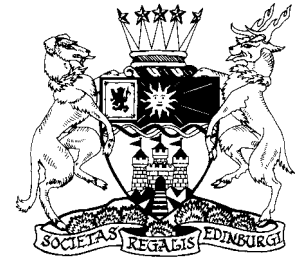


# *Bromidechinus*, a new Ordovician echinozoan (Echinodermata), and its bearing on the early history of echinoids

Andrew B. Smith and Jeremy J. Savill

**ABSTRACT:** A new genus and species of primitive echinozoan, *Bromidechinus rimaporus*, is described from the Upper Ordovician of Oklahoma, USA. This has a unique plate arrangement. There is a single perradial series of imperforate plates bounded on either side by a column of perforate ambulacral plates. A double column of interambulacral plates separates ambulacral zones. The sparse record of Ordovician echinozoans is reviewed and cladistic analysis suggests that *Bromidechinus* represents a lineage that diverged prior to the split between bothriocidarids and main-line echinoids. This leads to a revised interpretation of the earliest stages of morphological evolution of echinoids.

**KEY WORDS:** cladistic analysis, phylogeny



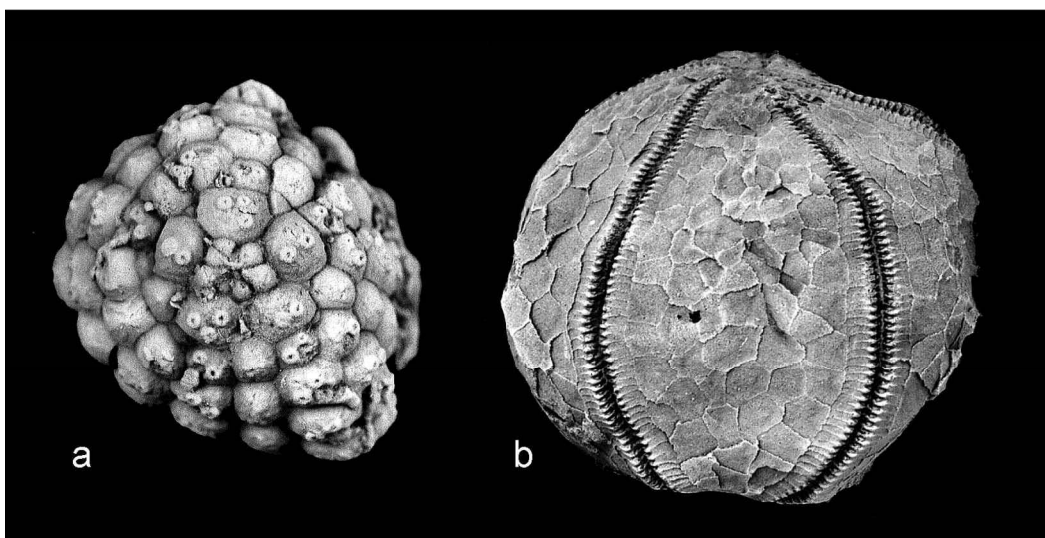
Echinoidea, one of the five classes of echinoderm, today comprises more than 800 extant species. They are a distinctive and easily recognisable clade with a characteristic tessellated skeleton composed of calcite plates covered in spines. This skeleton, or *test*, is typically globular in form. Except for a couple of highly derived groups, all have a complex internal dental apparatus known as the *Aristotle's lantern* that is used in feeding.

Recent morphological and molecular evidence (Littlewood & Smith 1995; Littlewood *et al* 1997; Mooi & David 1997; Sumrall & Sprinkle 1998) places echinoids as sister group to holothurians, and the Echinoidea and Holothuroidea together form the clade Echinozoa. Holothurians have reduced their body-wall skeleton to small plates or microscopic elements, and have the poorest of body fossil records (Smith & Galleml 1991). Luckily, their spicules are not uncommon in sediment

samples and from this much can be determined about their evolutionary history (Gilliland 1992).

Echinoids first appeared in the Ordovician, whereas undisputed holothurians did not appear until the late Silurian. However, neither the origins of the Echinozoa nor the split of holothurians from echinoids is properly understood. It is thus quite possible that forms described as echinoids from the Ordovician represent a mixture of stem-group Echinozoa and basal members of the Echinoidea and Holothuroidea. Indeed, there has been considerable dispute over which of the Ordovician forms represent true echinoids.

The root of the problem has been that the earliest echinozoans fall into two very distinct groups based on their overall test morphology, one exemplified by *Bothriocidaris* and the other by lepidocentrids such as *Aulechinus*. *Bothriocidaris* is a small, globular form with thick tessellate plates (Fig. 1a).



**Figure 1** The two contrasting morphologies of early Palaeozoic echinoids, as exemplified by *Bothriocidaris* and *Aulechinus*: (a) *Bothriocidaris pahlani* Schmidt, BMNH E83655, early Caradoc of Estonia, apical view,  $\times 5$ ; (b) *Aulechinus grayae* Bather & Spencer, BMNH E40522a, late Ashgill, Girvan, Ayrshire, lateral view of internal mould,  $\times 1.5$ .

Its test is made up of a double column of ambulacral plates with pore-pairs, and a single interambulacral column of plates. *Aulechinus* and related lepidocentrids by contrast have thin, flexible, globular tests with biserial ambulacra and a mass of irregular imbricate interambulacral plates (Fig. 1b).

In the early part of the twentieth century a major dispute arose amongst echinodermologists over the nature of *Bothriocidaris*. Mortensen (1928) believed that *Bothriocidaris* had

**Table 1** Ordovician Echinozoa

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*Aulechinus grayae* Bather & Spencer 1934, p. 557; McBride & Spencer 1938, p. 98. Starfish Bed, early Rawtheyan, late Ashgill; Ayrshire, Scotland.

*Bromidechinus rimaporus* Smith & Saville, this paper. Pooleville Member, Bromide Formation, Blackriverian [= Harnagian, early Burrellian], Caradoc; Oklahoma, USA.

*Bothriocidaris eichwaldi* Männil 1962, p. 152, pl. 1; figs 6–9. Pirgu Stage [= late Pugsillian to Rawtheyan], Ashgill; Estonia.

*Bothriocidaris globulus* Eichwald 1860; Männil, p. 160, text-figs 3 & 10. Vormsi Stage [= early Pugsillian], early Ashgill. Also Starfish Bed, early Rawtheyan, late Ashgill, Girvan, Ayrshire, Scotland (Paul 1967, p. 525, pl. 85, figs 1–4).

*Bothriocidaris kolatai* Kier 1982, p. 311, pl. 41, fig. 1, 2, text-fig. 74. Pooleville Member, Bromide Formation, Blackriverian [= Harnagian, early Burrellian], Caradoc; Oklahoma, USA.

*Bothriocidaris pahleni* Schmidt 1874; Männil (1963, p. 147, pl. 1, figs 1–5, pl. 2, figs 1, 2); Johvi Stage [= mid to late Burrellian], Caradoc; Estonia.

*Bothriocidaris parvus* Männil 1962, p. 156, pl. 2, figs 3, 4m, pl. 3, fig. 5. Vormsi Stage [= early Pugsillian], early Ashgill; Estonia.

*Bothriocidaris solemi* Kolata 1975, p. 66, pl. 14, figs 14–15. Walgreen Member, Grand Detour Formation, Platteville Group, Blackriverian [= Harnagian, early Burrellian], Caradoc; Illinois, USA.

*Bothriocidaris vulcani* Guensberg 1984, p. 67, pl. 14, figs 4–10. Lebanon Limestone, mid to late Blackriverian [= Harnagian, early Burrellian], Caradoc; Tennessee, USA.

