

# The morphologic and paleobiogeographic implications of a new early Silurian echinoid from Anticosti Island, Quebec, Canada

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## Abstract

The Ordovician and Silurian are an exceptionally important interval of time for understanding the effects of ancient climate change on the paleobiodiversity of echinoderms. Despite this importance, the fossil record of many echinoderm groups during this interval is sparse. The echinoids, or sea urchins, are no exception; and new fossil finds are necessary to better understand their initial diversification during the lower Paleozoic. We herein report on material from a new genus and species of echinoid, *Anticostiechinus petryki* gen. et sp. nov., from the Silurian of Anticosti Island, Canada. The morphology of the tubercles and spines of *A. petryki* are atypical for echinoids, and the surfaces for spine articulation consist of rounded, concave indentations. Additionally, the bases of the spines are subspherical. Furthermore, *A. petryki* belongs to the family Echinocystitidae, which increases the known diversity and distribution of this family during the Silurian and provides insight into the biogeography of echinocystitids from the Silurian to Devonian.

**Key words:** echinoderms, sea urchins, fossil, extinction

## Résumé:

L'Ordovicien et le Silurien constituent un intervalle de temps exceptionnellement important pour comprendre les effets des changements climatiques anciens sur la paléobiodiversité des échinodermes. Malgré cette importance, le registre fossile de nombreux groupes d'échinodermes au cours de cet intervalle est rare. Les échinoides, ou oursins, ne font pas exception; et de nouvelles découvertes de fossiles sont nécessaires pour mieux comprendre leur diversification initiale au cours du Paléozoïque inférieur. Nous présentons ici des données sur un nouveau genre et espèce d'échinoïde, *Anticostiechinus petryki* gen. et sp. nov., du Silurien de l'île d'Anticosti, Canada. La morphologie des tubercules et des épines d'*A. petryki* est atypique pour les échinoides, et les surfaces d'articulation des épines consistent en des indentations arrondies et concaves. En outre, les bases des épines sont subsphériques. Par ailleurs, *A. petryki* appartient à la famille des Echinocystitidae, ce qui augmente la diversité et la distribution connues de cette famille au cours du Silurien et donne un aperçu de la biogéographie des échinocystites, du Silurien au Dévonien.

**Mots-clés :** échinodermes, oursins, fossile, extinction

## Introduction

The biosphere collapsed during the Late Ordovician (Sepkoski 1996) as a result of global climate change and habitat destruction that were consequences of a Late Ordovician, southern hemisphere glaciation. The drivers for this climate change have been debated through the years with the following hypotheses advanced: a consequence of plate tectonic history, high cosmic ray flux, extensive volcanism, weathering of volcanic rocks, ocean euxinia, among others (Kump et al.

1999; Shaviv and Veizer 2003; Herrmann et al. 2004; Buggisch et al. 2010; Lefebvre et al. 2010; Nardin et al. 2011; Zou et al. 2018).

The primary obstacle for documenting the Late Ordovician to early Silurian faunal transition is a general lack of known fossils during this time interval. The most complete Hirnantian through Llandovery section known in shelly shelf strata is from Anticosti Island, Quebec (Copper 1989, 2001; Jin and Copper 2008; Desrochers et al. 2008, 2010;

Copper et al. 2013; and others). A rich crinoid fauna is now known from these strata (Ausich and Copper 2010; Ausich and Cournoyer 2019). However, the biodiversity dynamics of other echinoderms groups through this critical stage of Earth history are relatively poorly constrained (Guensburg and Sprinkle 2000; Sprinkle and Guensburg 2004; Webby et al. 2004; Peters and Ausich 2008; Lefebvre et al. 2013). Thus, all other echinoderm finds from Anticosti Island are quite significant. Today, only a few other echinoderm taxa have been described: asteroids (Billings 1857), rhombiferans (Billings 1857; Bolton 1970), edrioasteroids (Bolton 1970; Ewin et al. 2020), cyclocystoids (Glass et al. 2003; Ewin et al. 2019), diploporoids (Sheffield et al. 2017), and stylophorans (Lefebvre and Ausich 2021), and more taxa are under study.

