Pelmatozoan echinoderms from the Cambrian–Ordovician transition of the Iberian Chains (NE Spain): early diversification of anchoring strategies

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ABSTRACT

Three new echinoderm taxa representative of biodiversification across the Cambrian-Ordovician transition in the Iberian Chains are described in this paper. A new type of pelmatozoan columnal is described (in open nomenclature) from the Furongian Valtorres Formation. The primitive rhombiferan, *Macrocystella* aff. *pauli* is described based on disarticulated thecal plates and stem columnals, from the Tremadocian Santed Formation; it is a free-living organism with a flexible stem lying on a clay-rich seafloor allowing the theca to be held upright. A complete revision of the pelmatozoan *Oryctoconus* (characterized by its holdfast and nodal and internodal columnals) is made based on the description of the species *O. lobatus* and *O. josopaiti* n. sp. found in the Early Ordovician Valconchán and Santed Formations. The number and degree of development of anterior appendages in the *Oryctoconus* holdfasts (from absent to lobate and long spinose extensions), the length/diameter-ratio of the basal shields (ranging from amphora- to bowl-like morphologies), and the size (from slender millimetre-sized to robust centimetre-sized holdfats) are considered as the main anchoring strategies controlled by substrate consistency, grain size (ranging from clayey to sandy), and turbulence. The occurrence of nodal columnals mimicking the shape and size of holdfasts may represent distinct adaptations to soft substrates under high pulses of sedimentation rates. As a result, the morphological modifications of the reported holdfasts and nodal columnals are not necessarily phylogenetically related, but primarily controlled by substrate palaeoecological features.

RESUME

Ce travail présente la description de trois nouveaux taxons d'échinodermes pélmatozoaïres représentatifs de la biodiversification associée à la transition cambro-ordovicienne des chaînes Ibériques. Un nouveau type de columnales, en provenance de la Formation furongienne de Valtorres, est proposée en nomenclature ouverte. Le rhombifère primitif *Macrocystella* aff. *pauli*, de la Formation trémadocienne de Santed est décrit á partir des plaques de sa thèque et des columnales. Il représente un taxon dont la partie proximale de sa tige, qui s'étendait sur le substrat, était flexible et permettait d'élever la thèque. Une révision complète du genre *Oryctoconus*, représenté par un crampon et des columnales nodales et internodales, est réalisée à partir des espèces *O. lobatus* et *O. josopaiti* n. sp. des formations de l'Ordovicien inférieur de Valconchán et de Santed. L'hydrodynamisme, ainsi que la consistance et la granulométrie du substrat (variant d'argileux à sableux) sont considérés comme les principaux facteurs contrôlant le nombre et la taille des appendices antérieurs (depuis absents à lobés et épineux), la relation longueur/diamètre ainsi que la taille du crampon (depuis millimétriques et élancés à centimétriques et robustes). L'apparition de columnales nodales similaires en taille et forme aux crampons peut être interprétée comme une adaptation aux substrats mous qui subissent des taux de sédimentation significatifs. Par conséquent, les modifications morphologiques au sein des crampons et des columnales nodales décrits ne sont pas nécessairement d'origine phylogénique, mais principalement contrôlées par des facteurs paléoécologiques en relation avec le type de substrat.

Introduction

Echinoderms underwent a major radiation across the Cambrian-Ordovician transition leading to the highest-class diversity achieved by the phylum. Several classes, such as crinoids, rhombiferans and edrioasteroids, became common on Early Ordovician siliciclastic and carbonate platforms (Sprinkle & Guensburg 1995). Although these taxa can be found wholly articulated in clay-rich substrates, storms and volcanic events appear to have been the primary cause for the dominant preservation of both complete echinoderms and shell concentrations rich in their disarticulated ossicles.

In the western Mediterranean region (NW Gondwana), Tremadocian strata are characterized by the occurrence of a diverse and abundant fossil record of echinoderms that dominantly colonized soft substrates (for a synthesis see Lefebvre & Fatka 2003). This contrasts with the extremely poor record of Furongian (= late Cambrian) echinoderms, represented only by a single diversified fauna from the Montagne Noire (Ubaghs 1998), composed of edrioasteroids, stylophorans, and *Macrocystella*-like rhombiferan blastozoans, such as the endemic genera *Barroubiocystis* and *Velieuxicystis*.

The Early Ordovician of NW Gondwana is characterized by the apparition and diversification of different echinoderm

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groups. Appearance of new taxa includes diploporans, solutes, asterozoans and crinoids (Lefebvre & Fatka 2003). Edrioasteriods (Chauvel 1978; Ubaghs 1983; Vizcaïno & Lefebvre 1999; Vizcaïno et al. 2001) and blastozoans, including rhombiferans and eocrinoids (Chauvel 1978; Ubaghs 1983; Chauvel & Régnault 1986; Ubaghs 1994) and stylophorans (Lefebvre & Fatka, 2003), became more diversified. The eocrinoids dominated throughout the Middle Cambrian and Furongian forming chancelloriid-echinoderm-sponge meadows on carbonate and clay-rich shoreface and offshore substrates (Álvaro & Vennin 1997; Clausen 2004).

Echinoderm ossicles recently collected in the Iberian Chains (NE Spain) are described below. They are representative of the echinoderm biodiversification achieved across the Cambrian-Ordovician transition, and belong to the genera *Macrocystella* and *Oryctoconus*. *Macrocystella* is considered as an epibenthic, unattached, suspension-feeder rhombiferan and has a widespread palaeobiogeographic distribution. It has been reported from ?Furongian to Early Caradoc (Sandbian) strata of eastern Avalonia (England and Wales; Paul 1968, 1984), southwestern Europe (Montagne Noire, Bavaria, Bohemia, and Spain; Sdzuy 1955; Hammann, in Josopait 1972; Ubaghs 1983; Smith 1988; Gil Cid et al. 1996; Prokop & Petr 1999; Sdzuy et al. 2001), NW Africa (Morocco; Chauvel 1969), South and Middle America (Argentina, Bolivia, and Mexico; Robison & Pantoja-Alor 1968; Aceñolaza 1999), Australia (Tasmania, New Zealand; Jell et al. 1985), and Middle and East Asia (Salair, Korea; Kobayashi 1935). The occurrence of Early Ordovician disarticulated holdfasts (more abundant and diversified during the Arenig, e.g. *Balantiocystis*) was initiated in Early Tremadocian sandstone shoals and clay-rich substrates of Spain (Demanda Sierra, Iberian Chains and Cantabrian Mountains; Colchen & Ubaghs 1969; Josopait 1972; Álvaro & Colchen 2002; Seilacher & Macclintock 2005), Sardinia (Loi et al. 1995) and probably the Kistedal Formation of Finmark (Norway) (Erdtmann et al. 1984). There, the amphora-like *Oryctonocus* was previously interpreted as a holdfast joined to the distal end of a stalked pelmatozoan of uncertain affinity (Álvaro & Colchen 2002; Seilacher & MacClintock 2005).

The aim of this paper is to describe and illustrate the new pelmatozoan ossicles found in three new fossiliferous strata belonging to the Furongian Valtorres and the Early Ordovician Santed Formations of the Iberian Chains, NE Spain. Many of the studied ossicles are pelmatozoan holdfasts with a broad morphological variability that is interpreted in terms of substrate adaptation, a key factor to explain the ability of pelmatozoans to colonize new ecological niches.

