

Morphological and systematic reinterpretation of two enigmatic edrioasteroids (Echinodermata) from Canada

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Abstract: Reinterpretation of two enigmatic Canadian edrioasteroids, *Thresherodiscus ramosus* Foerste, 1914 from the Upper Ordovician Verulam Formation of Ontario and *Lispidecodus plinthotus* Kesling, 1967 from the Lower Mississippian Banff Formation of Alberta, shows that previous accounts of these taxa were largely erroneous. Unlike other isorophid edrioasteroids, *Thresherodiscus* has branching ambulacra, an unusual hydro-gonopore, differentiated interambulacral plates bearing respiratory structures, and ambulacra that extend onto the peripheral rim. Except for the turreted thecal shape, *Lispidecodus* is a rather typical discocystinid edrioasteroid. Phylogenetic analysis weakly supports the placement of *Thresherodiscus* within Agelacrinitidae and strongly places *Lispidecodus* within Discocystinae.

Résumé : Une réinterprétation de deux édrioastéroïdes canadiens, *Thresherodiscus ramosus* Foerste, 1914, de la Formation de Verulam de l'Ordovicien supérieur de l'Ontario, et *Lispidecodus plinthotus* Kesling, 1967, de la Formation de Banff du Mississippien inférieur de l'Alberta, démontre que les travaux antérieurs sur ces taxons étaient en bonne partie erronés. À l'encontre d'autres édrioastéroïdes isorophidés, *Thresherodiscus* présente des ambulacres ramifiés, un hydrogonopore inhabituel, des plaques interambulacraires différenciées portant des structures respiratoires, ainsi que des ambulacres qui se prolongent jusque sur le rebord périphérique. À l'exception de la forme en tourelle de sa thèque, *Lispidecodus* est un édrioastéroïde discocystinidé assez typique. Les résultats d'une analyse phylogénétique appuient faiblement l'affectation de *Thresherodiscus* aux Agelacrinitidés et fortement celle de *Lispidecodus* aux Discocystinés.

[Traduit par la Rédaction]

Introduction

Edrioasteroidea is a cosmopolitan echinoderm clade confined to the Paleozoic (Early Cambrian – Late Permian). Post-Cambrian taxa are divided into two main clades. Edrioasterida (Middle Cambrian through Middle Ordovician) is characterized by extremely wide ambulacra with externally exposed, biserial flooring plates, thick tessellate interambulacral plates, and a large globular theca. Isorophida (Middle Cambrian through Late Permian) is characterized, in post-Cambrian taxa, by a discoidal theca bordered by a well-developed peripheral rim, imbricate interambulacral plates, and extremely narrow ambulacra with hidden uniserial floor plates (Bell 1976b).

Among isorophids, two Canadian taxa, *Thresherodiscus ramosus* Foerste, 1914 from the Upper Ordovician (Caradocian) Verulam Formation of Ontario and *Lispidecodus plinthotus* Kesling, 1967 from the Lower Mississippian (Tournaisian) Banff Formation of Alberta, are morphologically puzzling. Previous descriptions of *T. ramosus* concentrated on the unusual branching nature of the ambulacral system but other-

wise confirmed that it possesses typical Ordovician isorophid morphology. Conversely, *L. plinthotus* was originally considered morphologically unique and placed in a family distantly related to all other edrioasteroids.

Here, we reinterpret the morphology of these two taxa using newly collected specimens of *Thresherodiscus* and the unique holotype of *Lispidecodus*. These taxa were placed in a phylogenetic context using a parsimony analysis of the reinterpreted morphology and data collected from closely related edrioasteroid taxa.

Previous investigations

Thresherodiscus ramosus was first described by Foerste (1914) as an unusual edrioasteroid with branching ambulacra. Until recently, this feature was almost unknown in other edrioasteroids, but it does occur in several other echinoderm groups including the glyptocystitoid rhombiferan *Strobillocystites*, the hemicosmitid rhombiferan *Caryocrinites*, and most notably in asterozoans and crinoids. Foerste commented on the triradial nature of the ambulacral system and correctly

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Fig. 1. Photographs of *Thresherodiscus ramosus* Foerste, 1914. **(1.1, 1.6, 1.11–1.14)** UMMP 73816. (1.1) Immersed view of the oral surface, $\times 2$. Note the dark covered diplopore-like structures along the ambulacral system. (1.6) Oral surface, whitened, $\times 2$. Note the elevated bulbous nature of the diplopore-like structures along the ambulacra. (1.11) Detail of the oral area showing the separate openings for the hydropore and gonopore and the diplopore-like structures, immersed, $\times 6$. (1.12) Detail of the left branch tips of the A ambulacrum, whitened, $\times 20$. Note the ambulacra extend epithecally onto the peripheral rim. (1.13) Detail of the right side of the C ambulacrum showing food groove, ambulacral cover plates, and bulbous diplopore-like structures on the adradial interambulacral plate series, whitened, $\times 8$. (1.14) Detail of the CD interambulacral area showing the periproct (p), the presumed hydropore (h), and presumed gonopore (g), whitened, $\times 4$. **(1.2, 1.4)** UMMP 73713, showing less well-developed ambulacral branching and proportionally wider peripheral rim, whitened and immersed, $\times 2$. **(1.3, 1.8–1.10)** UMMP 73714, interior view showing details of the ambulacral floor plates and oral frame. (1.3, 1.8) Entire specimen whitened and immersed, $\times 1.5$. (1.9) Detail of the floor plates and adjacent interambulacral plating showing internal expression of the diplopore-like structures, immersed, $\times 6$. (1.10) Detail of the oral frame showing the oval peristome and probable gonopore in the proximal CD interambulacral area along the midline, immersed, $\times 4$. **(1.5, 1.7)** UMMP 73819, showing nearly full development of the distal ambulacral branching and ambulacral tips beginning to encroach upon the peripheral rim, whitened and immersed, $\times 2$.

interpreted the ambulacral symmetry as what Sprinkle (1973) called the primitive 2–1–2 arrangement common to most early echinoderms. This symmetry is inherently triradial, with three main ambulacra, shared BC on the right, shared DE on the left, and the unitary A ambulacrum anteriorly extending from the centrally located peristome (Fig. 5). Five ambulacra developed as the distal shared ambulacrum bifurcates during ontogeny, whereas the A ambulacrum does not. Foerste (1914) also correctly noted that, unlike other Ordovician isorophids, *T. ramosus* lacks intrathecal extensions on the abradial ends of the cover plates, a feature common to more derived agelacrinitids (Bell 1976b), and the branching of the A ambulacrum.

More perplexing was the unusual but accurate description of interambulacral fields as being plated by central regions of large imbricating plates, separated from the ambulacra by “a continuous series of much smaller bordering plates arranged with their long axes more or less perpendicular to the adjoining branches of the ambulacral arms” (Foerste 1914, p. 437). The respiratory nature of these pore-bearing bordering plates was not recognized, however.

