A new species of Hirnantia (Orthida, Brachiopoda) and its implications for the Hirnantian age of the Ellis Bay Formation, Anticosti Island, eastern Canada

Authors: Zimmt, Joshua B., and Jin, Jisuo

Source: Journal of Paleontology, 97(1) : 47-62

Published By: The Paleontological Society

URL: https://doi.org/10.1017/jpa.2022.83

The BioOne Digital Library (https://bioone.org/) provides worldwide distribution for more than 580 journals and eBooks from BioOne's community of over 150 nonprofit societies, research institutions, and university presses in the biological, ecological, and environmental sciences. The BioOne Digital Library encompasses the flagship aggregation BioOne Complete (https://bioone.org/subscribe), the BioOne Complete Archive (https://bioone.org/archive), and the BioOne eBooks program offerings ESA eBook Collection (https://bioone.org/esa-ebooks) and CSIRO Publishing BioSelect Collection (https://bioone.org/csiro-ebooks).

Your use of this PDF, the BioOne Digital Library, and all posted and associated content indicates your acceptance of BioOne's Terms of Use, available at www.bioone.org/terms-of-use.

Usage of BioOne Digital Library content is strictly limited to personal, educational, and non-commmercial use. Commercial inquiries or rights and permissions requests should be directed to the individual publisher as copyright holder.

BioOne is an innovative nonprofit that sees sustainable scholarly publishing as an inherently collaborative enterprise connecting authors, nonprofit publishers, academic institutions, research libraries, and research funders in the common goal of maximizing access to critical research.

Downloaded From: https://complete.bioone.org/journals/Journal-of-Paleontology on 18 May 2025
Terms of Use: https://complete.bioone.org/terms-of-use

Journal of Paleontology, 97(1), 2023, p. 47–62

0022-3360/23/1937-2337
doi: 10.1017/jpa.2022.83

JOURNAL OF PALEONTOLOGY
A PUBLICATION OF THE Paleontological SOCIETY

A new species of *Hirnantia* (Orthida, Brachiopoda) and its implications for the Hirnantian age of the Ellis Bay Formation, Anticosti Island, eastern Canada

Joshua B. Zimmt[1]* and Jisuo Jin[2]

[1]Department of Integrative Biology and Museum of Paleontology, University of California Berkeley, Berkeley, CA, USA
<josh_zimmt@berkeley.edu>
[2]Department of Earth Science, University of Western Ontario, London, N6A 5B7, Canada <jjin@uwo.ca>

Abstract.—Anticosti Island, eastern Canada, records an exceptionally thick and well-exposed Ordovician/Silurian boundary section that hosts a series of diverse marine invertebrate faunas across the Late Ordovician mass extinction. However, the base of the terminal Ordovician stage, the Hirnantian, has been difficult to identify on Anticosti due to the lack of a traditional *Hirnantia* fauna within the Upper Ordovician Ellis Bay Formation. Previously, the eponymous taxon of the *Hirnantia* fauna, and type species of the genus *Hirnantia*, *H. sagittifera* (M'Coy, 1851) has been reported only from the uppermost Ellis Bay Formation, leading to uncertainty as to the age of the lower Ellis Bay Formation. Here we report *Hirnantia notiskuani* n. sp. from the lowermost Ellis Bay Formation. This new species is similar to the type species, *H. sagittifera*, but is distinguished by its strongly dorsibiconvex shell in mature forms and variously developed uniplicate anterior commissure. Occurrences of these two similar species of *Hirnantia*, *H. notiskuani* and *H. sagittifera*, within the lower and uppermost Ellis Bay Formation, respectively, indicate a Hirnantian age for the entire Ellis Bay Formation, a finding that is supported by recent palynological and chemostratigraphic studies. Brachiopod assemblages within the Ellis Bay Formation therefore are best characterized as a unique and diverse *Hirnantia* fauna, consisting of genera from both the typical *Hirnantia* fauna and the epeiric seas of Laurentia.

UUID: http://zoobank.org/1c1dff6a-ee38-4cd3-b8bd-3d803a2774ef

Introduction

Anticosti Island (Québec, Canada) is well known for its stratigraphically thick and fossiliferous Ordovician/Silurian boundary section, with a diverse marine invertebrate fauna consisting of corals, brachiopods, mollusks, trilobites, and crinoids that have been the subject of taxonomic investigations for over a century (Logan, 1863; Twenhofel, 1928; Bolton, 1981). Among these groups, the best documented have been the rhynchonelliform brachiopods, which have been described extensively in a series of monographs and papers (e.g., Jin, 1989; Copper, 1995; Dewing, 1999; Jin and Copper, 2000; Jin and Zhan, 2008; Copper and Jin, 2017). Turnovers within and among the orders of Rhynchonelliformea (Williams et al., 1996) have played a critical role in defining the terminal-Ordovician Hirnantian Stage, as well as the placement of the Ordovician/Silurian boundary on Anticosti Island (Bolton, 1981; Copper, 2001; Copper et al., 2013).

There are two major turnovers in brachiopod assemblages recorded throughout the Upper Ordovician on Anticosti Island. The first interval of brachiopod turnover is best observed along the western coast of Anticosti Island, where it is expressed as a gradual transition across the contact between the Vaureal and Ellis Bay formations. Notably, the lowermost member of the Ellis Bay Formation (sensu Copper et al., 2013) is marked by the first occurrences of the spire-bearing *Hindella* Davidson, 1882 and *Eospirigerina* Boucot and Johnson, 1967. Throughout the Ellis Bay Formation, there are no drastic turnovers in brachiopod assemblages, although Jin and Copper (2008) documented localized shifts in brachiopod associations. At the top of the Ellis Bay Formation, Jin and Zhan (2008) recognized the type species of *Hirnantia*, *H. sagittifera* (M'Coy, 1851), but extensive collections have demonstrated it is found only within the reefal Laframboise Member. Across the Ellis Bay/Becscie formational contact, a second major turnover in brachiopod assemblages is marked by the replacement of the typical Ellis Bay brachiopod assemblage by an assemblage dominated by smaller-shelled orthides, virginids, and athyrides (Jin et al., 1996; Li and Copper, 2006; Copper and Jin, 2017). This turnover is observable in every exposure of the contact between the Ellis Bay and Becscie formations.

---

*Corresponding author.

Recognizing these two major intervals of faunal turnover, Copper et al. (2013) interpreted the entire Ellis Bay Formation as Hirnantian in age, with each faunal transition representing a hypothesized pulse of the Late Ordovician mass extinction. In their framework, a Hirnantian age of the Ellis Bay Formation was supported by the first occurrences of the genera *Hindella* and *Eospirigerina* within the Fraise Member along the western coast of Anticosti Island, as well as the presence of *Hirnantia* in the uppermost Laframboise Member. According to Copper and Jin (2017), true *Hindella* species are confined largely to the Hirnantian, with only *Hindella terebratulina* (Wahlenberg, 1818) from the limestone capping the Boda reef mounds possibly extending downward in the uppermost Katian (Sheehan, 1977). In recent studies, however, the top of the Boda Limestone has been considered Hirnantian in age (e.g., Webby, 2002; Suzuki et al., 2009). This would imply *Hindella* is an "index" genus for the Hirnantian. However, *Eospirigerina* has been reported from notably older Late Ordovician rocks, such as the upper Dulankara Formation of Chu-Ili, Kazakhstan (Popov et al., 1999). Furthermore, the brachiopod assemblages of the Ellis Bay Formation lack many taxa of the classic *Hirnantia* fauna that are characteristic of the so-called cool-water Kosov faunal province in marginal and peri-Gondwana, expanding from high southern latitudes (e.g., Colmenar et al., 2018) to tropical latitudes during the Hirnantian (for a summary, see Rong et al., 2002; Huang et al., 2020a; Rong et al., 2020a).

Here we report a new species of *Hirnantia, H. notiskuani*, from eastern exposures of the lowermost Ellis Bay Formation (sensu Copper et al., 2013) on Anticosti Island. In many regards, this new species is similar to the morphologically plastic *H. sagittifera* except for the development of a uniplicate anterior commissure in both juvenile and mature specimens, a feature that has not been observed in the type species. Where it is most abundant, *H. notiskuani* is found in association with *Nasutimena fluctuosa* (Billings, 1860), a brachiopod characteristic of Laurentian epicontinental seas during the Katian. Given the significance of *Hirnantia* as an indicator of the Hirnantian Stage in tropical basins, its recognition from the sub-Laframboise Ellis Bay Formation provides new biostratigraphic context for understanding patterns of faunal turnover within the Ellis Bay Formation in central and eastern areas of Anticosti Island, thus providing strong evidence for placing the lower Ellis Bay Formation within the Hirnantian Stage.

Geologic setting

The exposed Upper Ordovician–lower Silurian stratigraphic succession of the Anticosti Basin is nearly a kilometer thick and divided into eight formations: the Upper Ordovician Vaureal and Ellis Bay formations and the lower Silurian Becscie (Copper and Jin, 2014), Merrimack (Copper and Long, 1989), Gun River (Copper et al., 2012), Menier, Jupiter, and Chicotte formations (Copper and Jin, 2015). In this paper, we focus on the stratigraphic interval spanning the uppermost Vaureal and lowermost Ellis Bay formations. These formations were deposited in a peripheral zone of the Appalachian foreland basin, the Anticosti Basin (Sanford, 1993), which was situated along the southern margin of Laurentia, approximately 20° south of the equator (Torsvik and Cocks, 2016). Subsidence rates in the Anticosti Basin peaked during the Late Ordovician but decreased markedly across the Ordovician/Silurian boundary, beginning with the deposition of the uppermost Vaureal and Ellis Bay formations (Long, 2007; Lavoie, 2008). Despite the influence of the Appalachian thrust sheet on the development of the Anticosti Basin, the stratigraphic succession on Anticosti Island was located on a promontory of the stable basement rock of the Canadian Shield beyond the Taconic deformation front and did not experience structural deformation associated with the Taconic Orogeny (Lavoie, 2008; Pinet et al., 2012). This allowed for the development of a gently dipping homoclinal carbonate ramp, with deposition largely controlled by storm processes (Sami and Desrochers, 1992; Long, 2007; Desrochers et al., 2010). The combination of high subsidence rates and gentle ramp gradient resulted in the deposition of a thick wedge of mixed carbonate and fine-grained siliciclastic sediments spanning the Ordovician/Silurian boundary.

Upper Ordovician and lower Silurian strata are exposed in an east–west trending belt spanning the entire length of Anticosti Island (~200 km), roughly oblique to the present southwestern dip of the ancient ramp (Desrochers and Gauthier, 2009). Upper Ordovician strata can be divided into a western facies suite, comprising largely mixed carbonate and shale facies deposited within the offshore transition zone, and an eastern facies suite, composed of mixed carbonate–siliciclastic facies deposited in environments ranging from the foreshore to the offshore transition zone (Long and Copper, 1986; Copper et al., 2013). While lithostratigraphic and sequence stratigraphic frameworks (e.g., Desrochers et al., 2010) have been proposed to correlate the western and eastern facies suites of the Upper Ordovician strata on Anticosti Island, in particular the members of the Ellis Bay Formation, rapid lateral facies shifts across the eastern and central parts of the basin continue to complicate regional stratigraphic correlation, as recognized in the original paper by Long and Copper (1986) describing the members of the Ellis Bay Formation. We therefore tentatively use the nomenclature of Long and Copper (1986) and Copper et al. (2013), pending further revision of correlation among eastern and central exposures of the Ellis Bay Formation.

Locality and stratigraphic information.—Collections were made at three localities spanning the easternmost exposures of the lowermost Ellis Bay Formation (Fig. 1).

Anse Mauvaise (Lousy Cove).—Samples were collected from the lower portion of the Prinsta Member at its type section at Anse Mauvaise (49.335°N, 61.887°W), where it overlies the cross-stratified sandstones of the uppermost Velleda Member of the Vaureal Formation (Fig. 2). Here the contact between the sandier Velleda Member and shalier Prinsta Member has been interpreted as a flooding surface coinciding with a regional rise in relative sea level (Desrochers et al., 2010). The Prinsta Member is expressed as nodular calcareous shales interbedded with very thin to thin-tabular grainstones and sandstones. The basal unit of the Prinsta Member contains half-meter-thick, reworked accumulations of aulacerids, stromatoporoids, and tabulate corals, referred to as "aulacerid biostromes" by Long and Copper (1986).

