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Variation in the Modified First Metatarsal of a Large Sample of *Tapirus polkensis* and the Functional Implications for Ceratomorphs.

Patrick Lawrence Hawkins

East Tennessee State University

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Variation in the Modified First Metatarsal of a Large Sample of *Tapirus polkensis,* and the Functional Implications for Ceratomorphs

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by

Patrick Lawrence Hawkins

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Steven C. Wallace, Chair

Blaine W. Schubert

Jim I. Mead

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ABSTRACT

Variation in the Modified First Metatarsal of a Large Sample of *Tapirus polkensis* and the Functional Implications for Ceratomorphs

by

Patrick Lawrence Hawkins

The Mio-Pliocene age Gray Fossil Site of northeastern Tennessee has the largest collection of tapir postcranial skeletons in the world. Though representing a single species, a few localized structures show high variability. This paper deals with variation of the first metatarsal, which in tapirs was reduced as an early adaptation for running and then retrofitted to serve as a special origin for flexors and adductors of the proximal phalanges. The first metatarsal connects the medial ankle with a posterior process of the third metatarsal in tapiroids. In *Tapirus indicus*, *T. webbi*, and 6 out of 31 *T. polkensis* feet at Gray, it extends more laterally to articulate with the fourth metatarsal. This condition is too variable for species distinction but is correlated with a decrease in the metatarsophalangeal joint facet, suggesting a mobility reduction likely related to the increased range and feeding strategy seen in extant *T. indicus*.

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Both the fossil site and museum at Gray are the successful culmination of too many individuals representing different organizations to specifically list here. Suffice it to say that ETSU, the scientific research community, and East Tennesseans have been enormously rewarded by this collective effort and will continue to be so for a long time. As research director for GFS, Dr. Wallace, has also provided me the opportunity for experience in paleontology ranging from excavation to publication.

Collections access has been given freely by Brett Woodward and April Nye (ETMNH), Jin Meng and Judy Galkin (AMNH Paleontology), Eileen Westwig (AMNH Mammalogy), Linda Gordon and Jeremy Jacobs (Smithsonian Division of Mammals), Michael Brett-Surman

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CHAPTER 1

INTRODUCTION

Paleontology is a science often conducted with a very limited number of specimens, but the sample of *Tapirus polkensis* recovered from the Gray Fossil Site (GFS) has over 75 individuals (Hulbert et al. 2009). It is numerous enough to show a natural amount of variation reflective of a living population. Most cranial and dental measurements of GFS individuals have coefficients of variation below 10 (Hulbert et al. 2009) indicating a single taxon (Simpson et al. 1960) and similar to extant *T. terrestris* (Simpson 1945). However, the fossil sample shows localized areas of substantial intraspecific variation such as sagittal crest morphology and the number of infraorbital foramina (Hulbert et al. 2009), which have formerly been used to differentiate species (Hatcher 1896; Simpson 1945; Ray and Sanders 1984). Cranial variation is also being treated elsewhere (Abernethy and Wallace 2011), so this project specifically investigates the first metatarsal and whether variable conditions in its articulation states can be correlated with the animal's locomotor function.

Postcranial variation is less well studied in general, but metatarsal articulations have partially defined extant and extinct tapir species (e.g. Hulbert, 2005). Although tapirs have a tridactyl pes, Radinsky (1963b) identified a vestigial first metatarsal (mt1) by tracing its homology through extinct tapiroids. He further stated that in extant New World tapirs (*T. bairdii*, *T. terrestris*, and *T. pinchaque*), the mt1 articulates laterally with a posterior process of the third metatarsal (mt3), but the facet between these bones is distinctly larger and better defined in the

Asian tapir (*T. indicus*), which includes a lateral expansion onto the fourth metatarsal (mt4). This extra facet between mt1 and mt4 was later found in *T. webbi*, an extinct New World species (Hulbert 2005) and subsequently used in a preliminary phylogenetic analysis (Hulbert and Wallace 2005).

Hulbert and Wallace (personal communication) found that the GFS sample exhibits both of these discrete character states, with the majority similar to extant New World tapirs (referred to herein as condition 0). Alternatively, condition 1 is an articulation between mt1 and mt4, which can be found in only 6 out of the 31 *T. polkensis* from GFS, as well as *T. indicus*, and *T. webbi*. Assessing and describing the anatomical variation associated with these character states is the focus of this research and is one of many projects intended to describe the population structure (Gibson and Wallace 2011) and variation (Hulbert et al. 2009; Abernethy and Wallace 2011; Hawkins and Wallace 2011) present in the GFS tapirs.

Though phylogenetically unacceptable, the metatarsal articulations are loose indicators of species, suggesting that factors unique to groups affect an individual's anatomy. To determine what may cause different foot morphologies, the functionality of bones and associated muscles must be investigated, along with behaviors and ecology of extant species. Living tapirs are rare, so little is known about them and anatomical dissection was unavailable. Functional morphology must be elucidated using traditional paleontological methods on fossils and modern osteological collections.

Examining tapirs and their extinct relatives in museums led to further areas of research. The vestigial mt1 is present in members of the superfamily Tapiroidea, but it is reduced to a fully fused posterior process of the first tarsal (t1) in modern rhinoceroses (Radinsky 1963b). The presence of a distinct mt1 may unite a paraphyletic Tapiroidea, while its assimilation with t1 may be an apomorphy for a monophyletic Rhinocerotoidea. Together, these superfamilies comprise Ceratomorpha (sensu McKenna and Bell 1997) and are tenuously distinguished using dental (Radinsky 1966a; Prothero 1998) and podial (Holbrook 1999; 2001) features. A separate mt1 has not been explicitly mentioned for rhinos (e.g. Prothero 2005), but they are a large and diverse group. Future work should consider this feature and appropriately scrutinize it as a potential uniting character.

The entire order of odd-toed ungulates (Perissodactyla) is defined by evolutionary specializations of their feet (Radinsky 1969), but postcranial fossils are relatively rare. The number of tapir skeletons at GFS allows a unique analysis of an important but understudied component of perissodactyl biology. This description of metatarsal anatomy, morphology in different taxa, and ecological importance is the product of having a large fossil sample and using it to understand more about the endangered living representatives of an important but rapidly vanishing group of large mammals.

CHAPTER 2

BACKGROUND

The Significance of the Gray Fossil Site

Northeastern Tennessee has an excellently preserved fossil site that has yielded informative research on the climate and biodiversity of the area since its discovery in 2000. The geologic ranges of *Teleoceras* (Prothero et al. 1989) and *Plionarctos* (Tedford and Martin 2001) constrain the sites age to late Miocene or early Pliocene and the Hemphillian North American Land Mammal Age (Wallace and Wang 2004). This time period marks the expansion of C4 grasslands in North America (Cerling et al. 1993) and is typically represented by open prairie and horse-rich faunas. However, GFS is dominated by tree macrofossils, pollen, and vertebrates that suggest a forested ecosystem (Wallace and Wang 2004). Moreover, isotopic work done by DeSantis and Wallace (2008) indicates that all species were either browsers or mixed feeders, except for one gomphothere, which suggests a biologically diverse patch of dense vegetation surrounded by vast Miocene grasslands. Holdovers from the earlier forests as well as new invaders could have lived in such a forested refugium (Wallace and Wang 2004; DeSantis and Wallace 2008).

The site provides unique clues for reconstructing the geologic history of North America. Chronologically, the time frame associated with GFS coincides with a worldwide replacement of C3 plants by C4 grasses during the Miocene-Pliocene transition that shaped the global vegetation currently visible (Jacobs et al. 1999). Geographically, East Tennessee is important because it coincides latitudinally with the division between the southern and northern Great Plains, typically used in western North America (Cerling et al. 1997). The west has a large number of fossil sites with which to biogeographically reconstruct a large area, whereas the inland east is sparse (Figure 1).

As a forested refugia for tapirs and other endemic North American taxa, as well some of the first South American invaders, GFS is indirectly associated with the Great American Biotic Interchange (GABI) (McDonald and Wallace 2011). Tapirs were widespread in North American forests beginning with the Eocene (DeSantis and MacFadden 2007), but since the Pleistocene have been limited to Central and South America (Padilla and Dowler 1994). The Oak-Hickory-Pine flora of GFS (Wallace and Wang 2004) is similar to the Pine-Oak forest that serves as a tapir habitat (and route to South America) present today in the Central American forest corridor (Kappelle 2008). These forests likely provide a food source such as acorns that can be eaten by *Tapirus bairdii* (Williams 1984). Oak forests in Central America vary depending on altitude and aridity, resulting in layers of biodiversity which may have provided the stage for GABI (Kappelle 2008). The north and south continents became physically connected around 2.5 Ma (Webb 1991), but sloths have been found in various North American locations, including GFS, as early as 8 Ma (McDonald and Wallace 2011).

Concentration and type of animals found at GFS are unique. With over 75 individual *T. polkensis* at Gray, the only locality that rivals this number is the Central Florida Phosphate District, which represents multiple faunas and lacks preservation of more fragile cranial characters (Hulbert et al. 2009). Tapirs are normally found in low numbers (Ray and Sanders 1984; Hulbert 2005), though they are geographically and chronologically widespread throughout the Cenozoic (DeSantis and MacFadden 2007). Perhaps the most similar site, biologically and geographically (Figure 1), is the Pipe Creek Sinkhole local fauna in Indiana. It was a pond environment with diverse plants and is also chronologically defined by *Teleoceras* and *Plionarctos*, although rodents have been used to designate Pipe Creek as late Hemphillian (Martin et al. 2002) or early Blancan (Martin 2003). No tapirs have been found at Pipe Creek (Farlow et al. 2001).

The GFS deposit formed within a sinkhole environment caused by collapsed karst topography (Whitelaw et al. 2008). Aquatic animals such as alligators, amphibians, and fish have been found throughout GFS, as well as a plethora of turtles and tapirs. Extant *Tapirus terrestris* are fond of water (Padilla and Dowler 1994) and their ancestors probably used the sinkhole environment more than the other large animals, hence the unusual abundance of *T. polkensis* at GFS (Hulbert et al. 2009).

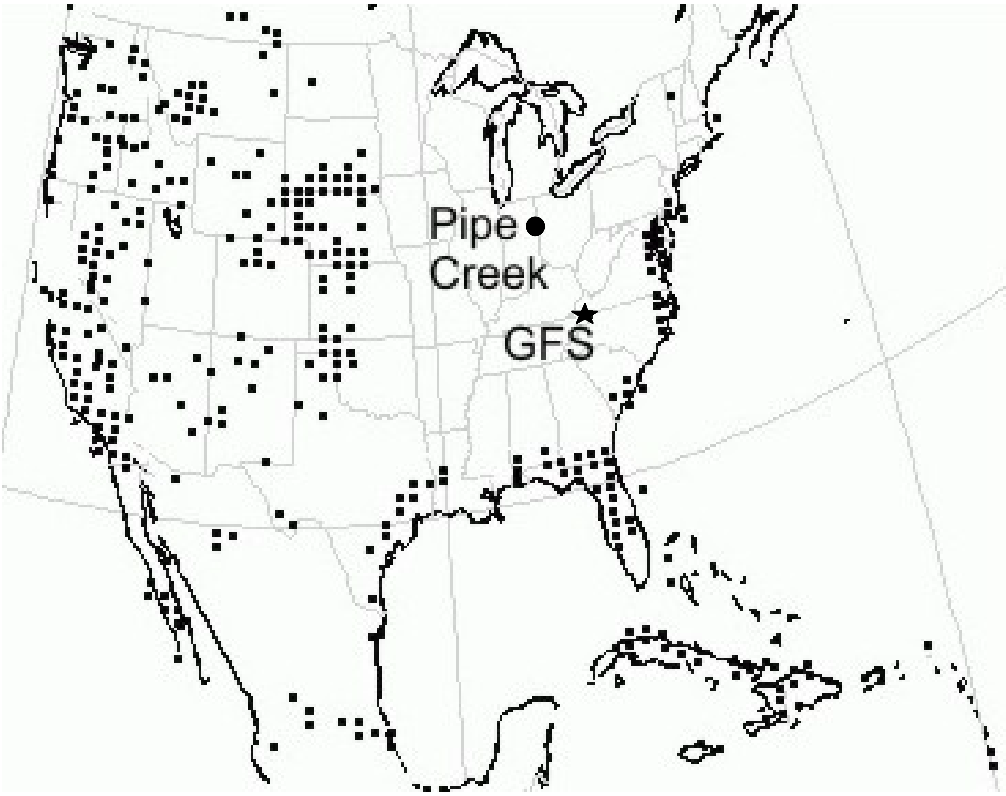


Figure 1. North American Miocene fossil localities. Map was generated using the Paleobiology Database (http://paleodb.org) on 17 November, 2010 using the time interval = Miocene. Pipe Creek Sinkhole (circle) and Gray Fossil Site (star).

The second-most abundant mammal at GFS (MNI=5) is *Teleoceras* cf *T. hicksi* (Wallace 2011). This rhinoceros is large but short-legged and has been considered a semiaquatic North American analog of *Hippopotamus amphibious* since Cope's (1879) description of *T. (Aphelops) fossiger*. Mihlbachler (2003) has shown that the population structure of *Teleoceras* from Florida is more like the modern black rhino than hippopotamus. MacFadden's (1998) isotopic evidence suggests they were terrestrial feeders. Rhinos from GFS have distinctively shortened limbs, indicative of *Teleoceras*, though the 2 complete individuals exhibit marginally longer, yet thinner, limbs (Wallace 2011). Like tapirs, *Teleoceras* probably lived on either land or water.

Tapir Biology

The distribution of tapirs in the past was larger than it is today. Living species are mostly limited to tropical forests near permanent water supplies (Eisenberg 1997), but *Tapirus pinchaque* is capable of living in colder temperatures and uses the dense forest canopy for shelter (Downer 1996). Fossils have been recovered far enough north that they are associated with boreal and temperate taxa, suggesting that temperature has not historically been an important limiting factor (Graham 2003). However, their dependence on forests, coupled with the worldwide expansion of grasslands, probably drove some species south (possible in North America after it joined with South America) while killing off others in the Pleistocene (Graham 2003). Tapir fossils have been used to map forest paleoenvironments based on stable carbon isotope analyses and their conservatively low-crowned teeth (DeSantis and MacFadden 2007). Fossils from the family Tapiridae have been found across Eurasia and the Americas, with inconclusive evidence as to their origin (Hulbert et al. 2009).

Tapir biogeography reflects their past widespread distribution. One species, *T. indicus*, is found in Southeast Asia and the remaining 3 are in Central and South America (Eisenberg 1997). This range reduction has continued as a result of anthropogenic habitat modification and is now a serious threat to *T. bairdii* (Matola et al. 1997) and *T. terrestris* (Bodmer and Brooks 1997). All 4 extant species are endangered or threatened (Baillie et al. 2004).

Southeast Asia's tapir (*T. indicus*) is dwarfed in size by elephants and rhinos with which it can be sympatric, but it is the largest living tapir. Osteologically, *T. indicus* is much more robust than other living tapirs, but third metatarsals are similar in length (Figure 2) to the other extant taxa. Body size, geographic location, and distinct bicolored pelage separate the Asian tapir from New World species. Morphologically, they are more similar to an even larger extinct Asian species, *T. augustus*, than to American taxa (Ray and Sanders 1984). Molecular work may support the monophyly of living Neotropical tapir species separate from *T. indicus* (Norman and Ashley 2000).

Behaviorally, *T. indicus* may be quite distinct, although like other tapirs, they are so rare and cryptic as to be difficult to study. A solitary male had a large home range of 12.75 km^2, which overlapped conspecifics (Williams and Petrides 1980). They are also not as inclined to use paths in the jungle or wallow in mud (Humphrey and Bain 1990). Khan (1997) found that the diet of *T. indicus* included 8.1% fruit, while this figure was around 33% (abnormally high for large herbivores) for *T. terrestris* (Bodmer 1990), so the Asian species is probably less selective. However, workers use inconsistent methods to study the diet of tapirs, making direct comparison difficult (Olmos 1997). Quantitative research on *T. indicus* is sparse compared to New World species (Olmos 1997).

Body mass can be used to easily distinguish new and old world tapirs, with *T. indicus* representing the largest living taxon (Hershkovitz 1954; Hulbert et al. 2009). Cranial osteology accurately reflects the body mass difference, but metatarsal measurements are less straightforward. Lengths of the long metatarsals overlap among species, but *T. indicus* is consistently more robust, while *T. pinchaque* is more gracile (Figure 2). Larger size may account for an enlarged home range of the former.

Figure 2. Relative third metatarsal sizes of the 4 extant species of *Tapirus* (posterior view). From left to right, *Tapirus terrestris* (AMNH 70321), *Tapirus pinchaque* (AMNH 169931)*, Tapirus bairdii* (AMNH 130104)*,* and *Tapirus indicus* (AMNH 54657). Notice the elongate articular facet on *Tapirus indicus* (white arrow) with a truncated lateral edge.

Tapirs travel constantly throughout their home ranges and can contribute greatly to the modification and health of their ecosystem. Their foraging behavior develops distinctive trails (Husson 1978), which create dispersal sites of intact seeds (Bodmer 1991; Rodrigues et al. 1993). This dispersal can occur over great distances, which increases the survival rate of seeds (Fragoso et al. 2003). The large size of tapirs contributes greatly to the survival rates and dispersion distances of seeds, leading some authors to refer to them as keystone species (Downer 1997).

