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Secular variation in seawater redox state during the Marinoan Snowball Earth event and implications for eukaryotic evolution

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ABSTRACT

The ocean is hypothesized to have been anoxic throughout the Marinoan 'Snowball Earth' event, from ca. 649-635 million years ago (Ma), with potentially catastrophic implications for the survival of eukaryotic life. However, the precise nature of ocean redox chemistry across this critical interval, and hence the factors that governed the persistence of eukaryotes, remain unknown. Here, we report records of pyrite Fe- and S-isotopes, combined with Fe-speciation, for glaciogenic diamictites from the Nantuo Formation of South China. These data provide constraints on seawater redox state across the Marinoan glaciation, and reveal that the redox state of the ocean fluctuated in concert with waxing and waning in the extent of glaciation, to include intervals of expanded oxygenation. The input of meltwater-derived oxygen provides a potential explanation for the persistence of eukaryotes through the Cryogenian 'Snowball Earth' events, which ultimately paved the way for subsequent intervals of rapid biological innovation.

INTRODUCTION

The Cryogenian Period is marked by two low-latitude glaciations, namely the Sturtian and Marinoan glaciations (Hoffman et al., 1998; Rooney et al., 2020). During these 'Snowball Earth' events, the ocean is generally considered to have been isolated from the atmosphere (Hoffman et al., 2017a). As such, the spatial development and persistence of anoxia, which was a prevalent feature of the deeper ocean prior to the glaciations (Canfield, 2008; Guilbaud et al., 2015), would have been exacerbated. The consequent global development of oceanic anoxia during the glacial period has been proposed as a major constraint on the persistence of eukaryotes (Runnegar, 2000; Hoffman, et al., 2017a). However, molecular clock and biomarker evidence suggests major eukaryotic assemblages that had evolved before the Sturtian glaciation persisted through the Cryogenian (Love et al., 2009; Erwin, 2015). The fossil record, although sparse, has also verified that some extant eukaryotes, such as macroalgae and possible sponges (Ye et al., 2015; Turner 2021), survived the glaciations, resulting in an absence of any apparent eukaryotic bottleneck during the Cryogenian Period (Erwin, 2015).

Various 'refugia' have been proposed as a potential solution to this apparent paradox, including small and perhaps intermittent open-water systems and ice shadows (Hoffman, 2016), but the suitability and full extent of these habitats for eukaryotes have been questioned (Moczydłowska et al., 2008; Hawes, et al., 2018). Here, we address this issue via pyrite Fe-S isotope and Fe-speciation analyses of glacial diamictite from the Nantuo Formation, South China, which allows a detailed reconstruction of oceanic redox state across the Marinoan glaciation.

GEOLOGICAL SETTING AND SEDIMENTARY INTERPRETATION

The Nantuo Formation is widely preserved on the Yangtze block, South China (Fig. 1; Text S1 in Supplementary Materials). Zircons from tuffaceous units constrain deposition to between ca. 649 ± 2.4 Ma and ca. 635 ± 0.6 Ma, corresponding to the Marinoan glaciation (Condon et al., 2005; Zhou et al., 2018). We focus our analyses on well-preserved samples from drill core ZK01, located in Taojiang city, Hunan Province. In drill core ZK01, the Nantuo Formation has a conformable contact with both the underlying interglacial deposits and the overlying post-glacial deposits, and can be divided into four units (Fig. 2). Unit I is composed of pebbly sandstone/siltstone underlying diamictite, showing a shallowing sequence, whereas Unit II consists of pebbly siltstone and mudstone/carbonate overlying diamictite, reflecting a deepening sequence. Similarly, units III and IV change from lower siltstone and pebbly sandstone through middle diamictite to upper pebbly sandstone/siltstone, recording another sedimentary cycle. These sedimentary cycles as recorded in drill core ZK01 are a common phenomenon on the Yangtze block, as well as on other continents (Fig. 1b; Shen et al., 2021).

