A test of whether rates of speciation were unusually high during the Cambrian radiation

Bruce S. Lieberman

Departments of Geology and Ecology and Department of Evolutionary Biology, University of Kansas, 120 Lindley Hall, Lawrence, KS 66045, USA (blieber@ku.edu)

The Cambrian radiation represents an interval when nearly 20 animal phyla appear in the fossil record in a short geological time span; however, whether this radiation also represents a period of extremely rapid speciation remains unclear. Here, a stochastic framework is used to test the null hypothesis that diversity changes in one of the dominant Early Cambrian groups, the olenelloid trilobites, could be produced by tempos of speciation known to have operated during later time periods. Two continuous-time models, the Yule model and the birth and death process model, and one discrete-time model, the Bienaymé–Galton–Watson branching process model, were used. No statistical evidence for uniquely high rates of speciation during the radiation in these trilobites was found when the continuous-time models were used with low or moderate extinction rates, the rates typically associated with the Cambrian radiation, although the p values are fairly low or, in one case, significant when high extinction rates were used. However, rates of speciation were higher than the average Phanerozoic rates of speciation. The discrete-time model produced equivocal results: either rates were unusually high or the model is inapplicable during the Cambrian radiation. This suggests that there was nothing unique about evolutionary processes relating to the tempo of speciation during the Cambrian radiation.

Keywords: Cambrian radiation; speciation rates; stochastic framework; trilobites

1. INTRODUCTION

The Early Cambrian marks a major episode in the history of life, the so-called Cambrian explosion or radiation, when the earth's biota shifted rapidly from an assemblage depauperate in metazoan taxa to a diverse metazoan fauna comprising at least 20 animal phyla occupying a range of habitats. Although the Cambrian radiation may not include the initial divergence of the major metazoan phyla (Runnegar 1982; Bengston & Zhao 1992, 1997; Briggs *et al.* 1992; Conway Morris 1993, 2000; Wills *et al.* 1994; Davidson *et al.* 1995; Fortey *et al.* 1996, 1997; Wray *et al.* 1996; Ayala *et al.* 1998; Bromham *et al.* 1998; Xiao *et al.* 1998), it was certainly a time of considerable diversification, including high rates of origination at higher taxonomic levels (Newell 1952; Raup 1978, 1981, 1991; Sepkoski 1979; Stanley 1979; Van Valen 1985*a*; Erwin *et al.* 1987; Gilinsky & Bambach 1987; Foote 1988; Gould 1989, 1991; Bengston & Zhao 1992, 1997; Conway Morris 1993; Valentine 1994). However, what remains largely untested is whether or not this radiation was accompanied by uniquely high rates of speciation. Uniquely high rates of speciation might suggest that there was something special about the rules of evolution during this time. By contrast, if rates of speciation were not unusually high, it would be another argument, along with those presented in Briggs & Fortey (1989), Briggs *et al.* (1992), Conway Morris (1993, 1998), Fortey *et al.* (1996, 1997), Xianguang & Bergström (1997), Bromham *et al.* (1998) and Hughes *et al.* (1999), that perhaps there was nothing truly unique about the evolutionary processes operating at this time.

The best way to approach the problem of whether rates of speciation were unusually high during the Cambrian radiation is to use a stochastic framework of the type outlined by Nee *et al.* (1992, 1994*a,b*), Sanderson &

Bharathan (1993), Harvey *et al.* (1994), Sanderson & Donoghue (1996), Pagel (1997, 1999), Paradis (1997, 1998) and Heard & Mooers (2000). Specifically, the goal was to match the approach that Pagel (1997) referred to as 'statistical palaeontology'. Here, the probability that the rates or probabilities of speciation prevailing during other times in earth's history could explain the change in diversity seen during the Cambrian radiation was calculated. In such a framework, the null hypothesis (H_0) to reject at some predetermined level of significance is that rates or probabilities of speciation in the Early Cambrian did not differ fundamentally from those at other times in earth's history. Speciation rates were used as a measure of rates of evolution following the arguments that these are among the fundamental data for determining rates of evolution (Stanley 1979; Vrba 1980; Stanley *et al.* 1981; Eldredge 1989), although the legitimate argument has been made by Sepkoski (1979) and others that differentiation of higher taxonomic categories are also important data for determining rates of evolution. Still, if speciation rates were uniquely high during the Cambrian radiation, it would indicate that the rules governing the tempo of evolution may have been different at that time. Several interesting and important palaeontological approaches to the quantification of speciation rates have been conducted by Raup (1978, 1981), Sepkoski (1979), Raup & Sepkoski (1982), Van Valen (1985*a*), Gilinsky & Bambach (1987) and Foote (1988). These approaches are clearly valid, but are not used here for two reasons: first, it would be extremely difficult, if not impossible, to adapt the phylogenetic database that this study relies on to these methods; and second, calculating a speciation rate during the Cambrian radiation does not by itself allow one to answer the statistical question of whether or not speciation rates were unusually high during the Cambrian radiation. Thus, the approach used here is

