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Morphology and ecological setting of the basal echinoid genus *Rhenechinus* from the early Devonian of Spain and Germany

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Based on new material from Germany and Spain, the echinoid "*Lepidocentrus*" *ibericus* from the Early Devonian (Emsian) of northern Spain is shown to be congeneric with *Rhenechinus* from the Hunsrück Slate of south-western Germany. New information on the lantern, pedicellariae and internal structure of the theca is provided, and confirms this genus as a member of the Echinocystitidae–Proterocidaridae clade and the most primitive of all Devonian echinoids. The two environmental settings in which *Rhenechinus* is found are very different: the Spanish specimens come from a relatively shallow-water bryozoan meadow setting while the German specimens are preserved in a deep-water setting. We deduce that the rare echinoid specimens from the Hunsrück Slate are all allochthonous, whereas the Spanish material is preserved in situ.

Key words: Echinodermata, Echinoidea, morphology, phylogeny, Devonian, Spain, Germany.

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Introduction

Although the fossil record of echinoids extends back to the Ordovician, Palaeozoic echinoids remain scarce and very poorly known. This is because their skeleton is much less robust compared to that of their post-Palaeozoic descendants, and they are rarely well preserved. Whereas the great majority of post-Palaeozoic echinoids have coronal plates that abut and are firmly sutured together, all Palaeozoic echinoids have a test constructed of imbricate plates that falls apart rapidly upon death. Consequently, our knowledge of the early evolutionary history of echinoids is patchy at best, and comes from a small number of localities and horizons where sedimentary conditions have favoured rapid burial.

The Devonian marks an important period in the diversification of echinoids and saw the start of several lineages that came to dominate in the upper Palaeozoic (Kier 1965: text-fig. 8; 1968). It is unfortunate, therefore, that so little is known about the echinoids and their ecology at this period. This stems from the paucity of well-preserved echinoids that have been described. Just 17 species in ten genera have been recorded from the Devonian, mostly from Germany or North America, and half of these are based on isolated spines, disarticulated plates or test fragments that are so incompletely known as to be effectively indeterminate (Smith 2011). Yet, judging from their morphological disparity, echinoids appear to have been rather diverse at this time. Of the six genera for which adequate material exists, three (*Albertechinus* Stearn, 1956, *Nortonechinus* Thomas, 1924, and *Deneechinus* Jackson, 1929) are members of the Archaeocidaridae, one (*Lepidechinoides* Cooper, 1931) is a lepidesthid, another (*Porechinus* Dehm, 1961) a palaechinid, and a third (*Rhenechinus* Dehm, 1953) an echinocystitid. The only Palaeozoic echinoids to have been previously reported from Spain are some disarticulated plates and spines that were referred to "*Archaeocidaris* sp." (Barrois 1882; Sieverts-Doreck 1951), and the poorly known *Lepidocentrotus ibericus* (Hauser and Landeta 2007). Newly collected material of *L. ibericus* allows us to establish the true identity of this species and reveals its close relationship to *Rhenechinus hopstaetteri* Dehm, 1953, from the German Lower Devonian Hunsrück Slate. *R. hopstaetteri* was established on the basis of a single partial test. A second, well-preserved individual of this species has recently come to light and we therefore take this opportunity to provide a detailed redescription of the German species and review our understanding of this genus and its phylogenetic position.

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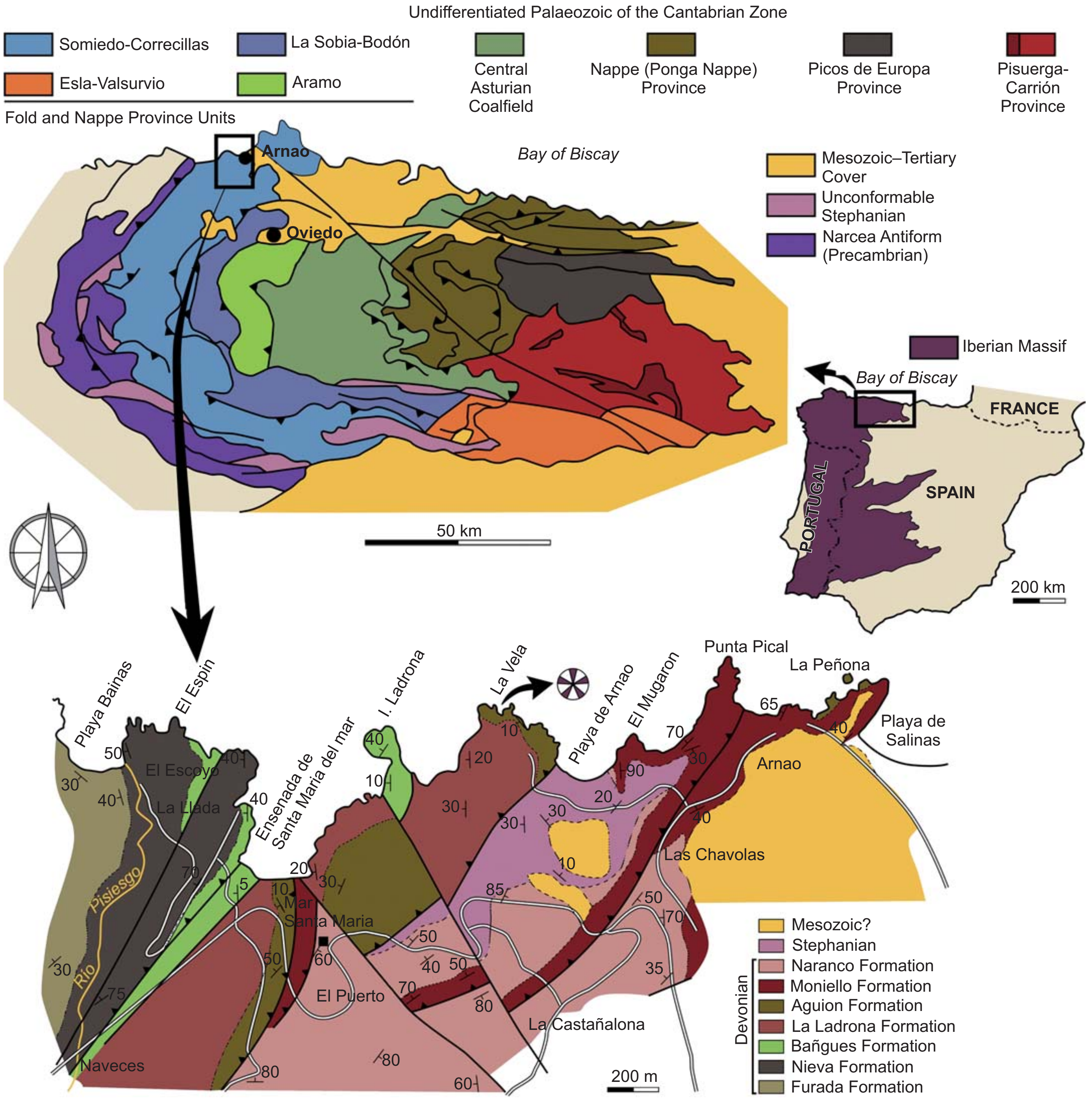

Fig. 1. Map showing the geographical position and geological setting of the Aguión Formation and the echinoid bearing horizon (arrowed symbol), modified from García-Alcalde (1992).

