

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

Paul Copper,¹ and Jisuo Jin²

¹Loupicoubas, 46220 Prayssac, France (pcopper@laurentian.ca)

²Department of Earth Sciences, University of Western Ontario, London, Ontario N6A 5B7, Canada (jjin@uwo.ca)

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 Phanerozoic 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 (atrypides, 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, atrypides, 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 athyrides and atrypides 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 athyride 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 Coelospirinae as compatible with atrypoid affinities (Alvarez et al., 1998, p. 836). These authors assigned *Hindella* to the Silurian Meristellinae (superfamily Meristelloidea), and considered *Cryptothyrella* as its junior

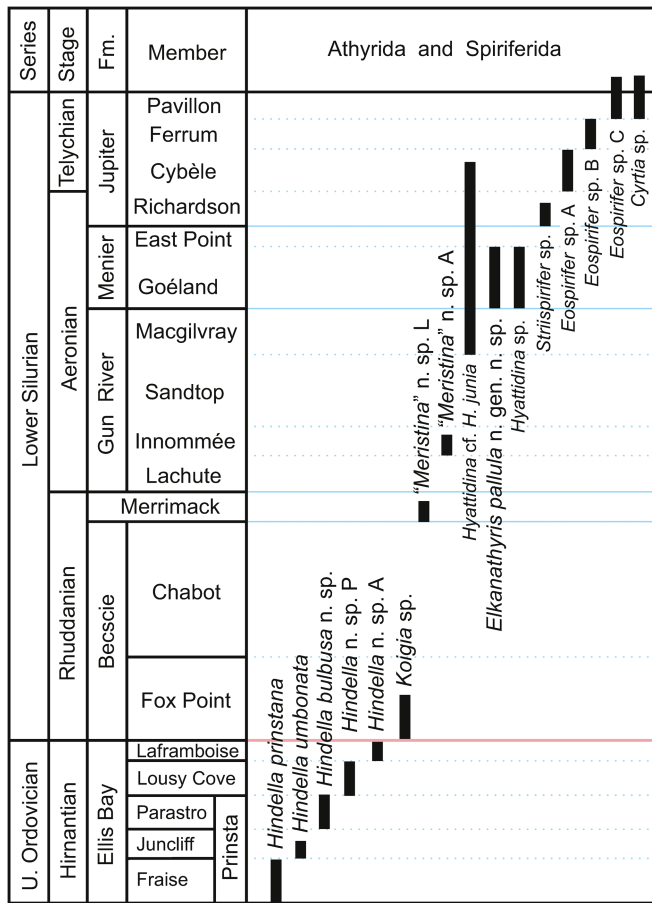


Figure 1. Stratigraphic ranges of the early hindellides *Hindella*, *Koigia*, *Hyattidina*, and *Elkanathyris* n. gen. across the Ordovician-Silurian boundary, Anticosti Island, eastern Canada. The early spiriferide occurrences are also shown for reference.

synonym. The Rhuddanian (early Silurian) genus *Koigia*, common in Estonia and on Anticosti, was allocated to their new subfamily Whitfieldellinae, to which they gave a range of Ashgill through late Silurian (Alvarez et al., 1998, p. 836). Thus Alvarez et al. (1998) abandoned the earlier name Hindellinae (Schuchert, 1894), used formally for the earliest athyrids by most Russian workers. We have found no evidence for any Katian–Rhuddanian Meristellinae, nor Whitfieldellinae on Anticosti Island, where athyrids are generally abundant and well preserved at numerous localities.

Modzalevskaya (1979, fig. 1; 1996) treated the classification of more-advanced athyrids of Silurian and Devonian age, including genera with a complex jugum (or jugal saddle and loops and “arcuate jugal plates”, such as *Glassina*, *Greenfieldia*, *Protathyris*, and *Pseudoprotathyris*). Such complex jugal structures and accessory lamellae are unknown or have not been described in athyrids of Late Ordovician and earliest Silurian (Rhuddanian) age, and did not become common until Wenlock–Ludlow time. Modzalevskaya (1979) also pointed out that the subfamily Protathyridinae Boucot, Johnson, and Staton, 1965 represents a junior synonym of the Athyrinae. Grunt (1989, fig. 41) included *Hindella* along with *Koigia*, *Hyattidina*, and *Cryptothyrella* (and others) within the Hindellinae as an ancestral group, although she did not discuss the simplicity of the brachidium as a key character. We effectively concur with that analysis.

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 athyrids 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 athyrids (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 Hyattidininae (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 superfamily Athyridoidea. 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 athyrids 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 athyrids 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 Parastro and Lousy Cove members, with the largest elongate shell at the top of the reefal Laframboise 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 umbonal blades curved from the jugal saddle, first appears much higher in Telychian strata of the Jupiter Formation, coeval with its occurrence in Baltica.

Koigia occurs in the basal Becscie Formation, within ~1 m of thin- to medium-bedded, hard, micritic mudstone and wackestone 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 *Zygospiraella*, *Becscia*, and *Viridita*. In Estonia, the type species of *Koigia* also occurs in the basal Rhuddanian (Rubel, 1970 initially 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 further study. The type species, *Cryptothyrella quadrangularis* (Foerste, 1906), as seen in Ohio, is characterized by an unusually large and prominently elongate shell (30–40 mm in length). The Rhuddanian ‘*Cryptothyrella* benthic 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 mid-Telychian. The genus is absent from the older Becscie, 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 northeast, 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 Hirnanian. 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 east and west ends of Anticosti reflect a curving shoreline along the 200 km long outcrop belt.

In such a carbonate-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 sediments. In the reefal Laframboise Member, *Hindella* was generally 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* community 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 monospecific), and extending into shallow and high-energy reefal settings. In the Parastro Member, a relatively small form of *Hindella* (*H. bulbosa* 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 Becscie Formation, especially in the lower Fox Point Member, associated with other small-shelled taxa (e.g., *Becscia* and *Viridita*; see Jin and Copper, 2010). The small shells usually show various degrees of distortion, damage, and disarticulation, with common geopodal 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 opportunist that thrived immediately after the Late Ordovician mass extinction events, but athyrides became scarce in the upper Becscie Formation (Chabot Member) when the monotypic, large-shelled *Virigiana* brachiopod community became dominant.

On Anticosti, *Hyattidina* and *Elkanathyris* n. gen. occur as common components of the *Pentamerus* community, indicating a mid-shelf depositional environment (Jin, 2008). They may also be associated with rich and diverse atrypides. 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 relatively 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 Survey of Canada, Ottawa. Well-preserved, pristine, calcitic specimens 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 specimens are housed in the Type Collections of the Geological Survey of Canada (GSC), Ottawa, the Cincinnati Museum

Center (CMC-IP), Cincinnati, and Ohio State University (OSU), Columbus, Ohio. General collections are also stored in the GSC, with a number prefixed with “A” or “C” to denote the Paul Copper Collection from Anticosti Island.

Systematic paleontology

Order Athyrida Boucot, Johnson and Staton, 1964

(nom.transl. Athyridae Davidson, 1881; =Incerti ordinis Nikiforova and Rzhonsnitskaya, 1960, part; ex Athyridoidea 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 Athyridae 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, *thyra*, 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 thyrid-, a proper family name is still Athyridae, as originally used by Phillips (1841) and Davidson (1881). Because Athyridae 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, Athyr- idida, etc.) should be avoided.

In light of the discussions above, we propose to retain the name Athyridae (and hence Athyr-ida), 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 Hyattidinae 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 atypide.

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, Selennyakh 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 atypoid *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.

Nikolaispira Nikitin and Popov in Nikitin et al., 1996.—Anderken Formation, Dulandkara Stage (mid-late Katian), Chu-Ili, Kazakhstan; its short, disjunct jugum differs 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 deltidial 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, Tadjikistan, ?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 *Nikolaispira* 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 spiralia 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 spiralia 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 spiralia 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, 1986, 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 “Athyracea” under *Incerti Ordinis*, somewhere between spiriferides and terebratulides (in that sense, they should be accredited with raising the athyrides to ordinal status because nearly all of the families they assigned are recognized as true athyrides today). Under the suborder Athyridoidea, Boucot et al. (1964; = suborder Athyridoidea in Boucot et al., 1965), however, excluded many groups that are recognized as athyrides today, such as the Athyrinoidea, Retzioidae, Dayioidea, Anoplothecidae, and Kayseriidae. Thus the “*Incerti Ordinis*” of Nikiforova and Rzhonsnitskaya (1960) matches more closely the order Athyrida as defined herein.

Externally, it is difficult to distinguish many athyrine taxa with smooth or capillate shells, due to their strong homomorphy. Copper (1986) reconstructed the spiralia and jugum of *Hindella* for the first time, based on topotype material, and demonstrated that there was no skeletal connection between the crura and spiralia 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 spiralia 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 atrypide genus *Cerasinella* Copper, 1995.

Sheehan (1977) abandoned the subfamily Hindellinae altogether, and allocated *Hindella* to the Meristellinae, and *Hyattidina* to a new subfamily, the Hyattidininae, 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 Hyattidininae. She did not use the subfamily Hindellinae Schuchert, 1894, but assigned *Greenfieldia* to the younger Didymothyrinae, and *Hindella* to the Meristellinae. 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 juga 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 Didymothyrinae 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 Retziidina, Koninckinidina and Athyridoidea, and did not recognize the subfamily Hindellinae.

Alvarez and Rong (2002, p. H1556) elevated the Hyattidinae to family status, but did not mention the subfamily Hindellinae, and assigned *Hindella* to the family Meristellidae within the superfamily Meristelloidea, and transferred the smooth-shelled *Hyattidina* Schuchert, 1913 to the superfamily Athyridoidae (herein we assign *Hindella* and *Hyattidina* to the same family, Hindellidae). They did not discuss the lack of skeletal connection between the crura and brachidium, nor the simple jugum, in such early athyrides. 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 athyride 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 athyrides, 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 athyrides, such as *Nikolaispira* 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 jugul processes that are not medially connected. The subfamily Hyattidinae, therefore, is subsumed in the family Hindellidae on account of their jugum and brachidium that resemble those of *Hindella*, *Koigia*, *Cryptothyrella*, 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.—Prinstana 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.

Atrypa cassidea Dalman, 1828.—Borenshult, Ostergötland, Sweden, *Dalmanitina* 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.—Cymy-brain Formation, Hirnantian, Denbighshire, U.K.

Hindella kiaeri Sheehan, 1977.—Nesoya, Asker Region, Oslo, “calcareous sandstones”, likely Hirnantian.

