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Earth and Planetary Science Letters



journal homepage: www.elsevier.com/locate/epsl

### Agglutinated tests in post-Sturtian cap carbonates of Namibia and Mongolia

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#### ARTICLE INFO

Article history: Received 8 December 2010 Received in revised form 17 March 2011 Accepted 17 May 2011 Available online 14 June 2011

Editor: P. DeMenocal

Keywords: snowball Earth Neoproterozoic eukaryote microfossil

#### ABSTRACT

Paleomagnetic data suggest that the early Cryogenian (Sturtian) glaciation extended to sea level at low latitude. The impact of this dramatic environmental change on biota, and the composition of ecosystems in the immediate aftermath of the Sturtian glaciation remain virtually unknown. Here we report the discovery of abundant agglutinated tests in organic-rich carbonates directly overlying Sturtian glacial deposits from two different paleocontinents; the Rasthof Formation of the Congo craton in northern Namibia and the Tsagaan Oloom Formation of the Dzabkhan terrane in Mongolia. The most abundant tests preserve morphological and compositional characters consistent with those found in at least two different families of modern lobose testate amoebae (Amoebozoa), a group of heterotrophic microbial eukaryotes. The presence of spatially and compositionally variable clay minerals, quartz and microcline on the test walls is a signature of widespread biological agglutination. The post-glacial fossil assemblages differ from the most common pre-Sturtian vase-shaped fossil testate amoebae, perhaps as a result of different preservational mechanisms or of the appearance of new forms after the glaciation. The apparent local abundance of eukaryotic body fossils in the post-Sturtian carbonates suggests that the Cryogenian limestones and dolostones may host a currently unexplored fossil record of modern eukaryotes.

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#### 1. Introduction

At least twice during the Cryogenian Period [750-635 million years ago (Ma)], glacigenic sediments were deposited at low latitudes and capped by sedimentologically and geochemically unusual carbonate rocks (Hoffman et al., 1998: Macdonald et al., 2010: Sohl et al., 1999). The "snowball Earth" hypothesis accounts for the deposition of these carbonates by predicting >1 million year long global glaciation followed by a greenhouse transient. The enhanced silicate weathering during this warm transient increases the flux of alkalinity to the oceans and promotes the precipitation of carbonate minerals (Hoffman and Schrag, 2002). Alternative views to the "snowball Earth" hypothesis propose the existence of large unfrozen regions in the tropical oceans or the existence of only a thin layer of ice (Allen and Etienne, 2008; Corsetti, 2009), but even these milder scenarios predict that primary productivity during the glaciations would have been restricted to low latitudes. The spatial isolation of ecosystems and the reduced zones of primary production at this time may have acted as evolutionary bottlenecks (Baker, 2006; Costas et al., 2008). The response of ecosystems and modern eukaryotic clades, which diverged ~1 Ga (e.g., Douzery et al., 2001), to these extreme environmental changes remains poorly constrained because of the lack of reported microfossil assemblages in strata unambiguously bound by Sturtian and Marinoan glacial deposits. This ~70 million year long gap in the fossil record has limited not only the understanding of ecosystems emerging from the Sturtian glaciation and entering the Marinoan glaciation, but also of the eukaryotic evolution during much of the Cryogenian period (Knoll et al., 2006).

Several authors have discussed the effect of Neoproterozoic glaciations on life. Corsetti et al. (2003) reported the preservation of vase-shaped microfossils, filamentous organisms, possible eukaryotes and cyanobacteria in silicified carbonates associated with the Sturtian-age Kingston Peak Formation in Death Valley. These microfossils and their host lithologies, identical to the assemblages and rocks described from the underlying Beck Springs Formation (Licari, 1978), are found in a structurally complicated area with copious olistostromes of the Beck Springs Formation (Walker et al., 1986). The syn-glacial origin of these fossiliferous localities is thus debated [3, supplementary material]. Moczydlowska (2008) discussed the occurrences of different acritarch taxa in strata that either predate the Sturtian glaciation or postdate the Marinoan glaciation by more than 70 million years and questioned the severity of both low-latitude glaciations. However, many questions still remain about the composition of ecosystems immediately after the Sturtian glaciation and the fossil record during ~70 million years between the Sturtian and the Marinoan glaciation. For example, although

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<sup>0012-821</sup>X/\$ – see front matter 0 2011 Elsevier B.V. All rights reserved. doi:10.1016/j.epsl.2011.05.030

fossil testate amoebae were ubiquitous in pre-Sturtian sediments, their distribution in the interglacial strata is unknown, and they are virtually absent in post-Marinoan marine strata. The rare, but exciting examples of non-acritarch pre-Ediacaran life (Hofmann et al., 1990; Maloof et al., 2010) also suggest that substantial ecological and evolutionary changes occurred between the two glaciations.

Here, we report the discovery of microfossil assemblages that occur unambiguously in post-glacial carbonate strata deposited in the immediate aftermath of the older Cryogenian (Sturtian) glaciation and prior to the younger Cryogenian (Marinoan) glaciation. Eukaryotic tests are present in the Rasthof Formation on the Congo craton in Namibia (Hoffman and Halverson, 2008; Hoffmann and Prave, 1996) (Fig. 1) and the Tsagaan Oloom Formation of the Dzabkhan terrane in Mongolia (Macdonald et al., 2009a). The discovery of these structures in the carbonates that cap glacial strata provides a new window into the eukaryotic survival and ecology during this critical period.

