Morphology and Ontogeny of the Cambrian Edrioasteroid Echinoderm Cambraster cannati from Western Gondwana

Authors: Zamora, Samuel, Sumrall, Colin D., and Vizcaïno, Daniel

Source: Acta Palaeontologica Polonica, 58(3) : 545-559

Published By: Institute of Paleobiology, Polish Academy of Sciences

URL: https://doi.org/10.4202/app.2011.0152

Morphology and ontogeny of the Cambrian edrioasteroid echinoderm *Cambraster cannati* from western Gondwana

SAMUEL ZAMORA, COLIN D. SUMRALL, and DANIEL VIZCAÏNO

Zamora, S., Sumrall, C.D., and Vizcaïno, D. 2013. Morphology and ontogeny of the Cambrian edrioasteroid echinoderm *Cambraster cannati* from western Gondwana. *Acta Palaeontologica Polonica* 58 (3): 545–559.

A review of the Cambrian edrioasteroid echinoderm *Cambraster cannati* is made based on new collections from the Iberian Chains (NE Spain) and Montagne Noire (France). New morphological data include a completely articulated oral area and details of ambulacra. Specimens ranging from 4 to 26 mm in diameter provide detailed information concerning the full ontogeny. Important changes through ontogeny mainly affect the marginal ring and the plating pattern of the aboral surface. Comparison with other species of *Cambraster* indicates that the aboral surface of *Cambraster tastudorum* from Australia shows strong resemblance to juvenile specimens of *C. cannati*. *Cambraster cannati* was attached directly to the substrate and inhabited relatively high energy, offshore environments from the west margin of Gondwana. Abnormalities in the skeleton are described for the first time in a Cambrian edrioasteroid.

Key words: Echinodermata, Edrioasteroidea, palaeobiology, Cambrian, Spain, France.

Samuel Zamora [samuel@unizar.es], Department of Palaeontology, The Natural History Museum, Cromwell Road, London SW7 5BD, UK;
Colin D. Sumrall [csumrall@utk.edu], Department of Earth and Planetary Sciences, University of Tennessee, Knoxville, TN 37996, USA;
Daniel Vizcaïno [daniel.vizcaino@wanadoo.fr], 7 rue J.-B. Chardin, Maquens, 11090 Carcassonne, France.

Received 10 October 2011, accepted 19 January 2012, available online 20 April 2012.

Introduction

Edrioasteroids are a clade of exclusively Palaeozoic sessile echinoderms with a 2-1-2 arrangement of ambulacra (Sprinkle 1973; Sumrall and Wray 2007), and display various thecal morphologies from globular to discoidal (Bell 1976a; Zhao et al. 2010). Post-Cambrian forms lived permanently attached to hardgrounds, skeletal debris, intraclasts, extraclasts, and living organisms (Bell 1976a; Brett and Liddell 1978; Waddington 1980; Wilson 1985; Sumrall 2000, 2001, 2010b; Sumrall et al. 2006a, b, 2009; Sumrall and Zamora 2011). In some cases, colonies of hundreds of individuals have been documented (Waddington 1980; Kammer et al.1987; Meyer 1990; Cornell et al. 2003; Shroat-Lewis et al. 2011). In contrast, Cambrian edrioasteroids had a more limited habitat, restricted to microtopographic skeletal debris or stabilized substrates (Dornbos 2006; Zamora and Smith 2010).

Well-preserved Cambrian edrioasteroids are rare fossils, but a few species have been described from North America, Europe, China, and Australia (Cabibel et al. 1959; Bell and Sprinkle 1978; Jell et al. 1985; Smith and Jell 1990; Zhao et al. 2010). Unfortunately, only a few are well enough known to provide an ontogenetic series. While edrioasteroid ontogenetic series are common in post-Cambrian species (Bell 1976b; Smith 1983; Kammer et al. 1987; Sumrall 2001; Sumrall et al. 2006a, b), ontogenies of Cambrian taxa are presently known only from *Totiglobus*, with specimens ranging from 2.5 mm to 31 mm in diameter (Bell and Sprinkle 1978), and *Kailidiscus*, with specimens ranging from less than 1 mm to 30 mm in diameter (Zhao et al. 2010).

Based on a new and relatively large collection of *Cambraster cannati*, we provide a third nearly complete ontogeny for a Cambrian edrioasteroid. *Cambraster* is a typical middle Cambrian edrioasteroid from Gondwana (Zamora et al. in press) known from Western Europe (France and Spain) and Australia (Cabibel et al. 1959; Jell et al. 1985; Zamora et al. 2007). It is distinct from other edrioasteroids by bearing a marginal ring composed of large plates restricted to the oral surface. Presently only two species of *Cambraster* are recognized; *C. cannati* from Montagne Noire (France) and the Iberian Chains (Spain), and *C. tastudorum* from Tasmania (Australia).

Cambraster is an important taxon for understanding the evolution of edrioasteroids and other Cambrian echinoderms for several reasons: (i) It is an early and well preserved echinoderm and many of its features can aid in understanding

http://dx.doi.org/10.4202/app.2011.0152

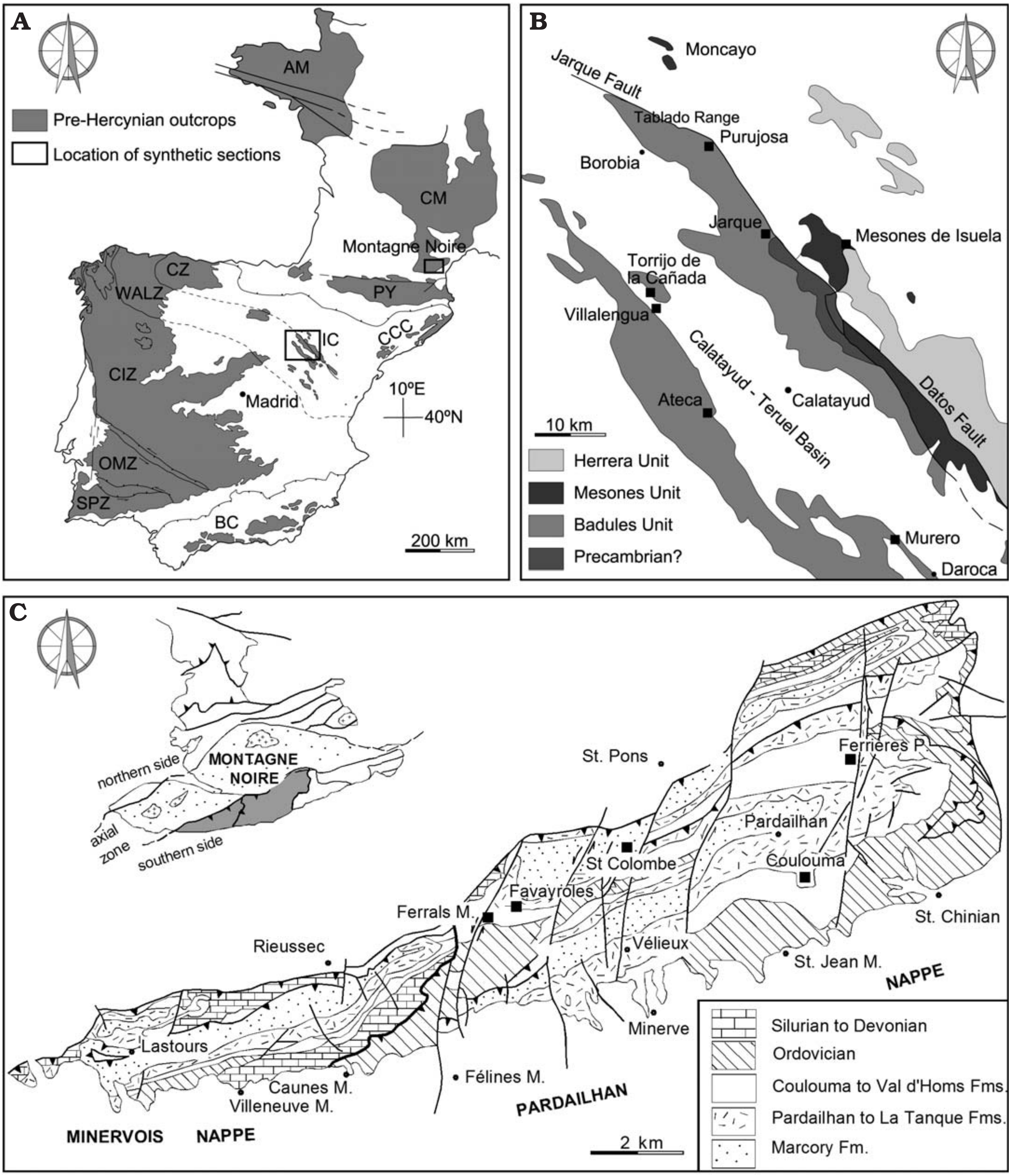

Fig. 1. Geological setting with indication of the studied localities. **A**. Map of Spain and France with the position of the Iberian Chains and Montagne Noire. **B**. Geological map of the Iberian Chains with indication of localities where specimens of *Cambraster* have been collected. **C**. Geological map of Montagne Noire (France) with indication of localities where specimens of *Cambraster* have been collected.

the early evolution of edrioasteroids and eleutherozoans in general (Smith 1985); (ii) it has been included in many edrioasteroid phylogenetic analyses (Smith 1985; Smith and Jell 1990; Guensburg and Sprinkle 1994; Sumrall and Zamora

2011) and used for tree rooting in asterozoans (Shackleton 2005); (iii) the phylogenetic position of *Cambraster* is controversial. The aim of this paper is to completely revise *Cambraster* based on new, well-preserved fossils. Also presented are discussions of the ontogeny, phylogeny, and palaeoecology of this early edrioasteroid.

Institutional abbreviations.—MPZ, Museo Paleontológico de la Universidad de Zaragoza, Spain; MNHN, Museum National d'Histoire Naturelle, Paris, France; NMVP, Museum of Victoria Palaeontological Collection, Victoria, Australia.

Other abbreviations.—AB, BC, CD, DE, EA refer to interambulacral areas.

Geological setting and stratigraphy

In the western Mediterranean regions of the Iberian Peninsula and Montagne Noire, the Middle Cambrian (or third Cambrian Series) is regionally subdivided into three stages including the Leonian, Caesaraugustan, and Languedocian (Liñán et al. 1993; Álvaro and Vizcaïno 1998). Specimens of *Cambraster* were collected from lower Languedocian aged rocks in both of these areas. Lithologically, specimens occur as molds preserved in fine sandstone and shale. The formations bearing these fossils are interpreted as having been deposited in offshore environments sporadically affected by storms.

