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Evolution

Counting dinosaurs: How many kinds were there?

(biodiversity/Mesozoic biostratigraphy/evolutionary rates)

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ABSTRACT **Dinosaurs figure prominently in discussions of mass extinctions and evolutionary metrics, but their usefulness is hampered by archaic taxonomy, imprecise biostratigraphy, and imperfect preservation that bias our understanding of dinosaur diversity. A critical evaluation shows that of 540 genera and 800 species of dinosaurs proposed since 1824, 285 genera and 336 species are probably valid. Nearly half of all genera are based on a single specimen, and complete skulls and skeletons are known for only 20% of all dinosaurs. Dinosaurs are known from every continent. Countries with the greatest known diversity of dinosaurs are (in descending order) the United States, Mongolia, China, Canada, England, and Argentina; the greatest future increases may be expected from Argentina and China. Nearly half of all dinosaur genera are of latest Cretaceous age (Campanian or Maastrichtian). Estimates of the average duration of a dinosaur genus range from 5 million to 10.5 million years, with the most likely value about 7.7 million years. Dinosaurs evolved as rapidly as Cenozoic mammals. Global dinosaur diversity during the Campanian and Maastrichtian is estimated at 100 genera per stage, using a logistic model to estimate future discoveries. A model of increasing diversity and a bottleneck model compensate for the biases in the preserved fossil record. The number of dinosaurs that have ever lived is estimated at 900–1200 genera. The fossil record of dinosaurs is presently about 25% complete. Dinosaurs disappeared in the Maastrichtian near the peak of their historic diversity.**

Current concerns about a decline in biodiversity (1, 2) and continued discussion about great extinction episodes in the past (3, 4) make it clear that the question "how many kinds of organisms are there?" is central to understanding our natural world. Dinosaurs are conspicuous in the terrestrial fossil record, and much has been made of trends in dinosaur diversity, especially near the Cretaceous/Tertiary boundary (5, 6). An understanding of dinosaur diversity may provide a model for the biodiversity of large animals today.

The utility of the dinosaur record for evolutionary studies has been seriously hampered by archaic taxonomy, imprecise stratigraphy, and taphonomic factors of biased preservation and collection. In addition, the study of dinosaurs has been hindered by the lack of a cogent higher level systematic scheme. This situation recently has changed with the application of cladistic methods to the problem of dinosaur relationships (7, 8). A consensus has emerged that the Dinosauria represent a monophyletic taxon (9, 10). A comprehensive synthesis of the Dinosauria exclusive of birds (11) now permits a critical summary of the fossil record of dinosaurs. Such a summary should include a comprehensive account of a reasonable taxonomy, precise stratigraphic assignment, and descriptions of provenance, abundance, and nature of the material. I assess the quality of the fossil record of dinosaurs and describe models for estimating the number of dinosaur genera that have ever lived. Such models take into account historic, geographic, stratigraphic, and biologic factors that bias our understanding of biodiversity.

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Taxonomic Considerations

Dinosaur taxa proposed since the description of *Megalosaurus* in 1824 number 540 genera and ≈800 species. Of these, 285 genera and 336 species are regarded as valid (11); that is to say, they represent taxa based on diagnostic materials that have been properly described in accordance with the rules of the International Commission of Zoological Nomenclature. A further 255 genera have been relegated to a state of taxonomic oblivion due to one of several types of deficiency (11). Of these, 60.8% are *nomina dubia*, based on material that is indeterminate and cannot be regarded as generically and specifically diagnostic; 27.1% are junior synonyms, 9.4% are preoccupied, and 2.8% are now regarded as nondinosaurian. The taxonomic characters of dinosaurs include a complex set of features distributed through the skull and the postcranial skeleton. Attempts to establish dinosaurian taxa on the basis of single cranial or postcranial elements are generally not successful. Teeth constitute the type material of 16.9% of the invalid genera. A further 16.1% of genera are based on collections of vertebrae, also rarely diagnostic.

Most dinosaur genera (246) are represented by a single species: 25 have a second species, 9 have three species, and 3 have four referred species. A ratio of 1.2 species per genus reflects our current understanding of dinosaur diversity.

