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VIRGIANID BRACHIOPODS OF THE MICHIGAN BASIN, AND ITS IMPLICATIONS FOR POST-EXTINCTION DIVERSIFICATION OF THE SILURIAN PENTAMERIDE FAUNA IN LAURENTIA

JISUO JIN[1] , DONALD MIKULIC[2] & JOANNE KLUESSENDORF[†]

[1]Department of Earth Sciences, University of Western Ontario, London, ON N6A 5B7, Canada. E-mail: jjin@uwo.ca
[2]Weis Earth Science Museum, University of Wisconsin-Oshkosh, Fox Valley Campus, Menasha, Wisconsin, USA; mikulic@illinois.edu
[†] Deceased

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Abstract. Three virgianid genera are present in the Michigan Basin. The oldest, *Virgiana mayvillensis* Savage from the Mayville Dolomite, is upper Rhuddanian in age and coeval with the same species on Anticosti Island in eastern Canada. "*Virgiana*" *major* Savage, 1916, from the uppermost Lime Island Dolomite (uppermost Rhuddanian), has an incipient cruralium supported anteriorly by a low median ridge, for which *Virgianoides* gen. nov. is proposed in this study. *Platymerella* in the Elwood Formation (uppermost Rhuddanian) was the most southerly virgianid occurrence in the American mid-continent. The early evolution of the *Brevilamnulella-Viridita-Virgiana* lineage was represented by the early-middle Rhuddanian fossil record of Anticosti Island. Available fossil data indicate that the *Virgiana* invasion into intracratonic basins did not begin until late Rhuddanian time, represented by the excellent record of *V. mayvillensis* in the Michigan Basin, and *V. decussata* in the Hudson Bay and Williston basins. Despite its late arrival, virgianids thrived for a somewhat longer geological time in the Michigan Basin, represented by *Virgianoides* and *Platymerella* in the latest Rhuddanian, when virgianids largely became extinct in other basins of Laurentia.

Introduction

The usually large pentameride brachiopod shells of *Virgiana* were the first well-known marine shelly benthos of Silurian aspect to evolve after the Late Ordovicain mass extinction event. In the middle and late Rhuddanian, *Virgiana* became widespread in Laurentia, Siberia, and some of their neighbouring terranes (Fig. 1; see Torsvik & Cocks 2017 for base paleomap), forming a well-known, high-abundance, low-diversity, and sometimes monospecific benthic shelly community (e.g., Twenhofel 1914, 1928; Nikiforova & Andreeva 1960; Menakova 1964; Lopushinskaya 1976; Berry & Boucot 1970; Boucot 1975; Sheehan 1980; Modzalevskaya 1985; Johnson & Lescinsky 1986; Kovalevskiy et al. 1991; Beznosova 1994; Watkins 1994; Jin et al. 1996; Jin 2008). *Virgiana* has been preserved commonly as easily recognizable shell beds, making them highly useful biostratigraphic markers for the middle and upper Rhuddanian (Jin et al. 1993, 1999; Watkins & Kuglitsch 1997; see also Fig. 2 herein).

Since the initial reports of *Virgiana* from the Michigan Basin, especially those from the lower Llandovery Mayville Dolomite of Wisconsin (Fig. 2), there has been a lack of information on morphological details of the two species, *Virgiana mayvillensis* Savage, 1916, and "*Virgiana*" *major* Savage, 1916. This is mainly because these shells in the Michigan Basin, from Wisconsin to Manitoulin Island (Onta-

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rio, Canada), are preserved exclusively in dolomite, often as moulds in weathered outcrops when the shell morphology can be observed. This problem was noted clearly by Ehlers (1973, p. 49) that "a very careful discrimination of the various species of *Virgiana* and further study of more extensive collections of fossil from the entire Mayville Dolomite will be necessary to determine the exact direction of migration of the Mayville fauna". Such an understanding will be key to biostratigraphic correlations of various *Virgiana* beds in the Anticosti, Michigan, Hudson Bay, and Williston basin across Laurentia. For example, both Twenhofel (1928) and Ehlers (1973) proposed that the *Virgiana barrandei* beds in the upper Becscie Formation of Anticosti Island were older than the *Virgiana*-bearing strata in the Michigan Basin. This interpretation was supported by the subsequent recognition of *Virgiana mayvillensis* in the Merrimack Formation that overlies the Becscie Formation (Copper & Long 1989; Jin & Copper 2000; see Fig. 2).

Much confusion remains regarding the identity of some finely ribbed forms of *Virgiana* from the Mayville Dolomite of Wisconsin and the Dyer Bay Formation of Manitoulin Island. This problem was partly exacerbated by the original illustration of "*Virgiana*" *major*, described by Savage (1916, p. 322, pl. 17, figs. 1, 2) as a finely ribbed species, but represented by a shell with limited details on shell ribbing and internal structures. Ehlers (1973, p. 75) considered some Mayville Dolomite shells with moderately coarse to fine ribs to be *Virgiana decussata*. This formed the basis for his preliminary biostratigraphic and paleogeographic interpretations of paleobiogeographic connections between the Michigan and the "Arctic" basins (i.e. Hudson Bay and Williston basins, where *V. decussata* predominates the Rhuddanian) in terms seaways and dispersal of benthic shelly faunas.

In recent years, new virgianid collections have been made separately by the authors from the Mayville Dolomite of Wisconsin, the Fisher Branch Formation of Manitoba, and the lower Severn River Formation of the Hudson Bay Lowlands. It is, therefore, the focus of this study to bring these collections together for a comparative study and to investigate the taxonomic identity of the finely ribbed virgianids in the Michigan Basin, as well as its biostratigraphic and paleobiogeographic implications.

Geological and stratigraphical background

Early Silurian rocks are extensively exposed along the cliff face of the Niagara Escarpment in northeastern and east-central Wisconsin. These exposures are, however, geographically and stratigraphically discontinuous and at no single location is the entire lower Silurian exposed. In addition, with the noteworthy exception of two locally thick intervals dominated by virgianids, the Silurian strata here are in general poorly fossiliferous. Although these outcrops have been studied for more than 170 years, the lack of sufficient fossiliferous zones has made it difficult to correlate these lower Silurian strata with those of other regions.