The type series of the type species of *Cambraster* were described from the Montagne Noire (Fig. 1), France (Miquel 1894). These fossils are relatively common in shales of the Coulouma Formation in different localities (Ferrals les Montagnes, Sainte-Colombe, Favayroles, Coulouma, Ferrières-Poussarou) that are lower Languedocian to basal middle Languedocian in age. Despite more than a century of collecting, only now is a large collection of specimens available for study. Associated fauna includes a wide diversity of trilobites representative of two distinct biozones (e.g., *Solenopleuropsis* [*Solenopleuropsis*] and *Jincella convexa*; for a list of trilobites, see Álvaro and Vizcaïno 1998) and echinoderms, including cinctans (*Sucocystis theronensis* and *Elliptocinctus barrandei*), stylophorans (*Ceratocystis vizcainoi*), ctenocystoids (*Ctenocystis smithi* and *Courtessolea monceretorum*), and blastozoans (*Gogia gondi* and *Vizcainoia languedocensis*) (see Álvaro et al. 2001 and references cited therein; Domínguez-Alonso 2004; Zamora and Smith 2012).

A second collection of *Cambraster* has been made from the lower part of the Borobia Formation (Middle Cambrian) in the Iberian Chains of North Spain (Fig. 1). These specimens were collected from three, new, poorly studied localities including, north to south, Borobia, Torrijo de la Cañada, and Villalengua (Zamora and Álvaro 2010). A single specimen was collected from the Borobia locality (Borobia Section 3) (see Gámez et al. 1991 for further details) and is associated with trilobites and other echinoderms including *Ceratocystis* sp. and indeterminate cinctans. *Cambraster* is much more common in the Torrijo de la Cañada and Villalengua sections. Specimens collected from Torrijo de la Cañada and Villalengua came from the base of the Borobia Formation (A1 unit sensu Schmitz 1971). In this area, a complete section of the Murero and Borobia Formations is present, and this section is one of the few areas where the base of the Borobia Formation is well exposed and fossiliferous. In both localities, road cuts and farm activity such as the ploughing of fields and excavation for irrigation pools, have provided an extensive amount of rock that is rich in trilobites and echinoderms. Trilobite species include *Solenopleuropsis* (*Solenopleuropsis*), *Eccaparadoxides pradoanus*, and *Bailiella levyi*, and echinoderms include the very common cinctan species *Elliptocinctus barrandei* and *Sucocystis theronensis* (see Zamora and Álvaro 2010), stylophorans (*Ceratocystis* sp. and Cothurnocystidae indet.), edrioasteroids described herein, and a single specimen of a gogiid eocrinoid.

Systematic palaeontology

Phylum Echinodermata De Brugière, 1791 (ex Klein, 1734)

Class Edrioasteroidea Billings, 1858

Order Stromatocystitida Bell, 1980

Emended diagnosis.—Edrioasteroid-grade echinoderms bearing interradial oral frame plates forming the mouth frame, ambulacra bearing biserial floor plates with sutural pores, cover plates arranged into multitiered series, interambulacral plates bearing epispires, aboral surface fully plated and bearing attachment disk with radially arranged elements.

Discussion.—Smith (1985) placed *Cambraster* within Isorophida, and Guensburg and Sprinkle (1994) left it in open nomenclature. Our restudy indicates that *Cambraster* is a stromatocystitid based on several features it shares with *Stromatocystites* including the interambulacral plating of the oral surface bearing epispires and the construction of the ambulacral system. Furthermore, both taxa have a fully plated aboral surface with a similarly arranged aboral disk. The primary differences between these taxa are the marginal ring and discoidal thecal construction in *Cambraster* vs. the more globular thecal shape and lack of marginal ring in *Stromatocystites*. Although these taxa live in very different environments, we do not interpret their differences as the result from ecophenotypic variation. The only substantial differences in individual edrioasteroid morphology noted result from ontogeny and teratology (Bell 1976b; Bell and Sprinkle 1978; Smith and Arbizu 1987; Sumrall and Wray 2007; Zhao et al. 2010; McKinney and Sumrall 2011).

Family Stromatocystitidae Bassler, 1935

Genus *Cambraster* Cabibel, Termier, and Termier, 1959

Type species: *Trochocystites cannati* Miquel, 1894 from the Languedocian (middle Cambrian) of Montagne Noire (France).

http://dx.doi.org/10.4202/app.2011.0152

Diagnosis.—Stromatocystitid with discoidal theca, bearing a marginal ring around the thecal ambitus bordered by peripheral skirt; aboral disk large with radially elongate plates centrally.

Discussion.—Miquel (1894) was the first to report specimens assignable to the genus *Cambraster*. These specimens were thought to be thecae of a cinctan and named *Trochocystites cannati*. Cabibel et al. (1959) determined that *T. cannati* was an edrioasteroid and erected the genus *Cambraster* to accept this species. They also described the edrioasteroid genus *Eikosacystis* with two species, *E. couloumanensis* and *E.*? *ferralsensis*. Termier and Termier (1969) described three additional species: *Cambraster elegans*, *Eikosacystis miqueli*, and *E. courtessolei* all based on very poorly preserved specimens.

Ubaghs (1971) concluded that the two species of *Cambraster* were valid, but synonymised *Eikosacystis* (Cabibel et al. 1959) with *Cambraster*, because the only difference between the two forms was their state of preservation. Subsequently, Smith (1985) determined that *C. cannati* and *C. elegans* were synonyms, arguing that the main difference between the two forms (i.e., presence of a larger portion of the aboral surface plating around the margin in *C. elegans*) was very likely a post-mortem preservational artefact.

A second valid species, *Cambraster tastudorum* was described by Jell et al. (1985) from the Cambrian of Tasmania, Australia. *Cambraster tastudorum* is represented by many well-preserved specimens, and is readily distinguished from *C. cannati* by the distribution of epispires on interambulacral plates, and by the plate pattern of the aboral disk surface (Jell et al. 1985).

Although *Cambraster* is similar in gross morphology to isorophids, these similarities are strictly superficial. The oral frame construction is formed from radial elements in isorophids whereas the elements are interradial in *Cambraster*. These elements are homologues of the integrated interradial plates of *Kailidiscus* (Zhao et al. 2010) and may be homologues of oral plates in other pentaradiate echinoderms (sensu Sumrall 2010a). Isorophids have uniserial floor plates that lack sutural pores in all groups, and in pyrgocystids a second series of outer biserial floor plates bearing pores are present (Sumrall and Zamora 2011). *Cambraster* bears biserial floor plates that bear double ambulacral pores along the sutures. Cover plates of isorophids are biserial or in multibiseries, whereas in *Cambraster* they are multitiered series. Interambulacral plates of isorophids lack epispires and are added along the margins of the interambulacral areas, whereas they bear epispires and are added throughout the interambulacral areas in *Cambraster*.

The greatest difference is seen in the construction of the thecal ambitus and aboral surface. In isorophids, a peripheral rim is present, consisting of a series of irregularly plated circlets that decrease in size distally. All of the plates are highly imbricate and are in contact with the substrate (Sumrall and Parsley 2003). The bottom surface is scored with a series of radial spur and groove structures. Interambulacral plates or plates of the pedunculate zone tuck under the edge of the peripheral rim rather than bearing a vertical suture (Sumrall 1993). The bottom surface of the theca is uniformly unplated (Bell 1976a).

In *Cambraster*, the marginal frame is constructed entirely different to that of a peripheral rim. The stout marginals are plates of the oral surface and are not in contact with the substrate. The interambulacral plates do not articulate with an imbricate suture beneath the plates, but abut with the upper surface of the plate with a vertical suture. Plates of the peripheral skirt, rather than being imbricate over one another, are adjacent and form a flexible portion of the peripheral wall of the theca along the ambitus. The bottom is fully plated in *Cambraster* rather than being unplated.

Several features of *Cambraster* are also similar to the early edrioasteroid-grade echinoderm *Kailidiscus chinensis* (Zhao et al. 2010). The mouth frame of both taxa bears six integrated interradial plates. In *Kailidiscus* these plates are bordered by a series of plates that correspond to the adradial series of floor plates, whereas in *Cambraster* this plate series is absent. Although both taxa bear multitiered cover plate series, they are more fully developed in *Kailidiscus* than in *Cambraster*. In both taxa the periproct is very large, offset to the left of the midline, and similar in construction with numerous small very narrow lathe shaped plates.

The poorly known early edrioasteroid-grade echinoderm *Camptostroma* is similar bearing numerous epispires in the interambulacral plates, but here the nature of the plating is much more complex in the arrangement of primary and secondary interambulacral plates to the epispires (Smith 1985). The nature of the ambulacral system is poorly constrained, but it is clear that the ambulacra are curved. The side walls of the theca are corrugated and complexly plated. Although the bottom of the theca is plated, there is no differentiation of the plates into a peripheral series and a central disc.

A final taxon similar to *Cambraster* is *Edriodiscus* Jell et al. (1985), which also bears a marginal ring, but constructed with many more medium-sized plates. Although the ambulacra are poorly known, they do bear biserial flooring plates. *Edriodiscus* is further differentiated from *Cambraster* by the plating of the aboral surface that bears more irregular plating with plates of approximately equal size. We tentatively assign *Edriodiscus* to Stromatocystitidae.

Geographic and stratigraphic range.—*Cambraster* is known from the Borobia and Coulouma Formations of West Gondwana (Spain and France) and in the Cateena Group of East Gondwana (Australia). The former corresponds to the Cambrian Series 3, Stage 5 and the Australian specimens occur in slightly younger strata from the Drumian stage of Series 3.

Cambraster cannati (Miquel, 1894)

Figs. 2–5.

1985 *Cambraster cannati* (Miquel, 1894); Smith 1985 and references cited there: 750, text-figs. 2, 3, 18, 19.

2007 *Cambraster* cf. *tastudorum*; Zamora et al. 2007: 255, fig. 4A, B.

Material.—This study is based on newly collected material from the middle Cambrian of the Iberian Chains (Spain) and

Montagne Noire (France). Collection from Spain, include four specimens from Torrijo de la Cañada (MPZ2011/97–100), one specimen from Borobia (MPZ2011/96), and 33 from Villalengua (MPZ2009/1232, MPZ2011/101–132). Material from Montagne Noire includes one specimen from Ferrières-Poussarou, two specimens from Favayroles, one specimen from Coulouma, five specimens from Sainte-Colombe, and 26 specimens from Ferrals-les-Montagnes. All specimens are preserved as natural moulds in shale that were studied from latex casts.

