

Corals and a cephalopod from the Whirlpool Formation (latest Ordovician, Hirnantian), Hamilton, Ontario: biostratigraphic and biogeographic significance

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Non-technical Summary.—The new coral species *Streptelasma rutkae* and a cephalopod belonging to the genus *Gorbyoceras* occur in nearshore shallow-marine sandstone of the Whirlpool Formation in Hamilton, southern Ontario. They are the first macrofossils contributing to a modern understanding of the geologic age and correlation of this formation. *Streptelasma rutkae* most closely resembles a species that occurs widely in the Edgewood Biogeographic Province of the east-central United States, in rocks dating to the latest part of the Ordovician Period. *Gorbyoceras* is present in Late Ordovician rocks in the Cincinnati Arch region. Thus, the occurrences of *Streptelasma rutkae* and *Gorbyoceras* support other fossil and chemical data suggesting that the age of the Whirlpool Formation is latest Ordovician, rather than earliest Silurian as traditionally thought. They also indicate paleogeographic connections between the area where the Whirlpool Formation was deposited in Ontario and the Edgewood Biogeographic Province and Cincinnati Arch region in the east-central United States.

Abstract.—Solitary rugose corals assigned to *Streptelasma rutkae* n. sp. and an annulated orthoconic cephalopod identified as *Gorbyoceras* sp. occur in nearshore shallow-marine sandstone of the Whirlpool Formation in Hamilton, southern Ontario. They are the first macrofossils contributing to a modern understanding of the age and correlation of this stratigraphic unit. *Streptelasma rutkae* most closely resembles *S. subregulare* (Savage, 1913), which occurs widely in the Edgewood Province of the east-central United States, in strata considered latest Ordovician (Hirnantian). *Gorbyoceras* ranges into the latest Katian (latest Richmondian) in the Cincinnati Arch region. Thus, the occurrences of *S. rutkae* and *Gorbyoceras* sp. support other biostratigraphic and chemostratigraphic data suggesting that the Whirlpool Formation is latest Ordovician, rather than earliest Silurian as traditionally thought. They also indicate paleogeographic connections between the area of Whirlpool deposition in Ontario and the Edgewood Province and Cincinnati Arch region in the east-central United States

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Introduction

The Whirlpool Formation is a unit of sandstone exposed along the Niagara Escarpment from the vicinity of Medina in northwestern New York westward to Hamilton in southern Ontario and northward from there to the Collingwood area (Rutka et al., 1991; Brett et al., 1995) (Fig. 1.1). The lower part of the formation is interpreted as a terrestrial deposit, with the upper part representing nearshore shallow-marine deposition during a transgression. The Whirlpool is separated from underlying shale of the Queenston Formation by the regional Cherokee Unconformity and is overlain gradationally by shale of the Power Glen Formation in the southeast and dolostone of the Manitoulin Formation in the northwest. On Bruce Peninsula

and Manitoulin Island, Ontario, where the Whirlpool Formation is absent, the Manitoulin Formation overlies the Cherokee Unconformity.

Traditionally, the Cherokee Unconformity was considered to mark the Ordovician–Silurian boundary (Brett et al., 1995). Although fossils representing various taxonomic groups were known from the Whirlpool Formation, they were thought to be biostratigraphically undiagnostic. Therefore, the Whirlpool was assigned an age on the basis of lateral correlation with strata of the Manitoulin Formation containing a fauna interpreted as earliest Silurian (Llandovery, Rhuddanian). More recently, the Hirnantian Isotopic Carbon Excursion (HICE) of latest Ordovician (Hirnantian) age has been identified in the upper Queenston, Whirlpool, and Manitoulin formations in southern Ontario, and brachiopods and conodonts in the Manitoulin have been reinterpreted as consistent with that age (Stott and Jin, 2007; Bergström

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et al., 2011). In northwestern New York, microfossils suggest that the Whirlpool and Power Glen formations are Late Ordovician (late Katian and/or Hirnantian) (Schröer et al., 2016).

In this paper, we present the first modern, systematic study involving macrofossils from the Whirlpool Formation. They are solitary rugose corals assigned to *Streptelasma rutkae* n. sp. and an annulated orthoconic cephalopod identified as *Gorbyoceras* sp., from Hamilton, Ontario (Fig. 1.1, white star). The occurrences of these taxa support other biostratigraphic and chemostratigraphic data suggesting that the Whirlpool Formation is latest Ordovician in age. They also point to paleogeographic connections with the Edgewood Province and Cincinnati Arch region in the east-central United States.

Geologic setting

Exposures of the Whirlpool Formation occur along the Niagara Escarpment in southern Ontario and northwestern New York, from the Collingwood area, to Hamilton, to the vicinity of Medina (Rutka, 1986, fig. 1-1; Middleton et al., 1987, fig. 1; Rutka et al., 1991, fig. 17; Brett et al., 1995, fig. 1) (Fig. 1.1). Southwest of the escarpment, the Whirlpool is present in the subsurface of Ontario, New York, northwestern Pennsylvania, and eastern Ohio (Castle, 1998; Johnson, 1998). The formation, rarely more than 9 m thick, is composed of very fine- to fine-grained subarkose to quartz arenite (Rutka, 1986; Rutka et al., 1991). The lower part of the Whirlpool is considered to represent terrestrial deposition in a braided river system, with sediment derived from the Appalachian region to the east. The upper part of the formation is a nearshore shallow-marine deposit that formed during a transgression.

The Whirlpool Formation is overlain gradationally by shale of the Power Glen Formation in the southeast and dolostone of the Manitoulin Formation in the northwest (Rutka, 1986; Middleton et al., 1987; Rutka et al., 1991; Brett et al., 1995). Northwest of Collingwood (Fig. 1.1), the Whirlpool pinches out beneath the Manitoulin Formation (Bergstrom et al., 2011) or grades laterally into it (Farnam et al., 2019), so the Manitoulin unconformably overlies the Queenston Formation on Bruce Peninsula. The Manitoulin Formation extends to Manitoulin Island, where it unconformably overlies carbonates and shales of the Georgian Bay Formation.

Rutka (1986, tables 5-1, 5-2, 5-3) tabulated the regional occurrence of various trace fossils, microfossils, and macrofossils found in her study of the Whirlpool Formation. Trace fossils

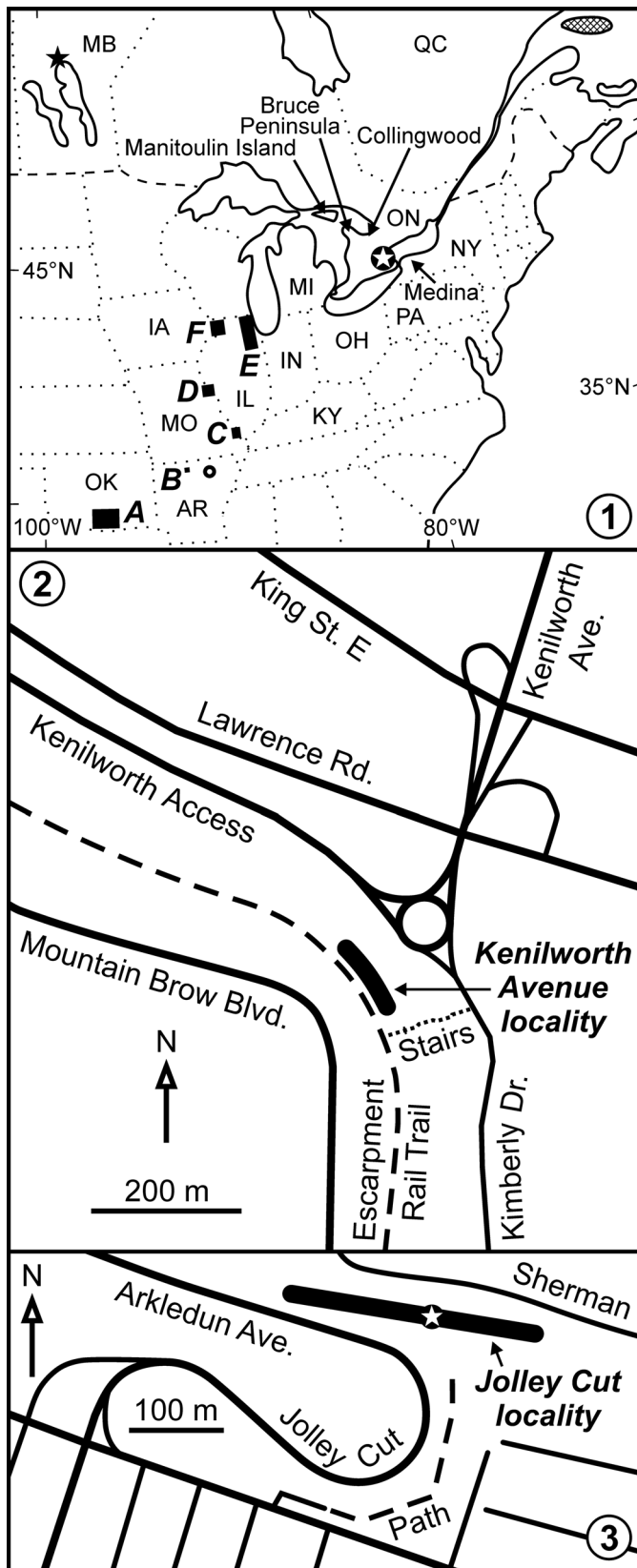


Figure 1. (1) Index map showing Hamilton, Ontario (white star), where studied corals and cephalopod were collected from Whirlpool Formation. Corals of Edgewood Province occur at stratigraphic sections in outcrop areas A–F; other corals mentioned in text occur on Anticosti Island, Québec (crosshatched area), at a locality in Grand Rapids Uplands, Manitoba (black star), and at St. Clair Spring section, Arkansas (open circle). AR = Arkansas; IA = Iowa; IL = Illinois; IN = Indiana; KY = Kentucky; MB = Manitoba; MI = Michigan; MO = Missouri; NY = New York; OH = Ohio; OK = Oklahoma; ON = Ontario; PA = Pennsylvania; QC = Québec. (2) Detail map showing Kenilworth Avenue locality where corals were collected in 1986. At that time, Escarpment Rail Trail was a Canadian National Railway line (Rutka, 1986, fig. A1–3a; Brusse et al., 1987, fig. 26). Whirlpool Formation is exposed below the former railway line (Rutka, 1986, p. A1–11; Brusse et al., 1987, p. 137). Locality is currently accessible by ascending stairs from Kimberly Drive; 30 steps below the top, there is access to a path leading northwest along the base of the stratigraphic section. (3) Detail map showing Jolley Cut locality (Rutka, 1986, p. A1–9, fig. A1–3a; Brusse et al., 1987, p. 140, fig. 26; Brett et al., 1991, fig. 44). Cephalopod was collected by Grant (1892, 1897a, b, 1900) from a Jolley Cut quarry; in 1985, R.A.H. located the probable site (white star).

appear only in the upper part of the formation, where they are common and diverse. Microfossils that occur in both the lower and upper parts of the Whirlpool include spore-like forms and tube-like fragments. In addition, acritarchs, chitinozoans, cuticle-like fragments, and scolecodonts are present in the upper part of the formation. In northwestern New York, Gray and Boucot (1971) listed spore tetrads, acritarchs, and scolecodonts ~2.5–3.0 m above the base of the Whirlpool Formation. From the bottom of the upper part of the Whirlpool, Schröer et al. (2016) reported cryptospores, acritarchs, glomalean fungi, chitinozoans, cuticle fragments, and small carbonaceous mandibles of unknown affinity. Miller and Eames (1982) documented spore-like microfossils and acritarchs from the upper part of the Whirlpool.

