Origin and evolution of the early Silurian (Rhuddanian) virgianiid pentameride brachiopods - the extinction recovery fauna from Anticosti Island, eastern Canada

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ABSTRACT - Discovery of a suite of post-mass extinction virgianiid brachiopods from the basal Silurian Beccs Formation of Anticosti Island demonstrates either that the Virgiana lineage originated from Brevilamnulella, or that the two lineages were sister groups. Gradational modifications are observed in a morphoseries from the Hirnantian genus Brevilamnulella, to the early Rhuddanian genus Viridita, and then to the middle-late Rhuddanian genus Virgiana. Four main evolutionary trends were ascertained: 1) adult shell size changed from < 15 mm to about 30 mm in length, and the shell outline from slightly transverse or equidimensional to markedly elongate, with a profile from nearly equibiconvex to strongly ventribiconvex; 2) the ventral umbo changed from low and narrow (1–2 mm above hinge line), with a suberect beak, to high, obtuse, and galeate, with a strongly incurved beak; 3) the shell surface is smooth in Brevilamnulella thebesensis, becoming quasi-smooth to gently costate in Viridita lenticularis, and then moderately costate in Viridita glomerosa sp. nov. and Virgiana barrandei; 4) the fold and sulcus are absent in Brevilamnulella and also in the early growth stage (up to 5 mm length) of Viridita lenticularis; at later growth stages, a ventral sulcus and a dorsal fold are developed extending to the anterior margin to produce a uniplicate commissure; such a fold and sulcus are present only in the early growth stage of Virgiana barrandei. On the basis of internal structures, it is also suggested that the Clorinda lineage had its origin in Brevilamnulella or Viridita during the late Rhuddanian, and became successful mainly in deeper-water, outer-shelf environments.

RIASSUNTO - [Origine ed evoluzione dei brachiopodi pentameridi virgianiidi del Siluriano inferiore - La fauna sopravvissuta all’estinzione dell’Isola di Anticosti, Canada orientale] - Dopo l’estinzione di massa della fine dell’Ordoviciano, le faune concligliatori bentoniche del Siluriano inferiore si ripresero piuttosto rapidamente con associazioni dominate in tutto il mondo da grandi brachiopodi pentameridi che occuparono gli ambienti marini poco profondi delle regioni paleotropicali.

L’origine dei pentameridi a grande guscio del Siluriano inferiore (e.g., i generi ad ampia diffusione paleogeografica Borealisa, Pentamerus, Stricklandia e Virgiana, comunque, ha sempre costituito un enigma data l’assenza di forme intermedie che suggeriscano uno stock ancestrale e indichino la transizione evolutiva da una serie dei Virgianidaceae ai pentameridi del Siluriano inferiore. Sono stati trovati recentemente brachiopodi virginiani nel Siluriano basale post-estinzione nel Fox Point Member della Beccs Formation nell’Isola di Anticosti. Questi virginiani dimostrano che la linea evolutiva di Virgiana, il primo gruppo di grossi pentameridi comparso dopo l’estinzione di massa dell’Hirnantia, può essere seguito fino all’ultimo genere orдовiciano Brevilamnulella. Variazioni graduali si osservano in una sequenza morfologica dal genere virnhtianum Brevilamnulella, al genere Viridita del Rhuddanian inferiore, e quindi al genere Virgiana del Rhuddanian medio-superiore. Sono state riscontrate quattro tendenze evolutive: 1) la lunghezza del guscio degli adulti cambiò da < 15 mm a circa 30 mm, la forma passò da leggermente obliqua o equidimensionale a marcamente elongata, con un profilo da quasi egualmente biconvesso a fortemente biconvesso nella parte ventrale; 2) l’umbone ventrale si modificò da depresso a stretto (1-2 mm sopra la linea della cerniera) con apice suberetto, ad alto, smussato e galeato, con un apice fortemente ricurvo; 3) la superficie del guscio, liscia in Brevilamnulella thebesensis, diventò quasi-liscia o leggermente costata in Viridita lenticularis, e successivamente moderatamente costata in Viridita glomerosa sp. nov. e Virgiana barrandei; 4) piega e solco sono assenti in Brevilamnulella e poi, fino a 5 mm in lunghezza, in Viridita lenticularis; negli studi di crescita successivi, si svilupparono un solco ventrale ed una piega dorsale che si estendevano fino al margine anteriore a produrre una commessura uniplicata; questo particolare tipo di piega e di solco è presente solamente negli studi di crescita iniziali di Virgiana barrandei. Sulla base delle strutture interne, viene proposto che la linea evolutiva di Clorinda si sviluppò da Brevilamnulella o Viridita nel Rhuddanian superiore, occupando prevalentemente gli ambienti di acque più profonde della piattaforma esterna.