Diagnosis.—Large *Cambraster* bearing numerous epispires at maturity, smooth peripheral skirt, proportionately shorter ambulacra in submature stages, and poorly demarked and organized central ventral disk.

Description

General shape.—*Cambraster* has a circular outline, mainly in juveniles, becoming pentagonal with maturity, with ambulacra extending to the corners of the thecal outline (Fig. 2). The aboral surface is flat and the oral surface is slightly convex (Fig. 3). In cross section it is plano-convex but with a very low profile.

Oral and ambulacral area.—The oral area is composed of a series of 6 primary interradial oral frame plates; each interambulacrum bears one plate and two are present in the interambulacrum CD (Figs. 2A, 3F$_3$, G$_2$, 5).

Interradial oral frame plates have a large, externally exposed area that forms the corners of the mouth frame and radially positioned limbs forming the proximal edges of the food grooves and peristomial opening. Around the ambulacral/peristomial margin are a series of large and small pits that mimic similar depressions of the ambulacral floor plates. The lateral margins of the plates extend into the food grooves where they contact adjacent plates forming the edge of the mouth frame. The distal adradial ends of the plates are notched by the proximal edge of the first podial pores of the ambulacral floor plates. The externally exposed portion of the interradial oral frame plates in the AB and AE position are large and broad, whereas they are smaller and more narrow in the BC and DE positions. In the CD position there are two plates with the plate on the left larger than the plate on the right; some specimens suggest a pore spanning the suture between the two plates (Fig. 3F$_1$). The mouth frame is covered by a poorly documented series of cover plates. A single large cover plate is positioned diagonally above the smaller right CD interradial oral frame plate. A series of small cover plates encircle the proximal and adradial edges of the externally exposed portions of the CD interradial oral frame plate in an undocumented arrangement. These cover plates are smaller than the primary series of cover plates seen in the proximal ambulacral series, but larger than the adradial secondary series into which they appear to merge in most rays (see Fig. 2A: reconstruction).

The oral surface bears five, straight, relatively wide ambulacra that show little taper and a somewhat pointed termination. They arise from the oral area in a distinct 2-1-2 pattern and extend from the mouth frame to the marginal ring. In larger specimens, an embayment is formed into the upper surface of the marginal frame where the ambulacra are inset (Figs. 3A$_1$, 4A$_1$). The ambulacra are formed from underlying biserial floor plates that structurally form the thecal wall and overlying cover plates arranged into multitiered series. The

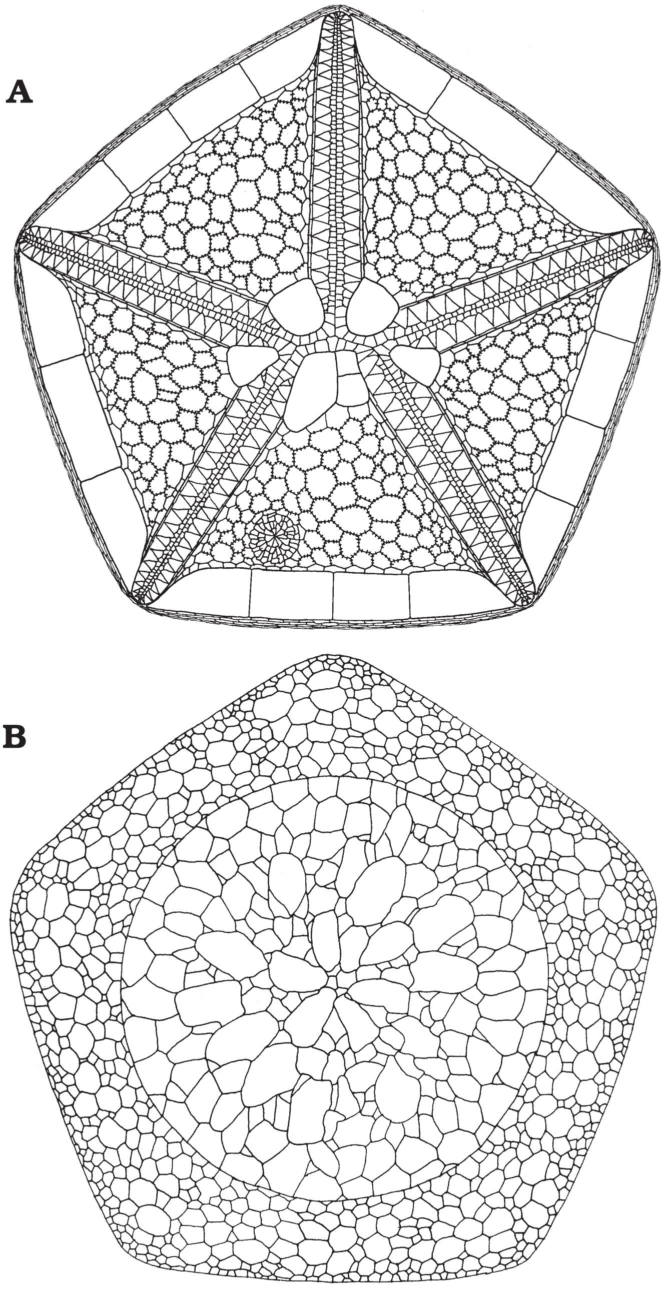

Fig. 2. Large mature specimen of Cambrian edrioasteroid echinoderm *Cambraster cannati* (Miquel, 1894). **A**. Oral view showing peristomial frame plates around central mouth, reconstructed oral and ambulacral cover plates, long straight ambulacra indenting large plates of marginal ring, interambulacral areas with small epispire-bearing plates, and peripheral skirt of tiny plates. **B**. Aboral view showing fully plated aboral surface composed of smaller-plated peripheral region lacking marginal ring surrounding larger-plated central region.

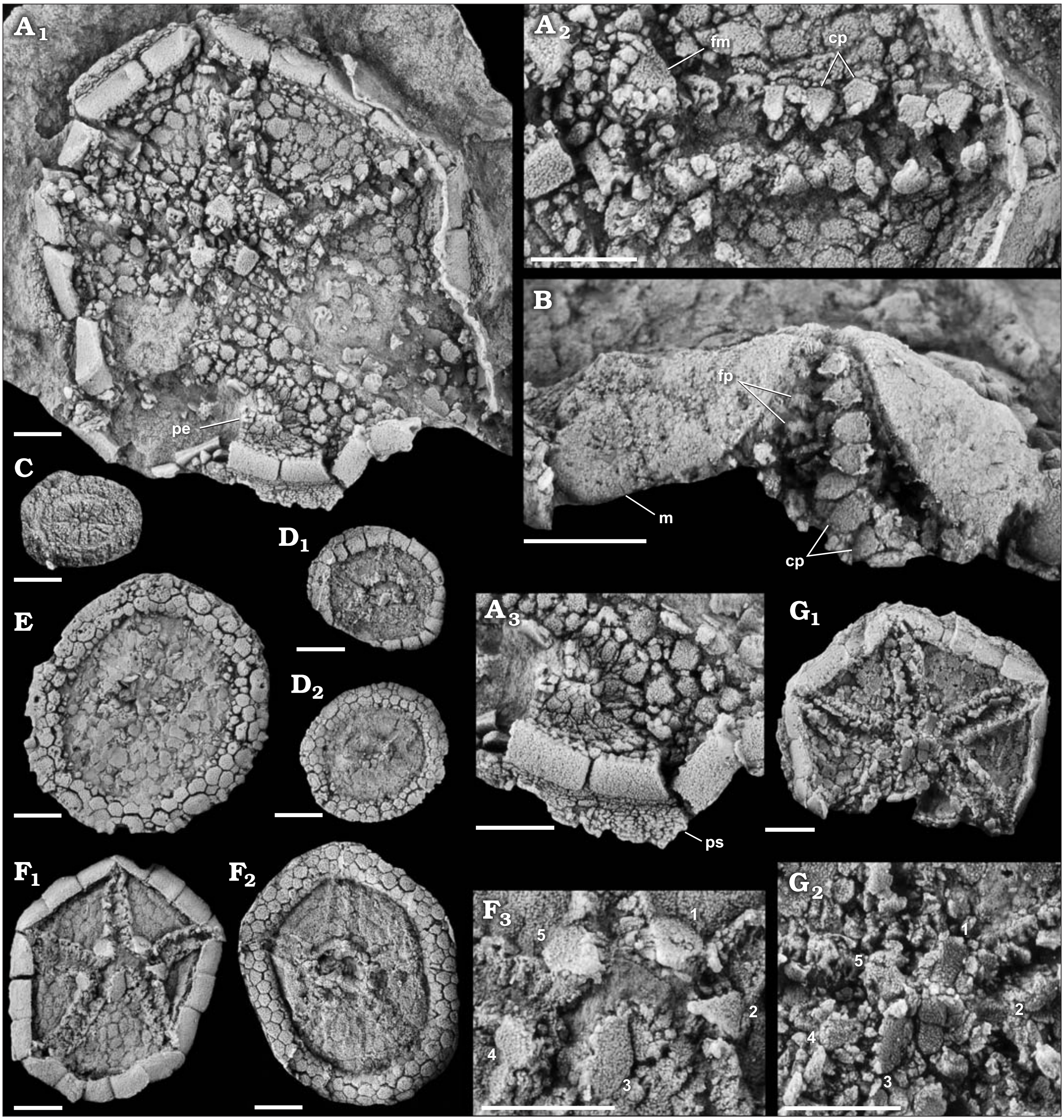

Fig. 3. Edrioasteroid echinoderm *Cambraster cannati* (Miquel, 1894) from the middle Cambrian of Borobia Formation (Spain) and Coulouma Formation (France). **A**. MPZ2011/101, complete adult specimen with a slightly distorted interambulacrum CD (A_1), detail of ambulacrum B (A_2), note the flooring plates with some cover plates articulated on them. Where cover plates are absent, ligamentary pits are identifiable. Detail of periproct and peripheral skirt bordering the marginal plates (A_3). **B**. MPZ2011/102, detail of contact between two marginal plates with invaginated borders to accommodate the ambulacral tip. **C**. MNHN.F.A45785, aboral view of an early juvenile with only few circlets of plates developed. **D**. MPZ2011/103, oral (D_1) and aboral (D_2) views of a juvenile that show a continuous marginal ring. **E**. MPZ2011/96, aboral view of an advanced juvenile. **F**. MPZ2009/1232a, b, oral (F_1) and aboral (F_2) views of an early adult specimen with marked pentameral shape; note impression of thicker ambulacra in F_2, oral frame plates, and possible hydropore showing though aboral plating. Detail of oral area, in which interradial oral plates are clearly visible (F_3). **G**. MPZ2011/104, oral view of a nearly complete specimen showing a nearly complete oral area. General view showing the oral area (G_1); detail of the oral area with the arrangement of interradial oral elements (G_2). Abbreviations: cp, cover plates; fm, peristomial frame plate; fp, flooring plates; m. Marginal plates; pe, periproct; ps, peripheral skirt. 1–5, peristomial frame plates. All specimens are photographs taken from latex casts whitened with NH_4Cl sublimate. Scale bars 2 mm.

floor plates are weakly exposed along the lateral margins, approximately 1.5 times as wide as long, and relatively thick. The perradial zig-zag suture is weakly developed and the floor plates are biserially alternate. Adjacent sutures between floor plates of the same side are marked by two pores that pass into the thecal interior. These pores are flared into the ambulacral tunnel and bear a weakly developed rim. The upper surface of the floor plates in the ambulacral tunnel is marked by two well-developed depressions abradially near the articulating surface for the cover plates. These depressions lead to a narrow dendritic network of strongly demarked, extremely thin channels that extend in branching arcs towards the perradial suture (Fig. 4A$_3$).

