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ScienceDirect
Palaeogeography, Palaeoclimatology, Palaeoecology 258 (2008) 180–188
PALAEO
www.elsevier.com/locate/palaeo

The Cambrian radiation of bilaterians: Evolutionary origins and palaeontological emergence; earth history change and biotic factors

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Accepted 3 May 2007

Abstract

Evidence from a variety of research areas, including phylogenetic palaeobiogeographic studies of trilobites, indicates that there may be a fuse to the Cambrian radiation, with a duration on the order of 20–70 myr. Evolution in trilobites appears to have been powerfully influenced by the tectonic changes occurring at the end of the Neoproterozoic: especially the breakup of Pannotia. This continental fragmentation may have also elevated opportunities for vicariance and speciation in trilobites, and other metazoans, given that speciation rates at this time period were high, though not phenomenally so. This provides clear evidence that abiotic factors played an important role in motivating evolution during this key episode in the history of life; biotic factors probably also played a role. The evidence for the role of biotic factors is considered in light of information from some problematic Cambrian taxa. These may show affinities with modern problematic pseudocoelomate phyla, although Cambrian and modern exponents differ dramatically in body size.

Keywords: Biogeography; Cambrian radiation; Phylogenetics; Trilobites; Ecdysozoans; Problematic taxa

1. Introduction

Scientific understanding of the status of the Cambrian radiation has grown significantly in the last decade; this growth has been accomplished by data from a variety of sources. These data derive from and include: the spectacular discoveries of metazoan embryos (Xiao et al., 1998; Steiner et al., 2004; Chen et al., 2006), with recognition of their possible triploblastic character (Xiao et al., 2000; Chen et al., 2006); analyses revealing the nature of ecological changes during the early and Middle Cambrian (Bottjer et al., 2000; Dornbos et al., 2005a); more accurate approaches to estimating divergence events in the modern biota using molecular dating techniques (Peterson et al., 2004); new evidence of bilaterians in the pre-Cambrian (Chen et al., 2004, 2006; Dornbos et al., 2005b), although some of these results have been challenged by Bengston and Budd (2004); advances in chronostratigraphy (Bowring et al., 2003; Condon et al., 2005); and new chemostratigraphic studies of the late Neoproterozoic and early Cambrian (Corsetti and Kaufman, 2003; Xiao et al., 2004; Maloof et al., 2005). Here, the growing consensus on the nature and timing of the Cambrian radiation emerging from these results will be considered in light of results derived from phylogenetic biogeographic analyses and studies of rates of evolution in trilobites. Further, the phylogenetic affinities some problematic Cambrian taxa share with modern problematic taxa, and the implications this may have for our understanding of the Cambrian radiation, will also be explored.

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doi:10.1016/j.palaeo.2007.05.021

2. Biogeographic patterns and the timing of the Cambrian radiation

2.1. Introduction

Although the Early Cambrian has for a long time been recognized as marking the geologically rapid proliferation of metazoan and especially bilaterian remains in the fossil record, its evolutionary significance has been debated since Darwin (1859). In particular, debate has centered around two distinct points of view: is there a long history of pre-Cambrian bilaterian divergence that for various reasons remains obscure in the fossil record?; or does the fossil record of the Cambrian radiation reasonably coincide with the timing of the evolutionary origins and proliferation of these clades. Lieberman (1999a) referred to these, respectively, as the Darwinian and Simpsonian views of the Cambrian radiation. There are a variety of ways of testing propositions about evolutionary divergence during the Cambrian radiation: one technique that has been used recently is phylogenetic biogeographic analysis (Lieberman, 2003a; Meert and Lieberman, 2004). The use of biogeography as a tool to infer the timing of the Cambrian radiation was first suggested by Fortey et al. (1996). In essence, this technique involves reconstructing biogeographic patterns and then discerning which tectonic events are most strongly replicated in the biogeographic patterns. When the tectonic events are of known timing this provides a means of minimally constraining the time of origin of the clade of interest (Meert and Lieberman, 2004; Lieberman, 2005). A similar approach has been used by Murphy et al. (2001) to constrain the origins of the modern mammalian orders. Our understanding of tectonics and palaeogeography during the late Neoproterozoic and early Cambrian has grown significantly in recent years. Although controversies remain (see discussions in Meert and Torsvik (2003) and Meert and Lieberman (2004)) we do have a

