

Review

The Location and Styles of Ice-Free “Oases” during Neoproterozoic Glaciations with Evolutionary Implications

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Received: 13 March 2012; in revised form: 10 April 2012 / Accepted: 17 May 2012 /

Published: 29 May 2012

Abstract: Evidence based on molecular clocks, together with molecular evidence/biomarkers and putative body fossils, points to major evolutionary events prior to and during the intense Cryogenian and Ediacaran glaciations. The glaciations themselves were of global extent. Sedimentological evidence, including hummocky cross-stratification (representing ice-free seas affected by intra-glacial storms), dropstone textures, microbial mat-bearing ironstones, ladderback ripples, and wave ripples, militates against a “hard” Snowball Earth event. Each piece of sedimentological evidence potentially allows insight into the shape and location, with respect to the shoreline, of ice-free areas (“oases”) that may be viewed as potential refugia. The location of such oases must be seen in the context of global paleogeography, and it is emphasized that continental reconstructions at 600 Ma (about 35 millions years after the “Marinoan” ice age) are non-unique solutions. Specifically, whether continents such as greater India, Australia/East Antarctica, Kalahari, South and North China, and Siberia, were welded to a southern supercontinent or not, has implications for island speciation, faunal exchange, and the development of endemism.

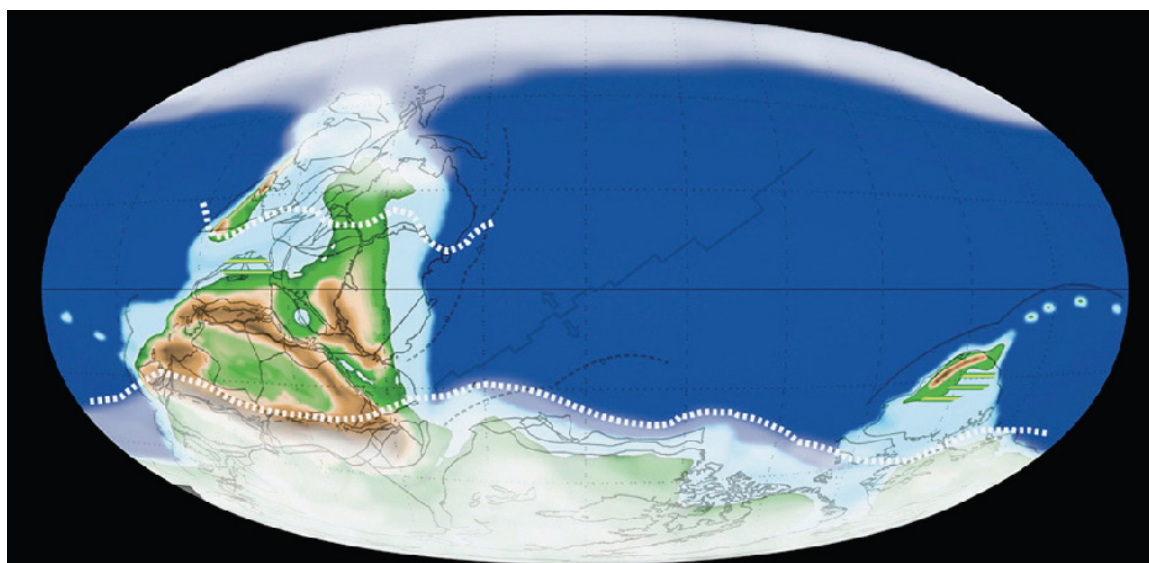
Keywords: Neoproterozoic; Snowball Earth; glaciation; evolution

1. Introduction

This paper reviews the style and likely location of ice-free “oases” that existed during severe Neoproterozoic glaciations, or Snowball Earth events [1,2]. Both Eyles and Januszcak [3] and Allen and Etienne [4] emphasize that the idea of a catastrophic global glaciation is not new, and can perhaps

be traced to the *Eiszeit* hypothesis of Louis Agassiz in 1837. One century on, based on his Arctic expeditions in the Spitsbergen archipelago beginning in 1948, W.B. Harland began to assemble evidence for a global Neoproterozoic glaciation, as summarized in his recent posthumous paper [5]. Four decades later, the evidence for Neoproterozoic glacial deposits on every continent was both comprehensively and succinctly documented by Mike Hambrey and Brian Harland in a benchmark tome entitled “Earth’s Pre-Pleistocene Glacial Record” [6]. In the decade that followed, Kirschvink had coined the term “Snowball Earth” [7] for the severe Neoproterozoic ice-house period in what is now known as the Cryogenian (850–635 Ma) (Figure 1). By the end of that decade, some interpretations of this Snowball Earth event became uncompromising; a vision of global ice cover affecting all of the planet at the same time, with geologically instantaneous meltback of the global ice sheets and deposition of “cap carbonates” in a greenhouse world [1]. Indeed, it has been suggested that global temperatures saw a swing from $-50\text{ }^{\circ}\text{C}$ during the glaciations to $+50\text{ }^{\circ}\text{C}$ following ice sheet decay and climate change into a “super-greenhouse” [2].

Figure 1. The image of an ice-encased Earth- a Snowball Earth, with oases of open water on which life could survive in refugia during a Neoproterozoic ice-house event? From Scotese (2009) [8], re-published with permission of the Geological Society of London.



The severity of the Cryogenian glaciations, together with their impact on life, has been vigorously debated. The glaciations themselves have been reviewed at length, with both a focus on sedimentary [4] and a holistic Earth systems approach [9] taken in recent years. The mechanisms to generate, or appear to generate, pan-glacial conditions as reviewed by Fairchild and Kennedy [9] include Snowball Earth itself, high obliquity/Earth tilt, the “Zipper Rift” model of diachronous glaciation during the rifting of Rodinia [3], and the “slushball Earth” compromise. This latter model is pertinent to the present paper as pockets of unfrozen water can provide the refugia for organisms that are required by advocates of the Snowball Earth theory [7].

