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MORPHOLOGY AND PHYLOGENETIC INTERPRETATION OF A NEW CAMBRIAN EDRIOASTEROID (ECHINODERMATA) FROM SPAIN

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Abstract: The edrioasteroid, *Aragocystites belli* gen. nov. sp. nov. from the middle Cambrian Murero Formation of Spain, is described based on a small number of very well-preserved specimens. Important anatomical characteristics include star-shaped and pseudoclavate theca, rare or absent epispires, well-developed interradially positioned oral plates and several unorganized cover plates associated with each widely exposed flooring plate. A phylogenetic analysis including several Cambro–Ordovician species shows it is more derived than *Stromatocystites* and *Totiglobus* but is a sister group to a clade comprising *Cambraster* and *Edriodiscus*. Ontogenetic observations based on juveniles of 5 mm in diameter suggest that this species changed thecal shape markedly during growth. *A. belli* gen. nov. sp. nov. probably lived in quiet environments where it attached directly to the sea floor on stabilized substrates.

Key words: Echinoderm, edrioasteroid, phylogeny, Cambrian, Spain.

Edrioasteroids are a group of sessile Palaeozoic echinoderms that are known from the Cambrian to the Permian (Sumrall 2009). They had a domed, globular, clavate or disc-shaped theca with five ambulacra displaying a 2–1–2 symmetry (Sumrall and Wray 2007). The five ambulacra are designated A–E and the anal pyramid always lies in the CD interambulacrum (Bell 1976).

Complete edrioasteroids from the Cambrian are rare (Fig. 1), but their limited fossil record shows they were distributed in all continents (Zamora *et al.* in press*a*). There are several genera and species described from North America (*Totiglobus*, *Stromatocystites*, *Walcottidiscus*), Asia (*Kailidiscus*), Europe (*Cambraster*, *Protorophus* and *Stromatocystites*), Australia (*Chatsworthia*, *Stromatocystites*, *Edriodiscus*, *Hadrodiscus*) and North Africa (*Stromatocystites*; Pompeckj 1896; Bassler 1935; Cabibel *et al.* 1959; Bell and Sprinkle 1978; Jell *et al.* 1985; Smith and Jell 1990; Zamora and Smith 2010; Zhao *et al.* 2010; Zamora *et al.* in press*b*).

It has been more than 25 years since the first rigorous cladistic analysis of Cambrian edrioasteroids (Smith 1985) and the taxonomy and phylogenetic relationships of some species are still disputed. *Cambraster* (Fig. 1B, E) is a clear example of this because it has been regarded as a primitive isorophid (Smith 1985), between *Totiglobus* and *Edriodiscus* (Smith and Jell 1990), closely related to stromatocystitids (Zamora *et al.* in press*b*) or in an uncertain position (Guensburg and Sprinkle 1994). *Kailidiscus* (Fig. 1G–H) is another example, being isorophid in some features but distinct in its ambulacral construction and in the separation of the gonopore and hydropore as two discrete pyramids. There are also some new species that were unknown when Smith (1985) published his cladistic analysis of Cambrian edrioasteroids (Zamora and Smith 2010; Zhao *et al.* 2010) and others that were poorly documented (Zamora *et al.* in press*b*).

Here, I report a new stromatocystitid-like edrioasteroid from middle Cambrian rocks from Spain based on very well-preserved specimens. These include both juveniles and adults, providing ontogenetic information. Phylogenetic analysis places *Aragocystites* into the evolutionary tree of edrioasteroids, thus providing a better understanding of the relationships of Cambrian taxa.

GEOLOGICAL SETTING AND STRATIGRAPHY

All specimens come from the Iberian Chains (north-east Spain) and have been collected from levels within the Murero Formation at two different localities, Murero and Jarque (Fig. 2, see also Liñán *et al.* 2008 for a recent update of stratigraphy).

The Murero Formation is composed mainly of shales and some interbedded carbonate nodules and is interpreted as having been deposited in offshore environments.

