



Perforocycloides nathaliae new genus and species, an unusual Silurian cyclocystoid (Echinodermata) from Anticosti Island, Québec, Canada

Timothy A. M. Ewin¹ · Mike Reich^{2,3,4} · Mark R. Graham⁵ · Mario E. Cournoyer⁶

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Abstract

Cyclocystoids are a poorly known, rare, extinct class of bi-facially flattened, disc shaped echinoderms, ranging from the Middle Ordovician to the Early Carboniferous. Articulated cyclocystoids are relatively common in the Ordovician but are rarer in younger strata. Here we describe *Perforocycloides nathaliae* new genus and species, from the early Silurian of Anticosti Island, Québec, Canada, the first articulated cyclocystoid from the Silurian of North America. This taxon is distinguished from other cyclocystoids by the number of variably sized marginal ossicles, the lack of interseptal plates, and the novelty of pores located in the distal part of the sutures between adjacent marginals on the dorsal surface. These dorsal intermarginal sutural pores led to canals which penetrated the contiguous area of the lateral surface of the marginals and emerged on the ventral surface between the cupules of adjacent marginals. These dorsal intermarginal sutural pores/canals appear to be unique to *Perforocycloides* and whilst their function is speculative, they provided some form of communication between the dorsal disc and the distal side of the ventral marginals/cupules. *Perforocycloides* most closely resembles the Ordovician–Silurian genus *Zygocycloides*, suggesting that this genus may have diversified more widely during the Silurian than previously reported. A review of global Silurian cyclocystoid distribution suggests taxa were geographically confined and that greatest diversity appears to have been located within Baltica. However, it also demonstrates our current limited knowledge. No specimens have been recorded from Gondwana (e.g. Africa, Australia, South America), Siberia, and North and South China, nor are any specimens known confidently anywhere from Přídolí strata.

Keywords Cyclocystoid · Anticosti Island · Canada · Jupiter Formation · Silurian · Palaeogeography

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✉ Timothy A. M. Ewin
t.ewin@nhm.ac.uk

✉ Mike Reich
reich@snsb.de

Mark R. Graham
m.graham@nhm.ac.uk

Mario E. Cournoyer
paleovision@videotron.ca

¹ Department of Earth Sciences, The Natural History Museum London, Cromwell Road, South Kensington, London SW7 5BD, UK

² SNSB–Bavarian State Collection of Palaeontology and Geology, Richard-Wagner-Strasse 10, 80333 Munich, Germany

³ Division of Palaeontology and Geobiology, Department of Earth and Environmental Sciences, Ludwig-Maximilians-Universität München, Richard-Wagner-Strasse 10, 80333 Munich, Germany

⁴ GeoBio-Center LMU, Richard-Wagner-Strasse 10, 80333 Munich, Germany

⁵ Core Research Laboratories, The Natural History Museum London, Cromwell Road, South Kensington, London SW7 5BD, UK

⁶ Musée de paléontologie et de l'évolution, 541, rue de la Congrégation, Montréal, QC H3K 2J1, Canada

Introduction

Cyclocystoids are a rare, extinct class of echinoderms ranging from the Middle Ordovician to the Early Carboniferous. They are typically small, circular to pentagonal, flattened organisms, which have been divided into two valid families, 21 genera, and about 40 species. They are known both from articulated and disarticulated material from North America, Europe, Australia, North Africa (Reich et al. 2017), and China (Reich et al. unpubl.), but with most articulated material known from Ordovician strata.

Cyclocystoids were extensively reviewed and monographed by Smith and Paul (1982), who erected the modern taxonomic and morphological framework within which all subsequent work has been based. Since this time, several new taxa and genera have been described, along with a new family lacking cupules (Reich et al. 2017).

Many aspects of the soft tissue and the life mode of cyclocystoids remain a matter of debate, particularly their orientation during life. Nichols (1969) and Smith and Paul (1982) presented several pieces of evidence supporting an interpretation that the mouth (ventral surface) faced toward substrate and that these creatures were vagile, using tube feet located along the rays for locomotion and consumed small organic particles from the sediment via cilia located in the cupules. However, Sprinkle et al. (2015) and Reich et al. (2017) favoured an orientation with the annular plate surface (dorsal) facing toward the substrate and the mouth (ventral surface) facing toward the water column, the organisms being sessile (and/or hemisessile), and with the radial tube feet used for capturing

suspended food particles (an orientation favoured by many previous workers including Sieverts-Doreck 1951, Kesling 1963, 1966 and Kolata 1975). Furthermore, questions as to their origins and interrelationships remain speculative (e.g. Smith and Paul 1982; Berg-Madsen 1987; Rowe 1988; Reich et al. 2017).

Whilst cyclocystoids have previously been reported from Ordovician strata of Anticosti Island (Glass et al. 2003), none have been reported from Silurian strata. Indeed, articulated specimens outside of the Ordovician are rare, and apart from the specimen described here, no other articulated non-Ordovician cyclocystoid has been previously described from North America. Thus, description of any new occurrence is significant.

