*Journal of Paleontology*, 97(2), 2023, p. 380–385

0022-3360/23/1937-2337
doi: 10.1017/jpa.2022.95

JOURNAL OF PALEONTOLOGY A PUBLICATION OF THE Paleontological SOCIETY

# Recovery of Laurentian cyclocystoids following Late Ordovician extinctions (Brassfield Formation, Llandovery; southwestern Ohio)

William I. Ausich[1]* and Nikki E. Zehler[2]

[1]School of Earth Sciences, 155 South Oval Mall, The Ohio State University, Columbus, Ohio 43210, USA <ausich.1@osu.edu>
[2]3018 Beaver Avenue, Cincinnati, Ohio 45213, USA <nzehler@gmail.com>

**Abstract.**—*Zygocycloides*? *foerstei* n. sp. is described from the Llandovery (Aeronian) Brassfield Formation of southwestern Ohio. This is among the oldest reported Silurian cyclocystoids from North America and is the only North American Llandovery cyclocystoid that is preserved with a complete rim of marginal ossicles. *Zygocycloides* Smith and Paul, 1982 is most similar to *Nicholsodiscus* Glass et al., 2003 (Katian) and *Perforocycloides* Ewin et al., 2019 (Llandovery, Telychian), both from Anticosti Island, Québec. Cyclocystoids (Ordovician to Mississippian) survived Late Ordovician extinctions, and this discovery documents that this echinoderm clade was part of shallow-water, marine paleocommunities during the initial post-extinction transgression onto the Laurentian platform.

UUID: http://zoobank.org/3d3e092e-267b-4841-9245-6275d1eb79a1

## Introduction

Cyclocystoids (phylum Echinodermata, subphylum Echinozoa) are one of the most enigmatic clades of Paleozoic echinoderms. Despite an Ordovician–Mississippian range, cyclocystoids are extremely rare echinoderms (e.g., Smith and Paul, 1982; Ewin et al., 2019), and their paleoecology has been debated regularly (e.g., Nichols, 1969; Smith and Paul, 1982; Glass et al., 2003; Sprinkle et al., 2015; Reich et al., 2017; Ewin et al., 2019). Much of their stratigraphic range is known from only isolated marginal ossicles. Ordovician specimens with complete rings of marginal ossicles are well documented from Avalonia, Baltica, and Laurentia (Smith and Paul, 1982), and this record has recently expanded both temporally and geographically (e.g., Reich et al., 2017; Ewin et al., 2019).

The cyclocystoid clade was clearly devastated by Late Ordovician extinctions (Smith and Paul, 1982, fig. 14), but relatively little is known about their recovery during the Llandovery. Although reports of Llandovery isolated marginal ossicles exist (Frest et al., 1999; Hints et al., 2022), only two Llandovery cyclocystoids with a complete ring of marginal ossicles have been described previously, including *Polytryphocycloides davisii* (Salter in Salter and Billings, 1858) from the Mulloch Hill Sandstone in Scotland (Smith and Paul, 1982) (upper Rhuddanian; Donovan et al., 2012, p. 155) and *Perforocycloides nathalieae* Ewin et al., 2019 from the Cybele Member, Jupiter Formation (Telychian) of Anticosti Island, Québec. In this report, a third cyclocystoid with a complete ring of marginal ossicles, *Zygocycloides*? *foerstei* n. sp., is reported from the Brassfield Formation (Aeronian) from Ohio. This new specimen is quite small and has a marginal ring with 15 ossicles and a few collapsed dorsal disc ossicles. This occurrence establishes the presence of cyclocystoids in Laurentian benthic faunas during the first major Silurian flooding of the North American continental interior after Late Ordovician extinctions. It also suggests promise for future discovery of Late Ordovician and early Silurian cyclocystoids in North America.

## Location and stratigraphy

*Zygocycloides*? *foerstei* n. sp. is from Oakes Quarry Park, ∼2 km (∼1.8 miles) east of Fairborn, Greene County, Ohio (39°48′53″N, 84°59′06″W) north of Ohio Highway 235 (Fig. 1). It was collected in float from the Brassfield Formation (upper or red Brassfield of Sullivan et al., 2016; Kleffner, 2020), which is Aeronian (Llandovery, Silurian) in age. The red Brassfield is within the *Pranognathus tenuis* Zone, which is middle Aeronian (M.A. Kleffner, personal communication, 2022).

The Brassfield Formation in Oakes Park Quarry contained a small, coral–stromatoporoid reef and reef-associated facies (Sheehy, 1979; Schneider and Ausich, 2002; Schmidt et al., 2007). Quarrying since the 1990s removed the core and flank beds of the primary Oakes Park Quarry reef. Today, the remaining Brassfield at this site has one poorly exposed reef northeast of the northern quarry face (Schneider and Ausich, 2002). Within the quarry, the exposed rocks are primarily encrinites with thin siliciclastic mudstone beds. The new cyclocystoid is preserved on the bedding surface of an encrinite bed. In addition to the echinoderms noted in the following (Table 1), the Brassfield Formation contains a diverse fauna that is largely

*Corresponding author.

