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**ALLOMETRIC TRENDS IN THE ONTOGENETIC GROWTH OF VARIOUS
PLEISTOCENE NORTH AMERICAN PROBOSCIDEANS AND THE
DWARFING OF COLUMBIAN MAMMOTH (*Mammuthus columbi*) THE
CHANNEL ISLANDS PYGMY MAMMOTH, (*Mammuthus exilis*)**

A Thesis

Presented to the

Faculty of

California State Polytechnic University, Pomona

In Partial Fulfillment

Of the Requirements for the Degree

Master of Science

In

Geological Sciences

By

Thein Htun

2020

SIGNATURE PAGE

THESIS: ALLOMETRIC TRENDS IN THE ONTOGENETIC GROWTH OF VARIOUS PLEISTOCENE NORTH AMERICAN PROBOSCIDEANS AND THE DWARFING OF COLUMBIAN MAMMOTH (*Mammuthus columbi*) THE CHANNEL ISLANDS PYGMY MAMMOTH, (*Mammuthus exilis*)

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ABSTRACT

Ontogenetic growth and phyletic dwarfing are both forms of body size alterations. Despite the former being an example of intraspecific, and the latter, interspecific size change, they are both subject to similar proportional changes known as allometry. They can become more robust or negatively allometric, gracile or positively allometric or undergo very little proportional change, also known as isometry. According to past studies, isometric growth trends are the most commonly observed in mammals, with positive allometry as the second most common. Furthermore, instances of phyletic dwarfing are often isometric or negatively allometric. Using methods devised by Kilbourne and Makovicky (2012) and Prothero and Sereno (1982), I tested for allometry in various North American proboscideans, more specifically, in the growth trends of the American mastodon, *M. americanum*, and the Channel Islands mammoth, *M. exilis*, and the dwarfing of the Columbian mammoth, *M. columbi* to the Channel Islands mammoth. I compared my results to similar past studied from which I found some unexpected results. I expected isometric growth in both the forelimbs and rear limbs of the American mastodon, but found that only the forelimbs were isometric, and the that the bones of the rear limbs grew with positive allometry in the humerus, and negative allometry in the tibia; which is a stark contrast from past studies, such as the one done by Kilbourne and Makovicky (2012) on modern African elephants, where they found that elephant limbs grew primarily with isometry. I reasoned it was the lack of the smaller neonates in my mastodon sample set as Kilbourne and Makovicky (2012) explained that a limited size range in a study can cause growth slopes to seem negatively allometric. I also found that the Channel Islands mammoth, while having isometric ontogenetic growth, became

more robust in their forelimbs as they dwarfed form their parent Columbian mammoth ancestor. This is also different from past studies on dwarf elephants, such as one done by Herridge (2010) where she found that Mediterranean dwarfed with isometry. This trend was possibly the result of the steep topography of the Channel Islands, and that robust forelimbs are not an uncommon adaptation in mountain-dwelling mammals. I speculated that the dwarfing was the result of heterochronic evolution that favored individuals that matured during what would be the smaller neonate stage of growth, when they would have more robust limb and reinforced limb bone growth trends, a form of paedomorphism. The results of both studies can be further understood with the use of histological techniques in future projects, from which it will be possible to ascertain differences of characteristics such bone density, ages and structural strength between different ontogenetic stages and species.

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GLOSSARY OF BIOLOGICAL TERMS FOR GEOLOGISTS s

Ontogeny: The growth and development of an organism throughout its life

Heterochrony: Pertains to the timing of development of certain traits throughout the growth of an organism

Allometry: The rates at which parts of an organism's body grows, and the associated changes in proportion

Isometry: Little to no change to proportion as an organism grows

Histology: Study of the structure of biological tissue at the microscopic level

Paedomorphism: Juvenile traits retained in adults

Proboscidea: The taxonomic order that includes all elephants

Phylogeny: Pertains to the evolutionary relationships between organisms

Diaphysis: The length of the shaft of a bone between the articular ends

Taxon: One or more populations of organisms that comprise a singular biological unit

Humerus: Upper arm bone that articulates with the scapula on the proximal(closer) end and with the radius and ulna on the distal(farther) end

Ulna: Lower arm bone that articulates with the humerus on the proximal end and carpals on the distal end; found in conjunction with the radius bone

Femur: Upper rear limb bone that articulates with the pelvis on the proximal end and the tibiae on the distal end

Tibia: Lower rear limb bone that articulates with the femur on the proximal end and the tarsal bones on the distal end

Osteon: cylindrical structural units that bones are comprised of

Artiodactyl: Mammalian taxonomic group defined by their even number of toes

Insular: Pertaining to islands

INTRODUCTION

ALLOMETRY AND SIZE INCREASE

When terrestrial tetrapods grow throughout their ontogeny, they undergo various physiological alterations in response to their size increase. For instance, their skeletal structure experiences growth in linear dimensions and density. As a result, their bones undergo modifications such as an increase in the number of osteons (Fig. 1) per area and greater cross-section thickness to provide stronger structural support, as the larger size will increase the biomechanical stress act on the bones (Carrier 1983; Gould 1966). The nature of these changes, such as the degree to which proportions change throughout growth, can vary between different taxonomic groups and different ontogenetic growth stages within a species. The change in proportion throughout its growth is also known as allometry. Positive allometry is when the bones grow longer faster than they grow thick, in which they become more gracile, and negative allometry is when they grow thick faster than they grow longer, in which they become more robust (Fig. 2). When an organism undergoes little to no proportional change, this phenomenon is known as isometry, or isometric growth (Fig. 2).

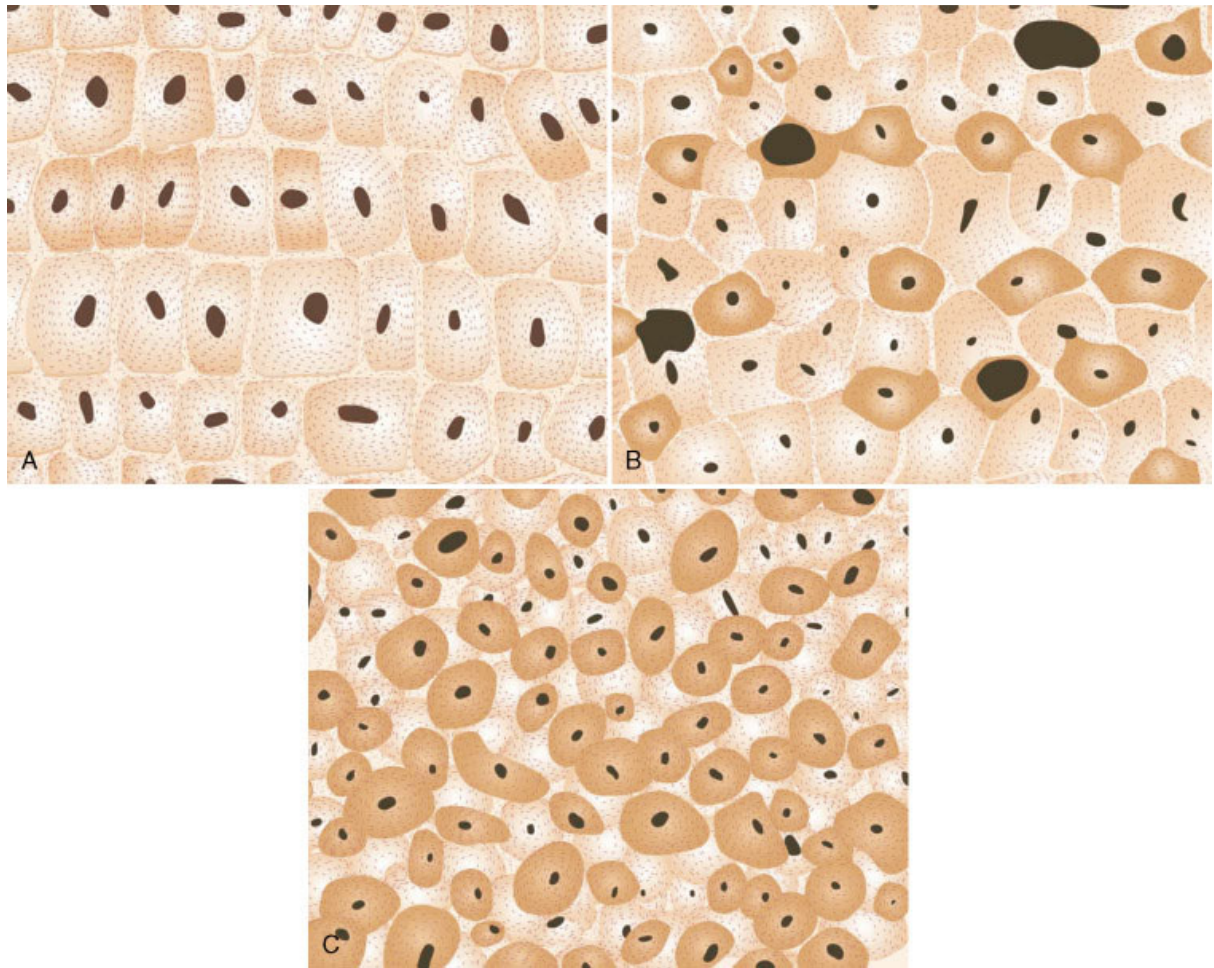


Figure 1: *Histological diagram of horse metacarpals at different ontogenetic stages, demonstrating changes in osteons per area. A. 54 day old neonate. B, 1-year-old juvenile C, 6-year-old adult (Adapted from Stover SM, et al.: Histological features of the dorsal cortex of the third metacarpal bone mid-diaphysis during postnatal growth in thoroughbred horses, J Anat 181:455, 199)*

