

PALAEOBIOLOGY OF THE PRIMITIVE ORDOVICIAN PELMATOZOAN ECHINODERM *CARDIOCYSTITES*

by JULIETTE DEAN *and* ANDREW B. SMITH

ABSTRACT. A new species of primitive cystoid, *Cardiocystites pleuricostatus*, is described from the Caradoc of Shropshire. Its superb preservation clarifies the morphology of this problematical taxon and shows it to belong to the Rhipidocystidae. Its highly flattened theca cannot be indicative of a recumbent mode of life, contrary to previous interpretations, since its arms and brachioles formed a conical filter. The flat, thin-plated theca may have been a specialization either for aiding gaseous exchange, or for providing hydrodynamic lift to the crown.

POORLY known taxa with apparently bizarre morphologies abound amongst early Palaeozoic echinoderms. They are of special interest for two reasons. First, they have proved difficult to place into a phylogenetic scheme, and in many cases have been elevated to high taxonomic rank. Determining their sister-group relationships is essential if we are to improve our understanding of the early evolution of echinoderms. It is especially important that the morphology of such poorly known taxa is interpreted correctly, so that estimates of disparity do not become overinflated. Second, where unexpected morphological combinations are encountered, these can shed light on the functional design and mode of life of primitive echinoderms.

Many of the taxa most difficult to place have traditionally been assigned to the eocrinoids, a paraphyletic group that comprises stem-group members of many of the better known cystoid groups (Smith 1984a; Paul 1988). Amongst the most poorly known of eocrinoids is *Cardiocystites*, erected by Barrande (1887) on the basis of two specimens from the middle Ordovician of the Czech Republic, neither of which was particularly well preserved. Although Barrande clearly recognized it to be a cystoid, he did not classify it further. Since its discovery no additional material of this species has been collected, and consequently its relationship to other cystoids has remained problematical. Ubaghs (1967, p. S491) accepted it as an eocrinoid, but left it unclassified within the class. Sprinkle (1973) redescribed and refigured Barrande's original material but was also unable to classify it, placing it in 'Order and Family indeterminate'. Broadhead (1982) placed *Cardiocystites* in the family Rhipidocystidae Jaekel, 1901, along with the other flattened eocrinoid genera *Rhipidocystis*, *Batherocystis*, *Petalocystis* and *Lingulocystis*. This placement was disputed by Lewis *et al.* (1987), when describing a new genus of rhipidocystid, *Mandalacystis*. They preferred to omit *Cardiocystites* and *Lingulocystis* from the Rhipidocystidae, but made no attempt to place either genus. Nevertheless, a cladistic analysis of cystoid genera carried out by Paul (1988) identified *Cardiocystites* as sister taxon to the clade *Rhipidocystis*, *Batherocystis* and *Petalocystis*.

Here we describe a new species of *Cardiocystites* which is much better preserved than the original and which consequently provides new information on the morphology and mode of life of this taxon. The material was collected more than 40 years ago by W. T. and J. F. Dean from the Caradoc of Shropshire. Although the Deans recognized that they had found a new and bizarre cystoid, the material remained undescribed in the collections of The Natural History Museum.

MORPHOLOGY OF *CARDIOCYSTITES*

Cardiocystites can be recognized immediately by its flattened cordiform theca bounded by a narrow marginal frame. A cylindrical stem attaches to the marginal frame distally, whilst from the centre of the proximal face arise five short, free-standing arms which bear long brachioles (Text-fig. 1). The mouth was presumably situated at the point of ambulacral convergence, as in all echinoderms, although no specimen shows the actual opening. The periproct is also not visible on any specimen but was probably positioned at the anterior corner on one side of the theca, the only region not clearly seen in our new material.

Stem

The stem is at least as long as the theca and tapers only very slightly distally. It is composed of cylindrical holomeric columnals throughout. The stem is heteromorphic proximally, with alternating nodals and internodals established immediately beneath the theca (Text-fig. 2). Distally, however, columnals become more uniform and each has a small spinose flange, at least in the type species. The stem attachment is shared equally between the two lower marginal ossicles. The distal end of the stem is missing.

