

Earltonella fredricksi n. gen n. sp. and *Thalassocystis striata* (Chlorophyta, Bryopsidales) from the Silurian (Llandoveryan) of the Timiskaming outlier, Ontario, Canada

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Abstract.—Specimens of macroalgae are reported and described herein from newly discovered algal-Lagerstätten within the Llandoveryan Earlton Formation at two localities separated by a distance of 45 km in the Timiskaming outlier of Ontario, Canada. Both localities are characterized by abundant specimens of the *Codium*-like bryopsidalean green alga *Thalassocystis striata*, the details of which, including within-assembly morphological variation, compare closely to material from the type locality. Previously, this noncalcified taxon was known only from the Llandoveryan Schoolcraft Formation in northern Michigan, ~500 km to the west. These new occurrences provide additional evidence that the alga-bearing intervals within the Earlton Formation at both Timiskaming localities correlate with the Schoolcraft Formation in the Michigan Basin. An associated noncalcified form at one of the Timiskaming localities is described as a new genus and species, *Earltonella fredricksi* LoDuca, n. gen. n. sp., the thallus architecture of which, with a creeping, runner-like stolon and numerous pinnate fronds, broadly resembles that of the living bryopsidalean alga *Caulerpa*. In broader terms, these new algal-Lagerstätten indicate that for a brief time during the late Llandoveryan, as with other times during the Silurian, unusual conditions conducive to both the proliferation and preservation of expansive ‘seaweed meadows’ were established across regional-scale areas of the Laurentian epeiric sea.

Introduction

Thalassocystis striata Taggart and Parker, 1976, was described as a noncalcified macroalga on the basis of material from the Llandoveryan Schoolcraft Formation near the city of Manistique in the Upper Peninsula of Michigan (Taggart and Parker, 1976). Recently, LoDuca et al. (2021) reported the first occurrence of this species from a locality outside the general Manistique area, a quarry exposure of the Schoolcraft Formation ~30 km to the east of the type locality. Based on that better-preserved material, LoDuca et al. (2021) redescribed the taxon as a green alga belonging to the Order Bryopsidales with a siphonous, multiaxial thallus architecture broadly similar to that of living *Codium* Stackhouse, 1797, and *Pseudocodium* Weber-van Bosse, 1896. In the present report, two additional occurrences of *T. striata* are described from newly discovered algal-Lagerstätten within the Llandoveryan Earlton Formation in the Timiskaming outlier (Lake Timiskaming area) of Ontario, Canada, ~500 km to the east of the type locality. In addition, a new form within one of the Timiskaming occurrences is proposed herein as a new genus and species of noncalcified bryopsidalean alga. This taxon is characterized by a thallus architecture broadly similar to that of living *Caulerpa*

Lamouroux, 1809, consisting of a creeping, runner-like stolon bearing numerous pinnate fronds and, as with *T. striata*, the specimens are preserved as carbonaceous compressions. Notably, the pinnate fronds of the new taxon show similarities to those of two macroalga genera previously described from the Ordovician and Silurian of North America.

Geologic setting and regional correlations

The specimens described herein were collected from two localities within the Timiskaming outlier in the Lake Timiskaming area of Ontario. One of these, the Dionne Concrete Products quarry, is located on the east side of Highway 11 ~10 km north of Earlton. The other, ~45 km to the south, is a shoreline exposure along the southern end of Wabi (Dawson) Point. In Bolton and Copeland (1972, fig. 1), these are localities 25 (= Macnamara quarry) and 8, respectively.

In the Dionne Concrete Products quarry, the 1–4 cm-thick alga-bearing slabs, which were collected by splitting blocks concentrated in spoil piles along a quarry road near the top of the pit, are composed of yellowish-brown to medium-gray dolomiticrite. Apart from the algae, the specimen-bearing surfaces are largely barren. The few associated shelly taxa include spiriferid brachiopods and the encrinurid trilobite *Rielaspis elegantula* (Billings, 1866). Rare horizontal burrows are evident on some surfaces (Fig. 1). Because the material described herein was not

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Figure 1. *Earltonella fredricksi* LoDuca, n. gen. n. sp., Earlton Formation (Llandoveryan), Dionne Concrete Products quarry, Earlton, Ontario. Top arrow, holotype, ROMIP 66270.1; lower right arrow, 66270.2; lower left arrow, 66270.3. Scale bar = 20 mm.

recovered in-situ, it cannot be definitively tied to a specific bed in the ~5 m-thick section exposed in the quarry. Spot excavations into the quarry wall during the course of this study identified several thin beds of alga-bearing dolomicrite in the middle part of the section, starting at ~1.5 m below the quarry top. These alternate with beds of biosparite and biomicrite. Since the alga-bearing intervals show exceptional preservation of non-biomineralized macroalgae and are lacking in comparably preserved animal remains, they represent examples of algal-Lagerstätten (see review in LoDuca et al., 2017).

The biosparite and biomicrite beds in the section are dominated by brachiopods and, especially in the upper part, corals, and include hardground surfaces at some levels (Copper and Armstrong, 1999). Bolton and Copeland (1972, fig. 2) placed the quarry section within the lower part of the Thornloe Formation. Later, Russell (1984) mapped strata in this area as belonging to his newly defined Earlton Formation, which includes the lower part of the Thornloe Formation as originally defined, and this assignment was followed in Copper and Armstrong (1999). Conodonts recovered from this quarry are indicative of the *celloni* Zone and point to an early to middle Telychian age (Radcliffe, 1998). Association of the algal material with *Rielaspis elegantula*, specimens of which were collected during the present investigation, also points to an early to middle Telychian age, because this trilobite previously has been reported only from strata of this age in the uppermost part of the Jupiter Formation (Pavillon Member) on Anticosti Island (Chatterton and Ludvigsen, 2004).

Algal material from the Wabi Point locality was recovered from blocks of fine-grained, thick-bedded dolomicrite that had fallen from the adjacent cliff face. These blocks appear to

have originated about three-quarters of the way up the section, from the “lithographic stone” interval of Hume (1925, p. 35). The largest specimen-bearing block, ~2 m on a side, yielded *Thalassocystis striata* material from several distinct levels. Breakage of this block in most cases resulted in highly irregular surfaces, but smooth splits were produced across algal thalli, in some cases showing shallow conchoidal fracture. The associated fauna is sparse, but includes crinoids, brachiopods, nautiloids, dendroid graptolites, ostracodes, and trilobites, including *Rielaspis elegantula* and a scutellid. As with the aforementioned Dionne quarry locality, the alga-bearing interval here qualifies as an algal-Lagerstätte. Russell (1984) mapped strata in this area as belonging to the Earlton Formation, and this assignment was followed by Copper and Armstrong (1999). Copper and Armstrong (1999) noted that the fauna is similar to that of the Fossil Hill Formation of the Bruce Peninsula and the Jupiter Formation (Pavillon Member) of Anticosti Island, both of which are early to middle Telychian in age.

Bolton and Copeland (1972, fig. 2) correlated the section at locality 25 (Dionne quarry, herein) with the middle part of the section at locality 8 (Wabi Point), but Colville and Johnson (1982, fig. 3) regarded the base of the former to lie stratigraphically immediately above the top of the latter. Both reports considered the section at locality 8 to be equivalent to the upper part of the Schoolcraft Formation in Michigan, and correlated a thick interval of *Pentamerus*-bearing strata at the nearby dock, ~10–15 m below the alga-bearing interval, with the upper *Pentamerus* bed of this unit. Colville and Johnson (1982, fig. 3), however, correlated the section at locality 25 with the Cordell Formation in Michigan, which immediately overlies the Schoolcraft Formation.

The recovery of *Thalassocystis striata* from both of these sections during the present investigation lends support to the Bolton and Copeland (1972) correlation. In addition, the age of the interval at locality 25, as indicated by recently obtained trilobite and conodont data, is also consistent with the Bolton and Copeland (1972) correlation. As noted above, these data, which were obtained after the Colville and Johnson study, point to an early to middle Telychian age for this interval. A similar age is indicated for the Schoolcraft Formation in the northern shelf area of the Michigan Basin (Al-Musawi, 2019), whereas the Cordell Formation is regarded as late Telychian to early Wenlockian, in part based on brachiopod and coral data (Colville and Johnson, 1982). Crucially, if the Bolton and Copeland (1972) correlation is correct, *T. striata* in the Lake Timiskaming area would be restricted to Schoolcraft-equivalent strata. This, then, suggests the possibility of high-resolution chronostratigraphic value for this alga-bearing interval over a regionally extensive area, spanning ~500 km, in a fashion akin to that known for the *Medusaegraptus* epibole, which is an algal-Lagerstätte that occurs in the slightly younger Lockport Group of western New York and has been traced for nearly 100 km across the outcrop belt (LoDuca and Brett, 1997).

