

Zeitschrift: Eclogae Geologicae Helvetiae
Herausgeber: Schweizerische Geologische Gesellschaft
Band: 97 (2004)
Heft: 3

Artikel: New Early Cambrian eocrinoids from the Iberian Chains (NE Spain) and their role in nonreefal benthic communities
Autor: Clausen, Sébastien
DOI: <https://doi.org/10.5169/seals-169118>

Nutzungsbedingungen

Die ETH-Bibliothek ist die Anbieterin der digitalisierten Zeitschriften. Sie besitzt keine Urheberrechte an den Zeitschriften und ist nicht verantwortlich für deren Inhalte. Die Rechte liegen in der Regel bei den Herausgebern beziehungsweise den externen Rechteinhabern. [Siehe Rechtliche Hinweise.](#)

Conditions d'utilisation

L'ETH Library est le fournisseur des revues numérisées. Elle ne détient aucun droit d'auteur sur les revues et n'est pas responsable de leur contenu. En règle générale, les droits sont détenus par les éditeurs ou les détenteurs de droits externes. [Voir Informations légales.](#)

Terms of use

The ETH Library is the provider of the digitised journals. It does not own any copyrights to the journals and is not responsible for their content. The rights usually lie with the publishers or the external rights holders. [See Legal notice.](#)

Download PDF: 26.11.2024

ETH-Bibliothek Zürich, E-Periodica, <https://www.e-periodica.ch>

New Early Cambrian eocrinoids from the Iberian Chains (NE Spain) and their role in nonreefal benthic communities

SÉBASTIEN CLAUSEN¹

Key words: Echinoderms, palaeoecology, Lower Cambrian, western Gondwana margin.

Mots clés: Echinodermes, paléocéologie, Cambrien inférieur, Marge occidentale du Gondwana.

ABSTRACT

The Early Cambrian echinoderm-sponge meadows, which colonized shallow carbonate-siliciclastic platforms, have received relatively little study despite their widespread occurrence in several regions of Gondwana. Their taxa are generally preserved disarticulated, reworked and deposited through the action of waves and storms. Silicified echinoderm-rich packstones from the uppermost Bilbilian limestones (latest Early Cambrian in age) of the Valdemiedes Formation (Iberian Chains, NE Spain) formed through growth and destruction of echinoderm-sponge colonies by storm-wave action. This fauna has been studied in thin section and after etching by acetic acid. Eocrinoid remains include the thecal basal-ossicle of *Rhopalocystis? mesonesensis* n. sp. and other indeterminate species. Echinoderm columnals, visible in thin section, are associated with sponge spicules, trilobites, calcite- and phosphate-shelled brachiopods, chancelloriid sclerites, and foraminiferans. This finding suggests that stemmed eocrinoids were already present on the western Gondwana margin at the end of the Early Cambrian.

RESUME

Malgré leur large distribution dans plusieurs régions du Gondwana, les colonies à échinodermes et éponges du Cambrien inférieur qui colonisèrent les plates-formes peu profondes en régime sédimentaire mixte demeurent relativement peu étudiées. Leur taxa sont généralement préservés désarticulés et remaniés au sein de dépôts hydrodynamiques sous l'influence des vagues et tempêtes. Des *packstones* silicifiés à échinodermes du Bilbilien terminal (fin du Cambrien inférieur) de la Formation de Valdemiedes (Chaînes Ibériques, Nord-Est de l'Espagne) ont été étudiés en lames minces et par dissolution à l'acide acétique. Ces bancs calcaires furent formés par la destruction répétée de colonies à éponges et échinodermes par l'action commune des vagues et tempêtes. Les restes d'éocrinoïdes extraits incluent la pièce basale de la thèque de *Rhopalocystis? mesonesensis* n. sp., ainsi que d'autres espèces indéterminées. Des columnales d'échinodermes sont également visibles en lames minces. Ces fossiles sont associés à des spicules d'éponges, des trilobites, des brachiopodes à valves calcaires et phosphatées, des sclérites de chancelloriides et des foraminifères. Cette étude suggère que les échinodermes à tige étaient présents sur la marge occidentale du Gondwana dès la fin du Cambrien inférieur.

1. Introduction

The Lower Cambrian sedimentary record is considered to represent the widest distribution of carbonate platforms during the Early Palaeozoic of the western Gondwana margin. Microbial and microbial-archaeocyathan buildups are representative benthic communities of the Lower Cambrian rocks in western Europe and northern Africa. These reef complexes are relatively well known for their syndimentary tectonic processes, preservation of primary textures, luxuriant growth of calcimicrobes, and biodiversity based on phosphatic- and siliceous-walled microfossils available after etching. Lower Cambrian reefal limestones developed from Morocco to the Iberian Peninsula, the Montagne Noire, the Armorican Massif (France), and Sardinia, recording a history of discontinuous

reef-building frameworks that evolved in the western Gondwana margin under a wide geodynamic extensional regime. Palaeogeographical reconstructions for the Early Cambrian, based on lithological indicators of climate (Álvaro et al. 2000), place the southward-drifting, western Gondwana margin in an arid subequatorial belt some 15–30°S, consistent with the presence of extensive reefs and evaporites.

By contrast, the sedimentary and palaeoecological patterns of the Early Cambrian nonreefal echinoderm-sponge meadows reported in the same marine platforms have been relatively ignored because of their limited outcrop exposure, mixed (carbonate-siliciclastic) character of their substrates, and drastic diagenesis. As envisaged by Álvaro & Vennin (1997) in the Iberian Chains (NE Spain), the ecological patterns of the nonreefal benthic communities were controlled by factors quite

¹ Université des Sciences et Technologies de Lille, U.F.R. Sciences de la Terre, Laboratoire de Paléontologie et Paléogéographie du Paléozoïque (LP3), UMR 8014 du C.N.R.S., F-59655 Villeneuve d'Ascq Cedex, France. E-mail: Sébastien.Clausen@ed.univ-lille1.fr