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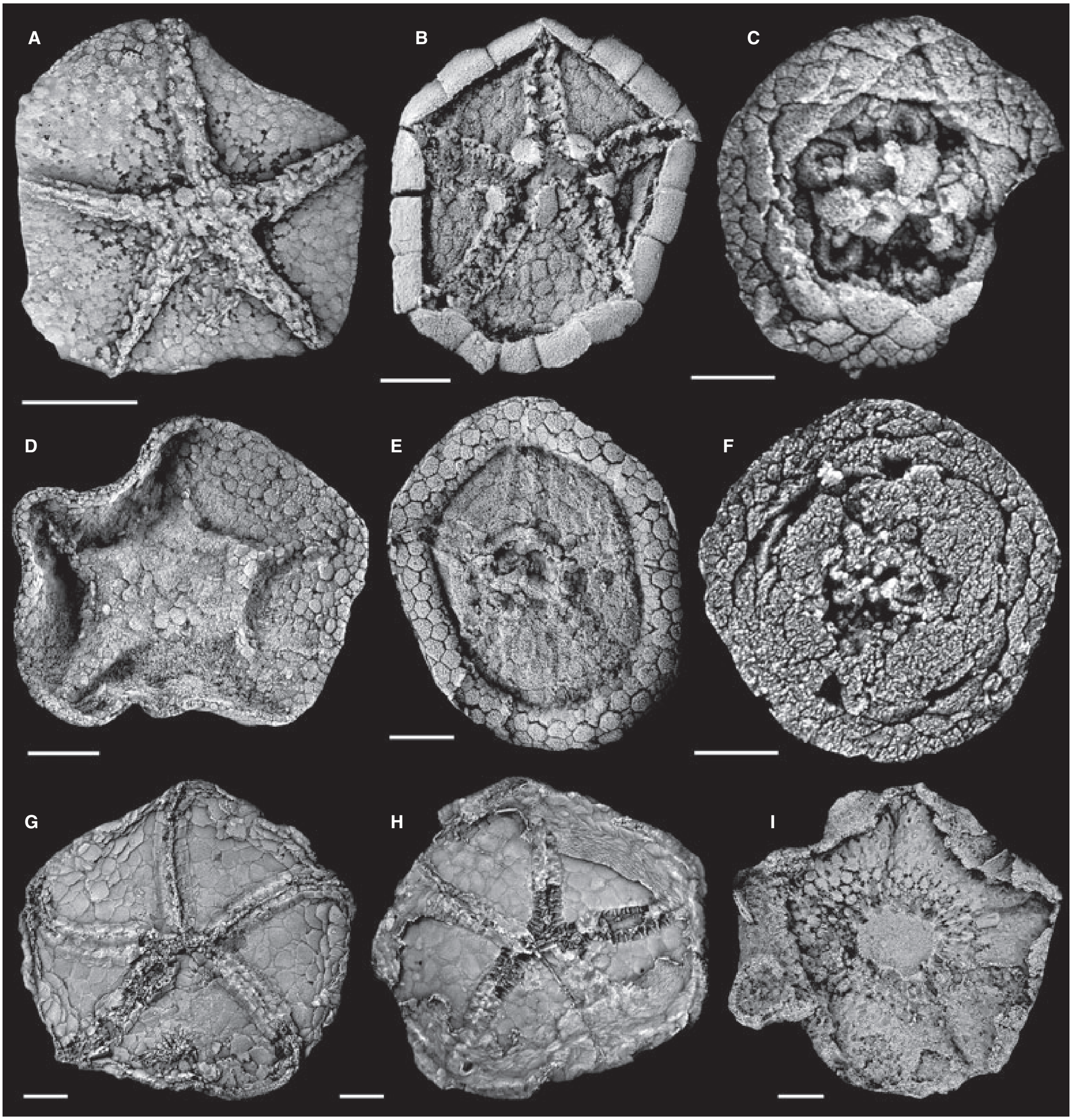


FIG. 1. General morphology of Cambrian edrioasteroids. A, D, oral and aboral views of *Stromatocystites pentangularis* from the Jince Formation (Bohemia). B, E, Oral and aboral views of *Cambraster cannati* from the Borobia Formation (Spain). C, F, oral and aboral views of a primitive isorophid *Protorophus hispanicus* from the Murero Formation (Spain). G–H, oral and aboral views of *Kailidiscus chinensis* from the Kaili Formation (China). I, aboral view of *Stromatocystites redunctus* from the Beetle Creek Formation (Australia). All specimens are from latex cast whitened with NH_4Cl sublimate. Scale bars represent 5 mm (A, D, G, H and I), 2 mm (B and E) and 1 mm (C and F).

It is the most fossiliferous Cambrian formation in the Iberian Chains with a high number of described taxa including trilobites, brachiopods, echinoderms, sponges, algae and rare nontrilobite arthropods (such as palaeoscolecids; Liñán and Gozalo 1986; García-Bellido *et al.* 2007; Zamora 2010*a*; Mergl and Zamora 2012).

The Murero locality (type locality for the Murero Formation) lies in the southern part of the Iberian Chains (Fig. 2). Specimens have been collected from a single stratigraphic level in the Rambla de Valdemiedes (RV1/17; Fig. 3), where edrioasteroids are very rare. Four complete specimens have been collected in association

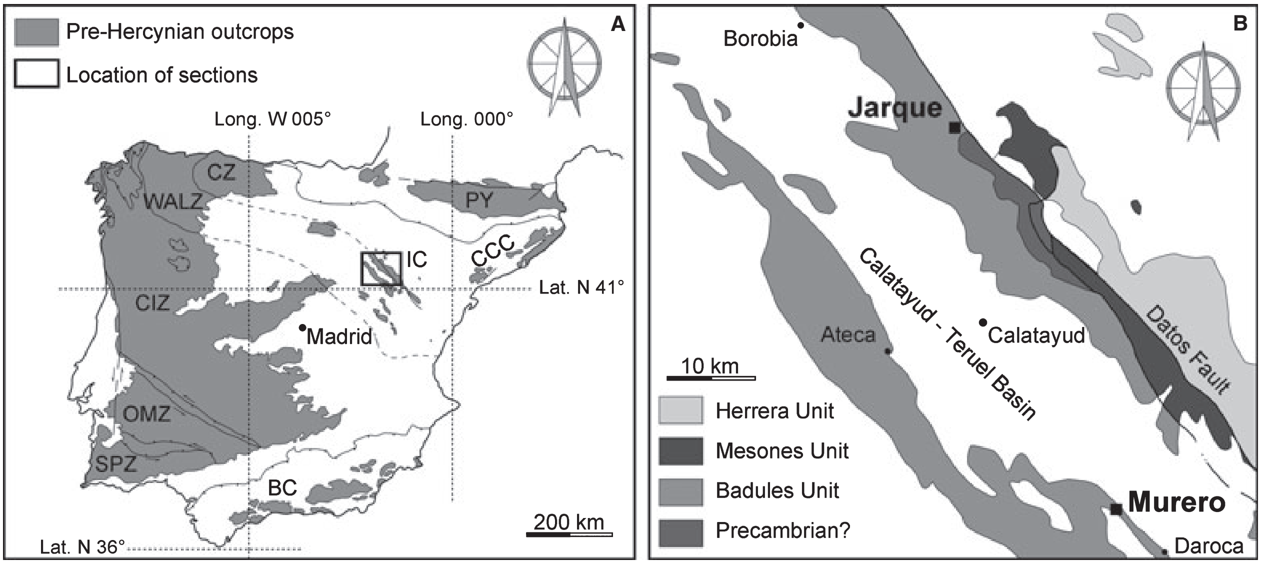


FIG. 2. A, map of Spain showing the location of the Iberian Chains. Abbreviations: BC, Betic Cordillera; CCC, Catalan Coastal Cordillera; CZ, Cantabrian Zone; IC, Iberian Chains; OMZ, Ossa–Morena Zone; PY, Pyrenees; SPZ, South Portuguese Zone; WAL, West Asturian–Leonese Zone. B, Map showing the localities studied and geological subdivision of the Iberian Chains (north-east Spain).

