Early athyride brachiopod evolution through the Ordovician-Silurian mass extinction and recovery, Anticosti Island, eastern Canada

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Abstract.—The subfamily Hindellinae is an early group of athyride brachiopods, characterized by a simple jugum that connects the laterally directed spiralia, which are disjunct from the crura. Four genera (Hindella, Cryptothyrella, Koigia, and Hyattidina) are reexamined on the basis of their internal structures, such as the crura and their connection to the hinge, the jugum, and spiralia. The internal brachidium and shell of the Aeronian genus Cryptothyrella differ substantially from those of Hindella. Elkanathyris pallula n. gen. n. sp. is recognized as a posteriorly ribbed hindellide of Aeronian age. These genera are transferred from the Meristellinae to the subfamily Hindellinae (family Hindellidae). On Anticosti Island, Hindella is confined to the Hirnantian (latest Ordovician); it became extinct at the end Ordovician during the last of several mass extinction events that also extinguished the Laframboise reefs at the top of the Ellis Bay Formation. Post-extinction recovery of athyrides was pioneered by small-shelled Koigia, which are abundant in the basal Silurian Becscie Formation. Hyattidina, with a simple brachidium, is abundant in the Aeronian and Telychian of Anticosti, but absent earlier. True meristellines, as envisioned here, first appeared in the Aeronian Gun River Formation. The revised taxonomy and stratigraphic ranges of these earliest athyrides shed light on the nature of the Ordovician–Silurian mass extinction and recovery, and help refine the biostratigraphy of the O-S boundary interval.

Introduction

The Ordovician culminated in one of the major Phanerzoic mass extinctions, ranked roughly fourth in severity, equivalent to the Cretaceous–Paleogene boundary mass extinction (Alroy, 2008, 2010a, b). Mass extinctions due to multiple glaciations in Gondwana severely affected the tropical coral-sponge reef ecosystem in the Late Ordovician (Copper, 2002, 2011; Webby, 2002), and its concomitant tropical shelly faunas, in which athyride brachiopods played a significant role. Several extinction events mark the Ordovician-Silurian (O-S) boundary section on Anticosti, as evident within the Hirnantian Ellis Bay Formation (Copper et al., 2013). The Hirnantian carbonate-dominated succession, ~80 m thick, was deposited over some two million years and marked the arrival of a rich and diverse suite of early spire-bearers (atyrids, hindellides, but no spiriferides), not seen in the Katian Vaureal Formation below. These all suffered losses at the end of the Hirnantian. The general recovery of brachiopod shelly faunas is recorded in the lower Silurian for Anticosti (Copper and Jin, 2012, 2014, 2015). The earliest shelly community of the Becscie Formation (Rhuddanian) was characterized by low diversity and small shells such as Koigia, described herein (Fig. 1). The upper Becscie Formation was marked by the appearance of the large-shelled pentameride Virgiana community, which became ubiquitous in Laurentia during the late Rhuddanian (Jin et al., 1996; Jin and Copper, 2000). Major diversification of Silurian-type athyrides, atyrids, and pentamerides began later in the Aeronian and Telychian.

Considerable confusion exists about the richly fossiliferous transitional Ordovician–Silurian boundary interval on Anticosti, and where to draw the boundary itself (Copper et al., 2013). The drastic environmental changes were reflected by critical evolution of the tropical marine faunas, such as those well preserved in the carbonate platforms of Baltica and Laurentia. Different species of spire-bearing athyrids and atyrids have, in the past, been variously assigned to the Late Ordovician or early Silurian, or sometimes to both. This study aims to clarify the morphology, evolution, and distribution of such key taxa in the Hirnantian and Rhuddanian, and provide an update and revision of the taxonomy proposed in the Treatise (Alvarez and Rong, 2002).

Athyrides were late arrivals in the spire-bearing brachiopod orders in Laurentia and Baltica during the Late Ordovician, and did not become major components of the benthic shelly fauna until the Hirnantian. On Anticosti Island, the genus Hindella (Figs. 2, 3) was an abundant component of the brachiopod fauna and locally formed shell beds in the Ellis Bay Formation. In their interpretation of athyrite evolution, Alvarez et al. (1998, p. 834–835) regarded Dayia, with laterally directed spiralia and a simple jugum, as derived from Lissatrypa via lateral compression of the muscle field, thus regarding the orientation of the spiralia as insignificant, although the spiralia in these two genera have opposite directions (Copper, 1986; Copper and Gourvennec, 1996). They also viewed the laterally directed double spiralia of the Coelspirinae as compatible with atyrid affinities (Alvarez et al., 1998, p. 836). These authors assigned Hindella to the Silurian Meristellinae (superfamily Meristelloidea), and considered Cryptothyrella as its junior

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In this study, the early athyride taxonomy adopted in the last Treatise (Alvarez and Rong, 2002) is revised, based on internal structures revealed through serial sections. Although Alvarez (1999) cautioned against the use of serial sections alone to reconstruct internal structures, we employ serial sections and acetate peels of pristinely preserved calcitic whole shells from Anticosti Island, especially when the serial-section peels were taken at close intervals (0.1 mm). These have proven accurate. Early athyrides have been described as having a smooth shell, but we discovered that many have a finely capillate shell. Hindella is the direct ancestor of Rhuddanian Koigia, an earliest Silurian recovery taxon, and both belong to the subfamily Hindellinae. This description probably fits all simple ancestral Ordovician athyrides (once their brachidia become better known), and their immediate descendants with such features. Complex juga and their extensions appear to have evolved first in the mid to late Aeronian (middle early Silurian). We note from serial sections that the subfamily Hyattidinae (Sheehan, 1977), and its type genus Hyattidina, which first arrives in the Gun River Formation (Aeronian) of Anticosti, has a very simple jugum, laterally directed spiralia, and crura unconnected with the spiralia and jugum. This is basically like that of Hindella (Copper, 1986, fig. 9). Alvarez et al. (1998, p. 841), in contrast, assigned these to the family Hyattidinidae and superfamly Athyridioidea. Herein, we consider that Hyattidina is most closely related to the subfamily Hindellinae.

**Stratigraphic distribution of Hindellidae on Anticosti Island**

Hindella is the only athyride genus known to date in the Upper Ordovician (Hirnantian) of Anticosti (Copper et al., 2013)—there are no earlier athyrides in the underlying Katian Vaureal Formation (see Fig. 1). It first appeared in the lower beds of the Ellis Bay Formation, without any predecessors on Anticosti or in North America. It must have evolved from athyrides of mid–upper Katian age, such as those known in the Anderken Formation (Dulankara strata) of Kazakhstan (Nikitin et al., 1996, 2006). Within the Ellis Bay Formation, Hindella evolved rapidly from the earliest species Hindella prinstana, through H. umbonata, and three younger species in the Parastros and Lousy Cove members, with the largest elongate shell at the top of the reefal Laramboise Member marking the last appearance of the genus (Fig. 1).

Alvarez and Rong (2002) reported the genus Whitfieldella from the Late Ordovician, although the validity of this lower range of this largely Silurian genus seems questionable. With the Hindellinae separated from the Meristellinae, as proposed in this study, the first appearance of Meristella and Meristina would be in the late Telychian or later. This agrees with the evolutionary scenario suggested by Schuchert (1894) and Modzalevskaya (1985, 1996) that the Hindellinae (excluding Whitfieldella and Meristina) form a natural ancestral group in the order Athyrida. In comparison, the more derived subfamily Didymothyridinae (Modzalevskaya, 1996), with complex umbo-nal blades curved from the jugal saddle, first appears much higher in Telychian strata of the Jupiter Formation, coeval with its occurrence in Baltica.

![Table showing stratigraphic distribution of Hindellidae on Anticosti Island](https://www.cambridge.org/core/altimg)
Koigia occurs in the basal Becsce Formation, within ~1 m of thin- to medium-bedded, hard, micritic mudstone and wacke- 
estone that overlie the Laframboise reefs at the O-S boundary 
(Copper and Jin, 2014). It is a much smaller-shelled athyride 
compared to Hindella in the Ellis Bay Formation, although their 
internal structures are similar. Koigia is locally abundant, 
alongside other Rhuddanian brachiopods, such as Zygospir-
aella, Becsceia, and Viridita. In Estonia, the type species of 
Koigia also occurs in the basal Rhuddanian (Rubel, 1970 ini-
cially cited it as Hindella).

So far, Cryptothyrella has not been found on Anticosti 
Island, although some athyride specimens from the Aeronian 
Gun River and Menier formations (Copper and Jin, 2012; 
Copper et al., 2012) may be assignable to the genus, pending 
future study. The type species, Cryptothyrella quadrangularis 
(Foerste, 1906), as seen in Ohio, is characterized by an unus-
ually large and prominently elongate shell (30–40 mm in 
length). The Rhuddanian ‘Cryptothyrella bentic community’, 
recognized by Cocks and McKerrow (1973, p. 293) for the 
platform setting in Laurentia and Baltica, has not been observed 
on Anticosti Island, nor has its presence been confirmed in the 
Rhuddanian of Laurentia.

Hyattidina is very abundant in the upper Gun River, 
Menier, and Jupiter formations, ranging from mid-Aeronian to 
to mid-Telychian. The genus is absent from the older Becsce, 
Merrimack, and lower Gun River formations (Fig. 1). It retained 
the simple jugum and brachidium of Hindella, but has a well-
developed fold and sulcus.

The early athyride shelly community on Anticosti 
Island

The carbonate sediments of Anticosti were deposited in the 
northern paleotropical latitudes, on a platform to ramp flanking 
the southeast side of Laurentia (Copper, 2002; Cocks and 
Torsvik, 2011). Strata are undeformed with dips <2° today.

