

Sizing the Jurassic Theropod Dinosaur *Allosaurus*: Assessing Growth Strategy and Evolution of Ontogenetic Scaling of Limbs

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ABSTRACT *Allosaurus* is one of the most common Mesozoic theropod dinosaurs. We present a histological analysis to assess its growth strategy and ontogenetic limb bone scaling. Based on an ontogenetic series of humeral, ulnar, femoral, and tibial sections of fibrolamellar bone, we estimate the ages of the largest individuals in the sample to be between 13–19 years. Growth curve reconstruction suggests that maximum growth occurred at 15 years, when body mass increased 148 kg/year. Based on larger bones of *Allosaurus*, we estimate an upper age limit of between 22–28 years of age, which is similar to preliminary data for other large theropods. Both Model I and Model II regression analyses suggest that relative to the length of the femur, the lengths of the humerus, ulna, and tibia increase in length more slowly than isometry predicts. That pattern of limb scaling in *Allosaurus* is similar to those in other large theropods such as the tyrannosaurids. Phylogenetic optimization suggests that large theropods independently evolved reduced humeral, ulnar, and tibial lengths by a phyletic reduction in longitudinal growth relative to the femur. *J. Morphol.* 267:347–359, 2006. © 2005 Wiley-Liss, Inc.

KEY WORDS: *Allosaurus*; bone histology; growth dynamics; scaling; allometry; theropod evolution

The growth dynamics of some theropod dinosaurs are well documented. Over the past decade, histological studies of bones have estimated growth dynamics for coelophysoids (Chinsamy, 1990; Padian et al., 2004), tyrannosaurids (Erickson et al., 2004; Horner and Padian, 2004), a troodontid (Varricchio, 1993), extinct avians (Chinsamy et al., 1998; de Ricqlès et al., 2003; Turvey et al., 2005), and living avians (Castanet et al., 2000; de Margerie et al., 2002, 2004). Those and other studies suggest that small basal dinosaur taxa (e.g., *Psittacosaurus*, *Massospondylus*, *Scutellosaurus*, and *Orodromeus*) grew at rates comparable to or exceeding rates in living reptiles and marsupials (Erickson and Tumanova, 2000; Erickson et al., 2001; Padian et al., 2001, 2004), whereas large derived taxa (e.g., sauropods, hadrosaurids, tyrannosaurids, and ceratopsids) grew at least as rapidly as living birds and placental

mammals (Curry, 1999; Sander, 1999; Horner et al., 1999, 2000; Erickson et al., 2001; Horner and Padian, 2004; Lee, 2004).

Changes in size as well as in body proportion accompany growth. For example, the femora of the large to gigantic tyrannosaurids lengthen more rapidly than do the humeri, ulnae, and tibiae (Russell, 1970; Currie, 2003). Such ontogenetic changes in limb bone proportions have implications on locomotion: smaller and younger tyrannosaurids probably ran faster than larger and older ones (Hutchinson and Garcia, 2002). That other large theropods show similar adult limb proportions as large tyrannosaurids (Christiansen, 1999; Middleton and Gatesy, 2000) suggests not only mechanical limits to locomotor performance at large size, but also raises the question of whether limb bone growth follows constrained patterns of ontogenetic scaling in other large theropods.

Allosaurus is a large and common basal tetanuran theropod. Approximately 60–80% of theropod occurrences from the Morrison Formation (Late Jurassic) are of *Allosaurus* (Dodson et al., 1980; Miller et al., 1996). Those occurrences are spread over a wide geographic range, including Colorado, Montana, New Mexico, Oklahoma, South Dakota, Wyoming, and Utah (Chure, 2000). One locality, the Cleveland-Lloyd Dinosaur Quarry (CLDQ) in east central Utah, has produced over 10,000 bones that represent the disarticulated remains of 44–60 individuals of *Allosaurus* (Madsen, 1976). Despite poor representation of extremely small and large individ-

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TABLE 1. Ontogenetic series of limb bones from *Allosaurus* found at the Cleveland-Lloyd Dinosaur Quarry

Element	Specimen	Length, mm	Circum., mm	LAG circumference, mm	# of preserved LAGs	# of retrocalculated LAGs	Est. age yrs	Est. mass. (DME mass), kg
Humerus	UUVP 4220	150	51	28,44	2	2	4	46 (64)
	UUVP 3312	184	64	50,59,62	3	3	6	109 (139)
	UUVP 40–227	255	97	60,62,68,72,77,84,88,93	8	4	12	297 (350)
	UUVP 5496	272	126	70,77,86,95,110,120	6	7	13	558 (627)
	UUVP 10154	336	146	98,131,134,138	4	11	15	789 (862)
Ulna	UUVP 3607	387	178	131,144,149,154,169,175	6	13	19	1423 (1481)
	UUVP 3689	111	35	13,16,31	3	0	3	27 (42)
	UUVP 2916	141	48	21,32,40,42	4	1	5	60 (88)
	UUVP 30–68	135	64	30,39,43,53,57	5	2	7	136 (187)
	UUVP 4740	172	87	42,51,54,59,64,71,79	7	4	11	323 (417)
	UUVP 3987	245	125	76,87,98,112,118,120	6	10	16	984 (1162)
	UUVP 40–264	370	125	110,113,120	3	3	6	76 (109)
Femur	UUVP 3164	468	153	138,144,146	3	4	7	130 (178)
	UUVP 30–737	485	190	104,112,119,126,134,143,153,158,162,165	10	3	13	181 (242)
	UUVP 11164	558	209	130,158,171,182	4	5	9	237 (310)
	UUVP 2656	656	286	135,152,163,202,260,262,279	7	5	12	760 (911)
	UUVP 3694	872	338	172,235,265,274,335	5	8	13	1252 (1445)
Tibia	UUVP 154	410	158	90,138	2	5	7	268 (344)
	UUVP 40304	596	214	102,114,124,129,133,152,158,168,196,212	10	5	15	892 (1043)
	UUVP 5300	622	239	119,143,155,168,201,235	6	9	15	1191 (1362)

uals, the CLDQ locality preserves individuals of a reasonably wide range in size. Those individuals range in length from 3–12 m and range in height, when fully upright, from 1–4.5 m (Madsen, 1976). The availability of skeletal material at CLDQ, which spans a broad size range and presumably ontogeny, presents an excellent opportunity to assess the growth dynamics of *Allosaurus* in the context of other theropods.

In this article we assess the growth dynamics of *Allosaurus* by analyzing a histological proxy for age. Lines of arrested growth (LAGs) occur in the bones of living poikilothermic and homeothermic tetrapods and are known to have an annual periodicity (Morris, 1970; Frylestam and Schantz, 1977; Fiala, 1978; Hemelaar and Van Gelder, 1980; Hutton, 1986; Castanet et al., 1988, 1993, 2004; Tucker, 1997). Although that annual periodicity cannot be empirically tested in the long bones of extinct tetrapods, inference by extant phylogenetic bracketing (Witmer, 1995) suggests that the presence of LAGs in extinct tetrapods also represents yearly intervals of bone growth. Bone resorption and remodeling, however, complicate age estimations. Resorption removes bone, and remodeling obscures the earliest LAGs. Both processes differ in extent across limb bones within an individual. Consequently, some bones will have more preserved LAGs than others, and age estimates will vary depending on the bone that is used (Horner et al., 1999). The number of missing LAGs is approximated by using retrocalculations, which use various models of periosteal bone growth rate (Chinsamy, 1993; Horner and Padian, 2004). When possible, however, the reliance on retrocalculations should be minimized by an ontogenetic series of bones (Horner et al., 1999). It is fortuitous that, for *Allosaurus*, an ontogenetic series of several limb bones is available. Here, we use bone

histology and image analysis to 1) test whether the growth strategy of *Allosaurus* is similar to similarly sized theropods (i.e., tyrannosaurids); 2) reconstruct patterns of limb bone scaling in *Allosaurus*; and 3) assess developmental mechanisms for evolutionary changes in the limb length of theropods.

MATERIALS AND METHODS

Histological Preparation

A total of six humeri, five ulnae, six femora, and three tibiae of *Allosaurus* (Marsh, 1877) was selected for histological analysis (Table 1). Those disarticulated limb bones came from the CLDQ in Utah and were collected by crews from the University of Utah, Salt Lake City, UT (UUVP) (Madsen, 1976). The bones represent a range of ontogenetic stages available at CLDQ from juveniles to subadults. Our histological sample does not provide robust ontogenetic scaling relationships between bone length and circumference, so we also measured CLDQ specimens currently stored at UUVP and Dinosaur National Monument (DINO) in Vernal, UT, as well as non-CLDQ specimens at the American Museum of Natural History (AMNH) in New York City and Brigham Young University (BYUVP) in Provo, UT (Appendix). The additional limb bones not only increase the statistical power of our analyses, but also allow us to characterize growth of the species.

