DINOSAUR DIVERSITY ANALYSED BY CLADE, AGE, PLACE AND YEAR OF DESCRIPTION

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INTRODUCTION

ALTHOUGH FUNDAMENTAL to Mesozoic palaeoecology, dinosaur diversity has received 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) and Fastovsky *et al*. (2004).

This study presents four analyses based on a database incorporating dinosaurian genera considered valid as of 31 March 2003. This database was compiled from the literature, principally from the publications of Glut (1997, 2000, 2002, 2003). Aves (*Archaeopteryx* + Neornithes) is excluded and *nomina nuda* and *nomina dubia* are omitted. The database was analysed in terms of the number of valid genera within each major clade, stratigraphic stage, place of discovery and year of description.

Taphonomy, diagenesis, erosion, collecting, preparation and publication present a series of filters that separate apparent from actual diversity. These results, based on apparent diversity, should therefore be interpreted with caution.

RESULTS

Number of genera by clade

Figure 1A shows the phylogeny used in this study and the number of genera in each clade. It is surprising that saurischians (300 genera) outnumber ornithischians (180 genera) so heavily – they are about 83% more diverse. More surprising still is the predominance of Theropoda: the total of 176 genera exceeds that for Sauropodomorpha (119 genera) and is only four fewer than Ornithischia (180 genera). Theropods account for 36% of all dinosaur genera, despite having a much more conservative body-plan than the ornithischians. If the clades Ornithomimosauria, Therizinosauroidea and Oviraptorosauria are considered herbivorous or omnivorous (see Barrett 2005) then the remaining carnivorous theropods number 139 genera (29% of all dinosaur genera). This is an unusually high proportion of total diversity for carnivores to attain within an ecosystem. The 95 coelurosaur genera represent 54% of Theropoda. Wilson and Upchurch's (2003) observation that titanosaurs represent approximately one third of sauropod diversity is corroborated by this study: they supply 32 of the 99 sauropod genera. This contrasts with Curry Rogers and Forster's (2004) assertion that titanosaurs comprise nearly half of sauropod genera.

Number of genera by age

Figure 1B shows how dinosaur diversity varied through the Mesozoic. Diversity generally increased through time, with 40 genera first appearing in the fossil record in the Triassic, 134 in the Jurassic, and 310 in the Cretaceous. This imbalance is partly due to the origin of the dinosaurs in the Late Triassic (Carnian) only, but even when diversity across the three periods is normalised by duration, the trend of increasing diversity is evident. The 40 Triassic genera arose in the 21.7 million years from the beginning of the Carnian to the end of Rhaetian, giving a genus density, or GD, of 1.84 genera per million years. The 134 Jurassic genera arose in 61.5 million years (GD 2.18) and the 310 Cretaceous genera in 79.2 million years (GD 3.91).

The large number of genera from the Carnian (19), the earliest age from which dinosaurs are known, implies that initial diversification was rapid. Of those genera, five are ornithischians (all of which are too basal to be assigned to major clades), 12 are saurischians and two are indeterminate. Of the saurischians, three are herrerasaurs, five are sauropodomorphs (all of them prosauropods) and the remaining four are theropods, of which only *Coelophysis* is clearly a neotheropod. Seventeen more genera are found in the Norian, including the earliest known sauropod, *Isanosaurus.*

