

Taking the Pulse of the Cambrian Radiation¹

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SYNOPSIS. The Cambrian radiation is that key episode in the history of life when a large number of animal phyla appeared in the fossil record over a geologically short period of time. Over the last 20 years, scientific understanding of this radiation has increased significantly. Still, fundamental questions remain about the timing of the radiation and also the tempo of evolution. Trilobites are an excellent group to address these questions because of their rich abundance and diversity. Moreover, their complex morphology makes them readily amenable to phylogenetic analysis, and deducing the nature of macroevolutionary processes during the Cambrian radiation requires an understanding of evolutionary patterns. Phylogenetic biogeographic analysis of Early Cambrian olenellid trilobites, based on a modified version of Brooks Parsimony Analysis, revealed the signature of the breakup of Pannotia, a tectonic event that most evidence suggests is constrained to the interval 600 to 550 Ma. As trilobites are derived metazoans, this suggests the phylogenetic proliferation associated with the Cambrian radiation was underway tens of millions of years before the Early Cambrian, although not hundreds of millions of years as some have argued.

Phylogenetic information from Early Cambrian olenellid trilobites was also used in a stochastic approach based on two continuous time models to test the hypothesis that rates of speciation were unusually high during the Cambrian radiation. No statistical evidence was found to support this hypothesis. Instead, rates of evolution during the Cambrian radiation, at least those pertaining to speciation, were comparable to those that have occurred during other times of adaptive or taxic radiation throughout the history of life.

INTRODUCTION

The Cambrian radiation is a key episode in the history of life that involves the apparent proliferation of many but not all bilaterian metazoan taxa in the fossil record (Conway Morris, 1993, 2000; Fortey *et al.*, 1996; Budd and Jensen, 2000). The study of this radiation has received rich attention for more than 100 years, and the last 20 years have witnessed particular progress. Still, several questions remain unanswered about the nature of that radiation. Among these questions, two of the important ones concern timing and tempo. Data from such areas as molecular biology and developmental biology have partly helped elucidate questions about the timing and tempo of the Cambrian radiation in an important way (*e.g.*, Davidson *et al.*, 1995; Wray *et al.*, 1996; Ayala *et al.*, 1998; Bromham *et al.*, 1998), but the fossil record remains an important place to test hypotheses about that radiation (Valentine, 1994; Fortey *et al.*, 1996; Conway Morris, 2000; Budd and Jensen, 2000). This paper will focus on how the analysis of trilobites using a phylogenetic framework has enhanced what we know about whether there was an early, hidden radiation preceding the apparent Cambrian radiation in the fossil record and also whether the rate of evolution was unusually high at this time.

Trilobites are among the best organisms to test hypotheses about the Cambrian radiation because of their rich abundance and diversity in Cambrian strata and also because they are perhaps the only diverse Cambrian metazoan group with a complex anatomy easily

amenable to phylogenetic analysis. Moreover, phylogenetic methods are central to addressing any questions about the rate of evolution and the timing of evolutionary events because calculation of an evolutionary rate presumes some knowledge about evolutionary relationships (Brooks and McLennan, 1991; Sanderson and Donoghue, 1996). Phylogenetic information, in conjunction with information from stratigraphy, can also help constrain the timing of speciation events (Novacek and Norell, 1982; Edgecombe, 1992).

THE TIMING OF THE CAMBRIAN RADIATION

The debate about the timing of the Cambrian radiation has a significant pedigree, and two primary viewpoints exist. Some have argued that the appearance of metazoan taxa in the Early Cambrian corresponds closely or directly to the evolutionary origin of these taxa (*e.g.*, Gould, 1989). In contrast, others have argued that the Metazoa must have originated much earlier (*e.g.*, Darwin, 1859, 1872; Runnegar, 1982; Davidson *et al.*, 1995; Fortey *et al.*, 1996; Wray *et al.*, 1996; Ayala *et al.*, 1998; Bromham *et al.*, 1998; Xiao *et al.*, 1998). These two viewpoints have been referred to, respectively, as the Simpsonian and Darwinian viewpoints by Lieberman (1999a). The former view treats the fossil record as a real evolutionary document (a view akin to G. G. Simpson's thoughts on evolution and the fossil record), while the latter view treats the fossil record as either fundamentally flawed, biased, or inaccurate (a view akin to C. Darwin's thoughts on evolution and the fossil record).

Information from trilobites can contribute in an important way to our understanding of the Cambrian radiation. Ostensibly, trilobites diversified during the Early Cambrian, and in fact roughly the first 10 to 15

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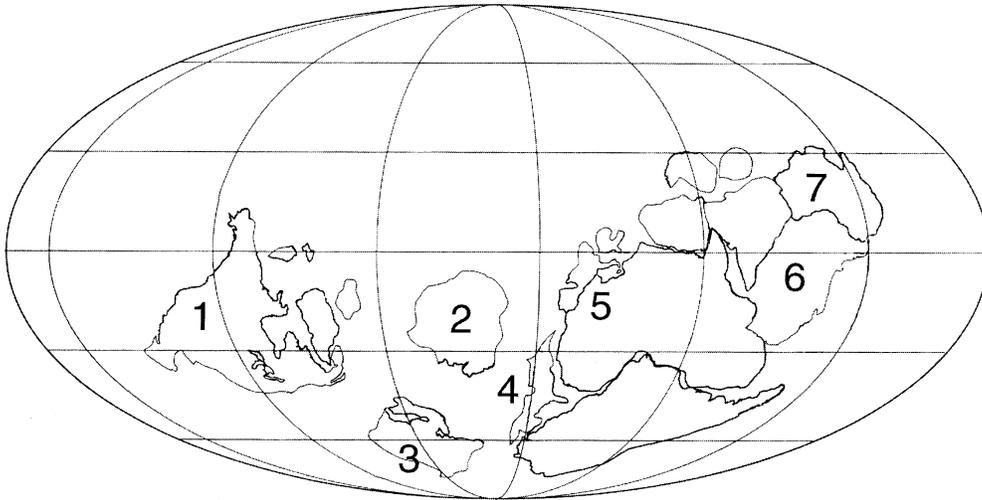