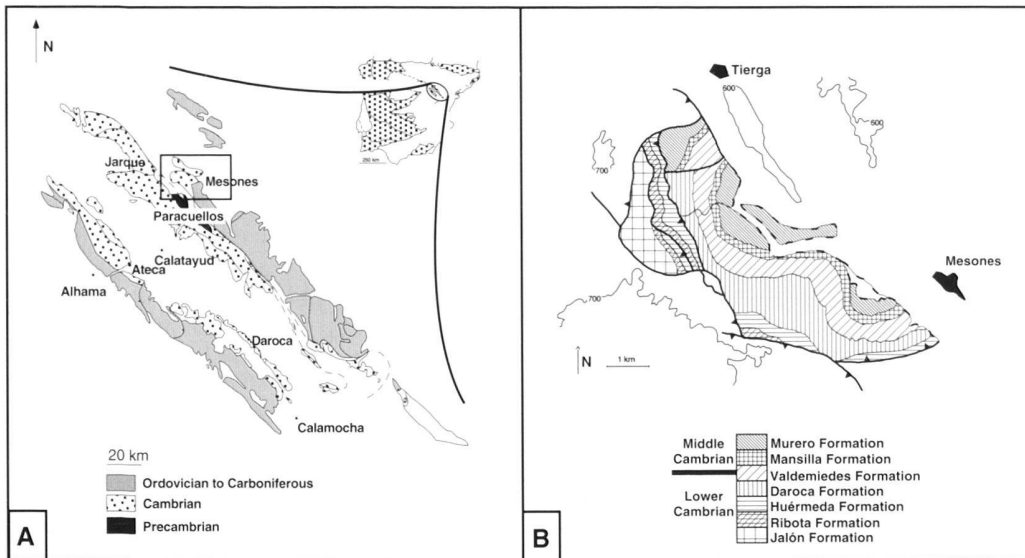


Fig. 1. Geological setting of the Iberian Chains in the context of the pre-Hercynian outcrops of the Iberian Peninsula (A) and geological sketch of the Cambrian outcrops of the Mesones de Isuela-Tierga area (eastern Iberian chain, boxed area in (A)) studied here (from Álvaro 1994).

different from those that governed the establishment and growth of reefs. Their taxa are rarely preserved in growth position but, instead, are disarticulated, reworked and deposited as hydrodynamic pavement (transported sediment accumulation) influenced by the action of waves and storms. Sponges bearing siliceous spicules can be studied after their extraction from limestone intercalations by dissolving the rock in dilute acids. However, thin sections are frequently the only way to study carbonate echinoderm plates.

The purpose of this paper is to present a study of Early Cambrian echinoderms based on thin sections and descriptions of new stemmed-eocrinoid skeletal elements after etching from silicified limestones. This case study is available because of the special diagenetic conditions recorded in some limestones of the Valdemedies Formation (Iberian Chains, NE Spain), whose silicification processes preserved the microstructure of some echinoderm skeletons. This will allow a better understanding of the role of echinoderms in the echinoderm-sponge meadows that covered the Lower Cambrian mixed substrates of the western Gondwana margin.

2. Geological setting and stratigraphy

The echinoderm ossicles reported here were found in the lower part of the Cambrian Valdemedies Formation (Iberian Chains, NE Spain; Fig. 1). The formation (20–150 m thick) consists of alternating beds of green marly shales and carbonates (Fig. 2). The carbonate intercalations are white limestones and yellow dolostones, up to 20 cm in thickness. The lower part of the formation contains stromatolitic limestones, whereas bioclastic limestones dominate its upper part. A lithofacies analysis of the Valdemedies Formation and its palaeogeographical distribution throughout the Iberian platform were recently established (Álvarez et al. 1993; Álvarez & Vennin

1996a–b, 1997). The Lower-Middle Cambrian boundary is in the Valdemedies Formation, the biostratigraphical chart of which has been established on the basis of trilobite zonation (Álvarez et al. 1993; Liñán et al. 1993). All the echinoderms analysed here were found from the limestone intercalations of the *Hamatolenus (H.) ibericus* zone, uppermost Bilbilian (Early Cambrian; Fig. 2).

The studied limestones consist of light to medium grey, echinoderm packstones, thinly bedded (less than 1.4 m thick), and partly bioturbated. Additional faunal elements include trilobites, calcite- and phosphate-shelled brachiopods, cancellorid sclerites, siliceous sponge spicules, and psammosphaerids (foraminiferans). The content of silt-size fraction is highly variable. Intervals without active reworking are indicated by the episodic occurrence of burrows, rarity of low-angle cross-bedding structures, and presence of an encrusting epibenthic fauna that suggests taphonomic feedback processes (*sensu* Kidwell 1991).

3. Systematic palaeontology

The described specimens are housed in the Museo Paleontológico of the Zaragoza University (prefixed MPZ).

Phylum Echinodermata KLEIN 1734
 Subphylum Blastozoa SPRINKLE 1973
 Class Eocrinoidea JAEKEL 1918

Family Rhopalocystidae UBAGHS 1968

Discussion. – The Family Rhopalocystidae was erected based on the genus *Rhopalocystis* (type species: *Rhopalocystis destombesi* UBAGHS 1963). Valid species are *R. destombesi* UBAGHS 1963, *R. grandis* CHAUVEL 1971, *R. zagoraensis*

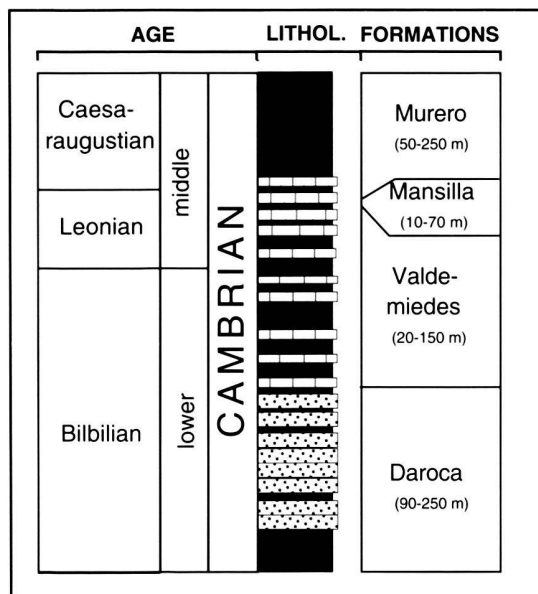


Fig. 2. Stratigraphical chart of the Lower-Middle Cambrian transition in the Iberian Chains.