Material and methods

The material examined during this study comprises 41 slabs in total, many of which bear multiple algal specimens. Of these, 33 are from the Wabi Point locality and were collected, in part, by KB during the summers of 2018 and 2019. The other eight slabs are from the Dionne Concrete Products quarry and were collected by MM and MP during the summer of 2020.

Reflected light images were obtained using a Canon Rebel digital camera fitted with a macrolens. To enhance contrast, specimens were photographed in some cases using polarizing filters. SEM study of the material was conducted using a JEOL JSM-7800F at the Electron Microbeam Analysis Laboratory (EMAL), Department of Earth and Environmental Science, University of Michigan. All specimens were imaged uncoated, and backscattered electron (BSE) images were obtained using an accelerating voltage of 25 keV. Measurements were obtained from digital images using the open source program ImageJ (Schneider et al., 2012).

Morphological terminology applied herein is that for algae. Bryopsidales terminology follows Taylor (1960).

Repositories and institutional abbreviations.—Types, figured, and other specimens from the Timiskaming area examined in this study are deposited in the Royal Ontario Museum (ROMIP), Toronto, and the Musée de paléontologie et de l'évolution (MPEP), Montreal, Canada.

Systematic paleontology

Division Chlorophyta Reichenbach, 1828
Order Bryopsidales Schaffner, 1922
Genus *Earltonella* LoDuca, new genus

Type species.—*Earltonella fredricksi* LoDuca, n. gen. n. sp., by monotypy, from the Earlton Formation (Llandoveryan) at the Dionne Concrete Products quarry near Earlton, Ontario.

Diagnosis.—As for the type species by monotypy.

Occurrence.—Silurian (Llandoveryan, Telychian); Lake Timiskaming area, Ontario, Canada (Laurentia paleocontinent).

Etymology.—In reference to the geographic origin of the material, near the town of Earlton, Ontario, Canada.

Remarks.—*Earltonella* LoDuca, n. gen. shares key characteristics with the early Paleozoic noncalcified macroalga genera *Buthograptus* Hall, 1861, and *Menieria* Wang et al., 2014. In particular, all three taxa are characterized by fronds consisting of a central axis bearing elongate pinnules. *Buthograptus*, which is known only from the Upper Ordovician Platteville Formation in southwestern Wisconsin and northern Illinois (LoDuca, 2019; Kolata, 2021), includes the species *B. laxus* Hall, 1861, *B. gundersoni* LoDuca, 2019, and *B. meyeri* LoDuca, 2019. *Buthograptus* was recently redescribed on the basis of new material and interpreted as a bryopsidalean alga with fronds similar to those of living *Caulerpa* (LoDuca, 2019). The fronds of *Buthograptus* are characterized by the same basic architecture as those of *Earltonella* LoDuca, n. gen., these consisting of elongate pinnules in opposite to subopposite arrangement along the supporting central axis, with the vertical spacing between adjacent pinnules (0.2–0.4 mm for *B. laxus*; 0.7–1.8 mm for *B. meyeri*) overlapping with the range present within individual fronds of the new genus (0.3–0.8 mm). *Earltonella* LoDuca, n. gen. is distinguished from *Buthograptus* on the basis of pinnule morphology. Specifically, the pinnules of *Buthograptus* are comparatively robust (widths of 0.4–0.7 mm vs. 0.15 mm) and, crucially, these never show branching. *Earltonella* LoDuca, n. gen. also differs from *Buthograptus* in that no specimens attributed to the latter show a stolon (LoDuca, 2019). The arrangement of multiple fronds in series on slabs that bear the holotypes of *B. laxus* and *B. meyeri* (see LoDuca, 2019, fig. 1.1, 1.8) is, however, suggestive of such a structure. A further difference between the new genus and *Buthograptus* concerns the details of pinnule spacing within a given frond. Specifically, in the new genus, this decreases by a factor of nearly three from the base to the top of a frond, whereas in *Buthograptus* this spacing remains essentially uniform within a particular frond.

The monotypic genus *Menieria* was erected by Wang et al. (2014) on the basis of *M. minuta* Wang et al., 2014, from the Silurian (Llandoveryan, Aeronian) Gun River Formation of Anticosti Island. This taxon differs from *Earltonella* LoDuca, n. gen. in that the “central axis,” as described by Wang et al. (2014, p. 361), is wider than the stolon of the new genus (1.0–1.6 vs. 0.7 mm) and bears fronds with highly irregular spacing. Differences are also evident with regard to the pinnules. Specifically, those of *Menieria* are larger in terms of both length (2.4–9.1 vs. 1.6–4.0 mm) and distal width (0.6–1.0 vs. 0.15 mm), with the latter difference being particularly pronounced, and show a different overall form, with a marked distal expansion, by roughly a factor of two. In addition, as with *Buthograptus*, the pinnules of *Menieria* never show branching. *Menieria* further differs from the new genus in the phyllotaxis of both the fronds and the pinnules. Although these give the appearance of having a distichous

alternate arrangement, after careful observation, Wang et al. (2014, p. 361) concluded that “lateral branches are attached to the central axis with a helical phyllotaxis” and determined the same arrangement for the pinnules. On the basis of the aforementioned differences, *Earltonella* LoDuca, n. gen. is regarded as distinct from *Menieria*. It must be noted, however, that the high degree of similarity in thallus morphology among *Menieria*, the new genus, and *Buthograptus* suggests that all three taxa share a very close evolutionary relationship.

Noncalcified stoloniform thalli somewhat similar to that of *Earltonella* LoDuca, n. gen. are also characteristic of *Parallelphyton* Wu and Zhao in Wu et al., 2011, from the Cambrian Kaili Biota of South China and an unnamed form with a similar thallus morphology from the Neoproterozoic of South China (Wu et al., 2011; Ye et al., 2015; Bykova et al., 2020). These, however, develop markedly simpler thalli than *Earltonella* LoDuca, n. gen., with the erect parts consisting only of unbranched cylindrical elements (analogous to central axes without pinnules). The nonbiomineralized Cambrian taxon *Margaretia* Walcott, 1931, which had been considered as a stoloniform *Caulerpa*-like green alga (Conway Morris and Robison, 1988), has since been reinterpreted as the tube of an enteropneust hemichordate (Nanglu et al., 2016). The same relationship has been proposed by Fatka and Vodička (2022) for the similar form *Krejciella* Obrhel, 1968b, from the Ordovician of the Prague Basin, which was previously interpreted as an alga by Havlíček et al. (1993). These taxa differ markedly from *Earltonella* LoDuca, n. gen. in having much wider axes (4–20 mm vs. 0.7 mm) and by the complete lack of pinnate fronds.

With regard to calcareous macroalgae, there are no taxa, living or fossil, similar to *Earltonella* LoDuca, n. gen. This is not surprising, given that heavy calcification in marine siphonous green macroalgae appears to be restricted to forms with densely packed side branches, particularly those that develop a cortex (Borowitzka, 1986). Such an architecture produces, in the micro-environment between the branches, conditions conducive to the precipitation of calcium carbonate (Pentecost, 1991). Calcareous bryopsidalean algae with complex thalli of this sort are known from the Silurian and include *Palaeoporella* Stolley, 1893, *Dimorphosiphon* Høeg, 1927, *Maslovina* Obrhel, 1968a, *Paralitanaiia* Mamet and Préat, 1985, and *Vitinellopsis* Vachard, Bucur, and Munnecke, 2022.

Earltonella fredricksi LoDuca, new species
Figures 1–6

Holotype.—ROMIP 66270.1 (Fig. 2.1) from the Earlton Formation (Llandoveryan) in the Dionne Concrete Products quarry, Lake Timiskaming area, Ontario, Canada (47.744004°N, 79.818975°W).

