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Population Structure Based on Age-Class Distribution of *Tapirus polkensis* from the Gray Fossil Site Tennessee.

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Population Structure Based on Age-Class Distribution of Tapirus polkensis from the Gray Fossil Site, Tennessee

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by

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ABSTRACT

Population Structure Based on Age-Class Distribution of Tapirus polkensis from the Gray Fossil Site, Tennessee

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Individuals of *Tapirus polkensis* from the Gray Fossil Site exhibit an excellent level of preservation. Intact skulls collected from the site were arranged in a rough age class system separated into 7 categories based on the teeth present and amount of dental wear. Such an eruption series is useful for general comparisons amongst the individual tapirs; however, the classes do not represent an age in years due to a lack of data on living tapirs. Consequently, it is possible that some age classes may contain several years of a tapirs life, or comparatively only a few months. In this study I placed ages on individuals of *T. polkensis* from the Gray Fossil Site based on age data taken from The Baird's Tapir Project of Costa Rica (Baird's Tapirs, *T. bairdii*) ranging from several months to 7 years in age. As eruption data is only useful for aging tapirs up to 7 years, this study also took dental wear into account for adult tapirs. After aging all possible individuals in the sample, the sample was compared to other studies on perissodactyl population structure. Interestingly, the *T. polkensis* sample is remarkably similar to modern populations of *Diceros bicornis*.

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CONTENTS

LIST OF TABLES

LIST OF FIGURES

LIST OF ABBREVIATIONS

Institutional Abbreviations

ETMNH, East Tennessee State University and General Shale Brick Museum of Natural History, Gray, Tennessee. **GFS**, Gray Fossil Site. **UF**, Florida Museum of Natural History, Gainesville, Florida.

Morphological Abbreviations

D, deciduous upper tooth; **I**, upper incisor; **C**, upper canine; **P**, upper premolar; **M**, upper molar; **d**, deciduous lower tooth; **i**, lower incisor; **c**, lower canine; **p** lower premolar; **m**, lower molar; **ES,** eruption series.

CHAPTER 1

INTRODUCTION

It is rare to observe the population structure of an extinct taxon. In most cases, interpretations are inferred based on closely related extant taxa. Consequently, localities that do record this type of data are extremely valuable to the understanding of extinct species. The Gray Fossil Site, Gray Tennessee is one such location that offers the largest sample of extinct tapir, a dwarf species (*Tapirus polkensis*), in the world. With more than 75 individuals (Hulbert et al. 2009), which span several general age groups, this sample offers a unique opportunity to study a facet of an extinct tapir population.

The Genus *Tapirus*

Tapirs are conservative perissodactyls, a group that also includes Equidae and Rhinocerotidae, with all members of the genus *Tapirus* possessing generalized skeletons and dentitions that allow for direct comparisons among the taxa. However, tapirs are easily distinguished from other perissodactyls by their mobile proboscis (Janis 1984), which is used for sensing the environment as well as manipulating shoots and other vegetation (Macdonald 1985). The genus *Tapirus* contains all of the extant tapirs: *T. bairdii* (Baird's Tapir), *T. pinchaque* (Mountain Tapir), *T. terrestris* (Brazilian or Lowland Tapir), and *T. indicus* (Malaysian Tapir) (Simpson 1945) as well as several extinct forms including *T. webbi*, *T. lundeliusi*, and *T. polkensis* (Hulbert 2005; Hulbert et al. 2009; Hulbert 2010).

T. polkensis was originally placed within the genus "*Tapiravus*" based on measurements taken from an isolated upper tooth, identified as a fourth premolar, and 2 partial jaw fragments

(Olsen 1960). Unfortunately, all of these elements lacked any stratigraphic data as they were recovered from a phosphate mine and had been removed from their original location (Olsen 1960; Hulbert et al. 2009). The designation of the species as *"Tapiravus" polkensis* was based almost exclusively on measurements taken from the upper forth premolar; however, buccal teeth are very difficult to distinguish when isolated, so (when available) it is more advantageous to compare more diagnostic cranial bones such as the lacrimal, nasal, frontal, or parietals (Hulbert et al. 2009). Cranial elements, however, are very frail and were most likely destroyed by the phosphate mining process, and so until recently such key elements were simply not available for study. Without such key elements, the placement of *"T." polkensis* was questionable.

The Gray Fossil Site

In 2000, an exquisite fossil locality was discovered near the town of Gray, Tennessee during the construction of a new roadway (Parmlee et al. 2002; Wallace et al. 2002; Wallace and Wang 2004; Hulbert and Wallace 2005; Shunk et al. 2006; Hulbert et al. 2009). A truly exceptional locality, the Gray Fossil Site (GFS), has yielded a wide variety flora and fauna not found in the region, including a variety of invertebrates, fish, amphibians, reptiles, and mammals (a compiled list is available in Hulbert et al. 2009); of these tapirs are by far the best represented animal at the site (Parmlee et al. 2002; Wallace and Wang 2004; Hulbert and Wallace 2005; Schubert and Wallace 2006; Hulbert et al. 2009). Specimens retrieved from the GFS are wonderfully preserved, with many specimens represented by articulated skeletons allowing for an in-depth reassessment of *"T." polkensis* (Hulbert et al. 2009). Newly available key elements called for "*T." polkensis* to be reassigned to the genus *Tapirus* (Hulbert and Wallace 2005) making it the smallest member of the genus (Hulbert et al. 2009).

Relative dates from the GFS are between 4.5 and 7 Ma (Late Miocene to Early Pliocene, Hemphilian North American Land Mammal Age; Tedford et al. 2004) based on 2 of the animals found at the site, the rhino *Teloceros* Hatcher, 1894 and the short-faced bear *Plionarctos* Frick, 1926 (Wallace and Wang 2004). Geologic analyses of the GFS have concluded that the site began as a sinkhole, which subsequently filled with water to become a small pond or lake (Wallace et al. 2002; Shunk et al. 2006; DeSantis and Wallace 2008); explaining both the lacustrine sediments found at the site, as well as the abundance of aquatic to semiaquatic animals such as fish, turtles, alligators, and tapirs (Hulbert et al. 2009). Wallace et al. (2002) also suggests that early on the sinkhole may have acted as a natural trap and later filled in preserving these animals. The large number of individuals as well as their relative even distribution among age classes suggest that the tapirs were most likely living near the pond and surrounding forest (DeSantis and Wallace 2008). Habitat use of secondary forests is also seen in the modern *T. bairdii* (Foerster and Vaughn 2002).

Procedure and Purpose

Tapirs are very conservative animals, often making fossil identifications difficult (Ray and Saunders 1984). Moreover, ages are usually determined on the basis of size or coat color (Maffei 2003), but these methods alone can be highly subjective. Size could potentially be used for fossil identification, and has in the past (Ray and Sanders 1984); however, there is a great deal of overlap between taxa. Extant tapirs share this conservatism in both skeletal and dental characteristics (Radinsky 1965); therefore, it is assumed that buccal teeth erupt and wear at a similar rate amongst both fossil and extant taxa. A generalized dentition for an adult tapir can be seen in Figure 1. By attributing dental eruption and wear to various tapir ages, it is possible to age both fossil and extant taxa. Consequently, this study seeks to compare individuals of *T.*

polkensis to those of extant tapir species with known ages, so age data can be recorded for this exceptional fossil sample.

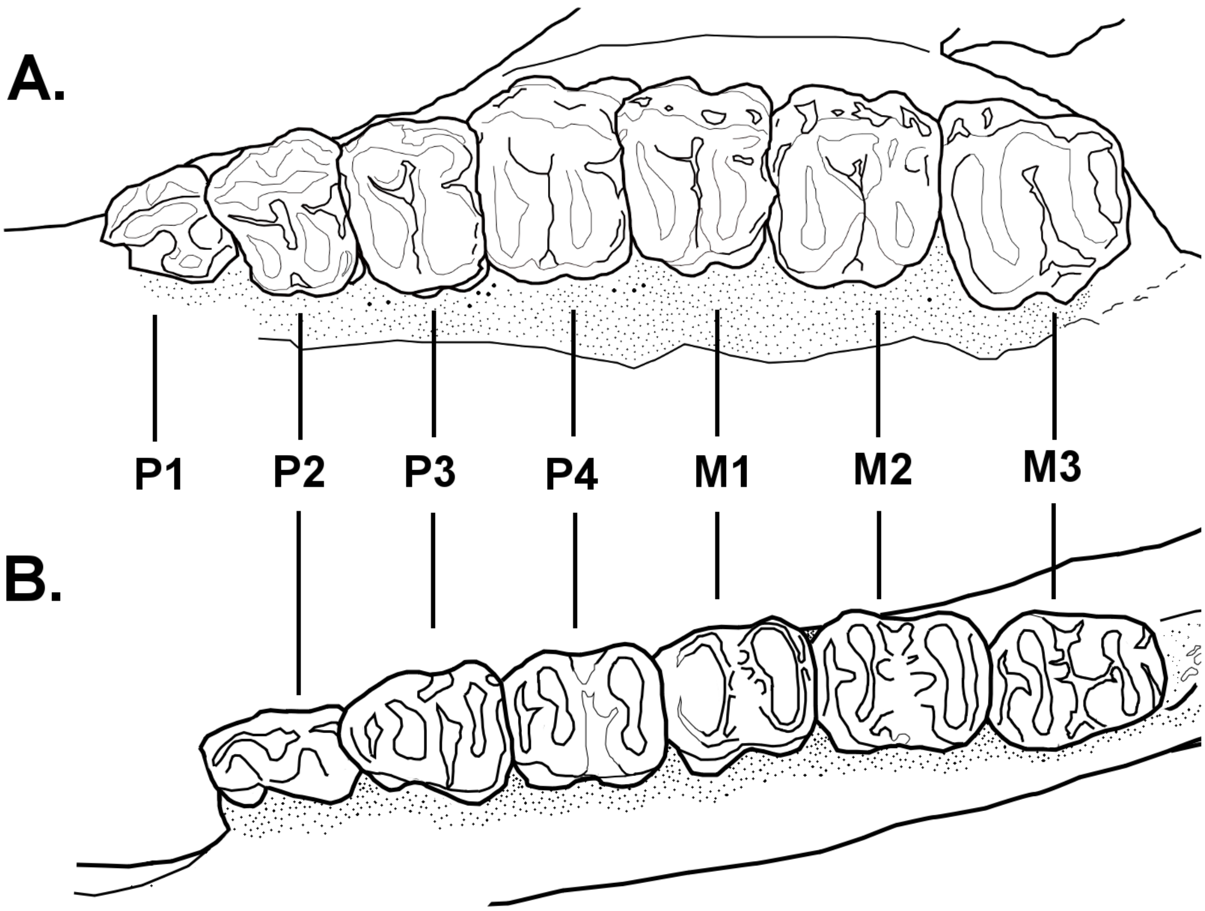

Figure 1: Generalized tapir dentition. A. Upper dentition. B. Lower dentition. Dental formula is I 3/3, C 1/1, P 4/3, M 3/3.