with eocrinoids (*Gogia gondi*), cinctans (*Gyrocystis platessa*), several species of trilobites (*Solenopleuropsis* spp., *Eccaparadoxides pradoanus*, *Conocoryphe heberti*) and palaeoscolecids.

The Jarque locality lies in the northern part of the Iberian Chains (Fig. 2). Specimens have been collected from the Jarque 1 section (Fig. 3), that is one of the most complete from all the Iberian Chains and encompasses many lower and middle Cambrian formations. Specimens come from a single bed where trilobites and other components are rare but clustered echinoderms are common, including the edrioasteroid described here and abundant cinctans (*Gyrocystis platessa*). There are also fragments of trilobites and brachiopods.

The age of both of these levels, based on associated trilobites, is uppermost Caesaraugustan – lowermost Languedocian in the Mediterranean time scale. This probably correlates with the Series 3-Stage 5 (*sensu* Álvaro *et al.* 2008) in the global time scale proposed by the ISCS (but see Gozalo *et al.* 2011 for a different interpretation).

Specimens from both localities are preserved fully articulated with associated well-preserved trilobites and other echinoderms. These beds probably formed via obrution events that entombed complete echinoderm specimens and other bioclasts derived from time-averaging processes. This environmental interpretation also is consistent with other finds of echinoderms and trilobites from the Murero Formation in other areas (see Zamora 2010*a*; Esteve *et al.* 2011 for more details).

SYSTEMATIC PALAEONTOLOGY

Repository. All specimens are housed in the Museo Paleontológico de la Universidad de Zaragoza with a repository number prefixed by MPZ.

Remarks. Orientation and ambulacral nomenclature of edrioasteroids follow Smith (1985). This is only possible after the identification of the main apertures of the body. The anal pyramid is always in the CD interambulacrum and the ambulacra are named clockwise from A to E according to their position (Fig. 4A). Adoral and aboral are used to designate positions closer or away from the oral area. The oral area was oriented facing away from the sea floor in life, and part of the aboral surface was in contact with the substrate. Proximal and distal refer to proximity to the mouth. Other useful terms for orientation are perradial or adradial that refer to a direction towards the perradial midline or towards the adradial sutures of ambulacra. The adradial suture is the zone of contact between the oral-ambulacral series plates and interambulacral plates (*sensu* Bell 1976).

Class EDRIOASTEROIDEA Billings, 1858

Genus ARAGOCYSTITES gen. nov.

Type species. Aragocystites belli sp. nov. from the middle Cambrian Murero Formation in Spain.

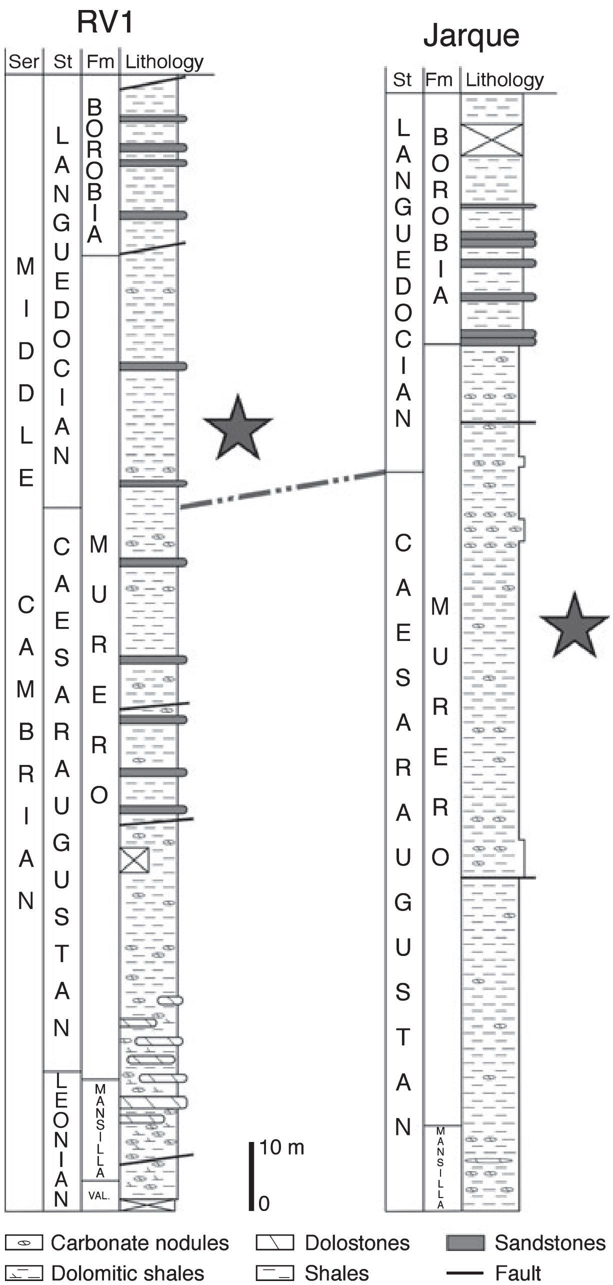


FIG. 3. Stratigraphic sections with the indication of levels where specimens have been collected. Modified from Liñán *et al.* 2008. RVI: Rambla de Valdemiedes 1 (Murero). Fm, Formation; RV1, Rambla de Valdemiedes section 1; Ser, Series; St, Stage; Val, Valdemiedes.

