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QUASIAULACERA, A NEW HIRNANTIAN (LATE ORDOVICIAN) AULACERATID STROMATOPOROID GENUS FROM ANTICOSTI ISLAND, CANADA

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ABSTRACT—A large and abundant columnar stromatoporoid, *Quasiaulacera* n. gen., from the Ellis Bay Formation, up to 3 m long and 40 cm in diameter, marks the Hirnantian (latest Ordovician) of Anticosti Island. Two species are present: *Quasiaulacera stellata* n. sp. from the basal Ellis Bay Formation (basal Prinsta Member, lower Hirnantian) along the northeastern coast of the island, and the type species *Q. occidua* n. sp. from the upper Ellis Bay Formation (Lousy Cove Member, upper Hirnantian) in the western carbonate facies of the island. *Quasiaulacera* is rare or absent in the reefal Laframboise Member (uppermost Hirnantian) of the formation. The new genus differs from *Aulacera* in the underlying Vaureal Formation (upper Katian) in having a large central axial zone marked by a single stack of large, convex-up cyst-plates, that is surrounded by a middle layer of small, concentric microcyst-plates, in places denticulate, and an outer layer composed of concentric laminae with dense pillars, in which microcyst-plates are either absent or rare. The outer two layers are defined by longitudinal fluting; there are no branching forms. Both species demonstrate a ball-like holdfast system, some with diameters of 30 to 70 cm, microbially cemented into the substrate. *Quasiaulacera* "gigantism" in the paleotropical Anticosti Basin evolved at a time of global cooling associated with the Hirnantian glaciation in south polar Gondwana, but terminated in mass extinction of the aulaceratids at the O/S boundary in Laurentia. This supports other evidence that the Hirnantian featured not only generic loss, but also innovation and migration in tropical latitudes.

INTRODUCTION

THE DISTINCTIVE giant columns or cylinders of the aulaceratid stromatoporoids have a stratigraphic range of over 200 m from the upper Vaureal Formation (Homard Member, upper Katian) through the top of the reefal Laframboise Member of the Ellis Bay Formation at the Ordovician/Silurian Mass Extinction boundary on Anticosti Island (Figs. 1, 2). There is no significant stratigraphic break at the O/S boundary in this area, and this is probably the most complete and thickest section of the world in the paleotropical carbonate platform setting. No specimens have been discovered in the lowermost Silurian strata of the island, despite over 150 years of fieldwork there by numerous geologists and paleontologists.

In this paper we provide the first formal description of two abundant new species of the exclusively Hirnantian *Quasiaulacera* n. gen., one early and one late Hirnantian in age (Figs. 2, 3), and elaborate on the genus reported provisionally in previous literature without a diagnosis, nor type species (Copper et al., 2011). For comparison, we also provide, for the first time, clear illustrations of topotype material of *Aulacera nodulosa* (Billings, 1857) and *A. undulata* (Billings, 1857) from their type localities, with precise stratigraphic and geographic data. A monograph covering all the aulaceratids is in preparation. A summary of their paleoecology and occurrence is available in Cameron and Copper (1994), and Copper et al. (2011). Aulaceratids, despite their abundance and good preservation, presented difficulties in collecting and preparation: 1) the large and heavy specimens created logistic difficulties for sampling and transportation in usually remote localities, and tidal flat outcrops were only accessible for about two hours daily during low tide; 2) most specimens were storm-disturbed and broken up post-mortem, although a few fell in situ on the bedding plane surfaces, but lost their apices; 3) the basal attachment structures were usually firmly cemented into the bedding planes, and difficult to extract; 4) large skeletons required multiple thin sections in transverse, axial and tangential views (type specimens required 15 to 30 large thin sections); and 5) partial recrystallization of the skeleton affected numerous specimens, and the axial cavity was usually vacant.

Richardson (1857) was the first to discover aulaceratids on Anticosti Island, assigning such specimens to his stratigraphic "Division B" (later the Vaureal Formation of Schuchert and Twenhofel, 1910). He measured his "tree-like fossils" with diameters of 3 to 7 inches (7–18 cm) and lengths of 5 feet (~1.8 m) on the tidal flats close to West Point lighthouse, the most westerly point of the island. Others were collected just east of the Salmon River at Battery Point some 200 km away, so named because sailors thought that the cylindrical fossils protruding from the bluffs looked like a battery of cannons. In addition, Richardson (1857, p. 216) discovered more such fossils on the tidal flats north of Cape Henry (Cap Henri), that mark the western approach to Ellis Bay itself. He collected these from beds stated to be some 5 to 12 feet (up to 3.6 m) below the Division C reefs, thus coming from the Lousy Cove Member that lies below the Laframboise Member (Ellis Bay Formation) capping the Ordovician section. Richardson (1857) also mentioned that those were "of larger size than before observed..." He measured those at 10 feet 6 inches (3.2 m) in length and 6 to 15 inches (15–38 cm) in diameter. Richardson extrapolated a total length of as much as 30 feet (9.1 m) for the broken specimens, as they barely tapered along their length, but such a vertical length seems highly unlikely. Small specimens are spindle-like, with a pointed top, and short (1 m), with diameters of <20 cm in complete specimens (one of these complete *Aulacera nodulosa*, on display at the Salmon River

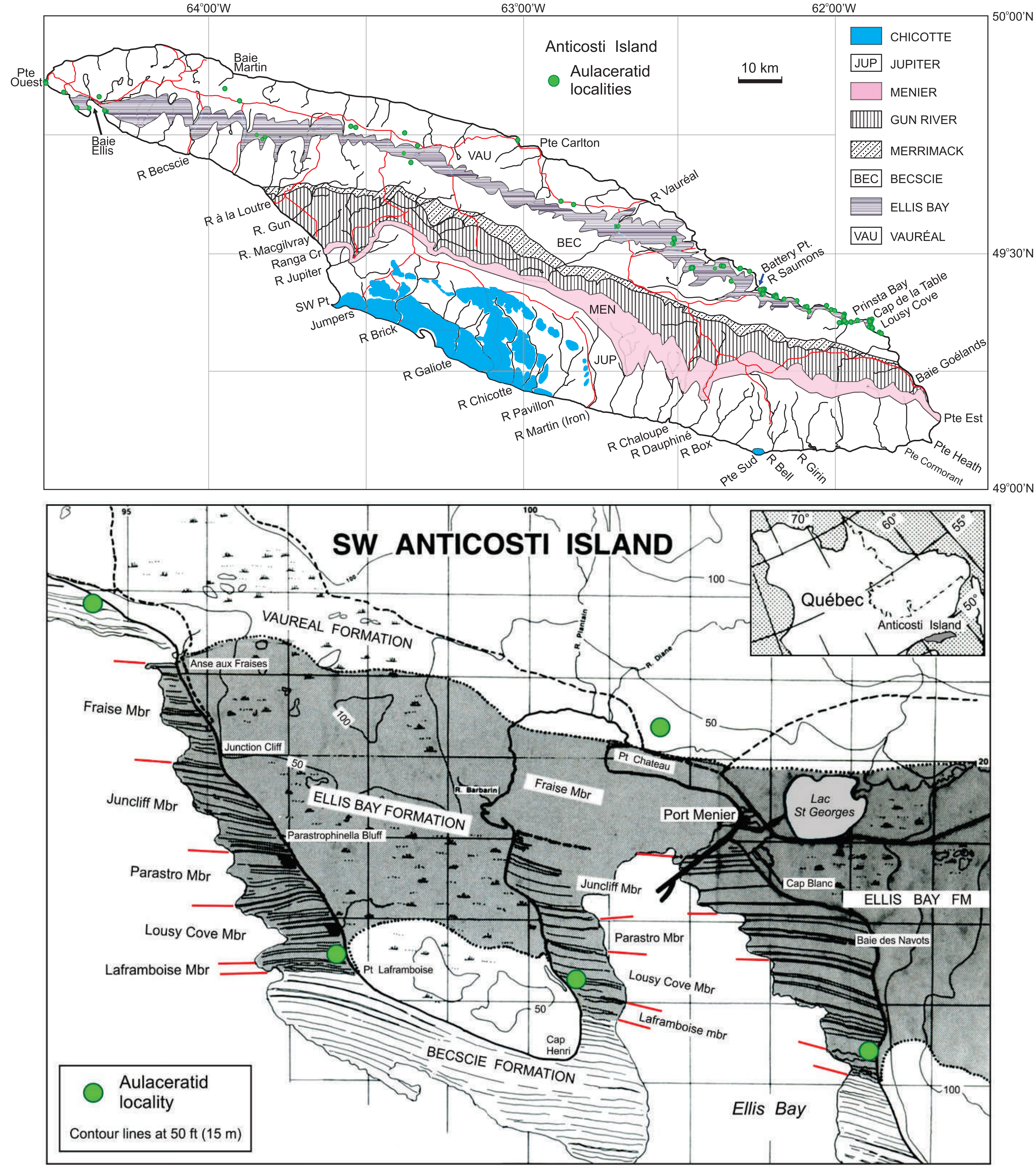

FIGURE 1—General geological map of Anticosti Island (top), and detailed map of the southwest coast (bottom), showing the geographic and stratigraphic distribution of known aulaceratid species (circles). Note that *Quasiaulacera occidua* n. sp. occurs almost exclusively in the western facies belt (see lower box), and *Q. stellata* n. sp. in the eastern facies belt (for a detailed map of the eastern place names, consult Long and Copper, 1987).