Specimens of *T. polkensis* from GFS have already been placed within ontogenetic groups (Table 1)(Hulbert et al. 2009) based on dental eruption and wear. However, these groupings do not represent ages in years but rather divide the individuals into general categories that allow for general statements about the sample and comparisons amongst individuals in each group (Hulbert et al. 2009). Consequently, I will correlate temporal data to these groupings by comparing the eruption and wear seen in the individuals of *T. polkensis* to those of extant member of the genus.

Table 1: Eruption Series groups used at the GFS and definitions

Eruption Series	**Characteristics**
Very Young Juvenile	DP1-DP3 and dp2-dp3 with little to no wear. DP4 and dp4 may be erupting.
Young Juvenile	DP1-DP4 and dp2-dp4 are all fully erupted and M1 and m1 may be erupting. Teeth are slightly worn.
Juvenile	DP1-M1 and dp2-m1 are all fully erupted and are in wear. Adult premolars and second molars fully formed in crypts.
Subadult	P1-P3, DP4, M1 and p2-p3, dp4, m1 are all fully erupted and in wear; M2 and m2 may be erupting. Little to no wear present on P1-P3 and p2-p3, but heavy wear on DP4 and dp4.
Young Adult	P4, M2, p4 and m2 have erupted and are in wear; M3 and m3 either erupting or fully erupted, but with little to no wear.
Full Adult	Lophs of M3 and m3 are moderately worn, but the dentine isn't exposed.
Old Adult	Lophs of M3 and m3 have heavy wear and exposed dentine.

Initially, problems arose from the inability to locate data on dental eruption from living members of the genus *Tapirus*. In the case of game preserves or in the wild, ages are often estimated based on size or coat color to differentiate juveniles from adults (Maffei 2003). Captive bred animals generally have good records of age, but depending on the animal, zoo staff may not collect other data that could be vital for morphological studies. For example, although many zoos house tapirs, the individuals are rarely anesthetized. Exceptions would only be made for animals that have been experiencing several medical issues (Trim et al. 1998). Because of this, zoo medical staff may observe a tapir's dentition but not take exact dental counts (M. Stancer and K. Jansen pers. comm.). Zoo staff may also lack the training to correctly identify teeth, leading to misrepresentations of which teeth should be present at a given age. This creates obvious hurdles when attempting to determine at what age teeth erupt. Currently, there is only one source for data on ages of dental eruption, The Baird's Tapir Project of Costa Rica (BTP), which is an ongoing ecological study focusing on collecting data from individuals of *T. bairdii* living in the Corcovado National Park in Costa Rica (Hernandez-Divers et al. 2005).

Since 1994 the BTP members have been observing and recording information on tapir diet, habitat use, pathologies, etc. Individuals are immobilized with anesthetic to allow various data to be collected and to be fit with radiotelemetry collars that allow their locations to be tracked (Foerster and Vaughn 2002; Hernandez – Divers et al. 2005). Additionally, since 1999 information has been collected on teeth present in individuals by making casts of their dentitions (K. Bauer and M. Colbert pers. com.). Presence/absence data for buccal teeth taken from these casts will be used as a comparison for dental eruption for the individuals of *T. polkensis* from the GFS because the physical casts themselves are currently being used for another study and are, therefore, not available for direct comparison.

Data collected by the BTP include individuals from roughly 1 to 7 years, so there are no comparative data for fossil tapirs that are less than 1 year or greater than 7. From the data collected, any Baird's tapirs (*T. bairdii*) that have all of their buccal teeth are older than 7 years. It is an inherent assumption of this study that it is the same for *T. polkensis*, as well as the rate at which the various teeth erupt. Tapirs are known to live to their mid-20s to early 30s in captivity, so it is unlikely that the oldest *T. polkensis* were only 7 years old. Fortunately, dental wear data could be useful in separating age groups after year 7; however, as the casts are currently unavailable, an analysis of wear for *T. bairdii* cannot be used at this time.

Other research has attempted to attribute an estimated age based on the amount of wear present on the teeth, which could be used to quantify ages older than 7 years. However, such estimates have proven to be difficult and have their own unique set of problems, namely inaccuracies depending on differences in rates of wear and diet among individual taxa (Morris 1972). Other studies that have attempted to ascertain more reliable ages by counting annuli in the cementum of teeth have been tested with various degrees of usefulness for several mammalian groups such as marine mammals, deer, rhinos, bats, bears, tapirs and humans (Laws 1952; Mitchell 1967; Hitchins 1978; Phillips et al. 1982; Carrel 1994; Maffei 2003; Wittwer-Backofen et al. 2004). Such studies are based on the assumption that alternating bands of cementum are likely caused by alternating seasons of growth and food restriction (Mitchell 1967). The cement forms on the dentine surface of adult teeth just below the gum line, and just under the crown on molars (Mitchell 1967). Mitchell (1967) also states that there is a correlation between the amount of dental cement and the rate of buccal tooth wear. Basically the more wear present on the teeth, the thicker the cementum rings.

Maffei (2003) attempted to evaluate the condition (threatened, endangered, etc.) of the population and the amount of hunting pressure existing on the lowland tapir, *T. terrestris*, residing the Chaco region of Bolivia. To accomplish this, Maffei aged individuals of *T. terrestris* using dental cementum counts. Skulls were collected from indigenous hunters, their incisors were decalcified using 30% formic acid, and dental annuli were counted. Once tentative ages were devised using this method, the state of wear present on buccal teeth was recorded for that age and were used to create dental wear keys for the various age classes of *T. terrestris*.

Data show that 63% of the individuals killed by natives are not reaching reproductive maturity, a sign of overhunting (Maffei 2003). Ages estimated for these tapirs are potentially underestimated, however, and Maffei (2003) states that due to the thickness of some of the roots and the time it took for those teeth to decalcify, some dental annuli may have been lost. Underestimated ages could pose a serious problem with my analysis, as this is the most analogue population comparison I could have hoped for.

Taking into consideration the possible underestimations of ages by loss of dental annuli in the study by Maffei (2003), my analysis also looks at dental wear keys devised by Hitchins (1978), which analyzed the amount of dental wear present in individuals of Black Rhino (*Diceros bicornis*) of known ages. Methods used by Hitchins (1978) are similar to those of Maffei (2003) in that dental cementum lines were counted to obtain age; however, 3 individuals within the study of known ages were used to calibrate and verify the system. A previous study on *D. bicornis* (Goddard 1970) stated that individuals gain their M1 at 3 years, and an individual used by Hitches at 4 years of age had its M1 present with single dental annuli. Using this, Hitchins (1978) devised keys by counting dental annuli, adding 3 years to the age, and then describing the amount of wear present at each given age. Unlike the previous two studies, Hitchins (1978) has a much higher maximum age of 37 years.

Using the techniques described above, the GFS sample can then be compared to the population structure of modern tapirs to document any differences. Consequently, here I attempt to answer: 1) does the sample at Gray give a relatively accurate representation of what the historical population structure was, or is there a preservation bias toward a certain age class, 2) if there is a bias toward a certain age class what could be the potential causes, (For example, if there is an inflation of older individuals is it possible that younger tapirs, due to their more fragile skeletons, do not preserve as well?), and finally 3) at what ages do epiphyses in the long bones fuse? Data from this study could prove invaluable for conservation efforts because although previous studies have been attempted to assess modern populations of tapirs, all lack a true natural setting (untouched by humans). If the Gray sample is a good, although averaged, representation of a natural population, it can be used as a comparison to modern tapir populations. The process of using a fossil taxon to assess the current state of a modern population is an incredibly exciting new prospect.

Conversely, if the Gray sample proves to be an unreliable representation of the population, this study still holds a great deal of validity. By aging the tapirs at the site and then attributing those ages to epiphyses fusion, paleontologists from other tapir sites can potentially give approximate ages to tapirs at their localities even if they lack dentitions. From a biological standpoint, this also gives insight into how tapirs grow, as well as when a tapir can be truly deemed an “adult” (a sexually mature individual), rather than basing it on possibly misleading characteristics such as size.