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

Species questionably assigned.—*Hindella shianensis* 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 Aeronian *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 athyride 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*” *terebratulina* (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 Webby (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 athyrids 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 athyrids, 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 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 Aeronian *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 filled 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 spiralia 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 Modzalevs-kaya (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 athyrids 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.
non 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 Juncliff 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* (Juncliff Member) and an underlying recessive lower unit of shales and limestones (Fraise Member, with *H. prinstana*). Here, the distinctive large elongate shell of *H. umbonata* can be easily distinguished from the smaller, rounded, globose shell of the older species, *H. prinstana*. The restricted type locality (C718) is defined here as the east end of Junction Cliff (UTM 20,

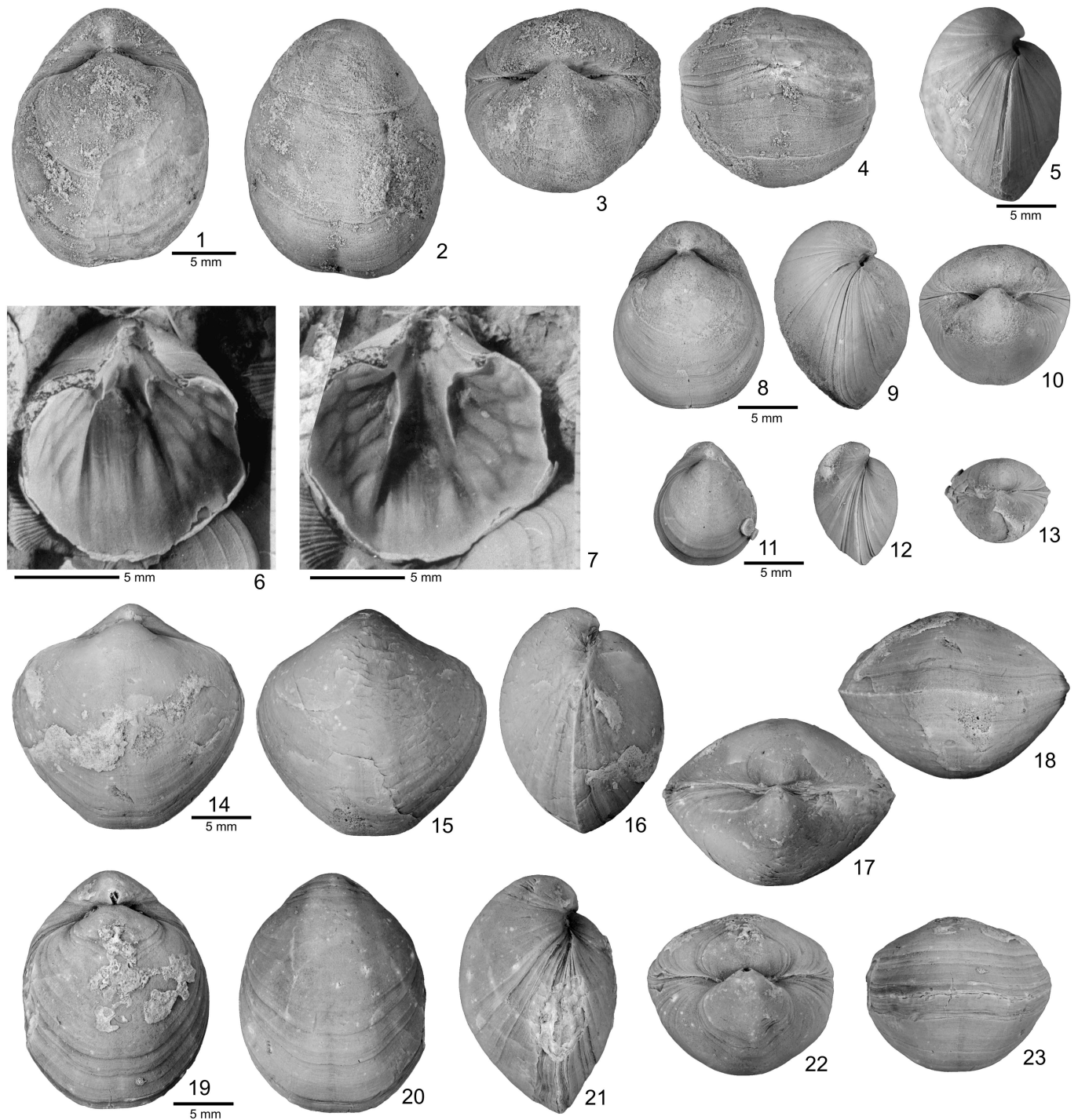


Figure 2. *Hindella* species from the Ellis Bay Formation (Hirnatian), Anticosti Island. (1–7) *Hindella umbonata* (Billings, 1862); GSC 137675 (1–4) and GSC134359 (5), Juncliff Member, locality A814, Prinista River (loc. A814); (6, 7) GSC 59097, interior of pedicle valve viewed at two different angles, Junction Cliff (A4, type locality). (8–13) *Hindella bulbosa* n. sp., Parastro Member, Parastrophinella Bluff (loc. A48); (8–10) GSC 137679, paratype; (11–13) GSC137680, paratype. (14–23) *Hindella prinstanta* (Billings, 1862), Fraise Member; (14–18) GSC 137666, wider variety; (19–23) GSC 137667, elongate form.

0396180E, 5519840N), 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. prinstanta*, and one resembling *H. bulbosa* 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 bulbosa* n. sp.). Thus, Richardson’s “Junction Cliff” collection is a mixture of three species of

Hindella from the Fraise, Juncliff, and Parastro members. This makes it impossible at this time to name a neotype for the lost *H. umbonata* “holotype” because the precise collecting locality or horizon is unknown for the extant types. This is left for a later revision, and complete description of all *Hindella* from the Hirnantian Ellis Bay Formation. Based on our new collections, the exact localities and stratigraphic positions of the three *Hindella* species from Junction Cliff to Parastrophinella Bluff can, however, be clearly defined.

Occurrence.—In addition to the type locality, collections of *Hindella umbonata* were also made from the following sites exposing the Juncliff Member:

C692 (= C701, A4a). Laloutre road, ~4.2 km south of main road. Light-gray weathering, thin- to medium-bedded micrites to coquinities, with abundant *Hindella umbonata*, rare *Eospirigerina*, *Mendacella*; middle-upper Juncliff Member. Map 12E/13, UTM 20, 53640E, 13150N.

C693. Laloutre road, ~4.2 km south of main road. Lithology and fauna similar to C692, but ~2 m higher stratigraphically. *Hindella umbonata* less common, more nested; upper Juncliff Member. Map 12E/13, UTM 20, 53650E, 13120N.

C721 (= A1, A426). Port Menier Quarry at Cap Blanc, south side of Port Menier, next to shoreline facing Ellis Bay. Light green-gray micrites at top of quarry (~3–4 m thick), capping recessive shale. Upper 1–2 m of quarry section consists of thin-bedded, gray micrite with shaly partings; *H. umbonata* co-occurs with abundant *Barbarorthis* and common *Mendacella*. Juncliff Member. Map 22H/16, UTM 20, 03120E, 18430N.

A813. Prinsta River, ~1 km upstream from mouth, at first sharp bend to south, north bank; 3–5 m thick section, with *Hindella umbonata* shelled in recessive blue-gray shale unit, and micrite at 1.45 m above a 20 cm thick sandstone bed with giant *Hormotoma*, corals marking the base of the Lousy Cove Member. Map 12F/5, UTM 20, 73480E, 66540N.

A1317b. Lac Cailloux road, 4.8 km south of main road; 3 m thick section of light gray, resistant micrite, with *Hindella umbonata* Juncliff Member. Map 12E/13, UTM 20, 39700E, 14360N.

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. bulbosa* n. sp. are smaller, with average width of 12 mm and 10 mm, respectively. *Hindella prinstana* also has a narrower apical angle, and *H. bulbosa* 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 Fraise 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 Fraise 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*, *Hormotoma*, 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*, aulacids, 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, Vaureal 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*, *Parastrophinella*, 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 *Vellamo*, *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

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

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

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

Hindella bulbosa new species
Figures 2.8–2.13, 3.1–3.17, 4

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 *Parastrophinella 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.

Diagnosis.—Relatively small, elongate, suboval shells of *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.

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.

Etymology.—From the Latin, *bulbus*, a swell, referring to the globular, pear-shaped shell typical of the new species.

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

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.

Genus *Cryptothyrella* Cooper, 1942

Type species.—*Whitfieldella quadrangularis* Foerste, 1906. Brassfield Formation, Aeronian, Dunkinsville (=“Duncansville” of Foerste, 1906), Adams County, Ohio.

Species assigned.—In addition to the type species, the following species are assignable to *Cryptothyrella*:

Atrypa crassa Sowerby, 1839.—Goleugoed Formation, late Rhuddanian, Girvan.

Terebratula furcata Sowerby, 1839.—Bog Quartzite, Aeronian, Shropshire.

Atrypa cylindrica Hall, 1852, p. 76, pl. 24, figs 2a–h.—Irondequoit Formation, basal Sheinwoodian, Niagara region, New York (strongly elongated shell with prominent capillae). The shells figured later as “*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 capillae.

Cryptothyrella bisulcata Gauri and Boucot, 1970.—Brassfield Limestone, Aeronian, near West Union, Ohio.

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

Hemithyris angustifrons M’Coy, 1851.—Mulloch Hill Formation, late Rhuddanian, Girvan. Internal structures poorly known.

Whitfieldella subquadrata Foerste 1906, p. 326, pl. 1, figs. 3a–f.—Indian Fields Formation, Aeronian, Berea, Kentucky. Regarded as junior synonym of the type species *Cryptothyrella quadrangularis* by Gauri and Boucot, 1970.

Diagnosis.—Shell medium to relatively large, elongate, globose, smooth to capillate, uniformly biconvex to bisulcate. Very small deltidial 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 infilled with prismatic callus posteriorly. Socket plates relatively thin, but inflated apically to support dental sockets; crura thin, delicate, parallel to each other, extending along commissural plane. Umbonal blades terminated as hooks, fused to crura; jugal saddle almost flat, positioned in mid-shell; spiralia with 8–10 whorls, directed laterally.

Remarks.—Based on Gauri and Boucot’s (1970) study of *Cryptothyrella*, Ziegler and Boucot (1970) proposed a *Cryptothyrella* community for North America. The genus, however, has had a shifting taxonomic history between a valid genus *Cryptothyrella* to a synonym of *Hindella*, resulting in a confusing stratigraphic range between the Late Ordovician (Hirnantian) and early Silurian. Various species have been