Before sectioning, bone lengths and midshaft circumferences were measured. Because length as measured along the outer curve (Madsen, 1976) produces a measurement that is ~10% larger and not directly comparable with measurements of theropods in other studies (Table 2), we measured length of femora, humeri, and tibiae as the maximum linear distance that is roughly parallel to midshaft. To minimize variations in ulnar length caused by individual variation in olecranon size, we measured ulnar length between the proximal and distal articular surfaces. Diaphyseal circumference was measured at 60% of the proximodistal length in the humerus and femur to avoid major regions of muscle insertion and, in the ulna and tibia, circumference was measured at 50% of the length. Positions for measuring circumference also helped to standardize positions for transverse sectioning in each ontogenetic series. Transverse sections were produced by standard hard tissue histological techniques (Wilson, 1994; Lamm, 1998). Photography of entire sections, which are quite large, under the high magnification of a microscope is space- and time-prohibitive. Instead, all 20 sections were backlit by a

TABLE 2. Measurements of limb bone length in selected theropods of nearly adult to adult size

Taxon	Source	Length, mm				Ratios		
		Humerus	Ulna	Femur	Tibia	H/F	U/F	T/F
<i>Eoraptor</i>	UCMP 177289 cast of PVSJ 512	75	56	152	175	0.49	0.37	1.15
<i>Herrerasaurus</i>	PVSJ 373: Novas, 1993; Sereno, 1993	175	152	364	347	0.48	0.42	0.95
<i>Coelophysis</i>	AMNH 7224	134	82	203	221	0.66	0.40	1.09
<i>Syntarsus</i>	QG/1: Raath, 1969	94	64	208	214	0.45	0.31	1.03
<i>Dilophosaurus</i>	UCMP 37302	285	191	558	527	0.51	0.34	0.94
<i>Deltadromeus</i>	SGM-Din 2: Sereno et al., 1996	(328)	(302)	740	(700)	0.44	0.41	0.95
<i>Aucasaurus</i>	MCF-PVPH-236: Coria et al., 2002	255	73	722	698	0.40	0.10	0.97
<i>Carnotaurus</i>	MACN-CH 894: Bonaparte et al., 1990	285	68	1030	(970)	0.28	0.07	0.94
<i>Piatnitzkysaurus</i>	PVL 4073: Bonaparte, 1986	294	179	563	518	0.52	0.32	0.92
<i>Suchimimus</i>	MNN GDF500: Sereno et al., 1998	560	331	1075	945	0.52	0.31	0.90
<i>Allosaurus</i>	USNM 4734: Gilmore, 1920	310	240	850	690	0.36	0.28	0.81
<i>Acrocanthosaurus</i>	NCSM 14345: Currie and Carpenter, 2000	370	217	1277	(960)	0.29	0.17	0.75
<i>Compsognathus</i>	UCMP 124884 cast of BSP AS I 536	(67)	42	110	133	0.61	0.38	1.21
<i>Sinornithomimus</i>	NIGP 127587: Currie and Chen, 2001	34	21	87	90	0.39	0.24	1.03
<i>Gorgosaurus</i>	USNM 12814: Russell, 1970	254	125	860	780	0.30	0.15	0.91
<i>Tyrannosaurus</i>	UCMP cast of MOR 555	380	160	1270	1100	0.30	0.13	0.87
<i>Struthiomimus</i>	AMNH 5339: Gilmore, 1920	309	206	515	577	0.60	0.40	1.12
<i>Sinornithomimus</i>	IVPP V11797-10: Kobayashi and Lü, 2003	212	145	323	335	0.66	0.45	1.04
<i>Microraptor</i>	CAGS 20-7-004: Hwang et al., 2004	61	(50)	74	94	0.82	0.73	1.27
<i>Bambiraptor</i>	AMNH 30556: Burnham, 2004	105	90	119	168	0.88	0.76	1.41
<i>Deinonychus</i>	MCZ 4371: Ostrom, 1976	254	192	336	368	0.76	0.57	1.10
<i>Falcarius</i>	Kirkland et al., 2005	(217)	(139)	(394)	(430)	0.55	0.35	1.09
<i>Alxasaurus</i>	IVPP 88402: Russell and Dong, 1993	375	245	555	(481)	0.68	0.44	0.87
<i>Nothronychus</i>	MSM P-2117: Kirkland and Wolfe, 2001	418	292	(692)	614	0.60	0.42	0.89
<i>Caudipteryx</i>	NGMC 97-9-A: Ji et al., 1998	70	59	149	182	0.47	0.40	1.22
<i>Ingenia</i>	GI 100/30: Barsbold et al., 1990	138	93	233	278	0.59	0.40	1.19
<i>Archaeopteryx</i>	Houck et al., 1990	83	71	71	92	1.17	1.00	1.30

AMNH, American Museum of Natural History, New York, NY, USA; BSP, Bayerische Staatssammlung für Paläontologie und Historische Geologie, Munich, Germany; CAGS, Chinese Academy of Geological Sciences, Beijing, China; GI, Geological Institute, Ulan Bator, People's Republic of Mongolia; IVPP, Institute of Vertebrate Paleontology and Paleoanthropology, Beijing, China; MACN-CH, Museo Argentino de Ciencias Naturales, Buenos Aires, Argentina; MCF-PVPH, Museo Municipal Carmen Funes, Plaza Huincul, Argentina; MCZ, Museum of Comparative Zoology, Harvard, MA, USA; MNN, Musée National du Niger, Niamey, Republic of Niger; MOR, Museum of the Rockies, Bozeman, MT, USA; MSM, Mesa Southwest Museum, Mesa, AZ, USA; NGMC, National Geological Museum of China, Beijing, China; NIGP, Nanjing Institute of Geology and Paleontology, Nanjing, China; NCSM, North Carolina State Museum of Natural Sciences, Raleigh, NC, USA; PVL, Fundación 'Miguel Lillo', San Miguel de Tucumán, Argentina; PVSJ, Museo Provincial de San Juan, San Juan, Argentina; QG, Zimbabwe Natural History Museum, Bulawayo, Zimbabwe; SGM, Ministère de l'Energie et des Mines, Rabat, Morocco; UCMP, University of California Museum of Paleontology, Berkeley, CA, USA; USNM, United States National Museum, Washington DC, USA. Estimated measurements in parentheses.

fiberoptic lightbox (Fostec, Auburn, NY) and imaged by digital macrophotography (DXC-330, Sony; D70, Nikon; 60 mm Micro-Nikkor, Nikon). Images of each section were digitally captured with some overlap and were reassembled in PhotoShop (Adobe, San Jose, CA). Periosteal borders, endosteal borders, and LAGs were digitally traced in Illustrator (Adobe) and exported for image analysis.

Estimation of Age and Growth Curve

Periosteal and LAG circumferences were measured by the perimeter function in NIH ImageJ (NIH, Bethesda, MD). We prefer to measure circumference because 1) estimates of circumference based on diameters are underestimates when sections are irregular in shape; 2) circumference is used to predict body mass (Anderson et al., 1985); and 3) circumference is easily comparable across sections of a given bone series. In Excel (Microsoft, Redmond, WA), LAG circumferences were visually aligned across each bone series and the circumferences of missing LAGs were retrocalculated using a significant power relationship. That power relationship predicts rapid growth early in ontogeny followed by slower growth during late ontogeny. Although some varanids can show rapid growth either during early or late ontogeny (de Buffrénil and Castanet, 2000), all assessed dinosaur taxa show higher periosteal growth rates earlier rather than later in ontogeny (Chinsamy, 1993; Curry, 1999; Horner et al., 1999,

2000; Erickson and Tumanova, 2000; Padian et al., 2004; Erickson et al., 2004; Horner and Padian, 2004). Age estimates are presented in Table 1.

Estimates of body mass were calculated using both an inter-specific (Anderson et al., 1985) and a developmental (Developmental Mass Extrapolation sensu Erickson and Tumanova, 2000; Erickson et al., 2004) relationship between body mass and femoral circumference. Because our femoral specimens span only the earlier half of ontogeny, we also estimated body mass using tibial, humeral, and ulnar circumferences. A relationship between body mass and age was determined by a nonconstrained three-parameter logistic regression (Zullinger et al., 1984) in SPSS (Chicago, IL), which uses an iterative least-squares criterion. Differences in growth curve parameters (i.e., asymptotic mass, growth rate constant, and inflection point) among *Allosaurus* and tyrannosaurids (Erickson et al., 2004) were considered significant if the 95% confidence intervals (CIs) of those parameters did not overlap. Maximum growth rate was calculated by finding the derivative of each regression equation at the inflection point.

Ontogenetic Limb Bone Scaling

Circumference–age and circumference–length regression equations were calculated for each bone series in SPSS. Both circumference and length are subject to error, so a Model II criterion (reduced major axis) for regression is appropriate. However,

when regressions are used for both functional relationships and prediction, a Model I (least-squares) criterion for regression is justified (Sokal and Rohlf, 1995). We used both regression techniques to compare the functional elements of the equations but only used Model I regressions for prediction. Circumference–age and circumference–length equations were combined to derive length–length equations between the femur and other limb bones. Femoral length was used as an indicator of body mass because it is positively correlated to body mass among living archosaurs (birds: Zeffer et al., 2003; crocodilians: Farlow et al., 2005) as well as among living mammals (McMahon, 1973; Christiansen, 1999), which show similar locomotor morphologies to non-avian theropods (Gatesy, 1991; Carrano, 1998; Christiansen, 1999). Limb bone lengths scale isometrically to femoral length if the power exponent equals 1. To assess the utility of the equations, we compared the predicted against measured lengths of articulated skeletal elements not included in our histological and scaling sample. Those skeletal elements are currently stored at the National Museum of Natural History (USNM) in Washington DC and the Museum of the Rockies (MOR) in Bozeman, MT.