Macrofossils occur in the upper part of the Whirlpool Formation but are sparse. They include corals, gastropods, bivalves, brachiopods (including linguloids), bryozoans, crinoids, ostracods, and trilobites (Foerste, 1923; Rutka, 1986; Brett et al., 1991, 1995). Cephalopods are represented by a single specimen, which Hewitt (1986) assigned to *Gorbyoceras* Shimizu and Obata, 1935. Rutka (1986) noted that brachiopods and crinoids are most widely distributed, and corals are present only in the area where the Whirlpool Formation is overlain by the Manitoulin Formation.

Regarding corals, Spencer (1883, p. 142) identified the solitary rugosan *Zaphrentis bilateralis* (Hall, 1852) from the Medina “Gray Band,” now known as the Whirlpool Formation (Hewitt, 1986, table 1). The assignment to that inadequately known species is doubtful. Bassler (1950) placed it in *Heliophrentis* Grabau, 1910 and indicated that the type material is from the Silurian Reynales Limestone in New York, which is substantially higher stratigraphically than the Whirlpool (Brett et al., 1995). Hill (1981) questionably synonymized *Heliophrentis* with *Zaphrentis* Rafinesque and Clifford, 1820 (misspelled *Zaphrentis* by Milne-Edwards and Haime, 1850), a Devonian genus. Grant (1897b, p. 136) listed *Favosites niagarensis* “(or closely allied)” from the unit he termed Medina, now known as the Whirlpool Formation (Hewitt, 1986, table 1). That identification requires verification. Type material of the tabulate coral *F. niagarensis* Hall, 1852 is from the Silurian Lockport Dolomite in New York (see Bassler, 1950), which is much higher stratigraphically than the Whirlpool (Brett et al., 1995).

More recently, corals from the Whirlpool Formation have been identified as the phaceloid colonial rugosan *Synaptophyllum* sp. (Salas, 1983) and the solitary rugosans *Blothrophyllum* sp. (Salas, 1983; Brett et al., 1991), *?Enterolasma* sp., and *Streptelasma* sp. (Rutka, 1986). However, the first three identifications are doubtful. *Synaptophyllum* Simpson, 1900 and *Blothrophyllum* Billings, 1859 as currently understood are Devonian in age (Pedder and Murphy, 2003; Pedder, 2010). *Enterolasma* Simpson, 1900 is considered a synonym of *Palaeoocyathus* Foerste, 1888, with assigned species ranging from the mid-Silurian (Wenlock) to Devonian (Weyer, 2007). *Streptelasma* Hall, 1847 is a possibility; confirmed species recognized by McLean and Copper (2013) range from *S. corniculatum* Hall, 1847 in the Late Ordovician (early Katian, Mohawkian, Chatfieldian) to *S. sibiricum* (Nikolaeva, 1955) of Latypov (1982) in the early Silurian (middle late Llandovery).

Kenilworth Avenue locality.—Corals of the Whirlpool Formation documented in the present study are from the Kenilworth Avenue locality in Hamilton, Ontario (Fig. 1.1, 1.2). This locality was described in detail by Rutka (1986). The Whirlpool Formation is ~2.5 m thick (Rutka, 1986, figs. 4-16, 4-17b, 4-19; Brusse et al., 1987, figs. 27, 28). The lower part, overlying the Queenston Formation, is a low-angle cross-laminated sandstone (Rutka, 1986, fig. 3-5). The upper part of the formation includes symmetrical ripple cross-laminated sandstone, trough and planar cross-laminated sandstone, interbedded sandstone and shale, and hummocky to bioturbated, amalgamated hummocky cross-stratified sandstone (Rutka, 1986, figs. 3-10a, b, 4-17b, 4-18). The upper part of the Whirlpool Formation is overlain by the Manitoulin Formation. Rutka (1986) considered the Whirlpool at this locality anomalous in being relatively thin, with a thin lower part. This was attributed to substantial reworking and/or scouring during the transgression in which the upper part of the formation was deposited.

Rutka (1986, tables 5-1, 5-2, 5-3) listed various trace fossils, microfossils, and macrofossils from the upper part of the Whirlpool Formation at the Kenilworth Avenue locality. The microfossils include spore-like forms, acritarchs, and tube-like fragments. Macrofossils include solitary rugose corals (identified as *Streptelasma* sp.) and unidentifiable brachiopods, crinoids, and bivalves. In the present study, corals from the Kenilworth Avenue locality are assigned to *Streptelasma rutkae* n. sp. (Fig. 2).

Jolley Cut locality.—The cephalopod documented in the present study is from the Jolley Cut locality in Hamilton, Ontario (Fig. 1.1, 1.3). The entire Jolley Cut locality was described in detail by Rutka (1986). Exposures occur over a lateral distance of 260 m (Rutka, 1986, figs. 4-14, 4-15; Brusse et al., 1987, figs. 29, 30; Brett et al., 1991, figs. 45, 46). The Whirlpool Formation has a maximum thickness of 4.3 m, including the lower and upper parts of the formation. The Whirlpool is underlain by the Queenston Formation and overlain by the Manitoulin Formation.

Rutka (1986, tables 5-1, 5-2, 5-3) listed various trace fossils, microfossils, and macrofossils from the upper part of the Whirlpool Formation at the Jolley Cut locality. The microfossils include spore-like forms, acritarchs, chitinozoans, tube- and cuticle-like fragments, and scolecodonts. Macrofossils include solitary rugose corals, brachiopods, and gastropods. A single cephalopod was collected from a quarry at the Jolley Cut by Grant (1892, 1897a, b, 1900), who identified the specimen as *Orthoceras* Bruguière, 1789. It was reassigned to *Gorbyoceras* by Hewitt (1986) and is described as *Gorbyoceras* sp. in the present study (Fig. 3). The occurrence of this cephalopod in the upper part of the Whirlpool Formation indicates normal marine, certainly not brackish, conditions during the transgression above the terrestrial lower part of the formation.

Materials and methods

Corals.—On 23 and 28 March 1986, R.A.H. collected silicified solitary rugose corals from the Whirlpool Formation at the

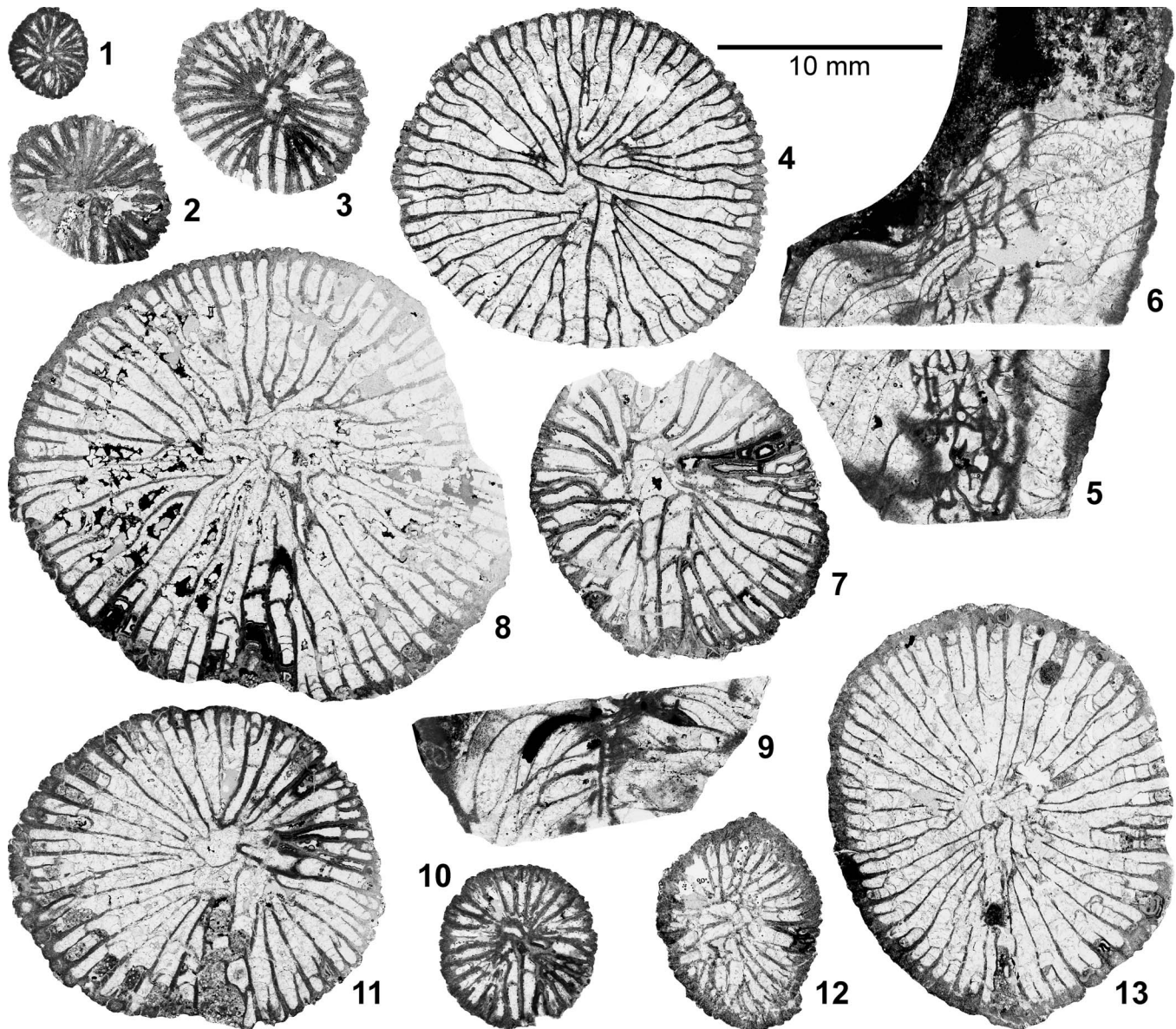
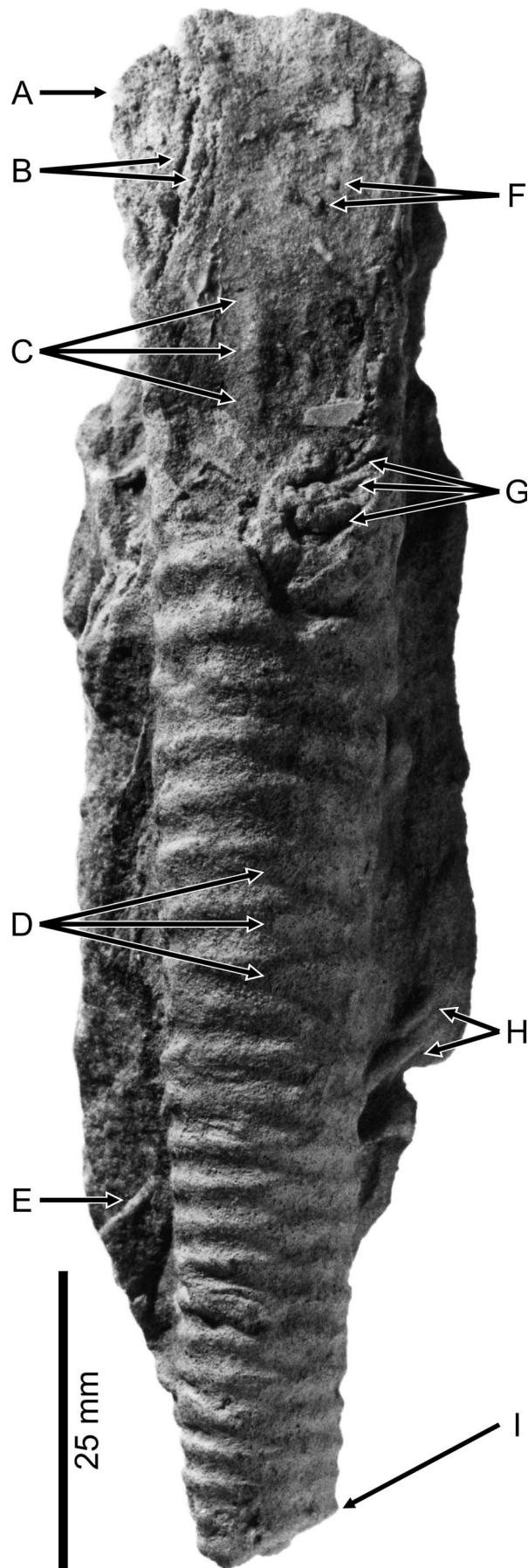


Figure 2. *Streptelasma rutkae* n. sp., transverse thin sections (1–4, 7, 8, 10–13; oriented with apical direction of corallum into the page and cardinal septum in six o'clock position) and longitudinal thin sections (5, 6, 9; oriented in cardinal-counter plane with cardinal fossula on left side and apical direction of corallum toward bottom of the page). (1) GSC 143183. (2–6) Holotype GSC 143181. (7) GSC 143188. (8) Paratype GSC 143182. (9) GSC 143186. (10, 11) GSC 143189. (12, 13) GSC 143187. Upper Ordovician, Hirnantian; sandstone bed 1.2 m above base of Whirlpool Formation; Kenilworth Avenue locality, Hamilton, Ontario.

