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A hydrozoan from the eurypterid-dominated Silurian Bertie Group Lagerstätten of North America

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Non-technical Summary.—Living disc-like hydrozoans such as the by-the-wind sailor and the blue button are often stranded in large numbers on beaches. These animals are delicate and rare as fossils as they require exceptional conditions for preservation. Here we describe a new example from the Bertie Group of upper New York State and Ontario (~420 Ma), which is famous for the remarkably preserved sea scorpions (eurypterids) that occur there. The new hydrozoan, which gets up to 17 cm across and is the second-oldest example known, adds an important new member to this assemblage. It floated on the surface of the ocean and was occasionally incorporated into layers rich in eurypterids and other fossils.

Abstract.—Fossil capitate hydrozoans require exceptional conditions for preservation. Here we describe *Bertratis ciurcae* new genus, new species from the Silurian (Pridoli) of southern Ontario and upper New York State, where it occurs in association with a diverse assemblage of eurypterids. Only the float (pneumatophore) is well preserved, surviving as a thick carbonaceous compression. The new taxon is the largest fossil capitate reported, reaching a width of 17 cm, and the third *Porpita*-like example known from the Paleozoic. It was a rare pelagic component of the biota of the well-known Bertie Group Lagerstätten.

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Introduction

The late Silurian (Pridoli) Bertie Group of Ontario, Canada, and upper New York State (Ciurca and Hamell, 1994) has long been known for its well-preserved and diverse fauna of eurypterids (Nudds and Selden, 2008; Briggs and Roach, 2020). The Bertie Group Lagerstätten also yield examples of other taxa (Nudds and Selden, 2008), including bivalve mollusks, gastropods and nautiloids, brachiopods, xiphosurans, scorpions, phyllocarids, an acanthodian (Burrow and Rudkin, 2014), and the plant *Cooksonia* (Edwards et al., 2004). Among additional rare fossils discovered in the Bertie Group by the late Samuel J. Ciurca, Jr. (Briggs and Roach, 2020), are six (possibly seven) specimens of a new disc-shaped taxon described here.

Disc-shaped fossils are often difficult to assign to a taxonomic group (Stanley, 1986; Lieberman et al., 2017; Landing et al., 2018; MacGabhann et al., 2019) as they normally represent soft-bodied organisms that have undergone modification during decay and fossilization. Most such fossils are assigned to one of three groups: cnidarian medusae (Young and Hagadorn, 2010, 2020), eldonids (MacGabhann et al., 2019), or capitate hydrozoans (Fryer and Stanley, 2004). Cnidarian medusae are usually preserved as molds and casts showing a distinct axial area and surrounding bell (Young and Hagadorn, 2010, 2020). They rarely occur in isolation and are not represented by a thick carbonaceous disc (Young and Hagadorn, 2010). Eldonids are an extinct group ranging from the lower Cambrian to the Upper Devonian. They are characterized by a coiled sac at their center that is interpreted as a coelom surrounding the gut (MacGabhann et al., 2019). The disc comprises internal lobes and radial fibers that bifurcate in a regular pattern (Lieberman et al., 2017; MacGabhann et al., 2019). The nature of their preservation indicates that the disc was composed of decay-resistant carbonaceous material (MacGabhann et al., 2019).

A diversity of rare disc-shaped fossils has been assigned to porpitoid hydrozoans. These fossils were placed historically within the suborder Chondrophorae of the order Siphonophorae (Caster, 1942) and referred to as chondrophorines. Garstang (1946) attempted to resolve the nature and interrelationships of the Siphonophorae, arguing that there are distinct differences between them and Chondrophorae, which led to the elevation of Chondrophorae to a separate order (Totton, 1954). More recently, Chondrophorae has been synonymized with order Anthoathecata, and porpitoids have been assigned to suborder Capitata (Schuchert, 2022). The extant families of Capitata are Velellidae, represented by the sail-bearing genus *Velella* (by-the-wind sailor), and Porpitidae such as *Porpita* (blue button). The main features of the Porpitidae include a chitinous float or pneumatophore surrounded by soft tissue that overlies

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the mouth and downward-directed tentacles (Mackie, 1959; Yochelson et al., 1983; Fryer and Stanley, 2004).