Cover plates are arranged into a multitiered series. Primary series are arranged with less than one set of primary plates per floor plate. A primary series consists of a large triangular plate with a smaller primary wedged between. A secondary series of smaller equant to elongate plates of unknown arrangement lie adradial to this series, and there is a hint of a tertiary series. Cover plate interiors poorly documented.

Interambulacra.—Interambulacral plates abut along vertical sutures forming a tessellate membrane (Figs. 3F$_1$, 4C$_2$). Plates in each interarea are differentiated into larger primary plates that are separated in plate corners by a series of smaller secondary plates. Primary plates are largest in proximal central interareas and smaller adradially and distally. Along the adradial edges of the interambulacra these plates are all small and radially elogate, forming one to two rows that articulate to the abradial notch on the floor plate series. Distally these plates are smaller and somewhat transversely elongate where they abut along the edge of the marginal ring articulating into a small notch along the proximal extremity of the ring. Interambulacral plates are also smaller along the margin of the periproct but do not form regular circlets.

Epispires are found only along the edges of interambulacral plates (Fig. 4C$_2$). These pores are small, vertical, and evenly spaced around the edges of each plate except at the extreme edges of the interambulacra where plates are smallest. Epispires are ovoid with the long axis perpendicular to the plate sutures and are equally developed on primary and secondary interambulacral plates. Small isolated platelets suggest that the epispires were covered with a few loosely articulated platelets embedded in soft tissues (Fig. 3A$_2$).

Marginal ring.—The marginal ring forms a stout frame of larger elements that are strongly differentiated from other plate series by their shape and position (Figs. 3, 4). The number of plates is slightly variable in different interambulacra of the same specimen and in the same interambulacra of different specimens, but does not seem to be diagnostic between different species (Table 1).

Table 1. Variability in the number of interradial and perradial marginal ring plates per interambulacrum. Normally the number of plates can change by just one plate but interambulacrum CD is an exception with the number being higher and more variable than the others.

Number of plates per interambulacrum	AB	BC	CD	DE	EA
Cambraster cannati specimens					
MPZ2009/1232; Fig. 3F$_1$	4	3	5	3	3
MPZ2011/101; Fig. 3A$_1$	4	?	6	3	3
MPZ2011/104; Fig. 3G$_1$	4	3	?	4	3
MPZ2011/104; Fig. 4B	3	?	?	3.5	2.5
MPZ2011/103; Fig. 3D$_1$	4	3?	?	?	4
MNHN.F.A45786; Fig. 4A$_1$	4	4	5	4	3
MNHN.F.A45788; Fig. 4C$_1$	4	3	?	?	?
MNHN.F.46475	3	?	?	3	3
Specimen figured in Smith (1985: text-fig. 2)	?	?	5	4	3
Cambraster tastudorum specimens					
NMVP107063B; Fig. 6A	3	3	4	3	3
NMVP107061; Fig. 6B	4?	3	5	3	3
NMVP107060; Fig. 6C$_1$	3	3?	?	3	3?

There are two somewhat different types of marginal plates constructing the frame; interradially positioned, rectangular marginals that do not support the distal ambulacra and paired-perradial marginals that together support the distal ambulacra. The interradial marginals vary between one and three per interambulacrum and, except for the CD interray where marginals are usually more numerous, the number does not follow any pattern within or between specimens nor ontogenetically (Table 1). They are triangular in radial cross section with an acute distal margin and slightly invaginated proximal margin. They have flat ventral surfaces and joint adjacent marginals by a weakly developed suture. In plan view they are transversely elongate but are more equant in juveniles. Perradial marginals are similar to interradial plates in gross features but differ along perradial margin. These plates are paired along the radii and meet along a long, radially positioned suture. They are trapezoidal in ventral aspect becoming widest along perradial margin, but triangular in dorsal aspect becoming narrowest perradial. The proximal edge of the dorsal surface is curved to create a radial invagination where the ambulacrum lies directly along this contact, becoming more exaggerated with age. The ambulacral embayment is cored by the ambulacral floor plates and radially elongate interambulacral plates extend along the ambulacrum in this area.

The marginal ring is surrounded by a peripheral skirt of tessellate to squamose and very tiny plates (Figs. 2A, 3A$_3$). Taphonomically, these plates appear to be somewhat flexible. These plates are variable in shape but most are rectangular and highly transversely elongate especially distally. The peripheral skirt articulates to the external part of the marginal plates along the distal dorsal surface. Up to 8–10 rows of these plates constitute this structure. In better-preserved specimens, the largest and more irregularly shaped plates lie proximally and smallest and more regularly plates distally. The peripheral skirt has a sharp transition between the plates of the oral surface and the equant tessellate plates of the aboral surface.

Aboral surface.—The aboral area is fully plated (Figs. 3C, E, D$_2$, F$_2$, 4A$_2$). Plates from this surface are nearly smooth, flat, polygonal, and sub-regularly arranged. The outermost edge of the aboral surface is formed from an irregular circlet of

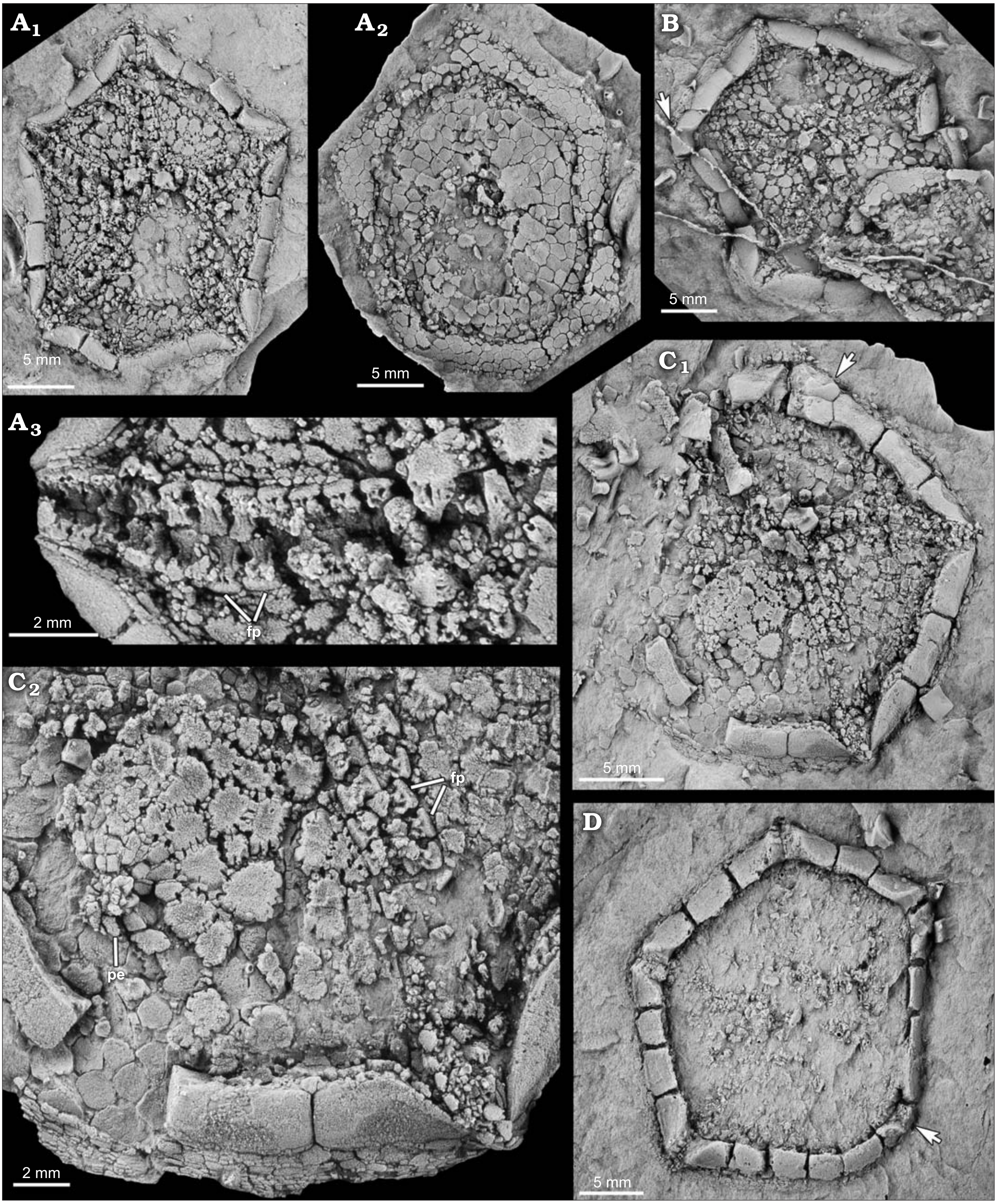

Fig. 4. Edrioasteroid echinoderm *Cambraster cannati* (Miquel, 1894) from the middle Cambrian of Borobia Formation (Spain) and Coulouma Formation (France). **A**. MNHN.F.A45786B, oral (A_1) and aboral (A_2) views of a complete adult specimen, detail of ambulacrum E showing the disposition of flooring plates (A_3). Note the position of the circular apertures for the water vascular system and the pits for cover plates articulation. **B**. MPZ2011/105, adoral view of a teratological specimen in which the ambulacrum E extends within a single marginal plate. **C**. MNHN.F.A45788, nearly complete specimen with →