Kenilworth Avenue locality in Hamilton, Ontario (Fig. 1.1, 1.2; 43°13'47.5"N, 79°48'55.4"W). The corals were obtained from a 15-mm-thick yellowish silicified sandstone bed 1.2 m above the base of the formation. That bed, which also yielded scolecodonts, was situated 0.3 m above a shale parting marking the likely change from terrestrial to marine deposition. The collecting site was 32 m southeast of the northwestern end of the 112-m-long exposure (see Rutka, 1986, fig. 4-19; Brusse et al., 1987, fig. 28). On 11 June 2022, R.J.E. verified that the exposure is still accessible, although largely overgrown. The 1986 collection yielded 14 coral specimens that are sufficiently well preserved for systematic study. From those specimens, 25 transverse and 10 longitudinal thin sections were prepared.

In addition to qualitative information, the following biometric data were obtained from transverse thin sections where possible: corallum diameter and radius, number of major septa, thickness of major septa (based on a typical septum on counter side of corallum, measured halfway between corallum periphery and axial end of septum), length of major septa (based on a typical septum, measured from corallum periphery to axial end of septum), thickness of cardinal septum (measured halfway between corallum periphery and axial end of septum), length of cardinal septum (measured from corallum periphery to axial end of septum), width of cardinal fossula (distance from median line of septum on one side of fossula to median line of septum on other side of fossula, measured midway between peripheral and axial ends of fossula), length of minor



septa (based on a typical septum, measured from corallum periphery to axial end of septum), and thickness of stereozone (measured midway between a typical major septum and adjacent minor septum).

In addition to qualitative information, the following biometric data were obtained from longitudinal thin sections where possible: thickness of tabulae (based on a typical tabula), spacing of tabulae in axial region (tabulae counted over a measured distance along corallum axis, then calculated as number per centimeter), and spacing of tabulae in septal region (tabulae counted over a measured distance along midline of septal region, then calculated as number per centimeter).

Cephalopod.—The only cephalopod known from the Whirlpool Formation was collected by Grant (1892, 1897a, b, 1900) at a Jolley Cut quarry in Hamilton, Ontario (Fig. 1.1, 1.3). On 2–4 March 1985, R.A.H. compared the lithology of the specimen with the still existing exposures and located the most closely matching occurrence (43°14'43.0"N, 79°51'35.4"W). The rock is weathered to the right color of pale yellow and composed of silica-cemented quartz grains (diameter 0.1–0.2 mm) with a green mineral and black phosphatic spots (diameter 0.3 mm). At the base of the bed are load structures (width 50 mm) and sinuous horizontal traces (width 2 mm) identified as *Planolites* Nicholson, 1873. This corresponds to the base of a low-angle cross-laminated interval at Section D of Rutka (1986, fig. 4-14; Brusse et al., 1987, fig. 29; Brett et al., 1991, fig. 46). The underlying 15-cm-thick sandstone layer has an irregular upper surface with shale patches and a smooth basal surface at the contact between the lower (terrestrial) and upper (marine) parts of the Whirlpool Formation.

The cephalopod is preserved on the underside of a 30-mm-thick, fine-grained, laminated sandstone bed as a cast with films of black phosphatic material (Fig. 3). It is envisioned that the ventral side of the annulated shell, with part of the wall broken away anteriorly, was imprinted in an area of mud on the seafloor. Elsewhere, traces of the *Planolites* producer were recorded in the mud. When a layer of fine-grained sand was deposited on top, load structures were produced, the traces were infilled (Fig. 3, arrows E, H), and infilling of the cephalopod imprint resulted in a three-dimensional cast. Several septa are weathered out as grooves in the sandstone (Fig. 3, arrow G) where the external wall was broken away anteriorly, revealing the interior of the shell. Therefore, the absence of septal sutures on the annulated part of the specimen, which are commonly superimposed on surfaces of annulated orthocones, is attributed to the sandstone and some phosphatic films replicating the exterior of a shell wall having no apparent preserved thickness. In the

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Figure 3. *Goryboceras* sp., cast on underside of sandstone bed, ventral view with anterior direction toward top of page; RM 1108. A, anterior end of annulated shell on lateral side of specimen; B, parallel grooves and ridges of uncertain origin; C, siphuncle; D, annulations of shell appear to wedge into each other along hyponomic sinus; E, horizontal *Planolites* trace; F, traces of vertical burrows; G, septa weathered out as grooves; H, horizontal *Planolites* traces; I, posterior end of shell is missing. Upper Ordovician, Hirnantian; sandstone bed 0.15 m above base of upper part of Whirlpool Formation; Jolley Cut locality, Hamilton, Ontario.

anterior portion of the shell, where the wall on the ventral side was broken away, the sandstone matrix has traces of vertical burrows (Fig. 3, arrow F); several horizontal parallel grooves and ridges with a width of 5 mm are of uncertain origin (Fig. 3, arrow B). Laterally, annulations of the shell wall extend to the anterior end of the specimen (Fig. 3, arrow A). The posterior end of the shell is missing (Fig. 3, arrow I).

Repositories and institutional abbreviations.—Specimens referred to in Systematic paleontology are deposited in American Museum of Natural History (AMNH), New York, New York; Geological Survey of Canada (GSC), Ottawa, Ontario; National Museum of Natural History (USNM), Washington, D.C.; Redpath Museum (RM), McGill University, Montréal, Québec; and University of Michigan Museum of Paleontology (UMMP), Ann Arbor, Michigan.

Systematic paleontology

Phylum Cnidaria Hatschek, 1888

Class Anthozoa Ehrenberg, 1834

Subclass Rugosa Milne-Edwards and Haime, 1850

Order Stauriida Verrill, 1865

Suborder Streptelasmatina Wedekind, 1927

Family Streptelasmatae Nicholson in Nicholson and Lydekker, 1889

Subfamily Streptelasmatinae Nicholson in Nicholson and Lydekker, 1889

Genus *Streptelasma* Hall, 1847

Type species.—*Streptelasma corniculum* Hall, 1847 (p. 69 as *Streptoplasma corniculum*, but generic name was corrected to *Streptelasma* on page facing p. 338; pl. 25, figs. 1a–d; fig. 1e was mentioned on p. 69 but not included in pl. 25), by subsequent designation (Roemer, 1861, p. 19); lectotype selected by Neuman (1969, p. 10), original number AMNH 645/1(a), current number AMNH 29548; from lower part of Trenton Limestone (Upper Ordovician, lower Katian; Mohawkian, Chatfieldian), Middleville, New York, USA.

Remarks.—The suprageneric classification below phylum level follows Hill (1981). Many morphologically simple Ordovician and Silurian streptelasmataid species and genera are poorly understood because their ontogeny and/or variability are insufficiently known. As new data and interpretations have emerged, numerous synonyms or possible synonyms have been suggested, as in the case of *Streptelasma* (e.g., Neuman, 1969; McLean, 1974; Elias, 1982; McAuley and Elias, 1990; McLean and Copper, 2013). Comparison with type species is an essential consideration in making generic assignments. Knowledge of the type species of *Streptelasma* is currently based only on the lectotype and a few additional specimens identified as *S. corniculum* from the Trenton Group of New York. They are documented in the following.

The lectotype of *S. corniculum* from Middleville was described and illustrated by Neuman (1969, p. 10, 11, figs. 4–6) and McLean and Copper (2013, p. 20, 21, pl. 1, figs. 1, 2, 6, 11). Transverse sections show only one side of the corallum,

which was cut longitudinally in the cardinal-counter plane. The major septa are moderately dilated and meet in small groups at the corallum axis in the early ontogenetic stage. They become thinner, shorter, and slightly wavy by the late stage (corallum diameter 17 mm), a short distance below the base of the calice, where their length is ~0.6 of the corallum radius and the axial region is open. Minor septa are generally confined to the narrow stereozone, extending a short distance beyond it in the late stage. Although the cardinal septum was removed by longitudinal cutting of the specimen, sediment beside its presumed location in the late stage suggests that tabulae were depressed in a fossula. In longitudinal section, tabulae are thin and widely spaced. They are convex upward in the septal region, with some slightly upturned where they join the stereozone, and slightly depressed in the axial region.

McLean and Copper (2013, p. 21, pl. 1, figs. 3–5, 7) also described and illustrated paralectotype AMNH 29551 from Middleville, which they considered conspecific with the lectotype. Moderately dilated major septa extending to the axis and the presence of a cardinal fossula are confirmed in transverse sections representing the intermediate stage. Features in a longitudinal section of the late stage are like those of the lectotype. Cox (1937, pl. 1, fig. 1) published a camera lucida drawing of the longitudinal section of USNM 322D, identified as *S. corniculum* from Middleville. Depression of tabulae in the axial region is less apparent than in the lectotype and paralectotype, but this section may be off-center or oblique.

McLean and Copper (2013, p. 21, pl. 1, figs. 8–10, 12) documented two relatively small paralectotypes, AMNH 29547 and AMNH 29549 from Watertown, which they suggested may represent juvenile forms of *S. corniculum*. The major septa are moderately dilated and extend to the axis in the early ontogenetic stage. Stumm (1963, pl. 1, figs. 4–6) illustrated transverse sections of UMMP IP 44327, identified as *S. corniculum* from near Watertown. However, the magnification and resolution of his figures are insufficient to verify certain details. Therefore, new photographs are presented here. In the early stage (Fig. 4.1), moderately to strongly dilated major septa extend to the axis. In the intermediate stage (Fig. 4.2), major septa meet in small groups at or near the axis. The long cardinal septum is thinner than other major septa, and it occurs in a prominent, straight-sided fossula that is sediment-filled, indicating depression of tabulae. In the late stage, the corallum diameter is 16 mm at the base of the calice (Fig. 4.3). The major septa are thin, slightly wavy, and shorter, reaching to ~0.8 of the corallum radius, with a few septal lobes extending into the axial region. The cardinal septum is distinctly shorter than other major septa. Minor septa extend a short distance beyond the stereozone.

Stumm (1963) figured two specimens identified as *S. corniculum* from Martinsburg. Corallum UMMP IP 45676 is considered to represent the intermediate stage of development. The external view (Stumm, 1963, pl. 1, fig. 1; diameter at calice rim 16 mm) shows that major septa extend to near the axis at the base of the calice, with the cardinal septum being the longest. In a longitudinal section of UMMP IP 44328 (Stumm, 1963, pl. 1, fig. 7), tabulae are widely spaced and arched upward in the septal region. The nature of tabulae in the axial region is unclear.