The 3 Neotropical species are the biggest endemic land mammals still living in South America (Olmos 1997). Despite their size, tapirs ably navigate dense forests and steep slopes (Padilla and Dowler 1994). Walking often occurs without visual help because they are crepuscular and have a better sense of smell than vision (Husson 1978). *Tapirus pinchaque* is active at night but sleeps most from midnight to dawn (Downer 1996). The lowland tapir, *T. terrestris*, has more intermittent sleeping patterns (Padilla and Dowler 1994), but this discrepancy may be because *T. pinchaque* inhabits the colder, higher Andes Mountains.

The forest habitats for which tapirs are superbly adapted are becoming increasingly rare, as are the tapirs themselves. Clearing land and overhunting are currently the greatest threats to the existence of tapirs (Downer 1996). All extant species are solitary in the wild and usually only interact with each other when mating or raising young (Padilla and Dowler 1994). There is no evidence (fossil or otherwise) to suggest that they have ever been gregarious animals, but conspecific males are not necessarily hostile to each other and sometimes drink or bathe together (Williams 1984; Matola et al. 1997). Low habitat densities replenished by very slow reproductive rates are hallmarks of the genus *Tapirus* (Eisenberg 1997).

Taphonomy

Fossils at GFS were first found in 2000 during the construction of a new road (see summary and references in Hulbert et al. 2009). In addition to road construction, a museum was later built over part of the fossiliferous layer, further disturbing the topography of the deposit, which was preserved as a gravel-capped hilltop (Wallace and Wang 2004). Because of these irregularities, fossils from GFS have been recovered from various locations, representing slightly different elevations and, most likely, different periods of time. One gravity survey (Whitelaw et al. 2008) shows that the site consisted of multiple sinkholes, which may have coalesced into one main basin. This basin formed a small paleolake (Shunk et al. 2006). Consequently, GFS probably filled with sediment over a long period of time (Hulbert et al. 2009; Shunk et al. 2009), and may preserve various moments of time that are not yet geologically identified. Currently, bones removed from the matrix are surveyed in 3 dimensional space with the intention of observing large scale trends as digging continues (Nave et al. 2002; Wallace 2004); however, results are only preliminary. Excavation at the site involves using a Geographical Information System to store location and descriptive data on individual skeletal elements (Burdick et al. 2002).

Over 80 individual tapirs have been recovered at GFS (Hulbert and Wallace 2011), intuitively implying that the remains of a heard are represented. However, extant tapirs are usually solitary animals (Padilla and Dowler 1994), so this accumulation is probably the result of an attritional deposition that represents many generations (Hulbert et al. 2009). Laminated clays and gravel, which compose the fossiliferous matrix, are at least 39 m thick (Wallace and Wang 2004; Whitelaw et al. 2008; Shunk et al. 2009), suggesting a long lifespan of a lacustrine environment is recorded. Tapirs probably spent a great deal of time in the water, as extant species do (Padilla and Dowler 1994).

The dramatic dominance of tapirs in the GFS fauna indicates that they successfully filled the forest dwelling amphibious mammal niche provided by the local habitat and water. Various age groups of tapirs, as indicated by different stages of epiphyseal fusion and dental wear, suggest that juveniles were not particularly prone to predation. Relative to the sustained population of large herbivores, there is a noticeable lack of large mammalian predators. Small carnivores are well represented by *Pristinailurus bristoli* (Wallace 2011), *Arctomeles dimolodontus*, and some material of the slightly larger *Plionarctos* sp. (Wallace and Wang 2004). *Machairodus* sp. is only known from isolated dental fragments (Wallace and Wang 2004). Alligators are more abundant than the mammalian carnivores and capable of consuming tapirs (Husson 1978), but crocodilian digestion characteristically demineralizes tooth enamel (Fisher 1981), and this has not been directly observed in GFS tapirs. Perhaps more excavation and investigation will explain what consumers were making use of the tapirs, but the current picture of numerous ungulates without pressure from large carnivore remains.

Institutional Abbreviations

AMNH: American Museum of Natural History, New York, NY.

ETMNH: East Tennessee State University and General Shale Brick Natural History Museum, Gray, TN.

GFS: Gray Fossil Site, Gray, TN.

USNM: United States National Museum, Washington, DC.

CHAPTER 3

ANATOMY

Anatomical Nomenclature

Human anatomy is the most extensively studied of any animal, which is understandable considering our self-interest and the relative ease with which a single species can be studied. It was also the first to be standardized (Wilson 2006). However, terminology for describing the human body has been developed over a long period of time and with multiple languages, adding complexity to an already intricate system, though multiple revisions have been published in Latin (Kachlik et al. 2008). For example, novel structures have traditionally been named after their discoverer (often concurrently in different countries and languages), which generated a notoriously redundant naming system (Waibl et al. 2005). Scientists throughout the world are familiar with Latin, which is also no longer a functionally evolving language, and therefore good for descriptive communication (Kachlik et al. 2008). Writing in English with part of the text in Latin is very cumbersome, so the approach here is to use recognizable English words that can easily translate into the Latin terms and appropriate abbreviations (Table 1) following Nomina Anatomica (Waibl et al. 2005).

Veterinary texts usually focus on economically important animals (i.e. not tapirs) and are modified *ad hoc* from human studies. Mammals all have the same general plan, with the greatest exception being the upright posture of humans, which leads mostly to confusion among anatomical directions such as anterior, superior, etc. (Prothero 2005). Perissodactyl anatomy is disproportionately focused on horses. Many texts have been written detailing equine anatomy for veterinarians or other professionals, often with little regard to homologous human structures or evolutionary biology (McFadyean 1902). Sisson (1910) recognizes homology between metatarsals in horses and other mammals but still refers to metatarsal 3 (mt3) as the large metatarsal bone along with the external (mt4) and internal (mt2). Moreover, horse legs have undergone a great deal of digital reduction, making their direct comparison with polydactyl tapirs difficult to describe with the available terms. Paucity of research on extant tapirs and the completely different orientation and morphology of tapir feet lead to further complications. Table 1 compares the terms used herein with other accepted nomenclature such as influential osteological work on tapirs and horses.

Table 1. Anatomical terms of authoritative works compared with this paper

Human	**Horse**	**Tapir**	**International**	**This paper**	
Gray 1918	Sisson 1910	Radinsky 1965	Nomina Anatomica 2005	English equivalent	Abbreviation
talus	tibial tarsal	astragalus	talus	talus	talus
calcaneus	fibular tarsal	calcaneum	calcaneus	calcaneus	calc.
naviculare	central tarsal	navicular	os tarsi centrale (os navicular)	navicular	nav.
first cuneiform	*(fused)* os tarsale primum et secundum, cuneiform parvum	ento-cuneiform	os tarsale I (os cuneiforme mediale	tarsal I (medial cuneiform)	t1
second cuneiform		meso-cuneiform	os tarsale II (os cuneiforme intermedium)	tarsal II (intermediate cuneiform)	t2
third cuneiform	third tarsal	ecto-cuneiform	os tarsale III (os cuneiforme laterale)	tarsal III (lateral cuneiform)	t3
cuboid	fourth tarsal	cuboid	os tarsale IV (os cuboideum)	tarsal IV (cuboid)	t4
first metatarsal	*absent*	vestigial first metatarsal	metatarsale I	metatarsal I	mt1
second metatarsal	internal metatarsal	second metatarsal	metatarsale II	metatarsal II	mt2
third metatarsal	large metatarsal	third metatarsal	metatarsale III	metatarsal III	mt3
fourth metatarsal	external metatarsal	fourth metatarsal	metatarsale IV	metatarsal IV	mt4
N/A	sagittal ridge	medial keel	N/A	sagittal ridge	sr
pisiform	accessory carpal	pisiform	os carpal accessorium (os pisiforme)	pisiform	p
greater multangular	first carpal	trapezium	os carpale I (os trapezium)	first carpal	c1

Perissodactyl Anatomy

Perissodactyl Families

Among extant perissodactyl families (i.e. Equidae, Rhinocerotidae, and Tapiridae), distinctions between feet are sufficient for grouping them. The manus for living genera in each of these families has 1, 3, and 4 functional digits, respectively. However, fossil forms fill all gaps between the living groups (Flower 1885). Horses have extreme cursorial adaptations (MacFadden 1992), and their extant species are monodactyl, though occasionally atavistically polydactyl (Gegenbaur et al. 1882; Marsh 1892). Postcranial anatomy of early equids was very similar to tapirs (Camp and Smith 1942), but hind feet of living ceratomorphs (tapirs and rhinos) are tridactyl and more similar to each other (Flower 1895). Modern rhino feet are graviportal, meaning that they are adapted to carrying the animal's large mass, but extinct members of the family were more lightly built and some were quite cursorial (Prothero 2005).

Metapodials of tapir fore and hind feet are very difficult to tell apart and nearly identical on the distal ends. Horse and rhino metapodials are also most easily discernable from proximal ends but show subtle differences in the distal facet and sagittal ridge. The metapodiophalangeal joint consists of 2 large sesamoid bones located just posterior to the proximal phalanx. Horses have a continuous facet between the articulations of the proximal phalanx and sesamoids but in the few individuals of *Teleoceras* at GFS there is a distinction between these facets, suggesting a more limited range of motion. However, this is to be expected when comparing a cursorial and graviportal foot. Tapir metatarsals look more like horses in this respect. On all feet, tapirs have a rounded facet anteriorly that develops a sagittal ridge posteriorly to separate the 2 sesamoids (and sesamoid ligaments) as well as restrict lateral motion of the phalanx, which has a corresponding posterior groove. Horses extend this groove anteriorly so that only backward and forward movements are allowed, regardless of how flexed the metapodiophalangeal joint is.

Fore and hind limb distal metapodials can also be discerned in horses because the sagittal ridge is more pronounced in metatarsals. In horses, MT3 also has a longer, more rounded shaft than MC3 in horses (Sisson 1910). Phalanges of fore and hind feet are nearly identical, differing only in length and width proportions (Sisson 1910). Distal differences are slight because the bones are dealing with similar biomechanical problems caused by landing on, and launching off, the ground. Extreme specializations towards elastically storing energy also dictate the distal structure, which occurs in both hind and forelimbs (Camp and Smith 1942; Payne et al. 2005). Proximally, more differences become apparent because those biomechanical issues are the result of muscular actions, which are different in form and function. Hind limbs do positive work to propel the animal forward, while forelimbs are assumed to perform a braking role by doing negative work (Dutto et al. 2006). Jumping over obstacles requires specializations in the hind limb for power and flexibility that are not needed by the fore limb (Dutto et al. 2004).

Unique Tapir Osteology

Tapirs have remained largely unchanged since the Eocene, earning them the popular title of ‘living fossils’ (Janis 1984). While this is superficially true of the postcranial skeleton and dentition, tapirs have achieved a highly specialized facial structure. Adaptations for the flexible proboscis (Witmer et al. 2001), including the “telescoping” of the cranium (Colbert 2005), differentiate tapirs from other perissodactyls, whereas their relatively small size and multiple toes are reminiscent of extinct relatives of both horses and rhinos.

Differing from both horses and rhinos, tapirs have altogether 14 functional toes, 4 on the front and 3 on the back feet. While rare in nature, drastically differing front and hind foot anatomy is (in a way) more adaptive. This arrangement gives tapirs 2 advantages, namely powerful speed in the hind limbs and maneuverability through unsteady substrate in the forelimbs. While horse evolution has followed extreme lengthening and distal reduction, useful in open terrain, tapir feet have long been adapted for running in a more closed environment. A tridactyl pes is already developed in the earliest true perissodactyls, and a reduction of the first digit is fully underway by the Eocene (Radinsky 1963b). However, after the first digit was reduced (typically a cursorial adaptation), its metatarsal became retrofitted as a muscle attachment site, and was therefore not completely lost as was the fifth digit. Reduction in digits usually involves the complete loss of hallux or pollex before others (Flower 1885), but in the specific case of tapiroids, mt1 remained. Therefore, while a reduced number of digits results from adaptation to running and is important throughout Perissodactyla, tapir hind feet are further specialized in a way not shared by any other mammal.

All tapirs have the same basic layout for the crus and pes. While the tibia and fibula remain unfused, they generally do not have well developed articular facets between them for motion. Articular surfaces at these joints, such as those found in primates, indicate a proclivity for supination and pronation. *Colodon* and *Deperetella*, which are extinct perissodactyl genera, have fused tibiae and fibulae (Holbrook 2001), as do many highly cursorial animals. This fusion is carried to the extreme in horses and some artiodactyls such as deer wherein the fibular shaft is reduced to a splint. The fibula's distal end, which makes up the lateral malleolus, can be completely separate from the proximal fibula and fused with the tibia in extremely modified animals such as the horse. Distal to and articulating with the tibia is the talus, which exhibits a groove in the middle to restrict lateral motion. This trochlear groove is very deep in cursorial horses, and indicative of ungulate running, as it is shared even by the unrelated artiodactyls (the distal end of the artiodactyls' talus is also grooved and therefore distinct from perissodactyls). The calcaneus is distal to the talus, and it also articulates with the fibula.

Distally touching both the talus and calcaneus on the lateral edge of the foot is the cuboid (t4), which directly supports the fourth metatarsal (mt4). The other weight bearing bone of the foot's middle section is the navicular, which is compressed between the talus and third tarsal (t3). A "saddle-shaped" facet between the talus and navicular with elevated sides and a depressed anterior and posterior serves as a good apomorphy for Perissodactyla (Radinsky 1966b). However, this character can be convergently derived in other groups and must therefore be used in conjunction with a suite of characters (Holbrook 2001). Between the navicular and third metatarsal (mt3), there is t3, which is similar in flatness and sometimes confused with the navicular. Fewer articular facets are present on t3, making it morphologically simpler than the navicular. The navicular has one proximal facet for the talus and distal facets for t2 and 3. All foot bones fit together very tightly and variation in shape and articulation is often great enough that trying to make composites between different individuals leaves noticeable gaps.

Metatarsal 4 has one main proximal tarsal facet for t4, just as mt3 has t3 and mt2 has t2. In addition, t2 has a facet on the proximo-medial side for the internal cuneiform (t1). Of the cuneiforms, t1 is most unique (Figure 3). It lacks the compact look of a weight supporting bone and articulates medially with mt2, t2 and often with the navicular. All tarsals except t1 are proximo-distally compressed. Uniquely, t1 has a tabular shape that curves laterally as it extends posteriorly. Its outside surface is broadly convex and wraps posteriorly around the medial edge of t2 to the posterior aspect of the metatarsals. Strongly attached to t1 is an even more unique bone that resembles tarsals in its irregular shape but had no known homologue until Radinsky (1963b) traced it back through the fossil lineage of tapirs to find that it was actually a first metatarsal (mt1). In *Deperetella*, an Eocene tapiroid, this metatarsal had an elongate shape, though distinctly reduced and still in contact with mt2. Since the Eocene, mt1 has undergone a change in position and shape, roughly reaching its current condition by the Oligocene (Radinsky 1963b).

Figure 3. Left second metatarsal and first tarsal in lateral view (ETMNH 8264) with arrow pointing to first metatarsal articulation with slight wear facet.

Previous workers have mentioned distinctions between the articular position of t3 regarding living species. Earle (1893) states that in *T. indicus*, t3 touches all 3 weight bearing metatarsals, while extant New World tapirs lack an articulation between mt4 and t3 (see figure 4). Radinsky's (1965) figure of *T. pinchaque* conforms with this view. It is not clear how many individuals Earle (1893) observed, but Simpson (1945) disagreed with this statement, at least regarding "several individuals" of *T. bairdii*, in which he says there is an articulation between t4 and mt3, which makes the previously mentioned configuration impossible. Simpson (1945) says that *T. excelsus* and *T. bairdii* have a well developed facet between mt4 and t3, but in *T.*

terrestris, t4 articulates with mt3 in several specimens. Concerning *T. indicus,* Simpson (1945) agrees with Earle (1893).

