

MACROEVOLUTION AND MACROECOLOGY THROUGH DEEP TIME

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Abstract: The fossil record documents two mutually exclusive macroevolutionary modes separated by the transitional Ediacaran Period. Despite the early appearance of crown eukaryotes and an at least partially oxygenated atmosphere, the pre-Ediacaran biosphere was populated almost exclusively by microscopic organisms exhibiting low diversity, no biogeographical partitioning and profound morphological/evolutionary stasis. By contrast, the post-Ediacaran biosphere is characterized by large diverse organisms, bioprovinciality and conspicuously dynamic macroevolution. The difference can be understood in terms of the unique escalatory coevolution accompanying the early Ediacaran introduction of eumetazoans, followed by their early Cambrian (Tommotian) expansion into the pelagic realm. Eumetazoans reinvented the rules of macroecology through their invention of multi-

trophic food webs, large body size, life-history trade-offs, ecological succession, biogeography, major increases in standing biomass, eukaryote-dominated phytoplankton and the potential for mass extinction. Both the pre-Ediacaran and the post-Ediacaran biospheres were inherently stable, but the former derived from the simplicity of superabundant microbes exposed to essentially static, physical environments, whereas the latter is based on eumetazoan-induced diversity and dynamic, biological environments. The *c.* 100-Myr Ediacaran transition (extending to the base of the Tommotian) can be defined on evolutionary criteria, and might usefully be incorporated into the Phanerozoic.

Key words: macroevolution, macroecology, Proterozoic, Ediacaran, Cambrian, eumetazoans, coevolution.

THE fossil record contributes uniquely to our understanding the evolutionary processes by tracking the biosphere through deep time, on a scale of millions to hundreds of millions of years. The long-term patterns recovered from the Phanerozoic fossil record demonstrate a range of phenomena not obvious from uniformitarian extrapolation, including widespread occurrence of evolutionary stasis/cladogenesis, long-term ecosystem stability, and recurrent intervals of major diversification and mass extinction (Gould 1985; Brett *et al.* 1996; Jablonski 2005). Whether or not these macroevolutionary patterns imply a hierarchy of emergent evolutionary processes (Erwin 2000; Jablonski 2000; Leroi 2000), they have rightly acquired a first-order role in resolving the structure and dynamics of the biosphere over the past 500–600 million years. That said, it is worth appreciating the much greater antiquity of life on Earth, extending back to at least 3500 Ma (Schopf 2006) – which poses an important question: are the macroevolutionary ‘rules’ drawn from Phanerozoic palaeobiology more generally, perhaps even universally, applicable? If so, then we have a valuable tool for addressing the early, mostly cryptic, record of life on Earth. If not, then new context-dependent rules will need to be derived, and their underlying mechanisms explored.

In the absence of evidence to the contrary, preference goes to the null hypothesis: that Phanerozoic-style macroevolution, like Darwinian-style microevolution, is universal. Indeed, these are the uniformitarian premises that sustain the search for ancient Phanerozoic-like life, both in the early fossil record and through the application of (Phanerozoic-calibrated) molecular clocks (e.g. Hedges *et al.* 2004; Peterson and Butterfield 2005; Berney and Pawlowski 2006). Extrapolation of Phanerozoic macroevolutionary modes are specifically invoked in hypotheses for pre-Phanerozoic mass extinctions (e.g. Vidal and Knoll 1982; Amthor *et al.* 2003; Grey *et al.* 2003), incumbent replacement (Grey *et al.* 2003) and major radiation (Knoll 1992; Philippe *et al.* 2000).

Cavalier-Smith (2002, 2006) has offered a challenging variation on this theme by focusing on Simpson’s macroevolutionary concept of ‘quantum evolution’. In this view, it is the Phanerozoic pattern of adaptive radiation that serves as the guiding principle, with the evolution of the eukaryotic cell expected to initiate a rapid and essentially saturating diversification. The absence of such a pattern in the early record thus becomes an argument for the absence of early (i.e. pre-Neoproterozoic) eukaryotes. Certainly the two billion-year interval separating the first

stratigraphic evidence of eukaryotes (in the late Archean; Brocks *et al.* 1999) from their first measurable radiation (in the early Ediacaran; Peterson and Butterfield 2005) strikes one as an extraordinarily long time, but it is important to appreciate that this temporal intuition derives solely from our Phanerozoic experience (Butterfield 2004). Macroevolutionary uniformity is perfectly legitimate as a null hypothesis, but to use it to infer pre-Phanerozoic tempo and mode merely begs the question. In this essay, I will argue that pre-Ediacaran macroevolution differed fundamentally from all that followed, owing to an absence of eumetazoans and their ‘quantum’ effects on macroecology.

THE PRE-PHANEROZOIC FOSSIL RECORD

The only useful test of pre-Phanerozoic macroevolution lies in an independent assessment of its fossil record. As in the Phanerozoic, this must be evaluated in the context of ecological variation, taphonomic/taxonomic bias, and the steep degradation of signal with age and outcrop area (Peters 2005); indeed, the paucity of Archaean data effectively limits this exercise to the Proterozoic. With notable exceptions in the transitional Ediacaran Period, the Proterozoic body-fossil record differs qualitatively from its Phanerozoic counterpart in the absence of biologically controlled biomineralization and the near absence of macroscopic forms, a habit often viewed as having more taphonomic than evolutionary significance (see Runnegar 1982). Despite the taphonomic challenges, the Proterozoic preserves a significant range of fossils, both prokaryotic and eukaryotic, which commonly equal or exceed the quality of preservation found in Phanerozoic fossil Lagerstätten (Butterfield 2003).

Cyanobacteria

Cyanobacteria and cyanobacteria-like microfossils dominate carbonate-hosted microbial mat biotas from at least the mid-Palaeoproterozoic (e.g. Hofmann 1976), and are conspicuous constituents of most Meso-/Neoproterozoic shale-hosted assemblages (e.g. Butterfield and Chandler 1992; Butterfield *et al.* 1994). At the same time, a pervasive expression of 2-methylhopanoid molecular biomarkers, even in deeper-water shales, points to a predominance of cyanobacteria in the Proterozoic plankton (Summons *et al.* 1999).

