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CHRONOCLINAL VARIATION AND SEXUAL DIMORPHISM IN *MAMMUT AMERICANUM* (AMERICAN MASTODON) FROM THE PLEISTOCENE OF FLORIDA

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CHRONOCLINAL VARIATION AND SEXUAL DIMORPHISM IN *MAMMUT AMERICANUM* (AMERICAN MASTODON) FROM THE PLEISTOCENE OF FLORIDA

Jeremy L. Green[1]

ABSTRACT

This study quantitatively and statistically analyzes chronoclinal variation in *Mammut americanum* fossils over a broad temporal range (~1.5 Ma to 10,000 year BP). A large sample of elements (third molars, mandibles, limb bones) from the Irvingtonian and Rancholabrean of Florida were measured and statistically compared for significant differences. Rancholabrean elements are generally found to be significantly larger than Irvingtonian elements. Florida *M. americanum* shows directional selection for increased body mass from the Irvingtonian to the Rancholabrean. Anterior mandibular height is the only measurement that demonstrates significant sexual dimorphism in Rancholabrean individuals, with males having a larger anterior mandibular height than females. Mandibular tusk presence/absence ratios in Florida *M. americanum* show directional selection against these small tusks from the Irvingtonian to the Rancholabrean. *M. americanum* demonstrates a heterochronic increase in growth rate at the onset of puberty from the Irvingtonian to the Rancholabrean. In addition, Rancholabrean *M. americanum* populations also exhibit holobiotic heteromorphism, with males growing at a faster rate than females. The results of this study demonstrate that throughout its ~1.5 Ma range in Florida, *M. americanum* was not static in its evolution.

Key Words: *Mammut americanum*, Florida, Pleistocene, morphologic evolution, sexual dimorphism.

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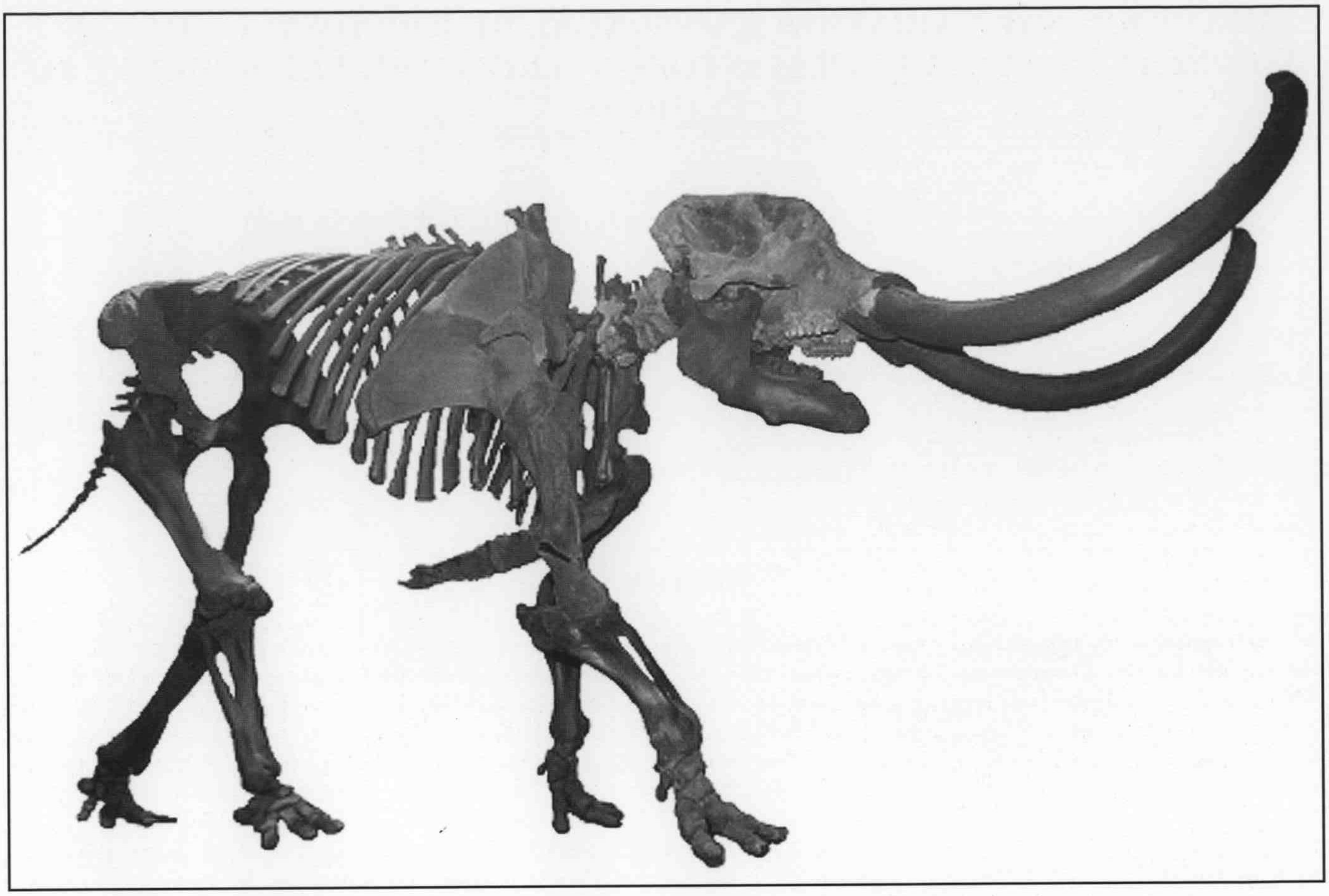


Figure 1. Mounted skeleton of *Mammut americanum* (UF 211300) from the Aucilla River (Rancholabrean) of Florida. Results of this study indicate this individual was an adult male. Photo by Jeff Gage; © Florida Museum of Natural History.

INTRODUCTION

Mammut (Family Mammutidae) is regarded as one of the most evolutionary conservative proboscidean taxa, experiencing little morphologic change across its temporal range from the late Miocene through the Pleistocene (Lambert and Shoshani 1998). This apparent evolutionary stasis is in contrast to the rapid morphological changes, especially in the dentition, demonstrated by other proboscideans, such as gomphotheres and elephantids (Saunders 1996). *Mammut americanum* (Kerr 1792) has traditionally been considered to be static in its morphologic evolution (e.g., Kurten & Anderson 1980). However, King and Saunders (1984) and Gingerich (1993) both found a small, yet significant, size change in Rancholabrean *M. americanum* molars from Missouri. Their findings suggest that *M. americanum* did experience some morphological evolution in the late Pleistocene. However, no study to date has quantitatively examined dental and postcranial size changes in *M. americanum* over longer timescales, nor examined chronologic change in growth or sexual dimorphism. Thus, the question of whether *M. americanum* demonstrates stasis or chronoclinal evolution across its full temporal range has never been adequately addressed.

Mammut americanum was the last surviving North American member of Mammutidae, thriving primarily in eastern North America (from southern Canada to Florida) (Shoshani 1990) and has been one of the most commonly recovered fossil mammals in this region (King & Saunders 1984). Descriptions of skeletons (Warren 1852; Osborn 1936; Corgan 1976; Fisher 1990; Harington et al. 1993; Daeschler 1996), molar morphology and metrics (Leidy 1869; Skeels 1962; Saunders 1977; King & Saunders 1984; Abraczinskas 1993; Green & Hulbert 2005) and discussions on extinction (Dreimanis 1968, 1967; King & Saunders 1984; Haynes 1991, 2002; Fisher 1996; Surovell et al. 2005), sexual dimorphism (Barbour 1931, 1932; Fisher 1990; Laub 1999, 2002) and paleodiet (Webb et al. 1992; Laub et al. 1994; Koch et al. 1998; Gobetz & Bozarth 2001; Gobetz & Green 2004; Green

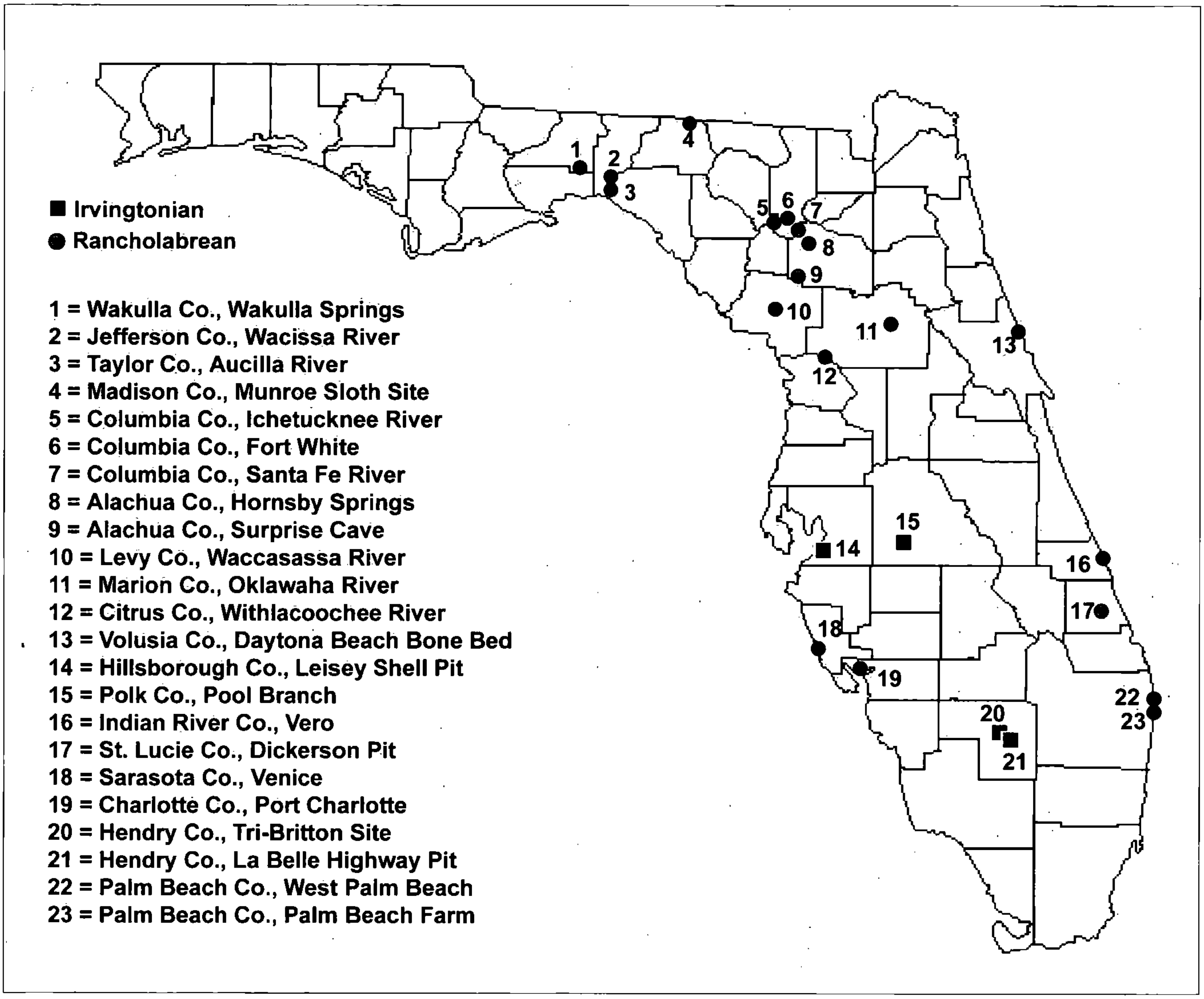


Figure 2. Map of Pleistocene Florida fossil vertebrate localities that yielded *Mammut americanum* remains used in this study. North American Land Mammal Age designation (i.e., Irvingtonian, Rancholabrean) for localities taken from Webb (1974), Morgan & Hulbert (2002), MacFadden (1997), Hulbert (2001), Meers & Hulbert (2002), and R.C. Hulbert (personal communication).

et al. 2005) constitute the majority of past research on this taxon.

Mammut americanum remains are common in fossil localities across Florida (Green 2002) and range in geologic age from about 2.5 mya to 10,000 ybp (Hulbert 2001) (Fig.2). The majority of Florida specimens are Rancholabrean (Webb 1974; Hulbert 2001), including three articulated and mounted skeletons: the Wakulla skeleton, on display at the Museum of Florida History, Tallahassee (Gunter 1931); the Aucilla skeleton (Fig.1), on display at the Florida Museum of Natural History, Gainesville; and the West Palm skeleton, on display at the South Florida Science Museum, West Palm Beach. Historically, considerably fewer *M. americanum* specimens of Irvingtonian or Blancan age had been recovered from this region (Webb 1974). In the past ten years, however, new Florida fossil localities have yielded a larger number of Irvingtonian *M. americanum* fossils, including dental and post-cranial remains (Webb & Dudley 1995; Meers & Hulbert 2002). This new material provides the opportunity to quantitatively study evolution and adaptation in different *M. americanum* populations representing a long temporal interval from a restricted geographical area (i.e., Florida). This study examines chronologic trends in morphologic size, sexual dimorphism, and growth in Florida *M. americanum* across the Pleistocene.

