

# ONTOGENETIC GROWTH IN THE PLEISTOCENE PRONGHORN *STOCKOCERAS* FROM SAN JOSECITO CAVE, MEXICO

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**Abstract**—San Josecito Cave, Nuevo Leon, Mexico, produced large samples of adult and juvenile bones of the Pleistocene pronghorn *Stockoceras conklingi*. The abundance of juvenile specimens allows the determination of the growth trends in ontogeny, and comparison of the growth trends in other pronghorns. We measured the four main limb bones (humerus, radius-ulna, femur, tibia), taking both the length of the bone (minus epiphyses in juveniles) and the midshaft circumference (following the conventions of Kilbourne and Makovicky, 2012). The Reduced Major Axis (RMA) fit was then calculated for all four limbs using both R and PAST software. RMA is more appropriate than a Least Squares Correlation because there is no dependent or independent variable. 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 (humerus slope = 0.82; radius-ulna = 0.73; femur = 0.88; tibia = 0.89). The RMA run in R software determined that all four limbs were significantly more robust, but in the PAST software, only the radius-ulna was significantly distinct from the isometric slope of 1.0, using 95% bootstrapped confidence intervals. 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.

## 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, scientists have focused on whether animals maintain the same limb proportions as they grow larger (isometric growth), or if some parts grow faster than others (allometric growth). Allometric growth in limbs has been especially well studied (McMahon, 1973, 1975; Alexander, 1977; Maloij et al., 1979; Alexander et al., 1979). For example, when a small animal grows to huge size, the limbs must grow more robust to support the greater body weight, because mass increases as a cube, whereas linear dimensions do not increase as fast. 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 the isometric slope of 1.0 (given their confidence intervals). All four limbs in the pygmy mammoth show isometric rather than allometric growth, contrary to commonly held expectations that proboscideans should 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. By contrast, Herridge (2010) found isometric growth in all four limbs in the Mediterranean dwarf elephants and mammoths.

However, proboscideans, hippos, and rhinos are all graviportal. What about cursorial mammals? Examples of taxa that have good samples of juvenile bones that allow us reconstruct a growth series are rare, but there are some cases. The collections of the Pleistocene pronghorn *Stockoceros conklingi* from San Josecito Cave in Nuevo Leon, Mexico, is particularly suited to this kind of study, since there are not only hundreds of adults, but quite a number of juvenile bones as well (Furlong, 1943). Detailed study of San Josecito Cave was undertaken by Arroyo-Cabrales (1994). The fossils from San Josecito Cave have been radiocarbon dated at 45,000-70,000 Ka (Arroyo-Cabrales et al., 1995). More recent work on San Josecito Cave was published by Chadeux et al. (2009).

## METHODS

We measured as many complete unbroken limb elements (humerus, radius, femur, tibia) of *Stockoceros conklingi* as we could find in the collections of the Natural History Museum of Los Angeles County. Sample sizes were 105 humeri, 122 radius-ulnae, 64 femora, and 60 tibiae. Some were measured by White using conventional calipers. Others were measured by Olson using 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 to 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 (from White's original data) 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 on a log-log plot. The size range of our sampled individuals spans more than one order of magnitude, so



FIGURE 1. Growth series of humeri of *Stockoceros conklingsi* from San Josecito Cave, with calipers for scale.

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). We also ran the same data with the PAST Paleo Stats software package (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 in Figure 2. As can be seen from Table 1, nearly all the statistics (whether run in R or in PAST) give a slightly negative (= greater robustness with increasing size) growth slope. In the R analysis, all of these slopes are significantly different from the isometric slope of 1.0, as shown by the confidence intervals, which do not include the value of 1.0. Thus, all four limbs are more robust than might be expected under the assumption of isometric growth. In the PAST analysis, the slopes are identical or almost identical to those calculated in R (except for the humerus), but the error estimates of the slope are slightly larger. These error estimates include the slope of 1.0 in the humerus, femur, and tibia, so these three limbs cannot be said to be significantly more robust than expected for isometry.

## DISCUSSION

The more robust growth in limbs as *Stockoceros conklingsi* grew is a bit surprising, since Prothero et al. (2021) noted that the growth in the limbs of *Capromeryx minor* were mostly isometric or gracile because pronghorns are highly cursorial animals whose limbs might be expected to grow more slender and gracile as they get larger and longer-legged. In addition, it might be expected that the limbs would grow more gracile as the body mass increased and an allometric tendency toward more gracile limbs would be the result. Instead, their growth was decidedly allometric with a significant trend toward greater robustness. These differences between dwarf pronghorn *C. minor*

TABLE 1. 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. *S. conklingsi* from this study, calculated in the R software package and the PAST (P) software package; *Capromeryx minor* from Prothero et al. (2021); *Antilocapra americana*, *Odocoileus virginianus* (white-tailed deer), *Okapia johnstoni* (okapi), and *Connocchaetes taurus* (wildebeest) data from Kilbourne and Makovicky (2012).