FIG. 1. Map of Early Cambrian paleogeography, emphasizing the regions considered in biogeographic analysis, modified from McKerrow *et al.* (1992), where: 1 = Laurentia; 2 = Siberia; 3 = Baltica; 4 = Avalonia; 5 = Morocco and southern Europe; 6 = East Antarctica; and 7 = Australia.

million years of the Cambrian are devoid of trilobites. Therefore, they might initially be treated as excellent candidates for the Simpsonian view of the Cambrian radiation. Fortey *et al.* (1996), however, have argued that there may be a signature of diversification events preserved in patterns of trilobite biogeography that actually indicates a much earlier origin and proliferation of the trilobites, supporting the Darwinian view of the radiation. A reconsideration of Fortey *et al.*'s (1996) study is now possible using a phylogenetic biogeographic approach.

Phylogenetic biogeography is a powerful research tool because it considers patterns of geographic change in the context of evolutionary events and because it is based on a rigorous, repeatable analytical method (Brooks, 1985; Wiley, 1988; Brooks and McLennan, 1991; Lieberman, 2000). It also can be used to identify both episodes of vicariance and congruent range expansion (geo-dispersal) that allow biogeographic patterns to be considered in the context of tectonic and climatic change. This enhances the value of biogeographic patterns because if the timing of tectonic events is known and if biogeographic patterns in a group resemble what is predicted to arise from a specific tectonic event, then the pattern can be treated as a temporal constraint on the origin and evolution of that group.

Fortey *et al.*'s (1996) study was pioneering, but it could not be based on the analysis of detailed phylogenetic biogeographic patterns since many studies of Early Cambrian trilobite phylogeny (*e.g.*, Lieberman, 1998, 1999b, 2001a, 2002) post dated their study. These phylogenetic data, when analyzed using techniques from phylogenetic biogeography, can be used to consider the tectonic signature preserved in patterns of trilobite biogeography and thus can be used to consider which viewpoint, the Simpsonian or the Darwinian, best describes the Cambrian radiation.

Key tectonic events

Three major tectonic events in the late Neoproterozoic and Early Cambrian might have influenced patterns of trilobite biogeography and evolution. Although the nature of these events and their timing are not ironclad, consensus seems to be emerging indicating this sequence: 1) breakup of the supercontinent Rodinia, occurring around 750 Ma and involving separation of western North America (Laurentia) and eastern Gondwana (East Antarctica, Australia, and possibly South China) (Hoffman, 1991; Moyes *et al.*, 1993; Powell *et al.*, 1993; Li *et al.*, 1996; Torsvik *et al.*, 1996; Dalziel, 1997; Scotese, 1997; Unrug, 1997; Wingate *et al.*, 1998; Karlstrom *et al.*, 1999); 2) ephemeral assembly and then breakup of the supercontinent Pannotia, occurring from 600 to 550 Ma and involving collision and later separation of Laurentia from western Gondwana (including northern Africa and the Amazon region of South America) and some smaller terranes marginal to Gondwana (Dalziel, 1992, 1997; Aleinikoff *et al.*, 1995; Powell, 1995; Faill, 1997; Scotese, 1997; Unrug, 1997; Scotese *et al.*, 1999) that included Avalonia (roughly southern Great Britain, eastern Newfoundland, and northern France) and also southern Europe; and 3) a potential episode of True Polar Wander involving large-scale rapid movement of most of the Earth's cratons in the Early Cambrian (Kirschvink *et al.*, 1997). A possible Early Cambrian paleogeography is shown in Figure 1. Major dissensions from this general sequence have been put forward by Bond *et al.* (1984) and Veevers *et al.* (1997), who argued that the breakup of Rodinia occurred around the earliest Cambrian at about 540 Ma. Although these authors did not consider the events related to the breakup and assembly of Pannotia, that event either would not have occurred or it would have been telescoped into the Early Cambrian. Other studies