CHAUVEL 1971, *R. fraga* CHAUVEL 1971, *R. havliceki* CHAUVEL 1978, *R. dehirensis* CHAUVEL & REGNAULT 1986, and *R. lehmani* CHAUVEL & REGNAULT 1986. These are all early to late Tremadocian in age (Chauvel & Regnault 1986, fig. 2) and were based on more or less articulated specimens preserved as internal and external moulds in shales and siltstones, which were studied through latex casts. As a result, the original diagnosis of the genus (after Ubaghs 1963, summarized in Ubaghs 1968, p. S481) lacks description of an inner cavity, information available herewith in silicified ossicles: 'Theca club-shaped, thick walled. Basal ossicle very thick, cup-shaped, infralaterals 4, pentagonal or hexagonal, largest plates of the theca; laterals 6, hexagonal or heptagonal; perradial series of 4 or 5 plates each (one radial and 2 or generally 3 supraradials); interradian areas typically resting on laterals, composed of 4 or 5 rows of interradian; CD interray larger than others, asymmetrically divided by a column of extra plates (anals). Peristome central, subpentagonal. Periproct with small anal pyramid. Ambulacra occupying a small stellate area around the oral pole, each one composed of 3 to 6 brachioliferous endothelial plates. Brachioles 20 to 30'. Ubaghs (1963) exhaustively listed the characters of the three parts of articulated eocrinoid skeletons: column, theca (with a single basal ossicle), and brachioles, and used them again in the family diagnosis (Ubaghs 1968). By contrast, only the basal part of the theca is available in the Iberian ossicles described below, even if other eocrinoid plates and ossicles (columnals?) are common in thin section (Pl. II). The plates described below are probably not *Rhopalocystis* although morphological differences are not significant, e.g. lower size, lack of other thick thecal plates from rest of the theca,

and age difference (early Cambrian vs Tremadocian). Nevertheless, the characters described in the new species share those of the basal ossicle with *Rhopalocystis* but none of the few eocrinoid genera known from the Cambrian. Furthermore, since the material collected is incomplete, it is referred to under open generic nomenclature. As a result, it is necessary to question the generic assignation of the new species described herein until more material permits to improve this uncertain assignation.

The nomenclature and orientation followed below is that used in the latest Treatise on Invertebrate Paleontology (Ubaghs 1968, p. S458) and in the original description of *Rhopalocystis destombesi* UBAGHS 1963. As the pieces described below are not elements from the oral part, but the basal circlet of a stemmed eocrinoid, the terms proximal and distal are used herein for features toward or away from the plane separating theca and stem (Fig. 3).

***Rhopalocystis? mesonesensis* species nov.**

Pl. I/1–13, Fig. 3-A

Etymology. – From Mesones, a village of the Iberian Chains (NE Spain), close to which the species was discovered.

Holotype. – MPZ 17070 (Pl. I/1–4)

Material. – About 25 specimens preserved as secondarily silicified, complete or broken ossicles. MPZ 17070–MPZ 17073.

Diagnosis. – Cylindrical to barrel-shaped, basal ossicle with hourglass-shaped axial canal, rounded proximal part with central depressed area; flat distal facet, ridge bounding the proximal opening of the axial canal from which 4 to 6 gutter-shaped branches diverge radially.

Description. – Cylindrical to barrel-shaped basal ossicle, circular in transverse section, sub-square to semi-elliptic in longitudinal section, with convex lateral sides, flat distal-facet, proximal part rounded with central depressed circular area; width (1.5 to 2.5 mm) equal or higher than height (0.75 to 2.5 mm); hourglass-shaped circular axial canal divided into two conical parts connected in the third to half way to proximal facet, minimal lumen about 0.25 mm in diameter, 0.5 to 0.75 mm at its distal opening (about 25% to 30% of the flat superior facet in diameter), 0.5 to 1.25 mm at its proximal opening (depressed rounded area); proximal part of the canal ringed by 2 or 3 peripheral 'septa' in some specimens; the distal opening of the canal is bounded by a ridge (up to 200 µm high and about 50 µm wide) from which 4 to 6 gutter-shaped branches (about 20 µm wide) diverge in radial symmetric pattern; inner cavity with triangular to semicircular outline in longitudinal section surrounding axial canal; wall about 200 to 300 µm thick in its lower part. A stereom-like microstructure can be outlined on the surface of some specimens. The pores of variable diameter