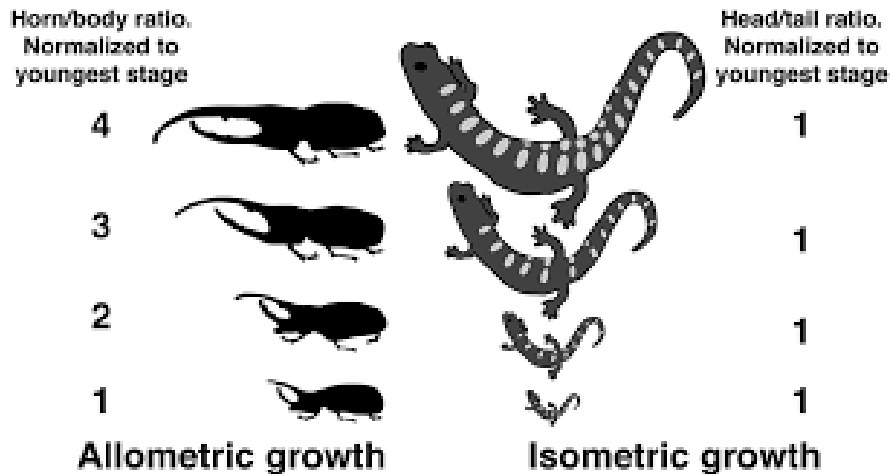


Figure 2: Left: Growth series demonstrating proportional changes in allometric growth. Right: Growth series representing little proportional change in isometric growth. (Adapted from Roselló-Díez, Alberto, and Alexandra L. Joyner. “Regulation of Long Bone Growth in Vertebrates; It Is Time to Catch Up.” *Endocrine Reviews*, vol. 36, no. 6, 2015, pp. 646–680., doi:10.1210/er.2015-1048)

It was a long-held belief that most mammals exhibit positive allometry, with various exceptions. Of these exceptions, it was thought that limb bones of large-bodied animals such as elephants underwent negative allometry to compensate for higher stress resulting from their greater mass. (Christiansen 2007). However, this notion was contradicted by Kilbourne and Makovicky (2012). They found that isometry is the most widespread with positive allometry as a very close second. They also found that the mode of growth often correlates with a variety of intraspecific and interspecific factors, ranging from stage of ontogeny, adult and birth mass, and type of metabolism. For instance, in a study about the growth of the bovid, *Ovibos moschatus*, Heinrich et al. (1999) reasoned that pre-juvenile neonates likely underwent negative allometric growth, then shifted to isometric growth when approaching adulthood, indicating that such mode of growth at an early age may have been to build up more robust morphology and later growth to maintain such

proportions to support its large size; this notion is supported by lower structural failure indices in mammalian neonates, as observed by Main and Biewener (2006) on a study of the safety factors of goat long bones. This was also observed by Long et al. (2018), who found that saber-toothed cat juveniles were born robust and grew with the normal trend that all other cats show until they reached adulthood. It is also pertinent to note that only a few limb allometry studies take into account the possibility of shifting modes; the few that have, have been limited to few species, mainly due to the lack of large sample sizes that also represent the entire ontogeny. More specifically, there is often a paucity of juvenile and neonate specimens. (Herridge 2010; Kilbourne and Makovicky 2012)

ALLOMETRIC TRENDS IN PROBOSCIDEANS

This study concerns the postnatal ontogenetic growth of different North American late Pleistocene proboscideans. Compared to most other mammalian groups, modern and recently extinct elephants are unique in that their limbs are kept in a near columnar stance during locomotion (Fig. 3). Consequently, their morphology is largely adapted to this locomotor style. With this gait, the limbs experience more axial stress and have reduced lateromedial bending range. As such, it would be reasonable to believe that to account for this increased stress, their limbs would grow increasingly more robust, or negatively allometric. However, in past studies, negative allometry has only been observed in a few species of elephants such as *Loxodonta africana* and *Elephas maximus* as observed in a study by Christiansen (2007). Those findings were contradicted by Kilbourne and Makovicky (2012). Using a much larger sample size, found that the mode of growth is mostly isometric, consistent with most other mammalian groups; they attributed this discrepancy to the lack of neonates in Christiansen's (2007) study, while their sample set

included them (Kilbourne and Makovicky 2012; Larramendi 2016). Using these past results, in this study, I will be comparing the growth curves of these elephants to that of the subjects of this study, of which are extinct mammoth and mastodon species. In addition, I will also be investigating proportional scaling associated with phyletic dwarfing, and how it compares to that of ontogenetic growth.

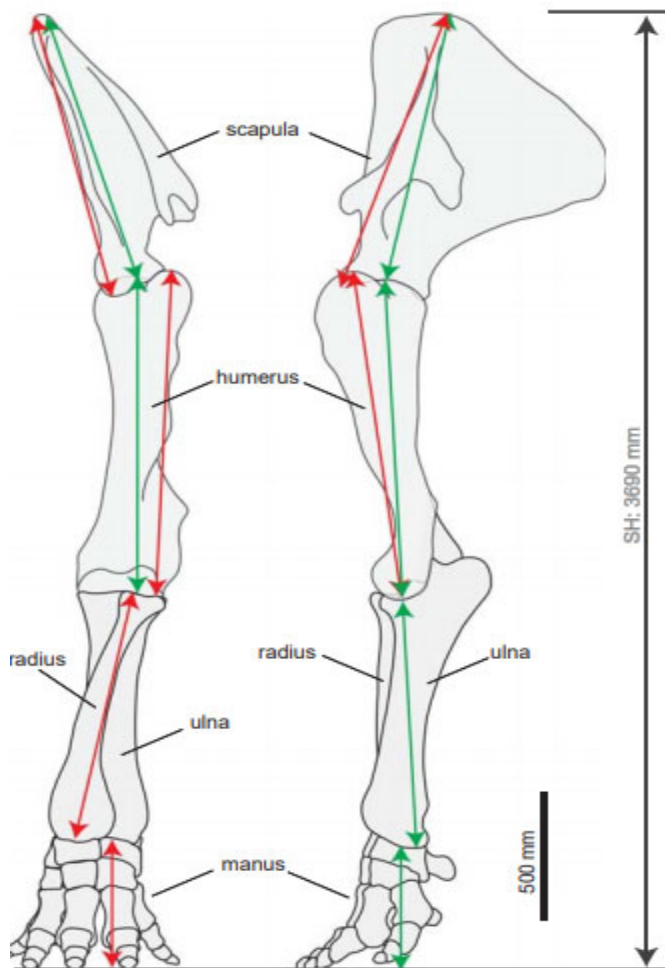


Figure 3: Diagram of a mammoth forelimb, demonstrating columnar profile (Adapted from Larramendi, A. 2016. Shoulder height, body mass, and shape of proboscideans. *Acta Palaeontologica Polonica* 61 (3): 537–574.)

PHYLETIC DWARFING AND ALLOMETRY

Phyletic dwarfing is the decrease in average body size of a species. It is often the result of a population of species becoming isolated in an area where selection pressures would favor smaller body sizes (Sondaar 1977). It is a phenomenon observed many times across different taxa, and proboscideans are no exception. Just as body proportions of an individual may change when undergoing ontogenetic growth, the overall body proportions of the dwarfed species may change compared to its ancestral species. As such, these changes can be isometric or positively/negatively allometric. Previous studies done on phyletic dwarfing in extinct mammals, such as one done by Prothero and Sereno (1982) on Pleistocene dwarfed hippos and Miocene dwarfed rhinoceroses have found that limb proportions became more robust or have negative allometry. However, studies of extinct dwarf proboscidean, such those done by Herridge (2010) on various Mediterranean dwarf elephants, have found that they had dwarfing slopes that trended isometric. In this project, I will be investigating the relationship between ontogenetic growth and dwarfing of the Channel Islands pygmy mammoth (*Mammuthus exilis*) from its mainland ancestor, the Columbian mammoth (*M. columbi*), and to the known growth trajectories of other proboscideans.

