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The oldest cinctan carpoid (stem-group Echinodermata), and the evolution of the water vascular system

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A new cinctan (***Protocinctus mansillaensis* gen. et sp. nov.**), from the early Middle Cambrian of the Iberian Chains (north-east Spain), is described with the aid of X-ray microtomography and three-dimensional computer models. Investigation in this manner was possible because of the unusual condition of the fossils, which are preserved as recrystallized calcite. ***Protocinctus* gen nov.** possesses an elongate body with a single left anterior feeding groove and an open posterior marginal frame (in ventral view): this combination of characters is unique amongst cinctans. Through the study of original specimens and 'virtual fossils' it was possible to reconstruct the palaeobiology of ***Protocinctus* gen. nov.**: cinctans are interpreted as pharyngeal basket feeders with a U-shaped gut, using their posterior appendage to aid stability on the sediment surface. Cinctans are critical to understanding the evolutionary history of the echinoderm stem group, as they illustrate the transition from a paired water vascular system (basal) to one constructed from just the left hydrocoel (derived). The former condition is also observed in another group of stem-group echinoderms, the ctenocystoids, and is hypothesized for the latest common ancestor of the echinoderms and hemichordates.

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INTRODUCTION

Cinctans are an enigmatic group of exclusively Middle Cambrian echinoderms. Together with ctenocystoids, stylophorans, and solutes they comprise the carpoids: an extinct group of deuterostomes, the biological affinities of which are extremely contentious because of their unusual character combinations. Carpoids possess a skeleton composed of calcite plates with a characteristic three-dimensional microstructure (stereom), a character that is restricted to the echinoderms amongst extant deuterostomes (Bottjer *et al.*, 2006). However, all living echinoderms exhibit pentamery (five-fold radial symmetry), whereas carpoids are asymmetrical or bilaterally symmetrical. In addition, some carpoids may have possessed gill slits (Domínguez, Jacobson & Jefferies, 2002; Smith, 2005, 2008), which do not occur in modern echinoderms, and the existence of an echinoderm-type water vascular system is still debated (Smith, 2005). As a result, there are a variety of palaeobiological and phylogenetic hypotheses for carpoids, with cinctans interpreted as: (1) derived blastozoans (Parsley, 1999; David *et al.*, 2000), (2) stem-group hemichordates (Domínguez & Jefferies, 2005) or (3) basal stem-group echinoderms (Jefferies, 1990; Smith, 2005).

Trochocystites bohemicus Barrande, 1887 was the first cinctan to be described, from the Skryje Shales of Bohemia (Czech Republic). Cinctans were subsequently reported from parts of western Gondwana and Siberia (Jaekel, 1918; Ubaghs, 1968b; Schröeder, 1973; Friedrich, 1993, 1995; Sdzuy, 1993; Fatka & Kordule, 2001; Rozhnov, 2006; Zamora & Smith, 2008). The oldest cinctan to date is a poorly preserved specimen of *Asturicystis* sp. (*sensu* Sdzuy, 1993),

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from the early Middle Cambrian (Lower Caesaraugustian, *Badulesia tenera* Zone) of Presa del Porma, northern Spain (Sdzuy, 1993). *Asturicystis havliceki* Fatka & Kordule, 2001, from the Jince Formation of the Czech Republic, may be older or equal in age; however, the stratigraphic correlation of Bohemian and Mediterranean faunas is problematic (Sdzuy, 1993; Álvaro & Vizcaïno, 1998; Fatka, 2006), and the morphology of this species is incompletely known. The next youngest finds are well-preserved specimens of *Asturicystis jaekeli* Sdzuy, 1993, *Sotocinctus ubaghsi* Sdzuy, 1993, and *Trochocystoides planus* Sdzuy, 1993, from a nearby locality in northern Spain (Soto de Caso), Lower Caesaraugustian, *Badulesia juliverti* Zone. This material comprises the so-called 'early Cincta' fauna, defined by Sdzuy (1993: 191).

A new cinctan, *Protocinctus mansillaensis* gen. et sp. nov., is here reported from the early Middle Cambrian of Spain. This material represents the oldest recorded occurrence of the group, thereby increasing the stratigraphic range of the Cincta. Cinctans are typically preserved as moulds; however, the specimens studied here are preserved in three dimensions as recrystallized calcite. As a result, they were suitable for study using a combination of conventional techniques and computed tomography. The anatomy of *Protocinctus* gen. nov. is described below, with morphofunctional information used to draw conclusions regarding cinctan palaeobiology. These findings improve our knowledge of this intriguing group, forming the basis for a discussion of the phylogenetic position and evolutionary history of cinctans.

GEOLOGICAL SETTING AND STRATIGRAPHY

The material described herein was collected from Cambrian rocks in the northern part of the Iberian Chains, north-east Spain (Fig. 1). There are two large Palaeozoic outcrops in this area, trending from the north-west to the south-east and separated by the Tertiary-aged Calatayud-Teruel basin (Lotze, 1929; Carls, 1983). Palaeozoic rocks are structured into three tectonostratigraphic units, the Mesones, Herrera, and Badules units (Gozalo & Liñán, 1988), with Cambrian outcrops common in all three. Fossils were found in Cambrian rocks from the south-west part of Purujosa village, and these deposits are located in the Badules Unit. Purujosa is part of the Tablado Range, situated 75 km west of Zaragoza, the major city in the area.

A well-developed section in Borraca Creek best displays the Middle Cambrian Mesones Group (Liñán *et al.*, 1992), which is divided into the following formations: Valdemiedes (50 m, pars), Mansilla (60 m), and Murero (70 m). The Mesones Group is sandwiched between the Daroca and Borobia formations: both are composed mainly of sandstones and are exposed in the same section. All three formations (Valdemiedes, Mansilla, and Murero) are composed of shales with interbedded carbonate nodules, deposited mainly in sublittoral environments (Liñán *et al.*, 1992; Sdzuy & Liñán, 1993; Gozalo *et al.*, 2004). *Protocinctus* gen. nov. is from the upper part of the Mansilla Formation (Fig. 2); this part of the section is composed of purple to reddish nodular limestones and shales, probably deposited in shoreface to offshore conditions (facies D of Álvaro & Vennin, 1997).

