

Neoproterozoic Glaciations and the Fossil Record

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Sedimentary, geochronological, and $\delta^{13}\text{C}$ chemostratigraphic data require that at least three glaciations—the Sturtian, Marinoan, and Gaskiers in geochronological order—occurred in the Neoproterozoic glacial interval (NGI; ca. 750–580 Ma); at least the Gaskiers glaciation has not been demonstrated global in nature. Available radiometric and $\delta^{13}\text{C}$ chemostratigraphic data also suggest that the fossil-rich Doushantuo Formation may have been deposited after the Marinoan but before the Gaskiers glaciation, thus representing a window between two glaciations. A review of the fossil record under this geochronological framework reveals the following patterns: 1) a broad decline in stromatolites and acritarchs occurred in the Cryogenian (ca. 750–600 Ma); 2) a taxonomically unique assemblage of large acanthomorphic acritarchs occurs between the Marinoan and Gaskiers glaciations; 3) multicellular algae diversified after the Marinoan glaciation, although they evolved earlier; 4) animals, probably in microscopic forms, evolved before the Gaskiers glaciation if not earlier; and 5) post-Gaskiers diversification of complex Ediacaran organisms/animals may have begun in deep-water slope environments and later expanded to shallow-water shelf environments where macrobilaterians and biomineralized animals first appeared. It is hypothesized that 1) the Cryogenian decline in stromatolites and acritarchs may have been causally related to glaciations; and 2) acanthomorphic acritarchs, algae, and animals may have suffered diversity loss related to the Gaskiers glaciation. The fossil record also implies that 1) at least some lineages of different algal clades survived all Neoproterozoic glaciations; and 2) some members of the animal clade survived the Gaskiers glaciation, probably in non-glaciated refugia.

1. INTRODUCTION

The causes, consequences, magnitude, and number of Neoproterozoic glaciations have been controversial [Kirschvink, 1992; Kaufman *et al.*, 1997; Hoffman *et al.*, 1998; Kennedy *et al.*, 1998; Hyde *et al.*, 2000; Kennedy *et al.*, 2001a; Kennedy *et al.*, 2001b; Hoffman and Schrag, 2002]. Nonetheless, the global distribution of Sturtian and Marinoan glaciogenic

deposits [Hambrey and Harland, 1981; Deynoux *et al.*, 1994] and the demonstrably low paleolatitude of some glaciated continents [Schmidt and Williams, 1995; Evans, 2000] indicate that these glaciations dwarf their Phanerozoic counterparts. Glaciation events of such magnitude are expected to have had significant impacts on biological evolution, causing biological extinctions followed by post-extinction recoveries and radiations. As yet, however, no carefully designed paleontological tests for these extinctions have been carried out. The delay stems from several obstacles. First, the geochronological resolution of many Neoproterozoic successions is poor, and as a result the precise temporal relationship between Neoproterozoic glaciations and evolutionary events has been elu-

Book Title
Book Series
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10.1029/Series#LettersChapter#

sive. Second, the Neoproterozoic fossil record is sketchy, and the phylogenetic interpretations of many Neoproterozoic fossils have been controversial. In the past few years, however, both the Neoproterozoic fossil record and geochronological resolution have been significantly improved, allowing a closer examination of the paleontological record in the broad context of climate changes. In this paper, I attempt to review currently available stratigraphic, geochronological, and paleontological data to bear on the relationship between Neoproterozoic glaciations and biological evolution. It is not the purpose of this paper, however, to differentiate among the end-member scenarios of Neoproterozoic glaciations [Hoffman *et al.*, 1998; Hyde *et al.*, 2000], although the proposed glaciation scenarios will have to eventually account for the paleontological record.

2. NEOPROTEROZOIC GLACIATIONS

As mentioned above, one of the key obstacles in the current analysis is the poor understanding of the temporal relationship between Neoproterozoic glaciations and the fossil record. In particular, the number of Neoproterozoic glaciogenic has been controversial [Kaufman *et al.*, 1997; Kennedy *et al.*, 1998; Halverson, 2002; Hoffman and Schrag, 2002; Bowring *et al.*, 2003; Rice *et al.*, 2003]. Kaufman *et al.* [1997], for example, argue that there may have been as many as five Neoproterozoic glaciations. Kennedy *et al.* [1998], on the other hand, recognize only two Neoproterozoic glaciations—the older Sturtian and younger Marinoan glaciation. Others [Brasier *et al.*, 2000; Brasier and Shields, 2000; Knoll, 2000; Corkeron and George, 2001; Zhou *et al.*, 2001; Halverson, 2002; Hoffman and Schrag, 2002; Bowring *et al.*, 2003; Rice *et al.*, 2003] suggest that at least three glaciations occurred in the Neoproterozoic. Below, I summarize our recent work in the Quruqtagh area [Xiao *et al.*, *in press a*] and in South China [Xiao *et al.*, 2003] that bears on the number of Neoproterozoic glaciations.

2.1. Quruqtagh

The Neoproterozoic Quruqtagh Group [Norin, 1937] in the Quruqtagh area, eastern Chinese Tianshan, is a >3 km thick, predominately siliciclastic succession. It consists of, in ascending order, the Bayisi, Zhaobishan, Altungol, Tereeken, Zhamoketi, Yukkengol, Shuiquan, and Hankalchough formations (Figure 1; [Gao and Zhu, 1984]). The Quruqtagh Group is bracketed between early Neoproterozoic stromatolitic dolomite and Early Cambrian (pre-trilobite Meishucunian to be exact) cherts and phosphorites. Diamictites exist in the Bayisi/Altungol, Tereeken, and Hankalchough formations. Large boulders set in silty matrix are common in all three diamictite formations, but unambiguous evidence for

glacial activities only occurs in the Tereeken and Hankalchough diamictites. Previous investigators interpreted these diamictite intervals as recording three Neoproterozoic ice ages in Quruqtagh [Gao and Zhu, 1984; Gao and Qian, 1985; Brookfield, 1994]. Our field investigation only confirms the glaciogenic nature of the Tereeken and Hankalchough diamictites; the Bayisi/Altungol diamictites may or may not be glaciogenic, but deformation and metamorphism make it difficult to identify unambiguous glaciogenic features.