During the Late Ordovician and early Silurian, Baltica was 
directly to the east at a similar paleolatitude, with an ocean 
~1000–1500 km wide separating it from Laurentia. To the 
neat south, Siberia was mostly north of the paleoequator. In the 
Anticosti Basin, siliciclastic sediments were rare, and consisted 
of episodic storm-generated or seismic deposits, marked by 
slumped beds, mostly during the late Katian and Hirnantian.

Wet coastal climates created an epeiric sea of mixed salinities 
(similar to the Java and Arafura epicontinental seas today) that 
affected the distribution of shelly and coral faunas in the early 
Silurian (Edinger et al., 2002). Facies differences between the 
est and west ends of Anticosti reflect a curving shoreline along 
the 200 km long outcrop belt.

In such a carbonated-dominated depositional setting of the 
Anticosti Basin, athyrides formed common shell clusters, or 
extensive shell beds. Their minute pedicle, as indicated by the 
small apical to trans-apical foramen, and common co-
occurrences with small and delicate bryozoans or broken 
shells suggest that they anchored on skeletal clasts in the sedi-
ments. In the reefal Laframboise Member, Hindella was gen-
nerally rare or only locally abundant (such as locality A1161), but 
in the reefal East Point Member (Aeronian) athyrides are 
generally common. This may indicate a later adaptation to 
shallow-water, higher-energy, reefal settings.

The athyrides were more common in mid-shelf settings, 
and rare in deeper waters of the Clorinda-Dicoelosia commu-
nity found in the Menier and Jupiter formations. Hindella 
habitats varied from deeper muddy seafloors (alongside solitary 
rugosans or bryozoans), to somewhat shallower, but still low-
energy, carbonate substrates (where it was commonly mono-
specific), and extending into shallow and high-energy reefal 
settings. In the Parastro Member, a relatively small form of 
Hindella (H. bulbusa n. sp.) occurs as a common component of 
the Parastrophinella pentameride association (Jin and 
Copper, 2008).

The small shells (<7 mm in width) of Koigia occur 
commonly in higher energy, storm-influenced settings 
represented by the Becsce Formation, especially in the lower 
Fox Point Member, associated with other small-shelled taxa 
(e.g., Becsceia and Viridita; see Jin and Copper, 2010). The small 
shells usually show various degrees of distortion, damage, and 
disarticulation, with common geopedal structures in conjoined 
shells, indicating rapid burial by micritic mud during storms 
(for more discussions on the depositional environments, see 
Copper and Jin, 2014). Koigia may be regarded as an opportu-
nist that thrived immediately after the Late Ordovician mass 
extinction events, but athyrides became scarce in the upper 
Becsce Formation (Chabot Member) when the monotypic, 
large-shelled Virgiana brachiopod community became 
dominant.

On Anticosti, Hyattidina and Elkanathyris n. gen. occur 
as common components of the Pentamerus community, indi-
cating a mid-shelf depositional environment (Jin, 2008). They 
may also be associated with rich and diverse atyrids. This 
agrees with the treatment of the Hyattidina community as 
equivalent to the Pentamerus or Stricklandia communities in the 
Welsh Borderlands (Cocks and McKerrow, 1973). It is rela-
tively rare in the Eocoelia community.

Materials and methods

The basis of the paper is the stratigraphic work that covers ~2000 
Anticosti localities, located on metric grid maps and with GPS 
coordinates (Copper et al., 2013; Copper and Jin, 2014, 2015). 
The large brachiopod collection is stored at the Geological Sur-
vey of Canada, Ottawa. Well-preserved, pristine, calcitic speci-
mens were serially sectioned with a Croft Parallel Grinder.

Acetate peels were taken at 0.1 mm intervals, mounted between 
35 mm glass slides, and examined and photographed under 
microscope. To prepare the serial section drawings, the peels 
were projected to a scale of x16 or x20, with the main internal 
features traced in ink and then scanned. The technique for 
reconstruction of the brachidia uses peels transposed into a 
view of the dorsal shell interior, employing the plane of 
symmetry as orientation (technique described in papers from 
1967 and earlier, accurate to within a millimeter, and available 
from first author).

Repositories and institutional abbreviations.—Figured speci-
mens are housed in the Type Collections of the Geological 
Survey of Canada (GSC), Ottawa, the Cincinnati Museum
Systematic paleontology

Order Athyrida Boucot, Johnson and Staton, 1964 (nom.transl. Athyridae Davidson, 1881; =Incerti ordinis Niki-forova and Rzhonsnishtskaya, 1960, part; ex Athyridoida Boucot, Johnson, and Staton, 1964, part)

Remarks.—Boucot et al. (1964) recognized that the family name Athyridae Phillips, 1841, used for a group of Leptaena species known at that time, was invalid because the genus Athyris M’Coy, 1844 was established later and, therefore, the family name could not have been derived from the genus Athyris. Boucot et al. (1964, 1965) accordingly assigned the authorship of the Athyridae to M’Coy (1844), but changed the family name to Athyrididae without any explanation. Later, Alvarez et al. (1980) identified the error in Boucot et al. (1964) (i.e., although M’Coy [1844] erected the genus Athyris, he assigned it to the family Delthyridae, but retained Phillips’ use of Athyridae for Leptaena and “Producta”). Alvarez et al. (1980) thereby assigned the authorship of Athyridae to Davidson (1881), who was the first to include Athyris in the family Athyridae. As in Boucot et al. (1964, 1965), however, Alvarez et al. (1980) and Alvarez and Brunton (1993) recommended the use of Athyrididae instead of Athyridae.

In terms of ICZN provisions, it should be noted that Athyridae Phillips, 1841 and Athyrididae Davidson, 1881 are effectively homonyms because the name was used for different genera of brachiopods. In this instance, the suppression of the senior homonym is warranted because neither Phillips (1841) nor M’Coy (1844) derived the family name Athyridae from the genus Athyris (from the Greek, thyrā, door, or its diminutive thyris, small opening, referring to the pedicle opening of the shell). As a result, Athyridae Davidson, 1881 becomes a valid name by default, and there is no justification to change the family name to Athyrididae, or to change the order name to Athyridida. According to ICZN (1999, Article 29.3.1.1), if the genitive singular stem of a noun ends in -id, these two letters should be elided before adding the family suffix -idae. An unelided form can be retained only if it has been in prevailing use. Therefore, even if the Greek word thyris is regarded as a latinized noun, and its genitive singular stem is thyrīs, a proper family name is still Athyridae, as originally used by Phillips (1841) and Davidson (1881). Because Athyrididae Davidson, 1881 is a valid family name that has been in use for over a century, we argue that its change to Athyrididae by Boucot et al. (1964) and subsequent use (Athyrididae, Athyridoidea, Athyridida, etc.) should be avoided.

In light of the discussions above, we propose to retain the name Athyridae (and hence Athyrida), as we have done in this study. A detailed discussion will be suitable for an ICZN Opinion note.

Family Hindellidae Schuchert, 1894
(nom. transl. Hindellinae Schuchert, 1894)
Subfamily Hindellinae Schuchert, 1894

Genera assigned.—As emended in this study, the subfamily Hindellinae Schuchert, 1894 includes the genera listed below.

Hindella, Davidson, 1882.—Hirnantian, Late Ordovician, Anticosti, Canada.
Cryptothyrella Cooper, 1942.—Aeronian, Llandovery, mid-western USA.
Tschatkalia Nikiforova, 1964.—Llandovery, Chatkal Mountain Range, Siberia.
Koigia Modzalevskaya, 1985.—early Rhuddanian, Estonia, and Anticosti Island, Canada (simple brachidia as in Hindella).

Genera questionably assigned.—For most of the genera below, the precise nature of the jugum is not yet known, although some are superficially similar to Hindella, such as the genera from North China (Fu, 1982).

Hyattidina Schuchert, 1913.—Aeronian, Llandovery, North America; the genus has a brachidium similar to that of Hindella, and the subfamily Hyatidininae is considered a junior synonym of Hindellinae.

Colongina Breivel and Breivel, 1970.—Early Devonian, eastern slope of Urals; designated by Grunt (1986, p. 25) as a hindelline, but its brachidia are unknown; doubtful assignment considering its much younger age; possibly an atrypide.
Apheathyris Fu, 1982.—Katian, Ningxia, North China (smooth, biconvex, rectimarginate shell, brachidia unknown).
Weibeia Fu, 1982.—Katian, Shaanxi, North China (smooth shell, weak fold and sulcus, brachidia unknown).
Argella Menakova and Nikiforova, 1986.—Pridoli, upper Silurian, Zeravshan Range, Tadzhikistan; elongate smooth shell, with simple brachidia like Hindella and Hyattidina, but posterior internal structures unclear (Alvarez and Rongs, 2002).
Cyclorhynchia Baranov, 1994.—Katian, Tscherkidium Beds, Seleynakh Range, NE Siberia (jugum unknown, and requiring assessment, but with laterally directed spiralia of three whorls); Copper (2002, p. H1472) incorrectly synonymized it with the atrypoid Cyclospira, which lacks a jugum, but has medially directed spiralia, the opposite to that of Cyclorhynchia.
Kellerella Nikitin and Popov in Nikitin et al., 1996.—Anderken Formation, Dulandkara Stage (mid–late Katian), Chu-Ili, Kazakhstan; its short, disjunct jugal processes differ from those found in typical hindellides.
Nikolaipsira Nikitin and Popov in Nikitin et al., 1996.—Anderken Formation, Dulandkara Stage (mid–late Katian), Chu-Ili, Kazakhstan; its short, disjunct jugal processes differ from that found in typical hindellides described in this study.
Elkanathyris n. gen. (herein).—Jupiter Formation, Aeronian–Telychian, Anticosti Island.