different and complementary to the approaches developed by Foote, Raup, Sepkoski and others.

2. MATERIAL AND MODELS

Potentially, an important part of testing H_0 is having a detailed phylogeny for some major group(s) of Early Cambrian taxa, because comparative data provide important information about the nature of evolutionary processes (Harvey & Pagel 1991; Hey 1992; Pagel 1993, 1997). Furthermore, without a phylogeny there may be taxa that are paraphyletic or even polyphyletic, and these can make the calculation of speciation rates problematic (Brooks & McLennan 1991; Smith 1994). Specifically, the calculation of a speciation rate depends on knowing what gave rise to what (Smith 1994). (However, as described below (§ 3), in this particular instance the phylogenetic topology does not affect the overall conclusions.) Recently, Lieberman (1998, 1999a) subjected clades of the exclusively Early Cambrian olenelloid trilobites to cladistic analysis. This procedure allows a hypothesis of relationship to be made for 78 species (figure 1). For the purposes of this analysis the phylogeny, along with stratigraphic information, was used to help constrain the relative timing of branching events to particular temporal intervals in the manner described by Smith (1994).

The olenelloid trilobites are well suited to the analysis of rates of speciation during the Cambrian radiation. They are one of the dominant Early Cambrian metazoan groups in terms of their relative abundance and diversity, and they also had a broad geographical distribution that encompassed Laurentia (North America and Greenland), Baltica (Scandinavia and the eastern European platform) and part of northern Africa. In addition, they have a complex morphology, which facilitates the character analysis requisite for phylogenetic studies. Some other major clades present during the Early Cambrian, such as the archaeocyathans, the small shelly fossils and the inarticulated brachiopods, are difficult or intractable subjects for phylogenetic analysis, because of their enigmatic affinities, their preservation as disarticulated fragments or their relatively simple morphology. Those non-trilobite taxa clearly referable to the metazoa that have a suitably complex morphology to permit rigorous character analysis, such as the echinoderms and the molluscs, are relatively species poor. Furthermore, the olenelloid trilobites are held to be representative of Early Cambrian faunas in general (Smith & Lieberman 1999); if any group would be anticipated to show a representative pattern, it is the olenelloids. Thus, the olenelloid trilobites are probably among the most appropriate Early Cambrian groups to consider in the analysis of probabilities and rates of speciation. Finally, studies of arthropods in general (Briggs & Fortey 1989; Gould 1989; Briggs *et al*. 1992; Wills *et al*. 1994, 1997; Budd 1997; Xianguang & Bergström 1997; Wills 1998), and trilobites in particular (Fortey *et al*. 1996; Hughes *et al*. 1999), have been important parts of studies of the nature of evolutionary processes during the Cambrian radiation.

Testing H_0 also requires some understanding of the relationship of speciation events to an absolute time scale. Stratigraphic correlation and absolute dating in the Cambrian interval are still controversial but recent studies have established new radiometric dates for horizons within the Early Cambrian (Bowring *et al*. 1993; Isachsen *et al*. 1994; Landing *et al*. 1998), and improved biostratigraphic and chemostratigraphic correlations have been developed (Yi & Bengston 1989; Ahlberg 1991; Kirschvink *et al*. 1991; Rozanov 1992; Brasier *et al*. 1996; Kaufman *et al*. 1996; Vidal & Moczydlowska-Vidal 1997), such
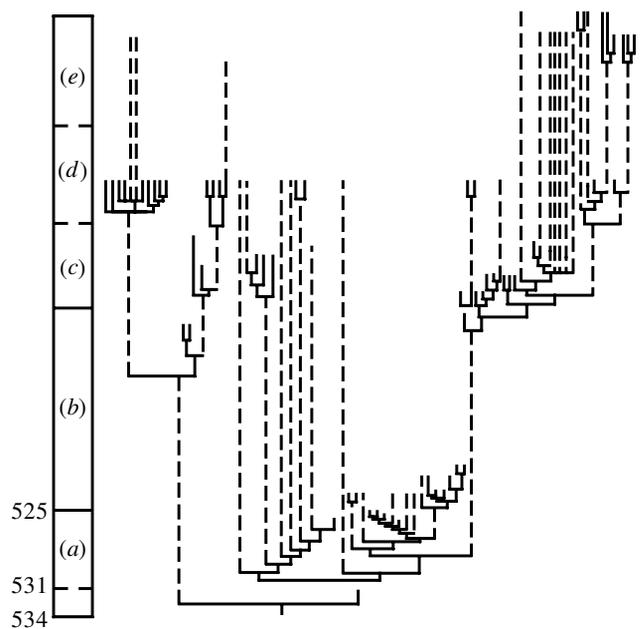

