Lucas et al., 2025, Fossil Record 10. New Mexico Museum of Natural History and Science Bulletin 100.

ALLOMETRIC TRENDS IN GROWTH OF THE CHALICOTHERE *MOROPUS ELATUS* (MAMMALIA: PERISSODACTYLA: CHALICOTHERIIDAE)

TYMBRI POTTER[1], DONALD R. PROTHERO[2,3], and ED WELSH[4]

[1] Department of Geological Sciences, California State University, Long Beach, CA 90840;
[2]Department of Geological Sciences, California State Polytechnic University, Pomona, CA;
[3]Department of Vertebrate Paleontology, Natural History Museum of Los Angeles County, Los Angeles, CA; [4]Badlands National Park, 25216
Ben Reifel Road, Interior, SD 57750

Abstract—The large clawed chalicothere *Moropus elatus* is known from dozens of skeletons from early Miocene quarries in western Nebraska, such as Agate Fossil Beds quarry and Morava Ranch Quarry. Using a flexible metric measuring tape, we measured all the unbroken juvenile and adult humeri, radii, femora, and tibiae in the sample, focusing on the diaphyseal shaft length (minus the epiphyses) vs. the midshaft diameter, following the conventions of Kilbourne and Makovicky (2012). Data were then plotted and reduced major axis (RMA) slopes of the data were calculated using PAST software. None of the four limbs were significantly different from isometric growth slope of 1.0, even though *Moropus* was thought to be robust in its limbs. Surprisingly, this is also true of the rhinoceroses *Diceros bicornis, Menoceras arikarense*, and *Teleoceras proterum*, and the zebra *Equus burchelli.* Allometric growth is relatively rare in most large hoofed mammals, even in animals as large as elephants.

INTRODUCTION

The subject of ontogenetic growth in fossils has been intensively studied in paleontology for many years (Gould, 1966, 1970, 1971, 1975, 1977; Kilbourne and Makovicky, 2012). In particular, the focus has long been on studying the rare fossil assemblages which have sample sizes of juvenile limb bones preserved, so they can be compared to the growth patterns in living mammals. What kinds of allometric growth patterns might be expected in different groups of mammals with known locomotor habits? For example, do highly cursorial ungulates show a tendency for their limbs to grow more gracile as they get larger? Do graviportal mammals (e.g. elephants, rhinos, and hippos) tend to develop more robust limbs as they grow larger?

Many of these patterns were examined in a study by Kilbourne and Makovicky (2012), which examined the ontogenetic growth in limbs of a wide range of large hoofed mammals, proboscideans and others. These data form the baseline for this study. So far, the studies conducted yield a wide spectrum of patterns. In proboscideans, the picture is complex. Htun et al. (2018a) found that ontogenetic growth slopes of the humerus, ulna, femur, and tibia of the Channel Islands pygmy mammoth (*Mammuthus exilis*) were 1.09, 0.91, 1.11, and 0.89, respectively, none of which were significantly different from an isometric growth slope of 1.0 given their confidence intervals. Thus, all four limbs in the pygmy mammoth show isometric rather than allometric growth, contrary to commonly held expectations that proboscidieans show develop more robust limbs as their mass increases allometrically. Growth of the Pleistocene pronghorn *Capromeryx minor* from the La Brea tar pits shows isometric slopes in the humerus, femur, and tibia, with a radius growth slope that is just slightly more gracile than isometric (Prothero et al., 2021). In the Pleistocene pronghorn *Stockoceros conklingi*, all four limb bones showed slopes that were less than 1.0, suggesting that their growth is negatively allometric, growing thicker as they mature, rather than more gracile or growing isometrically (Olson et al., 2022). This result is very similar to that of the extant *Antilocapra americana*, which was significantly more robust in three limbs, and isometric only in the radius (Kilbourne and Makovicky, 2012). Among deer, in proximal limb elements (humerus, femur), the Pleistocene deer *Navahoceros* exhibited negative allometry (growing more robust as it grew larger), consistent with the expectation based on the adult robustness, but the distal limb elements (radius and tibia) showed no significant difference from isometry (Kuo and Prothero, this volume). This contrasts with previous studies of growth in the white-tailed deer (*Odocoileus virginianus*), which was isometric in the humerus and radius, but gracile in the femur and robust in the tibia (Kilbourne and Makovicky, 2012).