Among the earliest descriptions of the lower Silurian rocks of northeastern Wisconsin, Hall, (1851) identified carbonate outcrops along the eastern shore of Green Bay near Sturgeon Bay, and considered it equivalent to the Clinton Group of the New York Silurian. Some of the evidence for this interpretation was based on finding typical fossils from this group, of which he specifically mentions the occurrence of strata "charged with casts of *Pentamerus oblongus*." It is now known, however, that the brachiopods he found in these outcrops are virgianids but Hall (1851) provided the earliest report of their occurrence in Wisconsin. Chamberlin (1877) was the first to make a comprehensive study of lower Silurian dolomites in eastern Wisconsin and subdivided these rocks into several units ("beds") based both on their lithology and fossil contents. He did not follow Hall's assignment of the lower Silurian dolomites in the region to the Clinton group but instead placed them higher in the Silurian as "subdivisions" of the overlying Niagara limestone. He named the lowest unit of his Niagara group the "Mayville beds" based on exposures he examined south of Mayville, Wisconsin. The highest strata in the Mayville beds were described as a coarse and thick layer "containing many obscure casts of a *Pentamerus* (*Gypidula*), very similar to the species *occidentalis*." Above the Mayville beds he described well-bedded and even-textured building stone strata, which he named the "Byron beds." This relationship in which the upper Mayville has a layer of abundant "pentamerids" and is overlain by the building stone strata of the Byron has been up until recently used by most others working on or discussing the Wisconsin Silurian.

Two specimens of "*Pentamerus occidentalis*" collected during Chamberlin's work were later included in Whitfield (1882, pls. 17 and 23) in a description of fossils occurring in the Guelph Limestone of Wisconsin. The figure legend for the specimen on plate 23 states it is from the Mayville beds at Williamstown although the plate carries the caption "Guelph Limestone." Mayville beds are well exposed at Williamstown, which is just north of the Mayville type section, but Guelph strata do not occur in this part of the state. It appears that these specimens were mistakenly attributed to the Guelph by Whitfield (1882).

Savage (1916) made important observations on what he called the Mayville Limestone of Wisconsin along with its conspicuous brachiopod horizon. Savage described the Silurian sections exposed in the quarries at Mayville and Marblehead in Fond du Lac County, Wisconsin, and recognized that the pentamerids found in the upper beds of the Mayville Limestone at both localities were *Virgiana*, not *Pentamerus*. He further determined that the Mayville Limestone was not equivalent in age to either the Clinton or the Niagara strata, and he correlated the Wisconsin *Virgiana* beds with those in the Becscie Formation of Anticosti Island. Most importantly however, he erected new species of *Virgiana*, with *V. barrandei* var. *mayvillensis* occurring in the Mayville limestone at Mayville while *V. barrandei* var. *major* is found in what he thought were the same Mayville beds at Marblehead.

Following Savage's (1916) work, most authors (e.g., Harris & Waldheuter 1996; Harris et al. 1996, 1998; Watkins 1994; Watkins & Kuglitsch 1997) continued to recognize only one *Virgiana* horizon in the region. It was assumed to always mark the top of the Mayville Dolomite and was overlain by the Byron Dolomite at both the Mayville and Marblehead quarries along with many other localities in the Wisconsin. In their work on the lower Silurian rocks of Wisconsin, however, Mikulic & Kluessendorf (1998, 2009, 2010) and Kluessendorf & Mikulic (2004) demonstrated that the Mayville and Marblehead sections are not time equivalent and represent two successive depositional sequences both starting with a virgianid rich horizon. The first sequence includes the virgianid horizon at the top of the Mayville Dolomite which is overlain by laminites of the Byron Dolomite. This virgianid horizon occurs as a biostromal coquina or in a zone around large algal mounds. Overlying the Byron Dolomite is the base of the next sequence which is represented by the widespread, bank-like virgianid coquinas of the Lime Island Dolomite which in turn is overlain by laminites of the Burnt Bluff Group. The depositional pattern, represented by these pentamerid shell beds to laminite cycles, indicates a shallowing-upward succession from subtidal to intertidal/supratidal depositional environments, in which prograding tidal flats cap the sequence (Kluessendorf & Mikulic 2004).

Savage (1916) recognized that the Mayville and Marblehead sections had different virgianid species and the subsequent recognition of the successive relationship of these sections provides an explanation for his observations. Both of these virgianid horizons extend north from east-central Wisconsin but no virgianids are found to the south through the Milwaukee area, although similar lithologies/environments are present. Southwards, *Platymerella* first occurs in Kenosha County, Wisconsin, at about the same horizon as the virgianid beds to the north, and characterizes this part of the lower Llandovery strata to the south through Illinois.

Materials and methods

Materials used for this study include the following collections:

Virgiana mayvillensis, sample MPM34700, Mayville Limestone Quarry 43.448056°N, 88.532175°W (centre of the quarry), Dodge County, Wisconsin; Mayville Formation; 9 small blocks of coquina, 7 isolated shells (including 3 photographed).

Virgiana mayvillensis, sample #712012; Hanke Quarry, near Mayville, Wisconsin; 6 small blocks of coquina, and more than 30 isolated but mostly incomplete valves. 43.443706°N, 88.512169°W.

Virgiana mayvillensis, Mayville White Lime Quarry, Mayville, Dodge County; Mayville Formation; 3 specimens. 43.448056°N, 88.532175°W (centre of the quarry).

Virgiana sp., one slab from top of Rademann Quarry, near Hamiltion, south of Fond du Lac, Wisconsin; 43.693420°N, 88.434457°W.

Virgiana "*decussata*", sample #3773, top of Mayville Formation, Mayville, Dodge County, Wisconsin, 5 specimens. 43.448056°N, 88.532175°W (centre of the quarry).

Virgianoides major, sample #9-06, Marblehead (43.70426°N, 88.388255°W), top part of Mayville Dolomite, Wisconsin. 43.703096°N, 88.386900°W (centre of the quarry).

All the virgianid material from Wisconsin consists of dolomitized shells in a dolostone matrix. Natural weathering has made some of the shell material preferentially soft and powdery, producing partial internal moulds or steinkerns. The internal structures (spondylium and hinge plates) were reproduced using a silicon-based moulding putty as a casting medium, similar to the traditional technique of liquid latex rubber replication.

