The oldest isorophid edrioasteroid (Echinodermata) and the evolution of attachment strategies in Cambrian edrioasteroids

SAMUEL ZAMORA and ANDREW B. SMITH

Zamora, S. and Smith, A.B. 2010. The oldest isorophid edrioasteroid (Echinodermata) and the evolution of attachment strategies in Cambrian edrioasteroids. *Acta Palaeontologica Polonica* 55 (3): 487–494.

Two new middle Cambrian edrioasteroid (Echinodermata), *Protorophus hispanicus* gen. et sp. nov., and Isorophida gen. et sp. indet., are described from the early middle Cambrian (Cambrian Series 3, Stage 5) of Spain. These are the oldest and probably the most primitive isorophids, a clade previously known from the upper Cambrian onwards. Specimens are attached to trilobite fragments indicating that edrioasteroids had by this time separated into two lineages each with different strategies for attachment, sediment attachers and hard substrate attachers. The single U-shaped ambulacral flooring plates of *Protorophus* are unique while Isorophida gen. et sp. indet. shares the presence of spines in common with some pyrgocystitid isorophids. The shift from facultative soft-bottom attachment to obligate hard-ground attachment in edrioasteroids involved the retention of a juvenile trait into adulthood and was already underway by the middle Cambrian.

Key words: Echinodermata, Isorophida, Edrioasteroidea, Cambrian, Spain.

Samuel Zamora [samuel@unizar.es], Área y Museo de Paleontología-IUCA, Departamento de Ciencias de la Tierra, Universidad de Zaragoza, E-50009 Zaragoza, Spain;
Andrew B. Smith [a.smith@nhm.ac.uk], Department of Palaeontology, The Natural History Museum, Cromwell Road, London SW7 5BD, UK.

Received 27 January 2010, accepted 20 April 2010, available online 27 April 2010.

Introduction

The Cambrian is one of the fulcrum points in the history of life. It is during the Cambrian that metazoans first start to appear in great numbers in the fossil record, which in turn precipitated a major change in the nature of the sea floor (Bottjer et al. 2000). Whereas the typical late Neoproterozoic sea floors are characterised by the presence of well-developed microbial mats and an absence of sediment mixing by vertically oriented burrowing, the Cambrian saw a marked increase in sediment disturbance (Gehling 1999; Droser et al. 1999) and the demise of microbial-stabilised firm grounds. The new Phanerozoic-style seafloors resulted in relatively greater water content of seafloor sediment and a blurry water-sediment interface, which led to the first appearance of a mixed layer (Bottjer et al. 2000). The effect of this change in dominant substrate types on the ecology and evolution of benthic metazoans has been termed the Cambrian Substrate Revolution (CSR), and was a global event of primary importance for the early diversification of echinoderms (Bottjer et al. 2000). During the early Cambrian the majority of echinoderms rested directly on non bioturbated soft substrates as sediment stickers and sediment attachers, but with increased disturbance and the formation of a well developed mixed layer echinoderms were supposedly propelled to develop new substrate-adaptative morphologies and strategies (Dornbos 2006).

The group of echinoderms that made the most dramatic shift from firm bottom sediment attachers to hardground cementers during this interval are the edrioasteroids. Edrioasteroids are an extinct clade of small, sessile forms with a globular to discoidal theca lacking exothecal appendages. The majority of edrioasteroids reported from the middle Cambrian are fully plated forms that have little or no modification of their lower surface for attachment. Forms such as *Stromatocystites* (Smith 1985; Smith and Jell 1990; Parsley and Prokop 2004), *Cambraster* (Jell et al. 1985; Smith 1985; Zamora et al. 2007), *Edriodiscus* (Smith and Jell 1990) and *Totiglobus* (Bell and Sprinkle 1978) all have upper and lower surfaces fully plated, and are never found attached to shells or recognisable hard substrates. As speculated by Parsley and Prokop (2004) these were probably only loosely attached to the sea floor through mucous adhesion. By the Ordovician, however, these forms had disappeared and been replaced by either deep infaunal forms with a retractable peduncle (rhenopyrgids; Smith 1985; Holloway and Jell 1983) or fixed epifaunal isorophids with an uncalcified aboral surface and well developed peripheral ring that are always found attached to hardgrounds and/or shells (Guensburg and Sprinkle 1994; Sumrall et al. 2006). These have uniserial ambulacral floor plates in contrast to the biserial or quadriserial flooring plates of stromatocystitids and their kin.