Our $\delta^{13}\text{C}$ chemostratigraphic data from sporadic carbonate units within the Quruqtagh Group suggest that the Hankalchough glaciation likely postdates the Marinoan glaciation [Brookfield, 1994]. This conclusion is supported by several lines of evidence. First, carbonate units between the Bayisi Formation and the Tereeken glacial interval have extremely positive $\delta^{13}\text{C}$ values up to +10.4‰ PDB but very negative $\delta^{18}\text{O}$ values (as low as -16‰ PDB). Such highly positive $\delta^{13}\text{C}$ values are characteristic of post-Sturtian but pre-Marinoan carbonates, such as the Etina Formation in the Adelaide Rift Complex [Walter *et al.*, 2000; McKirdy *et al.*, 2001], the middle Ombaatjie Formation in Namibia [Kennedy *et al.*, 1998; Halverson *et al.*, 2002; Hoffman and Schrag, 2002], the Keele Formation in NW Canada [Narbonne *et al.*, 1994; Kaufman *et al.*, 1997], and the lower Tsagan Oloom Formation in southwest Mongolia [Brasier *et al.*, 1996]. Neoproterozoic carbonate units characterized by similar magnitude of positive $\delta^{13}\text{C}$ excursion and interpreted of similar age also occur in Brazil [Iyer *et al.*, 1995], Scotland [Brasier and Shields, 2000], and western United States [Smith *et al.*, 1994]. The ~+10‰ $\delta^{13}\text{C}$ excursion in Quruqtagh is suggestive, although not compelling, evidence that the Tereeken and Hankalchough diamictites represent two post-Sturtian glacial deposits.

Second, a 10-m-thick cap carbonate sharply overlying the Tereeken diamictite shows sedimentary and geochemical similarities to Marinoan cap carbonates. The Tereeken cap consists of pinkish, macropeloidal dolomite and has a negative $\delta^{13}\text{C}$ profile, evolving from -4 ~ -5‰ near the base upward to more negative values. Declining $\delta^{13}\text{C}$ profile and macropeloidal dolomite are characteristic of Marinoan caps [Kennedy *et al.*, 1998; James *et al.*, 2001; Hoffman and Schrag, 2002], suggesting that the Tereeken is Marinoan and the Hankalchough, post-Marinoan.

Third, a strong positive $\delta^{13}\text{C}$ shift occurs in the Shuiquan Formation immediately below the Hankalchough diamictite (see also [Xu *et al.*, 2002]). This *positive* trend is in sharp contrast to the pronounced *negative* trend observed in carbonates immediately preceding the Marinoan glaciation [Halverson *et al.*, 2002; Hoffman and Schrag, 2002], indicating that the Hankalchough glaciation is probably not Marinoan in age.



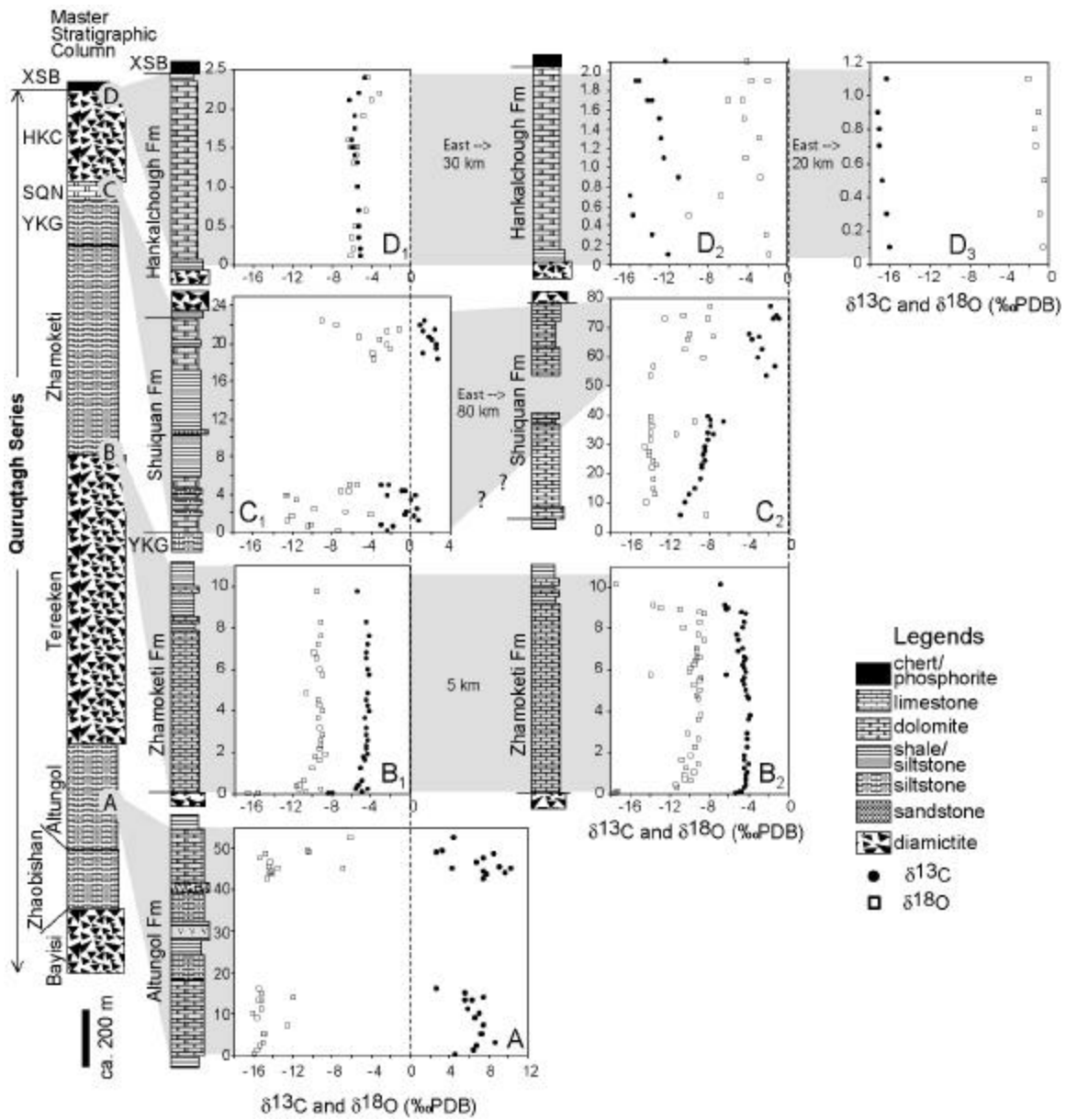


Figure 1. $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ profiles of carbonate units in the Quruqtagh Group. The complete stratocolumn is shown at left and the isotopic profiles are shown in panels. The approximate stratigraphic positions of these isotopic profiles are marked on the main stratocolumn. (A) Carbonate unit in the Altungol Formation. (B) Cap carbonate immediately overlying the Tereeken diamictite measured at two sections (B₁ and B₂ about 5 km apart). (C) Shuiquan Formation measured at two sections (C₁ and C₂). (D) Cap carbonate overlying Hankalchough diamictite measured at three sections (D₁, D₂, and D₃). Gray shading indicates stratigraphic correlation between measured sections. Vertical axes represent stratigraphic heights with arbitrary datum. XSB: Xishanblaq Fm (Cambrian); HKC: Hankalchough Fm; SQN: Shuiquan Fm; YKG: Yukkengol Formation. See Xiao *et al.* [in press a] for isotopic data.