Among other Anticosti echinoderms waiting description are the echinoids described herein. Though echinoids are abundant members of post-Paleozoic communities, their Paleozoic fossil record is comparatively poorer. Whereas most post-Paleozoic echinoids had tests comprised of rigidly sutured plates with interlocking stereom (Smith 1980b, 1984), many Paleozoic echinoids have predominantly imbricate, overlapping, test plates, and were prone to rapid disarticulation. This propensity to disarticulate has resulted in Paleozoic echinoid fossils often being overlooked taxonomically (Thompson and Ausich 2016; Thompson and Denayer 2017). Despite a general paucity of echinoids in the Paleozoic fossil record, the Silurian echinoid fossil record is particularly sparse, yielding fewer recorded echinoid species than any other period in the early Paleozoic (Kier 1965). Despite the rarity of echinoids in this period, the Silurian contains the first occurrence in the fossil record of two of the most abundant and long-ranging echinoid families in the Paleozoic, the Echinocystitidae Gregory, 1897 and Lepidocentridae Lovén, 1874, both of which have been hypothesized to give rise to all other Paleozoic, and by extension, post-Paleozoic echinoid families (Smith 1984). Because of the rarity of echinoids in the Silurian and its standing as an important period for understanding the later evolutionary history of echinoids, every new specimen is of key importance to understanding the early evolution of the group. Herein, we describe a new echinocystitid *Anticostiechinus petryki* gen. et sp. nov., the first Silurian echinoid known from Canadian strata. It has similarities to other Early and Middle Paleozoic genera globally, and, consequently, it is an important addition to our understanding of early echinoid evolution.

## Geography and stratigraphic occurrence

The Ordovician–Silurian boundary section on Anticosti Island (Fig. 1) is Katian (Late Ordovician) through Telychian (Llandovery). Richardson (1857) was the initial geologist who tried to understand Anticosti Island stratigraphy. Because of the importance of the Ordovician–Silurian boundary and the very fossiliferous strata on the island, Anticosti stratigraphy has been well studied (e.g., Schuchert and Twenhofel 1910; Twenhofel 1928; Bolton 1981; Cocks and Copper 1981; Petryk 1981; Long and Copper 1987; Barnes 1988; Copper 2001; Jin

and Copper 2008; and others). The most recent work has re-established the position of the Ordovician–Silurian boundary, which correlated Silurian strata from west to east based on a combination of biostratigraphy and sequence stratigraphy (Copper 1989; Desrochers et al. 2008; Desrochers et al. 2010; Copper et al. 2013). Stratigraphic nomenclature used here (Fig. 1) follows Copper et al. (2013).

The specimens of *Anticostiechinus petryki* described here are from the Allen A. Petryk collection. Many of these collections are now housed in the Musée de paléontologie et de l'évolution, Montréal, Canada (MPEP). The samples arrived in field bags, but unfortunately, the key identifying Petryk locality numbers has not been located. Consequently, stratigraphic occurrences were narrowed significantly utilizing the associated fauna (see Ausich and Cournoyer 2019). The lack of precise geographic and stratigraphic data on these fossils does not disqualify it for description because this echinoid is critical to understanding echinoid evolution, and there is a dearth of information on Silurian echinoids generally. The new echinoid described here was broken into four primary pieces and is from Petryk field locality 77AP15-4-1F (collected in 1977). In addition to the echinoid material, 50 additional fossil specimens are associated with the echinoid. Significant co-occurring fossils are *Encrinurus deomenos* Tripp, 1962 (MPEP488.2, known from either the Gun River or Jupiter formations), *Arctinurus Castelnau, 1843* fragments, *Stenopareia Holm, 1886* cephalons, *Gotatrypa Struve, 1966*, *Favosites Lamarck, 1816*, and *Coolinia pecten (Linnaeus, 1758)*, which is suggestive of the Jupiter Formation (sensu lato). In addition, *Katastrophomena radiireticulata (Twenhofel, 1928)* co-occurs with the new echinoid, and this brachiopod is known only from the Goéland Member, Menier Formation (late Aeronian) through the Ferrum Member of the Jupiter Formation (early Telychian) on Anticosti Island (Fig. 1). Conservatively, we regard this echinoid to be from strata that are late Aeronian to early Telychian in age from the Goéland Member, Menier Formation, Ferrum Member of the Jupiter Formation, or a unit between these two members. Future collecting will verify the exact occurrences of this important new echinoid.

## Diversity and distribution of Silurian echinoids

Silurian echinoids are rare globally and are known only from a handful of localities, most of which are limited to the Northern Hemisphere paleocontinents Baltica, Avalonia, and Laurentia (Table 1). Traditionally, Silurian echinoid faunas have included taxa belonging to three families of stem group echinoids; the Echinocystitidae, Lepidocentridae, and Bothriocidaridae (Order Bothriocidaroida) (Smith 1984; Thompson et al. 2022). Recent phylogenetic analyses, however, have disputed an echinoid affinity for the bothriocidaroids, instead favoring a stem group holothurian affinity for some species (Rahman et al. 2019). Because of this uncertainty, bothriocidaroids are excluded from the list of occurrences of Silurian echinoids in Table 1. Most early work on Silurian echinoids was based on fossils from the United Kingdom. Two of the best-known Silurian echinoids are the lepidocentrid *Palaeodiscus ferox* Salter, 1857 and the echinocys-

**Fig. 1.** Ordovician to Silurian stratigraphic column for Anticosti Island (modified from Copper et al. 2013). Grey bar indicates stratigraphic range where *Anticostiechinus petryki* gen. et sp. nov. was collected.

