Shape of Mesozoic dinosaur richness

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ABSTRACT

The richness of Mesozoic Dinosauria is examined through the use of a new global database. Mesozoic dinosaurs show a steadily increasing rate of diversification, in part attributable to the development of new innovations driving an increasing variety of behavioral strategies. The data do not suggest that dinosaurs were decreasing in richness leading to extinction during the last ~10 m.y. of the Cretaceous. Refinement of the dating of dinosaur fossils, rather than the collection of more dinosaurs, is the best way to resolve globally the rate of the Cretaceous-Tertiary dinosaur extinction.

Keywords: dinosaurs, richness, Mesozoic, diversity, rarefaction.

INTRODUCTION

Dinosaurs are generally reckoned to have been the dominant terrestrial vertebrates from the Late Triassic through the Cretaceous (e.g., Bakker, 1986). Here we quantitatively address what is known of the large-scale patterns of dinosaur richness. Because of a long-standing perception that dinosaurs were waning in richness toward the end of the Cretaceous (e.g., Archibald, 1996; Dodson, 1996), we focus attention on the Campanian–Maastrichtian interval.

Our analysis is based on a new global compilation of dinosaur genera by Weishampel et al. (2004). This new database is a 55% increase in size over an antecedent compilation (Weishampel, 1990); much of the new richness comes from continents other than North America.

METHODS

Coprolites, ichnotaxa, and ootaxa were culled from the Weishampel (2004) database, leaving 560 distinct, positively identified, skeleton-based genera from 1266 samples distributed among all continents. Multiple entries of a genus in the database result from multiple geographic records based upon first-order political subdivisions (states, departments, provinces, counties; see Weishampel, 1990; Weishampel et al., 2004). Genera whose age could not be identified within the level of temporal precision specified in the analyses (see following) were omitted from those analyses.

For dinosaurs (as for most fossil vertebrates), use of the generic level optimizes identification without sacrificing taxonomic resolution. The database resolves time into epochs, stages, and substages. The complete database is available (Table DR1[1]).

[1]GSA Data Repository item 2004151, Table DR1, global database of dinosaur genera, is available online at www.geosociety.org/pubs/ft2004.htm, or on request from editing@geosociety.org or Documents Secretary, GSA, P.O. Box 9140, Boulder, CO 80301-9140, USA.

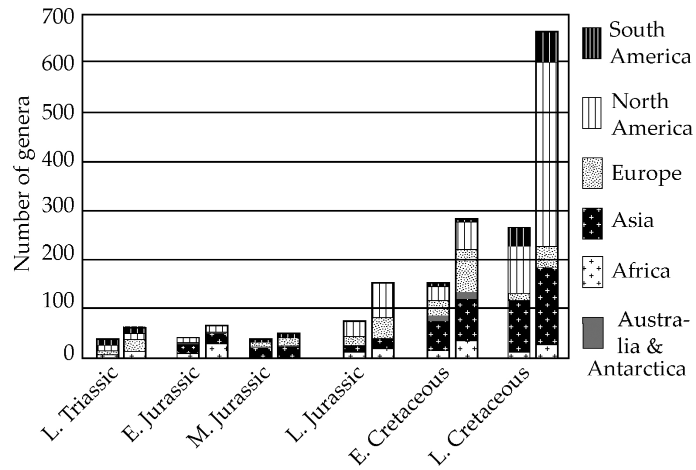

Figure 1. Dinosaur generic richness through Mesozoic by epoch. Each epoch has two metrics: left tabulation is absolute generic richness and consists of summation of different genera found during that time interval; right tabulation in each epoch is total sample counts, tallied from different geographic localities represented in that time interval. E.—Early; M.—Middle; L.—Late.

We use rarefaction (Sanders, 1968; Hurlbert, 1971; Simberloff, 1972; Heck et al., 1975) to compare generic richness among different sample sizes. In the rarefaction algorithm, $E(\hat{S}_n)$ is the number of genera expected in a sample, if the sample had the same richness structure as the smallest-sized sample, and s.e. $(\hat{S}_n)$ estimates the standard error for the expected number of species in a sample of size n.

