8-2011

Extreme Variation in the Sagittal Crest of Tapirus polkensis (Mammalia Perissodactyla) at the Gray Fossil Site Northeastern TN.

Aaron Randall Abernethy
East Tennessee State University

Recommended Citation

Extreme Variation in the Sagittal Crest of *Tapirus polkensis* (Mammalia, Perissodactyla) at the
Gray Fossil Site, Northeastern TN

———————————————

A thesis

presented to

the faculty of the Department of Biological Sciences

East Tennessee State University

In partial fulfillment

of the requirements for the degree

Master of Science in Biology

———————————————

by

Aaron Randall Abernethy

August 2011

———————————————

Steven C. Wallace, Chair

Jim I. Mead

Blaine W. Schubert

———————————————

Keywords: Tapirs, Sexual Dimorphism, Intraspecific Variation, Pathology, Ontogeny

ABSTRACT

Extreme Variation in the Sagittal Crest of *Tapirus polkensis* (Mammalia, Perissodactyla) at the
Gray Fossil Site, Northeastern TN

by

Aaron Randall Abernethy

The preservation and quantity of fossil tapirs (*Tapirus polkensis*) from the Gray Fossil Site in northeastern Tennessee provides a unique opportunity for comparison and analysis of skeletal characters. Intraspecifically, modern tapirs show little to no variation in the morphology of the sagittal crest. However, several different morphologies exist within the sample at Gray. No osteological evidence of sexual dimorphism exists for tapirs, and no correlation between crest shape and sex was observed. Several juveniles display well defined crests, while some adults have only minor thickening of the temporal ridges; therefore, no distinct correlation between age and crest state could be established. Three different patterns of wear exist within the sample, but there is no correlation between these and crest morphology. No cranial pathologies were found to be associated with a crest type. Despite some correlations the sagittal crest could simply be a variable character due to intraspecific variation.

ACKNOWLEDGEMENTS

CONTENTS

LIST OF TABLES

LIST OF FIGURES

Figure   Page

CHAPTER 1

INTRODUCTION

Tapirs are medium to large sized mammals belonging to the Order Perissodactyla, which also includes modern horses and rhinos (Janis 1984). They are more closely related to rhinos in the Suborder Ceratomorpha and are considered to be primitive in morphology (Janis 1984). Perissodactyls are defined as an ungulate with an odd number of digits and were much more diverse in the past (Janis 1984). Extinct groups such as chalicotheres and brontotheres were abundant during the Miocene and Eocene respectively (Coombs 1975; Mihlbachler 2008). Four modern species belong to the Family Tapiridae and all are considered threatened or endangered due to constricted habitats, habitat removal, and the lack of knowledge about their numbers in the wild (Bauer pers. com.). Tapirs are found today in tropical latitudes, with a disjunct distribution of Central America, northern South America, and Malaysia (Padilla and Dowler 1994; Padilla et al. 2010).

The Gray Fossil Site (GFS) in northeastern Tennessee has yielded the largest number of fossil tapirs than any other site in the world. With approximately eighty individuals and counting (Hulbert et al. 2009), the GFS provides an opportunity to study population dynamics and variation in a fossil species. Consequently, the goals of this study are to assess the amount of variation present within a single character, the sagittal crest, of the sample of fossil tapirs at the GFS and to compare the amount of variation observed with modern and extinct members of the genus *Tapirus*. Major questions of this study are as follows: What is responsible for the variation seen within the sagittal crest character; how does this variation compare to other tapirs;

and what does the variation observed within the character reflect about the habitat or behavior of these tapirs.

Sagittal crests are distinct features on many mammals, including tapirs, and are defined as a narrow ridge on the braincase formed by the migration and fusion of 2 parasagittal ridges (Holbrook 2002). This migration is typically attributed to ontogeny, and as the animal reaches adulthood the ridges merge to a medial position on the skull (Holbrook, 2001). However, complete fusion of the ridges is labeled a "true crest" by some authors (Simpson 1945; Holbrook 2001; Hulbert et al. 2009). In the genus *Tapirus*, each temporal ridge is formed on the parietals but also extends onto the frontals and is generally concave medially. Within *T. polkensis* from the GFS the interparietal varies in size and shape, being dorsoventrally flattened and triangular to reduced and laterally compressed in some individuals (Hulbert et al. 2009). This variation is typically not seen in adults of other species, where the interparietal shape is consistent much like the crest itself (Lundelius and Slaughter 1976; Hulbert et al. 2009). In modern tapirs 3 distinct morphologies of sagittal crest exist that are also present in early tapiromorphs and most fossil tapirs (Holbrook 2001). *Tapirus pinchaque* (Wooly Mountain Tapir) exhibits the true crest form and is the only modern tapir species that retains this morphology (Hulbert et al. 2009), which is considered primitive (Ray and Sanders 1984), and is described by Holbrook (2001) as occurring in many tapiromorphs and early perissodactyls. In *T. indicus* (Malayan Tapir) and *T. bairdii* (Baird's Tapir) temporal ridges never merge, but instead the process is suppressed, with the parietals and inter-parietal forming a sagittal table. Generally flattened from the frontals to the supraoccipital, this form occasionally also exhibits a concavity in the interparietal to form a small depression (Holbrook 2001). In the fourth extant taxon *T. terrestris* (Brazilian Lowland Tapir) the crest forms in a unique way, which so far has not been observed in any fossil species.

Specifically, crests in this species erupt directly out of the back of the skull medially and extend vertically very early in life (Holbrook 2002). However, Albright (1998) described one juvenile skull of *Nexuotapirus*, a Miocene form of Texas, which he postulates forms in the same way due to the high development at such a young age (before the eruption of the second upper molar). However, with only one described specimen it is not clear whether or not this is truly the same growth pattern as in *T. terrestris*.

Simpson (1945) declares the crest to be highly useful for fossil and modern tapir identification, claiming that each form is clearly the most diagnostic character available. However, *Tapirus polkensis* (Olsen 1960) from GFS exhibits a unique amount of variation in the sagittal crest character (Hulbert et al. 2009) where 4 separate crest types were observed and can be classified. These types include: 2 temporal ridges that come into close proximity of one another and sometimes are tangential, 2 temporal ridges which merge together to form a "true" crest, 2 temporal ridges that flatten anterio-posteriorly and create a flattened sagittal table, and sagittal table that is extended dorsally. Two of these 4 morphologies are exhibited by modern tapirs.

Several hypotheses to explain the variation include: 1) Sexual dimorphism, 2) ontogeny, 3) pathology, 4) multiple species, 5) preferential feeding, or 6) random intra-specific variation. As a result, the goals of this study are to analyze each possible source of this extreme variation to determine how the sagittal crest in *T. polkensis* is similar to and/or unique from that of other taxa and to better understand how osteological features respond to environmental parameters.

<u>Background</u>

<u>Sexual Dimorphism</u>

Perissodactyls often exhibit sexual dimorphism, as with most Ungulata (Nowak and Paradiso 1983). For example, Gingerich (1981) reported sexual dimorphism in canine and overall skull size in 2 separate species of the Eocene equiid *Hyracotherium*, and Coombs (1975) identified dimorphism in the radius and tibia lengths in Chalicotheres. Sexual dimorphism has also been noted in many modern and fossil rhinos from North America, Africa, and Asia (Dinerstein 1991; Mead 1999, 2000; Deng 2005; and Mihlbachler 2007). Dimorphic features were found in the Miocene rhino *Teleoceras major* by Mead (2000) for example, with males possessing a significantly greater size in many cranial and postcranial characters, especially fore and hind limb measurements over females. However, sexual dimorphism has never been reported in osteological characters of any *Tapirus* species or tapiromorphs. Fortunately, sexual dimorphism typically expresses itself in more than one osteological character; therefore, it is unlikely for a sample to display dimorphism in one character without a reaction to other features.

Sexual dimorphism of craniodental features is also prominent in many carnivorans, especially mustelids, procyonids, and felids (Gittleman and Van Valkenburgh 1997). Most significant are the differences seen in the canines, but this is correlated to breeding behavior and not body size like in many ungulates (Gittleman and Van Valkenburgh 1997). While most sexual dimorphism studies in Carnivora focus on craniodental features, studies that address postcranial material generally are used for locomotive and behavioral aspects. One of the most prevalent dimorphic features noted by Mead (2000) in *Teleoceras major* is the canine-like lower tusks, actually second incisors, that were significantly larger in males (around 1.5 times female

size). Despite the lack of canines in *Teleoceras*, this feature is comparable due to morphological and functional similarities and is another good example of sexual dimorphism in this character.

Ontogeny

Long considered to be a process of ontogeny, the development of the sagittal crest has been previously hypothesized to form from the migration of the temporal ridges from a lateral position in young juveniles merging toward a dorsal positioning in adult forms as the animal grows and the temporalis muscle develops (Simpson 1945; Ray and Sanders 1984; Holbrook 2001). However, Holbrook (2002) notes that the growth of the sagittal crest in *Tapirus terrestris* occurs almost immediately after birth and becomes fully developed quickly in very young juveniles. This could be due to the unique development of the sagittal crest in that species but could also reflect growth that all taxa take on; just not the pattern in that the crest develops into the adult morphology it exhibits later in life. Recently, Hagge (2010) described the ontogenic changes seen in the cranium of *Teleoceras major* (Rhinoceridae, Perissodactyla) and compared those to modern rhino taxa to develop several characters that uniformly change in aging rhinoceros. He noted that early developmental changes occurred in the lengthening of the skull, the timing of the development of tusks was similar across taxa, and strong development of the temporalis and masseter attachment areas were not prominent until adulthood. The excellent preservation and quantity of the ashfall rhinos provides the ability to create an ontogenic sequence that is not available with most fossil sites. The ashfall rhinos also prove vital for comparison to *Tapirus polkensis* at GFS.

Pathological Response

Pathogens present within a population can be reflective of the nutrition level in the surrounding environment. One example within *Felis concolor* was noted to contain high amounts of pathogens and geographic morphological variation between 2 separate populations (Duckler and Van Valkenburgh 1998). DeSantis and Wallace (2008) describe the GFS as a refugium in the late Miocene, maintaining a warm, wet climate with closed forests, in a North American continent becoming dominated by open grasslands. If the tapirs at GFS represent a single population and a cranial pathogen is prevalent within the sample, it could be correlated with changes in mastication behavior and development of the sagittal crest.

Multiple Species

Coefficients of variation calculated for the population based on linear measurements of the cheek teeth have indicated that the sample does support a single mammalian species, with most of the CV values being under 10 (Hulbert et al. 2009). The number 10 as a general upper limit has been documented in many osteological features of modern species (Yablokov 1974). Hulbert et al. (2009) focused their study on teeth, so this study will examined other cranial and post-cranial features to look for similar results.

Preferential Feeding

For decades very little was known about tapir diet, probably due to the cryptic nature of the animals, the endangered status, and the dense habitat in which they live. Early reports were inconclusive or unsubstantiated, basing the diet of individuals on observations of damaged plants found near tapir track ways (Medway 1974). Due to the lack of information on the diet, it is almost certain that zoo specimens were not fed a "natural" diet. Early reports of zoo raised

individuals (1930s) describe oatmeal and corn based diets with minor amounts of fruit; however, this could have been due to either ignorance of the natural diet or rationing of fruits during war times. Modern zoos typically feed many of their ungulates a generic tablet made of grains and corn, but some zoos use fruit, especially bananas, as a treat and/or manipulation tool for tapirs (Bauer pers.com; Jensen pers. com.).

Tapirs are considered to be opportunistic feeders, consuming any food source readily available including fruit, nuts, bark, stems, leaves, etc. (Olmos 1997). This behavior is also seen in zoo specimens that consume any plant mater, even sources that in large amounts will cause sickness (Jensen pers. com.). In the late 1990s and early 2000s many authors began describing in detail the feeding behavior and diet of the modern species. These works were published in a culmination of work printed by the Tapir Conservationist Group for a conservation action plan. The articles included detailed lists of plant species consumed and dispersed by tapirs and was the first and most detailed work to date documenting diets (Khan 1997; Olmos 1997; Galetti et al. 2001; Foerster and Vaughan 2002). Unlike before, this was accomplished by collecting tapir dung and the seeds within (Olmos 1997). Despite the wide variety of food sources, the diets of modern taxa vary geographically depending on availability of the corresponding plant species. Of the modern taxa *T. indicus* seems to have the most restrictive diet, which could be a product of lacking data rather than low plant species diversity in Malaysia. Medway (1972) noted many species in the same forests as he observed Malaysian tapirs 2 years later. These species included many fruits such as figs; however, these species are not described later as food sources, but Olmos (1997) notes that tapirs will prefer sugar rich foods such as fruits when available.