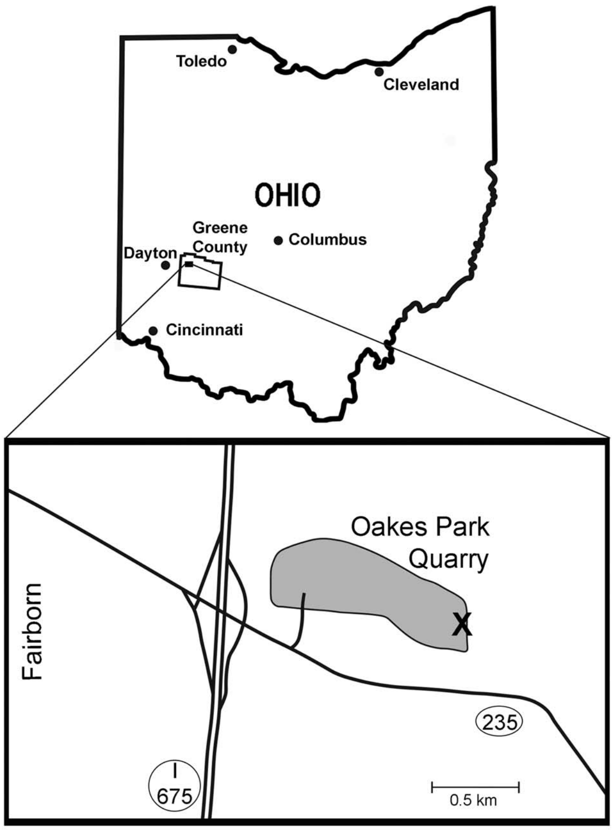


**Figure 1.** Locality map of the Oakes Quarry Park in Greene County, Ohio. "X" marks the approximate position where the holotype of *Zygocycloides*? *foerstei* n. sp. was collected.

**Table 1.** Brassfield Formation (Aeronian) echinoderms from Greene and Clark counties, Ohio.

| |
|---|
| ASTEROIDS |
| *Mesopalaeaster* (*Hemipalaeasater*) *schucherti* Foerste, 1919 |
| *Schuchertina magma* Foerste, 1919 |
| CYCLOCYSTOIDS |
| *Zygocycloides*? *foerstei* n. sp. |
| GLYPTOCYSTIDS |
| *Antartiocystis foerstei* Ausich and Shumacher, 1984 |
| *Brockocystis nodosaria* Foerste, 1919 |
| CRINOIDS |
| Diplobathrids |
| *Kyreocrinus constellatus* Ausich, 1986 (Ausich, 1986c) |
| *Rhachicrinus wrighti* Ausich, 1986 (Ausich, 1986c) |
| *Silfonocrinus siluricus* Ausich, 1986 (Ausich, 1986c) |
| *Stereoaster squamosus* Foreste, 1919 |
| *Turbocrinus punctum* Ausich, 1986 (Ausich, 1986c) |
| *Xysmacrinus greenensis* Ausich, 1986 (Ausich, 1986c) |
| Monobathrids |
| *Acacocrinus anebos* Ausich, 1987 |
| *Bikocrinus baios* Ausich, 1985 |
| *Clematocrinus ohioensis* Ausich, 1986 (Ausich, 1986b) |
| *Ibanocrinus petalos* Ausich, 1987 |
| *Manticrinus exaitos* Ausich, 1986 (Ausich, 1986b) |
| *Paiderocrinus asketos* Ausich, 1985 |
| *Paiderocrinus ochthos* Ausich, 1985 |
| *Patelliocrinus planus* Ausich, 1986 (Ausich, 1986b) |
| periechocrinid incertae sedis Ausich, 1987 |
| *Phrygilocrinus batheri* Ausich, 1985 |
| *Tirocrinus trochos* Ausich, 1987 |
| *Typannocrinus strombos* Ausich, 1985 |
| *Zirocrinus litos* Ausich, 1985 |
| Disparids |
| *Calceocrinus incertus* Foerste, 1936 |
| *Eomyelodactylus rotundatus* Foerste, 1919 |
| ?*Myelodactylus* sp. (Ausich, 1986b) |
| pisocrinid, genus and species undetermined (Ausich, 1986b) |
| *Stibarocrinus centervillensis* (Foerste, 1936) |
| *Trypherocrinus brassfieldensis* Ausich, 1984 (Ausich, 1984a) |
| Eucladids |
| *Dendrocrinus daytonensis* Ausich, 1986 (Ausich, 1986a) |
| dendrocrinid, gen. and sp. undetermined Ausich, 1986a |
| *Eoparisocrinus siluricus* Ausich, 1986 (Ausich, 1986a) |
| *Euspirocrinus heliktos* Ausich, 1986 (Ausich, 1986a) |
| ?*Euspirocrinus* sp. (Ausich, 1986a) |
| *Kanabinocrinus thyaros* Ausich, 1986 (Ausich, 1986a) |
| Flexibles |
| *Clidochirus americanus* Springer, 1920 |
| *Clidochirus springeri* Ausich, 1984 (Ausich, 1984b) |
| *Clidochirus ulrichi* Foerste, 1919 |

unstudied, including, among others, corals, stromatoporoids, brachiopods, and bryozoans.