RESULTS

Richness data are presented at three levels of temporal resolution: (1) Late Triassic–Late Cretaceous, by epoch; (2) Late Cretaceous, by stage; and (3) Campanian–Maastrichtian, by substage. At each level, two richness metrics are shown: (1) absolute generic richness, i.e., a compilation of different genera; and (2) total generic richness, incorporating the repeat sample counts, derived from different geographic localities.

Late Triassic–Late Cretaceous by Epoch

Absolute generic richness and total generic richness increased steadily from the Late Triassic to the Late Cretaceous (Table 1; Fig.

TABLE 1. DINOSAUR GENERIC RICHNESS THROUGH THE MESOZOIC BY CONTINENT

Epoch	Africa	Asia	Antarctica	Australasia	Europe	North America	South America	Total genera
L. Triassic	7/14	2/2	0/0	0/0	8/22	8/11	13/13	36/62
E. Jurassic	10/27	15/19	1/1	0/0	4/4	10/14	0/0	33/65
M. Jurassic	2/2	16/16	0/0	2/2	12/20	1/1	5/5	39/46
L. Jurassic	11/15	13/18	0/0	0/0	21/46	28/72	0/0	60/151
E. Cretaceous	15/29	58/84	0/0	10/15	35/89	26/56	8/8	147/281
L. Cretaceous	13/20	102/157	0/0	1/1	16/43	94/379	41/61	245/661
Total								560/1266

Note: Data presented as absolute/total generic richness. E.—Early; M—Middle; L.—Late.

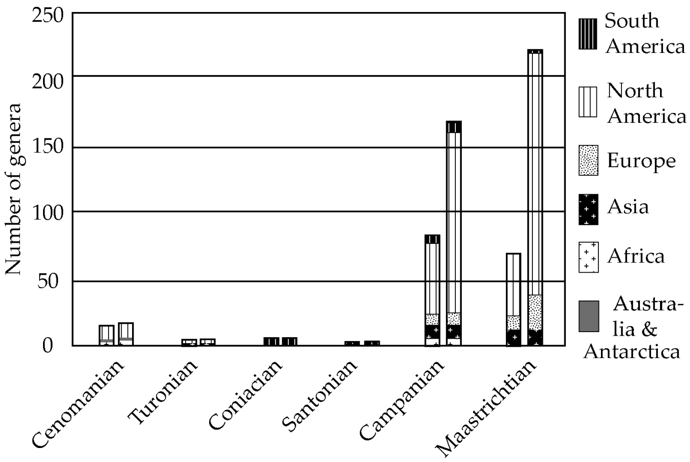

Figure 2. Dinosaur generic richness through Late Cretaceous by stage. Paired tabulations reported for each stage are same as those in Figure 1.

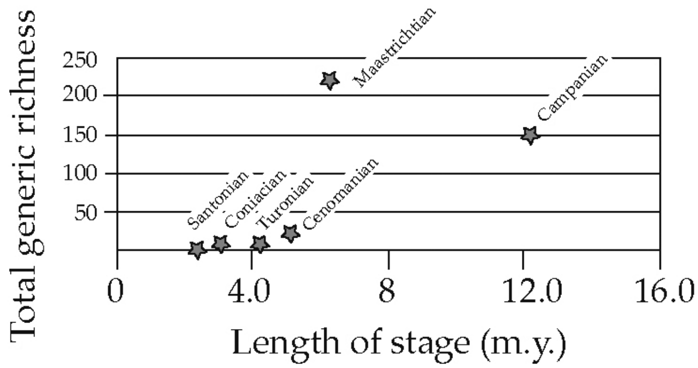

Figure 3. Total generic richness (as represented by total sample counts) in each stage of Late Cretaceous, plotted against duration of that stage. Lengths of stages are from Gradstein et al. (1995).

1). Dinosaur diversity culminated during the Late Cretaceous, which contains 44% of all genera, almost as much absolute richness as the earlier dinosaur-bearing epochs combined.