MATERIALS AND METHODS

One hundred and forty-two *Mammut americanum* specimens (upper third molars (M3), lower third molars (m3), limb bones, and mandibles from various localities in Florida were measured, including 109 elements from the Rancholabrean (21 M3s, 37 m3s, 30 mandibles, 10 humeri, 3 ulna, 4 femora, 1 tibia, 3 pelves) and 33 elements from the Irvingtonian (5 M3s, 10 m3s, 13 mandibles, 2 humeri, 1 ulna, 1 femur, 1 tibia). Selection of study elements was restricted to only those specimens with locality data yielding biochronological and stratigraphic data to merit designation to a specific NALMA; i.e., Irvingtonian or Rancholabrean. Florida fossil localities used in this study were placed in their respective NALMA using biochronologic information (Fig. 2). All specimens studied are listed in the Appendix.

One hundred and thirteen *Mammut americanum* specimens in this study are housed in Florida Museum of Natural History Vertebrate Paleontology Collection (UF) in Gainesville. Fifteen specimens are housed in other private and public institutions (i.e., Coastal Plains Institute and Land Conservancy, Tallahassee, Florida; Museum of Florida History, Tallahassee, Florida; Museum of Science and Industry, Tampa, Florida; South Florida Science Museum, West Palm Beach, Florida; Tall Timbers Research Station, Tallahassee, Florida). The remaining 14 specimens are in private collections in Florida. A thorough photographic record was made of each specimen in the final category and is available from the author upon request. Specimens in private collections were only used if they contained specific, reliable locality and associated faunal information, so that the geologic age of specimens could be ascertained.

Mammut americanum third molars are easily distinguished from other molars by the presence of four or more lophs (transverse ridges on upper teeth) and lophids (transverse ridges on lower teeth) (Fig. 3). Each tooth was identified as upper or lower, the eruption stage recorded (Table 1), and maximum length and maximum width measured using the methods of Saunders (1977). This study followed Smith and Dodsons's (2003) standardized terminology for anatomical orientation and notation in mammalian dentitions for describing morphology of *M. americanum* third molars.

Proboscidean limb bones, when not associated with dental elements, are not easily identified to taxa. Therefore, close comparison between other proboscidean limb bones (i.e., *Mammuthus*) and the criteria of Olsen (1972) were used to positively identify *Mammut americanum* limb bones (humerus, ulna, femur, tibia). In order to confine the study to fully-grown individuals (adults), only bones with both epiphyses fused were selected. Articular length and minimum mid-shaft circumference of each limb bone was measured using the methods of Saunders (1977).

Mammut americanum mandibles were measured following Tassy (1996). Only four of his measurements were used here on whole or partial mandibles: 1, anterior mandibular height, defined as the height of the mandible in front of the tooth row; measurement 16 of Tassy (1996:fig. 11.2); 2, posterior mandibular height, the height of the mandible behind the tooth row, in front of the ramus; measurement 17 of Tassy (1996:fig. 11.2); 3, anterior mandibular width, the width of the mandible in front of the tooth row, perpendicular to measurement 1; measurement 8 of Tassy (1996:fig. 11.2); and 4, poste-

Table 1. Criteria for age classes for *Mammut americanum* mandibles used in this study from the Irvingtonian and Rancholabrean of Florida.

Age Class	Criteria	Developmental Classification [a]
0	dp2/dp3 erupting to fully erupted; dp4 unerrupted	Juvenile
1	dp2/dp3/dp4 fully erupted, in wear	Juvenile
2	dp2 shed	Juvenile/Youth
3	dp3 shed	Youth
4	dp4 shed	Youth/Young Adult
5	m1 shed	Adult
6	m2 shed	Adult

[a] after Saunders (1977) and Green and Hulbert (2005).

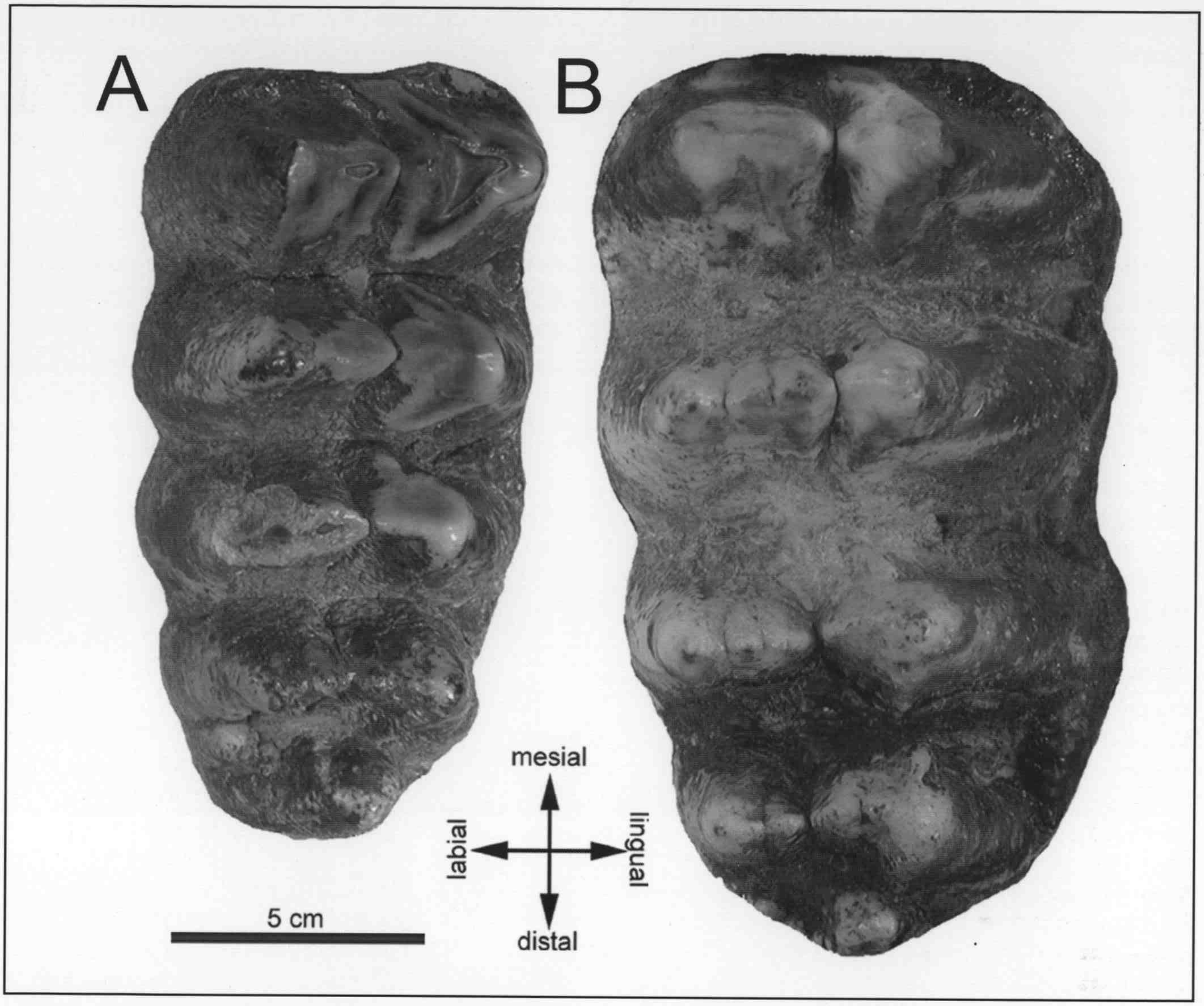


Figure3. A.) Irvingtonian Florida *Mammut americanum* M3 (UF 215058); B.) Rancholabrean Florida *M. americanum* M3 (UF 92216).

rior mandibular width, the width of the mandible behind the tooth row, perpendicular to measurement 2; measurement 7 of Tassy (1996:fig. 11.2). Seven age classes of Florida *Mammut americanum* (from fetal to adult) were defined by identifying molar wear and tooth replacement stages (Table 1).

Summary statistics (mean, standard deviation, coefficient of variation, sample size, and range) were computed for all quantitative variables (i.e., M3/m3 length/width, limb bone articular length/minimum circumference, anterior/posterior mandibular height/width). Coefficients of variation (V) were corrected for small sample size by calculating V* (Haldane 1955; Simpson et al. 1960), using the equation:

(1) $V^* = (1 + 1/4n)V$

Each mean measurement for Irvingtonian elements was statistically compared (using Microsoft Excel®) to the corresponding Rancholabrean mean measurement. Variance was calculated with a two-sample F-test (10 total variance tests), then the resulting variance (i.e., equal or unequal) two-tailed t-test (10 total t-tests) was applied to determine if statistically significant differences were present.

Two statistical tests were used to determine the degree of sexual dimorphism in Florida *Mammut americanum*, the mean method test (Plavcan 1994), and the coefficient of variation regression test:

(2) $Y = -0.47 + 0.0214{*}X$

where Y is the ln-transformed dimorphism and X is the combined-sex CV (Plavcan 1994). A total of 36 sexual dimorphism tests were performed (18 mean method tests; 18 CV regression tests). Both tests report estimated sexual dimorphism of a measurement as the ratio of male/female similarity, with ratios of 1.0 representing no difference between gender and those above 1.0 representing a difference. These two tests were selected based on the results of Plavcan (1994) and Van Valkenburgh and Sacco (2002), who found them to be among the most accurate in quantitatively estimating sexual dimorphism in extinct mammalian taxa. The mean value of both tests for each measurement was chosen to represent the overall sexual dimorphism estimate for that measurement.

Mandibles having one or more open oval shaped alveoli or tusk material present or absent in the symphysis were recorded (Appendix; coded 0 = absent, 1 = present). If present, the alveolus for a mandibular tusk lies in the deep medial portion of the symphysis (near the midline) and extends posteriorly to a point approximately level with the anterior mental foramen. The alveolus for the mandibular tusk can be observed on specimens missing the distal end of the symphysis in anterior and sometimes medial view if some bone rostral to the anterior mental foramen is preserved. In order to differentiate between deciduous and permanent lower tusks, the criterion of Tassy (1987) and Green and Hulbert

Table 2. Summary statistics for *Mammut americanum* M3/m3 length and width measurements from the Irvingtonian and Rancholabrean of Florida.

Statistical Category	Tooth Category	Irvingtonian Max Length (mm)	Irvingtonian Max Width (mm)	Rancholabrean Max Length (mm)	Rancholabrean Max Width (mm)
Mean	M3	159.3	87.9	176.3	97.2
Standard Deviation	M3	5.82	5.15	14.20	8.42
Coefficient of Variation	M3	3.88	6.35	8.16	8.77
Sample Size	M3	4	3	18	22
Maximum	M3	164.5	93.5	197.4	110.4
Minimum	M3	151.1	86.7	143.2	82.2
Mean	m3	171.9	90.1	184.2	96.5
Standard Deviation	m3	12.42	6.47	13.82	6.83
Coefficient of Variation	m3	7.41	7.38	7.57	7.13
Sample Size	m3	10	9	29	39
Maximum	m3	190.5	99.5	216.5	111.6
Minimum	m3	159.2	83.4	155	81.3

Table 3. Results of F-tests and t-tests between Florida Irvingtonian and Rancholabrean *Mammut americanum* measurements.

F-Test: Two Sample for Variances, One-Tail				t-test: Two Sample, Two-Tail			
Variables	F-Stat	P (alpha=0.05)	Variance	df	t-Stat	P (alpha=0.05)	Difference
M3 Length	0.401	0.195	Unequal	10	-2.619	0.026	Significant
M3 Width	1.170	0.345	Unequal	4	-0.849	0.444	Non-Significant
m3 Length	0.807	0.387	Unequal	17	-2.629	0.017	Significant
m3 Width	0.896	0.471	Unequal	12	-2.611	0.023	Significant
Humerus Length	0.003	0.044	Equal	10	-3.070	0.012	Significant
Humerus Circumference	0.014	0.093	Equal	10	-4.736	0.001	Significant
Anterior Mandible Height [a]	0.336	0.151	Unequal	12	-1.601	0.135	Non-Significant
Anterior Mandible Width [a]	0.508	0.269	Unequal	9	-2.652	0.026	Significant
Posterior Mandible Height [a]	0.265	0.075	Unequal	17	-2.302	0.034	Significant
Posterior Mandible Width [a]	0.555	0.268	Unequal	12	-3.294	0.006	Significant

[a] mandible measurements tested include only adult specimens (Age Class 5-6)

Table 4. Mean percentage increase from the Irvingtonian to the Rancholabrean in Florida *Mammut americanum* molar, limb bone, and mandible size measurements.

Measurement	% Increase[1]
M3 L[2]	7.77
M3 W[3]	4.42
m3 L	6.70
m3 W	6.55
Humerus L	15.70
Humerus C[4]	23.05
Femur L	10.60
Femur C	14.29
Ulna L	11.32
Ulna C	24.31
Tibia L	1.83
Tibia C	18.33
Anterior MH[5]	7.25
Anterior MW[6]	9.56
Posterior MH	5.97
Posterior MW	10.93

[1] % increase in measurement from the Irvingtonian to the Rancholabrean [2] element maximum length [3] element maximum width [4] limb bone minimum mid-shaft circumference [5] mandibular height [6] mandibular width

(2005) was used. Mandibular tusk presence frequency for Irvingtonian and Rancholabrean specimens was calculated for five different mastodon age groups: 1. percent all individuals possessing mandibular tusks (age classes 0-6); 2. percent individuals possessing deciduous tusks (age classes 0-1); 3. percent individuals possessing permanent tusks (age classes 2-6); 4. percent individuals possessing mandibular tusks (age classes 0-4; growth incomplete); 5. percent individuals possessing mandibular tusks (age classes 5-6; growth complete).

