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**Paleoenvironment of the Late Eocene Chadronian-Age Whitehead Creek Locality
(Northwestern Nebraska)**

by

Samantha M. Mills

A Thesis

Submitted to the Graduate Faculty of

St. Cloud State University

in Partial Fulfillment of the Requirements

for the Degree of

Master of Science

in Functional Morphology

October, 2019

Thesis Committee:

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Abstract

Toward the end of the Middle Eocene (40-37mya), the environment started to decline on a global scale. It was becoming more arid, the tropical forests were disappearing from the northern latitudes, and there was an increase in seasonality. Research of the Chadronian (37-33.7mya) in the Great Plains region of North America has documented the persistence of several mammalian taxa (e.g. primates) that are extinct in other parts of North America. This research aims to investigate the paleoenvironment of the Whitehead Creek locality, Nebraska, one Chadronian-age locality within the Great Plains, in order to better understand the circumstances surrounding the persistence of relict taxa during the late Eocene. To address the paleoenvironment at Whitehead Creek, this research evaluates locomotor guilds of 56 astragalar morphospecies, 43 calcaneal morphospecies, and a sample of 55 terminal phalanges. To evaluate paleoenvironment at Whitehead Creek, locomotor frequencies established for fossil morphospecies were compared with those found in 25 modern sites, representing a wide range of environments, using Sørensen's similarity index and the Euclidean Distance method. Results indicate that small mammals (< 1,000g) at Whitehead Creek practiced a wide range of locomotor activities including leaping, digging, climbing, and running in both arboreal and terrestrial habitats. Comparisons suggest that a gallery forest in the Cerrado of Brazil is a good modern analog for Whitehead Creek. The mixture of locomotor categories found at Whitehead Creek suggest that Whitehead Creek was a mosaic of water, overbanks, closed canopy forests (with an herbaceous understory), bamboo thickets and open woodlands.

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Chapter 1 - Introduction

Primates constituted a major part of mammalian faunas in North America during the early and middle Eocene (55-38mya) (Dunn, 2009). In the Uintan (46-40mya) and Duchesnean (40-38mya) in North America, certain taxa (e.g. primates, Ostrander, 1980; plesiadapiformes, Kihm & Tornow, 2014) were declining in diversity and abundance. By the end of the Uintan (46-42mya), primates were gone from the Rocky Mountains basins, but persisted as relicts in a few localities within the Great Plains (Tornow & Arbor, 2017). By the end of the middle Eocene and beginning of the late Eocene (Chadronian) in North America (38-33.7mya), the warmer, wetter and more stable climate of the early and middle Eocene was transitioning into a much cooler, more arid and seasonal climate (Janis, 1993; O'Terry, 2001; Retallack, 2007; Boardman & Secord, 2013; Tornow & Arbor, 2017).

Global climate change during the middle and late Eocene had a major impact on the tropical vegetation, as evidenced by a major reduction in the extent of tropical forests (Janis, 1993; Dunn, 2009) and the appearance of forests with an admixture of temperate and tropical plants (Wheeler & Landon, 1992; Miller, Smith, Sheldon & Strömberg, 2012). Many mammalian lineages were also affected, with extinction of most of the archaic groups (e.g. condylarths, uintatheres, plagiomenids and plesiadapiformes) (Prothero, 1985; Janis, 1993; Woodburne, Gunnell, Stucky & Berggren, 2009) and the appearance and diversification of most of the modern groups (e.g. artiodactyls and perissodactyls) (Janis, 1993; Retallack, 2007). The correlation between climate change and Eocene faunal and floral dynamics in North America is well documented. Studies (Prothero, 1985; Janis, 1993; Retallack, 2007; Woodburne et al., 2009) have highlighted the effects of climate change on floral and faunal diversity, whereby if there was a reduction in floral diversity there was a subsequent reduction in faunal diversity.

The disappearance of primates in the Rocky Mountains basins around 46-42mya (Dunn, 2009), and their persistence in Great Plains localities, such as Raben Ranch, Nebraska (Ostrander, 1980), Short Pine Hills, South Dakota (Krishtalka, 1978), and Medicine Pole Hills, North Dakota (Kihm & Tornow, 2014) indicates that biotic response to climate was heterogeneous. Site-specific changes occurred, whereby local environments responded to climate change at different times and rates and in different ways (Hren, Sheldon, Grimes, Collinson, Hooker, Bugler & Lohmann, 2013). Whereas fossil sites in the Rocky Mountains basins started to see the effects of climate change by the middle- middle Eocene (around 46-42mya) (Dunn, 2009), with mainly tropical paleofloras being mostly replaced by temperate paleofloras by the end of the late Eocene (around 33.7mya) (Lielke et al., 2012), fossil sites in the Great Basin Western Interior (Smith, Manchester, Ashwill, McIntosh & Conrey, 1998) and the Great Plains (O'Terry, 2001; Strömberg, 2004; Retallack, 2007; Zanzazi & Kohn, 2008; Boardman & Secord, 2013) were still seeing the effects of climate change, with paleofloras consisting of subtropical and temperate elements by the end of the late Eocene. As part of the Great Plains, the Chadronian-age Whitehead Creek locality may have served as a refugium for certain taxa (e.g. primates) (Tornow & Arbor, 2017), where, on the basis of phytoliths (Strömberg, 2004), paleosols (O'Terry, 2001; Retallack, 2007) and stable isotopes (Zanzazi & Kohn, 2008; Boardman & Secord, 2013), environmental reconstructions suggest an environment that was warmer, wetter and more stable than the Rocky Mountains basins.

Analyses of paleosols suggest a warm, wet, humid environment for northwestern Nebraska during the late Eocene (Retallack, 2007) with at least some closed canopy forests (O'Terry, 2001). A rain shadow formed by the Rocky Mountains produced considerably drier intermontane environments (Retallack, 2007). Whereas these cooler, drier, intermontane

environments were associated with a reduction in mammalian diversity during the late Eocene (Retallack, 2007; Woodburne et al., 2009), Oregon (west) and Nebraska (east) of the Rocky Mountains basins were warmer, wetter and more humid, with increased mammalian diversity (Retallack, 2007). These findings (Retallack, 2007; O'Terry, 2001) are corroborated by phytolith assemblages, which suggest a diverse array of forest indicators, such as woody dicots, dicots, conifers, ferns, palms and bambusoid grasses (Strömberg, 2004), and stable isotope analyses of mammalian teeth, which suggest not only the persistence of wet, dense, riparian habitats that cut through drier, more open biomes but also that mammalian habitats remained relatively stable across the Eocene-Oligocene boundary (Zanazzi & Kohn, 2008; Boardman & Secord, 2013). Research of the Chadronian in the Great Plains region has documented the persistence of several mammalian taxa that are elsewhere extinct (Krishtalka, 1978; Ostrander, 1980; Storer, 1996; Meyer, 2007; Kihm, 2013; Kihm & Tornow, 2014; Arbor & Tornow, 2015; Tornow & Arbor, 2017). This research aims to investigate the circumstances surrounding the persistence of these relict taxa (e.g. primates) in the Great Plains. More specifically, it seeks to interpret the environmental conditions that might have allowed these relicts to persist in the Great Plains after their extinctions elsewhere. The goal of this project is to reconstruct the paleoenvironment of one fossil locality, the Whitehead Creek locality, Nebraska (Figure 1.1, 1.2, 1.3 and 1.4), for the purpose of understanding its community ecology. This will be accomplished through the independent analysis of small mammal (< 1,000g) astragali, calcanei and terminal phalanges (Figure 1.5).

The flowchart outlined in Figure 1.5 is an incorporation of both the theoretical and methodological components of this project. This flowchart is designed to show how the ultimate goal will be reached and the necessary steps that will be taken to get there. The research design

of this project is as follows: bone features → locomotion → environment. The relationship between bone features and locomotion is known as functional morphology. More broadly, functional morphology is the study of the relationship between form and function. The relationship between locomotion and the environment is known as ecomorphology. More broadly, ecomorphology is the study of the link between the structure of an organism and the environment in which it occurs. This method assumes that postcranial morphology will covary with habitat structure, as the postcrania must allow the organism to function, or move, effectively in its environment. Functional morphology is a part of ecomorphology. These two methods, and their underlying theoretical concepts, will form the framework of this project. The results and subsequent discussion will add to this framework, creating a picture of what Whitehead Creek may have looked like 35mya and adding to our understanding of its community ecology.

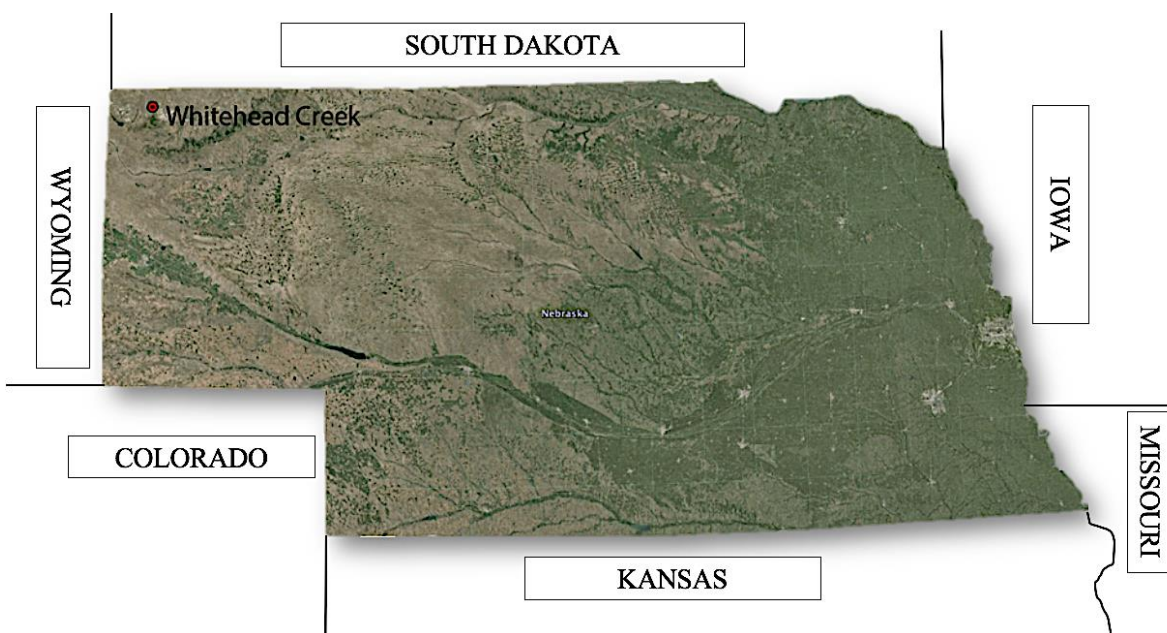


Figure 1.1. Location of the Whitehead Creek locality. Image modified from Arbor and Tornow (2015).



Figure 1.2. BA-01, anthill. Whitehead Creek locality, Oglala National Grasslands, northwestern Nebraska.



Figure 1.3. BA-04, anthill, looking south. Whitehead Creek locality, Oglala National Grasslands, northwestern Nebraska.



Figure 1.4. Whitehead Creek locality, Oglala National Grasslands, northwestern Nebraska. Picture of me in the field.

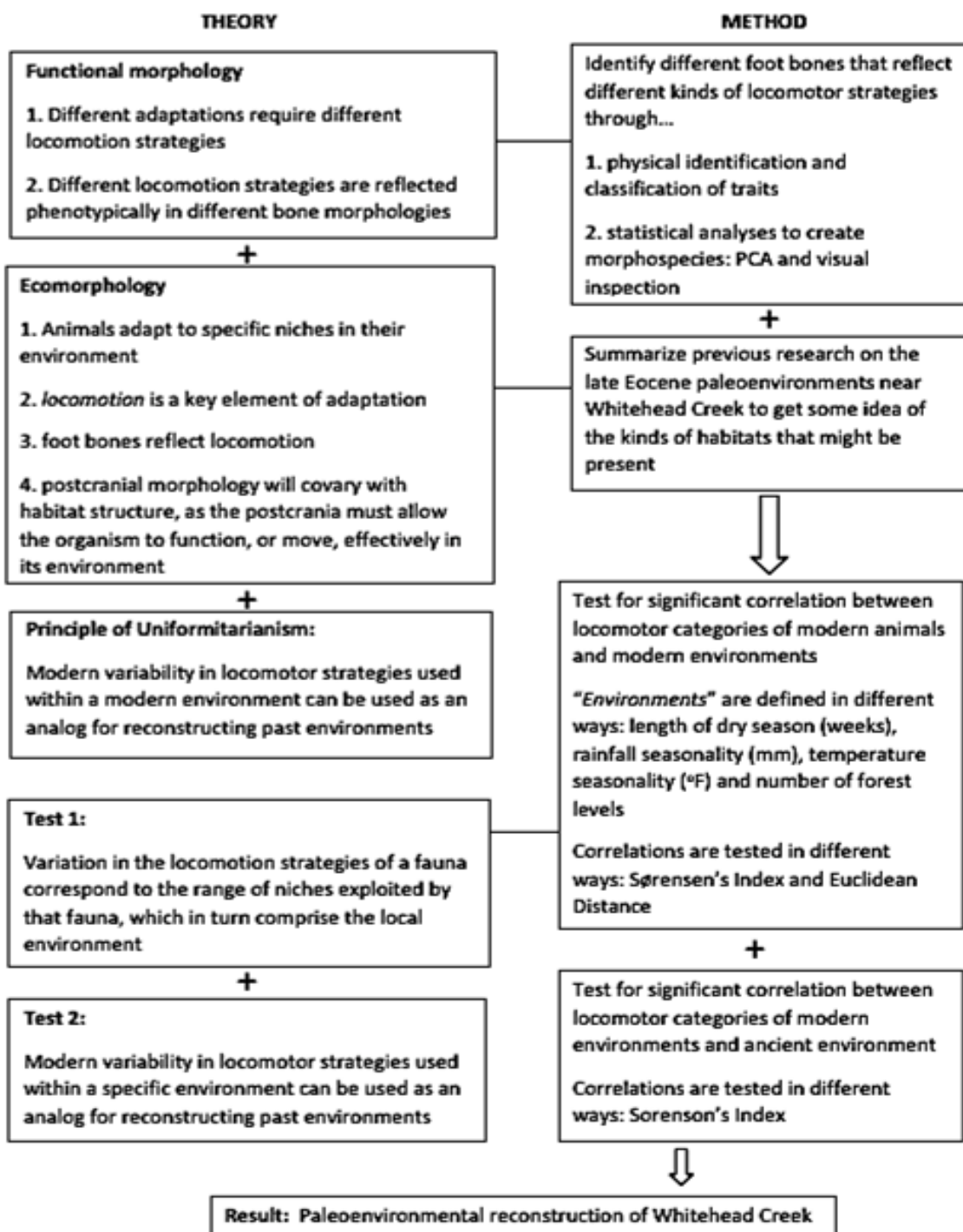


Figure 1.5. Flowchart outlining the research design of this project.

Chapter 2 – Background

Wood, Chaney, Clark, Colbert, Jepsen, Reeside and Stock (1941) subdivided the Eocene beds of North America into four land mammal ages – the Wasatchian, the Bridgerian, the Uintan and the Duchesnean. The Chadronian North American Land Mammal Age, named after the Chadron Formation in the Great Plains region, was considered to be early Oligocene. In 1992, new $^{40}\text{Ar}/^{39}\text{Ar}$ dates, combined with magnetostratigraphy and changes in the global time scale, showed that the Chadronian correlated with the late Eocene (Prothero & Emry, 2003). The Wasatchian, Bridgerian, Uintan and Duchesnean North American Land Mammal Ages also received new dates. The Wasatchian (about 55-50mya) and most of the Bridgerian (about 50-48mya) are now considered to be early Eocene. The last 2Ma of the Bridgerian (48-46mya), the Uintan (46-40mya) and the Duchesnean (about 40-38mya) are now considered to be middle Eocene.

According to LaGarry (1997), the late Eocene in Nebraska is comprised of the early-Chadronian Chamberlain Pass Formation and the middle- and late-Chadronian Chadron Formation. The Chadron Formation is made up of the Peanut Peak Member and the overlying Big Cottonwood Creek Member (LaGarry, 1997). The Peanut Peak and Big Cottonwood Creek members were defined on the basis of detailed lithologic correlations involving different soil types. Prothero and Emry (2003) further subdivided the Chadronian into four biostratigraphic units - the Earliest, Late Early, Middle and Late Chadronian. These subdivisions were based on FADS and LADS (first and last appearances of Chadronian-specific taxa).

The first 15 million years of the Eocene (about 55Ma-40Ma) were warm, wet and humid (Woodburne et al., 2009; NOAA, 2018); the climate was relatively stable on a global scale. At about 40mya, the final supercontinent of Gondwana separated into the continents of Australia

and Antarctica (Holroyd & Mass, 1994). Coupled with this separation was an initial reduction in the amount of atmospheric CO₂. These two events helped spur the rapid buildup and expansion of the Antarctic ice sheets. The resulting cooler waters formed a conveyor belt to the rest of the world, supplying cold ocean currents to different regions. This conveyor belt is what is known today as the North Atlantic Current (or North Atlantic Drift) (NOAA, 2017). The effects of colder sea surface temperatures and deep ocean temperatures had varying effects on continental Europe and North America (Hren et al., 2013). In Europe, climatic cooling, accompanied by a shift to drier conditions, was associated with a major mammalian faunal turnover otherwise known as the Grande Coupure (Costa, Garcés, Sáez, Cabrera, & López-Blanco, 2011). Many of Europe's endemic mammalian species became extinct and new Asian immigrants appeared (Costa et al., 2011). Costa et al. (2011) estimated an age for the pre- and post- Grande Coupure – 36.1Ma for the pre-Grande Coupure and 33.3Ma for the post-Grande Coupure. In North America, extinction rates were modest (Prothero, 1985). It was mostly the aquatic herpetofauna and land gastropods that were directly impacted (O'Terry, 2001).

The initial phases of the Eocene-Oligocene Transition (EOT) are characterized by an increase in local climatic variability relative to pre-EOT conditions (i.e. warm, wet and humid) and precede the major drop in temperature that coincides with the glacial event (40 Ma [Hren et al., 2013]). The range of responses associated with decreasing temperatures in continental North America began during the Uintan (46-42mya). It was at this time that primates in North America began to decline in diversity and abundance in the Rocky Mountains region (Dunn, 2009). This decline, in particular, has been linked to the reduction of tropical rainforests in the northern latitudes. Whereas the late Eocene of North America was marked by a general drying trend, environmental response to climate change was heterogeneous (Hren et al., 2013). Site-specific

changes occurred, whereby different, local environments responded to climate change at different times and rates and in different ways (Hren et al., 2013).

The various responses to climatic instability can be seen in several studies of Chadronian-age paleofloras (Wheeler & Landon, 1992; Smith et al., 1998; Lielke, Manchester & Meyer, 2012), which highlight the transition of plant communities with mainly tropical elements into plant communities with an admixture of subtropical/temperate elements. Lielke et al. (2012) describe the middle Chadronian, Mormon Creek paleoflora (36-35Ma) of the Fossil Basin locality in the Upper Ruby River Valley, southwestern Montana as being composed of two components, subtropical and warm-temperate, and lacking a xeric component. The subtropical component is eliminated in the late Chadronian Metzel Ranch (the Fossil Basin locality) paleoflora (35-34Ma), and the temperate component becomes prominent. The Ruby (the Fossil Basin locality) paleoflora, which spans the Eocene-Oligocene boundary (33.7Ma), has a significant proportion of gymnosperms (e.g. oaks and conifers).

Smith et al. (1998) found that there was a gradual transition from tropical to temperate conditions between 39Ma and 33Ma at the Gray Butte locality, central Oregon. Tropical paleofloras of the Clarno Formation are succeeded by cool-temperate paleofloras of the John Day Formation. Wheeler and Landon (1992) found that the late Eocene climate at an undisclosed locality adjacent to the Chadronia Pocket vertebrate locality, located in Dawes County, Nebraska, was seasonal; this is based off of their analyses of five different types of late Eocene woods. While studies of paleofloras were taking place, researchers began studying Chadronian-age fauna.

There are certain taxa that characterize the Chadronian; they have been found in the Great Basin Western Interior (Fremd, 2010; Samuels & Korth, 2017), the Rocky Mountains basins

(Donohoe, 1956; Ostrander, 1983; Emry, 1992; Emry & Korth, 1993; Tabrum, Prothero & Garcia, 1996; Lloyd & Eberle, 2012) and the Great Plains (Hough & Alf, 1956; Clark, Beerbower & Kietzke, 1967; Wood, 1969; Ostrander, 1980; Prothero, 1985; Pearson & Hoganson, 1995; Storer, 1996; Prothero & Emry, 2003; Meyer, 2007; Kihm & Schumaker, 2008; Kihm, 2011, 2013). Lagomorphs persist through the Oligocene, but a few species are restricted to the Chadronian – *Chadrolagus emryi* (Emry, 1992; Tabrum et al., 1996), *Palaeolagus temnodon* (Ostrander, 1980; Emry, 1992; Pearson & Hoganson, 1995) and *Megalagus brachyodon* (Ostrander, 1980; Emry, 1992; Storer, 1996; Tabrum et al., 1996; Lloyd & Eberle, 2012). Cylindrodontid rodents such as *Cylindrodon collinus* and *Pseudocylindrodon neglectus*, Pipestoneomyid rodents such as *Pipestoneomys*, Eomyid rodents such as *Aulolithomys* and *Litoyoderimys auogoleus* and Ischyromid rodents such as *Ischyromys junctus*, *I. douglassi* and *I. veterior* are all characteristic of Chadronian-age sites in the Great Plains (Clark et al., 1967; Wood, 1969; Ostrander, 1980; Storer, 1996; Kihm, 2011, 2013; Arbor & Tornow, 2015), Rocky Mountains basins (Donohoe, 1956; Ostrander, 1983; Emry & Korth, 1993; Lloyd & Eberle, 2012) and the Great Basin Western Interior (i.e. *Proischyromys perditus* only, Samuels & Korth, 2017).

Domnina thompsoni (a Soricomorph) and *Centetodon chadronensis* (a lipotyphlan) can be found at Chadronian-age sites in the Rocky Mountains basins (Tabrum et al., 1996) and the Great Plains (Ostrander, 1980; Emry, 1992; Storer, 1996; Kihm & Schumaker, 2008; Arbor & Tornow, 2015). The Apatemyid *Sinclairiella dakotensis* can be found in Chadronian-age deposits within the Great Plains (Clark et al., 1967; Ostrander, 1980; Arbor & Tornow, 2015; Tornow and Arbor, 2017). Other taxa that are characteristic of the Chadronian include Artiodactyls such as *Leptomeryx mammifer* (Storer, 1996; Tabrum et al., 1996; Emry, 1992; Arbor & Tornow, 2015)

and Perissodactyls such as *Mesohippus westoni* (Pearson & Hoganson, 1995; Storer, 1996), *Miohippus grandis* (Clark et al., 1967; Storer, 1996; Tabrum et al., 1996) and *Brontops* (Hough & Alf, 1956; Prothero & Emry, 2003). Unidentified species of the Perissodactyls *Mesohippus*, *Subhyracodon* and *Colodon* have been found at the Bridge Creek locality in the John Day Formation, central Oregon (Great Basin Western Interior), along with the unidentified species of the Artiodactyl *Archaeotherium* (Fremd, 2010).

The Great Plains (Clark et al., 1967; Wood, 1969; Ostrander, 1980; Storer, 1996; Meyer, 2007; Kihm, 2011, 2013; Kihm & Tornow, 2014; Arbor & Tornow, 2015; Tornow & Arbor, 2017), the Rocky Mountains basins (Donohoe, 1956; Ostrander, 1983; Emry & Korth, 1993; Lloyd & Eberle, 2012) and the Great Basin Western Interior (Fremd, 2010; Samuels & Korth, 2017) are known as faunal provinces. Based on differences in rodent taxa, Storer (1989) recognized seven faunal provinces: The High Arctic, the Great Plains, the Rocky Mountains basins, the Great Basin Western Interior, the Mexican Plateau-West Texas, Southern California-Baja California and the Florida-Gulf Coastal Plain (Figure 2.1). He defined a faunal province as a region with its own geological features, within which mammalian paleofaunas not only resemble each other but differ from mammalian paleofaunas of other regions. The Rocky Mountains basins, the Great Basin Western Interior and the Great Plains, are critical for understanding Whitehead Creek because they contain sites that have Chadronian-age exposures that are used as references to better understand the community ecology and paleoenvironment of the late Eocene of North America.



Figure 2.1. The faunal provinces (Storer, 1989) of continental North America. The image of North America was adopted from Nelson (2019).

Whitehead Creek

Whitehead Creek is a middle Chadronian (35.7-34.7mya [Prothero & Emry, 2003]) fossil locality (LaGarry & LaGarry, 1998; Tornow & Arbor, 2017) (Figure 2.2) that is located roughly 15 miles northwest of Crawford, Nebraska. It is located in Section 36 T34N R54W within the Oglala National Grasslands, northwestern Nebraska, about one mile north of Toadstool Park. Spatially, Whitehead Creek is located about four miles west-southwest of the Raben Ranch locality, about five miles north-northwest of Hough and Alf's (1956) anthills, about eight miles southwest of Ostrander's (1985) Twin Buttes locality and about thirteen miles northwest of Wood's (1969) "Chadronia" Pocket locality (Figure 2.3). Collection at Whitehead Creek began in 2013. Fossiliferous matrix was collected (Tornow, 2011-2015; Arbor & Tornow, 2015) from harvester anthills (Figure 2.4) using whisk brooms and dustpans, sweeping the surfaces of exposures, and limited subsurface sampling. This matrix was brought back to the Biological Anthropology Laboratory at St. Cloud State, where it was probed under a binocular microscope to recover fossils.

Whitehead Creek has produced a diverse, small mammalian fauna that includes 11 mammalian Orders that are represented by 20 families, which are represented by 31 genera (Arbor & Tornow, 2015). Arbor and Tornow (2015) provide a preliminary mammalian faunal list of the Whitehead Creek locality. This faunal list includes Multituberculata, Didelphimorphia, Leptictida, Lipotyphla, Soricomorpha, Apatotheria, Primates (including Plesiadapiformes and Omomyidae), Rodentia, Lagomorpha, Carnivora and Artiodactyla. The faunal list of Whitehead Creek is not exhaustive, and it is constantly being refined.

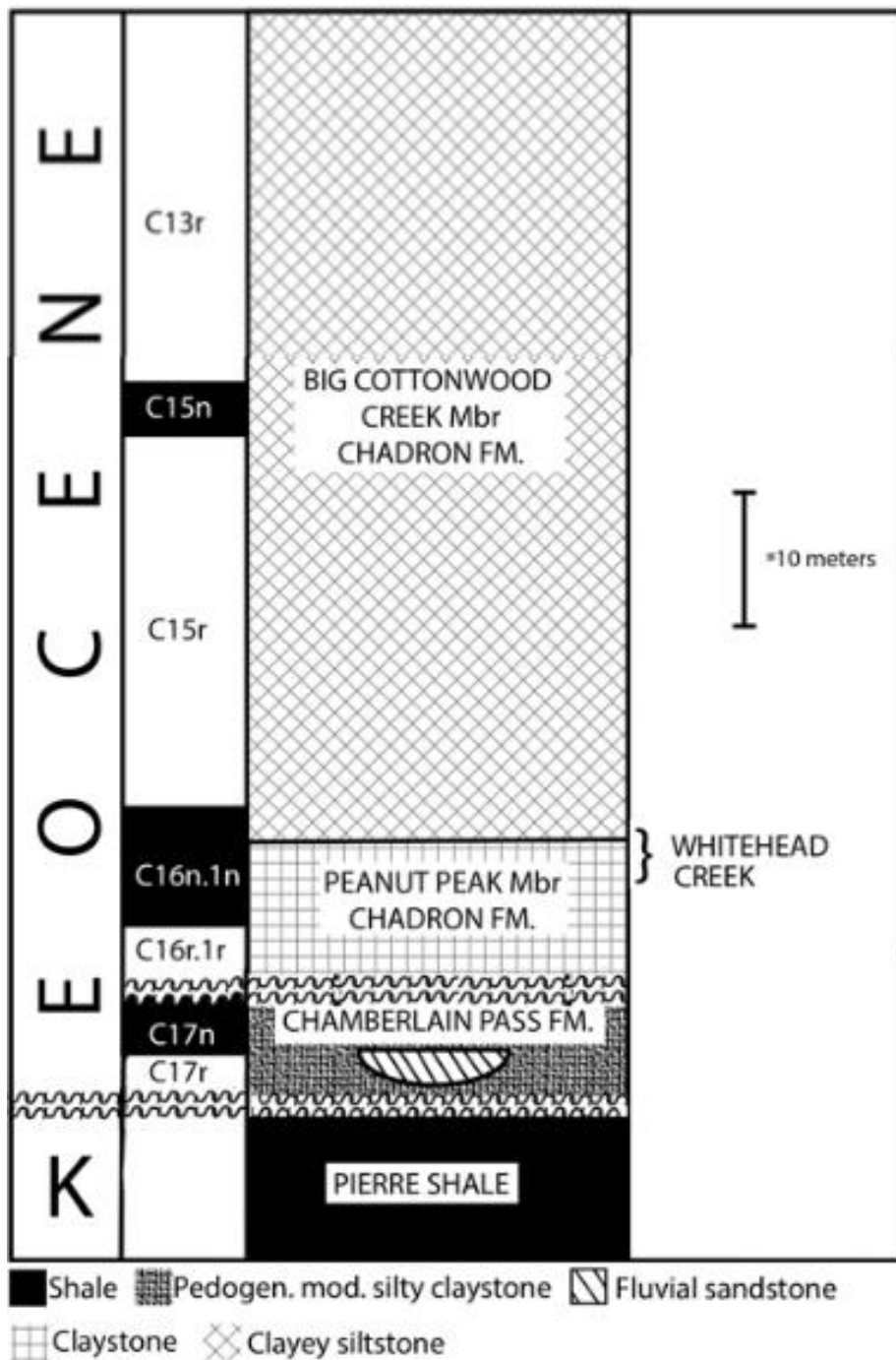


Figure 2.2. Whitehead Creek stratigraphy. Adopted from (Arbor and Tornow, 2015) and modified to show the relative date of the Whitehead Creek locality.

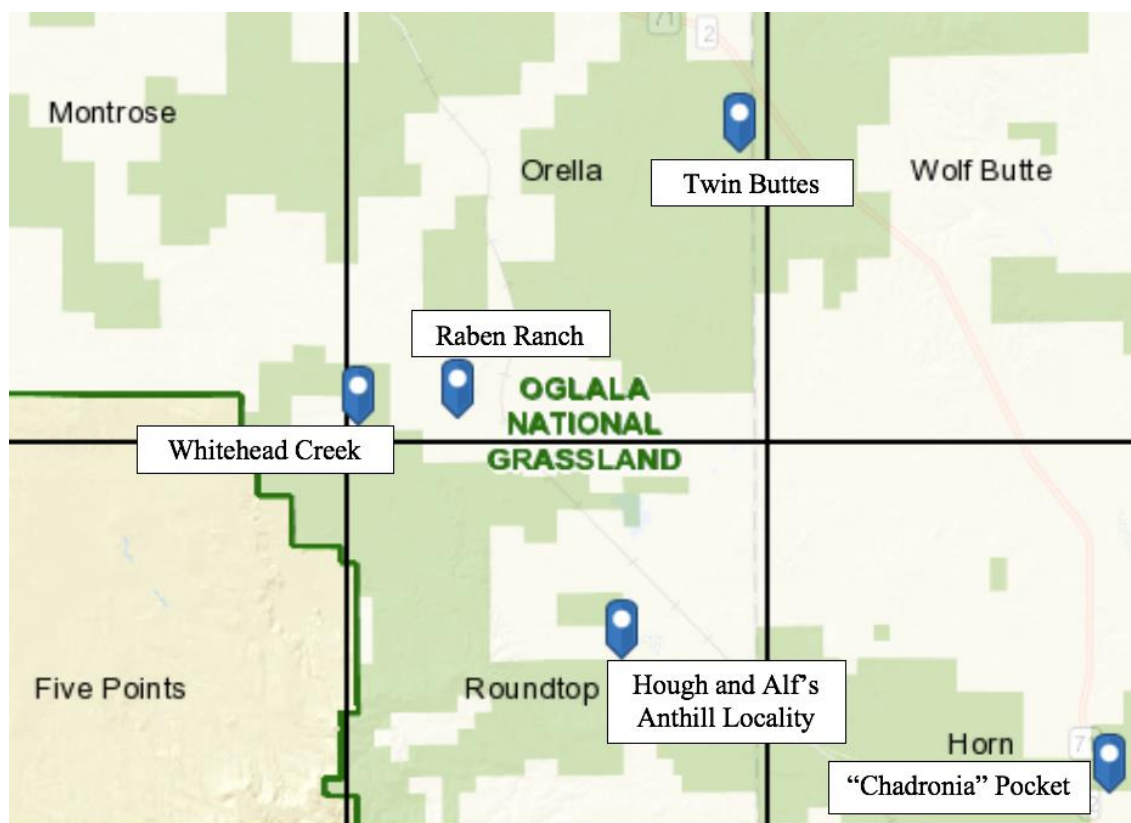


Figure 2.3. Whitehead Creek in relation to other Chadronian-age fossil localities within the Oglala National Grasslands, northwestern Nebraska. Modified from USDA Forest Service (2019).

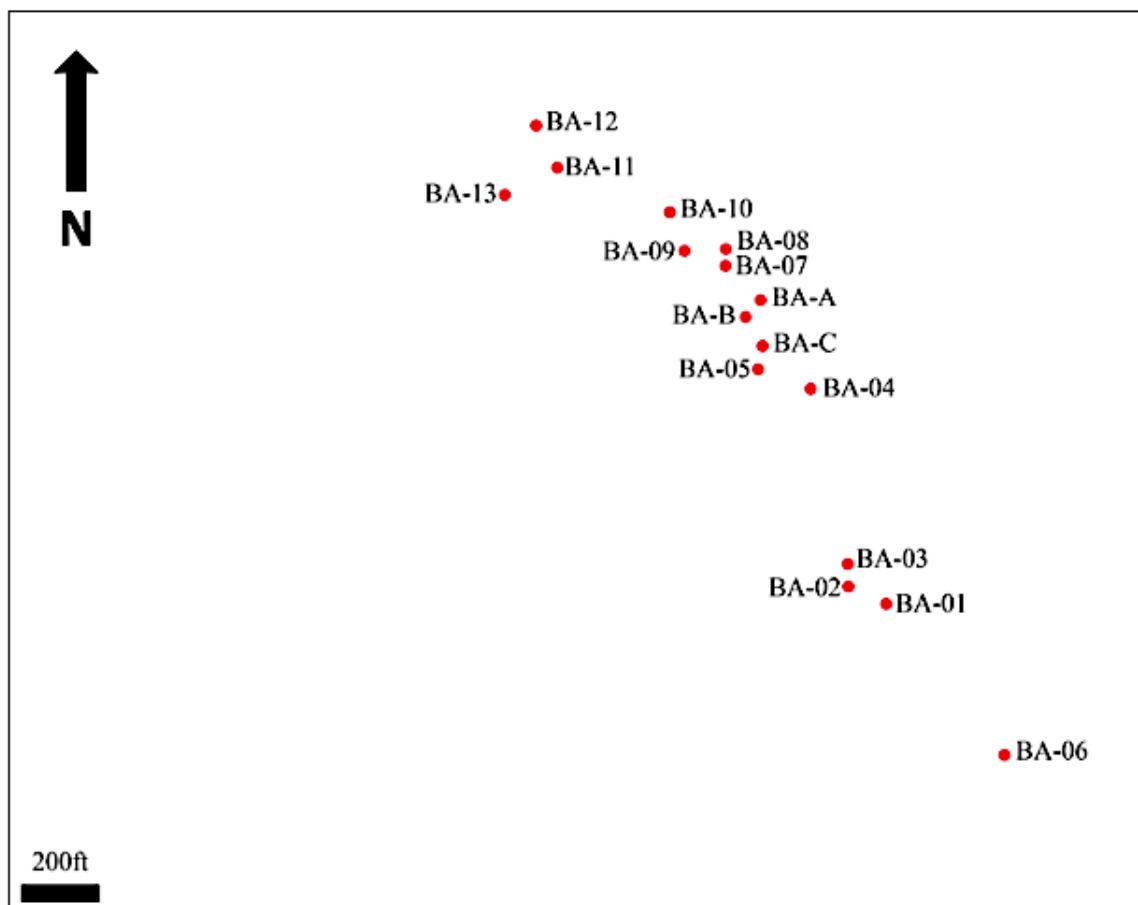


Figure 2.4. Spatial relationships of the harvester anthills at Whitehead Creek.

In addition to several mammalian species previously recognized at other Chadronian-age localities, the Whitehead Creek fauna demonstrates temporal and/or geographic range extensions for several taxa (Arbor & Tornow, 2015). Whereas the Whitehead Creek local fauna is largely consistent with the middle Chadronian, the presence of relict and immigrant taxa provides interesting data that mirrors other Chadronian localities of the Great Plains faunal province (Arbor & Tornow, 2015) – Calf Creek, Saskatchewan, Canada (Storer, 1996; Meyer, 2007);

Medicine Pole Hills, North Dakota (Pearson & Hoganson, 1995; Kihm & Schumaker, 2008; Kihm, 2011, 2013; Kihm & Tornow, 2014); Big Badlands, South Dakota (Clark et al., 1967); “Chadronia” Pocket, northwestern Nebraska (Wood, 1969); and Raben Ranch, northwestern Nebraska (Ostrander, 1980). Relict taxa are taxa that persist in a given area after their extinctions elsewhere.

Several relict taxa have been identified at Calf Creek, Saskatchewan, Canada such as the ischyromyid rodent *Leptotomus* and the Apatemyid *Apatemys* (Storer, 1996; Meyer, 2007). The sciuravid *Prolapsus* and two plesiadapiform primates – *Ignacius* and an unidentified Uintasoricine – have been found at Medicine Pole Hills (Kihm & Tornow, 2014). The omomyoid primate *Mytonius* has been identified at Short Pine Hills (Krishtalka, 1978). Ostrander (1980) identified the omomyoid primate *Chumashius* and the ischyromyid rodent *Leptotomus* at Raben Ranch. Arbor and Tornow (2015) and Tornow and Arbor (2017) have identified several relicts at Whitehead Creek – the plesiadapiform primate *Uintasorex*, an unidentified species of omomyoid primate, possibly two species of the sciuravid *Prolapsus*, the cylindrodontid rodent *Pseudocylindrodon tobei*, the eomyid rodent *Litoyoderimys lustrorum* and the apatemyid *Apatemys*.