museum, was collected at the wharf at the mouth of the Salmon River by Mr. Jean Gagnon). Richardson (1857), however, failed to notice the attachment bases of these pillar-like sponges on the tidal flats near Pointe Laframboise and along Ellis Bay. The last surviving Ordovician specimens of aulaceratids on Anticosti occur as broken fragments and attached bases in the reefal Laframboise Member, directly below the final Ordovician/Silurian mass extinction boundary; such specimens lack the

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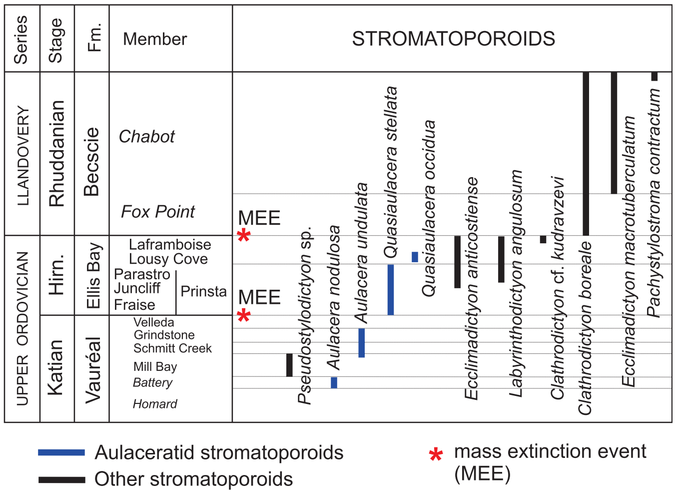

FIGURE 2—Range chart of presently described species of aulaceratids and other stromatoporoids in the Upper Ordovician and basal Silurian strata of Anticosti Island. The first stepped Ordovician/Silurian Mass Extinction Event (MME) is at or near the top of the Vaureal Formation (latest Katian) and the final MME is at the top of the Ellis Bay Formation (Hirnantian), marked by asterisks. Members in italics are provisionally named.

random pillars and the outer envelope of smooth laminae of typical *Aulacera* (Cameron and Copper, 1994, fig. 2c). The taxonomic position remains uncertain for other late surviving forms, with only large axial cyst-plates and smaller outer cyst-plate envelopes, which also occur in Katian strata of Manitoulin Island, Ontario (Copper and Grawbarger, 1978). Richardson (1857) made no mention of discovering any aulaceratids in the reefal topmost limestone bed (Laframboise Member), but they are indeed present in the reefs at the northeastern coast, and were noticed elsewhere by Petryk (1982). Lake (1981) failed to record the relatively common aulaceratids in the patch reefs of the lower Ellis Bay Formation on the Vaureal River.

No aulaceratids have been discovered in the Rhuddanian Becscie Formation that directly overlies the Hirnantian Ellis Bay Formation, even in the lowest few meters of the basal Silurian Fox Point Member. Oddly enough, Billings (1857, p. 253), who never went to Anticosti Island but only described the Richardson collections, listed "*Beatricea*" from his Division D, that later became part of the Becscie Formation. This is clearly an error.

At the tail end of the report on the geology and fossils of Anticosti Island, Billings (1857, p. 343–345) described a new genus of "Plantae" that he coined "*Beatricea*", for "certain tree-like fossils" collected by Richardson (1857). Billings (1857) assigned two species to his genus, one was *Beatricea nodulosa* from Battery Point, just east of the mouth of the Salmon River on the northern coast of Anticosti (see Fig. 4), and a second, younger species, *Beatricea undulata* (see Fig. 5), from a tidal flat locality near or at West Point lighthouse. Both those Katian-age localities are accessible today. Billings (1857, p. 344) stated that he examined specimens up to "10 ft 5 inches" (3.2 m) long that had been sampled by Richardson. Weston (1899), who later collected specimens from Anticosti, thought they might be either plants or "fucoids," and claimed he had found specimens some "20 feet" (~6 m) long. Both type localities have yielded new and fresh materials that are being revised.

When naming *Beatricia*, Billings was unaware that Plummer (1843) had already established the genus *Aulacera* based on similar cylindrical fossils from Indiana (USA) some 15 years earlier, interpreting them as nautiloids. Hyatt visited Anticosti Island in 1861, along with Verrill and Shaler, and collected many *Beatricea*, one specimen up to 13 ft. 6 in. (4.1 m) long, and first found their "basal attachments" (Schuchert, 1919, p. 294). Hyatt (1865) initially thought that *Beatricea* was a foraminiferan, and later a nautiloid (Hyatt, 1885). Nicholson (1886, p. 86–90) provided an extensive discussion on *Beatricea*, based on material from Anticosti, and documented Anticosti specimens of *Beatricea undulata* (pl. 8, figs. 4–8) from the West Point lighthouse locality, and assigned it to the stromatoporoids.

All previously described North American species of aulaceratids have been from middle to upper Katian strata (e.g., Foerste, 1909; Parks, 1910). Foerste (1909) described three new species or subspecies of aulaceratids from the classic Richmondian strata of Ohio and Kentucky. Galloway (1957) assigned *Aulacera* and *Cryptophragmus* to the Labechiidae. On Manitoulin Island, Ontario, aulaceratids occur at only the eastern end of the island, in outcrops near Manitowaning and Wikwemikong, and in the bluffs along the shoreline of Lake Huron, east of Wikwemikong (Copper and Grawbarger, 1978). Wider afield, aulaceratids from Siberia were described by Yavorsky (1955, 1963), who assigned eight Katian species to "*Beatricea*" (none from the Hirnantian), as well as recording previously described North American taxa. Nestor (1976) cited 12 *Aulacera* species from Siberia.

Schuchert and Twenhofel (1910) noted aulaceratid occurrences in their stratigraphic revision of Anticosti Island. Schuchert (1919) considered "*Beatricea*" a hydroid, and selected *Beatricea undulata* Billings, 1857 as type species of *Aulacera*, as Plummer (1843) originally did not select a type for the genus. Twenhofel (1928, p. 104–106) noted the presence of aulaceratids in both the Vaureal and Ellis Bay formations, but assigned all specimens to the two Billings (1857) species, and did not illustrate nor describe their internal structures. Petryk (1981) summarized the distribution of aulaceratids on Anticosti, and noted their presence in the uppermost Laframboise Member (his unit 7) of the Ellis Bay Formation. Later, Petryk (1982, pls.1, 2) illustrated aulaceratids from his Ellis Bay Member 4 at the Baie des Navots (east side cove in Ellis Bay) and Member 5 just north of Pointe Laframboise. Petryk (1982) interpreted the "*Aulacera*" attachment bases on the tidal flats at the west end to be of "cryptalgal" origin, but he provided neither thin-section illustration nor comparison with the Katian *Aulacera*. Bolton (1988) collected aulaceratids from roadside outcrops, and also resampled the Billings coastal localities of *Aulacera undulata* (West Point) and *A. nodulosa* (Battery Point). His aulaceratid localities, however, did not include precise geographic coordinates, and none of Bolton's samples are from the tidal flats of the Ellis Bay area or the northeast coast. None of the aulaceratids figured by Bolton (1988) showed the characteristic structures of *Quasiaulacera* n. gen. In terms of the recently revised stratigraphy, Bolton's aulaceratid localities, initially assigned to the Ellis Bay Formation, are here referred to the upper Vaureal Formation. In comparison, *Aulacera* occurs mostly in the Vaureal Formation, but rarely in the Ellis Bay Formation (Fig. 2). A possible *Aulacera* in the Laframboise reefs is an exteriorly smooth, cylindrical species with axial cyst-plates, surrounded by an outer envelope of microcyst-plates, and lacks radial pillars and an outer laminar layer (Cameron and Copper, 1994, fig. 2a, 2c).