Diagnosis (emended herein).—Smooth or gently plicate, commonly with capillae, biconvex; small, distinct interarea, with minute deltoidal plates, and apical to trans-apical foramen. Ventral valve mostly with relatively thick prismatic apical callus, deeply impressed muscle scars, and deep groove in the hinge plate. Dorsal valves with simple, arched jugum and medially aligned crura unconnected to the brachidium, with hooked terminations of the jugal blades. Laterally directed spiralia, <12 whorls. Loops, accessory lamellae, and extensions of the jugum absent.
Occurrence.—Late Ordovician (late Katian) and early Silurian (Llandovery), Laurentia, Baltica, Siberia, Tadzhikistan, ?Kazakhstan, and ?North China. Katian hindellide genera have not been reported from Laurentia. Some primitive or ancestral athyrides from the mid–upper Katian of Kazakhstan and North China, such as Nikolaaispira and Kellerella, are regarded as possible ancestral hindellides. During the Hirnantian, hindellides diversified to become a group of prominent and abundant brachiopods in tropical environments worldwide, forming extensive shell beds. The family may have survived into the late Silurian as Argella. An Early Devonian record is uncertain.

Remarks.—The order Athyrida is characterized by (1) medial crura oriented along the plane of symmetry, (2) laterally directed spiralia (some with double spiralal lamellae), and (3) a simple or complex jugum connecting the spiralia. The earliest forms, as represented by the Late Ordovician and early Silurian Hindellinae, have a smooth or finely capillate, impunctate shell, a simple jugum, and single, flat spiralial lamellae. Another consistent early feature is that the crura and brachidia approach each other at a sharp angle, but do not fuse. During the late Silurian and Devonian, the spiralium evolved double parallel whorls, developed from jugal extensions, or by transforming from U-shaped, trough-like spiral lamellae to double lamellae, as in the Anoplothecidae. Evolution of the brachidia demonstrates that by Aeronian–Telychian (mid-Llandovery) time, some athyrides developed complex jugal stems or extensions, such as in the Meristellinae and Whitfieldellinae.

The lateral projection of spiralia in athyrides and spiriferides suggests that they had a different feeding strategy, with feeding currents (from the spiral base inwards), opposite to that in atrypides (with medially or dorsally directed spiralia, and feeding current from the base outwards; see Copper, 1886, figs. 8, 9). Their Ordovician stratigraphic record shows that the original single spiral whorl stood in the central plane of symmetry, as seen in the Katian protozyginids (Copper, 1977). Nikiforova and Rzhonsnitskaya (1960) combined the superfamily Hyattidoidea, or complex jugum, and single, flat spiralial lamellae. Another consistent early feature is that the crura and brachidia approach each other at a sharp angle, but do not fuse. During the late Silurian and Devonian, the spiralium evolved double parallel whorls, developed from jugal extensions, or by transforming from U-shaped, trough-like spiral lamellae to double lamellae, as in the Anoplothecidae. Evolution of the brachidia demonstrates that by Aeronian–Telychian (mid-Llandovery) time, some athyrides developed complex jugal stems or extensions, such as in the Meristellinae and Whitfieldellinae.

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Externally, it is difficult to distinguish many athyride taxa with smooth or capillate shells, due to their strong homomorphy. Copper (1886) reconstructed the spiralia and jugum of Hindella for the first time, based on toptype material, and demonstrated that there was no skeletal connection between the crura and spiralium in either Hindella or Hyattidina, although there should have been soft tissue to hold them together in vivo. It is primarily the Russian workers (e.g., Modzalevskaya, 1985, 1996; Grunt, 1989) who have clarified the nature of the lophophore-supporting skeletal structures, and established evolutionary relationships between genera and subfamilies. A key to their understanding lies in the earliest subfamily, the Hindellinae.

Schuchert (1894, 1897), who named the Hindellinae, visualized them as encompassing Early Ordovician and Silurian athyrides possessing a simple jugum, although he unwittingly included later genera that are now known to be well outside that group, such as Anoplotheca and Coelospira, with double spiralial lamellae and a very complex jugum. Later, Schuchert (1928) revised his classification, and confined the Hindellinae to four smooth-shelled genera: Hindella, Hyattidina, Greenfieldia, and Whitfieldella (the latter two were moved to other subfamilies later). At that time, he also assigned the Hindellinae to the family Meristellidae of Waagen (1883).

Nikiforova and Rzhonsnitskaya (1960) and Menakova (1964) accepted the Hindellinae as a subfamily, and included it, besides Hindella, Whitfieldella, and Hyattidina, in the family Nucleospiridae. This is close to the Hindellinae defined in this study, except that we exclude the hindellines from the later Wenlock nucleospirids. An early origin for the Nucleospiridae is uncertain, although there are relatively flat, smooth athyrides, such as “Athyris” lara Billings (1866) in the Merrimack Formation of late Rhuddanian age. “Athyris” solitaria Billings 1866 from the same strata belongs to the smooth atrypine genus Cerasinella Copper, 1995.

Sheehan (1977) abandoned the subfamily Hindellinae altogether, and allocated Hindella to the Meristellidae, and Hyattidina to a new subfamily, the Hyattidinae, both within the Meristellidae.

Modzalevskaya (1985, fig. 29; 1996) proposed a comprehensive evolutionary scenario for the early athyrides of latest Ordovician–early Silurian age. She showed only Hindella in the Ordovician, but extended it into the Rhuddanian where Cryptothyrella was treated as a synonym. For the Rhuddanian, Modzalevskaya listed three genera: Koigia, Hyattidina, and Tschatkalia, and grouped them into the Hyattidinae. She did not use the subfamily Hindellinae Schuchert, 1894, but assigned Greenfieldia to the younger Didymothyrinidae, and Hindella to the Meristellidae. Notably, Modzalevskaya (1985) showed that the Meristellinae, Meristinae, and the genus Whitfieldella (and thus Whitfieldellinae) appear first in the Wenlock, characterized by the presence of a more complex jugum. In a series of elaborate diagrams, Modzalevskaya (1985, figs. 7–19) made detailed comparisons of the jugum in a range of genera for the first time, demonstrating that complex juga evolved later, and first appeared in such late Telychian–Wenlock genera as Meristella, Meristina, Didymothyris, and Collarothyris. On Anticosti Island, such complex jugu first appeared in the mid-Aeronian athyrides (work in progress).

Grunt (1986, 1989) adopted the Hindellinae of Schuchert (1894), and included in it nine genera, confining Cryptothyrella to the early Silurian. She employed Sheehan’s 1977 partial serial sections for “Hindella umbonata” from Junction Cliff. Grunt (1986) followed Schuchert (1928) in assigning the Hindellinae to the family Meristellidae. She elevated the Didymothyrinidae to family status and, on the basis of their complex jugum, placed it under the superfamily Athyridoidea.

Dagys (1996) reclassified the Order Athyrida (no author assigned) into three suborders, the Retziida, Koninckinida and Athyridida, and did not recognize the subfamily Hindellinae.
Alvarez and Rong (2002, p. H1556) elevated the Hyattidininae to family status, but did not mention the subfamily Hindellinae, and assigned Hindella to the family Meriellidae within the superfamily Meriellidae, and transferred the smooth-shelled *Hyattidina* Schuchert, 1913 to the superfamily Athyridoidae (herein we assign *Hindella* and *Hyattidina* to the same family, Meriellidae). They did not discuss the lack of skeletal connection between the crura and brachidium, nor the simple jugum, in such early athyrids. Davidson’s (1882) reconstruction of the *Hindella* brachidium (shown in Alvarez and Rong, 2002, p. H1564, fig. 1063v) incorrectly shows fused crura.

In the revised Treatise, Alvarez and Rong (2002) assigned various early athyrid genera (e.g., *Hindella*, *Hyattidina*, and *Koigia*) with a simple jugum into different families, abandoning the name Hindellinae. Herein, we propose to treat the Hindellinae as a natural group of early athyrids, and raise it to family status, the Hindellidae Schuchert 1894, characterized by a simple jugum and crura that may or may not directly connected to the spiralia. These early forms may have a smooth or capillate shell surface. These hindellides may have evolved from the older athyrids, such as *Nikolaiaspira* Nikitin and Popov in Nikitin et al., 1996 and *Kellerella* Nikitin and Popov in Nikitin et al., 1996, from the Anderken Formation (Dulankara Stage, mid–late Katian) of Chu Ili, Kazakhstan (see also Popov et al., 1999, 2002; Nikitin et al., 2006). These Kazakh forms show more primitive characters, such as short, spine-like jugal processes that are not medially connected. The subfamily Hyattidiinae, therefore, is subsumed in the family Hindellidae on account of their jugum and brachidium that resemble those of *Hindella*, *Koigia*, *Cryothyrella*, and *Elkanathyris* n. gen. (see descriptions of these genera below).

Genus *Hindella* Davidson, 1882

*Type species.*—*Athyris umbonata* Billings 1862; Juncliff Member, Ellis Bay Formation, Hirnantian, Anticosti Island.

*Species assigned.*—The following species are assigned to *Hindella*:

*Athyris umbonata* Billings, 1862.—Type species (see below).

*Athyris prinstana* Billings, 1862.—Prinsta Member and its stratigraphic equivalent to the west, Fraise Member, Ellis Bay Formation (see Copper et al., 2013).