Asia and North America dominate the database. Together they make up 67% of absolute Mesozoic generic richness and 80% of absolute Late Cretaceous generic richness.

Late Cretaceous by Stage

The Late Cretaceous is the only interval for which substages can be recognized, thus it is best suited to detailed examination (e.g., Fara and Benton, 2000). Figure 2 and Table 2 document absolute and total generic richness by stage in the Late Cretaceous.

Considered at face value, the Campanian represents a stunning (>90%) increase in richness from Cenomanian through Santonian levels. These results seem to suggest that the Campanian was the high water mark for dinosaur richness in the Mesozoic, a point reiterated by many workers (see following).

These observations need to be tempered in the context of the broad increase in dinosaur richness (Fig. 1). The low levels of richness that characterize the Cenomanian–Santonian intervals (Fig. 2) are likely artifacts rather than a true record of fluctuating dinosaur richness. If so, is the drop in absolute and total richness between the Campanian and Maastrichtian meaningful?

Several considerations mitigate the conclusion that dinosaur diversity decreased during the Campanian–Maastrichtian interval. First, the Campanian, with a maximum duration of 11.2 m.y. (Gradstein et al., 1995), is nearly twice as long as the maximum duration of the next longest stages in the Late Cretaceous (Maastrichtian, 5.8 m.y.; Cenomanian, 5.0 m.y.). Could high Campanian richness be simply an artifact of its length? Sample size compared to length of time interval for both the Late Cretaceous and Late Triassic–Cretaceous intervals (Fig. 3) shows no obvious relationship between time interval duration and dinosaur richness, suggesting that the richness patterns that we have observed are not directly related to stage duration.

Because Turonian, Coniacian, and Santonian sampling (5, 6, and 2, respectively) is likely underrepresented with respect to the rest of the database, we eliminated these from this analysis. Then, by using the smallest remaining sample size (Cenomanian, $n = 18$) to rarefy samples from the Campanian and Maastrichtian, we obtained the results shown in Table 3. Figure 4 shows the estimated expected number of genera, together with an ~95% confidence interval for each stage. This result suggests that at the 95% confidence level, we cannot reject the null hypothesis that the generic richness of the Campanian does not differ from that of the Maastrichtian.

This conclusion was obtained by comparing Campanian and Maastrichtian richness in the context of Cenomanian richness (our original intent). Considering only the Maastrichtian, however, the richness is less diverse than that of the Campanian (Table 4). With 95% confidence, the difference between Campanian and Maastrichtian is at least 18.4 and at most 27.6 genera, when rarefied to the observed Campanian level.

Campanian–Maastrichtian by Substage

The data also allow closer scrutiny of the proposed drop in diversity between the Campanian and Maastrichtian (Fig. 5; Table 5). It is highly unlikely that actual dinosaur richness within the Campanian and Maastrichtian varied as much as indicated by the raw data. (If so, the latest Maastrichtian would reflect a recovery after a major decline; see Fara and Benton, 2000.) We thus condensed the early and middle Campanian, and early and middle Maastrichtian, to allow comparison from the early Campanian through late Maastrichtian. At the 95% confidence level, we cannot reject the null hypothesis that the generic richness of the late Campanian does not differ from that of the late Maastrichtian (Fig. 6; Table 6). However, outside of their Late Cretaceous context, do the late Campanian and late Maastrichtian differ from each other? Data from Table 7 indicate that with 95% confidence, the late Campanian had at least 13.8 and at most 22.1 more dinosaur genera than the late Maastrichtian when rarefied to the late Campanian level.

DISCUSSION

Trends in Mesozoic Dinosaur Richness

At the epoch scale, Mesozoic dinosaurs steadily increased in richness from their appearance in the Triassic until their demise at the end of the Cretaceous. This pattern parallels the "logarithmic" phase (before stabilization) of the diversity curves of Sepkoski et al. (1981), Sepkoski (1997), and Benton (1999). While the morphological diver-

TABLE 2. DINOSAUR GENERIC RICHNESS THROUGH THE LATE CRETACEOUS BY STAGE

	Cenomanian	Turonian	Coniacian	Santonian	Campanian	Maastrichtian
Absolute richness	16	4	6	2	81	65
Total richness	18	4	6	2	167	221

Note: Data presented as absolute/total generic richness.