<u>Intraspecific Variation</u>

Within some morphological characteristics of mammals the amount of variation seen is considered high, thus deeming the character unsuitable for species identification. Such features are often evaluated by coefficients of variation (CV), which was first applied to *Tapirus* taxa by Simpson (1945) and *T. polkensis* by Hulbert et al. (2009). Simpson (1945) noted that *T. terrestris* skulls collected from certain localities had a higher range of CV values compared to those of all the combined samples from the geographical heterogeneous range. The complete geographic range of *T. polkensis* is yet unknown; however, specimens are also known from Florida localities as well as GFS. Hulbert et al. (2009) found most of the linear measurements recorded of the sample at GFS to indicate a single mammalian species (CV<10) but also noted that several characteristics within the sample were highly variable including the sagittal crest, shape of the nasals, and the number and strength of lingual cusps on the P1. Another character, the extra articular facet for the vestigial first metatarsal on the fourth metatarsal, has also been identified as being highly variable (Hawkins 2011).

CHAPTER 2

METHODS

Before addressing each hypothesis every individual with a preserved dorsal cranium at GFS was examined and classified into a new morphological classification scheme of sagittal crests which elaborates on Hulbert et al. (2009). Relative age classes determined by eruption of buccal teeth and the amount of wear to the teeth (usually based on the exposure of dentine) follow Hulbert et al. (2009). Seven age classes comprise the eruption series that range from very young juvenile to aged adults.

A morphological classification scheme is used to describe each "type" of sagittal crest within most *Tapirus* taxa. Extant specimens from the American Museum of Natural History (AMNH) including *T. pinchaque*, *T. terrestris*, *T. bairdii, and T. indicus* and fossil taxa (*T. haysii*, *T. lundeliusi*, and *T. veroensis*) from the collections of the University of Florida (UF) are included in this scheme to sample morphologies present within the genus. This classification scheme will also serve as a comparative tool for the description of *T. polkensis*. It is vital to note that this classification system will not represent a growth series of the sagittal crest within the genus *Tapirus* but instead classifies the observed states.

Sexual Dimorphism

Modern tapir collections at the AMNH were evaluated for sexual dimorphism in crest morphology. Many specimens in this collection have recorded sex upon death and therefore are optimal for a comparative control for this study. The fossil sample a GFS was evaluated using Mead's (2000) measurements of sexual dimorphism in *Teleoceras major*. Several other linear measurements are added to the data set including upper and lower antero-posterior canine length

16

and canine width, newly developed pelvic measurements, and the condylobasal skull length when available (Figures 1-8, Table 1). One individual (ETMNH 3719), which has been identified as a pregnant female due to the presence of a *in situ* fetus, serves as a "known" for labeling any observed bimodal characters. This method has been used with *Teleoceras major* as well (Voorhies and Stover 1978).

Ontogeny

Using the eruption series already provided by Hulbert et al. (2009) every individual that has both a preserved dorsal cranium and cheek teeth was examined for any correlation between eruption, wear, and crest morphology. A regression analysis using Minitab 15 statistical software was performed to analyze the potential correlation between age classes and crest type.

For a modern analog, crest morphology in juveniles of extant taxa was evaluated and compared to adult forms of the same species in order to construct a growth series for the sagittal crest. The AMNH vertebrate zoology collection houses specimens of all 4 modern taxa, including several juveniles, and was used for this aspect. Juveniles are designated by the lack of molars other than the M1 and generally lack completely fused suture lines

