8 Body-Size Evolution in the Dinosauria

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Introduction

The evolution of body size and its influence on organismal biology have received scientific attention since the earliest decades of evolutionary study (e.g., Cope, 1887, 1896; Thompson, 1917). Both paleontologists and neontologists have attempted to determine correlations between body size and numerous aspects of life history, with the ultimate goal of documenting both the predictive and causal connections involved (LaBarbera, 1986, 1989). These studies have generated an appreciation for the thoroughgoing interrelationships between body size and nearly every significant facet of organismal biology, including metabolism (Lindstedt & Calder, 1981; Schmidt-Nielsen, 1984; McNab, 1989), population ecology (Damuth, 1981; Juanes, 1986; Gittleman & Purvis, 1998), locomotion (McMahon, 1975; Biewener, 1989; Alexander, 1996), and reproduction (Alexander, 1996).

An enduring focus of these studies has been Cope's Rule, the notion that body size tends to increase over time within lineages (Kurtén, 1953; Stanley, 1973; Polly, 1998). Such an observation has been made regarding many different clades but has been examined specifically in only a few (MacFadden, 1986; Arnold et al., 1995; Jablonski, 1996, 1997; Trammer & Kaim, 1997, 1999; Alroy, 1998). The discordant results of such analyses have underscored two points: (1) Cope's Rule does not apply universally to all groups; and (2) even when present, size increases in different clades may reflect very different underlying processes. Thus, the question, "does Cope's Rule exist?" is better parsed into two questions: "to which groups does Cope's Rule apply?" and "what process is responsible for it in each?"

Several recent works (McShea, 1994, 2000; Jablonski, 1997; Alroy, 1998, 2000a, 2000b) have begun to address these more specific questions, attempting to quantify patterns of body-size evolution in a phylogenetic (rather than strictly temporal) context, as well as developing methods for interpreting the resultant patterns. Perhaps surprisingly, none of these studies has focused on body-size evolution in nonavian dinosaurs (hereafter referred to as "dinosaurs"), a group for which body size increases are

axiomatic. Although dinosaurs are commonly perceived to have undergone dramatic size increases (and certainly the thousandfold size difference between outgroup "lagosuchians" and sauropods is remarkable), few studies (Sereno, 1997) have attempted to quantify or analyze this pattern.

In this paper, I present the results of the first such study. Using measurement data and a composite phylogeny of dinosaurs, I reconstruct patterns of body-size evolution in this group. Ultimately, dinosaurs are brought into the context of Cope's Rule as the resulting patterns are assessed and interpreted in light of several potential underlying mechanisms.

Materials and Methods

Body-Size Estimation and Dinosaur Phylogeny

Estimating body size for any extinct organism is a difficult prospect, particularly taxa that differ significantly from extant forms in body size and shape. Dinosaurs have proven frustrating subjects for body-size estimation for this reason, and as a consequence different studies have generated widely varying results (Colbert, 1962; Bakker, 1975; Paul, 1988; Alexander, 1985; Anderson et al., 1985; Peczkis, 1994; Henderson, 1999; Seebacher, 2001). Much of this variation is tied to methodological differences (Alexander, 1985), the inherent subjectivity involved in creating full-body reconstructions of extinct animals (Paul, 1988), and the uncertainty surrounding predictions generated from the scaling relationships of extant taxa (Carrano, 2001). Thus, estimates of body masses for specific dinosaur taxa remain a subject of persistent debate.

However, it is not necessary to reconstruct absolute body masses to analyze patterns of body-size evolution; only *relative* body sizes need to be reconstructed. Therefore, it is possible to substitute proxies (or correlates) for body size in place of actual estimates, provided such proxies have a consistent, linear relationship to body size. This relationship need not even be specified, but the "fit" of the correlation and its linearity must be demonstrated. Such a linearly correlated variable would then reflect some multiple (or fraction) of body mass, allowing the relative sizes of taxa to be compared on a single scale. Changes between one taxon (ancestor) and the next (descendant) can then be measured while maintaining the same relationship (differing only in some multiple or fraction) that would have been present had actual masses been used.

In this study, I use femoral length (FL), anteroposterior diameter (FAP), and mediolateral diameter (FML) as separate proxies for body mass. These variables have been shown to be tightly linearly correlated

with body mass in many extant terrestrial taxa, particularly mammals (Alexander et al., 1979; Bou et al., 1987; Jungers et al., 1998; Christiansen, 1999) and birds (Maloiy et al., 1979; Cubo & Casinos, 1997). The linearity of this relationship is probably tied to the role of the femur (specifically, its cross-sectional area) in supporting body mass against gravity. Femoral measures have the added advantage of being relatively easily to obtain (even from photographs, when specimens are not directly accessible), and the femur is frequently preserved in dinosaur specimens.

I measured femoral length and diameters in 1,640 nonavian dinosaur specimens representing all major ingroup clades and nearly every taxon for which limb material is known ($N = 251$; appendix). I used the largest representative when multiple specimens were available, and excluded taxa when limbs were known only from juvenile specimens (e.g., *Lophorhothon, Pleurocoelus, Bellusaurus, Brachyceratops, Avaceratops, Maleevosaurus, Shanshanosaurus*). These measurements were mapped onto a composite phylogeny derived from several published sources (figs. 8.1, 8.2, 8.3, 8.4) and were analyzed by the methods described below. I incorporated several taxa that were not represented in published analyses into the phylogeny based on personal communications and observations. Although I attempted to include as many taxa as possible in this composite phylogeny, I omitted several taxa whose relationships were too uncertain to allow their placement in this context (e.g., *Saltopus, Kaijiangosaurus, Betasuchus, Tarascosaurus, Chuandongocoelurus, Podokesaurus, Tugulusaurus, Nanosaurus, Klamelisaurus,* "*Cetiosaurus*" *mogrebiensis, Lourinhasaurus*).

Controversy surrounds the details of several regions of this phylogeny and often extends to large collections of taxa. These groups include "ceratosaurian" theropods and "hypsilophodontid" ornithopods. In both cases, recent studies (Scheetz, 1999; Carrano et al., 2002) have favored rendering both formerly monophyletic groups as paraphyletic. For such examples, I rearranged the phylogeny to reflect these previous hypotheses and compared the reconstructed ancestral states. Similarly, I compared the effects of moving individual controversial taxa (e.g., *Euhelopus, Eoraptor, Heterodontosaurus*). In none of these instances were significant effects observed.

Identifying Evolutionary Patterns

Ideally, the identification and analysis of evolutionary trends are based on direct examination of actual ancestor-descendant pairs (Alroy, 1998), provided such forms and relationships could be identified. As few candidate ancestor-descendant pairs have been suggested among
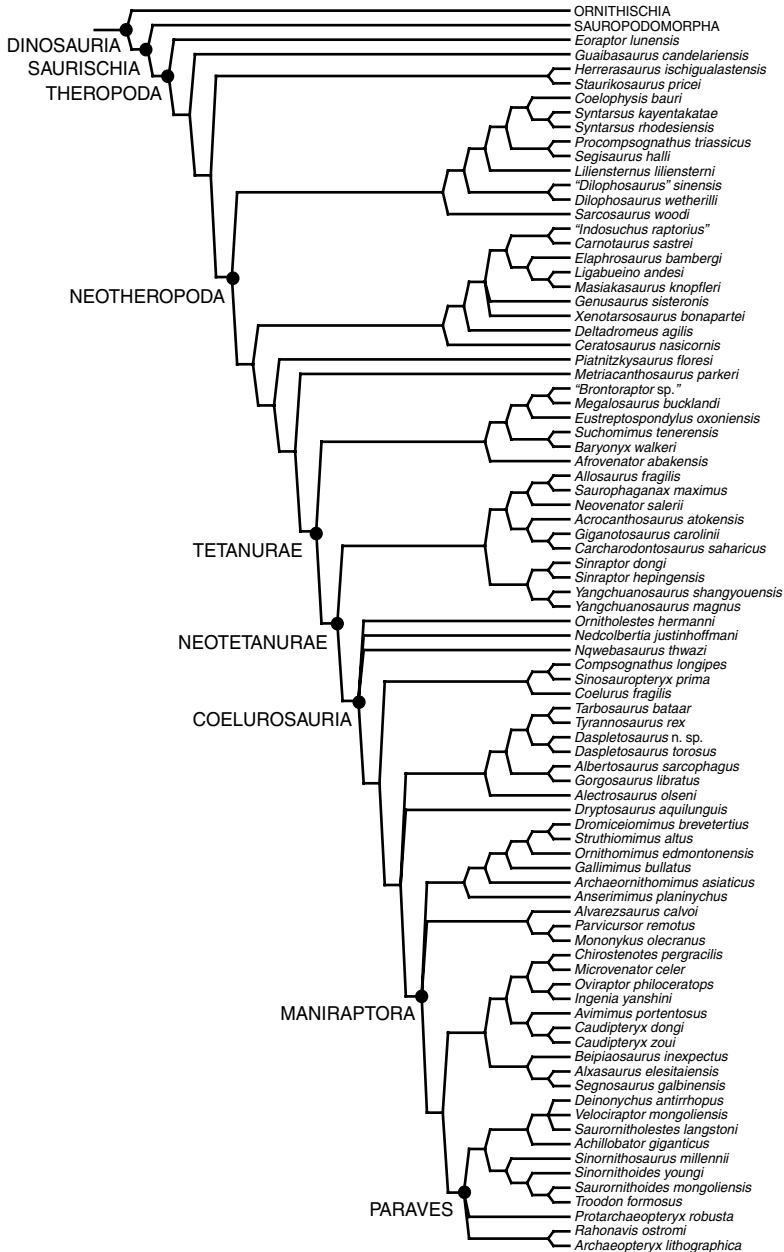
Figure 8.1. Phylogeny of Theropoda used in this study, after Sereno (1999), Holtz (2000), and Carrano et al. (2002). Additional taxa are included based on personal observations.
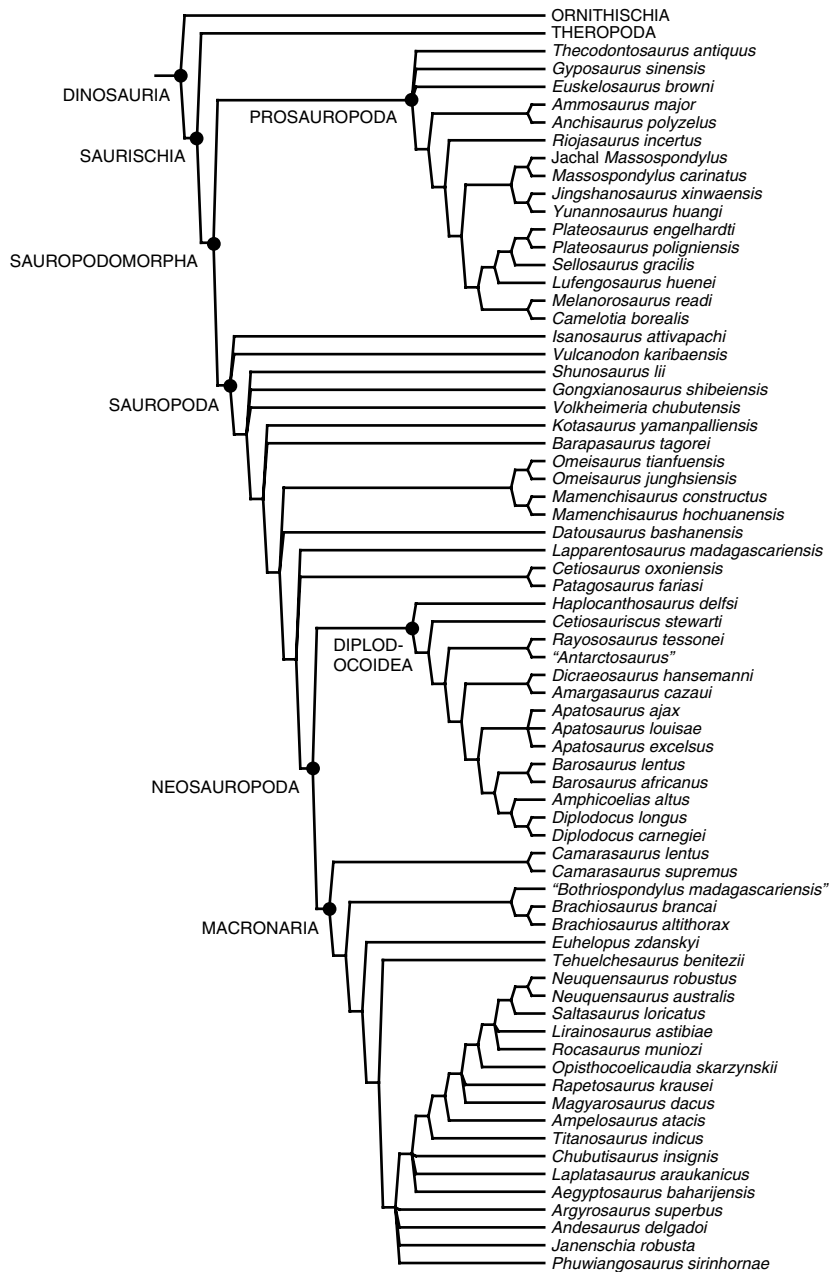
Figure 8.2. Phylogeny of Sauropodomorpha used in this study, after Wilson and Sereno (1998), Sereno (1999), Curry Rogers and Forster (2001), Wilson (2002), and K. A. Curry Rogers (personal communication). Additional taxa are included based on personal observations.
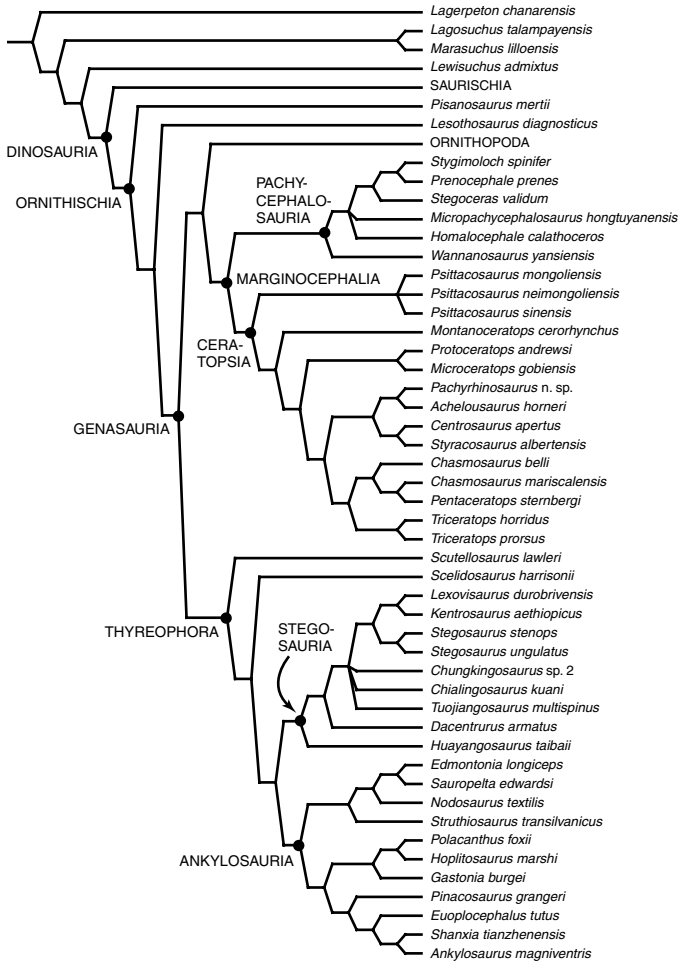
Figure 8.3. Phylogeny of Thyreophora and Marginocephalia used in this study, after Sereno (1999), Dodson et al. (2004), and R. V. Hill (personal communication.). Additional taxa are included based on personal observations.