Depositional environment

The Bertie Group was deposited along the north rim of the Appalachian Foreland Basin of Laurentia and on the paleo-southern side of the subsiding Algonquin Arch (Burrow and Rudkin, 2014). It crops out over 300 km from southern Ontario to the Herkimer County region of New York State (Edwards et al., 2004). During the late Silurian, massive evaporite deposits formed in the center of the basin due to the low paleolatitude, warm arid climate, and reduced connection to the open ocean (Vrazo et al., 2016, 2017). The Bertie Group was deposited in a near-shore ramp environment separate from these massive evaporite deposits and consists of calcareous shales and chemically precipitated dolomites (waterlimes) that originated in the subtidal and intertidal zone of a shallow lagoonal setting (Burrow and Rudkin, 2014; Vrazo et al., 2017).

The disc-shaped fossils described here occur in fine-grained, wavy-bedded, light gray dolostone. Associated thin evaporite layers (gypsum beds) and salt hoppers suggest that the marine environment was frequently hypersaline (Nudds and Selden, 2008). However, although the salinity was elevated at times, Vrazo et al. (2016) concluded that the eurypterids and associated animals inhabited a shallow subtidal normal marine environment following a transgression. A subsequent regression resulted in hypersaline and increasingly dysoxic conditions leading to desiccation cracks and supersaturated porewater promoting the nucleation of salt hoppers around organic material in the sediment. Thus the Bertie assemblage of eurypterids and associated fossils, including the new taxon described here, likely inhabited a near normal marine setting.

Taphonomy

The specimens are dark compression fossils preserved parallel to the bedding surface (Figs. 1.1, 1.2, 2.1, 2.3). Irregularly spaced concentric ridges around the periphery of the disc are a result of flattened convexity. Where the specimen is flattened at a slight inclination to bedding, these ridges are concentrated on one side (the right side of YPM IP 250362, for example, Fig. 1.1, 1.2), but the preserved specimens depart very little from bilateral symmetry and there is no evidence that outlines are significantly distorted. Energy-dispersive X-ray spectrometer (EDS) analysis with a scanning electron microscope showed that the dark color of the specimens is due to elevated levels of carbon (Fig. 3.1), which is also indicated by a striking contrast between specimen and matrix in back-scattered electron images. There is no evidence that the discs are biomineralized, and they are assumed to have been composed predominantly of chitin as are the floats of extant porpitoids (Bondyale-Juez et al., 2022). Where the dolomitic matrix is present on and around the margin of the specimens, it contains much less carbon and higher concentrations (wt%) of Ca, Mg, and O (Fig. 3.2). The presence of Si, Al, and low percentages of other minerals may indicate traces of clays and authigenic minerals that formed during diagenesis (Fig. 3). Analyses of eurypterid cuticle, presumably also originally chitinous, from the same locality yielded long-chain aliphatic components similar to type II kerogen as a result of diagenetic in situ polymerization (Gupta et al., 2007). The discs are darker in color than the eurypterids and have undoubtedly undergone a similar transformation.

Rapid burial of the Bertie Group eurypterids is attributed to sediment disruption during storms and/or wave action (Vrazo et al., 2017), agents that could have transported the disc-shaped organisms inshore and buried them. Only the decay-resistant internal float (pneumatophore) is well preserved; other morphological features would have degraded faster (Yochelson et al., 1983). Way up information is available for YPM IP 546800 only. It is preserved on the base of a slab providing a concave ventral view; thus, it was deposited convex upward in presumed life attitude. The lack of evidence of mass strandings, which frequently affect extant porpitids, suggests that the disc-shaped organisms were rare in the depositional environment. Their taphonomic pathway may have been promoted by sea-level transgression events as inferred for the eurypterids (Vrazo et al., 2016, 2017).

Methods

Specimens were photographed with a Canon EOS 60D and analyzed using a Hitachi SU7000 scanning electron microscope (SEM). Elemental analyses were carried out with an energy-dispersive X-ray spectrometer made by Oxford Instruments (Utilm Max-100 EDS system). The SEM was operated at acceleration voltage 15KV at variable pressure mode at 50 Pascals.

Repository and institutional abbreviation.—All specimens examined in this study are deposited in the Invertebrate Paleontology Division of the Yale Peabody Museum (YPM IP).

