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A new Middle Cambrian stem-group echinoderm from Spain: Palaeobiological implications of a highly asymmetric cinctan

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A new exquisitely preserved stem group echinoderm (cinctan), *Lignanicystis barriosensis* gen. et sp. nov., is described from the Middle Cambrian of Los Barrios de Luna, North Spain. This displays a unique asymmetrical body plan with ventral projecting nodes that raised the lower surface above the substratum. There are four openings through the body wall: mouth, anus, atrium, and an aligned row of sutural pores of uncertain function. Unlike other cinctans, *Lignanicystis* has a strongly asymmetrical shape convergent with that of some cornute carpoids. Like cornutes, the test is also elevated above the substratum to allow water flow beneath the theca. In both cases this is probably an adaptation to life in higher water flow regimes.

Key words: Echinodermata, Homostelea, carpoids, functional morphology, Cambrian, Spain.

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Introduction

In the Lower Palaeozoic a group of problematic fossils termed carpoids have long intrigued palaeontologists. These have a multiplated skeleton constructed of calcite with a very distinctive microstructural arrangement termed stereom. The genes responsible for stereom are unique to echinoderms amongst living phyla (Bottjer et al. 2006). However, carpoids differ from all living echinoderms in lacking any trace of radial symmetry, and have a strange anatomy that has been interpreted in several contrasting ways. Furthermore, some carpoids also appear to lack ambulacra, one of the defining features of crown group echinoderms. For these reasons carpoids have proved contentious.

There are four major groups of carpoids: stylophorans, ctenocystoids, cinctans, and solutes, all of which remain somewhat enigmatic. Cinctans, the subject of this paper, are known only from the Middle Cambrian. They are generally small and shaped like a tennis racquet with a plano-convex body (theca) and a posterior appendage (stele). A ring of large marginal plates forms a stout frame (cinctus) to the theca. Inside this frame the body is enclosed by dorsal and ventral plated integuments composed of small, tessellated plates. The body is pierced by several openings, some passing through the marginal frame, others through the dorsal integument. An asymmetrical pair of grooves leads into one of the marginal openings that is commonly assumed to be the mouth.

The first cinctan was described by Barrande from the Middle Cambrian of Bohemia (Czech Republic) (Barrande 1887). He considered them to be primitive stalked echinoderms. However, as they became better known and the uniqueness of their anatomical organization began to be appreciated, they were first raised to ordinal level within the class Carpoidea (Jaekel 1918) then elevated to their own subclass then class Homostelea (Gill and Caster 1960; Ubaghs 1968). Friedrich (1993) has provided a detailed review of the nomenclatorial history of the Carpoidea and resurrected the name Cincta Jaekel, 1918 for this group. Currently there are 12 genera and 24 species of cinctans, all from the Middle Cambrian of Western Gondwana, Avalonia, and Siberia (Friedrich 1993, 1995; Sdzuy 1993; Fatka and Kordule 2001; Rozhnov 2006). Friedrich (1993) and Sdzuy (1993) have all published detailed descriptive studies of the group and both accepted cinctans to be primitive echinoderms.

Because of their unusual morphology, the phylogenetic relationships of cinctans have been much debated. They have variously been interpreted as primitive, pre-radiate stem-group echinoderms (Bather 1930; Ubaghs 1971, 1975; Jefferies et al. 1996; Smith 2005), as stem-group Hemichordata (Domínguez and Jefferies 2005), or as unusual eocrinoid echinoderms that have secondarily lost their pentamery (David et al. 2000). Nor is there general consensus about their anatomy or mode of life, with the large opening at the anterior being interpreted as a mouth (e.g., Termier and Termier 1973), anus (e.g., Ubaghs 1968) or atrial opening to a pha-

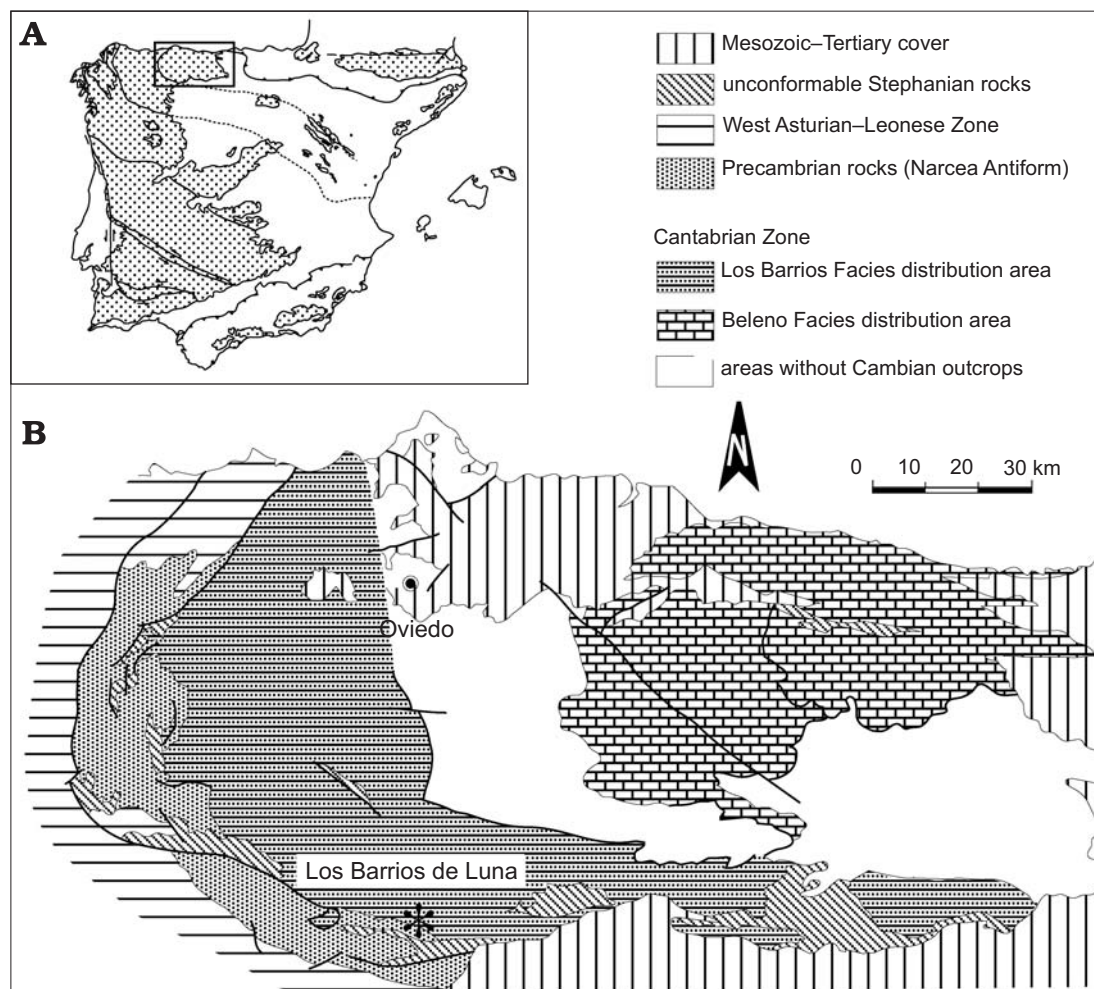


Fig. 1. **A.** Geographic map of Spain with the situation of Cantabrian Mountains. **B.** Geological setting of the section studied in Los Barrios de Luna (Cantabrian Mountains, North Spain). Based on Sdzuy and Liñán (1993).

ryngeal chamber (e.g., Bonik et al. 1978; Friedrich 1993; Smith 2005). The most widely held current view is that cinctans were active suspension feeders with their ventral surface resting on the sea floor, and with their slightly flexible appendage, upstream of the body, acting as an anchor in soft substrata (Friedrich 1993). Cinctans probably fed by filtering out fine particles through some form of pharyngeal basket, in an analogous way to extant tunicates (Bonik et al. 1978; Sdzuy 1985; Smith 2005).