Diagnosis.—Thallus noncalcified, comprising an elongate and creeping stolon (runner) bearing pinnate fronds at semi-regular intervals; stolon cylindrical; fronds consisting of a central axis (rachis) with delicate pinnules arrayed in opposite to subopposite fashion; pinnule form roughly cylindrical but slightly increasing in diameter distally, bifurcated at distal end, the resulting divisions being thin and hairlike; stolon, central axes, and pinnules without segmentation or serration.

Description.—Thallus of holotype, ROMIP 66270.1, noncalcified, preserved as a carbonaceous compression on bedding plane surface, oval in gross outline, 110 mm in length, 48 mm in width, comprising an elongate and creeping central stolon (runner) bearing pinnate fronds typically 18–22 mm in length, the latter in the flattened specimen oriented at roughly right angles to the stolon in the central part of the thallus but at progressively smaller angles toward the inferred thallus end, with those at the extreme end running nearly parallel to stolon (Figs. 1, 2.1, 3). Stolon cylindrical with fairly smooth margins (glabrous), hollow, 0.7 mm wide, with a subtle zigzag form along its length, the inflections spaced at intervals of ~2 mm, with fronds extending from both sides in a roughly distichous alternating pattern (Figs. 2.1, 3, 4.1). Fronds consisting of a central axis (rachis) with pinnules arrayed in opposite to subopposite fashion (Fig. 3, 4.2, 4.3). Central axis cylindrical, with a width of 0.3 mm proximally, expanding to a width of 0.4–0.5 mm along most of its length, rounded at tip, margin smooth, lacking cross-walls or other evidence of segmentation (Fig. 4.2–4.4). Pinnules continuous with central axis, without evidence of cross-walls at junctions (Fig. 4.4), in lower and middle parts of frond meeting central axis at an angle of ~80°, this angle progressively decreasing along upper part of frond, reaching a minimum of 40–50° along uppermost part of frond (Fig. 4.2, 4.3); vertically adjacent pinnules separated by intervals of 0.8 mm in lower part of frond, this distance decreasing to 0.3 mm in uppermost part of frond. Primary pinnule element roughly cylindrical, without pronounced basal constriction, increasing slightly in diameter from 0.11 mm at base to 0.15 mm at distal end and with a length of 1.1–1.3 mm (Fig. 4.2–4.4), distal end bifurcated, secondary elements hairlike, with a width of 0.08 mm and having a length roughly comparable to that of primary element or slightly longer, diverging at an angle of 20–40° (Fig. 4.2–4.4); primary elements in lower and middle part of frond fairly straight along their length but with subtle upward curvature, those along uppermost part of frond show strong upward curvature and extend well above tip of central axis (Fig. 4.3); pinnule margins fairly smooth, without serrations (Fig. 4.2–4.4). ROMIP 66270.2, 66270.3, and 66271 generally similar to holotype, but overall thallus form for 66270.2 and 66270.3 less elongate (Figs. 1, 2.2, 2.3, 5.1–5.5). SEM images of fronds show ‘mudcracked’ texture on central axes (Fig. 6.1, 6.2, 6.6) and, more subtly, on pinnules (Fig. 6.4), fairly smooth margins for both central axes and pinnules (Fig. 6.1–6.4), a rounded form for central axis tip (Fig. 6.6), and an expanded region at or near the base of some, but not all, pinnules (Fig. 6.7, 6.8), this appearing in reflected light images as a distinctly darkened area (Fig. 6.5, 6.9).

Etymology.—Named in honor of Dr. Walter Fredricks, Professor Emeritus of Biology at Marquette University, and his clan.

Materials.—ROMIP 66270.1–66270.5, 66271.

Remarks.—This form is known only from the Dionne Concrete Products quarry and, with specimens known from only two

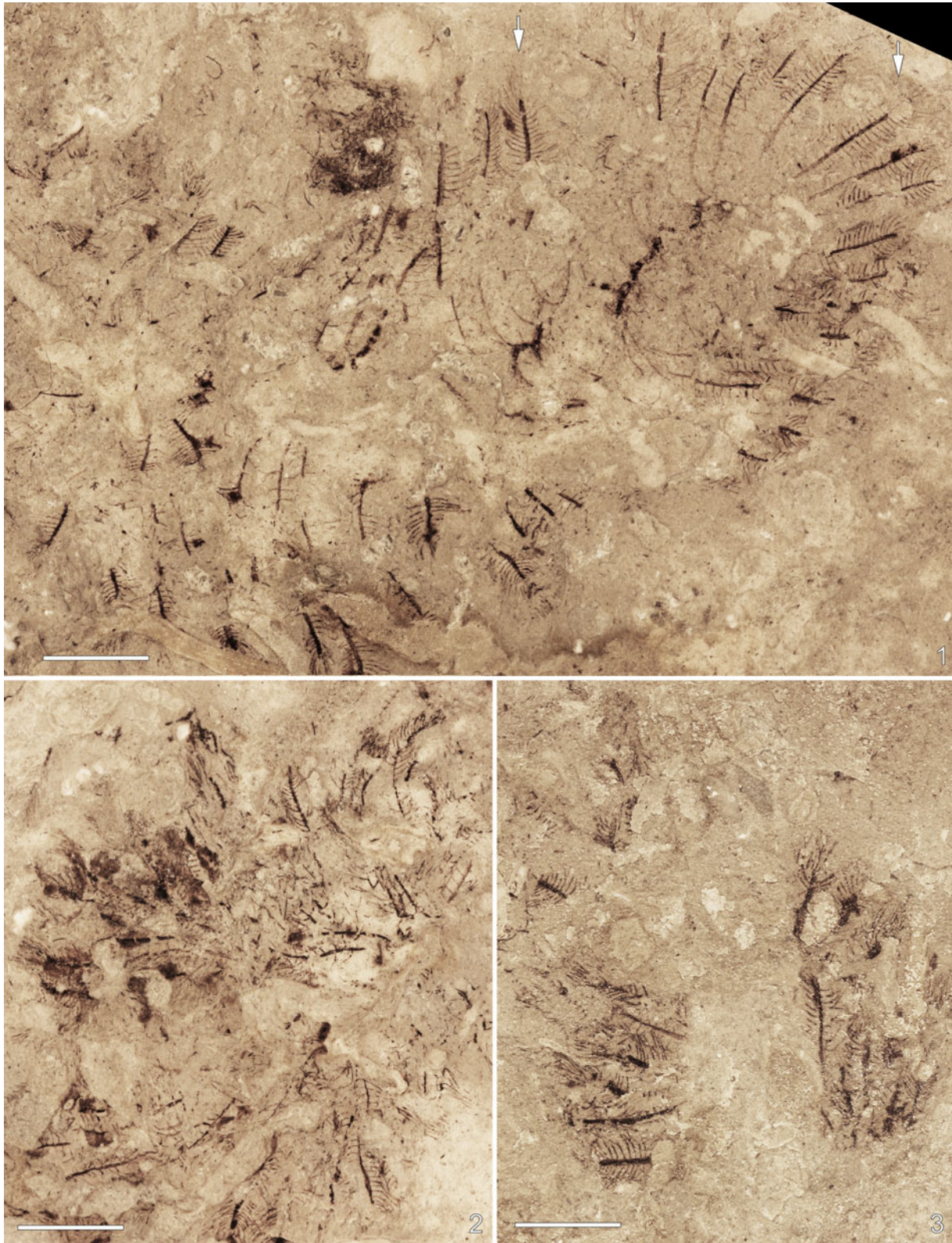


Figure 2. *Earlingtonella fredricksi* LoDuca, n. gen. n. sp., Earlington Formation (Llandoveryan), Dionne Concrete Products quarry, Earlington, Ontario: (1) holotype, ROMIP 66270.1; arrows indicate detailed views in Figure 4.2, 4.3; (2) 66270.2; (3) 66270.3. Scale bars = 10 mm.

slabs, is much less abundant at that locality than *Thalassocystis striata*. One of these slabs bears a single specimen (Fig. 5.1), the other appears to show several separate thalli (Figs. 1, 2.1–2.3).