At the turn of the 21st century, refugia for extremophiles were sought as an explanation for the survival of life during a “hard” Snowball Earth event (*viz.* a Snowball Earth with no free water on the surface and an arrested hydrological cycle) [2]. In particular, studies in modern high latitude glaciated

settings were undertaken in the hope that analogs for the Neoproterozoic icehouse world could be found. Vincent *et al.* [10] conducted work on the Ward Hunt ice shelf (Canada) and the McMurdo ice shelf (Antarctica), discovering communities of microbial mats in pools of meltwater on the ice shelves. These workers discovered that framework forming, photosynthetic, filamentous cyanobacteria provided a hospitable refuge for nematodes, flagellates, ciliates and rotifers. Cyanobacterial mats protect their communities from desiccation, freeze-thaw damage and also short-wavelength radiation. Collectively, the communities are frozen in a kind of stasis for almost all of the year, but are able to metabolize for days or weeks of the year during summertime [10].

At about the same time, McKay calculated that light can be transmitted through ice up to 30 m thick, and arctic lakes with ice 5 m thick harbor microbial life [11]. These findings provided a mechanism for life to continue under a “hard” Snowball Earth, with a realization that ice must still have been comparatively thin in places for photosynthesis to continue. Subsequently, based on biomarker evidence from black shales of the Vazante Group in Brazil, compelling evidence of photosynthesis during Cryogenian glaciation has been found [12].

From a theoretical point of view, there are several reasons why a snowball, rather than a slushball model (e.g., Figure 1) is, *a priori*, perhaps the most parsimonious climate scenario, which we shall elucidate below. Firstly, if a runaway ice albedo feedback of a sufficient extent has occurred to result in low latitude glaciation, the ice albedo feedback is required to stop before a hard snowball occurs. Under this scenario, there exists a maximum planetary albedo, and a minimum planetary temperature, which is not associated with increasing sea ice cover—despite the fact that lower albedo/higher temperature on the “way in” were associated with increasing ice cover. Modeling studies of slushball scenarios involve a range of assumptions about the hydrological cycle, such as low tropical evaporation/heat diffusion and the opacity of thin tropical sea ice [13], meridional diffusivity [14], cloud formation and heat transport [15]. The thin ice solution [13] requires a balance between basal freeze-on and sublimation on the sea ice surface, but this is difficult to achieve below comparatively mild temperatures (12 °C) [16]. Even hard snowball solutions may permit some refugia [17].

2. Impact of Global Glaciations on Evolution

2.1. Oxygenation

A substantial increase in free oxygen in the Earth’s atmosphere of between 10–5 and 10–2 times present atmospheric levels (PAL) [18] occurred at about 2.3 Ga: the so-called Great Oxygenation Event [19]. Bao *et al.* report that some glaciolacustrine limestones from the Wilsonbreen Formation of Spitsbergen show unusually depleted levels of the oxygen isotope ^{17}O [20]. These data, they argue, provide the first independent evidence pointing to a CO_2 -rich atmosphere during Snowball Earth. In this respect, the Cryogenian glaciations may bear some comparison to the Hirnantian glaciation of North Africa, where expansion of continent-scale ice sheets occurred in spite of CO_2 partial pressures elevated to 14 times their present value [21]. The high CO_2 values do not, of course, preclude the evolution of animals if oxygen levels were sufficiently elevated. The results of [19] allow a tentative link to be made between Paleoproterozoic glaciations and oxygen in the atmosphere. Based on time series data from multiple sulfur isotopes, together with sulfides from Transvaal Group sediments, it

can be argued that during the ~2.3 Ga Great Oxygenation Event, the release of free oxygen into the atmosphere enabled it to react with methane to produce the far less potent greenhouse gas CO₂ [19]. Given that a second major oxygenation occurred at the end of the Cryogenian [22], the so-called Neoproterozoic Oxygenation Event [23], it is possible that there may be a connection between oxygenation and the initiation of Cryogenian ice ages.

2.2. The Physical Fossil Record

Stromatolites, which first appeared in the early Archaean, experienced an increase in number and an increase in diversity, peaking between the mid Mesoproterozoic (1.35 Ga) to the late Cryogenian (~635 Ma) [24,25]. Acritarchs first appeared at about 3.2 Ga [26] and saw a gradual increase in diversity of forms and number throughout the Mesoproterozoic and Neoproterozoic [27,28]. Like the stromatolites, the acritarchs may have faced major pressures during the Cryogenian glaciations, but bounced back with a major explosion in biodiversity in the Ediacaran [29] (Figure 2). In Cryogenian assemblages, large acritarchs and complex acanthomorphic varieties with distinct peripheral processes are rare, suggesting that these forms, at least, suffered significant losses during the Cryogenian [28].

