

THE NEOPROTEROZOIC AND CAMBRIAN: A TIME OF UPHEAVALS, EXTREMES AND INNOVATIONS [☆]

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Contents

1.1. The Neoproterozoic World	3
1.2. Tectonic Upheaval and Geodynamic Twists: The Tale of Two Supercontinents	3
1.3. The Ocean and Atmosphere: Oxygenation and Anomalies	5
1.4. Climatic Extremes and Conundrums	7
1.5. Permissive Ecology and Neoproterozoic-Cambrian Climate	9
1.6. Emergence of Metazoa: A New World Order	10
1.7. Conclusions	11

1.1. THE NEOPROTEROZOIC WORLD

The Neoproterozoic Era (1,000–542 Ma) encompasses an eventful period in Earth history, comparable in length to the Phanerozoic Eon. Among the most notable events in the Neoproterozoic are the final amalgamation and demise of the oldest well-documented supercontinent (i.e. ‘Rodinia’: McMenamin and McMenamin, 1990; ‘Palaeopangaea’: Piper, 1982), the fusion of its cratonic pieces into Gondwana through an immense network of orogenic events, the most severe glaciations in Earth history (‘Snowball Earth’, Kirschvink, 1992a; Hoffman et al., 1998), large oscillations in the carbon and sulphur isotope composition of seawater in Earth history, the advent of animals, the first skeletonized organisms, the oldest evidence of predation and the colonization of the infaunal niche (‘agronomic revolution’: Seilacher, 1999). The large and ever increasing number of publications dealing with these and other aspects of the Neoproterozoic Earth suggests that in the years to come the list of extraordinary events and our understanding of the underlying mechanisms that drove them is likely to grow. The Neoproterozoic was without doubt a time of extremes, of evolution and innovation, which culminated in the birth of a habitable environment. This chapter aims to provide an updated summary of Neoproterozoic research and the intricate relationships between the solid Earth, the ocean–atmosphere, global climate and organismic evolution.

1.2. TECTONIC UPHEAVAL AND GEODYNAMIC TWISTS: THE TALE OF TWO SUPERCONTINENTS

The Neoproterozoic Era is bracketed by the end of the Grenvillian orogeny (1,300–900 Ma) and the Brasiliano–Pan–African system of orogenies (ca. 650–520 Ma, Figure 1.1): a full supercontinental cycle. On the basis of U–Pb detrital zircon ages found in major river mouths in four continents, Rino et al. (2008) argued that the Grenvillian and Brasiliano–Pan–African were the most intense orogenic events in Earth history. A legacy of the

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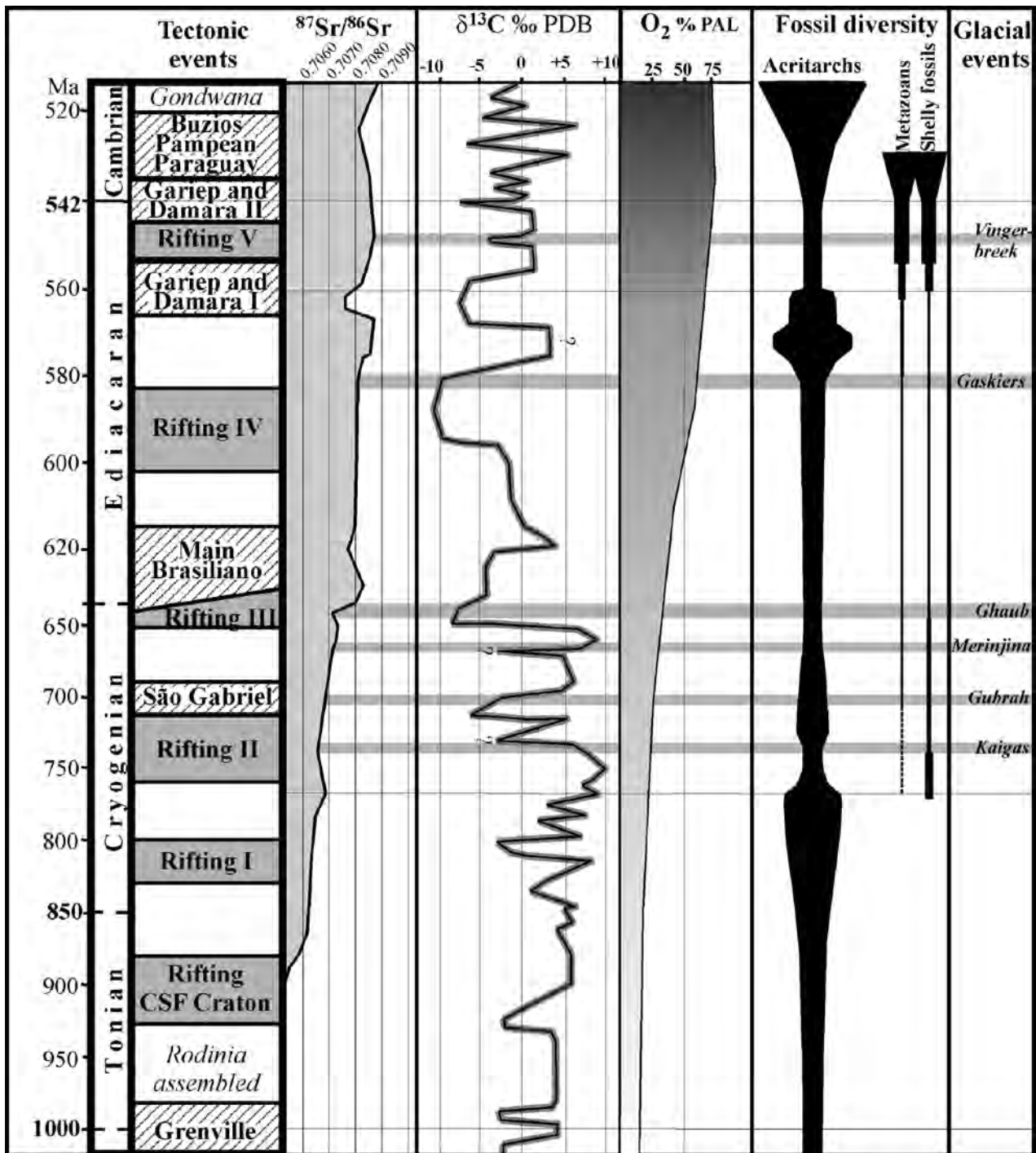