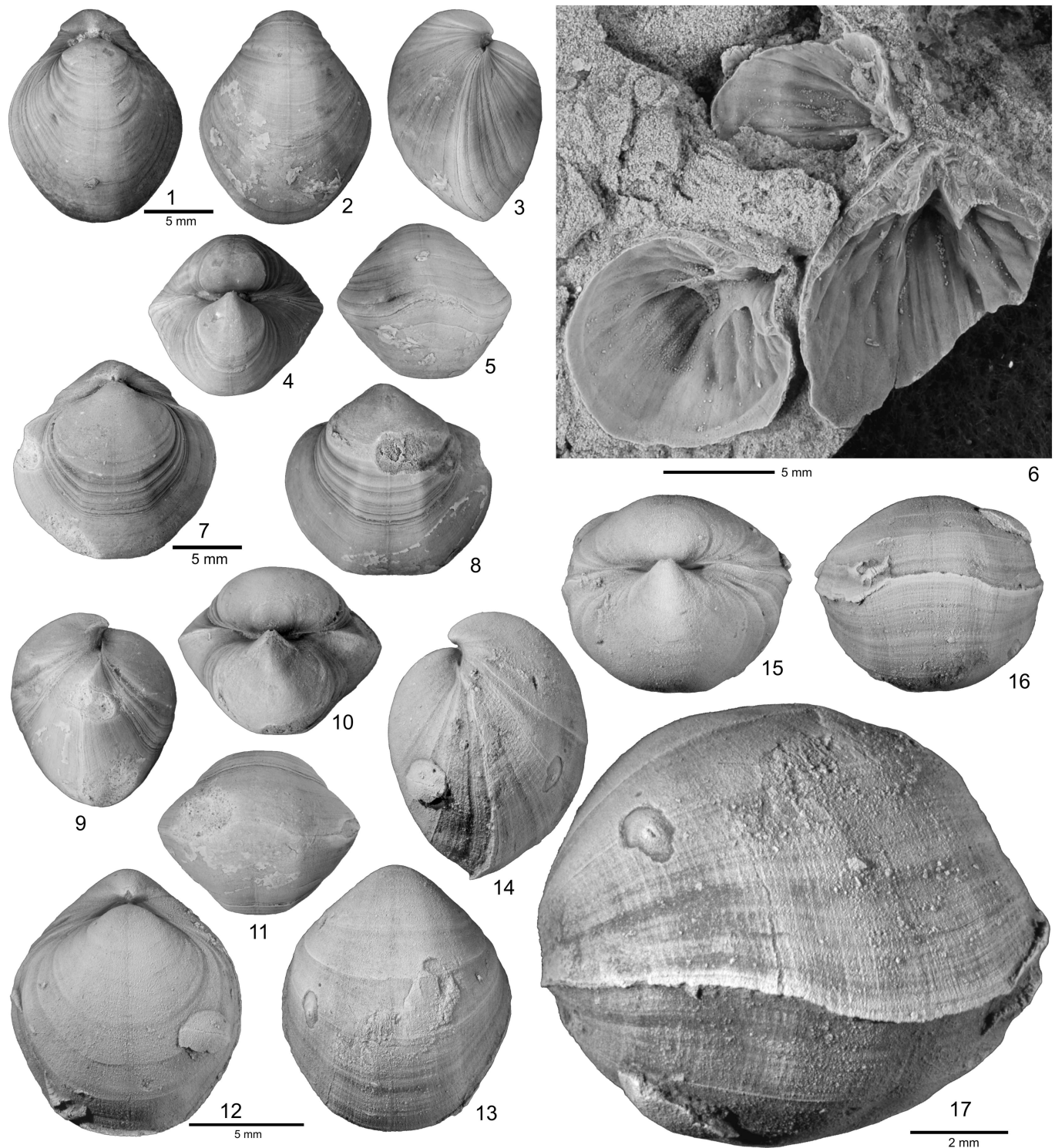


Figure 3. *Hindella bulbosa* n. sp. from Parastrophinella Bluff (loc. C720 = A48), Anticosti Island. (1–5) GSC 137671, holotype; (6) GSC 137681, paratype slab, interiors of ventral valves; (7–11) GSC 137670, paratype, subrhomboidal shell; (12–17) GSC 131790, well-preserved shell showing capillae in anterior part of shell.

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.

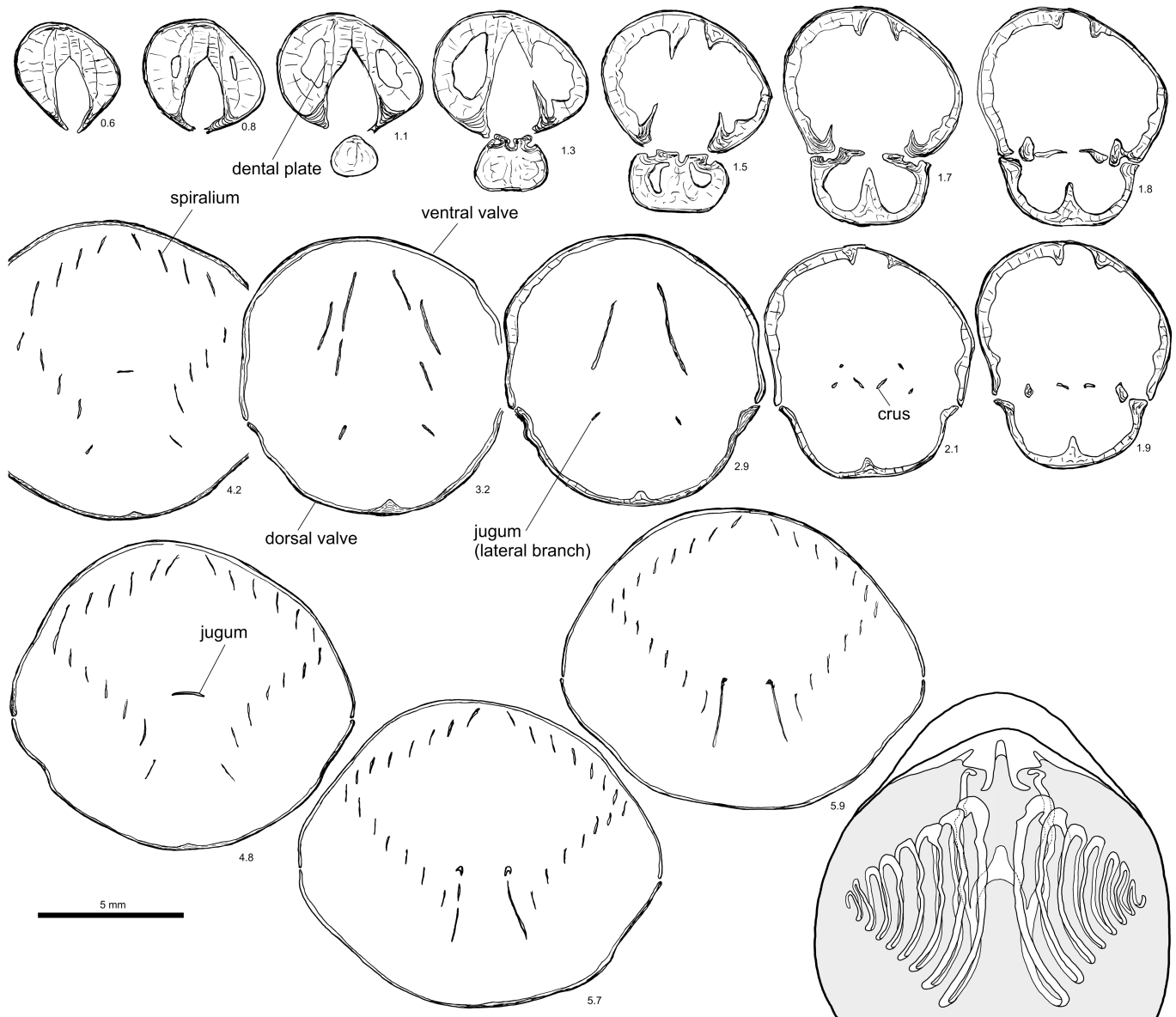


Figure 4. Selected serial sections and reconstruction of the spiralium and jugum of *Hindella bulbosa* n. sp. Paratype, GSC 131799, Parastro Member, Ellis Bay Formation, Parastrophinella Bluff (loc. A84), Anticosti Island. Note the simple jugum in the anterior central part of the shell cavity, the hook-like 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.

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 ventro-medially, 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 whorls 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

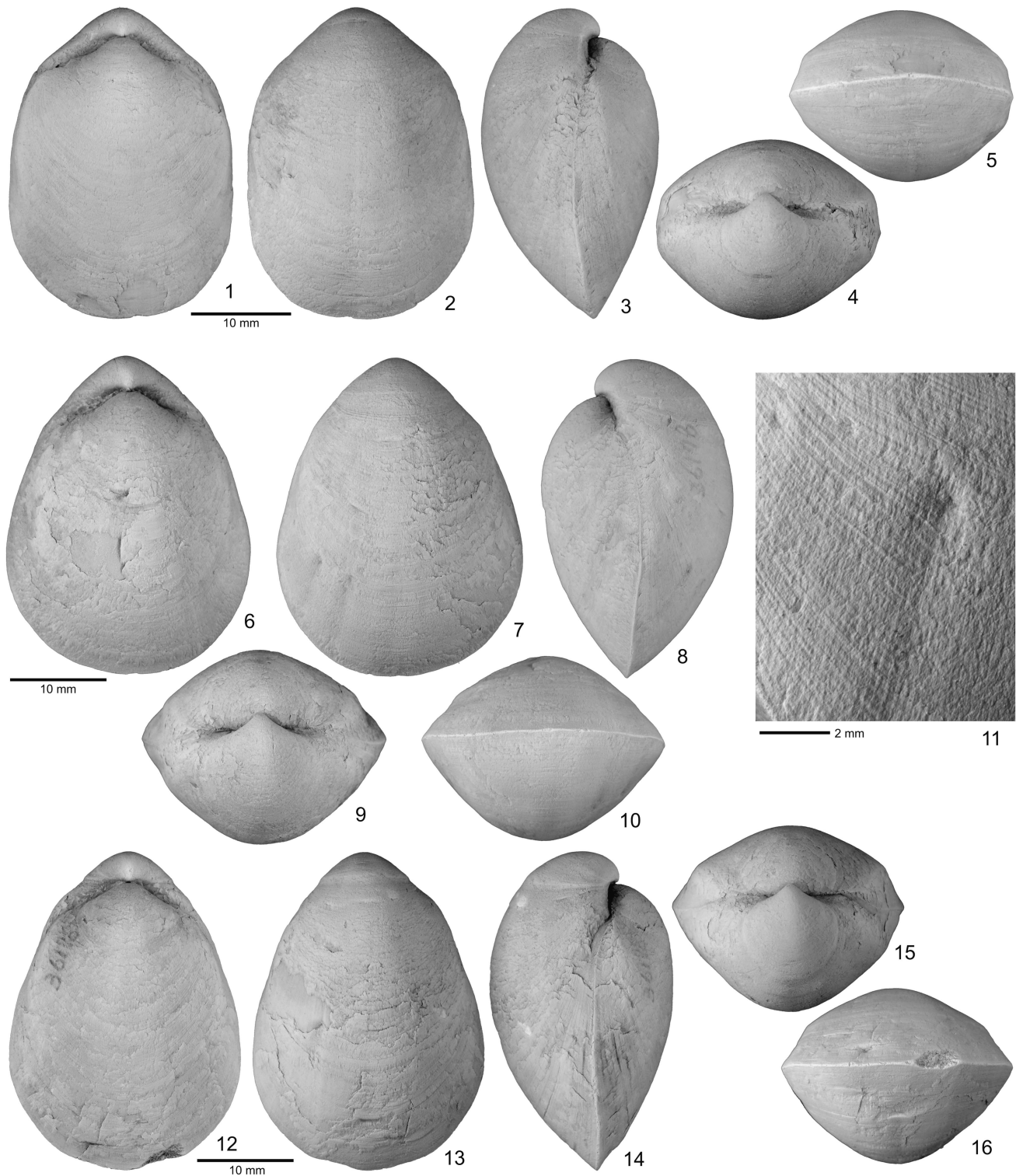


Figure 5. *Cryptothyrella quadrangularis* (Foerste, 1906), three topotype specimens from the Brassfield Formation, lower Aeronian, Dunkinsville (=Duncansville of Foerste, 1906), Adams County, Ohio. (1–5) CMC-IP 36178, #1, a subquadrate form; (6–11) CMC-IP 36178, #2, a suboval form, showing faint capillae (11) in antero-lateral part of ventral valve; (12–16), CMC-IP 36178, #3, a slightly narrower shell, with a rectimarginate anterior commissure typical of the species.