Institutional abbreviations.—BSPG, Bayerische Staatssammlung für Paläontologie und Geologie, München, Germany; DBM, Deutsches Bergbau-Museum, Bochum, Germany; GZG, Geowissenschaftliches Zentrum, Universität Göttingen, Germany; NHM, Natural History Museum, London, UK; NM.PWL, Naturhistorisches Museum Mainz, Landessammlung für Naturkunde, Mainz, Germany; SMF, Senckenberg Forschungsinstitut und Naturmuseum, Frankfurt/M, Germany; UO, Museum of Geology, Universidad de Oviedo, Spain.

Material and geological setting

Spanish material.—All the specimens come from the vicinity of Arnao village, Asturias, on the northern side of the Cantabrian Zone (North Spain) within the Somiedo-Correcilla Unit (Fig. 1).

In this area a Lower Devonian (upper Emsian) succession crops out in a series of old quarries between La Vela Cape and

Arnao beach. Here the lower 60 m of the Aguión Formation are exposed and have been informally divided into three lithostratigraphic units (sensu Álvarez Nava and Arbizu 1986); a lower calcareous unit, a middle marly-shaly unit and an upper unit of green and red marls (Fig. 2). The upper unit is 24 m thick and contains a rich fauna of pelmatozoans, fenestellid bryozoans, and brachiopods. Crinoids are diverse and sometimes very common, especially *Trybliocrinus flatheanus* and to a lesser extent *Pterinocrinus decembrachiatus*, *Orthocrinus* sp., and *Stamnocrinus intrastigmatus* (Schmidt 1931; Breimer 1962). Blastoids include *Pentremitidea lusitanica* and *Pleuroschisma verneuili* (Johnny Waters personal communication, May 2011). The commonest brachiopod is *Anathyris* and there are abundant large fenestellid bryozoan colonies (*Isotrypa* sp.). Articulated specimens of *Rhenechinus* come from a horizon towards the top of the upper unit (Fig. 2: arrow), although isolated plates are found throughout.

Argillaceous content varies within the upper unit of the Aguión Formation, indicating variability in the supply of terrigenous material. Arbizu et al. (1995) suggested this was a major factor in controlling the different fossil assemblages encountered within the unit. Levels where the crinoid *Trybolocrinus* are common probably represent turbid palaeoenvironments where there was abundant mud in suspension, whereas the level with echinoids has abundant fenestellids and other crinoids (i.e., *Pterinocrinus decembrachiatus*) and appears to have been deposited in a well-oxygenated and relatively tranquil environment. Arbizu et al. (1995) interpreted the entire unit as having been deposited in a typical platform environment, with highly variable rates of terrigenous supply. The presence of marl-rich levels with well-preserved echinoderm specimens alternating with tempestite encrinite levels suggests an offshore setting, sporadically affected by storm events.

The bed in which the echinoids are preserved is exposed on the foreshore at 43°34'44.6"N 5°59'02.2"W and is a firmground with attached crinoid holdfasts in places. Echinoids are preserved at the base of a red clay drape that covered this surface and appear to have been relatively common at this level. We deduce that echinoids were living in amongst the bryozoan meadows in a firm-ground, level bottom community.

German material.—Both specimens of *Rhenechinus hopstaetteri* come from the Lower Devonian (Early Emsian) Hunsrück Slate in the Rhineland-Palatinate of south-western Germany. The Hunsrück Slate is a Lagerstätte famous for its soft tissue preservation (Bartels et al. 1998; Sutcliffe et al. 1999). These mudrocks were deposited in a shelf-basinal environment separated by shallower swells on which a diverse benthic marine fauna thrived. Arthropods dominate, but there are also corals, sponges, brachiopods, gastropods, cephalopods, and echinoderms (Mittmeyer 1980; Bartels and Brassel 1990; Bartels et al. 1997, 1998; Kühl et al. 2011). Asteroids, ophiuroids and, to a lesser extent, crinoids dominate the echinoderm assemblages, but there are also rare holothurians and two monospecific echinoid genera (*Porechinus* Dehm, 1961 and *Rhenechinus* Dehm, 1953) as well as fragments of the echinoid *Lepidocentrus* Müller, 1856 (Table 1).

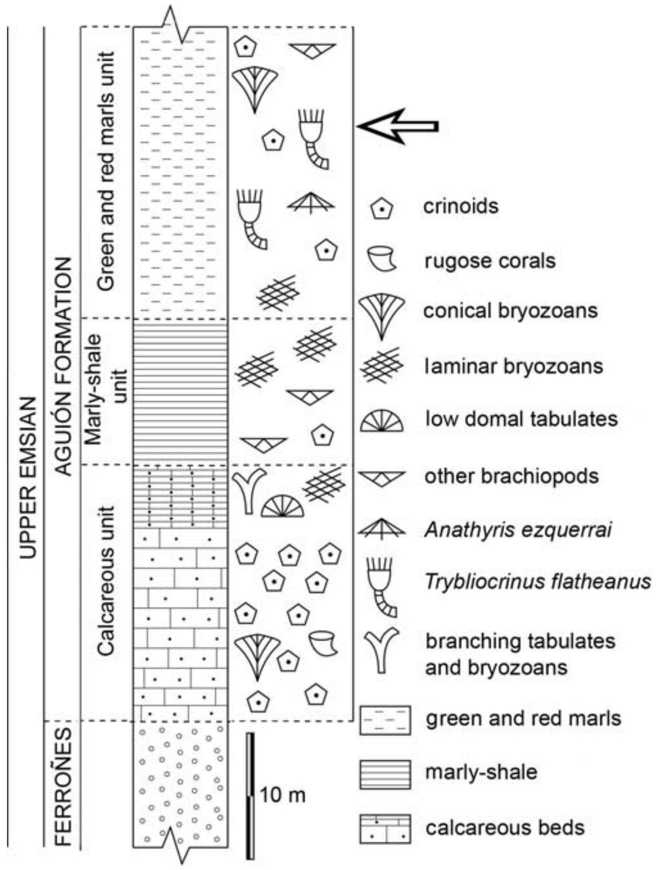

Fig. 2. Stratigraphical succession of the Aguión Formation at Arnao Platform showing lithological units, their faunal composition and types of communities. The level bearing echinoids is indicated by an arrow. From Arbizu et al. (1995).