System	Series	Stage	Formation	Member		
Silurian	Llandovery	Telychian	Chicotte			
			Jupiter	Pavillon		
				Ferrum		
				Cybèle		
			Aeronian	Richardson		
				Menier	East Point	
		Goéland				
		Gun River		Macgilvray		
				Sandtop		
			Innommée			
		Rhuddanian	Merrimack			
			Becschie	Chabot		
				Fox Point		
				Laframboise		
Ordovician	Late	Hirnantian	Lousy Cove			
			Ellis Bay	Parastro		
				Junction Cliff	Prinsta	
				Fraise		
				Katian	Vauréal	Velleda
			Grindstone			
		Schmitt Creek				
		Mill Bay				
		Battery				
		Homard				
		Tower				
		Easton				
		Lavache				
				west	east	

titid *Echinocystites pomum* Wyville Thomson, 1861, both described from the Ludfordian lower Lentwardine Formation of Herefordshire, UK (Hawkins and Hampton 1927) and representing occurrences from Avalonia. Additional occurrences from the United Kingdom include the lepidocentrids *Ap-tilechinus caledonensis* Kier, 1973 from the Telychian Deep-hope Formation of Scotland (representing a Laurentian occurrence); “*Maccoya*” *phillipsiae* (Forbes 1848) from the upper Llandovery of the Malvern Hills, Worcestershire, UK; and *Mytiastiches gigas* Sollas, 1899 from the lower Ludlow. The lepidocentrid *Koninckocidaris silurica* Jackson, 1912 is the only Silurian echinoid known from Laurentian strata in North America. At least three species are known from Silurian strata on Gotland, Sweden (Franzén 1979; Kutscher and Reich 2001, 2004). These include the echinocystitid *Gotlandechinus balticus* Regnéll, 1956, an indeterminate species of *Ap-tilechinus* (Franzén 1979) and large bulbous spines belong-

ing to a taxon assigned to the species *Silurocidaris clavata* Regnéll, 1956. Additional echinoid occurrences representing indeterminate taxa are known from both Baltic and Laurentian strata (Table 1) indicating that paleobiodiversity is likely vastly underrepresented from the known fossil record. Given that both the echinocystitids and lepidocentrids are first known from the Silurian, additional occurrences shed light on when these families originated, and how quickly they attained their paleobiogeographic distribution in the Silurian.

## Materials and methods

Material is deposited in collections of the Musée de paléontologie et de l'évolution in Montréal, Quebec, Canada (MPEP). All measurements are in millimetres.

