

Possible early foraminiferans in post-Sturtian (716–635 Ma) cap carbonates

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ABSTRACT

Foraminifera are an ecologically important group of modern heterotrophic amoeboid eukaryotes whose naked and testate ancestors are thought to have evolved ~1 Ga ago. However, the single-chambered agglutinated tests of these protists appear in the fossil record only after ca. 580 Ma, coinciding with the appearance of macroscopic and mineralized animals. Here we report the discovery of small, slender tubular microfossils in the Sturtian (ca. 716–635 Ma) cap carbonate of the Rasthof Formation in Namibia. The tubes are 200–1300 μm long and 20–70 μm wide, and preserve apertures and variably wide lumens, folds, constrictions, and ridges. Their sometimes flexible walls are composed of carbonaceous material and detrital minerals. This combination of morphological and compositional characters is also present in some species of modern single-chambered agglutinated tubular foraminiferans, and is not found in other agglutinated eukaryotes. The preservation of possible early Foraminifera in the carbonate rocks deposited in the immediate aftermath of Sturtian low-latitude glaciation indicates that various morphologically modern protists thrived in microbially dominated ecosystems, and contributed to the cycling of carbon in Neoproterozoic oceans much before the rise of complex animals.

INTRODUCTION

Recent molecular clock studies place the divergence of major eukaryotic supergroups at well before 635 Ma (Pawlowski et al., 2003; Douzery et al., 2004; Berney and Pawlowski, 2006; Peterson et al., 2008), but only few ancestral forms of modern eukaryotes can be unambiguously recognized in the fossil record before this time (Berney and Pawlowski, 2006; Knoll et al., 2006). This discrepancy is attributed to the microscopic size of many early-diverging modern eukaryotes, the absence of distinguishing morphological characters, the lack of resistant organic vesicles or tests (Knoll et al., 2006; Lipps, 2006), and the presence of adverse environmental conditions that prevented modern eukaryotes from becoming widespread (Li et al., 2010).

Reasons behind the absence of early Foraminifera from the fossil assemblages older than ca. 580 Ma remain unclear. Modern Foraminifera are an ecologically important group of heterotrophic eukaryotes that inhabit environments ranging from oxygenated ocean waters to deep-sea (Pawlowski and Gooday, 2009) or sulfidic (Bernhard et al., 2006) sediments. The earliest Foraminifera are reported in early Cambrian strata (Culver, 1991), while putative Foraminifera are reported in fossil assemblages younger than ca. 580 Ma (Lipps and Rozanov, 1996; Gaucher and Sprechmann, 1999; McIlroy et al., 2001). However, both molecular clocks (Douzery et al., 2004; Berney and Pawlowski, 2006) and the presence of filose testate amoebae, organisms related to the Foraminifera, in strata older than ca. 716 Ma (Porter et al., 2003) indicate that early Foraminifera should be present in the fossil record from 1150 to 690 Ma (Pawlowski et

al., 2003). At least some of early Foraminifera may have had mineral-rich tests (Pawlowski et al., 2003) and could have thrived in microbially dominated, oxygen-poor environments (Bernhard et al., 2006), leaving a fossil record. Here we report the discovery of agglutinated tubular microfossils interpreted as early-diverging foraminifera in ca. 715 Ma marine carbonates from the Rasthof Formation, Namibia. These fossil structures predate the earliest undisputed occurrences of fossil foraminifera by ~150 m.y.

GEOLOGIC SETTING

The Rasthof Formation is a carbonate succession that caps glaciogenic diamictite of the Sturtian Chuos Formation (Hedberg, 1979). The age of the Rasthof Formation is constrained below by the 746 ± 2 Ma (U-Pb zircon age) of volcanic rocks in the Naauwpoort Formation (Hoffman et al., 1996) and above by a 635.6 ± 0.5 Ma (U-Pb zircon age) rhyolite in the Ghaub Formation (Hoffmann et al., 2004); recent work suggests that the Sturtian glaciation occurred globally ca. 716 Ma (Macdonald et al., 2010). Microfossil assemblages occur in the basal ~100 m of microbially laminated dolostones at the Okaaru locality (Pruss et al., 2010). The most abundant microfossils preserved there are rigid oval (~170 μm long and ~115 μm wide) tests whose walls consist of carbonaceous material, muscovite, microcline, quartz, and hematite (Bosak et al., 2011a). These tests, morphologically consistent with the agglutinated tests of some modern lobose testate amoebae (Bosak et al., 2011a), are easily recognizable as grayish oval features in the dark brown and clear laminae of microbialaminites from the Okaaru locality (Fig. 1). The thin sections of microbialaminites also contain at least four specimens of >100- μm -long and ~30- μm -wide elongated structures (Fig. 1) that differ from all structures previously described by Bosak et al. (2011a). To examine them more closely, we extracted them from dolomite matrix (see the following).