Figure 1. Phylogeny of Early Cambrian olenelloid trilobites from Lieberman (1998, 1999a), used to test the null hypothesis about rates of speciation during the Cambrian radiation. Solid lines represent actual ranges of taxa, and dashed lines represent inferred ranges of taxa. The ghost-lineage method of Smith (1994) was used to constrain the time that sister taxa diversify. Stratigraphic sampling for some of the olenelloid species considered is not great, but additional sampling would only affect the calculation of ghost lineages if it extended a taxon's range downward. Such changes would reduce the overall magnitude of the diversity change during the Cambrian radiation, thereby reducing the speciation rates necessary to produce the radiation and making it less likely that the null hypothesis would be rejected. Therefore, based on the analyses in this study, additional sampling would not profoundly influence the overall conclusions. Radiometric dates and stratigraphic correlations are taken from Ahlberg (1991), Kirschvink *et al*. (1991), Rozanov (1992), Bowring *et al*. (1993), Isachsen *et al*. (1994), Brasier *et al*. (1996), Kaufman *et al*. (1996), Vidal & Moczydlowska-Vidal (1997) and Landing *et al*. (1998); ages are in millions of years. (a) *Schmidtiellus mickwitzi* zone, (b) *Holmia kjerulfi* group zone/ *Nevadella* zone, (c) lower *Olenellus* zone, (d) middle *Olenellus* zone and (e) upper *Olenellus* zone.

that the stratigraphic framework for studying the Early Cambrian is becoming relatively well understood (Knoll 1996) (see figure 1). The earliest part of the Early Cambrian is now recognized to be devoid of trilobites. Thus, the test of H_0 will be restricted to the earliest trilobitic parts of the Early Cambrian, which are still part of the Cambrian radiation. Tests of the tempo of evolution during the earliest, non-trilobitic, part of the Early Cambrian would be extremely difficult, if not impossible, because of the largely biologically depauperate nature of this interval. The definition of the base of the Early Cambrian in species-poor settings that precede the interval when most of the skeletonized metazoans diversified was done for purposes of biostratigraphic utility. However, this biostratigraphic action does not obviate or de-emphasize the evolutionary significance of the trilobitic part of the Cambrian-radiation interval. Testing H_0 for later parts of the Early Cambrian that post-date the Cambrian radiation would not specifically test whether or not rates were unusually high during the radiation.

In order to perform the broadest possible test of H_0, three different methods, each based on a separate model of evolution frequently applied to evolutionary studies, were used to calculate the probability that diversity changes in the Cambrian radiation can be explained by rates of speciation calculated for other groups at other times. The methods used, based on the Yule or pure-birth process, the birth and death process and the Bienaymé–Galton–Watson process, are the most statistically robust according to Sanderson & Donoghue (1996). Raup (1978, 1985), Sepkoski (1979), Raup & Sepkoski (1982), Van Valen (1985a), Foote (1988) and Gilinsky & Good (1991) have applied these methods to palaeobiological problems. These models are all based, to some extent, on an exponential model of diversification as opposed to a logistic model, in the sense that they do not suppose any density-dependent effects on diversity and they assume a branching model of evolution (Benton 1999). The issue of whether diversity best fits an exponential or a logistic pattern has been discussed extensively by Benton (1996, 1999) and has been the subject of considerable debate (for example, see Benton 1995, 1996, 1999 and Sepkoski 1979, 1996). The resolution of this debate depends on determining the role that competition plays in producing macroevolutionary patterns (see discussion in Gould & Calloway 1980; Benton 1983, 1987, 1999; Jablonski 1986; Rosenzweig 1995; and Sepkoski 1996). At this time, it appears that at the scale of the diversification of life, either model may adequately describe the data (Benton 1999). However, the Early Cambrian was one time when density-dependent effects on animal diversification are likely to have been less profound because there were fewer taxa and potentially more available ecospace, such that ecosystems were more open. In fact, the earliest phases of logistic diversification are essentially equivalent to exponential diversification, and the fact that broad patterns of Early Cambrian diversification appear to correspond to an exponential pattern has been acknowledged even in the works of those authors who have been strong advocates for the logistic model at the grand scale of life (e.g. Sepkoski 1979). Therefore, exponential models are certainly appropriate for considering diversification during the limited temporal interval of the Cambrian radiation, although consistent high rates of exponential diversification over tens of millions of years are not realistic.