**Table 1.** Known occurrences of echinoid taxa in the Silurian.

Species	Family	Locality	Formation	Stage	Reference	Reference for stratigraphy
<i>Koninckocidaris silurica</i>	Lepidocentridae	Rochester, New York, USA	Rochester Formation	Sheinwoodian, Wenlock	Jackson 1912	Cramer 2009
<i>Myriastiches gigas</i>	Lepidocentridae	?	?	Lower Ludlow	Sollas 1899	Lister and Downie 1967
<i>Echinocystites pomum</i>	Echinocystitidae	Lentwardine, Herefordshire, England, UK	Lower Lentwardine Formation	Ludfordian (Ludlow)	Salter 1857; Sollas 1899; Hawkins and Hampton 1927	Perrier et al. 2020
<i>Palaeodiscus ferox</i>	Lepidocentridae	Lentwardine, Herefordshire, England, UK	Lower Lentwardine Formation	Ludfordian (Ludlow)	Salter 1857; Sollas 1899; Hawkins and Hampton 1927	Perrier et al. 2020
" <i>Maccoya</i> " <i>phillipsae</i>	Lepidocentridae	Under Worcester Beacon, Malvern Hills, Worcestershire, England, UK	Miss Phillips' Conglomerate (Wych Formation)	Llandovery, Telychian	Forbes 1848	Cocks 2019
<i>Aptilechinus caledonensis</i>	Lepidocentridae	Pentland Hills, Scotland, UK	Deer Hope Formation	Llandovery, Telychian	Kier 1973	Clarkson et al. 2000
<i>Anticostiechinus petryki</i> n. sp.	Echinocystitidae	Anticosti Island, Precise details unknown	See <i>Systematic Palaeontology</i>	Llandovery	-	Copper et al. 2013
<i>Aptilechinus</i> sp.	Lepidocentridae	Vattenfallet, and Nyhamn/Gotland, Sweden	Lower Visby Marl	Llandovery, Telychian	Franzén 1979; Kutscher and Reich 2018	Calner and Jeppsson 2003; Jeppsson et al. 2006
<i>Gotlandechinus balticus</i>	Echinocystitidae	Klinterberget, Gotland, Sweden	Klinterberg Formation	C. <i>murchisoni</i> Zone; Wenlock, Homeric	Regnéll 1956	Calner and Jeppsson 2003; Jeppsson et al. 2006
Gen. et. sp. indet.	Inteterminate	Vattenfallet, Gotland, Sweden	Upper Visby Marl	Wenlock, Sheinwoodian	Regnéll 1956	Calner and Jeppsson 2003; Jeppsson et al. 2006
Gen. et. sp. indet.	Inteterminate	Samsugn, Gotland, Sweden	Slite Group	Wenlock, Sheinwoodian or Homeric	Regnéll 1956	Calner and Jeppsson 2003; Jeppsson et al. 2006
Gen. et. sp. indet.	Inteterminate	Tänglings hällar and Sandarve kulle, Gotland, Sweden	Hemse Marl	Ludlow, Gorstian or Ludfordian	Regnéll 1956	Calner and Jeppsson 2003; Jeppsson et al. 2006
Jaw-fragments, Gen. et. sp. indet.	Inteterminate	Samsugn, Gotland, Sweden	"About the age of the Slite Group"	Wenlock, Sheinwoodian or Homeric	Regnéll 1956	Calner and Jeppsson 2003; Jeppsson et al. 2006
<i>Lanternarius latens</i>	Inteterminate	Lansa, Farön, Sweden	"About the age of the Slite Group"	Wenlock, Sheinwoodian or Homeric	Regnéll 1956	Calner and Jeppsson 2003; Jeppsson et al. 2006
<i>Silurocidaris clavata</i>	Inteterminate	Mannegarde, Lye and Linde klint, Gotland, Sweden	Hemse Marl	Ludlow, Gorstian	Regnéll 1956	Calner and Jeppsson 2003; Jeppsson et al. 2006
<i>Tridentate pedicellariae</i>	Inteterminate	Vallance's Hill, Namina, New South Wales, Australia	?	Ludlow	Philip 1963	Philip 1963
" <i>Lepidocentrotus eifelianus</i> "	Indeterminate	Dudley, Worcestershire, England, UK	Wenlock Limestone	Wenlock, Homeric	Lewis and Donovan 1998	Perrier et al. 2020
Undescribed echinoid	Indeterminate	Eramosa Lagerstätte, Ontario, Canada	Upper Eramosa Formation	Wenlock	von Bittter et al. 2007	von Bittter et al. 2007

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## Systematic paleontology

Phylum Echinodermata De Brugière, 1791

Class Echinoidea Leske, 1778

Family Echinocystitidae Gregory, 1897

### *Anticostiechinus* gen. nov.

ZOOBANK LSID: urn:lsid:zoobank.org:act:F873A8BC-619E-4F3B-867C-93868EA164AC

DIAGNOSIS: As for species.

TYPE SPECIES: *Anticostiechinus petryki* by monotypy.

ETYMOLOGY: Named for Anticosti Island where the type species was located.

OCCURRENCE: Silurian (Llandovery, late Aeronian to early Telychian); Anticosti Island, Quebec.

REMARKS: See REMARKS for species.

### *Anticostiechinus petryki* sp. nov.

(Figs. 2a–2g, 3)

ZOOBANK LSID: urn:lsid:zoobank.org:act:319D1DF7-3553-4DD6-8F9E-6DCD1281737C

HOLOTYPE: MPEP488.1 (a single specimen that has been broken into four primary pieces).

ETYMOLOGY: The species name recognizes Allen Petryk, who collected the specimen.

OCCURRENCE: Silurian (Llandovery). The precise location is not known. The associated fauna indicates that this new echinoid was most probably from a horizon from the Goéland Member of the Menier Formation (late Aeronian) to the Ferrum Member of the Jupiter Formation (early Telychian), though the precise horizon is unknown.

DIAGNOSIS: Echinocystitid with heavily imbricate, scale-like interambulacral plates, and uniserial half-ambulacra. Ambulacral plates are about 1.5 times wider than high, and alternating plates are differentially enlarged or reduced in size. Interambulacral and ambulacral plates are covered with small pits, into which ball-like spine bases articulate. Some interambulacral plates have a large, sunken pit, which dominates the plate.

