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# The biotic response to Neoproterozoic snowball Earth

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## Abstract

The commonly held notion among earth scientists that Neoproterozoic low latitude glaciation (ca. 720–585 Ma), sometimes referred to as snowball Earth, caused major extinctions and imparted important evolutionary consequences upon the biosphere is not supported by the microfossil record. In particular, silicified microfossils from pre- and syn-glacial units in the Death Valley region, California, reveal little change during the glacial interval; in fact, the syn-glacial microbiota is slightly more diverse and contains more putative autotrophic and heterotrophic eukaryotes than underlying strata. In Australia, pre- and post-glacial acritarch assemblages from shale reveal no change in diversity across the glacial interval. In modern glacial environments, productive and diverse modern microbial communities live within and upon sea and glacial ice and may provide an analogue for a more robust snowball Earth biosphere than previously considered.

*Keywords:* Neoproterozoic; Glaciation; Snowball earth; Acritarchs; Microfossils; Biotic response

## 1. Introduction

Geologic and paleomagnetic evidence suggests that global glaciation extended into equatorial latitudes during Neoproterozoic time, between ~740 Ma and 580 Ma (but not without controversy, e.g., Eyles and Januszczak, 2003) (Fig. 1). The existence of purported Neoproterozoic low latitude glaciation has been known for many years (e.g., Harland and Rudwick, 1964), and more recently has been corroborated by robust paleomagnetic data (e.g., Schmidt et al., 1991; Schmidt and Williams, 1999; Sohl et al., 1999; Evans, 2000) and an immense amount of new geologic data (see references, below). Kirschvink (1992) coined the wonderfully descriptive phrase "snowball Earth" to describe low-latitude glaciation. Although the concept of a global Neoproterozoic ice age has existed for many years (e.g., Harland and Rudwick, 1964), a new wave of interest in Neoproterozoic glaciation can be traced to Hoffman et al. (1998). As such, we will differentiate between a descriptive use of the term "snowball Earth" to imply low latitude glaciation and the "Snowball Earth Hypothesis", sensu Hoffman et al. (1998), which is an attempt to explain the observations in the rock record. Building on the work of Kaufman and colleagues (e.g., Kaufman et al., 1991, 1993, 1997) and Kennedy (1996), Hoffman et al. (1998) demonstrated that major perturbations in carbon isotopic composition of carbonate characterize the lithologically unusual carbonates that cap the glacial deposits in most sections around the world and postulated a link between the glacial deposits below and the carbonate beds above, initiating the modern understanding of Neoproterozoic low latitude glaciation. This work has spawned a veritable gold rush of carbon isotopic studies in Neoproterozoic rocks (see references in Section 2.2).

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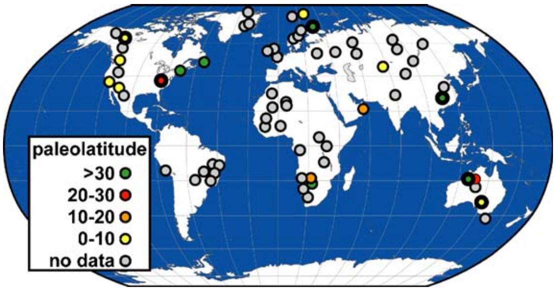

Fig. 1. Global distribution of Neoproterozoic glacial deposits and corresponding paleomagnetic data (original data from Evans, 2000; modified from Hoffman and Schrag, 2002). The thicker circles represent paleomagnetic data in which Evans (2000) had moderate to good confidence.

The imagery conjured by the phrase 'snowball Earth' has driven many of the recent studies: if the Earth was frozen like a snowball, how did life survive such a climatic deterioration? In reality, the direct record of life during snowball Earth in the form of tangible fossils is exceedingly small (e.g., Knoll et al., 1981; Corsetti et al., 2003). Rather, most studies rely upon indirect measures, commonly from the overlying cap carbonates, not the glacial deposits themselves, to constrain the effects of snowball Earth on the history of life (Hoffman and Schrag, 2000, 2002). Unfortunately, the measures in use (e.g., the carbon isotope record) provide non-unique solutions. Furthermore, it has not escaped attention that the major diversification of metazoan clades occurred briefly after the last glacial episode (more on the timing of snowball Earth will follow). Large frondose forms (some approach 2 m in length) occur in the Drook Formation, Newfoundland within 1500 m of the Gaskiers glacial deposits (Narbonne and Gehling, 2003), thought to have been deposited approximately 575 Ma (that is, ~10 m.y. after the last glacial interval). Could the cessation of snowball Earth then be related to the late Neoproterozoic–Cambrian diversification? Much has been speculated on very little data. Ultimately, we desire to know how Neoproterozoic low latitude glaciation affected the history of life and if the history of life can be used to constrain conditions during Neoproterozoic low latitude glaciation.

Here, we summarize the existing data on life during Neoproterozoic low latitude glaciation in order to address the points mentioned above. Others have discussed the record of life before and after the glacial events (e.g., Butterfield, 2000; Xiao, 2004) and the potential utility of molecular clocks with respect to the timing of the origin of major animal clades with respect to the glaciations (e.g., Peterson and Butterfield, 2005). Here, we will put the major focus upon the record of life *during* the glacial episodes. First, we will review the basic lithologic, geochemical, and geochronologic data available for the snowball Earth interval in order to set the stage for a discussion of life during low latitude glaciation, keeping in mind that this paper is not intended to be an exhaustive discussion of the snowball Earth hypotheses, but rather about life during snowball Earth. The available paleontological data will be presented next, followed by a discussion of the data. Finally, we will present an alternate view of life during snowball Earth, which we freely admit is speculation, based on a brief survey of the biological literature on life in modern icy environments, and end with a discussion of the kind of data we need to seek to truly answer the questions we pose.

## 2. Neoproterozoic low latitude glaciation: background

### 2.1. The rock record

Neoproterozoic glacial deposits are unusual for their global distribution (Fig. 1), the curious carbonate units that overlie them in nearly every succession (Fig. 2), and the carbon and sulfur isotopic records before and after the glacial events (Fig. 3). An excellent summary of Neoproterozoic glacial localities and their corresponding paleomagnetic signatures is provided in Evans (2000), on which Fig. 1 is based. Most deposits are identified as glacial in origin by the presence of diamictite (Fig. 2C) and laminated argillaceous strata with associated lonestones (interpreted as dropstones) (Fig. 2D). Some contain striated and faceted clasts indicative of glacial processes. Many of the diamictites contain abundant carbonate clasts, as if the glaciers directly eroded underlying carbonate banks. Generic diamict can be found in non-glacial environments and the presence of diamictite should not be used as the sole glacial indicator (Rampino, 1994; Eyles and Januszczak, 2003). However, the case for non-glacial lonestones (cf. Eyles and Januszczak, 2003) is probably overstated; thus the most parsimonious explanation for lonestones in most Neoproterozoic successions would suggest glacial processes. In addition, some, although not most, of the Neoproterozoic glacial deposits contain iron formation, not seen in the rock record since the Paleoproterozoic (Kirschvink, 1992; Kirschvink et al., 2000).