Geological setting and stratigraphy

The Iberian Chains are located in the NE of the Iberian Peninsula (Fig. 1), and contain a thick Early Palaeozoic sedimentary succession deposited on a platform situated on the northwestern margin of Gondwana. There, the Cambrian-Ordovician transition consists of siliciclastic strata that show successive alternations of shale- and sandstone-dominated sedimentary units (Álvaro et al. 2007). The echinoderm remains described below were found in the Valtorres (Acón Group) and Santed (Ateca Group) Formations, two shale-dominated units, *ca.* 300 m and
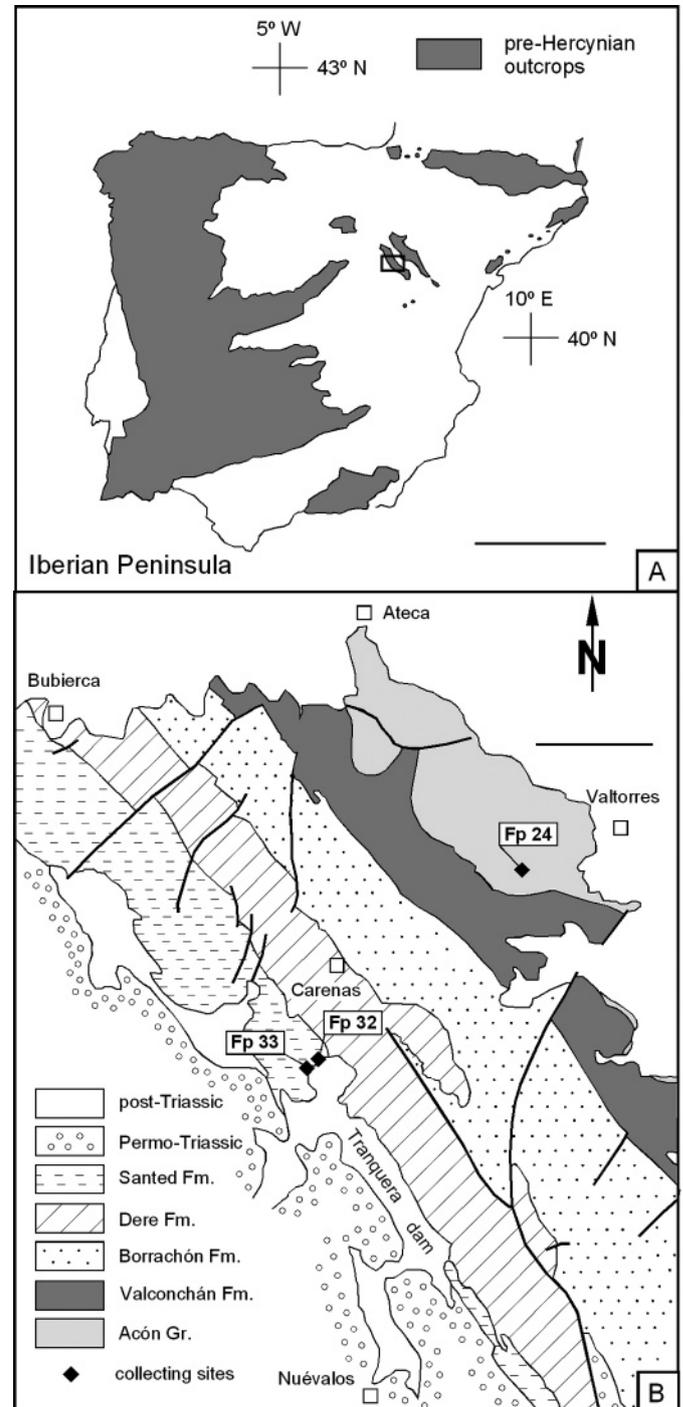
Fig. 1. Geological sketch of the pre-Hercynian outcrops of the Iberian Peninsula and setting of the study area in the Iberian Chains; modified from Josopait (1972). Scale bar in a is 200 km, and in b 2 km.

200–950 m thick, respectively, bracketed between sandstone-dominated formations (Wolf 1980; Álvaro 1995; Fig. 2).

Trilobites of the Valtorres Formation and the lowermost part of the overlying Valconchán Formation (Wolf 1980; Shergold & Sdzuy 1991; Álvaro 1995) form a Furongian association, determined for the first time by Sdzuy (in Josopait 1972), and subsequently described by Shergold & Sdzuy (1991). This faunal association includes agnostid, Aphelaspidine aff. *Aphelaspis rara* (ORŁOWSKI) *sensu* Żylińska (2001), *Elegantaspis* cf. *beta* IVSHIN 1962, *Parachangshania*? sp., *Pseudagnostus* sp., *Punctaspis*? *schmitzii* SHERGOLD & SDZUY 1991, solenopleuroidean, and *Valtorresia volkeri* SHERGOLD & SDZUY 1991 trilobites, which are associated with the brachiopods *Billingsella jalonensis* HAVLÍČEK & JOSOPAIT 1972, *B*. cf. *jalonensis*, and *B*. *perarea* HAVLÍČEK & JOSOPAIT 1972. According to Shergold & Sdzuy (1991), this fauna can be considered as probably early Franconian in age (Steptoean, according to the North American chronostratigraphic chart; Palmer 1998), and approximately equivalent to the *Parabolina spinulosa* Zone (Baltic region).

The Tremadocian-Arenig (Floian) boundary interval has been currently placed within the Santed Formation. Josopait (1970, 1972) and Hammann (in Wolf 1980: p. 128) reported the youngest Tremadocian and oldest Arenig trilobites of the Santed Formation in the vicinity of the Tranquera dam (Fig. 1). The uppermost Tremadocian fossil assemblage (a tuffitic bed named "*Fundpunkt* 32" – Fp 32 – by Josopait 1972; for a microfacies and geochemical analysis of the tuffite, see Álvaro et al. 2008) has yielded, among others, the trilobites *Euloma* cf. *filacovi* BERGERON 1889 and *Prionocheilus* cf. *languedocensis* (COURTESSOLE & PILLET 1975) whereas the lowermost Arenig assemblage (Josopait's Fp 33) contains *Prionocheilus* cf. *languedocensis* and *Megitaspis* (*Ekeraspis*) cf. *filacovi* MUNIER-CHALMAS & BERGERON, in Bergeron 1888. Hammann (in Wolf 1980) correlated biostratigraphically both levels with the 'faunizones' E and F of the southern Montagne Noire (Capéra et al. 1978; Vizcaïno et al. 2001). However, a recent re-evaluation of the biostratigraphic potential of both 'faunizones' has led Álvaro & Vizcaïno (2002) and Vizcaïno & Álvaro (2003) to propose them as two different fossil assemblages (not yet found in a same section of the Montagne Noire) of the *Euloma filacovi* Zone, which would include the Tremadocian-Floian boundary interval.

The echinoderms studied in this paper were sampled in three strata: (i) a carbonate nodule, up to 15 cm thick, embedded in the shale-dominated Valtorres Formation, and co-occurring with the aforementioned Furongian trilobite assemblage (Shergold & Sdzuy 1991); (ii) the aforementioned latest Tremadocian tuffitic bed (Fp32); the latter, up to 15 cm thick, has yielded a diverse fossil assemblage composed of disarticulated and partly fragmented trilobites, calcite- and phosphate-walled brachiopods, and echinoderm debris; and (iii) the ?earliest Floian shale bed Fp33, up to 40 cm thick.

Information of the latitude and longitude coordinates of these fossiliferous beds is regulated by the Law for the Protection of Palaeontological Sites in Aragón (Spain), and is available by request in the Museum of Palaeontology of Zaragoza
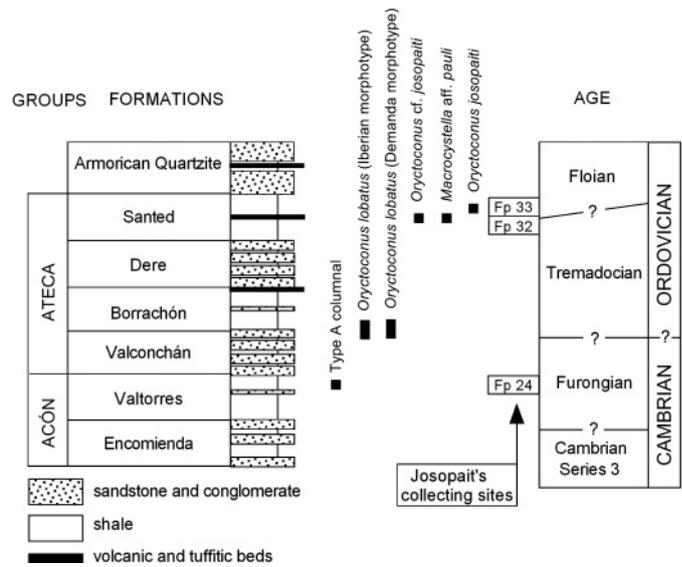
Fig. 2. Stratigraphic units of the Early Ordovician strata in the Iberian Chains showing the fossiliferous sites reported in the text.

University. The material described and illustrated in this paper is housed in the Museum of Palaeontology of the Zaragoza University-Gobierno de Aragón (institutional abbreviation MPZ).