dinosaurs, this option is not promising here. Instead, ancestral states must be either reconstructed or avoided.

Several methods have been developed for reconstructing ancestral states on a phylogenetic tree (Felsenstein, 1985; Schultz et al., 1996; Cunningham et al., 1998; Cunningham, 1999; Huelsenbeck & Bollback, 2001), perhaps the most straightforward being optimization of discrete characters directly onto a cladogram (Maddison et al., 1984). Continuous characters are problematic to reconstruct in this manner, largely because of the
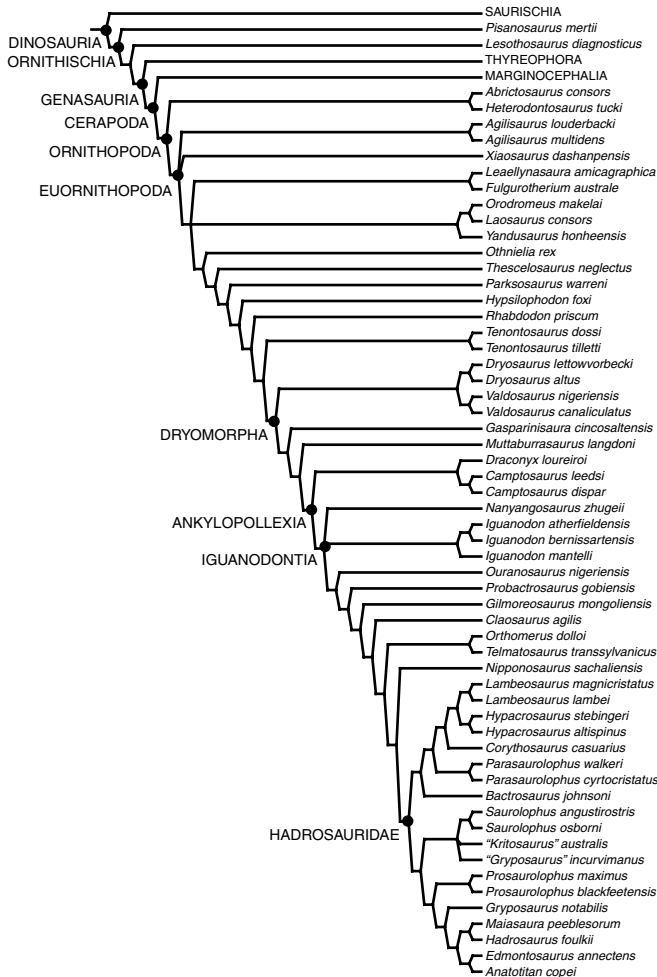
Figure 8.4. Phylogeny of Cerapoda used in this study, after Sereno (1999), Scheetz (1999), and Horner et al. (2004). Additional taxa are included based on personal observations.

difficulties associated with incorporating them into the discrete context of a cladistic analysis. Independent contrasts (Felsenstein, 1985) allows ancestral-state reconstructions of continuous characters, essentially by applying the mean of the two immediate daughter taxa to a given node. Unfortunately, this very procedure hampers its usefulness here, because averaging the changes contained within each set of ancestor-descendant pairs ultimately eliminates trends in the original data.

In this study, I used squared-change parsimony (SCP) to reconstruct

nodal values for body mass across Dinosauria (a similar procedure was used by Carrano, 2000). SCP is similar to independent contrasts but includes one further step: rather than using means as ancestral-state reconstructions, SCP modifies these values to minimize the sum of the squared changes across all the branches of the tree. The result is that a particular ancestral state is often not the mean of the descendant values and could even lie outside them. One particular problem with SCP (and other similar methods) is that there can be a very wide error associated with ancestral-state reconstructions, especially those near the base of the tree, which are most strongly affected by changes in terminal taxon values and positions. However, it has the benefit of potentially retaining trend signals within the data, although these signals are likely to be weak.

I reconstructed ancestral states with SCP using the "Trace Continuous" option in MacClade 4.0 (Maddison & Maddison, 2000) and the composite phylogeny. Unresolved nodes were treated as hard polytomies, as required of this option. Once ancestral values were obtained, I analyzed the ancestor-descendant changes within all of Dinosauria as well as several large ingroup clades. I also compared the changes between the ancestral value for a given clade and all its terminal taxa. Overall changes were evaluated by examining whether the mean change, sum change, and total number of changes for the group were positive or negative.

An alternative to SCP reconstruction is to eschew ancestral-state reconstructions altogether and examine only the original data associated with terminal taxa. Here I compared patristic distance with the measured body-mass proxies. Patristic distance was calculated by numbering all nodes based on their distance from the root node of the phylogeny (Sidor, 2001; note that this is identical to the "clade rank" method described by Carrano, 2000). I then used Spearman-rank correlation to test for correlation between patristic distance and body mass. If taxa with higher patristic distance values tend to have larger (or smaller) body masses, this would be evident as a significant positive (or negative) correlation. In this manner, body mass-clade rank correlation allows both identification and evaluation of trends within the data. Again, I examined Dinosauria as a whole and several less-inclusive clades.

Analyzing Evolutionary Trends

Evolutionary radiations (or trends) in morphology can often be described as changes in morphospace occupation over time for a given clade. Such changes can comprise expansion of the morphological range, resulting in a greater amount of morphospace occupied by the clade (Fisher, 1986). Expansion into a morphospace may resemble simple diffusion,

wherein the range of variation increases without bound through time from some ancestral condition. If, however, some maximum or minimum (or both) limits the variation expressed by the radiation, it can be described as diffusion with one (or more) bounds. Both situations fulfill McShea's (1994) definition of "passive" trends (see also McShea, 1998).

Change in morphospace occupation can also include displacement from one morphology to another, in which the location of a group or taxon shifts within the morphospace. In these cases, no range expansion is necessary, merely a change in the location of morphospace occupation; they conform to McShea's "driven" trends (1994) (here called "active"). (It should be noted that diffusion may also be overprinted on this pattern, so that range expansion may accompany a shift in location).

I employed McShea's (1994) three tests to determine whether trends in dinosaur body-size evolution could best be described as "passive" or "active":

1) The *minimum test* examines the behavior of the minimum bound of the size distribution through time. In a passive trend, this bound remains stable while the maximum bound increases, reflecting diffusive expansion of the group into morphospace. In contrast, the minimum and maximum bounds both increase in an active trend, reflecting the wholesale shift in morphospace occupation.

2) The *ancestor-descendant test* examines each change from an ancestor to its descendant and tallies the number of increases and decreases. Passive trends have near-equal numbers; active trends have a preponderance of one or the other.

3) The *subclade test* compares the frequency distributions of the state variable for ingroup clades with its distribution in the whole clade. Passively driven groups are expected to have distributions that deviate from the general pattern, whereas actively driven groups are expected to have patterns that mirror the general pattern.

The latter two tests are conducted on groups sufficiently far from the minimum bound so as to reduce the chance that the results are biased by it (McShea, 1994). For these two analyses, I examined taxa that were larger than the mean log size for each group (MacFadden, 1986).

Recently, Alroy (2000a) suggested that these tests did not adequately examine the subtleties present in many data sets but rather obscured them with the coarse designations "active" and "passive." He suggested that time-slice analyses were unlikely to reveal meaningful patterns, instead favoring examination of ancestor-descendant pairs. To illustrate this, Alroy presented twelve possible trend patterns based on plots of

descendant-ancestor differences versus ancestral states. I present similar plots here to investigate whether the pattern of body-size evolution in dinosaurs is likely to be the result of random or nonrandom changes.

Alroy's (2000a) objections to time-slice analyses have merit, and one possible alternative to avoiding them altogether is to replace temporal data with phylogenetic data. Superficially, this will cause little change in the overall pattern because most vertebrate clades (including dinosaurs) show some correlation between age rank and clade rank (Benton & Hitchin, 1997). However, by replacing time data with patristic distance, the comparisons become explicitly phylogenetic even when specific ancestor-descendant comparisons are not made. In dinosaurs, where the fossil record is extremely variable and long ghost lineages are inferred for several major clades (Sereno, 1999), this difference can interfere with resulting perceptions of evolutionary patterns. In particular, late first appearances of basal taxa (due to an incomplete record) may still be in proper sequence but can alter the overall pattern, especially if these taxa are located at the edges of the distribution. Thus, I also perform a *modified minimum test* in which the minimum bound is tracked on plots of body size versus patristic distance. For these analyses, patristic distance is rescaled to 1.0 for each of the major ingroup clades.

