Estimating the diversity of dinosaurs

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Despite current interest in estimating the diversity of fossil and extant groups, little effort has been devoted to estimating the diversity of dinosaurs. Here we estimate the diversity of nonavian dinosaurs at ≈1,850 genera, including those that remain to be discovered. With 527 genera currently described, at least 71% of dinosaur genera thus remain unknown. Although known diversity declined in the last stage of the Cretaceous, estimated diversity was steady, suggesting that dinosaurs as a whole were not in decline in the 10 million years before their ultimate extinction. We also show that known diversity is biased by the availability of fossiliferous rock outcrop. Finally, by using a logistic model, we predict that 75% of discoverable genera will be known within 60–100 years and 90% within 100–140 years. Because of nonrandom factors affecting the process of fossil discovery (which preclude the possibility of computing realistic confidence bounds), our estimate of diversity is likely to be a lower bound.

abundance-based coverage estimator | completeness | Cretaceous/Tertiary mass extinction | fossil record bias | rock availability

Quantifying the diversity of various animal groups has been a major focus of current research in paleontology (1). Despite their evolutionary success and their widespread popular appeal, however, little attention has been devoted to quantifying the diversity of dinosaurs. The study of dinosaur diversity has long been impeded by taxonomic difficulties and the incompleteness of the fossil record. Dinosaur taxonomy has at times been problematic, with many named genera having been invalidated because of synonymy, preoccupation, or being based on nondiagnostic material, particularly isolated teeth. Moreover, of currently recognized genera, 59% are known from only a single individual, and many of these only from very incomplete material. These factors have posed substantial challenges to assessing the diversity of dinosaurs (here used to refer only to nonavian dinosaurs).

Only two quantitative studies of the diversity of dinosaurs, including undiscovered as well as known taxa, appear in the literature. Dodson (2) estimated that 1,200 total genera existed, based on a model for estimating future discoveries and estimates of generic longevity. Russell (3) estimated that 3,400 genera existed, based on species–area relationships. An additional study by Weishampel and Jianu (4) estimated minimum species diversity curves for Ornithischia and Sauropodomorpha. However, although their work accounted for ghost lineages within phylogenies, they did not aim to enumerate all unknown dinosaur taxa.

Here we estimate the diversity (taxonomic richness) of dinosaurs, including those that remain to be discovered, by using data from a recently published compendium, *The Dinosauria* (5, 6), as well as an updated database compiled by the authors from the primary literature through May 2006. We apply a statistical method, the abundance-based coverage estimator (ACE) (7, 8), to account for the incompleteness of the fossil record. We also estimate diversity in the last two stages of the Cretaceous period to address whether dinosaurs were already in decline before their ultimate extinction. Finally, we assess the dependence of known diversity on the availability of fossiliferous rock outcrop, and we predict the trajectory of future dinosaur discoveries.

Most previous work in paleontology has focused on computing diversity curves by using rarefaction or sampling standardization (1, 9). Our work differs in that we estimate the absolute number of genera, including those not yet discovered, whereas rarefaction and related methods compare relative counts if all samples had the same size as the smallest sample (9). Our method thus uses all available data without being limited by the size of the smallest sample.

It is important to note that the ACE estimates the total number of discoverable genera, including future discoveries. By "discoverable," we mean that fossils of the genus could potentially be discovered by using techniques traditionally or currently used by paleontologists. A genus that left no fossils at all, because of lack of preservation, loss due to subduction or diagenesis, or other factors, can never be discovered, and its presence thus cannot be inferred by the ACE or any similar statistical method based only on abundance counts. Thus, our estimated diversity provides a lower bound on true original diversity (defined as the number of all dinosaur genera that ever existed, including those with no discoverable fossil record). Other authors have attempted to quantify true original diversity, but such methods require additional assumptions or information that is not available for dinosaurs (e.g., ref. 10 uses extant diversity in estimating the completeness of the fossil record of primate species).