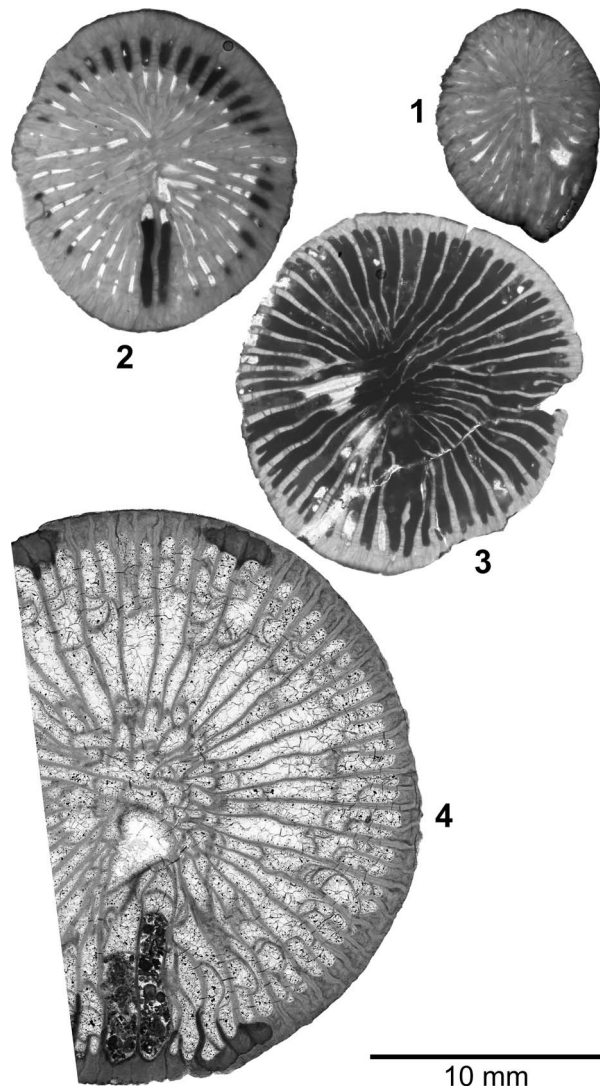


Figure 4. (1–3) *Streptelasma corniculum* Hall, 1847 of Stumm (1963), relatively thick transverse thin sections mounted in Canada Balsam (oriented with cardinal septum in six o'clock position). UMMP IP 44327; photographs taken by J.E. Bauer; images provided by the University of Michigan Museum of Paleontology under a CC-BY-NC 4.0 and published with permission here. Upper Ordovician, lower Katian (Mohawkian, Chatfieldian); Trenton Group (lower Cobourg); cut on Watertown–Syracuse Highway, ~9.7 km from Watertown (just within Watertown quadrangle), New York; collected by G.W. Sinclair. (4) *Streptelasma subregulare* (Savage, 1913), transverse thin section (oriented with apical direction of corallum into the page and cardinal septum in six o'clock position). USNM 423141. Upper Ordovician, Hirnantian; Kissenger Limestone Member, Bryant Knob Formation; cut on west side of State Route 79 just west of Kissenger Hill, Missouri (stratigraphic interval 3 at section 18 of McAuley and Elias, 1990; Fig. 1.1, area D).

There are several complicating factors in understanding *S. corniculum* and its variability, given the limitations of available data. The eight coralla documented in the preceding are from three geographic locations in New York, spanning a distance of ~50 km from Middleville to Watertown, with Martinsburg in between. Specimens may have been obtained from different stratigraphic positions within the Trenton Group. Lectotype AMNH 29548, selected from the collection on which Hall (1847) based the species, is from the lower part of the Trenton Limestone according to its original label (Neuman, 1969). However, it is uncertain how that relates to stratigraphic units within the Trenton

Group as currently recognized (Cornell et al., 2005). The three specimens illustrated by Stumm (1963; UMMP IP 44327, 44328, 44376) were reportedly from the lower Cobourg. The term Cobourg was formerly used for the upper Trenton; the lower Cobourg is now known as the Rust Formation of the Trenton Group (Cornell et al., 2005). Of the eight coralla documented in the preceding, only two provide information on the late ontogenetic stage. The length of major septa is ~0.6 of the corallum radius in lectotype AMNH 29548 and ~0.8 in UMMP IP 44327.

McLean and Copper (2013, p. 21, 27) distinguished *Streptelasma*, which they characterized as having “significantly shortened” major septa in the late ontogenetic stage, from *Helicelasma* Neuman, 1969 with “consistently longer” major septa. However, such a distinction seems arbitrary without quantification of a clear separation. The type species of *Helicelasma* is *H. simplex* Neuman, 1969 from the *Dalmanitina* Beds in Östergötland, Sweden. Those strata are now named the Loka Formation, which is Late Ordovician (Hirnantian) in age (Wang et al., 2019). The holotype of *H. simplex* is known only in longitudinal section (Neuman, 1969, figs. 23b, 26). A transverse section (diameter ~5 mm) from just below the calice of a small, preadult specimen shows that major septa nearly reach the corallum axis (Neuman, 1969, fig. 25c). In a larger, presumably mature individual, a transverse section (diameter ~8.5 mm) below the base of the calice has major septa that extend to ~0.8 of the corallum radius (Neuman, 1969, fig. 24e). The holotype of a large species, *H. mutabile* McLean and Copper, 2013, is from early Silurian (Llandovery, Telychian) strata in the Jupiter River Formation on Anticosti Island, Québec (Fig. 1.1, crosshatched area). In a transverse section (diameter ~36 mm) of the late stage below the calice, the length of major septa is ~0.7–0.8 of the corallum radius (McLean and Copper, 2013, pl. 4, fig. 6).

For comparison, *Streptelasma subregulare* (Savage, 1913) is an extraordinarily variable species that occurs in Hirnantian strata of the Edgewood Province in the east-central United States (Fig. 1.1). In the holotype, the length of major septa is ~0.4–0.6 of the corallum radius at a diameter of ~30 mm (Elias, 1982, pl. 4, fig. 7s). An extensive dataset including many specimens of *S. subregulare* shows a continuous range from major septa shorter than 0.4 of the corallum radius to major septa that extend to the corallum axis, even in the late stage of relatively large specimens at diameters of ≥ 25 mm (McAuley and Elias, 1990, fig. 14). Figure 4.4 shows a transverse section (diameter 25 mm) with major septa extending to ~0.8 of the corallum radius in the late stage a short distance below the calice. Detailed analysis of *S. subregulare* indicates a general relation between septal length and a paleoenvironmental gradient (Elias and Young, 2001, fig. 3). Major septa tended to be short in restricted, low-energy, high-turbidity conditions and progressively longer in more open, higher-energy, lower-turbidity conditions.

The preceding comparisons suggest that *Streptelasma* and *Helicelasma* cannot be clearly distinguished on the basis of major septal length in the late ontogenetic stage. *Helicelasma* is probably a junior synonym of *Streptelasma*.

Streptelasma rutkai new species
Figure 2

Types.—Holotype GSC 143181 (Fig. 2.2–2.6), paratype GSC 143182 (Fig. 2.8). Upper Ordovician, Hirnantian; sandstone bed 1.2 m above base of Whirlpool Formation; Kenilworth Avenue locality, Hamilton, Ontario.

Diagnosis.—Corallum trochoid, length and diameter up to ~40 mm and ~35 mm, respectively. Major septa moderately dilated and long in early ontogenetic stage, becoming thin and shorter during ontogeny, with length ~0.7–0.8 of corallum radius and a few septal lobes in axial region in late stage. Cardinal septum and fossula conspicuous in all ontogenetic stages. Stereozone thin; minor septa become relatively long during ontogeny. Tabulae convex upward in septal region, strongly depressed in cardinal fossula, slightly depressed and more closely spaced in axial region.

Occurrence.—Upper Ordovician, Hirnantian; Whirlpool Formation; Hamilton, Ontario.

Description.—Corallum trochoid, straight to very slightly curved with convex cardinal side; estimated maximum length ~40 mm based on longest nearly complete specimen (holotype GSC 143181), estimated maximum diameter ~35 mm based on broadest nearly complete specimen (GSC 143186); exterior with septal grooves and interseptal ridges. All specimens silicified; original microstructure of wall, septa, and tabulae obliterated.

Relation between number of major septa and corallum diameter shown in Figure 5. During early ontogenetic stage (Fig. 2.1, 2.2, 2.10), major septa moderately dilated, extend nearly to corallum axis where they meet in small groups. During intermediate stage (Fig. 2.3, 2.7, 2.12), major septa become less dilated, slightly shorter, may become slightly wavy, form slight

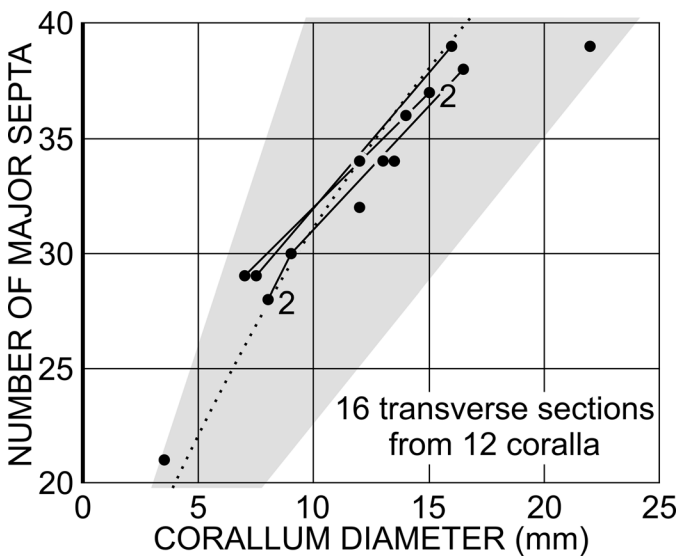


Figure 5. Relation between number of major septa and corallum diameter in *Streptelasma rutkae* n. sp. from Whirlpool Formation; data shown as filled circles, with numbers beside circles indicating frequencies greater than one and solid lines connecting data from same specimens. Shaded area shows range for *S. subregulare* from Edgewood Province, excluding a few anomalous values; dotted line used to compare data from different stratigraphic sections in Edgewood Province (see McAuley and Elias, 1990, fig. 13).

counterclockwise whorl in a few cases, meet in small groups from which a few septal lobes may extend. During late stage (Fig. 2.4, 2.8, 2.11, 2.13), major septa undilated and thin, shorter, slightly wavy; some ends meet; a few septal lobes extend axially. Relation between thickness of major septa and corallum diameter shown in Figure 6. Relation between length of major septa (as a fraction of corallum radius) and corallum diameter shown in Figure 7.

Cardinal septum and fossula conspicuous in all ontogenetic stages (Fig. 2.1–2.4, 2.7, 2.8, 2.10–2.13). Compared with typical major septa, cardinal septum usually thinner (as observed in 50% of 10 transverse sections), less commonly same thickness (30%), least commonly thicker (20%). Cardinal septum usually longer than typical major septa (as observed in 75% of 16 transverse sections) or less commonly same length (25%), may extend to corallum axis, may have axial lobe. Shape of cardinal fossula variable among coralla and usually among ontogenetic stages within coralla. Shapes correspond to four of five numbered categories defined by McAuley and Elias (1990, p. 37): usually biconvex with maximum width midway between peripheral and axial ends (category 4; as observed in 50% of 14 transverse sections), less commonly hourglass-shaped with constriction midway between peripheral and axial ends (category 5; 29%), uncommonly with width constant from peripheral end to axial end (category 2; 14%), rarely with width decreasing from peripheral end to axial end (category 1; 7%). Relation between width of cardinal fossula and corallum diameter shown in Figure 8.