Phylogenetic Comparisons and Tests

Phylogenetic relationships for theropod dinosaurs are based on cladistic analyses of independent morphological characters (Currie and Carpenter, 2000; Rahut, 2003; Sereno et al., 2004; Holtz and Osmólska, 2005). Because those cladistic analyses differ in the phylogenetic placement of several clades of basal theropods, we used two alternative cladograms of theropod relationships. In the first cladogram, the Ceratosauria is a paraphyletic grade of non-tetanuran theropods and Allosauroidae + Spinosauroidae is sister to the Coelurosauria (Rahut, 2003). In the second cladogram, the Ceratosauria is monophyletic and the Allosauroidae and the Coelurosauria are sister taxa to the exclusion of the Spinosauroidae (Holtz and Osmólska, 2005). In both, *Deltadromeus* is the sister taxon to the Abelisauridae (Sereno et al., 2004). Our study is limited to those taxa that have preserved forelimb and hindlimb elements. We chose 25 taxa that represent the major clades of theropods and *Eoraptor* and *Herrerasaurus* as outgroups in two phylogenetic comparative analyses: 1) phylogenetically independent contrasts, and 2) reconstruction of ancestral states.

We tested correlations between limb bone and femoral lengths using phylogenetically independent contrasts (Felsenstein, 1985). Humeral, ulnar, femoral, and tibial lengths from the theropods (Table 2) were log₁₀-transformed to improve normality and homoscedasticity and were mapped onto the theropod phylogeny within Mesquite (Maddison and Maddison, 2004). The PDAP module within Mesquite was used to calculate standardized contrasts as well as absolute values and standard deviations (SDs) of those contrasts. Correlations between the absolute value and SD of standardized contrasts were used to test the adequacy of using a speciation model of phenotypic evolution. A nonsignificant correlation ($P > 0.05$) between the absolute value and SD of contrasts for each character would suggest that branch length assumptions are adequate.

Limb bone length varies with body size, so we removed the effects of body size by calculating the residuals from the regressions of standardized contrasts. Regressions were performed in SPSS, but because Model I and Model II regressions for this dataset are similar, we only present Model I regressions. Significance of correlations between the residual contrasts of bone lengths and femoral length ($P < 0.05$) was judged with one-tailed t -tests because we predict a negative correlation between bone lengths and femoral length.

Ratios between humeral, ulnar, and tibial lengths and femoral length from selected theropods (Table 2) were mapped onto the phylogeny within the Mesquite system for phylogenetic computation (Maddison and Maddison, 2004). Branch lengths were set to unity, which assumes a speciation, “Brownian motion” model of phenotypic evolution (Rohlf et al., 1990). Ancestral ratios of bone length were estimated using squared-change parsimony

(Martins and Hansen, 1996; Garland et al., 1997) within Mesquite.

RESULTS

Previous studies of the long bone histology of large dinosaurs report fibrolamellar bony tissue (Reid, 1996; Curry, 1999; Horner et al., 1999, 2000; Horner and Padian, 2004). Our histological data from sections of *Allosaurus* humeri, ulnae, femora, and tibiae are consistent with previous observations. Furthermore, as in large hadrosaurids and *Tyrannosaurus rex* (Horner et al., 1999, 2000; Horner and Padian, 2004), vascular organization in *Allosaurus* varies across a section, among different bones, and through ontogeny. In summary, vascular canals in humeri, femora, and tibiae throughout ontogeny are predominantly circumferentially oriented, whereas those in ulnae are predominantly longitudinally oriented (Fig. 1). Secondary remodeling of fibrolamellar tissue also occurs in all sections but is particularly widespread in the sections of humeri and ulnae. In contrast, remodeling is localized to the anterior cortex in the femur and the lateral cortex in the tibia. Remodeling, which interrupts or removes ontogenetically older LAGs, is most extensive in the internal cortex.

LAGs occur in the cortex of all the bone sections of *Allosaurus* (Table 1). Although there is individual variation, circumferences of LAGs for each bone series generally overlap (Fig. 2). Estimates of age for our specimens range from 13–19 years. None of the sections, even the larger ones, have an external fundamental system (EFS) (Fig. 1). On the contrary, the outermost cortical bone remains highly vascularized, and only in the ulna does the spacing between successive LAGs decrease during ontogeny. All sections appear to represent individuals that were still actively growing before death.

Interlimb scaling relationships are presented below, where C = circumference, L = length, F = femur, T = tibia, H = humerus, U = ulna, \pm SE:

$$C_F = (0.10 \pm 0.02)L_F^{1.19 \pm 0.02}, n = 23, R^2 = 0.99 \quad (1)$$

$$C_T = (0.009 \pm 0.004)L_T^{1.58 \pm 0.08}, n = 25, R^2 = 0.94 \quad (2)$$

$$C_H = (0.04 \pm 0.02)L_H^{1.40 \pm 0.09}, n = 25, R^2 = 0.92 \quad (3)$$

$$C_U = (0.11 \pm 0.04)L_U^{1.26 \pm 0.08}, n = 16, R^2 = 0.95 \quad (4)$$

$$L_T = 4.23L_F^{0.74} \quad (5)$$

$$L_H = 0.65L_F^{0.94} \quad (6)$$

$$L_U = 0.37L_F^{0.97} \quad (7)$$

Femoral (one-tailed $P = 2.2 \times 10^{-6}$), tibial ($P = 1.1 \times 10^{-7}$), humeral ($P = 9.3 \times 10^{-5}$), and ulnar ($P = 2.9 \times 10^{-3}$) circumferences all show significant

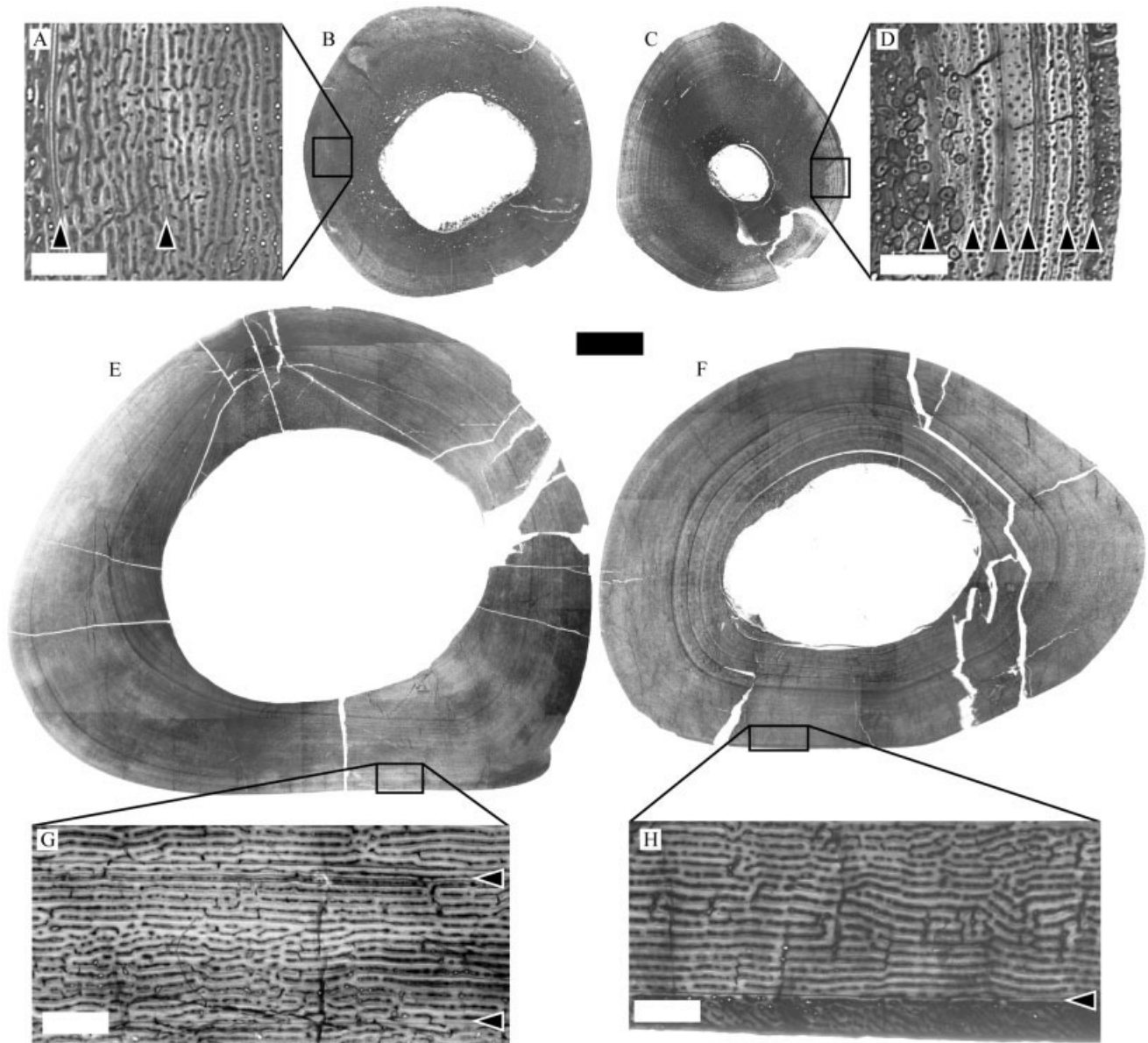


Fig. 1. Bone histology of *Allosaurus*. Transverse sections of a humerus (B), ulna (C), femur (E), and tibia (F). Magnified fields show fibrolamellar bony tissue and arrows indicate LAGs (A,D,G,H). UUVP 10154 (A,B); UUVP 3987 (C,D); UUVP 2656 (E,G); UUVP 5300 (F,H). Scale bars: (A,D,G,H) 1 mm; (B,C,E,F) 10 mm.

positive allometry with respect to lengths (Eqs. 1–4). Tibial length scales with strong negative allometry to femoral length (Eq. 5), whereas both humeral and ulnar length scale with weak negative allometry to femoral length (Eqs. 6, 7). Model II regression equations for circumference and length of the femur (one-tailed $P = 2.5 \times 10^{-7}$), tibia ($P = 2.6 \times 10^{-8}$), humerus ($P = 7.4 \times 10^{-6}$), and ulna ($P = 1.0 \times 10^{-3}$) show trends that agree with Model I trends (Eqs. 1–4). Furthermore, the trends of Model II regressions between femoral length and lengths of the tibia, humerus, and ulna are comparable to Model I trends (Eqs. 5–7).