Bassler (1935, 1936) and Regnéll (1966) reiterated Foerste's (1914) comments on ambulacral branching and the strongly triradial nature of the theca without adding any new information. Kesling (1960) clarified two important points concerning *Thresherodiscus*. First, the irregular plating of the anal pyramid was discussed. Second, a thecal opening in the proximal right CD interambulacrum was tentatively identified as the hydropore. Although present on all three of the new specimens that expose the external surface, this hydropore opening is unusual. In most edrioasteroids, the hydropore and gonopore are united into a single exterior vent called the hydro-gonopore, which is positioned on the border of the oral frame to the posterior right of the oral frame (Sumrall 1993). In *Thresherodiscus*, there are two apparent openings (unrecognized by Kesling 1960): one is surrounded by two hydropore oral plates in the posterior side of the oral frame along the midline, and the other (hydropore opening of Kesling 1960) lies more distally along the C ambulacrum and is formed from four hydropore oral plates (Figs. 1.11, 1.14).

Lispidecodus plinthotus was originally described by Kesling (1967) as so dissimilar to other known edrioasteroids to warrant the erection of a new family (Lispidecodidae) to receive it. This family was characterized by the unusual thecal shape, peristome and ambulacral positioning, and shape and

positioning of the hydropore and periproct, but no diagnosis was presented. The species was further characterized by two unusual features of the ambulacral system. First, the ambulacra, unlike those of other edrioasteroids, were described as being distinctly offset from the peristomal region rather than proximally grading into the peristome. Second, the ambulacral cover plate pattern was described as an alternation of large tong-shaped plates and U-shaped plates in an interlocking pattern. A reexamination of the type specimen shows both of these interpretations to be in error. The proximal ambulacral cover plates are taphonomically pressed into the proximal food groove, and the unusual cover plates are a misinterpretation of a typical six-plate pattern common to advanced agelacrinitids and discocystinids (Fig. 2) (Ehlers and Kesling 1958; Kesling and Ehlers 1958; Bell 1976b; Sumrall 1993, 1996). In a phylogenetic analysis of edrioasteroids, Smith and Arbizu (1987) and Sumrall (1993) placed *Lispidecodus* within Agelacrinitidae. Sumrall (1996) concurred and included *Lispidecodus* within Discocystinae without further comment.

Specimens, localities, and stratigraphy

The present information on *Thresherodiscus ramosus* Foerste, 1914 is based on four new specimens from the Upper Ordovician Verulam Formation of Ontario, Canada, that are deposited in the University of Michigan Museum of Paleontology (UMMP, Ann Arbor, Michigan). UMMP 73714 (Figs. 1.3, 1.8–1.10) is a very large individual (thecal diameter 42 mm) exposing the interior of the oral surface. This specimen provides information concerning the oral frame, plating of the ambulacral floor plates, and evidence for the respiratory nature of the differentiated adradial interambulacral plate series. UMMP 73816 (Figs. 1.1, 1.6, 1.11–1.14) is a large individual (thecal diameter 34 mm) preserving most of the oral surface, except for the distal BC interambulacrum and adjacent peripheral rim. The anal pyramid is weathered through, but otherwise the preservation is excellent. Specimen UMMP 73819 (Figs. 1.5, 1.7) is an intermediate-sized specimen (thecal diameter 25 mm) with good preservation of the nearly complete oral surface. The specimen is missing the peripheral rim along the AB interambulacrum and is slightly disrupted and deeply weathered along the E ambulacrum. Specimen UMMP 73713 (Figs. 1.2, 1.4) is a small specimen (thecal diameter 15 mm) with a largely weathered and overgrown surface. This specimen provides information