Systematic palaeontology

The description of *Macrocystella* is based on Paul's (1968) morphological terminology, and that of *Oryctoconus* on Brett (1981), Álvaro & Colchen (2002), and Seilacher & Mac-Clintock's (2005) nomenclature. As in the crinozoans, the terms proximal and distal are in reference to the planar surface that separates the calyx from the stem. Sampling, originally made by Josopait (1972) and Hammann (in Wolf 1980), was completed by the authors.

Class Rhombifera ZITTEL 1879

Superfamily: Glyptocystitida BATHER 1899
Family: Macrocystellidae BATHER 1899 (emend. JAEKEL 1918)
Genus: Macrocystella CALLAWAY 1877
Type species: Macrocystella mariae CALLAWAY 1877 from the *Shumardia pusilla* Zone of the Shineton Shales, upper Tremadocian of Shropshire, England.
Synonyms: Cystidea BARRANDE 1887, *Mimocystites* BARRANDE 1887, and *Mimocystis* CARPENTER 1891

Remarks: The assignation of *Macrocystella* to a class has been problematic; in fact, it has been assigned to the eocrinoids, the rhombiferan cystoids, and even as a link between them (Paul 1968; Sprinkle 1973). We follow Paul's (1968) proposal and include *Macrocystella* within the rhombiferan cystoids, an assignment subsequently followed by Sumrall & Sprinkle (1995),

Gil Cid et al. (1996), Ubaghs (1998), Aceñolaza (1999), and Sdzuy et al. (2001). Paul (1968) considered that the absence of pectinirhombs in the macrocystellids was a primitive character, and respiration would have taken place through the thecal plates and not using specialized thecal respiratory structures, such as epispires, pectinirhombs or diplopores.

Macrocystella aff. *pauli* GIL CID et al. 1996 (Figs. 3, 4)

1970   *Macrocystella* sp. – JOSOPAIT, p. 128.
1972   *Macrocystella* sp. – HAMMANN, in JOSOPAIT, p. 54.
1980   *Macrocystella* sp. – WOLF, p. 129.
2001   *Macrocystella* sp. – HAMMANN & SDZUY, in SDZUY et al., p. 234.
2002   *Macrocystella* sp. – ARROYO & LARA, p. 100.
2003   *Macrocystella.* – LEFEBVRE & FATKA, p. 88.

Locality: NW corner of the Tranquera dam, in the eastern side of the Carenas-Nuévalos road (Fig. 1).
Stratigraphic position: Tuffitic bed reported as collecting site Fp32 by Josopait (1972), Santed Formation, Tremadocian-Floian transition.
Material: About thirty-three disarticulated plates, six are thecal plates (MPZ2007/712–717), three columnals (MPZ2007/719–721), and a partial stem (bearing up to four articulated columnals) belonging to the distal part of the proximal stem (MPZ2007/718), preserved as natural external and internal moulds. Additional fragmentary material is MPZ2007/722–744.
Description: The reconstruction of the theca is based on disarticulated isolated plates. The thecal plates are polygonal (roughly hexagonal) in outline, ranging in size from 2.5 to 6.5 mm across (Figs. 3c–e; Figs. 4a–d). They bear a central umbo and several prominent radial ridges, which can be observed externally (as ridges) and internally (as folds). Folds never extend to the central part of the plate. Their internal and external surfaces are smooth, lacking any trace of pore openings or granules. The plates are thin-walled and commonly broken at their margins; they bear 6 prominent, ridge-like, radiating primary ridges, which begin at the margin and can reach or not the central umbo (Figs. 3c–e). The ridges narrow centripetally and show subtriangular longitudinal and transverse sections, with their

highest peaks at the plate margins. The transverse section of the primary ridges also displays a centripetal modification of their peaks, which grade from rounded to acute. Some further (commonly one, but rarely two) auxiliary ridges can appear intercalated between the primary ones, but they never reach the central umbo; the transverse section of their peaks is acute, and do not reach the height of the primary ridges. In these plates, traces of pectinirhombs are absent.

The proximal stem is disarticulated from the theca. The columnals of the proximal stem are preserved as both articulated and disarticulated (Fig. 3a & b; Figs. 4e–g). They are circular in outline, and have a large lumen. Their external diameter is 4 mm. They show both external (Ef) and internal (If) flanges, the widths of which are 500 μm and 250 μm, respectively. The fulcra are visible in just two ossicles, where they show small notches marking the articulation points (Figs. 3a & b; Fig. 4e). A fragment of the distal part of the proximal stem (Fig. 4g) is cylindrical; it shows the typical construction of a *Macrocystella* stem with outer proximals alternating with inner proximals, the latter abutting against the inner flanges of the former (*sensu* Paul 1968: p. 584). The lumen is large, raging from 0.8 mm (Fig. 4g) to 2.6 mm (Fig. 4f) in diameter. The external surface of the columnals (in transverse view) is smooth, lacking spines. The external borders of the outer proximal columnals are flanged (Fig. 4g). The distal stem and the brachioles are unknown.
Remarks: According to Paul (1968), Chauvel (1969) and Sdzuy et al. (2001), the key diagnostic features to identify the species of *Macrocystella*, on the basis of disarticulated material, are the shape of proximal columnals and the number and arrangement of (primary and auxiliary) ridges on thecal plates. Paul (1968) pointed out that the outline of thecal plates varies according to their position in the theca, thus in some special cases it is possible to identify the precise position of a disarticulated thecal plate. The periproct border plates, basals, radials, and orals are distinguishable, but the laterals and infralaterals are not. In the studied material, basal plates are not observed because these join proximally (aborally) forming an invagination around the stem, and invaginated borders have remained hidden. The periproct border plates, characterized by concave outlines and raised ridge-like margins, are also absent. As a result, the de-
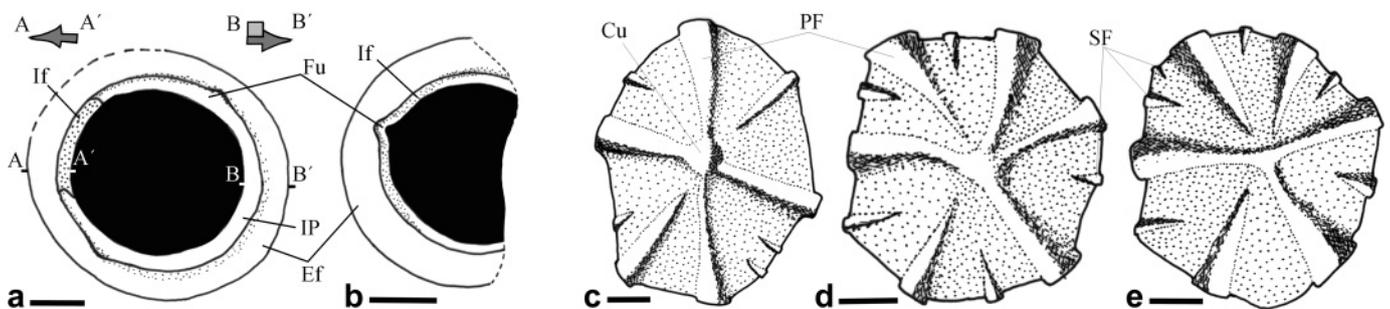
Fig. 3. Camera lucida draws of *Macrocystella* aff. *pauli*. a, b: isolated columnals MPZ2007/720, 719. Fu: fulcra, IP: inner proximal columnal, Ef: external flange, If: internal flange. c, d, e: Isolated thecal plates of specimens MPZ2007/713, 712, 717. PF: primary folds, SF: secondary folds, Cu: central umbo. All scale bars are 1 mm.
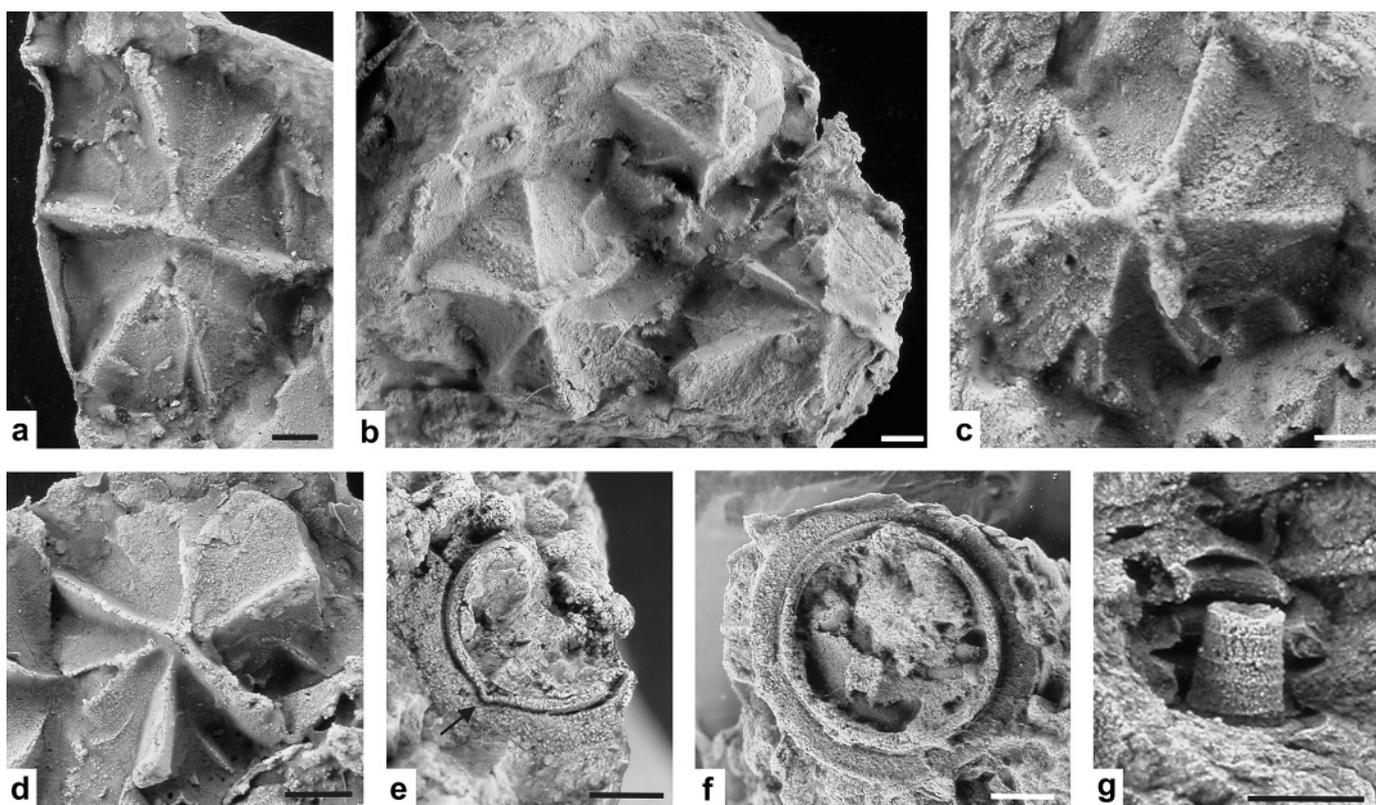
Fig. 4. *Macrocystella aff. pauli*. Photos a–d, f are of a latex cast whitened with ammonium chloride sublimate, and photos e, g of natural internal and external moulds. All scale bars are 1 mm. a–d: Isolated plates, probably infralaterals or laterals. a: Specimen MPZ2007/713. b: Specimen MPZ2007/715–717. c: Detail of specimen MPZ2007/717. d: Specimen MPZ2007/712. e: Broken isolated columnal showing fulcrum. Specimen MPZ2007/720. f: Complete columnal with a large lumen. Specimen MPZ2007/719. g: Mould of stem lumen for several columnals showing the transverse impressions for several flanged columnals. Specimen MPZ2007/718.

