

A Laurentian record of the earliest fossil eukaryotes

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ABSTRACT

The oldest evidence of eukaryotes in the fossil record comes from a recurrent assemblage of morphologically differentiated late Paleoproterozoic to early Mesoproterozoic microfossils. Although widely distributed, the principal constituents of this *Tappania-Dictyosphaera-Valeria* assemblage have not hitherto been recognized on Laurentia. We have recovered all three taxa from a shallow-water shale succession in the early Mesoproterozoic Greyson Formation (Belt Supergroup, Montana, USA). An exceptionally preserved population of *Tappania* substantially expands the morphological range of this developmentally complex organism, suggesting phylogenetic placement within, or immediately adjacent to, crown-group eukaryotes. Correspondence with *Tappania*-bearing biotas from China, India, Australia, and Siberia demonstrates an open-ocean connection to the intracratonic Belt Basin and, along with broadly co-occurring macrofossils *Grypania* and *Horodyskia*, supports the recognition of a globally expressed biozone. The Greyson Formation, along with contiguous strata in Glacier National Park, is unique in preserving all currently confirmed taxa of early eukaryotic and macroscopic fossils.

INTRODUCTION

The fossil record of eukaryotes extends back to at least the late Paleoproterozoic (Butterfield, 2015), and a recurrent assemblage of distinctive microfossils from China (Ruyang Group; Yin, 1997; Yin et al., 2005), Australia (Roper Group; Javaux et al., 2001; Javaux and Knoll, 2016), India (Semri Group; Prasad et al., 2005), and Siberia (Kamo Group; Nagovitsin, 2009) points to the presence of an ecologically coherent biota extending from ca. 1650 Ma to ca. 1400 Ma. Typified by process-bearing *Tappania*, reticulate-walled *Dictyosphaera/Shuiyoushaeridium*, and concentrically striated *Valeria*, these earliest fossil eukaryotes offer key insights into the early evolution of the clade, and enable practical applications to paleobiogeography and biostratigraphic correlation.

Proterozoic eukaryotes are also richly represented on Laurentia; however, their oldest confirmed records on this craton are of late Mesoproterozoic age (Butterfield and Chandler, 1992; Butterfield, 2000; Hofmann and Jackson, 1994). Older fossils are known from North America, notably *Grypania* and *Horodyskia* from the early Mesoproterozoic Belt Supergroup (Walter et al., 1976; Fedonkin and Yochelson, 2002), but neither of these macroscopic forms is unambiguously eukaryotic (Butterfield, 2009). Apart from our report of long-ranging *Valeria* in the Chamberlain Formation (Adam et al., 2016), the same is true for spheroidal and filamentous microfossils that have been recovered from Belt Supergroup strata (Horodyski, 1980). Here we report a full *Tappania-Dictyosphaera-Valeria* assemblage from the Greyson Formation of the lower Belt Supergroup, filling a major gap in the early eukaryotic record.

GEOLOGICAL SETTING

The Belt Supergroup contains as much as 15 km of strata, extending from British Columbia to central Montana, including an eastward-extending limb termed the Helena embayment (Winston and Link, 1993) (Fig. 1A). This intracratonic sedimentary succession has been interpreted