*Bothriocidaris* sp. nov., aff. *pahleni* Nestler 1968, p. 1224. F2, Hirnantian, late Ashgill; Gotland, Sweden [erratic block].

*Ectinechinus lamonti* McBride & Spencer 1938, p. 99. Starfish Bed, early Rawtheyan, late Ashgill; Ayrshire, Scotland.

*Eothuria beggi* McBride & Spencer 1938, p. 126. Starfish Bed, early Rawtheyan, late Ashgill; Ayrshire, Scotland.

*Neobothriocidaris minor* Paul 1967, p. 535, pl. 85, figs 5–8. Craighead Formation, Longvillian, late Burrellian, Caradocian; Ayrshire. Also from Starfish Bed, early Rawtheyan, late Ashgill; Ayrshire, Scotland.

*Neobothriocidaris peculiaris* Paul 1967, p. 535, pl. 85, figs 9–11. Starfish Bed, early Rawtheyan, late Ashgill; Girvan, Scotland. Also Kalvsjo Formation, Ashgill; Hadeland, Oslo Region, Norway (Brockelie & Briskeby 1980).

*Neobothriocidaris templetoni* Kolata 1975, p. 66, pl. 14, figs 1–2, text-figs 18, 19. Eagle Point Member, Dunleith Formation, Galena Group; early Trentonian [= Soudleyan, Burrellian], Caradoc; Illinois-Wisconsin, USA.

?*Neobothriocidaris* spp. Guensberg 1984, p. 69, pl. 14, fig. 11. Upper member of the Lebanon Limestone, mid to late Blackriverian [= Harnagian, early Burrellian], Caradoc; Tennessee, USA.

*Unibothriocidaris bromidensis* Kier 1982, p. 310, pl. 41, fig. 3, text-fig. 73. Pooleville Member, Bromide Formation, Blackriverian [= Harnagian, early Burrellian], Caradoc; Oklahoma, USA.

*Unibothriocidaris* sp. cf. *bromidensis* Kier; Kolata 1975, p. 68, pl. 14, figs 3–8 (as Genus & Species unknown). Briton Member, Mifflin Formation, Platteville Group, Blackriverian; [= Harnagian, early Burrellian], Caradoc; Illinois-Wisconsin, USA.

*Unibothriocidariskieri* Guensberg 1984, p. 68, pl. 14, figs 12–15. Lower Lebanon Limestone, Blackriverian [= Harnagian, early Burrellian], Caradoc; Tennessee, USA.

?*Unibothriocidaris* sp. Guensberg 1984, p. 64, pl. 13, fig. 15. Lower Lebanon Limestone, mid to late Blackriverian [= Harnagian, early Burrellian], Caradoc; Tennessee, USA.

*Volchovia mobilis* Hecker 1938, p. 425. *Megalaspis* Limestone, Volkhov Stage, early Middle Ordovician, Estonia.

*Volchovia norvegica* Regnéll 1948, p. 35, pl. 2, fig. 4. Expansus Shale, 3c $\beta$ , Harnagian Soudleyan, Burrellian, early Caradoc; Norway.

*Volchovia volborthi* Hecker 1938, p. 426. Vaginatum Limestone, Kunda Formation, late Arenig-early Llanvirn, Early to Middle Ordovician, Estonia.

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nothing to do with echinoids but was a peculiar cystoid. He argued that echinoids evolved from an edrioasteroid ancestor, such as the Cambrian *Stromatocystites*, and that the earliest and most primitive echinoids were the Silurian lepidocentrids *Echinocystis* and *Palaeodiscus* (Ordovician lepidocentrids were at that time unknown). Jackson (1929) and Hawkins (1931), however, strongly contested this opinion, arguing that *Bothriocidaris* was a true echinoid, and that echinoids could not therefore be derived from *Stromatocystites*.

A few years later Bather & Spencer (1934) recorded the first Ordovician lepidocentrid echinoid from the late Ordovician (Ashgill) of Scotland. McBride & Spencer (1938) subsequently gave detailed descriptions of this material and recognised two genera, *Aulechinus* and *Ectinechinus*. In addition, they described a third genus, *Eothuria*, which they attributed to the holothurians on the basis of its supposed anal plates. In the same year Hecker (1938, see also Hecker 1940) described the first Ordovician ophiocistioid, *Volchovia mobilis* from the Middle Ordovician of Estonia.

A major advance came with the first detailed description of *Bothriocidaris* by Männil (1962). Männil added greatly to our understanding of the morphology of this taxon and, for the first time, demonstrated that it had an Aristotle's lantern of sorts. For many this was convincing evidence that *Bothriocidaris* was indeed an echinoid.

Our understanding of ophiocistioids has also grown considerably, thanks to the careful work of Haude & Langenstrassen (1976) and Jell (1983). Critically, it was discovered that ophiocistioids have a lantern identical in structure to that of echinoids but a body wall skeleton reduced to microscopic wheel-shaped spicules identical to that of some holothurians. This prompted Smith (1984, 1988) to propose that ophiocistioids were sister-group to holothurians.

Our knowledge of Ordovician Echinozoa has steadily improved over the years. There are now eight genera and nineteen species described, including the new genus and species described here (Table 1). With the exception of *Volchovia*, all are now considered to come from the Upper Ordovician (Fig. 2). *Neobothriocidaris* was described from the late Caradoc and Ashgill of Girvan, Scotland by Paul (1967), and has subsequently been described from the early Caradoc of North America by Kolata (1975). *Bothriocidaris* and another new genus, *Unibothriocidaris*, were described from the early Caradoc of North America by Kier (1982) and Guensberg (1984). However, it is still true that Ordovician echinozoans are amongst the rarest of fossil echinoderms.

The discovery of a new taxon, intermediate between ophiocistioids and bothriocidarids, prompted us to reexamine the Ordovician record of Echinozoa. The description of this taxon and its relationship to other echinozoans form the subject of this paper.

## 1. Systematic description

Class Echinoidea Leske, 1778

Plesion (Genus) *Bromidechinus* gen. nov.

**Type species.** *Bromidechinus rimaporus* Smith & Saville sp. nov.

**Derivation of name.** Named after the Bromide Formation from which the two specimens came.

**Diagnosis.** Small, globular test with double column of ambulacral plates, single column of perradial plates and double column of interambulacral plates. Pores single and slit-like; fully enclosed within ambulacral plates. Apical disc an undifferentiated mass of small platelets.