doi:10.4202/app.2010.0012

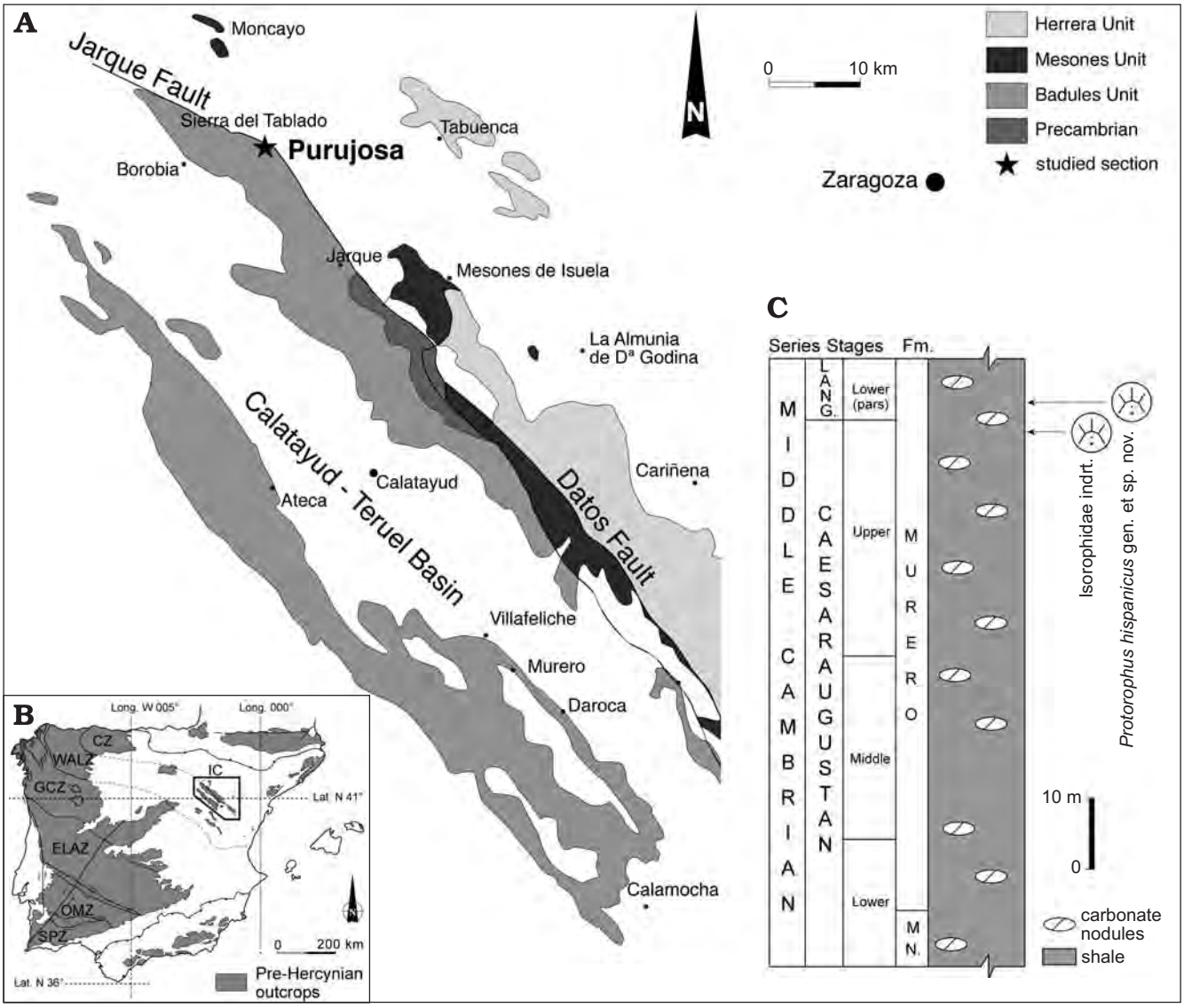

Fig. 1. **A**. Map showing the locality studied in the north part of Iberian Chains (Northeast Spain). After Gozalo and Liñán 1988. **B**. Map of Spain with the location of Iberian Chains. **C**. Synthetic stratigraphic column from Purujosa showing the levels from which the edrioasteroids were collected. CZ, Cantabrian Zone; ELAZ, East Lusitanian–Alcudian Zone; GCZ, Galician–Castilian Zone; IC, Iberian Chains; OMZ, Ossa-Morena Zone; SPZ, South Portuguese Zone; WAL, West Asturian–Leonese Zone.

There is, however, evidence that the upper Cambrian was a key period in edrioasteroid evolution. There are four records of edrioasteroids from this time interval. One indeterminate edrioasteroid from North America (Sumrall et al. 1997), a possible stromatocystitid from France (Ubaghs 1998) and two isorophid edrioasteroids from Australia, *Chatsworthia* and *Hadrodiscus* (Smith and Jell 1990), both of which have unplated aboral surfaces. Unfortunately, because the latter were recovered by acid preparation, it is not known whether these lived permanently attached or not. Furthermore, a new edrioasteroid from the middle Cambrian of China (Zhao et al. in press) shows intermediate characteristics. As a juvenile it appears very isorophid-like with a well-developed marginal ring forming a broad, aboral attachment area lacking aboral plates. However, it grows into a more stromatocystitid-like form that apparently adhered loosely to stabilised sediment.

We here report two new isorophid edrioasteroids from the early middle Cambrian (Cambrian Series 3) of Spain. These are not only the oldest members of this clade, but also demonstrate that the substrate revolution was already in progress, as both are clearly permanently attached to hard substrates.

Institutional abbreviations.—GM, Museum of Palaeontology, Guizhou University, Guiyang, China; MPZ, Zaragoza University Palaeontological Museum.

Geological setting and stratigraphy

The edrioasteroids were collected in the Purujosa 3 (Pur3) and Purujosa 4 (Pur4) sections in the northern part of the Iberian Chains (NE, Spain), 2 km south of Purujosa village (Fig. 1).

Both specimens come from the uppermost part of the Murero Formation but from different stratigraphic levels. This formation ranges in age in the studied area from early Caesaraugustan to early Languedocian (middle Cambrian). The Murero Formation consists of a siliciclastic succession with some interbedded carbonate nodules (Liñán et al. 2002) and has been interpreted as deposited in transgressive conditions representing offshore environments (Álvaro and Vennin 1997; Gámez et al. 2009). Edrioasteroids are restricted to two layers. The older consists of green silstones very rich in complete echinoderms, including the edrioasteroid reported here Isorophida gen. et. sp. indet., the gogiid eocrinoid *Gogia parsleyi*, the cinctan *Gyrocystis platessa*, as well as isolated *Ceratocystis*-like stylophoran plates and trilobite moults mainly belonging to *Eccaparadoxides brachyrachis* (see Zamora et al. 2009 for more details). The trilobite fauna does not provide a precise constraint on the age of this horizon, but based on levels above and below the layer yielding the edrioasteroid is uppermost Caesaraugustan–lowermost Languedocian in age.

The younger level is a thin layer (< 1 m in thickness) of red lutites that are richly fossiliferous. Associated fauna includes echinoderms (the edrioasteroid *Protorophus hispanicus* gen. et sp. nov., the cinctan *Gyrocystis platessa*, the stylophorans *Ceratocystis* sp., plus two different undescribed cothurnocystids, and the blastozoans *Gogia gondi*, Lichenoididae indet., and *Eocystites* sp.), polimerid trilobites (*Eccaparadoxides*? *pradoanus*, *Eccaparadoxides brachyrachis*, *Conocoryphe heberti*, *Solenopleuropsis thorali*, *Solenopleuropsis marginata*, *S. verdiagana*), agnostoid trilobites (*Condylopyge* sp., *Peronopsis acadica*, *P. ferox*, *Plaurocterium* sp., and *Megagnostus* sp.), and both orthid and lingulid brachiopods. Esteve et al. (in press) and Zamora (2010) provide further details on the fauna. The trilobite *Solenopleuropsis thorali*, indicates an age of earliest Languedocian (sensu Álvaro and Vizcaïno 1998) for this level.