Figure 1.1 Synthesis of Neoproterozoic chronostratigraphy, tectonic and glacial events, isotopic composition of seawater, atmospheric oxygenation and main extinction and radiation events. Note change in timescale at 635 Ma. $^{87}\text{Sr}/^{86}\text{Sr}$ curve mainly according to Halverson et al. (2007a); $\delta^{13}\text{C}$ curve from Halverson et al. (2005), Maloof et al. (2005) and Kah et al. (1999) with modifications to accommodate data from SW-Gondwana. Oxygenation curve according to Holland (2006). Rifting CSF Craton: Rifting in the Congo-São Francisco Craton (see Chapter 8 and references therein). Break-up of Rodinia (Li et al., 2008b; Chapter 8 and references therein): Rifting I: Greater India; Rifting II: South China, Kalahari Craton, Australia, East Antarctica; Rifting III: Amazonia and Río de la Plata cratons; Rifting IV: Baltica, northern Laurentia, Amazonia and Río de la Plata cratons; Rifting V: Opening of the Iapetus Ocean. Orogenic events shown are mainly referred to Gondwanan blocks (see Chapter 8 and references therein). Acritarch diversity (width in the Cambrian equals 75 species): see Chapter 9.1 and references therein. Shelly fossils and metazoan diversity: see Chapter 9.2.

break-up of Rodinia was a peak in passive margin abundance in the middle Neoproterozoic–Early Cambrian (Bradley, 2008), which accounts for the ample Neoproterozoic sedimentary record. Thus, it is clear that the Neoproterozoic was a tectonically dynamic period in Earth history; undoubtedly, these tectonic upheavals affected the concomitant evolution of the biosphere and dramatic fluctuations in seawater chemistry and climate (Section 1.3).

The early break-up of Rodinia appears to have been associated with one or more superplumes (Li et al., 1999, 2003, 2008b; Frimmel et al., 2001b; Puffer, 2002; Wang et al., 2007). The earliest superplume, temporally correlated with the initial break-up of Rodinia and situated beneath South China, India, East Antarctica and Australia, culminated ca. 825 Ma and may have been distinct from a subsequent peak in plume magmatism at ca. 780 Ma (Li et al., 2003). Whether these plumes triggered break-up or were a consequence of break-up remains a matter of debate. Mantle avalanches (Condie, 1998, 2000; Li et al., 2008b) or ‘slab graveyards’ (Rino et al., 2008), generated by the subduction of cold oceanic lithosphere at the margins of supercontinents, are often cited as possible mechanisms of plume inception (see Chapter 8). The shielding effect of supercontinents has been also invoked as a likely mechanism (Evans, 2003b). In combination, the global scale reorganizations of mass in the mantle may have been sufficient to drive large-scale, rapid true polar wander (Evans, 2003b). While such TPW events have been invoked as either a possible triggering mechanisms for Cryogenian glaciation or a means of rotating high latitude glacial deposits into the low latitudes (Kirschvink et al., 1997; Li et al., 2004), no data establishing this link has yet been established. The evidence for ca. 800 Ma TPW is derived from two unrelated sources (a) a compilation of radiometrically constrained palaeomagnetic data from mid-Neoproterozoic plume-related volcanics (Li et al., 2004) that suggests a single TPW event and (b) palaeomagnetic data from the mid-Neoproterozoic Akademikerbreen Group in Svalbard which suggests a pair of TWP events related to major shifts in the global carbon cycle (Maloof et al., 2006), but well in advance of the earliest evidence there for glaciation. Thus, independent data sets and theory are converging to imply at least one major TPW event sometime in the mid-Neoproterozoic. While this hypothesis is not yet fully tested and its potential connection to Cryogenian glaciation remains tenuous, it is a compelling idea that offers a potential means of elucidating the role of palaeogeography in the Earth system.

The break-up of Rodinia lasted >250 myr, with the final dispersion of Rodinia – the opening of the Iapetus Ocean – not beginning until ca. 600 Ma (Figure 1.1; Pisarevsky et al., 2008; see Chapter 8), after the nucleus of Gondwana had already begun to assemble (Collins and Pisarevsky, 2005). This protracted break-up of Rodinia is manifested in the seawater strontium isotope record, where a gradual rise from 0.7053 to 0.7072, related to erosion of old continental crust in the interior of Rodinia, characterizes the middle Neoproterozoic (Halverson et al., 2007a; Figure 1.1). A subsequent peak in $^{87}\text{Sr}/^{86}\text{Sr}$ of 0.7093 in the middle Cambrian (Montañez et al., 1996), the highest in Earth’s history (see Section 1.3), probably resulted from the unroofing of the extensive Brasiliano–Pan–African system of orogens (Figure 1.1).

As will be discussed below and in the ensuing chapters, the combination of supercontinental break-up and subsequent amalgamation of Gondwana likely played a central role in the climatic, geochemical and biospheric evolution of the Neoproterozoic–Cambrian world.

