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New multicellular marine macroalgae from the early Tonian of northwestern Canada

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ABSTRACT

Molecular phylogenetic data suggest that photosynthetic eukaryotes first evolved in freshwater environments in the early Proterozoic and diversified into marine environments by the Tonian Period, but early algal evolution is poorly reflected in the fossil record. Here, we report newly discovered, millimeter- to centimeter-scale macrofossils from outer-shelf marine facies of the ca. 950–900 Ma (Re-Os minimum age constraint = 898 ± 68 Ma) Dolores Creek Formation in the Wernecke Mountains, northwestern Canada. These fossils, variably preserved by iron oxides and clay minerals, represent two size classes. The larger forms feature unbranching thalli with uniform cells, differentiated cell walls, longitudinal striations, and probable holdfasts, whereas the smaller specimens display branching but no other diagnostic features. While the smaller population remains unresolved phylogenetically and may represent cyanobacteria, we interpret the larger fossils as multicellular eukaryotic macroalgae with a plausible green algal affinity based on their large size and presence of rib-like wall ornamentation. Considered as such, the latter are among the few green algae and some of the largest macroscopic eukaryotes yet recognized in the early Neoproterozoic. Together with other Tonian fossils, the Dolores Creek fossils indicate that eukaryotic algae, including green algae, colonized marine environments by the early Neoproterozoic Era.

INTRODUCTION

Understanding the early evolution and diversification of eukaryotes is a central objective in geobiology. Of particular importance are the archaeplastids, a key group that includes Rhodophyta (red algae) and Viridiplantae (green algae and land plants). With their primary chloroplasts derived from endosymbiosis, algae became significant contributors to primary productivity and photosynthetic oxygen production in the Neoproterozoic (1000–539 Ma; Brocks, 2018). Algae are proposed to have first evolved in freshwater environments in the early Proterozoic, but they then expanded into marine environments by the Tonian Period (1000–720 Ma)—leading to dramatic reorganizations of the marine biological pump, food webs, and benthic habitats (Sánchez-Baracaldo et al., 2017; Del Cortona et al., 2020). However, the early fossil record of algae—a polyphyletic group of photosynthetic eukaryotic organisms—is scarce and controversial (Berney and Pawlowski, 2006; Graham, 2019). While both fossils (Butterfield, 2000; Bykova et al., 2020; Tang et al., 2020) and biomarkers (Brocks, 2018) imply algal diversification by the Tonian, rare algal fossils provide limited geological constraints on the timing and environment of key nodes predicted by molecular data.

Various marine fossils as old as 1.9–1.5 Ga have been interpreted as algae (e.g., Han and Runnegar, 1992), including green algae (e.g., Agić et al., 2017). However, the phylogeny and habitat of many algal fossils remain contentious owing to their simple morphology and a lack of paleoenvironmental constraints. The oldest-known unequivocal rhodophyte fossil is the ca. 1050 Ma *Bangiomorpha pubescens* (Butterfield, 2000; Yang et al., 2016; Gibson et al., 2018). Also, *Proterocladus* from the ca. 795 Ma Svanbergfjellet Formation in Svalbard, Norway (Butterfield et al., 1994), and the ca. 1000 Ma Nanfen Formation in north China (Tang et al., 2020) has been interpreted as a siphonocladous green alga. This interpretation is inconsistent with some molecular clock results that suggest siphonocladous green algae did not diverge until the latest Neoproterozoic (e.g., Del Cortona et al., 2020). However, if confirmed, these fossils imply a much earlier origin and diversification of the chlorophytes. The ca. 1080 Ma Nonesuch Formation in North America contains a possible fragment of *Proterocladus* (Tang et al., 2020), but the setting (marine versus nonmarine) is