In the first model, the probability that the species diversity equals a particular value at time t is

$$P_n(t) = \binom{n-1}{n-i} e^{-i\lambda t}(1 - e^{-\lambda t})^{n-i}, \tag{1}$$

where t is the duration of the interval of interest, n is the number of species present at time t and i is the initial number of species present (Feller 1968). The probability that a lineage speciates is given by λdt; speciation is modelled as a time-homogeneous continuous-time Markov process that follows a Poisson distribution with parameter λ; each species is independent and has an equal probability of generating a new species (Feller 1968; Sanderson & Bharathan 1993). Then, the probability of a diversity change greater than or equal to the actual diversity change that occurred would be

$$1 - \sum_{j=i}^{n-1} P_j(t). \tag{2}$$

A shortcoming of the Yule model is that extinction is not factored in (Raup 1985).

In the birth and death process model, extinction is additionally factored in. With an initial diversity of one species, the probability that the species diversity equals a particular value at time t is (Feller 1968)

$$P_n(t) = (1 - \lambda B(t))(1 - \mu B(t))(\lambda B(t))^{n-1} \text{ for } n \geqslant 1 \tag{3}$$

and $P_0(t) = \mu B(t)$,

where $B(t) = \dfrac{1 - e^{(\lambda - \mu)t}}{\mu - \lambda e^{(\lambda - \mu)t}}$.

The parameter μ is the rate of decrease of diversity and the assumptions are the same as those of the Yule model (Feller 1968; Rannala & Yang 1996). This equation can be extended to initial diversity values greater than one, e.g. two. In fact, if one sets $G_n(t)$ equal to the probability that the species diversity equals n at time t, then if there are initially two species

$$G_n(t) = (n-1)[(1 - \lambda B(t))(1 - \mu B(t))]^2 (\lambda B(t))^{n-2}$$
$$+ 2\mu B(t)(1 - \lambda B(t))(1 - \mu B(t))(\lambda B(t))^{n-1}$$
$$\text{for } n \geqslant 2, \tag{4}$$
$$G_0(t) = \mu B(t)^2,$$
$$G_1(t) = 2\mu B(t)(1 - \lambda B(t))(1 - \mu B(t)).$$

Then, in the case of two initial species, the probability of a diversity change greater than or equal to the actual diversity change that occurred would be

$$1 - \sum_{j=0}^{n-1} G_j(t). \tag{5}$$

The model for the third method employs a discrete-time branching process and is based on a probability-generating function involving the sum of independent random variables, which is a polynomial in x, where the coefficients of the terms are the probabilities that are associated with changes in species diversity (represented by the powers to which x is raised) after one observed interval or generation with (Gilinsky & Good 1991)

$$f(x) = p_0 + p_1 x + p_2 x^2, \tag{6}$$

where p_0 is the probability that the size of the population changes from one to zero, p_1 is the probability that the size remains unchanged at one and p_2 is the probability that the size changes from one to two. This can be written more generally as $[f(x)]^{V_0}$ where V_0 is the initial standing species diversity. Also, this is an iterated generating function so that, for example, the probability that species diversity will change from one value to another over three generations is $[f(f(f(x)))]^{V_0}$ (Gilinsky & Good 1991). In this model, diversity changes occur during discrete generations. In the fossil record, our resolution of speciation and extinction events is often at the scale of formations or zones. Thus, when this model is applied to palaeobiological data, a generation is taken to mean some distinct stratigraphic interval. The model also makes the necessary assumptions that diversity no more than doubles in a single interval and that the diversity change observed should have occurred in the fewest possible generations. In the Early Cambrian each of these assumptions may not be valid, and this is discussed further in §4.