1.3. THE OCEAN AND ATMOSPHERE: OXYGENATION AND ANOMALIES

The ocean and atmosphere are intimately linked through gaseous exchange at the air–water interface and weathering of the continents. Ocean chemistry and the redox state of the ocean–atmosphere changed markedly in the Neoproterozoic, as manifested in the reprise of banded iron formation (BIF), after a gap of nearly 1 Gyr encompassing the whole Mesoproterozoic (e.g. Beukes and Klein, 1992; Klein and Beukes, 1992; Holland, 2006). Canfield (1998) suggested, based on a compilation of sulphur isotope data on sedimentary sulphides, that the late Palaeoproterozoic–Mesoproterozoic deep ocean was euxinic (i.e. sulphidic and anoxic) thus inhibiting deposition of BIF through iron sequestration by sulphides. Although this hypothesis has been challenged by Holland (2006), who envisioned the gap in BIF deposition to be due to a non-stratified, mildly oxidized ocean devoid of Fe^{2+} , it has also been widely supported by varied data sets. Molybdenum concentrations (Scott et al., 2008), Mo isotope compositions (Arnold et al., 2004), Fe speciation data, sulphides S isotope compositions (Shen et al., 2002) and biomarker data (Brocks et al., 2005; Brocks and Schaeffer, 2008) in late Palaeoproterozoic–Mesoproterozoic black shales all support this view of common, if not prevailing euxinic conditions in the deep ocean, analogous to the modern Black Sea. Anbar and Knoll (2002) and Anbar (2008) elaborated on the biogeochemical consequences (such as nutrient abundances) of the Canfield (1998) model of a tripartite evolution of Precambrian ocean chemistry.

Given that evidence is converging to indicate that the Neoproterozoic represents a transition between a dominantly euxinic to oxygenated deep ocean, two key questions remain: (a) what was the nature of that transition and (b) how did it relate to the biospheric evolution that culminated in the Cambrian explosion? While many authors have argued for at least periodically sulphidic deep oceans in the Neoproterozoic (e.g. Hurtgen

et al., 2005, 2006), Canfield et al. (2008) recently proposed instead, based on a large compilation of iron-speciation data, that at least during the latter half of the Neoproterozoic, the deep oceans were dominantly Fe-rich. The demise of sulphidic oceans could be a consequence, not of a return to the very low oxygen conditions that typified the Archaean, but rather a shortfall in the continental sulphur inventory, which limited the supply of sulphate to the oceans (Canfield, 2004). The well-known occurrence of BIF in glacial successions, such as the Rapitan Group of the northwest Canada (Klein and Beukes, 1993), the Sturtian of South Australia (Preiss, 1987), the Chuos (Beukes, 1973) and Numees (Frimmel et al., 2002) formations of Namibia and the Jacadigo Group and Puga Formation of the southern Paraguay belt in SW Brazil (Graf et al., 1994; Piacentini et al., 2007) clearly indicate widespread anoxic, non-sulphidic deep oceans. BIF and manganese formations unrelated to glacial deposits also occur, for example, in the Ediacaran Arroyo del Soldado Group of Uruguay (Gaucher, 2000; Gaucher et al., 2004b), and the Penganga Group of India (Mukhopayay et al., 1997; Holland, 2006), although the age of the latter is poorly constrained and may in fact be late Mesoproterozoic (Basu et al., 2008). While the iron-speciation data of Canfield et al. (2008) illustrate that the Neoproterozoic–Cambrian redox transition did not involve a simple switch from sulphidic to oxygenated deep oceans, the absence of persistent BIF deposition throughout the latest Neoproterozoic suggests that transitional ocean chemistry was not simply analogous to the iron-rich Archaean–Palaeoproterozoic deep oceans.

Fluctuations in the ocean redox state, in particular spanning the Cryogenian glaciations (see Chapter 10), appear likely. A number of authors argue that oceans were chemically stratified, with deep anoxic waters overlain by a thin, oxygenated water layer within the photic zone, where photosynthesis would provide the source of oxygen (Calver, 2000; Gaucher, 2000; Gaucher et al., 2004b; Shen et al., 2005). But it is becoming increasingly clear that the deep oceans became at least partially oxygenated some time in the middle Ediacaran Period, perhaps shortly after the Gaskiers glaciation (Fike et al., 2006; Canfield et al., 2007; Halverson and Hurtgen, 2007; McFadden et al., 2008).

Likely not coincidentally, the first Ediacaran fossils appear in deep water sediments in Newfoundland shortly after the Gaskiers glacials (Narbonne and Gehling, 2003). However, microfossils in South China suggest that the first Metazoa may have in fact evolved much earlier, in the earliest Ediacaran Period (Yin et al., 2007; Zhu et al., 2007). Since the redox state of the oceans has a profound impact on the biosphere, resolving the precise timing and nature of the Ediacaran oxygenation event and possible earlier fluctuations in the oxidation state of the oceans is required to clarify the still uncertain relationships between eukaryotic diversification and environmental change during the Neoproterozoic and Cambrian.