Abundance

The total number of dinosaur specimens in museum collections worldwide, narrowly defined as generically determinate, articulated specimens (12) or as diagnostic name-bearers, is ≈2100 (11). The fossil record of ornithischians (9.3 specimens per genus) is better than that of saurischians (6.2 specimens per genus). Certain dinosaurs are abundantly preserved. Perhaps the hadrosaur *Maiasaura* is the most abundant dinosaur, with at least 200 specimens (13). This is followed by *Psittacosaurus* with 120 specimens (14), *Coelophysis* with 100 specimens (15), *Plateosaurus* with 100 specimens (16), *Massospondylus* with 80 specimens (16), *Protoceratops* with 80 specimens (17), *Allosaurus* with 60 specimens (18), *Syntarsus* with 50 specimens (15), *Triceratops* with 50 specimens (17), and *Stegoceras* with 40 specimens (19).

However, 45.3% of dinosaur genera are represented by only a single specimen, and 74.0% have five specimens or fewer. Only 20.3% are based on essentially complete skulls and skeletons, and 56.8% include complete or partial skulls. Limited material often makes the convincing definition of variational biological species difficult. The level of genus is therefore a useful working unit for biostratigraphic studies of

Abbreviation: Ma, million years before present.

dinosaur diversity, although not the preferred unit for evolutionary studies.

Distribution in Time and Space

Dinosaurs are now known to have existed on all seven continents, including Antarctica (20). In the Cretaceous, known ranges extended from southern boreal regions (21) to northern boreal regions (22). More dinosaurs are known from the United States (64 genera) than from any other country. Other major sources of dinosaurs are Mongolia (40 genera), China (36 genera), Canada (31 genera), England (26 genera), and Argentina (23 genera). These six countries account for >75% of global dinosaur diversity. Stratigraphic and historical factors suggest that China and Argentina may rival the United States in the future. Most dinosaur genera (77.9%) are restricted to a single country; only 3.9% are known from three or more countries.

Dinosaurs extend stratigraphically from the Carnian stage of the Late Triassic, roughly 225 million years before present (Ma), through the Maastrichtian stage of the Late Cretaceous 65 Ma (23). The 160-million-year interval from first to last appearance is divided into 23 stages that average 7 million years in length [for the purposes of this report, the brief Rhaetian is subsumed within the Norian (24), and the Turonian, Coniacian, and Santonian are combined as a single interval of 7.4 million years duration]. It is a desideratum to refer each dinosaur occurrence to the precision of a marine stage. This is possible (11) for 52% of dinosaur genera; a further 38% are reported within two adjacent stages; only 9.8% are reported from more than two stages. Of 137 dinosaur genera reported from more than one stage, 77.4% represent uncertainty as to the correct stage and 22.6% represent legitimate records that span more than one stage.

Dinosaurs are by no means uniformly distributed through Mesozoic time (Fig. 1). The Campanian–Maastrichtian interval that comprises the final 10 million years of the Mesozoic includes 39.3% of all dinosaurs presently known; the Kimmeridgian–Tithonian includes 12.6% of dinosaur genera. These four stages comprise <20% of the total time span of the dinosaurs and contain 51.9% of dinosaur genera. Conversely, certain intervals—for example, the Pliensbachian to Bajocian in the Early to Middle Jurassic, the Berriasian through the Barremian in Early Cretaceous, and the Cenomanian in the Late Cretaceous—are poorly documented. Collectively, these nine stages, representing 35% of dinosaur time, account for only 9.8% of dinosaur genera.

Biases in the Fossil Record

Apparent diversity of fossils correlates highly with outcrop area (25) and the number of workers interested in fossils of a given age (26). These biases, first demonstrated for invertebrates, are also recognized for plants (27). Although the human bias is evident, dinosaur workers typically spread their studies over two or three geological periods; <10% of paleobotanists do so (27). A historical bias is evident: from 1824 to 1969, 65 first authors described 170 genera of dinosaurs, an effort of 2.6 genera per author and 0.45 author per year. From 1970 to 1990, 44 first authors described 115 genera, an identical effort of 2.6 genera per author but 2.32 authors per year, indicating a 5-fold increase in worker interest. In the United States, 27 first authors have described 64 genera, twice the number of workers in any other country. Dinosaur taxonomy began in the United States in 1856; only England (in 1824) was earlier. Corresponding dates were 1893 for Argentina, 1902 for Canada, and 1923 for China and Mongolia. Ultimately, diversity will be discovered whether workers be many or few.

