FROM COLTS TO HORSES: A STUDY OF THE ALLOMETRIC GROWTH IN THE LIMB BONES IN *EQUUS OCCIDENTALIS* FROM THE LA BREA TAR PITS

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Abstract—The fossil collections at the La Brea Tar Pits and Museum include huge numbers of juvenile limb bones in every stage of growth, allowing us to examine how limb bones changed shape as colts of *Equus occidentalis* grew from the smallest juvenile to adult size. We measured the diaphyseal length and circumference of a minimum of 50 juvenile specimens of humerus, radius-ulna, femur and tibia. Previous studies of the growth series of *E. quagga (= E. burchelli)*, the plains zebra, allows for comparison. We hypothesize that the distal limb segments (radius, tibia) grow longer more quickly than they grow thicker in cursorial animals like horses, becoming more gracile as they age. In the radius of *E. occidentalis* (n = 60), growth is significantly more robust (expected slope of radius vs. circumference = 1.0, actual slope = 0.73) as the colts grew, even more gracile than *E. quagga* (slope = 0.76). The tibia is isometric in its growth trends (slope = 1.04), while *E. quagga* has more robust tibial growth (slope = 0.88). The humerus (slope = 1.11) is also isometric, much like that of *E. quagga* (slope = 1.09). However, femora of *E. occidentalis* are gracile (slope = 1.24), while femora of *E. quagga* show the expected isometric slope (slope = 1.09). This is not surprising, because the adult limb proportions of *E. occidentalis* have been considered robust or normal for horses like zebras, and our data are consistent with this view.

INTRODUCTION

For decades, biologists have observed that cursorial mammals tend to have longer and more slender limbs that enhance running, lengthening the distal limb elements (radius-ulna, tibia, metapodials) at the expense of the proximal limb elements (humerus, femur) (Hildebrand, 1985; Hildebrand and Hurley, 1985; Kilbourne and Hoffman, 2015). While the systematics of the fossil species of *Equus* has been intensely studied for decades (Dalquest, 1978; Winans, 1989; Eisenmann, 1992; Azzaroli, 1998; Weinstock et al., 2006; Heintzman et al., 2017), relatively little attention has been paid to how and when did living and extinct horses (genus *Equus*) first show evidence of this pattern. How does their growth compare to the patterns in other cursorial mammals, such as ruminant artiodactyls? Very few fossil mammals are known from enough juvenile limb bones to assess this question. However, the collections of late Pleistocene fossils from Rancho La Brea asphalt deposits in Los Angeles, California, contains thousands of bones of the extinct horse *Equus occidentalis*, including dozens of juvenile bones in various ontogenetic stages (Fig. 1). These are among the few fossil collections in the world that allow investigation of postnatal ontogenetic allometry.

Until recently, there was very little published literature on postnatal ontogenetic allometry in living mammals to allow comparison with the fossil horses at Rancho La Brea. Kilbourne and Makovicky (2012) provided the first published data on postnatal long-bone growth in a number of living mammals, including the plains zebra (*Equus quagga;* formerly *E. burchelli*) and a number of cursorial artiodactyls. Their data and analyses provide a standard against which juvenile bones of La Brea horses can be compared.

Conventional interpretation of functional morphology has suggested that cursorial mammals should show evidence of more rapid growth of the length of their distal limb elements, relative to their cross-sectional area, so their limbs become more gracile as they grow. Biomechanical studies have shown that this decreases the rotational inertia in longer-limbed animals (Hildebrand, 1985; Hildebrand and Hurley, 1985; Kilbourne and Hoffman, 2015). In this study, we compare the limbs of the extinct horse *Equus occidentalis* to modern plains zebras to determine whether the Pleistocene species achieved its adult body proportions in the same way as do modern equids. We also wanted to see if juvenile *Equus occidentalis* aged with the same changes in their limb proportions as other cursorial mammals, or with a more robust ontogenetic limb growth pattern than observed in other species.

