A survey of dinosaur diversity by clade, age, place of discovery and year of description

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Dinosaur diversity is analyzed in terms of the number of valid genera within each major clade, Mesozoic age, place of discovery and year of description. Aves (*Archaeopteryx* + Neornithes) is excluded. Nomina nuda and nomina dubia are not counted. The results show 451 valid dinosaurian genera at the end of 2001, of which 282 are saurischian (112 sauropodomorphs and 170 theropods, including 93 coelurosaurs) and 169 ornithischian, including 11 pachycephalosaurs, 26 ceratopsians, 60 ornithopods, 12 stegosaurs, and 38 ankylosaurs. Thirty-eight genera arose in the Triassic, 124 in the Jurassic, and 289 in the Cretaceous, of which a disproportionately high number — 85 and 47 — are from the Campanian and Maastrichtian. The Kimmeridgian was the most productive age, with an average of 11.18 new genera per million years. The Kimmeridgian saw an unparalleled boom in sauropod diversity, with 20 new sauropod genera arising in its 3.4 million years, an average of one new sauropod every 170,000 years. Asia was the most productive continent with 149 genera, followed by North America (135), Europe (66), South America (52), Africa (39), Australasia (9), and finally Antarctica (1). Just three countries account for more than half of all dinosaur diversity, with 231 genera between them: the U.S.A (105), China (73), and Mongolia (53). The top six countries also include Argentina (44), England (30), and Canada (30), and together provide 335 dinosaur genera, nearly three quarters of the total. The rate of naming new dinosaurs has increased hugely in recent years, with more genera named in the last 19 years than in all the preceding 159 years. The results of these analyses must be interpreted with care, as diversity in ancient ecosystems is perceived through a series of preservational and human filters yielding observed diversity patterns that may be very different from the actual diversity.

Key words: Dinosauria, genera, diversity, phylogeny, biogeography, biostratigraphy, Kimmeridgian, Morrison Formation.

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Introduction

Although it is fundamental to matters of Mesozoic palaeoecology, the subject of dinosaur diversity has received surprisingly little attention in the literature. The principal contributions have been those of Dodson and his collaborators (Dodson 1990, Dodson and Dawson 1991, Dodson 1994, Holmes and Dodson 1997).

Dodson (1990) surveyed the non-avian dinosaur genera described at that time and concluded that only slightly more than half were valid (285 of 540). He briefly discussed the geographical distribution of the genera, and in more detail the changing levels of observed diversity through the Mesozoic. He estimated the total number of dinosaurian genera at 900-1200, based on estimated genus longevity of 7.7 million years, concluding that the record was at that time about 25% complete.

Dodson and Dawson (1991) discussed the process by which the fossil record of dinosaurs has been assembled, analysing the rate of description of new genera and considering this rate separately for the six countries most fertile in dinosaur genera. They also considered the differing levels of interest in different dinosaur groups and how this may have biased the publication record.

Dodson (1994) covered similar ground, but with more emphasis on the effect of geographical and taxonomic biases on the fossil record. He considered what the record in the last few million years of the Mesozoic implies about dinosaur extinction, concluding that a decline in diversity set in before the end of the Maastrichtian.

Finally, Holmes and Dodson (1997) updated Dodson's 1990 analysis with the 51 new genera named between 1989 and 1995, briefly discussing the age, country and infraorder of the new genera.

No published analysis considers the explosion in new genera since 1997, or analyzes diversity by clade or at all comprehensively by place of origin. The present study attempts to address these deficiencies by offering four different analyses of a single data-set describing the dinosaurian genera considered valid as at the end of 2001. The data-set itself and the analysis program are both freely available (Taylor 2004a, 2004b).

A distinction must be made between *observed diversity* and *actual diversity*. All these analyses necessarily work with information about the former. We can never know the actual levels of diversity in any ancient ecosystem: the set of valid genera that we have today is the result of a series of chances including which animals were fossilised, which fossils survived until the present, which surviving fossils are in exposed outcrops, which exposed fossils have been collected, which collected fossils have been prepared and which prepared fossils have been described. However, increased understanding of the preservational and human factors that bias the record of observed diversity may in the future allow increasingly accurate estimates of actual diversity to be made.

Materials and Methods

Source of Data

The analyses in this paper are all derived from a single data-set (Taylor 2004a) representing dinosaur phylogeny, geology, geography and history. The initial version of the data was obtained with permission from the Dinosauricon web-site (Keesey 2001). This data-set was assembled over several years by the web-site author, with reference to the scientific literature, to reflect a consensus of then-current ideas about dinosaurian phylogeny and taxonomy. The data-set has been progressively reviewed on an informal basis since its inception, so it is perhaps closer to being a peer-reviewed database than any other.

The initial data-set taken from this web-site has been modified by the author to include all valid genera named to the end of the year 2001, and to reflect a more up to date understanding of the classification and age of some taxa. This updating was done with reference to Glut 2003 and also to numerous papers referenced by the very helpful DinoData web site (Bervoets 2004). Genera described since 2001 are not included.

Analysis Program

The analyses are all produced by a single program (Taylor 2004b) which reads the entire data-set into memory and arranges the taxa into a prescribed phylogenetic tree. The clade Aves (birds) is then excised from the tree, and the remaining structure is processed in a number of ways to produce the different analyses. For the purposes of these analyses, the definition of Aves is that of Chiappe 1992, being the most recent common ancestor of *Archaeopteryx* and modern birds together with all its descendents.

Note that this program does not perform a phylogenetic analysis, but analyses genus data within the framework of a prescribed phylogeny. Phylogenies are always contentious, but for the purpose of the current study it seemed best to re-use rather than to replicate prior work, using an available phylogeny uncritically. The purpose of this paper is not to advocate a particular phylogeny: the phylogeny presented here is the hypothesis, not the conclusion. In any case, the more interesting results of this study mostly pertain to high-level clades and are therefore not much affected by uncertainties about the details of low-level phylogeny within those clades.

The first analysis is of the phylogeny itself, and simply lists all the taxa described in the data-set in a form that illustrates the hypothesised relationships, and counts the number of genera included in each taxon. The second analysis notes the first geological age in which each genus occurred and counts how many genera arose in each age, epoch and period of the Mesozoic. The third analysis counts the number of genera described from each country and state, aggregating up to continent and supercontinent. The fourth counts the number of genera described each year since 1824.

Genera and Species

This study only counts genera and makes no attempt to consider species. For extant animals, it can be argued that species are objectively real while genera are merely a convenient abstraction (Cantino *et al.* 1999, Lee 2003). For extinct animals, however, the converse appears to be the case. The biological concept of species is not testable with fossils, and therefore inapplicable, so a morphological concept must be used; and while there is broad consensus on the degree of variation that constitutes a generic difference between fossils, there is little agreement over how to separate fossil species in the Dinosauria. For example, the number of valid species in *Triceratops* has variously been placed at 10 (Hatcher *et al.* 1907), six (Lull 1933), one (Ostrom and Wellnhofer 1986; Lehman 1990) and most recently two (Forster 1990, 1996).

Although separation at the genus level is less contentious than at the species level for extinct animals, it is still by no means universally agreed upon. There are many dinosaur genera that some authorities consider distinct while others do not — for example, the allosaurid *Saurophaganax* (Chure 1995) is considered by some workers merely to represent large *Allosaurus* specimens (for example, Hunt and Lucas 1987, Paul 1988 pp. 312-313).

Ultimately, classification of dinosaur specimens into genera and species is as much an art as a science; so while there is some consensus at the genus level, there is no single, definitive list of valid genera. The genera considered valid in this study therefore represent one perspective among many.

In the current data set, 381 of the 451 valid genera are monospecific. Forty-six contain two species, 17 contain three species and only seven genera contain more than three recognised species. Of these, *Camarasaurus*, *Cetiosaurus*, *Chasmosaurus* and *Edmontonia* each have four species in this data-set, though Upchurch and Martin's (2002, 2003) recent work on *Cetiosaurus* has since reduced it to a single valid species, *C. oxoniensis*. *Iguanodon* and *Mamenchisaurus* each have seven species, and *Psittacosaurus* has eight. This gives a total of 562 dinosaur species, for an average of just 1.25 species per genus.

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Results

Number of Genera by Clade

[Fig. 1]

Fig. 1 gives a high-level overview of the phylogeny used in this study. See the Appendix for full details. Clade sizes are of course subject to the accuracy of the phylogeny used: however, high-level dinosaur phylogeny appears to have been relatively stable over the last few years, with instability largely at ‘‘family level’’ and lower within these higher clades, especially the Coelurosauria.

The 93 coelurosaurs represent 56% of the 170 theropods. Wilson and Upchurch’s (2003) observation that titanosaurs represent approximately one-third of sauropod diversity is corroborated by this study: they supply 34 of the 93 sauropod genera. This contrasts with Curry Rogers and Forster’s (2004) assertion that titanosaurs comprise nearly half of all known sauropod genera.

[Fig. 2]

Fig. 2 shows the relative sizes of the major dinosaur groups. It is surprising that saurischians outnumber ornithischians so heavily — they are about 66% more diverse. More surprising still is the predominance of theropods: the total number described (170) is greater than the number of sauropodomorphs (112) or ornithischians (169). They account for 37% of all known dinosaur genera. This is in spite of the theropods’ having a much more conservative body-plan than the ornithischians, which display remarkable morphological diversity encompassing ceratopsians, ornithopods and stegosaurs.

Of the total of 16 diplodocoidean genera, 12 fall within Flagellicaudata = Clade(*Dicraeosaurus* + *Diplodocus*), Harris and Dodson 2004. All but one of these 12 arose during the Kimmeridgian: the sole exception is *Amargasaurus* from the Hauterivian, about 20 million years later.

If the clades Ornithomimosauria and Therizinosauria are considered herbivorous or omnivorous (Kobayashi et al. 1999, Barsbold and Maryanska 1990) then the remaining, carnivorous, theropods number 151 — fully one third of all dinosaur genera. This is an unusually high proportion of total diversity for carnivores to attain within an ecosystem. (Holtz *et al.* (1998) have also suggested based on tooth-serration density that troodontids may have been omnivorous, but this idea is not widely accepted.)

Number of Genera by Geological Age

[Table 1]

Table 1 shows that observed dinosaur diversity generally increases through time, with 38 genera having arisen in the Triassic, 124 in the Jurassic, and 289 in the Cretaceous. This imbalance is partly due to the origin of the dinosaurs only in the Carnian (Late Triassic), but even when diversity across the three periods is normalised by duration, the trend towards greater diversity is evident. The 38 Triassic genera occurred in the 21.7 million years from the beginning of the Carnian to the end of Rhaetian, giving a genus density, or GD, of 1.75 genera per million years. The 124 Jurassic genera arose in 61.5 million years for a GD of 2.02 and the 289 Cretaceous genera arose in 79.2 million years for a GD of 3.65. One reason for this bias towards greater observed diversity in more recent times may simply be that older fossils have had more time in which to be destroyed by processes such as erosion (Molnar 1997).

[Fig. 3]

Fig. 3 shows the relative richness of the Mesozoic ages. The five most productive ages (Campanian, Maastrichtian, Kimmeridgian, Albian and Aptian) produced 223 of the 451 dinosaur genera — very nearly half.

[Table 2]

Table 2 shows the GD of individual ages. This gives a more realistic indication of the levels of dinosaurian diversity in each age than the non-normalised figures: for example, the Kimmeridgian is now seen to have been more fertile in its rate of producing new genera than the Campanian, even though the latter period gave rise to more than twice as many genera as the former. Similarly, the Santonian was more fertile than the Albian despite having originated fewer than one third as many new genera.

Three ages stand out as much more diverse than others. The Kimmeridgian has a very high GD of 11.18; and the last two ages of the Mesozoic, the Maastrichtian and Campanian, have GDs of 7.83 and 6.80 respectively. No other age has a GD greater than 4.00. While no doubt sampling biases account for some of the GD irregularity, there does appear to have been a substantial and sustained flurry of diversity in the last twenty million years or so of the Mesozoic.

The highest apparent spike, in the Kimmeridgian, is exaggerated by the rule used in this analysis that a genus is attributed only to the age in which it first arose and not also to subsequent ages in which it survived. Of the 38 genera designated as Kimmeridgian in this analysis, fully 22 may have persisted into the Tithonian, so the apparent fall-off of diversity between these ages is not entirely real.