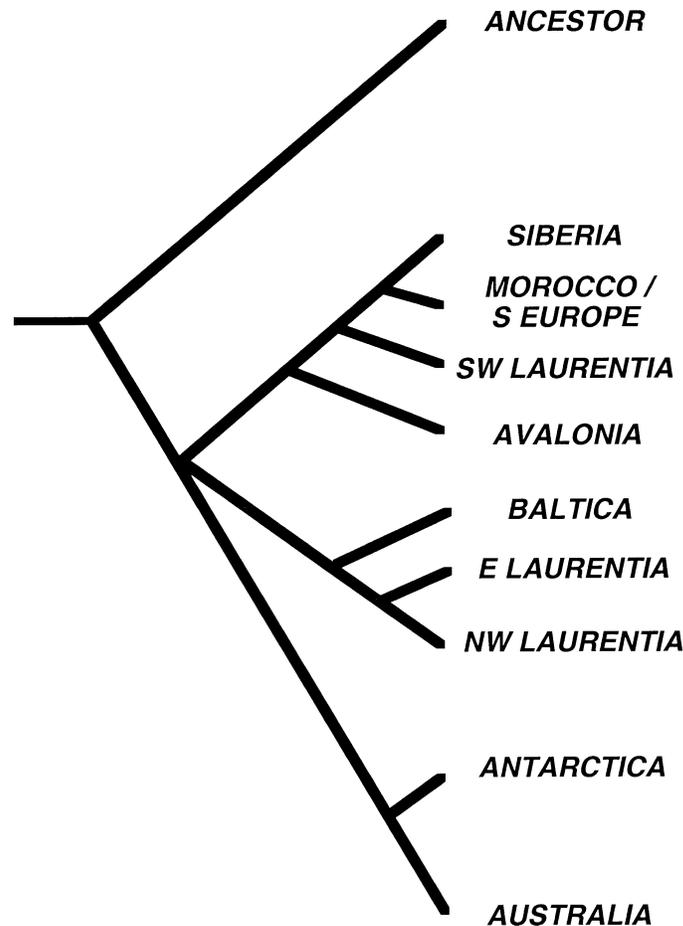


FIG. 2. Strict consensus tree of most parsimonious biogeographic patterns of vicariance displaying the relative time that regions became biogeographically isolated from one another; the closer two regions are, the more recently barriers emerged to separate them. Tree length 82 steps; produced from analysis of the data matrix in Table 1 using the exhaustive search option of PAUP 4.08b (Swofford, 2001). Tree rooted using a hypothetical ancestor (outgroup). The consistency index is 0.73, and the retention index is 0.58.

date, then my conclusions regarding the timing of the origin and diversification of trilobites would change accordingly.

Discussion

Because biogeographic patterns in Early Cambrian trilobites are most compatible with tectonic events that appear to date back to the late Neoproterozoic between 550 to 600 Ma it suggests this group had begun to diversify well before the Cambrian radiation's manifestation in the rock record. (The radiation is traditionally held to have begun approximately 543 Ma and ended around 515 to 520 Ma.) This result is given further significance when we consider the phylogenetic position of the trilobites within the Bilateria and the Metazoa. Recent phylogenetic topologies of the Arthropoda (*e.g.*, Briggs and Fortey, 1989; Wills *et al.*, 1998) suggest that trilobites are euarthropods, and these are in turn derived Bilateria and Metazoa. The result from biogeographic patterns thus suggests that numerous fundamental episodes of metazoan and bilaterian cladogenesis preceded the interval 550 to 600 Ma and thus the Cambrian radiation. Moreover, it

points out that there is a disjunction between the phylogenetic events we associate with the Cambrian radiation and the ecological and paleontological emergence of these taxa. This disjunction between evolutionary origin and ecological emergence is potentially a more general pattern in the history of life that deserves more scrutiny. For example, it has already been documented for various orders of Bryozoa (McKinney *et al.*, 1998), for Ordovician trilobites (Droser *et al.*, 1996) at smaller scales such as the radiation of trilobite clades like the Devonian calmoniids (Lieberman, 1993), and also in the sense that authors have argued for a pre-Cenozoic diversification of mammals at the superordinal level (*e.g.*, Archibald *et al.*, 2001).

The use of biogeographic patterns to constrain the timing of the Cambrian radiation is analogous to the use of biogeographic patterns by Murphy *et al.* (2001) to constrain the mammalian radiation in the Cretaceous. Moreover, these estimates on divergence times of the Bilateria and Metazoa are roughly in line with the predictions from the recent molecular clock analysis of Peterson and Takacs (2002). In spite of the fact that these results support an early, hidden Cambrian

radiation, biogeographic patterns from trilobites do not, however, support a diversification of the bilaterian metazoans far back into the Proterozoic that has been predicted by some authors (*e.g.*, Wray *et al.*, 1996). The history of bilaterian metazoan cladogenesis may extend that far back, but there is no evidence to that effect from such derived bilaterians as the trilobites. Furthermore, the fact that well-resolved biogeographic patterns were retrieved in these basal Early Cambrian trilobites and the fact that these patterns were congruent with a major tectonic event suggests that earth history events had a fundamental influence on the topology and perhaps the timing of the Cambrian radiation.

RATES OF EVOLUTION DURING THE CAMBRIAN RADIATION

Introduction

Determining the relative tempo of evolution during the Cambrian radiation is important because it helps elucidate the nature of macroevolutionary processes and how they may vary through time. Truly dramatic tempos of evolution during the Cambrian radiation would point to the uniqueness of this time period in the history of life. Tempos of evolution comparable to other time periods, by contrast, would de-emphasize the uniqueness of the Cambrian radiation, at least in terms of its relevance to our understanding of macroevolutionary processes.

There are two aspects of evolutionary rates. One involves the pace of cladogenesis or speciation. This is based on the recognition that some of the primary data bearing on rates of evolution are rates of speciation (Eldredge, 1979; Stanley, 1979; Vrba, 1980). Another aspect of the rate of evolution involves the amount of morphological change that occurs at speciation or cladogenetic events. This involves the topic of disparity, which has figured prominently in discussions about the nature of the Cambrian radiation. Some (*e.g.*, Gould, 1989, 1991; Hughes, 1991) have argued that the Cambrian radiation marks an interval of unusual evolutionary flexibility relative to subsequent times, such that the disparity of Cambrian faunas equals or exceeds modern faunas. Others have suggested that there is nothing unusual about Cambrian faunas in terms of their flexibility or disparity (*e.g.*, Briggs *et al.*, 1992; Wills *et al.*, 1994; Fortey *et al.*, 1996; Hughes *et al.*, 1999; Smith and Lieberman, 1999; Conway Morris, 2000).

The issue of disparity and the Cambrian radiation is still a topic that is being intensely debated by paleontologists and evolutionary biologists but will not be the focus of this analysis. Instead, here the focus will only be on the question of how, if at all, rates of speciation during the Cambrian radiation differed from rates of speciation documented at other time periods. Very high speciation rates at this time might suggest either that speciation per se occurred more easily in the Early Cambrian or that there were more opportunities for speciation, perhaps due to lower levels of

competition in the Early Cambrian (Conway Morris, 2000, 2002) or tectonic processes that facilitated vicariant differentiation and speciation (see Lieberman, 1997). This analysis will rely on the phylogenetic database of trilobites used in the previous part of this paper but will focus on trilobites of the Olenelloidea, the most diverse and abundant clade of olenelloids and also the clade containing those species with the most well-characterized stratigraphic ranges (Lieberman, 1998). Lieberman (2001*b*) discussed why a stochastic approach is the best way to test whether speciation rates were unusually high during the Cambrian radiation. The null hypothesis tested in such an approach is whether rates of speciation documented at other times in the history of life could produce the diversity change seen in Early Cambrian trilobites.