The Middle Cambrian of the Iberian Peninsula and France is subdivided into three stages: Leonian, Caesaraugustian, and Languedocian (Liñán *et al*., 1992, 2002, 2004; Álvaro & Vizcaïno, 1998). Trilobites associated with *Protocinctus* gen. nov. include *Eccaparadoxides asturianus* (Sdzuy, 1968), *Eccaparadoxides sulcatus* (Liñán & Gozalo, 1986), *Conocoryphe* (*Parabailiella*) sp., *Asturiaspis inopinatus* Sdzuy, 1968, and *Parasolenopleura ouangondiana* (Hartt, in Dawson, 1868). Thus, this level belongs to the *Eccaparadoxides asturianus* Zone, which is considered to be Upper Leonian (early Middle Cambrian) in age (Sdzuy, Liñán & Gozalo, 1999). A complete correlation of this interval with different regional stages is synthesized in Sdzuy *et al.* (1999) and Gozalo *et al.* (2007). In the 2008 version of the ICS international stratigraphic chart (http://www.stratigraphy.org/cheu.pdf), the *Eccaparadoxides asturianus* Zone belongs to Stage 5 of Cambrian Series 3.

MATERIAL AND METHODS

Six specimens are described in this paper, all of which were preserved three-dimensionally in red siltstones as recrystallized calcite. Two specimens (MPZ2007/2477 and MPZ2007/2478) were dissolved in hydrochloric acid (10%) to produce moulds that were studied using latex casts. Three specimens (MPZ2004/170, MPZ2004/171, and MPZ2004/172) were visualized using a combination of X-ray microtomography (XMT) and custom-built computer software (SPIERS). XMT is an ideal technique for imaging the interior of solid opaque samples such as fossils, as high-resolution images can be rapidly obtained without damaging specimens (Sutton, 2008). Before scanning, specimens were trimmed using a rock saw so that only thin (1–7-mm thick) matrix borders surrounded the fossils. XMT was performed on a Phoenix v|tome|x 's' system, and this generated data sets of several hundred two-dimensional section images (tomograms), with voxel sizes ranging from 20 to 30 μm^3 (depending on the sample size). Each tomographic data set was reconstructed using the custom-built SPIERS software suite to produce a three-

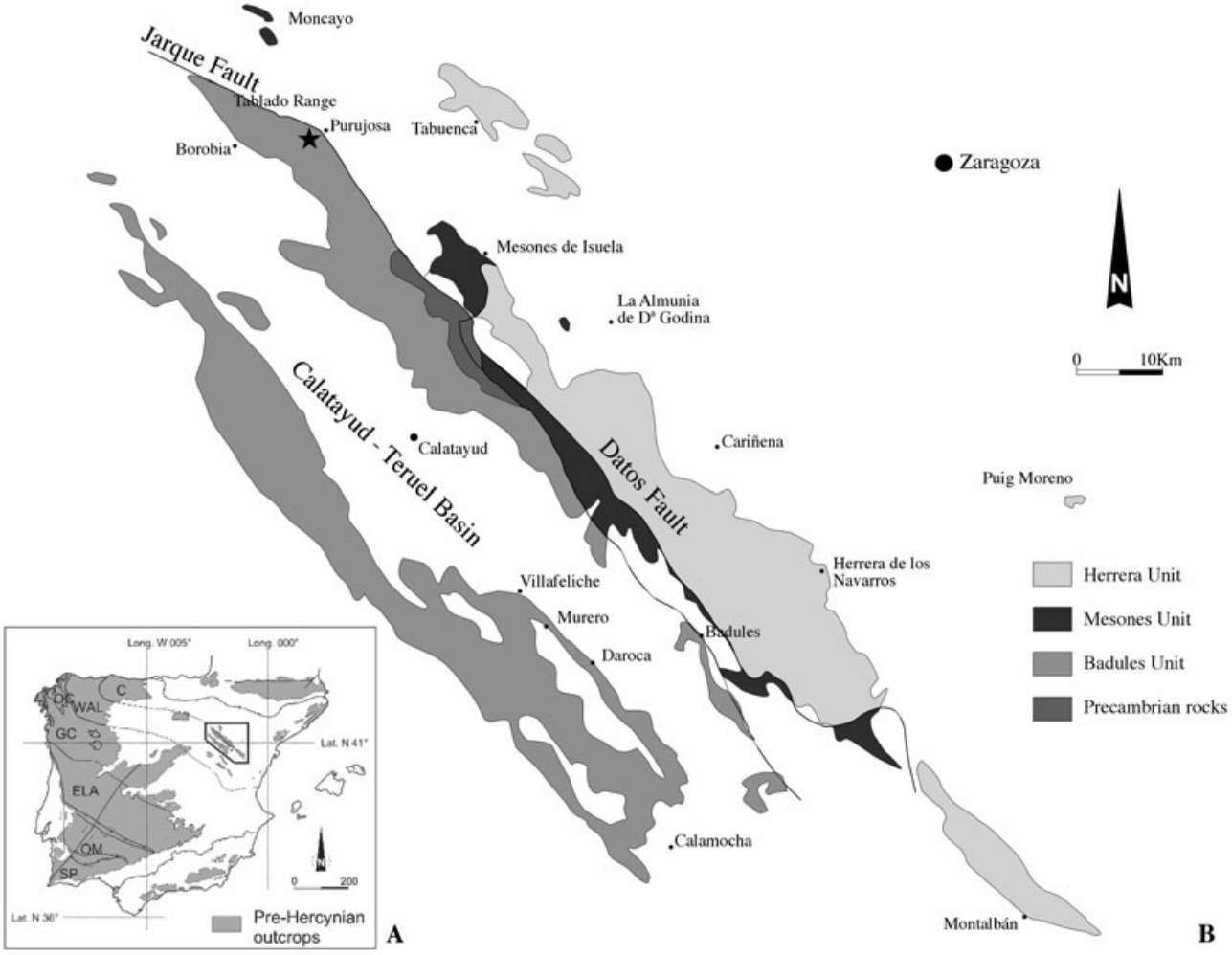

Figure 1. A, B, the geographic and geological setting of the Iberian Chains (north-east Spain), showing the type locality (indicated by a star), and surrounding areas. Modified from Gozalo & Liñán (1988).

dimensional 'virtual fossil', following the methodology of Sutton *et al* (2001, 2002). This process involved manual 'editing' of data sets to remove objects in the matrix that were irrelevant to the fossil and to accurately resolve plate boundaries. Reconstructions were studied on computer using stereo-capable viewing software, with virtual dissections performed to examine individual plate morphologies.