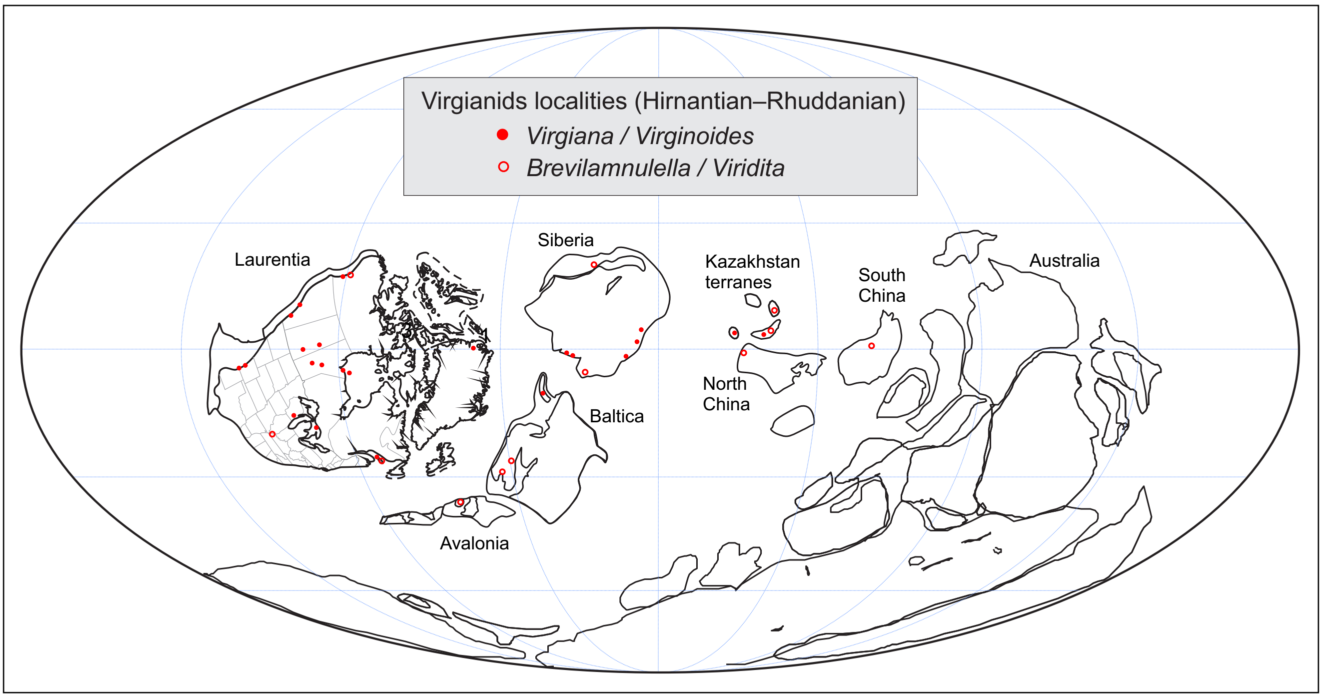

Fig. 1 - Paleogeographic occurrences of *Brevilamnulella*, *Viridita*, *Virgiana*, and *Virginoides* across the Ordovician–Silurian boundary interval (mainly Hirnantian–Rhuddanian). See text for details of occurrences. Base paleomap modified from Torsvik and Cocks (2017).

Repositories and institutional abbreviations

Figured specimens used in this study are housed in the Field Museum of Natural History (FMNH-PE), University of Chicago, Chicago, Illinois. Other materials examined during this study are in the following repositories: Milwaukee Public Museum (MPM), Milwaukee, Wisconsin; University of Illinois at Champaign-Urbana (UI), Illinois.

Paleoenvironmental and paleobiogeographical implications of the Michigan-basin *Virgiana* fauna

Large-shelled pentamerides constituted perhaps the most characteristic and paleoecologically significant marine shell benthos of the Silurian, particularly dominant in benthic shelly communities in carbonate shelves and platforms worldwide (Fig. 1). The *Virgiana* fauna of Laurentia was the earliest occurrence of such "Silurian-type" pentamerides, with its origin traceable to the Hirnantian *Brevilamnullela* and the earliest Rhuddanian *Viridita*, both being common in the tropical epeiric seas of eastern Laurentia (Fig. 2; see also Amsden 1974). Fossil data available hitherto suggest that eastern Laurentia was a hotspot for virgianid recovery and radiation starting from the earliest Rhuddanian because of its well-preserved fossil record of the *Brevilamnulella-Viridita-Virgiana* lineage (Jin & Copper 2010; Rasmussen & Harper 2011). The only other known record of the pre-*Virgiana* form of the Rhuddanian *Viridita* is *V. adakia* (Pershina & Beznosova *in* Beznosova 1985) from the basal Dzhagal beds, Yarenii horizon (Rhuddanian), northern Ural Mountains (see also Beznosova 1994).

The *Virgiana* paleocommunity

Boucot (1975) initially assigned the *Virgiana* brachiopod community to a rough-water Benthic Assemblage 3 (upper BA-3), equivalent to the mid-shelf *Pentamerus* Community of Ziegler (1965), interpreted to have lived in mid-shelf settings of moderate water depth. In pericratonic carbonate depositional settings, this interpretation has been supported by the *Virgiana barrandei* community of the Becscie Formation of Anticosti Island (Jin 2008), where *Virgiana* shell beds showing stacked hummocky cross stratification, indicative of deposition between fair-weather wave base and storm wave base (Fig. 3). The *Virgiana* community, however, was not confined to the BA-3 setting. The *Virgiana mayvillensis* community, preserved in the recessive-weathering, calcareous shale and micritic mudstone of the Merrimack Formation of Anticosti Island, was interpreted to have lived in a deeper-water (upper BA4) environment. On the other hand, the *Virgiana decussata* community in the basal Severn River Formation, often with well-preserved

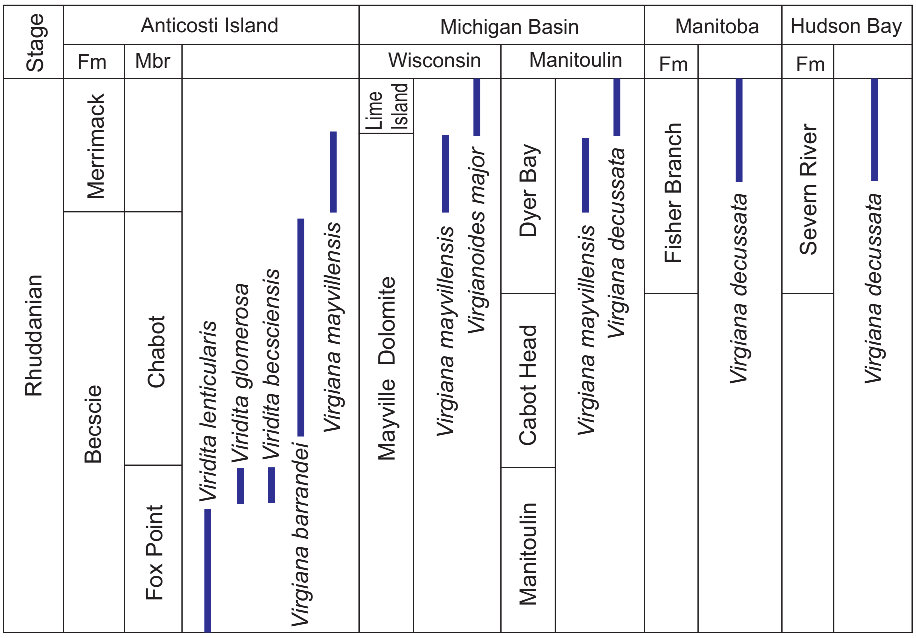

Fig. 2 - Stratigraphic ranges of *Virgiana* and closed related taxa in Laurentia. Note the earlier appearances of virgianids in the peri-cratonic Anticosti basin compared to those in inland basins.