Questo studio suggerisce che la linea evolutiva di Virgiana, il primo gruppo post-estinzione di pentameridi a grande guscio del Siluriano inferiore, si originò da Brevilamnulella e attinenti facies e relativamente profonde che si mantengono nelle regioni paleotropicali durante la glaciazione hirnantiana. Le serie morfologiche intermedie, rappresentate da Viridita lenticularis e Viridita glomerosa sp. nov. ritrovate nei carbonati del Siluriano basale (Rhuddanian inferiore) dell’Isola di Anticosti, documentano il percorso evolutivo dai piccoli gusci lenticolari di Brevilamnulella ai grandi gusci galeiformi di Virgiana, che divenne predominante nei mari tropicali poco profondi del continente di Laurentia e di altre paleo-placche e terranes nel Rhuddanian medio-superiore.

INTRODUCTION

The origin of large-shelled pentameride brachiopods that dominated the early Silurian shelly benthos worldwide has been an evolutionary puzzle. During the Late Ordovician, the family Virgianidae constituted a rising group of pentameride brachiopods (Suborder Pentameridina). The family originated during latest Katanian time and went through a moderate radiation before attaining global distribution. The oldest known virgianids are of latest Katanian (mid-Ashgill) age, represented by genera such as Brevilamnulella, Deloprosopus, Disulcatella, Eoconchidium, Holorhynchus, Proconchidium, Prostricklandia, and Tcherskidiun. It is difficult to determine which one of these genera appeared first because their fossils occur predominantly in shallow marine carbonate facies, where the biostratigraphic resolution tends to remain low. Despite uncertainty about
the precise timing and place of their origin, many of these early virgianids developed conspicuously large shells and rapidly formed a distinctive type of shelly community after their first appearance. They thrived especially in the shallow tropical seas of Laurentia, Baltic, Kazakhstan, Siberia, North China, South China, and their surrounding microplates and terranes (Amsden, 1974; Sapelnikov & Rukavishnikova, 1975; Nikolaev et al., 1977; Nikiforova, 1978, 1989; Rozman, 1978; Cocks, 1982; Oradovskaya, 1983; Sapelnikov, 1985; Temple, 1987; Blodgett et al., 1988; Kulkov & Severgina, 1989; Rong et al., 1989; Kovalevskii et al., 1991; Sapelnikov & Mizens, 1991; Beznosova, 1994; Cocks & Modzalevskaya, 1997; Jin & Chatterton, 1997; Rong & Boucot, 1998; Zhan & Cocks, 1998; Boucot et al., 2002, Modzalevskaya, 2003; Jin et al., 2006; Rong & Zhan, 2006; Harper et al., 2007). On the paleoequatorial carbonate platform of North Greenland (eastern margin of Laurentia), for example, *Proconchidium* formed frequently recurrent, monospecific shell beds spanning a 350 m thick succession of carbonate strata, interpreted as a stable, incumbent virgianid brachiopod community during the pre-Hirnantian Late Ordovician (Harper et al., 2007). During the Late Ordovician, there was a striking paleolatitudinal control on the virgianid distribution in Laurentia, although the controlling mechanism remains poorly known. Large-shelled virgianids were confined to the northern half of the paleocontinent (e.g., Baffin Island, North Greenland, and eastern Alaska), corresponding to the ‘northern hemispheric’ tropical regions of Laurentia. Their occurrence and dominance in the southern half of the paleocontinent did not occur until early Silurian (mainly Rhuddanian) time, when the *Virgiana* fauna became ubiquitous in North America (Boucot & Chiang, 1974; Sheehan, 1980; Jin et al., 1996; Jin & Copper, 2000).