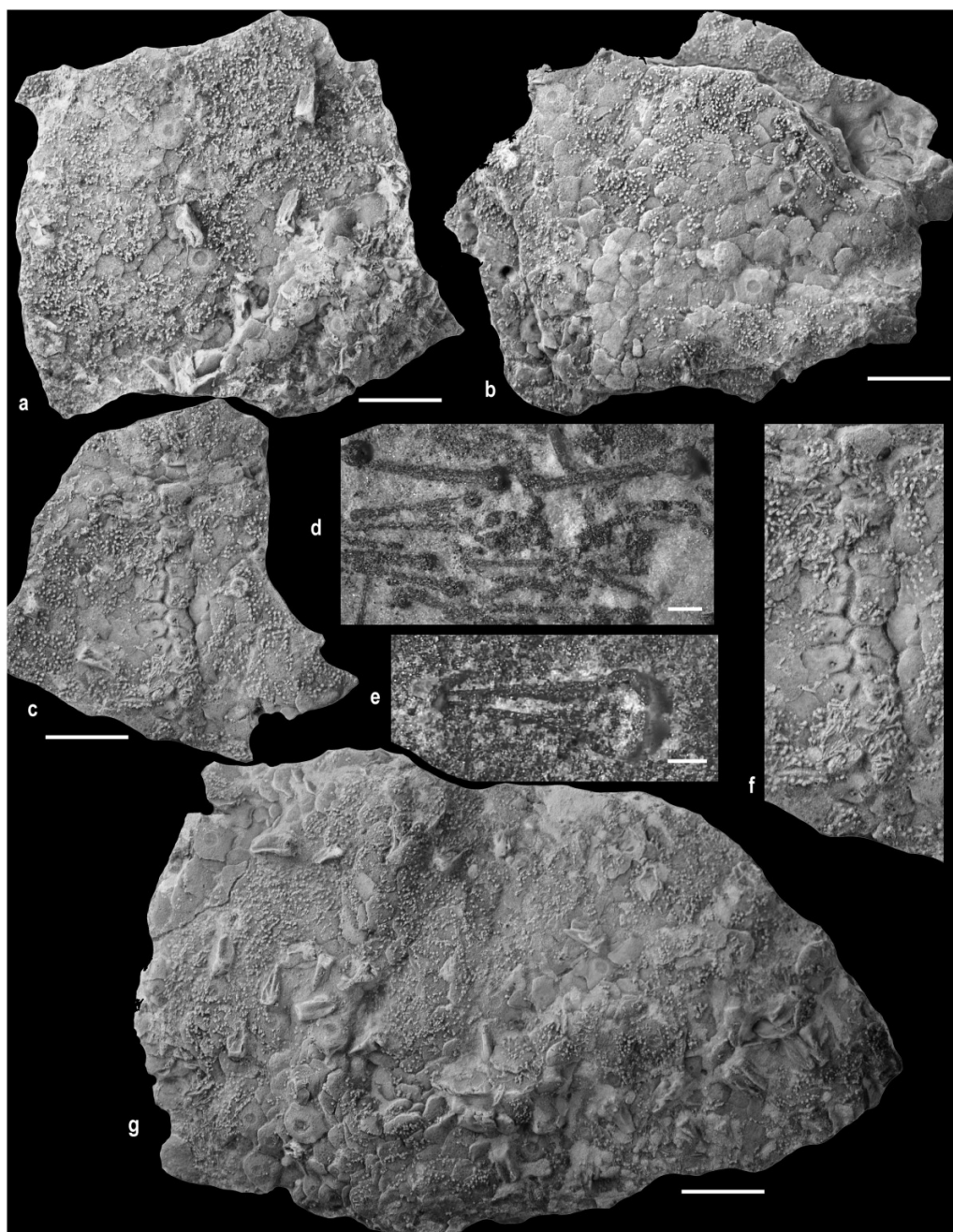
DESCRIPTION: This species is known from four fragmentary portions of a test and eight smaller fragments of ossicles. The outline of the test in profile and plan view and the diameter of the test are unknown. Test plating is strongly imbricate (Figs. 2a, 2b), with interambulacral plates imbricating over the ambulacra. One ambulacrum is 4.6 mm in diameter, and though no complete interambulacrum can be measured, the interambulacral areas are many times wider than ambulacral areas. Details of the apical disk and peristome are unknown, though various elements of the disarticulated Aristotle's lantern are preserved (Figs. 2a, 2g). Numerous fragmentary hemipyramids and epiphyses are scattered around the specimens, but no obvious rotulae or teeth were identified and the one-dimensional nature of the preservation of the

hemipyramids precludes a detailed description of their morphology.