[Fig. 4]

Fig. 4 shows that diversity levels correlate only weakly with eustatic level (that is, global sea level). Thus this study does not strongly corroborate the claims of Haubold 1990 and Hunt *et al.* 1994 that taphonomic biases cause observed dinosaur diversity to be highest at times of highest eustatic level.

The large genus-count of 24 for the Carnian, the earliest age in which dinosaurs appeared, implies that initial dinosaur diversification was rapid. Of those genera, one quarter are ornithischian, but all six are too basal to assign to more specific clades. Of the saurischians, four are sauropodomorphs (of which none are sauropods) and the remaining 14 are theropods, of which six fall within Neotheropoda and eight are more basal. Twelve more new genera arose in the Norian, including the earliest known sauropod, *Isanosaurus*.

[Table 3]

Table 3 shows long intervals between the earliest and subsequent genera within many of the major clades. For example, the next recorded coelurosaur after the therizinosauroid maniraptor *Eshanosaurus*, in the Hettangian, is *Ozraptor* from the Bajocian, 29 million years later. It has been suggested that *Eshanosaurus* may in fact be a prosauropod (Matthew C. Lamanna, pers. comm. to Xu, Zhao and Clark), though this alternative identification has not yet been published. Similarly *Yaverlandia*'s status as the oldest pachycephalosaur is not firmly established, as its pachycephalosaurian affinities have been questioned (Sullivan 2000).

A different situation pertains for ceratopsians. After *Chaoyangsaurus*, the next recorded genus seems to be *Archaeoceratops*. The exact ages of these genera are not firmly established; but the former may be Bathonian, and the Xinminbao Group in which latter was found seems to be Barremian (Tang *et al*. 2001), indicating a gap of about 42 million years. However, the ceratopsian identity of *Chaoyangsaurus* appears to be secure as the type specimen has a rostral bone (Zhao, Cheng and Xu 1999), implying a long ghost lineage.

Number of Genera by Place of Discovery

Dinosaur palaeontology begain in England, and shortly thereafter developed in mainland Europe. Accordingly, European genera dominated counts for the first 66 years (1824-1889) before the gathering pace of research in North America established it as the most productive continent for more than a hundred years. As late as 1883, Europe, with 17 genera, still had nearly twice as many dinosaurs as North America, with only nine. But in the late 1800s, the American railways moved west opening up new areas for fossil prospecting, so that by 1890 North America had overtaken Europe, with 19 genera to Europe’s 17. In the seven years since 1883, 10 new genera had been named from North America, but none were named in Europe that are still considered valid today. In 1890, the two established continents between them accounted for all but three of the dinosaur genera then known, with the others made up of two African dinosaurs (*Massospondylus* and *Euskelosaurus*, from Lesotho) and just one from Asia (*Titanosaurus*, from India).

After the description of *Titanosaurus* in 1877, there was a 45-year gap before the next Asian dinosaurs were named (*Indosuchus*, *Protoceratops* and *Psittacosaurus* in 1923). But since the early 1970s, the rate of new discoveries in Asia has been more rapid than in the West. By the end of 1993, Asia had finally overtaken North America as the most productive continent, with 104 genera compared to North America’s 99. By this point, the number of Europen genera had climbed only slowly to 51, less than half as many as Asia.

Europe’s first dinosaur (*Megalosaurus*) was described in 1824, Africa’s (*Massospondylus*) in 1854, North America’s (*Troodon*) in 1856, Asia’s (*Titanosaurus*) in 1877, South America’s (*Argyrosaurus*) in 1893, Australasia’s (*Rhoetosaurus*) in 1925. Finally, Antarctica’s first dinosaur, *Cryolophosaurus*, was described in 1994, so that dinosaurs are now known from all seven continents.

[Table 4]

Table 4 shows the breakdown of dinosaur genera by place of description as at the end of 2001.

[Fig. 5]

Fig. 5 shows that Asia remains the most productive continent with 149 genera, though North America is not far behind.

[Fig. 6]

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Fig. 6 shows that just three countries account for more than half of all dinosaur diversity, with 231 genera between them: the U.S.A (105), China (73), and Mongolia (53). The top six countries also include Argentina (44), England (30), and Canada (30), and together provide 335 dinosaur genera, nearly three quarters of the total.

Number of Genera by Year of Description

[Fig. 7]

[Fig. 8]

Fig. 7 shows the number of new dinosaur genera named by year from 1824 until 2001, and Fig. 8 shows the cumulative count of dinosaur genera. The first year to yield a large crop of new dinosaurs was 1877, at the height of the rivalry between Cope and Marsh. The seven new genera in that year, all but one from the Morrison Formation, more than doubled the previous record of three in 1869. They increased the total number of dinosaurian genera then known by a third. Despite the fragmentary remains on which most of these genera were established, all of the six Morrison genera are still considered valid: *Allosaurus* (Marsh), *Amphicoelias* (Cope), *Apatosaurus* (Marsh), *Camarasaurus* (Cope), *Dryptosaurus* (Marsh) and *Stegosaurus* (Marsh) are firmly established. *Titanosaurus*, though, now looks questionable (Wilson and Upchurch 2003) .

The last year in which no new dinosaurs were described was 1961; the last before that was 1949. This means that new dinosaurs have been described in every year but one of the last 52.

Of the 451 genera valid at the cut-off point for this study, just over half had been described in the previous 19 years (1983-2001). Naming the first half had taken 159 years (1824-1982). Until 1970, only three years had yielded more than six new genera (1877, 1914 and 1932). Since then, 17 years — more than half — have done so.

Apart from the general upward trend, there is little pattern to the year-by-year frequency of naming: for example, 1997, with just five new genera, was a relatively barren year sandwiched between two bumper crops: 14 in 1996 and 25 in 1998.

[Fig. 9]

Fig. 9 shows how naming frequency has varied decade by decade. A trend is evident: apart from anomalously low figures for the four decades from the 1930s to the 1960s, the tendency is for the naming rate to grow exponentially. This four-decade fall-off corresponds with a period in which mammal palaeontology dominated the field (Bakker 1975), brought to an abrupt end in the 1970s by the ‘‘dinosaur renaissance’’, widely considered to have been catalyzed by Ostrom’s description and osteology of *Deinonychus antirropus* (Ostrom 1969a, 1969b). After this period, the exponential naming rate seems to pick up as though the 30s-60s had never happened, with more than twice as many genera named in the 1970s (56) as in the last decade before the gap, the 1920s (25 genera). The 56 genera described in the 1970s outnumber the total of 48 from the previous four decades combined: 17 in the 1930s, four in the 1940s, 14 in the 1950s and 13 in the 1960s.

[Fig. 10]

The origin of dinosaur palaeontology in the northern hemisphere, and the more recent increase of work in the southern hemisphere, is reflected in the history of new genera from each of the two Mesozoic supercontinents (Fig. 10). As late as 1913, only four genera were known from Gondwana: *Massospondylus* (1854), *Euskelosaurus* (1866), *Argyrosaurus* (1893) and *Genyodectes* (1901). By that same year, 63 genera were known from Laurasia — nearly 16 times as many. By 1932, the situation had started to even up, with 16 Gondawanan genera to 98 Laurasian, for a factor of 6.13. At the end of 2001, the 230 Laurasian genera still significantly outnumber the 101 Gondwanan genera, but the factor of 2.28 indicates that the gap is closing.

These figures should not be taken at face value, however, as Gondwana and Laurasia did not exist as complete, distinct landmasses throughout the whole of the Mesozoic. Their history is rather complex, with the various plates repeatedly joining and dividing in various combinations, and with epicontinental seaways dividing individual plates into multiple palaeobioprovinces (Le Loeuff 1997). Note also that ‘‘Gondwana’’ in the sense used here includes only the modern southern continents Africa, Antarctica, Australasia and South America, omitting parts of Europe such as Italy and Austria that were part of the southern landmass during the Mesozoic.

Discussion

Reasons for Variations in Diversity

The greater observed diversity of certain groups and ages is due to many factors, some of which are discussed below.

Geological Preservational Bias. — Raup (1972), working with the record of marine invertebrates throughout the Phanerozoic era, demonstrated a strong correlation between observed diversity levels and the volume of sedimentary rock available from each age. This may be the single most significant factor affecting observed diversity through time.

Anatomical Preservational Bias. — Physical properties of the skeletons of different taxa affect the likelihood of preservation. The pneumatised and relatively fragile bones of theropods would generally be more susceptible to damage than the relatively robust bones of sauropods and ornithischians. However, observed diversity figures do not reflect this expectation, presumably because other factors outweigh this one.

Ecological Preservational Bias. — Many theropods, being opportunistic scavengers, would have favoured carrion-rich environments such as sea margins, which confer a greater likelihood of preservation than the open plains that might have been favoured by most herbivores. This factor goes some way towards explaining why we observe a disproportionately high number of theropod taxa. For example, the Santana Formation preserves four theropods and no other dinosaurs; the Solnhofen limestone preserves three theropods and no other dinosaurs. It is unlikely that there were no herbivorous dinosaurs in these ecosystems, but they probably lived and died in drier nearby environments, and so have not been preserved.

Differential Splitting and Lumping. — It is possible that some clades have been over-split by workers keen to establish new genera in ‘‘glamourous’’ families, when working with specimens for which the degree of morphological difference from existing genera is not as great as would otherwise be expected. For example, the eight genera in the morphologically conservative group Tyrannosauridae are perhaps more than would have been established for specimens varying to a similar degree in another family (Currie 2003).

In the same vein, there may be a tendency for large sauropods to be assigned new generic names when they are not really merited. For example, the dorsal vertebra that was the type specimen of ‘‘Ultrasauros’’ (Jensen 1985) is now referred to *Supersaurus*. (Curtice *et al.* 1996); *Dystylosaurus* (Jensen 1985) also appears to be synonymous with *Supersaurus* (Curtice and Stadtman 2002); and *Seismosaurus* (Gillette 1991) may be merely a large *Diplodocus* (Lucas and Heckert 2000).

Focus of Current Work. — The frequency with which new genera are described in different groups may simply reflect the number of workers in those groups. At present, there seem to be many more theropod workers than sauropod workers, and yet fewer who specialise in ornithischians. Many ornithopod specimens collected on expeditions remain in their plaster jackets while the theropods are prepared and described first. This current focus is reflected in the naming frequency in recent years, which is progressively skewing the record towards theropods. For example, in 1996, 10 new theropods were described but only two new ornithischians. The 111 new genera described in the years from 1996 to 2001 are made up of 47 theropods (42%), 32 sauropodomorphs (29%) and 32 ornithischians (29%).

Actual Diversity. — With these other factors taken into account, the observed diversity numbers are indicative of the actual diversity of the living animals. But caution must be exercised when interpreting observed diversity numbers. For example, the last fourteen years of history strongly indicate that Dodson's (1990) estimates of total dinosaur diversity at 900-1200 genera to be well short of the true number.

The Kimmeridgian Sauropod Boom

Among the diversity anomalies shown by this study, perhaps the most puzzling is the large number of new sauropod genera that arose during the Kimmeridgian. The total of 20 genera comprises 12 from the Morrison Formation of the U.S.A. (*Amphicoelias*, *Apatosaurus*, *Barosaurus*, *Brachiosaurus*, *Camarasaurus*, *Diplodocus*, *Dyslocosaurus*, *Dystylosaurus*, *Eobrontosaurus*, *Haplocanthosaurus*, *Seismosaurus* and *Supersaurus*), four from Tendaguru in Tanzania (*Dicraeosaurus*, *Giraffatitan*, *Janenschia* and *Tendaguria*), two from China (*Euhelopus* and *Omeisaurus*), and two from Portugal (*Dinheirosaurus* and *Lourinhasaurus*).

The two Chinese genera lie outside Neosauropoda, but the other 18 are all neosauropods, comprising 11 diplodocoids (all falling within Flagellicaudata) and six macronarians, with the position of *Haplocanthosaurus* uncertain: it resolves as a diplodocoid or macronarian, or just outside Neosauropoda, depending on which other taxa are included in the analysis (Upchurch 1998).

Apart from the Kimmeridgian, The next most diverse ages for sauropods are the Campanian (nine genera), Albian (eight), Maastrichtian (seven) and Bathonian (five). The average number of new sauropods that arose in each million years of the Kimmeridgian (sauropod Genus Density, or sauropod GD) is 5.88 — a new sauropod genus every 170,000 years. The ages with the next highest sauropod GDs are the Maastrichtian (1.17), Bathonian (1.04) and Hauterivian (0.80). This high value for the Maastrichtian is contrary to widespread orthodoxy that sauropods were in decline at the end of the Mesozoic.