*Athyris turgida* Shaler, 1865.—Probable junior synonym of *H. prinstana* (see below).

*Anomites terebratulinus* Wahlenberg, 1818.—Upper Boda reef-capping limestone, Hirnantian.

*Artrya cassidea* Dalman, 1828.—Borenschult, Ostergötland, Sweden, Dalmantinita Beds, Hirnantian.

*Whitfieldella ovoides* Savage, 1913.—Bryant Knob Formation, Hirnantian herein (the age of the Bryant Knob is debated because some have dated it as early RHuddanian).

*Whitfieldella speciosa* Savage, 1913.—Edgewood Group (Amsden, 1974 synonymized it with *W. ovoides*).

*Meristina crassa incipiens* Williams, 1951.—Cym-y-brain Formation, Hirnantian, Denbighshire, U.K.


*Hindella bulbosa* n. sp.—Parastro Member, Ellis Bay Formation (this study).

*Species questionable assigned.*—*Hindella shiamensis* Reed, 1912; Horizon 5, Shian, Pin Valley, Himalayas, precise age unknown (Hirnantian?); interior unknown, but the elongate shell resembles *H. umbonata*.

**Diagnosis.**—Relatively small to medium sized, smooth or capillate, globose, biconvex shell with incurved beak, apical to transapical foramen, small distinctive interarea, and minute deltidial plates; gently folded anterior commissure, rare median ventral groove. Internally, ventral muscle scars deeply incised, flanked by prominent dental plates and dental cavities, and vascular markings and ovarian pits; apical ventral cavity partially infilled by prismatic callus, leaving shallow groove; dental plates relatively straight, subparallel to plane of symmetry. Crura short and delicate, diverging slightly laterally; umbonal blades equally short and hooked; simple jugum postero-medial, gently arched posteriorly; spiralia with 6–8 whorls, laterally directed.

**Occurrence.**—A Hirnantian age for the genus is confirmed in Laurentia, Baltica, and South China (Rong, 1984). The Ashgill–Llandovery age was given by Alvarez and Rong (2002) because they synonymized Aaronian *Cryptothyrella* Cooper, 1942, with *Hindella*. There has been confusion about the age of the Ellis Bay Formation, but recent studies have confirmed its Hirnantian age based on microfossils, megafossils, geochemistry, and sequence stratigraphy (Achab et al., 2013; Copper et al., 2013; Mauviel and Desrochers, 2016). On Anticosti Island, *Hindella* is the only athyrid genus in the Hirnantian, co-occurring with *Hirnantia*, but it is absent lower in the Katian, or higher in the Silurian.

In Estonia, *Hindella* occurs in the Hirnantian Porkuni Stage. This distribution matches that of the type Hirnantian in the UK, where the species *Hindella incipiens* occurs (Harper and Owen, 1996). The Estonian “*Hindella crassa* (Sowerby)” is given a Juuru (early Rhuddanian) age by Modzalevskaya (1985, p. 46), but its affinity should be re-examined because it may be *Koigia*.

“*Cryptothyrella* terebratula* (Wahlenberg, 1818) from the Boda Limestone of Sweden was given a Late Ordovician age by Sheehan (1977); we consider it as true *Hindella*. Brenchley et al. (1997) suggested that the Boda Limestone was Katian, but Webb (2002) indicated that the top of the Boda mounds stopped growth in the mid-Hirnantian. The species comes from the upper part or tops of the Boda mounds and should be of Hirnantian age. Sheehan (1977) identified *Hindella crassa* (Sowerby, 1839) from the Hirnantian Dalmanitina Beds of Sweden. This suggests that all species of *Hindella* from Baltica and the UK are of Hirnantian age, as are those of Laurentia.

Amsden (1974) identified “*Cryptothyrella* ovoides” (Savage, 1913) from the Bryant Knob Formation and assigned it to the Edgewood Group. Amsden (1974) tentatively assigned the Bryant Knob (= Leemon Formation) to the early Llandovery, which should be reconsidered as Hirnantian because it shares nearly all the shelly fauna of the underlying Noix Formation, which has the genus *Hirnantia* as a component. Sheehan (1977, p. 25) referred the Edgewood “*Cryptothyrella* ovoides” to the Silurian (its external morphology is that of Hirnantian *Hindella*). More recently, Bergström et al. (2006)
re-dated the Leemon and Girardeau limestones of the Edgewood Group as Hirnantian.

Remarks.—There has been considerable confusion between *Hindella* and other homeomorphic athyrides that occur in the Ordovician-Silurian boundary interval. The deeply incised ventral muscle scars have been used as one criterion for *Hindella*, but these are similar in other early athyrides, and are also quite variable. Sheehan (1977) distinguished *Hindella* from *Cryptothyrella* mostly on external morphology: *Hindella* was noted to have a prominent beak with commonly well-developed concentric growth lines and a transapical foramen. We note that these features occur in most hindellines. *Hindella* with prominent concentric growth lines are rare amongst Anticosti shells. Sheehan (1977, p. 25) also remarked that the muscle fields were “more divergent” in *Cryptothyrella*, and the “cardinalia more robust.” Sheehan’s (1977) diagnosis, however, was based on different species assignments compared to what we propose in this study. For example, we assign the Hirnantian species *Anomites terebratulina* to *Hindella*, whereas he assigned it to *Cryptothyrella*. In our re-assessment of the type species of *Aeronia* *Cryptothyrella*, we show radial capillae on the shell surface (see description under that genus), which are also observed in some species of *Hindella*.

Herein, the internal architecture of the brachidia and dental apparatus are given primary taxonomic importance. Detailed serial sections of both *Hindella* and *Cryptothyrella*, demonstrate that *Hindella* differs from *Cryptothyrella* in its straight, almost vertically aligned dental plates, much less prismatic callus in the ventral apex, short and blunt teeth, a distinctive hinge plate, and median septum reaching to the hinge plate, forming the appearance of a “septalium” in globose, adult shells. In *Hindella*, the umbonal blades are short and weakly hooked close to the short crura (in contrast to the long crura and “walking-stick-shaped” umbonal blades in *Cryptothyrella*), the jugum is arched towards the posterior.

Davidson (1881, 1882), who described the genus *Hindella* based on specimens sent by Billings from the Junction Cliff locality on Anticosti, named it after the British geologist, George Hinde. Reconstruction of the shell spiralia and jugum was carried out by Norman Glass (Davidson, 1882, p. 130), and showed the lateral orientation of the spiral lophophore, and a single continuous brachidium starting with the crura. Hall and Clarke (1894, p. 64, figs. 46–51) copied, with sketches of the jugum and the internal umbonal area, and assumed the brachidia to continue, albeit at right angles from the crura. As shown in our serial sections, the curved umbonal blades of the brachidium are not connected to the crura, but approach as curved hooks close to the crura. During life, there must have been some connecting tissue that suspended the spiralia and jugum within the shell cavity, or else the spiralia would have been loose. The soft tissue endured long enough for the lophophore supports to be left more or less in their life orientation as mud infilled the shells, with spirals pointing to the sides of the shells. In atrypides there is no such crural-brachidial structure, as the laterally positioned crura continue into the spiridial lamellae, with no sharp angle of closure. This is, de facto, a fundamental distinction from the atrypides, as shown in Copper (1986).

Alvarez and Rong (2002) regarded *Hindella* and the junior genus *Cryptothyrella* as indistinguishable, and subsumed *Hindella* in the subfamily Meristellinae, thus combining forms with a complex and simple jugum. Cocks (2008) adopted the 2002 Treatise synonymy of *Hindella* and *Cryptothyrella*, referring them back to the subfamily Meristellinae. At the same time Cocks assigned a Llandovery age to *Hindella angustifrons* (Salter, 1851), *H. crassa* (Sowerby, 1839), and *H. furcata* (Sowerby, 1839), although labelling only *crassa* as *Hindella*. The only taxon remaining in the Hirnantian was *Hindella incipiens* (Williams, 1951). Sheehan (1977), and Modzalevskaya (1985) labelled *crassa* and *cassidea* as *Hindella*, but Hiller (1980) referred the species to *Cryptothyrella*. More recently, Niemeyer et al. (2010) assigned some Llandovery specimens (mostly steinkerns) from Chile to “*Hindella crassa incipiens*”, but the Chilean shells appear to have a somewhat more complex jugum, as shown in the serial sections by these authors, than the typical Hirnantian *Hindella* from Anticosti Island. Thus, the species *crassa* has zigzagged between two generic names. Specimens of such athyrides in the UK are rare, and poorly preserved as siliciclastic molds and casts, without brachidia, and thus muscle scar and hinge identifications are debatable. This leaves the Anticosti record of pristinely preserved shells with full brachidia, and *Hindella cassidea* (Dalman, 1828), as some of the few species that are true Hirnantian *Hindella*.

**Hindella umbonata** (Billings, 1862)

![Figure 2.1–2.7]

1862 *Athyris umbonata* Billings, p. 144, figs. 121a, b.
1863 *Athyris umbonata*; Logan, p. 317, figs. 331a, b.
1865 *Athyris umbonata*; Shaler, p. 69.
1866 *Athyris umbonata*; Billings, p. 46.
1882 *Hindella umbonata* (Billings); Davidson, p. 130.
1894 *Hindella umbonata*; Hall and Clarke, pl. 41, figs. 26, 27, 29, 30.
1928 *Hindella umbonata* (Billings); Twenhofel, p. 221, pl. 20, figs. 21–23.
1977 *Hindella umbonata*; Sheehan, pl. 1, figs. 26–28.