It has been proposed that such facies change in glacial deposits may have been induced by excessive topography relief during the global glaciation (Hoffman et al., 2017b). In this scenario, deposition of diamictite during ice sheet melting may have both created and destroyed topography within a short distance, leading to small-scale migration of the depocenter and complexity in the stratigraphic detail of glacial deposits (Hoffman et al., 2017b). However, this scenario does not appear to explain the facies variability in the Nantuo Formation, which can be correlated across the Yangtze block (Fig. 1b; Lang et al., 2018a). In particular, the thick sequence of siltstone/mudstones and carbonate beds in the Nantuo Formation cannot be simply interpreted as deposits during ice sheet melting (Fig. 1b; Shen et al., 2021). Rather, the Nantuo diamictites and pebbly sandstone/siltstone are generally considered to reflect deposition in a glacial marine environment, representing proximal glaciomarine and distal glaciomarine facies, respectively, whereas the pebble-free mudstone and carbonate may represent normal marine deposition without the influence of glaciation (Allen and Etienne, 2008; Lang et al., 2018a). Thus, the repetition of glacially influenced units separated by non-glacial units in the Nantuo Formation appears to record ice-sheet advancing-retreating cycles and sea-level fluctuations (Figs. 1b and 2; Shen et al., 2021), suggesting Marinoan glaciation dynamics (Text S2; Liu et al., 2020).

SAMPLING AND METHODS

Thin sections were prepared to guide the sampling of pyrite and fine-grained siliciclastic components (matrix). To avoid large-sized clasts in diamictites, matrix samples were obtained using a handheld drill. Under the optical and scanning electron microscope, pyrite morphologies are dominated by euhedral, subhedral, aggregates, and disseminated pyrite (Fig. 2), indicating a diagenetic origin rather than detrital pyrite. For total organic carbon (TOC) analyses, sample powders were combusted in a pure oxygen atmosphere and analyzed via a LECO CS–230. Fe speciation was performed via standard techniques (Poulton, 2021), with analysis via AAS. For Fe isotope ($\delta^{56}Fe_{py}$) measurements, large euhedral pyrite grains were hand-picked, and Fe was purified using ion-exchange chromatography and measured via Nu–MC–ICP–MS. For in situ S isotope ($\delta^{34}S_{py}$) analyses, euhedral pyrite (> 50 μm) was selected and measured via LA–MC–ICP–MS. More detailed methods are provided in the Supplementary Materials.

RESULTS

TOC concentrations are low throughout the section, whereas $\delta^{56}Fe_{py}$, $\delta^{34}S_{py}$ and Fe-speciation systematics show distinct variability (Fig. 3). In the lower part of Unit I, $\delta^{56}Fe_{py}$ values overall are negative, while $\delta^{34}S_{py}$ values decrease upwards. Highly reactive Fe (Fe_{HR}) to total Fe (Fe_T) ratios are particularly low (0.14 ± 0.01) throughout this interval. The extent of pyritization of Fe_{HR} is also low, and while the proportion of ferric (oxyhydr)oxides (Fe_{ox}/Fe_{HR}) shows an overall peak in the lower part of Unit I, ratios are low throughout the section. The upper part of Unit I is characterized by intermediate and fluctuating $\delta^{56}Fe_{py}$ values, a positive trend in $\delta^{34}S_{py}$ values, slightly increased average Fe_{HR}/Fe_T ratios, low Fe_{py}/Fe_{HR} ratios, and low Fe_{ox}/Fe_{HR} ratios that decrease through the interval (Fig. 3).

In Unit II, the majority of $\delta^{56}Fe_{py}$ values are positive (Fig. 3). $\delta^{34}S_{py}$ values show a general decrease, while Fe_{HR}/Fe_T and Fe_{ox}/Fe_{HR} ratios slightly increase through Unit II, coincident with a general decrease in Fe_{py}/Fe_{HR}. In units III and IV, $\delta^{56}Fe_{py}$ values show considerable variability, but there is a distinct shift from negative values to positive values, followed by a decrease to negative values, while $\delta^{34}S_{py}$ values show an inverse trend (Fig. 3). Fe_{HR}/Fe_T ratios progressively increase through units III and IV, while Fe_{ox}/Fe_{HR} ratios show the opposite trend, and Fe_{py}/Fe_{HR} ratios increase considerably towards the top of the section.

DISCUSSION

Variability in Seawater Redox State

Sedimentary pyrite Fe isotope data provide a first-order indication of seawater redox state (Zhang et al., 2015). In particular, positive $\delta^{56}Fe_{py}$ values are indicative of ferruginous conditions, whereas negative to near-zero $\delta^{56}Fe_{py}$ values can be observed under a variety of redox conditions (Text S4; Severmann et al., 2008; Planavsky et al., 2012). We thus interpret the large stratigraphic variability in $\delta^{56}Fe_{py}$ values to document variations in redox state (Fig. 3). Furthermore, the positive $\delta^{56}Fe_{py}$ values observed for many of the samples likely reflect ferruginous conditions, with partial oxidation of ferrous to ferric iron in the water column followed by reduction and transformation of ferric (oxyhydr)oxides into pyrite during early diagenesis. By contrast, the negative to near-zero $\delta^{56}Fe_{py}$ values for some samples may have developed under either euxinic or oxic conditions.