shells in situ in the Churchill area, are found to be quite common in localities within 50–500 m of the early Silurian rocky shoreline. Such a paleo-shoreline is interpreted have been subaerially exposed because of the wave scours infilled by a mixture of rock fragments from the Precambrian rocky shore and uppermost Ordovician-lower Silurian carbonates and fossils (nautiloids, corals, and brachiopods). Such shoreline exposures made up of Precambrian quartzite have been termed the "Jens Munk Archipelago" by Nelson and Johnson (2002). This clearly demonstrates that *Virgiana* shells could thrive in relatively shallow-water very close to the shoreline in the Hudson Bay Basin. This may have been possible because the northern Hudson Bay Basin was positioned close to the paleo-equator, where severe storms would be rare (Jin et al. 2013). This implies that the distribution of *Virgiana* shelly community was controlled more by water turbulence levels than by water depth or distance from the shoreline, as implied by some previous interpretations of Ziegler's (1965) brachiopod communities or Boucot's (1975) benthic assemblages.

In the Michigan Basin, well-exposed *Virgiana* shell beds on Manitoulin Island (Ice Lake area, northern margin of the basin) are also characterized by coquinas dominated by disarticulated valves, separated by thin carbonate mud drapes, with well-developed hummocky cross stratification (Fig. 3). This is similar to the *Virgiana barrandei* shell beds of Anticosti Island, indicative of deposition and accumulation between fair-weather and storm wave bases, in agreement with Boucot's (1975) rough-water upper BA3 interpretation. The *Virgiana mayvillensis* shell packstones in the upper Mayville Dolomite were interpreted by Watkins (1994) to have accumulated in even shallower-water settings above the fair-weather wave base, as indicated by predominant disarticulation and common breakage of the shells, winnowed into a clast-supported coquina fabric. Kluessendorf & Mikulic (2004) reported the virgianid beds of the Lime Island Dolomite at Marblehead as packstone or rudstone, with common to abundant disarticulated shells. The individual valves are randomly orientated, and in places, are imbricated or telescoped. Individual shells are approximately 1–5 cm in length and do not show recognizable sorting parallel to bedding plane. Some strata appear to be normally graded, however, either by size or abundance, with larger or more densely packed valves at the base. These virgianids lived in sub-tidal settings where near-monospecific composition of the brachiopod fauna and low diversity of the biota in general suggests that living conditions were somewhat stressed. Certain features of these deposits (e.g., disarticulation, imbrication, and telescoping of valves, grading of bioclasts, scoured basal contacts) indicate that the shells were deposited rapidly under high energy conditions, most likely reworked by severe storms, as the mud-sized sediment fraction was not winnowed out completely. In their study of the related Lime Island Dolomite at Eagle Bluff

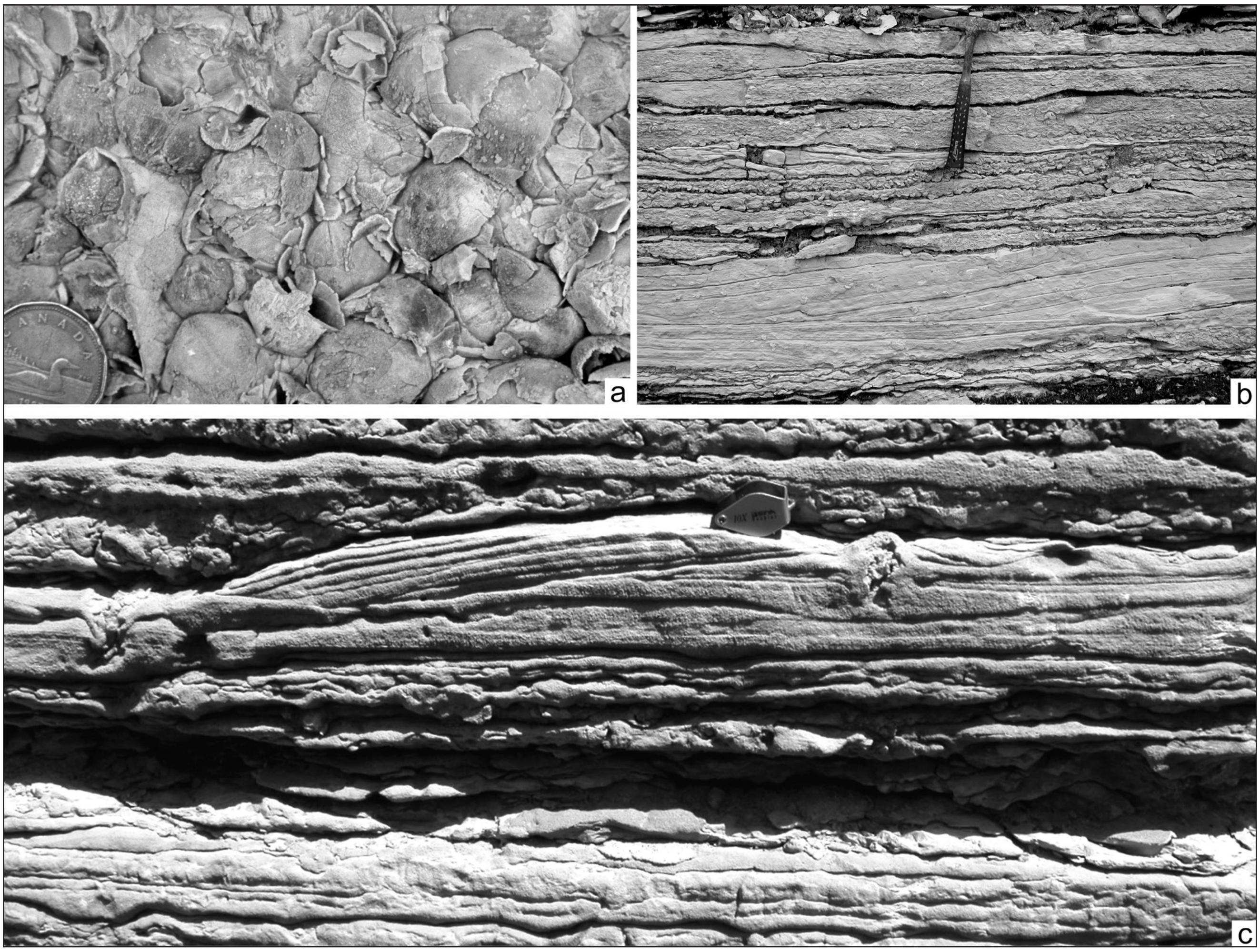

Fig. 3 - *Virgiana* shell coquina accumulated as severe storm deposits, as indicated by hummocky cross stratification (HCS), with shell concentrations covered by mud drapes. a-b) *V. barrandei* shell beds, Chabot Member, Becscie Formation, Anticosti Island (locality A1509; see Jin 2008). c) *Virgiana* shell beds, Dyer Bay Formation, Roadcut section along highway 540 near Ice Lake (45.896766°N, 82.413505°W), Manitoulin Island.