On the latter, however, the distribution of the material, together with the potential for concealment of some parts beneath matrix, leaves open the possibility that all or much of this material

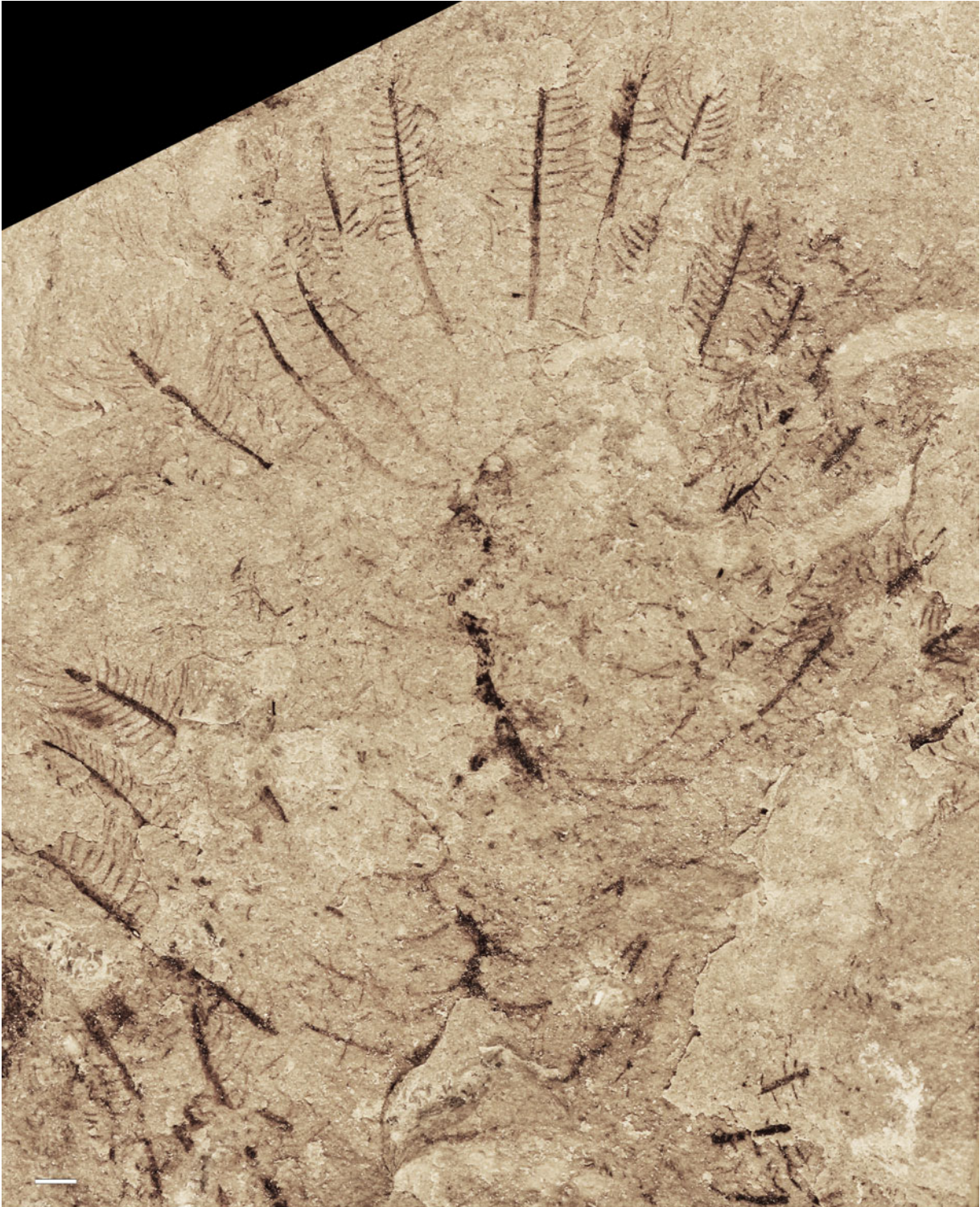


Figure 3. Detail of part of the holotype of *Earltonella fredricksi* LoDuca, n. gen. n. sp., Earlton Formation (Llandoveryan), Dionne Concrete Products quarry, Earlton, Ontario, ROMIP 66270.1. Scale bar = 2 mm.

belongs to a single large thallus. Rhizoidal features were not observed among any of the material. It is possible, however, that this aspect of thallus morphology is also concealed by matrix.

SEM images show a distinctive ‘mudcracked’ surface texture on the central axes and, to a lesser extent, on the pinnules (Fig. 6.2, 6.4, 6.6). A similar surface texture was reported for *Buthograptus*



Figure 4. Details of holotype of *Earlingtonella fredricksi* LoDuca, n. gen. n. sp., Earlington Formation (Llandoveryan), Dionne Concrete Products quarry, Earlington, Ontario, ROMIP 66270.1: (1) stolon, ring-shaped cross-section at far right (arrow) indicates hollow structure; (2) fronds at right arrow in Figure 2.1, arrows mark well-preserved pinnules that show bifurcated tips; (3) frond at left arrow in Figure 2.1; (4) enlargement of area indicated by arrow in (3) showing pinnules in continuity with central axis. Scale bars are (1–3) 2 mm; (4) 0.5 mm.

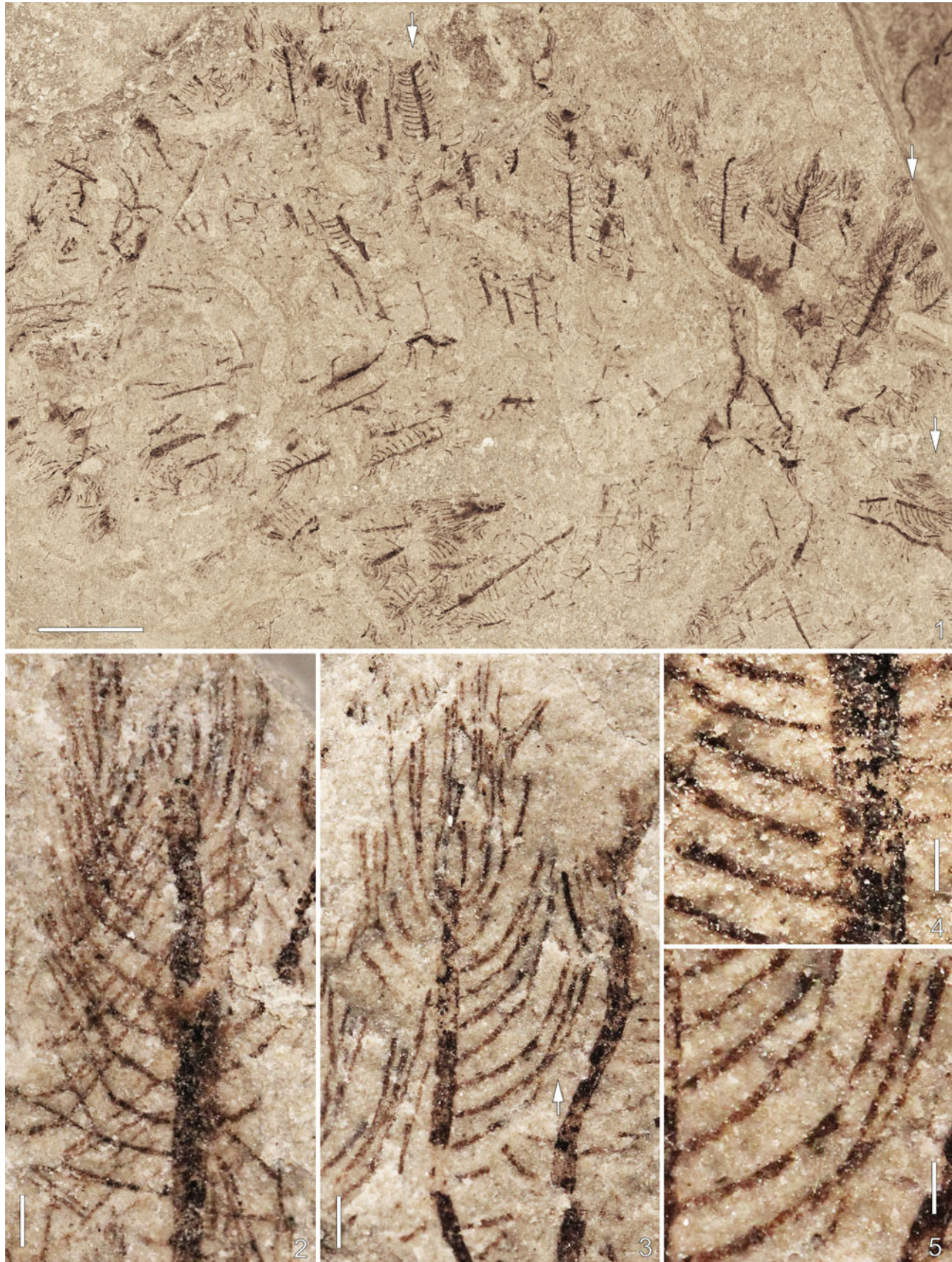


Figure 5. *Earlonella fredricksi* LoDuca, n. gen. n. sp., Earlon Formation (Llandoveryan), Dionne Concrete Products quarry, Earlon, Ontario, ROMIP 66271: (1) complete thallus; (2) detail of frond at upper right arrow in (1); (3) detail of frond at lower right arrow in (1); (4) detail of frond at left arrow in (1); (5) detail of frond at arrow in (3) showing pinnules with bifurcations. Images in (2–5) obtained using cross-polarized light. Scale bars are (1) 10 mm; (2, 3) 1 mm; (4, 5) 0.5 mm.