This research aims to investigate the circumstances surrounding the persistence of these relict taxa (e.g. primates) at the Whitehead Creek locality. More specifically, it seeks to interpret the environmental conditions that might have allowed these relicts to persist at the Whitehead Creek locality after their extinctions at sites to the west. The goal of this project is to apply an understanding of the relationship between locomotor adaptation among small mammals and the environment to reconstruct the paleoenvironment at Whitehead Creek.

Chapter 3 – Methods

Collection Methods

Fossiliferous matrix is collected from harvester anthills using whisk brooms and dustpans, by sweeping the surfaces of exposures and limited subsurface sampling (Tornow, 2011-2015; Tornow & Arbor, 2017). The matrix is brought back to the Biological Anthropology Laboratory at St. Cloud State, where it is screen washed down to 0.5mm. Once dry, the matrix is size-sorted into four size classes: > 10mm, < 10mm but > 1.4mm, < 1.4mm but > 1.0mm and < 1.0mm but > 0.5mm. Once the matrix is size-sorted, it is probed under a binocular microscope to recover the fossils. Fossils that are collected are put in plastic capsules that are placed inside plastic vials. The plastic vials are labeled with the locality information. Specimen recovery began in 2013 and is ongoing. All specimens are repositied with the University of Montana Paleontology Center (UMPC).

The fossils that are recovered from the matrix represent small mammals. Fossils of medium- and large-sized mammals are not represented at Whitehead Creek, as Whitehead Creek is a micromammal locality. Despite only being able to collect microfossils, small mammals are useful for fine-scale reconstruction of past habitats for a variety of reasons (Leichliter, Sandberg, Passey, Codron, Avenant, Paine, Codron, de Ruiter & Sponheimer, 2017). They occur in many sites (e.g. archaeological and paleontological), and when they are present, they are often abundant; this makes it easy to obtain a large sample size. In addition, small mammals are diverse in habitat preferences and dietary habits (Leichliter et al., 2017). They occur in a wide range of habitats, from desert to forest and unlike larger fauna, small mammals have quite limited lifespans and are therefore both temporally and spatially constrained (Leichliter et al., 2017).

Selection of Elements

The astragalus, calcaneus and terminal phalanx are chosen for analysis because they are well-studied and have been used to reconstruct locomotor behavior in diverse mammalian groups, including primates (Dagosto, 1983, 1986; Gebo, 1986, 1993; Dunn, 2009), “insectivores” (Rose, 1999; Dunn, 2009), rodents (Dunn, 2009; Ginot, Hautier, Marivaux & Vianey-Liaud, 2016) and carnivores (Van Valkenburg, 1987). Macleod and Rose (1993) have demonstrated a relationship between terminal phalangeal morphology and locomotor repertoire across mammalian groups. Once the postcranial bones were selected, they were recovered from the size-sorted matrix that was brought back from the Whitehead Creek locality. A total of 368 specimens (130 astragali, 126 calcanei and 112 terminal phalanges) were recovered.

Data Collection

Before running any analyses on the astragali and calcanei, specific measurements are taken. Total length of the astragalus (TAL), length of the lateral trochlear rim (LTL), length of the medial trochlear rim (MTL), maximum head width (MHW), maximum head height (MHH) and head-neck length are measured for each astragalar specimen when possible (Figure 3.1). Total length (TL), maximum width of the calcaneus (MWC), anterior length (AL), calcaneal neck length (CNL), calcaneal neck width (CNW), calcaneal neck height (CNH), ectal facet length (EFL), ectal facet height (EFH), cuboid facet width (CFW), cuboid facet height (CFH), calcaneal tuber width (CTW), calcaneal tuber height (CTH), sustentacular facet maximum length (SFL), sustentacular facet maximum width (SFW) and sustentacular facet projecting width (SFProj.W) are measured for each calcaneal specimen when possible (Figure 3.2). The astragalar (Figure 3.1) and calcaneal (Figure 3.2) measurements aren't characters, but they are the source of some characters. Quantitatively assessed, astragalar traits that involve astragalar measurements

include the head-neck-length index (HNLI), shape of the navicular facet (SNF) and trochlea symmetry. Quantitatively assessed, calcaneal traits that involve calcaneal measurements include anterior elongation (AE), posterior elongation (PE), morphology of the calcaneal tuber (CTM), outline of the ectal facet (OEF) and shape of the cuboid facet (SCF).

Before astragalar measurements are taken, each astragalus is embedded in some clay – ensuring that it is level. For astragalar length measurements – total astragalar length (TAL), length of the medial trochlear rim (MTL), length of the lateral trochlear rim (LTL) and head-neck length (HNL) – a level orientation involves a dorsal view, with both the medial and lateral trochlear rims being on the same plane. For height and width of the astragalar head (MHH and MHW), each astragalar specimen is oriented so that the head is facing straight up – anterior view. All measurements are made with Mitutoyo digital calipers.

Astragalus Measurements (Figure 3.1)

1. Total length of the astragalus (TAL)- From dorsal view, the TAL is measured from the anterior-most point of the astragalar head, to the posterior-most point on the posterior margin of the trochlear body. Adopted from Dagosto (1986).
2. Length of the lateral trochlear rim (LTL)- From dorsal view, the lateral trochlear rim length will be measured from the anterior-most point of the trochlear rim, to the posterior-most point. Adopted from Ginot et al. (2016).
3. Length of the medial trochlear rim (MTL)- From dorsal view, the medial trochlear rim length will be measured from the anterior-most point of the trochlear rim, to the posterior-most point. Adopted from Ginot et al. (2016).
4. Maximum head width (MHW)- From anterior view, this width extends across the talar head at the two points of greatest width. Adopted from Gebo (1986).

5. Maximum head height (MHH)- From anterior view, this height is measured from the plantar margin to the dorsal margin, just behind the elevated rim of the distal talar head- where the navicular facet starts. Adopted from Gebo (1986).

6. Head-neck length (HNL)- From dorsal view, this is the distance between the most distal point of the trochlea and the most distal point of the astragalar head. Adopted from Dagosto (1986).

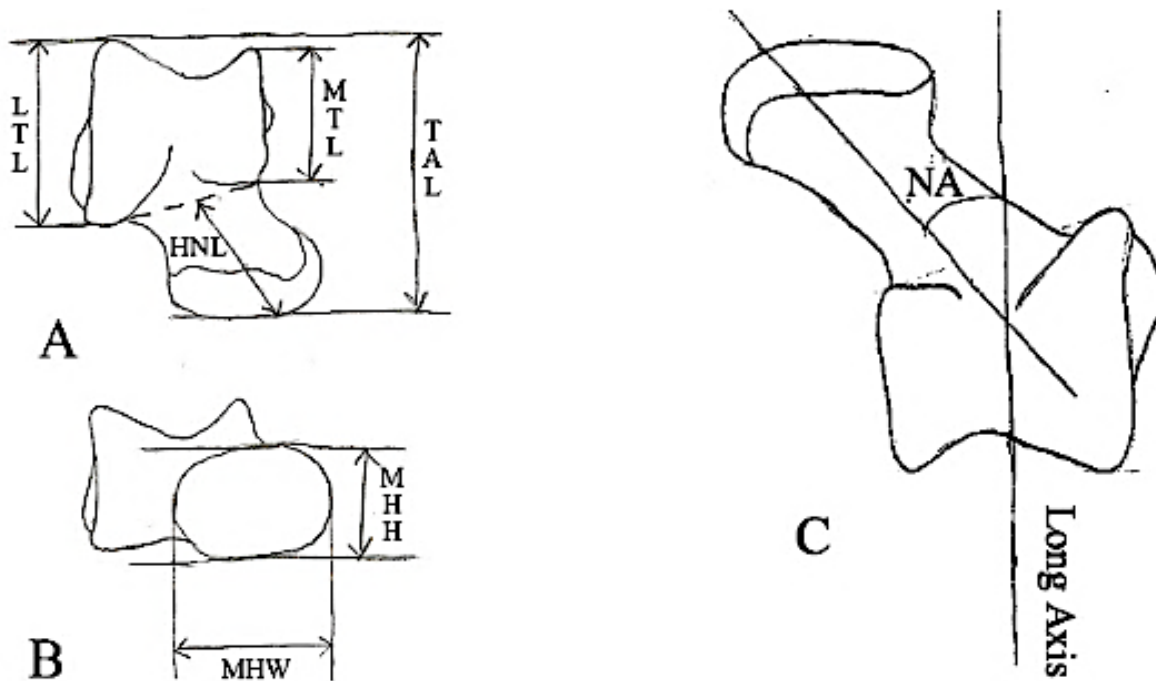


Figure 3.1. A: right astragalus in dorsal view. Anterior is down. TAL (Total Length of the Astragalus), HNL (Head-Neck Length), MTL (Length of the Medial Trochlear Rim) and LTL (Length of the Lateral Trochlear Rim). B: right astragalus in anterior view. MHW (Maximum Head Width) and MHH (Maximum Head Height). C: right astragalus in dorsal view. Anterior is up. NA (Astragalar Neck Angle).

Before calcaneal measurements are taken, each calcaneus is embedded in some clay – ensuring that it is level. For most of the calcaneal length and width measurements – total length (TL), maximum calcaneal width (MaxCalc.W.), anterior length (AL), calcaneal neck length (CNL), calcaneal neck width (CNW), ectal facet length (EFL), sustentacular facet length (SFL), sustentacular facet width (SFW) and sustentacular facet projecting width (SFProj.W.) – a level

orientation involves dorsal view, with the sustentacular facet and the peroneal process on a level plane that is parallel with the surface of the table. Cuboid facet width (CFW) and cuboid facet height (CFH) involve an anterior view, with the cuboid facet facing straight up. Measuring the height of the ectal facet (EFH) involves a lateral view with the bone oriented so that the sustentacular facet – which lies on the medial side of the bone – is facing straight down. The bone must also be parallel (or level) with the surface of the table. Measuring the width and height of the calcaneal tuber (CTW and CTH) involves a posterior view. The cuboid facet is placed straight down which results in the calcaneal heel facing straight up. Calcaneal neck height (CNH) can be measured in either medial (with the peroneal process [on the lateral side of the bone facing] straight down) or lateral view (with the sustentacular facet [on the medial side of the bone] facing straight down). All measurements are made with Mitutoyo digital calipers.

Calcaneus Measurements (Figure 3.2)

1. Total length of calcaneus (TL)- TL measures from the anterior-most point of the cuboid facet to the posterior-most point of the heel (i.e. spans the length of the entire bone).
2. Maximum width of the calcaneus (MWC)- The MWC is measured from the medial edge of the sustentacular facet to the lateral edge of the peroneal process (Gebo, 1986).
3. Anterior length (AL)- The AL will be measured from the anterior margin of ectal facet to anterior-most point of the cuboid facet.
4. Heel (neck) Length (CNL)- The CNL will be measured from the posterior margin of the ectal facet to the posterior-most point of the heel.
5. Heel (neck) Total Width (CNW)- This is a measurement of the widest point of the neck. I will be measuring from the lateral point to the medial point.

6. Heel (neck) total height (CNH)- This height is the most proximal heel height measured and extends from the plantar edge of the calcaneal heel to the dorsal edge (Gebo, 1986).
7. Length of the Ectal Facet (EFL)- EFL will be measured from the anterior-most point to the posterior-most point of the ectal facet.
8. Height of the Ectal Facet (EFH)- EFH will be measured from the midpoint of the base of the ectal facet to the highest point on the dorsal surface of the facet.
9. Cuboid facet width (CFW)- The CFW is measured from the medial-most point to the lateral-most point of the cuboid facet (anterior view) (Dagosto, 1986).
10. Cuboid facet height (CFH)- The CFH is measured from the plantar-most point to the dorsal-most point of the cuboid facet (anterior view) (Dagosto, 1986).
11. Calcaneal tuber maximum width (CTMW)- The CTMW is measured from the medial-most point to the lateral-most point of the calcaneal tuber (posterior view) (Ginot et al., 2016).
12. Calcaneal tuber maximum height (CTMH)- The CTMH is measured from the plantar-most point to the dorsal-most point of the calcaneal tuber (posterior view) (Ginot et al., 2016).
13. Sustentacular facet maximum length (SFL)- The SFL is measured from the most proximal point (posterior) to the most distal point (anterior) of the sustentacular facet (Gebo, 1986).
14. Sustentacular facet maximum width (SFW)- The SFW is measured from the most medial point to the most lateral point of the sustentacular facet (Gebo, 1986).
15. Sustentacular facet projection width (SFPW)- This width extends from the medial edge of the ectal facet to the medial edge of the sustentacular facet (Gebo, 1986).

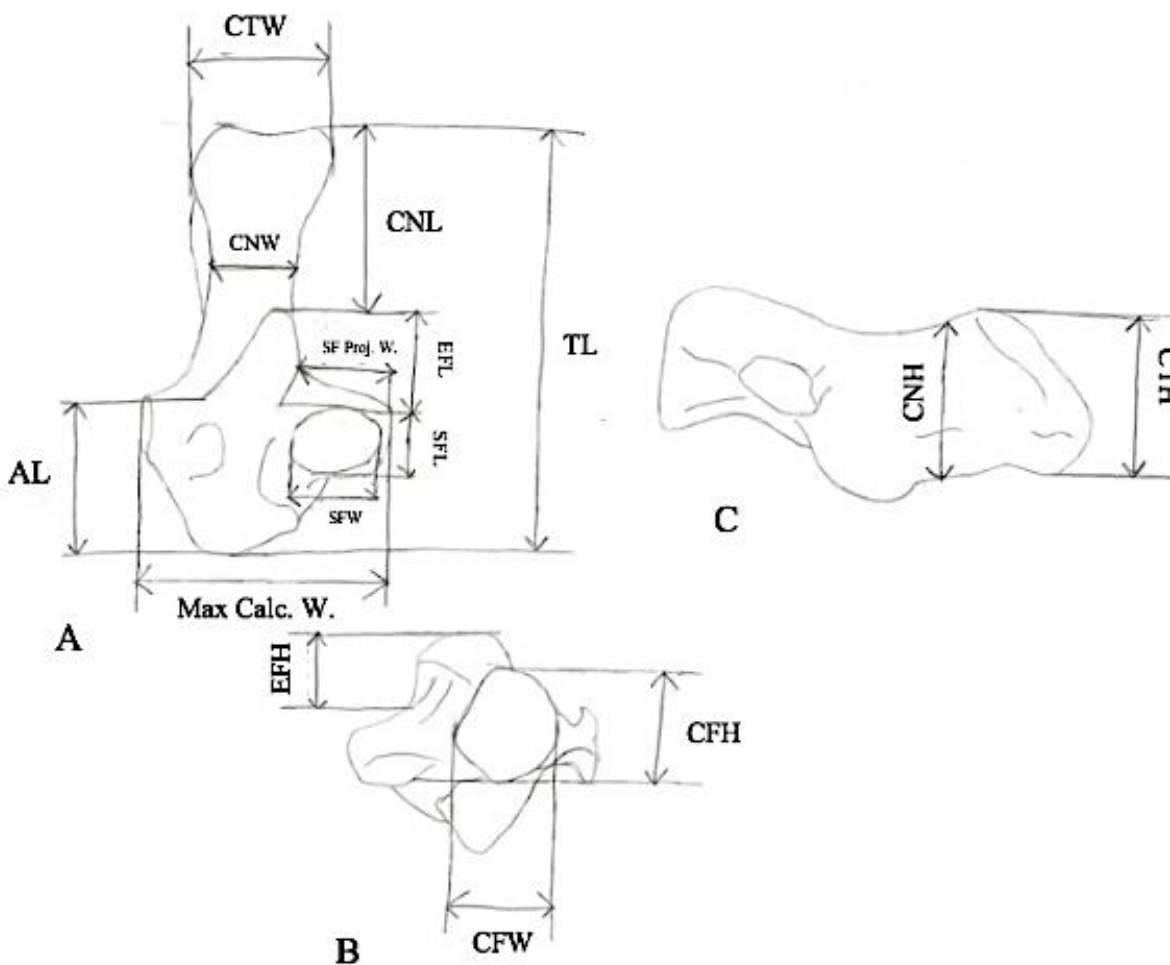


Figure 3.2. A: Right calcaneus in dorsal view. Anterior is down. TL (Total Length), AL (Anterior Length), MaxCalc.W. (Maximum Width of the Calcaneus), CNL (Calcaneal Neck Length), CNW (Calcaneal Neck Width), CTW (Calcaneal Tuber Width), EFL (Ectal Facet Length), SFL (Sustentacular Facet Maximum Length), SFW (Sustentacular Facet Maximum Width) and SFProj.W (Sustentacular Facet Projecting Width). B: Left calcaneus in anterior view. Medial is to the left. EFH (Ectal Facet Height), CFH (Cuboid Facet Height) and CFW (Cuboid Facet Width). C: Right calcaneus in lateral view. Anterior is to the right. CNH (Calcaneal Neck Height) and CTH (Calcaneal Tuber Height).

The University of North Carolina (2011) outlines four sources of measurement error.

“Zero offset”, a systematic error, occurs when taking measurements with a digital caliper. The zero reading may provide a negative number. In this case, the digital caliper must be “re-zeroed” so that it reads “0”. Failure to re-zero a digital caliper will result in constant error that is more

significant for smaller values than larger values. This type of systematic error was accounted for by “zeroing out” the digital caliper before every measurement was taken. “Parallax”, a systematic and/or random error, occurs whenever there is some distance between the object that is being measured and the person that is doing the measuring. If the observer’s eye is not squarely aligned with the part of the bone that is being measured, then the measurement(s) will be off. In this project, all of the tarsal specimens average 2-5mm in total length. Due to the small size of the specimens, all measurements were taken with the aid of a binocular microscope.

“Incomplete definition”, a systematic and/or random error, occurs when the measurement is not clearly defined. All measurements must be clearly defined so that when other people take the same measurement(s) they get the same, or nearly the same, results. To account for “incomplete definition”, all measurements were clearly defined so that they were replicable.

“Personal error” is another type of error that may affect the measurements used in this project. Personal errors come from carelessness, poor technique, or bias on the part of the person taking the measurements. “Personal error” was addressed by having randomly chosen five astragali and four calcanei and re-taking all of the appropriate measurements. An average error rate was calculated for each bone type. The five astragali had an average error rate of 0.014666667. One standard deviation for this error rate was 0.07. The four calcanei had an average error rate of 0.061666667. One standard deviation for this error rate was 0.29. Both average error rates are less than one tenth; this suggests that all of the initial measurements that were taken for all specimens of each bone type were fairly accurate.

Morphospecies

Specimens that are identical (or nearly identical) in size and shape might represent the same species. Only individual, unique specimens will be used to evaluate the paleoenvironment

of Whitehead Creek; this is to ensure an accurate representation of the Whitehead Creek faunal list. Principal Components Analysis (PCA) is used to identify specimens that are of the same size and shape. Side-by-side comparison of the specimens is performed to identify duplicate morphospecies. It is difficult to compare 100+ specimens side-by-side; thus, PCA is used to reduce the number of side-by-side comparisons that I would have to make. Those specimens that cluster together (particularly for Principal Component [PC] 1 – size) might be the same morphospecies.

Measurement data for each bone type (astragalus and calcaneus) is inputted into the statistical package, PAST3.22. Before running separate PCA analyses of the astragalus and calcaneus samples, badly damaged specimens were removed, along with any specimens that had either no measurement data, one measurement or two measurements; only astragali and calcanei with three or more measurements were included in their respective analysis. A PCA is run on a sample of 62 astragali (out of a total of 130) and 78 calcanei (out of a total of 126). After the PCAs are run, tight clusters of astragalar and calcaneal specimens are identified. Specimens in these tight clusters are visually assessed, and if any two are found to be identical (or nearly identical) in size and shape, only the more complete specimen is included in the final sample. The PCA results for the astragalus sample are given in Table 3.1. The first four principal components account for 98.0761% of the variance. Graphical representations of principal component one versus two, and two versus three, are provided in Figures 3.3 and 3.4 – respectively.

Table 3.1. Eigenvalues and percent variance of the PCA on the astragalus sample.

PC	Eigenvalue	% variance
1	1.20039	76.988
2	0.228433	14.651
3	0.0679215	4.3562
4	0.0324458	2.0809

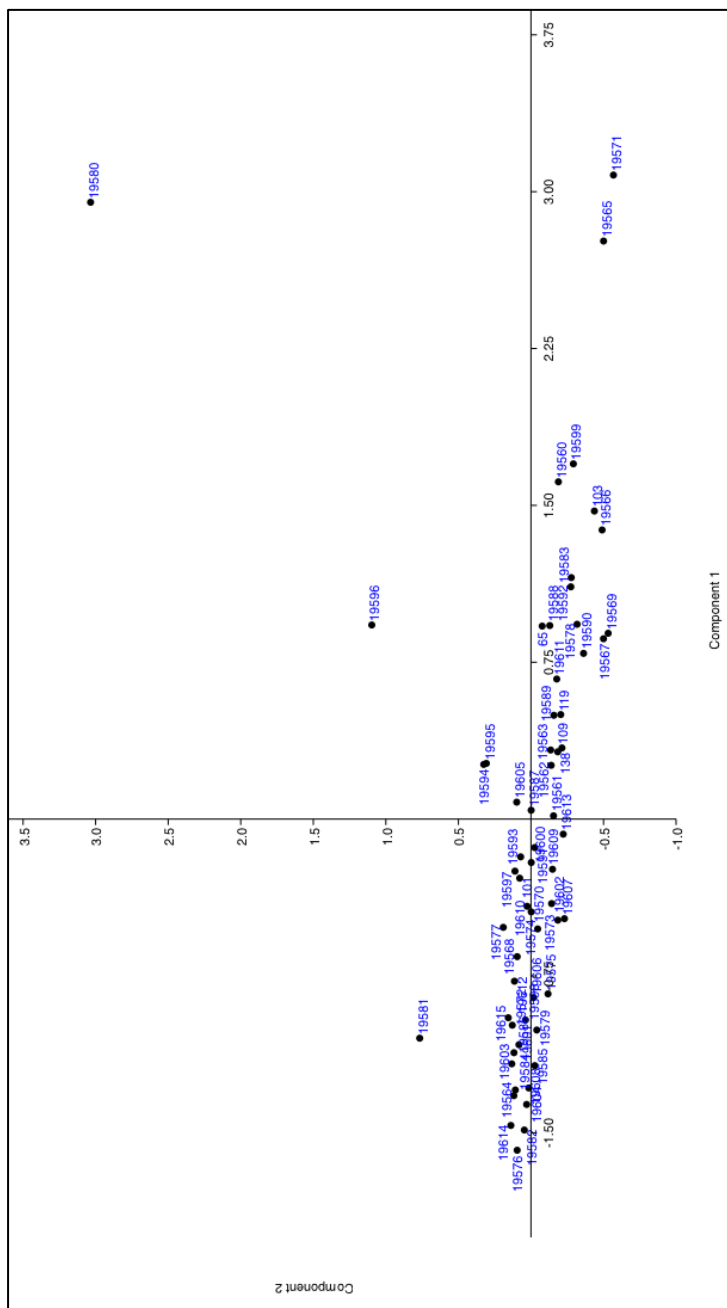


Figure 3.3. Results of PCA of astragalus sample: Component 1 versus Component 2.

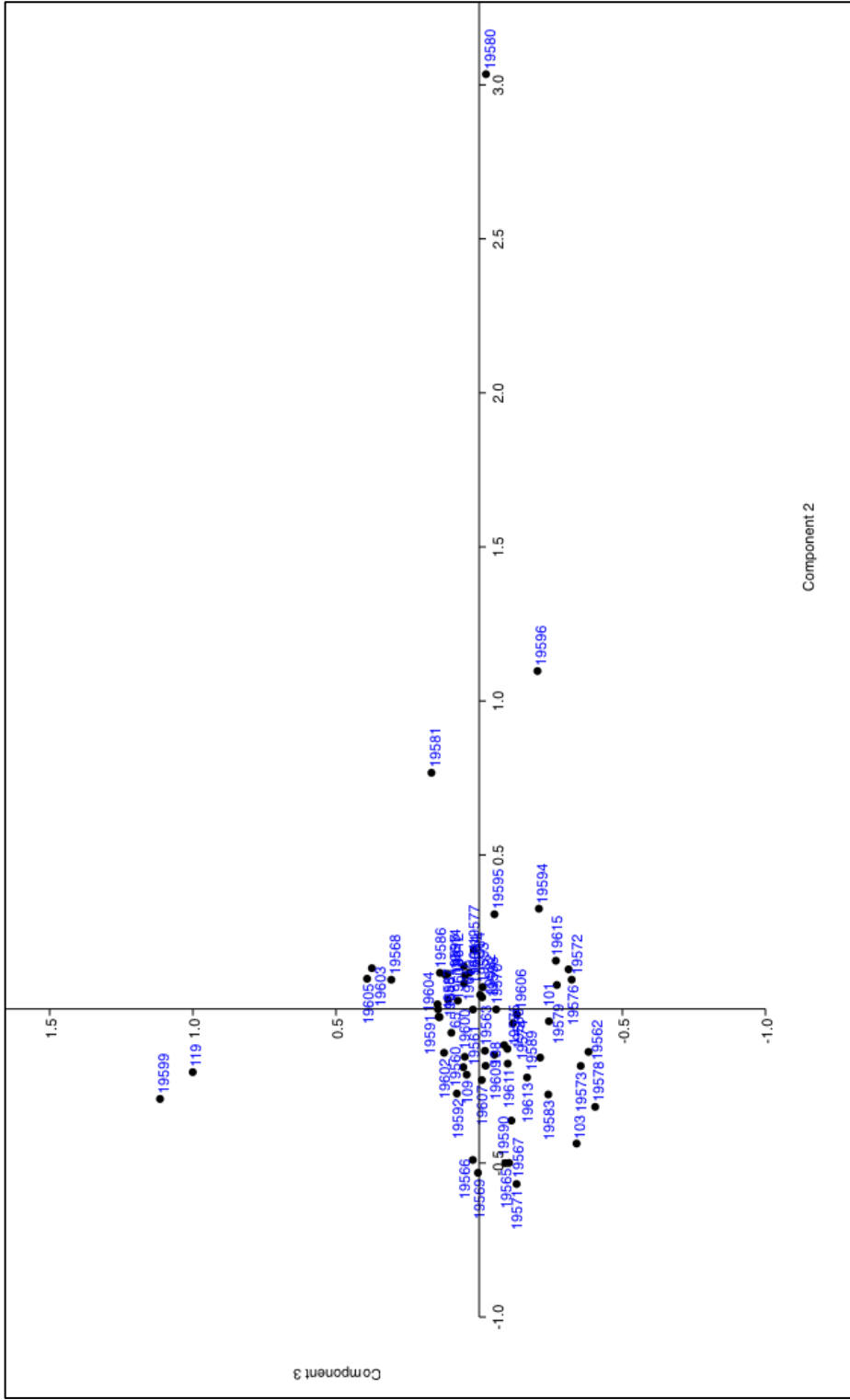


Figure 3.4. Results of PCA of astragalus sample: Component 2 versus Component 3.

The eigenvectors for astragali are provided in Table 3.2. An eigenvector of > 0.4 (or -0.4) is considered to be a strong loading. Thus, measurements (traits) that are > 0.4 (or -0.4) show strong positive (or negative) loadings respectively. PC 1 is always driven by size; in this case, size is represented by total astragalar length (TAL). This is important for this analysis because bones of similar size (i.e. that are similar in TAL) are likely representative of the same species. This is particularly true among species that lack sexual size dimorphism, which is the case for micromammals (personal communication, Dr. Matthew Tornow). PC 2 is driven by shape. In this case, shape is represented by TAL, maximum head width (MHW) and head-neck length (HNL). The eigenvalue for PC 3 (0.0679215) is being driven by medial trochlear length (MTL) and HNL. PC 4 (0.0324458) is being driven by length of the lateral trochlear rim (LTL), MHW and HNL.

Table 3.2. Eigenvectors for the astragalus sample.

	PC 1	PC 2	PC 3	PC 4
TAL	0.62006	-0.60001	-0.11298	-0.16205
LTL	0.33379	-0.32052	-0.15914	0.47368
MTL	0.33794	0.072325	0.83293	-0.30338
MHW	0.36008	0.45642	-0.010388	0.52791
MHH	0.31524	0.34798	0.14282	0.25308
HNL	0.40109	0.45013	-0.49762	-0.56089

The PCA results for the calcaneus sample are given in Table 3.3. The first three principal components account for 99.491% of the variance. Graphical representations of principal component one versus two, and two versus three, are provided in Figures 3.5 and 3.6 – respectively. The eigenvectors for calcanei are provided in Table 3.4. The eigenvalue for PC 1 (246.754) is being driven by the angle of the cuboid facet (CF ANGLE) and the height of the cuboid facet (CFH). The eigenvalue for PC 2 (93.972) is being driven by the CF ANGLE and the

CFH. The eigenvalue for PC 3 (76.096) is being driven by the angle of the ectal facet (EF ANGLE).

Table 3.3. Eigenvalues and percent variance of the PCA on the calcaneus sample.

PC	Eigenvalue	% variance
1	246.754	58.898
2	93.972	22.43
3	76.096	18.163

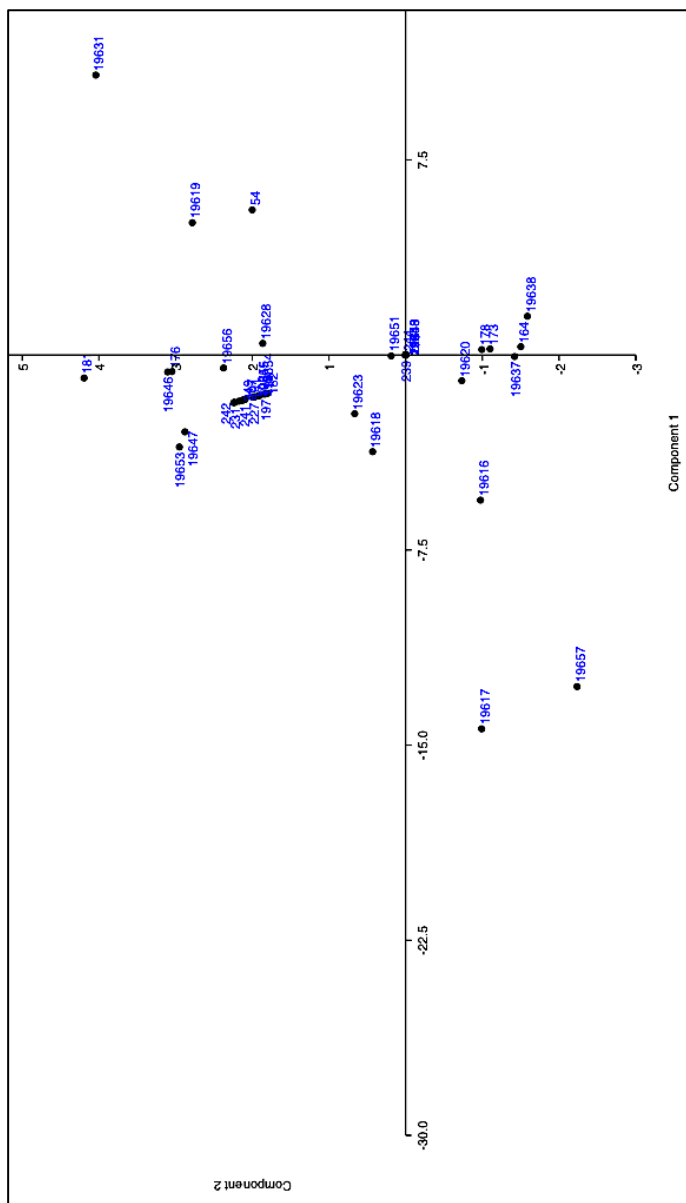


Figure 3.5. Results of PCA of calcaneus sample: Component 1 versus Component 2.

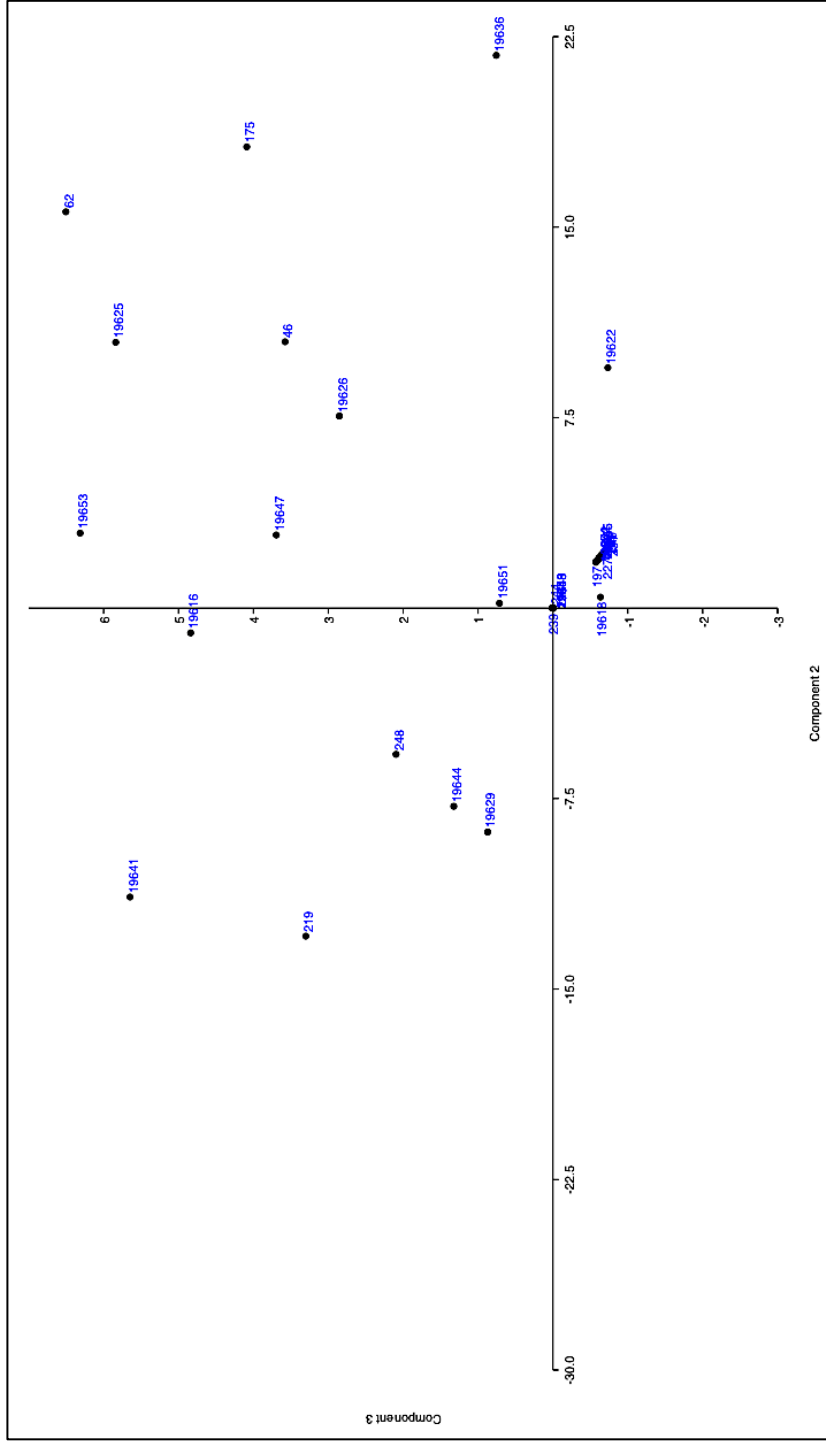


Figure 3.6. Results of PCA of calcaneus sample: Component 2 versus Component 3.

Table 3.4. Eigenvectors for the calcaneus sample.

	PC 1	PC 2	PC 3
TL	-0.0032124	0.013265	-0.011172
Max Calc. W.	0.00027005	-0.0014406	-0.0039586
AL	-0.0018365	0.0043735	-0.0069314
CNL	-0.0022543	0.0024596	-0.00035559
CNW	2.5842E-05	0.0039302	-0.0045135
CNH	-0.0013416	0.0025261	-0.0038763
EFL	0.00072543	-0.001675	-0.0056009
EFH	0.0017749	-0.0036124	-0.0034066

Table 3.4 (continued)

CFW	-0.00067076	0.0025474	-0.0041329
CFH	0.61523	-0.75244	0.23444
CTW	0.00046209	-0.00035827	-0.0021967
CTH	0.0014225	0.0016447	-0.0030534
SFL	0.0025321	-0.0053402	-0.0063806
SFW	0.00063229	-0.00085096	-0.00074974
SF Proj. W.	-0.00076814	-0.0022702	-0.0022599
AE	0.00022862	-0.00025965	0.0004586
PE	-0.00013724	-0.00068332	0.00094102

Table 3.4 (continued)

CNTW	0.00018255	0.0012815	-9.7361E-05
OEF	-0.0025461	0.0040436	-0.0029442
SCF	0.000845	0.00077173	0.0013745
CF ANGLE	0.78646	0.60638	-0.11706
EF ANGLE	-0.05411	0.25657	0.96487

Terminal phalangeal morphospecies were not identified due to the difficulty of assessing whether the specimens were manual or pedal, left or right and whether they were from digits one through five. A final sample of 55 terminal phalanges was obtained by removing any and all heavily damaged specimens from the overall sample of 112.

Character Definitions

With a final sample of 56 astragali (representing 56 morphospecies) and 44 calcanei (representing 43 morphospecies), morphological characters of the astragalus (Figures 3.7-3.12) and calcaneus (Figures 3.13-3.22) are identified. These characters have already been established in the literature using the comparative method (Dunn, 2009; Ginot et al., 2016) and the biomechanical method (Dagosto, 1983, 1986; Gebo, 1986, 1993; Carrano, 1997). Whereas the comparative method involves analyzing extant mammals with similar locomotor adaptations to see

how they move under various ecological constraints, the biomechanical method involves analyzing bones, joints and muscles as a system of struts and levers. The comparative and biomechanical methods are two different approaches to a much broader method known as functional morphology. Functional morphology is the study of the relationship between form and function (Bock & von Wahlert, 1965).

Form is the appearance (i.e. shape or structure) of a particular feature and function is the action of the feature or how it works. Form and function are combined to create the form-function complex, otherwise known as the faculty of a feature (Bock & von Wahlert, 1965). The faculty, comprising a form and a function of a particular feature, is what the feature is capable of doing in the life of the organism and is the unit that bears a relationship to the environment in which the organism resides (Bock & von Wahlert, 1965). The faculty is acted upon by natural selection and is the aspect of the feature adapted to the environment. The faculty is, therefore, the evolutionary unit of the feature.