Pathological Response

Simple observations for signs of pathologies within the sample at GFS can determine the validity of this hypothesis and all craniodental pathologies were documented and described.
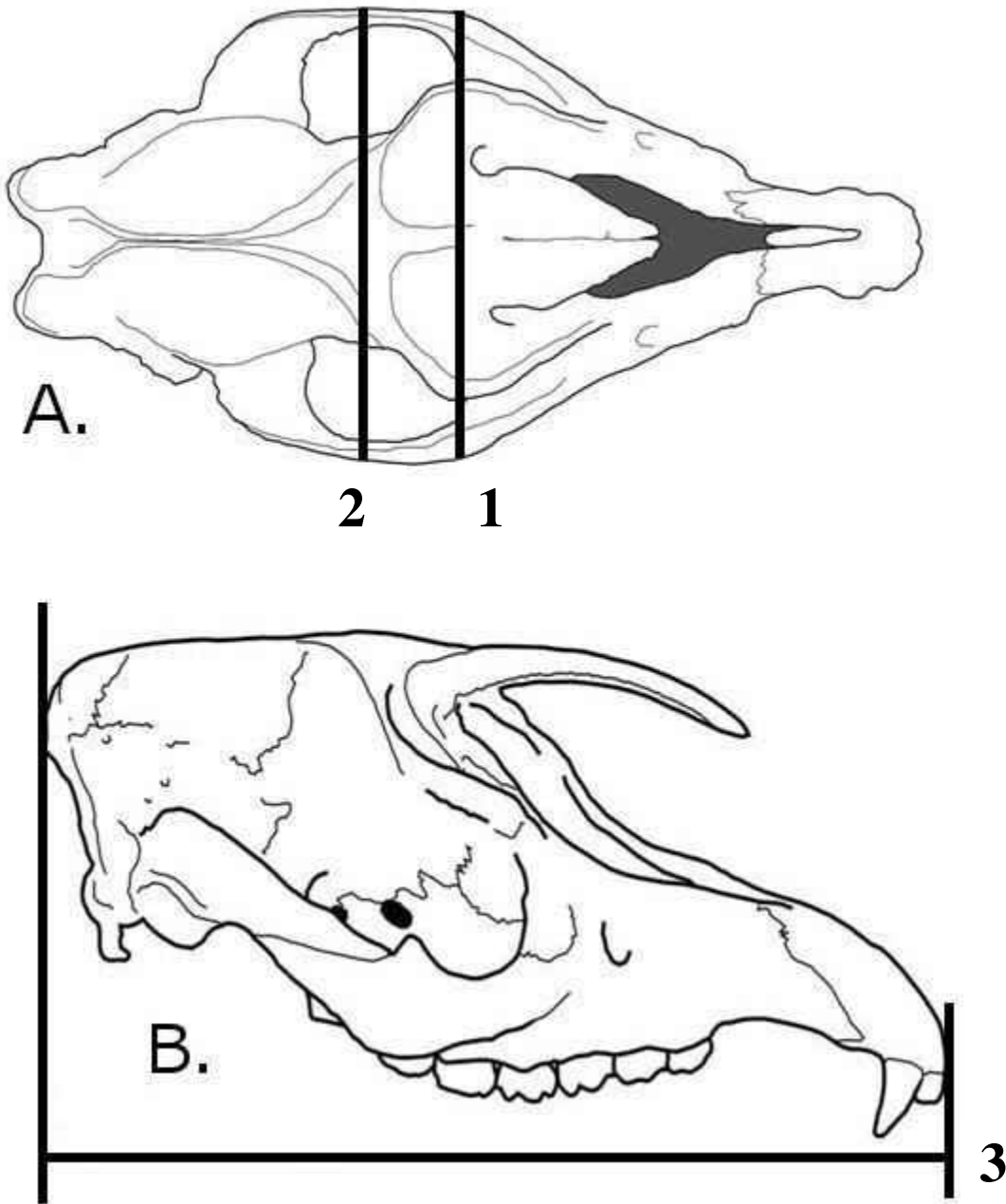
Figure 1: Cranial Measurements (1) taken in Sexual Dimorphism Study. Cranium measurements to assess sexual dimorphism in *Tapirus polkensis*. (A) Dorsal view (B) lateral view. Numbers are characters measured in Table 1. Not to scale.
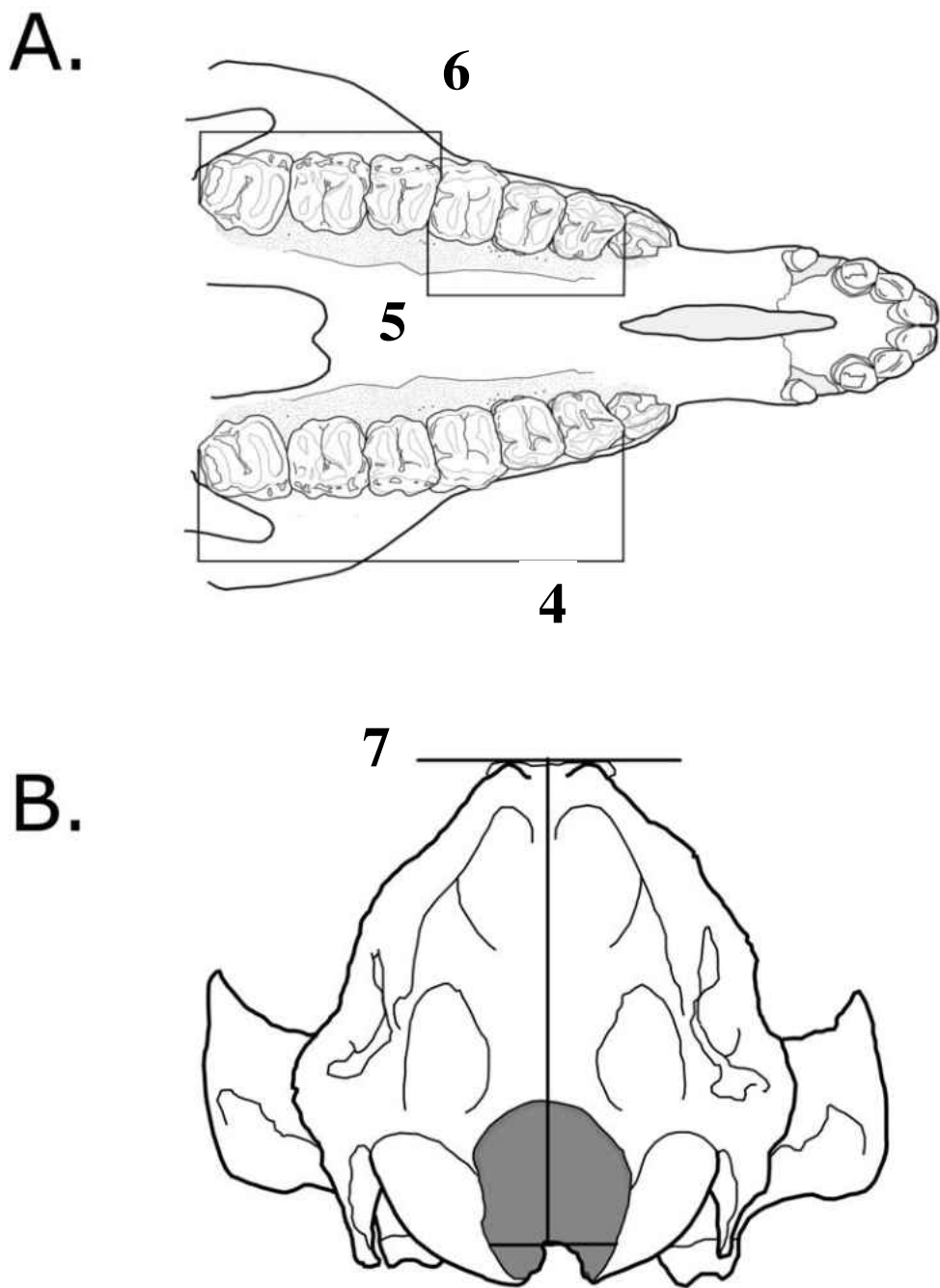
Figure 2: Cranial Measurements (2) taken in Sexual Dimorphism Study. Cranium measurements to assess sexual dimorphism in *Tapirus polkensis*. Palatal (A) and Posterior (B) views. Numbers are characters measured in Table 1. Not to scale.
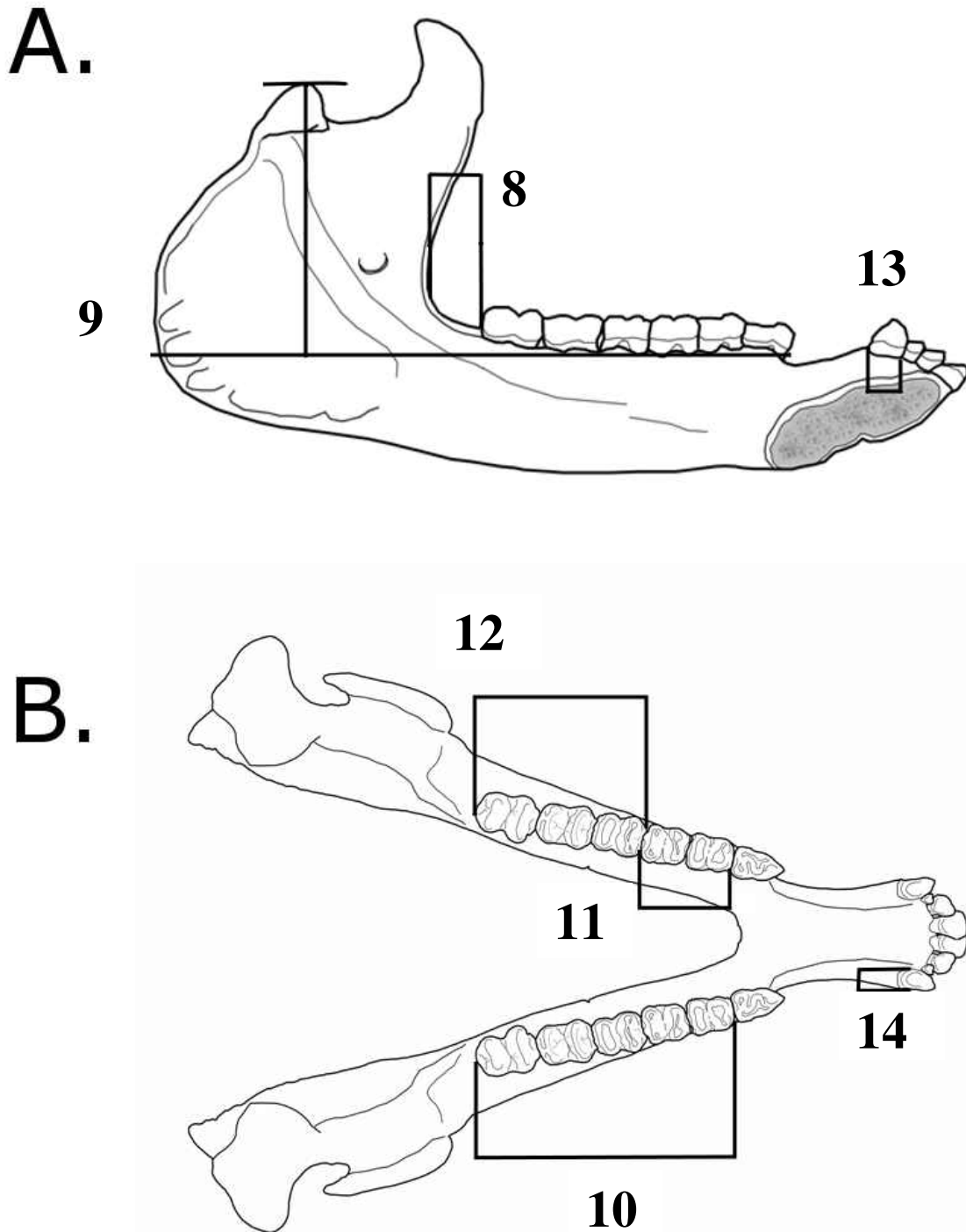
Figure 3: Dentary Measurements taken in Sexual Dimorphism Study, (A) lingual view, (B) dorsal view. Numbers are characters measured in Table 1.
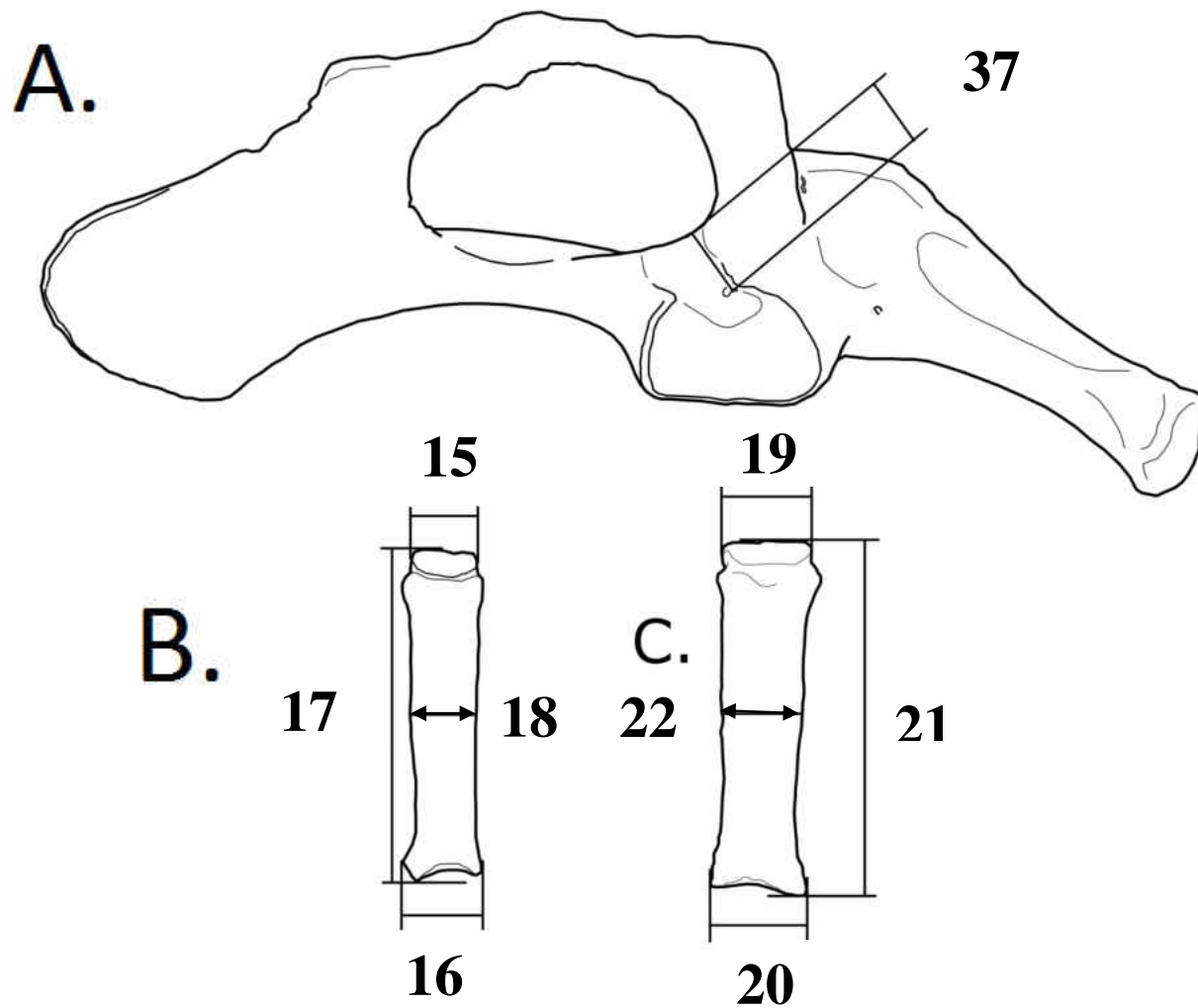
Figure 4: Pelvic & Metapodial Measurements taken in Sexual Dimorphism Study, (A) Pelvis, (B) metacarpal, and (C) metatarsal. Numbers are characters measured in Table 1. Not to scale.
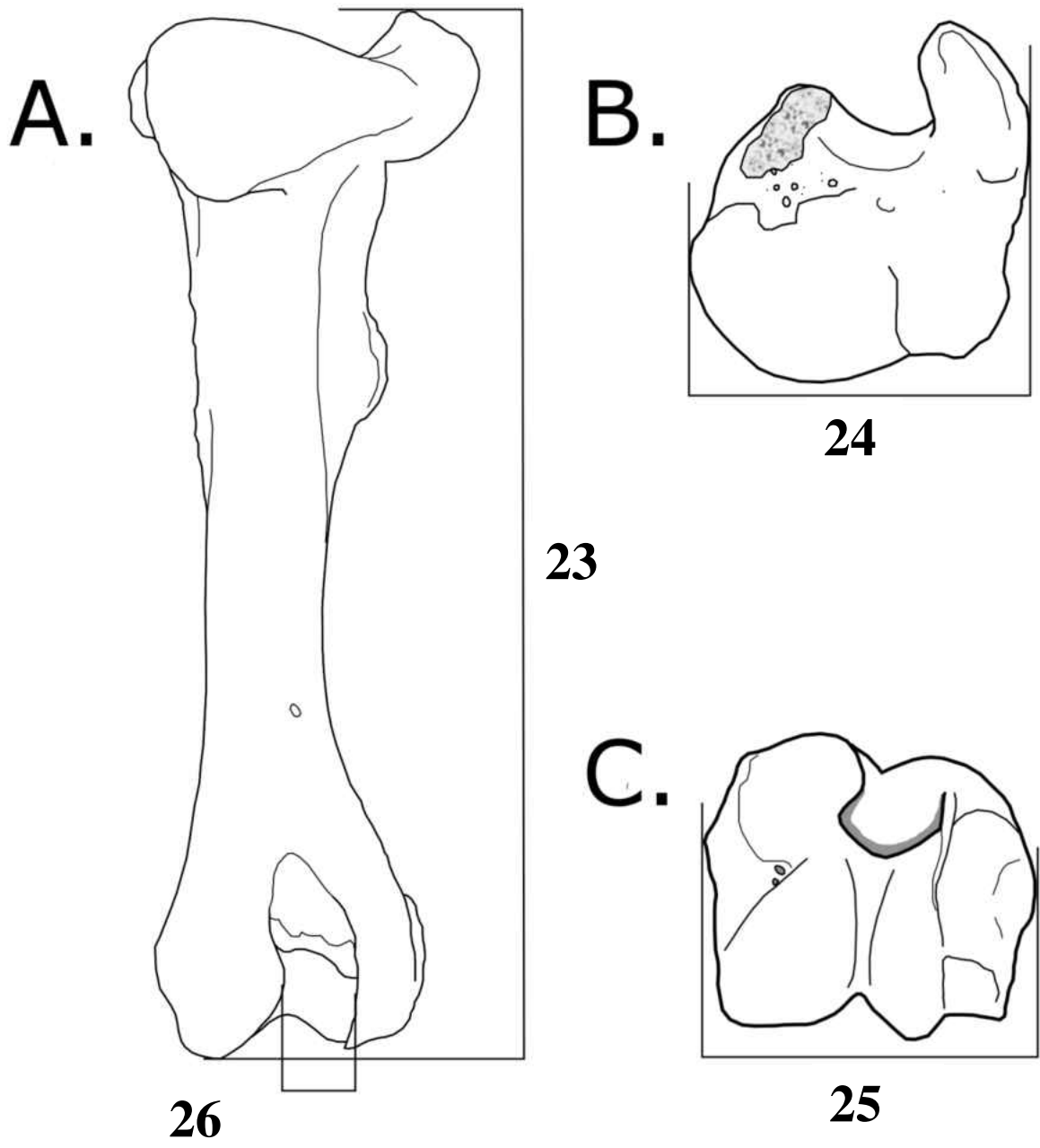
Figure 5: Humerus Measurements taken in Sexual Dimorphism Study, (A) Posterior, (B) Proximal, and (C) Distal views. Numbers are characters measured in Table 1. Not to scale.