New, excellently preserved material of a new species of cinctan, *Lignanicystis barriosensis* gen. et sp. nov., has been collected from the late Middle Cambrian of Spain and provides new information on the morphology and palaeobiology of this enigmatic group. This new cinctan genus is unusual in having a highly asymmetrical theca, convergent in overall shape with cothurnocystid and ceratocystid stylophoran carapoids. This raises the prospect that all three taxa were adapted for a similar mode of life and it is worth examining from a functional morphological perspective, what this might have been. Here we first describe the morphology of this new cinctan and then consider what it tells us about cinctan palaeobiology.

Institutional abbreviation.—MPZ, Museo Paleontológico, Universidad de Zaragoza, Spain.

Geological setting

All the specimens of *Lignanicystis barriosensis* gen. et sp. nov. were collected from outcrops around the village of Los Barrios de Luna in the Cantabrian Mountains, North Spain, about 50 km northwest of the city of León (Fig. 1). The Cambrian rocks cropping out here range from the early to late Cambrian in a continuous section called Los Barrios de Luna 1 (BL-1). They were deposited under marine conditions in the western margin of Gondwana. The Lower Cambrian Herrería Formation is a siliciclastic succession that discordantly overlies the Upper Proterozoic Mora Formation. Above this come the Láncara (150 m thick deposits, Lower–Middle Cambrian) and Oville (413 m thick deposits, Middle Cambrian) Formations, the former comprising a monotonous succession of purple carbonates (“griotte facies”) and the latter a siliciclastic succession of shales and sandstones divided into three members (called Genestosa, Adrados, and La

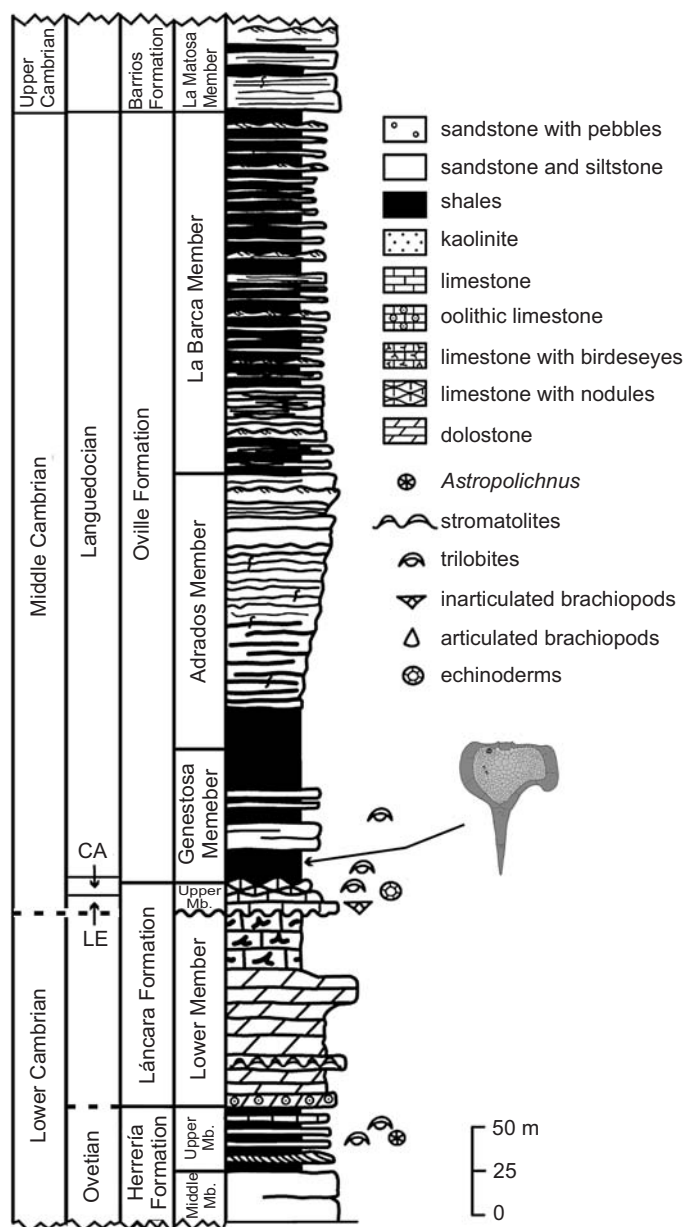


Fig. 2. Stratigraphic section at locality Barrios de Luna BL1 showing the horizon from which *Lignanicystis* was recovered. From Aramburu et al. 2006, derived from Zamarréño (1972) and Aramburu (1989). Abbreviations: CA, Caesaraugustian; LE, Leonian; Mb. Member.

Barca). The highest Cambrian rocks comprise the Barrios Formation (Middle Cambrian–Lower Ordovician), a siliciclastic sequence deposited in very deep-water conditions. A more detailed account of the stratigraphy of this section has been given by Aramburu et al. (2006).

The Lánacara Formation is very fossiliferous but echinoderms are rare and only isolated cinctan plates have been found, whereas the Oville Formation is very rich in trilobites, brachiopods, and echinoderms (Sdzuy 1961). Echinoderms recorded from the Oville Formation include the eocrinoid *Ubahscystis segurae* Gil Cid and Domínguez, 2002, undescribed cinctans, and *Gyrocystis* sp. (Zamora et al. 2007). All these echinoderms are well preserved and usually articulated

or partially articulated. The new cinctan described here comes from a thin level of siltstone at the base of the Genestosa Member of the Oville Formation (Fig. 2) where the only fossils are trilobites belonging to the species *Bailiella barriensis* and trace fossils. This horizon belongs to the *Solenopleuropsis thoralis* Zone, Lower Languedocian (early Middle Cambrian). The lithofacies and palaeontological evidence suggests a relatively shallow sublittoral environment of low to moderate energy, sporadically affected by storms. The presence of key trilobite taxa and archaeocyathans suggest a subtropical palaeolatitude (Courjault-Radé et al. 1992; Gozalo et al. 2003).

Systematic palaeontology

Phylum Echinodermata Brugière, 1791

(Stem group of the Echinodermata)

Cincta Jaekel, 1918

Family Trochocystitidae Jaekel, 1900

Genus *Lignanicystis* nov.

Derivation of the name: Named in honour of Prof. Eladio Liñán (Universidad de Zaragoza, Spain) in recognition of his lifetime dedication to the study of Spanish Cambrian fossils.

Type species: *Lignanicystis barriosensis* sp. nov., monotypic.

Diagnosis.—A cinctan whose theca is strongly asymmetrical in shape; anterior margin very wide and nearly straight; marginal plates M4r to M6r form an indented, bridge-like structure. Upper tegument of plates (supracentrals) differentiated into two discrete areas, the anterior central area formed of larger plates without pits or pores, the posterior and marginal areas of smaller plates with stellate ornamentation; an arc of small openings is developed towards the left side of the supracentralia separating these two areas. Long left and very short right marginal grooves, extending from plate M1l to M2r. Marginal plates M4l and M4r are hatchet-shaped, which becomes especially pronounced in larger individuals.

Lignanicystis barriosensis sp. nov.

Figs. 3–10.

1993 gen. et sp. nov. A; Friedrich 1993: 126, fig. 19.

Derivation of the name: After Barrios de Luna (León, North Spain), the locality where the material was collected.

Type material: The holotype (MPZ2007/776) is a complete specimen preserved as a natural mould in a siltstone. Paratypes (MPZ2007/778, 780, 784, 794, and 795) are partial complete specimens.

Type locality: Specimens were collected in a creek 500 meters to the southeast of Los Barrios de Luna village, near the road Mora-Los Barrios de Luna.

Type horizon: Middle Cambrian, Lower Languedocian, Oville Formation, Genestosa Member, *Solenopleuropsis thoralis* Zone.

Material.—Thirty four specimens (MPZ2007/776–809) in different states of preservation but fully articulated in many cases, suggesting rapid burial. They are preserved in siltstones as natural moulds coated with a very thin film of iron oxides. All fossils have been cast in latex prior to study.