Fourth, *Gao et al.* [1980] reported vendotaenid fossils from the Shuiquan Formation. True vendotaenid fossils typically occur in post-Marinoan Neoproterozoic rocks, again suggesting that the overlying Hankalchough glaciation is younger than the Marinoan.

Fifth, the Hankalchough diamictite is overlain by a non-classic cap carbonate. Homogenous dolomiticrite of the Hankalchough cap is characterized by extremely light and regionally variable $\delta^{13}\text{C}$ values (0 to -17‰) but normal $\delta^{18}\text{O}$ values (0 to -6‰). Part of the wide $\delta^{13}\text{C}$ range may be related to transgressive onlapping and spatial geochemical heterogeneity. Diagenetic alteration alone cannot satisfactorily explain the extremely light $\delta^{13}\text{C}$ values, given the normal $\delta^{18}\text{O}$ values. However, it is interesting to note that several post-Marinoan (and probably pre-Ediacaran) carbonate units in Australia (the Wonoka Formation; [Calver, 2000]), Oman (the Shuram Formation; [Burns and Matter, 1993; Brasier et al., 2000]), and possibly Lesser Himalaya [Jiang et al., 2002], are characterized by very negative $\delta^{13}\text{C}$ values.

Therefore, our preferred interpretation is that the Tereken and Hankalchough are respectively Marinoan and post-Marinoan in age, regardless whether the Bayisi/Altungol diamictites are glaciogenic. It is also possible that the Hankalchough glaciation predates Ediacaran animals if we push the chemostratigraphic significance of the extremely negative $\delta^{13}\text{C}$ excursion immediately overlying the Hankalchough diamictite. Of course, an ultimate test of the proposed age for the Hankalchough diamictite critically depends on reliable radiometric ages of the Quruqtagh deposits.

2.2. Other Post-Marinoan Diamictites

Although controversial, evidence for post-Marinoan Neoproterozoic glaciation(s) (sometimes referred to as the younger Varanger glaciation) has also been reported from South Australia [Di Bona, 1991], NW Australia [Grey and Corkeron, 1998; Corkeron and George, 2001], NW Canada [Kaufman et al., 1997], southern Namibia [Saylor et al., 1998], Death Valley [Corsetti and Kaufman, 2003], and southern Norway [Brasier et al., 2000; Knoll, 2000]. The Fersiga diamictite in western Africa is said to be Early Cambrian [Bertrand-Sarfati et al., 1995], but the dated granite (556 ± 12 Ma) in the Ahaggar inlier only provides an imprecise maximum age constraint for the Fersiga diamictite in the Taoudenni Basin.

The most unambiguously post-Marinoan diamictites are the Squantum [Thompson and Bowring, 2000], Gaskiers [Bowring et al., 2003], and Fauquier diamictites [Aleinikoff et al., 1995; Kaufman and Hebert, 2003] in eastern North America. The Squantum diamictite is constrained between 595.5 ± 2 Ma and 570 Ma [Thompson and Bowring, 2000], and the Gaskiers glaciation occurred around 580 Ma [Bowring et al.,

2003]. Cap carbonates overlying the Fauquier diamictite are interlayered with basalts of 564 ± 9 Ma [Aleinikoff et al., 1995; Kaufman and Hebert, 2003]. These diamictites were likely deposited after the Marinoan glaciation that ended before 599 ± 4 Ma [Barfod et al., 2002].

So far there is no paleomagnetic evidence suggesting that any of these post-Marinoan diamictites were deposited in the tropical ocean. And it is unclear whether all post-Marinoan Neoproterozoic diamictites record a single, widespread Gaskiers glaciation. But chemostratigraphic and radiometric data allow us to conclude that at least three glaciations—the Sturtian, Marinoan, and Gaskiers in geochronological order—occurred in the Neoproterozoic, although the Gaskiers glaciation may have been much less extreme than the other two.

2.3. South China

In South China, the Nantuo diamictite underlies the fossil-rich Doushantuo and Dengying formations and overlies siltstone, shale, and rhodochrosite of the Datangpo Formation (Figure 2B). The Nantuo is believed by most to be Marinoan in age and this is supported by a Marinoan-like cap dolostone atop the Nantuo diamictite. The Nantuo cap dolostone is characterized by tepee-like structures, barite precipitates, sheet cracks, and a declining $\delta^{13}\text{C}$ profile—features known to occur in many Marinoan caps but not common in Sturtian caps.

Two recently available radiometric dates help to constrain the age of the Nantuo (and Marinoan) glaciation. Phosphorites of the Doushantuo Formation are dated from 599 ± 4 Ma (Pb–Pb isochron; $n=5$) [Barfod et al., 2002], and an ash bed from the Datangpo Formation is dated from 663 ± 4 Ma (U–Pb zircon) [Xiao et al., 2003]. Together, these dates suggest that the Nantuo glaciation began after 663 ± 4 Ma and ended before 599 ± 4 Ma. This is consistent with other age constraints for the Marinoan glaciation. Detrital zircons put a maximum depositional age of ca. 650 Ma for the Marinoan glaciation in southern Australia [Ireland et al., 1998]. A maximum depositional age for the Laplandian (probably Marinoan) glaciation in southern Urals is provided by a U–Pb zircon age of 660 ± 15 Ma [Semikhatov, 1991]. The new radiometric dates from South China not only support a Marinoan age for the Nantuo diamictite, but also make it difficult to equate the Nantuo with either the Gaskiers [Bowring et al., 2003] or the Sturtian glaciations [Brasier et al., 2000].