It is difficult to document the effects of outcrop area on dinosaur diversity. Dinosaurs existed for only two and one-third periods. Thus, tabulations of period-level outcrop area (25, 27) have weak explanatory power. No comparable data exist at stage level. North American Cretaceous nonmarine outcrop area exceeds Jurassic outcrop area by a factor of 9 (27), but North American Cretaceous dinosaur diversity exceeds Jurassic diversity by a factor of only 2.6. This suggests that by comparison with the Jurassic, Cretaceous dinosaur diversity may be underrepresented. On the other hand, the diversity of dinosaurs from the 1000-km^2 outcrop of the Campanian Judith River Formation of Alberta, Canada (28, 29) exceeds the dinosaur diversity of the entire Kimmeridgian–Tithonian Morrison Formation that outcrops over 1,000,000 km^2 in the western United States (29, 30).

In accounting for these acknowledged biases, I regard the most intensively sampled intervals, the Campanian–Maastrichtian, and the Kimmeridgian–Tithonian, as providing the most reliable data and adjust poorly sampled, understudied intervals upward, according to one of several models (see below).

Longevity of Dinosaur Genera

There are three ways to estimate the average longevity of a genus of dinosaur, using successively more precise but smaller data sets. The first method accepts the data as unbiased. Of the 179 genera whose age is known, 82.7% are confined to a single stage. Indeed, 71.6% are confined to their

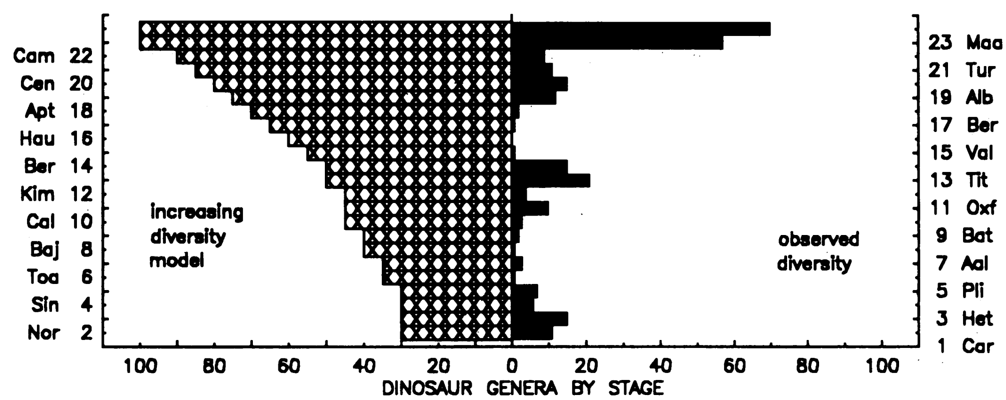

FIG. 1. Dinosaur diversity estimated by the model of increasing diversity. The fossil record of dinosaurs is arrayed by stratigraphic stage, from the oldest records of Late Triassic (Carnian) age (unit 1) to the youngest of Late Cretaceous (Maastrichtian) age (unit 23). Solid bars (right) represent the number of genera actually known from rocks of a given age; cross-hatched bars (left) represent the number of genera estimated by the model of increasing diversity. The pattern of increasing diversity reflects increasing provinciality as Pangaea broke up and the continents separated.

formation of discovery. One genus (*Bothriospondylus*) is reported (31) to range across four stages. Of the remaining 30, 16 are North American dinosaurs that range from the late Campanian to the mid-Maastrichtian (29) (i.e., Judith River Formation to Horseshoe Canyon Formation or Fruitland Formation to Kirtland Formation), and although straddling two stages, their ranges may not exceed the span of a single stage. By this reckoning, the modal longevity of a dinosaurian genus is one stage, and the average longevity is 1.1 stages per genus, or 7.7 million years. This may overestimate average longevity, as it assumes that a genus recorded in any stage lasted for the entire stage, an assumption whose validity is rarely documented.

The second method takes into account the fact that genera based on single specimens cannot in principle have a temporal distribution. If the 129 genera based on single specimens are eliminated, 48.1% of the remaining 156 genera are confined to a single formation and 51.9% are found in two or more formations. An additional 14 genera may be eliminated because of stratigraphic uncertainty. In this reduced data set, 52.1% are confined to a single stage, 45.7% span two stages, and 2.8% span three or more stages. This yields an estimated mean longevity of 1.5 stages or 10.5 million years per genus. This method may also overestimate longevity by eliminating legitimate single-stage occurrences.

The third method alone offers the potential to resolve rates at a time scale of less than a stage, by assessing taxonomic turnover among stratigraphically superimposed formations within the same geographic region, unfortunately a rare situation for dinosaurs. The best examples include the Judith River, Horseshoe Canyon, and Scollard Formations in Alberta, Canada, of late Campanian to late Maastrichtian age (29, 32); and the Djadochta, Barun Goyot, and Nemegt Formations in the Gobi Desert of Mongolia (32, 33), of approximately the same age.

