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Authors: Zamora, Samuel, Gozalo, Rodolfo, and Linñán, Eladio

Source: Acta Palaeontologica Polonica, 54(2) : 253-265

Published By: Institute of Paleobiology, Polish Academy of Sciences

URL: https://doi.org/10.4202/app.2008.0010

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Middle Cambrian gogiid echinoderms from Northeast Spain: Taxonomy, palaeoecology, and palaeogeographic implications

SAMUEL ZAMORA, RODOLFO GOZALO, and ELADIO LIÑÁN

Zamora, S., Gozalo, R., and Liñán, E. 2009. Middle Cambrian gogiid echinoderms from Northeast Spain: Taxonomy, palaeoecology, and palaeogeographic implications. *Acta Palaeontologica Polonica* 54 (2): 253–265. DOI: 10.4202/app.2008.0010

Gogia parsleyi Zamora sp. nov. and *Gogia* sp. are described from two different echinoderm assemblages, both from the middle Cambrian of the Murero Formation (Iberian Chains, NE Spain). *Gogia parsleyi* is reconstructed and described on the basis of fifteen complete or partial specimens and numerous isolated plates. It is characterised by spiralled brachioles, simple epispires, sometimes covered by stereomic domes or tiny cover plates, and by thecal plates arranged in subregular circlets. This gogiid population comprises juveniles, advanced juveniles and mature individuals. The material was found in the upper part of the Murero Formation (upper Caesaraugustian–lower Languedocian). *Gogia* sp. is represented by two almost complete specimens and several isolated plates from the lower part of the Murero Formation (lower Caesaraugustian). The genus *Gogia* was first described in Western Gondwana from the Languedocian (upper middle Cambrian) of France, but the material from Spain is older and represents the oldest record of this genus in Gondwana, suggesting an early migration from Laurentia. The gogiids are well preserved in two echinoderm Lagerstätten, which, together with other echinoderms, comprise the majority of the fossil fauna. Both levels are derived from obrution deposits produced in calm and open marine conditions, sometimes affected by sporadic storms. Their holdfast morphology suggests that these gogiids were low-tier suspension feeders, living attached to trilobite fragments in a soft, muddy environment.

Key words: Echinodermata, Eocrinoidea, Gogiida, Cambrian, Murero Formation, Spain.

Samuel Zamora [samuel@unizar.es] and Eladio Liñán [linan@unizar.es], Área y Museo de Paleontología, Departamento de Ciencias de la Tierra, Universidad de Zaragoza, E-50009 Zaragoza, Spain;
Rodolfo Gozalo [Rodolfo.Gozalo@uv.es], Departamento de Geología. Universitat de València.C/ Dr. Moliner n° 50. E-46100 Burjasot (Valencia), Spain.

Introduction

Echinoderms are an important component of middle Cambrian fossil assemblages from North Western Perigondwana. Two problems restrict their study: (i) complete and articulated echinoderms are rare; and (ii) isolated plates have limited taxonomic value, usually only assignable to class level or above (Donovan and Paul 1982). Of the eleven echinoderm classes recorded worldwide from the Cambrian (Sprinkle 1976), one of the most common is the Eocrinoidea Jaekel, 1918. This Linnaean class is a paraphyletic group that comprises stem-group members of the better known blastozoan clades (Sprinkle 1973; Smith 1984; Paul 1988). Major anatomical innovations of the eocrinoids include the development of erect brachioles for feeding and a long multiplated stalk, and later, a columnal-bearing stem to elevate the theca above the sea floor (Sprinkle and Collins 2006).

Among eocrinoids, representatives of the family Eocrinidae Jaekel, 1918 are the most common, primarily from Laurentia (Sprinkle 1973). Only a few fossils from Gondwana are considered as eocrinids. These are from the lower Cambrian of Spain (Ubaghs and Vizcaïno 1991), Morocco (Nardin 2006) and China (Zhao et al. 2007), and from the middle Cambrian of Bohemia (Barrande 1887; Fatka and Kordule 1984, 1991), France (Ubaghs 1987) and China (Zhao et al. 1994, 2007, 2008; Parsley and Zhao 2006).

At present, only two complete and articulated eocrinoid taxa are known from the Cambrian of Spain, *Alanisicystis andalusiae* Ubaghs and Vizcaïno, 1991 (Fig. 1) and *Ubaghsicystis segurae* Gil-Cid and Domínguez, 2002. The first is from the lower Cambrian of the Ossa Morena zone (South Spain). It was originally included as a subgenus within the genus *Gogia*, but certain features (for example the stereomic domes covering complex epispires) suggest a taxonomic position independent of, but closely related to *Gogia*. The second, *Ubaghsicystis segurae*, comes from the middle Cambrian of the Cantabrian zone (North Spain). It is the oldest articulated eocrinoid, with a xenomorphic stem composed of holomeric columnals (Gil-Cid and Domínguez 2002); these features suggest a derived position amongst Cambrian eocrinoids. In addition to these complete eocrinoids, isolated plates belonging to the eocrinoid *Rhopalocystis*? *mesonesensis* Clausen, 2004 from the upper lower Cambrian of the Iberian Chains, the enigmatic blastozoan *Eocystites* sp. (Gil-Cid and Domínguez 1998) from the middle Cambrian of Ossa Morena zone (South Spain), indeterminate eocrinoid plates (Álvaro and Vennin

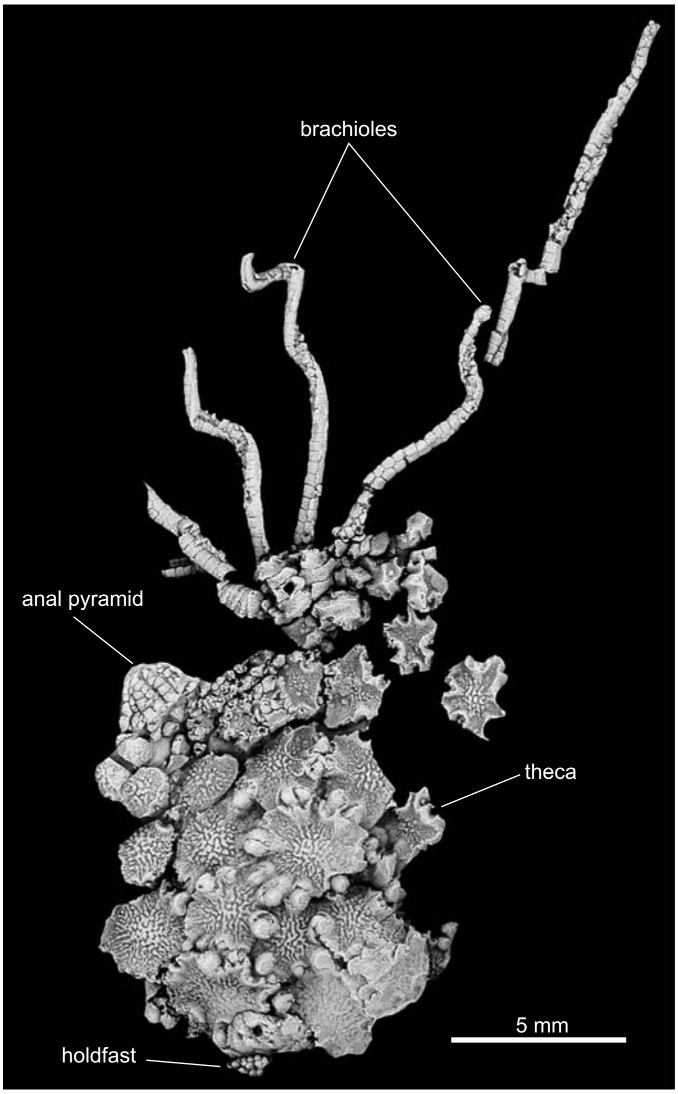

Fig. 1. Holotype (MGM2005K) of gogiid echinoderm *Alanisicystis andalusiae* Ubaghs and Vizcaïno, 1991 from the lower Cambrian of the Ossa Morena zone (South Spain). Photograph of latex cast whitened with NH_4Cl.

1997) from the middle Cambrian (Mansilla Formation, Iberian Chains) and columnals of uncertain affinity from the Furongian (Acón Group, Iberian Chains) (Zamora et al. in press), have also been described.

Echinoderms from the Murero Formation are extremely diverse, with a long and complete fossil record (Zamora et al. 2007), but few have been formally described so far (Friedrich 1993; Zamora and Rahman 2008). In this paper we report two new gogiid eocrinoids from the middle Cambrian Murero Formation. *Gogia parsleyi* Zamora sp. nov. and *Gogia* sp. are the first representatives of the group reported from the Iberian Chains. *Gogia* sp. is also the oldest representative of this genus in Western Gondwana and suggests taxa migrated to Gondwana from the Laurentian palaeocontinent.

These eocrinoids possess some plesiomorphic (primitive) characters, including an irregularly plated theca with larger primary and smaller secondary plates, epispires (sutural pores) for respiration, biserial brachioles and an expanded, probably short holdfast for attachment to hard substrates. The aims of this paper are twofold, firstly to describe new taxa from Spain, and secondly to analyse the geographic and stratigraphic distribution of gogiids. Some preliminary data on the palaeoecology of eocrinoids and other echinoderms from the Murero Formation is also discussed.