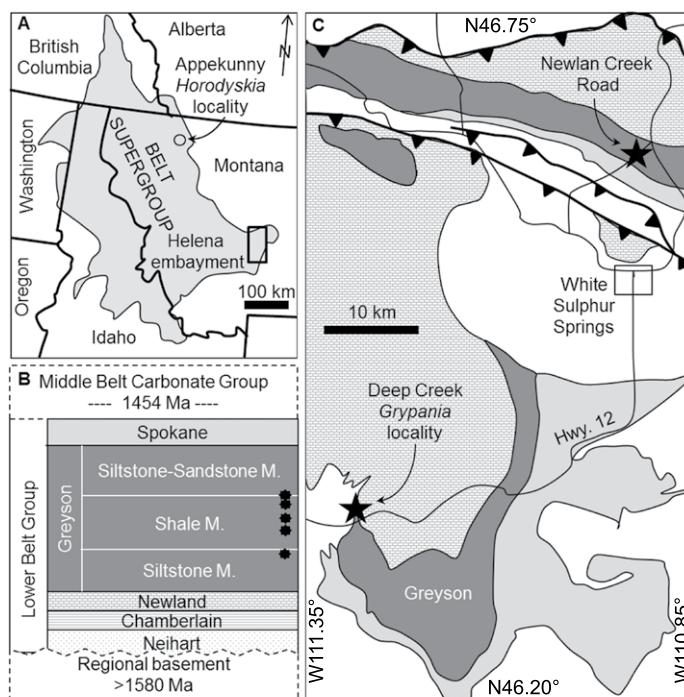


Figure 1. Geology of the fossiliferous Newlan Creek Road section of the Greyson Formation (Montana, USA). A: Extent of the Belt Supergroup, with the Helena embayment to the east. **B:** Stratigraphy of the Belt Supergroup within the Helena embayment; fossil horizons are marked by black stars. M.—member. **C:** Local bedrock geology, including the *Grypania* locality at Deep Creek and the *Tappania-Dictyosphaera-Valeria*-bearing section along Newlan Creek Road.

as a restricted marine (Horodyski, 1993; Lyons et al., 2000), possibly even a lacustrine (Winston, 1993), deposit. The paleogeographic relationships of the Belt Basin are poorly constrained, with different reconstructions identifying Siberia, Australia, or Antarctica as the conjugate rift margin (Sears and Price, 2003).

The Helena embayment preserves the lowermost strata of the Belt Supergroup, representing a broadly transgressive-regressive sedimentary succession. The fossils described here come from unoxidized shales of the Greyson Formation (Montana, USA) that overlie subtidal carbonate-shale deposits of the Newland Formation, and are overlain in turn by mud-cracked redbeds of the Spokane Formation (Fig. 1B). The Greyson Formation crops out extensively in the Little and Big Belt Mountains, including the type section of *Grypania* at Deep Creek (Walter et al., 1976), and is broadly correlative with the Appekunny Formation in Glacier National Park (Fig. 1A; Horodyski, 1993; Slotznick et al., 2016), including the type section of *Horodyskia* (Fedonkin and Yochelson, 2002). Our study is based on a roadcut section of the Greyson Formation ~50 km northeast of Deep Creek, along Newlan Creek Road near White Sulphur Springs, Montana (46.668°N, 110.884°W) (Fig. 1C), where it comprises ~1100 m of

finely laminated mudstones with isolated sandstone layers. We recognize three informal constituent units: (1) a lower siltstone member (~350 m); (2) a middle shale member (~435 m); and (3) an upper siltstone-sandstone member (~315 m). Multiple small-scale shallowing-upward sequences in the two upper members are interpreted to reflect sedimentation in shallow-shelf to subshoreface environments.

The age of the Greyson Formation is constrained by a 1454 ± 9 Ma U-Pb date from a bentonite layer in the overlying Helena Formation of the Middle Belt Carbonate Group (Evans et al., 2000), and is corroborated by 1470–1460 Ma sills intruding correlative Lower Belt Group strata of the Prichard Formation (Sears et al., 1998). The maximum age is set as 1710 Ma by the youngest age of a suite of zircons recovered from the underlying Neihart Quartzite (Mueller et al., 2016), although basement rocks in northern Idaho dated at 1576 ± 13 Ma underlie a unit thought to be correlative to the Neihart Quartzite (Evans and Fischer, 1986; see the GSA Data Repository¹).

PALEONTOLOGY

Nine unoxidized mudstone horizons of the Greyson Formation at Newlan Creek were collected for microfossil processing. Samples were broken into 1–3 cm fragments, allowed to disaggregate with minimal agitation in 48% hydrofluoric acid, and fossils were individually picked from rinsed slurries.

Microfossils were recovered from five horizons, all within or immediately below the shale member (Fig. 1B). The assemblages are dominated by simple spheroidal microfossils up to 300 μm in diameter (*Leiosphaeridia* spp.) regularly accompanied by a variety of paired, colonial, and budding forms, including *Satka favosa* and *Gemmuloides doncookii*; medial-split release structures are also common (Figs. 2C–2F, 2H). Such morphologies are common among extant protistan-grade eukaryotes, but the absence of any demonstrably crown-group features leaves these fossils taxonomically unresolved. Filamentous microfossils (*Siphonophycus*, *Oscillatoriopis*; Figs. 2A, 2B) are most likely benthic photosynthesizers (Butterfield and Chandler, 1992), providing an independent measure of shallow-water deposition in the Greyson Formation. The longitudinally striated filament *Lineaforma elongata* (Figs. 2G, 2I) may prove to be biostratigraphically useful with all currently reported occurrences limited to the early Mesoproterozoic (Vorob'eva et al., 2015; Adam et al., 2016; Javaux and Knoll, 2016).