Diagnosis. Same as for the species.

Derivation of name. In reference to the Kingdom of Aragón, where specimens were collected.

Remarks. The genus *Aragocystites* differs from other Cambrian edrioasteroids in several characteristics. It differs from *Stromatocystites* in the near absence of epispires, relatively larger thecal plates, well-defined interradial oral plates and having multiple primary cover plates to each flooring plate. It differs from *Cambraster* in lacking a marginal ring with stout single elements and in the less organized arrangement of aboral plates. *Cambraster* also lacks a clear disc for attachment. *Aragocystites* is different from *Kailidiscus* and its close relative *Walcottidiscus* (Smith 1985; Zhao *et al.* 2010) in the construction of its ambulacral flooring plates; having only outer biserial flooring plates in *Aragocystites* and both inner and outer flooring plates in the latter two. Furthermore, the aboral surface is fully plated in *Aragocystites* and unplated in *Kailidiscus*. *Totiglobus* has a similar arrangement of ambulacra with widely exposed biserial flooring plates but *Aragocystites* has a different thecal shape, rare epispires and a different construction of the attachment disc. *Aragocystites* differs from the Cambrian isorophids (i.e. *Protorophus*, *Chatsworthia*, *Hadrodiscus*) in the arrangement of flooring plates, uniserial and internal in isorophids and biserial and exposed in *Aragocystites*. Other differences are the unplated aboral surface in isorophids and their well-developed marginal ring composed of imbricate plates that is poorly developed and composed of tessellate plates in the new genus.

Aragocystites belli sp. nov.
Figures 4–6

2010*a* Stromatocystitid indet. Zamora, p. 40, fig. 4a, b.
2010*b* Stromatocystitid indet. Zamora, p. 509, fig. 4f.
2011 Stromatocystidae indet. Zamora, p. 72, fig. 10a.

Diagnosis. Edrioasteroid with a star-shaped outline in adults, disc-shaped theca in juveniles becoming more clavate during growth. Five straight and narrow ambulacra and wide interambulacral areas. Ambulacra with ?biserial, widely exposed flooring plates and well-developed interradially positioned oral plates. Cover plates small, about two per flooring plate and regularly organized. Relatively large interambulacral plates, tessellate and with epispires absent or extremely reduced. Aboral surface plating with attachment disc comprising two central plates and several surrounding plates. Marginal rim of larger tessellate plates well developed in juveniles but becoming more diffuse in adults.

Derivation of name. Species dedicated to Bruce M. Bell for his contribution to the understanding of Palaeozoic edrioasteroids.

Holotype. MPZ2007/1890 (Figs 4A–C and 6A), specimen with an oral area and details of ambulacra.

Paratypes. MPZ2007/1891a, b and MPZ2011/95a, b, part and counterpart preserved; MPZ 2012/3, aboral surface preserved.