CHAPTER 2

METHODS

Systematic Paleontology

Order PERISSODACTYLA Owen, 1848

Family TAPIRIDAE Burnett, 1830

Genus TAPIRUS Brünnich, 1771

TAPIRUS ("*TAPIRAVIS*") *POLKENSIS* (Olsen, 1960)

Ages Based on Dental Eruption

For this study, I only examined individuals of *T. polkensis* from the GFS that were found with either a complete upper or lower dentition (in some cases both). Initially, all individuals were given a rough age (ultimately +/- 1 year). Ages on buccal tooth eruption were based on direct comparisons to the presence/absence of data collected by BTP recorded in the form of dental casts. All of the data recorded for the *T. bairdii* were taken from the upper dentition. For at least this portion of my analysis the lower dentition could not be used for direct comparison because only a few individuals of *T. bairdii* actually had casts made of their lower teeth (as the mandible is difficult to stabilize on a live animal). Of those that were cast, few have age-data associated (M. Colbert pers. comm.). Therefore, for my analysis, it is assumed that the upper and lower buccal teeth are erupting at the same time, so ages based on dental eruption for upper dentition should be identical when using exclusively the lower. Previous work done by Hulbert et al. (2009) grouping the individuals of *T. polkensis* in to their respective ontogenetic classes corroborates this, at least for this taxon.

Incisors and canine eruption were not used in this analysis due to a lack of recorded data from BTP. Additionally, the rostrum in tapirs is often not well preserved; therefore, several individuals from GFS are lacking at least part of their rostrum and associated teeth. Individuals of *T. polkensis* with alveoli present allow for inferences based on the presence or absence of incisors and canines. Data were recorded on whether incisors and canines were present or absent for a given specimen based on teeth present in the skull when available but were not used in the actual aging of older individuals.

When comparing individuals of *T. polkensis* to the eruption data collected from *T. bairdii*, individuals were only used if the DP1, P1, or P1 alveoli and the anterior most portion of the zygomatic arch were used to ensure that the entire dentition was present and avoid underestimations in age. In individuals where alveoli were missing teeth, it was generally easy to determine if there were underlying unerupted adult teeth present. If the crowns of these adult teeth were still within the crypts, they were scored as if the deciduous tooth was still present, with this age score being verified using the lower dentition (if present).

In the case of buccal teeth, scores were assigned using a system developed and used by the BTP for *T. bairdii*. Each buccal tooth was given a score of 0, 1, or 2. For premolars the scores designate whether the 0) deciduous tooth is unerupted or erupting, 1) deciduous tooth has erupted or permanent tooth is erupting, or 2) adult tooth is fully erupted. Only 0 and 1 were used for either unerupted or erupted molars respectively. Once all individuals with full upper dentitions were scored, the individuals of *T. polkensis* were assigned approximate ages in years by comparing them to corresponding specimens of *T. bairdii* up to roughly 7 years. The oldest *T. bairdii* individual with a recorded dentition equaled 7 years 3 months and possessed an almost complete adult dentition, only lacking its M3. Therefore, all individuals of *T. polkensis* possessing an M3 were scored as simply being greater than 7 years in age.

Age Consensus Based on Eruption and Wear

To counteract the aforementioned limits placed on the study based on using solely the dental eruption data from the BTP, this study also attempts to place ages on the individuals of *T. polkensis* using gross dental wear. Amount of wear in adult ontogenetic groups range from wear only being present on the DP4, to wear so extreme that dentine is exposed throughout the entirety of the occlusal surface of each buccal tooth. Cusps develop on the deciduous teeth of rhinos in the same order as tapirs (Butler 1952), so this study assumes a similar progression of cusp development and wear between the 2 groups in the adult buccal dentition. Dental wear keys developed by Maffei (2003) and Hitchins (1978) were used to attribute "calendar" ages to individuals of *T. polkensis* that exhibit similar amounts of wear. Premolars range from 0) deciduous with little to no wear, 1) deciduous with heavy wear, 2) adult with little to no wear, 3) adult with moderate wear and slightly exposed dentine, and 4) adult with extreme wear causing the tooth to be concave. Molars range from 0) unerupted, 1) little to no wear, 2) moderate wear with slight exposed dentine, 3) slight concavity of the cusps, and 4) extremely worn with a majority of the tooth concave.

Attributing Age to Suture Fusion in Limbs

Once approximate ages have been attributed to the individuals at GFS, the degree of fusion of growth plates in long bones was recorded. Many of the *T. polkensis* skulls have associated postcranial material, which will be used to analyze the degrees of long bone fusion for the various age groups. An issue that may arise from this is the possible inclusion of tapir material that, although cataloged with a skull, is actually not the same individual. An example would be ETMNH 3573, which possess several extra elements. Any individuals in which "extra" associated elements are found were excluded from my study. Suture fusion data were plotted on a proposed "tapir timeline", which will superimpose the progression of fusion seen in a tapir skeleton as it matures to the eruption data.

CHAPTER 3

RESULTS

Initially, the first task was to take the eruption data collected from the BTP and create a key for comparison to the GFS sample. This key, shown in Table 2, shows which buccal teeth are present for given ages. The youngest tapir from the BTP is 9 months and the oldest is 7 years, 3 months. This constrains what can be said confidently on the youngest and oldest individuals, with those individuals being placed in the <1 year and >7 year groups respectively. Dental states in this key use the designations as the data collected by the BTP: 0, tooth is unerupted; 1, deciduous premolar or molar has erupted; 2, adult premolar has erupted.

Table 2: A dental eruption key for placing tapirs into rough age groups

Approximate Age Using Tooth Eruption	I1	I2	I3	C	P1	P2	P3	P4	M1	M2	M3
<1 – 1 year	1	1	1	1	1	1	1	1	0	0	0
1 - 2 years	1	1	1	1	1	1	1	1	1	0	0
2 - 3 years	1	1	1	1	2	2	1	1	1	0	0
3 - 4 years	2	2	2	1	2	2	2	2	1	1	0
4 - 5 years	2	2	2	2	2	2	2	2	1	1	0
5 - 6 years	2	2	2	2	2	2	2	2	1	1	0
6 - 7 years	2	2	2	2	2	2	2	2	1	1	1
> 7 years	2	2	2	2	2	2	2	2	1	1	1

Using the BTP data, attributing approximate ages based solely on dental eruption to juvenile individuals (and the younger end of ES 4) was a rather simple task. Buccal teeth present are clearly different among individuals from <1 to 1 year, 1 – 2 years, and 2 – 3 years. When compared to the eruption series classes: Eruption Series 1 (Very Young Juvenile) represents individuals <1 - 1 year; ES 2 (Young Juvenile) represents individuals from <1 year to 2, which overlaps both ES 1 and ES3; ES 3 (Juvenile) represents individuals from 1 – 2 years; The younger members of ES4 (Subadult) can also be determined using exclusively eruption data (Figure 2). Very young juvenile dentition consists of DP1 through DP4, at most. Young juvenile dentitions are characterized by presence of DP1 through DP4, as well as the eruption of M1. The eruption sequence is mirrored in both the upper and lower dentition, except that the lower dentition lacks a p1 (Figure 3). Of the 49 sample individuals from GFS, 23 individuals (47%) are juveniles.

Beginning with ES 4 tapirs are considered adults. Eruption series 4 contains individuals that are 2 - 3 and 3 - 4 years old. Tapirs that fall within the 3 - 4 year and higher age groups cannot be easily separated by only looking at buccal eruption, and therefore dental wear states would need to be scored to be used with dental eruption at higher ages. This key (Table 3) shows dental wear states created using a combination of methods from Hitchins (1978) and Maffei (2003). Premolars were scored based on whether they are deciduous or adult; 0, deciduous with little to no wear; 1, deciduous with heavy wear; 2, adult with little to no wear; 3, adult with moderate wear with partially exposed dentine; 4, adult with heavy wear causing the tooth to be concave. For molars: 0, unerupted; 1, little to no wear; 2, moderate wear with partially exposed dentine; 3, heavier wear with slight concavity on cusps; 4; heavy wear with majority of the tooth being concave.

Table 3: A dental wear key for placing tapirs into rough age groups

Approximate Age Using Dental Wear	P1	P2	P3	P4	M1	M2	M3
3 - 4 years	2	2	2	1	1	1	0
4 - 5 years	2	2	2	2	2	1	0
5 -6 years	3	3	3	3	3	2	1
6 - 7 years	4	4	3	3	3	2	1
7 - 8 years	4	4	4	4	3	3	1
8 - 9 years	4	4	4	4	4	3	2
9 - 10 years	4	4	4	4	4	4	2
10 - 11 years	4	4	4	4	4	4	3
> 11 years	4	4	4	4	4	4	4

Without also taking into consideration the eruption of canines and incisors, the only way to approximate age is to qualify the degree of wear present on the buccal teeth (Figures 4 - 5). For example, individuals within the 3 - 4 year and 4 - 5 year age groups both have heavy wear on their deciduous premolars 1 through 3. However, 4 -5 year individuals have more wear on their P4 as well as a little wear on their M1 (Figures 4 – 5). Degrees of dental wear have been recorded for approximate ages ranging from 3 – 4 years to >11 years (Appendix 2). Of the 49 sampled individuals from GFS, 26 individuals (53%) are adults. Each eruption series designation now relates to both a general ontogenetic designation as well as a specific age with some ES groups overlapping in age (Table 4). After assigning ages to each of the tapirs from GFS, it was a simple task to evaluate the state of fusion seen in postcranial elements. The results of the postcranial fusion analysis can be seen on the proposed tapir life in the conclusion of this study.