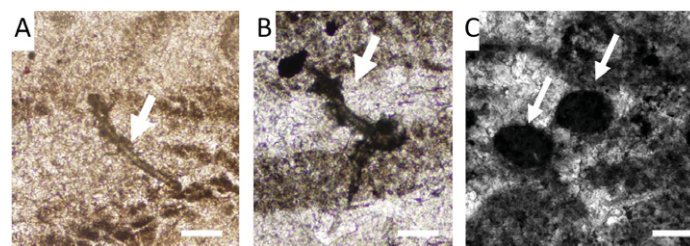


Figure 1. Photomicrographs of walled tests in thin sections of microbialaminites from basal Rasthof Formation at Okaaru (Namibia). Widths (10–15 μm) and lengths (110–400 μm) of tubular structures visible in thin sections are comparable to dimensions of smaller extracted tubular microfossils. A, B: Tubular microfossils are rare. C: Oval walled structures are abundant; hundreds of these morphologies have been extracted from Okaaru locality (Bosak et al., 2011). Scale bars: 100 μm .

MATERIALS AND METHODS

Samples (~20 g) of coarsely fragmented microbialaminites were placed in 10% HCl in clean containers overnight. These acid-cleaned samples were rinsed, pulverized, transferred to clean containers, and digested by 10% acetic acid buffered in ammonium acetate or by 10% HCl, following the general procedure for the extraction of acid-insoluble microfossils (Green, 2001). The residues were rinsed extensively in water, settled, and separated by filtration over nylon mesh filters (100 μm and 40 μm pore diameter; Millipore) and 0.2 μm pore diameter polycarbonate membrane (Whatman, Inc.), collected, and dried. Individual microfossils were picked under a 10–90 \times stereomicroscope (AmScope) and imaged under transmitted light using a Zeiss Axio-plan microscope. Tubular microfossils were only found in the fraction larger than 100 μm . Scanning electron microscopy was performed at the W.M. Keck Imaging Facility at the Whitehead Institute (Massachusetts Institute of Technology, MIT), using a JEOL 5600LV scanning electron microscope. Compositional analysis of individual grains on the surface of microfossils was performed at the MIT Electron Microprobe Facility, using a JXA-8200 Superprobe with a 15 keV acceleration voltage.

RESULTS

We recovered 15 organic- and mineral-rich tubular structures from the >100 μm size fraction of the acid-resistant residues of microbialaminites from the Rasthof Formation. These structures exhibit a range of lengths (200–1300 μm) and widths (20–70 μm) (Fig. 2) and are opaque under transmitted light. Their grayish-brown walls are flexible and less opaque when hydrated. The longest, slender structures (Fig. 2; Fig. DR1 in the GSA Data Repository¹) are also the most flexible, bending in two or three dimensions, while the two shortest tubes are rigid (Figs. 2B and 2C). The walls of all structures have a rough appearance under the transmitted light due to the presence of mineral grains, breaks, folds, and rare bright particles. Seven tubes have a rounded, closed end and a circular cross section (Figs. 2A–2C and 2E), three have a tapering end (Fig. 2D; Fig. DR1), while both the proximal and the distal ends of other specimens are split or broken (Fig. DR1). In two specimens, the rounded end is ~1.4 \times wider than the remaining test and contains a fold (Figs. 2A and 2B). The two most rigid tubes (Figs. 2B and 2C) are straight, preserving unornamented apertures and wide lumens (Figs. 2F and 2G; Fig. DR1). The less rigid structures can be gently curved in two or three dimensions when dry (Figs. 2A, 2D, and 2E; Fig. DR1) and have narrower lumens (Fig. 2H) that are best visible in broken structures (Fig. 2K; Fig. DR1). The diameters of most tubes vary along the length due to the presence of sinuous ridges (Fig. 2I), folds (Figs. 2A and 2B), and transverse constrictions (Figs. 2D, 2E, and 2J) in ~3–10- μm -thick walls (Figs. 2F, 2G, and 2K; Fig. DR1). The walls of all examined tubes contain carbonaceous material (Fig. DR2) and compositionally heterogeneous mineral grains (Fig. DR3). The characteristic grain size of these minerals is between 1 and 3 μm ; a few grains are larger than 5 μm (Figs. 2G, 2J, and 2K; Fig. DR1). Mineral grains can be seen both on the exteriors and in the exposed interiors of samples (Figs. 2F and 2G; Fig. DR1). X-ray diffraction spectra of the acid insoluble residue from the Okaaru locality identify these minerals as quartz, muscovite, hematite, and microcline (Bosak et al., 2011a), i.e., minerals distinct from the surrounding dolomite matrix. While silica and hematite may be precipitated during diagenesis as amorphous silica and iron oxides, respectively, muscovite and microcline have a detrital origin.