The carbon isotope record of marine carbonates ($\delta^{13}\text{C}_{\text{carb}}$) is exceptional within the scope of Earth's history. Neoproterozoic carbonates are characterized by typically highly positive $\delta^{13}\text{C}_{\text{carb}}$ values, with an average of approximately +5‰ (but with values commonly as high as +8‰ and rarely up to +12‰), punctuated by negative excursions that in some instances, drop below mantle values (−6‰; Halverson et al., 2005). Assuming a steady-state carbon cycle and constant, small fractionation between marine carbonate and seawater-dissolved inorganic carbon (DIC), the fraction of total carbon buried as organic matter (f_{org}) can be defined using the lever rule (e.g. Kump and Arthur, 1999) as

$$f_{\text{org}} = \frac{\delta^{13}\text{C}_{\text{carb}} + 6}{\Delta_p} \quad (1)$$

where Δ_p is the average net fractionation between contemporaneously produced carbonate and organic matter, essentially due to photosynthetic processes. For the Neoproterozoic, Δ_p is approximately 30‰ (Hayes et al., 1999) but in particular basins and at certain times, it appears to be highly variable (e.g. Fike et al., 2006). Assuming steady state, no drastic anomaly in the average value of mantle carbon during the Neoproterozoic, and an insignificant isotopic fractionation associated with carbonation of the oceanic crust (e.g. Hayes and Waldbauer, 2006), the lever rule requires $f_{\text{org}} \approx 0.4–0.5$ through most of the Neoproterozoic, plummeting during short periods to values as low as 0.1. If we consider that $f_{\text{org}} = 0.18$ in the present oceans (Hayes et al., 1999), the organic carbon burial rate during most of the Neoproterozoic Era must have been two to three times higher than today for most of the Neoproterozoic, decreasing to nearly half that value during glaciations.

This observation can be explained in terms of high rates of primary productivity, efficient organic carbon burial, or a combination of the two factors. In favour of the enhanced bioproductivity hypothesis (e.g. Kaufman et al., 1997; Gaucher, 2000; Gaucher et al., 2004b) are low-diversity, high-abundance acritarch assemblages interpreted to reflect recurrent eutrophic conditions in the Neoproterozoic (e.g. Gaucher, 2000, 2007; Gaucher et al., 2004b; Nagy et al., 2009). Enhanced bioproductivity has been also invoked as a mechanism of peak oil generation, black shale deposition and onset of climate cooling in the Phanerozoic (e.g. Cretaceous: Caldeira and Rampino, 1991; Barnes, 1999 and references therein). On the other hand, the alternative hypothesis of an unusually high organic carbon burial efficiency is supported by an above-average area of passive

margins in the Neoproterozoic (Bradley, 2008), many of which were clustered in the low latitudes (Kirschvink, 1992a; Evans, 2000; Li et al., 2008b) where primary productivity is concentrated. In either case, it is likely that the high average $\delta^{13}\text{C}$ of marine carbonates was directly linked to the unique tectonic history of the Neoproterozoic.

Negative $\delta^{13}\text{C}$ anomalies are the second hallmark of the Neoproterozoic–Cambrian carbon isotope record (Figure 1.1). While such anomalies can also be explained by steady-state solutions (most easily a drop in f_{org} ; Kump and Arthur, 1999), $\delta^{13}\text{C}$ values well below the canonical mantle value of -6‰ and, in places, apparently sustained for hundreds of thousands to millions of years (well in excess of the residence time of DIC in the oceans), strongly suggest non-steady state solutions. It should be noted that such extraordinary anomalies, such as the so-called Shuram (or Wonoka) anomaly in the middle Ediacaran, in which $\delta^{13}\text{C}$ drops as low as -12‰ and remained $< -6\text{‰}$ for at least a million years, if not much longer (e.g. Le Guerroué et al., 2006), invariably solicit suggestions of secondary origins (e.g. Kennedy et al., 2001; Bristow and Kennedy, 2008). Such scepticism is necessary in light of such highly unusual carbon isotope values. In the case of the ca. 580 Ma Shuram anomaly, however, virtually the identical carbon isotope pattern is reproduced in thick sections (usually several hundreds of metres; Halverson, 2006) on at least eight separate cratons. In the case of Siberia, the anomaly occurs in limestone preserving high ($> 3,000$ ppm) Sr concentrations (Pokrovskii et al., 2006). Not only would a diagenetic mechanism require an extremely massive transfer of sedimentary organic carbon into replacement carbonate minerals, but also to produce such a similar carbon isotope pattern through secondary processes in so many geographically separated locations seems even more non-actualistic than prevailing models to explain such anomalies in terms of carbon isotope composition of seawater.

If indeed primary, then seemingly the only explanation for the Shuram anomaly is a massive addition of carbon derived from a reduced (i.e. ^{13}C -depleted) carbon reservoir to the oceanic DIC reservoir. As discussed in more detail in Chapter 10, this could in theory be accomplished through release of methane from sedimentary clathrates or leakage of methane in a sulphate-poor ocean (e.g. Schrag et al., 2002), continental weathering of sedimentary organic matter (Workman et al., 2002) or the partial oxidation of a very large dissolved organic carbon reservoir in the oceans (Rothman et al., 2003). While the latter hypothesis is gaining traction (Fike et al., 2006; McFadden et al., 2008), it does not explain some of the earlier Neoproterozoic $\delta^{13}\text{C}$ anomalies (see Chapter 10) and no firm mechanism has been established to account for the unusual build up of DOC at this time. Another quandary regarding the Shuram anomaly is the huge demand of oxidants required to generate it (Bristow and Kennedy, 2008) at a time apparently immediately preceding and perhaps overlapping the first evidence for oxygenation of the deep ocean (Canfield et al., 2007) and first appearance of the Ediacaran biota (Narbonne and Gehling, 2003). The jury is still out on the driver, timing, timescale and significance of this extreme carbon isotope anomaly.

Even if the smoking gun for the Shuram anomaly can be identified, at least three and maybe four other prominent negative $\delta^{13}\text{C}$ anomalies, for which no consensus mechanism has been identified, occur in the middle Neoproterozoic. Like the Shuram anomaly, which appears to initiate prior to the middle Ediacaran Gaskiers glaciation (Halverson et al., 2005), negative anomalies presage two Cryogenian glaciations (Halverson et al., 2005; McCay et al., 2006). This consistent pattern of downturns in $\delta^{13}\text{C}$ preceding glaciation indicates a robust link between major perturbations to the global carbon cycle and icehouse events, begging the question of whether all such negative anomalies coupled to global cooling were driven by the same mechanism. But in this case, how do we explain negative anomalies that do not coincide with glaciation? Clearly, we have not yet decrypted the Neoproterozoic carbon isotope code.