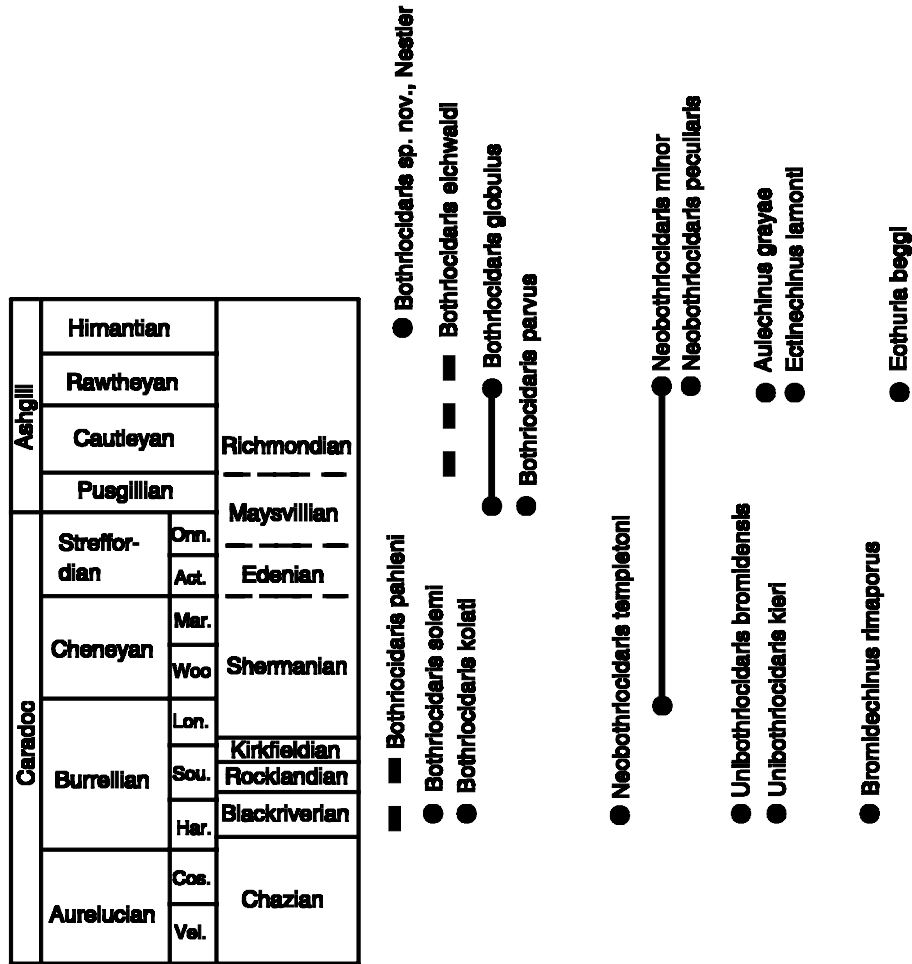


Figure 2 Geological distribution of all known echinozoan taxa from the Upper Ordovician; time scale and correlation taken from Fortey *et al.* (2000).

**Occurrence.** Bromide Formation, Blackriverian [= Harnagian, Burrellian, early Caradoc], Upper Ordovician of Oklahoma, USA.

**Description.** Test globular in form with an estimated uncrushed diameter of approximately 20 mm and height of maybe 25 mm. Plating is relatively thin and all plate boundaries are imbricate. However, overlap between plates is not extensive.

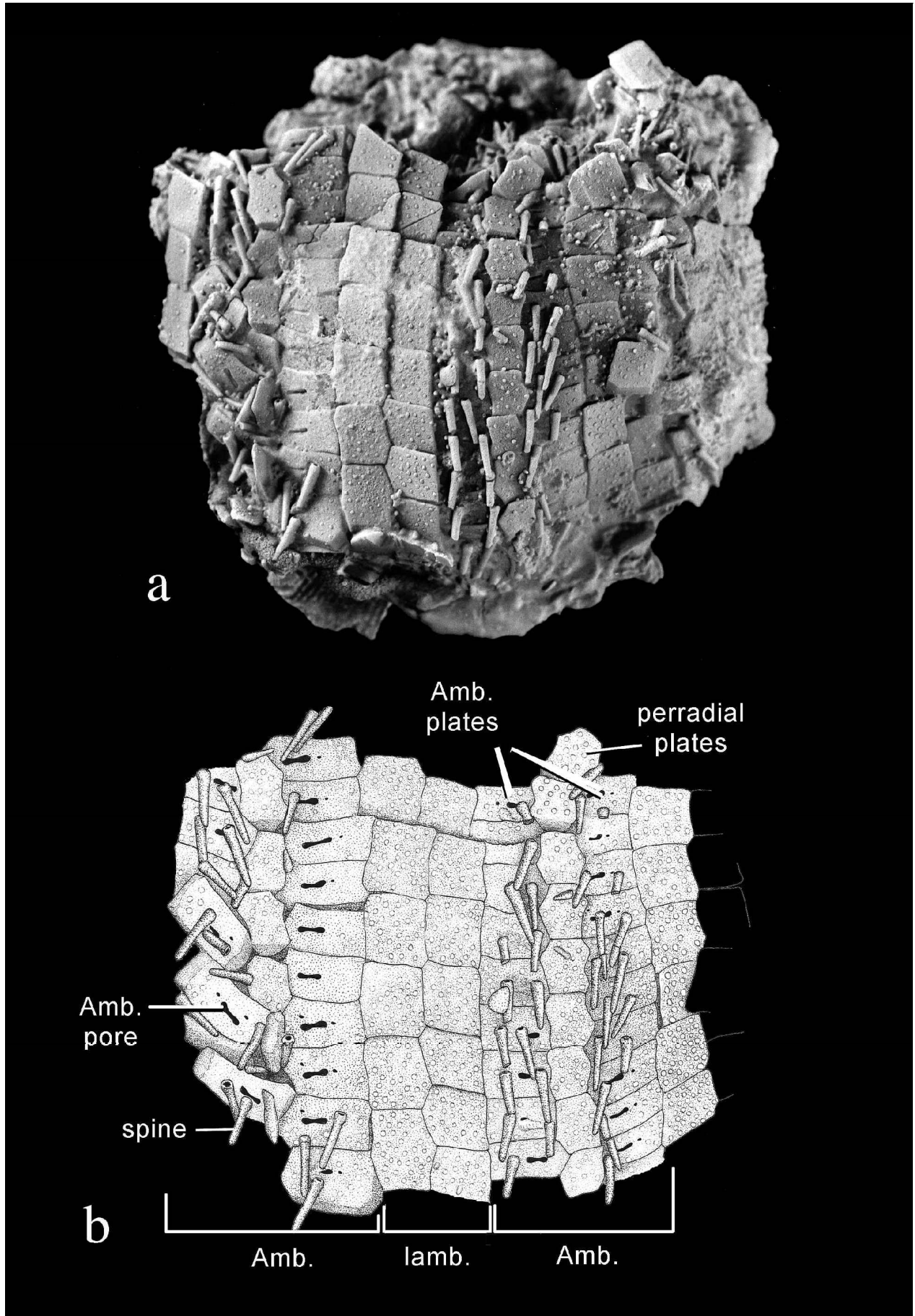
The corona is composed of three series of plates, arranged as five alternating ambulacral and interambulacral zones. The curvature of these zones seen in one specimen (Fig. 4) appears to be an artefact of preservation. The peristome and periproct are at opposite poles and both are relatively small. The aboral surface is reduced to a small adapical region (approximately 5.5 mm in diameter) made up of a mass of small platelets, presumably marking the position of the periproct. Both ambulacral and interambulacral columns extend to this mass of platelets (Fig. 4) and a ring of spines immediately surrounds the apical zone. There is no enlarged circlet of apical disc plates. However, preservation makes it impossible to tell whether a small ocular plate was present at the top of each ambulacral column or whether a single enlarged genital plate/madrepore was located in an interambulacral position. There is no evidence for an enlarged madreporic plate in the one specimen that preserves the apical disc (Fig. 4a, c).