METHODS

We measured every available unbroken juvenile humerus, fused radius-ulna, femur, and tibia, as well as some adult bones, of *Equus occidentalis* in the collections of the La Brea Tar Pits and Museum to obtain the largest sample size possible for this analysis. Measurements were made following the protocols of Kilbourne and Makovicky (2012), focusing on measuring 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 that had the epiphyses attached, 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. This allowed us to compare diaphysis lengths to both circumference, and also calculate cross-sectional area.

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 also 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 yield an isometric slope in log-log space of

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

approximately 1.0 (linear dimension vs. linear dimension), with allometric slopes greater than 1.0 if the limb is gracile (positive allometry), and less than 1.0 where the limb is robust (negative allometry). This allowed us to compare our results to data from living mammals examined by Kilbourne and Makovicky (2012).

RESULTS

Results of our analyses are shown in Figure 2, and in Tables 1-4. The prediction for most cursorial mammals would be that the proximal limb elements show isometric growth, or at least not show highly gracile growth trends. The modern plains zebra humerus has a slope of 1.09, which is isometric, and its femur has

the same slope (Kilbourne and Makovicky, 2012, tables 2, 4). In our analysis, the large Rancho La Brea horse data yielded slopes of 1.11 for the humerus, very similar to that of the plains zebra. However, its slope is 1.24 for the femur, which is significantly more gracile than expected. In fact, *Equus occidentalis* from Rancho La Brea exhibits the most gracile growth pattern of the femora of all the cursorial mammals shown in Table 1. This contrasts with the rest of the cursorial mammals studied, most of which are isometric or only slightly gracile (Table 3).

As stated above, the distal elements in cursorial ungulates are generally interpreted to be much more gracile than the proximal elements. However, Table 2 shows that the fused

TABLE 1. Humerus data of various mammals. **CI** = slope confidence interval limits; **L.S. SLOPE** = least squares slope; **RMA** = reduced major axis slope. **(G)** = gracile; **(I)** = isometric; **(R)** = robust. *Camelops hesternus* results from Htun et al. (this volume); *B. antiquus* from Galvez et al. (this volume); all other data from Kilbourne and Makovicky (2012). They are *Equus quagga*, the plains zebra; *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.

TAXON	N	L.S.SLOPE	Y-INTERCEPT	R²	CI	RMA
E. quagga	13		0.406	0.917	0.76,1.36	1.09 (I)
E. occidentalis	35	1.027	0.213	0.827	0.96,1.29	1.11(I)
B. antiquus	50	0.993	-0.364	0.919	0.95,1.12	1.03 (I)
B. bison	16		1.785	0.958	0.71,0.91	0.79 (R)
C. hesternus	29	1.048	-0.838	0.935	0.98,1.19	1.08 (I)
A. americana	19		2.069	0.946	0.63,0.82	0.75 (R)
O. virginianus	23		0.969	0.960	0.94,1.11	1.03 (I)
O. johnstoni	20		-0.304	0.982	1.16,1.37	1.26 (G)
C. taurinus	14		1.714	0.976	0.74,0.87	0.80 (R)