Middle Cambrian isorophid precursors

The two edrioasteroids recovered (Figs. 2, 3) are both rather small (4.3 mm and 11 mm in diameter) and have the body clearly divided into a peripheral rim and a central disc. Only the upper surface appears to be plated. The peripheral rim is circular and consists of a series of plates which become progressively smaller towards the edge of the rim. The largest innermost plates overlap on their oral face, but more or less abut to form a flat pavement aborally. The aboral surface of these plates lacks the radially aligned ridges and grooves that are commonly found in post-Cambrian isorophid edrioasteroids. Because of the arrangement of plates the peripheral rim is highest at its interior edge and slopes outwards.

The central disc is disrupted and largely missing in one specimen, but the other has a more or less undisrupted surface (Fig. 2A, B). The centre of the zone is covered by seven large, tall oral plates that appear to have abutted in life, although they are now slightly disrupted due to post-mortem collapse. Around the outside the most prominent elements are large U-shaped ossicles, three of which are clearly visible, one is partially visible and one further plate is presumably hidden by overlying platelets. These fill the space between the oral plates and the peripheral rim and are separated from each other by three or four small, somewhat imbricate plates. These U-shaped plates we interpret as ambulacral flooring plates. In close proximity to the U-shaped plates and overlying them are two or three small lath-like plates that, based on their shape and position, we interpret as disarticulated cover plates. In one interray there are a series of small lathe-like plates, again rather disrupted, that we interpret as the periproctal cone. The position of the periproct agrees with the inferred 2-1-2 pattern of oral plates in the central region.

Viewed from beneath (Fig. 2B, D) plate boundaries in the disc are difficult to make out, although the plates of the peripheral rim are clearly distinguished. While the central region beneath the oral plates and the periproct is clearly open and unplated, the outer part of the disc forms a flat calcified surface with few unambiguous plate boundaries. Large plates with a hemispherical outline coincide precisely in position with the U-shaped ambulacral plates seen in oral view, implying that these are the aboral view of the same plates.

A well developed peripheral rim is a characteristic of isorophid edrioasteroids, but is also seen in juvenile of the new edrioasteroid from China (Fig. 4B, C) (Zhao et al. in press). However, no edrioasteroid has ever been described with U-shaped terminal ambulacral flooring elements. The specimen that preserves disc plating is small, less than 5 mm in diameter, and thus potentially a juvenile. However, the ontogeny of the new edrioasteroid from China has been described in detail from individuals as small as 0.5 mm in diameter. At equivalent sizes (3–5 mm) Chinese specimens (Fig. 4B, C) clearly has paired adradial ambulacral, flooring plates that are visible both internally and externally, and a mouth frame constructed of six large integrated interradial plates (Zhao et al. in press). By contrast *Protorophus* has no clear mouthframe and single U-shaped terminal plates. It is this uniseriality of ambulacral flooring plates that suggests that *Protorophus* is closer phylogenetically to isorophids than to the new edrioasteroid from China.

Nor is our specimen likely to be a juvenile *Cambraster*. *Cambraster* is an edrioasteroid-like form that has a well developed marginal ring of stout plates which are bounded externally by a narrow peripheral rim of plates (see Jell et al. 1985; Smith 1985; Zamora et al. 2007). The ambulacra in adults are underlain by biserial flooring plates along almost all of their length, but the very tip of the ambulacra extends onto the marginal ring which has a corresponding U-shaped notch to house the distalmost coverplates.

Nevertheless, our specimen is not a juvenile *Cambraster* because firstly, the aboral surface is not fully plated, and secondly the complete ontogeny of *Cambraster* is now known (unpublished data) with specimens ranging from 6 to 35 mm