Functional morphology is a part of a much broader method known as ecomorphology. Ecomorphology is the study of the link between the structure of an organism and the environment in which it occurs (Bock, 1994; Dunn, 2009); it involves the covariation of morphology and ecology (Bock, 1994). This method assumes that morphology reflects the interaction between an organism and its environment, and theoretically, that postcranial morphology will covary with habitat structure because postcrania must allow the organism to function or move about effectively in its habitat. Ecomorphology also involves assessing whether individual mammalian lineages are adapting to changing environments at a single locality, or multiple localities, over time (Bock, 1994; Dunn, 2009). Ecomorphology, the main method used

in this project, is modified and used in a novel way. This project concentrates on a single locality, the Whitehead Creek locality, at a single point in time, the middle Chadronian.

Following are descriptions of the astragalar (Figures 3.7-3.12) and calcaneal characters (Figures 3.13-3.22), along with a discussion of the utility of each in discerning locomotor adaptations in small mammals. These tarsal characters reflect locomotor function within seven broad categories of locomotor behavior – arboreal leaping, terrestrial leaping (i.e. hopping), terrestrial running (i.e. cursorial), arboreal climbing (i.e. restricted to the trees; stays off of the ground), scansorial climbing (i.e. may frequent the ground; e.g. a squirrel), digging (i.e. fossorial) and swimming (i.e. semi-aquatic or natatorial). Identifying morphological characters in small, semi-aquatic mammals is difficult. Morphological characters will differ depending on the taxon (Salton and Szalay, 2004), how much time is spent in the water and the types of activities performed there (Stein, 1988); also, many terrestrial mammals (of various sizes) can swim, using cranio-caudal movements of the hind feet and/or forefeet (Wada, n.d.). These reasons make identifying semi-aquatic tarsal characters in the fossil record difficult; there are too many confounding variables. This difficulty prevents researchers from naming and describing small, semi-aquatic mammals in the fossil record – thus, there are very few (if any) articles to adopt semi-aquatic tarsal characters from. Dunn (2009) describes tarsal remains of fossil *Pantolestids*. A *Pantolestid* astragalus (20mm) is roughly six times larger than the average size of astragalar specimens used in this project (2-4mm). Morphological characters identified in medium and large, semi-aquatic taxa are not always present in small, semi-aquatic taxa mainly due to differences in body size (Stein, 1988; Salton & Szalay, 2004). In addition to Dunn (2009), semi-aquatic tarsal characters are also adopted from Ginot et al. (2016). Ginot et al. (2016) evaluate morphological characters of extant rodent taxa that exhibit different locomotor behaviors, but

most of these taxa are medium – large-sized. Any extant mammal that weighs more than 1,000g is too large to include in this study, as all of the postcranial elements (astragali, calcanei and terminal phalanges) recovered from Whitehead Creek represent small mammals. Given these challenges, semi-aquatic tarsal characters are adopted from Dunn (2009) and Ginot et al. (2016).

Astragalus Traits

A1. Trochlea Symmetry – Trochlea Symmetry (TS) = MTL/LTL (qualitative and quantitative; Figure 3.7; individual measurements given in Figure 3.1)

A1a. Marked Asymmetry (TS is ≤ 0.731): The medial trochlear rim is substantially shorter (in length and height) than the lateral trochlear rim (Dunn, 2009; Rose, Storch & Krohmann, 2015; Ginot et al., 2016).

A1b. Some Asymmetry (TS is > 0.731 but < 0.917): The medial trochlear rim is shorter (in length and height) than the lateral trochlear rim, but the differences aren't substantial (Ginot et al., 2016).

A1c. Symmetrical (TS is > 0.917 but ≤ 1): The trochlear rims are relatively equal in length, height, and shape (Ginot et al., 2016).

Marked asymmetry is representative of arboreal climbers, scansorial and fossorial taxa, while some asymmetry is representative of leaping (arboreal and terrestrial) and terrestrial generalist taxa (Dunn, 2009; Rose et al., 2015; Ginot et al., 2016). Marked asymmetry and some asymmetry add a transverse component to the plantar and dorsiflexion of the foot, so that as the foot plantar- or dorsiflexes it also inverts or everts (Ginot et al., 2016). This combination of movements allows the foot to adapt to uneven substrates. A symmetrical trochlea is representative of cursorial and semi-aquatic taxa. A reduction of the asymmetry means that the

foot will stay in the parasagittal plane during plantar- and dorsiflexion, allowing for more efficient running or paddling (Ginot et al., 2016).

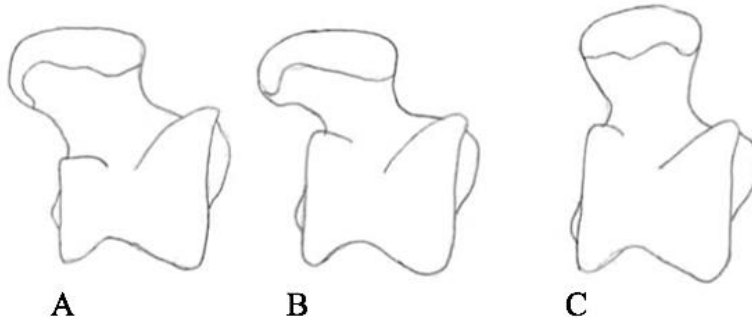


Figure 3.7. A, B and C: right astragalus in dorsal view. Anterior is up. A) is marked asymmetry, B) is some asymmetry, and C) is symmetrical.

A2. Length of Astragalar Neck and Head- Neck Length Index (HNLI) = $HNL/LTL \times 100$

(quantitative; individual measurements given in Figure 3.1)

A2a. Short: $HNLI \leq 0.50$

A2b. Intermediate: < 1 but > 0.50

A2c. Long: $HNLI \geq 1$

The HNLI is adopted from Dagosto (1983) and modified to take into account taxa other than primates. Using LTL alleviates uncertainty that comes from estimating body length when there is trochlear asymmetry. Semi-aquatic taxa have a short HNL. Whereas Ginot et al. (2016) suggest that a short HNL indicates less flexibility of the foot in regard with the ankle, Dunn (2009) suggests that a short astragalar neck, together with a short distal calcaneus, indicates that the organism is not a swift, terrestrial runner (i.e. it is not a cursor).

Cursorial, climbing, terrestrial generalist and fossorial taxa have an intermediate HNL. In cursorial taxa, the neck is lengthened antero-posteriorly. In generalist, climbing and fossorial taxa, the neck is lengthened, in part because it is deviated medially. An elongated and/or medially deflected neck increases the articular surface of the plantar sustentacular facet, along

which the calcaneus may slide (Ginot et al., 2016). Furthermore, the orientation of the sustentacular facet, following the axis of the neck, favors medial-lateral movements, which are required during inversion and eversion of the foot as it is adapting to uneven substrates (Chester, Bloch, Boyer & Clemens, 2015; Ginot et al., 2016).

Leaping (arboreal and terrestrial) taxa have a long HNL (Rose, 1999; Fostowicz-Frelik, 2007). The astragalar head is placed posteriorly in relation to the distal end of the calcaneus. This strengthens and stabilizes the ankle joint and limits mobility of the foot only to plantarflexion and dorsiflexion. This feature is enhanced by elongation of the astragalar neck (Fostowicz-Frelik, 2007).

A3. Astragalar Neck Angle (quantitative; measurement is given in Figure 3.1)

A3a. medially deflected, high angle $> 35^\circ$

A3b. medially deflected, moderate angle $< 35^\circ$ but $> 25^\circ$

A3c. little deflection, almost in-line with the long axis of the bone $< 25^\circ$

Neck angles fall into three distinct categories. Climbing and fossorial taxa have a medially deflected, high neck angle, whereas generalist and semi-aquatic taxa have a medially deflected, moderate neck angle. Medial deflection of the astragalar neck allows for, and enhances, transverse (i.e. medial-lateral) movements of the calcaneus below the astragalus (Ginot et al., 2016). Transverse movements allow the organism to adapt its foot to uneven substrates (Ginot et al., 2016).

Leaping (arboreal and terrestrial) and cursorial taxa exhibit a neck that has little medial deflection and is almost in-line with the long axis of the bone. As a consequence, the sustentacular facet is always oriented antero-posteriorly. This greatly reduces the transverse

movements of the calcaneus below the astragalus, making inversion or eversion of the foot extremely difficult or impossible (Ginot et al., 2016).

A4. Orientation of the Ectal Facet (qualitative; Figure 3.8)

A4a. Plantar

A4b. Lateral

The ectal facet is generally strongly projected laterally for leaping (arboreal and terrestrial) and cursorial taxa. This limits the transverse and anteroposterior mobility of the astragalus with regard to the calcaneus. As a result, these bones are more tightly linked, which allows for them to move as a single unit or complex rather than as independent entities (Ginot et al., 2016). Generalist, climbing, fossorial and semi-aquatic taxa have an ectal facet that is oriented more plantarly. This allows for increased mobility between the astragalus and calcaneus at the subtalar joint (STJ) (Ginot et al., 2016), thus allowing the organism to adapt its foot to uneven substrates (i.e. generalist, climbing and fossorial taxa) or to move more effectively and efficiently in the water (i.e. semi-aquatic taxa).

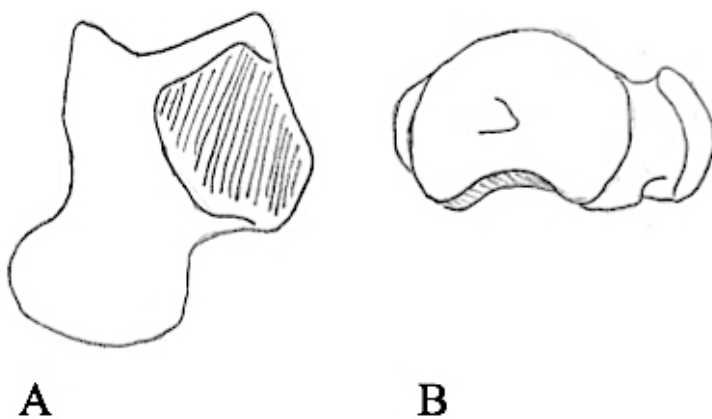


Figure 3.8. A: right astragalus in plantar view. Anterior is down. The ectal facet (shaded region) is oriented more plantarly. B: right astragalus in lateral view. Anterior is to the right. The ectal facet (shaded region) is oriented laterally.

A5. Trochlear Depth (qualitative; Figure 3.9)

A5a. deep

A5b. moderate

A5c. shallow

Trochlear depth is a qualitative assessment of how deep or shallow the trochlear surface is. Leaping (arboreal and terrestrial) and cursorial taxa have a deeply grooved trochlear surface (Van Valkenburgh, 1987; Dunn, 2009; Rose et al., 2015; Ginot et al., 2016). A deep trochlear groove is where both the medial and lateral trochlear rims are well-defined and steep. A deeply grooved trochlea provides the most stability to the upper ankle joint (UAJ), constraining movements to the parasagittal plane, mainly flexion/extension.

Scansorial (Ginot et al., 2016), generalist (Dunn, 2009; Ginot et al., 2016) and semi-aquatic (Dunn, 2009; Ginot et al., 2016) taxa have a moderately grooved trochlear surface. A moderate trochlear groove is defined by a “checkmark”-shaped trochlea – when viewed posteriorly (Ginot et al., 2016). Generally, the lateral trochlear rim is greater in height than the medial trochlear rim. A moderately grooved trochlea allows for some mobility of the UAJ.

Fossorial and arboreal climbing taxa have a shallow trochlear surface (Ginot et al., 2016). A shallow trochlear groove is where both the medial and lateral trochlear rims are really low in height; there is virtually no definition of the medial and lateral trochlear rims (Ginot et al., 2016). This allows for the greatest mobility of the UAJ. It allows for flexion/extension and inversion/eversion movements.

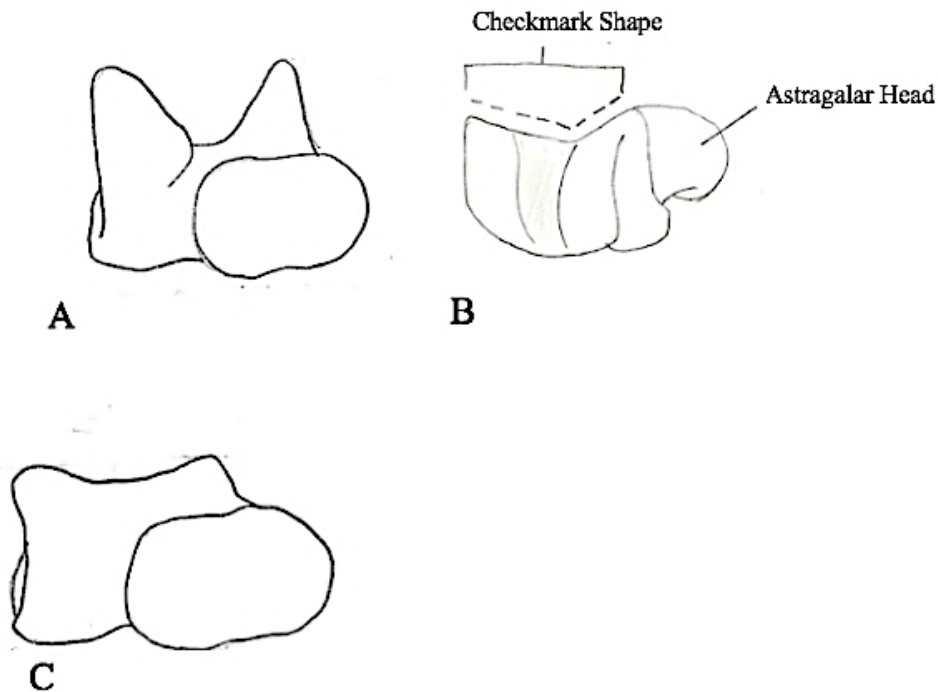


Figure 3.9. A: Right astragalus in anterior view showing deep trochlear depth. B: Left astragalus in posterior view showing moderate trochlear depth. C: Right astragalus in anterior view showing shallow trochlear depth.

A6. Shape of the navicular facet – Shape of the navicular facet (SNF) = MHW/MHH (qualitative and quantitative; Figure 3.10; individual measurements given in Figure 3.1)

A6a. round: < 1.1

A6b. ovoid: ≥ 1.1 but ≤ 1.636

A6c. ellipsoid: > 1.636

A6d. subcylindrical: visual assessment only

Arboreal leapers (Dagosto, 1986; Gebo, 1986, 1993), arboreal climbers (Dunn, 2009; Ginot et al., 2016) and terrestrial generalists (Ginot et al., 2016) display a round head, while scansorial (Dunn, 2009; Ginot et al., 2016), terrestrial leaping (Ginot et al., 2016) and semi-aquatic taxa (Dunn, 2009; Ginot et al., 2016) will display an ovoid shape of the navicular facet.

A round shape of the navicular facet indicates a highly mobile transverse tarsal joint (TTJ), whereas an ovoid shape of the navicular facet indicates a semi-mobile TTJ. If the shape of the navicular facet is more ellipsoid, there is less mobility at the TTJ. In this instance, movements at the TTJ are mainly constrained to medial and lateral movements only, rather than having a full range of motion. Cursorial (Rose et al., 2015; Ginot et al., 2016) and fossorial (Ginot et al., 2016) taxa exhibit this trait. The subcylindrical shape of the navicular facet is a diagnostic trait of lagomorphs only (Rose, DeLeon, Missiaen, Rana, Sahni & Smith, 2008). A subcylindrical shape is defined as being medio-laterally narrow and dorso-ventrally elongate; also, the astragalar head is slightly offset medially relative to the trochlear groove (Rose et al., 2008). In anterior view, the shape of the navicular facet may appear to be rectangular but with slightly rounded edges.

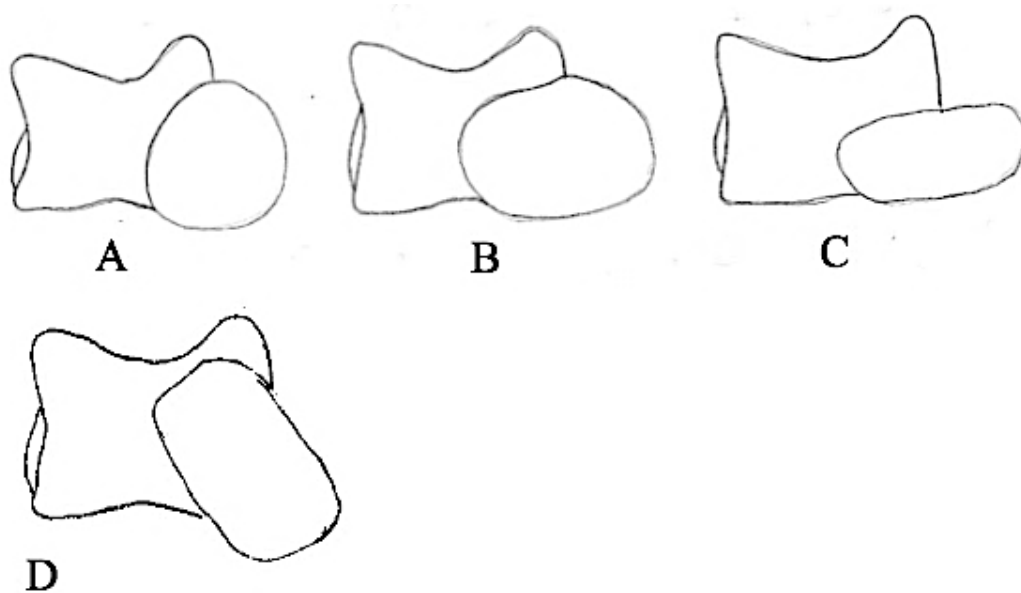


Figure 3.10. Right astragali in anterior view showing A: round, B: ovoid, C: ellipsoid, and D: subcylindrical astragalar heads.

A7. Squatting facet (qualitative; Figure 3.11)

A7a. present

A7b. absent

A squatting facet is defined as a facet on the dorsal surface of the astragalar neck that is bounded medially by a bony ridge (Dunn, 2009). The presence of a squatting facet can be diagnostic of habitual hyper-dorsiflexed or crouched squatting postures. The presence of this facet indicates that the astragalus came into repeated and prolonged contact with the tibia during dorsiflexion. A squatting facet can also be obtained through heritage rather than habitus. The following are examples of taxa that have obtained a squatting facet through their heritage: hedgehogs, tenrecs, lagomorphs and Macrocelideans (Dunn, 2009).



Figure 3.11. Right astragalus in dorsal view. Anterior is up. The squatting facet (shaded region) is separate from the trochlear surface and is bounded medially by a ring of bone. This trait is adopted from Ladeveze, Missiaen and Thierry (2010).

A8. Extension of the trochlea onto the astragalar neck (qualitative; Figure 3.12)

A8a. present: trochlear surface extends onto the dorsal surface of the astragalar neck

A8b. absent: trochlear surface does not extend onto the dorsal surface of the astragalar neck

This trait is adopted from Chester et al. (2015). According to Chester et al. (2015), extension of any part of the trochlea onto the dorsal surface of the astragalar neck is consistent with mammals whose feet abduct during dorsiflexion for climbing on vertical supports. This trait is modified to take into account the presence of a squatting facet. According to Dunn (2009), the presence of a squatting facet on the neck of the astragalus of *Ourayia* and *Chipetaia* suggests that the tibia and astragalus came into contact during dorsiflexion, which is known to occur in primates that demonstrate vertical clinging and leaping. However, the presence of this facet has been found to be nearly ubiquitous in many groups of primates, including those that do not engage in vertical clinging and leaping behavior, and has been suggested to be primitive for omomyids (Dagosto, 1985). This feature may also be indicative of plantigrade locomotion, where the knee is habitually bent. This requires a high degree of dorsiflexion (Dagosto, 1985).

In humans, a squatting facet exists in high frequencies in populations that habitually adopt a squatting posture for resting and is largely absent in populations that do not adopt a squatting posture for resting. This suggests that the presence of a squatting facet is a direct result of repeated contact between the astragalus and tibia and may be indicative of habitual hyperdorsiflexion (Dunn, 2009). A squatting facet can either be acquired through heritage (Dagosto, 1985) or habitus (Dunn, 2009). If the squatting facet is the result of heritage, it may be continuous with the trochlear surface. If it is continuous with the trochlear surface, its presence is marked as an arboreal trait for arboreal climbing, arboreal leaping and scansorial taxa. If the squatting facet is the result of habitus, it may be completely separate from the trochlea. Separation of the trochlea and squatting facet is not necessarily indicative of terrestriality. The organism can still be arboreal – displaying other arboreal astragalar characters (e.g. marked trochlear asymmetry, shallow trochlear grooving and a round navicular facet).

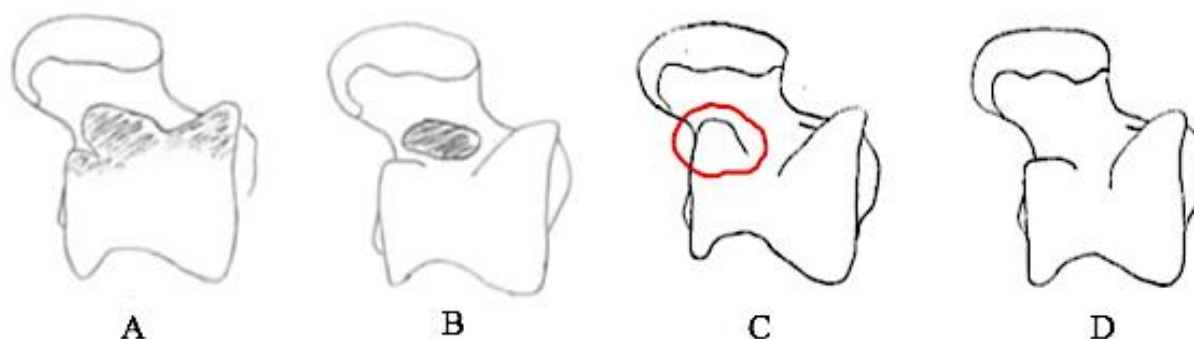


Figure 3.12. Right astragali in dorsal view, anterior is up, showing A: a trochlear surface that is continuous with the outline of the squating facet, B: a trochlea and squating facet that are separate, C: the medial trochlear rim extending onto the dorsal surface of the astragalar neck (red circle), and D: the trochlear surface and the medial trochlear rim not extending onto the dorsal surface of the astragalar neck. Extension of the trochlea onto the dorsal surface of the astragalar neck – A and C – is a trait that is adopted and modified from Chester et al. (2015) to account for habitus and heritage.

Astragalar neck angle, trochlear symmetry, trochlear depth, shape of the navicular facet, morphology and orientation of both of the ectal and sustentacular facets, and extension of the trochlea onto the astragalar neck, are given more weight than the other two identified astragalar characters (i.e. length of the astragalar neck and head and presence/absence of a squating facet) when it comes to assigning each astragalus specimen in the final sample to a locomotor category. The specified astragalar characters are given more weight over the other two characters because they have been shown to correspond to the degree of mobility at a particular ankle joint (i.e. UAJ, STJ or TTJ) (Dagosto, 1986; Gebo, 1986, 1993; Van Valkenburgh, 1987; Dunn, 2009; Chester et al., 2015; Rose et al., 2015; Ginot et al., 2016). The degree of mobility ranges from purely plantar- and dorsiflexion movements to a wide range of movements, involving both plantar- and dorsiflexion and medial-lateral movements. The sum total of the degree of mobility of all three ankle joints (UAJ, STJ and TTJ) generally indicates whether the organism is arboreal

(i.e. arboreal leaper, arboreal climber or scansorial) or terrestrial (i.e. terrestrial leaper, terrestrial cursor, terrestrial generalist or semi-aquatic).

Calcaneus Traits

C1. Anterior Elongation (AE)- length of the anterior portion of the calcaneus relative to the total length of the bone ($AE = AL/TL$) (quantitative; measurements are given in Figure 3.2)

C1a. Short ($< 35\%$)

C1b. Intermediate ($< 37\%$ but $\geq 35\%$)

C1c. Long ($\geq 37\%$)

Long anterior elongation creates a long load arm, which creates greater mechanical advantage; therefore, less effort is required to move a great distance (Gebo, 1986). Small primates (Gebo, 1986) and other small mammals require more muscle force to jump to the same height as a larger mammal, which has larger muscles and longer limbs. By lengthening the anterior calcaneus, small primates (Gebo, 1986) and other small mammals derive a better gear ratio in the foot which enables them to increase the distance of a leap without increasing muscle force or to decrease the muscle force necessary to leap a certain distance (Gebo, 1986) – more energy efficient. Leaping and cursorial taxa exhibit anterior elongation that is $\geq 37\%$, while generalist taxa demonstrate intermediate anterior elongation that is $< 37\%$ but $\geq 35\%$. A shorter load arm indicates that quadrupedal locomotion, possibly climbing, were more important than leaping and running (Dagosto, 1983; Gebo, 1986). Climbing, fossorial and semi-aquatic taxa exhibit shorter anterior elongation that is $< 35\%$.

C2. Posterior Elongation of the Calcaneal Heel (PE)- length of the posterior portion of the calcaneus relative to the total length of the bone ($PE = CNL/TL$) (quantitative; measurements are provided in Figure 3.2)

C2a. Short- ($< 38\%$)

C2b. Long- ($\geq 38\%$)

The length of the calcaneal heel can be thought of as the moment arm or “in-lever” (Carrano, 1997). The metatarsals act as the “out-lever” (Carrano, 1997). A shorter calcaneal heel (in-lever) would permit rapid motion of the metatarsals (out-lever) for a smaller amount of muscular shortening (Carrano, 1997). Therefore, a shorter calcaneal heel defines an animal that requires greater speed but that has less muscular force at its disposal (Carrano, 1997). Conversely, an animal which requires greater power in the foot stroke, but not speed of motion, has a longer calcaneal heel (Carrano, 1997). Climbing, generalist and fossorial taxa exhibit a short calcaneal heel (PE is $< 38\%$). Relative to climbers, slight lengthening of the heel in fossorial taxa produces greater power when the foot plantarflexes (Carrano, 1997). This helps to anchor the organism while it is using its forelimbs to dig (Ginot et al., 2016). Cursorial and semi-aquatic taxa exhibit a long calcaneal heel (PE is $\geq 38\%$) (Ginot et al., 2016).

The calcaneal heel may be long in leapers, but its length differs between arboreal leapers and terrestrial leapers. Arboreal leapers (e.g. primates) exhibit a somewhat shorter heel relative to terrestrial leapers) but tend to have greater anterior elongation (Dagosto, 1986; Gebo, 1986). In small-bodied primates, like tarsiers, the proportion of anterior length to posterior length (AL:PL) is greater. For example, *Tarsius bancanus* has a mean anterior length of 0.76 and a mean posterior length of 0.12 (Gebo, 1986). In larger primates, such as *Lemur catta*, the proportion of AL:PL is less, with a mean anterior length of 0.42 and a mean posterior length of 0.28 (Gebo, 1986). Terrestrial leapers (“hoppers”) such as rabbits tend to exhibit a long anterior length and a long posterior length. A long calcaneal heel, which provides greater force during plantarflexion (i.e. a powerful hop), combined with a long anterior length, which creates a

greater mechanical advantage, allows for repeated hopping (i.e. sustained locomotion).

Fostowicz-Frelik (2007) states that a long anterior length in *Hypolagus beremendensis*, an extinct species of leporid, is indicative of good jumping ability. Good jumping ability, or enhanced jumping potential, is seen in species with relatively longer feet. Species with relatively longer feet are known as forest species. Relatively longer feet allow the individual to perform powerful jumps of high steepness. Animals, living in more closed, bushy habitats are characterized by the greater angle of jump departure (Fostowicz-Frelik, 2007).

C3. Morphology of the Calcaneal Tuber (CTM)- Morphology of the Calcaneal Tuber (CTM) = CTW/CTH (quantitative; individual measurements given in Figure 3.2)

C3a. High, Narrow (Slender): ≤ 0.657

C3b. Low, Wide (Robust): > 0.657 but < 0.90

C3c. High, Wide (Very Robust): ≥ 0.90

A robust calcaneal heel is defined in terms of medio-lateral expansion of the calcaneal tuber (Rose et al., 2015; Ginot et al., 2016). The calcaneal tuber is the portion of the heel that is seen from a posterior view. According to Ginot et al. (2016), climbing taxa have a high, narrow tuber. Cursorial and semi-aquatic taxa have a low tuber of intermediate width (Ginot et al., 2016). Leaping taxa have a low, wider tuber relative to cursorial and semi-aquatic taxa (Ginot et al., 2016). Generalist taxa have a tuber that is intermediate in height and width relative to climbing, cursorial, semi-aquatic and leaping taxa, and fossorial taxa have the highest, widest tuber (Ginot et al., 2016).

CTM is a trait that is adopted and modified from Rose et al. (2015) and Ginot et al. (2016). CTW/CTH is a ratio that evaluates calcaneal tuber width relative to its height. Medial-lateral expansion of the tuber (low, wide) allows for less torque in the parasagittal plane but

provides greater mechanical advantage over a wider range of positions (as the ankle is moving) (Warburton & Prideaux, 2010). This is enhanced in fossorial taxa, where the tuber is both high and wide. This type of morphology produces a greater force during extension of the ankle, which helps to maintain the animal while it uses its forelimbs to dig. In contrast, a high, narrow tuber allows for more torque in the parasagittal plane (Warburton & Prideaux, 2010). More torque in the parasagittal plane would enhance ankle rotation as the foot is adapting to uneven substrates of various inclinations.

C4. Outline of the Ectal Facet (OEF)- height of the ectal facet relative to the length of the facet (OEF = EFH/EFL) (quantitative; measurements are provided in Figure 3.2)

C4a. short, strongly convex- (< 2)

C4b. long, slightly convex- (≥ 2)

A long, slightly convex ectal facet increases mobility at the STJ. This allows the astragalus and calcaneus to move independently of one another during movement of the ankle, thus enhancing the ability of the foot to adapt to uneven substrates (Ginot et al., 2016). Climbing and generalist taxa display a long, slightly convex calcaneal ectal facet. A short and strongly convex calcaneal ectal facet indicates that the astragalus and calcaneus should be maintained together as a unit during movement of the ankle, rather than being able to move independently of one another (Ginot et al., 2016). Leaping, cursorial, fossorial and semi-aquatic taxa display a short, strongly convex calcaneal ectal facet.

C5. Shape of the Cuboid Facet- Shape of the Cuboid Facet (SCF) = CFW/CFH (qualitative and quantitative; Figure 3.13; individual measurements are given in Figure 3.2)

C5a. crescent-shaped: higher than wide (< 1), wider than high (> 1)

C5b. circular: $\sim = 1$

C5c. triangular

Leaping (arboreal and terrestrial) and cursorial taxa exhibit a crescent shape of the cuboid facet that is higher than wide (< 1); generalist taxa are variable in this respect (either < 1 [higher than wide] or > 1 [wider than high]) (Ginot et al., 2016). Whereas a dorso-plantar main axis of the cuboid facet implies that the cuboid has limited transverse movements with respect to the calcaneus, a medio-lateral main axis implies that the cuboid does not have limited transverse movements with respect to the calcaneus (Ginot et al., 2016). In contrast, a more circular shape of the cuboid facet (approximately $= 1$) allows for a greater range of movements (Ginot et al., 2016). Climbing and fossorial taxa have a more circular shape of the cuboid facet. Only semi-aquatic taxa have a triangular-shaped cuboid facet. This shape is exhibited in some species of *Pantolestes* (Dunn, 2009).

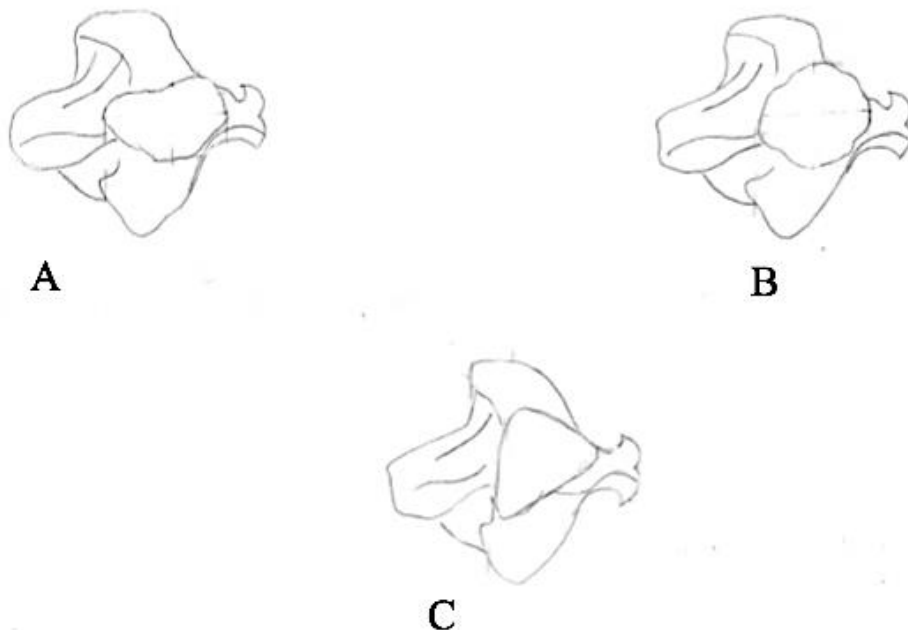


Figure 3.13. Left calcanei in anterior view showing A: crescent-shaped, B: circular, and C: triangular cuboid facets.

C6. Orientation of the Cuboid Facet (relative to the long-axis of the bone) (qualitative and quantitative; Figure 3.14)

C6a. oblique: either $>$ or $<$ 90°

C6b. perpendicular: close to 90°

When the cuboid facet is oriented perpendicular to the long-axis of the calcaneus, a greater range of movements are allowed at the TTJ- there is increased mobility. Climbing and generalist taxa display a cuboid facet that is perpendicular to the long-axis of the calcaneus. If the cuboid facet is oriented obliquely, the TTJ has more restriction or stability (Ginot et al., 2016). Leaping, cursorial, fossorial and semi-aquatic taxa display an obliquely-oriented cuboid facet.

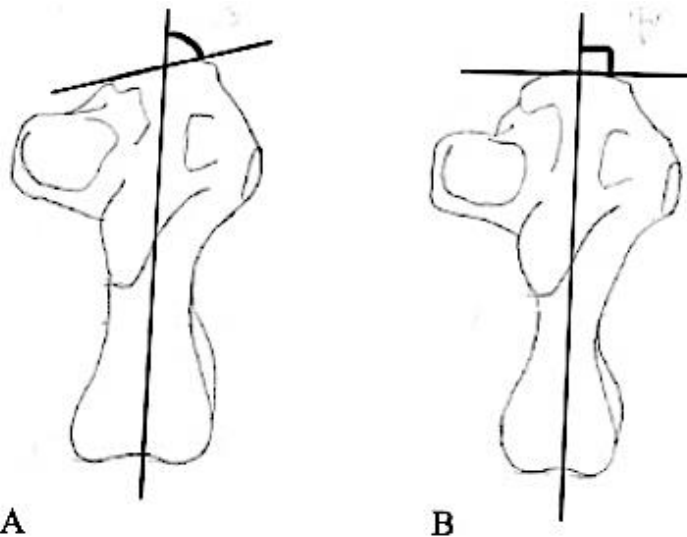


Figure 3.14. Right calcanei in dorsal view, anterior is up, showing A: an oblique, and B: a perpendicular orientation of the cuboid facet.

C7. Orientation of the Ectal Facet (relative to the long-axis of the bone) (qualitative and quantitative; Figure 3.15)

C7a. anteroposterior (in-line with the long-axis): $\leq 10^\circ$

C7b. oblique (oblique to the long-axis): $> 10^\circ$

Anteroposterior orientation of the ectal facet increases mobility at the STJ (Ginot et al., 2016) by allowing for inversion and eversion movements (Chester et al., 2015). In this way, the astragalus and calcaneus are able to move independently relative to one another (Ginot et al., 2016). Climbing and generalist taxa exhibit a calcaneal ectal facet that is oriented antero-posteriorly. Oblique orientation of the ectal facet provides stability at the STJ. This is enhanced by a short, strongly convex ectal facet morphology, which ensures that the astragalus and calcaneus are maintained together as a unit during movements of the ankle (Ginot et al., 2016). According to Dagosto (1986), an oblique orientation of the ectal facet indicates a combination of pure flexion-extension and eversion/inversion movements. When the calcaneus dorsiflexes it also everts, and when the calcaneus plantarflexes it also inverts. Leaping, cursorial, fossorial and semi-aquatic taxa display an ectal facet that is obliquely oriented to the long axis of the calcaneus (Ginot et al., 2016).

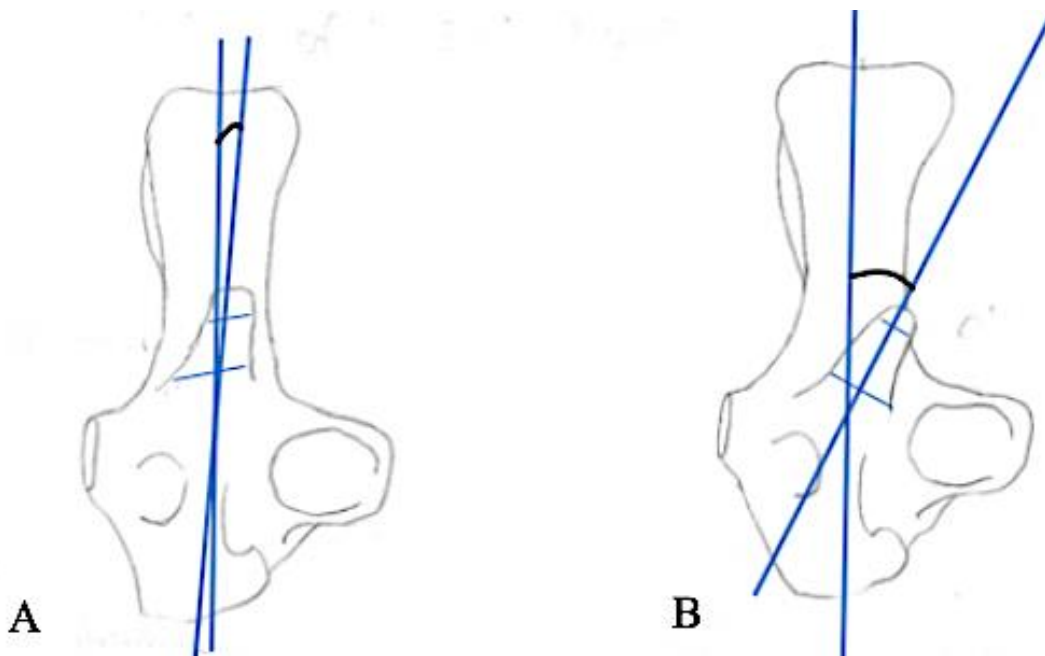


Figure 3.15. Right calcanei in dorsal view, anterior is down, showing an ectal facet that is A: antero-posteriorly, and B: obliquely oriented.