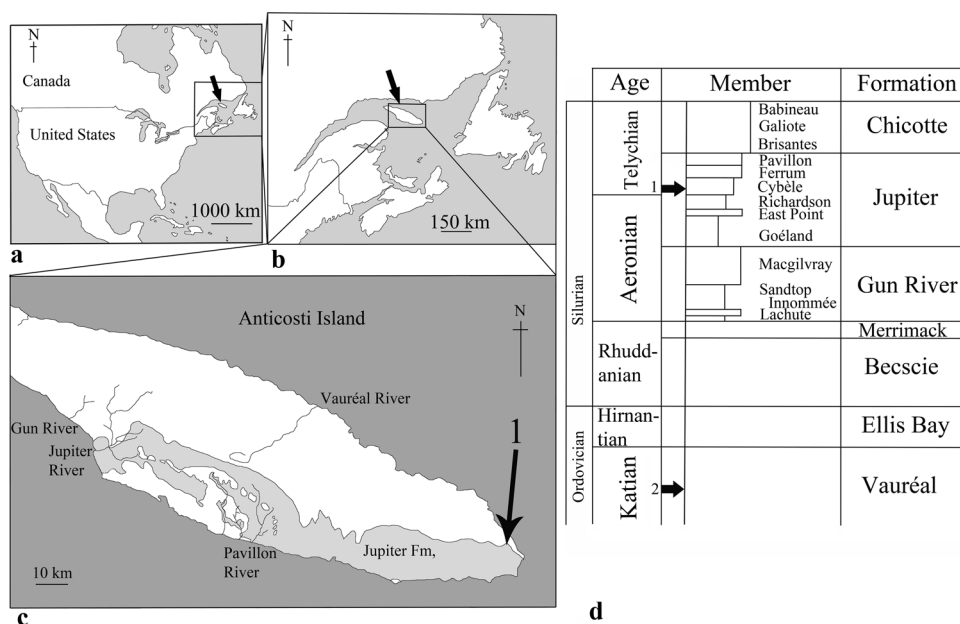
Here we describe a new genus and species based on a single specimen collected in the early 1990s by private collector Nathalie Daoust. The robust preservation of the specimen has enabled much of the marginal frame to be exposed through preparation, thereby facilitating a more complete knowledge of its morphology.

Geological setting

The geology of Anticosti Island comprises Upper Ordovician to Lower Silurian strata (Chatterton and Ludvigsen 2004), which dip gently to the southeast (see Fig. 1). The units are dominated by shallow marine carbonate ramp deposits of limestones and shales (Long 2007).

At the time of collection the specimen was identified as originating from the Richardson Member of the Jupiter Formation (Early Silurian). However, the subdivision of the Jupiter Formation was recently revised by Copper and Jin

Fig. 1 a–c, Maps showing location of specimen on Anticosti Island, Québec, Canada. **d** Column showing Ordovician and Silurian stratigraphy of Anticosti Island and the position of cyclocystoid remains; 1. *Perforocycloides nathalieae*; 2. *Nicholsodiscus anticostiensis*



(2015), who reassigned the limestone-dominated units of the upper part of the Richardson Member (units 4–7) to the overlying Cybèle Member on the grounds of closer affinities in the associated brachiopod faunas. The cyclocystoid studied here is preserved within an encrinite and is therefore more likely to have come from the Early Silurian Cybèle Member. The only other known cyclocystoids from Anticosti Island were published by Glass et al. (2003) from the Mill Bay Member, Vauréal Formation, Katian, Upper Ordovician, and are therefore significantly older (see Fig. 1d).

The Cybèle member comprises 32 m of grey, sparsely fossiliferous, lithographic limestone deposited on a broad, south-facing carbonate ramp. Fossils are relatively scarce, but dominated by trilobites and highly endemic crinoids (Ausich and Copper 2010). *Perforocycloides nathaliae* came from a medium grey, tempestite limestone, rich in crinoid columnals, bryozoans, and trilobite and brachiopod debris.

The parts of the specimen remaining are well preserved, retaining some 3-dimensionality, but have (probably) lost 1–3 marginal plates, most of the plates of the oral surface, and all plates of the aboral surface. This incomplete preservation and the host rock interpreted as a tempestite suggest short transportation with preservation occurring after rapid burial. This, along with the exsitu collection and lack of any sedimentological way-up structures, means there is no evidence for life position associated with this specimen.

Materials and methods

Specimen MPEP335.7 was recovered from roadside debris at locality MPEL189 (92-015 “Sandtop”), Anticosti Island, Québec, Canada by Nathalie Daoust on August 6, 1992 (see Fig. 1). The specimen shows the dorsal surface, while the ventral surface was buried in the matrix consisting of large detrital shelly fragments within a fine lime-rich mudstone (Fig. 2a). The dorsal surface is well preserved as calcified ossicles with secondary calcite infilling primary stereom (Fig. 2c). There are also some pyritic overgrowths.

To facilitate observation of more parts of this specimen, the matrix from both the exposed oral side and encased adoral side was prepared away (by M. Graham) under a Leica M80 model microscope. This was done using a pin and controlled air abrasion on the oral surface, and by tracing the position of the specimen and the surrounding block of the oral side onto a clear plastic film to act as a guide to the preparation of the aboral side. The oral side was set into a temporary mount made of fast setting two-part dental putty lined with protective plastazote foam. Adherent mud and pyrite was carefully removed using 7.5% CH₃COOH (acetic acid) applied with a pipette and flushed off with pure water after 2–3 min, and gentle abrasion with finely ground

carbide pins. To expose the ventral surface of the marginal plates, the bulk of the overburden was removed by scoring the matrix into cubes with a rotary cutter fitted with a diamond encrusted blade and then prising off the individual cubes of matrix. The final 1 mm depth of remaining matrix was removed by air abrasion using a Texas airsonics unit fitted with a 0.5 mm diameter nozzle. The abrasive powder was aluminium oxide delivered in short blasts at 30 psi. Final preparation was undertaken using 7.5% CH₃COOH and pins.

Repositories and institutional abbreviations. The specimen used in this study, prefixed MPEP, is housed in the Musée de paléontologie et de l'évolution, Montréal, Québec, Canada.