Ambulacral zones are composed of a single perradial column of imperforate plates and two lateral columns of perforated ambulacral plates (Fig. 3). Plates of the perradial series are

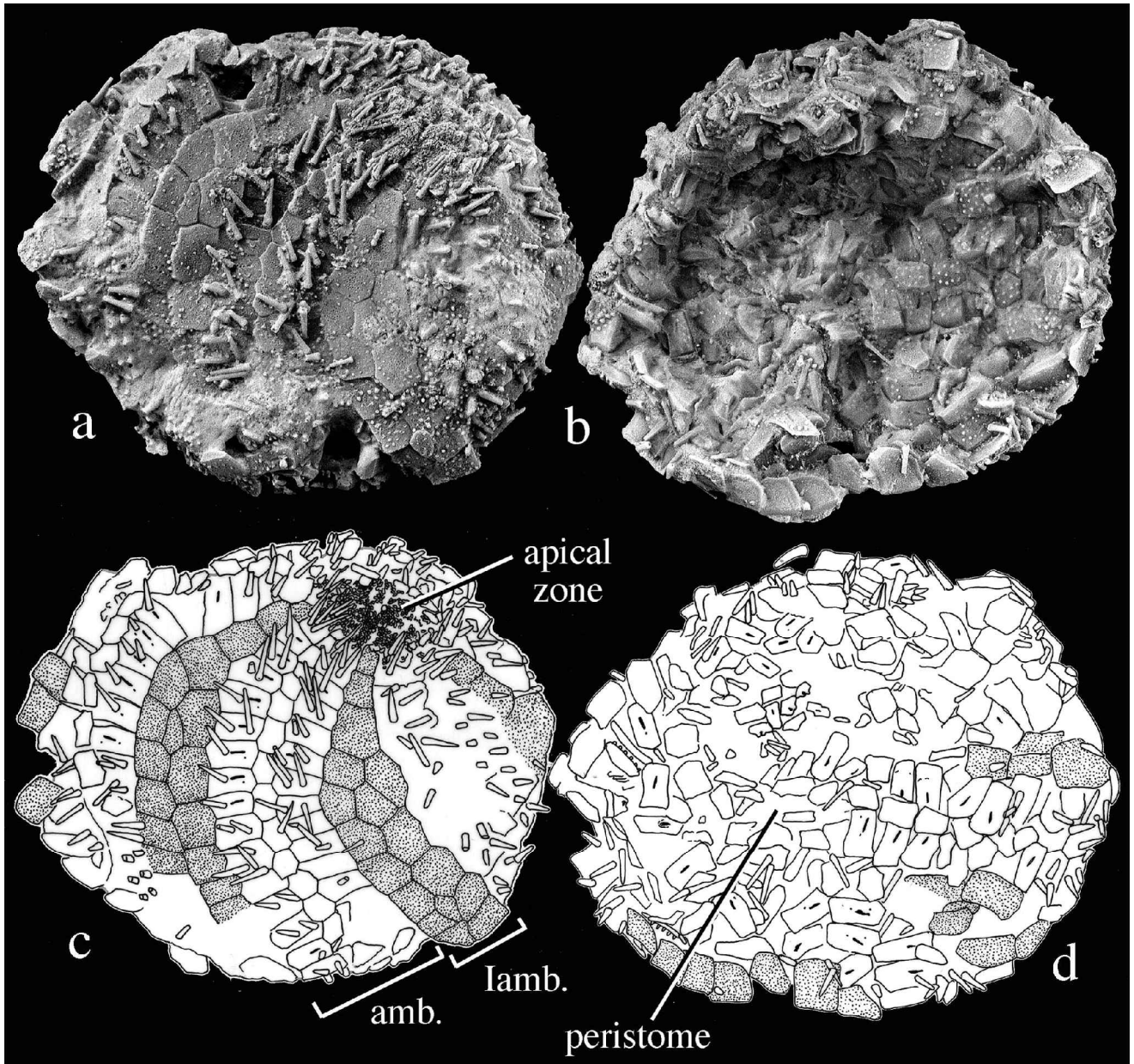
slightly taller than wide and rectangular to subhexagonal in outline. On either side lies a single column of ambulacral plates, each pierced by an ambulacral pore (Fig. 3). There are approximately twenty ambulacral plates in a column and slightly fewer imperforate perradial plates. The perradial plates imbricate with more adoral plates overriding adjacent adapical plates. They also overlap the perradial margins of adjacent ambulacral plates.

Ambulacral plates are about twice as wide as tall and form a regular uniserial column on either side of the perradial plate series. Each plate is weakly imbricate with its neighbours, and is slightly overlapped by both the perradial and the interambulacral series of plates. There is a single slit-like pore positioned on the perradial half of each plate (Figs 3, 5). This slit is slightly wider at each end and expands through the plate to open internally as a large tear-drop-shaped opening (Fig. 5c). On the inside the area around the pore is raised and the pore opening angled towards the perradius. Externally, a small tear-drop shaped pit is found immediately to the adradial side of the pore, and a second underneath the perradial end of the pore. These pits mark the attachment sites of the two primary spines associated with each plate.

Interambulacral zones are composed of a biserial series of imperforate plates. The interambulacral plates are slightly taller than wide and generally pentagonal in shape, with a more or less straight adradial suture and a more zig-zagged interradian suture (Figs 3, 4). They become taller adapically. The most adapical three or four plates are arranged uniserially,



**Figure 3** *Bromidechinus rimaporus* gen. et sp. nov., BMNH EE6607 (holotype). Pooleville Member, Bromide Formation, Blackriverian [= Harnagian Substage, Burrellian] early Caradoc, Late Ordovician, Criner Hills, Carter County, Oklahoma, USA; specimen in lateral profile (a) and interpretative line drawing (b);  $\times 4.5$ ; Amb = Ambulacral zone; lamb = interambulacral zone.



**Figure 4** *Bromidechinus rimaporus* gen. et sp. nov., BMNH EE6632 (paratype). Pooleville Member, Bromide Formation, Blackriverian [= Harnagian Substage, Burrellian] early Caradoc, Late Ordovician, Criner Hills, Carter County, Oklahoma, USA; specimen in apical (a) and adoral (b) views and interpretative line drawings (c, d);  $\times 3$ ; abbreviations as in Figure 3.

whereas, over the remainder of the test, plating is more or less strictly biserial, although an occasional small third plate may appear centrally in the interambulacral zone. Immediately adjacent to the peristome, plating is too disrupted to tell whether the interambulacral columns become uniserial, although this seems likely.

The peristome is small (c. 5 mm diameter). Unfortunately, preservation of this region is too poor to make out any further details. No elements of the lantern are discernible.

Spines are rather short and stout, being simple, elongate cones 2 mm in length. There are two to each ambulacral plate. Spines are absent from both perradial and interradian plates. All plates are covered in a fine ornament of blunt pegs, less than 0.05 mm in height. These may be granules attached directly to the plate surface, or (less likely) stereomic outgrowths from the plate surface. They are easily lost by abrasion.

*Bromidechinus rimaporus* sp. nov.

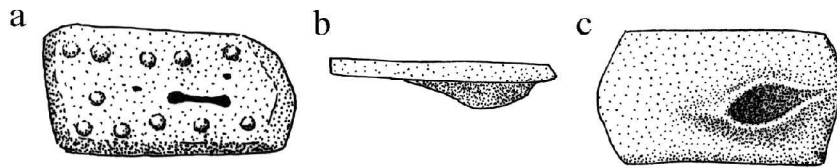
Figs 3–5

**Derivation of name.** From the Latin *rima*, a slit, and *porus*, pore, in reference to the distinctive form of ambulacral perforation.

**Types.** Holotype BMNH EE6607, paratype BMNH EE6632.

**Occurrence.** Both specimens come from Dunn Quarry (currently owned by Geological Enterprises from whom the specimens were purchased), Criner Hills, Carter County, Oklahoma, USA, from a level within the Pooleville Member, Bromide Formation, Blackriverian. This is correlated with the Harnagian substage of the Burrellian, early Caradoc, Upper Ordovician (for details of the stratigraphy and environmental setting of this locality, see Sprinkle 1982).