C8. Development and Placement of the Peroneal Tubercle (or process = small) (qualitative; Figure 3.16)

C8a. well-developed, placed distally

C8b. well-developed, placed proximally

C8c. reduced (or nearly absent), placed distally

* well-developed = tubercle

* less-developed (i.e. reduced or nearly absent) = process

A well-developed, and proximally placed, peroneal tubercle forms a fulcrum for the tendons *M. peroneus longus* and *brevis*, which help to abduct and evert the foot (Ginot et al., 2016). This may improve the mobility of the foot by facilitating its eversion and/or abduction through a change in the characteristics of the lever system of the *peroneus* muscles. This is a type-3 lever system, where the effort is exerted between the fulcrum and the resistance. The posterior position of the peroneal tubercle increases the in-lever length, producing a greater mechanical advantage for the *peroneus* muscles; it also increases the resistance to forces on the opposite (medial) side during inversion (Ginot et al., 2016). Climbing taxa have a well-developed and proximally placed peroneal tubercle which creates a “cruciform” shape, where the well-developed peroneal tubercle is situated directly across from the sustentacular facet.

A well-developed peroneal tubercle indicates that eversion and abduction of the foot are important behaviors, however, these behaviors do not serve the same purpose in fossorial taxa as they do in climbing taxa (Ginot et al., 2016). In fossorial taxa, the peroneal tubercle is placed distally, and its length is the highest. This development is linked to the passage of the tendons of the *peroneus* muscle group, which are responsible for eversion of the foot (Ginot et al., 2016). Semi-aquatic mammals also display a well-developed, distally-placed peroneal tubercle (Ginot et

al., 2016); however, its length and width will vary (Salton & Szalay, 2004) depending on the types of activities that small mammals are performing in/near the water and how much time they are spending in the water (Stein, 1988).

If the peroneal process is reduced and distally-placed, this changes the lever system of the *peroneus* muscle group into a direct pulling (Ginot et al., 2016). This greatly reduces the possibility of the foot abducting and/or everting (Ginot et al., 2016). Leaping, cursorial and generalist taxa exhibit a peroneal “process” that is reduced and placed distally.

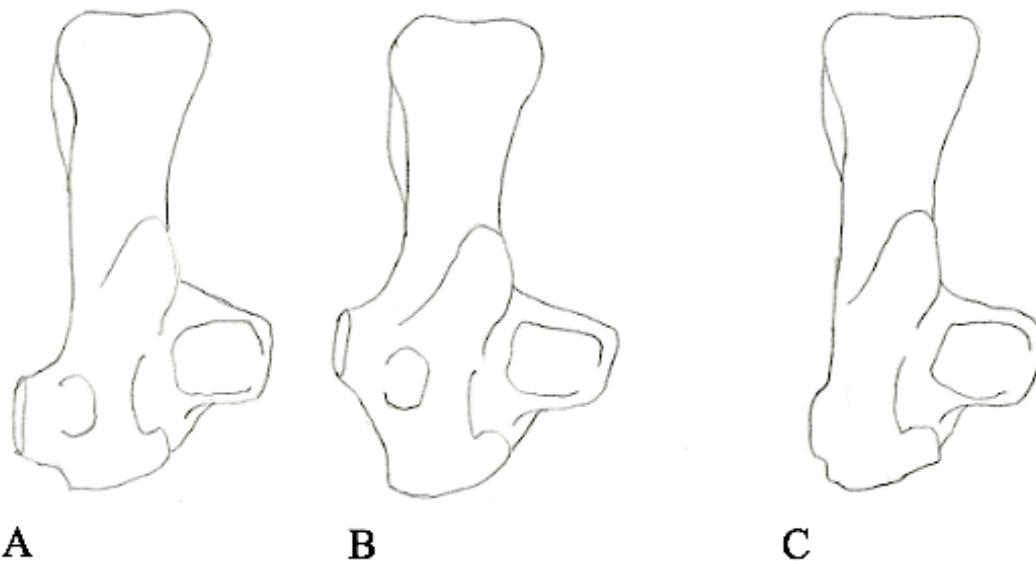


Figure 3.16. Right calcanei in dorsal view, anterior is down, showing a peroneal tubercle that is A: well-developed and placed distally, B: well-developed and placed proximally (“cruciform” shape), and C: reduced (or nearly absent) and placed distally.

C9. Calcaneal Heel Inflection (qualitative; Figure 3.17)

C9a. Curved (Medially and Plantarly)

C9b. Relatively Straight

A calcaneal heel that is curved medially and plantarly is linked to the direction of the forces that are the strongest and most often exerted during inversion and flexion of the foot

(Ginot et al., 2016). Dunn (2009) states that the plantar orientation of the heel indicates powerful pedal grasping, as necessitated by slow-climbing arboreal locomotion. Medial inflection of the heel can be seen in climbing taxa. Leaping, cursorial, generalist, fossorial and semi-aquatic taxa display a relatively straight heel.

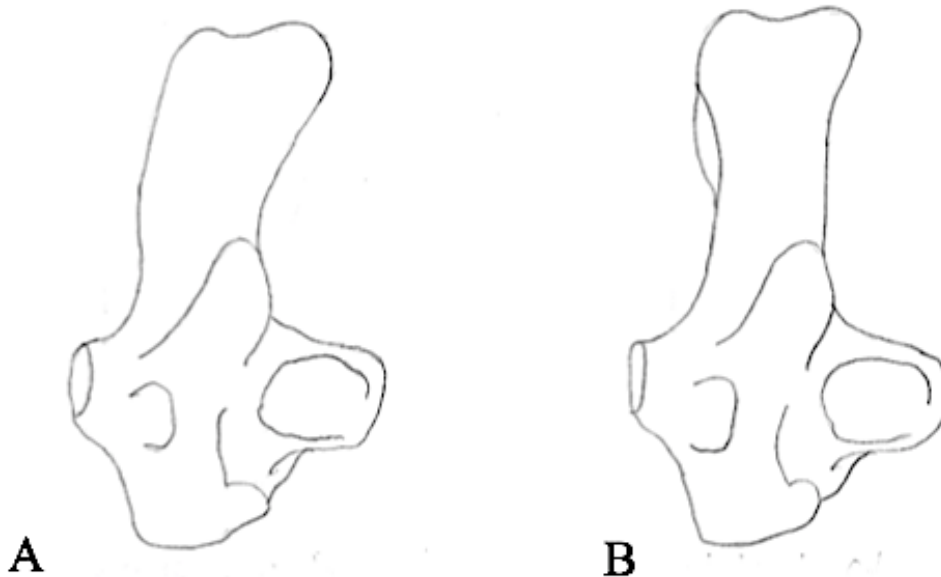


Figure 3.17. Right calcanei in dorsal view, anterior is down, showing A: medial inflection of the calcaneal heel, and B: a relatively straight calcaneal heel.

C10. Concavity of the Cuboid Facet (Figure 3.18)

C10a. yes

C10b. no

Concavity of the cuboid facet increases mobility at the TTJ by allowing the cuboid to rotate in a variety of ways (Chester et al., 2015). Climbing (Chester et al., 2015; Ginot et al., 2016) and arboreal leaping (Chester et al., 2015) taxa exhibit concavity of the cuboid facet. Terrestrial leaping, cursorial, generalist, fossorial and semi-aquatic taxa have more of a flat cuboid facet (Ginot et al., 2016). A relatively flat cuboid facet provides some stability at the TTJ. This stability is enhanced by an obliquely-oriented cuboid facet (Ginot et al., 2016).

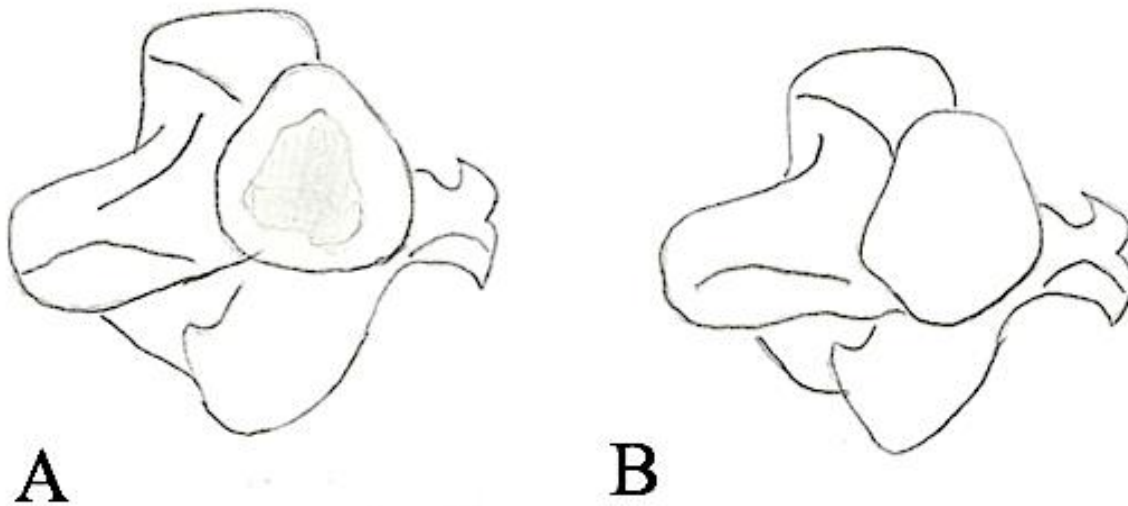


Figure 3.18. Left calcanei in anterior view, medial is to the left, showing a cuboid facet that is A: concave (shaded region), and B: not concave.

C11. Articulation of Fibula with the Lateral Side of the Ectal Facet (Figure 3.19)

C11a. yes

C11b. no

If the fibula made contact on the lateral side of the ectal facet, there will be a small facet present. If this small facet is absent, then the fibula did not make contact on the lateral side of the ectal facet. Contact between the fibula and the lateral side of the ectal facet restricts medial-lateral movements at the STJ (Chester et al., 2015). Arboreal climbing and arboreal leaping taxa do not exhibit articulation of the fibula on the lateral side of the ectal facet, whereas scansorial, terrestrial leaping, cursorial, generalist, fossorial and semi-aquatic taxa do exhibit articulation of the fibula on the lateral side of the ectal facet.

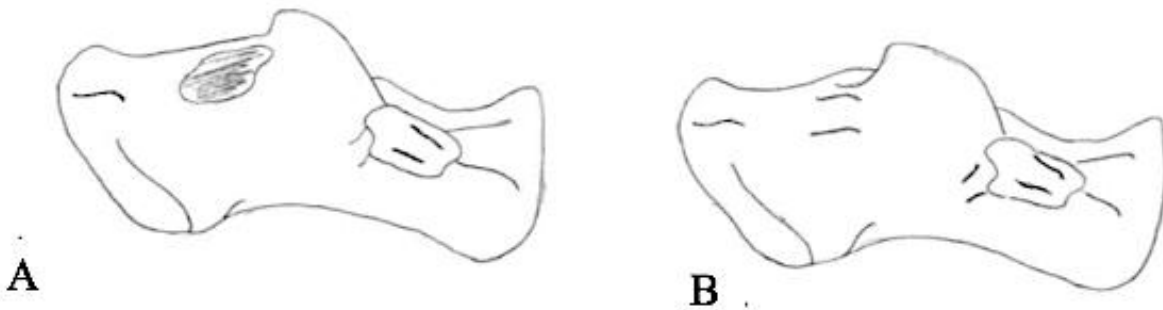


Figure 3.19. Right calcanei in lateral view, anterior is to the right, showing A: fibular contact (shaded region) on the lateral side of the ectal facet, and B: no fibular contact on the lateral side of the ectal facet.

C12. Extension of the Sustentacular Facet Beyond the Sustentacular Shelf (Figure 3.20)

C12a. yes

C12b. no

According to Chester et al. (2015), extension of the sustentacular facet beyond the sustentacular shelf lends support to a pronounced capacity for inversion and eversion of the foot. This trait can be found in climbing and arboreal leaping taxa. Terrestrial leaping, cursorial, generalist, fossorial and semi-aquatic taxa do not exhibit this trait.

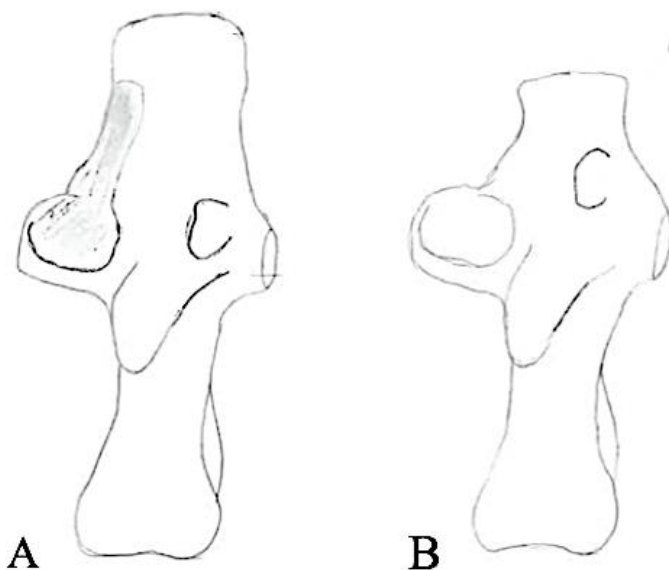


Figure 3.20. Right calcanei in dorsal view, anterior is up, showing A: extension of the sustentacular facet beyond the sustentacular shelf (shaded region), and B: no extension of the sustentacular facet beyond the sustentacular shelf.

C13. Cuboid Pivot (solely a primate trait [Ford, 1980]) (qualitative; Figure 3.21)

C13a. present- the size and depth (i.e. how well-defined it is) determines which of the multiple arboreal locomotor guilds it is

C13ai. well-defined, relatively large, slightly deep

C13aii. not well-defined, relatively shallow (i.e. present but the cuboid facet itself is slightly concave)

C13b. absent

The presence of a cuboid pivot allows the cuboid facet joint to function as a pivot. This type of articulation allows a greater degree of mobility, in particular inversion and eversion, while sacrificing stability (Ford, 1980). Increased mobility at the TTJ would allow the ankle to easily adapt to uneven substrates. The larger the pivot, the greater the mobility that is provided at the expense of stability. Arboreal quadrupeds (i.e. slow, cautious climbers), and generalized arboreal quadrupeds exhibit a well-defined, relatively large cuboid pivot that is slightly deep. A cuboid pivot that is not well-defined and relatively shallow is exhibited in primates that demonstrate vertical clinging and leaping (VCL) behaviors. According to Ford (1980), a cuboid pivot with this type of morphology is associated with the need for increased force and stability and the reduced need for inversion-eversion at the TTJ. A cuboid pivot is different from concavity of the cuboid facet. When the cuboid facet is concave, this concavity is even throughout the entire facet. A cuboid pivot is similar to this, but rather than being even throughout the entire facet, this concavity is restricted to a small “pivot” region that is situated in the plantar-medial portion of the cuboid facet.

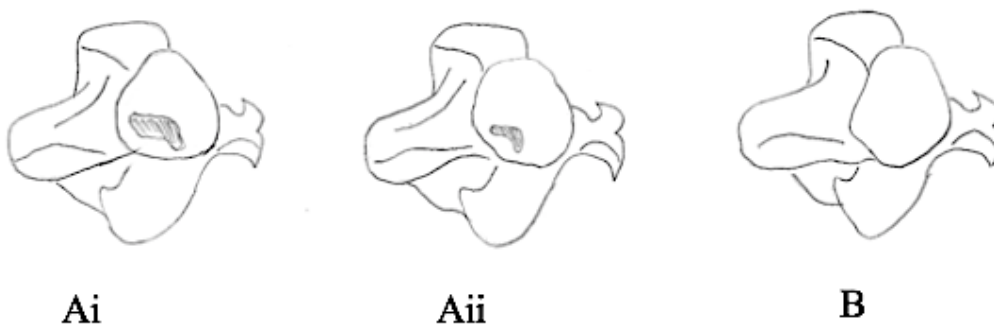


Figure 3.21. Left calcanei in anterior view, medial is to the left, showing Ai: a cuboid pivot (shaded region) that is present, well-defined, relatively large and slightly deep, Aii: a cuboid pivot (shaded region) that is not well-defined and relatively shallow, and B: the absence of a cuboid pivot. The presence of a cuboid pivot is solely a primate trait (Ford, 1980).

C14. Development and Length of the Distal Plantar Tubercle (qualitative; Figure 3.22)

C14a. Prominent and elongate

C14b. Reduced

Rose and Chinnery (2004) and Thorington, Schennum, Pappas and Pitassy (2005) note that a prominent and elongate distal plantar tubercle is characteristic of scansorial micro-mammals, for example ground squirrels. A reduced distal plantar tubercle is characteristic of arboreal climbing micro-mammals. Ginot et al. (2016) note that the distal plantar tubercle is an area of insertion of ligaments linked to the cuboid and the fifth metatarsal.

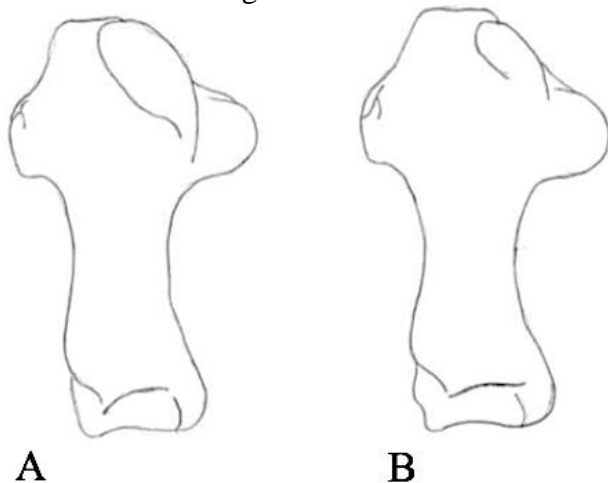


Figure 3.22. Right calcanei in plantar view, anterior is up, showing A: a distal plantar tubercle that is prominent and elongate, and B: a distal plantar tubercle that is reduced.

Morphology of the cuboid facet (including shape and concavity), morphology of the ectal facet, morphology of the calcaneal heel (slender/narrow or robust/wide), medial inflection of the calcaneal heel, development and placement of the peroneal tubercle, morphology of the sustentacular facet (including extension beyond the sustentacular shelf) and articulation of the fibula on the lateral side of the ectal facet are given more weight than the other identified calcaneal characters (i.e. anterior elongation, posterior elongation, orientation of the cuboid facet and orientation of the ectal facet), when it comes to assigning each calcaneus specimen in the final sample to a locomotor category. The specified calcaneal characters are given more weight than the other characters because they have been shown to correspond to a particular kind of locomotion, whether arboreal (Stein, 1988; Salton & Szalay, 2004; Dunn, 2009; Warburton & Prideaux, 2010; Chester et al., 2015; Rose et al., 2015; Ginot et al., 2016) or terrestrial (Dunn, 2009; Chester et al., 2015; Ginot et al., 2016). Development and length of the distal plantar tubercle is important for distinguishing between arboreal climbing and scansorial taxa (Rose & Chinnery, 2004; Thorington et al., 2005).

Terminal Phalanges

Terminal phalanges (Figure 3.23) have no defined characters (Macleod & Rose, 1993), therefore, the final sample of 55 terminal phalanges is evaluated morphometrically. 2-D coordinate data are gathered on 10, non-homologous landmarks and six semilandmarks. Landmarks 1, 5, 6, 7, 8, 10, 11, 12, 13 and 16 are non-homologous because each specimen may represent a different species (Webster & Sheets, 2010). If all of the specimens belonged to the same species then homologous, anatomical landmarks can be identified (Webster & Sheets, 2010). Landmarks 2, 3, 4, 9, 14 and 15 are semilandmarks. Semilandmarks capture the shape of a curve (Webster & Sheets, 2010). These 16 landmarks are used to capture the outline of each

specimen in lateral view (Figure 3.24). X, Y coordinates are obtained using the image software ImageJ (Schneider, Rasband & Eliceiri, 2012). In order to evaluate the 2-D coordinate data of the Whitehead Creek terminal phalanges in the final sample, with the goal of assigning each specimen to a locomotor category, a comparative data set must first be established. A comparative data set is formulated by scoring specimens figured in Macleod and Rose (1993) and Maiolino (2015).

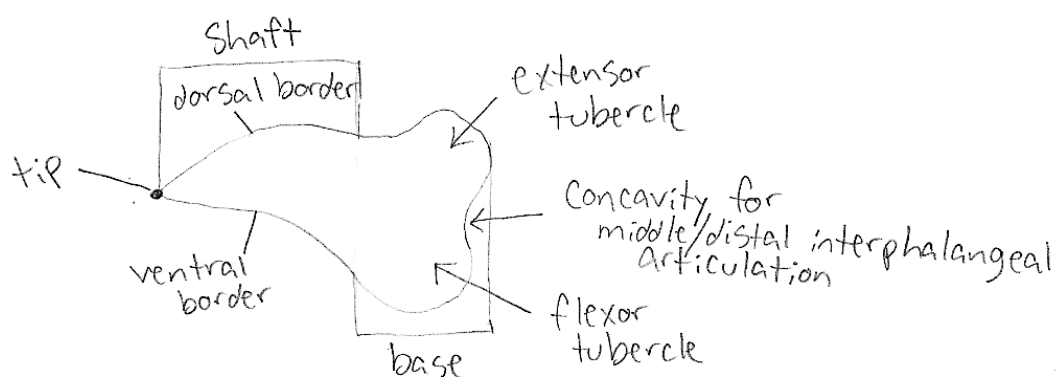


Figure 3.23. Terminal phalanx (claw) anatomy.

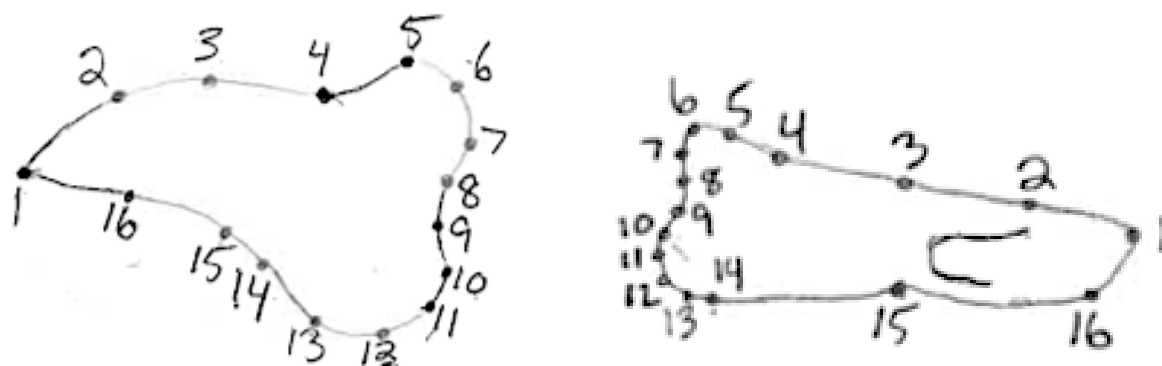


Figure 3.24. 16 coordinate points (lateral view). 16 coordinate points for a claw (left), and 16 coordinate points for a terminal phalanx with an apical tuft (right).

Assigning locomotor categories

Astragalus sample and calcaneus sample. After trait data are collected for each astragalus and calcaneus in the final samples, a tally mark system is used to score individual specimens (Table 3.5). For each trait scored, a tally mark is given to the locomotor category (or categories)

Table 3.5. Tally mark system used to score individual astragalus and calcaneal specimens.

AL	TL	C	TG	AC	SCAN	F	SA

that the trait corresponds with. For example, if an astragalus has a head-neck-length index (HNLI) value that is ≤ 0.50 (i.e. short; a semi-aquatic trait), a single tally mark is recorded for the presence of the semi-aquatic trait. However, not all traits are representative of a single locomotor category. Some traits, such as astragalus trochlear depth, are representative of multiple locomotor categories. For example, a deep trochlea can be found in both leaping and cursorial taxa. In this instance, three tally marks are given – one representing an arboreal leaping trait, one representing a terrestrial leaping trait and the other representing a cursorial trait.

In regard to calcaneal traits C10 (concavity of the cuboid facet, Figure 3.18) and C12 (extension of the sustentacular facet beyond the sustentacular shelf, Figure 3.20), presence of the trait is marked down as an arboreal leaping, arboreal climbing and scansorial trait. Absence of the trait is not necessarily indicative of terrestrial behaviors; small mammals can still be arboreal by exhibiting other arboreal tarsal characters. In regard to calcaneal trait C11 (articulation of the fibula with the lateral side of the calcaneal ectal facet, Figure 3.19), its absence is marked down as an arboreal leaping and arboreal climbing trait. Presence of this trait is not necessarily

indicative of terrestrial behaviors, although it is seen primarily in terrestrial small mammals. This tally mark system is applied to all 56 astragali and all 44 calcanei.

Once the 56 astragali and 44 calcanei are scored using the tally mark system, a majority rule criterion is used to assign each specimen to a locomotor category. If, for example, an astragalar specimen has two arboreal leaping traits, two terrestrial leaping traits, two cursorial traits, four arboreal climbing traits, five scansorial traits, one fossorial trait and zero semi-aquatic traits, the specimen is assigned to the scansorial locomotor category due to this category having the most tally marks. If the majority rule criterion is not applicable and the specimen has a tie between multiple locomotor categories, there are two options: 1) assign the specimen to the terrestrial generalist locomotor category, or 2) re-assess the specimen through character weighting. This last option is used if the combination of locomotor categories does not make sense. For example, UMPC - 19562 displays an equal representation of arboreal leaping, terrestrial leaping, cursorial and fossorial traits with three traits each. There are only two arboreal climbing traits, one scansorial trait and no semi-aquatic traits. This specimen is not assigned as a terrestrial generalist because it exhibits mobility at the UAJ, STJ and the TTJ. UMPC - 19562 has marked trochlear asymmetry and shallow trochlear grooving, indicating mobility at the UAJ. The sustentacular facet on the plantar surface of the astragalar neck is fully confluent with the navicular facet; this allows for increased mobility (with a transverse component) at the STJ (Ginot et al., 2016). The navicular facet is well-developed on the medial side of the astragalar neck, which allows for increased mobility at the TTJ. Increased mobility at the UAJ, STJ and TTJ indicate that the organism was able to adapt its feet to uneven substrates. This combination of traits allowed for the specimen to be assigned as an arboreal climber. In this case, the presence

of arboreal characters, such as marked trochlear asymmetry and shallow trochlear grooving, were given more weight than a long astragalar neck (a leaping and cursorial trait).

Terminal phalanx sample. Mean X, Y coordinates for each specimen in the comparative data set are determined in order to create a mean shape for each locomotor guild (i.e. cursorial, terrestrial generalist, arboreal climber, scansorial, fossorial and semi-aquatic). For example, X_1, Y_1 coordinates for all extant, small, fossorial mammals are averaged in order to create mean X_1 , mean Y_1 . This process is repeated for the other 15 coordinate points and for all of the other locomotor guilds. All coordinate data (for both Whitehead Creek, and the mean X,Y coordinates for each locomotor group [i.e. each mean shape]) are inputted into the statistical package PAST3.22 and converted into Procrustes residuals to remove size (Hammer, 1999-2018). This transformation centers all of the data points around the origin of the graph ($X = 0, Y = 0$), while minimizing the distance between them. A landmarks (2D) PCA (Table 3.6) of extant (Macleod & Rose, 1993; Maiolino, 2015) and fossil (Whitehead Creek) coordinate data is used to assign each specimen in the Whitehead Creek terminal phalanx sample to a locomotor guild. The minimum spanning tree option (Figure 3.25) is used to connect the dots between each fossil specimen and the mean shape of a locomotor group. This option minimizes the distance between all of the points; the goal of using this option is to be able to see how each of the fossil specimens compares with the mean shape of each locomotor group. If a fossil specimen fails to cluster with any particular locomotor group, the similarity and distance indices (Euclidean) option under the multivariate tab is used to determine statistically which locomotor group mean that particular specimen is closest to (Hammer, 1999-2018). The Euclidean Distance index ranges on a scale from 0-1, with 1 being the least similar and 0 being the most similar (Hammer, 1999-2018).

Results of a landmarks (2D) PCA on all coordinate data (with no mean shapes) is given in Figure 3.26; in this analysis, you can see the distinctiveness and/or overlap of the different locomotor categories. Note that the euprimates (Maiolino, 2018) and the Whitehead Creek primate nail (BA-5Q 2015) form a relatively distinct group; the fossorial group is also relatively distinct. The arboreal climbing, scansorial, terrestrial generalist and cursorial groups overlap each other to a certain degree.

Table 3.6. Eigenvalues and percent variance of the landmarks (2D) PCA on the terminal phalanx sample.

PC	Eigenvalue	% variance
1	0.00870992	32.202
2	0.00430473	15.915
3	0.00286595	10.596
4	0.00219772	8.1253
5	0.00176655	6.5312
6	0.00135121	4.9957
7	0.00107041	3.9575
8	0.000906074	3.3499
9	0.000671097	2.4812
10	0.000462426	1.7097
11	0.000434909	1.6079
12	0.000399244	1.4761
13	0.000331482	1.2255
14	0.00026235	0.96995
15	0.00025652	0.9484
16	0.000210614	0.77868
17	0.000161328	0.59646
18	0.00014375	0.53147
19	0.000137585	0.50867
20	9.01683E-05	0.33337
21	8.25974E-05	0.30538
22	6.36097E-05	0.23518
23	3.74224E-05	0.13836
24	3.27041E-05	0.12091
25	2.76946E-05	0.10239
26	2.35584E-05	0.087099
27	1.86294E-05	0.068876
28	1.39813E-05	0.051691

Table 3.6 (continued)

29	9.12215E-06	0.033726
30	4.41865E-06	0.016336
31	4.37529E-16	1.6176E-12
32	2.4238E-16	8.9612E-13

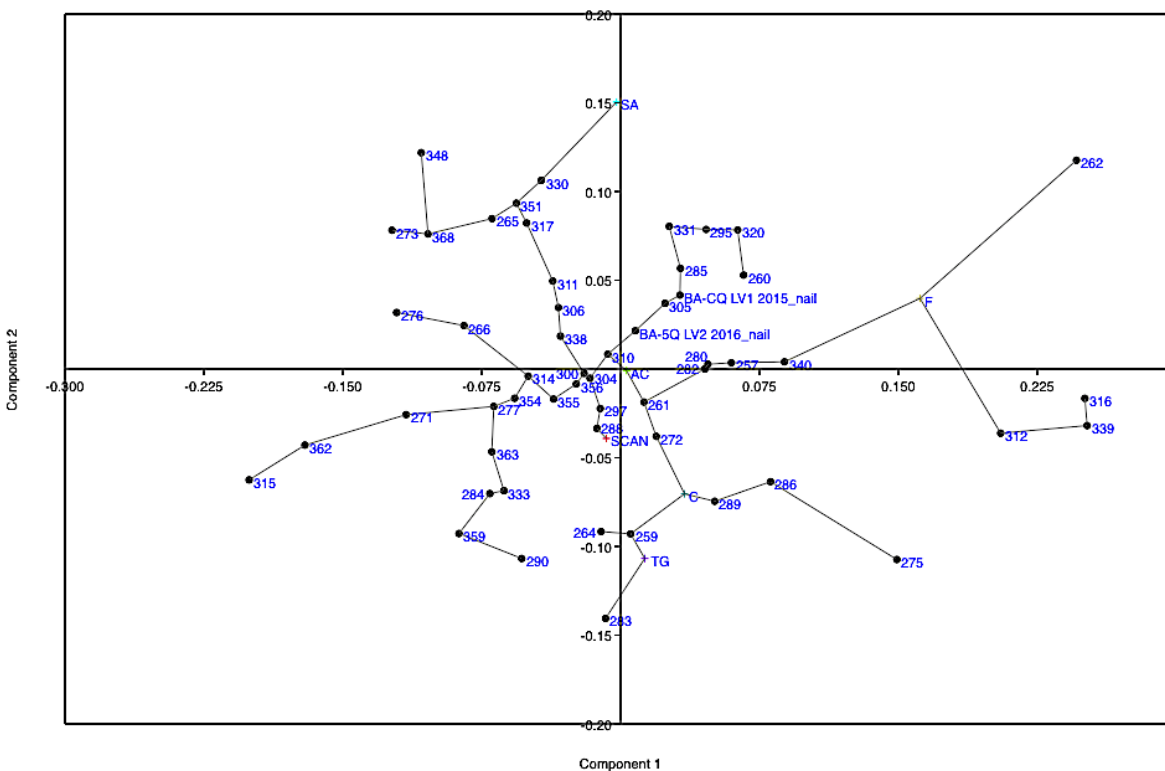


Figure 3.25. Minimum spanning tree results on the Whitehead Creek terminal phalanx sample. Mean shapes of locomotor guilds are represented by "+". AC (Arboreal Climber) is light green, SCAN (Scansorial) is red, TG (Terrestrial Generalist) is purple, C (Terrestrial Cursor) is cadet blue, F (Fossorial) is light brown and SA (Semi-Aquatic) is light blue. Whitehead Creek specimens are represented by solid, black circles. Each terminal phalanx specimen is represented by its assigned number. WHC_Primate Nail_BA-5Q 2015 is not included in this figure because it is the only euprimate in the sample, and it has been classified as an arboreal climber in the landmark PCA analysis.

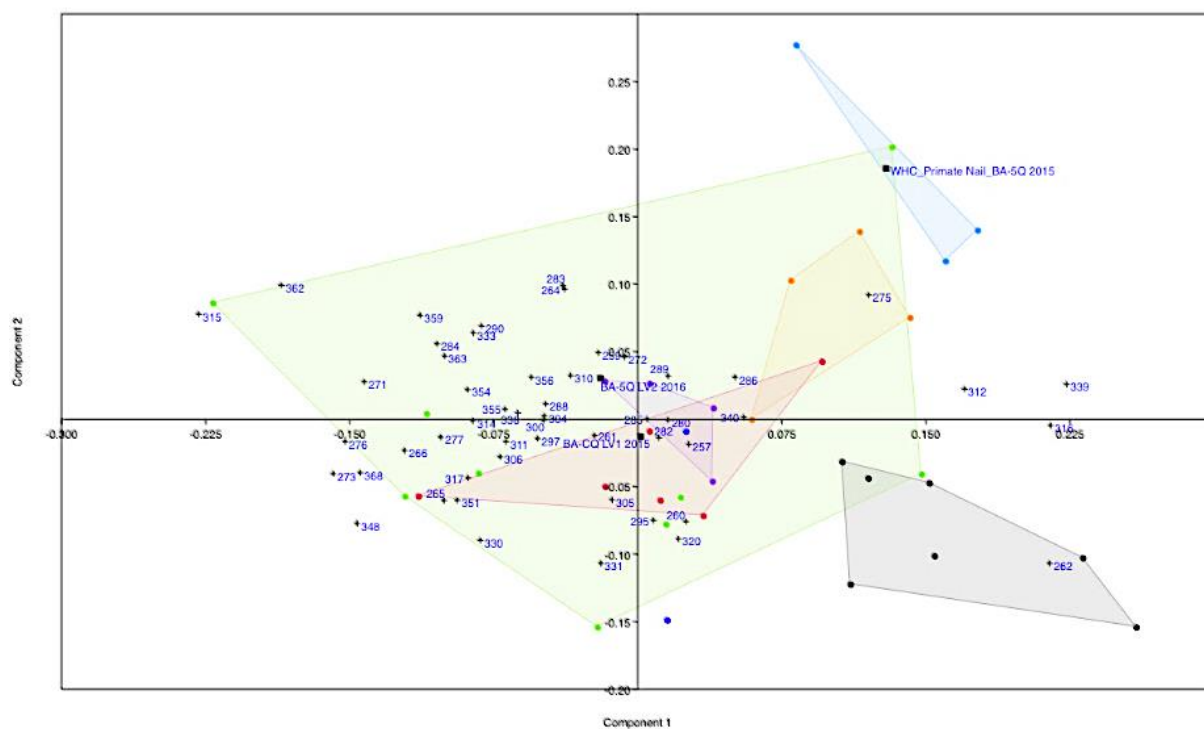


Figure 3.26. Landmarks (2D) PCA of extant (Macleod and Rose, 1993; Maiolino, 2018) and Whitehead Creek terminal phalangeal specimens. In a PCA, Component 1 is on the X-axis and Component 2 is on the Y-axis. Extant specimens are represented by dots, with the specific color of the dot corresponding to a particular locomotor category. Whitehead Creek terminal phalanx specimens that are claws are represented by “+” symbols and their corresponding specimen number, and Whitehead Creek terminal phalanx specimens with apical tufts (BA-CQ LV1 2015, BA-5Q LV2 2016, and WHC_Primate Nail_BA-5Q 2015) are represented by filled, black squares. Locomotor guilds – arboreal climbing (light green), scansorial (red), terrestrial generalist (purple), terrestrial cursor (dark orange), fossorial (black), semi-aquatic (blue), and the group containing the terminal phalanx specimens with apical tufts (light blue).

Locomotor guild frequencies of the three Whitehead Creek Samples

The Whitehead Creek astragalus sample consists of 56 specimens, representing 56 morphospecies (Table 3.7). There are zero arboreal leapers (0%), eight terrestrial leapers (14.29%), one terrestrial cursor (1.79%), eight terrestrial generalists (14.29%), eight arboreal climbers (14.29%), 30 scansorialists (53.57%), one fossorialist (1.79%) and zero semi-aquatic taxa (0%). The Whitehead Creek calcaneus sample consists of 44 specimens, representing 43 morphospecies (Table 3.7). UMPC - 19633/19659 is a composite specimen. There is one arboreal leaper (2.33%), three terrestrial leapers (6.98%), eight terrestrial cursors (18.60%), 13 terrestrial generalists (30.23%), one arboreal climber (2.33%), 13 scansorialists (30.23%), five fossorialists (11.63%) and zero semi-aquatic taxa (0%). The Whitehead Creek terminal phalanx sample consists of 55 specimens. There are 25 arboreal climbers (45.45%), 18 scansorialists (33.33%), three terrestrial generalists (5.56%), four terrestrial cursors (7.41%), four fossorialists (7.41%) and one semi-aquatic (1.85%) (Table 3.7). No data demonstrating the phalangeal morphology of leaping were available (Macleod and Rose, 1993).

Table 3.7. Locomotor guild frequencies of the three Whitehead Creek samples – astragalus, calcaneus and terminal phalanx.

Whitehead Creek Sample	Arboreal Leaper (AL)	Terrestrial Leaper (TL)	Terrestrial Cursor (C)	Terrestrial Generalist (TG)	Arboreal Climber (AC)	Scansorial (SCAN)	Fossorial (F)	Semi-Aquatic (SA)
Astragalus	0	8	1	8	8	30	1	0
Calcaneus	1	3	8	13	1	13	5	0
Terminal Phalanx	0	0	4	3	25	18	4	1

Locomotor comparisons between Whitehead Creek and modern localities

In order to reconstruct the paleoenvironment of Whitehead Creek, a comparative dataset consisting of locomotor guild frequencies from different modern sites must first be established.