scribed thecal plates are probably infralaterals (IL) or laterals (L), with exception of those infralateral and lateral plates that contribute to the periproct and have a distinguished margin (these are L1, L4, L5, and IL4, IL5 *sensu* Paul 1968).

Comparisons: The definition of *Macrocystella pauli* GIL CID et al. 1996, from ferruginous levels of the lower Caradoc (Sandbian) Cantera Shale Formation, Toledo Mountains, Spain, is based on a single specimen that comprises disarticulated thecal plates and an articulated proximal stem. The single specimen is missing and our comparison is based on the illustrations of the original paper that provides little detail (Gil Cid et al. 1996: Fig. 3). Disarticulated stem plates are not preserved and this precludes a complete comparison with our material. The thecal plates of *M. pauli* differs from those of *M*. aff. *pauli* in the type of transverse and longitudinal sections of the primary ridges, which are subrectangular in the former and subtriangular in the latter, and the relatively higher primary ridges of the former (Domínguez, pers. com. 2007). As both species are disarticulated specimens, further material is necessary to propose a formal systematic assignment of the Iberian material.

Other Tremadocian species of *Macrocystella* are *M. mariae* CALLAWAY 1877 (England and Wales), *M. bavarica* BARRANDE 1868 and *M. greilingi* HAMMANN & SDZUY (in Sdzuy et al. 2001;

Germany), *M. bohemicus* BARRANDE 1887 (Bohemia), *M. azaisi* THORAL 1935 (France), *M.? durandi* ACEÑOLAZA 1999 and *M.* sp. from the *Kainella meridionalis* Zone (Tremadocian) of the Rupasca Formation, northern Argentina (the latter not yet illustrated but assigned to *M*. cf. *mariae* by Gil Cid et al. 1996).

Macrocystella aff. *pauli* shares with *M. mariae* the rounded outline of proximal columnals, but differs in the shape of the primary ridges, which are narrow and sharper in the former and broad and rounded in the latter; in addition, *M. mariae* commonly has two auxiliary ridges, whereas *M*. aff. *pauli* commonly has a single auxiliary ridge and rarely two. *Macrocystella bohemicus* (senior synonym of *Mimocystites bohemicus* PAUL 1968) has two (rarely three) accessory ridges; its proximal stem is similar to that of *M. mariae*, differing only in the outer proximals, which display thicker and less blade-like flanges (Paul 1968). *M. azaisi* has more accessory ridges than *M*. aff. *pauli*, increasing up to five to eight in the subspecies *M. azaisi multicristata*; the proximal columnals are circular in both cases, but the flanges of *M. azaisi* bear fine irregular granules or spines encircling them. Only isolated thecal plates are known from *M.? durandi*, which are characterized by numerous accessory ridges not necessarily radially arranged. *M. bavarica* differs from *M*. aff. *pauli* in having proximal columnals with polygonal

outlines (in transverse view), and numerous auxiliary ridges (up to seven pairs). *M. greilingi* shows 4–9 pointed angles in proximal columnals (in transverse view), and the thecal plates have narrow notches and primary ridges radiating from a central boss toward the plate margins; the German material also has more abundant accessory ridges (between 3 and 7 pairs).

Class and Family Indeterminate

Genus *Oryctoconus* COLCHEN & UBAGHS 1969.
Type species *Oryctoconus lobatus* COLCHEN & UBAGHS 1969 from the lower Tremadocian uppermost part of the Najerilla Formation, Demanda Sierra, Spain.

Emended diagnosis: Bowl- to amphora-like shield, proximally pierced (holdfast) to longitudinally perforated (nodal columnal) by a straight axial canal (circular in cross-section), prolonged into a lobate to stellate crown of proximal appendages, unbranched, unsegmented, irregular in number (3–10), rather regularly spaced, and displaying radial symmetry. Heteromorphic stem composing of both cylindrical internodal columnals and amphora-shaped nodal columnals.

Remarks: As previously stated by Álvaro & Colchen (2002), the systematic description of *Oryctoconus* is done with the risk of developing a parataxonomic inflation among the pelmatozoans because these holdfasts are not distinctly associated with thecas and, as a result, cannot yet been assigned to formal species with certainty. The shields anteriorly pierced of the type species (*Oryctoconus lobatus*) have been interpreted as pelmatozoan holdfasts (Álvaro & Colchen 2002; Seilacher & Macclintock 2005), and must be considered as parataxonomic terms that need the description of joined thecas to become formal species. In addition, the shields mimicking the shape and size of holdfasts, but longitudinally perforated by a straight canal (bearing a distinct lumen at the distal end of the shield), had not been previously described, and are here interpreted as nodal columnals forming part of a heteromorphic stem.