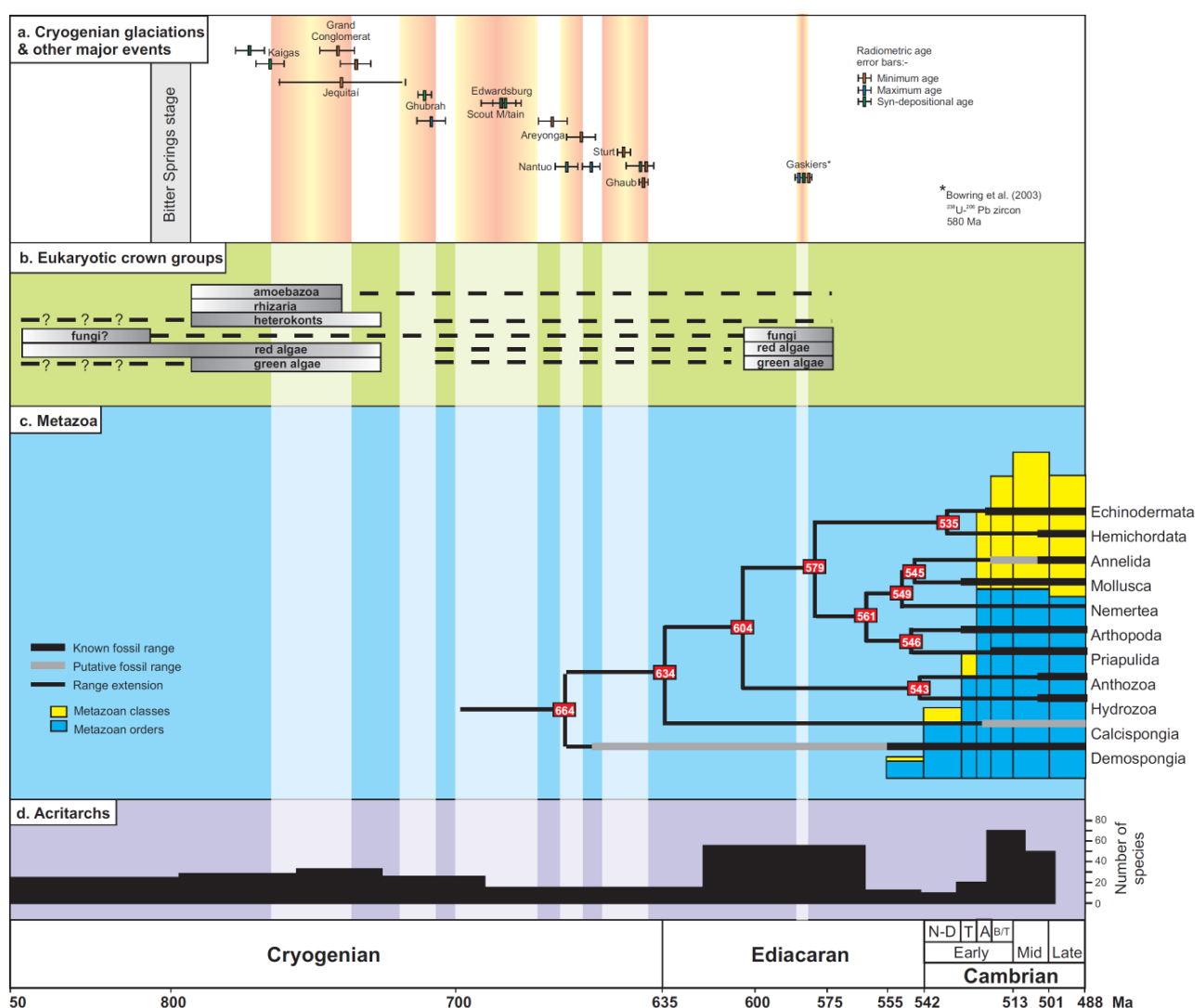
The coincidence between the appearance of Ediacara-type fossils in the rock record and Earth's recovery from major glaciations has been well documented [2] (Figure 2). During slowdown of the hydrological cycle, "evolutionary bottlenecks" are predicted under a snowball state [30]. Such bottlenecks presumably also affected eukaryotic crown groups other than the metazoa: notably the amoebozoa, rhizaria and heterokonts, as well as the algae, which were all well established prior to the first wave of Cryogenian glaciations [31–33] (Figure 2).

Whilst the fossil record clearly shows that several major photosynthetic clades, including green, red and chromophyte algae had also evolved and diversified well before the Cryogenian glaciations [34–36] (Figure 2), unambiguous animal fossils have not been documented in Cryogenian strata. Recent finds of discoidal structures discovered in Kazakhstan, of the type once argued to be molds of ancestral sea pens, are openly acknowledged to be of very uncertain origin: "it is possible (even probable?) that the discoidal fossils.....represent something other than metazoa and our >766 Ma age will lend support to those who wish to argue for a bacterial, lichen, Vendobiont, or non-biogenic for the impressions" [37] (Figure 2). However, amorphous structures have been interpreted as possible sponge ancestors from the Brachina Formation of South Australia [38]. Putative sponge ancestors are also described from the Cryogenian of the Damara Belt, Namibia [39], whereas possible early foraminera are also reported from the Rasthof Formation of northern Namibia [40].

The first purported fossil embryos first make their stratigraphic appearance, in Chinese strata, at about the same level as the famous Ediacara fossils in correlative South Australian strata [41–44]. The interpretation of microfossils as embryos, and eggs, is very controversial, and alternative interpretations that some of these forms are giant sulfur-oxidizing bacteria [44] have been proposed. Furthermore, owing to the general absence of late-stage developmental forms in some assemblages, an alternative interpretation may be that some clusters of cells represent non-metazoan holozoans [45]. Indeed, if the interpretation of Ediacaran microfossils seems fraught with difficulty, given that some can be reinterpreted as giant microbes, then problems also exist for recognizing the evidence for microbial forms themselves. Schopf *et al.* gave a detailed review of the difficulties of distinguishing true fossils

from pseudo-fossils produced by inorganic processes [46], highlighting the multidisciplinary approach needed in their analysis.

Figure 2. Evolutionary events in the Neoproterozoic plotted against the rhythm of glaciation. Data explanation of rows as follows. **(a)** The age ranges of named glaciations are based on minimum, maximum, and syn-depositional ages, from radiometric datasets with an error range. These data are tabulated in [4]. Age of the Gaskiers glaciation, constrained to start and finish within a 1 Ma timeframe, after [32]. The red/yellow vertical strips correspond to inferred major pan-glacial phases, considered the most likely yet, it is stressed, non-unique solution to the age range distribution [4]; **(b)** Eukaryotic crown groups—these are shown by appearances in the fossil record (in grey boxes) and inferred stratigraphic continuation (dashed lines). Data from [31]; **(c)** Metazoan branching and timing thereof from a single common animal ancestor believed to extend at least as far back as 700 Ma. Data based on molecular clocks and reproduced from [33]; **(d)** Distribution of acritarchs diversity over time, after [27] and [28]. Note the plunge in biodiversity during the interval affected by a wave of Cryogenian glaciation, and subsequent recovery into the Ediacaran.