Carbonates are found atop nearly every Neoproterozoic glacial unit, even in siliciclastic-dominated suc-

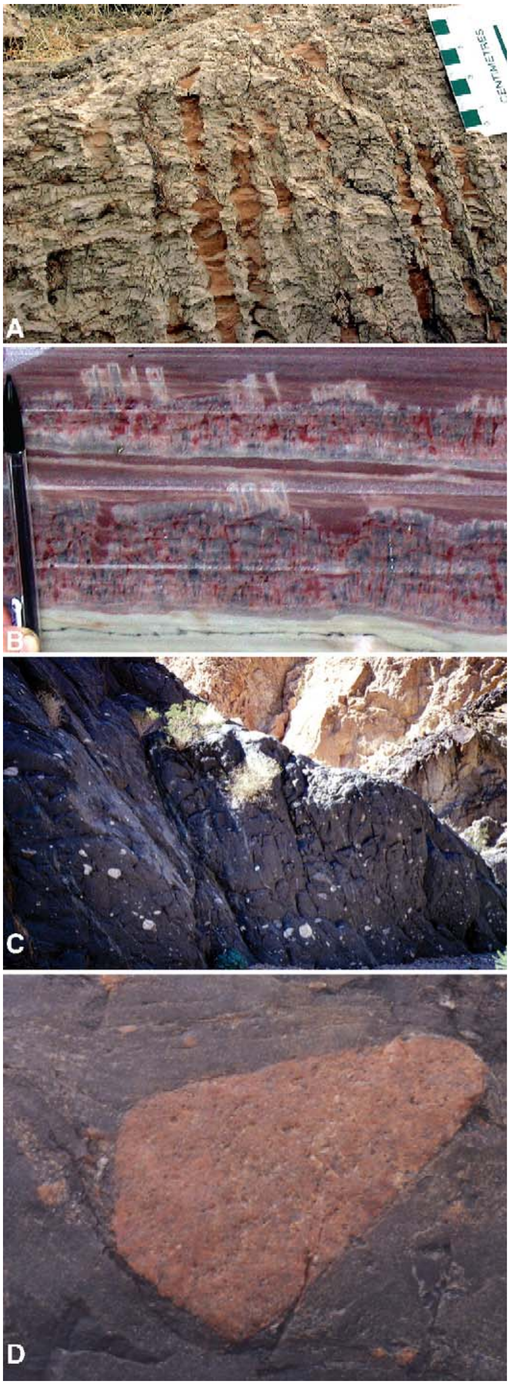

Fig. 2. Neoproterozoic glacial and cap carbonate features. A. Tubestones in Noonday Dolomite cap carbonate, Death Valley, California. B. Aragonite pseudomorph seafloor fans, Sete Lagoas Formation, Brazil. C. Typical diamictite, Wildrose Member, Kingston Peak Formation, Death Valley, California (largest clasts are ~1 m in diameter). The light-colored Noonday Dolomite cap carbonate is visible in the background. D. Glacially faceted granitic dropstone, Chiquerio Formation, San Juan, Peru (21 cm across).

cessions, and constitute one of the more unusual features of Neoproterozoic glacial successions (e.g., Kennedy et al., 1998; James et al., 2001; Hoffman and Schrag, 2002; Corsetti and Kaufman, 2003; Halverson et al., 2004) (Figs. 2A–B and 3). Such carbonate units have been called “cap carbonates” because of their position in sharp contact with the underlying glacial strata. In most successions, the basal portion of the cap carbonate is commonly laminated, allodapic or peloidal dolostone deposited upon the underlying glacial unit, and is generally a few meters thick (some would consider the basal portion to constitute *the* cap carbonate). The remainder of the cap carbonate sequence (Hoffman and Schrag, 2002; Halverson et al., 2004) may be quite thick in some successions (several hundred meters), may be limestone or dolostone, and can record unusual facies (e.g., seafloor precipitated aragonite–pseudomorph fans [Fig. 2B] (James et al., 2001), “tubestones” [Fig. 2A] (Corsetti and Grotzinger, 2005), sheetcrack cements and controversial tepee-like structures) (Allen and Hoffman, 2005). In at least one section, a thin layer of barite (commonly in the form of barite fans) separates the basal cap carbonate from the remaining cap carbonate sequence (Hoffman and Schrag, 2002).

### *2.2. The carbon isotopic record*

Kaufman et al. (1991) were among the first to recognize that the carbon isotopic record surrounding the Neoproterozoic glacial deposits was unusual and represented a global signal (Figs. 3 and 4). Since their initial study, thousands of carbon isotopic compositions ($\delta^{13}$C values) of inorganic carbon have been measured from pre-glacial and post-glacial carbonate units from around the world (including, but not limited to Kennedy et al., 1998; Misi and Veizer, 1998; Saylor et al., 1998; Jacobsen and Kaufman, 1999; Myrow and Kaufman, 1999; Prave, 1999; Brasier and Shields, 2000; Corsetti et al., 2000; Walter et al., 2000; Azmy et al., 2001; Kennedy et al., 2001a,b; Hurtgen et al., 2002; Corsetti and Kaufman, 2003; Gaucher et al., 2003; Jiang et al., 2003a,b; Rodrigues-Nogueira et al., 2003; de Alvarenga et al., 2004; Gaucher et al., 2004; Halverson et al., 2004; Hurtgen et al., 2004; Lorentz et al., 2004; Porter et al., 2004; Xiao et al., 2004). In general, these data demonstrate $\delta^{13}$C values $>+5$‰ PDB below the glacial interval; in some sections, the $\delta^{13}$C values decline to negative values in advance of the glacial deposits. The post-glacial cap carbonate $\delta^{13}$C values are negative, $\sim-3$ to $-6$‰ or even lower (see references presented

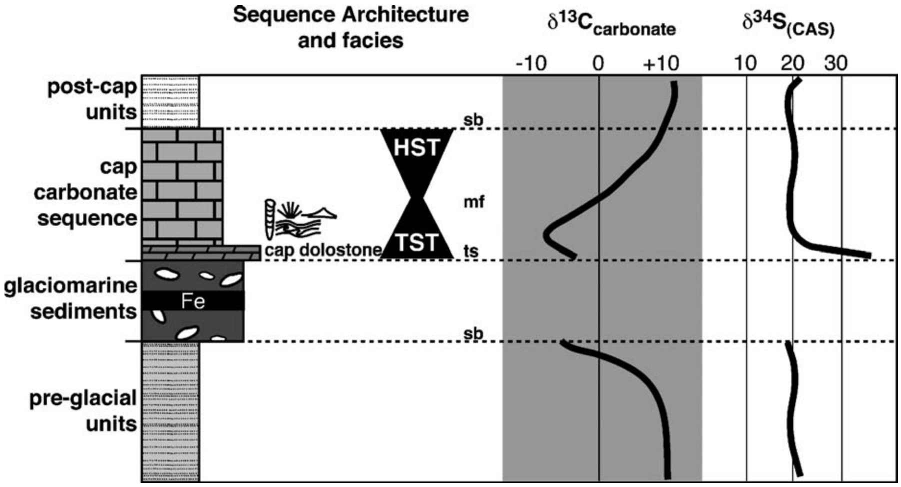

Fig. 3. Generalized cap carbonate sequence (after Hoffman and Schrag, 2002), $\delta^{13}C$ record (see references in text), and $\delta^{34}S$ record (Hurtgen et al., 2002, 2004) for a typical snowball Earth deposit. The unusual lithofacies are commonly associated with the transgressive portion of the sequence. All known cap carbonates record negative $\delta^{13}C$ values, but the shape of the profile may vary from the stylized view presented here (some cap carbonate sequences remain entirely negative from top to bottom, while others return to positive values more rapidly; see summary in Kennedy et al., 1998).