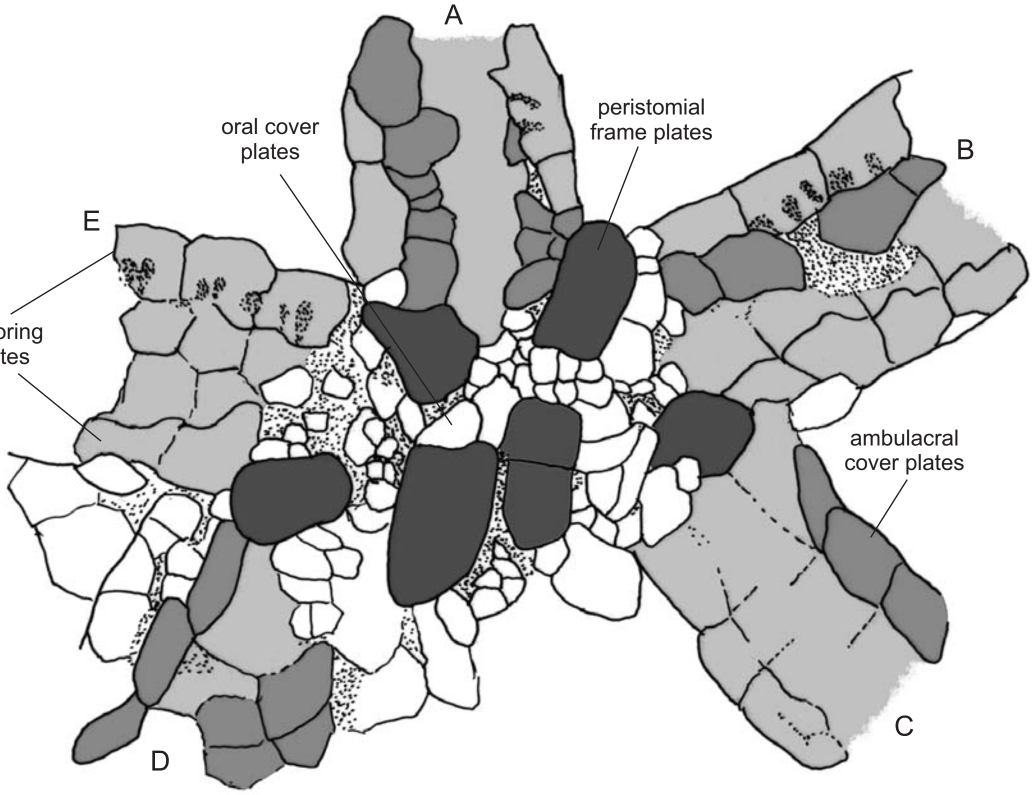

Fig. 5. Camera lucida drawing of oral frame in edrioasteroid echinoderm *Cambraster cannati* (Miquel, 1894); specimen MPZ2011/104. **A**–**E**. Ambulacral designation.

small equant peripheral plates that articulate with the plates of the peripheral skirt with a sharp transition. Distal to this peripheral plate series is a series of 5–6 poorly organized circlets that are arranged into a regular mosaic of larger plates toward the periphery and smaller plates centrally. Plates in this zone are thick, with vertical sutures and equant in outline. This zone lies directly beneath the marginal ring and may be functionally related. This zone shows an irregular transition over several irregular circlets to the central disk defined by thinner plates and differentiated plating style. The cental disk is demarked by a large circular suture and is plated with large, radially elongate primary plates that typically are twice as large as the largest plates of the peripheral series. These plates are irregularly arranged and separated in most places by smaller plates that vary between radially elongate to more equant. The central-most plating becomes irregular with many more small plates.

Anal pyramid/hydropore–gonopore.—Periproct placed in the distal interambulacrum CD left of the midline almost abutting the marginal ring. The structure is formed into a low cone and is plated with several highly irregular circlets of very thin, lathe-shaped plates that are radially arranged. The periproct is relatively large and becomes more complex adding plates ontogenetically.

Placement and nature of the hydropore and gonopore is poorly constrained. A possible pore between the two CD positioned interradial oral frame plates is not consistently seen in different specimens, and the proximal right interambulacrum CD is poorly preserved in all specimens. Interior views of the oral frame are obscured by the plating of the ventral integument, but one specimen suggests a bean-shaped mouth and a hydropore structure in the proximal right interambulacrum CD (Fig. 3F_3), similar to that reported for *C. tastudorum* by Jell et al. (1985).

Discussion.—*Cambraster* from the Western Mediterranean region includes only one species *C. cannati*. A recent specimen described from Spain as *Cambraster* cf. *tastudorum* (Zamora et al. 2007) corresponds to an aboral surface assignable as a later juvenile of *C. cannati*. *Cambraster cannati* differs from *C. tastudorum* (Fig. 6) primarily in the aboral plating, the relatively shorter ambulacra that do not extend as far over the perradial marginals, the lack of radial spines on the tiny peripheral skirt plates, and the relatively smaller number of marginals per interambulacrum.

---

well-preserved interambulacral plates, ambulacral flooring plates, and periproct. Also note the duplicated marginal ring in interambulacrum AB and close to the A ambulacra. General view (C_1) and detail of the interambulacra CD showing the periproct and interambulacral plating (C_2). **D**. MNHN.F.A45789, complete adult specimen with a well preserved marginal ring in which the tip of ambulacrum C extends within a single marginal plate rather than between two adjacent marginals. Abbreviations: cf, cover plates; fm, peristomial frame plate; fp, flooring plates; m, marginal plates; pe, periproct; ps, peripheral skirt. 1–5, peristomial frame plates. All specimens are photographs taken from latex casts whitened with NH_4Cl sublimate.

http://dx.doi.org/10.4202/app.2011.0152

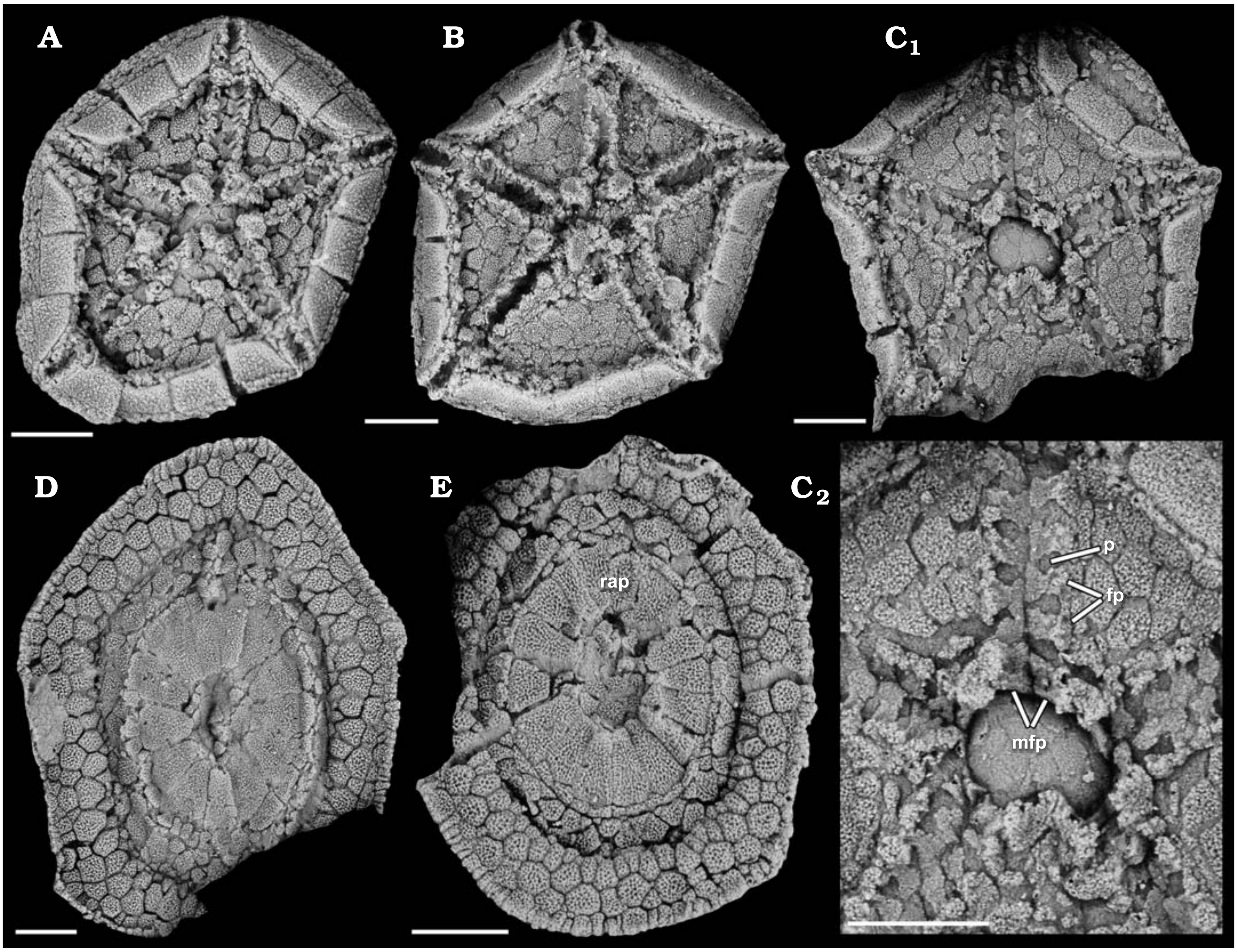

Fig. 6. Edrioasteroid echinoderm *Cambraster tastudorum* Jell, Burrett, and Banks, 1985 from the Cambrian Cateena Group, Australia. **A**. NMVP107063B, oral view of a complete specimen. **B**. NMVP107061, oral view of a complete specimen. **C**. NMVP107060, oral view of a nearly complete specimen showing the peristome bounded by interradial plates (mfp), flooring plates (fp), and apertures for the water vascular system (p). General view (C_1) and detail of the oral plating showing the interradial elements constructing the mouth frame (C_2). **D**, **E**. Aboral view of two specimens showing the plating pattern with large radial elements (rap). NMVP107068 (**D**) and NMVP107063A (**E**). Scale bars 2 mm.

Stratigraphic and geographic range.—*Solenopleuropsis* (*Solenopleuropsis*) Assemblage Zone from the lower Languedocian Borobia and Coulouma Formations of Spain and France respectively. *Jincella convexa* Zone from the middle Languedocian Coulouma Formation only in France.