Systematic paleontology

Phylum Cnidaria Verrill, 1865
Class Hydrozoa Owen, 1843
Subclass Hydroidolina Collins, 2000
Order Anthoathecata Cornelius, 1992
Suborder Capitata Kuhn, 1913
Superfamily Porpitoidea Goldfuss, 1818

Remarks.—Molecular data do not support a monophyletic Anthoathecata (Collins et al., 2006; Daley et al., 2007). Capitata is a paraphyletic assemblage of Aplanulata, but there is limited availability of molecular data. The family Porpitidae, which Collins et al. (2005) recovered as monophyletic, comprises two living genera, *Velella* and *Porpita*. Living porpitids are distinguished by a colonial pelagic stage, but it may be a modified individual polyp rather than a colony (Daly et al., 2007). The float has the greatest potential for fossilization but provides limited morphological characters (Fryer and Stanley, 2004).

Genus *Bertratis* new genus

Type species.—*Bertratis ciurcae* new genus, new species.

Diagnosis.—As for type species, by monotypy.

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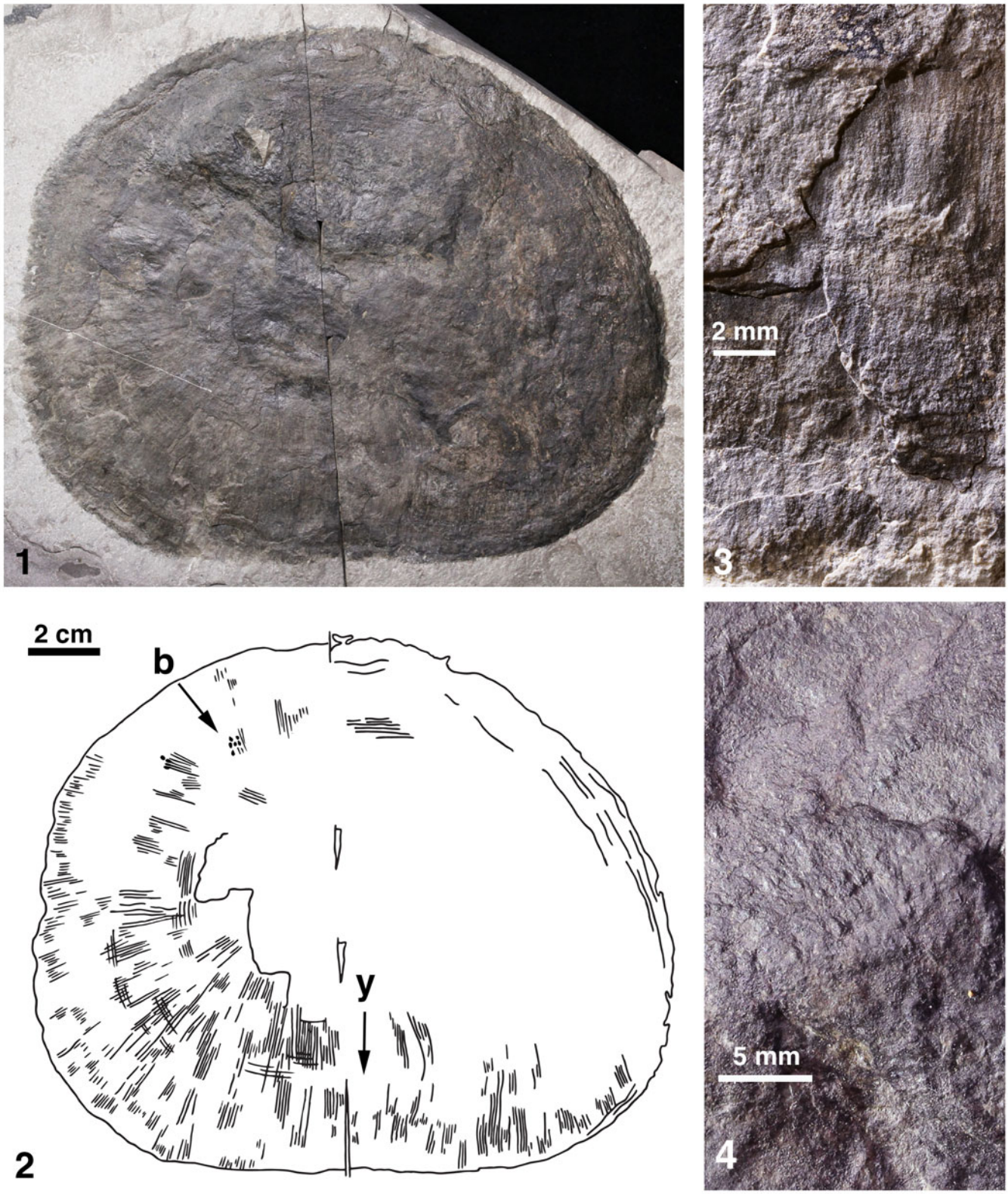