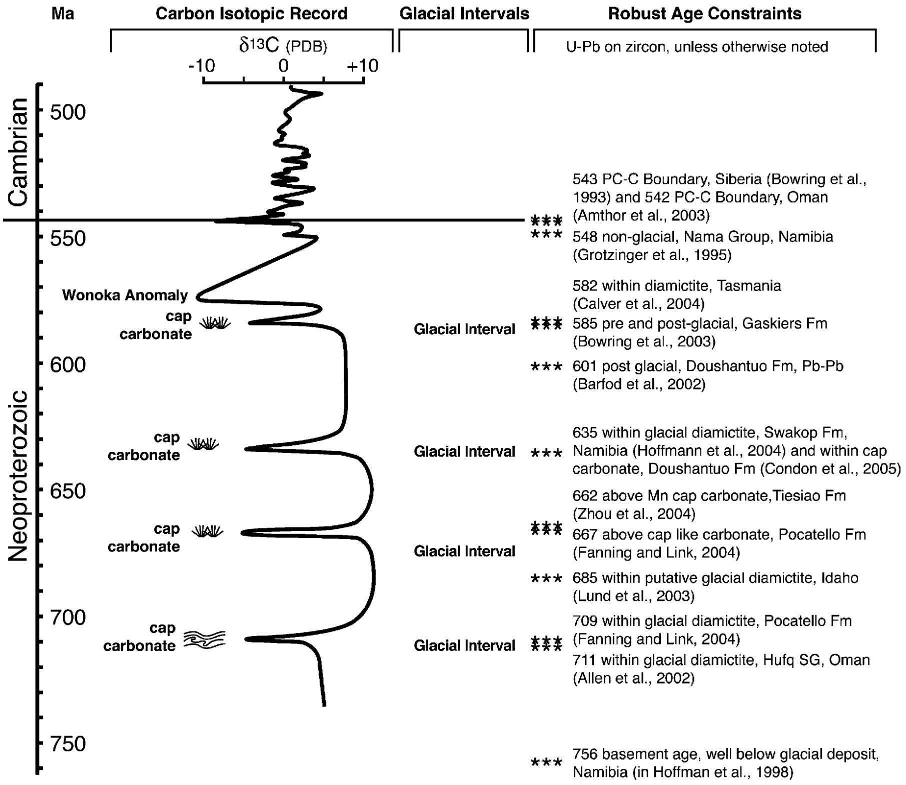

Fig. 4. Summary of age constraints for the Neoproterozoic glacial intervals. Three glacial episodes are revealed by the latest geochronology, although interregional correlations may allow additional glacial episodes (e.g., Knoll, 2000). Strata from Idaho (Lund et al., 2003; Lorentz et al., 2004) may imply a fourth, as shown here, but the glacial interpretation is tentative and other factors may create "cap-like" carbonates and negative $\delta^{13}C$ anomalies (Corsetti et al., 2004; Lorentz et al., 2004). The carbon isotopic profile is idealized (see Melezhik et al., 2001, for a detailed discussion on the construction of global carbon isotope plots). Additional radiometric dates from Amthor et al. (2003), Barfod et al. (2002), Bowring et al. (1993, 2003), Calver et al. (2004), Condon et al. (2005), Fanning and Link (2004), Grotzinger et al. (1995), Hoffmann et al. (2004), and Zhou et al. (2004).

above). The carbon isotopic compositions return to highly positive $\delta^{13}C$ values in overlying strata. The patterns described above have been used with some success as a correlation tool; however, the oscillatory nature of the record precludes robust correlation potential. Limited data are available from carbonate units deposited during the glacial intervals (Kennedy et al., 2001a,b; Corsetti et al., 2003; Halverson et al., 2004), which, in general, are rare. The available data would suggest that the syn-glacial $\delta^{13}C$ record was variable like the pre-and post-glacial record. Restricting the dataset to known primary marine carbonates, $\delta^{13}C$ values between $\sim -4.0$ and $+4.3$‰ have been reported. Although the negative $\delta^{13}C$ excursions characterize the cap carbonates, the temporal details of $\delta^{13}C$ secular variation in between the glacial events are not as clear (e.g., Melezhik et al., 2001).

### 2.3. The sulfur isotopic record of carbonate associated sulfate (CAS)

The rarity of sulfate rich evaporates in Neoproterozoic rocks precludes making detailed sulfur isotopic measurements from such strata. However, it is possible to analyze trace sulfate bound in the carbonate lattice (carbonate associated sulfate, CAS) and several studies have completed CAS analysis through the snowball Earth interval (Hurtgen et al., 2002; Hurtgen et al., 2004). In general, the sulfur isotopic record varies greatly over short stratigraphic distances and records highly positive $\delta^{34}S_{CAS}$ values within, but not limited to, the cap carbonates (Fig. 3).

### 2.4. Number and timing of low latitude glacial events

The number and timing of Neoproterozoic glacial events has been hotly debated, but recent geochronological studies have clarified the situation to a certain extent (Fig. 4). It is now clear that there were at least three glacial episodes in Neoproterozoic time, despite the fact that many successions around the world only preserve one or two events (cf., Kennedy et al., 1998). As currently defined, all three glacial episodes contain some paleomagnetic evidence for low-latitude glaciation (cf. Evans, 2000, taking into account the most recent geochronology). The oldest event took place some time between 723 Ma and 709 Ma. Diamictites from the Ghubrah Formation in Oman are dated at $723+16/-11$ Ma (Brasier et al., 2000), and have been recently redated at 711 Ma (Allen et al., 2002) and diamictites from the Pocatello Formation in southeastern Idaho are dated at $709 \pm 4$ Ma (Fanning and Link, 2004); dates from both localities overlap within analytical error. The actual duration of the ice age, or the possible existence of ice advance and retreats within a broadly defined event, is unclear. Putative glacial diamictites dated at 685 Ma (Lund et al., 2003) are also known from central Idaho, but the succession is somewhat metamorphosed and the glacial nature of the strata is difficult to confirm (Fanning and Link (2004) consider these deposits to represent a continuation of the previous glaciation). Diamictites of the Swakop Formation in Namibia are dated at 635 Ma (Hoffmann et al., 2004) and are correlated to the well-studied Ghaub Formation of the Otavi Group (Hoffman et al., 1998), and the basal Doushantuo Formation, a cap carbonate above the Nantuo Tillite in south China, has been dated at 635 Ma, as well (Condon et al., 2005). Glacial strata in Newfoundland (Bowring et al., 2003) and Tasmania (Calver et al., 2004) are dated at 585 Ma. Thus, there were *at least* three glacial episodes in Neoproterozoic time (cf., Xiao et al., 2004). It is likely that more glacial events occurred (e.g., Kaufman et al., 1997; Knoll, 2000; Corsetti and Kaufman, 2003), as revealed via stratigraphic correlation from one locality to another, but the successions in question generally lack radiometric control and the chemostratigraphic data used to correlate between them are somewhat equivocal. In Newfoundland, the duration of the glaciation is constrained to be less than one million years, within analytical error (Bowring et al., 2003). In the Otavi Group, Namibia, the duration of the glaciation represented by the Ghaub Formation glacial deposits was postulated to be much longer (up to 10 million years), based on thermal subsidence modeling (Hoffman et al., 1998). However, the modeling assumes trailing margin behavior; other workers interpret the succession as a foreland basin (Prave, 1996) and thus discount the 10 million year duration.

It has been common practice to apply names from glacial deposits in Australia to the rest of the world in a sort of unofficial chronostratigraphy, although intercontinental correlations were never certain. In Australia, most sections contain two glacial intervals: the older is called the Sturtian and younger the Marinoan (see Kennedy et al., 1998). In the absence of robust dates, the ages were commonly considered circa 700 Ma and circa 600 Ma, respectively. The names were commonly applied to glacial deposits on other continents that occupied a similar stratigraphic position (Sturtian for older one, and Marinoan for younger). The new dates discussed above call into question some of the prior intercontinental correlations. Therefore, the use of the terms Sturtian and Marinoan, which are entrenched in the Neoproterozoic literature, should be viewed with caution.