INSULAR DWARFING

As mentioned before, phyletic dwarfing is commonly observed in insular environments such as island environments. The ecological conditions associated with islands tend to be conducive to phyletic size change, due to new and different environmental conditions imposed by island environments. Smaller-bodied species tend to become larger, and larger-bodied animals tend to become smaller. This phenomenon, known as “Foster’s rule” or the “island effect/rule”, is a biological rule that explains the evolutionary trends of size changes in relation to amount of available resources (Foster 1964). The type of phyletic size reduction resulting from the conditions of Foster’s rule is known as insular or island dwarfism. One of the contentions of Foster (1964) is that when a population of a large-bodied animal species becomes isolated on an island environment, they are met with a series of environmental conditions that would be conducive to insular dwarfism. These conditions can be ecological challenges such as the reduced food supply and geographical range relative to the population’s original continental habitat. Such a reduction in food supply would create an environment in which selection pressures would favor individuals with smaller body sizes, as larger sizes would require more energy, and therefore more food to sustain itself (Sondaar 1977). At the same time, there could also be mitigations of other ecological challenges, such as reduced competition and predators that would otherwise make it no longer advantageous to have large body sizes. Insularity may also allow for traits that would otherwise be considered deleterious in the mainland environment, to be advantageous in island environments. Some small-bodied animals, such as various species of rodents, rabbits, shrews, and birds, can actually become larger. This phenomenon is called insular gigantism, and it results from the new environment

lacking factors such as predators, from whom a small body size would be advantageous to hide from. This would allow larger individuals to outcompete smaller ones, as they will have the size advantage (Foster 1964; Raia and Meiri 2007).

DWARFING AND HETEROCHRONIC EVOLUTION OF ONTOGENETIC GROWTH

There also may be connection between ontogenetic growth and phyletic dwarfing. Roth (1990), claims that size reduction of elephants is the result of heterochronic evolution. In other words, there was selection for individuals who were able to reach maturity faster and at smaller sizes. Such type of heterochronic evolution has been proposed to explain phyletic size change in other mammalian groups, such as the dwarfing of various late Miocene equids and some modern rabbits (Fiorello and German 1997; Oliveras et al. 2018). Studies of dwarf elephants have found evidence for paedomorphism, in which adults retain juvenile traits, such as proportion of different parts of the skull, while reaching reproductive maturity (Ambrosetti 1968; Palombo 2001). In addition, Raia et al. (2003) found evidence that the dwarf elephants species *E. falconeri* had faster life histories based on analysis of survivorship curves with a possible shift from r-selected to K-selected reproduction; this would indicate that dwarfism could be the result of positive selection for faster maturity, shorter life spans and higher/faster rate of reproduction.

EXAMPLES OF INSULAR DWARFING

The effects of Foster's rule have been observed multiple times across different clades in both the fossil record and extant taxa. However, it is among the larger megafauna, such as the proboscideans, rhinos, and hippos, that this trend is the most striking. For example, dwarfism has been observed in extinct and extant proboscideans at least 20 times (Aziz and Van de Bergh 1995; Herridge 2010). Furthermore, amongst hippopotamuses, there have been several instances of dwarfing, including at least one extant species (the living pygmy hippo, *Choeropsis liberiensis*), and amongst rhinos, at least three different species. (Prothero and Sereno 1982).

THE SUBJECTS OF THIS PROJECT

As I discussed earlier, the main subjects of this study of ontogenetic growth and phyletic dwarfing are going to be the various extinct proboscideans: the Channel Islands pygmy mammoth, *Mammuthus exilis* (Fig. 4A), their ancestral mainland species, the Columbian mammoth, *Mammuthus columbi* (Fig. 4B), and the distantly-related but contemporaneous American mastodon, *Mammut americanum* (Fig. 5A). The Columbian mammoth is a species of mammoths that lived in North America, except the polar regions, throughout the Pleistocene. They are close relatives of the smaller woolly mammoth, *Mammuthus primigenius* (Fig. 5B), and descendants of a population of steppe mammoths that migrated from Eurasia through the Bering Strait around the early Pleistocene, about 1.5 mya (Lister and Sher 2015). The Channel Islands pygmy mammoth are the dwarfed

descendants of the Columbian mammoth. A population of their ancestral species migrated to the Channel Islands, around the late Pleistocene, around

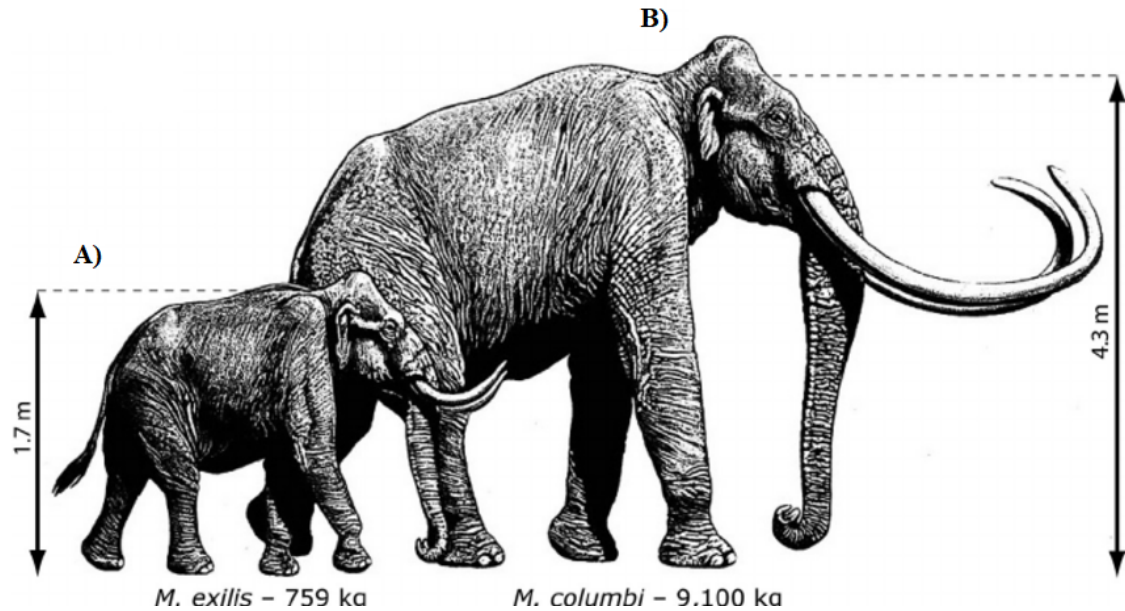


Figure 4:

- A) Channel Islands pygmy mammoth, *Mammuthus exilis*
- B) Columbian mammoth, *Mammuthus*

(Adapted from Semperebon, Gina & Rivals, Florent & Fahlke, Julia & Sanders, William & Lister, Adrian & Göhlich, Ursula. (2016). Dietary reconstruction of pygmy mammoths from Santa Rosa Island of California. *Quaternary International*. 406. 10.1016/j.quaint.2015.10.120.)

~120 ka, went extinct just prior other arrival of the first human inhabitants, around 13 ka, at the onset of the Holocene (Agenbroad 2001). The American mastodon, while superficially similar in appearance, are a part of a more primitive group of proboscideans whose lineage diverged (Fig. 6) from the last common ancestor of mammoths around the middle Oligocene (Shoshani 2005).

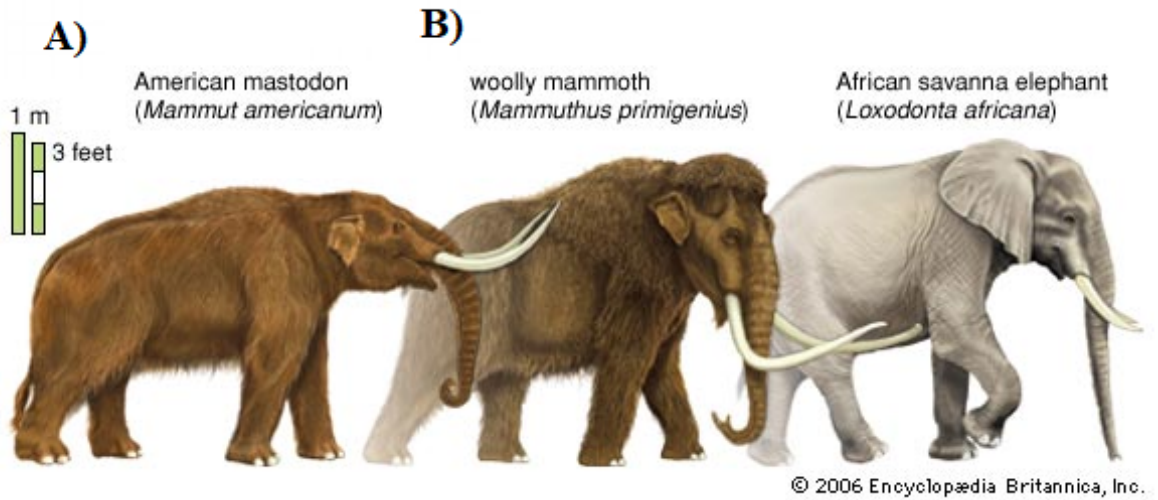


Figure 5: A) American mastodon, compared to other proboscideans B) Woolly mammoth (Adaped from Encyclopedia Britannica)