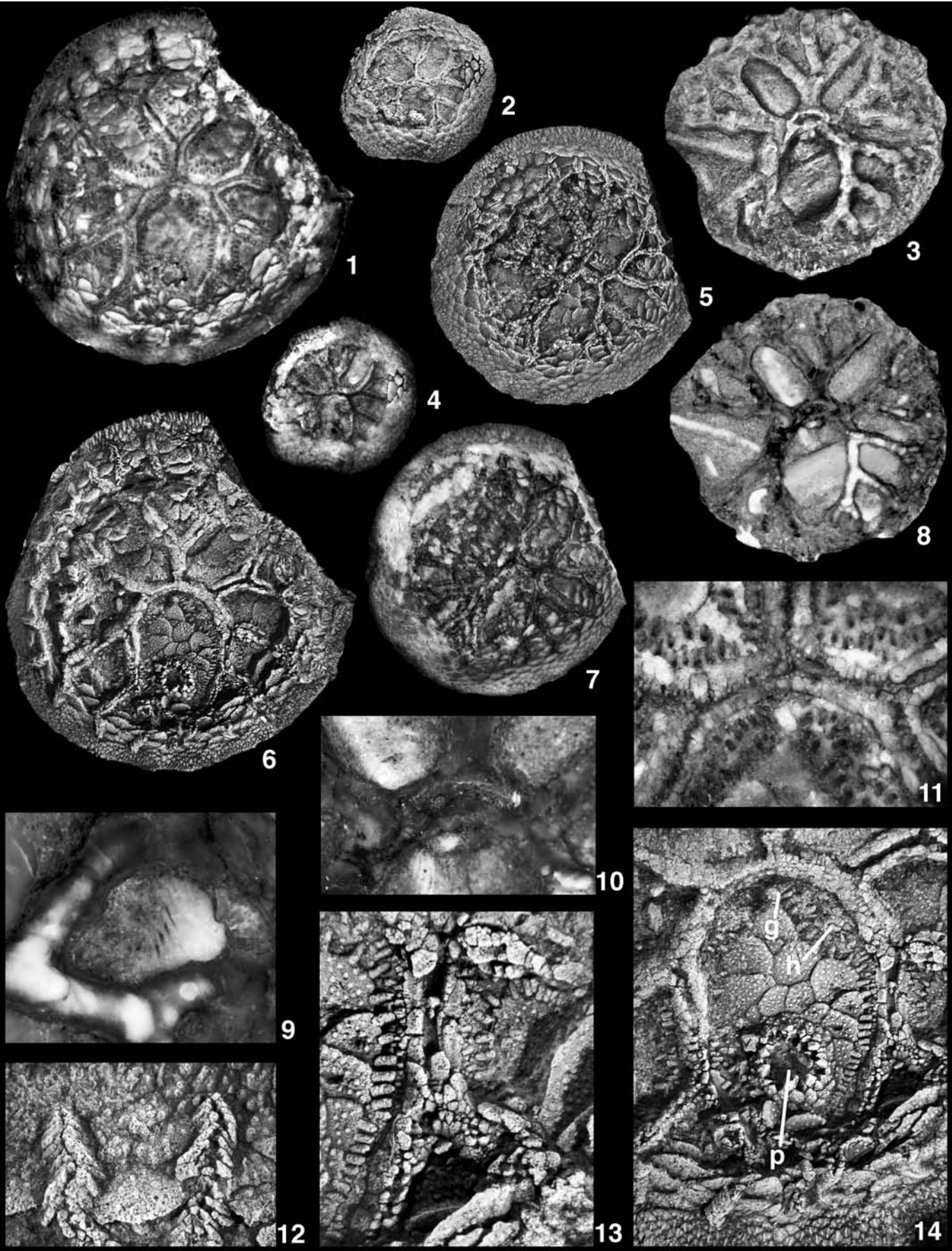
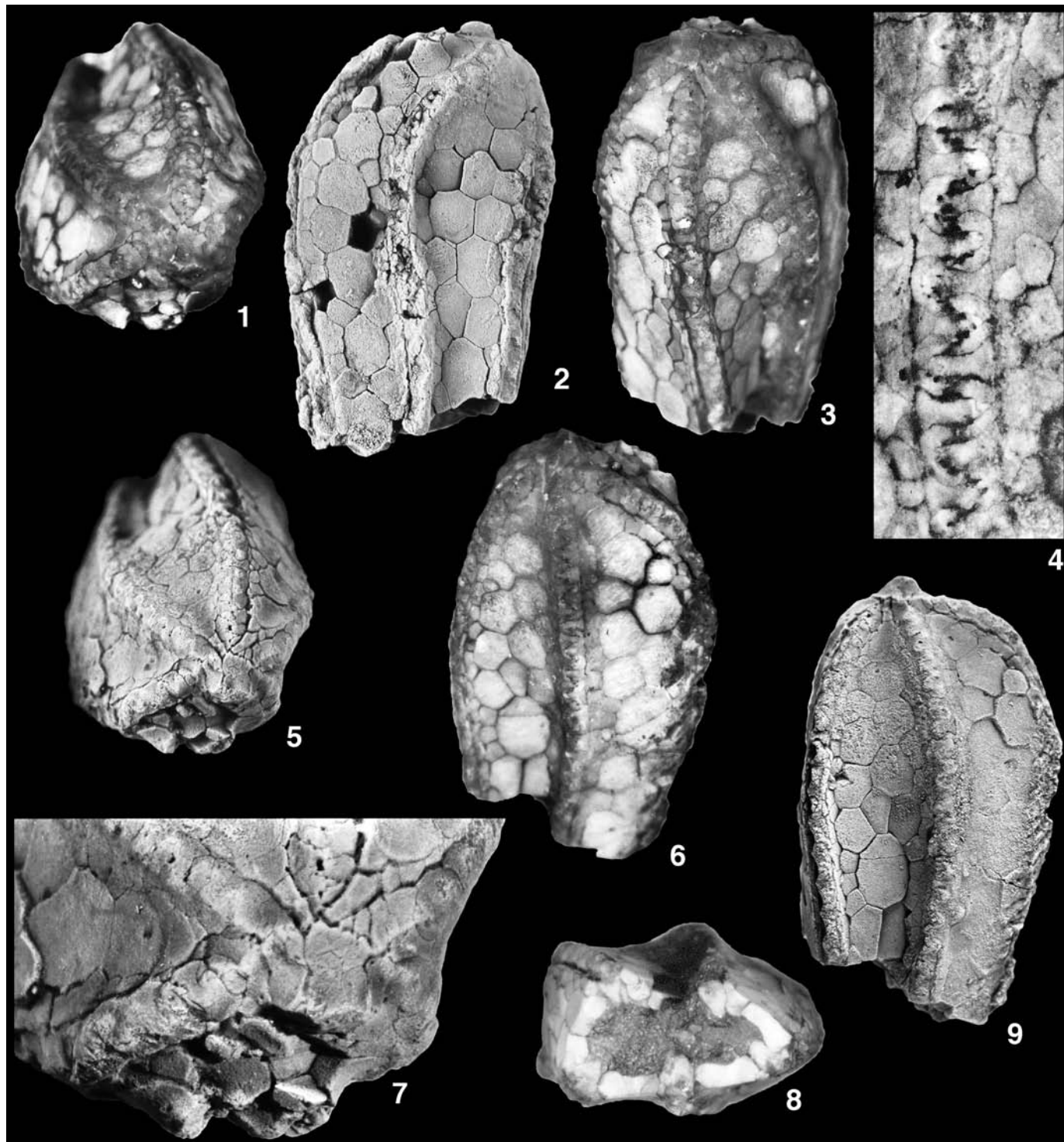


Fig. 2. Photographs of *Lispidecodus plinthotus* Kesling, 1967, USNM 154961. **(2.1, 2.5)** Oral view of holotype immersed and whitened, $\times 4$. Note the tessellate plating of the interambulacra and the high narrow ambulacra. **(2.2)** Lateral view centered on C ambulacrum, whitened, $\times 4$. Note the raised position of the hydropore and periproct at top. **(2.3)** Lateral view centered on the A ambulacrum, immersed, $\times 4$. **(2.4)** Cover plates of the E ambulacrum, immersed, $\times 15$. Note the six-plate pattern. Peristome is towards the top. **(2.6, 2.9)** E ambulacral view immersed and whitened, $\times 4$. **(2.7)** Enlargement of summit, whitened, $\times 8$. Note the integration of the ambulacra into the oral area and the relatively short shared ambulacra. **(2.8)** View of broken distal end of theca, immersed, $\times 4$. Note the deep ambulacral floor plates and the thick interambulacral plates.



about the respiratory pores and some ontogenetic information concerning the development of ambulacral branching.

The new *Thresherodiscus* specimens presented and described herein were collected from the Dufferin Aggregates Carden Quarry, Victoria County, Ontario, Canada. The Carden Quarry contains a complete section of the Upper Ordovician (Caradocian) Bobcaygeon Formation, and the upper 3–5 m of the quarry is capped by the overlying lower member of the Verulam Formation. These strata, which are exposed in many quarries and natural exposures in the vicinity of Lake Simcoe, Canada, are renowned for the preservation of an exceptionally diverse, well-preserved fauna of fossil echinoderms (Billings 1854; Springer 1911; Brett and Taylor 1999), including asteroids, carpoids, crinoids, cyclocystoids, edriasteroids, edrioblastoids, ophiurioids, parablasteroids, paracrinooids, rhombiferans, and possibly echinoids (Brett and Rudkin 1997).