*
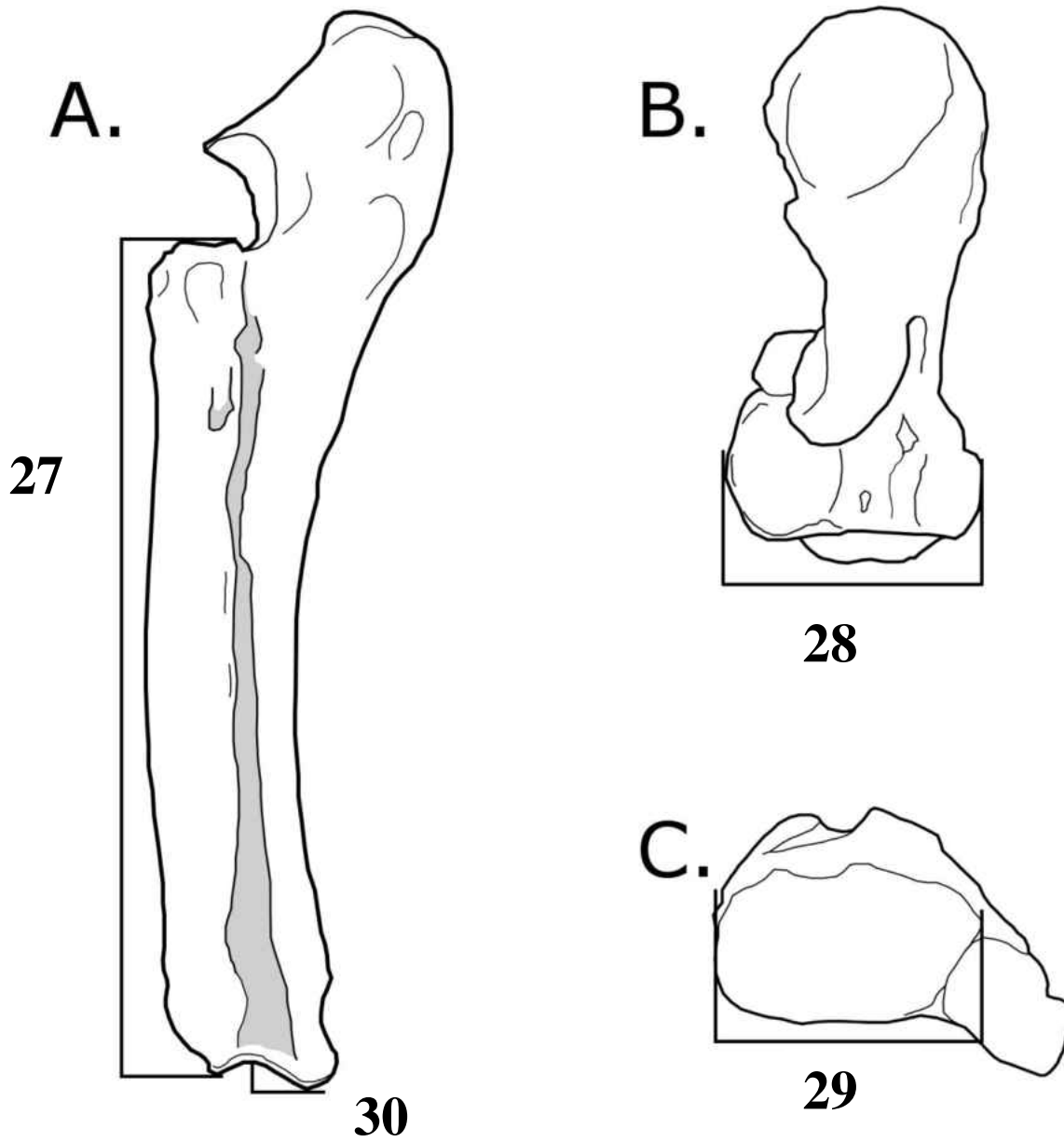
Figure 6: Radius Measurements taken in Sexual Dimorphism Study, A) Lateral, (B) proximal, and (C) distal views. Numbers are characters measured in Table 1. Not to scale.
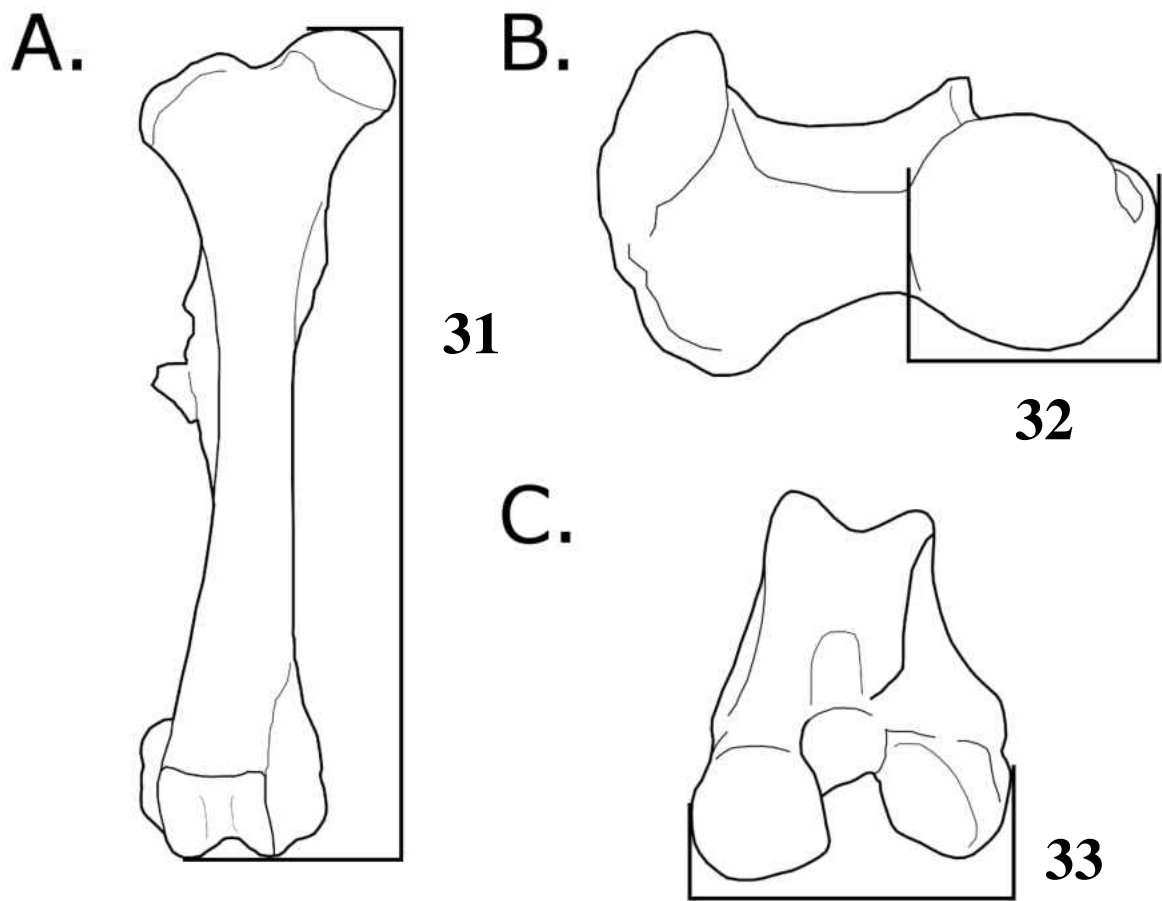
Figure 7: Femur Measurements taken in Sexual Dimorphism Study, (A) Anterior, (B) proximal, (C) distal views. Numbers are characters measured in Table 1. Not to scale.
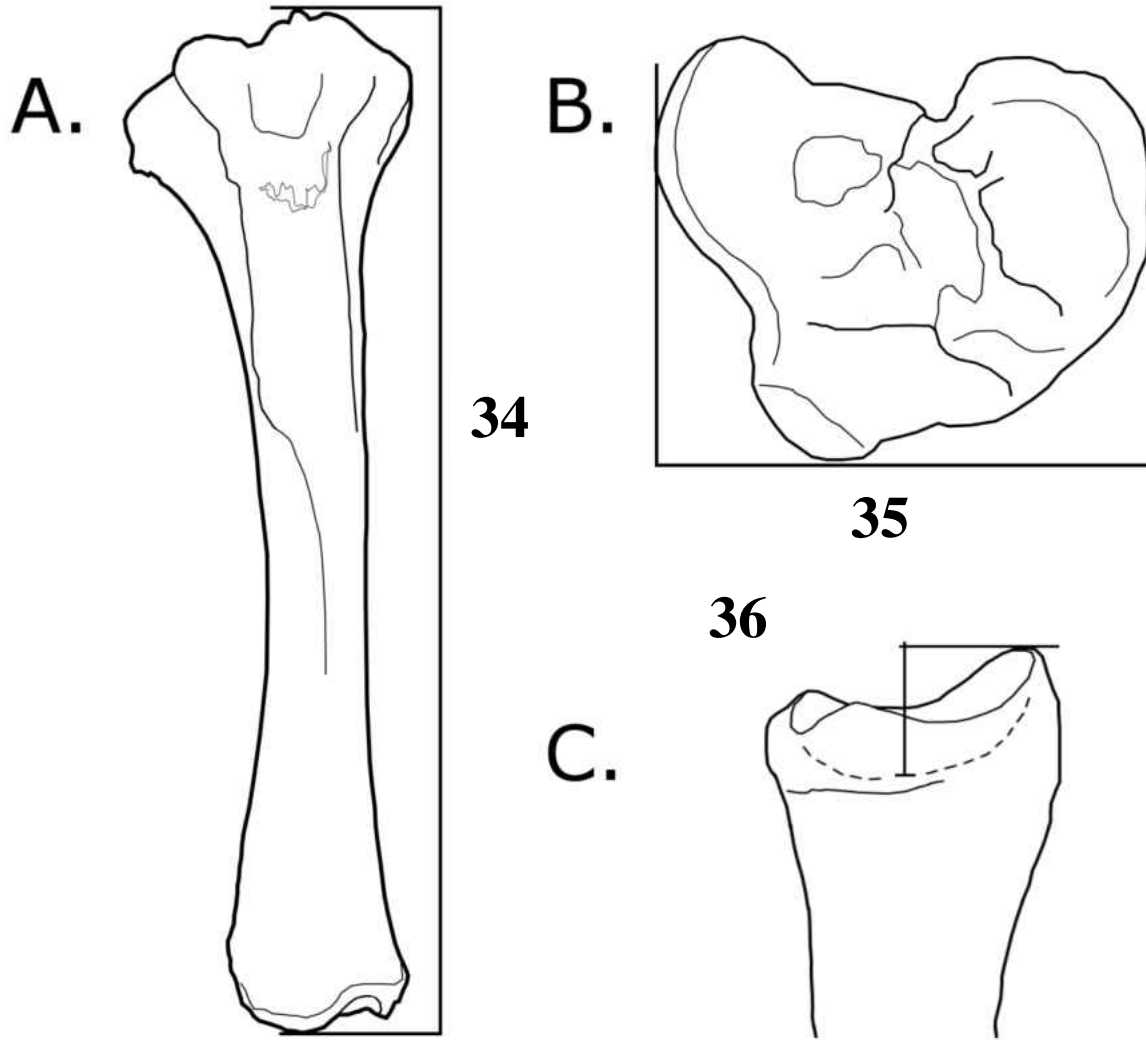
Figure 8: Tibia Measurements taken in Sexual Dimorphism Study, (A) Anterior, (B) proximal, and (C) lateral views. Numbers are characters measured in Table 1. Not to scale.

Table 1: Measurements of Sexual Dimorphism. The abbreviations and descriptions are of measurements taken in the sexual dimorphism study. Numbers correlate to measurements taken in Figures 1-8.

Character	Abbreviation	Description
1	BPOP	Maximum width at postorbital processes
2	MZW	Maximum skull width at zygomatic arches
3	CBL	Condylobasal skull length
4	P2-M3	Upper cheek teeth length along cervix (constricted part of tooth at crown/root junction)
5	P2-P4	Premolar row length along cervix (excluding first premolar)
6	M1-M3	Molar row length along cervix
7	LH	Ventral edge of foramen magnum to the dorsal edge of lambdoid crest
8	M3C	Horizontal distance from posterior edge m3 to anterior edge of ramus
9	CH	Height from ventral edge of m. angle to dorsal surface of m. condyle
10	p3-m3	Lower cheek tooth row length along cervix (excluding p2)
11	p3-p4	Lower premolar row length along cervix (excluding p2)
12	m1-m3	Lower molar row length along cervix
13	LCL	Lower canine length
14	LCW	Lower canine width
15	MC3PW	3rd Metacarpal proximal width
16	MC3DW	3rd Metacarpal distal width
17	MC3L	3rd Metacarpal length
18	MC3D	3rd Metacarpal mediolateral diameter at half the length
19	MT3PW	3rd Metatarsal Proximal width
20	MT3DW	3rd Metatarsal Distal width
21	MT3L	3rd Metatarsal Length
22	MT3D	3rd Metatarsal mediolateral diameter at half the length
23	HL	Humerus length
24	HPW	Humerus proximal width
25	HDW	Humerus distal width
26	HDWC	Humerus distal condyle width
27	RL	Radius length
28	RPW	Radius proximal width
29	RDW	Radius distal width
30	RDD	Radius distal depth on scaphoid articular surface
31	FL	Femur length
32	FHD	Femoral head diameter
33	FDW	Femur distal width
34	TL	Tibia length
35	TPW	Tibia proximal width
36	TDD	Tibia distal depth on astragalus articular surface
37	AT	Acetabulum wall thickness

Multiple species

To assess the presence of more than one species within the sample at GFS, CV values were calculated and compared to those previously obtained by Hulbert et al. (2009). If any CV values are greater than 10, this could support more than one species of tapir present at the GFS.

Preferential Feeding

A list of plant fossils was tabulated, and a comparison to modern tapir diets was made. Also, modern taxa diets were compared to crest morphologies to see if any correlation exists. Many specimens housed in the AMNH were collected from zoos and their dietary information is relatively unknown; however, these specimens were compared to individuals collected in the wild to look for morphological differences. A macrowear analysis was also performed on each specimen at GFS with a preserved dorsal cranium and cheek teeth. This analysis describes the overall wear on the cheek teeth, patterns visible between individuals, and whether or not dentine is exposed. A regression analysis was performed using Minitab15 statistical software to evaluate correlation between wear patterns and crest morphologies.