Mass estimates of *Allosaurus* based on both an interspecific (Anderson et al., 1985) and developmental (Erickson and Tumanova, 2000; Erickson et al., 2004) relationship between body mass and femoral circumference are similar (Table 1). Furthermore, growth curve parameters (i.e., asymptote, growth rate constant, and inflection point; see Fig. 3) have overlapping 95% CIs. Upper age limits for both mass estimation techniques are similar: 30 ± 4 (CI) years. Skeletal maturity, however, probably occurred between 13–19 years. The maximum growth rate was ~ 148 kg/year at year 15 ± 2 (CI) when mass is estimated by the interspecific relationship or

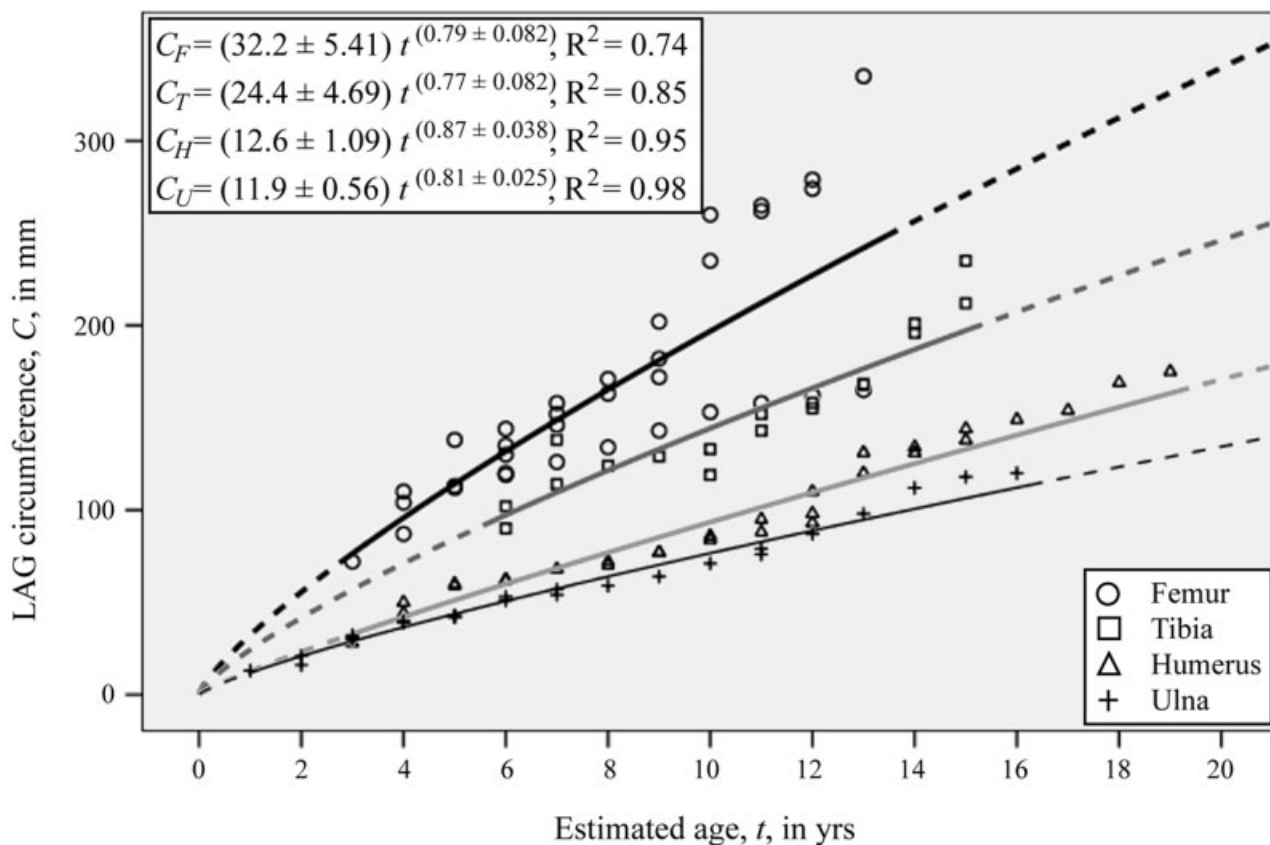


Fig. 2. Variation of LAG circumferences and circumference-to-age regressions in limb bones of *Allosaurus*.

~145 kg/year at year 15 ± 2 (CI) when mass is estimated by the developmental one. The growth curve parameters of *Allosaurus* and *Gorgosaurus*, which is a similarly sized tyrannosaurid, have overlapping confidence intervals (Fig. 3). Despite significantly larger adult mass, the growth rate constant and inflection point of *Tyrannosaurus* are not significantly different from either those of *Allosaurus* or *Gorgosaurus* (Fig. 3).

Figure 4 shows the negative relationships between either the residual contrasts in humeral, ulnar, or tibial length and femoral length. Significantly negative correlations exist between 1) the residual contrasts of humeral and femoral lengths ($n = 26$ contrasts, $R^2 = 0.86$, one-tailed $P < 0.001$); 2) the residual contrasts of ulnar and femoral lengths ($R^2 = 0.68$, one-tailed $P < 0.001$); and 3) the residual contrasts of tibial and femoral lengths ($R^2 = 0.99$, one-tailed $P < 0.001$). Alternative phylogenetic hypotheses (i.e., paraphyletic vs. monophyletic Ceratosauria) have little influence on those significantly negative correlations. Correlations between residual contrasts of bone length have no more error than if other models of phenotypic evolution were used because significant correlations do not exist between the absolute value and SD of standardized contrasts (humerus: $n = 24$ contrasts, $R^2 =$

6.14×10^{-6} , two-tailed $P = 0.99$; ulna: $R^2 = 8.50 \times 10^{-3}$, two-tailed $P = 0.67$; femur: $R^2 = 2.50 \times 10^{-3}$, two-tailed $P = 0.82$; tibia: $R^2 = 1.63 \times 10^{-3}$, two-tailed $P = 0.85$).

Character optimization using squared-change parsimony suggests that the adult ratios between bone length and femoral length in *Allosaurus* are substantially lower than the adult ratios in ancestral theropods (Fig. 5). Other large theropods such as *Carnotaurus*, *Gorgosaurus*, and *Tyrannosaurus* also show a similar reduction in limb bone ratios from ancestral ratios.

DISCUSSION

Growth strategy and ontogenetic limb bone scaling of *Allosaurus* resemble those of comparably sized theropods. As in other theropods, the four major long bones of *Allosaurus* are highly vascularized and are fibrolamellar in texture (Fig. 1). Both histological features suggest rapid periosteal growth. Age estimates of the largest sampled individuals from the CLDQ range from 13–19 years (Fig. 2). At 15 ± 2 (CI) years of age, the growth rate of *Allosaurus* reached a maximum (148 kg/yr), and that age and rate of maximum growth are similar in the tyrannosaurid *Gorgosaurus* (Fig. 3). Similarity in growth

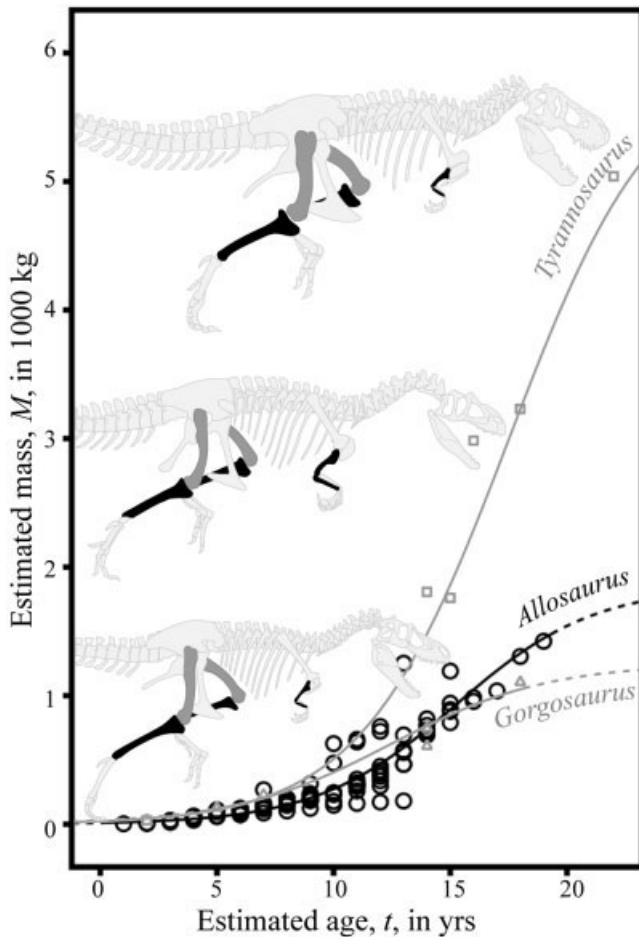


Fig. 3. Growth dynamics of some large theropods. Bones of the skeletal reconstructions (after Paul, 1988) show interlimb scaling during growth: isometry with respect to femur (dark gray) and negative allometry with respect to femur (black). Regression equations (\pm SE) are as follows: $M_{T. rex} = (5590 \pm 372)/(1 + e^{-(0.40 \pm 0.09)(t - (16 \pm 0.56))})$, $R^2 = 0.98$; $M_{Allo} = (1852 \pm 299)/(1 + e^{-(0.32 \pm 0.03)(t - (15 \pm 1.1))})$, $R^2 = 0.86$; $M_{Allo_DME} = (1871 \pm 295)/(1 + e^{-(0.31 \pm 0.03)(t - (15 \pm 1.1))})$, $R^2 = 0.84$; $M_{Gorgo} = (1414 \pm 449)/(1 + e^{-(0.30 \pm 0.11)(t - (14 \pm 2.5))})$, $R^2 = 0.97$.