SYSTEMATIC PALAEONTOLOGY

PHYLUM ECHINODERMATA BRUGUIÈRE, 1791
(EX KLEIN, 1734)

CLASS CINCTA JAEKEL, 1918

FAMILY SUCOCYSTIDAE? FRIEDRICH, 1993

GENUS ***PROTOCINCTUS* GEN. NOV.**

Derivation of name: Greek, *protos* (first) + cinctus.

Diagnosis: Relatively elongate, oval-shaped theca composed of ten marginal plates (M5r–M4l). Single and long left marginal groove, extending from M1r to M1l. Lintel composed of three suropercular plates. Supraoral plate boot-shaped. Anterior right embayment formed by M0, M1r, and M2r. Weakly developed ventral swellings on the lower surfaces of M0, M1r, and M2r. Marginal frame open in posterior ventral aspect, with an intercalated plate between M4l and M5r.

***PROTOCINCTUS MANSILLAENSIS* SP. NOV.**
(FIGS 3, 4)

Derivation of name: After the Mansilla Formation, where the material was collected.

Diagnosis: As for the genus (monotypic).

Holotype: MPZ2004/170 (Fig. 4A–G, J): a fully articulated specimen preserved as recrystallized calcite in a siltstone matrix.

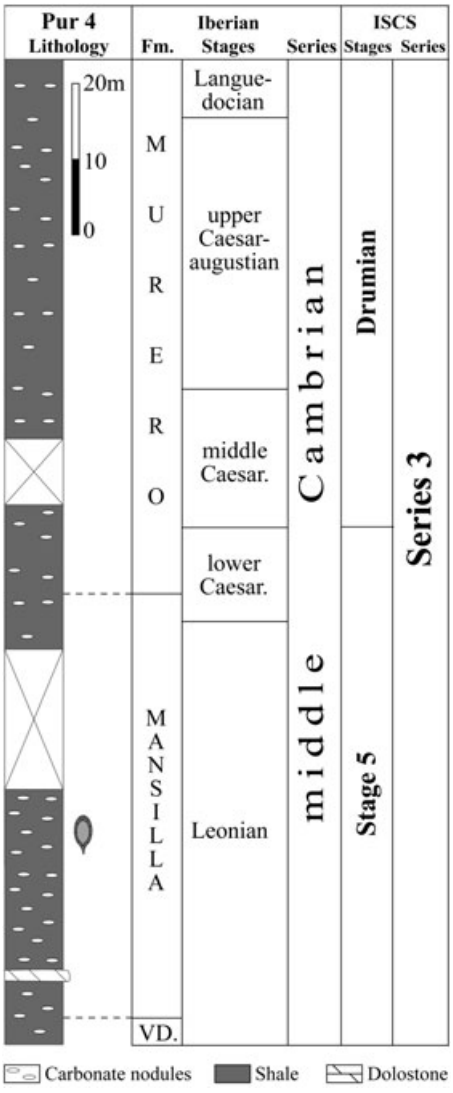

Figure 2. Stratigraphic section of the Mesones Group in Purujosa village (type horizon marked by a schematic diagram of ***Protocinctus mansillaensis*** **gen. et sp. nov.**). Abbreviations: Caesar, Caesaraugustian; VD., Valdemiedes Formation.

Other material: MPZ2004/171, MPZ2004/172 (Fig. 4H), MPZ2007/2476, MPZ2007/2477 (Fig. 4I), and MPZ2007/2478: nearly complete articulated specimens. Specimens are housed in the Área y Museo de Paleontología, Universidad de Zaragoza (MPZ). Virtual data sets are available on request.

Type locality: Borraca Creek, 3 km south-east of Purujosa village, in the northern part of the Iberian Chains.

Type horizon: Early Middle Cambrian (Cambrian Series 3, Stage 5), Upper Leonian, Mansilla Formation, *Eccaparadoxides asturianus* Zone.

Description: In the following description the orientation and plate notation follows that of Friedrich (1993), with the marginal plates abbreviated as M (Fig. 3). The anterior medial marginal plate is termed M0, and the other marginal plates are numbered sequentially around the margin (anterior to posterior) as M1l, M1r, M2l, M2r, etc., with l and r indicating their location to the left or right of M0 in dorsal aspect (Fig. 4B).

Protocinctus gen. nov. is composed of an anterior theca (body) and a posterior stele (appendage). The theca is flat (at least four times wider than thick), with a frame of ten marginal plates (the cinctus) enclosing the dorsal and ventral plated surfaces (the supracentral and infracentral integuments) (Figs 3, 4). The oval-shaped theca is longer than it is wide. In the holotype (MPZ2004/170) it is approximately 17 mm in length, with a maximum width of 10 mm (Fig. 4A, B). Other specimens are approximately 12–14 mm in length and 7.5–8.5 mm in width, with a mean length to width ratio of 1.6 : 1.

Orifices: Two openings are preserved in *Protocinctus* gen. nov. The first is a small circular aperture in the anterior right corner of the cinctus (best preserved in MPZ2004/170, and approximately 1.2 mm in diameter) that occurs between M1r and M2r (Figs 3E, 4D). It is bounded dorsally by the boot-shaped supraoral plate (approximately 1 mm in length and 2 mm in width; MPZ2007/2477), which articulates with the inner dorsal surfaces of M1r and M2r (Figs 3E, 4A, D, I). A single left marginal groove covered by multiple sets of small plates (the labrum, Sdzuy, 1993) leads into this opening (Figs 3E, 4C, D, I).

The second opening is also anterior but is much larger, being approximately 3.8 mm in diameter in MPZ2004/170 (Figs 3A, D, 4C, D): it is termed the porta (Sdzuy, 1993). The porta penetrates the marginal frame coincidently with the midline, is covered dorsally by a large rounded plate (the operculum; Figs 3C, E, 4A, C, D, G–I), and is bounded ventrally and laterally by M0, M1l. and M1r, which give the opening a concave lower border (Figs 3D, E, 4C, D). The upper posterior margin of the opening is delimited by three large polygonal plates from the supracentral integument (the lintel; Figs 3C, E, 4H, I). In MPZ2004/170 the operculum measures approximately 2.7 mm in length and 2.1 mm in maximum anterior width, filling the anterior of the porta. It is bowl-shaped, with a flat to concave dorsal surface and a convex ventral one. At its posterior margin the operculum articulates with all three lintel plates (Figs 3C, 4I).