The specimen of *Cambraster* described by Zamora et al. (2007) was based on museum collections and was assigned to the upper Caesaraugustan Murero Formation, but this age is in doubt because none of the more recent specimens come from this age or formation.

Cambraster tastudorum Jell, Burrett, and Banks 1985

Fig. 6.

Material.—Several latex casts obtained from the Museum of Victoria Palaeontological Collection including specimens NMVP107060, NMVP107061, and NMVP107063A, B. See Jell et al. 1985 for aditional information.

Diagnosis.—Small to medium *Cambraster* bearing relatively few epispires at maturity, spiny peripheral skirt, proportionately longer ambulacra at maturity, and well-organized central ventral disk with large, radially arranged plates.

Discussion.—*Cambraster tastudorum* Jell, Burrett, and Banks, 1985 conforms well to *Cambraster cannati* and these taxa are considered congeneric. Jell et al. (1985) listed two characteristics as diagnostic of *Cambraster tastudorum*: epispires developed on the central part of the oral surface in the interambulacra, and a circlet of large, radially arranged contiguous plates surrounding a small number of tiny plates on the aboral surface. Of these characteristics, we consider only the second one as clearly diagnostic of the species. Most of the described specimens of *C. tastudorum* are generally small, and only a few epispires are present in the largest ones. The relative paucity of epispires is also noted for similar sized specimens of *C. cannati* where small specimens lack epispires, medium-sized speci-

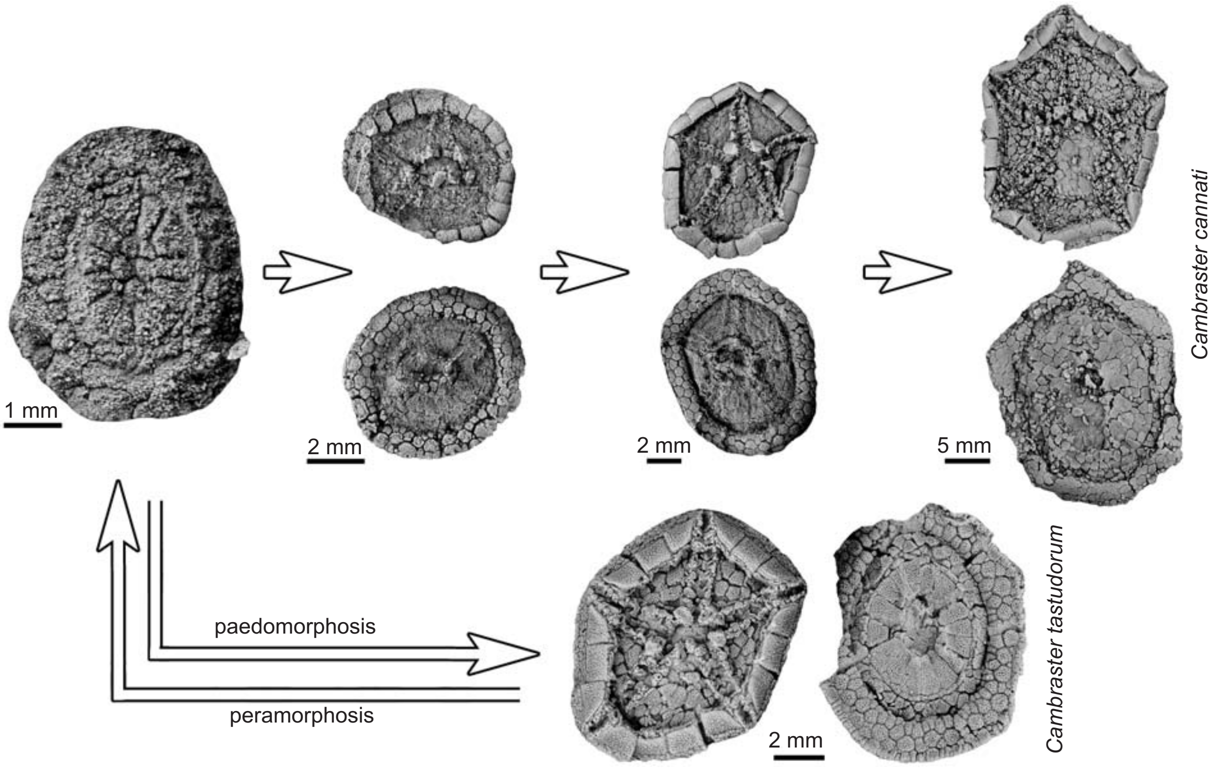

Fig. 7. Ontogenetic development of edrioasteroid echinoderm *Cambraster cannati* (Miquel, 1894). Note the similarity in the aboral plating between the most juvenile specimen of *C. cannati* and larger specimens of *Cambraster tastudorum* Jell, Burrett, and Banks, 1985.

mens have relatively few, and large specimens have very large numbers. If known specimens of *C. tastudorum* represent the mature condition for the species, than paucity of epispires is a valid taxobasis. If, however, known specimens are submature, and epispires are added later in ontogeny, this feature is non-diagnostic.

As mentioned above, the plating of the aboral surface of a large *Cambraster tastudorum* (Fig. 6D) shows a similar arrangement to only the smallest known specimens of *Cambraster cannati* suggesting heterochronic evolution. Unfortunately, there is no data to polarize this transformation to determine if *C. tastudorum* is paedomorphic with respect to *C. cannati* or if *C. cannati* is peramorphic with respect to *C. tastudorum.* Regardless, the relative juvenilization of the aboral surface of *C. tastudorum* serves to separate the two species.

However, the tips of the ambulacra are proportionately longer in *C. tastudorum* than they are in similar-sized specimens of *. cannati* (see below). If interpreted as heterochrony, the polarity of this transformation is in the opposite direction as the development of the aboral surface being more developed in *C. tastudorum* with respect to *C. cannati.* This feature is consistent between specimens of both species and serves to distinguish the two taxa.

Stratigraphic and geographic range.—Cateena Group, middle Cambrian (Cambrian series 3, Drumian), road cutting just S of Gawler River on Isandula Road, 8 km south of Ulverstone, N Tasmania, Australia.

Discussion

Ontogeny.—Specimens of *Cambraster cannati* from Spain and France provide the first data on ontogeny of *Cambraster* and a unique opportunity to examine the acquisition of characters along the ontogenetic trajectory. Ontogenetic sequences in edrioasteroids are especially important to analyze heterocronic evolution in echinoderms and several papers have focused on this topic (Bell 1976b; Sumrall 2001; Sumrall et al. 2006a; Zhao et al. 2010; McKinney and Sumrall 2011). Bell and Sprinkle (1978) and Zhao et al. (2010) provided ontogenetic sequences for the Cambrian edrioasteroids *Totiglobus* and *Kailidiscus* respectively. These taxa, however, are morphologically very different from *Cambraster*. *Totiglobus* has a globular, nearly spherical theca shape and different construction of the ambulacra and intermabulacral plating (Bell and Sprinkle 1978). The morphology of *Kailidiscus*, although well understood, is again very distinct from *Cambraster* in the construction of the ambulacra, interambulacra, and the naked lower surface of the theca (Zhao et al. 2010). These species, therefore, make poor models for a comparative study of the ontogenetic sequence found in *Cambraster*.

Specimens in the new collections of *Cambraster cannati* range in size from 4 to 26 mm in diameter. The smallest specimen available is 4 mm in diameter and only known from the aboral surface (Fig. 3C). By this ontogenetic stage the aboral plating is differentiated with an outer row composed with two irregular circlets of equant plates. The central disk is represented by a circlet of large, somewhat triangular plates that are radially elongate. The central portion of the central disk bears six irregularly polygonal plates. Although somewhat tectonically shortened, the theca at this stage is clearly circular in outline.

The next larger specimens in the new collections are 5 mm in diameter and include both oral and aboral surfaces (Fig. 3D$_1$, D$_2$). By this stage, five ambulacra are already visible. The mouth frame of integrated interradial plates is clearly differentiated including both plates in the CD interradius and their perradial expansions floor the proximal-most ambulacra. As in isorophids and *Kailidiscus*, the oral surface is dominated by the peristome, and the proportionately very wide ambulacra, while the interambulacral areas are relatively small bearing few plates (Bell 1976b; Zhao et al. 2010). At this stage epispires are not developed. The marginal ring is continuous without embayment at the tips of ambulacra (Fig. 8A), and the peripheral skirt is present, but poorly developed. The shape of marginals is also distinct with elements that are nearly longer than wide, although the number of marginals is consistent with that of mature specimens suggesting that addition of marginals does not occur ontogenetically. In aboral view new plates are added to the peripheral series forming three to four irregular series. The central disk has more plates in the proximal portion where primary plates begin to be outlined by secondary plates, and centrally the small, polygonal plates are more numerous. Overall, the plates and their distribution are very similar to the morphology of later stages.

The next larger specimens in the new collections are 11 mm in diameter (Fig. 3F$_1$, F$_2$). Many of the definitive mature characteristics are present at this stage. The interambulacra become proportionately larger and more pronounced but still lack well developed epispires. As the ambulacra elongate, the marginal frame begins to be stretched out and become angular where in contact with the ambulacral tips. Meanwhile, the interradial portion of the marginal frame becomes linear giving specimens a distinctly pentagonal outline that becomes more pronounced with age. Where the ambulacra contact the marginal frame, typically at the junction between two marginal plates, embayments form where ambulacral tips begin to override the marginal frame (Fig. 8B). This characteristic is somewhat variable because specimens of similar size may or may not express these embayments clearly (Fig. 3G$_1$). Development of the aboral surface is not much different from the previous size class only adding more circlets marginally and intercalating more plates centrally (Fig. 3E).

The largest specimens in the new collections include specimens from 20 mm onwards (Figs. 3A$_1$, 4A$_1$, A$_2$, C$_1$, D). At this ontogenetic stage the typical mature structures are fully established. The theca has a marked pentagonal outline and epispires are present all over the interambulacral plates. New plates in the interambulacral areas are being added along the radial and distal margins of the interareas as well as in the field interiors. The ambulacral tips extend out across the embayments of the marginal frame and in the most mature cases fully separate the marginal frame plates externally but remain in contact internally. In no cases do the tips of the ambulacra extend beyond the marginal frame onto the aboral surface of the theca. The bottom surface when fully developed looks little different than in previous stages except that more plates are present in the irregular plate circlets.