### 2.5. Summary of snowball Earth data

In summary, most workers agree that:

1. Glacial deposits are globally distributed in Neoproterozoic stratigraphic successions (Fig. 1);
2. There were at least three, if not more, glaciations in Neoproterozoic time ca. ~710, ~635 and ~585 Ma (Fig. 4);
3. The glacial deposits may contain iron-formation, but not all do;
4. The diamictites are sharply overlain by lithologically unusual "cap carbonates" (Figs. 2 and 3). In some sections, the basal cap dolostone is overlain by a cap carbonate sequence that includes unusual carbonate facies (carbonate and/or barite seafloor fans, sheet-crack cements, tubestones, and controversial tepee-like structures);
5. The pre-glacial $\delta^{13}C$ record is highly positive and in some sections declines to negative values just below the glacial units (Figs. 3 and 4). The syn-glacial $\delta^{13}C$ record is sparse, but varies between ~−4 and +4‰. The cap carbonates universally record negative $\delta^{13}C$ values and highly positive $\delta^{34}S_{CAS}$ values.

## 3. The snowball Earth hypotheses

Most would agree that the oceans were largely anoxic and likely low in sulfate during the glaciations, as demonstrated by the presence of iron formation and the sulfur isotopic data, and that the climate was warm during the formation of the post-glacial cap carbonates. Beyond these, no interpretive consensus exists on the data or the effects on the history of life. A survey of the geologic literature suggests that snowball Earth conditions would have caused widespread biotic crises and restricted the less-hardy eukaryotic organisms to "refugia." Furthermore, some envision strong evolutionary consequences, where successive glaciations would provide a bottleneck and flush style of evolution (Hoffman et al., 1998) that perhaps spurred the Cambrian explosion of metazoa. Specifically, three principal working hypotheses have been proposed to explain the geological and geochemical observations (in particular, the presence and isotopic signature of the cap carbonates), and all carry different consequences for the history of life (summarized in Table 1): the Snowball Earth Hypothesis (e.g., Hoffman et al., 1998; Hoffman and Schrag, 2002), the methane model (e.g., Kennedy et al., 2001a,b), and the overturn model (e.g., Grotzinger and Knoll, 1995; Kaufman et al., 1997). Most of the hypotheses speculate on syn-glacial processes primarily by examining the post-glacial cap carbonates and only

Table 1
Three competing hypotheses for the formation of cap carbonates in the aftermath of Neoproterozoic low latitude glaciation

| | Hard snowball | Methane model | Stagnant ocean |
|---|---|---|---|
| Hypothesis | Global ice cover separates ocean from atmosphere. $CO_2$ from volcanism builds up in atmosphere, causing global warming, ending glaciation. | Gas hydrates form in abundance during glaciation; disassociate during deglaciation. | Stratified ocean; $CO_2$ drawn down by biologic pump from surface and stored in deep, causes glaciation; overturn returns $CO_2$ to atm, causes warming, end of glaciation. |
| Cap carbonate | Resumption of hydrologic cycle causes intense weathering, flushing ions into the ocean, raising the alkalinity. | Anaerobic oxidation of methane in the water column increases alkalinity. | Sulfate reduction in anoxic water column during glaciation increases alkalinity. |
| Negative $\delta^{13}C$ in cap | Volcanogenic $CO_2$ is transferred from the atmosphere into ocean. | Gas hydrates input depleted $^{13}C$ into oceans. | Turnover brings depleted CO2 up to surface waters. |
| Potential weaknesses | Silica budget of ocean; ice-rafted debris suggests active hydrologic cycle; dated glacial interval indicates limited time for $CO_2$ build-up. | Cap carbonates only mildly depleted in $^{13}C$; postulated alkalinity too small to build large caps; seeps seen throughout record, not just with glacial episodes. | One overturn may have too few dissolved ions to form caps, nutrient flux in stagnant ocean may be too low for high productivity, alkalinity may be too low. |
| Geobiologic predictions | Primary production shuts down as ice retards photosynthesis, leads to loss of marine ecosystem and little organic matter burial during glaciation. | Primary production and organic matter burial would continue during glaciations; anaerobic (and perhaps aerobic) methane oxidation post-glaciation. | Primary production and organic matter burial would continue during glaciations; anaerobic photosynthetic and aerobic methane oxidizing bacteria may be present in abundance. |

secondarily via syn-glacial strata. All of them account for the observed negative $\delta^{13}C$ anomaly in post-glacial cap carbonates. None are directly contradicted by existing carbonate data from the cap carbonates, although many inconsistencies sill plague each hypothesis. Of the three hypotheses for cap carbonate formation, the Snowball Earth Hypothesis makes dire geobiologic predictions and will be covered in more detail.

### *3.1. Snowball Earth hypothesis predictions*

In this model, the tropical oceans freeze over because of an ice albedo runaway: when sea ice reaches a latitude of ~30°, the increased albedo causes enough heat to be reflected back to space that the earth quickly freezes and mean annual surface temperatures plummet to ~230 K; free water in surficial environments is thought to have been nonexistant. The oceans are separated from the atmosphere by a thick shell of ice (postulated to be >1.5 km thick). The thick sea ice provides the greatest challange for life, as photosynthesis would be precluded and prodctivity would crash. $CO_2$ would build up in the atmosphere via volcanic outgassing during this period because of the ice cover (rather than interacting with the oceans) until a critical threshold is reached (postulated near 10 times present values) and greenhouse warming would cause the ice to melt. As the snowball melts catastrophically and the hydrologic cycle returns, acid rain produced by the large amount of $CO_2$ in the atmosphere would cause intense carbonate and silicate weathering on the continents. The alkalinity of the oceans increases as weathering products are delivered, fostering the rapid precipitation of cap carbonates. The icehouse–greenhouse transition is predicted to be extremely rapid (ca. 1000 years).

Ultimately, the extent of ice cover predicted by the snowball Earth model is based on the postulated mechanism for cap carbonate deposition and the need to separate the ocean from the atmosphere. The affect of snowball Earth on the biosphere is intimately tied to the proposed thickness of sea ice and the ability for photosynthetic primary production to fuel the marine ecosystem. Where there was sunlight, there would have been little free water, and where there was abundant water (under the ice), there would have been no sunlight. Unfortunately, no robust proxy for the amount of sea ice cover, or the thickness of sea ice, currently exists. Models have been proposed (e.g., McKay, 2000; Goodman and Pierrehumbert, 2003; see also Donnadieu et al., 2003, for a discussion of ice on land), but none are universally accepted, as they make the a priori assumption that ice albedo feeback occurred, a fact we simply do not have the geologic record to support at this time.

## 4. Snowball Earth: the paleontological record

As previously mentioned, indirect means to assess the status of the biosphere during snowball Earth times, such as the carbon and sulfur cycles, can be interpreted in different ways, hence the different hypotheses presented in Table 1. Therefore, it would be best to examine the actual fossil record in order to assess the fate of life during extreme low latitude glaciation. The available fossil record is meager by Phanerozoic standards; life was largely unmineralized and microscopic (but see Hofmann et al., 1990) so the fossilization potential was low. Even some well-preserved microbiotas, considered diverse by Proterozoic standards, would be considered somewhat depauperate by Phanerozoic standards.