The distinctive morphologies and cell-division patterns of most of the subsections (orders) of extant cyanobacteria allow positive identification in the fossil record, with all but subsection V (=Stigonematales) recognized from

at least the early Neoproterozoic. Indeed, documentation of mid-late Palaeoproterozoic akinetes [differentiated reproductive structures limited to relatively derived subsections V and IV (=Nostocales)] presents a compelling case for the early establishment of all of the principal lineages of cyanobacteria (Tomitani *et al.* 2006). Such a conclusion is not particularly surprising in light of the considerably deeper record of cyanobacterial biomarkers (Brocks *et al.* 1999) and atmospheric oxygenation (Catling *et al.* 2005). What is surprising, however, is the remarkable evolutionary stasis experienced by cyanobacteria since that time: these are the ultimate in ‘living fossils’, neither going extinct nor giving rise to any significant daughter lineages (at least via cladogenesis) for the past 2000+ myr (Schopf 1994).

Billion-year evolutionary stasis is clearly at odds with the tempo and mode of the Phanerozoic record. Schopf (1994) described the pattern as one of extremely slow or ‘hypobradyletic’ turnover, and accounted for it in terms of the broad ecological tolerances seen in many cyanobacteria. Not all cyanobacteria are extreme generalists, however, and prokaryotes in general are rather better known for their high rates of evolutionary adaptation (e.g. Gogarten *et al.* 2002). In my opinion, the morphological stasis is more likely related to developmental limits set by the prokaryotic grade of organization, not least their single origin of genomic replication which constrains both genome size and morphological ‘evolvability’ (Poole *et al.* 2003). Among non-eukaryotes, cyanobacteria appear to have achieved close to maximum complexity with respect to differentiated cell-types, modes of multicellularity and large size (see Adams and Duggan 1999), and to have done so early in their evolutionary history.

Pre-Ediacaran eukaryotes (taxonomically resolved)

Exhaustion of morphogenetic potential may account for the profound stasis of cyanobacteria but this clearly does not extend to the eukaryotic domain. Cavalier-Smith (2002, 2006) notwithstanding, unambiguously eukaryotic body fossils are known from at least the early Mesoproterozoic (Javaux *et al.* 2003; Knoll *et al.* 2006), and diagnostically eukaryotic biomarkers have been recovered from both the late Archean (Brocks *et al.* 1999) and Palaeoproterozoic (Dutkiewicz *et al.* 2006). Identification of unique eukaryotic signature proteins (ESPs) among extant forms further implies a deep, independent origin for the lineage (Kurland *et al.* 2006). It is possible, even probable, however, that the full morphogenetic potential of eukaryotes was acquired incrementally along its stem-lineage, with their characteristic evolvability representing a relatively derived, possibly crown-group condition.

Only a handful of pre-Ediacaran fossils have been identified as members of extant eukaryotic clades, but these extend the record of crown eukaryotes back to at least the later Mesoproterozoic. Of these, most are multicellular organisms that owe their taxonomic resolution to the preservation of diagnostic cell division patterns. Late Mesoproterozoic (*c.* 1200 Ma) *Bangiomorpha pubescens*, for example, is indistinguishable from the modern filamentous red alga *Bangia* in its intercalary production of radially arranged wedge-shaped cells, distinctive inner and outer cell walls, and differentiation of at least two spore types borne on separate plants (Butterfield 2000). Indeed, the only significant difference between these two taxa is the cellular (vs. filamentous) basal holdfast of the fossil, though even this finds close counterparts within other extant bangiophytes (J. Brodie, pers. comm. 2005).

Late Mesoproterozoic (*c.* 1000 Ma) *Palaeovaucheria* likewise shows a one-to-one morphological comparison with an extant filamentous alga, in this case the largely coenocytic xanthophyte *Vaucheria* (see Butterfield 2004). Although not as character-rich as *Bangiomorpha*, its preserved reproductive structures and evidence for an associated, aestivating, ‘Gongrosira’ phase make a clear case for its assignment to the Vaucheriaceae. Likewise, the large semicoenocytic cells and branching thalli of *c.* 750 Ma *Proterocladus* compare precisely with those of cladophoralean green algae (Butterfield *et al.* 1994), even if their relative simplicity cannot entirely exclude the possibility of convergence. Among unicellular fossils, convincing taxonomic assignment is limited to certain middle Neoproterozoic vase-shaped microfossils (VSMs), which closely mirror the tests of modern testate amoebae (Porter *et al.* 2003).

The basis for this taxonomic resolution, of course, is that the fossils are essentially indistinguishable from their extant counterparts, implying some 750–1200 myr of morphological stasis. These are the ultimate in (eukaryotic) living fossils; but, unlike the case with cyanobacteria, this stasis cannot be ascribed to developmental constraints. By definition, crown-group eukaryotes have all of the basic morphogenetic machinery found in living eukaryotes, including cytoskeleton, multiple origins of chromosomal replication and sexual reproduction (Butterfield 2000, 2004; Poole *et al.* 2003).

Pre-Ediacaran eukaryotes (taxonomically unresolved)

Further evidence of the morphogenetic potential of early eukaryotes is found in a range of taxonomically unresolved fossils. Thus, the modestly macroscopic thalli of middle Mesoproterozoic *Grypania* and Meso-Neoproterozoic *Tawuia* demonstrate an early capacity for large body

size (Walter *et al.* 1990; Kumar 1995, 2001), while the conspicuously spinose walls of Meso-Neoproterozoic *Tappania*, *Trachystytrichosphaera* and *Germinosphaera* identify the early presence of a uniquely eukaryotic cytoskeleton and endomembrane system (see Cavalier-Smith 2002; Javaux *et al.* 2003; Butterfield 2005a; Knoll *et al.* 2006).

Pre-Ediacaran ‘problematica’ also document various grades of eukaryotic multicellularity, from the simple cellular networks/coenobia of *Eosaccharomyces* (*c.* 1000 Ma; see Knoll *et al.* 2006) and *Palaeastrum* (*c.* 750 Ma; Butterfield *et al.* 1994) to the large septate filaments of certain *Grypania* (Kumar 1995) and the semicoenocytic filament-vesicle complex comprising early Neoproterozoic *Cheilofilum* (Butterfield 2005b). Multicellular development of a conspicuously more complex grade is seen in early Neoproterozoic *Tappania* where a large central vesicle gives rise to a corona of multicellular, secondarily anastomosing filaments (with striking similarities to the hyphal fusion of higher fungi), as well as a morphologically distinct *Germinosphaera*-phase (Butterfield 2005a; Knoll *et al.* 2006). The most highly differentiated pre-Ediacaran eukaryote is middle Neoproterozoic *Valkyria*, which preserves at least six distinctive cell types (Butterfield *et al.* 1994).