**Diagnosis and description.** As for genus; no other species are known.



**Figure 5** Reconstruction of an ambulacral plate of *Bromidechinus rimaporus* gen. et sp. nov. seen in external (a), lateral (b) and internal (c) views.

## 2. Comparison with other Ordovician Echinozoa

*Bromidechinus* is clearly distinguished from other echinozoans on the basis of its test plating, but has features which link it to both ophiocistioids and to echinoids. The differences and similarities between *Bromidechinus* and the other Ordovician genera of Echinozoa previously described are highlighted below. The only taxon omitted from discussion is *Volchovia*, from the Middle Ordovician of Estonia (see Sprinkle *et al.* 1999 for the dating of these beds). The morphology of *Volchovia* is almost completely unknown. All three species of *Volchovia* have been described from aboral surfaces only, and there is as yet no convincing evidence that they are true ophiocistioids. *Volchovia* is clearly an eleutherozoan and very different from *Bromidechinus*, but a more precise placement of this taxon must await description of better material.

In this analysis three end-members act as our primary reference points: *Stromatocystites* Pompeckj, 1896, *Gillocystis* Jell, 1983, and *Aptilechinus* Kier, 1973. *Stromatocystites* is a stem-group eleutherozoan echinoderm from the Middle Cambrian most recently redescribed by Smith (1985). Phylogenetically it predates the separation of echinozoans from asteroids and ophiuroids (Smith 1984, 1988). *Gillocystis* comes from the Early Devonian of Australia and is the best-known ophiocistioid taxon thanks to the careful work of Jell (1983). Ophiocistioids are widely believed to be an extinct sister group to the holothurians (Smith 1988; Sumrall & Sprinkle 1998; Mooi & David 1997), and thus *Gillocystis* serves as a primitive holothurian representative. *Aptilechinus* is an undisputed echinoid from the Early Silurian of Scotland that was described by Kier (1973). The primary sources for descriptions of other taxa are listed in Table 1.

### 2.1. Shape and plating

Ordovician Echinozoa are all globular and relatively tall (i.e. melon-shaped). This body form is occasionally developed in certain Cambrian edrioasteroids (e.g. *Totiglobus* Bell & Sprinkle 1978), although *Stromatocystites* itself is rather depressed and cushion-shaped. A similar tall, melon-shaped test characterises *Aptilechinus*, but *Gillocystis* is more depressed, though still globular in form.

In terms of thecal construction there is a distinct dichotomy between those with thick tessellate plating (*Bothriocidarid*s, *Unibothriocidarid*s and *Neobothriocidarid*s) and those with thin, imbricate plating (*Stromatocystites*, *Ectinechinus*, *Aulechinus*, *Eothuria*, *Aptilechinus*, *Gillocystis*). *Bromidechinus* has relatively thin plates, but the sutures between plates are not strongly imbricate and plates only overlap slightly. It is therefore closer in form to lepidocentrid echinoids than to bothriocidarids.

The construction of the echinozoan corona is very variable (Fig. 6) *Bromidechinus* is unusual in having a test composed of three series of plates: interambulacral plates, perforate ambulacral plates and an imperforate perradial series. The only other group to have these three series of plates fully developed are the ophiocistioids, e.g. *Gillocystis* and *Eucladia*.

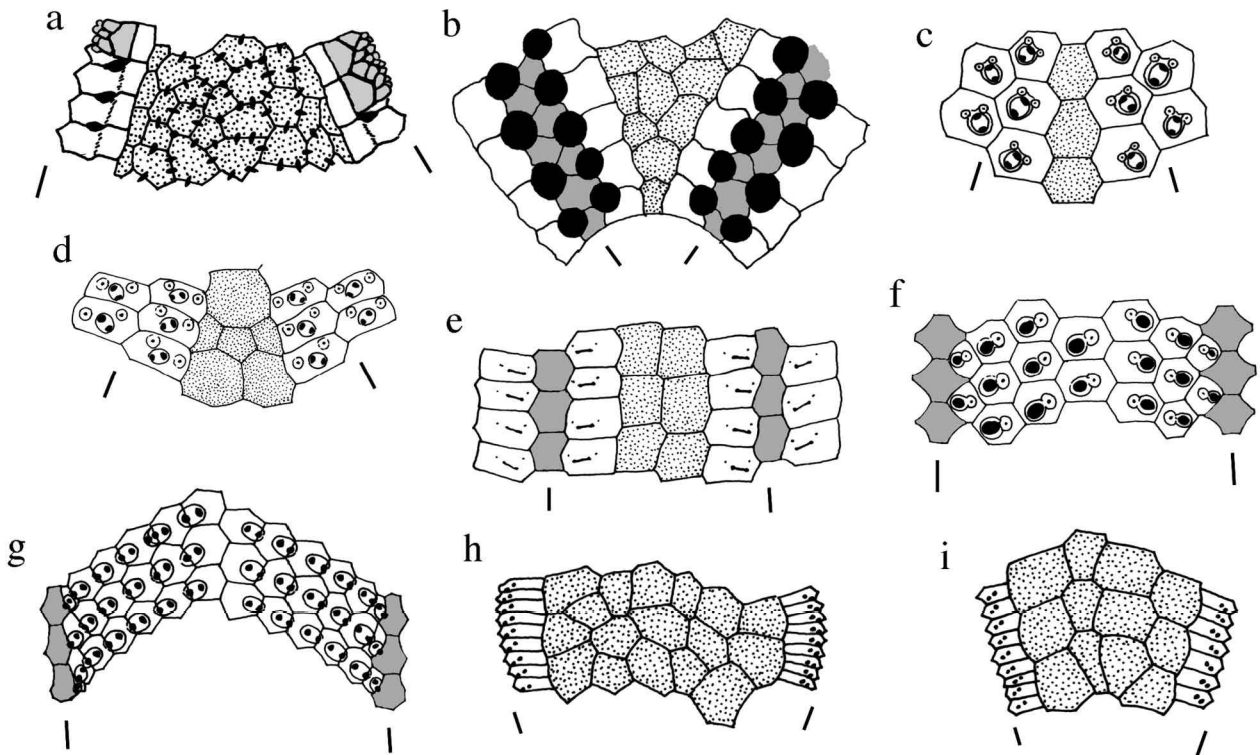
In ophiocistioids the perradial series is composed of T-shaped plates that are offset to left and right. *Neobothriocidarid*s has ambulacral series and a perradial series like *Bromidechinus* but plates of the interambulacral series are either completely missing (*N. peculiaris* Paul) or occur as small, disjunct diamond-shaped plates (*N. templetoni*, Kolata, *N. minor* Paul). In *Aptilechinus*, *Aulechinus*, *Ectinechinus* and *Eothuria* there are five narrow biserial ambulacra and five wider interambulacral zones but no perradial series of plates.

*Bothriocidarid*s has just fifteen columns of plates forming its test. There are five biserial columns of ambulacral plates and five uniserial columns of imperforate plates. The latter have been variously interpreted. Originally they were assumed to be homologous to interambulacral plates of other Echinozoa. However, Paul (1967) suggested that this uniserial column of imperforate plates might be perradial, by comparison with *Neobothriocidarid*s. Under Paul's model *Bothriocidarid*s completely lacks interambulacral plating. We prefer the standard interpretation, that there is a single column of interambulacral plates, for the following two reasons. Firstly, in *Bothriocidarid vulcani* Guensburg (1984), the imperforate column of plates starts off uniserial, but widens to include as many as three adjacent plates, suggesting homology with the interambulacral series of plates in *Bromidechinus*. Secondly, pore-pairs in *Bothriocidarid*s are inclined toward the ambulacral midline suture, forming a V-shaped arrangement with the Vs closing adorally. This arrangement is widely developed in echinoids and in every case the radial water vessel lies at the point of the V. This indicates that the radial water vessel in *Bothriocidarid*s ran down the midline of the ambulacral zones and not beneath the uniserial imperforate plate series.