Figure 1. *Bertratis ciurcae* n. gen. n. sp. YPM IP 250362, holotype. (**1, 2**) Image (**1**) and interpretive drawing (**2**) showing lineations (the oblique straight white line on the left side is a scratch that was present when the YPM received the specimen). (**3**) Enlargement of area arrowed "y" in (**2**) showing layers of radial structures. (**4**) Enlargement of area arrowed "b" in (**2**) showing beads on radial structures.

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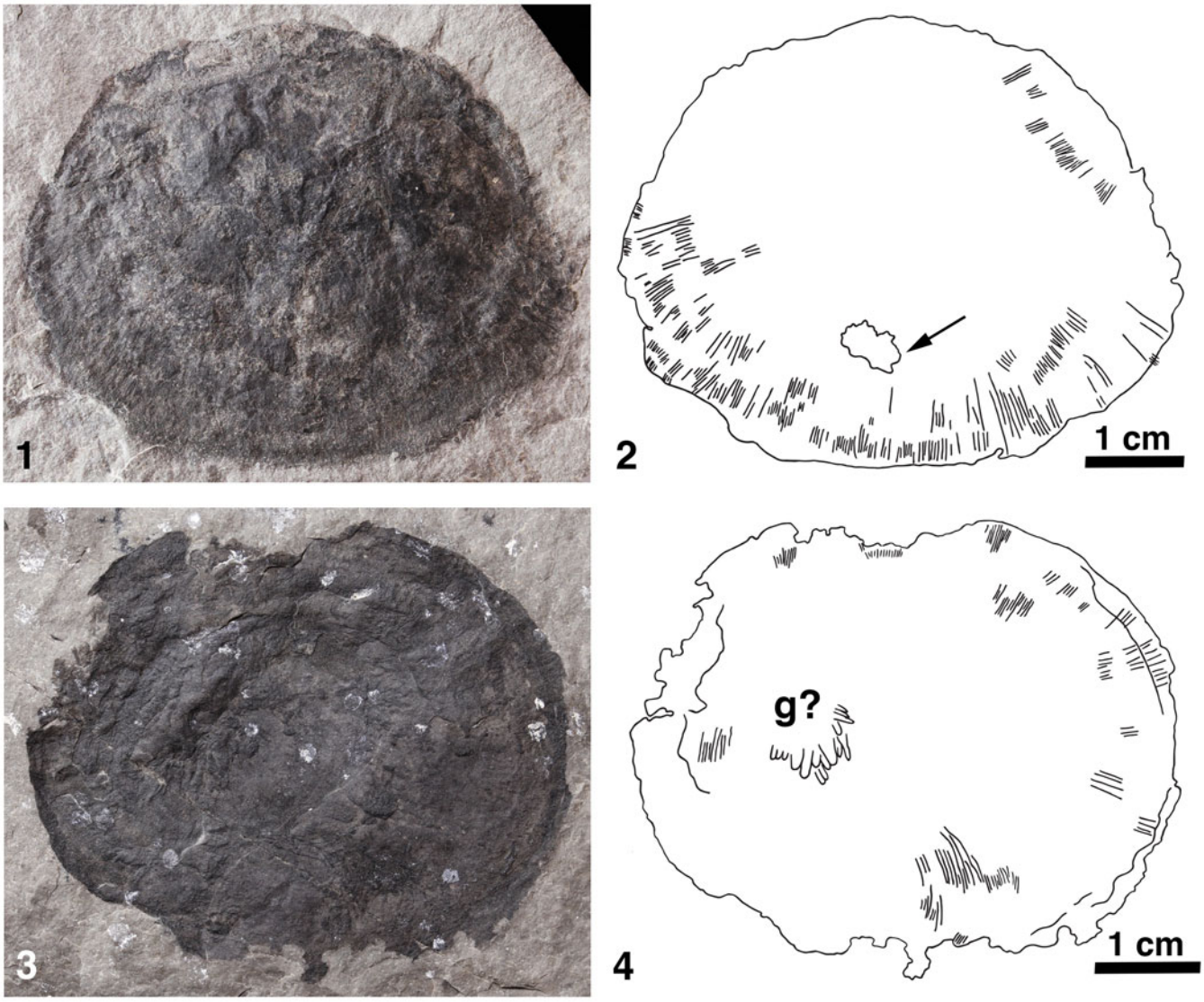