doi:10.4202/app.2010.0012

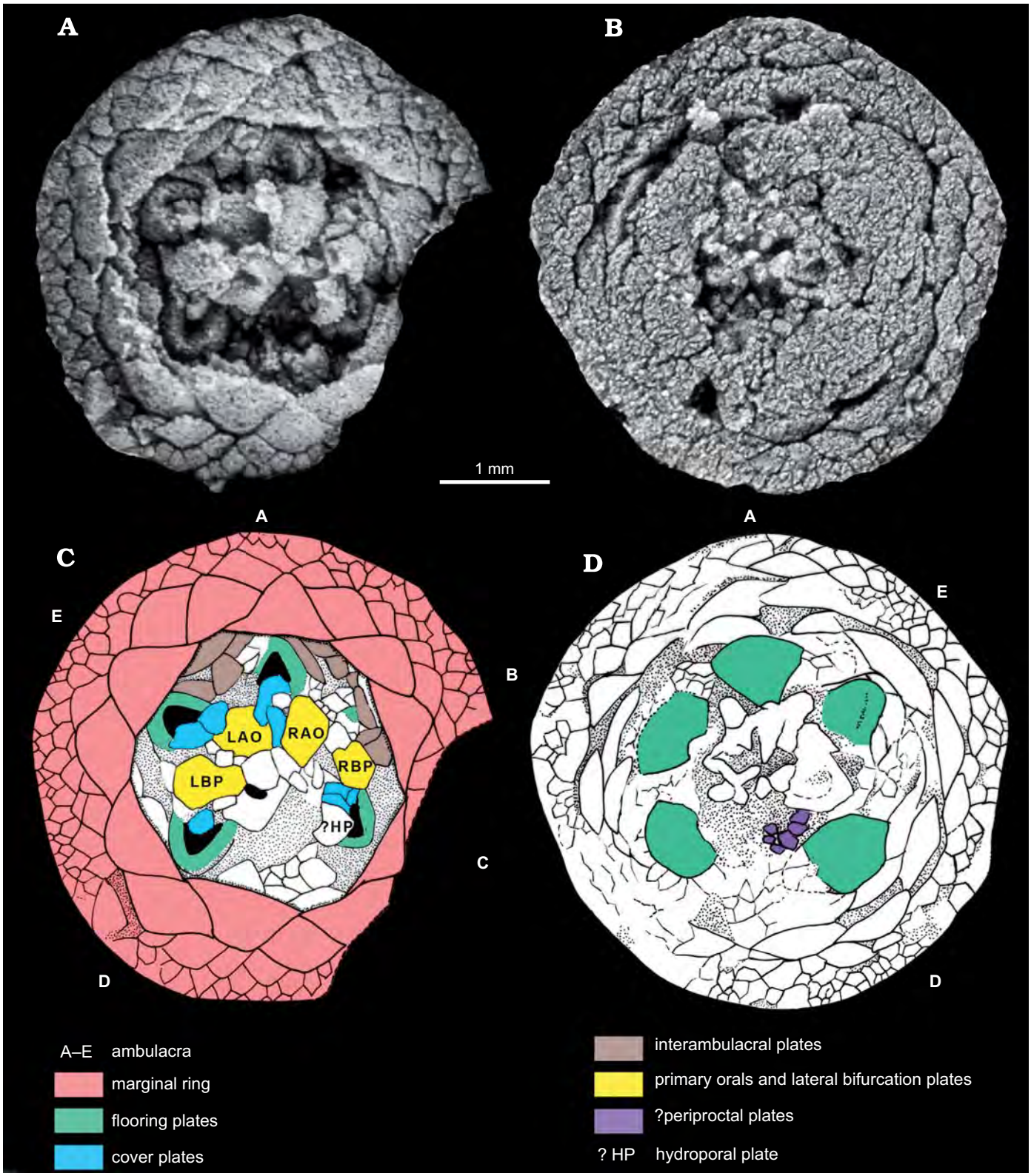

Fig. 2. Edrioasteroid *Protorophus hispanicus* gen. et sp. nov., Purujosa (Zaragoza Province, Spain). Holotype MPZ2009/1233 in adoral (**A**) and aboral (**B**) views; camera lucida drawing of the adoral view (**C**) with interpretation of major anatomical structures; camera lucida drawing of the aboral face (**D**). Note the base of the flooring plates. Scale bar is 1 mm for all specimens. Photographs are taken from latex casts whitened with NH_4Cl sublimate. Abbreviations: LAO, left anterior oral plate; LBO, left branching oral plate; RAO, right anterior oral plate; RBO, right branching oral plate.

in diameter. These clearly show that a continuous marginal ring of large plates is present from the earliest stages of growth, and is composed of its full adult complement of about 20 marginal plates by 6 mm diameter.

Attachment in echinoderms and the Cambrian substrate revolution

It seems highly likely that attachment at metamorphosis is primitive for echinoderms in general. Both crinoids and asteroids pass through an attached stage in their development, before becoming free living. Indeed it is the adoption of obligate attachment at the anterior and the subsequent body axis rotation that allowed echinoderms to break away from the straight-jacket of bilateral symmetry and explore new bodyplans (Smith 2008). Larval attachment at metamorphosis was therefore probably prevalent and possibly obligate amongst Cambrian echinoderms. Early in the Cambrian attachment was retained into adulthood by some stalked forms. Cambrian gogiids for example have plated holdfasts that allow them to attach directly to the bottom or to shell debris on the sea floor and were sessile throughout life (Sprinkle 1973; Parsley and Zhao 2006; Zamora et al. 2009). The same is also true for early solutes (Daley 1996).

Cambrian edrioasteroids, such *Stromatocystites*, *Totiglobus*, *Cambraster*, and the new Chinese taxa, have been interpreted as facultative sediment attachers (Bell and Sprinkle 1978; Smith and Jell 1990; Dornbos 2006; Parsley and Prokop 2004; Zhao et al. in press). Yet the discovery of immediately post-larval individuals in the new edrioasteroid from China (Zhao et al. in press) suggest that attachment of juveniles was crucial even in these Cambrian groups. By the beginning of the Ordovician almost all edrioasteroids had switched to become sessile cementers throughout life, utilising a variety of different substrates. These include exposed concretions, hardgrounds, shell pavements, isolated skeletal debris, microbial buildups and encrusting bryozoan colonies, living organisms and pebbles (see Sumrall et al. 2006, for a synthesis).

Our small individuals are clearly firmly attached to skeletal debris. Zhao et al. (in press) also report that very occasionally the new Chinese edrioasteroid is found attached to skeletal debris (presumably as small individuals). What this implies is that the basic isorophid mode of life arose by retention of the early larval attachment phase into adulthood. While skeletal debris was sparse and hardgrounds lacking this early attachment phase was abandoned in favour of free-lying. However, as the Cambrian substrate revolution progressed and bioturbation increased in both depth and intensity during the Cambrian (Bottjer et al. 2000), a transition occurred in the dominance of subtidal soft substrates from firm Proterozoic-style soft substrates without a well-developed mixed layer to soupier Phanerozoic style soft substrate with a well-developed mixed layer. This substrate change greatly affected the evolution of echinoderms with the apparition of new body plans and different ecological strategies. Dornbos (2008) examined the fossil record of three echinoderm groups (edrioasteroids, eocrinoids, helicoplacoids) indicating that genera adapted to a typical Proterozoic style soft substrates as sediment attachers, sediment resters and shallow sediment stickers were taxonomically dominant during the Early and Middle Cambrian.

The Cambrian substrate revolution clearly affected the evolution of echinoderms but in the case of edrioasteroids, their history was more closely tied to the development of hard-grounds in the fossil record. In the lower Cambrian, when skeletal debris were less common and hardgrounds absent, edrioasteroids attached only as juveniles and became free-living or sediment attachers as they developed. The origin of isorophids as obligate encrusters presumably involved retention of this larval stage into adulthood and became possible only with the expansion of hardground environments from the late Cambrian onwards (for a history of hardgrounds see review by Taylor and Wilson 2003). Nevertheless, this evolutionary shift was already underway by the Middle Cambrian, as our discovery of an 11 mm diameter adult attached to a trilobite moult (Fig. 3A) demonstrates. The fact that such occurrences are extremely rare (we have just one example from a horizon that has yielded more than 150 cinctans, 17 gogiids and only one edrioasteroid) implies that opportunities for hardground colonisation were few and far between at this time.