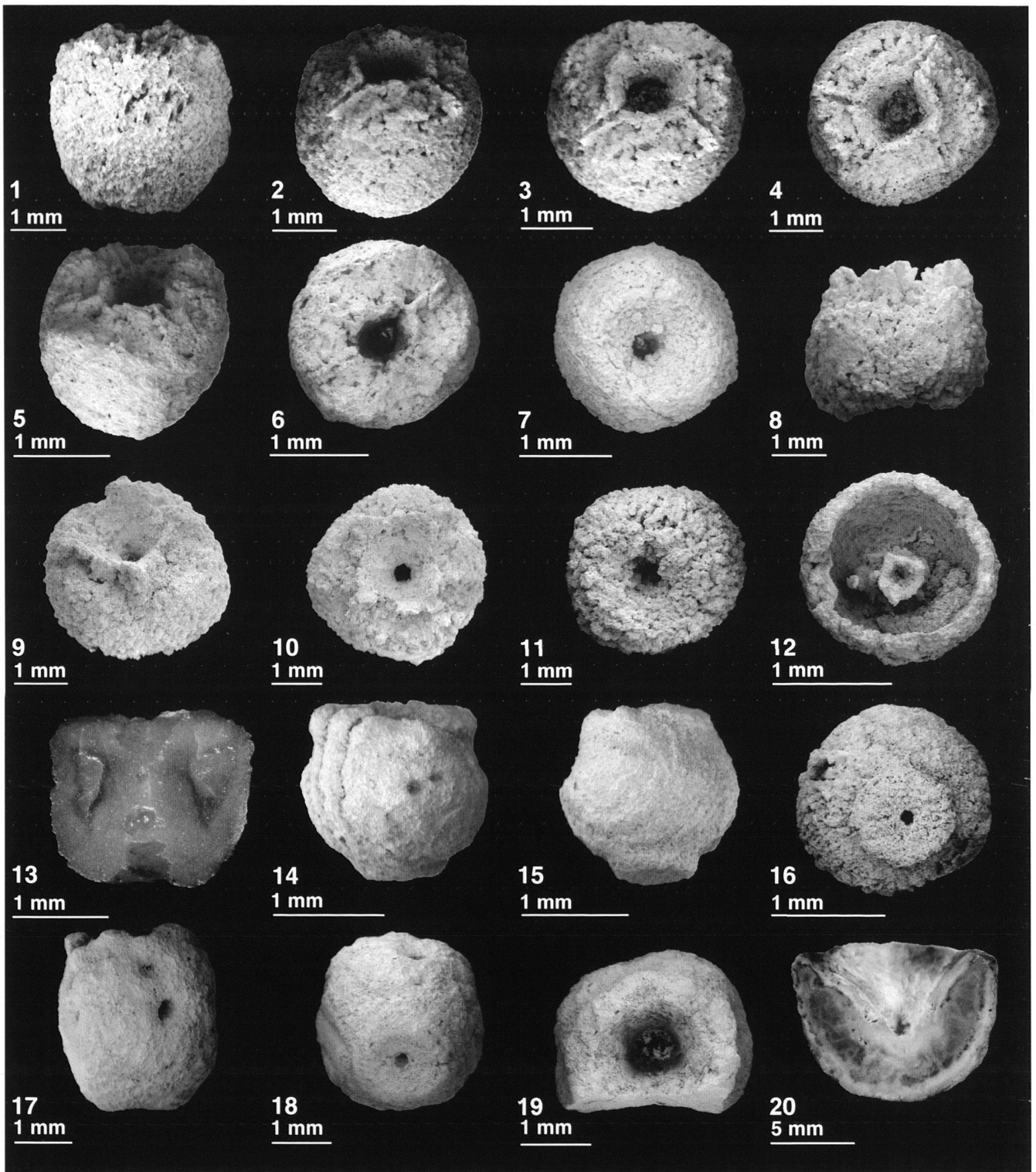


Plate I

- 1-14. *Rhopalocystis? mesonesensis*
 1-4. Holotype MPZ 17070: (1) lateral side, (2-3) oblique view of lateral side and superior facet, (4) distal facet.
 5-7. MPZ 17071: (5) oblique view of lateral side and superior facet, (6) distal facet, (7) proximal facet.
 8-11. MPZ 17072: (8) lateral side, (9) oblique view of lateral side and superior facet, (10) distal facet (11)
 12. MPZ 17073: transverse section showing the inner cavity.
 13. longitudinal section showing the outline of the inner cavity and the ridged inferior part of the hourglass-shaped axial canal.
 14-16. *Rhopalocystis? cf. mesonesensis*, MPZ 17074: (14) lateral side, (15) oblique view of lateral side and proximal facet, (16) proximal facet.
 17-19. Gen. et sp. indet. MPZ 17075: (17) lateral side, (18) oblique view of lateral side and proximal facet, (19) distal facet.
 20. *Cymbionites craticula* WHITEHOUSE 1941: longitudinal axial section showing the presence of an inner cavity secondarily filled with cement.

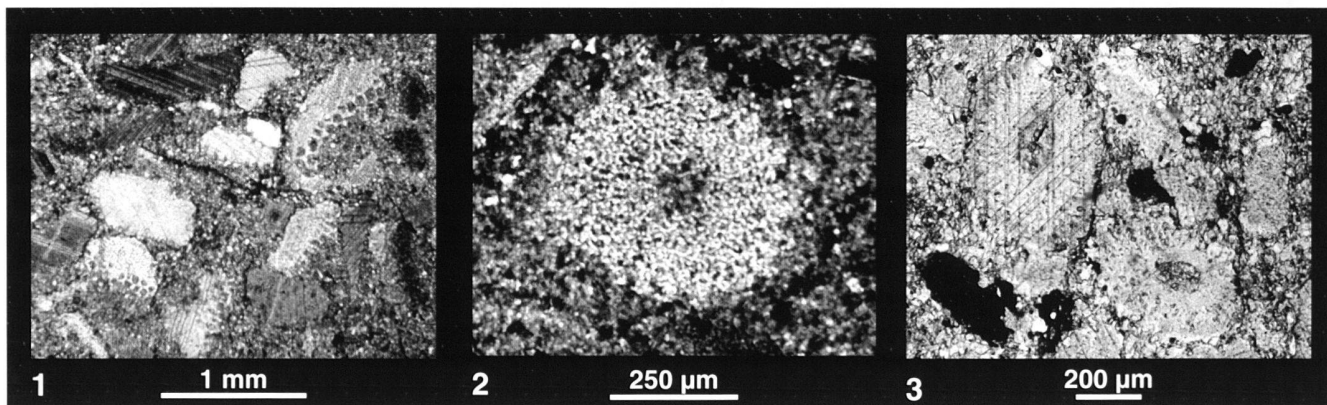


Plate II

1–3. Thin-sections of studied echinoderm packstones showing (1) eocrinoid plate sections, (2) characteristic transverse sections of columnals with original stereom, (3) or re-crystallized monocrystalline calcitic structure, still showing relics of stereom.

(10 to 40 µm) are not aligned, but the external surface shows oblique alignment of ridges. Possible plate sutures are not visible.

Discussion and comparison. – The general shape and radial symmetry of these specimens and the presence of a stereom-like framework are typical echinoderm features. Moreover, the porous microstructure on the external surface may be interpreted as stereom, even if insufficient information is available to undertake its complete description (Smith 1980).

Bilaterally symmetrical eocrinoids of the Family Rhipidocystidae JAEKEL 1901, such as *Batherocystis* BASSLER 1950 and *Petalocystites* SPRINKLE 1973 (Mid to Late Ordovician in age), have massive ossicles with axial canals in the proximal part of their theca and/or of their reduced stem. All of these skeletal elements and their axial canals are ovoid (flattened) in cross section, and none of them share the distal feature of *R.?* *mesonesensis*. The fused sets of basal marginals of *Petalocystites* and other unassigned rhipidocystid plates described by Sprinkle (1973) are composed of at least two and apparently three plates (2 big, 1 small; Sprinkle pers. com. 2004) three plates with apparent sutures on their flat side. They also differ from *R.?* *mesonesensis* by their general shape. Finally, the single columnal present in some specimens of *Petalocystites* does not have a distal facet, although others latex specimens have multiple columnals with facets at both ends (Sprinkle pers. com. 2004).