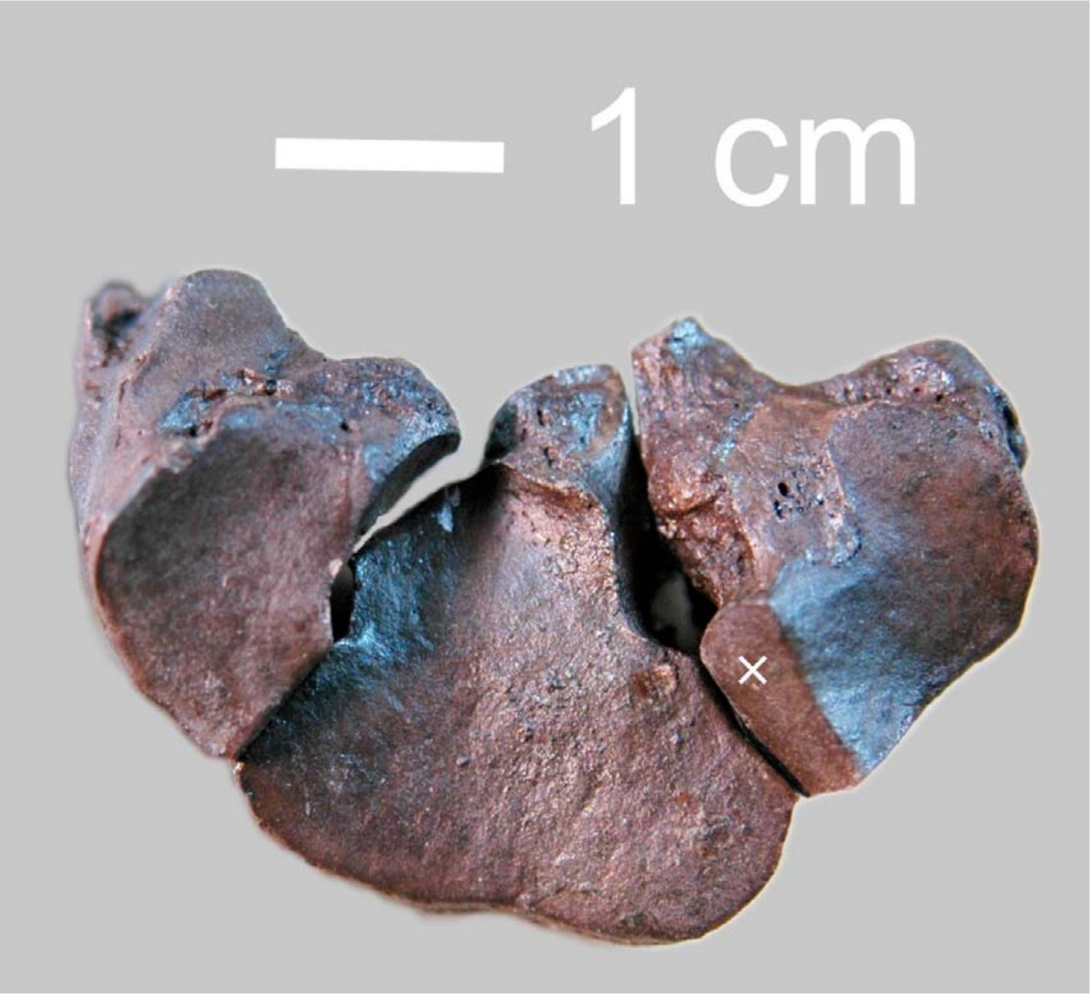


Figure 4. Proximal view of mt2-4 (from left to right) with third tarsal facet marked (X) on mt4 (ETMNH 8264).

Tapirs at GFS have an articulation between t3 and mt4 (Figure 4), as does a *T. webbi* (Hulbert 2005: Figure 12). Prothero (2005) states that rhinos have an articulation between t3 and mt2, but not mt4. If such a feature of the pes proves common for all members of Rhinocerotidae, it may be considered the primitive character state and therefore useful for reconstructing tapir evolution. Some species are known to exhibit a highly variable manus (Harrison and Manning 1983), and an equally variable pes may be expected, therefore care must be taken when inferring phylogenetic relationships from foot bones.

All of the facets so far mentioned are smooth and fit well against each other. However, the articulation between t1 and mt1 is decisively different because commonly, instead of a gliding surface there is a jagged suture holding these 2 bones together (Figure 5). In Radinsky's (1963b) dissection of a *T. indicus* foot, he makes special mention of ligaments binding t1 and mt1. The joint between these small bones is strong and apparently immobile, but the medial and lateral sides allow for a great deal of motion. Medially, t1 fits loosely in a concavity formed by mt2, t2 and the navicular. Mt1 laterally touches the other metatarsals, but this joint can vary widely (Figure 6).

Figure 5. Anterior view (ETMNH 3519) of first metatarsal and tarsal in anatomical articulation (left), and the same bones reflected to show a lack of smooth facet between (right).

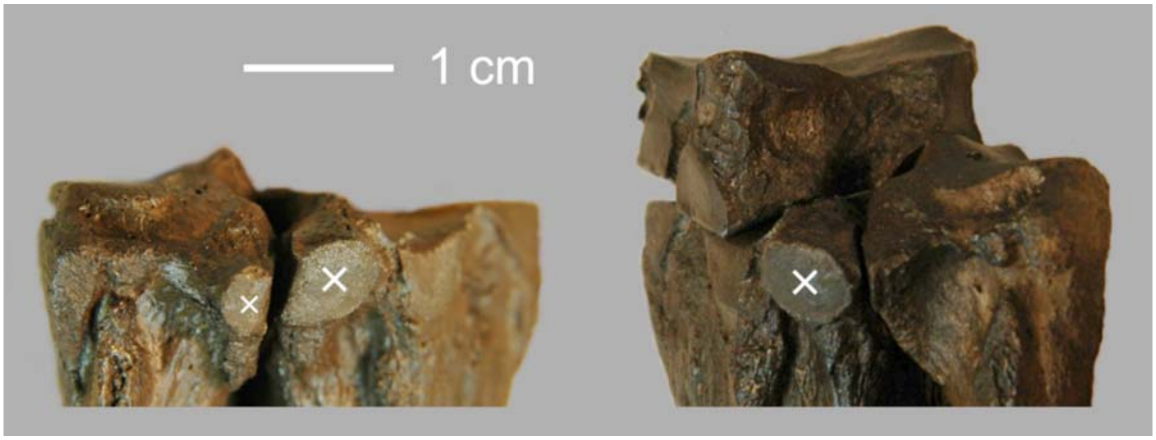


Figure 6. Two states of articular facets. Posterior view of left (condition 1, ETMNH 8264) and right (condition 0, ETMNH 3519) metatarsal 3 and 4. Right pes has tarsal 3 proximal to metatarsal 3.

Most often, tapirs have a single articular facet on the posterior projection of the proximal end of mt3. This condition is generally present on tapirs in the western hemisphere, including most *T. polkensis* from GFS. *Tapirus indicus* was noted by Radinsky (1963b) to consistently have mt1 articulate with mt3, but in addition abut laterally against a similar posterior projection on mt4. Hulbert (2005) used this feature in conjunction with many others to distinguish a new species of tapir, *T. webbi*, from others in the New World with comparable postcranial material.

Soft Tissue

To evaluate the functional significance of tapir foot osteology, Radinsky (1963b) dissected the tarsals and ligaments of *T. indicus* and determined that mt1 is firmly attached to the plantar side of the metatarsals and serves as the origination of digital flexors (Figure 7). Proposing a double function provides 2 useful hypotheses for which dimensions should be correlated with the mt4 facet. If mt1s main purpose is to brace the tarsus, the robustness of the proximal end of the mt3 should coincide with the extra articulation. Alternatively, if the action of the muscles attaching distally to the phalanges is more important, there would be a correlation with the size of the distal articular facet.

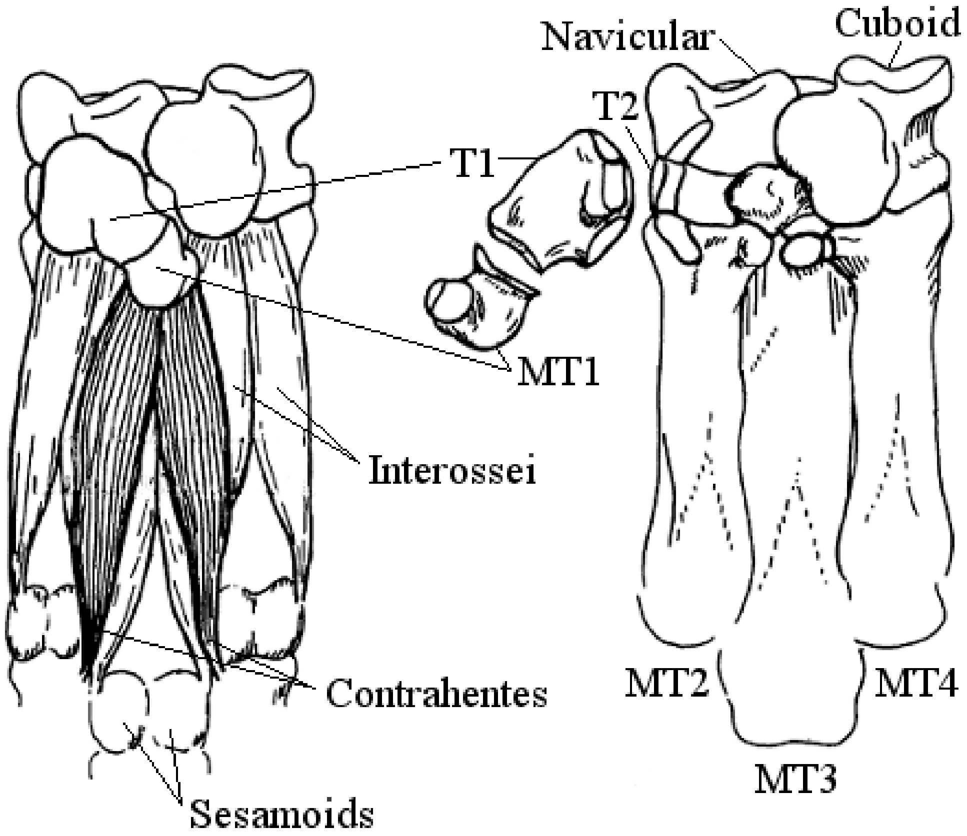


Figure 7. Plantar view of right *Tapirus indicus* hind foot with musculature (left) and with first tarsal and first metatarsal reflected medially (modified from Radinsky 1963b).

The contrahentes of tapirs originates from the mt3-mt1 joint and inserts on the proximal phalanges of the side toes (Radinsky 1963b). Adduction and flexion of toes is the inferred action, but no anatomical studies explicitly state this. The adductor pollicis in humans may be a derived remnant of the contrahentes (Yamamoto et al. 1988), which is present in hind and forefeet in most mammals. Horses have lost these muscles, and basically all others that do not help either flex or extend joints (Sisson 1910; although see Soffler and Hermanson 2006 and Meyers and Hermanson 2007). Horses have gained long, light limbs at the expense of toe loss, rhinoceroses retain lateral toes to support their graviportal body plan, but tapirs remain able to use important flexors and adductors. Because of the unstable substrate tapirs usually run through, this ability to push off with digits besides the middle third toe is likely adaptive towards their preferred habitat.

Comparison of tapirs with other ungulates illustrates the importance of side digit adduction. In artiodactyls the major weight bearing cannon bone consists of mt3 and mt4, so contrahentes insert on the toes of the second and fifth digit (Campbell 1945). Even though peccaries have lost digit 5, the lateral muscle of this group fuses with the fibular flexor brevis profundus to insert on mt4 (Campbell 1945). In tapirs, Campbell (1945) describes the origin of both these muscles as the tarsal ligaments, less specific than Radinsky's (1963b) description, but still compatible. Interestingly, the contrahentes origin for hippopotamus (and pig by association) is listed as the tarsal ligaments and sesamoid by Campbell (1945). This plantar sesamoid is present in all artiodactyls (Flower 1885), which may serve a comparable function as mt1 in tapirs. Possibly, this sesamoid is a similar vestige of the lost first digit.

The Horse as a Comparison

Most detailed anatomical descriptions of perissodactyls use horses, so investigating the soft tissue associated with a 3-toed perissodactyl has inherent limitations. Also, many publications of fossils portray only the anterior view (e.g. Simpson 1945; Radinsky 1965) although there are exceptions (Radinsky 1963b; Hulbert 2005; Prothero 2005), which is largely useless for this study and must be supplemented with multiple views and descriptions of veterinary horse anatomy. Despite shortcomings, many similarities exist. Tarsal 1 is remarkably similar in *Equus*, although there is no indication of mt1. One major difference is the fusion between t1 and t2, also known as the cuneiform parvum (Sisson 1910). This unique tarsal is obviously 2 bones fused together, though there is no suture delineating them. Ossification centers can be observed for each of the tarsals, including 2 for the cuneiform parvum but not for a vestigial first metatarsal (Soana et al. 1998).

The tibialis anterior is an important flexor of the ankle and originates on the lateral aspect of the tibia (Bressou 1961). In most animals, including humans, this muscle's medial attachment on t1 and mt1 also allows inversion of the foot, but this is not possible in horses because they lack mt1 and the ability to invert or evert the foot. As for origins, the normal digital flexors and adductors are reduced or absent in horses (Sisson 1910). Those that remain are the interossei and lumbricales, which are considered so similar to those of the forelimb that they are deprived of specific mention by Sisson (1910). Most important is the highly modified median interossei, or suspensory ligament, which contains little actual muscle tissue (Payne 2005). Positioned posteriorly on the ankle joint, t1 lies at a critical junction between muscular flexion and the tendinous suspensory system. This area also marks the transition between the distal foot, identical regardless of pelvic or pectoral limb, and the proximal leg where divisions of adaptations require differing morphologies.

The Forelimb as an Analog

Tarsal 1 is highly analogous in morphology to the pisiform of the forelimb. Horse pisiforms, or accessory carpal bones, make up a portion of the anterior annular ligaments (McFadyean 1902) under which tendons are redirected. In horses and tapirs the posterior process of the pisiform is larger than t1, but both attach similarly to the joint. Tarsal 1 remains closer to the metatarsals as it extends laterally, while the pisiform sticks out more posteriorly. Alternatively, mt1 is so close to the ankle that they touch. If mt1 and t1 are considered a single unit, as inferred by the strong connection and occasional fusion, together they make an arch situated on the back of the metatarsals. There is no indication that an annular ligament similar to that in horses is formed by these bones, but the proximal projection is a mechanically advantageous place for muscle attachment.

The anterior annular ligament made up of distal portions of various ligaments and carpals creates a carpal tunnel through which tendons and the median nerve travels in humans (Davis 1913). In horses, the first carpal (c1) is imbedded in the internal lateral ligament, which often fuses posteriorly to this annular ligament (Sisson 1910). In location, c1 is more similar to mt1 than the pisiform because it articulates with the distal row of carpals and is on the medial side. In perissodactyls, c1 is small and does not normally articulate with anything but c2. Sisson (1910) noted that it is absent in about half of the individuals he dissected, sometimes present on only one side, occasionally rests against the second metacarpal (mc2), and rarely forms an articular facet. Carpal 1 is therefore also more similar to mt1 in its variation.

The tibialis anterior is an important flexor on the medial leg of horses (Payne 2005). It arises from the lateral portion of the proximal tibia and is located mostly on the anterio-lateral side of the leg. It divides into 2 tendons, one of which inserts on the metatarsal tuberosity (anterio-proximally) and another on t1 and t2 (Sisson 1910). A similar configuration occurs in tapirs (Bressou 1961) but has been described in less detail. Campbell's (1945) foot dissections have a figure of tibialis anterior on the medial side, probably inserting very proximally on the metatarsus but does not mention it. In a description of the Asian tapir, Murie (1871) writes that the tibialis anterior inserts on mt2s inner side with no mention of the tarsals. This type of disagreement among anatomical descriptions, especially in the parts that authors leave out is typical. The flexor ulnaris lateralis of the horse forelimb originates on the lateral epicondyle of the humerus, inserts on the pisiform and fourth metacarpal (by splitting into 2 tendons), and flexes the carpal joint (Sisson 1910). This indicates an analogous function between the flexor ulnaris lateralis and tibialis anterior.

Wrist and ankle structures may be analogous for various reasons. Causative factors could be genetic (Davis 1964; Newman and Müller 2005), developmental (Oster et al. 1988; Hinchliffe 2002), or external. The adaptive limb may not be immediately obvious. Differences between hind and fore limbs may reflect a division of labor between the pelvic and thoracic girdle (Kharlamova et al. 2007). However, variation of skeletal articulations may be more noticeable in the pes because the facets on those bones are almost always more clearly delineated. Tapir carpals also do not articulate on both sides (i.e. variation may be present in life, but the facets present on bone are the only indicators of it in fossils). Because mt1 and t1 make a strongly bonded single unit, differences in their articulation will be seen through the distal (lateral) facet, which in tapirs can be considered the joint between mt1 and mt3(or mt4).

CHAPTER 4

PERISSODACTYL PHYLOGENY

Perissodactyls are defined as ungulates that have an axis of symmetry through the third digit of their feet (Owen 1848). This originally included hyraxes because of their mesaxonic feet, which was previously supported by various studies (Fischer 1989; Prothero and Schoch 2002). However, more recent molecular (Beck et al. 2006) and morphological (Sieffert 2007; Asher and Lehmann 2008) evidence is now showing that hyraxes have a shared ancestry with proboscideans. Although hyrax placement is definitely outside the well agreed upon Perissodactyla (Mesaxonia sensu Schoch 1989), this association illustrates the need for a more thorough investigation of foot anatomy. Some of the best synapomorphies for Perissodacytla involve the foot, including the complete loss of the pollex (Matthew 1917), a saddle shaped facet on the talus for articulation with the navicular (Radinsky 1966b), and a lateral reorientation of the medial tarsal (Radinsky 1963b; Holbrook 2001). Considering these synapomorphies, Owen (1848) was correct to define and name the perissodactyls after their odd toes.

Taxonomic Divisions of Perissodactyla

The most common usage of Perissodactyla (McKenna and Bell 1997; MacFadden 1992), which is adopted here, refers to horses, tapirs, rhinoceroses, calicotheres, brontotheres, and all of their most recent common ancestors. Perissodactyls in this sense are usually viewed as monophyletic, although multiple characters must be used to succinctly define the group

(Holbrook 2001). Two suborders, the Hippomorpha and the Ceratomorpha, can be easily defined within the perissodactyls (Wood 1937), but the affinities of the extinct calicotheres and brontotheres have never been clear (Simpson 1945; Hooker 1989); likely reflecting the great diversity achieved by the order and their subsequent modern paucity. Despite this lack of resolution, many perissodactyl families are represented in the North American fossil record, so they have been frequently used for ecological and biostratigraphic studies (Holbrook 2001).