Photographs and X-radiographs were taken at the Natural History Museum, London.

Systematic palaeontology

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

Stem group Echinoidea

Family Echinocystitidae Gregory, 1897

Genus *Rhenechinus* Dehm, 1953

Type species: *Rhenechinus hopstaetteri* Dehm, 1953, by original designation; Lower Devonian (Early Emsian), Hunsrück Slate from the Rhineland-Palatinate of south-western Germany.

Diagnosis.—Ambulacral zones narrow and straight; plating quadriserial throughout with every other plate a demiplate occluded from the adradial suture. Pore-pairs uniform and with a surrounding peripodial rim, alternately displaced to left and right forming a biseries down the centre of each half-ambulacrum. Interambulacral zones broad and com-

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Table 1. Echinoid specimens from the Lower Devonian Hunsrück Slate.

Museum acronym and number	Original collection	Species	Locality	Authors
BSPG 1955 I 585	leg. n. n. 1949; donated by Helmut Hopstätter (Simmern), 1952	*Rhenechinus hopstaetteri* Dehm, 1953	Quarry Kaisergrube, Gemünden	Hopstätter 1952; Dehm 1953
BSPG 1960 I 164	donated by Maria Bodtländer-Gross (Bundenbach), 1960	*Porechinus porosus* Dehm, 1961	Bundenbach	Dehm 1961
GZG.INV.19996	purchased in 1963	*Lepidocentrus* sp.	Quarry Mühlenberg near Bundenbach	–
SMF.HS.426	J. Schmitt, 1966	gen. et sp. indet.	Quarry Eschenbach, Bundenbach	–
private collection	E. Halisch (Rotenburg W.)	*Lepidocentrus* sp.	Bundenbach	Beyer 1979
private collection	A. Seilacher (Tübingen)	*Lepidocentrus* sp.	?Bundenbach	–
DBM.HS.285	–	*Rhenechinus hopstaetteri* Dehm, 1953	Quarry Eschenbach-Bocksberg, Bundenbach	Bartels and Brassel 1990; Bartels et al. 1997, 1998
DBM.HS.337	–	*Lepidocentrus* sp.	Quarry Kreuzberg near Weisel	Bartels and Brassel 1990; Bartels et al. 1998
NM.PWL.1992/234-LS	–	*Lepidocentrus* sp.	Quarry Eschenbach-Bocksberg, Bundenbach	–
NHM.E76446	purchased from F. Krantz in 1905	?*Rhenechinus hopstaetteri*	Bundenbach	–

posed of a large number of small, polygonal plates forming semi-regular *en chevron* rows; plates imbricate. Basicoronal plate present adorally. Coronal plates with small secondary tubercles or granules only, bearing short simple spines. Teeth oligolamellar.

Remarks.—*Rhenechinus* closely resembles the late Silurian *Echinocystites*, but in that taxon the interambulacral plates are more scale-like and more irregular in arrangement, not forming semi-organized rows, and the outer column of primary ambulacral plates always extend to the perradius. *Rhenechinus* is distinguished from all other Devonian echinoids by its quadriserial pore-pair arrangement and demiplates in the ambulacra. In *Albertechinus*, *Deneechinus*, *Nortonechinus*, *Lepidechinoides*, and *Porechinus* the ambulacral pore-pairs are uniserial and there are no demiplates. Proterocidarids, such as *Proterocidaris* and *Pholidocidaris,* differ from *Rhenechinus* in having enlarged oral pore-pairs and more than four columns of plates in their ambulacral zones.

Stratigraphic and geographic range.—Emsian, Lower Devonian; Spain and Germany.

Rhenechinus ibericus (Hauser and Landeta, 2007)

Figs. 3, 4, 5A–E.

2007 *Lepidocentrus ibericus*; Hauser and Landeta 2007: 66, text-figs. 2, 3.

Holotype: Specimen referred to by Hauser and Landeta (2007), housed in a private collection and unnumbered in the original description.

Type horizon: Aguión Formation, Emsian, Lower Devonian.

Type locality: Cap la Vela, Arnao, Asturias, NW Spain.

Material.—Five specimens, UO DGO-23000–23003, NHMEE 13984, all from the type loclity and horizon.

Diagnosis.—A species of *Rhenechinus* with just four columns of interambulacral plates in each zone. Surface of interambulacral plates with pitted ornament.

Description.—All specimens have collapsed post-mortem but are estimated to have been up to 45 mm in diameter. They were almost certainly globular in shape. The apical disc is not seen but in UO DGO-23002 there is a single genital plate in isolation (Fig. 5B). This has a single gonopore and no hydropore openings and is pentagonal in outline. Ambulacral zones are relatively narrow and composed of four columns of plates throughout. In each half column a large primary element extends from adradial to perradial suture and alternates with a smaller demiplate, which is excluded from the adradial suture (Figs. 3B, 4B, 5A). In external view the ambulacra are flush and each element has a single rather large pore-pair with a subcircular tube-foot attachment rim slightly less than 1 mm in diameter. The pore-pairs are offset on the demiplates so that there are two biserial columns of pore-pairs in each ambulacral zone. There is usually one large mamelon (ca. 0.4 mm diameter) without a boss on the lower adradial side of the pore-pair on primary plates, accompanied by two or three small granules (ca. 0.2 mm diameter). The occluded plates have just one or two granules at most. On the internal surface each primary plate thickens perradially, giving rise to a haft that arches inwards towards the perradius forming a ridge (Fig. $4A_3$). This internal ridge is more strongly developed on adoral plates than on adapical plates. The perradial edge of these plates is notched by a longitudinal groove for the radial water vessel, which therefore lay enclosed within the ambulacral plates. There is also a lateral canal that leads to the pore-pair on the primary ambulacral plate, and which is also therefore enclosed. Ambulacral elements close to the peristome become narrower with long adradial projections, and their pore-pairs become smaller (Fig. 3A). All plate edges are bevelled, with the adradial edge of ambulacral plates passing under the adjacent interambulacral plates.