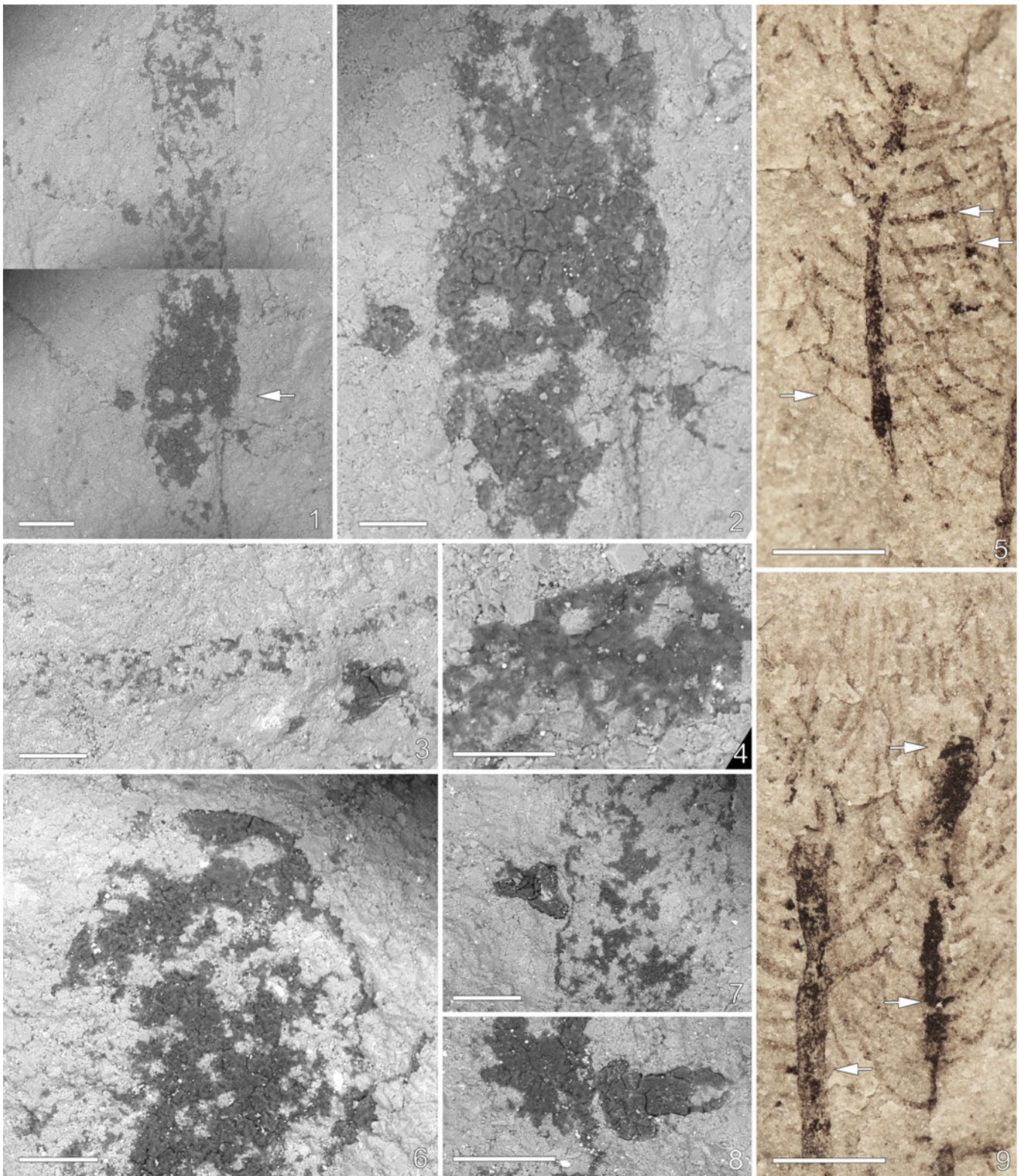


Figure 6. Fronds of *Earlingtonella fredricksi* LoDuca, n. gen. n. sp. from the holotype slab, ROMIP 66270: (1) composite SEM-BSE image of area at left arrow in (5); (2) detail of area at arrow in (1) showing mudcracked texture on central axis; (3) SEM-BSE image of pinnule at lower right arrow in (5); (4) SEM-BSE image of pinnule at upper right arrow in (5); (5) reflected light image of distal part of frond, 66270.4; (6) SEM-BSE image of area at upper right arrow in (9); (7) SEM-BSE image of area at left arrow in (9); (8) SEM-BSE image of area at lower right arrow in (9); (9) reflected light image of distal parts of two fronds, 66270.5. Scale bars are (1, 3, 6–8) 0.2 mm; (2, 4) 0.1 mm; (5, 9) 2 mm.

laxus (LoDuca, 2019, fig. 3.3). SEM images also clearly reveal the presence of an expanded region at or near the base of some, but not all, pinnules (Fig. 6.7, 6.8). This, too, has been reported for specimens of *B. laxus* (Whitfield, 1894, pl. 1, fig. 3; LoDuca, 2019, fig. 3.3), and it is evident in specimens of *Buthograptus meyeri* (LoDuca, 2019, fig. 1.8). For all of these taxa, however, it is not evident on all pinnules, including those on a given frond, and it is entirely absent on *Buthograptus gundersoni* and *Menieria minuta*. The significance of this feature remains unclear.

The thallus of *Earltonella fredricksi* LoDuca, n. sp., in broad terms, resembles those produced by the living bryopsidalean alga *Caulerpa*. In particular, as with the well-known extant taxa *C. sertularioides* Howe, 1905 (Fig. 7) and *C. taxifolia* Agardh, 1817, the thallus consists of an elongate creeping cylindrical stolon that bears a series of pinnate, complanate fronds. In addition, as with all bryopsidalean algae, the new species appears to have had a siphonous thallus organization. For the stolon, this is indicated by its hollow nature, as conveyed by the ring-like form of this feature in cross-section view (Figs. 3, 4.1), and for the entire thallus this is indicated by a lack of evident cross walls or segmentation. Trabeculae (i.e., irregular, strut-like cell wall ingrowths), which are ubiquitous for living *Caulerp*aceae and traverse the cell wall lumen to provide structural support, have not been observed in the new species, but it is doubtful that such internal structures would be evident in compressed fossil specimens. In terms of pinnule morphology, the new species shows pinnules with bifurcated tips, and pinnules of this nature are known for *Caulerpa*, including *C. taxifolia*. Key morphometric aspects also fall within the range known for *Caulerpa*, with width values for the stolon,

central axes, and pinnules, as well as frond lengths, being comparable to those displayed by smaller species within the genus, albeit only about one-half to one-third those observed in the aforementioned *C. taxifolia* and *C. sertularioides*. In addition, the fairly wide pinnule spacing is comparable to that known for *C. ashmeadii* Harvey, 1858. No species of *Caulerpa*, however, shows pinnules with an overall shape that precisely matches that of the new species, particularly with regard to the relatively long secondary elements. *Earltonella fredricksi* LoDuca, n. sp. also appears to differ from all known *Caulerpa* species in the manner in which the fronds are arranged along the stolon. In *Caulerpa*, these are arranged in a single row along the top. In the new species, by contrast, the fronds seem to emerge from the sides of the stolon, in an alternating pattern. Such an arrangement for the new species must, however, be regarded as equivocal, owing to the flattened condition of the fossil thalli. In this regard, if the fronds were arranged largely upright in a single row along the top, but were tilted relative to perpendicular in an alternating pattern down the length of the stolon, a rapid influx of mud from above could have produced the pattern of frond distribution shown by the specimens. The orientation of some of the associated specimens of *Thalassocystis striata* is consistent with burial dynamics of this sort (e.g., Fig. 8.2). Moreover, flattening in this manner could have distorted the stolon into the zigzag form evident in the specimens (Figs. 3, 5.1). Some herbarium specimens of *Caulerpa* would appear to be comparable in these regards (Fig. 7).