Institutional abbreviation.—MGM, Museo Geominero, Madrid, Spain; MPZ, Museo de Paleontología, University of Zaragoza, Spain.

Geological setting and stratigraphy

The Murero Formation is exposed in several Cambrian localities (Fig. 2) in the Iberian Chains (NE Spain), all of which are rich in trilobites, echinoderms, brachiopods, and Burgess Shale-type fossils. Trace fossils are also present. Two large Palaeozoic outcrops trending NW-SE, separated by the Tertiary Calatayud-Teruel basin, constitute the central part of the Iberian Chains. In this region, Palaeozoic rocks are structured into three tectonostratigraphic units, the Mesones Unit, Herrera Unit and Badules Unit (Gozalo and Liñán 1988), and Cambrian rocks are common in all three.

The Cambrian stratigraphy of the Iberian Chains was established by Lotze (1929); the lithostratigraphic nomenclature has subsequently undergone minor modifications (Lotze 1958, 1961; Schmitz 1971; Liñán et al. 1992; Álvaro 1995). The units in this sequence (in ascending stratigraphic order) are: the Bámbola Formation, Embid Formation, Jalón Formation, Ribota Formation, Huérmeda Formation and Daroca Formation for the lower Cambrian; the Mesones Group (Valdemiedes, Mansilla and Murero formations) for the lower–middle Cambrian; and the Acón Group for the middle Cambrian–Furongian. The palaeontological contents of each unit were summarised by Liñán et al. (1996, 2002) and Gozalo et al. (2008).

The fossils described herein came from two different localities, Murero and Purujosa villages; both are situated in the Badules unit, which is considered to be the prolongation of the West Asturian-Leonese Zone to the southeast (Fig. 2A). They are from two different beds in the Murero Formation. This formation represents a monofacial deposit of green lutites with interbedded carbonate nodules and very fine sandstones. The original sediments were deposited in a shallow marine environment (sublittoral facies, sensu Liñán 1995). The *Dyctionina–Acrothele* brachiopod assemblage is well represented throughout the formation and indicates the predominance of low-energy deposits (Liñán and Mergl 2001).

The presence of agnostoid and polimeroid cosmopolitan trilobites suggests an outer sublittoral facies for the Murero Formation.

Locality 1.—Murero is a small village situated on the western branch of the Iberian Chains, located 80 km south of Zaragoza (Fig. 2B). The Cambrian rocks in this area show a

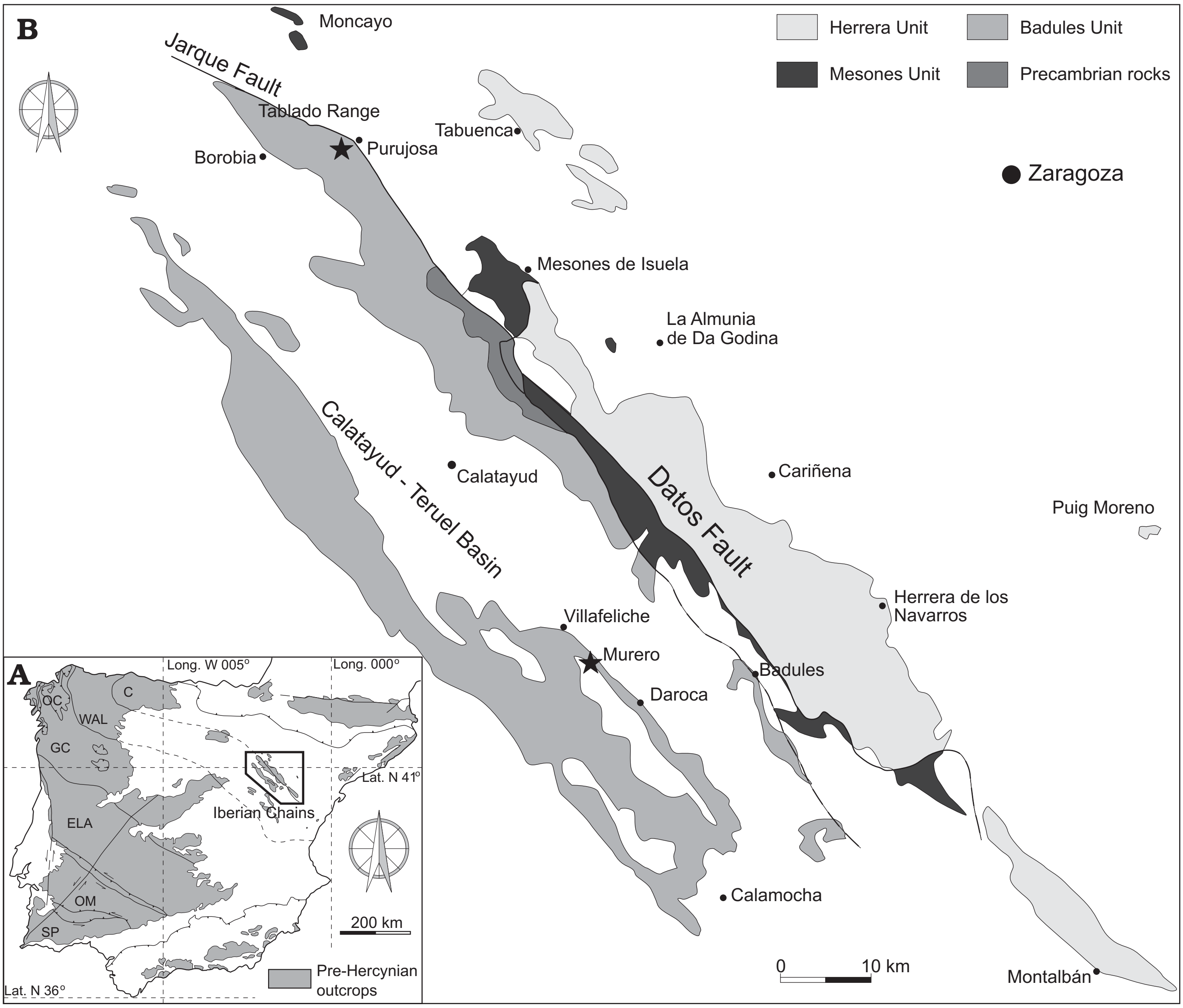

Fig. 2. Geological setting of the two discussed localities in the Iberian Chains (after Liñán et al. 2008). **A**. Pre-Hercynian outcrops and tectono-stratigraphic zones of the Iberian Peninsula; the Iberian Chains are framed. Zones: CZ, Cantabrian; WALZ, West Asturian-Leonese; GCZ, Galician-Castilian; ELAZ, East Lusitanian-Alcudian; OMZ, Ossa-Morena Zone; SPZ, South Portuguese. **B**. Pre-Hercynian outcrops and tectono-stratigraphic zones and units of the Iberian Chains; Murero and Purujosa (indicated by stars) (Modified from Gozalo and Liñán 1988).

lower and middle Cambrian sequence divided into Valdemiedes, Mansilla, and Murero formations in a normal succession dipping to the south (Liñán and Gozalo 1986). Eocrinoids were collected in the upper part of level 12 of Rambla de Valdemiedes 1 section, which represents the base of the Murero Formation (Fig. 3). This level is five metres thick, comprising green shales and carbonate nodules (see Liñán and Gozalo 1986, and García-Bellido et al. 2007), and containing trilobites, echinoderms, brachiopods, sponges, and ichnofossils. The presence of the trilobite *Badulesia granieri* (Thoral, 1935), indicates that the level belongs to the *Badulesia granieri* Zone (lower Caesaraugustian).

The eocrinoids from this locality were found in a thin level associated with the trilobites *Eccaparadoxides asturianus* (Sdzuy, 1968), *Badulesia granieri* (Thoral, 1935), *Conocoryphe* (*Parabailiella*) *languedocensis* Thoral, 1946 and *Condylopyge* sp. The presence of both agnostoid and polimeroid trilobites suggests open marine conditions; however, the sponge *Leptomitus conicus* is also present, which is typical of soft substrates in low or moderately low energy conditions (García-Bellido et al. 2007).