Fig. 1. A reconstruction of the Earth's palaeogeography at 580 Ma, based on the work of J. Meert, Department of Geological Sciences, University of Florida (see Meert and Torsvik (2003) and Meert and Lieberman (2004)), and emphasizing the major cratonic blocks. The small trilobite icons represent the approximate positions of early Cambrian sediments containing relevant trilobite material.

reasonable understanding of the critical events and the Earth's palaeogeography during this interval (see Fig. 1).

2.2. Materials and methods

In order to rigorously apply biogeographic analysis to the problem of dating the Cambrian radiation, phylogenies are necessary. Lieberman (1998, 1999b, 2001a, 2002) presented a series of phylogenetic analyses of early Cambrian trilobites encompassing approximately 115 species; trilobites constitute the most diverse and abundant Cambrian organisms that are readily amenable to phylogenetic analysis. These phylogenies, along with the geographic distributions of their component taxa, were then subjected to a modified Brooks Parsimony Analysis; this method relies on constructing data matrices to consider patterns of vicariance and patterns of geodispersal; these are then analyzed using a parsimony algorithm. The method has been described in detail by Lieberman and Eldredge (1996), Lieberman (2000, 2003a,b), and Brooks and McLennan (2002).

2.3. Discussion

2.3.1. Timing early, but not too early

The results of the biogeographic analysis suggest several salient features: 1) there is only limited evidence for coordinated dispersal by trilobites between different biogeographic regions; 2) tectonic processes, rather than repeated episodes of sea-level rise and fall, played the primary role in structuring biogeographic and evolutionary patterns during the Cambrian radiation; 3) the predominant biogeographic process influencing biogeographic patterns in the trilobites studied appears to have been vicariance, suggesting numerous opportunities for allopatric speciation mediated by geological change; and 4) vicariance biogeographic patterns in trilobites are most congruent with the breakup of the supercontinent Pannotia, a tectonic event constrained to have occurred between 600–550 Ma (Meert and Lieberman, 2004).

The compatibility of the vicariance patterns with a distribution of trilobites across a once united Pannotia that subsequently fragmented (between 600–550 Ma), along with the limited or absent evidence for congruent dispersal in trilobites, provides an age estimate for the origin of trilobites. In particular, it suggests that trilobites had originated at least 20–70 myr before they first appeared in the fossil record. Given that trilobites are euarthropods, and thus derived bilaterians (Wills et al., 1998), this indicates a significant portion of bilaterian divergence occurred at least 20–70 million years before the trilobitic part of the Cambrian radiation.

These results on timing derived from biogeographic analyses of trilobites are congruent with the results from Xiao et al. (1998, 2000) and Chen et al. (2006) and Dornbos et al. (2005b) which identified animal embryos in the Ediacaran, congruent with the results in Chen et al. (2004) which identified small bilaterians in the Ediacaran, and also with the results from recent molecular clocks estimates of bilaterian divergence in Peterson et al. (2004). The convergence of these separate and distinct data sets on a largely similar inferred timing for bilaterian cladogenesis may provide broad support for the notion that there is a significant fuse (perhaps 20–70 myr or so) to the Cambrian radiation. However, the duration of this fuse is far shorter than that posited by Darwin (1859) and by the early molecular clock studies of Wray et al. (1996).

These results may be significant because they suggest some gap in the fossil record between the origin and divergence of bilaterians and their subsequent appearance and proliferation. The value of the fossil record is not obviated though, because notably the signatures of these earlier events are preserved in the evolutionary and biogeographic patterns (Lieberman, 2005).