GEOGRAPHIC AND STRATIGRAPHIC DISTRIBUTION

The aulaceratids have an unusual geographic distribution on Anticosti Island, arriving during a long-term shallowing episode, and vanishing at the O/S boundary on top of the reefal Laframboise Member of the Ellis Bay Formation (Twenhofel,

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FIGURE 3—*1, 2*, biostromal beds formed by *Quasiaulacera stellata* n. sp., Prinsta Member, Ellis Bay Formation (lower Hirnantian), locality A595 (12F/5, 80920:64800), coastal outcrop on west side of Lousy Cove, northeast end of Anticosti Island: *1*, bedding surface view of toppled trunks and remnant vertical bases; *2*, perpendicularly cut coastal section exposing the biostromal bed, as well as transverse and longitudinal sections of the aulaceratid skeleton; *3–6*, "tree-trunk-like", toppled skeletons of upper Hirnantian *Quasiaulacera occidua* n. sp., and the microbially cemented holdfast in the substrate of the Lousy Cove Member, Ellis Bay Formation, locality A1175 (22H/16, 00280:17630), tidal flat exposure, west side of Ellis Bay: *3*, fragmented *Quasiaulacera occidua* n. sp. ~1.5 m long, 20 cm diameter, on the bedding plane surface of the tidal flats, eastern side of Ellis Bay, south of Baie des Navots, ~2 km south of Port Menier (locality A1163, 22H/16, 04620:17270); *4*, tidal flat outcrop of bedding plane surface with two parallel skeletons of *Q. occidua* (longest ~1 m in length), western side of Ellis Bay, Lousy Cove Member, Ellis Bay Formation, locality A1175 (see above); *5, 6*, attachment bases on the bedding plane surface of the Lousy Cove Member, ~400 m north of Pointe Laframboise, adjacent to the mouth of Laframboise Creek, western Anticosti (A972, 22H/16, 97500:17900); larger attachment base is ~50–60 cm in diameter, with the diameter of *Quasiaulacera* itself ~15 cm in the center. Such abundant attachment bases are scattered over a tidal outcrop area of ~1 km^2. Hammer length=35 cm; lens cap diameter=52 mm.

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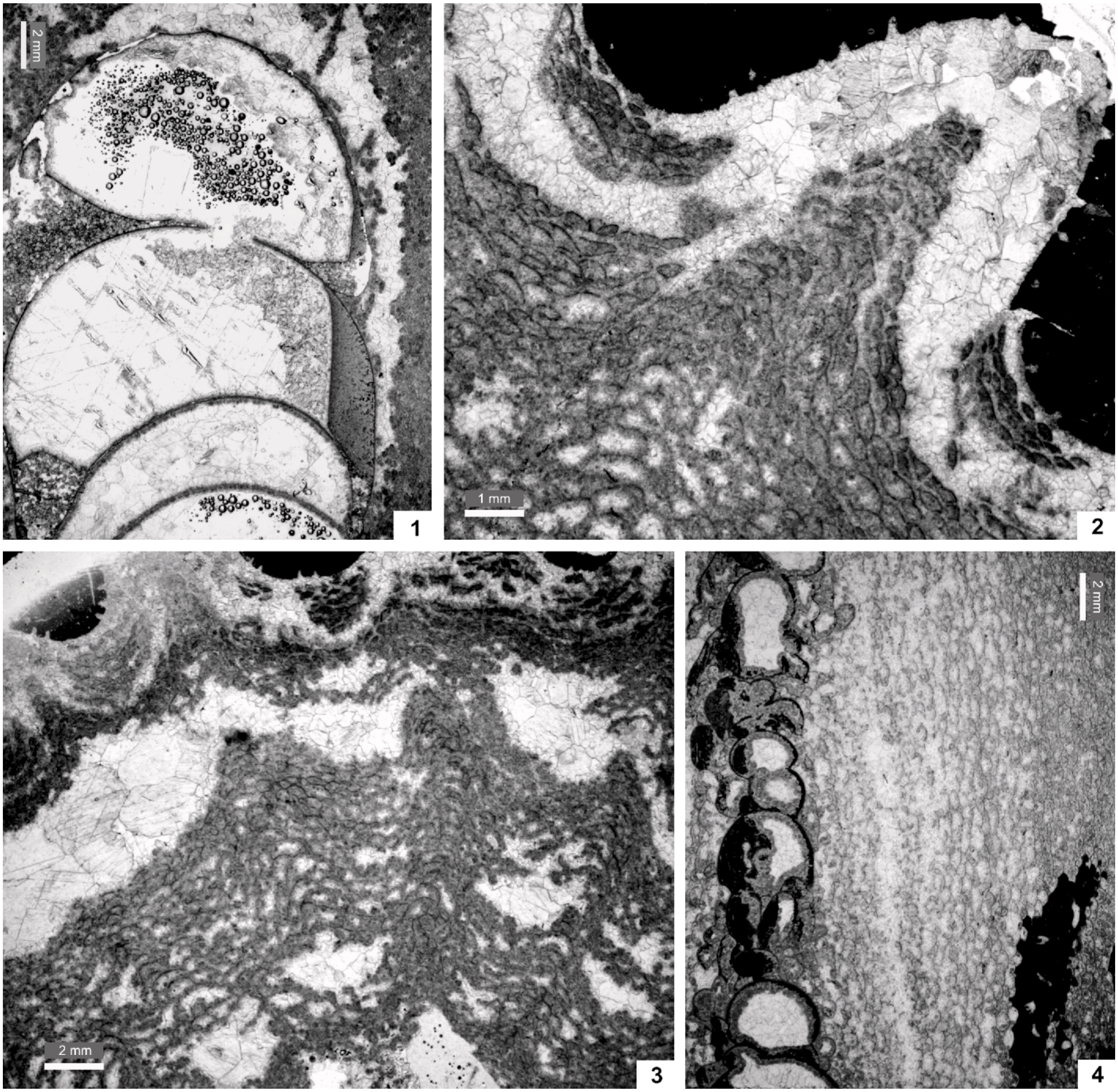

FIGURE 4—*Aulacera nodulosa* (Billings, 1857), Battery Member, upper Vaureal Formation, upper Katian; all specimens from locality A891 (12E/8, 55500–56000:74050), 300–400 m long coastal bluff at type locality, Battery Point. *1*, hypotype GSC 129372, axial longitudinal view of the central cyst-plates, large specimen; *2*, *3*, hypotype GSC 129373, transverse skeletal view; *4*, hypotype GSC 129380, small specimen, axial view of cyst-plates surrounded by microcyst-plates; note the relatively variable but narrow axial cavity in *A. nodulosa*, and the laterally overlapping axial cyst-plates typical of the species.

1928; Petryk, 1981; Copper, 1989; Copper et al., 2011). Petryk (1981, 1982) associated their frequency with shallowing sedimentary "megacycles" on the Anticosti Platform, influenced by Late Ordovician glaciation in North Africa. Within the upper Katian–Hirnantian of Anticosti there are three regressive cycles, one in the upper Vaureal Formation, one in the middle Ellis Bay Formation, and one at the top of the Ellis Bay Formation; these may coincide with Gondwana glacial episodes (Copper et al., 2011). In the Katian Vaureal Formation, especially the upper parts, *Aulacera* occurs mostly in shallower carbonate facies from west to east along strike for some 250 km: some were reworked in sandstone units in the upper Vaureal Formation (the Mill Bay, Grindstone, and Velleda members; see Long and Copper, 1987 for maps of localities on the northeast coast).