2.3. The Molecular Clock Record

In their review of the events leading up to the appearance of animals, Peterson *et al.* concluded that the “Cambrian explosion was the inevitable outcome of the evolution of macrophagy near the end of the Marinoan glacial interval” [33]. These workers published an evolutionary tree showing their envisaged tempo of evolution, with the nodes of animal groups placed on the basis of molecular clock estimates [33] (Figure 2). Several significant node events were postulated, and the coincidence between radiometrically-dated glaciations and evolutionary events is at its clearest in the molecular clock data. These events were:

- (1) Branching from a node at about 664 Ma in the mid Cryogenian to yield the Demospongia.
- (2) At 635 Ma, a node yielding the Calcispongia. This divergence is almost exactly coincident with the Ghaub glaciation in northern Namibia, which has been robustly dated using the Pb-Pb technique on an ash bed [47].
- (3) Splitting of the common lineage at 604 Ma, giving rise to two further branches of hypothetical metazoan ancestors.
- (4) A very significant node at 579 Ma, roughly coincident with the Gaskiers glaciation, just before the appearance of the oldest frondose-bearing Ediacaran *Lagerstätte* at ~575 Ma (in the Drook Formation, Newfoundland) [32].

Based on their molecular clock data, [33] envisage a common ancestor stretching back to ~700 Ma. In this interpretation, a much younger common ancestor for animals is proposed than [48]. Indeed, the latter workers suggest that vertebrates diverged from chordates at about 1 Ga.

2.4. The Molecular Fossil Record

Molecular fossils are chemical residues interpreted as either (1) directly derived constituents of life, (2) their excreta, or (3) “daughter” constituents modified by diagenetic alteration. Their presence, in the absence of body fossils, gives greater clarity to the nature of Cryogenian microbial ecosystems. Glacial diamictites of the Vazante Group, São Francisco Basin, Brazil, are $>740 \pm 22$ Ma, based on Pb-Pb isochrons from aragonite pseudomorphs in their overlying cap carbonates of the Sete Lagoas Formation [49]. The diamictites are intercalated with inter-glacial black shales that contain up to 3% total organic carbon [12].

A suite of molecular fossils have been successfully extracted from the Vazante Group shales. These include 2-methyl-hopanes, which derive from cyanobacteria, and alkylated 2,3,6 trimethylbenzenes, from green sulfur bacteria [50]. The latter are anaerobic and use H₂S for photosynthesis in an oxygen-depleted, hydrogen sulfide-rich photic zone [51]. Gammacerane (a C₃₀ triterpane) is also found, and is thought to derive from a protozoan tetrahymanol [52] produced by a predator of green and purple sulfur bacteria. Steranes, not methylated at C-4, were also recovered: these are exclusively associated with aerobic eukaryotes and may represent an algal contribution in the organic matter.

To summarize, the inter-diamictite shale intervals of the Vazante Group reveals the presence both of photosynthetic bacteria and eukaryotes, in a stratified ocean with oxic surface waters, yet euxinic conditions in the photic zone [12]. The molecular fossils hence illustrate the existence of sea-ice-free conditions in at least some areas and at some times either during, or between, glaciations [12].

Molecular fossil biomarkers have also been recovered by [53] from the late Cryogenian of Oman, from the Ghadir Manquil Formation of the Huqf Supergroup, stratigraphically below the deglacial “cap carbonate” succession. There, biomarker evidence includes steranes, which are proxies for eukaryotes, the affinity of which is typical of the Demospongiae. These biomarkers suggest that the first animals evolved prior to the end of the Marinoan glaciation at about 635 Ma [53].

2.5. Strikes of Extinction and Adaptive Radiations

Possible insight into the response of late Neoproterozoic ecosystems to glaciation might be provided by the analog of the Hirnantian glaciation of North Africa, which represents the earliest expansion of major ice sheets in the Phanerozoic. The glaciation was associated with two mass extinction “strikes”, collectively representing the second largest in Earth’s history and the first of the “big five” of the Phanerozoic [54]. Both extinction “strikes” are calibrated against the oxygen isotope record, with the first associated with enrichment in $\delta^{18}\text{O}$ values as a result of ice sheet growth, and a dilution in $\delta^{18}\text{O}$ values as a result of ice sheet decay [55].

The first strike of Hirnantian extinction saw the destruction of shelfal habitats as North Gondwanan ice sheets expanded to the shelf edge. The extinction affected not only benthic, but also pelagic organisms, notably the graptolites. The second wave of extinction occurred an estimated 0.5 Ma later [56], and is believed to have been the result of rapid, global eustatic sea level rise, killing off a second collection of genera in their refugia, almost eliminating the graptolites [55]. Indeed, a full recovery of the marine ecosystem, with clades recovering to their pre-glacial levels, did not occur until about five to ten million years later in the late Llandovery [57]. An adaptive radiation of specialized forms of brachiopod, the so-called Hirnantia fauna, occurred in response to climatic cooling and these forms populated high paleo-latitude, ice proximal areas [58].

In the Cryogenian, by comparison, metazoan fossils are vigorously debated, and communities more primitive, and hence the assertion that ecosystems responded in a comparable manner to those in the Hirnantian crises is a great oversimplification, if not an overstatement. However, as noted above, acritarchs did appear to respond to environmental pressures during Cryogenian glaciations (Figure 2). Acanthomorphic acritarchs are interpreted as indicative of nearshore environments [59]: should this interpretation extend to all Neoproterozoic acritarchs, then their adaptation to deep “blue-water” refugia (*i.e.*, ice-free tropical areas) during glaciations [30] seems very likely. If this is the case, then the acanthomorphic acritarchs may show evidence of improvisation under environmental pressure.

Following the Gaskiers glaciation in the Ediacaran (Figure 2), a switch to oxygenated deep ocean floors appears to have occurred with implications for nurturing the deep benthic Ediacara fauna. These conclusions are based on iron extraction techniques—fundamentally the low ratio of highly reactive iron to total iron, in the Ediacaran strata in Newfoundland [22]. It is thought that the newly oxygenated conditions paved the way for the Ediacara fauna, with a low diversity assemblage established some 5 Ma following the Gaskiers glaciation, succeeded by a much more diverse assemblage later in the Ediacaran [22] (and refs. therein).