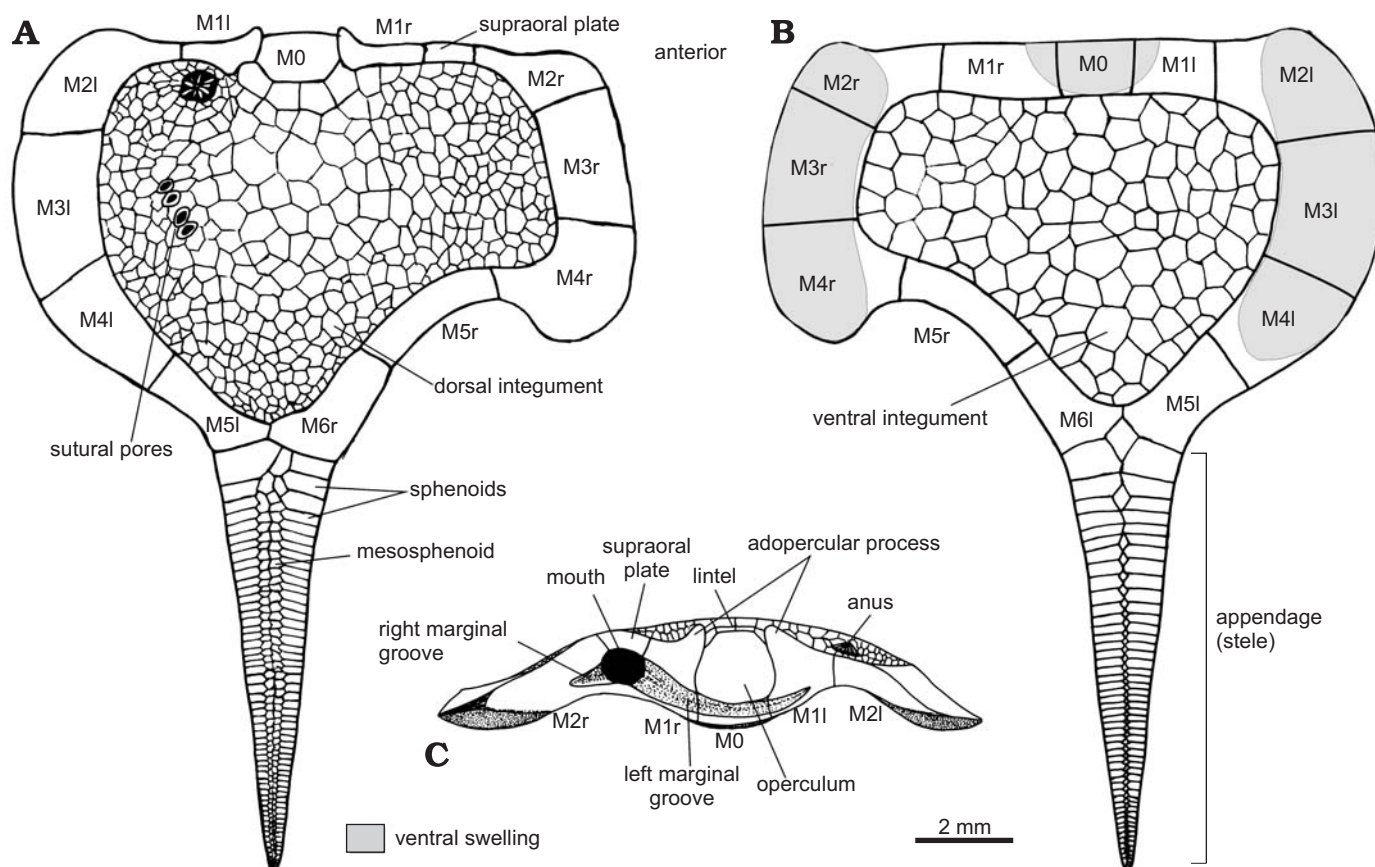


Fig. 3. Reconstruction of *Lignanicystis barriosensis* gen. et sp. nov. in dorsal (A), ventral (B), and anterior (C) views to show anatomical terms and orientation.

Diagnosis.—As for the genus, by monotypy.

Stratigraphic and geographic range.—Middle Cambrian, Lower Languedocian, Oville Formation, Genestosa Member (Fig. 2).

Description

In the following description orientation and plate nomenclature follows Friedrich (1993) (see Fig. 3). Marginal plates are referred to with the letter M. The anterior marginal plate that coincides with the axial plane and which underlies the operculum is called M0. Marginal plates are then numbered successively around the margin towards the posterior appendage as M1r, M1l, M2r, M2l etc. with l and r indicating their position to the left or the right of the M0 plate in dorsal view.

Like all cinctans the body is composed of an anterior body, or theca, and a posterior appendage or stele. The theca is formed of a frame of stout marginal plates (the cinctus) which enclose dorsal and ventral plated surfaces. In *Lignanicystis* the shape of the theca is highly asymmetric compared to that in other species, with a large posterior embayment on the right-hand side of the stele (Figs. 3, 4). The holotype (Fig. 4A) has a thecal length of 8.5 mm and a width of 12.5 mm. The stele is estimated to be approximately 11 mm in length. The largest theca (MPZ2007/777) is 14 mm in length and 19 mm in width.

Orifices.—There are four different openings or sets of openings in *Lignanicystis*.

(1) In the anterior right side of the cinctus there is a small circular aperture that is located between the marginal plates M1r and M2r and covered dorsally by the supraoral plate (Figs. 3, 4B). The opening is flattened dorso-ventrally and wider than tall in external view (1.5 mm in width and 1.0 mm in height MPZ2007/778). The bounding marginal plates are thin so that the passageway through to the interior is short. On the interior ventral surface plates M1r and M2r form a broad, expanded platform to the interior of the opening (Fig. 4A₄). Externally, two marginal grooves lead into this aperture from left and right marginal plates. This we interpret as the mouth.

(2) There is a small cone of wedge-shaped plates towards the anterior left dorsal plated surface (Figs. 3, 4A₃). It is 0.5–0.8 mm in diameter and composed of a single ring of about nine plates that radiate from a central point. Surrounding this cone is a narrow zone of small irregular plates. This conforms in shape and size to a periproct in crown group echinoderms.

(3) The largest aperture, termed the porta by Sdzuy (1993), lies at the anterior, passing through the marginal frame and coinciding with the axial plane. This opening is covered by a large, spoon-shaped plate called the operculum, and is bounded ventrally and laterally by marginal plates M0,