Materials and methods

Four items, all in place, are required to pursue this analysis. 1) Phylogenetic patterns are needed for without knowledge of lineage relationships the calculation of speciation rates is tenuous (Lieberman, 2001*c*). Phylogenies can be combined with information from stratigraphy to constrain the time when lineages diversified in the manner described by Novacek and Norell (1982) and Edgecombe (1992). Here the phylogenetic framework described above and based on the work of Lieberman (1998, 1999*b*) was used. 2) A chronology for the interval being studied is needed because calculating rates of speciation requires dates. Although stratigraphic correlation in the Cambrian interval is not without controversy (Landing, 1996; but see Knoll, 1996), the publication of several new radiometric dates for the Early Cambrian (Bowring *et al.*, 1993; Isachsen *et al.*, 1994; Landing *et al.*, 1998) as well as several chemostratigraphic (Kirschvink *et al.*, 1991; Brasier *et al.*, 1996; Kaufman *et al.*, 1996) and biostratigraphic studies (Qian and Bengtson, 1989; Ahlberg, 1991; Rozanov, 1992; Vidal and Moczyłowska-Vidal, 1997) now make it possible to constrain with some degree of confidence the duration of the entire Cambrian radiation and even the duration of some of the sub-intervals within that time span. 3) Knowledge of speciation rates from other time periods is needed. This involved collecting a database using results from Walker and Valentine (1984), Vrba (1987), Hulbert (1993), and Lieberman (1999*c*). These studies were chosen because they focused on species-level fossil taxa for which the phylogenetic context was at least roughly known and because they concentrated on a time interval roughly comparable to those considered for the Early Cambrian trilobites. Moderately high rates of speciation (75th and 90th percentile) were used in the test because past authors have suggested that rates of speciation were extremely high during the Cambrian radiation; low to moderate rates of extinction were used because it has never been argued that the Cambrian radiation was a time of unusual extinction. Furthermore, using high extinction rates could make it artificially difficult or even impos-

sible to reject the null hypothesis. 4) Some model of the evolutionary process is needed. Lieberman (2001*b*, *c*) considered different models that have been used to evaluate speciation rates and concluded that the Yule or pure-birth process and the birth and death process were the most robust continuous time models, following the recommendations of Sanderson and Donoghue (1996).

Results

When the test of the null hypothesis was implemented with all of the four items described above in place, the null hypothesis could not be rejected; in short, speciation rates among olenellid trilobites in the Cambrian radiation were not unusually high (Lieberman, 2001*b*). Speciation rates were somewhat elevated during the Cambrian radiation, relative to the Phanerozoic average, but they have been elevated at other times in the history of life too. In fact, a much greater diversity change would have to have occurred for the null hypothesis to be rejected. These results were also resilient to substantial changes in phylogenetic topology and Early Cambrian chronostratigraphy (Lieberman, 2001*b*).

Discussion

If the results from trilobites can be extended to other groups, they suggest no need to invoke special rules of evolution, at least those pertaining to rates of speciation, to explain that radiation. Instead, the Cambrian radiation is perhaps best viewed as a time of taxic radiation equivalent to radiations at other major era boundaries, for example, those known to have occurred at the start of the Mesozoic and the start of the Cenozoic. Thus, if there is anything unique about the macroevolutionary processes operating during the Cambrian radiation, it must involve the issue of disparity discussed by Gould (1989, 1991), Briggs and Fortey (1989), Briggs *et al.* (1992), Conway Morris (1993, 2000), Foote (1995), Wills *et al.* (1994), Fortey *et al.* (1996), and Smith and Lieberman (1999).

CONCLUSIONS

A clearer picture of the Cambrian radiation is beginning to emerge. Although high rates of evolution may have prevailed during the Cambrian radiation, they were not phenomenally high nor high enough to merit the formulation of new rules of evolution relating to the tempo of speciation. Furthermore, some period of cryptic diversification must be acknowledged to have occurred prior to the appearance of Early Cambrian organisms in their eponymous stratigraphic sections. Evidence suggests derived bilaterian metazoans such as trilobites had already begun to diversify anywhere from 20 to 70 million years before their appearance in the fossil record, if support for the timing of key tectonic events used as calibration points remains strong. This estimate is comparable to estimates for the diversification of crown group Metazoa derived

from the recent molecular clock analysis of Peterson and Takacs (2002).

This recognition may at first appear troubling to paleontologists because it implies some inadequacy in the fossil record between the transition from evolutionary origin to either ecological dominance or paleontological emergence of the Metazoa; however, this need not be the sole interpretation. First of all, it is comforting that even though the actual late Neoproterozoic diversification of trilobite taxa is not preserved in the fossil record, the evolutionary signature of these events is retained in the history of life preserved in phylogenetic trees.

In addition, the inferred gap between evolutionary origin and paleontological appearance is relatively small compared to the inferred total duration of the derived Metazoa (on the order of ten percent or less). This type of postulated small discrepancy between macroevolution and the fossil record at the grand scale of life may be analogous to the discrepancy at smaller scales such as the divergence of species argued to occur under the punctuated equilibria hypothesis of Eldredge and Gould (1972). The punctuated equilibria hypothesis predicts that speciation events comprise about ten percent of a species' total duration. Further, it posits that very rarely can paleontologists observe speciation in the fossil record; instead, the appearance of a new species in the fossil record represents a migration of that species from other regions where they originated as small, environmentally marginal populations that are unlikely to be preserved in the fossil record. In fact, it was a species' restriction to small population sizes in marginal environments that made them more likely to differentiate and also less likely to be preserved as fossils (Eldredge and Gould, 1972). At the grand scale of initial metazoan cladogenesis this may also have been true, with species restricted to small population sizes in narrow, marginal environments. Again, by analogy, this may have masked their paleontological presence while facilitating their evolutionary diversification.