Two to three representatives of each biome type are chosen for this project – temperate

grasslands (Swan Lake National Wildlife Refuge, Missouri [Eulinger & Burt, 2006]; Giant's Castle Game Reserve, South Africa [Rowe-Rowe & Meester, 2015]), deciduous forests (Swan Lake National Wildlife Refuge, Missouri [Eulinger & Burt, 2006]; Washington and Jefferson National Forests, Virginia [McShea, Pagels, Orrock, Harper & Koy, 2003]), dry deciduous forests (Colima, Mexico [Poindexter, Schnell, Sánchez-Hernández, Romero-Almaraz, Kennedy, Best & Owen, 2012]), gallery forests (Cerrado of Brazil [Redford & da Fonseca, 1986]; Tana River, Kenya [Andrews, Groves & Horne, 1975]; Lankoci-Forest, upper section of the Drava River, Central Europe [Gyozo, Daniel & Gergely, 2005]), primary tropical lowland forests (Greater Palawan, Busuanga, Philippines [The Field Museum, 2010]; near Maroantsetra, Toamasina Province, northeastern Madagascar [Stephenson, 1995]), secondary tropical lowland forests (Greater Palawan, Busuanga, Philippines [The Field Museum, 2010]; near Maroantsetra, Toamasina Province, northeastern Madagascar [Stephenson, 1995]), montane forests (Quezon Province of the Philippines [The Field Museum, 2010]; southwestern Jalisco and northeastern Colima, Mexico [Vazquez, Medellín & Cameron, 2000]), bamboo thickets (Mt. Tay Con Linh II, Vietnam [Lunde, Musser & Truong Son, 2003]), bamboo forests (Salak Phra Wildlife Sanctuary, southwestern Thailand [Wiles, 1981]) and taiga forests (Thunder Bay, Canada [Morris, 2005]; Hokkaido, Japan [Hiashi, 1994]). For each modern site, locomotor data is collected on all documented small mammals (< 1,000g) (Table 3.8). Data on locomotion are obtained from a variety of sources, including the Animal Diversity Web (ADW, 2014) and IUCN (IUCN, 2018). Once locomotor guild frequencies for each modern site are obtained, they are compared with locomotor guild frequencies for the Whitehead Creek samples of *astragali*, *calcanei* and terminal phalanges using Sørensen's similarity index in the statistical package PAST3.22 (Hammer, 2018).

Table 3.8. Locomotor guild frequencies for modern sites. For each modern site, a citation is provided in the far right-hand column.

Modern Biome Type	Site	AL	TL	TQ	AC	SCAN	F	SA	Citation
Gallery Forest	Cerrado of Brazil	0	1	20	7	5	6	11	Redford and da Fonseca, 1986
High Ground, Old-Growth Forest	Cocha Cashu, Peru	1	0	6	2	11	0	6	Terborgh et al., 1984
Lowland Bamboo Forest	Salak Phra Wildlife Sanctuary, SW Thailand	0	0	2	0	4	1	0	Wiles, 1981
Primary Tropical Lowland Forest	Greater Palawan, Busuanga, Philippines	0	0	2	0	4	0	0	The Field Museum, 2010
Primary Tropical Lowland Forest	Near Maroantsetra, Toamasina Province, NE Madagascar	0	0	2	0	3	1	0	Stephenson, 1995
Upland Bamboo Forest	Salak Phra Wildlife Sanctuary, SW Thailand	0	0	3	1	4	1	0	Wiles, 1981
Woodland Gallery Forest	Tana River, Kenya	1	0	2	0	3	0	0	Andrews et al., 1975
Montane/Cloud Forest	SW Jalisco and NE Colima, Mexico	0	0	2	0	3	0	1	Vazquez et al., 2000
Bamboo Thicket (1650-1850m)	Mt. Tay Con Linh II, Vietnam	0	0	2	0	3	0	1	Lunde et al., 2003
Secondary Tropical Lowland Forest	Greater Palawan, Busuanga, Philippines	0	0	2	0	6	0	0	The Field Museum, 2010
Temperate Grassland	Swan Lake National Wildlife Refuge, Missouri	0	1	4	0	2	5	1	Eulinger et al., 2006

Table 3.8 (continued)

Alder Gallery Forest	Lankoci-Forest, upper section of the Drava River, Central Europe	0	1	4	0	2	2	0	Gyozo et al., 2005
Old-Growth Forest	Olympic Peninsula, Olympic National Park, Washington	0	2	5	0	2	2	2	Carey and Jonson, 1995
Oak/Hickory Forest	Swan Lake National Wildlife Refuge, Missouri	0	0	4	0	4	3	1	Eulinger et al., 2006
Chestnut/Oak Forest	Washington and Jefferson National Forests, Virginia	0	2	4	0	6	5	0	McShea et al., 2003
Taiga	Thunder Bay, Canada	1	2	5	0	4	1	0	Morris, 2005
Taiga	Hokkaido, Japan	0	1	7	1	2	0	0	Hiashi, 1994
Tropical Dry Deciduous Forest	Colima, Mexico	0	0	4	0	2	0	1	Poindexter et al., 2012
Tropical Dry Deciduous Forest	Colima, Mexico	0	0	5	0	2	0	1	Poindexter et al., 2012
Tropical Dry Deciduous Forest	Colima, Mexico	0	0	3	1	2	0	1	Poindexter et al., 2012
Bamboo Thicket (1850-2100m)	Mt. Tay Con Linh II, Vietnam	0	0	3	0	2	0	2	Lunde et al., 2003
Tall Grassland	Giant's Castle Game Reserve, South Africa	0	0	2	0	1	1	0	Rowe-Rowe and Meester, 2015

Table 3.8 (continued)

Temperate Grassland (2700m)	Giant's Castle Game Reserve, South Africa	0	0	1	0	2	1	0	Rowe-Rowe and Meester, 2015
Secondary Tropical Lowland Forest	Near Maroantsetra, Toamasina Province, NE Madagascar	0	0	1	0	3	2	0	Stephenson, 1995
Montane Forest	Quezon Province of the Philippines	0	0	4	3	0	1	0	The Field Museum, 2010

Sørensen's similarity index analysis

Sørensen's similarity index is a beta diversity index that uses binary data (presence/absence) (Hammer, 2018) to evaluate similarity in taxonomic composition between sites (Lyman, 2008). It allows for comparisons between heterogeneous samples of varying sample sizes (e.g. Whitehead Creek and modern localities) by using only the presence data to evaluate similarity, not the absence data (i.e. absence data plays no role). By only using the presence data, Sørensen's similarity index is evaluating the shared (i.e. joint) occurrences of the different taxa across different sites (Lyman, 2008). Relative to other similarity indices (e.g. Jaccard), Sørensen's similarity index puts more weight on joint occurrences than on mismatches, however, in doing so, it also doubles any error that might be present in the data (Schroeder & Jenkins, 2018). According to Schroeder and Jenkins (2018), there are three types of error – taxonomic misidentification, geographic undersampling and numerical undersampling. Taxonomic misidentification occurs while sampling (e.g. during counts in the field) or in subsequent sample processing (e.g. preserved samples) (Schroeder & Jenkins, 2018). Geographic undersampling is the use of an insufficient number of sampled sites, and numerical undersampling is the inclusion of insufficient individuals in a sample, which may result in the

exclusion of rare species (i.e. the sample size is too small) (Schroeder & Jenkins, 2018); rare species can affect the value of most beta indices (especially those based on presence-absence data) and so their exclusion can result in large errors.

Sørensen's similarity index is being applied in a different way for this research. It is being used to evaluate "functional similarity" (Siefert, Ravenscroft, Weiser & Swenson, n.d.; Silva & Brandão, 2014; García-Cárdenas, Montoya-Lerma & Armbrecht, 2018) rather than "taxonomic similarity" (i.e. species beta diversity). Using Sørensen's similarity index as a functional similarity index, rather than a species beta diversity index, which compares species composition between communities, has become increasingly popular amongst ecologists and biologists (Silva & Brandão, 2014). One key weakness of species beta diversity indices is that they ignore functional similarities between communities (Siefert et al., n.d.). A niche-based community involves the separation of species based on their functional traits (e.g. locomotor behaviors). Differences in the functional composition between different communities captures the signals of niche-based assembly processes (i.e. environmental filtering). Environmental filtering drives community assembly (Siefert et al., n.d.); in other words, biotic and abiotic components of the environment influence the functional composition of the local community (i.e. the relationship between physical properties of the environment and locomotor guild frequencies of a single site). Similarity (or difference) between different communities is not captured when using Sørensen's Index in the traditional way (i.e. species beta diversity). Using Sørensen's Index as a functional index enables appropriate description of communities and it displays a higher degree of similarity between different communities (if there is any similarity) relative to the traditional Sørensen's Index (Siefert et al., n.d.; Silva & Brandão, 2014; García-Cárdenas et al., 2018).

The results of a functional comparison are more telling because they bring the ecology component into the equation. Studies that use Sørensen's Index in this way demonstrate the importance of niche-based processes in driving community turnover and the necessity of functional composition to detect these patterns. In other words, functional comparisons allow researchers to track changes in the functional composition of different communities and how these changes are influenced by changes in the environment (Siefert et al., n.d.).

In using Sørensen's similarity index as a functional similarity index, locomotor repertoires are substituted for taxa; locomotor repertoires are placed as column headers, while the different localities (both Whitehead Creek and modern) are placed as row headers. Each column in the matrix represents a functional unit (Figure 3.27). A functional unit (e.g. SCAN 1) is different than another functional unit (e.g. SCAN 2) of the same site, as each functional unit represents a small mammal that fills a different scansorial niche. Comparing the same functional unit (e.g. SCAN 1) of different sites amounts to comparing like with like, as each site has at least one small mammal that fills the scansorial niche. The maximum number of columns for a single locomotor guild is determined by the site (whether modern or Whitehead Creek) with the most counts of that guild. For example, the Whitehead Creek terminal phalanx sample has 25 arboreal climbers; this indicates that there will be (at the most) 25 AC columns. Adding additional sites (i.e. modern localities) creates a continuous matrix, whereby Sørensen's similarity index evaluates the shared, functional units between sites (i.e. all of the joint occurrences represented by 1s). Sørensen's similarity index does not take into account all of the 0s, and the order of the 1s and 0s does not matter. The order of the sites does not matter either.

	SCAN	SCAN	SCAN	SCAN	SCAN
PTL1-Phil	1	1	1	1	0
STL1-Phil	1	1	1	1	1
PTLF2-NEMad	1	1	1	0	0
STLF2-NEMad	1	1	1	0	0
TG1-Swan	1	1	0	0	0
Oak/Hick1-Swan	1	1	1	1	0
TallG2-S.Africa	1	0	0	0	0
TG2700(2)-S. Africa	1	1	0	0	0
ChestOakF2-Virginia	1	1	1	1	1
WGF1-Brazil	1	1	1	1	1
WGF1-Kenya	1	1	1	0	0
AlderGF2-S.Cent.Eur.	1	1	0	0	0
HGOGF1- Peru	1	1	1	1	1
OGF2- Washington	1	1	0	0	0
Taiga1-Japan	1	1	0	0	0
Taiga2-Canada	1	1	1	1	0
UpBF1-Thai	1	1	1	1	0
LowBF1-Thai	1	1	1	1	0
TropDDF2.1-Mexico	1	1	0	0	0
TropDDF2.2-Mexico	1	1	0	0	0
TropDDF2.3-Mexico	1	1	0	0	0
BamT1650-1850(2)-Viet.	1	1	1	0	0
BamT1850-2100(2)-Viet.	1	1	0	0	0
MontF1-Phil	0	0	0	0	0
Mont/CloudF2-Mexico	1	1	1	0	0
WHC-ASTRAG	1	1	1	1	1
WHC-CALC	1	1	1	1	1
WHC-TP	1	1	1	1	1

Figure 3.27. Construction of the Sørensen's similarity index matrix (Hammer, 2018). Locomotor repertoires are substituted for taxa; the locomotor repertoires are placed as column headers. Sites, including Whitehead Creek and all modern sites, are placed as row headers. The order of the 1s and 0s in the matrix does not matter; order of the sites does not matter. See chapter 4 – results for meaning of the colored dots.

Environmental characteristics of modern sites (MANOVA and Euclidean Distance)

Preliminary analysis shows no relationship between locomotion and biome name, as like biomes do not cluster together in Sørensen's similarity index (see Figure 4.1 in chapter 4).

Because the preliminary analysis reveals that there is no relationship between locomotion and biome name, the relationship between locomotion and characteristics of the environment is evaluated. To evaluate the relationship between small mammal locomotor guild frequencies and physical characteristics of the environment (Table 3.9), each modern site is scored for length of

the dry season (in weeks), seasonality in precipitation (2 driest months/2 wettest months [x 100]), temperature difference (2 warmest months – 2 coldest months) and number of forest levels.

These data are evaluated using two methods in PAST3.22. First, clusters of modern sites identified using the Sørensen's similarity index analysis are compared using Hotelling's p (part of a MANOVA analysis) to investigate whether clusters identified on the basis of locomotor guild frequencies differ significantly in physical, environmental properties. Second, modern sites are clustered on the basis of physical characteristics of the environment using a Euclidean Distance analysis. The composition of the cluster obtained using Euclidean Distance on environmental data is compared with the composition of the cluster obtained using Sørensen's similarity index on locomotor data.

Table 3.9. Physical characteristics of the environment that are used in the MANOVA and Euclidean Distance analyses in PAST3.22.

Biome	Dry Season (weeks)	Rainfall Seasonality (mm) (2 driest months/2 wettest months [x100])	Temperature Seasonality (°F) (2 warmest months – 2 coldest months)	Forest Levels
WGF-Brazil	24	28.1501	10.2	4
HGOGF1-Peru	24	17.9724	27	4
LowBF1-Thai	27	3.3333	22.3	3
PTL1-Phil	8.5	1.3233	16.2	4
PTLF2-NEMad	26	28.6036	14.4	6
UpBF1-Thai	27	3.3333	22.3	3
WGF1-Kenya	39	15	12.6	4
Mont/CloudF2-Mexico	31	2	10.8	4
BamT1650-1850(2)-Viet.	33	5.523	22	3
STL1-Phil	8.5	1.3233	16.2	4
TG1-Swan	7	31.6107	58	1
AlderGF2-S.Cent.Eur.	15	40.8654	43.2	3
OGF2-Washington	12	10.4712	25	6

Table 3.9 (continued)

Oak/Hick1-Swan	7	31.6107	58	3
ChestOakF2-Virginia	8	57.3604	18	4
Taiga2-Canada	24	42.6036	151	3
Taiga1-Japan	15	38.8379	48	3
TropDDF2.1-Mexico	15	1.8145	16.2	3
TropDDF2.2-Mexico	15	1.8145	16.2	3
TropDDF2.3-Mexico	15	1.8145	16.2	3
BamT1850-2100(2)-Viet.	33	5.523	22	3
TallG2-S.Africa	20	5.3824	16.2	1
TG2700(2)-S.Africa	20	5.3824	5.4	1
STLF2-NEMad	26	28.6036	14.4	6
MontF1-Phil	19	1.2176	9	3

Table 3.9 Key. WGF (Woodland Gallery Forest), HGOGF (High-Ground, Old-Growth Forest), LowBF (Lowland Bamboo Forest), UpBF (Upland Bamboo Forest), Thai (Thailand), PTL (Primary Tropical Lowland), PTLF (Primary Tropical Lowland Forest), NEMad (Northeastern Madagascar), Mont/Cloud (Cloud Forest), BamT1650-1850 (Bamboo Thicket at an Elevation of 1650-1850m), Viet (Vietnam), STL (Secondary Tropical Lowland), STLF (Secondary Tropical Lowland Forest), Phil (Philippines), TG (Temperate Grassland), Swan (Swan Lake National Wildlife Refuge, Missouri), AlderGF (Alder Gallery Forest), S.Cent.Eur (South-Central Europe), OGF (Old-Growth Forest), Oak/Hick (Oak-Hickory Deciduous Forest), ChestOakF (Chestnut Oak Xeric Deciduous Forest), TropDDF (Tropical Dry Deciduous Forest), BamT1850-2100 (Bamboo Thicket at an Elevation of 1850-2100m), TallG (Tall Grassland), S.Africa (South Africa), TG2700 (Temperate Grassland at an Elevation of 2700m) and MontF (Montane Forest).

Chapter 4 – Results

Whitehead Creek astragalus and calcaneus samples with assigned locomotor guilds

The Whitehead Creek astragalus sample consists of 56 specimens, representing 56 morphospecies (Table 4.1 and 4.2). The Whitehead Creek calcaneus sample consists of 44 specimens, representing 43 morphospecies (Table 4.3, 4.4 and 4.5). Locomotor categories of those specimens marked with an asterisk are assigned on the basis of criteria other than the majority rule and receive further discussion.

Table 4.1. Whitehead Creek astragalus sample with four traits.

Specimen #'s (University of Montana Paleontology Center)	Trochlea Symmetry	Head-Neck-Length Index	Neck Angle	Position of Ectal Facet
* UMPC – 19560	Symmetrical (C and SA)	1.09 (AL and TL)	20.49° (AL, TL and C)	Plantar (TG, AC, SCAN, F and SA)
* UMPC – 19561	Some (AL, TL and TG)	0.739 (C, TG, AC, SCAN and F)	20.58° (AL, TL and C)	Lateral (AL, TL and C)
* UMPC – 19562	Marked (AC, SCAN and F)	1.051 (AL and TL)	23.061° (AL, TL and C)	Lateral (AL, TL and C)
UMPC – 19563	Some (AL, TL and TG)	0.836 (C, TG, AC, SCAN and F)	19.49° (AL, TL and C)	Plantar (TG, AC, SCAN, F and SA)

Table 4.1 (continued)

UMPC – 19564	Marked (AC, SCAN and F)	0.716 (C, TG, AC, SCAN and F)	6.995° (AL, TL and C)	Plantar (TG, AC, SCAN, F and SA)
UMPC – 19565	Some (AL, TL and TG)	0.87 (C, TG, AC, SCAN and F)	14.583° (AL, TL and C)	Plantar (TG, AC, SCAN, F and SA)
UMPC – 19566	Marked (AC, SCAN and F)	0.718 (C, TG, AC, SCAN and F)	23.26° (AL, TL and C)	Plantar (TG, AC, SCAN, F and SA)
UMPC – 19567	Marked (AC, SCAN and F)	0.775 (C, TG, AC, SCAN and F)	18° (AL, TL and C)	Plantar (TG, AC, SCAN, F and SA)
UMPC - 19568	Symmetrical (C and SA)	0.652 (C, TG, AC, SCAN and F)	20.157° (AL, TL and C)	Lateral (AL, TL and C)
UMPC - 19569	Marked (AC, SCAN and F)	0.676 (C, TG, AC, SCAN and F)	20.132° (AL, TL and C)	Plantar (TG, AC, SCAN, F and SA)
UMPC – 19570	Marked (AC, SCAN and F)	0.752 (C, TG, AC, SCAN and F)	19.65° (AL, TL and C)	Plantar (TG, AC, SCAN, F and SA)
UMPC – 19571	Marked (AC, SCAN and F)	0.784 (C, TG, AC, SCAN and F)	17.045° (AL, TL and C)	Plantar (TG, AC, SCAN, F and SA)

Table 4.1 (continued)

* UMPC – 19572	Marked (AC, SCAN and F)	0.841 (C, TG, AC, SCAN and F)	23.182° (AL, TL and C)	Plantar (TG, AC, SCAN, F and SA)
UMPC – 19573	Marked (AC, SCAN and F)	0.886 (C, TG, AC, SCAN and F)	24.207° (AL, TL and C)	Plantar (TG, AC, SCAN, F and SA)
UMPC – 19574	Marked (AC, SCAN and F)	0.771 (C, TG, AC, SCAN and F)	18.41° (AL, TL and C)	Plantar (TG, AC, SCAN, F and SA)
UMPC – 19575	Marked (AC, SCAN and F)	0.8 (C, TG, AC, SCAN and F)	27.882° (TG and SA)	Plantar (TG, AC, SCAN, F and SA)
* UMPC – 19576	Marked (AC, SCAN and F)	1.0 (AL and TL)	38.303° (AC, SCAN and F)	Plantar (TG, AC, SCAN, F and SA)
UMPC - 19577	Marked (AC, SCAN and F)	0.763 (C, TG, AC, SCAN and F)	17.633° (AL, TL and C)	Plantar (TG, AC, SCAN, F and SA)
UMPC - 19578	Marked (AC, SCAN and F)	0.864 (C, TG, AC, SCAN and F)	19.51° (AL, TL and C)	Plantar (TG, AC, SCAN, F and SA)
* UMPC - 19579	Some (AL, TL and TG)	1.225 (AL and TL)	24.89° (AL, TL and C)	Plantar (TG, AC, SCAN, F and SA)

Table 4.1 (continued)

UMPC – 19580	N/A	N/A	7.022° (AL, TL and C)	Lateral (AL, TL and C)
UMPC – 19581	N/A	N/A	N/A	Plantar (TG, AC, SCAN, F and SA)
UMPC – 19582	Marked (AC, SCAN and F)	0.74 (C, TG, AC, SCAN and F)	20.625° (AL, TL and C)	Plantar (TG, AC, SCAN, F and SA)
UMPC – 19583	Marked (AC, SCAN and F)	0.732 (C, TG, AC, SCAN and F)	19.665° (AL, TL and C)	Plantar (TG, AC, SCAN, F and SA)
UMPC – 19584	Marked (AC, SCAN and F)	0.761 (C, TG, AC, SCAN and F)	15.764° (AL, TL and C)	Plantar (TG, AC, SCAN, F and SA)
* UMPC - 19585	Some (AL, TL and TG)	0.738 (C, TG, AC, SCAN and F)	14.304° (AL, TL and C)	Plantar (TG, AC, SCAN, F and SA)
UMPC – 19586	Some (AL, TL and TG)	0.691 (C, TG, AC, SCAN and F)	14.039° (AL, TL and C)	Plantar (TG, AC, SCAN, F and SA)
UMPC - 19587	Some (AL, TL and TG)	0.857 (C, TG, AC, SCAN and F)	21.862° (AL, TL and C)	Plantar (TG, AC, SCAN, F and SA)

Table 4.1 (continued)

* UMPC - 19588	Some (AL, TL and TG)	0.943 (C, TG, AC, SCAN and F)	13.743° (AL, TL and C)	Lateral (AL, TL and C)
* UMPC - 19589	N/A	0.876 (C, TG, AC, SCAN and F)	13.706° (AL, TL and C)	Lateral (AL, TL and C)
* UMPC - 19590	Marked (AC, SCAN and F)	0.735 (C, TG, AC, SCAN and F)	19.219° (AL, TL and C)	Lateral (AL, TL and C)
UMPC – 19591	Some (AL, TL and TG)	0.742 (C, TG, AC, SCAN and F)	20.671° (AL, TL and C)	Lateral (AL, TL and C)
UMPC – 19592	Some (AL, TL and TG)	0.844 (C, TG, AC, SCAN and F)	13.17° (AL, TL and C)	Lateral (AL, TL and C)
* UMPC – 19593	Some (AL, TL and TG)	0.917 (C, TG, AC, SCAN and F)	20.143° (AL, TL and C)	Lateral (AL, TL and C)
* UMPC – 19594	N/A	N/A	9.309° (AL, TL and C)	Plantar (TG, AC, SCAN, F and SA)
* UMPC – 19595	N/A	N/A	15.103° (AL, TL and C)	N/A

Table 4.1 (continued)

UMPC – 19596	N/A	N/A	N/A	N/A
UMPC - 19597	N/A	0.824 (C, TG, AC, SCAN and F)	17.595° (AL, TL and C)	Plantar (TG, AC, SCAN, F and SA)
UMPC – 19598	Some (AL, TL and TG)	0.873 (C, TG, AC, SCAN and F)	13.124° (AL, TL and C)	Plantar (TG, AC, SCAN, F and SA)
UMPC - 19599 (Marsupial)	Marked * Medial rim is longer than lateral (AC, SCAN and F)	0.625 (C, TG, AC, SCAN and F)	8.142° (AL, TL and C)	Lateral (AL, TL and C)
* UMPC 19600	Some (AL, TL and TG)	0.972 (C, TG, AC, SCAN and F)	22.839° (AL, TL and C)	Lateral (AL, TL and C)
* UMPC – 19601	Some (AL, TL and TG)	0.802 (C, TG, AC, SCAN and F)	16.444° (AL, TL and C)	Lateral (AL, TL and C)
* UMPC – 19602	Some (AL, TL and TG)	0.793 (C, TG, AC, SCAN and F)	15.507° (AL, TL and C)	Lateral (AL, TL and C)

Table 4.1 (continued)

* UMPC – 19603	N/A	0.836 (C, TG, AC, SCAN and F)	16.967° (AL, TL and C)	Lateral (AL, TL and C)
* UMPC – 19604	Some (AL, TL and TG)	0.726 (C, TG, AC, SCAN and F)	19.16° (AL, TL and C)	Lateral (AL, TL and C)
* UMPC - 19605 (Marsupial)	Marked * Medial rim is longer than lateral (AC, SCAN and F)	1.052 (AL and TL)	8.389° (AL, TL and C)	Lateral (AL, TL and C)
* UMPC – 19606	Marked (AC, SCAN and F)	0.747 (C, TG, AC, SCAN and F)	34.651° (AC, SCAN and F)	Lateral (AL, TL and C)
UMPC – 19607	Some (AL, TL and TG)	0.883 (C, TG, AC, SCAN and F)	13.344° (AL, TL and C)	Plantar (TG, AC, SCAN, F and SA)
UMPC – 19608	Some (AL, TL and TG)	0.736 (C, TG, AC, SCAN and F)	8.872° (AL, TL and C)	Plantar (TG, AC, SCAN, F and SA)
UMPC – 19609	Some (AL, TL and TG)	0.854 (C, TG, AC, SCAN and F)	17.657° (AL, TL and C)	Lateral (AL, TL and C)
* UMPC - 19610	Some (AL, TL and TG)	0.851 (C, TG, AC, SCAN and F)	21.8° (AL, TL and C)	Lateral (AL, TL and C)

Table 4.1 (continued)

UMPC – 19611	Some (AL, TL and TG)	0.911 (C, TG, AC, SCAN and F)	19.53° (AL, TL and C)	Lateral (AL, TL and C)
* UMPC – 19612	Some (AL, TL and TG)	0.825 (C, TG, AC, SCAN and F)	31.179° (TG and SA)	Lateral (AL, TL and C)
UMPC – 19613	Marked (AC, SCAN and F)	0.808 (C, TG, AC, SCAN and F)	13.562° (AL, TL and C)	Plantar (TG, AC, SCAN, F and SA)
* UMPC – 19614	Some (AL, TL and TG)	0.921 (C, TG, AC, SCAN and F)	13.632° (AL, TL and C)	Lateral (AL, TL and C)
* UMPC - 19615	Marked (AC, SCAN and F)	1.167 (AL and TL)	22.987° (AL, TL and C)	Plantar (TG, AC, SCAN, F and SA)

Table 4.2. Whitehead Creek astragalus sample with the other four traits and assigned locomotor guilds.

Specimen #'s (University of Montana Paleontology Center)	Trochlear Depth	Shape of the Navicular Facet	Squatting Facet	Extension of Trochlea onto the Astragalar Neck	Assigned Locomotor Guild
* UMPC – 19560	Shallow (AC and F)	Round (AL, TG and AC)	Absent	Yes (AL, AC and SCAN)	AC
* UMPC – 19561	Moderate (TG, SCAN and SA)	Ellipse (C and F)	Present	Yes (AL, AC and SCAN)	SCAN

Table 4.2 (continued)

* UMPC – 19562	Shallow (AC and F)	Ellipse (C and F)	Absent	No	AC
UMPC – 19563	Moderate (TG, SCAN and SA)	Ovoid (TL, SCAN and SA)	Present	Yes (AL, AC and SCAN)	SCAN
UMPC – 19564	Deep (AL, TL and C)	Ovoid (TL, SCAN and SA)	Present	Yes (AL, AC and SCAN)	SCAN
UMPC – 19565	Moderate (TG, SCAN and SA)	Ovoid (TL, SCAN and SA)	Absent	No	SCAN
UMPC – 19566	Moderate (TG, SCAN and SA)	Ovoid (TL, SCAN and SA)	Present	Yes (AL, AC and SCAN)	SCAN
UMPC – 19567	Moderate (TG, SCAN and SA)	Ovoid (TL, SCAN and SA)	Absent	No	SCAN
UMPC - 19568	Deep (AL, TL and C)	Ovoid (TL, SCAN and SA)	Present - huge	No	C
UMPC - 19569	Moderate (TG, SCAN and SA)	Ovoid (TL, SCAN and SA)	Present	Yes (AL, AC and SCAN)	SCAN
UMPC – 19570	Deep (AL, TL and C)	Ovoid (TL, SCAN and SA)	Present	Yes (AL, AC and SCAN)	SCAN
UMPC – 19571	Moderate (TG, SCAN and SA)	Ovoid (TL, SCAN and SA)	Present	Yes (AL, AC and SCAN)	SCAN
* UMPC – 19572	Shallow (AC and F)	Ovoid (TL, SCAN and SA)	Absent	No	TG

Table 4.2 (continued)

UMPC – 19573	Deep (AL, TL and C)	Ovoid (TL, SCAN and SA)	Absent	No	SCAN
UMPC – 19574	Moderate (TG, SCAN and SA)	Ellipse (C and F)	Absent	Yes (AL, AC and SCAN)	SCAN
UMPC – 19575	Deep (AL, TL and C)	Ovoid (TL, SCAN and SA)	Present	Yes (AL, AC and SCAN)	SCAN
* UMPC – 19576	Shallow (AC and F)	Ovoid (TL, SCAN and SA)	Present	Yes (AL, AC and SCAN)	AC
UMPC - 19577	Moderate (TG, SCAN and SA)	Ovoid (TL, SCAN and SA)	Present	Yes (AL, AC and SCAN)	SCAN
UMPC - 19578	Moderate (TG, SCAN and SA)	Ovoid (TL, SCAN and SA)	Present	Yes (AL, AC and SCAN)	SCAN
* UMPC - 19579	Shallow (AC and F)	Ovoid (TL, SCAN and SA)	Absent	No	F
UMPC – 19580	Deep (AL, TL and C)	Subcylindrical (lagomorphs only)	Absent	No	TL
UMPC – 19581	Shallow (AC and F)	Round (AL, TG and AC)	Absent	No	AC
UMPC – 19582	Moderate (TG, SCAN and SA)	Ovoid (TL, SCAN and SA)	Present	Yes (AL, AC and SCAN)	SCAN

Table 4.2 (continued)

UMPC – 19583	Moderate (TG, SCAN and SA)	Ovoid (TL, SCAN and SA)	Present	Yes (AL, AC and SCAN)	SCAN
UMPC – 19584	Moderate (TG, SCAN and SA)	Ovoid (TL, SCAN and SA)	Present	Yes (AL, AC and SCAN)	SCAN
* UMPC - 19585	Deep (AL, TL and C)	Ovoid (TL, SCAN and SA)	Present	No	TG
UMPC – 19586	Moderate (TG, SCAN and SA)	Ovoid (TL, SCAN and SA)	Present	Yes (AL, AC and SCAN)	SCAN
UMPC - 19587	Moderate (TG, SCAN and SA)	Ovoid (TL, SCAN and SA)	Present	Yes (AL, AC and SCAN)	SCAN
* UMPC - 19588	Moderate (TG, SCAN and SA)	Ovoid (TL, SCAN and SA)	Present	Yes (AL, AC and SCAN)	SCAN
* UMPC - 19589	Moderate (TG, SCAN and SA)	Round (AL, TG and AC)	Present - small	Yes (AL, AC and SCAN)	SCAN
* UMPC - 19590	Deep (AL, TL and C)	Round (AL, TG and AC)	Absent	No	TG
UMPC – 19591	Moderate (TG, SCAN and SA)	Ovoid (TL, SCAN and SA)	Absent	No	TL

Table 4.2 (continued)

UMPC – 19592	Deep (AL, TL and C)	Ovoid (TL, SCAN and SA)	Present	Yes (AL, AC and SCAN)	TL
* UMPC – 19593	Moderate (TG, SCAN and SA)	Ovoid (TL, SCAN and SA)	Present	Yes (AL, AC and SCAN)	SCAN
* UMPC – 19594	Moderate (TG, SCAN and SA)	Ovoid (TL, SCAN and SA)	Present	Yes (AL, AC and SCAN)	TG
* UMPC – 19595	Moderate (TG, SCAN and SA)	Ovoid (TL, SCAN and SA)	Present	Yes (AL, AC and SCAN)	TG
UMPC - 19596	Deep (AL, TL and C)	Ovoid (TL, SCAN and SA)	Absent	No	TL
UMPC - 19597	Shallow (AC and F)	N/A	Present	Yes (AL, AC and SCAN)	AC
UMPC – 19598	Moderate (TG, SCAN and SA)	Ovoid (TL, SCAN and SA)	Present	No	SCAN
UMPC - 19599 (Marsupial)	Shallow (AC and F)	Round (AL, TG and AC)	Absent	No	AC
* UMPC 19600	Moderate (TG, SCAN and SA)	Ovoid (TL, SCAN and SA)	Present	Yes (AL, AC and SCAN)	SCAN

Table 4.2 (continued)

* UMPC – 19601	Moderate (TG, SCAN and SA)	Ovoid (TL, SCAN and SA)	Present	Yes (AL, AC and SCAN)	SCAN
* UMPC – 19602	Moderate (TG, SCAN and SA)	N/A	Absent	Yes (AL, AC and SCAN)	TG
* UMPC – 19603	Shallow (AC and F)	Ovoid (TL, SCAN and SA)	Present - small	Yes (AL, AC and SCAN)	TG
* UMPC – 19604	Deep (AL, TL and C)	Ovoid (TL, SCAN and SA)	Present	Yes (AL, AC and SCAN)	TL
* UMPC - 19605 (Marsupial)	Shallow (AC and F)	Ovoid (TL, SCAN and SA)	Present	No	TG
* UMPC – 19606	Shallow (AC and F)	Ovoid (TL, SCAN and SA)	Present	No	AC
UMPC – 19607	N/A	Ovoid (TL, SCAN and SA)	Present - huge	No	SCAN
UMPC – 19608	Moderate (TG, SCAN and SA)	Ovoid (TL, SCAN and SA)	Absent	No	SCAN
UMPC – 19609	Moderate (TG, SCAN and SA)	Ovoid (TL, SCAN and SA)	Absent	No	TL
* UMPC - 19610	Moderate (TG, SCAN and SA)	Ovoid (TL, SCAN and SA)	Present	Yes (AL, AC and SCAN)	SCAN
UMPC – 19611	Moderate (TG, SCAN and SA)	Ovoid (TL, SCAN and SA)	Absent	Yes (AL, AC and SCAN)	TL

Table 4.2 (continued)

* UMPC – 19612	Moderate (TG, SCAN and SA)	N/A	Absent	Yes (AL, AC and SCAN)	SCAN
UMPC – 19613	Deep (AL, TL and C)	Ovoid (TL, SCAN and SA)	Present	Yes (AL, AC and SCAN)	SCAN
* UMPC – 19614	Deep (AL, TL and C)	Ovoid (TL, SCAN and SA)	Present	Yes (AL, AC and SCAN)	TL
* UMPC - 19615	Deep (AL, TL and C)	Ovoid (TL, SCAN and SA)	Absent	No	AC

UMPC - 19560 demonstrates two locomotor behaviors, arboreal climbing and arboreal leaping. This specimen mainly exhibits arboreal climbing traits; however, it does exhibit several arboreal leaping traits. The arboreal climbing traits include plantar orientation of the ectal facet and a shallow trochlea. This specimen exhibits a long head-neck length, and a low neck angle, characteristics of leapers (Dagosto, 1983; Ginot et al., 2016). Arboreal leapers and arboreal climbers share several traits. UMPC – 19560 demonstrates some of these traits: a round shape of the navicular facet and extension of the trochlear surface onto the dorsal surface of the astragalar neck.

Whereas UMPC - 19561 exhibits a majority of characteristics consistent with arboreal leaping and cursorial behaviors, it is classified as scansorial due to the presence of some asymmetry of the trochlea and moderate trochlear grooving. Moderate trochlear grooving allows for some mobility in the upper ankle joint (Ginot et al., 2016). In this specimen, the medial trochlear rim is shorter than the lateral trochlear rim in both length and height. The unequal sizes of the medial and lateral trochlear rims are often seen in arboreal mammals that utilize inverted

and everted ankle postures (Dunn, 2009). This specimen also demonstrates some mobility at the subtalar joint. The ectal facet is less concave and extends both medial and antero-posteriorly (Ginot et al., 2016).

Whereas UMPC - 19562 exhibits a majority of characteristics consistent with leaping, cursorial and fossorial behaviors, it is classified as an arboreal climber because the sustentacular facet is fully confluent with the navicular facet. This trait, in addition to the sustentacular facet having a transverse component (i.e. antero-posterior reduction and medio-lateral expansion), allow for increased mobility at the subtalar joint (Ginot et al., 2016). The navicular facet is well-developed on the medial side of the neck, which allows for increased mobility at the transverse tarsal joint. The trochlea displays shallow grooving. This allows the upper ankle joint to have some medial and lateral mobility (Ginot et al., 2016). This specimen demonstrates mobility at all three ankle joints – the upper ankle joint, subtalar joint and transverse tarsal joint.

Whereas UMPC - 19572 exhibits a majority of characteristics consistent with climbing and fossorial behaviors, it is classified as a terrestrial generalist because, while this specimen demonstrates good mobility at all three ankle joints, it exhibits a wide, moderately deep groove between the ectal facet and the sustentacular facet, which suggests the presence of moderately strong ligaments between the astragalus and calcaneus (Ginot et al., 2016). This groove is more pronounced in primarily terrestrial mammals, whereas it is less pronounced in primarily arboreal mammals (Ginot et al., 2016).

Whereas UMPC - 19576 exhibits a majority of characteristics consistent with climbing and fossorial behaviors, it is classified as an arboreal climber due to the presence of marked trochlear asymmetry, with the lateral trochlear rim being twice as long as the medial trochlear rim. Marked trochlear asymmetry and shallow trochlear grooving are two arboreal climbing

traits that allow for added mobility at the upper ankle joint (Dunn, 2009; Rose et al., 2015; Ginot et al., 2016). While marked trochlear asymmetry is primarily seen in mammals that utilize inverted and everted ankle postures (Dunn, 2009), a shallow trochlea further adds to mobility in the upper ankle joint by allowing for some lateral mobility (Ginot et al., 2016).

