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

HOW DID EXTINCT RHINOCEROS LIMBS GROW? ALLOMETRIC GROWTH IN RHINOCEROS LIMBS

SUNSHYNE M. SANTOS[1], DONALD R. PROTHERO[1,2], KRISTIN I. WATMORE[3] and ED WELSH[4]

[1]Department of Geological Sciences, California State Polytechnic University, Pomona, CA; smsantos@cpp.edu; [2]Department of Vertebrate Paleontology, Natural History Museum of Los Angeles County, Los Angeles, CA; [3]Department of Geosciences, University of Southern California, Los Angeles, CA 90089; [4]Badlands National Park, 25216 Ben Reifel Road, Interior, SD 57750

Abstract—Fossil rhinoceroses came in many different shapes and sizes, from goat-sized creatures to enormous indricotheres that were among the largest land mammals that ever lived. How did rhinos grow into these different shapes? We looked at two extreme examples: the pony-sized early Miocene rhinoceros *Menoceras arikarense*, which had long slender legs, from Agate Fossil Beds National Monument in Nebraska; and the hippo-like rhinoceros *Teleoceras proterum*, with its stumpy short legs, from the late Miocene Mixson's Bone Bed in northern Florida. These are not only two extreme variants of rhinoceros body form, but they are also among the few species that are known from large quarry samples with lots of juvenile bones that allow us to examine how their limbs changed shape and size over ontogeny. We measured diaphyseal length (minus the epiphyseal caps) and midshaft circumferences of the humerus, radius, femur, and tibia of both rhinos from several museum collections. We calculated the reduced major axis (RMA) slope for their growth, using PAST software. The slopes for most of the *Menoceras* limbs were slightly greater than 1.0 (slightly gracile), while most of the *Teleoceras* limbs had slopes less than 1.0 (slightly robust). However, these slopes are not significantly different from the isometric slope of 1.0 because the error estimates in the slope are large. This is consistent with the data from Kilbourne and Makovicky (2012), who found that even graviportal animals like the black rhinoceros (*Diceros bicornis*), as well as elephants and hippos, showed isometric growth in most of their limbs, despite their large body masses.

INTRODUCTION

Rhinoceroses have been one of the most widespread and successful large mammals in the Northern Hemisphere for over 40 million years (Prothero, 2005). We know rhinos today as one of the largest horned mammals. However, the group experienced a great diversity over its evolution. They ranged over a wide variety of sizes, some of which were as small as a sheep, and one species (*Paraceratherium bugtiense*) was one of the largest terrestrial mammals to exist. Most rhinos did not have horns. There were a variety of other features that may seem unusual to our modern understanding of what a rhino is, but they experienced a lot of variation throughout their evolution.

The two species that will be examined in this project are *Menoceras arikarense*, from the earliest Miocene (latest Arikareean, about 19 Ma) Agate Fossil beds, Sioux County, Nebraska, and *Teleoceras proterum,* from the late Miocene (early Hemphillian, about 8 Ma) Mixson's Bone Bed, Levy County, Florida (Tedford et al., 2004). These two Miocene rhinoceroses present a striking contrast in the extremes of rhino body shapes. The pony-sized *Menoceras arikarense* was a small rhino (barely over a meter in shoulder height) with two paired horns on its nose, and relatively slender limbs compared to most rhinos. *Teleoceras proterum* had a small single nasal horn with a barrel-like body and had short limbs. Its body type is often compared to that of a modern-day hippopotamus. These two rhinos were chosen, not only because they represent two extremes in rhinoceros body shape, but also because they are represented by huge quarry samples (typically hundreds of bones), with lots of juvenile limbs (Fig. 1), so there are enough specimens to get robust plots of growth from smallest juveniles to largest adults.

The thick robust limbs of living rhinoceroses are adapted to support their great weight, so it might be expected that the limbs should grow more robust through ontogeny as their mass increases by a cube, but the cross-sectional area of the limb bones only increases as a square (Gould, 1966, 1970, 1971, 1977). In other words, they should show allometric growth, with the cross-sectional area (here represented by the circumference of the limb) increased proportionately faster than the length as they grew larger during their lifetimes.

However, recent studies do not support this expectation. According to Kilbourne and Makovicky (2012), the modern African black rhino (*Diceros bicornis*) shows isometric growth in its humerus, radius, and tibia, and yet its femur was significantly more gracile than isometric (see Table 1). No other modern rhinos have been studied to see if this is a common pattern among the members of the family.