2.3.2. Possible explanations for the gap in the fossil record

The results from palaeobiogeography and other disciplines do appear to indicate the existence of a gap, albeit not as profound as some have argued, in the fossil record. (Note, here I am not going to consider at all the status of the organisms of the Ediacaran biota which could conceivably close up some of this gap, because their affinities still are too enigmatic and contentious; see Xiao et al., 2005 for discussion.) The growth in palaeontological knowledge of the Proterozoic in general, and the Ediacaran in particular, demonstrates that the fossil record from this time period is not unusually incomplete, and thus ideas akin to Walcott's Lipalian interval, which invoked a large stratigraphic gap between the pre-Cambrian and Cambrian, are no longer tenable. Given this, explanations for the perceived palaeontological gap have typically focused on three major possibilities, though they need not be mutually exclusive: 1) late Neoproterozoic animals lacked hard parts and were unlikely to fossilize; 2) late Neoproterozoic animals were unusually small and perhaps akin to modern larvae with set aside cells; or 3) late Neoproterozoic animals were extremely rare and occupied marginal environments unlikely to leave a geological record; in this case "marginal" implies both an environment at the margin or periphery of the species range and also an environment that might not be the same as the optimal environment typically occupied by the species.

Hypothesis one, although of course possible, seems insufficient because if abundant large sized bilaterians lacking hard parts were present in the Neoproterozoic they should have left a trace fossil record; the ichnological data, however, do not support this (Crimes, 1992; Fortey et al., 1996; Knoll, 1996; Budd and Jensen, 2000). Hypothesis two has been discussed by several authors including Fortey et al. (1996) and Xiao et al. (1998). Davidson et al. (1995) argued that Neoproterozoic bilaterians were small larvae. Lieberman (1999a) discussed difficulties with the larvae hypothesis, but this does not mean that Neoproterozoic bilaterians were not all rather small compared to their Phanerozoic descendants. Indeed, the fossils described in Chen et al. (2004) and Dornbos et al. (2005b) lend credence to this view (though Bengston and Budd (2004) have challenged the interpretation of some of these). Some analogous facts about possible changes in the size range of organisms in the Cambrian are treated more fully below in the discussion of problematic taxa. Hypothesis three was discussed by Lieberman (2003c), who argued that the very conditions that would have encouraged rapid early animal diversification would have made them less likely to be preserved in the fossil record. The argument was based on an analogy to the punctuated equilibria hypothesis of Eldredge and Gould (1972). They argued that the early stages of allopatric speciation would only be rarely preserved, both because population sizes were small and populations were restricted to marginal environments less likely to be preserved. Thus, species would tend to appear suddenly in the fossil record, only after they had reached sufficient abundance and entered more typical environments.

Perhaps early bilaterians consisted of taxa at low population densities that were diverging in marginal environments that rarely are preserved. A taphonomic question relevant to this problem is what general levels of abundance or population density are necessary for a taxon to become palaeontologically emergent? In principle, this could be deduced using studies like that of Valentine (1989) but where one would also calculate population densities of those modern species that had fossilized remains and compare those with taxa that did not have fossilized remains. These density values might be taken as a minimum measure of density values necessary for a taxon to be fossilized. Further, to what extent these values resemble modern marine taxa, including those with small allopatric distributions, could be determined. Finally, to test the hypothesis of Lieberman (2003c) one could ask to what extent are the maximum implied densities of hypothetical late Neoproterozoic bilaterians, in total, plausible or implausible over long periods (20–70 myr) of time.