Cinctus: The cinctus or marginal frame is composed of the following plates: M0, M1l, M2l, M3l, M4l, M1r, M2r, M3r, M4r, and M5r (Fig. 3A, B). These plates

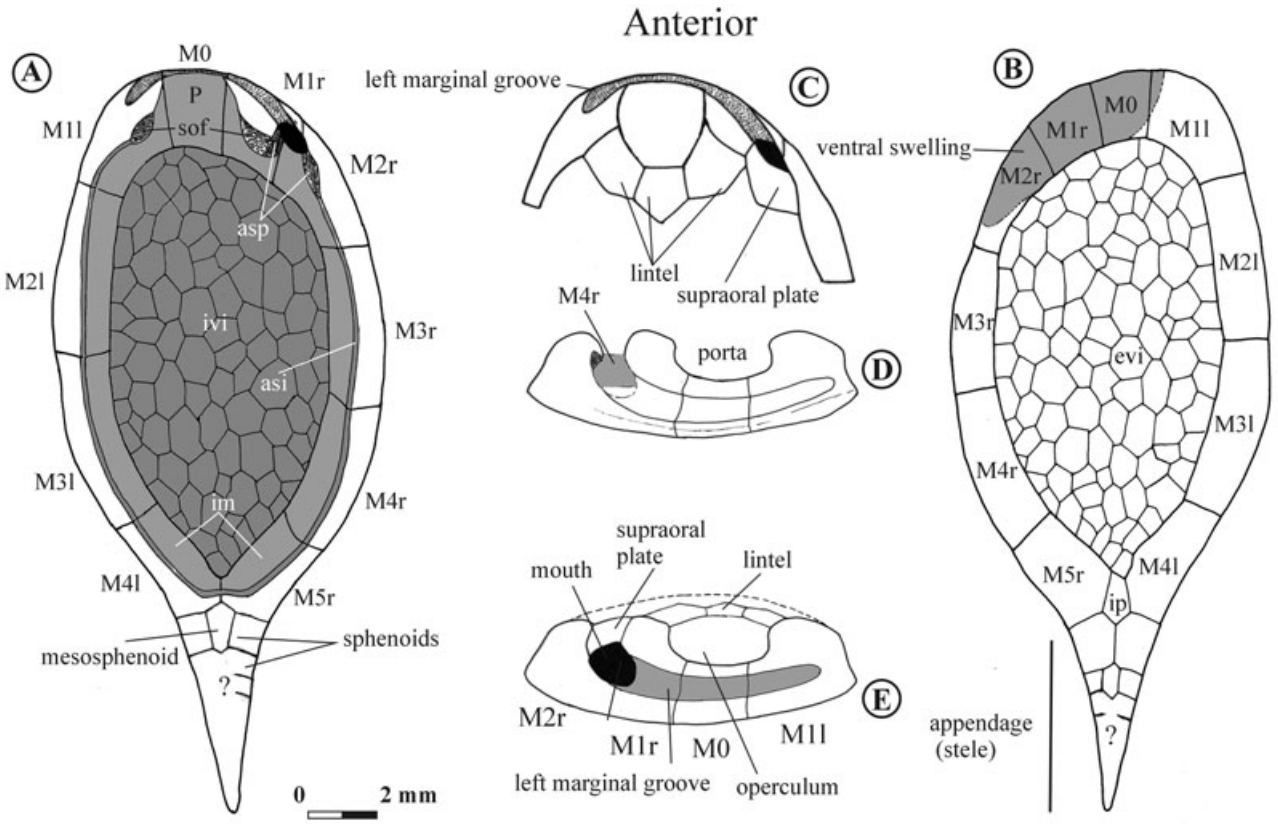

Figure 3. ***Protocinctus mansillaensis*** **gen. et sp. nov.** reconstruction. A, C, dorsal view. B, ventral view. D, E, frontal views. Abbreviations: asi, articulation with the supracentral integument; asp, articulation with the supraoral plate; divi, depression in the interior ventral integument; evi, exterior of ventral integument; im, interior of the marginal plates; ip, intercalated plate; ivi, interior of the ventral integument; M0–5, marginal plates 0–5 (l, left and r, right); P, porta; sof, suropercular facets.

confer a rigid structure to the animal. Marginal plates are subtriangular in cross section: the lower surface of the frame is wide and flat or slightly convex (Fig. 4E, F), whereas the upper surface is thin and strongly convex (Fig. 4A, G). On their inner faces plates are strongly concave, and their outer faces are gently curved (Fig. 4G). Ventral swellings in the marginal plates are greatly reduced compared with those seen in other cinctans. *Protocinctus* gen. nov. has only one indistinct swelling, located in the ventral surfaces of M0, M1r, and M2r (Figs 3B, 4B); this is most obvious in larger individuals. Dorsal and ventral furrows run continuously along the inside of the cinctus, close to the upper and lower borders of the frame (Figs 3A, 4A, G). These furrows presumably acted as insertions for the supracentral and infracentral integuments. The inner junctions between the marginal plates were apparently flat.

At the anterior of the cinctus, M0 (Figs 3A, B, E, 4B, D) articulates with M1l and M1r, forming the floor of the porta. It is subrectangular in outline and longer than it is wide, with a length to width ratio of approximately 1.5 : 1. A distinct groove is present in the anterior margin of M0, occupying almost one half of the anterior plate height: this is part of the left marginal groove.

Both M1l and M1r possess dorsal articulation facets and portions of the marginal groove. M1l is curved in shape (Figs 3A, B, 4A, B), and articulates rigidly with M0 and M2l, but more flexibly with the infracentral integument and the lintel. The length of the plate is approximately twice the width, with the width decreasing in the posterior of the plate. The marginal groove occurs on the anterior margin of the plate, but weakens and then disappears completely as the plate curves laterally (Figs 3D, E, 4D). On the dorsal inner surface of M1l, the articulation facet occurs at almost one half of the distance from the anterior margin of the plate; this was likely to have been an articulation surface with lintel plate 1 (Figs 3A, C, 4A, I).

