

Modeling growth rates for sauropod dinosaurs

Thomas M. Lehman and Holly N. Woodward

Abstract.—Sauropod dinosaurs were the largest terrestrial animals and their growth rates remain a subject of debate. By counting growth lines in histologic sections and relating bone length to body mass, it has been estimated that *Apatosaurus* attained its adult body mass of about 25,000 kg in as little as 15 years, with a maximum growth rate over 5000 kg/yr. This rate exceeds that projected for a precocial bird or eutherian mammal of comparable estimated body mass. An alternative method of estimating limb length and body mass for each growth line, and fitting the resulting age/mass data to the von Bertalanffy growth equation, yields a revised growth curve suggesting that *Apatosaurus* adult mass was reached by 70 years with a maximum growth rate of 520 kg/yr. This alternative method for growth rate determination can also be applied to histological studies of other sauropods. At only about half the mass of *Apatosaurus*, *Janenschia* took between 20 and 30 years to attain its adult size (over 14,000 kg). This result is supported by independent evidence of estimated bone apposition rates. Despite having an adult body mass greater than *Apatosaurus*, the titanosaurid *Alamosaurus* attained a mass over 32,000 kg within 45 years and a maximum growth rate of 1000 kg/yr. Titanosaurids may have been the fastest growing of all sauropods. Even so, sauropod growth rate estimates produced using the von Bertalanffy equation fall between those projected for reptiles and those for precocial birds of equivalent projected body mass. These results are comparable to those found for smaller dinosaurs, and suggest that sauropods grew at rates similar to other dinosaurs in spite of their great size.

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Introduction

Many dinosaurs grew to very large size, and so the question of how rapidly they grew has long been a subject of interest and debate (e.g., see reviews by Padian et al. 2001; Erickson 2005; Lehman 2007). How many years were required for large dinosaurs to achieve sexual maturity (age at first reproduction)? How long were their life spans? Answers to such questions are of natural interest, but are also essential for understanding dinosaurian population ecology (e.g., Case 1978b). For instance, on the basis of likely demographic and physiological factors, Dunham et al. (1989) theorized that large dinosaurs must have required more than five years and probably less than 20 years to reach maturity. Moreover, because growth rates of vertebrate animals vary with thermal physiology (Case 1978a), assessments of dinosaurian growth rates provide constraints on interpretation of their metabolism. The growth rate, age at sexual maturity, longevity, and metabolic rate of sauropod dinosaurs are matters of particular interest, con-

sidering these were the largest of all terrestrial animals.

Until recently, however, a means to actually determine absolute rates of growth for dinosaurs had not been presented. Many authors (e.g., Reid 1987, 1997; Sander 2000) concluded that the fibrolamellar bone tissue typical of dinosaurs indicates that they grew *continuously* and *rapidly* at rates comparable to those observed in extant mammals and birds. That many dinosaurs grew *continuously* seems unequivocal, because growth lines are often poorly developed or absent in their bones, and so there is commonly no evidence for periodic interruption of growth. However, just how *rapidly* dinosaurs grew remained a matter of conjecture because the very lack of growth lines made it impossible to determine the ages of individuals at different points in their life history, and thus provided no means to establish their actual rate of growth quantitatively. Moreover, Horner et al. (1999) pointed out that an alligator (ectothermic poikilotherm) growing under optimum conditions may produce bone tissues also lacking growth lines, and

conversely, an elk (endothermic homeotherm) growing under harsh conditions may produce bones with distinct lines of arrested growth (LAGs). As a result, bone tissue type and presence or absence of growth lines alone cannot establish the metabolic physiology of dinosaurs or their growth rates in absolute terms.

The general conclusion therefore that dinosaurs grew “rapidly” based on their bone tissue is an ambiguous assessment because rates of growth depend not only on how much growth an animal undergoes in a given span of time, but also on the size it ultimately attains. For example, a “slowly” growing alligator actually grows at a more rapid absolute rate (27 g/day) than a “rapidly” growing rodent (1–3 g/day), rabbit (10–20 g/day), gorilla (16 g/day), or human (8 g/day) (data from Case 1978a). Rodents, rabbits, and primates attain their adult size more quickly, but the alligator achieves a substantially greater adult weight. Of course, growth rate also varies during the life of an individual, from slow during the period immediately following birth, accelerating to reach the maximum growth rate approaching maturity, and then slowing again or halting completely at adult size. Hence, a means of standardization is required for suitable comparison of growth rates among different animals.

Growth rates are often measured in various ways, for example, in terms of increase in length (e.g., shoulder height, snout-vent length, total body length), and some have presented idealized growth curves for dinosaurs showing their increase in body length with age (e.g., Carpenter 1999; Sander et al. 2004). However, rates of growth in body length are difficult to compare among animals having, for example, short necks and tails (e.g., elephants) with those having relatively long necks and tails (e.g., sauropods). Instead, determinations of growth rate in terms of body weight allow for the most pertinent comparison of animals having markedly different body plans. The pioneering work of Case (1978a,b) provides the context in which to evaluate growth rates among vertebrates of varied adult body weight and varied physiology by comparing their maximum growth rate with their maximum adult body weight.

In Case’s studies, and in most of the works cited therein, the term “weight” is used interchangeably with the more appropriate term “mass,” and the two terms are likewise used synonymously here.

Recent studies of dinosaurian bone histology that use Case’s (1978a) means of comparison have revealed that many dinosaurs did not grow either continuously or rapidly. Many dinosaurs experienced interrupted or cyclic growth expressed histologically in the form of varied growth increments that range from striking LAGs with conspicuous annuli (Reid 1981) to less evident “resting lines” (Reid 1990), “modulations” (Ricqlès 1983), and subtle “polish lines” (Sander 2000). Thus, for some dinosaurs it is possible to apply the method of skeletochronology to determine the minimum ages of individuals at their time of death. Several methods (discussed below) can be used to estimate the weights of the individuals, and growth rates can be calculated for comparison with Case’s (1978a) data on extant animals. Such studies indicate that many dinosaurs actually did not grow extraordinarily rapidly, but instead had growth rates slightly higher than in extant reptiles and generally less than for birds or mammals of comparable adult weight. For example, quantitative estimates of growth rate based on skeletochronology were presented for a variety of dinosaurs by Erickson et al. (2001) and Lehman (2007); and although their methods are slightly different, the results obtained are similar. The model growth curves presented for several smaller dinosaurs (*Shuvuuia*, *Syntarsus*, *Troodon*, *Saurornitholestes*, *Psittacosaurus*, *Masospondylus*) are uncontroversial because they indicate maximum growth rates somewhat higher than those in extant reptiles, but lower than for extant birds and eutherian mammals of comparable adult body mass. Only the model growth rates for the hadrosaur *Maiasaura* and sauropod *Apatosaurus* exceed this (Erickson et al. 2001). As discussed by Lehman (2007), there are reasons to doubt the growth curve for *Maiasaura* (Erickson et al. 2001), which indicates an unreasonable birth weight (160 kg at time = 0), a sustained interval of no growth at all (from birth to age five),

followed by a short burst of rapid growth to adult size (1500 kg) in a single year.

The hypothesized growth curve for the sauropod dinosaur *Apatosaurus* is also extraordinary, and requires a maximum growth rate (over 5000 kg/yr) greater than in any extant terrestrial animal and exceeding those projected for a eutherian mammal of comparable estimated adult body mass (Erickson et al. 2001). Herein we reexamine the data on which the model growth curve for *Apatosaurus* was based. We illustrate an alternative method for constructing a growth curve for *Apatosaurus* based on the same data. And we use this method to construct growth curves for larger (*Alamosaurus*) and smaller (*Janenschia*) sauropod dinosaurs. Our results indicate that sauropods achieved maximum growth rates ranging from about 180 to 1100 kg/yr and approached adult body mass in 20 to 80 years. These growth rates are substantially lower than those previously proposed for sauropods, but comparable to those estimated for smaller dinosaurs (Erickson et al. 2001; Lehman 2007).

Growth in Sauropods

Most previous studies of sauropod growth have focused primarily on their likely metabolic physiology. Weaver (1983) argued on the basis of energy considerations that sauropod dinosaurs could not have been endothermic because of their large size, low estimated feeding rates, and diet of low caloric value. Spotila et al. (1991) and Paladino et al. (1997) added that sauropods were likely homeothermic "mass" ectotherms ("gigantothermic") whose sheer size limited their metabolism and growth rate. However, others (e.g., Wedel 2003) have pointed out that sauropod pulmonary air sac systems may have allowed for more efficient heat dissipation, elevated metabolism, and more rapid growth rates.

Only a few absolute growth rate estimates have been presented for sauropods. Paul (1994: p. 250) plotted a maximum growth rate of about 900 g/day (330 kg/yr) for a "sub-adult" sauropod with an estimated adult body mass of ten tons; however, he did not provide any information about how these values were determined or on which specimen(s)

they were based. On the basis of previous studies, long-term "average" growth rates can be determined for several sauropods by dividing the number of growth lines (assumed to be annual) observed in histologic sections by the estimated weight of the animal. For example, Reid (1987) counted and estimated about 28 or 29 growth lines in a sauropod pubis and suggested that it came from an animal weighing five to six tons. He did not indicate how this weight was determined. A crude estimate of average growth rate based on these values ranges from 172 to 214 kg/yr.