Systematic palaeontology

Phylum Echinodermata Bruguière, 1791 (ex Klein 1734)

Class Edrioasteroidea Billings, 1858

?Order Isorophida Bell, 1976a

Genus *Protorophus* nov.

Etymology: A combination of the greek *proto*—the first or earliest and Isorophida.

Type species: *Protorophus hispanicus* sp. nov., see below.

Diagnosis.—Edrioasteroid with a discoidal theca with a wide and clearly differentiated peripheral rim composed of imbricate plates. Central area dominated by oral plates, six or seven in number. Ambulacra floored by a single large U-shaped plate. Aboral surface uncalcified.

Discussion.—With only one small specimen it is likely that many of the features of *Protorophus* are juvenile. However, the highly distinctive U-shaped terminal flooring plates of this genus are unique and seen in no isorophids whose ontogeny has been described (Bell 1976a, b). The well-developed peripheral rim, lack of aboral plating and the uniserial nature of the ambulacral terminal flooring plates all suggest affinities with Isorophida rather than any of the other Cambrian non-isorophid edrioasteroid groups.

Geographic and stratigraphic range.—Iberian Chains (North Spain), middle Cambrian (Cambrian Series 3).

Protorophus hispanicus sp. nov.

Fig. 2.

Etymology: From the Spanish *hispano, hispánico* in reference to its occurrence.

doi:10.4202/app.2010.0012

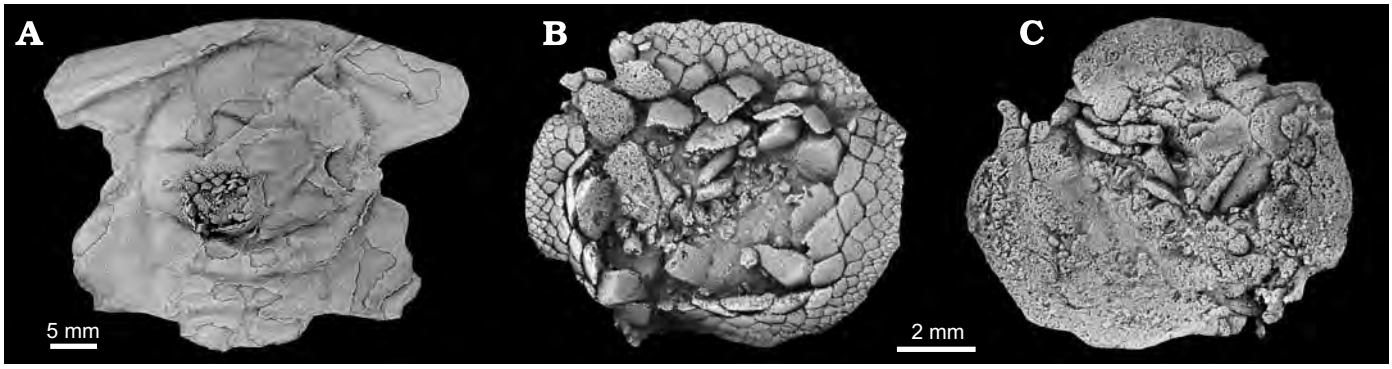

Fig. 3. Isorophida gen. et sp. indet., MPZ2010/857, Purujosa (Zaragoza Province, Spain). **A**. General view of specimen attached to a paradoxidid cranidium. **B**. Detail of the oral surface of the theca, note the well developed marginal ring and the disarticulated spines in the central theca. **C**. Aboral surface of the same specimen. Photographs are taken from latex casts whitened with NH_4Cl sublimate.

Type material: Holotype and only known specimen, part and counterpart preserved as natural moulds in siltstones: MPZ2009/1233a, b.

Type locality: Moncayo Natural Park, close to the village of Purujosa (north Iberian Chains, Zaragoza province, Spain).

Type horizon: Purujosa 3 section (Pur3), level 10, *Solenopleuropsis thorali* Zone, Murero Formation, Lower Languedocian sensu Álvaro and Vizcaïno, 1998, Middle Cambrian (equivalent to Cambrian Series 3, Stage 5).

Diagnosis.—As for genus.

Description.—Interambulacra AB, BC, CD, DE, EA following Bell (1976a). Orientation of specimen is based on the identification of a structure we interpret as the periproct. As this structure is in the interray CD in all known edrioasteroids, the other ambulacra are numbered according with this position.

Small (4.3 mm diameter) isorophid-like, circular in plan view, with a discoidal theca clearly separated into a peripheral rim and a central disc; thecal plating without ornament.

Central area of theca covered with large, prominent, oral cover plates that slope upwards towards the middle. Opposite the inferred position of the periproct there are a pair of oral plates to left and right of the U-shaped plate that we identify as left and right anterior orals (Fig. 2A, C). Two further plates sit in interambulacra AB and DE, which are left and right lateral bifurcation plates (Fig. 2A, C). Finally, in the CD interray there are three oral plates, two on the left-hand side and a single plate on the right-hand side, presumably equivalent to the posterior orals and hydropore plate of isorophids. The pattern thus conforms to the standard 2-1-2 symmetrical pattern of other edrioasteroids, although now slightly disrupted. Gonopore and hydropore unknown due to the state of preservation.

There is a single ambulacral flooring plate in each radius. This is a large ossicle with a U-shaped facet in oral view (Fig. 2A, C) and a flat aboral surface. The deep food groove defined by this U-shaped facet faces adorally. Cover plates are relatively large (ca. 250 μm), but lie scattered above the ambulacral plates and their poor preservation preludes detailed description. There are two or three coverplates to each flooring plate. Interambulacral plates few, with three or four preserved in each interray.