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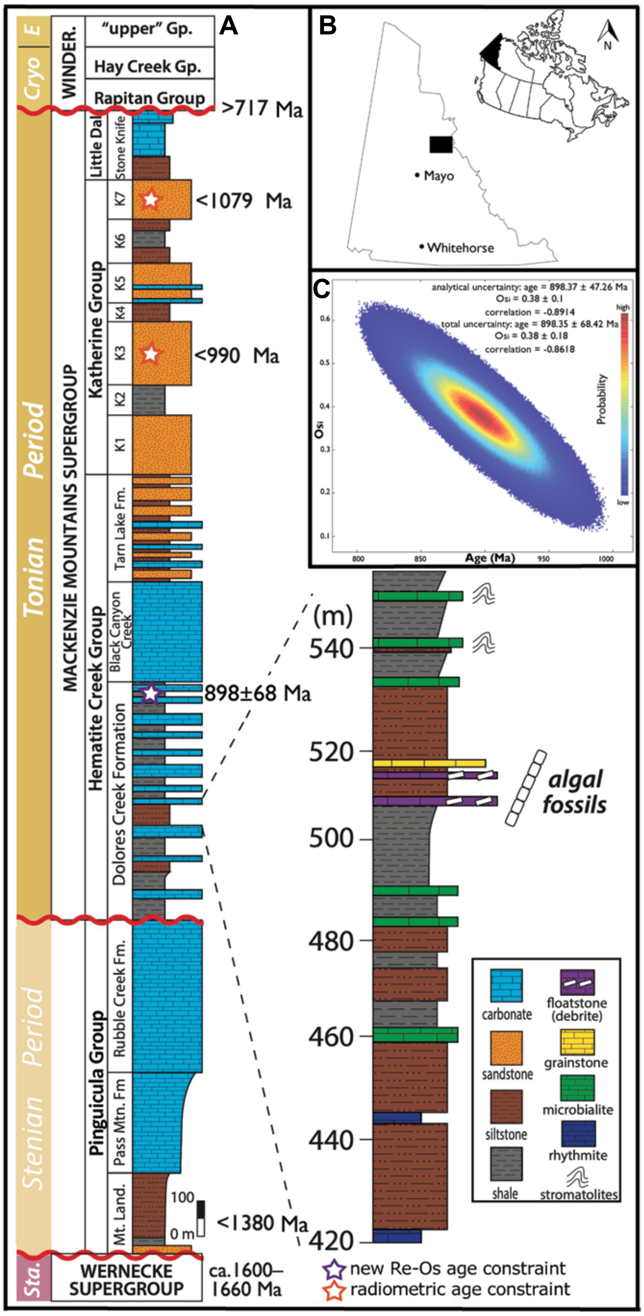

Figure 1. Geologic setting. (A) Stratigraphic log of the Dolores Creek Formation in the study area (Yukon, Canada, 64°41′17.6″N; 133°14′30.3″W), with radiometric age constraints and fossil interval enlarged. See the Supplemental Material (see footnote 1) for regional correlations. (B) Map of Yukon, Canada showing field location in the Wernecke Mountains. (C) Contour plot of a Monte Carlo simulation that yields a nearly identical age to the benchmark Isoplot algorithm (898 ± 68 Ma including both analytical and model age uncertainties). Gp.—Group; Fm.—Formation; Sta.—Statherian Period; Cryo—Cryogenian Period; E—Ediacaran Period, Winder.—Windermere Supergroup.

disputed (Jones et al., 2020). These uncertainties highlight the pressing need to document Proterozoic algal fossils from geochronologically and paleoenvironmentally resolved successions.

We report two populations of exceptionally well-preserved, macroscopic, filamentous fossils from ca. 950 Ma marine strata of the lower Dolores Creek Formation in the Wernecke Mountains, Yukon, Canada. Phylogenetic and paleoenvironmental interpretations of these fossils reveal novel insights into early eukaryotic evolution and ecology.

GEOLOGIC SETTING

The ca. 950–900 Dolores Creek Formation (Fig. 1; Figs. S1–S4 in the Supplemental Material[1]) is the basal unit of the ca. 950–775 Ma Mackenzie Mountains Supergroup, which outcrops along the border between Yukon and Northwest Territories (Canada) and represents one of the most complete early–middle Tonian successions globally (Turner, 2011). In most locations, the formation consists of ∼300 m of shale, siltstone, and microbial dolostone deposited in outer-shelf settings (Fig. 1). The conformably overlying Black Canyon Creek Formation is composed of tidally influenced meter-scale carbonate-shale cycles, implying a marine setting (Turner, 2011) (Figs. S5–S7). At the fossil locality (Fig. S3), the Dolores Creek Formation is expanded to ∼1 km thick and includes a thick basal succession, absent in most sections, that consists of dark-gray siltstones and shales with minor stromatolitic bioherms and debrites. The macrofossils described here are associated with debrite beds near the middle of the formation in facies interpreted to record deposition via gravity flows into relatively deep water (below storm wave base; Fig. 1C). We infer that the fossils were transported from a shallow marine shelf edge and redeposited by episodic slope failure events resulting in rapid burial and aiding fossil preservation. Increasingly abundant stromatolite bioherms above the debrite interval record progradation of the shallower, photic-zone shelf-edge facies from which the fossils were likely derived. Thus, the fossils likely represent organisms that inhabited the seafloor between stromatolite mounds that rimmed the margin.