Lighthouse to the north in Door County, Mikulic & Kluessendorf (2010) reported the occurrence of microbial-algal laminites and mounding, laminoid fenestrae, and mud cracks in strata that underlie, overlie, or interbedded with the virgianid strata. These sedimentary structures indicate an intertidal-supratidal depositional environment, probably susceptible to substantial salinity fluctuations.

Virgiana paleobiogeography

A the global scale, the paleogeographic distribution of the Rhuddanian *Virgiana* fauna was closely associated with that of its ancestral *Brevilamnulella* in the Hirnantian, although *Brevilamnulella* spread across a greater number of tectonic plates (Fig. 1). During the latest Ordovician, *Brevilamulella* occurred in Laurentia (Amsden 1974; Jin & Chatterton 1997), Avalonia (Temple 1987), Baltica (Cocks 1982; Rasmussen et al. 2010); Siberia and peri-Siberian terranes (Rozman 1978; Oradovskaya 1983; Kulkov & Severgina 1989); Kazakhstan terranes (Sapelnikov & Rukavishnikova 1975; Menakova 1984, 1991), South China and North China (Rong et al. 2008). All the occurrences are confined to shallow carbonate facies in the paleotropical regions, with greater abundance towards the paleoequator. After the end-Hirnantian extinction event, *Brevilamnulella* disappeared from most of the regions listed above, with the genus itself or its immediate descendent *Viridita* surviving into the early Rhuddanian in eastern Laurentia, Avalonia (Welsh borderlands), and Timan (Beznosova 1994; Jin & Copper 2000, 2010).

The re-diversification and paleogeographic expansion of virgianids started in the middle Rhuddanian and culminated in the late Rhuddanian. The fossil record hitherto available suggests that eastern Laurentia was at least part of an evolutionary hotspot of virgianids. Whereas the rich and diverse virgianids of North Greenland remain to be systematically studied (Hurst & Sheehan 1982), the abundant fossils of the *Viridita-Virgiania* lineage from Anticosti Island (Jin & Copper 2010) provide a detailed record on both the timing and process of its evolution from throughout the Rhuddanian. The occurrences of the early Rhuddanian *Viridita* in eastern Laurentia and Timan (boreal Urals, paleogeogaphically northern Baltica) indicate an early virgianid faunal connection between these two tectonic plates, as this earliest Silurian form has not been found elsewhere. By the mid-late Rhuddanian, *Virgiana barrandei* and other congeneric species became abundant throughout much of Laurentia (for a summary see Jin & Copper 2000), Timan, the Tunguska region and Verkhoyansk margin of Siberia, and other small terranes (e.g. Tadzhikistan; Nikiforova & Andreeva 1961; Menakova 1964; Kovalevskii et al. 1991; Beznosova 1994), achieving a semi-cosmopolitan distribution.

In Laurentia, the highest abundance and diversity and greatest stratigraphic range of *Virgiana* are found in peri-cratonic settings, such as the Anticosti Basin and North Greenland (Hurst & Sheehan 1982; Jin & Copper 2000, 2010). The occurrences tend to become increasingly sporadic paleogeographically and episodic stratigraphically in intracratonic seas, suggesting periodic invasions from continental margin to inland basins. This is further supported by the greater range of water depth occupied by various species of *Virgiana* in the Anticosti Basin (Jin 2008), but predominantly near-shore, shallow-water settings in inland basin. With each marine transgression, *Virgiana* probably relied on their rapid growth rate to colonize newly created shallow-water habitats in inland seas most successfully, resulting in the widespread shell beds we see today in the Michigan, Hudson Bay, Williston, and Franklinian basin.

Systematic paleontology

Order **Pentamerida** Schuchert & Cooper, 1931
Suborder **Pentameridina** Schuchert & Cooper, 1931
Superfamily Pentameroidea M'Coy, 1844

Family Virgianidae Boucot & Amsden, 1963

Genus *Virgiana* Twenhofel, 1914

Type species - *Pentamerus Barrandi* [sic] Billings, 1857, p. 296. Becscie River Bay, Becscie Formation (mid-Rhuddanian), Anticosti Island, Quebec.

Diagnosis (*sensu* Jin & Copper 2000): Shell medium to large, elongate, suboval, ventribiconvex, weakly to strongly costate, with tumid ventral umbo and incurved beak; ventral sulcus and dorsal fold generally present, better developed posteriorly; spondylium relatively long and shallow, supported posteriorly by short median septum, bearing comb structure distally; outer plates usually shorter than inner plates; brachial processes rod-like or ribbon-like.

Virgiana mayvillensis Savage, 1916

Fig. 4

1916 *Virgiana barrandei* var. *mayvillensis* Savage, p. 321, pl. 17, figs. 3-7.
1971 *Virgiana mayvillensis*; Boucot et al., p. 273, pl. 1, figs. 5-11; pl. 6, fig. 13.
1971 *Virgiana barrandi* (Billings); Boucot et al., p. 272, pl. 1, figs. 1-4.
1973 *Virgiana decussata*; Ehlers (*non* Whiteaves, 1891), p. 74, pl. 11, figs. 28, 29, 33–35 (*non* figs. 30–32).
1985 *Virgiana barrandei*; Sapelnikov (*non* Billings, 1857), p. 29, pl. 6, figs. 3a, b, v.
1996 *Virgiana mayvillensis*; Jin et al., p. 602, figs. 3g-m; p. 603, figs. 4a–h.
2000 *Virgiana mayvillensis*; Jin and Copper, p. 31, pl. 7, figs. 5-17.

Types: Three specimens were originally illustrated from the "upper part of the Mayville Limestone; near Mayville, Wisconsin" (Savage 1916, p. 324), uppermost Rhuddanian (Watkins & Kuglitsch, 1997).

Other material: See Materials and methods section.

Description (topotype material, new collection). Shell large, elongate oval in outline, ventribiconvex, with relatively large shells (sternkeins) reaching 50 mm in length, 37 mm in width, and 30 mm in thickness (Fig. 4). Maximum shell width slightly anterior of the mid-length of shell. Hinge line short and curved. Interarea absent; delthyrium open; palintrope poorly delimited. Anterior commissure rectimarginate. Ventral valve strongly and uniformly convex, with high, smoothly arched ventral umbo extending about 17 mm above hinge line in large shells; beak incurved, nearly oppressed onto dorsal umbo. Dorsal valve moderately convex and half as deep as ventral valve, without clearly defined fold or sulcus, although antero-medial portion of valve having tendency to flatten compared to dorsal umbo. Shell strongly costate, with rounded ribs increasing in number anteriorly by bifurcation or intercalation, reaching 7 or 8 per 10 mm in anterior part of shell (Fig. 4a, e, h).