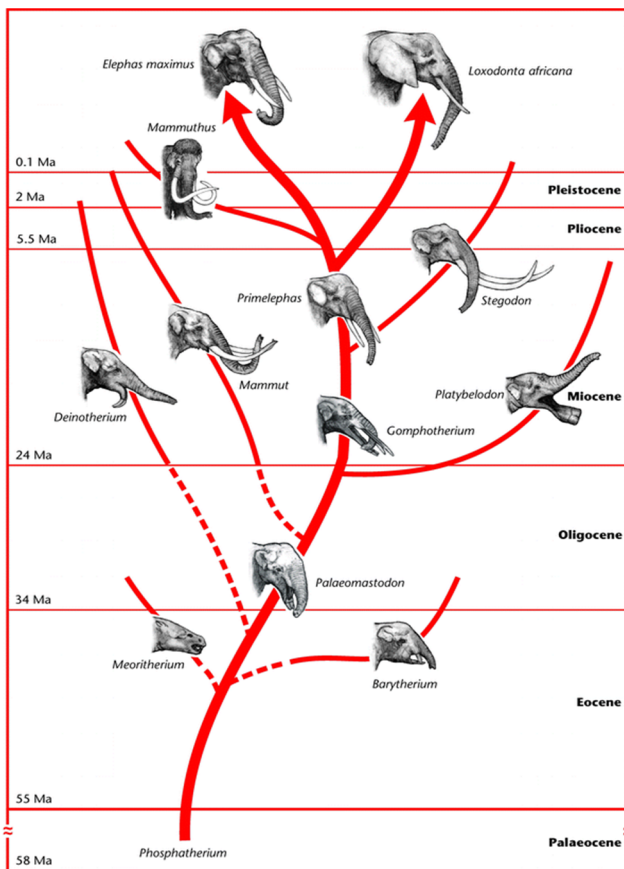


Figure 6: Phylogeny of Proboscidea; note the divergence in the middle Oligocene (Adapted from Shoshani (Jul 2001) Proboscidea (Elephants). In: eLS. John Wiley & Sons Ltd, Chichester. <http://www.els.net> [doi: 10.1038/npg.els.0001575])

THE GOALS OF THIS PROJECT

I will be comparing the growth trends of the limb bones of the different species.

Furthermore, I will also be comparing these growth trajectories with that of the dwarfing trends of Channel Islands mammoth from its continental ancestor. This will determine whether the rate of proportional changes associated getting smaller with dwarfism is comparable to the rate of getting larger during ontogenetic growth.

These types of studies are often hampered by the lack of specimens, as post-cranial elements seldom remain intact in large numbers and even more sparse are specimens of juvenile individuals of a species. (Juvenile bones tend to be thinner and more fragile, so they are usually destroyed and rarely known from most mammalian fossil species).

However, I was fortunate enough to be able to procure a relatively large collection of adult specimens of all of the species, and juveniles of the Channel Islands mammoth and American mastodon. While the museum collections I visited had an abundance of Columbian mammoth material, there was a shortage of juvenile limb elements. This lack of juveniles, unfortunately, made it impossible to determine an accurate ontogenetic growth trajectory for that one species. However, I still had plentiful adult specimens, which were needed to determine the dwarfing trend. Even more abundant was the American mastodon material; if anything, this is one of the largest sample sizes of this type of study done on any proboscidean.



Figure 7: *Map of the Channel Islands*

Adapted from USGS maps

GEOLOGICAL SETTING OF THE CHANNEL ISLANDS

In order to understand how the Channel Island dwarf mammoths became isolated and dwarfed, it is important to also understand the geological history and settings of their habitat. The Channel Islands are an archipelago, about ~18km off the coast of Ventura and Santa Barbara Counties in southern California (Fig. 7). They are a geographically isolated portion of the Transverse Ranges, which are a group of mountain ranges that share a common orientation of east-west (Fig. 8), which is different from the north-south orientation of other mountain ranges throughout California. This orientation is the result

of a complex of tectonic forces stemming from the relative motions of the Pacific and North American plates due to the San Andreas fault, which



Figure 8: Map of the Transverse Ranges. The Channel Islands are circled in black. Note the East-West orientation (adapted from USGS maps)

caused a clockwise rotation (Fig. 9) of the mountains (Hornafius et al. 1991). The island chain consists of 8 different islands. The islands from which the fossils were excavated are San Miguel, Santa Rosa, and Santa Cruz. The bones were primarily found in Pleistocene alluvial deposits that formed from dissected terraces (Stock and Furlong 1928). In terms of stratigraphy, the basement consists of pre-late Jurassic metavolcanics that were intruded by a late Jurassic plutonic complex and is overlain by alternating

sequences of marine and non-marine sandstones, interbedded with episodes of volcanism throughout the mid-Cenozoic (Dibblee 1982).

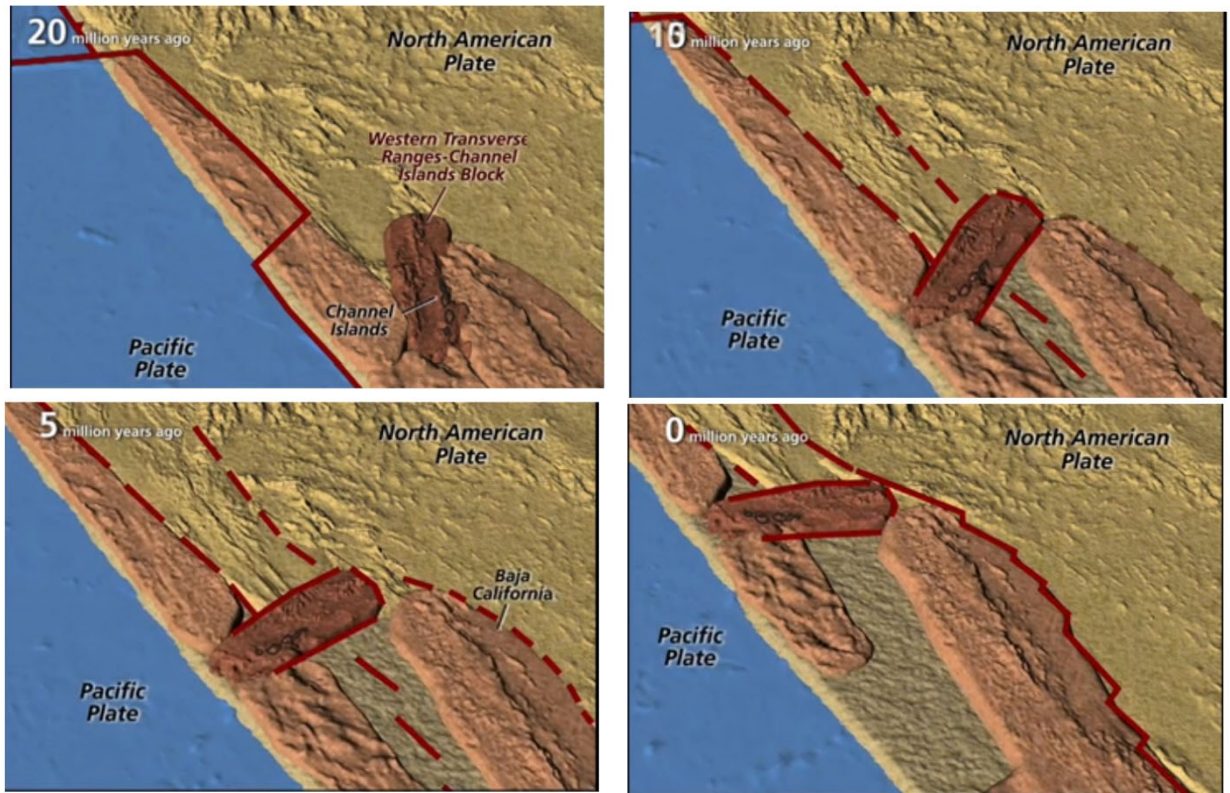


Figure 9: Chronology of the relative plate motions and rotation (Adapted from National Parks Service website animations)

PALEOCLIMATOLOGY

Probably one of the most crucial aspects of the biogeography of the dwarfed mammoths is the record of past climate change events. Like the rest of the world, the Channel Islands were subject to alternating glacial and interglacial events throughout the Pleistocene and

were likely the result of alternating changes of orbital eccentricity, tilt and precession known as the Milankovitch cycles (Berger 1988). These alternating cycles forced periods of glaciation which lasted about 100,000 years, coinciding with the changes in orbital eccentricity. However, prior to the mid-Pleistocene transition, glaciation cycles were likely forced by orbital precession, as evidenced by climatic shifts every 41,000 years, corresponding to the tilt or obliquity cycle. Periods of glaciation are often associated with oceanic regression; this reduction in sea levels and distance between the Channel Islands and the mainland facilitated the migration of Columbian mammoths onto the islands (Fig. 10). The gap between the mainland can be as narrow as 6 km, which is a short and easy distance of travel for the mammoths, since modern elephants have been known to swim considerable distances across oceans to reach islands (Johnson 1978).