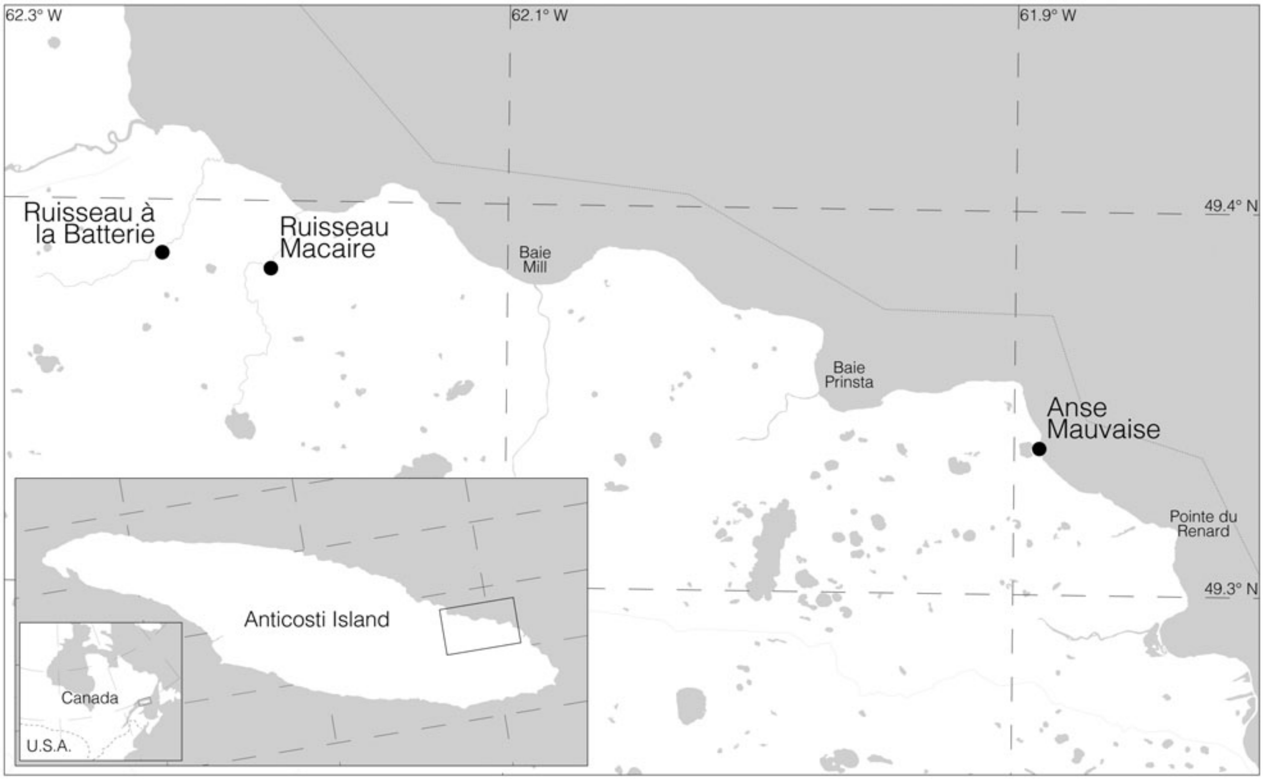

Figure 1. Map of the northeastern coast of Anticosti Island (Québec, Canada), marking the locations of *Hirnantia*-bearing exposures of the Prinsta Member (black circles). Inset map shows the location of Anticosti Island and the area detailed in the main map (Datum: WGS84).

Ruisseau Macaire.—Samples were collected from Ruisseau Macaire (49.381°N, 62.193°W) within an interval that is correlative with the type section of the Prinsta Member at Anse Mauvaise (Fig. 2). Here the base of the Prinsta Member is tentatively placed at the contact between recessive-weathering calcareous shales and the underlying weathering-resistant thin wavy-bedded bryozoan packstones to grainstones interbedded with laminar shale. Across this contact, the packstone to grainstone beds of the Prinsta Member gradually thin, while the relative proportion of calcareous shale increases, a trend that may reflect the rise in sea level observed across the Velleda/Prinsta contact at Anse Mauvaise. Throughout the measured section, the packstones to grainstones are gradually replaced by very thin to thin-tabular calcareous siltstone beds. The member is capped by nearly two meters of thin nodular very fine sandy grainstones with laminar shale interbeds, which is overlain by the argillaceous limestones of the Lousy Cove Member.

Ruisseau à la Batterie.—Samples were collected from the uppermost Prinsta Member at Ruisseau à la Batterie (49.385°N, 62.237°W). Here the lower part of the Prinsta Member is not exposed due to damming of the river by beavers. The exposed part of the formation consists of calcareous shales interbedded with very thin to thin-tabular calcareous siltstone beds, which are overlain by nearly two meters of thin nodular very fine sandy grainstones with laminar shale interbeds (Fig. 2). This nodular interval is erosively overlain by the argillaceous limestones of the Lousy Cove Member, similar to the stratigraphic succession at Ruisseau Macaire.

Materials and methods

CT scanning.—Specimens were scanned using a GE Phoenix Nanotom M micro-CT system in the Functional Anatomy and Vertebrate Evolution Laboratory, University of California, Berkeley, with an energy setting of 120 kV and current setting of 190 mA. The raw project images were reconstructed in the Phoenix Datos software at 0.126 microns per voxel and exported as an image stack in TIFF format.

SEM imaging.—Before imaging, specimens were sputter coated in a layer of osmium (~14 nm thick) using a Filgen OPC 80T. Specimens were imaged using a Zeiss 1540XB field emission scanning electron microscope in the Western University Nanofabrication Facility.

Repositories and institutional abbreviations.—Specimens figured and otherwise referenced in this study are deposited in the following institutions: American Museum of Natural History (AMNH-FI), New York, United States of America; the Nanjing Institute of Geology and Palaeontology (NIGP), Nanjing, China; and the Geological Survey of Canada (GSC), Ottawa, Canada.

Systematic paleontology

Order Orthida Schuchert and Cooper, 1932
Superfamily Enteletoidea Waagen, 1884

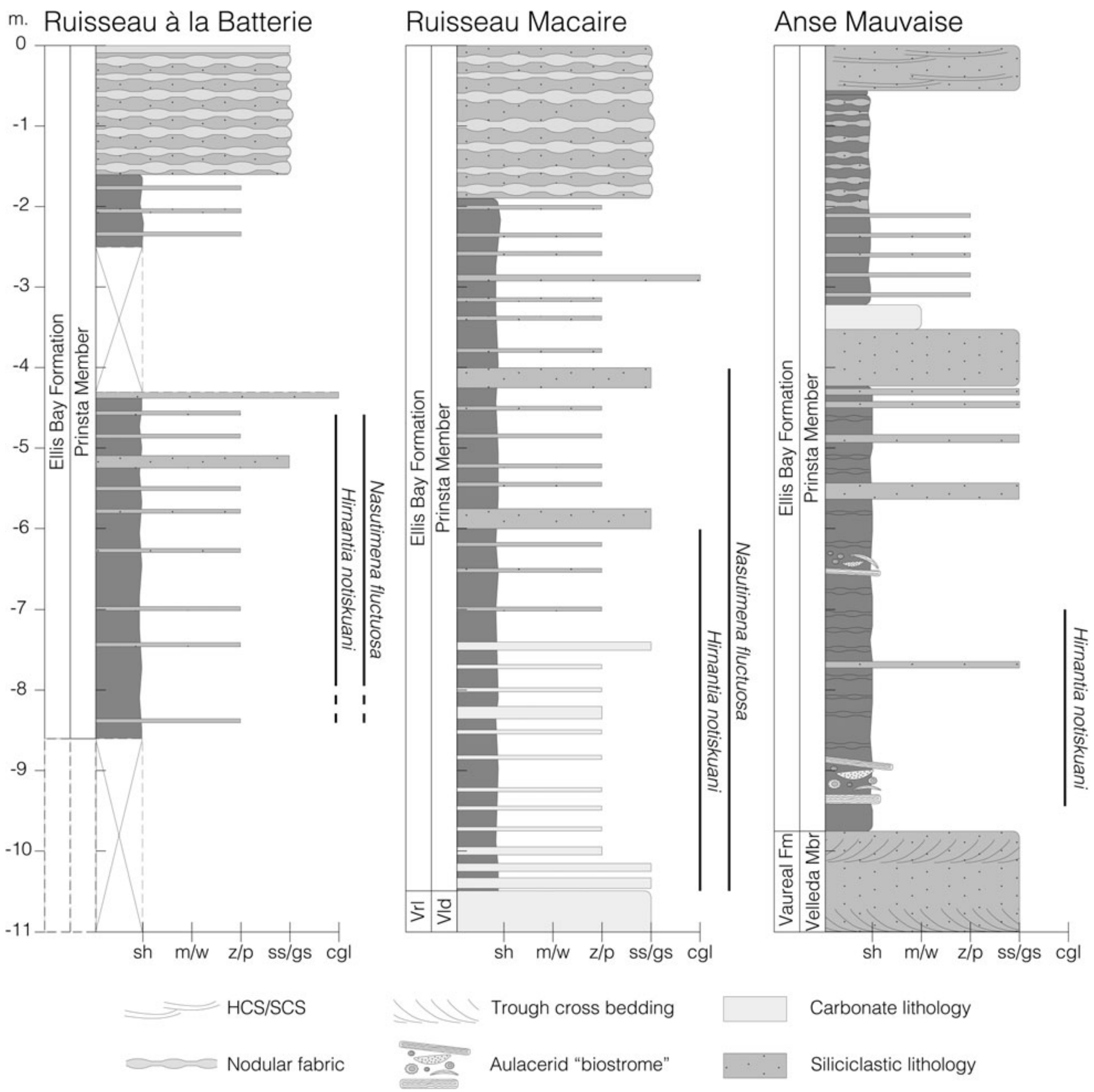

Figure 2. Stratigraphic columns illustrating the uppermost Velleda Member (Vaureal Formation) and Prinsta Member (Ellis Bay Formation) for each of the three localities in this study, as well as the stratigraphic range of *Hirnantia notiskuani* n. sp. and *Nasutimena fluctuosa* at each locality. The datum for each column is the base of the Lousy Cove Member of the Ellis Bay Formation (sensu Long and Copper, 1986). sh = shale; m/w = lime mud or wackestone; z/p = silt or packstone; ss/gs = sandstone or grainstone; cgl = conglomerate.

Family Draboviidae Havlíček, 1950
Genus *Hirnantia* Lamont, 1935

Type species.—*Orthis sagittifera* M'Coy, 1851, Foel-y-Ddinas Mudstone Formation (Hirnantian), Wales, UK.

Hirnantia notiskuani new species
Figures 3–8

2008 *Hirnantia* sp. nov. A, Jin and Zhan, p. 53, pl. 35, figs. 1–16.

Types.—Holotype, AMNH-FI 137221 (Fig. 3.1–3.7); Prinsta Member (Hirnantian), Ellis Bay Formation, Ruisseau Macaire locality, eastern Anticosti Island, Québec, Canada. Figured paratypes (all from the same locality and stratigraphic interval), AMNH-FI 137220 (Fig. 4.1–4.8), AMNH-FI 137223 (Fig. 5.1–5.5), AMNH-FI 137224 (Fig. 5.6–5.14), and one dorsal valve AMNH-FI 137222 (Figs. 3.8–3.9, 4.9).