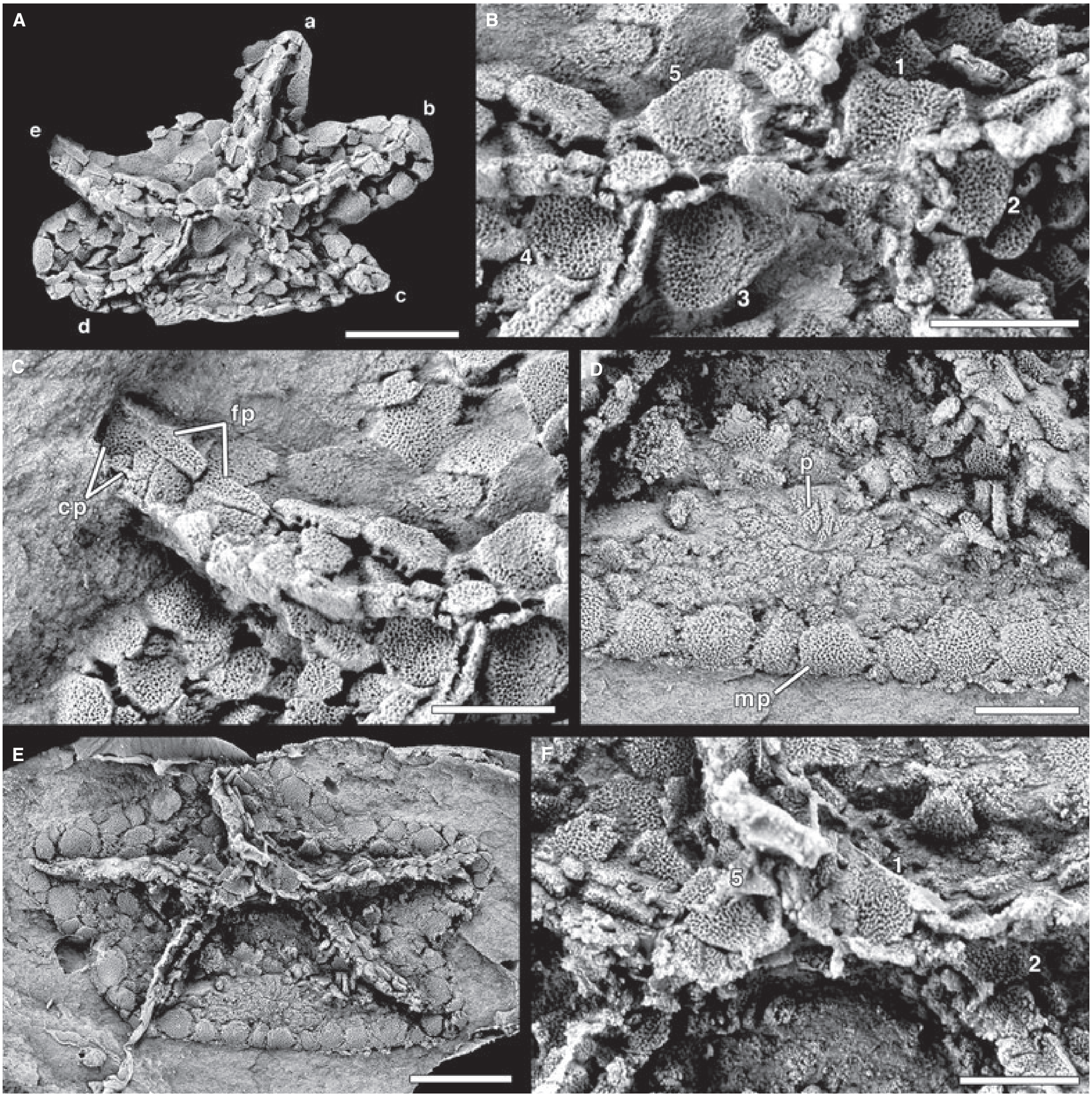


FIG. 4. *Aragocystites belli* gen. nov. sp. nov. from the middle Cambrian Murero Formation (Spain). A–C, oral view of the holotype MPZ2007/1890; A, complete theca showing the five ambulacra with a clearly marked 2–1–2 pattern. B, detail of the oral area with indication of the five interradially positioned oral plates. C, detail of ambulacrum E showing the exposed flooring plates and the unorganized cover plates. D–F, oral view of paratype MPZ2007/1891a. D, detail of interambulacrum CD with the anal pyramid. E, complete specimen in oral view showing the diffuse marginal ring. F. Detail of the oral area showing three of the five interradially positioned oral plates and oral cover plates. Abbreviations: a–e, ambulacral nomenclature; 1–5, interadially positioned oral plates; cp, cover plates; fp, flooring plates; p, periproct; mp, marginal plates from the distal ring. All specimens are from latex cast whitened with NH_4Cl sublimate. Scale bars represent 5 mm (A and E) and 2 mm (B–D and F).

Additional material. Other investigated material but more poorly preserved specimens are MPZ 2012/1 and MPZ 2012/2.

Type locality. Murero, Iberian Chains, Spain.

Type and horizon. All specimens are from the upper levels of the Murero Formation (uppermost Caesaraugustan – lowermost Languedocian; Cambrian – corresponding to the international Cambrian Series 3, Stage 5 *sensu* Álvaro *et al.* 2008).

Description. Aragocystites belli has a slightly inflated star-shaped theca in large individuals but is circular in juveniles (Figs 4A and 5E). Thecae range from 9 to 25 mm in diameter although specimens are slightly distorted due to tectonic deformation. In cross–section, specimens were probably biconvex with a domed oral surface and a subclavate aboral part.

The oral area is composed of five primary interradial oral frame plates (Figs 4B, F and 6). These plates are externally exposed and are larger than any other plates of the oral area. They form the corners of the mouth frame. Their inside connection with ambulacra is unknown. The mouth frame is covered by large oral cover plates (Fig. 4F).

The oral surface bears five straight ambulacra with a clear 2–1–2 pattern and wide interambulacral areas (Fig. 4E). Only the exposed parts of flooring plates are visible. They are large (about 5–6 per ambulacra), and elongate, and their arrangement suggests that they are biserial but their internal expression is not visible in any specimen (Fig. 4C). The cover plates articulate with the outer floor plates half way along the width, in a series of pits. Cover plates are smaller than flooring plates (Fig. 4C) and in multiple series with an organized arrangement. Primary large cover plates alternate between bigger and smaller elements followed by a second row of secondary and smaller cover plates. There are two cover plates abutting each floor plate. The primary series articulate with flooring plates and they are larger than the secondary series.

The interambulacral areas are proportionately wide and composed of large, polygonal interambulacral plates. These plates are irregularly arranged (Fig. 4A). Epispires occur only rarely and along the plate margins of largest plates.

There is a well-organized circlet of plates in the distal most oral area (?marginal ring). This is composed of a primary ring of large and tessellate elements that in some cases are surrounded by a discrete number of smaller plates (Fig. 4D). The marginal ring has about 9–10 plates per interambulacra with the exception of interambulacra CD that shows eleven. The marginal ring is more clearly seen in juveniles.

The aboral surface is fully plated with a distinct central region that is composed of two central plates surrounded by 7–8 large plates (Figs 5B and 6). This central region has a finer stereom texture. Epispires are lacking on the aboral surface. The other aboral plates form a tessellate pavement and probably provided a pseudoclavate shape to the theca elevating the oral area above the substrate.

The periproct is located in the distal CD interambulacrum, slightly left of the middle line (Fig. 4D). It is relatively large and almost abuts the marginal ring. The structure is a well-developed cone of irregular and very thin plates arranged concentrically. The placement and nature of hydropore and gonopore are unknown. A granular stereom microstructure covers all thecal plates with the exception of the attachment disc (Figs 4C and 5B).

Remarks. The internal arrangement of flooring plates is not observed in any available specimen, but based on the exposed part of these plates and comparison with other edrioasteroids with a similar arrangement, they are probably organized biserially. Another significant feature is the presence of a possible primitive marginal ring obvious in juveniles but looses distinction ontogenetically.

This structure is composed of a better organized circlet of plates that appear in the distal part of the oral area. The construction is different from that observed in isorophids and more similar to that in *Cambraster*, but in the later these elements are clearly different from other thecal plates and in *Aragocystites* the plates constructing the ring are undifferentiated from other thecal plates.