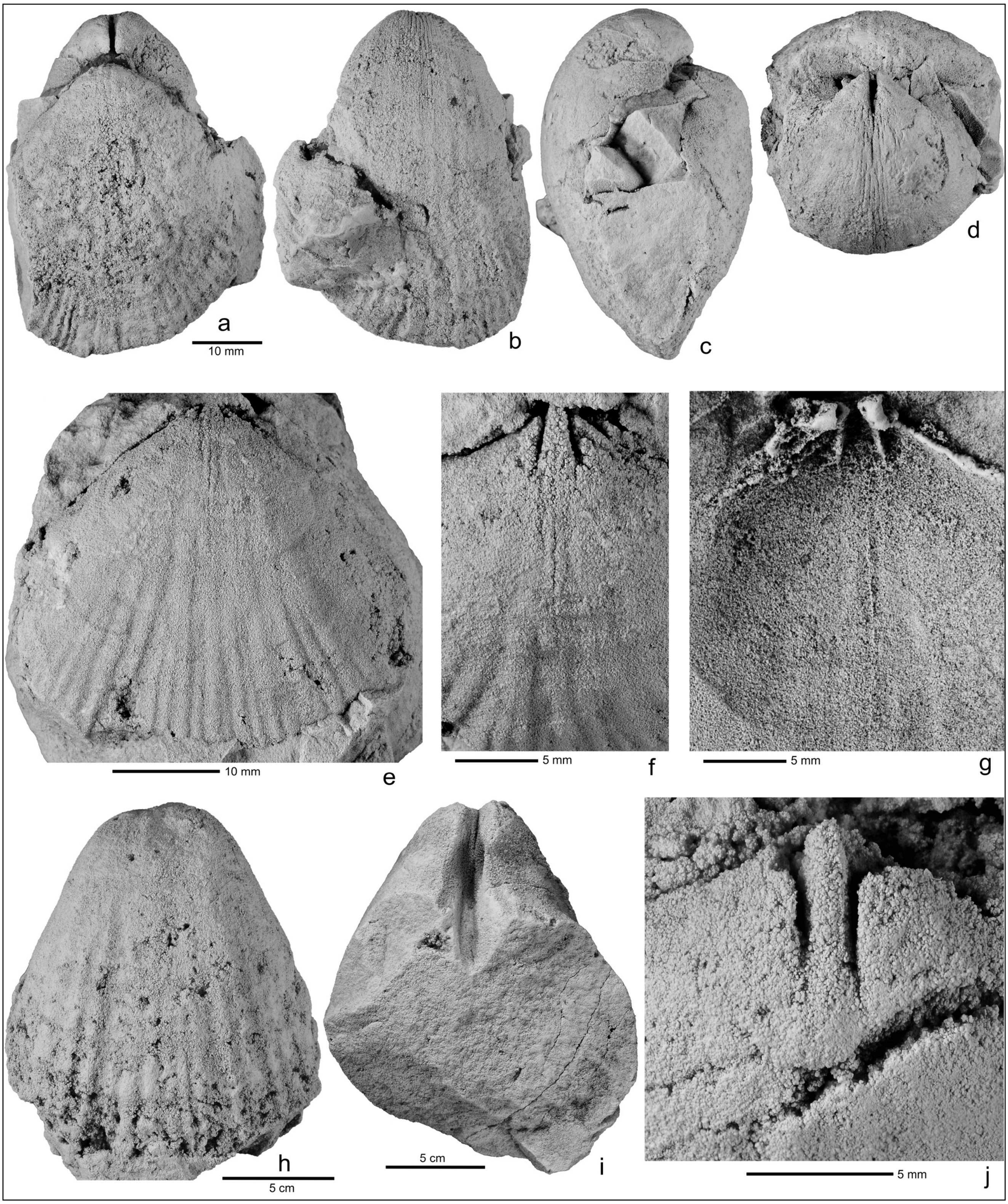

Fig. 4 - *Virgiana mayvillensis* Savage, 1916, topotype material from Mayville Dolomite, Mayville Limestone Quarry, Dodge County, Wisconsin (MPM locality 34700). a-d) FMNH-PE 91170, dorsal, ventral, lateral, and posterior views of average-sized shell steinkern. e-g) FMNH-PE 91171, internal mould of dorsal valve, enlarged view of cardinalia, and silicon rubber cast to show discrete hinge plates. h) FMNH-PE 91172, internal mould of ventral valve showing strong costae. i) FMNH-PE 99173, internal mould of ventral valve showing relatively large spondylium. j) FMNH-PE 99174, apical view of internal mould of dorsal valve, showing discrete, subparallel inner hinge plates.

Spondylium broadly V-shaped (Fig. 4i), with about half of its length extended anterior of hinge line, supported by median septum in apical area only, becoming free anteriorly. Median septum short, thick, and relatively high in umbonal area, becoming rapidly thinner and lower distally, generally confined to apical area posterior of hinge line. Teeth very weak.

Inner hinge plates short, rarely exceeding 6 mm in sagittal length, discrete, diverging slightly from each other at junctions with valve floor from posterior to anterior (Fig. 4e-g, j). Outer hinge plates longer than inner hinge plates. Crura rod-shaped. Adductor muscle scars slender, developed anterior of hinge plates, divided by incipient medial ridge (Fig. 4f).

Ovarian pits strongly developed on inner surface in umbonal portions of both valves.

Remarks. Between the two subspecies of *Virgiana barrandei* established by Savage (1916), based on materials reportedly from the "upper Mayville Dolomite" in Wisconsin, "*V. barrandei* var. *mayvillensis*" was described as a strongly ribbed shell than "*V. barrandei* var. *major*", among other morphological differences. The number and strength of the ribs in *V. mayvillensis*, however, vary greatly, partly due to the variable degree of rib bifurcation in relatively large shells. The shell illustrated Savage (1916, pl. 17, figs. 3, 6, 7) clearly has rather numerous and somewhat weakened ribbing compared to the generally coarse and strong ribs of the species. As noted by Savage (1916, p. 321), there is a wide range of variation in the shell size of *V. mayvillensis*, with the type specimen being average-sized for the species, measuring 57 mm in length, 30 mm in width, 32 mm in thickness. The large new collection generally supports these early observations - the large forms of this species tend to be strongly elongate and the dorsal valve and its umbo strongly convex.