Pelves of the three mounted *Mammut americanum* skeletons from Florida (listed above) were used to determine gender using the ratio of the maximum ilium width (IW; measurement 5 in Lister (1996:fig. 25.2) to the maximum horizontal pelvic aperture width (PAW; measurement 3 in Lister (1996:fig. 25.2), and the ratio of IW to the diagonal pelvic aperture height (DPAH; measurement 2 in Lister (1996:fig. 25.2)). Lister and Agenbroad (1994) and Lister (1996) showed that the IW:PAW and IW:DPAH ratios were the most accurate in determining gender in mammoths and elephants. The gender estimate based on the pelvis for each skeleton was compared to those based on molars, limb bones, and the mandibles of each skeleton in order to support the gender determination of each individual and determine the relative accuracy of sexual dimorphism estimates (based on mean method and CV regression tests) on isolated specimens in this study.

MORPHOLOGIC EVOLUTION IN FLORIDA *MAMMUT AMERICANUM*

MOLARS

Molar size in Florida *Mammut americanum* increased significantly over time (Tables 2, 3; Figs. 3, 4), although at less of an overall rate than other elements across the Pleistocene (Table 4). Late-Irvingtonian (~500,000 ybp) mastodon teeth from the Tri-Britton Site and La Belle Highway Pit show a slight trend of being smaller than early-Irvingtonian specimens (~ 1 Ma) from Leisey Shell Pit (Appendix). In order to ascertain whether such chronologic differences affect lumped mean Irvingtonian molar values, four additional two-tailed t-tests were performed for m3 and M3 length and width between late- and early-Irvingtonian *M. americanum* molars. All four tests showed the differences to be nonsignificant (M3 length: df = 3, $p = 0.8852$; M3 width: df = 1, $p = 0.2486$; m3 length: df = 7, $p = 0.8894$; m3 width: df = 5, $p = 0.4269$), so the time-averaging of Irvingtonian samples does not affect the results of this study.

Mean M3 length increased slightly more than mean m3 length from the Irvingtonian to the Rancholabrean (Table 4), although Irvingtonian M3 sample sizes are small and caution should be taken with their interpretation. The width in m3 increased much more than M3 width (Table 4). In addition, length and width in m3 increased proportionally, whereas in M3 they increased disproportionately (length increased much more than width; Table 4). These results are interesting because they correlate with those of King and Saunders (1984). From the Mid-Late-Wisconsinan to the Late-Wisconsinan, Missouri *M.americanum* M3 length increased 6.66% and width increased 2.76%, m3 length increased 5.13% and width increased 4.09%. Also of interest is the fact that the King and Saunders (1984) sample interval is much smaller (tens of thousands of years) than this study (hundreds of thousands of years), yet the results show similar trends and the approximately the same percentage difference. These results suggest that *Mammut americanum* followed a conservative pattern in its dental evolution, with M3 length increasing disproportionately to width and m3 length increasing proportionately to width.

LIMB BONES AND BODY SIZE

Limb bone size (i.e., articular length and mid-shaft circumference) also increased significantly over time from

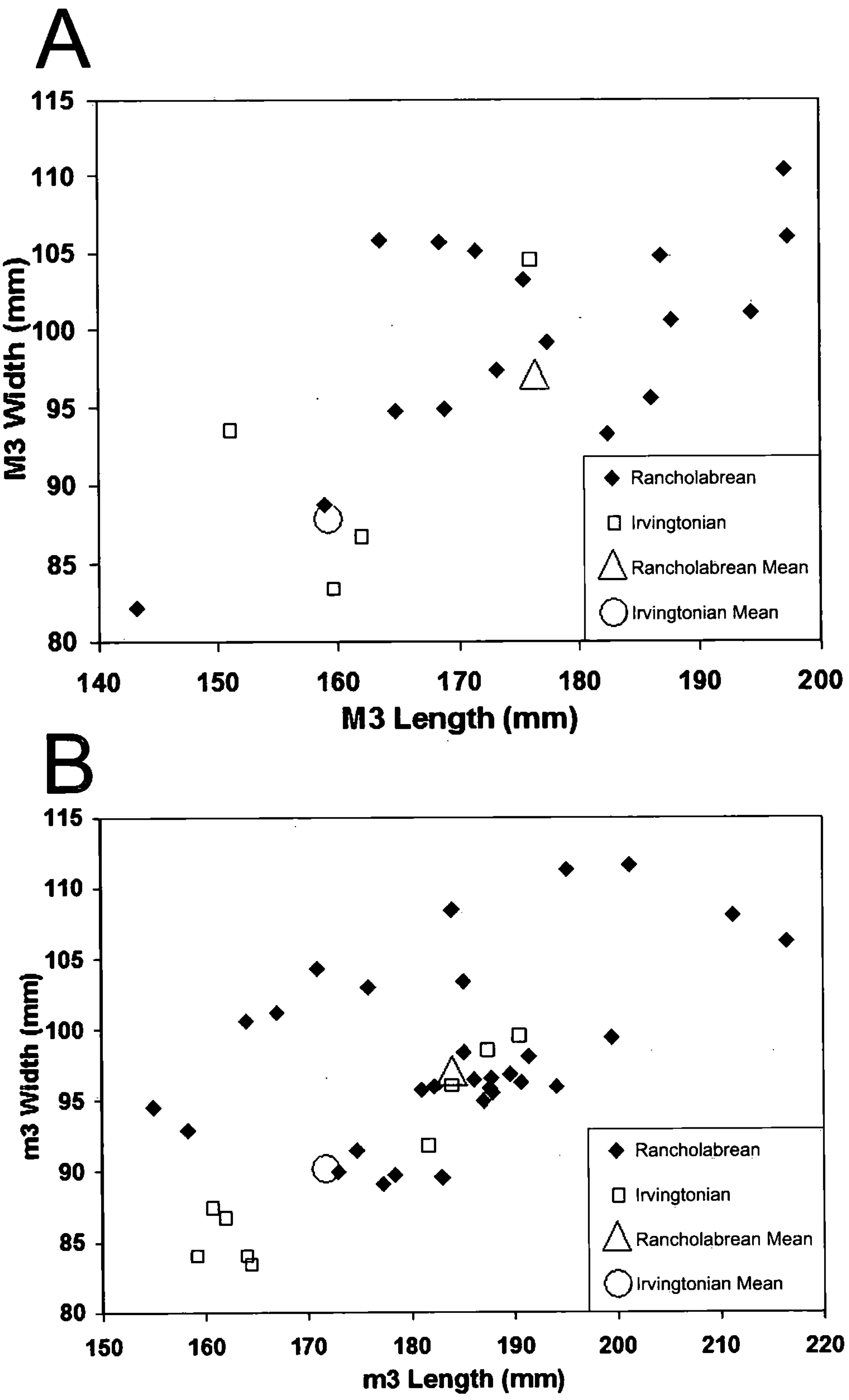


Figure 4. A.) *Mammut americanum* M3 length vs. width plot for Rancholabrean and Irvingtonian specimens; B.) *M. americanum* m3 length vs. width plot for Rancholabrean and Irvingtonian specimens.

Table 5. Summary statistics for *Mammut americanum* limb bone (humerus, femur, ulna, tibia) measurements from the Irvingtonian and Rancholabrean of Florida.

Statistical Category	Limb Bone	Irvingtonian Articular Length (mm)	Irvingtonian Min Circumference (mm)	Rancholabrean Articular Length (mm)	Rancholabrean Min Circumference (mm)
Mean	Humerus	762.5	342.5	904.5	445.1
Standard Deviation	Humerus	3.54	3.54	62.93	29.46
Coefficent of Variation	Humerus	0.52	1.16	7.13	6.78
Sample Size	Humerus	2	2	10	10
Maximum	Humerus	765	345	1020	508
Minimum	Humerus	760	340	795	410
Mean	Femur	950	380	1062.7	443.3
Standard Deviation	Femur	-	-	96.93	57.74
Coefficent of Variation	Femur	-	-	9.88	14.11
Sample Size	Femur	1	1	3	3
Maximum	Femur	-	-	1143	510
Minimum	Femur	-	-	955	410
Mean	Ulna	710	275	800.7	363.3
Standard Deviation	Ulna	-	-	81.95	63.31
Coefficent of Variation	Ulna	-	-	11.09	18.88
Sample Size	Ulna	1	1	3	3
Maximum	Ulna	-	-	895	435
Minimum	Ulna	-	-	747	315
Mean	Tibia	645	245	657	300
Standard Deviation	Tibia	-	-	-	-
Coefficent of Variation	Tibia	-	-	-	-
Sample Size	Tibia	1	1	1	1
Maximum	Tibia	-	-	-	-
Minimum	Tibia	-	-	-	-

the Irvingtonian to the Rancholabrean (Tables 3, 5; Figs. 5, 6). Limb bone size increased at a larger rate (~20%) than any other variable for Florida *Mammut americanum* (Table 4). Because limb bone size is highly correlated with body mass in extant and extinct mammals (Alexander et al. 1979; Anderson et al. 1985; Gingerich 1990), as limb bone size increased for Florida *M. americanum*, body mass almost certainly increased as well. A significant increase in body size is not surprising as this kind of pattern is well documented in late Cenozoic mammals (Kurten 1968; Hulbert & Morgan 1993; Lister 1993; Purdue & Reitz 1993; Seymour 1993).

Unfortunately, sample sizes are low for limb bone elements (resulting in large CV values for some elements in Table 5), so caution should be taken to not overinterpret the results of this study. The humerus (n=3) is the limb element with the strongest possibility for describing chronologic change. The Irvingtonian sample contains two humeri approximately equal in size, from different late-Irvingtonian localities (Appendix). Two separate limb bones from different localities of late-Irvingtonian age having nearly equal dimensions support the large mean percentage difference in humeral circumference between Irvingtonian and Rancholabrean *Mammut americanum* (Table 4). An additional partial humerus (UF 214719; Hendry Co.) from the La Belle Highway Pit, while not measurable, appears to be of approximately the same size as the other two Irvingtonian humeri, further supporting such a small size trend among Irvingtonian populations. In addition, both Irvingtonian

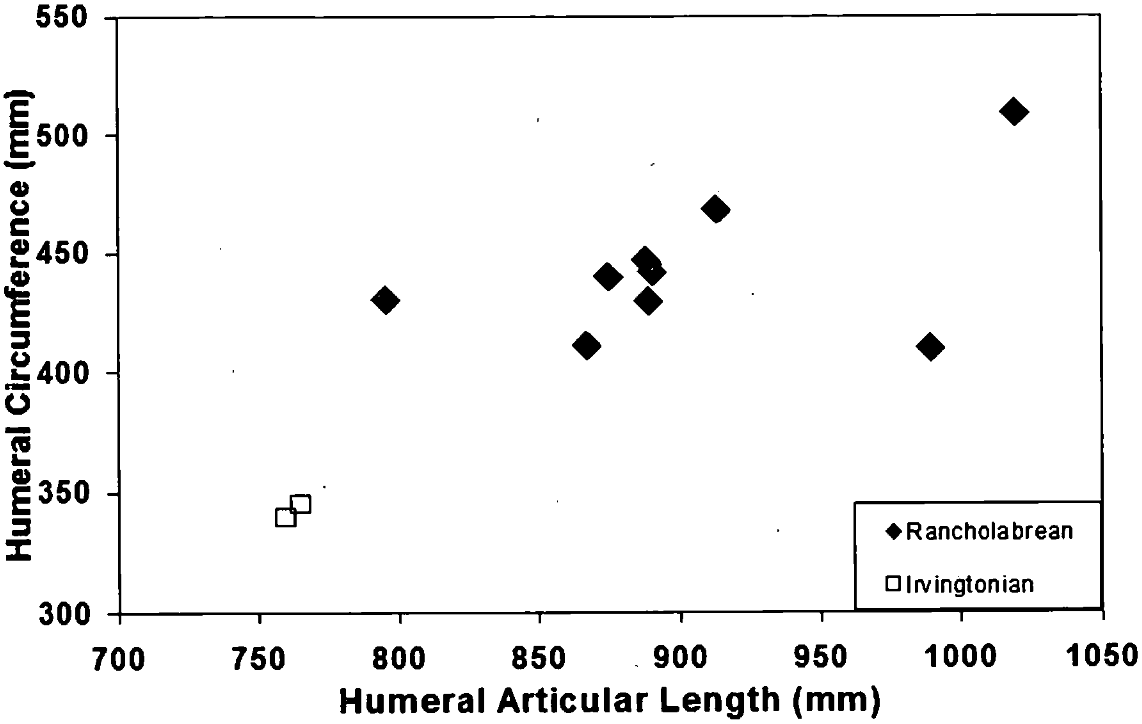


Figure 5. Humerus articular length vs. mid-shaft minimum circumference plot for Rancholabrean and Irvingtonian Florida *Mammut americanum.*

humeri are smaller than the smallest Rancholabrean specimen.

The observed change in *Mammut americanum* body mass is probably not an artifact of sample size, but rather represents a true increase in adult mass from the Irvingtonian to the Rancholabrean of Florida. The sample sizes for the other three limb elements (femur, tibia, ulna) are too small to test for statistical significance, but these elements apparently show the same trend, with Irvingtonian limb bones always being smaller than Rancholabrean elements (Table 5; Appendix).