## Llandovery echinoderm faunas

August Foerste (1884, 1919, 1936) described the first echinoderm fossils from the Brassfield Formation of Ohio, which then included one glyptocystoid, five crinoids, and three asteroids (one of which was subsequently recognized as a crinoid holdfast) (Foerste, 1919, 1936; Ausich, 1986a) (Table 1). During the late 1970s, an exceedingly rich echinoderm fauna in reef-associated facies was discovered in what is now the Oakes Quarry Park near Fairborn, Ohio. Ausich and Schumacher (1984) and Ausich (1984a, b, 1985, 1986a, b, c, 1987) described one new glyptocystoid and 31 crinoids (Table 1). This is the locality where the new cyclocystoid was collected, and with this new cyclocystoid, 33 echinoderm species assigned to four subclasses are known from the Brassfield Formation in Greene and Clark counties, Ohio. In addition, Broadhead and Ettensohn (1981), Ausich and Dravage (1988), Blake and Ettensohn (2009), Boyarko and Ausich (2009), and Ausich et al. (2015) described additional crinoids and asteroids from the Brassfield Formation elsewhere in Ohio and Kentucky. Oakes Quarry Park has one of the richest Llandovery echinoderm faunas known, with other important faunas (with 10 or more taxa) from the Cabot Head Formation (Rhuddanian), New York and Ontario (Brett, 1978; Eckert 1984); Farmer's Creek Member, Hopkinton Formation (Aeronian), Iowa (Witzke and Strimple, 1981); Leijiatum Formation (Aeronian), China (Mao et al., 2017); Chicotte Formation, Cybele Member of the Jupiter Formation, and Ferrum Member of the Jupiter Formation (Telychian), Québec (Ausich and Copper, 2010; Ausich and Cournoyer, 2019); Osgood Formation (Telychian to Wenlock), Indiana (Frest et al., 1999); the Welton Member of the Scotch Grove Formation (Telychian–Wenlock), Iowa; Wolcott Limestone (Telychian), New York (Eckert and Brett, 2001); and the lower Visby Formation (Telychian), Sweden (Angelin, 1878). Of these diverse Llandovery echinoderm faunas, only the Cybele Member of the Jupiter Formation and now the Brassfield Formation have reported cyclocystoids with complete marginal rings. Other Llandovery occurrences with only isolated marginal ossicles have been reported, including those from the Blanding Formation, Iowa (lower Aeronian), the Brassfield Formation in Indiana (Aeronian) (see Frest et al., 1999), and the Telychian of eastern Estonia (Saaremaa) (Hints et al., 2022).

https://doi.org/10.1017/jpa.2022.95 Published online by Cambridge University Press

## Methods

Minimal preparation was possible due to the fragility of the specimen. Photographs were taken with an Apple iPhone SE attached to the eye piece of a Wild stereomicroscope. The new cyclocystoid specimen is preserved on a bedding surface of crinoidal grainstone, so there is no density contrast between the lower surface of the specimen and the matrix. Thus, implementation of X-ray computerized tomography (CT) scanning techniques would not reveal any morphological detail of the aboral surface of USNM PAL 777895.

*Repositories and institutional abbreviations.*—The holotype of *Z.*? *foerstei* n. sp. is deposited in the Springer Room, Smithsonian National Museum of Natural History (USNM PAL).

## Systematic paleontology

Classification and terminology follow Smith and Paul (1982). All measurements are in millimeters.

Class Cyclocystoidea Miller and Gurley, 1895
Family Cyclocystoididae Miller, 1882
Genus Zygocycloides Smith and Paul, 1982

*Type species.*—*Zygocycloides variabilis* Smith and Paul, 1982.

*Included species.*—*Z. magnus* (Miller and Dyer, 1878); *Z. marstoni* (Smith and Paul, 1982); *Z. variabilis* Smith and Paul, 1982; and *Z?. foerstei* n. sp.

*Occurrence.*—Ordovician (Sandbian) to Silurian (Wenlock). North America, Scotland, England, Sweden (Smith and Paul, 1982; Reich and Kutscher, 2010).

*Remarks.*—This single, partial cyclocystoid Brassfield specimen with a complete rim of marginal ossicles is a challenge to interpret (Figs. 2, 3). Is the preserved morphology that of an adult; and what, if any, details, including plate sculpturing, have been erased as a result of weathering? The total diameter of this specimen is 6.3 mm. The relatively large marginal rim of ossicles results in a radius of 1.8 mm for the central disc. Thus, the central disc is only ∼23.9% of the area of the specimen, which is substantially smaller than any previously described taxon. The percentage of the disc area for *Nicholsodiscus* Glass et al., 2003 is ∼47%, and other genera are 60% or more (Glass et al., 2003). Similarly, this Brassfield cyclocystoid has 15 marginal ossicles. *Perforocycloides* Ewin et al., 2019 has 17–20, and *Zygocycloides* Smith and Paul, 1982 has 18–20. All other cyclocystoids have more, with *Polytryphocycloides* having as many as 60 marginal ossicles. The ontogenetic stage of this new specimen remains a question. Regardless, this specimen needs to be interpreted.

*Perforocycloides* is distinguished from all other cyclocystoid genera by the presence of pores between marginal ossicles, and *Zygocycloides* is distinguished by the presence of interseptal ossicles on the dorsal surface. Pores between marginal ossicles are absent in the new Brassfield specimen, but interseptal ossicles are interpreted to be present. The depth of the sutural grooves between adjacent marginal ossicles is present from nearly the distal margin to the proximal margin of these ossicles. However, in a few examples, the distal margin is filled with calcite. This is not a filling of debris and has the surface texture of the remainder of the marginal plate. Indistinct plate sutures and a few plate edges of these presumed interseptal ossicles are visible but very small. The size and preservation make positive identification of these ossicles difficult to verify.