Using average bone apposition rates and cortex thickness, Sander and Tuckmantel (2003) estimated the likely minimum and maximum ages for the large adult Tendaguru sauropods *Brachiosaurus* (27 to 50 years), *Barosaurus* (21 to 39 years), and *Dicraeosaurus* (11 to 22 years). Paul (1997) provided weight estimates for comparable adult individuals of the same sauropods (31,500, 11,600, and 5000 kg, respectively). From the age estimates given by Sander and Tuckmantel (2003) and the weight estimates given by Paul (1997), it is possible to determine long-term average growth rates for these sauropods: *Brachiosaurus* (630 to 1167 kg/yr), *Barosaurus* (297 to 552 kg/yr), and *Dicraeosaurus* (227 to 455 kg/yr). Such estimates do not take into account the slower rates of growth early and late in life history, but they suggest long-term average growth rates for sauropods in the range of 200 to 1000 kg/yr. Only the maximum growth-rate estimate determined for *Apatosaurus* by Erickson et al. (2001) is strictly comparable with those given by Case (1978a) for extant vertebrates.

The Case of Apatosaurus.—The *Apatosaurus* growth curve given by Erickson et al. (2001) was based on observations of bone histology presented by Curry (1999). In the histological sections studied by Curry, annual cycles of bone growth ("growth lines") were described and illustrated for limb girdle and appendicular bones from individuals about one-third to one-half adult body length. No sections were described for bones smaller than one-third adult length, and it was not possible to count growth lines in bones larger than about two-thirds adult length because secondary

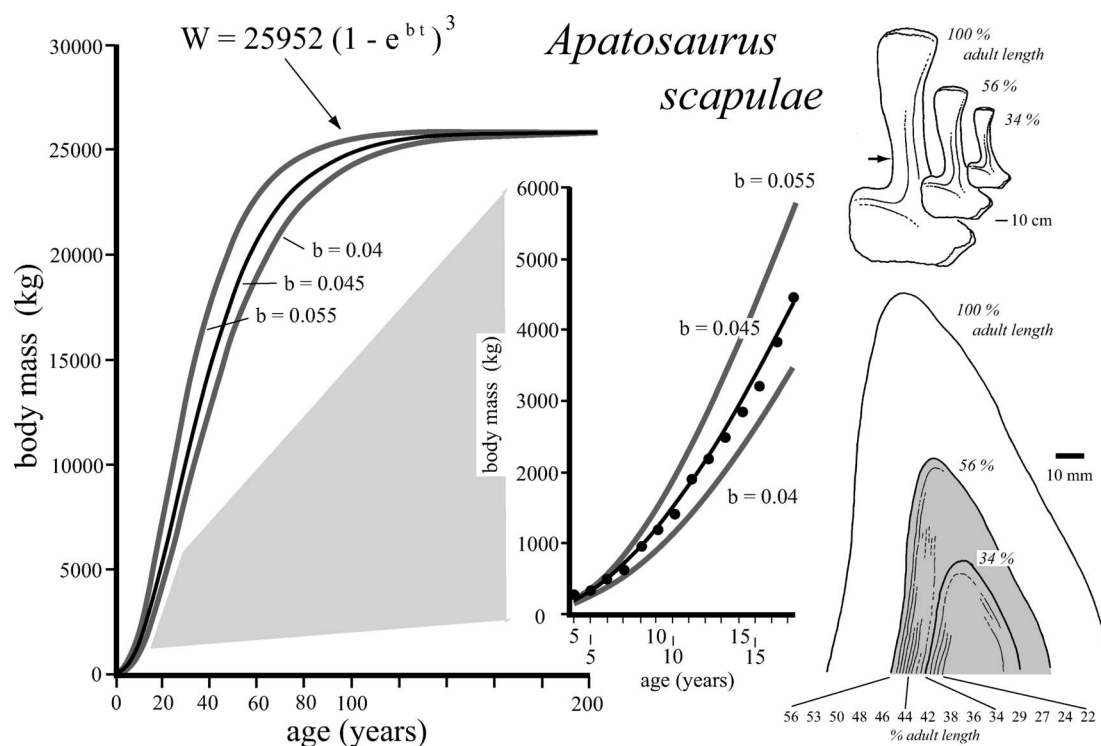


FIGURE 1. Growth annuli preserved on the medial surfaces of two subadult *Apatosaurus* scapulae, redrawn from photographs given by Curry (1999). The percentage of adult length is determined relative to the largest individual of *Apatosaurus excelsus* reported by Curry (1999). The growth history in terms of body mass (W) versus age (t) for *Apatosaurus* is based on fitting estimated masses for 14 yearly growth increments (Tables 1, 2) to the von Bertalanffy growth equation, and varying exponent (b) between 0.04 and 0.055. The asymptotic value for adult body mass (25,952 kg) is that given by Erickson et al. (2001).

bone remodeling had obliterated the primary bone tissue. Therefore, it is possible to document growth history unequivocally only for animals in a limited size range. Critical to construction of the *Apatosaurus* growth curve are two scapulae illustrated by Curry (1999). These are the only elements described by Curry (1999) that preserve annual growth lines suitable for estimating age minima. These are the same two bones on which the growth curve presented by Erickson et al. (2001) was based. The smaller of the two scapulae is 34% adult length and preserves about five growth lines. The larger specimen is 56% adult length and preserves about ten growth lines. We choose a conservative approach of counting only the most obvious growth lines; additional vague or discontinuous lines are present. We also assume that the increment of bone between the outermost line and the preserved periosteal surface in each specimen records

about one year of growth. Together the two specimens record a minimum of 14 years of growth because the innermost two lines in the larger likely equate with the outermost two in the smaller; a determination made by graphically removing successive increments of bone between annuli in the larger specimen and calculating the percent adult length for each annulus (Fig. 1). The two specimens reveal that at least 14 years of life were required for *Apatosaurus* to grow from 22% to 56% adult length, or from 1% to 18% adult body mass (utilizing the method for mass estimation given by Erickson et al. 2001).

Histological data given by Curry (1999) do not reveal how many years of growth were required to achieve 34% adult length (1% adult mass), nor do they reveal how many years were required to grow from 56% adult length (18% adult mass) to 100% adult size. The *Apatosaurus* growth curve presented by Erick-

TABLE 1. Mass estimates for preserved growth annuli in four sauropod dinosaurs. The number of preserved growth annuli (No.) for each sauropod with the percentage adult length (%) and mass (kg) estimates for each annulus are shown. Mass estimates for each growth increment are determined in the manner of Erickson et al. (2001) as [(femur length)³/(adult femur length)³]-adult mass. The length of a preserved skeletal element (e.g., scapula) is assumed to vary proportionally with femur length. Adult femur length for *Apatosaurus* = 177.5 cm, *Alamosaurus* = 161 cm, *Janenschia* = 127 cm, Northampton sauropod = 132 cm (estimated). Adult mass estimates for *Apatosaurus* = 25,952 kg, *Alamosaurus* = 32,663 kg, *Janenschia* = 14,029 kg, Northampton sauropod = 9000 kg.

<i>Janenschia</i>			<i>Alamosaurus</i>			<i>Apatosaurus</i>			Northampton sauropod		
No.	%	kg	No.	%	kg	No.	%	kg	No.	%	kg
1	46.5	1411	1	30	882	1	22	276	1	62	2434
2	51.2	1883	2	33	1174	2	24	359	2	64	2645
3	53.5	2148	3	36	1524	3	27	511	3	66	2869
4	59.3	2925	4	41	2251	4	29	633	4	67	2985
5	64	3678	5	45	2976	5	34	978	5	69	3227
6	66	4033	6	48	3612	6	36	1211	6	70	3353
7	68.6	4529	7	51	4333	7	38	1424	7	72	3614
8	72	5236	8	56	5736	8	42	1923	8	73	3749
9	76.7	6330	9	59	6708	9	44	2211	9	74	3888
10	80	7183				10	46	2526	10	76	4176
11	83.7	8226				11	48	2870	11	77	4325
12	84.3	8404				12	50	3244	12	78	4478
13	85	8616				13	53	3864	13	79	4634
14	86	8923				14	56	4477	14	80	4794
15	87.2	9302							15	82	5124
16	87.8	9495							16	83	5295
17	88.4	9691							17	84	5470
18	89	9890							18	85	5648
19	91.3	10,677							19	87	6016
20	91.9	10,889							20	89	6400
21	92.4	11,067							21	90	6598
22	94.2	11,727							22	91	6800
23	96.5	12,607									
24	97.1	12,844									
25	97.7	13,083									
26	98.8	13,530									
38	100	14,029									

son et al. (2001) must therefore be incorrect because it indicates attainment of full adult body mass in 15 years and it is clear from Curry's observations that a minimum of 14 years were required simply to attain 18% adult body mass.