The chronologic difference in limb bone size could also be attributed to sexual dimorphism rather than chronoclinal change, as suggested by the bimodal distribution of humeri (Fig. 5). It is possible that limb bones in the Irvingtonian sample (n=2) come only from females, and Rancholabrean specimens from male and female *Mammut americanum.* However, the Rancholabrean humeral sample does include the female West Palm skeleton (Table 6), which is very small in comparison to confirmed males. This specimen is comparable in articular length, but much larger in circumference, than Irvingtonian humeri (Appendix), implying a large difference in body mass. It is not currently possible to determine the gender of Irvingtonian specimens as no limb bones have been recovered with associated pelves. It is possible that the entire sample of Irvingtonian limbs is from female animals, and no true male elements (which could have dimensions much closer to Rancholabrean values) have been recovered yet.

A ~20% increase in *Mammut americanum* humeral circumference is significant as the largest Rancholabrean individuals have recently been suggested to have weighed as much as 8,000 kg (Christiansen 2004). Using the allometric equation calculating proboscidean body mass from humeral circumference of Christiansen (2004):

(3) $\log \text{mass (kg)} = -1.598 + 2.062(\log X)$

late-Irvingtonian *M. americanum* from Florida would have weighed on average about 4200 kg, while Rancholabrean individuals from Florida would have weighed on average about 7500 kg, a 44% increase. Such an increase in body mass over a short period (~500,000 years) is quite impressive and possibly implies an ecophenotypic response, which will be discussed in more detail later.

Mammut americanum molar size (both length and width) did not increase proportionally to mid-shaft humeral circumference from the Irvingtonian to the Rancholabrean (Table 4). As previously stated, mid-shaft circumference of the humerus is a direct indicator of body mass in proboscideans (Christiansen 2004). Therefore, body mass in Florida *M. americanum* may

Table 6. Pelvic measurements and corresponding gender determination for three Rancholabrean *Mammut americanum* mounted skeletons from Florida.

Pelvic Measurements	West Palm Skeleton[1]	Aucilla Skeleton[2]	Wakulla Skeleton[3]
IW[4]	170	233	225
PAW[5]	461	555	588
DPAH[6]	-	535	467
Ratio = IW:PAW	2.711	2.382	2.613
Ratio = IW:DPAH	-	2.296	2.076
Gender [7]	Female	Male	Male

[1] uncatalogued specimen (Palm Beach Co.) displayed at the South Florida Science Museum, West Palm Beach, FL

[2] UF 211300 (Taylor Co.) displayed at Florida Museum of Natural History, Gainesville, FL

[3] uncatalogued Florida Geological Survey specimen (Wakulla Co.) displayed at the Museum of Florida History, Tallahassee, FL

[4] minimum width of ilium (only 1 L.) shaft (see Lister 1996)

[5] maximum horizontal width of pelvic aperture (see Lister 1996)

[6] diagonal pelvic aperture height (see Lister 1996)

[7] gender determined from pelvic ratios IW:PAW (males = ratio < 2.6); IW:DPAH (males = ratio < 2.4)

not have increased proportionally to tooth size from the Irvingtonian to the Rancholabrean. A similar result was found in Hulbert and Morgan's (1993) study of the giant armadillo, *Holmesina*, in Florida, which expressed directional evolution for increased total body mass more than the area of tooth occlusion during its 2.5 Ma. In addition, the Aucilla skeleton (UF 211300) is a very large male specimen (Table 6) with the largest humerus currently identified from Florida (Appendix). However, m3 dimensions of this specimen are unusually small, with length being well below the Rancholabrean mean and width just above the Rancholabrean mean (Table 2; Appendix). According to the geometrical similarity model, molar area (length x width) should increase at 2/3 the rate of body mass (which is proportional to volume) in order to maintain isometry (Cock 1966; Gingerich et al. 1982; LaBarbera 1989). The presence or lack of isometry can be tested using allometric scaling, but examining intraspecific tooth area to body mass allometric relationships requires measuring associated molars and body mass estimators (i.e., limb bones) (Gingerich et al. 1982). The samples presented in this study constitute mostly unassociated, individual skeletal elements, so testing temporal change in the allometric relationship between tooth size and body mass in *M. americanum* is currently not possible, but would be interesting to examine in future studies.

A confirmed lack of correlation between tooth size and body mass in *M. americanum* would be surprising as the opposite has been traditionally accepted for mammalian lineages (Carroll 1997), especially for ungulates (Janis 1990) and primates (Gingerich et al. 1982). However, MacFadden and Hulbert (1990) found that predicting body mass from molar size of Miocene gomphotheres from Florida yielded grossly inflated results.

MANDIBLES

As with all other elements in this study, Florida *Mammut americanum* mandibular size increased from the Irvingtonian to the Rancholabrean (Tables 4, 7; Figs. 7, 8), although anterior mandibular height was not significantly different (Table 3). Only posterior mandibular width showed a substantial increase. Because proboscidean lower molars form and erupt from the posterior portion of the mandible (Saunders 1996), the increased width of the posterior mandible could be correlated with increased m3 width, or vice versa. The increase in m3 size would have less selection pressure on the posterior height and anterior portions of the mandible to grow larger, thus explaining the less substantial increase. It is also significant that while the sample size for anterior mandibular height is large (n=15), the CV is unusually high (Simpson et al. 1960) (Table 7). This could be a result of sexual dimorphism and will be discussed below.

SEXUAL DIMORPHISM IN FLORIDA *MAMMUT AMERICANUM*

SEXUAL DIMORPHISM ESTIMATES

Mammut americanum sexual dimorphism has been addressed (Haynes 1989, 1991; Fisher 1990) but

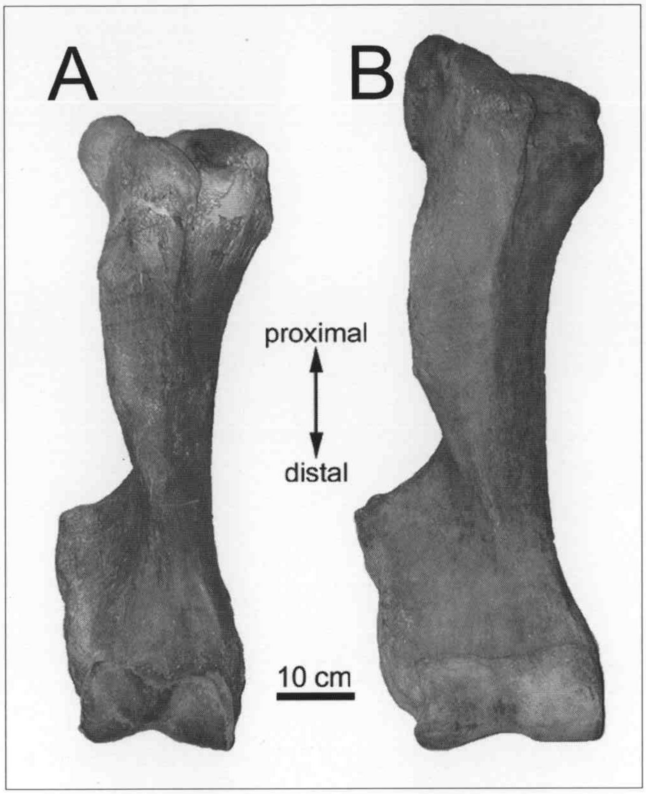


Figure 6. A.) Irvingtonian Florida *Mammut americanum* humerus (UF 210415); B.) Rancholabrean Florida *M. americanum* humerus (UF 137891).

not quantitatively analyzed like that of modern elephants (Haynes 1991; Lister 1996), mammoths (Haynes 1991; Lister & Agenbroad 1994; Averianov 1996; Lister 1996) or gomphotheres (Tassy 1996). *M. americanum* presumably had a polygynous-mating system (Haynes 1989, 1991) with males being substantially larger in body and tusk size than females (Fisher 1990; Haynes 1991), resulting in strong male competition for mates, as in modern elephants and other polygynous ungulates (Perez-Barberia et al. 2002).

Pelvic measurements may be applied with some confidence to sexing skeletons of *Mammut americanum* (Table 6). The Wakulla skeleton IW:PAW ratio is just above the dividing line for males as defined by Lister (1996), who expressed caution in sexing mammoth pelves with the IW:PAW ratio in the 2.6-2.7 range. However, the IW:DPAW ratio is clearly in the male region, so this animal was determined to be a male that shows slight overlap with female IW:PAW ratios (also seen in *Mammuthus*; Lister 1996). The IW:PAW ratio of just above 2.7 (Table 6) indicates that the West Palm skeleton is of a female individual. Haynes (1991) reported that minimum ilium shaft width is dimorphic for proboscideans, with males consistently having values above 160 mm and females never exceeding about 160 mm. Haynes' results suggest that the West Palm specimen represents a female and further supports the male determination of the Wakulla and Aucilla skeletons (Table 6).

The average sexual dimorphism ratio for each *Mammut americanum* element studied is in Table 8.

Table 7. Summary statistics for *Mammut americanum* mandible measurements from the Irvingtonian and Rancholabrean of Florida.

Statistical Category	NALMA	Anterior Depth (mm)	Anterior Width (mm)	Posterior Depth (mm)	Posterior Width (mm)
Mean	Irvingtonian	171.1	109.8	176.5	152.5
Standard Deviation	Irvingtonian	13.23	7.79	7.82	11.00
Coefficient of Variation	Irvingtonian	8.12	7.45	4.61	7.52
Sample Size	Irvingtonian	5	5	6	6
Maximum	Irvingtonian	190	119	190	173
Minimum	Irvingtonian	153.5	100	169	144
Mean	Rancholabrean	184.5	121.4	187.7	171.2
Standard Deviation	Rancholabrean	22.82	10.93	15.16	14.77
Coefficient of Variation	Rancholabrean	12.58	9.14	8.20	8.74
Sample Size	Rancholabrean	15	17	17	18
Maximum	Rancholabrean	228	155	220	202
Minimum	Rancholabrean	159.5	106	160	143

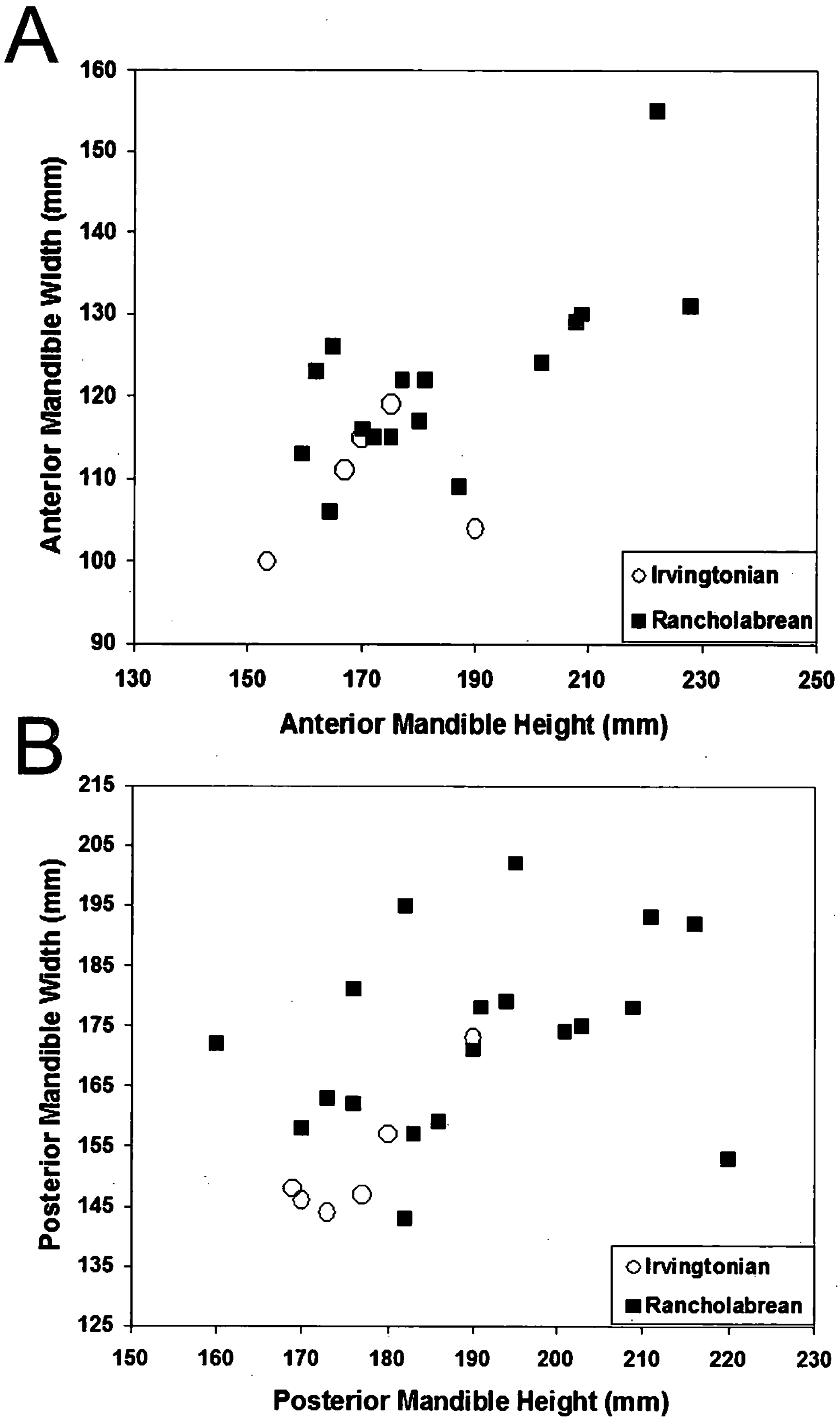


Figure 7. A.) Anterior mandibular height vs. anterior mandibular width for Rancholabrean and Irvingtonian *Mammut americanum* from Florida; B.) Posterior mandibular height vs. posterior mandibular width for Rancholabrean and Irvingtonian *M. americanum* from Florida.