Diagnosis.—Dorsibiconvex shells of *Hirnantia* with a uniplicate anterior commissure, best developed at gerontic

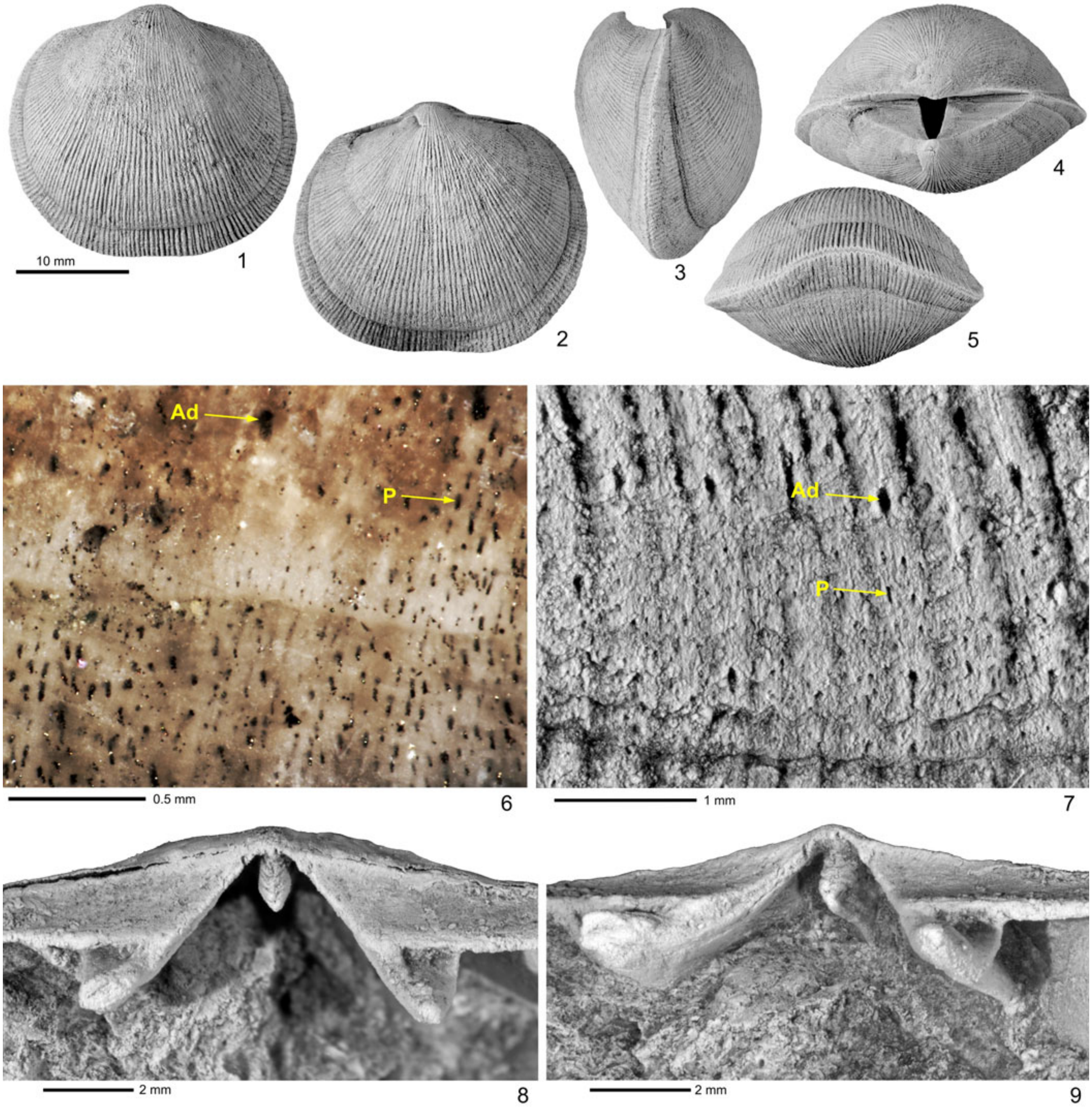

Figure 3. *Hirnantia notiskuani* n. sp. from the Prinsta Member of the Ellis Bay Formation, Hirnantian, at Ruisseau Macaire, eastern Anticosti Island. (**1–7**) Holotype AMNH-FI 137221: (**1**) dorsal, (**2**) ventral, (**3**) lateral, (**4**) posterior, and (**5**) anterior views of a strongly dorsibiconvex shell, demonstrating the well-developed uniplicate anterior that distinguishes this species; (**6, 7**) local enlargement showing aditicules and densely spaced punctae that characterize the shell microstructure. (**8, 9**) Paratype AMNH-FI 137222: enlargement of the dorsal interior of a uniplicate shell illustrating the cardinalia of *H. notiskuani*, with a high shaft and relatively small, bilobed, crenulated myophore; (**8**) perpendicular view; (**9**) oblique view. Ad = aditicule; P = punctae.

stage. Predominantly one column of aditicules per rib. Cardinal process consisting of relatively narrow, bilobed myophore with chevron-like crenulations and high, blade-like shaft merging anteriorly with a low median ridge. Brachiophore plates sitting directly on valve floor, diverging anteriorly from each other at ~80°.

Occurrence.—All specimens are from the Prinsta Member of the Ellis Bay Formation (Late Ordovician) at Ruisseau Macaire, Ruisseau à la Batterie, and Anse Mauvaise sections along the northeastern coast of Anticosti Island, Québec, Canada.

Description.—Shell medium to large for draboviids, subcircular to transversely ellipsoid in outline, biconvex to dorsibiconvex in profile; maximum width located around mid-length of shell. Hinge line straight, with rounded cardinal extremities,

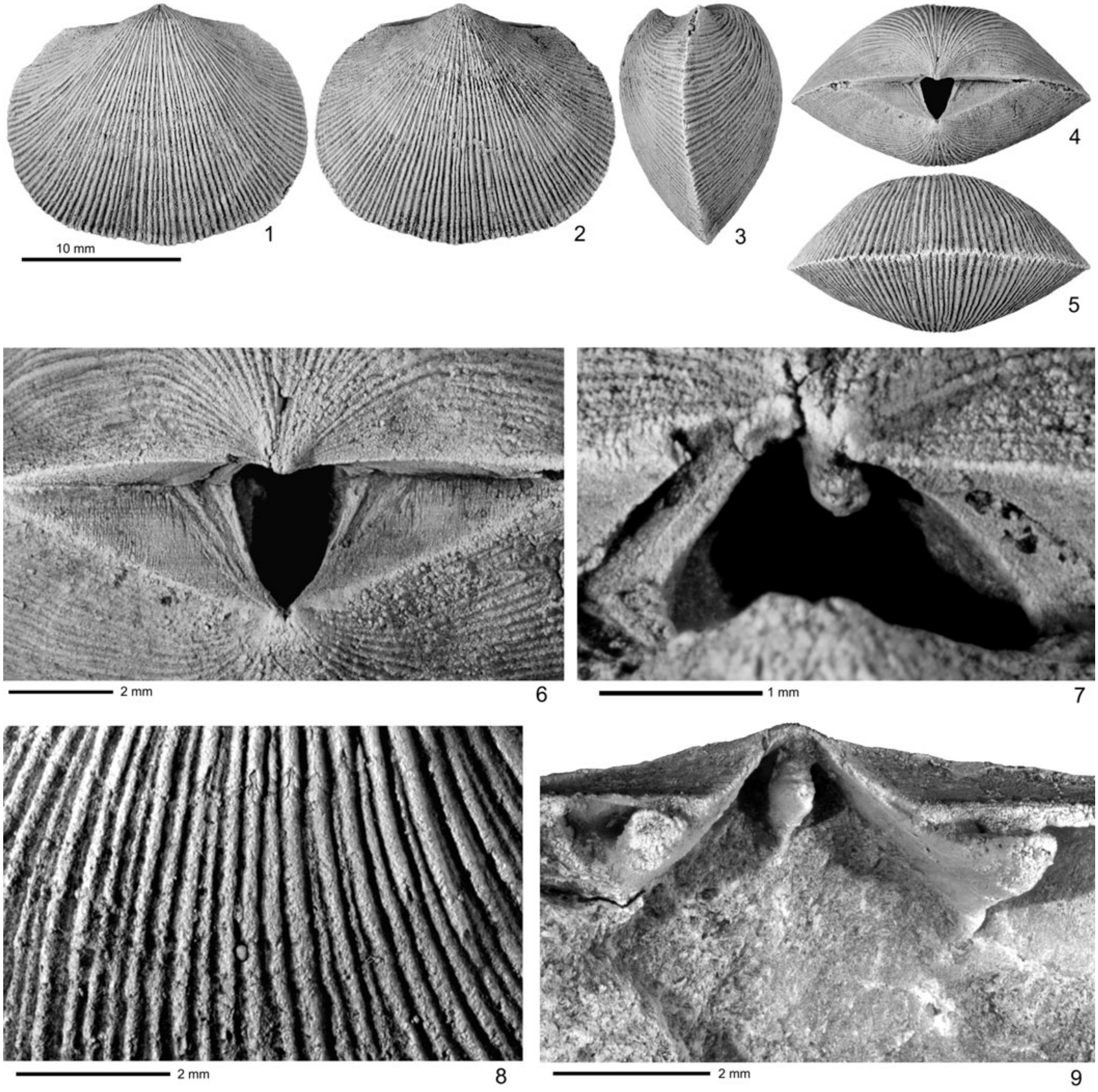

Figure 4. *Hirnantia notiskuani* n. sp. from the Prinsta Member of the Ellis Bay Formation, Hirnantian, at Ruisseau Macaire, eastern Anticosti Island. (**1–8**) Paratype AMNH-FI 137220: (**1**) dorsal, (**2**) ventral, (**3**) lateral, (**4**) posterior, and (**5**) anterior views of a juvenile individual with a rectimarginate anterior commissure; (**6–8**) local enlargement of (**6**) shell posterior, depicting transverse striae on ventral interarea, (**7**) interior of dorsal umbo as in (**6**) but rotated, revealing cardinal process, and (**8**) aditicules. (**9**) Paratype AMNH-FI 137222: oblique view of dorsal interior of a uniplicate shell.

reaching 50–60% of maximum shell width. Anterior commissure rectimarginate in some small and medium-sized specimens (Fig. 4.5), often gently uniplicate, particularly in large, gerontic (strongly convex) specimens (Figs. 3.5, 5.10). Shell surface multicostellate, with costellae increasing in number by both intercalation and bifurcation on both valves (Fig. 4.8). Fine capillae present between some costellae. Growth lines usually better developed in anterior parts of shell. Predominantly single column of aditicules per rib, sporadically interspersed with two columns of aditicules, densely spaced at shell margin (Fig. 5.11–5.14). Punctae fine, densely spaced, oriented at fairly low angles to the shell surface (Figs. 4.8, 5.13).

Ventral exterior.—Umbo weakly convex with suberect to slightly incurved beak. Interarea relatively high, apsacline curved in longitudinal profile, bearing transverse striae (Fig. 3.3, 3.4). Delthyrium open (Fig. 3.4). Gentle sulcus developed in anterior part, particularly of large specimens (Fig. 3.5).