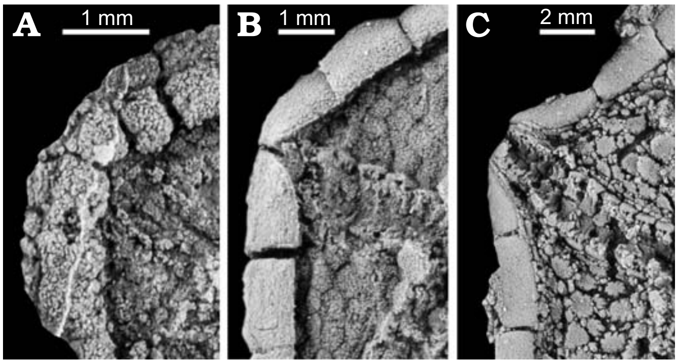

Fig. 8. Ontogenetic development of marginal ring and ambulacral tips in edrioasteroid echinoderm *Cambraster cannati* Miquel (1894) from early juveniles (**A**), late juveniles (**B**), and adult (**C**) specimens. The three photographs represent ambulacrum E.

The ontogeny of *Cambraster tastudorum* is poorly known because many well-preserved specimens are approximately 10 mm in diameter (Fig. 6). The oral surface of this species conforms fairly closely with similarly sized individuals of *Cambraster cannati* characterized by the absence or poor representation of epispires. However, the ambulacra are proportionately longer with nearly all ambulacral tips extending through the embayment of the marginal rim as in more mature specimens of *Cambraster cannati.* The aboral plating of *Cambraster tastudorum*, bears 4–5 irregular circlets of tessellate, polygonal plates, an intermediate circlet with large radial elements forming a uniform pavement and a central disc with small plates (Jell et al. 1985). This plating is nearly identical to that seen in the 4 mm diameter specimens of *C. cannati*. The ontogeny of *Cambraster cannati* also demonstrates that juvenile specimens lack epispires, a character also seen in other Cambrian echinoderm groups bearing epispires (Sprinkle 1973; Parsley 2012). The similar-sized (circa 10 mm) figured specimens of *C. tastudorum* (Fig. 6) have only scattered epispires, suggesting that this character may not necessarily be considered as diagnostic. If other features, such as the well-developed marginal ring embayments, suggest these specimens of *C. tastudorum* are mature, then perhaps poorly developed epispires may turn out to be diagnostic.

State of preservation.—All specimens of *Cambraster cannati* are preserved as natural moulds of the original calcite skeletons and thus were studied from latex casts. Many specimens were collected as part and counterpart allowing the examination of both the upper and lower surfaces of the thecae. The plating of the aboral surface, however, obscures details of the internal anatomy of the ambulacral system and oral frame. Because specimens are lithologically compressed, the oral surface is pressed against the aboral surface when the inflated theca of the living animal collapsed. Oral areas are also always somewhat disrupted except for one specimen (Fig. $3G_2$). In general the preserved height of the thickly plated ambulacra is exaggerated with respect to the thinly plated interambulacra as commonly noted for other taxa (Bell 1976a). Aboral views are in some cases striking because they seem to preserve a ring-like bulge (but no marginal plates), an impression of the ambulacral system, and an oral frame with a possible hydropore (Fig. 3E, F_2). In these cases, the thick marginal ring plates, ambulacral system, and oral frame have been compressed onto the aboral surface during compaction.

Mode of life.—Several authors have discussed the life mode of *Cambraster* based mainly on morphology (Termier and Termier 1969; Smith 1985; Guensburg and Sprinkle 1994), but a model including both morphological adaptations and paleoenvironments has not emerged. Termier and Termier (1969) proposed that *Cambraster* and the closely related genus *Stromatocystites* were infaunal animals. This hypothesis was rejected by Smith (1985) based on the absence of paxillae to maintain a water-filled space around their buried thecae that would have enabled the papillae to function infaunally. Smith (1985) also suggested that *Cambraster* was probably a sessile form laying directly on the sea floor. Guensburg and Sprinkle (1994) agreed with Smith (1985) in the mode of life of *Cambraster* and provided explanations for the marginal ring function. They suggested that the marginal ring did not contact the substrate and presumably stiffened the theca. Later this structure was incorporated into the peripheral rim of all isorophids and helped seal the thecal margins to the substrate. Reanalysis of the construction of these structures shows them to be entirely different and probably served a different function.

Other Cambrian edrioasteroids, such as *Totiglobus*, *Stromatocystites*, and *Kailidiscus* have globular thecae that are hydrodynamically unstable thereby more consistent with a quiet water environment. These forms apparently attached directly to the substrate (Dornbos 2006; Domke and Dornbos 2010; Zhao et al. 2010). In contrast, *Cambraster* bears a marginal ring and a low profile, disc-shaped theca with a hydrodynamically stable, plano-convex cross section. We interpret this shape as an adaptation to relatively high-energy environments. A similar streamlined profile is shared with other younger edrioasteroids living in similar environments. The marginal ring was probably a protective structure weighing down the edge of the theca and creating laminar flow across the theca.

The peripheral skirt of *Cambraster* borders the animal and is composed of several rows of tiny plates. This structure is very flexible and attaches the edge of the marginal ring to the aboral surface. Flexibility in the skirt is related to changes in thecal volume during thecal extension and contraction though probably minor in this taxon as compared to later forms (Sumrall 1993).

The echinoderm fauna associated with *Cambraster* provides further valuable paleoenvironmental information. *Cambraster* in both western Mediterranean occurrences are found in off-shore environments sporadically punctuated by storm deposition. In both cases, associated fauna is considered para-autochthonous and appears associated with a rich assemblage of trilobites, brachiopods, and other echinoderms. Ventral swellings on the cinctans *Elliptocinctus barrandei* and *Sucocystis theronensis* associated at these levels are adaptations to relatively energetic environments (Zamora and Smith 2008; Zamora and Álvaro 2010). The armoured stylophoran *Ceratocystis*, also present in both *Cambraster* occurrences, has been interpreted to inhabit relatively shallow, energetic environments (Lefebvre 2007).

Although other edrioasteroids including ?*Stromatocystites* and *Protorophus* are found in the Iberian Chains, these forms come from very quiet water, offshore facies of the Murero Formation where they attach to stabilized substrate and shell fragments respectively (Zamora 2010; Zamora and Smith 2010). The upper Murero Formation and lower Borobia Formation record a regression sequence resulting in a coarser grained, more proximal, and energetic offshore environment (Álvaro and Vennin 1996) more suitable to *Cambraster* colonization.

Another interesting feature of *Cambraster* is the extension of ambulacra beyond the marginal ring. Juveniles lack indented marginal plates, whereas this feature increases throughout ontogeny. This is probably another case of increasing ambulacra surface during ontogeny, as has been suggested for other edrioasteroid taxa (McKinney and Sumrall 2011).

The morphological features and environment all indicate that *Cambraster* was sessile, attached directly on the substrate, and inhabited relatively high energy, offshore environments.

Abnormalities in *Cambraster*.—Edrioasteroid teratologies are rare but can be found in large collections. There are several reports of specimens with extra ambulacra, missing ambulacra, and ambulacra curving opposite from the normal direction (Bell 1976a; Smith and Arbizu 1987; Sumrall 1996, 2001; Sumrall et al. 2006b; Sumrall and Zamora 2011). Generally these occur at low frequency, but in the Ordovician pyrgocystid *Cysaster*, specimens with between four and nine ambulacra are relatively common (Bell 1976a).

Three specimens of *Cambraster* reported herein show possible abnormalities in the growth of the marginal ring. Typically, as the ambulacra extend through the marginal ring, the ambulacral embayment lies along the suture between two marginal plates. One of our reported specimens (Fig. 4D) shows an ambulacrum (probably C) extending through the marginal embayment formed in a single marginal plate. A second specimen shows a similar situation but affecting ambulacrum E (Fig. 4B). A similar specimen was illustrated by Ubaghs (1971: fig. 9) and Smith (1985: fig. 19D), in which two of the five embayments are within single plates and also Jell et al. (1985: 188, fig. 4B), discussed and illustrated a specimen of *C.* sp. cf. *tastudorum* with the E, A, and B ambulacral grooves all centered on single, slightly curved marginals.

http://dx.doi.org/10.4202/app.2011.0152

A third specimen shows a marginal embayment formed in three plates. The left side is normal, but the right side shows duplication of the marginal plate with one plate forming the proximal features and one forming the distal features. The left side of these plates are somewhat wider than normal but forms the marginal embayment similarly to the normal condition. The right side forms a three plate junction with the adjacent interradial marginal plate (Fig. 5E). This type of teratology probably occurred early in development where the growth center of the plate was split resulting in two marginal plates.

Conclusions

Cambraster cannati was one of the first Cambrian edrioasteroids described in detail and its morphology has been reviewed in tens of papers about the early evolution of echinoderms. Despite these well documented studies, we demonstrate that larger collections of new material can still provide valuable information on morphology. Base on the ambulacral construction, *Cambraster* is probably related with stromatocystitids rather than with any other edrioasteroid clade. The atypical morphology of *Cambraster* is probably an adaptation to living in high energy environments where the marginal ring played a protective role. This is suggested from morphology, and associated, facies and faunal assemblage occurring with these edrioasteroids.

The first ontogenetic data for *Cambraster* is also provided. These data indicate that the main ontogenetic changes affect the morphology of marginal ring, the relative length of ambulacra and the thecal outline. Juvenile specimens of *Cambraster cannati* show a very strong resemblance to adult specimens of *C. tastudorum* from Australia suggesting heterocronic evolution. The large number of specimens also highlights two main types of teratologies. One is a duplication of a marginal plate, and the other is an extension of ambulacra through a single marginal plate rather than between two marginal plates.

Acknowledgements

We thank Isabel Pérez (MEC-FSE, Zaragoza University, Spain) for preparing the plates and some photographs for this paper. Special thanks are given to Fernando Gracia (Zaragoza, Spain) for his help in the field. David Holloway (Museum of Victoria, Victoria, Australia) and Bertrand Lefebvre (Université Lyon, France) provided latex casts from collections they curate. We are grateful to Peter Jell (Queensland Museum, Queensland, Australia) for important systematic discussions. Bertrand Lefebvre (Université Lyon, France) and James Sprinkle (University of Austin, USA) reviewed the completed manuscript. This work is a contribution to the Project CGL 2011-24516 from MEC and to the project CGL 2010-19491 from MICINN-FEDER. SZ has a postdoctoral grant financed from MEC-Spain, and grants NSF EAR-0745918 and NSF DEB-1036260 funded the visit of CDS to Spain.