Kilbourne and Makovicky (2012) reported that three of the four limbs (humerus, femur, tibia) in the African elephant, *Loxodonta africana*, show isometric growth, with slopes of 0.90, 0.95, and 0.97 for the humerus, femur, and tibia respectively, all within the confidence limits that include the isometric slope of 1.0 (Table 1). Only the ulna (slope = 0.86) was significantly more robust. In *Hippopotamus amphibius*, three limbs (humerus, femur, tibia) are isometric, and only the radius show significantly more robust growth. Across their entire sample, Kilbourne and Makovicky (2012) showed that most mammals, even graviportal large-bodied mammals like elephants already mentioned, and hippos, show isometric growth in most their limbs, a result that contradicts the expectations based on the idea that larger animals should develop more robust limbs as they grow. However, previous studies have shown that dwarf rhinos often end up with proportionally more robust limbs than their mainland counterparts, and this is a common pattern with insular dwarfs, including dwarfed hippos, mammoths, and elephants (Prothero and Sereno, 1982).

Compared to living black rhinos, what is the growth of our two fossil rhinos like? Are they also largely isometric in most limbs, or do they show significant allometry? That is the focus of this study.

METHODS

We measured as many complete unbroken limb elements (humerus, radius, femur, tibia) of our two rhinos as we could find in the collections listed below. Sample sizes are given in Table 1,

FIGURE 1. Typical drawers of the limbs of (**A**) *Menoceras arikarense* tibiae, and (**B**) *Teleoceras proterum* radii, showing part of the huge sample available.

and most of the limbs are represented by at least 32 specimens; the largest sample was 77. To make all the data comparable with the measurements of growing mammalian limbs made by Kilbourne and Makovicky (2012), we used a flexible metric tape measure to find the circumference of the midshaft and the length of the diaphysis (shaft of the limb elements) excluding the epiphyseal caps. These 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. It is not possible to determine the sex of individual disarticulated limb bones, so we cannot determine whether sexual dimorphism will influence the results. Nor is it possible to determine the exact ontogenetic age of individual specimens by things such as partial fusion or complete fusion of the epiphyses. In most cases, the epiphysis was either completely missing, or completely fused, and there were no other clues about the age of the specimen other than size.

One reviewer suggested to us that a study of the juvenile *Teleoceras major* from Ashfall Fossil Bed State Park in Nebraska might be useful, because the skeletons are articulated and attached to skulls whose dental eruption and wear stage might give a clue to ontogenetic age. However, one of us (Prothero) has already examined those specimens. Not only are there too few juveniles in the sample to make a real difference (less than a dozen), but nearly all of them are of about the same ontogenetic age, because the calves were apparently birthed at the same time before they met their abrupt end with the volcanic eruption that killed all the animals at Ashfall.

Our data comes from a variety of museums, including the American Museum of Natural History, New York, New York (which had all the *Teleoceras proterum* specimens, and most of the *Menoceras arikarense* specimens); the Carnegie Museum of Natural History, Pittsburgh, Pennsylvania; the University of Nebraska State Museum, Lincoln, Nebraska; and the Field Museum of Natural History, Chicago, Illinois. We also examined the collections at the Florida Museum of Natural History in Gainesville, Florida, but they did not have any *T. proterum* limbs that were complete enough to add to the sample.

Data were collected, analyzed, and plotted using Excel spreadsheets. Following the conventions of most allometric studies, raw data were converted to natural logs and plotted in log-log graphs, so that the exponential slope of allometry would give a simple linear slope. Since there is no dependent or independent variable in this study (an assumption of the least-squares regression method), we adopted the commonly used Reduced Major Axis (RMA) method of correlation to determine the slope between the two variables (calculated using the PAST software (Hammer et al., 2001). The PAST software gives the RMA slopes, and the bootstrapped 95% confidence intervals on either side of the slope, as well as values like the coefficient of correlation, r^2.