The most significant fossils in the Greyson microbiota are morphologically differentiated vesicles assignable to *Tappania plana*, *Dictyosphaera macroreticulata*, and *Valeria lophostriata*. Only *Valeria* (Figs. 3D, 3E) has been previously documented on Laurentia: in the middle Neoproterozoic Chuar Group of Arizona (Porter and Riedman, 2016), the late Mesoproterozoic Bylot basin system of Canada (Butterfield and Chandler, 1992; Hofmann and Jackson, 1994), and the Lower Belt Group Chamberlain Formation (Adam et al., 2016). With a total age range exceeding 700 m.y., it offers no useful stratigraphic resolution (Hofmann, 1999). There are, however, good grounds for recognizing its fine concentric microstructure as diagnostically eukaryotic (Javaux et al., 2001); modern analogs are found in the microfibrillar cell-wall construction of glaucophyte algae (cf. Willison and Brown, 1978).

Dictyosphaera is distinguished by its relatively large vesicles (50–300 μm) and a complex polygonal wall structure well beyond the limits of prokaryotic morphogenesis (Yin et al., 2005; Agić et al., 2015). Although the inner surface of the wall is not seen in the Greyson population (Figs. 3A–3C), the specimens correspond closely with the Ruyang Group type material in terms of outer wall ornamentation, size, medial split structures, and the presence of a large intracellular inclusion in some unsplit specimens

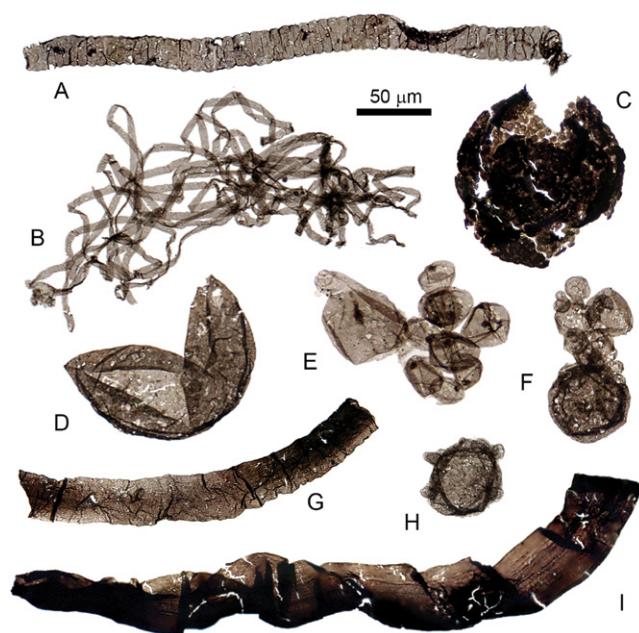


Figure 2. Filamentous and spheroidal microfossils from the Greyson Formation (Montana, USA). A: *Oscillatoriopis longa*. B: *Siphonophycus* sp. C: Colonial *Satka favosa*. D: *Leiosphaeridia* sp. with a medial split. E: Colonial spheroidal form with single larger cell developing a lateral extension. F: Colonial *Coneosphaera* sp. G, I: *Lineaforma elongata*. H: *Gemmuloides doncookii*. Scale bar applies to all images.