Nevertheless, the 14 years of growth recorded in the two specimens illustrated by Curry (1999) provide an alternative means to model growth in *Apatosaurus*. Here we use a simple form of the well-known von Bertalanffy growth equation, wherein the mass (W) at any given age (t) is an exponential function limited by the asymptotic adult mass (Fig. 1) (reviewed in Lehman 2007). We use the general form of this equation employed in an extensive study of growth in birds (Ricklefs 1968, 1973), the closest living relatives of dinosaurs, and in elephants (Laws et al. 1975), the largest living terrestrial animals. Because there re-

mains substantial disagreement regarding the accuracy of methods for estimating mass in dinosaurs (e.g., Paul 1997), and considerable uncertainty regarding the assumptions used in this analysis (see discussion), a high degree of precision in curve fitting is unwarranted. Here we use the same asymptotic value for *Apatosaurus* adult body mass (25,952 kg) estimated by Erickson et al. (2001), assume that the hatchling weight is negligible relative to adult body mass, and adjust the value of exponent b in the growth equation to obtain a match with the estimated body masses for each of the 14 years of growth recorded in Curry's (1999) specimens (Table 1, Fig. 1). Although a set of growth curves is shown here to bracket the array of yearly growth increments, it is possible to determine the best-fit curve by rearranging the von Bertalanffy equation to solve for exponent b for each

TABLE 2. Estimated maximum growth rates in four sauropod dinosaurs. The varied values of exponent b are those shown for growth equations in Figures 1 to 4.

	exponent b	Maximum growth rate (kg/year)	Age at first preserved growth ring (years)	Age at 90% adult mass (years)
<i>Apatosaurus</i>	0.04	460	5	80
	0.045	520	5	70
	0.055	630	4	60
<i>Alamosaurus</i>	0.065	940	5	55
	0.075	1090	4	45
	0.08	1160	4	40
<i>Janenschia</i>	0.1	623	6	29
	0.16	993	4	18
Northampton sauropod	0.045	180	24	75
	0.065	260	16	50

growth increment, and adjusting the entire array up a year at a time to obtain the minimum standard deviation in the set of exponent b values. A reasonable fit to the data is obtained with a value of 0.045 for the exponent. Values less than 0.04 result in substantially lower estimated masses, whereas values greater than 0.055 produce much higher estimated masses at the upper end of the growth series (Table 2). Hence, the innermost annulus in the smaller of Curry's (1999) specimens was produced at an age of about five years, whereas the outermost increment of bone in the larger specimen was produced at an age of about 18 years. Curry estimated the minimum age of the smaller specimen as five years, and the larger as ten years. Our method indicates ages of eight or nine and of 17 or 18 for the two individuals, respectively. These results are not dramatically different, considering that Curry's (1999) age estimates are acknowledged to be minima.

If our model growth curve is correct, *Apatosaurus* required about 70 years to approach full adult body mass and attained a maximum growth rate of about 520 kg/yr. These results differ substantially from the maximum growth rate of 5466 kg/yr and the 15 years to attain full adult body mass given by Erickson et al. (2001); however, they accord with those modeled for smaller dinosaurs where the maximum growth rates exceed those found in extant reptiles but are less than those observed in birds or eutherian mammals (Erickson et al. 2001).

The Case of Alamosaurus.—The same method

can be used to model growth in the sauropod dinosaur *Alamosaurus*, which attained a maximum adult body mass (32,663 kg) somewhat greater than that estimated for *Apatosaurus* (Lehman and Coulson 2002). A histological study of *Alamosaurus* (Woodward 2005) included a section taken from a subadult humerus (59% adult length, 20% estimated adult mass) that revealed a minimum of nine annual cycles of bone growth, including the preserved periosteal surface of the specimen (Woodward 2005; Woodward and Lehman 2006). Here, only the most obvious growth lines are counted, and the percent adult length and mass estimates are determined in the same manner as for *Apatosaurus* (Table 1). In the case of *Alamosaurus*, a value of 0.075 for the exponent in the growth equation results in a reasonable fit to the data, with the first preserved growth line produced at age four, and the outermost at age 12 (Fig. 2). Values for b less than 0.065 result in underestimation of mass, whereas values greater than 0.08 result in substantial overestimation at the upper end of the growth series (Table 2). The resulting growth curve for *Alamosaurus* indicates that adult body mass was approached after about 45 years of growth, and the maximum growth rate attained was about 1090 kg/yr. This estimated growth rate exceeds that determined for *Apatosaurus* and approaches that projected for a precocial bird of comparable adult body mass.

The Case of Janenschia.—The sauropod growth rates estimated above are also compatible with observations reported for other

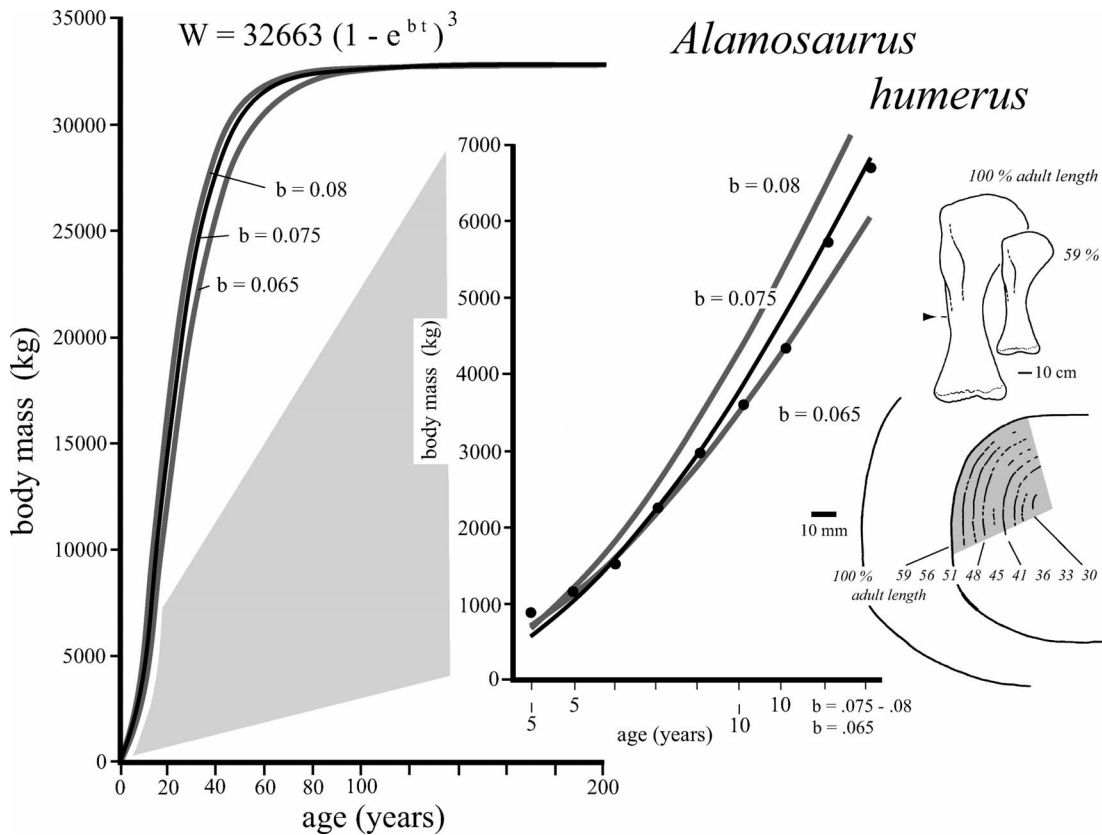


FIGURE 2. Growth annuli preserved on the lateral surface of a subadult *Alamosaurus* humerus, redrawn from a photograph given by Woodward (2005). The percentage of adult length is determined relative to the largest individual of *Alamosaurus sanjuanensis* reported by Lehman and Coulson (2002). The growth history in terms of body mass (W) versus age (t) for *Alamosaurus* is based on fitting estimated masses for nine yearly growth increments (Tables 1, 2) to the von Bertalanffy growth equation, and varying exponent (b) between 0.065 and 0.08. The asymptotic value for adult body mass (32,663 kg) is based on the largest specimen reported by Lehman and Coulson (2002).

sauropods that attained lesser adult body masses (approximately 5 to 15 tons). For example, a histological section of an adult femur of *Janenschia* illustrated by Sander (2000) preserves 38 growth lines and provides the most complete record of growth for any sauropod. The outermost 12 growth lines are very closely spaced LAGs, indicating that this specimen is from a senile individual. Sander (2000) presented no weight estimate, growth curve, or growth rate estimate for *Janenschia*, but these can be obtained from the data he provided. We estimate the adult body mass of *Janenschia* as 14,029 kg (Fig. 3), and utilize the same method of mass estimation for each increment of bone growth as described above (Table 1). A value of 0.1 for the exponent in the growth equation results in a reasonable fit to the data at the

lower end of the growth series, whereas a value of 0.16 results in a better fit at the upper end. If these sufficiently bracket the likely growth history, then the first growth line preserved in the specimen was produced at age four to six, the maximum growth rate was between 623 and 993 kg/yr, and adult mass was approached after about 20 to 30 years of growth (Table 2). This estimate agrees with an age of 19 to 35 years suggested for this specimen on the basis of bone cortical thickness and apposition rate (Sander and Tuckmantel 2003). Interestingly, although this specimen preserves striking growth lines it records a relatively rapid growth rate, especially considering that its estimated adult mass is substantially lower than that of *Apatosaurus* or *Alamosaurus*. Hence, the presence of marked