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

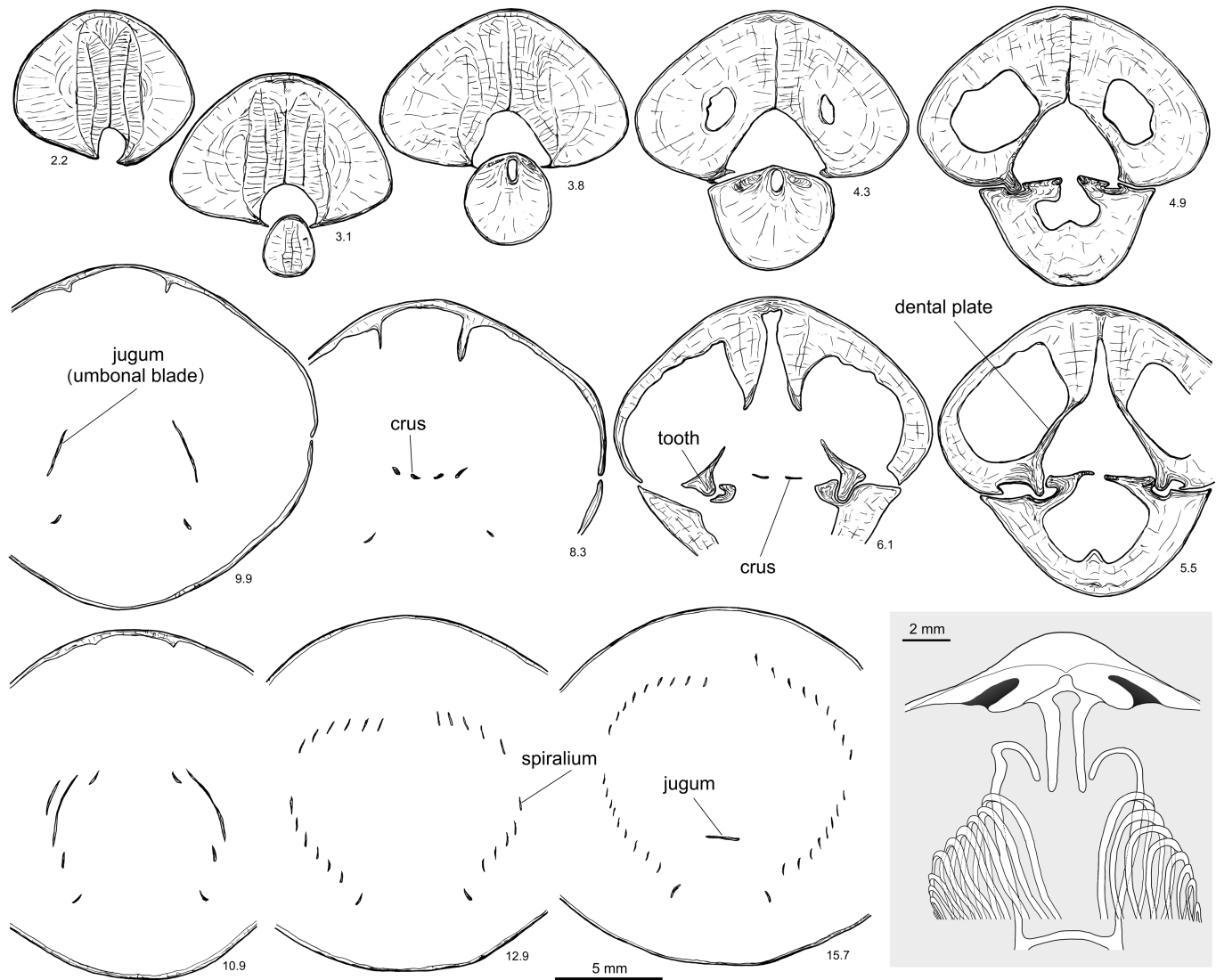


Figure 6. Serial sections and brachidium reconstruction of *Cryptothyrella quadrangularis* (Foerste 1906). OSU 18250, topotype, Brassfield Formation, lower Aeronian, Dunkinsville (=Duncansville of Foerste, 1906), Adams County, Ohio. Note the development of massive prismatic thickening of the ventral umbo divided by a deep groove, baso-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.

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 deltidial 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.

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 intraspecific 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 vental 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); Vakhtrapa, 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;

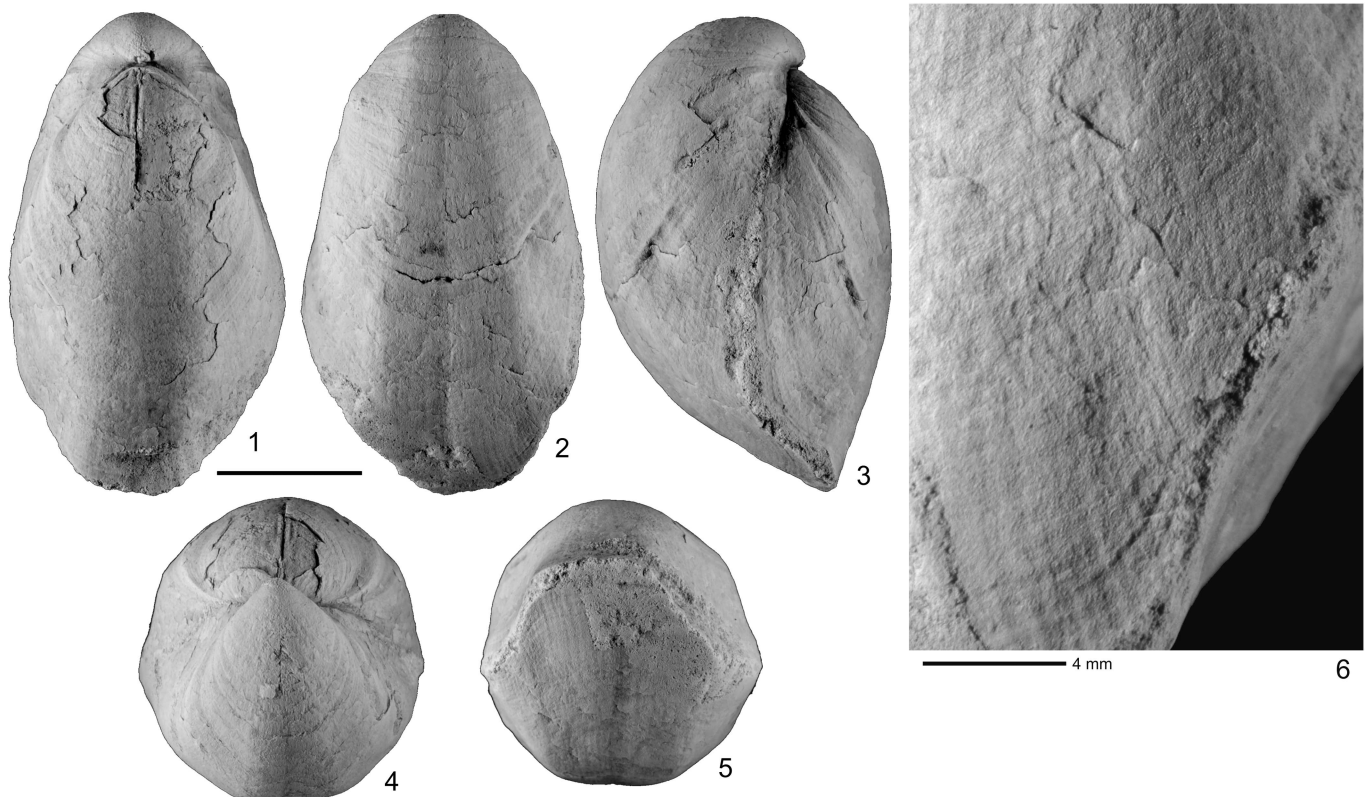


Figure 7. (1–6) *Cryptothyrella cylindrica* (Hall, 1852), OSU 14066, Bisher Formation, Hillsboro, Ohio. Note the presence capillae in anterior part of shell (6). Scale bar = 10 mm unless noted otherwise.

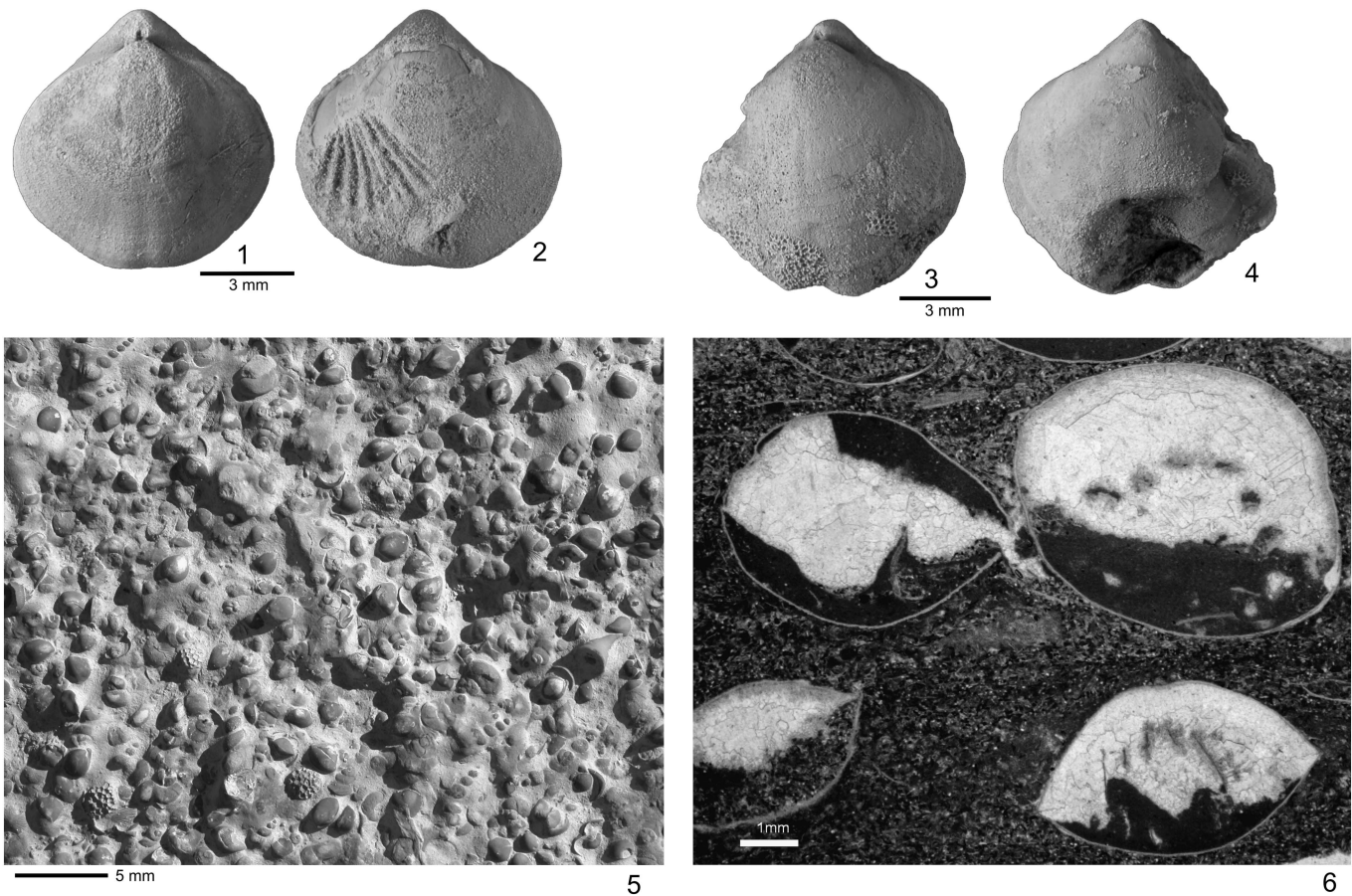


Figure 8. *Koigia* from the Fox Point Member (basal Rhuddanian), Becscie Formation, Anticosti Island. (1, 2) GSC 134362, dorsal and ventral views, with ventral valve partly impacted by another shell; (3, 4) GSC 134363, dorsal and ventral views, with anteriorly crushed ventral valve; (5) small slab showing bedding surface covered by shells of *Koigia* sp., small favositid corals, and conispiral gastropods, loc. A1450; (6) thin section of slab at right angles to bedding plane showing shells in resting position, loc. A313d. Note the thin-walled shells with geopedal infill and spiralia preserved.

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 Rhuddanian 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, Llandoverly.

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; spiranium with 6–8 whorls, laterally directed.