Among the cursorial artiodactyls studied by Kilbourne and Makovicky (2012), it is surprising that only the okapi *Okapia johnstoni*, showed gracility in the growth of the radius-ulna and tibia. Yet the okapi is a giraffid that lives in dense jungles and does not rely on speed to escape predators. But it is related to *Giraffa*, which has both long limbs and a long neck (but has not yet been analyzed for its limb growth trends). By contrast, the pronghorn and wildebeest, both open-grassland runners, did not show the expected gracile pattern.

Htun et al. (2018b) found that of the limbs of the Pleistocene La Brea camelid *Camelops hesternus* grew with the expected pattern: robust or isometric in the proximal limb elements (humerus, femur), but showed an allometric trend toward more gracile distal limb elements, like the radius-ulna and tibia. Galvez et al. (2018) found that in the humerus, the growth trend in the late Pleistocene La Brea species *Bison antiquus* was isometric (slope = 1.03), while *Bison bison* was significantly more robust. In the radius-ulna, *B. antiquus* was robust (slope = 0.89), about the same as in *B. bison* (slope = 0.87). The femur showed the same growth trends, with highly robust (slope = 0.85) growth in *B. antiquus,* while *B. bison* had a slope of 0.92. However, the tibia (slope = 1.05) shows isometric growth, compared to the robust slope of 0.75 for the tibia in *B. bison*. In short, a wide variety of different growth trends in large hoofed mammals have been documented, not only by Kilbourne and Makovicky (2012), but also by studies that have been done since then.

Another candidate for such a study is the chalicothere *Moropus elatus*. First fully described by Holland and Peterson (1914), large samples of this animal were collected from what is now Agate Fossil Beds National Monument in Sioux County, western Nebraska, mostly by the American Museum of Natural History, University of Nebraska State Museum, and Carnegie Museum of Natural History (Osborn, 1919; Coombs, 1978, 1982). Additional specimens were collected from the nearby Morava Ranch Quarry (Coombs and Coombs, 1997).

Coombs (1975) showed that there was sexual size dimorphism in *Moropus elatus*, with presumed females having smaller limbs than presumed males. However, it is impossible to assign disarticulated limb elements to sex without making the *a priori* assumption that smaller limbs are female and larger limbs are from males, just by virtue of size. In this study, we only care whether limbs are adult (with fused epiphyses) or juvenile (with unfused epiphyses). The difference in size of the adult bones due to sexual dimorphism should not bias our results, because juvenile bones are so much smaller than either adult female or male bones. Kilbourne and Makovicky (2012) had both male and female individuals in their sample of modern mammals, and it made no difference in their results.

Moropus limbs have long been described as robust (Holland and Peterson, 1914; Coombs, 1978, 1983), particularly in the context of trying to interpret form and function for their peculiar, clawed unguals. It would be worthwhile to measure the large sample of individuals, from juveniles to adults, to see how their limbs changed proportions as they grew.

METHODS

We measured as many complete unbroken limb elements (humerus, radius, femur, tibia) of *Moropus elatus* (Fig. 1) as we could find in the collections of the American Museum of Natural History, University of Nebraska State Museum, the Field Museum of Natural History, and Carnegie Museum of Natural History, which have the bulk of the Agate Fossil Beds collections, as well as a few specimens from Morava Ranch Quarry in the AMNH. Sample sizes are given in Table 1. We used a flexible metric tape measure to find the length of diaphysis (shaft of the limb elements) excluding the epiphyseal caps to make all the data comparable. Epiphyseal caps are often missing in juvenile limb elements, since they are still cartilage or only poorly ossified and weakly attached the growth surface of the diaphysis. We measured the midshaft circumference directly with the measuring tape to facilitate comparisons with the measurements of growing mammalian limbs made by Kilbourne and Makovicky (2012).