We followed the conventions of Kilbourne and Makovicky (2012) in plotting length on the Y axis vs. circumference on the X axis. If the slope of the RMA line is significantly less than 1.0, then the growth is negatively allometric, or in other words, the limbs are becoming more robust as they grow. This might be expected for an animal with short stocky limbs, like *Teleoceras*. If the slope is significantly greater than 1.0, then the growth in positively allometric, that is, more gracile and long-limbed. This might be predicted for *Menoceras*, which had long thin legs

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), *Hippopotamus amphibius*, and *Loxodonta africana* (African elephant) data from Kilbourne and Makovicky (2012).

TAXON	N	r^2	CI	RMA
Humerus				
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)
H. amphibius	11	0.584	0.85, 1.37	1.00(I)
L. africana	11	0.632	0.38, 1.08	0.90(I)
Radius				
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)
H. amphibius	9	0.407	0.44, 0.95	0.75(R)
L. africana	7	0.849	0.63, 0.94	0.86(R)
Femur				
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)
H. amphibius	12	0.733	0.91, 1.21	1.02(I)
L. africana	11	0.565	0.70, 1.07	0.95(I)
Tibia				
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)
H. amphibius	11	0.406	0.91 1.21	1.01(I)
L. africana.	10	0.901	0.60 1.09	0.97 (I)

compared to most rhinos.

RESULTS

Results of our analysis are shown in Table 1 and in Figures 2-3. The limbs of *Menoceras arikarense* all had slopes that could not be statistically distinguished from 1.0 (isometric), largely because the scatter of the data was so large (Fig. 2) and the error estimates of the slopes (Table 1) were also correspondingly large as well, as shown by the r^2 value. However, the scatter on the data from the humerus and femur was so large that fitting a line through them is not very meaningful (Figs. 2A, 2C). It is hard to determine why the growth data for these rhinos is not more tightly correlated. The likeliest reason is that the Agate Quarry sample does not really include many very young juveniles, which would anchor and extend the bottom end of the slope and give more tightly correlated results. As discussed above, there is no way to determine if there are different sexes represented in these bones, because sex cannot be identified from isolated disarticulated limb bones. Nor was it possible to determine the actual ontogenetic age of the individual limb bones—all we have is their dimensions. In addition, Kilbourne and Makovicky (2012) report r^2 values of 0.5 and lower for some *Diceros bicornis* limbs, so even in an animal with good constraints on ontogenetic age and growth, rhinoceroses tended to have less robust correlation with greater scatter. For what it's worth, three of the four limbs (humerus, radius, and tibia) did give slopes that