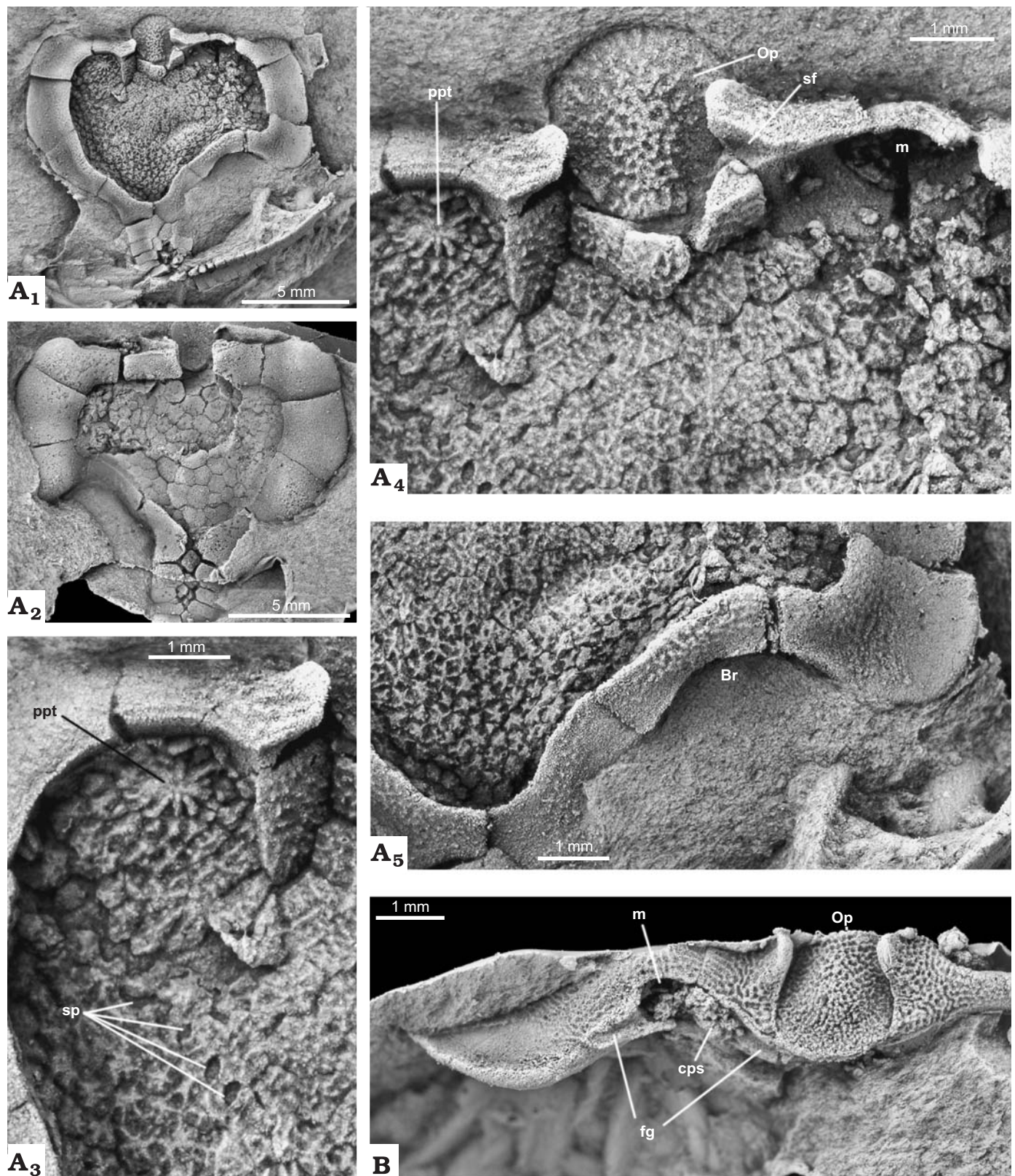


Fig. 4. Cinctan echinoderm *Lignanicystis barriosensis* gen et sp. nov. from the Middle Cambrian of Cantabrian Mountains, North Spain. **A.** Holotype MPZ2007/776 in dorsal (A₁) and ventral (A₂) views; A₃, detail of dorsal integument on left-hand side; A₄, detail of anterior part of theca in dorsal view; A₅, detail of posterior right-hand side of theca in dorsal view. **B.** Paratype MPZ2007/778: anterior of theca in lateral view. Abbreviations: Br, bridge plate; cps, cover plates; fg, food groove; m, mouth; Op, operculum; ppt, periproct; sf, suropercular facet; sp, sutural pore. All photographs are of latex casts taken from natural moulds.

M1l and M1r. The upper margin of the opening is bounded by four large plates of the dorsal tegument, which are not markedly differentiated from other tegumental plates (Fig. 4A₄). The large opercular plate, which in MPZ2007/779 measures 4.5 mm by 3.5 mm, fills the entire opening (Fig. 4A₄, B). It is smooth on its inner, concave face but ornamented with a coarse reticular stereom on its external, convex face (Fig. 5B). Small swellings at the posterior corners of the plate probably mark articulation surfaces. Its placement and setting is such that it can only open outwards.

(4) Finally there is a uniserial row of small ovate openings lying towards the upper left side of the supracentral tegument (Figs. 3, 4A₃). In the best-preserved specimen, there are four clear openings, and probably more extending towards the anterior left. Each opening is ca. 200–300 µm by 120–150 µm in diameter and lies suturally, bordered by three tegumental plates raised to form a low rim. These are the dorsal sutural pores.

Cinctus.—The cinctus, or marginal frame, is composed of twelve stout plates (M6r–M5l) which differ markedly in shape around the ring, and which consequently are readily identifiable in isolation. All are approximately triangular in cross-section with a short, thick internal face that is concave, and a wide wedge-shaped outer face. The abutment facets between adjacent plates have a slightly sunken centre bordered by a raised marginal rim (Fig. 5C). They presumably housed ligamentous soft tissue binding the plates together. The morphology of the plates and the type of articulation suggest that marginal plates had only very limited capacity of movement.

Plate M0 lies at the anterior and forms the floor to the porta (Fig. 3). It is distinctly swollen on its ventral surface, rectangular and a little wider than long in plan view, and bears the left ambulacral groove on its outer face. There is no broad anterior shelf to this plate so that the ambulacral groove runs beneath the ambitus and faces ventrally (Fig. 4B). Plates M1r and M1l form the lateral frame to the porta each giving rise to a dorsal adopercular process (Fig. 3) that has, on its inner face, a small, flat, triangular suropercular facet (Fig. 4A₄). These plates are rectangular in ventral view, but in anterior view are raised to form a low arch (Fig. 4B). M1r and M1l articulate with three specific plates each and with the ventral and dorsal integuments. M1r articulates with one tegumental plate, M0 and M2r, while M1l articulates with a tegumental plate, M0 and M2l. The suropercular facets mark the articulation points with supracentral plates. The adopercular processes are inclined slightly towards the anterior. M1r and M1l both carry the left marginal groove on their outer surface.

Plate M2r carries the small right marginal groove on its exterior surface (Figs. 3, 4B). The distal part of this plate is

expanded outwards as a wide platform, which narrows when reaching the start of the marginal groove. Plate M3r is very like other mid-cinctus plates, having a flat, ventral surface with a rectangular outline and a dorsal surface that has an outer flange and inner thickened rim.

Plates M4r, M5r, and M6r form the posterior embayment and are raised to create a bridge-like (arch) structure in the posterior right side of the animal (Figs. 3, 4A₅). The anterior part of M4r continues the broad outer platform developed on M3r but, towards its posterior side, becomes narrower and elevated to begin the bridge. Plate M4 consequently has a very distinct hatchet-shaped outline in plan view. Plate M5r is curved, forming an arch, and it is raised above the substratum. The anterior part of M6r contributes to the distal part of the bridge while its posterior side completes the cinctus and is in contact with the stele. In the largest individuals the outer margin of these plates is thickened as a rim (Fig. 5A). A similar rim is also developed on plates M4l and M5l.

The left marginal plates of the cinctus are very like those observed in other species of cinctans. All have a wide margin that becomes slightly narrower on the plates that are near the stele. Plates M4l and M5l narrow towards their abutment and are raised forming an arch, which is smaller and less developed than that on the right-hand side.