References

Álvaro, J.J. and Vennin, E. 1996. The Middle–Upper Cambrian transition in the Iberian Chains (NE Spain). An integrated approach. *Rivista Italiana di Paleontologia e Stratigrafia* 102: 341–352.

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.

Álvaro, J.J., Lefebvre, B., Shergold, J.H., and Vizcaïno, D. 2001. The Middle–Upper Cambrian of the southern Montagne Noire. *Annales de la Société Géologique du Nord (2^{e} série)* 8: 205–211.

Bassler, R.S. 1935. The classification of the Edrioasteroidea. Smithsonian *Miscellaneous Collections* 93: 1–11.

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

Bell, B.M. 1976b. Phylogenetic implications of ontogenetic development in the class Edrioasteroidea (Echinodermata). *Journal of Paleontology* 50: 1001–1019.

Bell, B.M. 1980. Edrioasteroidea and Edrioblastoidea. *In*: T.W. Broadhead and J.A. Waters (eds.), Echinoderms: Notes for a Short Course. *University of Tennnessee Department of Geological Sciences, Studies in Geology* 3: 158–174.

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

Billings, E. 1858. *On the Asteriadae of the Lower Silurian rocks of Canada. Geological Survey of Canada, Figures and Descriptions of Canadian Organic Remains, Decade 3*, 75–85. J. Lovell, Montreal.

Brett, C.E. and Liddell, W.D. 1978. Preservation and paleoecology of a Middle Ordovician hardground community. *Paleobiology* 4: 329–348.

Cabibel, J., Termier, H., and Termier, G. 1959. Les échinodermes mésocambriens de la Montagne Noire (Sud de la France). *Annales de Paléontologie* 44: 281–294.

Cornell, S.R., Sumrall, C.D., and Brett, C.E. 2003. Paleoecology and taphonomic implications of an edrioasteroid encrusted hardground from the lower Devonian of eastern New York State. *Palaios* 18: 212–224.

De Brugière, J.G. 1791. *Tableau encyclopédique et méthodique des trois règnes de la nature, Vol. 7, L'helminthogie*. 83 pp.

Domínguez-Alonso, P. 2004. *Sistemática, anatomía, estructura y función de Ctenocystoidea (Echinodermata Carpoidea del Paleozoico inferior)*. 538 pp. Unpublished Ph.D. thesis, Universidad Complutense, Madrid. http://eprints.ucm.es/tesis/bio/ucm-t23248.pdf

Domke, K.L. and Dornbos, S.Q. 2010. Paleoecology of the middle Cambrian edrioasteroid echinoderm *Totiglobus*: Implications for unusual Cambrian morphologies. *Palaios* 25: 209–214.

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.

Gámez, J.A., Fernández-Nieto, C., Gozalo, R., Liñán, E., Mandado, J., and Palacios,T. 1991. Bioestratigrafía y evolución ambiental del Cámbrico de Borobia (Provincia de Soria. Cadena Ibérica Oriental). *Cuadernos del Laboratorio Xeolóxico de Laxe* 16: 251–271.

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.

Jell, P.A., Burrett, C.F., and Banks, M.R. 1985. Cambrian and Ordovician echinoderms from eastern Australia. *Alcheringa* 9: 183–208.

Kammer, T.W., Tissue, E.C., and Wilson, M.A. 1987. *Neoisorophusella*, a new edrioasteroid genus from the Upper Mississippian of the eastern United States. *Journal of Paleontology* 61: 1033–1042.

Lefebvre, B. 2007. Early Palaeozoic palaeobiogeography and palaeoecology of stylophoran echinoderms. *Palaeogeography, Palaeoclimatology, Palaeoecology* 245: 156–199.

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.

McKinney, M.L. and Sumrall, C.D. 2011. Ambulacral growth allometry in edrioasteroids: functional surface-volume change in ontogeny and phylogeny. *Lethaia* 44: 102–108.

Meyer, D.L. 1990. Population paleoecology and comparative taphonomy of two edrioasteroid (Echinodermata) pavements: Upper Ordovician of Kentucky and Ohio. *Historical Biology* 4: 155–178.

Miquel, J. 1894. Note sur la géologie des terrains primaires du département de l'Hérault. Le Cambrien et l'Arenig. *Bulletin de la Société d'étude des Sciences naturelles de Béziers* 17: 5–36.

Parsley, R.L. 2012. Ontogeny, functional morphology, and comparative morphology of lower (stage 4) and basal middle (stage 5) Cambrian gogiids, Guizhou Province, China. *Journal of Paleontology* 86: 569–583.

Shackleton, J.D. 2005. Skeletal homologies, phylogeny and classification of the earliest asterozoan echinoderms. *Journal of Systematic Palaeontology* 3: 29–114.

Schmitz, U. 1971. Stratigraphie und Sedimentologie im Kambrium und Tremadoc der Westlichen Iberischen Ketten nördlich Ateca (Zaragoza), NE Spanien. *Münstersche Forschungen zur Geologie und Paläontologie* 22: 1–123.

Shroat-Lewis, R.A., McKinney, M.L., Brett, C.E., Meyer D.L., and Sumrall, C.D. 2011. Paleoecologic assessment of an edrioasteroid (Echinodermata) encrusted hardground from the Upper Ordovician (Maysvillian) Bellevue Formation, Maysville, Kentucky. *Palaios* 26: 470–483.

Smith, A.B. 1983. British Carboniferous edrioasteroids (Echinodermata). *Bulletin of the British Museum of Natural History (Geology)* 37: 113–138.

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

Smith, A.B. and Arbizu, M.A. 1987. Inverse development in a Devonian edrioasteroid from Spain and the phylogeny of the Agelacrinitidae. *Lethaia* 20: 49–62.

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

Sprinkle, J. 1973. *Morphology and Evolution of Blastozoan Echinoderms*. 283 pp. Harvard University Museum of Comparative Zoology, Special Publication, Cambridge.

Sumrall, C.D. 1993. Thecal designs in isorophinid edrioasteroids. *Lethaia* 26: 289–302.

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

Sumrall, C.D. 2000. The biological implications of an edrioasteroid attached to a pleurocystitid rhombiferan. *Journal of Paleontology* 74: 67–71.

Sumrall, C.D. 2001. Paleoecology of two new edrioasteroids from a Mississippian hardground in Kentucky. *Journal of Paleontology* 75: 136–146.

Sumrall, C.D. 2010a. A model for elemental homology for the peristome and ambulacra in blastozoan echinoderms. *In*: L.G. Harris, S.A. Böttger, C.W. Walker, and M.P. Lesser (eds.), *Echinoderms*, 269–276. Durham, CRC Press, London.

Sumrall, C.D. 2010b. The systematics of a new Maysvillian (Upper Ordovician) edrioasteroid pavement from northern Kentucky. *Journal of Paleontology* 84: 783–794.

Sumrall, C.D. and Parsley, R.L. 2003. Morphology and biomechanical implications of isolated discocystinid plates (Edrioasteroidea, Echinodermata) from the Carboniferous of North America. *Palaeontology* 46: 113–138.

Sumrall, C.D. and Wray, G.A. 2007. Ontogeny in the fossil record: diversification of body plans and the evolution of "aberrant" symmetry in Paleozoic echinoderms. *Paleobiology* 33: 149–163.

Sumrall, C.D. and Zamora, S. 2011. Ordovician edrioasteroids from Morocco: Faunal exchanges across the Rheic Ocean. *Journal of Systematic Palaeontology* 9: 425–454.

Sumrall, C.D., Brett C.E., and Cornell, S. 2006a. The systematics and ontogeny of *Pyrgopostibulla belli*, a new edrioasteroid (Echinodermata) from the Lower Devonian of New York. *Journal of Paleontology* 80: 187–192.

Sumrall, C.D., Sprinkle, J., and Bonem, R.M. 2006b. An edrioasteroid-dominated echinoderm assemblage from a Lower Pennsylvanian marine conglomerate in Oklahoma. *Journal of Paleontology* 80: 229–244.

Sumrall, C.D., Brett, C.E., and McKinney, M.L. 2009. A new agelacrinitid edrioasteroid attached to hardground clasts from the McKenzie Member of the Mifflintown Member (Silurian) of Pennsylvanian, *Journal of Paleontolog*y 83: 794–803.

Termier, H. and Termier, G. 1969. Les stromatocystitoďdes et leur descendance. Essai sur l'évolution des premiers échinodermes. *Geobios* 2: 131–156.

Ubaghs, G. 1971. Diversité et spécialisation des plus anciens échinodermes que l'on connaisse. *Biological Reviews* 46: 157–200.

Waddington, J.B. 1980. A soft substrate community with edrioasteroids, from the Verulam Formation (Middle Ordovician) at Gamebridge, Ontario. *Canadian Journal of Earth Sciences* 17: 674–679.

Wilson, M.A. 1985, Disturbance and ecologic succession in an Upper Ordovician cobble-dwelling hardground fauna. *Science* 228: 575–577.

Zamora, S. 2010. Middle Cambrian echinoderms from North Spain show echinoderms diversified earlier in Gondwana. *Geology* 38: 507–510.

Zamora, S. and Álvaro, J.J. 2010. Testing for a decline in diversity prior to extinction: Languedocian (latest Mid-Cambrian) distribution of Cinctans (Echinodermata) in the Iberian Chains, NE Spain. *Palaeontology* 53: 1349–1368.

Zamora, S. and Smith, A.B. 2008. A new Middle Cambrian stem-group echinoderm from Spain: Palaeobiological implications of a highly asymmetric cinctan. *Acta Paleontologica Polonica* 53: 207–220.

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: 487–494.

Zamora, S. and Smith, A.B. 2012. Cambrian stalked echinoderms show unexpected plasticity of arm construction. *Proceedings of The Royal Society B* 279: 293–298.

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.

Zamora, S., Lefebvre, B., Álvaro, J.J., Clausen, S., Elicki, O., Fatka, O., Jell, P., Kouchinsky, A., Lin, J.-P., Nardin, E., Parsley, R., Rozhnov, S., Sprinkle, J., Sumrall, C.D., Vizcaïno, D., and Smith, A.B. (in press). Cambrian echinoderm diversity and palaeobiogeography. *Geological Society of London*.

Zhao, Y.L., Sumrall, C.D., Parsley, R.L., and Peng, J. 2010. *Kailidiscus*, a new plesiomorphic edrioasteroid from the basal Middle Cambrian Kaili Biota of Guizhou Province, China. *Journal of Paleontology* 84: 668–680.

http://dx.doi.org/10.4202/app.2011.0152