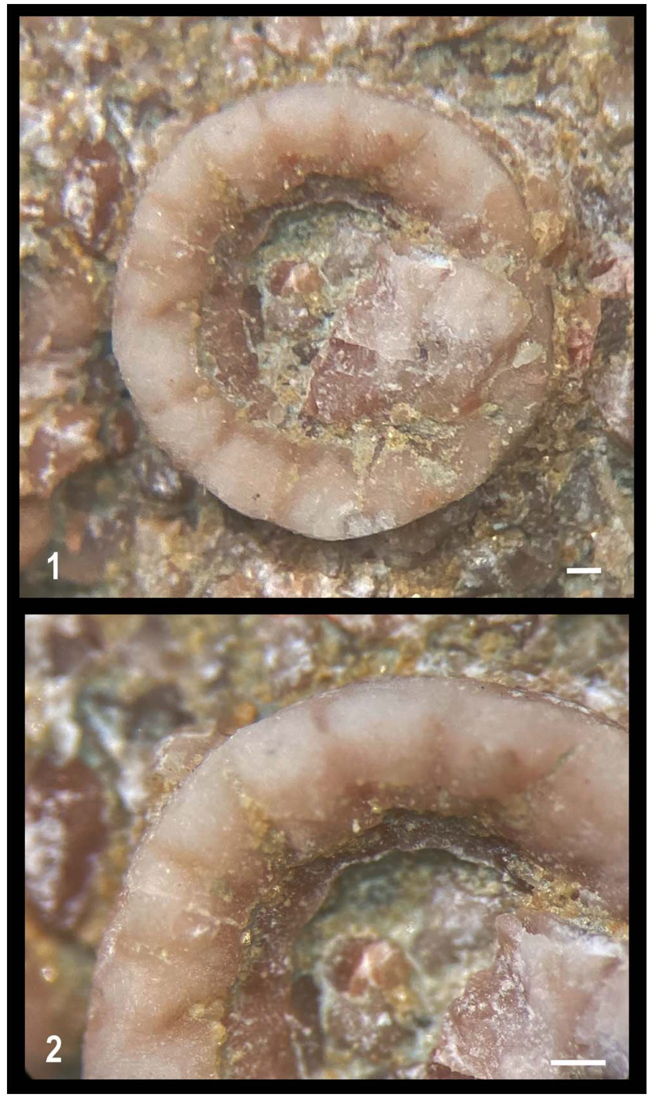

**Figure 2.** *Zygocycloides*? *foerstei* n. sp., holotype, USNM PAL 777895. (**1**) Entire specimen. (**2**) Enlargement of marginal ring ossicles; note that the sutures between ossicles are obscured by calcite interpreted to be interseptal ossicles. Scale bars = 0.5 mm.

Due to the relatively small number of marginal ossicles and the likelihood that interseptal ossicles are present, this cyclocystoid is assigned to *Zygocycloides*? Furthermore, as will be discussed, it is very different from other described species of *Zygocycloides*, and it is considered the new species *Z.*? *foerstei.*

Named species of *Zygocycloides* range in age from Sandbian to Wenlock. *Zygocycloides magnus* is reported from Katian

https://doi.org/10.1017/jpa.2022.95 Published online by Cambridge University Press

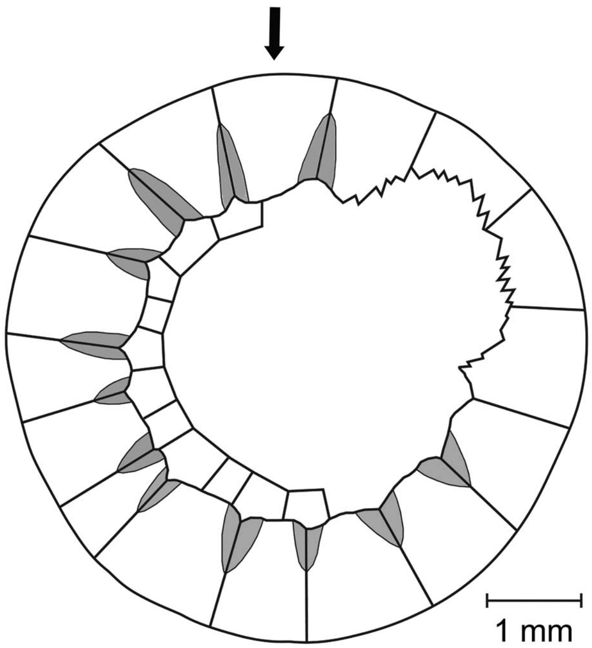


**Figure 3.** Camera lucida drawing of *Zygocycloides*? *foerstei* n. sp., holotype, USNM PAL 777895; compare with Figure 2.1. Shaded areas are depressions along plate sutures of adjoining marginal ossicles; arrow above the specimen designates the beginning of measured marginal ossicles in Figure 4. Scale bar = 1.0 mm.