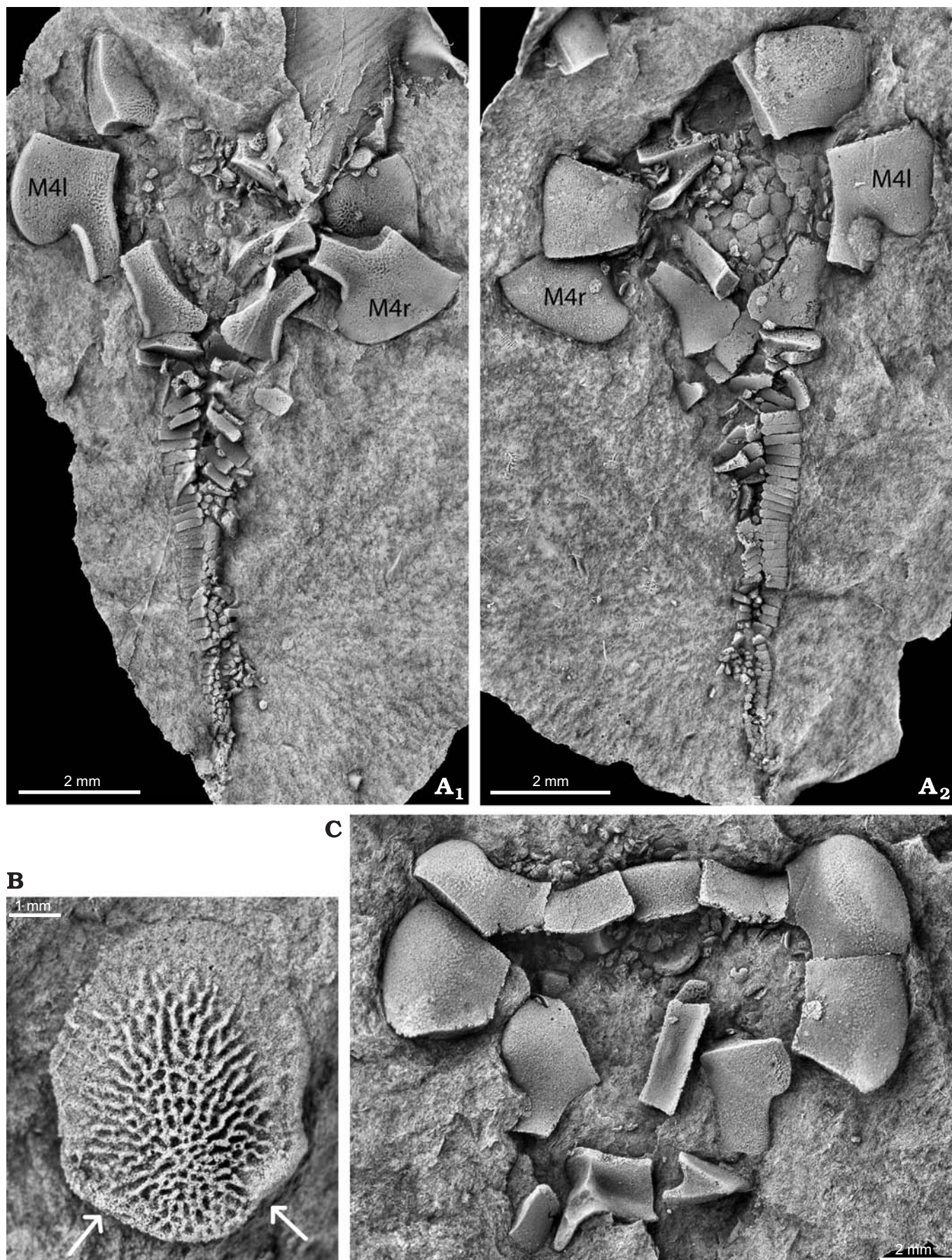
The ventral surface of the marginal ring is thus not flat, as in many other cinctans, but undulose. Plates M2–M4 all are swollen on their ventral outer surface, as is plate M0 (Fig. 5C). Consequently much of the lower surface of the disc is raised above the level of the sea-floor. In particular, the bridge-like structure formed on either side of the stele by plates M4r–M6r and M4l–M5l ensures that some parts of the marginal ring were elevated well above the substratum.

All marginal plates show similar stereom ornamentation (Figs. 4–6). On its dorsal surface the inner part of the plate bears a coarse labyrinthic ornament overlying finer stereom, while the outer flange is a dense, almost imperforate calcite. The ventral surface is smooth and unornamented.

Dorsal and ventral integuments.—The dorsal (supracentral) and ventral (infracentral) integuments are formed from a large number of polygonal plates.

Dorsal integument: Plates of the dorsal integument are differentiated into two areas, a large anterior zone contiguous with the operculum and a lateral and posterior peripheral zone (Figs. 3, 4A₁, A₃). The plates forming the anterior zone are relatively large (ca. 0.8–1.0 mm major axis—comparable in size to central plates of the ventral surface), and polygonal in outline. They form a continuous tessellated pavement without sutural pores. They are ornamented with a radial pattern of rugose ornament (epistroma) on their external surface and are smooth internally. Lateral faces of these plates are

Fig. 5. Cinctan echinoderm *Lignanicystis barriosensis* gen et sp. nov. from the Middle Cambrian of Cantabrian Mountains, North Spain. **A.** Paratype MPZ2007/784; theca in dorsal (A₁) and ventral (A₂) views. Note the distinctive shape of plates M4l and M4r. **B.** Specimen MPZ2007/779; operculum in external view: arrows point to articular facets. **C.** Paratype MPZ2007/780; ventral view of partially disarticulated specimen showing marginal articulation facets and ventral swellings on plates M2–M4. All photographs are of latex casts taken from natural moulds. →



vertical and smooth. The most anterior part of this pavement is formed of the four plates that border the dorsal edge of the porta-operculum complex, and which remain undifferentiated from adjacent dorsal plates (Figs. 3, 4A₄). The entire region appears to be cohesive and forms a rather rigid zone.

In the peripheral zone, dorsal plates are considerably smaller (400–550 µm in length) and have a very strong stellate ornamentation created by 5–7 ridges that radiate from the centre of each plate (Fig. 4C). Plates decrease slightly in size towards the marginal frame. Plates abut, but there are deep pits around the margins of the plates that match similar pits on adjacent plates. However, none of these are true pores through the tegument, rather they are simply thinner zones on the plate. This peripheral zone of plates seems to be more flexible than the anterior zone, as the plates are smaller and it has become wrinkled in places during preservation. It is through this zone that the periproct opens and it is along the border between the peripheral and anterior zones that the row of sutural pores is found. The interior face of supracentral tegument plates is smooth and unornamented.

Ventral integument: Plates forming the ventral integument are fewer in number and somewhat larger than those of the dorsal integument. Largest infracentral plates lie centrally along the anterior posterior axis while those to left and right gradually decrease in size towards the marginals (Fig. 4A₂). Large infracentral plates are approximately 0.8–1.0 mm in diameter and decrease in size by about half close to the marginal plates. These plates are relatively thick, entirely unornamented and tessellated together to form a continuous pavement.

Marginal grooves.—Two well-defined grooves run from the peristome around the outer face of the marginal ring. The right groove is short and extends only half-way along plate M2r, tapering rapidly towards its distal end (Figs. 3, 4B). The left groove is much longer, extending around the anterior, passing underneath the operculum and finally ending about half way along plate M1l. Around the anterior the groove lies below the ambitus and thus faces slightly downwards. Small wedge-shaped plates ca. 150 µm lie scattered in the groove in MPZ2007/778 and partially cover the peristome (Fig. 4B). Over the peristome these cover plates are a little larger and have a stellate ornament, like plates of the dorsal integument. There is a faint groove running along upper and lower rims of the marginal grooves presumably for accommodation of the cover plates.

Appendage (Stele).—The stele is long and originates as a direct continuation from the marginal frame. It is between 1 and 1.5 times the length of the theca and is constructed from a marginal series of wedge-shaped sphenoid plates, and smaller polygonal mesosphenoid plates that run down the midline of the stele both dorsally and ventrally (Figs. 3, 4A, 6). A small enclosed canal, bounded by sphenoid plates laterally and mesosphenoid plates dorsally and ventrally, runs the length of the stele. For the proximal two-thirds of the stele sphenoid plates are much wider than long and have a broad lateral

flange, rather flat ventral surface and an inner raised dorsal portion, exactly as in lateral marginal frame plates. The two posterior marginal frame plates (M5l and M6r) are offset relative to each other, and this left-right offset continues down the length of the stele. Furthermore the mesosphenoid plates are not symmetrically arranged at least proximally (Fig. 6B). The sphenoid plates have large, flat abutment faces and proximal mesosphenoid plates are thick and tessellate, suggesting that for much of its length the stele was relatively rigid. In the distal portion of the stele the sphenoid plates become much smaller and lose their distinct flange, while mesosphenoid plates become arranged as an alternating biseries dorsally and a single series of diamond-shaped plates ventrally which may not be contiguous. In cross-section the proximal part of the stele is initially lozenge-shaped but rapidly becomes more triangular. Towards the distal extremity the stele becomes more circular in cross-section and the difference in size between sphenoid and mesosphenoid plates is greatly reduced. The flat abutment of plates and the disposition of the alternating mesosphenoids suggest that the stele was probably rigid in the anterior portion but became somewhat more flexible distally.