Locality 2.—Purujosa is located in the Moncayo Natural Park at the Tablado Range, 75 km west of Zaragoza in the north of the Iberian Chains (Fig. 2B). Eocrinoids were collected from the top of the Murero Formation in the Purujosa-4 section (Fig. 3); in the study area, this formation occurs as a 75 m sequence of shales, nodular carbonates and

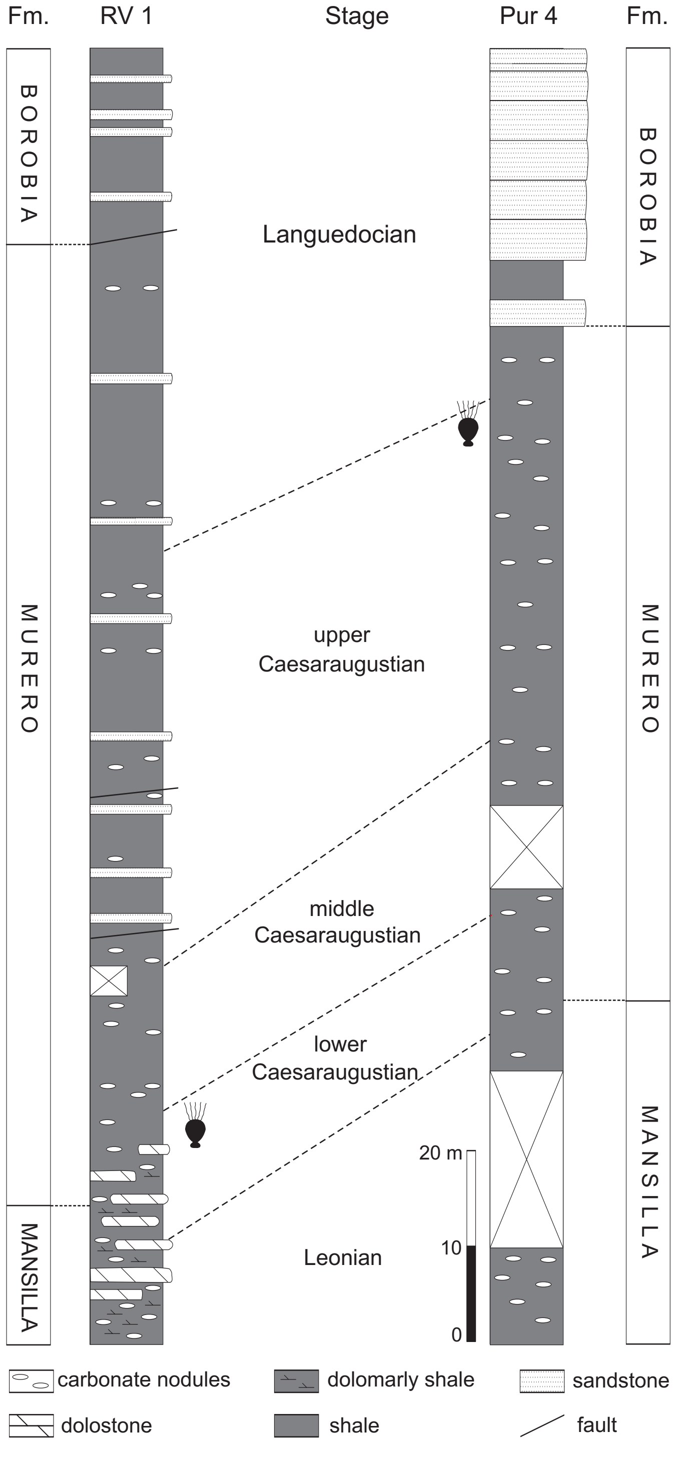

Fig. 3. Sections of the middle Cambrian Murero Formation in Murero and Purujosa indicating the levels with *Gogia* sp. and *Gogia parsleyi* Zamora sp. nov.

fine sandstones. Fossils were collected in a thin (35 cm) level of green-grey shale, rich in cinctans (*Gyrocystis platessa* Jaekel, 1918) and eocrinoideans. Trilobite fragments and trace fossils are also present, but so far only the trilobite *Eccaparadoxides brachyrachys* (Linnarsson, 1883) has been identified. The trilobite assemblage in the overlying level is composed of *Eccaparadoxides*? *pradoanus* (Verneuil and Barrande, 1860), *Peronopsis acadica* (Hart, 1868), *Peronopsis ferox* (Tullberg, 1880), *Solenopleuropsis simula* Sdzuy, 1958, *S. marginata* Sdzuy, 1958, *S. thorali* Sdzuy, 1958, *Conocoryphe* (*Conocoryphe*) *heberti* Munier-Chalmas and Bergeron, 1889, and *Ctenocephalus* aff. *coronatus* (Barrande, 1846); these taxa suggest a lower Languedocian age (middle Cambrian). Thus, the age of the echinoderm level containing eocrinoidean fossils is likely to be uppermost Caesaraugustian or lowermost Languedocian.

The oldest cinctan echinoderm is also reported from this section, in the underlying Mansilla Formation (Rahman and Zamora in press).

Systematic palaeontology

(by Samuel Zamora)

Phylum Echinodermata Bruguière, 1791 (ex Klein, 1734)

Subphylum Blastozoa Sprinkle, 1973

Class Eocrinoidea Jaekel, 1918

Order Gogiida Broadhead, 1982

Family Eocrinidae Jaekel, 1918

Genus *Gogia* Walcott, 1917

Type species: *Gogia prolifica* Walcott, 1917, lower Middle Cambrian, British Columbia (Canada).

Discussion.—*Gogia* is the most abundant and diverse Cambrian eocrinoid (Sprinkle 1973). Thirteen species have been described in the lower and middle Cambrian of Laurentia; only one of these, *Gogia ojenai* Durham, 1973, is from the lower Cambrian (Robison 1965; Sprinkle 1973; Sprinkle and Collins 2006). There are, however, several new species from the lower Cambrian of Laurentia that still require formal description (Bryan C. Wilbur, personal communication 2005). Until now, the first convincing appearance of *Gogia* in Western Perigondwana was in the upper middle Cambrian of Montagne Noire (France), where *Gogia gondi* Ubaghs, 1987 is reported. The Spanish material described here suggests an older first occurrence of the genus *Gogia* in Gondwana, in the lower middle Cambrian.

One point of discussion within the genus *Gogia* is the subgenus *Alanisicystis* Ubaghs and Vizcaïno, 1991, from the lower Cambrian of Southern Spain (Fig. 1). This subgenus is characterised by "single or partioned epispires provided with external dome-like stereomic cover". There are no other *Gogia* species that show this peculiar type of epispire (complex and covered) (Sprinkle 1976; Ubaghs 1987). For this reason, we believe that *Alanisicystis* Ubaghs and Vizcaïno, 1991 should be a separate genus rather than a subgenus of *Gogia* (note, type material of *Alanisicystis andalusiae* Ubaghs and Vizcaïno, 1991 previously deposited in Carcassone, France [Vizcaïno collection numbers: VCE 11, *1–3*, 23, 24, 25, 26] is now deposited in the MGM. New collection numbers are