The Bobcaygeon Formation is dominated by thin- to medium-bedded limestones ranging in lithology from mudstone to grainstone, frequently with interbedded shales, and was deposited in lagoonal, shoaling, and shallow-shelf environments (Brookfield and Brett 1988). The overlying Verulam Formation is typically thinner bedded, contains a larger percentage of interbedded shale, and is interpreted as being deposited in a distal-shelf environment. The Bobcaygeon and Verulam formations were likely deposited in a subtropical environment 15°–20° south of the Upper Ordovician paleoequator (Brett and Taylor 1999), although Brookfield (1988) has suggested that these strata were deposited in a more temperate climate.

The Bobcaygeon and Verulam formations contain abundant, often stacked hardgrounds, each characterized by a unique morphology and biota. The Bobcaygeon Formation is most famous for the “Kopf hardground,” a stratigraphically persistent surface that is characterized by hummocky and undercut topography, and contains abundant *Trypanites* borings (Brett and Liddell 1978). The Kopf hardground typically supports a fauna dominated by the large edriasterid edriasteroid *Edriaster bigsbyi* (Billings 1854), the paracrinooid *Amygdalocystites*, and the crinoids *Cremacrinus* and *Hybocystites* (Brett and Liddell 1978). Crinoid holdfasts are also common on this hardground, especially those of *Cleiocrinus*. Hardgrounds of the lower Verulam Formation are characterized by low-topography, smooth, rolling surfaces that are not heavily bored (Brett and Brookfield 1984). The biota preserved on the Verulam hardgrounds is typically much smaller than those of the Bobcaygeon Formation and is dominated by the isorophid edriasteroid *Isorophusella*. Literally thousands of *Isorophusella* specimens have been recovered from the Verulam hardgrounds in densities as high as 250/m² (Waddington 1980). Hardgrounds of the Verulam Formation also yield other isorophid edriasteroids, including species of *Foerstediscus*, *Cystaster*, and the *Thresherodiscus* specimens described herein.

The holotype and only known specimen of *L. plinthotus* (Fig. 2) is a small turreted theca (height 17.4 mm, maximum diameter 10.0 mm) free of matrix. It preserves the oral area, interambulacra, and proximal ambulacra, but the distal theca and attachment surface are broken off and not preserved. The periproctal opening in the proximal CD interambulacrum is somewhat crushed, and the plates of the anal pyramid are missing.

The specimen was collected as float near Maligne Lake, Jasper National Park, ~50 km southeast of Jasper, Alberta, Canada. Although the stratigraphic provenance of *L. plinthotus* is uncertain, Kesling (1967, p. 197) suggested the following: “From the location of the discovery site and the nature of preservation, it is reasonably certain that the specimen came from the Mississippian Banff Limestone.” The Lower Mississippian (Tournaisian) Banff Formation varies in thickness from at least 160 to 600 m, the thickest surface exposures being located in Sunwapta Pass (Chatellier 1988). It is underlain by the Late Devonian Exshaw Formation and overlain by the Mississippian (Tournaisian–Visean) Rundle Group (Spreng 1953; Chatellier 1988).

Sparsely fossiliferous, dark-colored shales and mixed carbonates and fine-grained siliciclastics dominate the Banff Formation in the vicinity of Jasper. Crinoid–bryozoan packstones and grainstones, however, containing abundant black chert make up a large part of the middle and upper parts of the formation. Although several smaller scale sedimentary sequences are recognized within the Banff Formation, it is generally interpreted as a shallowing-upward succession with most deposition occurring well below wave base on a structurally controlled carbonate ramp situated ~10° north of the Early Mississippian paleoequator (Laudon et al. 1952; Spreng 1953; Chatellier 1988; Webster 1989).

Rapidly deposited crinoid–bryozoan wackestones and packstones preserve numerous articulated echinoderms in the Banff Formation. The echinoderm fauna is especially renowned for its exceptionally preserved crinoids: several thousand specimens representing over 50 species have been described (Laudon et al. 1952). Articulated blastoids and echinoids are also found commonly, in addition to exceedingly rare ophiurioids, stelleroids, and edriasteroids. Only two edriasteroid specimens have been reported from the Banff Formation, *L. plinthotus*, described here, and *Postubulla? jasperensis* (Harker 1953), described from a single juvenile. Other common macrofossils from the Banff Formation include diverse Mississippian marine invertebrates such as brachiopods, ramose and fenestrate bryozoans, platyceratid gastropods, and solitary corals (Spreng 1953).

Phylogenetic position

To determine the phylogenetic position of *Thresherodiscus* and *Lispidecodus*, a phylogenetic analysis was performed on 13 representative isorophinid taxa with 24 characters, most of which were binary (Appendix A; Appendix B, Table B1), and derived primarily from Sumrall (1993). Alternate character states were weighted equally and unordered. The character matrix was assigned character polarity using the outgroup criterion. *Carneyella pilea* (Hall 1866) and *Foerstediscus grandis* (Bassler 1935) were used as outgroup taxa because they are well-known members of Carneyellidae, the sister taxon of Isorophida (interpreted from Bell 1976b). The matrix was analyzed with PAUP* (Swofford 2002) using the branch and bound search algorithm to assure recovery of all equally most parsimonious trees and bootstrapped 1000 times to assess tree robustness.

This analysis recovered 27 trees of 35 steps: consistency index CI = 0.77, retention index RI = 0.88, and rescaled consistency index RC = 0.68. The results were largely con-

gruent with trees recovered by Sumrall (1993). The placement of *Neoisorophusella* as derived from the Agelacrinitidae rather than as a sister taxon to *Isorophusella* results largely from reanalysis and recoding, however (Fig. 3). Furthermore, in this analysis, the monophyly or paraphyly of Isorophinidae is equivocal.