The Middle Cambrian enigmatic echinoderm *Cymbionites craticula* WHITEHOUSE 1941, is now considered to be a basal circling of a non-stemmed eocrinoid acting as a stabilising organ for the bottom-dwelling animal (Gislén 1947; Schmidt 1951; Smith 1982). Specimens of *Cymbionites* with an internal cavity visible in transverse section (Pl. I/20) are quite common. According to Whitehouse (1941), this cavity results from successive preservation processes differently affecting external and internal parts of the plates. Such an

interpretation (external silicification and internal carbonate cementation) is also possible for *R.?* *mesonesensis* even if the systematic observation of this character and the diagenetic pattern of the Valdemiedes Formation (Álvaro & Vennin 1998) make this point questionable. In addition, *Cymbionites* shares its general shape with the forms described herein. *Cymbionites* is usually composed of five (sometimes six) plates strongly fused by a secondary stereom overgrowth, so that neither articulating furrow nor sutures are visible on well-preserved specimens. These plates, which are ‘united laterally and apically’ (Whitehouse 1941, p. 9), define a deep and conical central cavity with a single upper opening (Smith 1982). Thus, *Cymbionites* diverge from *R.?* *mesonesensis* in the lack of an axial canal. Moreover, ‘the outer surface of the [*Cymbionites*] cup is completely smooth and shows no sign of sutures, attachment area, or stem’ (Smith 1982, p. 94); therefore, a close relationship of *R.?* *mesonesensis* with *Cymbionites* seems improbable.

Ubaghs (1963) noted a superficial similarity of *Cymbionites* with the eocrinoid species *Rhopalocystis destombesi*. As described before, a single basal plate characterizes this stemmed eocrinoid. The *Rhopalocystis* basal plate and the new Iberian forms have a similar vase-shape and share the presence of an axial canal. Moreover, the distal facet of *Rhopalocystis* is divided into 4 sub-equal areas by 4 ridges corresponding to the sutures between the 4 overlying infralateral plates. The rounded inferior facet is truncated by a depressed circular area, which is occupied by the proximal part of the columnal in articulated specimens.

The difference in preservation of the materials compared herein makes it impossible to compare the internal features, such as the presence of an internal cavity or several constitutive plates secondarily fused. Nevertheless, because of the similarity of the ossicles described herein with the basal of *Rhopalocystis* and the presence of distinctive plates of eocrinoids in thin section (Pl. II), the new species described

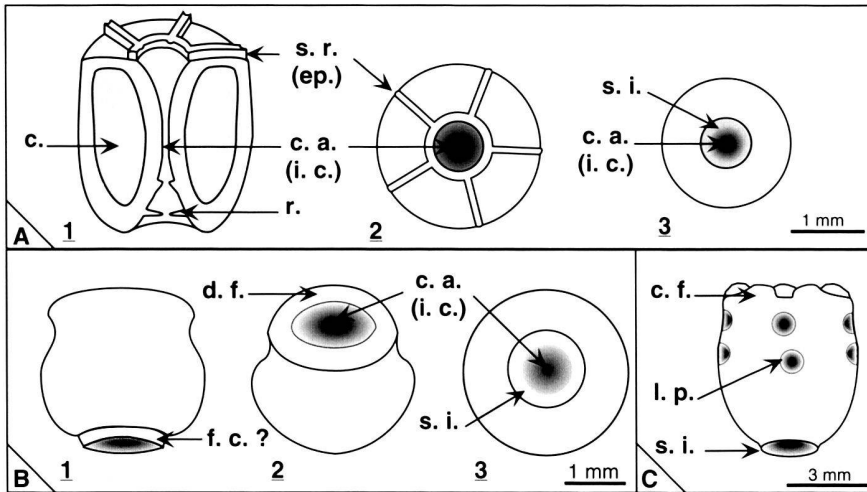


Fig. 3. Interpretative reconstruction of the basal ossicle of (A) *R.?* *mesonesensis* (1: longitudinal section; 2: distal facet; 3: proximal facet); (B) *R.?* cf. *mesonesensis* (1: lateral side; 2: oblique view of lateral side and superior facet; 3: proximal facet); (C) Gen. et sp. indet (lateral side). Abbreviations: c.: cavity; c.a.: canal axial defined by Ubaghs (1963) as internal cavity (i.c.) of the basal ossicle; c. f.: crenulated distal-facets; d. f.: distal facet of articulation between the basal ossicle and the infralateral plates; f. c.?: proximal part interpreted as the first columnal which might be fixed to or included into the basal ossicle of the theca; l. p.: lateral pores; r.: ridges visible in several specimen at the inner face of the axial canal; s. i.: proximal surface of insertion of the columnal to the theca; s. r.: sutural ridge corresponding to the attachment of the infralateral plates to the basal ossicle and to each other, the grooves at the top of which could be interpreted as epispire (? , ep.)

herein is considered to represent the one-piece basal circlet (less likely the entire theca) of a stemmed eocrinoid (see interpretative reconstruction, Fig. 3).

Rhopalocystis?* cf. *mesonesensis

Pl. I/14–16, Fig. 3-B

Material. – One specimen preserved as secondarily silicified ossicle. MPZ 17074.

Description. – Bell-shaped basal ossicle, circular in transverse section; lateral side composed of convex proximal half-part and constricted (concave) distal half-part; width (1.75 mm) higher than height (1.5 mm); distal facet flat, with large canal opening (about 0.65 mm, 50 % of the facet) bounded by narrow smooth surface (0.4 mm to 0.65 mm wide); axial canal narrowing progressively downward; small proximal opening (0.15 mm in diameter); proximal facet smooth and totally flat, occupied by a discoid part, about 1 mm in diameter (50 % of maximum diameter), 0.25 mm height (about 15 % of the total height). Two perforations (0.15 mm) line up obliquely on slightly eroded outer face. A stereom-like microstructure can be seen on the outer surface. Possible plate sutures are not observed.

Comparison. – *Rhopalocystis?* cf. *mesonesensis* differs from *R.?* *mesonesensis* in the bell shape, the lack of ridge on the distal facet, and the presence of a discoid part constituting the proximal facet. This part could be interpreted as the first columnal that might be fixed to or included into the basal ossicle of the theca. Chauvel & Regnault (1986) noted the presence of a constricted aboral-end in the “morphological suite” observed within the genus *Rhopalocystis* (*R. lehmani*; Chauvel & Regnault 1986 fig. 3/K). The scarcity of material does not permit me to undertake the study of its internal structure by sectioning.

Gen. et sp. indet

Pl. I/17–19, Fig. 3-C

Material. – One incomplete specimen preserved as secondarily silicified ossicle. MPZ 17075.

Description. – Barrel-shaped basal ossicle, sub-square in transverse section, sub-rectangular in longitudinal section, slightly convex lateral side with constricted (concave) distal part (25% of total length), width (2.85 mm) narrower than height (3.15 mm); distal facet with large canal-opening (about 1.5 mm in diameter, 60 % of the facet), bounded by relatively narrow crenulated surface (about 1 mm wide); the axial canal narrows progressively toward the proximal facet; proximal facet composed of discoid part (about 1.5 mm) faintly differentiated from remainder of ossicle, in which a large depressed circular-area (about 1 mm in diameter) bounds axial-canal opening (0.17 mm); two pores (about 0.3 mm in diameter) line up obliquely on each lateral side. A porous stereom-like microstructure is on the outer surface. Potential plate sutures were not observed.