The first and second models are fairly similar but both differ significantly from the third model. These differences manifest themselves for several reasons, but one is that the first and second models are continuous-time processes whereas the third

model is a discrete-time process. There has been significant debate about which type of model, continuous or discrete, best exemplifies the evolutionary process (Gilinsky & Good 1991). If the evolutionary process is largely continuous, with speciation and extinction not clustered and episodic, then the first and second models may be more appropriate. If evolution is better viewed as a discrete process, with speciation and extinction occurring episodically, then the discrete approach may be more appropriate. Of course, a discrete model can approach a continuous model as the intervals become more finely divided.

To implement the first two stochastic models, estimates of the parameters λ and μ were obtained from the literature (Walker & Valentine 1984; Vrba 1987; Hulbert 1993; Lieberman 1999*b*). These studies were chosen to derive the values of λ and μ for two reasons: first, because they were based on species-level diversity changes analysed in fossil clades for which a phylogenetic context existed; and second, because they considered groups that had diversity changes over time intervals comparable to those seen in the olenelloids. Without these two constraints, parameter values would not be strictly comparable with the example considered herein, which would complicate the testing of H_0. Datasets were obtained for fossil invertebrates only, and for both fossil invertebrates and vertebrates, in case there were some biological differences between invertebrate and vertebrate taxa, even though the invertebrate taxon is meaningless phylogenetically. In this case, the H_0 being tested is whether rates differed statistically from high rates that have prevailed at other times during the Phanerozoic. Thus, 90th percentile values of λ were chosen, while 10th percentile (low), mean (moderate) and 90th percentile (high) values of μ were chosen. (However, low and moderate extinction probabilities are likely to be the most realistic based on previous studies that suggest that the extinction probability was low or moderate through the early part of the Early Cambrian, and became rather high only towards the end of the Early Cambrian (Raup & Sepkoski 1982; Van Valen 1985*b*; Foote 1988; Raup 1991; Sepkoski 1994), after the studied interval had ended.) Values from Early Cambrian taxa were not included. Rates were provisionally treated as homogeneous across branches within an interval. Rates can, in actuality, vary across individual branches within any given interval (see Sanderson & Bharathan 1993; Pagel 1993, 1997, 1999; and Heard & Mooers 2000) but the H_0 here considers the entire duration of the radiation not individual branches within that interval, because otherwise the problem is hard to frame stochastically (see Sanderson & Donoghue 1996). Diversity changes in olenelloid trilobites are greatest in the earliest trilobitic part of the Early Cambrian (the *S. mickwitzi* zone). If H_0 cannot be rejected for the diversity change during the 6-million-year long *S. mickwitzi* zone, then it cannot be rejected for subsequent intervals. To use the Bienaymé–Galton–Watson process, values of p_0, p_1 and p_2 are necessary. These are only available from Gilinsky & Good (1991). Whether these are strictly comparable with the entities considered herein is debated by Gilinsky & Good (1991) and Gilinsky (1994). The values of p_2 from Gilinsky & Good (1991) are based on higher taxa and could be too low for species, making it easier to reject H_0. As was the case for the parameters of the continuous-time models, high values of origination probability (p_2) were sought because the H_0 being tested is whether rates of speciation during the Cambrian radiation differ statistically from high rates of speciation that have prevailed at other times during the Phanerozoic. Again, probabilities for Early Cambrian taxa were not included. The 90th percentile values and the maximum values of p_2 were

Table 1. Yule (pure birth) and birth and death (BD) process models, along with their associated parameters (in units of per million years), used to determine the probability that a diversity change as great or greater than the one seen in the Cambrian radiation could have been produced by rates of speciation that have operated at other times in earth's history.