The 2 commonly used suborders within the Perissodactyla often include different names of taxa. McKenna and Bell (1997) for example, include the infraorders Selenida (Brontotheres and Calicotheres) and Tapiromorpha (superfamilies Rhinocerotoidea and Tapiroidea) in the suborder Ceratomorpha. Wood's (1937) original use of Ceratomorpha (as opposed to Tapiromorpha) was explicitly chosen to prevent confusion and reflect a close association between tapiroids and rhinocerotoids. Holbrook (1999) further defines Ceratomorpha as an infraorder-level group by its inclusion of tapirs, rhinoceroses, and their closest relatives.

Within the Ceratomorpha, Tapiridae and Rhinocerotidae are both extant families and generally considered monophyletic (Holbrook 2001), but relationships between their respective superfamilies, Tapiroidea and Rhinocerotoidea, are much more complicated. If together they make a monophyletic group, and all genera of ceratomorphs fall into one or another of these superfamilies, then one would have to be paraphyletic while the other, ideally, monophyletic. Therefore it is not surprising that recent cladistic analyses (e.g. Holbrook 1999, 2001) support the common perception that rhinocerotoids and tapiroids are closely related but distinct groups.

Placement of Hyrachyus *Within Ceratomorpha*

Despite the efforts to sort out the ceratomorphs, much disagreement remains. The contested placement of Hyrachyidae exemplifies this quagmire because it is considered a tapiroid (Radinsky 1966b, 1967), the sister group to rhinocerotoids (Holbrook 1999), or at least the most primitive rhino (Prothero 1989). Colbert and Schoch (1998) acknowledge the confusion discussing the genus in their Tapiroidea chapter but place *Hyrachyus* within Rhinocerotoidea. The upper molars of *Hyrachyus* do resemble those of the rhinocerotoids; however, the lowers look like tapirs (Cope 1873; Wood 1934). Size was used by Wood (1934) to differentiate 4 genera within Hyrachyidae, but these were later synonymized under the genus *Hyrachyus* by Radinsky (1967).

The discussion of the placement of Hyrachyidae is largely the product of one's philosophy of systematics (Hopson 1989). Wood's (1934) revision of Hyrachyidae recognized their similarities with tapirs but grouped them with rhinos, despite doubting that their ancestors were true rhinoceroses. Radinsky (1966b, 1967) placed *Hyrachyus* in the subfamily Helaletidae (Tapiroidea) based on its primitive dental characters, reflecting a paraphyletic concept of tapiroids, and an attempt to more concisely define the Rhinocerotoidea, which he considered polyphyletic. However, most workers at least agreed that *Hyrachyus* marks the differentiation of Rhinocerotoidea from the remaining ceratomorphs, but a long series of disagreements (Radinsky 1966b; Savage et al. 1966; Radinsky 1967; Schoch 1982; Radinsky 1983; Prothero et al. 1986) about the definitions of primitive characters, phylogenetic concepts, apomorphies, and even how these disagreements should be published followed Radinsky's (1966b) placement of *Hyrachyus* in Tapiroidea.

CHAPTER 5

METHODS AND MATERIALS

Fossil Material

All fossils used in this study were found at the GFS and are curated in the collections at ETMNH. Preparation includes consolidation in Butvar-98 and reconstruction with Butvar-76. Bones are partially permineralized. Measurements were taken only if the entire area was competent bone, although some were pieced together in the lab. Articular surfaces are all clearly visible and discernable from non-articular bone. Juvenile individuals with unfused distal epiphyses were not used (proximal epiphyses fuse first). Weathered metatarsals with undefined edges of articular surfaces were not used. Complete skeletons, isolated bones, and fragments were included as long as the articular condition of mt1 could be determined. Sex cannot be determined osteologically (Simpson 1945) and was not considered in the analysis.

Extant Material

Modern skeletal material was examined from the American Museum of Natural History in New York (AMNH) and the United States National Museum in Washington, D.C. (USNM). Most tapirs were taken from the wild, but some had unclear provincial information, including zoos in which they died. Sex was not identified in many individuals. As with the fossils, young individuals were only excluded if they had unfused epiphyses. Most individuals were complete, but a small number were partially inaccessible (Table 2).

Table 2. Number of third metatarsals compared from each collection with points of interest

Collection	*Tapirus* Species	Feet	Left	Right	Points of Interest
AMNH	*bairdii*	0	0	0	NA
	indicus	4	2	2	all mt4
	pinchaque	2	1	1	all mt3
	terrestris	17	9	8	all mt3
USNM	*bairdii*	4	3	1	all mt3
	indicus	9	4	5	USNM 155410 has no distal mt1 articular facet and mt1 is fused with t1 on right pes
	pinchaque	4	2	2	all mt3
	terrestris	4	2	2	USNM 270353 has both feet with mt1 articulation only on mt4
ETMNH	*polkensis*	31	11	20	ETMNH 8264 has mt4 articulation only on the left

Survey Data

At GFS, skeletal elements are surveyed in 3 dimensions using a total station before being completely exhumed from the matrix (Nave et al. 2002; Wallace et al. 2002; Wallace 2004). Digging is done by hand in 1 meter squares, so even if small bones are overlooked, along with the matrix they are water screened and found later. Screening the material removes clay so that only bones, wood, and rock remain in a concentrated collection of sediment with both location and time data. The date serves as an approximation for depth and the meter grid coincides with the Tennessee State Plane Coordinate System (Burdick et al. 2002).

Linear Morphometrics

Measurements were taken with Titan digital calipers to the nearest hundredth of a millimeter on multiple bones of the tarsus. The state of the articular facet can be determined by viewing mt1, mt3, or mt4 but only mt3s were used in the final analysis. Originally 20 exploratory measurements (Table 3) were taken to search for correlations between character states and articular facets, including multiple measurements of anterior and posterior mt4 and mt2 articulations. After some initial statistics showed that some of the proximal facets were too variable to show any trends, a simplified set of measurements was statistically analyzed (Table 4; Figure 8).

Comparison Statistics

Data were maintained in Microsoft Excel spreadsheets and some basic statistics were performed with this program. Coefficient of Variation (standard deviation divided by the mean) was multiplied by 100. In order to determine correlation with the articular character states, measurements were analyzed with a 2 tailed Student's t-test, assuming unequal variance because the sample number is so different between the groups, and because the direction of difference was not important. Minimum breadth and depth of the metatarsals were excluded from some statistical analyses because they vary greatly and those measurements are difficult to replicate.

Table 3. Exploratory measurements initially used

Measurement	Description	Abbreviation
maximal length	total length including distal sagittal ridge and proximo-lateral ridge	maxL
medial length	length from median keel to proximal articular facet	medL
minimal breadth of diaphysis	shortest breadth of metatarsal shaft in medio-lateral orientation	mB
minimum depth of diaphysis	shortest depth of metatarsal shaft in anterio-posterior orientation	mD
proximal articular width	proximal facet for t3 in medio-lateral orientation	paw
proximal articular depth	proximal facet for t3 in anterio-posterior orientation	pad
ventro-dorsal mt1 articulation	mt1 articular facet in ventro-dorsal orientation	vmt1
medio-lateral mt1 articulation	mt1 articular facet in medio-lateral orientation	lmt1
mt2 anterior height	height of anterior facet for mt2	mt2ah
mt2 anterior width	width of anterior facet for mt2	mt2aw
mt2 posterior height	height of posterior facet for mt2	mt2ph
mt2 posterior width	width of posterior facet for mt2	mt2pw
mt4 anterior height	height of anterior facet for mt4	mt4ah
mt4 anterior width	width of anterior facet for mt4	mt4aw
mt4 posterior height	height of posterior facet for mt4	mt4ph
mt4 posterior width	width of posterior facet for mt4	mt4pw
distal flange	width of distal flange for muscle attachment	df
distal constriction	width of shaft slightly distal to flange in shallow depressions	dc
distal facet width	width of distal articular facet in medio-lateral orientation	dfw
distal medial facet	depth of distal articular facet sagittal ridge in anterio-posterior orientation	dmf

Table 4. Measurements used for Student's t test

	Measurement	**Description**	**Abbreviation**
1	maximal length	total length including distal sagittal ridge and proximo-lateral ridge	maxL
2	medial length	length from median keel to proximal articular facet	medL
3	minimal breadth	shortest breadth of metatarsal shaft in medio-lateral orientation	mB
4	minimum depth of diaphysis	shortest depth of metatarsal shaft in anterio-posterior orientation	mD
5	proximal articular width	proximal facet for t3 in medio-lateral orientation	paw
6	proximal articular depth	proximal facet for t3 in anterio-posterior orientation	pad
7	proximal depth with posterior process	front of proximal facet to the most posterior point	padp
8	distal flange	width between tubercles above proximal joint for attachment of lateral ligaments of metatarsophalangeal joint	df
9	distal constriction	width between fossa between tubercle and distal articular facet	dc
10	distal facet width	width of articular facet in medio-lateral orientation	dfw
11	distal medial facet	depth of distal facet at sagittal ridge of metatarsophalangeal joint	dmf
12	distal facet depth	depth of distal facet in anterio-posterior orientation	dfd
13	medial sesamoid	depth of distal facet medial to sagittal ridge of metatarsophalangeal joint	ms
14	lateral sesamoid	depth of distal facet lateral to sagittal ridge of metatarsophalangeal joint	ls

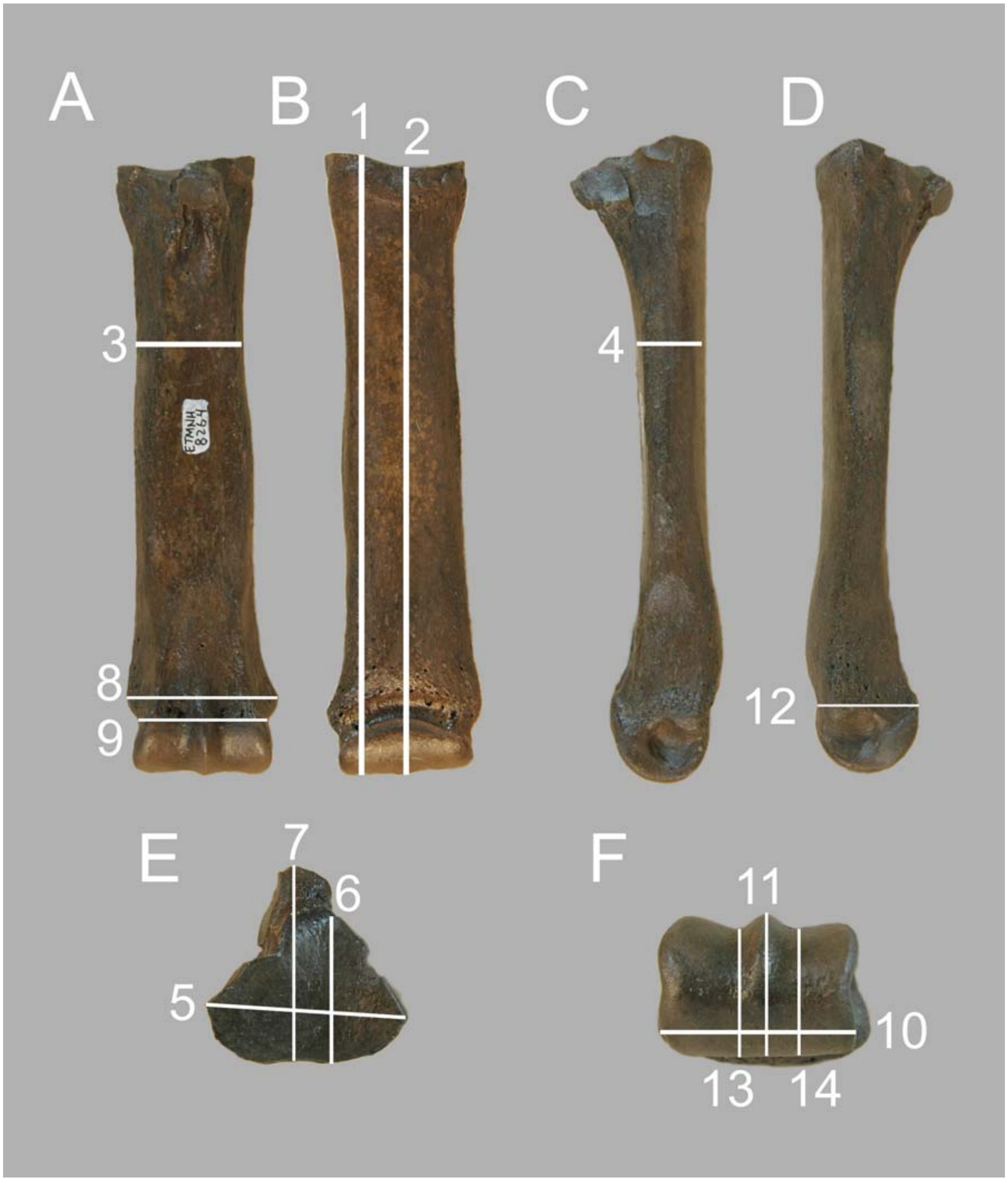


Figure 8. Explanation of 14 measurements used for Student's t test. Posterior A, anterior B, lateral C, medial D, proximal E, and distal views F of a right third metatarsal; see Table 4 for definitions.

CHAPTER 6

RESULTS

Metatarsal Variation in GFS Tapirs

Although the unique metatarsal arrangement has been considered by some workers to be phylogenetically significant at the species level (Radinsky 1963b; Hulbert 2005; Hulbert and Wallace 2005), its variable representation at GFS suggests otherwise. Coefficients of variation (CV) for cranial and dental measurements fall mostly within a normal species range (Hulbert et al. 2009), including measurements of mt3 (Table 5). High CV values for minimum breadth and depth are likely signatures of difficulties involved in measuring the same area of the diaphysis. The total GFS sample had higher CV than both groups in 5 measurements. First is the proximal articular facet with posterior process (Table 5), which is structurally related to articulation with mt1. Four more measurements with higher CV values in the total group, (dmf, dfd, ms, and ls in Table 5) are located distally on mt3. Mean linear measurements of mt3s with condition 0 are all greatest (except minimum breadth). Differences in standard deviation typify what was expected; less numerous (condition 1) mt3s have lower standard deviations, while the regular types drive up the standard deviation of the combined sample.

Exploratory statistical analyses suggested a significant difference in distal measurements (Figures 9 and 10). Student's t-test of GFS individuals yielded a correlation between condition 1 and measurements of the distal metatarsal (Tables 6 and 7). Proximal articular facet depth, where mt1 articulates with mt3 (padp), also had a low p-value. Depth and breadth values are considered problematic because of their inconsistency while measuring. The same test, using all available species gave low p-values for many measurements, probably reflecting their specific differences.