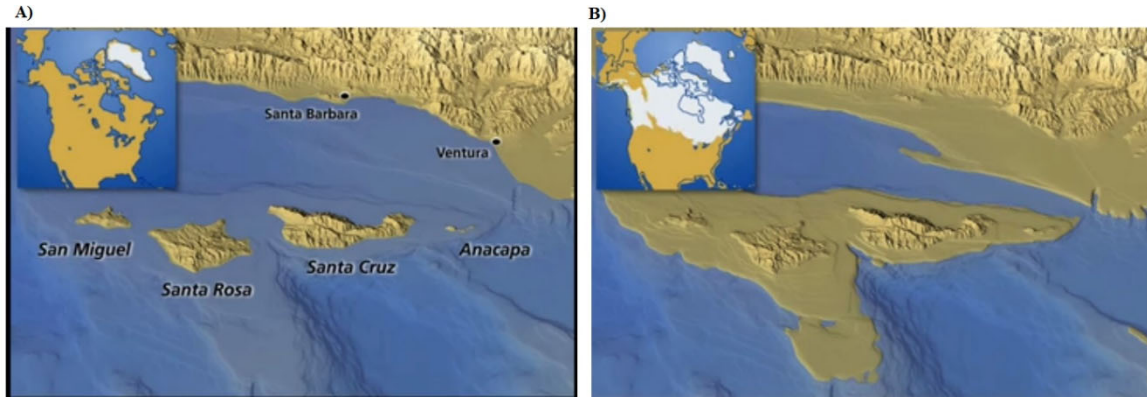


Figure 10: *Map of the Channel Islands during*

A) Interglacial period, with higher sea levels

B) Glacial period, with lower sea levels

(Adapted from National Parks Service website animations)

METHODOLOGY

The method for determining the growth and dwarfing trajectories was largely influenced by Kilborne and Makovicky (2012) and Prothero and Sereno (1982), respectively. To determine the growth trajectories, I measured both the length and circumference of all available juvenile and adult specimens, plotted the natural log of the measurements in a log-log graph, and determined the growth slope with the use of a RMA (Reduced Major Axis regression) analysis. This method also gave error estimates for each slope, so I could determine whether slopes were significantly different at the 95% confidence level. To determine the dwarfing slope, I averaged measurements of adult specimens, in the same manner as the previous method, of both the Columbian and Channel Islands pygmy mammoth plotted the data, and calculated the slope between these two means for different species. This is necessary, because it is inappropriate to confuse the intraspecific change within a single species with the intraspecific differences between two different species (Prothero and Sereno 1982). The resulting slope values is what I used to determine whether the trends are allometric or isometric.

I visited various many different fossil collections around the United States, including the American Museum of Natural History in New York, the University of Nebraska State Museum in Lincoln, Nebraska, the Natural History Museum of Los Angeles County, the La Brea Tar Pits Museum, the Santa Barbara Museum of Natural History, the New Mexico State Museum, and the Sternberg Museum in Hays, Kansas. In addition, I received data measured by colleagues from the Denver Museum of Nature and Science (especially from the Snowmass Mastodon Site), the Waco Mammoth Site, and the Hot Springs Mammoth Site in Hot Springs, South Dakota. I looked specifically for four types

of limb bones; in the forelimbs, I measured the humerus and ulnae; in the rear limbs I measured the femur and the tibia (Fig. 11). I measured every unbroken Columbian and Channel Islands dwarf mammoth limb bone I could find, as well as every American mastodon bone in their collections.



Figure 11: *The different limb bones; with scale bar and line that marks approximates the landmarks on the diaphyseal suture used for measurements*

- A) *Femur*
- B) *Humerus*
- C) *Tibia*
- D) *Ulna*

Using a flexible metric tape measure, I started by measuring the circumference of the bone at the midshaft to the nearest millimeter. Afterwards, I measured the diaphyseal length, which I considered to be length between the sutures that demarcate the articular

ends and the shaft (Fig. 11) for each type of bone. To keep measurements as consistent as possible, I chose two landmarks, one on each side of the diaphysis, to use as a point of reference when measuring. I kept the landmarks the same between the different specimens of each type of bone. In addition, I measured the epiphyseal length, which was the total length of the entire bone with the epiphyses fused to the ends, though this was not always possible as the articular ends are not always preserved, especially among juveniles as they have not completely ossified yet. If the bones were disarticulated, I would measure them on top a flat and level surface such as a table or their storage drawer(Fig 12). If the bones were articulated in an exhibit, I would measure them directly from the display (Fig 13).



Figure 12: *Measuring loose disarticulated bones*



Figure 13: *Measuring a Channel Islands pygmy mammoth directly from the display*

To test for error and reproducibility of the measurements, I conducted an experiment with some of the bones from the La Brea Tar Pits Museum. I measured the same bones ten times in a row, starting from a standing position and then crouching down on the floor to reach the key measurement landmarks, then returning to standing position and trying to measure the same dimensions in the same way. I then processed the measurements in

Excel to find the standard deviation. The results of this experiment are discussed and discussed in the Results section.

The statistical analysis used to test for allometry is the Reduced Major Axis (RMA) regression, also occasionally called the Standard Major Axis (SMA) regression. It is a commonly used regression analysis in the biological sciences to model growth trends. This method resolves various issues with the more commonly seen Least Squares Regression, which is the standard regression analysis used by most commercially available statistical programs such as Microsoft Excel. A significant advantage of RMA analyses has over the Least Squares regressions is that it makes no assumptions about which one is the dependent variable, and which one is the independent variable, whereas in Least Squares Regression must assume that one variable is independent and one variable is dependent. In addition, RMA accounts for the errors of both the horizontal and vertical distances, as opposed to the Least Squares which assumes that independent (horizontal) variables were measured without any error and thus only calculates the errors of the vertical axis (Harper 2014).

To perform this statistical analysis, I used R, which is an open-source programming language that is commonly used in the biological sciences. Before calculating the slopes, I uploaded my measurements into Excel, and converted them to the natural logs; doing so standardizes the measurements values to produce a linear slope. Nearly all size dimensions in biology are analyzed on log-log plots, because size is a dimension that increases exponentially, so linear plots do not reflect this. I proceeded to plot the natural log values with the values pertaining to the lengths on the x axis, and the values pertaining to the circumference on the y axis, which gave us the growth and

dwarfing slopes. I used the “smatr” library, which contained the script to perform the RMA analysis.

In the dwarfing analysis, if there is an overrepresentation of one of the species in relation to the other, as there was for the Columbian mammoth compared to the Channel Islands pygmy mammoth, it may end up causing the overall slope to be rather skewed trending towards the scaling of the overrepresented species. To remedy this issue, I calculated the mean values of each of the species sample sets and found the slope between them following the methods of Prothero and Sereno (1982).

Slope values significantly less than 1.0 (after comparing the error estimates of the slope calculated by the RMA program) are considered to be a negatively allometric, indicating that they became more robust over time; slope values significantly greater than 1.0 (again, after comparing the error estimates of the slope calculated by the RMA program) are considered to be positively allometric indicating that their proportions became more gracile over time and slope values of 1.0 or very close to is considered to be isometric (or not significantly different from 1.0, based on the error estimates calculated by the RMA program), meaning that proportions hardly changed over time.

RESULTS

ERROR ESTIMATION

Measurement reproducibility experiment: The methods of this experiment were discussed above. With the humerus, I got a standard deviation of 1.85, mean of 80.36 for the diaphysis and the circumference, 0.920 and mean of 32.75. The femur had standard deviation of 1.47 for the diaphysis with a mean of 63.41 and 0.171 for the circumference with mean of 33.49. The ulnae had standard deviation of 0.823, with a mean of 61.7 for the diaphysis and 0.497 with a mean of 34.55 for the circumference. The tibia had standard deviation of 0.831 with a mean of 80.36 for the diaphysis and .171 with a mean of 21.1 for the circumference (Table 4). These standard deviations are very small compared to lengths and circumferences of bones that are in the hundreds of millimeters, so they demonstrate that the measurement error is negligible. In addition, since the bones are plotted on log-log plots, such small differences are less important than they would be on linear plots.

COLUMBIAN MAMMOTH RESULTS

Even though there were plenty of adult and juvenile Channel Island pygmy mammoths and American mastodons, and an abundance of adult Columbian mammoth specimens, there was a shortage of the Columbian mammoth juvenile specimens. Because of this, all our growth slopes associated with the Columbian mammoths were

significantly negatively skewed. The humerus had a slope of 0.76 (Table 2), the ulna had a slope of 0.571 (Table 3), the femur had 0.76 (Table 4) and the tibia had a rather anomalous slope of -1.49 (Table 5). These slopes are not representative of a growth series of an ontogeny as they almost exclusively consist of adult specimens. Because of this issue, I considered these results to be unusable for the purpose of my analysis. In the future, I hope to find more juvenile specimens to fix these issues and get a proper slope.

CHANNEL ISLANDS MAMMOTH GROWTH TRENDS

We had enough juveniles of the Channel Islands pygmy mammoths to properly determine their growth trends. They tended to be isometric to negatively allometric (Tables 2-5). The humerus had an isometric slope of 1.09 (Table 2), the ulna had an isometric slope of 1.06 (Table 3), the femur was near isometric at 1.11 (Table 4) and the tibia was isometric at 0.89 (Table 5). (Error estimates and significance of each is shown in each of the tables).