2.3.3. Earth history change as the pacemaker of evolution

Another pattern emerging from the biogeographic analysis of Meert and Lieberman (2004) is that tectonic events have left a clear and significant stamp on evolutionary patterns. First, the tectonic events are faithfully replicated in those patterns (Lieberman, 2005). This suggests that tectonic events can have a significant effect on evolution, and it is notable that the Cambrian radiation, one of the key episodes in the history of life, also corresponds with a time of major earth history change (Lieberman, 2003a,b, 2005). Further, there is congruence between the predominant biogeographic pattern in trilobites, vicariance, and the primary tectonic changes occurring at this time, the breakup of a supercontinent. Not only does this suggest a prominent association between earth history change and evolution during a key episode in the history of life, but it also provides a motor for accelerating the tempo of evolution at this time. In particular, the Cambrian radiation represents a time of high, though not phenomenally high, rates of speciation (Lieberman, 2001b).

The excessive opportunities for allopatric speciation via vicariance created by continental fragmentation at the end of the Neoproterozoic would have provided a means for ramping up the speciation motor at the end of the Neoproterozoic and the start of the Cambrian, thereby contributing to the Cambrian radiation (Lieberman, 2001b, 2005; Meert and Lieberman, 2004). Of course it needs to be established to what extent earth history changes, particularly tectonic events, play in motivating other key episodes in the history of life, but at least in the case of the Cambrian radiation it is clear that earth history change played an important, though not the only role in fomenting evolutionary divergence at this time. In addition, tectonic events may not have been the only type of earth history changes that contributed to the Cambrian radiation. For example, there were several major episodes of climatic change, including profound cooling, towards the end of the Neoproterozoic (Hoffman et al., 1998; Evans, 2000); the climatic amelioration afforded by the termination of episodes of major glaciation may have also played a role.

3. Changing ecological processes during the Cambrian radiation: the significance of problematic taxa

3.1. Introduction

The important role that earth history played in motivating the Cambrian radiation does not preclude a role for biotic processes. This topic can be considered using a variety of approaches. For example, the detailed

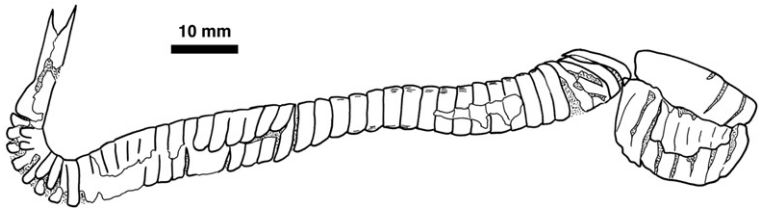

Fig. 2. A reconstruction of the vetulicolian *Skeemella clavula* Briggs, Lieberman, Halgedahl, and Jarrard, 2005, Middle Cambrian, Utah, adapted from Briggs et al. (2005).

studies by Bottjer et al. (2000), Droser et al. (2002), and Dornbos et al. (2005a) have greatly increased our knowledge of the nature of ecological interactions during this time period; in particular, these studies argued that a major change occurred through the Cambrian radiation interval in the depth and intensity of bioturbation with a concomitant change in the style of benthic substrates and the form of the sediment–water interface.

The nature of problematic taxa (*sensu* Bengston, 1986) during and after the Cambrian radiation also may shed light on this. It has been amply documented that the Cambrian period preserves a significant array of taxa that are "problematic" (Whittington, 1985; Briggs and Fortey, 1989; Gould, 1989; Briggs et al., 1992; Conway Morris, 1993; Fortey et al., 1996; Budd and Jensen, 2000; etc.), and how problematic these taxa may be continues to inspire debate (e.g., Conway Morris, 2003; Briggs and Fortey, 2005). Fortey et al. (1996), Budd and Jensen (2000), and Briggs and Fortey (2005) have elucidated in detail the notion of stem and crown group taxa and how these influence our understanding of the Cambrian radiation; thus, I will not reiterate their points here. Instead, I will focus on a limited set of Cambrian "problematic" taxa, using examples to discuss their possible affinities with modern forms and how they differ from these forms.