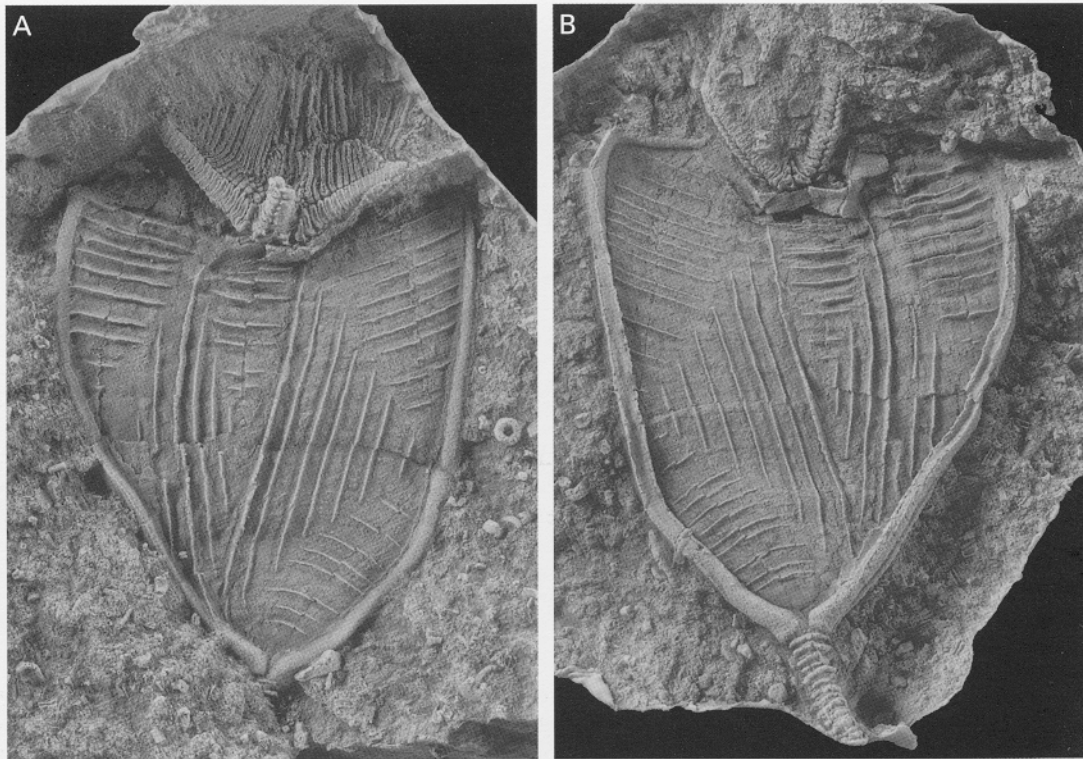
Theca

Thecal plating is very similar in *C. bohemicus* and *C. pleuricostatus* and comprises an outer series of frame plates and an internal series of large polygonal plates. Plating is clearly differentiated into a proximal and distal series separated by a horizontal suture line mid-way down the theca (Text-figs 1, 3). The marginal frame plates have a thickened external rim, c. 0.5–1.0 mm wide, which is smooth and slightly faceted. Upper right and upper left frame elements are similar, consisting of an L-shaped marginal ridge and a triangular internal flange. Sutures coincide exactly on the two surfaces. The flange arises from below the top of the marginal rim, so that the rim projects above the level of the central tessellate region on both surfaces.

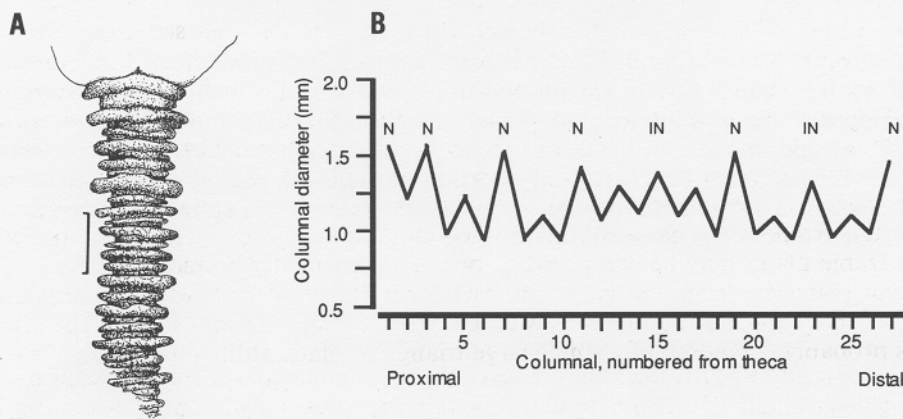
In the lower half of the theca, frame elements differ on left and right sides. One side is formed of a single frame element similar to the proximal element. This is bow-shaped, with a short internal flange that narrows and more-or-less disappears at either end. An identical plate, again with coincidental sutures, is found directly underneath on the opposite surface. By contrast, the lower half of the other side of the frame is composed of two (*C. bohemicus*) or three (*C. pleuricostatus*) elements, each composed of a thickened rim and narrow internal flange. The plate sutures in this area are not clearly defined in any specimen, but the marginal sutures again coincide on each face. In side view the external face has a sharply defined longitudinal groove, raising the possibility that these lower frame plates may be composed of two elements tightly bound together.

The interior plates are large and very thin. Two large rectangular plates in the proximal half of the theca are subequal in size and meet down the midline along a straight suture. The lower half of the theca is probably composed of a single large triangular plate, although in neither species is the plating clearly seen. In *C. bohemicus* two ridges cross the theca, running from the oral mound and converging a little to one side of the stem attachment. These are also present in *C. pleuricostatus*, but are joined by a large number of other ridges set perpendicular to plate sutures. These appear to be structural ribs rather than pleats in the surface of the plate since, where they are displaced and seen in cross section, they appear solid.