Ehlers (1973, p. 74-75, p. 75, pl. 11, fig. 31) assigned some Mayville Dolomites shells to *Virgiana decussata* and compared them to a shell from the Fisher Branch Formation of Manitoba. The shape and ribbing of the material figured from the Mayville Dolomite, however, fit well within the range of *V. mayvillensis* described and illustrated by Savage (1916, pl. 17, figs. 3, 6, 7; compare with Ehlers 1973, pl. 11, fig. 28, 29, 22-35). *V. decussata* from Manitoba and the Hudson Bay region is distinguished by a much larger adult shell, with very fine (>10 per 10 mm) and usually faint ribbing from posterior to anterior parts of the shell, and an extremely prominent ventral umbo and beak (Jin et al. 1993). *V. mayvillensis* from both Wisconsin and Anticosti Island has much stronger and coarser (commonly 7 or 8 per 10 mm) ribs over the entire shell.

Genus *Virgianoides* gen. n.

Type species - *Virgiana barrandei* var. *major* Savage, 1916 (see below).

Diagnosis: Large, ventribiconvex shells of virgianids, with posteriorly discrete inner hinge plates converging anteriorly onto low median ridge to form incipient cruralium.

Etymology: After *Virgiana*, its closely related genus.

Discussion. The new genus is the only genus so far known in the Family Virgianidae to develop an incipient cruralium. Some other virgianids may have basomedially inclined inner hinge plates, but they remain discrete along their entire length and do not unite at the base to form a cruralium. So far, the new genus includes the type species only. In the type species of *Virgiana*, the inner hinge plates are predominantly subparallel in transverse section (Jin & Copper 2000, p. 30, text-fig. 15). In *Virgiana decussata* from the Hudson Bay and Williston basins, the inner hinge plates are predominantly discrete, although their orientation is variable, ranging from subparallel, to basomedially inclined (but they are not united towards the valve floor).

Virgianoides major (Savage, 1916), new combination

Fig. 5, 6

1916 *Virgiana barrandei* var. *major* Savage, p. 322, pl. 17, figs. 1, 2.
1973 *Virgiana decussata*; (*non* Whiteaves); Ehlers, p. 74, pl. 11, fig. 32 only.

Types: One internal mould of a conjoined shell from the "upper part of the Mayville Limestone; Marblehead, Wisconsin" (Savage 1916, p. 324), uppermost Rhuddanian (Watkins & Kuglitsch 1997). Recent stratigraphic study assigns the *V. major* beds in the Marblehead area to the Lime Island Formation (uppermost Rhuddanian; Mikulic & Kluessendorf 2009, 2010).

Other material: See Materials and methods section.

Description (topotype material). Shell large, elongate-oval, ventribiconvex, with maximum width at about two-thirds shell length from apex. Ventral valve strongly convex, with broad, tumid, arched and rostrate umbo and incurved beak; ventral medial fold variously developed, slightly broader and bet-

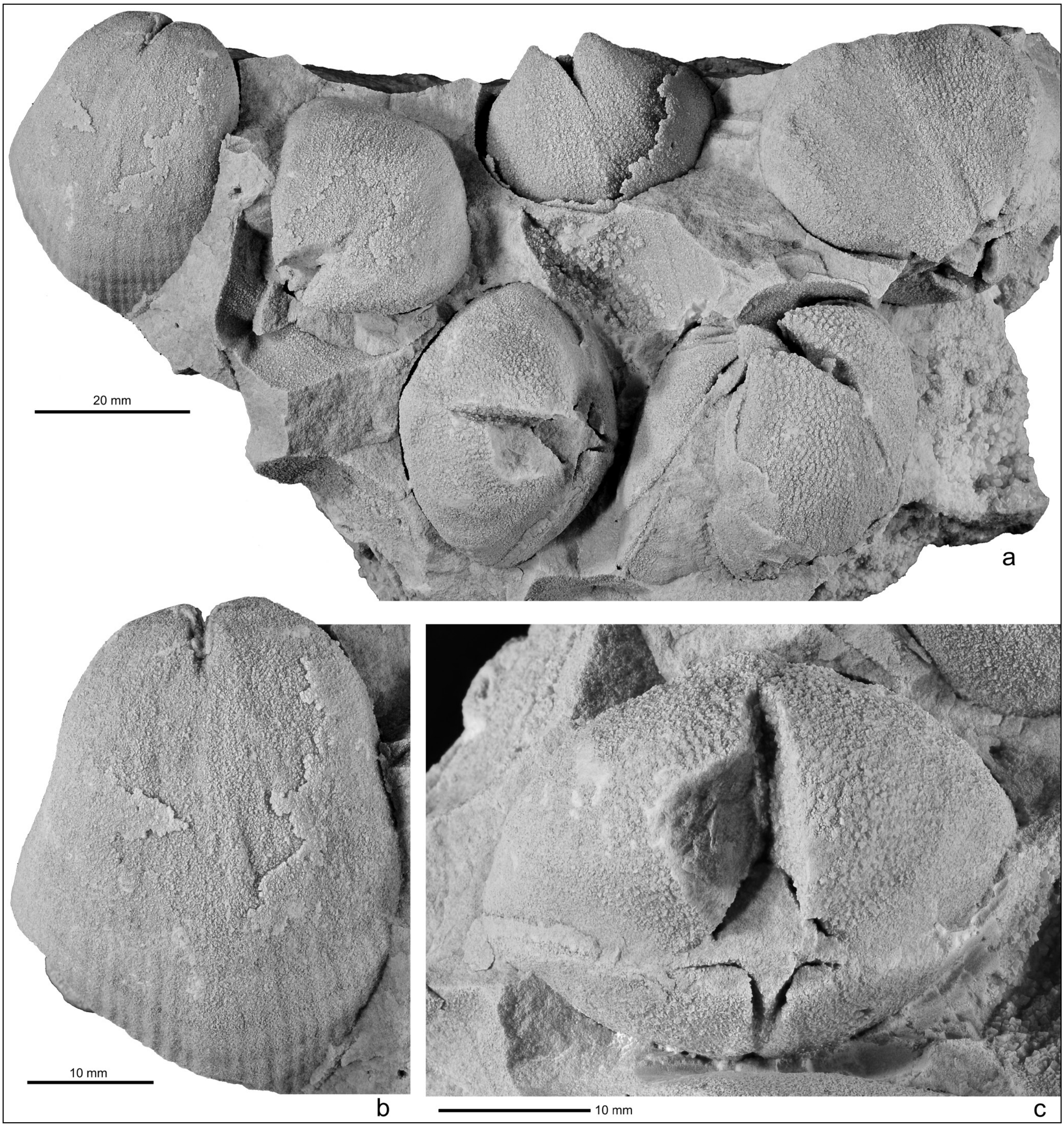

Fig. 5 - *Virgianoides major* (Savage, 1916) new combination, topotype material from the Lime Island Dolomite at Marblehead Quarry, Marblehead, Wisconsin (Sample 9-06), approximately 37 m (122 ft) above the *Virgiana mayvillensis* horizon in the Mayville area (see Fig. 4). a) FMNH-PE 91175, block of shell coquina preserved as internal mounds, with mixed conjoined shells and disarticulated valves. b) Further enlarged view of ventral valve in coquina as in image (a), showing relatively fine costae, and strong median septum. c) Posterior part of conjoined shell in coquina as in image (a), showing V-shaped spondylium and posteriorly discrete and anteriorly united inner hinge plates. Note impressions of well developed ovarian pits in umbonal parts of ventral valves.