M1r is similar to M0 in ventral aspect (Figs 3B, 4B): approximately equal in width, but greater in length (length of M0 approximately 0.8 times the

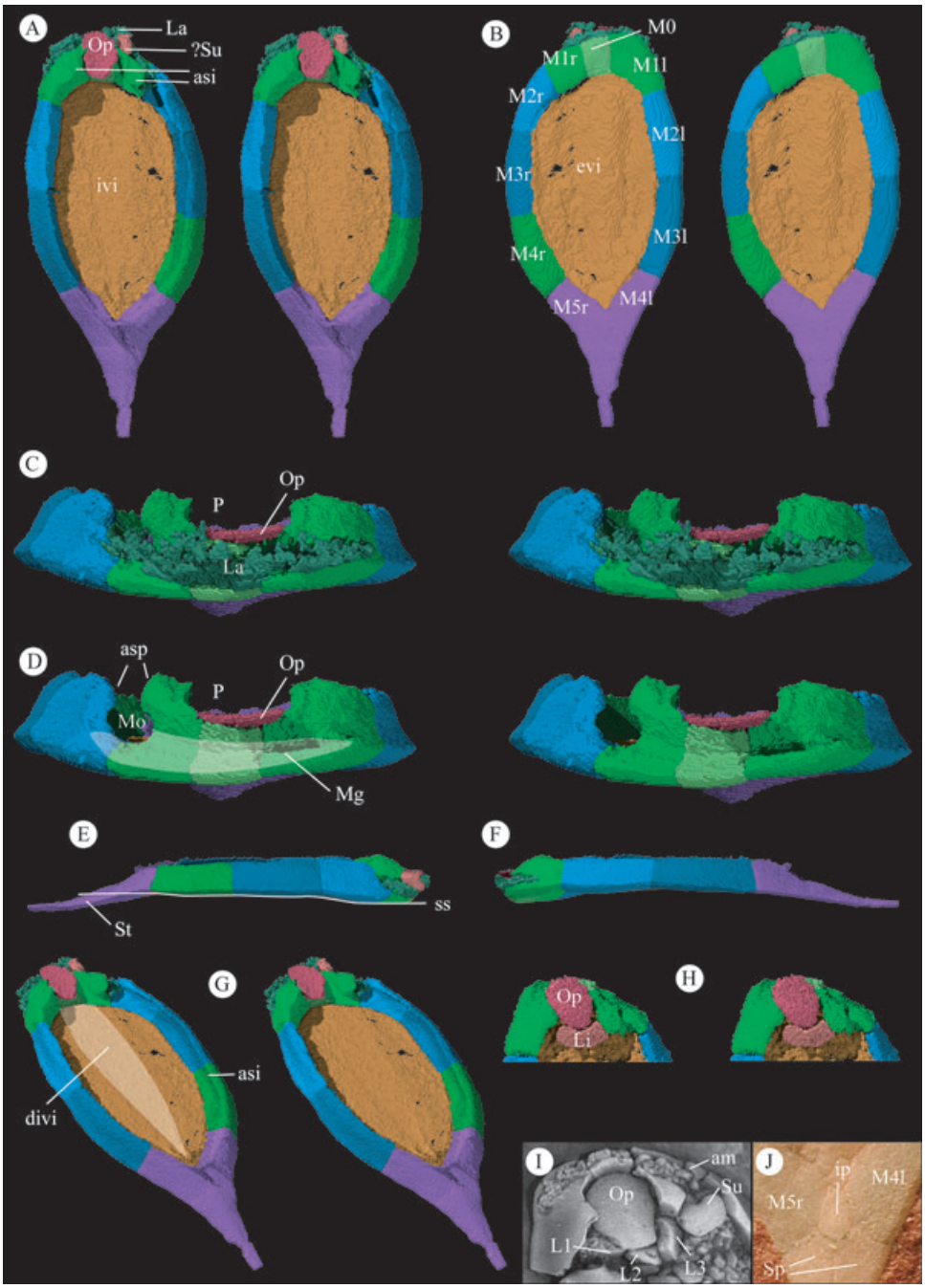

Figure 4. ***Protocinctus mansillaensis*** **gen. et sp. nov.** A–G, J, holotype, MPZ2004/170. G, MPZ2004/172. H, MPZ2007/2477. A–H, 'virtual' reconstructions; I, latex cast from an artificial mould of MPZ2007/2477, cast whitened with ammonium chloride sublimate. J, holotype specimen in matrix. A, B, dorsal and ventral stereo-pairs, ×3.6. C, D, Anterior stereo-pairs, without the ?supraoral plate, with and without the labrum, ×7.2. E, F, left and right lateral views, ×3.3. G, posterolateral stereo-pair, ×3.4. H, anterior region, dorsal stereo-pair, ×5.0. I, anterior region, dorsal view, ×4.6. J, posterior region of the cinctus, ventral view, ×9.0. Abbreviations: am, abnormal marginal plate; asi, articulation with supracentral integument; asp, articulation with supraoral plate; divi, depression in the interior ventral integument; evi, exterior of the ventral integument; ip, intercalated plate; ivi, interior of the ventral integument; L1–3, lintel plates 1–3; La, labrum; Li, lintel (undifferentiated); M0–5, marginal plates 0–5 (l, left and r, right); Mg, marginal groove; Mo, mouth; Op, operculum; P, porta; Sp, sphenoids; ss, sediment surface; St, stele; Su, supraoral plate.

length of M1r). It articulates with M2r, M0, the supraoral plate, infracentral plates, and the lintel (as in M1l, articulations are rigid with plates from the cinctus, and loose with other plates). The lateral margin of M1r is strongly concave where the marginal groove (Figs 3E, 4D) leads into the right circular aperture (located just below the right articulation facet). The articulation facet on M1r was for lintel plate 3 (Figs 3A, C, 4A, I): it occurs in the same plane as the facet on M1l and is similar in size.

The anterior right corner of the cinctus (M0, M1r, and M2r) curves at a greater angle than the left corner (approximately 60 ° on the right, and 40 ° on the left), forming the diagnostic anterior right embayment (Figs 3A, 4A). The inner anterior margin of M2r is strongly incised where the circular aperture occurs, giving the plate a concave shape similar to the lateral margin of M1r. In other respects it is similar to M2l, M3l, M3r, and M4r, which have a near identical elongate shape. Plates on the left of the frame are longer than those on the right (length to posterior width ratio approximately 3 : 1 on the left, and 2.5 : 1 on the right; Figs 3A, 4A).