1.4. CLIMATIC EXTREMES AND CONUNDRUMS

Neoproterozoic glacial sediments are widespread across the globe, so much so that both Douglas Mawson and Briand Harland recognized, over half a century ago, that these *infraCambrian* ice ages must have been unusually severe. Despite the episodic challenges to the glacial origin (e.g. Schermerhorn, 1974; Eyles and Januszczak, 2004; Direen and Jago, 2008) of many of the diamictites and associated deposits typically classified as glaciogenic, the prevailing view is that there were multiple, widespread glaciations. Establishing the age and global correlation of these glacial deposits, on the other hand, remains a topic of considerable disagreement and debate. It is now clear that there were three or more separate glaciations: at least two during the Cryogenian, and at least one (ca. 580 Ma; Thompson and Bowering, 2000; Bowering et al., 2003b; Calver et al., 2004) during the Ediacaran Period. But whereas new radiometric ages appear to be validating a synchronous end to the end-Cryogenian (i.e. Marinoan or Elatina) glaciation at 635 Ma (Hoffmann et al., 2004; Condon et al., 2005; Zhang et al., 2008b), the timing of earlier glaciations is becoming increasingly convoluted, with ages on alleged middle Cryogenian

glacial deposits spanning nearly 100 myrs, from ca. 745 Ma in southern Africa (e.g. Kaigas and Chuos formations, Frimmel et al., 1996c; Key et al., 2001) to ca. 658 Ma from the *sensu stricto* Sturtian glacials (Merinjina Formation) of South Australia (Fanning, 2006), with a host of ages in between (Figure 1.1; for a recent review of these ages, see Allen and Etienne, 2008 and Xu et al., 2009). Slightly younger Re-Os ages from the Tapley Hill Formation and other equivalent interglacial sediments in Australia (Kendall et al., 2007, 2006) appear to reinforce a relative young age for the Sturtian glaciation, but imply a very short duration for the interglacial succession if the base of the type Ediacaran section is truly 635 Ma. These young ages for the interglacial sediments also conflict with a single U-Th-total Pb age of 680 ± 23 Ma from an authigenic monazite in the Enorama Shale, that overlies the Tapley Hill Formation (Mahan et al., 2007). In summary, controversy remains over the ages and correlation of the earlier Cryogenian glaciations and new ages seem to raise as many new questions as they resolve.

All reliable palaeomagnetic determinations thus far obtained for cratons glaciated during the Cryogenian Period¹ indicate middle to low palaeolatitudes (e.g. Evans, 2000; Hoffman and Schrag, 2002). Since many of these syn-glacial deposits, including the famous tidal rhythmites of the Elatina Formation in South Australia (e.g. Williams, 1996) were deposited in the oceans, it is thus clear that glaciers reached sea level in the tropics, in many places transgressing carbonate platforms – a scenario that has not arisen since the Neoproterozoic. The superposed, thick carbonates that were deposited in many cases with little or no evidence of a depositional hiatus or reworking of the uppermost glacial deposits (Williams, 1979; Fairchild, 1993; Kennedy, 1996; Hoffman and Schrag, 2002) complete the picture of extreme climate switches that epitomize the Neoproterozoic Earth system. These cap carbonates invariably preserve negative carbon isotope excursions, which illustrate unequivocally that the most severe glacial events in Earth's history were intimately linked to perturbations to the global carbon cycle (Kaufman et al., 1997). Hypotheses abound for the origin of the cap carbonates and their affiliated negative $\delta^{13}\text{C}$ signatures (Kaufman and Knoll, 1995; Kennedy et al., 2001; Shields, 2005) and both are pillars of the snowball Earth hypothesis (Hoffman et al., 1998), but are not easily explained in other models that attempt to account for low-latitude glacial deposits, such as the high obliquity hypothesis (e.g. Williams, 1975, 1993) and the collapse of orbiting ice rings into the atmosphere (Sheldon, 1984). An alternative attempt to challenge the global nature of the glaciations, the 'zipper-rift' hypothesis (Eyles, 2008), which explains the Neoproterozoic glacial deposits as products of glaciated rift shoulders in the low latitudes, cannot account for the many low-latitude and extensive, end-Cryogenian glacial deposits that are found on tectonically stable, thermally subsiding basins, such as in northern Namibia, South Australia and northwestern Canada.

The so-called cap carbonates are extraordinary by any measure, hosting a suite of unusual sedimentary and geochemical features (Hoffman and Schrag, 2002) that cannot be easily explained by any modern analogue. For example, the 'cap dolostones' and associated barite and aragonite seafloor cements forming the base of the 635 Ma post-glacial transgressive sequence (Hoffman et al., 2007) contain isotopic signatures (e.g. boron isotopes in carbonate and triple oxygen isotopes in sulphate; Kasemann et al., 2005; Bao et al., 2008) indicative of very high $p\text{CO}_2$ in the aftermath of glaciation, while mega-oscillation ripples suggest sustained, intense winds whose shear could penetrate 200–400 m water depth (Allen and Hoffman, 2005). The barite cements and other physical and chemical features of the cap carbonate are also consistent with a highly physically and chemically stratified ocean, a predictable consequence of rapid melting of an immense volume of continental ice (e.g. Shields, 2005; Hoffman et al., 2007). However, the timescale of the meltback from snowball glaciation is a matter of serious debate (Hoffman et al., 2007). While it has commonly been assumed that continental ice sheets would melt in just a few thousand years, based on the large positive albedo feedback and assumed high $p\text{CO}_2$ (e.g. Hyde et al., 2000), palaeomagnetic data showing multiple magnetic reversals in coeval cap dolostones in the Paraguay Belt, Brazil (Trindade et al., 2003) and South Australia (Raub and Evans, 2006) challenge this assumption. If these are true reversals contemporaneous with deposition of the cap dolostone, then they imply a timescale for post-glacial melting on the order of hundreds of thousands to millions of years, inconsistent with catastrophic deglaciation as envisaged in the snowball Earth hypothesis.