Results

How Many Kinds of Dinosaurs Were There? The publication of the first edition of *The Dinosauria* (5) in 1990 occasioned a comprehensive critical review of the dinosaurian fossil record in which 285 genera were recognized as valid (2). The decade and a half since then has seen a tremendous increase in the number of genera described. Since 1990, an average of 14.8 genera have been described annually, compared with 5.8 genera annually between 1970 and 1989 and 1.1 genera annually between 1824 and 1969. In 1990, six countries accounted for 75% of all known dinosaur genera; in order, they are the United States, Mongolia, China, Canada, England, and Argentina. Today, the same six countries continue to have the highest known diversities, but in four of the six the number of genera has increased substantially as follows: United States (127 known genera, +48% increase since 1990), China (109, +132%), Argentina (61, +165%), Mongolia (61, +45%), Canada (43, +5%), and England (33, +14%). (Note that some genera are known from multiple countries.) In total, we currently recognize 527 valid known genera of dinosaurs, excluding genera based on isolated teeth or single elements. All together, 242 new genera have been described since 1990, an 85% increase. This remarkable pace of discovery presents an opportunity to revise earlier estimates of the diversity of dinosaurs.

By using the ACE, we currently estimate dinosaur diversity, including genera that remain to be discovered, at 1,844 genera. Accordingly, 29% of all discoverable genera are currently known, whereas 71% remain unknown (Table 1). We also

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Abbreviation: ACE, abundance-based coverage estimator.

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Table 1. Estimated diversity for the entire Mesozoic and by subperiod

Interval	Known diversity (genera)	Estimated diversity (genera)	Percentage known
Entire Mesozoic	527	1,844	29
Late Cretaceous	237	784	30
Early Cretaceous	139	575	24
Late Jurassic	64	224	29
Middle Jurassic	49	246	20
Early Jurassic	33	79	42
Late Triassic	34	62	55

Known generic diversity, estimated diversity using the ACE, and percent completeness at the genus level. Note that the column totals do not add to the overall totals for the entire Mesozoic. This occurs because (*i*) some genera, particularly those occurring in stages near subperiod boundaries, cannot be resolved to a single subperiod and are thus included in more than one subperiod; and (*ii*) the ACE is a nonlinear method, so its output is not additive.

estimated the total number of genera and percentage of known genera for each subperiod ("epoch" *sensu* ref. 11) in which dinosaurs were extant (Table 1). Because of reduced sample sizes, estimates for the Late Triassic and Early Jurassic are less reliable than that for the entire Mesozoic. There is a generally increasing trend in diversity through the Mesozoic, peaking in the Late Cretaceous. The Middle Jurassic, which is known to be particularly poorly sampled (see ref. 12, pp. 383–384), has the lowest estimated percentage of known genera. These results are generally consistent with those of Fara and Benton (13), who estimated the completeness of the tetrapod fossil record based on proportions of Lazarus taxa.

Were Dinosaurs in Decline Before the Cretaceous/Tertiary Boundary? Extensive debate has centered on whether dinosaurs were declining in diversity in the last 10 million years of the Cretaceous before their ultimate extinction (9, 14–21). Answering this question requires stage-level data on dinosaur ages. Of Late Cretaceous dinosaur genera, 70% have ages resolvable to the stage level. Of these well resolved genera, 86 are known from the Campanian and 76 from the Maastrichtian (including 16 known from both stages), so it appears that diversity was declining near the end of the Cretaceous. However, because the decline may result from sampling bias (9), and also because the Campanian (12.9 million years) is more than twice as long as the Maastrichtian (5.1 million years) (22), this apparent pattern should not be accepted at face value.

To assess whether diversity was declining at the end of the Cretaceous, we first divided Late Cretaceous dinosaurs into well resolved and poorly resolved genera, depending on whether each genus could be dated to the stage level. We then applied the ACE to only the well resolved genera. This procedure yielded an estimated diversity of 209 genera in the Campanian and 213 genera in the Maastrichtian. We thus found no evidence for a decline using only well resolved genera. Next, to avoid excluding poorly resolved Late Cretaceous genera, we used a randomization procedure to assign the poorly resolved genera to individual stages. Such genera were randomly assigned to a stage within their known age range with the probability of being assigned to any particular stage proportional to the number of well resolved genera in that stage. [A similar procedure is commonly used for tabulations of the Sepkoski compendium of marine invertebrates (23).] We then estimated diversity in each stage by applying the ACE to all genera associated with that stage (i.e., well resolved genera plus the poorly resolved genera randomly assigned to that stage). This procedure was repeated 100 times to assess the variability introduced by the randomization process.