Remarks.—*Lignanicystis* has many of the typical features of cinctans, but is unique in having a strongly asymmetrical thecal outline. The large embayment in the posterior right of the marginal frame (Fig. 4A) is seen in no other cinctan, all of which have ovate, more or less bilaterally symmetrical marginal frames.

The degree to which left and right ambulacral grooves are developed varies markedly amongst cinctan genera and is an important taxonomic character (summarized in Fig. 7). *Lignanicystis* has a relatively long left ambulacral groove, while the right ambulacral groove is much reduced and extends no further than half-way across plate M2r. Amongst cinctans *Sucocystis*, *Sotocinctus*, *Trochocystoides*, *Asturicystis*, *Trochocystites*, and *Elliptocinctus* all have left and right ambulacral grooves. However, those of *Trochocystites*, *Trochocystoides*, *Sotocinctus*, and *Asturicystis* are much longer than in *Lignanicystis*, with the left ambulacral groove extending onto plate M3r. The ambulacral development in *Lignanicystis* is very similar to that observed in *Elliptocinctus* and in some species of *Sucocystis* (i.e., *S. undata*, *S. melendezi*, *S. acrofera*, and *S. quadricornuta*).

Another feature that varies amongst cinctan genera is the extent to which the suropercular plates are differentiated from dorsal tegumental plates (Fig. 8). In *Gyrocystis*, *Sucocystis*, and *Elliptocinctus* there are just three (rarely four or two) suropercular plates that are enlarged and clearly differentiated from plates of the dorsal integument. These differentiated plates form a clear lintel above the operculum. By contrast in both *Lignanicystis* and *Trochocystites* there are four small suropercular plates that remain undifferentiated from other dorsal integument plates. In other taxa, such as *Sotocinctus* and *Asturicystis* there are 6 or 7 dorsal tegumental plates bordering the operculum.

The degree to which nodes and protuberances are developed on the ventral surface of marginal plates is another tax-

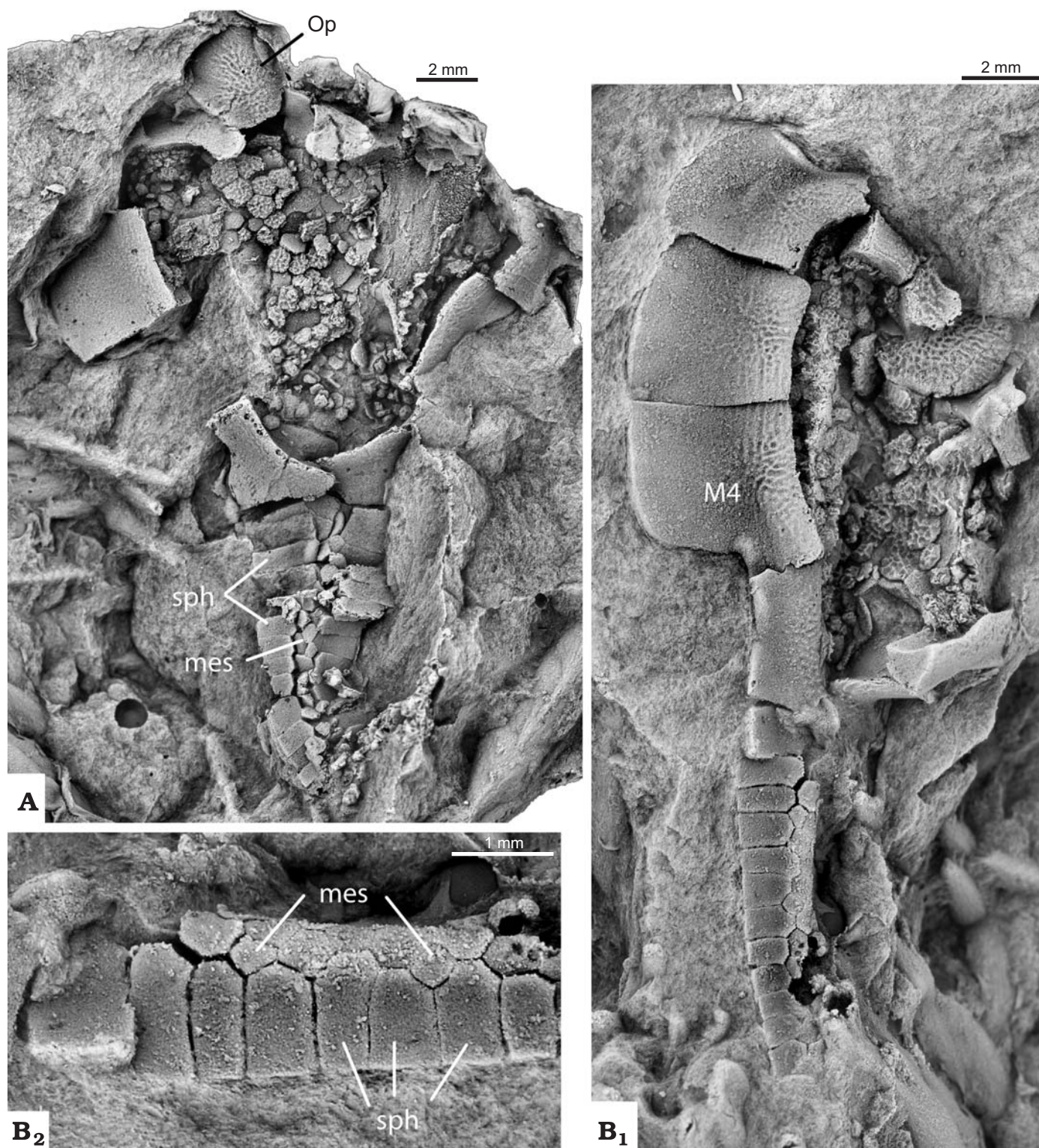


Fig. 6. Cinctan echinoderm *Lignanicystis barriosensis* gen et sp. nov. from the Middle Cambrian of Cantabrian Mountains, North Spain. **A.** Paratype MPZ2007/794; theca in dorsal view. **B.** Paratype MPZ2007/795; theca in dorsal view; general (**B₁**) and detail of appendage (**B₂**). Abbreviations: M4, hatchet-like marginal plate M4l; mes, mesosphenoidal plate; Op, operculum; sph, sphenoidal plate. All photographs are of latex casts taken from natural moulds.

onomically important character that varies amongst cinctans (summarized in Fig. 7). Although *Lignanicystis* and *Trochocystites* both have protruberances developed on the ventral

surface of their marginal plates, these protruberances are on different plates (Fig. 7). The hatchet-shaped plate M4 (Fig. 5A, B) is unique to *Lignanicystis*.

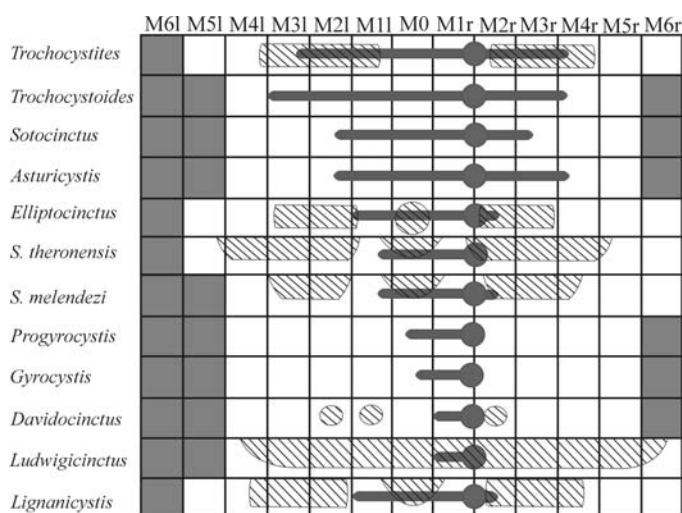


Fig. 7. Schematic summary of number of marginal plates in the cinctus, food groove distribution and ventral swelling development on marginal plates for genera of cinctans. M1–M6 marginal plates; l, left, r, right; open boxes, marginal plate present; grey circle, position of mouth; thick grey line, extent of left or right food groove; oblique hatching, presence of ventral swelling on marginal plate; S, *Sucocystis*.