The theca is unusual in that there appears to be almost no internal cavity between the two plated surfaces. The marginal rim, which in *C. pleuricostatus* is only 1 mm deep, is elevated above the central plates on both surfaces. In effect this means that the flanges and central plates are closely appressed, only a fraction of a millimetre apart. We initially thought that the part and counterpart

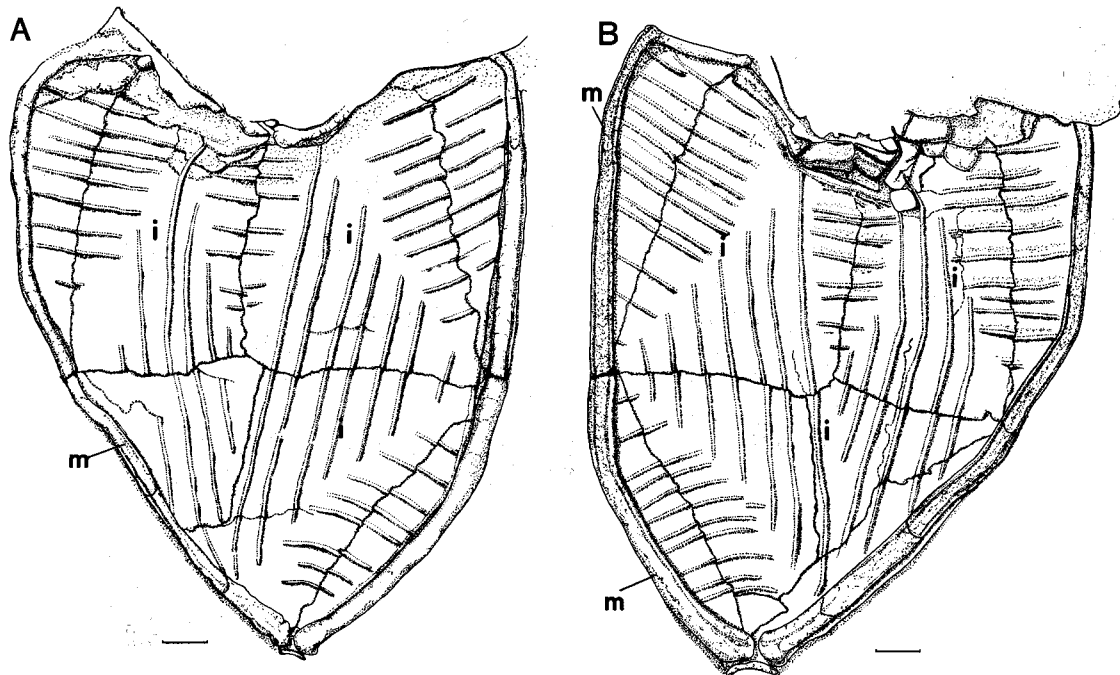


TEXT-FIG. 1. *Cardiocystites pleuricosatus* sp. nov.; BMNH E23706a-b, holotype; Smeathen Wood Beds, *Reuscholithus reuschi* Zone, Burrellian Stage, Harnagian Substage, Caradoc Series; Smeathen Wood, Horderley, Shropshire; part (A) and counterpart (B); $\times 3$.



TEXT-FIG. 2. *Cardiocystites pleuricosatus* sp. nov. A, BMNH E23706b; *Camera lucida* drawing of stem; scale bar represents 1 mm. B, columnal diameter plotted against distance from theca; N = nodal, IN = internodal.

of the holotype of *C. pleuricosatus* were showing the internal and external of the same surface, since suture lines exactly coincided on the two surfaces. However, the ridging is not exactly identical on the two surfaces, and in some places the ridges on the underside can be seen to be weakly corrugating



TEXT-FIG. 3. *Cardiocystites pleuricostatus* sp. nov.; BMNH E23706a–b, holotype; *Camera lucida* drawings of thecal plating, part (A) and counterpart (B). i = interior plate; m = marginal frame plate. Scale bars represent 1 mm.

the upper surface. The superb preservation of the arms and brachioles shows that there has been no skeletal disarticulation of the theca that might have resulted in the loss of a second plated surface.