Figure 2. *Bertratis ciurcae* n. gen. n. sp. (**1, 2**) YPM IP 209925, image (**1**) and interpretive drawing (**2**) showing lineations (arrow indicates thin surface cuticle analyzed in Fig. 3.1). (**3, 4**) YPM IP 546800, image (**3**) and interpretive drawing (**4**) showing lineations (g? = possible gonozooids; white areas are paint splashes).

Occurrence.—Silurian (Pridoli) Bertie Group. Member A, Williamsville Formation, Ridgemount Quarry South about 8 km west of Fort Erie, Ontario, with the exception of YPM IP 255247, which is from the Phelps Member, Fiddlers Green Formation, Lang (Langheinrich) Quarry, 0.5 km south of Brewer Road, ~1 km southeast of Elizabethtown, Herkimer County, New York State. The locality of YPM IP 250663 is unknown.

Etymology.—Bertie, referring to the stratigraphic source of the specimens, and *ratis* (Latin, feminine) meaning float or raft.

Remarks.—Previous reliable records of Paleozoic porpitoids (Table 1) are late Silurian (Ludlovian Series) to Early Devonian in age (Landing et al., 2018; Giribet and Edgecombe, 2020) represented by the *Velella*-like *Plectodiscus discoideus* (Rauff, 1939) and the *Porpita*-like *Pseudodiscophyllum* Fryer and Stanley, 2004. All fossil *Velella*-like forms were synonymized with *Plectodiscus* Ruedemann (1916) by Yochelson et al. (1983) in their redescription of pyritized material from the Devonian Hunsrück Slate, which yields the most complete examples, preserving even the tentacles. The float of *Plectodiscus* is characterized by pronounced overlapping concentric chambers interpreted as pneumatocysts (Yochelson et al., 1983). The float of the *Porpita*-like *Pseudodiscophyllum*, by contrast, is dominated by a regular series of pronounced radial ribs, which are beaded near the center of the disc and bifurcate near the margin at the outer of just two circular ribs (Fryer and Stanley, 2004). The float of the new Bertie Group taxon, like *Pseudodiscophyllum*, lacks well-defined concentric chambers, but it consists of layers of closely spaced fine radial structures that show traces of beading in one place on YPM IP 250362. *Bertratis* differs from *Pseudodiscophyllum* in lacking a circular outline and regularly arranged ribs, necessitating the erection of a new genus and species to accommodate it.

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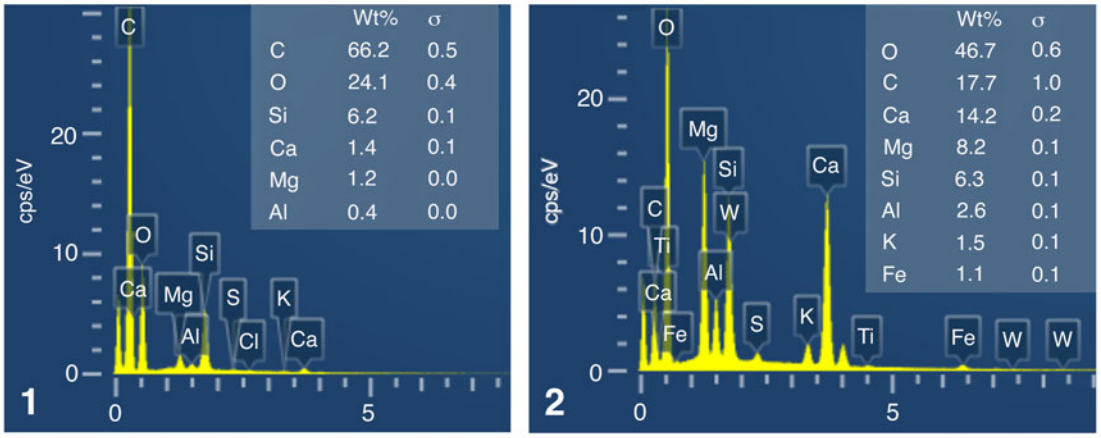