ter delimited anteriorly in some shells. Dorsal valve much less convex, attaining less than one-third of ventral-valve depth; dorsal umbonal area moderately to weakly convex; antero-medial portion of dorsal valve flattened, bearing gentle medial depression. Costae relatively fine, faint, averaging 10 per 10 mm, increasing anteriorly by bifurcation and intercalation.

Spondylium broadly V-shaped in transverse section in its posterior portion (Figs. 5c, 6), with depth approximately equal to opening; median septum posteriorly strong, high, supporting spondylium, becoming lower, thinner, and free anteriorly, exten-

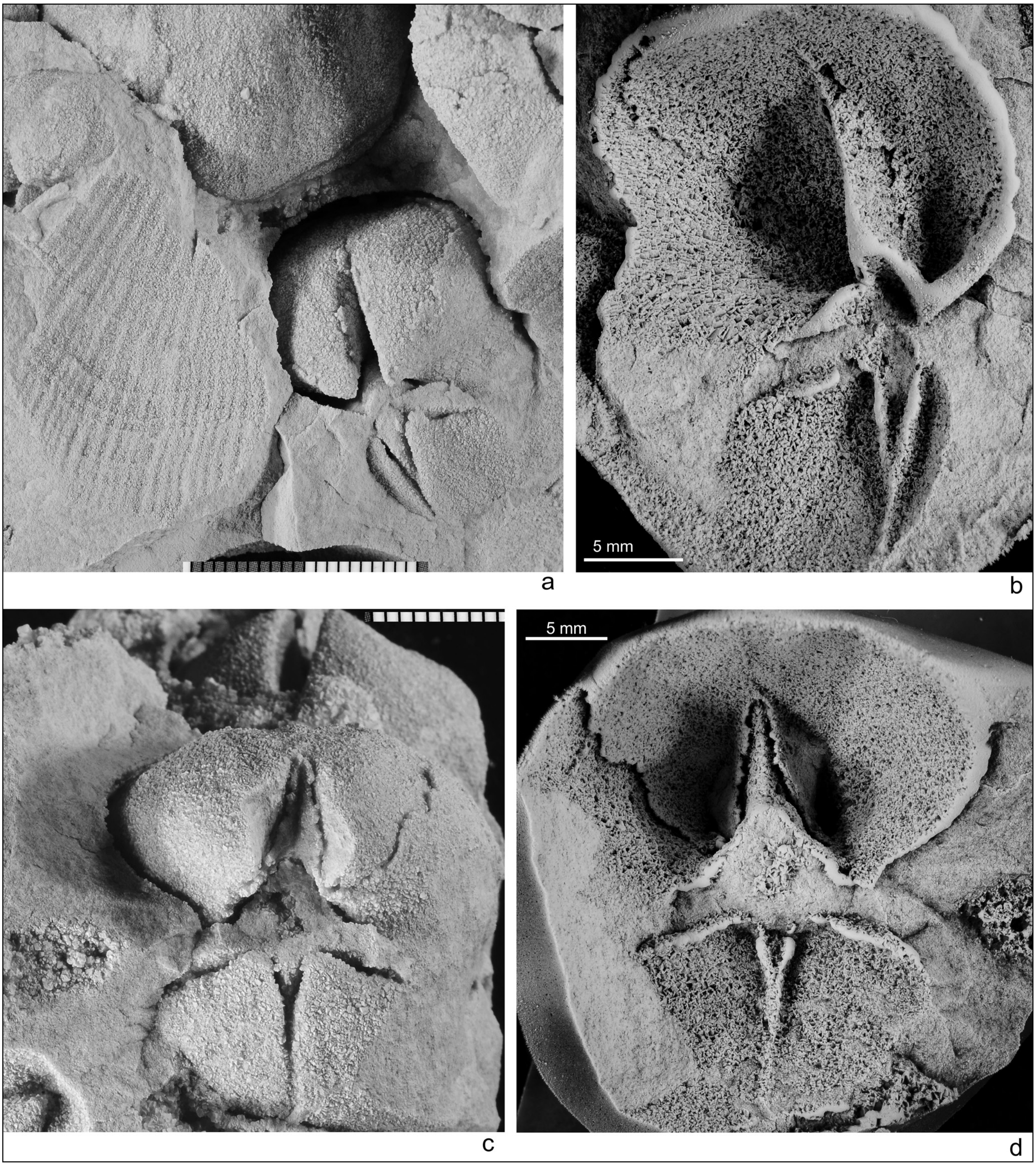

Fig. 6 - *Virgianoides major* (Savage, 1916) new combination, topotype material from the Lime Island Dolomite at Marblehead Quarry, Marblehead, Wisconsin (Sample 9-06). a-b) FMNH-PE 91176, internal mould and its silicon rubber cast of conjoined shell, showing strong median septum and incipient cruralium; note external mould to the left, showing relatively fine costae. c-d) FMNH-PE 91177, another internal mould and its silicon rubber cast showing similar spondylium and cruralium. Thicks of scale bars in (a) and (c) are in mm.

ding for about one-fourth of sagittal length of shell (or one-fifth of linear length from shell apex to anterior margin), decreasing in height distally to become low ridge and forming wider gap from its ventral edge to base of spondylium.

Inner hinge plates discrete posteriorly, basomadially inclined in transverse section, becoming united onto low median ridge anteriorly for form cruralium (Figs. 5c, 6a-d). Crural bases and crura not observable in material preserved as moulds.

Remarks. A large collection of new topotype material of this species from the Marblehead Quarry of Wisconsin also yielded mostly internal moulds of both originally disarticulated or articulated shells (for example, see Fig. 5a). In external morphology, *V. major* resembles *V. decussata* from the Williston and Hudson Bay basins in its large shell size, prominent ventral umbo, and numerous but faint ribs. In the anterior lateral part of the shell, the ribs average 10 per 10 mm (in comparison to 11-12 in *V. decussata*; 7-8 in *V. mayvillensis*).

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