(Results are expressed as unconditional p values and as conditional p values conditioned on the non-occurrence of early lineage extinction, with values of $p < 0.05$ implying inapplicability of the model or rejection of the null hypothesis presented in § 1. Conditional p values are expressed as lower bounds and the actual value will be higher. λ is the parameter of the Yule process, and λ and μ are the parameters of the birth and death process. Parameters are derived from Walker & Valentine (1984), Vrba (1987), Hulbert (1993) and Lieberman (1999*b*).)

model	λ	μ	unconditional p value	conditional p value
Yule	0.89[a]	0[b]	0.996	> 0.980
Yule	0.77[c]	0[b]	0.985	> 0.939
BD	0.89[a]	0.05[d]	0.980	> 0.921
BD	0.89[a]	0.30[e]	0.730	> 0.525
BD	0.89[a]	0.69[f]	0.114	> 0.054
BD	0.77[c]	0.05[d]	0.950	> 0.848
BD	0.77[c]	0.28[g]	0.598	> 0.383
BD	0.77[c]	0.69[f]	0.030	> 0.019

[a] 90th percentile value of λ based on invertebrate taxa only.
[b] Zero by definition for a pure birth process.
[c] 90th percentile value of λ based on a combined database of invertebrate and vertebrate taxa.
[d] Lowest non-zero value (roughly 10th percentile) of μ based on invertebrate taxa or a combined database of invertebrate and vertebrate taxa.
[e] Mean value of μ based on invertebrate taxa only.
[f] 90th percentile value of μ based on invertebrate taxa or combined database of invertebrate and vertebrate taxa.
[g] Mean value of μ based on a combined database of invertebrate and vertebrate taxa.

used. The 10th percentile (or lowest non-zero) and mean values of extinction probability (p_0) were used. As defined in Gilinsky & Good (1991), $p_0 + p_1 + p_2 = 1$. Again, only the earliest trilobitic part of the Early Cambrian, the *S. mickwitzi* zone, was considered. Provisionally, this zone was treated as representing the smallest resolvable biostratigraphic interval, or generation. However, following Gilinsky & Good (1991), diversity is allowed to no more than double in a single generation. Therefore, the observed diversity change in the *S. mickwitzi* zone required a minimum of four discrete generations of the Bienaymé–Galton–Watson branching-process model. The relevant polynomial expansion is thus $[f(f(f(f(x))))]^2$. This was evaluated using MAPLE V v. 3 (Waterloo Maple Software, Waterloo, Canada).

3. RESULTS

Analyses using the continuous-time models are presented in table 1. As can be seen, for several different high, but not anomalously high, speciation rates and for low or average extinction rates, H_0 and the continuous-time model cannot be rejected. In fact, a much greater diversity change would be required in the Early Cambrian in order to reject H_0. The high p values imply

that there is no evidence that the assumptions of the continuous-time model are violated. These results are resilient to changes in the duration of the *S. mickwitzi* zone. For example, even if future chronostratigraphic revisions indicate that the studied interval actually occupies only half as much time (3 million years), H_0 still cannot be rejected unless extinction probabilities are assumed to have been very high, and, as described in §2, existing evidence suggests that these probabilities were not high during the studied interval.

Random phylogenies were generated from the phylogeny in figure 1 using the equiprobable setting of MACCLADE v. 3.04 (Maddison & Maddison 1992) to determine whether the results were highly dependent on the phylogenetic topology of figure 1. These random phylogenies differed dramatically in overall topology from one another and from figure 1, and were far less parsimonious, but H_0 still could not be rejected (nor were the *p* values close to 0.05) unless, again, extinction probabilities were assumed to have been very high during the Cambrian radiation. Thus, the results are not affected if a phylogenetic topology different from, and slightly (one or two steps) or far (30 or 40 steps) less parsimonious than, the one in figure 1 was used.

The *p* values described above are unconditional probability values. Thus, they do not take into account the obvious fact that the lineage analysed, the olenelloids, did not become extinct before it could be observed in the fossil record. However, it is interesting to consider how probability values are affected if we take into account the fact that early lineage extinction did not occur. This requires evaluating a conditional probability. Most palaeontological and biological studies that have considered speciation rates within a probabilistic framework have focused solely on unconditional probabilities, with the study of Foote *et al.* (1999) being a notable exception. To help better constrain the results, probabilities conditional on the non-occurrence of early lineage extinction were also calculated for the birth and death process. This requires derivation of the following conditional-probability expression:

$$P(X_{6 \times 10^6} \geqslant 20 \,|\, X_a \geqslant 1), \tag{7}$$

where X_t is the number of species at time t. This is the probability that there are 20 or more species after 6 million years, given that there is at least one species after a certain short period of time, a. Because palaeontological speciation rates are typically calculated per million years, a is set to 1 million years in the subsequent calculations; however, any other value could be used without perturbing the derivation. Then, the derived expression was used to calculate a minimal conditional *p* value for the various parameters of λ and μ used in the analysis.