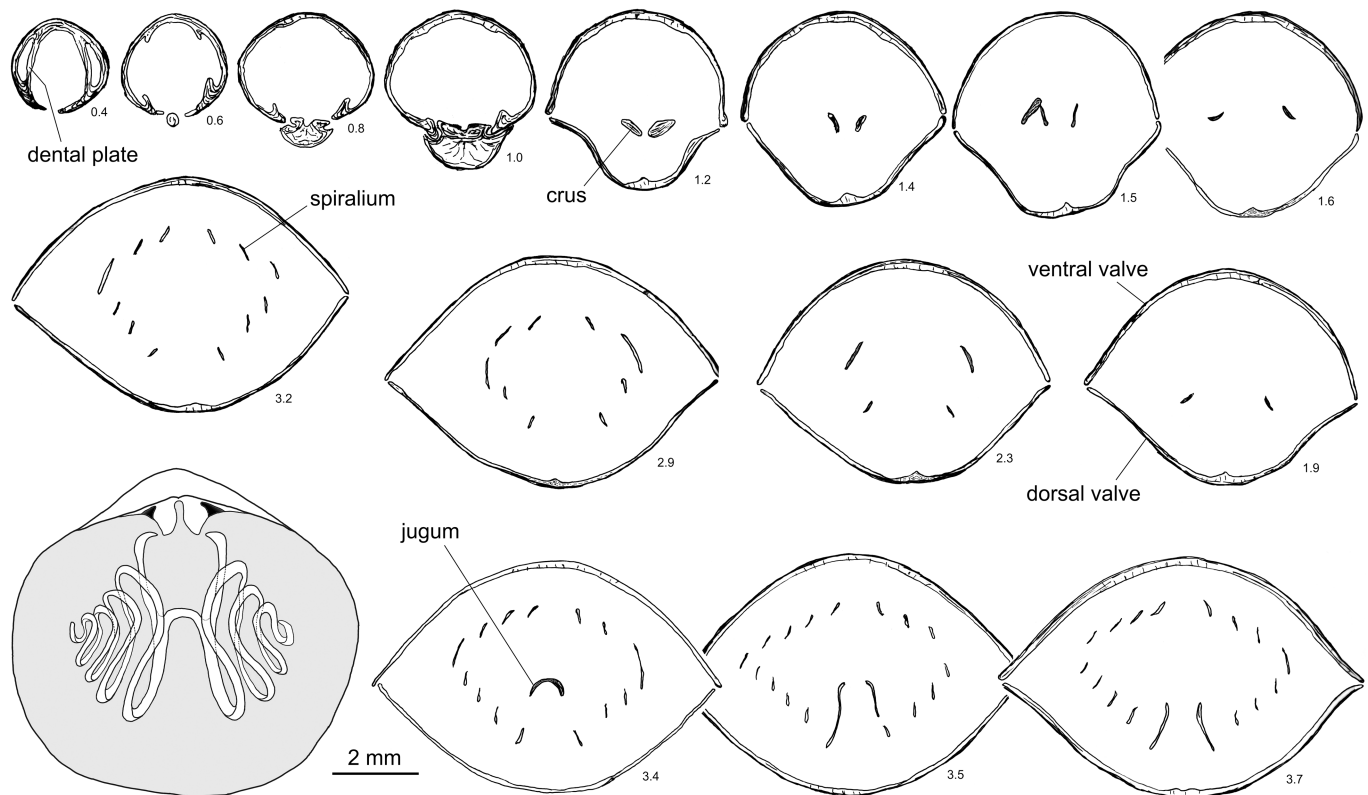


Figure 9. Serial sections and reconstruction of *Koigia* sp. Specimen GSC 131800 from a coastal bluff section on the east side of the cove at Ruisseau aux Algues (loc. A314), Fox Point Member (basal 3 m), Becschie Formation. Note the lack of skeletal connection between the crura and jugal blades. Number below each serial section denotes distance (mm) from shell apex.

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 spiridium 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, p. H1556) used the “numerous growth lines” to assign the genus to the superfamily Athyridoidea. Our data makes such assignment doubtful. 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, and shell-bed forming, or packed in large nests, is in the Macgilvray Member of the upper Gun River Formation (mid-Aeronian; Copper et al., 2013). It retains this abundance into 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 athyrines, *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 callus 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 junea* 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 rhynchonellide *Platyrochalos*;

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.

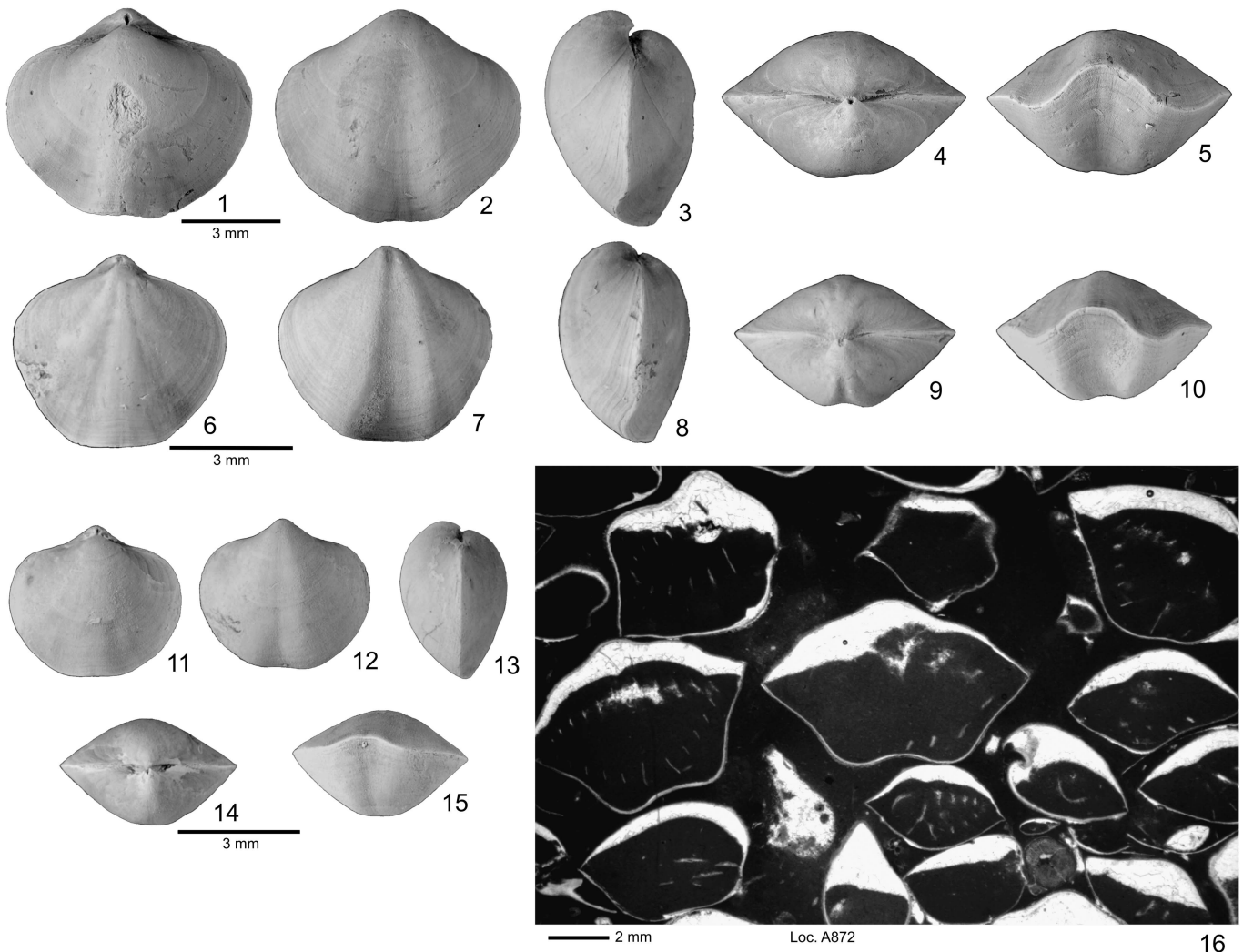


Figure 10. (1–15) *Hyattidina* sp. from the Goéland Member, Menier Formation, locality A852a; (1–5) GSC 134443; (6–10) GSC 134441; (11–15) GSC 134442. (16) Thin sections of *Hyattidina* cf. *H. junia* (Billings, 1866) from the Cybèle Member, Jupiter Formation, coastal bluff section, just southeast of Richardson Cliff (loc. A872).

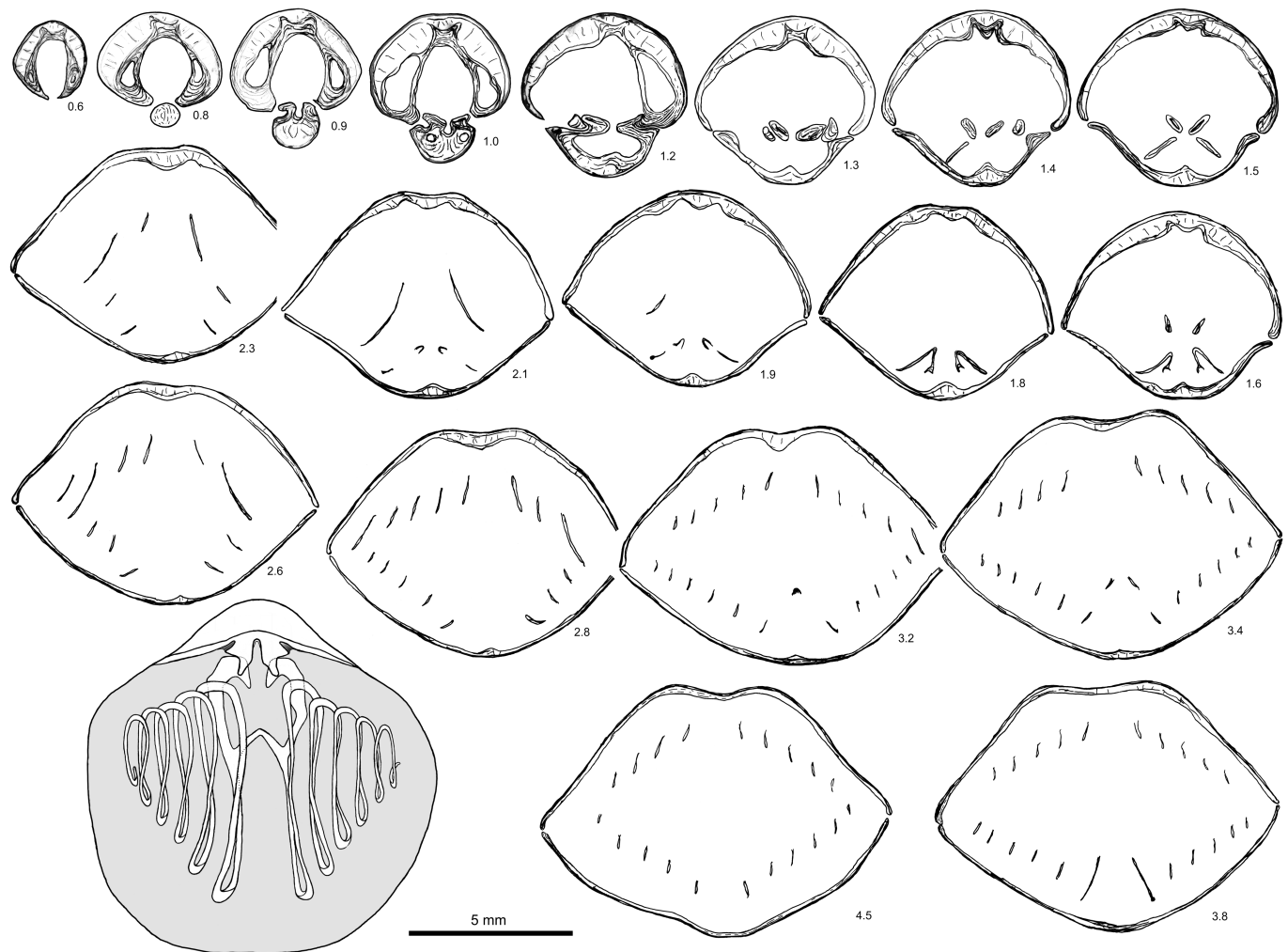


Figure 11. Serial sections and reconstructed brachidia of *Hyattidina* cf. *H. junia* (Billings 1866). Specimen GSC 131801 from locality A163c, Cybèle Member, Jupiter Formation. Note the thin, relatively straight dental plates flanking small lateral cavities, buried median septa in both valves, minute stubby crura, hooked umbonal blades, small, and a pointed jugal saddle. Number below each serial section denotes distance (mm) from shell apex.