2.4. Correlation

Since the goal of this paper is to evaluate the evolutionary patterns in the context of Neoproterozoic glaciations, the following discussion on stratigraphic correlation will be based on physical stratigraphic, chemostratigraphic, and radiometric

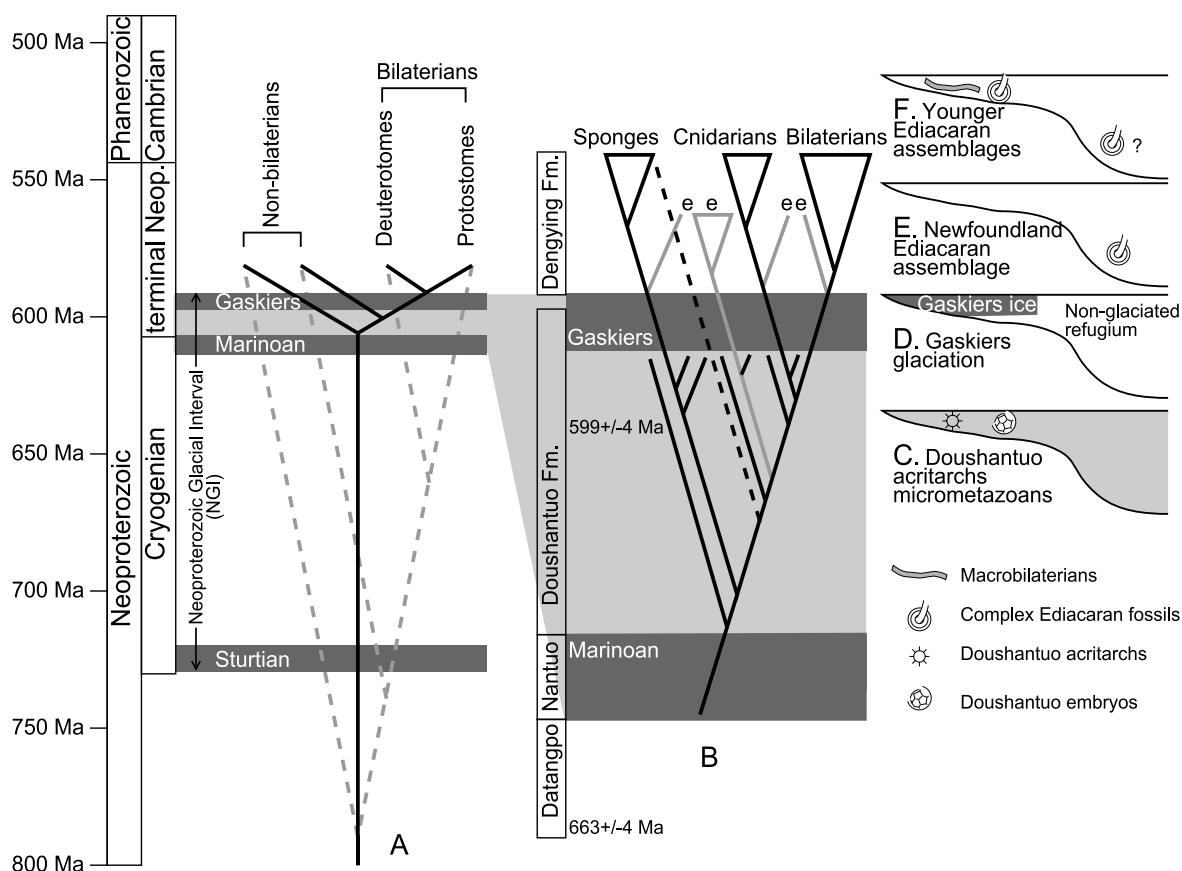


Figure 2. Neoproterozoic glaciations and evolution. (A) Superimposed on the three Neoproterozoic glaciations are two phylogenetic trees of living animals. The deep tree (dashed gray) is based on molecular clock estimates, while the shallow tree (solid black) on paleontological record. (B) Expanded view (light gray shadow) assuming a shallow tree. Many Neoproterozoic animal fossils can be conceptually regarded as stem groups at different phylogenetic levels. Stem groups in solid black lines show possible phylogenetic positions of Doushantuo animals. Stem groups in gray lines (labeled “e”) represent possible phylogenetic positions of Ediacaran animals (non-animal Ediacaran organisms not considered here). Dashed black line indicates uncertainty about sponge paraphyly [Medina *et al.*, 2001]. The upper Doushantuo Formation has been dated from 599 +/- 4 Ma [Barfod *et al.*, 2002] and an ash bed in the Datangpo Formation that immediately underlies the Nantuo Formation has been dated from 663 +/- 4 Ma [Xiao *et al.*, 2003]. (C–F) Environmental distribution of Neoproterozoic biodiversity during the Doushantuo (C), Gaskiers (D), early Ediacaran (E), and late Ediacaran time (F).

data. Biostratigraphic data, although consistent with the proposed correlations, are not used to develop the correlations, in order to avoid circularity.

Insofar as the Nantuo diamictite in South China is not followed by another Neoproterozoic glacial deposit, it becomes critical to determine the age of the fossil-rich Doushantuo Formation relative to the Gaskiers glaciation. In the Yangtze Gorges area, the lower and upper Doushantuo Formation is separated by a sequence boundary [Wang *et al.*, 1998; Wang *et al.*, 2001]. On carbonate platforms in central Guizhou Province, this sequence boundary is expressed as a karstification surface [Xiao and Knoll, 2000a]. It is therefore tempting to consider that this sequence boundary represents a glacioeustatic event

related to the Gaskiers glaciation. This correlation, however, is inconsistent with the radiometric date of 599 +/- 4 Ma [Barfod *et al.*, 2002] from upper Doushantuo phosphorite above the mid-Doushantuo sequence boundary. Unless this radiometric date overestimates the depositional age by more than 20 million years, the mid-Doushantuo sequence boundary cannot be correlated with the 580 Ma Gaskiers glaciation.

The preferred alternative is that the sequence boundary near the Doushantuo–Dengying boundary [Wang *et al.*, 2001] is glacioeustatically related to the Gaskiers glaciation. This preferred correlation converges with the opinion of Zhou *et al.* [2001] who argue that the Doushantuo Formation predates the Moelv glaciation in southern Norway, as long as the Moelv

is equivalent to the Gaskiers [Brasier *et al.*, 2000; Brasier and Shields, 2000; Knoll, 2000]. Their argument is based on the occurrence of large (>100 μm in diameter) acanthomorphic acritarchs (Doushantuo–Pertatataka microflora, or DPM; [Zhou *et al.*, 2001]). In both South China and the Amadeus Basin, Australia, DPM occurs in rocks deposited after the Marinoan (or Nantuo) glaciation but before the radiation of complex Ediacaran organisms [Zang and Walter, 1992; Zhang *et al.*, 1998a; Knoll and Xiao, 1999]. Several elements of the DPM also occur in the Biskopås Conglomerate below the Moelv diamictite [Vidal, 1990]. This led Zhou *et al.* [2002] to conclude that the Doushantuo was deposited after the Marinoan but before the Moelv glaciation.

If we ignore the acritarch biostratigraphic data to avoid circularity, circumstantial chemostratigraphic evidence is consistent with the proposition that the Doushantuo probably predates the Gaskiers. Carbonates in the uppermost Doushantuo Formation are characterized by a negative $\delta^{13}\text{C}$ excursion [Yang *et al.*, 1999; Wang *et al.*, 2002a; Wang *et al.*, 2002b], possibly equivalent to negative $\delta^{13}\text{C}$ excursions in the Gaskiers cap carbonate [Myrow and Kaufman, 1999; Bowring *et al.*, 2003] and other post-Marinoan but pre-Ediacaran successions discussed above. In some sections, the uppermost Doushantuo beds are characterized by $\delta^{13}\text{C}$ values as low as -8‰ but normal $\delta^{18}\text{O}$ values around 0‰ to -2‰ [Wang *et al.*, 2002a], reminiscent of the cap carbonate overlying the Hankalchough diamictite that is interpreted as post-Marinoan in age (see above).