Results

Evolutionary Patterns

SCP reconstructions of ancestral (nodal) states produce a general pattern consistent with an overall size increase throughout Dinosauria. This is evident in the positive mean, sum, and median changes as well as the left-skewed distribution of changes (tables 8.1–8.3). The results from comparisons between each ancestor and descendant are similar to those from comparisons between the single reconstructed ancestral value for Dinosauria and all its terminal taxa (table 8.4). This pattern is consistent regardless of which measured variable is examined.

The pattern is robust but complex, largely due to the overlap of numerous internal patterns associated with less-inclusive dinosaurian clades. When performed on these clades, the SCP analysis reveals size increases in most, but not all, dinosaur groups (tables 8.1–8.3). Again, the patterns are consistent for most measured variables, with a tendency for some clades to show weaker trends with diameter measures. The most notable exception occurs in coelurosaurian theropods, which occasionally show negative mean and sum changes, as well as a negative median change for FML, that suggest overall size decreases. The coelurosaur pat-

Table 8.1. Body-size statistics for Dinosauria and ingroup clades, using squared-change parsimony reconstructions based on measurements of femoral length

Group	Mean	Sum	Skew	Median	N	+	−	χ^2
Dinosauria	0.012	5.773	−0.442	0.018	466	**279**	187	18.163*
Saurischia	0.008	2.267	−0.482	0.016	273	116	**157**	6.158*
Theropoda	0.004	0.576	−0.694	0.018	154	**92**	62	5.844*
Coelurosauria	−0.001	−0.050	−0.465	0.006	78	**43**	35	0.821
Sauropodomorpha	0.013	1.523	0.493	0.009	118	**52**	43	1.661
Prosauropoda	0.003	0.094	0.132	0.019	28	**16**	12	0.571
Sauropoda	0.014	1.203	0.771	0.006	89	**47**	42	0.281
Macronaria	0.006	0.233	0.349	0.006	41	**21**	20	0.024
Ornithischia	0.019	3.491	−0.354	0.021	185	**118**	67	14.059*
Thyreophora	0.034	1.376	−0.197	0.041	41	**27**	14	4.122*
Stegosauria	0.037	0.559	0.390	0.041	15	**9**	6	1.389
Ankylosauria	0.021	0.438	−0.679	0.033	21	**14**	7	2.333
Marginocephalia	0.027	1.060	−0.480	0.041	38	**27**	11	6.737*
Pachycephalo	0.022	0.218	−0.159	0.057	10	**6**	4	0.400
Ceratopsia	0.029	0.823	−0.637	0.044	28	**21**	7	7.000
Ornithopoda	0.012	1.175	−0.407	0.016	99	**61**	38	5.343*

Notes: Statistics summarize differences between each reconstructed ancestral node and each descendant taxon. Skew, skewness; +, number of positive ancestor-descendant changes; −, number of negative ancestor-descendant changes; χ^2, chi-square results. Asterisks indicate χ^2 values that are significant to at least $P < 0.05$. Pachycephalo = Pachycephalosauria.

tern is also manifest at a higher level, within Theropoda as a whole. Sauropoda and Pachycephalosauria also show evidence of size decreases, although these are more weakly evident (usually as a right-skewed distribution of changes). The small sample size for Pachycephalosauria hampers further investigation, but the sauropod pattern seems to be influenced by size decreases concentrated within Macronaria.

Patristic-distance correlations clarify these trends, albeit at the expense of the increased number of data points afforded by SCP reconstructions (fig. 8.5; tables 8.5–8.7). These results are very similar to those produced by SCP, revealing size increases in nearly all dinosaur clades as well as in Dinosauria, and are consistent among the three measured variables. Spearman-rank correlations reveal positive trends in most groups, although these are not significant in Ankylosauria and Stegosauria for FAP, or Pachycephalosauria for FML. Negative correlations are also present—significant in Macronaria, Sauropoda, and Theropoda but nonsignificant in Saurischia and Coelurosauria—indicating trends toward size decreases in these groups.

Table 8.2. Body-size statistics for Dinosauria and ingroup clades, using squared-change parsimony reconstructions based on measurements of femoral anteroposterior diameter

Group	Mean	Sum	Skew	Median	N	+	−	χ^2
Dinosauria	0.006	2.400	−0.331	0.015	385	**216**	169	5.738*
Saurischia	0.002	0.545	−0.310	0.018	226	**127**	99	3.469
Theropoda	−0.005	−0.644	−0.428	0.020	130	**74**	56	2.492
Coelurosauria	−0.028	−1.850	−0.124	0.003	66	**34**	32	0.061
Sauropodomorpha	0.010	0.960	0.257	0.015	118	**64**	54	0.847
Prosauropoda	0.003	0.063	−0.206	0.011	24	**13**	11	0.167
Sauropoda	0.009	0.641	0.331	0.011	70	**38**	32	0.514
Macronaria	−0.013	−0.400	0.583	−0.003	32	15	**17**	0.125
Ornithischia	0.013	1.913	−0.265	0.014	151	**85**	66	2.391
Thyreophora	0.031	0.866	−0.177	0.004	28	**15**	13	0.143
Stegosauria	0.043	0.391	0.989	0.008	9	**6**	3	1.000
Ankylosauria	0.007	0.098	−0.267	−0.005	15	6	**9**	0.600
Marginocephalia	0.034	1.023	−0.060	0.049	30	**20**	10	3.333
Pachycephalo	0.023	0.162	0.488	−0.018	7	3	**4**	0.143
Ceratopsia	0.037	0.860	−0.316	0.059	23	**17**	6	5.260*
Ornithopoda	0.002	0.165	−0.463	0.013	87	**48**	39	0.931

Note: Statistics summarize differences between each reconstructed ancestral node and each descendant taxon. Abbreviations are as in Table 8.1.

Evolutionary Trends

Minimum Test. When plotted against time (i.e., age rank), body-size distribution in Dinosauria shows a rapid expansion in range throughout the Mesozoic, most of which occurs during the Late Triassic (age ranks 1–4) (fig. 8.6). However, this range expansion is almost entirely confined to the right of the distribution, representing size increases. Few taxa decrease in size from the ancestral dinosaurian condition, and as a result the distribution shows a relatively stable minimum bound, suggesting that the pattern is passive.

Within Dinosauria, the patterns are more complex: most groups mirror this overarching passive pattern, but a few do not. These exceptions—Sauropodomorpha, Thyreophora, and (although inconsistently among different variables) Stegosauria and Ceratopsia—instead show a loss of taxa at the minimum bound while the maximum bound increases. Thus, the entire distribution shifts toward the right, although an increase in range may also be present. Interestingly, macronarians show the reverse pattern: loss of larger taxa as smaller taxa appear, thus shifting

Table 8.3. Body-size statistics for Dinosauria and ingroup clades, using squared-change parsimony reconstructions based on measurements of femoral mediolateral diameter

Group	Mean	Sum	Skew	Median	N	+	−	χ^2
Dinosauria	0.014	5.110	−0.364	0.030	375	**225**	150	15.000*
Saurischia	0.006	1.352	−0.472	0.019	215	**123**	92	4.470*
Theropoda	−0.002	−0.225	−0.593	0.034	120	**67**	53	1.633
Coelurosauria	−0.009	−0.508	−0.356	−0.007	56	27	**29**	0.071
Sauropodomorpha	0.014	1.308	0.181	0.009	94	**55**	39	2.723
Prosauropoda	0.002	0.053	−0.293	0.038	23	**13**	10	0.391
Sauropoda	0.013	0.911	0.239	0.008	70	**41**	29	2.057
Macronaria	−0.001	−0.050	0.079	0.005	35	**20**	15	0.714
Ornithischia	0.024	3.758	−0.135	0.036	154	**99**	55	12.570*
Thyreophora	0.041	1.463	−0.337	0.046	36	**25**	11	5.444*
Stegosauria	0.038	0.573	0.521	0.027	15	**10**	5	1.667
Ankylosauria	0.028	0.471	−0.784	0.058	17	**12**	5	2.882
Marginocephalia	0.035	1.041	−0.539	0.044	30	**23**	7	19.200*
Pachycephalo	0.035	0.244	0.413	0.021	7	**5**	2	1.286
Ceratopsia	0.105	0.797	−0.914	0.048	23	**18**	5	7.348*
Ornithopoda	0.016	1.324	0.086	0.027	82	**48**	34	2.390

Note: Statistics summarize differences between each reconstructed ancestral node and each descendant taxon. Abbreviations as in Table 8.1.

the distribution to the left. Both types of exceptions may be described as active.

Ancestor-Descendant Test. When taxa greater than the mean log-size are considered, most dinosaur clades (including Coelurosauria) show a greater number of increases between ancestors and descendants than decreases (table 8.8). This active pattern is also seen in Dinosauria as a whole. There is only one weak instance of the reverse pattern (Macronaria, FAP), although a few groups (Macronaria, Sauropoda, Sauropodomorpha) show near-equal values for increases and decreases.

Subclade Test. The body-size distribution for Dinosauria is strongly right skewed, as is typical for most animal groups (fig.8.7; Stanley, 1973). When subclades whose means are larger than the mean log size are analyzed, their distributions are quite variable (table 8.9). This variation ranges from positively skewed distributions (very similar to that for Dinosauria) to near-normal and negatively skewed distributions, often differing for the same group depending on the measured variable.

Table 8.4. Body-size statistics for Dinosauria and ingroup clades, using squared-change parsimony reconstructions based on measurements of femoral length

Group	Mean	Sum	Skew	Median	N	+	−	χ^2
Dinosauria	0.826	208.036	−0.664	0.937	252	**246**	6	228.571*
Saurischia	0.404	60.159	−0.701	0.519	149	**118**	31	50.799*
Theropoda	0.277	22.419	−0.334	0.357	81	**60**	21	20.753*
Coelurosauria	0.068	2.870	0.060	0.015	42	**22**	20	0.009
Sauropodomorpha	0.399	27.151	−1.112	0.466	68	**62**	6	46.118*
Prosauropoda	0.133	2.128	−0.270	0.221	16	**10**	6	1.000
Sauropoda	0.209	10.879	−0.588	0.239	52	**46**	8	30.769*
Macronaria	−0.084	−2.108	−0.333	−0.035	25	10	**15**	1.000
Ornithischia	1.571	155.577	−0.635	1.675	99	**99**	0	99.000*
Thyreophora	0.528	11.609	−1.027	0.566	22	**21**	1	18.182*
Stegosauria	1.002	9.018	−0.343	1.004	9	**9**	0	9.000*
Ankylosauria	0.098	1.077	−0.933	0.138	11	**9**	2	4.455*
Marginocephalia	1.269	26.645	−0.092	1.272	21	**21**	0	21.000*
Pachycephalo	−0.154	−0.925	0.035	−0.101	6	1	**5**	2.667
Ceratopsia	0.392	5.880	−0.556	0.587	15	**11**	4	3.267
Ornithopoda	0.590	31.839	−0.747	0.725	54	**50**	4	39.185*

Note: Statistics summarize differences between the basal reconstructed ancestral node for each clade and all its descendant terminal taxa. Abbreviations as in Table 8.1.

Change Versus Ancestor Plots. When descendant-ancestor differences are plotted against ancestral states for Dinosauria, the resulting pattern suggests that body-size evolution is an active pattern, rather than due to simple random diffusion (fig. 8.8). Although the mean change is nearly zero, there is a weak trend within the data: the regression slope is small but significantly positive ($y = 0.72x - 0.193; r^2 = 0.062; P < 0.001$). Given the negative autocorrelation between the x and y variables, the corrected positive correlation would be even stronger (Alroy, 1998). Indeed, this pattern is remarkably similar to that for Cenozoic mammals in that it can also be described by a cubic equation favoring moderate-to-large body sizes.

The positive regression pattern is repeated at many more inclusive levels within Dinosauria. The best-sampled ingroups (Saurischia, Ornithischia, Theropoda, Thyreophora, Ornithopoda, Coelurosauria) have significant patterns that are very similar to that of Dinosauria. They can also be described by similar cubic equations. Other groups also have positive regression slopes but not significantly so. In addition, the re-

duced sample sizes of these other clades make it difficult to determine whether a cubic equation could also be appropriately fit to those data.

