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Middle Cambrian echinoderms from north Spain show echinoderms diversified earlier in Gondwana

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ABSTRACT

New fossil discoveries in the middle Cambrian of Spain have considerably expanded our knowledge of the temporal and spatial distribution of some major clades of echinoderms including sucocystid cinctans, isorophid edrioasteroids, cothurnocystid stylophorans, ctenocystoids, and a new group of blastozoans ("eocystitids"). Because many of these taxa appear close to the beginning of the middle Cambrian, it seems likely that their origins must be placed in the early Cambrian. These results, based on articulated specimens provided from Echinoderm Lagerstätten, agree with the hidden diversity provided from isolated ossicles from other Gondwanan areas.

INTRODUCTION

Echinoderms are a major deuterostome phylum found living in Holocene seas and comprise such well-known groups as the sea urchins and starfishes. Crown-group echinoderms are easily distinguished by their unique pentaradially symmetrical body plan, by the presence of a water vascular system derived from the left hydrocoel, and by their skeleton composed of calcitic plates with a three-dimensional microstructure called stereom.

According to current evidence, the fossil record of echinoderms began slowly in the early Cambrian (ca. 520 Ma) with the appearance of first helicoplacoids, followed by edrioasteroids and eocrinoids (lepidocystids and gogiids) (Durham, 1978, 1993; Sprinkle, 1973; Zhao et al., 2007). The group then diversified during the middle Cambrian and Early Ordovician, reaching peak diversity during the Middle Ordovician (Sprinkle and Guensburg, 1997, 2004). However, there are reasons to believe that Cambrian faunas remain incompletely documented and that this may not be an accurate record of the pattern of diversification. Our knowledge of the Cambrian radiation has come largely from North America (Laurentia), but the study of isolated ossicles in bioclastic limestones from North Africa and Australia (Jell et al., 1985; Clausen, 2004; Clausen and Smith, 2005, 2008; Clausen et al., 2009) hints at much greater hidden diversity in Gondwanan shelf settings than those reported from Echinoderm Lagerstätten. Furthermore, the order of appearance of echinoderm groups in the fossil record does not fit with current ideas of their cladistic relationships with putative crown-group echinoderms predating the appearance of the earliest preradiate stem-group echinoderms in the Cambrian (sensu Smith, 2008; Swalla and Smith, 2008). Finally, molecular clock studies suggest that there is a short period of early diversification that has not been captured by the fossil record (Swalla and Smith, 2008). These various lines of evidence suggest that much remains to be discovered about the Cambrian history of echinoderms.

Here I report a new, diverse fauna of echinoderms from the early middle Cambrian of north Spain, which lay on the western margin of Gondwana during the Cambrian (Fig. 1A). This earliest middle Cambrian diversification event includes the earliest representatives of some echinoderm clades.

A few of these taxa were recently described (Zamora and Smith, 2008; Zamora et al., 2009; Rahman and Zamora, 2009), but the majority are reported here for the first time and await formal description. This new fauna provides critical data suggesting that the divergence for some clades occurred earlier in Gondwana than previously thought.

GEOLOGIC SETTING AND STRATIGRAPHY

The material described in this paper comes from 20 localities located in the Cantabrian Mountains (Cantabrian Zone) and the Iberian Chains, north Spain (Fig. 1B; Table DR1 in the GSA Data Repository[1]). Specimens from the Cantabrian Zone come from the shales of