Fe-speciation systematics (Text S4; Raiswell and Canfield, 1998; Poulton, 2021) allow a more nuanced evaluation of the precise nature of redox variability. $Fe_{HR}/Fe_T > 0.38$ generally provides a robust indication of water column anoxia (Raiswell and Canfield, 1998), whereas ratios for oxic conditions are generally significantly lower (0.14 ± 0.08; Poulton and Raiswell, 2002). However, due to inherent variability in the source rocks deposited in a particular region, wherever possible, an oxic baseline should be derived for the precise rocks being analysed (Poulton, 2021). This is particularly significant, since rapid deposition (as would likely be the case for the Nantuo Formation diamictites) may mask the Fe_{HR} depositional flux from an anoxic water column. Where samples show evidence of anoxic deposition, Fe_{py}/Fe_{HR} ratios above 0.6–0.8 distinguish a euxinic water column from ferruginous depositional conditions (Poulton, 2021).

The negative $\delta^{56}Fe_{py}$ values in the lower part of Unit I coincide with very low Fe_{HR}/Fe_T ratios and peak Fe_{ox}/Fe_{HR} ratios, strongly supporting oxic deposition and allowing an oxic Fe_{HR}/Fe_T baseline ratio (0.14 ± 0.01) to be defined for the Nantuo Formation (Fig. 3). The $\delta^{56}Fe_{py}$ values for the lower part of Unit I can thus be considered to document oxic depositional conditions followed by conversion of a proportion of the Fe (oxyhydr)oxide pool to pyrite during diagenesis. $\delta^{56}Fe_{py}$ values in the upper part of

Unit I fluctuate between negative and positive, while Fe_{HR}/Fe_T ratios are either similar to, or slightly above, the oxic baseline. We interpret these samples to represent a fluctuating redox state, with low Fe_{py}/Fe_{HR} ratios supporting oxic through to ferruginous conditions. This overall more reducing state relative to the lower part of Unit I is also supported by a general decrease in the preservation of Fe (oxyhydr)oxides (i.e., lower Fe_{ox}/Fe_{HR}).

More stable (but potentially fluctuating) ferruginous anoxia is then indicated throughout Unit II (positive $\delta^{56}Fe_{py}$ values, combined with slightly elevated Fe_{HR}/Fe_T and low Fe_{py}/Fe_{HR}), but a transition to dominantly oxic conditions is indicated at the base of Unit III (negative $\delta^{56}Fe_{py}$ values, combined with a progressive increase in Fe_{ox}/Fe_{HR}) (Fig. 3). The main part of Unit III shows a clear redox progression (Fig. 3), with the initial development of stable ferruginous conditions (positive $\delta^{56}Fe_{py}$ values, combined with a transition to highly elevated Fe_{HR}/Fe_T, lower Fe_{ox}/Fe_{HR}, and persistently low Fe_{py}/Fe_{HR}). Subsequently, however, the transition to negative $\delta^{56}Fe_{py}$ values, combined with highly elevated Fe_{py}/Fe_{HR} ratios in Unit IV, indicates the development of water column euxinia. Here, the negative to near-zero $\delta^{56}Fe_{py}$ values indicate near-quantitative uptake of ferrous Fe into pyrite.

The seawater redox variability we document is further supported by $\delta^{34}S_{py}$ data. Generally, relatively heavy $\delta^{34}S_{py}$ values suggest a smaller seawater sulfate reservoir (SSR), which may be driven by the expansion of anoxia (Text S4; Canfield, 1998; Habicht et al., 2002). Thus, gradually decreasing $\delta^{34}S_{py}$ values in Unit II and the lower part of Unit I suggest an expanding SSR, which is likely tied to our evidence for an increase in seawater oxygenation through these intervals. Conversely, gradually increasing $\delta^{34}S_{py}$ values in units III-IV and in the upper part of Unit I support a diminishing SSR due to expanded anoxia (Fig. 3).

Mechanisms for Seawater Redox Evolution

This dynamic redox history, particularly the intervals of expanded seawater oxygenation, is perhaps surprising given the prevalence for the development of ocean anoxia during ‘Snowball Earth’ events (Hoffman et al., 2017a). However, there are several potential explanations for redox instability. Firstly, fluctuations in sea-level, may have brought the site of sedimentation into and out of a more oxygenated surface ocean. However, there is an apparent contradiction between seawater redox state and sea-level, whereby seawater oxygenation corresponds to rising sea-levels in Unit II (Fig. 3; Text S5), suggesting that this is an unlikely explanation.