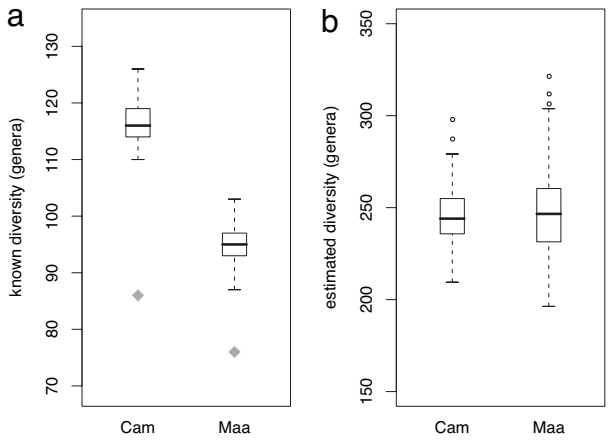

Fig. 1. Known and estimated diversity in the last two Late Cretaceous stages (Cam, Campanian; Maa, Maastrichtian). Results from 100 sets of randomizations to assess whether dinosaur diversity was declining near the end of the Cretaceous. (*a*) Number of genera associated with each stage, comprising well-resolved genera and the poorly resolved genera randomly assigned to that stage. The number of well-resolved genera known from each stage is marked by a gray diamond. (*b*) Estimated diversity in each stage. Box plots show middle 50% of values (represented by box) with the median shown as a horizontal line within the box.

For the 100 sets of randomizations, the number of known genera associated with the last two Late Cretaceous stages is shown in Fig. 1*a*, and estimated diversity for each stage using the ACE is shown in Fig. 1*b*. Fig. 1*a* shows that known diversity declined from the Campanian to the Maastrichtian. By contrast, Fig. 1*b* shows that estimated diversity held steady over these two stages. Averaged over the 100 sets of randomizations, the Campanian was estimated to have a diversity of 245.9 genera and the Maastrichtian 246.3. These results suggest that the apparent decline in dinosaur diversity in the Maastrichtian may be a result of sampling bias rather than a true decline, consistent with the results of Fastovsky *et al.* (9) using rarefaction. This finding is particularly surprising because known diversity is higher in the Campanian than in the Maastrichtian. However, we estimate that the Campanian dinosaur record is more complete than the Maastrichtian record, 48% complete at the generic level compared with 39%, so the decline in known diversity is misleading. It is possible that a gradual decline in diversity occurred within the Maastrichtian rather than between the Campanian and the Maastrichtian. To test such a hypothesis, however, data resolved to the substage level would be necessary, and too few dinosaur genera can currently be dated with such precision. Given the temporal resolution currently available, then, we find no evidence for a decline in dinosaur diversity near the end of the Cretaceous, a result consistent with a sudden extinction due to bolide impact.

Bias Due to Rock Availability. It has long been recognized that known diversity is influenced by the availability of fossiliferous rock (11, 24–29). Dodson (2) acknowledged this bias, but at that time tabulations of outcrop area were available only at the period level. Because dinosaurs existed for only two periods and part of a third, such data have little explanatory power. Here we use subperiod-level data on the number of formations (11) to assess the correlation of diversity with rock availability. These data record the number of terrestrial formations listed in the U.S. Geological Survey Lexicon of Geologic Names (30) for each subperiod. Although the number of formations is an imperfect proxy for rock availability, such data are the best currently available at the subperiod level. Peters and Foote (11) argue that