One consistent (albeit not universal) pattern replicated in some Cambrian problematic taxa is their affinity to modern problematic phyla, especially those belonging to the para- or polyphyletic pseudocoelomate grade; this may be informative regarding the nature of ecological patterns and processes during the Cambrian radiation. In particular, assuming phylogenetic affinities between some Cambrian problematica and modern problematica there is still at least one fundamental way that Cambrian problematic differ from typical (though not all, see below) modern pseudocoelomates: in their overall body size; Cambrian taxa greatly dwarf modern taxa (for discussions of modern pseudocoelomates see Brusca and Brusca, 1990, 2003; Ruppert and Barnes, 1994); in particular, and in one possible case size differences that are roughly factors of 100,000: 10′s of centimeters versus 100's of microns.

3.2. Are some Cambrian problematica modern problematica?

As a microcosm of the debate about the nature of Cambrian soft-bodied problematica the Phylum Vetulicolia are worth consideration (Fig. 2). They have an unusual and distinctive body form that has been discussed in detail by Hou (1987), Chen and Zhou (1997), Shu et al. (2001), Hou et al. (2004), Briggs and Fortey (2005), and Briggs et al. (2005). Moreover, their unusual and distinctive morphology has led to hypotheses suggesting various phylogenetic placements for the group including those of Gee (2001), Shu et al. (2001, 2003, 2004), Lacalli (2002), Mallatt et al. (2003), and Briggs et al. (2005).

Briggs et al. (2005) discussed several possible phylogenetic affinities for the group: one of these was based on their resemblance to the problematic kinorhynchs (Fig. 3). With these they share: a segmented organic cuticle that has discretely cuticularized posterior segments; a terminal, circular mouth; a similar number of total divisions in the body (shared only with some vetulicolians); and a bifid trunk termination (again, shared only with some vetulicolians); both also lack eyes and limbs. Some vetulicolian characters are also shared with

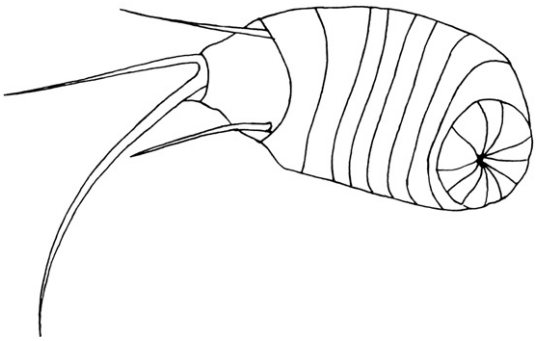

Fig. 3. Anatomy of a larval kinorhynch, modified from Hou et al. (1995) following information in Nyholm (1947) and Kozloff (1972); shown approximately X150,000.

arthropods: notably, arthropods and vetulicolians also share mid-gut glands (Butterfield, 2003). (Digestion in kinorhynchs is little known, but they appear to possess structures at least analogous to these too (Brusca and Brusca, 1990, p. 348). One pronounced difference between kinorhynchs (see Nyholm, 1947; Kozloff, 1972) and vetulicolians is that vetulicolians are dramatically larger. Although vetulicolians do share various characters in combination with arthropods, they lack several fundamental arthropod characters including appendages and eyes (Shu et al., 2001, 2003, 2004), thus precluding their presence in the arthropod crown group. Their terminal, circular mouth is also atypical of arthropods.

Relevant here are numerous molecular systematic analyses (reviewed and discussed in Adoutte et al., 2000) that have consistently recognized a clade referred to as Ecdysozoa including the arthropods along with other non-arthropod yet molting and segmented (sometimes ambiguously) phyla. Included towards the base of the ecdysozoans are such pseudocoelomates as nematodes; meanwhile, the pseudocoelomate priapulids and kinorhynchs are basal among extant Ecdysozoa (Mallatt and Giribet, 2006). If vetulicolians do show affinities with the kinorhynchs then they may sit at the very base of Ecdysozoa or within the ecdysozoan stem group (Fig. 4). This does not, however, obviate the detailed character discussions and evidence presented in Shu et al. (2001, 2003, 2004). Note that there may actually be relatively little phylogenetic space between a basal ecdysozoan and a basal deuterostome (see Fig. 4). The characters developed in vetulicolians might indeed be primitive retentions held in common with a basal deuterostome. (Of course it is conceivable that vetulicolians are basal deuterostomes, or slightly down the metazoan tree relative to both ecdysozoans and deuterostomes, etc., see Fig. 4.).