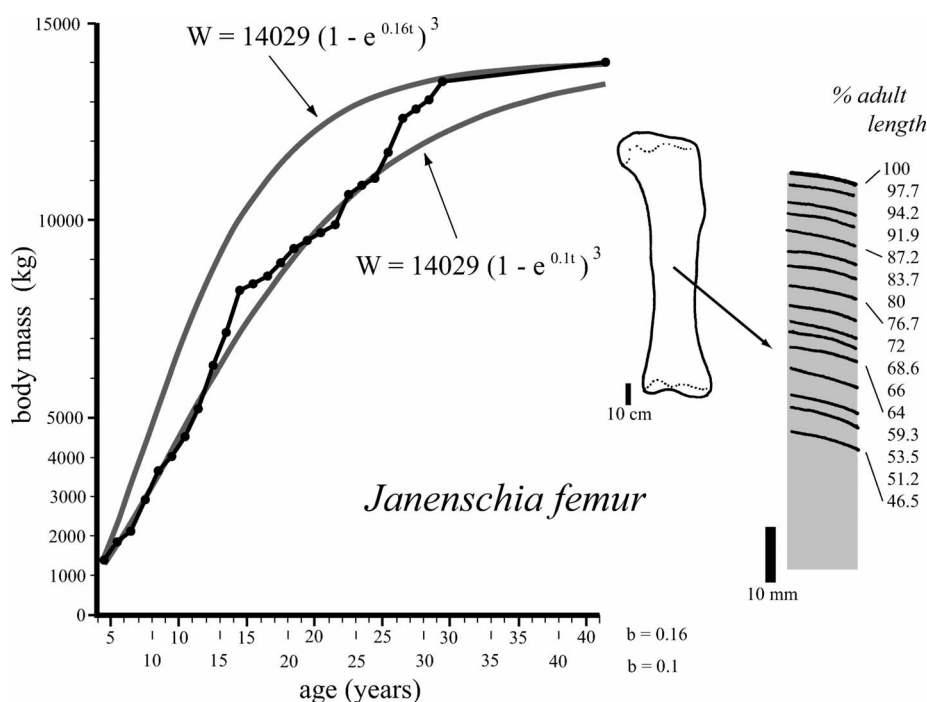


FIGURE 3. Growth annuli preserved in a section taken from the diaphysis of an adult *Janenschia robustus* femur, redrawn from a photograph given by Sander (2000). The percentage of adult length is determined assuming that this specimen attained the maximum adult size at the time of its death. The growth history in terms of body mass (W) versus age (t) for *Janenschia* is based on fitting estimated masses for 38 yearly growth increments (Tables 1, 2) to the von Bertalanffy growth equation, and varying exponent (b) between 0.1 and 0.16. The asymptotic value for adult body mass (14,029 kg) assumes that the femur sectioned and illustrated by Sander (length = 1270 mm, circumference = 570 mm) represents the maximum adult length, and that a compatible humerus (estimated circumference 458 mm) would have proportions similar to those in other titanosaurian sauropods. The summed circumferences were then used in the empirical equation of Anderson et al. (1985) as modified by Alexander (1989) to estimate the asymptotic adult body mass.

growth lines alone does not indicate “slow” growth as is sometimes assumed.

The Northampton Sauropod.—Reid (1990) reported approximately 22 growth lines in the pubis of an unidentified sauropod from the Northampton Sands in England. In this case, well-defined LAGs are documented in the outermost cortex of the bone but they are not more closely spaced approaching the preserved periosteal surface, suggesting that the asymptotic adult phase of growth had not been achieved at the time of this individual’s death. This specimen exhibits the most distinct type of growth lines found in sauropod bones, presumably resulting from the slowest rates of growth, and is frequently cited as evidence for ectothermic physiology in at least some sauropods (Reid 1981). It provides an opportunity therefore to model the likely slowest growth rates in sauropods, as well as

to test the method of growth curve approximation with a fragmentary specimen. Because the identity of the Northampton sauropod is uncertain, and the maximum adult body mass for this species is unknown, a more conjectural approach must be used to reconstruct its growth history. An appropriate femur length and body mass must be estimated on the basis of the pubis (Fig. 4), but otherwise following the same method as for *Apatosaurus* where scapula dimensions were used instead. Mass estimates are then determined for each increment of bone growth as before (Table 1). In this case, the first growth line preserved in the specimen was produced at age 16 to 24, the maximum growth rate was between 180 and 260 kg/yr, and adult mass was approached after about 50 to 75 years of growth (Table 2). These results are compatible with the “average” growth rate of 172 to 214 kg/yr that can

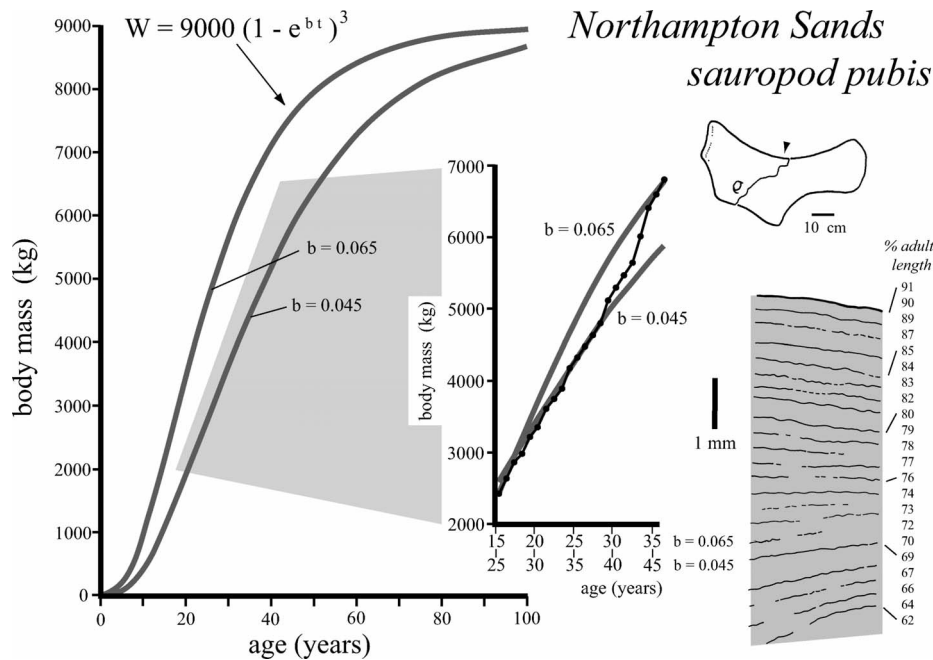


FIGURE 4. Growth annuli preserved in a section taken from the pubis of an unidentified sauropod from the Northampton Sands, redrawn from a photograph given by Reid (1990). The restored length of the pubis (0.75 m) was determined from the proportions in *Apatosaurus* as shown. A relationship ($r = 0.65$) between pubis length and body mass [mass (t) = 32.8 · pubis length (m) – 17.8] obtained for 13 sauropods with masses given by Paul (1997) yields an estimated body mass of 6800 kg for the Northampton specimen. Yearly mass estimates for this individual were then determined for each of 22 growth rings in the same manner as for the other specimens. The asymptotic limit for adult body mass (9000 kg) was estimated by incremental selection of values above 6800 kg in the growth equation until the 22-year set of growth data could be bracketed by model growth curves. The growth history in terms of body mass (W) versus age (t) is based on fitting estimated masses for 22 yearly growth increments (Tables 1, 2) to the von Bertalanffy growth equation, and varying exponent (b) between 0.045 and 0.065 (Tables 1, 2).

be deduced from Reid's (1987) original analysis of the same specimen, and with the maximum plotted sauropod growth rate of 330 kg/yr from Paul's (1994) study, which cites Reid's study but might not refer to this particular specimen.

Discussion

In the four sauropods examined above, which attained maximum adult weights between about 10 and 30 tons, the maximum estimated growth rates range from about 200 to 1100 kg/yr and are within the limits projected for reptiles and for precocial birds of comparable body masses (Fig. 5) (Case 1978a). These rates are in line with those determined for smaller dinosaurs and typically two to five times greater than for reptiles of comparable size (Erickson et al. 2001; Lehman 2007). Sauropods, like other dinosaurs, did not achieve growth rates projected for eutherian mam-

mals or altricial birds, which are ten to 30 times greater than in reptiles (Case 1978a). The estimated sauropod growth rates do exceed those measured in the largest living terrestrial mammalian herbivores (e.g., 150 kg/yr in elephants [Case 1978a]), but sauropods grew much larger and required at least several decades (30 to 80 years) to attain full adult size. It is interesting to note that the two titanosaurs (*Alamosaurus* and *Janenschia*) exhibit the most rapid growth rates of the few sauropods studied. Titanosaurs are generally placed among the more derived sauropods (e.g., Wilson and Sereno 1998).