3. The Concept of and Evidence for Ice-Free Oases

An intriguing problem that remains is the style of refugia for organisms during glaciations. Even if the latest candidates for the earliest animal fossils [37–39] are unsupported by further investigation, the most conservative molecular clock analyses postulate the existence of the common ancestor at about 700 Ma [33]. Thus, since simple metazoa were probably in existence during the Cryogenian glaciations, suitable refugia must be found for them. Oxygenation of the ocean floor below the photic zone is evident at 580 Ma following the Gaskiers glaciation (*i.e.*, in the Ediacaran) [22], but it is not clear whether the deep marine environment would have been oxygenated earlier, in the Cryogenian. If this was the case, then available refugia would have been significantly more extensive during the glaciations. Below, we discuss the role of paleocontinent configuration, and review recent sedimentological data for ice-free areas.

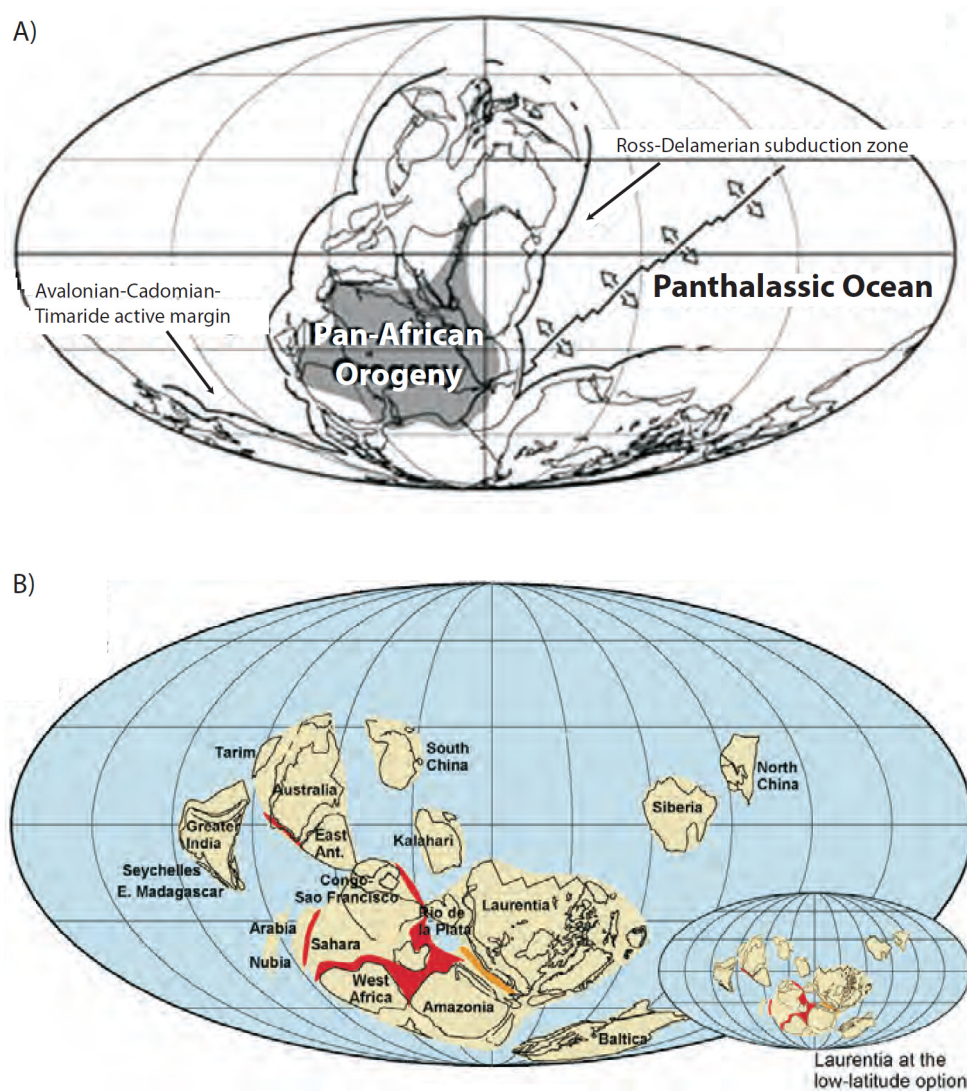
3.1. Numerical Modeling and Paleogeographic Reconstructions

Hyde *et al.* were the first to propose that, on the basis of a coupled ice-sheet/ climate model, ice-free pockets may have existed at equatorial latitudes during Snowball Earth intervals [15]. Using energy-balance models and general climate circulation models, these workers simulated the extent of ice for the ~590 Ma “Varanger” glaciation, albeit based on the paleogeography of 545 Ma and earlier published in [60]. Hyde *et al.*’s interpretation [15] subsequently became popularized as depicting a Slushball Earth state [9], and was the first to propose a “soft” Snowball Earth scenario. Subsequent hints at ice-free conditions at the equator have also been depicted more recently in more modern paleogeographic reconstructions, albeit with the admission that their construction for the Snowball Earth periods, and presumably therefore ice sheet extent, is a “very difficult task” [8]. As such, it seems reasonable to state that there have been many strong paleogeographic hints for the absence of sea ice at low paleolatitudes, but no firm evidence based on those datasets.

An important issue is the distribution of the continents with respect to one another, in the context of a very sparse paleomagnetic dataset for the Cryogenian [7,60]. An understanding of distribution of continents is important for two reasons. Firstly, as a result of their weathering, cratons and islands alike supply nutrients to marine ecosystems. Second, the positions of nutrient-rich thermohaline currents might be postulated. On the basis of Parsimony Analysis of Endemism (PAE) studies, the Ediacara fauna have played an important role in testing latest Neoproterozoic plate reconstructions [61,62]. Few to no latitudinal diversity gradients are acknowledged in most cases, although “tubular” Ediacaran forms were confined to equatorial areas. The isolation of marine ecosystems, due to their separation by vast oceans, and the role of this separation in producing very distinct taxa, was illustrated by the work of C.D. Walcott in the early 20th century in his comparison of Laurentian and Avalonian trilobites in the Cambrian. Perhaps the same is true of simple ecosystems in the Cryogenian. Taking an Ediacaran timeslice at 600 Ma, about 20 million years before the “Gaskiers” glaciation, one can appreciate distinct differences in the global paleogeographic reconstructions of [8] and [63] (Figure 3). The former model depicts Baltica and Laurentia forming the core of Rodinia at high southern hemisphere latitudes, and all other landmasses adjoined to the supercontinent, albeit with the existence of epicontinental seaways (Figure 3). The latter model, by contrast, envisages a totally separate North

China, South China, Siberia, Kalahari and Greater India, strewn out in northern hemisphere equatorial latitudes, with Australia and east Antarctica also barely in contact with the southern supercontinent (Figure 3). This latter reconstruction, representing an interval through which the Ediacara fauna appeared, does not exclude the possibility that separate populations, separated by ocean basins, evolved. Meanwhile, the Scotese model for 600 Ma implies that faunal exchange across a vast epicontinental shelf area would likely occur.