Cambrian stromatocystitids have well-developed interambulacral and ambulacral columns but no perradial series of plates. However, they do have a biserial column of cover plates that attach to ambulacral plates and meet perradially, roofing over the radial water vessel. These may be homologues to the perradial series (see Discussion).

### 2.2. Apical system

Unfortunately, little is known about the apical disc structure of *Bromidechinus* other than it was very reduced in area and enclosed the periproct. In modern echinoids the apical disc is composed of five ocular plates at the summits of ambulacra, and five interradial genital plates. Ocular plates are pierced by the tip of the radial water vessel and one of the genital plates is perforated by the hydropore. The situation in Ordovician echinozoans is very different. There is a large plate at the summit of ambulacral columns in *Bothriocidarid*s, but this is not perforated by the tip of the radial water vessel. Furthermore, in one ray one of these plates has the opening to the hydropore. It is doubtful whether these plates are directly homologous to the ocular plates of modern echinoids. In *Aulechinus*, *Aptilechinus* and *Ectinechinus* there is a differentiated terminal plate at the summit of the ambulacra, but this again is not perforated. In these three taxa the madreporite opening is associated with an enlarged interradial plate at the



**Figure 6** Test construction in early Palaeozoic echinozoans: (a) *Stromatocystites*; (b) ophiocistioid (*Eucladia*); (c) *Bothriocidarid pahlani* Schmidt; (d) '*Bothriocidarid*' *vulcani* Guensburg; (e) *Bromidechinus*; (f) *Uniboethriocidarid*; (g) *Neoboethriocidarid*; (h) *Ectinechinus*; (i) *Aptilechinus*. In all diagrams the interradius is central and the perradial on either side are marked by dashes. Shading as follows: interambulacral series, stippled; ambulacral series, unshaded; perradial series and coverplate series, grey.

apex of one of the interambulacral zones. In *Eothuria* there does not appear to be a differentiated terminal plate nor an enlarged interradial madreporic plate, although a small opening is reported near the summit of one interambulacrum that is presumably the hydropore. In *Gillocystis* the tip of the radial water vessel does extend through the test and is associated with a small pyramid of plates (Jell 1983). However, it does not appear to be associated with a single enlarged terminal element. In *Gillocystis* the madreporic plate is situated in one of the interambulacra at the edge of the peristome. The hydropore in stromatocystitids has a similar interradial position close to the mouth.

The periproct in stromatocystitids consists of a pyramid of plates situated midlength in one of the interambulacral zones. It has a similar position in *Gillocystis*, but is apical, and composed of a mass of small plates in *Aulechinus*, *Eothuria*, *Ectinechinus*, *Bromidechinus* and *Bothriocidarid*. In all those taxa the oral (ambulacra-bearing) surface is greatly enlarged and the aboral surface reduced to the small periproctal region. By contrast the aboral surface in ophiocistioids and stromatocystitids is almost as large as the oral surface. *Totiglobus*, amongst stromatocystitids, has a markedly reduced aboral surface.

### 2.3. Ambulacra and the water vascular system

Ambulacral plates are perforated and in life would have supported the tube-feet. In stromatocystitids, *Bothriocidarid*, *Aulechinus*, *Ectinechinus* and *Aptilechinus* ambulacral plates meet perradially, but in *Gillocystis*, *Neoboethriocidarid*, *Uniboethriocidarid* and *Bromidechinus* the two columns of plates are separated by a single perradial series of plates. In most taxa there are just two columns of ambulacral plates in each

zone, but in *Neoboethriocidarid* and *Uniboethriocidarid* there are multiple columns (up to six abreast).

The shape of ambulacral plates offers a further differential character. In *Uniboethriocidarid*, *Neoboethriocidarid* and all species of *Bothriocidarid* except *B. vulcani*, ambulacral plates are pentagonal or hexagonal and as wide as tall. Those in *B. vulcani* are laterally more elongate and only weakly hexagonal. These are much more similar to ambulacral plates of *Bromidechinus* and *Aptilechinus*, which are rather flat and rectangular in outline. *Eothuria* and *Gillocystis* also have similar ambulacral plates, but in *Aulechinus* and *Ectinechinus* the plates appear even thinner and more imbricate, and are distinctly kinked.

Ambulacral pore morphology is particularly variable amongst these taxa. In *Bromidechinus*, *Eothuria*, *Uniboethriocidarid* and *Bothriocidarid*, pores are placed well within ambulacral plates clearly separated from the suture. In others the pore passes along the adoral suture and is marginal in position. *Aptilechinus* is rather unusual in this respect, in that its pores are sutural when seen from the interior, but open a little removed from the suture on the outer surface. Pores are double in *Bothriocidarid*, *Neoboethriocidarid*, *Aulechinus*, *Aptilechinus* and *Ectinechinus*, but single in *Gillocystis* and all ophiocistioids, all stromatocystitids and in *Bromidechinus* and *Uniboethriocidarid*. Pores are particularly large in ophiocistioids.

*Stromatocystites* is inferred to have had an external radial water vessel, lying on top of the ambulacral plates. In *Aulechinus*, *Aptilechinus* and *Ectinechinus* the radial vessel is enclosed within ambulacral plates, while in other taxa, the vessel is fully internal, lying beneath the ambulacral plates. Paul (1967) described the radial vessel of *Neoboethriocidarid* as enclosed, but casts of the specimen (not available to Paul) show clearly that the perradial plates have an internal groove

with shallower oblique lateral grooves on their inner surface. The water vessels of *Neobothriocidaris peculiaris* are thus internal rather than enclosed within plates. *Eothuria* and *Bromidechinus* have a broadly similar plate structure. The inner surface of the plate surrounding the ambulacral pore is elevated and projects towards the perradius. In both the water vessel remains open and fully internal. In *Gillocystis* the perradial plates are grooved internally, as are the adradial portions of ambulacral plates, creating a channel for the internal radial water vessel and its lateral branches.

#### 2.4. Interambulacra

Interambulacral zones are present in all taxa except for species of *Unibothriocidaris* and *Neobothriocidaris peculiaris*. Small, disjunct diamond-shaped plates, which we interpret as interambulacral plates, are found down the interradius of *N. templetoni* and *N. minor*.

All species of *Bothriocidaris*, with the exception of *B. vulcani*, have a single uniserial column of interambulacral plates in each zone. In *B. vulcani*, although single plates predominate adapically, there can be up to three plates abreast in interambulacral zones. In *Bromidechinus* interambulacra are almost exclusively biserial, but become uniserial adapically and possible adorally. In *Gillocystis* the most adoral portion of interambulacral zones has uniserial plating, but plating rapidly becomes multiserial, with around three or four plates abreast by the ambitus. Similarly the interambulacral zones in *Aulechinus*, *Ectinechinus*, *Aptilechinus* and *Eothuria* begin with a single interambulacral plate orally, but rapidly expand into an irregular series up to five abreast at the ambitus. *Aptilechinus* is similar but with only three interambulacral plates abreast at the ambitus.