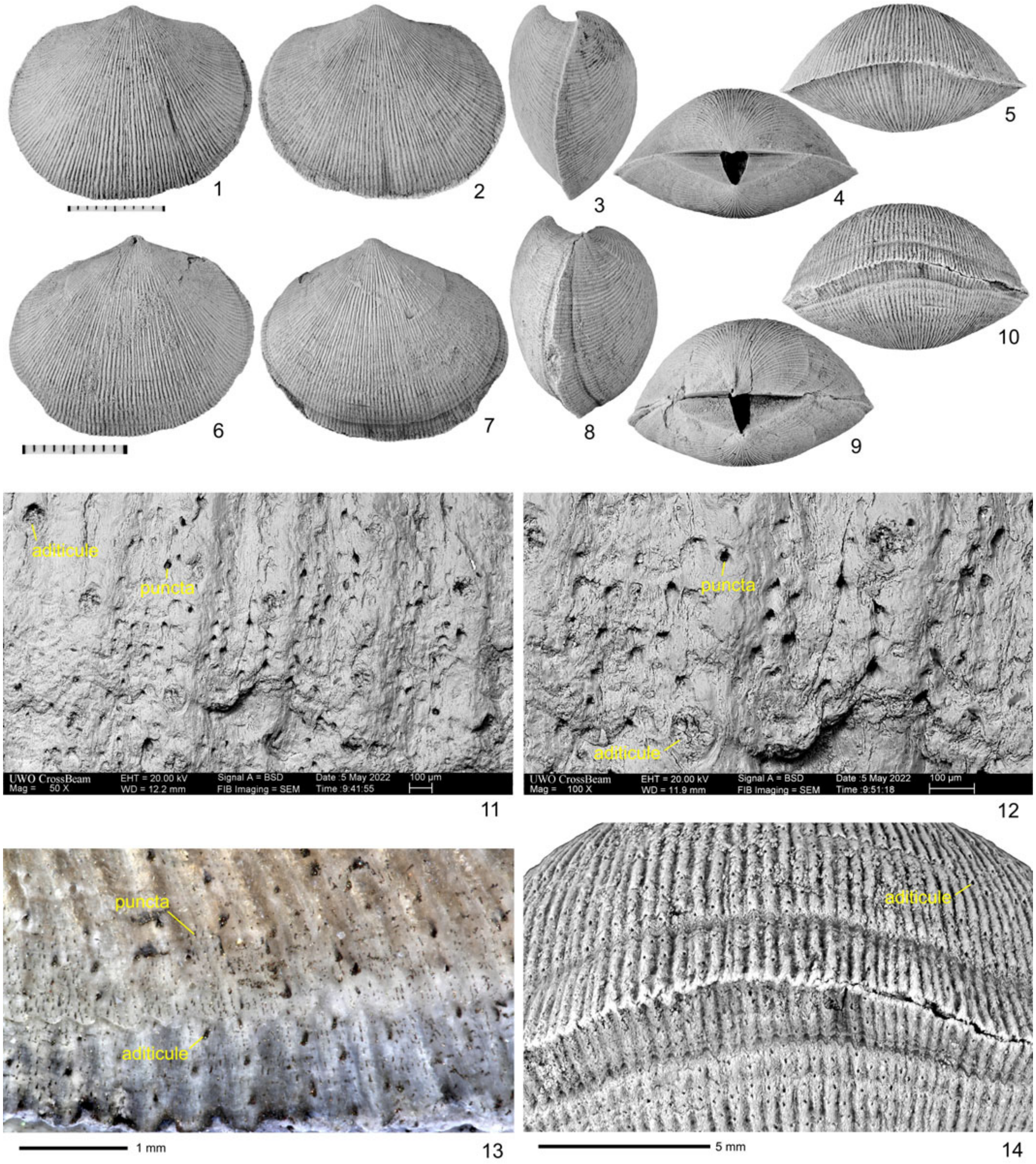

Figure 5. *Hirnantia notiskuani* n. sp. from the Prinsta Member of the Ellis Bay Formation, Hirnantian, at Ruisseau Macaire, eastern Anticosti Island. (**1–5**) Paratype AMNH-FI 137223: (**1**) dorsal, (**2**) ventral, (**3**) lateral, (**4**) posterior, and (**5**) anterior views of a juvenile individual with a broadly uniplicate margin. (**6–14**) Paratype AMNH-FI 137224: (**6**) dorsal, (**7**) ventral, (**8**) lateral, (**9**) posterior, and (**10**) anterior views of a moderately convex, broadly uniplicate shell; (**11, 12**) SEM images of shell surface showing aditicules (often filled with pyrite, see (**13**)) and densely spaced punctae; (**13**) enlargement of shell, photographed while immersed in alcohol, to highlight punctae and aditicules, both filled by pyrite; (**14**) enlargement of anterior commissure showing densely spaced aditicules along the anterior margin of the shell: note that aditicules can be variably arranged in single and double columns.

Dorsal exterior.—Valve moderately to strongly but uniformly convex, resulting in central part of valve having greatest convexity and depth, particularly in mature specimens. Umbo more strongly convex than ventral umbo, with ventrally directed beak sometimes extending slightly beyond commissural plane (Figs. 3.3, 5.3). Interarea lower than that of ventral valve, very slightly anacline to orthocline, with slightly curved longitudinal profile. Notothyrium open (Fig 4.7). Gentle fold developed anteriorly in large specimens to accommodate anterior sulcus of opposite valve (Fig. 3.5).

Ventral interior.—Dental plates present, weakly divergent anteriorly, extending anteriorly into low lateral bounding ridges of muscle field (Fig. 6.5–6.12). Pedicle callist present in apical area of umbonal cavity, represented by thin, transverse plate located just below delthyrial opening (Fig. 7).

Dorsal interior.—Brachiophores moderately robust, wedge shaped, supported by high, straight, brachiophore plates that diverge from each other anterolaterally at ~80° (Fig. 3.8, 3.9). Sockets small, triangular, bounded anteromedially by brachiophores, open anterolaterally, with socket floor raised above the valve floor, supported by fulcral plates that are directly attached to the brachiophore plates (Fig. 3.9). Brachiophore plates sitting directly on valve floor, without forming delthyrial platform (Fig. 6.4–6.9). Cardinal process consisting of high, thin, plate-like shaft (Fig. 6.1–6.4) that extends anteriorly as low, rounded median ridge (Fig. 6.4–6.12); myophore delicate, with bilobate, crenulated top (Figs. 3.8, 4.7). Muscle scars poorly preserved in dorsal valves available for study.

Etymology.—After the traditional Innu name for Anticosti, *Notiskuan*, which translates from the Innu-aimun language to “where bears are hunted.”

Materials.—Conjoined shells (22) isolated from matrix plus seven embedded in slab; ventral valve (one); dorsal valves (two).

Remarks.—*Hirnantia notiskuani* n. sp. is similar to the type species with regard to several external and internal characters. Externally, the gradual change in convexity throughout ontogeny, from a biconvex to dorsibiconvex profile, is consistent with the description of the type species by Temple (1965). Other external characteristics, including a punctate shell, fine multicostellate ornamentation, and an apsacline, slightly curved ventral interarea, are consistent with the description of the type species from several regions (e.g., Melou, 1987; Villas et al., 1999; Hints et al., 2012; Rong et al., 2020b). Internally, the high, divergent brachiophore plates braced by fulcral plates, bilobed myophore, and high shaft of the cardinal process, which extends anteriorly as a broad median ridge, are also common features shared with the type species of *Hirnantia* (Amsden, 1974; Lespérance and Sheehan, 1976; Melou, 1987; Villas et al., 1999; Hints et al., 2012; Benedetto, 2013). The configuration (size and orientation) of the ventral interarea and the pedicle callist in the new species resemble most closely those of *H. sagittifera* from the Hirnantian Kuanyinchiao beds at the Hirnantian type section in Hubei, China (Fig. 9), although the pedicle callist was not reported specifically in previous studies of *H. sagittifera* from South China (e.g., Rong, 1984; Rong et al., 2002; Huang et al., 2020a, b). A similar pedicle callist was described, but not illustrated, by Havlíček (1977, p. 267) for *H. sagittifera* from the Kosov (Hirnantian) strata of Bohemia. While Havlíček (1977) described several other species of *Hirnantia* from Katian (pre-Kosov) strata of Bohemia, most of those forms do not have the fine multicostellae or the subquadrate-outlined dorsal muscle field that are characteristics of the type species. The generic validity of the Bohemian species, therefore, needs further detailed investigations, especially as some of Havlíček’s species occur in Katian strata of Anti-Atlas, Morocco (Mergl, 1983; Colmenar et al., 2018).

In contrast to the type species of *Hirnantia,* which has a rectimarginate to weakly unisulcate anterior commissure (Harper, 2000), *H. notiskuani* is characterized by a uniplicate anterior commissure that is best developed in large and strongly convex (presumably gerontic) forms. However, this feature can be highly variable in both large forms (pronounced anterior plication to broad, shallow plication) and small to medium forms (broad, shallow plication to rectimarginate commissure; Fig. 8). A similar variation in anterior commissure has been observed in the orthoid genus *Plaesiomys* Hall and Clarke, 1892 from the same stratigraphic interval of the Ellis Bay Formation (Jin and Zhan, 2008). *Plaesiomys anticostiensis* (Shaler, 1865), for example, has a gently uniplicate anterior margin, whereas the type species, *P. subquadrata* (Hall, 1847), has a rectimarginate anterior. Despite the great degree of morphological variation in both internal and external structures of the type species of *Hirnantia* (Temple, 1965; Rong, 1984; Villas et al., 1999; Hints et al., 2012; Huang et al., 2020b; Rong et al., 2020b), *H. notiskuani* is the only species with a uniplicate anterior commissure. Juvenile specimens of *H. notiskuani* that lack a uniplicate anterior commissure can be distinguished externally from *H. noixella* Amsden, 1974 by their more evenly biconvex profile, in contrast to the ventribiconvex shell of *H. noixella*.

Order Strophomenida Öpik, 1934
Superfamily Strophomenoidea King, 1846
Family Strophomenidae King, 1846
Genus *Nasutimena* Jin and Zhan, 2001

Type species.—*Strophomena fluctuosa* Billings, 1860, Vaureal Formation (Richmondian), Anticosti Island, Canada.

Nasutimena fluctuosa Billings, 1860
Figure 10

1860 *Strophomena fluctuosa* Billings, p. 57, fig. 6.
1862 *Strophomena fluctuosa*; Billings, p. 123, figs. 102a, b.
1863 *Strophomena fluctuosa*; Logan, p. 221, fig. 207A.
1892 *Strophomena fluctuosa*; Hall and Clarke, p. 251, pl. llA, figs. 4, 5.
1924 *Strophomena fluctuosa*; Foerste, p. 119, pl. 12, figs. 8a, b.
1928 *Strophomena fluctuosa*; Twenhofel, p. 193, pl. 22, figs. 3–5.
1928 *Strophomena fluctuosa*; Troedsson, p. 93, pl. 22, fig. 13.
1970 *Strophomena fluctuosa*; Macomber, p. 440, pl. 78, figs. 16–24.
1972 *Strophomena fluctuosa*; Bolton, p. 22, pl. 1, fig. 9.