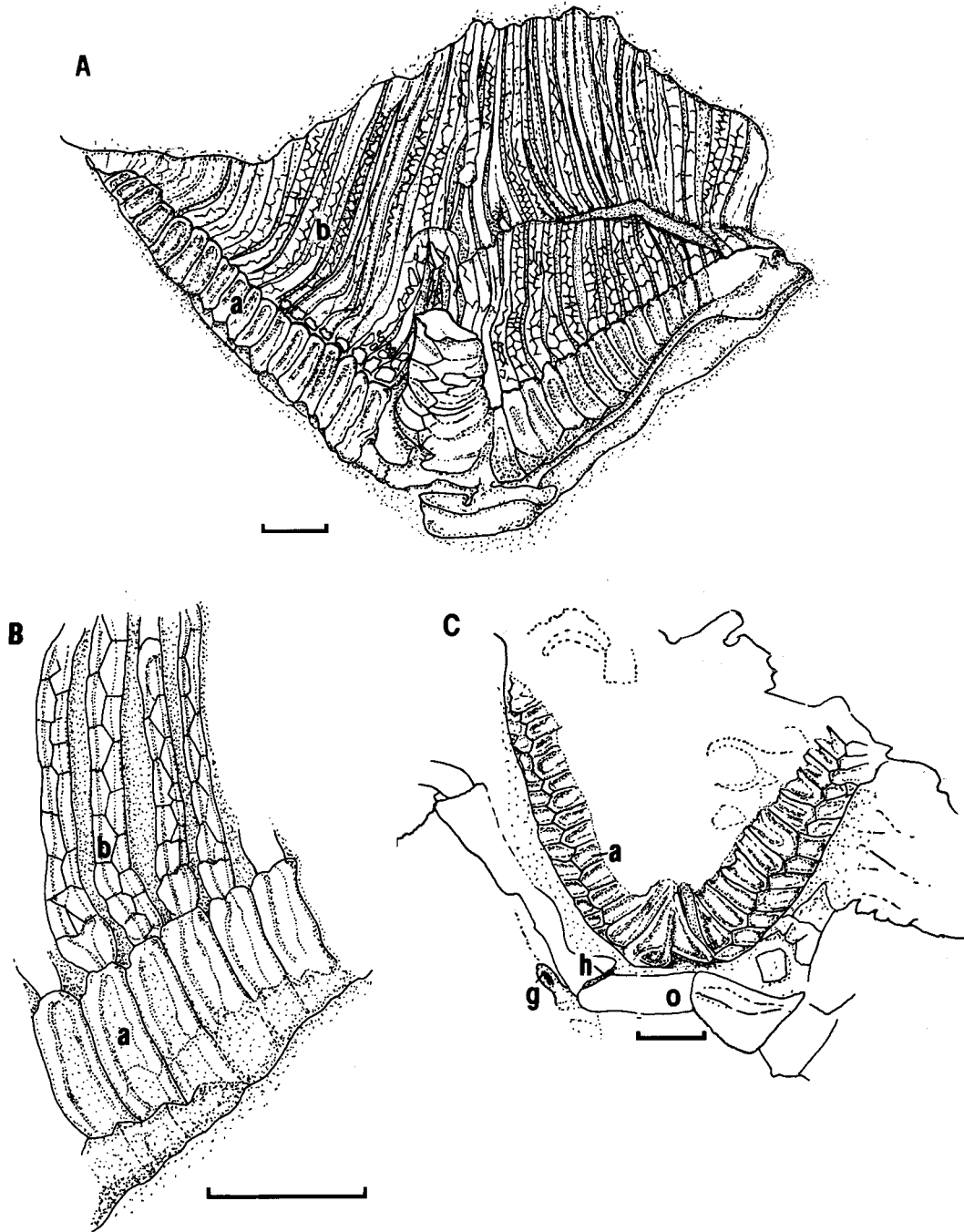
Oral area

The oral area forms a small rounded and flat-topped region in the middle of the distal face of the theca. Its structure remains poorly known, but in *C. pleuricostatus* the five arms diverge from the centre of a ring of some seven plates, 1.5–4.5 mm long. Sutures of some of these plates appear to coincide with the mid-line of arm bases, but plating in this area has collapsed and the arrangement of these plates is uncertain. This is the only portion of the theca that appears to have any depth. On one side there is a small oval opening immediately adjacent to a sutural groove (Text-fig. 4c); we interpret these as the gonopore and hydropore slit.