Microfossil diversity compilations are available for the Neoproterozoic (e.g., Schopf, 1992; Knoll, 1994; Vidal and Moczydlowska-Vidal, 1997), but only a limited number of studies specifically address microfossils within or bracketing glacial deposits (Vidal, 1976; Pierce and Cloud, 1979; Zhao et al., 1985; Corsetti et al., 2003; Grey et al., 2003). Currently, two styles of fossil preservation are available for examination: chert (fossils are entombed in chert and examined in thin section), and shale (fossils are preserved as organic-walled structures disseminated in shale and examined as disarticulated extracts from macerated shale). Silicified microbiotas generally provide a survey of benthic organisms with some pelagic input. They are relatively rare in the fossil record by Phanerozoic standards and are most common in paleoenvironments suitable to early silicification (in the Neoproterozoic, this would bias the record towards shallow water communities living in carbonate-dominated environments [Maliva et al., 1989; Maliva et al., 2005]). Once entombed in chert, the microfossils can withstand a substantial amount of post-depositional alteration. Microfossils preserved in shale, however, commonly contain an abundance of pelagic organisms with relatively robust organic walls (e.g., acritarchs, organisms of largely uncertain affinity, but commonly interpreted as the cysts of planktonic eukaryotic algae) that are able to withstand mild diagenetic alteration; less robust microfossil remains are not preserved. Although some well-preserved acritarch assemblages are quite diverse (e.g., Grey et al., 2003), they are highly susceptible to post-depositional thermal alteration. They do provide a survey of the pelagic realm not captured in most silicified microbiotas, as they commonly occur in somewhat deeper water shales. Thus, both styles of Proterozoic microfossil preservation are subject to particular environmental biases that could limit their utility, especially because the number of microfossil localities is low.

### 4.1. Silicified microfossils from Death Valley

The best studied and, to our knowledge, the only known silicified microfossil assemblage within a Neoproterozoic glacial deposit, is found in the Kingston Peak Formation in the Death Valley region of eastern California (Pierce and Cloud, 1979; Corsetti et al., 2003) (Fig. 5). The age of the Kingston Peak Formation is undoubtedly Neoproterozoic (Fig. 5A), but it is not clear which Neoproterozoic glaciation correlates to the unit in question (note that Corsetti et al., 2003 opt for the older Neoproterozoic glaciation, based on lithologic comparisons to better-dated units elsewhere in the western North America). The microfossils occur in a thin (~2 m thick) oncolitic carbonate unit (Fig. 5B) found interbedded with dropstone-laden shales, cross-bedded fine sandstones, and carbonate clast diamictite. Many of

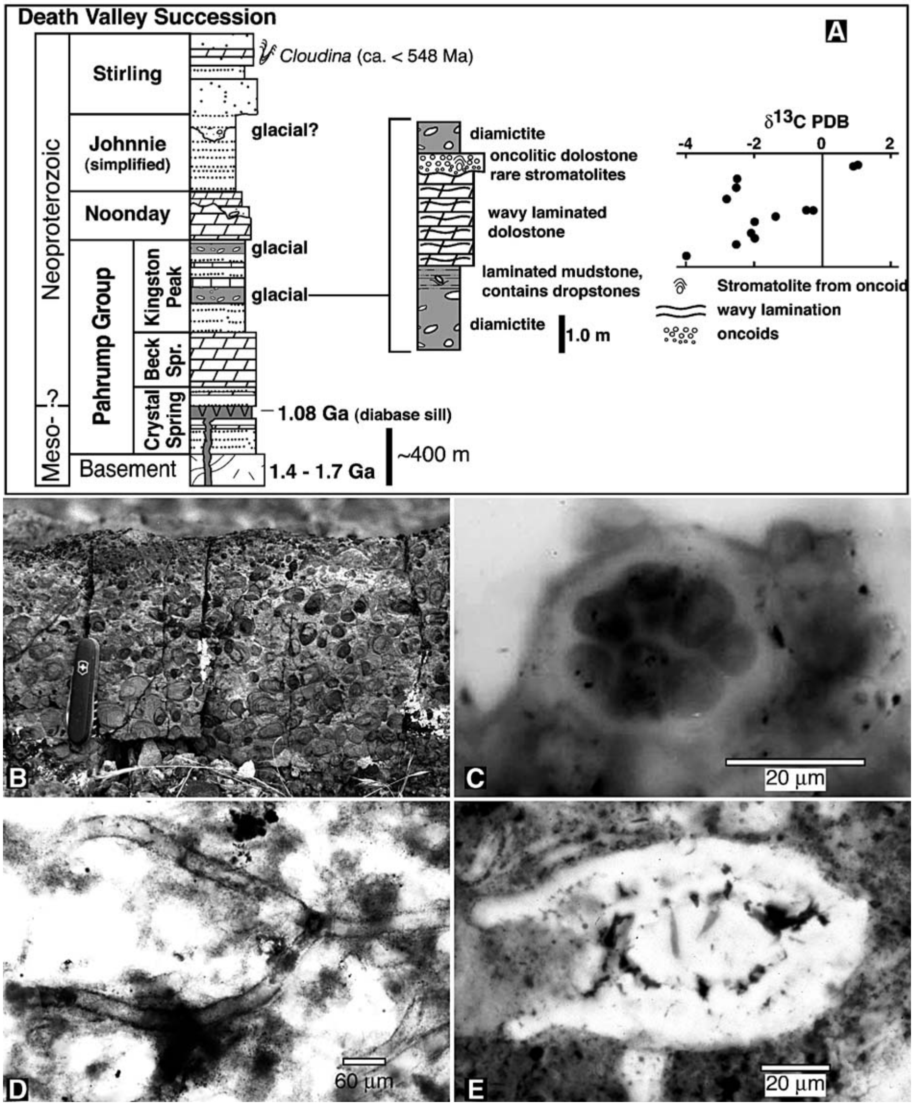

Fig. 5. Syn-glacial microfossils from the Kingston Peak Formation, Death Valley, California (modified from Pierce and Cloud, 1979 and Corsetti et al., 2003). A. General stratigraphic column for the Neoproterozoic Death Valley succession. The inset column and isotopic profile originate from the syn-glacial oncolite bed, discussed in the text (Corsetti et al., 2003). B. Field photograph of the oncolite bed. Silicified microfossil bearing carbonate stands in slight relief versus the dolostone. C. Putative pluricellular cyanobacterium from the silicified oncolite bed. D. *Palaeosiphonella*, a putative branched autotrophic eukaryote from the oncolite bed. E. Vase-shaped microfossil, a putative testate amoeba (cf., Porter and Knoll, 2000) from the oncolite bed.

the larger oncoids appear to have stabilized and display vertical growth into small columnar stromatolites. Weakly stratified diamictite is found above and below the oncolite unit, and iron-rich strata are found within a few tens of meters below the unit. As the diamictites above and below appear identical, Corsetti et al. (2003) interpret the oncolite unit to have been deposited during glaciation. Taken in isolation, the oncolite bed appears to have been deposited in a typical, agitated, shallow marine setting. Given its position within the diamictites, the depositional setting is less certain, and they conclude that the carbonate unit may represent a shallow marine environment or it could represent a non-marine glacial environment akin to those found today in the Antarctic Dry Valley lakes (see detailed discussion in Corsetti et al., 2003). Interestingly, Walter and Bauld (1983) noted stromatolitic carbonates within diamictite from the Neoproterozoic Wanapi Dolomite Member in the Ngalia basin in Australia and suggested comparison with the Antarctic Dry Valley lakes, as well. The thin carbonate unit is used as a marker bed throughout the Kingston Range area; regional relations rule out the idea that the thin unit somehow represents structural duplication from underlying units. The $\delta^{13}C$ profile forms a coherent trend from $-4‰$ at the base to $+1.1‰$ at the top (Corsetti et al., 2003). The $\delta^{13}C$ profile from the underlying units is well-known (Corsetti and Kaufman, 2003) and does not match the strongly negative to mildly positive trend from the oncolite unit, confirming that the unit does not represent duplication from underlying units.

