

Shape of Mesozoic dinosaur richness: Comment and Reply

COMMENT

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The recent article by Fastovsky et al. (2004) examines the Mesozoic record of dinosaur diversity. For this study they utilized recently published dinosaur distribution data compiled by Weishampel et al. (2004). A major concern of Fastovsky et al. (2004) was the dinosaur record during the closing 10 m.y. of the Cretaceous. It is this aspect of their paper on which I am commenting.

The authors conclude: "The database does not support the claim that dinosaur richness was decreasing toward extinction during the ~10 m.y. preceding the Cretaceous-Tertiary boundary" (p. 880). Note that the authors qualified this statement with the phrase "decreasing toward extinction." This is a subjective opinion separate of the more objective issue of whether there was such a decline. When read carefully it is quite clear that their own data show a decline. For example note their absolute richness for this interval in Table 5 with a decline of 51 genera from late Campanian to 41 genera in the late Maastrichtian. Note a similar pattern for the left hand bars in Figure 5.

The authors do not accept these results but rather introduce what they call "total generic richness." The authors are not explicit as to how "total generic richness" was obtained, but they do note: "Multiple entries of a genus in the database result from multiple geographic records based upon first-order political subdivisions (states, departments...)" (p. 877). If this is in fact what they did, parsing the data according to political subdivisions can be a useful although crude way of examining relative degrees of spatial distribution (e.g., endemism, cosmopolitanity), but such groupings are not relevant to questions of taxonomic diversity through time.

Next, the authors introduce a rarefaction analysis, but fail to provide a description of which of the many forms of this technique they used. Tipper (1979) reviewed the problems with a naive application of rarefaction to diversity data, listing four critical assumptions implicit in its use in paleoecological studies. As these problems are not discussed by the authors, they apparently are unaware of the pitfalls of rarefaction as used in paleoecology. This is clear when they apply the unwarranted assumption that the "number of genera expected in a sample" can be estimated "if the [expected] sample had the same richness structure as the smallest-sized sample" (p. 877). This is an erroneous assumption given that they are trying to test for total generic richness through the Mesozoic for notoriously rare dinosaur taxa. In fact, rarefaction estimates are sensitive to both the relative diversity and the evenness of the comparison faunas. Determining which aspect(s) of these factors is/are similar or different between populations using the rarefaction results is impossible, especially when broad discrepancies in the protocols used to obtain samples may exist.

As the authors show, their results are largely based upon the much better North America record. I examined the same Weishampel et al. (2004) data set noted by the authors dealing with North America. I utilized genera in the data set that were identified without qualification (e.g., cf., aff., ?, etc.), apparently similar to that done by the authors. I only used localities for which unambiguous age ranges were provided. By use of these data I am not implying that I agree with all taxonomic and age assignments, but rather wish to show that these data clearly show a decline between the Campanian and Maastrichtian in North America.

¹GSA Data Repository item 2005064, Table DR1, generic counts of dinosaurs through the Campanian and Maastrichtian of North America, is available online at www.geosociety.org/pubs/ft2005.htm, or on request from editing@geosociety.org or Documents Secretary, GSA, P.O. Box 9140, Boulder, CO 80301-9140, USA.

TABLE 1. SUMMARY OF GENERIC COUNTS OF DINOSAURS THROUGH THE CAMPANIAN AND MAASTRICHTIAN OF NORTH AMERICA TAKEN FROM WEISHAMPEL ET AL. (2004)

E. Campanian	L. Campanian	E. Maastrichtian	L. Maastrichtian
4 genera	48 genera	23 genera	32 genera
7 localities	14 localities	3 localities	18 localities
8 occurrences	92 occurrences	32 occurrences	119 occurrences

Note: Below each subage are: number of genera for each subage, number of dinosaur-bearing localities referred to that subage, and the number of localities at which particular genera occur during the given subage. See text for further explanation. See Table DR1¹ for complete generic listings for each subage. E.—early; L.—late.