Figure 3. Two contrasting paleogeographic visions for a common interval at 600 Ma (early Ediacaran). (A) The Scotese model [8]; (B) The Li *et al.* reconstruction [63].



Smith and Pickering [64] hypothesized that the presence of oceanic seaways were critical to the initiation of major glacial phases during the Phanerozoic. Citing several examples, they argued that the opening of straits (such as the modern day Bering Strait in southern South America) contributed to the thermal isolation of polar continents by increasing the vigor of high latitude thermohaline currents around continental margins. Given the paleogeographic uncertainties discussed above, it is difficult to comment whether such seaways were instrumental in initiating Cryogenian glaciations, although they would almost certainly be a major source of nutrients to support life. Secondly, contingent on more

robust paleogeographic reconstructions being available in future, an understanding of the influence of trade winds on bioproductivity may be possible. For example, the modern day coast of Mauritania is an upwelling zone in the Atlantic where NE trade-winds blow the warm coastal waters seaward. These are replaced by cool waters rich in phosphate and nitrate, stimulating blooms of phytoplankton, and in turn zooplankton and fish feeding in a system that is active throughout the year, e.g., [65].

3.2 Subglacial Lakes and Pressure-Melting “Oases”

The east Antarctic ice sheet is underlain by vast subglacial lakes, resulting from the combined effects of pressure melting and locally elevated geothermal heat fluxes [66]. Such lakes both lubricate and initiate fast flowing ice streams [67]. In 1998, Vostok hole 5 G was drilled by a team of Russian, French and US scientists through the modern east Antarctic ice sheet, terminating at a depth of 3650.2 m beneath the ice surface [68]. In the following year, coccoid and rod-shaped bacteria were extracted from accreted ice at the base of the ice sheet that were considered to be surrogate evidence for microbial life in Lake Vostok [69]. Pressure melting is believed to keep Lake Vostok liquid at -3°C but basal freeze-on occurs in areas of lower subglacial pressure, accreting pristine, microbe-bearing ice to the basal part of the ice sheet [66].

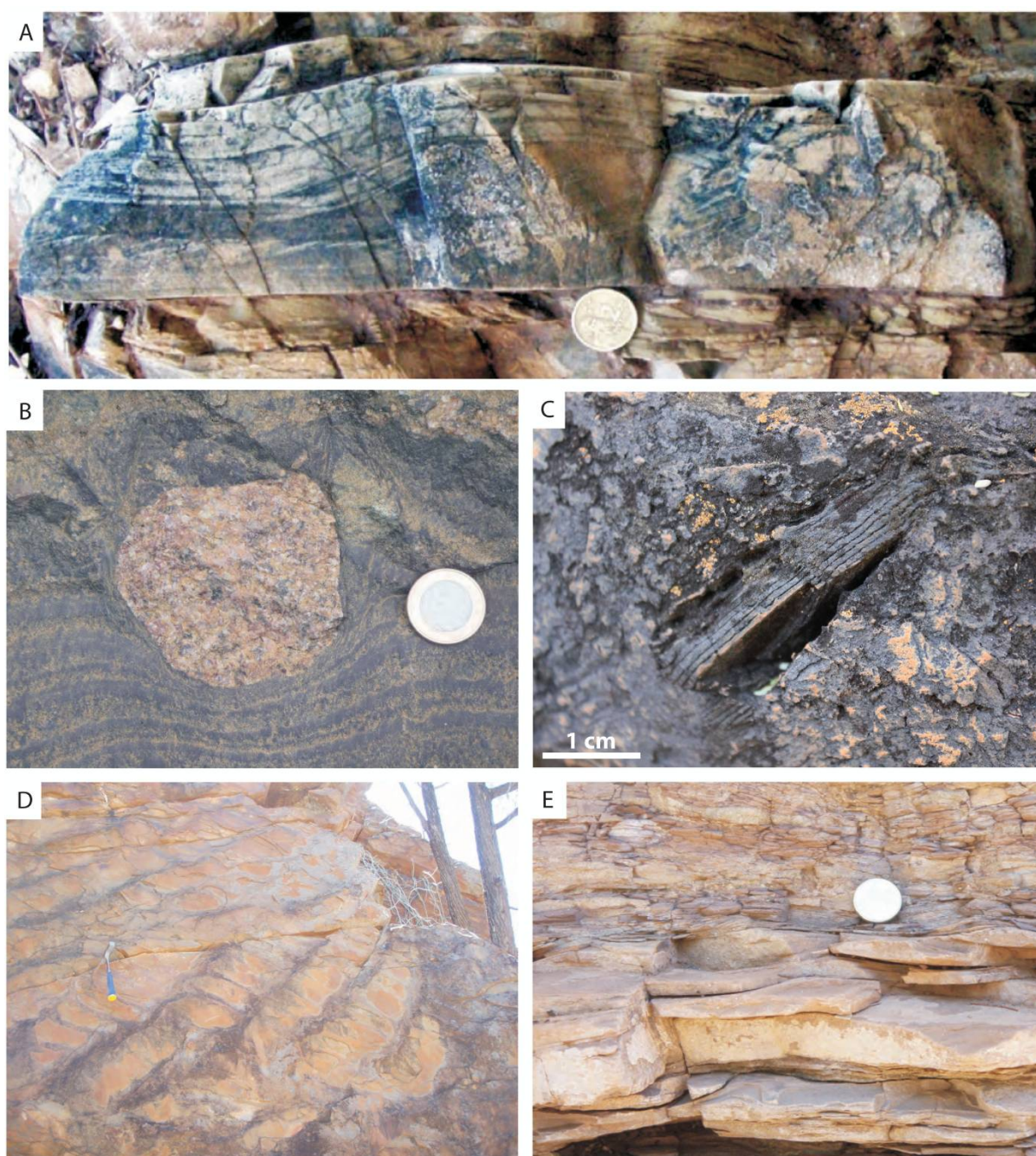
Given the existence of endemic, microbial life forms in basally accreted ice in Vostok 5G, and presumably the subglacial lake itself [69], pressure-melting “oases” offer an intriguing possibility for the survival of life during Neoproterozoic pan-glacial conditions. In the Late Ordovician paleo-glaciological record of North Africa, evidence for “pure” ice streams, resulting from the lateral flux of ice, includes mega-scale glacial lineations, which probably require the presence of a water film to form [70]. These structures, therefore, enable the effects of pressure melting to be inferred in the ancient paleo-glacial record. Under a “hard” Snowball Earth, these meltwater films could represent refugia. Similar structures have not yet been observed in Cryogenian strata, probably owing to the limitations of the sedimentary record, although candidate ice streams have been postulated [71].