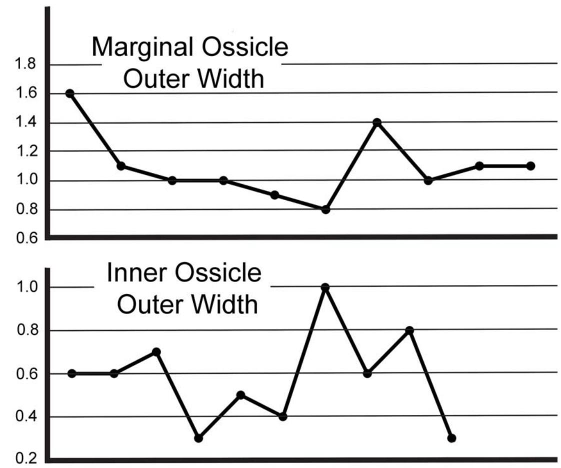


**Figure 4.** Outer and inner widths of marginal ossicles around the ring of marginal ossicles (holotype, USNM PAL 777895). The arrow above the specimen in Figure 3 is the first (left) ossicle for which measurements are recorded; subsequent measurements are for marginal ossicles in a clockwise direction from the marginal ossicle indicated by an arrow.

strata in the Fairmont and Arnheim formations of southwestern Ohio and southeastern Indiana; *Z. marstoni* is reported from the Acton Scott Beds of Cheney Longville Beds of Shropshire, U.K., Sandbian, and the Katian of Ottawa, Canada, and Cincinnati, Ohio; and *Z. variabilis* is from the Katian Drummock Group of Threave Glenn and Quarrel Hill, Ayrshire, Scotland, and the Fauquez Shales, Katian?, near Fauquez Castle, Belgium. In addition to the named species, *Zygocycloides* sp. has been reported from the base of the Eagle Point Member, Dunleith Formation, Galena Group (Katian) of Illinois (Kolata, 1975); *Z.*? sp. has been reported from the Telychian of Estonia (Hints et al., 2022), *Zygocycloides* n. sp. 1 has been reported from the lower Visby Formation (Wenlock, Sheinwoodian) on Gotland, Sweden (Reich and Kutscher, 2010), and *Z.* sp. was reported from the Wenlock (Homerian) of Gotland, Sweden (Reich and Kutscher, 2010).

*Zygocycloides*? *foerstei* new species
Figures 2–4

*Type.*—Holotype: USNM PAL 777895.

*Diagnosis.*—Based on characters of the dorsal surface: circular to elliptical test shape, 15 marginal ossicles, dorsal surface of marginal ossicles smooth and slightly convex, dorsal outline of marginal ossicles either modestly tapering trapezoid or rectangular, proximal margin of two adjacent marginal ossicles with slight indentation, and narrow and relatively shallow sutural grooves between adjacent marginal ossicles.

*Occurrence.*—Brassfield Formation (red Brassfield of Sullivan et al., 2016; Kleffner, 2020), Oakes Quarry Park, ~2 km east of Fairborn, Greene County, Ohio (39°48′53″N, 84°59′06″W) (Fig. 1); Silurian (Llandovery, middle Aeronian).

*Description.*—Circular test shape (Figs. 2.1, 3), diameter of specimen 63 mm, marginal rim with 15 ossicles (Figs. 2.1, 3). Marginal ossicles relatively large and robust; only dorsal surface exposed; subequal in size but no discernable pattern (Fig. 4); modestly tapering trapezoid or rectangle in dorsal outline (Fig. 4); and surface smooth and slightly convex. Distal margin of marginal ossicles broadly convex with smooth sculpturing; proximal margin between adjacent marginal ossicles sharply convex into an indentation along sutures. Contact between adjacent ossicles along a straight suture in a relatively narrow and shallow radial groove that extends from the outer margin to the inner margin, groove widens slightly proximally. Interseptal ossicles interpreted to be present (but most are not preserved) (Fig. 2b). Pores between marginal ossicles absent.

Disk diameter 3.6 mm, 32.5% of total area. A few distalmost annular ossicles are preserved but collapsed into central cavity; no distinction between radial and interradial annular ossicles. The distal edges of a few peripheral skirt ossicles may be preserved under a small portion of the marginal ossicles. Other details not preserved.

*Etymology.*—The species name *foerstei* recognizes August Foerste (1862–1936), who was a very influential paleontologist from Dayton, Ohio, and the first person to document many echinoderms from the Brassfield Formation in the Dayton area.

*Measurements.*—Total diameter, 6.3 mm; disk diameter, 3.6 mm.

https://doi.org/10.1017/jpa.2022.95 Published online by Cambridge University Press