There is some difference in the relative size of the ventral plates amongst cinctans. In *Lignanicystis*, as in *Trochocystites* and *Trochocystoides*, ventral plates are relatively small and numerous, differing little in size from dorsal plates. By contrast ventral plates in *Sucocystis* are much larger and fewer in number. Finally only *Lignanicystis* and *Trochocystites* have a row of sutural pores along the line separating the two regions of the dorsal integument.

Overall *Lignanicystis* appears to share at least one synapomorphy with *Trochocystites* (the presence of a line of sutural pores in the dorsal membrane). However, the development of its marginal groove is much closer to that seen in *Sucocystis* and *Elliptocinctus*. No detailed analysis of how these genera are related is presented here, however, as a cladistic analysis of the entire group is currently in progress.

Cinctan palaeobiology

Anatomical organization.—Faced with a problematic fossil such as cinctans, the anatomical orientation is established by first identifying the function of the various openings. *Lignanicystis barriosensis* has four openings or sets of openings that perforate the theca and we start by reviewing their probable functions and homologies.

All cinctans have a moderately large circular opening between plates M1r and M2r in the lateral right front of the marginal frame that passes from the exterior to interior. In most cinctans a left and right groove, running around the outside of the marginal frame, converge on this opening and are covered with a sheet of plates (Friedrich 1993). The structure of this plated covering sheet is not well known but

is partially preserved in *Trochocystites*, *Gyrocystis*, *Asturicystis*, and *Sotocinctus* (Friedrich 1993; Sdzuy 1993) and in life it fully covered the opening. The obvious interpretation is that the opening is the mouth and that the paired and covered grooves are food grooves. David et al. (2000) noted that the marginal ossicles and covering plates hold the same spatial relationships as ambulacral flooring and cover plates in crown group echinoderms. However, it is unlikely that marginal frame plates in cinctans and ambulacral flooring plates in helicoplacoids and crown group echinoderms are strictly homologous since they are very different in position and structure.

The small cone of plates in the left anterior dorsal integument is interpreted either as an anal opening (e.g., Sdzuy in Jefferies 1990: 673; Friedrich 1993; Sdzuy 1993; Smith 2005) or as a gonopore (Parsley 1999; David et al. 2000). This structure is seen in *Trochocystites*, *Gyrocystis*, and *Sotocinctus*, and is probably best preserved in *Lignanicystis barriosensis*. No other echinoderm has a gonopore in the form of a cone of plates through a flexible membrane, whereas this is the typical structure taken by the periproct in a variety of echinoderms.

The largest opening in cinctans is the porta, which is protected in life by the big spoon-shaped plate or operculum. This is located in the anterior side of the theca framed by the dorsal integument and marginal frame plates. It is clear that the operculum hinged to open outwards, not inwards, and thus must have acted as a one-way valve. Ubaghs (1968), Parsley (1999) and David et al. (2000) have this orifice as the anus. It is the largest opening in the body that is at least six times the size of the anal opening in *Lignanicystis barriosensis*, so must be designed to cope with a large volume of discharge. If we are correct in interpreting cinctans as pharyngeal basket feeders the porta would represent the exhalent orifice to the pharyngeal chamber.

The fourth set of openings is the series of small sutural pores along the boundary between the anterior and marginal plated zones of the dorsal tegmen. These extend only a short distance from the lower left extremity of the anterior zone towards the periproct. A similar, but more extensive line of sutural pores is seen in *Trochocystites* (Ubaghs 1967), again

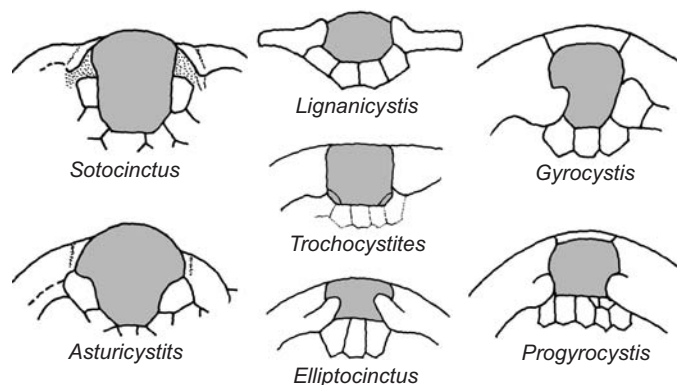


Fig. 8. Schematic diagrams of plating associated with the dorsal porta-operculum complex for different genera of Cincta. Opercula are shaded.

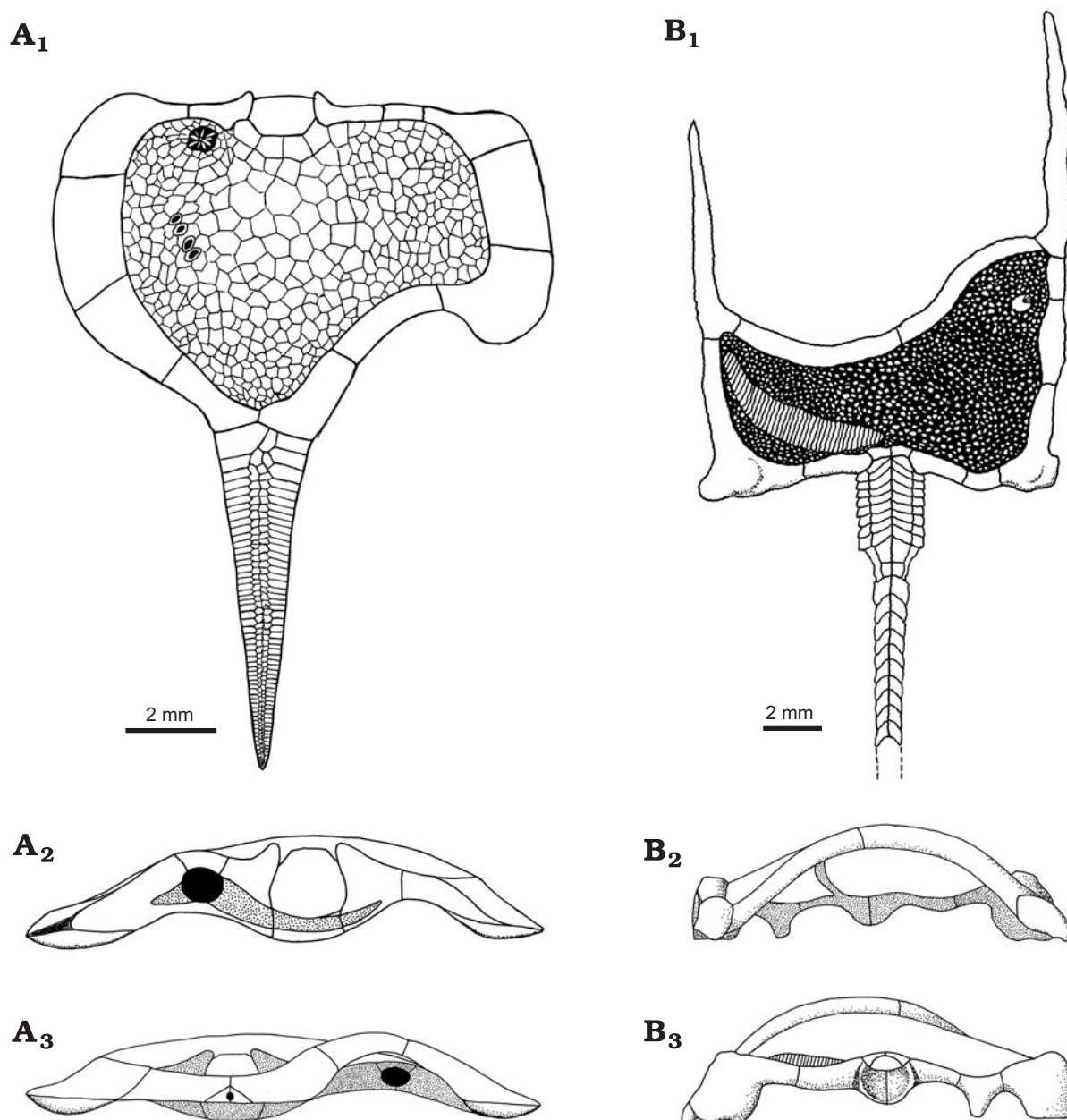


Fig. 9. Reconstruction of the marginal frame of cinctan echinoderm *Lignanicystis barriosensis* (A) and the cothurnocystid *Scotiaecystis collapsa* (B) (redraw from Cripps 1988) in dorsal (A₁, B₁) and anterior (A₂, B₂) views, and posterior view showing the distinctive bridge-like structure (A₃, B₃). Mouth opening—black; dorsal and ventral integuments omitted for clarity.