Comparison. – This third taxon differs significantly from the two described previously in the presence of two pores on each side of the ossicle. This character could be interpreted as intra-plate thecal pores (cystoid) or sutural pores (eocrinoid). The absence of plate sutures, even secondary, makes the interpretation questionable. Nevertheless, the presence of pores demonstrates that this ossicle was most likely part of the perforate extraxial skeleton (following Extraxial-Axial Theory; David & Mooi 1996, 1999) and not a columnal (imperforate extraxial skeleton), even if some imperforated parts of the theca (e.g. stem) have rare pores (Sprinkle, pers. com. 2004). This specimen could be derived ontogenically from the specimen described as *R.?* cf. *mesonesensis* by resorption of the aboral discoid part and development of the pores. Neverthe-

less, the lack of better preserved material displaying a continuum between both specimens does not permit its assignation to the same taxon.

4. Hydrodynamic patterns and facies control

The late Bilbilian palaeogeographical framework of the Iberian platform consists of a peritidal, mixed belt passing seaward into discontinuous shelly limestones and further offshore (and in coeval tectonically induced depressions) into open-sea shale substrates. The late Bilbilian Iberian platform has the geometry of an intra-shelf ramp (Álvarez & Vennin 1996b, 1997) with maximum carbonate accumulation some distance from the shore. The limestone banks that have yielded the above-described echinoderms represent three storm deposits within the peritidal history of the Iberian platform. These are densely fossiliferous beds of bioclastic accumulations that functioned as long-term banks comprising many amalgamated, event-scale concentrations.

In the Valdemiedes Formation, eocrinoid ossicles are very abundant in wackestone and packstone textures (Pl. I/22), in which no complete or even partially articulated skeletons have been reported. The ossicles, observed in thin section, consist of highly porous calcite crystals, whose small pores are filled with calcite cement (in optical continuity), and rare epitaxial rings are recognized. The ossicles are neither micritized nor bearing micritic envelopes. Calcite cements are relatively poorly developed, as carbonate mud is dominant component of the facies, except intra-skeletal and shelter cementation (Álvarez & Vennin 1998). Intra-skeletal porosities are composed of sutural and stereom pores (Pl. II). Physical processes were important in the accumulation of echinoderm skeletal elements based on to the presence of erosive bases, low-angle laminae, and fining-upward, centimetre-scale sequences. These characters indicate sediment transport and rapid burial events, which were episodic because of the local abundance of mud-supported textures and partly articulated skeletons. During episodic storms, wave and landward oriented wind drift currents would be able to pile up skeletal debris and construct nearshore echinoderm sand pavements. The subsequent hydrodynamic echinoderm banks were formed through growth and destruction of echinoderm-sponge colonies by storm-wave action. The low- to middle-level, suspension-feeding, eocrinoid-sponge meadows developed on seaward parts of the platform below the fair-weather wave base but above the storm-wave base, where water movement was sufficient to provide a well-oxygenated water, a sufficient food supply, and probably relatively clear waters (Boucot & Carney 1981).

5. Discussion: palaeoecological implications

The Early Cambrian echinoderm-sponge meadow community was dominated by suspension feeders, such as echinoderms, sponges, but it also included calcite- and phosphate-shelled brachiopods and rare cancelloriids. High-energy disturbance of the seafloor caused extensive winnowing, providing a firm,

shelly or hard substrate necessary for the attachment of encrusting epibenthos, such as agglutinated foraminifera (psammosphaerids) and polychaeta tubes (serpulids; Clausen & Álvarez 2002). This community contained neither echinoderm holdfasts nor other encrusting organisms. Sprinkle & Guensburg (1995) and Guensburg & Sprinkle (2001) argued that hard attachment surfaces, at least shells in soft-sediment environments ('benthic islands', Taylor & Wilson 2002a), were required and constituted a limiting factor for the diversification of Cambrian echinoderms. Even if some Cambrian echinoderms were pre-adapted to attachment as episkeletozoans (Taylor & Wilson 2002b), it is remarkable that eocrinoids, such as the most widespread genus *Gogia* and the Laurentian eocrinoid *Lepidocystis* occurred attached only occasionally (Guensburg & Sprinkle 2001).

The arguments for the interpretation of a stem in the latest Early Cambrian species *R.?* *mesonesensis* are (i) the homology of its basal ossicle to that of the Tremadocian *Rhopalocystis*; (ii) the existence of a basal opening connected with an axial canal; and (iii) the presence of a proximal facet surrounding the axial canal opening, which indicates its articulation with columnals according to Sprinkle (1973). Thus, the new species described herein provides evidence for the existence of stemmed echinoderms with columns well differentiated from the cup in the latest Early Cambrian of the western Gondwana margin. The previous oldest occurrence of this character was from the early Middle Cambrian of Denmark (Berg-Madsen 1986). The absence of preserved anchorage structures and the presence of microbial matgrounds in the peritidal environment suggest that the latest Early Cambrian eocrinoids may have been mat-stickers (Seilacher 1999) with the distal, attenuated and recurved part of the stems inserted into soft substrates (Ubaghs 1968), and partly stabilized by microbial films. Evidence from the eocrinoid-sponge meadows in the Early Cambrian of the Iberian Chains thus agrees with the interpretation of Smith (1990), Smith & Jell (1990), Dornbos & Bottjer (2000, 2001), and Lefebvre & Fatka (2003) on the role of microbial mats in firming Lower to Middle Cambrian substrates.

The Early Cambrian eocrinoid-sponge meadows belong to shallow, mixed-substrate nonreefal communities. The higher sessile tier was occupied by stemmed eocrinoids (Burzin et al. 2001 table 10.1), which were simply partially inserted into the firm substrate. Their differentiated column allowed them to elevate above the bottom, competing with low to high filters (foraminifers, brachiopods, sponges; Burzin et al. 2001) and less frequent cancelloriids, whose feeding behaviour is questionable, although organisms in different tiers will not compete directly with one another. This community depended on the presence of microbial films to stabilise the substrate, which was permitted by the scarcity of grazers such as helcionelloid molluscs, the latter occurring only in the lowermost Middle Cambrian of the studied outcrops. The increase in bioturbation and mat-ground scratchers across the Early-Middle Cambrian transition led to the progressive disappearance of the microbial community ('agroneomic revolution', Seilacher &

Pflüger 1994). In the Iberian Chains, the latest Early to earliest Middle Cambrian had the widespread development of echinoderm-sponge meadows, with a progressively decreasing rate of carbonate productivity in shallow-water environments, whereas the transgressive character of the late Leonian (early Middle Cambrian) is consistent with the appearance of cinctans, which were epi-benthic, unattached suspension feeders dominating deeper, low-energy, distal-muddy environments (Friedrich 1993; Liñán et al. 1996).