The ambulacra are straight to slightly sinusoid (Figs. 2c, 2f, 3). All ambulacral plates are imbricate, with more adapical ambulacral plates imbricating over more adoral plates. Where preserved, each ambulacrum is arranged into two columns of plates. Each ambulacral plate is pierced by two pore pairs, the more perradial of which is located slightly adoral to the more adradial (Fig. 3). These pore pairs are sunken into a small peripodial ring and are typically located toward the more adoral edge of the plate, and are, on average, located 40% of the total height of the plate from the adoral suture (Table 2). These pores are also on average located closer to the perradial suture than adradial suture (Table 2). Ambulacral plates are on average 1.5 times wider than high, and the shapes of the plates are irregularly polygonal (Fig. 2f). The perradial suture displays a distinct zig-zag morphology, as the perradial margin of each plate tapers to a point per radially (Fig. 2f). Within each half-ambulacrum, every other plate seems to be enlarged relative to the plates above or below them (Fig. 2f). Though all plates appear to be in contact with the adradial suture, these larger plates have more of their adradial margins in contact with the adradial suture than do the smaller plates (Fig. 2f). All plates are in contact with the perradial suture, and there is no discernible variation in morphology from the adoral to aboral surface, though only a small portion of the ambulacrum is visible. All ambulacral plates are densely covered with numerous small spines and the small pits into which the spines articulate (Fig. 2c). The interior of plates are not visible, thus it is not possible to tell if the radial water vessel is enclosed within the plates or any arch-like protrusions.

The interambulacral areas are wide and comprised of numerous heavily imbricate plates (Figs. 2a, 2b, 2g). The precise organization of the interambulacra is unknown due to the fragmentary nature of these specimens, and the number of columns of plates in each interambulacrum is unknown, though there are likely as many as 10 columns, and probably more. Plates imbricate adambulacrally and adorally, with a substantial portion of a given plate covered by imbricating adjacent plates (Fig. 2b). Plates are rounded to rhomboidal in shape and are scale-like with rounded adambulacral margins (Figs. 2b, 2g). The interradian margins that are visible are scalloped to imbricate underneath the rounded adambulacral margins of the adjacent plates. Plates are about as wide as high, or slightly wider than high, but if viewed in place the imbrication of adjacent plates makes many plates appear higher than wide (Fig. 2b). Each plate is covered in numerous, densely packed, small indentations or pockets, into which the bases of each spine articulated. Some plates have a larger, circular indentation or pit (Figs. 2a, 2b), which may have borne large spines or may be similar to a sunken tubercle. These larger circular indentations or pits are not located in the center of the plate, but due to the large degree of imbrication in interambulacral plates in this species are located more toward the adambulacral edge of plate. Plates with these large indentations are present in some of the adambulacral interambulacral columns, in some places for multiple rows (Fig. 2c), though it is not possible to determine if this

**Fig. 2.** *Anticostiechinus petryki* gen. et sp. nov. (a) MPEP488.1c part of the test of *A. petryki* showing imbricate interambulacral plating and numerous tiny spines covering the surface of the test. Additionally scattered elements of the aristotles lantern are present. Scale bar = 5.0 mm. (b) Interambulacral plating of MPEP488.1d showing imbricate plating of interambulacral, as well as large, circular indentations that may have been attachment sites for spines. Scale bar = 5.0 mm. (c) Ambulacra of *A. petryki* (MPEP488.1c) Note pore pairs that are enclosed entirely within the plates. Additionally, the pore pairs on each plate are located closer to the perradial suture than the adradial suture. Scale bar = 5.0 mm. (d) MPEP488.1a, enlargement of Fig. 2g. Small spines covering interambulacral plates of *A. petryki*. Note there is no milled ring, and the base of spines consists of a rounded bump. Scale bar = 0.5 mm. (e) MPEP488.1a, enlargement of Fig. 2g. with a single pedicellariae showing two valves. Scale bar = 0.25 mm. (f) Close up of ambulacra shown in Fig. 2c, MPEP488.1b. (g) Semi-disarticulated test of specimen MPEP488.1a.



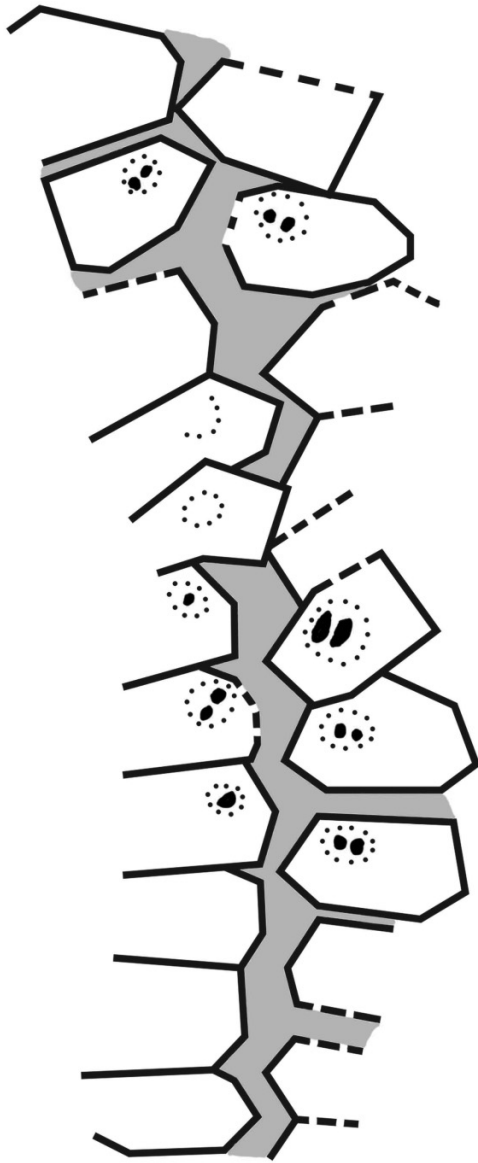
was present in any particular arrangement adorally-aborally. It is not possible to tell if all adambulacral interambulacral plates bear these large indentations.