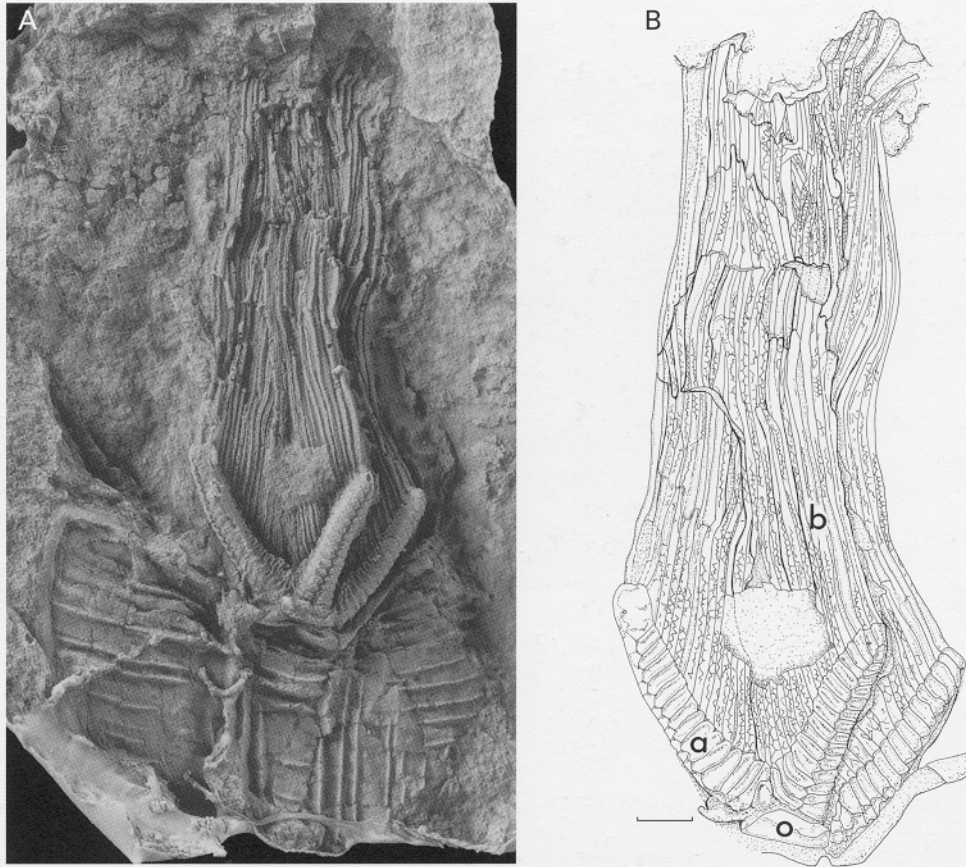
Arms and brachioles

Five arms are seen in both species, but are better preserved in *C. pleuricostatus* (Text-fig. 5). They diverge upwards and outwards from the centre of the theca, are equal in length, relatively short and stubby, 6.5 mm long and 1.0–1.5 mm in diameter. They are thus only about one-third the length of the theca. Arm plating is biserial, composed of a double series of stout ossicles with a smooth outer surface slightly raised to form a rim at distal and proximal edges. There are *c.* 16 elements in each column. Each arm plate gives rise to a single brachiole (Text-fig. 4b). Basal arm elements are larger and more triangular in form than other elements (Text-fig. 4c).

Brachioles are much finer and very much longer than the arms. Each is biserial and the basal articulation occupies virtually the full width of the arm plate from which it arises. Brachioles are approximately 20 mm long and 0.1–0.2 mm wide and are formed of a large number of small



TEXT-FIG. 4. *Cardiocystites pleuricosatus* sp. nov.; BMNH E23706a-b, holotype; *Camera lucida* drawings. A, C, arms and brachioles of part and counterpart. B, detail showing biserial brachioles attaching to ambulacral ossicles of the arm. a = arm; b = brachiole; g = gonopore; h = hydropore slit; o = oral plates. Scale bars represent 1 mm.



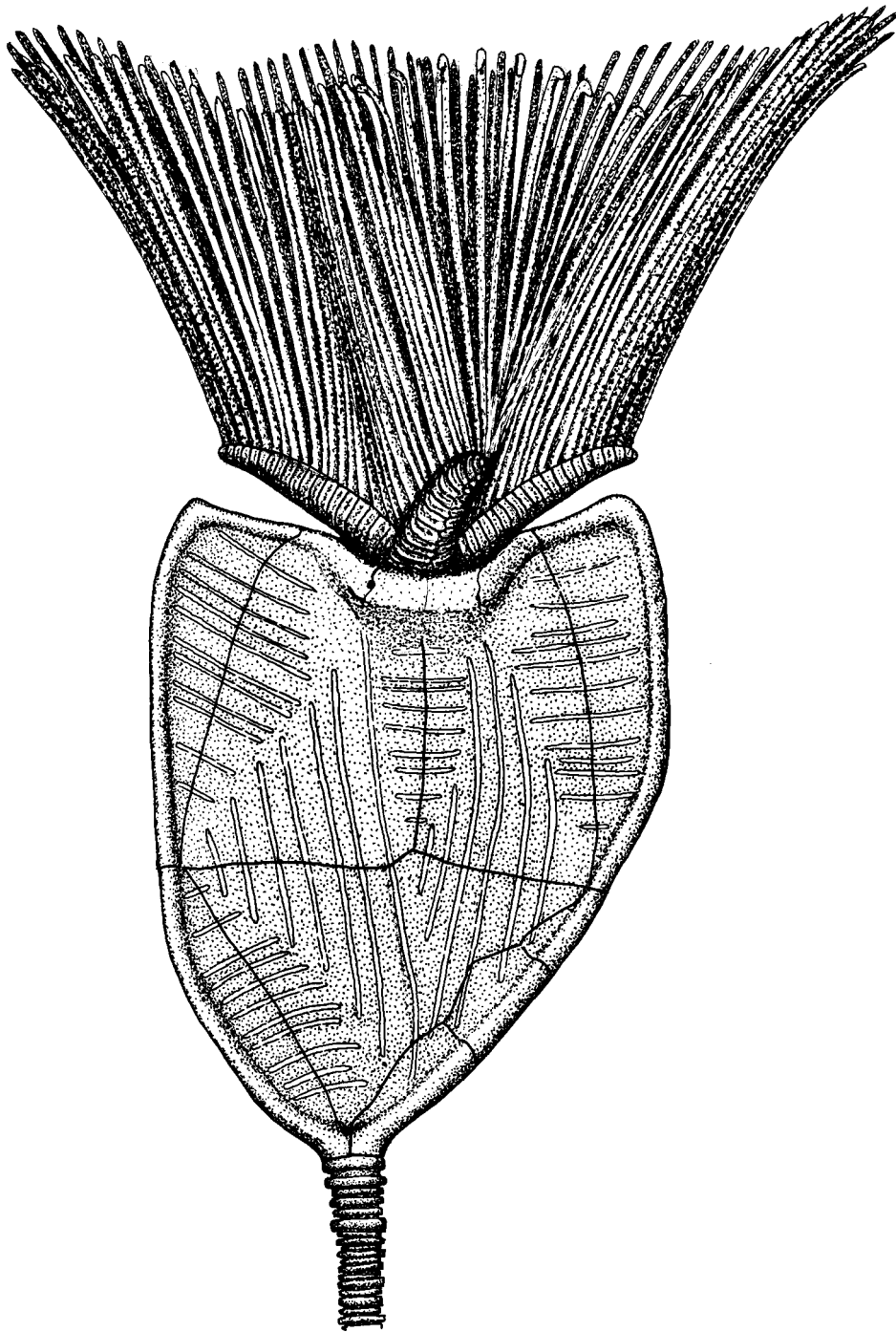
TEXT-FIG. 5. *Cardiocystites pleuricostatus* sp. nov.; BMNH E23709, paratype. A, latex cast; $\times 3$. B, *Camera lucida* drawing of same showing arms (a), brachioles (b) and oral frame plates (o). Scale bar represents 1 mm.