The gross morphology and carbonaceous composition of *Earltonella fredricksi* LoDuca, n. sp. also invite comparisons with hydroid colonies, particularly those produced by extant aglaopheniids (feather hydroids), and with the pinnule-bearing arms of crinoids. With regard to a hydroid affinity, the hydrocladia of living hydroids can resemble the general form of the pinnules in the new species, including the development of distal bifurcation (e.g., Henry and Kenchington, 2004, fig. 1), and fossils of early Paleozoic age with a form somewhat resembling the pinnate fronds of the new species have been described as hydroids. Among these are the Ordovician taxon *Webbyites* Kraft, Kraft, and Prokop, 2001, and *Plumalina* Hall, 1858, the latter known mainly from the Devonian but also reported from the Silurian (Wenlockian) of New York (Muscente and Allmon, 2013). Nonetheless, a hydroid affinity for the new species is regarded as unlikely for several reasons. First, specimens of the new species show no evidence of hydrotheca, including in SEM images. Specifically, the pinnule margins appear fairly smooth and continuous, and their surfaces lack sculpture or patterning that might point to the presence of such structures (Fig. 6.3, 6.4). Second, the hydrocladia of *Plumalina*, although lacking preserved hydrotheca or polyps, show in some cases distinctive box-like modules with a central pore or groove, which have been interpreted as polyp bases (Sass and Rock, 1975; Muscente and Allmon, 2013). The pinnules of the new species, however, do not show features along these lines. Finally, the strongly upcurved nature of the distal (uppermost) pinnules and the lack of internodes on the central axes would seem to be inconsistent with a hydroid affinity (LoDuca, 2019; Song et al., 2021). With regard to a crinoid affinity, decalcified examples of pinnule-bearing crinoid arms preserved as carbonaceous material that occur in direct association with a rich, noncalcified

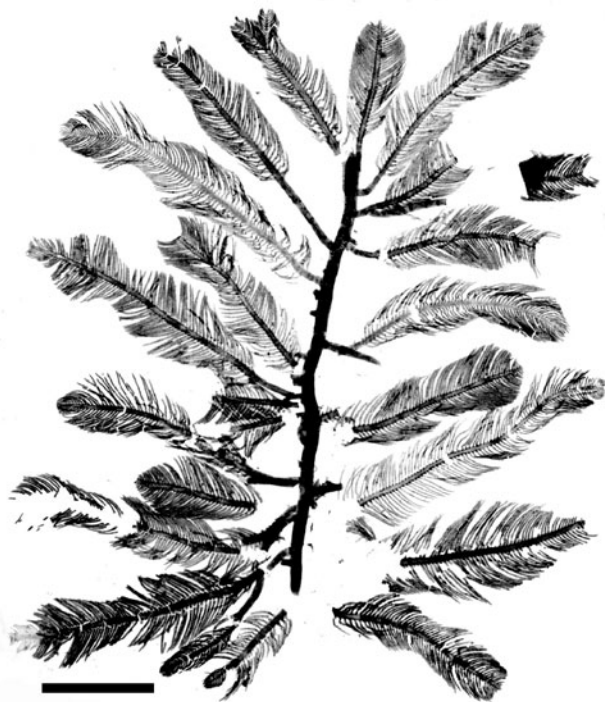


Figure 7. Herbarium specimen of *Caulerpa sertularioides* Howe, 1905, University of Michigan Herbarium, 682353. Scale bar = 20 mm.

macroalgal flora in the Llandoveryan (Aeronian) of Estonia (Tinn et al., 2009; Ausich et al., 2020) have a gross morphology somewhat similar to the individual fronds of the new species. The pinules of crinoids, however, are not known to show distal bifurcation. In addition, the new species lacks key crinoid features (e.g., a calyx or a stem constructed of columnals).

A terrestrial habitat for the new species can be excluded by its direct association with marine taxa, including trilobites and brachiopods, and by its general lack of disarticulation and fragmentation, indicating that the material was buried in situ or very nearly so. This, then, serves to effectively eliminate the possibility that it represents an early non-vascular land plant, such as a liverwort.

In consideration of the foregoing, together with co-occurrence with the noncalcified bryopsidalean alga *Thalassocystis striata* and broad similarity to the noncalcified Late Ordovician–Early Silurian macroalga taxa *Buthograptus* and *Menieria*, it is concluded that *Earltonella fredricksi* LoDuca, n. sp. is best regarded as a bryopsidalean alga with a stoloniform thallus (sensu LoDuca et al., 2017) roughly comparable to that of frondose forms of *Caulerpa*, such as *C. taxifolia*, although it must be noted that an animal affinity cannot be entirely excluded on the basis of the available data. Given the uncertainties regarding precise arrangement of the fronds along the stolon, and in consideration of the considerable age of the material, the new species is not assigned to *Caulerpa*. In this regard, molecular studies cast doubt on a close phylogenetic affinity between the new species and *Caulerpa*. According to the chronogram provided in Draisma et al. (2014), Caulerpaceae did not diverge from the sister-clade *Pseudochlorodesmis* until sometime after the Devonian, between the late Carboniferous and Late Triassic. Molecular clock analyses do, however, readily accommodate a bryopsidalean affinity for *Earltonella fredricksi* LoDuca, n. sp. (Verbruggen et al., 2009; Draisma et al., 2014; Del Cortona et al., 2020) and, as noted above, both calcified and noncalcified bryopsidalean algae with diverse and complex forms have been described from Ordovician and Silurian strata.

Considered as a bryopsidalean alga and in view of the molecular evidence, it is conceivable that *Earltonella fredricksi* LoDuca, n. gen. n. sp. belongs to an extinct lineage within this group, together with *Buthograptus* and *Menieria* and, perhaps, *Parallelphyton*. A similar scenario was raised in regards to the Silurian *Codium*-like taxa *Thalassocystis* and *Inocladus* (LoDuca et al., 2021). The possibility of such a scenario, in general, is supported by well-documented examples of convergent evolution of complex thallus form among extant Bryopsidales, including between *Codium* and *Pseudocodium* and even within *Caulerpa* itself in terms of frond morphology where, as noted by Draisma et al. (2014, p. 1029), “Vesiculate, terete, and flattened ramuli [pinules] all evolved multiple times” (see also Famà et al., 2002).

Considered in broader terms, the appearance of complex *Caulerpa*-like thalli within Bryopsidales during the Late Ordovician–Early Silurian is part of a major revolution in macroalgal thallus morphology during this time documented by LoDuca et al., 2017. As suggested by that study, the Ordovician macroalgal revolution may signal a defensive response to intensified grazing pressure by meso-herbivores that arose as an outcome of the Great Ordovician Biodiversification Event (GOBE). Specifically, ‘complicating’ a simple siphonous thallus, consisting only of an unbranched cylindrical siphon, by developing

dense outgrowths of lateral appendages (secondary elements) yields benefits by providing (1) a physical barrier (‘palisade’) between grazers and critical central parts of the thallus, and (2) a measure of anatomical compartmentalization, which in turn allows the cell walls of the secondary elements to be relatively thin for enhanced assimilation efficiency without incurring marked costs in survivorship (LoDuca and Behringer, 2009). Numerous variations on this theme originated among siphonous green macroalgae during the GOBE, of which complex *Caulerpa*-like thalli are but one example, along with a proliferation of heavily calcified thalli (LoDuca et al., 2017).

Genus *Thalassocystis* Taggart and Parker, 1976

Type species.—*Thalassocystis striata* Taggart and Parker, 1976, by monotypy.

Thalassocystis striata Taggart and Parker, 1976

Figures 8–11

Holotype.—FMNH 43982 from the Schoolcraft Formation (Llandoveryan) in an exposure along the Lake Michigan shoreline two miles east of Manistique, Michigan, U.S.A. (Taggart and Parker, 1976, fig. 1).