UMPC - 19579 is classified as fossorial because it demonstrates increased mobility in the upper ankle joint. In fossorial taxa, flexibility of the ankle mainly depends on the upper ankle joint (Ginot et al., 2016). This specimen has a shallow trochlea and a trochlear body that is broad and shallow. A fairly wide trochlea is associated with a slight lateral projection of the sustentacular facet, while the flatter body shape is linked to a lesser arc of parasagittal movements (Ginot et al., 2016). According to Dunn (2009), a flatter trochlear body indicates a significant amount of lateral mobility at the upper ankle joint. The ectal facet of this specimen is moderately concave. Strong curvature of the ectal facet would limit movements of the calcaneus in regard to the astragalus (Ginot et al., 2016).

UMPC - 19585 is classified as a terrestrial generalist because it demonstrates a mix of leaping, cursorial and scansorial behaviors. This specimen exhibits deep trochlear grooving, which is characteristic of leaping and cursorial taxa (Ginot et al., 2016). Deep trochlear grooving restricts movements of the upper ankle joint to purely plantar- and dorsi-flexion, which adds to the stability of this joint (Ginot et al., 2016). Whereas there is stability in the upper ankle joint, there is some mobility in the subtalar joint and transverse tarsal joint. The ectal facet is plantarly-oriented, and the sustentacular facet is ovoid in shape. An ovoid shape of the sustentacular facet produces a slight transverse component. Increased width of the sustentacular facet permits medio-lateral movements at the subtalar joint which increases mobility (Ginot et al., 2016). The

navicular facet is ovoid in shape. An ovoid shape of the navicular facet suggests frequent use of inverted and everted ankle postures (Chester et al., 2015).

Whereas UMPC - 19588 exhibits a majority of characteristics consistent with leaping and scansorial behaviors, it is classified as scansorial due to the presence of moderate trochlear grooving, an ovoid shape of the navicular facet, and a sustentacular facet that takes up almost the whole width of the plantar surface of the trochlear neck, which indicates a transverse component. The medial and lateral trochlear rims are unequal in length and height. Unequal sizes of the medial and lateral trochlear rims are often seen in arboreal mammals that utilize inverted and everted ankle postures (Dunn, 2009). This produces mobility at the upper ankle joint. A transverse component of the sustentacular facet permits medio-lateral movements at the subtalar joint, which increases mobility (Ginot et al., 2016). An ovoid shape of the navicular facet also suggests frequent use of inverted and everted ankle postures (Chester et al., 2015).

Whereas UMPC - 19589 exhibits a majority of characteristics consistent with leaping, it is classified as scansorial due to the presence of moderate trochlear grooving, a slight transverse component of the sustentacular facet and a round shape of the navicular facet. Whereas the posterior margin of the medial trochlear rim is gone, the medial trochlear rim is still higher than the lateral rim from a posterior view. Unequal sizes of the medial and lateral trochlear rims are often seen in arboreal mammals that utilize inverted and everted ankle postures (Dunn, 2009). A transverse component of the sustentacular facet permits medio-lateral movements at the subtalar joint. A round shape of the navicular facet allows for a wide range of movements, adding significant mobility to the transverse tarsal joint (Ginot et al., 2016).

Whereas UMPC - 19590 exhibits a majority of characteristics consistent with arboreal leaping and cursorial behaviors, it is classified as a terrestrial generalist. Whereas this specimen

exhibits deep trochlear grooving, a leaping (Dunn, 2009; Ginot et al., 2016) and terrestrial cursor (Ginot et al., 2016) trait, the sustentacular facet has a transverse component and the navicular facet has a round shape. The sustentacular facet takes up almost the whole width of the plantar surface of the astragalar neck. A transverse component of the sustentacular facet permits medio-lateral movements at the subtalar joint, increasing mobility (Ginot et al., 2016). A round shape of the navicular facet allows for a wide range of movements, adding significant mobility to the transverse tarsal joint (Ginot et al., 2016).

Whereas UMPC - 19593 exhibits a majority of characteristics consistent with leaping and scansorial behaviors, it is classified as scansorial due to the presence of moderate trochlear grooving, a sustentacular facet with a transverse component and an ovoid-shaped navicular facet. These traits are consistent with mobility at all three ankle joints. The medial trochlear rim is shorter and higher than the lateral trochlear rim. Unequal sizes of the medial and lateral trochlear rims are generally seen in arboreal mammals that utilize inverted and everted ankle postures (Dunn, 2009). The lateral trochlear rim, being low in height, allows for some lateral mobility at the upper ankle joint (Dunn, 2009; Ginot et al., 2016). The trochlear surface merges, and is confluent with, the outline of the squatting facet. Extension of the trochlear surface onto the dorsal surface of the astragalar neck is an arboreal trait (Chester et al., 2015). A transverse component of the sustentacular facet permits medio-lateral mobility at the subtalar joint (Ginot et al., 2016), and an ovoid shape of the navicular facet suggests frequent use of inverted and everted ankle postures (Chester et al., 2015).

Whereas UMPC - 19594 exhibits a majority of characteristics consistent with climbing behaviors, it is classified as a terrestrial generalist because of a low neck angle. Climbing taxa generally exhibit a high neck angle (Ginot et al., 2016). Relative to a high neck angle, a low neck

angle causes the sustentacular facet to be more antero-posteriorly oriented, which greatly reduces transverse movements of the calcaneus below the astragalus (Ginot et al., 2016). Despite having a low neck angle, this specimen exhibits moderate trochlear grooving, a plantarly-oriented ectal facet and an ovoid-shaped navicular facet. Moderate trochlear grooving allows for some mobility at the upper ankle joint (Dunn, 2009), while an ovoid-shaped navicular facet allows for some mobility at the transverse tarsal joint (Chester et al., 2015).

UMPC - 19595 is classified as a terrestrial generalist due to the presence of moderate trochlear grooving, a navicular facet that is ovoid in shape, and a low neck angle. Moderate trochlear grooving permits some lateral movement at the upper ankle joint (Dunn, 2009), while an ovoid-shaped navicular facet indicates frequent use of inverted and everted ankle postures (Chester et al., 2015). The presence of a low neck angle causes the sustentacular facet to be more antero-posteriorly oriented, which greatly reduces transverse movements of the calcaneus below the astragalus (Ginot et al., 2016). Climbing taxa generally have a high neck angle, which increases the articular surface of the sustentacular facet, along which the calcaneus may slide (Ginot et al., 2016).

Whereas UMPC - 19600 exhibits a majority of characteristics consistent with leaping and scansorial behaviors, it is classified as scansorial due to the presence of moderate trochlear grooving, a transverse component of the sustentacular facet and a navicular facet that is ovoid in shape. Whereas leapers are characterized by having a very stable upper ankle joint (Dagosto, 1986; Gebo, 1986; Dunn, 2009; Ginot et al., 2016), UMPC - 19600 demonstrates some mobility at the upper ankle joint, as indicated by moderate trochlear grooving. This allows for some lateral movement at the upper ankle joint. A transverse component of the sustentacular facet permits medio-lateral movements at the subtalar joint (Ginot et al., 2016), and an ovoid-shaped

navicular facet suggests frequent use of inverted and everted ankle postures (Chester et al., 2015).

UMPC - 19601 is classified as scansorial because it demonstrates moderate trochlear grooving, a transverse component of the sustentacular facet and an ovoid-shaped navicular facet. Unequal sizes of the medial and lateral trochlear rims allow for some lateral movement at the upper ankle joint (Dunn, 2009). A transverse component of the sustentacular facet permits medio-lateral movements at the subtalar joint, and an ovoid-shaped navicular facet indicates frequent use of inverted and everted ankle postures (Chester et al., 2015). This specimen does not have a deep trochlea, a trait that is consistent with leaping behaviors (Dagosto, 1986; Gebo, 1986; Dunn, 2009; Ginot et al., 2016).

Whereas UMPC - 19602 exhibits a majority of characteristics consistent with arboreal leaping behaviors, it is classified as a terrestrial generalist because it demonstrates moderate trochlear grooving, which allows for some lateral movement at the upper ankle joint (Dunn, 2009). Leaping and cursorial taxa have a relatively stable upper ankle joint, as indicated by deep trochlear grooving (Dagosto, 1986; Gebo, 1986; Dunn, 2009; Ginot et al., 2016). Due to the absence of several significant traits, such as shape of the navicular facet and morphology of the sustentacular facet, a full assessment of mobility at the subtalar joint and transverse tarsal joint is difficult.

UMPC - 19603 is classified as a terrestrial generalist because it demonstrates a majority of characteristics consistent with leaping, cursorial and climbing behaviors. This specimen exhibits a shallow trochlea, a huge sustentacular facet with a transverse component and an ovoid-shaped navicular facet. A shallow trochlea allows for increased mobility at the upper ankle joint (Dunn, 2009; Ginot et al., 2016). A transverse component of the sustentacular facet permits

medio-lateral movements at the subtalar joint (Ginot et al., 2016), and an ovoid-shaped navicular facet suggests frequent use of inverted and everted ankle postures (Chester et al., 2015). Whereas this specimen demonstrates mobility at the upper ankle joint, subtalar joint and transverse tarsal joint, it exhibits a characteristic that is often seen in terrestrial mammals, a laterally-oriented ectal facet. Lateral orientation of the ectal facet limits transverse and antero-posterior movements of the astragalus in regard to the calcaneus (Ginot et al., 2016).

Whereas UMPC - 19604 exhibits a majority of characteristics consistent with arboreal leaping and terrestrial leaping, it is classified as a terrestrial leaper due to the presence of an ovoid-shaped navicular facet. An ovoid shape of the navicular facet suggests frequent use of inverted and everted ankle postures (Chester et al., 2015). Arboreal leapers demonstrate characteristics that enhance mobility and flexibility of the ankle, key attributes that allow them to move in an arboreal environment (Warburton & Prideaux, 2010). One such trait is a navicular facet that is round in shape. A round navicular facet allows for a wide range of movements, adding significant mobility to the transverse tarsal joint (Ginot et al., 2016).

UMPC - 19605 is a marsupial specimen that is different from the other marsupial specimen (UMPC - 19599) in this sample. UMPC - 19605 exhibits a squatting facet. The presence of a squatting facet indicates the use of habitual, hyper-dorsiflexed foot postures (Dunn, 2009; Ladeveze et al., 2010). The presence of a squatting facet in this specimen suggests that it was doing something different with its ankles.

Whereas UMPC - 19606 exhibits a majority of characteristics consistent with climbing and fossorial behaviors, it is classified as an arboreal climber due to the presence of a shallow trochlea, marked trochlear asymmetry, a high neck angle, a navicular facet that is ovoid in shape and a transverse component of the sustentacular facet. A shallow trochlea, combined with

marked trochlear asymmetry, allow for increased mobility at the upper ankle joint (Ginot et al., 2016). A high neck angle increases the articular surface of the sustentacular facet, along which the calcaneus may slide (Ginot et al., 2016). A transverse component of the sustentacular facet permits medio-lateral mobility at the subtalar joint (Ginot et al., 2016), and an ovoid-shaped navicular facet suggests frequent use of inverted and everted ankle postures (Chester et al., 2015).

Other informative traits that UMPC - 19606 exhibits involve an ectal facet that is transversely compressed, strongly concave, and extremely laterally-oriented. This combination of traits limits the transverse and antero-posterior movements of the calcaneus in regard to the astragalus, which indicate that the astragalus and calcaneus are maintained together, as a unit, during rotation of the ankle rather than being allowed to move as independent entities (Ginot et al., 2016). Extreme lateral orientation of the ectal facet is not a characteristic that is seen in arboreal mammals (Dunn, 2009).

Whereas UMPC - 19610 exhibits a majority of characteristics consistent with leaping and scansorial behaviors, it is classified as scansorial due to the presence of moderate trochlear grooving and an ovoid-shaped navicular facet. Unequal sizes of the medial and lateral trochlear rims allow for some lateral mobility at the upper ankle joint (Dunn, 2009). A navicular facet that is ovoid in shape suggests frequent use of inverted and everted ankle postures (Chester et al., 2015). The navicular facet of this specimen is deeper on the lateral side, likely reflecting forces frequently transmitted on the lateral side of the head during habitual pedal eversion (Chester et al., 2015).

Whereas UMPC - 19612 exhibits a majority of characteristics consistent with arboreal leaping and scansorial behaviors, it is classified as scansorial due to the presence of moderate

trochlear grooving and a sustentacular facet that takes up the whole width of the plantar surface of the neck. A moderately-grooved trochlea allows for some lateral movement at the upper ankle joint (Ginot et al., 2016). A transverse component of the sustentacular facet permits medio-lateral movements at the subtalar joint (Ginot et al., 2016).

Whereas UMPC - 19614 exhibits a majority of characteristics consistent with arboreal and terrestrial leaping behaviors, it is classified as a terrestrial leaper because it exhibits a navicular facet that is ovoid in shape. An ovoid-shaped navicular facet suggests a frequent use of inverted and everted ankle postures, which allows for some mobility at the transverse tarsal joint (Chester et al., 2015). An arboreal leaper displays characteristics that enhance mobility and flexibility of the ankle, which allow it to move in an arboreal environment (Warburton & Prideaux, 2010). An example of an arboreal leaper trait is a navicular facet that is round in shape (Chester et al., 2015). A round shape of the navicular facet allows for a wide range of movements, adding significant mobility to the transverse tarsal joint (Ginot et al., 2016).

UMPC - 19615 demonstrates two locomotor behaviors, arboreal climbing and arboreal leaping. This specimen demonstrates some significant arboreal characteristics such as marked trochlear asymmetry and a plantarly-oriented ectal facet. Marked trochlear asymmetry suggests that the rotation axis of the foot has a transverse component (Ginot et al., 2016). This allows the foot to adapt to substrates of variable inclination, usually by different degrees of inversion and eversion (Dunn, 2009; Ginot et al., 2016). A plantar orientation of the ectal facet allows for increased mobility at the subtalar joint (Ginot et al., 2016). The ectal facet of this specimen is also less concave and extends medially and antero-posteriorly. This ectal facet morphology permits movement of the calcaneus in regard to the astragalus (Ginot et al., 2016).

UMPC - 19615 also demonstrates some significant leaping characteristics such as a deep trochlea, a long neck with a low neck angle and a sustentacular facet with an antero-posterior component. A deep trochlea provides stability to the upper ankle joint by limiting medio-lateral movements (Dagosto, 1986; Gebo, 1986; Dunn, 2009; Ginot et al., 2016). A long neck and a low neck angle are characteristic of leapers (Dagosto, 1983, 1986; Gebo, 1986). An antero-posterior component of the sustentacular facet indicates that plantar- and dorsiflexion movements are favored (Ginot et al., 2016).

Table 4.3. Whitehead Creek calcaneus sample with six traits.

Specimen #'s (University of Montana Paleontology Center)	Anterior Elongation (AE)	Posterior Elongation (PE)	Morphology of the Calcaneal Tuber (CTM)	Outline of the Ectal Facet (OEF)	Shape of the Cuboid Facet (SCF)	Orientation of the Cuboid Facet
UMPC - 19616	30.37% (AC, SCAN, F and SA)	39.26% (AL, TL, C, and SA)	0.6632 (AL, TL, C, TG, and SA)	1.865 (AL, TL, C, F, and SA)	0.83 (AL, TL, and C)	81.491° (AL, TL, C, F, and SA)
* UMPC – 19617	37.37% (AL, TL and C)	44.89% (AL, TL, C, and SA)	0.9565 (F)	1.7 (AL, TL, C, F, and SA)	1.41 (TG)	72.627° (AL, TL, C, F, and SA)
UMPC - 19618	30.74% (AC, SCAN, F and SA)	42.91% (AL, TL, C, and SA)	0.7532 (AL, TL, C, TG, and SA)	2.8 (TG, AC, and SCAN)	1.548 (TG)	84.482° (AL, TL, C, F, and SA)

Table 4.3 (continued)

UMPC – 19619	35.48% (TG)	N/A	N/A	1.612 (AL, TL, C, F, and SA)	1 (AC, SCAN, and F)	94.585° (TG, AC, and SCAN)
UMPC – 19620	25.71% (AC, SCAN, F and SA)	30.57% (TG, AC, SCAN, and F)	0.6567 (AC and SCAN)	2.28 (TG, AC, and SCAN)	1 (AC, SCAN, and F)	87.294° (TG, AC, and SCAN)
UMPC – 19621	28.13% (AC, SCAN, F and SA)	38.09% (AL, TL, C, and SA)	0.6474 (AC and SCAN)	1.642 (AL, TL, C, F, and SA)	1.4625 (TG)	77.335° (AL, TL, C, F, and SA)
UMPC – 19622	31.40% (AC, SCAN, F and SA)	36.13% (TG, AC, SCAN, and F)	0.7778 (AL, TL, C, TG, and SA)	1.842 (AL, TL, C, F, and SA)	0.782 (AL, TL, and C)	99.125° (AL, TL, C, F, and SA)
* UMPC - 19623	N/A	N/A	N/A	1.657 (AL, TL, C, F, and SA)	1.862 (TG)	86.269° (TG, AC, and SCAN)
UMPC - 19624 Marsupial	N/A	N/A	N/A	1.058 (AL, TL, C, F, and SA)	N/A	77.617° (AL, TL, C, F, and SA)
UMPC – 19625	28.63% (AC, SCAN, F and SA)	38.74% (AL, TL, C, and SA)	0.6647 (AL, TL, C, TG, and SA)	1.635 (AL, TL, C, F, and SA)	N/A	97.607° (AL, TL, C, F, and SA)
* UMPC - 19626	27.66% (AC, SCAN, F and SA)	36.05% (TG, AC, SCAN, and F)	0.6369 (AC and SCAN)	1.34 (AL, TL, C, F, and SA)	1.11 (TG)	94.114° (TG, AC, and SCAN)
UMPC – 19627	26.04% (AC, SCAN, F and SA)	33.80% (TG, AC, SCAN, and F)	0.8421 (AL, TL, C, TG, and SA)	2.069 (TG, AC, and SCAN)	1.397 (TG)	75.158° (AL, TL, C, F, and SA)

Table 4.3 (continued)

* UMPC - 19628	24.52% (AC, SCAN, F and SA)	30.58% (TG, AC, SCAN, and F)	0.6589 (AL, TL, C, TG, and SA)	1.83 (AL, TL, C, F, and SA)	1.082 (AC, SCAN, and F)	89.452° (TG, AC, and SCAN)
UMPC – 19629	32.92% (AC, SCAN, F and SA)	29.23% (TG, AC, SCAN, and F)	0.5729 (AC and SCAN)	1.622 (AL, TL, C, F, and SA)	0.675 (AL, TL, and C)	69.993° (AL, TL, C, F, and SA)
UMPC - 19630 Marsupial	33.95% (AC, SCAN, F and SA)	45.32% (AL, TL, C, and SA)	N/A	1.18 (AL, TL, C, F, and SA)	1.333 (TG)	67.784° (AL, TL, C, F, and SA)
UMPC - 19631	N/A	N/A	N/A	2.635 (TG, AC, and SCAN)	N/A	99.778° (AL, TL, C, F, and SA)
UMPC – 19632	31.27% (AC, SCAN, F and SA)	40.87% (AL, TL, C, and SA)	0.5094 (AC and SCAN)	1.9 (AL, TL, C, F, and SA)	0.747 (AL, TL, and C)	120.548° (AL, TL, C, F, and SA)
* UMPC - 19633 Marsupial	N/A	N/A	N/A	1.343 (AL, TL, C, F, and SA)	1.234 (TG)	72.341° (AL, TL, C, F, and SA)
UMPC - 19634	N/A	N/A	N/A	2.646 (TG, AC, and SCAN)	0.715 (AL, TL, and C)	87.194° (TG, AC, and SCAN)
UMPC – 19635	30.67% (AC, SCAN, F and SA)	34.48% (TG, AC, SCAN, and F)	0.5291 (AC and SCAN)	1.683 (AL, TL, C, F, and SA)	1.6 (TG)	122.471° (AL, TL, C, F, and SA)
UMPC – 19636	27.78% (AC, SCAN, F and SA)	38.67% (AL, TL, C, and SA)	0.6376 (AC and SCAN)	1.843 (AL, TL, C, F, and SA)	N/A	120.896° (AL, TL, C, F, and SA)

Table 4.3 (continued)

UMPC – 19637	31.17% (AC, SCAN, F and SA)	33.44% (TG, AC, SCAN, and F)	0.6549 (AC and SCAN)	2.039 (TG, AC, and SCAN)	1 (AC, SCAN, and F)	88.211° (TG, AC, and SCAN)
UMPC – 19638	30.30% (AC, SCAN, F and SA)	36.97% (TG, AC, SCAN, and F)	0.7544 (AL, TL, C, TG, and SA)	1.792 (AL, TL, C, F, and SA)	0.951 (AL, TL, and C)	89.872° (TG, AC, and SCAN)
* UMPC - 19639	27.50% (AC, SCAN, F and SA)	42.86% (AL, TL, C, and SA)	0.4632 (AC and SCAN)	2.5 (TG, AC, and SCAN)	0.928 (AL, TL, and C)	65.035° (AL, TL, C, F, and SA)
UMPC – 19640	24.85% (AC, SCAN, F and SA)	41.27% (AL, TL, C, and SA)	0.6688 (AL, TL, C, TG, and SA)	2.077 (TG, AC, and SCAN)	N/A	79.535° (AL, TL, C, F, and SA)
UMPC - 19641	N/A	N/A	N/A	2.014 (TG, AC, and SCAN)	1.089 (AC, SCAN, and F)	63.489° (AL, TL, C, F, and SA)
* UMPC - 19642	30.57% (AC, SCAN, F and SA)	38.22% (AL, TL, C, and SA)	0.5043 (AC and SCAN)	2.75 (TG, AC, and SCAN)	0.87 (AL, TL, and C)	102.081° (AL, TL, C, F, and SA)
UMPC – 19643	30.83% (AC, SCAN, F and SA)	41.04% (AL, TL, C, and SA)	0.6859 (AL, TL, C, TG, and SA)	1.985 (AL, TL, C, F, and SA)	0.925 (AL, TL, and C)	81.135° (AL, TL, C, F, and SA)
UMPC – 19644	25.30% (AC, SCAN, F and SA)	43.60% (AL, TL, C, and SA)	0.6614 (AL, TL, C, TG, and SA)	1.554 (AL, TL, C, F, and SA)	0.789 (AL, TL, and C)	70.794° (AL, TL, C, F, and SA)
UMPC - 19645	N/A	N/A	N/A	N/A	1.102 (TG)	90° (TG, AC, and SCAN)

Table 4.3 (continued)

UMPC – 19646	N/A	37.50% (TG, AC, SCAN, and F)	0.6039 (AC and SCAN)	1.47 (AL, TL, C, F, and SA)	N/A	N/A
UMPC – 19647	N/A	N/A	N/A	1.93 (AL, TL, C, F, and SA)	1.117 (TG)	86.067° (TG, AC, and SCAN)
UMPC – 19648	N/A	N/A	N/A	1.634 (AL, TL, C, F, and SA)	N/A	N/A
UMPC - 19649	N/A	N/A	0.8095 (AL, TL, C, TG, and SA)	1.652 (AL, TL, C, F, and SA)	N/A	N/A
UMPC – 19650	33.20% (AC, SCAN, F and SA)	41.20% (AL, TL, C, and SA)	0.608 (AC and SCAN)	1.738 (AL, TL, C, F, and SA)	N/A	66.691° (AL, TL, C, F, and SA)
UMPC - 19651 Marsupial	N/A	N/A	0.9241 (F)	1.621 (AL, TL, C, F, and SA)	N/A	N/A
UMPC – 19652	N/A	N/A	N/A	1.833 (AL, TL, C, F, and SA)	N/A	73.482° (AL, TL, C, F, and SA)
UMPC - 19653	26.70% (AC, SCAN, F and SA)	41.30% (AL, TL, C, and SA)	0.6148 (AC and SCAN)	1.549 (AL, TL, C, F, and SA)	1.021 (AC, SCAN, and F)	85.352° (TG, AC, and SCAN)
* UMPC – 19654	N/A	N/A	N/A	N/A	0.94 (AL, TL, and C)	N/A

Table 4.3 (continued)

UMPC – 19655	N/A	N/A	N/A	N/A	1.063 (AC, SCAN, and F)	N/A
UMPC – 19656	N/A	N/A	N/A	1.325 (AL, TL, C, F, and SA)	N/A	N/A
UMPC – 19657	30.50% (AC, SCAN, F and SA)	41.40% (AL, TL, C, and SA)	0.7368 (AL, TL, C, TG, and SA)	1.722 (AL, TL, C, F, and SA)	1.138 (TG)	74.095° (AL, TL, C, F, and SA)
UMPC – 19658	N/A	N/A	N/A	2.206 (TG, AC, and SCAN)	N/A	N/A
* UMPC - 19659 Marsupial COMPOSITE SPECIMEN WITH UMPC - 19633	N/A	N/A	N/A	1.259 (AL, TL, C, F, and SA)	1.473 (TG)	139.008° (AL, TL, C, F, and SA)

Table 4.4. Whitehead Creek calcaneus sample with five traits.

Specimen #'s (University of Montana Paleontology Center)	Orientation of the Ectal Facet	Development & Placement of the Peroneal Process	Calcaneal Heel Inflection	Concavity of the Cuboid Facet	Articulation of the Fibula with the lateral side of Ectal Facet
UMPC - 19616	28.678° (AL, TL, C, F, and SA)	Well-developed, placed distally (F and SA)	Relatively straight (AL, TL, C, TG, F, and SA)	No	Yes
* UMPC – 19617	45.427° (AL, TL, C, F, and SA)	Well-developed, placed distally (F and SA)	Relatively straight (AL, TL, C, TG, F, and SA)	Yes (AL, AC, and SCAN)	No (AL, AC, and SCAN)
UMPC - 19618	23.586° (AL, TL, C, F, and SA)	Reduced, placed distally (AL, TL, C, and TG)	Relatively straight (AL, TL, C, TG, F, and SA)	Yes (AL, AC, and SCAN)	N/A
UMPC – 19619	9.258° (TG, AC, and SCAN)	Well-developed, placed proximally; Cruciform (AC and SCAN)	Some medial flare (AC and SCAN)	Yes (AL, AC, and SCAN)	No (AL, AC, and SCAN)
UMPC – 19620	11.929° (AL, TL, C, F, and SA)	Well-developed, placed proximally; Cruciform (AC and SCAN)	Some medial flare (AC and SCAN)	Yes (AL, AC, and SCAN)	Yes
UMPC – 19621	17.001° (AL, TL, C, F, and SA)	Development??. placed distally	Relatively straight (AL, TL, C, TG, F, and SA)	No	Yes

Table 4.4 (continued)

UMPC – 19622	25.169° (AL, TL, C, F, and SA)	N/A	Some medial flare (AC and SCAN)	Yes (AL, AC, and SCAN)	Yes
* UMPC - 19623	19.52° (AL, TL, C, F, and SA)	Well-developed, placed distally (F and SA)	N/A	Yes (AL, AC, and SCAN)	No (AL, AC, and SCAN)
UMPC - 19624 Marsupial	9.809° (TG, AC, and SCAN)	N/A	Medial Inflection (AC and SCAN)	Yes (AL, AC, and SCAN)	No (AL, AC, and SCAN)
UMPC – 19625	31.863° (AL, TL, C, F, and SA)	N/A	Relatively straight (AL, TL, C, TG, F, and SA)	Yes (AL, AC, and SCAN)	Yes
* UMPC - 19626	28.378° (AL, TL, C, F, and SA)	Reduced, placed distally (AL, TL, C, and TG)	Relatively straight (AL, TL, C, TG, F, and SA)	Yes (AL, AC, and SCAN)	Yes
UMPC – 19627	18.385° (AL, TL, C, F, and SA)	Reduced, placed distally (AL, TL, C, and TG)	Relatively straight (AL, TL, C, TG, F, and SA)	No	Yes
* UMPC - 19628	16.978° (AL, TL, C, F, and SA)	Development??. placed distally	Relatively straight (AL, TL, C, TG, F, and SA)	Yes (AL, AC, and SCAN)	Yes
UMPC – 19629	23.277° (AL, TL, C, F, and SA)	Well-developed, placed proximally (AC and SCAN)	Relatively straight (AL, TL, C, TG, F, and SA)	Yes (AL, AC, and SCAN)	No (AL, AC, and SCAN)

Table 4.4 (continued)

UMPC - 19630 Marsupial	33.043° (AL, TL, C, F, and SA)	Well-developed, placed distally (F and SA)	High degree of medial inflection (AC and SCAN)	Yes (AL, AC, and SCAN)	No (AL, AC, and SCAN)
UMPC - 19631	9.579° (TG, AC, and SCAN)	Well-developed, placed proximally; Cruciform (AC and SCAN)	N/A	N/A	Yes
UMPC – 19632	23.178° (AL, TL, C, F, and SA)	Reduced, placed distally (AL, TL, C, and TG)	Relatively straight (AL, TL, C, TG, F, and SA)	Yes (AL, AC, and SCAN)	Yes
* UMPC - 19633 Marsupial	6.027° (TG, AC, and SCAN)	Well-developed, placed distally (F and SA)	Some medial inflection (AC and SCAN)	Yes (AL, AC, and SCAN)	No (AL, AC, and SCAN)
UMPC - 19634	3.112° (TG, AC, and SCAN)	Well-developed, placed proximally (AC and SCAN)	N/A	No	Yes
UMPC – 19635	38.560° (AL, TL, C, F, and SA)	Reduced, placed distally (AL, TL, C, and TG)	Relatively straight (AL, TL, C, TG, F, and SA)	Yes Very little (AL, AC, and SCAN)	Yes
UMPC – 19636	28.760° (AL, TL, C, F, and SA)	Reduced, placed distally (AL, TL, C, and TG)	Relatively straight (AL, TL, C, TG, F, and SA)	N/A	Yes
UMPC - 19637	6.766° (TG, AC, and SCAN)	Well-developed, placed proximally (AC and SCAN)	Some medial flare (AC and SCAN)	Yes (AL, AC, and SCAN)	Yes

Table 4.4 (continued)

UMPC – 19638	2.142° (TG, AC, and SCAN)	Well-developed, placed proximally (AC and SCAN)	Relatively straight (AL, TL, C, TG, F, and SA)	No	Yes
* UMPC - 19639	30.965° (AL, TL, C, F, and SA)	Reduced, placed distally (AL, TL, C, and TG)	Relatively straight (AL, TL, C, TG, F, and SA)	Yes (AL, AC, and SCAN)	Yes
UMPC – 19640	16.358° (AL, TL, C, F, and SA)	Development??. placed distally	Relatively straight (AL, TL, C, TG, F, and SA)	Yes (AL, AC, and SCAN)	Yes
UMPC - 19641	27.510° (AL, TL, C, F, and SA)	N/A	N/A	Yes (AL, AC, and SCAN)	No (AL, AC, and SCAN)
* UMPC - 19642	41.549° (AL, TL, C, F, and SA)	Well-developed, placed distally (F and SA)	Relatively straight (AL, TL, C, TG, F, and SA)	Yes Very little (AL, AC, and SCAN)	Yes
UMPC – 19643	23.166° (AL, TL, C, F, and SA)	N/A	Relatively straight (AL, TL, C, TG, F, and SA)	Yes (AL, AC, and SCAN)	Yes
UMPC – 19644	23.92° (AL, TL, C, F, and SA)	N/A	Relatively straight (AL, TL, C, TG, F, and SA)	N/A	Yes
UMPC - 19645	N/A	Development??. placed proximally (AC and SCAN)	N/A	Yes (AL, AC, and SCAN)	N/A

Table 4.4 (continued)

UMPC – 19646	35.972° (AL, TL, C, F, and SA)	N/A	Some medial flare (AC and SCAN)	N/A	Yes
UMPC – 19647	28.333° (AL, TL, C, F, and SA)	Development?, placed proximally (AC and SCAN)	Relatively straight (AL, TL, C, TG, F, and SA)	Yes (AL, AC, and SCAN)	No (AL, AC, and SCAN)
UMPC – 19648	N/A	N/A	N/A	N/A	N/A
UMPC - 19649	N/A	N/A	N/A	N/A	Yes
UMPC – 19650	28.727° (AL, TL, C, F, and SA)	N/A	Relatively straight (AL, TL, C, TG, F, and SA)	No	Yes
UMPC - 19651 Marsupial	24.624° (AL, TL, C, F, and SA)	N/A	Some medial flare (AC and SCAN)	N/A	Yes
UMPC – 19652	43.029° (AL, TL, C, F, and SA)	Well-developed and placed proximally (AC and SCAN)	Some medial flare (AC and SCAN)	N/A	No (AL, AC, and SCAN)
UMPC - 19653	30.905° (AL, TL, C, F, and SA)	N/A	Relatively straight (AL, TL, C, TG, F, and SA)	Yes (AL, AC, and SCAN)	Yes

Table 4.4 (continued)

* UMPC – 19654	N/A	Well-developed, placed distally (F and SA)	N/A	Yes (AL, AC, and SCAN)	N/A
UMPC – 19655	N/A	Well-developed, placed distally (F and SA)	N/A	Yes (AL, AC, and SCAN)	N/A
UMPC – 19656	33.236° (AL, TL, C, F, and SA)	N/A	Medial inflection (AC and SCAN)	N/A	No (AL, AC, and SCAN)
UMPC – 19657	37.196° (AL, TL, C, F, and SA)	Reduced, placed distally (AL, TL, C, and TG)	Relatively straight (AL, TL, C, TG, F, and SA)	No	Yes
UMPC – 19658	N/A	N/A	N/A	Yes (AL, AC, and SCAN)	N/A
* UMPC - 19659 Marsupial COMPOSITE SPECIMEN WITH UMPC - 19633	14.772° (AL, TL, C, F, and SA)	N/A	Medial inflection (AC and SCAN)	Yes (AL, AC, and SCAN)	No (AL, AC, and SCAN)

Table 4.5. Whitehead Creek calcaneus sample with three traits and the assigned locomotor guilds.

Specimen #'s (University of Montana Paleontology Center)	Extension of the Sustentacular Facet Beyond the Sustentacular Shelf	Presence of a Cuboid Pivot	Development and Length of the Distal Plantar Tubercle	ASSIGNED LOCOMOTOR GUILD
UMPC - 19616	No	Absent	N/A	C
* UMPC – 19617	No	Absent	N/A	F
UMPC - 19618	No	Absent	N/A	C
UMPC – 19619	No	Absent	distal plantar tubercle is prominent and elongate (SCAN)	SCAN
UMPC – 19620	No	Absent	distal plantar tubercle is prominent and elongate (SCAN)	SCAN
UMPC – 19621	No	Absent	N/A	C
UMPC – 19622	No	Absent	N/A	TG, with some climbing tendencies

Table 4.5 (continued)

* UMPC - 19623	Yes (AL, AC, and SCAN)	Absent	N/A	F
UMPC - 19624 Marsupial	N/A	Absent	Distal plantar tubercle is prominent and elongate (SCAN)	SCAN
UMPC – 19625	No	Absent	N/A	C
* UMPC - 19626	No	Absent	N/A	TG
UMPC – 19627	No	Absent	N/A	C
* UMPC - 19628	No	Absent	N/A	TL
UMPC – 19629	N/A	Absent	N/A	F
UMPC - 19630 Marsupial	N/A	Absent	Distal plantar tubercle is prominent and elongate (SCAN)	SCAN
UMPC - 19631	No	N/A	N/A	SCAN

Table 4.5 (continued)

UMPC – 19632	No	Absent	N/A	C
* UMPC - 19633 Marsupial	N/A	Absent	Distal plantar tubercle is prominent and elongate (SCAN)	SCAN
UMPC - 19634	No	Absent	Distal plantar tubercle is prominent and elongate (SCAN)	SCAN
UMPC – 19635	No	Absent	N/A	TG
UMPC – 19636	N/A	Absent	N/A	TG
UMPC - 19637	No	Absent	Distal plantar tubercle is prominent and elongate (SCAN)	SCAN
UMPC – 19638	No	Absent	N/A	TG
* UMPC - 19639	No	Absent	N/A	TG
UMPC – 19640	No	Absent	N/A	TL

Table 4.5 (continued)

UMPC - 19641	N/A	Present	Distal plantar tubercle is reduced? (AC)	AC
* UMPC - 19642	No	Absent	N/A	TG
UMPC – 19643	No	Absent	N/A	AL
UMPC – 19644	No	Absent	N/A	C
UMPC - 19645	No	Absent	Distal plantar tubercle is prominent and elongate (SCAN)	SCAN
UMPC – 19646	N/A	Absent	N/A	TG
UMPC – 19647	No	Absent	N/A	TG
UMPC – 19648	No	N/A	N/A	TG

Table 4.5 (continued)

UMPC - 19649	No	N/A	N/A	TG
UMPC – 19650	No	Absent	N/A	C
UMPC - 19651 Marsupial	N/A	Absent	Distal plantar tubercle is prominent and elongate (SCAN)	SCAN
UMPC – 19652	No	Absent	Distal plantar tubercle is prominent and elongate (SCAN)	SCAN
UMPC - 19653	N/A	Absent	N/A	TG
* UMPC – 19654	No	Absent	N/A	F
UMPC – 19655	N/A	Absent	N/A	F
UMPC – 19656	N/A	N/A	N/A	SCAN

Table 4.5 (continued)

UMPC – 19657	No	Absent	N/A	TL
UMPC – 19658	No	N/A	N/A	TG
* UMPC - 19659 Marsupial COMPOSITE SPECIMEN WITH UMPC - 19633	N/A	Absent	Distal plantar tubercle is prominent and elongate (SCAN)	SCAN

Whereas UMPC - 19617 exhibits a majority of characteristics consistent with an arboreal leaping behavior, it is classified as fossorial due to the presence of a well-developed and distally-placed peroneal process, a transverse component of the sustentacular facet, an ectal facet that is short and strongly convex and a cuboid facet that is concave. A well-developed, distally-placed peroneal process indicates that eversion and abduction of the foot are important (Ginot et al., 2016). Whereas a reduction in the length of the sustentacular facet limits antero-posterior movements of the calcaneus in regard to the astragalus, an increase in the width of this facet permits medio-lateral movements at the subtalar joint (Ginot et al., 2016). An ectal facet that is short and strongly convex mirrors the morphology of the astragalar ectal facet, which would be short and strongly concave. This ectal facet morphology indicates that the astragalus and calcaneus are maintained together as a complex during movements of the ankle, rather than being allowed to move as independent entities (Ginot et al., 2016). Concavity of the cuboid facet allows the cuboid to glide through its range of movements (Chester et al., 2015).