Table 8. Sexual dimorphism ratios (from mean method and CV tests) in molar, limb bone, and mandibular measurements of Irvingtonian and Rancholabrean *M. americanum* from Florida.

Irvingtonian Measurement	Mean Method SD Ratio	CV SD Ratio	Average SD Ratio
M3 L	1.08	1.08	1.08
M3 W	1.16	1.2	1.18
m3 L	1.14	1.12	1.13
m3 W	1.13	1.12	1.13
Anterior Mandibular Height	1.11	1.14	1.13
Anterior Mandibular Width	1.13	1.12	1.12
Posterior Mandibular Height	1.07	1.05	1.06
Posterior Mandibular Width	1.13	1.12	1.12
Rancholabrean Measurement	**Mean Method SD Ratio**	**CV SD Ratio**	**Average SD Ratio**
M3 Length	1.13	1.14	1.14
M3 Width	1.17	1.16	1.16
m3 Length	1.12	1.12	1.12
m3 Width	1.12	1.11	1.11
Humerus Length	1.11	1.11	1.11
Humerus Mid-shaft Minimum Circumference	1.12	1.1	1.11
Anterior Mandibular Height	1.23	1.25	1.24
Anterior Mandibular Width	1.14	1.16	1.15
Posterior Mandibular Height	1.15	1.14	1.15
Posterior Mandibular Width	1.15	1.15	1.15

Of all studied elements, only Rancholabrean anterior mandibular height shows a large dimorphic ratio (1.24). In fact, the highest SD estimates overall come from the Rancholabrean mandible rather than from limb bones or molars (Table 8). Significant sexual dimorphism in anterior mandibular height could be the cause of the insignificant statistical increase (Table 3), with the distribution of the smaller female specimens overlapping more with Irvingtonian measurements. Additionally, the increase of sexual differences results in more phenotypic variation, which could also explain the unusually large CV for this measurement (Table 5).

Figure 8 compares two mandibles from the Aucilla River (Taylor Co.) which are assigned to age class 5 and demonstrate this sexual dimorphism, with the male mandible being noticeably larger in the anterior portion than the female mandible. Figure 9 represents male and female morphospaces for the anterior portion of the mandible. Despite the clear bivariate plot, some overlap was probably present between the two groups.

A study by Tassy (1996) documented strong mandibular sexual dimorphism in a *Gomphotherium angustidens* (Cuvier 1817) population from the locality of En Pejouan (middle Miocene) in France. His data showed that horizontal ramus height was more dimorphic relative to horizontal ramus width (Tassy 1996: Fig. 11.5, 11.6). Therefore, a similar pattern of mandibular sexual dimorphism exists between Tassy's (1996) sample of *G. angustidens* from the Miocene of France and this study's *Mammut americanum* sample from the Rancholabrean of Florida. However, Tassy (1996) also noted that the *G. angustidens* sample showed strong sexual dimorphism in m3 length and width, while *M. americanum* from this study does not (Table 8). It is possible that mandibular sexual dimorphism is evident in other extinct proboscideans, but such remains to be studied.

All sexual dimorphism estimates in this study constitute low sexual dimorphism ratios (less than 1.3; Table 8) (Plavcan 1994). The particularly low sexual dimorphism ratios for humeral measurements are interesting because sexual size dimorphism in polygynous extant mega herbivores, like elephants and rhinoceroses, etc., is pronounced (Owen-Smith 1988; Haynes 1991).

Table 9. Mandibular tusk frequency in *Mammut americanum* mandibles from the Irvingtonian and Rancholabrean of Florida.

NALMA	% DT[1]	N[2]	% PT[3]	N	% All[4]	N	% J-YA[5]	N	% A[6]	N
Irvingtonian	100.00	4	100.00	7	100.00	11	100.00	6	100.00	5
Rancholabrean	66.67	3	21.05	19	27.27	22	33.33	9	23.07	13

[1] % deciduous tusks (in mandibles with Age Class 0-1)
[2] sample size
[3] % permanent tusks (in mandibles with Age Class 2-6)
[4] % all mandibles with tusks (permanent/deciduous; Age Class 0-6)
[5] % tusks in juvenile – young adult mandibles; having not terminated growth (Age Class 0-4)
[6] % tusks in adult mandibles; terminated growth (Age Class 5-6)

Mammut americanum appears to have distinct dimorphism in shoulder height and body mass (Haynes 1991), and the Florida skeletons studied here follow that trend, with the Aucilla and Wakulla males being larger in postcranial dimensions than the West Palm female (Appendix). While males were larger in mass than females, overlap in dimorphic limb bone dimensions still exists for *M. americanum*, as expressed in the low sexual dimorphism limb bone estimate (Table 8). Small sample size or time-averaged samples may be the cause of this unexpected observation.

In summary, anterior mandibular height has the highest sexual dimorphism ratio of all other elements studied here and is probably a more reliable indicator of gender than most isolated postcrania for *Mammut americanum.* Gender determination using pelvic dimensions are probably more accurate overall, as *M. americanum* appears to follow the same trend in pelvic dimorphism as modern elephants and mammoths, but complete pelves are rare. Maxillary tusk size should also not be ignored, as *M. americanum* shows clear size dimorphism of maxillary tusks (Fisher 1990; Haynes 1991). In recovered skeletons where pelvic sexual dimorphism estimates and tusk size are not available or are questionable, anterior mandibular height is the most reliable indicator of gender. While males did grow much larger than females (Fisher 1990; Haynes 1991), body size alone (based on limb bone dimensions in this study) is probably not a good gender indicator.

The trend for *Mammut americanum* to grow larger in body mass in the Rancholabrean of Florida allowed for an increase in sexual size dimorphism, although much overlap in body mass between genders is still evident. This directional selection for sexual size dimorphism in male individuals could have been the result of increased competition between males for females or sexual selection by females for larger male body size. While Plavcan (2000) states that the sexual dimorphism estimate of extinct animals alone is not a good indicator of social behavior or social structure, the interpretations about *M. americanum* behavior provided here are supported by extant elephant behavior and social structure (Haynes 1989, 1991; Sukumar 2003). Therefore, it is likely that *M. americanum* sexual dimorphism estimates indicate similar mating behaviors as extant elephants.

MANDIBULAR TUSKS

Mammut americanum mandibular tusks have been historically attributed to be present only in males (Barbour 1931, 1932; Osborn 1936; Laub & Fisher 1996; Laub 1999, 2002). The hypothesis of male-specific mandibular tusks was actually first proposed in 1807 by William Clark in a letter to Thomas Jefferson that described fossils from the Big Bone Lick in Kentucky (Rice 1951). All adult Irvingtonian Florida *Mammut americanum* mandibles in this study had mandibular tusks, yet only ~27% of adult Rancholabrean specimens had such tusks (Table 9). Furthermore, deciduous mandibular tusks (67% frequency; Table 9) were more common than permanent ones (21% frequency; Table 9) in Rancholabrean populations. The data suggest both that Irvingtonian and Rancholabrean juveniles usually had deciduous tusks, but Florida Rancholabrean *M. americanum* very frequently did not retain, or simply did not develop, permanent mandibular tusks, whereas all Irvingtonian individuals developed and retained them throughout life.

Loxodonta africana (Blumenbach 1797) and *Elephas maximus* (Linnaeus 1758) have sex ratios close to parity for male and female offspring (Owen-Smith 1988). If *Mammut americanum* is assumed to also have offspring sex ratios of 1:1, then the sample of *M. americanum* elements used here represent both sexes.

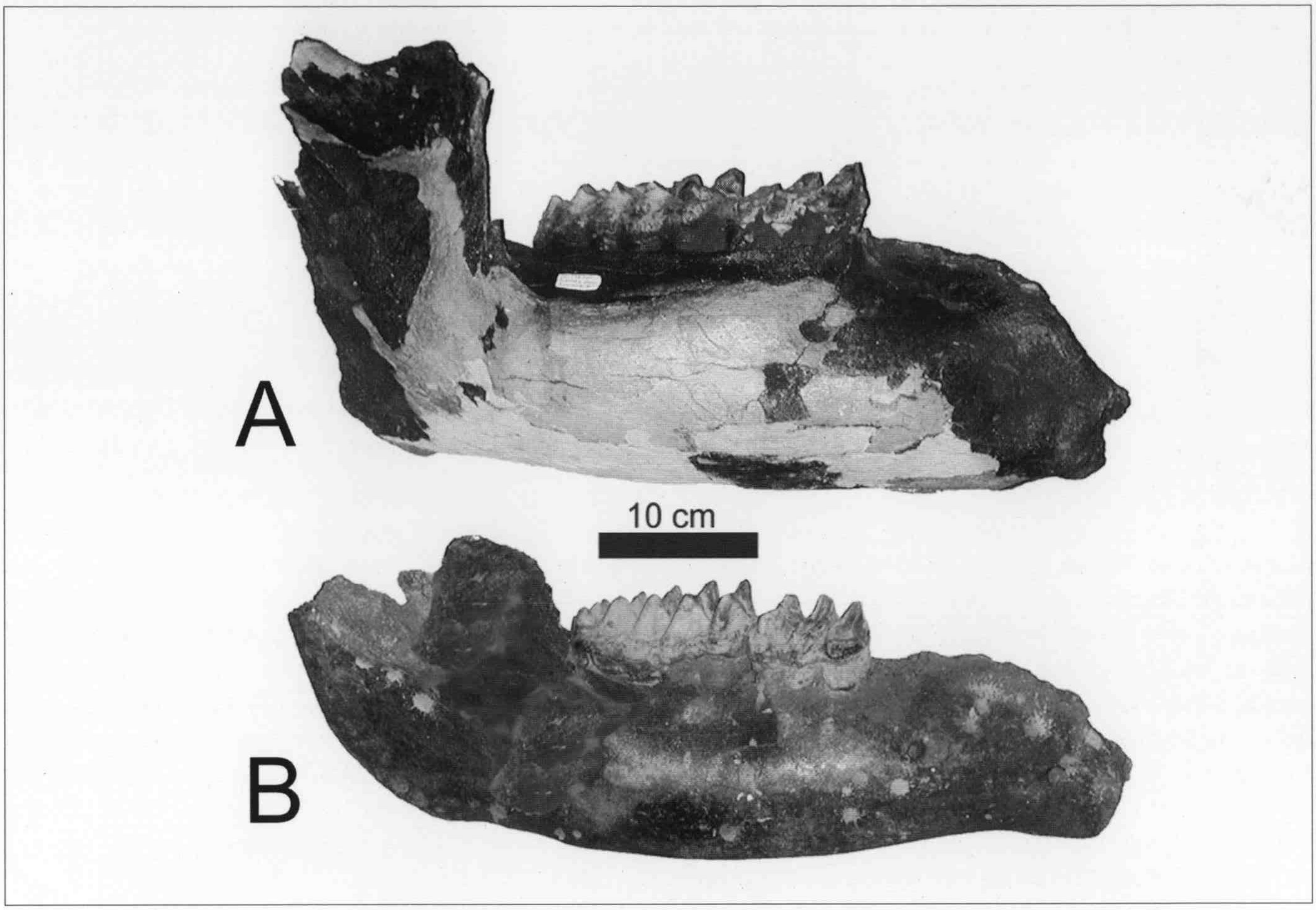


Figure 8. A.) Rancholabrean "male" *Mammut americanum* mandible (UF 135704); B.) Rancholabrean "female" *M. americanum* mandible (UF 135705).

Thus, the drastically different tusk presence ratios here do not suggest sexual dimorphism in the presence/absence of permanent lower tusks, but rather a decrease in frequency through time.

In addition, neither of the two Rancholabrean male skeletons (Aucilla and Wakulla) had mandibular tusks, nor open symphyseal alveoli, which further rejects the hypothesis that mandibular tusks are a male-specific character. Even more interesting is the observation that the three Rancholabrean mandibles that do show evidence of mandibular tusks are among the smallest Rancholabrean mandibles in this study (Fig. 8; Appendix), suggesting females. In summary, mandibular tusks should neither exclusively nor inclusively be used to determine gender in Florida *M. americanum*.

Male *Mammut americanum* individuals display sexual size dimorphism for large maxillary tusks, which aided in inter-male dominance competition (Fisher 1990). However, mandibular tusks are much smaller in diameter (usually <50.0 mm) than maxillary tusks (Laub 2003; Green 2005). Previous authors that suggested *M. americanum* mandibular tusks were male-specific (Barbour 1931, 1932; Osborn 1936; Laub 1999, 2002) have not discussed the reason such small tusks were male-specific; i.e., their intended function has not been addressed like that of maxillary tusks. The results of this study suggest that *M. americanum* females sometimes retained mandibular tusks, while males may not always have retained them. The lack of sexual dimorphism, as well as the small size of mandibular tusks, suggests they did not function in male-male competition. Although Haynes (1991) and Green (2005) suggested possible feeding adaptations for these tusks, this hypothesis remains to be further tested.