Figure 3. *Bertratis ciurcae* n. gen. n. sp., YPM IP 209925, EDS analyses. (**1**) Thin surface cuticle arrowed in Figure 2.2. (**2**) Matrix at edge of specimen.

Table 1. Paleozoic genera of probable porpitoids best represented in the fossil record.

Taxon	Major reference	Age	Location	Features	Maximum dimensions (mm)
Pseudodiscophyllum windermerensis Fryer and Stanley, 2004	Fryer and Stanley, 2004	Late Silurian, Ludlow, Ludfordian, Bannisdale Formation	Cumbria, England	Radial lines and beads, concentric lines	117 × 111
Plectodiscus discoideus (Rauff, 1939) (formerly *Palaeonectris discoidea*)	Yochelson et al., 1983	Early Devonian, Emsian, Hunsrück Slate	Rhineland-Palatinate, Germany	Concentric lines, sail, tentacles, radial structures at periphery	67 × 49
Plectodiscus molestus Ruedemann, 1916	Ruedemann, 1916	Late Devonian	Near Ithaca, New York State	Concentric lines, crumpled	123 × 105
Plectodiscus cortlandensis Caster, 1942	Caster, 1942	Late Devonian	Near Cortland, New York State	Concentric lines, diagonal sail	135 × 104
Plectodiscus circus Chamberlain, 1971	Chamberlain, 1971	Middle Pennsylvanian, Moscovian, Atoka Formation	Southeast Oklahoma	Central cone, sail, concentric lines	42 × 32
Plectodiscus casteri (Fisher, 1957) (formerly *Silurovelella*)	Fisher, 1957	Late Silurian, Ludlow, Vernon Shale	Near Vernon, New York State	Concentric lines, faint radial lines	145 × 100
Bertratis ciurcae	This paper	Late Silurian, Pridoli, Bertie Group	Upper New York State and southern Ontario	Radial lines, concentric lines	172 × 140

Bertratis ciurcae new species
Figures 1, 2

Holotype.—YPM IP 250362.

Diagnosis.—Subcircular float, bilaterally symmetrical, narrowing slightly to presumed anterior margin, layers of closely spaced radiating structures, faint concentric features, no obvious sail or similar.

Description.—The float (pneumatophore) is subcircular in outline and bilaterally symmetrical (Figs. 1.1, 1.2, 2), allowing the anterior–posterior axis to be identified. For the purposes of description, we designate the more convex margin as anterior. The maximum width lies just over half the distance from front to rear. The posterior margin is slightly convex to nearly straight, showing a shallow indentation in some specimens (Fig. 1.1, 1.2). The four specimens sufficiently well preserved to be measured range in dimensions from 42 × 51 mm (Fig. 2.3, 2.4) to 140 × 172 mm (Fig. 1.1, 1.2). There is no evidence of allometry (Fig. 4). The float is flattened, and its thickness cannot be determined. Specimens show some relief in the central region, which was gently convex whereas the margins were more inclined (Figs. 1.1, 2.1, 2.3).

The float was made up of several thin layers although these rarely separate cleanly where the part and counterpart separate. Three morphological features are evident on the better-preserved specimens. Most obvious are fine radial structures that are present on some part of most specimens (Figs. 1.1, 1.2, 2). They vary in their degree of resolution and spacing but are less than 1 mm wide. They are most pronounced toward the periphery, where they form several layers (Fig. 1.3), and they do not appear to extend to the center (Figs. 1.1, 1.2, 2). A smooth featureless layer underlies the radial lines in the central area of YPM IP 250362, and they are overlain in places by a rougher layer, which may represent adhering sediment. YPM IP 209925 (Fig. 2.1, 2.2) preserves patches of thin cuticle above the radial structures, which may represent the outer cuticle of the float. Concentric lines are more rarely evident than radial ones, but where they are present they appear to be at a similar level