In the lower Hirnantian Prinsta Member of the Ellis Bay Formation, *Quasiaulacera stellata* are virtually confined to the northeastern coast of the island, in some places occurring helter-skelter in dense layers of broken skeletons detached from their bases (Fig. 3). These are associated and overgrown with the tabulate coral *Ellisites* (Cameron and Copper, 1994, fig. 3b, 3c, 3d). In the center of the island, along the Vaureal River,

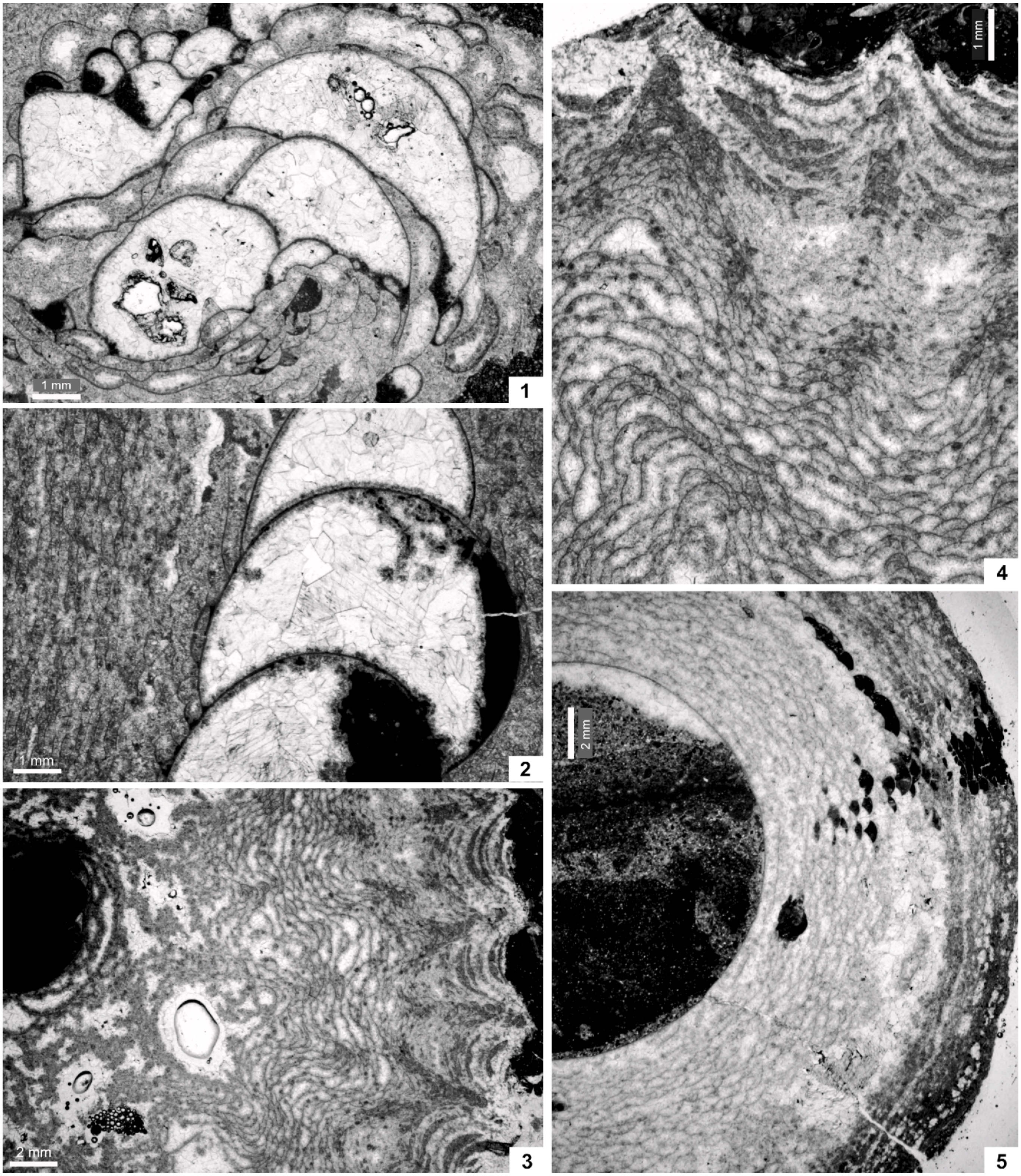

FIGURE 5—*1–4*, *Aulacera undulata* (Billings, 1857), carbonate facies of the Velleda Member, upper Vaureal Formation, uppermost Katian, type locality at West Point lighthouse, western Anticosti Island: *1*, hypotype GSC 129606; *2*, hypotype GSC 129610, longitudinal-oblique axial section with irregular cyst-plates, locality A971c (22H/16, 90400:23900); *3*, *4*, GSC 129603, transverse sections of the skeleton demonstrating the undulose overall structure of microcyst-plates towards the outer wall, note a faint tendency to develop larger continuous flatter cyst-plates in the outer few mm (precursor of the laminae in *Quasiaulacera*?), Grindstone Member, upper Vaureal Formation, locality A951a (12E/8, 52540:73770), Homard roadcut, 400 m west of lower Salmon River bridge; *5*, *Aulacera* sp., GSC 129608, immature, smooth cylindrical form, one of the oldest specimens in the Anticosti section, Homard Member, middle Vaureal Formation, locality A486, (12E/8, 52620:78240, Harvey Creek mouth section).

aulaceratids make a rare appearance in the small coral patch reefs of the lower Ellis Bay Formation, described by Lake (1981), who, however, did not mention the presence of aulaceratids that occur in these reefs, describing the laminar encrusting coral *Ellisites* as a stromatoporoid, and the abundant solenoporid rhodoliths as the stromatoporoid *Ecclimadictyon*. Aulaceratids are absent or very rare in the Fraise, Juncliff, and Parastro members of the lower Ellis Bay Formation at the western end of the island (Fig. 1). Those beds are dominated by rich shelly faunas, with scarce small tabulate and solitary rugose corals, and lacking stromatoporoids. At the western end, *Quasiaulacera occidua* is common in outcrops of the Lousy Cove Member of the Ellis Bay Formation along the tidal flats just north of Laframboise Pointe, and north of Cap Henri and Cap à l'Aigle along the shores of Ellis Bay (Fig. 1; see also Petryk, 1982, pls. 1, 2). Thus *Quasiaulacera* are present only in the lower Ellis Bay Formation on the northeastern coast, and only in the upper Ellis Bay Formation on the western coast. This may be attributed to their prevalence in the shallower-water, coral-rich facies of the Ellis Bay Formation, and their absence in deeper shelly communities. Petryk (1981, 1982) suggested that aulaceratids were important elements in Hirnantian reef construction on Anticosti. However, this is not corroborated from our sampling of numerous outcrops, and from collections of over 250 specimens; reefs had fewer specimens, and at best aulaceratids were concentrated in biostromal layers with favositids and the encrusting heliolitids *Ellisites* and *Protrochiscolithus*, or in isolated perireefal or non-reefal clusters or "forests" (e.g., Desrochers et al., 1998, fig. 3; Nestor et al., 2010, fig. 8). We have not recorded any *Quasiaulacera* in the Pointe Laframboise patch reefs, nor did Petryk (1982; the specimen he shows is from the Lousy Cove Member).

The stratigraphic distribution of the aulaceratids of Anticosti places them in the upper 100–150 m of the Katian Vaureal Formation, continuing through the overlying Hirnantian Ellis Bay Formation. The oldest aulaceratids on Anticosti occur in the equivalent of the provisionally named Homard Member of the Vaureal Formation (Fig. 2), consisting of ~60 m of rhythmically bedded micrites that underlie the Battery Member at Battery Point (Fig. 4). The Homard Member is well exposed in the bluffs stretching west from the Salmon River mouth past Anse Harvey, to Baie des Homards and Homard Creek; it contains rare, small aulaceratids (<5 cm diameter) with a smooth cylindrical wall (Figs. 4, 5). Aulaceratids in general do not make an abundant appearance until the upper part of the Vaureal Formation (Mill Bay Member or higher), and other stromatoporoids are virtually absent. *Aulacera undulata* (Billings, 1857) occurs in the stratigraphic equivalents of the lower Grindstone Member of the Vaureal Formation at the eastern end (see Figs. 2, 4.1–4.4). Only rare non-aulaceratids such as *Pseudostylodictyon* occur in the upper Vaureal Formation (Nestor et al., 2010). We note that *Aulacera* occurs in both the Velleda and Grindstone members, formerly assigned to the Ellis Bay Formation (Long and Copper, 1987), but now to the Vaureal Formation (Desrochers et al., 2008; Copper et al., in press).

The aulaceratids saw a renewed evolutionary burst on Anticosti during deposition of the Hirnantian Ellis Bay sediments, but they became abruptly extinct at the top of the uppermost reefal Laframboise Member of the Ellis Bay Formation. Reworked aulaceratids occur in the basal oncolite unit of the Laframboise Member. There are no aulaceratids (and indeed no stromatoporoid sponges, nor colonial rugose corals) in the lowermost Rhuddanian Becscie Formation, directly above the reefs (as already noted by Twenhofel, 1928, p. 108). We thus define the final mass extinction boundary, and the Ordovician–Silurian boundary on Anticosti Island, at the top of the uppermost reefs, or the top of the oncolite bed, where reefs are absent (Fig. 2). This level is also marked by the extinction of many invertebrate shelly fossils, as well as planktic microfauna such as chitinozoans (Soufiane and Achab, 2000; Achab et al., 2012) and acritarchs (Delabroye et al., 2011). Lecompte (1956) and Dong (2001) stated that aulaceratids continued into the Silurian, but this is not the case on Anticosti.