Re-Os Geochronology

Black shale from the Dolores Creek Formation yielded a Re-Os date of 896 ± 45 Ma (2σ, $n = 5$, mean square of weighted deviates [MSWD] = 0.92; total uncertainty includes that of the ^{187}Re decay constant) with an initial ^{187}Os/^{188}Os composition of 0.38 ± 0.09 (Fig. S1; Dataset S2; see Supplemental Material). This date is similar to that obtained using a Monte Carlo resampling approach (898 ± 68 Ma) that propagates both analytical and model age uncertainties (Fig. 1; Fig. S1; Li et al., 2019). Here, we consider the date derived using the Monte Carlo method to be the best estimate of the depositional age of the Dolores Creek Formation and minimum age for the macrofossils.

MACROFOSSILS

We analyzed 339 specimens of macrofossils (Figs. 2 and 3; Table 1; Figs. S8–S15; Dataset S2) that ranged from exceptional preservation with rare three-dimensional morphological details to poor preservation with only outlines of the fossils. Fossils are casted by clays and pyrite (often weathered as Fe oxides; Figs. 3C and 3D) with limited carbon remaining. Accounting for variations in preservation, the specimens maintain a ribbon-like shape with consistent widths along the entire length (Figs. 2A and 2B). Two populations were identified based on their widths (Fig. S9): Large specimens range from 0.60 to 0.80 mm in width, whereas small specimens range from 30 to 50 μm. The large fossils reach up to 36 mm in length, while the small forms can be up to 4.9 mm long; because the specimens are likely fragmented, their observed lengths provide only minimum estimates.

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[1] Supplemental Material. Detailed description of methods, geological setting, Proterozoic life, and additional figures for each morphologic characteristic. Please visit https://doi.org/10.1130/GEOL.S.14120384 to access the supplemental material, and contact editing@geosociety.org with any questions.