Systematic palaeontology

This publication is registered under ZooBank LSID urn:lsid:zoobank.org:pub:20BC3F65-897D-4CC2-B912-69380712A3AF. Terminology is mostly based on Smith and Paul (1982).

Subphylum **Echinozoa** Haeckel *in* von Zittel, 1895

Class **Cyclocystoidea** Miller and Gurley, 1895

Family **Cyclocystoididae** Miller, 1882

Genus ***Perforocycloides*** Ewin, Reich, Graham, and Cournoyer, nov.

Type and only species. *Perforocycloides nathaliae* gen. et sp. nov.

LSID ZooBank. This new genus is registered under urn:lsid:zoobank.org:act:154FC5CF-D59A-4205-8A1D-9AA9656F3AEB.

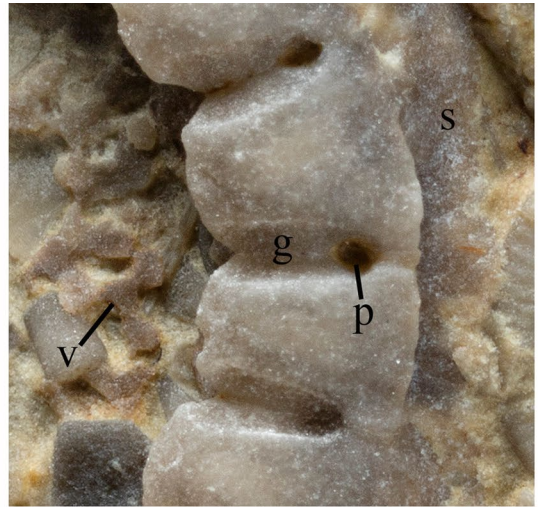
Diagnosis. Test circular, disc 60% of test, marginal ring composed of 17–20 variously sized, frequently paired marginals with larger wedge-shaped and smaller rectangular ossicles. Dorsally, marginals only contiguous at distal tip but otherwise widely separated by broad sutural grooves which link to a circular inter-marginal sutural pore adjacent to contiguous part. Inter-marginal sutural pore leads to a canal which penetrates marginal ring and opens on dorsal surface between cupulate zones on the external edge of adjacent marginals. Ventral marginal surfaces square, smooth, gently curved, and narrowly separated. Probably 2–3 cupules per marginal.

Description. See species description.

Etymology. From Latin *perforare* = perforated, to highlight the distinguishing feature of this genus, the conspicuous



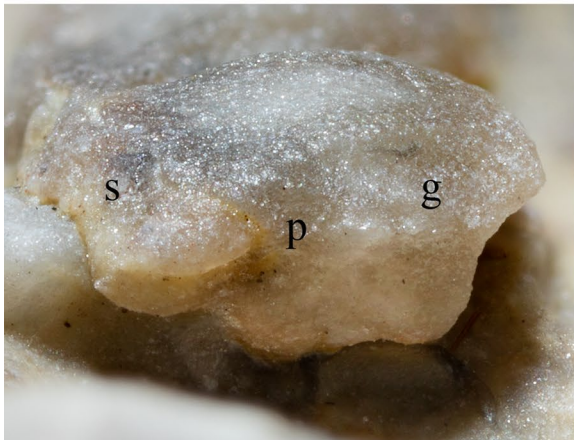
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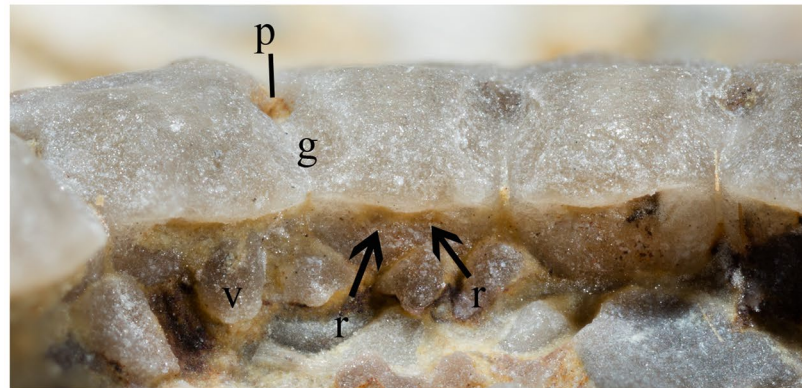
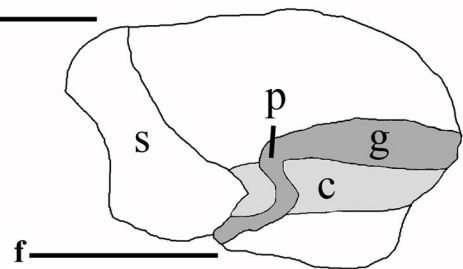
b —



d —



c —



e —



g —

Fig. 2 *Perforocycloides nathalieae* gen. et sp. nov., MPEP335.7. Early Silurian, Upper Llandovery, Jupiter Formation, Cybèle Member. **a** Dorsal view of entire specimen. **b** Detail of dorsal marginal ossicle, distal ventral disc plating and peripheral skirt. **c** Lateral view of marginal ossicle suture. **d** Same view as Fig. 2c, but coated in ammonium chloride sublimate. **e** Proximal surface of marginal ossicles. Note prominent crescentic facet area extended well beyond the ventral crest. Arrows point to radial ducts still filled with sediment. **f** Camera lucida of lateral view of marginal in Fig. 2c, d. Darker grey corresponds to the dorsal sutural groove which leads to a pore and sinusoidal canal that penetrates the contiguous area of the lateral surface (in light grey) and emerges on the distal side of the ventral marginal surface, adjacent to the cupules. **g** Ventral view of marginal ossicles (top of the crest). *c* contiguous area of lateral suture of marginal, *g* groove on distal surface suture between marginal ossicles, *p* intermarginal sutural pore, *r* radial ducts, *s* peripheral skirt, *v* ventral disc plating

dorsal intermarginal sutural pores, and from Greek *κύκλος* (*kýklos*) = circle, in reminiscence of other cyclocystoid genera. Gender masculine.