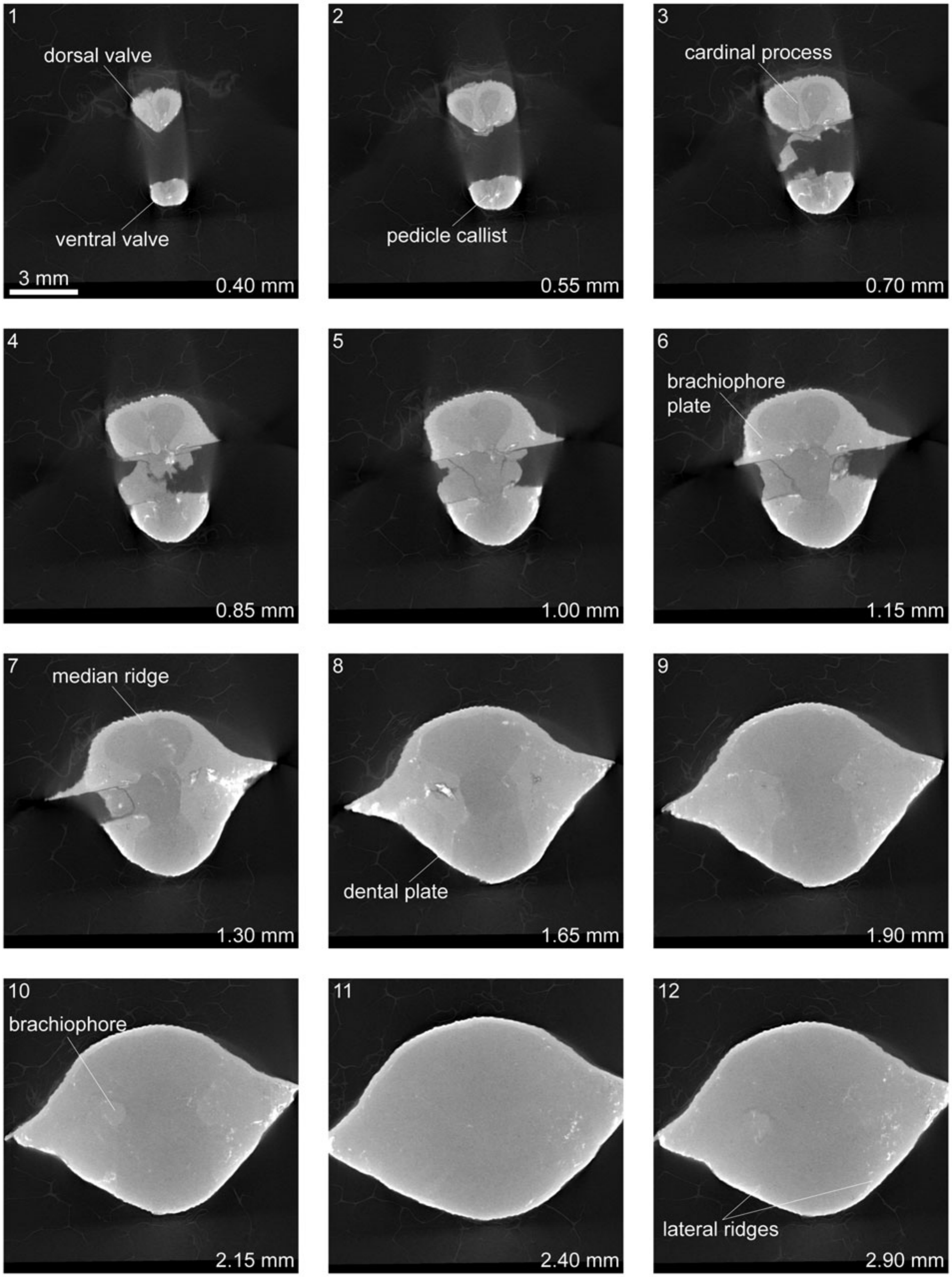

Figure 6. Serial cross sections of *Hirnantia notiskuani* n. sp. (AMNH-FI 137220), created using micro-CT scanning, progressively moving from the posterior to the anterior part of the shell. Lighter gray areas indicate shell calcite, while darker gray areas indicate infilling matrix; note the low contrast between the shell and enclosed carbonate-rich matrix. White splotches and lines are likely pyritized grains; the smearing effect above the specimen is caused by the positioning of the electron source. CT images reveal several internal morphological features: (**1–4**) a high, thin, plate-like shaft of the cardinal process, (**4–12**) which extends anteriorly as a low, rounded median ridge; (**5–9**) weakly divergent dental plates, (**10–12**) extending as low lateral bounding ridges of the ventral muscle field.

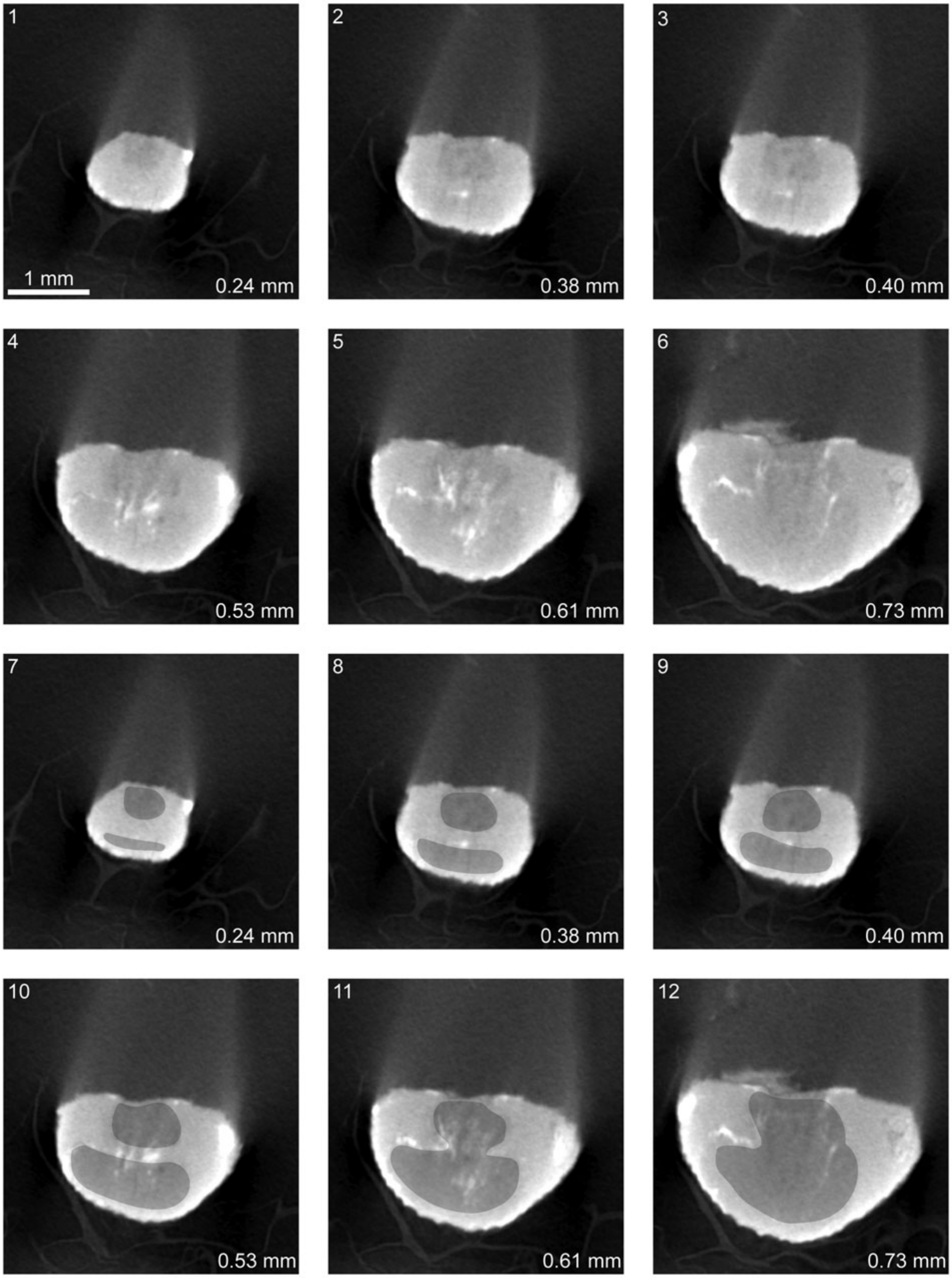

Figure 7. Serial cross sections of the ventral umbo of *Hirnantia notiskuani* n. sp. (AMNH-FI 137220) created using micro-CT scanning. Images are taken at a slightly oblique angle to avoid imaging artifacts created by pyrite within the enclosed matrix. Coloration as seen in Figure 6. (**1–6**) CT images of the ventral umbo reveal two separate chambers that are separated by a thin pedicle callist, which starts near the apex of the umbo and parts anteriorly. (**7–12**) Images as in (**1–6**), but with each chamber shaded.

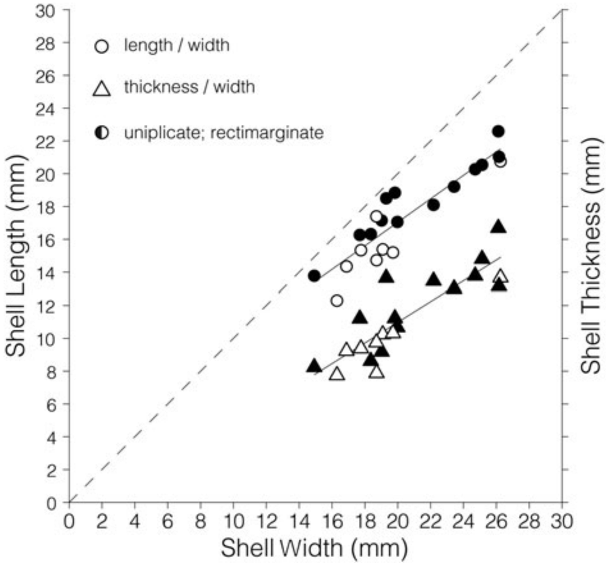

Figure 8. Shell dimensions of *Hirnantia notiskuani* n. sp. from the Prinsta Member of the Ellis Bay Formation at Ruisseau à la Batterie, Ruisseau Macaire, and Anse Mauvaise (Lousy Cove). Note that although there is variability in the anterior commissure, both small- and large-sized shells can possess a uniplicate commissure that is characteristic of the species.

1981 *Strophomena fluctuosa*; Bolton, p. 50, pl. 3, fig. 4.
1995 *Luhaia fluctuosa* (Billings); Dewing, p. 139, pl. 10, figs. 2, 4–8, pl. 11, figs. 1–13.
1997 *Strophomena fluctuosa*; Jin et al., p. 26, pl. 5, figs. 1–16, pl. 6, figs. 1–7.
1999 *Gunnarella fluctuosa* (Billings); Dewing, p. 20, pl. 6, figs. 2, 4–8, pl. 7, figs. 1–13.
2001 *Nasutimena fluctuosa* (Billings); Jin and Zhan, p. 31, pl. 6, figs. 9–19, pl. 7, figs. 5–12, pl. 20, figs. 1–7, pl. 21, figs. 5, 6, figs. 16, 17.

Holotype.—The original holotype of *Strophomena fluctuosa* collected by Billings (1860) from the Vaureal Formation (per Jin and Zhan, 2001) was misplaced before 1945 (Wilson, 1945, p. 142). However, a published hypotype (GSC 2017) from the Vaureal Formation, Carlton Point, Anticosti, was illustrated by Twenhofel (1928, pl. 22, fig. 5) and subsequently by Jin et al. (1997, pl. 5, figs. 1–4).

Occurrence.—All specimens are from the Prinsta Member of the Ellis Bay Formation (Late Ordovician) at Ruisseau Macaire and Ruisseau à la Batterie on eastern Anticosti Island, Québec, Canada.

Description.—Shells medium sized, subtriangular in outline; resupinate in lateral profile with sharp ventrally directed geniculation (110–120°); trail high, with anteromedial dorsal fold and ventral sulcus (Fig. 10.1–10.5). Hinge line long, strophic, with rounded to alate cardinal extremities, commonly maximum width of specimen. Ribbing well defined, parvicostellate (Fig. 10.7). Concentric rugae variably developed on disc as either continuous (uninterrupted by costae) or discontinuous (interrupted by costae) wrinkles (Fig. 10.6). Concentric growth lines fine, strongly expressed on the trail. Pseudopunctae fine, densely spaced.

Ventral exterior.—Valve weakly convex in umbonal area, becoming flat and concave anteriorly. Low planar interarea 2–3 mm high, weakly striated, slightly apsacline; delthyrium covered by thick, strongly convex pseudodeltidium (Fig. 10.4). Trail with anteriomedial fold to accommodate fold of dorsal valve.

Dorsal exterior.—Valve flat to weakly concave in umbonal area, becoming convex anteriorly. but with distinctive cleft running down middle of disk (Fig. 10.1). Planar interarea approximately 1 mm high and anacline; notothyrium covered by thick, strongly convex chilidium. Protruding fold developed on trail medioanteriorly (Fig. 10.1, 10.5).

Ventral interior.—Teeth robust and triangular, strongly divergent; dental plates extending anteriorly to form well-developed ridges that laterally bound deeply impressed subcircular to diamond-shaped muscle field, but often with 2–3 mm gap anterior of muscle field. Adductor scars lanceolate, divided by median ridge that tapers anteriorly, terminates just beyond anterior margin of muscle field. Diductor scars anteriorly divergent, enclosing adductor scars laterally. Peripheral rim well developed, starting laterally of muscle-bounding ridges and extending to line of geniculation where it curves anteriorly and continues along margin of the disc. Trail marked by well-developed radial thickenings of the shell, forming distinct ridges on interior and exterior of trail.

Dorsal interior.—No dorsal interiors were recovered during collection.

Materials.—Conjoined valves (6); ventral valves (5; often broken along anterior margin).