MAMMOTH DWARFING TRENDS

The dwarfing slopes seemed to show quite a bit of variation. The slope associated with the humerus was 0.93 (Table 2), which is nearly isometric (based on the error estimates of the slope). The femur (Table 4) was near isometric at 0.95 (based on the error estimates of the slope). The ulna was significantly negatively allometric with a slope of 0.81 (Table 3). The tibia had a slope that was completely isometric with a value of 1.00 (Table 5).

MASTODON RESULTS

We also had plenty of juvenile specimens of the American mastodon. The forelimb elements were not significantly different from isometry, while in the rear limbs, the femur was positively isometric, while the tibia was significantly negatively allometric. The humerus (Table 2) had an isometric slope of 1.026 (not significantly different from isometric), the ulna (Table 3) had a slope of 0.909 (not significantly different from isometric), the femur was positively allometric with a slope of 0.1314 (Table 4) while the tibia had a negatively allometric slope of 0.789 (Table 5).

Table 1. *Calculated values pertaining to error estimation. STD = Standard deviation. D = Diaphyseal length. C= circumference*

All measurements are in cm

Bone type	STD(D)	STD (C)	Mean(D)	Mean(C)
Ulnae	0.823273	0.497214	61.7	34.55
Humerus	1.851246	0.920447	80.36	32.75
Femur	1.465492	0.08756	63.41	33.49
Tibia	0.831665	0.936898	64.45	21.1

Table 2. Data of various proboscidean humeri. *N* = total number of samples. *CI* = slope confidence interval limits; *AVG* = Slope between average of each species; *RMA* = reduced major axis slope; *SD* = standard deviation from error analysis. *SD(L)* = standard deviation of diaphyseal length; *SD(C)* = standard deviation of circumference. (*G*) = gracile; (*I*) = isometric; (*R*) = robust. Regression slopes of intraspecific growth. Mammoth dwarfing slope, calculated from the pooled data of *M. exilis* and *M. columbi* in two ways: *RMA* analysis from pooled data of all adults, and Average between the means of each species. R^2 = coefficient of determination.

Taxon	N	Y-int	AVG	R ²	P value	CI	RMA	SD(L)	SD(C)
								1.94	
<i>M. americanum</i>	29	0.326	1.003	0.957	< 0.0001	0.925,1.113	1.03(I)		
<i>M. exilis</i>	14	0.452	1.06	0.94	< 0.0001	0.94, 1.27	1.09(I)		
<i>M. columbi</i>	19	1.83	0.494	0.421	< 0.0001	0.52, 1.12	0.76(R)		
<i>L. Africana</i>	11	1.68		0.9	< 0.0001	0.62,1.03	0.90(I)		
<i>M. exilis</i> + <i>M. columbi</i> dwarfing <i>RMA</i>	30	1.68	0.754	1.68	< 0.0001	0.78, 1.12	0.93(I)		
<i>M. exilis</i> + <i>M. columbi</i> dwarfing means	2	1.58	0.757		< 0.0001				

Table 3. Data of various proboscidean ulnae. *N* = total number of samples. *CI* = slope confidence interval limits; *AVG* = Slope between average of each species ; *RMA* = reduced major axis slope; *SD* = standard deviation from error analysis. *SD(L)* = standard deviation of diaphyseal length; *SD(C)* = standard deviation of circumference. (*G*) = gracile; (*I*) = isometric; (*R*) = robust. Regression slopes of intraspecific growth. Mammoth dwarfing slope, calculated from the pooled data of *M. exilis* and *M. columbi* in two ways: *RMA* analysis from pooled data of all adults, and Least Squares analysis between the means of each species. R^2 = coefficient of determination.

Taxon	N	Y-int	AVG	R2	P value	CI	RMA	SD(L)	SD(C)
								0.823	0.497
<i>M. americanum</i>	24	0.724		0.795	< 0.0001	0.742, 1.115	0.909(I)		
<i>M. exilis</i>	11	0.452		0.879	< 0.0001	0.70, 1.17	0.91(I)		
<i>M. columbi</i>	12	0.452		0.82	< 0.0001	0.426, 0.767	0.57(R)		
<i>L. africana</i>	7	1.85		0.984	< 0.0001	0.63,0.95	0.86(R)		
<i>M. exilis</i> + <i>M. columbi</i> dwarfing RMA	12	1.06	0.538	0.9477	< 0.0001	0.72,0.91	0.81(R)		
<i>M. exilis</i> + <i>M. columbi</i> dwarfing means	2	1.58	0.757		< 0.0001				

Table 4. Data of various proboscidean femora. *N* = total number of samples. *CI* = slope confidence interval limits; *AVG* = Slope between average of each species ; *RMA* = reduced major axis slope; *SD* = standard deviation from error analysis. *SD(L)* = standard deviation of diaphyseal length; *SD(C)* = standard deviation of circumference. (*G*) = gracile; (*I*) = isometric; (*R*) = robust. Regression slopes of intraspecific growth. Mammoth dwarfing slope, calculated from the pooled data of *M. exilis* and *M. columbi* in two ways: *RMA* analysis from pooled data of all adults, and Least Squares analysis between the means of each species. R^2 = coefficient of determination.

Taxon	N	Y-int	AVG	R2	P value	CI	RMA	SD(L)	SD(C)
								0.823	0.497
<i>M. americanum</i>	24	0.724		0.795	< 0.0001	0.742, 1.115	0.909(I)		
<i>M. exilis</i>	11	0.452		0.879	< 0.0001	0.70, 1.17	0.91(I)		
<i>M. columbi</i>	12	0.452		0.82	< 0.0001	0.426, 0.767	0.57(R)		
<i>L. africana</i>	7	1.85		0.984	< 0.0001	0.63,0.95	0.86(R)		
<i>M. exilis</i> + <i>M. columbi</i> dwarfing RMA	12	1.06	0.538	0.9477	< 0.0001	072,0.91	0.81(R)		
<i>M. exilis</i> + <i>M. columbi</i> dwarfing means	2	1.58	0.757		< 0.0001				

Table 5. Data of various proboscidean tibiae. *N* = total number of samples. *CI* = slope confidence interval limits; *AVG* = Slope between average of each species; *RMA* = reduced major axis slope; *SD* = standard deviation from error analysis. *SD(L)* = standard deviation of diaphyseal length; *SD(C)* = standard deviation of circumference. (*G*) = gracile; (*I*) = isometric; (*R*) = robust. Regression slopes of intraspecific growth. Mammoth dwarfing slope, calculated from the pooled data of *M. exilis* and *M. columbi* in two ways: *RMA* analysis from pooled data of all adults, and Least Squares analysis between the means of each species. R^2 = coefficient of determination.

Taxon	N	Y-int	AVG	R2	P value	CI	RMA	SD(L)	SD(C)
								0.171	0.831
<i>M. americanum</i>	31	0.356	0.726	0.795	< 0.0001	0.680, 0.914	0.789 (R)		
<i>M. exilis</i>	30	1.15	0.778	0.753	< 0.0001	0.74, 1.08	0.89(I)		
<i>M. columbi</i>	22	1.67		0.228	< 0.0001	0.512, 1.14	0.763(R)		
<i>L. africana</i>	11	-2.63	-0.597	0.159	< 0.0001	-1.49,	-1.763		
<i>M. exilis</i> + <i>M. columbi</i> dwarfing RMA	41	1.38	0.888	0.896	< 0.0001	0.88, 1.14	1.00(I)		
<i>M. exilis</i> + <i>M. columbi</i> dwarfing means	2	3.38	1.111		< 0.0001				

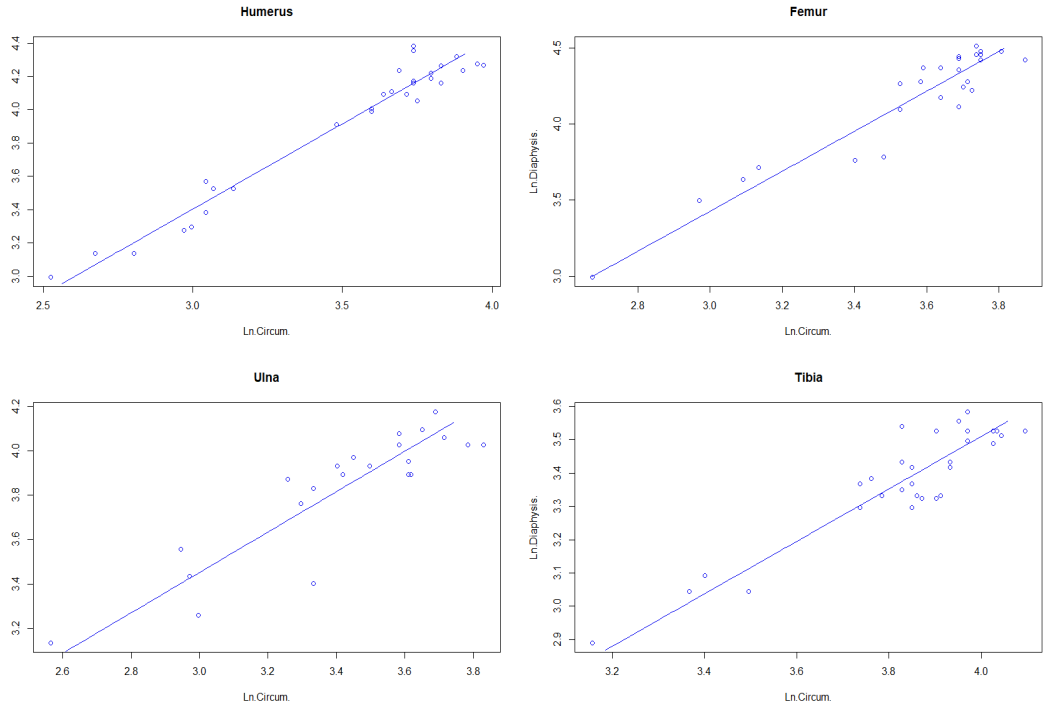


Figure 14: RMA regression plots of the mastodon bones. Associated slopes and confidence intervals can be found in table