SYSTEMATIC PALEONTOLOGY

All specimens were recorded by their GSC number, Anticosti locality number, topographic map sheet number, and metric grid references, with a digital file of the locality database stored at the Geological Survey of Canada (GSC), Ottawa.

Phylum Porifera Grant, 1836
Class Stromatoporoidea Nicholson and Murie, 1878
Order Labechiida Kühn, 1927
Family Aulaceratidae Kühn, 1927

Remarks.—This is equal to Family Beatricidae Raymond, 1931 (p. 178; see Stearn et al., 1999). For a thorough review of the family characteristics and assignments see Webby (2012, p. 32–40). The family includes the following genera, with tentative geological ranges: *Aulacera* Plummer, 1843 (=*Beatricea* Billings, 1857; middle–upper Katian, ?Hirnantian); unbranched *Cryptophragmus* Raymond, 1914 (upper Sandbian); branching *Thamnobeatricea* Raymond, 1931 (=?*Cladophragmus* Raymond, 1931, upper Darriwilian–Katian); *Sinodictyon* Yabe and Sugiyama, 1930 (upper Darriwilian); *Ludictyon* Ozaki, 1938 (upper Darriwilian, but said to extend into the Silurian of China by Dong, 2001); *Alleynodictyon* Webby, 1971 (lower Katian); *Quasiaulacera* n. gen. (Hirnantian).

Yavorsky (1955, 1963) showed that aulaceratids were widely expanded across the Siberian Platform, as they were in North America (Foerste, 1909). Ancestral genera appear to have been derived from North China and Korea. In Estonia, there are few Hirnantian stromatoporoids, and aulaceratids are absent in the Ordovician (Nestor, 1997). Bolton (1988, p. 24) regarded *Aulacera* as a *nomen oblitum*, but he continued to follow the example of Galloway and St. Jean (1961), and ultimately retained the name *Aulacera*, whose type species was designated as *A. plummeri* by Galloway (1957). There are 12–15 species of Ordovician aulaceratids described so far (see Yavorsky, 1955, 1963; and Nestor, 1976 for Siberian taxa). Stearn et al. (1999) assigned two columnar genera, *Ludictyon* from Guizhou (Silurian), and *Pararosenella* from the Caucasus and Ukraine (Famennian) as long-range post-O/S boundary survivors of the aulaceratids.

Genus Quasiaulacera new genus

Type species.—*Quasiaulacera occidua* n. sp.

Diagnosis.—Large, columnar, non-branching aulaceratids, generally fluted on outside, up to ~2 to 3 m long, 20 to 40 cm in diameter. Small, immature specimens may be smooth on outside. Skeleton consisting of three layers: central axial zone with cyst-plates occupying about 20 to 50 percent of the skeleton, surrounded by envelope of microcyst-plates, and ultimately covered by outer layer of multiple, thin, concentric laminae, penetrated by thick, radiating, superposed pillars. Outer surface has papillose appearance due to penetration of pillars through laminae. Growth stages marked by ontogenetically early slender smooth columnar form with large axial column, until that reaches diameter of up to 2 to 3 cm. Beyond that stage, microcyst-plates and outer laminar layers become fluted. Astrorhizae unknown.

Etymology.—Latin, *quasi*, alike or similar to. Plummer (1843) did not state the derivation of his genus name *Aulacera*. It is probably from the Greek, *aulon* or *aulos*, a hollow flute or pipe, and *keros*, horn, referring to the cylindrical shape with tapering ends.

Occurrence.—Lousy Cove Member, Ellis Bay Formation, western Anticosti Island, upper Hirnantian, uppermost Ordovician. It is abundant in the Hirnantian of Anticosti Island where it is characterized by a lower Hirnantian species, *Q. stellata* n. sp., and a higher Hirnantian species, *Q. occidua* n. sp. We are uncertain at present if this genus also occurs in the uppermost Hirnantian reefal Laframboise Member of Anticosti.

Remarks.—We introduce new internal skeletal macrostructures, the *microcyst-plates*. These structures are markedly smaller than cyst-plates; the latter average 2 mm (range 1.2–3.5 mm, by comparison to *Pachystylostroma* from Anticosti) in width, whereas microcyst-plates average 0.5 mm (range 0.3–0.6 mm) in width.

The new genus is readily differentiated from its older counterpart, *Aulacera* Plummer, 1843, by possession of an outermost multiple layered envelope of thin laminae, intersected by densely packed pillars. In the central axial zone there is a stack of much larger, convex-up, widely spaced cyst-plates; in *Aulacera* the central cavity is normally much narrower by about 50 percent (compare Figs. 4.1–4.4, 5.1, 5.2). On Anticosti *Aulacera* from the Katian Vaureal Formation commonly possesses axial cyst-plates that overlap each other laterally in a large axial cavity. This large axial cavity for *Quasiaulacera* is especially notable in the type species *Q. occidua* n. sp., where it may form more than 50 percent of the skeleton's volume. *Aulacera* has only two skeletal layers and lacks the dense clusters of long pillars that are a feature of the outer laminar envelope. *Aulacera* pillars tend to be rare, short (<1 mm), discontinuous, and spine-like, or denticulate (see Figs. 4.1, 5.3). The Sandbian–lower Katian genus *Cryptophragmus* Raymond, 1914 is distinct in being a small, finger-sized aulaceratid with a large axial portion filled by convex cyst-plates, and an outer, thin envelope of laminae with pillars; it lacks microcyst-plate layers. Darriwilian–Sandbian–lower Katian *Thamnobeatricea* Raymond, 1931 is a branching form probably ancestral to *Cryptophragmus*.

Quasiaulacera seems likely to have evolved from late Katian *Aulacera* such as *A. undulata* (Billings, 1857), by developing layers of thin, outer laminae from extended flat cyst-plates, through which pillars were extended from the microcyst-plate layers within. Indeed, *A. undulata* have some flat cyst-plates like that in the outermost layers of the skeleton (Fig. 5.3, 5.4). There are no *Quasiaulacera* specimens that have a nodular outer appearance, as seen in the *Aulacera* of Katian age, such as *A. nodulosa* (Billings, 1857). All specimens were fluted (i.e., possessing outer, longitudinal, rounded ridges and grooves), though small specimens were virtually smooth on the outside. Very small diameter (1–2 cm) skeletons from the lowermost Ellis Bay Formation may have only the thinnest layer of one or two outer laminae and radiating pillars, suggesting that the addition of the outer laminae led to the evolution of *Quasiaulacera* from *Aulacera* in early Hirnantian time. As for *Aulacera undulata*, Twenhofel (1928, p. 106) noted that "in the young stages the surfaces of the stems are smooth ..."

The genus *Quasiaulacera* is confined to the Ellis Bay Formation, whereas *Aulacera* dominates in the Vaureal Formation. Small specimens in the lower Prinsta Member of the Ellis Bay Formation along the Prinsta River, and in the bluffs east of the river mouth, have only a very thin, <1–2 mm, outer laminar layer, and may be confused with *Aulacera* (e.g., coastal bluffs east of the Prinsta River mouth, locality A135, 12F/5, 74480:66450). This distinction in the distribution of *Quasiaulacera* came about with the sequence stratigraphic work of Desrochers et al. (2008) on the northeastern coast of the island, and the acritarch and chitinozoan analyses of Delabroye et al. (2011) at both ends of the island. That called into question the correlations of Schuchert and Twenhofel (1910), who assumed that the two thick sandy members extending from Lousy Cove through Prinsta Bay and Mill Bay belonged to the lower Ellis Bay Formation, a correlation followed by Long and Copper (1987) in the lack of shelly evidence (e.g., absence of the diagnostic Hirnantian brachiopods *Hindella* and *Hirnantia*).

QUASIAULACERA OCCIDUA new species
Figures 3.3–3.6, 6, 7

1857 "tree-like fossil" RICHARDSON, p. 216.
1886? *Beatricea nodulosa* Billings; NICHOLSON, pl. 8, figs. 6, 7.
1982 "aulacerid" Petryk, 1982, pl. 1, figs. 1–3, pl. 2, fig. 1.
1994 "New aulacerid genus" CAMERON AND COPPER, fig. 2b, 2d.
1998 "*Quasiaulacera*" (idealized reconstruction); DESROCHERS ET AL., fig. 3.
2011 "*Quasiaulacera* sp. B" COPPER, NESTOR, AND STOCK, fig. 1A, 1D, 1E.