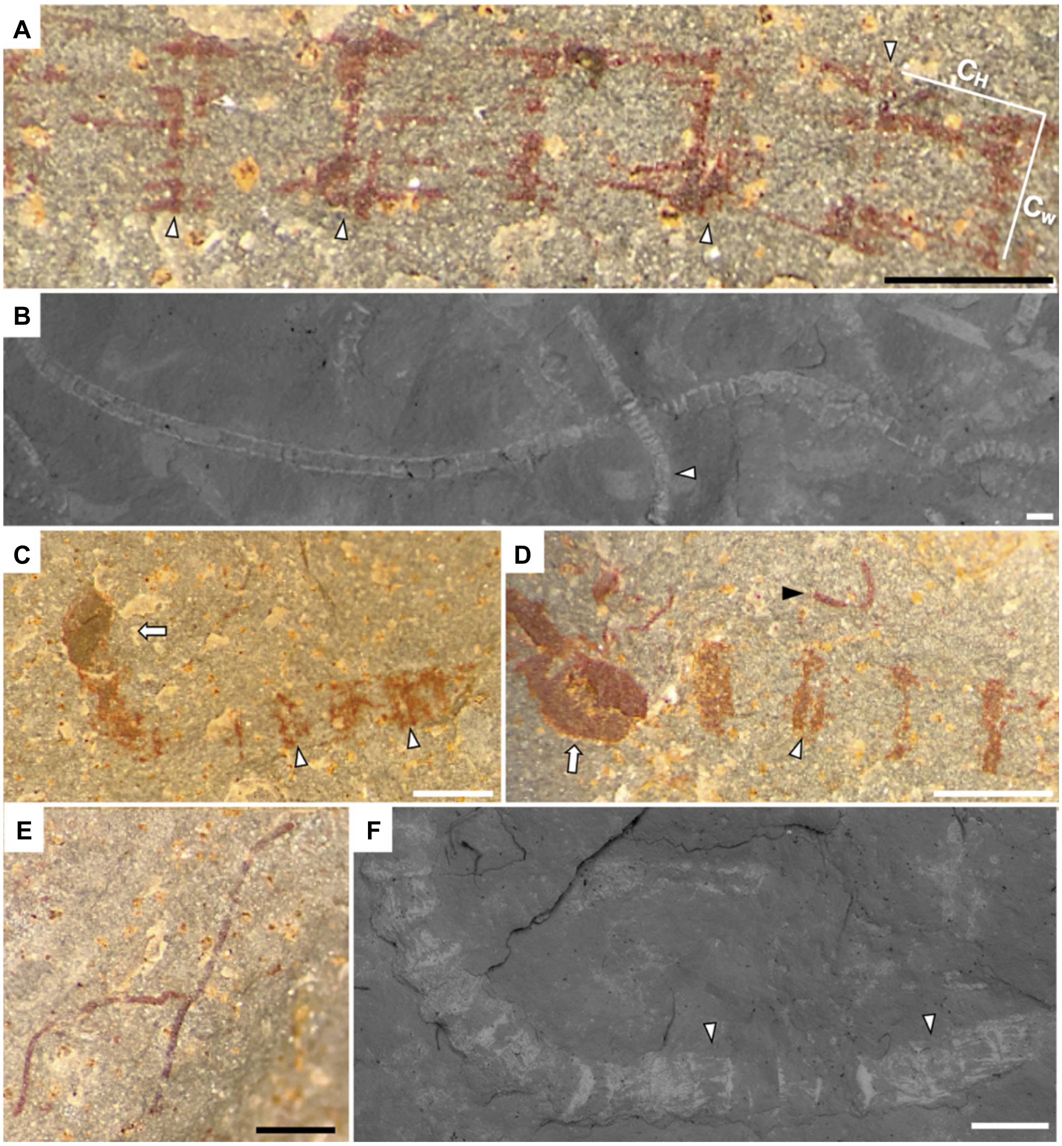

Figure 2. Dolores Creek Formation (Yukon, Canada) macrofossils. (A) Large macrofossil divided by double septa (arrowheads) into cells (C_H—cell height, C_w—cell width) with longitudinal striations. (B) One large specimen (arrowhead) overlying another perpendicular to the first. (C) Large macrofossil with septa (arrowheads) and probable holdfast (arrow). (D) Holdfast (arrow) of large macrofossil overlapping another with double septa (white arrowhead). Note small fossils (black arrowhead). (E) Small macrofossil with branching. (F) Large macrofossil with longitudinal striations (arrowheads). White scale = 1 mm; black scale = 0.5 mm. See the Supplemental Material (see footnote 1) for additional examples of morphological characteristics. Specimens in A, D, and F are from sample HCS-W18–56 (Royal Ontario Museum specimen ROMIP66167), specimen in C is from sample HCS-W18–59 (ROMIP66169), and specimens in B and E are from sample HCS-W18–72 (ROMIP66170).

The large fossils are subdivided by a series of double septa into uniform, repeating segments with no evidence of pit connections (Figs. 2A–2D; Figs. S10 and S11). These segments range in length from 0.45 to 0.53 mm (mean = 0.49 ± 0.017 mm), they are consistently spaced, and >30 segments occur in the best-preserved examples. Where specimens are preserved in three dimensions, the double septa exhibit higher relief (Fig. S8; Video S1). Longitudinal striations (<0.03 mm in width) within the segments and extending between the septa (Figs. 2A and 2E) may be the result of compression of a tube (Cohen et al., 2009). However, the observation of these striations in the three-dimensionally preserved specimens (Fig. 2E) suggests that they were biological features. Exceptionally preserved larger specimens bear an elongated, ellipsoidal-to-globose, club-like structure at one of the termini (*n* = 15; Figs. 2C and 2D; Fig. S12). The small specimens display branching (Fig. 2F; Fig. S13) but lack visible segments or other characteristic features.

DISCUSSION

Taphonomy

Taphonomic bias contributes to the sparse fossil record of Proterozoic macroalgae. Nonbiomineralizing macroalgae have low preservation potential and are primarily preserved as two-dimensional carbonaceous compressions (Xiao and Dong, 2006). This is similar to Burgess Shale–type preservation, which, in addition to the characteristic carbonaceous films, also include accessory minerals such as pyrite and clays, implicated as taphonomically important in algal fossils from the Ediacaran to Cambrian (Anderson et al., 2011; LoDuca et al., 2015), as well as other postulated green algae from the Tonian (Anderson et al., 2020). The Dolores Creek macrofossils show both of these accessory minerals (Figs. 3C and 3D; Figs. S14 and S15) but retain little remnant organic carbon, implying a similar preservational pathway but enhanced degradation and removal of carbonaceous remains (Schiffbauer et al., 2014).