The shape of holdfasts and nodal columnals is similar, although the former are pierced in the proximal facet, and the latter in both proximal and distal facets. When the distal part of these ossicles is not visible their distinction is impossible, and the term shield refers to both holdfast and nodal columnal.

Two different species of *Oryctoconus* displaying amphora-like ossicles are known: *O. dorecki* SDZUY 1955 from the Tremadocian Leimitz Shales of Frankenwald, and *O. lobatus* COLCHEN & UBAGHS 1969 from the lower Tremadocian uppermost part of the Najerilla Formation in the Demanda Sierra (Colchen & Ubaghs 1969), the Valconchán Formation of the Iberian Chains (Álvaro & Colchen 2002), the Cabitza Formation of SW Sardinia (Loi et al. 1995), and probably Finmark, Norway (described by Erdtmann et al. 1984, but designated by Berg-Madsen 1986). According to Álvaro & Colchen (2002), their main differences are the number of appendages (5–10 *vs* 3–6, respectively) and, which is more important, the proximal face of the shield, which is convex (trapezoidal in cross-section)

and bearing a central funnel-like depression in the former and flat in the latter. Álvaro & Colchen (2002) distinguished two end-member morphotypes of *O. lobatus* that can co-occur in a single coquina displaying gradual morphological transitions: (i) the Demanda morphotype (Fig. 5.o), in which the anterior appendages are lobate and short, and its height/anterior diameter–ratio is 0.4–0.6; and (ii) the Iberian morphotype (Figs. 5k & n), with long spinose anterior appendages and a ratio of 0.4–2.

Oryctoconus josopaiti n. sp. (Figs. 5a–j, l, m, s)

non 1970 "*Calyx*" *dorecki*. – JOSOPAIT, p. 127–128
non 1972 "*Calyx*" *dorecki*. – HAMMANN, in JOSOPAIT, p. 54

Name: After Volker Josopait, the palaeontologist of the Münster University who found the fossil ossicles in the 1960s.
Holotype: MPZ2007/750. (Figs. 5a–b)
Paratypes: MPZ2007/751, 752, 754, 755, 757, 761. (Figs. 5c–g)
Type locality: NW corner of the Tranquera dam, in the eastern side of the Carenas-Nuévalos road (Fig. 1).
Type stratum: "Tuffitic" bed reported as collecting site Fp33 by Josopait (1972), Santed Formation, Tremadocian-Floian transition.
Material: Thirteen shields (holdfasts plus nodal columnals) (MPZ2007/749–761), two isolated internodal columnals (MPZ2007/747–748), in one case displaying up to ten joined plates (MPZ2007/745), and several partly articulated plates that probably represent a poorly preserved theca (MPZ2007/746), all of them preserved as natural external and internal moulds.
Diagnosis: A species of *Oryctoconus* with bowl-shaped shield; anterior faces of shield convex anteriorly, subtrapezoidal in cross-section and bearing a central funnel-like depression. Three anterior spinose appendages, slender and up to seven times longer than the basal shield.
Description: Three kind of ossicles can be distinguished: holdfast, nodal and internodal columnals. Bowl-shaped shield, up to 8 mm long, reduced to the junction of the anterior appendages, anteriorly prolonged into three slender and spiniform appendages, up to 7 mm long (Figs. 5a–d, f & g). The internodal columnal plate, directly joined anteriorly, has an inflated base with a central perforation (lumen); at the anterior face/columnal contact, the latter shows a prolongation with a distinct depression (interpreted as the articulation of the stem, probably occupied with ligaments; Fig. 5m). The articulation facet is raised on a truncated cone-shaped shaft with a central lumen (about 1/5 of the facet diameter) surrounded by a large concavity (areola) and narrow, smooth, peripheral, articulation surface (articulum). One specimen (Fig. 5e) shows the shield articulated with an internodal columnal, which has a relatively small, circular central lumen (*ca.* 100 μm in diameter) surrounded by a depression (*ca.* 600 μm in diameter) and a peripheral raised articulum. The internodal columnals are cylindrical (Figs. 5e & j), up to 1 mm in diameter in isolated specimens and 600 μm in the specimen that is articulated with the shield (Fig. 5e). The surface of articulation with other internodal columnals is smooth and concave. The stem that has preserved ten joined columnals
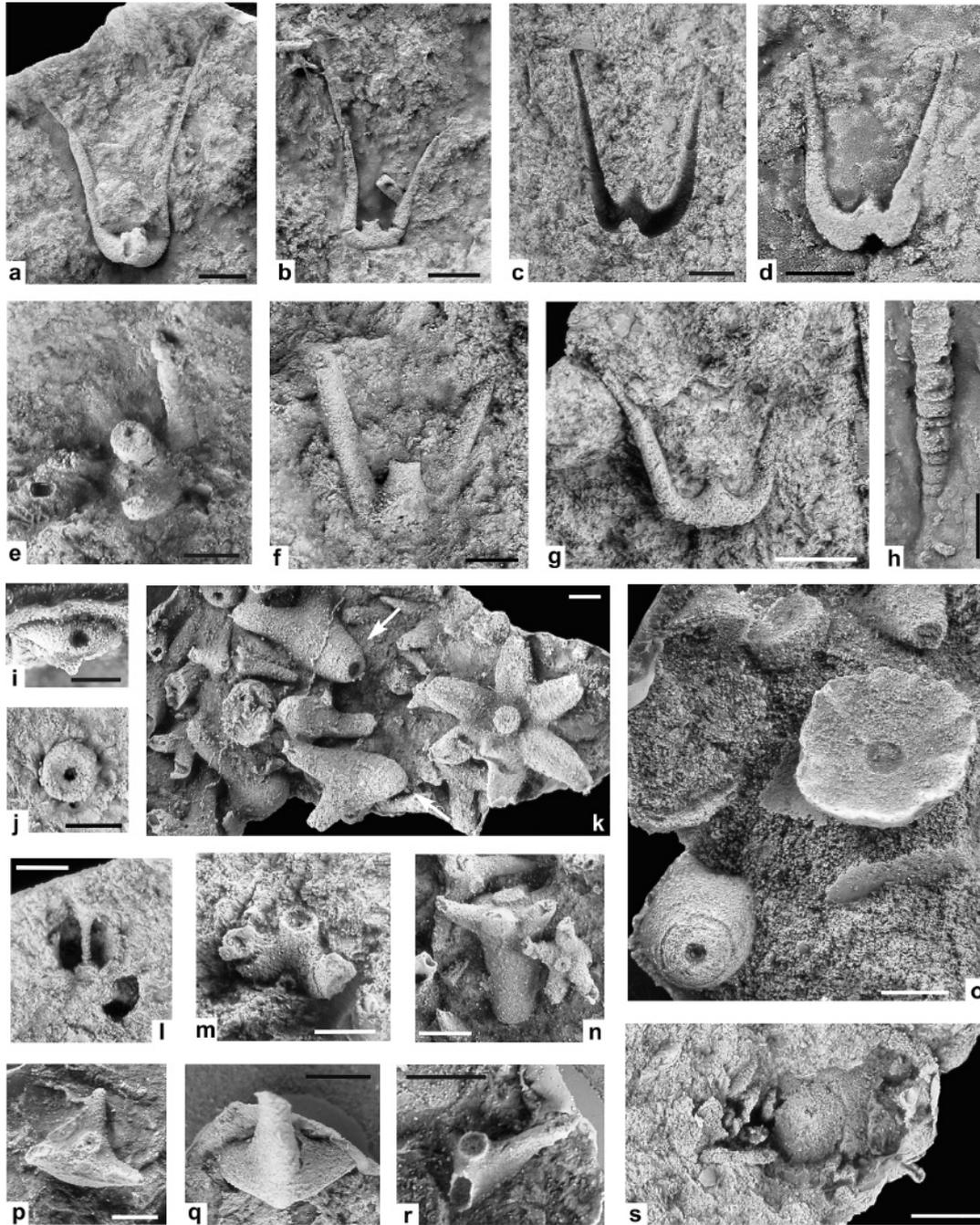
Fig. 5. *Oryctoconus*. Photos a, b, d–k, m–s are of a latex cast whitened with ammonium chloride sublimate. Photos c and l of natural internal and external moulds. Scale bars are 1 mm in c–f, h–j, l, m, p–s; 2 mm in a, b, k; and 3 mm in g, n, o.