In the Red Deer River Valley of Alberta, a fauna of 42 genera of Late Cretaceous dinosaurs has been recovered from three formations spanning the interval from 76 to 65 Ma, roughly late Campanian to terminal Maastrichtian. The fauna of the Judith River Formation includes 30 genera of dinosaurs, of which 56.7% are confined to the formation, 36.7% continue into the early Maastrichtian, and 6.7% continue into the late Maastrichtian. The fauna of the early Maastrichtian Horseshoe Canyon Formation includes 18 genera, of which 66.7% carry over from the Judith River Formation, and 33.3% represent new appearances. The Scollard fauna comprises 9 genera of dinosaurs, 66.7% of which are new, and 33.3% of which are carried over, two from the Judith River and one from the Horseshoe Canyon. Assigning the ages 76–73 Ma to Judithian faunas, 71–68 Ma to Edmontonian faunas, and 68–65 Ma to Lancian faunas (29), the average duration of a genus of Late Cretaceous dinosaur in Alberta appears to be 4.2 million years, or 0.6 stage per genus.

In the Gobi Desert of Mongolia, the time successive Upper Cretaceous units are the Djadochta, Barun Goyot, and Nemegt Formations, which preserve a fauna of 22 genera of dinosaurs. The Gobi formations are less well constrained temporally than the Alberta sediments due to the lack of marine beds. Osmolska (33) suggests the formations are, respectively, early, middle, and late Campanian or early Maastrichtian in age, while Fox (34) and Lillegraven and McKenna (35) suggest that the formations are late Campanian and early and late Maastrichtian, respectively. In either case, the time span between oldest and youngest formations is similar to the span of the Alberta units. The average duration of a genus of Mongolian Late Cretaceous dinosaur appears to be similar to that for Alberta.

In both Alberta and Mongolia, it is assumed that dinosaurs appearing in the Judith River or Djadochta Formations originated at that time rather than at an earlier undocumented time. Origination earlier or survival elsewhere later would increase the longevity of genera somewhat. Range extensions increase the figure for average generic longevity to 5.0 million years, or 0.7 stage per genus. Also, the comparative brevity of the Albertan and Mongolian sequences necessarily rules out ranges of two stages or more in duration, thus biasing these estimates toward the short side. Nonetheless, the impression remains both in Alberta and Mongolia that faunal turnover at the generic level during the Late Cretaceous occurs at intervals substantially shorter than one stage.

It is difficult to choose among the three rates calculated, especially as the two more refined estimates diverge in opposite directions from the first value. The most precise value is biased against long-lived genera. It also has the least generality for the entire Mesozoic, as it can be demonstrated only for the last ten million years of the Cretaceous, a time when intense biotic interactions with angiosperms and mammals have been postulated (36–38). Similarly, the upper value of 1.5 stages or 10.5 million years per genus is biased against short-lived genera and seems more sluggish than indicated by Late Cretaceous dinosaurs. Consequently, the middle estimate of 1.1 stages of 7.7 million years per genus may give the most reasonable middle ground for estimating the duration of a genus of dinosaur. All three rates are used in the calculations that follow.

How Many Kinds of Dinosaurs Were There?

The data summarized above can be used as a basis for estimating the number of dinosaur genera that have ever lived. One approach is to estimate the number of dinosaur genera that will be found. The rate of description of newly identified genera has been ≈6 per year for the past 20 years. Were this high rate to continue unabated, the current figure of 285 genera would double in 50 years. A logistic growth curve fitted to data on the rate of description of newly identified genera of dinosaurs from 1824 to the present suggests that a maximum of 725 genera ultimately will be described. This estimate forms the lower bounding limit but compensates least effectively for the recognized biases.

A more sophisticated approach is to project diversity sampled at selected intervals over the entire span of the Mesozoic, taking into account rates of evolution and models of diversity. Dinosaurs not buried due to taphonomic filtering, destroyed by erosion, or that remain deeply buried beneath Cenozoic strata will never be described. Also, dinosaurs clearly existed during certain intervals for which there is almost no record (e.g., Aalenian and Berriasian). For estimating the number of dinosaur genera that have ever lived, the starting point must be the best sampled interval adjusted for future discoveries. The dual interval of Campanian and Maastrichtian includes 112 genera, or 56 per stage. A logistic fit of rate of discovery of genera suggests that this number may stabilize at 150 genera or 75 per stage. I estimate the actual worldwide diversity, adjusting for those that will never be found, at 100 genera each for the Campanian and the Maastrichtian.