pentagonal elements. Cover-plates appear to be absent. Brachioles arise from every arm ossicle and create a dense filtration fan. Basal elements are slightly enlarged, but otherwise there is no differentiation of plating either along the length of an individual brachiole, or distally along the length of the ambulacrum.

WHY DOES *CARDIOCYSTITES* HAVE SUCH A PECULIAR THECAL DESIGN?

The functional morphology and mode of life of cystoids such as rhipidocystids and *Cardiocystites* are not well understood. It has generally been assumed that their flattened thecal morphology indicates that they lived resting on the sea-floor (e.g. Bockelie 1981, p. 145; Lewis *et al.* 1987, p. 1229; Paul 1988, p. 206). The flattened theca is sometimes thought of as analogous to a snowshoe, functioning to distribute weight so that the animal remains on the surface when living on soft, unconsolidated sediment. Yet this is not the only possible explanation for why a flattened theca evolved, and there are now strong reasons for believing that flattened eocrinoids may have lived elevated above the sea-floor.

First, Lewis *et al.* (1987) discovered that the stem of the highly flattened rhipidocystid *Mandalacystis* ends in a holdfast, at least in smaller individuals. This is strong evidence that *Mandalacystis* lived attached by its stem in an upright posture rather than detached and recumbent. Lewis *et al.* were uncertain how to interpret this and, as a compromise, postulated that juveniles



TEXT-FIG. 6. Reconstruction of *Cardiocystites pleuricostatus* sp. nov.

lived erect but that larger individuals became detached and adopted a recumbent mode of life similar to that postulated for other rhipidocystids. Wilson *et al.* (1992) later reported finding abundant holdfasts of rhipidocystids covering an early Ordovician hardground.

Secondly, we now know that *Cardiocyttites* has five erect arms and a dense brachiolar filtration fan. Its five arms are splayed radially outwards and not confined to the plane of thecal flattening (Text-fig. 6). Furthermore, there is a complete absence of any bilateral symmetry to the conical filtration fan. Such a filtration fan could only have functioned if it was held well above the sediment-water interface and consequently *Cardiocyttites* could not have lain on the sea-floor.

If the highly flattened body form seen in *Cardiocyttites* and *Mandalacystis* is not an adaptation for a recumbent mode for life then it must have served another purpose. There are several possibilities: protective camouflage, providing hydrodynamic lift and/or stability, or enhancing rates of gaseous exchange.

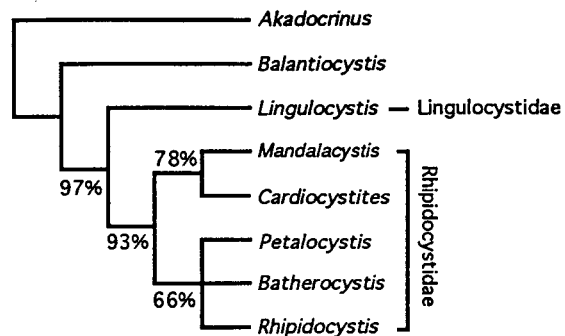
Camouflage. Some modern cidaroid echinoids develop large paddle-shaped spines that are attractive to epiflora and epifauna and thus provide natural camouflage (Smith 1984b). It is therefore conceivable that the broad flat theca of eocrinoids might have served a similar purpose, since we know that encrusting biota were flourishing by this time. However, this explanation seems highly unlikely since none of the specimens shows any evidence of encrustation. Furthermore, the skeleton in echinoderms is mesodermal and thus tissue-covered in life. Cidaroid spines are exceptional in having a cortical overgrowth that is tissue-free, and thus attractive to epibionts. Such a cortex is clearly not developed on plates of *Cardiocyttites*. Finally, this interpretation does not provide an explanation for the thinness of the plates forming the theca. It therefore seems highly implausible that the flattened theca served any role in camouflage.