strategy to reach a particular size in closely related theropod lineages suggests that the mechanism by which the independent evolution of gigantism occurred may be similar. The acceleration of growth rate as seen in *Tyrannosaurus rex* relative to more basal tyrannosaurids (Erickson et al., 2004; Fig. 3) may also explain how allosauroids such as *Acrocanthosaurus* (Stovall and Langston, 1950), *Giganotosaurus* (Coria and Salgado, 1995), and *Carcharodontosaurus* (Stromer, 1931; Sereno et al., 1996) became gigantic. Rapid growth in those gigantic allosauroids is not unreasonable because growth in amniotes is generally more rapid in clades of large adult size than in clades of small size (Case, 1978; Erickson et al., 2001; Padian et al., 2001, 2004).

During ontogeny, the linear dimensions of *Allosaurus* limb bones change proportions. Circumfer-

ences of humeri, ulnae, femora, and tibiae scale with positive allometry to respective bone length (Eqs. 1–4). That pattern of allometry suggests that long bones of older individuals are relatively stouter than those of younger individuals. In addition, ontogenetic changes in proportional length occur between forelimb and hindlimb bones. With respect to femoral length, humeral, ulnar, and tibial lengths scale negative allometrically (Eqs. 5–7). Unfortunately, skeletal disarticulation precludes any statistical test of significance for the patterns of interlimb allometry. In a qualitative sense, however, the relatively high coefficients of allometry for the humeral and ulnar equations suggest only weak negative allometry, whereas the low coefficient for the tibial equation suggests strong negative allometry.

To test those equations, we compared predicted length to measured length for an incompletely articulated and a completely articulated specimen of *Allosaurus*. The incompletely articulated specimen of *Allosaurus* (USNM 4734) was found with a femur and tibia in articulation (Gilmore, 1920). Our predicted tibial length (Eq. 5: 602 mm) is 13% shorter than the measured length (690 mm). In the fairly complete skeleton of *Allosaurus* (MOR 693), our prediction for tibial length (Eq. 5: 554 mm) is 15%

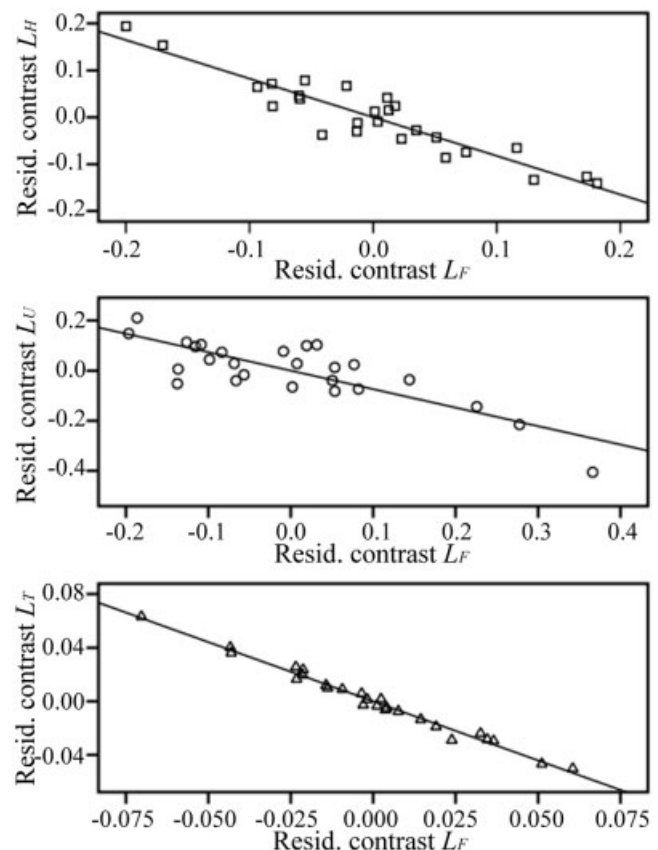


Fig. 4. Correlations between residual contrasts of humeral, ulnar, or tibial lengths and femoral length. Abbreviations follow text.

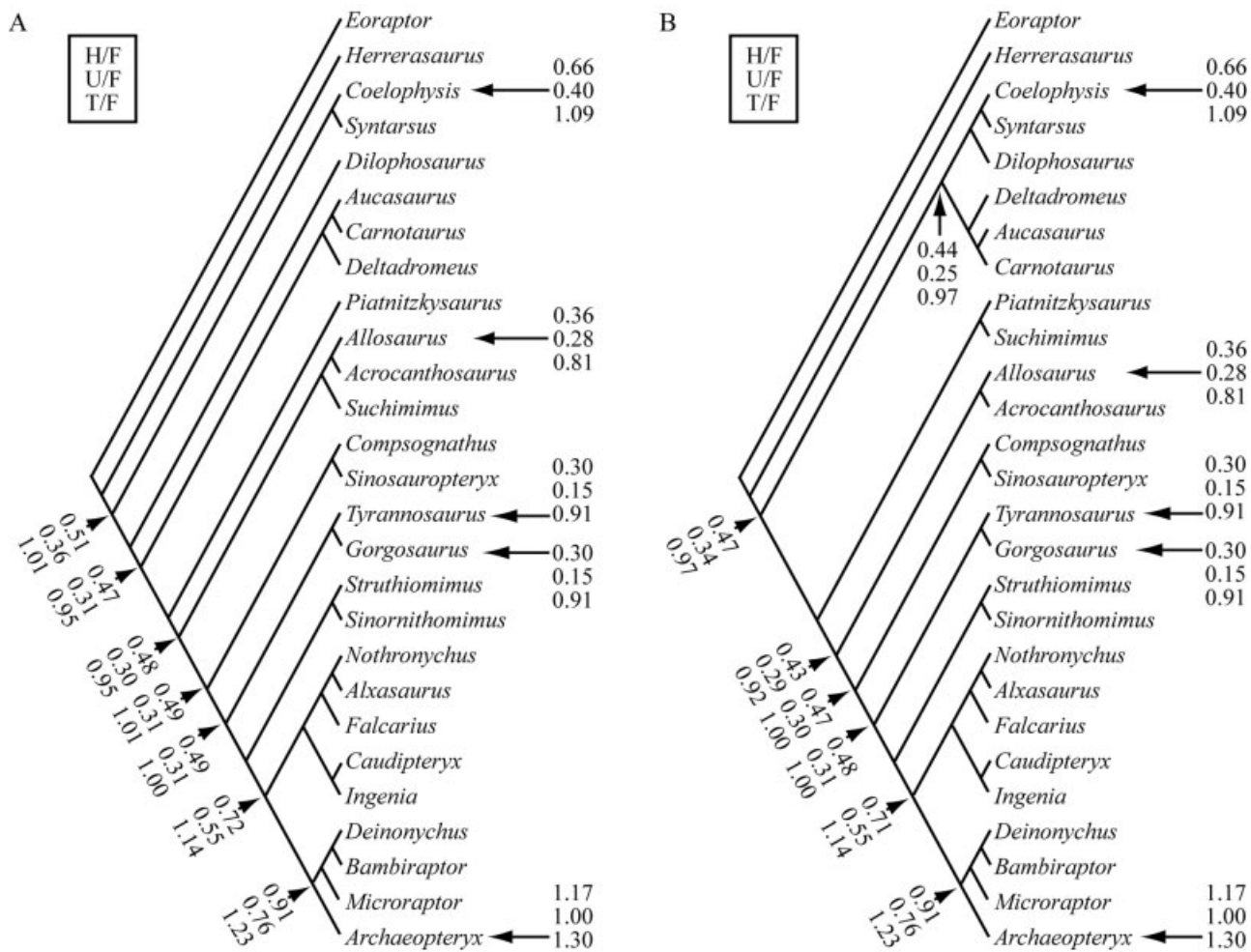


Fig. 5. Estimates of ancestral adult ratios between bone length and femoral length. One phylogenetic reconstruction features a paraphyletic Ceratosauria (A), whereas a second reconstruction features a monophyletic one (B). Abbreviations follow text.

shorter than the measured length (650 mm). Humeral (Eq. 6: 327 mm) and ulnar (Eq. 7: 221 mm) predictions for MOR 693 differ from measurements (314 mm and 200 mm, respectively) by about 4%. The scaling equations predict allometric growth in *Allosaurus* limb bones fairly well and suggest that the growth dynamics of *Allosaurus*, which are largely based on CLDQ specimens, reflect those of the species.