Models of Diversity. Three models of diversity may be considered. A model of constant diversity anchored on a single interval (the Campanian–Maastrichtian) provides an upper bounding limit. Using low, middle, and high estimates of average generic longevity (0.7, 1.1, and 1.5 stages per genus) in a model of constant diversity projected across 23 stages from Carnian to Maastrichtian, the number of dinosaurs that have lived may be estimated at 3285, 2100, and 1525 genera.

Such estimates, based on the assumption of a cylindrical clade geometry, form an upper bounding limit but are not biologically reasonable. Spindles representing a defined point of origin, a time of diversification, a period of peak diversity, and a period of decline are typical of plots of organic diversity through time (39, 40). Furthermore, a clade may show several peaks of diversity followed by moderate declines. Two more reasonable models may be used to estimate dinosaur diversity through time: a model of increasing diversity (Fig. 1) and a bottleneck model (Fig. 2). Both models are anchored on the best sampled points: 100 genera for the Campanian and the Maastrichtian (as estimated above), 50 genera for the Kimmeridgian and Tithonian (twice the number observed to allow for future discoveries), and 30 genera each (also twice the number observed) for the Carnian through the Sinemurian. The trend toward increasing diversity is consistent with trends both of within-community dinosaur diversity and with increasing provinciality through the Mesozoic as the continents separated and migrated toward their current positions (42). In the increasing diversity model, diversity is smoothly integrated from the Sinemurian to the Kimmeridgian, and from the Tithonian to the Campanian. This procedure yields estimates of 1850, 1175, and 865 genera.

The bottleneck model follows patterns of the known fossil record more closely than the preceding model. This model interprets gaps in the terrestrial fossil record as representing times of marine transgression that reduced habitable land area and thus decreased biotic diversity on land (43–45). Although the fossil record is almost blank for these intervals, the continuity of families across these hiatuses demonstrates that nonpreservation rather than massive extinction is the correct explanation. The low diversity of late Early Cretaceous dinosaur communities (32, 41) as compared with preceding Kimmeridgian–Tithonian ones (30, 32) is consistent with the bottleneck model. In this model, diversity following the Tithonian is halved to 25 genera for the Berriasian through the Hauterivian and integrated for the remainder of the Cretaceous; similarly, diversity is halved after the Sinemurian to 15 genera for the Pliensbachian through Bajocian, followed by integration through the rest of the Jurassic. This approach yields 1380, 875, and 645 genera.

Discussion. The approach taken to estimate total dinosaur diversity is analogous to that taken by Signor (46), who estimated Cenozoic invertebrate diversity using a single diversity datum (Recent diversity), three estimates of mean species duration, and three patterns of change of diversity through time. In this study, three rates of generic longevity and three models of diversity are used to calculate nine estimates for the total dinosaur genera that have ever lived. The estimates range from a maximum of 3285 genera to a minimum of 645. As a model of constant diversity has no biological plausibility, the three figures from this model are not considered further. The lowest estimate, that of 645 genera derived from the bottleneck model using the sluggish rate of evolution, is lower than the estimate of 725 genera derived from the logistic fit of rate of description of actual new taxa. This figure too is eliminated, leaving five estimates ranging from 865 to 1850 genera. The most conservative estimates are associated with the middle value for generic longevity. Thus, the range for the most probable figures for the number of dinosaurs that have ever lived is 900–1200 genera. It thus follows that the fossil record of dinosaurs is 24–32% complete at present. By comparison, Signor (46) estimated that the record of Phanerozoic marine invertebrates is 12% complete on average (but the Silurian record at 30% is the most complete because the total size of the fauna is the smallest). Taphonomic biases may favor the preservation of animals of large size (47).

Given the imperfection of the fossil record, it is impossible to specify precisely the number of dinosaur genera that have existed. The application of a logistic growth model borrowed from population biology is based on the assumptions that the population of dinosaur genera is finite, that the past history of discovery of dinosaurs is relevant to the future, and that as the number of undiscovered dinosaurs decreases the rate of discovery of additional kinds will decline asymptotically. The estimates of generic longevity are consistent within a factor of two, allowing reasonable boundaries for establishing the desired estimates. An important feature of the models of diversity used is that they assume the fossil record is biased and compensate for it; i.e., dinosaurs were present even though not yet discovered or even unpreserved. If the fossil record were interpreted literally, the apparent diversity would be much lower. Perhaps the most sensitive assumption is that 100 genera represents the greatest global diversity that dinosaurs ever attained at any one time, and that diversity was considerably lower when Pangaea was assembled in the Triassic. However, the figure of 100 genera seems defensible empirically and by comparison with living large-bodied mammals.