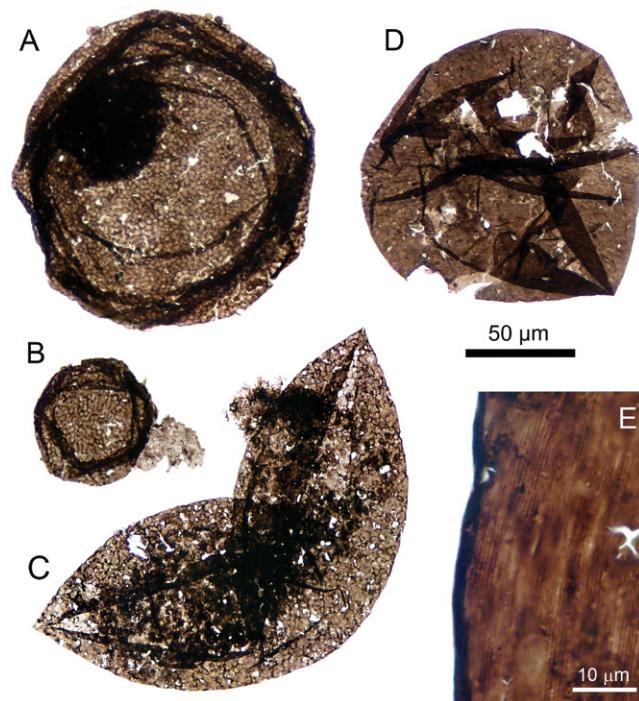


Figure 3. Eukaryotic microfossils from the Greyson Formation (Montana, USA). A–C: *Dictyosphaera macroreticulata*, with reticulate wall structure, intracellular inclusion (A) and medial split (C). D, E: *Valeria lophostriata*, with concentric wall microstructure. Dark scale bar applies to A–D.

¹GSA Data Repository item 2017114, geochronological constraints on the Greyson Formation, is available online at <http://www.geosociety.org/datarepository/2017/> or on request from editing@geosociety.org.

(Fig. 3A; cf. Pang et al., 2013). The absence of an acanthomorphic (*Shuiyousphaeridium*) phase seen in the late Paleoproterozoic Ruyang Group and Semri Group biotas (Pang et al., 2013; Singh and Sharma, 2014; Agić et al., 2015) is most likely due to small sample size and local taphonomy.

The most conspicuous and common eukaryote in the Greyson Formation biota is *Tappania plana* (Fig. 4), a microfossil distinguished by tubular processes and broader neck-like extensions (Yin, 1997). Most Greyson Formation *Tappania* specimens correspond to previously described populations, but the large sample size reveals a substantially new account of its anatomy. Vesicles range from 30 to 150 μm (\bar{x} = 89 μm , standard deviation = 23 μm , N = 53) with shapes varying from equidimensional to elongate (Fig. 4C). Both the processes (N \leq 20) and neck-like extensions (N \leq 4) vary in number and are randomly distributed on vesicles, although many specimens show clear evidence of hemispherical polarization (Figs. 4B, 4D, 4E, 4H–4J). Process branching shows a broad range of expression, including equidimensional (Figs. 4B, 4E, 4H, 4I) and size-reductive bifurcations (Figs. 4B, 4I, 4J), second-order branching (Figs. 4B, 4H), and vesicles bearing multiple branched process (Figs. 4B, 4I). As in the Kamo Group and Roper Group populations, there are rare instances of processes with internal partitions (Fig. 4F). Some specimens also bear outgrowths directly comparable to *T. tubata* (Fig. 4J), a putative second species.

Greyson Formation *Tappania* specimens exhibit a number of features not seen in other populations, most notably the differentiation of an outer wall (Figs. 4A, 4B, 4G). Although often expressed as a simple enveloping sheath, this relatively translucent layer can also be seen forming processes that are not present, or only partially developed, on the more robust inner wall; such independent morphogenesis demonstrates a particularly sophisticated level of cytoskeletal control. A further subset of specimens has terminally flared processes (Figs. 4A, 4B, 4D, 4G, 4H), suggesting suspension within a third (unpreserved) outer envelope or adventitious substrate attachment.

In a conventional form-taxonomic context, the novel features and variation exhibited by Greyson Formation *Tappania* specimens would warrant the establishment of multiple new form genera and form species. Even within this relatively large population, however, there are no obvious modes in size or form. Such morphological continuity, anchored to the presence of diagnostic neck-like extensions, points to pronounced ontogenetic and/or ecophenotypic variation (cf. Yin et al., 2005; Javaux and Knoll, 2017). On the basis of current evidence, *Tappania* represents a single biological species, *T. plana*.

DISCUSSION

The complex wall morphologies and microstructures exhibited by Greyson Formation *Tappania*, *Dictyosphaera*, and *Valeria* specimens are diagnostically eukaryotic. Such features are entirely outside the capacity of any organisms lacking a fully motorized cytoskeleton and endomembrane system (Javaux et al., 2001; Cavalier-Smith, 2002; Pang et al., 2013; Agić et al., 2015; Butterfield, 2015). The sophistication of this cytological machinery is particularly apparent in *Tappania*, where the inducible development of at least three separate components (neck-like extensions, processes, and independently deployed outer wall) demonstrates a level of morphogenetic control comparable to that of all but the most derived living protists. In this light, there is an increasingly secure case for placing *Tappania* within, or immediately adjacent to, crown-group Eukarya, despite its unresolved affiliations (Javaux and Knoll, 2016). This same conclusion may be drawn for *Dictyosphaera* and *Shuiyousphaeridium* (Pang et al., 2013; Agić et al., 2015), although not for fundamentally simpler *Valeria*.