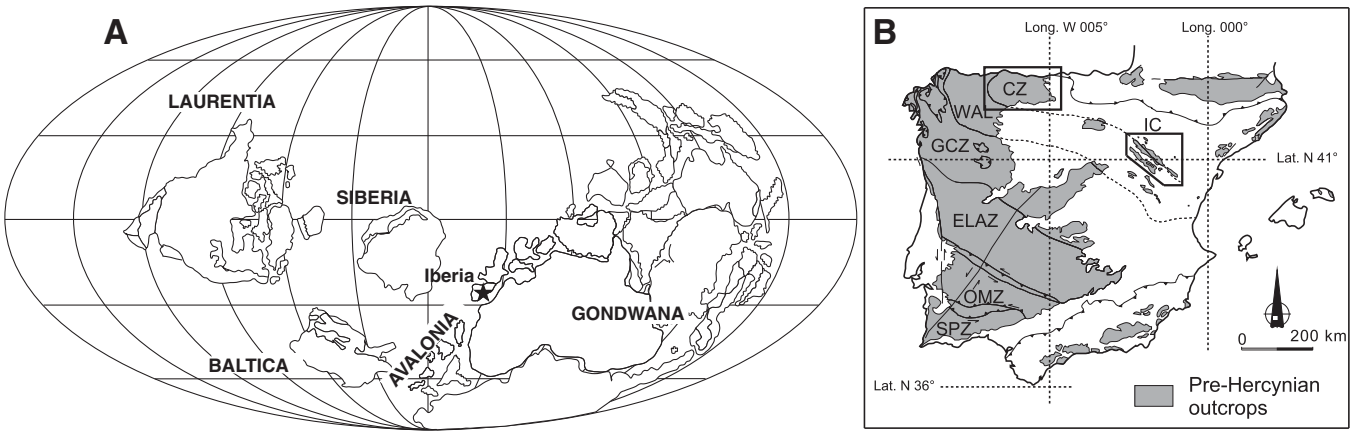

Figure 1. A: Paleogeographic reconstruction for the middle Cambrian indicating the position of Iberia (star), after McKerrow et al. (1992). B: Map of Spain indicating the locality of studied areas. CZ—Cantabrian Zone; IC—Iberian Chains; WAL—West Asturian-Leonese Zone; GCZ—Galician-Castilian Zone; ELAZ—East Lusitanian-Alcudian Zone; OMZ—Ossa-Morena Zone; SPZ—South Portuguese Zone.

[1]GSA Data Repository item 2010148, Table DR1 (list of the taxa recorded from each locality) and Table DR2 (list of all taxa recorded from the middle Cambrian from Spain and their ages), is available online at www.geosociety.org/pubs/ft2010.htm, or on request from editing@geosociety.org or Documents Secretary, GSA, P.O. Box 9140, Boulder, CO 80301, USA.

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the Genestosa Member, Oville Formation. The diachrony of this formation (Zamarreño, 1972) means that faunas ranging from the early Caesaraugustan to the early Languedocian (Mediterranean time scale sensu Liñán et al., 1993; Álvaro and Vizcaïno, 1998) have been studied. Specimens from the Iberian Chains come from the Valdemiedes, Mansilla, Murero, Borobia, and Torcas Formations, which range in age from the early Leonian to the late Languedocian (middle Cambrian). During the Cambrian the north part of the Iberian Peninsula was located in a mid-latitude, temperate-water platform of West Gondwana (sensu McKerrow et al., 1992).

Both trilobite and echinoderm abundance and diversity fluctuated in parallel with relative sea level. Diversity peaks, related to immigration and radiation of major groups, were achieved during transgressive events and close to maximum floodings, whereas major regressive trends dramatically reduced sampled benthic community diversity.

MATERIALS AND METHODS

About 2000 specimens of articulated or partially articulated echinoderms have been collected. All localities have been sampled in detail with trilobites providing biostratigraphical control. One level near the top of the Murero Formation at Purujosa (Moncayo Natural Park, Iberian Chains) (for stratigraphic details see Esteve et al., 2010) contains eight different echinoderms: the cinctan *Gyrocystis platessa*, eocrinoids (*Gogia gondi*, a new Lichenoididae, and "eocystitids"), stylophorans (*Ceratocystis* sp. and two new cothurnocystids), and isorophid edrioasteroids. This is the highest recorded Cambrian diversity of echinoderms known worldwide for a single level.

RECORDED GROUPS

In the middle Cambrian of Spain, echinoderms fall into one of five broad groups (Fig. 2; Table DR2). These coincide with those proposed by Sprinkle (1992) as representative of the middle Cambrian radiation (with the exception of the problematic *Echmatocrinus* and *Eldonia*, whose echinoderm affinities are questionable). Solutes are absent and probably represent an endemic group from Laurentia. By contrast, cinctans are diverse but are endemic to Gondwana (including Avalonia) and Siberia. A brief description and the most relevant data for these groups are presented below.

Cinctans

Cinctans are the most abundant and diversified group of middle Cambrian echinoderms (Fig. 2) (~49% of total). These racquet-shaped animals are interpreted as stem-group echinoderms (Rahman and Zamora, 2009), although other workers consider them to be modified blastozoans (David et al., 2000). Several species have been recorded in the middle Cambrian of Spain, including members of two main clades (gyrocystids and sucocystids) and the basal genera *Sotocinctus* and *Asturicystis*. They are ubiquitous in the Spanish fossil assemblages. The Spanish Cambrian now has the oldest known cinctans with isolated marginal plates in the lower-Leonian Mansilla Formation, as well as the oldest named species *Protocinctus*, from the upper-Leonian part of the same formation (Rahman and Zamora, 2009) (Fig. 3A). The cinctan record extends into the upper Languedocian, but only in the Iberian Chains.