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, Llandoverly; Anticosti Island.

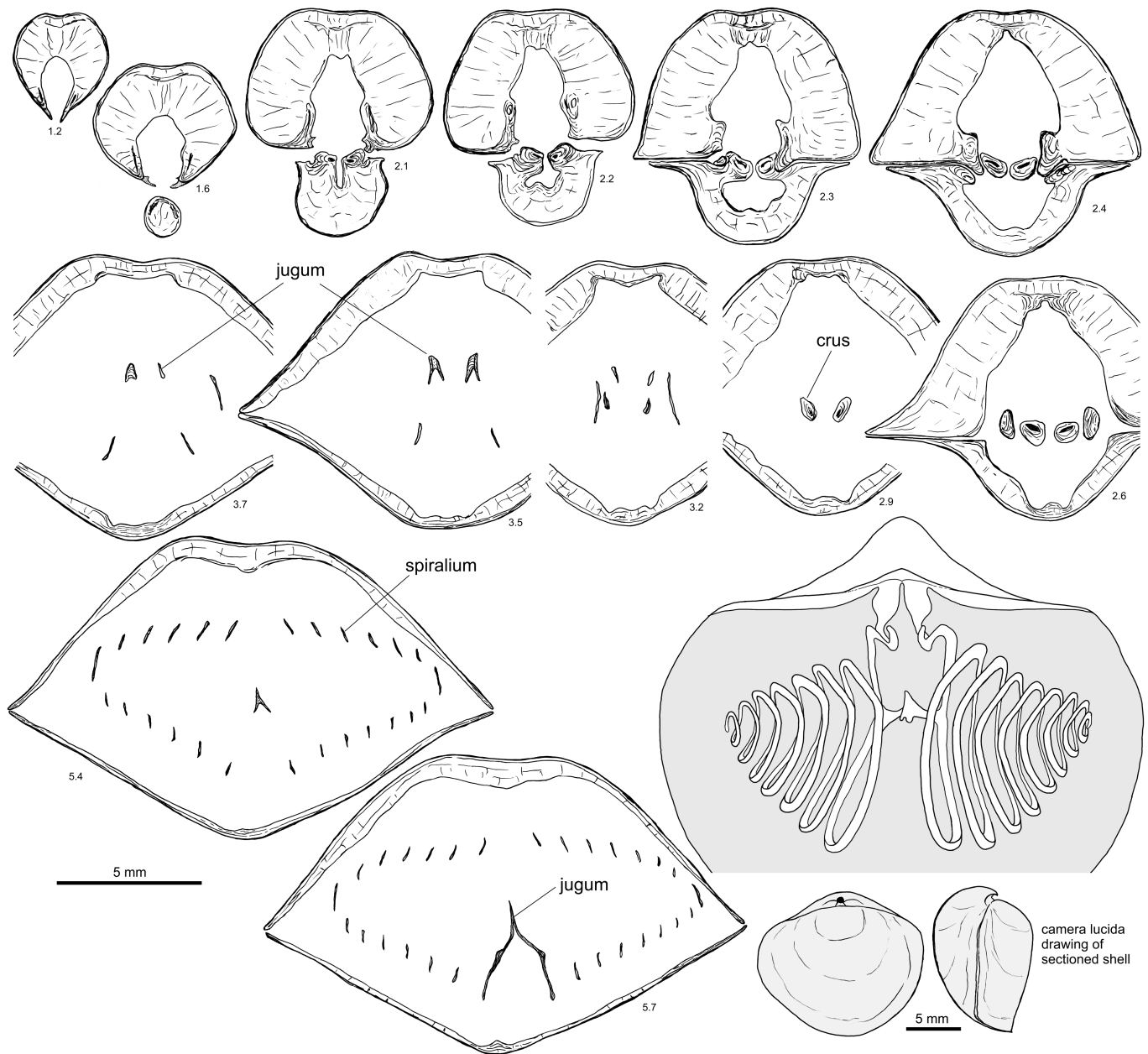


Figure 12. Serial sections and reconstructed brachidia of *Hyattidina* sp. Specimen GSC 131802 from locality A708, Goéland Member, Menier Formation. Note the thick shell posterior wall, minute, pointed jugal arch, and slit-like dental cavities. Number below each serial section denotes distance (mm) from shell apex.

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

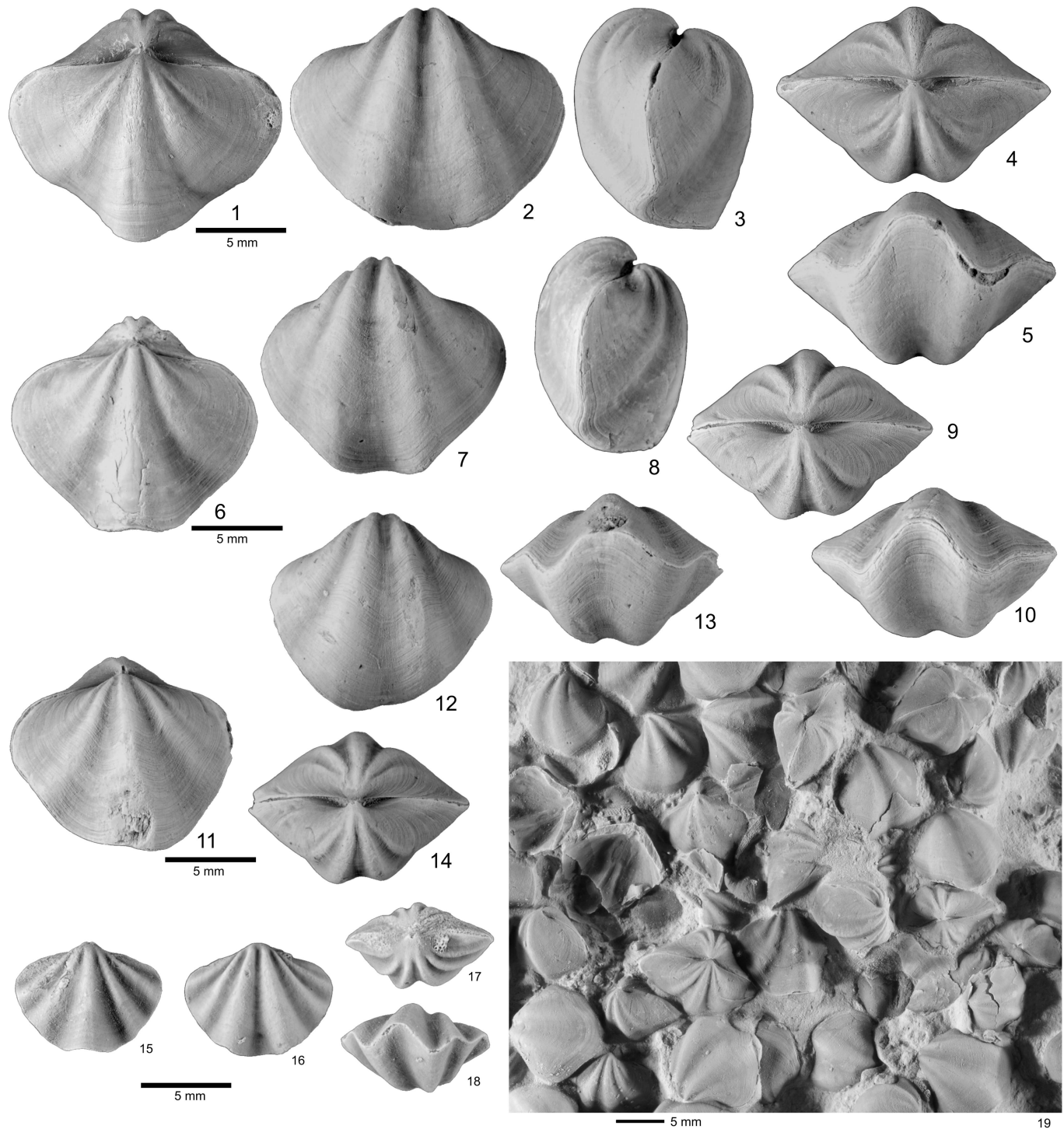


Figure 13. *Elkanathyris pallula* n. gen. n. sp. from the Goéland Member, Menier Formation, locality A852a. (1–5) 134439, holotype; (6–10) GSC 134440, paratype; (11–14) GSC 134437, paratype; (15–18) GSC 134438, paratype, immature shell showing strong ribs; (19) shell bed with densely packed *E. pallula* n. sp. shells.

dorsal valve constrained laterally by teeth from the ventral valve, and a sharp angular jugum connecting a spiralia 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.

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 *Triplesia*, in addition to the new species. Goéland Member, upper unit 5, Menier Formation.

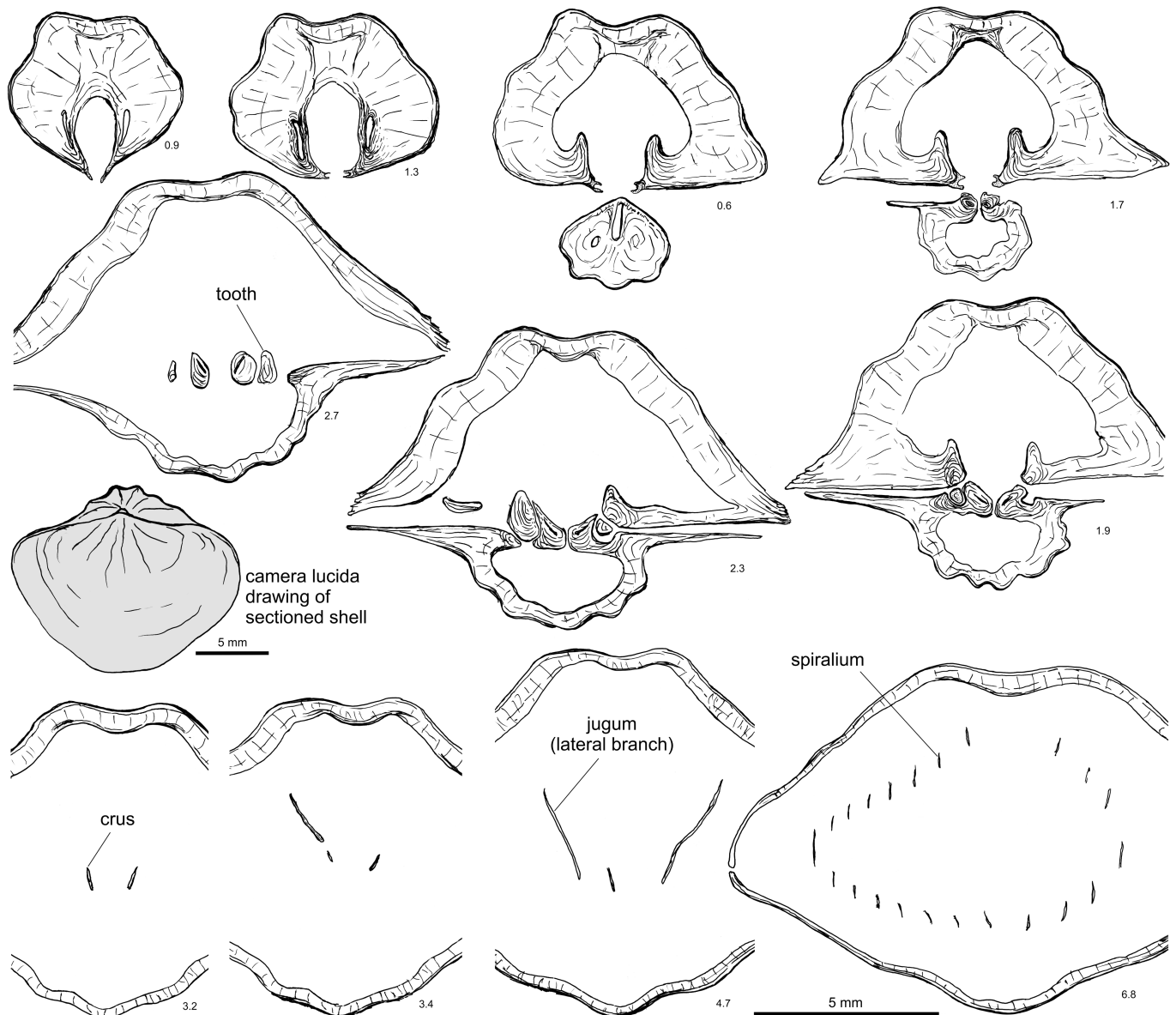


Figure 14. Serial sections of *Elkanathyris pallula* n. gen. n. sp. Specimen GSC 131803 from locality A708, Goéland Member (unit 5), Menier Formation. Note that the left spiralium has broken off, causing the jugum and spiralium to be displaced posteriorly towards the hinge, making it difficult to reconstruct the connection between the umbonal blades and the crura. Number below each serial section denotes distance (mm) from shell apex.