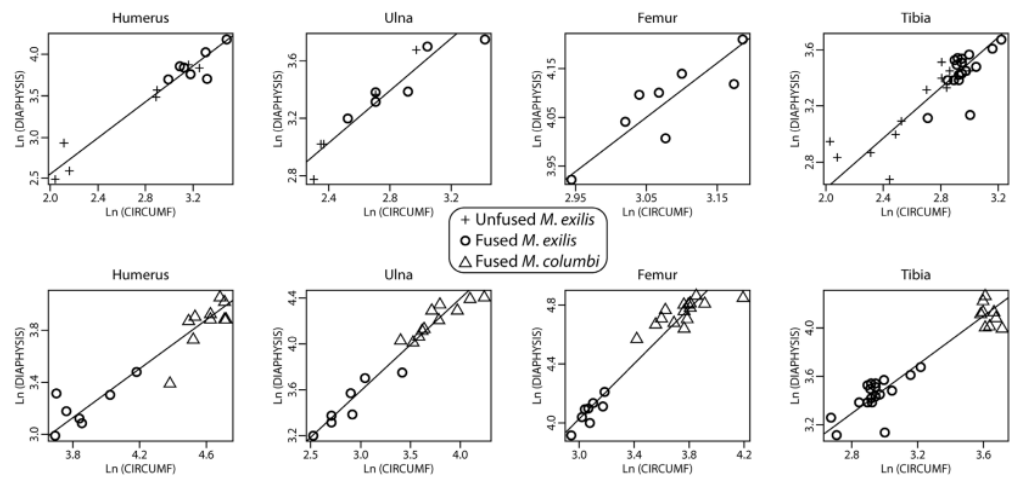


Figure 15:
 Top row: RMA growth slopes of the Channel Islands mammoth
 Bottom row: Dwarfing slopes of the pooled data of both the Columbian and Channel Islands mammoth

DISCUSSION

ERROR RESULTS DISCUSSION

I tested for reproducibility of my measurements for each type of limb bones; I measured each one 10 times and calculated the standard deviation. I found that there was relatively low variation in the circumferences of the humeri having a standard deviation of 0.9204 compared the higher variation of the diaphyseal length at 1.851. A similar trend also occurred in the ulnae, with a standard deviation of 0.497 for the circumference and 0.823 for the diaphyseal length. Similar trends were also observed in the femora, the diaphyseal length had a standard deviation of 1.465 while the circumference was 0.08756. In the tibiae, the diaphyseal length had a standard deviation of 0.171 while the circumference was 0.936. It seems like overall, there is a general trend of lower deviations in the circumference compared to their associated diaphysis measurement. I suspect that this variation is a result of the impression of the tape measure that I used, and possibly my hand not being the steadiest when measuring the length of the shaft, while it may have been easier to keep a steadier hand when measuring the circumference. Nonetheless, the deviation is quite low for all of the bones and statistically insignificant, being only a few millimeters of difference. When converted to natural logs and plotted, these small deviations make very little difference to the overall slope.

MASTODON RESULTS DISCUSSION

The slopes associated with the American mastodon seem to differ quite a bit from what I expected. I initially expected mostly near isometric growth, consistent with that of modern elephants, *Loxodonta africana*, as calculated by Kilbourne and Makovicky (2012) and other proboscideans (Johnson and Buss 1965; Laws 1966; Laws et al. 1970; Roth 1982, 1984, 1990; Raia et al. 2001). However, the results were quite different from what I expected. The humeri had a slope of 1.03 not significantly different from isometry, comparable to the isometric slope of the humeri of *L. africana* which has a value of 0.90. The ulnae had a slope of 0.909, not significantly different from isometric and rather different from the negative allometric slope of 0.86 of *L. africana*. In the hindlimbs, the femora had a slope of 1.314, which is significantly positively allometric and quite different from the slope of *L. africana*, which has a slope of 0.95 and not significantly different from isometric. Similarly, the tibia has a significantly negative allometric slope of 0.789 compared to the isometric slope of *L. africana* of 0.97.

The American mastodon exhibits negative allometry in the lower rear limb; it becomes more robust as it grows. This seems to be somewhat contrary to what I expected, as Kilbourne and Makovicky (2012) established in their analysis of the African elephant, *L. africana*, that like most mammalian taxa, proboscideans scale isometrically. Interestingly, Christiansen (2007) argued that elephants grew with negative allometry, though his study was criticized by Kilbourne and Makovicky (2012) for its relatively narrow size and age range. Kilbourne and Makovicky did a similar analysis, but with a sample set that included a wider range of ages, including neonates and overall a larger sample size. They found that because they included neonates in their study, they got isometric slopes;

without the neonates they would get negatively allometric slopes. As I found in my Columbian mammoth analysis, lacking smaller and juvenile specimens cause the slopes to skew very negative; although I had a large sample size, possible one of the largest of any proboscidean study of this type, I am likely running into the same problem that Christiansen(2007) did: having little not no neonates in my collection. As a result, this may have caused the tibia to have a very negatively allometric slope.

My analysis was done on a much larger sample size compared to Kilbourne and Makovicky's (2012) study; and while the slopes of the forelimbs had trends that were consistent with the results of Kilbourne and Makovicky in that they were mostly isometric, the rear limbs were quite different. The humerus had a positively allometric slope of 1.31, while the tibia was negatively allometric with a slope of 0.789.

Interestingly, the presence of neonates in their study increased the growth slopes to isometry while in my study, with the presence of neonates, my results yielded a negative = and positive growth slope in the rear limbs. However, this does not explain the presence of the positive growth slope of the femur; if anything, the lack of neonates should reduce all of the slopes to negative, and yet there is a positively allometric growth slope.

The lack of shifting growth trajectories, as proposed by Heinrich et al. (1999) may be an explanation for these trends. The musk oxen of the study by Heinrich et al. (1999) study underwent negative allometric growth due to their being born with relatively weak limb bones; after a certain point, when the bones become mineralized and more robust, the mode of growth shifts to isometry. The opposite could be the case here, where it's quite possible that much like the study of Long et al. (2018) of saber-tooth cats, the mastodons

were born with relatively reinforced bones, and as a result, underwent growth that underwent a form of growth that would not require it to reinforce the bones that much more. In other words, it could have undergone positive allometric growth; if the bones were reinforced from birth, positive allometric growth would not decrease the safety factors as much, and neither would there be a need for negative allometric growth to further reinforce the bones. It's also possible that in order to maintain proportions, this positive allometric growth is needed to compensate for the very negatively allometric growth of the tibia; though like I explained before, this negative allometric growth was calculated without the presence of neonate specimens, and thus may not accurately represent the true growth trend. It would be pertinent to find out how well reinforced these bones are, and to what extent, at different ontogenetic stages, especially to see if the femur is denser compared to the other limb bones. Future projects to resolve these issues should involve histology techniques for cross sectional analysis in conjunction with determining things such as failure indices and safety factors.

MAMMOTH RESULTS DISCUSSION

Because of the lack of juvenile Columbian mammoth specimens, I believe that comparing its growth slopes to that of the Channel Islands mammoths would not be a valid comparison due to its highly skewed values. This is unfortunate, as knowing whether the growth trends are allometric or isometric could help explain the dwarfing trends. However, I still had enough juveniles and adults of pygmy mammoths to

determine the dwarfing trends. The dwarfing slopes of the Channel Islands pygmy mammoth seemed to be near isometric in the hind limbs, with the femoral and tibia elements having slopes of 0.92 and 0.94, respectively (Table 3 and Table 4). This is largely consistent with past studies, such as one done by Herridge (2010), in which it was determined that the dwarfing of the various Mediterranean elephant limbs was largely isometric. The slopes of dwarfing in this case are quite similar to that of the ontogenetic growth slopes of the Channel Islands mammoth, with the femur having a slope of 1.11, and the tibia being near isometric with a slope of .89, but within the margin of error. These slope values are also consistent with that of most proboscidean growth trajectories.