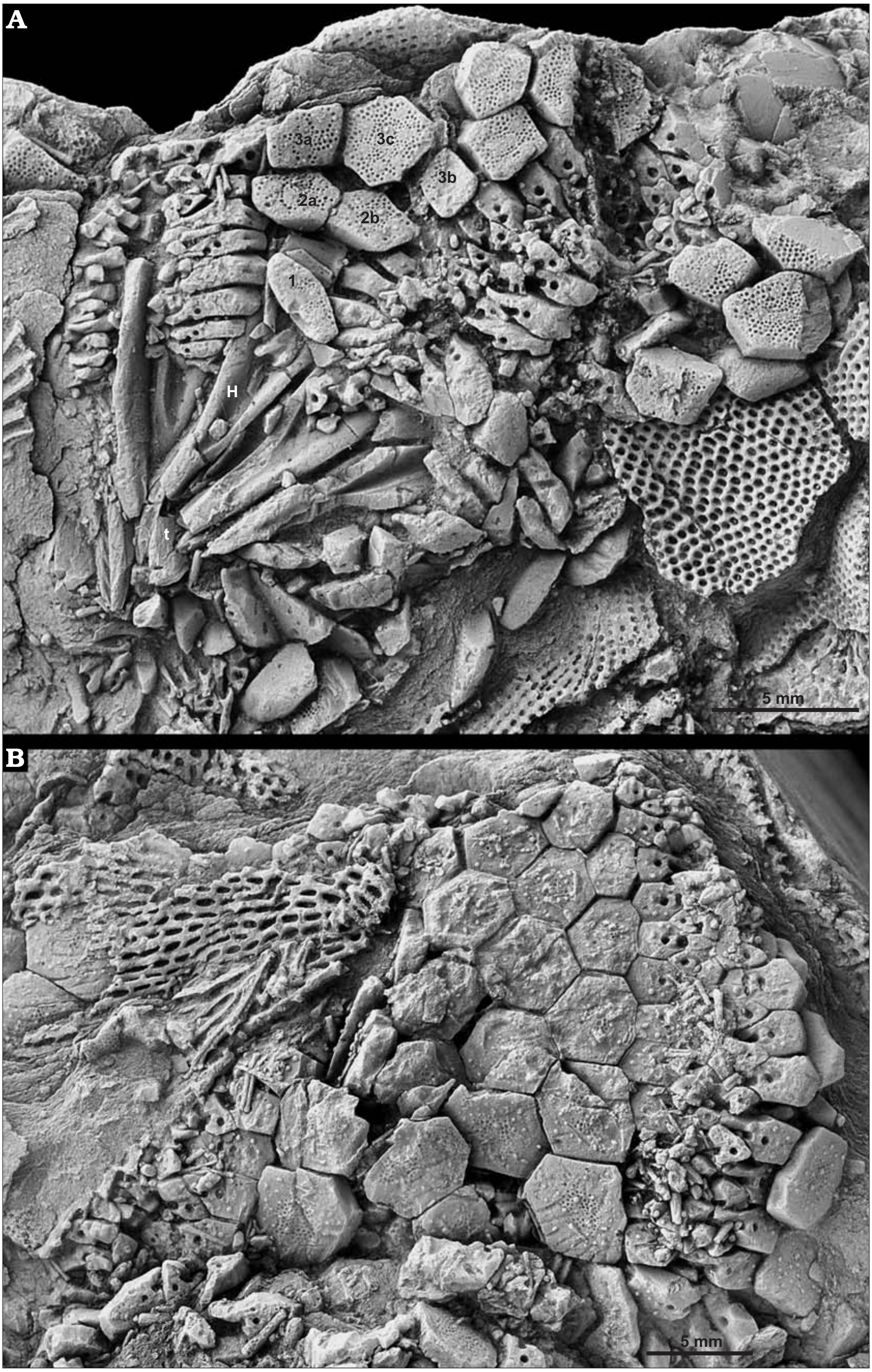

Fig. 3. Echinocystitid echinoid *Rhenechinus ibericus* (Hauser and Landeta, 2007). Aguión Formation, Emsian, Lower Devonian, Arnao, Asturias, NW Spain. **A**. UO DGO-23001 showing adoral plating and elements of the lantern. **B**. UO DGO-23000 showing partially articulated plating of the upper surface. Abbreviations: H, hemipyramid; t, tooth; 1, 2a, b, 3a–c, first three rows of interambulacral plates.

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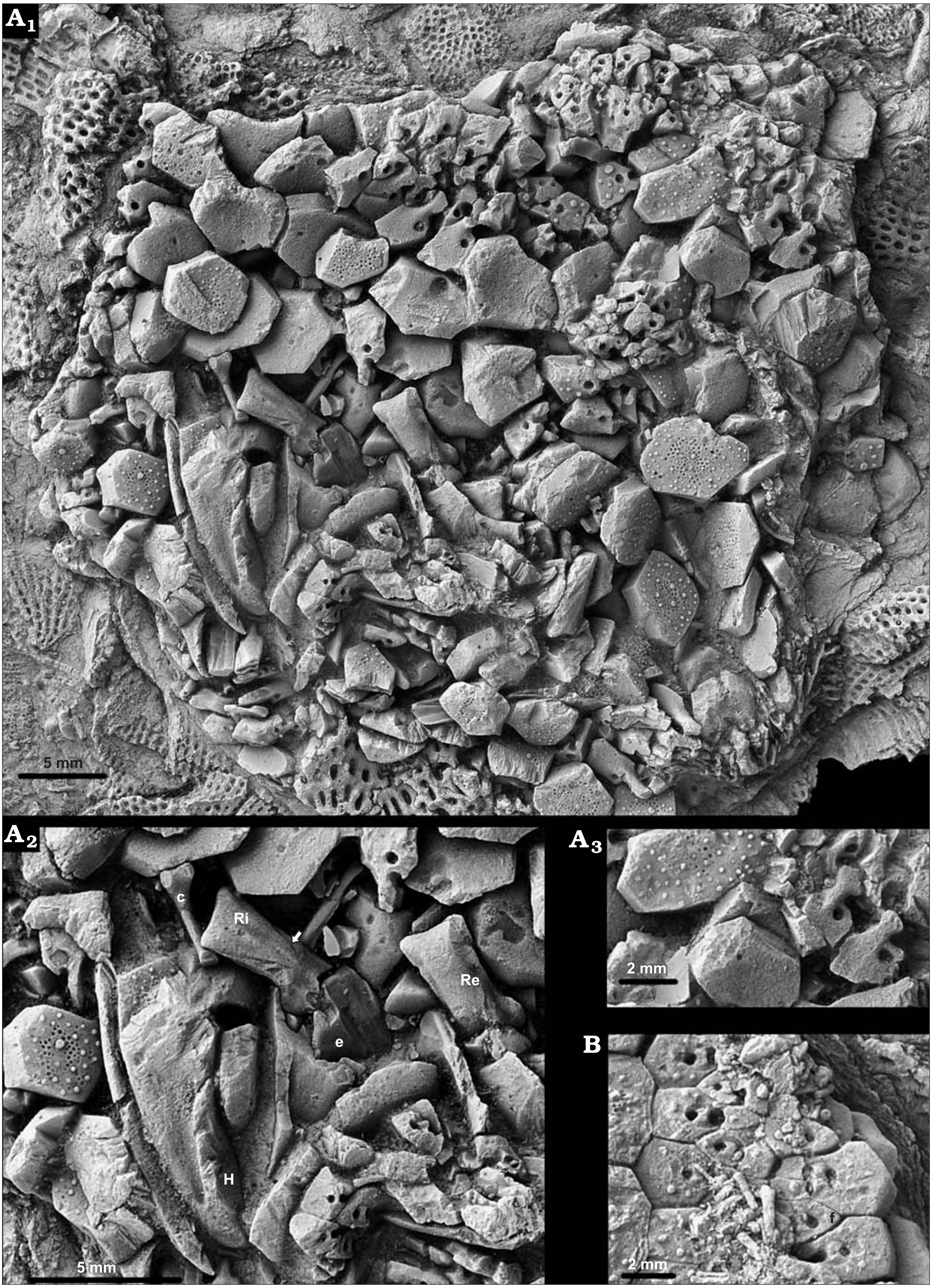
A1
5 mm
A2
c
Ri
Re
e
H
5 mm
A3
2 mm
B
f
2 mm

