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THE SHAPE OF MESOZOIC DINOSAUR RICHNESS: A REASSESSMENT

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Abstract—The premise that the number of dinosaur taxa increased near the end of the Cretaceous Period is not accepted based on a simple tabulation of valid dinosaur species during the late Campanian, early Maastrichtian and late Maastrichtian. The data demonstrate that the both the number of genera and species declined toward the K-boundary.

INTRODUCTION

The extinction "event" of the non-avian dinosaurs at the end of the Cretaceous Period has been the focus of much attention over the past two decades. Unfortunately, most of the discussions have centered on the thesis that an asteroid impact somehow caused, or more precisely, selected, non-avian dinosaurs for extinction. Largely ignored are the facts that: (1) the non-avian dinosaurs are a polyphyletic (unnatural) group; (2) that dinosaur extinction occurred throughout the entire Mesozoic Era; and (3) the terminal extinction is really no different than some of those extinctions that preceded it (Sullivan, 1987). Here, I present data that demonstrate there is no evidence for an increase in the number of dinosaur species during the last 15 million years of the Cretaceous (late Campanian through late Maastrichtian), as claimed by Fastovsky et al. (2004).

MEASURING DINOSAUR DIVERSTY

The recent assessment of changing dinosaur diversity presented by Fastovsky et al. (2004) based on data published in the new edition (2nd) of *The Dinosauria* (Weishampel et al., 2004) is flawed, from both the perspective of dinosaur taxonomic resolution and biostratigraphic distribution. The premise that (non-avian) dinosaur richness (generic diversity) increased throughout the Mesozoic Era needs further rigorous scrutiny, as does the claim that this apparent increase in richness is demonstrable in the late Campanian-Maastrichtian interval.

The notion that measuring dinosaur genera is a precise quantification of "richness" is somewhat misleading, and has been critiqued elsewhere by Archibald (2005). Moreover, a true measure of dinosaur richness does not require statistical testing using rarefaction as claimed by Fastovsky et al. (2005).

The method of determining generic richness proposed by Fastovsky et al. (2004, 2005) is here rejected on the grounds that genera in themselves do not reflect true diversity and that it is at the level of species that evolution and extinction take place (Newell, 1982). For example, a taxon such as the ceratopsid *Chasmosaurus*, known by four species in the late Campanian, is reduced to one taxon, using their "genera count method." The hadrosaurid *Parasaurolophus*, known by three species in the late Campanian, is also reduced to one. In contrast, the genus *Tyrannosaurus*, only known by one Maastrichtian species, is also counted as one taxon. Although most of the dinosaur genera are monospecific, the resultant tabulation produced by Fastovsky et al. (2004) is inaccurate because they do not account for individual species. Other issues, such as tabulating taxa that are either "form genera" (e.g., the long-ranging *Richardoestesia*), recognition of taxa that are arguably *nomina dubia* (e.g., *Gravotholus*), or synonyms (e.g., *Colepiocephale*, *Hanssuesia* vs. *Stegoceras* [*sensu lato*]), also skew the results. Other taxa (e.g., *Judinoris nogotsavensis*, *Titanosaurus indicus*, *Euronychodon portucalensis*, and others) are known from inadequate material. It should be noted that although *The Dinosauria* is an admirable compilation of data, not all these data are correct or universally agreed upon.

Assessing biostratigraphic distribution can also be misleading. Some taxa (e.g., *Rhabdodon septmanicus*) reported in Weishampel et al. (2004) as being from the Campanian-Maastrichtian are based on a single specimen, so they do not have a broad temporal distribution. Many of the specimens cited as being Maastrichtian from South America, Asia, and elsewhere, lack the necessary marine "tie-ins" (to corresponding terrestrial sequences), or absolute dates, that unequivocally support either an early or late Maastrichtian age determination. The same is true for some of the Campanian taxa. Biostratigraphic occurrences of some taxa (e.g., *Pachycephalosaurus*, in the late Campanian) are not accepted (Sullivan, 2003, 2006b). While others, such as the occurrence of *Pentaceratops*, are simply incorrect. This taxon is cited as present in the Maastrichtian, but it is known only from upper Campanian strata (Sullivan and Lucas, 2003, 2006). Lastly, the recent relocation of the Campanian-Maastrichtian boundary (Lerbekmo and Braman, 2002) may cause the biostratigraphic occurrence of a taxon to be counted twice (once in the Campanian and once in the Maastrichtian).

Fastovsky et al. (2004, p. 877) claimed that absolute (dinosaur) richness and total generic richness increased steadily from the Late Triassic to the Late Cretaceous is undermined by the fact that dinosaur richness for the Turonian through Santonian (see their fig. 2), is lower than that for the Late Triassic. This paucity of genera reflects biases that are grounded in inadequate samples stemming from incomplete collecting efforts, recovery of inadequate sample sizes and by a dominance of marine facies in the Middle Cretaceous record.