¹GSA Data Repository item 2012024, Figures DR1–DR4, is available online at www.geosociety.org/pubs/ft2012.htm, or on request from editing@geosociety.org or Documents Secretary, GSA, P.O. Box 9140, Boulder, CO 80301, USA.

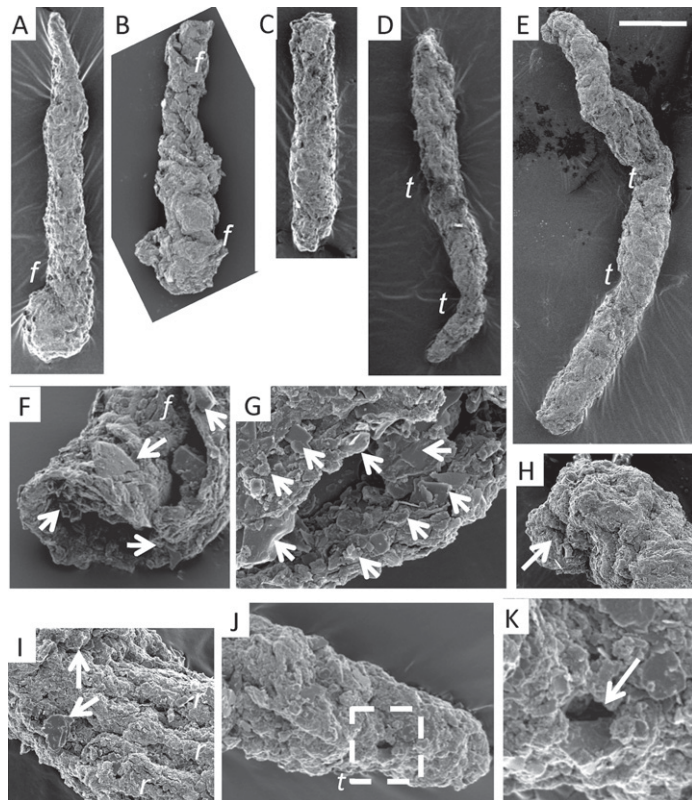


Figure 2. Representative morphologies of tubular tests from Rasthof Formation (Namibia). All images are scanning electron micrographs. A–E: Tubular tests with transverse constrictions (*t*) and folds (*f*). F: Aperture of B showing small mineral grains on exterior and in lumen (arrows). G: Aperture of C showing small mineral grains coating lumen and exterior (arrows). H: Upper terminus of E exposing wall thickness and lumen (arrow). I: Detail of D showing sinuous ridges (*r*) and larger mineral grains (arrows). J: Tapering end of D (detail) showing transverse constrictions (*t*). K: Detail of J outlined by white rectangle exposing wall thickness and hollow interior (arrow). Platy mineral grains are visible on surface. Scale bar in E (in μm): 100 in A–E; 25 in F; 8 in G; 30 in H; 20 in I; 14 in J; 6.7 in K.