Earlier mammutids, (e.g., *Eozygodon*, *Zygolophodon*) had much larger mandibular tusks than *Mammut* (Lambert and Shoshani 1998). A *Mammut americanum* mandible, UF 144175, from the Blancan of Florida (Webb 1974) has alveoli that Lambert and Shoshani (1998) describe as abnormally large for the taxon, being "near-*Zygolophodon* proportions." It is possible that *M. americanum* mandibular tusks decreased in size through time (i.e., from the Blancan to the Rancholabrean), although this observation also remains

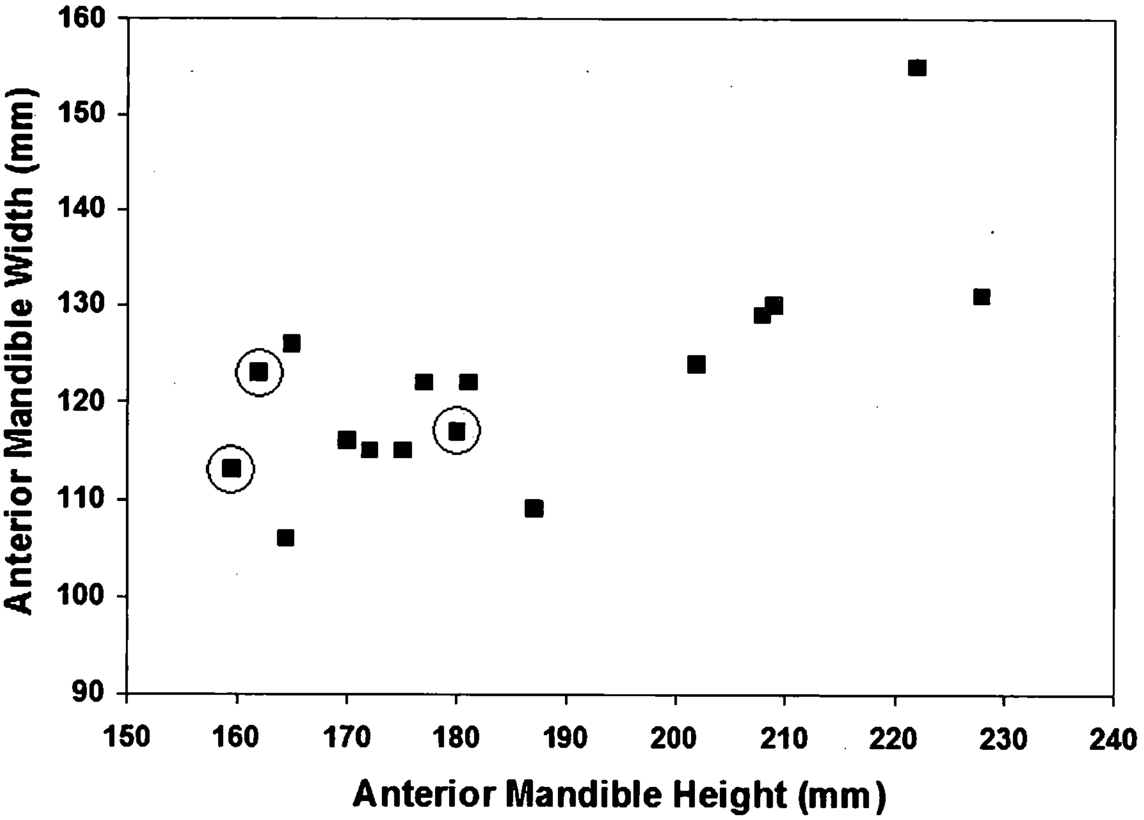


Figure 9. Anterior mandibular height vs. anterior mandibular width graph for Rancholabrean *Mammut americanum*, showing a bivariate, sexually dimorphic plot. Circled data points represent mandibles with mandibular tusks present.

to be tested. A separate study that quantifies mandibular tusk chronologic size trends in *M. americanum* would be ideal, but sufficient sample sizes again are currently lacking.

GROWTH OF FLORIDA *MAMMUT AMERICANUM*

Figure 10 (A-D) demonstrates that Florida *Mammut americanum* experienced a heterochronic change in growth rate from the Irvingtonian to the Rancholabrean. The general shapes of the growth curves (Fig. 10 A-D) are not very different from each other, except that the Rancholabrean curves are higher overall than Irvingtonian curves. No representative Irvingtonian specimens of age class 3 were available for this study, which limits the ability to reconstruct a complete curve. However, the end points (age class 6) of all four Irvingtonian growth curves are below Rancholabrean end points. Therefore, it is likely that the complete Irvingtonian growth curve mirrors the Rancholabrean curve, only smaller. Growth patterns for a *Gomphotherium angustidens* population from the Miocene of France (Tassy 1996) are similar to *M. americanum* growth curves (both show a polynomial S-shaped growth curve) but the trend is more pronounced in *M. americanum* probably because the gomphothere curves utilized more age classes per curve (n=26) than those in this study (n=7).

Mammut americanum growth appears to have terminated at age class 5 (signifying the eruption of the m3) for Rancholabrean individuals. Irvingtonian mandibular values have more varied and wider intervals between age class 5 and 6 than Rancholabrean values. It is possible that Irvingtonian mastodons were still growing at age class 5, but it is difficult to confirm this observation due to small sample size. To test this hypothesis, four two-tailed t-tests were performed between each Irvingtonian mandibular value for age classes 5 and 6. All four two-tailed t-tests showed non-significant differences (anterior height: df = 2, $p = 0.183$; anterior width: df = 3, $p = 0.387$; posterior height: df = 3, $p = 0.392$; posterior width: df = 3, $p = 0.391$), so Irvingtonian individuals probably terminated growth at age class 5, and even if they continued growth, the increase was not sig-

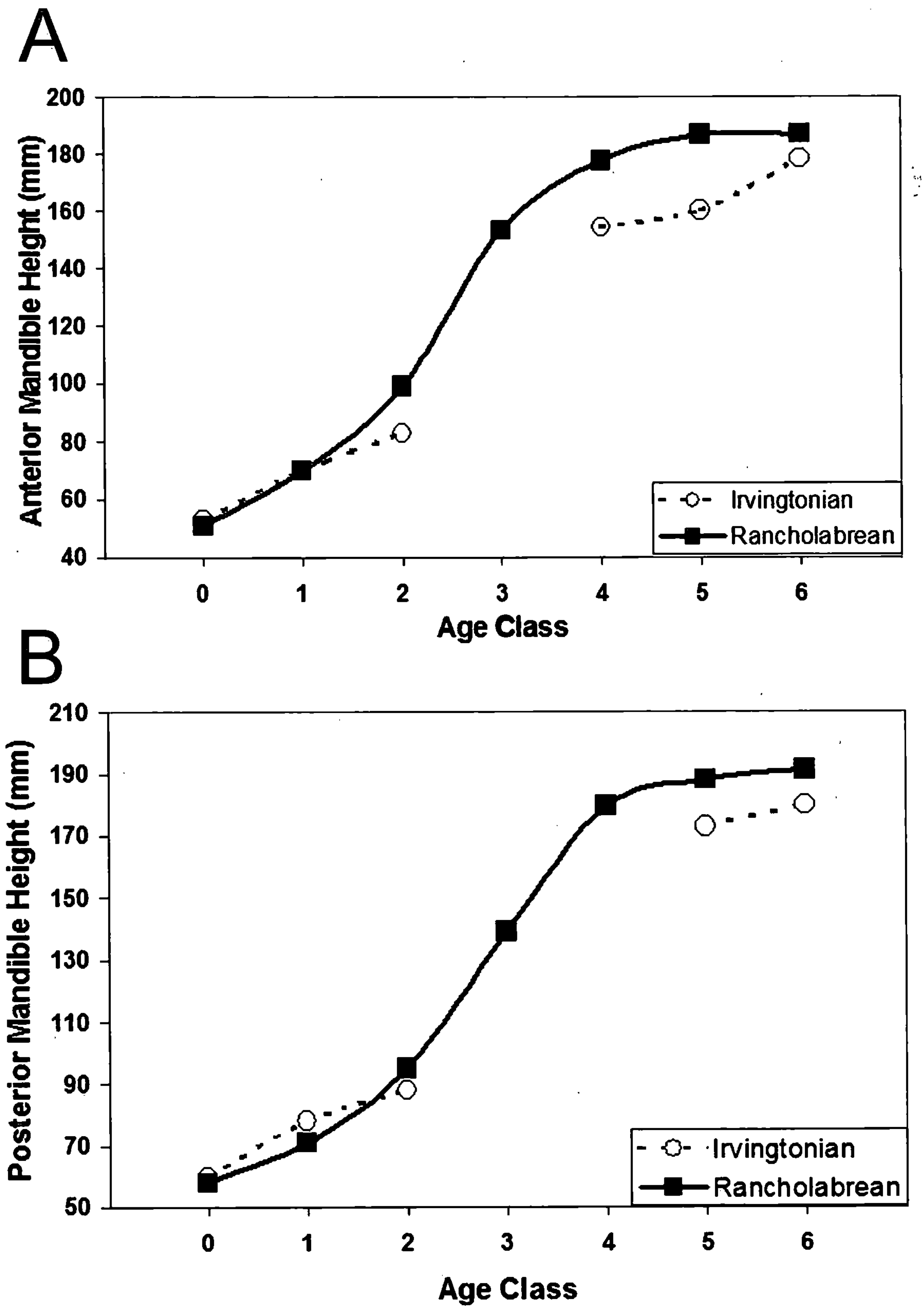
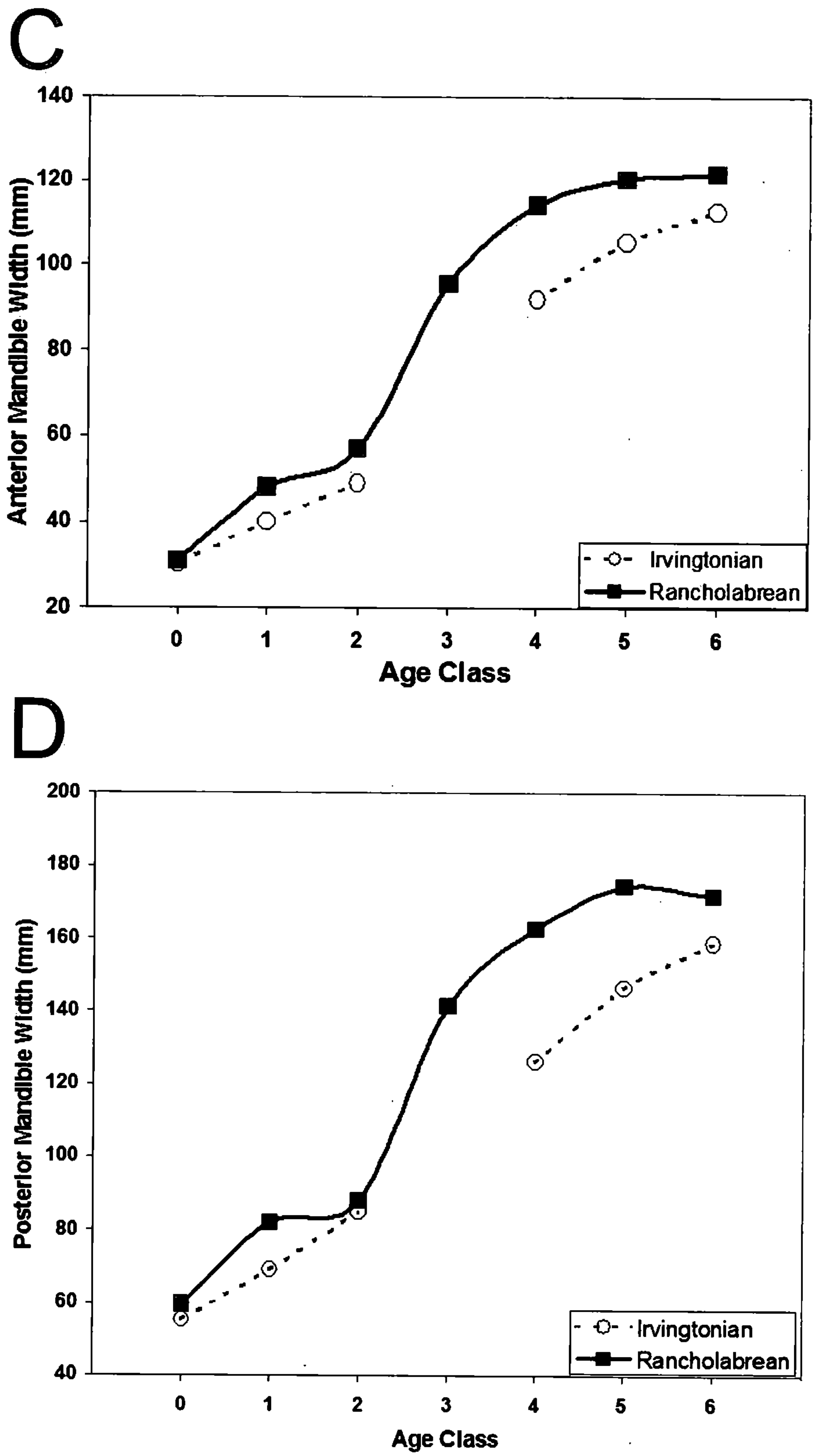


Figure 10. A.) Growth curve of anterior mandibular height for Rancholabrean vs. Irvingtonian *Mammut americanum* from Florida; B.) Growth curve of posterior mandibular height for Rancholabrean vs. Irvingtonian *M. americanum* from Florida.;



C.) Growth curve of anterior mandibular width for Rancholabrean vs. Irvingtonian *Mammut americanum* from Florida; D.) Growth curve of posterior mandibular width for Rancholabrean vs. Irvingtonian *M. americanum* from Florida.