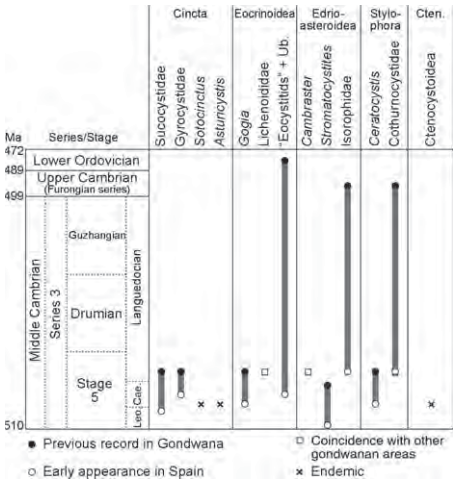

Figure 2. Diagram showing the stratigraphic range of the major echinoderm groups that occur in the Cambrian of Gondwana. Solid circles indicate previous known earliest occurrence from Gondwana; open circles their current oldest occurrence after the new discoveries in Spain reported here. Time scale and correlation of global to Mediterranean series based on chemostratigraphic data from Álvaro et al. (2008).

Eocrinoids

Eocrinoids are the second group in order of diversity and abundance (Fig. 2) (~23% of total). These are a paraphyletic group of blastozoans (Sprinkle, 1973) with a body plan composed of a theca, feeding biserial appendages called brachioles, and a stem with a final pad for attachment. There are four discrete groups in the Spanish middle Cambrian. (1) Gogiids (Fig. 4A) are the most common of them including two named species, *Gogia gondi* Ubaghs 1987 and *G. parsleyi* Zamora 2009 (in Zamora et al., 2009), and several species in open nomenclature. Gogiids have been found in the Murero and Borobia Formations of the Iberian Chains. (2) Lichenoidids, previously recorded from the middle Cambrian of Bohemia (Ubaghs, 1953), are represented by two different species of a new genus (Fig. 4I). These have a very short stalk for attachment to skeletal debris. Specimens are very uncommon. (3) *Ubaghsicystis segurae* Gil Cid and Domínguez 2002 is the single member of a new group of eocrinoids (Fig. 4G), differing from gogiids in having a holomeric stem and a pair of arms arising from an oral spout. (4) "Eocystitids" constitute a new group of blastozoans (Fig. 2). The middle Cambrian rocks of Gondwana often yield star-shaped isolated plates informally named *Eocystites*. This group has been traditionally assigned to paraphyletic eocrinoids (Sprinkle, 1973). The first complete and articulated specimens have now been discovered (Fig. 3C) and show a theca composed of star-shaped plates with two feeding appendages constructed of multiserial plates. They show a tripartite stem with a proximal pentaradial arrangement, an intermediate cone-shaped plate, and a distal stiff part composed of holomeric columnals.

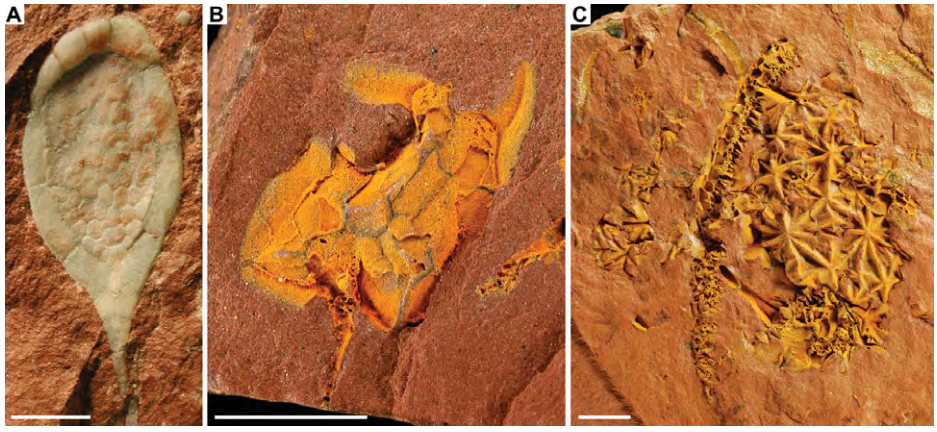

Figure 3. Middle Cambrian echinoderms from Spain. A: Cinctan *Protocinctus mansillaensis* from the upper Leonian of Iberian Chains (MPZ2004/170). B: Stylophoran *Ceratocystis* sp. A from the lower Languedocian of Iberian Chains (MPZ2009/167a). C: "Eocystitid" from the lower Languedocian of Iberian Chains (MPZ2009/1230a). Scale bars indicate 5 mm for all photographs. MPZ: repository numbers (Palaeontological Museum, Zaragoza University, Spain).