Taxonomically problematic microfossils with a central non-mineralized vesicle are referred to the ‘Acritarcha’ where they are classified by means of artificial form taxonomy. Even so, most acritarchs have been interpreted as the remains of unicellular protists, primarily phytoplankton cysts (e.g. Knoll 1994; Vidal and Moczydlowska-Vidal 1997), thus conferring a measure of biological as well as macroevolutionary significance. Such promotion may well be legitimate for early Palaeozoic forms, but this patently does not extend to the Proterozoic where major sectors of (eukaryotic) acritarch diversity are now recognized as benthic, vegetative, multicellular and non-protistan (Butterfield 1997, 2001a, 2004, 2005a, b; Knoll *et al.* 2006). Unlike unicellular phytoplankton, an actively growing multicellular organism can be represented by a host of different forms during the course of its accumulative ontogeny and degradative taphonomy, not least through the production of multiple ‘organ taxa’. The lesson from recent population-level studies of pre-Ediacaran acritarch assemblages is that true fossil diversity has been grossly over-estimated as a consequence of simplistic form-taxonomy (see also Alroy 2002): hence, the huge synonymy lists associated with *Tawuia*-type macrofossils (Butterfield *et al.* 1994; Kumar 2001) and the conspicuously declining diversity estimates of pre-Ediacaran fossil Lagerstätten following taxonomic revision (for a sobering example, compare Butterfield and Rainbird 1998 with Butterfield 2005a, b).

The practice of acritarch form-taxonomy has also had a deeply corrupting effect on inferred macroevolutionary patterns, where highs and lows in documented diversity have tended to be interpreted in terms of radiation and extinction (Knoll 1994; Vidal and Moczydlowska-Vidal 1997; Knoll *et al.* 2006). Considered in their biological and stratigraphic context, however, the fluctuations in pre-Ediacaran acritarch diversity are fundamentally less dramatic. Indeed, there is a reasonable case to be made for viewing these fluctuations as little more than a product of sampling (e.g. Peters 2005), compounded by facies-specific ecology (Butterfield and Chandler 1992) and the myriad artefacts of acritarch form-taxonomy (Butterfield 2004, 2005a, b). Knoll *et al.* (2006) have argued that a major Meso-Neoproterozoic radiation of eukaryotes can be detected on the basis of increasing *within-biota* diversity; however, their three exemplars of elevated early-middle Neoproterozoic diversity have yet to be critically re-evaluated: in my estimation, the Svanbergfjellet biota preserves no more than 15 unambiguously eukaryotic species (vs. the 25 estimated by Knoll *et al.* 2006), while the counts from the Chuar and Visingsö biotas are supported by spikes of demonstrably unreconstructed form-taxa.

Huntley *et al.* (2006) found conspicuously more monotonous trends in the pre-Ediacaran acritarch record using a taxon-free morphometric approach, but even here there are obvious sampling biases. By failing to include the relatively diverse Tindir assemblage in their Cryogenian (N2) bin (see Kaufman *et al.* 1992), for example, they recorded a non-existent drop in post-Sturtian/pre-Marinoan disparity. Ongoing work also continues to raise the known diversity and disparity of the earlier record (e.g. Knoll *et al.* 2006; Butterfield, unpublished), leaving conspicuously little to distinguish Mesoproterozoic (M1 and M2) biotas from their early-middle Neoproterozoic (N1 and N2) counterparts.

Despite its shortcomings, the pre-Ediacaran acritarch record preserves a modest diversity of forms that are sufficiently complex to diagnose as biologically distinct entities, and sufficiently common to yield long-term macroevolutionary trends. Almost universally, the emerging pattern is one of profound stasis, with the evolutionary turnover (taxonomic origination and extinction) of pre-Ediacaran acritarchs typically running one to two orders of magnitude more slowly than their early Cambrian counterparts (Knoll 1994), and disparity essentially static from the mid-Mesoproterozoic to the Ediacaran (cf. Huntley *et al.* 2006). Distinctively spinose *Trachyhystrichosphaera*, for example, ranges for some 400 myr without obvious morphological change, while *Tappania* persists for at least 600 myr (Butterfield 2005a), *Chuararia/Tawuia* macrofossils for c. 1000 myr (Kumar 2001; Butterfield 2004), and concentrically sculptured *Valeria*

for over 1100 myr (Hofmann 1999; Knoll *et al.* 2006). Not surprisingly, the pre-Ediacaran acritarch record has yet to yield any useful patterns of biostratigraphic zonation (or indeed any biogeographical partitioning; see below).

Thus, the overarching pattern of pre-Ediacaran eukaryotes, including both taxonomically resolved and problematic forms, is one of minimal morphological diversity and profound evolutionary stasis. Apart from the Mesoproterozoic disappearance of macroscopic *Grypania* (and *Hordyskyia*, if this string-of-beads structure proves to be a eukaryotic fossil; see Knoll *et al.* 2006) there is no compelling evidence of extinction among early eukaryotes, and only the most modest indications of innovation. Pre-Ediacaran communities appear to have been composed almost entirely by 'living fossils' and their ancient equivalents.