If the Gaskiers glaciation occurs near the Doushantuo–Dengying boundary, then the Doushantuo Formation represents a window between two Neoproterozoic glaciations, while the overlying Dengying Formation and other classic Ediacaran successions record post-Gaskiers evolution (Figure 2).

3. NEOPROTEROZOIC FOSSIL RECORD AND GLACIATIONS

It has been proposed that the beginning and end of the Cryogenian Period be defined by, respectively, the initiation of the Sturtian and the conclusion of the Marinoan glaciation [Knoll, 2000]. This may be justifiable because the Marinoan diamictites are the most widespread and covered by a well-developed cap carbonate. A precise definition of the Cryogenian–terminal Proterozoic boundary is pending upon the ratification of a GSSP section. For the sake of simplicity and convenience, however, in the following discussion I use the term “Neoproterozoic glacial interval” (NGI; Figure 2A) to encompass all three Neoproterozoic glaciations: Sturtian, Marinoan, and Gaskiers; this would be a geological interval about 140 myr, longer than any Phanerozoic periods.

3.1. Stromatolites

Cyanobacteria and stromatolites clearly survived all Neoproterozoic glaciations. The survival of photoautotrophic groups, particularly the presence of stromatolites in carbonates interbedded with diamictites [Corsetti *et al.*, 2003], places a limit on the nature of NGI glaciations. The survival of high-ranking taxonomic groups, however, does not invalidate biotic perturbation or extinction events that occurred at lower taxonomic level.

Indeed, the abundance and morphological “diversity” of stromatolites began to decline in late Neoproterozoic, before the NGI [Awramik, 1971; Walter and Heys, 1985; Awramik, 1990; Awramik, 1992; Semikhatov and Raaben, 1994; Semikhatov and Raaben, 1996; Awramik and Sprinkle, 1999; Grotzinger and Knoll, 1999]. This decline has been traditionally related to the appearance of grazing and burrowing animals [Awramik, 1971; Walter and Heys, 1985], but significant grazing and burrowing did not occur until after the NGI [Droser *et al.*, 2002]. In addition, Phanerozoic stromatolites commonly coexisted with grazing and burrowing animals [Pratt, 1982; Farmer, 1992]. Grotzinger [Grotzinger, 1990; Grotzinger and Knoll, 1999] proposed that the stromatolite decline was caused by decreasing carbonate saturation of seawater (and hence probability of stromatolite preservation) throughout the Proterozoic. An additional, and more obvious, culprit of the stromatolite decline is Neoproterozoic glaciations, because the most significant decline in stromatolite abundance and “diversity” occurred during the NGI. Glacioeustatic sea level drop could greatly reduce the carbonate platform environments available to phototrophic microbial mats. Glaciations would also initiate other environmental changes affecting, directly or indirectly, microbial habitats, abundance, or diversity. The stratigraphic resolution is still insufficient for us to determine whether the broad declining trend starting before the NGI is a mega-Signor–Lipps artifact [Signor and Lipps, 1982] and whether stromatolites briefly recovered between glaciations.

3.2. Acritarchs

At the broad scale, acritarchs (traditionally interpreted as resting cysts of photoautotrophic eukaryotes but likely including heterogeneous groups) also suffered significant diversity loss between the Sturtian and Marinoan glaciations [Knoll, 1994; Vidal and Moczydlowska-Vidal, 1997]. The global diversity pattern is supported by assemblage-level data; the α -diversity of all described Cryogenian assemblages is extremely low [Knoll *et al.*, 1981; Vidal, 1981; Vidal and Nystuen, 1990; Yin, 1990], suggesting that the Cryogenian diversity decline is real at both local and global scales.

A taxonomically unique acritarchs assemblage, characterized by large acanthomorphs, diversified shortly after the Marinoan glaciation. In South China, this acritarchs assemblage occurs in the Doushantuo Formation and includes such forms as *Asterocapsoides sinensis*, *Bacatisphaera baokangensis*, *Castaneasphaera speciosa*, *Dicrospinasphaera zhangii*, *Distosphaera speciosa*, *Echinosphaeridium maximum*, *Eotylotopalla delicata*, *Eo. dactylos*, *Ericiasphaera magna*, *Er. rigida*, *Er. sparsa*, *Mastosphaera changyangensis*, *Meghys-tricosphaeridium chadianensis*, *Me. magnificum*, *Me. reticulatum*, *Papillomembrana compta*, *Pustulisphaera membranacea*, *Sinosphaera rupina*, and *Tianzhushania spinosa* [Yuan and Hofmann, 1998; Zhang et al., 1998a; Yin, 1999]. Elements of the Doushantuo acritarch assemblage have also been reported in the Pertatataka Formation, Amadeus Basin, central Australia [Zang and Walter, 1992], the Scotia Group, Svalbard [Knoll, 1992b], the lower Krol Group (Krol A), Less Himalaya [Tiwari and Knoll, 1994], and lower Vendian rocks in eastern Siberia [Moczydlowska et al., 1993]. All these units locally overlie glacial deposits interpreted as Marinoan in age.

In the Yangtze Gorges area, large acanthomorphic acritarchs first appear within meters above the Nantuo cap carbonate [Yin et al., 2001]. Accepting the Pb-Pb date from the upper Doushantuo Formation [Barfod et al., 2002], Doushantuo acritarchs first appeared before 599 ± 4 Ma. In South Australia, however, similar acritarchs radiated after the ca. 580 Ma Acraman impact ejecta layer [Grey et al., 2003]. The apparent delay in South Australia may be related to unsuitable taphonomic or paleoenvironmental conditions.

Available evidence also suggests that the Doushantuo acritarch assemblage disappeared around the Gaskiers glaciation. Many Doushantuo acritarchs are preserved in both cherts and phosphorites [Xiao, in press]. The overlying Dengying Formation contains beautifully phosphatized fossils [Ding et al., 1992], but no Doushantuo-type acritarchs. Basal Cambrian acritarchs [Moczydlowska, 1991] are entirely different from those preserved in the Doushantuo Formation. Accepting that the Gaskiers glaciation occurred near the Doushantuo–Dengying boundary, the simplest interpretation is that most Doushantuo-type acritarchs are restricted between the Marinoan and Gaskiers glaciations.