Types.—Billings (1862, p. 144) established the species based on specimens from “Junction Cliff, Anticosti, Division 1.” In modern stratigraphy, this locality at western Anticosti Island exposes the Junciff Member, Ellis Bay Formation, as well as the underlying the recessive Fraise Member (see Copper et al., 2013, fig. 4c, d for the type locality; Jin and Copper, 1997 for a map), Hirnantian, latest Ordovician. Junction Cliff is readily accessible, and shows a 10 m thick upper unit of resistant, partly nodular micrite with shaly partings, with *H. umbonata* (Junciff Member) and an underlying recessive lower unit of shales and limestones (Fraise Member, with *H. pristana*). Here, the distinctive large elongate shell of *H. umbonata* can be easily distinguished from the smaller, rounded, globose shell of the older species, *H. pristana*. The restricted type locality (C718) is defined here as the east end of Junction Cliff (UTM 20,
where H. umbonata occurs in the resistant upper ledges of the lower Juncliff Member.

The original type lot of H. umbonata Billings in the GSC type collection consists of six specimens, labelled “GSC 2284, GSC2284a–e” collected by J. Richardson from “Junction Cliff.” The shell figured by Billings (1862), GSC2284, listed as the holotype, is lost. The remaining five shells, GSC 2284a–e are not assignable to the species, with four belonging to H. prinstana, and one resembling H. bulbusa n. sp. Richardson (1857) collected brachiopods from the lower Fraise to Parastro members, stretching from Junction Cliff to Parastrophinella Bluff (the latter being the type locality of Parastrophinella reversa and Hindella bulbusa n. sp.). Thus, Richardson’s “Junction Cliff” collection is a mixture of three species of

Figure 2. Hindella species from the Ellis Bay Formation (Hirnatian), Anticosti Island. (1–7) Hindella umbonata (Billings, 1862); GSC 137675 (1–4) and GSC134359 (5), Juncliff Member, locality A814, Prinsta River (loc. A814); (6, 7) GSC 59097, interior of pedicle valve viewed at two different angles, Junction Cliff (A4, type locality). (8–13) Hindella bulbusa n. sp., Parastro Member, Parastrophinella Bluff (loc. A48); (8–10) GSC 137679, paratype; (11–13) GSC137680, paratype. (14–23) Hindella prinstana (Billings, 1862), Fraise Member; (14–18) GSC 137666, wider variety; (19–23) GSC 137667, elongate form.
**Remarks.**—Hindella umbonata is a common species of the genus on Anticosti Island, and can be readily distinguished from other congeneric species on the island by its larger (average shell width 16 mm), strongly elongate, globose shell with parallel sides. Both H. prinstana and H. bulbusa n. sp. are smaller, with average width of 12 mm and 10 mm, respectively. Hindella prinstana also has a narrower apical angle, and H. bulbusa n. sp. is pear-shaped (see below).

**Hindella prinstana** (Billings, 1862)

Figure 2.14–2.23

1862 Athyris Prinstana [sic] Billings, p. 145, figs. 122a, b.
1865 Athyris turgida Shaler, p. 69.
1866 Athyris Prinstana [sic] Billings, p. 46 (no figures).
1894 Hindella prinstana (Billings); Hall and Clarke, pl. 41, fig. 28, pl. 49, fig. 1 (specimen illustrated from the Prinsta Member, in the lower unit at Junction Cliff).

1928 Hindella prinstana (Billings); Twenhofel, p. 220, pl. 22, figs. 12, 13.
1977 Hindella umbonata; Sheehan, pl. 1, figs. 26–28.

**Type locality and horizon.**—Billings (1862, p. 145) reported the species from “Prinsta Bay, Anticosti, Division 1”, but his original types have not been located. At this locality on the northeast coast, the species occurs in the lower Prinsta Member, stratigraphically coeval to the Prinsta Member of the west coast, lower Hirnantian. This low bluff locality on the east side of the Prinsta River mouth (= A135 or A362 of the new collections; map sheet 12F/5, UTM 20, 74480E, 66450N), consists of the following units, in descending order:

1. 105 cm of calcareous sandy shales with rare nodules.
2. 319 cm of nodular shale and limestone. Upper 289 cm nodular shale and calcarenites with nodules at top, sandy, upper resistant ledge with Hindella prinstana, Hornotoma, and sandstones at 30 cm and 95 cm above base. Most Hindella occur ~30 cm above base at ledge in this 5 cm bed with broken Hindella, aulacercids, cup corals; units less sandy and calcarenitic at base then near top. The base of the western Prinsta Member (= Fraise Member) is at this level.
3. 145 cm nodular, wavy bedded and platy calcareous sandstone (Velleda Member, Vaulare Formation).

**Occurrence.**—In addition to the type locality, the species occurs in the localities listed below:

A134a. Prinsta River mouth, first outcrop on NW bank, ~3 m recessive, silty dark green-gray shale and sandstone interbeds at base, overlain by 2 m of nodular limestone, with loose valves of Hindella prinstana. Prinsta Member (base). Map sheet 12F/5, UTM 20, 74360E, 66570N.

A134b. Prinsta River, NW bank, ~200 m upstream, same stratigraphic level as A134a, with H. prinstana. Map sheet 12F/5, UTM 20, 74130E, 66510N.

C717. Jupiter road, ~3 km south of main road. Recessive green-brown soft shales, nodular calcarenites, with abundant Hindella prinstana and Eospirigerina. Fraise Member. Map sheet 12E/11, UTM 20, 69480E, 10370N.

A431. Anse aux Fraises. Thinly bedded, dark gray shale, with nests of Hindella prinstana, Plaesiomys, and Eospirigerina in tidal flat outcrops. Fraise Member, ~15 m above base. Map sheet 22H/16, UTM 20, 95660E, 20680N.

A432. Anse aux Fraises, tidal flat outcrop, ~150 m south of A431, with localized nests of Hindella prinstana, Parastrophiolina, and Leptaena. Fraise Member (middle). Map sheet 22H/16, UTM 20, 95780E, 20430N.

A1317a. Lac Cailloux road, 4.8 km south of main road, 3–5 m lower recessive weathering shales, and brown-green soft to blocky, nodular micrite, with Velldia, Plaesiomys, and Hindella prinstana. Fraise Member. Map sheet 12E/13, UTM 20, 39700E, 14360N.

**Remarks.**—There are five species of Hindella in the Ellis Bay Formation, suggesting a relatively rapid evolution of Hindella during the Hirnantian. Other species occur in the higher Parastro, Prinsta, and Laframboise members. The oldest species, Hindella prinstana is smaller (~12 mm wide), and about equally

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as wide as long (instead of elongate, as in \emph{H. umbonata}), less inflated, and with a more pronounced anterior fold. In eastern Anticosti, this is the stratigraphically lowest species of \emph{Hindella}, occurring directly above sandstones of the Velleda Member of the Vaureal Formation. The elongate shells of \emph{Hindella umbonata} occur upstream on the Prinsta River at locality A813 (see localities of \emph{H. umbonata}). \emph{Hindella prinstana} is abundant in the Prinsta and Fraise members at both ends of the island.

Shaler (1865) reported his species “\emph{Athyris turgida}” from “1/2 mile north of White Cliff”, which posits it within the Fraise Member, and is thus a probable synonym of \emph{H. prinstana}.

The specimen illustrated by Sheean (1977) resembles those from the lower recessive shales of the Fraise Member at Junction Cliff, and is thus assignable to \emph{H. prinstana}.

\textbf{\emph{Hindella bulbosa} new species}

Figures 2.8–2.13, 3.1–3.17, 4

\textbf{Types.}—Holotype, GSC 137671 (Fig. 3.1–3.5); figured paratypes, GSC 131790, 137670, 137679–137681 (Figs. 2, 3), and 131799 (serially sectioned specimen; Fig. 4). Parastrophinella Bluff, southwest coast of Anticosti Island, locality A84 (=C720; see Jin and Copper, 1997). First coastal bluff scree outcrops ~700 m southeast of Junction cliff (UTM 20, 0397126E, 5518771N). Lower half of bluffs of thinly bedded micrites, shales with abundant \emph{Parastrophinella} \emph{reversa} in several layers (type locality), and a diverse benthic fauna (see Jin and Copper, 2008, fig. 6C). Upper Parastro Member, Ellis Bay Formation, middle Hirnantian.

\textbf{Diagnosis.}—Relatively small, elongate, suboval shells of \emph{Hindella}, with narrow apical angle and low beak; usually prominent growth disruptions, concentric filae, and more distinctive radial capillae; gentle fold and sulcus developed towards anterior commissure. Dental plates straight, flanking wide lateral cavities; small teeth; 7 or 8 spiral whorls; simple low jugum and flat jugal arch.

\textbf{Description.}—Shells relatively small, longer than wide, bulbous, ovoid to pear-shaped, wider anteriorly than posteriorly. Apical angle relatively narrow, rounded. Adult shells 8–10 mm wide (average = 10 mm), with average thickness of ~9 mm. Umbo strongly convex, inflated. Anterior commissure weakly plicate. Internal structures as in diagnosis.

\textbf{Etymology.}—From the Latin, \emph{bulbus}, a swell, referring to the globular, pear-shaped shell typical of the new species.

