ALLOMETRIC TRENDS IN GROWTH AND DWARFING IN THE DWARF PRONGHORN *CAPROMERYX*: DOES DWARFING FOLLOW THE SAME TRENDS AS GROWTH?

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Abstract—Phyletic dwarfing in the fossil record is quite common, and numerous studies of allometric size reduction after dwarfing are documented. Studies of ontogenetic growth in the fossil record are also popular, but with a different set of expectations. But only rarely has anyone compared the trends of ontogenetic growth in a fossil organism with the slope of reduction in size with specific attention given to dwarfing. Do animals get smaller the same way they grow up? We compared the postnatal ontogenetic trend (i.e., slope) in each of the four main limb bones of the late Pleistocene dwarf pronghorn, *Capromeryx minor*, to the slope for its larger early Pleistocene ancestor *C. arizonensis* to determine how ontogenetic slopes compare to the slope of dwarfing. We compared the large sample sizes of *C. minor* (both juveniles and adults) with the adult limb bones of *C. arizonensis* from the early Pleistocene Inglis locality in Florida. *Capromeryx* decreased by 14-30% in size from the early to late Pleistocene species, but almost all the dwarfing slopes were isometric, with a slope very close to 1.0. Growth of the juvenile *C. minor* from the La Brea sample shows isometric slopes in the humerus, femur, and tibia, with a radius growth slope that is just slightly more gracile than isometric. Thus, the overall trend in growth in most limbs is isometric, and so is the trend in dwarfing, so these pronghorns do not show allometric size changes in either process.

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 addition, there are many examples of phyletic dwarfing documented in the fossil record, showing the opposite trend of size reduction in contrast to size increase during ontogenetic growth (Boucot, 1976; Sondaar, 1977; Gould, 1975; Marshall and Corruccini, 1978; Ford, 1980). Rarely, however, has it been possible to compare the two trends and answer the question: do animals get small in the same way they grow large? In the handful of cases where we have a clear phyletic dwarfing trend, we usually do not have an ontogenetic growth series as well. And in most cases where we have an ontogenetic growth trend, we do not have a dwarfing event as well. Nevertheless, it is worth asking the question to see if there are common trends in the way organisms change their size and body proportions, and see if growth and dwarfing follows the same processes or not.

In the past, the topic of phyletic dwarfing has received some attention, although rarely are there enough fossil materials of both ancestral and descendant populations. Allometric growth in limbs has been especially well studied (McMahon, 1973, 1975; Alexander, 1977; Maloiy et al., 1979; Alexander et al., 1979). In most of these studies, the length of the limb element (y axis) is compared to the midshaft circumference (x axis) on log-log plots. If the slope of these two variables is 1.0, then growth is isometric. If the slope is significantly less than 1.0, then the limb is growing allometrically, and becoming more robust as it grows. If the slope is greater than 1.0, then the limb is becoming more elongate and gracile during ontogeny.

Among the published studies, dwarfed hippo and rhino limbs were found to become more robust as the animals decreased in body size (Prothero and Sereno, 1982). In proboscideans, the picture is more complex. Htun et al. (2018) 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 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 proboscideans show develop more robust limbs as their mass increases allometrically. The growth in the pygmy mammoth is consistent with the results of the African elephant (*Loxodonta africana*), where three of the four limbs (humerus, femur, tibia) in *L. 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 (Kilbourne and Makovicky, 2012). Only the ulna (slope = 0.86) was significantly more robust. In the case of dwarfing, the dwarfing slope of the humerus was 0.71, and for the ulna was 0.53, and both of these values are significantly more robust than expected for isometric growth, so they follow the trend of increased robustness with size decrease. But the slopes for the femur (0.92) and tibia (0.94) do not depart significantly from isometry, so the robustness trends occurs only in the forelimb. By contrast, Herridge (2010) found isometry in all four limbs in the Mediterranean dwarf elephants and mammoths.

What about other mammals that are not graviportal like proboscideans, hippos, and rhinos? Examples of taxa that have good juvenile bones and growth series, and also a larger ancestor that is not dwarfed are rare, but there are some cases. The late Pleistocene (Rancholabrean) dwarf pronghorn *Capromeryx minor* was first described by Taylor (1911) based on teeth and jaws and a few isolated postcranials from the UCMP excavations at Rancho La Brea. As early as 1914, a plaque mount based on some of the specimens was made from replicas of the original LACM sample, known as the "Hancock Collection". Chandler (1916) described some additional bones of *C. minor* from the Hancock Collection, including a partial skull with the distinctive

horn cores, and additional lower jaws. He gave a brief description of a few of the skeletal elements but he provided no illustrations or measurements. No further descriptions of the rest of skeleton were published until Prothero et al. (this volume) did so. This description allows the first large data set of a growth series of the limbs of *Capromeryx minor*.