#### 2.5. Peristome and lantern

The peristomial region and lantern are very poorly known in early echinozoans. *Bothriocidaris*, *Gillocystis*, *Aulechinus*, *Aptilechinus* and *Ectinechinus* are all known to possess a lantern, whereas a lantern is definitely absent from all stromatocystitids. In *Bothriocidaris* there are five pairs of internal, finger-like elements that converge adorally to form V-shaped hemipyramids. The adoral point of each hemipyramid is interradianal. These are clearly differentiated from the first ambulacral plates on which they rest. In *Aulechinus* there are similar paired elongate ossicles meeting interradianally forming the pyramids, but these are much more recognisably modified ambulacral plates. In *Ectinechinus*, *Aptilechinus* and *Gillocystis* the hemipyramids are more inflated and triangular in form and less clearly ambulacral in origin. The 'oral valves' of *Eothuria* are also V-shaped structures and are almost certainly also hemipyramids.

Teeth in *Bothriocidaris* are represented by small, poorly defined structures that may simply be spinelets, like the teeth of ophiuroids. In *Aulechinus* the teeth are broad plank-shaped structures with strong longitudinal grooves. They possibly represent a fused amalgam of spines. Similar structures are present in *Ectinechinus* and *Aulechinus*, but the ribbing on the teeth is less pronounced than in *Aulechinus*.

The lantern of ophiocistioids is highly developed with pyramids, V-shaped goniodonts and rotulae (see Haude & Langenstrassen 1976). Epiphyses are present in both *Aptilechinus* and ophiocistioids but have not been identified in any Ordovician echinozoan.

#### 2.6. Spines, tubercles, pedicellariae and tube feet

Spines are completely absent from stromatocystitids and ophiocistioids. In *Bromidechinus* and *Aptilechinus* there is a pair of stout spines on each ambulacral plate, positioned on either side of the ambulacral pore. In *Aulechinus* there are no primary spines present at those positions, but there may be

very small, almost rudimentary pegs. Primary spines are also absent from *Ectinechinus* and *Eothuria*. *Bothriocidaris* has stout spines very much like those of *Bromidechinus* and *Aptilechinus*. In most species there are just two spines, one on either side of the ambulacral pore-pair. In *B. kolatai* there is a cluster of spines around the upper margin of the pore-pair. *Neobothriocidaris* and *Unibothriocidaris* have a single spine immediately above each pore-pair.

In *Unibothriocidaris*, *Neobothriocidaris* and *Bothriocidaris*, spines attach onto obvious tubercles which are perforate and have a distinct mamelon. In all other taxa there are no differentiated tubercles and the spines simply attach directly onto the plate. Their point of attachment is generally marked by a small perforation or ligament pit.

Interambulacral spines are present only in a few species of *Bothriocidaris*. They have the same appearance as ambulacral spines and attach to similar well-developed tubercles.

Nestler (1968) described the valves of pedicellariae isolated from a glacially derived block of late Ordovician age together with plates and spines of a *Bothriocidaris*. Although these are clearly pedicellariae, some doubt must remain as to their identity, since they were isolated loose, and no articulated specimen of *Bothriocidaris* has ever been found with similar structures.

All plates of *Bromidechinus* are covered in fine peg-like structures. They are easily abraded and are either small granules embedded in the outer tegmen or (less likely) are direct outgrowths of the plate surface stereom. Identical granulation is present in *Aulechinus*, *Aptilechinus*, *Eothuria* and *Gillocystis*, but is absent from *Bothriocidaris*, *Neobothriocidaris* and *Unibothriocidaris*.

### 3. Cladistic analysis

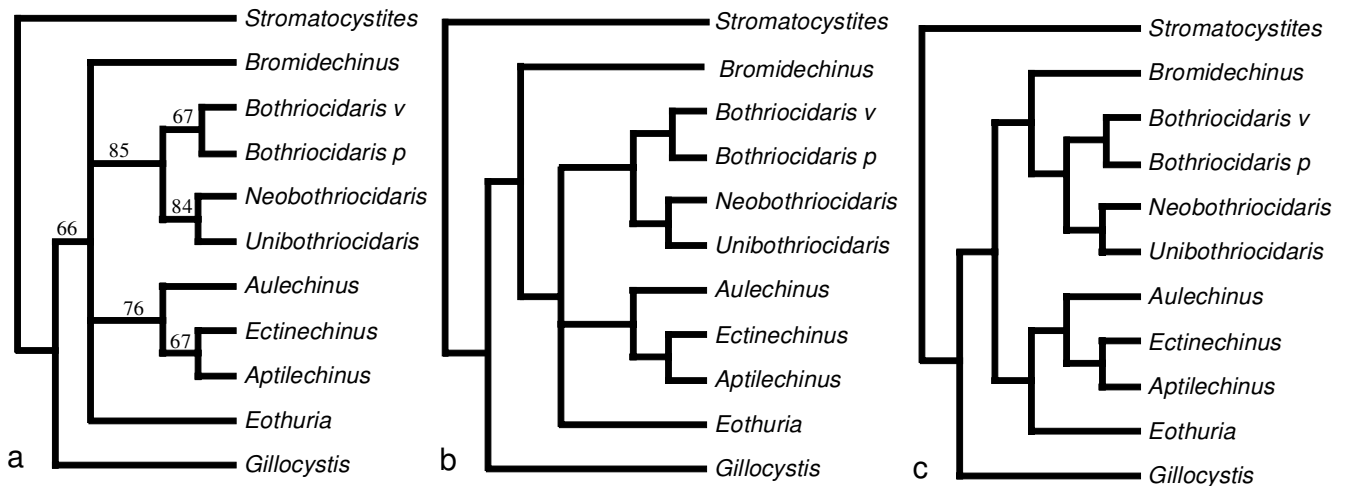
#### 3.1. Methods

To establish how *Bromidechinus* is related to other echinozoan taxa, we undertook a cladistic analysis using PAUP 4\* (Swofford 1999). We included seven Ordovician genera (*Bromidechinus*, *Bothriocidaris*, *Neobothriocidaris*, *Unibothriocidaris*, *Aulechinus*, *Ectinechinus* and *Eothuria*). Because *Bothriocidaris* encompasses species with significant differences in plating, we included *B. vulcani* as well as the type species, *B. pahlani*. We also included the Silurian echinoid *Aptilechinus caledonensis* (Kier 1973), and the ophiocistioid *Gillocystis* (Jell 1983) as early members of the Echinoidea and Ophiocistioida, respectively. As outgroup we included the Middle Cambrian stem-group eleutherozoan *Stromatocystites* (see Smith 1984).

These eleven taxa were scored for twenty-seven morphological characters, listed in Appendix 1. All characters were given equal weight and treated as unordered. Analyses were run using the Exhaustive Search option, which guarantees to find the most parsimonious solutions. One thousand bootstrap replicates were carried out to test the robustness of the resultant topology.

#### 3.2. Results

Four maximally parsimonious trees, length 44 steps, with a consistency index of 0.76 and a retention index of 0.75, were recovered. These place *Bromidechinus* in one of two positions, either as sister group to all other echinozoans other than *Gillocystis*, or as sister group to the bothriocidarids (Fig. 7). A strict consensus of the four trees identifies a very early split between ophiocistioids (*Gillocystis*) and the rest. Reweighting characters on the basis of their rescaled consistency index and rerunning the analysis resulted in just three trees, all with *Bromidechinus* as basal to both lepidocentrids and bothriocidarids (i.e. Fig. 6a).



**Figure 7** Phylogenetic hypotheses for the placement of *Bromidechinus* based on parsimony analysis of data presented in Appendix 1: (a) strict consensus of the four most equally parsimonious trees that were found; *Bromidechinus* falls in just one of two places; (b) strict consenses of the three most parsimonious trees that place *Bromidechinus* as sister taxon to all echinozoans other than *Gillocystis*; (c) the fourth most parsimonious tree, which places *Bromidechinus* as sister taxon to the bothriocidarids; bootstrap values are given for the strict consensus.