\textbf{Remarks.}—The new species is readily distinguished from \emph{Hindella umbonata} (Billings, 1862) and \emph{H. prinstana} (Billings, 1862) of the underlying Juncliff and Fraise members by its smaller size (with average width 10 mm versus 16 mm for \emph{H. umbonata}, and average thickness 9 mm versus 12 mm for the large shells of \emph{H. umbonata}), slightly wider apical angle, more bulbous shape, and less robust shell wall. \emph{Hindella umbonata} is strongly elongate, with parallel sides, whereas \emph{H. bulbosa} n. sp. reaches its maximum width anteriorly, giving it a pear shape. The umbo of \emph{H. bulbosa} n. sp. is relatively pinched, given its narrow apical angle of ~110°, versus 100° in \emph{H. umbonata}.

\textbf{Hindella bulbosa} n. sp. is common only at the western (e.g., Parastrophinella Bluff) and middle parts of Anticosti Island, and appears to be absent at the east coast.

\textbf{Genus Cryptothyrella} Cooper, 1942

\textbf{Type species.}—\emph{Whitfieldella quadrangularis} Foerste, 1906. Brassfield Formation, Aeronian, Dunkinsville (= “Duncansville” of Foerste, 1906), Adams County, Ohio.

\textbf{Species assigned.}—In addition to the type species, the following species are assignable to \emph{Cryptothyrella}:

- \emph{Atrypa crassa} Sowerby, 1839.—Goleuogoed Formation, late Rhuddanian, Girvan.
- \emph{Terebratula furcate} Sowerby, 1839.—Bog Quartzite, Aeronian, Shropshire.
- \emph{Atrypa cylindrica} Hall, 1852, p. 76, pl. 24, figs 2a–h.—Irondequoit Formation, basal Sheinwoodian, Niagara region, New York (strongly elongated shell with prominent capilla).

Shells figured later as “\emph{Whitfieldella cylindrica} Hall” by Hall and Clarke (1894, pl. 40, figs. 16–22) are from the “Niagara group” (=Bisher Formation, coeval with the Irondequoit Formation; C.E. Brett, personal communication, 2017), “Hillsboro, Ohio” and have anterior plicae and capilla.

- \emph{Cryptothyrella bisulcata} Gauri and Boucot, 1970.—Brassfield Limestone, Aeronian, near West Union, Ohio.

\textbf{Species questionably assigned.}—The following species require further study to establish their generic affinities:

- \emph{Hemithyris angustifrons} M’Coy, 1851.—Mulloch Hill Formation, late Rhuddanian, Girvan. Internal structures poorly known.
- \emph{Whitfieldella subquadrama} Foerste 1906, p. 326, pl. 1, figs. 3a–f.—Indian Fields Formation, Aeronian, Berea, Kentucky. Regarded as junior synonym of the type species \emph{Cryptothyrella quadrangularis} by Gauri and Boucot, 1970.

\textbf{Diagnosis.}—Shell medium to relatively large, elongate, globose, smooth to capillate, uniformly biconvex to bisulcate. Very small deltoidal plates flanking transapical foramen in adult shells; beak incurved. Ventral umbo thickened internally by callus fill, leaving narrow medial groove; teeth small, rounded; dental plates short, with thin terminations, medially inclined, fused posteriorly through prismatic thickening, becoming discrete anteriorly; dental cavities mostly filled with prismatic callus posteriorly. Socket plates relatively thin, but inflated apically to support dental sockets; crura thin, delicate, parallel to each other, extending along commisural plane. Umbonal blades terminated as hooks, fused to crura; jugal saddle almost flat, positioned in mid-shell; spiralia with 8–10 whorls, directed laterally.

\textbf{Remarks.}—Based on Gauri and Boucot’s (1970) study of \emph{Cryptothyrella}, Ziegler and Boucot (1970) proposed a \emph{Cryptothyrella} community for North America. The genus, however, has had a shifting taxonomic history between a valid genus \emph{Cryptothyrella} to a synonym of \emph{Hindella}, resulting in a confusing stratigraphic range between the Late Ordovician (Hirnantian) and early Silurian. Various species have been
allocated to one or the other genus (Sheehan, 1977), thus making the community analysis unreliable. Gauri and Boucot (1970) provided a single transverse section that showed large lateral cavities, ventro-medially inclined dental plates, and flat, thin, divided horizontal hinge plate, which are similar to those in the topotype shell of *C. quadrangularis* examined in this study.

Gauri and Boucot (1970, fig. 1) did not examine the crura, jugum, or spiralia, but noted a questionable “septalium”, which is not present in the shell serially sectioned herein, although a median septum is present. More detailed internal structures were provided by Grunt (1980, 1986, 1989), through serial sections of topotype material.

Figure 3. *Hindella bulbusa* n. sp. from Parastrophinella Bluff (loc. C720 = A48), Anticosti Island. (1–5) GSC 137671, holotype; (6) GSC 137681, paratype slab, interiors of ventral valves; (7–11) GSC 137670, paratype, subrhomboidal shell; (12–17) GSC 131790, well-preserved shell showing capillae in anterior part of shell.
Cryptothyrella is externally distinct from Hindella by its notably larger and more elongate shell (commonly twice as long as Hindella), commonly with a ventral medial groove (a dorsal medial groove may also be present in some shells). Internally, the ventral apical cavity has a much thicker prismatic callus than in Hindella, and dental plates are strongly inclined ventromedially, almost forming a “pseudospondylium”—a feature that is not prominent in Hindella. Internally, the crura of Cryptothyrella are much longer (about twice the length), and straight anteriorly, parallel to each other. The umbonal blades form long hooks, which are double the size seen in Hindella. The mid-shell-positioned jugal saddle of Hindella is rounded, and tilted slightly to the posterior, whereas in Cryptothyrella it is flat, and more anteriorly positioned in the shell. A larger number of spiral whors in Cryptothyrella may be related to its larger shell size (Fig. 4). A “pseudoseptalium” may be seen in Hindella sections near the dorsal umbo, but this is absent in Cryptothyrella. There is no true septalium present in either genus.

Cocks (1978) assigned a loose valve (the lectotype) of Hemithyrias angustifrons Salter from the Rhuddanian Mulloch Hill Formation to Cryptothyrella, but later transferred it to Hyattidina (Cocks, 2008). However, Cocks (1978) also assigned the holotype of Atrypa crassa Sowerby, 1839, a Rhuddanian shell, to Hindella, which would make the two genera coeval in the UK. These assignments seem doubtful.

Cryptothyrella quadrangularis (Foerste, 1906)  
Figures 5.1–5.16, 6

Figure 4. Selected serial sections and reconstruction of the spiralium and jugum of Hindella bulbusa n. sp. Paratype, GSC 131799, Parastro Member, Ellis Bay Formation, Parastrophanella Bluff (loc. A84), Anticosti Island. Note the simple jugum in the anterior central part of the shell cavity, the hook-like attachment points of the jugal blades, and the lack of skeletal connection to the crura. Number below each serial section denotes distance (mm) from shell apex.
1906  *Whitfieldella quadrangularis* Foerste, p. 327.
1906  *Whitfieldella subquadrata* Foerste, p. 326.
1970  *Cryptothyrella quadrangularis* (Foerste); Gauri and Boucot, p. 125, pl. 29, 30.
1986  *Cryptothyrella quadrangularis*; Grunt, p. 18, fig. 3.
1989  *Cryptothyrella quadrangularis*; Grunt, p. 39, fig. 23.

*Types.*—Foerste (1906, p. 327, pl. 1, figs. 4a–c) reported the type species from a “ravine...northeast of Duncansville, east of Sprow’s bridge...in Adams county, Ohio...38 feet above the...
base of the Clinton.” Foerste (1906, p. 41) further described the quadrangularis bed within a measured 54 ft (16 m) section in which it forms a “6 inch” (15 cm) layer. In modern stratigraphy, the type species is from the Brassfield Formation, lower Aeronian (C.E. Brett, personal communication, 2017). Whifieldella subquadrata Foerste, 1906, synonym of C. quadrangularis (see Gauri and Boucot, 1970), is from the basal Plum Creek Shale, which overlies the C. quadrangularis bed and is separated from it by a minor disconformity (C.E. Brett, personal communication, 2017). The serially sectioned specimen in this study (Fig. 6) is a topotype provided by W. Ausich of Ohio State University.

Diagnosis (emended herein).—Large, elongate, strongly biconvex shells, commonly with gentle ventral sulcus, and faint radial capillae. Anterior commissure broadly uniplicate; beak incurved with obscured small denticidial lates and apical to transapical foramen. Both valves thickened by prismatic infill, marked by narrow median groove on ventral interior. Large dental cavities flanked by thin dental plates; teeth small, solid. Crura long, straight, subparallel to each other; dorsally flat hinge plates; median septum present; umbonal blades with hook-like terminations, not connected to crura; simple jugum flat, saddle-shaped; laterally directed spiralia with 8–11 whorls.

Remarks.—The large, elongate shell (Fig. 5) easily distinguishes the Aeronian genus Cryptothyrella from Hirnantian Hindella and Rhuddanian Koigia. Striking are the internal massive, prismatic anterior deposits of the shell wall that would have weighted the shell in an umbo-down position during life (Fig. 6; 2.2–6.1 mm from shell apex). The jugum is simple, with a flat arch (at 15.7 mm), similar to that in Hindella, both of which share a finely capillate shell surface, although the faint capillae can be observed only on well-preserved shells.

Figure 6. Serial sections and brachidium reconstruction of Cryptothyrella quadrangularis (Foerste 1906). OSU 18250, topotype, Brassfield Formation, lower Aeronian, Dunkinsville (= Duncansville of Foerste, 1906), Adams County, Ohio. Note the development of massive prismatic thickening of the ventral umbo divided by a deep groove, base-ventrally inclined dental plates, long and straight crura, and the anteriorly positioned jugum, which differentiate Cryptothyrella from Hindella. Number below each serial section denotes distance (mm) from shell apex.
Serial sectioning in this study revealed that the crura are not fused directly to the umbonal blades that have a hook-like ending (Fig. 6).