Over the years, a number of additional species of *Capromeryx* have been named, but few had any associated limb elements. Skinner (1942) named and described another new species, *C. arizonensis*, from the early Pleistocene of Dry Mountain, Arizona. The original Arizona material did not include postcranials, but according to the online catalogue, there are over 1600 specimens from early Pleistocene localities in Florida (such as Inglis and Santa Fe River) referred to *C. arizonensis* in the Florida Museum of Natural History. These provide us with a comparison of a larger ancestral species with its dwarfed descendant, and determine the slopes of the dwarfing curve.

METHODS

We measured as many complete unbroken limb elements (humerus, radius, femur, tibia) of *Capromeryx minor* as we could find in the collections of the La Brea Tar Pits Museum and of *C. arizonensis* in the Florida Museum of Natural History. Sample sizes are given in Table 1. To make all the data comparable, we used a flexible metric tape measure to find the length of diaphysis (shaft of the limb elements) excluding the epiphyseal caps (Fig. 1). 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. We measured the midshaft circumference directly with the measuring tape, or calculated it using the midshaft diameter measured with metric dial calipers

to facilitate comparisons with the measurements of growing mammalian limbs made by Kilbourne and Makovicky (2012).

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 give a simple linear slope. The size range of our sampled individuals cover orders 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 R program "smatr")(Warton et al., 2007, 2012). For size reduction data during dwarfing, however, we simply calculated the Cartesian slope for the means of adult specimens of the two species in log-log space, since it is invalid to calculate an RMA slope for all the raw data when mixing two species together, especially if the sample size of one species is much larger than the other (Prothero and Sereno, 1982).

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 Tables 1 and 2, and in Figure 2. Examining the dwarfing trend, nearly all the limbs
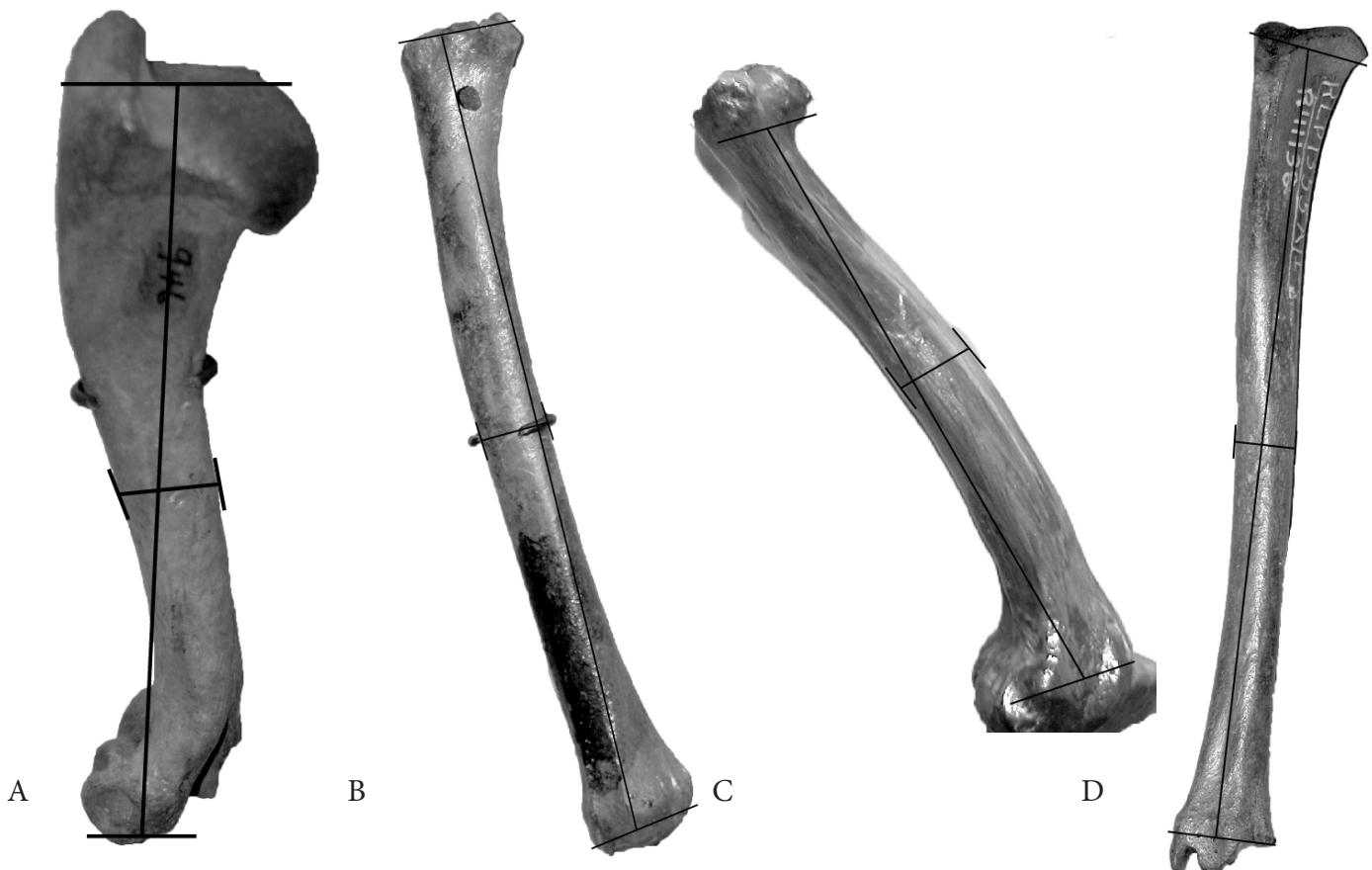