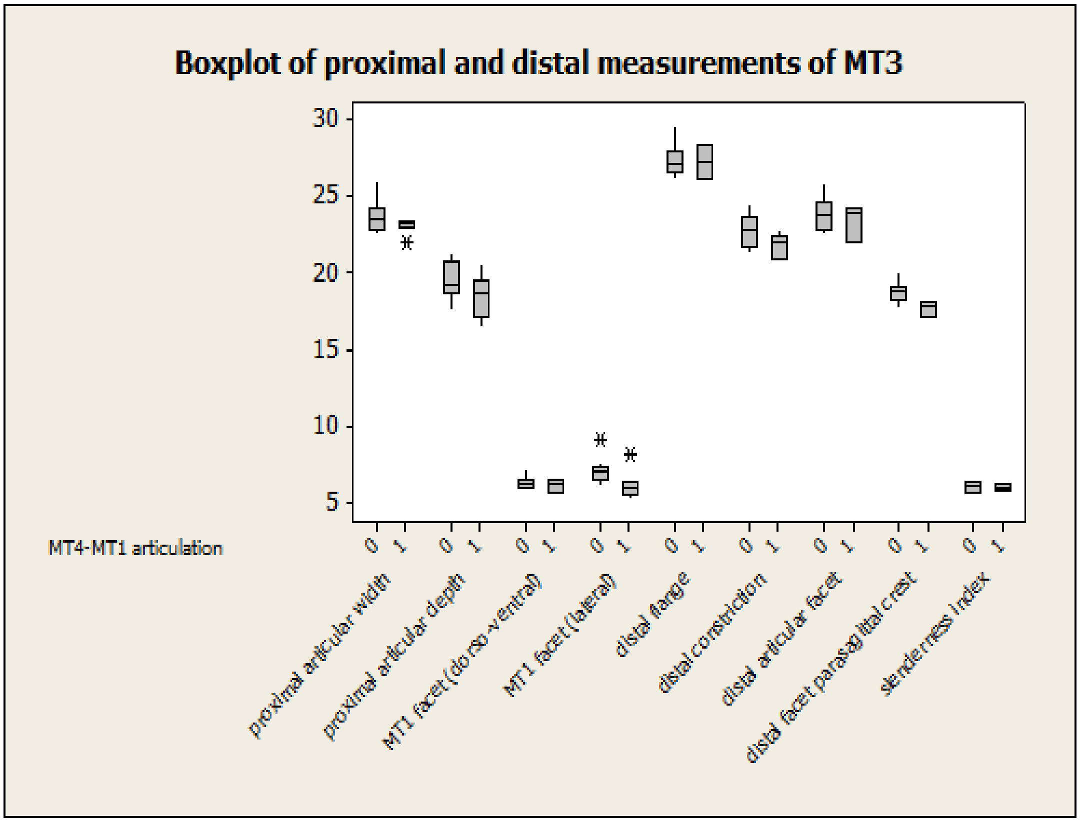
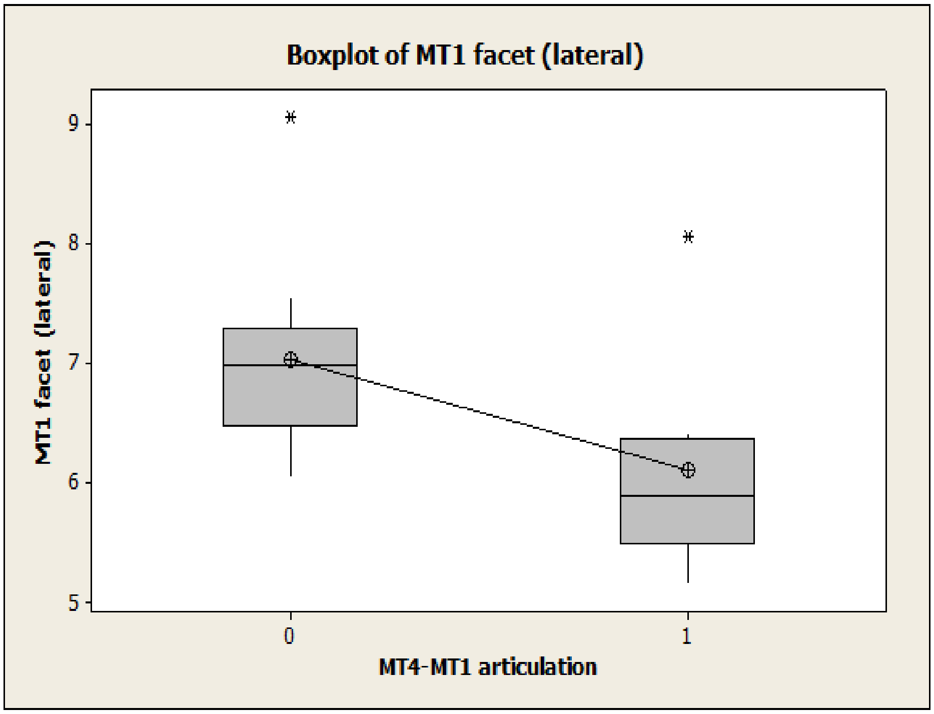


Figure 9. Comparison of selected measurements indicating distal correlation. Condition 0 is the presence of a facet between mt1 and mt3, whereas 1 is presence of an extra articulation between mt1 and mt4. Distal facet parasagittal crest (distal medial facet, dmf) shows the clearest distinction besides the lateral mt1 facet (lmt1).



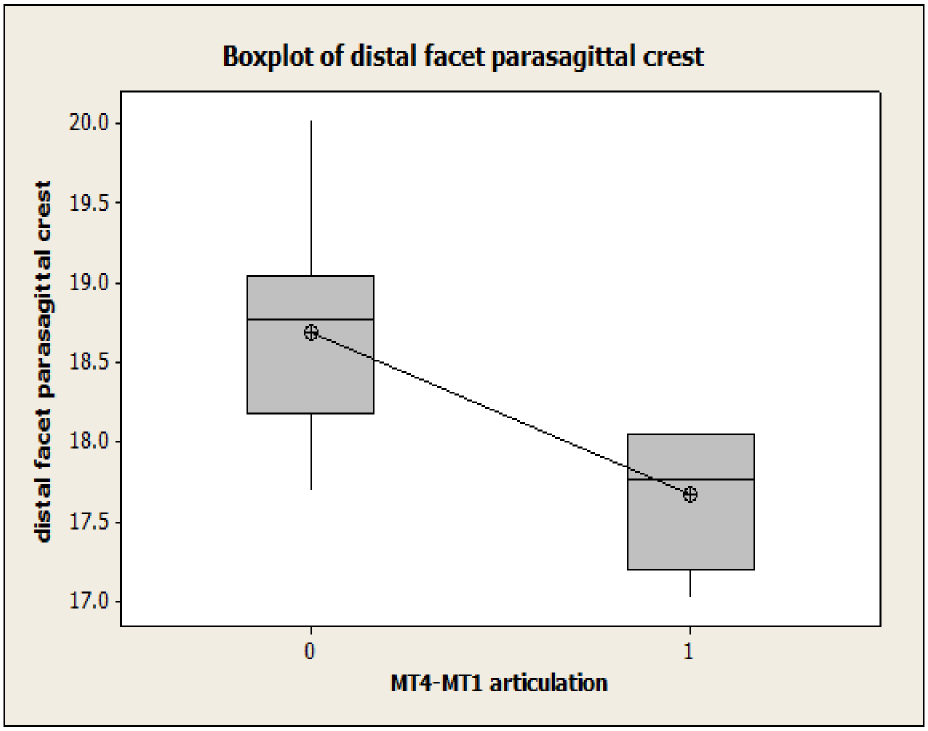


Figure 10. Detailed graph of statistically significant boxplots p-value = 0.032 (medio-lateral measurement of first metatarsal facet, above) and 0.001 (distal medial facet, below).

Table 5. Mean and CV for GFS *Tapirus polkensis* mt3 measurements in millimeters

	Mt3 facet		**Mt3 and mt4 facet**		**Total**	
	mean	CV	mean	CV	mean	CV
maxL	111.33	2.61	109.63	1.82	111.03	2.54
medL	107.46	2.44	105.67	1.56	107.10	2.37
mB	17.84	8.71	18.73	3.49	18.00	8.12
mD	12.60	11.86	11.30	6.84	12.35	11.90
paw	23.72	4.05	23.31	1.55	23.64	3.75
pad	19.00	4.73	18.01	7.28	18.81	5.53
padp	24.66	3.45	23.14	3.62	24.36	4.27
df	27.48	3.47	27.19	3.76	27.43	3.49
dc	22.63	3.25	21.71	4.07	22.45	3.74
dfw	24.24	3.21	23.43	4.16	24.07	3.60
dmf	18.69	3.01	17.97	1.94	18.55	3.22
dfd	18.91	3.43	18.15	2.58	18.76	3.65
ms	17.08	3.50	16.13	2.98	16.89	4.08
ls	16.39	3.10	15.52	3.76	16.22	3.85

Table 6. P values for t-test using only GFS third metatarsals. Asterisk denotes significant P values (α =0.05)

Measurement			GFS	All species	Area
1	maxL	maximal length	0.172465	0.051668	**length**
2	medL	medial length	0.067874	0.046209*	
3	mB	minimal breadth of diaphysis	0.048883	0.048883*	**shaft**
4	mD	minimum depth of diaphysis	0.009337*	0.009337*	
5	paw	proximal articular width	0.148529	0.070708	**proximal**
6	pad	proximal depth with posterior process	0.003661*	0.189865	
7	padp	proximal articular depth	0.142288	0.655079	
8	df	distal flange	0.508632	0.027728*	**distal width**
9	dc	distal constriction	0.042964*	0.022291*	
10	dfw	distal facet width	0.083598	0.037762*	
11	dmf	distal medial facet	0.003136*	0.037633*	**distal depth**
12	dfd	distal facet depth	0.010279*	0.032835*	
13	ms	medial sesamoid	0.002595*	0.045452*	
14	ls	lateral sesamoid	0.013533*	0.070481	

Table 7. P values for all tapirs, grouped by articulation without regard to species. Asterisk denotes significant P values (≤0.05)

Two tailed independent t test	
Measurement	**P-value**
maximal length	0.051668
medial length	0.046209*
minimal breadth of diaphysis	0.048883*
minimum depth of diaphysis	0.009337*
proximal articular width	0.070708
proximal depth with posterior process	0.189865
proximal articular depth	0.655079
distal flange	0.027728*
distal constriction	0.022291*
distal facet width	0.037762*
distal medial facet	0.037633*
distal facet depth	0.032835*
medial sesamoid	0.045452*
lateral sesamoid	0.070481

Correlation with Sides

Using only adult right third metatarsals, a Minimum Number of Individuals (MNI) of 20 can be calculated. There are of course many more individual tapirs at GFS (Hulbert et al. 2009), but this illustrates how common the feet are. Sides can be easily identified by the raised lateral portion of the proximal head. The left side is underrepresented, accounting for only 12 of the 35 mt3s. Only 8 individuals have both feet represented in this study, and 2 of these have condition 1 on both feet. Another individual, which has a nearly complete postcranial skeleton, ETMNH 8264, has a right mt1 with condition 0, but the opposite on the left side.

The GFS sample of tapirs is dominated by a singular articulation between the mt1 and mt3 (condition 0). Of 6 bones with condition 1, four are from 2 individuals with symmetrical sides, and one is the individual (ETMNH 8264) with condition 1 only on the left. The validity of this individual was questioned at first because 3 legs were originally given the same catalog number (ETMNH 3719 in Hulbert et al. 2009) because of their close proximity. However, there is no question about the shared character states of this one individual, because the extra metatarsal (ETMNH 3719) is from a right foot and has the same articular condition as the more complete right leg. The size difference between the compete individual (ETMNH 8264) and the foot (ETMNH 3719) also supports this conclusion. This is the only example of one individual with both character states. ETMNH 3519 has 2 feet with the extra articulation, but its right mt4 is highly weathered. It has a definite posterior protrusion equal to that found on mt3, but its character state, defined here as the extra articulation, is not certain.

Condition 1 is seen completely in 2 individuals, while the remaining 2 (one foot of ETMNH 8264 and one unarticulated mt3) in this category are from the left side. Eight mt3s with condition 0 are from left feet. There is an extremely small sample size for condition 1, but they tend to occur on the left side (4 of 6). Most (18 of 20) right sides exhibit condition 0 (Table 8), but most metatarsals recovered happen to be from the right side, which is certainly a simple preservation bias.

Table 8. Distribution of articulation states among left and right *T. polkensis* mt3

Condition 0		**Condition 1**		**Total**	
left	right	left	right		
7	18	4	2	31	
percent left 28%	percent right 72%	percent left 66.667%	percent right 33.333%	percent left 35.48%	percent right 64.52%

Location

From the early stages of excavation, recording location data on fossils has been a prime concern (Nave et al. 2002; Burdick et al. 2002; Wallace et al. 2002). The high degree of precision with which many fossils have been surveyed is beyond the scope of this project. However, it is interesting to point out that the few unique mt3s with condition 1 appear to be concentrated in Test Pit 2-2004 (informally known as the Rhino Pit), which was started in 2004 at grid position 356 North and 123 East. Coincidently, one of the best preserved tapirs (ETMNH 3519) was later found within the same square in which the pit was started. ETMNH 3519 has 2 complete hind feet with condition 1. The other tapir with condition 1, ETMNH 3573, was found about 3 meters away, but a slightly different level. Yet another tapir, ETMNH 8264 (originally designated ETMNH 3719, see above), has one foot of each state, and was also found in the Rhino Pit. This excavation pit is the largest (and best surveyed) of GFS and also has tapirs with mt1-mt3 articulations only (Figure 11), so any conclusions at this time would be speculative. Future expansion of the digging area will test these curiosities and whatever tentative conclusions are drawn from them.

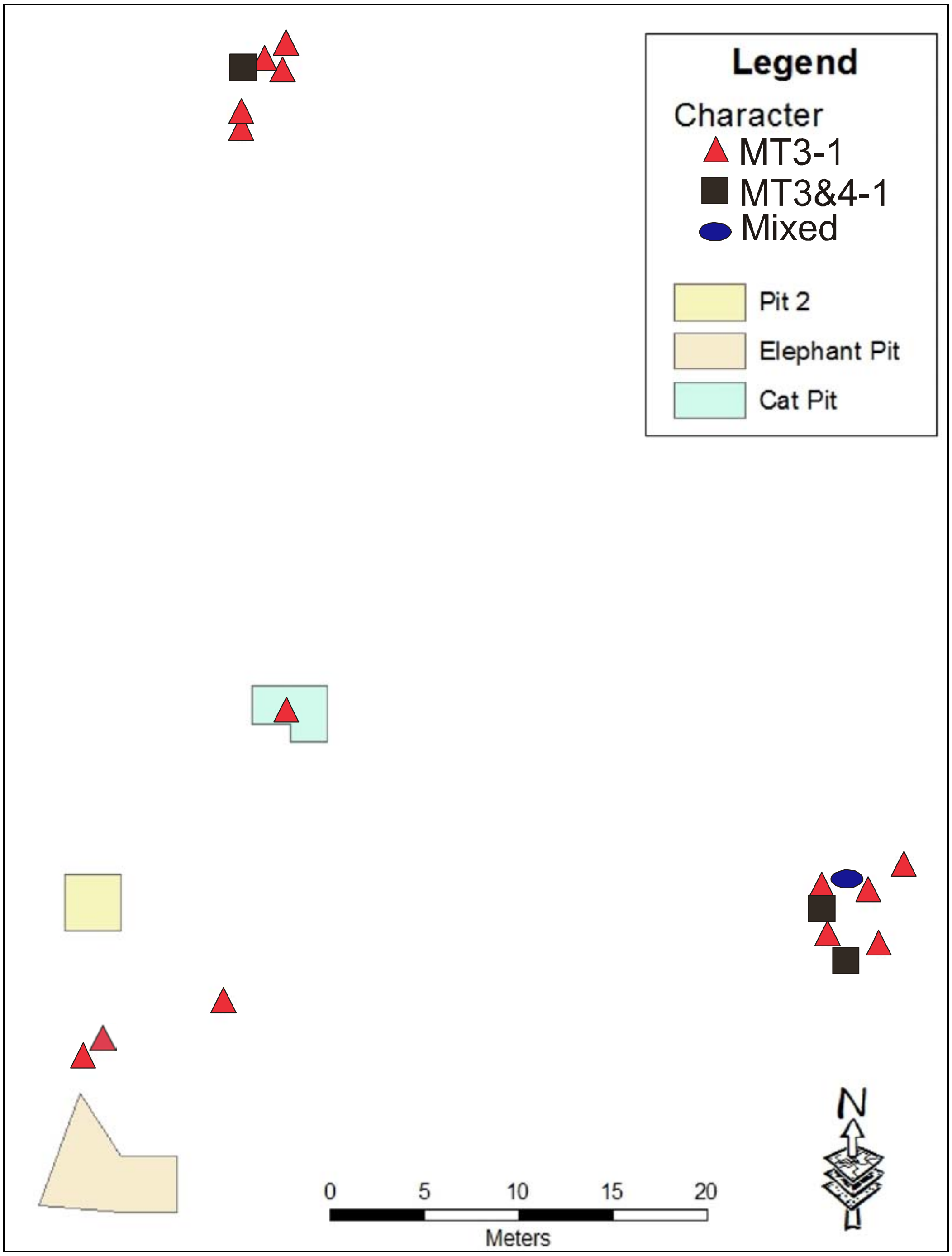


Figure 11. Map of 18 individual tapirs with metatarsals having good survey data. Southeast cluster is Test Pit 2-2004 (Rhino Pit) with one individual having both articular states and 2 individuals with condition 1 on both feet.

Variation in Different Tapir Species

Condition 1 is present in only a few species. Extant *T. indicus* usually, but not consistently, exhibits condition 1, as well as all known individuals (n≈43) of the extinct North American taxon, *T. webbi* (Hulbert 2005). Simpson (1945) hints at the mt4 articulation in *T. excelsus* (AMNH 39406, probable junior synonym for *T. veroensis* [Ray and Sanders 1984]), but I have not had the opportunity to see it. Likewise, some *T. indicus* metatarsals showed only the mt3 articulation. The presence of the extra articulation holds up as a decent character for species identification but should always be verified with a large sample.

One individual *T. terrestris* (USNM 270353), of the 11 examined, has an alternate condition that has not been previously described in this paper or the literature. Both mt1s are unfused and articulated laterally only with mt4 (Figure 12). The other New World species have condition 0, as described by Radinsky (1963b), although they are represented by smaller samples within collections. The most variable extant species is *T. indicus*, which has 2 individuals that do not have the mt4 facet. One of these individuals (USNM 267510) has the same condition 0, and another (USNM 155410) essentially lacks any of the characters states, exhibiting no articulation between mt1 and the other metatarsals (Figure 13). This latter individual has uncertain locality information and may have lived a long time in captivity. Trends of this character state as previously stated are mostly true, but there is enough variation within the extant specimens to rule out its use as a phylogenetic character.