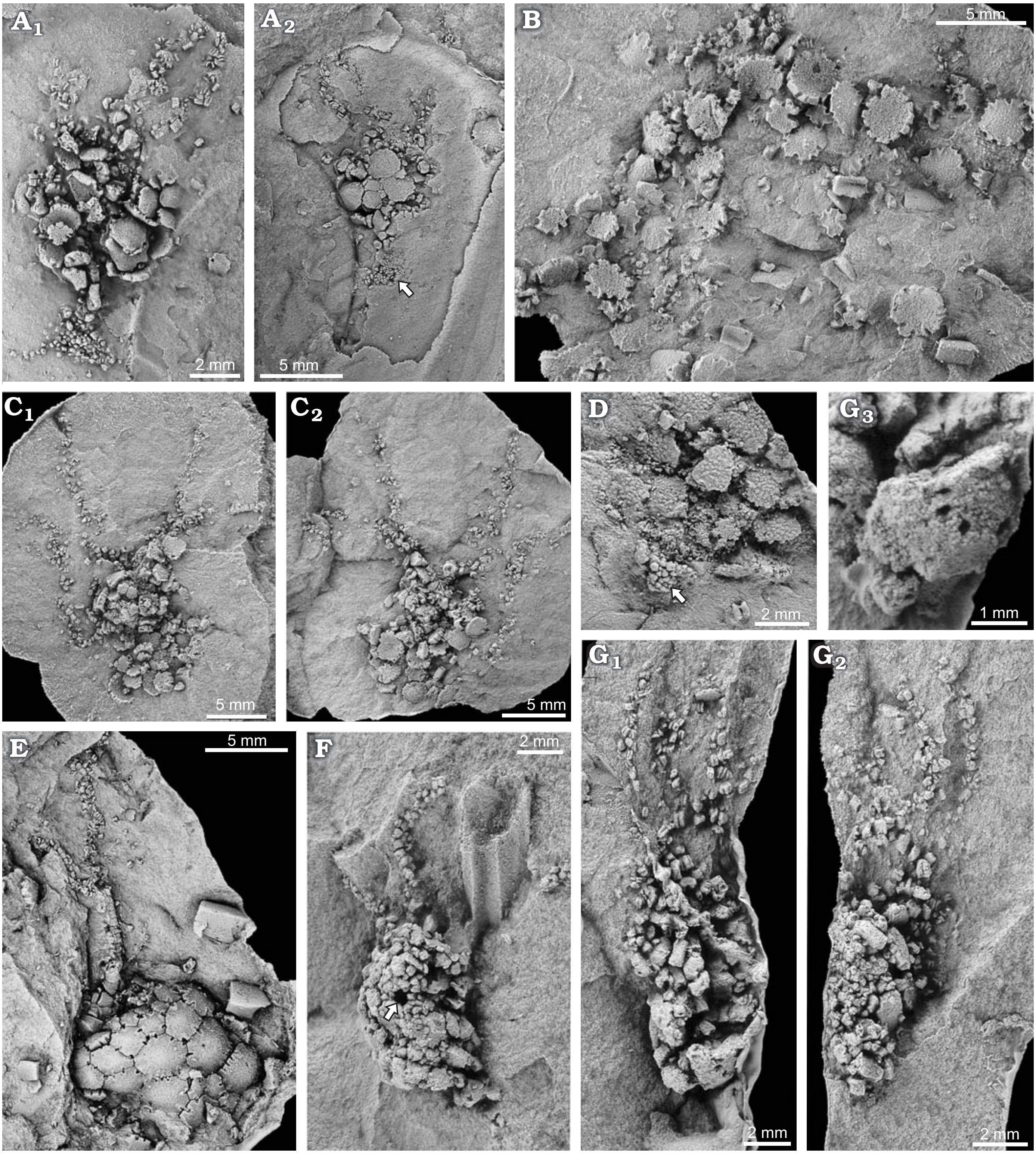

Fig. 4. **A**–**E**. Eocrinoid blastozoan *Gogia parsleyi* Zamora sp. nov. **A**. Paratype MPZ2006/556a, b; part (A_1) and counterpart (A_2) of a slightly disturbed small specimen attached to a free cheek of *Eccaparadoxides* sp. fragment. The arrow indicates where the holdfast attaches to the trilobite element. **B**. MPZ2006/559b; accumulation of disarticulated plates from eocrinoids (*Gogia parsleyi* Zamora sp. nov.) and cinctans. **C**. Paratype MPZ2006/557a, b; nearly complete specimen with thecal plates slightly disturbed. **D**. Paratype MPZ2004/215; partial theca with ornamented plates and a very short holdfast (indicated by the arrow). **E**. Paratype MPZ2004/214; specimen with an almost complete theca. **F**, **G**. *Gogia* sp. **F**. MPZ2004/194a; partly complete specimen with a possible periproct on the lateral surface (see white arrow). **G**. MPZ2004/195a, b; partially disarticulated specimen (G_1), counterpart of the same specimen (G_2), detail of two adjoined plates with epispires (G_3). Photographs of latex casts whitened with NH_4Cl.

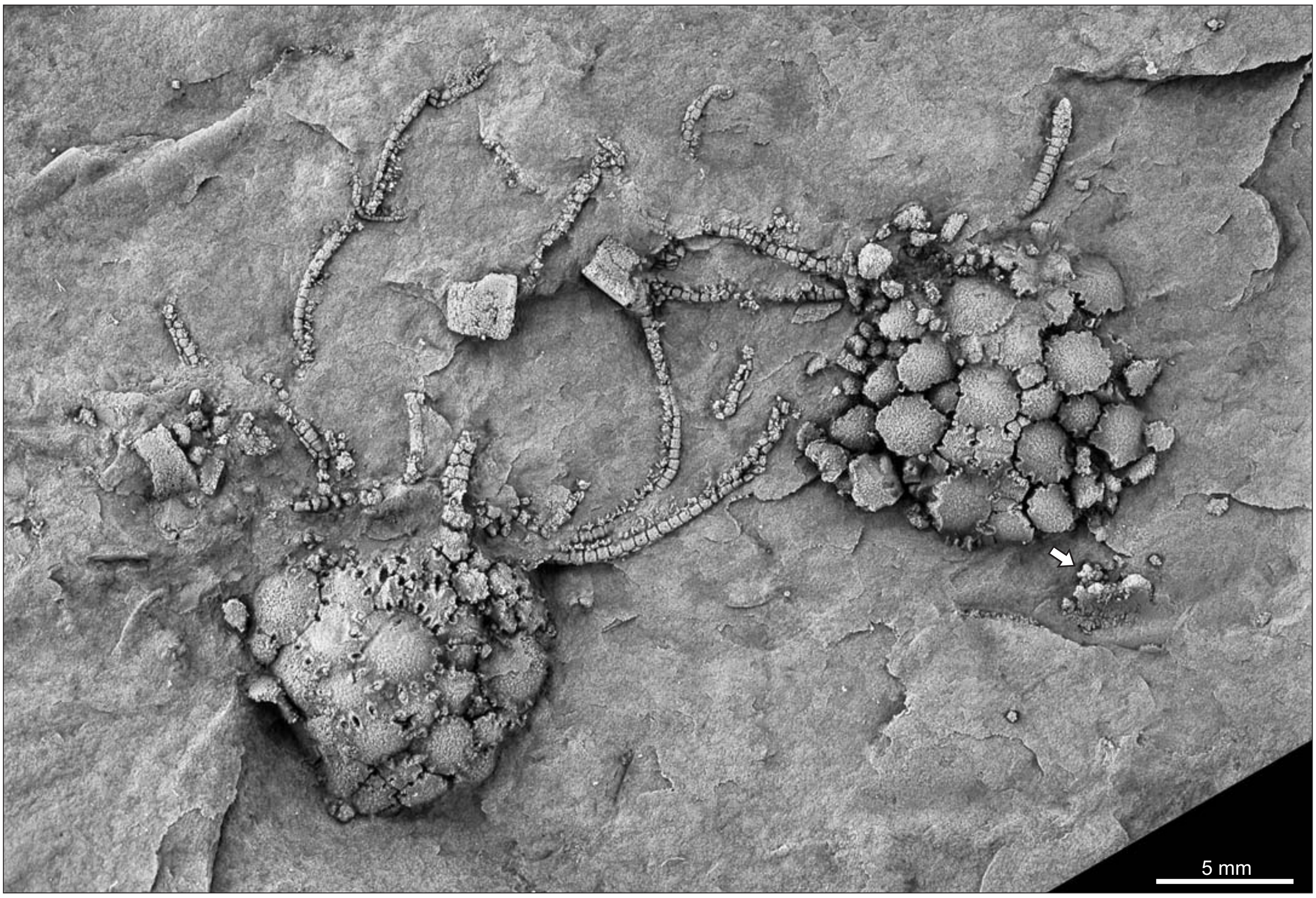

Fig. 5. Slab with two nearly complete, articulated and exquisitely preserved specimens of eocrinoid blastozoan *Gogia parsleyi* Zamora sp. nov., with some isolated plates belonging to cinctan carpoids. Both specimens probably represent an early mature stage (TH = 12 mm). The left specimen (holotype MPZ2004/162a) shows many of the diagnostic features referred to in the text. The right specimen (paratype MPZ2004/161a) shows the holdfast separated from the theca (indicated by an arrow). Photograph of latex cast whitened with NH_4Cl.

MGM2003K *1–3*, MGM2004K, MGM2005K, MGM2006K, MGM2007K).

Gogia parsleyi Zamora sp. nov.

Figs. 4A–F, 5–9.

Etymology: In honour of Prof. Ronald L. Parsley (Tulane University, New Orleans), for his contributions to the understanding of gogiid eocrinoids and Palaeozoic echinoderms in general.

Type material: Holotype: MPZ2004/162a, b, almost complete specimen without holdfast (Fig. 5). Paratypes: MPZ2004/161, 163, 214, 215, 238; MPZ2006/556–558, 560; MPZ2008/160–164, complete or partial specimens.

Type locality: La Borraca Creek, four kilometers to the southwest of Purujosa village (Zaragoza, NE Spain) in the Moncayo Natural Park.

Type horizon: Murero Formation, uppermost Caesaraugustian or lowermost Languedocian, Middle Cambrian.

Diagnosis.—Eocrinid with globular-shaped theca and large, slightly convex thecal plates (slightly ornamented). Epispires are simple and numerous, with a well developed raised rim sometimes covered by a stereomic dome or by small plates. Thecal plates are arranged into six or seven subregular circlets. At least seven long, narrow biserial and spiralled brachioles. Almost no stalk, except for an expanded holdfast composed of tiny globular plates.

Material.—14 articulated and nearly complete specimens (ten with both part and counterpart), MPZ2004/161–163, 214, 215, 238; MPZ2006/556–558, 560; MPZ2008/160–162, 164. Two disarticulated specimens, MPZ2006/559 and MPZ2008/163, and 23 isolated plates (MPZ2004/216–237, 239). All fossils are preserved as natural moulds in a grey-green shale. Articulated specimens with delicate, intact structures suggest rapid burial while alive by a storm-induced obrution deposit.

Description.—The shape of the theca is ellipsoidal to rounded; the size of the holotype theca is 12 × 11 mm (Fig. 5). All the recovered specimens have been flattened by collapse and/or compaction. There are 35 thecal plates per exposed side, which exhibit polygonal outlines and subregular arrangements in 6 or 7 circlets; a number of the plates are large (up to 3 mm) (see reconstruction, Fig. 6). There is no clear gradient in the size of the plates, but the larger ones are concentrated in the lower–middle portions of the theca; plates decrease in size aborally and especially adorally. Additional plates are intercalated along sutures, as shown by the juvenile specimen MPZ2006/556 (Fig. 4A). Plates are slightly domed on their external surface and are typically ornamented with tiny granules (Fig. 4D). On the internal surface, they are unornamented and slightly concave (Fig. 4B). Some stereomic structures are well preserved (Fig. 7).