The curve-fitting technique utilized by Erickson et al. (2001) to model sauropod growth requires that the age at death (based on growth line counts) is known for multiple individuals representing different ontogenetic stages of the same species. Because of medullary expansion and bone remodeling with

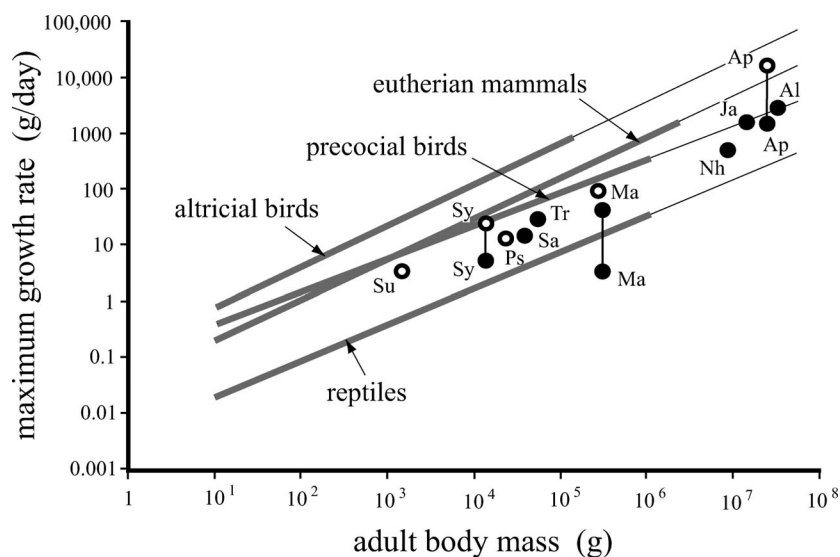


FIGURE 5. Comparison of estimated maximum growth rates in dinosaurs with regression lines determined by Case (1978a) based on data for extant tetrapods. The regression lines are extended (right) beyond the domain of the data on which they are based to the range of estimated body masses for sauropod dinosaurs. Dinosaurian maximum growth rates typically lie in the realm between those for reptiles and precocial birds of comparable projected adult body masses. Estimates (open circles) for *Shuvuuia* (Su), *Syntarsus* (Sy), *Psittacosaurus* (Ps), *Massospondylus* (Ma), and *Apatosaurus* (Ap) are from Erickson et al. (2001). Estimates (closed circles) for *Syntarsus* (Sy), *Saurornitholestes* (Sa), *Troodon* (Tr), and *Massospondylus* (Ma, low to high range) are from Lehman (2007). Estimates for *Alamosaurus* (Al), *Apatosaurus* (Ap), *Janenschia* (Ja), and the Northampton sauropod (Nh) are those presented herein.

growth, age estimates based on growth-line counts for most individuals will represent their minimum ages. In contrast, the method of growth curve approximation proposed herein requires only the growth record of a single individual, and does not require knowledge of the individual's age at the time of its death. Growth lines most useful for this method are those found in individuals that died during the exponential phase of growth, from about one-third to two-thirds adult length, when growth rates are highest and growth lines most widely separated, but before later bone remodeling obscures or obliterates the earlier growth record. In the examples of *Apatosaurus* and *Alamosaurus* discussed above, only the early part of the exponential growth phase was completed prior to death. More complete individual growth records, such as preserved in the specimen of *Janenschia* are exceptional.

Of course, there are several assumptions and potential sources of error in an analysis of the sort presented above. Several critical assumptions are that (1) the cyclicity in bone growth is annual, (2) the asymptotic limit for

adult weight is known, (3) weight estimates for each growth increment are accurate, (4) allometric growth of limb and girdle elements relative to the femur is not significant, (5) each skeletal element maintains its proportions with growth, and (6) the individuals sampled are representative of their species.

Periodicity of Growth Lines.—It is assumed here, as in other studies of dinosaur bone histology (including those of Erickson et al. 2001) that the preserved cycles of bone growth were produced annually. Comparison with cyclical bone growth in living tetrapods (e.g., Castanet et al. 1993) and bone apposition rates (Sander and Tuckmantel 2003) suggests that this is a reasonable assumption. However, some studies have demonstrated that the number of growth lines may vary even between different skeletal elements in the same individual (e.g., Horner et al. 2000) and so their varied development would result in different model growth curves. Horner et al. (1999) found that there is no optimal bone to use for dinosaur skeletochronology, and that counting growth lines in a single bone would likely yield an unreliable age estimate in any case. The most ac-

curate assessment of age and growth rate will be obtained in those bones where the highest numbers of growth lines are found in the cortex and if present, in the outermost periosteal layers (external fundamental system). So, the model growth curves obtained for the four sauropods examined here should be considered as representing their *maximum* rates of growth. If additional bones from the same individuals were to reveal a greater number of growth lines, the result would be a lower and more accurate estimated rate of growth in a model curve. Moreover, if vague or less continuous growth lines also evident in the histologic sections of the four sauropods were included, lower growth rates than those determined above would result. Such complications apply equally, however, to all studies that utilize osteological growth lines to reconstruct growth history.

Because of cortical drift or asymmetric growth in some skeletal elements, the number of growth lines and the thicknesses of each growth increment may also vary between sides of the same bone. In a complete cross-section of a bone this complication would be evident, and can be addressed by careful measurement. For instance, complete cross-sections of the scapulae in *Apatosaurus* reveal that the growth lines are only well preserved on the medial side, but that growth was relatively symmetrical. In contrast, asymmetric growth may not be evident in a sample taken only from one side of a bone. For example, the section of the Northampton sauropod pubis illustrated by Reid (1990) was taken on the medial side of the bone, where the growth increments are relatively thin. Growth increments are thicker on the lateral side (Reid 1981), and a growth curve based on measurements taken there would therefore yield a higher growth rate. Measurements between growth lines taken on multiple sides of such a bone would bracket the lowest and highest growth rates on resulting model growth curves. The effect of asymmetric growth is likely to be more pronounced in girdle elements than in limb bones, and therefore use of limb bones for growth studies minimizes this complicating factor (e.g., Sander 2000). Nevertheless, growth rate determinations based on girdle el-

ements such as the scapula (Curry 1999) or pubis (Reid 1987) are frequently cited and certainly valid as long as growth was not markedly asymmetric.

Asymptotic Limit for Adult Weight.—Paul (1997) argued that utilizing the summed circumferences of the humerus and femur (the method of Anderson et al. 1985) typically overestimates weight in many dinosaurs. Because of their avian-style pulmonary air sac system and pneumatic vertebrae, sauropods may have had considerably lower bulk body densities than previously assumed (Paul 1997; Wedel 2003). For example, using scaled skeletal restorations Paul (1997) determined the adult weight of *Apatosaurus* as 13 to 19 tons (17.5 tons for Carnegie Museum specimen CM 3018). The method of Anderson et al. (1985), used herein and by Erickson et al. (2001), yields a maximum adult weight for similar specimens over 25 tons. Russell (1989) suggested an upper limit of 43 tons. Hence, reported estimates for maximum adult weight in *Apatosaurus* vary substantially below and above the value determined by the sum of limb bone shaft circumferences. To test the sensitivity of the growth curve approximation method to varied asymptotic adult weight, the values given by Paul (1997) and Russell (1989) are chosen to represent reasonable lower and upper limits for *Apatosaurus* (Fig. 6). The maximum adult femur length and the percentage increase in length for each growth increment remain constant in any case, but as the asymptotic value for adult weight decreases, the weights estimated for each growth increment also decrease, as does the maximum growth rate. In all cases, however, the same exponent ($b = 0.045$) results in a best fit to the 14 years of growth data. The relationship between maximum adult weight and maximum growth rate remains the same (Fig. 6), defining a line of constant slope between the regressions for reptiles and precocial birds on the log-log plot of Case (1978a). This reflects the fact that the weight estimate for each growth increment is itself a function of the maximum weight estimated for the adult. Given the findings of Paul (1997) and the likely case that the method of Anderson et al. (1985) overestimates mass, then the true

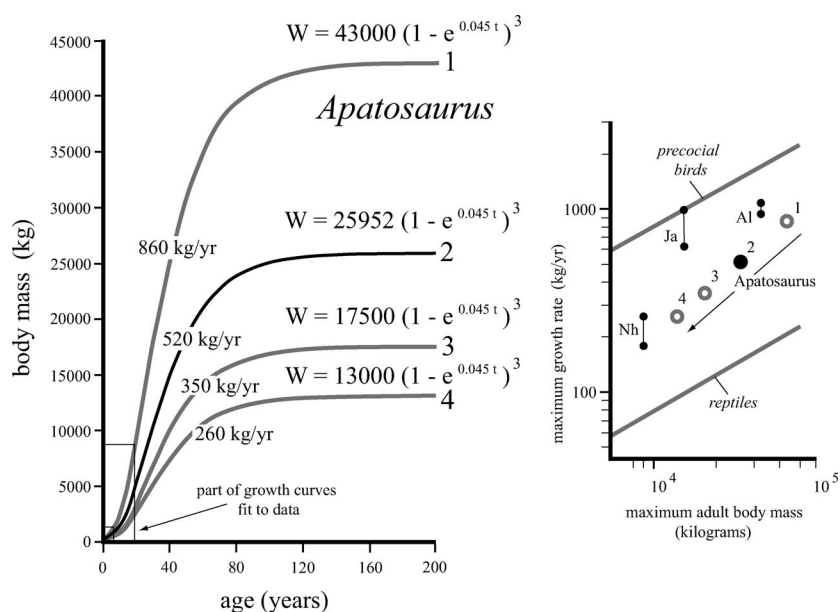


FIGURE 6. Alternative *Apatosaurus* growth curves based on varied estimates for asymptotic limit of adult mass. Estimates of 43 ton from Russell (1989), ~25 tons from Erickson et al. (2001), 17.5 and 13 tons from Paul (1997) are shown along with associated maximum growth rates (kg/yr). In each case the weight estimates for 14 yearly growth increments given in Table 1 are recalculated using the appropriate asymptotic limit and fit to a von Bertalanffy growth equation with exponent $b = 0.045$. The 14 years of growth data record the lower part of the exponential phase of growth (Fig. 1). On right are shown corresponding points for each of the four alternative *Apatosaurus* growth curves on Case's (1978a) log-log plot of maximum adult body mass and maximum growth rate (enlarged from Fig. 5); also shown are upper and lower limits determined for *Alamosaurus* (Al), *Janenschia* (Ja), and the Northampton sauropod (Nh).

growth rates for *Apatosaurus* would likely be even lower than the 520 kg/yr determined above. The same is true for the growth rates determined for *Alamosaurus* and *Janenschia* because their maximum adult weights are also estimated by using the method of Anderson et al. (1985). If the adult weight estimates for these taxa are revised downward, the corresponding maximum growth rates will be lowered accordingly and would plot at points along a line with slope comparable to that shown for *Apatosaurus* (Fig. 6).