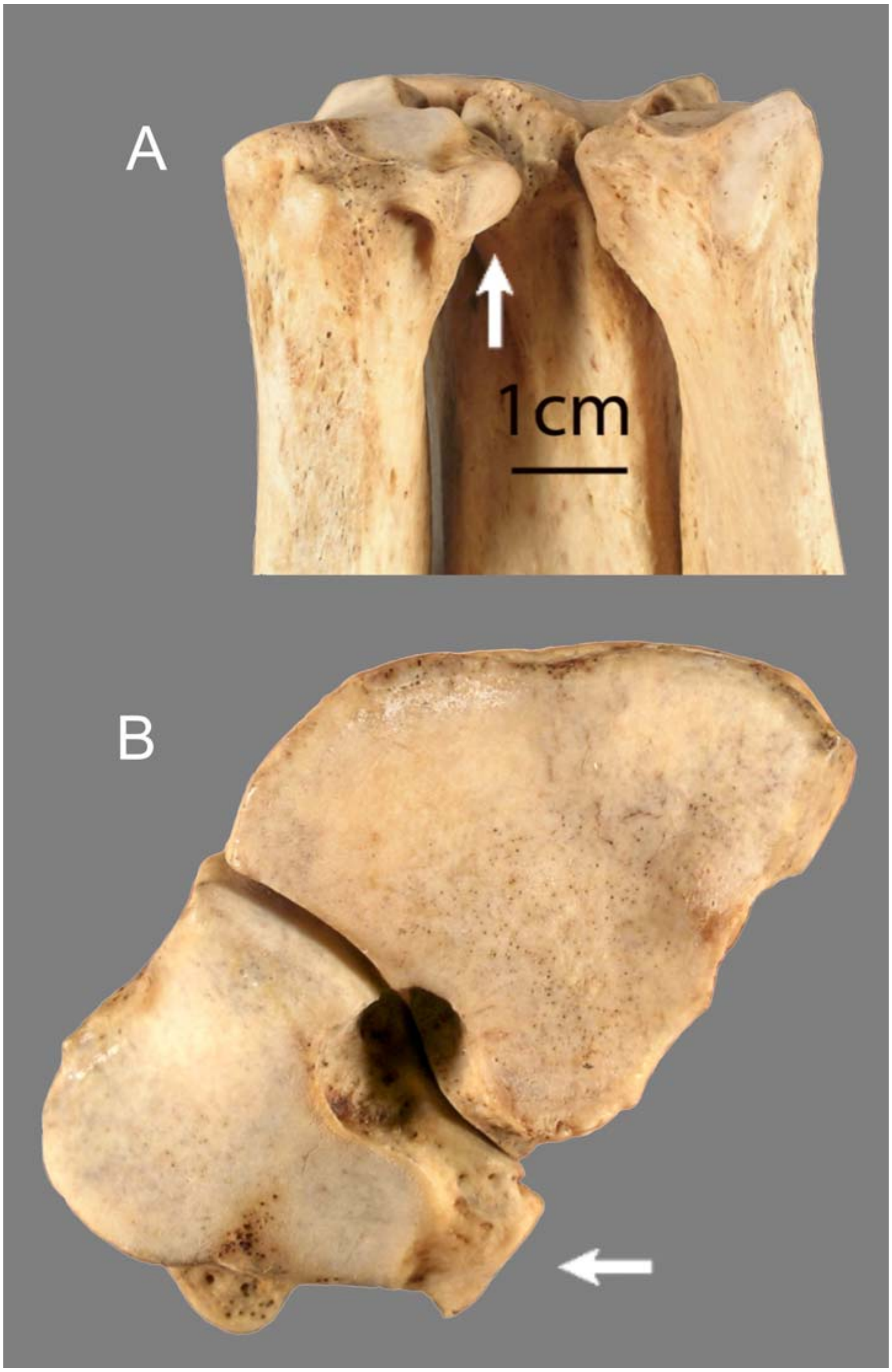


Figure 12. Posterior (A) and proximal (B) views of *T. terrestris* (USNM 270353) showing an articular state, which has not been previously documented. Arrow highlights that the facet for the first metatarsal is entirely on the fourth metatarsal.

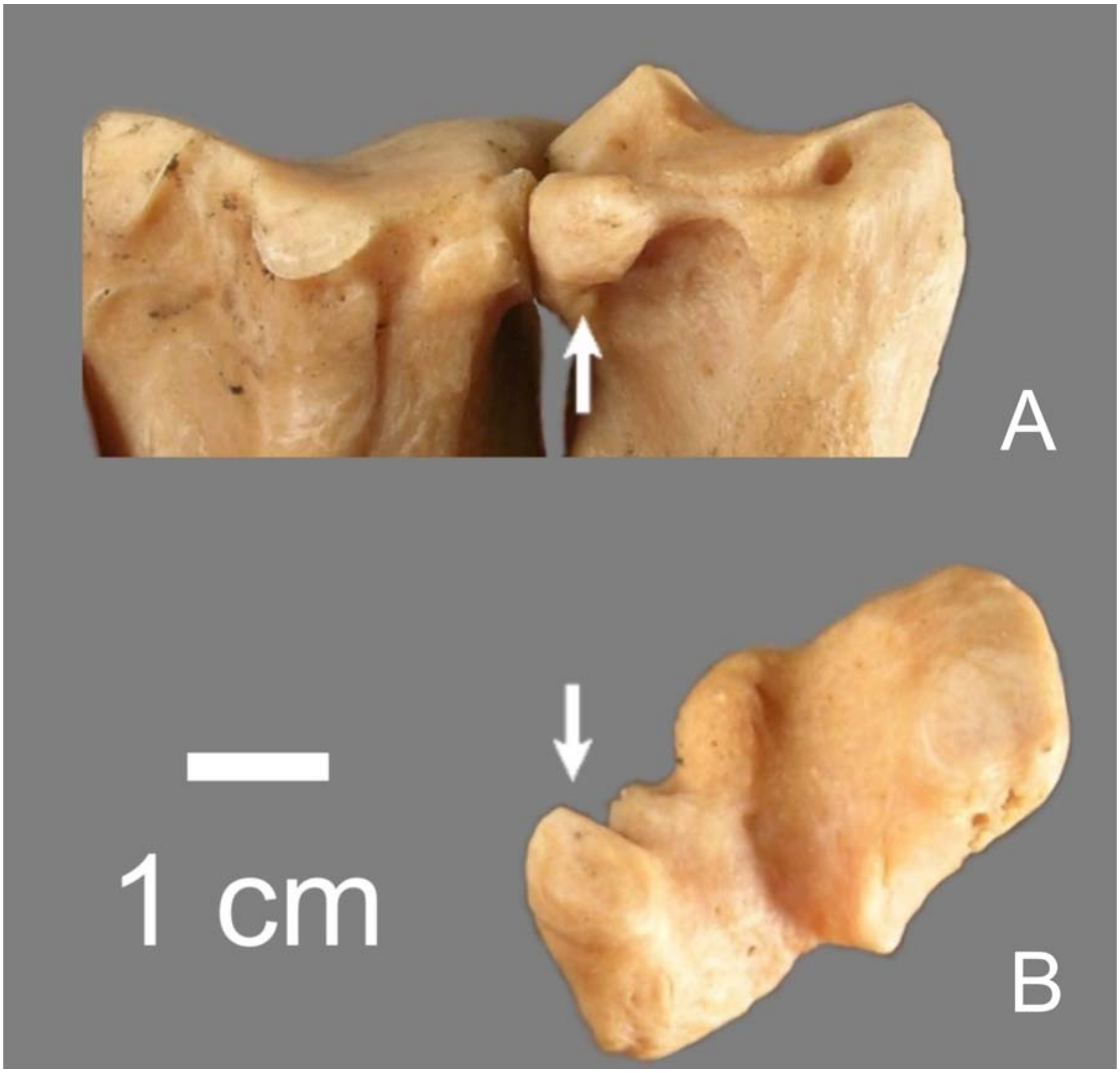


Figure 13. Posterior view of USNM 155410 (*Tapirus indicus*) proximal end of third and fourth metatarsals (A) and anterior view of fused first metatarsal and tarsal (B). Note the lack of facet indicated by white arrows. Its locality is unknown.

CHAPTER 7

DISCUSSION

First Metatarsal Applied to Phylogeny

Articular states are general trends and should not be considered good indicators of species. *Tapirus polkensis* exhibits the most variation of any species living or extinct, but most have only the mt3 articulation. Of course, *T. polkensis* is also the most numerous and it is worthwhile to mention that variable conditions were only found in taxa with many individuals (i.e. *T. polkensis*, *T. indicus*, and *T. terrestris*).

Placement of the mt1 articulation relative to other metatarsals is therefore not a valid character for species identification. However, the presence of a separate mt1 may be useful on a larger taxonomic scale. The first metatarsal is an individual bone in all tapiroids, with fusion between mt1 and t1 leaving a distinct suture (Figure 14). Rhinocerotoids lack a separate mt1, as it is reduced to a small lateral process on t1 (Radinsky 1963b). *Teleoceras* from GFS exhibit this excellently (Figure 15) and I could find no mention of a separate mt1 in any true rhinocerotoid. Scott et al. (1941) describe the odd shape of t1 in *Colodon* stating that the only difference between it and *Hyracodon* is an articulation with mt3 (the *Hyracodon* t1 articulates distally with mt2) and a rugosity separating 2 portions of the bone. Tarsal 1 is highly variable, even within the small *Teleoceras* sample from GFS (Figure 16). Ceratomorphs are too diverse geographically and morphologically for a full description of their feet here, but this character is suggested as a starting point for research that is possibly better able to define a monophyletic Rhinocerotoidea within Ceratomorpha.

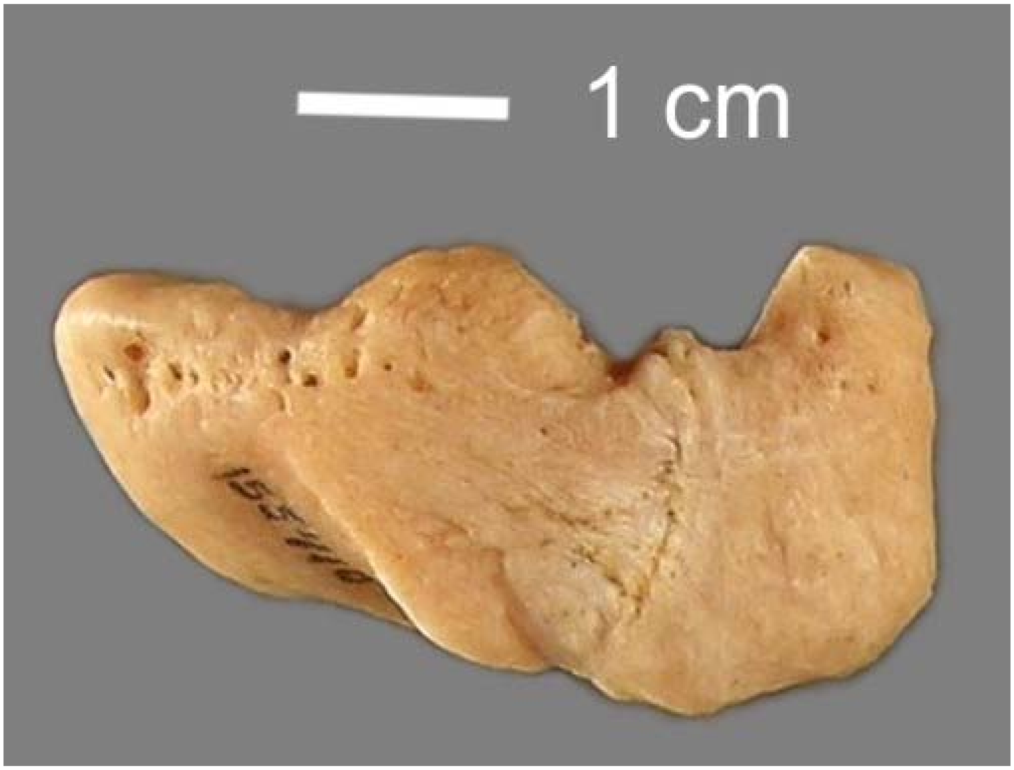


Figure 14. Posterior view of fused right first tarsal (left) and the first metatarsal (right) of *Tapirus indicus* (USNM 155410). Note clear, yet fully closed suture.

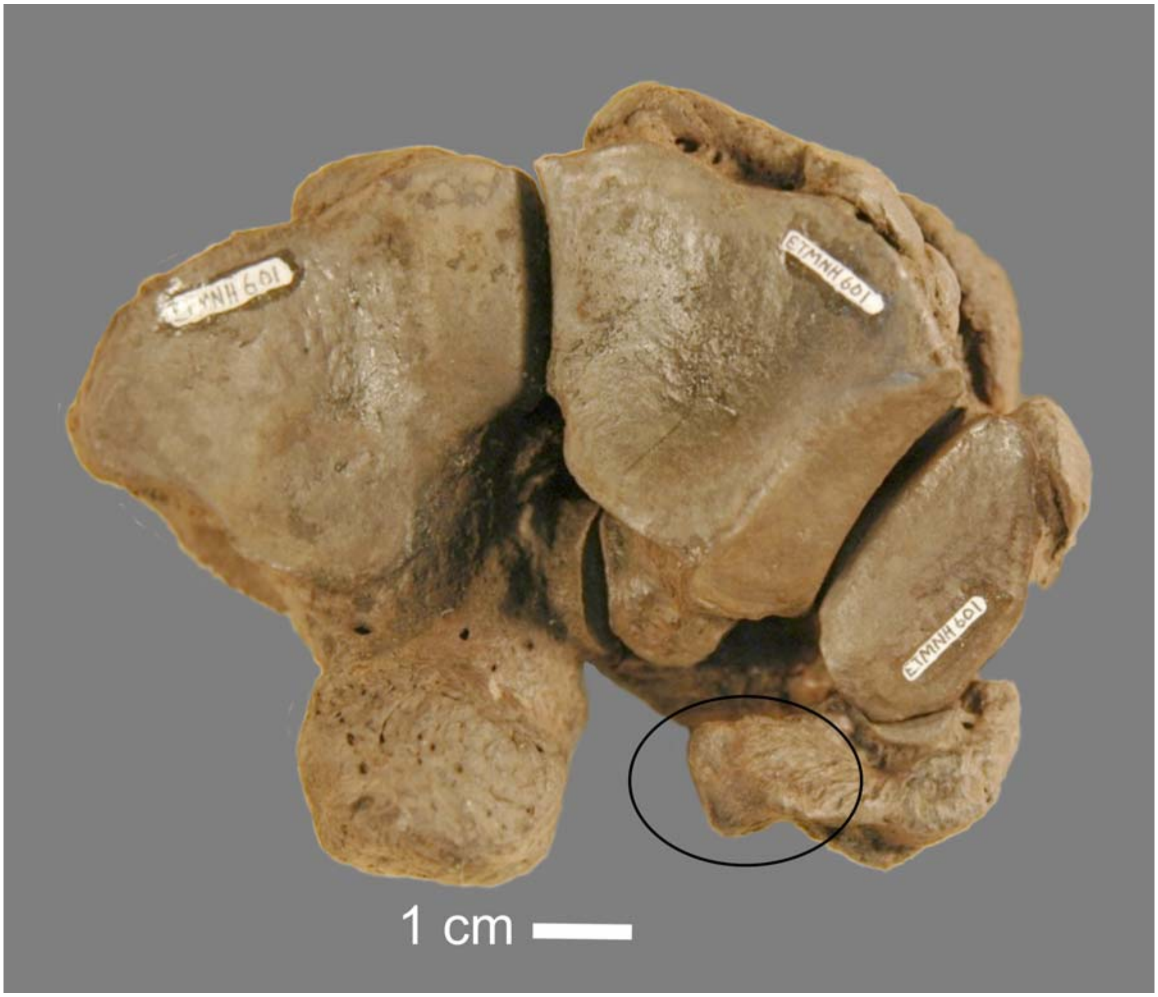


Figure 15. Distal view of distal tarsals from the left pes of *Teleoceras* cf *T. hicksi* (ETMNH 601) from GFS showing posterior-lateral process of the first tarsal, which does not articulate with the third or show a suture joint.

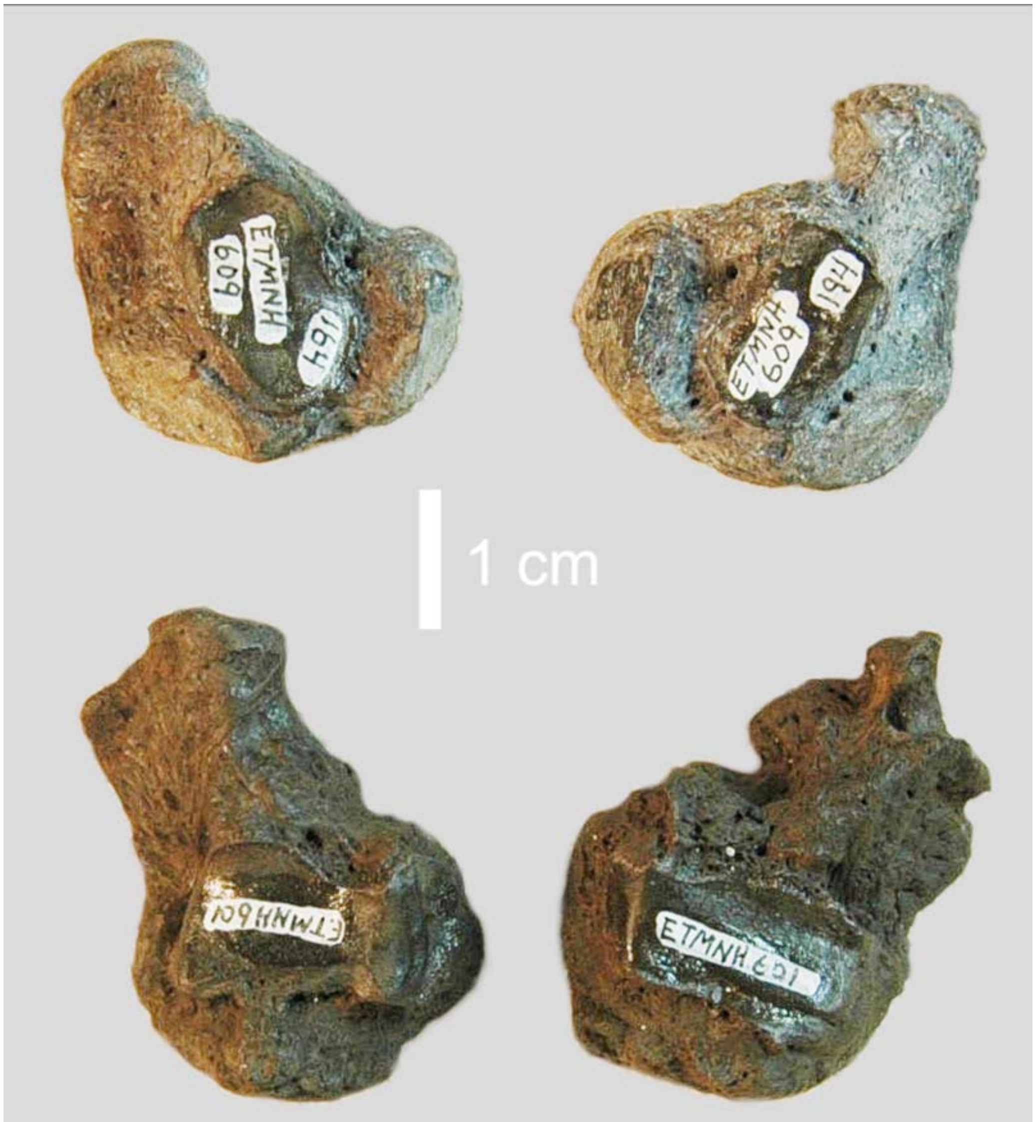


Figure 16. Left and right first tarsals of *Teleoceras* cf. *T. hicksi*, (above ETMNH 609 and below 601) from GFS, posterior views.