Finally, the data from trilobites and also other studies (*e.g.*, Budd, 2002) suggest that the gap in timing between the visible manifestation of the Cambrian radiation and the evolutionary diversification of its component fauna, at least for such derived metazoans as the trilobites, is not as profound as some earlier studies had argued. In fact, Budd (2002) argues that the gap is even smaller than the one favored here. For example, Runnegar (1982), Wray *et al.* (1996), and Ayala *et al.* (1998) suggested that divergence events we associate with the Cambrian radiation happened back between 670 to 1,200 Ma. Even Darwin (1859, 1872) suggested the diversification seen in the Cambrian radiation should have required a period of time equal to the length of the entire Phanerozoic, which would actually make his estimate for metazoan origins similar to that of Wray *et al.* (1996). Although these interpretations are still possible, they are not initially supported by the data presented herein or even from other

studies deriving from the reanalysis of molecular clock data (*e.g.*, Peterson and Takacs, 2002). Thus, of the two competing legacies of the Cambrian radiation both appear to be vindicated. Data presented here suggest there likely is a gap in the fossil record between the evolutionary origin of Early Cambrian faunas and their appearance in the fossil record, according well with the Darwinian view. An important record of this early Cambrian radiation, however, is preserved in the fossil record, especially in phylogenetic and biogeographic patterns; this accords well with the Simpsonian view. In addition, the implied gap in the quality of the fossil record is not so profound as to obviate the value of the fossil record for addressing macroevolutionary questions in general.

In the end, what will become important to know about the Cambrian radiation and indeed other major evolutionary radiations in the fossil record is why there appears to be a lag between evolutionary origin and paleontological manifestation. It is possible that this lag represents a basic flaw in the fossil record, but it may represent something more significant. For example, in the case of the Cambrian radiation, some have argued that the delay represents the origin of skeletons or some biomineralization event (Kazmierczak *et al.*, 1985), although Bengtson (2002) has presented cogent arguments against this. Moreover, the trace fossil record also does not support this interpretation (Crimes, 1992; Fedonkin, 2002; Jensen, 2002). (Note though, this explanation could not in any event apply to other radiations preserved in the fossil record.) It is possible that the Cambrian radiation represents the origins of large size in several metazoan lineages as Davidson *et al.* (1995) argued. Finally, this apparent discrepancy between evolutionary origin and paleontological emergence may have something to do with the interplay of diversity dynamics. Perhaps a group's probability of becoming visible in the fossil record depends on its attaining a level of diversity; especially when speciation rates are low for whatever reason or speciation and extinction rates are nearly identical at low diversity levels, groups will not reach sufficient levels of diversity to be seen typically in the fossil record. Instead, maybe events like the Cambrian radiation or even the Cenozoic radiation of mammals represent times when speciation rates quite suddenly outstripped extinction rates. At least in the case of the Cambrian radiation, this may have been caused by geological changes including continental rifting leading to multiple episodes of vicariance (Lieberman, 1997) or ecological opportunities (Conway Morris, 1993, 2000, 2002). These processes, acting alone or in concert, may have allowed diversity levels to rise and groups to reach levels where they became in a sense paleontologically emergent. In any event, it is clear that the analysis of the fossil record will continue to yield insight into the nature of the Cambrian radiation and evolutionary radiations in general.

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REFERENCES

- Ahlberg, P. 1991. Trilobites in the Lower Cambrian of Scandinavia. *Geologiska Föreningens Stockholm Förhandlingar* 113:74–75.
- Aleinikoff, J. N., R. F. Zartman, M. Walter, D. W. Rankin, P. T. Lytle, and W. C. Burton. 1995. U-Pb ages of metarhyolites of the Catoctin and Mount Rogers Formations, central and southern Appalachians: Evidence for two pulses of iapetan rifting. *Amer. J. Sci.* 295:428–454.
- Archibald, J. D., A. O. Averlanov, and D. G. Ekdale. 2001. Late Cretaceous relatives of rabbits, rodents, and other extant eutherian mammals. *Nature* 414:62–65.
- Ayala, F. J., A. Rzhetsky, and F. J. Ayala. 1998. Origin of the metazoan phyla: Molecular clocks confirm paleontological estimates. *Proc. Natl. Acad. Sci. U.S.A.* 95:606–611.
- Bengtson, S. 2002. Biomineralized skeletons—when, where, and why did they evolve? SICB Ann. Meeting Final Prog. Abstracts: 121–122.
- Bond, G. P., P. A. Nickeson, and M. A. Kominz. 1984. Breakup of a supercontinent between 625Ma and 555Ma: New evidence and implications for continental history. *Earth Plan. Sci. Lett.* 70:325–345.
- Bowring, S. A., J. P. Grotzinger, C. E. Isachsen, A. H. Knoll, S. M. Pelechaty, and P. Kolosov. 1993. Calibrating rates of Early Cambrian evolution. *Science* 261:1293–1298.
- Brasier, M. D., G. Shields, V. N. Kuleshov, and E. A. Zhegallo. 1996. Integrated chemo- and biostratigraphic calibration of early animal evolution: Neoproterozoic-Early Cambrian of southwest Mongolia. *Geol. Mag.* 133:445–485.
- Bremer, K. 1994. Branch support and tree stability. *Cladistics* 10: 295–304.
- Briggs, D. E. G. and R. A. Fortey. 1989. The early radiation and relationships of the major arthropod groups. *Science* 246:241–243.
- Briggs, D. E. G., R. A. Fortey, and M. A. Wills. 1992. Morphological disparity in the Cambrian. *Science* 256:1670–1673.
- Bromham, L., A. Rambault, R. A. Fortey, A. Cooper, and D. Penny. 1998. Testing the Cambrian explosion hypothesis by using a molecular dating technique. *Proc. Natl. Acad. Sci. U.S.A.* 95: 12386–12389.
- Brooks, D. R. 1985. Historical ecology: A new approach to studying the evolution of ecological association. *Ann. Miss. Bot. Gard.* 72:660–680.
- Brooks, D. R. and D. A. McLennan. 1991. *Phylogeny, ecology, and behavior*. University of Chicago Press, Chicago, Illinois.
- Budd, G. E. 2002. The fossil record of bilaterians. SICB Ann. Meeting Final Prog. Abstracts: 136–137.
- Budd, G. E. and S. Jensen. 2000. A critical reappraisal of the fossil record of the Bilaterian phyla. *Biol. Revs.* 75:253–295.
- Conway Morris, S. 1993. The fossil record and the early evolution of the Metazoa. *Nature* 361:219–225.
- Conway Morris, S. 2000. The Cambrian 'explosion': Slow-fuse or megatonnage? *Proc. Natl. Acad. Sci. U.S.A.* 97:4426–4429.
- Conway Morris, S. 2002. The Cambrian explosion: What's the problem? SICB Ann. Meeting Final Prog. Abstracts: 156–157.
- Crimes, T. P. 1992. Changes in the trace fossil biota across the Proterozoic-Phanerozoic boundary. *J. Geol. Soc. London* 149:637–646.
- Dalziel, I. W. D. 1992. On the organization of American plates in the Neoproterozoic and the breakout of Laurentia. *Geol. Soc. Amer. Today* 2:237–241.
- Dalziel, I. W. D. 1997. Neoproterozoic-Paleozoic geography and tec-