Alternative Weight Estimates.—The proposed method of growth curve approximation assumes that weights calculated for each growth increment are adequately predicted by the "developmental mass extrapolation" method of Erickson et al. (2001). Weight at any given size is taken to be a function of the ratio of cubed length to adult length and the maximum adult weight (Table 1). As a result, incremental weights at each growth line are specified by the values chosen for maximum adult length

and weight. It is useful therefore to examine alternative methods for weight determination wherein values obtained for each growth increment are independent of the maximum adult value. The method of Anderson et al. (1985) allows weights to be estimated as a function of the summed shaft circumferences of the humerus and femur. To test the effect of this weight estimation method on the resulting growth curve in *Apatosaurus*, weights are calculated for each growth increment assuming that the summed circumferences of the limb bones vary proportionally with each increment of growth in the scapula (Fig. 7). Weights determined in this manner are progressively greater with each growth increment than those found previously. Hence, a growth curve fit to the adjusted set of weight data is found with a higher exponent ($b = 0.05$) and the maximum growth rate is slightly higher (576 kg/yr) for the growth curve. This is not dramatically different from the curve presented previously. Because the method of Ander-

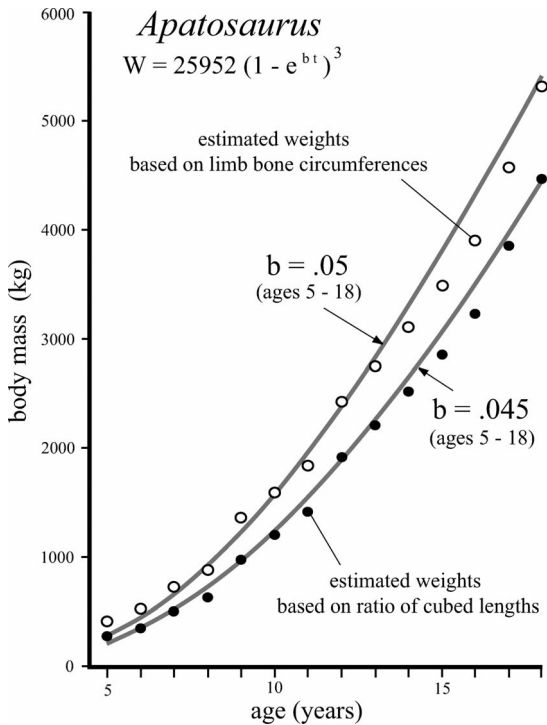


FIGURE 7. Alternative *Apatosaurus* growth curves showing the effect of different methods of mass estimation. The “developmental mass extrapolation” method of Erickson et al. (2001) uses the ratio of cubed length to adult length and the estimated maximum adult mass; the resulting mass estimates for 14 yearly growth increments (filled circles) and growth curve on right are also shown in Figure 1. The method of Anderson et al. (1985) uses the summed circumferences of the humerus and femur. In this case, it is assumed that the sum of limb bone circumferences varies directly with the scapula cross-section (e.g., 22% adult diameter corresponds with 22% adult circumference). The recalculated mass estimates (open circles) are greater, as is the exponent ($b = 0.05$) fitting the growth curve (left), resulting in a higher growth rate.

son et al. (1985) may overestimate weight even in adult animals (e.g., Paul 1997), and therefore inaccurately predict weight in juvenile animals (Erickson et al. 2001), the growth curve based on these weight estimates likely provides a maximum limit on growth rate.

Another technique for mass estimation is the “polynomial method” of Seebacher (2001), wherein polynomial equations are fitted to the outlines of skeletal reconstructions and used to determine body volume. With this method, Seebacher (2001) obtained a weight estimate of 22,407 kg for *Apatosaurus* using the same specimen (CM 3018) for which Paul (1997) had

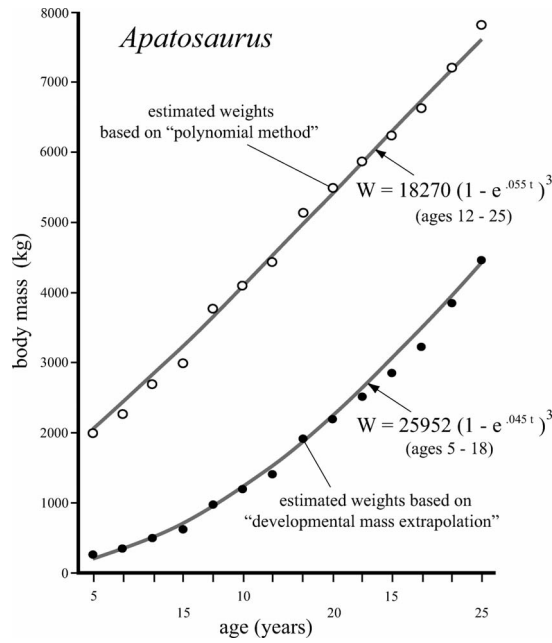


FIGURE 8. Alternative *Apatosaurus* growth curves showing the effect of different methods of mass estimation. The “developmental mass extrapolation” method of Erickson et al. (2001) results in mass estimates for 14 yearly growth increments (filled circles) and growth curve also shown in Figure 1. The “polynomial method” of Seebacher (2001) results in a relationship between mass (y , in kg) and total body length (x , in m) for 13 sauropod dinosaurs, such that $y = 214.44 x^{1.46}$. This equation yields a mass of 18,270 kg for *Apatosaurus* (CM 3018, 21 m length). The recalculated weights (open circles) using this equation for each of the 14 yearly growth increments, and assuming that scapula length varies directly with total body length are substantially greater than those determined by “developmental mass extrapolation.” The resulting growth curve has a slightly higher exponent ($b = 0.055$), fits to older ages (12 to 25), and results in a lower maximum growth rate (446 kg/yr).

determined a value of 17,500 kg. He also produced a regression that relates mass estimates for 13 sauropods to their total body length (Fig. 8). This equation yields an estimated weight of 18,270 kg for *Apatosaurus* (CM 3018, length = 21 m), somewhat lower than what Seebacher (2001) had more precisely determined because the regression reflects a best fit for the 13 specimens. Although the regression is based on adult specimens with a wide range of body sizes, it can be used to produce an alternative set of weight estimates for each of the growth increments in *Apatosaurus* if total body length is assumed to vary directly with scapula length (Fig. 8). In this case, weight is a function of length only, not estimated max-

imum adult length or adult weight. The weight estimates obtained are substantially greater than those found with either of the previous methods, diminishing from about ten times to two times greater through the 14 yearly growth increments. If these weight data are fit to the von Bertalanffy equation using 18,270 kg as the asymptotic limit for adult weight, a fit is found with a slightly higher exponent ($b = 0.055$) than determined previously, and for ages 12 to 25, rather than 5 to 18 as before. However, the growth curve results in a lower maximum growth rate of 446 kg/yr, compared to 520 or 576 kg/yr with the other methods, and approximately 60 years is still required to achieve 90% adult mass.

Regardless of which method of mass estimation is used, there are potential sources of error when utilizing either linear dimensions or circumferences of limb bones along with measurements in histologic sections to deduce mass. Inasmuch as mass increases with growth more rapidly than length, small errors in length measurement may result in substantial errors in mass estimation. Many sauropod limb girdle and appendicular bones for which histologic sections are obtained are distorted or partly restored (particularly their articulation surfaces), resulting in imprecise dimensions. Nevertheless, whether “developmental mass extrapolation” (Erickson et al. 2001), the summed circumferences of limb bones (Anderson et al. 1985), or the “polynomial method” of Seebacher (2001) is used, the estimated maximum growth rates for *Apatosaurus* range from 400 to 600 kg/yr and adult size is approached after 60 to 80 years of growth.

Allometric Growth.—The proposed method of growth curve approximation assumes that all bones in the skeleton grow at the same rate as the femur (i.e., isometric growth). For example, in *Apatosaurus* the increments of growth in width of the scapula are assumed to equate with identical increments of growth in length of the femur. Sauropod limb elements do not exhibit strong allometries (Sander 2000; see also Ogier cited in Ricqlès 1983). Over a limited range of body size the assumption of isometric growth is therefore probably a reasonable one. However, sauropods known from a more complete ontoge-

netic series exhibit at least slightly allometric growth in dimensions of many skeletal elements relative to the femur. For instance, Ikejiri (2004) found that the length of the scapula in *Camarasaurus* exhibits slightly negative allometric growth relative to length of the femur (i.e., it increases in length more slowly than the femur with growth).