FIGURE 1. Skeletal elements of *Capromeryx minor*, showing the measurement landmarks. A. Humerus. B. Radius. C. Femur. D. Tibia.
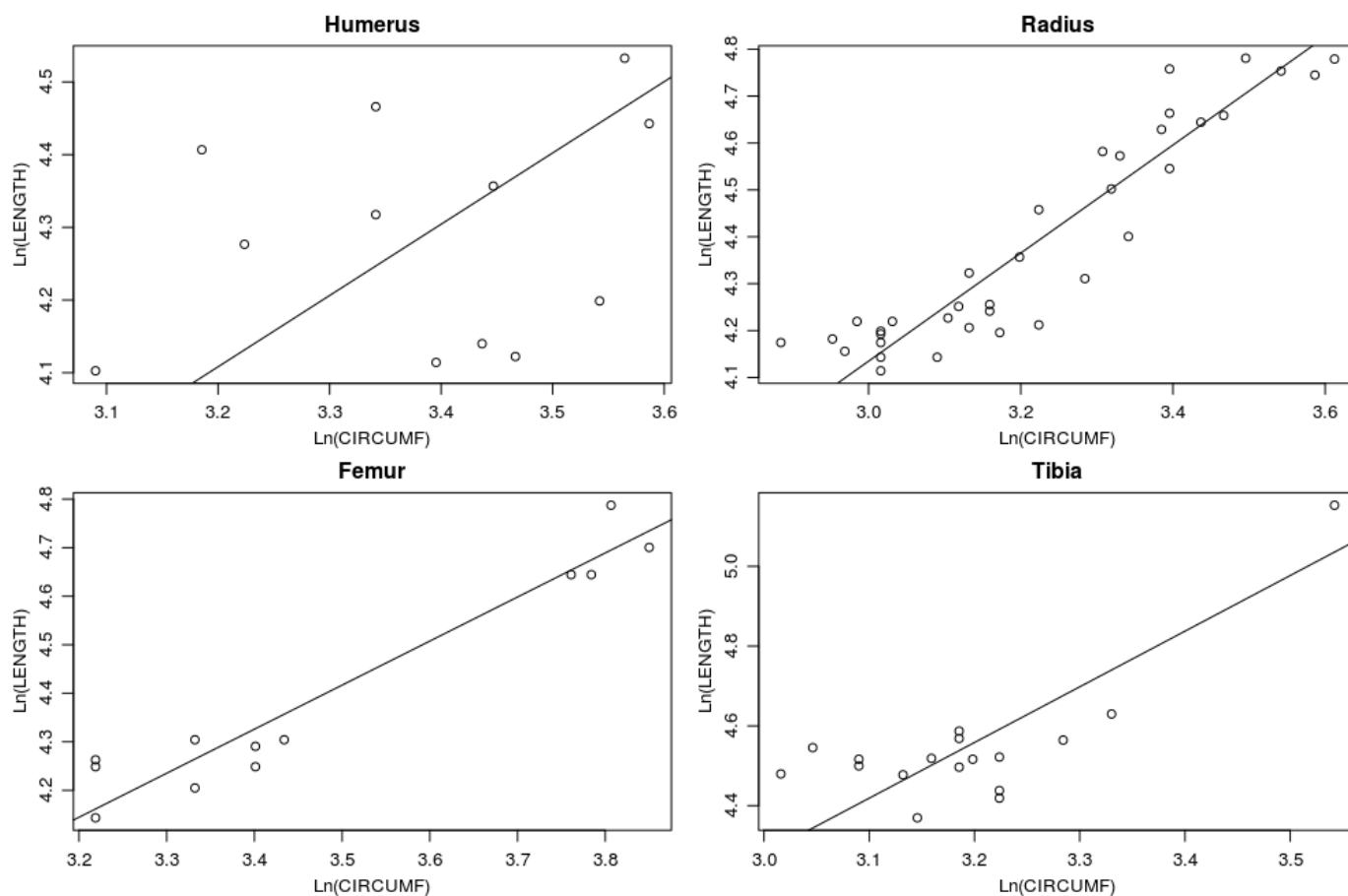
FIGURE 2. Log-log plots of the growth of *C. minor* from Rancho La Brea.