Table 4: Eruption series designations and the ages they represent

Eruption Series	Age Range
Very Young Juvenile	< 1 - 1 yr
Young Juvenile	< 1 - 2 yr
Juvenile	1 - 2 yr
Subadult	2 - 4 yr
Young Adult	4 - 9 yr
Full Adult	6 - 9 yr
Old Adult	9 - >11yr

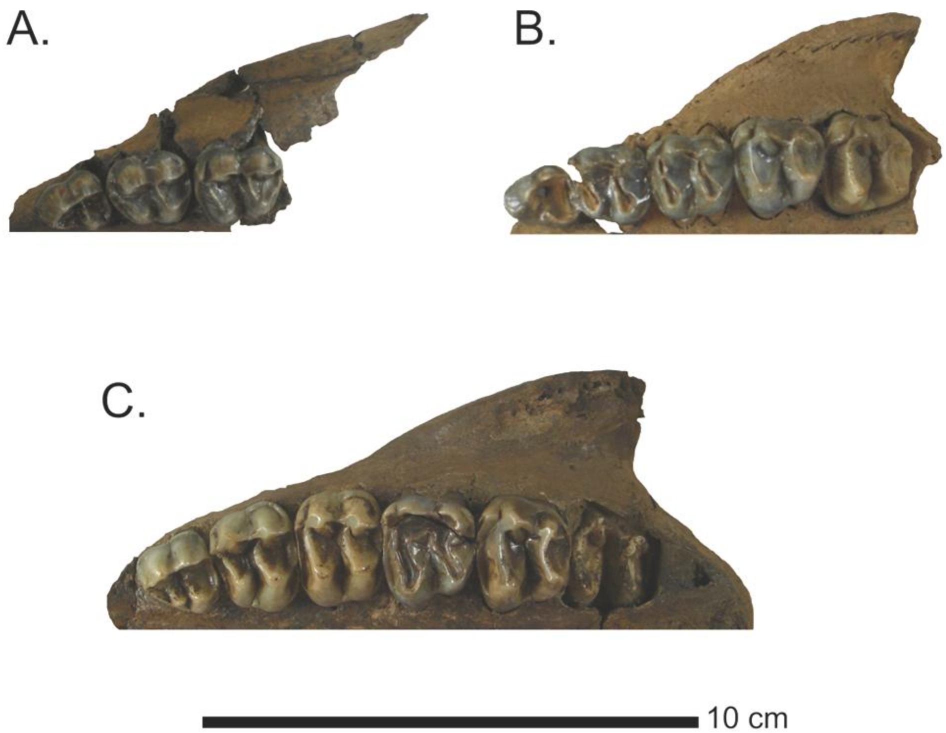

Figure 2: Upper dentitions of juvenile individuals of *Tapirus polkensis*. A) ETMNH 3680, <1 - 1 year; dentition consists of deciduous premolar through deciduous premolar 4, at most. As this individual does not have its DP4, it is on the younger end of this range. B) ETMNH 3689, 1 - 2 years; dentitions are characterized by presence of DP1 through DP4, as well as the possible eruption of M1. C) ETMNH 611, 2 - 3 years; individuals have lost DP 1 - 3, which have been replaced by adult premolars. DP4 is heavily worn and M2 is fully formed in its crypt.

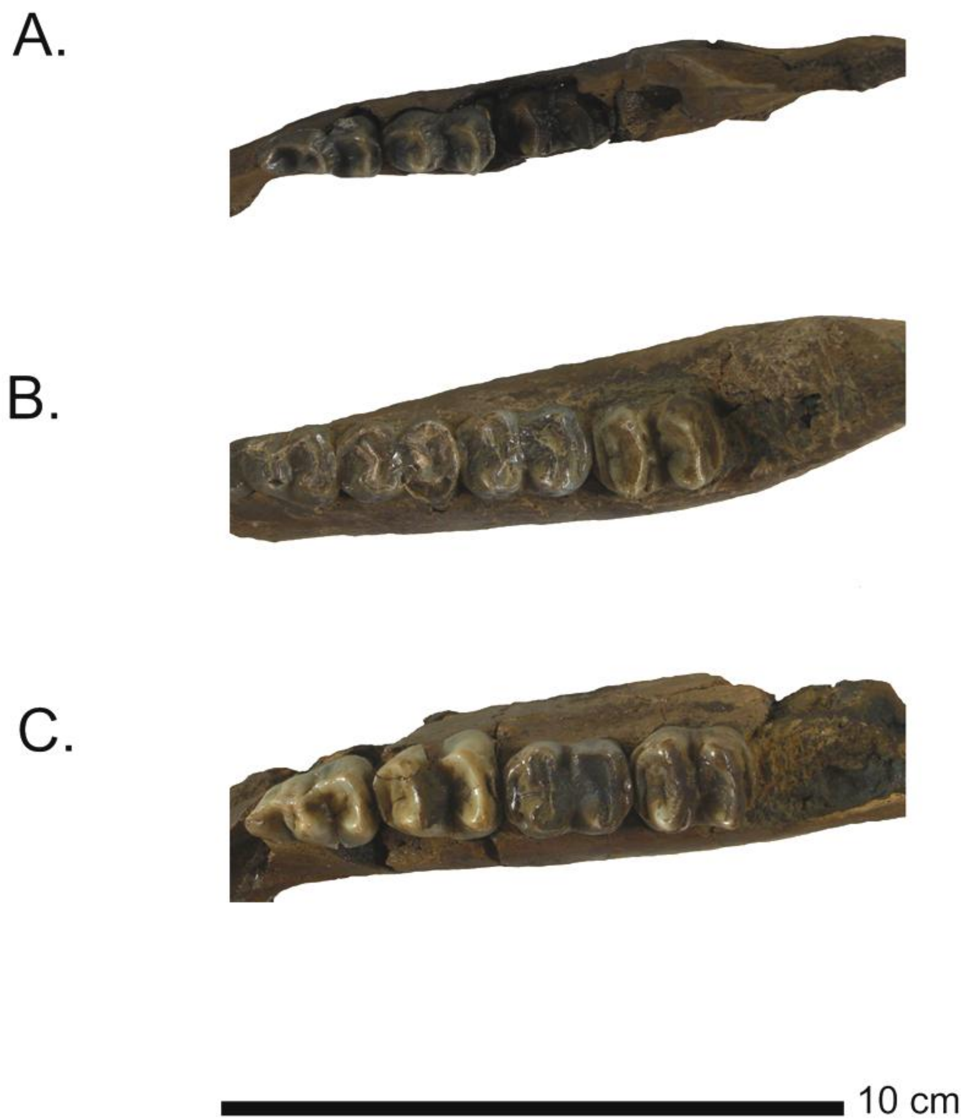

Figure 3: Lower dentitions of juvenile individuals of *Tapirus polkensis*. A) ETMNH 610, (<1 – 1 year) dentition consists of deciduous premolar 2 through deciduous premolar 4. B) ETMNH 3687, (1 - 2 years) dentition in which dp2 through m1 have erupted. C) ETMNH 611, (2 - 3 years), dp 2 and dp3 have been replaced by p2 and p3, but dp4 is still present.

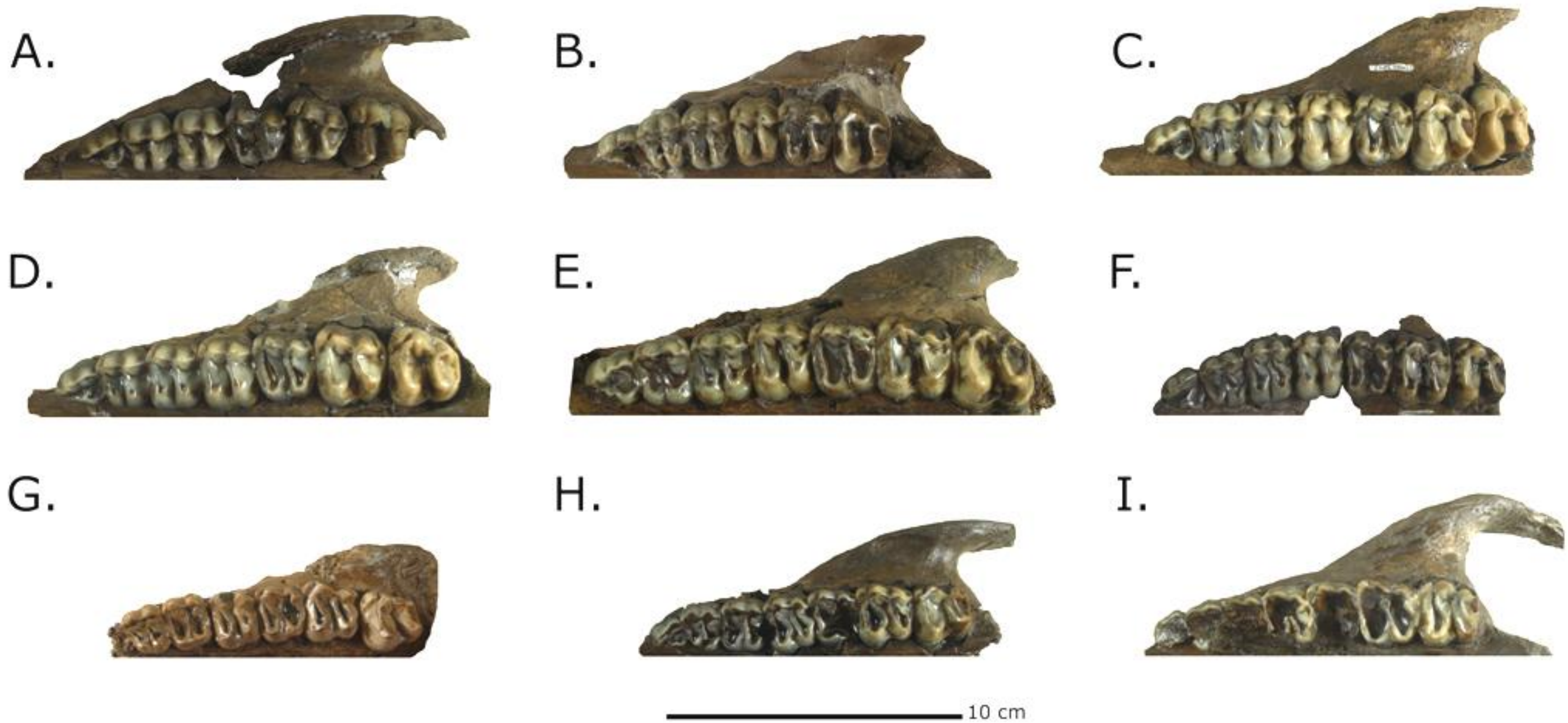

Figure 4: Upper dentitions of adult individuals of *Tapirus polkensis*. A) ETMNH 3699, Subadult (3 - 4 years); B) ETMNH 3426, Young Adult (4 - 5 years; C) ETMNH 3843, Young Adult (5 - 6 years); D) ETMNH 3719, Young Adult (6 - 7 years); E) ETMNH 680, Full Adult (7 - 8 years); F) ETMNH 682, Full Adult (8 - 9 years); G) ETMNH 606, Full Adult (9 - 10 years); H) ETMNH 5285, Old Adult (10 - 11 years); I) ETMNH 3519, Old Adult (11 - >11 years).