4. Sedimentological Evidence for Ice-free “Oases”

The sedimentological argument against a “hard” Snowball Earth is now well rehearsed [72], and includes evidence for ice waxing and waning cycles or parasequences [73], dropstone-bearing diamictite sequences intercalated with non-glacial deposits [74], and most simply the thickness of the diamictites themselves [75]. However the specific impact of glacial processes on simple ecosystems is less well understood. Some of the evidence for thin-ice or ice-free conditions is shown on Figure 4, and discussed in detail below.

Both [76] and [4] emphasized the uniformitarian nature of Neoproterozoic glaciations, with dynamic ice masses delivering sediment to ocean basins. In order for a flux of ice to occur, topography must exist on the ice surface. In order for ice flowage to take place, ablation of tidewater ice sheets is necessary, in addition to a steady supply of snowfall in the accumulation areas in the highlands. A number of parasequences, or stacked coarsening upward sequences that record repeated intervals of ice sheet advance interspersed with stillstands, were identified in Omani Cryogenian successions [4]. During the stillstands, localized ice sheet melting may have occurred, and in these stillstands, organic rich black shales were deposited [12].

Figure 4. Sedimentary features that illustrate ice-free or discontinuous ice conditions in Cryogenian glacial successions. **(A)** Hummocky cross stratification in sandstones of the Wilyerpa Formation, central Flinders Ranges, Australia; **(B)** Granite lonestone, interpreted as an ice-rafted dropstone, in the Bebedouro Formation of the Chapada Diamantina, Brazil; **(C)** Microbial laminate-bearing ironstone within the Chuos Formation, Ghaub Farm, Otavi Mountainland of Namibia; **(D)** Ladderback ripples on a dipping sandstone surface in the Elatina Formation, Warren Gorge, South Australia; **(E)** Wave ripples in sandstone in cross section, immediately above the basal diamictite of the Elatina Formation, Bulls Run, central Flinders Ranges, Australia. All photos by D. Le Heron; photo A is taken from [72].



In east Svalbard and east Greenland, latest Cryogenian glacial deposits are punctuated by limestones of the Slangen Member, bearing mudcracks [77] and interpreted as sabkha-like deposits [17]. These

are sandwiched between lonestone-bearing shales of the MacDonaldryggan Member below and intercalated sandstones and diamictites of the Wilsonbreen Member above. The presence of the limestone member is reconciled with the Snowball Earth by invoking a landward-dipping slope, and a sill onto which sea ice (a “sea glacier”) was attached [17]. Onshore-directed winds resulted in sublimation of the ice between the main glacier and the sea ice, resulting in a so-called “sikussak” oasis [17]. This interpretation has recently been retracted [78].

In the Chuos Formation of northern Namibia, microbial laminites are present as clasts in ironstone intervals, where they are sandwiched between diamictites of the Chuos Formation, northern Namibia Figure 4C. Either the microbial laminites represent primary precipitation of iron, such as that observed in modern acid mine drainage environments [79] or, alternatively represent clasts derived from (a) debris flows or (b) sea-ice fallout. The development of extremophile bacterial communities beneath modern sea ice has been well studied [80–83], but the potential for carbonate fixing in such environments is unclear.

In southern Australia, a wealth of evidence exists for dynamic ice sheets and the existence of “oases” on a Snowball Earth. The type area of the so-called Sturtian glaciation [2] occurs in the Adelaide Fold Belt. Evidence for glaciation was first published in 1908 [84] and the significance of lonestones of exotic clasts within pelites, interpreted as ice-rafted debris, is also long since established [85,86]. The central Flinders Ranges, at Holowilena, [72] document the occurrence of hummocky cross-stratification within a 5 km thick sequence, recording the advance and recession of Sturtian ice sheets. Hummocky cross-stratified sandstones (Figure 4A) are interpreted to record deposition upon a storm-agitated sea floor, either through pure oscillatory motion or combined flows involving an oscillation with a geostrophic component superimposed [74,87]. In South Australia, hummocky cross-stratified sandstones were recorded below a 500 m thick succession of lonestone-bearing pelites, some 2 km below the Tindelpina Shale Member where the absence of lonestones has long been recognized to record the termination of the Sturtian glaciation [85]. Because the formation of hummocky cross-stratification requires the “coupling” between storm waves and the sea floor [72], it is argued that sandstones bearing these structures offer the strongest evidence yet for ice-free conditions during the Sturtian glaciation.