INTERPRETATION

The tubular structures from the cap carbonates of the Rasthof Formation exhibit a narrow range of widths and lengths and contain flexible <20- μm -thick walls composed of an organic matrix and small mineral grains. The recurring presence of apertures, narrow or wide lumens, domed and tapering closed ends, folds, and striations provide crucial support for the interpretation of the tubes as agglutinated tests, rather than as elongated fecal pellets or algal thalii encased in detrital minerals. The presence of a lumen indicates that the tubes did not originate as fecal pellets, whereas the presence of compositionally heterogeneous minerals in the interiors of tubes and the presence of apertures are inconsistent with the interpretation of tubes as fossil algal thalii encased in detrital minerals.

The close association of minerals with the fossil organic matrix resembles that found in modern test-forming organisms that actively agglutinate minerals. Active agglutination of detrital minerals, as opposed to the precipitation of authigenic minerals from solution, is supported by the compositional difference between the minerals in tubular tests and dolomite rock matrix (Bosak et al., 2011a), the heterogeneous spatial distribution of minerals on the surface of individual tests (Fig. DR3), and the uniformly small sizes of mineral grains on the surfaces of individual tests. The latter is particularly consistent with the size selection of mineral grains by modern agglutinating microscopic eukaryotes (e.g., Brady,

1884; Gooday et al., 2005; Arminot du Chatelet et al., 2008; Pawlowski et al., 2008). Agglutinated tubular microfossils have not been reported in pre-Sturtian microfossil assemblages preserved in carbonate rocks. The apparent absence of these morphologies from microfossil assemblages preserved at a different locality of the Rasthof Formation and from carbonates capping the Sturtian diamictites of the Tsagaan Oloom Formation (Bosak et al., 2011a) suggests that agglutinated tubes may be uncommon even in postglacial microfossil assemblages.

Two major groups of unicellular eukaryotes contain representatives with >100- μ m-thick walled mineral-rich tubular tests: Foraminifera (Rhizaria) and lobose testate amoebae (Amoebozoa). The combined set of characters preserved by the Cryogenian tests (morphologically simple tubular, finely agglutinated tests 200–1200 μ m long and <100 μ m wide, domed ends of tests, apertures, bulbous ends, wrinkles, ridges, and constrictions) is found in a subset of modern benthic agglutinated monothalamous foraminiferans. For example, the finely agglutinated tubes of *Hippocrepinella* and small *Pelosina*-like foraminifera and various silver saccaminids (Fig. 3; Fig. DR4) often contain collapsible and variably large apertures, flexible or more rigid tests with ridges, wrinkles, folds, transverse constrictions, rounded, globular ends, and a variably thick coating of clay or silt-sized mineral grains (Brady, 1884; Gooday et al., 2005; Pawlowski et al., 2008). The uniformly small size of mineral grains on the tests of these modern organisms is a result of biological selectivity with respect to the size and composition of agglutinated minerals that can be compositionally very distinct from the bulk carbonate sediment (Arminot du Chatelet et al., 2008).

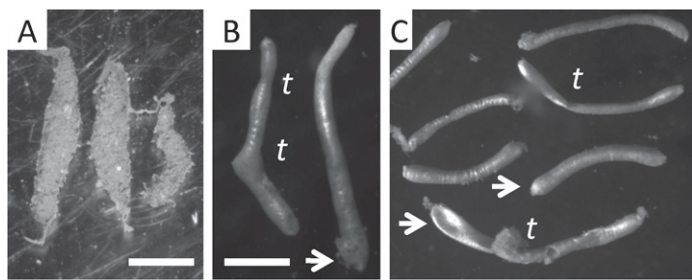


Figure 3. Photographs of modern agglutinated tubular monothalamous foraminiferans. **A:** Modern *Pelosina* sp.; scale bar is 200 μ m. **B, C:** Modern silver-brown saccaminids with constricted tests (*t*) and bulbous ends (arrows). Some tests in **C** are collapsed due to flexible walls, as well as covered by mineral grains. Scale bar in **B** is 100 μ m. Tests in **C** are as much as 2 mm long.