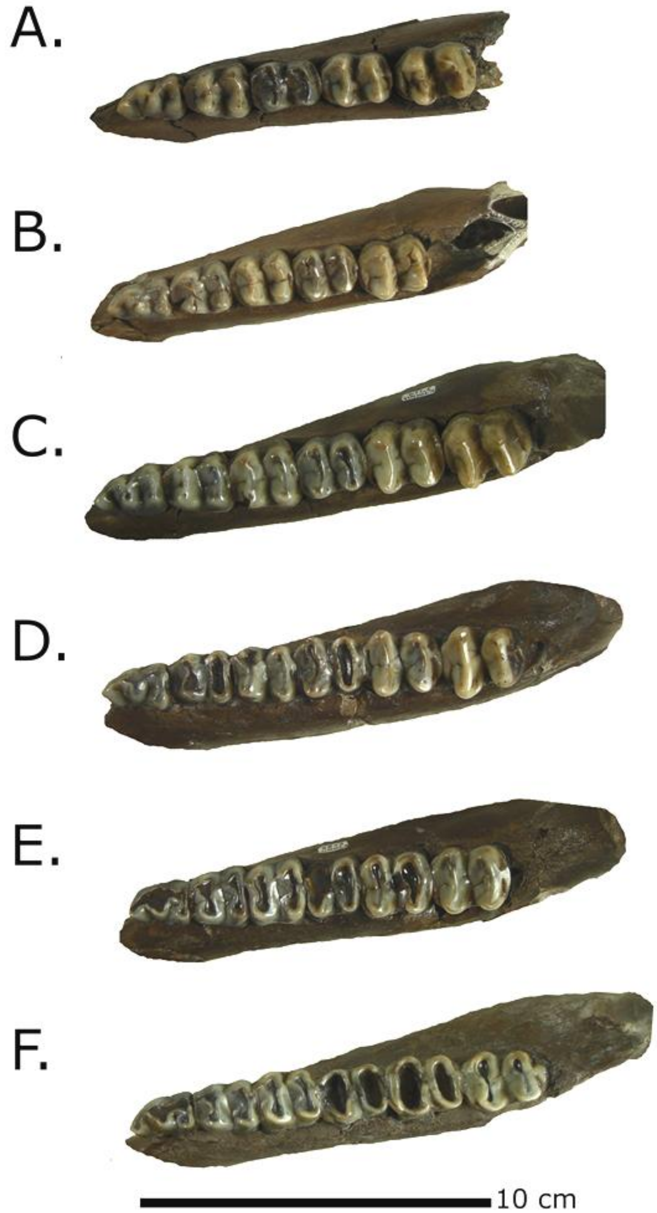

Figure 5: Lower dentitions of adult individuals of *Tapirus polkensis*. A) ETMNH 3699, Subadult (3 - 4 years); B) ETMNH 3426, Young Adult (4 - 5 years); C) ETMNH 3719, Young Adult (6 - 7 years); D) ETMNH 682, Full Adult (8 - 9 years); E) ETMNH 5285, Old Adult (10 - 11 years); F) ETMNH 3519, Old Adult (11 - >11 years). The individuals representing 5 - 6 years, 7 - 8 years, and 9 - 10 years lack lower dentitions; however, based on those that do, the lower dentitions mirrors the eruption seen in the upper dentition.

CHAPTER 4

DISCUSSION

Data collected from the BTP proved to be an invaluable starting point for this study. As the only known-age tapir analysis available for comparison, the data not only created the baseline of this study but also lacked the assumptions that caused problems when using other methods. The limits of the data, however, namely the lack of data for individuals less than 9 months or older than 7.5 years, required that other studies be brought in to better define these groupings. Unfortunately, dental records simply do not exist for individuals less than 9 months.

Based on the very young juveniles (ES1) individuals from GFS and the 9 month old tapir from BTP, it's safe to assume that when dental records for these infants do become available that incisors and canines will be important for determining age in very young juveniles. Data collected for the 9 month old BTP individual show that I1 and I2 had erupted but not I3 or the canine. When compared to very young juveniles from GFS, all of those sampled have at least alveoli for I1 and I2, suggesting that even the youngest tapir at the GFS is at least 9 months old. There are several possibilities that may explain why skulls of individuals less than 9 months old have yet to be recovered (excluding one fetus). One possibility may be that at these ages the skull is too frail to survive the fossilization process. Many of the very young juvenile individuals recovered from the GFS are very fragmentary, so this is likely. Another possibility is that the tapirs are giving birth some distance away from the sinkhole at Gray and then walking in later. This is also highly possible as watering holes inhabited by alligators can be a dangerous place for a very young and inexperienced juvenile tapir. Baird's Tapirs lose their juvenile markings by 6 months, and are relatively similar in overall size to adults (by that time) based on observations of captive individuals from the Nashville Zoo (Figure 6). Weights do differ, however, with the adult weighing more than 200 lbs than the juvenile. For example, Romeo (adult male, 9 years old) weighed 226.7 kg (as of 12/1/10) and Noah (juvenile male, 6 months old) weighed 133 kg (as of 11/13/10). The female Houston, not pictured, weighed 244.5 as of 11/30/10 (K. Jansen pers. comm.). With respect to overall size, this trend is not seen in *T. polkensis*, as young individuals appear to differ greatly in overall size from significantly older individuals based on comparisons of skull and long bone length. This could be due to differences in rate of maturity or simply differences based on tapir diets in a natural setting compared to that of captive tapir diets. For example, the tapirs at the Nashville Zoo are fed a diet of of 18lbs Mazuri Wild Herbivore and 1200g of cracked corn per day. Each of the three tapirs then get its own produce diet mix which consists of 125g carrot, 125g sweet potato, 170g papaya, 7 whole bananas, and 200g daily variety root vegetable (either turnips, rutabaga, sweet potato, yucca, beets, parsnips, or radishes). By comparison wild individuals of *T. bairdii* feed on mainly bamboo, plant leaves, twigs, and fruit when available (Tobler, 2002). This can lead to different rates of wear.

The more nutritious captive diet most likely lends to the overall weight difference; however, the similarities in over body size seen between Romeo and Noah are real representation of how quickly tapirs grow. Although records for the amount of time it takes *T. bairdii* to reach adult size aren't readily available, work with *T. terrestris* has found that individuals of *T. terrestris* reach their full adult size by 18 months (Young, 1961). It would appear that *T. bairdii* reaches adult size quicker, which suggests that the age which the individual tapir reaches adult size varies from species to species.

Figure 6: Size difference in captive Baird's Tapirs. These individuals of *Tapirus bairdii* are on display at the Nashville Zoo, Nov. 2010. Romeo, seen on the left, is the father of Noah, seen on the right. At the time of this photograph Romeo is 9 years old, whereas Noah is merely 6 months old. The overall size difference between the two does not equal the disparity in age.

Once a tapir reaches 3 – 4 years, dental eruption of buccal teeth may not give an accurate approximation of the individual's age. Using dental wear in addition to eruption has helped alleviate this problem, but it assumes that all individuals are eating the same items and wearing their teeth at the same rate. All tapirs, as well as the black rhinos used in this study, are browsers, and even though it is still possible that teeth in these individuals wear at different rate, the black rhinos remain one of the closest possible comparisons. Although the study on *T. terrestris* (Maffei 2003) is the most directly comparable to the tapirs in this study, problems with Maffei's conclusions meant that other less directly related ungulate studies would have to be compared as well. As a result, Hitchins' (1978) work with aging black rhinos was used alongside Maffei's (2003) study to create dental wear keys.

The main problem with Maffei's (2003) study of wear on buccal teeth *T. terrestris* was the possible underestimations of ages. One of the main bases of the *T. terrestris* wear key is that individuals that do not have their M3 erupted are less than 2 years of age (Maffei 2003). This creates a significantly large spike of individuals <2 years of age (before they reach sexual maturity). Maffei (2003) interprets this as evidence of overhunting of *T. terrestris* by indigenous hunters. However, data collected by the BTP refute this. Even their oldest known age individual (7 years, 3 months) lacks an erupted M3. This verifies that the age data were underestimated and causing a false inflation in the number of individuals considered to be less than 2 years of age. As the work was done in Bolivia, it is likely that outdated lab equipment probably reduced the quality of the results (L. Maffei pers. comm.). Unfortunately, this means the data cannot be used to determine how the amount of hunting is affecting the population of *T. terrestris* in the Chaco like Maffei attempted to do and is of little use as an age comparison to the GFS sample. For example, if the individuals at the GFS were interpreted as <2 years of age if they lack an erupted M3, there would also be a large spike of individuals that are <2 years from the GFS. This would insinuate that *T. polkensis* would also have an extremely high mortality from overhunting, which is not the case as there is little evidence of predation or even scavenging on the bones. Because of this, the dental keys in Maffei (2003) are not representative of their true respective ages and could not be used for direct comparison for this study.

