

POSTNATAL ALLOMETRIC LIMB GROWTH IN JUVENILE CAMELS FROM THE PLEISTOCENE OF RANCHO LA BREA TAR PITS

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Abstract—Cursorial mammals, especially long-limbed running artiodactyls, are well known for having lengthened their distal limb segments (radius-ulna, tibia, metapodials). Studies of the growth of juvenile limbs in many artiodactyls suggest that these same limbs grow allometrically so that the rate at which they lengthen is greater than the rate at which they thicken. Large samples of juvenile limb bones of the extinct llama camel *Camelops hesternus* from the late Pleistocene of Rancho La Brea were measured to see what growth trends they exhibited. All of the limbs of *Camelops* grow with the expected pattern: robust or isometric in the proximal limb elements (humerus, femur), but an allometric trend toward more very gracile distal limb elements, like the radius-ulna and tibia. This is in contrast with other long-legged artiodactyls, such as pronghorns, white-tailed deer, wildebeests, and okapis, which also tended to be isometric or slightly gracile in their proximal elements, but robust in their tibiae and occasionally their radii.

INTRODUCTION

Juvenile fossils of extinct mammalian species are very rare, and seldom are there enough bones to form a growth series and study ontogenetic growth through time. A notable exception to this rule is the Pleistocene tar pits of Rancho La Brea, in Los Angeles, California, where there are typically hundreds to thousands of bones of the common species, including juveniles. In the case of the common mammals (such as dire wolves, *Canis dirus*, and saber-toothed cats, *Smilodon fatalis*), there are literally hundreds of juvenile elements for every bone in the skeleton. Fossils of the Pleistocene camel, *Camelops hesternus* (Fig. 1) (Webb, 1983; Kurtén and Anderson, 1980; Honey et al., 1998), are not as common but there are typically 20-30 examples of nearly every limb element in the collections of the La Brea Tar Pits Museum (formerly the George C. Page Museum of La Brea Discoveries).

Until recently, there were not many comprehensive studies of limb allometry in living mammals as they grow from tiny juveniles to adults. However, Kilbourne and Makovicky (2012) studied a wide spectrum of juvenile mammal limb bones, including a number of long-limbed artiodactyls. They found that cursorially adapted mammals such as long-limbed artiodactyls tended to thicken the distal elements (radius-ulna, tibia) of each limb faster than the same bones got longer. This is surprising, given the common trend of cursorial animals to have long, thin, gracile distal limb bones compared to proximal limb segments (humerus, femur). Such long, slender distal limbs not only increase stride length in running, but minimize the rotational inertia of the bones as they go through each stride (Hildebrand, 1985; Hildebrand and Hurley, 1985; Kilbourne and Hoffman).

Kilbourne and Makovicky (2012) did not have any camelids in their sample, but did have deer, okapis, pronghorns, and several bovids, so it would be expected that camelids might follow similar trends. In this study, we examine postnatal ontogenetic limb allometry in the camelid *Camelops hesternus*, to see if they follow the trend of gracile distal limb elements seen in other cursorial artiodactyls.

METHODS

We measured nearly every unbroken juvenile humerus, radius, femur, and tibia of *Camelops hesternus* in the collections of the La Brea Tar Pits Museum to obtain the largest sample size

possible for this analysis. Measurements were made by taking the length of the diaphysis of the shaft of each bone, and the circumference of the midshaft. In the case of adult or subadult bones, measurements of shaft length were made from the diaphyseal-epiphyseal sutures. Measurements shorter than 460 mm were made with metric digital calipers; those over 460 mm, and circumference measurements, were made with a flexible metric measuring tape. In addition to measuring diaphysis length, we measured midshaft circumference.