To test the effect of allometry on growth curve estimation, the scapula in *Apatosaurus* is assumed to exhibit negative allometry comparable to that documented in *Camarasaurus* (Ikejiri 2004). In this test, the same allometric coefficient (0.94) is used for *Apatosaurus*, but the intercept is adjusted such that the regression passes through the maximum adult dimensions for the femur and scapula in *Apatosaurus* (Fig. 9). The resulting equation is used to estimate corresponding femur lengths for scapula lengths ranging from 22% to 56% adult size. These allometrically adjusted femur lengths are used to calculate weights for each growth increment as before. The adjusted weight estimates are slightly lower than those determined previously, but a growth curve of the same form ($b = 0.045$) fits these data if shifted to ages 4 to 17, rather than 5 to 18 (Fig. 9). The maximum growth rate remains the same. Much more striking allometry is required to dramatically change the form of the growth curve. Sauropod limb girdle and appendicular bones that yield histologic samples used in growth studies typically exhibit nearly isometric growth (e.g., allometric coefficients between 0.89 and 1.10 in *Camarasaurus* [Ikejiri 2004]).

A second form of allometric growth should be considered, however. The method of growth curve approximation assumes that each bone also maintains the same proportions with growth. For example as the humerus grows, its diameter- or circumference-to-length ratio is assumed to remain constant. In sauropods, over a wide range of body size, this assumption is valid (e.g., Tidwell and Wilhite 2005). Carpenter and McIntosh (1994) found that the circumference-to-length ratio remained constant in juvenile *Apatosaurus* humeri as small as 20% adult length.

However, a series of four *Alamosaurus* humeri of 30%, 40%, 59%, and full adult length,

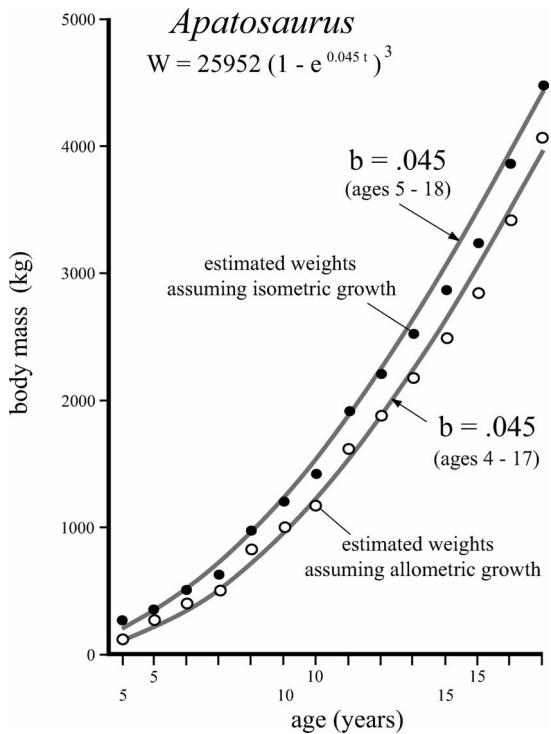


FIGURE 9. Alternative *Apatosaurus* growth curves showing the possible effect of allometry, in this case, varied growth rate between two skeletal elements. Weight estimates based on assumed isometric growth of the scapula relative to femur (filled circles) and resulting growth curve (right) are those also given in Figure 2. Weight estimates adjusted for allometry (open circles) assume that the scapula in *Apatosaurus* exhibits negative allometric growth compared to the femur, as found in *Camarasaurus* (Ikejiri 2004), where $y = 0.94x + 0.21$ ($y = \log$ scapula length, $x = \log$ femur length) but with intercept adjusted for regression to pass through adult scapula and femur dimensions for *Apatosaurus* (lengths 210.0 and 177.5 respectively). The growth curve adjusted for allometry (right) has the same form ($b = 0.045$) shifted one year younger to fit the recalculated data.

exhibit varying circumference-to-length ratios of 0.38, 0.39, 0.43, and 0.44 (Fig. 10). Hence, in *Alamosaurus* the proportions of the humerus show significant ontogenetic change. In the growth curve for *Alamosaurus*, it is assumed, however, that each growth increment in diameter of the humerus equates with an identical increment of growth in length.

To test the effect of this form of allometry on growth curve estimation, a relationship is established between percent adult diameter and percent adult length based on the four *Alamosaurus* humeri (Fig. 10). From the measured percent adult diameters (ranging from

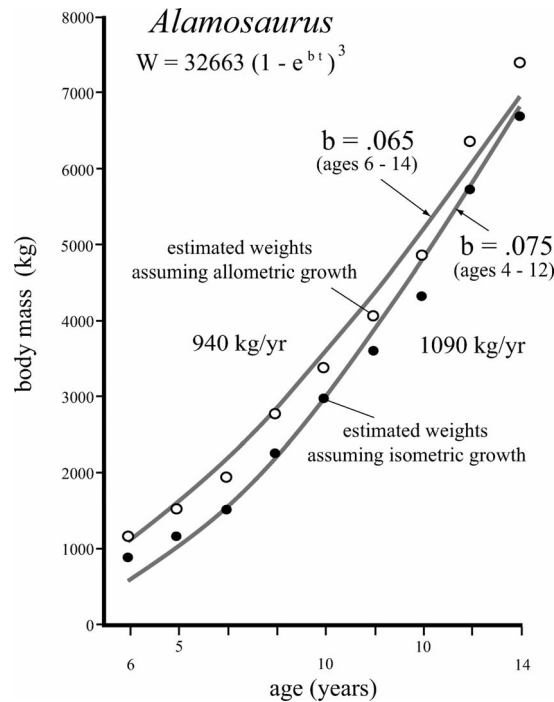


FIGURE 10. Alternative *Alamosaurus* growth curves showing the possible effect of allometry, in this case varied proportions in a skeletal element with growth. Weight estimates based on assumed isometric growth of the humerus (filled circles) and resulting growth curve (right) are those also given in Figure 2. Weight estimates adjusted for allometry (open circles) recognize that the humerus in *Alamosaurus* increases proportionally in diameter relative to length with growth. Four Texas Memorial Museum specimens (TMM 41541-1, 43621-1, 43600-2, 45600-1) yield $y = 0.95x + 4.74$ ($y = \log$ percent adult length, $x = \log$ percent adult diameter); this relationship is used to calculate appropriate humerus lengths for each growth increment measured in diameter (Fig. 2). The resulting weight estimates are higher, but the growth curve adjusted for allometry (left) has a lower exponent ($b = 0.065$) and is shifted two years older (ages 6 to 14) to fit the recalculated data.

30% to 59% in the histologic section; Fig. 2) corrected estimates of percent adult length can then be calculated for each growth increment. These corrected length estimates range progressively from 3% to 2% greater than the original length estimates, and yield weight values correspondingly greater than those determined previously (Fig. 10). However, this set of weight estimates fit best to a growth curve having a slightly lower exponent ($b = 0.065$) and adjusted to older ages (6 to 14), compared to the original estimates. The result is a slightly lower maximum growth rate (940 kg/yr) than in the previous growth curve.

More significant allometry of this sort would be required to alter the projected growth curve dramatically. Moreover, the general observation that limb girth and appendicular elements tend to increase proportionally in girth relative to length with growth will result in lower projected growth rates because increments of growth recorded in the girth of such elements correspond to lesser increments of growth in their length.

Individual Variation.—Many large land animals exhibit a fairly broad range of body mass at a given age, most commonly a manifestation of sexual dimorphism but also reflecting variability in diet or habitat conditions. This is also the case with at least some dinosaurs known from an adequate population sample (e.g., Sander and Klein 2005). Other dinosaurs are thought to exhibit a more constrained growth trajectory with little individual variation in growth rate or maximum adult size (e.g., Erickson 2005). However, the growth curve fitting technique using several individuals of known age at death (e.g., Erickson et al. 2001) will always result in a single growth curve even if the individuals actually followed slightly different growth trajectories. Multiple individuals of the same age at death are required to demonstrate a low level of developmental plasticity. There are few dinosaur population samples that allow for body masses to be determined for multiple individuals of the same age. Regardless, it seems unlikely that the largest known or preserved specimen in each of the four cases presented above could represent the maximum adult size and therefore the asymptotic limit for growth in each species. Likewise, different individuals no doubt grew somewhat faster or slower than those few examined here.

The possibility also exists that the four examples described above may represent unusual individuals that perhaps lived in poor habitat or under stressed conditions, possibly leading to the development of marked growth lines or ultimately to their selective preservation. A greater census of the sort conducted by Sander and Klein (2005) may reveal a broader range of individual variation in some sauropod species. Varied growth “spurts” evident in the more complete growth records of some

individuals (*Janenschia* and the Northampton sauropod; Figs. 3, 4) are in keeping with slightly slowed or accelerated growth pulses in individual life histories, resulting perhaps from alternating periods of harsh or favorable growth conditions. However, such peculiarities might instead simply reflect a failure to recognize some growth lines actually present but poorly expressed in the histologic sections. Even so, an individual's growth record is not expected to fit precisely to a specific growth curve. Preservation of only a segment of the growth record (e.g., the early exponential phase of growth in *Apatosaurus* and *Alamosaurus*; Figs. 1, 2) may result in a less accurate reflection of the long-term growth history of the individual. Questions regarding individual variability may ultimately be resolved by producing a series of model growth curves of the sort developed here for multiple individuals of the same species.