Diagnosis.—Small to medium sized, transversely 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 hyattidid 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 athyrids 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

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 only) 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 *Zygospiraella*, *Becscia* and *Viridita* (Jin and Copper, 2010; Copper and Jin, 2014). In the Aeronian–Telychian, athyrides 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 athyrides. 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 athyrides, combining such genera within the *Hindellidae* Schuchert, 1894. The evolution of such early athyrides 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.

Acknowledgments

We jointly thank NSERC's Discovery Grant Program (Natural Sciences and Engineering Research Council) for its long-term support of stratigraphic work on Anticosti Island. J. Dougherty and M. Coyne provided access and curation for the Billings collection (Geological Survey of Canada, Ottawa), in charge of the curation of the Anticosti collections, now in Ottawa, made by us since 1966. Specimens of *Cryptothyrella* were kindly provided for study by W. Ausich (Ohio State University) and B. Hunda (Cincinnati Museum Center, Ohio). Stratigraphic information on the *Cryptothyrella* occurrences in Ohio and New York was provided by C.E. Brett (University of Cincinnati) and M. Kleffner (Ohio State University). The constructive comments of journal reviewers R.-Y. Li and F. Alvarez and journal editor B. Hunda greatly helped improve the presentation and

discussions. This paper is a contribution to the International Geoscience Programme (IGCP) Project 653—The onset of the Great Ordovician Biodiversification Event.

References

- Achab, A., Asselin, E., Desrochers, A., and Riva, J.F., 2013, The end-Ordovician chitinozoan zones of Anticosti Island, Québec: definition and stratigraphic position: Review of Palaeobotany and Palynology, v. 198, p. 92–109.
- Alroy, J., 2008, Dynamics of extinction and origination in the fossil record: Proceedings of the National Academy of Sciences, v. 105, p. 11536–11542.
- Alroy, J., 2010a, The shifting balance of diversity among major marine animal groups: Science, v. 329, p. 1191–1194.
- Alroy, J., 2010b, Geographical, environmental and intrinsic biotic controls on Phanerozoic marine diversification: Palaeontology, v. 53, p. 1211–1235.
- Alvarez, F., 1999, Shape, growth, and evolution of the brachio-jugal system developed by the retziidines (Brachiopoda, Athyridida): Senckenbergiana Lethaea, v. 79, p. 131–143.
- Alvarez, F., and Brunton, C.H.C., 1993, Athyridida versus Athyrida (Brachiopoda): Journal of Paleontology, v. 67, p. 310.
- Alvarez, F., and Rong, J.-Y., 2002, Athyridida, in Kaesler, R.L., ed., Treatise on Invertebrate Paleontology, pt. H, Brachiopoda (revised): Lawrence, Kansas, Geological Society of America and University of Kansas Press, v. 4, p. H1475–H1614.
- Alvarez, F., Brime, C., and Brunton, C.H.C., 1980, The authorship of the family Athyrididae (Brachiopoda): Journal of Paleontology, v. 54, p. 1134.
- Alvarez, F., Rong, J.-Y., and Boucot, A.J., 1998, The classification of athyridid brachiopods: Journal of Paleontology, v. 72, p. 827–855.
- Amsden, T.W., 1974, Late Ordovician and Early Silurian articulate brachiopods from Oklahoma, southwestern Illinois and eastern Missouri: Oklahoma Geological Survey Bulletin, v. 119, p. 1–154.
- Baranov, V.V., 1994, Paleozoic athyridids (brachiopods) from northeast Asia: Paleontologicheskii Zhurnal, v. 4, 28–37. [in Russian]
- Bergström, S.M., Saltzman, M.M., and Schmitz, B.S., 2006, First record of the Hirnantian (Upper Ordovician) $\delta^{13}\text{C}$ excursion in the North American Midcontinent and its regional implications: Geological Magazine, v. 143, p. 657–678.
- Billings, E., 1862, On some new species of fossils in the Quebec Group: Geological Survey of Canada, Palaeozoic Fossils, v. 1, p. 25–168.
- Billings, E., 1866, Catalogue of Lower Silurian fossils of the island of Anticosti, with descriptions of some new genera and species: Geological Survey of Canada Publications, n. 427, 93 p.
- Bolton, T.E., 1981, Late Ordovician and Early Silurian Anthozoa of Anticosti Island, Québec, in Lespérance, P.J., ed., Field meeting Anticosti-Gaspé, Québec, 1981: Subcommittee on Silurian Stratigraphy, Ordovician–Silurian Boundary Working Group, Université de Montréal, v. 2, p. 107–135.
- Boucot, A.J., 1975, Evolution and Extinction Rate Controls: New York, Elsevier, 427 p.
- Boucot, A.J., Johnson, J.G., and Staton, R.D., 1964, On some atrypoid, retzioid and athyridoid Brachiopoda: Journal of Paleontology, v. 38, p. 805–822.
- Boucot, A.J., Johnson, J.G., and Staton, R.D., 1965, Suborder Athyridina, in Moore, R.C., ed., Treatise on Invertebrate Paleontology, Part H, Brachiopoda: Lawrence, Kansas, University of Kansas Press, p. H654–H667.
- Breivel, I.A., and Breivel, M.I., 1970, Novye vidy gidpidulid i rod *Colongina* iz podgranitnykh Siluro-Devonskikh otlozheni vostochnogo sklona Urala: Materialy po Geologii Urala, Sverdlovsk, p. 57–63.
- Brenchley, P.J., Marshall, J.D., Hints, L., and Nolvak, J., 1997, New isotopic data solving an old biostratigraphic problem: the age of the Upper Ordovician brachiopod *Holorhynchus*: Journal of the Geological Society London, v. 154, p. 335–342.
- Cocks, L.R.M., 1978, A review of British Lower Palaeozoic brachiopods, including a synoptic revision of Davidson's Monograph: Monographs of the Palaeontographical Society, no. 131, p. 1–256.
- Cocks, L.R.M., 2008, A revised review of British Lower Palaeozoic brachiopods: Palaeontographical Society of London, Monograph, v. 629, p. 1–276.
- Cocks, L.M.R., and McKerrow, W.S., 1973, Brachiopod distributions and faunal provinces in the Silurian and Lower Devonian: Special Papers in Palaeontology, no. 12, p. 291–304.
- Cocks, L.R.M., and Torsvik, T.H., 2011, The Palaeozoic geography of Laurentia and western Laurussia: a stable craton with mobile margins: Earth-Science Reviews, v. 106, p. 1–51.