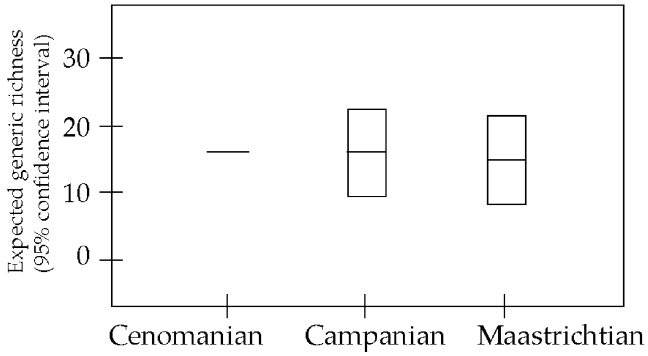

Figure 4. Plot of 95% simultaneous confidence intervals for expected number of different dinosaur genera during Late Cretaceous. Coniacian, Turonian, and Santonian samples were removed from analysis because of inferred sampling artifacts (see text). Campanian and Maastrichtian generic richness is thus rarefied against Cenomanian generic richness. All confidence intervals are based upon normal assumptions.

sity of Triassic theropods was grossly limited to size (e.g., Fastovsky and Smith, 2004), Late Cretaceous theropods developed considerable morphotypic disparity, presumably reflecting a larger range of behaviors. Weishampel and Norman (1989) tracked similar changes in herbivorous dinosaurs (sauropodomorphs and ornithischians); these changes focused primarily on their increasing range of food-processing strategies. As in marine invertebrates (Bambach, 1983), the ability to colonize heretofore unavailable ecospace by the invention of new feeding mechanisms and behaviors may have been a key driving force in the striking and continuous Jurassic–Cretaceous dinosaur diversification.

Richness Through the Campanian–Maastrichtian Interval

The published consensus is that dinosaurs were a group in decline at the Cretaceous-Tertiary boundary. Marsh (1882) concluded that dinosaurs reached their peak in the Jurassic; Colbert (1961, 1965) reconstructed a 68% decrease in genera in North America in what would now be considered the last 15 m.y. of the Cretaceous. Swinton (1971) restated the idea, attributing the decline to a now-discredited cause (racial senescence). Bakker (1986) used diversity indices to show that North American Campanian faunas were more diverse than Maastrichtian faunas. Sloan et al. (1986) and Clemens et al. (1981) reconstructed the peak in dinosaurian richness as 76–73 Ma (but see Sheehan and Morse, 1986).

Explicit statements that dinosaur richness waned during the last 10 m.y. of the Cretaceous can be found in Marsh (1882), Colbert (1961), Schopf (1982), Bakker (1986), Archibald (1996), Dodson and Tartarinov (1990; citing Bakker [1986]), Dodson (1996), and Russell and Dodson (1997). All of these claims (except Marsh, 1882) were based upon the North American record and thus constituted best-guess estimates, given the absence of global data. In contrast, far fewer paleontologists have stated that the fossil record is moot, not to say mute, on this point (Russell, 1982; see also attributions in Lessem, 1992).

The data presented here fail to demonstrate any decrease in richness between the Campanian and Maastrichtian. Figure 5 shows the richness of those genera for which an early, middle, or late Campanian or an early, middle, or late Maastrichtian age assignment could be made. There is a drop in richness from the Campanian, but a rise at the end of the Maastrichtian is also apparent, reflecting the strength of the latest Cretaceous North American record and the ambiguity of age assignments for the Asian record. Without the inclusion of the Asian record at this level of temporal resolution, the early and middle Maastrichtian evidence may be artificially depauperate, whereas the late Maastrichtian numbers are artificially elevated, reflecting the comparative precision of North American age assignments relative to those from Asia (which in many cases cannot be constrained more precisely