O. josopaiti n. sp. a–b: Holotype (MPZ2007/750) in lateral view showing the three slender appendices and the proximal elevation. c: Natural external mould of specimen MPZ2007/761. d, f, g: Several specimens in lateral view. Specimens MPZ2007/761–752–755. e: Oblique view of a holdfast? with an internodal columnal attached. Specimen MPZ2007/757. h: Partial stalk with some articulated internodal columnals of different length. Specimen MPZ2007/745. i: Distal part of a nodal columnal with the central perforation. Specimen MPZ2007/761. j: Isolated internodal columnal showing the central lumen. Specimen MPZ2007/748. l: Internal and external natural mould showing the axial canal infilled with sediment. Specimen MPZ2007/749. m: Oblique view a shield (nodal columnal or holdfast) showing the facet of articulation. Specimen MPZ2007/754. s: A possible thecal fragment of *Oryctoconus* with polygonal and very thin plates. Specimen MPZ2007/746.

O. lobatus COLCHEN & UBAGHS 1969 Iberian morphotype. k: Several specimens of holdfast (lower arrow) and nodal columnals (upper arrow) in the same slab showing the typical anchor shape of these ossicles, proximal and distal parts and distribution of appendages. Specimen MPZ2007/670. n: Specimen with the central proximal elevation slightly developed. MPZ17150. o: *O. lobatus* COLCHEN & UBAGHS 1969, Demanda morphotype. Holotype (Specimen MPZ17143).

O. cf. *josopaiti* n. sp. p–r: Several specimens in proximal, oblique distal and oblique proximal view respectively. All specimens are probably holdfast as they are never pierced in the distal face. (Specimen numbers are; p = MPZ2007/763; q = MPZ2007/768b, r = MPZ2007/765).

(Fig. 5h) is narrow; the height of their columnals is variable, alternating higher and lower columnals. The stem is heteromorphic alternating cylindrical internodal columnals with shield-shape nodals.

Some probable plates of the theca show polygonal outlines with smooth surfaces (Fig. 5s). No apertures in these plates were observed.

Comparisons: O. *josopaiti* n. sp. differs from the other species of the genus in the bowl-shaped aspect of the shield (both holdfast and nodal columnal), the number and shape of the spinose and long anterior appendages (up to five times longer than the basal shield), and the concavity of its anterior face.

As stated above, we do not know the morphology of their respective thecas, and the species of *Oryctoconus* are proposed as parataxonomic species. An example of intra-specific variability exclusively affecting the holdfasts was documented by Le Menn (1985): *Ancyrocrinus armoricanus* MORZADEC 1967, from the Devonian of the Armorican Massif, France, comprises two holdfast end-members grading from bowl- to amphora-like shields that mimic the external morphologies of *O. lobatus* (Iberian morphotype), *O. dorecki* and *O. josopaiti* n. sp. (Figs. 7A & B). The holdfasts of *Ancyrocrinus* (a Devonian crinoid) differ from those of *Oryctoconus*, among other characters, in the greater size of *Ancyrocrinus* and in the shape and symmetry of the anterior perforation, which is star-shaped in the former and circular in the latter.

Oryctoconus cf. *josopaiti* (Figs. 5p–r)

Locality: NW corner of the Tranquera dam, in the eastern side of the Carenas-Nuévalos road (Fig. 1); Josopait's (1972) collecting site Fp32 in the Santed Formation, Tremadocian-Floian transition.

Material: Twenty-five specimens (MPZ2007/762–775, 943–953) preserved as natural external and internal moulds.

Description: Bowl-shaped shields (all of them are probably holdfast) with a very small size (*ca.* 2 to 3 mm). The proximal face is slightly raised in the middle of a triangular proximal face of the shield. On this morphotype, the proximal appendages are joined forming a triangular proximal face in upper view, in the middle of which the articular facet is slightly raised. The proximal face of the shield is slightly convex and perforated, where a small circular depression marks the point of articulation with the stem. The diameter of the circular depression (facet) is up to 0.5 mm. The distal part of the shield is concave and not pierced in any specimen.

Discussion: Oryctoconus cf. *josopaiti* differs from *O. josopaiti* in the relative length of the anterior appendages much more developed in the later. The proximal appendages of *Oryctoconus* cf. *josopaiti* are joined forming a triangular proximal face in plan view, in the middle of which the articular facet is slightly raised. By contrast, in *O. josopaiti* the three appendages are more differentiated or isolated and raised from the bottom of a truncated cone-shaped basal shield, displaying the typical convexity of the distal face.

Despite the co-occurrence of *Oryctoconus* cf. *josopaiti* and *Macrocystella* aff. *pauli*, the former can not be considered as the holdfast of the latter because all the species known from *Macrocystella* are free living.

Columnal type A (Figs. 6a–h)

1972 Pelmatozoen-Reste (Typ A). – JOSOPAIT, p. 62–65, Fig. 10.

Locality: These ossicles were found by Josopait (1972) in a partly limonitized dolostone nodule, up to 15 cm thick, embedded in the offshore shales of the Furongian Valtorres Formation that crop out along the Encomienda valley, Iberian Chains (Josopait's collecting site Fp24 and stratigraphic section At$_{22}$ of Álvaro & Vennin 1996; Fig. 1).

Material: More than one hundred specimens (Fig. 6a) preserved as natural moulds in a dolomitic nodule. Material from Josopait's collection (Münster University, Germany) as repository number L51/16/4a.

Description: Smooth, bell- to amphora-like columnal with convex and perforated base (Fig. 6b, d), circular transverse section, up to 2 mm long and 3.5 mm of diameter, and length/diameter ratio ranging between 0.5 and 1.5. The stereom microstructure was not observed, either in latex cast or in thin-section (Figs. 6f & g). Flat to slightly vaulted anterior face, lacking any anterior appendage, but bearing a concentric expansion of its lateral margin in some specimens, and displaying a central axial canal, up to 1 mm in diameter. The axial canal is straight, simple, circular in cross-section, unbranched, and crosses the columnal longitudinally. The lumen is sometimes surrounded by a thin rim.

Comparisons: These ossicles differ from *Oryctoconus* nodal columnals in the lack of anterior appendages. Their only difference with the Demanda morphotype of *O. lobatus* is the smooth outline of their anterior face. The Iberian columnals differ from the eocrinoid? spiny columnals described by Sumrall et al. (1997), from the Furongian of the western United States, in the lack of lateral spines. Rozhnov (2001, p. 242) and Kruse & Zhuravlev (2008) illustrated some eocrinoid ossicles from a hardground slab sampled in the late Middle Cambrian Mila Formation, Elburz Mountains, Iran, which are apparently identical, both in size and morphology, to the Iberian material. Rozhnov (2001) interpreted them as eocrinoid holdfasts but, as they are pierced in both faces, they are better considered as columnals.