Remarks.—These specimens are virtually identical to those described by Dewing (1999) from the Vaureal Formation (Katian) on Anticosti Island and are assigned to the species on the basis of their distinctive subtriangular outline marked by an anteromedial fold, sharp ventrally directed geniculation, and variably developed rugae covering the disc (Jin and Zhan, 2001). However, in contrast to the description of Dewing (1999), the teeth of the specimens described from the Ellis Bay Formation are more robust, a trait observed in specimens from southern Manitoba (Jin and Zhan, 2001). Specimens from the Ellis Bay Formation also have a prominent cleft running down the midline of the dorsal disk, a trait that has not been described in other specimens of this species.

Discussion

A Hirnantian age for the Ellis Bay Formation.—The newly described occurrences of *Hirnantia notiskuani* in the sub-Laframboise Ellis Bay Formation provide a critical biostratigraphic constraint for understanding the Upper Ordovician succession on Anticosti Island. By expanding the stratigraphic range of the genus *Hirnantia* to the base of the Ellis Bay Formation, *H. notiskuani* provides compelling evidence for a Hirnantian age of the Ellis Bay Formation. A member of the cool-water "Kosov faunal province" in marginal and peri-Gondwana, *Hirnantia* was a cool-water, high-latitude genus

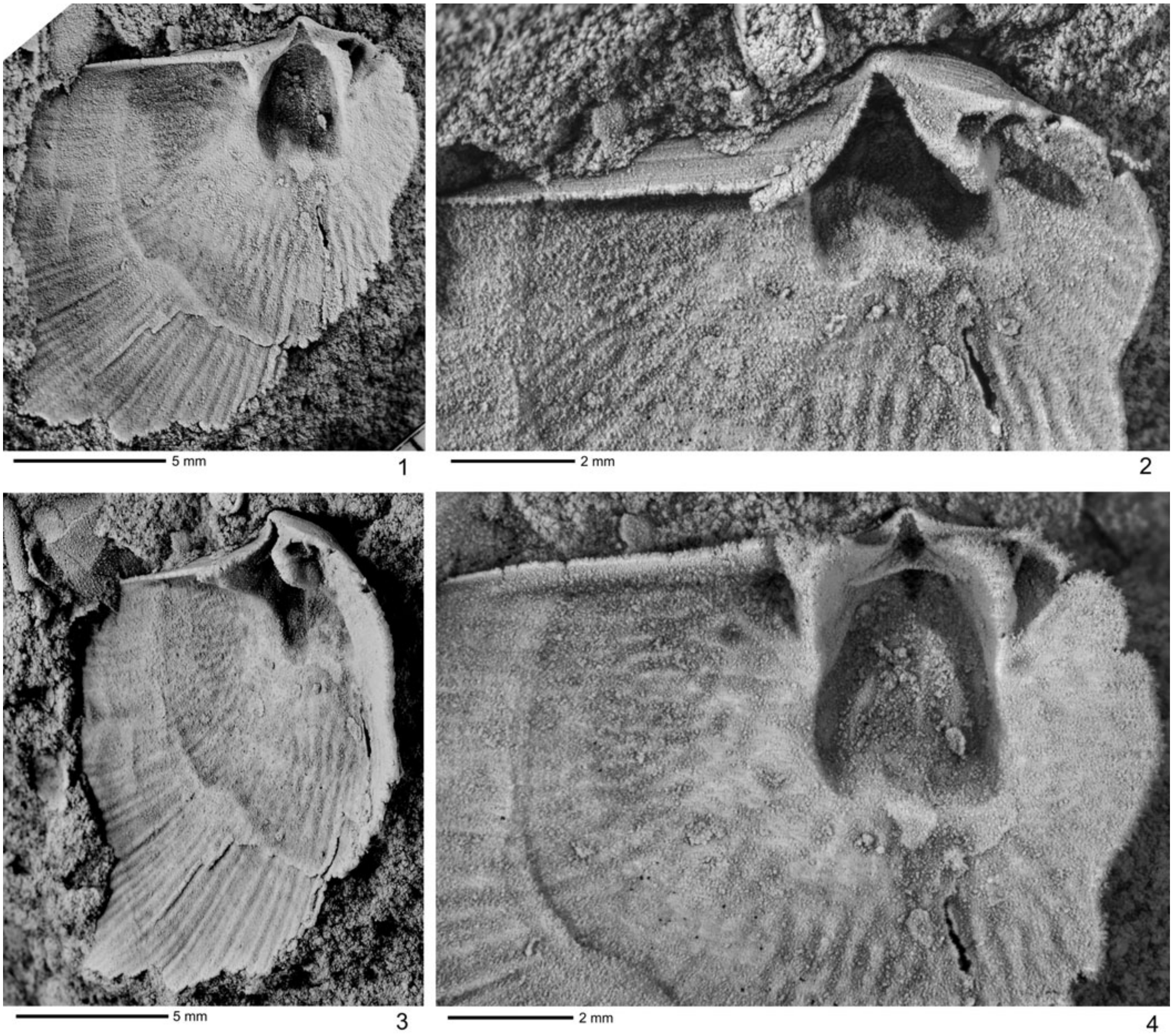

Figure 9. Silicon rubber cast of a ventral internal mold of *Hirnantia sagittifera*, specimen NIGP180325, Kuanyinchiao beds, GSSP section for the base of the Hirnantian Stage, Wangjiawan, Yichang district, Hubei, China. (**1–4**) Various enlarged views of the ventral interior; note the presence of pedicle callist, a thin transverse plate situated in the apical area, characteristic of the type species.

that did not begin to expand its range to tropics until the onset of global cooling at the start of the Hirnantian Stage (Sheehan, 2001; Rong et al., 2002; Huang et al., 2020a). While several species of *Hirnantia* have been reported in Sandbian and Katian strata of high-latitude sites such as Bohemia (Havlíček, 1977), these are represented mostly by relatively small, coarsely ribbed shells, unlike the typical shells of *Hirnantia*. So far, the type species and the new species from Anticosti Island, characterized by large, strongly dorsibiconvex shells with fine multicostellae, appear to be confined predominantly to the Hirnantian. Furthermore, in the rare instances where *Hirnantia* has been identified in lower-latitude, pre-Hirnantian strata, such as at the top of the Wufen Formation in Southwest China, the genus is found over a restricted stratigraphic interval only a few centimeters below an abrupt shift in facies and fossil assemblages that marks the base of the Hirnantian (Rong et al., 2002). On Anticosti Island, the first occurrences of *Hirnantia*, represented by *H. notiskuani*, are found above major shifts in the stratigraphic and fossil records that mark the base of the Ellis Bay Formation. The differences in regional context between these patterns of first occurrences of *Hirnantia* provide greater confidence that the occurrences of *H. notiskuani* at the base of the Prinsta Member signify a Hirnantian age for the Ellis Bay Formation on Anticosti Island. These results are consistent with a growing number of palynological and chemostratigraphic studies that, in contrast to earlier studies (e.g., Brenchley et al., 1994; Bergström et al., 2006), suggest that the entire Ellis Bay Formation falls within the Hirnantian Stage (Delabroye et al., 2011; Achab et al., 2013; Mauviel and Desrochers, 2016; Mauviel et al., 2020).

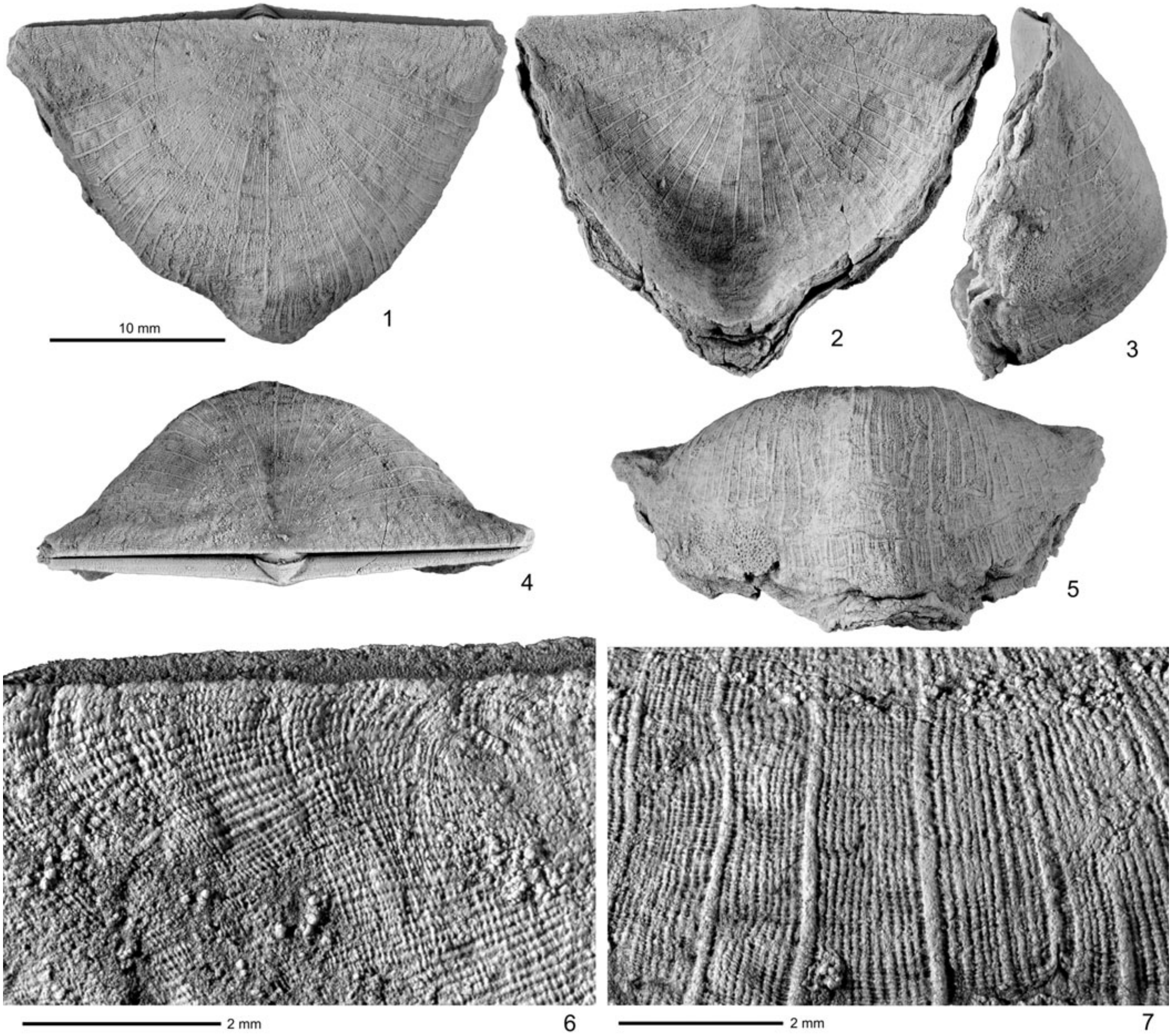

Figure 10. *Nasutimena fluctuosa* from the Prinsta Member of the Ellis Bay Formation, Hirnantian, at Ruisseau Macaire, eastern Anticosti Island. AMNH-FI 137239: (**1**) dorsal, (**2**) ventral, (**3**) lateral, (**4**) posterior, and (**5**) anterior views of a well-preserved shell, with enlargement of (**6**) the ventral posterior, displaying rugae, characteristic of the species, and (**7**) trail with well-developed parvicostellate ribbing.