Basic statistics and regressions were calculated and plotted using Microsoft Excel. Following the conventions of most allometric studies, raw data were converted to natural logs and plotted in log-log space, so that the exponential slope of allometry would give a simple linear slope. We used Excel to calculate the simple least-squares regression of the data. Since there is no dependent or independent variable in this study (an assumption of the least-squares regression method), we adopted the more commonly used Reduced Major Axis (RMA) method of correlation to determine the slope between the two variables (calculated using the R program “smatr”) (Warton et al., 2006, 2008).

We followed the conventions of Kilbourne and Makovicky (2012) in plotting length on the Y axis vs. circumference on the X axis, which should give an isometric slope in log-log space of 1.0 (linear dimension vs. linear dimension), and allometric slopes greater than 1.0 if the limb is gracile (positive allometry), and less than 1.0 if it is robust (negative allometry). This allowed us to compare our results to the data of living mammals examined by Kilbourne and Makovicky (2012). We also calculated the confidence intervals of the slopes to see if the differences are significantly different from isometry or not, following the methods used by Kilbourne and Makovicky (2012).

RESULTS

Length vs. Circumference

Results of our analyses are shown in Figure 2, and in Tables 1-4. For the humerus (Fig. 2A, Table 1), *Camelops* has a RMA slope of 0.79, which is significantly robust given the confidence intervals around the slope. This would be expected in the proximal limb elements. The humeri of other artiodactyls in Kilbourne and Makovicky (2012) tended to show gracile or isometric growth trends, but the pronghorn and the bison had



FIGURE 1. Growth series of juvenile to adult humeri of *Camelops hesternus* in the collections of the La Brea Tar Pits Museum. (Photo by D.R. Prothero).

TABLE 1. Humerus data of various artiodactyls. C.I. = slope confidence interval limits; L.S. SLOPE = least squares slope; RMA = reduced major axis slope. (G) = gracile; (I) = isometric; (R) = robust. *C. hesternus* results from this study; *Bison antiquus*, the extinct Pleistocene bison, from Galvez et al. (this volume); all other data from Kilbourne and Makovicky (2012). They are *Antilocapra americana*, the pronghorn; *Odocoileus virginianus*, the white-tailed deer; *Okapia johnstoni*, the okapi; *Connochaetes taurinus*, the wildebeest; and *Bison bison*, the American Plains bison. No least squares slopes were given by Kilbourne and Makovicky (2012).

TAXON	N	L.S.SLOPE	Y-INTERCEPT	R ²	C.I.	RMA
Length vs. circumference						
<i>Camelops hesternus</i>	29	1.048	-0.838	0.958	0.71,0.91	0.79 (R)
<i>A. americana</i>	19		2.069	0.946	0.63,0.82	0.75 (R)
<i>O. virginianus</i>	23		0.969	0.960	0.94,1.11	1.03 (I)
<i>O. johnstoni</i>	20		-0.304	0.982	1.16,1.37	1.26 (G)
<i>C. taurinus</i>	14		1.714	0.976	0.74,0.87	0.80 (R)
<i>B. bison</i>	16		1.785	0.958	0.71,0.91	0.79 (R)
<i>B. antiquus</i>	50	0.993	-0.364	0.919	0.95,1.12	1.03 (I)

TABLE 2. Radius-ulna data of various artiodactyls. Conventions as in Table 1.

TAXON	N	L.S. SLOPE	Y-INTERCEPT	R ²	C.I.	RMA
Length vs. circumference						
<i>Camelops hesternus</i>	17	1.2766	-2.656	0.881	1.12,1.64	1.36 (G)
<i>A. americana</i>	18		1.889	0.858	0.65,1.09	0.87 (I)
<i>O. virginianus</i>	12		1.742	0.965	0.77,1.02	0.89 (I)
<i>O. johnstoni</i>	12		0.251	0.955	0.95,1.43	1.21 (G)
<i>C. taurinus</i>	13		1.844	0.988	0.80,0.92	0.86 (R)
<i>B. bison</i>	12		1.560	0.971	0.81,0.99	0.87 (R)
<i>B. antiquus</i>	50	0.856	0.567	0.928	0.83,0.97	0.89 (R)