Taphonomic and ontogenetic features: The distinction between original skeletal walls and secondary artefacts produced by taphonomic alteration is key for the reconstruction of any skeleton microstructure. The columnal type A preserved in a carbonate nodule shows a strong difference in preservation when comparing with the specimens of *Oryctoconus* preserved as moulds in shales and sandstones: dolostone-hosted specimens retained details of the skeleton microstructure and ontogeny. Despite the entire replacement of the original calcite composition by iron-rich dolomite, the skeletons have hardly suffered from additional recrystallization. Sparry mosaics are rare and easily recognisable by the asymmetric pat-
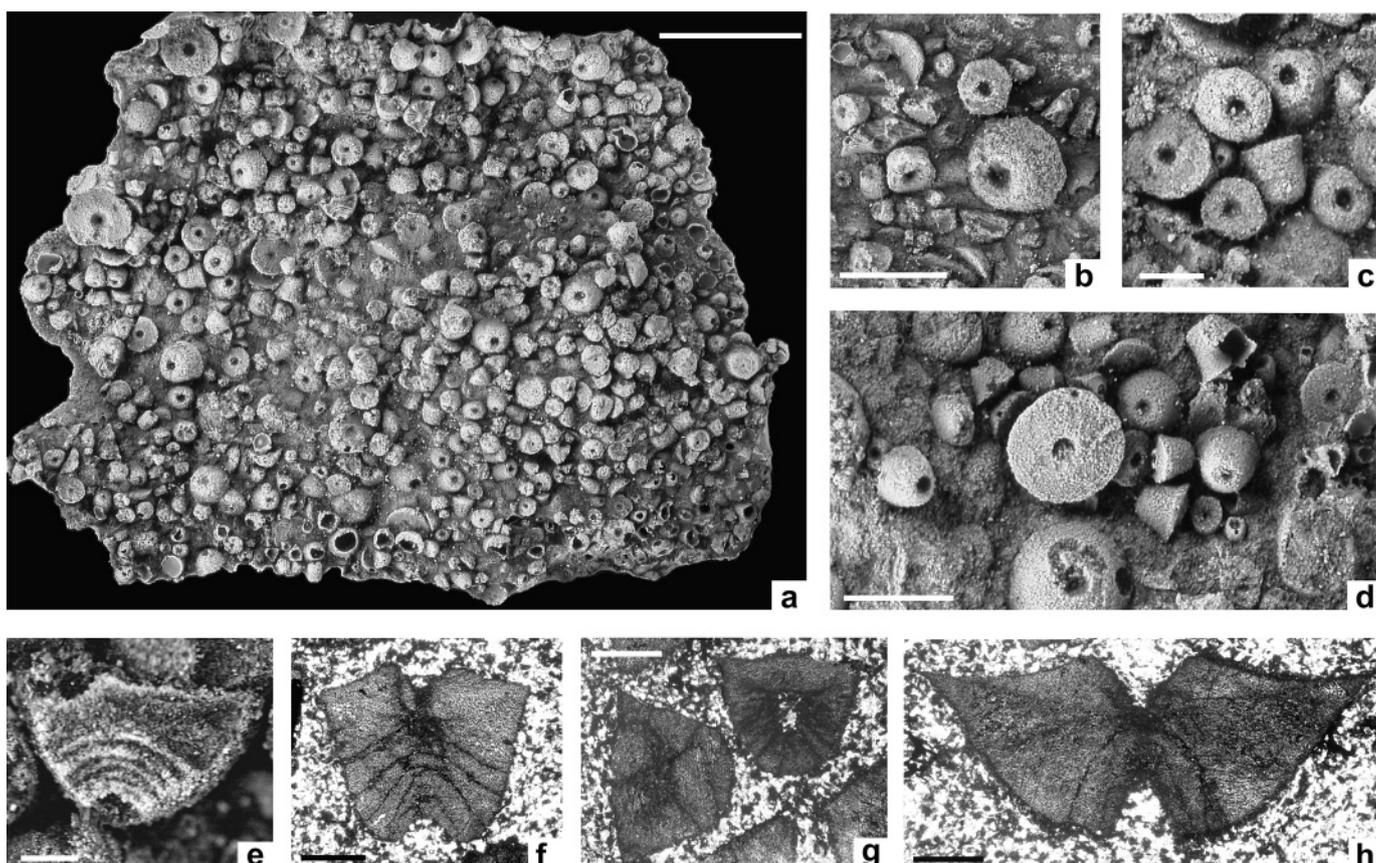
Fig. 6. Pelmatozoan columnals type A. All photos are of latex cast whitened with ammonium chloride sublimate. Scale bar are 1 cm in a; 4 mm in b & c; 3 mm in d, and 500 μm in e–h. a, General view of a concretion with tens of columnals. b, c, d: Details of different ossicles. e: Latex cast of a columnal with the outer wall dissolved that shows growth stages. f–h: Different specimens in thin sections preserved as iron-rich dolomite. Specimen L51/16/4a.

terns of their dolomite crystals. By contrast, the symmetric arrangement of dolomite crystals exhibited by their transverse and longitudinal sections reflects the original superposition of growth stages (Figs. 6e–h). Latex casts of some laterally flattened skeletons, with their outer walls broken, also allow identification of growth stages (Fig. 6e). The inner cavity of the columnal type A is not empty but occupied by up to 5 transverse laminae, up to 100 μm thick, anteriorly convex, which subdivide the posterior three fourths of the shield. An axial canal passes through the centre of the laminae and commonly penetrates the distal apex of the columnal. This framework points to a complex skeletal growth, not simply achieved by accretion of carbonate, but also by precipitation of successive proximal surfaces.

Implications and concluding remarks

Both the Valtorres and Santed Formations are thick shale-dominated strata that have yielded scattered fossil assemblages. This can be result from either original development of impoverished shell communities or to the onset of early diagenetic processes that destroyed their mineralized carcasses. However, two event shell concentrations have yielded a rich and diversified fossiliferous fauna, composed of disarticulated and partly fragmented trilobites, calcite- and phosphate-walled brachiopods, and echinoderm debris: event beds are tempestitic (Fp24) and tuffitic (Fp32), shell accumulations. The tuffite reported as Fp32 by Josopait (1972) indicates the onset of an active neighbouring volcanism that provided a locus for coquina deposition, as other rare Early Ordovician echinoderm and linguliformean brachiopods have also been exclusively found in fine-grained volcaniclastic strata of NW Gondwana (e.g., Emig & Gutiérrez-Marco 1997; Sdzuy et al. 2001). In both event types, a broad parautochthonous/allochthonous–ratio can be estimated based on the variations in the degree of articulation of the multi-element fossils (such as echinoderms and trilobites). This feature is directly related to the fluctuations in the energy of benthic currents and the distance of transport. There, the debris of *Macrocystella* and *Oryctoconus* are disarticulated to partly articulated, indicating a short transport from their substrate. As a result, it is possible to interpret a clay-rich soft substrate for both of them. In the case of *Macrocystella*, it does not represent a sessile mud-sticker echinoderm, as it may have rested with the distal stem lying on the seafloor, the flexible proximal stem
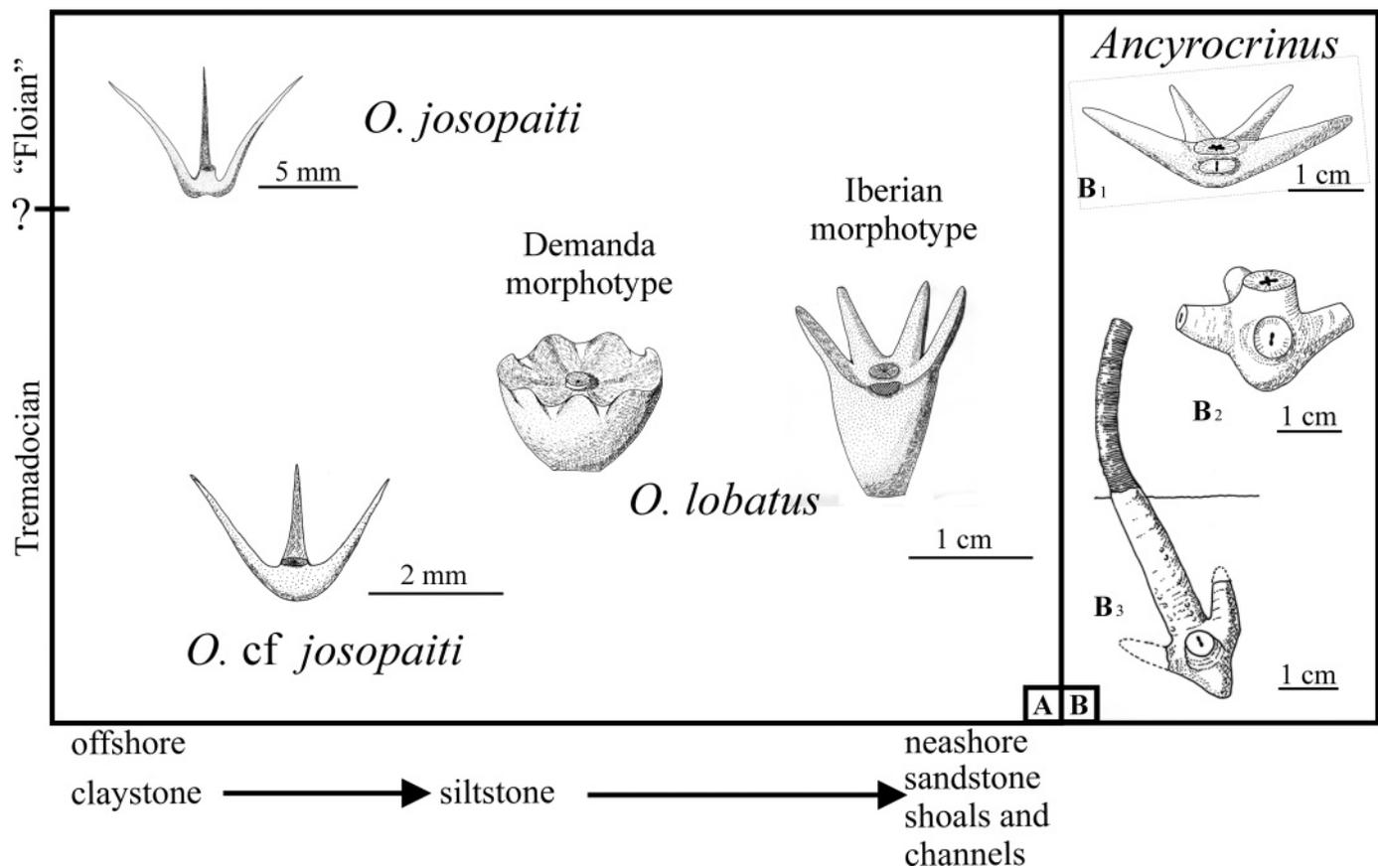
Fig. 7. Comparison between *Ancyrocrinus* and *Oryctoconus*. A: Reconstruction of different grapnel-like *Oryctoconus* holdfasts related to their occurrences, environments and inferred type substrata. B: B₁. Reconstruction of *Ancyrocrinus armoricanus* based on Le Menn 1985 (pl. 20, Figs. 8–12). B₂. Sections of the proximal part and appendages of *Ancyrocrinus* (after Seilacher & MacClintock, 2005). B₃. Supposed mode of life of *Ancyrocrinus* where the grapnel stuck deep in the sediment (after Seilacher & MacClintock, 2005).