Hydrofoil for lift or stability of filtration cone. The filtration cone of *Cardiocyttites* needs to be elevated into the water column to function. The semi-rigid stem clearly serves to raise the crown, and enables the filtration cone to become orientated perpendicular to the current direction. However, there is also a possibility that lift could be generated from the current itself such that the crown acts in a manner analogous to a kite, and the stem its tether. The development of the theca into a broad blade-like foil immediately upstream of the filtration fan certainly had hydrodynamic consequences. Such a blade would presumably stabilize the orientation of the cone in the face of oscillating currents and possibly help optimize the angle of the crown.

Baumiller (1992) doubted whether crinoids ever utilized hydrodynamic lift because current velocities had to be extremely high before measurable lift was obtained. However, his calculations were based solely on the lift provided by a porous filtration cone. The foil-like theca of *Cardiocyttites* may have provided additional and possibly more effective hydrodynamic lift, although we have no experimental evidence to support this. Furthermore, the light construction of the theca with its strengthening ribs is consistent with a hydrodynamic explanation.

Gaseous exchange. Efficiency of gaseous exchange was clearly an important issue for the survival of early Palaeozoic cystoids since many developed highly specialized respiratory structures (e.g. Paul 1979). These structures often dominate the theca and involve pores or thin-walled regions of the theca with large surface areas across which gases could diffuse readily. It is therefore possible that the flattened, thin-walled theca represents an adaptation for more efficient gaseous exchange. The thick-walled globular theca of standard eocrinoids must have been considerably more of a barrier to gases than the thin-walled, flattened theca of *Cardiocyttites*. Internal volume was tiny, further enhancing the efficiency of the theca as an exchange surface. Thinness of thecal plates would have been crucial for effective gaseous exchange but also must have greatly reduced the mechanical strength of the theca. The ridges that cross the theca are unlikely to have functioned to increase the available surface area analogous to flanges on a radiator, since they appear to be solid and do not always coincide on the two surfaces. Rather, their primary rôle seems to have been in strengthening the plates.

TEXT-FIG. 7. Single most parsimonious cladogram for flattened eocrinoid taxa. Tree length = 23, Consistency Index = 0.78, Retention Index = 0.76. Bootstrap values for internal branches are based on 1000 replicates.



On the other hand, one might question whether a flattened theca was really the most efficient way to improve gaseous exchange. Why, for example, did one surface not simply remain uncalcified?

PHYLOGENETIC RELATIONSHIPS

Paul (1988) provided the first serious assessment of the relationships of cystoids, including *Cardiocystites*. His cladistic analysis placed *Cardiocystites* as sister-group to rhipidocystids and identified *Lingulocystis* as the immediate outgroup to both taxa. In the light of our new data on the morphology of *Cardiocystites* we have undertaken a reanalysis of its relationships. For outgroups we include *Akadocrinus* (Paul's original outgroup) and *Balantiocystis*. *Balantiocystis* appears to be the most closely related eocrinoid; not only is its theca distinctly compressed but amongst its multiple polygonal plates are larger thickened nodulose plates that may be homologous to the marginals of rhipidocystids. Furthermore, its oral area and brachiolar arrangement are very similar to that seen in *Rhipidocystis*. *Balantiocystis* comes from the lower Ordovician of the Montagne Noire, France and its morphology was superbly described by Ubaghs (1972).

The Appendix lists the character scorings used in our analysis along with our data matrix. Morphological information comes from the following sources: *Rhipidocystis* – Ubaghs (1967); Bockelie (1981); *Petalocystis* – Sprinkle (1973); *Mandalacystis* – Lewis *et al.* (1992); *Akadocrinus* – Sprinkle (1973); *Lingulocystis* – Ubaghs (1960, 1994); *Balantiocystis* – Ubaghs (1972); *Batherocystis* – Ubaghs (1967). *Batherocystis*, although clearly a member of the Rhipidocystidae, remains poorly known and no arm and brachiolar characters can be scored for this taxon.

Parsimony analysis using the exhaustive search option of PAUP (Swofford 1993) found one tree, which places *Petalocystis*, *Batherocystis* and *Rhipidocystis* in a trichotomy (Text-fig. 7). Lack of resolution in this part of the cladogram is due solely to the lack of information concerning the morphology of *Batherocystis* rather than conflict amongst characters. The remaining relationships are all supported with reasonably high bootstrap values. *Cardiocystites* is placed as sister taxon to *Mandalacystis*, and together these form the sister group to the clade *Rhipidocystis*–*Petalocystis*–*Batherocystis*. Since Lewis *et al.* (1992) accepted that *Mandalacystis* should be placed in the Rhipidocystidae, *Cardiocystites* must also belong in this family. *Lingulocystis* was identified as the immediate outgroup to Rhipidocystidae. This supports the findings of Paul (1988).

SYSTEMATIC PALAEOLOGY

Family RHIPIDOCYSTIDAE Jaekel, 1901

Genus CARDIOCYSTITES Barrande, 1887

Type species. By monotypy; *Cardiocystites bohemicus* Barrande, 1887, p. 120, pl. 31, figs 10–12, from the Zahořany Formation of Zahořany, Bohemia.