CHAPTER 3

RESULTS

Each individual tapir specimen from the GFS with a preserved dorsal cranium (n=23)

was assigned a value based on morphology that can be viewed in a classification scheme (Table

2). Additionally, the sagittal crest classification scheme was produced for other *Tapirus* taxa

(Table 3). Four different crest morphologies are visible within the sample. The first and more

common (n=7) contains 2 distinct sagittal ridges that are heavily convex towards the midline of

the skull and occasionally touch (Figure 9). It is also common to see parallel growth lines,

although faint, adjacent to these sagittal ridges. Morphology 2, long been considered to be a

"true" crest by previous workers (Simpson 1945; Lundelius and Slaughter 1976; Ray and

Sanders 1984; Holbrook 2001, 2002), exhibits 2 distinct and relatively thin temporal ridges

merge and run along the midline of the skull for an undefined distance before separating again.

Morphology 2 is commonly seen in older individuals (Eruption series 5-7) and can be seen in

Figure 10. Figure 11 shows the third morphology that is a flattened area atop the skull created

by the terminated migration of the temporal ridges. Typically, this area has a concavity created

by warping of the interparietal that is more rounded and less triangular than morphologies 1 and

2. Morphology 4 is nearly identical to the third; however, the flattened area is exaggerated

vertically and occasionally expressed by the lack of ventral sloping within the supraoccipital of

individuals categorized in the third morphology. Figure 12 shows a lateral and dorsal view of

morphology 4 for comparison with morphology 3.

Figure 9: ETMNH 3719 exhibiting Crest Morphology 1. Two parasagittal temporal ridges proximal to one another along midline of skull. Scale = 10 cm.

Figure 10: ETMNH 3519 exhibiting Crest Morphology 2. "True" crest composed of two thin parasagittal ridges which merge and run for a distance before separating. Scale = 10 cm.

Figure 11: ETMNH 3718 exhibiting Crest Morphology 3. Flattened table created by terminated migration of temporal ridges. Scale =10 cm.
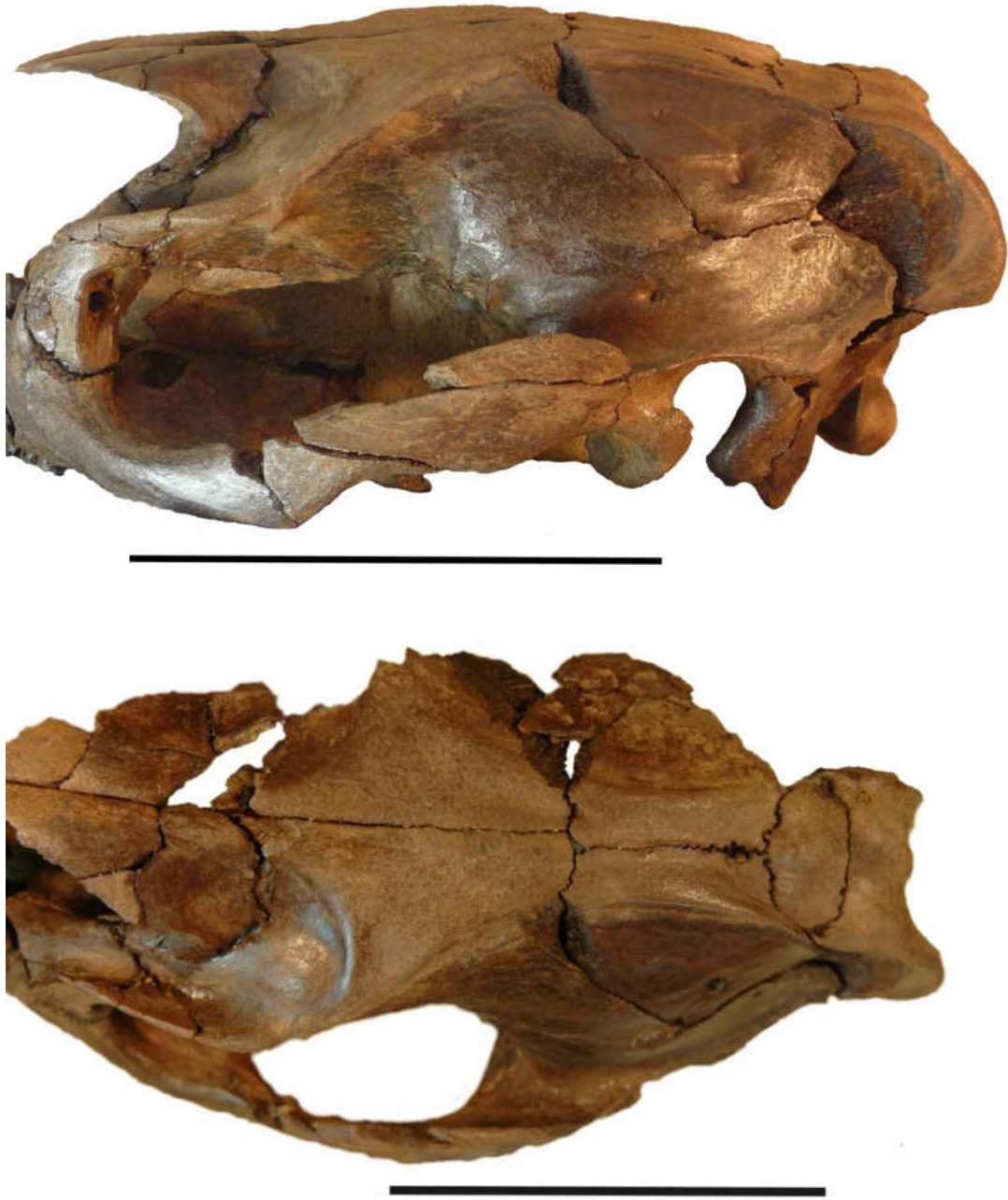
Figure 12: ETMNH 605 exhibiting Crest Morphology 4. ETMNH 605 in (A) lateral view and (B) dorsal view to express vertically extension of crest. Scales = 10 cm.

Table 2: Sagittal Crest Classification Scheme for all Gray Fossil Site Specimens. *Tapirus polkensis* with a preserved sagittal crest, eruption series class, and crest morphology. Asterisk denotes poorly preserved specimens.

SPECIMEN NUMBER	ERUPTION SERIES	CREST MORPHOLOGY
ETMNH 3680	1	0
ETMNH 3690	1	0
ETMNH 3718	1	3
ETMNH 605	2	1
ETMNH 3687	2	4
ETMNH 3691	2	3
ETMNH 3794*	2	1
ETMNH 6821	2	0
ETMNH 600	3	4
ETMNH 3701	3	3
ETMNH 3695*	4	3
ETMNH 3699	4	1
ETMNH 3705	5	3
ETMNH 3843	5	2
ETMNH 606	6	2
ETMNH 607	6	3
ETMNH 680	6	1
ETMNH 682	6	1
ETMNH 3719	6	1
ETMNH 683	7	2
ETMNH 3519	7	2
ETMNH 3716	7	1
ETMNH 3717	7	1
ETMNH 3753*	7	2

0 = Juvenile with no temporal ridges

1 = Temporal ridges proximal to one another, in some cases tangential.

2 = "True crest" morphology in which two temporal ridges merge for a distance.

3 = Migration of the temporal ridges is terminated, creating a sagittal table.

4 = A sagittal table that exhibits vertical exaggeration, supraoccipital does not slope ventrally.

Table 3: Sagittal Crest Classification Scheme for members of Tapirus. Classification scheme applied in Table 2 (*Tapirus polkensis*) to classify all modern and several fossil taxa of the genus *Tapirus*. Class 5 is included here due to the unique morphology of the sagittal crest of *T. terrestris* (Holbrook, 2002).

CREST MORPHOLOGY	*TAPIRUS*
0	Juveniles
1	*T. polkensis*
2	*T. polkensis, T. lundeliusi, T. veroensis, T. pinchaque, T. haysii*
3	*T. polkensis, T. bairdii*
4	*T. polkensis, T. indicus*
5	*T. terrestris*

Sexual Dimorphism

Nearly all the specimens of modern taxa housed in the AMNH collections show a consistent gross morphology within the same species regardless of sex. Each taxon displays the morphologies previously described in the introduction of this study and no individual examined deviated from this pattern. These specimens were collected from both natural locales and zoos during the early part of the 20th century. Multiple males and females from each species were examined, but juveniles were excluded from this study in order to remove ontogenetic bias.

Basic descriptive statistics of the linear measurements obtained for this study are in Table 4. Based on an eruption series score of 4 or higher, 13 individuals with preserved dorsal craniums were considered to be young adult or older and used in this study. Only one of the characters measured showed a clear bimodal distribution. Twenty-one measurements of acetabulum thickness show a distinct separation into 2 ranges of 4.9 - 6.8 mm and 8.7 – 10.8 mm, respectively. These data were averaged for individuals with left and right measurements. A 2 sample t-test shows a statistically significant difference between the ranges, P value ≤ 0.05 (Table 5, Figure 13). Only 3 individuals (ETMNH 3705, 3519, and 3719) with preserved acetbaulums also contained a preserved dorsal cranium. Each of the 3 individuals exhibits a separate crest morphology, while ETMNH 3705 and 3519 belong to the thinner acetabulum group, and ETMNH 3719 belongs to the thicker group.

Ontogeny

Of the 23 specimens preserved with dorsal craniums, 10 were considered to be juveniles based on a lack of fusion in skeletal features and eruption series constraints. Any individual that displayed all deciduous premolars and a completely erupted first molar and erupting second molar were considered to be eruption series 3 state. Typically, in eruption series 3, the first