*Remarks*.—*Zygocycloides*? *foerstei* can be distinguished on the basis of dorsal surface characters. *Zygocycloides variabilis* has a circular to elliptical test shape, 18–20 marginal ossicles, dorsal surface of marginal ossicles smooth and slightly convex, dorsal outline of marginal ossicles modestly tapering trapezoid, proximal margin of two adjacent marginal ossicles with modest indentation, and broad and relatively deep sutural grooves between adjacent marginal ossicles. *Zygocycloides magnus* has a circular test shape, 20 marginal ossicles, the dorsal surface of marginal ossicles smooth and flat, dorsal outline of marginal ossicles modestly tapering trapezoid, proximal margin of two adjacent marginal ossicles with modest indentation, and broad and relatively deep sutural grooves between adjacent marginal ossicles. *Zygocycloides marstoni* has a subcircular test shape, 18–20 marginal ossicles, dorsal surface of marginal ossicles smooth or very weakly pitted and flat, dorsal outline of marginal ossicles strongly tapering trapezoid, proximal margin of two adjacent marginal ossicles with deep indentation, and broad and relatively deep sutural grooves between adjacent marginal ossicles. *Zygocycloides*? *foerstei* has a circular to elliptical test shape, 15 marginal ossicles, dorsal surface of marginal ossicles smooth and broadly convex, dorsal outline of marginal ossicles either modestly tapering trapezoid or rectangular, proximal margin of two adjacent marginal ossicles with slight indentation, and narrow and relatively shallow sutural grooves between adjacent marginal ossicles.

## Paleobiogeography

A major shift among dominant crinoid clades occurred following the Late Ordovician mass extinction from the Ordovician early Paleozoic crinoid fauna to the Silurian to middle Mississippian middle Paleozoic crinoid fauna (Ausich et al., 1994; Baumiller, 1994; Ausich and Deline, 2012; Deline et al., 2012). Global recovery of crinoid faunas during the early Silurian was dominated by clades previously established in Laurentia (Ausich and Deline, 2012).

As argued by Sheffield et al. (2022), understanding biogeographic aspects of the Silurian recovery among other Paleozoic echinoderms has not been accomplished because of a general lack of understanding of clades based on modern phylogenetic methods. However, the sphaeronitid diploporans form a well-defined clade, and their paleobiogeographic history was explored by Sheffield et al. (2022). They concluded that sphaeronitid diploporans dispersed from Baltica to Laurentia during the Late Ordovician. Silurian Laurentian dispersal was confined to Laurentia.

Cyclocystoids are a well-defined clade, but their fossil record is poor, and determination of phylogenetic relationships within the clade is needed. The new Brassfield Formation cyclocystoid is assigned to *Zygocycloides*?. As noted, Smith and Paul (1982) recognized three species in *Zygocycloides*: *Z. variabilis* from the Katian of Scotland and Belgium, *Z. marstoni* from the Sandbian of England and Katian of North America, and *Z. magnus* from the Katian of North America. Reich and Kutscher (2010) also reported *Zygocycloides* from the Wenlock of Sweden on the basis of isolated marginal ossicles. *Zygocycloides*? sp. is also reported from the Telychian of Baltica (Estonia). Thus, as known, *Zygocycloides* was present on both Laurentia and Avalonia during the Ordovician. *Zygocycloides* questionably remained on Laurentia into the Llandovery, and perhaps by the Telychian, this genus migrated to Baltica and persisted through to at least the Wenlock.

Smith and Paul (1982) recognized two cyclocystoid genera that survived through the Late Ordovician mass extinction, Reich and Kutscher (2010) extended the range of *Cyclocystoides* from the Ordovician to the Silurian, and *Zygocycloides* also has an Ordovician through Silurian range. All four of these genera were present in the Ordovician of Laurentia with *Zygocycloides* known from both Laurentia and Avalonia. Silurian occurrences of these genera include *Polytryphocycloides* on both Baltica and Avalonia, *Apycnodiscus* and *Cyclocystoides* on Baltica, and *Zygocycloides* on both Laurentia and Baltica. Judging from these occurrences, it is possible that the four Ordovician–Silurian boundary-crossing cyclocystoids had Laurentia as their center for dispersal to Avalonia and Baltica.

Further, Ewin et al. (2019) suggested that both cyclocystoids reported from Anticosti Island, Québec (*Nicholodiscus* and *Perforocycloides*), were closely related to *Zygocycloides*, making it possible that *Zygocycloides*, *Nicholodiscus*, and *Perforocycloides* may represent a Laurentian clade. The biogeographic and evolutionary hypotheses suggested in the preceding must be verified with an increased number of fossil occurrences and modern phylogenetic analyses, as discussed by Sheffield et al. (2002).

## Acknowledgments

We thank D.B. Blake and M.A. Kleffner for their recommendations on Brassfield asteroids and chronostratigraphy, respectively. We also thank B. Lefebvre, M. Reich, J.R. Thompson, and S. Zamora for their thoughtful reviews that greatly improved this manuscript.