Diagnosis. Pelmatozoan with heteromorphic stem, flattened heart-shaped theca bounded by a thickened rim and composed of an upper and lower series of large polygonal plates, five erect arms and long brachioles.

Occurrence. Upper Ordovician (Caradoc Series) of the Czech Republic and England.

Cardiocyttites pleuricostatus sp. nov.

Text-figures 1-6

Types. Holotype: Natural History Museum, London, BMNH E23706a, b; paratype BMNH E23709.

Other material. National Museum of Wales 97.43G.1 (arm fragment).

Occurrence. The holotype and NMW 97.43G.1 come from the Smeathen Wood Beds, *Reuscholithus reuschi* Zone, Burrellian Stage (Harnagian Substage), Caradoc Series at Smeathen Wood, Horderley, Shropshire. The paratype comes from the Harnagian Substage of 'Onny Valley', almost certainly from the Horderley district in the vicinity of Round House or Smeathen Wood.

Diagnosis. A *Cardiocyttites* with multiple small corrugations running perpendicular to the plate margins towards the centre of the plate.

Description. The most proximal 6.5 mm of the stem is visible in the holotype, fully articulated. The stem is holomeric and heteromorphic with up to three series of internodals developed between nodals. Nodal and internodal cycles are readily discernible from sequential alternation in columnal diameter (Text-fig. 2). The nodal-internodal pattern becomes established rapidly beneath the theca, after the third nodal has formed.

The holotype, preserved as part and counterpart, has a maximum thecal width of 18 mm and a length from stem to the centre of the oral surface of 17.5 mm. It has a relatively narrow marginal rim, 0.75 mm wide and c. 0.5-1.0 mm deep; it is rectangular in cross section. On one face (?upper) the rim is weakly concave with rounded edges, while the other (?lower) is convex.

The organization of the distal series of plates is problematical. Marginal plates on either side bound a triangular area. The holotype shows possible fracture lines or sutures marking a small triangular area near the stem attachment and another approximately sagittal. However, the pattern of ribbing suggests that the entire area inside the marginal frame is composed of a single element.

All central plates are ribbed, with ribbing perpendicular to sutures. Ribs from adjacent plates meet across the suture line with little or no displacement. Ribs are c. 0.1 mm wide and 0.1 mm high. The median longitudinal ribs are the longest, with the two largest extending from the oral area to the marginal frame slightly to one side of the stem. Ribbing on upper and lower surface is often, but not always, coincidental.

Remarks. *C. pleuricostatus* is easily differentiated from *C. bohemicus* by its strongly ribbed thecal plates. In *C. bohemicus* just two ribs cross the theca, running obliquely from the oral area. These ribs are present in *C. pleuricostatus*, but are accompanied by a large number of other ribs, set perpendicular to plate sutures.

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JULIETTE DEAN

ANDREW B. SMITH

Department of Palaeontology
The Natural History Museum
Cromwell Road
London SW7 5BD, UK

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APPENDIX

Characters used in determining the phylogenetic position of *Cardiocystites*. The data matrix is given at the end.

1. Thecal form: globular to ovate (0); strongly flattened in one plane (1).
2. Stem: columnals, polyplated (0); holomeric (1).
3. Stem: homeomorphic (0); heteromorphic, with large and small columnals alternating (1); reduced to a few large elements (2).
4. Stem attachment to theca: attaches equally to two basals (0); attaches to three basals (1); attaches to four basals (2); attaches to five basals (3).
5. Marginal frame plates: undifferentiated (0); present (1).
6. Marginal plates with internal flanges: absent (0); present (1).
7. Marginal frame plates: double, at least distally (0); single (1).
8. Number of plates forming lateral and distal margins of theca: more than ten (0); seven or eight (1).
9. Centrals: tessellate (0); imbricate (1).
10. Number of centrals: more than six (0); three or four (1).
11. Transverse strutting: absent (0); present (1).
12. Arms: absent (oral frame plates give rise to brachioles direct) (0); present (1).
13. Oral area and arms: basically pentaradial (0); strongly bilateral (1).
14. Brachioles: biserial (0); uniserial (1).
15. Brachioles: contiguous forming filtration net (0); in scattered clumps (1).

16. Oral area: narrow, not stretching across entire proximal face (0); wide, occupying entire width of theca proximally (1).
17. Oral area: flush (0); depressed, below horn-like processes of the theca (1).
18. Periproct: lateral half-way down theca (0); in upper corner of theca close to peristome (1); on oral surface (2).

<i>Cardiocyttites</i>	11101	10101	11001	011
<i>Rhipidocystis</i>	11201	10101	00110	101
<i>Petalocystis</i>	11201	10101	00100	001
<i>Mandalocystis</i>	11011	10101	01101	111
<i>Lingulocystis</i>	11121	01010	10100	000
<i>Batherocystis</i>	11201	10101	00???	001
<i>Balantiocystis</i>	01110	0?000	00000	000
<i>Akadocrinus</i>	01030	0?000	00000	002