Diagnosis.—*Quasiaulacera* with relatively thick outer laminar layer of 10–20 concentric, closely spaced laminae penetrated by continuous, superposed pillars up to ~10 mm long, 0.2–0.3 mm in diameter, protruding through successive outer laminae, and thicker at base of each lamina than at top. Pillars begin at base of outer laminar layer, but absent in intermediate microcyst-plate layer. Large, smooth-sided axial cavity filled with stack of single large cyst-plates. This is surrounded by middle layer of microcyst-plates, outer parts of which form grooves and ridges reflected in outer laminar envelope as fluting.

Description.—Long, continuous single columnar skeletons may be up to or exceed 2 m in length, with diameters in the range of 15–20 cm, and are longitudinally grooved on the outside; basal diameters of mature specimens measured in situ on the bedding plane average ~20 cm in diameter (Fig. 3.5, 3.6). Specimens are commonly broken or crushed in the recumbent position, as the large hollow axial cavity, usually missing the central cyst-plates due to bioerosion or dissolution, led to fractures. Outer surface of well preserved specimens are minutely pustulose, due to the pillars in the outer laminae evident on the surface. Outer laminar layer consists of 10–20 distinctive laminae, cumulatively 1–3 cm thick, penetrated by numerous long, non-branching pillars over 10–12 mm (Figs. 6, 7) in extent, and 0.3 mm in diameter, evenly but irregularly spaced at 0.5 to 1.0 mm (Fig. 7.1–7.4). New pillars are inserted between older pillars with skeletal expansion (Fig. 6.2, 6.3). The laminae are more densely packed in the grooves (4 per mm) than in the ridges, where they are spaced at about 3 per mm (see Fig. 6.2). Middle layer (Fig. 6.1, 6.3) composed of small microcyst-plates up to ~0.5 mm in diameter and 0.2–0.3 mm high; this layer may occupy 30–40 percent of the skeleton overall; wave-like expansion of the outer part of the middle layer, and expanded through variations in the spacing of the laminar layers, led to the fluted external skeletal form. The large axial cavity makes up about 40–50 percent of the skeleton, but cyst-plates are almost never preserved here, and thus their nature is obscure; where preserved, fragments of cyst-plates are extremely thin.

Etymology.—Latin, *occidua*, from *occiduus*, "setting, sinking, or westerly [sun]," referring to the westerly occurrence of this species on Anticosti Island, and the fact that it is one of the last aulaceratids to survive in the late Hirnantian, prior to the O/S mass extinction.

Types.—Holotype GSC 129346. The type locality is A972, tidal-flat outcrops adjacent to Laframboise Creek, ~300 m NNW of Pointe Laframboise, western Anticosti Island, NTS 22H/16,

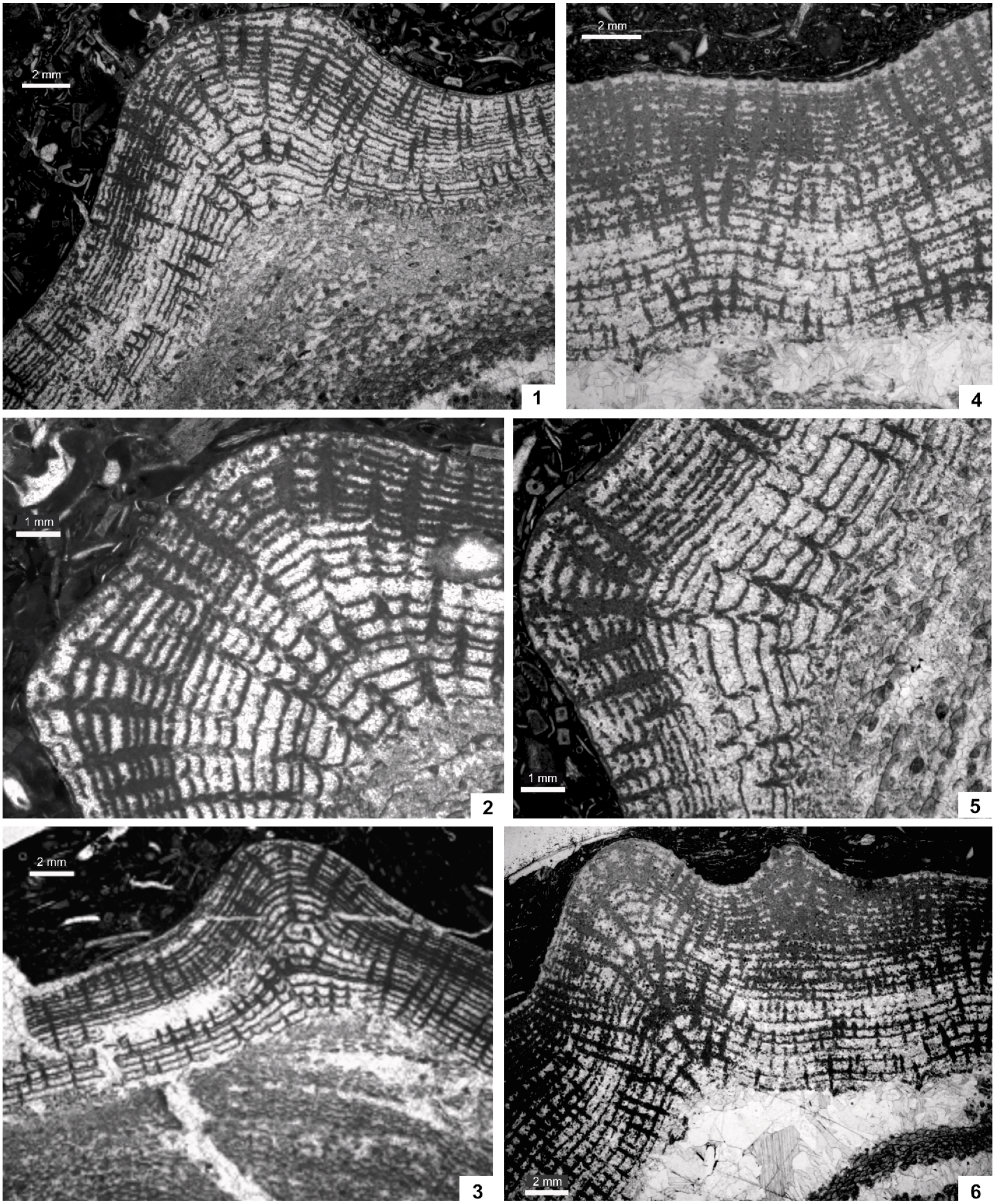

FIGURE 6—*Quasiaulacera occidua* n. sp., transverse thin section views of the skeleton. *1*, *4–6*, paratype GSC 129355, showing distinctive outer layer of densely packed smooth laminae intersected by long pillars (features that are absent in *Aulacera*), upper Lousy Cove Member, Ellis Bay Formation; locality A1163 (22H/16, 04620:17270; see Fig. 2.3), eastern side of Ellis Bay; *2*, *3*, holotype GSC 129346, locality A972 (22H/16, 97500:17900; see Fig. 2.5, 2.6), tidal flat outcrops south of Laframboise Creek, ∼400 m north of Pointe Laframboise, western coast.