## References

Angelin, N.P., 1878, Iconographia Crinoideorum in stratis Sueciae Siluricis fossilium: Holmiae, Samson and Wallin, 62 p.
Ausich, W.I., 1984a, Calceocrinids from the early Silurian (Llandoverian) Brassfield Formation of southwestern Ohio: Journal of Paleontology, v. 58, p. 1167–1185.
Ausich, W.I., 1984b, The genus *Clidochirus* from the early Silurian of Ohio (Crinoidea: Llandoverian): Journal of Paleontology, v. 58, p. 1341–1346.
Ausich, W.I., 1985, New crinoids and revision of the superfamily Glyptocrinacea (early Silurian, Ohio): Journal of Paleontology, v. 59, p. 793–808.
Ausich, W.I., 1986a, Early Silurian rhodocrinitacean crinoids (Brassfield Formation, Ohio): Journal of Paleontology, v. 60, p. 84–106.
Ausich, W.I., 1986b, Early Silurian inadunate crinoids (Brassfield Formation, Ohio): Journal of Paleontology, v. 60, p. 719–735.
Ausich, W.I., 1986c, New camerate crinoids of the suborder Glyptocrinina from the lower Silurian Brassfield Formation (southwestern Ohio): Journal of Paleontology, v. 60, p. 887–897.
Ausich, W.I., 1987, Brassfield Compsocrinina (early Silurian crinoids) from Ohio: Journal of Paleontology, v. 61, p. 552–562.
Ausich, W.I., and Copper, P., 2010, The Crinoidea of Anticosti Island, Québec (Late Ordovician to early Silurian): Palaeontographica Canadiana, no. 29, 157 p.
Ausich, W.I., and Cournoyer, M.E., 2019, New taxa and revised stratigraphic distribution of the crinoid fauna from Anticosti Island, Québec, Canada (Late Ordovician–early Silurian): Journal of Paleontology, v. 93, p. 1137–1158.

Ausich, W.I., and Deline, B., 2012, Macroevolutionary transition in crinoids following the Late Ordovician extinction event (Ordovician to early Silurian): Palaeogeography, Palaeoclimatology, Palaeoecology, v. 361, p. 38–48.

Ausich, W.I., and Dravage, P., 1988, Crinoids from the Brassfield Formation of Adams County, Ohio: Journal of Paleontology, v. 62, p. 285–289.

Ausich, W.I., and Schumacher, G.A., 1984, New lower Silurian rhombiferan cystoid (Echinodermata, Callocystitidae) from southwestern Ohio: Journal of Paleontology, v. 58, p. 9–15.

Ausich, W.I., Kammer, T.W., and Baumiller, T.K., 1994, Demise of the middle Paleozoic crinoid fauna: a single extinction event or rapid faunal turnover?: Paleobiology, v. 20, p. 345–361.

Ausich, W.I., Peter, M.E., and Ettensohn, F.R., 2015, Echinoderms from the lower Silurian Brassfield Formation of east-central Kentucky: Journal of Paleontology, v. 89, p. 245–256.

Baumiller, T.K., 1994, Patterns of dominance and extinction in the record of Paleozoic crinoids, *in* David, B., Guille, A., Feral, J.P., and Roux, M., eds., Echinoderms Through Time: Rotterdam, Balkema Press, p. 193–198.

Blake, D.B., and Ettensohn, F.R., 2009, The complex morphology of a new lower Silurian asteroid (Echinodermata): Journal of Paleontology, v. 83, p. 63–69.

Boyarko, D., and Ausich, W.I., 2009, New calceocrinids from the Brassfield Formation of northern Kentucky and southern Ohio: Southeastern Geology, v. 46, p. 103–108.

Brett, C.E., 1978, Description and paleoecology of a new lower Silurian camerate crinoid: Journal of Paleontology, v. 52, p. 91–103.

Broadhead, T.W., and Ettensohn, F.R., 1981, A new *Brockocystis* (Echinodermata: Rhombifera) from the lower Silurian (Llandovery) of Kentucky: Journal of Paleontology, v. 55, p. 663–779.

Deline, B., Ausich, W.I., and Brett, C.E., 2012, Comparing taxonomic and geographic ranges in the morphological disparity of Ordovician through early Silurian Laurentian crinoids: Paleobiology, v. 38, p. 538–553.

Donovan, S.K., Lewis, D.N., Fearnhead, F.E., and Widdison, R.E., 2012, The British Silurian Crinoidea, Part 3, addendum to parts 1 and 2, Camerata and columnals: Monographs of the Palaeontographical Society, London, v. 166, p. 135–259.

Eckert, J.D., 1984, Early Llandovery crinoids and stelleroids from the Cataract Group (lower Silurian), southern Ontario, Canada: Royal Ontario Museum Life Sciences Contributions, no. 137, 83 p.

Eckert, J.D., and Brett, C.E., 2001, Early Silurian (Llandovery crinoids from the Lower Clinton Group, western New York State: Bulletins of American Paleontology, no. 360, 88 p.

Ewin, T.A.M., Reich, M., Graham, M.R., and Cournoyer, M.E., 2019, *Perforocycloides nathalieae* new genus and species, an unusual Silurian Cyclocystoidea (Echinodermata) from Anticosti Island, Québec, Canada: Paläontologische Zeitschrift, v. 93, p. 625–635.

Foerste, A., 1884, The power of motion in crinoid stems: American Naturalist, v. 18, p. 57–58.

Foerste, A., 1919, Echinodermata of the Brassfield (Silurian) Formation of Ohio: Bulletin of the Scientific Laboratories of Denison University, v. 19, p. 3–31.

Foerste, A., 1936. Several new Silurian cephalopods and crinoids, chiefly from Ohio and Hudson Bay: Ohio Journal of Science, v. 36, p. 261–272.

Frest, T.J., Brett, C.E., and Witzke, B.J., 1999, Caradocian–Gedinnian echinoderm associations of central and eastern North America, *in* Boucot, A.J., and Lawson, J.D., eds., Paleocommunity Analysis. A Silurian–Lower Devonian Example: Cambridge, Cambridge University Press, p. 638–783.