There are several possible causes for the sudden (in geological terms) Kimmeridgian boom in observed sauropod diversity.

Availability of Strata. — Although high observed diversity in the Kimmeridgian is most pronounced for sauropods, diversity is also high for theropods (five) and ornithischians (13). This is due in part to the exposure of Morrison-Formation strata across a wide area of more than a million square kilometers in 12 states (Dodson *et al.* 1980). Accordingly, the Morrison Formation is particularly well studied.

Similarly, the observed diversity spike in the Campanian is partially attributable to the exposure of the Two Medicine Formation across a wide area of Montana and Alberta (and

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also partly just to the length of this age — 12.5 million years, more than three times the length of the Kimmeridgian). Horner and Dobb (1997, pp. 192-196) observed that the high diversity of ostensibly contemporary Campanian centrosaurines actually represents a stratigraphic sequence, in which *Styracosaurus*, ‘‘centrosaurine 1’’ (not yet described), *Einiosaurus*, *Achelousaurus* and *Pachyrhinosaurus* occur successively within and immediately above the upper Two Medicine Formation. In other words, the seeming high diversity is really an artifact of over-coarse granularity in our time divisions, and the large number of genera actually reflects an unusually rapid turnover rather than many contemporary centrosaurines. However, this situation does not pertain in the case of Morrison sauropod diversity, as the Morrison sauropods all overlap in time (Turner and Peterson 1999).

Preservational Environment. — Morrison sediments represent an enormous alluvial plain rich in lucustrine and floodplain environments that were conducive to fossilisation (Dodson *et al.* 1890). So an unusually high proportion of the Morrison fauna has probably been preserved well enough to be identified reliably.

Taxonomic Over-Splitting. — As discussed above, several of the Kimmeridgian sauropods currently considered valid may in fact belong to the same genus. Following on from the *Dystylosaurus* and *Seismosaurus* referrals previously mentioned, more synonymisations are likely. For example, *Supersaurus* may be congeneric with *Barosaurus* (Curtice 2003), and *Giraffatitan* may not be distinct from *Brachiosaurus* (Wilson and Sereno 1988).

In general, larger animals seem to be more susceptible to over-splitting than small ones. In part, this is because they tend to live longer, so they have more time in which to accumulate individual variations that can be mistaken for generic differences. Over time, individual muscles may hypertrophy or atrophy, with consequent changes in the skeleton. Furthermore, variation is easier to see in larger specimens. These effects may go some way towards explaining why more genera are erected for large animals than for smaller ones.

Niche Partitioning. — Even allowing for biases arising from availability of strata, preservational environment and taxonomic over-splitting, the Kimmeridgian in general, and the Morrison ecosystem in particular, still appears remarkably diverse. No recent ecosystem even approaches such richness of large animals. Some areas of Africa support four herbivores massing 1000 kg or more (elephants, rhinos, hippos and giraffes), but no more; and the last three of these, while ‘‘large’’ by contemporary standards, are small compared with even the smallest of the 12 Morrison sauropods. One candidate explanation for this diversity is niche partitioning: an ecology in which different sauropod genera favoured different foods, or lived in different environments, thereby avoiding intergeneric competition.

Stevens and Parrish (1999) investigated neck mobility in *Apatosaurus* and *Diplodocus* by computer modelling of the cervical zygapophyseal articulations. Their results indicate that the former, despite its shorter neck, could feed rather higher than the latter (6m vs. 4m above ground level). *Brachiosaurus* could reach much higher still: a feeding height of 15m has been suggested (Paul 1998). These differing feeding heights suggest different dietary specialisations. In general, of course, the sauropods with higher reach would have been equally capable of browsing at lower levels; but Christian and Heinrich (1998) suggest, rather improbably, that *Brachiosaurus brancai* may have had a very limited vertical feeding range due to the difficulty of moving its neck far from the vertical pose that their study favours.

Studies of dental wear (Fiorillo 1998) indicate that different sauropods may have fed on different plants: coarse scratches on *Camarasaurus* teeth suggest that its food was gritty, whereas the finer scratches on *Diplodocus* teeth indicate a grit-free diet. As the concentration of grit tends to be higher at lower levels, this implies a low-level feeding strategy for *Camarasaurus* while *Diplodocus* probably browsed at a higher level — a conclusion that contradicts the horizontal neck posture suggested for *Diplodocus* by Stevens and Parrish (1999).

Barrett and Upchurch (1994) argued that specialisations in the skull of *Diplodocus* indicate an unusual mechanism for cropping vegetation, with the characteristic labial wear-facets on both upper and lower teeth explained by its use of different jaw actions for high and low browsing. They speculated that the differences between this feeding method and the less specialised method used by *Brachiosaurus* and *Camarasaurus* indicates some ecological separation.

In modern ecosystems, hippos and rhinos do not compete with each other because the former are largely aquatic. (Although they feed mostly on land, hippos remain close to water, whereas rhinos favour open grassland.) It is tempting to imagine that the Morrison sauropods might have niche-partitioned similarly, with some but not all being semi-aquatic. However, multiple lines of evidence show that sauropods were very poorly adapted for such a lifestyle: their feet are proportionally smaller than those of almost all terrestrial vertebrates, generating pressures about twice those of domestic cattle (Alexander 1989); and Coombs (1975) makes a strong biomechanical argument that the deep, relatively narrow torsos of sauropods are an adaptation for carrying weight in terrestrial locomotion.

While all Morrison sauropods were primarily terrestrial, some difference in partiality to wetter and dryer environments may nevertheless be indicated. For example, differences in limb and foot bones suggest that *Apatosaurus* and *Diplodocus* were better suited to traversing wet sediments than *Camarasaurus* was (Bonnan in press). However, Dodson *et al*. (1980) analysed the occurrence of several sauropod taxa within the four major lithofacies of the Morrison and concluded that large herbivorous dinosaurs were not aquatic, nor even semi-aquatic in the style of the hippo. “Diplodocus and *Camarasaurus* resemble elephants in their patterns of distribution.’’ However, the same authors also ‘‘believe that the distribution of large dinosaurs in the Morrison reflects ecological factors, not patterns of rapid evolution or extinction at the generic level.’’

Future Work

Follow-up studies might usefully relate the results of the individual analyses in this report to each other. For example, more work could be done on the age-distribution of particular clades, and on the tendency of certain clades to occur more commonly within particular continents. Similarly, the changing ‘‘fashionability’’ of different clades through history could be determined by observing the varying rates at which new genera have been named within those clades at different times.

It would be interesting to investigate the correlation between observed diversity levels and variables such as the level of atmospheric oxygen (Berner and Canfield 1989), the level of atmospheric carbon dioxide (Berner 1990, 1994) and average surface temperature (Frakes *et al.* 1992).

The Kimmeridgian sauropod boom is worthy of treatment in much greater depth than it has received in this study. The Morrison ecosystem that simultaneously supported so many very large animals is without parallel. It is a mystery not only how so many sauropod genera survived as contemporaries, but also how they arose within so short a space of time from one another. In order to fully explain the Kimmeridgian boom, it will be necessary to understand why relatively few sauropods arose during the immediately preceding Oxfordian (four sauropod genera) and Callovian (three); and why so few new sauropods arose in the immediately subsequent Tithonian (one genus) and Valanginian (two).

Finally, much effort is wasted at present by numerous workers each maintaining their own databases of valid dinosaur genera, their ages, countries, etc., similar in spirit to the one used in this study. It would be useful to establish a single canonical list, maintained by a committee of experts, and made freely available on the Internet in a well-defined format for all who wish to work with it.

Conclusions

Analysing dinosaur diversity data yields a number of surprising results, chief among which are the high diversity of theropods compared with ornithischians, the diversity spikes in the Kimmeridgian, Maastrichtian and Campanian, the long intervals between the first and subsequent recognised genera of some clades, and the increasing rate in the naming of new genera.

It is apparent that the diversity patterns observed from current data are extremely uneven. It is difficult to interpret some of the findings of this study, particularly those pertaining to geographical distribution, because observed diversity is affected by so many factors, both preservational and human. Dinosaur diversity is a system of many variables (taxonomic, geographic, geological, historical and others), correlated in complex ways and to varying degrees. It is not always possible to study variations in any one of these variables in isolation.

Much work remains to be done in analysing dinosaur diversity, particularly in correlating phylogenetic, geographic and stratigraphic information. That work could best be facilitated by collaboration on the creation and maintenance of a publicly owned database of dinosaur genera, so that different workers could more easily devise and perform different analyses without first having to replicate each other's spadework in assembling data.

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Table 1

Number of dinosaur genera by geological age, from oldest to youngest. The number of genera shown for each epoch includes those for all the ages it contains as well as those of uncertain position within the epoch. The number of genera shown for each period includes those for all the epochs it contains. Numbers in square brackets after epoch names indicate genera whose first occurrence is within the epoch but cannot be more precisely stated. Each genus is counted only in the earliest age in which it occurs, so that the total number of genera counted in this analysis is equal to the total number of valid genera. The bar-graph clearly shows the bias in the fossil record towards the Carnian, Kimmeridgian and mid- and late Cretaceous.

Period	**Epoch**	**Age**	**Definition (Mya)**	**Number of Genera**	
Triassic				38	
	Late Triassic [1]			38	
		Carnian	227.4-220.7	24	||||||||||||||||||||||||
		Norian	220.7-209.6	12	||||||||||||
		Rhaetian	209.6-205.7	1	|
Jurassic				124	
	Early Jurassic [4]			29	
		Hettangian	205.7-201.9	12	||||||||||||
		Sinemurian	201.9-195.3	4	||||
		Pliensbachian	195.3-189.6	3	|||
		Toarcian	189.6-180.1	6	||||||
	Middle Jurassic [4]			34	
		Aalenian	180.1-176.5	2	||
		Bajocian	176.5-169.2	3	|||
		Bathonian	169.2-164.4	16	||||||||||||||||
		Callovian	164.4-159.4	9	|||||||||
	Late Jurassic [3]			61	
		Oxfordian	159.4-154.1	8	||||||||
		Kimmeridgian	154.1-150.7	38	||||||||||||||||||||||||||||||||||||||
		Tithonian	150.7-144.2	12	||||||||||||
Cretaceous				289	
	Early Cretaceous [10]			102	
		Berriasian	144.2-137.0	2	||
		Valanginian	137.0-132.0	4	||||
		Hauterivian	132.0-127.0	9	|||||||||
		Barremian	127.0-121.0	24	||||||||||||||||||||||||
		Aptian	121.0-112.2	25	|||||||||||||||||||||||||
		Albian	112.2-98.9	28	||||||||||||||||||||||||||||
	Late Cretaceous [14]			187	
		Cenomanian	98.9-93.5	16	||||||||||||||||
		Turonian	93.5-89.9	10	||||||||||
		Coniacian	89.9-85.8	7	|||||||
		Santonian	85.8-83.5	8	||||||||
		Campanian	83.5-71.0	85	|||||||||||||||||||||||||||||||||||||||||||||||||||||||||||||||||||||||||||||||||||||
		Maastrichtian	71.0-65.0	47	|||||||||||||||||||||||||||||||||||||||||||||||

Table 2

Genus Density (GD) by geological age, found by dividing the number of genera arising in each age by the length of the age in millions of years. Each genus is counted only in the earliest age from which it is known.