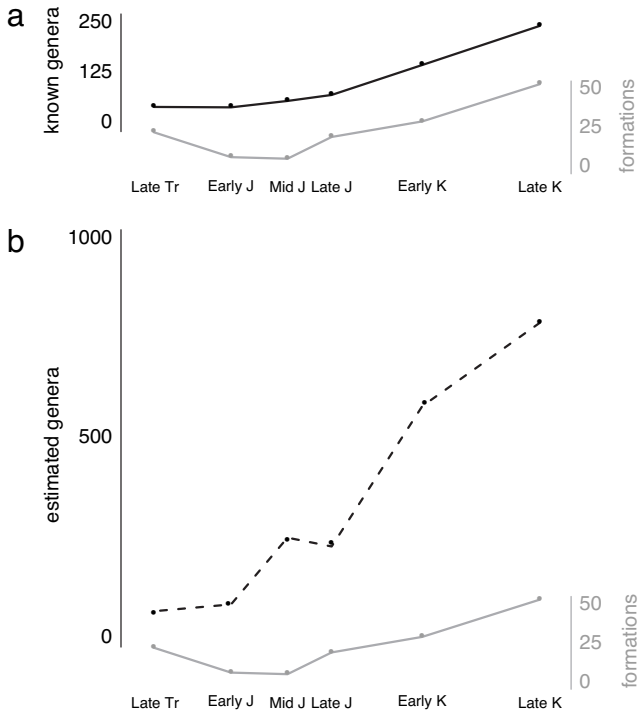

Fig. 2. Relationship of known and estimated diversity with rock availability (Tr, Triassic; J, Jurassic; K, Cretaceous). (*a*) Known diversity (solid black line) and number of terrestrial U.S. Geological Survey formations (gray line), a proxy for rock availability (11). (*b*) Estimated diversity using the ACE (dashed black line) and number of formations (gray line). Known diversity is strongly correlated with rock availability ($R^2 = 60.3\%$ for first differences), but estimated diversity is only weakly correlated ($R^2 = 12.8\%$ for first differences).

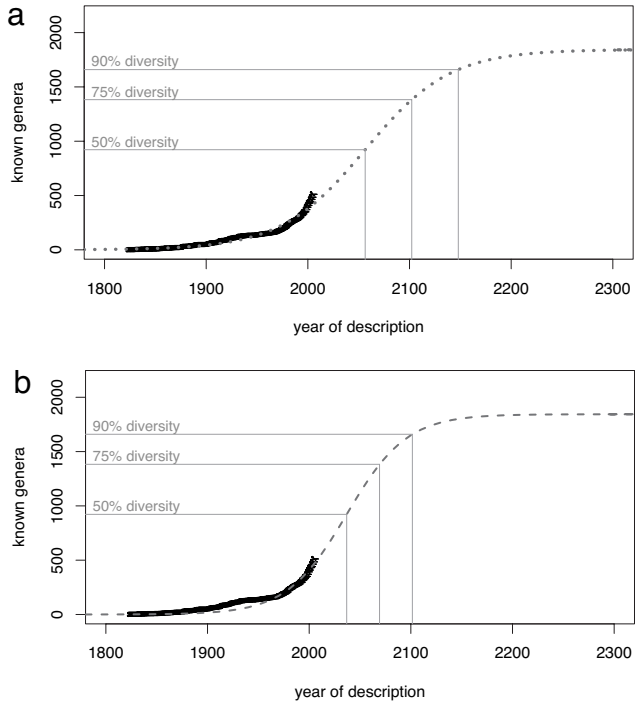

Fig. 3. Predicted rate of future dinosaur discoveries. Logistic accumulation curves fitted to known cumulative genus counts and constrained with a horizontal asymptote at 1,844 genera. Curves have the form $y = 1844/(1 + \exp\{-[\beta_0 + \beta_1(x - \beta_2)]\})$. Gray lines indicate predicted dates at which 50%, 75%, and 90% of discoverable generic diversity will be known. (*a*) Curve fitted using unweighted least-squares. Estimated parameter values are $\beta_0 = 0.23$, $\beta_1 = 0.024$, $\beta_2 = 2066$. (*b*) Curve fitted using weighted least-squares, with recent observations given more weight so that the curve better fits recent rates of discovery. Estimated parameter values are $\beta_0 = -1.05$, $\beta_1 = 0.034$, and $\beta_2 = 2006$.

the number of formations represents an amalgamation of global record quality, research effort, and lithological variability, although their conclusion is better supported for marine than for terrestrial formations.