FIGURE 1. Comparison of juvenile and adult humerus of *M. elatus*.

TABLE 1. Limb growth data of ungulates. N = number of specimens; CI = slope confidence interval limits; RMA = reduced major axis slope. (G) = gracile; (I) = isometric; (R) = robust, calculated in the PAST software package; *Diceros bicornis, Equus burchelli, Antilocapra americana, Odocoileus virginianus* (white-tailed deer), *Okapia johnstoni* (okapi), and *Connochaetes taurus* (wildebeest) data from Kilbourne and Makovicky (2012).The rhinoceroses *Menoceras arikarense* and *Teleoceras proterum* after Santos et al. (this volume).

TAXON	N	r^2	CI	RMA
Humerus				
M. elatus	14	0.554	0.35, 1.19	0.903(I)
M. arikarense	55	0.015	0.45, 2.15	0.688(I)
T. proterum	37	0.155	0.46, 1.18	0.865(I)
D. bicornis	14	0.931	0.75, 1.03	0.910(I)
E. burchelli	13	0.917	0.77, 1.36	1.09(I)
O. virginianus	23	0.960	0.94, 1.11	1.03 (I)
A. americana	19	0.946	0.63, 0.82	0.75 (R)
O. johnstoni	20	0.982	1.16, 1.37	1.26 (G)
C. taurinus	14	0.976	0.65, 0.77	0.71 (R)
Radius-Ulna				
M. elatus	13	0.695	0.44, 1.06	0.798(I)
M. arikarense	69	0.463	0.91, 1.59	1.19(I)
T. proterum	44	0.458	0.70, 1.08	0.94(I)
D. bicornis	15	0.590	0.601, 1.05	0.89(I)
E. burchelli	12	0.815	0.47, 1.02	0.76(I)
O. virginianus	12	0.965	0.77, 1.02	0.89 (I)
A. americana	18	0.858	0.65, 1.09	0.87 (I)
O. johnstoni	12	0.955	0.95, 1.43	1.21 (G)
C. taurinus	13	0.988	0.81, 0.99	0.86 (R)
Femur				
M. elatus	16	0.832	0.68, 1.06	0.90(I)
M. arikarense	45	0.505	0.79, 1.47	1.10(I)
T. proterum	32	0.116	0.53, 2.19	0.79(I)
D. bicornis	15	0.946	1.04, 1.46	1.21(G)
E. burchelli	13	0.933	0.77, 1.40	1.09(I)
O. virginianus	23	0.961	1.02, 1.21	1.13 (G)
A. americana	18	0.955	0.73, 0.92	0.85 (R)
O. johnstoni	20	0.970	1.7, 1.43	1.31 (G)
C. taurinus	15	0.989	0.92, 1.01	0.96 (I)
Tibia				
M. elatus	18	0.524	0.0.24, 1.03	0.92 (I)
M. arikarense	77	0.246	0.79, 1.22	1.01 (I)
T. proterum	75	0.609	1.22, 2.03	1.67(G)
D. bicornis	14	0.877	0.70, 1.13	0.95(I)
E. burchelli	13	0.914	0.65, 1.13	0.88(I)
O. virginianus	20	0.962	0.80, 0.98	0.90 (R)
A. americana	17	0.932	0.69, 0.97	0.89 (R)
O. johnstoni	21	0.977	1.16, 1.41	1.29 (G)
C. taurinus	14	0.989	0.82, 0.93	0.88 (R)

Following the conventions of most allometric studies, raw growth data were converted to natural logs and plotted in log-log graphs, so that the exponential slope of allometry would