molar shows some degree of wear, but this is not always the case. Eruption series 4 state is defined by occurrence of a deciduous P4 only and erupted second molar. The eruption series 1-3 denotes a juvenile, while the eruption series 4 state is considered to be a sub-adult. Regression analysis results (R-squared value = 0.2%) display no correlation between eruption series (here used as a proxy for age) and crest morphology (Figure 14). Distribution of eruption series states within the sample was normal, with a standard deviation of 2.21. Several young individuals display well developed crests, most notably ETMNH 600, 3687, 3691, 3701, and 3718.   No individual displaying eruption series states 1-4 exhibit morphology 2. Several individuals that display eruption series 6 and 7 exhibit developing or developmental crest forms (crest morphology 1).
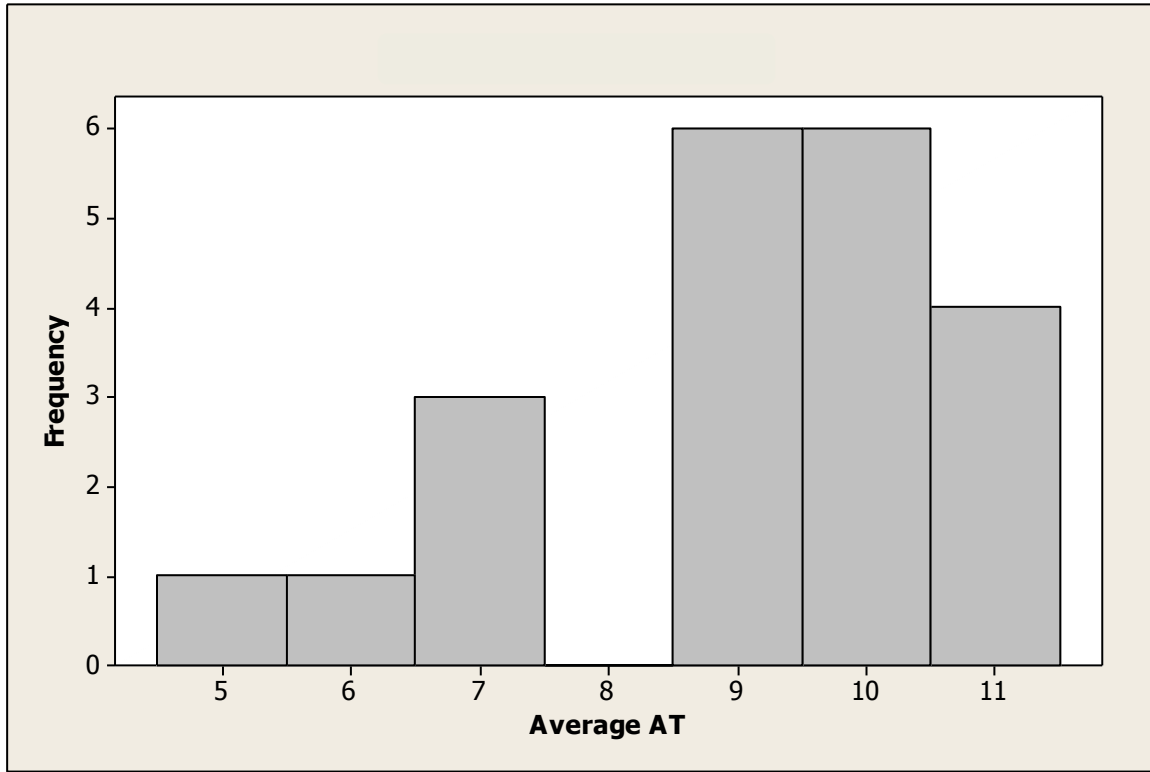
Figure 13: Histogram of Acetabulum Thickness Data from GFS. Histogram displays bimodal distribution of acetabulum thickness (AT; mm) for 21 individuals of *Tapirus polkensis* from the Gray Fossil Site.
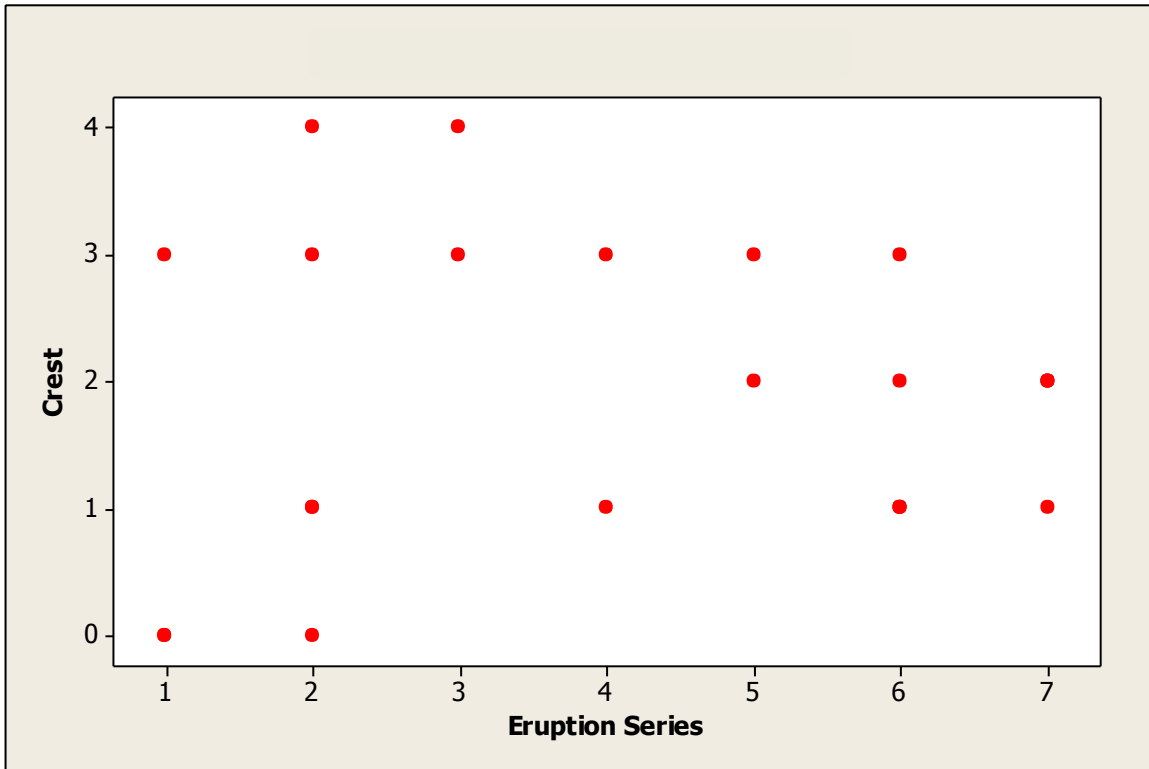
Figure 14: Regression Analysis Scatter Plot of Crest Morphology vs. Eruption Series. Results of a regression analysis using eruption series (ES) data (as a proxy for age) as the independent variable and classification scheme created for crest morphologies as the dependent variable. Scatterplot of Crest versus ES displaying no correlative pattern. S-value = 1.245, adjusted R-sq = 0.2%, Equation = (Crest = 1.78 + 0.022 ES).

Table 4: Basic Descriptive Statistics for Sexual Dimorphism Study. Basic descriptive statistics of sexual dimorphism study. Measurements in millimeters. Characters are from Table 1. Note: Characters with only one measurement taken were not included. These include: CBL, RDD, and AT (for which data are shown in Table 5).

Number: Character	N	MEAN	SD	MIN	MAX
1. BPOP	2	159.5	2.12	158.00	161.00
2. MZW	2	164.27	1.17	163.45	165.10
4. P2-M3	8	101.76	5.43	95.37	112.31
5. P2-P4	8	45.51	3.11	42.17	50.54
6. M1-M3	8	56.22	3.10	52.19	61.91
7. LH	6	83.36	2.13	80.87	86.15
8. m3C	5	14.65	2.47	8.42	22.34
9. CH	5	73.80	2.81	66.48	81.39
10. p3-m3	7	86.62	1.37	82.52	93.81
11. p3-p4	7	30.79	0.62	29.19	33.92
12. m1-m3	7	55.80	0.87	52.31	59.86
13. LCL	6	9.618	0.97	8.35	10.90
14. LCW	6	8.29	1.11	6.57	9.75
15. MC3PW	4	23.83	1.03	20.97	25.73
16. MC3DW	4	22.57	0.52	21.37	23.89
17. MC3L	3	108.90	1.46	107.13	111.80
18. MC3D	4	10.52	0.46	9.32	11.55
19. MT3PW	3	23.45	0.75	22.07	24.64
20. MT3DW	3	23.81	0.73	22.36	24.57
21. MT3L	3	109.40	1.17	107.85	111.70
22. MT3D	3	10.76	0.23	10.47	11.20
24. HPW	3	68.17	1.23	65.81	69.92
25. HDW	4	52.46	0.89	50.89	54.41
26. HDWC	4	45.70	1.10	43.68	47.89
27. RL	2	193.70	1.70	192.00	195.40
28. RPW	3	42.27	0.28	41.76	42.73
29. RDW	2	34.21	0.45	33.76	34.65
31. FL	2	264.27	4.25	260.03	268.52
32. FHD	3	35.47	0.47	34.79	36.36
33. FDW	3	59.62	1.00	58.34	61.58
34. TL	4	241.51	1.11	238.22	243.12
35. TPW	4	64.30	0.78	62.73	66.30
36. TDD	4	10.54	0.39	9.59	11.51

Table 5: Acetabulum Thickness Data for Groups 1 & 2 and Results for t-test. Acetabulum thickness data for Group 1 (n = 6) and Group 2 (n = 15) and results of t-test performed. Histogram displays bimodal distribution of acetabulum thickness (mm) for 21 individuals of *Tapirus polkensis* from Gray Fossil Site.

GROUP 1	GROUP 2	t-value	P-value
6.77	9.56	t = 8.82	p ≤ 0.000
6.93	10.86		
4.92	9.15		
6.33	9.78		
6.57	9.32		
	9.97		
	8.69		
	10.12		
	10.01		
	10.83		
	9.27		
	9.43		
	8.84		
	10.61		
	10.06		

Pathological Response

Two individuals with major pathological conditions and preserved dorsal crania exist in the GFS sample. ETMNH 607 (Figure 15) and ETMNH 3519 (Figure 16) both contain spongy growths along the lingual side of the cheek teeth and on the palate. In some cases this pathology is seen in alveoli of missing teeth, as is the case in the right P3s of ETMNH 607 and ETMNH 3519 and the right P2 of ETMNH 3519. ETMNH 607 has significant wear and breakage on all of the upper premolars, which are devoid of enamel. Many individuals, especially those exhibiting eruption series 5-7, have broken and heavily worn teeth with dentine exposed in the cheek teeth. In the case of ETMNH 682, no dentine is left in most of the dentary molars. Juveniles from the GFS sometimes display exposed dentine in newly erupted teeth or premolars with blunt surfaces. Cases of extreme wear were observed in some individuals in the AMNH collections but not to the frequency seen in the GFS sample. This trend was also not apparent in Plio-Pleistocene fossil samples of *T. veroensis, T haysii,* and the newly described *T. lundeliusi* (Hulbert 2010) from the University of Florida collection.

Figure 15: ETMNH 607 Palate with Dental Pathologies. ETMNH 607 exhibits a spongy growth in alveoli of the missing right P3. Enamel is not present on first 2 premolars that are heavily worn. Scale = 5 cm.

Figure 16: ETMNH 3519 Palate with Dental Pathologies. ETMNH 3519 exhibits a spongy growth located on palate on lingual side of both cheek tooth rows. Scale = 5 cm.

The current GFS floral list is composed of 13 orders containing 14 families (Table 6). GFS is rich in flowering plants, especially hickory, oak, and pine (Wallace and Wang 2004), and contains many potential food sources including grapes (*Vitis*) (Gong et al 2010), nuts from hickory (*Carya*), pine (*Pinus*), and walnut (*Jugalans*) trees, and stems and leaves of flowering plants such as *Fraxinus* and sunflowers (Ochoa pers. com.).

Tooth wear is typically more developed on the lingual surfaces of the upper cheek teeth and the labial surfaces of the lower cheek teeth, an expected pattern given tapir occlusion. However, 4 separate macrowear patterns are visible within the sample at Gray. The first and most frequently observed pattern (n=6) is designated W1 and consists of heavily worn posterior cusps of the M1 and anterior cusps of the M2, creating a concave "groove". The second pattern (W2) is similar to the first but shifted forward on the palate to encompass the entire P4 and anterior cusps of the M1. Teeth displaying W2 wear are heavily worn compared to others in the maxilla, but only 4 individuals share this pattern. The third pattern (W3) is only seen in 2 individuals that both belong to eruption series 7. This pattern shows even wear and exposed dentine across all cheek teeth. Both individuals (ETMNH 683 and 3717) display concave molars with moderate to extensive wear of the dentary. The fourth pattern (W4), observed in only 2 individuals (ETMNH 3687 and 3716), is very different from patterns W1-3. In this pattern the premolars are all heavily worn with exposed dentine and unusually blunt occlusal surfaces, while the molars show little wear. While ETMNH 3687 is a sub-adult, with a M3 still erupting, there is little to no wear visible on any of the molars. ETMNH 3716 is a full grown adult displaying eruption series 7, has moderate wear on the M3, a concave M1, and completely worn premolars. It is important to note that although ETMNH 607 may have been suffering from a dental

Table 6: Gray Fossil Site Floral List (Wallace and Wang 2004; Gong et al. 2010).

ORDER	FAMILY	GENUS/Description (Common name)
Pinales	Pinaceae	*Pinus* (Pine)
		Abies (Fir)
		Thuja (Arbor vitae "Green Giant")
Asterales	Compositae	Low Spine (Sunflowers)
		High Spine
		Fenestrate
Myrtales	Onagraceae	(Evening Primrose)
Fagales	Fagaceae	*Quercus virginian* (live oak)
		Quercus sp. (oak)
		Distylium (winter hazel)
	Juglandaceae	*Carya* (hickory)
		Juglans (walnut)
Saxifragales	Hamamelidaceae	(witch hazel)
Ranunculales	Menispermaceae	*Sinomenium* (moonseed)
Cornales	Nyssaceae	*Nyssa* (black gum "Tupelo")
Lamiales	Oleaceae	*Fraxinus* (black ash)
Poales	Poaceae	*Sargentodoxaceae sargentodoxa* (flowering vines)
Rosales	Ulmaceae	*Ulmas-Zelkova* (dwarf Chinese elm)
Symplocales	Symplocaceae	Flowering plants
Vitales	Vitaceae	*Parthenocissus* (Virginia creeper)
		Vitis (grape vine)
Malvales	Malvaceae	(mallow)

pathology, the premolars are also heavily worn with no enamel preserved and flattened occlusal surfaces.

No correlation exists between the 4 wear patterns observed and the crest morphologies of the classification scheme. Coefficient for the independent variable of wear is shown in Table 7 to be zero; however, it is likely just a small number due to the expression in Minitab 16. This is also evident in the R-squared value, which is extremely low. Equal sample sizes for the 2 variables in this study prevent sample bias, and thus a larger sample is not needed to further test this hypothesis.

<div align="center">Random Intraspecific Variation</div>

Intraspecific variation in the phenotype of a species is based on 2 factors, the genetic sequencing of individual organisms and the impact of the environmental surroundings they inhabit. Because no direct correlation could be found so far in this study, it is possible that the variation seen within the sagittal crest character is due to genetic mutations that are not critical to the survival and viability of individuals who exhibit them.