Large theropods, such as *Allosaurus*, are not known for proportionately long humeri, ulnae, or tibiae. On the contrary, when corrected for phylogenetic affinity they have relatively shorter humeri, ulnae, and tibiae than small adult theropods (Fig. 4). Those strongly negative correlations suggest that the independent evolution of large size in non-avian theropods involved similar developmental constraints. The pattern of limb bone development (i.e., ontogenetic scaling) is strikingly similar in *Allosaurus* and tyrannosaurids. In both taxa, negative allometric growth relative to femur length (i.e., a proxy

for size) produces an adult morphology of reduced humeral, ulnar, and tibial lengths (Russell, 1970; Currie, 2003; Fig. 3). If *Allosaurus* and tyrannosaurids evolved from relatively longer-limbed ancestors as nodal reconstructions (Fig. 5) and recent discoveries (Xu et al., 2004) suggest, then presumably the patterns of negative allometric growth represent independent reductions from an ancestral state. Such a conclusion is contingent on 1) knowledge of ontogenetic scaling in theropods that have ancestral limb proportions, and 2) a strong correspondence between limb proportions and ontogenetic scaling relationships.

Unfortunately, ontogenetic data are rare for small non-avian theropods. Small forms, such as the coelophysoid *Syntarsus*, show similar limb proportions as ancestral allosauroids and tyrannosaurids (Table 2; Fig. 5), but skeletal disarticulation has precluded a thorough analysis of limb growth (Raath, 1990). Enough ontogenetic data are available for another coelophysoid, *Coelophysis*. A reevaluation of the

growth of *Coelophysis* (Colbert, 1964, 1989) suggests that humeral length scales with significant positive allometry relative to femoral length ($n = 7$, $R^2 = 0.94$, one-tailed $P = 0.01$), whereas ulnar and tibial lengths scale isometrically relative to femoral length ($n = 6$, $n = 16$, $R^2 = 0.90$, $R^2 = 0.97$, $P = 0.08$, $P = 0.11$, respectively). *Coelophysis*, however, does not accurately reflect ancestral theropod limb growth because it has relatively long humeri, ulnae, and tibiae (Fig. 5). Limb growth in *Coelophysis* does help to bracket the ancestral states in lineages where the evolution of large size occurred. Although growth in *Coelophysis*, *Allosaurus*, and tyrannosaurids suggests that a phyletic reduction in limb length relative to the femur evolved independently in the lineages of large theropods, the magnitude of that reduction remains unknown.

Our analysis is contingent on a strong correspondence between the ontogenetic trajectories and adult proportions of limb bones. That correspondence seems strong in *Coelophysis*, *Allosaurus*, and tyrannosaurids. Relatively long limb bones lengthen either more rapidly or at a pace with increases in body size, whereas relatively shorter limb bones lengthen more slowly during growth. Ontogenetic limb bone scaling in *Archaeopteryx*, however, suggests caution when inferring growth trajectory from adult proportions. Indeed, the humeri and ulnae show positive allometric lengthening relative to body size, which produces relatively long forelimbs (Houck et al., 1990). The tibiae, however, do not show an equivalent correspondence. Relatively long tibiae in adults develop not by positive allometric lengthening but by negative allometric lengthening with respect to body size.

We cannot directly test whether *Allosaurus* had indeterminate growth. None of the sections in our sample show evidence of an external fundamental system (EFS), which is a histological proxy for skeletal maturity (Chinsamy, 1990; Horner et al., 1999, 2000; Erickson et al., 2004; Horner and Padian, 2004). This suggests that our sample is likely an incomplete ontogenetic series. We estimate the ages of a larger femur and tibia to be 22 years (AMNH 680: $L_F = 981$ mm, $C_F = 375$ mm) and 28 years (AMNH 680: $L_T = 810$ mm, $C_T = 317$ mm), but histological examination of the femur does not reveal an EFS (Camp, 1935; per. obs.). Absence of an EFS is not evidence for indeterminate growth in *Allosaurus* because the largest known elements have not been sampled. Some evidence, however, supports determinate growth in *Allosaurus*. A large, isolated, and fragmentary fibula of *Allosaurus* shows an incipient EFS (UVP 6346: Bybee, 1997). Furthermore, some bones of closely related theropods and other dinosaurs have EFSs (Chinsamy, 1990; Varricchio, 1993; Horner et al., 1999, 2000; Erickson et al., 2004; Horner and Padian, 2004).

Individuals of *Allosaurus* did not all grow alike. The variation in LAG circumference at a given age

in the femur (Fig. 2) might represent individual differences in growth trajectory or sexual dimorphism. Dimorphism in the limb bones of *Allosaurus* seems unlikely because only the femur shows “robust” and “gracile” trajectories. Rather, those trajectories appear to be a function of size. The femur is the largest limb element and, by a statistical argument, should experience absolutely more variation than smaller elements (e.g., humerus and ulna). Residual plots, which remove the confounding effects of size on measurements, suggest that variation in femoral growth trajectory is not different from the variation in other limb bones. Alternatively, the CLDQ may contain more than one allosaurid taxon. This is apparently the case with the Late Cretaceous Dinosaur Park Formation, which contains two tyrannosaurids: *Gorgosaurus* and *Daspletosaurus* (Ryan et al., 2001; Currie, 2003). Variation aside, the general growth dynamics of *Allosaurus* are consistent with our knowledge of growth in other large theropods (Erickson et al., 2004; Horner and Padian, 2004) and dinosaurs in general (Erickson et al., 2001; Padian et al., 2004).

CONCLUSIONS

The growth dynamics of *Allosaurus* are similar to those in equally large theropods. Similarities in growth strategy suggest that the evolution of gigantism in those respective lineages might involve similar increases in maximum growth rate. Furthermore, similarities in the ontogenetic scaling of limb bones and phylogenetic optimization suggest that large theropods independently evolved reduced humeral, ulnar, and tibial lengths by a phyletic reduction in longitudinal growth relative to the femur.

We cannot directly reject or support the hypothesis of indeterminate growth in *Allosaurus*. There is, however, independent evidence to suggest that growth was determinate. A large fibula of *Allosaurus* shows an incipient external fundamental system (Bybee, 1997), as do bones from closely related theropods and other dinosaurs (Chinsamy, 1990; Varricchio, 1993; Horner et al., 1999, 2000; Erickson et al., 2004; Horner and Padian, 2004).