If vetulicolians do share affinities with kinorhynchs, this would not be the first case where a Cambrian problematicum has been posited to share a relationship with a modern problematic, pseudocoelomate taxon. Hou et al. (1995) presented arguments that anomalocaridids shared several features in common with pseudocoelomates in general and kinorhynchs in particular. Setting aside that there exists phylogenetic evidence for placing anomalocaridids within the arthropod stem group (e.g., Briggs and Fortey, 1989; Budd, 1993, 1996, 2002; Collins, 1996; Wills et al., 1998), Hou et al. (1995) did recognize salient features anomalocaridids share with ecdysozoan pseudocoelomates: indeed, anomalocaridids may lie up the tree from vetulicolians, but still near the basal part of the Ecdysozoa and close to the origins of the arthropods.

Again, body size constitutes a fundamental difference between anomalocaridids and modern kinorhynchs, with the former larger by many orders of magnitude (see Briggs, 1994 for some discussion on the dimensions of anomalocaridids). In important respects, the possible association posited between vetulicolians

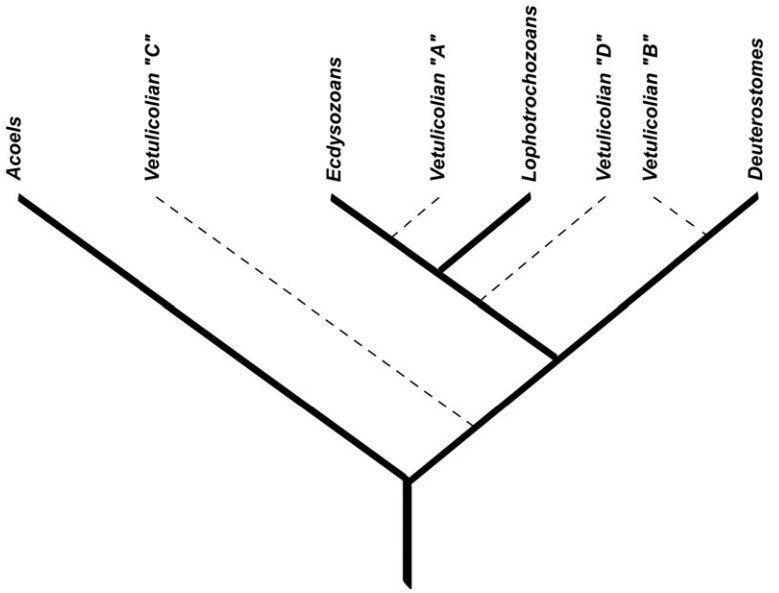

Fig. 4. Possible phylogenetic positions for the vetulicolians: "Vetulicolian A", they are basal ecdysozoans with affinity to kinorhynchs, discussed herein and in Briggs et al. (2005); "Vetulicolian B", they are basal deuterostomes, discussed in Shu et al. (2001, 2003, 2004); "Vetulicolian C" and "Vetulicolian D", other possible placements.

and kinorhynchs here and in Briggs et al. (2005) is based on analogy and phylogenetic extension of the arguments in Hou et al. (1995).