Modified Minimum Test. Several differences from the minimum test are detected in these patterns when body size is plotted against patristic distance instead of time (fig. 8.5). Dinosauria, Saurischia, Theropoda,
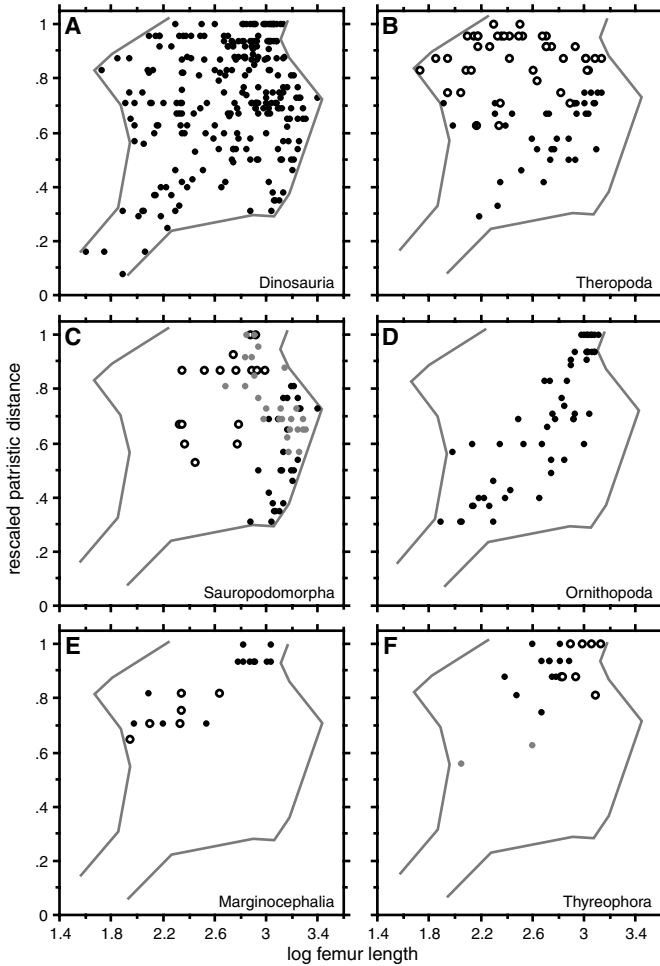

Figure 8.5. Patristic distance analyses results. Patristic distance (rescaled to 1.0 for major ingroup clades) is plotted against log femur length for Dinosauria and several representative ingroup clades. (A) Dinosauria. (B) Theropoda: open circles, Coelurosauria; closed circles, all other theropods. (C) Sauropodomorpha: open circles, Prosauropoda; gray circles, Macronaria; closed circles, other sauropods. (D) Ornithopoda. (E) Marginocephalia: open circles, Pachycephalosauria; closed circles, Ceratopsia. (F) Thyreophora: gray circles, basal thyreophorans; open circles, Stegosauria; closed circles, Ankylosauria.

Table 8.5. Spearman-rank correlations of body size (based on femoral length) and patristic distance for Dinosauria and ingroup clades

Group	rho	Z	P	rho†	Z†	P†
Dinosauria	0.285	6.142	<0.001*	0.283	6.118	<0.001*
Saurischia	−0.071	−1.169	0.243	−0.073	−1.206	0.228
Theropoda	−0.175	−2.162	0.031*	−0.178	−2.206	0.027*
Coelurosauria	−0.020	−0.174	0.862	−0.030	−0.265	0.791
Sauropodomorpha	0.340	3.681	<0.001*	0.339	3.664	<0.001*
Prosauropoda	0.556	2.891	0.004*	0.550	2.855	0.004*
Sauropoda	−0.104	−0.973	0.331	−0.106	−0.998	0.318
Macronaria	−0.718	−3.515	<0.001*	−0.727	−3.526	<0.001*
Ornithischia	0.745	10.100	<0.001*	0.744	10.093	<0.001*
Thyreophora	0.593	3.749	<0.001*	0.587	3.711	<0.001*
Stegosauria	0.571	2.135	0.033*	0.562	2.102	0.036*
Ankylosauria	0.548	2.450	0.014*	0.535	2.394	0.017*
Marginocephalia	0.831	5.120	<0.001*	0.829	5.107	<0.001*
Pachycephalo	0.858	2.573	0.010*	0.855	2.564	0.010*
Ceratopsia	0.802	4.166	<0.001*	0.798	4.148	<0.001*
Ornithopoda	0.913	9.035	<0.001*	0.913	9.034	<0.001*

Note: Asterisks highlight *p*-values that are significant to at least the 0.05 level; daggers indicate values that are corrected for ties.

and Coelurosauria retain the basic pattern described above, with a stable minimum bound and an expanding upper bound. Sauropoda and Sauropodomorpha instead show increases away from the most primitive size toward both smaller and larger forms; the distribution resembles an expanding cone. Most other clades exhibit a distributional shift toward larger forms with a concomitant loss of smaller taxa, but macronarians again show the unusual reverse pattern. The three variables show consistent overall patterns.

Discussion

Evolutionary Patterns and Trends

Body-size increases have been implicitly noted as a characteristic feature of dinosaur evolution since the early days of paleontological study. This was partly based on a tacit understanding of these immense animals as having necessarily descended from some smaller-sized member(s) of the Paleozoic fauna. Subsequent discoveries bolstered this opinion by documenting small early dinosaurs (Cope, 1889; Talbot, 1911; Huene,

Table 8.6. Spearman-rank correlations of body size (based on femoral anteroposterior diameter) and patristic distance for Dinosauria and ingroup clades

Group	rho	Z	P	rho[†]	Z[†]	P[†]
Dinosauria	0.296	5.827	<0.001*	0.295	5.806	<0.001*
Saurischia	−0.067	−0.998	0.318	−0.069	−1.030	0.303
Theropoda	−0.202	−2.294	0.022*	−0.205	−2.331	0.020*
Coelurosauria	−0.030	−0.242	0.809	−0.039	−0.315	0.753
Sauropodomorpha	0.292	2.828	0.005*	0.290	2.813	0.005*
Prosauropoda	0.476	2.281	0.023*	0.471	2.258	0.024*
Sauropoda	−0.201	−1.671	0.095*	−0.204	−1.697	0.090*
Macronaria	−0.205	−0.869	0.385	−0.211	−0.894	0.371
Ornithischia	0.746	9.233	<0.001*	0.746	9.228	<0.001*
Thyreophora	0.524	2.772	0.006*	0.518	2.743	<0.006*
Stegosauria	−0.212	−0.601	0.548	−0.271	−0.767	0.443
Ankylosauria	0.338	1.266	0.206	0.322	1.205	0.228
Marginocephalia	0.857	4.692	<0.001*	0.855	4.682	<0.001*
Pachycephalo	0.777	1.903	0.057*	0.771	1.888	0.059*
Ceratopsia	0.842	4.166	<0.001*	0.798	4.148	<0.001*
Ornithopoda	0.878	8.178	<0.001*	0.878	8.186	<0.001*

Note: Symbols as in Table 8.5.

1914) along with increasingly larger Jurassic and Cretaceous forms. This general notion became ensconced in scientific opinion, even coming to fulfill a perceived role in contributing both to their success and extinction (Benton, 1990).

From the many descriptive analyses presented here, it is clear that dinosaur evolution is indeed characterized by a marked, pervasive pattern of body-size increase. This is evident in most of the major ingroup clades as well, indicating that the overall pattern is not merely an artifact of overlapping—and potentially discordant—internal patterns. This perhaps belabors the rather obvious point that dinosaurs did, in fact, get bigger as time proceeded in the Mesozoic. However, the specificity of these analyses also allows a more complex pattern to be determined. For example, at least two less-inclusive clades (Macronaria and Coelurosauria) are typified by size *decreases.*

These two groups are interesting in their own right as the most diverse and morphologically divergent components of their parent clades. Macronarians (including "titanosaurs") display a host of unusual synapomorphies among sauropods that are likely tied to unique locomotor and

Table 8.7. Spearman-rank correlations of body size (based on femoral mediolateral diameter) and patristic distance for Dinosauria and ingroup clades

Group	rho	Z	P	rho[†]	Z[†]	P[†]
Dinosauria	0.243	4.717	<0.001*	0.241	4.691	<0.001*
Saurischia	−0.053	−0.783	0.435	−0.055	−0.815	0.415
Theropoda	−0.167	−1.817	0.070*	−0.170	−1.853	0.064*
Coelurosauria	−0.058	−0.432	0.666	−0.072	−0.531	0.596
Sauropodomorpha	0.287	2.796	0.005*	0.285	2.777	0.006*
Prosauropoda	0.386	1.853	0.064*	0.376	1.803	0.071*
Sauropoda	−0.219	−1.833	0.067*	−0.223	−1.863	0.063*
Macronaria	−0.552	−2.467	0.014*	−0.563	−2.519	0.012*
Ornithischia	0.592	7.347	<0.001*	0.591	7.361	<0.001*
Thyreophora	0.683	4.095	<0.001*	0.679	4.073	<0.001*
Stegosauria	0.553	2.068	0.039*	0.543	2.033	0.042*
Ankylosauria	0.631	2.525	0.012*	0.624	2.495	0.013*
Marginocephalia	0.782	4.282	<0.001*	0.779	4.267	<0.001*
Pachycephalo	0.634	1.553	0.121	0.624	1.529	0.126
Ceratopsia	0.762	3.576	<0.001*	0.758	3.555	<0.001*
Ornithopoda	0.845	7.604	<0.001*	0.845	7.602	<0.001*

Note: Symbols as in Table 8.5.

postural specializations in this group (Wilson & Sereno, 1998; Wilson & Carrano, 1999). Appearing during the Middle Jurassic (Wilson & Sereno, 1998), macronarians attained very large body sizes (e.g., *Brachiosaurus, Chubutisaurus, Argentinosaurus*), but eventually produced taxa as "small" as elephants (saltasaurines). It has been suggested that at least one taxon (*Magyarosaurus*) was the product of dwarfing within Macronaria (Jianu & Weishampel, 1999).

Coelurosaurs are most noteworthy as the clade including birds (although avians are excluded from this study), and marked size decrease has been specifically implicated in the origin of the latter group (Sereno, 1997; Carrano, 1998). However, this pattern extends well into the more basal nodes of Coelurosauria, with the largest taxa (tyrannosaurids) also representing the most basal major clade in the group. Only therizinosaurs—sister taxa to oviraptorosaurs—show a significant reversal of the size-decrease trend. Furthermore, coelurosaurs include the most dramatic size decrease in all of Dinosauria: five orders of magnitude from 1,000-kg tyrannosaurs to 0.1-kg basal avians. (If Neornithes are included, this size decrease spans *seven* orders of magnitude, down to 0.001-kg hummingbirds.)