<table>
<tr><th>Age</th><th>Definiton (Mya)</th><th>Duration (Ma)</th><th>Number of Genera</th><th>Genus Density</th><th></th></tr>
<tr><td>Carnian</td><td>227.4-220.7</td><td>6.70</td><td>24</td><td>3.58</td><td>|||||||||||||||||||||||||</td></tr>
<tr><td>Norian</td><td>220.7-209.6</td><td>11.10</td><td>12</td><td>1.08</td><td>|||||||</td></tr>
<tr><td>Rhaetian</td><td>209.6-205.7</td><td>3.90</td><td>1</td><td>0.26</td><td>|</td></tr>
<tr><td>Hettangian</td><td>205.7-201.9</td><td>3.80</td><td>12</td><td>3.16</td><td>||||||||||||||||||||||</td></tr>
<tr><td>Sinemurian</td><td>201.9-195.3</td><td>6.60</td><td>4</td><td>0.61</td><td>||||</td></tr>
<tr><td>Pliensbachian</td><td>195.3-189.6</td><td>5.70</td><td>3</td><td>0.53</td><td>|||</td></tr>
<tr><td>Toarcian</td><td>189.6-180.1</td><td>9.50</td><td>6</td><td>0.63</td><td>||||</td></tr>
<tr><td>Aalenian</td><td>180.1-176.5</td><td>3.60</td><td>2</td><td>0.56</td><td>|||</td></tr>
<tr><td>Bajocian</td><td>176.5-169.2</td><td>7.30</td><td>3</td><td>0.41</td><td>||</td></tr>
<tr><td>Bathonian</td><td>169.2-164.4</td><td>4.80</td><td>16</td><td>3.33</td><td>|||||||||||||||||||||||</td></tr>
<tr><td>Callovian</td><td>164.4-159.4</td><td>5.00</td><td>9</td><td>1.80</td><td>||||||||||||</td></tr>
<tr><td>Oxfordian</td><td>159.4-154.1</td><td>5.30</td><td>8</td><td>1.51</td><td>||||||||||</td></tr>
<tr><td>Kimmeridgian</td><td>154.1-150.7</td><td>3.40</td><td>38</td><td>11.18</td><td>||||||||||||||||||||||||||||||||||||||||||||||||||||||||||||||||||||||||||||||</td></tr>
<tr><td>Tithonian</td><td>150.7-144.2</td><td>6.50</td><td>12</td><td>1.85</td><td>||||||||||||</td></tr>
<tr><td>Berriasian</td><td>144.2-137.0</td><td>7.20</td><td>2</td><td>0.28</td><td>|</td></tr>
<tr><td>Valanginian</td><td>137.0-132.0</td><td>5.00</td><td>4</td><td>0.80</td><td>|||||</td></tr>
<tr><td>Hauterivian</td><td>132.0-127.0</td><td>5.00</td><td>9</td><td>1.80</td><td>||||||||||||</td></tr>
<tr><td>Barremian</td><td>127.0-121.0</td><td>6.00</td><td>24</td><td>4.00</td><td>||||||||||||||||||||||||||||</td></tr>
<tr><td>Aptian</td><td>121.0-112.2</td><td>8.80</td><td>25</td><td>2.84</td><td>|||||||||||||||||||</td></tr>
<tr><td>Albian</td><td>112.2- 98.9</td><td>13.30</td><td>28</td><td>2.11</td><td>||||||||||||||</td></tr>
<tr><td>Cenomanian</td><td>98.9- 93.5</td><td>5.40</td><td>16</td><td>2.96</td><td>||||||||||||||||||||</td></tr>
<tr><td>Turonian</td><td>93.5- 89.9</td><td>3.60</td><td>10</td><td>2.78</td><td>|||||||||||||||||||</td></tr>
<tr><td>Coniacian</td><td>89.9- 85.8</td><td>4.10</td><td>7</td><td>1.71</td><td>|||||||||||</td></tr>
<tr><td>Santonian</td><td>85.8- 83.5</td><td>2.30</td><td>8</td><td>3.48</td><td>||||||||||||||||||||||||</td></tr>
<tr><td>Campanian</td><td>83.5- 71.0</td><td>12.50</td><td>85</td><td>6.80</td><td>|||||||||||||||||||||||||||||||||||||||||||||||</td></tr>
<tr><td>Maastrichtian</td><td>71.0- 65.0</td><td>6.00</td><td>47</td><td>7.83</td><td>||||||||||||||||||||||||||||||||||||||||||||||||||||||</td></tr>
</table>

Table 3

First and second genera occurring within some important clades, with the difference between their ages, measured from the beginning of the age in each case. The difference between the ages of the earliest and subsequent genera within each clade is the length of the implied ghost lineage at the base of that clade. Genera whose age is not known to the resolution of a single age are discounted: for example, *Losillasaurus* is only known to be Late Jurassic, so it is ineligible to be the oldest Diplodocoid.

Clade	First genus	Age	Second genus	Age	Gap (Mya)
Sauropoda	*Isanosaurus*	Norian	*Vulcanodon*	Hettangian	15
Neosauropoda	*Atlasaurus*	Bathonian	*Bellusaurus*	Oxfordian	10
Diplodocoidea	Eleven genera	Kimmeridgian	*Amargasaurus*	Hauterivian	22
Titanosauria	*Tendaguria*	Kimmeridgian	*Macrurosaurus*	Valanginian	17
Carnosauria	*Cryolophosaurus*	Pliensbachian	*Gasosaurus*	Bathonian	26
Coelurosauria	*Eshanosaurus*	Hettangian	*Ozraptor*	Bajocian	29
Pachycephalosauria	*Yaverlandia*	Barremian	*Goyocephale*	Santonian	41
Ceratopsia	*Chaoyangsaurus*	Bathonian	*Archaeoceratops*	Barremian	42
Ornithopoda	*Yandusaurus*	Bathonian	Five genera	Kimmeridgian	15
Stegosauria	*Huayangosaurus*	Bathonian	*Lexovisaurus*	Callovian	5
Anklyosauria	*Tianchisaurus*	Bathonian	*Sarcolestes*	Callovian	5

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Table 4

Number of genera by place of discovery. The number of genera shown for each country includes those for all the states it contains; numbers for continents include those for their countries; and numbers for the supercontinents include those for the continents that make them up. Each genus is counted only in the country in which it was first discovered, even if specimens have subsequently been discovered in other countries.

<table>
<tr><th>Supercontinent</th><th>Continent</th><th>Country</th><th>State</th><th>Number of Genera</th><th></th></tr>
<tr><td>Laurasia</td><td></td><td></td><td></td><td>350</td><td></td></tr>
<tr><td></td><td>Asia</td><td></td><td></td><td>149</td><td></td></tr>
<tr><td></td><td></td><td>China</td><td></td><td>73</td><td>|||||||||||||||||||||||||||||||||||||||||||||||||||||||||||||||||||||||||</td></tr>
<tr><td></td><td></td><td>India</td><td></td><td>9</td><td>|||||||||</td></tr>
<tr><td></td><td></td><td>Japan</td><td></td><td>1</td><td>|</td></tr>
<tr><td></td><td></td><td>Kazakhstan</td><td></td><td>3</td><td>|||</td></tr>
<tr><td></td><td></td><td>Laos</td><td></td><td>1</td><td>|</td></tr>
<tr><td></td><td></td><td>Mongolia</td><td></td><td>53</td><td>|||||||||||||||||||||||||||||||||||||||||||||||||||||</td></tr>
<tr><td></td><td></td><td>Russia</td><td></td><td>2</td><td>||</td></tr>
<tr><td></td><td></td><td>S. Korea</td><td></td><td>1</td><td>|</td></tr>
<tr><td></td><td></td><td>Thailand</td><td></td><td>4</td><td>||||</td></tr>
<tr><td></td><td></td><td>Uzbekistan</td><td></td><td>2</td><td>||</td></tr>
<tr><td></td><td>Europe</td><td></td><td></td><td>66</td><td></td></tr>
<tr><td></td><td></td><td>Austria</td><td></td><td>1</td><td>|</td></tr>
<tr><td></td><td></td><td>Belgium</td><td></td><td>1</td><td>|</td></tr>
<tr><td></td><td></td><td>Croatia</td><td></td><td>1</td><td>|</td></tr>
<tr><td></td><td></td><td>France</td><td></td><td>9</td><td>|||||||||</td></tr>
<tr><td></td><td></td><td>Germany</td><td></td><td>8</td><td>||||||||</td></tr>
<tr><td></td><td></td><td>Hungary</td><td></td><td>1</td><td>|</td></tr>
<tr><td></td><td></td><td>Italy</td><td></td><td>1</td><td>|</td></tr>
<tr><td></td><td></td><td>Portugal</td><td></td><td>6</td><td>||||||</td></tr>
<tr><td></td><td></td><td>Romania</td><td></td><td>3</td><td>|||</td></tr>
<tr><td></td><td></td><td>Spain</td><td></td><td>5</td><td>|||||</td></tr>
<tr><td></td><td></td><td>United Kingdom</td><td></td><td>30</td><td></td></tr>
<tr><td></td><td></td><td></td><td>England</td><td>30</td><td>||||||||||||||||||||||||||||||</td></tr>
<tr><td></td><td>N. America</td><td></td><td></td><td>135</td><td></td></tr>
<tr><td></td><td></td><td>Canada</td><td></td><td>30</td><td></td></tr>
<tr><td></td><td></td><td></td><td>Alberta</td><td>30</td><td>||||||||||||||||||||||||||||||</td></tr>
<tr><td></td><td></td><td>U.S.A.</td><td></td><td>105</td><td></td></tr>
<tr><td></td><td></td><td></td><td>Alabama</td><td>1</td><td>|</td></tr>
<tr><td></td><td></td><td></td><td>Alaska</td><td>1</td><td>|</td></tr>
<tr><td></td><td></td><td></td><td>Arizona</td><td>8</td><td>||||||||</td></tr>
<tr><td></td><td></td><td></td><td>Colorado</td><td>16</td><td>||||||||||||||||</td></tr>
<tr><td></td><td></td><td></td><td>Connecticut</td><td>2</td><td>||</td></tr>
<tr><td></td><td></td><td></td><td>Kansas</td><td>3</td><td>|||</td></tr>
<tr><td></td><td></td><td></td><td>Maryland</td><td>1</td><td>|</td></tr>
<tr><td></td><td></td><td></td><td>Montana</td><td>18</td><td>||||||||||||||||||</td></tr>
<tr><td></td><td></td><td></td><td>N. Carolina</td><td>1</td><td>|</td></tr>
<tr><td></td><td></td><td></td><td>New Jersey</td><td>1</td><td>|</td></tr>
<tr><td></td><td></td><td></td><td>New Mexico</td><td>12</td><td>||||||||||||</td></tr>
<tr><td></td><td></td><td></td><td>Oklahoma</td><td>3</td><td>|||</td></tr>
<tr><td></td><td></td><td></td><td>Pennsylvania</td><td>1</td><td>|</td></tr>
<tr><td></td><td></td><td></td><td>S. Dakota</td><td>3</td><td>|||</td></tr>
<tr><td></td><td></td><td></td><td>Texas</td><td>8</td><td>||||||||</td></tr>
<tr><td></td><td></td><td></td><td>Utah</td><td>13</td><td>|||||||||||||</td></tr>
<tr><td></td><td></td><td></td><td>Wyoming</td><td>13</td><td>|||||||||||||</td></tr>
<tr><td>Gondwana</td><td></td><td></td><td></td><td>101</td><td></td></tr>
<tr><td></td><td>Africa</td><td></td><td></td><td>39</td><td></td></tr>
<tr><td></td><td></td><td>Egypt</td><td></td><td>4</td><td>||||</td></tr>
<tr><td></td><td></td><td>Lesotho</td><td></td><td>5</td><td>|||||</td></tr>
<tr><td></td><td></td><td>Madagascar</td><td></td><td>5</td><td>|||||</td></tr>
<tr><td></td><td></td><td>Malawi</td><td></td><td>1</td><td>|</td></tr>
<tr><td></td><td></td><td>Morocco</td><td></td><td>3</td><td>|||</td></tr>
</table>

<table>
<tr><td></td><td>N. Zimbabwe</td><td></td><td>1</td><td>|</td></tr>
<tr><td></td><td>Niger</td><td></td><td>6</td><td>||||||</td></tr>
<tr><td></td><td>S. Africa</td><td></td><td>7</td><td>|||||||</td></tr>
<tr><td></td><td>Tanzania</td><td></td><td>6</td><td>||||||</td></tr>
<tr><td></td><td>Zimbabwe</td><td></td><td>1</td><td>|</td></tr>
<tr><td>Antarctica</td><td></td><td>1</td><td></td><td>|</td></tr>
<tr><td>Australasia</td><td></td><td>9</td><td></td><td></td></tr>
<tr><td></td><td>Australia</td><td></td><td>9</td><td>|||||||||</td></tr>
<tr><td>S. America</td><td></td><td>52</td><td></td><td></td></tr>
<tr><td></td><td>Argentina</td><td></td><td>44</td><td>||||||||||||||||||||||||||||||||||||||||||||</td></tr>
<tr><td></td><td>Brazil</td><td></td><td>8</td><td>||||||||</td></tr>
</table>

Appendix. Number of Genera by Clade

This appendix shows the phylogeny assumed for this study (Taylor 2004a), including definitions for the more important clades. The phylogeny and definitions are modified from Keesey 2001. Vertical lines join sister groups, which are indented to the same level. Each clade's subclades are listed below it, indented by a single additional level. The counts in the left margin indicate the number of valid genera within each clade. The count for a high-level clade includes the counts of all the subclades contained within it, as well as genera basal within the high-level clade and those whose position within that clade cannot be more precisely determined. For example, the count of nine genera in Diplodocidae includes the two in Apatosaurinae and the five in Diplodocinae, plus two other diplodocid genera (*Dinheirosaurus* and *Dyslocosaurus*) that cannot be more precisely located.