Interestingly, when data from my study are compared to the information from the Maffei (2003) study, the curves are relatively similar (Figure 7). The major difference between the 2 population studies is the exaggerated spike for 1 - 2 year old individuals of *T. terrestris* as a result of the error discussed previously. I would expect that after removing all of the falsely underestimated individuals of *T. terrestris* and regrouping them the curve would more closely resemble that of *T. polkensis*.

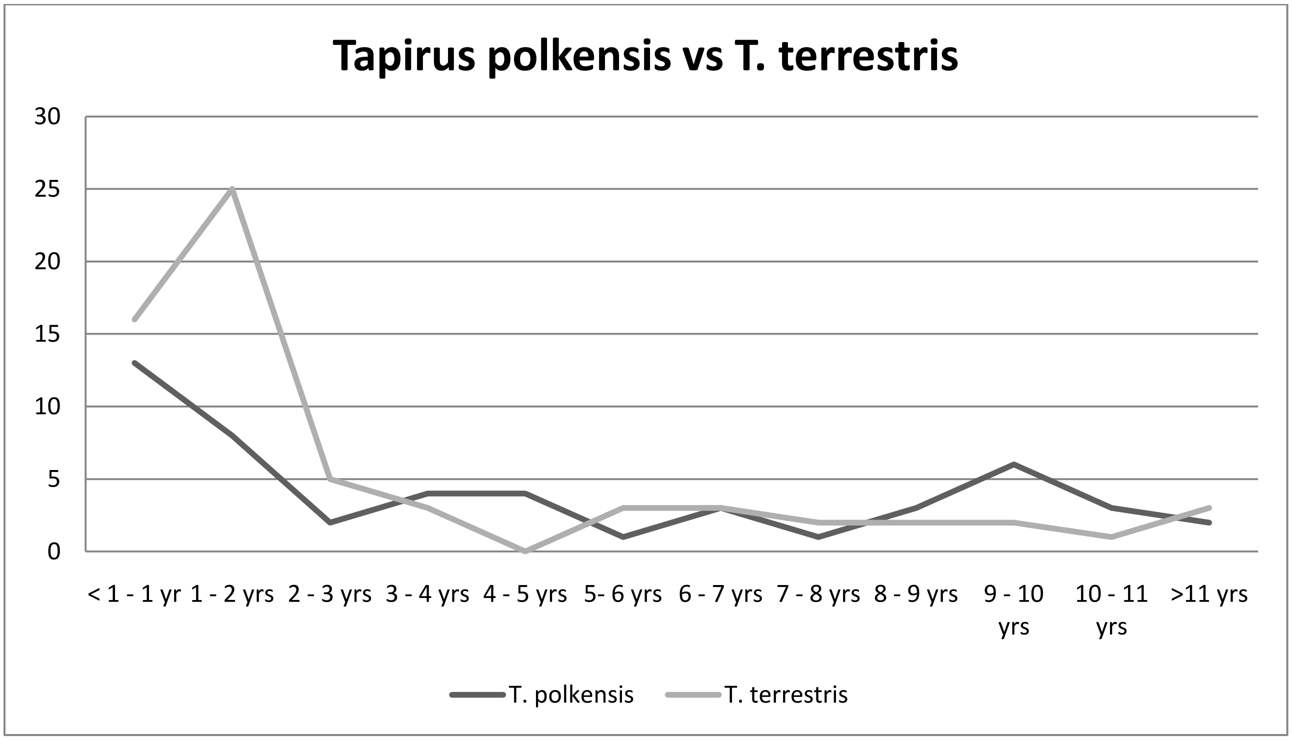

Figure 7: Sample of *Tapirus polkensis* from the Gray Fossil Site compared to the sample of *T. terrestris* from the Bolivian Chaco. Due to underestimations in age, the *T. terrestris* curve is inflated in the 1 – 2 year category.

With the Maffei (2003) study proving to be no longer directly applicable, I turned to data collected from 1960 – 1972 by Hitchins (1978) on black rhinos (*Diceros bicornis*) from the Hluhluwe Game Reserve. From this, Hitchins (1978) created 17 age classes; each with a respective dental key showing buccal teeth present and degrees of wear based on ages determined by the number of cementum rings present in the M1. Because the M1 erupts at age 3 in black rhinos (Goddard 1970), and based on a known age 4 year old that had one cementum ring, Hitchins (1978) determined the actual age could be calculated by adding 3 years to the cementum-ring based age. Therefore, black rhinos that have their M1 erupted (black rhino ES 5) represent the youngest age group for which cementum ages were calculated.

I compared the state of eruption and wear for this group to when the M1 erupts in tapirs (tapir ES 2) and found that the age estimated for the black rhinos is roughly double that seen in tapirs. Using this, I estimated ages of tapirs by comparing them to the degree of wear seen in rhinos, assigning ages based on the rhinos, and then dividing that number by two. For example, a tapir that has its M1 just beginning to erupt would be 4 years old using the rhino key, but according to the data collected by the BTP it would be between 1 - 2 years old. In addition to allowing me to age the tapirs at GFS, I also used the black rhino data as a comparison population sample (Figure 8). Both populations are relatively similar, with major differences being lack of rhino data (see age groups 6 -7 yrs, 8 - 9 years, and 9 - 10 years in Figure 8).

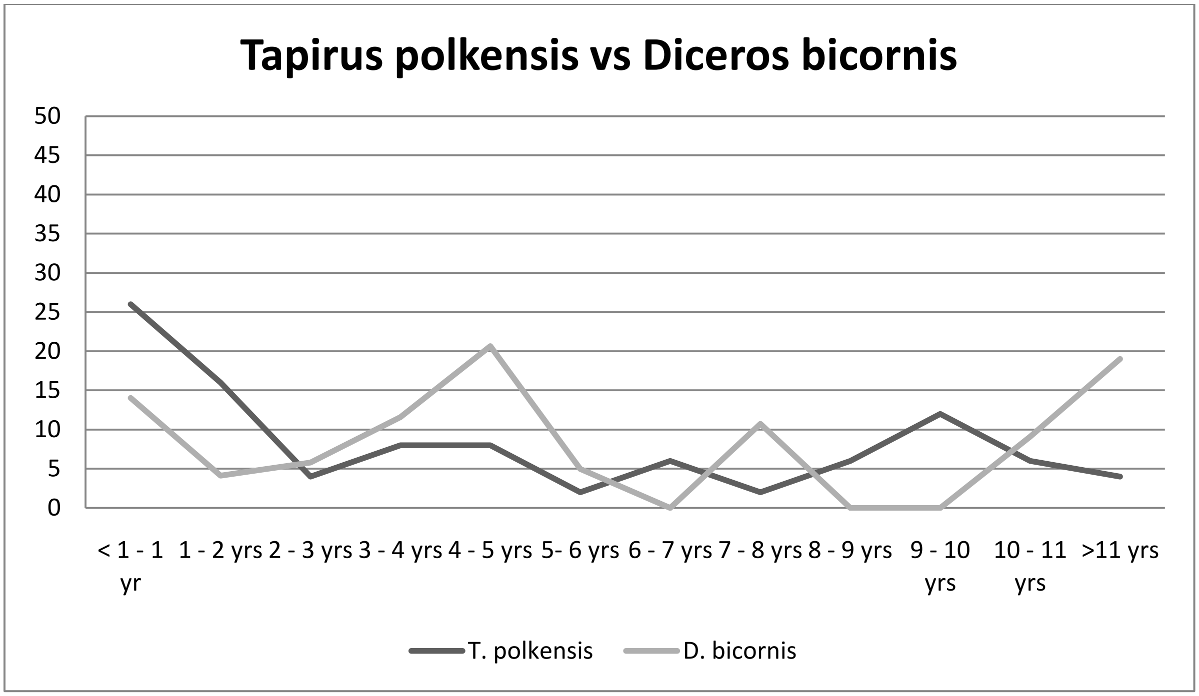

Figure 8: Sample of *Tapirus polkensis* from the Gray Fossil Site compared to the sample of *Diceros bicornis* from the Hluhluwe Game Reserve. Due to the larger sample size for the black rhinos (n = 121; Appendix, Table 3), percentages were used on the y –axis rather than number of individuals. Addtionally, rhino ages were divided by two to allow for direct comparison to tapir ages.

Overall, the rhino and tapir trend lines (Figure 8) represent a high mortality in the younger age groups, an increase once individuals reach roughly 2 years, and then fluctuating for the remainder of the graph. The greater number of recovered tapirs from ages <1 - 1 and 1 - 2 years is possibly due to greater hunting pressures on juvenile tapirs compared to rhinos of the same individual age. This stands to reason as rhinos have fewer natural predators, are larger with very thick hide, and tend to herd to protect young, which increase difficulty for predators to make successful kills. Modern tapirs only have their size as defense as they do not herd. *Tapirus polkensis*, as a dwarf tapir, is much smaller in size. Based on the faunal list for the GFS, tapirs may have been preyed upon by alligators and the saber-toothed cat, *Machairodus.* However, none of the tapir individuals from the GFS show any indication of hunting or even scavenging so although it is a possibility there is no fossil evidence to support this hypothesis. The other possibility is that there simply more juveniles present living near the sinkhole and, therefore, are well represented. Once the tapirs reach roughly 2 years of age (sexual maturity in modern species) the trend line becomes relatively stable. This seems to validate that the tapirs recovered from the GFS were most likely living the forested areas surrounding the sinkhole deposit, routinely traveling to the sinkhole to use it as a water source.