TABLE 3. RESULTS OF RAREFACTION IN THREE LATE CRETACEOUS STAGES

	Cenomanian	Campanian	Maastrichtian
$E(\hat{S}_n)$	(16)	16	15
s.e. $(\hat{S}_n)$	(0)	2.8	2.9

TABLE 4. RESULTS OF RAREFACTION WHEN CAMPANIAN DINOSAUR RICHNESS IS COMPARED TO THAT OF MAASTRICHTIAN

	Campanian	Maastrichtian
Absolute richness	81	65
Total richness	167	221
$E(\hat{S}_n)$	(81)	58
s.e. $(\hat{S}_n)$	(0)	2.33

TABLE 5. DINOSAUR GENERIC RICHNESS THROUGH THE LATE CRETACEOUS BY STAGE

	Early to middle Campanian	Late Campanian	Early to middle Maastrichtian	Late Maastrichtian
Absolute richness	20	52	31	41
Total richness	29	88	49	144

Note: Data presented as absolute/total generic richness.

TABLE 6. RESULTS OF RAREFACTION IN SUBSTAGES OF THE CAMPANIAN AND MAASTRICHTIAN

	Early to middle Campanian	Late Campanian	Early to middle Maastrichtian	Late Maastrichtian
$E(\hat{S}_n)$	(20)	24	22	19
s.e. $(\hat{S}_n)$	0	2.8	2.3	2.7

TABLE 7. RESULTS OF RAREFACTION WHEN LATE CAMPANIAN DINOSAUR RICHNESS IS COMPARED TO THAT OF LATE MAASTRICHTIAN

	Late Campanian	Late Maastrichtian
Absolute richness	52	41
Total richness	88	144
$E(\hat{S}_n)$	(52)	34
s.e. $(\hat{S}_n)$	(0)	2.13

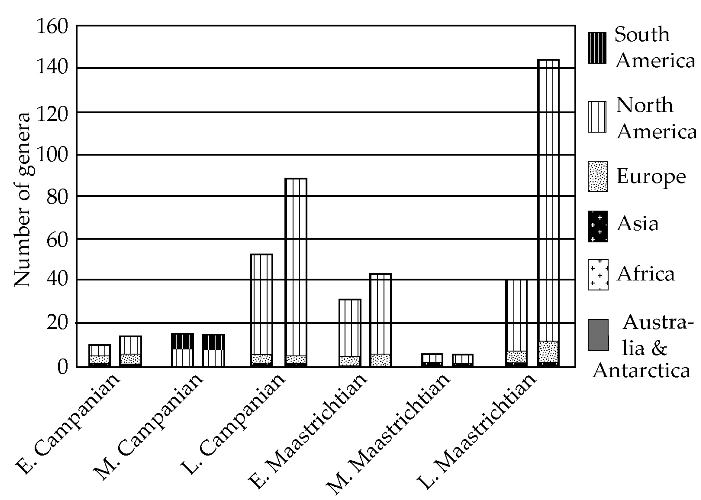

Figure 5. Dinosaur generic richness through latest Cretaceous by substage. Paired tabulations reported for each stage are same as those in Figure 1. E.—early; M.—middle; L.—late.

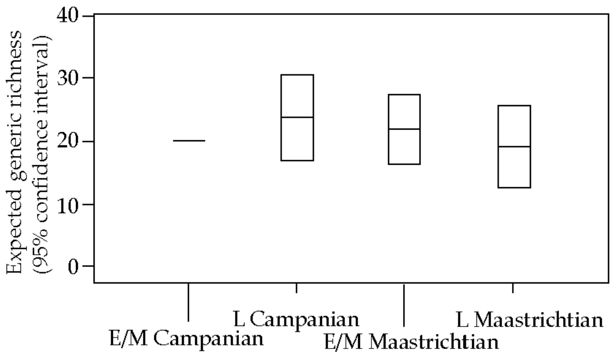

Figure 6. Plot of 95% simultaneous confidence intervals for expected number of different dinosaur genera during latest Cretaceous. Early Campanian and middle Campanian are combined (E-M Campanian) and early Maastrichtian and middle Maastrichtian are combined (E-M Maastrichtian) because of inferred sampling artifacts (see text). Late Campanian, E-M Maastrichtian, and late Maastrichtian were thus rarefied against E-M Campanian. All confidence intervals are based upon normal assumptions.

than ''Late Cretaceous''). The viewpoint that, globally, dinosaurs were decreasing in richness from the Campanian to the Maastrichtian is thus poorly supported by the data.