METHODS AND CONCLUSIONS

I have re-tabulated the counts for both genera and species using *The Dinosauria*, (making minor corrections where necessary), and they are presented here in Table 1. Additional data come from this volume (Currie and Varricchio, 2004; Bakker et al., 2006; Lucas et al., 2006; Sullivan, 2006a,b). For dinosaur species: late Campanian: 103 maximum, 77 minimum; early Maastrichtian: 75 maximum, 68 minimum; late Maastrichtian: 49 maximum, 46 minimum. For dinosaur genera: late Campanian: 92 maximum, 69 minimum; early Maastrichtian: 67 maximum, 60 minimum; late Maastrichtian: 46 maximum, 43 minimum. In either case, there is a noticeable decline of taxa in both the genera and species from the late Campanian to late Maastrichtian. I would argue that the best precision here lies with assessing taxa at the species level, and such an assessment shows a noticeable decline from late Campanian to late Maastrichtian (Sullivan, 1987).

Any apparent increase in dinosaur diversity can be correlated, in large part, to an increase (more complete) of the strata preserved. In general, the younger the stratum, the less likely it has been subjected to forces of uplift and erosion. Although *apparent* dinosaur diversity has increased through time (Dodson, 1990), so too has the extinction of non-avian dinosaur taxa. However, over the last 9-10 million (76-65 Ma) years of the Cretaceous, there is an undeniable decrease in both the genera and species of dinosaurs of nearly 60%. The late Maastrichtian remnant of 45-48 species of the Cretaceous non-avian dinosaurs represents a small percentage of all the non-avian dinosaur taxa that lived during the Mesozoic Era. Not only did most of the non-avian dinosaur taxa become extinct prior to the

TABLE 1

Taxon	LC	EM	LM
CERATOSAURIA			
Laevisuchus indicus	?		
Noasaurus leali	x	x	x
Majungatholus atopus	?		
Carnotaurus sastrei	x	x	x
Masiakasaurus knopfleri	?		
Majungasaurus crenatissmus	?		
Basal TETANURAE			
Richardoestesia gilmorei	x	x	x
Richardoestesia isoceles	x	x	x
Bahariasaurus ingens		x	x
TYRANNOSAURIDAE			
Bagaraatan ostromi		x	
Dryptosaurus aquilungus	x	x	
Albertosaurus sarcophagus	x	x	
Gogosaurus libratus	x		
Alioramus remotus		?	
Daspletosaurus torosus	x		
Tyrannosaurus rex	?	x	x
Nanotyrannus lancensis			x
Tarbosaurus bataar	x	x	
ORNITHOMIMOSAURIA			
Ornithomimus edmontonensis	x	x	
Ornithomimus antiquus	x	x	x
Struthiomimus altus	x	x	
Archaeornithiomimus asiaticus	?		
Anserimimus planinychus		x	
Gallimimus bullatus		x	
Deinocheirus mirificus		x	
THERIZINOSAUROIDEA			
Erlianosaurus bellamanus	?		
Nanshiungosaurus brevispinus	?		
Therizinosaurus cheloniformis		x	
OVIRAPTOROSAURIA			
Avimimus portentosus	?		
Chirostenotes elegans	x	x	x
Chirostenotes pergracilis	x	x	
Nomingia gobiensis		x	
Rinchenia mongoliensis			
Elmisaurus rarus		x	
Heyuannia huangi	?	?	
Ingenia yanshini	?	?	?
	x	x	
TROODONTIDAE			
Troodon formosus	x	x	?
Saurornithoides junior		x	
Borobovia gracilicrus		x	
Tochisaurus nemegtensis		x	

Taxon	LC	EM	LM
DROMAEOSAURIDAE			
Adasaurus mongoliensis		x	
Atrociraptor marshalli		x	
Bambiraptor feinbergorum	x		
Dromaeosaurus albertensis	x	x	x
Euronychodon portucalensis	x	x	
Saurornitholestes langstoni	x		
Saurornitholestes robustus	x		
Pyroraptor olympius		x	
Unquillosaurus ceibalii	?		
Variraptor mechinorum	x	x	
Basal AVIALAE			
Avisaurus archibaldi	?	x	x
Avisaurus gloriae	x		
Enantiornis leali	?	x	x
Gurilynia nessov		x	
Lectavis bretincola	?	x	x
Gargantuavis philoinos		x	
Coniornis altus	x		
Hesperornis regalis	x		
Judinornis nogontsavensis		x	
Potamornis skutchi			x
incertae sedis			
Abelisaurus comahuensis		x	
Indosaurus matleyi		x(m)	
Indosuchus raptorius		x(m)	
SAUROPODA			
Nemegtosaurus mongoliensis		x	
Opisthocoelocaudia skarzynskii			x
Jianosaurus septentrionalis			x
"Titanosaurus" colberti			x
Titanosaurus indicus			x
Magyarosaurus dacus			x
Laplatasaurus araukanicus	x	x	?
Rapetosaurus krausei	?		
Lirainosaurus astibiae	x		
Saltasaurus loricatus	?	x	x
Alamosaurus sanjuanensis	x	x	
Argyrosaurus superbus	x	x	x
Antarctosaurus wichmanniannus	x	x	x
ANKYLOSAURIDAE			
Ankylosaurus magniventris			x
Euoplocephalosaurus tutus	x	x	
Nodocephalosaurus kirtlandensis	x		
Tarchia gigantea	?	x	
Edmontonia longiceps	x		
Edmontonia rugosidens	x		
Panoplosaurus mirus	x		
"Struithiosaurus'" transilvanicus			x