Acritarchs from the Biskopås Conglomerate in southern Norway [Vidal, 1990] share similarities to those from the Doushantuo Formation, but the Biskopås Conglomerate is stratigraphically below the Moelv diamictite. This leads to one of the following two conclusions: either the Moelv represents a Marinoan diamictite and several genera (e.g. *Papillomembrana* and *Ericiasphaera*) of the Doushantuo assemblage sailed through the Marinoan glaciation, or the Moelv is equivalent to the Gaskiers and the entire Doushan-

tuo assemblage is restricted between the Marinoan and Gaskiers glaciations. Because of the uncertain age of the Moelv diamictite, it is difficult to distinguish these two alternatives. However, that the Pertatataka assemblage may be bracketed by the Marinoan and Egan (?=Gaskiers) glaciations [Grey and Corkeron, 1998] lends support to the latter alternative.

More systematic paleontological sampling of the Doushantuo and other units is required to refine the picture and to distinguish the signals of environmental heterogeneity, preservational bias, and evolutionary trend in the observed fossil record. If it can be confirmed that the Doushantuo acritarch assemblage is restricted between the Marinoan and Gaskiers glaciations, it raises the question whether the appearance and disappearance of this assemblage were related to glaciations.

3.3. Algae

Various eukaryotic clades, including both photoautotrophic and heterotrophic protists such as red algae, green algae, stramenopiles, alveolates, and both lobose and filose amoebae, also diverged before the NGI [Knoll, 1992a; Butterfield et al., 1994; Butterfield, 2000; Porter and Knoll, 2000]. Obviously, these high-ranking groups also survived all NGI glaciations.

The history of algal evolution broadly parallels to that of acritarchs. Multicellular algae are poorly known between the Sturtian and Marinoan, but are abundant and diverse in Doushantuo shales, phosphorites, and cherts [Zhang, 1989; Zhang and Yuan, 1992; Zhang et al., 1998a; Xiao et al., 1998; 2002; in press b; Xiao, in press]. Cellular preservation in Doushantuo phosphorites allows us to understand the possible phylogenetic relationships of phosphatized Doushantuo algae; most can be interpreted as stem group florideophyte red algae or stem group coralline algae [Xiao et al., in press b]. It is possible that these stem groups went extinct at the same time when Doushantuo-type acritarchs disappeared. But the conclusion is less secure in this case because, unlike acritarchs, post-Doushantuo algal fossils are rare or poorly preserved for meaningful comparison.

3.4. Animals Before or During the NGI

3.4.1. Molecular clock studies. Molecular clock studies indicate that animals, plants, and fungi may have diverged from each other in the Mesoproterozoic [Doolittle et al., 1996; Wang et al., 1999; Heckman et al., 2001; Nei et al., 2001; Hedges, 2002]. Similar studies also suggest that the deepest (protostomes–deuterostomes) divergence within the crown-group bilaterian animals probably occurred either before or within the NGI, although the range and uncertainty of these estimates are large [Runnegar, 1982; Doolittle et al., 1996;

Wray *et al.*, 1996; Ayala *et al.*, 1998; Bromham *et al.*, 1998; Gu, 1998; Lee, 1999; Lynch, 1999; Wang *et al.*, 1999; Smith and Peterson, 2002]. If correct, they indicate that minimally one lineage each of the protostome, deuterostome, and non-bilaterian clades survived one or more glaciations. While the survival of ancestral animals puts limits on the extreme nature of Neoproterozoic glaciations, the molecular clock studies themselves say nothing about the physiological and ecological selectivity of the survivors. Nor do they provide any insights into the morphology, diversity, and phylogeny of early diverging but subsequently extinct stem lineages. Hence, molecular clock studies alone are not sufficient to understand the dynamic relationship between environmental perturbations and biological turnovers in the NGI. We will have to depend on the fossil record, however sketchy or biased it is, to determine the morphology (e.g. body size and related physiological constraints) and ecology (e.g. shallow-water shelf vs. deep-water slope environments) of ancestral animals. The currently available fossil record does not allow us to answer all these questions, but some general patterns can be learned.

3.4.2. Pre-NGI animals. Reports of millimeter-wide bedding plane traces in the Paleo- and Mesoproterozoic rocks [Seilacher *et al.*, 1998; Rasmussen *et al.*, 2002a; Rasmussen *et al.*, 2002b; Ray *et al.*, 2002] are attractive, but interpretations of these markings as animal traces remain controversial. The often-cited pre-NGI worm-like fossil, *Protoarenicola*, from North China [Sun *et al.*, 1986] has been shown to be a holdfast-bearing benthic alga [Qian *et al.*, 2000]. At the present, there do not appear to be any unequivocal body or trace fossils of pre-NGI animals.

3.4.3. Discoidal fossils. There are several reports of discoidal or circular fossils from rocks underlying Neoproterozoic diamictites. Discoidal fossils from the Twitya Formation in the Mackenzie Mountains, northwestern Canada, are bracketed by the Rapitan (=Sturtian) and Ice Brook (=Marinoan) glaciations [Hofmann *et al.*, 1990]. Simple discoidal fossils from the Cheikhia Group in the Taoudenni Basin, Algeria, predate the Fersiga diamictite [Bertrand-Sarfati *et al.*, 1995], whose age is poorly constrained but possibly equivalent to the Gaskiers glaciation. Assemblages dominated by discoidal or circular fossils also occur in other Neoproterozoic (e.g. [Narbonne and Hofmann, 1987; Farmer *et al.*, 1992; Zhang and Shu, 2002]) and possibly Cambrian deposits [Crimes *et al.*, 1995]. The biological interpretation of such simple forms is challenging. Some have been interpreted as cnidarian animals [Glaessner, 1984; Hofmann *et al.*, 1990; Bertrand-Sarfati *et al.*, 1995], coenocytic algae [Xiao *et al.*, 2002; Knoll and Xiao, 2003], holdfasts of frondose Ediacaran organisms [Gehling *et al.*, 2000], or scratch marks [Jensen *et al.*, 2002].

Each interpretation makes its own predictions: coenocytic algae lived (but were not necessarily preserved) in the photic zone, and frondose Ediacaran organisms must occur in the same geological interval as their holdfasts.

If the Twitya discs are correctly interpreted as stem-group cnidarians [Hofmann *et al.*, 1990], they imply that at least stem-group sponges and possibly stem-group bilaterians, depending on the exact phylogenetic relationships between cnidarians and bilaterians [Collins, 1998; Kim *et al.*, 1999; Medina *et al.*, 2001], existed before the Marinoan glaciation.