TABLE 1: Statistics of interspecific differences between *Capromeryx minor* and C. *arizonensis*.

Species	N	Mean L	%Decr.	Mean Circ.	%Decr.	Slope
HUMERUS						
C. arizonensis	16	110.7	20%	41.1	16%	0.956
C. minor	2	89.0		34.5		
RADIUS						
C. arizonensis	10	145.7	22%	38.8	21%	0.901
C. minor	4	114.0		34.6		
FEMUR						
C. arizonensis	8	156.5	30%	47.4	30%	0.998
C. minor	2	110.0		33.4		
TIBIA						
C. arizonensis	14	200.4	20%	42.9	14%	1.046
C. minor	1	173.0		34.5		

were about 14-30% shorter in *C. minor* than in *C. arizonensis*. The slope associate with interspecific dwarfing ranged from 0.901 to 1.046, essentially indistinguishable from the isometric slope of 1.0. These slopes were calculated from the means of the two samples, and since there are only two points, it is not possible to conduct error analysis or calculate confidence limits. However, these values are so close to isometry (especially if they are rounded) that isometry is the most likely interpretation.

The data for the ontogenetic growth sequence of *C. minor* are shown in Table 2. The slopes show no statistical difference from isometry in the humerus, femur, or ulna (Table 2). Only the radius was significantly more gracile than isometry and its lower confidence limit of 1.01 falls just outside the isometric slope of 1.0. It is interesting, however, that the scatter of the data varies widely from limb to limb. The data for the femur and radius had very tight coefficients of determination ($r^2 = 0.922$ and 0.866 respectively) while the data for the humerus ($r^2 = 0.063$) and the tibia ($r^2 = 0.591$) are much more scattered. We are not sure why this is so, because there is no obvious reason why some of the La Brea bones should give such scattered data, while others provide tight correlation. Perhaps they are more prone to taphonomic distortion, but there is no apparent problem with deformation of the specimens when examining them in the collections.

TABLE 2: Limb growth data of artiodactyls. N = number of specimens; CI = slope confidence interval limits; RMA = reduced major axis slope. (G) = gracile; (I) = isometric; (R) = robust. *C. minor* results from this study; *Antilocapra americana, Odocoileus virginianus* (white-tailed deer), *Okapia johnstoni* (okapi), and *Connochaetes taurus* (wildebeest) data from Kilbourne and Makovicky (2012).

TAXON	N	R²	CI	RMA
Humerus				
C. minor	13	0.063	0.52, 1.85	0.98 (I)
A. americana	19	0.946	0.63, 0.82	0.75 (R)
O. virginianus	23	0.960	0.94, 1.11	1.03 (I)
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				
C. minor	36	0.866	1.01, 1.31	1.15 (G)
A. americana	18	0.858	0.65, 1.09	0.87 (I)
O. virginanus	12	0.965	0.77, 1.02	0.89 (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				
C. minor	12	0.922	0.75, 1.10	0.91 (I)
A. americana	18	0.955	0.73, 0.92	0.85 (R)
O. virginianus	23	0.961	1.02, 1.21	1.13 (G)
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				
C. minor	17	0.591	0.98, 1.97	0.1.4 (I)
A. americana	17	0.932	0.69, 0.97	0.89 (R)
O. virginianus	20	0.962	0.80, 0.98	0.90 (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)

DISCUSSION

The isometric change in limbs as dwarfing occurred is a bit surprising, since Prothero et al. (this volume) noted that the limbs of *C. minor* appeared to be a lot more slender proportionately than the limbs of larger pronghorns, and it might be expected that the limbs would grow more gracile as the body mass decreased and an allometric tendency toward more gracile limbs would be the result. Instead, their size decrease occurred without any allometric change in shape. This contrasts with what Prothero and Sereno (1982) found with dwarfed hippos and dwarfed rhinos.

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 2, 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 ruminant. Such also is the case of the limbs of *C. minor*, with the exception of the radius which just missed being isometric within the confidence limits of the analysis—but many of the animals in Table 2 have even more robust, and even more gracile, growth trends in the radius, so there is quite a bit of variability around the expectation of isometry.

CONCLUSION

As 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 is true of the growth of pronghorns such as *Capromeryx minor* as well. Interestingly, recent studies have also shown that dwarfing typically tend to be isometric rather than allometric, whether it be in pygmy mammoths or dwarf pronghorns analyzed in this study.

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