Age and Occurrence. Early Silurian, Jupiter Formation (Upper Llandovery: Telychian), Cybèle Member, Anticosti Island, Québec, Canada.

Discussion. 17 marginals are preserved; however, the space between the broken ends could be comfortably occupied by three further marginals, thus giving a total of 20 (Fig. 2a). However, it is conceivable that there are just 17 marginals (or < 20), and the broken parts have simply moved apart during fossilization without loss of many/any marginals. It is also possible that there are more than 20 ossicles and that the existing marginal frame has been pushed together. However, we think this is unlikely as there is little suggestion of deformation to the existing curvature of the marginals present to make such a scenario likely. As such, until more complete material is recovered, a broader range of the number of marginal ossicles is provided for in the diagnosis.

Perforocycloides is unusual as it possesses distinct pores situated in the distal suture between marginal ossicles, adjacent to the contiguous (most distal) part of the dorsal marginal surface (Fig. 2b). This leads to a canal that penetrates along the suture and opens adjacent to and between the cupules of separate marginals. These pores and canals are here termed the marginal sutural pores, and are entirely separate structures from the “radial ducts” and the “facet canals” of Smith and Paul (1982: fig. 9d). Marginal sutural pore and canal systems have not been recognized in any other previously described cyclocystoid taxa.

The number and variable morphology of the marginal ossicles, the presence of the marginal sutural pores, and the lack of interseptal plates precludes assignment of this specimen to any previously described cyclocystoid genus. In addition to the previously stated characters, *Perforocycloides* clearly

differs from *Nicholsodiscus* Glass et al. (2003), the only other cyclocystoid described from Anticosti Island, by the smaller number of marginals (20 compared to 24), which are more widely separated proximally, and the relatively larger disk to marginal ratio (60% as opposed to 47% in *Nicholsodiscus*).

Perforocycloides appears to be most similar to *Zygocycloides* Smith and Paul (1982) in the number, morphology, relatively large size in relation to disc ratio, and variability of the marginal ossicles. With so many aspects of *Perforocycloides* coinciding with *Zygocycloides*, intermarginal sutural pores and canals were extensively searched for in members of the latter, working on the hypothesis that these pores may be covered by interseptal plates. However, none were detected. Apart from these pores, *Perforocycloides* differs only in the lack of interseptal plates. While it is conceivable that interseptal plates were lost in *Perforocycloides* during fossilization, it is thought their presence is unlikely as there are no obvious suture lines on the marginals suggesting that they were once there. So, while the two genera are distinct, the many similarities suggest it is not unreasonable to assume some form of relationship.

Nicholsodiscus, was also closely compared with *Zygocycloides* by Glass et al. (2003), suggesting that it differed only in the number of marginals (24 versus 20) and the shape of the interseptal plates (long and thin as opposed to equidimensional). Indeed, there are many similarities in the marginal ossicles between *Zygocycloides*, *Perforocycloides* and *Nicholsodiscus*, which again suggest some sort of relationship between them. If so, *Perforocycloides* is perhaps particularly notable, as it suggests that the *Zygocycloides* lineage diversified up to and through the Ordovician boundary. *Zygocycloides* was originally suggested by Smith and Paul (1982) to have become extinct at the end of the Ordovician; however Reich and Kutscher (2010) reported isolated marginals from the Silurian of Gotland, Sweden (cf. Table 1), thereby demonstrating that its range should be extended.

Perforocycloides nathalieae Ewin, Reich, Graham, and Cournoyer, new species
Figure 2

Material. Holotype MPEP335.7.

LSID ZooBank. This new species is registered under urn:lsid:zoobank.org:act:7D616CEC-7283-4919-AB66-1CC52B7ED03D.

Diagnosis. As for genus.

Age and occurrence. Early Silurian, Upper Llandovery: earliest Telychian, Jupiter Formation, Cybèle Member.

Table 1 Stratigraphic and geographic distribution of Silurian cyclocystoid taxa (genera and species) compiled after Smith and Paul 1982; Frest et al. 1999, 2011; Reich and Kutscher 2006, 2010; Donovan et al. 2008