Grunt (1986) was the first to illustrate the complete internal structure of the species, with serial sections based on “Whitfieldella subquadrata” material from Indian Fields of Kentucky (Smithsonian collections). Cryptothyrella subquadrata forms a distinct marker bed in the Brassfield Formation, traceable from Kentucky to Ohio (C.E. Brett, personal communication, 2017), and its synonymy with C. quadrangularis by Gauri and Boucot (1970) is justified because the quadrate form is within the intraspecies variation of C. quadrangularis based on examination of the topotypes (e.g., Fig. 5.1–5.5). The serial sections of a shell from the original type locality (Duncansville, Ohio) of C. quadrangularis, as is shown for the first time here, display internal structures that are largely the same as those in the topotype of “W. subquadrata” as illustrated by Grunt (1986, fig. 3), especially in the development of a simple jugum.

The prismatic pedicle callus that fills most of the ventral umbo, as seen in the serial sections, is also shown in Grunt (1986, 1989). The teeth are supported by dental plates with prismatic thickening, with the blunt teeth directed inwards into opposing dorsal sockets. The dorsal hinge plate is strong, separated by a notothyrial pocket, and reinforced by prismatic layer under the crura. The crural bases are minute, imbedded in the hinge plate, and stretch to form thin, long, flat, parallel plates (Fig. 6; 5.5–6.1 mm from shell apex), narrowing anteriorly to points in the medial plane. The umbonal blades from the jugum start before the crura, extend posteriorly, forming a round arch, like a shepherd’s crook, disconnected from the crura (Fig. 6).

Cryptothyrella cylindrica (Hall, 1852) reported from New York and Ohio, is early Sheinwoodian, thus much younger species than the Aeronian C. quadrangularis. It differs from the latter in having a more elongate shell, with well-developed dorsal fold and ventral sulcus towards the anterior, forming a highly uniplicate anterior commissure, and marked by well-developed anterior capillae (Fig. 7.1–7.6), originally described as “radiating striae” by Hall (1852, p. 77).

Genus Koigia Modzalevskaya, 1985
Figures 8.1–8.6, 9

Type species.—Hindella extenuata Rubel, 1970 (p. 48, pl. 25, figs. 1–9), Juuru Regional Stage, Koigi Member, Varbola Formation (basal Rhuddanian, Nestor, 1997); Vakhtrepa, Koigi, Estonia. See Koigia serial sections in Modzalevskaya (1985, p. 38).

Diagnosis.—Shell small, smooth, approximately as wide as long, moderately biconvex, with incurved beak. Ventral apical cavity with little callus. Dental plates thin, defining open lateral cavities. Dorsal valve with relatively flat hinge plates; crura short, thin, flat, not connected to jugal blades, forming sharp angle at junction with primary lamellae; jugum simple, with flat jugal saddle positioned at mid-length to posterior of shell;
modest median septum connected to hinge plate; spiralia with 5–7 whorls, laterally directed (Fig. 8).

Remarks.—Koigia has a small shell (usually <10 mm wide) compared to other genera of the Hindellinae (Fig. 8). Using serial sections, Rubel (1970, figs. 15–17) reconstructed six whorls of laterally directed spiralia, a simple jugum, and a hooked, right-angle connection of the umbonal blades of the first spiral whorl with the crura. This type of connection is not observed in the Anticosti shells of Koigia (Fig. 9). All hindellines from Anticosti Island show a disconnection between the crura and brachidia. Thus, it is likely that this disconnection between crura and brachidia was overlooked in the Estonian material during sectioning and reconstruction. The small-shelled Koigia differs from Hindella in its larger and more distinctive lateral cavities, and thin dental plates, as well as a thinner shell wall. Lateral cavities are infilled with thick callus in the ventral apex of Hindella. The crura in Koigia are short and stubby; the simple jugal arch is rounded, versus flat in Hindella. Externally, the shell of Hindella tends to be more elongated and globose, and commonly larger. Capillae, observed in well-preserved shells of Hindella, are unknown so far in Koigia. The younger Rhuddanian genus Koigia bears similarities to its presumed Hirnantian ancestor Hindella. The smaller Koigia shells may have been an example of dwarfism immediately after the Hirnantian mass extinctions. This agrees with many other small-shelled brachiopod taxa in the basal Ruddanian strata on Anticosti Island, such as the atrypides Becscia and Zygospiraella, the orthides Isorthis and Mendacella, and the pentameride Viridita.

Genus Hyattidina Schuchert, 1913

Type species.—Atrypa congesta Conrad, 1842, New York, Clinton Group, Llandovery.

Diagnosis (emended herein).—Small, biconvex, inflated, smooth shells with strongly incurved beak, minute hollow deltidial plates, and prominent angular fold-sulcus. Internally ventral umbo with thick callus; teeth short, blunt, directed medially; dental plates relatively strong, straight, defining small lateral cavities. Dorsal hinge plate stout, divided by narrow groove, with bulbous inner socket ridges; median septum weak; crura short, not fused with but approaching umbonal blades at sharp angle, in non-touching “handshake” pattern; jugum simple, with angular saddle pointing ventro-dorsally; spiralium with 6–8 whorls, laterally directed.
Occurrence.—Aeronian to Telychian, ?Wenlock.

Remarks.—When proposing the genus *Hyattella*, Hall and Clarke (1893) compared *Athyris junia* Billings, 1866 with the type species *H. congesta*. Schuchert (1913, p. 415) renamed the genus *Hyattidina* because the name *Hyattella* was pre-occupied.

The shells of *Hyattidina* show considerable variability, ranging from almost smooth and round to those with an angular fold and sulcus. The brachidia, however, are quite consistently developed, with a simple jugum and laterally directed spiralia. The reconstruction of the jugum and spiralium by Hall and Clarke (1894, pl. 40, fig. 26), based on a silicified shell from “Reynale’s Basin, New York”, is essentially correct, but missed the sharp angle and juxtaposition of the crura and umbonal blades (which are shown as a straight connection). Our material, presented herein, is very similar in shape and size to the type *Hyattidina congesta* from the “Clinton... Lockport, New York” as figured by Hall and Clarke (pl. 40, fig. 26). Alvarez and Rong (2002, p. H1556) selected a neotype from the Hall collection, which has a more prominent fold-sulcus than seen commonly in the Anticosti specimens, which are flatter, with a weaker fold. Hall and Clarke (1893, p. 61; 1894, p. 767) illustrated the type species *H. congesta* with a simple jugum (referred to as a “loop top”), similar to that of the Anticosti species.

Alvarez and Rong (2002) described *Hyattidina*, and its subfamily, as lacking a median septum and a jugal saddle, and having a shell with numerous growth lines and thin dental plates. Based on the new data from this study, these criteria should be emended to describe a smooth shell (without prominent growth lines), a distinct septum, relatively thick dental plates, and a jugal saddle. The information on the shape and configuration of umbonal blades, crura, jugum and spiralia, as presented in this study, is also new. Alvarez and Rong (2002) also allocated a Ludlow age to the genus, but the type and most other species of the genus are Telychian in age, thus much older. On Anticosti, the lowermost occurrence of the genus, which is often abundant, is in the Macgilvray Member of the upper Gun River Formation (mid-Aeronian; Copper et al., 2013). It retains this abundance into to the Ferrum Member of the Jupiter Formation (early middle Telychian; for example, see *Hyattidina cf. junia*, below), becoming rare in the Pavillon Member (mid-Telychian). In the richly fossiliferous Anticosti succession with abundant athyrids, *Hyattidina* is absent from the upper Katian through lower Aeronian strata.

Internally, the brachidia of Anticosti *Hyattidina* are quite similar to those of *Hindella* in the jugum and short crura, but differ from *Koigia*, which has a simpler, rounded jugum, and fewer spiral whorls. Thus there is little to distinguish the brachidia in the hyattidines and hindellines, and we thus place them in the same family Hindellidae. *Hyattidina* and *Koigia* have much less ventral apical prismatic callosity than either *Hindella* or *Cryptothyrella*.
suggesting that *Hyattidina* may have its ancestry in Rhuddanian *Koigia*.

*Hyattidina cf. H. junia* (Billings, 1866)
Figures 10.16, 11

1866 *Athyris junia* Billings, p. 46 (no illustrations).

?1894 *Hyattella junia* Billings; Hall in Hall and Clarke, pl. 40, figs. 29–31.

1928 *Hyattidina congesta junia* Billings; [sic] Twenhofel, pl. 30, figs 4–6.

1981 *Hyattidina junea* (Billings); [sic] Bolton, 1981, pl. 5, fig. 4.

*Types.*—Lectotype, herein selected, GSC 2374, from “six miles east of Otter River, Anticosti Island, ... Divs 2,3,4 Richardson” (Billings, 1866, p. 47, based on Richardson’s collections). Twenhofel (1928, p. 223 and explanation of pl. 30) illustrated the type specimen and labeled it as from “Hannah Cliff, east of Gun River, zone 2.” This places the type locality within the Macgilvray Member of the Gun River Formation (see Copper et al., 2012), where the genus becomes abundant for the first time. The species reaches its largest shell size in the Goéland Member of the Menier Formation (Copper and Long, 1990; Copper et al., 2012), and fades away in the Richardson and Cybèle members of the Jupiter Formation (Copper and Jin, 2015).