Whereas UMPC - 19623 exhibits a majority of characteristics consistent with an arboreal leaping behavior, it is classified as fossorial due to the presence of a well-developed and distally-placed peroneal process. A peroneal process that is well-developed and distally-placed indicates that eversion and abduction of the foot are important (Ginot et al., 2016). Leapers and terrestrial cursors have a reduced and distally-placed peroneal process. This changes the lever system at the peroneal process into a direct pulling with no fulcrum, which greatly reduces the possibility of abduction and/or eversion of the foot (Ginot et al., 2016). This specimen demonstrates other significant traits. The ectal facet is short and strongly convex. This indicates that the calcaneus and astragalus are maintained together as a complex during movements of the ankle, rather than being allowed to move as independent entities (Ginot et al., 2016). The cuboid facet is concave. Concavity of the cuboid facet allows the cuboid to glide through its range of movements (Chester et al., 2015; Ginot et al., 2016). There is no facet present on the lateral side of the ectal facet which would indicate that the fibula made contact. No contact between the fibula and the lateral side of the ectal facet indicates that medio-lateral movements were permitted at the subtalar joint (Chester et al., 2015).

Whereas UMPC - 19626 exhibits a majority of characteristics consistent with arboreal leaping, arboreal climbing and scansorial behaviors, it is classified as a terrestrial generalist due to increased stability at the subtalar joint. The ectal facet is obliquely-oriented, which limits movement of the calcaneus in regard to the astragalus (Ginot et al., 2016). The fibula made contact on the lateral side of the ectal facet, which indicates that medio-lateral movements are limited (Chester et al., 2015). Whereas the subtalar joint is relatively stable, the transverse tarsal joint has some mobility. The cuboid facet is concave. Concavity of the cuboid facet allows the cuboid to glide through its range of movements (Chester et al., 2015).

Whereas UMPC - 19628 exhibits a majority of characteristics consistent with a fossorial behavior, it is classified as a terrestrial leaper due to the presence of a facet on the lateral side of the ectal facet. This indicates that the fibula made contact. This kind of contact limits medio-lateral movements, adding stability to the subtalar joint (Chester et al., 2015). This specimen demonstrates another significant leaping trait. The anterior portion of the ectal facet is oriented perpendicularly to the dorsal surface of the calcaneal body. This corresponds to the strong curvature of the astragalar ectal facet, further adding to the stability of the subtalar joint (Ginot et al., 2016).

Whereas UMPC - 19639 exhibits a majority of characteristics consistent with an arboreal leaping behavior, it is classified as a terrestrial generalist because it demonstrates mobility at the transverse tarsal joint. The cuboid facet is slightly higher than wide, which approaches a circular shape. This shape gives a great deal of flexibility to the transverse tarsal joint, allowing the distal part of the foot to move independently from the ankle (Ginot et al., 2016). The cuboid facet is also concave, which permits the cuboid to glide through its range of movements (Chester et al., 2015). According to Ginot et al. (2016), leaping taxa have a crescent-shaped cuboid facet with a dorso-plantar main axis. Such a shape implies that the cuboid has limited transverse movements in regard to the calcaneus (Ginot et al., 2016).

Whereas UMPC - 19642 exhibits a majority of characteristics consistent with arboreal leaping and semi-aquatic behaviors, it is classified as a terrestrial generalist because it displays mobility at the subtalar joint and transverse tarsal joint. The sustentacular facet has a transverse component, which permits medio-lateral movements at the subtalar joint (Ginot et al., 2016), however, the fibula did make contact on the lateral side of the ectal facet, thus moderately restricting medio-lateral movements (Chester et al., 2015). The cuboid facet is concave.

Concavity of the cuboid facet allows the cuboid to glide through its range of movements (Chester et al., 2015).

UMPC - 19654 is classified as fossorial because the peroneal process is well-developed and placed distally, the sustentacular facet has a transverse component and there is a huge, distal plantar tubercle. A well-developed and distally-placed peroneal process indicates that eversion and abduction of the foot are important (Ginot et al., 2016). A transverse component of the sustentacular facet adds mobility to the subtalar joint by permitting medio-lateral movements (Ginot et al., 2016). A huge, distal plantar tubercle is linked to the strong connection between the cuboid and the calcaneus, emphasizing stability and power of the forefoot (Ginot et al., 2016).

UMPC - 19633/19659 is a composite specimen. Together, they represent an almost complete marsupial calcaneus. UMPC - 19633 is missing most of its heel. UMPC - 19659 has most of its heel. Whereas UMPC - 19659 is missing its peroneal process, UMPC - 19633 has its peroneal process. The peroneal process is well-developed and placed distally. It also has a ridge of bone that runs along its dorsal surface, starting anteriorly and moving posteriorly about half the length of the peroneal process. Both UMPC - 19633 and UMPC - 19659 have a sustentacular facet that is present and in good condition. The sustentacular facet is like a shelf that juts out medially and then extends anteriorly and joins with the anterior portion of the calcaneus at the cuboid facet. Both UMPC - 19633 and UMPC - 19659 have an ectal facet that is present and in good condition. The ectal facet is short, broad and strongly convex. This type of ectal facet morphology indicates that the astragalus and calcaneus are maintained together during movements of the ankle rather than being allowed to move as independent entities (Ginot et al., 2016). The cuboid facet is in good condition in both specimens. This facet is divided into two

halves, one medial and one lateral, that are at an angle to each other. The cuboid facet has a “scooped-out” appearance.

Whitehead Creek terminal phalanx sample with assigned locomotor guilds

Terminal phalangeal morphospecies are not identified due to the difficulty of assessing whether the specimens are lefts or rights, manual or pedal and which digit they came from. A final sample of 55 specimens was obtained by removing any and all heavily damaged specimens from an overall sample of 112. The 55 terminal phalanges are evaluated morphometrically (landmarks [2D] PCA) in order to assign them to locomotor categories. Table 4.6 contains a list of the specimens, along with their assigned locomotor categories.

Table 4.6. Assigned locomotor guilds of the Whitehead Creek terminal phalanx sample.

Specimen Number (WHC-PC)	ASSIGNED LOCOMOTOR GUILD
WHC-PC 257	AC
WHC-PC 259	TG
WHC-PC 260	AC
WHC-PC 261	AC
WHC-PC 262	F
WHC-PC 264	TG
WHC-PC 265	AC
WHC-PC 266	SCAN
WHC-PC 271	SCAN
WHC-PC 272	C
WHC-PC 273	AC
WHC-PC 275	C
WHC-PC 276	SCAN
WHC-PC 277	SCAN
WHC-PC 280	AC
WHC-PC 282	AC
WHC-PC 283	TG
WHC-PC 284	SCAN
WHC-PC 285	AC
WHC-PC 286	C
WHC-PC 288	SCAN
WHC-PC 289	C

Table 4.6 (continued)

WHC-PC 290	SCAN
WHC-PC 295	AC
WHC-PC 297	SCAN
WHC-PC 300	SCAN
WHC-PC 304	SCAN
WHC-PC 305	AC
WHC-PC 306	AC
WHC-PC 310	AC
WHC-PC 311	AC
WHC-PC 312	F
WHC-PC 314	SCAN
WHC-PC 315	SCAN
WHC-PC 316	F
* WHC-PC 317	AC
WHC-PC 320	AC
WHC-PC 330	SA
WHC-PC 331	AC
WHC-PC 333 (grooming claw?)	SCAN
WHC-PC 338	AC
WHC-PC 339	F
WHC-PC 340	AC
WHC-PC 348	AC
WHC-PC 351	AC
WHC-PC 354	SCAN
WHC-PC 355	SCAN
WHC-PC 356	AC
WHC-PC 359	SCAN
WHC-PC 362	SCAN
WHC-PC 363	SCAN
WHC-PC 368	AC
*** WHC_Primate Nail_BA-5Q 2015	AC
* BA-5Q LV2 2016_nail	AC
* BA-CQ LV1 2015_nail	AC

Table 4.6 Key: WHC-PC (Whitehead Creek postcrania), AC (Arboreal Climber), SCAN (Scansorial), TG (Terrestrial Generalist), C (Terrestrial Cursor), F (Fossorial) and SA (Semi-Aquatic). Specimens marked with an “*” are unidentified taxa with an apical tuft. The specimen marked with a “***” is the only primate specimen (i.e. an unidentified species of an Omomyoid primate). WHC-PC 333 may be a grooming claw; its shape is compared with the general grooming claw morphology as seen in Maiolino (2015).

Sørensen's similarity index results

Results of the Sørensen's similarity index analysis are given in Figure 4.1. The Whitehead Creek tarsal and phalangeal samples cluster with a gallery forest from the Cerrado of Brazil and a high-ground, old-growth forest from Peru. The Whitehead Creek calcaneus sample clusters with Brazil at a similarity index value of 0.69. Peru is external to this group and clusters with it at a similarity index value of 0.53. The Whitehead Creek astragalus sample clusters with the Whitehead Creek terminal phalanx sample at a similarity index value of 0.61. This group is external to the group containing Brazil, the Whitehead Creek calcaneus sample, and Peru and clusters with it at a similarity index value of 0.48.

Sites in the neotropics are highly complex and heterogeneous (Vieira & Monteiro-Filho, 2003; Ramkumar & Menier, 2017). To evaluate the possibility that the neotropical sites might look so different because they consist of a mosaic of different environments, a second Sørensen's similarity index analysis is run using combined locomotor guild frequency data from different habitat types within a single site. Raw counts of locomotor guilds are combined for the three tropical dry deciduous forests in Mexico, the upland and lowland bamboo thickets in Vietnam, the upland and lowland bamboo forests in Thailand, the primary and secondary tropical lowland forests in the Philippines, the primary and secondary tropical lowland forests in northeastern Madagascar, the temperate grasslands in south Africa, and the deciduous forest and temperate grassland in Missouri. Raw counts of combined locomotor guilds are converted into presence-absence data. I am applying the same method to Sørensen's similarity index as addressed in the methods.

Results of the second Sørensen's similarity index analysis are given in Figure 4.2. Eight modern sites form a cluster, six of which are heterogeneous – Mexico (tropical dry deciduous

forests), Vietnam (bamboo thickets), Thailand (bamboo forests), Philippines (tropical lowland forests), northeastern Madagascar (tropical lowland forests) and Swan Lake (deciduous forest and temperate grassland). This cluster has a similarity index value of 0.60, which approaches the similarity index threshold value of 0.70. Peru (high-ground, old-growth forest) and Virginia (Chestnut Oak forest) are included in this cluster. Brazil and the Whitehead Creek samples still form a cluster which is external, and basal to, a larger group containing the other 16 modern sites.

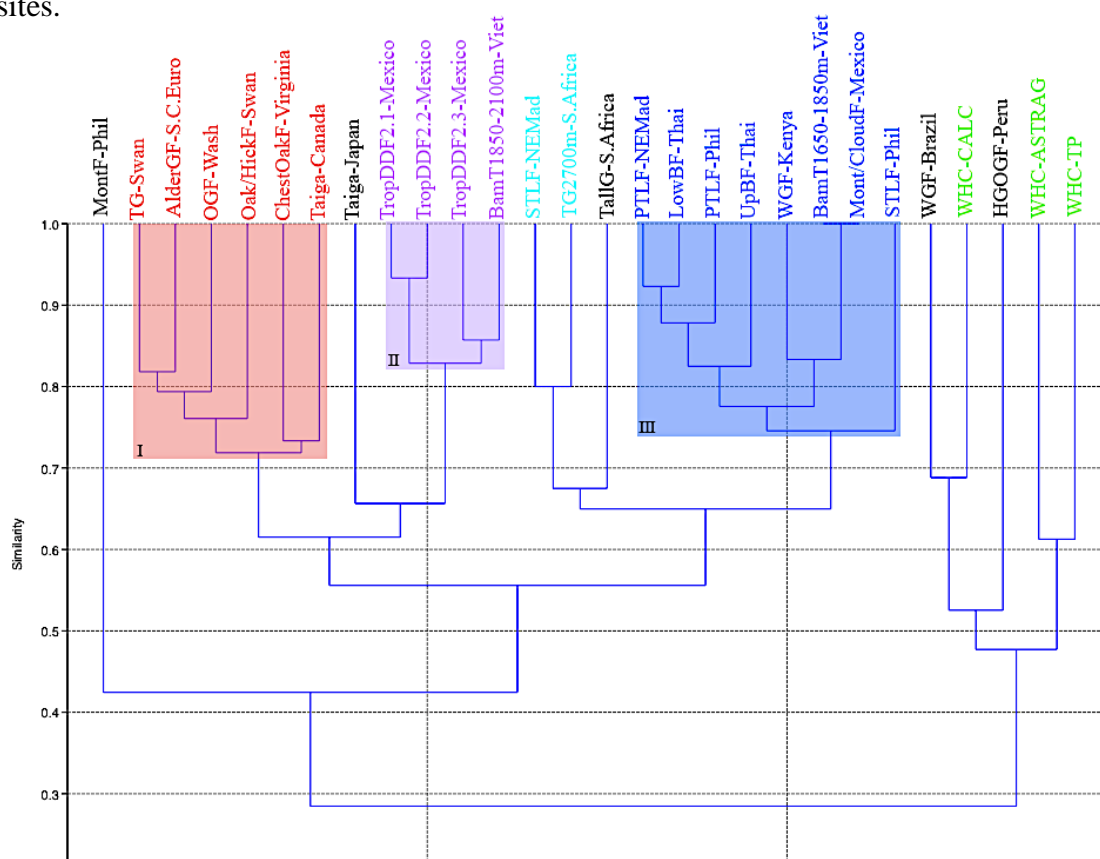


Figure 4.1. Initial results of the Sørensen's similarity index analysis. The similarity index scale on the left-hand side ranges from 0-1, with 1 being the most similar and 0 being the least similar (Hammer, 2018). Cluster I is highlighted in red. This cluster largely consists of temperate modern localities. Cluster III is highlighted in blue. This cluster consists of tropical modern localities. Cluster II is highlighted in purple. This cluster consists of three tropical, dry deciduous forests from Mexico and a bamboo thicket (elevation 1850-2100m) from Vietnam. A group consisting of a secondary tropical lowland forest from northeastern Madagascar and a temperate grassland (elevation 2700m) from South Africa is highlighted in light blue. Modern localities

that are considered to be outliers are highlighted in black. Whitehead Creek tarsal and phalangeal samples are highlighted in light green.

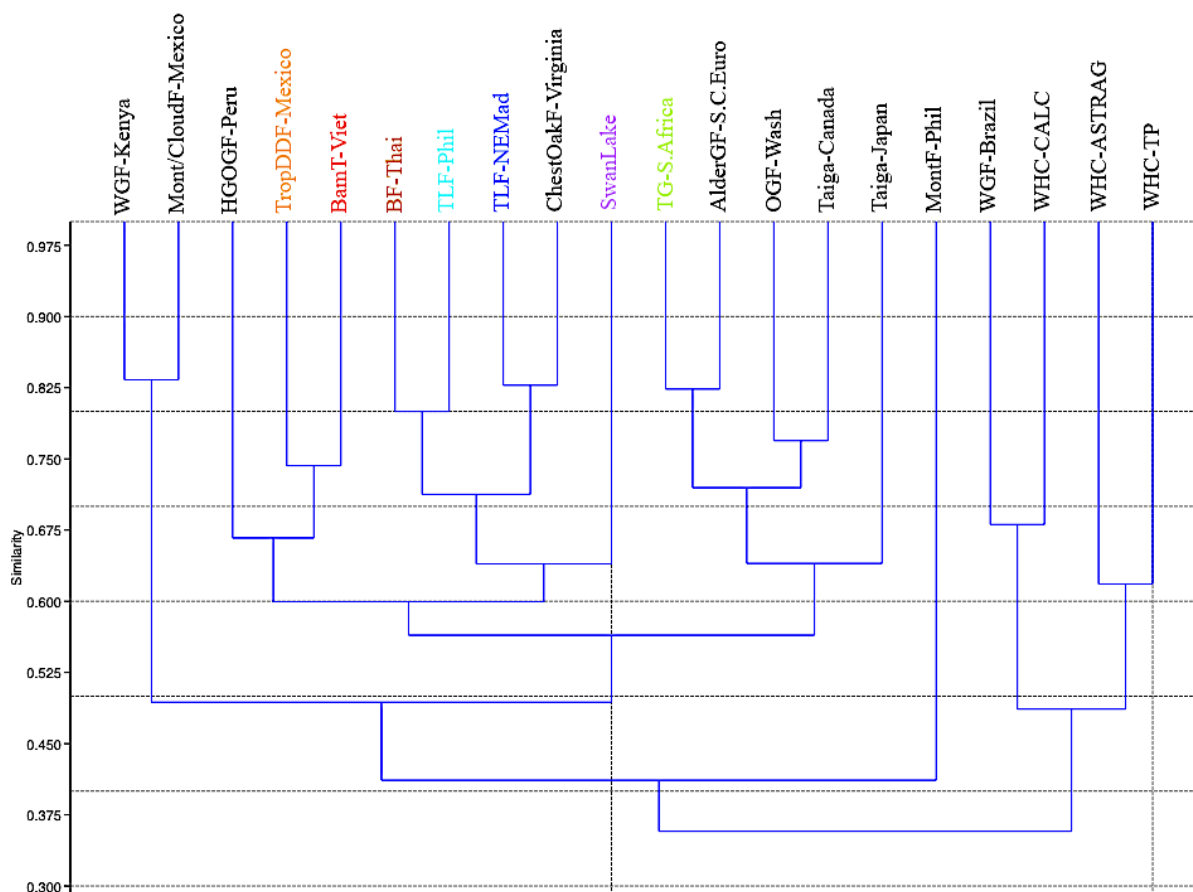


Figure 4.2. Results of the second Sørensen's similarity index analysis - evaluating mosaic habitats. Key: Similarity index is on the left-hand side of the graph. Values range from 0.300 to 0.975. The closer to "1", the more similar the sites in the cluster are to each other relative to other sites. The modern, "mosaic" sites are color coded. The colors have no significance other than to signify that the modern site is composed of a mosaic of different habitats.

In the initial Sørensen's similarity index analysis (Figure 4.1), the cluster containing all three Whitehead Creek samples, Brazil and Peru is external, and basal to, a cluster consisting of the other 23 modern sites. Within this large group, Sørensen's similarity index has identified three distinct clusters with similarity index values that are greater than or equal to 0.70.

According to Sørensen (1948), the limit value for the Quotient of Similarity (QS) is chosen arbitrarily and must depend on how high values are represented in the results. Cluster I,

highlighted in red, has a similarity index value of 0.72. This cluster consists of a temperate grassland (Swan Lake National Wildlife Refuge, Missouri), an alder gallery forest (Lankoci-Forest, upper section of the Drava River, Central Europe), an old-growth forest (Olympic Peninsula, Olympic National Park, Washington), an oak/hickory deciduous forest (Swan Lake National Wildlife Refuge, Missouri), a chestnut oak deciduous forest (Washington & Jefferson National Forests, Virginia) and a taiga forest (Thunder Bay, Canada). Cluster II, highlighted in purple, has a similarity index value of 0.83. This cluster consists of three tropical dry deciduous forests (Colima, Mexico) and a bamboo thicket (elevation 1850-2100m) (Mt. Tay Con Linh II, Vietnam). Cluster III, highlighted in blue, has a similarity index value of 0.75. This cluster consists of a primary tropical lowland forest from northeastern Madagascar, a lowland bamboo forest from Thailand, a primary tropical lowland forest from the Philippines, an upland bamboo forest from Thailand, a woodland gallery forest from Kenya, a bamboo thicket (elevation 1650-1850m) from Vietnam, a cloud forest from Mexico and a secondary tropical lowland forest from the Philippines.

Sørensen's similarity index fails to cluster like biomes on the basis of locomotor guild frequencies. This indicates that either there is no relationship between environment and small mammal locomotor frequencies or that biome names aren't capturing the environmental characteristics that influence locomotor adaptations among small mammal communities. To test this second idea, I evaluate whether localities within any given cluster share environmental components with each other. By evaluating biotic and abiotic components of the environment, I am seeing if these modern localities are clustering by environmental characteristics in the same manner that they cluster on the basis of locomotor guild frequencies. If they do, then there is a

relationship between small mammal locomotor guild frequencies and characteristics of the environment.

MANOVA analysis results

Clusters of modern sites identified using Sørensen's similarity index (i.e. cluster I, cluster II and cluster III) are compared using MANOVA to investigate whether clusters identified on the basis of locomotor guild frequencies differ significantly in physical, environmental properties. MANOVA performed on site-specific environmental characteristics of the three main clusters demonstrates that they are significantly different ($p < 0.05$; $p = 0.01839$), and pairwise comparisons using Hotelling's p (Table 4.7) indicate that clusters I and III are significantly different ($p = 0.0029288$). If Bonferroni correction is relaxed, the difference between Clusters I and II is significant as well.

Table 4.7. Results of Hotelling's p .

	Cluster III	Cluster I	Cluster II
Cluster III		0.0029288	0.7556
Cluster I	0.0029288		0.044004
Cluster II	0.7556	0.044004	

Table 4.7 Key: Cells highlighted in yellow indicate the significant differences between clusters. Cells highlighted in green indicate the significant differences between clusters if Bonferroni correction is relaxed.

Euclidean Distance results

Results of the Euclidean Distance analysis are given in Figure 4.3. Clusters identified using Sørensen's similarity index (i.e. cluster I, cluster II and cluster III) remain relatively unchanged in the Euclidean Distance analysis on environmental characteristics. The integrity of cluster I holds up, with the exception of the taiga forest from Canada that herein is external to a group containing the other 24 modern localities. The old-growth forest in Washington is also pulled out, clustering with the high-ground, old-growth forest in Peru. The integrity of cluster II

holds up, with the exception of the bamboo thicket (elevation 1850-2100m) from Vietnam; this modern locality lies within cluster III. The integrity of cluster III holds up, but with a few exceptions. The primary and secondary tropical lowland forests from the Philippines, and the primary tropical lowland forest from northeastern Madagascar, are external to cluster III.

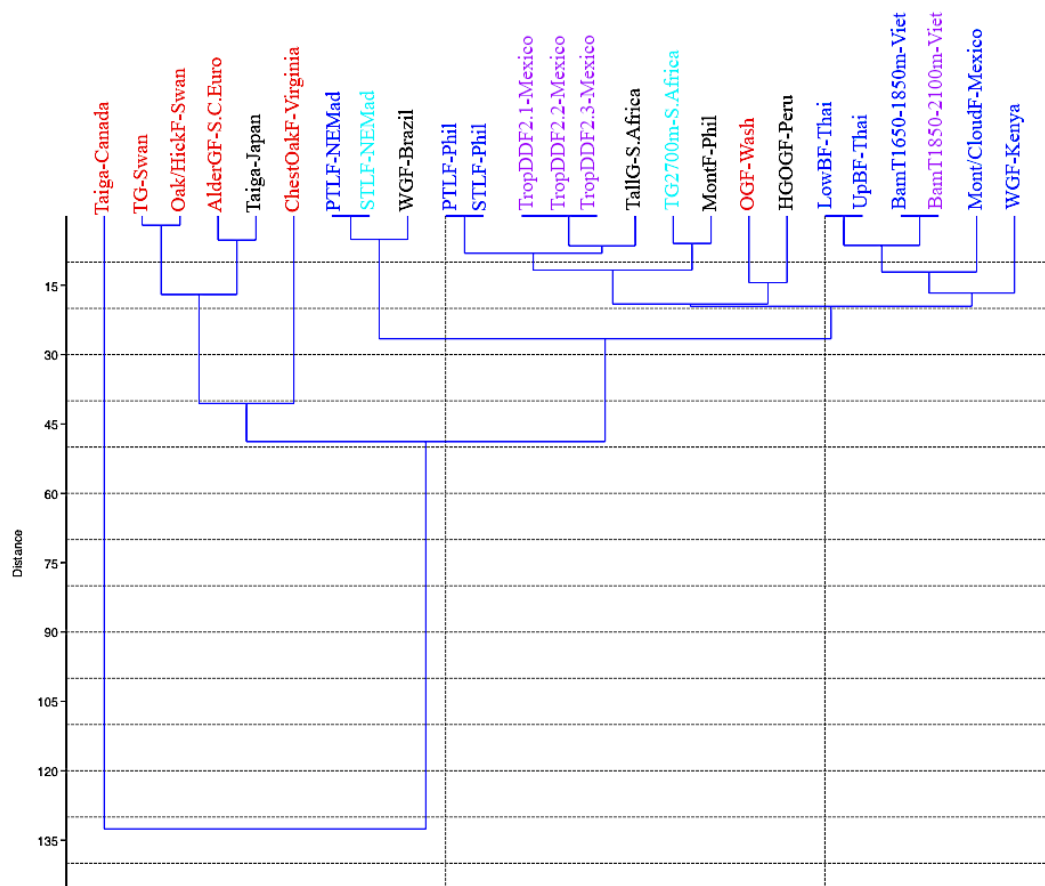


Figure 4.3. Results of the Euclidean Distance analysis. The distance index scale on the left-hand side ranges from 0-100+. Closer to 0 indicates the most similarity, while further from 0 indicates the least similarity (Hammer, 2018). Modern localities from cluster I are highlighted in red. Modern localities from cluster II are highlighted in purple, and modern localities from cluster III are highlighted in blue. A temperate grassland (2700m) from South Africa and a secondary tropical lowland forest from northeastern Madagascar are highlighted in light blue. Modern localities that are considered to be outliers are highlighted in black.

Whereas the neotropical sites (Brazil and Peru) cluster with each other on the basis of small mammal locomotor guild frequencies, they fail to cluster with each other when environmental data are evaluated. An investigation of why Brazil and Peru don't cluster together

on the basis of physical, environmental properties reveals that temperature difference ($^{\circ}\text{F}$) is influencing the outcome of the initial Euclidean Distance analysis. When temperature difference ($^{\circ}\text{F}$) is temporarily removed from the Euclidean Distance analysis, Brazil and Peru cluster together (Figure 4.4).

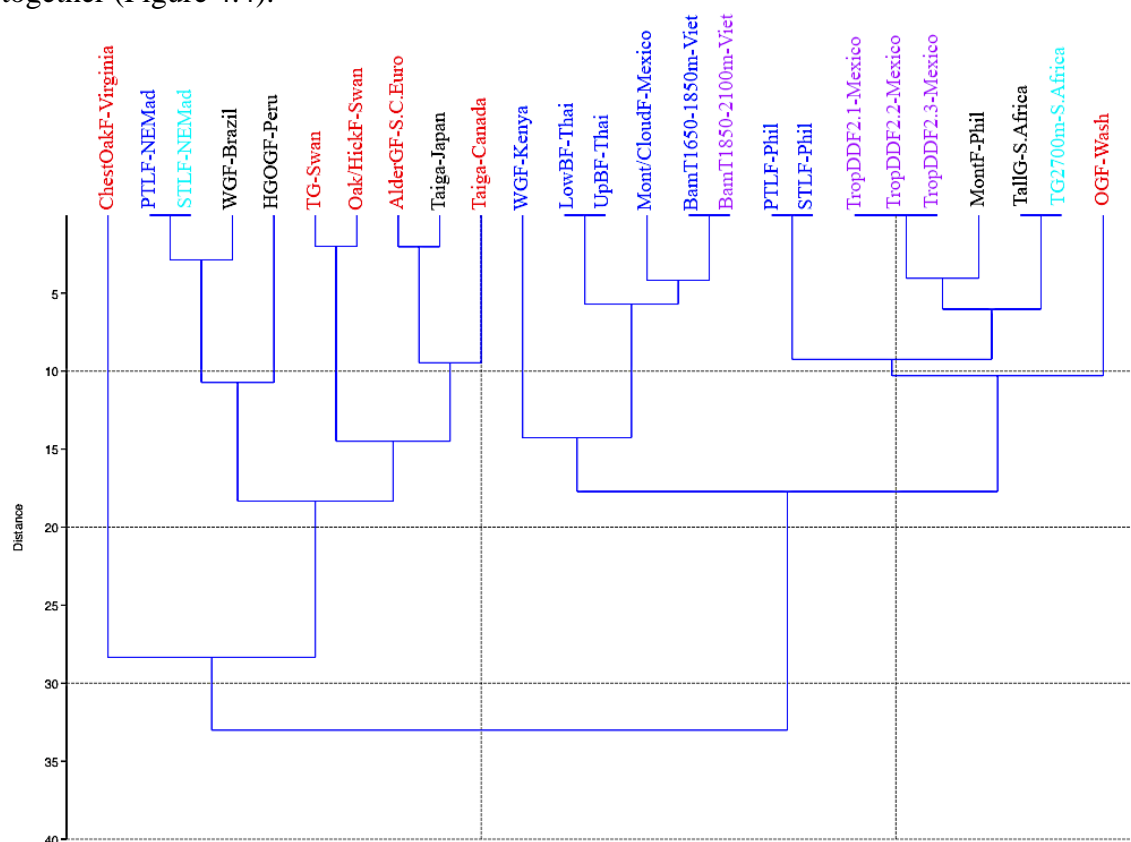


Figure 4.4. Euclidean Distance analysis evaluating temperature difference ($^{\circ}\text{F}$). The closer to “0”, the more similar the sites in the cluster are to each other relative to other sites. If temperature seasonality ($^{\circ}\text{F}$) were removed from the analysis, Brazil and Peru would cluster together. Cluster I is highlighted in red. Cluster II is highlighted in purple, and cluster III is highlighted in blue. A secondary tropical lowland forest from northeastern Madagascar and a temperate grassland (2700m) in South Africa are highlighted in light blue. Modern sites that are outliers in the analysis are highlighted in black.

Chapter 5 – Discussion

Visual comparison of Sørensen's similarity index and Euclidean Distance clusters

Visual comparison of the Sørensen's similarity index analysis of locomotor guild frequencies (Figure 4.1) and the Euclidean Distance analysis of environmental data (Figure 4.3) suggests that, while there is no relationship between biome name and the frequencies of locomotor guilds, there is a relationship between characteristics of the environment and locomotor guild frequencies, as both analyses yield clusters with similar constituencies. This indicates that there is a relationship between environmental variables and locomotor guild frequencies. MANOVA (Table 4.7) adds additional support to this conclusion, where clusters that are well-supported by locomotor data are also distinguished on the basis of environmental data. Having established that there is a relationship between locomotion and the environment, or more specifically, locomotor guild frequencies and characteristics of the environment, now Whitehead Creek can be compared with all modern sites to see if there is a good modern analog for the 35Ma fossil site.

Euclidean Distance analysis: the influence of temperature difference (°F)

Whereas the neotropical sites (Brazil and Peru) cluster with each other on the basis of small mammal locomotor guild frequencies, they fail to cluster with each other on the basis of environmental characteristics (Figure 4.3). An investigation reveals that temperature difference (°F) is influencing this outcome. Temperature difference refers to stability; a low value indicates a relatively stable temperature, while a high value indicates an unstable temperature (i.e. major temperature swings). If temperature difference is temporarily removed from the analysis, Brazil and Peru cluster together and clusters I, II and III remain relatively unchanged (Figure 4.4).

Further evaluation of the environmental data reveals that most temperate modern sites that are situated at an elevation that is less than or equal to 2,300m (e.g. taiga forest in Canada, temperate grassland in Swan Lake, Missouri, or an alder gallery forest in South Central Europe) have a high temperature difference (151°F, 58°F and 43.2°F, respectively). There are three modern sites that sit above 2,300m – a gallery forest from Brazil (2,854m), a montane/cloud forest from Mexico (2,750m) and a temperate grassland from South Africa (2,700m). These three sites have a low temperature difference – 10.2°F, 10.8°F and 5.4°F, respectively. In addition to site elevation, geographical location also seems to influence temperature difference. Most tropical sites (e.g. Mexico, Kenya, South Africa and northeastern Madagascar) have a temperature difference value that ranges from 5 – 17°F. Southeast Asian sites (e.g. Thailand and Vietnam) and a single neotropical site, Peru, have a temperature difference value that is approximately 23°F.

Visual comparison of both Sørensen's similarity index clusters (initial and mosaic)

Visual comparison of the initial Sørensen's similarity index analysis (Figure 4.1) and the Sørensen's similarity index analysis evaluating mosaic habitats (Figure 4.2) suggests that a gallery forest from the Cerrado of Brazil is a good modern analogue for Whitehead Creek, as Whitehead Creek clusters with Brazil in both analyses. While Whitehead Creek and Brazil are not exactly the same, some broad inferences can be made about the paleoenvironment of Whitehead Creek, including how these data corroborate previous paleoenvironmental studies of late Eocene northwestern Nebraska. Analyses of paleosols suggest a warm, wet and humid environment for northwestern Nebraska during the late Eocene (Retallack, 2007) with at least some closed canopy forests (O'Terry, 2001). These findings are corroborated by phytolith assemblages, which suggest a diverse array of forest indicators such as woody dicots,

dicots/conifers/ferns, palms, bambusoid grasses and Costaceae (Strömberg, 2004), and stable isotope analyses of mammalian teeth, which suggest the persistence of wet, dense, riparian habitats cutting through drier, more open biomes during the Chadronian (Boardman & Secord, 2013). A warm, wet Eocene environment in northwestern Nebraska, as suggested by Retallack (2007), is corroborated by analyses of oxygen isotope data from *Mesohippus* (Zanazzi, Kohn, MacFadden & O'Terry, 2007) and analyses of fossil *Alligator* at late Eocene sites in the Great Plains (Whiting & Hastings, 2015; Whiting, 2016), which suggest a mean annual temperature range of 51.62°F - 87.98°F (with an average of approximately 70°F), and analyses of paleosols (Sheldon & Retallack, 2004) and *Alligator* fossils (Whiting, 2016), which suggest mean annual precipitation values that range from 696mm – 1,008mm.

Warm, wet Eocene climates in the Great Plains gradually transition into cool, dry climates by the end of the Miocene (Sheldon & Retallack, 2004; Retallack, 2007; Zanazzi et al., 2007; Whiting, 2016). Paleotemperature records for Nebraska show a long-term cooling trend (Sheldon & Retallack, 2007), although the mean annual temperature fluctuates, from approximately 56°F in the Oligocene (Zanazzi et al., 2007) to being greater than 62.6°F in the early Miocene (Whiting, 2016) to being less than 62.6°F in the middle- and late Miocene (Whiting, 2016). These findings are corroborated by analyses of enamel ¹⁸O, which suggest that temperature seasonality remained relatively stable during the EOT, with only a slight increase in the early Oligocene (Zanazzi et al., 2007). Paleoprecipitation records for Nebraska show a long-term aridification trend – 852mm (36-35Ma), 752mm (35-33.7Ma), 628mm (33.7-33Ma), 474mm (33-31Ma) and 433mm (31-29Ma) (Sheldon & Retallack, 2004).

According to Retallack (2007), successive appearances and expansion of bunch grassland at 35-34Ma, sod-forming short grassland at 19-16 Ma, and sod-forming tall grassland at 7-6 Ma

were each followed by long-term climatic drying and cooling during the Oligocene (33-23 Ma), late Miocene (15-10 Ma) and Pliocene-Pleistocene (5-0 Ma), respectively, with dry-cool conditions coinciding with sagebrush expansion. These findings (Retallack, 2007) are corroborated by phytolith assemblages, which suggest a decrease in the relative abundance of forest indicators and a subsequent increase in the abundance of grasses by the end of the Miocene.

The Whitehead Creek ecosystem, similarities and differences with Brazil – vegetation structure and climate

Eiten (1972) describes the Cerrado of Brazil as consisting of dry forests situated on the interflaves and slopes of the gently rolling terrain and narrow, moist gallery forests situated in the bottoms of valleys along the streams. The gallery forests are closed canopy tall forests that may be bordered by strips of moist or marshy grasses (Eiten, 1972). The savanna portion of the Cerrado, which lies on the other side of the strips of marshy grasses, is heterogeneous in terms of canopy cover (Eiten, 1972). In using the vegetation structure of a gallery forest from the Cerrado of Brazil as a baseline, the data of this project, in co-occurrence with the Whitehead Creek faunal list, will be used to paint a picture of what Whitehead Creek may have looked like 36-35mya.

The presence of arboreal, scansorial, and terrestrial species is consistent with previous interpretations of the late Eocene paleoenvironment of northwestern Nebraska, suggesting that the Whitehead Creek sample includes representatives from a mosaic of environments, characteristic of a complex, heterogeneous habitat. Small sandstone fragments (Figure 5.1), in addition to fish fossils found at Whitehead Creek, suggest the presence of water. The Whitehead Creek faunal list suggests that obligatory arborealists (e.g. arboreal climbers and leapers) may be underrepresented in the Whitehead Creek tarsal sample. Whereas the tarsal sample does contain



Figure 5.1. Sandstone fragments found at Whitehead Creek. Sandstone fragments are the remnants of an ancient streambed or other type of seasonal or permanent water source that once existed in the area.

arboreal morphospecies, there are no tarsals that can be assigned confidently to *Ectypodus*, either of the apatemyid species, a plesiadapiform or a eupimate; however, a tooth belonging to *Uintasorex*, a plesiadapiform primate, and a terminal phalanx belonging to an omomyid primate have been found at Whitehead Creek, thus suggesting the presence of closed canopy forests in the Whitehead Creek ecosystem. *Leptomeryx* fossils have also been found at Whitehead Creek. *Leptomeryx* possessed low-crowned teeth, which were suitable for browsing (Ostrander, 1980). Based on stable isotope analyses of mammalian teeth, Zanazzi and Kohn (2008) suggest that *Leptomeryx* preferred woodland habitats. ^{13}C values indicate that its diet consisted of 90% C_3 vegetation, while ^{18}O values indicate that it was relatively water-dependent.

In sampling late-Chadronian sites in northwestern Nebraska, Strömberg (2004) has identified *Chusquea* phytoliths. *Chusquea* is known as the South American Mountain Bamboo (Cooper, 2007); it is a clumping bamboo (i.e. grows in clumps rather than spreading out when it grows [i.e. running bamboo]) (Cooper, 2007). This type of bamboo is native to the neotropics and is usually dependent on humidity, shade and warm temperatures (55°F – 70°F) (Strömberg, 2004). *Chusquea* also thrives in habitats that have a mean annual precipitation value that ranges from 1,000mm – 6,000mm (Cooper, 2007). This type of clumping bamboo is naturally associated with forest habitats, either as understory or inhabiting forest margins in the shade of taller vegetation (Strömberg, 2004). Based on the data of this project and the Whitehead Creek faunal list, the Whitehead Creek ecosystem once contained water, closed canopy forests with an herbaceous understory, bambusoid thickets and open woodlands. In addition to this, the Big Cottonwood Creek sample used in Strömberg's (2004) study contained moderate counts of diatoms and sponge spicules, suggesting proximity to water or higher soil moisture. The sample that she used comes from a paleosol that likely formed on over-bank deposits on the Big Cottonwood Creek member paleovalley floodplain in the basal part of the member (close to the contact point with the Peanut Peak member) (Strömberg, 2004). This adds another potential component to the Whitehead Creek ecosystem – water, overbank, closed canopy forests with an herbaceous understory, bambusoid thickets and open woodlands.