Ediacaran eukaryotes

All this changes with the onset of the Ediacaran, which begins with a major radiation of large, conspicuously ornamented acritarchs (Zang and Walter 1992; Knoll 1994; Zhang *et al.* 1998; Grey 2005; Huntley *et al.* 2006; Knoll *et al.* 2006), the first measurable radiation in the whole of the fossil record (Peterson and Butterfield 2005). At the same time, the distinctive and hitherto extinction-proof acritarchs of the pre-Ediacaran disappear, never to return, documenting the first (more or less) measurable extinction event in the whole of the fossil record (Peterson and Butterfield 2005). Most significantly, this turnover of acritarch biotas is accompanied by an unprecedented, order-of-magnitude increase in evolutionary rates, such that all of these novel early Ediacaran acritarchs have disappeared within 50 myr of their arrival (Knoll 1994; Peterson and Butterfield 2005). With similar alacrity, the famously problematic macrofossils of the late Ediacaran appear, flourish and disappear in the course of the next 40 myr (Grazhdankin 2004; Narbonne 2005), possibly in concert with a novel diversity of macroscopic algae (Gnilovskaya 1990; Xiao *et al.* 2002; Knoll *et al.* 2006). Acritarchs in the late Ediacaran and earliest Cambrian are represented by a default biota of unornamented sphaeromorphs, followed by a major Tommotian (530–520 Ma) radiation of small, rapidly evolving ornamented forms, probably phytoplankton cysts coevolving with newly introduced meso-zooplankton (Butterfield 1997, 2001a, 2003; Knoll *et al.* 2006). The first unambiguous evidence for eumetazoans occurs in the form of late Ediacaran (> 558 Ma) trace fossils (Martin *et al.* 2000; Grazhdankin 2004), which are preceded by problematic metazoan-like embryos of early Ediacaran age (Xiao 2002).

PRE-PHANEROZOIC MACROEVOLUTION

Much of what is known about Proterozoic diversity derives from exceptionally preserved, but correspondingly rare, biotas offering limited stratigraphic confidence with respect to first and last appearance. Even so, the sampling is sufficient to establish the mutually exclusive distributions of pre-Ediacaran, early Ediacaran and Cambrian ornamented acritarchs. More importantly, even sparse sampling is capable of demonstrating long-term stasis, with a minimum requirement of just two temporally separated data points. The fact that most pre-Ediacaran fossils with a diagnosable morphology exhibit stasis on a 100- to 1000-myr time-scale (vs. the *c.* 10-myr-scale longevity of Ediacaran and younger forms; Knoll 1994, table 3) marks a fundamental break in macroevolutionary expression.

So, what might account for the shift? Certainly there are major geological perturbations associated with this interval, and most of these have at some stage been promoted as environmental triggers (though usually with reference to the considerably younger Cambrian ‘explosion’). Thus, the dramatic glacial episodes immediately preceding the Ediacaran (Hoffman *et al.* 1998), and the marginally younger Acraman impact (Grey *et al.* 2003; Grey 2005) have been interpreted as ecological bottlenecks followed by adaptive radiation, after the manner of the K/T replacement of dinosaurs by mammals. Alternatively, Brasier (1992) and Elser *et al.* (2006) have argued that the biological innovations were induced by substantial shifts in nutrient availability, as reflected in the widespread deposition of Ediacaran phosphorites and black-shales. Major perturbations in $\delta^{13}\text{C}$ and $\delta^{32}\text{S}$ signatures have also been used to infer increases in Neoproterozoic oxygen levels, which may have impacted evolutionary mode by meeting a minimum threshold for large motile metazoans, and/or indirectly through the oxidative release of trace metals necessary for nitrogen fixation (Canfield and Teske 1996; Anbar and Knoll 2002). Undoubtedly some of these phenomena are related to one another, and potentially to the macroevolutionary divide of the early Ediacaran, but the causal connections remain unclear (Butterfield 1997, 2004; Budd and Jensen 2000): unlike the relatively simple biotic replacements associated with the K/T boundary, the pre-Ediacaran/Ediacaran/Cambrian transition entailed a fundamental reorganization of evolutionary and ecological context (see Marshall 2006), while geological/geochemical data point to planetary-scale continuity in nutrient supply and primary productivity since at least the Palaeoproterozoic (Butterfield 1997; Bjerrum and Canfield 2002). Further, neither ice nor nutrients offer any obvious explanation for the appearance of novel morphologies or order-

magnitude increase in evolutionary turnover. A more compelling case can be made for the role of oxygen thresholds (Catling *et al.* 2005), but only on the assumption that eumetazoans were previously present and respiratorially constrained.

The other class of explanation focuses on internal, genetic/developmental thresholds, of which the most unqualified is Cavalier-Smith’s (2002, 2006) hypothesis of late (i.e. early Neoproterozoic), eukaryote-induced, ‘quantum evolution’. In this account, the profound morphological stasis of pre-Ediacaran life is simply the expression of an exclusively prokaryotic biosphere, combined (somewhat less elegantly) with a 400–500-myr delay in eukaryote expansion imposed by the Cryogenian glaciations. The problem here, of course, is the diverse and compelling evidence for a much earlier eukaryotic presence. The mistake is to limit the discussion to developmental potential. Evolution, even macroevolution, is not simply a matter of ‘evolvability’; it is also a reflection of the external selective pressures that make it happen.

The real question, then, is what drives morphological evolution (as opposed to what merely allows it, or might hold it back – the focus of most Ediacaran/Cambrian explosion models). In the Phanerozoic, at least, it is clear that organismal morphology is largely a product of coevolution, whereby novel characteristics in one biological compartment induce secondary novelty in others, giving rise to enhanced sensory and locomotory systems, ecological specialization and escalatory arms races (Vermeij 1994). Indeed, it is this pervasive ‘biological environment’ that gives the Phanerozoic its dynamic character, with special explanation required only for those few lineages that fail to take part; e.g. ‘living fossils’ (Parsons 1993).

In the Phanerozoic, morphological coevolution is driven overwhelmingly by animals, specifically eumetazoans. Unlike sponges, eumetazoans have differentiated tissues and actively interact with organisms capable of morphological response, i.e. other eukaryotes (Peterson and Butterfield 2005). The impact of eumetazoan coevolution, both antagonistic and mutualistic, is widely reflected in the diversification of Phanerozoic protists (e.g. Butterfield 1997, 2001a; Hamm *et al.* 2003), fungi (e.g. Blackwell and Jones 1997), land plants (e.g. Dilcher 2000; Fenster *et al.* 2004) and animals themselves. Indeed, it was the unique ability of eumetazoans to extend coevolutionary ecology into multicellular/macrosopic morphospace, by way of animals preying on animals, that gave rise to Phanerozoic-type trophic structures (Butterfield 2001b), which in turn accounts for the vast majority of all documented diversity. Some three-quarters of described living species are animals, while most of the rest are readily recognized as the product of animal coevolution (Hutchinson 1959; May 1994; Rosselló-Mora and Amann 2001, table 2).