*Remarks.*—The serially sectioned specimen (Fig. 11) comes from the Cybèle Member of the Jupiter Formation, Cape Billings at the north end of Wreck Bay (locality A163, map sheet NTS 12F/4, UTM 20, 96180E, 41640N), a ~8 m thick low bluff section leading to the sea. The sampled beds include, in descending order:

- A163d, thin-bedded micrites and green-gray shales within the top 1 m of section, with the rhyonochelid *Platyrochaloa*;
- A163c, 1–2 m of thinly bedded, shaly micrites, with *Hyattidina*; A163b, ~2 m of poorly fossiliferous gray shales and micrites, with the atrypide *Clintonella* and small favositid corals;
- A163a basal 2 m of thin-bedded coquina, with small-shelled *Gotatrypa, Coolinia*, small favositids, and gastropods.

Figure 10. (1–15) *Hyattidina* sp. from the Goéland Member, Menier Formation, locality A852a; (1–5) GSC 134443; (6–10) GSC 134441; (11–15) GSC 134442. (16) Thin sections of *Hyattidina cf. H. junia* (Billings, 1866) from the Cybèle Member, Jupiter Formation, coastal bluff section, just southeast of Richardson Cliff (loc. A872).
The specimen is from the northeast coast, as was the material sent by Billings to Hall and Clarke (1893), but lies stratigraphically well above the smaller shells in the Macgilvray Member, Gun River Formation, on the south coast.

The specimen illustrated as *Hyattella junia* by Hall and Clarke (1894, pl. 40) and labeled as from "East cape", was most likely sent by Billings from the Richardson collection from bluffs east of East Point. This would place them in the Cybèle Member of the Jupiter Formation, similar to the serially sectioned specimen in this study. The strata of the Goéland Member (Menier Formation) were never sampled by either Richardson (1857) or Twenhofel (1928) because of the usually stormy northeast coastline, with its high cliffs (there was no road access at their time).

The type specimen of *Hyattidina congesta* (Conrad, 1842, as illustrated by Hall and Clarke, 1894, pl. 40, figs. 23–28) differs from the type of *Hyattidina junia* in its larger size, and smoother shell, with a prominent dorsal fold and ventral sulcus. The shell of *H. junia* illustrated by Hall and Clarke (1894, explanation to pl. 40) came from the Cybèle Member, stratigraphically much higher than the type stratum in the Gun River Formation. The shell illustrated in 1894 as *Hyattella congesta* by Hall and Clarke (1894) bears strong similarity to *Hyattidina* sp. (see below), which occurs in the Goéland Member of the Menier Formation (Aeronian). There are several undescribed species of the genus on Anticosti Island.

*Hyattidina* sp.
Figures 10.1–10.15, 12

Remarks.—Smooth, biconvex shells with a distinct ventral sulcus and broad dorsal fold (Fig. 10.1–10.15) are herein referred to the genus *Hyattidina* under open nomenclature. They occur together with *Elkanathyris pallula* n. gen. n. sp. in the lower Goéland Member of the Menier Formation. *Hyattidina* sp. differs from typical *H. junia* from the Gun River Formation in that the unusual umbonal blades seen in *H. junia* are absent in *Hyattidina* sp. (compare Figs. 11, 1.8–2.1 mm with Fig. 12, 2.6–3.5 mm from apex).

*Elkanathyris* new genus

Type species.—*Elkanathyris pallula* n. gen. n. sp., Menier Formation, upper Goéland Member, mid-Aeronian, Llandovery; Anticosti Island.
Species assigned.—Type species only.

Diagnosis.—Shell small to medium sized, wider than long, posteriorly plicate, with 4–6 strong ribs; hinge line relatively straight, long. Dental plates straight, delimiting relatively small lateral cavities. Inner socket ridges strong and bulbous; umbonal blades curved in sharp juxtaposition to crura; spiralia with <12 whorls; simple jugum with pointed jugal saddle.

Etymology.—After Elkanah Billings, the first Canadian paleontologist of the Geological Survey of Canada, who described numerous fossils from Anticosti Island, and Athyris, the eponymous genus of the order Athyrida.

Remarks.—Large collections from shell nests in the Gun River and Menier formations of Anticosti demonstrate considerable variability in the development of coarse ribs (plicae). The strong ribs are most prominent in the apical area, clearly defined in the posterior half of most shells, but fade anteriorly and laterally, extending to the anterior margin only in some immature shells. This may be an endemic genus to Anticosti Island, and its development of apical plicae is similar to that in some unrelated brachiopods lineages on Anticosti, such as Phricoclorinda Jin and Copper, 2000, which evolved radial and crisscross ribbing from the normally smooth Clorinda. In New York, Clinton strata (Aeronian–Telychian) contain abundant Hyattidina, but no ribbed forms are known to be related to Hyattidina.

Elkanathyris n. gen. differs from the older Hyattidina in its long straight hinge plates, bulbous inner socket ridges on the
Elkanathyris pallula new genus new species

Figures 13.1–13.19, 14

Type.—Holotype, GSC 134439 (Fig. 13.1–13.5), from locality A708 (=A852a, map sheet NTS 12F/4, UTM 20, 92900E, 49400N), exposures along Sandtop gravel road, 2.4 km south-east of South Sandtop Creek. Soft-weathering, blue-gray shales and micrites, with local shell beds or lenses rich in Pentamerus, Hyattidina, Joviatrypa, Stricklandia, and Trilesia, in addition to the new species. Goéland Member, upper unit 5, Menier Formation.

dorsal valve constrained laterally by teeth from the ventral valve, and a sharp angular jugum connecting a spiralium with up to 10 whorls. As in Hyattidina, there is a median septum buried in both valves; the crural bases are small and delicate within the bulbous inner socket ridges.
Diagnosis.—Small to medium sized, transversed extended, posteriorly plicate hindellide shells, with very narrow dental cavities, bulbous socket ridges, and a simple jugum with pointed jugal saddle.

Description.—Shell small to medium sized, generally wider than long, subquadrate, biconvex; coarse ribs (plicae) in posterior half of adult shell, two or more medial ribs on ventral valve, single strong median rib on dorsal valve, and two or three lateral ribs; remainder of shell smooth; concentric growth lines weak or absent; hinge line relatively long, straight; beak incurved, with minute apical, or transapical foramen flanked by small, hollow deltidial plates. Ventral umbonal interior with narrow, slit-like dental cavities, leading to dorso-medially directed teeth; inner socket ridges bulbous, obscuring thin crural bases; jugum simple with pointed jugal saddle; laterally directed spiralia of 9–10 whorls.

Remarks.—In this study only one new species of the new genus is described. The genus ranges through ~150 m of strata, found above and below the type stratum. Some of these hyattidinid nests, but not all, include both smooth Hyattidina and ribbed Elkanathyris n. gen. shells, which occur in the Stricklandia or Triplesia brachiopod community, with the Pentamerus community in the strata above. This suggests that the athyrides lived in relatively deeper water, mid-shelf carbonate settings (equivalent to a BA-4 setting of Boucot, 1975).

Population variants at the type locality include smooth shells (without the undulating ribs or plicae) that are internally identical to Elkanathyris pallula n. gen. n. sp. (Figs. 13, 14), as confirmed by serial sections of several specimens of both

Figure 14. Serial sections of Elkanathyris pallula n. gen. n. sp. Specimen GSC 131803 from locality A708, Goeland Member (unit 5), Menier Formation. Note that the left spiralium has broken off, causing the jugum and spiralium to be displaced posteriorly towards the hinge, making it difficult to reconstruct the connection between the umbonal blades and the crura. Number below each serial section denotes distance (mm) from shell apex.
variants in this study. Pending a broader investigation into the internal structures of *Cryptothyrella* and *Elkanathyris* n. gen., the smooth form that co-occurs with the ribbed *Elkanathyris pallula* n. gen. n. sp. is assigned provisionally to *Hyattidina* sp. under open nomenclature.

**Conclusions**

An abundant and well-preserved suite of athyride brachiopods is present in the Late Ordovician (Hirnantian) and early Silurian (Llandovery) sequence of Anticosti Island. Their stratigraphic distribution provides clues as to the change-over in shelly communities crossing the Ordovician-Silurian mass extinction boundary. Marked are rapid evolution of *Hindella* species during deposition of the Hirnantian Ellis Bay Formation, and their disappearance at the top of the Ordovician, alongside the last occurrence of the orthide genus *Hirnantia*. *Hindella* is replaced by the athyride *Koigia* in the Rhuddanian, a smaller genus that is locally abundant along with the new Early Silurian shelly fauna of *Zygospiraelia, Beccia* and *Viridita* (Jin and Copper, 2010; Copper and Jin, 2014). In the Aeronian-Telychian, athyrids diversified further into the meristelline and whitfieldelline subfamilies that mark the Telychian through Wenlock in Laurentia.

Detailed serial sections using acetate and butyrate peels are reconstructed in three dimensions to demonstrate the nature of the calcified skeletal supports of the lophophore in these early athyrids. This sheds a new, and different, light on their rise in the Silurian. For the first time we note: (a) Hindellide brachidia lack a skeletal connection between the spiralia and the dorsal hinge crura (this is thus unlike what is normally shown in figures), (b) the umbonal blades of the brachidium and crura are bent at their tips into a hook-like structure (new discovery), and (c) the jugum of hindellides is a simple arch, either rounded or angular. Using the crura, and brachidium, we modify and simplify the existing taxonomy of early athyrids, combining such genera within the *Hindellidae* Schuchert, 1894. The evolution of such early athyrids provides a stratigraphically useful tool that explains the westward migration of pentameride, rhychonellide, and atrypide shelly communities in the early Silurian equatorial belt of Laurentia and Baltica.

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