Minor septa extend beyond stereozone, increase in length during ontogeny (Fig. 2.1–2.4, 2.7, 2.8, 2.10–2.13), average length 0.21 of corallum radius (range 0.12–0.36 based on 16

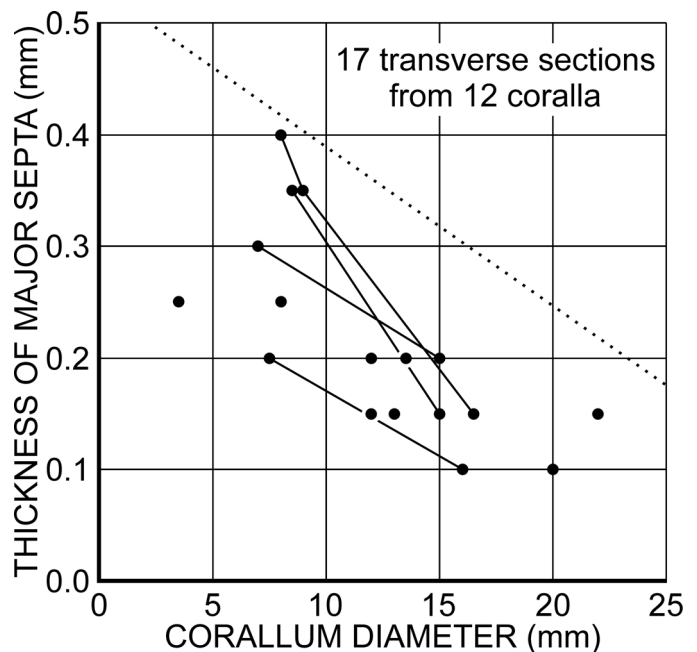


Figure 6. Relation between thickness of major septa and corallum diameter in *Streptelasma rutkae* n. sp. from Whirlpool Formation; data shown as filled circles, with solid lines connecting data from same specimens. Dotted line used for comparison with *S. subregulare* at different stratigraphic sections in Edgewood Province (see McAuley and Elias, 1990, fig. 15).

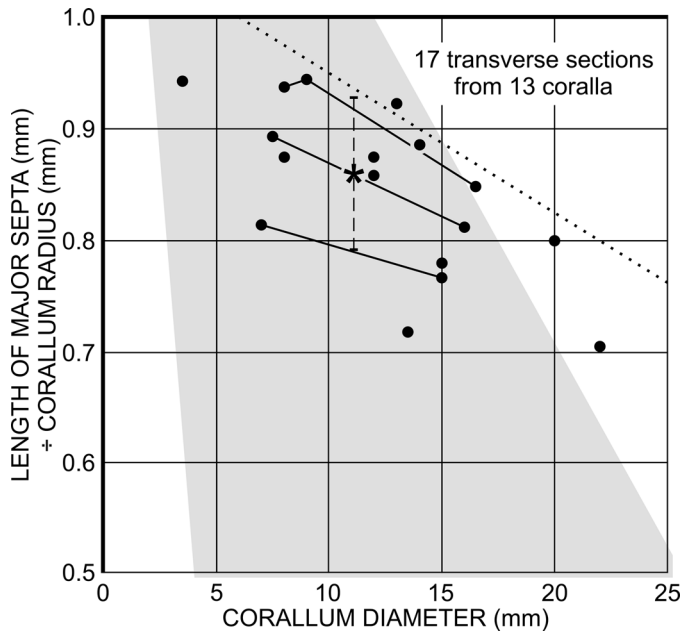


Figure 7. Relation between length of major septa and corallum diameter in *Streptelasma rutkae* n. sp. from Whirlpool Formation. Length of a typical septum was divided by corallum radius, yielding a value ≤ 1.0 . Data shown as filled circles, with solid lines connecting data from same specimens. Asterisk is mean value (0.86) and dashed line is standard deviation (0.07) for transverse sections at corallum diameters of 5–15 mm (average 11.2 mm; based on 12 sections from 10 coralla). Shaded area shows range of typical data for *S. subregulare* from Edgewood Province; values as low as 0.2 occur in the province (see McAuley and Elias, 1990, fig. 14, lower graph). For *S. subregulare* from stratigraphic intervals 3 and 4 at section 18, most values plot in the shaded and unshaded areas above dotted line (see McAuley and Elias, 1990, fig. 14, upper graph).

transverse sections), in some cases longest adjacent to counter septum, rarely slightly contraclined. Stereozone thin, average thickness 0.11 of corallum radius (range 0.05–0.20 based on 18 transverse sections).

Tabulae mostly incomplete (Fig. 2.5, 2.6, 2.9), convex upward in septal region, may be slightly upturned at stereozone, strongly depressed in cardinal fossula, slightly depressed in axial region, thin (thickness of typical tabula 0.10 mm in five

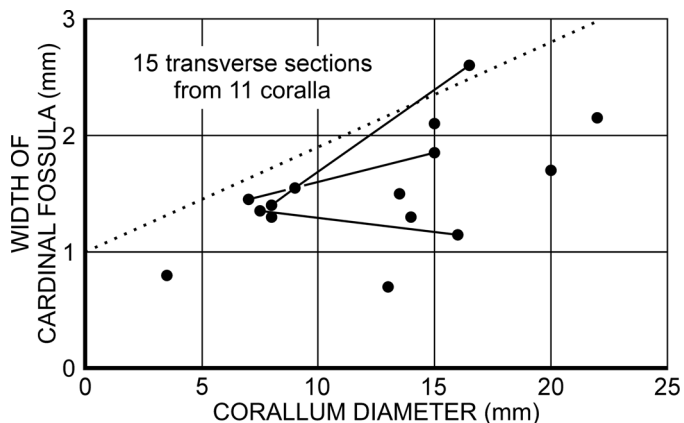


Figure 8. Relation between width of cardinal fossula and corallum diameter in *Streptelasma rutkae* n. sp. from Whirlpool Formation; data shown as filled circles, with solid lines connecting data from same specimens. Dotted line used for comparison with *S. subregulare* at different stratigraphic sections in Edgewood Province (see McAuley and Elias, 1990, fig. 16).

longitudinal sections), spacing greater in septal region (average 15 tabulae per centimeter based on five longitudinal sections) than in axial region (average 22 tabulae per centimeter based on two longitudinal sections).

Etymology.—The species is named for Margaret A. Rutka, in recognition of her research on the Whirlpool Formation.

Materials.—In addition to the types: GSC 143183 (Fig. 2.1), GSC 143184, GSC 143185, GSC 143186 (Fig. 2.9), GSC 143187 (Fig. 2.12, 2.13), GSC 143188 (Fig. 2.7), GSC 143189 (Fig. 2.10, 2.11), GSC 143190–143194. Upper Ordovician, Hirnantian; sandstone bed 1.2 m above base of Whirlpool Formation; Kenilworth Avenue locality, Hamilton, Ontario.

Remarks.—Coralla from the Whirlpool Formation will be compared with *Streptelasma corniculum* to verify the generic assignment, with *S. subregulare* to demonstrate that they represent a new species and with *S. affine* (Billings, 1865) to show their difference from another species that occurs in North American Hirnantian strata.

Comparison with *S. corniculum*.—The morphology of *S. corniculum*, the type species of *Streptelasma*, was described in Remarks under the genus. Characters of the Whirlpool coralla that resemble those of *S. corniculum* include moderately dilated major septa that meet in small groups axially in the early ontogenetic stage; major septa that become thinner, shorter, and slightly wavy by the late stage; a conspicuous cardinal septum and fossula in which tabulae are depressed; a narrow stereozone; and thin, relatively widely spaced tabulae that are slightly depressed in the axial region and convex upward in the septal region, with some slightly upturned at the stereozone.

In *S. corniculum*, the late ontogenetic stage is known in the lectotype, where the length of major septa is ~ 0.6 of the corallum radius, and in another specimen, where the length is ~ 0.8 (Fig. 4.3). Major septa in the Whirlpool coralla extend to ~ 0.7 – 0.8 of the corallum radius in the late stage (Fig. 7). Lengths of major septa in a large collection of *S. subregulare* (see Fig. 7) range from much shorter than in *S. corniculum* to longer than in the Whirlpool coralla, indicating that a wide range of septal lengths can be accommodated within the genus. In the late ontogenetic stage, the axial region is open in the lectotype of *S. corniculum*; a few septal lobes extend into the axial region in another corallum (Fig. 4.3). In *S. subregulare*, a few septal lobes occur in some coralla (McAuley and Elias, 1990; Fig. 4.4). The axial region in *S. affine* varies from open to having septal lobes (Elias, 1982, pl. 5, figs. 13, 18). A few septal lobes are present in the Whirlpool coralla. All things considered, the Whirlpool coralla are assigned to the genus *Streptelasma*.

Comparison with *S. subregulare*.—Coralla from the Whirlpool Formation are most closely comparable to *S. subregulare*, which is the most abundant and widespread coral in the Hirnantian-age Edgewood Province of the east-central United States (Elias and Young, 1998; Elias et al., 2013a). For information on stratigraphic sections and collecting intervals in outcrop areas of the Edgewood Province, see McAuley and Elias (1990) and Elias (1992); the outcrop areas are shown in Figure 1.1.

Streptelasma subregulare is an extraordinarily variable species. Modern descriptions and photographs have been provided by Elias (1982, p. 57, 58, pl. 4, figs. 7–22; 1992, pl. 1, figs. 1–9), McAuley and Elias (1990, p. 34–42, pl. 1, figs. 1–19, pl. 2, figs. 1–12, pl. 3, figs. 1–18, pl. 4, figs. 1–13, pl. 5, figs. 1–10), and Elias and Young (1992, fig. 3g–i); see also Figure 4.4.

Corallum shape and size are far more variable in *S. subregulare* than in the Whirlpool materials. In addition to trochoid coralla that are straight to very slightly curved, as in the Whirlpool Formation, *S. subregulare* also includes ceratoid to rarely subcylindrical forms and moderately to in some cases greatly curved shapes (McAuley and Elias, 1990, table 4). Coralla of *S. subregulare* attain a greater maximum size (length 102 mm, diameter 44 mm) than those in the Whirlpool Formation (length ~40 mm, diameter ~35 mm).

The relation between number of major septa and corallum diameter for the Whirlpool coralla is typical of *S. subregulare* at most stratigraphic sections in the Edgewood Province (Fig. 5). However, compared with the Whirlpool coralla, the proportion of data points that plot above an arbitrary dotted line (see Fig. 5) is much greater for *S. subregulare* at stratigraphic sections 20 and 31 (in outcrop area C), and the proportion of data points that plot below the dotted line is much greater for *S. subregulare* at section 21 (in area A) and section 19 (in area C) (McAuley and Elias, 1990, fig. 13, table 5).

Data points for the thickness of major septa in the Whirlpool coralla plot below the dotted line in Figure 6 but are within the overall range for *S. subregulare* (McAuley and Elias, 1990, fig. 15). Similarly, data for *S. subregulare* plot predominantly below the dotted line at sections 19, 20, and 31 (in area C) and section 32 (in area F); however, data plot predominantly above the dotted line at sections 14 and 18 (in area D) (McAuley and Elias, 1990, fig. 15, table 5). Data points for the length of major septa in the Whirlpool coralla plot mostly within the typical range for *S. subregulare*, but values for the Whirlpool coralla are ~0.7 or higher (Fig. 7); values for *S. subregulare* are commonly as low as 0.5 and the range extends down to 0.2 (McAuley and Elias, 1990, fig. 14, lower graph). Furthermore, unlike the Whirlpool coralla, data for *S. subregulare* in stratigraphic intervals 3 and 4 at section 18 (in area D) plot mostly above the dotted line that is shown in Figure 7 (McAuley and Elias, 1990, fig. 14, upper graph). In the late ontogenetic stage, septal lobes are present in the axial region of Whirlpool coralla, whereas the axial region is usually open in *S. subregulare*.