Table 7: Regression Analysis of Tooth Wear and Crest Morphology. Tooth wear patterns were assigned values based on description of wear. Crest morphologies were assigned using crest classification scheme.

WEAR	ETMNH #	CREST
1	606	2
1	607	3
1	3519	2
1	3699	1
1	3705	3
1	3753	2
2	600	4
2	680	1
2	682	1
2	3719	1
3	683	2
3	3717	1
4	3687	4
4	3716	1

S-value = 1.1547

R-sq% = 0.00

Equation = Crest Morphology = 2.00- 0.00 Wear

CHAPTER 4

DISCUSSION

Variation seen in the sagittal crest of *Tapirus polkensis* is unique compared to other members of the genus. So much so that attempting to quantify the amount seen is extremely difficult due to the complexity of the feature and inconsistency of obtainable measurements. A fragile component of the skeleton, the braincase, is often crushed or simply not preserved during the fossilization process. When the sample size at the GFS increases to a more substantial quantity and also includes more relatively complete individuals, an expansion of this study may be able to refine the results shown and accurately quantify the true variation seen within the character. With the magnitude of the site itself this should only be a matter of time, rather than a question of possibility.

Sexual Dimorphism

Bimodal distribution of the acetabulum thickness of *T. polkensis* is potentially the first osteological record of sexual dimorphism within the genus *Tapirus*. Age can be ruled out as a possibility for the groupings because individuals belonging to eruption series 1, 5, and 7 are seen in the larger range of approximately 8-11 mm, whereas two adults, ETMNH 3519 (ES7) and ETMNH 3705 (ES5), belong to the lower range (~5-7mm). This shows no correlation between age and acetabulum thickness (AT).

Distribution of the acetabulum thickness measurements (Figure 13) also displays a skewed relationship, with more than twice as many individuals falling within the thicker group. Sampling bias is unlikely because all specimens at the GFS are collected; however, preservation bias due to thinner elements not preserving as well is a possibility. Conditions under which

preservation would occur at the GFS were relatively calm (low energy environment) characterized by the thin, sometimes laminated beds of fine clays, indicative of a fresh water (lake/pond) environment (Shunk et al. 2006). Very few specimens have been observed with worn, rounded edges or striations from abrasion, suggesting few specimens have been transported over a distance.

Unfortunately only 3 individuals (ETMNH 3519, 3705, 3719) have both preserved sagittal crests and pelvises. This is most likely due to the distance between these 2 features, creating an unlikely probability for preservation of both. ETMNH 3519 and 3705 belong to the thinner/smaller grouping of AT measurements while 3719 belongs to the larger/thicker grouping. ETMNH 3719 was discovered with a fetus *in situ*, giving the unique insight of sex of the individual. It is possible that the thicker acetabulum is unique to females in this sample making this measurement useful in identifying females and providing sex ratios for populations at the GFS. If this is the case, the sample is female dominated with a ratio of 2.5/1. Gibson (2011) reports that the GFS sample represents a population with a greater number of juveniles as opposed to adults. GFS could represent an area in which a large amount of breeding is occurring skewing the population numbers towards both juveniles and females. This skew could also be a product of behavior as modern males spend a majority of time encircling the home range (Bauer, pers. com.). Very little is known on the sex ratios in populations of modern tapirs, so few conclusions can be drawn from that comparison. Their cryptic behavior and locales create difficulties in accurately studying these animals. Workers of the Baird's Tapir Project in Costa Rica have noted that small, isolated populations of *T. bairdii* to be composed of family groups with a male, breeding female, and juveniles; however, they also have observed juvenile to sub-

adult males being forced from populations at certain ages (Bauer pers. com.). If the sample at Gray follows this behavior, the sex-ratio observed at the GFS could be explained.

It is also possible that the pelvises preserved are all female and that the differences in acetabulum thickness are due sexual maturity of the females. This is unlikely, because juveniles are seen in both groupings therefore rejecting the hypothesis that child birth is affecting the acetabulum thickness. The lack of preservation of any male is unlikely as well.

<u>Ontogeny</u>

Ray and Sanders (1984) suggest that a sampling bias of all modern and fossil tapirs exists in which individuals with unerupted upper and lower M3s are over abundant due to the exceptionally long developmental period between the eruption of the M2s and the M3s. This "young adult" range, which falls out between eruption series 6 and 7, is postulated to indicate a time of vulnerability in the animal's life or a slowing of dental development (Ray and Sanders 1984). GFS sample is likely a representative sample of an actual population rather than a skewed sample indicative of a trap environment (Hulbert et al. 2009), and this bias has not been observed (Gibson 2011). R-squared values of the regression analysis between eruption series and crest morphology are definitively low, expressing no correlation between tooth eruption and wear and a certain crest morphology. To date eruption series stands as the best proxy for age determination in the sample. Other research is being done that estimates actual age in years based on the eruption series application to Baird's tapirs (*T. bairdii*) for which age is known (Gibson 2011) in Costa Rica.

If the modern taxa show similar amounts of variability in the morphology of the sagittal crest as seen in the sample of *T. polkensis* at GFS, this could support the hypothesis that growth

causes different crest morphologies within a sample. However, consistency of gross morphology between juveniles and adults in modern taxa does not support this hypothesis. Only juveniles that were considered extremely young (no erupted cheek teeth) were morphologically different, and this is undoubtedly due to the migration process of the temporal ridges. *Tapirus terrestris* juveniles are an exception, exhibiting the unique morphology that is more prominent in adults at a very young age (Holbrook 2002). It is evident that the sagittal crest is a product of growth, but the mechanism for its variability is unlikely determined by age.

Pathological Response

Not enough individuals (n = 2) at the GFS exhibit dental or cranial pathologies to support the hypothesis that pathologies could be correlated to crest morphology. ETMNH 607 and ETMNH 3519 have different crests yet similar pathologies, supporting that there is no direct correlation between the spongy growths visible on those individual's palates and crest morphology. However, more individuals with this specific pathology need to be found before a definitive answer can be made. High amounts of tooth wear and broken teeth in the sample covering every eruption series provides no insight to a possible relationship between dental degradation and crest morphology.

Duckler and Van Valkenburgh (1998) have shown a correlation between poor nutrition and tooth breakage in Florida pumas (*Felis concolor*). This trend was also observed in giraffes kept in zoos (Clauss et al. 2007). It is possible that the environment at the GFS presented the sample with a nutritionally poor diet. However, due to the wide variety of plant taxa consumed by modern forms, this is highly unlikely. Moreover, the presence of arrested growth lines (Harris lines) in long bones would be a good indicator of this poor nutrition (Duckler and Van

Valkenburgh 1998), but the presence of Harris lines were not analyzed in this study due to the destructive nature of cross sectioning bone.

The presence of sugar-rich food sources such as grapes could suggest that the dental pathogens observed are related to cavities and/or abscesses that in some cases could have completely dissolved the enamel. No other evidence of cavities (such as holes in the teeth) could be found, but abscesses could have occurred in broken teeth where the pulp was open to bacterial infection.

<div align="center">Preferential Feeding</div>

The amount of wear observed in the sample of tapirs at the Gray site far exceeds that of other samples, modern or fossil. Browsers are typically known to select foods that are less abrasive, rather than silica rich foods such as grasses. Captive giraffes (*Giraffa camelapardis*) have shown considerable tooth wear due to dietary differences from free-ranging giraffes, which are browsers of acacia (Clauss et al. 2007). If dietary differences explain why browsers would exhibit more tooth wear, the flora at the GFS could hold clues to the extensive wear observed in *T. polkensis* from the site. Dietary differences would also be expected in zoo raised/kept specimens of *Tapirus* compared to free-ranging.

Environments inhabited by modern tapir taxa typically have more tropical plants, with higher amounts of sugar-rich fruits than are seen in the preserved flora at the GFS. In some areas, it is estimated that one-third of the diet of *T. terrestris* can consist of fruit (Bodmer 1990). Individuals of *T. bairdii* being studied in Costa Rica by the Baird's Tapir Project prefer bananas over almost any other food (Bauer pers. com.). This preference is also observed in zoo raised specimens in the Knoxville Zoo (Jensen pers. com.).

Crests examined in zoo kept specimens did not differ in gross morphology from those collected in the wild dating back to the early 20th century. While this seemingly contradicts the theory that diet is related to crest morphology, it is unknown to what age specimens were captured or if any specimens were raised from birth in early 20th century zoos. It is known however that diet was indeed different. Early reports of tapir diets in captivity include oatmeal, various vegetables, fruit, and corn (Medway 1974). Many zoos today rely on tablets composed of corn, grain, and vegetable matter; however, tapirs will consume almost anything in their enclosure including nuts, stems, leaves, grass, and bark (Jensen pers. com.). The specimens in the collections of the AMNH were donated in the 1920s when little was known on tapir diet. If the organisms were collected as sub-adults or full grown adults, the crest may have already been fully formed before a dietary change occurred.

"Grooves" documented in the sample at GFS (see page 33) may be heavily worn areas where nuts were cracked repetitively. Highly abrasive nut shells would undoubtedly wear down the teeth if consumed in high amounts. Competition for food sources could provide pressure for dietary modification in some individuals. This competition could be intraspecific or interspecific, with the presence of other low level browsers in the fauna (DeSantis and Wallace 2008). Sugar-rich grapes were almost certainly a staple in the diet, but if this source was dominated by certain individuals, or another species, others might have relied on nuts to supplement their diet. While this is speculative, no other evidence for the extreme wear seen in the cheek teeth can be identified at this time, but future microwear analyses could shed light on this issue. It is also possible however that a lower amount of predators at the site could reduce selective pressures on the population and thus cause individuals to live as long as dentition

would allow. However, some juveniles display this extreme wear as well, which is evidence that rejects this hypothesis.

During growth, if an organism uses particular muscles it is presumed that evidence of such would show in the osteology. Tapirs therefore eating food sources with more abrasive qualities should strengthen the muscles associated with mastication like the temporalis. In response larger muscle scars for attachment of broader/bulkier muscles would also be expected. Despite this, no correlation can be found between the 4 wear patterns and crest shape, suggesting tooth wear is not related to the formation of the crest.

Intraspecific Variation

Coefficients of variation on linear measurements of the cheek teeth of the sample at GFS support a single mammalian species (Hulbert et al. 2009). Yet, the crest is not the only variable feature present within the sample. Presence of an articulation for the vestigial first metatarsal on the third metatarsal is variable as well (Hawkins 2011). These variable characters among the sample could be occurring due to a lack of selective pressure on the populations at the GFS. Very few large predators have been discovered to date, and it is possible the predator/prey ratio is fairly low. There are alligators present at the site, but very little evidence of predation, such as pitting or gnaw marks on bones. The aggressive movements involved in alligator feeding would leave these marks on bone, but this is not seen despite the excellent sample size. Most other characters measured for the sexual dimorphism study showed normal distributions with few outliers and typically low standard deviations when appropriate sample sizes were met.   One explanation of the variation could be biotopic variability, as described by Yablokov (1974), where variation is manifested by different sets of conditions in different populations or micro-

populations. It is also possible that if GFS is a refugium (DeSantis and Wallace 2008), several separate populations from a larger historic range could be represented and be responsible for the different morphologies observed. If this is the case, it is impossible to test at this time due to the lack preserved individuals at other sites.

Other perissodactyls also exhibit polymorphism, most notably the morphology of the premolars (Radinsky 1963; Mihlbachler 2008). Brontotheres, an extinct group of Eocene perissodactyls resembling rhinos in gross morphology, display intraspecific variation in horn shape, canine size, and overall skull size, although these are mostly attributed to sexual dimorphism (Mihlbachler et al. 2004). The presence of and size of the hypocone on the M3 in brontotheres is also variable but is not considered to be related to sex (Mihlbachler 2008). Hulbert et al. (2009) also reported higher amounts of variation in linear measurements of the P1 in *Tapirus polkensis*. Some fossil rhinos and brontotheres also exhibit intraspecific variation within crest morphologies (Mihlbachler pers. com.), meaning this is not unique to tapirs. Van Valen in the foreword for Variability of Mammals (Yablokov 1974) writes:

> "Phenotypic variation is the raw material for natural selection, yet a century after Darwin it is an almost unknown subject. To a considerable extent this may be true because even to see the significance of studying variation within a populations (rather than taking it as a given) requires an appreciation of several ordinarily separate disciplines: morphology, ecology, genetics, developmental biology, and to some extent systematics and paleontology."