- tonics: Review, hypothesis, environmental speculation. *Bull. Geol. Soc. Amer.* 190:16–42.
- Darwin, C. 1859. *On the origin of species by means of natural selection; or the preservation of favored races in the struggle for life* (Reprinted 1st edition). Harvard University Press, Cambridge, Massachusetts.
- Darwin, C. 1872. *On the origin of species by means of natural selection; or the preservation of favored races in the struggle for life* (Reprinted 6th edition). Mentor, New York.
- Davidson, E. H., K. J. Peterson, and R. A. Cameron. 1995. Origin of bilaterian body plans: Evolution of developmental regulatory mechanisms. *Science* 270:1319–1325.
- Droser, M. L., R. A. Fortey, and L. Xing. 1996. The Ordovician radiation. *Am. Sci.* 84:122–131.
- Edgecombe, G. D. 1992. Trilobite phylogeny and the Cambrian-Ordovician “event”: A cladistic reappraisal. In M. J. Novacek and Q. D. Wheeler (eds.), *Extinction and phylogeny*, pp. 144–177. Columbia University Press, New York.
- Eldredge, N. 1979. Alternative approaches to evolutionary theory. *Bull. Carnegie Mus. Nat. Hist.* 13:7–19.
- Eldredge, N. and S. J. Gould. 1972. Punctuated equilibria: An alternative to phyletic gradualism. In T. J. M. Schopf (ed.), *Models in paleobiology*, pp. 82–115. Freeman, Cooper, San Francisco, California.
- Faill, R. T. 1997. A geologic history of the north-central Appalachians. Part 1. Orogenesis from the Mesoproterozoic through the Taconic Orogeny. *Am. J. Sci.* 297:551–619.
- Faith, D. P. 1991. Cladistic permutation tests for monophyly and nonmonophyly. *Syst. Zool.* 40:366–375.
- Fedonkin, M. A. 2002. Megascopic trace and body fossils of the oldest metazoans. SICB Ann. Meeting Final Prog. Abstracts: 191.
- Foot, M. 1995. Morphological diversification of Paleozoic crinoids. *Paleobiology* 21:273–299.
- Fortey, R. A. 1990. Ontogeny, hypostome attachment and trilobite classification. *Palaeontology* 33:529–576.
- Fortey, R. A., D. E. G. Briggs, and M. A. Wills. 1996. The Cambrian evolutionary ‘explosion’: Decoupling cladogenesis from morphological disparity. *Biol. J. Linn. Soc.* 57:13–33.
- Fortey, R. A. and R. M. Owens. 1997. Evolutionary history. In R. L. Kaesler (ed.), *Treatise on invertebrate paleontology, O (Arthropoda 1, Trilobita, Revised)*, pp. 249–287. Geological Society of America and University of Kansas Press, Lawrence, Kansas.
- Gould, S. J. 1989. *Wonderful life*. W. W. Norton, New York.
- Gould, S. J. 1991. The disparity of the Burgess shale arthropod fauna and the limits of cladistic analysis. Why we must strive to quantify morphospace? *Paleobiology* 17:411–423.
- Hillis, D. M. 1991. Discriminating between phylogenetic signal and random noise in DNA sequences. In M. M. Miyamoto and J. Cracraft (eds.), *Phylogenetic analysis of DNA sequences*, pp. 278–294. Oxford University Press, Oxford.
- Hoffman, P. F. 1991. Did the breakout of Laurentia turn Gondwana inside out? *Science* 252:1409–1412.
- Hughes, N. C. 1991. Morphological plasticity and genetic flexibility in a Cambrian trilobite. *Geology* 19:913–916.
- Hughes, N. C., R. E. Chapman, and J. M. Adrain. 1999. The stability of thoracic segmentation in trilobites: A case study in developmental and ecological constraints. *Evol. Devel.* 1:24–35.
- Hulbert, R. C., Jr. 1993. Taxonomic evolution in North American Neogene horses (subfamily Equinae): The rise and fall of an adaptive radiation. *Paleobiology* 19:216–234.
- Isachsen, C. A., S. A. Bowring, E. Landing, and S. D. Samson. 1994. New constraint on the division of Cambrian time. *Geology* 22:496–498.
- Jensen, S. 2002. The Proterozoic and earliest Cambrian trace fossil record; patterns, problems and perspectives. SICB Ann. Meeting Final Prog. Abstracts: 250.
- Karlstrom, K. E., M. L. Williams, J. McLelland, J. W. Geissman, and K.-I. Åhäll. 1999. Refining Rodinia: Geologic evidence for the Australia-Western U. S. connection in the Proterozoic. *Geol. Soc. Amer. Today* 9:1–7.