bent to allow the theca to be held upright and the brachioles extended to feed (Paul 1968).

All the reported holdfasts and nodal columnals of *Oryctoconus* were found densely crowed both in sandstone and shale substrates. The shields are considered to have been displaced short distances by wave or current scouring, because most of them are disarticulated but not broken, and do not show any preferred orientation: some are lying with the convex apex facing down and others with them up or laterally. Local abundance suggests that they were gregarious pelmatozoans that possessed a high-reproductive potential.

Holdfast attachment structures were responsible for stabilizing and supporting the stalk and theca above the substrate and for anchoring the organism against lateral movement across the seafloor. On clay-rich soft substrates, the *Oryctoconus* pelmatozoan was faced with a problem common to sessile 'mud-sticker' organisms: how to maintain a suitable life position on or within soft bottoms submitted to accidental disturbances, such as bottom current stress, substrate consistency, and high rates of sedimentation. Grapnel-like holdfasts (*sensu* Brett 1981), such as *Ancyrocrinus* and *Oryctoconus* (Fig. 7), are characterized by a distinct intra-specific diversity that is

probably associated with morphological adaptations to specific substrate conditions. A common change exhibited with pelmatozoan holdfasts is the production and modification of appendages (or radices) depending on the firmness of the substrate (Brett 1981; Álvaro & Colchen 2002). In the case of *Ancyrocrinus armoricanus* MORZAZEC 1967, a certain degree of variation on a basic holdfast morphotype was interpreted as a result of intra-specific variability (Le Menn 1985). The author described both massive amphora-like holdfasts with short and robust appendages (pl. 18, Fig. 25, and pl. 20, Figs. 9–12) and bowl-like holdfasts with slender and long appendages (pl. 20, Fig. 8) mimicking the geometries of *O. lobatus* (Iberian morphotype *sensu* Álvaro & Colchen 2002) and *O. josopaiti* n. sp., respectively.

Two end-member morphologies are also recognisable in *O. lobatus*, the so-called Iberian and Demanda morphotypes (Álvaro & Colchen 2002). The Iberian morphotype of *O. lobatus* occurs both in the Cantabrian Mountains and the Iberian Chains as lag deposits on sandstone bedding and foreset planes (Álvaro & Colchen 2002; Seilacher & Macclintock, 2005), rarely associated with disarticulated stem internodal columnals. By contrast, the Demanda morphotype of *O. lobatus*, characterized by lobate appendages, dominantly occurs in silty substrates,

commonly associated with stem internodal columnals, and can show gradual variations into the Iberian morphotype.

The Iberian morphotype of *O. lobatus* approaches to the functional paradigm represented by the *Ancyrocrynus* grapnel. Both skeletons were interpreted by Seilacher & Macclintock (2005) as a partly buried weighted anchor that would function as ballast in high-energy substrates. High-energy environments and sandy substrates would therefore have favoured the production of robust and centimetre-sized holdfasts to afford increased anchorage. In this case, internodal columnals were commonly washed away during transport in sandy substrates. In contrast, *O. dorecki* and *O. josopaiti* n. sp. occur in tuffitic beds as partly disarticulated stem columnals and holdfasts, reworked short distances from clayey substrates. In this case, the contact with soft clayey substrates may have induced production of numerous longer appendages and miniaturization (millimetre-sized) of the holdfasts (Fig. 7A). Development of slender and spiniform appendages (e.g., in *O. dorecki* and *O. josopaiti* n. sp.), in which a large resting surface is acquired by increasing the number and length of appendages, would have increased the stability of pelmatozoans on soft clay-rich substrates (the so-called "snowshoe effect" *sensu* Savazzi 1982, 1999). The development of nodal columnals mimicking the shape and size of holdfasts in *Oryctoconus* may be useful for stabilizing the whole pelmatozoan in soft substrates (again the "snowshoe effect") under high sedimentation rates. Under these conditions, once the holdfast and distal part of the attached stem is buried, the development of a bowl-shaped nodal columnal may contribute to the stability of the echinoderm.

As a result, the reported pelmatozoans possessed both size- and shape-parameters sensitive to the degree of turbulence characteristic of their respective quiet- and rough-water environments. The phenotypic gradient illustrated in Figure 7 appears to fit well with factors suggestive of quiet and turbulent conditions. Correlation between holdfast (and bowl-shaped nodal columnal) form and size and grain size does provide real possibilities for employing shell morphology as an index of current strength; it must be kept in mind that grain size correlates with depth as well as with current velocity.

Another question is related to the taxonomic affinity of *Oryctoconus*. The origin of true stems with columnals on primitive pelmatozoams is an enigmatic question. According to Sprinkle (1973: p. 39), early members of both the blastozoan eocrinoids and crinozoan crinoids apparently made a similar but independent transition from a primitive and perhaps ancestral holdfast attachment appendage (now termed stalk; see Sprinkle & Guensburg 2001: p. 61) to a true and very similar columnal-bearing stem. The eocrinoids apparently made this transition in the middle Cambrian to Early Ordovician. Two middle Cambrian representatives, *Eustypocystis* SPRINKLE 1973 from the Secret Canyon Formation of Nevada and *Ubaghsicystis* GIL CID & DOMÍNGUEZ ALONSO 2002 from the Genestosa Member of the Cantabrian Mountains, Spain, share the holomeric character of their cylindrical stem columnals. In contrast, the oldest crinoids (Tremadocian in age), named pro-

tocrinoids by Guensburg & Sprinkle (2003: p. 7), are characterized by a pentameric stem and a large lumen. These traits are considered by the same authors as representing a pleisomorphic (primitive) crinoid character, and a key to separating the protocrinoids from other stemmed echinoderms. Subsequently, two other scenarios concerning the origin of columnals in pelmatozoans have been envisaged: (i) the crinoids may have evolved from rhombiferans either with retention of or change to a pentameric column (Ausich 1998); in this case, pentamerism would be an apomorphic character; and (ii) pentamerism can be considered as a crinoid-derived character and holomeric columnals are plesiomorphic and inherited from blastozoans (this hypothesis is based on the observations of well-preserved pelmatozoan columnals from the early Middle Cambrian of Morocco; Clausen & Smith 2008).

The fact that the stem internodal columnals articulated with *Oryctoconus* holdfasts (or nodal columnals) are cylindrical with small circular lumens may suggest an assignation of *Oryctoconus* to the blastozoans, likely to eocrinoids. This is based on the lack of reported crinoids bearing holomeric stems predating the Tremadocian-Floian transition (Sprinkle 1973; Sprinkle & Guensburg 2001), and the widespread distribution of blastozoans with holomeric stems since the middle Cambrian.

Acknowledgements

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