The family Virgianidae all but became extinct at the Katin-Hirnantian boundary, associated with the first major pulse of the glacially induced Late Ordovician mass extinctions, that spanned nearly two million years (445.6–443.7 Ma; see Gradstein et al., 2004). Only two Late Ordovician genera of the Suborder Pentameridina (mainly Rhuddanian) carbonate strata of Anticosti Island, eastern Canada. The new material provides a rare opportunity for investigating the origin and early diversification of the early Silurian virgianids and related pentamerides. This study constitutes a preliminary report of this investigation. For a preliminary cladistic analysis, the reader is referred to Jin et al. (2006), and a more comprehensive cladistic study is not feasible with currently available data and awaits information on biometric measurements and internal structures of virgianids from several other regions.

Figured specimens are housed in the Type Collection of Invertebrate and Plant Fossils, Geological Survey of Canada (GSC), Ottawa, and the Department of Earth Sciences, the University of Western Ontario (W). Locality and sample numbers prefixed with the letter A or C denote the P. Copper collections from Anticosti Island, and detailed data are available in Jin & Copper (2000), or directly from the authors.

**STRATIGRAPHIC SETTING**

In this study, the base of the Becscie Formation (i.e., the Ordovician-Silurian boundary) follows the definition of Schuchert & Twinhokel (1910), placed at the top of the last Laframboise reefs, or at the top of the coeval...
The Fox Point Member

On the northeast coast of Anticosti Island, the Fox Point Member has a minimum thickness of 8.2 m, exposed continuously from the top of the oncelite unit of the Laframboise Member (top unit of the Hirnantian Ellis Bay Formation) in the direction of eastern Fox Bay (see Jin & Copper, 2000 for a map and stratigraphic chart with pentameride ranges of Anticosti Island). The basal contact is exposed in the bluffs and tidal flats 50-150 m west of Ruisseau aux Algues. The upper contact with the Chabot Member is gradational at Fox Point and can only be arbitrarily identified in the coastal sections. The typical lithology in the eastern outcrops comprises medium grey, thin-bedded micrites alternating with thinner calcareous limestones of the Chabot Member. Asymmetric ripples, gutter casts, and hummocky beds are common; ball-and-pillow structures are locally present. This indicates a sedimentary suite influenced by periodic severe storms (Sami & Desrochers, 1992). The somewhat deeper water Fox Point Member is evenly and thinly bedded, as is evident from both ground observation and air photos. The overlying Chabot Member is thick-bedded and locally biostromal, interpreted as a shallowing-upward succession (Long, 2007).

The Chabot Member

The Member is well exposed along the coast around Anse à Chabot, about 10 km west of the Beccie River mouth (locality A292). The dominant lithology consists of yellowish-grey, medium- to thick-bedded micrite, common bioclastic packstone and grainstone, and coral-stromatoporoid biostromes. Shale and argillaceous lime mudstone are virtually absent. The upper contact of the Chabot Member with the Merrimack Formation is well exposed at the 24 mile bridge over the Jupiter River (see Copper & Long, 1989), where the bluish-grey lime mudstone of the Merrimack Formation begins at the river bank. Stromatoporoids, corals, and brachiopods are occasionally silicified on upper bedding surfaces. Intraformational conglomerates, hardgrounds, and ripple marks, cross-stratification, and scours are common sedimentary structures (Sami & Desrochers, 1992; Long, 2007).