Internal fluctuations within the data are large (as seen in both the stage and the substage records). The magnitude of the difference between the Campanian and Maastrichtian (and between the late Campanian and late Maastrichtian) is not as great as the fluctuations that we have recorded between other stages and substages. It is premature to rule out the possibility that the increase in richness from the early Campanian to the late Campanian, or from the Early Maastrichtian to the late Maastrichtian, is an artifact of the incomplete database. Decreases in richness from the Campanian to the Maastrichtian, or from the late Campanian to the late Maastrichtian, have little significance when considered in the context of unambiguously increasing Mesozoic dinosaur richness.

Paradoxically, the authors cited above could be correct in that the data show an increasing dominance of North American faunas in the most resolved intervals under study (Figs. 2 and 5) and thus do not preclude a drop in diversity between the Campanian and Maastrichtian in North America. But, considered in the context of Mesozoic—or even Late Cretaceous—richness, the data cannot be used to support claims of a decrease in dinosaur richness between the Campanian and Maastrichtian that would lead to extinction. This view echoes that of Dodson (1990, p. 7612), who in his treatment of the earlier version of the Weishampel (1990) database wrote, ''There is nothing to suggest that dinosaurs in the Campanian or the Maastrichtian were a group that had passed its prime and were in a state of decline.''

CONCLUSIONS

This analysis indicates that, as a group, dinosaurs had an ascending diversity curve through the Mesozoic. The database does not support the claim that dinosaur richness was decreasing toward extinction during the ~10 m.y. preceding the Cretaceous-Tertiary boundary.

The data suggest that both South America and Asia have much to contribute to the question of Late Cretaceous dinosaur diversity. They indicate that the key to better understanding Mesozoic dinosaur richness is not collecting more dinosaurs, but obtaining better temporal control on the ones that we already have.

REFERENCES CITED

Archibald, J.D., 1996, Dinosaur extinction and the end of an era: New York, Columbia University Press, 235 p.

Bakker, R.T., 1986, The dinosaur heresies: New York, William Morrow and Company, 481 p.

Bambach, R.K., 1983, Ecospace utilization and guilds in marine communities through the Phanerozoic, *in* Tevesz, M.J.S., and McCall, P.L., eds., Biotic interactions in recent and fossil benthic communities: New York, Plenum Press, p. 719–746.

Benton, M.J., 1999, The history of life: Large databases in palaeontology, *in* Harper, D.A.T., ed., Numerical palaeobiology: Computer-based modelling and analysis of fossils and their distributions: New York, John Wiley and Sons, p. 249–283.

Clemens, W.A., Archibald, J.D., and Hickey, L.J., 1981, Out with a whimper not a bang: Paleobiology, v. 7, p. 293–298.

Colbert, E.H., 1961, Dinosaurs: Their discovery and their world: New York, E.P. Dutton and Co., 300 p.

Colbert, E.H., 1965, The age of reptiles: London, Weidenfeld and Nicolson, 228 p.

Dodson, P., 1990, Counting dinosaurs: National Academy of Sciences Proceedings, v. 87, p. 7608–7612.

Dodson, P., 1996, The horned dinosaurs: Princeton, New Jersey, Princeton University Press, 346 p.

Dodson, P., and Tartarinov, L.P., 1990, Dinosaur extinction, *in* Weishampel, D.B., et al., eds., The Dinosauria: Berkeley, University of California Press, p. 55–62.