$$P(X_{6 \times 10^6} \geqslant 20 \,|\, X_a \geqslant 1) = \frac{P(X_{6 \times 10^6} \geqslant 20 \cap X_{1 \times 10^6} \geqslant 1)}{P(X_{1 \times 10^6} \geqslant 1)}, \tag{8}$$

$$= \frac{\sum_{j=1}^{\infty} P(X_{6 \times 10^6} \geqslant 20 | X_{1 \times 10^6} = j) P(X_{1 \times 10^6} = j)}{P(X_{1 \times 10^6} \geqslant 1)}, \tag{9}$$

and by time homogeneity

$$= \frac{\sum_{j=1}^{\infty} P(X_{5 \times 10^6} \geqslant 20 \,|\, X_0 = j) P(X_{1 \times 10^6} = j)}{P(X_{1 \times 10^6} \geqslant 1)}. \tag{10}$$

Equation (10) is

$$\geqslant \frac{\sum_{j=2}^{\infty} P(X_{5 \times 10^6} \geqslant 20 \,|\, X_0 = j) P(X_{1 \times 10^6} = j)}{P(X_{1 \times 10^6} \geqslant 1)}, \tag{11}$$

since one non-negative term is removed from the sum. Equation (11) is

$$\geqslant \frac{\sum_{j=2}^{\infty} P(X_{5 \times 10^6} \geqslant 20 \,|\, X_0 = 2) P(X_{1 \times 10^6} = j)}{P(X_{1 \times 10^6} \geqslant 1)}, \tag{12}$$

since $P(X_{5 \times 10^6} \cdot 20 \,|\, X_0 \cdot j) \geqslant P(X_{5 \times 10^6} \geqslant 20 \,|\, X_0 = 2)$ for all $j \cdot 2$.

Equation 12 is

$$= \frac{P(X_{5 \times 10^6} \geqslant 20 \,|\, X_0 = 2) \sum_{j=2}^{\infty} P(X_{1 \times 10^6} = j)}{P(X_{1 \times 10^6} \geqslant 1)}, \tag{13}$$

$$\begin{aligned} = \; & P(X_{5 \times 10^6} \geqslant 20 \,|\, X_0 = 2) \\ & \times \left[\frac{1 - P(X_{1 \times 10^6} = 0) - P(X_{1 \times 10^6} = 1)}{1 - P(X_{1 \times 10^6} = 0)} \right], \end{aligned} \tag{14}$$

$$\begin{aligned} = \; & \left[1 - \sum_{n=0}^{19} G_n(5 \times 10^6) \right] \\ & \times \left[\frac{1 - P(X_{1 \times 10^6} = 0) - P(X_{1 \times 10^6} = 1)}{1 - P(X_{1 \times 10^6} = 0)} \right], \end{aligned} \tag{15}$$

where G_n refers to equation (4).

When this expression was evaluated for the various parameters used with the birth and death process, the lower bounds recovered for these conditional probabilities were all greater than 0.38 when low or moderate extinction probabilities were assumed (table 1). Thus, even when conditional-probability values are considered, the results remain unchanged. However, with high extinction probabilities the minimum value for the conditional probability does in one case approach 0.05, although this is a lower bound, and in one case is less than 0.05 (table 1).

Analyses using the discrete-time model are presented in table 2. These results are very different from those presented in table 1, and, again, the results are resilient to changes in phylogenetic topology based on the protocol used for the other analyses. However, these results are not resilient to certain other modifications. In particular, the discrete-time model assumes that the diversity change occurs in the minimum possible number of generations. However, when the minimum-generations assumption is slightly relaxed by increasing the number of generations from four to five, the diversity change is no longer significant.

Table 2. Bienaymé–Galton–Watson branching-process model, along with the associated parameters (in units of per generation), used to determine the probability that a diversity change as great or greater than the one seen in the Cambrian radiation could have been produced by rates of evolution that have operated at other times in earth's history.

(Results are expressed as unconditional p values, with values of $p < 0.05$ implying inapplicability of the Bienaymé–Galton–Watson model or rejection of the null hypothesis. Parameters are p_0, the probability of extinction, p_1, the probability of persistence, and p_2, the probability of origination, and were derived from Gilinsky & Good (1991).)

p_0	p_1	p_2	p value
0.004^a	0.665	0.331^b	0.006
0^c	0.526	0.474^d	0.007
0.004^a	0.522	0.474^d	0.009
0.144^e	0.382	0.474^d	0.005
0.144^e	0.525	0.331^b	< 0.001

[a] Lowest non-zero value (roughly 10th percentile).
[b] 90th percentile value.
[c] Minimum value.
[d] Maximum value.
[e] Mean value.