Metatarsal 1 Fused with Tarsal 1 as an Apomorphy for Rhinocerotoidea

Rhinocerotoids are closely related to tapiroids but more derived and possibly monophyletic (Colbert and Schoch 1998). Members of the Rhinocerotidae are defined by their chisel shaped upper first incisor occluding with a tusklike lower second incisor (Radinsky 1966b; Prothero 1998). Using these criteria, Radinsky (1966b) excluded the genera that had previously made Rhinocerotidae polyphyletic. Holbrook (1999; 2001) proposed using an “offset” neck of the talus (astragalus) to unite Rhinocerotoidea, including *Hyrachyus*, but excluding *Juxia*, (Indricotheriidae) a primitive rhinocerotoid. The offset talus is normally easy to see but subjective in nature; compare the straight *T. polkensis* tali (Figure 17) with intermediate nature of *Teleoceras* cf. *T. hicksi* (Figure 18), an advanced, but aberrant member of Rhinocerotidae (Prothero 2005). Another character used by Holbrook (1999) to potentially define rhinocerotoids is a joining of the sustentacular and distal calcaneal facet on the talus, which is more objective, but this groups *Hyrachyus* and “some *Tapirus*” (Figure 17) with Rhinocerotoids. *Teleoceras* cf. *T. hicksi* from GFS consistently has a very deep groove between these facets on the talus that creates a canal proximally to disto-laterally (Figure 19), but I can find no mention of any anatomical structure that might pass through it.

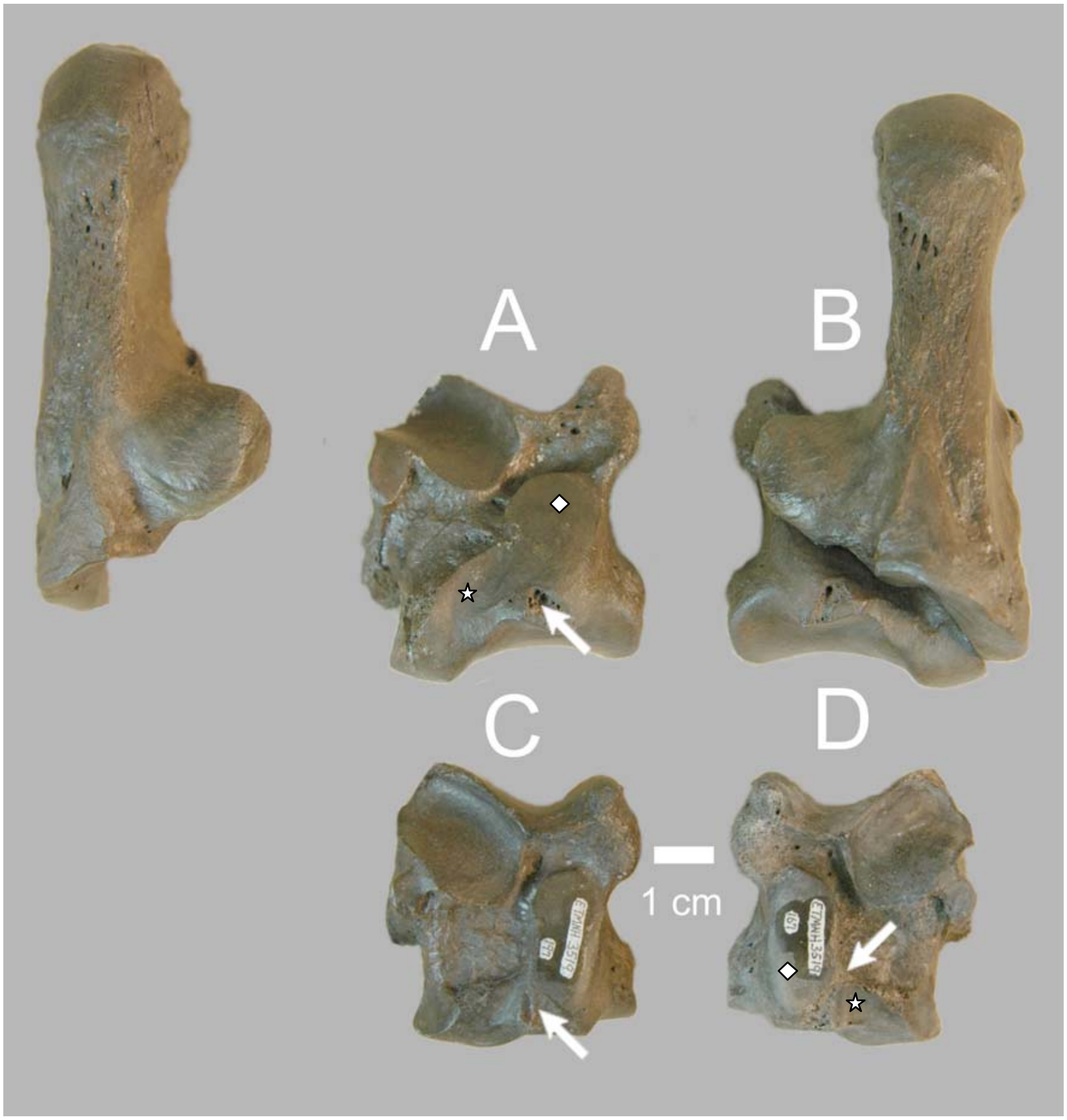


Figure 17. Right and left tali of ETMNH 8264 (above) and 3519 (below, with confluent sustentacular (diamond) and distal calcaneal facets (star) on A and C, but separated on D.

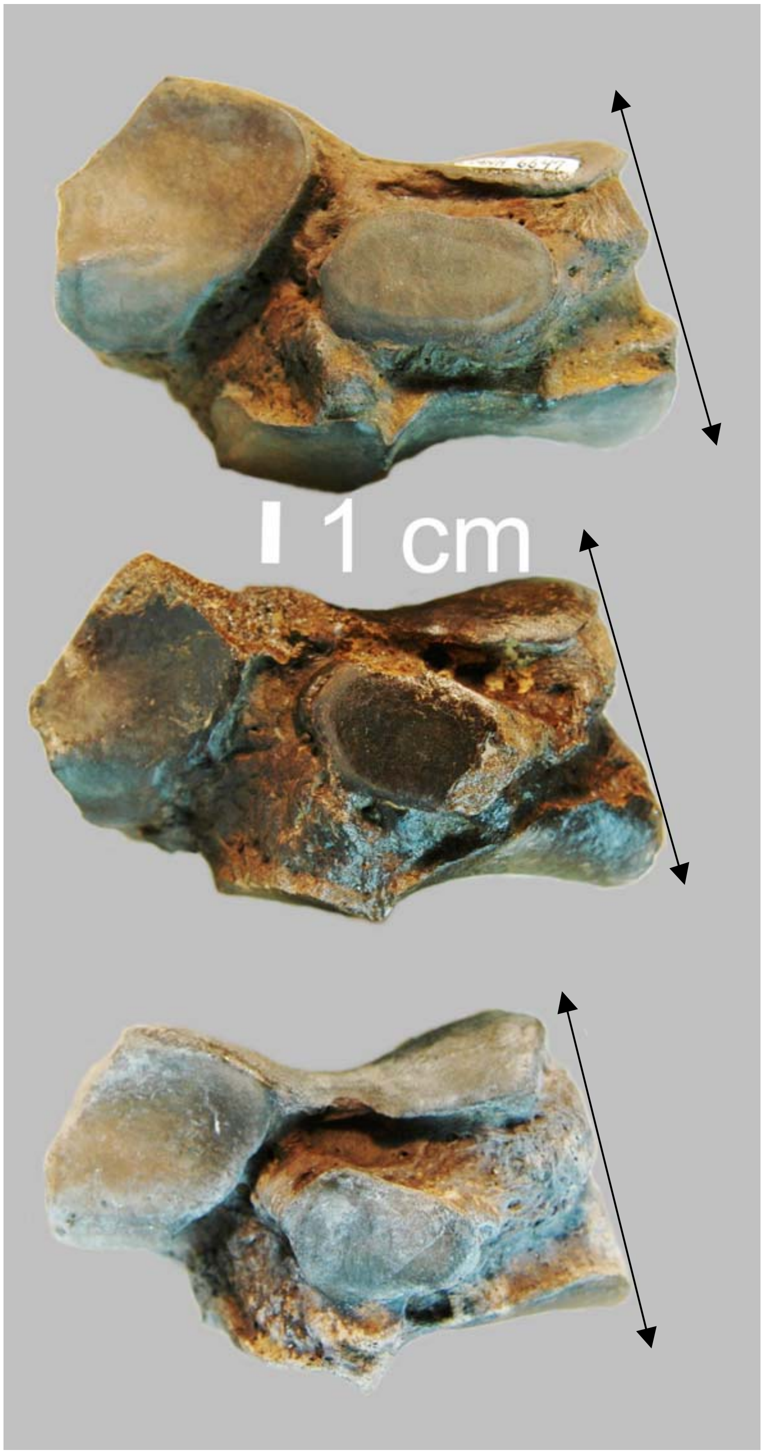


Figure 18. Tali of 3 *Teleoceras* cf. *T. hicksi* (ETMNH 6647 above, 1901 middle, and 609 below) from GFS, posterior view. Notice proximo-distal compression and only a slight offset of trochlea (arrow) compared with relative straightness of tapirs.

Figure 19. Distal view of 3 *Teleoceras* cf *T. hicksi* left tali showing deep separation between distal and sustentacular facets. Left to right: ETMNH 609 (with calcaneus anatomically placed), ETMNH 6647, and ETMNH 1901. Star shows distal facet and diamond shows sustentacular facet, while arrows show a passage between facets.

Regardless of location, a distinct first metatarsal may help define Tapiroidea, grouping *Hyrachyus, Tapirus, Helaletes, Deperetella,* and *Colodon* together. More ceratomorph fossil material will be found, so the unique structure of the tarsus should be carefully examined to support or refute this assertion. As a discrete character, separation of the mt1 and t1 is less subjective than an offset talus. Cranial differences between tapirs and *Hyrachyus* may suggest a phylogenetic distance, but the similarity of their pes indicates a high level of conservation that is probably a constraining plan for their intermediates (i.e. Witmer 1995). The placement of *Hyrachyus* within Ceratomorpha is largely inconsequential to the phylogeny of the rest of the group, but it may help define character polarities for future analyses as a sister group to rhinocerotoids. As for the polarity of mt1, should that be used as a character, articulating with mt3 is a derived state (mt4 would be even more derived).

Anatomy

Articular surfaces are useful in paleontology because they are easily identifiable and offer some insight into the animal's skeletal interactions. Smooth facets indicate a healthy amount of wear between bones, but this can deteriorate with age, disease, or disuse. Not all joints are designed to allow for movement. Between t1 and the reduced mt1, for example, there is much variation in the type of joint; ranging from a normal smooth facet to jagged articulations that look more like a suture. However, bony sutures can show a great deal of variation within a species and are sometimes indicative of age or arthritis. Of the individuals found at GFS with both feet present, fusion is roughly the same on both right and left, suggesting that internal development affects this anatomy more than asymmetrical pathology. Fusion in these bones is herein documented for both fossil species and living species, including a single (broken) individual from GFS.

Because Radinsky's (1963b) original description of this bone provided one proximal and one distal function, the statistical results support a role connected with the distal end of the metatarsal. More specifically, the anterio-posterior depth of the distal articular facet seems to be smaller in those individuals with the extra mt4 facet, which would be directly related to the amount of flexion allowed in the third metatarsophalangeal joint. This is a complex joint in perissodactyls, contributing greatly to the springing apparatus that stores energy for efficient motion. In addition, tapirs retain a muscular component to this joint for active motion.

Digital reduction in the ancestors of tapirs led eventually to a reduced vestige of their most medial metatarsal, but they were unable to follow that trend as far as horses. Most animals, including tapirs, use t1 and mt1 as an insertion for the tibialis anterior, which provides dorsiflexion by its anterior attachments but also everts the foot by wrapping around posteriorly.

Tapirs need to control more variable motions in their feet and this led to retention of mt1. Eventually, this arrangement led to more laterally displaced mt1, which was bound to the rest of the tarsus and now serves as a point of origin for the contrahentes.

Metatarsal 1 developed into a continuous connection between tibialis anterior and contrahentes that allowed for more control over pes eversion. Because tapirs still have distinct contrahentes for each of their side digits (Campbell 1945, Bressou 1961), their contraction is considered here to be somewhat independent of each other. This arrangement is the product of tapir's feet needing to be dexterous because of the inconsistent nature of their preferred habitat's substrate.

Tapirus polkensis is considered a smaller species relative to the rest of Tapiridae (Hulbert et al. 2009; Hulbert and Wallace 2011), whereas *T. indicus*, the species most likely to exhibit the extra metatarsal articulation, is the largest extant member. Therefore, exhibiting condition 1 cannot be a direct product of body size. There is probably a similarity in the habits of these 2 tapirs, which could lead to the occasional lateral displacement of mt1. Although Asian tapirs are remarkably similar to the New World cousins, a few differences that have already been pointed out may be crucial for their foot development. Indirectly related to their body size is their increased amount of foraging space, with *T. indicus* being known to have a much larger range (Kahn 1997). Moreover, *T. indicus* does not make well worn paths (Humphrey and Bain 1990), which could heavily influence hind feet development through ontogeny. Consequently, USNM 155410 is an exceptional individual because it is without any posterior articulation on mt1 and is from a zoo. Such a captive would have had a greatly reduced home range as a result of being confined (although I cannot say when it was brought into captivity), so the lack of articulation could support my hypothesis.

Perissodactyl Adaptations

Two major themes in perissodactyl history are adaptations for running speed and herbivorous digestion (Radinsky 1966a) as popularly exemplified by the modern *Equus*. These adaptations are intimately tied to each other and the natural environment. As herbivorous hindgut fermenters, perissodactyls process large amounts of relatively low quality food (Shipley 1999), making increased hypsodonty and cheek tooth surface area logical traits for the order. Horses are more derived and often considered better in these respects, but low crowned teeth are advantageous for the environments preferred by tapirs (Janis 1984). Their primitive brachydont dentition has been accompanied with the development of a specialized masticatory apparatus and proboscis (Radinsky 1965), possibly allowing for more discriminating foraging.

Cheek teeth of perissodactyls show distinctive patterns that can be diverse (Radinsky 1969). Molars are often used in paleontological descriptions because of their superior preservation, morphological variation, and ease of comparison, but it is possible that when paleontologists focus on molar cusp patterns, they are using a feature that is so closely tied to a universal function (i.e. mastication) that an abnormal amount of convergence is present. Premolars are also variable and have been used to describe brontotheres, which led to an unrealistic number of species (Mihlbachler 2008).

Considering the variation present in the diet of browsers and the ebb and flow of abundances of different kinds of food, it is easy to see how adaptive tooth patterns would be quickly reversed and redeveloped. Postcranial features are equally important adaptations for perissodactyls and may be less likely to have rapid convergence. Evolving long limbs is convergent between all animals adapted for speed, but they can always be grouped by subtle anatomical differences in the feet. As an example, artiodactyls can be extremely adapted for speed, and superficially similar to perissodactyls, but individual ankle bones such as the talus can always be used to tell them apart. The same is true for the living perissodactyls.

Modifications for Speed and Maneuverability

Though lengthening limbs as cursorial adaptations is the other main aspect of perissodactyl evolution (Radinsky 1966b, 1969), reversals may have occurred (Schoch 1984). As the family Tapiridae evolved, traditional cursorial modifications developed (e.g. reduction of acromion and fusion of radius and ulna) but were mostly confined to the forelimb, which Radinsky (1965) attributes to existing specializations of the hind limb. Hind limb musculature agrees with this idea, being more specialized and simplified in both perissodactyls and artiodactyls (Campbell 1945).