To focus on short-term diversity changes and reduce the effects of large-scale trends, we take first differences (11). Over the entire Mesozoic, known diversity is strongly correlated with the number of formations at the subperiod level ($R^2 = 60.3\%$) (Fig. 2*a*). However, the correlation of estimated diversity and number of formations (Fig. 2*b*) is substantially lower ($R^2 = 12.8\%$), as would be expected because dinosaur diversity is unlikely to be strongly correlated with rock availability. Although this analysis is necessarily tentative because it is based on only five data points, it suggests that (*i*) known dinosaur diversity is biased by rock availability, and (*ii*) our estimates are adjusting known diversity for the incompleteness of the fossil record.

Predicting the Rate of Future Discoveries. To predict the trajectory of future discoveries, we fit logistic accumulation curves ("collector's curves") to cumulative counts of known genera. Note that the description rate of new genera is steeply increasing, so it would be difficult to fit such a curve without the constraint imposed by our estimate of the total number of discoverable genera, which implies that the curve must reach an asymptote at 1,844 genera. The best-fit curve found by using standard least-squares (Fig. 3*a*) appeared to underestimate recent rates of increase, so we also fit a logistic curve by using weighted least-squares to gave greater weight to more recent years (Fig. 3*b*). The unweighted curve forecasts that 50% of the 1,844 estimated genera will be discovered by the year 2056, 75% by 2102, and 90% by 2148. The weighted curve forecasts that 50% of the 1,844 estimated genera will be discovered by 2037, 75% by 2069, and 90% by 2102. This last prediction requires that 1,133 additional genera be discovered in less than a century or ≈12 genera per year. This rate of discovery is modest compared with recent years: At least 12 genera have been described in 7 of the last 8 years and at least 20 in 6 of those years. However, recent rates are historically high and largely a result of burgeoning activity in China and Argentina. To sustain similar rates of discovery for another century, new sources of dinosaur discoveries must continue to be found.

Discussion

We estimate that 29% of discoverable dinosaur genera are now known. Other authors have estimated the percentage of known diversity for other fossil groups, but these studies have been at the species level and thus are not directly comparable with our estimate. However, 90% of dinosaur genera are monospecific (the mean number of species is 1.2, with 98.3% of genera having 3 or fewer species), so the percentage completeness at the species level is likely to be close to the generic figure of 29%. Using this figure, the dinosaur fossil record is less complete than that of North American fossil mammal species, of which 56–67% are estimated to be known (31–33). Considering the extensive history of exploration in North America and the more recent age of mammal fossils, it is not surprising that the mammal record is better known than that of dinosaurs. However, the dinosaur fossil record is substantially more complete than that of primate species in particular, of which Tavare *et al.* (10) estimated <7% are known. The primate fossil record is sparse, because primates (particularly early species) were likely small-bodied, had limited

populations, and were arboreal, characteristics unfavorable to fossilization (10).

The dinosaur record also appears to be more complete than that of Phanerozoic marine invertebrate species as a whole, of which an estimated 12% are known (34). This overall figure of 12% combines soft-bodied groups whose fossil record is very sparse (e.g., ctenophores and nematodes) and well skeletonized taxa whose fossil record is relatively complete [e.g., crinoids, bivalves, brachiopods, and trilobites (31, 35)]. In general, marine ecosystems should be more conducive to fossilization than terrestrial ones, but the lack of hard parts of many invertebrates makes them less likely to fossilize than vertebrates such as dinosaurs. Moreover, although small animals often have larger population sizes, large animals such as dinosaurs may be more likely to be preserved because of taphonomic biases (36, 37).

Other studies have quantified the completeness of the fossil record for various groups [e.g., Phanerozoic marine invertebrates (35), Late Cretaceous mammals (38), Cretaceous tetrapods (13), and Phanerozoic animals and plants (39)]. These studies express their results as preservation rates per time interval (35, 38), the percentage of living families with fossil representatives (35), an index of completeness based on the prevalence of Lazarus taxa (13), and indices of congruence with published phylogenies (39). Because we calculate the percentage of genera that are known, our results and theirs cannot be compared directly.