The pervasive coevolutionary influence of eumetazoans means that their presence can be detected via the traits of contemporaneous, coevolving organisms: thus, metabolically expensive pollination syndromes imply pollinators (e.g. Fenster *et al.* 2004) and metabolically expensive defences imply predators. In a palaeontological context, such secondary effects offer a powerful means of assessing the presence/absence/activity of taphonomically cryptic eumetazoans. Like sedimentary trace fossils, coevolved morphological adaptations induced by eumetazoans tend to be much more diverse and readily preserved than the animals themselves (Butterfield 2003). More generally, the inherent 'coevolvability' of eumetazoans means that emergent macroevolutionary signatures provide an independent measure of their activity; thus evolutionary conservatism is recognized as a feature of physically stressed, largely competitor-free environments (e.g. Parsons 1993), not least the ongoing Phanerozoic stasis of *Bangia*-, *Vaucheria*- and *Cladophora*-type metaphytes in desiccating, euryhaline and/or eutrophic settings (see Harlin 1995; Butterfield 2000, 2004). In this light, the conspicuously low diversity and extreme stasis of the pre-Ediacaran fossil record present a compelling case for the absence of pre-Ediacaran eumetazoans (Peterson and Butterfield 2005).

There are, of course, arguments for a considerably earlier appearance of eumetazoans, including inferences from molecular clocks (e.g. Hedges *et al.* 2004; Berney and Pawlowski 2006) and early Cambrian biogeography (Fortey *et al.* 1996; Lieberman 2002), as well as a direct record of putative body and trace fossils (Hofmann *et al.* 1990; Seilacher *et al.* 1998; Rasmussen *et al.* 2002; Fedonkin 2003). Significantly, each of these claims assumes that small, non-biomineralizing and/or planktic eumetazoans will be palaeontologically invisible, thereby justifying 100–1000-Myr lacunae in the fossil record. Such absence might be warranted in the case of body fossils, or even small trace fossils, but it is fundamentally more difficult to mask the impact of eumetazoans on associated organisms and macroevolutionary mode. Eumetazoans do not live in a vacuum, and any reasonable claim for their pre-Ediacaran presence needs also to explain their early ecological and macroevolutionary invisibility. On current evidence, tissue-grade animals capable of preying on other eukaryotes first appeared in the early Ediacaran (Peterson and Butterfield 2005) where they drove hitherto extinction-proof acritarchs to extinction, provoked a radiation of novel ornamented acritarchs, and revolutionized (co)evolutionary tempo and mode. No other hypothesis accounts for these data.

PRE-PHANEROZOIC MACROECOLOGY

Although the introduction of eumetazoan ecology provides a sufficient mechanism for the Ediacaran/Cambrian

radiations, it does not of itself explain the macroevolutionary structure of the pre-Ediacaran biosphere, or its conversion to Phanerozoic/modern rules. For this it is necessary to understand how organismal ecology, diversity, biogeography and productivity interrelate to yield functioning ecosystems, and how such systems would have worked in the absence of eumetazoans. Neither is known with precision, but consideration of the pre-Ediacaran to Phanerozoic record in the light of recent macroecological theory (Brown 1995; Rosenzweig 1995) promises some illumination.

Species-area relationship

The only ecological rule that comes close to being general is the species-area relationship (SAR), whereby species diversity increases in proportion to the area studied following a constant power law (Godfray and Lawton 2001; Martín and Goldenfeld 2006). In the modern biosphere the SAR appears to hold for animals and plants at moderately high values, whereas the relationship for unicellular protists and bacteria is close to flat, a consequence of their small size and high dispersability (Green *et al.* 2004; Horner-Devine *et al.* 2004). Indeed, Finlay (2002) and colleagues argued that organisms smaller than *c.* 1 mm have essentially no biogeography/provinciality (but see Green and Bohannan 2006; Woodcock *et al.* 2006). Combined with astronomical population sizes, global distribution is expected to result in reduced evolutionary turnover as both the opportunities for allopatric speciation and the likelihood of extinction become increasingly limited (Norris 2000). Lynch and Conery (2003) extended this concept to argue for fundamental differences in the genomic evolution of prokaryotes vs. unicellular eukaryotes vs. multicellular eukaryotes.

Small size, global distribution and minimal turnover are also characteristic of pre-Ediacaran eukaryotes, which might then be modelled on the relatively flat SARs of extant phytoplankton and microbial protists (e.g. Finlay 2002; Green *et al.* 2004; Smith *et al.* 2005). Lack of provinciality, however, is not expected to impinge on *global* diversity (see Rosenzweig 2001), and it is clear from the Phanerozoic microfossil record (Norris 2000) that neither small size nor global distribution offers sufficient explanation for the extraordinary morphological conservatism of pre-Ediacaran eukaryotes. The pre-Ediacaran expression of a flat SAR and minimal morphological diversity compares most closely with that of extant bacteria (cf. Horner-Devine *et al.* 2004), despite the fundamentally different controls on prokaryotic/eukaryotic evolvability.

The non-uniformitarian, prokaryote-like, SAR of pre-Ediacaran eukaryotes is largely a product of profound evolutionary stasis. Under such conditions all forms,

regardless of size, would eventually acquire a global distribution, thereby eliminating any biogeographical partitioning (see Willis 1926). The modern SAR is an emergent property of Phanerozoic-style species richness and evolutionary turnover which, in turn, is contingent upon the uniquely disruptive ecology of eumetazoans. Interestingly, the transitional Ediacaran interval was marked by significant increases in organismal size, diversity and evolutionary turnover, but nonetheless remained devoid of biogeographical partitioning (Grazhdankin 2004; Grey 2005), a pattern consistent with the still considerable levels of stasis documented for this time (see Knoll 1994).

Ecosystem stability

One of most debated issues in modern macroecology is the relationship between diversity and stability: the ability of an ecosystem to resist change or to return to equilibrium following perturbation (Lehman and Tilman 2000; McCann 2000). Contrary to May's (1973) linear stability models, most real ecosystems become more stable as species richness increases; thus, it is the unusually simple or simplified communities such as boreal forests and agricultural monocultures that are prone to invasion and/or catastrophic reorganization. Diversity is thought to contribute to stability in a variety of ways, most of which can be viewed as ecological 'insurance', e.g. ecological redundancy, negative covariance and/or 'portfolio' effects (Lehman and Tilman 2000). In multitrophic structures, diversity increases 'connectance' and reduces the average strength of trophic interactions, thereby disbursing the impact of any perturbation (McCann 2000; Butterfield 2001b; Duffy 2002).