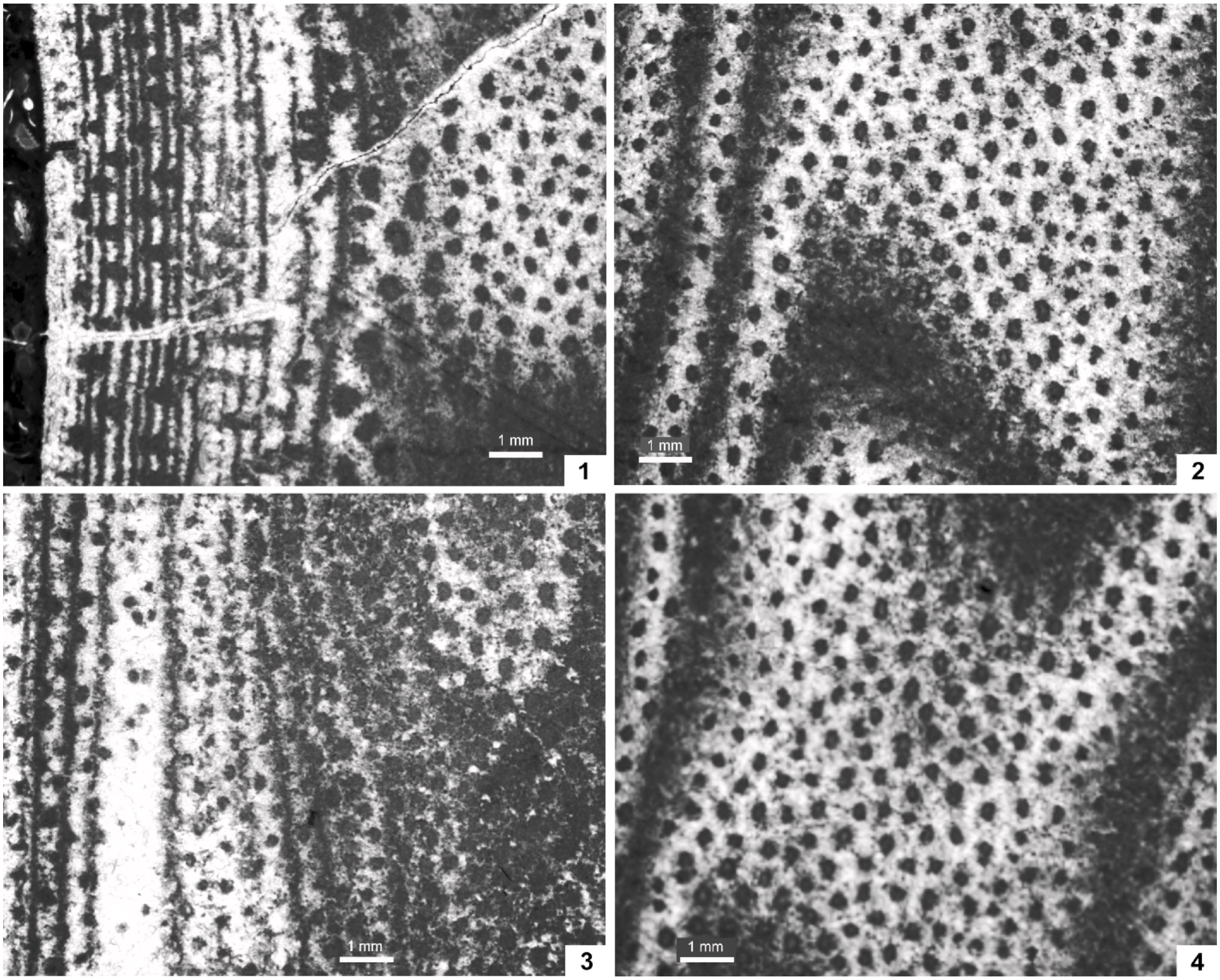

FIGURE 7—*Quasiaulacera occidua* n. sp., tangential, longitudinal views of the skeleton; holotype GSC 129346, upper Lousy Cove Member, Ellis Bay Formation, locality A972 (22H/16, 97500:17900). Note that the laminar layers appear to consist of granular structure, and that the intersecting pillars are circular in cross-section, and may appear hollow close to the intersection with laminae; they are spaced regularly at from 0.5 to 0.8 mm, and are ∼0.2–0.3 mm in diameter.

975550:17920 (Figs. 1, 3, 6, 7); upper Lousy Cove Member, 5–8 m below the reefal Laframboise Member, Ellis Bay Formation, upper Hirnantian. The basal attachment site of the holotype was not located, but these ∼40–70 cm diameter bases are abundant on the tidal flats, standing out in stark contrast to the darker gray host carbonates (Fig. 3.5, 3.6). Paratype GSC 129355, locality A1163, eastern side of Ellis Bay, south of Baie des Navots, towards Cap à l'Aigle, 22H/16, 04260:17270, Lousy Cove Member, Ellis Bay Formation (see Fig. 3.3; this is probably the locality cited by Richardson, 1857, p. 216). Material includes about 30 specimens. Similar recumbent cylindrical specimens occur on the tidal flats on the western (Cap Henri) and eastern sides of Ellis Bay (Cap à l'Aigle, Fig. 3.3), at the same stratigraphic level (Fig. 1).

Occurrence.—Richardson (1857, p. 216) found a partial specimen on the tidal flats near Cap à l'Aigle in the equivalents of the Lousy Cove Member, 17 ft (∼5 m) below the Laframboise coral bed, and described it as a "tree-like fossil . . . One specimen now in the museum of the Survey is 10.5 feet long, six inches in diameter at the larger end, and but an inch or so less at the other." (Note: this specimen is missing from the GSC Billings collection). He estimated its total length as some 30 ft (∼9 m). Nearly all material comes from the western end of the island in the Lousy Cove Member. Rare specimens occur in the eastern part of the upper Ellis Bay Formation outcrop belt in the Homard road outcrops (e.g., locality A895, 12E/8, 48460:7610). The total stratigraphic range of this species is uncertain; Petryk (1981, 1982) and Bolton (1988) cited specimens of aulaceratids from roughly the middle of the Ellis Bay Formation, but none have been illustrated, so we are uncertain if the ranges of species overlap. We have found no specimens in the lower three members of the Ellis Bay Formation at the western end (nor did Petryk, 1982).

Remarks.—Richardson's (1857) specimens were collected from within "grey limestone" (p. 216) 12–17 feet (3.7–5.2 m) below the "coral limestone bed" (=Laframboise Member). Twenhofel (1928) cited aulaceratids from his "Ellis Bay zones 5–8," but he made no thin sections, nor did he illustrate any specimens to note their internal differences from older Vaureal forms of *Aulacera*.