Phylogenetic Affinity

An animal affinity can be ruled out for the macrofossils because no animals are known to have a septate filamentous construction. A fungal affinity is also unlikely for the larger fossils because septate fungal hyphae are much thinner (micrometer versus millimeter scale), and often associated with diagnostic spore-bearing structures (Alexopoulos et al., 1996). Large filaments with differentiated cell walls (double septa) organized into an unbranching thallus are consistent with a cyanobacterial or algal interpretation (Graham and Wilcox, 2000).

Distinguishing between these interpretations is complicated by the morphological convergence among extant filamentous cyanobacteria and algae. However, the large size,

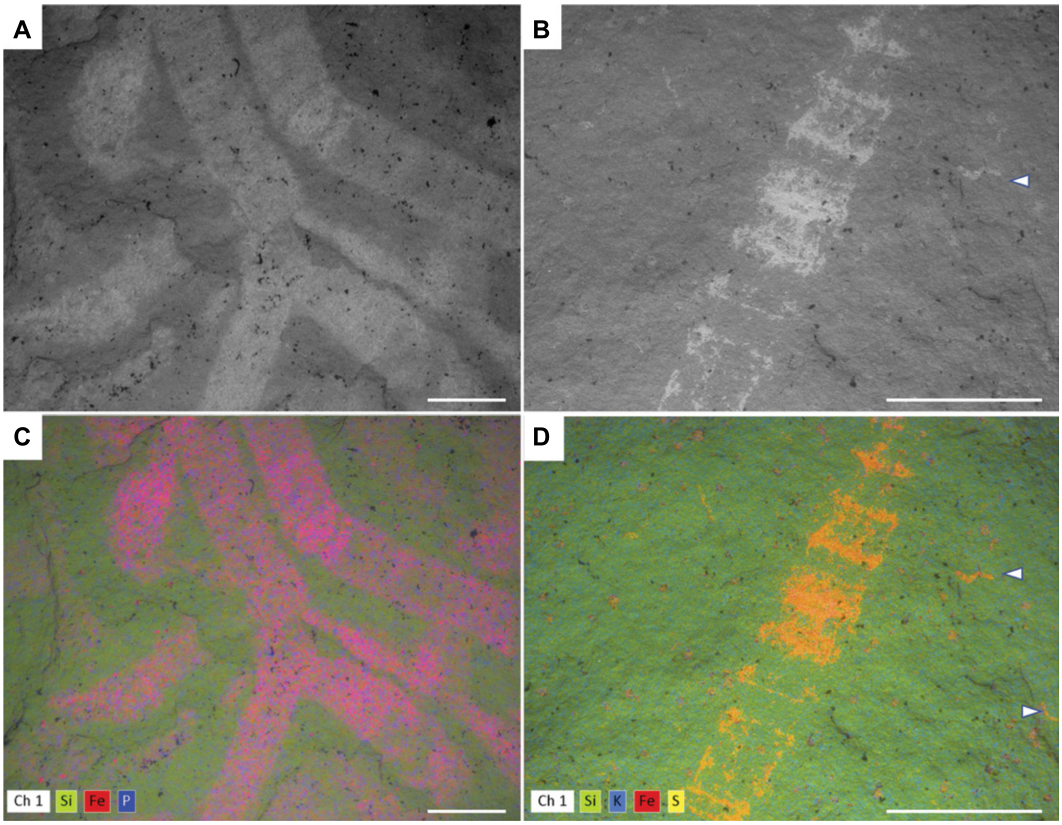

Figure 3. Electron microscopic images and elemental maps. (A–B) Backscattered electron image of large macrofossils. (C) Energy-dispersive X-ray spectroscopy (EDS) map of the area in A with relative abundances of Fe, Si, and P. Note the apparent branching is a result of overlapping fossils, and apparent red color is from Fe (red) enrichment. (D) EDS map of area in B with relative abundances of Fe, Si, K, and S. Note: orange color is the result of a combination of Fe (red) and sulfur (yellow). Arrowheads denote small fossils. Scale = 1 mm. Specimens in A and C are from sample HCS-W18–40 (Royal Ontario Museum specimen ROMIP66164), and specimens in B and D are from HCS-W18–59 (ROMIP66169).