The tubular tests from the Rasthof Formation share characteristics with a subset of latest Neoproterozoic and early Cambrian tubular microfossils *Platysolenites* that are widely interpreted as early Foraminifera (Lipps and Rozanov, 1996; McIlroy et al., 2001). Although *Platysolenites* can be more than an order of magnitude larger (Lipps and Rozanov, 1996; McIlroy et al., 2001), the sizes of its smaller representatives match those of the Cryogenian tubes described here. Lobose testate amoebae (Amoebozoa) from the family Diffflugidae can also have elongated agglutinated tests similar to that in Figure 2B that are always shorter than 300 μ m (e.g., *Diffflugia lanceolata*; Lahr and Lopes, 2006). However, unlike fossil tubes from the Rasthof Formation, modern tubular lobose testate amoebae have tapering necks and apertures and rigid, coarsely agglutinated tests coated by mineral grains as wide as 30 μ m, but lack transversal or longitudinal ridges, folds, breaks, and striated surfaces (Lahr and Lopes, 2006). The rare agglutinated representatives of modern filose testate amoebae (euglyphids and amphitremids in Rhizaria) are neither tubular, nor do they exceed ~100 μ m in length. Although some Annelida (Animalia) construct agglutinated tubes, the ages and the very simple morphologies of

the Cryogenian tests are inconsistent with this origin. Not only are even the smallest agglutinated Annelida longer than 1 mm (Berrill, 1977), but molecular clocks also estimate a post-635 Ma divergence of these organisms (Peterson et al., 2008).

The emerging record of testate protists (Bosak et al., 2011a, 2011b) and other putative eukaryotes (Malooof et al., 2010) in 716–635 Ma carbonate strata is consistent with molecular clock studies. These studies estimate the divergence of Rhizaria, a major eukaryotic supergroup, and Foraminifera, as a lineage within Rhizaria, as ca. 1 Ga (Pawlowski et al., 2003; Douzery et al., 2004; Berney and Pawlowski, 2006; Peterson et al., 2008). The fossil record of Rhizaria may be older than that of Foraminifera: some pre-Sturtian vase-shaped microfossils were attributed to a different lineage of Rhizaria, filose testate amoebae (Porter et al., 2003), but this interpretation is inconsistent with the molecular data that place the Neoproterozoic divergence of Foraminifera much before the Phanerozoic divergence of euglyphids (Berney and Pawlowski, 2006).

ENVIRONMENTAL IMPLICATIONS

The microbially laminated strata preserving putative foraminiferal tests in the Rasthof Formation were deposited under low-energy conditions that may have included intermittent or permanent anoxia very close to the water-sediment interface (Pruss et al., 2010). The presence of abundant bladed cements in the light laminae of fossiliferous microbialaminites indicates that portions of the carbonates precipitated and lithified rapidly (Pruss et al., 2010); this likely fostered preservation of these organic-rich forms. The Cryogenian tubular organisms may have grazed on microbial mats, fed on organic detritus, preyed on bacteria, other protists, and, possibly, any early animals (Bowser et al., 1992). Modern analogs of laminated sediments from the Rasthof Formation are microbially dominated, stratified, oxygen-poor sediments (Bernhard et al., 2006) that typically harbor calcareous foraminiferal taxa, but also include some benthic monothalamous organic-walled species (Bernhard et al., 2006). In contrast, strata harboring latest Precambrian and early Cambrian foraminiferans were deposited in shallow, more turbulent, and probably well-oxygenated waters (McIlroy et al., 2001).

The presence of previously unreported tubular microfossils in the Rasthof Formation adds to the record of morphologically modern eukaryotic body fossils from the 716–635 Ma carbonate strata (Bosak et al., 2011a, 2011b), and suggests that agglutination was present in multiple eukaryotic groups, including early Foraminifera. This compositional innovation would have increased the robustness of body fossils, facilitating the preservation of organic material associated with the tests in the rapidly accumulating post-Sturtian cap carbonate strata. Therefore, a closer look at preglacial carbonates may help identify even earlier occurrences of agglutination in the rock record, extending a new taphonomic window into Neoproterozoic eukaryotic diversification, evolutionary innovations, increasing ecological complexity, and environmental changes that brought complex animals to the fore.

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ERRATUM

Remarkably extensive glaciation and fast deglaciation and climate change in Turkey near the Pleistocene-Holocene boundary

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There was an error in typesetting in the RESULTS AND DISCUSSION section (in the middle of column three on p. 1052) of this paper. In the paragraph beginning with “Deglaciation occurred in two phases...” the term “$\frac{1}{8}$” should be “$\frac{1}{8}$”.