Another significant Cambrian problematicum that may show affinities to a modern problematicum is *Dinomischus* Conway Morris, 1977a. This taxon possesses several traits in common with entoprocts (Conway Morris, 1977a), a problematic phylum of interstitial pseudocoelomate (or possibly even acoelomate) organisms (Brusca and Brusca, 1990; Ruppert and Barnes, 1994). However, the phylogenetic position of *Dinomischus* is still controversial (see Briggs et al., 1994; Hou et al., 2004), and Chen and Zhou (1997) preferred to link it with echinoderms. Again, repeating the familiar pattern, *Dinomischus* is massive relative to modern entoprocts: all modern entoprocts are <5 mm (see Ruppert and Barnes, 1994) while the standard size for *Dinomischus* is a few centimeters (Briggs et al., 1994; Hou et al., 2004) (excluding the long tube that extends above the bracts). Note that the size disparity here is not as dramatic as that suggested for the kinorhynchs relative to the vetulicolians.

A salient point that bespeaks to the potentially unique ecological nature of the Cambrian radiation is the size difference between these early and Middle Cambrian organisms and their possible modern relatives. A dramatic increase or decrease in body size, or in the geographic area occupied by a taxon, may imply an important change in ecological conditions has occurred, freeing up (or restricting) available ecospace. (These and related ecological topics are treated and reviewed in the detailed works of Rosenzweig (1995), Brown and Lomolino (1998), and Maurer (1999) and the references cited therein.) One of the best anecdotal examples is the increase in mammalian body size after the large non-avian representatives of the dinosaurs went extinct. The one modern pseudocoelomate group that still sometimes attains relatively large size are the priapulids, yet these show an important difference between Cambrian and modern representatives in their patterns of geographic and environmental distribution (Gould, 1989): in the Cambrian large priapulids are far-flung geographically (see Conway Morris, 1977b; Wills, 1998; Lieberman, 2003d), whereas today large priapulids are restricted to polar and boreal environments (Brusca and Brusca, 1990).

Cyanobacteria and stromatolites show a related pattern. Cyanobacteria still have cosmopolitan distributions today, as they seemingly have had for billions of years, but the distinctive reefal frameworks they built, which were widespread in the Archaean and Proterozoic, are today restricted to unusual environments that otherwise exclude their metazoan predators; throughout the Phanerozoic they are typically only found during times of environmental overturn and organismal stress (e.g., Nisbet, 1991; Knoll, 2003). The large-scale restriction of macroscopic cyanobacterial stromatolites to the pre-Cambrian world bespeaks of the changing nature of Phanerozoic ecology: grazing bilaterians became sufficiently abundant to eliminate their macroscopic manifestation without eliminating the taxa that produced them. A problem with this type of hypothesis, however, is that it is difficult to test (Rosenzweig, 1995), especially in long extinct taxa.

Still, were this analogy to hold, with vetulicolians, *Dinomischus*, and possibly even the anomalocaridids related to diminutive modern pseudocoelomates in interstitial environments, it implies that in the Cambrian there were greater ecological opportunities for these types of organisms in standard marine environments; opportunities that were subsequently removed. Of course the ecological pressures and processes are unspecified and we do not know why these opportunities are no longer available, but it could be that the culprits were other increasingly abundant bilaterian taxa; further, this transition may have possibly occurred by the late Cambrian.

4. Conclusions

It appears that physical, abiotic factors play one of the primary roles in motivating evolutionary patterns during the Cambrian radiation (Lieberman, 2000, 2003a,b,c, 2005), but this does not preclude other factors from playing an important role. For instance, evidence is emerging attesting to the changing ecological dynamics during this time period (e.g., Dornbos et al., 2005a). If the possible changes in body size in the problematic pseudocoelomates discussed herein are substantiated it would provide further support for the notion that an understanding of ecological dynamics will also shed further light on the nature of the Cambrian radiation.

Acknowledgements

Thanks to S. Dornbos and S. Xiao for inviting me to participate in this volume. Thanks to S. Dornbos, J. Hendricks, J. Meert, and two anonymous reviewers for comments on an earlier version of this manuscript; thanks to J. Meert for contributing the palaeogeographic reconstruction used in Fig. 1; thanks to D. E. G. Briggs for discussions related to the nature of vetulicolians. This research was supported by NSF EAR-0518976, NASA Astrobiology NNG04GM41G and a Self Faculty Fellowship.

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