The nonreefal echinoderm-sponge meadows represent an intermediate benthic community between microbial-dominated earliest Cambrian ecosystems and the younger post-Cambrian, soft-bottom, diversified, echinoderm communities occupying the high-paleolatitude seas of the northwestern Gondwana margin (Lefebvre & Fatka 2003), which is well illustrated in the earliest Tremadocian of the Iberian Peninsula, Sardinia, and Germany by the 'bloom' of the anchor like grapple *Oryctoconus* COLCHEN & UBAGHS 1969 (Álvarez & Colchen 2002). On the northwestern Gondwana margin, the blastozoan clade (following Extraxial-Axial Theory, David & Mooi 1996; David et al. 2000), which includes the eocrinoids, followed more significant radiation during the Early Cambrian than usually proposed in previous works: from stalks developed from the aboral ends of the calyx into an irregularly plated outgrowth with a large central lumen continuous with the thecal cavity (*Gogia*; Ubags 1975) to well-differentiated stems composed of holomeric columnals. When compared to the different known stratigraphic ranges, the cladograms of major groups of echinoderms (David & Mooi, 1999) suggest that the evolution of early Palaeozoic echinoderms was continuous and exponential on the Gondwana margins from the earliest Cambrian times. However, many important aspects of this Cambrian history were, unfortunately, affected by taphonomic processes (Smith 1988). Most primitive echinoderms had a membrane-embedded skeleton that rapidly disarticulated after death into individual plates. Even though the systematic assignment of the isolated plates reported herein within one eocrinoid taxon remains debatable, this work suggests that their study is a new step to improve the knowledge of the Early Cambrian echinoderm diversity and palaeoecology.

Acknowledgements

The author thanks Peter Jell from the Queensland Museum for loaning material of *Cymbionites*, M. Caridroit, J.M. Degardin, G. Ponchel and P. Recourt for technical help and comments in learning scanning electron microscopy techniques, P. Dorn for successive sections of specimens, J. J. Álvarez, D. Vizcaíno, and particularly B. Lefebvre for critical remarks, and W. I. Ausich and J. Sprinkle for their constructive revision of the manuscript. The fossil-bearing limestones were sampled in 1991 by J.J. Álvarez.

REFERENCES

ÁLVARO, J. J. 1994: El Cámbrico Inferior terminal y Medio de las Cadenas Ibéricas. Bioestratigrafía y Paleogeografía. Doctoral thesis, University of Zaragoza, 1–250 [unpublished].

- ÁLVARO, J. J. & COLCHEN, M. 2002: Earliest Ordovician pelmatozoan holdfasts from western Europe: the *Oryctoconus* problem revisited. *Eclogae geol. Helv.* 95, 451–459.
- ÁLVARO, J. J. & VENNIN, E. 1996a: Spicules d'éponges et Chancelloriidae cambriens des Chaînes Ibériques, NE Espagne. *Rev. Micropal.* 39, 293–304.
- 1996b: Tectonic control on Cambrian sedimentation in south-western Europe. *Eclogae. geol. Helvetiae* 89, 935–948.
- 1997: Episodic development of Cambrian eocrinoid-sponge meadows in the Iberian Chains (NE Spain). *Facies* 37, 49–64.
- 1998: Petrografía y diagénesis de las calizas cámbricas del Grupo Mesones (Cadenas Ibéricas, NE de España). *Bol. R. Soc. Esp. Hist. Nat. (Sec. Geol.)* 93, 33–53.
- ÁLVARO, J. J., GOZALO, R., LIÑÁN, E. & SDZUY, K. 1993: The palaeogeography of northern Iberia at the Lower-Middle Cambrian transition. *Bull. Soc. géol. France* 164, 843–850.
- ÁLVARO, J. J., ROUCHY, J. M., BECHSTÄDT, T., BOUCOT, A., BOYER, F., DEBRENNE, F., MORENO-EIRIS, E. & VENNIN, E. 2000: Evaporitic constraints on the southward drifting of the western Gondwana margin during Early Cambrian times. *Palaeogeogr., Palaeoclimat., Palaeoecol.* 16, 105–122.
- BASSLER, R. S. 1950: New genera of American Middle Ordovician "Cystoidea". *J. Washington Acad. Sci.* 40, 273–277.
- BERG-MADSEN, V. 1986: Middle Cambrian cystoid (*sensu lato*) stem columnals from Bornholm, Denmark. *Lethaia* 19, 67–80.
- BOUCOT, A. J. & CARNEY, R. S. 1981: Principles of benthic Marine Paleocology. Academic Press, New York.
- BURZIN, M. B., DEBRENNE, F., & ZHURAVLEV, A. Y. 2001: Evolution of shallow-water level-bottom communities. In: *The Ecology of the Cambrian Radiation* (Ed. by ZHURAVLEV, A. Y. & RIDING, R.). Columbia University Press, New York, 217–237.
- CHAUVÉL, J. 1971: *Rhopalocystis* UBAGHS: un échinoderme Eocrinoïde du Trémadocien de l'Anti-Atlas marocain. *Mémoires du B.R.G.M.* 73 (Colloque Ordov-Silur. Brest), 43–46.
- 1978: Compléments sur les échinodermes du Paléozoïque marocain (Diploporites, Eocrinoïdes, Edrioastroïdes). *Notes du Service Géologique du Maroc*, 39, 27–78.
- CHAUVÉL, J. & REGNAULT, S. 1986: Variabilité du Genre *Rhopalocystis* UBAGHS, Eocrinoïde du Trémadocien de l'Anti-Atlas marocain. *Geobios* 19, 863–870.
- CLAUSEN, S. & ÁLVARO, J. J. 2002: Encrusting strategies in a Cambrian nonreefal epibenthic community. *Bull. Soc. géol. France* 173, 553–559.
- COLCHEN, M. & UBAGHS, G. P. 1969: Sur des restes d'Echinodermes du Cambro-Ordovicien de la sierra de la Demanda. *Bull. Soc. géol. France* 11, 649–654.
- DAVID, B. & MOOI, R. 1996: Embryology supports a new theory of skeletal homologies for the phylum Echinodermata. *C. R. Acad. Sci. Paris* 319, 577–584.
- 1999: Comprendre les échinodermes: la contribution du modèle extraxial-axial. *Bull. Soc. géol. France* 170, 91–101.
- DAVID, B., LEFEBVRE, B., MOOI, R., PARSLEY, R. 2000: Are homalozoans echinoderms? An answer from the extraxial-axial theory. *Paleobiology* 26, 529–555.
- DORNBOSS, S. Q. & BOTJER, D. J. 2000: Evolutionary paleoecology of the earliest echinoderms: helicoplacoids and the Cambrian substrate revolution. *Geology* 28, 839–842.
- 2001: Taphonomy and environmental distribution of helicoplacoid echinoderms. *Palaios* 16, 197–204.
- FRIEDRICH, W. P. 1993: Systematik und Funktionsmorphologie mittelkambrischer Cincta (Carpoidea, Echinodermata). *Beringeria* 7, 3–190.
- GISLÉN, T. 1947: On the Haplozoa and the interpretation of *Peridionites*. *Zool. Bidrag. Uppsala* 25, 402–408.
- GUENSBURG, T. E. & SPRINKLE, J. 2001: Ecologic radiation of Cambro-Ordovician echinoderms. In: *The Ecology of the Cambrian Radiation* (Ed. by ZHURAVLEV, A. Y. & RIDING, R.). Columbia University Press, New York, 428–444.
- JAEKEL, O. 1901: Über Carpoideen, eine neue Klasse von Pelmatozoen. *Deutsch. Geol. Gesell., Zeitschr.*, for year 1900, 666–677.
- 1918: Phylogenie und System der Pelmatozoen. *Paläont. Z.* 3, 1–128.