following the same boundary. These have a similar position and shape as the left thecal openings of the stylophoran *Ceratocystis* (Jefferies 1969), which have been interpreted as gill slits. One possibility therefore is that these pores represent secondary pharyngeal openings. However, this seems unlikely to us for several reasons. Firstly, there are no deutero-stomes that have both an exhalent orifice and a series of small gill slits. Second, only *Lignanicystis* and *Trochocystites* have a well-defined row of sutural pores. Finally *Gyro-cystis* has somewhat similar sutural openings through the dorsal tegmen but they are always in the right side and are scattered rather than aligned (Friedrich 1993). The alternative interpretation is that they are epispires, which are mem-

brane-covered gaps used for increasing oxygen flow to internal organs. In *Lignanicystis* and *Trochocystites* the sutural pores follow the boundary between the strong more rigid anterior part of the tegment and the more flexible peripheral zone. This presumably marks an anatomic boundary and the line of pores could specifically follow one of the internal organs such as the gut or gonads.

Convergence on cornute stylophorans.—Stylophorans are another group of aberrant asymmetric, calcite-plated animals whose affinities have been disputed. Like cinctans, the skeleton in stylophorans is composed with two parts, the theca and an appendage, and the calcite-plated skeleton has a micro-

structure of stereom. They are subdivided in two groups: cornutes, that can be boot-shaped asymmetrics or nearly symmetric in shape (Lefebvre 2003), and mitrates that are much more symmetric. Depending the different “schools” they are interpreted as primitive chordates (Jefferies 1968, 1969; Jefferies et al. 1996), primitive non radial echinoderms (Bather 1925; Ubags 1971, 1975; Paul and Smith 1984; Smith 2005; Clausen and Smith 2005) or derived echinoderms (Sumrall 1997; David et al. 2000; Lefebvre 2003). Each interpretation imparts its own set of assumptions concerning the body axis orientation and anatomical organization of these animals. Recent discovery of a primitive stylophoran with well-preserved stereom has demonstrated that the appendage is a muscular locomotory organ (Clausen and Smith 2005). Consequently, we interpret stylophorans as having their mouth opening on the anterior right side of the body and the left apertures are taken to be pharyngeal openings (Smith 2005; Clausen and Smith 2005).

In thecal shape *Lignanicystis* resembles ceratocystid and cornute stylophorans in that both have a well-developed marginal frame enclosing a flexible membrane and a single appendage that is rather stiff and inflexible distally (Fig. 9). More importantly both have a strongly asymmetrical thecal outline, and adoral knobs and projections around the margin to help raise the bulk of the theca off the sea-floor. Both animals have the mouth opening on the right side.

The similarity between cornutes and cinctans, however, is not exact. In *Lignanicystis* the embayment is posterior, on the same side as the appendage, whereas in cothurnocystids the embayment is anterior on the opposite side to the appendage. Despite this difference, the striking convergence in design between *Lignanicystis* and cothurnocystids such as *Nevadaecystis* and *Scotiaecystis* suggests both followed a similar mode of life. This probably had something to do with their adopting similar feeding strategies.

The feeding strategy of cinctans appears to have been very different from that of pentaradial echinoderms. Cinctans were flattened and recumbent, and had their two food-gathering grooves wrapped around the anterior margin of their body, close to the sea floor. This is a very unusual pattern compared with crown-group echinoderms, whose network of food-grooves generally face away from the sea floor in filtration feeders and downwards in deposit feeders. It is, however, similar to that of other stem group echinoderms such as ctenocystoids (Robison and Sprinkle 1969) and stylophorans. There are flattened eocrinoids (e.g., Dean and Smith 1999; Nardin 2007) but these have an erect filtration fan of arms and lived tethered and kite-like in areas of strong current. The fact that the marginal grooves can become extremely reduced in some cinctans such as *Gyrocystis* suggests they did not have to meet the same functional requirements as the ambulacral surfaces of pelmatozoan and edrio-asteroid echinoderms. Pelmatozoans feed by capturing small food particles suspended in the water using their network of ambulacral tube-feet, as presumably did the extinct edrio-asteroids. In both cases feeding efficiency is increased by en-

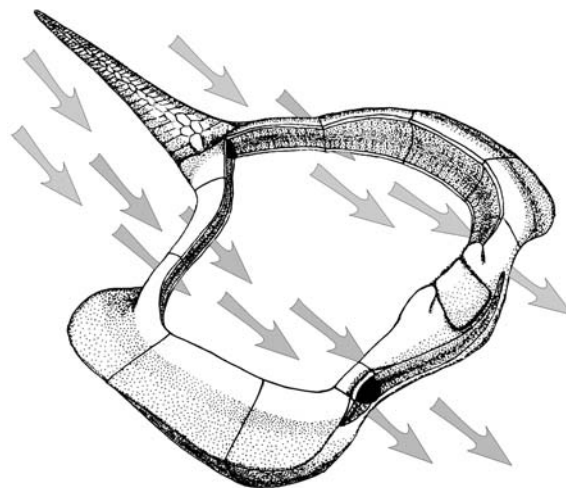


Fig. 10. Reconstruction of cinctan echinoderm *Lignanicystis* showing inferred current directions passing beneath the theca. Dorsal and ventral teguments omitted for clarity.

larging the size and density of the filtration net, not by decreasing it.

Friedrich (1993) suggested that cinctans were suspension feeders somewhat comparable to crinoids that capture the food particles downstream (Meyer 1979). In *Lignanicystis barriosensis* the marginal groove is best developed immediately around the operculum and faces down towards the surface. Their source of food was therefore presumably resuspended organic material from the sea floor.

The marginal grooves in cinctans are thought to have housed a left and right ambulacral tentacle (Ubags 1968; David et al. 2000; Smith 2005), but, because of their small extent and position, did not form an extensive filtration fan and may therefore simply have been used to stir up or pick over the sediment immediately in front of the animal. It is possible that these grooves were then used to canalize an inflow of water to the mouth, with food particles being filtered and captured internally through a pharyngeal basket. In the case of *Lignanicystis* the marginal grooves would be well placed to funnel the boundary layer with its suspended load into the peristome.

In both cornutes and cinctans props on the lower surface raised the body away from the seafloor (Fig. 9). In *Lignanicystis* these create two clear passageways at the posterior margin, which would have allowed flow beneath the animal (Fig. 10). We can infer the direction of water flow from the fact that the operculum is likely to have faced downstream to ensure efficient venting. In both cases this may have been to avoid too much bottom sediment clogging up the filtration system. Another possibility is that it could have been to prevent dislodgement under higher current regimes. As benthic animals living in water currents they would have been prone to dislodgement and lifting. Current flowing over shallow-domed organisms such as sand dollars creates lift (Telford 1981, 1983). Raising the test off the sea-floor to allow flow of water to pass underneath can help increase traction and

thus better resist dislodgement. It may be that both cothurnocystid cornutes and *Lignanicystis* were adapting to feed in higher flow regime environments.

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