Description.—Thallus of ROMIP 66272.1 noncalcified, unsegmented, extending 46 mm above holdfast, comprising dichotomously branched axes; branching highly irregular (anisotomous); individual axes with a length of 22–27 mm, these in some cases narrow, with a maximum width of 3 mm, but in other cases broad and obovate with a maximum width of 7 mm; proximal parts of axes with a width of 1–3 mm; axis terminations obtuse; angle between axes at bifurcation typically between 30–40°; medullary tubes with a width of 0.16 mm, poorly preserved; cortical tubes not evident; holdfast small relative to thallus, 7 mm wide, 11 mm long, consisting of a loose array of thin filaments, each having a width of 0.3–0.4 mm (Fig. 8.1). Thalli of ROMIP 66272.2 and 66273 generally similar to 66272.1, but 66272.2 somewhat smaller, with a height of 32 mm (Fig. 8.1), and 66273 preserved in overhead as opposed to lateral view (Fig. 8.2, 8.3). ROMIP 66274 (Fig. 9.1) shows only relatively narrow axes, some with a papillate surface texture, others with well-preserved medullary and cortical tubes (Fig. 9.2); some axes show a strong degree of 3D preservation (Fig. 9.3). ROMIP 66272.3 shows in lower part of thallus well-preserved cortical tubes with a cylindrical form, a length of 0.5–1.0 mm, and a width of 0.1 mm, these arrayed along the supporting medullary tube in a single row and oriented to it at an angle of ~90°, with spacing between adjacent tubes of less than one tube width (Fig. 9.4, 9.5). ROMIP 66272.3 and 66275 show well-preserved holdfasts (Fig. 9.4, 9.6, 9.7). ROMIP 662726 appears to show a greater amount of decay relative to the other specimens (Fig. 9.8). Thalli from Wabi Point (Figs. 10.1–10.7, 11) generally similar to aforementioned Dionne quarry thalli in terms of branching details, surface texture, and internal features, and with a comparable range of thallus sizes and axis forms. Some show a pronounced degree of 3D preservation (Fig. 10.4).

Materials.—ROMIP 66272–66277; MPEP 1501.1–1501.33.

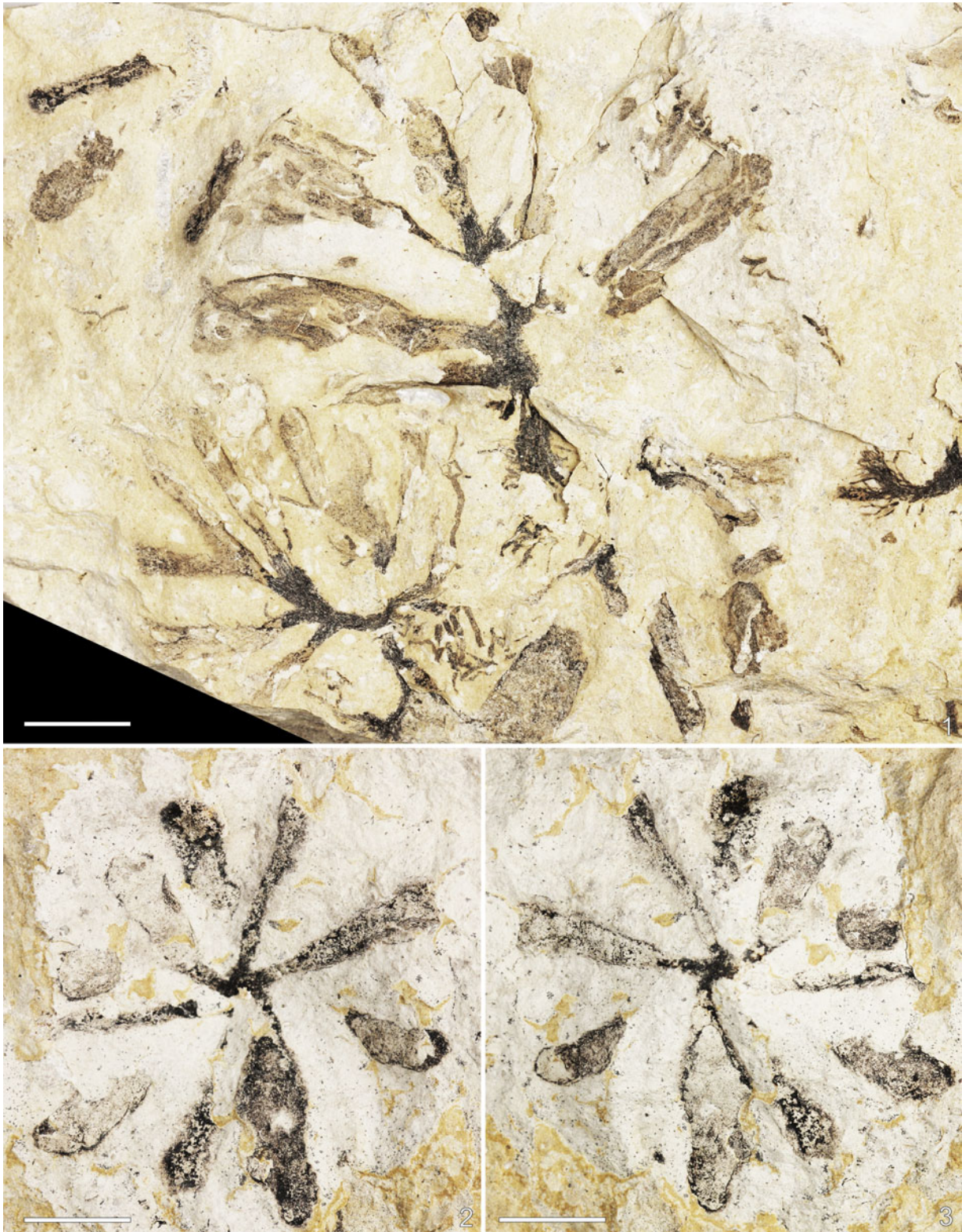


Figure 8. *Thalassocystis striata* Taggart and Parker, 1976, Earleton Formation (Llandoveryan), Dionne Concrete Products quarry, Earleton, Ontario: (1) two thalli preserved in lateral view, ROMIP 66272.1 (top) and 66272.2 (bottom); (2) thallus preserved in overhead view, ROMIP 66273A; (3) counterpart of specimen in (2), ROM 66273B. Scale bars = 10 mm.

Remarks.—This species is locally abundant at both of the Timiskaming localities, with dozens of thalli having been collected from each. In all key morphological respects, the

Timiskaming material is entirely consistent with Michigan material, as described by LoDuca et al. (2021). This includes (1) thallus branching pattern; (2) axis shape, size,