Genus	Species	Age	Location	Country	Paleocontinent
APYCNODISCUS Smith and Paul, 1982	<i>Apynodiscus insularis</i> (Regnéll, 1945)	Wenlock; ?Sheinwoodian	Gotland	Sweden	Baltica
	<i>Apynodiscus</i> sp. nov. 1 [sensu Reich and Kutscher 2010]	Wenlock; Homerian	Gotland	Sweden	Baltica
	<i>Apynodiscus</i> sp. nov. 2 [sensu Reich and Kutscher 2010]	Wenlock; Homerian	Gotland	Sweden	Baltica
	<i>Apynodiscus</i> sp. indet. [sensu Reich and Kutscher 2010]	Wenlock; Homerian	Gotland	Sweden	Baltica
	<i>Apynodiscus</i> sp. indet. [sensu Reich and Kutscher 2010]	Ludlow; Gorstian	Gotland	Sweden	Baltica
CYCLOCYSTOIDES Salter and Billings, 1858	<i>Cyclocystoides</i> sp. nov. 1 [sensu Reich and Kutscher 2010]	Wenlock; Sheinwoodian	Gotland	Sweden	Baltica
	<i>Diastocystoides</i> (?) sp. [sensu Smith and Paul 1982; Donovan et al. 2008]	Wenlock; Sheinwoodian	Dudley, West Midlands	England, U.K.	Avalonia
PERFOROCYCLOIDES Ewin, Reich, Graham and Cournoyer, this paper	<i>Perforocystoides nathalieae</i> gen. et sp. nov.	Liandover; Telychian	Anticosti Island	Québec, Canada	Laurentia
	POLYTRYPHOCYCLOIDES Smith and Paul, 1982	<i>Polytrypheocystoides davisii</i> (Salter in Salter and Billings, 1858)	Liandover; Rhuddanian	Ayrshire	Scotland, U.K.
<i>Polytrypheocystoides</i> sp. [sensu Frest et al. 1999]		Liandover; Rhuddanian/Aeronian	Cass Township	Iowa, U.S.A.	Laurentia
<i>Polytrypheocystoides davisii</i> (Salter in Salter and Billings, 1858)		Liandover; Telychian	May Hill Inlier, Gloucestershire	England, U.K.	Avalonia
<i>Polytrypheocystoides</i> sp. [sensu Frest et al. 1999]		Wenlock; Sheinwoodian	Adams (Decatur Co.), St. Paul	Indiana, U.S.A.	Laurentia
<i>Polytrypheocystoides lindstroemi</i> (Regnéll, 1945)		Wenlock; Sheinwoodian	Gotland	Sweden	Baltica
<i>Polytrypheocystoides cf. lindstroemi</i> (Regnéll, 1945)		Wenlock; Homerian	Gotland	Sweden	Baltica
<i>Polytrypheocystoides cf. lindstroemi</i> (Regnéll, 1945)		Ludlow; Gorstian	Gotland	Sweden	Baltica
<i>Sievertsia</i> sp. [sensu Frest et al. 1999]		Liandover; Rhuddanian/Aeronian	Cass Township	Iowa, U.S.A.	Laurentia
<i>Sievertsia</i> sp. [sensu Frest et al. 1999]		Liandover; Rhuddanian/(Aeronian)	Mount Summer	Illinois, U.S.A.	Laurentia
<i>Sievertsia</i> sp. nov. [sensu Frest et al. 1999]		Liandover; (Aeronian)/Telychian	St. Paul	Indiana, U.S.A.	Laurentia
SIEVERTSIA Smith and Paul, 1982	<i>Sievertsia</i> sp. [sensu Frest et al. 1999, 2011]	Wenlock; Sheinwoodian	Napoleon	Indiana, U.S.A.	Laurentia
	<i>Sievertsia</i> sp. [sensu Frest et al. 1999]	Wenlock; Sheinwoodian	Adams (Decatur Co.), Waldron	Indiana, U.S.A.	Laurentia
	<i>Sievertsia</i> sp. [sensu Frest et al. 1999]	Wenlock; Sheinwoodian	Newsom's Station	Tennessee, U.S.A.	Laurentia
	<i>Sievertsia</i> sp. nov. [sensu Frest et al. 1999]	Wenlock; Sheinwoodian	Clifton, Iron City, Riverside	Tennessee, U.S.A.	Laurentia
	<i>Sievertsia</i> n. sp. [sensu Frest et al. 1999]	Wenlock; Sheinwoodian	McC(J)ory Lane/Nashville	Tennessee, U.S.A.	Laurentia
	<i>Sievertsia</i> n. sp. [sensu Frest et al. 1999]	Ludlow/Pfidiol	McC(J)ory Lane/Nashville	Tennessee, U.S.A.	Laurentia
	<i>Sievertsia</i> sp. indet. [sensu Reich and Kutscher 2010]	Wenlock; Sheinwoodian	Gotland	Sweden	Baltica
	<i>Sievertsia</i> sp. [sensu Frest et al. 1999]	Wenlock; Sheinwoodian	St. Paul	Indiana, U.S.A.	Laurentia
	<i>Sievertsia</i> sp. indet. [sensu Reich and Kutscher 2010]	Wenlock; Homerian	Gotland	Sweden	Baltica
	<i>Sievertsia</i> sp. indet. [sensu Reich and Kutscher 2010]	Ludlow; Gorstian	Gotland	Sweden	Baltica
	<i>Sievertsia</i> sp. nov. 1 [sensu Reich and Kutscher 2010]	Ludlow; Gorstian	Gotland	Sweden	Baltica
	<i>Sievertsia</i> sp. nov. 2 [sensu Reich and Kutscher 2010]	Ludlow; Ludfordian	Gotland	Sweden	Baltica
<i>Sievertsia</i> sp. nov. 1 [sensu Reich and Kutscher 2010]	Ludlow; Ludfordian	Gotland	Sweden	Baltica	
<i>Sievertsia</i> sp. nov. 2 [sensu Reich and Kutscher 2010]	Ludlow; Ludfordian	Gotland	Sweden	Baltica	
<i>Sievertsia</i> cf. sp. nov. 2 [sensu Reich and Kutscher 2010]	Ludlow; Ludfordian	Gotland	Sweden	Baltica	
<i>Sievertsia</i> n. sp. [sensu Frest et al. 1999]	(Ludlow)/Pfidol	White Mound (Murray Co.)	Oklahoma, U.S.A.	Laurentia	
ZYGOCYCLOIDES Smith and Paul, 1982	<i>Zygocystoides</i> sp. nov. 1 [sensu Reich and Kutscher 2010]	Wenlock; Sheinwoodian	Gotland	Sweden	Baltica
	<i>Zygocystoides</i> ? sp. [sensu Reich and Kutscher 2010]	Wenlock; Homerian	Gotland	Sweden	Baltica
NEW GENUS	gen. et sp. nov. [sensu Reich and Kutscher 2010]	Ludlow; Gorstian	Gotland	Sweden	Baltica
UNKNOWN GENUS	gen. et sp. indet. [sensu Smith and Paul 1982]	Liandover; Telychian	near Coalbrookdale, Shropshire	England, U.K.	Avalonia
	gen. et spp. indet./nov. [sensu Frest and Paul 1971; Smith and Paul 1982]	Wenlock; Sheinwoodian	Sandusky	Indiana, U.S.A.	Laurentia

Description. Circular outline, 13 mm total diameter, composed of a few distal parts of the ventral disc plating, 17 prominent marginals, trapezoidal in dorsal view, organised into alternating groups of large and small plates, and a multiplied, marginal skirt.