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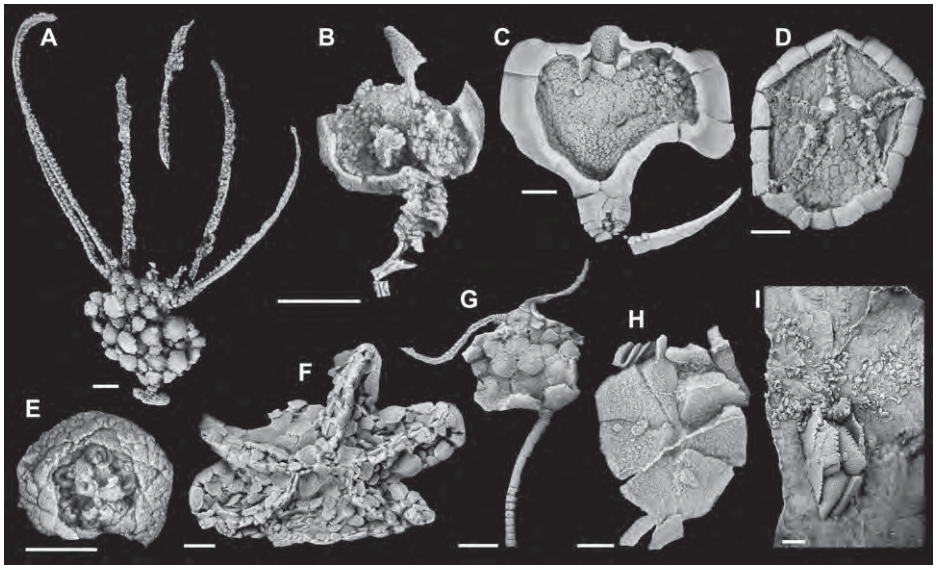

Figure 4. Different echinoderm groups recorded in the middle Cambrian of north Spain. A: The gogiid eocrinoid *Gogia gondi* Ubaghs 1987 (MPZ2009/164b). B: Cothurnocystid stylophoran (MPZ2009/1231a). C: The cinctan *Lignanicystis barriosensis* Zamora and Smith 2008 (MPZ2007/776b). D: The edrioasteroid *Cambraster cannati* (Miquel, 1894) (MPZ2009/1232a). E: Isorophid edrioasteroid (MPZ2009/1233a). F: Stromatocystitid edrioasteroid (MPZ2007/1890). G: The eocrinoid *Ubaghsicystis segurae* Gil Cid and Domínguez Alonso, 2002 (MNCN-I-30849). H: Ctenocystoid (MPZ2009/1234b). I: Lichenoidid eocrinoid (MPZ2009/165). MNCN: Museo Nacional Ciencias Naturales (Madrid, Spain). Photographs of latex casts whitened with NH_4Cl. Scale bars indicate 2 mm for all photographs.

Edrioasteroids

Edrioasteroids are cushion-shaped echinoderms with a pseudo-fivefold ambulacrum arrangement (Sumrall and Wray, 2007) (Fig. 2) (~10% of total). They are represented by three major clades found in Spain only in the Iberian Chains: stromatocystitids (Fig. 4F), cambrasterids (Fig. 4D), and isorophids (Fig. 4E). Stromatocystitids are fully plated and lack a marginal ring, and occur from the early Leonian to the Languedocian. Cambrasterids are also fully plated but have a strongly developed peripheral ring of ossicles. They occur in the early Languedocian. Rare isorophids have been found in the early Languedocian. These have uniserial ambulacral flooring plates, and lived attached by their uncalcified aboral surface to skeletal debris.

Stylophorans

Stylophorans are an asymmetric to bilateral symmetric group of echinoderms that comprise two major clades: cornutes and mitrates. They represent ~13% of the total (Fig. 2). Up to now, the middle Cambrian of Gondwana has only yielded the armored stylophoran *Ceratocystis* (Lefebvre, 2007). This genus is very abundant in Spain (Fig. 3B), but in the Iberian Chains it coexisted with two new cothurnocystid stylophorans (Fig. 4B), one related to *Ponticulocarpus* (Sumrall and Sprinkle, 1999) and a second taxon that is more *Cardiocystella*-like in shape (Sumrall et al., 2009). The oldest articulated specimens of *Ceratocystis* have been found in the lower Caesaraugustan.