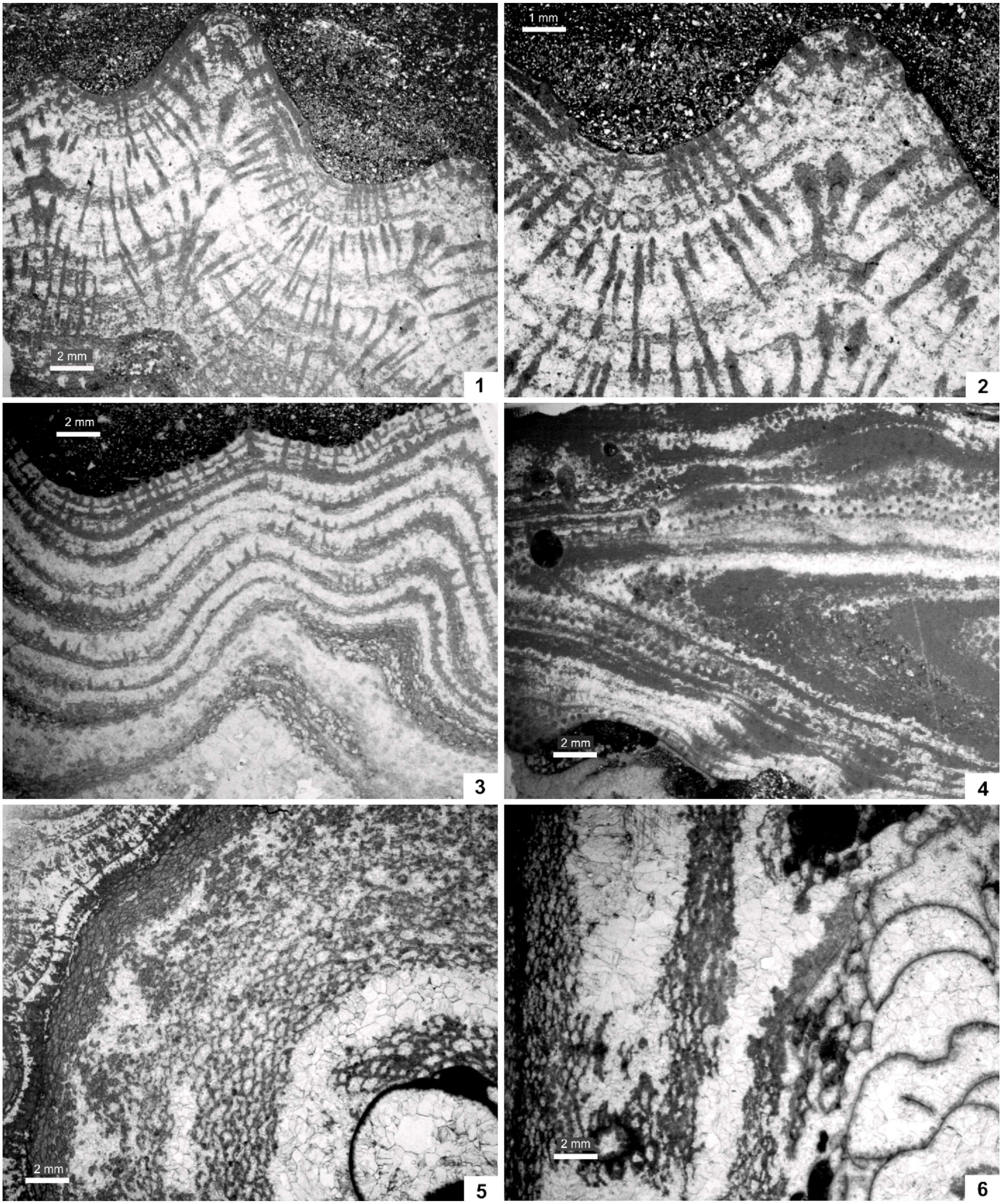

FIGURE *8*—Thin sections of *Quasiaulacera stellata* n. sp. demonstrating the basic structural features, with an outer set of laminae that are partly interrupted by microcyst-plates. *1*, *2*, holotype GSC 129342, transverse views (*2* as local enlargement of *1*) of the outer laminar layers and pillars, locality A315 (12F/5, 80920:64780); *3*, paratype GSC 129657, transverse section of the outermost laminar layer and pillars, and part of the middle microcyst-plate layer, demonstrating that in *Q. stellata* the microcyst plates disappear progressively towards the outside of the skeleton, locality A315; *4*, paratype GSC 129627, tangential longitudinal view along the outer laminar layers, locality A315; *5*, paratype GSC 129592, transverse view showing the axial cavity, surrounding microcyst-plate and outer laminar layers of small specimen, locality A496 (12F/5, 80380–700:65760–66480), Table Head upper cliffs, east end (specimens toppled on beach from upper Prinsta Member); *6*, paratype GSC 129796, axial longitudinal view showing cyst-plates and surrounding envelope of microcyst-plates, locality A315. All basal Prinsta Member, Ellis Bay Formation, lower Hirnantian.

This species is distinguishable from its older Hirnantian ancestor, *Quasiaulacera stellata* n. sp., by a larger axial cavity with large, stacked cyst-plates, and a much thicker, continuous outer layer of 10–20 multiple laminae penetrated by pillars (Figs. 6, 7). In addition, the microcyst-plates do not appear in the outer laminar layers, as they do in *Q. stellata* n. sp., nor do pillars or denticles appear in the microcyst-plate layer inside that. This suggests that the evolutionary trend within the Hirnantian Ellis Bay Formation, from *Q. stellata* n. sp. to *Q. occidua* n. sp. is marked by stronger development of the outer laminae and pillars, and progressive loss of the microcyst-plates within the laminar layers, and denticles between the microcyst-plates. Many specimens of *Q. occidua* are crushed; this feature very likely relates to the very large axial cavity, commonly hollow, thus post-mortem, making the skeleton vulnerable to fracture and early diagenesis. This is not seen in *Quasiaulacera stellata*, nor in older *Aulacera* on Anticosti. In examining a specimen from the "West Point lighthouse" (sent by Whiteaves), Nicholson (1886, pl. 8, figs. 6, 7) noted a laminar outer layer with strong pillars, as known from *Q. occidua*. It is likely that this sample came from the Ellis Bay locality of Richardson (1857, cited above) and not from West Point (see Fig. 5 for specimens of *A. undulata*).

QUASIAULACERA STELLATA new species
Figures 3.1, 3.2, 8

1982 "aulacerid" Petryk, p. 397, pl. 2, figs. 3, 4 (from Prinsta Bay).
1994 "New aulacerid genus" CAMERON AND COPPER, fig. 3a–3f (type locality).
2011 "*Quasiaulacera* sp. A" COPPER, NESTOR, AND STOCK, fig. 1B (type locality).

Diagnosis.—*Quasiaulacera* with smaller diameter axial zone possessing laterally overlapping cyst-plates. Variably developed outer laminar layers commonly interrupted by microcyst-plate layers or lenses, which led to accentuation of exterior ridges and grooves. Gradual transition of appearance of pillars within outer regions of microcyst-plate layer, and accentuation of laminar layers outwards. Outer laminar layer commonly has clusters of microcyst-plates in ridges and troughs of grooved exterior. Central core of skeleton is surrounded by envelope of microcyst-plates, initially forming a smooth outer ring; in larger specimens fluted structure of skeleton begins in microcyst-plate layer. On outer part of microcyst-plate envelope, microcyst-plates began to form ridges and grooves that persist through outer laminar envelope; small, short, spine-like denticles $<$0.1–0.2 mm long rest on some microcyst-plates, but do not penetrate overlying microcyst-plates. Outer skeleton appearance is fluted in mature specimens, but may be smooth in immature finger-sized specimens.

Description.—Diameters of some broken skeletons of *Q. stellata* from the lower Prinsta Member exceed 35–40 cm; lengths indeterminable but at least 0.8 m, and judging from wide diameters of broken specimens, possibly $>$2 m. Axial zone occupying $<$20 percent of volume, marked by single or overlapping cyst-plates, and in some outlined by larger, bubble-like cyst-plates. Middle layer of microcyst-plates commonly with denticles. Outer laminar layers variably developed, from being relatively thick in mature specimens (Fig. 8.1–8.3), to being thinner and showing latilaminar interruptions by layers or lenses of microcyst-plates (Fig. 8.1, 8.2, 8.4). Densely packed pillars up to 0.2 mm in diameter, packed at 2–3 per mm laterally (Fig. 8.1–8.4). Middle microcyst-plate layer initially smooth towards the axis, then fluted in outer parts (Fig. 8.5). Axial zone relatively narrow, with cyst-plates that commonly overlap laterally (Fig. 8.5, 8.6).

Etymology.—*Stellata*, Latin, "starry," due to its star-shaped transverse section.

Types.—Holotype GSC 129342; paratypes GSC 129370 and 129796, immature smooth specimen. The type locality is A315 (=A468b), Lousy Cove, north side, 12F/5, 80900:64850, lower Prinsta Member, Ellis Bay Formation. At this tidal-flat outcrop, the lower reaches may be covered in some years by up to 2 m thick of boulders and cobbles brought by winter storms, as shown in Cameron and Copper (1994, fig. 3d–3f). Access to the locality is by a bush trail from the Table Head lighthouse to Lousy Cove, or by boat from the sea. Specimens are scattered in the bluff outcrop, in the same bed, 12F/5, 80920:64780; lower 1–2 m of the Prinsta Member, Ellis Bay Formation. Specimens also occur in outcrop in lower part of bluff extending north to Table Head, in the same bed, 12F/5, 80920:64780. Specimens of the index genus *Hirnantia* also occur in the lower Prinsta Member at Lousy Cove, seen on the front cover of the monograph by Jin and Zhan (2008).

Occurrence.—The basal (1–2 m) Prinsta Member is packed with broken and overturned, as well as attachment bases, of *Quasiaulacera stellata* n. sp. at the type locality, and this bed may be followed for $\sim$1 km along strike in the direction of Table Head (Figs. 1, 3). It is less common in the bluffs east of the Prinsta River mouth (Petryk, 1982), and upstream along the river bank. The species has been found in only the Prinsta Member (lower Ellis Bay Formation) from the eastern facies belt as far west as the western side of the Salmon River, and along Homard road leading to Baie des Homards (see Fig. 8 and map in Long and Copper, 1987).

Remarks.—The species is distinguished from the younger *Quasiaulacera occidua* n. sp. by having a thinner, and less regularly spaced, outer envelope of laminae that is interrupted by thin lenses of microcyst-plates (Fig. 7.1–7.3). Pillars are usually smaller in diameter, and more closely spaced (Fig. 7.1, 7.3, 7.5). Small denticles appear within the middle microcyst-plate layer, that are not seen in the type species *Q. occidua* (Fig. 8.5, 8.6). The axial cavity has a smaller diameter, occasionally with laterally overlapping or irregularly stacked cyst-plates (Fig. 8.5, 8.6). At the type locality, and towards Table Head, broken specimens were commonly bored and eroded on the outside (Fig. 8.2), and covered by encrusting tabulate corals, thus preserving their outer features in detail.

CONCLUSIONS

The Hirnantian (uppermost Ordovician, Ellis Bay Formation) was marked by evolution of a new and abundant suite of columnar aulaceratid stromatoporoids featuring gigantism, largely replacing *Aulacera* of the Katian in the first O/S extinction wave. Two species form this unusual assemblage, *Quasiaulacera stellata* n. sp. and *Q. occidua*. n. sp.

The last aulaceratids on Anticosti disappeared at the end of a reefal phase of sedimentation, i.e., at the top of the Laframboise Member, Ellis Bay Formation, marking the O/S boundary.

The final Ellis Bay Formation reefs of the Laframboise Member were dominated by clathrodictyid stromatoporoids, replacing the aulaceratids as a common element in the Ordovician. No aulaceratids occur in the Lower Silurian (Rhuddanian) Becscie Formation.

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