Regarding the length of major septa at corallum diameters of 5–15 mm, the Whirlpool coralla have a higher mean value (Fig. 7, asterisk) than all but two occurrences of *S. subregulare* (Elias and Young, 2001, fig. 3); mean values for *S. subregulare* are slightly higher at section 15 and in the combined stratigraphic intervals 3 and 4 at section 18 (in area D). Compared with the Whirlpool coralla, mean values for *S. subregulare* are significantly lower at section 19 (in area C) and section 34 (in area E) (Elias and Young, 2001, fig. 3). The standard deviation of the mean value for the Whirlpool coralla (Fig. 7, dashed line) is considerably smaller than that for occurrences of *S. subregulare* (Elias and Young, 2001, fig. 3).

The cardinal septum is conspicuous in all ontogenetic stages of the Whirlpool coralla, usually being thinner and longer

than typical major septa. In *S. subregulare*, however, the cardinal septum is most commonly inconspicuous, being the same length and thickness as other typical major septa, but the range of variability is high (McAuley and Elias, 1990, table 6). The cardinal septum in *S. subregulare* is predominantly thinner and longer than typical major septa only at section 31 (in area C) (McAuley and Elias, 1990, table 6). Regarding shape of the cardinal fossula, category 4 is predominant in the Whirlpool coralla, followed by category 5; category 3 (width increasing from peripheral end to axial end) is absent. In *S. subregulare*, category 4 is predominant at sections 19, 20, and 31 (in area C), but category 2 ranks second and category 3 occurs at those sections (McAuley and Elias, 1990, table 7). Data points for width of the cardinal fossula in Whirlpool coralla (Fig. 8) plot within the typical range for *S. subregulare* (McAuley and Elias, 1990, fig. 16). However, data for *S. subregulare* at section 18 (in area D) and section 19 (in area C) differ in plotting predominantly above the dotted line shown in Figure 8 (McAuley and Elias, 1990, fig. 16, table 5).

In ontogenetic stages where major septa are thin, minor septa are relatively long in the Whirlpool coralla (Fig. 2.4, 2.8, 2.11, 2.13). They are seldom as long in *S. subregulare* (Elias, 1982, pl. 4, figs. 17, 22; McAuley and Elias, 1990, pl. 1, figs. 3, 12, 16, 19, pl. 2, figs. 2, 3, pl. 5, fig. 10; Fig. 4.4). In Whirlpool coralla, as in *S. subregulare*, minor septa are in some cases longest adjacent to the counter septum. Width of the stereozone in Whirlpool coralla (0.05–0.20 of corallum radius) is similar to that in *S. subregulare* (0.05–0.15; McAuley and Elias, 1990, p. 38).

The close spacing of tabulae in the axial region of Whirlpool coralla (average 22 tabulae per centimeter) is comparable to some specimens of *S. subregulare* at section 17 (in area D) (McAuley and Elias, 1990, fig. 17). However, tabulae in the septal region are closely spaced in those specimens of *S. subregulare* (e.g., McAuley and Elias, 1990, pl. 3, fig. 6), whereas they are relatively widely spaced in Whirlpool coralla (Fig. 2.5, 2.6, 2.9).

In summary, the tremendous overall range of variability in *S. subregulare* encompasses morphologic characters of the Whirlpool coralla; however, the particular combination of features in the Whirlpool coralla makes them distinct. Although a few characters of the Whirlpool coralla are notably consistent with coralla of *S. subregulare* at several stratigraphic sections, other characters of *S. subregulare* at those sections are different. The combination of features that distinguish the Whirlpool coralla as a group includes major septa that become thin during ontogeny; the length of major septa that decreases during ontogeny to ~0.7–0.8 of the corallum radius, with a few septal lobes present in the axial region; the conspicuous cardinal septum and fossula in all ontogenetic stages; minor septa that become relatively long during ontogeny; and tabulae that are closely spaced in the axial region. It is concluded that the Whirlpool coralla represent a new species, *S. rutkae*, which shows relatively little intraspecific variability.

Comparison with *S. affine*.—*Streptelasma affine* is known from the Upper Ordovician (upper Katian–Hirnantian; Richmondian–Gamachian) on Anticosti Island, Québec (Bolton, 1981, pl. 3, figs. 3–8; Elias, 1982, p. 59, 60, pl. 5, figs. 4–18) (Fig. 1.1, crosshatched area). It is an exceptionally large species

(maximum length 170 mm, diameter 55 mm), far larger than *S. rutkae* (maximum length ~40 mm, diameter ~35 mm). Coralla of *S. affine* are initially ceratoid to trochoid and slightly to moderately curved, becoming subcylindrical and usually straight in later stages; coralla of *S. rutkae* are trochoid and straight to very slightly curved. Like *S. rutkae*, the major septa in *S. affine* become thin and slightly wavy and withdraw from the axis during ontogeny. However, in some cases they extend to <0.5 of the corallum radius, which is considerably less than the minimum value of ~0.7 in *S. rutkae*. In *S. affine*, there is variation from coralla with an open axial region to those with septal lobes; all coralla of *S. rutkae* have a few septal lobes in the axial region. The cardinal septum is generally indistinct in *S. affine*, whereas *S. rutkae* has a conspicuous cardinal septum in a pronounced fossula with depressed tabulae. The stereozone is usually thicker in *S. affine* than in *S. rutkae*. *Streptelasma affine* and *S. rutkae* are easily distinguishable from one another on the basis of the combinations of features exhibited by coralla.

Phylum Mollusca Linnaeus, 1758
 Class Cephalopoda Cuvier, 1797
 Subclass Orthoceratoidea Kuhn, 1940
 Order Orthocerida Kuhn, 1940
 Family Pseudorthoceratidae Flower and Caster, 1935
 Genus *Gorbyoceras* Shimizu and Obata, 1935

Type species.—*Orthoceras gorbyi* Miller, 1894 (p. 322, pl. 10, fig. 2), by original designation (Shimizu and Obata, 1935, p. 4); holotype USNM 64337 (Flower, 1946, p. 148; Frey, 1995, p. 64); from Saluda Formation (Upper Ordovician, upper Katian; Cincinnati, Richmondian), Indiana, USA.

Remarks.—The type species, *Gorbyoceras gorbyi*, was described by Miller (1894) from two fragmentary casts showing highly oblique, low annulations and no axial lirae. Flower (1946, p. 145–149, pl. 2, figs. 1, 9, 10, pl. 4, figs. 3, 6, 7) and Frey (1995, p. 63, 64, pl. 12, figs. 12, 13) also studied other specimens from the Saluda Formation in Indiana and Ohio and the basal Whitewater Formation (Upper Ordovician, upper Katian; Cincinnati, Richmondian) in Ohio.

Gorbyoceras sp.
 Figure 3

- 1892 *Orthoceras*; Grant, p. 149.
- 1897a *Orthoceras*; Grant, p. 28.
- 1897b *Orthoceras* species; Grant, p. 136.
- 1900 *Orthoceras*; Grant, p. 83.
- 1986 *Gorbyoceras*; Hewitt, fig. 2.

Occurrence.—Upper Ordovician, Hirnantian; Whirlpool Formation; Hamilton, Ontario.

Description.—Annulated orthocone with slightly exogastric curvature of chord height around 3 mm in ventral 90 mm exposed length. At posterior end of specimen, crest of annulation has diameter ~13.2 mm (measured laterally and dorsoventrally) and height 0.6 mm, and wavelength of annulations is 3.6 mm. At a distance 124 mm and 30

annulations anteriorly, crest of annulation has diameter 27.4 mm (measured laterally) and height ~1.0 mm, and wavelength of annulations is 4.5 mm. Annulations appear to wedge into each other (Fig. 3, arrow D), bending into a ventral hyponomic sinus. At diameter ~20 mm, external surface has faint axial striae spaced 3 mm apart. Exposed interior of shell shows septa with radius of curvature 14 mm (Fig. 3, arrow G). Siphuncle in subcentral position laterally and dorsoventrally (Fig. 3, arrow C), extends 15 mm anteriorly beyond last unbroken septum, visible diameter 2 mm with transverse ridges spaced at intervals of 5 mm. These ridges appear to be cyrtocoanitic necks of septa that were broken off.

Material.—Specimen RM 1108. Upper Ordovician, Hirnantian; 0.15 m above base of upper part of Whirlpool Formation; Jolley Cut locality, Hamilton, Ontario.

Remarks.—The suprageneric classification follows Frey (1995). Two named species of annulated orthocones have been based on fragments from units formerly interpreted as basal Silurian in eastern North America (see “Cephalopod data” in the section “Age of Whirlpool Formation and associated strata”), as follows.

Spyroceras microtextile Foerste, 1923 is from the Centerville Member of the Whippoorwill Formation in Ohio. Judging from the description and photographs (Foerste, 1923, p. 87, pl. 15, fig. 2a–c), the shell is “very slowly enlarging” to a diameter of only 9 mm, with five transverse annulations in 9 mm and with fine longitudinal striae that are more conspicuous than the fine transverse ones. Flower (1946) noted that generic reassignments are necessary for annulated Ordovician species placed by earlier workers in the Devonian genus *Spyroceras* Hyatt, 1884. Likely possibilities are *Gorbyoceras* and *Anaspyroceras* Shimizu and Obata, 1935, in which he placed some of those species. However, internal structures in many of the other species (including *S. microtextile*) are insufficiently known for assignment to a particular genus.

Dawsonoceras tenuilineatum Savage, 1913, from the Wilhelmi Formation in northeastern Illinois, was documented by Savage (1913, p. 119, pl. 7, fig. 22). The illustrated portion of the specimen was said to be from about half the greatest diameter. At a diameter of 25 mm, there are five transverse annulations in ~25 mm, showing no hint of expansion. Longitudinal ornaments look less conspicuous than the transverse ones between the annulation crests on the photograph. Flower (1962) accepted the generic name *Dawsonoceras* Hyatt, 1884 for this species, which he cited as the only known local species of that genus of early Silurian age. Like the mid-Silurian (Wenlock) type species *D. annulatum* (Sowerby, 1818) specified by Hyatt (1884), and the specimen from the Jolley Cut (above the crinoidal lithology in the Gasport Formation) on which his generic concept was based, *D. tenuilineatum* as well as *S. microtextile* differ from the Whirlpool specimen in giving no hint at a large apical angle and axial curvature. Three *Dawsonoceras* specimens were seen by R.A.H. (3 March 1989) on a 12 m² bedding plane in the Goat Island Formation, which served as the basement floor of a house built on top of the Niagara Escarpment at 21 East 9th Street in

Hamilton. The shells were remarkably straight and slowly enlarging up to the body chamber (30 to 70 mm diameter in a length of 670 mm, 20 to 50 mm in 470 mm, and ? to 50 mm in 350 mm). The transverse annulations disappeared at the body chamber.

In the specimen from the Whirlpool Formation, the visible diameter of the longitudinal ridge with transverse ridges (Fig. 3, arrow C) is too small to be the whole siphuncle, which in both *Dawsonoceras* and *Gorbyoceras* is ~20% of the diameter of the chambers around them. In *Dawsonoceras* and other orthocones with short septal necks (orthochoanitic), siphuncles are preserved as segmented cylindrical fillings of their lumen. The deep and transverse grooves of such siphuncles are not seen on the convex and probably partly buried surface of the siphuncle in the Whirlpool specimen. In contrast with *Dawsonoceras*, septal necks in *Gorbyoceras* are longer and curved into swollen siphuncle connecting rings (cyrtchoanitic), with posterior endosiphuncular deposits (Frey, 1995, pl. 12, fig. 6). It is therefore possible that the transverse ridges in the Whirlpool specimen represent gradual expansions defined by long septal necks from less obvious thin septal contraction grooves, and that the connecting rings were not yet reinforced by endosiphuncular or cameral deposits in the broken anterior chambers. According to Frey (1995), endosiphuncular deposits are seen only to a shell diameter of 15 mm in *G. hammelli* (Foerste, 1910).