Sutural pores (epispires) occur over the entire theca, with a regular distribution and size (Figs. 5, 7B, C, 8A, B, 9C). Epispires are surrounded by a prominent raised rim (Figs. 6, 7C, 8E, F, 9C), which usually crosses the associated plate suture(s). Epispires are present on the sutures between two plates or at the corners between three plates (Fig. 8F); and they are sometimes more developed in one of the two adjacent plates. The pores show an almost uniform diameter. The number of epispires per plate ranges from 4 (MPZ2004/162a) to 17 (MPZ2004/217) and there are up to four epispires per plate side. Some epispires show an external dome-like stereomic cover (Figs. 6, 8E), others are covered by numerous tiny plates (Figs. 4E, 8F). The covered epispires are only present in the lower–middle theca and sometimes these structures do not cover the whole pore. These epispires are rounded to elliptical and have an epispire H/W ratio varying from 1 to 3.

Brachioles are attached in groups of two to a modified single thecal plate, which is projected at the periphery of the oral region (Fig. 8C). They are spiralled with a quite loose twist (approximately 0.5 mm) (Fig. 8G) and are sometimes coiled at their tips (Figs. 5, 8D). The length of the brachioles is at least 25 mm, twice the length of the theca. Seven brachioles are preserved in the most complete specimens (MPZ2004/162a), there were probably more in living animals. Brachioles are biserial, with the alternating brachiolar plates numbering about three or four per millimetre (Figs. 8A, G, 9A). Cover plates are not well preserved; there are

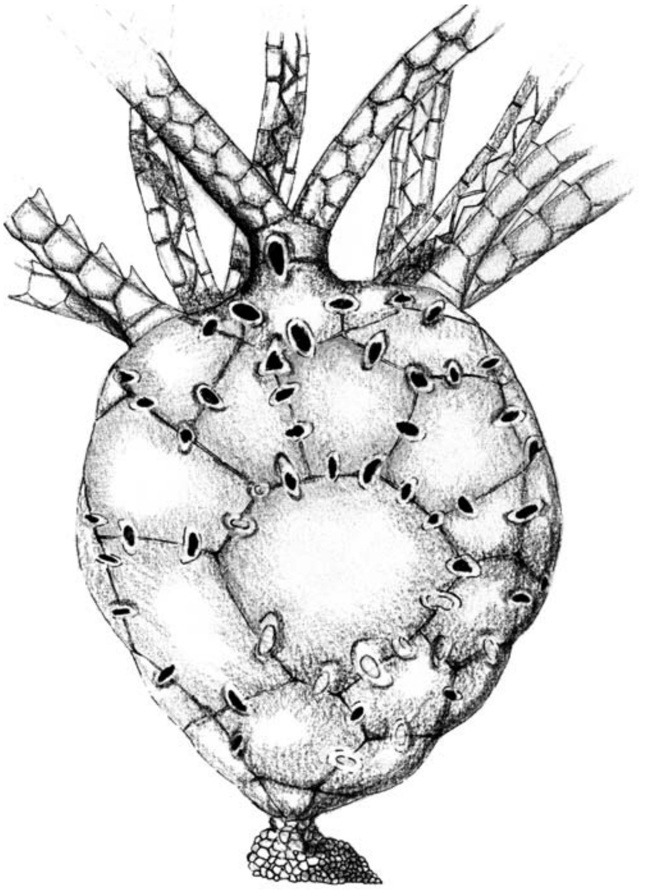

Fig. 6. Reconstruction of eocrinoidean blastozoan *Gogia parsleyi* Zamora sp. nov. (by Santiago Alberto, after a sketch by SZ), based on the holotype MPZ2004/162a. The holdfast, not preserved in the holotype, is reconstructed based on paratypes MPZ2004/161 and MPZ2004/215.

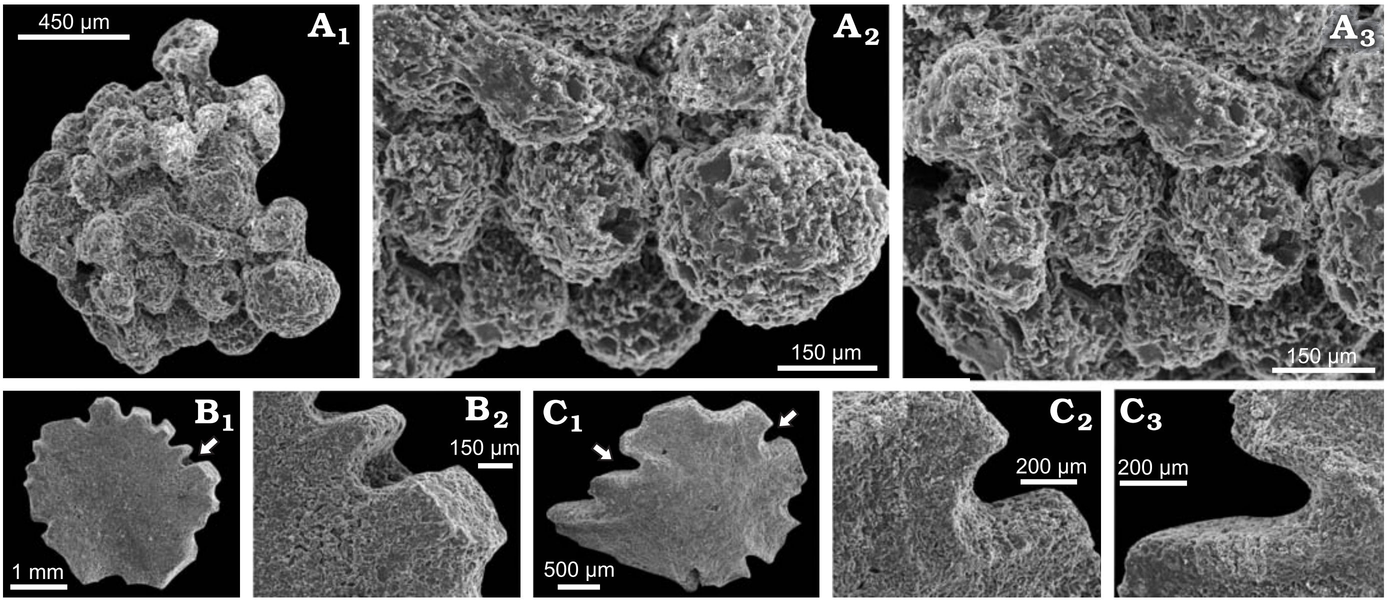

Fig. 7. Details of element structures in eocrinoidean blastozoan *Gogia parsleyi* Zamora sp. nov. (SEM photos of latex casts). **A**. Fragment of a holdfast from the specimen MPZ2004/161, consisting of an aggregate of globular plates (A_1), details of specimen (A_2, A_3). **B**. Internal view of a plate showing sutural pores of epispires (MPZ2004/225); general view of an isolated plate (B_1), detail of the epispire (B_2). **C**. External surface of a plate (MPZ2004/232) (C_1), details of the epispires showing the raised rim and stereomic structures (C_2, C_3). Arrows indicate enlarged details.