Conclusions

Individual growth records in histologic specimens of four sauropod dinosaurs enable estimation of body mass for successive increments of bone growth. Assuming that growth lines in the sections were produced annually, and that each skeletal element varied proportionally in length with the femur during growth, the yearly body mass estimates result in a set of age/body mass data that can be fit to a general form of the von Bertalanffy growth equation. Sauropod dinosaur growth rates estimated in this way are comparable to those determined for other dinosaurs. Although the proposed method of growth curve approximation relies on multiple crucial assumptions, tests that allow for reasonable deviation from those assumptions result in only modest change in the growth curves. Such sensitivity tests suggest that the method provides reasonable bounds on the likely growth rates in sauropods. The maximum growth rates range from about 200 to 1000 kg/yr. These rates exceed those typical for the largest extant mammalian herbivores, but sauropods grew much larger and required at least several decades to approach adult size. Titanosaurians exhibit the highest growth rates among the few sauropods examined. However, sau-

ropods likely weighed appreciably less than is estimated on the basis of the summed circumferences of their limb bones, and so their actual growth rates were probably lower than these estimates. Dinosaurian growth rates, including those of sauropods, typically exceed rates projected for reptiles by two to five times, and approach those estimated for precocial birds of comparable body masses. Sauropods did not achieve growth rates comparable to those projected for eutherian mammals or altricial birds of similar size. Bones of individuals between one-third and two-thirds adult length are most likely to preserve evidence for the rapid early exponential phase of growth, and so additional specimens in this size range should be sought and sectioned to substantiate the findings of the present study.

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Literature Cited

- Alexander, R. M. 1989. Dynamics of dinosaurs and other extinct giants. Columbia University Press, New York.
- Anderson, J. F., A. Hall-Martin, and D. A. Russell. 1985. Long-bone circumference and weight in mammals, birds and dinosaurs. *Journal of Zoology A* 207:53–61.
- Carpenter, K. 1999. Eggs, nests, and baby dinosaurs. Indiana University Press, Bloomington.
- Carpenter, K., and J. McIntosh. 1994. Upper Jurassic sauropod babies from the Morrison Formation. Pp. 265–278 in K. Carpenter, K. Hirsch, and J. Horner, eds. *Dinosaur eggs and babies*. Cambridge University Press, Cambridge.
- Case, T. J. 1978a. On the evolution and adaptive significance of postnatal growth rates in the terrestrial vertebrates. *Quarterly Review of Biology* 53:243–282.
- . 1978b. Speculations on the growth rate and reproduction of some dinosaurs. *Paleobiology* 4:320–328.
- Castanet, J., H. Francillon-Vieillot, F. J. Meunier, and A. de Ricqlès. 1993. Bone and individual aging. Pp. 245–283 in B. K. Hall, ed. *Bone*, Vol. 7. Bone growth. CRC Press, Boca Raton, Fla.
- Curry, K. A. 1999. Ontogenetic histology of *Apatosaurus* (Dinosauria: Sauropoda): new insights on growth rates and longevity. *Journal of Vertebrate Paleontology* 19:654–665.
- Dunham, A. E., K. L. Overall, W. P. Porter, and C. A. Forster. 1989. Implications of ecological energetics and biophysical and developmental constraints for life-history variation in dinosaurs. Pp. 1–19 in J. O. Farlow, ed. *Paleobiology of the dinosaurs*. Geological Society of America Special Paper 238.
- Erickson, G. M. 2005. Assessing dinosaur growth patterns: a microscopic revolution. *Trends in Ecology and Evolution* 20:677–684.
- Erickson, G. M., K. C. Rogers, and S. A. Yerby. 2001. Dinosaurian growth patterns and rapid avian growth rates. *Nature* 412:429–433.
- Horner, J. R., A. de Ricqlès, and K. Padian. 1999. Variation in dinosaur skeletochronology indicators: implications for age assessment and physiology. *Paleobiology* 25:295–304.
- . 2000. Long bone histology of the hadrosaurid dinosaur *Maiasaura pebblesorum*: growth dynamics and physiology based on an ontogenetic series of skeletal elements. *Journal of Vertebrate Paleontology* 20:115–129.
- Ikejiri, T. 2004. Relative growth and timing of ontogenetic changes in *Camarasaurus* (Dinosauria, Sauropoda). *Journal of Vertebrate Paleontology* 42:74A.
- Laws, R. M., I. S. Parker, and R. C. Johnstone. 1975. Elephants and their habitats: the ecology of elephants in North Bunyoro, Uganda. Clarendon, Oxford.
- Lehman, T. M. 2007. Growth and population age structure in the horned dinosaur *Chasmosaurus*. Pp. 259–317 in K. Carpenter, ed. *Horns and beaks: ceratopsian and ornithomimid dinosaurs*. Indiana University Press, Bloomington.
- Lehman, T. M., and A. B. Coulson. 2002. A juvenile specimen of the sauropod dinosaur *Alamosaurus sanjuanensis* from the Upper Cretaceous of Big Bend National Park, Texas. *Journal of Paleontology* 76:156–172.
- Padian, K., A. J. de Ricqlès, and J. R. Horner. 2001. Dinosaurian growth rates and bird origins. *Nature* 412:405–408.
- Paladino, F. V., J. R. Spotila, and P. Dodson. 1997. A blueprint for giants: modeling the physiology of large dinosaurs. Pp. 491–504 in J. O. Farlow and M. Brett-Surman, eds. *The complete dinosaur*. Indiana University Press, Bloomington.
- Paul, G. S. 1994. Dinosaur reproduction in the fast lane: implications for size, success, and extinction. Pp. 244–255 in K. Carpenter, K. Hirsch, and J. Horner, eds. *Dinosaur eggs and babies*. Cambridge University Press, Cambridge.
- Paul, G. S. 1997. Dinosaur models: the good, the bad, and using them to estimate the mass of dinosaurs. Pp. 129–154 in D. L. Wolberg, E. Stump, and G. D. Rosenberg, eds. *DinoFest international*. Academy of Natural Sciences, Philadelphia.
- Reid, R. E. H. 1981. Lamellar-zonal bone with zones and annuli in the pelvis of a sauropod dinosaur. *Nature* 292:49–51.
- . 1987. Bone and dinosaurian "endothermy." *Modern Geology* 11:133–154.
- . 1990. Zonal "growth rings" in dinosaurs. *Modern Geology* 15:19–48.
- . 1997. Dinosaurian physiology: the case for "intermediate" dinosaurs. Pp. 449–473 in J. O. Farlow and M. Brett-Surman, eds. *The complete dinosaur*. Indiana University Press, Bloomington.
- Ricklefs, R. E. 1968. Patterns of growth in birds. *Ibis* 110:419–451.
- . 1973. Patterns of growth in birds. II. Growth rate and mode of development. *Ibis* 115:177–201.
- Ricqlès, A. de 1983. Cyclical growth in the long limb bones of a sauropod dinosaur. *Acta Palaeontologica Polonica* 28:225–232.
- Russell, D. A. 1989. An odyssey in time: the dinosaurs of North America. National Museum of Natural Sciences, Ottawa.
- Sander, P. M. 2000. Long bone histology of the Tendaguru sau-

- ropods: implications for growth and biology. *Paleobiology* 26: 466–488.
- Sander, P. M., and N. Klein. 2005. Developmental plasticity in the life history of a prosauropod dinosaur. *Science* 310:1800–1802.
- Sander, P. M., and C. Tuckmantel. 2003. Bone lamina thickness, bone apposition rates, and age estimates in sauropod humeri and femora. *Paläontologische Zeitschrift* 77:161–172.
- Sander, P. M., N. Klein, E. Buffetaut, G. Cuny, V. Suteethorn, and J. Le Loeuff. 2004. Adaptive radiation in sauropod dinosaurs: bone histology indicates rapid evolution of giant body size through acceleration. *Organisms, Diversity and Evolution* 4: 165–173.
- Seebacher, F. 2001. A new method to calculate allometric length-mass relationships of dinosaurs. *Journal of Vertebrate Paleontology* 21:51–60.
- Spotila, J. R., P. Dodson, and F. V. Paladino. 1991. Hot and cold running dinosaurs: body size, metabolism and migration. *Modern Geology* 16:203–227.
- Tidwell, V., and D. R. Willhite. 2005. Ontogenetic variation and isometric growth in the forelimb of the Early Cretaceous sauropod *Venenosaurus*. Pp. 187–196 in V. Tidwell and K. Carpenter, eds. *Thunder lizards*. Indiana University Press, Bloomington.
- Weaver, J. C. 1983. The improbable endotherm: the energetics of the sauropod dinosaur *Brachiosaurus*. *Paleobiology* 9:173–182.
- Wedel, M. J. 2003. Vertebral pneumaticity, air sacs, and the physiology of sauropod dinosaurs. *Paleobiology* 29:243–255.
- Wilson, J. A., and P. C. Sereno. 1998. Early evolution and higher-level phylogeny of sauropod dinosaurs. *Society of Vertebrate Paleontology Memoir* 5.
- Woodward, H. N. 2005. Bone histology of the sauropod dinosaur *Alamosaurus sanjuanensis* from the Javelina Formation, Big Bend National Park, Texas. Masters's thesis. Texas Tech University, Lubbock.
- Woodward, H. N., and T. M. Lehman. 2006. Using limb circumference and body mass to estimate sauropod dinosaur growth rates. *Journal of Vertebrate Paleontology* 26:141A.