Studies on survivorship done on other large ungulates have shown that mortality is very high in the first 2 years of life. Loison et al. (1999) recorded male/female survivorship data for one population of Isard (*Rupicapra pyrenaica*), 2 populations of Roe deer (*Capreolus capreolus*), and 2 populations of Big Horn Sheep (*Ovis canadensis*). When compared to the sample from GFS, it appears that population trend line is negatively correlated to the annual survival rate for Big Horn sheep, female Roe deer, and female Isard (Figure 9). This seems to show that tapirs have a low survival probability early in life, roughly until they reach 2 – 2.5 years of age, and then they reach a level of relative stability. Interestingly, the GFS tapir trend line does not increase significantly for older tapirs as the other ungulate survivorship lines suggest that it would (which would show a greater mortality with age). This may suggest the population was relatively dense, as proportions of older individuals increase in denser populations (Festa-Bianchet et al. 2003). This could also be due to the small sample size, which when added to the current count, would change the length of the trend line. With more individuals it is possible that the number of tapirs older than 11 years would increase to mirror the higher mortality of older individuals seen in Loison et al. (1999). It is also possible, however, that due to the longer life span seen in tapirs compared to most ungulates that tapirs simply experience a longer period of stability before the mortality increases.

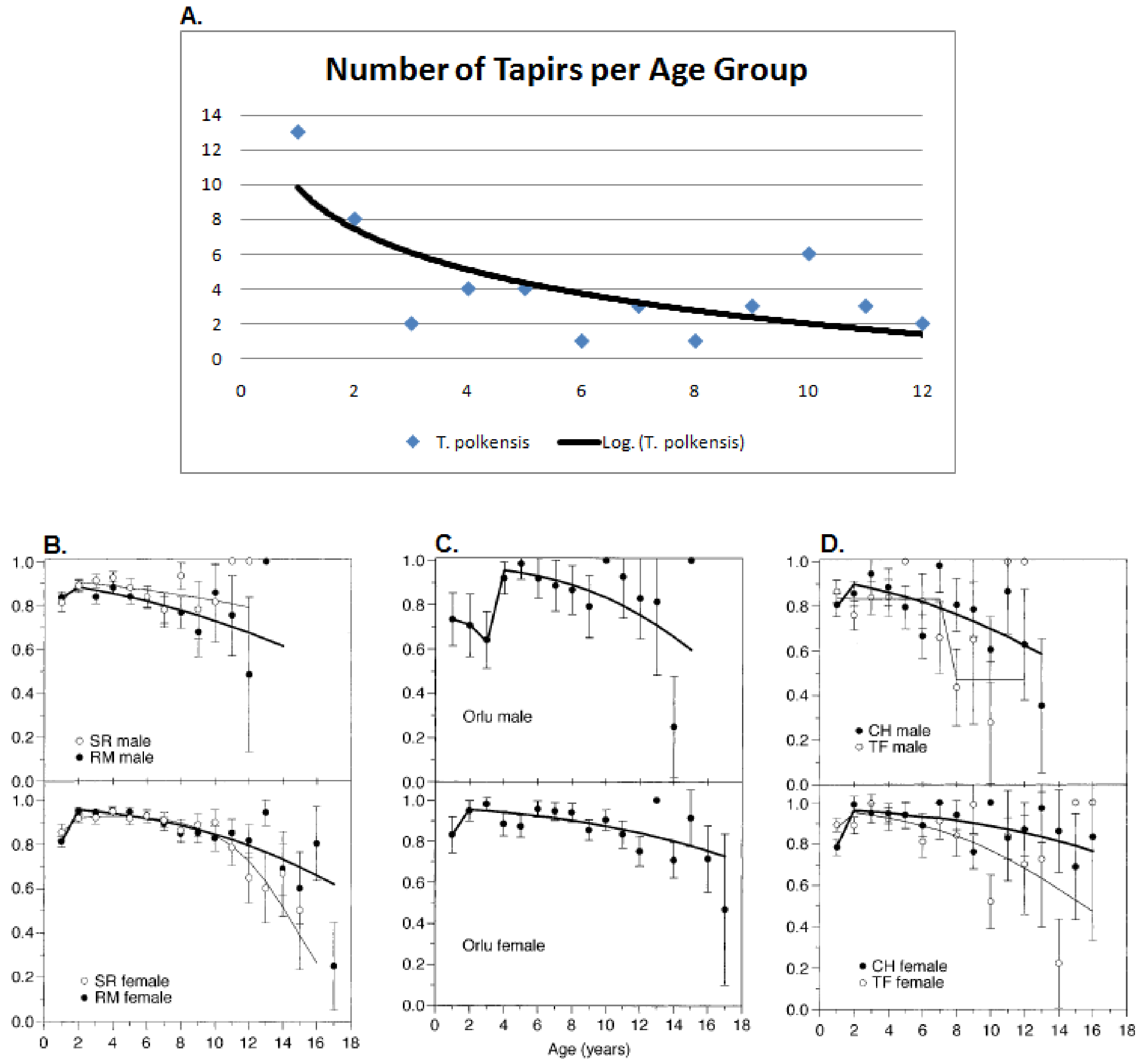

Figure 9: Sample of *Tapirus polkensis* compared to the annual survival rates of three species of large ungulates (in part modified from Loison et al. 1999). A) Number of *T. polkensis* individuals grouped into respective age groups. B) Survival rate of Big Horn Sheep. SR, Sheep River population; RM, Ram Mountain population. C) Survival rate of Isard, Orlu population. D) Survival rate of Roe deer. CH, Chizé population; TF, Trois-Fontaines population.

Future Work

As the GFS sample is a good representation of the tapir population's age structure, the next step would be to attempt to identify any sexual dimorphism that could be observed from the fossils. As seen in other ungulates, survivorship between males and females can potentially be very different. It would be interesting to see if that same trend can be observed in the GFS tapir population. Some studies are currently being conducted to assess any skeletal evidence of sexual dimorphism in the GFS, and they could prove promising. Currently, only one individual is known to be definitively female as it was found with a fossilized tapir fetus (Hulbert et al 2009). It would be interesting to see if there were any skews in the sample toward one gender similar to what is seen in the ungulate studies conducted by Loison et al. (1999).

As more work is conducted on the population structures of modern and extinct species of tapir, comparisons between populations through time could be an interesting pursuit as well. Research in this particular area could prove very helpful for conservation efforts as it would allow comparisons between historical and modern populations that have many factors that could affect the population, such as human hunting pressures, habitat loss, or competition with livestock. Historical populations would lack these unnatural pressures, and provide a better proxy to which modern populations could be compared. In doing so, not only could species be more easily identified as threatened or endangered, but the degree of that danger could also be assessed.

Conclusion

This study used data collected by the BTP on *T. bairdii*, Maffei's (2003) study on *T. terrestris*, and Hitchins's (1978) study of *D. bicornis* to create dental keys for accessing age of tapirs based on dental eruption and degrees of dental wear. These keys were then used to age fossil tapirs, *T. polkensis*, from the GFS. The youngest individuals from the GFS appear to be roughly 9 months with the exception of one fetal individual. The lack of individuals between fetal and 9 months of age could potentially be a result of the frail skeletal elements of these individuals not preserving well. As this study focused on skulls with complete dentitions, any poorly preserved specimens of very young juveniles would have likely been excluded. Another scenario, however, is that the tapirs are calving in the nearby forest with tapirs venturing to the sinkhole once they are older.

Prior to this study, virtually no studies have attempted to assess the age structure of tapir populations. Aside from the *T. bairdii* studied by the BTP, only *T. terrestris* (Maffei 2003) has been the focus of such a study. Unfortunately, a flaw in the methodology has shown that the age structure data represented by Maffei (2003) is not a reliable representation of the *T. terrestris* population in the Chaco. It is possible that once this flaw is rectified, the T. terrestris population can then be compared to the GFS sample.

The sample from GFS seems similar to the sample from Hitchins (1978). This suggests that tapir and rhino populations have very similar age structures. This is not surprising as both are large perissodactyls that occupy similar niches. However, this validates that the tapirs were living relatively near the sinkhole since the sample obviously represents a viable population both shown by this study and the discovery of the pregnant female described in Hulbert et al. (2009).

In closing, this study has also created a proposed timeline for the life of a tapir (Figure 10). This timeline compiles of all the information collected from the known age *T. bairdii* individuals studied by the BTP as well as information compiled by this study by aging individuals and then taking note of fusion in long bones. This timeline will be useful in assessing the ages of tapirs in other populations, both living and fossil, and in turn increase our understanding of an enigmatic and little understood taxa.