Filamentous and coccoidal morphologies interpreted as putative cyanobacteria (Fig. 5C) are the most common microfossil within the silicified oncolite unit, and appear entwined in mat-like arrays that probably represent near-life positions. More importantly, the oncolite unit contains several significant non-cyanobacterial microfossils: branched, septated tubular microfossils (Fig. 5D), provisionally assigned to *Palaeosiphonella*, vase-shaped microfossils (Fig. 5E) and several other complex but unassigned forms, some with double wall partitioning indicating eukaryotic affinity (Pierce and Cloud, 1979; Corsetti et al., 2003). *Palaeosiphonella* is probably an autotrophic eukaryote (alga), while vase-shaped microfossils are morphologically identical to testate amoebae (Porter and Knoll, 2000; Porter et al., 2003) and are thus considered eukaryotic heterotrophs. When compared to microfossils from the underlying pre-glacial Beck Spring Dolomite, the syn-glacial oncolite unit contains more putative eukaryotes than the pre-glacial Beck Spring Dolomite microbiota (Corsetti et al., 2003). The diversity of the assemblage is typical of most other Neoproterozoic silicified microbiotas. In modern marine glacial sediments, it is common to find “old” microfossils, such as diatoms, coccoliths, foraminifera, and the like, that were transported from ancient sediments exhumed by glacial process and resedimented (Webb et al., 1984). The delicate, well preserved, unmineralized Kingston Peak Formation microfossils, however, would not survive desiccation and transport, and are found within and around oncoids that formed in place; thus it is highly unlikely that they were transported from underlying units.

### 4.2. Microfossils in shale

Several Neoproterozoic syn-glacial localities preserve microfossils in shale (Vidal, 1976; Knoll et al., 1981; Zhao et al., 1985). The Tillite Group in Greenland contains a low diversity assemblage of simple spherical acritarchs (Vidal, 1976). The Tillite Group is commonly considered “Varanger” in age (yet another colloquial age term), which likely correlates to one of the younger glacial episodes. A similarly low diversity assemblage originates from the glacial Mineral Fork Formation in Utah (Knoll et al., 1981); the quantity of microfossils was characterized as “extremely abundant”, but entirely dominated by *Bavlinella faveolata*, a form that consists of many micron-sized cells packed together in a “raspberry-like multisphere” (p. 250, Knoll et al., 1981; see Vidal and Nystuen, 1990, for a discussion of *Bavlinella* and its affinities to *Sphaerocongregus sp.*, which they suggest could represent anoxygenic photosynthesizing bacteria). The unit is commonly correlated to the Pocatello Formation and thus would represent the older of the Neoproterozoic glacial episodes, ca. 710 Ma. Similar forms were reported from the nearby and correlative Formation of Perry Canyon, Utah, and from siltstones interbedded with Neoproterozoic diamictite in the Conception Bay Group, Newfoundland (Knoll et al., 1981). Vidal and Nystuen (1990) report organic walled microfossils from the Moelv Tillite (Hedmark Group, southern Norway). Unpublished reports also indicate syn-glacial shale-based microfossil assemblages from the Neoproterozoic of northern Norway and Namibia (G. Vidal, pers. comm. to Knoll, *in* Knoll et al., 1981). Acritarchs have also been reported from the Nantuo Tillite (Zhao et al., 1985), likely deposited ca. 635 Ma, in south China, but the details are little known.

Perhaps the best and most diverse dataset of glacially related organic walled microfossils brackets the Marinoan glacial deposits in Australia (Grey et al., 2003) (Fig. 6). The dataset was compiled from several basins

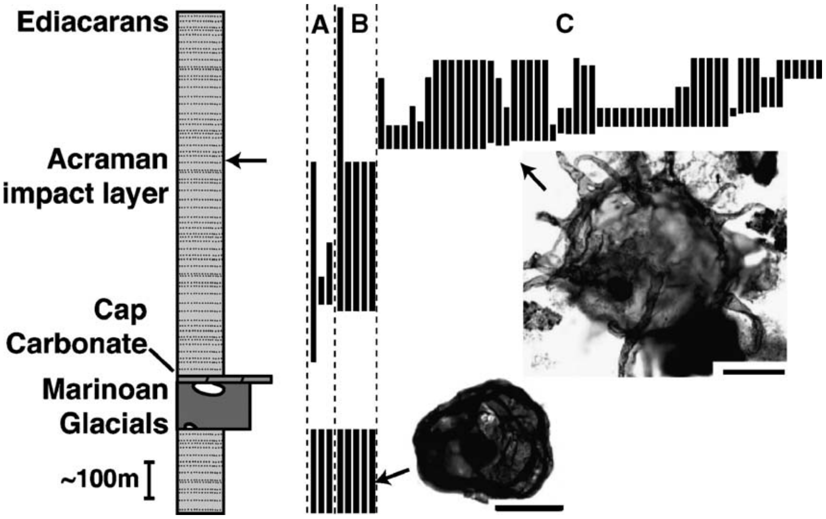

Fig. 6. Acritarch biodiversity data bracketing the Marinoan glaciation in Australia, modified from Grey et al. (2003). Thickness is relative to the individual sections used to construct the diagram, but in some sections, the Acraman impact layer is as much as 600 m above the cap carbonate (Grey et al., 2003). A: Non-unique morphotypes with long stratigraphic ranges; B. Leiosphere assemblage occurs before and after the glacial units (see Grey et al., 2003). C: Acanthomorph assemblage, occurs well above B and is likely not related to glacial turnover (see Grey et al., 2003). Scale bar on photomicrographs: 25 μm.

and includes microfossil data from at least 13 drill cores and 12 measured sections, and thus represents the most statistically robust glacially related dataset. At least 8 taxa occur before and after the Marinoan glacial event. The glacial interval is apparently barren of microfossils, although it is unclear whether the abundance pattern results from actual biotic crisis or paleoenvironmental/preservational bias. The fact that the same morphotypes reappear unchanged above the glacial interval may suggest that the syn-glacial absence is at least in part facies controlled. The pre- and post-glacial acritarch assemblages are virtually identical and show no major extinction or turnover in relationship to the glacial deposits. Instead, the turnover is entirely disconnected from the Marinoan glaciation, as the older low-diversity leiosphere-dominated flora is replaced by a highly diverse acanthomorph (e.g., spiny) flora well above the glacial termination (greater than 600 m above, in some cases).

### *4.3. Global microfossil compilations*

Neoproterozoic microfossil diversity compilations suffer from the lack of available geochronology, relatively low diversity assemblages, few localities, problematic taxonomy, and unclear global correlation. The geochronology of all of the available datasets are simply too coarse to accurately comment on life during snowball glaciation. Nevertheless, it is appropriate to cautiously consider the available data, given that fossil data is so scarce. Knoll (1994) compiled a list of acritarchs from 1700 Ma to 520 Ma; five of his time slices (800–750, 750–700, 700–650, 650–600 and 600–575 Ma) span the glacial intervals in question (Fig. 7). Admirably, this study was largely restricted to specimens the author observed personally, thereby circumventing taxonomic issues inherent in literature-based compilations. Little change in acritarch diversity is noted between 800 and 650 Ma, when diversity remained nearly constant at ~30 species. Even allowing for potential age reassignment of certain microbiotas,

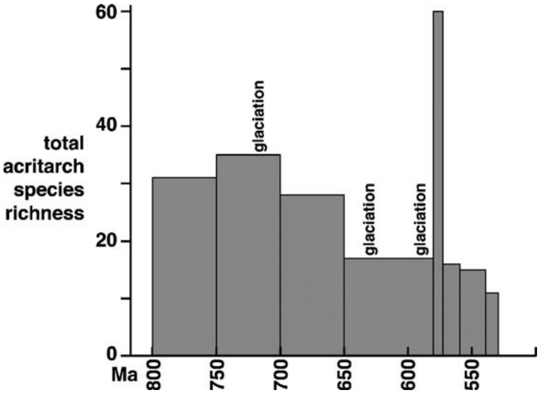

Fig. 7. Acritarch biodiversity between 800 and 538 Ma, replotted from Knoll (1994). The time bins are coarse, but essentially no change is noted with the older glaciation, and some change is noted for the younger glaciations. The diversity spike after the last glacial has been moved forward in time from the original diagram to account for new information (e.g., Grey et al., 2003).

this time interval would certainly encompass the older of the snowball Earth intervals. A decline in diversity is observed between 650 and 600, which, in this compilation, constitutes what was considered the younger glacial interval. An 'explosion' of diversity to ~60 species occurred between 600 and 575 Ma (the diagram presented here was modified slightly from the original to account for the presence of two glacial deposits between 635 and 585 Ma, placing the burst in diversity to well after 585 Ma in accordance with the new data found in Grey et al., 2003). Diversity then crashed back to glacial diversity levels, less than 20 species, between 575 and 538 Ma, apparently in the absence of glacial pressures. Vidal and Moczydlowska-Vidal (1997) provided the most recent microfossil compilation, but the time intervals used to bin the data were too coarse to provide information that would supersede the data presented above, and the diversity patterns are ultimately similar.