Interambulacral plates in the best-preserved specimen form four columns towards the ambitus (Fig. 3B). The outer columns are composed of irregularly pentagonal plates while the middle two columns are composed of strictly hexagonal plates (Fig. 5A). Plates are 5–6 mm in diameter and rather thick (0.8 mm) compared to those of *R. hopstaetteri*. Plate edges are bevelled with adradial faces overlapping ambulacral plates and interradial faces underlapping adjacent plates. Towards the apex the outer columns of plates are pinched out leaving just two interambulacral columns. At the peristome there is a single basicoronal plate followed by two equal-sized plates, which in turn abut a large central hexagonal plate plus two adradial plates (Fig. 3A). Externally interambulacral plates are ornamented by a dense circular pitting, with pits approximately 0.2 mm in diameter (Fig. $4A_1$). In between the pits there are scattered small granules again approximately 0.2 mm in diameter.

Primary spines are preserved only in the ambulacral regions. They are up to 2 mm in length, circular in cross-section, and without a hollow core. There is a very short base of fine stereom mesh and the exterior of the shaft has fine longitudinal ridges of stereom. Smaller secondary spines up to 1 mm in length are also present and are the only spines found on interambulacral plates.

There are two forms of pedicellaria present; large spinate tridentate forms and short, bulbous tridentate forms (Fig. 5D, E). The large spinate tridentate forms are 1.2–1.6 mm in length and have a broad, expanded base (0.3 mm in width) and long spine-like blades that meet for almost their entire length and are subcircular in cross-section. Close to the base is there a narrow gap between the blades, occupying no more than one-third of the blade length. The interior structure and appearance of the valves is unknown. These spinate tridentates are found along the ambulacral zones. The second type of pedicellaria is similar only smaller, between 0.3 and 0.6 mm in length, and with shorter, stubbier blades. They have a rounded base without handles which grades into short blades that contact along most of their length. Again there is a narrow opening, much shorter than the length of the blades, close to the base. Their interior structure is also unknown. These small pedicellariae are found in association with both ambulacral and interambulacral zones.

The lantern is preserved in two specimens, NHM EE13984 and UO DGO-23001. Large hemipyramids are present but are always partially buried under other plates of the test so that their overall shape is impossible to reconstruct. They taper adorally and each has a deep, well-defined outer groove for retractor and protractor muscle attachment (Fig. 3A). Rotulae are of the hinge-construction type (Fig. $4A_2$). Both internal (Ri) and external (Re) surfaces are clearly displayed and show the articulation facets and symmetrical ligament insertion furrows for attachment to the epiphyses. Adaxially the rotula is notched and ends as two rounded projections while proximally there is a flattened condyle with a distinctive V-shaped groove on its lower surface. Epiphyses were presumably present but are nowhere clearly seen. A flat plate seen in Fig. $4A_2$: e may be an epiphysis. This has only a weak lateral section unlike the axe-shaped epiphyses of crown-group echinoids illustrated by Kroh and Smith (2010: fig. 19A–C). On one surface there is a long median groove, presumably to house the rotula. A single ossicle with a narrow subcircular shaft that ends in a bent head with a double condyle (Fig. $4A_2$: c) is interpreted to be a compass. Teeth are up to 3 mm wide with a flat axial face and convex abaxial face. They are simple oligolamellar in structure (see Reich and Smith 2009), constructed of a biseries of stout lath-like elements (Fig. 5B). At any one point there are some five laths abreast on each side of the tooth.

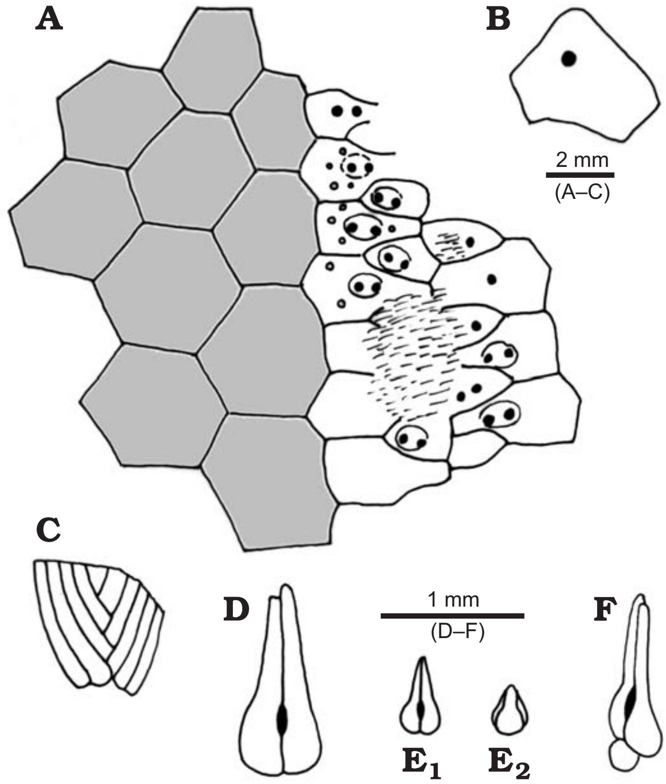

Fig. 5. Camera lucida drawings of test plating, tooth, and pedicellariae. **A**–**E**. *Rhenechinus ibericus* (Hauser and Landeta, 2007), Aguión Formation, Emsian, Lower Devonian, Arnao, Asturias, NW Spain. **A**. UO DGO-23000, adapical ambulacral and interambulacral (shaded) plating. **B**. UO DGO-23002, genital plate. **C**. UO DGO-23001, tip of oligolamellar tooth seen in axial view. **D**. UO DGO-23001, spinate tridactylous pedicellaria. **E**. UO DGO-23000, two small tridactylous pedicellariae (E_1 and E_2). **F**. *Rhenechinus hopstaetteri* Dehm, 1953, DBM.HS.285, spinate tridactylous pedicellaria with basal element.