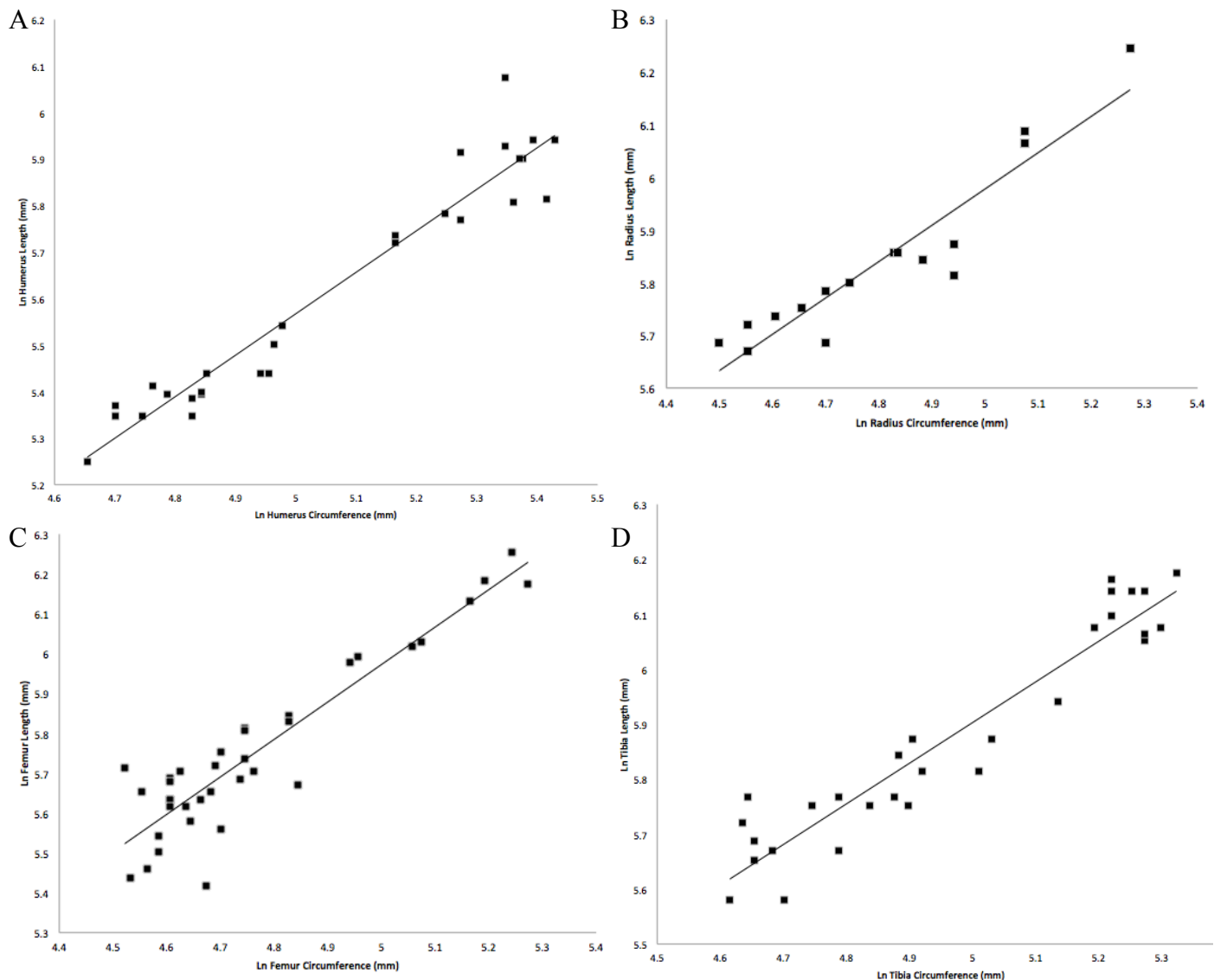


FIGURE 2. Plots of natural log (ln) of circumference (X-axis) vs. natural log (ln) of length (Y-axis) for limb bone elements of *Camelops hesternus*, with the RMA slope shown. **A.** Humerus. **B.** Radius-ulna. **C.** Femur. **D.** Tibia.