Tapir modifications for running must allow them not only to be fast but to be stable in a forested environment. Their hind limbs may have been so specialized (i.e. Radinsky 1965) that further changes may have been deleterious for the tapir lifestyle and anatomy, but as evidenced by comparisons with horses, the possibility for lengthening and thinning the limb further is mechanically feasible. Radinsky (1963b) regards the fusion of the mt1 with t1 in rhinos as a cursorial adaptation. Extant rhinos are mostly graviportal, but their ancestors were often small and quick (Prothero et al. 1989). Tapirs are not usually thought of as modified for running, but their evolution since the Eocene is marked by development and subsequent reversal of cursorial trends (Radinsky 1965; Schoch 1984).

Comparisons Between Perissodactyls

Perissodactyl feet are always adaptive tools modified for running, but tradeoffs exist between a slender build for speed and a more robust power. For example, extant horses are wonderfully adapted to open plains speed. On the other extreme, extant rhinoceroses have become large in size and graviportal as a consequence. Tapirs, on the other hand, are better adapted to navigate through dense foliage. Though these strategies are different, basic adaptations for running (i.e. limb weight reduction and lengthening) are universal and dependant only on pervasive aspects of the animal's habitat or lifestyle.

Anatomical features adapted for locomotion in some ways unite the order Perissodactyla and in others highlight the differences between them. Veterinary research on horses experimentally assigns specific functions to features that can be used to make inferences for fossils. For example, the horse suspensory ligament system lengthens legs while conserving elastic energy (Hildebrand 1987) and is presumed to be the similar for tapirs, despite more muscle tissue distally. Tracing the phylogeny of these specialized digital ligaments back to the tapir-like ancestors of horses shows that as the springing mechanism evolved from muscular attachments, while the fleshy cushion characteristic of tapir feet was lost (Camp and Smith 1942).

Because the ceratomorphs are endangered now but prevalent in the fossil record, there is great potential to study these species without disturbing them directly by conducting paleontological analyses. Fossils can also be used in large numbers to develop hypotheses about the variation present in a population or to make inferences on the natural history of extinct taxa. GFS has the largest collection of individual tapirs, which probably accumulated over periods of time that dwarf the era early in the 20th century when scientists collected animals for study.

Comparing bones of extant groups to large fossil samples can generate ideas about what needs to be studied indirectly in the endangered species.

Species Concepts

In order to meaningfully address what changes are likely to be seen between species, the species concept used must be addressed. Paleontologists often use the morphological species concept (MSC) out of necessity, even though other biologists must choose from a wide range of ideas about what constitutes a species. Philosophically, MSC follows from the idea that structural variation between 2 individuals is great enough that they would not be able to hybridize in a single viable population. Stated this way, MSC is rooted in the biological species concept (BSC), which states that creating viable offspring is the sole criterion for determining a valid species. Metatarsal variation does not fall in this category, nor would many dental differences that have previously been used to oversplit paleontological groups such as brontotheres (Mihlbachler 2008).

Quantitatively, the rule of thumb for MSC involves coefficients of variation in skeletal structures. Normal species variation is considered to be below 10 (Simpson et al. 1960), such as those listed here for the GFS sample of *Tapirus polkensis*. High variation would indicate a species difference or a discrete intraspecific variation such as sexual dimorphism. Cranial foramina and sagittal crest differences already described (Hulbert et al. 2009) and metatarsal variations of *T. polkensis* do not necessarily reflect species differences, or even incipient speciation. If GFS represented a mass death assemblage involving a very short amount of time, these differences could be considered normal variation in a breeding population. However, GFS represents a long enough period of time that skeletal features fluctuate enough for differences to be present in the fossil record. Theories must be developed to explain the source of variation, especially regarding an inconsistent and vestigial structure like mt1.

Variability in a Vestigial Structure

Vestigial is usually understood to mean a reduced structure that is no longer functional but lacks the deleterious effects on the organism to be heavily selected against and removed from the population (Fong et al. 1995). Relatively large amounts of intraspecific variation in a skeletal feature have previously been used to support vestigiality (Tague 2002). Bilateral asymmetry may also result from loss of function (Maxwell and Larsson 2007). Consequently, the modified first metatarsal of tapirs is here given as an example of a bone that was previously vestigial and underwent reduction early in their evolution (Radinksy 1963b) but was not completely lost.

Increased variation due to a bone's vestigial nature can sometimes lead to it being retrofitted for another function, famously known in the pandas as the radial sesamoid which developed into a flexible thumb-like structure when digit 1 was otherwise occupied (Davis 1964; Gould 1992). Initial loss of function frees the bone to be available for other purposes. As a result, high variation can indicate vestigiality (or possibly historical trends towards vestigiality), and in the carpals of *Teleoceras* for example, Harrison and Manning (1983) hypothesized that such variance is associated with the ability to rapidly evolve adaptive structures. Similarly, increased dental variation has been attributed to fast evolution in living rodents (Guthrie 1965).

Osteological Remodeling and Adaptation

A basic assumption in most paleontological research is that skeletal changes over time are heavily influenced by selective pressures so that they potentially reflect specific differences. Ideally, differences indicating something about the way the animal lived will also be preserved. In reality, however, osteological variations are used to study species because it is normally all that is left from fossilization. Tooth wear is an obvious example of differences that lack phylogenetic or genetic causes but still are apparent in the fossil record. In certain circumstances fortunately, it may make little difference whether an osteological feature is determined by genetics or usage because the inference made will reflect an adaptation.

Functionality is also important for determining the value of a phylogenetic character (Bock 1981). Unfortunately, many apomorphic characters are not chosen based on function. Moreover, if a feature is vitally important, a high degree of conservation is typical, resulting in a character that is phylogenetically useless. Alternatively, if a feature varies so much that evolution leads it to be convergent with those in other groups, it can again become useless. In practice, a compromise is met by studying small variations in analogous bones, although the presence or absence of a bone becomes useful on a larger taxonomic scale. Small differences between species may be adaptive characters, but within a species they must be considered individual variations or responses to the animal's environment.

Body tissues are remarkably variable because they are the result of genetic blueprints dictating the initial development of a structure but in turn are effected by environmental factors (both within and outside the body). Bone may be considered the most consistent of all tissues; school children are taught an invariable number of bones exist in the human body. Even though it is hard and mineralized, bone tissue undergoes the same programmed destruction and replacement that other tissues do (Huiskes et al. 2000), sometimes resulting in osteoporosis through osteoclast activity exceeding that of osteoblasts (Teitelbaum 2000).

Wolff's law is the popular conception of bone adaptation, but it is no longer considered valid in the original mathematical sense (Ruff et al. 2006). Despite disagreements about the mechanism by which bone responds to a stimulus, experimental data dealing with human athletes (Alfredson et al. 1997), bed rest (Zerwekh et al. 1998), and measured stress of long bones (Demes 2007) consistently shows that osteological tissue changes with environmental pressure. The lateral displacement of mt1 in some tapirs as a response to environmental, developmental, or preferential factors is therefore quite plausible.

Spatial or Temporal Differences Between Character States

In the future, more data will be available with which to test hypotheses, but currently it seems that there is a slight clustering of GFS tapirs with condition 1. Because those with the extra articulation show an increased occurrence in Test Pit 2-2004 relative to other areas of GFS, they likely had a similar time of deposition. Also, there are so few of them, we could easily postulate that they represent some part of a closely related family group. Asserting that these tapirs are close in time or space is independent from any adaptive hypotheses that may be generated to explain morphologic similarity.

Testable Hypotheses Explaining Metatarsal Variation

Paleontological questions cannot be formulated until fossil specimens are found and observations made. Previous workers who had the insight to consider metatarsal articulations as important characters (e.g. Radinsky 1963b and Hulbert 2005) did so with a very limited sample size, which happened to coincide with known species differences. It is still possible, but highly unlikely, that there were 2 species present at GFS and the differences therein are interspecific. Moreover, information on tapir sexual dimorphism is anecdotal and contradictory, but Simpson (1945) found no osteological differences. Intraspecific fighting appendages such as enlarged canines or horns are also completely absent in all tapir species. Dimorphism has been documented in horses and rhinoceroses (mostly in dental measurements), so it is still theoretically plausible.

Ontogenetic difference is the other main factor that can generate high morphological variation. Using only isolated mt3's, there is no way to account for the age of the individual beyond complete epiphyseal fusion. In the future when larger samples are available and foot bones can be associated with cranial material to further define age groups, this question can be more fully addressed. It may also be possible to devise an age scheme based only on mt3 growth plate fusion, for example 1) both plates unfused 2) proximal plate fused but visible 3) proximal suture completely closed 4) distal plate fused but visible 5) both sutures closed. When species differences, sexual dimorphism, and ontogeny are ruled out as sources of variation, more unorthodox hypotheses must be formulated. These alternate hypotheses are more speculative but could at least provide points for future research on extant animal behavior and fossil assemblages. The following hypotheses provide causes for increased variation but will tend to do so over a range, while bimodal distribution would be more common for the traditional hypothesis listed above.

Alternative Theories to be Tested

Tapirs are cryptic in the wild and the small amount of biological research on their behavior and preferences reflects this. Some hypotheses presented here can be easily supported or refuted by specific experiments that have yet to be done (Table 9). Because one extant taxon shares condition 1, any differences between them and New World species can be considered. Some reported differences lack rigorous supporting research but nevertheless fit very well with the proposed function of the modified metatarsal.

The basis for many of these hypotheses lies in the association between osteological adaptations of the distal metatarsals and associated musculotendinous features. As a point of origin for muscles that proceed distally to the phalanges, mt1 placement (medial or lateral) should be affected by reactions to the substrate. In general, tapirs have retained a muscular tridactyl pes to cope with their forested environment. While the forelimb has 4 toes for extra stability, hind limbs are modified more for a powerful thrust, which must efficiently push off the ground in order to be effective.

All tapirs inhabit forested areas of some sort, but *T. indicus* differs from the other species by preferring primary forest and having a more generalist diet (Williams and Petrides 1980; Fragoso 1991). Although *T. indicus* feeds near water and swims, they apparently do not wallow in mud (Humphrey and Bain 1990). Another line of research to pursue would be intensive study of *T. pinchaque* because it is the least likely to remain in dense jungles and muddy riverbanks.

Environmental factors are most likely dictating the articular states of tapir metatarsals, and there may not be one single factor that is particularly responsible. The favored hypotheses (i.e. the use of paths, muddy substrates, and inhabiting primary vs. secondary forests, and range size) should be considered related and potentially correlated with each other. *Tapirus indicus* lives in a more open primary forest, probably walks further (large body size and measured home range), and doesn’t use paths or mud. These may all result in a less flexible metatarsophalangeal joint as indicated by their smaller distal facet measurements.

Size cannot be an influencing factor for *T. polkensis* because it is smaller than extant species at around 125 kg (Hulbert et al. 2009). Their abundance with the aquatic fauna at GFS is strongly indicative of a preference for mud wallowing, similar to other American tapirs. The home range of *T. polkensis* at GFS cannot currently be determined. Though the fossiliferous deposits cover a relatively small area, the tapirs certainly ranged over an area too big to be preserved at the fossil site, so this remains a valid hypothesis. While GFS is highly centralized in one area, other sites are not. It will be important in the future to determine how tapirs with condition 1 are geographically distributed. *Tapirus webbi* from Florida is the species showing condition 1 most consistently, and it too may have a functional home range larger than other American species, although this is not possible to verify with fossils. Research on extant species is needed to test this hypothesis by determining range sizes for extant animals in Asia and in America.

Table 9. Summary of hypotheses explaining metatarsal variation

Hypotheses	**Pro**	**Con**
Two species	Localized variation	Low Coefficient of Variation for metatarsal and craniodental measurements
Sexual dimorphism	Males have larger home ranges	Unknown in tapirs
Ontogeny	Tarsal one could be displaced laterally with age	All individuals show adult fusion of epiphyses
"Follower or hider" behavior in juveniles	Occurs during developmental stage of young animal when bone tissue is highly plastic	Would require a great deal of wild tapir research over many years
Preferential foot use	Most mt3 with extra articulation are left and most mt3 without are right	Needs a functional reason for osteological response
Size of home domains	*Tapirus indicus* has a large range	Requires range research for all extant species, which should be done anyway
Use of paths	*Tapirus indicus* may not create paths as often as New World species	
Preference for muddy substrate	Use of digital adduction	All tapirs probably use water
Swimming	Requires walking on unsteady substrate	Adduction of digits is not affected
Time averaging	Naturally fluctuating expression of the different character states over a long period of time would give the appearance of more variation than is real	The length of deposition is poorly understood at this time
Random variation	Plastic character based on variation present in *Tapirus polkensis* as well as other taxa	Character states are correlated with distal metatarsals

CHAPTER 8

CONCLUSION

Location of mt1 relative to other metatarsals in tapirs has been suggested to be useful for distinguishing species (Radinsky 1963b; Hulbert 2005; Hulbert and Wallace 2005). However, facets that indicate metatarsal locations are variable in a large sample of a single species (Hulbert et al. 2009) from GFS, invalidating this character's phylogenetic use. Inspection of this obscure bone in modern skeletal collections also showed its variability among extant species represented by decent numbers of individuals.

All tapirs have a distinct mt1 despite varying degrees of fusion with t1. Metatarsal 1 was also present in fossil members of the superfamily Tapiroidea examined. With the exception of a dubiously placed genus *Hyrachyus* (see Hopson 1989), mt1 is lost in the superfamily Rhinocerotoidea. Further study of mt1 within this large group of perissodactyls may produce an apomorphy for defining a monophyletic Rhinocerotoidea within Ceratomorpha.

While phylogenetically insignificant, the position of mt1 is instead considered anatomically adaptive in *Tapirus*. When mt1 is positioned laterally enough to articulate with mt4, the distal articular facet is smaller and less mobile in the GFS sample. This correlation makes sense considering that tarsals and proximal metatarsals of tapirs serve as origin for flexors and adductors of the digits (Radinsky 1963b), providing a muscular connection between the proximal and distal ends of mt3. Metatarsal1 and its associated tarsals are located at a critical junction between proximal muscles for stride propulsion and distal muscles that push off the ground, so the bone's placement is likely connected with how tapirs use their habitat. While they have cursorial adaptations, tapirs probably modified their hind limbs as much as possible (Radinsky 1965). Because further digit reduction is possible (e.g. horses), the tridactyl pes and tetradactyl manus of tapirs are assumed necessary for the unsteady substrate associated with their forested environment.

The minority of tapirs (6 of 31 mt3s) at GFS are anatomically similar to the extant Asian tapir, *T. indicus* (Radinsky 1963b) and extinct American species *T. webbi* (Hulbert 2005). Modern descriptions of *T. indicus* suggest they are less inclined to use jungle trails and mud wallows (Humphrey and Bain 1990) than New World species (Husson 1978; Padilla and Dowler 1994). *Tapirus indicus* may also have a larger home range than other extant species (Williams and Petrides 1980). Both behaviors can be plausibly connected to a more flexible metatarsophalangeal joint than in extant New World tapirs. Future research may provide more solid evidence linking the location of mt1 with a particular environmental feature. However, for the time being, variation in the metatarsal anatomy of *T. polkensis* from GFS may help develop hypotheses regarding differences between the last endangered representatives of a once diverse and successful family.

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VITA

PATRICK LAWRENCE HAWKINS

Personal Data:	Date of Birth: March 24, 1983 Place of Birth: East Ridge, Tennessee
Education:	Public Schools, Murfreesboro, Tennessee B.S. Biology, Geology Minor, East Tennessee State University, Johnson City, Tennessee 2005 M.S. Biology, Paleontology concentration, East Tennessee State University, Johnson City, Tennessee 2011
Professional Experience:	Head science teacher for Korea Poly School in Seoul, South Korea, 2007-2008 Graduate Assistant, East Tennessee State University, College of Arts and Sciences, 2008-2010
Field Experience:	Pleistocene cave excavations, Virginia and Tennessee, 2006-2008 Pleistocene excavation at Saltville, Virginia, 2009 Miocene excavation at Gray Fossil Site, Tennessee, 2010
Peer Reviewed Publications:	Hawkins PL, Wallace SC, Schubert BW. 2009. A New Pleistocene Faunal Assemblage from Morrill Cave, Sullivan County,

	Tennessee: With a Preliminary Discussion of the Arvicoline Rodents. Current Research in the Pleistocene 26:152-154.
Abstracts:	Hawkins PL, Wallace, SC. 2010. Comparing Fossil Species to Endangered Zoo Animals and Local Roadkill. South Eastern Association of Vertebrate Paleontology. Abstracts. Hawkins PL, Wallace SC. 2010. Simple Femoral Indicators of Locomotion Derived From Anatomical Studies. Journal of Vertebrate Paleontology 30 (3, supplement). Hawkins PL, Wallace SC. Forthcoming 2011. *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.
Honors and Awards:	Jackson School of Geosciences Student Travel Grant, 2009 East Tennessee State University Graduate and Professional Student Association Travel Grant, 2009 and 2010
Professional Affiliations:	Society of Vertebrate Paleontology Don Sundquist Center for Excellence in Paleontology ETSU Graduate and Professional Student Association