The most surprising result of my results is how negatively allometric the dwarfing trends of the forelimbs were. The humerus had a near isometric slope of 0.93, the ulnae had a robust slope of 0.81. The slope of the ulna is a significant departure from its corresponding ontogenetic growth slope of 0.91. The humerus was closer to its corresponding growth slope of 1.09. Furthermore, these results are not consistent with that of other proboscidean dwarfing trends of the limbs, as they tend to be isometric (Herridge 2010). This would mean that the forelimbs of the Channel Islands mammoth would be proportionally shorter compared to that of its mainland ancestor.

The forelimbs being more robust contradicts the results of Agenbroad et al. (1999), which suggested that the forelimbs were proportionally longer compared to the rear limbs. In this case, the proportions of the forelimbs dwarfed with negative allometry, while the proportions of the rear limbs changed little. My study had a much greater number of specimens that were studied by Agenbroad et al. (1999), more than double the number of

ulnae, 11 (compared to 5), and thirty times the number of tibiae, 30, compared to 1. Furthermore, in a later study, taking cues from Sondaar (1977) and after a bone metric analysis, Agenbroad concluded that the Channel Islands mammoths do indeed have proportionally shorter forelimbs compared to their rear limbs (Agenbroad 2001).

A possible reason for this trend could pertain to the environment the mammoths lived in. The Channel Islands have a rather steep mountainous topography, consistent with that of the rest of the Transverse Ranges. In such an environment, having more robust forelimbs would be advantageous. Sondaar (1977) observed that many mammalian species that live in mountainous environments tend to have more robust forelimbs; he coined this phenomena as “Low Gear Locomotion”. Such form of locomotion is the result of proportionally shorter but thicker forelimbs. It is mechanically advantageous because the resulting gait would entail a lower center of gravity that would make the foot bones less prone to breakage due to reduced stress; this would be especially useful in mountainous environments, where the traversal of the steeper slopes would result in greater stress placed upon the forelimbs. This adaptation would however, result in lower running speeds for the animal due to the shorter limbs; however, being an insular environments and therefore lacking predators, the ability to move quickly to evade being preyed upon is no longer an advantageous trait. As mentioned earlier, this trend has been observed in many extinct and extant different mammalian taxa including various species of mountain goats and an extinct mountain dwelling camelid, *Capricamelus gettyi* (Whistler and Webb 2003). In addition, Sondaar (1977) noted at least one other species of proboscideans, a dwarfed species of *Stegodon* has been observed to also have robust

forelimbs; which was likely an adaptation to help exploit resources in more mountainous environments .

As I discussed earlier, the process of phyletic dwarfing is the result of heterochronic evolution. In the case studies of the various Mediterranean dwarf elephants, pedomorphic traits were commonly observed in mature individuals. There was also a marked shift towards faster and earlier maturation, to reproduce as early as possible in line with a shift towards r- selection reproduction (Raia et al. 2003; Herridge 2010). Thus, a possible explanation for the dwarfing of the Channel Islands mammoth is that perhaps there were selection pressures for Columbian mammoth individuals that matured quicker, perhaps during an earlier juvenile stage, more specifically. As I mentioned earlier, there is evidence for shifting modes of growth in mammalian ontogenies, with neonate growth primarily being defined by negative allometry. A possible explanation for the negatively allometric dwarfing is the ontogenetic truncation in which maturation occurs at an earlier state, perhaps a stage that is in between postnatal and a neonate stage. If Columbian mammoths neonates underwent negative allometric growth before shifting to isometric growth, the truncation of maturation occurring at some point between the neonate and juvenile stages, then it would make sense that the dwarf adults would have proportions and bone densities more in line with that of a younger juvenile or neonate of the parent species; hence possibly explaining why the forelimbs of the Channel Islands mammoth are more robust. The steep topography of the Channel Islands would place increased physical stress on the forelimbs, and in line with trends observed in other mammalian taxa, favor those with more robust forelimbs. Hence, it would make sense

that individuals that reached maturity during the neonate growth stage, when the structural failure indices were likely lower, would have an advantage.

However, the intraspecific scaling of Channel Island mammoths suggest that they underwent isometric growth for of all the limbs. This could indicate the Channel Island mammoths were born relatively robust. Perhaps one of the reasons why the Columbian mammoth individuals that underwent faster maturation is because they had relatively reinforced bones from birth, hence why their period of neonate negative allometric growth was shorter. As a result, their dwarfed descendants were more likely to have reinforced bones, especially in the forelimbs, hence why they grew with isometry, much like the saber tooth cats in the study of Long et al. (2018) study. It should be noted that the forelimbs dwarfed negatively allometric, while the rear limbs were isometric. I speculate that this could be explained by the intraspecific forelimb growth of the ancestral individuals being much more negatively allometric in relation to the rear limbs; such a phenomenon is possible in proboscidean growth trends, as observed in the slopes of the mastodon growth of this study. The growth trends of the ancestral Columbian species are currently unknown due to the lack of specimens; at this point I can only speculate on the relationship and differences between the intraspecific growth trends.

FUTURE PROJECTS

A series of potential future projects could elucidate these results. An obvious one is to obtain more juvenile Columbian mammoth specimens and get its growth trends. We have tried every museum and collection we could locate, but so far no one seems to have any unbroken juvenile Columbian mammoth limbs. A more substantial project can involve the use of histological techniques; mainly to observe bone densities/osteons per area.

More specifically, I would like to determine the ages and sizes at which the differing bone densities occur. From these observations, it would be perhaps pertinent to compare the bone densities of specimens from different species that are similar in size (i.e., an adult of the Channel Islands mammoth, and a smaller juvenile of a Columbian mammoth). Furthermore, it would also be useful to compare specimens of similar ages from the two species, via observing the CGM (cyclical growth marks); in doing so, it may be possible to gain further evidence to support the idea that dwarves are the result of maturation at an earlier life stage. A similar study was undertaken by Oliveras et al, (2018), in which they were able to determine, based on histological analysis, that the dwarfing of various species of hipparionins were the result of the heterochronic evolution of maturation.

It is quite possible that the Channel Island mammoths are born with more reinforced bones, especially in the forelimbs, hence why they don't really become more robust as they grow. It would be possible to use cross sectional data from the bone histology to determine failure indices or safety factors. If the Channel Island mammoths bones, especially those attributed to the younger individuals, have relatively high safety factors compared to their ancestral species at comparable ontogenetic stages and sizes, it would further lend credence that the Channel Island mammoths were born with more reinforced bones. Although the dwarf mammoth sample set lacked limb neonate limbs, there are other neonate cranial and post cranial elements in the collections. Those specimens may be of interest for histological studies, as they may provide some insight on the bone densities of Channel Island mammoth neonates.

CONCLUSIONS

I investigated the growth trends of the limb bones of various North American Pleistocene proboscideans, and the dwarfing of the Columbian mammoth to the Channel Islands mammoth. I found that the ontogenetic growth of the American mastodon seem to differ markedly from my expectations. I expected isometric growth for all the limbs, in line with most mammalian taxa. However, the results seem to show that only the forelimbs grew with isometry, and that the rear limbs grew positively and negatively allometric, in the femur and tibia, respectively. I reasoned that this is due to the lack of neonates in my sample. In a similar study, using the same methods on modern African elephants, Kilbourne and Makovicky (2012) found that the lack of neonates in a sample set can cause a growth slope to skew more negative. This however, only explains the negative allometry of the tibia, but not the humerus; I speculated that this may be related to how reinforced the bone is at birth, and that it perhaps could have grown with positive allometry, while still maintaining a relatively high safety factor.

The Channel Islands mammoth had isometric intraspecific scaling, as I expected. However, I found that when the Columbian mammoths dwarfed to the Channel Islands mammoth, the forelimbs become more robust, while the rear limbs scaled isometrically. I speculate that the reason for this trend is that the steep-sloped environments of the Channel Islands would favor a low gear locomotion that would result from more robust forelimbs as such similar instances have been observed in other mammalian species that live in mountainous areas. I argued that the mechanism for this kind of dwarfing is the result of heterochronic evolution, in particular, the result of a shift to earlier and faster maturation that would occur in an early ontogenetic stage, particularly, during the

neonate stage, when they are possibly undergoing negatively allometric growth, as argued by Heinrich et al. (2007), before it shifts to isometry. As a result of maturing at growth stage when they are undergoing negative allometry, they would have proportions and bone densities that are more in line with a neonate, essentially a form of paedomorphism. However, due to the lack of neonate limb specimens of both the parent and dwarf species, this is still largely speculation, and will require further investigation, possibly involving the use of other skeletal elements not covered in this study.

Histological analyses could be useful in future studies. My proposed explanations for my results often relate to factors such as bone density, age and ontogenetic stage; all of which can be determined from cross sectional analysis. Furthermore, I can also apply these techniques to specimens that couldn't be included in this study, such as broken limb bones, as they can now be used without the presence of an intact diaphysis and non-limb elements belonging to individuals of a poorly represented ontogenetic stage, like a cranium of a Channel Islands mammoth neonate.

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