In the Chabot Member, large shells of *Virgiana barrandeii* (Billings, 1866) are the predominant brachiopod, and it appears immediately above the base of the member. Locally, monospecific *Virgiana* shell beds are prominent, with individual beds of 20-50 cm stacking up vertically for several meters of section, usually composed of entirely disarticulated but not severely broken shells; conjoined and well-preserved shells may also form small patches of shell beds, some buried in situ or even in life position (Jin et al., 1996; Copper, 1997; Jin, 2008). *Zygospiraella*, which first appears in the upper Fox Point Member, is a rare taxon in the Chabot Member. Other rare brachiopods include the orthide

![Diagram](image-url)
Mendacella and the strophomenide Brachyprion. The overall brachiopod diversity of the Chabot Member is much lower than the Fox Point fauna.

A rich stromatoporoid and colonial coral fauna is present in the Chabot Member, especially in the upper part exposed along the coast from the Becscie River to Rivière au Cailloux. Clathrodictyon and Ecclimadictyon reach large sizes exceeding 20 cm, representing the recovering stromatoporoids from the Hirnantian mass extinctions. Colonial rugose corals are characterized by the phaceloid genera Paleophyllum and Donacophyllum. Solitary rugosans (e.g., Dinophyllum, Amplexoides, and Cyathactis) do not become common until later in the overlying Merrimack Formation of deep-water origin. Tabulate corals, such as Propora and Paleoefavorites, are typically small, hemispheroidal forms in the Chabot Member, rarely attaining large sizes up to 1 m (e.g., costal sections at the mouth of Rivière au Cailloux: A1336-1337). Virgiana shell patches, comprising a mixture of disarticulated and conjoined shells, have been found among the coral-stromatoporoid biostromes at locality A1337.

**VIRGIANID EVOLUTION DURING THE EARLIEST SILURIAN**

The phylogenetic relationship between the latest Ordovician *Brevilamnulella* and the earliest Silurian *Virgiana* has been enigmatic because the type species of *Brevilamnulella* from North America usually has a small, predominantly smooth shell, without fold and sulcus, and with proportionally small internal structures (such as the spondylium, ventral median septum, and hinge plates), whereas *Virgiana* has a large, costate shell with a strongly arched ventral valve and much enlarged internal structures. There has been little previous evidence for forms intermediate between *Brevilamnulella* and *Virgiana* during the Ordovician-Silurian transition.

New collections of virgianids from the Fox Point Member and the lower Chabot Member (early-middle Rhuddanian) provide clues to the origin and early evolution of the early Silurian *Virgiana* lineage, particularly regarding the temporal changes in shell size, outline, globosity, ribbing, the development of fold and sulcus, and the configuration of internal plate structures. This morphologies strongly suggests that either the *Virgiana* lineage originated from *Brevilamnulella*, or the two lineages shared an immediate common, but yet unknown, ancestor. In the sections below, we show modifications from the Hirnantian *Brevilamnulella* to the early Rhuddanian *Viridita*, and then to the middle-late Rhuddanian *Virgiana*.

**Shell size and shape**

In *Viridita lenticularis* (Billings, 1866) from the basal few metres of the Fox Point Member, the shells are slightly wider than long, and transversely subelliptical. Some shells may become equidimensional with equal length and width (Figs. 2-3). At its early growth stage, *V. lenticularis* resembles *Brevilamnulella thebesensis* from Hirnantian strata of the Edgewood Group in eastern USA (Amsden, 1974) in its lenticular shell of moderate biconvexity. In *Viridita glomerosa* sp. nov. from the upper Fox Point Member of the Becscie Formation, there is a notable increase in both the average and maximum shell size per individual populations, as well as an increase in shell globosity (measured by T/W ratio; see Figs. 3-4), although the shells remain subequally biconvex. Despite a trend for shell enlargement, accelerated longitudinal growth is not yet obvious in *Viridita glomerosa*. Among several populations examined, however, there is a trend for the shells to transform from transversely subelliptical (slightly wider than long; samples A1540b and C712) to approximately equidimensional (length about the same as width; sample from GSC Loc. 36366). Allometric elongation of the shell is diagnostic only for *Virgiana barrandei*, which first appears in the lower Chabot Member (middle Rhuddanian), although there is some overlap in shell size between the largest *Viridita glomerosa* and the small shells of *Virgiana barrandei* (Figs. 4-5). Among shells of similar length, *Viridita glomerosa* is always wider than long, and *Virgiana barrandei* always longer than wide, possibly a trend towards an umbo-down, ‘mud-sticker’ shell adaptation to the substrate.