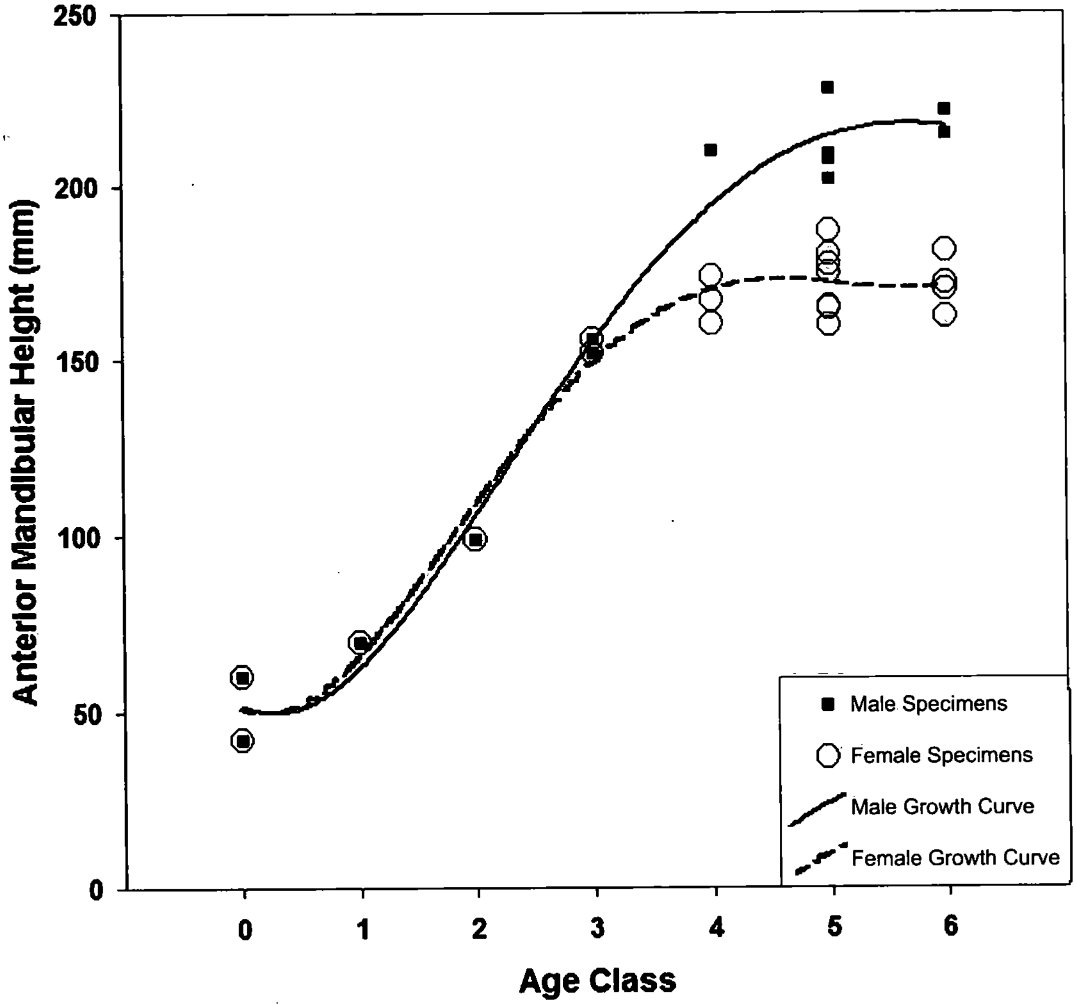


Figure 11. Growth curves for male and female Rancholabrean *Mammut americanum* anterior mandibular height.

nificant into age class 6.

Irvingtonian and Rancholabrean *Mammut americanum* individuals grew at approximately the same rate from birth until age class 2. The transition from age class 2 to 3 shows Rancholabrean individuals suddenly growing larger. The boundary between age class 2 and 3 is the transition from the juvenile to the youth developmental stage (Table 1) and could correspond to the onset of puberty and an increase in sexual dimorphism.

Modern elephants have family groups that generally consist of related adult females and juvenile animals (both males and females) (Owen-Smith 1988). Males usually leave the group at the onset of spermatogenesis (beginning of puberty), while females remain (Owen-Smith 1988). The onset of adulthood is slightly different for African and Asian elephants. For the former, males start puberty between 7 to 15 years and females between 11 to 14 years; yet in the latter, males start puberty between 7 to 10 years and females between 7 to 8 years (Owen-Smith 1988). If *Mammut americanum* ages correspond to African elephant ages for similar developmental stages, then *M. americanum* would transition from juvenile and youth developmental stages between 5-12 African elephant years, according to Laws (1966).

Figure 11 illustrates male-female growth differences for Rancholabrean *Mammut americanum*, with males accelerating growth well beyond females between age classes 3-4 (the onset of puberty in modern elephants; Owen-Smith 1988). The lack of bimodalism for age class 3 (Fig. 11) is probably due to small sample size (n=2). This differential growth rate between genders was termed "holobiotic heteromorphism" by Jarman (1983). Pronounced sexual dimorphism in *M. americanum* was thus achieved through males growing at an accelerated rate relative to females, as opposed to a difference in relative maturation ages between genders (progenesis or relative hypermorphosis) (McNamara 1995). This type of heteromorphism is visible in other large mammalian taxa, such as *Loxodonta africana* (Jarman 1983; McNamara 1995).

RESPONSE OF *MAMMUT AMERICANUM* TO ECOGEOGRAPHIC AND CLIMATIC CHANGE IN FLORIDA

The body mass of *Mammut americanum* increased substantially from the Irvingtonian to the Rancholabrean of Florida, as previously discussed. Much research has already documented body size fluctuations in Cenozoic mammals, as well as the mechanisms responsible for these changes (Kurten 1968; Prothero & Sereno 1982; Koch 1986; Hulbert & Morgan 1993; Lister 1993; Purdue & Reitz 1993; Seymour 1993; Lister 1997). Underlying causes for drastic body mass shifts (in a few generations or more) in mammals can be "ecophenotypic" (direct effect of the environment), "evolutionary" (modification through genetic change), or a combination of the two (genetic assimilation or facultative adaptation) (see Lister 1997 for a more detailed review). It is possible that one or all of these factors influenced body mass fluctuations in *M. americanum* from the Pleistocene of Florida. Concerning ecophenotypic changes, variables in the surrounding environment that can induce drastic, short-term changes in body size in organisms include food quality (nutritive value) and quantity, as well as climatic change (Jarman 1974; Prothero & Sereno 1982; Lister 1997). This section explores possible "ecophenotypic" response scenarios to further explain the noted body mass increase in *M. americanum*.

FOOD QUANTITY AND QUALITY

A direct relationship exists between the quantity of food consumed and body size in mammals (Jarman 1974). The late Cenozoic (~2.5 Ma) saw the start of the Great American Biotic Interchange, with multiple migrations of land mammals between North and South America (Webb 1991). The transition between the Irvingtonian and Rancholabrean age in North America saw an increase in land mammal diversity and the majority of immigrants were both small and large grazers and large browsers (Webb 1984). The increase of large browsing taxa in the Rancholabrean could imply that more browsing habitat and food was readily available, thus *Mammut americanum* could have increased food consumption. Nutritive value of the consumed food is also reflected in herbivore body size, as large herbivores generally feed on foods low in nutritive value because they are available in higher quantities than foods with high nutritive value (Jarman 1974). Larger herbivores are also less selective in feeding and physiologically adapted to surviving on a low nutritive value diet than smaller herbivores (Jarman 1974). Thus, an increase in consumed food quantity with a corresponding decrease in food quality could account for increased body mass in *Mammut americanum* from the Irvingtonian to the Rancholabrean. However, this hypothesis implies a temporal dietary change. Green et al. (2005) examined paleodiet in both Irvingtonian and Rancholabrean Florida *M. americanum* and both appear to have maintained the same browsing strategy, although this was not statistically tested due to limited samples. In addition, dietary change could correspond with a significant morphological change in third molars. While M3 measurements (length, width) show a slight disproportional increase, m3 measurements increased approximately proportional to each other (Table 4). Future research studying temporal shifts in *M. americanum* diet (perhaps through isotopic analyses) is needed to further test this hypothesis.

ENVIRONMENTAL AND CLIMATIC CHANGE

The environment and ecogeography of North America changed drastically during the late Cenozoic due to the rapidly changing climates invoked by Milankovik Cycles and corresponding glacial and interglacial phases, resulting in one of the most stressful times in geologic history for fauna and flora (Carroll 1997; Clark et al. 1999; Wang & Deng 2005). Temporal change in *Mammut americanum* body mass could have been in response to fluctuating environmental and climatic conditions induced by interglacial/glacial cycles, as the environmental effects of these shifts were registered in Florida (Watts & Hansen 1988; Webb 1991). Kurten (1968) documented several European species, including *Mammuthus primigenius* (Blumenbach 1803), changing body size rapidly in response to glacial advance and retreat. Mean global temperatures also decreased throughout the Pleistocene until the end of the last glacial maximum (Zachos et al. 2001). *Mammut americanum* may have followed Bergmann's Rule through increasing body mass in order to adapt to the cooler conditions in the Rancholabrean, as large bodied mammals (>500 g) show a strong tendency to follow Bergmann's Rule (Meiri & Dayan 2003). While climate change could be responsible for the body mass fluctuation in *M. americanum*, Alroy et al. (2000) suggests the impact of climatic change on body mass in mammals may be less important than biotic factors. The small sample sizes of this study preclude further explanation for Florida *Mammut americanum* increased body mass. A more comprehensive, comparative study of chronoclinal body mass change in multiple Pleistocene mammals from Florida would support further explanation of *M. americanum* temporal change, as well as help elucidate any possible correlation of environmental and climatic change with body mass fluctuations in fossil mammals over time.

CONCLUSIONS

This study examines morphological, sexually dimorphic, and growth differences between Irvingtonian and Rancholabrean *Mammut americanum* populations from Florida. This study demonstrates that *M. americanum* was as not conservative in its evolution as previously thought, because Florida populations showed directional selection for increased third molar, limb bone, and mandibular size, as well as increased growth rate and decreased mandibular tusk frequency from the Irvingtonian to the Rancholabrean. M3 length, m3 length and width, humeral length and mid-shaft circumference, anterior mandibular width, and posterior mandibular height and width were found to be significantly larger in Rancholabrean individuals. Florida *M. americanum* also showed more dramatic directional selection for limb bone circumference (which increased ~20%) than tooth size (length and width, which increased only ~5%) and could indicate that *M. americanum* did not follow isometry in growth between molars and body mass, although this remains to be allometrically tested. Even though statistically significant differences in means are lacking in some measurements, the values of all Irvingtonian specimens in this study are smaller than those from the Rancholabrean.

While *Mammut americanum* demonstrates a strong increase in body mass into the Rancholabrean of Florida, the underlying cause for this shift is not currently known. It is possible this trend is correlated with either a shift in food quantity and quality, or perhaps with the rapidly changing environmental and climatic conditions in the Pleistocene, or perhaps a mixture of both scenarios. Further investigation with larger samples is needed to indicate the exact cause for this observed shift in body mass.

Mammut americanum mandibles show significant sexual dimorphism in the anterior portion of the mandible in Rancholabrean specimens. Sexual dimorphism appears lacking in Irvingtonian mandibles, but sample sizes may be too small to accurately demonstrate gender differences. Mandibular dimorphism in Rancholabrean *M. americanum* is further supported by examination of mandibles associated with gender determined skeletons – males had larger anterior mandibular height than females. This observation could help support gender determination of skeletons that lack an associated pelvis.

Mammut americanum mandibular tusks, while traditionally regarded as sexually dimorphic, were found to not be sexually dimorphic in either Irvingtonian or Rancholabrean Florida populations. Mandibular tusks also demonstrate a decrease in presence/absence frequencies through time, as all Irvingtonian mandibles studied had tusks, while only 27% of Rancholabrean specimens had them.

Finally, *Mammut americanum* experienced a heterochronic change in growth rate over time, with Irvingtonian individuals growing more slowly (but following the same growth pattern) than Rancholabrean ones. Growth ended at the time of complete eruption of the m3 (age classes 5-6). Rancholabrean and Irvingtonian *M. americanum* were born at roughly the same size and grew at the same rate until age class 2-3, when Rancholabrean individuals increased growth rate more than Irvingtonian ones. The Rancholabrean growth increase probably corresponds with the onset of sexual maturity (which occurred at ~12.7 years of age; Shipman 1992), and is the result of males growing faster than females (i.e., holobiotic heteromorphism). The relative acceleration of male growth beyond female growth created pronounced sexual dimorphism in *M. americanum.*

Time-averaging of chronologically diverse Florida fossil localities into two subsets, Irvingtonian and Rancholabrean, is important to interpret the results of this study. The Rancholabrean sample includes elements from 20 different localities, which could vary in geologic age from 300,000 to 10,000 ybp (Webb 1974; Hulbert 2001) and most do not possess absolute ages, as opposed to the Irvingtonian sample, which is only limited to four localities with estimated absolute ages of 1.5-1.0 Ma (Leisey Shell Pit, Pool Branch) (Morgan & Hulbert 1995; Hulbert 2001) and ~0.6-0.5 Ma (La Belle Highway Pit, Tri-Britton Site) (Meers & Hulbert 2002). Therefore, the time averaging of elements from 20 different localities across a 300,000-year interval could inflate observed phenotypic variance (Bush et al. 2002; Barnosky et al. 2004; Hunt 2004). This inflation is reflected in the overall high CV estimates for Rancholabrean *Mammut americanum* samples (Tables 2, 5, 7). Thus, true Rancholabrean phenotypic variance of *M. americanum* is interpreted to be less than observed phenotypic variance in this study.