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

| TAXON	N	L.S. SLOPE	Y-INTERCEPT	R²	CI	RMA
E. quagga	12		2.093	0.815	0.46, 1.15	0.76 (I)
E. occidentalis	60	0.673	2.359	0.899	0.66,0.79	0.73 (R)
B. antiquus	50	0.993	-0.364	0.928	0.83,0.97	0.89 (R)
B. bison	16		1.785	0.958	0.71,0.91	0.79 (R)
C. hesternus	29	1.048	-0.838	0.881	1.12,1.64	1.36 (G)
A. americana	19		2.069	0.946	0.63,0.82	0.75 (R)
O. virginianus	23		0.969	0.960	0.94,1.11	1.03 (I)
O. johnstoni	20		-0.304	0.982	1.16,1.37	1.26 (G)
C. taurinus	14		0.778	0.976	0.74,0.87	1.22 (G)
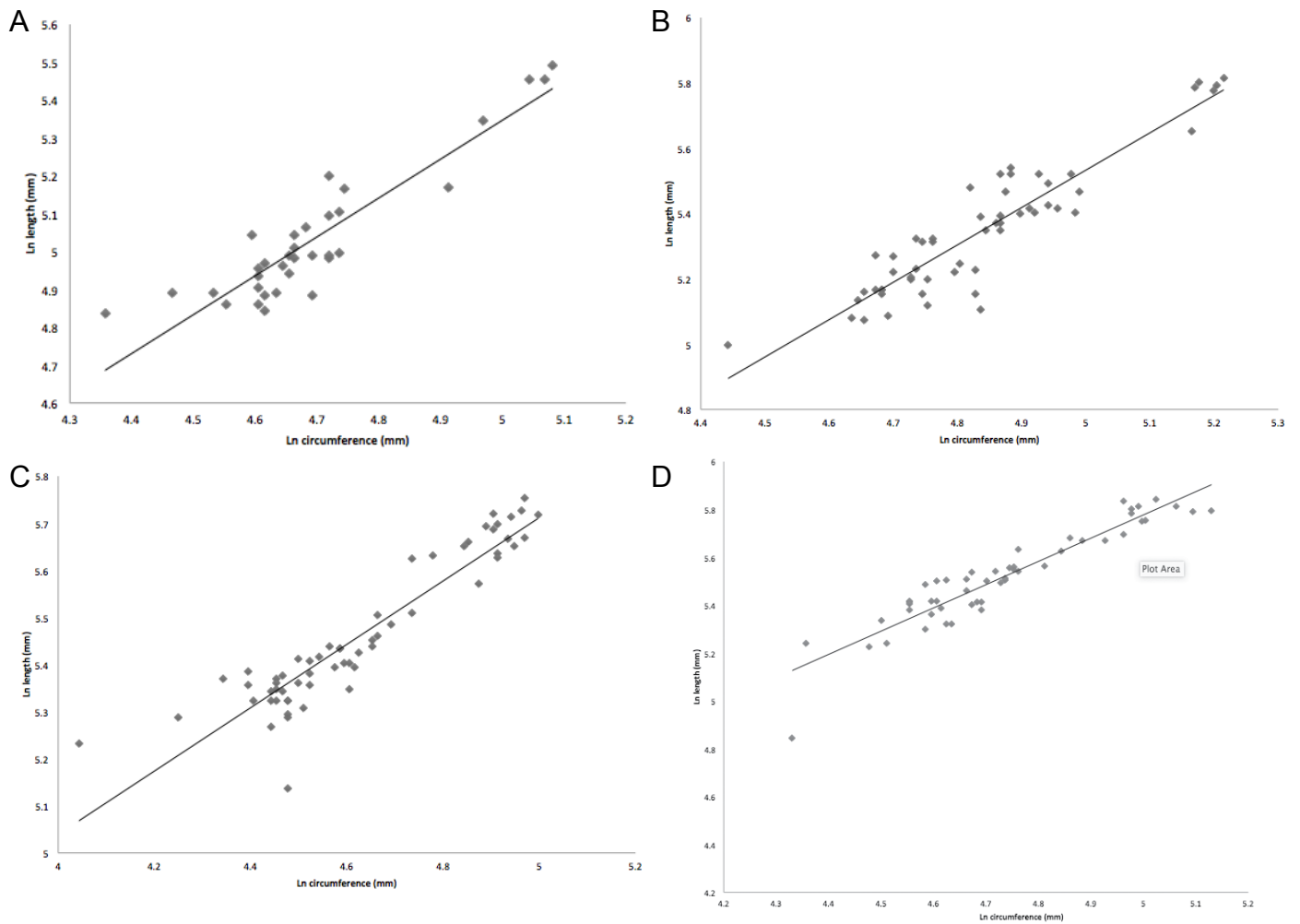
FIGURE 2. Plots of natural log (ln) of circumference (X-axis) vs. natural log (ln) of length (Y-axis) for limb bone elements of *Equus occidentalis*, with the RMA slope shown. **A**, Humerus. **B**, Radius-ulna. **C**, Femur. and **D**, Tibia.