Fara, E., and Benton, M.J., 2000, The fossil record of Cretaceous tetrapods: Palaios, v. 15, p. 161–165.

Fastovsky, D.E., and Smith, J., 2004, Dinosaur paleoecology, *in* Weishampel, D.B., et al., eds., The Dinosauria (second edition): Berkeley, University of California Press, p. 614–626.

Gradstein, F.M., Agterberg, F.P., Ogg, J.C., Hardenbol, J., Van Veen, P., Thierry, J., and Huang, Z., 1995, A Triassic, Jurassic, and Cretaceous time scale, *in* Berggren, W.A., et al., eds., Geochronology, time scales, and global stratigraphic correlation: SEPM (Society for Sedimentary Geology) Special Publication 54, p. 95–126.

Heck, K.L.J., Van Belle, G., and Simberloff, D., 1975, Explicit calculation of rarefaction diversity measurement and the determination of sufficient sample size: Ecology, v. 56, p. 1459–1461.

Hurlbert, S.H., 1971, The non-concept of species diversity: A critique and alternative parameters: Ecology, v. 59, p. 577–586.

Lessem, D., 1992, Kings of creation: New York, Simon and Schuster, 367 p.

Marsh, O.C., 1882, Classification of the Dinosauria: American Journal of Science, v. 23, p. 81–86.

Russell, D.A., 1982, A paleontological consensus on the extinction of the dinosaurs?, *in* Silver, L.T., and Schultz, P.H., eds., Geological implications of impacts of large asteroids and comets on the Earth: Geological Society of America Special Paper 190, p. 401–413.

Russell, D.A., and Dodson, P., 1997, The extinction of the dinosaurs: A dialogue between a catastrophist and a gradualist, *in* Farlow, J.O., and Brett-Surman, M.K., eds., The complete dinosaur: Bloomington, Indiana University Press, p. 662–672.

Sanders, H.L., 1968, Marine benthic diversity: A comparative study: Biometrics, v. 25, p. 517–535.

Schopf, T.J.M., 1982, Extinction of the dinosaurs: A 1982 understanding, *in* Silver, L.T., and Schultz, P.H., eds., Geological implications of impacts of large asteroids and comets on the Earth: Geological Society of America Special Paper 190, p. 415–422.

Sepkoski, J.J., 1997, Ten years in the library: New data confirm paleontological patterns: Paleobiology, v. 19, p. 43–51.

Sepkoski, J.J., Bambach, R.K., Raup, D.M., and Valentine, J.W., 1981, Phanerozoic marine diversity and the fossil record: Nature, v. 293, p. 435–437.

Sheehan, P.M., and Morse, C.L., 1986, Cretaceous-Tertiary dinosaur extinction: Science, v. 234, p. 1171–1172.

Simberloff, D.S., 1972, Properties of the rarefaction diversity measurement: American Naturalist, v. 106, p. 414–418.

Sloan, R.E., Rigby, J.K., Jr., Van Valen, L.M., and Gabriel, D.L., 1986, Gradual dinosaur extinction and simultaneous ungulate radiation in the Hell Creek Formation: Science, v. 234, p. 1173–1175.

Swinton, W.E., 1971, The dinosaurs: New York, John Wiley and Sons, 331 p.

Weishampel, D.B., 1990, Dinosaurian distribution, *in* Weishampel, D.B., et al., eds., The Dinosauria: Berkeley, University of California Press, p. 63–139.

Weishampel, D.B., and Norman, D.B., 1989, Vertebrate herbivory in the Mesozoic: Jaws, plants, and evolutionary metrics, *in* Farlow, J.O., ed., Paleobiology of the dinosaurs: Geological Society of America Special Paper 238, p. 87–100.

Weishampel, D.B., Barrett, P.M., Coria, R.A., Le Loeuff, J., Xu, X., Zhao, X., Sahni, A., Gomani, E.M.P., and Noto, C.R., 2004, Dinosaur distribution, *in* Weishampel, D.B., et al., eds., The Dinosauria (second edition): Berkeley, University of California Press, p. 517–606.

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