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LITERATURE CITED

- Anderson JF, Hall-Martin A, Russell DA. 1985. Long bone circumference and weight in mammals, birds, and dinosaurs. *J Zool* 207:53–61.
- Barsbold R, Maryańska T, Osmólska M. 1990. *Oviraptorosauria*. In: Weishampel DB, Dodson P, Osmólska H, editors. *The Dinosauria*. Berkeley: University of California Press. p 249–258.
- Bonaparte JF. 1986. Les Dinosauriens (Carnosauriens, Allosauridés, Sauropodes, Cétosauridés) du Jurassique moyen de Cerro Cónor (Chubut, Argentino). *Ann Paléontol* 72:247–289.
- Bonaparte JF, Novas FE, Coria RA. 1990. *Carnotaurus sastrei* Bonaparte, the horned, lightly built carnosaur from the middle Cretaceous of Patagonia. *Contrib Sci Nat Hist Mus Los Angeles County* 416:1–42.
- Burnham DA. 2004. New information on *Bambiraptor feinbergi* (Theropoda: Dromaeosauridae) from the Late Cretaceous of Montana. In: Currie PJ, Koppelhus EB, Shugar M, Wright J, editors. *Feathered dragons: studies on the transition from dinosaurs to birds*. Bloomington: Indiana University Press. p 67–111.
- Bybee PJ. 1997. Histological bone structure differences in various sized elements from the Late Jurassic dinosaur, *Allosaurus fragilis*, of central Utah. Ph.D. dissertation. Provo, Utah: Brigham Young University.
- Camp CL. 1935. Dinosaur remains from the province of Szechuan, China. *Univ California Publ Bull Dept Geol Sci* 23: 467–472.
- Carrano MT. 1998. Locomotion in non-avian dinosaurs: integrating data from hindlimb kinematics, in vivo strains, and bone morphology. *Paleobiology* 24:450–469.
- Case TJ. 1978. Speculations on the growth rate and reproduction of some dinosaurs. *Paleobiology* 4:320–328.
- Castanet J, Newman DG, Saint-Girons H. 1988. Skeletochronological data on the growth, age and population structure of the tuatara, *Sphenodon punctatus*, on Stephens and Lady Alice Islands, New Zealand. *Herpetologica* 44:25–37.
- Castanet J, Francillon-Vieillot H, Meunier FJ, de Ricqlès A. 1993. Bone and individual aging. In: Hall BK, editor. *Bone*, vol. 7. Bone growth. B. Boca Raton, FL: CRC Press. p 245–283.
- Castanet J, Curry Rogers K, Cubo J, Boisard J-J. 2000. Periosteal bone growth rates in extant ratites (ostrich and emu). Implications for assessing growth in dinosaurs. *Comptes Rendus Acad Sci Ser III-Sci Vie-Life Sci* 323:543–550.
- Castanet J, Croci S, Aujard F, Perret M, Cubo J, de Margerie E. 2004. Lines of arrested growth in bone and age estimation in a small primate: *Microcebus murinus*. *J Zool* 263:31–39.
- Chinsamy A. 1990. Physiological implications of the bone histology of *Syntarsus rhodesiensis* (Saurischia: Theropoda). *Palaeontol Afr* 27:77–82.
- Chinsamy A. 1993. Bone histology and growth trajectory of the prosauropod dinosaur *Massospondylus carinatus* Owen. *Mod Geol* 18:319–329.
- Chinsamy A, Martin LD, Dodson P. 1998. Bone microstructure of the diving *Hesperornis* and the volant *Ichthyornis* from the Niobrara Chalk of western Kansas. *Cretac Res* 19:225–235.
- Christiansen P. 1999. Long bone scaling and limb posture in non-avian theropods: evidence for differential allometry. *J Vertebr Paleontol* 19:666–680.
- Chure DJ. 2000. A new species of *Allosaurus* from the Morrison Formation of Dinosaur National Monument (UT-CO) and a revision of the theropod family Allosauridae. Ph.D. dissertation. New York: Columbia University Press.
- Colbert EH. 1964. The Triassic dinosaur genera *Podokesaurus* and *Coelophysis*. *Am Mus Novit* 2168:1–12.
- Colbert EH. 1989. The Triassic dinosaur *Coelophysis*. *Mus North Ariz Bull* 57:1–160.
- Coria RA, Salgado L. 1995. A new giant carnivorous dinosaur from the Cretaceous of Patagonia. *Nature* 377:224–226.
- Coria RA, Chiappe LM, Dingus L. 2002. A new close relative of *Carnotaurus sastrei* Bonaparte 1985 (Theropoda: Abelisauridae) from the Late Cretaceous of Patagonia. *J Vertebr Paleontol* 22:460–465.
- Currie PJ. 2003. Allometric growth in tyrannosaurids (Dinosauria: Theropoda) from the Upper Cretaceous of North America and Asia. *Can J Earth Sci* 40:651–665.
- Currie PJ, Carpenter K. 2000. A new specimen of *Acrocanthosaurus atokensis* (Theropoda, Dinosauria) from the Lower Cretaceous Antlers Formation (Lower Cretaceous, Aptian) of Oklahoma, USA. *Geodiversitas* 22:207–246.
- Currie PJ, Chen P-J. 2001. Anatomy of *Sinosauropteryx prima* from Liaoning, northeastern China. *Can J Earth Sci* 38:1705–1727.
- Curry KA. 1999. Ontogenetic histology of *Apatosaurus* (Dinosauria: Sauropoda): new insights on growth rates and longevity. *J Vertebr Paleontol* 19:654–665.
- de Buffrénil V, Castanet J. 2000. Age estimation by skeletochronology in the Nile Monitor (*Varanus niloticus*), a highly exploited species. *J Herpetol* 34:414–424.
- de Margerie E, Cubo J, Castanet J. 2002. Bone typology and growth rates: testing and quantifying 'Amprino's rule' in the mallard (*Anas platyrhynchos*). *C R Biol* 325:221–230.
- de Margerie E, Robin J-P, Verrier D, Cubo J, Groscolas R, Castanet J. 2004. Assessing a relationship between bone microstructure and growth rate: a fluorescent labelling study in the king penguin chick (*Aptenodytes patagonicus*). *J Exp Biol* 207: 869–879.
- de Ricqlès AJ, Padian K, Horner JR, Lamm E-T, Myhrvold N. 2003. Osteohistology of *Confuciusornis sanctus* (Theropoda: Aves). *J Vertebr Paleontol* 23:373–386.
- Dodson P, Behrensmeyer AK, Bakker RT, McIntosh JS. 1980. Taphonomy and paleoecology of the dinosaur beds of the Jurassic Morrison Formation. *Paleobiology* 5:208–232.
- Erickson GM, Tumanova TA. 2000. Growth curve of *Psittacosaurus mongoliensis* Osborn (Ceratopsia: Psittacosauridae) inferred from long bone histology. *Zool J Linn Soc* 130:551–566.
- Erickson GM, Curry-Rogers K, Yerby SA. 2001. Dinosaur growth patterns and rapid avian growth rates. *Nature* 412:429–433.
- Erickson GM, Makovicky PJ, Currie PJ, Norell MA, Yerby SA, Brochu CA. 2004. Gigantism and comparative life-history parameters of tyrannosaurid dinosaurs. *Nature* 430:772–775.
- Farlow JO, Hurlburt G, Else RM, Britton ARC, Langston WL. 2005. Femoral dimensions and body size of *Alligator mississippiensis*: estimating the size of extinct mesoeucrocodylians. *J Vertebr Paleontol* 25:354–369.
- Felsenstein J. 1985. Phylogenies and the comparative method. *Am Nat* 125:1–15.
- Fiala P. 1978. Age-related changes in the substantia compacta of the long limb bones. *Folia Morphol* 4:316–321.
- Frylestam B, Schantz T. 1977. Age determination of European hares based on periosteal growth lines. *Mammal Rev* 7:151–154.
- Garland T Jr, Martin KLM, Díaz-Uriarte R. 1997. Reconstructing ancestral trait values using squared-change parsimony: plasma osmolality at the origin of amniotes. In: Sumida SS, Martin KLM, editors. *Amniote origins*. San Diego: Academic Press. p 425–501.
- Gatesy SM. 1991. Hind limb scaling in birds and other theropods: implications for terrestrial locomotion. *J Morphol* 209:83–96.
- Gilmore CW. 1920. Osteology of the carnivorous Dinosauria in the United States National Museum, with special reference to the genera *Antrodemus* (*Allosaurus*) and *Ceratopsus*. *Bull US Natl Mus* 110:1–159.
- Hemelaar ASM, Van Gelder JJ. 1980. Annual growth rings in phalanges of *Bufo bufo* (Anura, Amphibia) from the Netherlands and their use for age determination. *Neth J Zool* 30:129–135.
- Holtz TR, Osmólska H. 2005. Saurischia. In: Weishampel DB, Dodson P, Osmólska H, editors. *The Dinosauria*. Berkeley: University of California Press. p 21–24.
- Horner JR, Padian K. 2004. Age and growth dynamics of *Tyrannosaurus rex*. *Proc R Soc Lond B* 271:1875–1880.
- Horner JR, de Ricqlès AJ, Padian K. 1999. Variation in dinosaur skeletochronology indicators: implications for age assessment and physiology. *Paleobiology* 25:295–304.