Spines are present in both the interambulacra and ambulacra of *Anticostiechinus petryki* gen et sp. nov. Spines are small

and tapered distally. They lack a milled ring and any ornamentation along the shaft and appear to have been radially symmetrical in cross section (Fig. 2d). The longest spine is about 1.3 mm in length, and ambulacral spines consistently appear to be longer than interambulacral spines, though this



**Fig. 3.** Close up view of ambulacral plating of *Anticostiechinus petryki* gen. et sp. nov. Grey area indicates space between plates due to post-mortem disarticulation. Dotted circles represent peripodial indentations in which pore pairs are found on each plate. Dashed lines represent unclear or obscured plate boundaries. Compare with Fig. 2c.



could be a taphonomic artifact. A few pedicellariae are preserved on specimen (Fig. 2e). These consist of at least two slender valves, though a third was likely present, each of which is wider at the base and tapers distally. These elements have a flattened wider base where the valves meet.

**REMARKS:** *Anticostiechinus petryki* gen et sp. nov. is similar to other Silurian and Devonian echinoids, such as *Palaeodiscus ferox* Salter, 1857, *Echinocystites pomum* Wyville Thomson, 1861, and *Lepidocentrus eifelianus* Müller, 1857, in that it has scale-like interambulacral plates that are heavily imbricate. It is differentiated from most lepidocentrids, however, by the morphology of its ambulacral plates, which are higher

than the short, rectangular ambulacral plates that characterize lepidocentrids. It is also differentiated from other echinocystitids like *Echinocystites*, *Rhenechinus* Dehm, 1953 and *Gotlandechinus* in having uniserial half-ambulacra, instead of having biserial half-ambulacra as a result of the demi-plate reduction present in those genera. Whereas *A. petryki* lacks demi-plates, alternating plates in the half-ambulacrum of each ambulacrum are reduced in size, which may be indicative of a transitional morphology related to those of other echinocystitids. The ambulacral plates of *A. petryki* are most similar to those of the Devonian *Porechinus porosus* Dehm, 1961. *Porechinus* has long been considered to be closely related to echinoids of the family Palaechinidae M'Coy, 1849 based on the morphology of its interambulacral plates, which are regular and hexagonal (Dehm 1961). However, the morphology of interambulacral plates in *Anticostiechinus* and their similarity to those of *Porechinus* may indicate either that regular hexagonal plating evolved convergently in *Porechinus* and *A. petryki*, or that *Anticostiechinus* and *Porechinus* share a common ancestor that had ambulacra like those in both taxa, and that *Porechinus* gave rise to Palaechinids. Nevertheless, *Rhenechinus* also has regular hexagonal plating, which may indicate that this plating is non-diagnostic of Palaechinids. Despite these similarities, *A. petryki* is strongly differentiated from *Porechinus*, which has very slightly imbricate to tessellate plating, because of its heavily imbricate interambulacral plates. *A. petryki* is also noteworthy given that pedicellariae are preserved on the test (Fig. 2e). Pedicellariae are rare in the echinoid fossil record, especially during the Paleozoic (Coppard et al. 2012). The pedicellariae preserved on *A. petryki* are similar to those preserved on other echinocystitids *Echinocystites pomum* Wyville Thomson, 1861 and *Rhenechinus ibericus* (Hauser and Landeta 2007).

## Discussion

The Ordovician and Silurian were an exceptionally important interval of time for the evolutionary history of echinoderms (Guensburg and Sprinkle 2000; Sprinkle and Guensburg 2004; Peters and Ausich 2008; Lefebvre et al. 2013; Thompson et al. 2022). This is in part because of widespread global climatic changes which influenced the evolutionary dynamics of multiple echinoderm groups. To gain a richer understanding of the impact of Ordovician and Silurian extinction and origination on the macroevolutionary dynamics of echinoids, a more thorough understanding of the morphology and distribution of echinoids during this interval of time is necessary. Below, we outline the implications of *Anticostiechinus* on the current state of early Paleozoic echinoid morphology and paleobiogeographic distribution.