CHAPTER 5

CONCLUSIONS

No significant correlation could be made between any of the proposed hypotheses and the variation seen in the sagittal crest of the sample of *Tapirus polkensis* at the GFS. Several of the hypotheses need more data (i.e., more complete individuals) to be adequately addressed. While variability within the sagittal crest character is rarely observed in perissodactyls, intraspecific variation is fairly common across the order. *Tapirus polkensis* is considered the oldest member of the genus (Hulbert et al. 2009) and its phylogenetic position may hold insight to the amounts of variability within the sample at the GFS. With the unique environmental setting that the GFS is interpreted to be during the late Miocene (DeSantis and Wallace 2008), selective pressures could have been at a minimum, causing high amounts of variation in certain osteological characters. Examination of the sagittal crest is difficult when compared to other cranial features due to its qualitative nature.

Hulbert et al. (2009) suggest that the "reduced" parasagittal crest (described as a sagittal table) is a juvenile condition retained by some adults in the population, and that it is related to increased reliance of the masseter and pterygoideus muscles during mastication. However, the heightened or raised table condition observed in crest morphology 4 would suggest an increase in the growth and heavy usage of the temporalis muscle in those individuals and that an underlying functional connection between the variation observed in the sagittal crest of *T. polkensis* and its diet. Muscle mass and bite force calculations could render insight into the variation observed but were out of the scope of this study. If the mechanism for this variability can be determined, it could help clarify how environmental parameters affect the growth and bone structure in tapirs and possibly other mammals.

With many studies on variability since Yablokov (1974), the subject is becoming clearer, yet sometimes difficult to quantify. Describing qualitative variability is vital in helping explain variation seen within samples, populations, and taxonomic levels and can also be important in phylogenetic and ecologic studies. Understanding in detail the habits and health of these organisms could be vital in helping to preserve an endangered genus whose modern diversity is minimal compared to the fossil record. Usually, researchers infer paleobiological knowledge on a taxon through closely related modern representatives. However, preservation at the GFS provides a converse relationship where studies of fossil taxon can provide valuable information on the ecology and biology of the modern related taxa. Consequently, GFS provides the avenue from which to study the osteology of these cryptic animals in detail, furthering our knowledge on population variation and dynamics with ongoing research.

BIBLIOGRAPHY

Albright LB. 1998. New genus of tapir (Mammalia: Tapiridae) from the Arikareean (earliest

Miocene) of the Texas Coastal Plain. Journal of Vertebrate Paleontology 18:200-217.

Bodmer RE. 1990. Fruit patch size and frugivory in the lowland tapir, *Tapirus terrestris*.

Journal of Zoology 222:121-128.

Clauss M, Franz-Odendaal TA, Brasch J, Castell JC, Kaiser T. 2007. Tooth Wear in Captive

Giraffes (*Giraffa camelopardalis*): Mesowear analysis classifies free-ranging specimens

as browsers but captive ones as grazers. Journal of Zoo and Wildlife Medicine 38(3):433-

445.

Coombs MC. 1975. Sexual Dimorphism in Chalicotheres (Mammalia, Perissodactyla).

Systematic Zoology 24(1):55-62.

Deng T. 2005. New Discovery of *Iranotherium morgani* (Perissodactlya, Rhinocerotidae) from

the Late Miocene of the Linxia Basin in Gansu, China, and its Sexual Dimorphism.

Journal of Vertebrate Paleontology 25(2):442-450.

DeSantis LRG, Wallace SC. 2008. Neogene forets from the Appalchians of Tennessee, USA:

Geochemical evidence from fossil mammal teeth. Palaeogeography, Palaeoclimatology,

Palaeoecology 266:59-68.

Dinerstein E. 1991. Sexual Dimorphism in the Greater One-Horned Rhinoceros (*Rhinoceros

unicornis*). Journal of Mammalogy 72(3):450-457.

Duckler GL, Van Valkenburgh B. 1998. Osteological corroboration of pathological stress in a
    population of endangered Florida pumas (*Felis concolor coryi*). Animal Conservation
    1:39-46.

Foerster CR, Vaughan C. 2002. Home Range, Habitat Use, and Activity of Baird's Tapir In
    Costa Rica. Biotropica 34(3):423-437.

Galetti M, Keuroghlian A, Hanada L, Morato MI. 2001. Frugivory and Seed Dispersal by the
    Lowland Tapir (*Tapirus terrestris*) in Southeast Brazil. Biotropica 33(4):723-726.

Gibson ML. 2011. Population Structure Based on Age Class Distribution of *Tapirus polkensis*
    from the Gray Fossil Site, TN. Unpublished Masters Thesis. Department of Biology.
    East Tennessee State University.

Gingerich PD. 1981. Sexual Dimorphism and Social Structure in the Early Eocene Horse
    Hyracotherium (Mammalia, Perissodactyla). Paleobiology 7(4):443-455.

Gittleman JL, Van Valkenburgh B. 1997. Sexual dimorphism in the canines and skulls of
    carnivores: effects of size, phylogeny, and behavioral ecology. Journal of the Zoological
    Society of London 242:97-117.

Gong F, Karsai I, Liu C. 2010. *Vitis* seeds (Vitaceae) from the Late Neogene Gray Fossil Site,
    northeastern Tennessee, U.S.A. Review of Palaeobotany and Palynology 162:71-83.

Hagge MD. 2010. A Functional and Ontogentic Skull Analysis of the Extant Rhinoceroses and
    Teleoceras major, an Extinct Miocene North American Rhinoceros. Unpublished
    Masters Thesis. Department of Geology and Geophysics, Louisiana State University.
    173 p.

Hawkins PL, Wallace SC. 2010. *Tapirus polkensis* foot bones and their environmental importance at the Gray Fossil Site. In: Schubert BW, Mead JI, editors. Gray Fossil Site Symposium. p 34-35.

Hawkins PL. 2011. Variation in the Modified First Metatarsal of a Large Sample of Tapirus polkensis, and the Functional Implications for Ceratomorphs. Graduate Thesis submitted to the Department of Biology, ETSU. 100p.

Holbrook LT. 2001. The unusual development of the sagittal crest in the Brazilian tapir (*Tapirus terrestris*). Journal of the Zoological Society of London 256:215-219.

Holbrook LT. 2002. Comparative osteology of the early Tertiary tapiromorphs (Mammalia, Perissodactyla). Zoological Journal of the Linnaean Society 132:1-54.

Hulbert Jr. RC. 2005. Late Miocene *Tapirus* (Mammalia, Perissodactyla) from Florida, with description of a new species, *Tapirus webbi*. Bulletin of the Florida Museum of Natural History 45(4):465-494.

Hulbert Jr. RC, Wallace SC, Klippel WE, Parmalee PW. 2009. Cranial Morphology and Systematics of an Extraordinary Sample of the Late Neogene Dwarf Tapir, *Tapirus polkensis* (Olsen). Journal of Paleontology 83(2):238-262.

Hulbert RC. 2010. A new early Pleistocene tapir (Mammalia: Perissodactyla) from Florida, with a review of Blancan tapirs from the state. Florida Museum of Natural History Bulletin 49(3):67-126.

Janis C. 1984. Tapirs as Living Fossils. In Living Fossil. New York. (7)80-86.

Khan M. 1997. Status and action plan of the Malayan tapir (*Tapirus indicus*). In: Brooks DM,
Bodmer RE, Matola S, editors. Tapirs: Status, Survey and Conservation Action Plan.
Gland, Switzerland and Cambridge, England: IUCN/SSC Tapir Specialist Group.

Lundelius E, Slaughter BH. 1976. Notes on American Pleistocene Tapirs. In essays on
Paleontology in honor of Loris Shano Russell 226-243. edited by Churcher CS. Life
Science Misc. Publishing. Royal Ontario Museum

Mead AJ. 1999. Aspects of the Systematics and Paleoecologies of the Middle to Late Miocene
North American Rhinoceros *Peraceras*, *Teleoceras*, and *Aphelops*. An unpublished
Ph.D. Dissertation. Department of Geosciences. University of Nebraska. 315 p.

Mead AJ. 2000. Sexual Dimorphism and Paleoecology in *Teleoceras*, A North American
Miocene Rhinoceros. Paleobiology 26(4):689-706.

Medway LDS. 1972. Phenology of a tropical rain forest in Malaya. Biological Journal of the
Linnaean Society 4:117-146.

Medway LDS. 1974. Food of a tapir, *Tapirus indicus*. Malayan Nature Journal 28: 90-93.

Mihlbachler MC, Lucas SG, Emry RJ. 2004. A new brontotheres (Brontotheriidae,
Perissodactlya, Mammalia) from the Eocene of the Ily Basin of Kazakstan and a
phylogeny of Asain "horned brontotheres. American Museum Noviates (3439):1-43.

Mihlbachler MC. 2007. Sexual Dimorphism and Mortality Bias in a Small Miocene North
American Rhino, *Menoceras arikarense*: Insights into the Coevolution of Sexual
Dimorphism and Sociality in Rhinos. Journal of Mammalian Evolution 14(2):217-238.

Mihlbachler MC. 2008. Species Taxonomy, Phylogeny, and Biogeography of the

    Brontotheriidae (Mammalia: Perissodactyla). Bulletin of the American Museum of

    Natural History (311):1-475.

Nowak RM, Paradiso JL. 1983. Walker's Mammals of the World. Fourth ed. The John Hopkins

    University Press. Baltimore (2):569-1362.

Olmos F. 1997. Tapirs as seed dispersers and predators. In: Brooks DM, Bodmer RE, Matola S,

    editors. Tapirs: Status, Survey and Conservation Action Plan. Gland, Switzerland and

    Cambridge, England: IUCN/SSC Tapir Specialist Group.

Olsen SJ. 1960. Age and Faunal Relationship of *Tapiravus* remains from Florida. Journal of

    Paleontology 34(1):164-167.

Padilla M, Dowler RC. 1994. *Tapirus terrestris*. Mammalian Species 481:1-8.

Padilla M, Dowler RC, Downer CC. 2010. *Tapirus pinchaque*. Mammalian Species 42(863):166-

    182.

Radinsky L. 1963. Origin and Early Evolution of North American Tapiroidea. Peabody Museum

    of Natural History. Yale University Bulletin (17)106 p.

Ray CE, Sanders AE. 1984. Pleistocene Tapirs in the Eastern United States. Special Publication

    of the Carnegie Museum of Natural History. (8):283-315.

Shunk AJ, Driese SG, Clark GM. 2006. Latest Miocene to earliest Pliocene sedimentation and

    climate record derived from paleosinkhole fill deposits, Gray Fossil Site, northeastern

    Tennessee, U.S.A. Palaeogeography, Palaeoclimatology, Palaeoecology 231(3):265-278.

Simpson GG. 1945. Notes on Pleistocene and Recent Tapirs. Bulletin of the American Museum
of Natural History 86(2):33-82.

Voorhies MR, Stover SG. 1978. An Articulated Fossil Skeleton of a Pregnant Rhinoceros,
Teleoceras major, Hatcher. Proceedings of the Nebraska Academy of Sciences 88:47-48.

Wallace SC, Wang X. 2004. Two new carnivores from an unsual late Tertiary forest biota in
eastern North America. Nature 431:556-559.

Yablokov AV. 1974. Variability of Mammals, revised edition. Smithsonian Institution, Amerind
Publishing Co. Pvt. Ltd. New Delhi. 350 p.

VITA

AARON RANDALL ABERNETHY

Education:	Public Schools, Maiden, North Carolina
	B.S. Geology, Appalachian State University, Boone, North Carolina, 2008
	M.S. Biology, Paleontology concentration, East Tennessee State University, Johnson City, Tennessee 2011
Professional Experience:	Teaching Assistant, Appalachian State University, Dept. of Geology, 2004-2007
	Graduate Assistant, East Tennessee State University, College of Arts and Sciences, 2008-2010
Field Experience:	Triassic excavations, New Mexico, 2006-2007
	Pleistocene excavation at Saltville, Virginia, 2010
	Miocene excavation at Gray Fossil Site, Tennessee, 2010

Abstracts: Abernethy AR, Wallace SC. 2010. Sexual Dimorphism in the

                               Black-Footed Ferret (Mustela nigripes) from a captive bred

                               population. South Eastern Association of Vertebrate

                               Paleontology. Abstracts.

                               Abernethy AR, Wallace SC. 2010. Extreme variation in the sagittal

                               crest of *Tapirus polkensis* from northeastern Tennessee. In:

                               Schubert BW, Mead JI, editors. Gray Fossil Site

                               Symposium. p 12-14.

                               Abernethy AR, Wallace SC. 2011. First record of sexual

                               dimorphism in a fossil tapir (Tapirus polkensis) from the

                               Gray Fossil Site, Northeastern, TN, USA. Abstracts with

                               programs.

Honors and Awards: Appalachian State University Dept. Scholarship, 2004

                               East Tennessee State University Graduate and Professional Student

                               Association Travel Grant 2011

Professional Affiliations: Don Sundquist Center for Excellence in Paleontology

                               ETSU Graduate and Professional Student Association