The CD interray is the widest and retains a few small lath-like plates that mark the remains of the periproct.

The peripheral rim is composed of 3 to 4 circles of plates that are tesselate on their aboral contact but which imbricate orally. These plates decrease in size towards the outer edge. Ten large peripheral plates, alternately radial and interradial in position, form the inner edge of the peripheral rim. Ten rhomb shaped and slightly smaller secondary peripheral plates are intercalated between each pair of primaries. They are rhomb shaped and slightly smaller. The other peripheral plates rapidly decrease in size distally.

Aboral surface unplated. The aboral surface of peripheral rim plates is flat and smooth and plate boundaries are clearly distinguished (Fig. 2B, D). It occupies ca. 30 % of the radius. Inside the peripheral rim there are two zones, an outer calcified zone that is in contact with the substrate at the same level as the peripheral rim, and an inner zone where plating is elevated away from the surface. Plate boundaries in the outer zone are difficult to discern but a small number of large, flat elements that are approximately oval in outline can be made out. The best defined of these coincide exactly in position with the U-shaped flooring plates. Although this might be a separate calcified surface, it seems more likely that what is observed is the aboral surface of the ambulacral flooring plates and interradial elements that have collapsed onto the substrate. Only the elevated oral plates remain separated from the base, creating the central cavity. The inner face of at least some of the oral cover plates appear to have a spike-like projection (Fig. 2B, D).

Discussion.—*Protorophus* is unique in having a single large flooring plate to each ambulacrum. This element is flat-based and has a prominent U-shaped notch on its oral surface. In specimens of the new edrioasteroid from China of similar size (Fig. 4B, C) there is an oral frame of interradial plates and paired ambulacral flooring plates (Zhao et al. in press: fig. 6). In early isorophid taxa the flooring plates are simple U-shaped elements underlying the ambulacra that decrease in size distally (Bell 1976a, b; Sumrall 1996; Sumrall and Zamora in press). Chinese taxa, by contrast, has ambulacra that have a double biseries of flooring plates (Fig. 4A). *Cambraster* has a strongly developed marginal ring of ossicles and a fully plated aboral surface. The lack of a complete

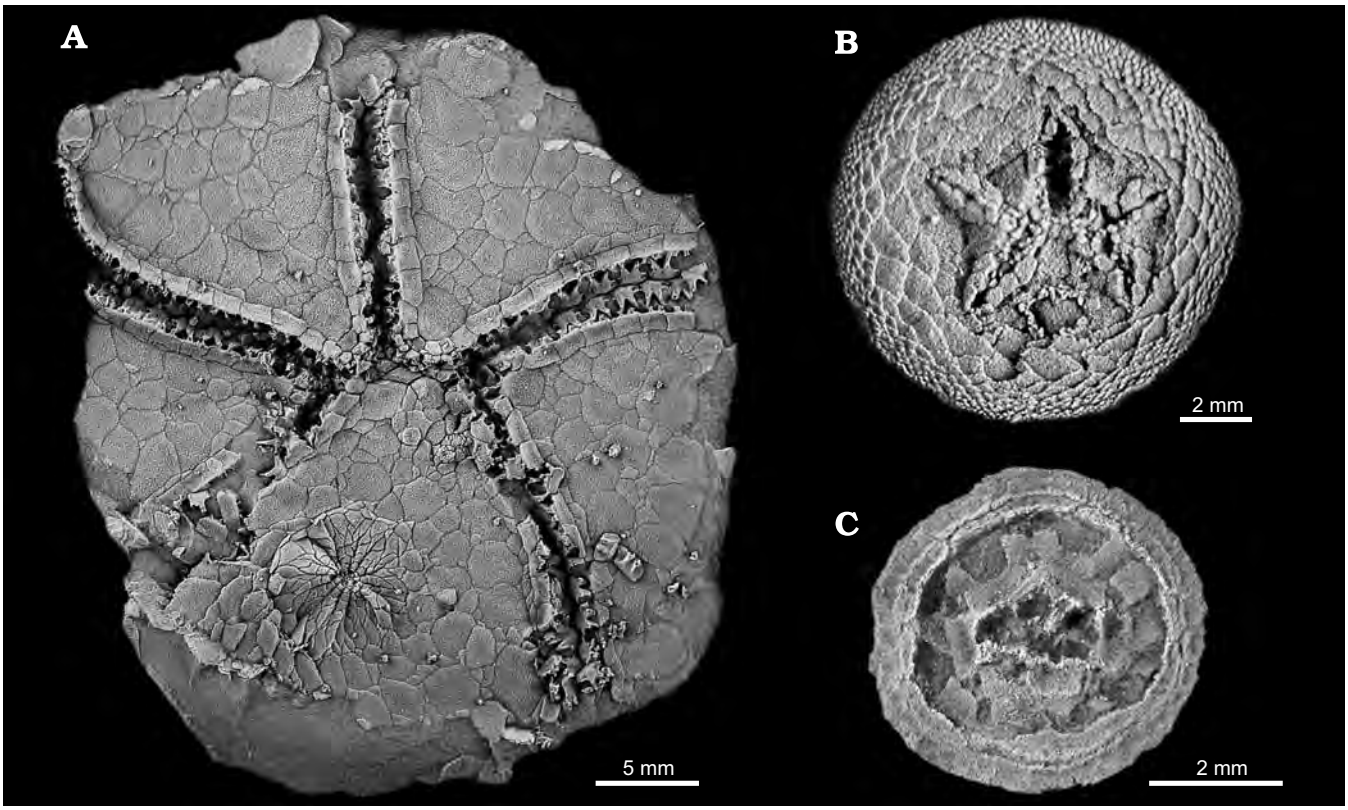

Fig. 4. New edrioasteroid from the middle Cambrian of China (Zhao et al. in press). **A**. Adoral view of an adult specimen GM2103. **B**. Adoral view of a juvenile specimen GM1331 **C**. Aboral view of a juvenile specimen GM1670. B, C show a marginal ring. Photographs are taken from latex casts whitened with NH_4Cl sublimate. Courtesy of Colin Sumrall.

rim of stout marginal ossicles in *Protorophus* readily distinguishes it from similar sized juveniles of *Cambraster*.