Ecosystem stability has been documented at a variety of scales in the Phanerozoic fossil record, including instances of 'coordinated stasis' where fossil 'communities' exhibit taxonomic coherency on a million-year time scale (Brett *et al.* 1996; DiMichele *et al.* 2004). Exactly how this geological-scale stasis relates to the stability phenomena studied by neo-ecologists has yet to be resolved, but there is little doubt that Phanerozoic ecosystems can be modelled broadly on actualistic phenomena, at least some of which can be scaled up to yield macroevolutionary expression (see Butterfield 2001a). For example, the relatively rapid turnover of Cambrian taxa can be related to the simple, direct trophic links of that time, whereas the increasing persistence of post-Cambrian biotas most likely derive from their substantially greater levels of complexity and interconnectedness (see Butterfield 2001b; Bambach *et al.* 2007).

Pre-Ediacaran ecosystems were also stable, but this stability was of a fundamentally different kind: biotas were profoundly simple, yet remained unchanged for hundreds

of millions to billions of years. Undoubtedly the constituent communities enjoyed a degree of dynamic stability relating to metabolic trade-offs and trophic interactions made at a (mostly) unicellular level (cf. Naeem and Li 1998; Bell *et al.* 2005), but this cannot be equated with the myriad, often idiosyncratic effects of eumetazoans and eumetazoan-derived diversity that stabilize most Phanerozoic ecosystems (see Vermeij 1994; Menge 1995; Verity and Smetacek 1996; McCann 2000; Worm and Duffy 2003). It is clear, for example, that the added ecological complexity accompanying the Ediacaran–Cambrian rise of eumetazoans induced a pronounced *reduction* in overall stasis/stability, counter to the expectations of actualistic ecology but intriguingly consistent with May's (1973) widely dismissed linear models (see Sinha and Sinha 2005).

One of the important stabilizing effects in modern ecosystems relates to the availability of diverse life-history strategies among multicellular/macroscopic organisms and the emergent concept of ecological succession, i.e. the tendency of communities to become occupied by increasingly larger, longer-lived, 'K-selected' organisms that increasingly buffer and modify physical environment (Odum 1969). But this is a peculiarly Phanerozoic (and transitionally Ediacaran) phenomenon. Pre-Ediacaran communities were essentially 'instantaneous' owing to the rapid life cycles and global distribution of their microbial, 'r-selected' constituents, the ultimate in environmental trackers (Finlay *et al.* 1997; see DiMichele *et al.* 2004, p. 312). Unbuffered physical environments can of course be highly variable locally, but on a planetary scale these have not changed since the early Proterozoic rise in atmospheric oxygen (Catling 2005). Without the contribution of coevolutionary 'biological environments', this combination of taxonomic ubiquity and physical continuity imparted a decidedly monotonous tone to pre-Ediacaran evolution.

For the same reason, microbes, particularly prokaryotic microbes, are largely immune from extinction. There is no evidence for cyanobacterial extinction over the past 2+ billion years (indeed, such terminology is probably inappropriate in the context of prokaryotic 'species': see Finlay *et al.* 1997; Rosselló-Mora and Amann 2001; Gogarten *et al.* 2002), while distinctive pre-Ediacaran acritarchs typically managed 500–1000 myr before checking out. Extinction, particularly mass extinction, is essentially a phenomenon of the Phanerozoic biosphere, imposed by the eumetazoan forcing of organism size (Maurer 2003), ecological specialization (Vermeij 1994), and corresponding reductions in population sizes and geographical range (Jablonski 2005). Probably the greatest contribution of eumetazoans to extinction dynamics was the emergence of extended trophic hierarchies which, despite their inherent stability, are subject to system-wide collapse. This kind of mass extinction is of course unique to

eumetazoan ecosystems and, as such, introduced a unique macroevolutionary mode to the Phanerozoic biosphere (see Jablonski 2000, 2005; Roopnarine 2006). It remains to be seen whether a comparable process operated during the transitional Ediacaran interval, and whether it offers a realistic trigger for the Cambrian explosion (cf. Amthor *et al.* 2003; Marshall 2006).

Productivity

In addition to the dynamics of biodiversity, macroecology is concerned with metabolism and the flow of energy and materials through organisms (Brown *et al.* 2004). These too will have been perturbed by the introduction of eumetazoans as they diverted primary productivity through extended trophic structures and enhanced primary productivity through a combination of nutrient recycling and various diversity effects (Lehman and Tilman 2000; Worm and Duffy 2003; Tilman *et al.* 2006). The truly revolutionary impact, however, relates to the increased biomass spectrum accompanying the invention of multitrophic food webs. In the modern oceans, total standing biomass is invariant with respect to body size across all pelagic organisms from unicellular plankton to whales, owing to the simple size structuring of marine food webs ('big fish eat little fish') and the three-quarter allometric scaling of metabolic rate to body mass (Sheldon *et al.* 1972; Kerr and Dickie 2001; Cohen *et al.* 2003; Brown *et al.* 2004), i.e. there is just as much 'whale' as there is 'cod' as there is phytoplankton in the (undisturbed) modern ocean. With the body mass of pelagic organisms extending over 20 orders of magnitude, and predators typically four orders of magnitude larger than their prey (Brown *et al.* 2004), some 80 per cent of modern marine biomass is likely to be eumetazoan [not including heterotrophic/chemoautotrophic prokaryotes (see Whitman *et al.* 1998), but also not including the considerable biomass of benthic metazoans, which also exhibit an essentially flat biomass spectrum (Schwinghamer 1983; Kerr and Dickie 2001)]. Even more remarkably, all this animal biomass comes essentially free of charge. The addition of new trophic layers does not require any additional primary productivity (cf. Bambach 1993); apart from a modest increase in biologically sequestered phosphorus and nitrogen (Elser *et al.* 1996), it is little more than a diversion of primary productivity through a series of incrementally larger, longer lived and more slowly metabolizing organisms.