4. DISCUSSION

Based on the analyses employing frequently used continuous-time models of evolution that are statistically robust according to Sanderson & Donoghue (1996), there is no statistical evidence to show that rates of speciation during the Cambrian radiation in one of the dominant Cambrian organisms were anomalously high relative to the rest of the history of life, unless high extinction probabilities are assumed to have prevailed during the Cambrian radiation, and previous studies by Raup & Sepkoski (1982), Van Valen (1985*b*), Foote (1988), Raup (1991) and Sepkoski (1994) suggest that extinction probabilities remained low or moderate until the end of the Cambrian radiation, millions of years after the interval considered in this study. This result matches Sepkoski's prediction that 'little if anything really spectacular in terms of cladogenesis occurred during the [Cambrian radiation]' (Sepkoski 1979, p. 228). However, this is not to say that rates of speciation were not high during the Cambrian radiation relative to the average rate of speciation for the entire Phanerozoic. Raup (1991) estimated that, for the Phanerozoic, $\lambda = 0.249$ per million years and $\mu = 0.250$ per million years. When equation (5) is evaluated using these parameters, the p value is 1.5×10^{-4}, a highly significant value. Similarly, even if we take very high parameter values, for example $\lambda = 1.45$ per million years, the highest value known for invertebrates, and a nearly equal value of μ ($\mu = 1.44$ per million years), the resultant p value is still significant ($p = 0.03$). Thus, rates of speciation were elevated during the Cambrian radiation, but they have been equivalently elevated at other subsequent times during the history of life, and there is no need to ascribe unique evolutionary processes pertaining to rates of speciation to the Cambrian-radiation interval. The results from the discrete-time model imply either that there was something unique and anomalously high

about rates of speciation during the Early Cambrian or that the assumptions of the discrete-time model might not apply to the Cambrian radiation. Two assumptions of the discrete-time model may be violated here: that diversity is allowed to no more than double in a single interval, and that the diversity change observed must have occurred in the fewest possible generations. When these assumptions are slightly relaxed, the results from the discrete-time model are no longer statistically significant. By contrast, the results from the analyses using continuous-time models appear robust. Furthermore, the employed values of the parameter p_2 of the discrete-time model are likely to be too low when treated as speciation rates (Gilinsky & Good 1991; Gilinsky 1994), which would make it artificially easier to reject H_0. For this reason, as indicated by the results from the analyses using continuous-time models, it appears more likely that the assumptions of the discrete-time model, including those relating to the number of generations, or the parameters available to implement that model, are not valid for species during the Cambrian radiation. However, the results from the discrete-time model do need to be explored further. They suggest that there is still potentially something unique about the nature of the Cambrian radiation, because the discrete-time model is capable of modelling diversity at other times in the history of life (see Gilinsky & Good 1991).

If we accept the results from the continuous-time models and that the assumptions necessary to implement the discrete-time model may not have been applicable in the Early Cambrian, the failure to find anomalously high rates of speciation during the Cambrian radiation conforms to the more general pattern that during major evolutionary radiations at higher taxonomic levels speciation rates are often not profoundly elevated (Hallam 1998). Rates of speciation during the Cambrian radiation were clearly high, as demonstrated by Raup & Sepkoski (1982), Van Valen (1985*a*) and Foote (1988), but they have been high at other times during the Phanerozoic. Thus, one would have to conclude that the tempo of speciation was not uniquely high in the Early Cambrian, and that the Cambrian radiation should be viewed as comparable with other episodes of adaptive or taxic radiation witnessed throughout earth's history. Several authors have considered whether any other evolutionary processes may have been unique during the Cambrian radiation. Gould (1989, 1991), Foote (1991, 1992, 1995), Wagner (1995) and others have suggested that there were still unique evolutionary processes intrinsic to the Early Cambrian, but this study adds a different type of data to the evidence described by Briggs & Fortey (1989), Briggs *et al.* (1992), Conway Morris (1993, 1998), Fortey *et al.* (1996, 1997), Xianguang & Bergström (1997), Bromham *et al.* (1998), Hughes *et al.* (1999) and Smith & Lieberman (1999) that, although the Cambrian radiation is clearly an important episode in the history of life, it may not have been a time of distinctive or unusual evolutionary processes.

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