Protorophus has greater similarity to the upper Cambrian *Chatsworthia* and *Hadrodiscus* from Australia in the plate arrangement of the marginal ring. Poor preservation in these Australian taxa prevents us making a detailed comparison, and their flooring plate arrangement remains unknown. Individuals in both taxa range from about 6 mm in diameter but by that stage both *Chatsworthia* and *Hadrodiscus* clearly show long straight series of ambulacral coverplates in contrast to *Protorophus*. None shows the large terminal U-shaped plates of *Protorophus* even in partially disarticulated material.

Geographic and stratigraphic range.—Iberian Chains (west Gondwana margin), lower Languedocian.

Isorophida gen. et sp. indet.

Fig. 3.

Material.—One specimen, MPZ2010/857, preserved as natural moulds in part and counterpart.

Description.—Theca in plan view subcircular in outline and preserving only the marginal ring and some collapsed plates of the central disc. The aboral face is uncalcified. The thecal diameter is 11 mm. The marginal rim is composed of tesselate plates, arranged into 5 to 6 circles of plates: plates are polygonal, diamond to rhombic in shape, and arranged in decreasing size towards the periphery.

Plating of the disc is largely lost, with just a few scattered plates remaining. Prominent amongst these are five spines, 2 mm in length and approximately cylindrical in cross-section (Fig. 3B, C). The specimen is attached to the glabella of a trilobite (Fig. 3A).

Discussion.—This specimen has a peripheral ring that is very similar to that seen in *Protorophus*, and in juveniles of the new edrioasteroid from China. Unlike both of those taxa, however, there are prominent spines, possibly associated with the innermost plates of the peripheral rim.

Edrioasteroids with spines are unusual and are confined to pyrgocystids and an aberrant ?agelacrinitid. These include *Pyrgocystis* sp. from the middle Ordovician of North America, with spines around all the oral area (Guensburg and Sprinkle 1994), *Hystrichopsydrax sandersi* from the late Ordovician of North America which has spines in the interambulacral area (Guensburg 1988), *Epipastron ixine* and Isorophida gen. et. sp. indet, from the Silurian of Australia (Holloway and Jell 1983) which have large spines in the interior part of the marginal frame, and *Epipastron* sp. from the Silurian of Tasmania which shows flexible spines in the marginal ring (Holloway 1992).

This specimen comes from the same locality as *Protorophus* but from a slightly older horizon. It probably represents a new taxon, but as we know so little about its morphology we simply note its occurrence here and place it in open nomenclature.

doi:10.4202/app.2010.0012

Geographic and stratigraphic range.—From Moncayo Natural Park, close to the village of Purujosa (north Iberian Chains, Spain). Murero Formation, latest Caesaraugustan–earliest Languedocian of the Mediterranean stratigraphic chart of Liñán et al. 1993 and Ávaro and Vizcaïno 1998; Middle Cambrian (equivalent to Cambrian Series 3, Stage 5).

Acknowledgements

Isabel Pérez (MEC-FSE) has provided us excellent photograph assistance and Fernando Gracia and Jorge Esteve (Zaragoza University, Spain) invaluable field sampling help. Colin D. Sumrall (University of Tennessee, Knoxville, TN, USA) provided us excellent photographs of the new edrioasteroid from China. Two reviewers Ron Parsley (Tulane University, New Orleans, LA, USA) and anonymous one, provided comments that improved the resulting manuscript. This work is a contribution to the Project Consolíder MURERO number CGL2006-12975/BTE from MEC of Spain-FEDER-EU and Grupo Consolidado E-17 from Gobierno de Aragón.

References

Álvaro, J.J. and Vennin, E. 1997. Episodic development of Cambrian eocrinoid-sponge meadows in the Iberian Chains (NE Spain). *Facies* 37: 49–64. http://dx.doi.org/10.1007/BF02537370.

Álvaro, J.J. and Vizcaïno, D. 1998. Révision biostratigraphique du Cambrien moyen du versant méridional de la Montagne Noire (Languedoc, France). *Bulletin de la Société géologique de France* 169: 233–242.

Bell, B.M. 1976a. A study of North American Edrioasteroidea. *New York State Museum, Memoirs* 21: 1–447.

Bell, B.M. 1976b. Phylogenetic implications of ontogenetic development in the class Edrioasteroidea. *Journal of Paleontology* 52: 243–266.

Bell, B.M. and Sprinkle, J. 1978. *Totiglobus*, an unusual new edrioasteroid from the Middle Cambrian of Nevada. *Journal of Paleontology* 52: 243–266.

Bottjer, D.J., Hagadorn, J.W., and Dornbos, S.Q. 2000. The Cambrian substrate revolution. *GSA Today* 10: 1–7.

Daley, P. 1996. The first solute, which is attached as an adult: a Mid-Cambrian fossil from Utah with echinoderm and chordate affinities. *Zoological Journal of the Linnean Society* 117: 405–440.

Dornbos, S.Q. 2006. Evolutionary palaeoecology of early epifaunal echinoderms: Response to increasing bioturbation levels during the Cambrian radiation. *Palaeogeography, Palaeoclimatology, Palaeoecology* 237: 225–239. http://dx.doi.org/10.1016/j.palaeo.2005.11.021.

Dornbos, S.Q. 2008. Tiering history of early epifaunal suspension-feeding echinoderms. *In*: W.I. Ausich and G.D. Webster (eds.), *Echinoderm Paleobiology,* 132–143. Indiana University Press, Bloomington.

Droser, M.L., Gehling, J.G., and Jensen, S. 1999. When the worm turned: concordance of Early Cambrian ichnofabric and tracefossil record in siliciclastic rocks of South Australia. *Geology* 27: 625–628. http://dx.doi.org/10.1130/0091-7613(1999)027<0625:WTWTCO>2.3.CO;2

Esteve, J., Zamora, S., Gozalo, R., and Liñán, E. (in press). Sphaeroidal enrollment in middle Cambrian solenopleuropsine trilobites. *Lethaia*. http://dx.doi.org/10.1111/j.1502-3931.2009.00205.x.