Existing statistical methods for estimating diversity, including the ACE, assume random sampling of specimens. In reality, fossil discoveries are correlated in time and space depending on rock availability (see above) and numerous social and historical factors (40, 41). The dinosaur fossil record is especially patchy, because a substantial fraction of known diversity in some intervals derives from a single formation (e.g., Hell Creek, Morrison). No method yet exists to account for such temporal and spatial correlations, however, and authors disagree on how these correlations affect estimated diversity (42, 43). As a result, standard confidence intervals are likely to underestimate the true degree of uncertainty. We therefore do not attempt to calculate confidence intervals for our diversity estimates, because such intervals would be misleadingly narrow. For dinosaurs in particular, temporal and spatial correlations may cause the ACE, which assumes that undiscovered genera are inherently rare (see *Methods*), to underestimate diversity. Although many or even most undiscovered genera may in fact be rare, it is nonetheless probable that some abundant genera remain to be discovered, especially in time intervals or areas in which little terrestrial rock outcrop is available. If so, diversity would exceed our estimates.

Our estimate of 1,844 genera exceeds that of Dodson (2) by ≈50%, which is not surprising in light of recent growth in the rate of new genera being described, and is slightly over half of Russell's (3) estimate. The latter is not incompatible with our estimate, because it includes genera having no discoverable fossil record, whereas our estimate does not. If both our estimate and Russell's are correct, it would imply that 46% [(3,400–1,844)/3,400] of dinosaur genera have no discoverable fossil record.

It is an open question to what extent our estimates of discoverable genera mirror true original diversity. Our estimated diversity is surely a better proxy for true original diversity than is known diversity, because estimated diversity attempts to account for future discoveries. Furthermore, we posit that genera become undiscoverable primarily through initial failure to enter the fossil record (e.g., living in nondepositional environments) or subsequent loss of fossiliferous rock (e.g., subduction). (Other factors, such as size bias or erosion, might cause genera to be rare but not in principle undiscoverable.) If so, the issue of extrapolating to true original diversity from estimated diversity is analogous to inferring global diversity trends from a subset of localities, that is, showing that total richness mirrors alpha diversity. Research on marine invertebrates has shown that alpha diversity does in fact reflect global diversity (44–46). Furthermore, evidence suggests that dinosaur diversity trends at the formation level for well sampled formations (e.g., Morrison, Cloverly, Judith River) reflects global diversity trends (47). It is therefore plausible that estimated diversity reproduces the pattern of true original diversity in dinosaurs. This conclusion is strengthened by our results on rock availability bias: We expect that rock availability should have relatively little correlation with true original diversity, and its correlation with our estimated diversity is in fact low (Fig. 2*b*; $R^2 = 12.8\%$).

Assuming that estimated diversity parallels true original diversity, Fig. 3 may provide additional insight into the correlation of known diversity and rock availability. The plots in Fig. 2 *a* and *b* can be thought of as corresponding to the left and right parts of the logistic accumulation curve, respectively. At the left part of the curve (Fig. 3 *a* or *b*), known diversity is low compared with the number of discoverable genera, and additional sampling is likely to yield new genera. Thus, known diversity and rock availability are expected to be correlated, because extraneous (e.g., geological, historical, or social) biases should have a relatively larger impact when our knowledge of the dinosaur record is incomplete. At the right part of the curve, known diversity and rock availability should not be highly correlated, because for that part of the curve, known diversity is close to estimated diversity (and therefore mirrors true original diversity). Over the next century or two, as we move rightward and upward on the curve and completeness of the dinosaur record improves, we should expect known diversity to become less correlated with rock availability. However, because we have not yet reached such a point on the curve, we thus find that current known diversity is correlated with rock availability.