In comparison to *Viridita*, the earliest form of *Virgiana barrandei* exhibits not only an increase in shell size, globosity, and accelerated elongation, but also a strongly allometric, accelerated increase in the ventral valve convexity. At an early growth stage, as indicated by the umbonal areas of both valves, the shell of *V. barrandei* was approximately equibiconvex or with the ventral valve slightly deeper than the dorsal. During ontogeny, the ventral valve became increasingly deeper and more strongly arched, whereas the dorsal valve less convex and
even flattened towards the anterior margin. Thus around the anterior margin, some shells of *V. barrandei* may be strongly ventribiconvex, or nearly planoconvex (see Jin & Copper, 2000).

The strongly transverse shell of *Viridita becsciensis* (Twenhofel, 1928) appears to be a rare and extreme case for the genus on Anticosti Island (Jin & Copper, 2000) but, in its wide outline and strong ventral sulcus, it resembles *Brevilamnula curta* Menakova, 1984 from the uppermost Katian Archalyk Formation of Tadzhikistan, except that it is much smaller than the Anticosti species.

**Height of the ventral umbo**

In relatively small shells of *Viridita lenticularis*, the ventral and dorsal umbones are low (1-2 mm above hinge line) and of similar height, with the ventral umbo slightly higher in larger specimens. In general appearance, the umbal areas of both valves hardly rise above the hinge line, but only the suberect beaks protrude posteriorly (Figs. 3a-k, 5a-e). With increased shell size and globosity in *Viridita glomerosa*, the ventral umbo in particular becomes higher and more strongly convex, and the ventral beak more incurved to a degree that the posterior
extremity of the ventral valve (i.e., the shell apex) is not marked by the beak but by the arched umbo (Figs. 3l–u). In sample C712, for example, the ventral umbo may be up to 4 mm above the hinge line in the largest shells of *Viridita glomerosa*, and the beak becomes dorsally pointed.

The galeiform shell (i.e., the shell umbo resembling the shape of a helmet), in which the ventral umbo and beak become high, tumid, and arched over the dorsal umbo, is not attained until the appearance of *Virgiana barrandei* in the basal Chabot Member. However, the relatively small, globose, and presumably mature shells of *Viridita glomerosa* are essentially similar to the virgianids of Anticosti Island, as in the Hirnantian species *Brevilamnulella thebesensis* (Fig. 3f). A similar interarea is retained in *Virgiana barrandei* (see Jin et al., 2006, p. 73, figs. 1.15, 1.21), but becomes largely obsolete in *V. mayvillensis* from the overlying Rhuddanian Merrimack Formation.

**Shell costae, fold, and sulcus**

The type species of *Brevilamnulella, B. thebesensis* (Savage, 1913), has a relatively small (< 15 mm in maximum length or width), essentially smooth shell, without any clearly delimited fold or sulcus (Amsden, 1974). Among large collections of *Viridita lenticularis* from the basal Fox Point Member, shells less than 10 mm in length or width are typically smooth, as are the early growth stages of larger shells (Figs. 3a–k). Gentle, undulating costae or plicae are developed in the anterior, especially the antero-medial, portion of shells larger than 10 mm long. Contrary to common belief, *Virgiana barrandei*, the type species of mid-Rhuddanian age, is only weakly costate. The ribs of some shells are clearly visible only with the help of coating and low-angle lighting (Figs. 5f–o; see also Jin & Copper, 2000). Stronger and more consistently developed costae are not developed until the late Rhuddanian, in such species as *Virgiana mayvillensis* from the Merrimack Formation of Anticosti Island and the Mayville Dolomite in Wisconsin, mid-continent USA. In the development of shell costae, the rather strong and consistent costae in the older, relatively small shells of *Viridita glomerosa* (compared to *Virgiana*) are evolutionarily puzzling - these small shells show a tendency to become more globose and more strongly ribbed than many of the larger shells of *Virgiana barrandei* that occur immediately above *Virgiana glomerosa* in the Becscie Formation. This implies that ribbing is not a quintessential character for deciphering the speciation process from *Viridita* to *Virgiana* because the change from quasi-smooth to distinctly ribbed shells appears to have happened independently in the two genera.