All previous records of *Tappania* and *Dictyosphaera* came from a relatively narrow range of late Paleoproterozoic to early Mesoproterozoic strata, pointing to their utility as biostratigraphic markers (Yin et al., 2005; Agić et al., 2015; Javaux and Knoll, 2017). This potential is bolstered by the presence of two distinct forms exhibiting the same temporal distribution, along with a third (*Valeria*) that is conspicuously different. Extension of a *Tappania*-*Dictyosphaera*-*Valeria* assemblage zone into Laurentia now

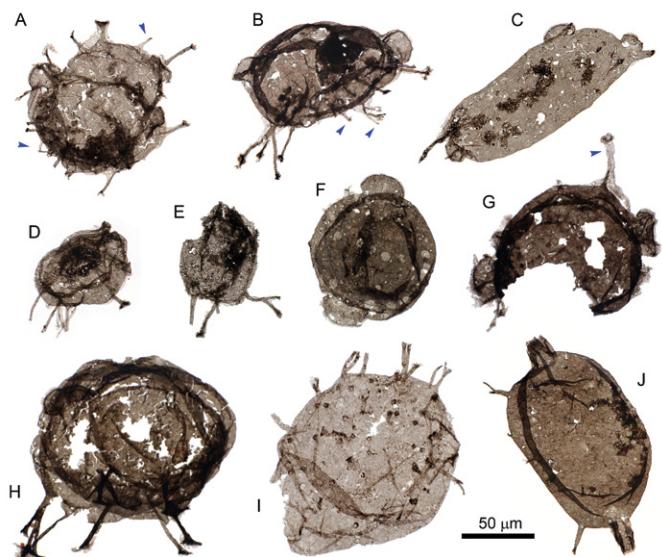


Figure 4. Eukaryotic *Tappania plana* from the Greyson Formation (Montana, USA), showing variably branched processes (B, E, H–J), terminally flared processes (A, B, D, G, H), hemispherically polarized processes (B, D, E, H–J), septate processes (F), tubular outgrowth comparable to *T. tubata* (J), and an outer wall capable of independent process formation (blue arrows in A, B, G). Scale bar applies to all images.

confers a corroborating global signal. Notably, the ca. 1450 Ma minimum age for the Greyson Formation biota overlaps the age of Roper Group fossils (cf. Javaux et al., 2001), which are bracketed in turn by the marginally younger Kamo Group and older Ruyang Group and Semri Group biotas.

A *Tappania*-*Dictyosphaera*-*Valeria* biozone is further supported by the accompanying occurrence of *Grypania* and *Horodyskia*. Despite the fundamentally unresolved affiliations of these oldest-known macrofossils, both contribute a possible biostratigraphic signal. In addition to its type occurrence in the Greyson Formation, *Grypania spiralis* is known from the early Mesoproterozoic Changchengian System of north China (Du et al., 1986) and the late Paleoproterozoic Semri Group of India (Sharma and Shukla, 2009), along with a less resolved population in the 1.87 Ga Negaunee Iron-Formation of Michigan, USA (Han and Runnegar, 1992). *Horodyskia* is biologically more problematic and extends from the early Mesoproterozoic Appekunny Formation in Glacier National Park (Montana) through Mesoproterozoic–Neoproterozoic strata in Australia (Grey et al., 2010; Calver et al., 2010) and the Ediacaran of south China (Dong et al., 2008). Even so, its first appearance notably is within the narrow time frame delineated by the cooccurrence of *Tappania plana*, *Dictyosphaera macroreticulata*, *Valeria lophostriata*, and *Grypania spiralis*.

Insofar as the Greyson Formation in the Helena embayment is stratigraphically contiguous with the Appekunny Formation in Glacier National Park, this shallow shelf succession is unique in preserving a complete roster of all known early eukaryotic and macroscopic fossil taxa, along with a comprehensive record of simple spheroidal and filamentous form taxa. The succession demonstrates a clear connection between the Helena embayment and the global oceans (cf. Winston, 1993), with important implications for early Proterozoic paleogeography and the global distribution of the planet's oldest known eukaryotes.

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