PHYLOGENETIC POSITION

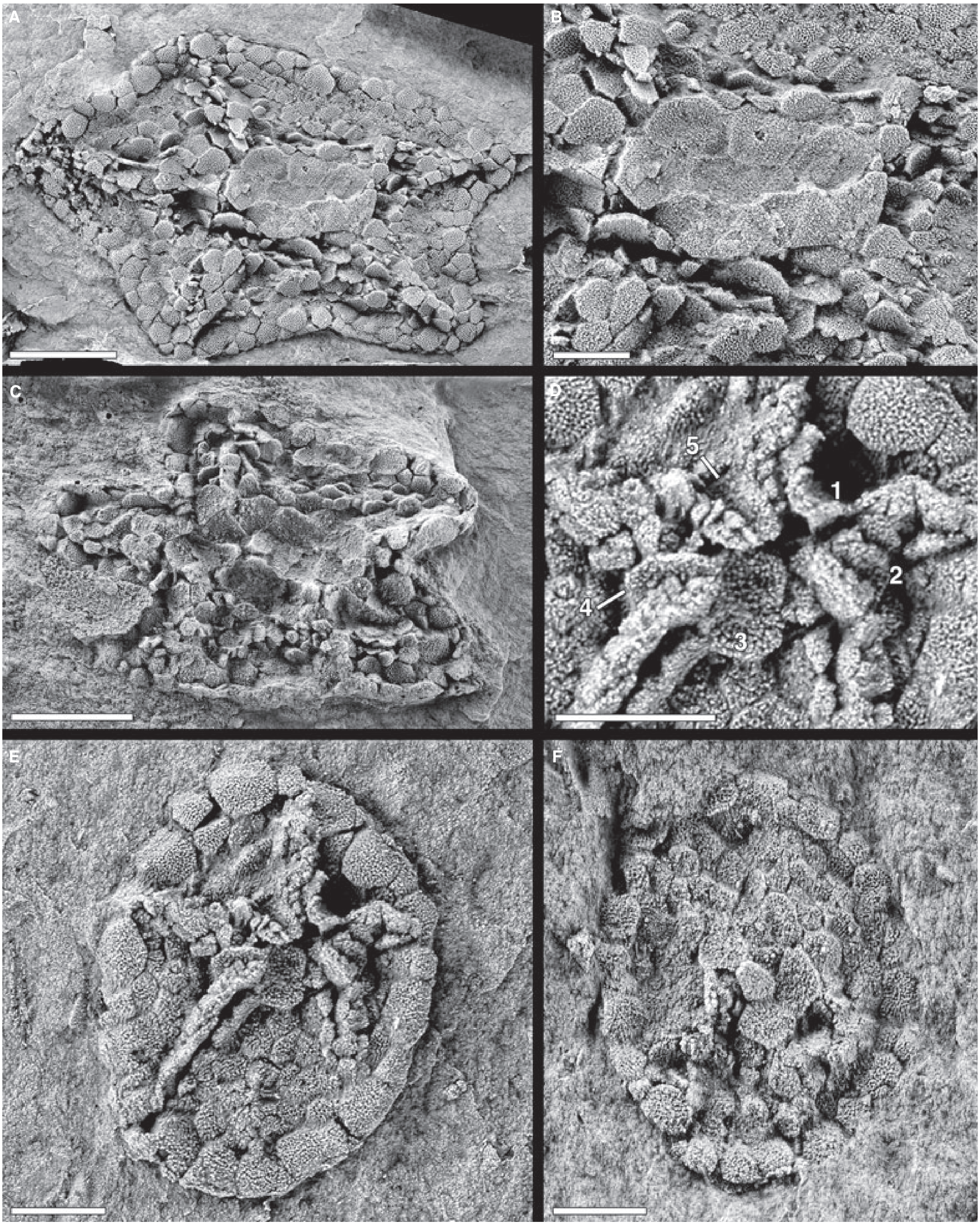
Material and methods

To evaluate the phylogenetic position of *Aragocystites belli* gen. nov. sp. nov. with respect to other Cambrian and Ordovician taxa, a cladistic analysis has been performed. Taxa included are *Stromatocystites pentangularis*, *S. reduncus*, *Cambraster cannati*, *Kailidiscus chinensis*, *Totiglobus nimius*, *Protorophus hispanicus*, *Chatsworthia spinosa*, *Hadrodiscus parma* and *Edriodiscus primoticus* from the Cambrian and *Argodiscus espilezorum* and *Edrioaster bigsbyi* from the Ordovician. The latter two are representatives of the two major post-Cambrian clades, the Isorophida and Edrioasterida.

Almost all specimens have been studied directly from museum collections, especially from the Natural History Museum (London) where there are original specimens or replicas of *Stromatocystites pentangularis*, *S. reduncus*, *Chatsworthia spinosa*, *Hadrodiscus parma*, *Edriodiscus primoticus* and *Edrioaster bigsbyi*. The Palaeontological Museum (Zaragoza University) has type material of *Protorophus hispanicus* and a large collection of *Cambraster cannati*. Types of *Afropyrgocystis espilezorum* are in the Faculté des Sciences et Techniques Guéliz, Université Cadi

FIG. 5. *Aragocystites belli* gen. nov. sp. nov. from the middle Cambrian Murero Formation (Spain). A–B, aboral view of paratype MPZ2007/1891b. A, general view of the aboral side showing the central attachment disc and the impression of the five ambulacra from the oral area. B, detail of attachment disc constructed with a couple of central plates and one circlet of surrounded polygonal plates. Note that a coarse stereom ornament is absent in the plates of the attachment disc. C, aboral view of paratype MPZ 2012/3. D–F, juvenile specimen MPZ2011/95. D, detail of oral area showing the distribution of cover plates and interradially positioned oral plates. E, oral view with a circular and disc-shaped theca showing five ambulacra, anal pyramid, and well-developed marginal ring. F, aboral view showing a poorly developed central disc for attachment. Abbreviations: See Figure 4. All specimens are from latex cast whitened with NH_4Cl sublimate. Scale bars represent 5 mm (A and C) and 2 mm (B and D–F).