Disc—60% of total size, plates poorly preserved, revealing only a small number of weathered and loosely articulated proximal plates. Radial/interradial plates indistinguishable. Those plates preserved resemble imbricated branching rods forming a reticulate lattice interspersed with fairly wide sutural pore spaces (Fig. 2b). Radial/interradial plates drape over the proximal face of the marginals, suggesting that they were attached below the radial ducts (Fig. 2e) in a manner consistent with the interpretations of Smith and Paul (1982).

Annular plates—Lost but crescentic sutures on the proximal dorsal surface of the marginals suggest at least 2 or 3 per marginal (Fig. 2b, d).

Marginal ossicles—Fairly large and robust. Cupules obscured by fairly large frontal plates (Fig. 2g), but probably numbered 2 on small ossicles and perhaps 3 on larger ones (as suggested by the number of crescentic facets). The presence of intervening walls and tubercles in *Perforocycloides* is not currently known, as it was not possible to effectively clear the cupules of matrix during preparation. However, as they are seen in all representatives of the suspected closely related genus *Zygocycloides*, we suggest they are likely to be present.

Dorsal surface widely exposed, showing alternating sets of large and small wedge-shaped/trapezoidal to rectangular marginal ossicles with gently curved, smooth surfaces, and greatly extended, broad, slightly rounded, annular facet (crescentic facet) zone (Fig. 2a). Crescentic facets poorly preserved but suggesting at least 2–3 per marginal (Fig. 2b, e). Dorsal surfaces of adjacent marginals widely spaced proximally by a prominent, smooth sided, concaved trough which extends most of the length of the marginals and terminates in a deep circular pore (the dorsal intermarginal sutural pore) adjacent to where the dorsal surfaces become contiguous distally (Fig. 2b). Contiguous area of the dorsal marginal surface is fairly short and comprises about 20% of total length (3 mm of a total 15 mm).

Lateral surfaces of marginals show that the dorsal intermarginal sutural pore forms the opening to a canal (the intermarginal sutural canal), which penetrates the contiguous area a short distance, before bending through 90° and then emerging between the margins of cupules of adjacent marginals (which are presumably walled) (Fig. 2c, d, f). Contiguous area of the lateral surface of the marginals is fairly small and smooth, gently tapering from the mid-point ventrally and lacking any obvious ridges or striations.

Ventral marginal ossicle morphology displays a smooth, low, slightly domed crest, square in outline (when viewed

ventrally), and which is only narrowly separated from neighbours (Fig. 2g).

Proximal marginal surface is mostly formed by an inclined wall perforated by at least two radial ducts (Fig. 2e). However, this surface is dominated dorsally by the proximally extended area of the crescentic sutures. Preservation is insufficient to reveal any other pores/ducts on this surface with confidence.

Peripheral skirt—Broad and robust, composed of numerous small polygonal plates. Although preservation prevents identification of the shape or arrangement of individual ossicles, including if they are or are not imbricate. Frontal plates not clearly seen in the only available specimen but appear to be fairly large, as the cupulate zone is obscured by an apparent plate when viewed ventrally and laterally.

Etymology. Named in honour of Nathalie Daoust who originally found the specimen studied here, and in recognition of her support of the Musée de paléontologie et de l'évolution (Montréal, Canada).

Discussion. While the up-direction of the specimen is unknown, the loss of various organs mainly follows the general sequence outlined for cyclocystoids by Smith and Paul (1982: 604). Annular and cover plates are completely lost, along with most of the proximal radial/interradial plates. However, it differs in that much of the peripheral skirt remains entire and articulated, despite some of the marginal ossicles most likely being lost or, at least, the marginal ring being broken. This suggests the peripheral skirt was unusually robust or flexible.

The narrowing of the contiguous zone between adjacent marginals of both the dorsal and ventral surfaces was suggested by Smith and Paul (1982) to facilitate flexibility of the marginal frame to assist with movement. However, the broad, smooth walled, channel-like appearance of the groove between adjacent marginals on the dorsal surface, which terminate in a pore and canal system, suggests that they facilitated communication of some kind between the proximal dorsal and distal ventral surfaces through the marginal ring, rather than simply allowing a wider range of movement (see Fig. 2a–d, f). In the imperfectly preserved material available to us, the canal appears to maintain the same diameter along its entire length and does not greatly constrict, as occurs in the radial ducts, although the groove between adjacent marginals on the dorsal surface appears to increase in size proximally (towards the disk).