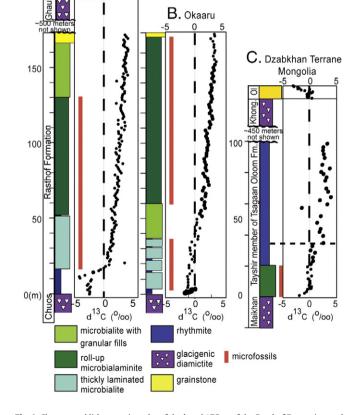
#### 2. Geological setting

A. Ongongo

Ma

5

The Rasthof Formation of northern Namibia overlies diamictite and conglomerate of the Chuos Formation of presumed Sturtian age. The age of the Rasthof Formation is constrained below by  $746 \pm 2$  Ma (U–Pb TIMS



**Fig. 1.** Chemo- and litho-stratigraphy of the basal 175 m of the Rasthof Formation at the A) Ongongo and B) Okaaru localities in northern Namibia (Halverson et al., 2007), and C) at the Tayshir and Khongoryn localities in Mongolia (Hoffman and Halverson, 2008). In the Mongolian column, the lower 20 m of section is from the Tayshir locality and the upper 155 m is from Khongoryn. Solid red lines indicate strata where structures are present, but do not preclude the presence of structures in other, currently unexamined strata. All carbonate carbon isotopic values are relative to VPDB. The rarity of detrital sediment and the preservation of soft organic vesicles in all cap carbonates indicate that the structures were not transported from preglacial sediments. Pre-glacial sediments ovelcanic rocks.

zircon age) volcanic rocks in the Naauwpoort Formation (Hoffman et al., 1996) and above by a  $635.6 \pm 0.5$  Ma (U–Pb TIMS zircon age) rhyolite in the Ghaub Formation (Hoffmann et al., 2004). The Rasthof Formation can be correlated with other post-Sturtian cap carbonates with carbon and strontium isotope chemostratigraphy (Halverson et al., 2007; Macdonald et al., 2009a) (Fig. 1). We identified fossil tests in ~150 m thick microbially laminated dolostones of the lower Rasthof Formation at two localities, Ongongo and Okaaru, separated by ~50 km near the town of Sesfontein (Fig. 1). The lack of erosional features, desiccation cracks, ripple marks or other bedforms indicates that the microbialites in the lower Rasthof Formation were subtidal (Pruss et al., 2010).

Cryogenian strata of the Tsagaan Oloom Formation in Mongolia consist of the Maikhan Ul diamictite, organic-rich limestone of the Tayshir Member, and the Khongoryn diamictite (Brasier et al., 1996; Khomentovsky and Gibsher, 1996; Macdonald, 2011). A maximum age constraint on the Tsagaan Oloom Formation is provided by a 773.5  $\pm$  6.6 Ma age on the underlying Dzabkhan Volcanics (Levashova et al., 2010, LA-ICPMS). The lower portion of the overlying Tayshir member can be correlated with other post-Sturtian cap carbonates with carbon and strontium isotope chemostratigraphy (Macdonald et al., 2009a; Shields et al., 2002), suggesting that the Maikhan-Ul is a Sturtian-age glacial deposit (Fig. 1). The cap carbonate at the base of the Tayshir member is succeeded by tens to hundreds of meters of shale and marl, consistent with a prominent transgression (Macdonald et al., 2009a) (Fig. 1). Microfossils in these facies are found in allodapic limestone and dolostones (Fig. 1). The lack of any current- and wave-generated structures and the absence of scour and exposure surfaces within the lower Tayshir member suggest that these facies were also subtidal. The Tayshir member is overlain by the Khongoryn diamictite and the Ol cap carbonate. The latter shares geochemical and sedimentary characteristics with other ca. 635 Ma basal Ediacaran cap carbonates (Macdonald et al., 2009b).

#### 3. Results

3.1. Morphological and compositional characteristics of microfossils in thin section

Cap carbonates of the Rasthof Formation were not previously described as fossiliferous, but the thin sections of microbialaminites contain abundant gray and brown structures with  $6 \pm 2 \mu m$  (N = 15) thick organic-rich dark brown or gray walls and oval cross-sections (Fig. 2). These structures often occur as groups (Fig. 2A, B) and are common in both dark and light laminae of the thinly laminated microbialites. The structures in the thin sections from the Okaaru locality are elliptical, with a 30–290 µm long axis and a 30–170 µm short axis (median = 110  $\mu$ m and 70  $\mu$ m, respectively, N = 193). Fewer than 10% of the structures seen in thin section have vase-shaped crosssections with possible necks (Fig. 2C) or thinner walls at the blunt end along the long axis (Fig. 2E). The structures at Ongongo are also oval (Fig. 2B), but exhibit possible breaks or openings at one end of the short axis, rather than the long axis (Fig. 2F). The walls of oval structures are enriched in Si, Al and K, elements that are considerably less common in the surrounding dolomite matrix (Fig. 3).

Structures with common and distinct morphologies are also present in thin sections of the allodapic carbonates from the basal Tayshir member of the Tsagaan Oloom Formation. These include dark, ~60–160  $\mu$ m long elongated structures with a rounded end or a blunt, sometimes curved end (Fig. 2D, G, I) and numerous ~5  $\mu$ m diameter orange structures with a dark center (Fig. 2H).

## 3.2. Morphological and compositional characterization of structures extracted from cap carbonates

To further characterize structures present in the laminae of cap carbonates, we dissolved individual ~10 g samples from Okaaru,

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