A diverse Hirnantia *fauna.*—The new occurrences of *H. notiskuani* from the basal Ellis Bay Formation provide new context for assessing the biostratigraphic significance of the brachiopod assemblages throughout the Hirnantian on Anticosti Island. In contrast to other occurrences of *Hirnantia*, *H. notiskuani* does not frequently occur in direct association with other common members of the *Hirnantia* fauna (Jin and Zhan, 2008). Long and Copper (1986) reported *Hindella* from the lower Prinsta Member at Anse Mauvaise, while subsequent collection by Jin and Zhan (2008) yielded specimens of *Eospirigerina*. Common members of the *Hirnantia* fauna, including brachiopod genera such as *Leptaena* Dalman, 1828, *Coolinia* Bancroft, 1949 (=*Fardenia*, Lamont, 1935; per Rong et al., 2013), *Aphanomena* Bergström, 1968 (=*Eostropheodonta*, Bancroft, 1949; per Rong and Cocks, 1994), co-occur in a variety of different assemblages throughout the Ellis Bay Formation (see Jin and Copper, 2008), either stratigraphically above or outside the geographic range of *H. notiskuani* (Jin and Copper, 2008; Copper et al., 2013), a pattern similar to the diachronous temporal and spatial distribution of the *Hirnantia* fauna observed in other Upper Ordovician sections (Rong et al., 2002). These genera, inclusive of *Hirnantia*, range up to the top of the reefal Laframboise Member (Jin and Zhan, 2008; Copper et al., 2013). On this basis, the brachiopod assemblages of the Ellis Bay Formation should be considered a part of the *Hirnantia* fauna.

Here we consider the *H. notiskuani* association of the basal Ellis Bay Formation on eastern Anticosti Island to represent a moderate-diversity *Hirnantia* fauna, associated with surviving brachiopod taxa from late Katian (Richmondian) epeiric seas of Laurentia, such as *Hesperorthis* Schuchert and Cooper, 1931, *Gnamptorhynchos* Jin, 1989, *Plaesiomys*, *Furcitella* Cooper, 1956, *Nasutimena*, *Hypsiptycha* Wang, 1949, and *Rostricellula* Ulrich and Cooper, 1942 (see Jin and Zhan, 2008). A similar assemblage, although lacking *Hirnantia*, has been observed in Hirnantian strata in southern Ontario (Stott and Jin, 2007), as well as in marginal Laurentian Hirnantian strata in Girvan, Scotland (Harper, 1981). Together, these assemblages show the presence of a unique Laurentian-affinity fauna composed of taxa typical of epeiric seas as well as the typical *Hirnantia* fauna. The *H. sagittifera* association in the Laframboise Member, however, represents a more “typical” *Hirnantia* fauna, associated with common *Vinlandostrophia* Zuykov and Harper, 2007, *Mendacella* Cooper, 1930, *Leptaena*, *Coolinia* (=*Fardenia*), *Aphanomena* (=*Eostropheodonta*), *Eospirigerina*, and *Hindella* (Copper et al., 2013). In this regard, if the entire Ellis Bay brachiopod fauna is to be treated as a *Hirnantia* fauna, it would be a highly diverse assemblage (see faunal list in Copper et al., 2013). Finally, across the Ellis Bay/Becscie formational contact, the brachiopod assemblages abruptly transition to an assemblage with an Edgewood–Cathay affinity (sensu Rong et al., 2020a), consisting of genera such as *Koigia* Modzalevskaya, 1985, *Mendacella*, *Diceromyonia* Wang, 1949, *Platystrophia* King, 1850, *Leptaena*, and *Biparetis* Amsden, 1974, and higher up in the Becscie Formation, *Viridita* Jin and Copper, 2000 (Li and Copper, 2006). Biostratigraphy based on brachiopod assemblages would therefore ascribe an early to middle Hirnantian age to the entire Ellis Bay Formation, inclusive of the Laframboise Member, and a late Hirnantian age to the lowermost Becscie Formation. Given its potentially unique and well-preserved Hirnantian fossil and stratigraphic records, future studies of Upper Ordovician strata from Anticosti Island should focus on the incorporation of paleobiological and chemostratigraphic data from Anticosti Island into our global understanding of the sequence of climate (e.g., Finnegan et al., 2011) and extinction (e.g., Copper et al., 2013) events across the Ordovician/Silurian boundary.

Acknowledgments

J.B.Z. thanks the Anticosti-UNESCO Steering Committee for financial and logistical support. We thank A. Desrochers and P. Copper for invaluable field guidance, E. Bōgner and J. Tseng for their assistance in collecting and processing CT data, and T. Goldhawk for his assistance in producing the SEM images included in this study. J.B.Z.’s fieldwork is funded by the Marland Pratt Billings and Katharine Fowler-Billings Research Award from the Geological Society of America (grant no. 12320-19), the William B.N. Berry Fund from the University of California Museum of Paleontology, and the Lerner–Gray Memorial Fund of the American Museum of Natural History. J.J.’s work is funded by the Natural Sciences and Engineering Research Council of Canada. Collections were made under authorization issued by Ministère de l’environnement et de la Lutte contre les changements climatiques (MELCC) under the Natural Heritage Conservation Act (permit no. 7912-09-01-0000201; reference 402036698). The constructive comments of two journal reviewers helped greatly improve the clarity of our discussion.

Declaration of competing interests

The authors declare none.

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.

Amsden, T.W., 1974, Late Ordovician and early Silurian articulate brachiopods from Oklahoma, southwestern Illinois and eastern Missouri: Oklahoma Geological Survey Bulletin, v. 119, 154 p.

Bancroft, B.B., 1949, Welsh Valentian brachiopods and the *Strophomena antiquata* group of fossil brachiopods: Quarry Manager’s Journal: Mexborough, Time Printing Co., 16 p.

Benedetto, J.L., 2013, Upper Ordovician brachiopods from the San Benito Formation, Cordillera del Tunari Bolivia: Ameghiniana, v. 50, p. 418–428.

Bergström, J., 1968, Upper Ordovician brachiopods from Västergötland, Sweden: Geologica et Paleontologica, v. 2, p. 1–35.

Bergström, S.M., Saltzman, M.W., and Schmittz, B., 2006, First record of the Hirnantian (Upper Ordovician) δ^{13}C excursion in the North American midcontinent and its regional implications: Geological Magazine, v. 143, p. 657–678.

Billings, E., 1860, Description of some new species of fossils from the lower and middle Silurian rocks of Canada: The Canadian Naturalist and Geologist, v. 5, p. 49–69.

Billings, E., 1862, New species of fossils from different parts of the lower, middle, and upper Silurian rocks of Canada: Geological Survey of Canada, Palaeozoic Fossils, v. 1, p. 96–168.

Bolton, T.E., 1972, Geological map and notes on the Ordovician and Silurian litho- and biostratigraphy, Anticosti Island, Quebec: Geological Survey of Canada, Paper 71, 45 p.

Bolton, T.E., 1981, Ordovician and Silurian biostratigraphy, Anticosti Island, Quebec, *in* Lesperance, P.J., ed., UGS Field Meeting, Anticosti-Gaspe, Quebec, Vol. 2, Stratigraphy and Paleontology: Montreal, Universite de Montreal, p. 41–59.

Boucot, A.J., and Johnson, J.G., 1967, Silurian and Upper Ordovician atrypids of the genera *Plectatrypa* and *Spirigerina*: Norsk Geologisk Tidsskrift, v. 47, p. 79–101.

Brenchley, P.J., Marshall, J.D., Carden, G.A., Robertson, D.B.R., Long, D.G.F., Meidla, T., Hints, L., and Anderson, T.F., 1994, Bathymetric and isotopic evidence for a short-lived Late Ordovician glaciation in a greenhouse period: Geology, v. 22, p. 295–298.

Colmenar, J., Villas, E., and Rasmussen, C.M.Ø., 2018, A synopsis of Late Ordovician brachiopod diversity in the Anti-Atlas, Morocco, *in* Hunter, A.W., Álvaro, J.J., Lefebvre, B., van Roy, P., and Zamora, S., eds., The Great Ordovician Biodiversification Event: Insights from the Tafilalt Biota, Morocco: Geological Society, London, Special Publications, n. 485, p. 153–163.

Cooper, G.A., 1930, New species from the Upper Ordovician of Percé: American Journal of Science, ser. 5, v. 20, p. 51–56.

Cooper, G.A., 1956, Chazyan and related brachiopods: Smithsonian Miscellaneous Collections, v. 127, 1025 p.

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., 2001, Reefs during multiple crises towards the Ordovician–Silurian boundary: Anticosti Island, eastern Canada, and worldwide: Canadian Journal of Earth Sciences, v. 38, p. 143–151.

Copper, P., and Jin, J., 2014, The revised lower Silurian (Rhuddanian) Becscie Formation, Anticosti Island, eastern Canada records the tropical marine faunal recovery from the end-Ordovician mass extinction: Newsletters on Stratigraphy, v. 4, p. 61–83.

Copper, P., and Jin, J., 2015, Tracking the early Silurian post-extinction faunal recovery in the Jupiter Formation of Anticosti Island, eastern Canada: a stratigraphic revision: Newsletters on Stratigraphy, v. 48, p. 221–240.

Copper, P., and Jin, J., 2017, Early athyride brachiopod evolution through the Ordovician–Silurian mass extinction and recovery, Anticosti Island, eastern Canada: Journal of Paleontology, v. 91, p. 1123–1147.

Copper, P., and Long, D.G.F., 1989, Stratigraphic revisions for a key Ordovician/Silurian boundary section, Anticosti Island, Canada: Newsletters on Stratigraphy, v. 21, p. 59–73.

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 megafaunal correlations: Stratigraphy, v. 10, p. 213–227.

Dalman, J.W., 1828, Uppstallning och Beskrifning af de i sverige funne Terebratuliter: Kungliga Svenska Vetenskapsakademien Handlingar, v. 3, p. 85–155.

Davidson, T., 1882, A monograph of the British fossil Brachiopoda: Palaeontographical Society Monographs, supplement, v. 5, p. 1–134.

Delabroye, A., Munnecke, A., Vecoli, M., Copper, P., Tribovillard, N., Joachimski, M.M., Desrochers, A., and Servais, M., 2011, Phytoplankton dynamics across the Ordovician/ Silurian boundary at low palaeolatitudes: correlations with carbon isotopic and glacial events: Palaeogeography, Palaeoclimatology, Palaeoecology, v. 312, p. 79–97.

Desrochers, A., and Gauthier, É., 2009, Carte géologique de l'île d'Anticosti (1/250,000): Ministère des Ressources naturelles et de la Faune du Québec (DV 2009-03).

Desrochers, A., Farley, C., Achab, A., Asselin, E., and Riva, J.F., 2010, A far-field record of the end Ordovician glaciation: the Ellis Bay Formation, Anticosti Island, Eastern Canada: Palaeogeography, Palaeoclimatology, Palaeoecology, v. 296, p. 248–263.

Dewing, K., 1995, Late Ordovician and early Silurian strophomenid brachiopods from Anticosti Island, Quebec [Ph.D. thesis]: London, University of Western Ontario, 487 p.

Dewing, K., 1999, Late Ordovician and early Silurian strophomenid brachiopods of Anticosti Island, Quebec, Canada: Paleontographica Canadiana, v. 17, 143 p.

Finnegan, S., Bergmann, K., Eiler, J.M., Jones, D.S., Fike, D.A., Eiseman, I., Hughes, N.C., Tripati, A.K., and Fischer, W.W., 2011, The magnitude and duration of Late Ordovician–early Silurian glaciation: Science, v. 331, p. 903–906.

Foerste, A.F., 1924, Upper Ordovician faunas of Ontario and Quebec: Geological Survey of Canada, Memoir 138, 255 p.

Hall, J., 1847, Descriptions of the organic remains of the lower division of the New York System: New York State Geological Survey, Palaeontology of New York, v. 1, 338 p.

Hall, J., and Clarke, J.M., 1892, An introduction to the study of the genera of Palaeozoic Brachiopoda: New York State Geological Survey, Palaeontology of New York, v. 8, 367 p.

Harper, D.A.T., 1981, The stratigraphy and faunas of the Upper Ordovician High Mains Formation of the Girvan district: Scotland Journal of Geology, v. 17, p. 247–255.

Harper, D.A.T., 2000, Dalmanellidina, *in* Kaesler, R.L., ed., Treatise on Invertebrate Paleontology, Part H, Brachiopoda (revised), Volume 1, Introduction: Boulder, Colorado, and Lawrence, Kansas, Geological Society of America and University of Kansas Press, p. 782–844.

Havlíček, V., 1950, Ramenonozci Českého Ordoviku: Rozpravy Ústředního Ústavu Geologického, v. 13, p. 1–72.