← Fig. 4. Echinocystitid echinoid *Rhenechinus ibericus* (Hauser and Landeta, 2007). Aguión Formation, Emsian, Lower Devonian, Arnao, Asturias, NW Spain. **A**. NHM EE13984; entire specimen (A_1), detail of lantern elements (A_2), detail of internal haft on ambulacral plates (A_3). **B**. UO DGO-23000, showing detail of ambulacral plating. Abbreviations: c, compass; e, epiphysis; H, hemipyramid; h, haft on internal face of ambulacral plate; Ri, rotula-internal face; Re, rotula-external face.

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Remarks.—This species differs from *Rhenechinus hopstaetteri* in having fewer more regularly polygonal interambulacral plates with rather thicker and more upright sutures. Furthermore, the surface of interambulacral plates shows a distinctive pattern of fine circular pits towards their centre, which is never seen in *R. hopstaetteri*.

Stratigraphic and geographic range.—Emsian, Lower Devonian; Cap la Vela (Arnao), northern Spain.

Rhenechinus hopstaetteri Dehm, 1953

Figs. 6, 7.

1952 "Ein Seeigel aus dem Hunsrückschiefer"; Hopstätter 1952: 33.
1953 *Rhenechinus hopstätteri*; Dehm 1953: 93, pl. 5: 1–4.
1961 *Rhenechinus hopstätteri* Dehm, 1953; Kuhn 1961: 33, figs. 15, 16.
1966 *Rhenechinus hopstatteri* Dehm, 1953; Kier 1966: U303, fig. 224.2.
1970 *Rhenechinus hopstätteri* Dehm, 1953; Kutscher 1970a: 40.
1970 *Rhenechinus hopstätteri* Dehm, 1953; Kutscher 1970b: 96.
1980 *Rhenechinus hopstaetteri* Dehm, 1953; Mittmeyer 1980: 38.
1990 *Rhenechinus hopstätteri* Dehm, 1953; Bartels and Brassel 1990: 181, fig. 169.
1997 "Seeigel *Rhenechinus hopstätteri* mit erhaltenen Stacheln"; Bartels et al. 1997: 49, fig. 61.
1998 *Rhenechinus hopstaetteri* Dehm, 1953; Bartels et al. 1998: 210, fig. 188.
1999 *Rhenechinus hopstätteri* Dehm, 1953; Jahnke and Bartels 1999: 43.
2000 *Rhenechinus hopstätteri* Dehm, 1953; Jahnke and Bartels 2000: 43.

Holotype: BSPG. 1955 I 585.

Type horizon: Hunsrück Slate, Lower Emsian, Lower Devonian.

Type locality: Bundenbach, Rhineland-Palatinate, Germany.

Material.—One specimen, DBM.HS.285, Eschenbach-Bocksberg mine, Bundenbach, Rhineland-Palatinate, Germany.

Diagnosis.—A species of *Rhenechinus* with up to 8 interambulacral columns in a zone with plates of rather irregular shape and size; surface of plates lacking pitted ornamentation.

Description.—The holotype (Fig. 6) shows an articulated test in oral view and the new specimen (Fig. 7) is a complete test squashed in lateral profile. The test must have been subglobular in life and taller than wide, with a diameter up to approximately 10 cm. Apical disc unknown but relatively small, as the ambulacra converge adapically (Fig. 7A).

Ambulacral zones are narrow and biserial with a primary element alternating with a small demiplate in each half ambulacrum (Fig. 6B). Pore-pairs are prominent and offset forming a double series in each column. The pore-pairs are about 1 mm in width with an obvious periporal rim; the inner pore pierces the plate rather than forming a marginal notch. There are small granules scattered on the adradial and perradial sides of the zone of pore-pairs. Towards the peristome plates become narrower and wider, and pore-pairs become smaller. Ambulacral plating appears to extend further onto the peristome than interambulacral plates (Fig. 6C).

Interambulacral plates are up to 6 mm in width and irregularly polygonal in outline. At the widest point there are some nine plates abreast. Only the adradial series of plates form a regular column and these may bear slightly larger tubercles than other plates. Plates are relatively thin—not much more than 0.6 mm in thickness, and have bevelled edges. A single plate forms the adoral boundary to the peristome and this is followed by two plates that just touch interradially and then by three plates, a large central hexagonal plate and two adradial pentagonal plates (Fig. 6C).

A membrane of small platelets covers the peristome (Fig. 6C), which is about 20 mm in diameter. While ambulacral plates extend a little way onto this membranous region, they are confined to the outer region.

Spines are up to 4 mm in length and are concentrated in the peristomial and ambulacral zones (Figs. 6A, 7B). There are several slender spines to each ambulacral plate, with somewhat longer spines being found adradially and shorter spines perradially. Small spines are also found on interambulacral plates but are not nearly as dense nor as long. Small spinate tridactylous pedicellariae are present on interambulacral plates (Figs. 5E, 7B). These are approximately 1 mm long and have a swollen base and long spine-like blades that are in contact along most of their length. The pedicellarial head rests on a small element some 0.2 mm in width that is either a stem element (as described by Haude 1998) or a small tubercle (preservation is not adequate to distinguish).

The lantern is present but internal. Hemipyramid tips can be seen (Fig. 7C) and show a deep abaxial groove for retractor and protractor muscle insertion. The teeth that protrude have a flat axial face and are simple oligolamellar in strucure with four or five laths abreast on each half. They end at a simple point.

Remarks.—The original description given by Dehm (1953) is detailed and largely correct. The new specimen provides additional information about the test shape and about the distribution of spines and pedicellariae. This is a species that attains almost twice the size of the Spanish species but we do not think the diagnostic differences are simply size related. Although *R. ibericus* may increase the number of interambulacral columns in each zone as it grows, the surface ornament in the two species is quite distinct with the Spanish species having a strongly pitted surface and the German species a smooth, unpitted surface.

One other echinoid, *Porechinus porosus* is known from the same formation (Dehm 1961) and this does have a strongly pitted ornament to its plate surfaces. However, it differs in having distinctly thicker plating and ambulacral plates that are uniserially arranged. All the other echinoid specimens of the Lower Emsian Hunsrück Slate (*Lepidocentrus* spp.; Table 1) are based on fragmentary material and need to be revised. This is made especially difficult by the incomplete nature of the type material of *Lepidocentrus* (Müller 1857).

Stratigraphic and geographic range.—Hunsrück Slate, Lower Emsian, Lower Devonian; Gemünden and Bundenbach, Rhineland-Palatinate, Germany.