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

TAXON	N	L.S. SLOPE	Y-INTERCEPT	R²	CI	RMA
E. quagga	13		0.515	0.933	0.77, 1.40	1.09 (I)
E. occidentalis	55	1.141	-0.189	0.848	1.11, 1.38	1.24 (G)
B. antiquus	46	0.796	0.437	0.873	0.76,0.95	0.85 (R)
B. bison	16		1.427	0.975	0.86,0.99	0.92 (R)
C. hesternus	36	0.906	-0.445	0.851	0.86,1.12	0.98 (I)
A. americana	18		1.916	0.955	0.73,0.92	0.85 (I)
O. virginianus	23		0.805	0.961	1.02,1.21	1.13 (G)
O. johnstoni	20		-0.419	0.970	1.17,1.43	1.31 (G)
C. taurinus	15		1.261	0.989	0.92, 1.01	0.96 (I)

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

TAXON	N	L.S. SLOPE	Y-INTERCEPT	R²	CI	RMA
E. quagga	13		1.606	0.914	0.64, 1.13	0.88 (I)
E. occidentalis	53	0.971	0.920	0.870	0.94, 1.15	1.04 (I)
B. antiquus	70	1.025	0.905	0.949	0.99, 1.11	1.05 (I)
B. bison	17		2.232	0.923	0.64,0.89	0.75 (R)
C. hesternus	29	1.219	-2.201	0.902	1.13,1.45	1.28 (G)
A. americana	17		1.986	0.932	0.69,0.97	0.89 (R)
O. virginianus	20		1.892	0.962	0.80,0.98	0.90 (R)
O. johnstoni	21		-0.179	0.977	1.16,1.41	1.29 (G)
C. taurinus	14		1.851	0.989	0.82,0.93	0.88 (R)

radius-ulna is isometric in the plains zebra (slope = 0.76), while the large Rancho La Brea horse is slightly more robust (slope = 0.73). Surprisingly, many other cursorial artiodactyls in Table 2 are also isometric or even robust, although the okapi and wildebeest are the most gracile taxa studied. The data for the tibia (Table 4) give similar results. The plains zebra is isometric (slope = 0.88), while the large Rancho La Brea horse is also isometric (slope = 1.04). Nearly all the cursorial artiodactyls in Table 4 have robust growth in their tibiae except again for the okapi, which is gracile. In other words, the colts are born with gracile limbs, and keep those same proportions through isometric growth to adulthood.

DISCUSSION

These results are consistent with the previous hypotheses about the large Rancho La Brea horse, *Equus occidentalis*. Conventionally, it has been interpreted to have been relatively stout-limbed compared to some of the noticeably stilt-legged Pleistocene horses, such as *Equus* (now *Haringtonhippus*) *francisci* (Kurtén and Anderson, 1980; Heintzman et al., 2017). Our growth data clearly show a pattern of isometric or even slightly robust growth of limbs compared not only to the living plains zebra, but also to many other even more cursorial living artiodactyls. This is the pattern exhibited by living wild equids such as zebras.

CONCLUSION

Examination of the growth of limbs in the extinct Pleistocene horse *Equus occidentalis* from the Rancho La Brea asphalt deposits has demonstrated that colts grew with an isometric or slightly robust growth pattern, excepting the gracile femora, similar to other living equids, and comparable to other living cursorial artiodactyls. The La Brea horse grows much like the living zebra and other cursorial mammals, except for the growth of its femur.

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