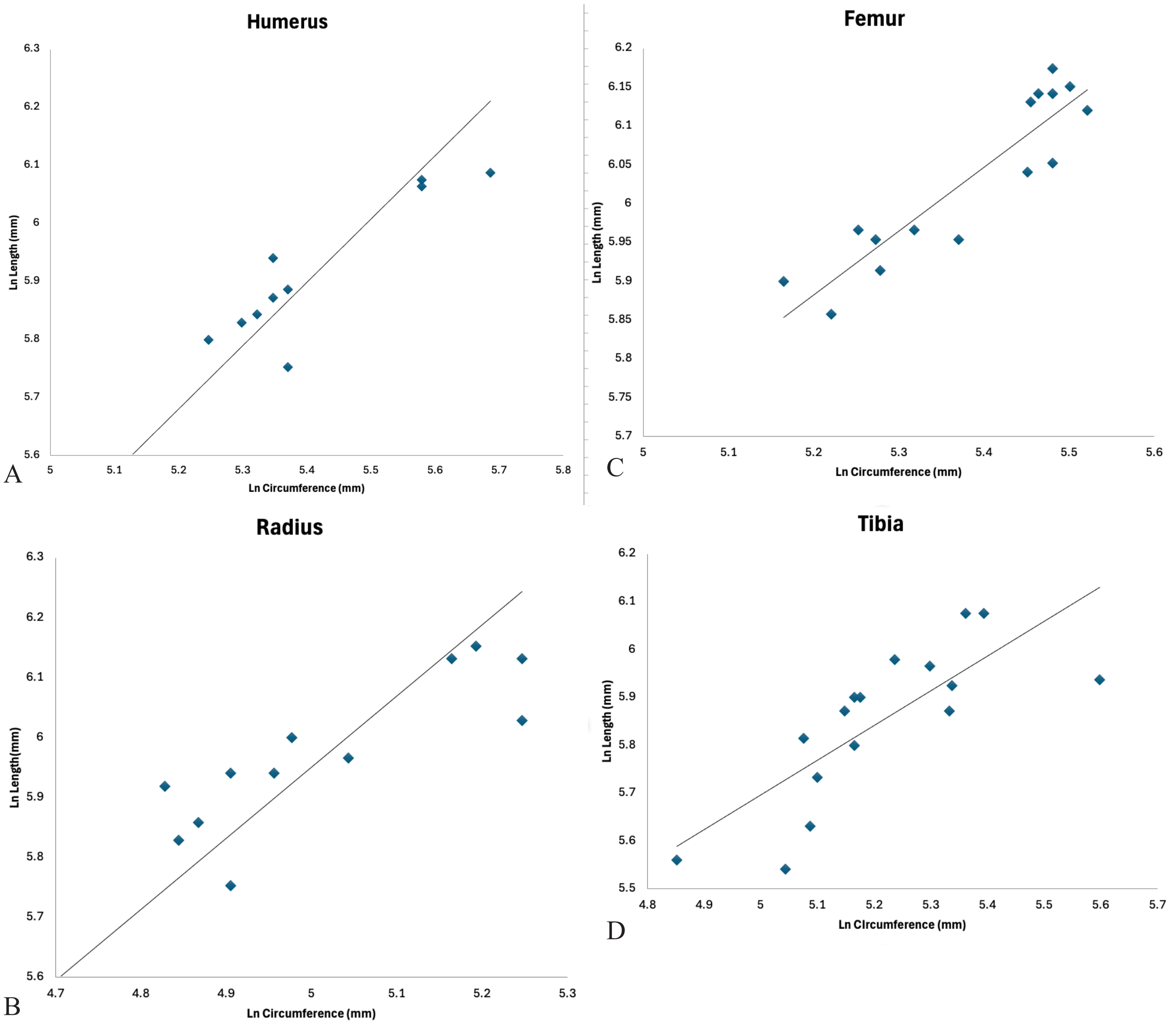

FIGURE 2. Plots of the data and RMA slopes for the four limbs of *M. elatus*. **A,** Humerus. **B,** Radius. **C,** Femur. **D,** Tibia.

give a simple linear slope. The size range of our sampled individuals cover almost an order of magnitude, so only log-log plots are appropriate to calculate the growth slope. 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 PAST program—Hammer et al., 2001).