Trend analyses do not produce consistent results for all groups or for all methods. Table 8.10 shows that several clades show characteristics of either active or passive trends depending on the test employed. Specifically, the ancestor-descendant test suggests that size increases in nearly all groups are the result of active trends, whereas many saurischian trends are characterized as passive under the minimum and modified minimum tests. A few of the passive trends in the minimum test results are identified
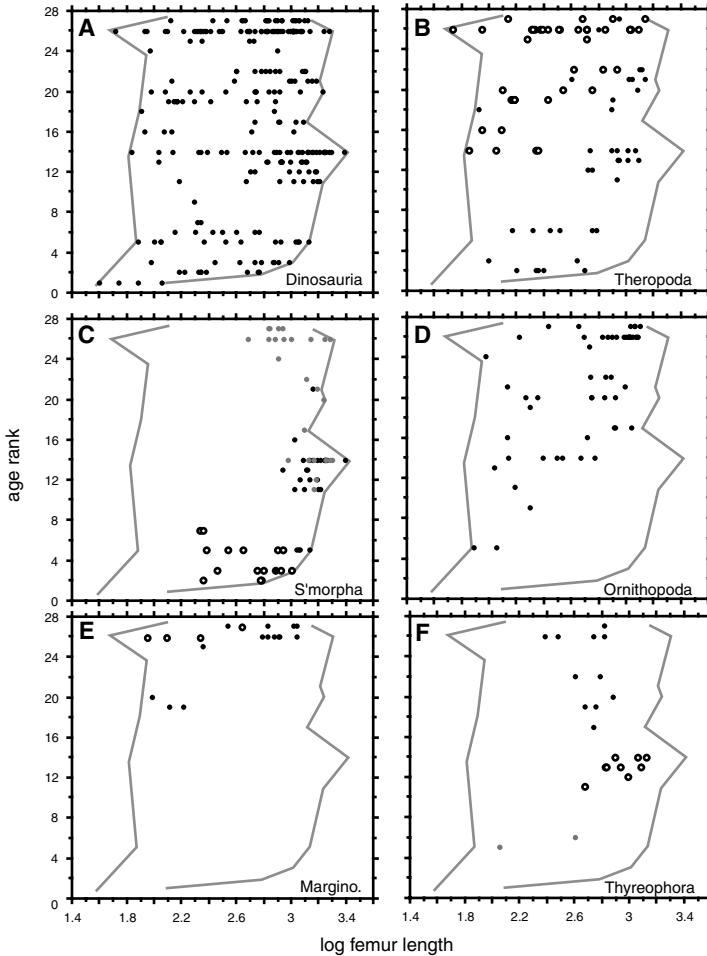

Figure 8.6. Minimum test results. Age rank is plotted against log femur length for Dinosauria and several representative ingroup clades. The gray lines indicate the total distribution for Dinosauria for successive ingroup graphs. (A) Dinosauria. (B) Theropoda: open circles, Coelurosauria; closed circles, all other theropods. (C) Sauropodomorpha: open circles, Prosauropoda; gray circles, Macronaria; closed circles, other sauropods.(D) Ornithopoda. (E) Marginocephalia: open circles, Pachycephalosauria; closed circles, Ceratopsia. (F) Thyreophora: gray circles, basal thyreophorans; open circles, Stegosauria; closed circles, Ankylosauria.

Table 8.8. Ancestor-descendant test results, using taxa larger than the mean size for each variable

Group	FL			FAP			FML		
	+	−	χ^2	+	−	χ^2	+	−	χ^2
Dinosauria	193	77	49.837*	157	69	34.265*	158	66	39.786*
Saurischia	116	53	23.485*	94	44	18.116*	91	43	17.194*
Theropoda	56	9	33.985*	45	10	22.273*	40	9	19.612*
Coelurosauria	19	0	19.000*	14	2	9.000*	12	2	7.143*
Sauropodomorpha	60	44	2.462	49	34	2.711	51	34	3.400
Prosauropoda	13	3	6.250*	11	3	4.571*	10	5	1.667
Sauropoda	47	41	0.409	38	31	0.710	41	29	2.057
Macronaria	21	19	0.100	15	16	0.032	20	15	0.714
Ornithischia	77	24	27.812*	63	25	16.409*	67	23	21.511*
Thyreophora	18	5	7.348*	14	3	2.882	22	7	7.759*
Stegosauria	9	5	1.143	6	3	1.000	10	5	1.667
Ankylosauria	9	0	9.000*	6	0	6.000*	11	2	6.231*
Marginocephalia	15	2	9.941*	13	2	8.067*	14	2	9.000*
Pachycephalo	0	0	N/A	0	0	N/A	1	0	1.000
Ceratopsia	15	2	9.941*	13	2	8.067*	13	2	8.067*
Ornithopoda	44	17	11.951*	36	20	4.571*	31	14	6.422*

Note: FL, femoral length; FAP, femoral anteroposterior diameter; FML, femoral mediolateral diameter. Other abbreviations as in Table 8.1.

as active trends by the modified minimum test. The subclade test is generally inconclusive.

Some of the differences between the minimum and modified minimum tests are probably due to the nature of the dinosaur fossil record. Because many time intervals are poorly sampled, numerous dinosaur taxa appear later in time than their phylogenetic relationships suggest—i.e., later than the first appearance of their sister taxon. Although the *order* of appearance is not strongly affected (as demonstrated by strong age rank-clade rank correlations), the specific pattern is. As basal taxa are drawn into later time intervals, the size distribution of these primitive forms is drawn with them. This effect is mitigated by using the modified minimum test: by restoring primitive taxa to their "proper" position relative to other taxa, the size distribution is modified.

This discrepancy suggests that the active results may be inaccurate. It is largely due to the presence of small-bodied, derived taxa late in the Mesozoic, because these late-surviving taxa retain low patristic-distance values. Here the incompleteness of the fossil record is probably
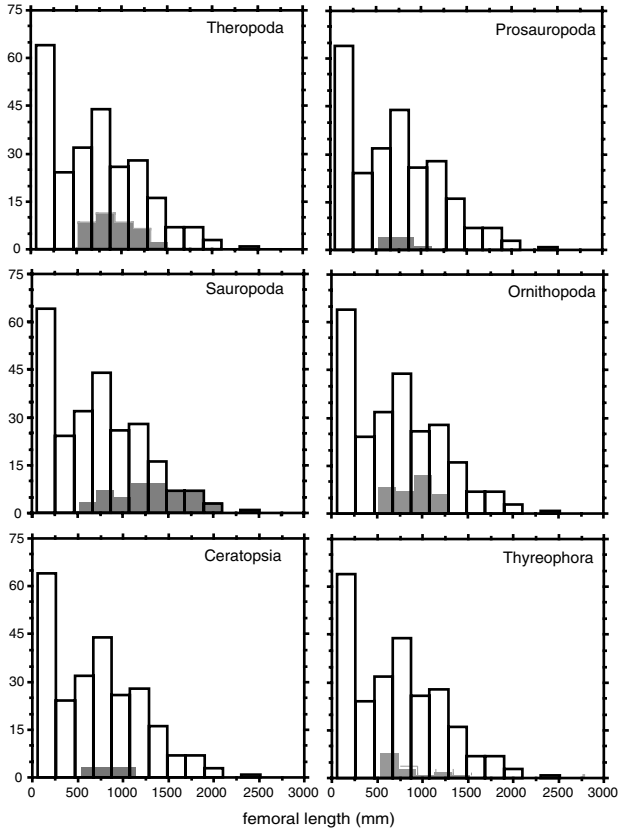
Figure 8.7. Subclade test results for representative ingroup clades. In each graph, the overall distribution for Dinosauria is shown by the open bars; each clade is represented by the black bars within it.

Table 8.9. Subclade test results, using raw data from subclades with means larger than (or close to) that for Dinosauria

	FL		FAP		FML	
Group	**Mean**	**Skew**	**Mean**	**Skew**	**Mean**	**Skew**
Dinosauria	717.71	0.618	75.45	1.025	98.31	0.930
Tetanurae	943.01	−0.086	100.20	1.212	114.13	1.154
Sauropoda	1324.73	0.188	138.66	0.905	201.02	0.033
Macronaria	1240.32	0.094	115.44	1.532	193.34	0.102
Iguanodontia	892.73	−0.477	100.38	−0.115	110.26	0.131
Stegosauria	911.89	0.109	96.90	1.043	133.50	−0.218

Note: FL, femoral length; FAP, femoral anteroposterior diameter; FML, femoral mediolateral diameter.
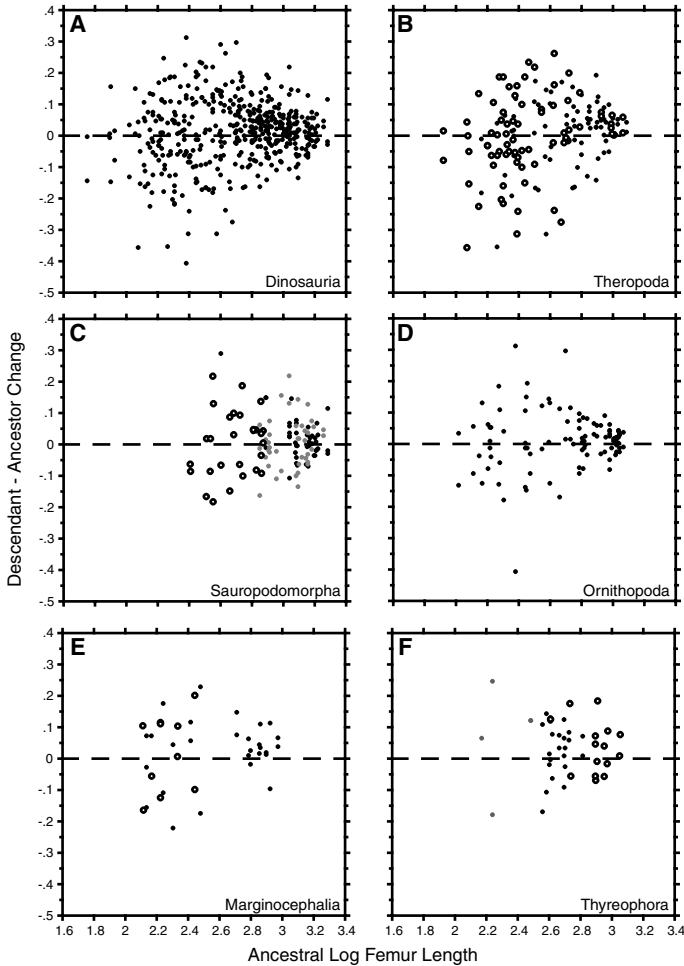
Figure. 8.8. Difference-versus-ancestor plots. The difference between each descendant and its reconstructed ancestor is plotted against the ancestral log femur length for that pair. The dashed line indicates zero change. (A) Dinosauria. (B) Theropoda: open circles, Coelurosauria; closed circles, all other theropods. (C) Sauropodomorpha: open circles, Prosauropoda; gray circles, Macronaria; closed circles, other sauropods. (D) Ornithopoda. (E) Marginocephalia: open circles, Pachycephalosauria; closed circles, Ceratopsia. (F) Thyreophora: gray circles, basal thyreophorans; open circles, Stegosauria; closed circles, Ankylosauria.

interfering with the underlying pattern. Because small-bodied forms are likely to be more poorly sampled, the forms that are sampled will have patristic distance values that are too low relative to those of large-bodied forms. For example, it is highly improbable that the ornithopod *Thescelosaurus* actually represents a single surviving form that originated in the

Table 8.10. Summary of trend analyses results

Group	min	mod min	anc-desc
Dinosauria	+++	+++	+++
Saurischia	− − −	− − −	+++
Theropoda	− − −	− − −	+++
Coelurosauria	− − −	− − −	+++
Sauropodomorpha	+++	+++	+++
Prosauropoda	− − −	− − −	+++
Sauropoda	− − −	− − −	+++
Macronaria	− + +	+++	+ − +
Ornithischia	+++	+++	+++
Thyreophora	+++	+++	+++
Stegosauria	+ − +	+++	+++
Ankylosauria	− − −	+++	+++
Marginocephalia	+++	+++	+++
Pachycephalo	+++	+++	00+
Ceratopsia	+++	+++	+++
Ornithopoda	+++	+++	+++

Note: min, minimum test; mod min, modified minimum test; anc-desc, ancestor-descendant test; +, active; −, passive; 0, insufficient sample. Each symbol refers to one variable illustrating that pattern, in the order FL, FAP, FML. Symbols in boldface represent significant trends for the ancestor-descendant test.

Early Jurassic and survived into the Maastrichtian without any other sister taxa along its lineage. Instead, its patristic distance is made artificially low by the absence of an intervening record. This problem is most apparent at the low end of the body-size range and affects most of the ornithischian lineages. The comparatively (and disproportionately) well-studied theropods do not exhibit this problem to the same degree, nor do the large-bodied sauropodomorphs. In this light, it is particularly interesting that the size decreases in Coelurosauria and Macronaria appear to be active trends.

The presence of upper and lower bounds is more difficult to discern. If the passive pattern most accurately describes the size increase in dinosaurs, then a lower size bound likely exists. Circumstantial evidence—specifically, the total lack of adult dinosaurs below FL $\sim$ 45 mm and nonoverlap of dinosaurian and Mesozoic mammalian size ranges—supports such an inference. Similarly, size reduction in macronarians may be a reflective response to an upper size bound. This upper bound is very similar for most nonsauropod dinosaurs (in the 10-ton range), with sauropods alone achieving sizes a full order of magnitude larger. Why sauropods

were uniquely free of the size constraint evident in other groups remains a mystery.