Taxon	LC	EM	LM
Basal ORNITHOPODA			
Bugenosaurua infernalis			x
Orodromeus makelai	x	x	
Parksosaurus warreni		x	
Thescelosaurus neglectus	?	?	x
Basal IGUANODONTIA			
Rhabdodon priscus	x	x	x
Rhabdodon septmanicus	x	x	x
Zalmoxes robustus			x
Zalmotes shqiperorum			x
HADROSAURIDAE			
Telmatosaurus transsylvanicus			x
Gilmoreosaurus mongoliensis	?		
Tanius sinensis		?	
Gryposaurus notabilis	x		
Gryposaurus incurvimanus	x		
Kritosaurus navajovius	x		
"Kritosaurus" australis	x	x	
Brachylophosaurus canadensis	x		
Anasazisaurus horneri	x		
Naashoibitosaurus ostromi	x		
Maiasaura peeblesorum	x		
Prosaurolophus maximus	x		
Prosaurolophus blackfeetensis	x		
Saurolophus osborni		x	
Saurolophus angustirostris	?	?	
Edmontosaurus regalis		x	x
Edmontosaurus annectens			x
Edmontosaurus sakatchewansis			x
"Hadrosaurus" minor	x	x	
Bactrosaurus johnsoni	?		
Corythosaurus casuarius	x		
Hypacrosaurus altispinus		x	
Hypacrosaurus stebingeri	x		
Lambeosaurus lambei	x		
Lambeosaurus magnicristatus	x		
"Lambeosaurus" laticaudus	?		
Olorotitan arhanensis		x	x
Parasaurolophus walkeri	x		
Parasaurolophus tubicen	x		
Parasaurolophus cyrtocristatus	x		
Amurosaurus riabinini			x
Barsboldia sicinskii	?	x	
Tsintaosaurus spinorhinus	?		

Taxon	LC	EM	LM
PACHYCEPHALOSAURIDAE			
Alaskacephale gangloffi	x		
Colepiocephale lambei	x		
Homalocephale calathoceros	?	?	
Hanssuesia sternbergi	x		
Prenocephale brevis	x	x	
Prenocephale edmontonensis		x	x
Prenocephale goodwini	x		x
Prenocephale prenes	x		
Dracorex hogwartsia			x
Pachycephalosaurus wyomingensis			x
Stygimoloch spinifer			x
Basal CERATOPSIA			
Leptoceratops gracilis			x
Montanoceratops cerorhynchus		x	
CERATOPSIDAE			
Brachyceratops montanus	x		
Avaceratops lamersi	x		
Centrosaurus apertus	x		
Monoclonius crassus	x		
Pachyrhinosaurus canadensis		x	
Stryracosaurus albertensis	x		
Anchiceratops ornatus	x	x	
Aguaceratops marisalensis	x		
Arrhinoceratops brachyops		x	
Chasmosaurus belli	x		
Chasmosaurus russelli	x		
Chasmosaurus irvinensis	x		
Diceratops hatcheri			x
Einiosaurus procurvicornis	x		
Achelousaurus horneri	x		
Prenoceratops pieganensis	x		
Pentaceratops sternbergii	x		
Torosaurus latus			x
Torosaurus utahensis		x	
Triceratops horridus			x

TABLE 1. Global biostratigraphic distribution of valid non-avian dinosaur species for the late Campanian, early Maastrichtian (pre-Lancian) and late Maastrichtian(Lancian).Key: LC = late Campanian; EM = early Maastrichtian; LM = late Maastrichtian; ? = possible occurrence; (m) = original recorded as "middle" Maastrichtian; x = positive occurrence. Additional taxa from Currie and Varricchio (2004), Bakker etal. (2006) and Sullivan (2006a, b) (this volume).

late Campanian, the number of species from the late Campanian through the late Maastrichtian was demonstrably diminished.

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