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

RESULTS

Results of our analysis are shown in Table 1 and Figures 1-4. In all four limbs, *Moropus elatus* did not show a slope significantly different from the isometric slope of 1.0. However, it should be noted that the sample sizes were not very large (between 14 and 18 specimens for each limb), and the data were a bit scattered, so the r^2 values for each RMA analysis were not as high as would be preferred (from 0.554 to 0.832). Still, it is clear from these slopes that there is no statistically significant trend towards either robust growth or gracility as *M. elatus* grew larger.

DISCUSSION

Comparing *M. elatus* to other perissodactyls, it is clear that isometric growth is the norm, whether the animal is graviportal like the black rhinoceros *Diceros bicornis*, or gracile like the Plains zebra *Equus burchelli* (Table 1). Likewise, studies of the gracile long-legged rhinoceros *Menoceras arikarense* (from the same Agate Fossil Beds quarries as *M. elatus*) or the stumpy-legged "hippo-like rhino" *Teleoceras proterum* from Mixson's Bone Bed showed isometry in nearly all the limb growth (Table 1), regardless of whether it had slender limbs or stumpy limbs as an adult (Santos et al., this volume). The only exception to this general trend was the femur in *D. bicornis*, which was gracile (Table 1), according to Kilbourne and Makovicky (2012), even in a graviportal thick-legged animal like a rhinoceros.

Likewise, the long-held expectation that growth in larger mammals would be allometric has not turned out to be true. Instead, almost all the larger mammals surveyed by Kilbourne and Makovicky (2012) or the pygmy mammoths studied by Htun et al. (2018a) show isometric growth trends in ontogeny. As can be seen in Table 1, the growth trends in other long-legged cursorial artiodactyls, such as the American pronghorn, the white-tailed deer, the okapi, and the wildebeest are mostly isometric, but some are robust and some are gracile, with no consistent trend in any particular limb, or in any particular group of ruminants.

CONCLUSION

The results of this work are congruent with what was apparent in the work of Kilbourne and Makovicky (2012), By far, the most common growth trend in larger mammals is not allometric growth, but isometric growth, even in animals with huge body masses, such as elephants and mammoths. This also holds true for our study of *Moropus elatus*, which does not deviate from isometric growth in all four limb elements (within the 95% confidence level of the slopes). Other known perissodactyls retain similar growth patterns, like the rhinoceroses *Diceros bicornis, Menoceras arikarense*, and *Teleoceras proterum*, and the zebra *Equus burchelli*. In fact, examples of allometric growth are very rare in larger hoofed mammals, and show no general pattern corresponding with cursoriality, graviportality, or any other expectations of growth based on body size or mode of locomotion.

ACKNOWLEDGMENTS

We thank Meng Jin and Judy Galkin of the American Museum of Natural History, Ashley Poust and George Corner of the University of Nebraska State Museum, Bill Simpson of the Field Museum, and Matt Lamanna and Amy Henrici of the Carnegie Museum for access to specimens. We thank E. Prothero for Photoshopping the illustrations in Figure 1. We thank M. Mihlbachler and M. Coombs for reviewing the manuscript.

REFERENCES

Coombs, M.C., 1975, Sexual dimorphism in chalicotheres (Mammalia, Perissodactyla): Systematic Zoology, v. 24, p. 55-62.

Coombs, M.C., 1978, Reevaluation of early Miocene North American *Moropus* (Perissodactyla, Chalicotheriidae, Schizotheriinae): Bulletin of the Carnegie Museum, v. 4, p. 1-62.