This evident complexity is manifest across several hierarchical levels, highlighting one problem fundamental to macroevolutionary trend analysis: scale. The pattern described for Dinosauria does not hold for all its constituent clades; is it an artifact? Could the pattern for each clade be broken down further, possibly revealing ingroup patterns that are equally discordant with the larger one? At some point these clades will have been atomized to their furthest level (in the case of fossil taxa, that of specimens), but long before this point we will have ceased to focus on "macroevolutionary" patterns.

Pattern Biases and Robustness

Certainly the patterns described here are potentially sensitive to analytical biases. For example, SCP attempts to minimize the sum of squared changes across all branches of the tree but in doing so effectively minimizes (although does not eliminate) trends within the data. Thus, it is not surprising that the values for overall mean and median changes are very close to zero. In light of this, it is considered significant that SCP fails to reduce these values to zero, and this "failure" is interpreted as support for the presence of a general size trend in the data.

The data sample itself is certainly not an unbiased representation of true dinosaur diversity, but it is difficult to assess the specific effects of various potential factors. Certain time periods are poorly sampled, and others exhibit strikingly dense sampling. Yet these variations can affect taxa of all sizes alike, especially when particular times and places have no known dinosaur record whatsoever. In these cases, there is no clear bias against any specific body size.

Smaller taxa face a number of preservational biases in the fossil record, the result being that smaller taxa should be relatively less common overall. This tendency should become more pronounced in older strata, as overall preservation quality (and rock outcrop area) declines. The expected result would be a record that lacks smaller taxa in older sediments. In fact, the actual record finds that early dinosaurs are predominantly small-bodied forms. The predicted taphonomic bias should be opposite this pattern, but instead small forms are most commonly found basally in their respective clades (and therefore earlier in time).

Interestingly, larger taxa also face a sampling bias—one involving collection. Large dinosaurs are more difficult to collect and harder to prepare and curate than smaller forms. As a result, collectors often sample—and museums curate—larger dinosaurs less frequently and less thoroughly

than smaller forms (see Dodson 1996, 297, endnote 36 for one such story). As a result, although many small dinosaur taxa are certainly entirely missing from the current fossil record, it is equally likely that some larger taxa have been discovered but deliberately left uncollected.

Finally, the fundamental link between these patterns and the phylogenetic history of Dinosauria means that subsequent changes and refinements in dinosaur systematics will result in alterations to these patterns. These changes are unavoidable as new taxa are discovered and placed into the existing phylogenetic context, but also as that context shifts with future study. Nevertheless, the most basic aspects of the patterns described here are likely to remain relatively robust to such changes. For the overall pattern of size increase to be reversed, the currently sampled dinosaur record would have to entirely misrepresent the actual pattern— a large number of derived, smaller taxa would have to be missing along with a large number of primitive, larger taxa.

Underlying Mechanisms

In quantitatively documenting the patterns of body-size evolution in dinosaurs, this paper provides a structure within which hypotheses of underlying causal mechanisms, scenarios of competition and purported structural limits may be framed and, ultimately, tested. Although these are not exhaustively treated here, a few points warrant discussion.

The dinosaurian pattern of body-size evolution appears to be consistent whether within-lineage or among-lineage patterns are compared, implying that it is not an artifact of the latter (e.g., caused by preferential extinction of small-bodied lineages). The predominant absence of derived small-bodied taxa in numerous clades instead suggests that there is a significant within-lineage trend for size increase. However, it is also likely that this trend is the result of several competing (and coordinating) influences rather than one single underlying mechanism, as was recently suggested for similar patterns in North American Cenozoic mammals (Alroy, 1998). The resolution of the dinosaurian record makes investigation of these potential mechanisms difficult.

Without identifying any underlying mechanism per se, it can still be noted that size changes occur passively during the evolution of dinosaurs (and many other vertebrates). However, if these trend analyses are accurate, then dinosaurs are not characterized by a uniform pattern of body-size increase (or even of body-size change). Instead, numerous groups show patterns suggestive of active trends, including many ornithischians but few saurischian clades. The strongest active signal is present in Ornithopoda, which exhibits a steady progression from small to large body

sizes through the Mesozoic. A similar trend is evident in Ceratopsia and probably also in Pachycephalosauria. For the reasons discussed above, these active signals are viewed with suspicion.

Like many animal groups, dinosaurs (and most of their constituent clades) originated at small body sizes relative to their later size diversity. Possible reasons for the commonness of this pattern among animals have been discussed elsewhere (Cope, 1896; Simpson, 1953; Stanley, 1973). One consequence is that the larger populations and higher turnover rates among smaller taxa would favor the more frequent generation of descendant taxa with different body sizes. With the presence of a lower size bound (structural, ecological, or competitive), the result would be a tendency to expand the size range at its upper end until some upper size limit were reached. This general pattern is observed in dinosaurs, having originated at sizes near the minimum of their range, as well as in most less-inclusive clades.

More recently, Burness et al. (2001) noted a strong correlation between the maximum body size in endotherms and ectotherms and the land area occupied by these taxa, which they linked to metabolic requirements. However, the authors noted that dinosaurs seem to achieve significantly larger sizes than would be predicted by any of the metabolic equations, based on estimated Mesozoic land areas. This suggests that whereas land area may impose one constraint on maximum body size, it may not represent the only such constraint. An additional factor (or factors) may act to restrict maximum body sizes for mammals below that seen in dinosaurs. For example, Farlow (1993) suggested that theropods were able to achieve significantly larger body sizes than carnivorous terrestrial mammals due to a combination of factors, potentially including higher population densities, lower metabolic rates, and higher turnover rates. Similar differences between dinosaurs and mammals may have extended to other dinosaur groups as well (Farlow et al., 1995).

Janis and Carrano (1992) suggested that mammals are constrained below a certain maximum size due to the positively allometric relationship between gestation period and body size. Increasingly large mammals require disproportionately long gestation times, which in turn limit reproductive turnover rates and increase susceptibility to population perturbations. Dinosaurs, as oviparous animals, were likely free from this constraint and able to achieve very large body sizes with little or no impact on reproductive turnover. This assumes that both groups (or, indeed, any group) eventually would have evolved both smaller and larger taxa unless and until some constraint prevented them from further doing so. However, birds do not appear to have benefited from oviparity in the same

manner. Perhaps birds (even flightless forms) were constrained from reaching very large body sizes by the numerous biological modifications that occurred during the origin of flight, much as they appear to be constrained from evolving viviparity (Blackburn & Evans, 1986).

Conclusions

This study clearly demonstrates a significant, consistent pattern of body size increase in nonavian dinosaurs through the Mesozoic. This pattern is evident in nearly every ingroup clade, although it is difficult to detect in poorly sampled ones (e.g., Pachycephalosauria). Only two clades—Coelurosauria and Macronaria—are characterized by size decreases. These patterns are detected when either phylogenetic or temporal data are used, but the former allows more precision and alleviates problems associated with long unsampled lineages.

Trend analyses produce some conflicting interpretations of these patterns, but most size increases are ascribed to active patterns in ancestor-descendant and some minimum and modified minimum tests. Subclade test results are inconsistent. The overall pattern for Dinosauria appears to be due to passive trends, and there is some evidence of the existence of both lower and upper bounds. Size increases in ornithischians tend to be more strongly described as active compared with those in saurischians, but this is likely skewed by the poor record of small-bodied forms. Sauropods appear to have reached the upper bound on size, and macronarians may have decreased in size preferentially partially in response to this.

These patterns are unlikely to be the result of various sampling or methodological biases, despite the obvious incompleteness of the dinosaur fossil record and the dependence of this study on the underlying phylogenetic framework. In addition, the complexity of these patterns suggests that no single explanation is appropriate to describe body-size evolution in all dinosaurs. Instead, future studies should focus on less-inclusive dinosaur clades as taxa within them become more densely sampled. Parallel comparisons between dinosaur and terrestrial mammal clades are also likely to be fruitful in illuminating similarities and differences in body-size evolution in these two phylogenetically independent groups.

and Chris Sidor. The data used in this study were gathered at many different institutions throughout the world, thanks to the hospitality of many curators, collections managers, and other colleagues. Finally, this manuscript was improved thanks to the comments of two anonymous reviewers.

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Appendix 8.1.

Body-size measurements used in this study: FL, femoral length; FAP, femoral anteroposterior diameter; FML, femoral mediolateral diameter. Original measurements in millimeters. Data were log-transformed before analysis.

Institutional abbreviations: AM, Albany Museum, Grahamstown, South Africa; AMNH, American Museum of Natural History, New York; ANSP, Academy of Natural Sciences, Philadelphia; BHI, Black Hills Institute, Hill City, South Dakota; BMNH, The Natural History Museum, London; BSP, Bayerische Staatssammlung für Paläontologie, München; BYU, Brigham Young University, Provo, Utah; CEUM, College of Eastern Utah Prehistoric Museum, Price; CH/P.W., Department of Mineral Resources, Bangkok; CM, Carnegie Museum of Natural History, Pittsburgh; CMNH, Cleveland Museum of Natural History, Ohio; CV, Municipal Museum of Chungqing, China; FMNH, Field Museum of Natural History, Chicago; GMNH, Gunma Museum of Natural History, Japan; GMV, China Geological Museum, Beijing; HMN, Humboldt Museum für Naturkunde, Berlin, Germany; IGM/GIN, Institute of Geology, Ulan Baatar, Mongolia; IRSNB, Institute Royale des Sciences Naturelles de Belgique, Brussels; ISI, Indian Statistical Institute, Kolkata; IVPP, Institute of Palaeoanthropology and Palaeontology, Beijing; JM, Jura-Museum, Eichstatt, Germany; KMV, Kunming Museum of Vertebrate Palaeontology, China; LV, Laboratory of Vertebrate Palaeontology, Geological Survey of China, Beijing; MACN, Museo Argentino de Ciencias Naturales "Bernardino Rivadavia," Buenos Aires; MAFI, Geological Institute of Hungary, Budapest; MCN, Museu de Ciências Naturais, Rio Grande do Sul, Brazil; MCNA, Museo de Ciencias Naturales de Alava, Vitoria-Gasteiz, Spain; MCZ, Museum of Comparative Zoology, Harvard University, Cambridge; MDE, Musée des Dinosaures, Esperaza, France; MIWG, Museum of Isle of Wight Geology, Sandown, U.K.; ML, Museu da Lourinha, Portugal; MLP, Museo de La Plata, Argentina; MNA, Museum of Northern Arizona, Flagstaff; MNHN, Muséum National d'Histoire Naturelle, Paris; MNN, Musée National d'Histoire Naturelle, Niamey, Niger; MNUFR, Mongolian National University, Ulan Baatar; MOR, Museum of the Rockies, Bozeman, Montana; MPCA, Museo Provincial "Carlos Ameghino," Cipoletti, Argentina; MPEF, Museo Paleontolòlogico "Egidio Feruglio," Trelew, Argentina; MUCP, Museo de Ciencias Naturales de la Universidad Nacional del Comahue, Neuquén, Argentina; NCSM, North Carolina State Museum of Natural Sciences, Raleigh; NGMC, National Geological Museum, Beijing; NIGP, Nanjing Institute of Geology and Palaeontology, China; NMC, Canadian Museum of Nature, Ottawa; OMNH, Sam Noble Oklahoma Museum of Natural History, University of Oklahoma, Norman; OUM, Oxford University Museum, UK; PIN, Paleontological Institute, Moscow; PMU, Palaeontological Museum, University of Uppsala, Sweden; POL, Musée de Poligny, Jura, France; PVSJ, Museo Provincial de San Juan, Argentina; PVL, Instituto Miguel Lillo, Tucumán, Argentina; PVPH, Paleontología de Vertebrados, Museo "Carmen Funes," Plaza

Huincul, Argentina; QG, Queen Victoria Museum, Harare, Zimbabwe; ROM, Royal Ontario Museum, Toronto; RTMP, Royal Tyrrell Museum of Palaeontology, Drumheller, AB; SAM, South African Museum, Cape Town; SGM, Société Geologique de Morocco, Rabat; SMNS, Staatliches Museum für Naturkunde, Stuttgart; SMU, Shuler Museum of Paleontology, Southern Methodist University, Dallas; TATE, Tate Geological Museum, Casper College, Wyoming; UA, Université d'Antananarivo, Madagascar; UALB, University of Alberta, Edmonton, Canada; UCMP, University of California Museum of Paleontology, Berkeley; UC OBA, Department of Organismal Biology and Anatomy, University of Chicago; UHR, Hokkaido University, Sapporo, Japan; UMNH, Utah Museum of Natural History, Salt Lake City; UNPSJB, Universidad Nacional de la Patagonia "San Juan Bosco," Comodoro Rivadavia, Argentina; UPLR, Universidad Provincial de La Rioja, Argentina; USNM, National Museum of Natural History, Smithsonian Institution, Washington, DC; YPM, Peabody Museum of Natural History, Yale University, New Haven, Connecticut; ZDM, Zigong Dinosaur Museum, Dashanpu, China; ZPAL, Muzeum Ziemi Polska Akademia Nauk, Warsaw.