Although the Whirlpool specimen lacks the more highly oblique annulations illustrated from various *Gorbyoceras* species in the Richmondian of the Cincinnati Arch region (Flower, 1946; Frey, 1995), it is assigned to that genus because there is curvature of the shell axis, while the septa within the annulations appear more concave and closely spaced than those of the sectioned *Anaspyroceras* specimen of Richmondian age from Manitoulin Island, illustrated by Copper (1978, pl. 5, fig. 3). Having examined the photograph of the Whirlpool specimen, R.C. Frey (R.C. Frey, personal communication to R.A.H., 1986) stated: “*Anaspyroceras* typically has subtubular and suborthochoanitic necks. *Gorbyoceras*, as you pointed out, has more expanded segments and cyrtchoanitic necks. The impression of the siphuncle in your specimen does suggest it is *Gorbyoceras*.”

The cephalopod from the Whirlpool Formation differs in ornament from the type species of *Gorbyoceras*, *G. gorbyi*. A better match among other Cincinnati species assigned to this genus (Flower, 1946; Frey, 1995) is *G. duncani* Flower, 1946, from the lower and upper Whitewater Formation and Saluda Formation in Ohio and Indiana (Flower, 1946, p. 156, 157, pl. 1, figs. 1, 6, pl. 4, fig. 12; Sweet, 1964, fig. 185.4). The latter species has transverse annulations and axial lirae and is a similar size and shape to the Whirlpool specimen. However, given the state of preservation of the cephalopod from the Whirlpool Formation and the lack of additional material, it is identified as *Gorbyoceras* sp. rather than assigned to a new species or a previously named species based on better-preserved Richmondian material from the Cincinnati Arch region, for which internal structures are known.

The wedging of annulations on the Whirlpool specimen (Fig. 3, arrow D) is comparable to that seen in the original figure of *Spyroceras mcfarlani* Foerste, 1932 from the

Chatfieldian-age Perryville Member of the Lexington Limestone in Kentucky (Foerste, 1932, pl. 14, fig. 5), reillustrated as “*Spyroceras*” *mcfarlani* by Flower (1946, pl. 5, fig. 5). Foerste (1932, p. 107, 108) did not comment on that structure before noting that annulations fade on one side in *Gorbyoceras*, something not seen as wedges on photographs of various *Gorbyoceras* species in Flower (1946) and Frey (1995). Significantly, the longitudinal lirae of the Kentucky specimen pass undeflected across the wedge-like annulations, indicating that the latter were not due to pathological damage during formation of the shell aperture or to deformation during fossilization.

Age of Whirlpool Formation and associated strata

Fossils in the Whirlpool Formation were once considered biostratigraphically undiagnostic (Brett et al., 1995). The formation was therefore assigned an age on the basis of lateral correlation with strata of the Manitoulin Formation, containing a fauna thought to be early Silurian (Llandovery, Rhuddanian). However, Hewitt (1986, fig. 2) identified a cephalopod from the Whirlpool Formation as “Richmondian *Gorbyoceras*,” thereby suggesting a Late Ordovician age for the formation. More recently, Stott and Jin (2007) pointed out that the brachiopod fauna in the Manitoulin Formation is very similar to that in the Mosalem Formation of eastern Iowa (Fig. 1.1, area F). A $\delta^{13}\text{C}$ curve in the lower Mosalem had been interpreted as the HICE, indicating a latest Ordovician (Hirnantian) age (Kleffner et al., 2005; Bergström et al., 2012). Stott and Jin (2007) also noted similarity of the Manitoulin brachiopod fauna with that in the Ellis Bay Formation on Anticosti Island, Québec (Fig. 1.1, crosshatched area), which also records the HICE (Mauviel and Desrochers, 2016).

Sharma and Dix (2004) reported elevated $\delta^{13}\text{C}$ values in ooids near the top of the Queenston Formation in southern Ontario. Bergström et al. (2011) identified the HICE in the upper Queenston Formation, Whirlpool Formation, and overlying Manitoulin Formation in the vicinity of Collingwood, Ontario (Fig. 1.1) and in the upper Queenston and Manitoulin on Bruce Peninsula, where the Whirlpool is absent. However, the HICE was not detected on Manitoulin Island, where the Queenston Formation is missing and the Georgian Bay Formation underlies the Manitoulin Formation. Bergström et al. (2011) concluded that strata of the Manitoulin Formation on Manitoulin Island represent only the upper part of the formation. They considered available conodont data from the Manitoulin Formation consistent with a Hirnantian age. Diagnostic fossils have not been documented from the upper Queenston Formation, but macrofossils and conodonts in the middle Queenston suggest a Late Ordovician (late Katian; Richmondian) age (Liberty and Bolton, 1971; Rudkin et al., 1998; Bergström et al., 2011). The upper (Kagawong) submember of the upper member, Georgian Bay Formation, is considered Late Ordovician (late Katian; Richmondian) on the basis of conodonts and macrofossils (Barnes and Bolton, 1988; Bergström et al., 2011).

Farnam et al. (2019) did not detect the HICE in the Manitoulin Formation near Hamilton, Ontario (Fig. 1, white star), where it overlies the Whirlpool Formation. In northwestern New York, data based on chitinozoans, cryptospores, acritarchs, and scolecodonts, as well as a prominent $\delta^{13}\text{C}$ peak at the base of

the Whirlpool Formation, suggest that the Whirlpool and overlying Power Glen Formation are Late Ordovician (late Katian and/or Hirnantian) in age (Schröder et al., 2016).

The Whirlpool Formation has been traced in the subsurface from southern Ontario and northwestern New York to northwestern Pennsylvania and eastern Ohio (Castle, 1998; Johnson, 1998). In southern Ohio, strata representing the Whirlpool Formation are thought to grade westward into the Centerville Member of the Whippoorwill Formation, with the overlying Belfast Member of the Whippoorwill corresponding at least in part to the Power Glen Formation in northwestern New York (Waid, 2018). On the eastern side of the Cincinnati Arch region in Ohio and Kentucky, a small $\delta^{13}\text{C}$ excursion that may represent the HICE has been detected in the Centerville (Farnam et al., 2019; Farnam and Brett, 2021), and conodonts in the Belfast could be Hirnantian in age (Waid, 2018).

Coral data.—*Streptelasma rutkae* n. sp. from the Whirlpool Formation is considered most closely related to *S. subregulare*, which is the most abundant and widespread coral in the Edgewood Province of the east-central United States (Elias and Young, 1998; Elias et al., 2013a) (Fig. 1.1). The coral fauna in the Edgewood Province was initially thought to range from the latest Ordovician (Hirnantian; Gamachian) to earliest Silurian (Llandovery, Rhuddanian), based primarily on earlier interpretations of conodonts and brachiopods, as well as the corals themselves (McAuley and Elias, 1990; Elias and Young, 1992; Young and Elias, 1995). More recently, the HICE has been recognized in some units containing Edgewood corals including *S. subregulare*, as follows: the lower Mosalem Formation in eastern Iowa (Fig. 1.1, area F), Wilhelmi Formation in northeastern Illinois (Fig. 1.1, area E), and Leemon Formation in southeastern Missouri (Fig. 1.1, area C) (Kleffner et al., 2005; Bergström et al., 2006, 2012). Consequently, the coral fauna in the Edgewood Province is now regarded as only Hirnantian in age (Elias et al., 2013a). Wang et al. (2019) placed this fauna in their globally identifiable Transitional Benthic Fauna 3, probably limited to the late Hirnantian on the basis of biostratigraphic and chemostratigraphic data.

Given the apparent close relationship of *S. subregulare* and *S. rutkae*, the occurrence of *S. rutkae* is consistent with the interpretation that the Whirlpool Formation is Hirnantian. Also noteworthy, McAuley and Elias (1990) mentioned that some coralla of *S. subregulare* are similar to *S. affine* from the Vaureal and Ellis Bay formations on Anticosti Island, Québec (Fig. 1.1, crosshatched area). Those strata are Late Ordovician in age, ranging from late Katian to Hirnantian (Richmondian–Gamachian) (Mauviel and Desrochers, 2016).

Corals have been reported from the Manitoulin Formation at some localities where it overlies the Whirlpool Formation (Rutka, 1986). For example, Williams (1919) listed *Enterolasma* cf. *E. geometricum* (Foerste, 1890) and *Paleofavosites asper* (d'Orbigny, 1850) at Hamilton (Fig. 1.1, white star) and *Enterolasma* cf. *E. geometricum* and *Streptelasma* cf. *S. hoskinsoni* Foerste, 1890 at adjacent Stoney Creek, Ontario. He illustrated specimens of those three species from the Manitoulin Formation on Manitoulin Island (Fig. 1.1), but the identifications and implied ages are questionable.

Enterolasma cf. *E. geometricum* from the Manitoulin Formation is unidentifiable on the basis of the lateral view of a corallum and a view of its calice, showing a morphologically simple solitary rugosan (Williams, 1919, pl. 5, figs. 4a, b). That species was originally described by Foerste (1890) as *Streptelasma callicula* var. *geometricum* from the Brassfield Formation of Ohio, which is considered Llandovery (Rhuddanian–Aeronian) in age (Sullivan et al., 2016). Foerste (1893) subsequently identified it as *Streptelasma? geometricum*. Later, Foerste (1931) listed the species as *E. geometricum* but refigured it as *Zaphrentis (?) geometricum*. Weyer (2007) considered it a questionable species of *Palaeocyathus*.

Streptelasma cf. *S. hoskinsoni* from the Manitoulin Formation is unidentifiable on the basis of the lateral view of a solitary rugosan (Williams, 1919, pl. 5, fig. 5). *Streptelasma hoskinsoni* was originally described by Foerste (1890) from Ohio, probably from the Brassfield Formation (Laub, 1979). It was assigned to *Dinophyllum* Lindström, 1882 by Laub (1979), but could belong to *Helicelasma* or *Parastreptelasma* Li and Gong, 1996 according to McLean and Copper (2013). A silicified solitary rugosan from the Manitoulin Formation on Manitoulin Island was figured as *Streptelasma* sp. by Bolton (1966, pl. 1, figs. 22, 27; 1968, fig. 12.2). The generic assignment cannot be confirmed on the basis of the lateral view of the corallum and a view of its calice, which shows a morphologically simple species with radially arranged septa and possibly a cardinal fossula (Bolton, 1966, pl. 1, fig. 22). The calice of a different specimen, also identified as *Streptelasma* sp., was illustrated by Bolton and Copeland (1972, pl. C, fig. 18). The corallum is morphologically simple, with major septa that join in small groups from which a few septal lobes may extend near the axis. Information on its ontogeny is required to confirm the generic assignment.

Regarding the tabulate coral *Paleofavosites asper* from the Manitoulin Formation, Williams (1919, pl. 6, figs. 1a, b) illustrated the exterior and longitudinal view of a broken corallum. The type area of that species is in the Welsh Borderland, where it occurs in the mid–late Silurian (Wenlock–Ludlow) (Powell and Scrutton, 1978). The Manitoulin material illustrated by Williams (1919) was considered by Laub (1979) to be conspecific with specimens from the Brassfield Formation of Ohio, which he identified as *P. prolificus* (Billings, 1865). Bolton (1966, pl. 1, figs. 25, 26; 1968, fig. 12.20) and Bolton and Copeland (1972, pl. C, fig. 11) also illustrated coralla identified as *P. asper* from the Manitoulin Formation on Manitoulin Island and Bruce Peninsula (Fig. 1.1). Laub (1979) noted the similarity of those coralla and his Brassfield material identified as *P. prolificus* but was uncertain whether they are conspecific.