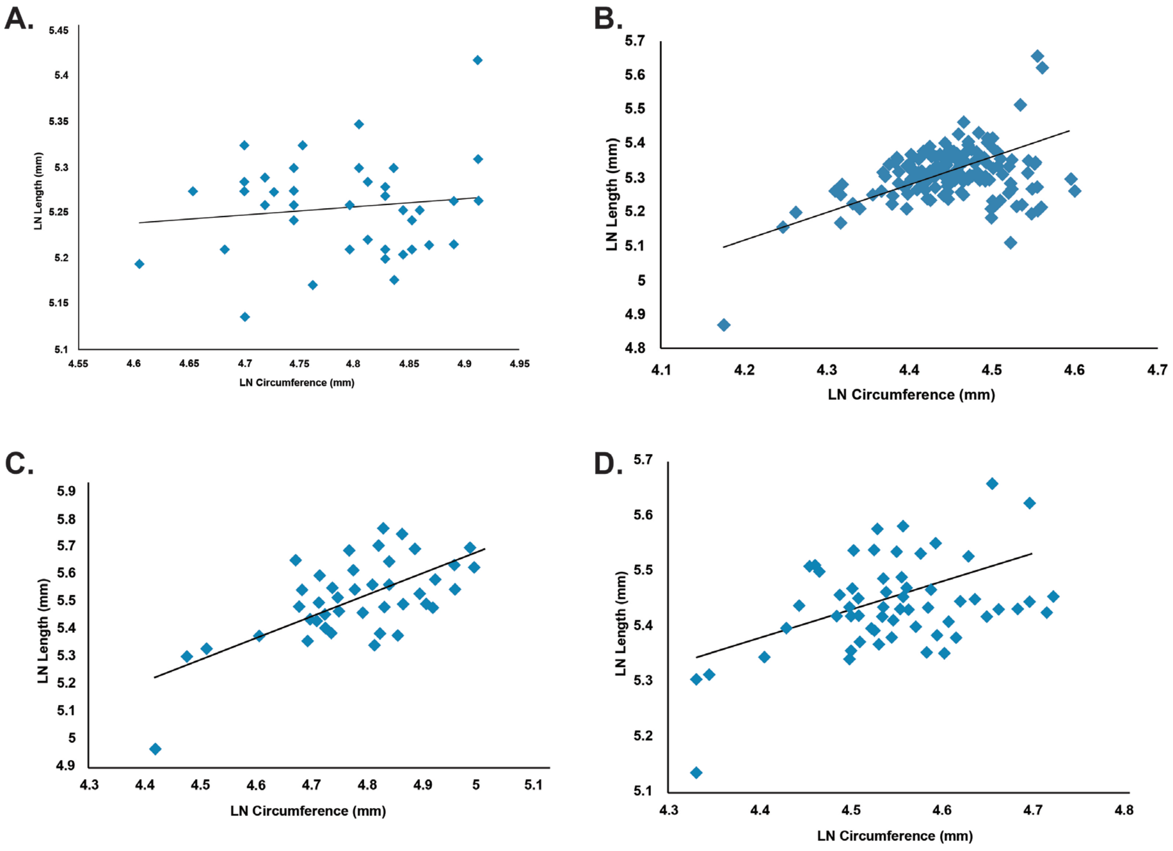

FIGURE 2. Plots of the data and RMA slopes for the four limbs of *Menoceras arikarense*. **A**. Humerus. **B**. Radius. **C**. Femur. **D**. Tibia.

were greater than 1.0, suggesting gracility, although they were not significantly different from isometry.

Similar results occurred with most of the limbs of *Teleoceras proterum* (Table 1). The humerus, radius, and femur slopes were not significantly different from isometry, due to the large error estimates from the highly scattered data with a low r^2 value (Fig. 3, Table 1). Nevertheless, the scatter was less and the r^2 values for these bones was closer to 1.0 (perfect correlation), because the Mixson sample includes some very small juvenile bones that the Agate sample lacked. For what it's worth, three of the four limbs (humerus, radius, and femur) gave slopes that were less than 1.0, suggesting a tendency toward robustness.

Strangely, the tibia gave a slope of 1.21, and it was significantly more gracile based on the slope error estimates. We are not sure why this is, except that the data was more scattered than in most of our samples, so the slope may reflect this scatter. In this case, most of the shortening of the stumpy *Teleoceras* limb occurs in both the proximal elements (humerus, femur) as well as the flattened stumpy metapodials, rather than in the distal elements (radius, tibia), so by comparison the tibia might be relatively gracile.

DISCUSSION

Comparing our fossils to those of 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). As we can see in Table 1, the gracile long-legged rhinoceros *Menoceras arikarense* or the stumpy-legged "hippo-like rhino" *Teleoceras proterum* from Mixson's Bone Bed showed isometry in nearly all the limb growth, regardless of whether it had slender limbs or stumpy limbs as an adult. The only exception to this general trend was the femur in *D. bicornis*, which was gracile (Table 1), according to Kilbourne and Makovicky (2012), as well as the tibia in *T. proterum*, 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. (2018) show isometric growth trends in ontogeny. As can be seen in Table 1, even the growth trends in other long-legged cursorial artiodactyls, such as the 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 element, or in any particular group of ruminants.

CONCLUSION

The results of this work are consistent 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 studies of these two rhinos, which shows isometric growth in all four limb elements. Other known perissodactyls retain similar growth patterns, like the rhinoceroses *Diceros bicornis* and the zebra *Equus burchelli*. In fact, examples of allometric growth are very rare in larger hoofed mammals, and show no general pattern corresponding