Glass, A., Ausich, W.I., and Copper, P., 2003, New cyclocystoid (phylum Echinodermata) from Anticosti Island, Québec, and its bearing on cyclocystoids life modes: Journal of Paleontology, v. 77, p. 949–957.

Hints, L., Pärnaste, H., Männik, P., Reich, M., and Rozhnov, S., 2022, Development of faunal diversity during the late Llandovery–early Wenlock in the easternmost part of the Baltic Palaeobasin—implications for the Ireviken Event: Estonian Journal of Science, v. 71, p. 89–110.

Kleffner, M.A., 2020, Revised middle to upper Aeronian and Telychian (lower Silurian) conodont biostratigraphy for the eastern portion of the midwestern portion of the basins and arches region (New York, Ohio, Kentucky, and Indiana): GSA Connects Online, paper no. 35-2, https://gsa.confex.com/gsa/2020AM/webprogram/Paper350459.html

Kolata, D.R., 1975, Middle Ordovician echinoderms from northern Illinois and southern Wisconsin: Paleontological Society Memoir, no. 7, 74 p.

Mao, Y., Ausich, W.I., Li, Y., Lin, J.-P., and Lin, C., 2017, New taxa and phyletic evolution of the Aeronian (Llandovery, Silurian) Petalocrinidae (Echinodermata: Crinoidea) in Guizhou, South China Block: Journal of Paleontology, v. 91, p. 477–492.

Miller, S.A., 1882, Description of three new orders and four new families in the class Echinodermata and eight new species from the Silurian and Devonian formations: Journal of the Cincinnati Society of Natural History, v. 5, p. 221–231.

Miller, S.A., and Dyer, G.B., 1878, Contributions to palaeontology: Journal of the Cincinnati Society of Natural History, v. 1, p. 24–39.

Miller, S.A., and Gurley, W.F.E., 1895, Description of new species of Palaeozoic Echinodermata: Illinois State Museum of Natural History Bulletin, v. 6, 62 p.

Nichols, D., 1969, The origin of echinoderms, *in* Millott, N., ed., Echinoderm Biology. Symposium of the Zoological Society of London: London, Academic Press, p. 209–229.

Reich, M, and Kutscher, M., 2010, Cyclocystoids (Echinodermata: Echinozoa) from the Silurian of Gotland, Sweden, *in* Harris, L.G., Böttger, S.A., Walker, C.W., and Lesser, M.P., eds., Echinoderms: Durham: London, Taylor and Francis Group, p. 144–171.

Reich, M., Sprinkle, J., Lefebvre, B., Rössner, G.E., and Zamora, S., 2017, The first Ordovician cyclocystoid (Echinodermata) from Gondwana and its morphology, paleoecology, taphonomy, and paleogeography: Journal of Paleontology, v. 91, p. 735–754.

Salter, J.W., and Billings, E., 1858, On *Cyclocystoides*, a new genus of Echinodermata from the lower and middle Silurian rocks: Geological Survey of Canada, Figures Describing Canadian Organic Remains, v. 3, p. 86–90.

Schmidt, D.A., Carney, C.K., and Ausich, W.I., 2007, Stromatoporoid–tabulate coral reefs, USA, *in* Vennin, E., Aretz, M., Boulvain, F., and Munnecke, A., eds., Facies from Paleozoic reefs and bioaccumulations: Mémoires du Muséum Nationale d'Histoire Naturelle, no. 95, p. 117–119.

Schneider, K.A., and Ausich, W.I., 2002, Paleoecology of framebuilders in early Silurian reefs (Brassfield Formation, southwestern Ohio). PALAIOS, v. 17, p. 237–248.

Sheehy, T.J., 1979, Carbonate petrology of a carbonate buildup in the Brassfield Formation near Fairborn, Ohio [M.S. thesis]: Dayton, Ohio, Wright State University.

Sheffield, S.L., Lam, A.R., Phillips, S.F., and Deline, B., 2022, Morphological dynamics and response following the dispersal of Ordovician–Silurian diploporan echinoderms to Laurentia: Contributions from the Museum of Paleontology, University of Michigan, v. 34, p. 123–140.

Smith, A.B., and Paul, C.R.C., 1982, Revision of the Cyclocystoidea (Echinodermata): Philosophical Transactions of the Royal Society of London, v. 296, p. 577–684.

Springer, F., 1920, The Crinoidea Flexibilia: Smithsonian Institution Publication, no. 2501, 486 p.

Sprinkle, J., Reich, M., and Lefebvre, B., 2015, Computed tomography (CT) scans of a new Ordovician cyclocystoid from Morocco and its orientation and life mode, *in* Zamora, S., and Rábino, I., eds., Progress in Echinoderm Paleobiology: Madrid, Instituto Geológico y Minero Españo, p. 163–167.

Sullivan, N.B., McLaughlin, P.I., Brett, C.E., Cramer, B.D., Kleffner, M.A., Thomka, J.R., and Emsbo, P., 2016, Sequence boundaries and chronostratigraphic gaps in the Llandovery of Ohio and Kentucky: the record of early Silurian paleoceanographic events in east-central North America: Geosphere, v. 12, p. 1813–1832.

Witzke, B.J., and Strimple, H.L., 1981, Early Silurian crinoids of Eastern Iowa: Proceedings of the Iowa Academy of Science, v. 88, p. 101–137.


Accepted: 12 September 2022