Metazoan trophic structures of course had to be constructed from the bottom up, first through the invention of small herbivores, then incrementally larger (and longer-lived) primary, secondary and tertiary carnivores (Butterfield 2001a, b). Thus, the early evolution of

eumetazoans and their trophic hierarchy would have rapidly increased standing biomass, while at the same time radically extended the upper limit of its size spectrum (see Schwinghamer 1983; Kerr and Dickie 2001). Simply as particles, this novel distribution of biomass would have had a profound impact on contemporaneous biogeochemistry (e.g. Logan *et al.* 1995; Butterfield 1997), but it is the accompanying ecological novelty that reinvented ecology and evolution. Larger organisms, for example, are capable of engaging in a fundamentally broader range of activities than their microscopic counterparts (e.g. burrowing and deposit feeding; Jumars *et al.* 1990), which in turn have major biogeochemical, macroecological and macroevolutionary effects (e.g. McIlroy and Logan 1999). Organism size also correlates with organism age, such that a biosphere of large multicellular organisms gives rise to life-history trade-offs, allowing diversity to be partitioned in time as well as space (see Odum 1969; Bonsall *et al.* 2004). Notably, it is the extended age of larger organisms that multiplied standing biomass in the early Phanerozoic, in much the same way that trees did in terrestrial ecosystems [though aquatic ecosystems do not exhibit an equivalent biomass pyramid (Cohen *et al.* 2003; Brown *et al.* 2004) because of the rapid life cycles of primary producers and nested, size-structured food webs].

Eumetazoans can also be held accountable for a major shift in the source of marine primary productivity, from predominately cyanobacteria in the Proterozoic to predominately (eukaryotic) algae in the Phanerozoic (Summons *et al.* 1999). In a world devoid of grazers, phytoplankton are expected to evolve to minute size without morphological elaboration (Butterfield 1997; Jiang *et al.* 2005), playing strongly to the strengths of cyanobacteria (Lynch and Conery 2003; Poole *et al.* 2003). With the introduction of herbivorous mesozooplankton, however, the ability of eukaryotes to respond morphologically, by adding protective ornamentation and increasing size (see Jiang *et al.* 2005), gave them a unique selective advantage, and an unprecedented role in marine primary productivity. (Why exactly earlier protistan-grade predation failed to induce such coevolutionary response warrants further consideration, but it most likely relates to the ecological limitations of unicellularity, including a minimal capacity to detect/ambush prey at a distance, escape viscous fluid flow, or generate large-prey-entraining feeding currents; see Kiørboe *et al.* 1996; Naganuma 1996; Jakobsen 2002.) Larger, eukaryotic phytoplankton, in turn, have profound effects on biogeochemical cycling, on the one hand preferentially raining out as export carbon, and on the other preferentially directed into pelagic food webs where it is suspended as long-lived biomass or jettisoned as rapidly sinking, nutrient-rich faecal pellets (Logan *et al.* 1995; Butterfield 1997, 2001a, b; Wassmann 1998). With knock-on implications for bottom water

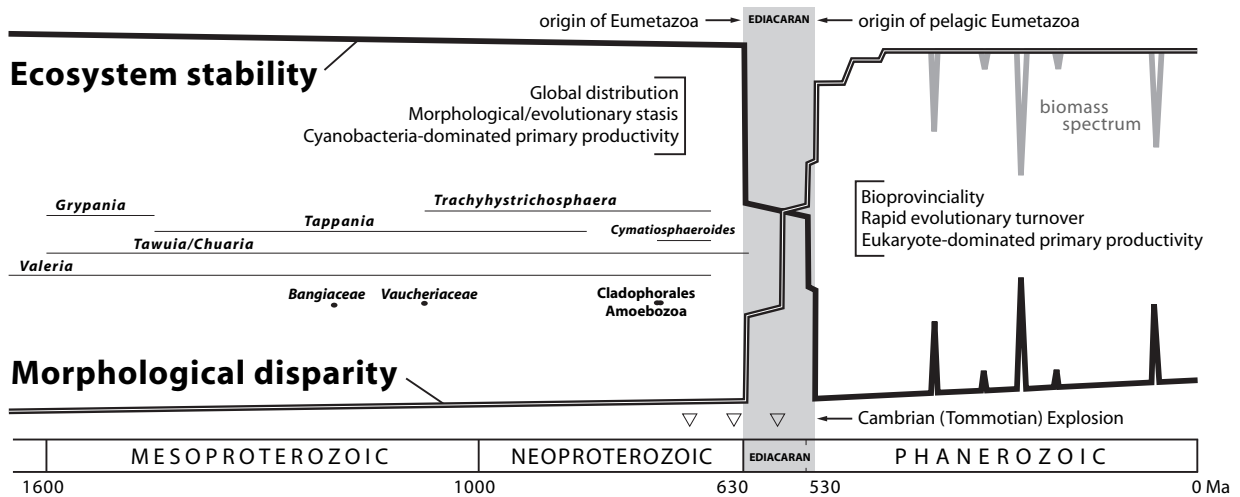
oxygenation, nutrient cycling and benthic metazoans (e.g. McIlroy and Logan 1999), these biologically induced shifts in productivity would have played a key role in establishing modern-style biogeochemical cycles.

The transition from pre-Ediacaran to modern-type marine productivity did not happen overnight. Certainly standing biomass would have increased dramatically as the first tier of eumetazoan consumers was introduced in the early Ediacaran, and again with the addition of a second trophic level in the late Ediacaran, as reflected by the appearance of biomineralization (Vermeij 1989), predatory borings (Hua *et al.* 2003) and macroscopic trace fossils (Jensen 2003). Even so, the acritarch and biomarker records suggest that eukaryotes remained relatively minor constituents of the plankton until the early Cambrian (Tommotian), at which point the entire system shifted rapidly into Phanerozoic mode via the ‘Cambrian explosion’ (Butterfield 1997, 2001a, b, 2003; Zhuravlev 2001). The Atdabanian appearance of metre-long anomalocaridids (Hou *et al.* 2004) points to a rapid expansion of pelagic food webs to four or five trophic levels (and equivalent biomasses; cf. Kerr and Dickie 2001), while the addition of a further level may have contributed to the substantial increases of standing biomass in the early Ordovician (see Payne and Finnegan 2006). Large amounts of suspended biomass are of course susceptible to collapse, despite dynamic stability, and there is little doubt that the biogeochemical pertur-

bations associated with Phanerozoic mass extinctions derive in large part from the reversion of the marine biomass spectrum to pre-Tommotian-like conditions, including a return of primary productivity to smaller, less exportable, possibly cyanobacteria-dominated, phytoplankton (Text-fig. 1).