M4l and M5r comprise the posterior of the cinctus (Figs 3A, B, 4A, B, G, J). They possess the same general shape, being less elongate than the other cinctus plates. Posterior portions of both plates decrease in width (to approximately two thirds the width of anterior parts), giving a relatively narrow posterior margin. The cinctus is open in ventral aspect, with a single intercalated plate inserted between plates M4l and M5r (Figs 3B, 4J). This plate is polygonal, with a pentagonal outline (1.3 mm in length and 1 mm in width; MPZ2004/170).

Integuments: The dorsal (supracentral) and ventral (infracentral) integuments (Figs 3A, B, 4A, B, G) are made up of numerous polygonal plates, which confer a tessellate structure to the theca. The integuments were inserted into the furrows close to the upper and lower borders of the cinctus during life (Figs 3A, 4G). The integument plates lack external ornamentation, and are typically pentagonal-shaped in marginal areas, and hexagonal in the centre. The infracentral integument is composed of approximately 75–100 plates, a much lower number than the supracentral integument (plate number uncertain). The plates are quite homogeneous in size, with the infracentral plates approximately two or three times the size of the supracentral plates. A cone-shaped depression, which narrows posteriorly, occurs in the central interior portion of the infracentral integument (Fig. 4G): this measures approximately 12 mm in length and 2.8 mm in maximum width (MPZ2004/170).

Marginal grooves: Protocinctus gen. nov. possesses a single left marginal groove (Figs 3D, E, 4D). It is horizontally oriented, running from the anterior right opening along the exterior of the cinctus, and terminating around halfway along the length of M1l. The groove is at its maximum size where it enters the anterior right opening (approximately 0.9 mm in height; MPZ2004/170). It decreases in size left of this, and maintains a relatively constant height of approximately 0.75 mm (MPZ2004/170) across M0 and the anterior of M1l, before it ends abruptly. The total length of the groove is approximately 5 mm. As briefly mentioned above, the groove is covered by numerous small plates that collectively form a structure termed the labrum (Fig. 4A, C, I). The plates that comprise the labrum are small (approximately 0.4–0.6-mm wide; MPZ2004/170) and polygonal. The organization of individual plates comprising this structure is uncertain.

Appendage (stele): The stele is most completely known in the holotype (MPZ2004/170), where it measures approximately 6.5 mm in length, and forms an angle of approximately 145 ° with M4l and M5r (Figs 3A, B, 4A, B). The ratio of stele length to theca length is approximately 1 : 2.5. The stele is composed of lateral pairs of polygonal-shaped sphenoids (Figs 3A, B, 4J), with diamond-shaped mesosphenoids inserted centrally in alternate pairs of sphenoids. The size of the stele plates decreases posteriorly. On the ventral surface, the cinctus articulates with two large, elongate sphenoids, and a single intercalated plate (Figs 3B, 4J). The preservation of the dorsal stele is incomplete (Figs 3A, 4A, G), and it cannot be described in detail; the dorsal articulation between the cinctus and the stele probably included two mesosphenoids (Fig. 3A). In cross section the stele is triangular, with a flat ventral surface; this shape is constant along the length of the stele. The ventral part of the stele is oriented so that it projects below the ventral cinctus (Fig. 4E, F).

Remarks: The characters displayed by *Protocinctus* gen. nov. are all known from other cinctans, but the character combination is unique; consequently, assigning *Protocinctus* gen. nov. to an existing cinctan family is problematic. The presence of a single left marginal groove that reaches M1l is a trait shared with some species of *Sucocystis* Cabibel, Termier & Termier, 1959; however, *Protocinctus* gen. nov. differs from these forms in other respects (the shape and height of the theca, the number of marginal plates, and the development of ventral swellings). The elongate thecal shape of *Protocinctus* gen. nov. is similar to that of *Gyrocystis* Jaekel, 1918, *Progyrocystis* Friedrich, 1993, or *Elliptocinctus* Termier & Termier,

1973. The arrangement of three plates in the lintel is similar to *Gyrocystis*, *Sucocystis*, and *Elliptocinctus*, and the absence of prominent ventral swellings is a feature shared with *Trochocystoides parvus* Jaekel, 1918, *T. planus*, *S. ubaghsi*, *A. jaekeli*, and *Gyrocystis platessa* Jaekel, 1918. We tentatively assign *Protocinctus* gen. nov. to the family Sucocystidae, based on the presence of a single long left marginal groove and the anterior continuity of the ventral swellings. *Protocinctus* gen. nov. is probably basal within the family, because it possesses an elongate theca and relatively reduced ventral swellings. This assignment is preliminary, and will be tested in a cladistic analysis to be published by the second author (Smith & Zamora, in press).

In one specimen (MPZ2007/2477), a small marginal plate is inserted between M1r and M2r (Fig. 4I). The number of marginal plates can vary within a single species of cinctan (Friedrich, 1993), but in no known specimen does an additional plate occur in the anterior frame. Although it is uncertain how cinctans added plates during growth, it is doubtful that additions could have occurred in the anterior of the frame; here, distinctive processes occur on M1l and M1r that are never transposed to other plates. Instead, because of the similarity of the marginal plates and proximal sphenoids, it is more likely that cinctans added new plates to the cinctus from the stele. As the presence of a small plate between M1r and M2r is not seen in any other cinctans, it probably resulted from abnormal plate growth. Similar abnormalities occur in stylophoran carpoids (Ware & Lefebvre, 2007).

DISCUSSION

Palaeobiology

Three major openings into the body cavity have been described in cinctans (Smith, 2005); however, only two are preserved in *Protocinctus* gen. nov. The aperture located on the anterior right side of the cinctus is widely agreed to be the mouth, with the associated marginal groove(s) being involved in feeding (Ubaghs, 1968b; Jefferies, 1990, 1991, 1997; Friedrich, 1993; Sdzuy, 1993; Jefferies, Brown & Daley, 1996; Domínguez, 1999; Parsley, 1999; David *et al.*, 2000; Smith, 2005; Zamora & Smith, 2008).