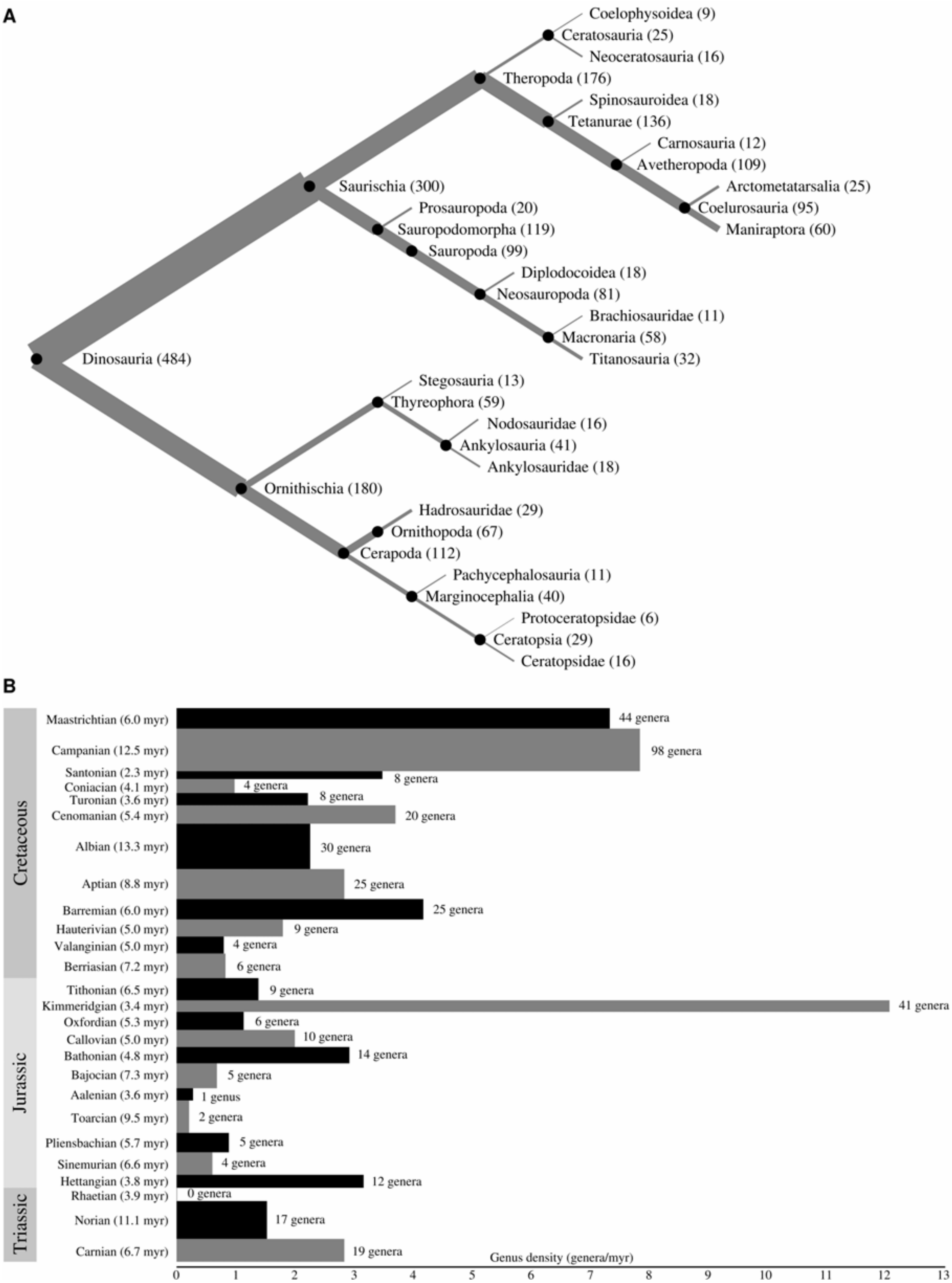

Figure 1. Dinosaur diversity. A, cladogram of Dinosauria indicating sizes of illustrated clades: thickness of branches is proportional to number of genera, including those in subclades; B, diversity by stratigraphic age: thickness of bars indicates duration of age, length indicates genus density (genera per myr) and area indicates number of genera.

The six most productive stages are the Campanian (98 genera), Maastrichtian (44), Kimmeridgian (41), Albian (30), Aptian (25) and Barremian (25). These stages total 50 million years (31% of the Carnian–Maastrichtian interval) and produced 263 of the 484 genera (54%).

GD gives a more realistic indication of diversity in each age than simple genus counts. Three ages stand out as much more diverse than others: the Kimmeridgian (GD 12.06), Campanian (7.84) and Maastrichtian (7.33). These ages total 21.9 million years (13%) and supply 183 genera (38%). No other stage has a GD greater than 4.17. While sampling biases account for some of the irregularity, there does appear to have been a substantial, sustained diversification in the last twenty million years of the Mesozoic.

Genus counts correlate only weakly with global sea-level (R^2 = 0.208), and GD more weakly still (R^2 = 0.177). Thus, this study does not support the claims of Haubold (1990) and Hunt *et al*. (1994) that taphonomic biases cause apparent dinosaur diversity to be highest at times of highest sea-level.

Number of genera by place

Asia was the most productive continent with 166 genera, followed by North America (141), Europe (75), South America (52), Africa (38), Australasia (11), and finally Antarctica (1).

Three countries account for more than half of all dinosaur diversity, with 247 genera between them: the USA (108), China (80), and Mongolia (59). The top six countries also include Argentina (46), England (34), and Canada (32), and together provide 359 genera, nearly three quarters of the total.

All 32 Canadian genera are from Alberta. The most productive American states are Montana (17), Wyoming (16), Colorado (16), Utah (13) and New Mexico (12), which together account for two thirds of all American dinosaurs.