Dropstones (Figure 4) are common in shale-prone successions throughout the South Australian record. They are also globally ubiquitous in Cryogenian glacial successions of South America, North America, Arctic and mainland Europe, Asia, Africa, Australia and Antarctica [6,88]. The dropstones certainly represent the disintegration of debris-laden ice. Their ambiguity, however, revolves around (1) the extent to which debris is glacially entrained, as opposed to passively entrained by sea ice, and (2) whether they form part of a glacial retreat, glacial advance, or glacial stillstand succession. Note that in the case of the “sikussak” oasis model developed for the Svalbard sections [17], an alternative interpretation based on the stratigraphic relationship between the dropstone-bearing shales (MacDonaldryggan Member) below and the limestone and sabkha deposits above (Slangen Member) is that the dropstones were shed from an iceberg armada as Earth entered a snowball interglacial. In South Australia, dropstone-bearing intervals are clearly associated with a glacial re-advance stratigraphic motif in the Holowilena area [72].

Ladderback ripples (Figure 4D) form in intertidal environments, and they are extremely well preserved in the Elatina Formation of Warren Gorge, South Australia [89]. A primary set of ripple

crests develop either through wave or current agitation under subaqueous conditions (during high tides). As the tide recedes, the sediment surface is largely exposed, but remaining water on intertidal sandflats drains seawards between the crests of the ripples. In doing so, a secondary set of ripple crests form, producing ladderback ripples such as those spectacularly preserved in the Elatina Formation, South Australia (Figure 4D). The presence of ladderback ripples demonstrates an incomplete ice cover of intertidal ice on sand flats during the late Cryogenian glaciations [90]. Wave ripples, as discussed above, are clear sedimentary evidence for ice-free oases in the Huqf of Oman [4], but are also clearly expressed in the Elatina Formation (Figure 4E) where, significantly, they occur directly above the basal diamictite [89,90]. These observations demonstrate that meltwater produced early on in the Elatina glaciation drained with access to the open air, illustrating that ice was locally absent. This complements the interpretations of [72] that ice-free conditions persisted in the early Cryogenian (Sturt) glaciation of South Australia. Moreover, the presence of wave ripples demonstrates the absence of sea ice early on in the Elatina glaciation and hence further evidence for ice-free oases in this younger Cryogenian glaciation. The stratigraphic position of these wave ripples most likely indicates the occurrence of ice-free conditions during the waxing phase of glaciation.

A suite of other sedimentological structures is also well known from the Port Askaig Tillite of the Cryogenian age in western Scotland that likely imply ice-free conditions. Large-scale cross-beds, interpreted to represent subaqueous simple and compound barforms of probable subtidal origin in a shelf setting, are intimately associated with diamictites and conglomerates [91]. The open shelf tidal bars occur within, and not at the top of, the Port Askaig Tillite, implying gradual ice meltback and re-advance behavior rather than catastrophic ice sheet retreat [91].

Thus far, no systematic attempt has been made to catalogue the distribution of the facies indicative of thin sea ice, or ice-free conditions, on a global scale, although huge strides have been made to catalogue the current state-of-the art in the Neoproterozoic glacial world by the encyclopedic work on Neoproterozoic glaciations by Arnaud, Halverson and Shields-Zhou [87]. The stratigraphic distribution of hummocky cross-stratified intervals could, for example, be used to infer mega-regional oases or ice-free zones, provided that temporal resolution of the datasets is sufficient. The recent review of Allen and Etienne ([4]; see Figure 2) pointed out quite clearly that this is not yet possible. Nevertheless, it is hoped that a trend toward increasingly better-constrained Cryogenian stratigraphic successions on each continent may allow the areas of open ocean to be mapped on the basis of these facies types, independently of any preconceived notion on ice extent. Given that intense glaciations may have stimulated altruism, increasing the evolutionary likelihood of macroscopic life [92], these efforts may lead to a better understanding of life-supporting oases in the Cryogenian icehouse world.

5. Conclusions

There is a complex relationship between the fossil record and late Neoproterozoic glaciation. Recent evidence for mid Cryogenian, Ediacara-like discoids from Kazakhstan [36] and shelly fossils possibly of sponge reef derivation in Australia [37] must be tested rigorously. If confirmed, suitable refugia must be found for them as they represent evidence for metazoa prior to branching from a common ancestor, at least based on molecular clock analyses [32].

It is suggested that the analogue of the Hirnantian (~443 Ma) glaciation and deglaciation of Gondwana, in terms of its influence on the biosphere, may have some use in understanding evolutionary pressures and the location of evolutionary “sweetspots” during a Neoproterozoic ice-house event. The analogue can only be partial since major animal groups had evolved by the latest Ordovician, but the glaciation is also the soonest major glaciation after the Gaskiers event. Extinctions during ice advance to the shelf edge are inferred, resulting from decimation of habitat, squeezing life to the shelf edge. Evolutionary adaptation of life to ice house conditions, in the Hirnantian, gave rise to specialized forms, which then died out as the ice melted under a new wave of mass extinction.

Deglaciation appears to have given rise to new forms both after the Ghaub glaciation and the Gaskiers glaciation but there was a delay of about 5 Ma before the first appearance of soft-bodied animals in the Ediacaran strata of Newfoundland [21]. The length of this delay is comparable to the full ecological recovery of the Silurian oceans following Hirnantian deglaciation [57].

The configuration of the continents, at a 600 Ma time slice (20 Ma prior to the Gaskiers glaciation), remains uncertain. The precise linkage between shallow seas, land bridges, and in particular the putative location of life-giving thermohaline currents is indeterminable from the present dataset. Certainly, models that argue for separate landmasses at equatorial latitudes favor speciation in “island-like” ecosystems, whereas models favoring single continents do not.

The sedimentological data for thin ice or sea-ice-free conditions has, until quite recently, been largely overlooked. The data includes the presence of thick diamictite successions, wave rippled sandstones, ladderback rippled sandstones, hummocky cross-stratification, intra-diamictite ironstones with microbial structures, and non-glacial facies such as limestones. It is suggested that, provided a sufficiently robust chronostratigraphic framework develops, the global recognition of these structures, and their systematic mapping, may allow mega-regional areas of open water to be located.

Acknowledgments

A critical pre-review of this work by Erwan Le Ber improved an initial version of the manuscript, and the author benefited from the critical eye of Richard Boyle and four anonymous reviewers.

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