3.4.4. Doushantuo animals. The Doushantuo Formation contains multiple taphonomic windows of exceptional preservational quality, in its cherts, shales, and phosphorites. Doushantuo chert nodules, deposited in subtidal environments in the Yangtze Gorges area and elsewhere in South China, preserve abundant cyanobacteria, acanthomorphic acritarchs, as well as multicellular algae [Zhang *et al.*, 1998a; Xiao, in press]. Rare triaxonal spicules preserved in Doushantuo chert nodules have been interpreted as hexactinellid spicules ([Tang *et al.*, 1978; Ding *et al.*, 1985; Zhao *et al.*, 1988]; but see [Steiner *et al.*, 1993]). No other animals have been reported from the chert nodules.

Subtidal (below wave-base) shales in the uppermost Doushantuo Formation in the Yangtze Gorges area preserve carbonaceous compressions, many of which can be unambiguously interpreted as macroscopic (centimeter- to decimeter-sized) algae [Xiao *et al.*, 2002]. The preservational style and quality of these algae is comparable to that of Burgess Shale and Chengjiang algae [Briggs *et al.*, 1994; Butterfield, 1995; Chen *et al.*, 1996; Butterfield, 2003]. A taphonomic test can be therefore carried out: if there existed in subtidal environments macroscopic animals with reasonably recalcitrant structures such as extracellular cuticles, they should be preserved in Doushantuo shales. A couple of Doushantuo fossils resemble and may be equivocally interpreted as sponges or cnidarians. But no macrobilaterians have been documented in Doushantuo shales. Nor are there any macroscopic resting traces or crawling tracks on Doushantuo bedding planes. This leads to one of the following hypotheses: 1) macrobilaterians (and their pattern formation mechanisms) had not evolved; 2) macrobilaterians with extracellular cuticles had not evolved; 3) macrobilaterians with extracellular cuticles had not invaded into subtidal platform environments. This leaves several possibilities of NGI bilaterians: microbilaterians [Davidson *et al.*, 1995], bilaterians without any recalcitrant structures, or bilaterians living in offshore pelagic environments [Runnegar, 2000]. Expanding our search into deeper paleoenvironments and into taphonomic windows that can preserve microscopic and more labile organic structures will provide key tests of these possibilities.

Doushantuo phosphorites, deposited in shallow subtidal (above wavebase) environments at Weng'an and several other localities in South China, represent a NGI taphonomic window that has the potential to preserve labile micrometazoans. At Weng'an, phosphatic horizons occur in both the lower and upper Doushantuo Formation, separated by a subaerial exposure surface [Xiao and Knoll, 2000a]. Rare earth element patterns in the lower Doushantuo phosphorite are consistent with phosphatization in an anoxic sedimentary/diagenetic environment [Chen *et al.*, 2003]. The absence of not only algal and animal fossils but also cyanobacteria and acritarchs in the lower phosphorite horizon is probably related to the anoxic preservational and/or paleoenvironmental conditions.

The best-preserved and most diverse fossils come from the upper Doushantuo Formation. In addition to filamentous and coccoidal cyanobacteria, acanthomorphic acritarchs, and multicellular algae, sub-millimeter-sized animal embryos at successive cleavage stages also occur in the upper phosphorite horizon [Xiao *et al.*, 1998; Xiao and Knoll, 2000b; Xiao, 2002]. It is difficult to determine which animal clade(s) these fossil embryos belong to. But they display a chimeric combination of features that individually occur in crown group sponges, cnidarians, and bilaterians, suggesting that these embryos may belong to stem groups at the animal, eumetazoan, or bilaterian levels [Xiao and Knoll, 2000b]. Phosphorites of the upper Doushantuo Formation also yield sub-millimeter-sized, tabulated tubes [Xue *et al.*, 1992; Li *et al.*, 1997]. These tubular fossils can be interpreted as either stem-group eumetazoans or stem-group cnidarians [Xiao *et al.*, 2000] or crown group anthozoans [Chen *et al.*, 2002]. Finally, microscopic sponge body fossils and putative gastrulas have been reported from the upper Doushantuo Formation [Li *et al.*, 1998; Chen *et al.*, 2000; 2002], although the interpretation of such forms are highly debatable [Zhang *et al.*, 1998b; Xiao *et al.*, 2000].

Despite the interpretative uncertainties surrounding the Doushantuo fossils, the important messages from Doushantuo phosphorites are 1) animals evolved before the Gaskiers glaciation; 2) none of them can be unambiguously interpreted as macroscopic bilaterians; and 3) many of them can be regarded as stem groups at deep phylogenetic levels.

3.5. Post-NGI Radiation

3.5.1. Complex Ediacaran fossils. Post-NGI evolution is characterized by the arrival of complex Ediacaran fossils. Some Ediacaran fossils have been interpreted as lichens, possible fungi, or extinct groups phylogenetically unrelated to animals [McMenamin, 1986; Seilacher, 1989; Seilacher, 1992; Zhuravlev, 1993; Retallack, 1994; Peterson *et al.*, 2003]. The Ediacaran biotas as a consortium, however, represent merely a sampling of the Neoproterozoic biodiversity (Figure 2B;

[Runnegar, 1995; Waggoner, 2003]) that includes, among others, animals such as sponges [Gehling and Rigby, 1996], stem-group eumetazoans [Buss and Seilacher, 1994], cnidarians or cnidarian-grade animals [Glaessner, 1984; Conway Morris, 1993b], and bilaterians [Fedonkin and Waggoner, 1997].

Among the best-known Ediacaran fossils, the Newfoundland assemblage is probably the oldest [Benus, 1988; Gehling and Narbonne, 2002; Bowring *et al.*, 2003; Narbonne and Gehling, 2003]. The White Sea and South Australia assemblages are younger [Martin *et al.*, 2000], and the Namibia assemblage is the youngest in the Neoproterozoic [Grotzinger *et al.*, 1995]. A few Ediacaran fossils may extend into the Cambrian [Conway Morris, 1993a; Jensen *et al.*, 1998; Hagadorn *et al.*, 2000]. Quantitative analysis also delineates the Newfoundland, White Sea–South Australia, and Namibia assemblages [Waggoner, 2003].

The temporal succession of Ediacaran assemblages is accompanied by paleoenvironmental shift and evolutionary progress. The Newfoundland assemblage occurs in a deep-water slope environment [Myrow, 1995], while the younger assemblages in White Sea, South Australia, and Namibia are from shallow-water (within photic zone) platform environments. There do not appear to be any unambiguous macrobilaterians in the Newfoundland assemblage [Clapham and Narbonne, 2002; Guy Narbonne, personal communication, 2003]. The White Sea and Namibia assemblages, on the other hand, include body and trace fossils of macrobilaterians, and the latter also includes partially biomineralized animals (e.g. *Cloudina*, *Namapoikia*, *Namacalathus* in Namibia) [Fedonkin, 1994; Grotzinger *et al.*, 1995; 2000; Jenkins, 1995; Fedonkin and Waggoner, 1997; Jensen *et al.*, 2000; Droser *et al.*, 2002; Gehling, 2002; Wood *et al.*, 2002]. The difference in macrobilaterian diversity unlikely represents poorer preservation in the Newfoundland assemblage, considering its *in-situ* preservation beneath volcanic ash covering [Clapham and Narbonne, 2002; Narbonne and Gehling, 2003]. Rather, the diversity difference probably results from evolutionary (temporal) change and/or ecological (spatial) heterogeneity.