Count	Taxon
451	Dinosauria sensu Padian, May 1993 = Clade(Neornithes, Triceratops)
282	. . Saurischia sensu Gauthier 1986 = Clade(Neornithes not Triceratops)
112	. . . . Sauropodomorpha sensu Gauthier 1986 = Clade(Saltasaurus not Neornithes)
2	. . . . . . Plateosauridae
2	. . . . . . Melanorosauridae
5	. . . . . . Massospondylidae
2	. . . . Yunnanosaurinae
93	. . . . . . Sauropoda sensu Wilson, Sereno = Clade(Saltasaurus not Plateosaurus)
89	. . . . Clade(Saltasaurus not Vulcanodon)
84	. . . . Eusauropoda = Clade(Saltasaurus not Barapasaurus, Ohmdenosaurus, Vulcanodon, Zizhongosaurus)
2	. . . . Mamenchisauridae
68	. . . . Neosauropoda = Clade(Saltasaurus, Diplodocus)
16	. . . . Diplodocoidea = Clade(Diplodocus not Saltasaurus)
3	. . . . Rebbachisauridae
12	. . . . Flagellicaudata = Clade(Diplodocus, Dicraeosaurus)
2	. . . . Dicraeosauridae
9	. . . . Diplodocidae
2	. . . . Apatosaurinae
5	. . . . Diplodocinae
48	. . . . Macronaria = Clade(Saltasaurus not Diplodocus)
46	. . . . Camarasauromorpha = Clade(Camarasaurus, Saltasaurus)
3	. . . . Camarasauridae
43	. . . . Titanosauriformes = Clade(Titanosaurus, Brachiosaurus)
4	. . . . Brachiosauridae
34	. . . . Titanosauria sensu Wilson, Sereno 1998
24	. . . . Clade(Epachthosaurus, Saltasaurus, Argyrosaurus, Lirainosaurus)
17	. . . . Clade(Saltasaurus, Argyrosaurus, Lirainosaurus)
3	. . . . Nemegtosauridae
4	. . . . Saltasauridae = Clade(Saltasaurus, Opisthocoelicaudia)
3	. . . . Saltasaurinae = Clade(Saltasaurus not Opisthocoelicaudia)
2	. . . . Saltasaurini
170	. . . . Theropoda = Clade(Neornithes not Saltasaurus)
4	. . . . . . Herrerasauria
4	. . . . Herrerasauridae sensu Novas 1992 = Clade(Herrerasaurus, Staurikosaurus)
161	. . . . . . Neotheropoda sensu Sereno = Clade(Neornithes, Ceratosaurus)
28	. . . . Ceratosauria sensu Gauthier 1984 = Clade(Ceratosaurus not Neornithes)
10	. . . . Coelophysoidea = Clade(Coelophysis not Ceratosaurus)
6	. . . . Coelophysidae = Clade(Coelophysis, Procompsognathus)
2	. . . . Procompsognathinae = Clade(Procompsognathus not Coelophysis)
4	. . . . Coelophysinae = Clade(Coelophysis not Procompsognathus)
17	. . . . Neoceratosauria = Clade(Ceratosaurus not Coelophysis)
14	. . . . Abelisauroidea implied Bonaparte, Novas 1985 = Clade(Carnotaurus not Ceratosaurus, Elaphrosaurus)
11	. . . . Abelisauria = Clade(Abelisaurus, Noasaurus)
4	. . . . Noasauridae