Unfortunately, radiometric dating seems unlikely to resolve this debate any time soon, for not only would it be remarkable to find volcanic horizons at the right levels of a cap dolostone, but even the highest resolution zircon U-Pb ages are unlikely to resolve the difference between a few thousands of years and few hundred thousand years (Bowring and Schmitz, 2003). Nor has geochronology proved decisive in testing the time span of the presumed snowball Earth events, which are predicted to last approximately 10 myrs (Hoffman et al., 1998). While some attempts to constrain the time span of the Neoproterozoic glaciations have proven consistent with the snowball hypothesis, such as subsidence analysis (Hoffman et al., 1998) and measurement of Ir anomalies in cap carbonates (Bodiselsch et al., 2005), these methods are indirect and not as convincing as direct radiometric ages.

¹ The Cryogenian Period has not yet been formally defined, but its upper boundary is already set to the base of the Ediacaran Period (ca. 635 Ma) and will surely span all prior Neoproterozoic glaciations.

This difficulty in precisely dating the time span of Neoproterozoic glaciations and using the sedimentary record to test the snowball hypothesis is also due to the fact that this record is fundamentally incomplete. Thus, even where there are thick glacial successions, determining their timing of deposition relative to the history of the glacial event is difficult (Hoffman, 2005). The documentation of thick and complex glacial successions (e.g. Christie-Blick et al., 1999; McMechan, 2000; Allen and Etienne, 2008) alone does not contradict the snowball Earth hypothesis, for coupled climate-ice sheet modelling suggests that even under full snowball conditions, thick, wet-based glaciers would grow on the continents within a few hundreds of thousands of years of the initial freeze over (Donnadieu et al., 2003). Furthermore, a large part of the glacial record may have been deposited during either the initial, pre-snowball phases or just prior to total meltback (Hoffman, 2005). Thus, it is likely that the physical processes responsible for the Neoproterozoic glacial sedimentary record would not be radically different than those operating in present glacial environments.

More crucial to the snowball Earth hypothesis is evidence of persistent open water during the glaciation, if it can be demonstrated that this open water existed in the low latitudes at any time other than the end of the glaciation. This question is not simply an academic debate over whether the Earth experienced a 'hard' or 'soft' (i.e. 'Slushball Earth') global glaciation, for even as little as 10^4 km² of open water in the tropics might be sufficient to prevent sufficient CO₂ to build up in the atmosphere to overcome the high albedo of a virtually ice covered globe due to removal of carbon alteration of oceanic crust (Le Hir et al., 2008) – this assuming less than 0.2 bar of CO₂ is sufficient to initiate melting, which has been questioned by Pierrehumbert (2004). Evidence for such open water may be found in the form of oscillation ripples in the upper part of multiple cycles in the late Cryogenian Fig Formation in Oman (Leather et al., 2002; Allen and Etienne, 2008). Others have argued for extensive open water based on computer climate simulations (Hyde et al., 2000; Peltier et al., 2007), the survival of several fossil taxa through glacial events (Corsetti et al., 2003; Moczyłowska, 2008a), biomarkers (Olcott et al., 2005) and the theoretical effects of global ice cover on phytoplankton and the rest of the marine biota (Gaidos et al., 1999; Corsetti et al., 2006).

This list of papers in support of or opposition to the snowball Earth hypothesis is too long to review in full in this chapter. However, a pair of recent papers by Bao et al. (2008, 2009) establishes convincingly that at least the end-Cryogenian glaciation was an exceptional event. Specifically, they have documented large negative $\Delta^{17}\text{O}$ anomalies in sulphate, which are most readily explained by extremely high $p\text{CO}_2$, both during (12,500–80,000 ppm) and after (> 10,000 ppm) the glaciation. High $p\text{CO}_2$ in the aftermath of glaciation is consistent with, but not unique to the snowball Earth hypothesis, but no other current hypothesis can rationalize such high $p\text{CO}_2$ during glaciation.

1.5. PERMISSIVE ECOLOGY AND NEOPROTEROZOIC-CAMBRIAN CLIMATE

Neoproterozoic glaciations may have played a key role in the diversification of eukaryotes and especially metazoans (Knoll and Walter, 1992). In the concept of 'permissive ecology' (Knoll, 2003b), Neoproterozoic ice ages provide both a negative and a positive influence on organisms. On the negative side, harsh glacial conditions, followed by extremely hot climates were an ecological bottleneck, clearly associated with acritarch extinction events (Vidal and Knoll, 1983; Vidal and Moczyłowska-Vidal, 1997; Moczyłowska, 2008a; see Chapter 9.1). Indeed, a compilation of acritarch diversity through the Neoproterozoic and Cambrian (Figure 1.1; Knoll et al., 2006, see Chapter 9.1) reveals a conspicuous dearth of acritarchs spanning at least two Cryogenian glaciations.