Table A8.1. List of taxa, specimens, and measurements used in this study

Taxon	Specimen	FL	FAP	FML
Dinosauriformes				
Lagerpeton chanarensis	PVL 06	76.8	7.7	
Lagosuchus talampayensis	UPLR 09	40.6	2.5	122.2
Lewisuchus admixtus	PVL 4629	1115.0		
	PVL 3456		112.0	
	PVL 3454			7.7
Marasuchus lilloensis	PVL 3871	56.3		5.1
	PVL 3870		3.7	
Dinosauria				
Saurischia				
Theropoda				
Eoraptor lunensis	PVSJ 512	154.0	19.6	12.7
Guaibasaurus candelariensis	MCN-PV 2355	214.0	25.0	19.0
Herrerasaurus ischigualastensis	PVL 2566	482.0	54.4	55.1
Staurikosaurus pricei	MCZ 1669	220.0	24.7	
Coelophysoidea				
Coelophysis bauri	UCMP 129618	245.0	22.0	19.0
"Dilophosaurus" sinensis	KMV 8701	587.0		
Dilophosaurus wetherilli	UCMP 37302	552.0	35.9	67.8
Liliensternus liliensterni	HMN R.1291	424.0	37.8	31.1

Table A8.1. (*continued*)

Taxon	Specimen	FL	FAP	FML
Procompsognathus triassicus	SMNS 12951	96.0	9.4	7.1
Sarcosaurus woodi	BMNH 4840	321.0	31.4	35.9
Segisaurus halli	UCMP 32101	142.9		
Syntarsus kayentakatae	MNA V2623	272.0	21.6	23.1
Syntarsus rhodesiensis	QG 1	203.0	16.5	17.0
Neoceratosauria				
Carnotaurus sastrei	MACN-CH 894	1018.0	95.6	94.6
Ceratosaurus nasicornis	UMNH VP 5278	759.0	71.7	90.4
Deltadromeus agilis	BSP 1912 VIII 70	1230.0	138.0	147.0
Elaphrosaurus bambergi	HMN Gr. S. 38–44	529.0	59.0	45.0
Genusaurus sisteronis	MNHN Bev-1	390.0	34.1	33.7
"*Indosuchus raptorius*"	ISI R 401–454	872.0	77.0	
Ligabueino andesi	MACN-N 42	81.4		7.0
Masiakasaurus knopfleri	UA 8681	202.5		
	UA 8684		21.5	19.8
Xenotarsosaurus bonapartei	UNPSJB-Pv 184	611.0	77.0	69.0
Tetanurae				
Metriacanthosaurus parkeri	OUM J.12114	849.0	85.0	96.1
Piatnitzkysaurus floresi	PVL 4073	548.0	67.3	91.3
Spinosauroidea				
Baryonyx walkeri	BMNH R.9951		92.0	100.0
"*Brontoraptor* sp.*"	TATE 1012	832.6	110.9	123.6
Afrovenator abakensis	UC OBA 1	761.0	65.0	83.0
Eustreptospondylus oxoniensis	OUM J.13558	510.0	56.1	56.2
Megalosaurus bucklandi	OUM mount	830.0	102.7	111.3
Suchomimus tenerensis	MNN GDF 500	1080.0	85.7	145.2
Allosauroidea				
Acrocanthosaurus atokensis	NCSM 14345	1180.0		
	SMU 74646		189.7	214.2
Allosaurus fragilis	AMNH 630	1001.0		133.6
	AMNH 680		115.7	
Carcharodontosaurus saharicus	BSP 1922 X46	1260.0		126.0
Giganotosaurus carolinii	MUCPv-CH-1	1350.0	151.0	
Neovenator salerii	MIWG 6348	780.0		90.0
Saurophaganax maximus	OMNH 01123	1135.0	107.0	150.0
Sinraptor dongi	IVPP 87001	869.5	78.7	91.4
Sinraptor hepingensis	ZDM 0024	995.0		100.0

(*continued*)

Table A8.1. (*continued*)

Taxon	Specimen	FL	FAP	FML
Yangchuanosaurus magnus	CV 00216	1200.0		
Yangchuanosaurus shangyouensis	CV 00215	850.0	96.0	
Coelurosauria				
Coelurus fragilis	YPM 1991	220.0	17.0	
Compsognathus longipes	MNHN CNJ 79	109.7	9.2	
Dryptosaurus aquilunguis	ANSP 9995/10006	778.0	83.5	88.0
Nedcolbertia justinhoffmani	CEUM 5071	144.8		18.2
Nqwebasaurus thwazi	AM 6040		11.0	
Ornitholestes hermanni	AMNH 619	215.0	17.0	24.1
Sinosauropteryx prima	NIGP 127587	86.4		
	NIGP 127586		6.0	
Tyrannosauroidea				
Albertosaurus sarcophagus	ROM 807	1066.0	85.2	123.6
Alectrosaurus olseni	AMNH 6554	661.0	72.3	
Daspletosaurus n. sp.	OMNH 10131	1033.0	118.0	132.0
Daspletosaurus torosus	AMNH 5438	1030.0		108.3
	FMNH 5336		125.3	
Gorgosaurus libratus	NMC 2120	1040.0		
	NMC 530		133.0	103.0
Tarbosaurus bataar	PIN 551-1	1200.0	110.0	
	PIN 551-2			110.0
Tyrannosaurus rex	FMNH PR 2081	1342.5		188.1
	BHI 3033		168.0	
Ornithomimosauria				
Anserimimus planinychus	GIN AN MPR 100/300	433.0		
Archaeornithomimus asiaticus	AMNH 6570	402.0	46.0	
Dromiceiomimus brevitertius	NMC 12228	468.0		
	ROM 852		41.0	33.5
Gallimimus bullatus	ZPAL MgD-I/1	680.0	63.1	59.2
Ornithomimus edmontonensis	NMC 12441	500.0		
	ROM 851		29.2	25.3
Struthiomimus altus	AMNH 5375	501.0	39.8	
	AMNH 5339			44.0
Alvarezsauria				
Alvarezsaurus calvoi	MUCPv-54		9.7	10.3
Mononykus olecranus	GIN 107/6	132.5	11.5	10.3
Parvicursor remotus	PIN 4487/25	52.6	3.3	3.1

Table A8.1. (*continued*)

Taxon	Specimen	FL	FAP	FML
Oviraptorosauria				
Alxasaurus elesitaiensis	IVPP 88402	555.0	70.0	70.0
Avimimus portentosus	PIN 3907/1	185.9	16.3	14.3
Beipiaosaurus inexpectus	IVPP V.11559	260.0		38.0
Caudipteryx dongi	IVPP 12344	149.0	16.0	17.0
Caudipteryx zoui	NGMC 97-9-A	149.0		
Chirostenotes pergracilis	RTMP 79.30.1	311.0	16.6	30.7
Ingenia yanshini	GIN 100/30	228.1	22.2	22.8
Microvenator celer	AMNH 3041	122.8	11.2	10.7
Oviraptor philoceratops	AMNH 6517	262.0		
Segnosaurus galbinensis	GIN 100/82	840.0		
Deinonychosauria				
Achillobator giganticus	MNUFR-15	505.0		67.3
Deinonychus antirrhopus	MCZ 4371	335.0	32.1	37.8
Saurornithoides mongoliensis	AMNH 6516	198.0		
	IVPP V.10597		6.5	6.5
Saurornitholestes langstoni	RTMP 88.121.39	212.0	22.1	15.6
Sinornithoides youngi	IVPP V.9612	140.0	11.0	
Sinornithosaurus millenii	IVPP V.12811	148.0	9.5	
Troodon formosus	MOR 748	317.0		
	MOR 553s		32.8	32.9
Velociraptor mongoliensis	IGM 100/988	238.0	25.2	26.1
Protarchaeopteryx robusta	GMV 2125	120.0		16.0
Archaeopteryx lithographica	Solnhofen specimen	70.0		
	JM SoS 2257		2.9	
Rahonavis ostromi	UA 8656	86.9	6.0	5.5
Prosauropoda				
Ammosaurus major	YPM 208	221.0	33.2	42.3
Anchisaurus polyzelus	YPM 1883/2128	210.0	20.0	24.3
Camelotia borealis	BMNH R.2870	985.7	114.2	132.8
Euskelosaurus brownii	SAM 3349/02	590.0	70.0	88.0
Gyposaurus sinensis	IVPP V.27	235.5		
	IVPP V.26		28.0	
	IVPP V.43			27.7
Jingshanosaurus xinwaensis	LV003	845.0		
Lufengosaurus huenei	IVPP V.98	780.0		
	IVPP V.82			115.0

Taxon	Specimen	FL	FAP	FML
Massospondylus carinatus	QG 1159	335.0	40.6	42.1
Jachal *Massospondylus*	PVSJ uncat.	220.0	25.6	24.9
Melanorosaurus readi	SAM 3450	583.3	59.1	81.6
Plateosaurus engelhardti	SMNS uncat.	750.0	82.3	90.8
Plateosaurus poligniensis	POL 75	821.0		138.6
	POL 76		96.0	
Riojasaurus incertus	PVL 3808	608.0		106.2
	PVL 3669		67.2	
Sellosaurus gracilis	SMNS 12843	551.0		
	SMNS 17928		65.1	
	SMNS 5715			66.9
Thecodontosaurus antiquus	SMNS uncat.	280.0	43.4	
Yunnanosaurus huangi	IVPP AS V20	435.0	54.6	60.0
Sauropoda				
Gongxianosaurus shibeiensis	holotype	1164.0		270.0
Isanosaurus attavipachi	CH4-1	760.0	71.5	121.6
Vulcanodon karibaensis	QG 24	1100.0	140.0	174.0
Eusauropoda				
Barapasaurus tagorei	ISI R.50	1365.0	131.0	187.0
Cetiosaurus oxoniensis	OUM J.13899	1626.0		305.0
Datousaurus bashanensis	IVPP V.7262	1057.0	147.0	
Kotasaurus yamanpalliensis	111/S1Y/76	1130.0	80.0	160.0
Lapparentosaurus madagascariensis	"individu taille max"	1590.0	240.0	
Mamenchisaurus constructus	IVPP V.948	1280.0	207.0	
Mamenchisaurus hochuanensis	IVPP holotype	860.0		
Omeisaurus junghsiensis	IVPP AS holotype		103.0	
Omeisaurus tianfuensis	ZDM T5701	1310.0		206.0
Patagosaurus fariasi	PVL 4076	1542.0	135.5	
	PVL 4170			255.0
Shunosaurus lii	IVPP V.9065	1250.0		188.0
Volkheimeria chubutensis	PVL 4077	1156.0	148.0	75.1
Neosauropoda				
Diplodocoidea				
Amargasaurus cazaui	MACN-N 15	1050.0	128.8	180.0
Amphicoelias altus	AMNH 5764	1770.0	210.0	216.0
Apatosaurus ajax	YPM 1860	2500.0		
Apatosaurus excelsus	FMNH 7163	1830.0	310.0	310.0

Table A8.1. (*continued*)