The development of a ventral sulcus and dorsal fold is highly variable and inconsistent, both ontogenetically and among shells of similar size and presumably at similar growth stages. In the lower Fox Point Member at the east end of Anticosti Island (sample A1450b), the shells usually have a weak fold and sulcus, and these originate anterior to the umbonal area and remain broad and shallow to the anterior margin, resulting in a very gently uniplicate or nearly rectimarginate commissure. In contrast, shells from the upper Fox Point Member at the west end of the island (sample A294) tend to have a stronger fold and sulcus, originating in the umbonal area, about 2-3 mm from the beak, and persisting to the anterior margin, producing a clearly uniplicate commissure (see Jin & Copper, 2000, pl. 4, figs. 6-19), although shells with poorly defined fold and sulcus also exist in the same
collection, characterized by an essentially rectimarginate anterior commissure.

The fold and sulcus in *B. lenticularis*, when well-developed (Figs. 5a–e), appear to be very similar to the early growth stage of *Virgiana barrandei* (Figs. 5f–o). A flattening of the dorsal valve and development of an antero-medial depression, together with notable shell elongation, mark the beginnings of true *Virgiana*, represented by *Virgiana barrandei*, that first appears in lower middle Rhuddanian strata of the Becscie Formation. In *V. barrandei*, the uniformly convex state (or the ‘Brevilamnula state’), without a fold or sulcus, is confined to the apical 2-5 mm. At 3 mm to 8 mm length, the dorsal fold and ventral sulcus are well defined and broaden notably with ontogeny, usually with a single costa in the sulcus. This can be referred to as the ‘*Viridita lenticularis* state’. The fold and sulcus disappear more anteriorly; the dorsal fold inverts to a gentle medial depression that broadens towards anterior margin. The corresponding anteromedial carina in the ventral valve is usually less well delimited than the medial depression of the dorsal valve. The result is a weakly sulciplicate anterior commissure in large or gerontic shells of *V. barrandei*. In small to medium-sized shells between 8–30 mm long, the anterior commissure may be rectimarginate because the inversion of fold and sulcus develops gradually in individual shells (Figs. 5f–j).

In addition to other characters, the high degree of similarity in the development of fold and sulcus between *Viridita lenticularis* and the early growth stage of *Virgiana barrandei* is interpreted here as evidence for a close phylogenetic relationship.

In *Viridita glomerosa*, the fold and sulcus have a tendency to become flattened near the anterior margin, concomitant with a moderate increase in shell size and convexity. The result is a rectimarginate anterior commissure, although the coarse costae make the margin denticulate (Figs. 3p, u). Thus, despite its intermediate
nature between *Viridita lenticularis* and *Virgiana barrandei* in terms of shell size, *Viridita glomerosa* is not likely a phylogenetic intermediate that lies on the main line of transition from *Viridita* to *Virgiana*, but rather represents a side branch from this line (cladogenesis).