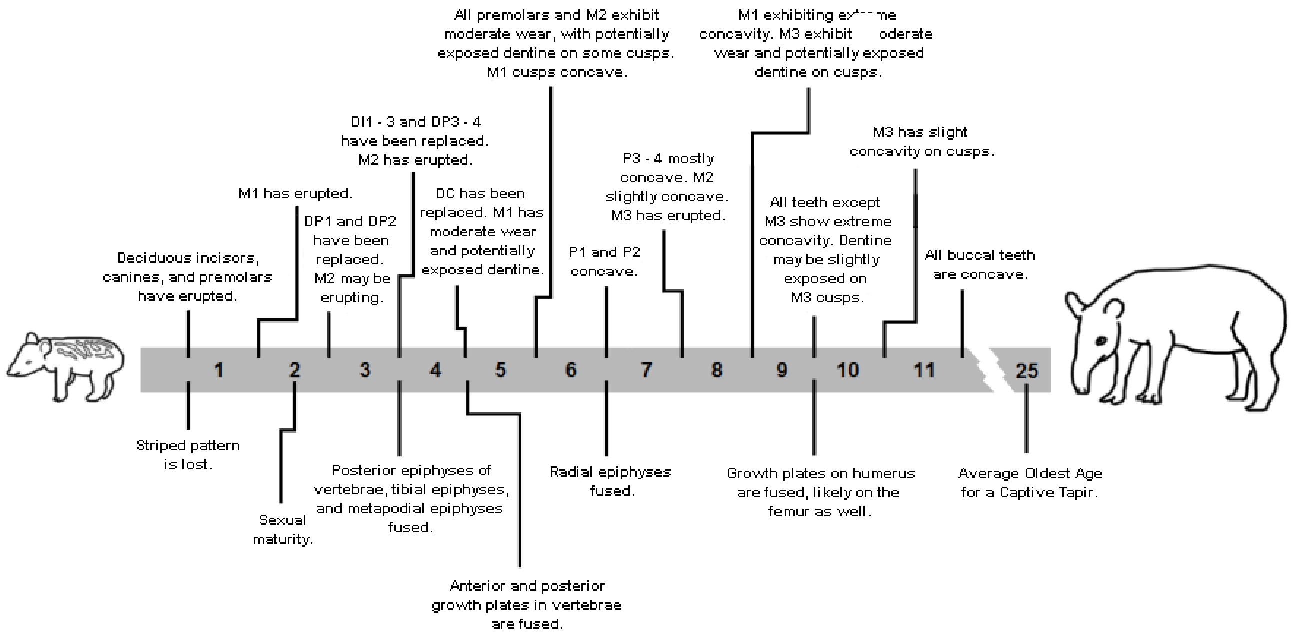

Figure 10: Proposed tapir life timeline. This timeline is based on data collected for *Tapirus bairdii* by the Baird's Tapir Project of Costa Rica and comparisons to the fossil taxon *T. polkensis* from the Gray Fossil Site, Tennessee. Oldest captive age tapir taken from Parera, 2002.

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APPENDICES

APPENDIX A

Data Collected from the GFS Juvenile Individuals of *Tapirus polkensis* (Eruption Series 1 – 3)

	UPPER DENTITION											LOWER DENTITION									
ETMNH	I1	I2	I3	C	P1	P2	P3	P4	M1	M2	M3	i1	i2	i3	c	p2	p3	p4	m1	m2	m3
ES1																					
610	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	1	1	0	0	0	0
3677	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	1	1	0	0	0	0
3678	A	A	A	A	A	1	A	0	A	A	A	A	A	A	A	1	1	0	0	0	0
3680	A	A	A	P	1	1	1	0	0	0	0	A	A	A	A	A	A	A	A	A	A
3681	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	1	1	1	0	0	0
3683	A	A	A	A	A	A	A	A	A	A	A	A	A	1	A	1	1	0	0	0	0
3685	A	A	A	A	1	1	1	1	0	0	0	A	A	A	A	1	1	1	0	0	0
3692	A	A	A	A	A	1	1	1	0	0	0	A	A	A	A	1	1	1	0	0	0
3806	A	A	A	A	1	1	1	1	0	0	0	A	A	A	A	A	A	A	A	A	A
ES2																					
605	P	P	P	P	1	1	1	1	1	0	0	D	D	P	P	1	1	1	1	0	0
3687	A	A	A	A	1	1	1	1	1	0	0	A	A	A	A	1	1	1	1	0	0
3689	A	A	A	A	1	1	1	1	1	0	0	A	A	A	A	A	A	A	A	A	A
3692	A	A	A	A	1	A	1	1	0	0	0	A	A	A	A	1	1	1	0	0	0
3794	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	1	1	1	0	0	0
6821	A	A	A	A	1	1	1	1	0	0	0	A	A	A	A	A	A	A	A	A	A
ES3																					
600	A	A	A	A	1	1	1	1	1	0	0	P	P	P	P	A	1	1	1	0	0
3694	A	A	A	A	A	A	A	A	A	A	A	A	P	A	P	1	1	1	1	0	0
3698	A	A	A	A	1	1	1	1	1	0	0	A	A	A	A	A	A	A	A	A	A
3720	A	A	A	A	1	1	1	1	1	0	0	A	A	A	A	1	1	1	1	0	0
3808	A	A	A	A	A	A	A	A	A	A	A	A	P	P	P	1	1	1	1	0	0

Prescence (P) and Absence (A) data was collected for incisors and canines. Eruption designations are the same as those used by BTP. For premolars: 0, deciduous tooth unerupted or erupting; 1, deciduous tooth erupted or permanent tooth erupting; 2, permanent tooth erupted. For molars: 0, unerupted or erupting; 1, molar erupted.

APPENDIX B

Data Collected from the GFS Adult Individuals of *Tapirus polkensis* (Eruption Series 4 – 7)

	UPPER DENTITION											LOWER DENTITION									
ETMNH	I1	I2	I3	C	P1	P2	P3	P4	M1	M2	M3	i1	i2	i3	c	p2	p3	p4	m1	m2	m3
ES4																					
611	P	P	P	P	2	2	2	1	1	0	0	P	P	P	P	2	2	1	0	0	0
3695	A	A	A	A	A	A	A	A	A	A	A	P	P	P	P	2	2	1	1	0	0
3699	A	A	A	A	2	2	2	1	1	1	0	A	A	A	P	2	2	1	1	1	0
3700	2	2	2	2	2	2	2	1	1	1	0	A	A	A	A	A	A	A	A	A	A
4144	A	A	A	A	A	A	A	A	A	A	A	A	A	A	P	2	2	2	1	1	0
7280	A	A	A	A	A	A	A	A	A	A	A	P	A	A	P	2	2	1	1	0	0
ES5																					
595	A	A	A	A	2	2	2	2	1	1	1	A	A	A	A	A	A	A	A	A	A
602	A	A	A	P	2	2	2	2	1	1	0	A	A	A	A	A	A	A	A	A	A
3426	A	A	A	A	2	2	2	2	1	1	0	A	A	A	P	2	2	2	1	1	0
3705	A	A	A	A	A	2	2	2	1	1	0	A	A	A	A	A	A	A	A	A	A
3712	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	2	2	2	1	1	1
3719	P	P	P	P	2	2	2	2	1	1	1	A	A	A	A	A	A	A	A	A	A
3843	A	A	P	A	2	2	2	2	1	1	0	A	A	A	A	A	A	A	A	A	A
5171	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	2	2	2	1	1	0
ES6																					
606	P	P	P	P	A	2	2	2	1	1	1	A	A	A	A	A	A	A	A	A	A
607	P	P	P	P	A	A	A	2	1	1	1	A	A	A	A	A	A	A	A	A	A
608	A	A	A	A	A	A	2	2	1	1	1	A	A	A	A	2	2	2	1	1	1
680	P	P	P	P	2	2	2	2	1	1	1	A	A	A	A	A	A	A	A	A	A
682	P	P	P	P	2	2	2	2	1	1	1	P	P	P	P	2	2	2	1	1	1
687	P	P	P	P	2	2	2	2	1	1	1	P	P	P	P	2	2	2	1	1	1
3573	P	P	P	P	2	2	2	2	1	1	1	P	P	P	P	2	2	2	1	1	1
3719	P	P	P	P	2	2	2	2	1	1	1	P	P	P	P	2	2	2	1	1	1
10383	A	A	A	A	A	A	A	A	A	A	A	P	P	P	P	2	2	2	1	1	1
10585	A	A	A	A	2	2	2	2	1	1	1	A	A	A	A	A	A	A	A	A	A
ES7																					
683	P	P	P	P	2	2	2	2	1	1	1	P	P	P	P	2	2	2	1	1	1
3519	P	P	P	P	2	2	2	2	1	1	1	P	P	P	P	2	2	2	1	1	1
3714	A	A	A	A	A	A	A	A	A	A	A	A	A	P	A	2	2	2	1	1	1
3716	A	A	A	A	2	2	2	2	1	1	1	A	A	A	P	2	2	2	1	1	1
3717	P	P	P	P	2	2	2	A	A	A	A	P	P	P	P	2	2	2	1	1	1
5285	P	P	P	P	2	2	2	2	1	1	1	P	P	P	P	2	2	2	1	1	1

Presence (P) and absence (A) data was collected for incisors and canines. Eruption designations are the same as those used by BTP. For premolars: 0, deciduous tooth unerupted or erupting; 1, deciduous tooth erupted or permanent tooth erupting; 2, permanent tooth erupted. For molars: 0, unerupted or erupting; 1, molar erupted.

APPENDIX C

Ages in Years for Black Rhinos (*Diceros bicornis*) from the Hluhluwe Game Reserve from 1960 to 1972 as Determined by Dental Cementum Counts, Adapted from Hitchins (1978)

Age Class	n	Rhino Age Range	Equivalent Tapir Age
I	2	-	<1 - 1 yr
II	2	-	<1 - 1 yr
III	2	-	<1 - 1 yr
IV	11	-	<1 - 1 yr
V	5	4	2
VI	7	4 - 5	2.25
VII	4	6 -7	3.25
VIII	10	6 -7	3.25
IX	11	7 - 10	4.25
X	12	8 - 12	5
XI	2	10	5
XII	6	11 - 12	5.75
XIII	13	14 - 18	8
XIV	11	20 - 23	10.75
XV	20	22 – 31	13.25
XVI	2	33 - 34	16.75
XVII	1	37	18.5
SUM	121		

*Tapir ages based on dental eruption and wear are equivalent to half of the estimated ages of black rhinos.

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