A coral that better contributes to an understanding of the age of the Manitoulin Formation is the tabulate *Propora thebesensis paucivesiculosa* (Bolton, 1957), which occurs on Bruce Peninsula and Manitoulin Island. Young and Elias (1995) concluded that it is probably a geographic subspecies of *P. thebesensis* (Foerste, 1909). *Propora thebesensis* is widespread in the Hirnantian Edgewood Province and ranges into the upper Mosalem Formation in northwestern Illinois (Fig. 1.1, area F) (Elias and Young, 1992; Young and Elias, 1995). The upper Mosalem may be Rhuddanian in age (Bergström et al., 2012). Young and Elias (1995) noted that *P. thebesensis* also occurs on Anticosti

Island in the Ellis Bay and Becscie formations, which range in age from Hirnantian to Rhuddanian (Mauviel and Desrochers, 2016). Thus, *P. thebesensis paucivesiculosa* is consistent with the interpretation that the Manitoulin Formation is latest Ordovician to possibly earliest Silurian.

On Manitoulin Island, corals occur in the upper (Kagawong) submember of the upper member, Georgian Bay Formation, which underlies the Manitoulin Formation. They include *Streptelasma divaricans* (Nicholson, 1875) and representatives of the colonial rugosan genus *Cyathophylloides* Dybowski, 1873 and the tabulate genera *Calapoecia* Billings, 1865 and *Nyctopora* Nicholson, 1879 (Elias, 1982; Elias et al., 2013a). McLean and Copper (2013) placed *S. divaricans* in the poorly known genus *Parastreptelasma* on the basis of its long, thin major septa in the late ontogenetic stage. They noted that the type species of *Parastreptelasma*, *P. raritabulatum* Li and Gong, 1996, has long, slender major septa throughout ontogeny. However, *S. divaricans* is a highly variable species that includes some coralla with short major septa and an open axial region in the late stage and some with moderately dilated septa in the early stage (Elias, 1982). Those characters are typical of *Streptelasma* (see Systematic paleontology). The coral fauna in the upper Georgian Bay Formation is characteristic of the Richmond Province in eastern North America, which is Late Ordovician (late Katian; Richmondian) in age (Elias et al., 2013a).

Within the Cincinnati Arch region, rugose corals are present in the basal bed of the Belfast Member, Whippoorwill Formation, in Kentucky (Brett and Ray, 2005). Foerste (1923, p. 74) reported *Enterolasma caliculum* (Hall, 1852) from just below the “typical Belfast” in Ohio. That taxonomic identification is questionable as it has been applied to solitary rugosans from a wide range of Silurian strata in eastern North America (e.g., see Bassler, 1915). Nevertheless, it suggests a taxon that is different from the Richmondian species in the Cincinnati Arch region—*S. divaricans* and *Grewingia canadensis* (Billings, 1862)—with which Foerste was familiar (Elias, 1982, 1983).

Cephalopod data.—The presence of the annulated orthoconic cephalopod *Gorbyoceras* sp. in the Whirlpool Formation supports other evidence indicating a latest Ordovician, rather than Silurian, age for the formation. *Gorbyoceras* has a lengthy range in the Late Ordovician of North America (Flower, 1946; Frey, 1995). The youngest Richmondian occurrences are in the Cincinnati Arch region, where *G. hammelli* and *G. crossi* Flower, 1946 are present in the Hitz Member of the Saluda Formation in southeastern Indiana. The Hitz is latest Richmondian in age (Brett et al., 2020).

Some annulated orthocones occur in strata that may be, or are, Hirnantian in age. Within the Cincinnati Arch region, Foerste (1923) described *Spyroceras microtextile* from beneath the Brassfield limestone in southwestern Ohio, in strata he later provisionally termed “Centerville formation” (Foerste, 1931, p. 185). That unit is now known as the Centerville Member of the Whippoorwill Formation (Waid, 2018). Foerste (1923) considered *S. microtextile* to have Ordovician affinity. Annulated cephalopods from the “typical massive Belfast bed” in southern Ohio were identified by Foerste (1923, p. 74) as possibly *Dawsonoceras*. Those strata are now known as the Belfast Member of the Whippoorwill Formation (Waid, 2018).

The Whippoorwill may be Hirnantian in age (Waid, 2018; Farnam et al., 2019; Farnam and Brett, 2021). Foerste (1928) described *S. ferum* (Billings, 1866) and *S. microcancellatum* Foerste, 1928 from the Ellis Bay Formation (Hirnantian; Mauviel and Desrochers, 2016) on Anticosti Island (Fig. 1.1, cross-hatched area). Flower (1946) suspected that *S. ferum* is very closely related to *G. hammelli*. The only cephalopod identified from Hirnantian strata in the area of the Edgewood Province is *Dawsonoceras tenuilineatum* Savage, 1913. Savage (1913, p. 119) described it from the “Channahon limestone” in northeastern Illinois (Fig. 1.1, area E), now known as the Wilhelmi Formation (Willman, 1973). Savage (1913, table on p. 24–25) also reported *Dawsonoceras* cf. *D. tenuilineatum* from the “Edgewood formation” near Edgewood, northeastern Missouri (Fig. 1.1, area D). It presumably occurs in the “Cyrene member” (Savage, 1913, p. 22), now known as the Cyrene Formation (Thompson and Satterfield, 1975). Flower (1962) noted that *D. tenuilineatum* is inadequately known but nevertheless listed it with other described species of that genus.

Cephalopods have been identified from the Manitoulin Formation where it overlies the Georgian Bay Formation on Manitoulin Island, overlies the Queenston Formation on Bruce Peninsula, and overlies the Whirlpool Formation in southern Ontario (Williams, 1919; Bolton, 1957). They have also been listed from the Power Glen Formation where it overlies the Whirlpool in southern Ontario (Bolton, 1957). These cephalopods are not annulated; they are unrelated to *Gorbyoceras* sp. from the Whirlpool Formation.

The youngest cephalopods in the Queenston Formation have been reported from a limestone interval (Prairie Point biostrome) in about the middle of the formation on Bruce Peninsula (Liberty and Bolton, 1971). On Manitoulin Island, cephalopods occur in the upper (Kagawong) submember of the upper member of the Georgian Bay Formation (Foerste, 1924; Caley, 1936). The cephalopod-bearing strata in both those units are considered Richmondian in age. None of the cephalopods are annulated; they bear no resemblance to *Gorbyoceras* sp. from the Whirlpool Formation. On Manitoulin Island, cephalopods also occur in the Richmondian-age lower (Meaford) submember of the upper member of the Georgian Bay Formation (Foerste, 1924; Caley, 1936; Copper, 1978). Among them are *Gorbyoceras hammelli* and *Spyroceras parksi* Foerste, 1924. The latter species, considered closely similar to *G. crossi* by Flower (1946), was placed in *Anaspyroceras* by Copper (1978).

Biogeographic implications

Corals.—*Streptelasma subregulare* and *Propora thebesensis* in the Edgewood Province of the east-central United States (Fig. 1.1) most closely resemble *S. rutkae* n. sp. in the Whirlpool Formation and *P. thebesensis paucivesiculosa* in the Manitoulin Formation of southern Ontario, respectively. The species- and subspecies-level differences presumably resulted from genetic differentiation of populations and geographic speciation in the latest Ordovician (Hirnantian), given the following evidence that the epeiric sea extended between those areas. In northeastern Illinois (Fig. 1.1, area E), *S. subregulare* occurs in the Schweizer and overlying Birds members comprising the Wilhelmi Formation (McAuley and

Elias, 1990; Elias, 1992). *Propora thebesensis* is also present in the Wilhelmi (Young and Elias, 1995). A $\delta^{13}\text{C}$ excursion in the Wilhelmi Formation has been identified as the HICE (Bergström et al., 2012). The Schweizer Member extends into the subsurface of northwestern Indiana as the lower unit of the Sexton Creek Limestone (Rexroad and Droste, 1982). A small-amplitude $\delta^{13}\text{C}$ excursion, thought to represent the upper part of the HICE, occurs in the lower Sexton Creek (Degraeuwe, 2019). Associated chitinozoans indicate an age in the range of latest Ordovician to earliest Silurian (Degraeuwe, 2019). In the subsurface of northeastern Indiana, the Sexton Creek Limestone grades into the Cataract Formation, with the Manitoulin Dolomite Member at its base (Rexroad and Droste, 1982). The Manitoulin Dolomite continues in the subsurface of southern Michigan (Lilienthal, 1978) and northwestern Ohio (Larsen, 1998), to the Manitoulin and Whirlpool formations in southern Ontario (Johnson, 1998).

Corals were also able to spread elsewhere in the cratonic interior during the Hirnantian. In the Grand Rapids Uplands of Manitoba (Fig. 1.1, black star), a poorly preserved fauna occurs in the upper Stonewall Formation (Demski et al., 2015). It includes the tabulates *Propora* cf. *P. thebesensis* (Elias et al., 2013b, fig. 39b, c), *Paleofavosites* sp., and *Aulopora* sp. and the solitary rugosans *Streptelasma* sp. and *Rhegmaphyllum* sp. Associated conodonts and a positive $\delta^{13}\text{C}$ excursion in the upper Stonewall indicate a Hirnantian age (Demski et al., 2015). The coral fauna in the upper Stonewall Formation is somewhat similar to that in the Edgewood Province, where *P. thebesensis* and representatives of *Paleofavosites* Twenhofel, 1914 and *Streptelasma* are widespread, although *Aulopora* Goldfuss, 1829 is rare (Elias and Young, 1998). In the geographic area of the Edgewood Province, *Rhegmaphyllum* sp. appears in strata immediately above those containing characteristic Edgewood corals (McAuley and Elias, 1990; Elias, 1992). It occurs in the upper Mosalem Formation (Fig. 1.1, area F), lower Elwood Formation (Fig. 1.1, area E), and lower Bowling Green Dolomite (Fig. 1.1, area D), which have been considered earliest Silurian (Rhuddanian) in age (Bergström et al., 2012). However, in northern Arkansas (Fig. 1.1, open circle), *Rhegmaphyllum* sp. is present in oolite of the lower Cason Formation (McAuley and Elias, 1990); associated brachiopods and conodonts indicate a Hirnantian age (Amsden, 1986; Barrick, 1986). In correlative shale of the lower Cason (Fig. 1.1, area B), *Rhegmaphyllum* sp. is absent from a coral fauna belonging to the Edgewood Province (McAuley and Elias, 1990; Young and Elias, 1995).

Beyond the paleocontinent Laurentia, corals resembling those of the Edgewood Province have been recognized in South China, Baltica, and Kolyma, forming a widespread “Edgewood coral fauna” that is probably limited in age to the late Hirnantian (Wang et al., 2019, p. 17).

Cephalopods.—The annulated cephalopod *Gorbyoceras* sp. is considered to have arrived in the depositional area of the Whirlpool Formation in southern Ontario during a Hirnantian marine transgression. A likely source area was the Cincinnati Arch region, where *G. hammelli* and *G. crossi* are present in latest Richmondian strata in southeastern Indiana. Cephalopods also occur in the Centerville Member of the

Whippoorwill Formation in southwestern Ohio (Foerste, 1923, 1931), which may prove to be Hirnantian (Farnam et al., 2019; Farnam and Brett, 2021). One of them is an annulated species, *Spyroceras microtextile*, in need of modern study and generic reassignment. In the subsurface, the Centerville grades eastward into the Whirlpool Formation (Waid, 2018). Thus, there was a pathway for cephalopods from the Cincinnati Arch region to the area of Whirlpool deposition in southern Ontario.

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Declaration of competing interests

The authors declare none.

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