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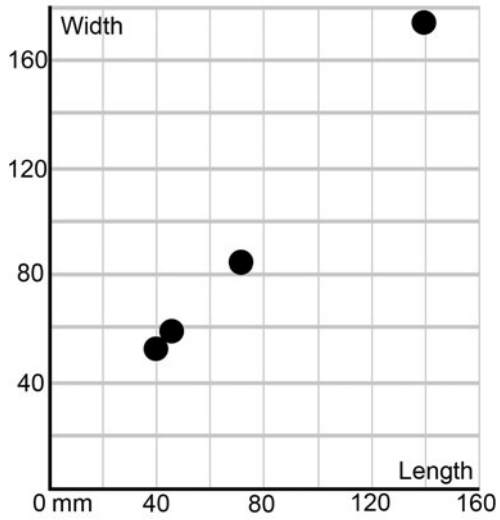

Figure 4. *Bertratis ciurcae* n. gen. n. sp., plot of dimensions of four measurable specimens (YPM IP 209925, 250362, 255247, and 546800) revealing strong correlation and absence of allometry.

(Fig. 1.1, 1.2). They too are generally spaced less than 1 mm apart. In some cases, elongate bead-like structures up to 1 mm long are aligned with the radial lines (left anterior area of YPM IP 250362: Fig. 1.1, 1.2, 1.4). YPM IP 546800 is unusual in preserving a cluster of bulbous structures (center left of the specimen, which was buried convex upward, as viewed from the concave ventral side; Fig. 2.3, 2.4), some up to 1 mm wide. These are reminiscent, in their position and variable orientation, of gonozooids. However, these bulbous structures are preserved at the level of the pneumatophore, so could represent gonozooids only if there were some displacement during flattening of the specimen. There is no clear evidence of a sail.

Etymology.—After the discoverer Samuel J. Ciurca, Jr.

Materials.—YPM IP 250362 holotype, YPM IP 209925, 255247, 255284, 255285, and 546800 and possibly 250663. All specimens were collected by Samuel Ciurca except for YPM IP 255247 and 250663, which he purchased on eBay.

Remarks.—We assign *Bertratis ciurcae* to the Porpitoidea but do not place it in a family. The absence of information on the life cycle and lack of preserved morphology other than the float prevent a confident placement in the living family Porpitidae.

Discussion and conclusions

Waggoner and Collins (2004) argued that the occurrence of Paleozoic, as well as Neoproterozoic, porpitids (chondrophorines) is improbable because their use in calibrating molecular clock estimates placed the origin of Cnidaria at more than 1,500 Ma. Phylogenomics of Cnidaria have become more refined (e.g., Park et al., 2012; Kayal et al., 2018) and Landing et al. (2018), in their review of the early evolution of colonial animals, concluded that the oldest undoubted examples of porpitoids are Silurian. *Bertratis* adds a third genus to the list of Paleozoic porpitoids (Table 1). The other Silurian example (Fryer and Stanley, 2004) is older.

Bertratis reaches a maximum dimension of just over 17 cm, making it the largest Paleozoic capitate float known and suggests that these hydrozoans were important consumers of zooplankton. Schuchert (2010, p. 480) noted that living *Porpita* reaches diameters of 5 cm whereas *Velella* reaches sizes of up to 10 × 5 cm. Thus the largest specimen of *Bertratis* is notably larger than living porpitids, but its maximum dimension is less than twice that of the largest *Velella*. The occurrence of *Bertratis* in the Bertie Group Lagerstätten reflects the need for exceptional conditions to facilitate preservation. The Bertie Group represents nearshore marine settings with a restricted fossil assemblage dominated by eurypterids, which may have congregated to molt. Open marine taxa are uncommon but include nautiloids. The discovery of *Bertratis ciurcae* adds a rare taxon to the Bertie Group biota. Its thick organic float indicates a preservation potential at least as high as that of eurypterid cuticle. The range of size and low number of specimens show that it was not aggregated by wind or currents in this case. It was rare in this depositional setting and may have lived on the surface of the open ocean like modern porpitids.

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Declaration of competing interests

The authors declare that they have no competing interests.

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