## Morphology of *Anticostiechinus* spines and tubercles

The spines and tubercles of *Anticostiechinus* are strikingly different from those of all other Paleozoic echinoids and are worth comment. As opposed to many stem group echinoids and all crown group echinoids, where tubercles consist of a rounded, spherical boss onto which a rounded spine base ar-

**Table 2.** Measurements (in millimetres) of morphology of ambulacral plates of *Anticostiechinus petryki* gen et sp. nov.

	Ambulacral plate height	Ambulacral plate width	Plate width/height	Distance from pore pairs to adoral suture	Location of pore pairs relative to adoral margin of plate	Distance from pore pairs to perradial suture
Plate 1	1.4	2.0	1.4	0.5	0.4	0.7
Plate 2	1.3	2.0	1.5	0.3	0.2	0.4
Plate 3	1.5	1.9	1.3	0.8	0.5	0.7
Plate 4	1.3	2.3	1.8	0.4	0.3	0.6
Mean	1.4	2.1	1.5	0.5	0.4	0.6

articulated (Smith 1980a), on *Anticostiechinus*, the base of the spine is spherical and fits into a rounded socket or pit on the plate. The bases of spines are enlarged, bulbous, and spherical (Fig. 2d). Interambulacral plates are covered in shallow pits, into which these bulbous spines articulated. Additional larger indentations on some interambulacral plates may also be articulation surfaces for larger spines that are not preserved. Small pits are also known on the surface of interambulacral and ambulacral plates of the Devonian palaechinid *Porechinus*. In *Porechinus*, the nature of these pits was not particularly well known, but given that they bear spines in *Anticostiechinus*, this was likely their role in that taxon. Furthermore, small spines with a rounded, enlarged base and similar to those in *Anticostiechinus* are also present on the test of *Porechinus* (Dehm 1961). The small, pit-borne spines present across these echinoids are also similar to those in some pyrogocystid edrioasteroids (Sumrall et al. 2013) and are indicative of potential similarities between these eleutherozoan groups. The spine and tubercle morphology of *Anticostiechinus* further demonstrates that the morphological and taxonomic diversity of known Silurian echinoids likely vastly underestimates the diversity present during the Silurian. Future discoveries of Silurian echinoid fossils are likely to inform additional novel morphologies that will aid in our understanding of early echinoid biodiversity and diversification.

### Implications of *Anticostiechinus* for understanding Silurian echinoid distribution

*Anticostiechinus petryki* gen. et sp. nov. bolsters previous knowledge of the diversity and distribution of echinoids during the Silurian. The Silurian fossil record of echinoids is sparse, with only approximately nine named non-bothriocidaroid species (Table 1). *Anticostiechinus petryki* represents the first occurrence of a Laurentian echinocystitid, expanding the known biogeographic range of the clade. The Silurian occurrence of *A. petryki* indicates that the echinocystitids were widespread, occupying environments in Laurentia, Baltica (represented by the Homeric *Gotlandechinus*), and Avalonia (represented by the Ludfordian *Echinocystites*). Unfortunately, due to the uncertainty surrounding the precise age of *A. petryki* and the general rarity of echinoids from Silurian strata, analyses of fluctuating echinocystitid distributions throughout the stages of the Silurian are not possible, but at the very least, it appears that the family was represented across all sectors of Laurussia (Cocks and Torsvik 2005). The distribution of echinocystitids is similar to that

observed for the lepidocentrid echinoids during the Silurian. No echinoid fossils have been identified from Silurian strata in Gondwana, so it remains an open question whether or not echinoids were restricted to Laurentia, Baltica, and Avalonia during the Silurian.

Two species of *Rhenechinus* from Emsian strata of Spain and Germany (Dehm 1953; Smith et al. 2013) are the youngest echinocystitid echinoids known. One of these, *Rhenechinus hopstaetteri* Dehm, 1953, also co-occurs with the echinocystitid *Porechinus porosus* Dehm, 1961 in the Hunsrück slate of Germany (Dehm 1953; Dehm 1961). The Hunsrück slate is thought to represent deep paleoenvironments along the southeastern margin of Laurussia (Übelacker et al. 2016), whereas the Spanish occurrences from the Cantabrian Zone represent shallower water deposits from slightly farther south (Korn and De Baets 2015). This indicates that echinocystitids may have continued to inhabit the oceans around Laurussia and its precursors from the Silurian into Devonian times.

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## Data availability

All data that underlies this work are available within the manuscript.

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### Competing interests

The authors declare there are no competing interests.

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