Taxon	Specimen	FL	FAP	FML
Apatosaurus louisae	CM 3018	1785.0	174.0	332.3
Barosaurus africanus	HMN NW 4	1361.0	150.6	204.2
Barosaurus lentus	AMNH 6341	1440.0	120.2	204.3
Cetiosauriscus stewarti	BMNH R.3078	1360.0	190.0	195.0
Dicraeosaurus hansemanni	HMN m	1220.0	142.5	
	HMN dd 3032			192.3
Diplodocus carnegii	CM 84	1542.0	174.0	
	CM 94			186.0
Diplodocus longus	YPM 1920	1645.0		
	AMNH 223		143.0	
Haplocanthosaurus delfsi	CMNH 10380	1745.0		
	CM 572		207.0	
Rayososaurus tessonei	MUCPv-205	1440.0		220.0
Macronaria				
"*Bothriospondylus madagascariensis*"	MNHN uncat.	1460.0	110.0	
Brachiosaurus altithorax	FMNH P25107	2000.0		365.0
Brachiosaurus brancai	HMN St	1913.0	151.7	299.0
Camarasaurus lentus	DINO 4514	1470.0		252.0
	CM 11338		86.5	
Camarasaurus supremus	AMNH 5761a	1800.0	255.0	
	GMNH-PV 101			228.0
Euhelopus zdanskyi	PMU R234	955.0	100.0	142.0
Titanosauriformes				
Aegyptosaurus baharijensis	BSP 1912 VIII 61	1290.0	75.0	223.0
Ampelosaurus atacis	MDE uncat. 1	802.0		157.5
	MDE uncat. 2		66.0	
Andesaurus delgadoi	MUCPv-132	1550.0		226.0
Argyrosaurus superbus	PVL 4628	1910.0	160.0	300.0
Chubutisaurus insignis	MACN 18222	1715.0	265.0	
Janenschia robusta	HMN IX	1330.0		
	HMN P		131.5	188.8
Laplatasaurus araukanicus	MLP-Av 1047/1128	1000.0		
Lirainosaurus astibiae	MCNA 7468	686.0		97.0
Magyarosaurus dacus	BMNH R.3856	488.0	43.7	66.8
Neuquensaurus australis	MLP-Cs 1121/1103	700.0	110.0	
Neuquensaurus robustus	MLP-Cs 1094	799.0		134.5
	MLP-Cs 1480		120.0	

Taxon	Specimen	FL	FAP	FML
Opisthocoelicaudia skarzynskii	ZPAL MgD-I/48	1395.0	108.0	280.0
Phuwiangosaurus sirinhornae	P.W. 1-1/1-21	1250.0	85.0	215.0
Rapetosaurus krausei	SUNY uncat.	687.0	91.2	63.1
Rocasaurus muniozi	MPCA-Pv 56	768.0		117.0
Saltasaurus loricatus	PVL 4017-80	875.0		164.6
	PVL 4017-79		90.0	
Tehuelchesaurus benitezii	MPEF-PV 1125	1530.0		243.0
Titanosaurus indicus	BMNH R.5934	865.0	67.3	80.9
Ornithischia				
Lesothosaurus diagnosticus	BMNH RU B.17	102.0	10.5	12.3
Pisanosaurus mertii	PVL 2577	170.3	9.8	6.6
Marginocephalia				
Ceratopsia				
Psittacosauridae				
Psittacosaurus mongoliensis	AMNH 6254	162.0		
	AMNH 6541			22.9
Psittacosaurus neimongoliensis	IVPP 12-0888-2	129.5	15.0	
Psittacosaurus sinensis	IVPP V.740-741	96.0	11.8	
Neoceratopsia				
Microceratops gobiensis	holotype	123.0		12.0
Montanoceratops cerorhynchus	MOR 300	346.0	33.7	42.6
Protoceratops andrewsi	AMNH 6416	226.0		
	AMNH 6424		28.3	29.0
Ceratopsidae				
Achelousaurus horneri	MOR 591	612.0	68.2	85.9
Centrosaurus apertus	AMNH 5427	800.0		
	YPM 2015		99.3	111.6
Chasmosaurus belli	ROM 839	825.0		
	BMNH R.4948		71.1	130.8
Chasmosaurus mariscalensis	UTEP P.37.3.031	676.5		97.5
Pachyrhinosaurus n. sp.	RTMP 87.55.57	676.0	99.6	106.5
Pentaceratops sternbergi	OMNH 10165	1096.0		226.5
	PMU R286		114.5	
Styracosaurus albertensis	AMNH 5372	749.0	112.0	
Triceratops horridus	AMNH 5033	1033.5	105.2	175.2
Triceratops prorsus	USNM 4842	1104.0	120.0	190.0

Table A8.1. (*continued*)

Taxon	Specimen	FL	FAP	FML
Pachycephalosauria				
Homalocephale calathoceros	GI SPS 100/1201	218.0		25.2
Micropachycephalosaurus hongtuyanensis	IVPP V.5542	125.8	14.2	
Prenocephale prenes	ZPAL MgD-I/104	221.5	22.0	26.0
Stegoceras validum	UALB 2	221.0	19.5	17.9
Stygimoloch spinifer	RTMP 97.27.4	441.0	46.7	69.1
Wannanosaurus yansiensis	IVPP V.447.1	90.0		
Thyreophora				
Scelidosaurus harrisonii	BMNH R.1111	403.0	56.5	52.4
Scutellosaurus lawleri	MNA.Pl.1752	114.0		
	MCZ 8797		19.2	12.2
Stegosauria				
Chialingosaurus kuani	IVPP V.2300	690.0		101.0
Chungkingosaurus sp. 2	CV 00205	670.0		110.0
Dacentrurus armatus	BMNH R.46013	1232.0		176.0
				135.0
Huayangosaurus taibaii	ZDM T7001	475.0		75.5
Kentrosaurus aethiopicus	HMN bbl	784.0	88.0	120.0
Lexovisaurus durobrivensis	BMNH R.1989	979.0	82.0	138.0
Stegosaurus stenops	YPM 1387	1157.0		
	AMNH 650		78.5	172.0
Stegosaurus ungulatus	YPM 1853	1348.0		
	YPM 1858		101.0	168.0
Tuojiangosaurus multispinus	CV 00209	872.0		141.0
Ankylosauria				
Ankylosauridae				
Ankylosaurus magniventris	AMNH 5214	660.0	76.4	136.8
Euoplocephalus tutus	AMNH 5404	547.5	85.6	
	ROM 784			103.2
Pinacosaurus grangeri	ZPAL MgD-II/1	243.0	23.0	42.0
Shanxia tianzhenensis	IVPP V.11276	402.6		67.7
Nodosauridae				
Edmontonia longiceps	NMC 8531	660.0		
Gastonia burgei	CEUM 1307	574.4		103.8
Hoplitosaurus marshi	USNM 4572	476.0	41.0	90.0
Nodosaurus textilis	YPM 1815	609.0	63.4	101.1

Table A8.1. (*continued*)

Taxon	Specimen	FL	FAP	FML
Polacanthus foxii	BMNH R.175	548.0	41.0	
Sauropelta edwardsi	AMNH 3032	764.0	88.0	104.0
Struthiosaurus transylvanicus	MCNA 6531/6540	300.0		
	BMNH R.11011		26.5	33.5
Ornithopoda				
Heterodontosauridae				
Abrictosaurus consors	BMNH RU B.54	77.1	8.4	6.2
Heterodontosaurus tucki	SAM K337	113.2	12.8	8.9
Euornithopoda				
Agilisaurus louderbacki	ZDM 6011	198.5	24.5	
Agilisaurus multidens	ZDM T6001	153.4	18.8	11.9
Fulgurotherium australe	NMV P208186	186.5	24.5	
	NMV P186326			17.4
Hypsilophodon foxii	BMNH R.5829	200.0		
	BMNH R.192a		22.2	21.2
Laosaurus consors	YPM 1882	246.0	29.5	27.1
Leaellynasaura amicagraphica	NMV P186047	135.0	17.0	
	NMV P186333			12.7
Orodromeus makelai	MOR 473	166.1		
	PU 23443		116.0	15.0
Othnielia rex	BYU ESM-163R	139.1	15.8	15.4
Parksosaurus warreni	ROM 804	270.0		
Thescelosaurus neglectus	AMNH 5891	448.0	56.3	61.2
Xiaosaurus dashanpensis	IVPP V.6730A	110.0		11.6
Yandusaurus honheensis	holotype			77.0
Ankylopollexia				
Camptosaurus dispar	YPM 1877	591.0		
	YPM 1880		80.0	100.3
Camptosaurus leedsi	BMNH R.1993	311.0	40.0	
Draconyx loureiroi	ML 434		64.0	66.0
Dryosaurus altus	CM 1949	470.0		
	YPM 1876		40.3	42.1
Dryosaurus lettowvorbecki	BMNH R.12777	343.0		45.0
	BMNH R.12278		42.0	
Gasparinisaura cincosaltensis	MUCPc-208	94.7	11.7	10.3
Rhabdodon priscum	MNHN uncat.	550.0	92.0	
	BMNH 3814			43.0

Taxon	Specimen	FL	FAP	FML
Tenontosaurus dossi	FWMSH 93B1	557.0		84.6
Tenontosaurus tilletti	UALB 22	700.0		
	YPM 5535		70.8	81.8
Valdosaurus canaliculatus	BMNH R.184/185	135.4	15.9	14.8
Valdosaurus nigeriensis	MNHN GDF 332	224.0	26.8	26.3
Iguanodontia				
Claosaurus agilis	YPM 1190	673.0		
Gilmoreosaurus mongoliensis	AMNH 6551	704.0	84.3	
Iguanodon atherfieldensis	BMNH R.3741	840.0		
	BMNH R.5764		79.0	
	IRSNB 1551			95.4
Iguanodon bernissartensis	BMNH 2649	1090.0	121.0	185.1
Iguanodon mantelli	BMNH 2650	822.0	84.8	131.4
Muttaburrasaurus langdoni	BMNH R.9604	990.0	108.9	168.8
Nipponosaurus sachaliensis	UHR 6590	544.0	57.0	59.0
Nanyangosaurus zhugeii	IVPP V.11821	517.0	62.0	
Orthomerus dolloi	BMNH 42955	495.0	57.0	57.0
Ouranosaurus nigeriensis	MNHN GDF 381	830.7	86.2	99.7
Probactrosaurus gobiensis	PIN AN SSR 2232/1	565.0		
Telmatosaurus transsylvanicus	MAFI v.10338	731.0		104.0
Hadrosauridae				
Anatotitan copei	AMNH 5730	1150.0	140.0	
Bactrosaurus johnsoni	AMNH 6553	781.0	103.0	
Corythosaurus casuarius	AMNH 5240	1080.0	130.0	
	RTMP 80.40.1			143.7
Edmontosaurus annectens	ROM 801	1278.5		
	NMC 8399		140.8	
	ROM 867			126.0
"*Gryposaurus*" *incurvimanus*	ROM 764	1053.0	122.8	
	RTMP 80.22.1			119.6
Gryposaurus notabilis	AMNH 5465	1215.0	137.8	
Hadrosaurus foulkii	ANSP 10005	1055.0		
Hypacrosaurus altispinus	NMC 8501	1074.0		
	AMNH 5217		106.8	
	RTMP 81.10.1			100.9
Hypacrosaurus stebingeri	MOR 773	1190.0	100.1	142.4
"*Kritosaurus*" *australis*	MACN-RN 02	790.0	80.7	109.2

(*continued*)

Table A8.1. (*continued*)

Taxon	Specimen	FL	FAP	FML
Lambeosaurus lambei	NMC 351	1117.0		
	ROM 6474		104.7	
	RTMP 82.38.1			155.2
Lambeosaurus magnicristatus	RTMP 66.4.1	1000.0	102.8	
Maiasaura peeblesorum	MOR 005 1989	960.0	138.3	
	MOR 005 7-12-91-45			93.3
Parasaurolophus cyrtocristatus	FMNH P27393	1041.5	124.5	142.4
Parasaurolophus walkeri	ROM 768	1059.0	146.8	98.7
Prosaurolophus blackfeetensis	MOR 454	855.0	62.7	104.8
Prosaurolophus maximus	RTMP 84.1.1	1050.0		
	ROM 7871		107.9	190.1
Saurolophus angustirostris	PIN 551-8	1200.0		
Saurolophus osborni	AMNH 5220	1150.0		
	AMNH 5271		145.5	