A small cone of tooth-shaped plates is preserved in the anterior left of the supracentral integument in some genera (e.g. *Gyrocystis*, *Lignanicystis* Zamora & Smith, 2008, *Sotocinctus* Sdzuy, 1993, and *Trochocystites* Barrande, 1859): this is interpreted as either an anal opening (Jefferies, 1991, 1997; Friedrich, 1993; Sdzuy, 1993; Jefferies *et al.*, 1996; Domínguez, 1999; Smith, 2005; Zamora & Smith, 2008) or a gonopore (Parsley, 1999). Although gonopores are sometimes enclosed by small pyramids (e.g. in the caryocystitid rhombiferan *Echinosphaerites* Wahlenberg, 1818), these structures normally occur along the sutures between adjacent thecal plates (Kesling, 1967); in contrast, the cinctan pyramid is embedded in a flexible plated integument, similar to the anal pyramids of pleurocystitid rhombiferans (Kesling, 1967). Furthermore, the narrow zone of small plates surrounding the cinctan pyramid is very similar in shape and size to the periprocts of cheirocrinid and pleurocystitid rhombiferans (Parsley, 1970; Sprinkle, 1974; Paul, 1984). The cinctan cone-shaped structure is best interpreted as the anus, perhaps combined with other accessory orifices (i.e. the gonopore and/or hydropore). The apparent absence of this opening in *Protocinctus* gen. nov. and other cinctans is almost certainly a taphonomic artefact, relating to poor preservation of the supracentral integument. Thus, the cinctan gut can be inferred to have passed from the anterior right mouth to the anterior left anus in a U-shaped path (Domínguez, 1999).

The function of the porta is also controversial: it was covered by a large plate (the operculum), and has been interpreted to be either an anus (Ubaghs, 1968b; Parsley, 1999) or an atrial opening (Bonik, Gutmann & Haude, 1978; Friedrich, 1993; Smith, 2005; Zamora & Smith, 2008). In life, the operculum articulated loosely at its posterior with the lintel. As a result, it was capable of considerable vertical rotation: movement of the operculum upwards created an external opening into the porta. Whereas large movable plates may have controlled the anal openings of some solutes and stylophorans (Caster, 1968; Lefebvre, 2003), the operculum is more specialized than these simple valve-like structures. Moreover, assuming that the operculum could move sufficiently to expose the majority of the porta, the associated opening would be considerably larger than the mouth (up to three times the size in *Protocinctus* gen. nov.); the cone-shaped aperture represents a better candidate for the cinctan anus (see above).

Several features of the porta suggest that it was involved in expelling large volumes of water (Zamora *et al.*, 2007); here, it is considered to be an atrial opening, with the operculum acting as an outlet valve (moving outwards under internal pressure from atrial outflow). If this is correct, then cinctans may be interpreted as pharyngeal basket feeders with internal gill slits piercing a pharynx, similar to extant tunicates (Bonik *et al.*, 1978; Sdzuy, 1985; Domínguez, 1999; Smith, 2005; Zamora & Smith, 2008). The marginal grooves may have directed water into the mouth, with food particles being filtered and captured via an internal pharyngeal basket (Smith, 2005; Zamora & Smith, 2008). Following this, compression of the flexible supracentral integument

served to compact the pharynx, forcibly expelling water through the atrial opening (Zamora *et al.*, 2007). The large depression in the central part of the interior infracentral integument of *Protocinctus* gen. nov. (Fig. 4G), which was previously poorly known, was most probably associated with the position of internal soft tissues. Assuming cinctans were analogous to tunicates in their internal anatomy, the depression may relate to the position of the pharynx.

Previous workers have argued that cinctans were oriented with the stele facing into water currents, and the flat surface of the theca resting on the sea floor (Ubaghs, 1968b; Friedrich, 1993; Jefferies *et al.*, 1996). The posterior appendage was therefore used to increase stability in the soft substratum (Ubaghs, 1968b). Cinctans used the stele to improve their stability in two different ways. Genera like *Elliptocinctus*, with long and straight steles, only inserted the distal tip of the stele into the sediment. This is evident from specimens where only the distal part of the stele is bent. A similar situation occurs in some solute carpoids, for example *Dendrocystites* Barrande, 1887 or *Dendrocystoides* Jaekel, 1918 (Caster, 1968; Jefferies, 1990), which converge with cinctans in this mode of anchoring. Our computer reconstructions clearly show that the stele of *Protocinctus* gen. nov. is preserved in an oblique orientation (Fig. 4E, F). It is highly unlikely that this position is a taphonomic effect: proximal stele plates are tightly sutured to the posterior cinctus, suggesting that the orientation of the stele was not greatly affected by the post-mortem decay of inner soft tissues. During life, the animal sat on the sediment surface, with the stele occupying a position under the cinctus (Fig. 4E, F). Consequently, the majority of the stele was inserted into the sediment, where it acted as an anchor. This alternative strategy for stability may have arisen because *Protocinctus* gen. nov. lacked the strong ventral swellings seen in forms such as *Elliptocinctus*.

Phylogenetic position

Recent molecular studies of extant animals have produced a robust phylogeny for the inter-relationships of chordates, echinoderms, and hemichordates (Bourlat *et al.*, 2006; Delsuc *et al.*, 2006). By correctly placing fossils within this cladogram, it may be possible to determine the relative order in which characters were acquired during deuterostome evolution; however, the phylogenetic position of the cinctans within the Deuterostomia is controversial.

Domínguez & Jefferies (2005) suggested that cinctans were stem-group hemichordates, stemward of ctenocystoid carpoids. Although ctenocystoids and cinctans show some similarities (see below), there are no characters that unite cinctans and hemichordates to the exclusion of other deuterostome groups. Indeed, the presence of a stereomic calcite skeleton is almost certainly a synapomorphy of echinoderms (Bottjer *et al.*, 2006). The lack of hemichordate characters in cinctans (and ctenocystoids) makes their interpretation as stem-group hemichordates unconvincing: we treat them as echinoderms, in accordance with other workers (Ubaghs, 1968b; Jefferies, 1990, 1991, 1997; Friedrich, 1993; Sdzuy, 1993; Jefferies *et al.*, 1996; David *et al.*, 2000; Smith, 2005).