Ctenocystoids

Ctenocystoids are the rarest group of echinoderms (5% of total) (Fig. 2). They are more or less bilaterally symmetric, with a marginal ring of plates and two integuments of small plates closing the body cavity. They are easily differentiable by the presence of a ctenidial organ resting in the anterior theca and covering the mouth and associated food grooves (Rahman and Clausen, 2009). In the Cambrian of Spain, there are two different taxa, one of which has just a single marginal ring of ossicles (Fig. 4H).

IMPLICATIONS FOR ECHINODERM DIVERSIFICATION

The middle Cambrian of Spain provides some of the earliest records of major echinoderm clades and an important window onto Gondwanan faunas (Fig. 2; Table DR2). The oldest cinctan carpoid has been described from the upper Leonian of the Iberian Chains (Rahman and Zamora, 2009) and represents the most primitive sucocystid (Smith and Zamora, 2009). The eocrinoid *Ubaghsicystis* represents the oldest member of this group with holomeric columnals and a xenomorphic stem, and with "eocystitids" represent likely forerunners of the pleurocystitid rhombiferans. Isorophid edrioasteroids, previously known from the upper Cambrian, now extend their fossil record to the middle Cambrian. They were the oldest edrioasteroids living permanently attached to hard substrates (skeletal debris). Cothurnocystid stylophorans have been found for the first time in the middle Cambrian rocks outside of North America (Ubaghs and Robison, 1988). Coexistence of three different stylophorans in the same bed (cothurnocystid-ceratocystid assemblage) not only is a unique example but also suggests more complex synecologic interactions than were previously argued for this group (Lefebvre, 2007). Spain also now has the oldest and most primitive ctenocystoids, represented in the basal middle Cambrian by a form showing a single marginal ring and other primitive features. "Eocystitid" isolated plates are found since the upper Leonian, and the oldest articulated specimens are middle Caesaraugustan in age. The strange arrangement of characters they show needs a phylogenetic re-evaluation of this new group, but suggests a link between eocrinoids such as *Ubaghsicystis* and more derived rhombiferan cystoids.

Sprinkle (1992) has argued that echinoderms underwent a major diversification in the middle Cambrian, preceding the so-called Great Ordovician Diversification (Sprinkle and Guensburg, 1997). The new Spanish data suggest that a number of the clades involved in this diversification (such as sucocystid cinctans, cothurnocystid stylophorans, ctenocystoids, and isorophid edrioasteroids) appeared significantly earlier in Gondwanan settings than previously thought (Fig. 2). This shows that, even by the earliest middle Cambrian, a variety of novel body plans and ecological strategies already existed among echinoderms, pushing back the timing of important divergences into the lower Cambrian.

Furthermore, the middle Cambrian echinoderm communities in Spain appear to be the most diverse of anywhere. The eight different echinoderm species that coexisted in the top of the Murero Formation from the Purujosa locality (Iberian Chains) show very different body plans adapted for very different ecologic niches. There are low to medium suspension feeders (such as gogiids, lichenoidids, or isorophid edrioasteroids) that lived permanently attached; others are free-living forms, such as cinctans, stylophorans, and "eocystitids". Both gogiids and isorophids were commonly attached to skeletal debris. Previous lichenoidids known (*Lichenoides priscus* for example; see Ubaghs, 1953) rested on the substrate, but the new specimens from Spain were also attached to skeletal debris. Cinctans and stylophorans rested on the seafloor and captured particles from the water-sediment interface.

The rich and diverse fauna from the middle Cambrian of Spain also significantly improves our knowledge of paleobiogeographic

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distributions at this time. Some cinctans (*Sucocystis theronensis*, *Elliptocinctus barrandei*), previously considered endemic to the Montagne Noire (France), are known now from Spain. The lichenoidids represented an endemic group of eocrinoids from Bohemia, but now their distribution extends to Spain. The gogiids, previously known from North America, France, Czech Republic, and China, are also now shown to be diverse in the middle Cambrian of Spain. Edrioasteroids such as *Cambraster* and *Stromatocystites*, known from France and Australia, and Czech Republic, Australia, and Newfoundland, respectively, also occur in Spain. Cothurnocystids, only previously known from the middle Cambrian of North America, are here present but in a shallower water environment. Finally, the most primitive known ctenocystoids are found in the middle Cambrian of Spain and later diversified, spreading to other paleocontinents.

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