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   7   | . . | . . | . . | . . | . . | . . | . . | . . Abelisauridae sensu Novas 1997
   3   | . . | . . | . . | . . | . . | . . | . . | . . | . . Carnotaurinae = Clade(Carnotaurus not Abelisaurus)
 129   | . . | . . | . . | . . Tetanurae = Clade(Neornithes not Ceratosaurus)
 121   | . . | . . | . . | . . | . . Clade(Neornithes, Torvosaurus)
   4   | . . | . . | . . | . . | . . | . . Torvosauridae = Clade(Torvosaurus not Spinosaurus)
 108   | . . | . . | . . | . . | . . | . . Avetheropoda = Clade(Neornithes, Allosaurus)
  14   | . . | . . | . . | . . | . . | . . | . . Carnosauria sensu Gauthier 1986 = Clade(Allosaurus not Neornithes)
  10   | . . | . . | . . | . . | . . | . . | . . | . . Allosauroidea = Clade(Allosaurus, Sinraptor)
   4   | . . | . . | . . | . . | . . | . . | . . | . . | . . Sinraptoridae = Clade(Sinraptor not Allosaurus)
   5   | . . | . . | . . | . . | . . | . . | . . | . . | . . Allosauridae sensu Padian, Hutchinson 1997 = Clade(Allosaurus not Sinraptor)
   3   | . . | . . | . . | . . | . . | . . | . . | . . | . . | . . Carcharodontosaurinae
  93   | . . | . . | . . | . . | . . | . . | . . Coelurosauria sensu Gauthier 1986 = Clade(Neornithes not Allosaurus)
  89   | . . | . . | . . | . . | . . | . . | . . | . . Maniraptoriformes = Clade(Neornithes, Ornithomimus)
   2   | . . | . . | . . | . . | . . | . . | . . | . . | . . Avimimidae
   2   | . . | . . | . . | . . | . . | . . | . . | . . | . . Compsognathidae
   9   | . . | . . | . . | . . | . . | . . | . . | . . | . . Arctometatarsalia emended 1996 = Clade(Ornithomimus not Neornithes)
   9   | . . | . . | . . | . . | . . | . . | . . | . . | . . | . . Ornithomimosauria = Clade(Ornithomimus, Pelecanimimus)
   8   | . . | . . | . . | . . | . . | . . | . . | . . | . . | . . | . . Ornithomimidae sensu Smith, Galton 1990
   5   | . . | . . | . . | . . | . . | . . | . . | . . | . . | . . | . . | . . Ornithomiminae implied Marsh 1890
   3   | . . | . . | . . | . . | . . | . . | . . | . . | . . | . . | . . | . . | . . Ornithomimini implied Marsh 1890
  43   | . . | . . | . . | . . | . . | . . | . . | . . | . . Maniraptora sensu Holtz 1996 = Clade(Neornithes not Ornithomimus)
  41   | . . | . . | . . | . . | . . | . . | . . | . . | . . | . . Clade(Neornithes, Oviraptor)
  22   | . . | . . | . . | . . | . . | . . | . . | . . | . . | . . | . . Clade(Oviraptor not Neornithes)
   9   | . . | . . | . . | . . | . . | . . | . . | . . | . . | . . | . . | . . Oviraptorosauria sensu Padian, Hutchinson, Holtz 1998
   3   | . . | . . | . . | . . | . . | . . | . . | . . | . . | . . | . . | . . | . . Caenagnathidae = Clade(Chirostenotes not Oviraptor)
   2   | . . | . . | . . | . . | . . | . . | . . | . . | . . | . . | . . | . . | . . | . . Caenagnathinae
   5   | . . | . . | . . | . . | . . | . . | . . | . . | . . | . . | . . | . . | . . Oviraptoridae = Clade(Oviraptor not Chirostenotes)
  10   | . . | . . | . . | . . | . . | . . | . . | . . | . . | . . | . . | . . Therizinosauria sensu D. A. Russell 1997
   9   | . . | . . | . . | . . | . . | . . | . . | . . | . . | . . | . . | . . | . . Therizinosauroidea sensu D. A. Russell, Dong 1995
   6   | . . | . . | . . | . . | . . | . . | . . | . . | . . | . . | . . | . . | . . | . . Therizinosauridae = Clade(Therizinosaurus not Alxasaurus)
   5   | . . | . . | . . | . . | . . | . . | . . | . . | . . | . . | . . | . . | . . | . . | . . Therizinosaurinae
  19   | . . | . . | . . | . . | . . | . . | . . | . . | . . | . . | . . Paraves = Clade(Neornithes not Oviraptor)
  14   | . . | . . | . . | . . | . . | . . | . . | . . | . . | . . | . . | . . Eumaniraptora = Clade(Neornithes, Deinonychus)
  10   | . . | . . | . . | . . | . . | . . | . . | . . | . . | . . | . . | . . | . . Deinonychosauria sensu Gauthier 1986 = Clade(Deinonychus not Neornithes)
   4   | . . | . . | . . | . . | . . | . . | . . | . . | . . | . . | . . | . . | . . | . . Dromaeosauridae = Clade(Dromaeosaurus, Velociraptor)
   3   | . . | . . | . . | . . | . . | . . | . . | . . | . . | . . | . . | . . | . . | . . | . . Velociraptorinae = Clade(Velociraptor not Dromaeosaurus)
   5   | . . | . . | . . | . . | . . | . . | . . | . . | . . | . . | . . | . . Alvarezsauria
   5   | . . | . . | . . | . . | . . | . . | . . | . . | . . | . . | . . | . . | . . Alvarezsauridae
   3   | . . | . . | . . | . . | . . | . . | . . | . . | . . | . . | . . | . . | . . | . . Mononykinae = Clade(Mononykus, Parvicursor, Shuvuuia)
   7   | . . | . . | . . | . . | . . | . . | . . | . . | . . Troodontidae sensu Varricchio 1997
  13   | . . | . . | . . | . . | . . | . . | . . | . . | . . Tyrannosauroidea = Clade(Tyrannosaurus not Ornithomimus, Neornithes)
   8   | . . | . . | . . | . . | . . | . . | . . | . . | . . | . . Tyrannosauridae
   6   | . . | . . | . . | . . | . . | . . | . . | . . | . . | . . | . . Tyrannosaurinae = Clade(Tyrannosaurus not Alectrosaurus, Aublysodon)
   3   | . . | . . | . . | . . | . . | . . | . . | . . | . . | . . | . . | . . Tyrannosaurini = Clade(Tyrannosaurus not Albertosaurus, Gorgosaurus)
   6   | . . | . . | . . | . . | . . | . . Spinosauria
   5   | . . | . . | . . | . . | . . | . . | . . Spinosauridae = Clade(Spinosaurus, Baryonyx)
   2   | . . | . . | . . | . . | . . | . . | . . | . . Baryonychinae implied Charig, Milner 1986 = Clade(Baryonyx not Spinosaurus)
   3   | . . | . . | . . | . . | . . | . . | . . | . . Spinosaurinae implied Stromer 1915 = Clade(Spinosaurus not Baryonyx)
   2   | . . | . . | . . | . . | . . | . . | . . | . . | . . Irritatorini implied Martill, al. 1996
 169   | . . Ornithischia sensu Padian, May 1993 = Clade(Triceratops not Neornithes)
 159   | . . | . . Genasauria = Clade(Triceratops, Ankylosaurus)
 102   | . . | . . | . . Cerapoda = Clade(Triceratops, Iguanodon)
  38   | . . | . . | . . | . . Marginocephalia = Clade(Triceratops, Pachycephalosaurus)
  11   | . . | . . | . . | . . | . . Pachycephalosauria = Clade(Pachycephalosaurus not Triceratops)
   9   | . . | . . | . . | . . | . . | . . Goyocephalia = Clade(Goyocephale, Pachycephalosaurus)
   7   | . . | . . | . . | . . | . . | . . | . . Homalocephaloidea = Clade(Homalocephale, Pachycephalosaurus)
   6   | . . | . . | . . | . . | . . | . . | . . | . . Pachycephalosauridae
   5   | . . | . . | . . | . . | . . | . . | . . | . . | . . Pachycephalosaurinae
   2   | . . | . . | . . | . . | . . | . . | . . | . . | . . | . . Pachycephalosaurini
  26   | . . | . . | . . | . . | . . Ceratopsia = Clade(Ceratops not Pachycephalosaurus)
  25   | . . | . . | . . | . . | . . | . . Neoceratopsia = Clade(Ceratops not Psittacosaurus)
  20   | . . | . . | . . | . . | . . | . . | . . Coronosauria = Clade(Triceratops, Protoceratops)
  17   | . . | . . | . . | . . | . . | . . | . . | . . Ceratopsoidea = Clade(Ceratops, Montanoceratops)
  16   | . . | . . | . . | . . | . . | . . | . . | . . | . . Ceratopsomorpha = Clade(Ceratops, Zuniceratops)
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14     | . . | . . | . . | . . | . . | . . | . . | . . | . . | . . Ceratopsidae = Clade(Ceratops, Centrosaurus)
 7     | . . | . . | . . | . . | . . | . . | . . | . . | . . | . . | . . Centrosaurinae = Clade(Centrosaurus not Ceratops)
 2     | . . | . . | . . | . . | . . | . . | . . | . . | . . | . . | . . | . . Centrosaurini
 4     | . . | . . | . . | . . | . . | . . | . . | . . | . . | . . | . . | . . Pachyrhinosaurini
 7     | . . | . . | . . | . . | . . | . . | . . | . . | . . | . . | . . Ceratopsinae = Clade(Ceratops not Centrosaurus)
 2     | . . | . . | . . | . . | . . | . . | . . | . . | . . | . . | . . | . . Chasmosaurini
 4     | . . | . . | . . | . . Heterodontosauridae
 3     | . . | . . | . . | . . | . . Heterodontosaurinae
 2     | . . | . . | . . | . . | . . | . . Heterodontosaurini
60     | . . | . . | . . | . . Ornithopoda = Clade(Iguanodon not Triceratops)
 2     | . . | . . | . . | . . | . . Zephyrosauridae
 2     | . . | . . | . . | . . | . . Othnieliidae
 2     | . . | . . | . . | . . | . . | . . Othnieliinae
48     | . . | . . | . . | . . | . . Euornithopoda = Clade(Iguanodon, Hypsilophodon)
46     | . . | . . | . . | . . | . . | . . Iguanodontia = Clade(Iguanodon not Hypsilophodon)
41     | . . | . . | . . | . . | . . | . . | . . Euiguanodontia = Clade(Iguanodon, Gasparinisaura)
40     | . . | . . | . . | . . | . . | . . | . . | . . Dryomorpha = Clade(Dryosaurus, Iguanodon)
 2     | . . | . . | . . | . . | . . | . . | . . | . . | . . Dryosauridae
38     | . . | . . | . . | . . | . . | . . | . . | . . | . . Ankylopollexia = Clade(Parasaurolophus, Camptosaurus)
 2     | . . | . . | . . | . . | . . | . . | . . | . . | . . | . . Camptosauridae
34     | . . | . . | . . | . . | . . | . . | . . | . . | . . | . . Styracosterna = Clade(Parasaurolophus not Camptosaurus)
30     | . . | . . | . . | . . | . . | . . | . . | . . | . . | . . | . . Iguanodontoidea = Clade(Iguanodon, Hadrosaurus)
29     | . . | . . | . . | . . | . . | . . | . . | . . | . . | . . | . . | . . Hadrosauroidea = Clade(Hadrosaurus not Iguanodon)
26     | . . | . . | . . | . . | . . | . . | . . | . . | . . | . . | . . | . . | . . Hadrosauridae
21     | . . | . . | . . | . . | . . | . . | . . | . . | . . | . . | . . | . . | . . | . . Euhadrosauria = Clade(Hadrosaurus, Lambeosaurus)
10     | . . | . . | . . | . . | . . | . . | . . | . . | . . | . . | . . | . . | . . | . . | . . Lambeosaurinae = Clade(Lambeosaurus not Hadrosaurus)
 3     | . . | . . | . . | . . | . . | . . | . . | . . | . . | . . | . . | . . | . . | . . | . . | . . Parasaurolophini
 6     | . . | . . | . . | . . | . . | . . | . . | . . | . . | . . | . . | . . | . . | . . | . . | . . Lambeosaurini
11     | . . | . . | . . | . . | . . | . . | . . | . . | . . | . . | . . | . . | . . | . . | . . Hadrosaurinae = Clade(Hadrosaurus not Lambeosaurus)
 2     | . . | . . | . . | . . | . . | . . | . . | . . | . . | . . | . . | . . | . . | . . | . . | . . Maiasaurini
 3     | . . | . . | . . | . . | . . | . . | . . | . . | . . | . . | . . | . . | . . | . . | . . | . . Hadrosaurini
 4     | . . | . . | . . | . . | . . | . . | . . | . . | . . | . . | . . | . . | . . | . . | . . | . . Edmontosaurini
 2     | . . | . . | . . | . . | . . | . . | . . | . . | . . | . . | . . | . . | . . | . . | . . | . . Saurolophini
55     | . . | . . | . . Thyreophora = Clade(Ankylosaurus not Triceratops)
53     | . . | . . | . . | . . Thyreophoroidea = Clade(Ankylosaurus not Scutellosaurus)
51     | . . | . . | . . | . . | . . Eurypoda = Clade(Ankylosaurus, Stegosaurus)
12     | . . | . . | . . | . . | . . | . . Stegosauria = Clade(Stegosaurus not Ankylosaurus)
10     | . . | . . | . . | . . | . . | . . | . . Stegosauridae = Clade(Stegosaurus not Huayangosaurus)
 5     | . . | . . | . . | . . | . . | . . | . . | . . Stegosaurinae
 2     | . . | . . | . . | . . | . . | . . | . . | . . | . . Stegosaurini
38     | . . | . . | . . | . . | . . | . . Ankylosauria sensu Carpenter 1997 = Clade(Ankylosaurus not Stegosaurus)
36     | . . | . . | . . | . . | . . | . . | . . Ankylosauroidea = Clade(Ankylosaurus, Nodosaurus)
 2     | . . | . . | . . | . . | . . | . . | . . | . . Stegopeltini
13     | . . | . . | . . | . . | . . | . . | . . | . . Nodosauridae = Clade(Nodosaurus not Ankylosaurus)
 4     | . . | . . | . . | . . | . . | . . | . . | . . | . . Edmontoniinae
 3     | . . | . . | . . | . . | . . | . . | . . | . . | . . Panoplosaurinae
21     | . . | . . | . . | . . | . . | . . | . . | . . Ankylosauridae = Clade(Ankylosaurus not Nodosaurus)
 6     | . . | . . | . . | . . | . . | . . | . . | . . | . . Polacanthinae = Clade(Polacanthus not Ankylosaurus, Shamosaurus)
 3     | . . | . . | . . | . . | . . | . . | . . | . . | . . | . . Polacanthini
 2     | . . | . . | . . | . . | . . | . . | . . | . . | . . Shamosaurinae = Clade(Shamosaurus not Ankylosaurus, Polacanthus)
10     | . . | . . | . . | . . | . . | . . | . . | . . | . . Ankylosaurinae = Clade(Ankylosaurus not Polacanthus, Shamosaurus)
 8     | . . | . . | . . | . . | . . | . . | . . | . . | . . | . . Syrmosaurini
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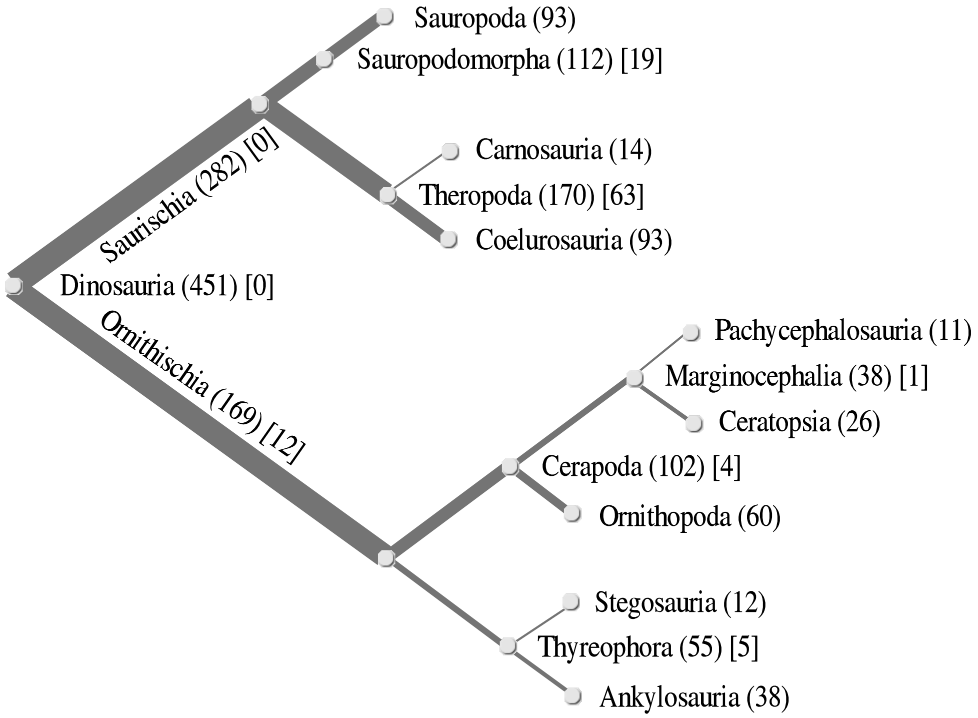

Fig. 1. Breakdown of dinosaur diversity by phylogeny. The number of genera included in each clade is indicated in parentheses. Non-terminal clades additionally have, in square brackets, the number of included genera that are not also included in one of the figured subclades. For example, there are 63 theropods that are neither carnosaurs nor coelurosaurs. The thickness of the lines is proportional to the number of genera in the clades they represent.

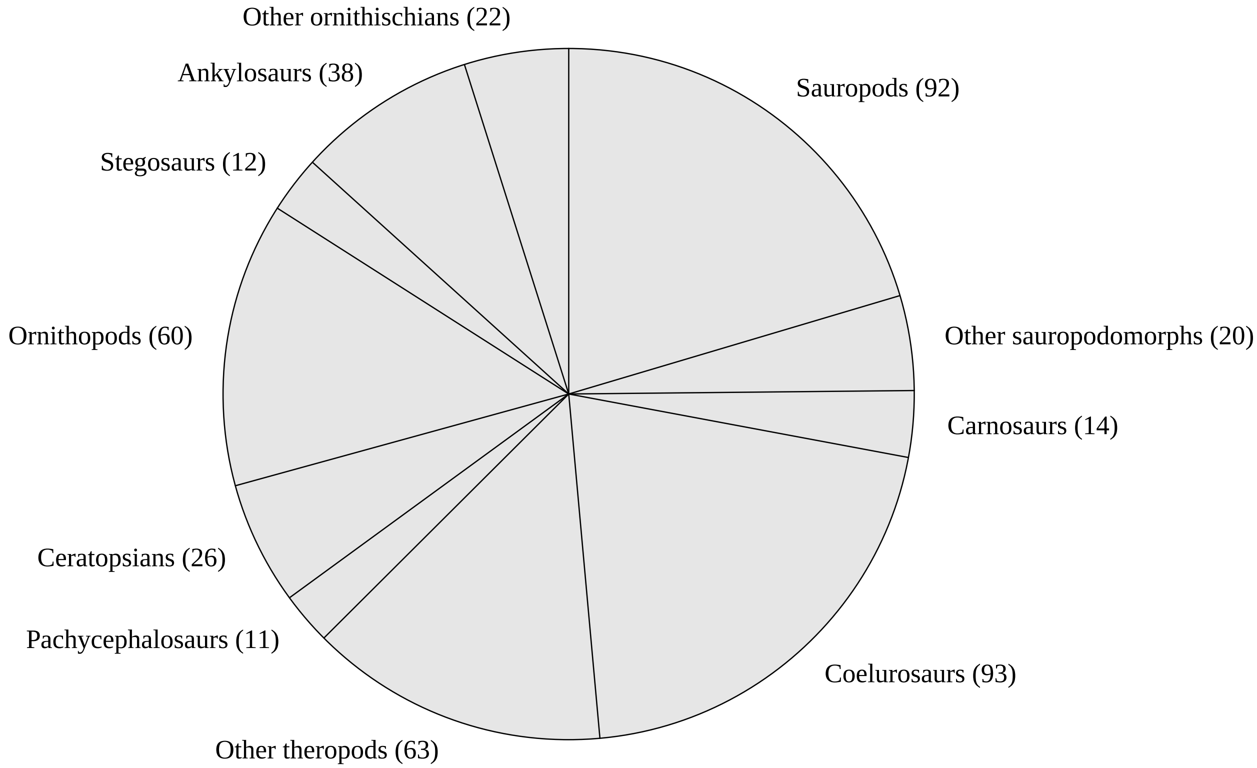

Fig. 2. Breakdown of dinosaurian diversity by high-level taxa. ‘‘Other sauropodomorphs’’ are the ‘‘prosauropods’’ sensu lato. ‘‘Other theropods’’ include coelophysoids, neoceratosaurs, torvosaurs (= megalosaurs) and spinosaurs. ‘‘Other ornithischians’’ are basal forms, including heterodontosaurs and those that fall into Marginocephalia or Thyreophora but not into a figured subclade.