Parsley (1999) and David *et al.* (2000) interpreted cinctans as flattened blastozoans displaying a pair of recumbent brachioles. Under the David *et al.* (2000) model (extraxial–axial theory, EAT), brachioles accommodated elements of the water vascular system: cinctan marginal grooves housed radial water vessels, with the overlying labrum plates interpreted as biserial cover plates. However, in basal cinctans the plates covering the marginal grooves were organized into three or more rows (Sdzuy, 1993), or were irregularly arranged (Smith, 2005). Only a few (probably derived) species of cinctans developed a biserial arrangement of the labrum plates (Friedrich, 1993). Flooring plates were almost certainly absent, as they were not observed in our computer reconstructions, and have never been reported previously. Thus, basal cinctan food grooves incised directly into thecal plates, and were covered by multiple sets of small plates; this precise arrangement is not seen in any other echinoderm. The ambulacra of some eocrinoids (e.g. *Ascocystites* Barrande, 1887) approach this organization; however, in these forms grooves typically follow the sutures between specialized plates, and are not borne by 'ordinary' thecal plates (Ubaghs, 1968a). As the arrangement of the skeletal elements associated with cinctan food grooves differs from that of other blastozoan ambulacral systems, it seems unlikely that these structures are strictly homologous, suggesting that cinctans did not possess brachioles.

Flattened thecas, similar to those observed in cinctans, evolved independently in some eocrinoids and rhombiferans (Sumrall, Sprinkle & Guensburg, 2001). These forms share several plesiomorphies with their radial ancestor: for instance, cardiocystitids and a few rhipidocystids display pentamery in the construction of their ambulacra (Sumrall *et al.*, 2001). Moreover, all flattened blastozoans retain some traces of radial symmetry in their body plan; however, there is no evidence of radial (let alone pentaradial) symmetry in any part of the cinctan skeleton. The probable lack of brachioles and complete absence of radial symmetry cast significant doubts on the interpretation of cinctans as blastozoans. If we are correct in our interpretation of cinctans as pharyngeal basket feeders, this represents another difference between cinctans and blastozoans, as no blastozoans are

thought to have possessed an internal pharynx. For these reasons, the affiliation of cinctans with blastozoans is herein rejected.

Having contested close phylogenetic relationships with hemichordates and blastozoans, we conclude that cinctans were stem-group echinoderms primitively lacking radial symmetry, in agreement with Jefferies (1990, 1991, 1997), Jefferies *et al.* (1996), Domínguez (1999), Smith (2005), and Zamora & Smith (2008). As basal stem-group echinoderms, cinctans may share some plesiomorphies with the latest common ancestor of echinoderms and hemichordates (Ambulacraria). Ancestral characters predicted by the phylogeny for extant deuterostomes include pharyngeal gill slits, a paired water vascular system (constructed from left and right hydrocoels), and an adult body plan with fundamental bilateral symmetry (Smith, 2005, 2008; Swalla & Smith, 2008). In addition, a filter-feeding pharynx may be a symplesiomorphy of all deuterostomes (Cameron, 2002, 2005; Sato, Rickards & Holland, 2008).

Based on their functional morphology and anatomical comparisons with living tunicates, cinctans are herein interpreted as pharyngeal basket feeders, possessing a pharynx perforated by gill slits. As suggested by Ubaghs (1968b) and Smith (2005), the anterior marginal grooves were probably associated with tentacular extensions of a water vascular system that aided feeding. Ubaghs (1968b) proposed that these tentacles were partially exothecal in some taxa; however, it is extremely speculative to infer the presence of free tentacular extensions without evidence of a supporting skeleton or attachment facets. It is more plausible to interpret tentacles as wholly recumbent structures (confined to the marginal grooves).

The body plan of cinctans varies from asymmetrical to nearly bilaterally symmetrical; symmetry is expressed in the shape of the theca and the size/number of the anterior feeding grooves (Fig. 5). The degree of asymmetry in cinctans may relate to the degree of torsion experienced during their metamorphosis from larva to adult. Where paired marginal grooves are present, torsion was presumably less extensive, with cinctans developing both left and right paired hydrocoels, but to differing extents. As the right marginal groove is always shorter than the left one, the right hydrocoel must have been partly suppressed during ontogeny. Cinctans such as *Protocinctus* gen. nov. that lack a right marginal groove may have undergone more marked torsion, and consequently completely lost the right hydrocoel in their development (like living echinoderms). Two feeding grooves, housing a functional hydrovascular system constructed from left and right hydrocoels, was almost certainly the plesiomorphic state for cinctans, as it is most similar to the inferred condition for the latest common ancestor of the ambulacrarians. So, although *Protocinctus* gen. nov. is the oldest known cinctan, the organization of its feeding grooves suggests it is relatively derived within the class.

Cinctans share several traits with another group of probable stem-group echinoderms: the ctenocystoids. These resemblances include the anterior feeding grooves, the dorsal and ventral integuments bounded by a marginal frame, and an anterior chamber accommodating pharyngeal gill slits (Rahman & Clausen, in press). As ctenocystoids always possess a pair of bilaterally symmetrical anterior feeding grooves (Fig. 5), they more closely approximate the hypothetical ambulacrarian ancestor described by Smith (2005), and were probably stemward of cinctans in the echinoderm stem group. Ctenocystoids possess an anterior mouth and a posterior anus, so their intestinal tract was presumably uncoiled, as hypothesized for the latest common ancestor of the Ambulacraria by Holland (1988). The transition from ctenocystoids to cinctans involved increased torsion during development, and thecal flattening in an anterior–posterior direction. This caused the anus to migrate into an anterior position and the gut to coil into a U-shape in cinctans.

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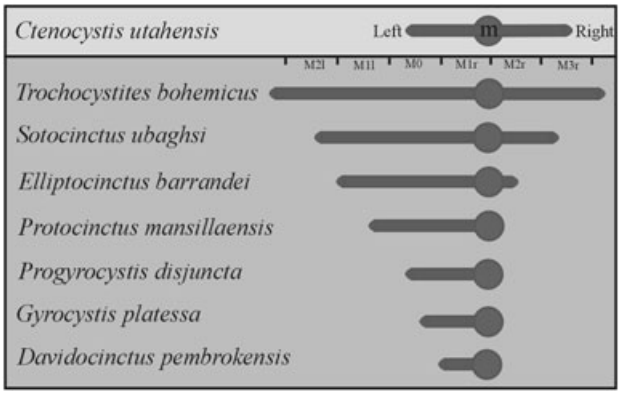

Figure 5. Schematic diagram comparing the number/symmetry of anterior food grooves in cinctans and a ctenocystoid. M and m indicate the positions of marginal plates and the mouth, respectively.

tion of trilobites, and made several useful suggestions regarding Spanish geology. This work is a contribution to the Project Consolíder MURERO, number CGL2006-12975/BTE, from the MEC of Spain-FEDER-EU, and Grupo Consolidado E-17, from Gobierno de Aragón.

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