**Internal structures**

Internally, there do not seem to be fundamental differences between *Viridita* and *Virgiana* in the relative size and configuration of the median septum and spondylium in the ventral valve and the hinge plates and crura in the dorsal valve. In proportion to shell size, the spondylium is the only internal structure that is lengthened in *Virgiana barrandei* (from one-third to two-fifths shell length) compared to *Viridita lenticularis* (less than one-third shell length). In both *Viridita* and *Virgiana*, however, the spondylium is rather broad and shallow, and only its apical portion is supported by a median septum, so that the spondylium is mostly free hanging. The wedge-shaped junction between the median septum and the valve floor, typical of *Pentamerus* that evolved later during the Aeronian, is only weakly developed in *Viridita* and *Virgiana* (see Jin & Copper, 2000 for more details).

In the dorsal valve, the inner and outer hinge plates (= outer and inner plates of older usage) are similarly short in *Viridita* and *Virgiana*, confined essentially to the umbonal area. Also, the inner hinge plates have a similar orientation in cross section, with a slight basomedial inclination, but are never coalesced to form a cruralium. One of the diagnostic microstructures of these virgianids is the lack of clearly developed prismatic layers in the hinge plates, so that the lamellar layers of the inner hinge plates and the valve floor are continuous and smoothly merged. In this respect, a close phylogenetic relationship among *Brevilamnulella*, *Viridita*, and *Clorinda* is conceivable because *Clorinda* differs from the two virgianids only in having baso-laterally inclined inner hinge plates and somewhat better defined prismatic layers, but lacking shell ribbing. Their general similarity explains why some species of *Brevilamnulella, Viridita*, and *Clorinda* were described initially as *Clorinda* (Twenhofel, 1928; St. Joseph, 1938), Boucot (1975) initially suggested that *Clorinda* evolved from *Brevilamnulella* in mid-Llandovery time, but the presence of early forms of *Clorinda* in lower Rhuddanian strata of the Welsh Borderland (Temple, 1987) points to a much earlier origin of the *Clorinda* lineage.

**SUMMARY**

*Viridita* from the lower Rhuddanian strata of the Fox Point Member, Beccscie Formation, provided clues to the evolutionary pathway from the Hirnantian *Brevilamnulella* to the middle and late Rhuddanian *Virgiana* by bridging several key morphological gaps between the two genera. Ontogenetic and populational variations of *Viridita lenticularis* demonstrate that smooth shells without fold and sulcus (*Brevilamnulella*-type) could evolve into weakly costate shells with a well-defined ventral fold and dorsal sulcus. On the small side, the range of shell sizes of *Viridita glomerosa* overlaps with that of *V. lenticularis* and, on the larger side, with that of *Virgiana barrandei*. *Viridita glomerosa* also has a globose shell, with rather strong costae like some late forms of *Virgiana*. Pronounced shell elongation and loss of the ventral sulcus and dorsal fold in the anterior half of the shell are the only autapomorphic characters of the *Virgiana* lineage. A comprehensive cladistic analysis is to be conducted when detailed morphological data of virgianids from other regions become available.

**SYSTEMATIC NOTES**

Order **Pentamerida** Schuchert & Cooper, 1931  
Suborder **Pentameridina** Schuchert & Cooper, 1931  
Superfamily **Pentameroidae** M'Coy, 1844  
Family **Virgianidae** Boucot & Amsden, 1963

Genus *Viridita* Jin & Copper, 2000  

**Type species** - *Camerella lenticularis* Billings, 1866, uppermost Fox Point Member, Beccscie Formation, Reef Point, Anticosti Island.

*Viridita glomerosa* sp. nov.  
(Figs. 3 l-u; 6) 1972 *Parastrophinella lenticularis* Bolton (non Billings, 1866), p. 32, pl. 6, figs. 2, 4.

Etymology - Latin, *glomerosus*, round like a ball. The feminine adjective *glomerosa* depicts the globular shell of the new species.

**Types** - Holotype, GSC 29640 (see Bolton, 1972, p. 32, pl. 6, fig. 2), a conjoined shell; Fox Point Member, Beccscie Formation, Ste. Marie River road at the top of an escarpment southwest of the south end of Petit Lac Ste. Marie, GSC locality 33630. Paratypes, GSC 29641 (see Bolton, 1972, p. 32, pl. 6, fig. 4), and 47 shells uncatalogued and unfigured specimens from the same locality and stratum. Bolton initially reported the brachiopod collection from his Member 6, Ellis Bay Formation. These strata have now been assigned to the Fox Point Member of the Beccscie Formation (Long & Copper, 1994; Jin & Copper, 2000; Long, 2007).