Number of genera by year of description

Apart from a 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 23 in 1998. Aggregating the decades, the tendency is for the naming rate to grow exponentially. The exception is a four-decade fall-off from the 1930s to the 1960s, which corresponds with a period in which mammal palaeontology dominated the field (Bakker 1975). This was brought to an abrupt end in the 1970s by the "dinosaur renaissance", widely considered to have been catalysed by Ostrom's descriptions of *Deinonychus antirrhopus* (Ostrom 1969*a*, *b*). After this period, the exponential naming rate recovered as though the trough of the 1930s–60s had never happened.

The first year to yield a large crop of new dinosaurs was 1877, at the height of the Marsh-Cope rivalry. The eight genera named in that year (all but *Titanosaurus* and *Dryptosaurus* from the Morrison Formation), more than doubled the previous record of three (named in 1869) and increased the total number of dinosaurian genera then known by nearly a quarter.

The last year in which no new dinosaurs were described was 1965; the last before that was 1956. New dinosaurs have therefore been described in every year but one of the last 47. Until 1977, only four years (1877, 1914, 1924 and 1932) yielded more than six new genera. Since then, 19 years – more than two thirds – have done so. Of the 484 genera valid at the cut-off point for this study, just over half (243) had been described in the previous 23 years (1981–2003). Naming the first half had taken 156 years (1825–1980).

The origin of dinosaur palaeontology in the northern hemisphere, and the subsequent increase of work in the southern hemisphere, is reflected in the history of new genera from the two Mesozoic supercontinents (counting India and Croatia as Gondwanan). As recently as 1913, when 81 dinosaur genera had been named, only six were Gondwanan: *Massospondylus* (1854, South Africa), *Euskelosaurus* (1866, South Africa), *Titanosaurus* (1877, India), *Argyrosaurus* (1893, Argentina), *Genyodectes* (1901, Argentina) and *Algoasaurus* (1904, South Africa). At the end of March 2003, the 373 Laurasian genera (77%) still dominate the 111 Gondwanan genera (23%), but the gap is closing.

DISCUSSION

First occurrences and ghost lineages

The earliest and next known genera for some clades are here shown, together with the elapsed time (myr) between the ages in which these genera originated, indicating the minimum length of the ghost lineage from their common ancestor:

Sauropoda: *Isanosaurus* (Norian) and *Vulcanodon* (?Hettangian), 15.0 myr;
Spinosauroidea: *Magnosaurus* (?Aalenian), *Poekilopleuron* and others (Bathonian), 10.9 myr;
Avetheropoda: *Eshanosaurus* (Hettangian) and *Cryolophosaurus* (?Pliensbachian), 10.4 myr;
Carnosauria: *Cryolophosaurus* (?Pliensbachian) and ?*Piatnitzkysaurus* (Callovian), 30.9 myr;
Coelurosauria: *Eshanosaurus* (Hettangian) and *Proceratosaurus* (Bathonian), 36.5 myr;
Maniraptora: *Eshanosaurus* (Hettangian), *Ornitholestes* and others (Kimmeridgian), 51.6 myr;
Ankylosauria: *Sarcolestes* (Callovian) and *Dracopelta* (Kimmeridgian), 10.3 myr;
Pachycephalosauria: *Stenopelix* (Berriasian) and *Yaverlandia* (Barremian), 17.2 myr;
Ceratopsia: *Chaoyangsaurus* (Bathonian) and *Psittacosaurus* (Valanginian), 32.2 myr;
Ornithopoda: *Yandusaurus* (Bathonian), *Camptosaurus* and others (Kimmeridgian); 15.1 myr.

These results must be interpreted with caution, as the ages of some of the cited genera (e.g. *Magnosaurus*) are not certain, and the taxonomic affinities of others have been disputed. Specifically, M. Lamanna (personal communication cited in Kirkland and Wolfe 2001) has argued that the type dentary of *Eshanosaurus* is that of a prosauropod – an identification which, if accepted, would significantly reduce the ghost lineages for Avetheropoda, Coelurosauria and Maniraptora. The pachycephalosaurian identity of *Yaverlandia* has also been questioned. If it is removed from that clade, then the next oldest pachycephalosaur is *Goyocephale* (?Santonian), extending the pachycephalosaur ghost lineage to 58.4 myr. The mean of these ghost lineages is 23 myr, indicating that the early diversification of these clades remains poorly understood.

The Kimmeridgian sauropod boom

The Kimmeridgian saw an unparalleled boom in sauropod diversity, with 19 sauropod genera appearing during its 3.4 million years. The “sauropod genus density” of 5.59 is equivalent to a new sauropod every 179,000 years. The next most sauropod-dense ages were the Hauterivian (1.40) and Maastrichtian (1.00). Kimmeridgian sauropods include all seven of the diplodocids (*sensu* Taylor and Naish 2005); and of these, all but the Portuguese *Lourinhasaurus* are from the Morrison Formation. So this clade, widely considered successful, was in fact extremely limited in time and space.

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