Conclusions

Is an estimate of 900–1200 genera for the total diversity of dinosaurs over 160 million years of time a reasonable estimate? On the face of it, this number seems small. By comparison, mammals today number 1010 genera and 4170 species (48). Approximately 40% of mammals are rodents, 20% are bats, and 10% are insectivores, none of which are close ecological analogues of dinosaurs (49). Thus, it is more reasonable to restrict the comparison to larger mammals—that is to the orders Carnivora, Artiodactyla, Perissodactyla, and Proboscidea, which include those mammals that are the most reasonable ecological analogues of dinosaurian herbivores and their predators. These four orders of mammals

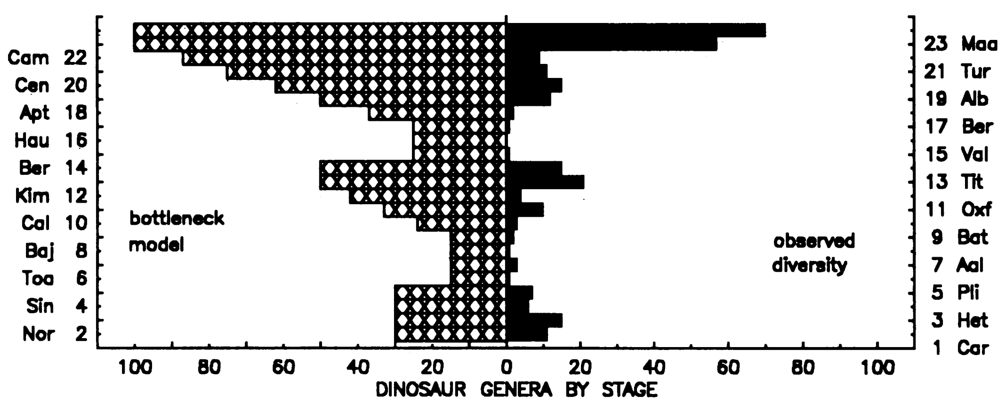

FIG. 2. Dinosaur diversity estimated by the bottleneck model. As in Fig. 1, solid bars (right) represent the number of genera actually known from rocks of a given age and cross-hatched bars (left) represent the number of genera estimated by the bottleneck model. Not only does global diversity decline from the Kimmeridgian–Tithonian to the Aptian–Albian, so does community diversity, as when the diversity of Morrison dinosaur faunas (30) is compared with Cloverly dinosaur faunas (41); this suggests that the bottleneck model has merit.

comprise 175 genera and 461 species (50). It is well known that dinosaurs were on average larger than the majority of mammals (51) and that diversity decreases with increasing body size (1). Accordingly, it would appear that the estimate of 100 genera of dinosaurs at any one time interval is a reasonable estimate of diversity. Furthermore, the average duration of a genus of mammal, 7–8 million years (52, 53), is comparable to the average duration of a genus of dinosaur, which I variously estimate at 5.0–10.5 million years. Thus, the generic longevities of dinosaurs and mammals compare remarkably well. A major difference is that mammals today average 4 species per genus, and the subset of larger mammals averages 2.6 species per genus, but dinosaurs average only 1.2 species per genus. Paleontologists must be satisfied with fewer criteria for recognizing species than are available to neontologists, but the tendency for reduced numbers of species seems consistent with relatively large body sizes typical of dinosaurs.

This critical systematic and stratigraphic summary points out the elusiveness of a precise estimate of the kinds of dinosaurs that have lived. Depending on the assumptions, the number ranges from 645 to 3285 genera, with most probable values between 900 and 1200 genera. Nonetheless, when the biases are understood, patterns in biodiversity can be explored. For instance, it is clear that dinosaurs were evolving at rates comparable to those of Cenozoic land mammals. It is less important to specify with precision the number of dinosaurs than it is to understand the nature of the dinosaur fossil record and the legitimate uses to which it may be applied.

The decisive role of dinosaurs in the terminal Cretaceous mass extinctions is open to question (54). The data presented record phenomena over 7 million years as a single datum and thus lend support to neither a gradual nor an abrupt disappearance of the dinosaurs. Nonetheless, 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.

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