While the results of this study are conclusive about certain aspects of *Mammut americanum* evolution, sample sizes for some results in this study are still lacking and need to be increased, especially those for

Irvingtonian elements. Such a sample increase would further test the conclusions made in this paper.

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Appendix. Specimen number, element identification, locality, NALMA, and raw data results for Florida Irvingtonian and Rancholabrean *Mammut americanum* measurements for this study. UF, UF/FGS, DMAS=catalogued specimens deposited in Florida Museum of Natural History Vertebrate Paleontology collection, Gainesville, Florida; MOSI=catalogued specimens deposited in Museum of Science and Industry, Tampa, Florida; TTRS/WA=catalogued specimen deposited in Tall Timbers Research Station, Tallahassee, Florida; BF, BFa, GO, JS, JT=uncatalogued specimens in private collections; CPI-BM, HM, RM=uncatalogued specimens deposited in Coastal Plains Institute and Land Conservancy, Tallahassee, Florida; W=Wakulla mastodon, uncatalogued skeleton mounted in Museum of Florida History, Tallahassee, Florida; WP=West Palm mastodon, uncatalogued skeleton mounted in South Florida Science Museum, West Palm Beach, Florida. For the Tusks column under Mandibles: 0 = mandibular tusks not present, 1 = mandibular tusks present, - = indeterminate.

Part 1. Upper third molar measurements (M3s)

Specimen	Locality	Max Length	Width 1	Width 2	Width 3	Max Width
Irvingtonian						
UF 215058	Hendry Co., La Belle Highway Pit	162	86.7	85.7	86.5	86.7
UF 215060	Hendry Co., La Belle Highway Pit	164.5				
UF 206855	Hendry Co., Tri-Britton Site	159.7			83.4	83.4
GO 6	Hillsborough Co., Leisey Shell Pit	151.1	93.5	93.5	86.1	93.5
BF 19	Hillsborough Co., Leisey Shell Pit	176	104.5	99.5		104.5
Rancholabrean						
JS 2	Alachua Co., Santa Fe River	163.5	105.3	105.8	102.5	105.8
JS 1	Alachua Co., Santa Fe River	173.2	97.4	93.7	92.8	97.4
UF 40001	Columbia Co., Ichetucknee River	187	104.8	99.4	96.2	104.8
UF 210253	Levy Co., Wacassa River	168.8		94.7	94.9	94.9
UF 16454	Levy Co., Wacassa River		84.4	84.3		84.4
UF 210254	Levy Co., Wacassa River				87.5	87.5
UF 206884	Madison Co., Munroe Sloth Site	182.4	91.7	93.3	91.8	93.3
UF 13505	Palm Beach Co., West Palm Beach	186	91.5	95.6	92.3	95.6
UF 135709	Taylor Co. Line, Aucilla River	164.8	93.4	94.8	84.6	94.8
UF 192226	Taylor Co., Aucilla River	175.5	103.4	102.8	99.4	103.4
UF 135724	Taylor Co., Aucilla River	159.1	88.3	88.7	86.9	88.7
UF 135722	Taylor Co., Aucilla River	168.3	101.8	105.7	100.5	105.7
UF 135725	Taylor Co., Aucilla River	171.3	98.5	105.2	98.1	105.2
UF 135713	Taylor Co., Aucilla River	177.3	99.2	94.2	99.2	
UF 135726	Taylor Co., Aucilla River	187.7	98.2	100.6	98.8	100.6
UF 135723	Taylor Co., Aucilla River	197.2	110.4	108.7	105.4	110.4
CPI-RM 4	Taylor Co., Aucilla River	197.4	106	103.7	101.2	106
UF 135727	Taylor Co., Aucilla River		86.6	82.6	82.7	86.6
CPI-BM 3	Taylor Co., Aucilla River	194.3	98.5	101.3	94.6	101.3

DMAS 705	Volusia Co., Daytona Beach Bone Bed	143.2	82.2	80.9	76.5	82.2
DMAS 449	Volusia Co., Daytona Beach Bone Bed		79.8	85	81.3	85

Part 2. Lower third molar measurements (m3s)

Irvingtonian						
UF 215057	Hendry Co., La Belle Highway Pit	162	75.3	86.7	83.1	86.7
UF 215061	Hendry Co., La Belle Highway Pit	181.7	80	86.1	91.8	91.8
UF 215059	Hendry Co., La Belle Highway Pit	184	84.1	96	93	96
UF 206851	Hendry Co., Tri-Britton Site	164.1	77.9	84	82.3	84
Rancholabrean						
UF 210251	Levy Co., Wacassa River	181	86.3	95.7	94.7	95.7
UF 210252	Levy Co., Wacassa River	189.6	86.1	96	96.9	96.9
UF 16463	Levy Co., Wacassa River				94.7	94.7
UF 48920	Levy Co., Wacassa River				85.1	85.1
UF 51192	Palm Beach Co., Palm Beach Farm	178.4	79.2	89.7	86.5	89.7
UF 18504	Palm Beach Co., West Palm Beach	187.6	81.8	95.8	95.9	95.9
UF 11492	Sarasota Co., Venice		84.3		88.3	88.3
CPI-HM 9	St. Lucie Co., Dickerson Pit	185	89	95.5	98.4	98.4
UF 135705	Taylor Co. Line, Aucilla River	183	79.1	89.4	89.5	89.5
UF 135712	Taylor Co., Aucilla River	158.3	85.6	92.9	89.6	92.9
UF 135721	Taylor Co., Aucilla River	164	89.8	100.6	94.7	100.6
UF 211300	Taylor Co., Aucilla River	167	87.4	97.4	101.2	101.2
UF 135720	Taylor Co., Aucilla River	173	86.3	89.9	88.3	89.9
UF 135714	Taylor Co., Aucilla River	177.2	85.7	89.1	88.3	89.1
UF 135715	Taylor Co., Aucilla River	186.1	86.1	96.5	95.5	96.5
UF 135703	Taylor Co., Aucilla River	187	83.4	94.7	94.9	94.9
UF 135704	Taylor Co., Aucilla River	187.7	86.8	95.8	96.6	96.6
UF 135717	Taylor Co., Aucilla River	187.9	83.6	95.5	90.2	95.5
UF 135701	Taylor Co., Aucilla River	199.5	91.9	99.3	99.4	99.4
UF 135718	Taylor Co., Aucilla River	216.5	97	105.5	106.2	106.2
CPI-BM 1	Taylor Co., Aucilla River	155	94.5	93.1	91.9	94.5
CPI-BM 8	Taylor Co., Aucilla River	201.3	99	111	111.6	111.6
UF 200661	Taylor Co., Aucilla River, Sloth Hole	174.8	83.6	91.5	90.5	91.5
UF 200681	Taylor Co., Aucilla River, Sloth Hole	182.3	88.7	96	93.6	96
DMAS 578	Volusia Co., Daytona Beach Bone Bed	191.4	86.7	98.1	94.9	98.1
DMAS 445	Volusia Co., Daytona Beach Bone Bed			80.1	81.3	81.3
CPI-RM 3	Volusia Co., Daytona Beach, Intracoastal Waterway		95.7	99.3	101.3	101.3

Part 3. Limb bone measurements

Irvingtonian

Specimen	Limb Bone	Locality	Art Length	Mid Circum
UF 214718	Humerus	Hendry Co., La Belle Highway Pit	765	345
UF210415	Humerus	Hendry Co., Tri-Britton Site	760	340
UF 210414	Femur	Hendry Co., Tri-Britton Site	950	380
UF 214726	Ulna	Hendry Co., La Belle Highway Pit	710	275
UF 214711	Tibia	Hendry Co., La Belle Highway Pit	645	245
Rancholabrean				
JS 1	Humerus	Alachua Co., Santa Fe River	913	468
UF 61905	Humerus	Columbia Co., Santa Fe #18	890	445
UF 156814	Humerus	Jefferson Co., Wacissa River	875	440
TTRS/WA 103-5	Humerus	Jefferson Co., Wacissa River	889	429
WP	Humerus	Palm Beach Co., West Palm Beach	795	430
UF 204652	Humerus	Charlotte Co., Port Charlotte	990	410
UF137981	Humerus	Taylor Co., Aucilla River	868	412
UF 211300	Humerus	Taylor Co., Aucilla River	1020	508
UF 14778	Humerus	Taylor, Aucilla River	891	442
W	Humerus	Wakulla Co., Wakulla Springs	914	467
WP	Femur	Palm Beach Co., West Palm Beach	955	
UF 137891	Femur	Taylor Co., Aucilla River	1090	410
UF 211300	Femur	Taylor Co., Aucilla River		510
W	Femur	Wakulla Co., Wakulla Springs	1143	410
UF 211300	Ulna	Taylor Co., Aucilla River	895	435
UF 137891	Ulna	Taylor Co., Aucilla River	747	315
UF 14778	Ulna	Taylor Co., Aucilla River	760	340
UF 14778	Tibia	Taylor Co., Aucilla River	657	300

Part 4. Mandibular measurements

Irvingtonian

Specimen	Age Class	Locality	Post Depth	Ant Width	Post Width	Ant Depth	Tusks
UF 88875	0	Hillsborough Co., Leisey Shell Pit	60	32	53	59	1
UF 80286	0	Hillsborough Co., Leisey Shell Pit	60	29	60	57	1
MOSI 030601	0	Hillsborough Co., Leisey Shell Pit		30	53	43	1
UF 27901	1	Polk Co., Pool Branch	78	40	69	70	1
UF 210411	2	Hendry Co., Tri-Britton Site	77	44	79	81	1
UF 81453	2	Hillsborough Co., Leisey Shell Pit	99	54	91	85	1
MOSI 1	4	Hillsborough Co., Leisey Shell Pit		92	126	154.1	1

UF 215057	5	Hendry Co., La Bell Highway Pit	177	111	147	167	1
UF 210408	5	Hendry Co., Tri-Britton Site	173		144		-
UF 215061	5	Hendry Co., La Bell Highway Pit	169	100	148	153.5	1
UF 210450	6	Hendry Co., Tri-Britton Site	170	115	146	170	1
UF 210409	6	Hendry Co., Tri-Britton Site	190	104	173	190	1
UF 215059	6	Hendry Co., La Bell Highway Pit	180	119	157	175	1
Rancholabrean							
UF 47217	0	Alachua Co., Hornsby Springs	61	35	63	60	0
UF 160000	0	Alachua Co., Surprise Cave	55	27	56	42	1
UF 131987	1	Marion Co., Ocklawaha River	71	48	82	70	1
UF 135706	2	Taylor Co., Aucilla River	95	57	88	99	0
UF 135707	3	Taylor Co., Aucilla River	141	96	137	152	0
UF/FGS 5446	3	Indian River Co., Vero	140	97	148	156	-
UF 135708	3	Taylor Co., Aucilla River	136	94	139	152	-
UF 135702	4	Taylor Co., Aucilla River		112	157	167	0
WP	4	Palm Beach Co., West Palm Beach	180.8			173.8	0
JT 1	4	Citrus Co., Withlacoochee River	161	111	155	160	1
UF 135703	4	Taylor Co., Aucilla River	190	115	162		-
UF 180220	4	Taylor Co., Aucilla River	187	119	176	210	0
UF 137891	5	Taylor Co., Aucilla River	160	121	172		-
UF 3356	5	Alachua Co., Hornsby Springs	176	106	181	164.5	0
DMAS 578	5	Volusia Co., Daytona Beach Bone Bed	176	113	162	159.5	1
UF 3372	5	Alachua Co., Hornsby Springs	191	109	178	187	0
UF 135701	5	Taylor Co., Aucilla River	182	131	195	228	0
UF 211300	5	Taylor Co., Aucilla River	209	130	178	209	0
UF 135705	5	Taylor Co., Aucilla River	183	126	157	165	0
UF 11492	5	Sarasota Co., Venice	182	122	143	177	-
UF 2124	5	Columbia Co., Santa Fe River		122	182		-
UF 135704	5	Taylor Co., Aucilla River	203	115	175	175	-
UF 18504	5	Palm Beach Co., West Palm Beach	170	117	158	180	1
UF 135778	6	Aucilla River, Taylor Co.	195	155	202	222	0
UF 32309	6	Columbia Co., Ichetucknee River	201	121	174		0
UF 217282	6	Columbia Co., Ichetucknee River	173	115	163	172	0
W	6	Wakulla Co., Wakulla Springs	220		153	215	0
UF 1965	6	Marion Co., Ocklawaha River	186	116	159	170	0
UF 3064	6	Columbia Co., Ichetucknee River	190	123	171	162	1
UF 65644	6	Columbia Co., Ichetucknee River	194	122	179	181	-

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