On the other hand, ice ages also foment biological diversification by providing vast ecospace to be colonized when ice retreats and climate stabilizes (Knoll, 2003b). This effect is presumably evidenced by the diversification of vendobionts and metazoans in the aftermath of the Gaskiers glacial event (Narbonne and Gehling, 2003). Perhaps even more impressive is the apparent diversification of acanthomorphic acritarchs (Zhou et al., 2007; Figure 1.1). In the latter case, however, an alternative hypothesis linking the Acraman impact in Australia to acritarch diversification cannot be ruled out (Grey et al., 2003; Grey, 2005; see Chapter 9.1), but in any case, still links diversification with environmental catastrophe. Knoll (2003b) further hypothesized that similar evolutionary radiations of eukaryotes did not take place in the aftermath of the older Cryogenian glaciations because there was not enough oxygen to sustain complex eukaryote physiology. A review of the possible relationships and feedbacks between Neoproterozoic ice ages and the biosphere has been provided by McMenamin (2004).

Decreasing amplitudes and increasing frequency of $\delta^{13}\text{C}$ oscillations characterize the Neoproterozoic-Cambrian transition (Brasier and Sukhov, 1998; Shields and Veizer, 2002; Maloof et al., 2005; Chapter 10) and coincide with a shift to a prevailing warm climate (Gaucher et al., 2007b). A warm Cambrian climate is indicated by apparently high $p\text{CO}_2$ at this time (e.g. Berner, 2004; Bao et al., 2008) and consistent with cyanobacterial and algal calcification events (Riding, 1994) and skeletal carbonate mineralogy (Zhuravlev and Wood, 2008). Change from a highly

unstable Neoproterozoic global climate into a relatively stable and warm Cambrian environment has been ascribed to the progressive exhaustion of nutrients and establishment of a Cambrian superoligotrophic ocean (Martin, 1996; Barnes, 1999). From a permissive ecology point of view, both climate warming and climate stabilization removed a pre-existing stress factor, likely enabling the explosive diversification of metazoans. However, as we will discuss below, other, non-ecological factors were paramount in triggering the ‘Cambrian explosion’.

The Cambrian explosion was preceded by a Neoproterozoic evolutionary radiation. Indeed, we may say that the Cambrian explosion had a long Neoproterozoic fuse. At the dawn of the Neoproterozoic, the oceans were already inhabited by eukaryotes that had reached macroscopic size and a multicellular grade of organization (Butterfield and Rainbird, 1998; Butterfield, 2000; Porter, 2004a; Knoll et al., 2006). Eukaryotic phytoplankton (the presumed affinity of most acritarchs) underwent two major periods of diversification in the Neoproterozoic (Figure 1.1), the first in the Tonian-early Cryogenian and the second (i.e. the ECAP: Ediacaran Complex Acanthomorph Palynoflora: Grey et al., 2003) in the early-middle Ediacaran. The Tonian-Cryogenian assemblage suffered a severe mass extinction in the Cryogenian, presumably related to glaciation. Acritarch diversity then remained low throughout the remainder of the Cryogenian, but a few taxa survived through to the Ediacaran Period (Moczyłowska, 2008a). The appearance of the ECAP in the middle Ediacaran, as suggested by the Australian record (Grey et al., 2003) or in the early Ediacaran, as suggested by the South China record (Zhu et al., 2007) was a truly explosive event (Vidal and Moczyłowska-Vidal, 1997; Knoll et al., 2006; Moczyłowska, 2008a; see Chapter 9.1). The ECAP suffered arguably the most severe Neoproterozoic mass extinction in the middle Ediacaran, with 75–90% of all species becoming extinct (Vidal and Moczyłowska-Vidal, 1997; see Chapter 9.1).

Judging from their fossil record, protozoans were also a Neoproterozoic innovation. The oldest fossil protozoans are the so-called vase-shaped microfossils (VSM), which appear in the pre-glacial Cryogenian (ca. 800 Ma) and have been convincingly classified as testate amoebae (Vidal, 1976; Porter et al., 2003). Agglutinated foraminifers (*Titanotheca coimbrae*) have been described from the late Ediacaran Arroyo del Soldado Group in Uruguay (Gaucher and Sprechmann, 1999; see Chapters 4.3 and 9.2), showing that amoeboid protozoans continued to diversify in the later Neoproterozoic. Ciliates have been recently described from the Doushantuo Formation in China (Ediacaran, 580 Ma), adding to the known diversity of Neoproterozoic Protozoa (Li et al., 2007). The advent and diversification of protozoans shows that heterotrophy reached a new level of complexity in the Neoproterozoic, although its origins may be considerably older (Bengtson, 2002). The enhanced primary productivity characteristic of Neoproterozoic oceans, leading to acritarch blooms (Gaucher, 2000, 2007; Gaucher et al., 2004b), may have promoted the diversification of eukaryotic predators/grazers (Porter and Knoll, 2000). The first evidence of macrophagous predation among metazoans and their implications will be dealt with below.

1.6. EMERGENCE OF METAZOA: A NEW WORLD ORDER

Arguably the most important Neoproterozoic biotic innovation was the advent of metazoans. Among the *bona fide* metazoan fossils occurring in Neoproterozoic successions are sponges (*Palaeophragmodictya*: Gehling and Rigby, 1996; Brasier et al., 1997), cnidarians (*Namacalathus*: Grotzinger et al., 2000; *Vendoconularia*: Ivantsov and Fedonkin, 2002; *Corumbella*: Babcock et al., 2005; *Quadratitubus* and *Ramitubus*: Liu et al., 2008), molluscs (*Kimberella*: Fedonkin and Waggoner, 1997; Fedonkin et al., 2007b), arthropods (*Parvancorina*: Lin et al., 2006) and possibly annelids (*Cloudina*: Hua et al., 2005). The interpretation of the problematic fossil *Otavia* in middle Cryogenian rocks in Namibia as a sponge (Brain et al., 2001, 2003, 2008) and the occurrence of biomarkers typical of sponges in equivalent rocks in Oman (Love et al., 2009) suggest that the Porifera may have evolved significantly earlier and prior to the final global glaciation. The evolutionary picture of the synoptic palaeontological record closely resembles molecular clock estimates of key divergences of early Metazoa, the ages of which have been significantly reduced in recent years by the use of more precise calibration methods (i.e. based on invertebrates rather than vertebrates; Peterson and Butterfield, 2005). In their recent compilation of genetic data by Peterson et al. (2008), while Metazoa are rooted in the Cryogenian (with, e.g., the calcisponges diverging by ca. 760 Ma), bilaterian diversification was concentrated in the Ediacaran Period.