In summary, we estimate that 71% of discoverable dinosaur genera remain unknown to science and that new genera will continue to be discovered for at least another century. We also find that the known dinosaur fossil record is biased by the availability of fossiliferous rock. Furthermore, contrary to the known fossil record, we find no evidence that diversity declined from the Campanian to the Maastrichtian. Previous studies (1, 48) have demonstrated that a literal reading of the fossil record can be misleading. Our analyses confirm that the incompleteness of the fossil record must be taken into account.

Methods

Numerous methods have been developed to estimate the diversity of a population including as-yet-undiscovered taxa (7, 8, 49–55). Here we used the ACE, a nonparametric statistical method (7, 8) based on abundance counts. The ACE has been shown to perform well in the statistics and ecology literature (49, 51, 53–55). Anderson *et al.* (52) used the ACE to estimate Triassic plant diversity, but to our knowledge, the method has not been applied to fossil animals. We used a variant of the ACE designed for populations in which taxon abundances vary widely (7), as is the case for dinosaurs. Because diagnosing dinosaur fossils at the species level is often problematic (2), we used the genus as our unit of analysis. As required by the ACE, we divided genera into groups of rare and abundant genera. We considered abundant genera to be those represented by >10 individuals, as recommended in the literature (8, 56). Only rare genera are used to estimate diversity, a procedure that has several advantages for dinosaurs. First, it is often difficult to determine the exact number of individuals of very abundant genera. For example, in a large bonebed, we may be able to determine only that there are approximately several hundred individuals. Using only rare genera avoids the need

for precise counts of abundant genera. Second, finds of very abundant genera are less likely to be collected or reported in the literature. For example, a new find of a rare genus such as *Neuquenraptor* (known from only one individual) is more likely to be reported than a new find of a common genus such as *Protoceratops* (known from nearly 100 individuals). Third, rare genera provide the best information about undiscovered genera. Undiscovered genera are inherently rare and would likely be represented by only a few individuals if discovered, so only similarly rare known genera are relevant to estimating the number of undiscovered genera.

The ACE uses the number of known rare genera to estimate "coverage," defined as the total relative abundance of all known genera. Stated mathematically, suppose there are a total of K known and unknown genera, with p_i denoting the probability that a fossil find (i.e., individual) belongs to genus i for $i = 1, 2, \ldots, K$. Coverage is defined as the sum of the p_i values for the known genera. This quantity can be estimated from fossil abundance data and is a function of the number of genera known from only a single individual (7). A high coverage suggests that few unknown genera remain to be found, whereas a low coverage suggests that many unknown genera remain to be found. Estimated diversity is then calculated as follows:

$$\text{Estimated diversity} = D_{\text{abun}} + \frac{D_{\text{rare}}}{\hat{C}_{\text{rare}}} + \frac{f_1}{\hat{C}_{\text{rare}}}\,\tilde{\gamma}^2_{\text{rare}}.$$

Here,

$$\tilde{\gamma}^2_{\text{rare}} = \max\left\{\max\left(\frac{D_{\text{rare}}}{\hat{C}_{\text{rare}}}\frac{\Sigma i(i-1)f_i}{(\Sigma i f_i)^2} - 1,\ 0\right)\cdot\left(1 + \frac{1-\hat{C}_{\text{rare}}}{\hat{C}_{\text{rare}}}\frac{\Sigma i(i-1)f_i}{\Sigma i f_i - 1}\right),\ 0\right\}$$

is a measure of the heterogeneity of the p_i values (reflecting the dominance or evenness of the relative abundance distribution), D_{abun} is the number of known abundant genera, D_{rare} is the number of known rare genera, $\hat{C}_{\text{rare}} = 1 - f_1/n_{\text{rare}}$ is the coverage estimated from rare genera, f_i is the number of genera known from exactly i individuals, n_{rare} is the number of individuals among rare genera, and the index i in the definition of $\tilde{\gamma}^2_{\text{rare}}$ ranges from 1 to 10 (the cutoff for rare vs. abundant genera). Raw data needed to calculate these quantities are given in Data Set 1, which is published as supporting information on the PNAS web site. See refs. 7 and 8 for details on the ACE methodology. All calculations were performed by using code written by S.C.W. for the statistical software R (www.r-project.org).

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