However, as with so much of cyclocystoid functional morphology, we are at a loss to explain with any certainty what the function of such a canal system is. If these cyclocystoids were vagile benthic feeders, then this system might have served to remove unwanted processed particles from the cupule margins, ejecting it dorsally without the need to

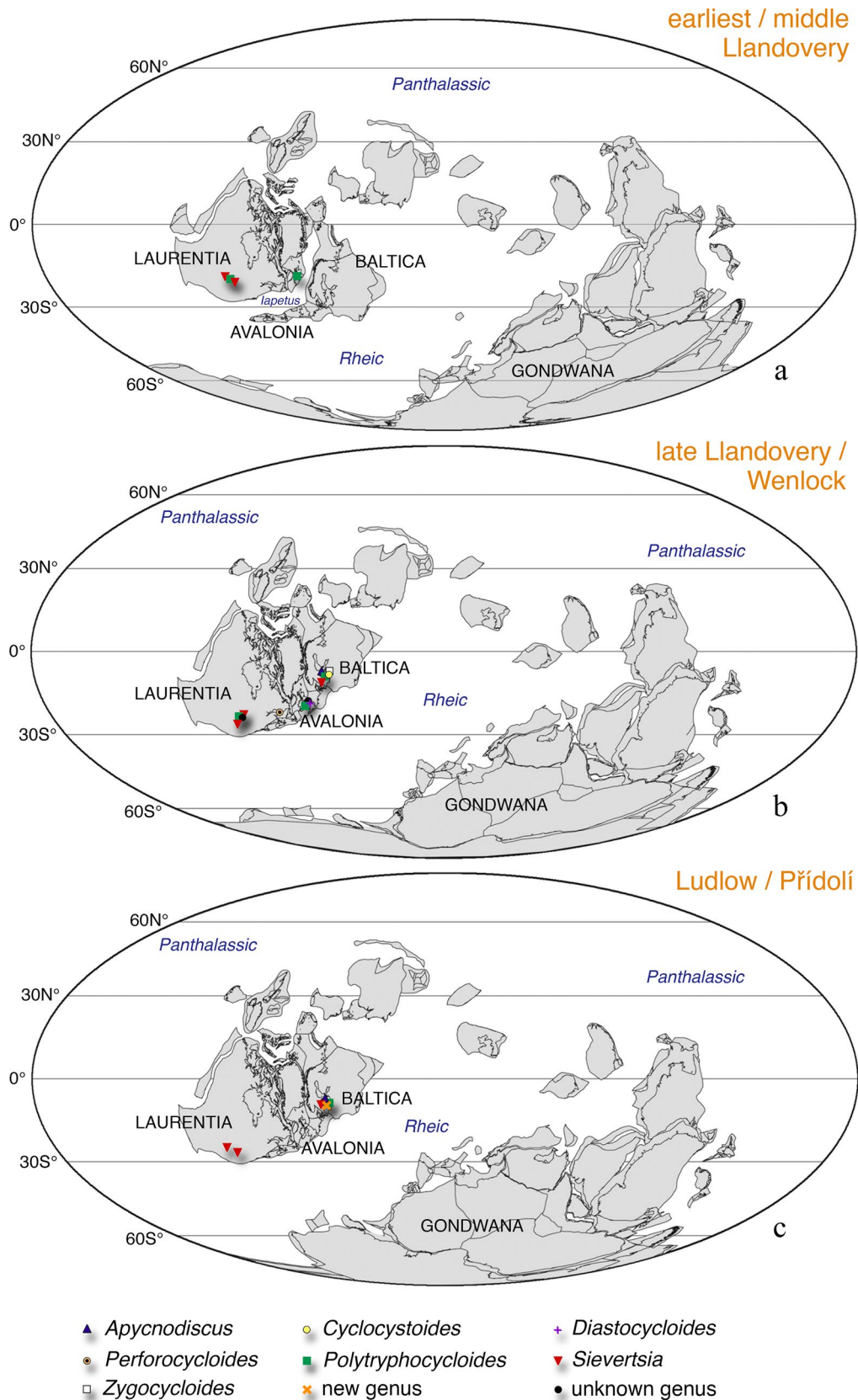


Fig. 3 Distribution of the major palaeocontinents and terranes during the **a** earliest Silurian (Llandovery: Rhuddanian + Aeronian), **b** late Early/Middle Silurian (Llandovery: Telychian + Wenlock), and **c** Late

Silurian (Ludlow + Přídolí), showing the geographical distribution of the known Silurian cyclocystoid genera (cf. also Table 1) (palaeogeography from Torsvik and Cocks 2013 modified)

open the marginal skirt. If, however, the animal was sessile or hemisessile with the annular plates facing the substrate, then the grooves would have formed tubes (floored by the substrate) and facilitated communication from the disk through to the distal side of the marginals to the cupules, and thereby the water column, if the peripheral skirt and frontal plates were open. Being so numerous, maybe these intermarginal sutural canal/pore/groove systems were related to gamete dispersal. More material is really needed to explore these possibilities further. Any account also needs to take into consideration that such pores and canals are not currently observed in any other cyclocystoid.

The only other cyclocystoid genus with a broad dorsal separation of the marginals, and which could have potentially facilitated communication from the proximal dorsal surface of the disk through to the distal side of the marginals, is the Late Ordovician taxon *Diastocycloides* Smith and Paul (1982). The large separation opens distally between the cupules of adjacent marginals in an identical position as proposed for the canals of *Perforocycloides*. However, the passage formed by this broad separation differs in that it does not penetrate the medial contiguous zone of the marginal lateral surface. While this separation may have facilitated communication, there are no specialised structures suggesting it acted in this manner, unlike in *Perforocycloides*. As such, it appears more likely to have facilitated a broader range of movement of the marginal frame.