TAXON	N	r <sup>2</sup>	CI	RMA
<b>Humerus</b>				
<i>S. conklingsi</i> (R)	105	0.536	0.75, 0.97	0.82(R)
<i>S. conklingsi</i> (P)	105	0.536	0.65, 1.05	0.85 (I)
<i>C. minor</i>	13	0.063	0.52, 1.85	0.98 (I)
<i>A. americana</i>	19	0.946	0.63, 0.82	0.75 (R)
<i>O. virginianus</i>	23	0.960	0.94, 1.11	1.03 (I)
<i>O. johnstoni</i>	20	0.982	1.16, 1.37	1.26 (G)
<i>C. taurus</i>	14	0.976	0.65, 0.77	0.71 (R)
<b>Radius-Ulna</b>				
<i>S. conklingsi</i> (R)	122	0.851	0.68, 0.78	0.73(R)
<i>S. conklingsi</i> (P)	122	0.851	0.68, 0.81	0.73(R)
<i>C. minor</i>	36	0.866	1.01, 1.31	1.15 (G)
<i>A. americana</i>	18	0.858	0.65, 1.09	0.87 (I)
<i>O. virginianus</i>	12	0.965	0.77, 1.02	0.89 (I)
<i>O. johnstoni</i>	12	0.955	0.95, 1.43	1.21 (G)
<i>C. taurus</i>	13	0.988	0.81, 0.99	0.86 (R)
<b>Femur</b>				
<i>S. conklingsi</i> (R)	64	0.936	0.82, 0.93	0.87(R)
<i>S. conklingsi</i> (P)	64	0.936	0.79, 1.03	0.87(I)
<i>C. minor</i>	12	0.922	0.75, 1.10	0.91 (I)
<i>A. americana</i>	18	0.955	0.73, 0.92	0.85 (R)
<i>O. virginianus</i>	23	0.961	1.02, 1.21	1.13 (G)
<i>O. johnstoni</i>	20	0.970	1.7, 1.43	1.31 (G)
<i>C. taurus</i>	15	0.989	0.92, 1.01	0.96 (I)
<b>Tibia</b>				
<i>S. conklingsi</i> (R)	60	0.844	0.80, 0.99	0.892 (R)
<i>S. conklingsi</i> (P)	60	0.844	0.61, 1.10	0.892 (I)
<i>C. minor</i>	17	0.591	0.98, 1.97	1.04 (I)
<i>A. americana</i>	17	0.932	0.69, 0.97	0.89 (R)
<i>O. virginianus</i>	20	0.962	0.80, 0.98	0.90 (R)
<i>O. johnstoni</i>	21	0.977	1.16, 1.41	1.29 (G)
<i>C. taurus</i>	14	0.989	0.82, 0.93	0.88 (R)

and the much larger *S. conklingsi* likely reflect the difference in adult size of the two species or a different adaptation in feeding, and hence locomotor, strategies, or both. White and Morgan (2011) discussed the feeding ecology and social structure of *Capromeryx*, but did not make comparisons to *Stockoceros*.

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, the living pronghorn *Antilocapra americana* shows significantly more robust growth than expected in three out of four limbs, and the radius-ulna has a robust growth trend, but it is not significant (because the sample sizes are so small, only 17–19 individuals, in Kilbourne and Makovicky, 2012). Comparing the growth trends to other long-legged cursorial artiodactyls, such as the white-tailed deer, the okapi, and the wildebeest (Table 1), we find that they are mostly isometric, while some are robust and some are gracile, with no consistent trend in any particular limb, or in any particular group of ruminants. In fact, many of the mammals studied by