TABLE 1. GENERAL MORPHOMETRICS OF THE TWO FOSSIL SIZE CLASSES

Size class	n	Minimum width	Maximum width	Mean width	σ	Maximum length	Mean length	σ
Large	250	600	800	700	30	36	9	4.78
Small	89	30	50	40	5	4.9	0.95	0.70

Note: Widths are reported in μm, and lengths are in millimeters.

longitudinal striations, and probable holdfasts all favor an epibenthic algal interpretation for the large fossils. Cyanobacteria lack a holdfast to support an erect epibenthic habit (Xiao et al., 2002). Some cyanobacteria such as *Rivularia* and *Calothrix* can develop apical cells (Castenholz, 2001), but these are typically conical in shape or specialized heterocysts that are unlikely to occur only at the terminal end of the organism (cf. Fig. 2C). The probable holdfasts represent the only variation in the width from the thallus and differ in shape from heterocysts by their elongated structure. Additionally, the longitudinal striations (Figs. 2A and 2E) likely represent rib-like cell wall ornamentation. Such striations are unknown from cyanobacterial cell walls but are broadly similar to the longitudinal ridges on the cell walls of some green algae (e.g., desmidaceans; Gontcharov and Watanabe, 1999). Finally, filamentous cyanobacterial cells have an upper size limit of ~0.2 mm in width (Pang et al., 2018), whereas the cells in the larger macrofossils are up to 0.8 mm in width. Thus, the larger population is most parsimoniously interpreted as epibenthic eukaryotic macroalgae. The smaller branching specimens somewhat resemble other Tonian fossils interpreted as crown-group green algae (Butterfield et al., 1994; Tang et al., 2020); however, with their simple morphology, they could plausibly represent either algae or cyanobacteria.

Extant filamentous green algae provide the best analog for the larger populations based on their large cell size, typical of extant siphonocladaleans (Leliaert et al., 2007), and the presence of rib-like ornamentation on their cell walls, reminiscent of extant desmidaceans (Gontcharov and Watanabe, 1999). Most multicellular red and brown algae have either pseudoparenchymatous or true parenchymatous thalli (Graham and Wilcox, 2000), distinct from the uniseriate filamentous construction of the Dolores Creek fossils. Red algae also have pit connections (Yang et al., 2016) and smaller cell size compared with most multicellular lineages, possibly due to their minimal cytoskeleton (Brawley et al., 2017), while larger cells are common in green algae (e.g., siphonocladaleans; Leliaert et al., 2007). A uniseriate filamentous thallus is common among green algae (South and Whittick, 1987), including both streptophytes and chlorophytes (Leliaert et al., 2012), some of which can develop simple holdfasts as well (South and Whittick, 1987). An extant analog for the large fossils could be *Chaetomorpha melagonium*, a cladophoralean green alga with a uniseriate filament composed of cells up to 850 μm in width and a discoidal holdfast (Blair, 1983).

Broader Implications

The larger macrofossils from the Dolores Creek Formation, together with recognized Tonian chlorophytes from China (Tang et al., 2020) and Spitsbergen (Butterfield et al., 1994), provide evidence that benthic macroalgae inhabited marine habitats by the early Tonian Period. This finding is consistent with a Paleoproterozoic–Mesoproterozoic divergence between Rhodophyta and Viridiplantae (Sánchez-Baracaldo et al., 2017; Gibson et al., 2018), and it indicates that chlorophytes had already colonized oceans by ca. 900 Ma, ~200 m.y. before the first Cryogenian snowball glaciation and 300 m.y. before the earliest biomarker evidence for green algae–dominated marine ecosystems (Brocks, 2018). This discrepancy between the fossil and biomarker record may be an artifact of preservation (or sampling bias), or, alternatively, it may indicate that marine algae were ecologically restricted, perhaps due to severe nutrient limitation in Tonian seawater (Ozaki et al., 2019). This distinction is important because the ecological expansion of benthic macroalgae may have influenced marine oxygenation due to their greater burial potential compared to phytoplankton (LoDuca et al., 2017). The Dolores Creek fossil locality represents a depositional setting that was optimized for fossil preservation due to rapid burial by gravity flow(s), and thus it offers a rare glimpse into early eukaryotic macroalgae.

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