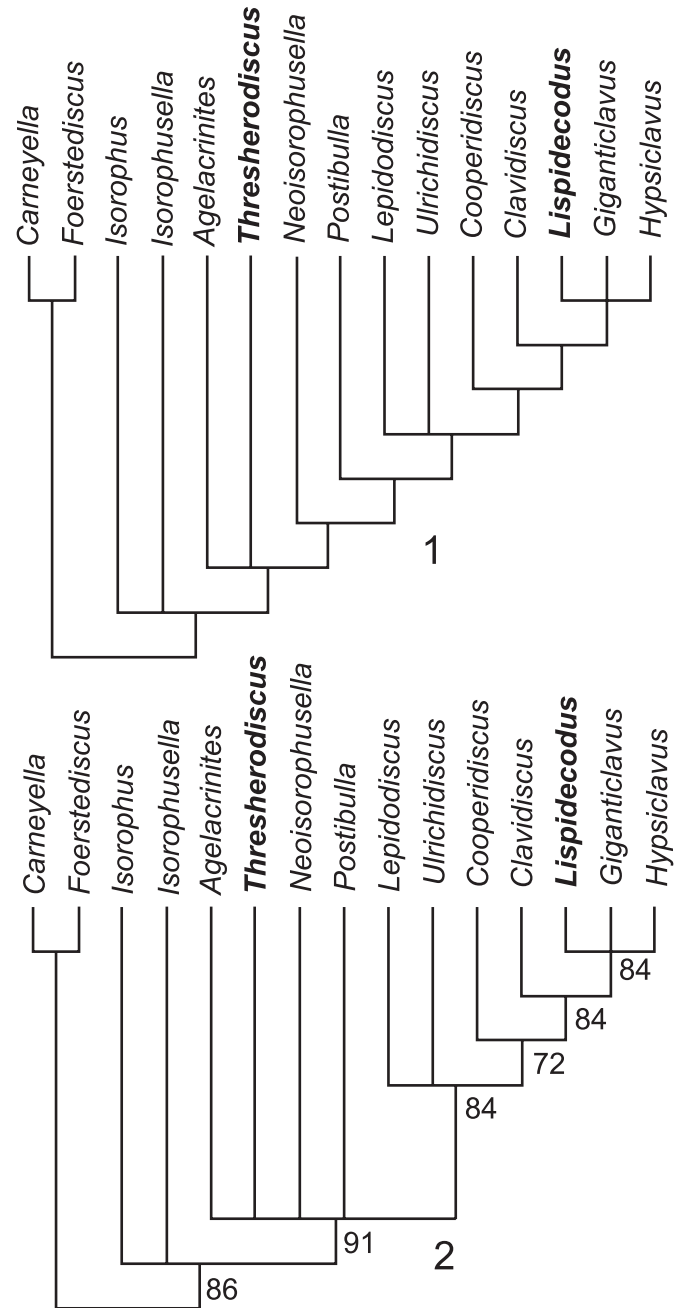
The placement of *Thresherodiscus* within Agelacrinitidae (Fig. 3) is based on the lack of a single posterior oral (character 1), the lack of intrathecal extensions of the cover plates (character 4), and the presence of numerous sets of shared oral cover plates (character 6). Two aspects of this placement are puzzling, however. First, *Thresherodiscus* is much older than any other known agelacrinitid; the oldest known is *Pyrgopostibulla belli* from the earliest Devonian of New York State (Cornell et al. 2003; Sumrall et al. 2006). Second, the anal pyramid is very similar to those in all non-isorophinid edrioasteroids, having a series of lathe-shaped plates that decrease in size centrally rather than the advanced inner and outer circlet of plates seen in more derived isorophinids (Bell 1976b; Sumrall and Parsley 2003). Furthermore, it is conceivable that the loss of the intrathecal extensions of the ambulacral cover plates is functionally linked to the respiratory structures of the ambulacral bordering plates unique to *Thresherodiscus*. Bearing intrathecal cover plate extensions requires no direct articulation between the adradial interambulacra and the ambulacral floor plates. The ambulacral bordering plates are tightly sutured to the flooring plates, however, precluding intrathecal cover plate extensions. Indeed, the placement of the primary cover plates on the floor plates without a hinge notch is very different in construction details as compared to the typical agelacrinitid condition (Sumrall and Parsley 2003).

Three autapomorphic features of *Thresherodiscus* were not included in the analysis because they are uninformative and, therefore, cannot influence the results of the analysis: the presence of distal branching of the ambulacral system, separate openings for the hydropore and gonopore, and the presence of covered diplopore-like respiratory structures along the edges of the ambulacral system. These respiratory structures are reminiscent of what Guensburg and Sprinkle (1994) described for the pyrogocystids as "hood plates." The respiratory plates in *Thresherodiscus* differ from these hood plates in the presence of a hollow stereom bulb with two passages to the coelom and the non-correspondence between the cover plate position and the hood plates.

We tentatively assign *Thresherodiscus* to Agelacrinitidae. Although there are some problems with this, including the presence of primitive features of the periproct and the large stratigraphic gap with other agelacrinitids, this is the most reasonable placement with our present knowledge. The other possibility is *Thresherodiscus* possesses several highly apomorphic characters but is a more primitive isorophid. Although this is perhaps more consistent with the stratigraphic discrepancy and the plating of the periproct, it is inconsistent with the three relatively advanced characters that place it within Agelacrinitidae. Pending discovery of additional taxa along this lineage to help clarify the relationships, we tentatively assign *Thresherodiscus* to Agelacrinitidae.

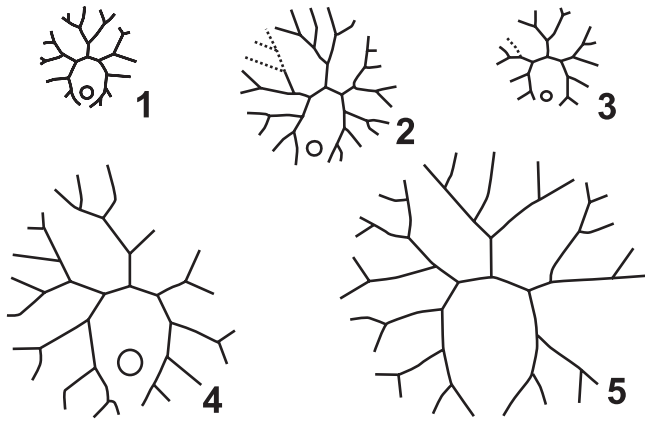
The placement of *Lispidecodus* is much clearer (Fig. 3). This taxon is nested within Discocystinae based on the high ambulacral floor plates (character 9), adjacent interambulacral

Fig. 3. Phylogenetic placement of *Thresherodiscus ramosus* Foerste, 1914 and *Lispidecodus plinthotus* Kesling, 1967. (1) A strict consensus tree summarizing the common relationships found in the 27 equally most parsimonious trees. (2) The results of a bootstrap analysis. Numbers at nodes represent bootstrap proportions. Nodes lacking numbers have bootstrap proportions < 50%.



plates (character 11), lateral extensions of the adradial interambulacral plates (character 12), presence of the left hydropore oral (character 15), thick interambulacral plates (character 16), and the foreshortened posterior-right interambulacral plates (character 21). One character reversal is notable, hydro-gonopore girdle absent (character 22). The unusually narrow oral area and turreted thecal shape are autapomorphic for *Lispidecodus* and belie the multitude of characters that support its well-nested placement within Discocystinae.

Fig. 4. Line drawings of the ambulacral system of the five known specimens of *Thresherodiscus ramosus* Foerste, 1914. All drawings $\times 1$. Note the similarity in branching pattern between the specimens. (1) Holotype, CGS 8446. (2) UMMP 73819. (3) UMMP 73713. (4) UMMP 73816. (5) UMMP 73714. Note that the image for (5) has been inverted left to right because the specimen exposes the interior surface.