Another possible control on the dynamic redox history concerns the periodic development of open water, leading to enhanced productivity and O_2 production (Ye et al., 2015), as well as exchange of O_2 between the atmosphere and ocean (Johnson et al., 2017). However, while these two scenarios may have contributed to the redox dynamics, we note that there is no significant shift in TOC burial (albeit on a highly local scale) that might otherwise indicate enhanced oxygen production (Fig. 3). Furthermore, rapid equilibration between the atmosphere and ocean due to the periodic open water may be expected to lead to abrupt intervals of seawater oxygenation (Le Hir et al., 2008). Thus, while such a process may explain the more rapid fluctuations in oxygenation observed in upper part of Unit I, it does not provide a compelling explanation for the progressive changes recorded in other parts of the Nantuo Formation.

We thus additionally consider that during the ‘Snowball’ glaciation, air bubbles would have been readily trapped within the snow (meteoric ice) and subsequently incorporated into glacial ice (Hoffman et al., 2017a). Upon melting of the glacier, O_2 derived from the air bubbles would lead to the formation of oxygenated meltwater. When subglacial drainage was channeled, oxygenated meltwater would have short residence time and would be transported to ice shelf waters (Jenkins, 1999), resulting in oxidized seawater (Lechte et al., 2019). Conversely, the distributed drainage and longer residence time of oxygenated meltwater may have had little influence on subglacial seawater anoxia (Tranter, 1997; Lechte et al., 2019). The sedimentology of the studied Marinoan deposits appears to record ice-sheet advancing-retreating cycles, controlling meltwater supply and subglacial drainage scale (Fig 2; Text S2; Shen et al., 2021), and hence seawater redox. Specifically, during ice sheet retreat, ice thinning and sufficient meltwater favored formation of an interconnected drainage system, likely driving expanded oxygenation of the ocean, whereas the meltwater supply and drainage system during ice sheet advance were far less efficient, leading to possible ocean deoxygenation (Fig. 4).

The ice-sheet dynamics and associated fluctuations in meltwater-derived O_2 influx provide a compelling explanation for longer-term changes in seawater redox state observed in the Nantuo Formation. During the first ice retreat, a relative increase in meltwater-derived O_2 influx controlled the seawater oxygenation documented in Unit II (Fig. 3), and ultimately resulted in oxic conditions at the base of Unit III. By contrast, the seawater deoxygenation recorded in Unit III and the upper part of Unit I may have been linked to a decrease in meltwater-derived O_2 influx during the second and first ice advances, respectively (Fig. 3). The euxinic conditions recorded in Unit IV, even with increasing meltwater-derived O_2 during the second ice retreat, were mainly driven by significant sulfate reduction in the water column (Lang et al., 2018b).

Implications for Eukaryotic Evolution

While the secular variation in seawater redox state we document was likely linked to a variety of factors, including potential changes in productivity and air-sea O_2 exchange during intervals of open water, a dynamic meltwater-derived O_2 influx due to Marinoan glaciation dynamics was likely more important and of widespread significance (Fig. 4). The oceanic influx of meltwater-derived O_2, although decreased during ice-sheet advance, was long-lived and widespread throughout the glaciation, thus meeting the basic requirement for survival of subglacial eukaryotic assemblages. This persistence of eukaryotic life ultimately paved the way for the subsequent shift in ecosystem complexity (e.g., the Lantian biota; Yuan et al., 2011) witnessed shortly after the terminal Marinoan glaciation.

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FIGURE CAPTIONS

Fig. 1. **a**) Late Neoproterozoic tectonic division and facies distribution in South China. **b**) Cyclicity in the Nantuo Formation at a basin-to-platform scale. Photographs of the Nantuo Formation showing **c)** diamictites, **d)** dropstone**, e)** lonestone, and **f)** shale.

Fig. 2 Sedimentology and petrography characteristics of the Nantuo Formation in drill core ZK01. Radiometric ages from Condon et al. (2005) and Zhou et al. (2018).

Fig. 3. Geochemistry related to sedimentary records through the Nantuo Formation in drill core ZK01.

Fig. 4. Schematic diagram showing seawater redox evolution during the Marinoan glaciation. **a**) During ice-sheet advance, anoxic conditions prevailed in the ice-covered ocean. **b**) During ice-sheet retreat, an abundant influx of meltwater-derived O_2 led to expanded seawater oxygenation.