- Conrad, T.A., 1842, Observations on the Silurian and Devonian systems of the United States, with descriptions of new organic remains: Journal Academy of Natural Sciences Philadelphia, v. 8, p. 228–280.
- Cooper, G.A., 1942, New genera of North American brachiopods: Journal of the Washington Academy of Sciences, v. 32, p. 228–235.
- Copper, P., 1977, *Zygospira* and some related Ordovician and Silurian atrypid brachiopods: Palaeontology, v. 20, p. 295–335.
- Copper, P., 1986, Filter-feeding and evolution in early spire-bearing brachiopods: Biostratigraphie du Paléozoïque, n. 4, p. 219–230.
- Copper, P., 1995, Five new genera of Late Ordovician–early Silurian brachiopods from Anticosti Island, eastern Canada: Journal of Paleontology, v. 69, p. 846–862.
- Copper, P., 2002, Atrypida, in Kesler, R.L., ed., Treatise on Invertebrate Paleontology, pt. H, Brachiopoda (revised): Lawrence, Kansas, Geological Society of America and University of Kansas Press, v. 4, p. H1377–H1474.
- Copper, P., 2011, 100 million years of reef prosperity and collapse: Ordovician to Devonian interval, in Stanley, G.D., ed., Corals and Reefs: Crises, Collapse and Change: Paleontological Society Papers, v. 17, p. 15–32.
- Copper, P., and Gourvenec, R., 1996, Evolution of the spire-bearing brachiopods (Ordovician–Jurassic), in Copper P., and Jin, J., eds., Brachiopods: Rotterdam, Balkema Press, p. 81–88.
- Copper, P., and Jin, J., 2012, Early Silurian (Aeronian) East Point coral patch reefs of Anticosti Island, eastern Canada: first reef recovery from the Ordovician/Silurian mass extinction in eastern Laurentia: Geosciences, v. 2, p. 64–89.
- Copper, P., and Jin, J., 2014, The revised Lower Silurian (Rhuddanian) Becscie Formation, Anticosti Island, eastern Canada records the tropical marine recovery from the end-Ordovician Mass Extinction: Newsletters on Stratigraphy, v. 47, p. 61–83.
- Copper, P., and Jin, J., 2015, Tracking the early Silurian post-extinction faunal recovery in the Jupiter Formation of Anticosti Island: a stratigraphic revision: Newsletters on Stratigraphy, v. 48, p. 221–240.
- Copper, P., and Long, D.G.F., 1990, Stratigraphic revision of the Jupiter Formation, Anticosti Island, a major reference section above the Ordovician–Silurian boundary: Newsletters in Stratigraphy, 23: 11–36.
- Copper, P., Long, D.G.F., and Jin, J., 2012, The Early Silurian Gun River Formation of Anticosti Island, eastern Canada: a key section for the mid-Llandovery of North America: Newsletters on Stratigraphy, v. 45, p. 263–280.
- Copper, P., Jin, J., and Desrochers, A., 2013, The Ordovician–Silurian boundary (late Katian–Hirnantian) of western Anticosti Island: revised stratigraphy and benthic faunal correlations: Stratigraphy, v. 10, p. 213–227.
- Dagys, A., 1996, On the classification of the order Athyridida, in Copper, P., and Jin, J., eds., Brachiopods: Rotterdam, Balkema Press, p. 89–90.
- Dalman, J.W., 1828, Uppställning och beskrifning af de i Sverige Terebratuliter: Konglige Svenska Vetenskaps Akademiens Handlingar, v. 3, p. 85–155.
- Davidson, T., 1881, On the genera and species of spiral-bearing Brachiopoda: Geological Magazine, v. 8, p. 1–13.
- Davidson, T., 1882, A monograph of the British fossil Brachiopoda: Palaeontographical Society Monographs, no. Supplement, v. 5, p. 1–134.
- Edinger, E.N., Copper, P., Risk, M.J., and Atmojo, W., 2002, Oceanography and reefs of Recent and Paleozoic tropical epeiric seas: Facies, v. 47, p. 127–150.
- Foerste, A.F., 1906, The Silurian, Devonian and Irvine formations of east-central Kentucky, with an account of their clays and limestones: Bulletin of the Kentucky Geological Survey, v. 7, p. 1–332.
- Fu, L.-P., 1982, Brachiopoda, in Xi'an Institute of Geology Mineral Resources, ed., Paleontological Atlas of Northwest China—Precambrian and Early Paleozoic, Shaanxi-Gansu-Ningxia: Beijing, Geological Publishing House, p. 95–179.
- Gauri, K.L., and Boucot, A.J., 1970, *Cryptothyrella* (Brachiopoda) from the Brassfield Limestone (lower Silurian) of Ohio and Kentucky: Journal of Paleontology, v. 44, p. 125–132.
- Grunt, T.A., 1980, Atridydy Russkoi platform: Akademiya Nauk SSSR, Trudy Paleontologicheskogo Instituta, v. 182, p. 1–164. [in Russian]
- Grunt, T.A., 1986, Systematics of the brachiopod order Athyridida: Trudy Akademiya Nauk SSSR, v. 215, p. 1–200.
- Grunt, T.A., 1989, Order Athyridida, evolutionary morphology and historical distribution: Trudy Akademiya Nauk SSSR, v. 238, p. 1–139.
- Hall, J., 1852, Containing descriptions of the organic remains of the lower middle division of the New York System (equivalent in part to the Middle Silurian rocks of Europe): New York State Geological Survey, Palaeontology of New York, v. 2, p. 1–353.
- Hall, J., and Clarke, J.M., 1893–1895, An introduction to the study of the genera of Palaeozoic Brachiopoda. Natural History of New York, Palaeontology, Volume 8, Part 2. New York Geological Survey. Charles van Benthuysen and Sons Albany, 394 p. [Fascicle I, 1–176 was published in July 1893; fascicle II, 177–317, was published in December 1893; pages 318–394 and the plates were published for the first time in 1895. The date on the title page is 1894 but the book was not released until early 1895.]
- Harper, D.A.T., and Owen, A.W., 1996, Fossils of the Upper Ordovician: Palaeontological Association, Field Guides to Fossils, n. 7, p. 1–312.
- Hiller, N., 1980, Ashgill Brachiopoda from the Glyn Ceiriog District, north Wales: Bulletin British Museum of Natural History, v. 34, p. 209–216.
- ICZN, 1999, International Code of Zoological Nomenclature: London, The Natural History Museum, 306 p.
- Jin, J., 2008, Environmental control on temporal and spatial differentiation of Early Silurian pentameride brachiopod communities, Anticosti Island, eastern Canada: Canadian Journal of Earth Sciences, v. 45, p. 159–187.
- Jin, J., and Copper, P., 1997, *Parastrophinella* (Brachiopoda): its paleogeographic significance at the Ordovician–Silurian boundary: Journal of Paleontology, v. 71, p. 369–380.
- Jin, J., and Copper, P., 2000, Late Ordovician and Early Silurian pentamerid brachiopods of Anticosti Island, Québec, Canada: Palaeontographica Canadiana, n. 18, 140 p.
- Jin, J., and Copper, P., 2008, Response of brachiopod communities to environmental change during the Late Ordovician mass extinction interval, Anticosti Island, eastern Canada: Fossils and Strata, v. 54, 41–51.
- Jin, J., and Copper, P., 2010, Origin and evolution of the Early Silurian (Rhuddanian) virgianid pentameride brachiopods—the extinction recovery fauna from Anticosti Island, eastern Canada: Bolletino della Società Paleontologica Italiana, v. 49, p. 1–11.
- Jin, J., Long, D.G.F., and Copper, P., 1996, Paleocology of the Early Silurian *Virgiana* pentamerid brachiopod community of Anticosti Island, Québec: Palaios, v. 11, p. 597–609.
- Logan, W.E., 1863, Report on the geology of Canada: Geological Survey of Canada, Report of Progress to 1863, 983 p.
- Mauviel, A., and Desrochers, A., 2016, A high-resolution, continuous $\delta^{13}\text{C}$ record spanning the Ordovician–Silurian boundary on Anticosti Island: Canadian Journal of Earth Sciences, v. 53, p. 795–801.
- M'Coy, F., 1844, A synopsis of the characters of the Carboniferous Limestone fossils of Ireland: Dublin, University Press, 207 p.
- M'Coy, F., 1851, On some new Cambro-Silurian fossils: Annals and Magazine of Natural History, v. 8, p. 387–443.
- Menakova, G.N., 1964, Brakhiopody iz nizhnasiluriiskikh otlozhenii Zeravshano-Gissarskoi Gornoi Oblasti: Trudy Upravleniya Geologii i Okhrany Nedr pri Sovete Ministrov Tadzhikskoi SSR, Paleontologiya i Stratigrafiya, v. 1, p. 1–51.
- Menakova, G.N., and Nikiforova, O.I., 1986, Novye predstaviteli pozdnasiluriiskikh brakhiopod Zeravshano-Gissarskoi Gornoi Oblasti: Paleontologicheskii Zhurnal, n. 4, p. 65–76.
- Modzalevskaya, T.L., 1979, Systematics of the Paleozoic Athyrididae: Paleontologicheskii Zhurnal, n. 2, p. 48–63.
- Modzalevskaya, T.L., 1985, Brakhiopody silura i rannego devona evropeiskoi chasti SSSR, Otryad Athyridida: Akademiya Nauk SSSR, Paleontologicheskii Institut, 128 p.
- Modzalevskaya, T.L., 1996, Principle trends in early athyrid evolution, in Copper P., and Jin, J., eds., Brachiopods: Rotterdam, Balkema Press, p. 179–183.
- Nestor, H., 1997, Silurian, in Raukas, A., and Teedumäe, A., eds., Geology and Mineral Resources of Estonia: Tallinn, Estonian Academy Publishers, p. 89–106.
- Niemeyer, H., Alvarez, F., Boucot, A.J., and Bruna, M., 2010, Brachiopods from Cordon de Lila, lower Silurian (Llandovery) Quebrada Ancha Formation, Antofagasta region, Chile: Special Papers in Palaeontology, v. no. 84, p. 287–307.
- Nikiforova, O.I., 1964, Nakhodki novykh siluriiskikh brakhiopod v Chatkalskom Khrebtse: Paleontologiya i Stratigrafiya, Trudy Vsesoyuznogo Nauchno-Issledovatel'skogo Geologicheskogo Instituta (VSEGEI), v. 93, p. 81–90.
- Nikiforova, O.I., and Rzhonsnitskaya, M.A., 1960, Incerti ordinis, in Sarycheva, T.G., ed., Osnovy Paleontologii, Mshankii i Brakhiopody: Moskva, Izdatelstvo Akademii Nauk SSSR, p. 280–286.
- Nikitin, I.F., Popov, L.E., and Holmer, L.E., 1996, Late Ordovician brachiopod assemblage of Hiberno-Salarian type from Central Kazakhstan: GFF, v. 118, p. 84–96.
- Nikitin, I.F., Popov, L.E., and Bassett, M.G., 2006, Late Ordovician rhynchonelliformean brachiopods of north-eastern Central Kazakhstan: National Museum of Wales Geological Series, v. 25, p. 223–294.
- Phillips, J., 1841, Figures and Descriptions of the Palaeozoic Fossils of Cornwall, Devon, and West Somerset: London, Longman & Co., 231 p.
- Popov, L.E., Nikitin, I.F., and Sokiran, E.V., 1999, The earliest atrypides and athyridides (Brachiopoda) from the Ordovician of Kazakhstan: Palaeontology, v. 42, p. 625–661.

- Popov, L.E., Cocks, L.R.M., and Nikitin, I.F., 2002, Upper Ordovician brachiopods from the Anderken Formation, Kazakhstan: their ecology and systematics: *Bulletin of the Natural History Museum London (Geology)*, v. 58, p. 13–79.
- Reed, F.R.C., 1912, Ordovician and Silurian fossils from the central Himalayas: *Memoirs of the Geological Survey of India*, v. 7, p. 1–168.
- Richardson, J., 1857, Report for the year 1856, of Mr James Richardson, Explorer, in Logan, W.E., Report of Progress for the years 1853, 54, 55, 56: Montreal, Geological Survey of Canada, p. 190–245.
- Rong, J.-Y., 1984, Brachiopods of latest Ordovician in the Yichang district, western Hubei, central China, in *Nanjing Institute of Geology and Palaeontology*, ed., *Stratigraphy and Palaeontology of Systemic Boundaries in China, Ordovician–Silurian boundary 1: Hefei, Anhui Science and Technology Publishing House*, p. 111–176.
- Rubel, M.P., 1970, Brachiopody Pentamerida i Spiriferida Silura Estonii: Tallinn, Valgus, Eesti NSV Teaduste Akadeemia Geoloogia Institut, 75 p.
- Salter, J.W., 1851, List of some of the Silurian fossils of Ayrshire: *Quarterly Journal of the Geological Society of London*, v. 7, p. 170–178.
- Savage, T.W.E., 1913, Alexandrian Series in Missouri and Illinois: *Bulletin Geological Survey of America*, v. 24, p. 351–376.
- Schuchert, C., 1894, A revised classification of the spire-bearing Brachiopoda: *American Geologist*, v. 13, p. 102–107.
- Schuchert, C., 1897, A synopsis of American fossil Brachiopoda, including bibliography and synonymy: *Bulletin of the United States Geological Survey*, v. 87, p. 1–463.
- Schuchert, C., 1913, Class Brachiopoda, in Zittel, K.A., von (translated by Eastman, C.R.), *Textbook of Palaeontology*: London, MacMillan, v. 1, p. 355–420.
- Schuchert, C., 1928, Classification of brachiopod genera, fossil and recent, in Schuchert, C., and Levene, C.M., *Fossilium Catalogus, Animalia, Brachiopoda*: Berlin, W. Junk, 140 p.
- Shaler, N.S., 1865, List of the Brachiopoda from the island of Anticosti: *Bulletin of Harvard Museum Comparative Zoology*, v. 1, p. 61–70.
- Sheehan, M., 1977, Late Ordovician and earliest Silurian meristellid brachiopods in Scandinavia: *Journal of Paleontology*, v. 51, p. 23–43.
- Sowerby, J. de C., 1839, Organic remains, in Murchison, R.I., *The Silurian System*: London, John Murray, p. 579–765.
- Twenhofel, W.H., 1928, *Geology of Anticosti Island*: Geological Survey of Canada Memoir, v. 154, p. 1–481.
- Waagen, W.H., 1883, Salt Range fossils: *Paleontologia Indica*, v. 3, p. 391–546.
- Wahlenberg, G., 1818, *Petrificata telluris suecanae*: *Nova Acta Regia Societatis Scientiarum Uppsaliensis*, v. 8, p. 1–116.
- Webby, B.D., 2002, Patterns of Ordovician reef development, in Kiessling, W., Flügel, E., and Golonka, J., eds., *Phanerozoic Reef Patterns*: SEPM Special Publications, n. 72, p. 129–180.
- Williams, A., 1951, Llandovery brachiopods from Wales with special reference to the Llandovery District: *Quarterly Journal of the Geological Society of London*, v. 107, p. 85–136.
- Ziegler, A.M., and Boucot, A.J., 1970, North American Silurian animal communities, in Berry, W.B.N., and Boucot, A.J., eds., *Correlation of the North American Silurian Rocks*: Geological Society of America, Special Paper, v. 102, p. 95–112.

Accepted 27 June 2017