Silurian cyclocystoids—diversification and their palaeogeographical distribution

The worldwide fossil record of Silurian cyclocystoids is sparse (Table 1; Fig. 3). Articulated Silurian cyclocystoid specimens have only been recorded from Scotland, England (Smith and Paul 1982; Donovan et al. 2008—*Polytryphocycloides*, *Diastocycloides*?), Sweden (Lindström 1885, 1888; Regnéll 1945; Smith and Paul 1982—*Apynodiscus*, *Polytryphocycloides*), and now Anticosti Island. Isolated Silurian cyclocystoid material broadens their palaeogeographical distribution and currently, the most diverse material has been reported from Gotland/Sweden, which includes representatives of *Apynodiscus*, *Cyclocystoides*, *Polytryphocycloides*, *Sievertsia*, *Zygocycloides* and a new genus (Franzén 1979; Reich and Kutscher 2006, 2010). Disarticulated Silurian material has also been recorded from Illinois, Indiana, Iowa, Oklahoma, and Tennessee, USA (Frest and Paul 1971: 425; Smith and Paul 1982: 677; Frest et al. 1999: 670, 671, 672, 679, 711, 714, 715, 717, 718, 724, 728, 734, 738, 742, 743, tables 45.12, 45.35, 45.36, 45.37, 45.38, 45.39, 45.41, 45.43, 45.46, 45.49, 2011: table 6; Frest 2005: 301, 302; Thomka 2015: 357), and England (Smith and Paul 1982: 677), with taxa of *Polytryphocycloides*, *Sievertsia*, and gen. indet.

mentioned or listed. Unfortunately, these numerous disarticulated cyclocystoid occurrences were neither illustrated nor described, so it is impossible to compare them with published material.

Additional unpublished articulated specimens, predominantly from Gotland, (> 12 taxa) and housed in private collections, further suggest greater diversity in Silurian strata than currently known (Reich pers. observ.). However, there are still regions known to contain rich Silurian echinoderm faunas but which have been poorly investigated with regards to cyclocystoids, for example Africa, Australia, and China (Reich pers. observ.). With greater knowledge of these areas, palaeogeographical analysis will become more refined. The early taxa described by Salter and Billings (1858) as being “Silurian” in age are now regarded as Ordovician (Smith and Paul 1982).

The present Silurian cyclocystoid data (Table 1) suggest that different regions were characterised by certain taxa, with Baltica, Avalonia and Laurentia each containing different genera (Fig. 3a–c), allowing some tentative palaeobiogeographical information. While the Llandovery epoch is almost as long as all the other Silurian epochs combined, the published data for cyclocystoid sites from this time interval are limited to Avalonia and Laurentia only (Table 1). The following Wenlock epoch suggests cyclocystoids were situated on Avalonia, Baltica and Laurentia, with highest diversity during the Sheinwoodian age (Table 1; Fig. 3b). In contrast, younger Silurian cyclocystoids are known from only Baltica and Laurentia (Table 1; Fig. 3c), and all are assigned to the Ludlovian epoch. No Cyclocystoidea fossils have yet been described from strata confidently assigned to Přídolí strata anywhere. Only a single preliminary report of disarticulated ossicles from sedimentary rocks, only identified as Ludlow/Přídolí age from Laurentia (Oklahoma and Tennessee), is known (Frest et al. 1999).

Based on current published data, it appears that Baltica was a hot spot for cyclocystoid diversification during much of Silurian times. However, because of limited knowledge and missing information from Gondwana (e.g. Africa, Australia, South America), Siberia, North- and South China as well as Laurentia, the discussion on biogeographical patterns remains speculative.

Timing of the origin of cyclocystoids

The origin of cyclocystoids are poorly understood. The putative earliest member of the Cyclocystoidea consists of isolated marginals from the early Middle Ordovician of the western US (Whiterockian/Dapingian; Frest pers. comm. in Smith and Paul 1982), but which are still undescribed. Slightly younger cyclocystoid material from the early Darriwilian (Volkhov regional stage, Langevoja regional

substage) was reported from Baltica and includes: (1) *Cyclocystoides* from Estonia (Männil 1983, 1987); and (2) *Monocycloides* from Öland, Sweden (Berg-Madsen 1987). However, both these records are again based on isolated material. The first articulated specimens (*Moroccodiscus*) were recently described from the early late Darriwilian of Gondwana (Reich et al. 2017).

Thus, all three stratigraphically oldest records of cyclocystoids have been reported from three different palaeocontinents. However, the timing of this origin seems to be related to that of other significant (eleutherozoan) echinoderm groups (e.g. echinoids, and sea cucumbers) as part of a major Ordovician diversification event (Sprinkle and Guensburg 2004; Lefebvre et al. 2013). Distributions of Ordovician cyclocystoid taxa are clearly affected by a lack of knowledge of examples from outside Europe and North America (e.g. Reich et al. 2017: fig. 11). Undoubtedly patterns of cyclocystoid specific distribution and diversification do occur in Ordovician/Silurian times and will be further described and refined in the future.

Conclusion

A new genus and species of cyclocystoid from the Silurian of Anticosti Island is the first report of an articulated Silurian example in North America. It has affinities to *Zygo-cycloides* and *Nicholsodiscus*, suggesting the zygocycloid lineage may have diversified up to and through the end Ordovician boundary.

The defining feature of the new genus is the apparently unique possession of intermarginal sutural pores and canals that penetrated the contiguous parts of the lateral surface of the marginals. However, beyond communication between the distal dorsal surface of the disk and the distal side of the ventral marginal ossicles/cupules, their function is not clear, partly because the life orientation of cyclocystoids is still debatable.

Based on current evidence, Silurian cyclocystoids are known from only Laurentia, Avalonia, and Baltica, with the latter appearing to be a hotspot of diversity. However, this may be the result of limited study in other areas.

The three earliest occurrences of cyclocystoids are reported from the Dapingian/Darriwilian on three different palaeocontinents. This coincides with an Ordovician bio-diversification event which also saw the first occurrence of echinoids and holothurians.

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