Havlíček, V., 1977, Brachiopods of the order Orthida in Czechoslovakia: Rozpravy Ústředního Ústavu Geologického, v. 44, 327 p.

Hints, L., Pärnaste, H., and Gailite, L.I., 2012, *Hirnantia sagittifera* (Brachiopoda) and *Mucronaspis mucronata* s.l. (Trilobita) in the Upper Ordovician of the East Baltic: taxonomy and distribution: Estonian Journal of Earth Sciences, v. 61, p. 65–81.

Huang, B., Zhou, H.H., Harper, D.A.T., Zhan, R., Zhang, X.L., Chen, D., and Rong, J.Y., 2020a, A latest Ordovician *Hirnantia* brachiopod fauna from western Yunnan, Southwest China and its paleobiogeographic significance: Palaeoworld, v. 29, p. 31–46.

Huang, B., Rong, J.Y., Harper, D.A.T., and Zhou, H., 2020b, A nearshore Hirnantian brachiopod fauna from South China and its ecological significance: Journal of Paleontology, v. 94, p. 239–254.

Jin, J., 1989, Late Ordovician–early Silurian rhynchonellid brachiopods from Anticosti Island, Quebec: Biostratigraphie du Paleozoique, v. 10, 127 p.

Jin, J., and Copper, P., 2000, Late Ordovician and early Silurian pentameric brachiopods from Anticosti Island, Québec, Canada: Palaeontographica Canadiana, no. 19, 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, no. 54, p. 41–51.

Jin, J., and Zhan, R., 2001, Late Ordovician articulate brachiopods from the Red River and Stony Mountain Formations, Southern Manitoba: Ottawa, NRC Research Press, 117 p.

Jin, J., and Zhan, R, 2008, Late Ordovician Orthide and Billingsellide brachiopods from Anticosti Island, eastern Canada: diversity change through mass extinction: Ottawa, NRC Research Press, 159 p.

Jin, J., Long, D.G.F., and Copper, P., 1996, Early Silurian *Virgiana* pentamerid brachiopod communities of Anticosti Island, Québec: PALAIOS, v. 11, p. 597–609.

Jin, J., Caldwell, W.G.E., and Norford, B.S., 1997, Late Ordovician brachiopods and biostratigraphy of the Hudson Bay Lowlands, northern Manitoba and Ontario: Geological Survey of Canada, Bulletin 513, 115 p.

King, W., 1846, Remarks on certain genera belonging to the class Palliobranchiata: Annals and Magazine of Natural History, v. 18, p. 26–42.

King, W., 1850, A monograph of the Permian fossils of England: Palaeontographical Society Monograph, 258 p.

Lamont, A., 1935, The Drummuck Group, Girvan: a stratigraphical revision, with descriptions of new fossils from the lower part of the group: Transactions of the Geological Society of Glasgow, v. 19, p. 288–332.

Lavoie, D., 2008, Appalachian foreland basin of Canada, *in* Miall, A., ed., The Sedimentary Basins of the United States and Canada, Volume 5: Amsterdam, Elsevier, p. 65–103.

Lespérance, P.J., and Sheehan, P.M., 1976, Brachiopods from the Hirnantian Stage (Ordovician–Silurian) at Percé, Quebec: Paleontology, v. 19, p. 719–731.

Li, R.Y., and Copper, P., 2006, Early Silurian (Llandovery) Orthhide Brachiopods from Anticosti Island, Eastern Canada: The O/S Extinction Recovery Fauna: Special Papers in Palaeontology 76, 80 p.

Logan, W.E., 1863, Geology of Canada. Geological Survey of Canada, Report of Progress from Its Commencement to 1863: Montreal, Dawson Brothers, 983 p.

Long, D.G.F., 2007, Tempestite frequency curves: a key to Late Ordovician and early Silurian subsidence, sea-level change, and orbital forcing in the Anticosti foreland basin, Quebec, Canada: Canadian Journal of Earth Sciences, v. 44, p. 413–431.

Long, D.G.F., and Copper, P., 1986, Stratigraphy of the Upper Ordovician upper Vaureal and Ellis Bay formations, eastern Anticosti Island, Quebec: Canadian Journal of Earth Sciences, v. 24, p. 1807–1820.

Macomber, R.W., 1970, Articulate brachiopods from the upper Bighorn Formation (Late Ordovician) of Wyoming: Journal of Paleontology, v. 44, p. 416–450.

Mauviel, A., and Desrochers, A., 2016, A high-resolution, continuous delta δ^{13}C record spanning the Ordovician–Silurian boundary on Anticosti Island, eastern Canada: Canadian Journal of Earth Sciences, v. 53, p. 795–801.

Mauviel, A., Sinnesael, M., and Desrochers, A., 2020, The stratigraphic and geochemical imprints of Late Ordovician glaciation on far-field neritic carbonates, Anticosti Island, eastern Canada: Palaeogeography, Palaeoclimatology, Palaeoecology, v. 543, n. 109579, https://doi.org/10.1016/j.palaeo.2019.109579

M'Coy, F., 1851, On some new Cambro–Silurian fossils: Annals and Magazine of Natural History, v. 8, p. 387–443.

Melou, M., 1987, Découverte de *Hirnantia sagittifera* (M' Coy, 1851) (Orthida, Brachiopoda) dans l'Ordovicien supirieur (Ashgillien) de l'extrémité occidentale du Massif Amoricain: Geobios, v. 20, p. 679–685.

Mergl, M., 1983, New brachiopods (Cambrian–Ordovician) from Algeria and Morocco (Mediterranean Provinces): Casopis pro Mineralogii a Geologii (Prague), v. 28, p. 337–348.

Modzalevskaya, T.L., 1985, Брахиоподы силура и раннего девона Европейской части СССР, Отряд Athyridida: Академия Наук СССР, Палеонтологический институт, 128 p. [in Russian]

Öpik, A.A., 1934, Uber Klitamboniten: Tartu University, Acta & Commentationes, ser. A, v. 26, 239 p.

Pinet, N., Keating, P., Lavoie, D., Dietrich, J., Duchesne, M.J., and Brake, V., 2012, Revisiting the Appalachian structural front and offshore Anticosti Basin (northern Gulf of St. Lawrence, Canada) by integrating old and new geophysical datasets: Marine and Petroleum Geology, v. 32, p. 50–62.

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.

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: Hefei, Anhui Science and Technology Publishing House, p. 111–176.

Rong, J.Y., and Cocks, L.R.M., 1994, True *Strophomena* and a revision of the classification and evolution of strophomenoid and 'strophodontid' brachiopods: Palaeontology, v. 37, p. 651–694.

Rong, J.Y., Chen, X., and Harper, D.A.T., 2002, The latest Ordovician *Hirnantia* fauna (Brachiopoda) in time and space: Lethaia, v. 35, p. 231–249.

Rong, J.Y., Huang, B., Zhan, R., and Harper, D.A.T., 2013, Latest Ordovician and earliest Silurian brachiopods succeeding the *Hirnantia* fauna in Southeast China: Special Papers in Palaeontology 90, 142 p.

Rong, J.Y., Harper, D.A.T., Huang, B., Li, R., Zhang, X., and Chen, D., 2020a, The latest Ordovician Hirnantian brachiopod faunas: new global insights: Earth-Science Reviews, v. 208, n. 103280, https://doi.org/10.1016/j.earscirev.2020.103280

Rong, J.Y., Aung, K.P., Zhan, R., Huang, B., Harper, D.A.T., Chen, D., Zhou, H.H., and Zhang, X.L., 2020b, The latest Ordovician *Hirnantia* brachiopod fauna of Myanmar: significance of new data from the Mandalay Region: Palaeoworld, v. 29, p. 1–30.

Sami, T., and Desrochers, A., 1992, Episodic sedimentation on an early Silurian, storm- dominated carbonate ramp, Becscie and Merrimack formations, Anticosti Island, Canada: Sedimentology, v. 39, p. 355–381.

Sanford, B.V., 1993, St. Lawrence Platform, *in* Wheeler, J.O., Scott, D.F., and Aitken, J.D., eds., Sedimentary Cover of the Craton in Canada: Geological Survey of Canada, Volume 5, p. 723–786.

Schuchert, C., and Cooper, G.A., 1931, Synopsis of the brachiopod genera of the suborders Orthoidea and Pentameroidea, with notes on the Telotremata: American Journal of Science, v. 22, p. 241–251.

Schuchert, C., and Cooper, G.A., 1932, Brachiopod genera of the suborders Orthoidea and Pentameroidea: Peabody Museum of Natural History Memoir, v. 4, 270 p.

Shaler, N.S., 1865, List of the Brachiopoda from the island of Anticosti sent by the Museum of Comparative Zoology to different institutions for exchange for other specimens, with annotations: Bulletin of the Museum of Comparative Zoology at Harvard College, v. 1, p. 61–70.

Sheehan, P.M., 1977, Late Ordovician and earliest Silurian meristellid brachiopods in Scandinavia: Journal of Paleontology, v. 51, p. 23–43.

Sheehan, P.M., 2001, The Late Ordovician mass extinction: Annual Review of Earth and Planetary Sciences, v. 29, p. 331–364.

Stott, C.A., and Jin, J., 2007, Rhynchonelliformean brachiopods from the Manitoulin Formation of Ontario, Canada: potential implications for the position of the Ordovician–Silurian boundary in cratonic North America: Acta Palaeontologica Sinica, v. 46, supplement, p. 449–549.

Suzuki, Y., Shiino, Y. and Bergström, J., 2009, Stratigraphy, carbonate facies and trilobite associations in the Hirnantian part of the Boda Limestone, Sweden: GFF, v. 131, p. 299–310.

Temple, J.T., 1965, Upper Ordovician brachiopods from Poland and Britain: Acta Palaeontologia Polonica, v. 10, p. 379–427.

Torsvik, T.H., and Cocks, L.R.M., 2016, Ordovician, *in* Earth History and Palaeogeography: Cambridge, Cambridge University Pres, p 101–123.

Troedsson, G.T., 1928, On the Middle and Upper Ordovician faunas of northern Greenland, Part 2: Meddelelser om Gronland, v. 72, 197 p.

Twenhofel, W.H., 1928, Geology of Anticosti Island: Geological Survey of Canada, Memoir 154, 481 p.

Ulrich E.O., and Cooper G.A., 1942, New genera of Ordovician brachiopods: Journal of Paleontology, v. 16, p. 620–626.

Villas, E., Lorenzo, S., and Gutiérrez-Marco, J.C., 1999, First record of a *Hirnantia* fauna from Spain, and its contribution to the Late Ordovician palaeogeography of northern Gondwana: Transactions of the Royal Society of Edinburgh: Earth Sciences, v. 89, p. 187–197.

Waagen, W., 1884, Salt Range fossils, Part 4: Brachiopoda: Palaeontologia Indica, v. 1, p. 329–770.

Wahlenberg, G., 1818, Petrificata telluris suecanae: Nova Acta Regia Societatis Scientiarium Uppsaliensis, v. 8, p. 1–116.

Wang, Y., 1949, Maquoketa Brachiopoda of Iowa: Geological Society of America, Memoir 42, 55 p.

Webby, B.D., 2002, Patterns of Ordovician reef development, *in* Kiessling, W., Flügel, E., and Golonka, J., eds., Phanerozoic Reef Patterns: SEPM Special Publications, v. 72, p. 129–180.

Williams, A., Carlson, S.J., Brunton, C.H.C., Holmer, L.E., Popov, L., 1996, A supra-ordinal classification of the Brachiopoda: Philosophical Transactions of the Royal Society B, v. 351, p. 1171–1193.

Wilson, A.E., 1945, Strophomena and its homomorphs *Trigrammaria* and *Microtrypa* from the Ottawa Limestone of the Ottawa–St. Lawrence lowlands: Transactions of the Royal Society of Canada, ser. 3, v. 39, p. 121–150.

Zuykov, M.A., and Harper, D.A.T., 2007, *Platystrophia* (Orthida) and new related Ordovician and early Silurian brachiopod genera: Estonian Journal of Science, v. 56, p. 11–34.

Accepted: 2 September 2022