TABLE 3. Femoral data of various artiodactyls. Conventions as in Table 1.

TAXON	N	L.S. SLOPE	Y-INTERCEPT	R ²	C.I.	RMA
Length vs. circumference						
<i>Camelops hesternus</i>	36	0.906	-0.445	0.851	0.86,1.12	0.98 (I)
<i>A. americana</i>	18		1.916	0.955	0.73,0.92	0.85 (I)
<i>O. virginianus</i>	23		0.805	0.961	1.02,1.21	1.13 (G)
<i>O. johnstoni</i>	20		-0.419	0.970	1.17,1.43	1.31 (G)
<i>C. taurinus</i>	15		1.261	0.989	0.92, 1.01	0.96 (I)
<i>B. bison</i>	16		1.427	0.975	0.86,0.99	0.92 (I)
<i>B. antiquus</i>	46	0.796	0.437	0.873	0.76,0.95	0.85 (R)

slightly more robust humerus growth. The same was true of the femur, the other proximal limb segment (Fig. 2C, Table 3). In *Camelops*, the slope is 0.98, the confidence limits indicating isometry, and all the other artiodactyls reported by Kilbourne and Makovicky (2012) are either isometric or gracile.

The crucial difference, however, should be apparent in the distal limb segments, which would generally be predicted to become more gracile as the animal became more cursorial. In *Camelops*, the fused radius-ulna has an RMA slope of 1.36 (Fig.

2B, Table 2), which is highly gracile, more so than any other artiodactyl studied by Kilbourne and Makovicky (2012). All the rest of the artiodactyls reported by Kilbourne and Makovicky (2012) had robust radius-ulna proportions, and only the okapi was gracile but not outside the confidence limits for isometry. The other distal limb segment is the tibia (Fig. 2D, Table 4). *Camelops* has a gracile slope of 1.36, more gracile than any other mammal reported by Kilbourne and Makovicky (2012), including the okapi. This is in contrast with most of the other

TABLE 4. Tibia data of various artiodactyls. Conventions as in Table 1.

TAXON	N	L.S. SLOPE	Y-INTERCEPT	R ²	C.I.	RMA
Length vs. circumference						
<i>Camelops hesternus</i>	29	1.219	-2.201	0.902	1.13,1.45	1.28 (G)
<i>A. americana</i>	17		1.986	0.932	0.69,0.97	0.89 (R)
<i>O. virginianus</i>	20		1.892	0.962	0.80,0.98	0.90 (R)
<i>O. johnstoni</i>	21		-0.179	0.977	1.16,1.41	1.29 (G)
<i>C. taurinus</i>	14		1.851	0.989	0.82,0.93	0.88 (R)
<i>B. bison</i>	17		2.232	0.923	0.64,0.89	0.75 (R)
<i>B. antiquus</i>	70	1.025	0.905	0.949	0.99, 1.11	1.05 (I)

artiodactyls studied by Kilbourne and Makovicky (2012), which had slopes less than 1.0, suggesting that their tibiae were also more robust in proportions.

CONCLUSIONS

Cursorial animals generally tend to lengthen their distal segments by allometric growth of length compared to thickness of limb bones. However, during postnatal ontogeny, *Camelops hesternus* juvenile limb bones show more gracile growth trends in distal limb elements (radius-ulna, tibia) than most of the other artiodactyls studied by Kilbourne and Makovicky (2012). Only the okapi showed any degree of gracility, and most artiodactyls, such as bison and wildebeest, have more robust growth trends, contrary to predictions.

ACKNOWLEDGMENTS

We thank A. Farrell and G. Takeuchi for access to the La Brea material. We thank T.S. Kelly and B.M. Kilbourne for their helpful reviews of the paper.

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