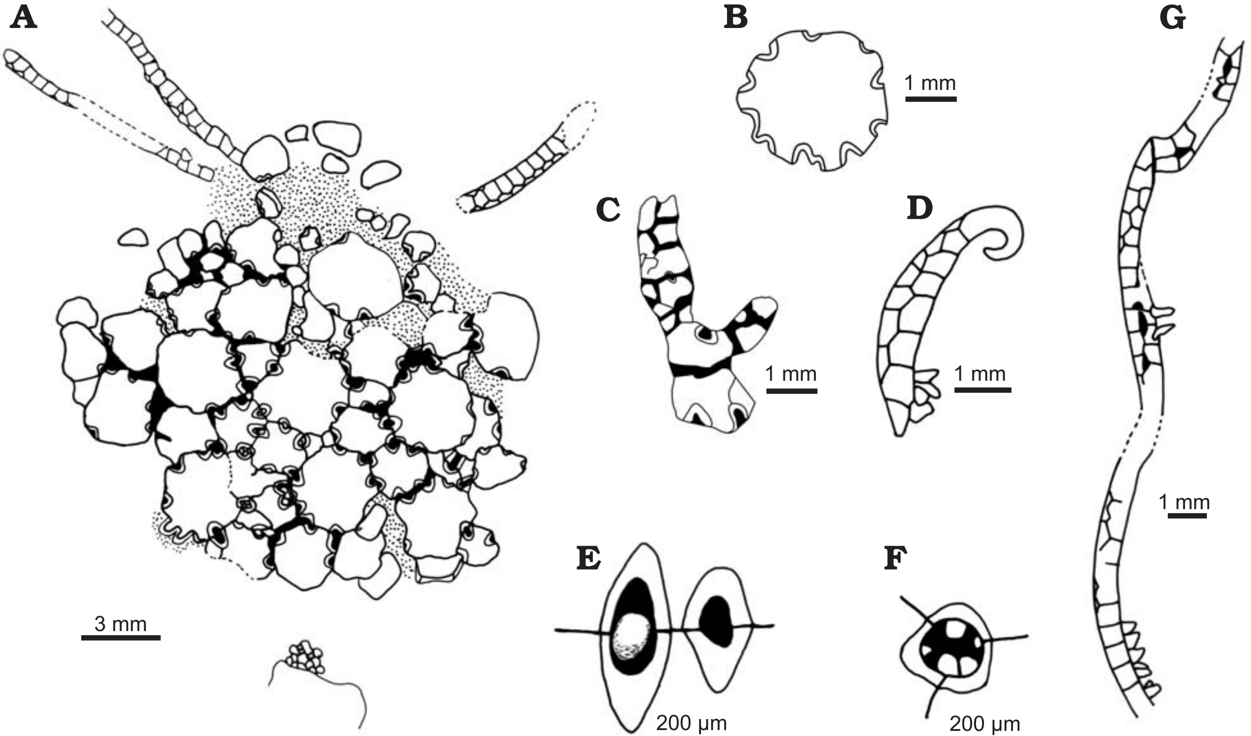

Fig. 8. Camera lucida drawings of eocrinoid blastozoan *Gogia parsleyi* Zamora sp. nov. **A**. General view of the paratype MPZ2004/161, detached holdfast below. **B**. Thecal plate, half-epispires with their prominent rim indicated. **C**. Two brachioles on a single thecal plate. **D**. Biserial brachiole terminally enrolled. **E**. Epispire covered by a single domal plate. **F**. Epispire covered by tiny plates. **G**. Spiralled brachiole.

two on a brachiolar plate, with a spinous projection in lateral view. The preservation of the brachioles in the holotype suggests that they were flexible.

The holdfast is preserved in some specimens, but no stalk is apparently present. In MPZ2004/161a (Fig. 5) the holdfast appears disarticulated, in specimens MPZ2004/215 (Fig. 4D) and MPZ2008/162 (Fig. 9A) it is apparently still connected to the base of the theca. It is composed of numerous tiny, globular plates, which are clearly visible in SEM images (Fig. 7A). The transition between the holdfast and theca is abrupt, consisting of a change in the type and size of plates.

Discussion.—*Gogia parsleyi* Zamora sp. nov. conforms to the diagnosis proposed by Walcott 1917 (see also, Sprinkle 1973; Sprinkle and Collins 2006) for the genus *Gogia*. It has a unique character combination of simple covered epispires; large thecal plates arranged in subregular circlets; spiralled brachioles; and the absence of a stalk connecting the expanded holdfast with the theca.

The general body structure of *Gogia parsleyi* Zamora sp. nov. (Fig. 6) shows many features that are shared with other gogiids, such as erect biserial brachioles, thecal plates arranged in poorly developed circlets, epispires and an attachment appendage consisting of only a holdfast.

This species differs from other Cambrian gogiids in several characteristics; for example, thecal plates organised into subregular arranged circlets and the presence of covered epispires. One undescribed species of *Gogia* from North America also shows stereomic domes covering epispires (James Sprinkle, personal communication 2008). *Gogia parsleyi* Zamora sp. nov. is similar to *Gogia hobbsi* Sprinkle, 1973, particularly in the ornamentation of the thecal plates and the spiralled brachioles; however, *Gogia hobbsi* has a conical thecal shape, is smaller in size with fewer plates and has a stalk.

Gogia parsleyi is likely to be closely related to *Alanisicystis* Ubaghs and Vizcaïno, 1991, because both have stereomic cover domes on some epispires in the lower part of the theca, but it differs from this species by having simple epispires and plate ornamentation composed of a slightly rough surface texture. Moreover, in *Gogia parsleyi* some epispires are covered by tiny plates rather than domes, which are always observed in *Alanisicystis* (Fig. 1). This feature is equally well shown in *Rhopalocystis destombesi* Ubaghs, 1963, in which a group of small plates covers the sutural pores (Ubaghs 1963: fig. 8.5–7) and in *Globoeocrinus globulus* Zhao, Parsley, and Peng, 2008. A new gogiid from Morocco that is under description (Nardin 2006) shares many features with *Gogia parsleyi*, such as the presence of covered epispires, but they differ mainly in the type of epispires, which are simple in the Spanish material and complex in the Moroccan specimen (Elise Nardin, personal communication 2006).

Sinoeocrinus Zhao, Huang, and Gong, 2004 differs by lacking the stereomic domes or tiny plates covering epispires. *Gogia parsleyi* differs from *Akadocrinus* Prokop, 1962 in the stalk, which is nearly absent in the former and composed of many fusular rings in the later. Furthermore, they differ in general thecal shape.

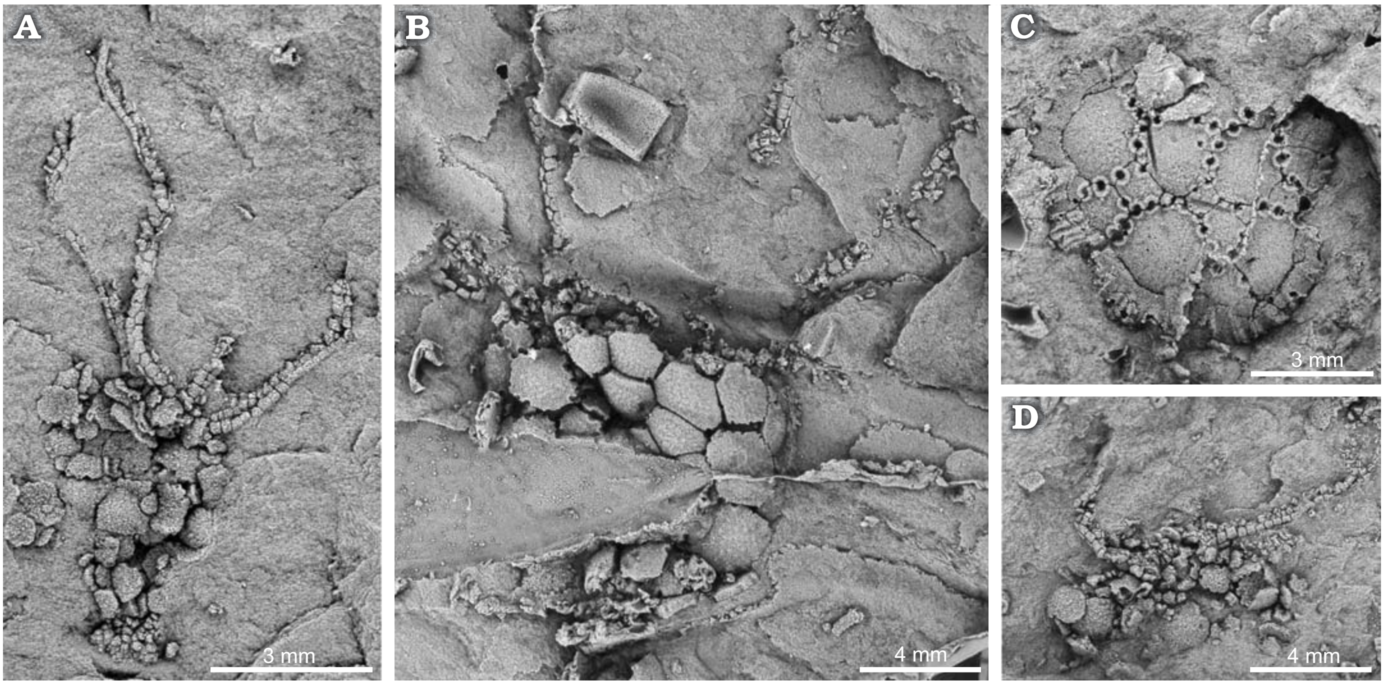

Fig. 9. Eocrinoid blastozoan *Gogia parsleyi* Zamora sp. nov. **A**. Paratype MPZ2008/162. Complete juvenile specimen (length of theca is about 5 mm); brachioles are spiralled and probably show a 2-2 pattern. **B**. Paratype MPZ2006/558a. Advanced juvenile specimen (length of theca is 11 mm). **C**. Paratype MPZ2008/164b. Fragment of theca with tessellated plates, epispires with characteristic rim. **D**. Paratype MPZ2008/161, upper part of theca. Photographs are of latex casts taken from natural moulds whitened with NH_4Cl.

Marjumicystis Ubaghs and Robison, 1985 also appears to lack a stalk, but differs principally in lacking well developed epispires.