- Kaufman, A. J., A. H. Knoll, M. A. Semikhatov, J. P. Grotzinger, S. B. Jacobsen, and W. Adams. 1996. Integrated chronostratigraphy of Proterozoic-Cambrian boundary beds in the western Anabar region, northern Siberia. *Geol. Mag.* 133:509–533.
- Kazmierczak, J., V. Ittekkott, and E. T. Degens. 1985. Biocalcification through time: Environmental challenge and cellular response. *Paläont. Zeitsch.* 59:15–33.
- Kirschvink, J. L., M. Magaritz, R. L. Ripperdan, and A. Y. Zhuravlev. 1991. The Precambrian-Cambrian boundary: Magnetostratigraphy and Carbon isotopes resolve correlation problems between Siberia, Morocco, and South China. *Geol. Soc. Amer. Today* 1:69–71.
- Kirschvink, J. L., R. L. Ripperdan, and D. A. Evans. 1997. Evidence for a large-scale reorganization of Early Cambrian continental masses by Inertial Interchange True Polar Wander. *Science* 277:541–545.
- Knoll, A. H. 1996. Daughter of time. *Paleobiology* 22:1–7.
- Landing, E. 1996. Avalon: Insular continent by the latest Precambrian. *Geol. Soc. Amer. Spec. Pap.* 304:29–63.
- Landing, E., S. A. Bowring, K. Davidek, S. R. Westrop, G. Geyer, and W. Heldmaier. 1998. New U-Pb zircon dates from Avalon and Gondwana and duration of the Early Cambrian. *Can. J. Earth Sci.* 35:329–338.
- Li, Z.-X., L. Zhang, and C. McA. Powell. 1996. Positions of the East Asian cratons in the Neoproterozoic supercontinent Rodinia. *Austral. J. Earth Sci.* 43:593–604.
- Lieberman, B. S. 1993. Systematics and biogeography of the “*Metacryphaeus* Group” Calmoniidae (Trilobita, Devonian), with comments on adaptive radiations and the geological history of the Malvinokaffric realm. *J. Paleontol.* 67:549–570.
- Lieberman, B. S. 1997. Early Cambrian paleogeography and tectonic history: A biogeographic approach. *Geology* 25:1039–1042.
- Lieberman, B. S. 1998. Cladistic analysis of the Early Cambrian olenelloid trilobites. *J. Paleontol.* 72:59–78.
- Lieberman, B. S. 1999a. Systematic revision of the Olenelloidea (Trilobita, Cambrian). *Bull. Yale Univ. Peabody Mus. Nat. Hist.* 45:1–150.
- Lieberman, B. S. 1999b. Testing the Darwinian legacy of the Cambrian radiation using trilobite phylogeny and biogeography. *J. Paleontol.* 73:176–181.
- Lieberman, B. S. 1999c. Evaluating the turnover-pulse hypothesis in proetid trilobites during the Acadian orogeny. *Virg. Mus. Nat. Hist. Spec. Publ.* 7:99–108.
- Lieberman, B. S. 2000. *Paleobiogeography: Using fossils to study global change, plate tectonics, and evolution*. Kluwer Academic Press/Plenum Publishing, New York, New York.
- Lieberman, B. S. 2001a. Phylogenetic analysis of the Olenellina Walcott, 1890 (Trilobita, Cambrian). *J. Paleontol.* 75:96–115.
- Lieberman, B. S. 2001b. A test of whether rates of speciation were unusually high during the Cambrian radiation. *Proc. Roy. Soc. London, Biol. Sci.* 268:1707–1714.
- Lieberman, B. S. 2001c. Analyzing speciation rates in macroevolutionary studies. In J. Adrain, G. D. Edgecombe, and B. S. Lieberman (eds.), *Fossils, phylogeny, and form: An analytical approach*, pp. 323–339. Kluwer Academic Press/Plenum Publishing, New York.
- Lieberman, B. S. 2002. Phylogenetic analysis of some basal early Cambrian trilobites, the biogeographic origins of the Eutrilobita, and the timing of the Cambrian radiation. *J. Paleontol.* 76:692–708.
- Lieberman, B. S., and N. Eldredge. 1996. Trilobite biogeography in the Middle Devonian: Geological processes and analytical methods. *Paleobiology* 22:66–79.
- McKerrow, W. S., C. R. Scotese, and M. D. Brasier. 1992. Early Cambrian continental reconstructions. *J. Geol. Soc. London* 149:599–606.
- McKinney, F. K., S. Lidgard, J. J. Sepkoski, Jr., and P. D. Taylor. 1998. Decoupled temporal patterns of evolution and ecology in two post-Paleozoic clades. *Science* 281:807–809.
- Moyes, A. B., J. M. Barton, Jr., and P. B. Groenewald. 1993. Late Proterozoic to Early Palaeozoic tectonism in Dronning Maud Land, Antarctica: Supercontinental fragmentation and amalgamation. *J. Geol. Soc. London* 150:833–842.
- Murphy, W., J. E. Eizirik, S. J. O’Brien, O. Madsen, M. Scally, C.