Discussion and conclusions

Rhenechinus was originally treated as a lepidocentrid by Dehm (1953) and Hauser and Landeta (2007) also assigned

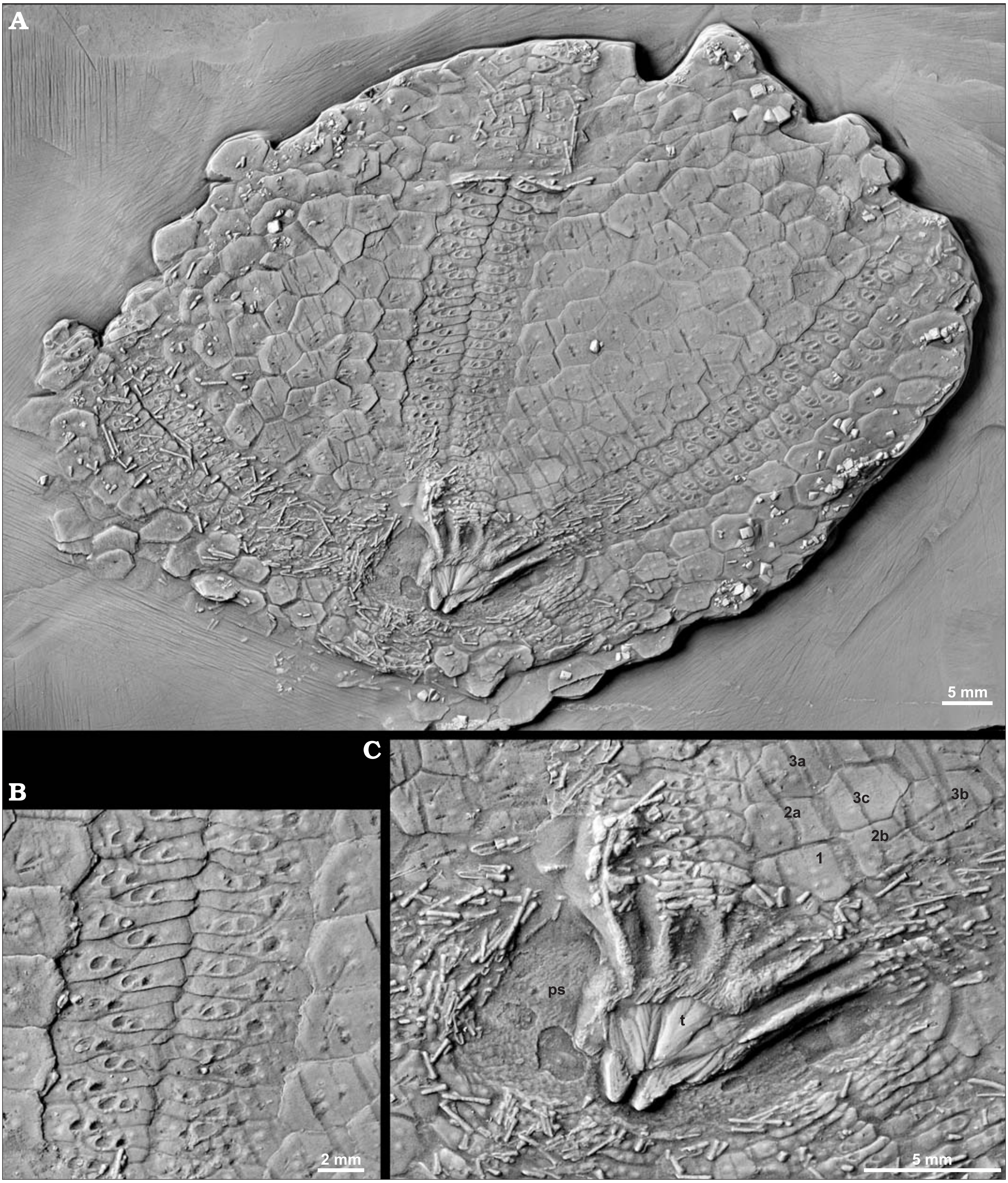

Fig. 6. Echinocystitid echinoid *Rhenechinus hopstaetteri* Dehm, 1953, BSPG.1955 I 585 (holotype), Hunsrück Slate, Lower Emsian, Lower Devonian; Gemünden, Rhineland-Palatinate, Germany. **A**. General view. **B**. Detail of ambulacral plating. **C**. Detail of oral region. Abbreviations: ps, peristomial membrane; t, tooth; 1, 2a, b, 3a–c, first three rows of interambulacral plates.

their Spanish specimen to *Lepidocentrus*. Kier (1965: 450, 1966) transferred *Rhenechinus* to the Echinocystidae on the basis of its plesiomorphic similarity to *Echinocystites*. However, much of its anatomy was at that time incompletely