Gámez Vintaned, J.A., Schmitz, U., and Liñán, E. 2009. Upper Vendian– lowest Ordovician sequences of the western Gondwana margin, NE Spain. *In*: J. Craig, J. Thurow, B. Thusu, A. Whitham, and Y. Abutarruma (eds.), Global Neoproterozoic Petroleum Systems: The Emerging Potential in North Africa. *Geological Society, London, Special Publications* 326: 231–244. http://dx.doi.org/10.1144/SP326.130305-8719/09/$15.00.

Gehling, J.G., 1999. Microbial mats in terminal Proterozoic siliciclastics: Ediacaran death masks. *Palaios* 14: 40–57.

Gozalo, R. and Liñán, E. 1988. Los materiales hercínicos de la Cordillera Ibérica en el contexto del Macizo Ibérico. *Estudios Geológicos* 44: 399–404.

Guensburg, T.E. 1988. Systematics, functional morphology, and life modes of Late Ordovician edrioasteroids, Orchard Creek Shale, southern Illinois. *Journal of Paleontology* 62: 110–126.

Guensburg, T.E. and Sprinkle, J. 1994. Revised phylogeny and functional interpretation of the Edrioasteroidea based on new taxa from the Early and Middle Ordovician of western Utah. *Fieldiana* (*Geology*) 29: 1–43.

Holloway, D.J. 1992. An edrioasteroid from the Silurian of Tasmania. *Alcheringa* 16: 188. http://dx.doi.org/10.1080/03115519208619117

Holloway, D.J. and Jell, P.A. 1983. Silurian and Devonian edrioasteroids from Australia. *Journal of Paleontology* 57: 1001–1016.

Jell, P.A., Burrett, C.F. and Banks, M.R. 1985. Cambrian and Ordovician echinoderms from eastern Australia. *Alcheringa* 9: 183–208. http://dx.doi.org/10.1080/03115518508618967

Liñán, E., Perejón, A., and Sdzuy, K. 1993. The Lower–Middle Cambrian stages and stratotypes from the Iberian Peninsula: a revision. *Geological Magazine* 130: 817–833.

Liñán, E., Gozalo, R., Palacios, T., Gámez Vintaned, J.A., Ugidos, J.M., and Mayoral, E. 2002. Cambrian. *In*: W. Gibbons and T. Moreno (eds.), *The Geology of Spain*, 17–29. The Geological Society, London.

Parsley, R.L. and Prokop, R.J. 2004. Functional morphology and palaeoecology of some sessile Middle Cambrian echinoderms from Barrandian region of Bohemia. *Bulletin of Geosciences* 79: 147–156.

Parsley, R.L. and Zhao, Y. 2006. Long-stalked eocrinoids in the basal Middle Cambrian Kaili Biota, Taijiang County, Guizhou Province, China. *Journal of Paleontology* 80: 1058–1071. http://dx.doi.org/10.1666/0022 3360(2006)80[1058:LSEITB]2.0.CO;2

Smith, A.B. 1985. Cambrian eleutherozoan echinoderms and the early diversification of edrioasteroids. *Palaeontology* 28: 715–756.

Smith, A.B. 2008. Deuterostomes in a twist: the origins of a radical new body plan. *Evolution and Development* 10: 492–502. http://dx.doi.org/10.1111/j.1525-142X.2008.00260.x

Smith, A.B. and Jell, P.A. 1990. Cambrian edrioasteroids from Australia and the origins of starfishes. *Memoirs of the Queensland Museum* 28: 715–778.

Sprinkle, J. 1973. *Morphology and Evolution of Blastozoan Echinoderms*. Harvard University Museum of Comparative Zoology, Special Publication: 284 pp.

Sumrall, C.D. 1996. Late Paleozoic edrioasteroids (Echinodermata) from the North Americ2an midcontinent. *Journal of Paleontology* 70: 969–985.

Sumrall, C.D., Sprinkle, J., and Guensburg, T.E. 1997. Systematics and paleoecology of Late Cambrian echinoderms from the western United States. *Journal of Paleontology* 71: 1091–1109.

Sumrall, C.D., Sprinkle, J., and Bonem, R.M. 2006. An edrioasteroid-dominated echinoderm assemblage from a Lower Pennsylvanian marine conglomerate in Oklahoma. *Journal of Paleontology* 80: 229–244. http://dx.doi.org/10.1666/0022-3360(2006)080[0229:AEEAFA]2.0.CO;2

Sumrall, C.D. and Zamora, S. (in press). Ordovician edrioasteroids from Morocco: faunal exchanges across the Rheic Ocean. *Journal of Systematic Palaeontology*. http://dx.doi.org/10.1080/14772019.2010.499137

Taylor, P.D. and Wilson, M.A. 2003. Palaeoecology and evolution of marine hard substrate communities. *Earth-Science Reviews* 63: 1–103. http://dx.doi.org/10.1016/S0012-8252(02)00131-9

Ubaghs, G. 1998. Echinodermes nouveaux du Cambrien supérieur de la Montagne Noire. *Geobios* 31: 809–829.

Zamora, S. 2010. Middle Cambrian echinoderms from North Spain show echinoderms diversified earlier in Gondwana. *Geology* 38: 507–510. http://dx.doi.org/10.1130/G30657.1

Zamora, S., Liñán, E., Domínguez Alonso, P., Gozalo, R., and Gámez Vintaned, J.A. 2007. A Middle Cambrian edrioasteroid from the Murero biota (NE Spain) with Australian affinities. *Annales de Paléontologie* 93: 249–260. http://dx.doi.org/10.1016/j.annpal.2007.09.003

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

Zhao, Y., Sumrall, C.D., Parsley, R.L., and Peng, J. (in press). *Kailidiscus*, a new plesiomorphic edrioasteroid from the basal middle Cambrian Kaili Biota of Guizhou Province, China. *Journal of Paleontology*. http://dx.doi.org/0022-3360/10/0084-0668$03.00