Ayyad. Marrakech, Morocco. *Camptostroma* has been studied from latex casts from the United States National Museum. The remaining taxa (*Totiglobus nimius* and *Kailidiscus chinensis*) have been scored from data in Bell and Sprinkle (1978) and Zhao *et al.* (2010). Only four taxa could be scored for all the characters.



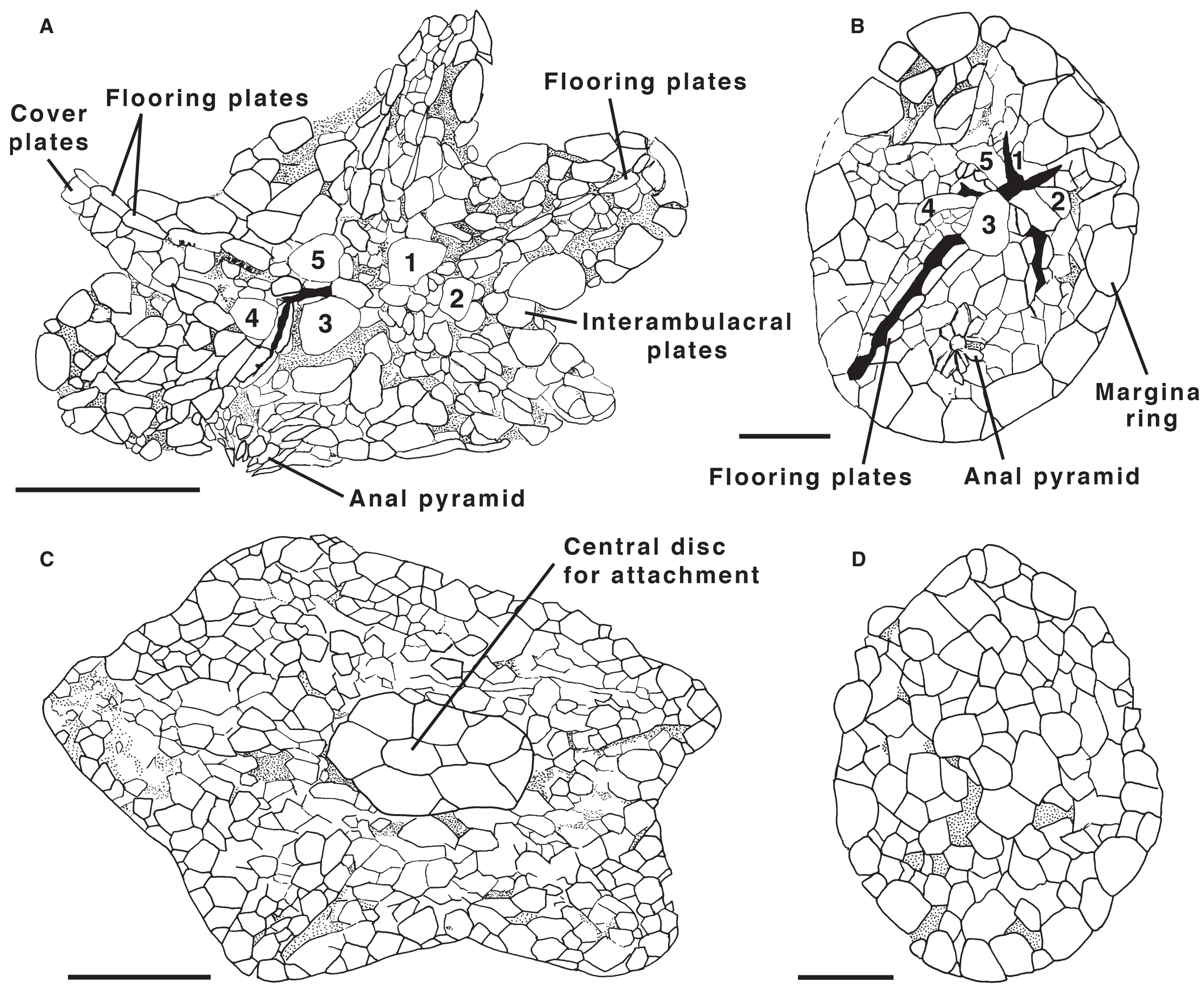


FIG. 6. Camera lucida drawings of *Aragocystites belli* gen. nov. sp. nov. with indication of major anatomical details. A, holotype MPZ2007/1890; B, paratype MPZ2007/1891b; C–D, paratype MPZ2011/95. For legend see Figure 4. Scale bars represent 5 mm (A and C) and 2 mm (B and D).

Camptostroma roddyi was selected as outgroup to root the analysis, in accordance with previous studies (Smith 1985; Smith and Jell 1990; Guensburg and Sprinkle 1994).

Characters. A total of 20 characters have been scored (Appendix). These have been taken from original descriptions and previous cladistic analyses (Smith, 1985; Smith and Jell 1990; Guensburg and Sprinkle 1994; Sumrall and Zamora 2011) with some additional characters based on personal observations. Wherever possible, characters were scored as the presence/absence of homologous characteristics. The matrix has a total of 17 binary characters and two multistate characters.