In Table 1, I have divided the sampling into the normally recognized time subdivisions (early and late) of the Campanian and Maastrichtian (e.g., Gradstein et al., 1995). Localities identified as "middle" Campanian and Maastrichtian were included with late Campanian and late Maastrichtian, respectively. Although the Campanian is decidedly longer than the Maastrichtian, Fastovsky et al. (2004) show that this is not a factor in differences in dinosaur diversity. The very low early Campanian diversity is almost certainly an artifact, as probably is the early Maastrichtian as well. This interpretation is supported because five genera (*Avisaurus*, *Leptoceratops*, *Pachycephalosaurus*, *Pentaceratop*, *Troodon*) are reported from the late Campanian and late Maastrichtian but not the intervening early Maastrichtian. The much better sampled late Campanian and late Maastrichtian intervals show a clear decline from 48 to 32 genera—a 33% drop. As Table 1 shows, this is the case even though there are four more localities and 27 more repeated generic samplings for the late Maastrichtian compared to the late Campanian of North America. Interestingly, if one were to follow the logic of Fastovsky et al. (2004), these data would suggest that the late Campanian is more poorly sampled than the late Maastrichtian, opposite of what they are arguing.

Another method that does not have the potential problems of using unequal intervals of time and is more ecologically meaningful compares the taxonomically richest dinosaurian faunas from the Campanian and Maastrichtian. For the Campanian, this is from the Dinosaur Park Formation, Alberta, Canada, which has 31 genera, while for the Maastrichtian, this is from the Lance Formation, Wyoming, United States, which has 20 genera (Weishampel et al., 2004). This is a 35% decline.

These data speak for themselves. Whichever method is employed, there is clearly a decline of over 30% for dinosaur genera in North America during the ~10 m.y. preceding the Cretaceous-Tertiary boundary. I invite readers to examine these data for themselves.

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REPLY

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We thank J.D. Archibald for his comment on our study (Fastovsky et al., 2004) because his misunderstanding of our work provides the opportunity to clarify ideas that may have similarly confused other readers.

The raw data show high abundance in the late Campanian, decreased abundance in the early–middle Maastrichtian, and increased abundance in the late Maastrichtian. Given the stunning overall increase in dinosaur generic richness toward the end of the Mesozoic, there are clearly concerns about artifacts of sampling and, as acknowledged by Archibald, interpretation is required. Our view is that the significance of any change in diversity (in this case, that from the Campanian to the Maastrichtian) can be assessed only in the context of the magnitude of other diversity fluctuations in the time interval under study (in this case, the Late Cretaceous). It was thus never a question of whether we did or did not “accept (our) results”; it was only about constructing a context in which to be able to intelligently interpret them.

That context was developed by the use of total generic richness and statistically tested via rarefaction. Total generic richness is analogous to ecological sampling (counts per unit area), and was necessary for quantitative treatment of the data. Thus, we do not accept Archibald’s preemptory assertion that “the groupings are not relevant to questions of taxonomic diversity through time.”

The citations in our manuscript indicate “which of the many forms” of rarefaction we used. The one we applied to this problem was developed by Sanders (1968) and corrected by Hurlbert (1971) and Simberloff (1972). Thus,

$$E(\hat{S}_n) = \sum_{i=1}^S \left[1 - \frac{\binom{N-N_i}{n}}{\binom{N}{n}} \right] \quad (1)$$

where $E(\hat{S}_n)$ equals the expected number of species in a sample of size n ; N equals the total number of individuals in the entire sample; N_i equals the number of individuals in species i ; S equals the total number of species in the entire sample of size N ; and n equals the sample size chosen for standardization ($n < N$). Heck et al. (1975) gave the formula of $\text{var}(\hat{S}_n)$ for estimating the variance of the expected number of species in a sample of size n .

Archibald’s suggestion that comparison of the taxonomically richest units from Campanian and Maastrichtian (Dinosaur Park Formation and Lance Formation, respectively) is “more ecologically meaningful” is absurd. There is no reason to suppose that the richest formations of each time interval are spatially equivalent or preserve faunas with equal fidelity. That is why we undertook the analyses presented in Fastovsky et al. (2004).

Archibald constructed his own database from our original source (Weishampel et al., 2004), inviting “readers to examine these data for themselves.” Having done so, we are reassured that Archibald’s data and ours are generally in agreement. The late Maastrichtian has fewer taxa recorded than the Late Campanian, but it also has more taxa than any other interval in the Mesozoic. We again see the apparent decline in generic richness from the Campanian to the Maastrichtian, which we clearly acknowledged before (Tables 4 and 7, and accompanying text), and we again see the apparent increase in diversity between the early and late Maastrichtian. So we again ask ourselves, as we did when we wrote our manuscript, are these fluctuations significant or are they due to sampling? And again we conclude that the only way to assess their significance is to consider them in the context of other generic diversity fluctuations throughout the Late Cretaceous. When that is done, it cannot be shown that the drop from late Campanian to late Maastrichtian is remarkable. And that, of course, is the conclusion reached in Fastovsky et al. (2004).

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