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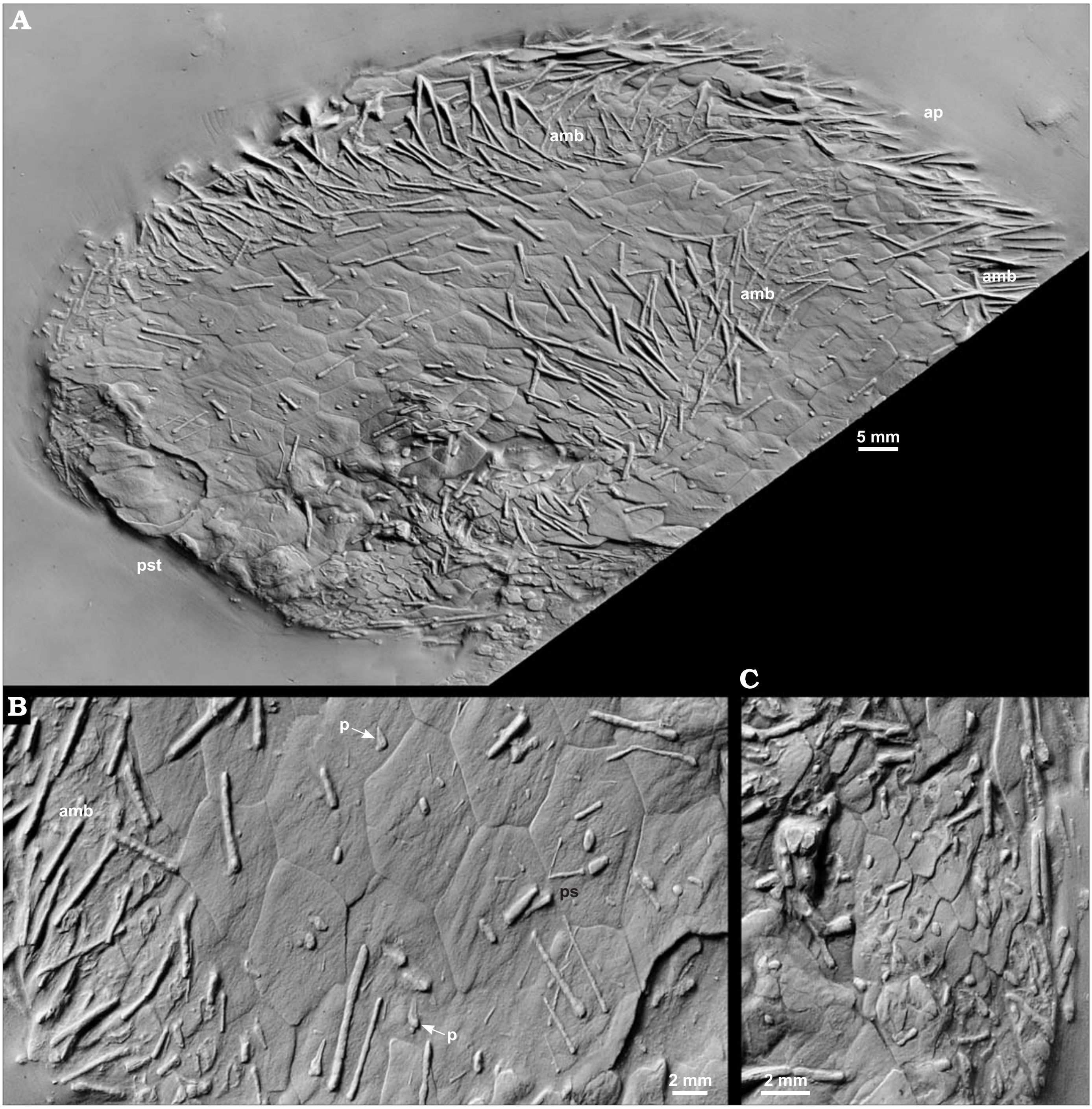

Fig. 7. Echinocystitid echinoid *Rhenechinus hopstaetteri* Dehm, 1953, DBM.HS 285, Hunsrück Slate, Lower Emsian, Lower Devonian; Eschenbach-Bocksberg mine, Bundenbach, Rhineland-Palatinate, Germany. **A**. General view. **B**. Detail of adoral plating showing pedicellariae and spines. **C**. Detail of adoral ambulacral plating. Abbreviations: amb, ambulacral zone; ap, apical disc region; p, pedicellaria; ps, pedicellarial stalk element; pst, peristome.

known. The new specimens from Spain (Figs. 3–5) and Germany (Fig. 7) provide important new information on the morphology of *Rhenechinus* and help confirm its phylogenetic position as lying between *Echinocystites* and the Proterocidaridae. Based on our new material we now confirm that *Rhenechinus* retains many primitive features compared to other Devonian echinoids. Firstly, as first noted by Jesionek-Szymańska (1982), its teeth have a very primitive construction-termed simple oligolamellar (Reich and Smith 2009), like those of *Echinocystites* but in marked distinction to the teeth of archaeocidarids, lepidesthids, lepidocentrids, and palaechinids, all of which have true lamellar teeth. Secondly, the radial water vessel in *Rhenechinus* is enclosed within the ambulacral plates, at least adorally. Each primary ambulacral plate has a large internal haft that projects perradially to underlie the radial water vessel (Fig. $4A_3$), again a feature seen in all Ordovician and Silurian echinoids, including *Echinocystites*, but in none of the other Devonian forms except *Albertechinus*. Thirdly, the lack of enlarged primary tubercles and spines distinguishes *Rhenechinus* from other Devonian echinoids with the exception of *Porechinus*. Larger tubercles and spines are wanting from all Silurian and Ordovician echinoids and it is only in the Devonian that echinoids with larger articulated spines are first encountered. Finally, the ambulacral plating in *Rhenechinus* is identical to that seen in *Echinocystites*, and consists of a primary plate alternating with a demiplate. This pattern of plating is not found in any other Devonian echinoid. All these features confirm the primitive status of *Rhenechinus* and its close similarity to *Echinocystites*. However, compared to *Echinocystites*, *Rhenechinus* has more regularly organized interambulacral plating and distinct peripodial rims around its pore-pairs, as in proterocidarids. *Rhenechinus* is therefore phylogenetically intermediate between *Echinocystites* and the Proterocidaridae.

Rhenechinus provides further information on the types of pedicellariae present in Palaeozoic echinoids. It possessed only tridactylous pedicellariae, although these were of two forms, large and small. The large spinate pedicellariae are similar in appearance to those that have been found in other Devonian echinoids (*Lepidocentrus*; Haude 1998). They are three-bladed and rest either on a small basal element or directly onto a tubercle. Ophicephalous and globiferous pedicellariae, which have been reported from some Carboniferous taxa (Geis 1936; Coppard et al. 2012), are wanting. This supports the view that ophicephalous and globiferous pedicellariae evolved only in archaeocidarids. Larger pedicellariae are more common along the ambulacra suggesting that their primary role may have been to protect the tube-feet from pests and parasites. Smaller pedicellariae are found scattered over interambulacral plates and may have been rather common, although they are now preserved only in small patches.

Our new material also provides information on the structure of Palaeozoic echinoid lanterns. Specifically we recognize for the first time that compass elements were present (Fig. $4A_2$). These slender elements act to regulate the volume of the peripharyngeal coelom as the lantern moves in and out of the test during feeding. Although lanterns have been described for a small number of Ordovician and Silurian echinoids (*Aulechinus*, *Palaeodiscus*, *Echinocystites*, and *Aptilechinus*) none have preserved compasses. Compasses are slender and rather fragile elements by comparison to the other elements that make up the lantern of sea urchins, so their absence may be taphonomic rather than genuine. Their definitive presence in *Rhenechinus* suggests that they must also have been present in many of the other Palaeozoic echinoids by phylogenetic implication.

It is unusual to find the same echinoid genus in two such very different environmental settings and this requires comment. The main difference between the Spanish and German deposits is that the former were formed under normal shallow marine conditions on a terrigeonous-carbonate ramp (Arbizu et al. 1995; see above), while the Hunsrück Slate lacks carbonates and was deposited under deeper-water, shelf-basin conditions (Bartels et al. 1998). The fact that the echinoids are common, and preserved so well at Arnao, indicates they are autochthonous. By contrast, after hundreds of years of work on the fauna of the Hunsrück Slate there are only two definite specimens of *Rhenechinus* known. Because echinoids preserved in the Hunsrück Slate are so rare (around ten specimens only are known; Table 1) they are presumably allochthonous, washed into the basins from shallower habitats in nearby local swells.

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