**Other material** - GSC locality 76179 (logging road from House Creek tote to Jupiter River road, about 800 m south from House Creek tote), 6 shells and a small block with about 10 shells embedded; this collection also contains 7 loose shells of *Virgiana barrandei* and thus the sample is probably a mixture of brachiopods from the upper Fox Point and the basal Chabot members. C712, 35 shells from Ste. Marie road, close to GSC locality 33630, uppermost Fox Point Member, Beccscie Formation.

Diagnosis - Small, strongly biconvex to globular, costate shells of *Viridita*, generally lacking fold or
sulcus. Ventral and dorsal interareas narrow but well defined. Spondylium shallow, broadly V-shaped, apically supported by short median septum, anteriorly free. Inner and outer hinge plates short, less than one-fifth length of shell; inner hinge plates subparallel to each other and crudely lyre-shaped in cross section.

**Description** - Shell usually small (<20 mm in length), rarely attaining medium size (20–40 mm in length), subcircular to transversely subelliptical, equidimensional to slightly wider than long, strongly biconvex to globular in lateral profile. Hinge line short, less than one-third width of shell, with rounded cardinal extremities. Shell widest at about mid-length. Ventral umbo relatively narrow, strongly convex, extending 2–3 mm above hinge line; beak small, incurved to point dorsally. Ventral interarea minute, slender, but sharply defined, moderately apsacline (Figs. 3o, t); with open delthyrium. Dorsal umbo somewhat lower and slightly less convex than ventral umbo; dorsal interarea similarly small but orthocline to slightly apsacline. Fold and sulcus absent. Costae rounded, relatively strong for genus except for quasi-smooth umbonal areas, 8–14 on each valve, with occasional bifurcation or intercalation. Concentric growth lines fine, irregularly developed. Anterior commissure rectimarginate, denticulate (Figs. 3p, u).

Ventral interior: Teeth weak, knob-like. Spondylium duplex, shallow, broadly V-shaped, posteriorly supported by median septum up to 2 mm length of shell, anteriorly free (see Fig. 6, 1.1-1.9 mm from apex). Median septum short, confined largely to umbonal cavity, but extending anteriorly along valve floor as low ridge, tapering out before reaching one-third length of shell; junction of median septum with valve floor wedge-shaped. Ovarian pits prominently developed on inner surface of valve posterior (Fig. 6), with one “Ziegler’s blister” observed. Dorsal interior: Hinge sockets small, delimited mainly by small, inner socket ridges. Both inner and outer hinge plates short, less than one-fifth length of shell. Inner hinge plates subparallel to each other, slightly arched laterally to be vaguely lyre-shaped, but baso-laterally inclined near junction with valve floor (see Fig. 6, 0.9 mm from apex). Outer hinge plates slightly longer than inner hinge plates along longitudinal axis of shell. Crura plate-like, each forming small flange at junction with outer hinge plates.

**Discussion** - The new species is similar to the type species, *Viridita lenticularis* in overall shell size and general configuration of internal structure, especially the curvature of inner hinge plates in cross section. It differs from *V. lenticularis* in having a more strongly convex
shell with stronger and more consistently developed costae. The ventral sulcus and dorsal fold, which are variously developed in the type species, are usually absent in *V. glomerosa* sp. nov. Although the average shell size is similar for the two species, a few specimens of *V. glomerosa* attain a maximum shell size (length 25.4 mm, width 28.5 mm) that is considerably larger than that of *V. lenticularis*. The ovarian pits, especially in the posterior part of the ventral valve, of *Viridita glomerosa* are much more prominent than those of *V. lenticularis*, but are similar to those in various species of *Virgina* (Jin & Copper, 2000).

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