Adaptations and implications

In *Thresherodiscus*, the distal ambulacral branching becomes more complex ontogenetically, and the ambulacral tips over-run the peripheral rim only in larger specimens. More complex branching of the *Thresherodiscus* ambulacra is an example of one of several ways large edrioasteroids increase the surface area of the alimentary system. Ontogenetically, edrioasteroids, just post-metamorphosis, have no ambulacra, but as they mature the ambulacra increase in length at a much greater rate than the thecal diameter (Bell 1976a; Sumrall 2001; Hall and Sumrall 2003). As volume increases, however, ambulacra often exhibit a range of different curvatures to compensate for the increased thecal volume, including simple curvature as in most edrioasteroids, distal ambulacral curling as in *Bostryclavus sampsoni* (Sumrall 1996), spiraling ambulacra as in *Giganticlavus bennisoni* Sumrall and Bowsher, 1996, and meandering distal ambulacra as in *Torquerediscus kypsi* and *Parapostibulla belli* (Sumrall 2001; Cornell et al. 2003; Sumrall et al. 2006). Foerste (1914) argued that the branching of the ambulacra in *T. ramosus* was a similar adaptation. This hypothesis is supported by the presence of more complex ambulacral branching in more mature specimens of *T. ramosus* (Fig. 4).

The respiratory structures in *T. ramosus* are unusual for isorophid edrioasteroids. These structures are small plates adjacent to the ambulacra that have two small pores that enter the coelom and connect through a hollow bulb of stereom. Presumably, coelomic fluid passes through the bulb, where gas exchange takes place with the ambient seawater. Guensburg and Sprinkle (1994) described similar hood plates that lack pores in pyrgocystids as possibly serving a respiratory function, but no other isorophids have a pore network of any kind. Bell (1977) and Sumrall (1993) suggested instead that cloacal pumping may have been a common form of respiration in these taxa.

The adaptive significance of the unusual shape of

L. plinthotus is less clear. Sumrall and Parsley (2003) argued that discocystinids fed by bending away from prevailing currents and feeding from more rapid currents generated as water passed over the thecal ambitus. This scenario is not possible in *Lispidecodus* because the oral surface does not have the sharp-edged morphology of all other discocystinids.

Systematic paleontology

Class Edrioasteroidea Billings, 1858
Order Isorophida Bell, 1976a
Family Agelacrinitidae? Chapman, 1860

Discussion

Thresherodiscus is tentatively placed within Agelacrinitidae. However, the stratigraphic range (Upper Ordovician) considerably predates the previous oldest agelacrinitid (*Parapostibulla belli*; Sumrall et al. 2006) of Early Devonian age. Nevertheless, such large range extensions are not an uncommon occurrence in many groups of echinoderms (e.g., Kolata et al. 1991; Sumrall et al. 2000). Furthermore, the plating of the anal pyramid is very uncharacteristic of Agelacrinitids. A more definite placement of *Thresherodiscus* cannot be made without the discovery of additional material.

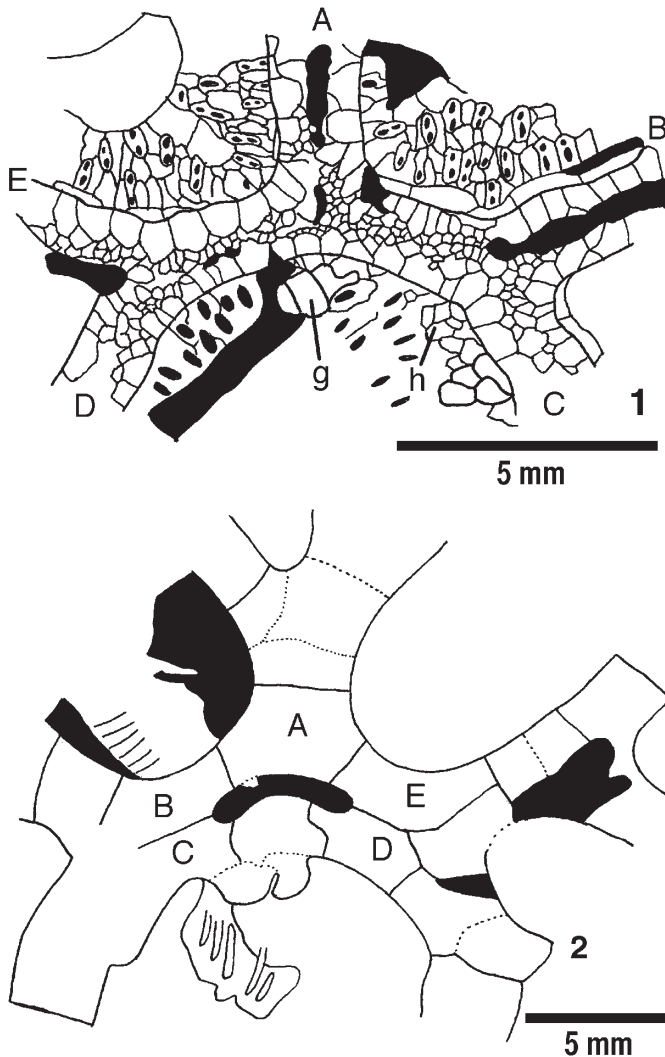
Genus *Thresherodiscus* Foerste, 1914
Thresherodiscus ramosus Foerste, 1914
Figs. 1, 4, 5

DIAGNOSIS: Isorophinid with covered diplopore like respiratory structures adjacent to ambulacra, branching ambulacra, irregularly plated anal pyramid and lacking intrathecal cover plate extensions.

MATERIAL: The redescription herein is based on UMMP 73713, UMMP 73714, UMMP 73816, and UMMP 73819.

DESCRIPTION: Theca large discoidal, circular in outline, ambulacral system radiates from central peristome in 2–1–2 arrangement. Extremely wide oral area plus bifurcation of A ambulacrum exaggerate triradial appearance of ambulacral system. Oral frame composed of five radially positioned oral frame plates and one posterior plate bordering bean-shaped peristomal opening. Transition onto ambulacral floor plates unclear in known material. Peristome covered by series of oral cover plates. Primary orals and lateral bifurcation plates undifferentiated from oral cover plates and laterally shared cover plates. Shared cover plates tiered with large abradial primary cover plates articulating to oral frame plates and smaller secondary cover plates apparently somewhat irregularly placed adradially along periradial suture. Ambulacra radiate from central peristomal region with five main ambulacral trunks typical of Echinodermata. Distal ambulacra formed from uniserial floor plates and articulating cover plates. Food grooves straight, but ambulacra branch distally. A, B, and D ambulacra with primary food groove trending left (when viewed from proximal to distal) with side branches developing along right side. C and E ambulacra with primary food groove trending to right with secondary branches to the left (Figs. 1, 6, 4). Larger secondary branches may in turn branch distally, resulting in a heterotomous branching pattern. In large specimens, distal ambulacral tips extend epithecally