- J. Douady, E. Teeling, O. A. Ryder, M. J. Stanhope, W. W. de Jong, and M. S. Springer. 2001. Resolution of the early placental mammal radiation using Bayesian phylogenetics. *Science* 294:2348–2351.
- Novacek, M. J. and M. A. Norell. 1982. Fossils, phylogeny, and taxonomic rates of evolution. *Syst. Zool.* 31:366–375.
- Peterson, K. J. and C. M. Takacs. 2002. Molecular clocks, snowball earth, and the Cambrian explosion. *SICB Ann. Meeting Final Prog. Abstracts*: 341.
- Powell, C. McA. 1995. Are Neoproterozoic glacial deposits preserved on the margin of Laurentia related to fragmentation of two supercontinents? *Geology* 23:1053–1054.
- Powell, C. McA., M. W. McElhinny, J. G. Meert, and J. K. Park. 1993. Paleomagnetic constraints on timing of the Neoproterozoic breakup of Rodinia and the Cambrian formation of Gondwana. *Geology* 21:889–892.
- Prave, A. R. 1999. Two diamictites, two cap carbonates, two $\delta^{13}\text{C}$ excursions, two rifts: The Neoproterozoic Kingston Peak Formation, Death Valley, California. *Geology* 27:339–342.
- Qian, Y. and S. Bengston. 1989. Paleontology and biostratigraphy of the Early Cambrian Meishucunian Stage in Yunnan Province, south China. *Fossils and Strata* 24:1–156.
- Rozanov, A. Y. 1992. Some problems concerning the Precambrian-Cambrian transition and the Cambrian faunal radiation. *J. Geol. Soc. London* 149:593–598.
- Runnegar, B. 1982. A molecular-clock date for the origin of the animal phyla. *Lethaia* 15:199–205.
- Sanderson, M. J. and M. J. Donoghue. 1996. Reconstructing shifts in diversification rates on phylogenetic trees. *Trends Ecol. Evol.* 11:15–20.
- Scotese, C. 1997. *Paleogeographic atlas*. PALEOMAP Project, University of Texas, Arlington, Texas.
- Scotese, C., A. J. Boucot, and W. S. McKerrrow. 1999. Gondwanan palaeogeography and palaeoclimatology. *J. Afr. Earth Sci.* 28: 99–114.
- Smith, L. H. and B. S. Lieberman. 1999. Disparity and constraint in olenelloid trilobites and the Cambrian radiation. *Paleobiology* 25:459–470.
- Stanley, S. M. 1979. *Macroevolution: Pattern and process*. W. H. Freeman, San Francisco, California.
- Swofford, D. L. 2001. *PAUP. Phylogenetic analysis using parsimony*. Version 4.08b. Sinauer Associates, Sunderland, Massachusetts.
- Torsvik, T. H., M. A. Smethurst, J. G. Meert, R. Van Der Voo, W. S. McKerrrow, M. D. Brasier, B. A. Sturt, and H. J. Walderhaug. 1996. Continental break-up and collision in the Neoproterozoic and Palaeozoic—A tale of Baltica and Laurentia. *Earth-Sci. Revs.* 40:229–258.
- Unrug, R. 1997. Rodinia to Gondwana: The geodynamic map of Gondwana supercontinent assembly. *Geol. Soc. Amer. Today* 7: 1–7.
- Valentine, J. W. 1994. Late Precambrian bilaterians: Grades and clades. *Proc. Natl. Acad. Sci. U.S.A.* 91:6751–6757.
- Veevers, J. J., M. R. Walter, and E. Scheibner. 1997. Neoproterozoic tectonics of Australia-Antarctica and Laurentia and the 560 Ma birth of the Pacific Ocean reflect the 400 m. y. Pangean super-cycle. *J. Geol.* 105:225–242.
- Vidal, G. and M. Moczydlowska-Vidal. 1997. Biodiversity, speciation, and extinction trends of Proterozoic and Cambrian phytoplankton. *Paleobiology* 23:230–246.
- Vrba, E. S. 1980. Evolution, species and fossils: How does life evolve? *South Afr. J. Sci.* 76:61–84.
- Vrba, E. S. 1987. Ecology in relation to speciation rates: Some case histories of Miocene-Recent mammal clades. *Evol. Ecol.* 1:285–300.
- Walker, T. D. and J. W. Valentine. 1984. Equilibrium models of evolutionary species diversity and the number of empty niches. *Am. Nat.* 124:887–899.
- Wiley, E. O. 1988. Vicariance biogeography. *Ann. Revs. Ecol. Syst.* 19:513–542.
- Wills, M. A., D. E. G. Briggs, and R. A. Fortey. 1994. Disparity as an evolutionary index: A comparison of Cambrian and Recent arthropods. *Paleobiology* 20:93–130.
- Wills, M. A., D. E. G. Briggs, R. A. Fortey, M. Wilkinson, and P. H. A. Sneath. 1998. An arthropod phylogeny based on fossils and recent taxa. In G. D. Edgecombe (ed.), *Arthropod fossils and phylogeny*, pp. 33–105. Columbia University Press, New York.
- Wingate, M. T. D., I. H. Campbell, W. Compston, and G. M. Gibson. 1998. Ion microprobe U-Pb ages for Neoproterozoic basaltic magmatism in south-central Australia and implications for the breakup of Rodinia. *Precam. Res.* 87:135–159.
- Wray, G. A., J. S. Levinton, and L. H. Shapiro. 1996. Molecular evidence for deep Precambrian divergences among Metazoan phyla. *Science* 274:568–573.
- Xiao, S., Y. Zhang, and A. H. Knoll. 1998. Three-dimensional preservation of algae and animal embryos in a Neoproterozoic phosphorite. *Nature* 351:553–558.