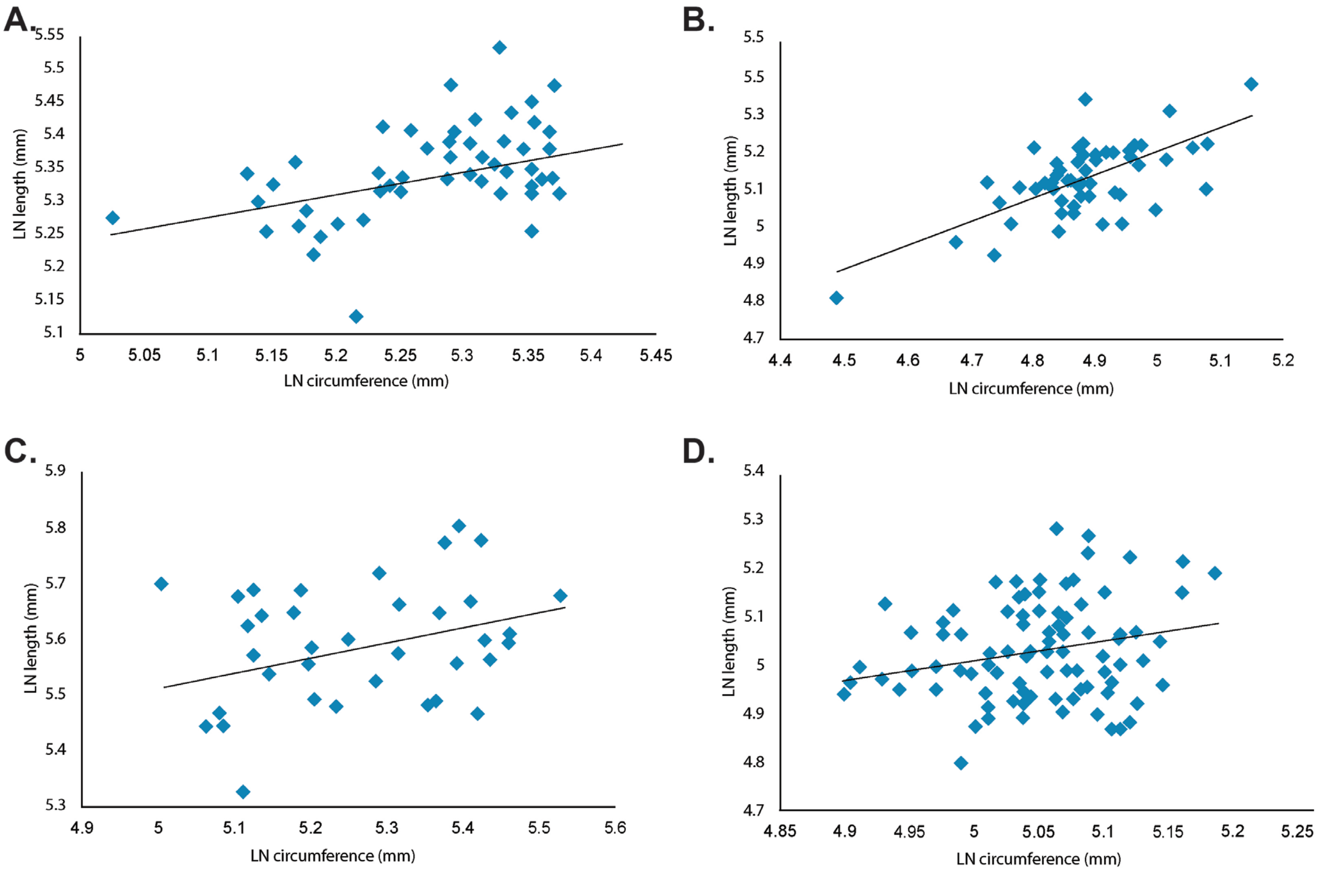

FIGURE 3. Plots of the data and RMA slopes for the four limbs of *Teleoceras proterum*. **A**. Humerus. **B**. Radius. **C**. Femur. **D**. Tibia.

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, Bruce MacFadden and Richard Hulbert of the Florida Museum of Natural History, 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 W. McLaughlin, M. Mihlbachler, and D. Wilcots for reviewing the manuscript.

REFERENCES

Gould, S.J., 1966, Allometry and size in ontogeny and phylogeny: Biological 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., 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.

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

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.

Prothero, D.R., 2005, The Evolution of North American Rhinoceroses: Cambridge University Press, Cambridge, UK.

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.

Tedford, R. H., Albright III, L.B., Barnosky, A.D., Ferrusquia-Villafranca, I., Hunt, Jr., R.M., Storer, J.E., Swisher III, C.C., Voorhies, M.R., Webb, S.D., and Whistler, D.P., 2004, Mammalian biochronology of the Arikareean through Hemphillian interval (late Oligocene through early Pliocene Epochs); *in* Woodburne, M.O., ed., Late Cretaceous and Cenozoic Mammals of North America: Biostratigraphy and Geochronology: Columbia University Press, New York, p. 169–231.