Fig. 5. Line drawings of the oral area of *Thresherodiscus ramosus* Foerste, 1914. (1) Exterior view of UMMP 73816, showing cover plate cycles and respiratory structures. (2) Interior view of UMMP 73714, showing the bean-shaped peristomal opening, two hydropore orals, and the oral frame plates. A–E, ambulacral designations; g, gonopore; h, hydropore.



onto peripheral rim up to one half to two thirds width of peripheral rim (Figs. 1.12, 1.14). Cover plate pattern as in shared ambulacra with large primary plates and somewhat irregular secondary plates adradially along perradial suture; details unknown because of poor preservation in available material. Interambulacral plates of two types: centrally, plates larger, imbricate, slightly tessellate, outer surface covered with small pustules; adradially, interambulacral plates very small, generally perpendicularly elongate, fully adjacent. Adradial interambulacral plates of two types: non-respiratory plates more common with smooth surface; respiratory plates small, oval in outline, developed into thin-walled elongate bulb leading to two pores at opposite ends of plate, giving the appearance of diplopores (Figs. 1.1, 1.4, 1.7, 1.11, 5.1), bulbs all perpendicular to plate surface. Peripheral rim surrounds theca surface, plated with approximately five poorly defined circlets of highly imbricate plates. Most proximal

circlet differentiated with much larger plates. Plates of more distal circlets generally decreasing in size and becoming more radially elongate, especially in distalmost circlet. Bottom surface with radial spur and groove structures. Apparent hydropore–gonopore structure present in proximal right CD interambulacrum along proximal C ambulacrum. In small specimens, hydro-gonopore formed from two plates differentiated from adjacent ambulacral bordering plates with transverse slit-like opening (Fig. 1.4). In UMMP 73816, structure apparently formed from four plates (Figs. 1.11, 5.1). No apparent internal expression of this opening. Second possible pore in proximal central CD interambulacrum formed from two differentiated plates. Internal expression of these plates as two small plates slightly to right of midline with possible opening in between them (Figs. 1.10, 5.2); plating of each of these openings unclear. Periproct located in distal CD interambulacrum. Opening covered by irregularly plated pyramid of lath-shaped plates (Fig. 1.14).

DISCUSSION: The nature of the hydropore and gonopore is unclear at the present time. In most agelacrinitids the hydropore and gonopore are integrated with two internal openings and one external opening (Sumrall 1993). In *Thresherodiscus*, however, there seems to be two separate openings externally, but the obvious external opening along the C ambulacrum first described by Kesling (1960) has no obvious internal expression.

The extension of the distal ambulacra over the proximal portion of the peripheral rim is highly unusual in Edrio-asteroidea. There are a few examples (S.V. Rozhnov, personal communication, 2001) but none so dramatically displayed. The ambulacral tips are apparently epithelial extensions of the ambulacra rather than either free appendages or formed through intercalation between the plates of the peripheral rim as on UMMP 73816. This feature is only developed on the most mature specimens and may be a further adaptation to increase the amount of nutrient intake needed by large individuals.

OCCURRENCE: *Thresherodiscus ramosus* Foerste (1914) is known only from the lower Trenton section on Goat Island, Ontario, and the lower Verulam Formation of Victoria County, Ontario, Canada.

Subfamily Discocystinae Sumrall, 1996

Genus *Lispidecodus* Kesling, 1967

Lispidecodus plinthotus Kesling, 1967

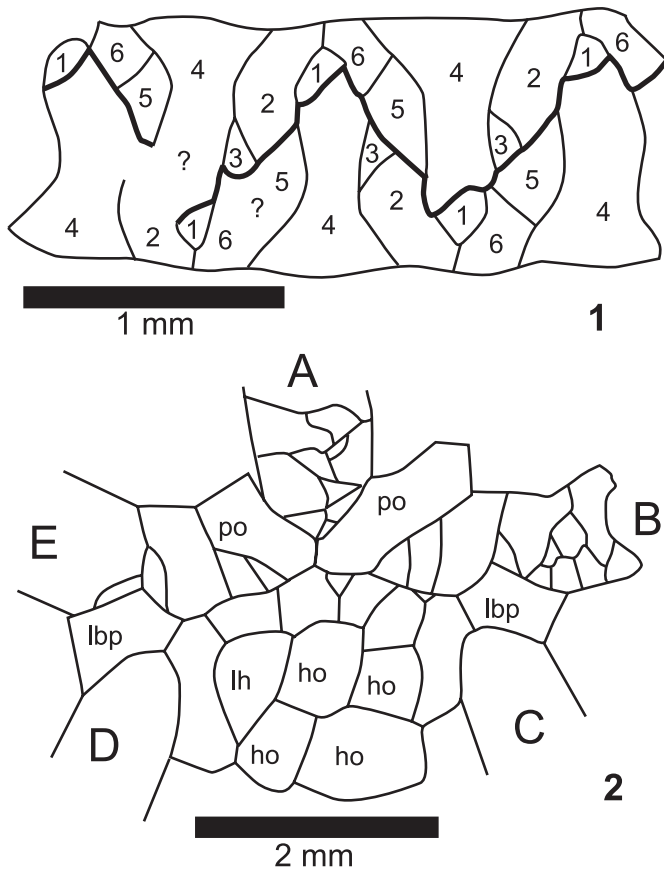
Figs. 2, 6

DIAGNOSIS: Discocystinid with fully tessellate interambulacral plates, turreted oral surface, one primary oral cover plate separating primary oral plate (po) from lateral bifurcation plate (lbp), and highly protuberant anal pyramid.

MATERIAL: The description is based on the unique holotype USNM 154961 (USNM, US. National Museum of Natural History, Washington, D.C.).

DESCRIPTION: Theca small with highly turreted oral surface 17.4 mm high, 10.0 mm maximum width. Oral area with distinct 2–1–2 symmetry. Anterior primary orals and lateral bifurcation plates undifferentiated. Laterally shared ambulacra poorly developed with one primary oral cover plate anteriorly

Fig. 6. Line drawings of the cover plates and peristome of *Lispidecodus plinthotus* Kesling, 1967. (1) Ambulacral cover plates in six-plate cycles. Plate designations follow Sumrall (1996). (2) Oral cover plating of the summit. Note the relatively short shared ambulacra. A–E, ambulacral designation; ho, hydropore oral; lbp, lateral bifurcation plate; lh, left hydropore oral; po, primary oral plate.



with associated secondary cover plates (Figs. 2.7, 6.2). Primary ambulacra grade into oral surface, but taphonomic distortion gives appearance of ambulacra being offset from oral cover plate system. Hydro-gonopore slit-like, in proximal right CD interambulacrum, offset from oral rise, highly elevated, with two anterior, two posterior, and one left hydropore orals, girdle absent (Fig. 6.2). Primary ambulacra straight, narrow termination unknown, maximum width 0.9 mm with little taper distally, composed of floor plates and ambulacral cover plates. Floor plates extremely high and narrow, length unknown, with opposite lateral extensions that connect with adradial floor plates. Cover plates in six-plate pattern with primary cover plates alternating with secondary cover plates (Figs. 2.4, 6.1): plate 1, offset orally, small; plate 2, medium-sized; plate 3, very small; plate 4, largest plate with perradial salient; plate 5, slightly smaller than plate 2; plate 6, small. Interambulacra long and narrow, concave, with large thick tessellate interambulacral plates centrally and smaller thicker interambulacral plates adambulacrally. Adambulacral interambulacra with lateral extensions. Anal pyramid relatively large, in proximal CD interambulacrum, bordered by seven modified interambulacra forming a pedestal presumably in which anal pyramid articulated. Actual pyramid not preserved.