## 5. Discussion

Did snowball Earth have a major effect on the course of evolution? With the image of a frozen world, it is easy to understand why major effects are hypothesized, but do they make geobiologic sense? After all, complex multicelled algal clades are known from before and after the glacial interval (Butterfield, 2000; Xiao, 2004). The three major hypotheses (snowball, methane, and stagnation) predict different effects on the biosphere, with the snowball scenario offering the most severe situation. The available fossil record, however problematic, can be used to address the speculation surrounding the biotic and evolutionary effects of what may be the most severe glaciations recorded in the stratigraphic record.

### 5.1. Fossil record versus snowball Earth

The silicified microbiota in the syn-glacial Kingston Peak Formation is more diverse than underlying units in the region. The presence of likely autotrophs and heterotrophs implies a robust trophic structure (Corsetti et al., 2003) and, most importantly, the fact that sunlight penetrated into the environment. The large dataset found before and after the Marinoan glaciation in Australia (Grey et al., 2003) demonstrates no difference in the pre- and post-glacial assemblages; the barren interval within the diamictites is reasonably interpreted as a preservational bias, at least in part. In fact, the major post-glacial diversification event does not occur until well above the post-glacial cap carbonate and is therefore disconnected from the glaciation itself. The coarse temporal resolution of the global microfossil diversity investigations precludes detailed interpretation, but the broad scale trends suggest that the older Neoproterozoic glaciation had little effect on global diversity and that the younger glaciation(s) had a mild effect (Knoll, 1994; Vidal and Moczydlowska-Vidal, 1997), certainly not the massive extinction predicted by the snowball model. Thus, the fossil record does not support the major extinctions predicted to have occurred during snowball Earth.

The depauperate but abundant syn-glacial microfossil assemblages from the Mineral Fork Formation (Knoll et al., 1981) and the Tillite Group (Vidal and Moczydlowska-Vidal, 1997) could indeed indicate a biotic response to environmental stress, as abundant, monospecific assemblages have been associated with environmental perturbation (Knoll et al., 1981). Thus, the fossil record does support some effect on the marine biosphere. This is not unexpected, as similar monospecific microfossil assemblages are known from other, less severe glacial intervals. For example, the taxon *Tasmanites*, a distinctive organic walled microfossil, forms significant syn-glacial monospecific accumulations in association with Permian glacial deposits (Revill et al., 1994). Thus, the fact that the Mineral Fork, Tillite Group, and Nantuo strata contain microfossils at all, whether monospecific or diverse, indicates that primary productivity continued at some level during the glaciations. Thus, the actual fossil record suggests that the dire geobiologic predictions of a snowball Earth do not stand further scrutiny.

The fossil record can be used to argue against the refugia hypothesis. This hypothesis, considered by some to be a loophole for life during snowball Earth, suggests that eukaryotes and prokaryotes survived in some refugia where conditions remained equitable and then repopulated the post-snowball Earth (Hoffman et al., 1998). Hydrothermal vents are commonly considered a likely refugia (Runnegar, 2000). However, the putative photosynthetic phytoplankton found in many of the deposits discussed above would clearly not be adapted to life near deep, dark mid-ocean ridge vents. Additionally, the nearly identical microbial components of the pre- and syn-glacial microbiotas from Death Valley, its more diverse glacial assemblage, and the indistinguishable pre- and post-glacial microbiotas from Australia, all argue against life retreating to refugia. The likelihood of the same taxa and community structure that existed prior to the onset of glaciation adapting to, and surviving in, refugia unchanged, and then repopulating the marine environment is remote.

### *5.2. Did snowball conditions drive the Cambrian explosion?*

The fossil record does not support the hypothesis that successive Neoproterozoic glacial episodes somehow pushed evolution towards the origin and diversification of metazoan clades, for the concept of "bottleneck and flush" (Hoffman et al., 1998) is not consistent with the available data. The stasis demonstrated by the Kingston Peak microfossils and the Australian data clearly downplays the role of snowball glaciation with respect to evolutionary innovation. It is possible that the cessation of successive glaciations *permitted* the Cambrian explosion to proceed, in the sense that many large metazoans would not survive a snowball scenario, but there is no evidence for a direct connection between evolutionary innovation and snowball Earth.

### *5.3. Alternate hypotheses*

The presence of the syn-glacial microbiotas would at first seem to be inconsistent with the hard snowball scenario, which requires vast, virtually unbroken sea-ice cover in order to separate the atmosphere from the ocean. While the thickness of the sea ice is debated, it is presumed to be thick enough by the snowball hypothesis to prevent abundant sunlight penetration, which is detrimental to photosynthetic phytoplankton and by association, the rest of the biosphere. However, it is entirely possible that this logic is flawed and that life is simply more robust that we presume.

A survey of life in modern icy environments, our closest accessible modern analogue to snowball Earth, reveals some relevant observations. Biologists have long known that complex communities of photosynthetic and heterotrophic bacteria, and microbial eukaryotes including metazoa thrive within seasonal sea ice, perennial lake ice, glacial ice, and ice shelves (Priscu et al., 1998; Mueller et al., 2001; Thomas and Dieckmann, 2002; Vincent et al., 2004). In some cases, the ice communities are so productive that the ice appears colored (Fig. 8; see also Vincent et al., 2004, Fig. 2, p. 106). Such environments have been suggested as likely habitats during snowball Earth (Vincent et al., 2000; Vincent et al., 2004; Domack et al., 2005), while others have remarked upon the lithologic similarity between some Neoproterozoic stromatolitic carbonates within glacial diamictites and modern Antarctic dry valley lakes (Walter and Bauld, 1983).

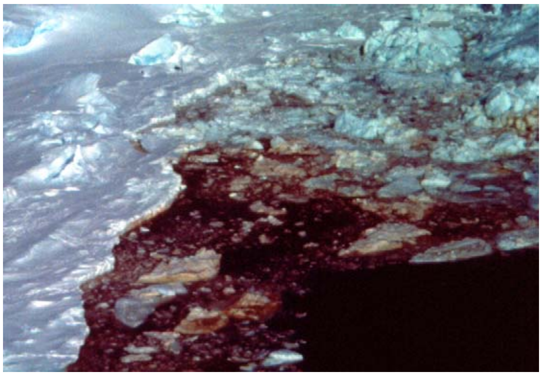

Fig. 8. Pack ice of the northern Ross Sea, January 1999. When broken by the ship, the underside of the ice (so-called "dirty ice") is visible and is covered with a diverse microbial community (courtesy of D. Caron, USC).