Parsley and Zhao (2006) provided a complete ontogenetic sequence for the Cambrian eocrinoid *Sinoeocrinus lui* Zhao, Huang, and Gong, 2004, describing, for the first time, the ontogenetic changes occurring in a gogiid population. These ontogenetic stages were described in terms of thecal height (TH) and were thus divided into juvenile, advanced juvenile, mature and advanced mature, or gerontic, stages. The material of *Gogia parsleyi* described in this paper is not very abundant, but a few different ontogenetic stages can be recognised; these stages are important to understand feature changes in specimens of different sizes. The TH of specimens ranges from 5 mm to 12 mm. The smallest specimens (Figs. 4A, 9A), with a TH of 6 mm and 5 mm, respectively, probably represent juveniles or early advanced juveniles (sensu Parsley and Zhao 2006). They have a 2-2 ambulacral pattern (Fig. 9A), lack of ornamentation and very small epispires without a raised rim. The specimen which is intermediate in size, with a TH of ca. 7.5 mm (Fig. 9B), shows intermediate features, lacking ornamentation and possessing an incipient raised rim bordering epispires, which are very small. It probably represents an advanced juvenile. The largest specimens have a TH of ca. 12 mm and show some very distinctive features. They possess more than five brachioles, probably in a 2-1-2 pattern, ornamented thecal plates and well developed, sometimes covered epispires with prominent raised rims. All these features are probably indicative of early mature specimens.

Stratigraphic and geographic distribution.—Upper part of Murero Formation, uppermost Caesaraugustian or lowermost Languedocian (middle Cambrian).

Gogia sp.

Fig. 4F, G.

Material.—Two incomplete specimens partially articulated (MPZ2004/194, 195) and several isolated plates that probably belong to a single disarticulated specimen (MPZ2004/196). All the material is preserved as natural moulds coated with limonite in green shale.

Description.—The most complete specimen (Fig. 4F) (MPZ2004/194) possesses a rounded, conical theca, with a narrow base and expanded adoral surface. The theca height/width ratio is approximately 2; the number of plates is approximately 70 per exposed surface. Plates are irregular in shape and ornamented with small crests; they are irregularly arranged with the primary plates surrounded by many small secondary ones. Plates are thick compared to those of other gogiids. Epispires are rare and confined to larger plates. They are small and lack a raised rim (Fig. $4G_3$), with a height/width ratio of about 1.7. A rounded lateral opening is observed in one specimen, with a diameter of 0.65 mm (Fig. 4F), which corresponds (in position) to the anal pyramids of other gogiids.

Brachioles are disarticulated in two of the specimens; as a result it is impossible to know their exact number and detailed morphology. They were probably quite low in number

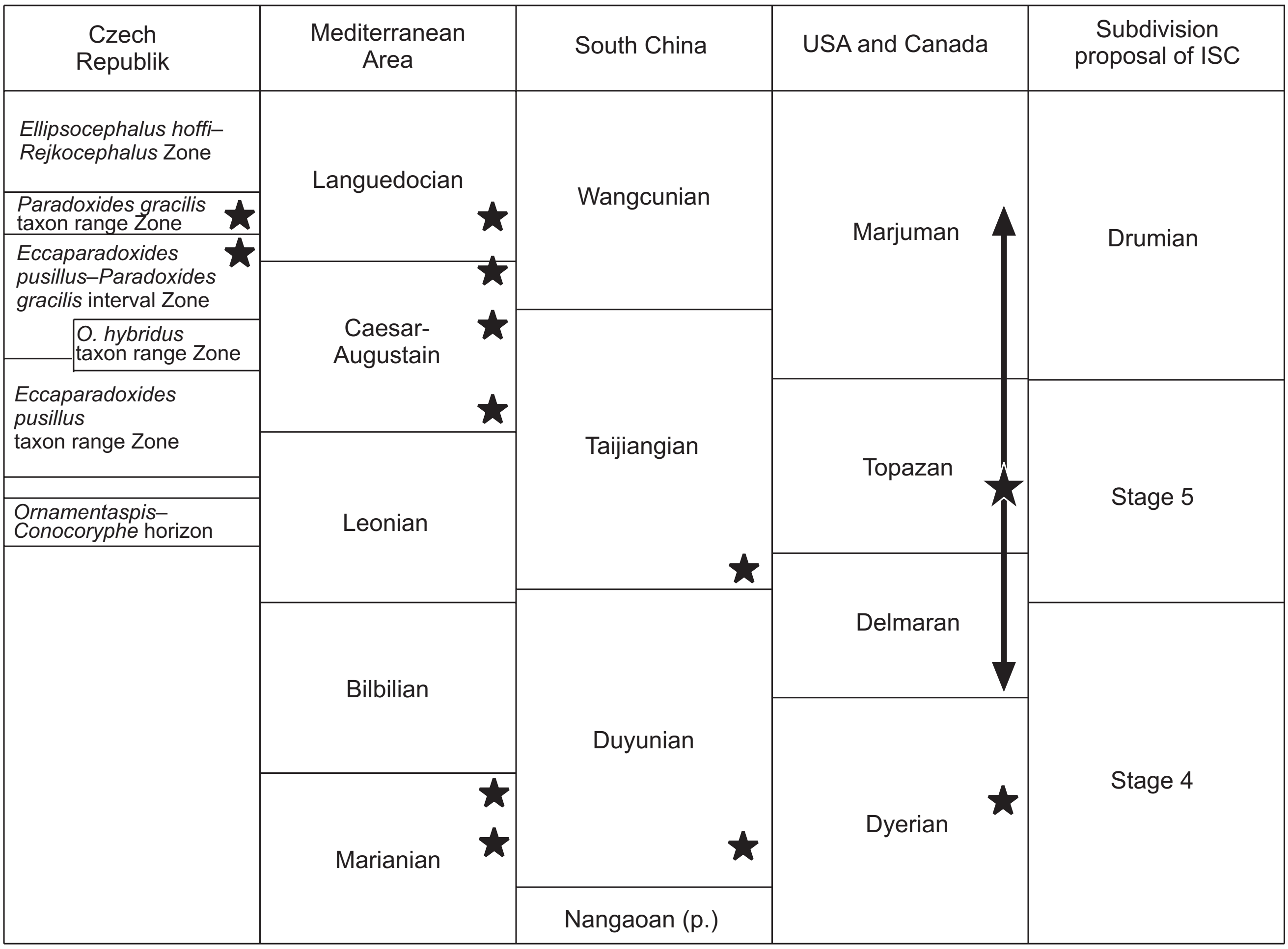

Fig. 10. Stratigraphic distribution of gogiids (indicated by stars) in the early and middle Cambrian. The biostratigraphy for the Czech Republic is based on Fatka (2006); the stages for the Mediterranean area are from Liñán et al. (2002) and Gozalo et al. (2008); the stages for South China are taken from Peng and Babcock (2001) and Peng (2003); the stages for USA and Canada (Laurentia) are from Sundberg and McCollum (2003) and Sundberg (2005). The Subdivision proposal of ISC for the Cambrian System is from Zhu et al. (2006).

(4?), and fairly long and large. The brachiolar plates show a well developed food groove.

Discussion.—The general morphology of the theca, disposition of plates and the structure of epispires suggest that the material should be included in the genus *Gogia*.

Stratigraphic and geographic distribution.—Lower part of the Murero Formation, *Badulesia granieri* Zone, lower Caesaraugustian.

Palaeobiogeography and palaeoecology of gogiids

Stratigraphic occurrence and palaeobiogeography.—The oldest known gogiids were reported from the early Cambrian of California, USA (see Sprinkle 1976), Ossa Morena, Spain (Ubaghs and Vizcaïno 1991), Anti-Atlas, Morocco (Nardin 2006), and China (Zhao et al. 2007); all of these are approximately the same age (Fig. 10). The next oldest records also occur in the USA; there is a nearly continuous sequence of different *Gogia* species from the basal Delamaran to the middle Marjuman (stages from the North American chronostratigraphic scale, see Sprinkle 1976). This extensive record strongly suggests that North America was the area where *Gogia* first evolved, although it probably migrated, at least once, to northern Perigondwana (France, Ubaghs 1987; and Spain, herein).