CONCLUSION

Macroevolution as we know it is limited almost exclusively to the Phanerozoic, for the simple reason that it derives from the activities and emergent macroecological phenomena of Phanerozoic-like organisms, i.e. eumetazoans and the byproducts of eumetazoan coevolution. Unlike their pre-Ediacaran counterparts, Phanerozoic ecosystems are dominated by large, diverse, evolutionarily dynamic organisms that exhibit unique SARs (including biogeographical partitioning), unique modes of ecosystem (in)stability (including mass extinction) and unique distributions of biomass (including eukaryote-dominated primary productivity and long-lived, trophically nested, secondary productivity). Certainly the morphogenetic evolvability of crown eukaryotes was a prerequisite for such patterns, as was an oxygenated atmosphere, but this potential remained largely unexploited in the absence of eumetazoan-driven coevolution. Under these benign conditions, pre-Ediacaran



TEXT-FIG. 1. A conceptual view of the macroecological differences between the pre-Ediacaran and post-Ediacaran marine biospheres, and the transitional Ediacaran. The disparity curve is derived from acritarch data and estimated number of cell types (McShea 1996; Huntley *et al.* 2006), and ecosystem stability from estimated rates of evolutionary turnover (Sepkoski 1984; Knoll 1994). The spikes in ecosystem stability following Phanerozoic mass extinctions are inferred from observed and modelled recovery times (Solé *et al.* 2002). Biomass spectrum very broadly tracks disparity through this interval (see Bell and Mooers 1997) except during mass extinctions, which are characterized by the loss of large organisms but not cell types. Also shown are the age ranges of pre-Ediacaran eukaryotes discussed in the text, and the Cryogenian and Ediacaran glaciations (triangles). Note that the Ediacaran/Cambrian boundary as depicted here (at the base of the Tommotian; c. 530 Ma) differs from the IUGS-ratified position, which corresponds to the base of the preceding Nemakit-Daldyn Stage (c. 542 Ma). Vertical scale for all curves is qualitative only.

eukaryotes competed with prokaryotes on essentially equal terms; hence, their peculiarly prokaryote-like macroevolution.

Lack of morphological diversity does not of course preclude an underlying wealth of genetic diversity, as is increasingly being recognized among extant microbes (e.g. Moreira and López-García 2002; Sogin *et al.* 2006; but see Rosselló-Mora and Amann 2001; Berney *et al.* 2004), or indeed an underlying ecological dynamism, as seen in microbial microcosm experiments (e.g. Naeem and Li 1998; Bell *et al.* 2005). Even so, it is a mistake to view organism ecology and ecosystems as infinitely fractal (contra Suess 1954). Unicellular and microbial organisms represent a trivial fraction of available morphospace and corresponding diversity, a consequence of their small size, restriction to viscous fluid regimes and limited modularity (e.g. Koehl 1996; Naganuma 1996; Bell and Mooers 1997; Carroll 2001; Poole *et al.* 2003). Moreover, the substantial top-down role of eumetazoans in driving the diversification of Phanerozoic protists (Verity and Smetacek 1996; Thingstad 1998; Duffy 2002; Hamm *et al.* 2003; Worm and Duffy 2003) points to fundamentally lower pre-Tommotian and pre-Ediacaran microbial diversity, obviating any uniformitarian macroecological or macroevolutionary generalizations. Proterozoic microbes were unquestionably more diverse than can be resolved in the morphological fossil record, but morphology nonetheless remains a key measure of diversity and its impact on ecosystem function. Indeed, most of the novelties of Phanerozoic macroevolution can be ascribed to the eumetazoan-induced 'invention' of organismal size and morphology.

The most pronounced increase in early morphological diversity/disparity was unquestionably the Cambrian (Tommotian) 'explosion' of animals and protists (see Zhuravlev 2001), but it was the first appearance of eumetazoans, in the early Ediacaran, that marks the more fundamental transition (Text-fig. 1). In between lies what must have been a most remarkable 100 million years, where the ponderous habits of pre-Ediacaran macroevolution were replaced by the dynamism of the Phanerozoic. Notably, this was a step-wise transition, with fully fledged Phanerozoic rules only attained with the Tommotian expansion of metazoan ecology into the pelagic realm and the establishment of modern-style benthic-pelagic coupling (Butterfield 1997, 2001a, b, 2003; see Thingstad 1998; Wassmann 1998). In this light, there is a certain attraction to recognizing the Tommotian Stage as the base of the Cambrian (see Khomentovskii and Karlova 2005) and, even more idealistically, the Ediacaran Period as the base of the Phanerozoic (Text-fig. 1). Thus construed, the Ediacaran would begin with the first appearance/evidence of (benthic) eumetazoans and end with their expansion into the water column (cf. Knoll *et al.* 2006), while the

Phanerozoic would circumscribe the entire age of eumetazoans.

Whatever the nomenclature, it is clear that life on Earth has occupied two more or less coherent, stable modes separated by an extended, but ultimately unstable transition (Text-fig. 1). During its first *c.* 3000 million years the biosphere followed distinctively pre-Ediacaran rules based on microbes, metabolism and monotonously physical environments, whereas the past *c.* 530 million years has operated in the uniformitarian context of large organisms, complex ecologies and historical contingency. And while it was the 'quantum' effects of eumetazoans and pelagic eumetazoans that invented post-Ediacaran macroevolution, there is little doubt that these key innovations were discovered via underlying microevolutionary experimentation. Given the lethargic, almost ahistorical rates of pre-Ediacaran/pre-eumetazoan evolution (and our $n = 1$ sample size; Lineweaver and Davis 2002), we can expect all possible biospheres to exhibit Darwinian microevolution (DesMarais *et al.* 2003), but very few to be playing by advanced Phanerozoic rules.

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