Sea ice develops annually as a semisolid matrix of ice with brine pores and channels yielding a variety of microenvironments that vary in temperature (−2 to −35 °C), salinity (3 ppt to 150 ppt), space (up to 2 m thick), nutrient concentration, and light intensity (Maykut, 1986; Staley and Gosink, 1999). Nutrients are trapped within the ice from the sea water during initial freezing, may also be obtained from the atmosphere, and are affected by brine drainage (Dieckmann et al., 1991; Golden et al., 1998; Kaartokallio, 2001). As a result, DOC concentrations are generally significantly higher in sea ice than in bulk seawater (Thomas and Papadimitrou, 2003). Subsequently, complex communities dominated by diatoms form visible inclusions in the bottom 10 to 20 cm of sea ice (Staley and Gosink, 1999; Thomas and Dieckmann, 2002). A vast array of heterotrophic bacteria have been catalogued from sea ice communities and act to mineralize the organic matter trapped or produced (Friedmann, 1993; Bowman et al., 1997; Junge et al., 2002; Thomas and Dieckmann, 2002). Based on high bacterial production rates (10–15% of primary production), it is estimated that 20–30% of the primary carbon cycles through the heterotrophic bacteria (Kottmeier et al., 1987; Kottmeier and Sullivan, 1987; Friedmann, 1993). Protozoa and metazoa (polychaetes, amphipods, and euphausiids [krill]) are also present and take advantage of the abundant food source (Garrison and Buck, 1989; Garrison, 1991; Thomas and Dieckmann, 2002). Sea ice hosts a diverse and productive community of organisms; in fact, 5% of the total annual productivity of the sea-ice influenced zone of the Southern Ocean comes from Antarctic sea ice (Thomas and Dieckmann, 2002). The benthic community from the Kingston Peak Formation was likely photosynthetic (based on morphology) and demonstrates that light was able to penetrate into the environment; thus, the sea ice analogue may be suitable for some, but not all, of the snowball Earth environments.

Permanently ice-covered lakes and ice shelves may be more suitable analogues for snowball Earth conditions as the ice is thicker (several lakes in Antarctica have ice covers of 3 to 6 m; while ice shelves vary in thickness from 10 to 80 m) and the surface ice is more isolated from the water column. In the 4 m thick perennial lake ice of Lake Bonney, Antarctica, microbial communities thrive in association with aeolian deposits at a depth of 2 m (Priscu et al., 1998). The depth of the sediment layer is determined by the steady-state equilibrium between the downward movement of sediments as the top layers of ice melt extensively in the summer and the upward movement of ice as it ablates at the surface and freezes onto the bottom. Nutrients are abundant in the sediment layer; indeed, dissolved inorganic nitrogen and dissolved organic carbon concentrations peak at the same depth (Priscu et al., 1998). Microbial assemblages in Lake Bonney ice are comprised primarily of filamentous cyanobacteria (Priscu et al., 1998; Gordon et al., 2000). Heterotrophic bacteria and green non-sulfur bacteria were also identified and may contribute to nutrient recycling (Gordon et al., 2000). Significantly, the lake ice microorganisms do not resemble the eukaryotic plankton predominant in the lake water, but are more similar to organisms found in terrestrial mats in the nearby area (Priscu et al., 1998; Gordon et al., 2000).

Ice shelf communities of the Ward Hunt, Markham, and McMurdo ice shelves, probably the best analogue for snowball Earth ice, are dominated by filamentous cyanobacteria that form mats in association with sediments found in meltwater ponds and lakes on the surface of the ice (Vincent et al., 2000; Vincent et al., 2004). The sediment originates from the marine environment and moves upward through the ice as water freezes to the base and ablates from the surface (Vincent et al., 2004). Nutrient concentrations (DIC, DOC, total nitrogen and phosphorus) in the meltwater are high and increase in the mat pore waters (Vincent et al., 2004). The photosynthetic capacity of microalgal communities from Weddel Sea pack ice is similar to Antarctic phytoplankton (Lizotte and Sullivan, 1992). Cyanobacteria dominate these communities (~$10^5$ cells/cm$^2$), although eukaryotic algae are also present (Vincent et al., 2004). Heterotrophic bacteria are also present in significant numbers (~$10^7$ cells/cm$^2$) and likely contribute to nutrient recycling (Vincent et al., 2000). Primary production in ice shelf communities is significant and provides the basis for a food chain that supports other organisms such as ciliates, flagellates, nematodes, rotifers, platyhelminthes, and tardigrades (Vincent et al., 2000, 2004).

It has been suggested that the Permian *Tasmanites* accumulations (noted previously), which contain up to 30% organic matter, may represent organic sedimentation from microbial communities that lived within the ice (Revill et al., 1994). The Permian and modern analogues demonstrate that a significant amount of organic matter can be transferred from the ice into the underlying marine realm. It is likely that even a snowball Earth would have some ice-free marine environments, particularly in marginal marine environments where putative sea ice would intersect the marginal marine realm. In the modern ocean, Antarctic ice-margin environments are some of the most productive on Earth (Lizotte and Sullivan, 1992). Glacially produced detritus may have been an important source of nutrients during snowball Earth, as well. Finally, in the present day, snow can support a diverse community of algae, heterotrophic bacteria, fungi, insects, copepods, and ice worms with eolian deposition as the major source of nutrient input (Hoham and Duval, 2001). While activity and growth of microbes in snow is difficult to conclusively demonstrate, cold-adapted microorganisms (beta-proteobacteria and actinobacteria) were found to dominate and increase in number seasonally in mountain snow (Segawa et al., 2005). Snow environments, if they existed during snowball Earth, could have represented an important, albeit difficult to quantify, component of the ecosystem. Thus, as demonstrated by the fossil record and the modern analogues, it is entirely possible for life to continue on unimpeded during Neoproterozoic low latitude glaciation, even one completely entombed in ice; the record of life, therefore, cannot be used to falsify the Snowball Earth hypothesis itself, but rather some of its geobiologic predictions.

## 6. Conclusion

As stated in the introduction, we set out to explore how Neoproterozoic low latitude glaciation affected the history of life and if the history of life can be used to constrain conditions during Neoproterozoic low latitude glaciation. The fossil record, however limited and problematic, reveals little change between pre-, syn-, and post-glacial microbiota with respect to individual Neoproterozoic low latitude glacial events. The extinctions predicted during snowball Earth and the evolutionary consequences are not supported by the available data. Apparently, there was no diversity bottleneck during Neoproterozoic low latitude glaciation, nor glacially induced radiation following the termination of glaciation. Interestingly, there are modern analogues that may be consistent with microbial life surviving a snowball Earth. Thus, the fossil record may not be used to constrain the existence of a snowball Earth, but rather that the original geobiological predictions were overstated.

Paleontologists generally develop a search image for their samples based on past experience and overlook strata that do not fit the preconceived image. Perhaps a more systematic sampling, although time intensive, would produce additional paleontologic data with which to evaluate the biosphere during snowball Earth. Indirect means of biosphere assessment, such as the inorganic carbon isotope record, are largely equivocal and are broadly consistent with several different snowball Earth hypotheses. While an immense amount of carbon isotopic data from carbonate has been collected in recent years that confirm the overall pattern of secular variation, it is not clear that these data alone are very useful to understanding life during snowball Earth. On its present course, our knowledge of the snowball Earth biosphere will not likely improve without the input of some new sources of data. Additional organic carbon isotope analyses would perhaps provide a better indication of the snowball Earth biosphere, in concert with the $\delta^{13}C_{carbonate}$ data. The $\delta^{34}S_{CAS}$ method appears highly promising and should be expanded to more sections (currently, data are available for three sections globally). Other means for checking the pulse of the biosphere should be developed and employed if we desire the field to move forward.

## 7. Note added in proof

Lithologic and biomarker evidence consistent with synglacial primary productivity and photosynthesis, corroborating our results presented here, has recently been reported in Neoproterozoic glacial deposits from Brazil (Olcott, A., Sessions, A., Corsetti, F.A., Kaufman, A.J., de Oliviera, T. F., 2005. Biomarker evidence for photosynthesis during Neoproterozoic glaciation: Science 310, 471-474).

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