- Horner JR, de Ricqlès AJ, Padian K. 2000. Long bone histology of the hadrosaurid dinosaur *Maiaasaura peeblesorum*: growth dynamics and physiology based on an ontogenetic series of skeletal elements. *J Vertebr Paleontol* 20:115–129.
- Houck MA, Gauthier JA, Strauss RE. 1990. Allometric scaling in the earliest fossil bird, *Archaeopteryx lithographica*. *Science* 247:195–198.
- Hutchinson JR, Garcia M. 2002. *Tyrannosaurus* was not a fast runner. *Nature* 415:1018–1021.
- Hutton JM. 1986. Age determination of living Nile crocodiles from the cortical stratification of bone. *Copeia* 1986:332–341.
- Hwang SH, Norell MA, Ji Q, Gao K. 2004. New specimens of *Microraptor zhaoianus* (Theropoda: Dromaeosauridae) from northeastern China. *Am Mus Novit* 3381:1–44.
- Ji Q, Currie PJ, Norell MA, Ji S-A. 1998. Two feathered dinosaurs from northeastern China. *Nature* 393:753–761.
- Kirkland JJ, Wolfe DA. 2001. First definitive therizinosaurid (Dinosauria; Theropoda) from North America. *J Vertebr Paleontol* 21:410–414.
- Kirkland JL, Zanno LE, Sampson SD, Clark JM, DeBlieux DD. 2005. A primitive therizinosaurid dinosaur from the Early Cretaceous of Utah. *Nature* 435:84–87.
- Kobayashi Y, Lü J-C. 2003. A new ornithomimid dinosaur with gregarious habits from the Late Cretaceous of China. *Acta Palaeontol Pol* 48:235–259.
- Lamm E-T. 1998. New methods for the preparation and systematic organization of histological sections. *J Vertebr Paleontol* 18:58A.
- Lee AH. 2004. Ontogenetic histology of *Centrosaurus*: testing the relationship between limb bone form and function. *J Vertebr Paleontol* 24:82A.
- Maddison WP, Maddison DR. 2004. Mesquite: a modular system for evolutionary analysis. V. 1.05: <http://mesquiteproject.org>
- Madsen JH. 1976. *Allosaurus fragilis*: a revised osteology. *Utah Geol Min Surv Bull* 109:1–163.
- Marsh OC. 1877. Notice of new dinosaurian reptiles from the Jurassic Formation. *Am J Sci* 14:514–516.
- Martins EP, Hansen TF. 1996. The statistical analysis of interspecific data: a review and evaluation of phylogenetic comparative methods. In: Martins EP, editor. *Phylogenies and the comparative method in animal behavior*. New York: Oxford University Press. p 22–75.
- McMahon T. 1973. Size and shape in biology. *Science* 179:1201–1204.
- Middleton KM, Gatesy SM. 2000. Theropod forelimb design and evolution. *Zool J Linn Soc* 128:149–187.
- Miller WE, Horrocks RD, Madsen JH. 1996. The Cleveland-Lloyd Dinosaur Quarry, Emery County, Utah: a U.S. natural landmark (including history and quarry map). *Brigham Young Univ Geol Stud* 41:3–24.
- Morris P. 1970. A method for determining absolute age in the hedgehog. *J Zool* 161:277–281.
- Novas FE. 1993. New information on the systematics and postcranial skeleton of *Herrerasaurus ischigualastensis* (Theropoda: Herrerasauridae) from the Ischigualasto Formation (Upper Triassic) of Argentina. *J Vertebr Paleontol* 13:400–423.
- Ostrom JH. 1976. On a new specimen of the Lower Cretaceous theropod dinosaur *Deinonychus antirrhopus*. *Breviora* 439:1–21.
- Padian K, de Ricqlès AJ, Horner JR. 2001. Dinosaurian growth rates and bird origins. *Nature* 412:405–408.
- Padian K, Horner JR, de Ricqlès AJ. 2004. Growth in small dinosaurs and pterosaurs: the evolution of archosaurian growth strategies. *J Vertebr Paleontol* 24:555–571.
- Paul GS. 1988. *Predatory dinosaurs of the world: a complete illustrated guide*. New York: Simon & Schuster.
- Raath MA. 1969. A new coelurosaurian dinosaur from the Forest Sandstone of Rhodesia. *Arnoldia* 4:1–25.
- Raath MA. 1990. Morphological variation in small theropods and its meaning in systematics: evidence from *Syntarsus rhodesiensis*. In: Carpenter K, Currie PJ, editors. *Dinosaur systematics: approaches and perspectives*. Cambridge, UK: Cambridge University Press. p 91–105.
- Rauhut OWM. 2003. The interrelationships and evolution of basal theropod dinosaurs. *Special papers in palaeontology* 69. London: Palaeontological Association.
- Reid REH. 1996. Bone histology of the Cleveland-Lloyd dinosaurs and of dinosaurs in general. I. Introduction to bone tissues. *Brigham Young Univ Geol Stud* 41:25–72.
- Rohlf FJ, Chang WS, Sokal RR, Kim J. 1990. Accuracies of estimated phylogenies: effects of tree topology and evolutionary model. *Evolution* 44:1671–1684.
- Russell DA. 1970. *Tyrannosaurs* from the Late Cretaceous of western Canada. *Natl Mus Nat Sci Publ Palaeontol* 1:1–34.
- Russell DA, Dong Z. 1993. The affinities of a new theropod from the Alxa Desert, Inner Mongolia, People's Republic of China. *Can J Earth Sci* 30:2107–2127.
- Ryan MJ, Russell AP, Eberth DA, Currie PJ. 2001. The taphonomy of a *Centrosaurus* (Ornithischia: Ceratopsidae) bone bed from the Dinosaur Park Formation (Upper Campanian), Alberta, Canada, with comments on cranial ontogeny. *Palaios* 16:482–506.
- Sander PM. 1999. Life history of Tendaguru sauropods as inferred from long bone histology. *Geowissenschaftliche Reihe* 2:103–112.
- Sereno PC. 1993. The pectoral girdle and forelimb of the basal theropod *Herrerasaurus ischigualastensis*. *J Vertebr Paleontol* 13:425–450.
- Sereno PC, Duthiel DB, Iarochene M, Larsson HCE, Lyon GH, Magwene PM, Sidor CA, Varricchio DJ, Wilson JA. 1996. Predatory dinosaurs from the Sahara and Late Cretaceous faunal differentiation. *Science* 272:986–991.
- Sereno PC, Beck AL, Dutheil DB, Gado B, Larsson HCE, Lyon GH, Marcot JD, Rauhut OWM, Sadleir RW, Sidor CA, Varricchio DJ, Wilson GP, Wilson JA. 1998. A long-snouted predatory dinosaur from Africa and the evolution of spinosaurids. *Science* 282:1298–1302.
- Sereno PC, Wilson JA, Conrad JL. 2004. New dinosaurs link southern landmasses in the Mid-Cretaceous. *Proc R Soc Lond B* 271:1325–1330.
- Sokal RR, Rohlf FJ. 1995. *Biometry*. New York: W.H. Freeman.
- Stovall JW, Langston WL. 1950. *Acrocanthosaurus atokensis*, a new genus and species of Lower Cretaceous Theropoda from Oklahoma. *Am Midl Nat* 43:696–728.
- Stromer E. 1931. Wirbeltier-Reste der Bajarijstufe (unterstes Cenoman). 10. Ein Skelett-Rest von *Carcharodontosaurus* nov. gen. *Abhandl Bayer Akad Wiss Math-Naturwiss Abt* 9:1–23.
- Tucker AD. 1997. Validation of skeletochronology to determine age of freshwater crocodiles (*Crocodylus johnstoni*). *Mar Freshw Res* 48:343–351.
- Turvey ST, Green OR, Holdaway RN. 2005. Cortical growth marks reveal extended juvenile development in New Zealand moa. *Nature* 435:940–943.
- Varricchio DJ. 1993. Bone microstructure of the Upper Cretaceous theropod dinosaur *Troodon formosus*. *J Vertebr Paleontol* 13:99–104.
- Wilson JW. 1994. Histological techniques. In: Leiggi P, May P, editors. *Vertebrate paleontological techniques*. New York: Cambridge University Press. p 205–234.
- Witmer LW. 1995. Homology of facial structures in extant archosaurs (birds and crocodilians), with special reference to paranasal pneumatization and nasal conchae. *J Morphol* 225:269–327.
- Xu X, Norell MA, Kuang X, Wang X, Zhao Q, Jia C. 2004. Basal tyrannosauroids from China and evidence for protofeathers in tyrannosauroids. *Nature* 431:680–684.
- Zeffer A, Johansson LC, Marmebro Å. 2003. Functional correlation between habitat use and leg morphology in birds (Aves). *Biol J Linnean Soc* 79:461–484.
- Zullinger EM, Ricklefs RE, Redford KH, Mace GM. 1984. Fitting sigmoidal equations to mammalian growth curves. *J Mammal* 65:607–636.

APPENDIX. Measurements of limb elements from *Allosaurus*

Element	Specimen	Length, mm	Circum, mm
Humerus	UUVP 1980	156	51
	UUVP 1981	162	55
	UUVP 566	199	72
	UUVP 30-77	202	72
	UUVP 5423	205	76
	UUVP 40-729	240	90
	UUVP 2327	244	84
	UUVP 2765	251	90
	UUVP 4387	254	102
	UUVP 3342	255	105
	UUVP 4792	264	109
	UUVP 4909	277	90
	UUVP 2998	280	91
	UUVP 30-778	280	127
	UUVP 4908	280	118
	UUVP 273	290	123
	UUVP 5501	295	115
	UUVP 549	330	132
	UUVP 5982	330	135
	UUVP 5577	333	151
Ulna	UUVP 1334	334	144
	UUVP 3435	343	180
	UUVP 5472	351	155
	UUVP 1169	379	187
	UUVP 2913	135 (151)	52
	UUVP 5595	142 (158)	53
	UUVP 4844	143 (160)	50
	UUVP 30-69	143 (158)	59
	UUVP 30-65	145 (162)	51
	UUVP 2764	148 (170)	64
	UUVP 1996	151 (160)	56
	UUVP 30-64	153 (173)	61
	UUVP 5206	179 (200)	75
	UUVP 11658	180 (210)	81
	UUVP 4103	206 (238)	95
Femur	UUVP 10616	220 (255)	93
	BYUVP 5146	220 (255)	100
	UUVP 30-62	230 (240)	98
	BYUVP 13240	250 (285)	103
	BYUVP 11567	265 (310)	118
	UUVP 6023	239	75
	CLDQ 05-48	251	75
	UUVP 3872	336	103
	UUVP 11162	344	102
	CLDQ 103	357	106
	UUVP 2559	413	140
	UUVP 847	431	140
	UUVP 492	471	161
	UUVP 3208	482	160
	UUVP 30-724	511	170
	UUVP 30-16	513	180
	UUVP 40-268	514	175
	UUVP 718	523	171
	CLDQ 01-377	533	197
	UUVP 30743	541	175
	UUVP 5991	563	204
	UUVP 5302	678	257
	UUVP 5993	751	290
	DINO 2560	870	322
	AMNH 408	810	291
	AMNH 257	930	358
	AMNH 6125	930	337
	AMNH 680	980	380

APPENDIX. (Continued)

Element	Specimen	Length, mm	Circum, mm
Tibia	UUVP 30-55	343	97
	UUVP 2584	358	73
	UUVP 40-299	379	106
	UUVP 2977	433	122
	UUVP 3233	444	122
	UUVP 40-306	525	180
	UUVP 40-298	525	182
	UUVP 3835	540	197
	UUVP 40-308	540	205
	UUVP 249	542	197
	UUVP 3249	543	194
	UUVP 5990	546	191
	UUVP 40-301	552	181
	UUVP 40-304	552	183
	UUVP 3833	553	195
	UUVP 5301	567	177
	UUVP 5988	577	195
	UUVP 5361	596	202
	UUVP 40-297	612	231
	AMNH 5750	640	253
	UUVP 10248	695	267
	AMNH 6125	700	294
	AMNH 408	700	265
	AMNH 680	810	317
	AMNH 290	859	327

Ulnar length including olecranon process in parentheses. Abbreviations follow text.