Distal theca including pedunculate zone and peripheral rim not preserved.

DISCUSSION: In the original description, Kesling (1967) discussed at length whether or not *Lispidecodus* was an edrioasteroid. Of this there can be no doubt, as it has several synapomorphies of Discocystinid edrioasteroids, including the plating of the hydropore and the tessellate interambulacral plating. The lateral extensions of the floor plates and the six-plate pattern of ambulacral cover plates clearly place it as highly derived within Agelacrinitidae. Kesling's (p. 198) description of the cover plates is puzzling: "Two types of plates: long, narrow, tong-like plates alternating with short, broad, U-like plates along each side." Kesling and Ehlers (1958) were the first to recognize the cyclic nature of ambulacral cover plates. The misinterpretation of the true six-plate pattern seems to derive from the clear suture between plate 4 on one side of the ambulacrum and plates 1, 2, 3, 5, and 6 on the opposite side, and the perradial suture is rather vague in most places (Figs. 2.4, 6.1). The separation of the ambulacra from the oral area described by Kesling results from the large size of the pos and lbps coupled with the taphonomic sinking of the first cover plates of each ray into the food groove. The relatively high nature of the ambulacra associated with the low depressed interambulacra is common in discocystinids and is probably the life condition. The adradial interambulacral plates articulate along a beveled facet that is at an angle to the adjacent floor plates. The elevated periproct positioned very proximally is unknown in edrioasteroids but is a common feature of some other echinoderms.

OCCURRENCE: The exact occurrence of *L. plinthotus* is uncertain. The specimen was discovered in talus below outcrops of the Mississippian Banff Limestone ~30 miles (50 km) southeast of Jasper, Alberta, in 1956. The locality and preservation are consistent with the Banff Limestone.

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Appendix A. Morphological characters used in the phylogenetic analysis

- (1) Primary oral plates strongly differentiated from oral cover plates (0) or not differentiated (1)

- (2) Three primary oral plates differentiated (0) or four (1)
 (3) Ambulacra straight at maturity (0) or curved (1)
 (4) Cover plates with intrathecal extensions (0) or lacking intrathecal extensions (1)
 (5) Secondary cover plates absent (0), or present between primary cover plates (1), or tiered above primary cover plates (2)
 (6) Oral area with one set of shared cover plates (0) or numerous sets of shared cover plates (1)
 (7) Primary cover plates undifferentiated (0) or in three-plate cycles (1)
 (8) Lateral extensions of ambulacral floor plates absent (0) or present (1)
 (9) Floor plates low (0) or high (1)
 (10) Cover plates lie atop floor plate (0) or articulate into hinge-notch in floor plate (1)
 (11) Interambulacral plates imbricate (0) or adjacent (1)
 (12) Lateral extensions of adradial interambulacral plates absent (0) or present (1)
 (13) Hydropore integrated into oral rise (0) or offset (1)
 (14) One hydropore oral (0) or many (1)
 (15) Left hydropore oral absent (0) or present (1)
 (16) Interambulacral plates thin (0) or thick (1)
 (17) Pedunculate zone not present between ambulacra and peripheral rim (0) or present (1)
 (18) Pedunculate zone not differentiated (0) or differentiated into pedunculate zone and recumbent zone (1)
 (19) Peduncular plates irregular (0) or aligned into columns (1)
 (20) Peripheral rim very large (0) or with smaller diameter than oral surface (1)
 (21) Posterior right oral cover plates undifferentiated (0) or foreshortened adjacent to hydro-gonopore (1)
 (22) Hydro-gonopore not bounded by girdle (0) or bounded (1)
 (23) Periproct with irregular plating (0) or simple cone (1)
 (24) Ambulacra curved CCW-CW as 4-1 (0), 3-2 (1), 5-0 (2), 0-5 (3)

Appendix B

Table B1. Character matrix used in the phylogenetic analysis.

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24
<i>Cameyella</i>	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	?	?	0	0	0	0	0
<i>Foerstediscus</i>	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	?	?	0	0	0	0	3
<i>Isorophus</i>	0	1	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	?	?	0	0	0	1	0
<i>Isorophusella</i>	0	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	?	?	0	0	0	1	?
<i>Agelacrinites</i>	1	?	1	1	1	0	0	0	0	1	0	0	1	0	0	0	0	?	?	0	0	0	1	1
<i>Thresherodiscus</i>	1	?	0	1	2	1	0	0	0	0	0	0	?	?	?	0	0	?	?	0	0	0	0	?
<i>Neosorophusella</i>	1	?	0	1	1	1	0	0	0	1	0	0	1	0	0	0	0	?	?	0	0	0	1	?
<i>Postibulla</i>	1	?	1	1	1	1	1	0	0	1	0	0	1	0	0	0	0	?	?	0	0	0	1	1
<i>Utrichidiscus</i>	1	?	1	1	1	1	1	1	0	1	0	0	1	1	0	0	1	0	0	0	0	0	1	2
<i>Lepidodiscus</i>	1	?	1	1	1	1	1	1	0	1	0	0	1	1	0	0	1	0	0	0	0	0	1	0
<i>Clavidiscus</i>	1	?	1	1	1	1	1	1	1	1	0	0	1	1	1	0	1	0	1	1	1	1	1	0
<i>Hypsiclavus</i>	1	?	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	0
<i>Giganticlavus</i>	1	?	1	1	1	?	1	1	1	1	1	1	?	?	?	1	1	1	1	1	?	?	1	2
<i>Cooperidiscus</i>	1	?	1	?	?	?	?	?	?	1	0	0	1	?	?	0	1	0	0	1	?	0	1	3
<i>Lispidecodus</i>	1	?	?	1	1	0	1	1	1	1	1	1	1	1	1	1	?	?	?	?	1	0	1	?

Note: The numbers 0-3 indicate alternate morphological states; a question mark (?) indicates that the character cannot be coded for a given taxon.