The evolution of the Vendobionta (Seilacher, 2007b and references therein) likely represents a separate radiation of organisms comparable to the Cambrian radiation of metazoans (Shen et al., 2008a). According to Shen et al. (2008a), the ‘Avalon explosion’ represents an independent, failed experiment with an evolutionary pattern similar to that of the Cambrian explosion. The affinities of the Vendobionta remain elusive, and recent hypotheses even deny their multicellular nature, suggesting that they represent giant foraminifera (xenophyophores, Seilacher, 2007b). Many, if not most, discoidal forms may actually represent microbial colonies, as argued by Grazhdankin and Gerdes (2007).

The advent of skeletons was a major Neoproterozoic innovation (Figure 1.1), which had many important repercussions: (a) it significantly changed the surface cycles of several elements, such as Ca, Si, P and C; (b) it enabled the eukaryotes to become reef builders and take over the reef ecosystem, a role previously monopolized by prokaryotes (cyanobacteria); and (c) it set the stage for a ‘Darwinian arms race’ (Vermeij, 1989), which fully developed in the Cambrian. Neoproterozoic shelly fossils include carbonate skeletons as in *Cloudina* (Germs, 1972a), *Namacalathus* (Grotzinger et al., 2000) and *Namapoikia* (Wood et al., 2002), siliceous scales as in the Tindir biota (Allison and Hilgert, 1986; McMenamin, 2004) and testate amoebae (Porter and Knoll, 2000), siliceous sponge spicules (Brasier et al., 1997), possibly phosphatic skeletons as in *Waltheria* (Gaucher and Sprechmann, 1999) and agglutinated protists like *Titanotheca* (Gaucher and Sprechmann, 1999; see also Chapter 9.2).

What may have triggered the advent of skeletons in the Neoproterozoic? A hint is provided by predatorial borings in *Cloudina* shells (Bengtson and Zhao, 1992; Hua et al., 2003) and in unmineralized tubular fossils (*Sinocyclocyclus*, Liu et al., 2008), clearly showing that macrophagous predators were extant and food webs were likely complex by late Ediacaran times (Bengtson, 2002). The ‘Darwinian arms race’ or ‘trophic escalation’ frequently invoked as one of the main drivers of the Cambrian explosion (Vermeij, 1989; Gaucher and Sprechmann, 1999, Dzik, 2007; Chapter 9.2) was already underway in the late Neoproterozoic. The gap of ca. 40 myr between the earliest evidence of macrophagous predation and the Cambrian explosion may be explained by an ecological ‘inhibitor’, such as climatic instability and oxygen deficiency, typical of the Cryogenian and Ediacaran. Removal of these ecological barriers may have been a key factor leading to the Cambrian evolutionary radiation.

The response of eukaryotes to predation has been recently summarized by Jim Gehling as the ‘Dig, Defend or Depart’ (or Die!) strategy. Benthic organisms that could not build a mineralized skeleton (‘Defend’) may have become planktic (‘Depart’) to escape selective pressure (Bengtson, 2002). Butterfield (1997) argued that the advent of spiny acritarchs (acanthomorphs) may have followed this strategy. The third possible anti-predatory response was to dig for shelter, a behaviour aptly referred to as the ‘Verdun Syndrome’ by Dzik (2007). This author argued that the vast majority of latest Ediacaran and earliest Cambrian infaunal trace fossils represent shelters of animals feeding above the sediment surface, highlighting the protective function of the burrows. Finally, the ‘agronomic revolution’ (Seilacher, 1996, 1999), whereby animals were able to exploit the resources contained in the sediment, initiated near the Ediacaran/Cambrian boundary and radically changed the benthic ecosystem by the recycling of sediments and nutrients and the grazing of biomats, with obvious implications for the carbon cycle (McMenamin, 2004; Chapter 9.3). The Precambrian ‘matgrounds’ were irreversibly succeeded by Phanerozoic ‘mixgrounds’ (Seilacher, 1999). The final decline of stromatolites in the late Neoproterozoic may also be related to grazing pressure (see discussion in Bengtson, 2002). The agronomic revolution opened up a whole new set of ecological niches, which must have contributed to the Cambrian explosion.

1.7. CONCLUSIONS

The Neoproterozoic stands out as a period of innovations and upheavals. The extreme palaeoclimatic, palaeoceanographic and biotic events that characterize the Neoproterozoic Era may ultimately be a result of its unusual tectonic history. The final accretion and subsequent break-up of Rodinia, followed by the amalgamation of Gondwana were probably paramount in influencing Earth’s surface environments, although the precise mechanisms remain controversial. Deep-Earth processes, such as mantle avalanches and superplumes, may have been the unheralded engines of a dynamic Neoproterozoic tectonic regime. Rapidly evolving palaeogeography may have in turn contributed to biogeochemical and climatic oscillations, which themselves were likely inextricably linked to biospheric evolution and ultimately the Cambrian explosion. Thus, Neoproterozoic–Cambrian Earth history is a case in point of the complexity and intrigue of the interactions between the deep Earth, the lithosphere, the oceans, the atmosphere and the biosphere. Without a doubt, continued vigorous research and debate about this fascinating Era will yield ever greater insight into the behaviour of the Earth system.