Bootstrap analysis shows that while some parts of the topology are reasonably well supported, other parts are rather weakly supported and much less robust. It is likely that the large number of unknown character states that are included in the matrix is contributing to the low bootstrap support values.

#### 4. Discussion

Our analysis identifies *Bromidechinus* as lying close to the split between echinoids and ophiocistioids. This has several implications for our interpretation of the early evolution of echinoids.

The most striking feature of *Bromidechinus* is its distinctive test, composed of three series of plates. The only other groups with a similar test construction are ophiocistioids and the bothriocidaroid *Neobothriocidarid*. Given that *Bromidechinus* and the ophiocistioids have a basal position in the cladogram, it is probable that this was the primitive condition for echinozoans.

In considering the origin of the perradial series of plates, one possibility is that they are derived from cover plates. In *Stromatocystites* there is a single primary cover plate to each ambulacral plate, and this is attached centrally, leaving an exposed adradial portion and a covered perradial portion of the ambulacral plate. Immediately inside the cover plate is the sutural pore for the ambulacral tube foot. Cover plates form an alternating biseries of plates meeting perradially above the radial water vessel. In ophiocistioids, the perradial plates form an alternating series meeting perradially and positioned above the radial water vessel, but the ambulacral pores are now on the external portion of the ambulacral plate and the internal portion is greatly reduced. In *Bromidechinus* the perradial plates have become strictly uniserial.

The enclosure of the radial water vessel within ambulacral plates in *Aptilechinus* and its relatives has generally been viewed as an intermediate stage between having a fully external water vessel and a fully internal water vessel. However, this does not agree with the character changes suggested by the cladogram. The earliest Echinozoa (exemplified by *Bromidechinus*, *Eothuria* and ophiocistioids) had a fully internal radial

water vessel. So too did the bothriocidarid *Neobothriocidarid*. The enclosed water vessel in *Aptilechinus* therefore represents a secondary modification. It may be that the internal projections to ambulacral plates which created a channel for the water vessel in *Eothuria* and *Bromidechinus* came to underlie the water vessel with the loss of the perradial series of plates.

Another interesting outcome is that bothriocidarids cannot be considered as stem-group holothurians, as previously proposed (Smith 1984). Bothriocidarids appear as sister-group to the main-line echinoid clade and thus post-date the split with ophiocistioids. Smith suggested affiliation between bothriocidarids and ophiocistioids on the basis that they shared a perradial series of imperforate plates. This is now shown to be primitive for echinozoans as a whole. Characters that place ophiocistioids as basal include the position of the periproct, which opens laterally within an interambulacral zone, and the oral position of the madreporic plate.

Furthermore, the lantern in bothriocidarids must be derived rather than primitive. Both *Aptilechinus* and *Gillocystis* have comparable lantern structure, with paired hemipyramids, rotulae and epiphyses. It seems highly unlikely that such a complex structure would evolve independently, and again implies that the basic elements were present in the latest common ancestor of these two taxa.

Our knowledge of primitive early echinozoans comes almost entirely from just two horizons in the late Ordovician, the Rawtheyan and the Harnagian. By the early Caradoc there was already a considerable diversification on body form of echinoids, and it is obvious that the origins of the group must lie deeper. There remains much hidden history of the group to be discovered in the Early and Middle Ordovician.

#### 5. Appendix

Characters scored for Ordovician Echinozoa, and data matrix used in analysis. All characters are treated as unordered so that numerical values assigned to character states are arbitrary.

1. Test plating: basically imbricate = 0; ambulacral and interambulacral plates uniformly block-like and tessellate = 1.

2. Aboral plate system: extensive and almost as well developed as oral plate system = 0; highly reduced to small apical zone of circumperiproctal plates = 1.
3. Enlarged plates at adapical end of ambulacra forming contiguous circlet of apical disc plates: no = 0; yes = 1.
4. Hydropore opening: a simple sutural pore = 0; a multi-perforate madreporic plate = 1.
5. Position of hydropore opening: oral, immediately adjacent to the peristome = 0; apical, associated with the aboral plating system = 1.
6. Position of hydropore opening: radial = 0; interradial = 1.
7. Ambulacral zones with a central perradial series of plates: absent = 0; present, as a series of plates incorporated into the thecal wall = 1; present, as a series of cover plates = 2.
8. Ambulacral plates (i.e. tube-foot bearing plates): arranged as a single column on each side of the perradius = 0; arranged into multiple columns on each side of the perradius = 1.
9. Ambulacral plate shape: basically rectangular = 0; hexagonal, approximately as wide as tall = 1; narrow and geniculate = 2.
10. Ambulacral zone with a distinct perradial channel externally: no = 0; yes = 1.
11. Ambulacral pores: single = 0; paired = 1; multiple, forming sieve plate = 2.
12. Ambulacral pores: passing partially or completely along the suture between adjacent plates = 0; entirely within a single plate = 1.
13. Ambulacral pores surrounded by a distinct periporal rim: no = 0; yes = 1.
14. Radial water vessel: external to ambulacral plates = 0; internal to ambulacral plates = 1; enclosed within ambulacral plates = 2.
15. Internal surface of ambulacral plates: flat = 0; raised to form a distinct channel perradially = 1; differentiated into a haft and blade = 2.
16. Interambulacral plating: absent = 0; present = 1.
17. Interambulacral plating: uniserial throughout = 0; uniserial plating adapically and adorally but biserial or triserial at ambitus = 1; wide irregular band of plates but uniserial close to peristome = 2.
18. Position of periproct: opening within interambulacral zone in oral plating system = 0; opening apically within aboral plating system = 1.
19. Primary spines: absent = 0; present = 1.
20. Spine attachment: attached directly to plate via a ligament pit = 0; attached and articulating onto a proper tubercle with mamelon = 1.
21. Primary spine arrangement on ambulacral plates: a single spine positioned immediately adapical of the ambulacral pore = 0; a cluster of ambulacral spines on the aboral margin of the ambulacral pore = 1; two spines, one on either side of the ambulacral pore = 2.
22. Spines: present on interambulacral plates: no = 0; yes = 1.
23. Plates smooth = 0; covered in peg-like granules = 1; with finer secondary tubercles and spines = 2.
24. Proximal ambulacral plates differentiated as hemipyramids that are sutured interradially: no = 0; yes = 1.
25. Hemipyramids: rod-like = 0; wide and shield-shaped = 1.
26. Teeth: undifferentiated = 0; broad plate of bound spines = 1; echinoid tooth = 2; goniodont = 3.
27. Perradial plates bounding ambulacral pore: no = 0; yes = 1.

Data matrix:

<i>Stromatocystites</i>	00000	12001	00000	1200?	?000?	??
<i>Bromidechinus</i>	010?1	?1000	01011	11110	001??	?0
<i>Bothriocidarid vulcani</i>	11111	00020	11010	11111	012??	??
<i>Bothriocidarid pahlani</i>	11111	00020	11010	10111	00210	1?
<i>Neobothriocidarid</i>	11???	?1120	10110	10?11	101??	?1
<i>Unibothriocidarid</i>	11???	?1120	01110	0?211	1?1??	?0
<i>Aulechinus</i>	01011	10011	?0022	1210?	?0111	??
<i>Ectinechinus</i>	01011	10010	10022	1210?	?0011	??
<i>Apitolechinus</i>	01011	10010	10022	12110	00011	2?
<i>Eothuria</i>	010?1	10010	21011	1210?	?0111	??
<i>Gilocystis</i>	00010	11000	00011	1200?	?0111	31

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