All other gogiids found in parts of Gondwana are middle Cambrian (Fig. 10), these generally occur as isolated records of single species in different levels. The earliest are *Sinoeocrinus lui* Zhao, Huang, and Gong, 1994 and *Globoeocrinus globulus* Zhao, Parsley, and Peng, 2008, from the base of the Taijiangan stage of China (Peng and Babckock 2001; Peng 2003). The next representative, in ascending stratigraphical order, is *Gogia* sp., from the lower Caesaraugustian of Spain (herein). Finally, the latest occurrences are known from four horizons in the Czech Republic (Fatka 2006), France (Ubaghs 1987), and Spain (herein); these horizons all have a similar age, uppermost Caesaraugustian to lowermost Languedocian

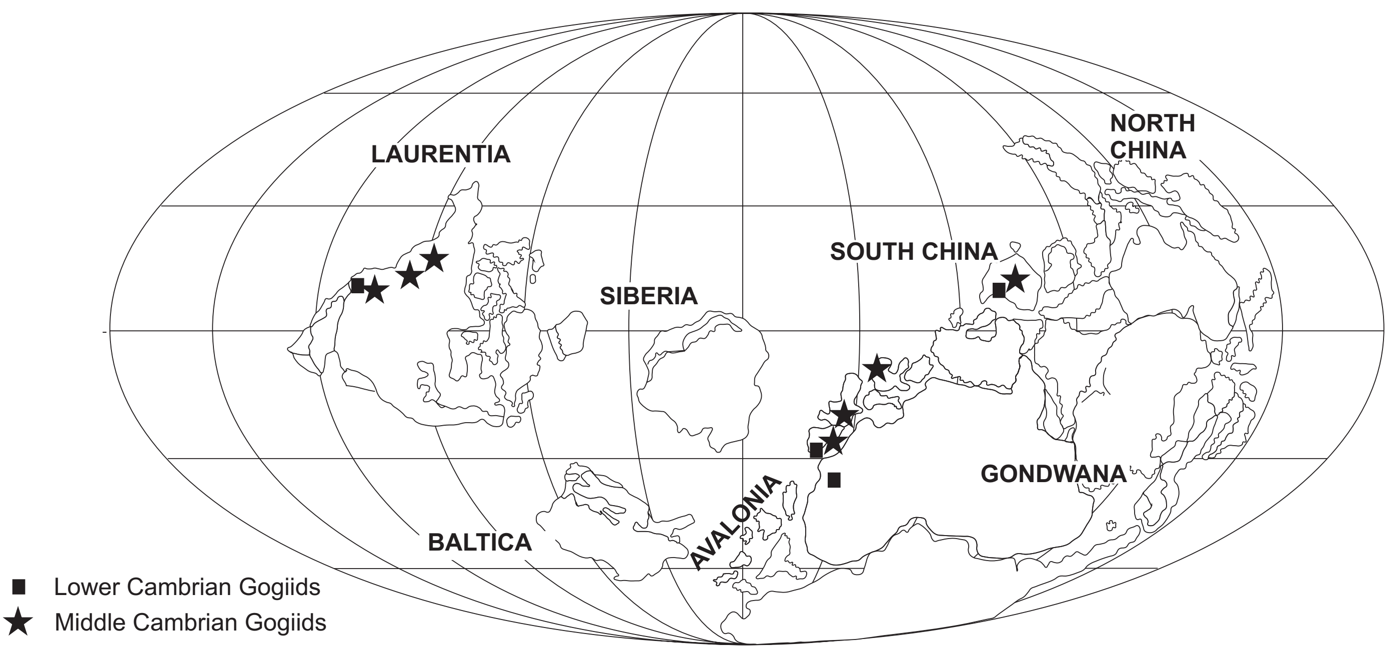

Fig. 11. Palaeogeographic distribution of gogiids in the early and middle Cambrian; reconstruction after McKerrow et al. (1992).

(Fig. 10). The youngest gogiids from Europe and North America are similar in age.

Gogiids are known from three distinct biogeographic areas: the Rocky Mountains (western North America), with the exclusive presence of the genus *Gogia*; northern Perigodwana (Europe and North Africa), where *Gogia* and another three genera have been found; and South China, where three additional genera are reported.

The distribution of gogiids (Fig. 11) is apparently restricted to tropical and subtropical regions when we plot their occurrences on the Cambrian palaeogeographic reconstruction of McKerrow et al. (1992). This pattern has also been described for other groups, including trilobites, bradoriids, and demosponges, and could be interpreted as a climatic control on the geographic distribution of gogiids.

Another suggestion is that two main lineages existed; one is the genus *Gogia* that evolved in the Rocky Mountains, which migrated to Europe during the middle Cambrian. The other lineage comprises genera of gogiids that are exclusively from Gondwana regions.

Palaeoecology.—The gogiids from the Iberian Chains provide a good opportunity to document the palaeoecology of this group in the Perigondwanan margin during the middle Cambrian. Fossil echinoderms from the two studied beds are exquisitely preserved, with some examples of complete and articulated eocrinoids with the brachioles still attached, and the theca and holdfast intact; furthermore, cinctan carpoids are preserved with the delicate labrum in place and with complete steles. All these features of excellent preservation are associated with the same lithology type, suggesting that echinoderms were living together and killed, probably by obrution processes caused by storms. In all cases, abundant isolated echinoderm plates appear unabraded, perhaps indicating a time averaging process, compaction of the surrounding sediment or the action of infaunal animals. Further work is needed to explain the association of both articulated specimens and disarticulated plates. Similar modes of origin have been proposed for other Cambrian echinoderm assemblages (Sprinkle 1976; Bell and Sprinkle 1978; Ubaghs and Robison 1985; Ubaghs 1987; Friedrich 1993; Lin et al 2008).

Locality 1, in the lower part of the Murero Formation (*Badulesia granieri* Zone), is a clay-shale containing a fossil assemblage made up of abundant echinoderms, sponges and trilobites. The echinoderms include the eocrinoid *Gogia* sp., the enigmatic blastozoan *Eocystites* sp., and a new cinctan carpoid.

Locality 2 is located in the upper part of the Murero Formation (uppermost Caesaraugustian or lowermost Languedocian). The echinoderms are the eocrinoid *Gogia parsleyi,* the cinctan *Gyrocystis platessa* Jaekel, 1918 and isolated plates that probably belong to the stylophoran carpoid *Ceratocystis*?

As has been suggested for other Cambrian echinoderm groups (Lefebvre 2007), dense assemblages of echinoderms seem relatively incompatible with a rich and diverse associated fauna. This is illustrated in the two assemblages described herein, where echinoderms are the major fossil group and trilobites show little diversity. Furthermore, the complete absence of phosphatic brachiopods and the scarcity of agnostoid trilobites, which are common in other levels of the Murero Formation, may imply relatively shallow water conditions for the two echinoderm assemblages.

Different strategies of attachment have been proposed for primitive eocrinoids living on this poorly consolidated sediment (Sprinkle 1973; Parsley and Prokop 2004; Sprinkle and Wilbur 2005; Dornbos 2006). The most common hypothesis is attachment by bioglue to hard elements, such as brachiopods or trilobite carapace fragments. Gogiids from the middle Cambrian of China recently provided further information on attachment strategies. Based on a large collection, Lin et al. (2008) indicated that 73% of gogiids are preserved attached to skeletal substrates. One specimen of *G. parsleyi* appears to be fixed to a trilobite fragment (Fig. 4A), in this case a librigena of *Eccaparadoxides* sp.; the attachment structure of this specimen is composed of numerous tiny globular plates that make a holdfast.

In summary, the eocrinoids described herein were one of the most important components of the soft-bottom communities that lived in the calm, shallow, open marine conditions associated with the Murero Formation. They coexisted with other echinoderms that make up the most important component of these fossil assemblages within eocrinoids. Other fossils associated with echinoderms include trilobites, sponges, and small shelly fossils, which are always a minor part of the community. This peculiarity has been observed in other Cambrian and lower Ordovician areas where echinoderms are the most important fossil group (Sprinkle 1973; Sprinkle 1976; Ubaghs and Robison 1985; Lefebvre 2007). The most common feature of the two echinoderm assemblages described herein is that eocrinoids commonly show low diversity, being represented by one taxon per bed. When other echinoderms appear, they show a distinct body plan that suggests a different ecological niche. "One-species-to-one-locality" (sensu Sprinkle 1976) is the most common situation among eocrinoids from the early–middle Cambrian of Laurentia (Sprinkle 1976; Ubaghs and Robison 1985), but the data reported in this paper (as well as previous works by Ubaghs [1987] and Ubaghs and Vizcaïno [1991]) confirms this scenario also for Gondwana. Perhaps this comes from the apparent gregarious nature of the individuals in each species, which exclude other species from a single "garden" or colony (Sprinkle 1976). Finally, the association of different types of echinoderms in the same levels was probably controlled for the relatively similar ecological requirements (Lefebvre 2007).

Acknowledgments

We thank Ronald L. Parsley (Tulane University, New Orleans, USA) not only for accepting the dedication of the new species described herein, but also for reviewing this paper and making useful comments. We also thank Elise Nardin (University of Rennes, France) for sending latex casts of French specimens and comments on Moroccan eocrinoids, Daniel Vizcaïno (Carcassone, France) for his comments on the Cambrian stratigraphy of Montagne Noire (France) and Bryan C. Wilbur (University of Texas, Austin, USA) for interesting discussions about lower Cambrian eocrinoids from the western USA. We thank Isabel Pérez (Zaragoza University, Spain) for photographs and help us with Fig. 3. Imran Rahman (Imperial College, London, UK) and Sarah Shackleton (Zaragoza, Spain) reviewed the English grammar of this paper. Fernando Gracia and Jorge Esteve (Zaragoza University, Spain) provided field support. Two reviewers, James Sprinkle (University of Texas, Austin, USA) and Reimund Haude (University of Göttingen, Germany), made many useful suggestions for improvement. The research was partly supported by the Project BTE2006-12975 of the Spanish Ministerio de Ciencia y Tecnología, and by the Grupo Consolidado E-17 and PM067/2006 of the Aragón Government. SZ holds a pre-doctoral research grant from the Departamento de Educación, Cultura y Deporte of the Aragón Government.

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