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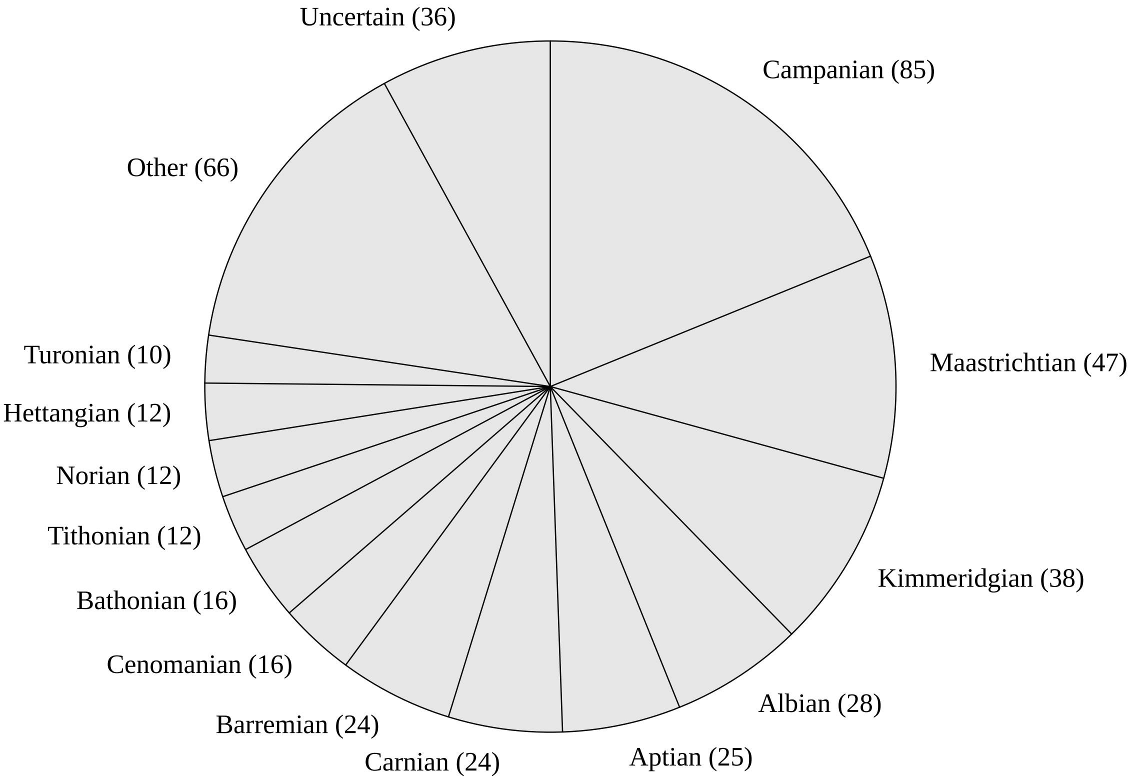

Fig. 3. Breakdown of dinosaurian diversity showing the most productive ages. The ‘‘uncertain’’ segment represents genera whose age is known only to the epoch level.

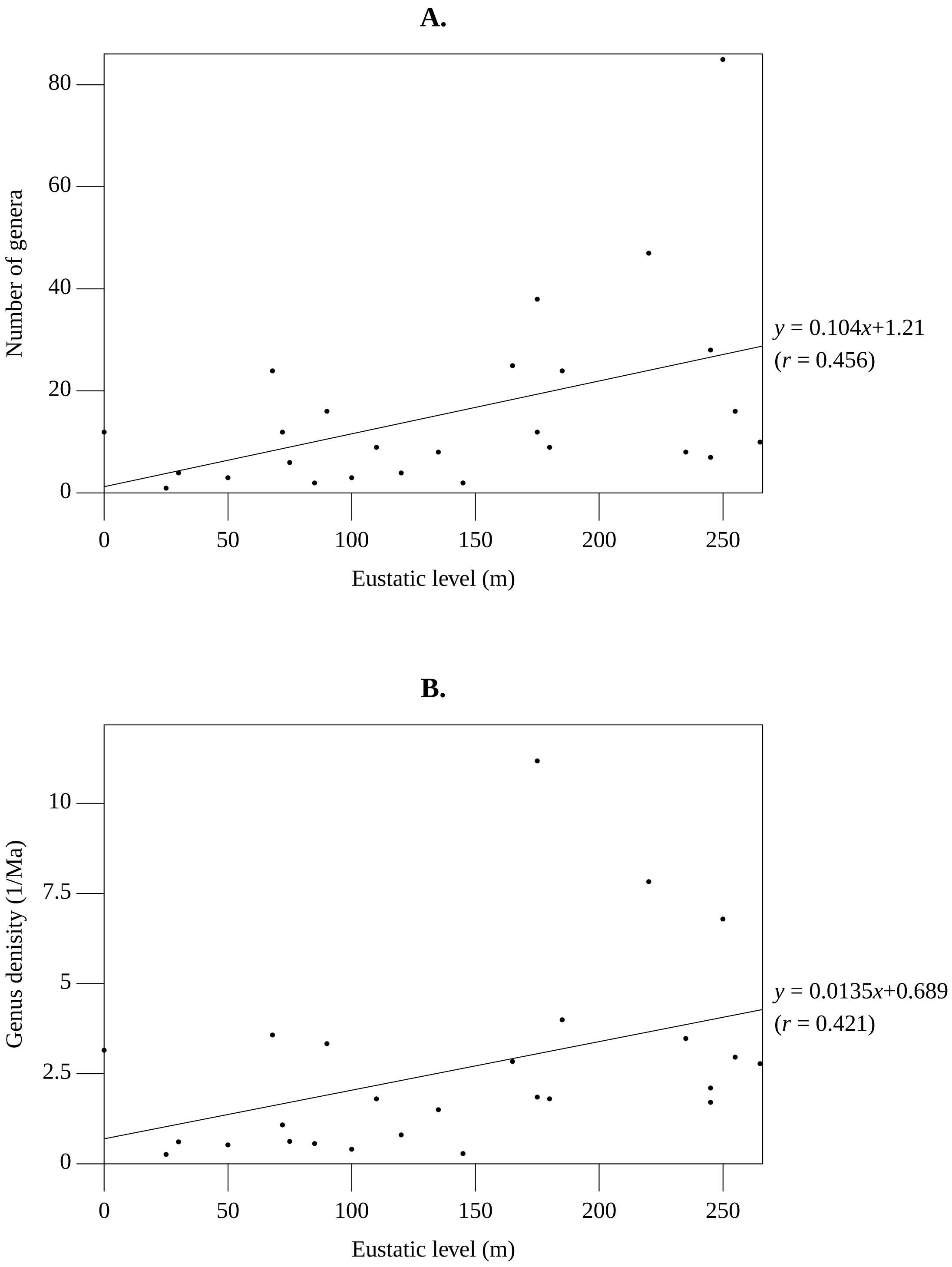

Fig. 4. Correlation between eustatic level (measured in meters above the present-day level) and dinosaur diversity. **A.** Eustatic level vs. number of new dinosaur genera per age. **B.** Eustatic level vs. genus density. Solid lines are best fits for the data. Correlation coefficients (*r*) appear below the regression equations. Data on eustatic levels during

each age from Figures 3-5 of Haq *et al.* 1987.

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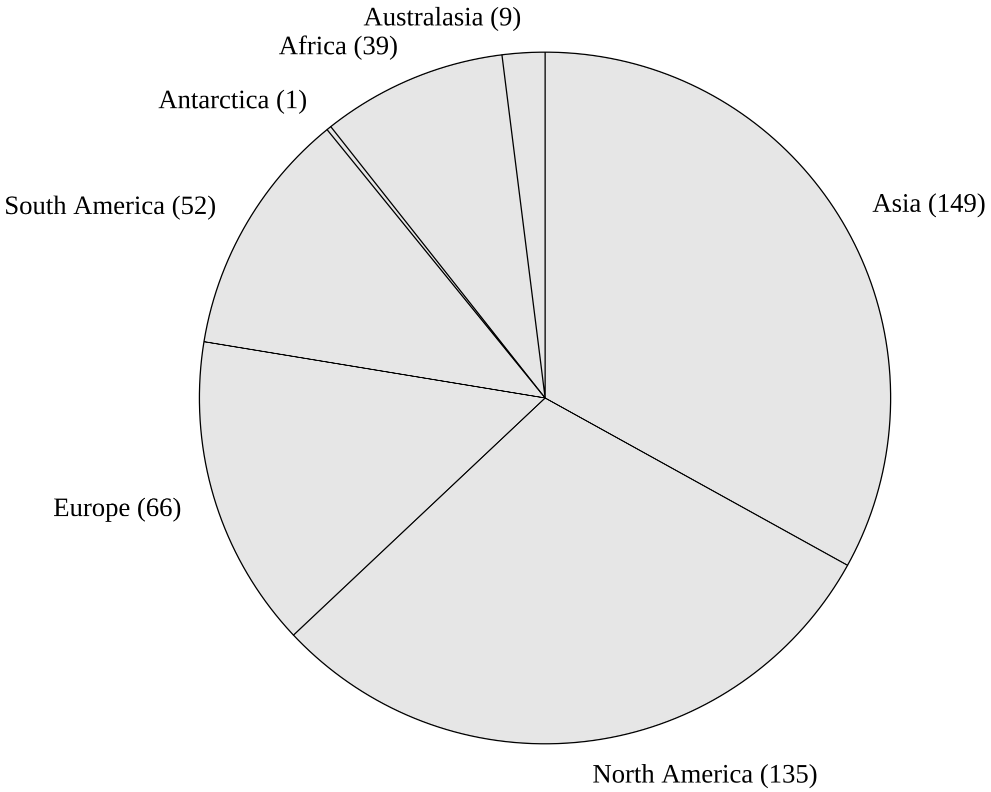

Fig. 5. Breakdown of dinosaurian diversity showing the relative productivity of the continents.

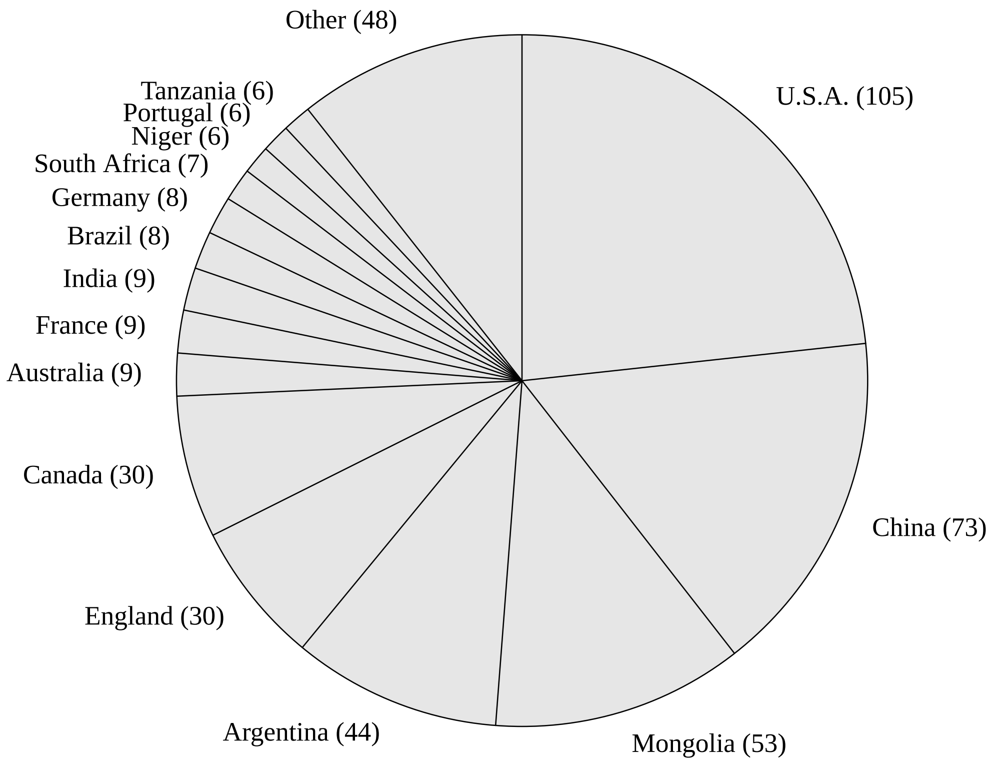

Fig. 6. Breakdown of dinosaurian diversity showing the most productive countries. No country not listed here has yielded more than five new dinosaur genera.