- KIDWELL, S. M. 1991: Taphonomic feedback (live/dead interactions) in the genesis of bioclastic beds: keys to reconstructing sedimentary dynamics. In: *Cycles and Events in Stratigraphy* (Ed. by EINSELE, G., RICKEN, W. & SEILACHER, A.). Springer-Verlag, Berlin, 268–282.
- KLEIN, J. T. 1734: *Naturalis dispositio Echinodermatum. Accessit lucubratiuncula de aculeis Echinorum marinorum, cum spicilegio de Belemnitis*. Gedani, Schreiber.
- LEFEBVRE, B. & FATKA, O. 2003: Palaeogeographical and palaeoecological aspects of the Cambro-Ordovician radiation of echinoderms in Gondwana Africa and peri-Gondwana Europe. *Palaeogeogr., Palaeoclimat., Palaeoecol.* 195, 73–97.
- LIÑAN, E., PEREJÓN, A. & SDZUY, K. 1993: The Lower-Middle Cambrian stages and stratotypes from the Iberian Peninsula: a revision. *Geological Magazine* 130, 817–833.
- LIÑAN, E., VILLAS, E., GÁMEZ VINTANED, J. A., ÁLVARO, J. J., GOZALO, R., PALACIOS, T. & SDZUY, K. 1996: Síntesis paleontológica del Cámbrico y Ordovicio del Sistema Ibérico (Cadenas Ibéricas y Cadenas Hespéricas). *Rev. Esp. Paleont., no. extr.*, 21–32.
- SCHMIDT, H. 1951: Whitehouse's Ur-Echinodermen aus der Cambrium Australiens. *Paläont. Z.* 24, 142–145.
- SEILACHER, A. 1999: Biomat-related lifestyles in the Precambrian. *Palaaios* 14, 86–93.
- SEILACHER, A. & PFLÜGER, F. 1994: From biomats to benthic agriculture: a biohistoric revolution. In: *Biostabilization of Sediments* (Ed. by KRUMBEN, W. E., PATERSON, D. M. & STAL, L. J.). Bibliotheks und Informations system der Carl von Ossietzky, Univ. Oldenburg, 97–105.
- SMITH, A. B. 1980: Stereom microstructure of the echinoid test. *Special Papers in Palaeontology* 25: 1–81.
- 1982: The affinities of the Middle Cambrian Haplozoa (Echinodermata). *Alcheringa* 6, 93–99.
- 1988: Patterns of diversification and extinction in Early Palaeozoic echinoderms. *Palaeontology* 31, 799–828.
- 1990: Evolutionary diversification of echinoderms during the early Palaeozoic. In: *Major Evolutionary Radiations* (Ed. by TAYLOR, P. D. & LARWOOD, G. P.). Clarendon Press, Oxford, 265–286.
- SMITH, A. B., JELL, P. A. 1990: Cambrian edrioasteroids from Australia and the origin of starfishes. *Mem. Queensland Mus.* 28, 715–778.
- SPRINKLE, J. 1973: Morphology and evolution of blastozoan echinoderms. *Mus. Compar. Zool. Harvard Univ., Spec. Publ.*, 1–283.
- SPRINKLE, J. & GUENSBURG, T. E. 1995: Origin of echinoderms in the Paleozoic evolutionary fauna: the role of substrates. *Palaaios* 10, 437–453.
- TAYLOR, P. D. & WILSON, M. A. 2002a: Palaeoecology and evolution of marine hard substrate communities. *Earth Sci. Rev.* 1274, 1–103.
- 2002b: A new terminology for marine organisms inhabiting hard substrates. *Palaaios* 17, 522–525.
- UBAGHS, G. 1963: *Rhopalocystis destombesi* n. g. n. sp. Eocrinoïde de l'Ordovicien inférieur (Trémadocien supérieur) du Sud marocain. *Notes du Service Géologique du Maroc* 23, 25–45.
- 1968: Eocrinoïdea. In: *Treatise on Invertebrate Paleontology Pt. 5, Echinodermata 1(2)* (Ed. by MOORE, R. C.). Geol. Soc. America, New York, and Univ. Kansas Press, Lawrence, S455–495.
- 1975: Early Palaeozoic echinoderms. *Ann. Rev. Earth Planet. Sci.* 3, 89–98.
- WHITEHOUSE, F. W. 1941: The Cambrian faunas of North-Eastern Australia, part 4: Early Cambrian echinoderms similar to the larval stages of recent forms. *Mem. Queensland Mus.* 12, 1–28.

Manuscript received November 1, 2003

Revision accepted August 20, 2004