Coombs, M.C., 1982, Chalicotheres (Perissodactyla) as large terrestrial mammals: Third North American Paleontological Conference, Proceedings, v. 1, p. 99-103.

Coombs, M.C., 1983, Large mammalian clawed herbivores: A comparative study: Transactions of the American Philosophical Society, v. 73, p. 1-100.

Coombs, M.C., and Coombs, W.P., 1997, Analysis of the geology, fauna, and taphonomy of Morava Ranch Quarry, early Miocene of northwest Nebraska: PALAIOS, v. 12, p. 165-187.

Galvez, S., Prothero, D.R., and Syverson, V.J.P., 2018, How did bison calves grow up? Postnatal limb allometry in *Bison antiquus* from La Brea tar pits: New Mexico Museum of Natural History Bulletin v. 79, p. 213-217.

Gould, S.J., 1966, Allometry and size in ontogeny and phylogeny: Biology Reviews, v. 41, p. 587-640.

Gould, S.J., 1970, Evolutionary paleontology and the science of form: Earth Science Reviews, v. 5, p. 77-119.

Gould, S.J., 1971, Geometric similarity in allometric growth: a contribution to the problem of scaling in the evolution of size: American Naturalist, v. 705, p. 113-136.

Gould, S.J., 1975, Allometry in primates, with emphasis on scaling and evolution of the brain: Contributions to Primatology, v. 5, p. 244-292.

Gould, S.J., 1977, Ontogeny and Phylogeny: Cambridge, Massachusetts, Belknap Press.

Hammer, Ø., Harper, D.A.T., and Ryan, P.D., 2001, PAST: Paleontological Statistics Software Package for Education and Data Analysis: Palaeontologia Electronica, v. 4, no. 1.

Holland, W. J., and Peterson, O.A., 1914, Osteology of the Chalicotheroides: Memoirs of the Carnegie Museum, v. 3, n. 2, p. 189-406.

Htun, T., Prothero, D.R., Hoffman, J.M., Lukowski, S., and Syverson, V.J.P., 2018a, Allometric trends in growth and dwarfing in the extinct Pleistocene Channel Islands pygmy mammoth *Mammuthus exilis*: New Mexico Museum of Natural History and Science, Bulletin 79, p. 261-265.

Htun, T., Prothero, D.R., and Syverson, V.J.P., 2018b, Postnatal allometric limb growth in juvenile camels from the Pleistocene of Rancho La Brea tar pits: New Mexico Museum of Natural History and Science, Bulletin 79, p. 267-270.

Kilbourne, B.M., and Makovicky, P.J., 2012, Postnatal long bone growth in terrestrial placental mammals: Allometry, life history, and organismal traits: Journal of Morphology, v. 273, p. 1111–1126.

Olson, S.M., White, R.S, Prothero, D.R., Balassa, D., Marriott, K.L., and V.J.P. Syverson, 2022, Ontogenetic growth in the Pleistocene pronghorn *Stockoceros conklingi* from San Josecito Cave, Mexico: New Mexico Museum of Natural History and Science, Bulletin, v. 90, p. 321-324.

Osborn, H.F., 1919, Seventeen skeletons of *Moropus*: Probable habitats of this animal: Proceedings of the National Academy of Sciences, v. 5, no. 7, p. 250–252.

Prothero, D.R., and Sereno, P.C., 1982, Allometry and paleoecology of Medial Miocene dwarf rhinoceroses from the Texas Gulf Coastal Plain: Paleobiology, v. 8, p. 16–30.

Prothero, D.R., Syverson, V.J.P., Hulbert, R.H., Jr., De Anda, E.E., and Balassa, D., 2021, Allometric trends in growth and dwarfing in the dwarf pronghorn *Capromeryx*: does dwarfing follow the same trends as growth? New Mexico Museum of Natural History and Science, Bulletin 82, p. 335-339.