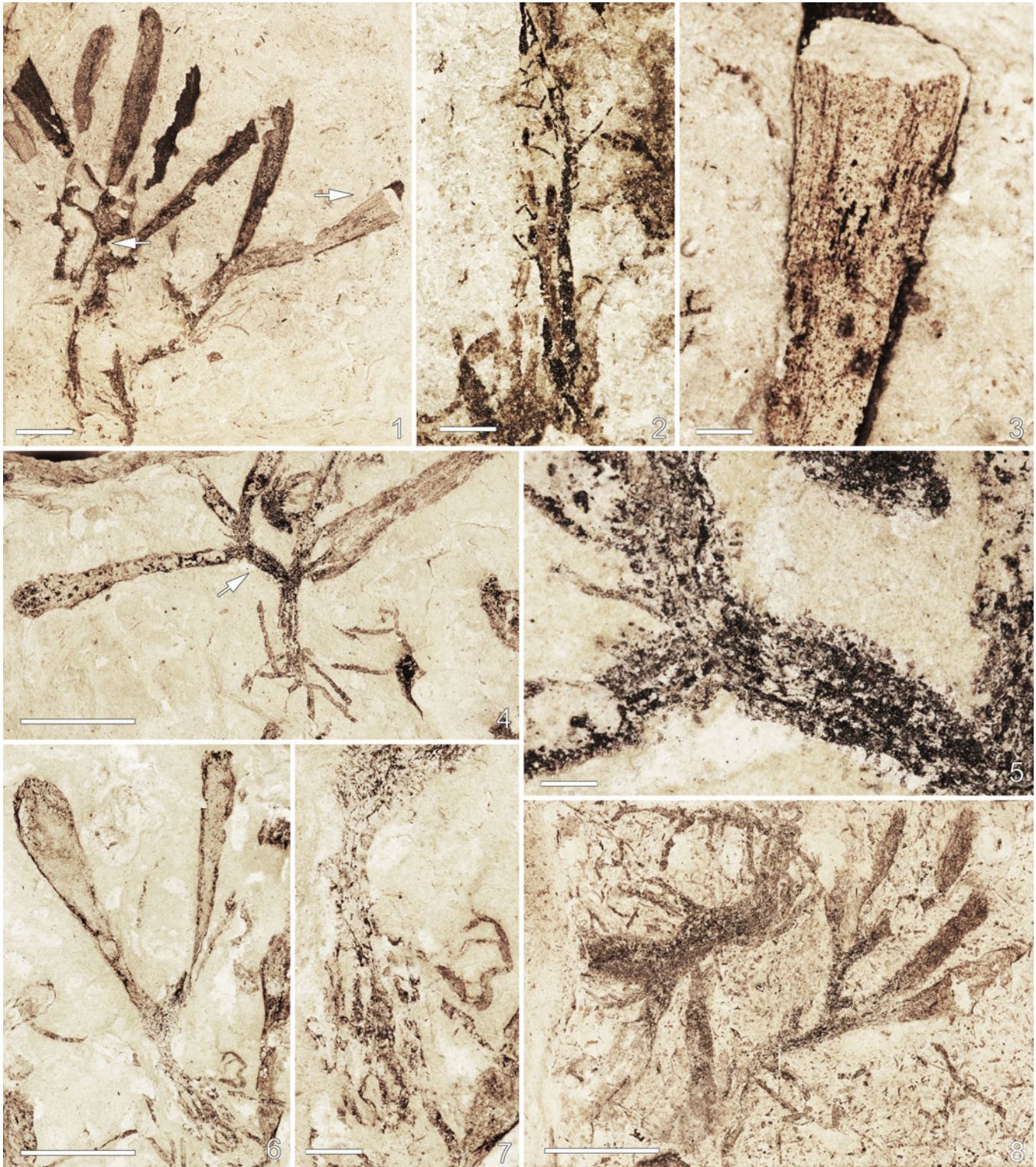


Figure 9. *Thalassocystis striata* Taggart and Parker, 1976, Earleton Formation (Llandoveryan), Dionne Concrete Products quarry, Earleton, Ontario: (1) complete thallus, ROMIP 66274; (2) detail of area at lower arrow in (1) showing medullary and cortical tubes; (3) detail of area at upper arrow in (1) showing axis with strong degree of 3D preservation; (4) thallus with well-preserved holdfast, ROMIP 66272.3; (5) detail of area at arrow in (4) showing medullary and cortical tubes; (6) thallus with sparse branching, ROMIP 66275; (7) detail of thallus in (6) showing holdfast; (8) complete thallus, ROMIP 66276. Scale bars are (1, 4, 6, 8) 10 mm; (2, 5) 1 mm; (3, 7) 2 mm.

and surface texture; (3) details of the medullary and cortical tubes, including shape, size, and arrangement; and (4) holdfast configuration and size. In addition, all key variations among Michigan specimens are fully represented

among the Timiskaming material. In this regard, as with all of the Michigan localities, some of the individual thalli from both of the Timiskaming localities show a mix of narrow axes and wider, distinctly bulbous axes (compare



Figure 10. *Thalassocystis striata* Taggart and Parker, 1976, Earleton Formation (Llandoveryan), Wabi (Dawson) Point, Ontario: (1) nearly complete thallus, ROMIP 66277; (2) nearly complete thallus, MPEP 1501.2a; (3) nearly complete thallus, MPEP 1501.9a; (4) nearly complete thallus showing a single dichotomy and a strong degree of 3D preservation, MPEP 1501.20; (5) an axis showing medullary tubes, MPEP 1501.14a; (6) nearly complete thallus, MPEP 1501.30b; (7) an axis showing medullary tubes, MPEP 1501.16a (images in 2–7 courtesy of Mario Courmoyer). Scale bars are (1–4, 6, 7) 10 mm; (5) 2.5 mm.



Figure 11. *Thalassocystis striata* Taggart and Parker, 1976, Earleton Formation (Llandoveryan), Wabi (Dawson) Point, Ontario. Large slab bearing complete and partial thalli, MPEP 1501.32 (image courtesy of Mario Courmoyer). Scale bar = 20 mm.

Figs. 8.1, 10.2 with LoDuca et al., 2021, fig. 15.8), whereas others comprise only narrow axes (compare Figs. 9.1, 10.3 with LoDuca et al., 2021, fig. 15.1). In addition, thalli with

limited branching, in some cases comprising just a single dichotomy, are known from all occurrences (compare Fig. 9.6 with LoDuca et al., 2021, fig. 16.2, 16.6).

Taphonomic details are also comparable between the Timiskaming and Michigan material. In particular, specimens in both areas usually show the thallus in lateral view, although overhead views are known (compare Fig. 8.2 with LoDuca et al., 2021, fig. 16.10), and they tend to be fairly flat, although examples with a strong degree of 3D preservation are occasionally encountered (Figs. 9.3). The latter characteristic is particularly well developed among thalli from the Michigan type locality as well as the Wabi Point locality (Fig. 10.4). Specimens from the Michigan type locality are also similar to those from the Wabi Point locality in that detached axes (Figs. 10.4, 10.5, 11) are not uncommon, whereas specimens from the other localities tend to be complete or nearly so. Finally, as with the Michigan material, some of the Timiskaming specimens show only surficial details of the axes, including in some cases a distinctive papillate texture (Figs. 8.2, 8.3, 9.1, 9.6, 10.6), whereas others show internal details pertaining to the siphons (Figs. 9.2, 9.4, 9.5, 10.3, 10.5, 10.7). With regard to preservation of internal features, the Timiskaming specimens are more similar to those from the Manistique area than they are to those from the Carmeuse quarry near Gulliver, Michigan, in that the best specimens from the latter show these features in greater detail compared to specimens from all of the other localities.

Conclusions

Lagerstätten bearing an abundance of exceptionally preserved noncalcified macroalgae, or algal-Lagerstätten, are known from a number of locations and stratigraphic levels within the Silurian of North America, including localities in Michigan, Wisconsin, New York, Ontario, Nunavut, New Brunswick, and Quebec (LoDuca et al., 2017). Here, algal-Lagerstätten are reported for the first time from the Silurian of the Timiskaming outlier in eastern Ontario. These alga-bearing deposits, which occur within the Llandoveryan Earleton Formation in sections exposed near Earleton and at Wabi Point, are separated geographically by a distance of 45 km and are characterized by an abundance of the *Codium*-like bryopsidalean green alga *Thalassocystis striata*. This noncalcified taxon was known previously only from the Llandoveryan Schoolcraft Formation in northern Michigan, and these new occurrences provide additional key evidence that the alga-bearing intervals within the Earleton Formation at both Timiskaming localities correlate with the Schoolcraft Formation in the Michigan Basin. Notably, the Timiskaming specimens compare closely in all respects, including within-assembly variation, with material from Michigan, including the type locality. The Earleton-area section also contains a new form of noncalcified bryopsidalean alga, *Earltonella fredricksi* LoDuca, n. gen. n. sp., which is characterized by a stoloniform thallus architecture similar to that of *Caulerpa*, a common extant bryopsidalean alga, and its distinctive pinnate fronds resemble those of the macroalgal taxa *Buthograptus* and *Menieria* from the Upper Ordovician of Wisconsin and Lower Silurian of Quebec, respectively. In broader evolutionary terms, this new taxon adds to the diversity of morphologically complex macroalgae that originated during and shortly after the Great Ordovician Biodiversification Event (GOBE).

In a paleoenvironmental context, these new algal-Lagerstätten indicate that, for a brief time during the late Llandoveryan, as with

other times during the Silurian, unusual conditions conducive to both the proliferation and preservation of expansive ‘seaweed meadows’ were established across regional-scale areas of the Laur-entian epeiric sea. Further study of these and other Silurian algal-Lagerstätten, particularly in a sequence stratigraphic framework and aided by stable carbon isotope analyses, should help to increase understanding of the broad-scale causal mechanism(s) behind their formation, including possible relationships to climate change.

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