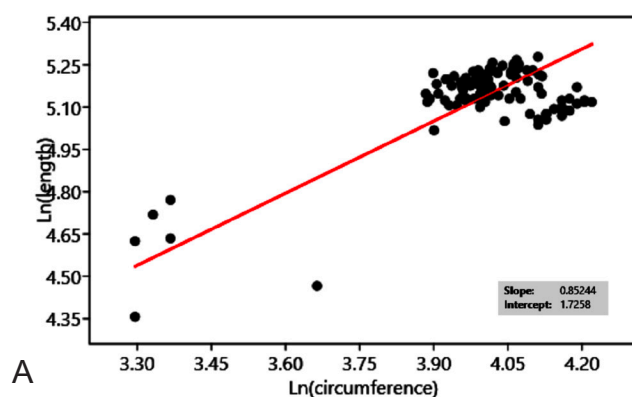
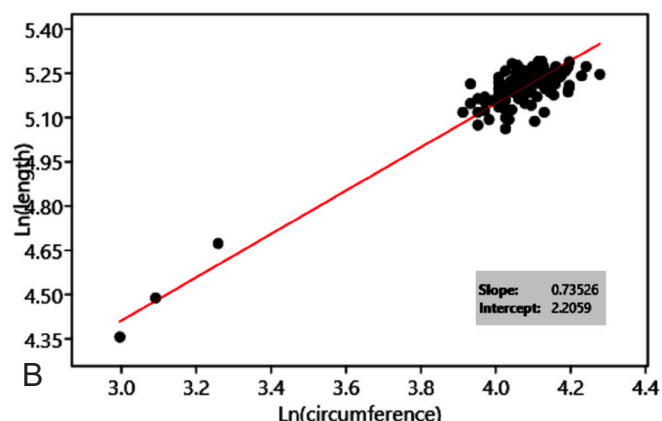
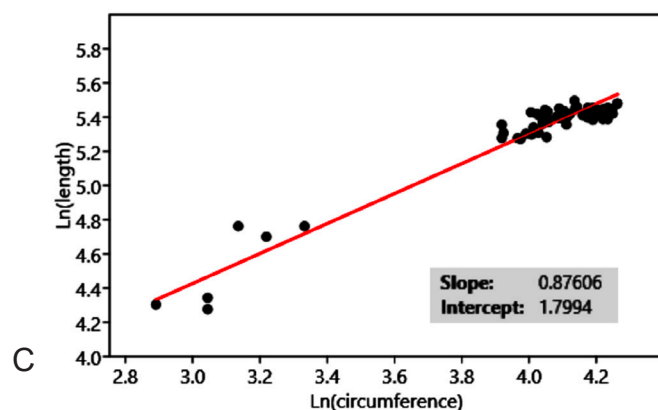
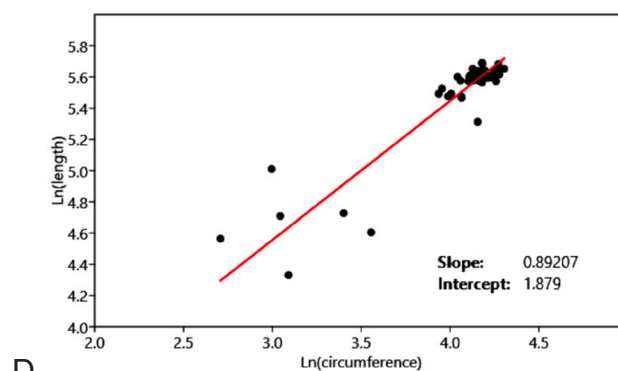
**Stockoceros Humerus****Stockoceros Radius/Ulna****Stockoceros Femur****Stockoceros Tibia**

FIGURE 2. RMA plots of the four primary limbs of *Stockoceros conklingi* from San Josecito Cave, with the line fit and slope shown as well. **A**, Humerus. **B**, Radius-ulna. **C**, Femur. and **D**, Tibia.

Kilbourne and Makovicky (2012) exhibit the extremes of long-bone allometric growth in the radius—in terms of both greater robustness and gracility—so there is quite a bit of variability around the expectation of isometry.

The R method and PAST method of calculating RMA slopes gave slightly different results for the same data, which is a bit surprising. The  $r^2$  values were identical, and the slopes were identical or nearly identical, but the biggest difference seems to be that the PAST consistently gave larger confidence intervals (CI) for the same data and the same slopes. Thus, all four limbs were significantly more robust than a slope of 1.0 in R because their small confidence interval excluded the slope of 1.0, but only one of the four limbs was significantly more robust in PAST (in other words, the confidence intervals for three out of four limbs included values greater than 1.0). We are not quite sure why this difference exists. For the humerus, it might be explained by the low  $r^2$  value (0.536) but for the femur the  $r^2$  was 0.936 and for the tibia it was 0.844, so this is not a satisfactory explanation. However, the  $r^2$  can be deceptive because the number of juvenile specimens is so small that the slope is strongly influenced by the scatter of the adult specimens (Fig. 2).

Perhaps the two different software routines are sensitive in different ways to the distribution of the data. In all our data sets, the data formed a large cluster of adults, and a smaller cluster of juveniles, with almost no subadult specimens in between. Perhaps the PAST software is more sensitive to odd distributions than the R software routine. Maybe they are calculated using

different confidence intervals, and not the standard 95% confidence interval.

## 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. However, the Pleistocene pronghorn *Stockoceros conklingi* grew with a negative allometry, in which the limbs got more robust as the animal grew, a surprising result for a gracile runner with cursorial limbs. However, the same trends appear in most of the limbs of modern pronghorns, *Antilocapra americana*, so this may be true of many antilocaprids. This contrasts with the dwarf pronghorn *Capromeryx minor*, which showed a tendency toward isometric or even gracile limbs as it grew, consistent with many other cursorial ruminants.

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