Of all characters, floor plates are the most complicated in edrioasteroids. In *Kailidiscus*, they are quadriserial; the outer plates of the floor plate system are topologically and structurally similar to those forms with biserial arrangement as edrioasterids and other taxa with similar arrangement (i.e. *Cambraster*, *Stomatocystites*), and they are considered homologous based on the following: (1) they bear pores, (2) they are biserial and (3) they show broad expression along the edge of the ambulacra. Sumrall and Zamora (2011) argued that these plates are also homologous with the hood plates in pyrgocystids. The inner floor plates of *Kailidiscus* are interpreted as homologues of the floor plates of isorophids that, except for pyrgocystids, lack the outer floor plates.

Analytical techniques. The data matrix was constructed using the computer program MacClade (Maddison and Maddison 2000) and then analysed using PAUP* (Swofford 2002). All characters with the exception of Character 1 were treated as unordered. All analyses used the branch

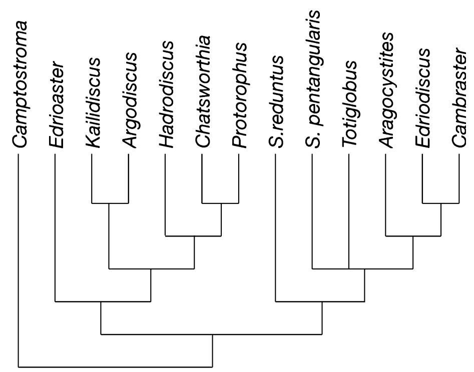


FIG. 7. Cladogram obtained from the cladistic analysis showing the phylogenetic position of *Aragocystites belli* gen. nov. sp. nov.

and bound search option, a method guaranteed to find the most parsimonious solutions.

Results

One most parsimonious tree (Fig. 7) was obtained from the unweighted analysis with a Consistency Index of 0.628, Retention Index of 0.72 and Rescaled Consistency Index of 0. 458. The analysis defines two clades but both lack clear autopomorphies being defined by homoplastic characters. One includes *Stromatocystites*, *Totiglobus*, *Aragocystites*, *Cambraster* and *Edriodiscus*. *Aragocystites* falls with *Cambraster* and *Edriodiscus* in a single clade, being more primitive than the latter two but more derived than stromatocystitids and *Totiglobus*. The other clade defines edrioasterids and isorophids based on two homoplastic characters (7, 10). *Edrioaster* lies at the base of the tree as the sister group of isorophids that also includes the aberrant *Kailidiscus*. Isorophids are supported with three characters (1, 13, 17), but only the two latter are autopomorphies. These are defined by an uncalcified aboral surface and the presence of inner flooring plates.

ONTOGENY

The ontogeny of Cambrian edrioasteroids is known for only a few taxa. Bell and Sprinkle (1978) described the ontogeny of *Totiglobus* from specimens ranging from 2.5 to 31 mm; and Zhao *et al.* (2010) provided a complete ontogenetic sequence of *Kailidiscus* including specimens ranging from less than 1 up to 30 mm. Lastly, Zamora *et al.* (in press*b*) described the ontogeny of *Cambraster* from specimens ranging from 4 to 26 mm.

Although there is not a complete ontogenetic sequence of *A. belli*, some conclusions can be drawn from comparing the smallest specimen of 9 mm (Figs 5E–F and 6) with the larger forms. The smallest specimen has a circular theca with a well-developed marginal ring, fewer interambulacral plates and large interradially positioned oral plates. By this size flooring plates, cover plates and anal pyramid are well differentiated.

The aboral surface in the juvenile shows a developed but poorly fused attachment disc and few aboral plates. Specimens of 20–25 mm are, by comparison, more clavate and star shaped with a poorly differentiated marginal ring and have more numerous and larger interambulacral plates which bear a few small epispires. At this stage, the aboral surface shows a very strong and easily identifiable attachment disc.

Some of the features expressed during ontogeny are probably related to changes in the ecological requirements. Smallest specimens probably rested with the entire aboral surface and the well-developed marginal ring on the substrate, providing a stronger attachment. The disc-shaped theca also offered less resistance against water currents. By contrast adult forms with a greater requirement for food needed to elevate the theca above the substrate for more efficient filter feeding. They attached to the sediment only with the fused disc of plates. This is also observed in other edrioasteroids like *Kailidiscus* in which juveniles show a discoidal theca that became more globular as adults (Zhao *et al.* 2010).

Apparently adults of *Aragocystites* retain some characters that are typical of juveniles of other genera that are more plesiomorphic, such as the absence of epispires or the marginal ring. Sprinkle and Bell (1978) suggested that the evolution of edrioasteroids is controlled by heterochronic processes. Based on the cladistic analysis, there is a possibility that morphologies *Cambraster* and *Edriodiscus* are derived from juvenile specimens of *Aragocystites* in which epispires were absent or very rare and show a better developed marginal ring (Fig. 5E).

PALAEOECOLOGY

The Murero formation was deposited in quiet water in an offshore marine environment. Sedimentological and palaeontological evidence suggest that an obrution event was responsible for entombing the palaeocommunities where these edrioasteroids lived. *Aragocystites belli* therefore most likely lived on stabilized mud with the aboral disc of plates attached to the substrate. The disc has a finer stereom texture ornamentation than is seen elsewhere suggesting cementation (Fig. 5B). The globular to pseudo-clavate shape of the theca also supports a mode of life in quiet environments and this interpretation also agrees with previous observations in other globular edrioasteroids (Smith and Jell 1990; Sumrall, 1993).

Other fauna that probably lived along side *A. belli* include other echinoderms typical of soft bottom communities such as the cinctan *Gyrocystis platessa* and the gogiid eocrinoid *Gogia gondi*, several species of trilobites (*Solenopleuropsis* spp., *Conocoryphe heberti*, *Eccaparadoxides pradoanus*), agnostoids and palaeoscolecids.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Appendix S1. List of characters.

Appendix S2. Character codification for each taxa.

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