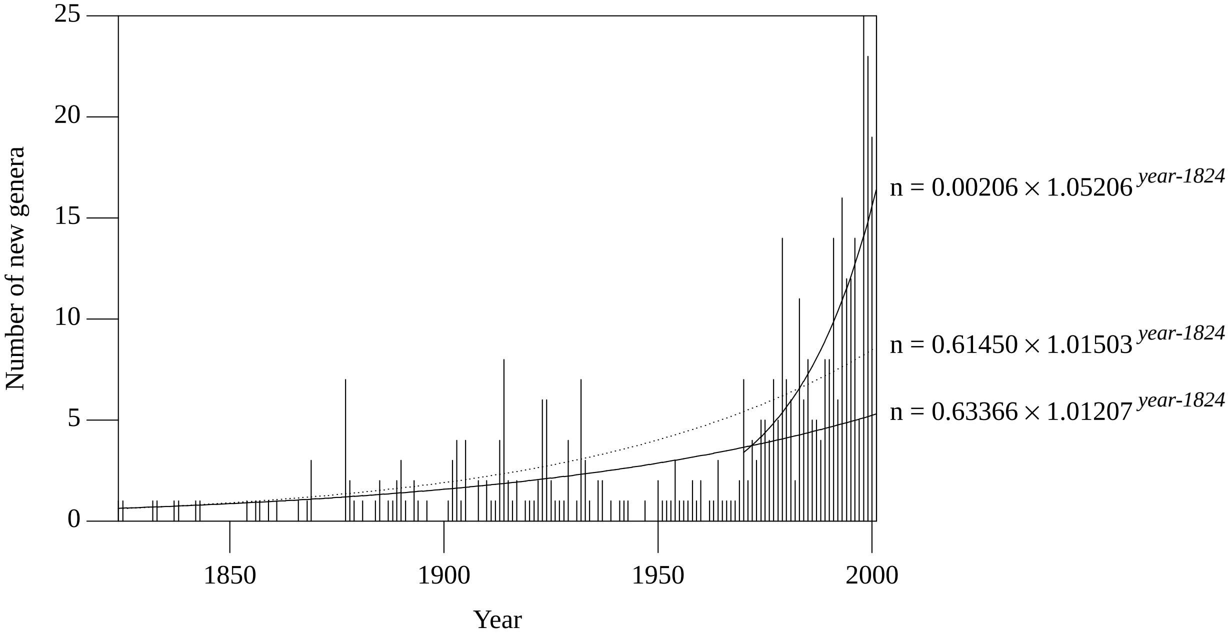

Fig. 7. Number of new dinosaur genera by year. The lines represent best-fit exponential curves for the number of new genera per year, as follows: the long solid line takes all the data into account; the long dotted line omits the anomalously low numbers of new genera during the four decades from 1930 to 1969, before the dinosaur renaissance; and the short solid line uses only the counts from the renaissance era, from 1970 onwards.

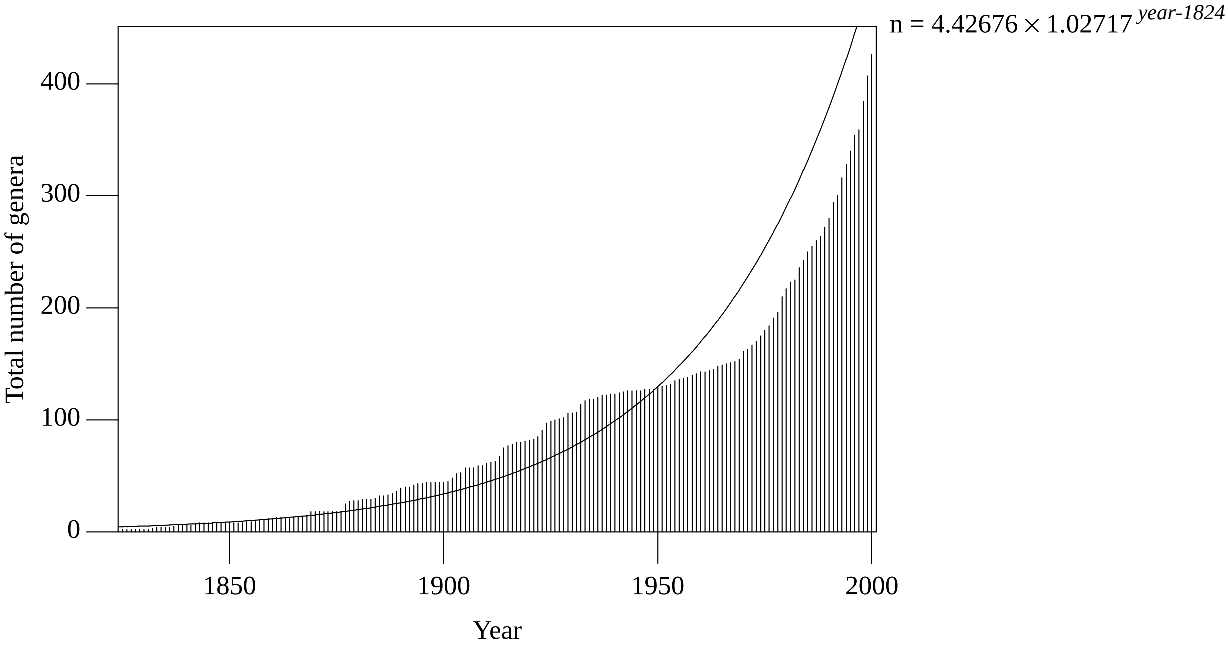

Fig. 8. Total number of known dinosaur genera by year. The solid line is a best-fit exponential curve, which emphasises the levelling off in the 1930s-1960s

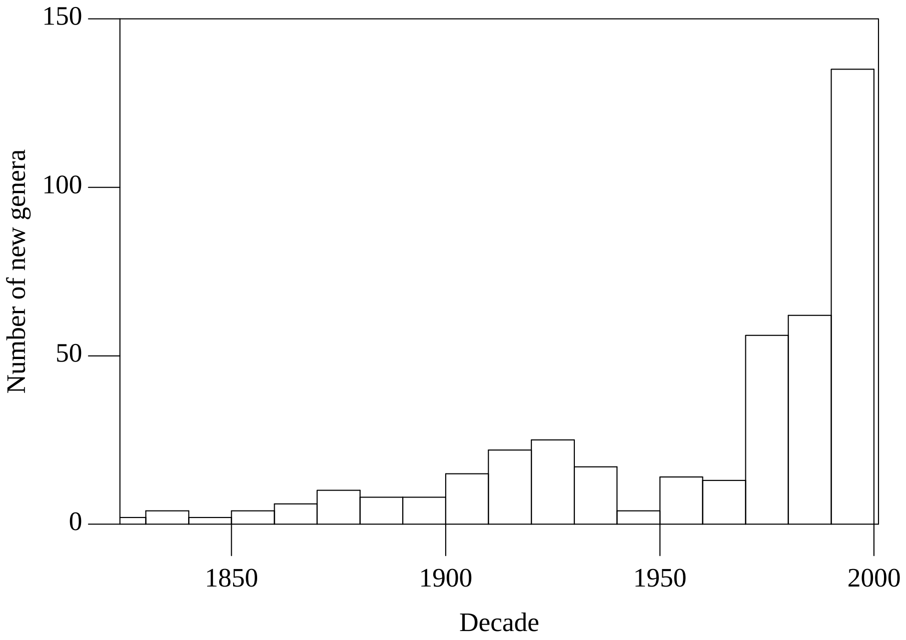

Fig. 9. Number of new dinosaur genera by decade.

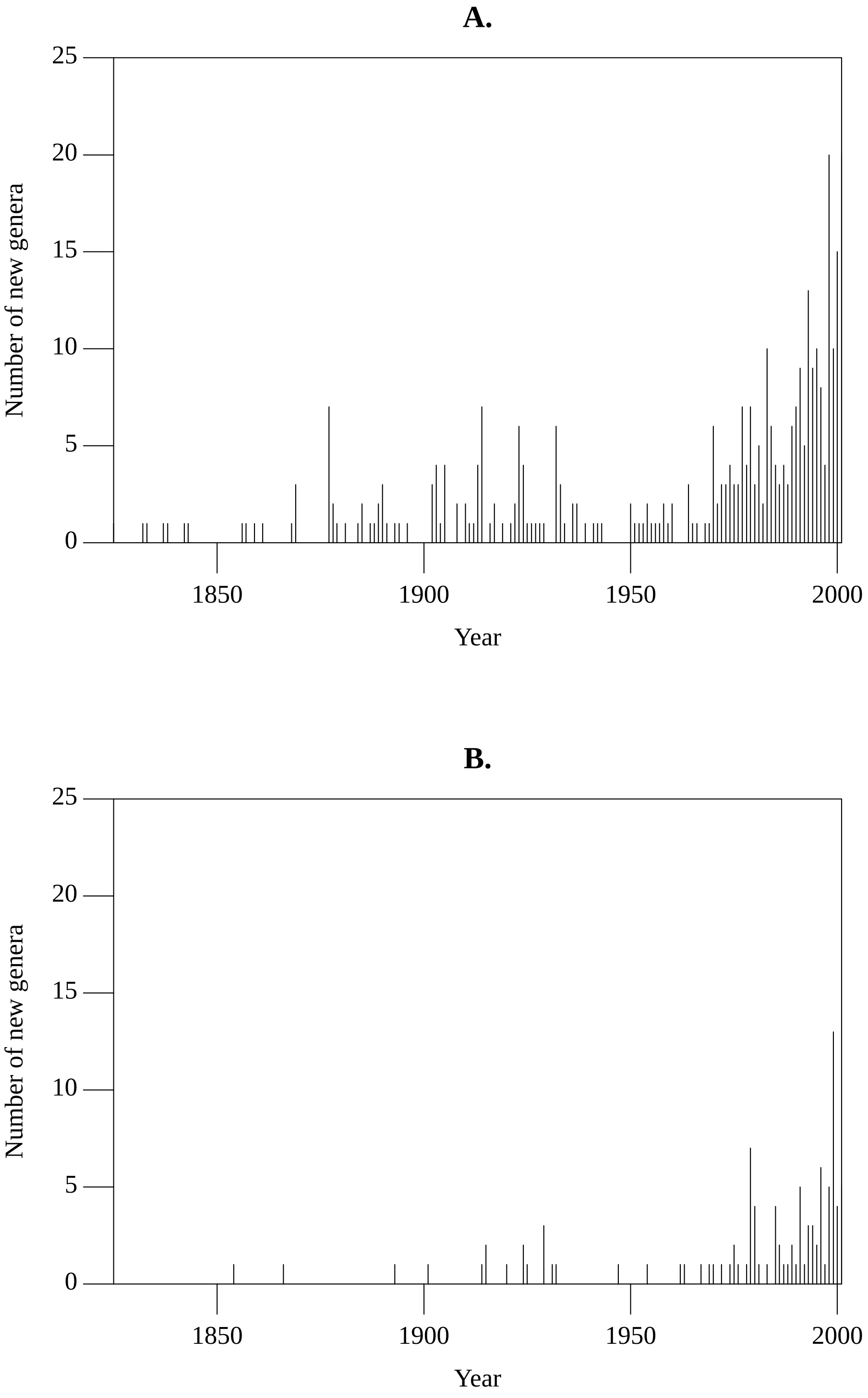

Fig. 10. Number of new dinosaur genera by year, graphed separately for the two supercontinents. **A.** Laurasia. **B.** Gondwana. Note that ‘‘Gondwana’’ in the sense used here includes only the modern southern continents Africa, Antarctica, Australasia and South America, omitting parts of Europe such as Italy and Austria that were part of the

southern landmass during the Mesozoic.