Taken at face value, the temporal succession of Ediacaran assemblages indicates that post-NGI radiation of macroscopic, complex Ediacaran organisms began in deep-water slope environments and later expanded into shallow-water shelf environments where macrobilaterians first evolved. This hypothesis predicts that the oldest shallow-water assemblage post-dates the oldest deep-water assemblage, although it does not preclude Ediacaran organisms persisting in deep-water environments. Key tests of this hypothesis include more precise dating of additional complex Ediacaran assemblages from both shallow- and deep-water environments (e.g., shallow-water: South Australia, South China, Siberia; deep-water: Mackenzie Mountains, North Carolina, Charnwood Forest; [Ford, 1958; Sun,

1986; Fedonkin, 1990; Narbonne and Aitken, 1990; Narbonne, 1994; Gehling, 2000; MacNaughton *et al.*, 2000; Compston *et al.*, 2002)).

Available paleontological evidence does not allow us to tell whether ancestors of complex Ediacaran organisms survived the Gaskiers glaciation in deep-sea refugia, although the moderate phylogenetic diversity, ecological complexity, and morphological disparity of the Newfoundland assemblage [Clapham and Narbonne, 2002; Narbonne and Gehling, 2003] do suggest that there may have been some Ediacaran forerunners in pre-Gaskiers oceans.

3.5.2. Bilaterian animals. One of the important tie points in the Proterozoic animal fossil record is the presence of millimeter- to centimeter-sized body and trace fossils of macrobilaterians in younger, shallow-water Ediacaran assemblages in White Sea, Australia, and Namibia [Fedonkin, 1994; Grotzinger *et al.*, 1995; Fedonkin and Waggoner, 1997; Jensen *et al.*, 2000; Droser *et al.*, 2002; Gehling, 2002], suggesting that bilaterian animals diverged no later than 555 Ma [Martin *et al.*, 2000].

3.5.3. Animal biomineralization. Partially biomineralized tubular fossils have been known in the youngest Ediacaran assemblage—the shallow-water Namibia assemblage [Grant, 1990; Grotzinger *et al.*, 2000; Waggoner, 2003]. Similar fossils also occur in the upper Miette Group in British Columbia [Hofmann and Mountjoy, 2001] and the middle Dengying Formation in South China [Chen *et al.*, 1981; Conway Morris *et al.*, 1990; Ding *et al.*, 1992; Bengtson and Zhao, 1992; Chen and Sun, 2001]. The middle Dengying Formation also yields a rare frondose Ediacaran fossil identified as *Paracharnia dengyingensis* [Sun, 1986]. It would be interesting to learn whether the upper Miette Group and middle Dengying Formation have depositional ages similar to that of the Kuibis and Schwarzrand subgroups where *Cloudina* and *Namacalathus* occur in Namibia.

To summarize, the post-Gaskiers fossil record suggests that complex Ediacaran organisms, at least some of which were animals, emerged from deep-water slope environments shortly after the Gaskiers glaciation. Although animals evolved during the NGI, it is not until the later stage of Ediacaran diversification when macroscopic bilaterian animals evolved and colonized the shallow-water shelf environments. And animal biomineralization evolved still later—very close to the Precambrian–Cambrian boundary (Figure 2).

4. DISCUSSION AND CONCLUSIONS

The above analysis suggests that the marine communities did respond to climate changes associated with Neoproterozoic

glaciations. The Cryogenian decline in stromatolites and acritarchs may have been causally related to the Sturtian and Marinoan glaciations. The brief diversification and eventual disappearance of Doushantuo-type acritarchs near the Doushantuo–Dengying boundary points to a possible extinct event caused by the Gaskiers glaciation. The prevalence of many stem group red algae and animals in the Doushantuo Formation is also consistent with a Gaskiers extinction event; stochastic and massive trimming of a phylogenetic tree is expected leave many twigs as stem groups.

On the other hand, the intensity of these possible extinction events is less than what would be expected from hard snowball Earth events [Hoffman *et al.*, 1998]. At least some members of several photoautotrophic groups (e.g., cyanobacteria and algae) survived all Neoproterozoic glaciations. Some animals must have survived the Gaskiers glaciation if post-Gaskiers animals did not evolve *de novo*.

Perhaps more can be learned by studying the paleoenvironmental distribution of Neoproterozoic biodiversity before and after each glaciation. Did organisms lived in the photic zone suffer more during Neoproterozoic glaciations? Did deep-sea environments or other non-glaciated areas serve as effective refugia during the glaciations? Did post-glacial radiation indeed begin in deep-sea refugia? Answers to these questions would provide paleobiological constraints on the nature of Neoproterozoic glaciations.

To answer these questions and further test the ideas expressed in this paper, future work should be aimed 1) to sharpen the geochronological resolution of Neoproterozoic successions; 2) to improve the stratigraphic and phylogenetic resolution of Neoproterozoic fossils; 3) to better understand the environmental distribution and taphonomic biases embedded in the Neoproterozoic fossil record. To achieve these requires more paleontological, stratigraphic, paleoenvironmental, and taphonomic analyses of carefully measured successions. The current Neoproterozoic fossil record is mostly based on sporadic sampling of cherts, phosphorites, or carbonaceous shales, rather than bed-by-bed sampling as practiced in the Phanerozoic. There are of course taphonomic issues in the Neoproterozoic because virtually all Neoproterozoic organisms are non-biomineralized and their preservation requires unusual taphonomic conditions. But there are Neoproterozoic sections with abundant shales or chert nodules, allowing high-resolution paleontological sampling. Such data will allow us to obtain a high-resolution picture of the Neoproterozoic diversity dynamics at local, regional, and global levels.

Acknowledgments. I would like to thank Gregory Jenkins for inviting me to contribute. I would also like to thank Huiming Bao, Frank Corsetti, Whitey Hagadorn, Paul F. Hoffman, Ganqing Jiang, Alan J. Kaufman, Andrew H. Knoll, Guy M. Narbonne, Zhanxiong Peng,

Curt Pueschel, Bob Tucker, Leiming Yin, Xunlai Yuan, and Chuanming Zhou for sharing data and ideas. My research on the Neoproterozoic geobiology is supported by National Science Foundation and National Geographic Society.

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