One of the major similarities between Brazil and Whitehead Creek is that both sites are described as containing ancient vegetation. For fossil sites within the Great Plains, ancient vegetation refers to the recession and subsequent restriction of tropical vegetation to small tracts or pockets. For the Cerrado, ancient vegetation refers to flora that was once more widespread but is now restricted to small tracts or pockets in relict communities – mesic forest surrounded by

xeric habitats (Cole, 1960). In both instances, the relict floral communities likely functioned to increase the species diversity in two ways. First, they serve as mesic corridors allowing vast range, and in the case of Whitehead Creek, temporal extensions of species which are basically forest dwellers. The second way in which gallery forests increase diversity is by providing refuge, food and/or water for species not confined to forests (Redford & da Fonseca, 1986). Not only the water, which is always present in a gallery forest, but the structure of the forest itself helps to sustain species (Redford & da Fonseca, 1986), as it creates numerous niches to be filled.

The Whitehead Creek ecosystem is different than a gallery forest from the Cerrado of Brazil in a number of ways. A gallery forest in the Cerrado is only a few hundred meters wide (Redford & da Fonseca, 1986); in the Whitehead Creek ecosystem, the closed canopy forests may be slightly larger in size, as they would have to be large enough to support populations of plesiadapiform primates and omomyid primates. Based on the calculated average home range size for three, tiny, extant primates (pygmy tarsier [50g; 12,000m²] [ADW, 2014], pygmy marmoset [124g; 5,500m²] [ADW, 2014] and mouse lemur [60g; 21,500m²][Gron, 2009]), which is 13,000m², it is assumed that this is the average home range size for omomyid and plesiadapiform primates. An average home range size of 13,000m² is calculated for an extant primate with an average body mass of approximately 78g. Some species of *Uintasorex*, a tiny plesiadapiform primate, which has been identified at Whitehead Creek, can weigh as little as 20-25g (Gunnell, 2012); so, the average home range size for a plesiadapiform primate may be smaller than 13,000m² (3,333m²). The equation for this is as follows: (13,000m² x 20g)/78g.

The understory of the closed canopy forests in the Whitehead Creek ecosystem likely contained an herbaceous or shrubby layer (Strömberg, 2004), while the understory in the gallery forests in the Cerrado usually have a sparse understory (Redford & da Fonseca, 1986). Unlike

the Cerrado, where the gallery forests are separated from the open woodlands by strips of marshy grasses (Eiten, 1972; Redford & da Fonseca, 1986), the closed canopy forests in the Whitehead Creek ecosystem are likely separated from the open woodlands by bambusoid thickets.

The large tracts of closed canopy forests needed to support populations of plesiadapiform primates and omomyid primates would have needed to be sustained by stable, warm temperatures. Due to insufficient paleotemperature records for late Eocene northwestern Nebraska, estimates were calculated from three modern sites in Indonesia (central Sulawesi), Brazil (Amazonas) and Madagascar (Tulear; southwest Madagascar), from which three extant, small-bodied (48-124g) primates live. *Tarsius pumilus* (pygmy tarsier) lives high up in the mountains in the montane forests in central Sulawesi (ADW, 2014). *Callithrix pygmaea niveiventris* (eastern pygmy marmoset) lives in river-edge forests in Amazonas, Brazil (ADW, 2014). *Microcebus murinus* (gray mouse lemur) lives primarily in dry deciduous forests on the island of Madagascar (Duke Lemur Center, 2019). Based on climate data for these three modern sites (World Weather and Climate Information, 2010 – 2016), estimates for MAT (°F) and temperature difference (°F) are calculated. MAT is estimated to be 76.5°F, and temperature difference is estimated to be 15.8°F. The estimated MAT and temperature difference (°F) are similar to values of the Cerrado – 76.1°F and 10.2°F, respectively. Based on these values for small-bodied primates living in tropical regions, it is reasonable to suggest that MAT and temperature difference values were similar in late Eocene northwestern Nebraska, especially at Whitehead Creek.

In addition to stable, warm temperatures, large tracts of tropical vegetation would also need a steady/constant supply of moisture. Clark et al. (1967) and Retallack (2007) suggest an environment in northwestern Nebraska with distinct wet and dry seasons. Thirty-six to thirty-five

million years ago, the wet season likely saw precipitation amounts totaling 908mm –1,008mm (Sheldon and Retallack, 2004). Based on the presence of fossil *Alligator* at late Eocene sites in northwestern Nebraska (Whiting & Hastings, 2015) and north central Nebraska (Cherry County; Whiting, 2016), precipitation values have been predicted to be between 720mm and 1,840mm, with greater than 115mm during the dry season. These precipitation values are major constraints for extant *Alligator*, to which fossil *Alligator* is most closely related (Whiting, 2016). In addition to MAP, Retallack (2007) estimates a seasonality in precipitation value of approximately 40mm during the late Eocene in northwestern Nebraska. It is possible that, while the large tracts of tropical vegetation (i.e. gallery forests) weren't the vast tropical forests of the early and middle Eocene, they were supported by a constant supply of moisture, even though the wet season saw no more than 1,000mm of rainfall.

While the rainfall seasonality value that Retallack (2007) estimated for late Eocene northwestern Nebraska (40mm) is comparable to values of some modern temperate sites (e.g. Canada [42.6036mm], Japan [38.8379mm] and south-central Europe [40.8654mm]), it is only moderately comparable to the values of Swan Lake (31.6107mm), northeastern Madagascar (28.6036mm) and Brazil (28.1501mm). Rainfall seasonality values > 20mm but < 30mm indicate that there is some fluctuation in rainfall throughout the year (i.e. moderate seasonality). Rainfall seasonality values > 30mm indicate that there is little fluctuation in rainfall throughout the year (i.e. little seasonality). Most of the modern African and southeast Asian sites have rainfall seasonality values that average around 5-15mm. These sites exhibit much seasonality; the dry season receives a lot less rain than the wet season. Based on estimated values for MAP (Sheldon and Retallack, 2004; Retallack, 2007; Whiting, 2016) and seasonality in precipitation (Retallack,

2007) for late Eocene northwestern Nebraska, it is reasonable to assume that Whitehead Creek had similar values – approximately 1,008mm and 40mm, respectively.

The Whitehead Creek ecosystem had a climate much similar to Brazil and other modern sites containing small-bodied primates (Indonesia and Madagascar). Based on estimated values, Whitehead Creek may have had a MAT of 76.5°F, temperature difference of 15.8°F, MAP of 800-1,000mm and rainfall seasonality of 40mm. These estimated values corroborate other paleoenvironmental studies of late Eocene northwestern Nebraska, which suggest a paleoenvironment that is warm, wet and humid; this helps to place Whitehead Creek within the climate change continuum (Figure 5.2). While the Whitehead Creek ecosystem is similar to Brazil in some respects, it is different from it in other respects. Brazil has a rainfall seasonality value of 28.1501mm, which indicates that there is some fluctuation in rainfall throughout the year (i.e. moderate seasonality). In regard to the Whitehead Creek ecosystem, there was little fluctuation in rainfall throughout the year (40mm).



Figure 5.2. How Whitehead Creek is placed within the climate change continuum.

With a picture of what the Whitehead Creek ecosystem may have looked like 35mya, how the plants and animals may have interacted will bring the picture to life (Figure 5.3). The Whitehead Creek ecosystem supported a diversity of rodents (e.g. *Prosciurus*, *Adjidaumo*, *Paradjidaumo*, *Heliscomys*, *Ischyromys*, *Prolapsus*, *Pseudocylindrodon* and *Litoyoderimys*) which occupied the various arboreal, semi-arboreal and terrestrial niches. Ischyromyids

demonstrated burrowing behaviors but likely foraged above ground (Ostrander, 1980). Most of the Eomyid rodents are not well known (Ostrander, 1980); however, a few of them are.

Adjidaumo are thought to be ground-dwelling scamperers. Paradjidaumo are thought to be typical running rodents, and *Heliscomys* are thought to have filled the scampering, seed, fruit, insect eating niche. *Prosciurus vetustus*, an aplodontid, was a scansorial insectivore.

Herpetotherium valens and *Peradectes*, both marsupials, occupied the semi-arboreal niche.

Primates (plesiadapiformes and omomyids), apatemyids (*Sinclairella* and *Apatemys*) and multituberculates occupied the arboreal niche. The unknown species of multituberculate found at Whitehead Creek likely filled the arboreal climbing, herbivorous niche. Ostrander (1980) describes multituberculates as omnivores. Lagomorphs (*Palaeolagus*), artiodactyls (*Leptomeryx*) and soricids (*Domnina*) occupied the terrestrial niches. Wood (1940) states that the Great Plains in the late Eocene were not the open plains of today. Rather, they once supported a considerable growth of trees and clumps of bushes. *Palaeolagus*, a lagomorph known from the Chadronian of Nebraska, likely lived in these clumps of bushes (Ostrander, 1980). *Leptomeryx*, a browser (Ostrander, 1980; Zanazzi and Kohn, 2008) likely inhabited the woodlands (Zanazzi and Kohn, 2008), while *Domnina* burrowed underground.

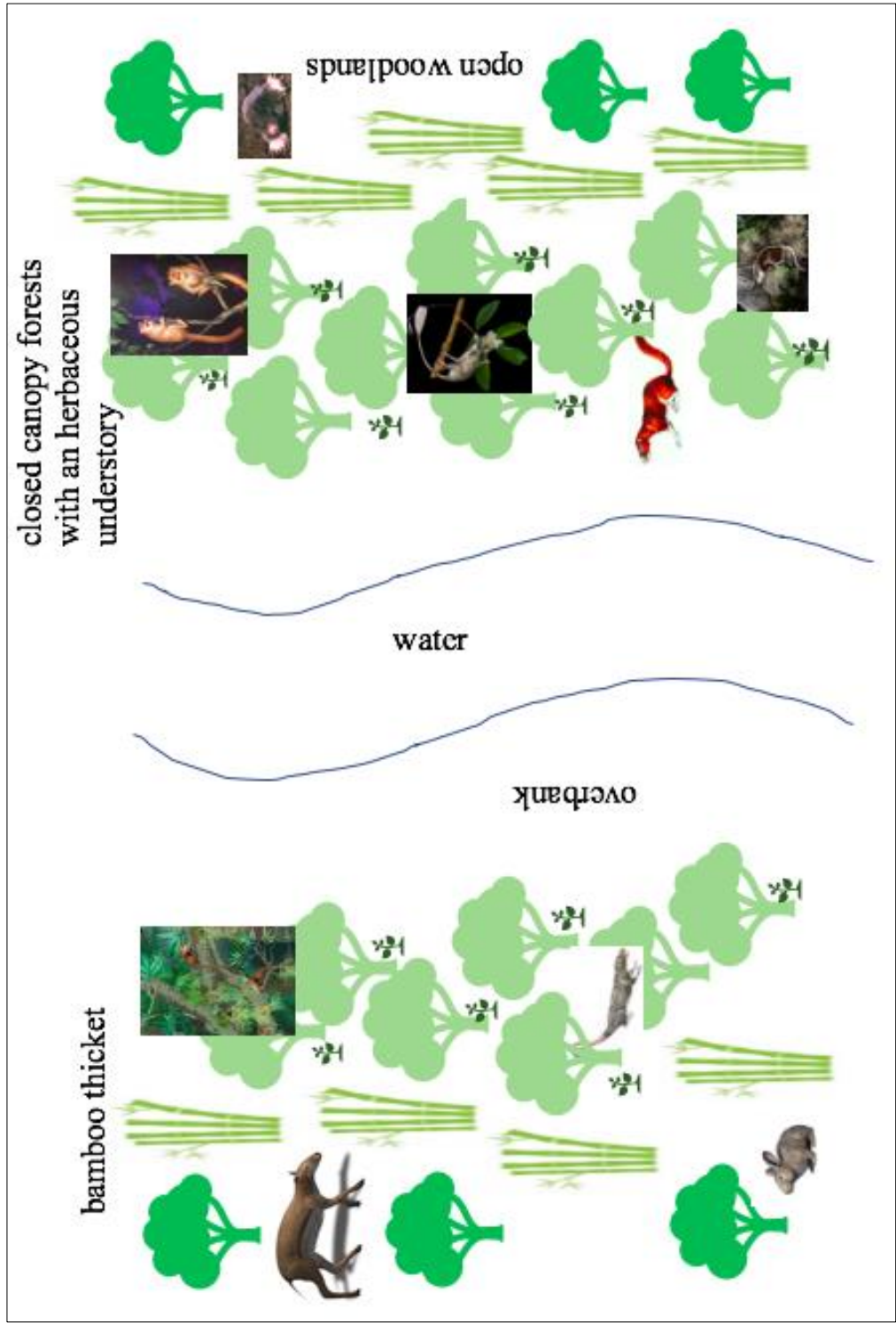


Figure 5.3. What Whitehead Creek may have looked like 35mya. The Whitehead Creek fauna are depicted in their natural habitats; the images are not to scale. Plesiadapiform primates, omomyid primates, apatemyids and multituberculates fill the arboreal niche. Marsupials occupy the semi-arboreal niche. The various rodents occupy the arboreal, semi-arboreal and terrestrial niches. Soricids, lagomorphs and artiodactyls occupy the terrestrial niche in the more semi-open habitats.

In what ways are modern analogs good for interpreting paleoenvironments?

Modern analogs are useful for interpreting paleoenvironments because they can be used as a baseline or outline. This outline is then filled in with details based on the results of the project. In this project, a gallery forest from Brazil is the outline; the results of this project, and the Whitehead Creek faunal list, help fill in the details, bringing the Whitehead Creek ecosystem to life. There are similarities and differences between Whitehead Creek and Brazil, both in terms of vegetation structure and climate; however, the fact that the two sites are not one hundred percent similar speaks volumes. The same idea applies to the other modern sites as well.

Climate change has occurred on various spatial (global, regional and local) and temporal scales (short-term versus long-term), affecting sites at different times/rates and in different ways. For example, a long-term cooling and drying trend is evident in continental North America, specifically within the Great Plains; however, short-term changes are not showing this. The environment may be changing over the course of millions of years, but this change fluctuates on a much smaller scale, perhaps over the course of thousands of years. The complexity of climate change and how it has affected continental North America (broadly), the Great Plains (specifically) and Nebraska (more specifically), has influenced how this ancient environment is compared with modern environments, as no modern environment looks like any ancient environment in terms of the landscape and climate. These ever-changing factors can not simply be captured at a single point in time and compared with another single point in time, whether past or present. It is for this reason that modern analogs are used as baselines or outlines, with which one can fill in the details using one's data.

Chapter 6 – Conclusion

The Chadronian-age Whitehead Creek locality located in northwestern Nebraska has produced diverse and rich fossil mammal samples (Arbor & Tornow, 2015), and like other Chadronian sites within the Great Plains faunal province, includes relict taxa that persist long after their extinctions from sites further west (Tornow & Arbor, 2017). As part of the Great Plains faunal province (Storer, 1989), Whitehead Creek may have served as a refugium for some mammalian species during the late Eocene (Arbor & Tornow, 2015; Tornow & Arbor, 2017), where, on the bases of phytoliths (Strömberg, 2004), paleosols (O'Terry, 2001; Retallack, 2007), and stable isotopes (Zanazzi & Kohn, 2008; Boardman & Secord, 2013) environmental reconstructions suggest an environment that was warmer, wetter, and more stable than the Rocky Mountains basins.

The goal of this project was to reconstruct the paleoenvironment of the late Eocene Whitehead Creek locality. This was done through an analysis of small mammal (< 1,000g) astragali, calcanei and terminal phalanges and their relationship to locomotor behavior and the environment. Having evaluated the relationship between locomotor guild frequencies among small mammals and the environment in modern biomes, I examined this relationship at Whitehead Creek to make inferences about its paleoenvironment and to contextualize these environmental data within a broader body of work on the Chadronian paleoenvironment of the Great Plains.

Thirty-five million years ago, the Whitehead Creek ecosystem consisted of a mosaic of different habitats, including water, overbanks, closed canopy forests, bamboo thickets and open woodlands. These various habitats were sustained by stable (temperature difference of 15.8°F), warm temperatures (76.5°F) and a steady/constant supply of moisture (rainfall seasonality of

40mm). The wet season saw anywhere from 800mm-1,000mm of precipitation, while the dry season saw less amounts. This complex, heterogeneous habitat supported a diversity of rodents (e.g. *Prosciurus*, *Adjidaumo*, *Paradjidaumo*, *Heliscomys*, *Ischyromys*, *Prolapsus*, *Pseudocylindrodon* and *Litoyoderimys*) that occupied the various arboreal, semi-arboreal and terrestrial niches. Primates (plesiadapiformes and omomyids), apatemyids (*Sinclairiella* and *Apatemys*) and multituberculates occupied the arboreal niche. Marsupials (e.g. *Herpetotherium valens* and *Peradectes*) occupied the semi-arboreal niche, while lagomorphs (*Palaeolagus*), artiodactyls (*Leptomeryx*) and soricids (*Domnina*) occupied the terrestrial niches.

Future contributions

Due to the fact that the outcome of this project may have been influenced by the underrepresentation of semi-aquatic taxa in the Whitehead Creek samples, future work is needed to identify and describe semi-aquatic tarsal characters in the fossil record. This may be possible with research on extant semi-aquatic taxa and a thorough understanding of how semi-aquatic tarsal characters differ between taxa in accordance with the amount of time spent in the water and the types of activities performed there (including how the animal swims).

References

- Andrews, P., Groves C.P. & Horne, J.F.M. (1975). Ecology of the Lower Tana River Flood Plain (Kenya). *Journal of the East Africa Natural History Society and National Museum*, 151:1-31.
- Animal Diversity Web. (2014). Browse Animalia: Mammalia. *University of Michigan*. DOI: <https://animaldiversity.org>
- Arbor, T.C. & Tornow, M.A. 2015. Small Mammals of the Middle Chadronian (Late Eocene) Whitehead Creek Local Fauna of Nebraska.
- Boardman, G.S. & Secord, R. (2013). Stable isotope paleoecology of White River ungulates during the Eocene-Oligocene climate transition in northwestern Nebraska. *Palaeogeography Palaeoclimatology, Palaeoecology* 375:38-49.
- Bock, W.J. & von Wahlert, G. (1965). Adaptation and the Form-Function Complex. *International Journal of Organic Evolution*, 19(3):269-299.
- Bock, W.J. (1994). Concepts and methods in ecomorphology. *J. Biosci.*, 19(4):403-413.
- Carey, A.B. & Johnson, M.L. 1995. Small mammals in managed, naturally young, and old-growth forests. *Ecological Applications*, 5:336-352.
- Carrano, M.T. (1997). Morphological indicators of foot posture in mammals: a statistical and biomechanical analysis. *Zoological Journal of the Linnean Society*, 121:77-104.
- Chester, S.G.B., Bloch, J.I., Boyer, D.M. & Clemens, W.A. Oldest known euarchontan tarsals and affinities of Paleocene Purgatorius to Primates. *National Academy of Sciences*, 112(5):1487-1492.

- Clark, J., Beerbower, J.R. & Kietzke, K.K. (1967). Oligocene Sedimentation, Stratigraphy, Paleocology and Paleoclimatology in the Big Badlands of South Dakota. Chicago Field Museum of Natural History.
- Cole, M.M. (1960). Cerrado, Caatinga and Pantanal: The Distribution and Origin of the Savanna Vegetation of Brazil. *The Geographical Journal*, 126(2):168-179.
- Cooper, G. (2007). *Chusquea* – mountain bamboo of Latin America. Tradewinds/Bamboo Direct Nursery, Oregon, USA. DOI: <http://www.bamboodirect.com/bamboo/info/chusquea.pdf>
- Costa, E., Garcés, M., Sáez, A., Cabrera, L. & López-Blanco, M. (2011). The age of the ‘Grande Coupure’ mammal turnover: New constraints from the Eocene-Oligocene record of the Eastern Ebro Basin (NE Spain). *Palaeogeography, Palaeoclimatology, Palaeoecology*, 301:97-107.
- Dagosto, M. (1983). Postcranium of *Adapis parisiensis* and *Leptadapis magnus* (Adapiformes, Primates) Adaptational and Phylogenetic Significance. *Folia primatol*, 41: 49-101.
- Dagosto, M. (1985). The distal tibia of primates with special reference to the omomyidae. *International Journal of Primatology*, 6(1):45-75.
- Dagosto, M. (1986). The Joints of the Tarsus in the Strepsirhine Primates: Functional, Adaptive, and Evolutionary Implications. *City University of New York*. (Thesis Dissertation). Pg. 1-352.
- Donohoe, J.C. (1956). New Aplodontid Rodent from Montana Oligocene. *Journal of Mammalogy*, 37(2):264-268.
- Duke Lemur Center. (2019). *Microcebus murinus*. DOI: <https://lemur.duke.edu/discover/meet-the-lemurs/grey-mouse-lemur/>

- Dunn, R. (2009). *Mammalian Postcranial Evolution and Primate Extinction in the Middle Eocene of North America*. (Electronic Theses and Dissertations). Washington University, St. Louis.
- Eiten, G. (1972). The Cerrado Vegetation of Brazil. *Botanical Review*, 38(2): 201-341.
- Emry, R. J. (1992). Mammalian Range Zones in the Chadronian White River Formation at Flagstaff Rim, Wyoming. In D. R. Prothero, W. A. Berggren (eds.), *Eocene-Oligocene Climatic and Biotic Evolution*, 106-115.
- Emry, R.J. & Korth, W.W. (1993). Evolution in Yoderimyinae (Eomyidae: Rodentia), with New Material from the White River Formation (Chadronian) at Flagstaff Rim, Wyoming. *Journal of Paleontology*, 67(6):1047-1057.
- Eulinger, K., Luensmann, P., & Burt, M.S. (2006). The Mammals of Swan Lake National Wildlife Refuge. *Missouri Academy of Science*, 40:30-36.
- The Field Museum. (2010). Synopsis of Philippine Mammals: Search by Location (Greater Palawan-Busuanga). *The Field Museum, Lake Shore Dr., Chicago, Illinois*.
http://archive.fieldmuseum.org/philippine_mammals/maps_location3/LOC_20.asp
- Fremd, T.J. (2010). SVP Field Symposium 2010 John Day Basin Field Conference. John Day Fossil Beds National Monument (and surrounding basin) Oregon, USA.
- Ford, S.M. (1980). A Systematic Revision of the Platyrrhini Based on Features of the Postcranium. (Electronic Theses and Dissertations). University of Pittsburg, Pittsburg, Pennsylvania.
- Fostowicz-Frelik, L. (2007). The hind limb skeleton and cursorial adaptations of the Pliocene rabbit *Hypolagus beremendensis*. *Acta Palaeontologica Polonica*, 52(3):447-476.

- García-Cárdenas, R., Montoya-Lerma, J., & Armbrrecht, I. (2018). Ant Diversity Under Three Coverages in a Neotropical Coffee Landscape. *Rev. Biol. Trop.*, 66(4):1373-1389.
- Gebo, Daniel L. (1986). The Anatomy of the Prosimian Foot and its Application to the Primate Fossil Record. *Duke University*. (Thesis Dissertation). Pg. 1-553.
- Gebo, Daniel L. 1993. Functional Morphology of the Foot in Primates. In: Postcranial Adaptation in Nonhuman Primates. DeKalb, Illinois: Northern Illinois University Press. p 175-196.
- Ginot, S., Hautier, L., Marivaux, L., & Vianey-Liaud, M. (2016). Ecomorphological Analysis of the Astragalo-Calcaneal Complex in Rodents and Inferences of Locomotor Behaviors in Extinct Rodent Species. *Institut des Sciences de l'Evolution de Montpellier, Université de Montpellier, Montpellier, France*. DOI: <https://peerj.com/articles/2393/#materials|methods>
- Gron, K.J. (2009). Primate Factsheets: Mouse lemur (*Microcebus*) Taxonomy, Morphology, and Ecology. DOI: http://pin.primate.wisc.edu/factsheets/entry/mouse_lemur/taxon
- Gunnell, G. F. (2012). New Uintasoricine (?Primates, Plesiadapiformes) from the Earliest Bridgerian, Latest Early Eocene of Wyoming. *Journal of Paleontology*, 86(6):973-978.
- Gyozo, H., Daniel, M., & Gergely, C. (2005). Population dynamics and spatial pattern of small mammals in protected forest and reforested area. *Natura Somogyiensis*, 7:191-207.
- Hammer, Øyvind. (1999-2018). PAleontological STatistics, Version 3.21. Natural History Museum, University of Oslo.
- Hiashi, A. (1994). A pictorial guide to the mammals of Japan. *Tokai University Press*. <http://www.ne.jp/asahi/kitutuki/kobo/11ysi/e-mammals.html>

- Holroyd, P.A. & Maas, M.C. (1994). Paleogeography, paleobiogeography, and anthropoid origins. In J.G. Fleagle and R.F. Kay (eds.) *Anthropoid Origins*. New York: Plenum Press, pp. 297-334.
- Hough, J., & Alf, R. (1956). A Chadron Mammalian Fauna from Nebraska. *Journal of Paleontology*, 30(1):132-140.
- Hren, M.T., Sheldon, N.D., Grimes, S.T., Collinson, M.E., Hooker, J.J., Bugler, M. & Lohmann, K.C. (2013). Terrestrial cooling in Northern Europe during the Eocene-Oligocene transition. *PNAS*, 110(19):7562-7567.
- IUCN. (2018). The IUCN Red List of Threatened Species. *International Union for Conservation of Nature and Natural Resources*. DOI: <http://www.iucnredlist.org>
- Janis, C.M. (1993). Tertiary Mammal Evolution in the Context of Changing Climates, Vegetation, and Tectonic Events. *Annu. Rev. Ecol. Syst.*, 24:467-500.
- Kihm, A.J. & Schumaker, K.K. (2008). *Domnina* (Mammalia, Soricomorpha) from the latest Eocene (Chadronian) Medicine Pole Hills Local Fauna of North Dakota. *Paludicola*, 7(1):26-36.
- Kihm, A.J. (2011). Rodents from the Chadronian (Latest Eocene) Medicine Pole Hills Local Fauna, North Dakota. Part 1. Eutypomyidae, Cylindrodontidae and *Pipestoneomys*. *Paludicola*, 8(2):75-90.
- Kihm, A.J. (2013). Rodents from the Chadronian (Latest Eocene) Medicine Pole Hills Local Fauna, North Dakota. Part 2. Ischyromyidae, Sciuravidae, Aplodontidae, Sciuridae and Heliscomyidae. *Paludicola*, 9(2):41-55.
- Kihm, A.J., & Tornow, M.A. (2014). First Occurrence of Plesiadapiform Primates From the Chadronian (Latest Eocene). *Paludicola*, 9(4):176-182.

Krishtalka, L. (1978). Paleontology and geology of the Badwater Creek area, central Wyoming.

Part 15. Review of the Late Eocene Primates from Wyoming and Utah, and the Plesitarsiiformes. *Annals of the Carnegie Museum*, 47:335-360.

Ladeveze, S., Missiaen, P., & Thierry, S. (2010). First skull of *Orthaspidotherium edwardsi* (Mammalia, "Condylarthra") from the late Paleocene of Berru (France) and phylogenetic affinities of the enigmatic European family Pleuraspidotheriidae. *Journal of Vertebrate Paleontology*, 30:1559-1578.

LaGarry, H.E. (1997). Geology of the Toadstool Park Region of Northwestern Nebraska, With the Lithostratigraphic Revision and Re-description of the Brule Formation and Remarks on Oligocene Bone Processing. (Electronic Theses and Dissertations). University of Nebraska.

Leichliter, J., Sandberg, P., Passey, B., Codron, D., Avenant, N.L., Paine, O.C.C....Sponheimer, M. (2017). Stable carbon isotope ecology of small mammals from the Sterkfontein Valley: Implications for habitat reconstructions. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 485:57-67.

Lielke, K., Manchester, S. & Meyer, H. (2012). Reconstructing the Environment of the Northern Rocky Mountains during the Eocene/Oligocene Transition: Constraints from the Paleobotany and Geology of Southwestern Montana, USA. *Acta Palaeobotanica*, p. 11-67.

Lloyd, K.J. & Eberle, J.J. (2012). A late Eocene (Chadronian) mammalian fauna from the White River Formation in Kings Canyon, northern Colorado. *Rocky Mountain Geology*, 47(2):113-132.

- Lunde, D.P, Musser, G.G. & Truong Son, N. (2003). A survey of small mammals from Mt. Tay Con Linh II, Vietnam, with the description of a new species of *Chodsigoa* (Insectivora: Soricidae). *Mammal Study*, 28:31-46.
- Lyman, R.L. (2008). *Quantitative Paleozoology*. New York, Cambridge University Press.
- Macleod, N. & Rose, K.D. (1993). Inferring Locomotor Behavior in Paleogene Mammals Via Eigenshape Analysis. *American Journal of Science*, 293-A:300-355.
- Maiolino, S.A. (2015). Comparative Morphology of Primate Distal Phalanges: Implications for Early Primate Evolution and the Origins of the Primate Nail. (Electronic Theses and Dissertations). Stony Brook University, Stony Brook, NY.
- McShea, W.J., Pagels, J., Orrock, J., Harper, E., & Koy, K. (2003). Mesic deciduous forest as patches of small-mammal richness within an appalachian mountain forest. *Journal of Mammalogy*, 84(2):627-643.
- Meyer, T. (2007). Chadronian “Insectivores” of the Cypress Hills, Saskatchewan. (Electronic Theses and Dissertations. University of Saskatchewan, Saskatoon, Canada.
- Miller, L.A., Smith, S.Y., Sheldon, N.D., & Stromberg, C.A.E. (2012). Eocene vegetation and ecosystem fluctuations inferred from a high-resolution phytolith record. *GSA Bulletin*, 124(9-10):1577-1589.
- Morris, D.W. (2005). On the roles of time, space and habitat in a boreal small mammal assemblage: predictably stochastic assembly. *OIKOS*, 109:223-238.
- Nelson, K. (2019). Geography for Kids: North American - flags, maps, industries, culture of North America. *Ducksters*. Retrieved from <https://www.ducksters.com/geography/northamerica.php>

- NOAA. (2017, Oct. 10). What is the global ocean conveyor belt? *National Oceanic and Atmospheric Administration, U.S. Department of Commerce*.
<https://oceanservice.noaa.gov/facts/conveyor.html>
- NOAA. (2018). Early Eocene Period – 54 to 48 Million Years Ago. DOI:
<https://www.ncdc.noaa.gov/global-warming/early-eocene-period>
- Ostrander, G.E. (1980). Mammalia of the Early Oligocene (Chadronian): Raben Ranch Local Fauna of Northwestern Nebraska. (Electronic Theses and Dissertations). South Dakota School of Mines and Technology, Rapid City, South Dakota.
- Ostrander, G.E. (1983). A New Genus of Eomyid (Mammalia, Rodentia) from the Early Oligocene (Chadronian), Pipestone Springs, Montana. *Journal of Paleontology*, 57(1):140-144.
- Ostrander, G.E. (1985). "Correlation of the early Oligocene (Chadronian) in northwestern Nebraska". *Dakoterra*, 2(2):205-231.
- O'Terry, Jr., Dennis. (2001). Paleopedology of the Chadron Formation of Northwestern Nebraska: implications for paleoclimatic change in the North American midcontinent across the Eocene-Oligocene boundary. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 168:1-38.
- Pearson, D.A. & Hoganson, J.W. (1995). *Proceedings of the North Dakota Academy of Sciences*, 49.
- Poindexter, C.J., Schnell, G. D., Sánchez-Hernández, C., Romero-Almaraz, M., Kennedy, M.L., Best, T.L.,...Owen, R.D. (2012). Co-occurrence of small mammals in a tropical dry deciduous forest: comparisons of communities and individual species in Colima, Mexico. *Journal of Tropical Ecology*, 28(1):65-72.

- Prothero, D.R. (1985). North American Mammalian Diversity and Eocene-Oligocene Extinctions. *Paleobiology*, 11(4):389-405.
- Prothero, Donald R. & Emry, Robert J. 2003. The Chadronian, Orellan, and Whitneyan North American Land Mammal Ages. In: Michael, O. W., *Late Cretaceous and Cenozoic Mammals of North America: Biostatigraphy and Geochronology*. Columbia University Press pp. 156-168.
- Ramkumar, M. & Menier, D. (2017). Defining Habitat and Habitat Heterogeneity. DOI: https://www.researchgate.net/publication/316343549_Defining_Habitat_and_Habitat_Heterogeneity
- Redford, K.H., & da Fonseca, Gustavo A.B. (1986). The Role of Gallery Forests in the Zoogeography of the Cerrado's Non-volant Mammalian Fauna. *BIOTROPICA*, 18(2):126-135.
- Retallack, G.J. (1983). Late Eocene and Oligocene paleosols from Badlands National Park, South Dakota. *Geological Society of America, Special Paper 193*, Boulder, Colorado.
- Retallack, G.J. (2007). Cenozoic Paleoclimate on Land in North America. *Department of Geological Sciences, University of Oregon, Eugene, Oregon 97403*. Pg. 271-288.
- Rose, K.D. (1999). Postcranial Skeleton of Eocene Leptictidae (Mammalia), and Its Implications for Behavior and Relationships. *Journal of Vertebrate Paleontology*, 12(2):355-372.
- Rose, K.D. & Chinnery, B.J. (2004). The Postcranial Skeleton of Early Eocene Rodents. *Bulletin of Carnegie Museum of Natural History, Number 36*:211-244.

- Rose, Kenneth D., DeLeon, Valerie, B., Missiaen, P., Rana, R.S., Sahni, A., Singh, L., & Smith, T. (2008). Early Eocene Lagomorph (Mammalia) from Western India and the Early Diversification of Lagomorpha. *Proceedings: Biological Sciences*, 275(1639):1203-1208.
- Rose, K.D., Storch, G., & Krohmann, K. (2015). Small-mammal postcrania from the middle Paleocene of Walbeck, Germany. *Paläontol Z*, 89:95-124.
- Rowe-Rowe, D.T., & Meester, J. (2015). Habitat preferences and abundance relations of small mammals in the Natal Drakensberg. *South African Journal of Zoology*, 17(4):202-209.
- Salton, J.A., & Szalay, F.S. (2004). The Tarsal Complex of Afro-Malagasy Tenrecoidea: A Search for Phylogenetically Meaningful Characters. *Journal of Mammalian Evolution*, 11(2):73-104.
- Samuels, J.X. & Korth, W.W. 2017. The first Eocene rodents from the Pacific Northwest, USA. *Palaeontologia Electronica* 20.2.24A: 1-17. <https://doi.org/10.26879/717> palaeo-electronica.org/content/2017/1874-eocene-rodents-from-oregon
- Schneider, C.A., Rasband, W.S., & Eliceiri, K.W. (2012). NIH Image to ImageJ: 25 years of image analysis. *Nature methods*, 9(7):671-675.
- Schroeder, P.J. & Jenkins, D.G. (2018). How robust are popular beta diversity indices to sampling error? *Ecosphere*, 9(2):1-14.
- Siefert, A., Ravenscroft, C., Weiser, M.D. & Swenson, N.G. (n.d.). Functional beta diversity patterns reveal deterministic community assembly processes in eastern North American trees. DOI:
http://andrewsiefert.weebly.com/uploads/9/6/8/8/9688764/final_manuscript.pdf

- Sheldon, N.D. & Retallack, G.J. (2004). Regional Paleoprecipitation Records from the Late Eocene and Oligocene of North America. *The Journal of Geology*, 112:487-494.
- Silva, R.R. & Brandão, C.R.F. (2014). Ecosystem-Wide Morphological Structure of Leaf-Litter Ant Communities along a Tropical Latitudinal Gradient. *PLoS ONE*, 9(3):1-11.
- Smith, G.A., Manchester, S.R., Ashwill, M., McIntosh, W.C., and Conrey, R.M. (1998). Late Eocene-early Oligocene tectonism, volcanism, and floristic change near Gray Butte, central Oregon. *GSA Bulletin*, 110(6):759-778.
- Sørensen, T. (1948). A Method of Establishing Groups of Equal Amplitude in Plant Sociology Based on Similarity of Species Content and Its Application to Analyses of the Vegetation on Danish Commons. *Biologiske Skrifter*, Bind V, Nr. 4:1-41.
- Stein, B.R. (1988). Morphology and Allometry in Several Genera of Semiaquatic Rodents (Ondatra, Nectomys and Oryzomys). *Journal of Mammalogy*, 69(3):500-511.
- Stephenson, P.J. (1995). Small mammal microhabitat use in lowland rain forest of north-east Madagascar. *Acta Theriologica*, 40(4):425-438.
- Storer, J.E. (1989). Rodent Faunal Provinces, Paleocene-Miocene of North America.
- Storer, J.E. (1996). Eocene-Oligocene faunas of the Cypress Hills Formation, Saskatchewan, p. 240-261. In Prothero, D.R., and Emry, R.J. (eds.), *The Terrestrial Eocene-Oligocene Transition in North America*. Cambridge University Press, New York.
- Strömberg, Caroline A.E. (2004). Using phytolith assemblages to reconstruct the origin and spread of grass-dominated habitats in the Great Plains of North America during the late Eocene to early Miocene. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 207:239-275.

- Tabrum, A.R., Prothero, D.R. & Garcia, D. (1996). Magnetostratigraphy and biostratigraphy of the Eocene-Oligocene transition, southwestern Montana. In D.R. Prothero and R.J. Emry (eds.), *The Terrestrial Eocene-Oligocene Transition in North America*, 278-311.
- Terborgh, J.W., Fitzpatrick, J.W. & Emmons, L.H. 1984. Annotated checklist of bird and mammal species of Cocha Cashu Biological Station, Manu National Park, Peru. *Fieldiana: Zoology, new series*, 21:1-19.
- Thorington Jr., R.W., Schennum, C.E., Pappas, L.A. & Pitassy, D. (2005). The Difficulties of Identifying Flying Squirrels (Sciuridae: Pteromyini) in the Fossil Record. *Journal of Vertebrate Paleontology*, 25(4):950-961.
- Tornow, M.A. 2011-2015. Interim and final reports on paleontological investigations within the Oglala National Grassland 2011-2015 field seasons, U.S. Department of Agriculture Forest Service Special Use Permit PRD130.
- Tornow, Matthew A. & Arbor, Taflin C. 2017. Apatemyids (Mammalia, Apatotheria) from the middle Chadronian (late Eocene) of Sioux County, Nebraska, USA. *Palaeontologia Electronica*, 20.1.9A: 1-16 palaeo-electronica.org/content/2017/1770-apatemyids-from-nebraska
- University of North Carolina. (2011). Measurements and Error Analysis. Advanced Instructional Systems Inc. and University of North Carolina, Chapel Hill. DOI: https://www.webassign.net/question_assets/unccolphysmechl1?measurements/manual.html
- USDA Forest Service. (2019). FSTopo Map Product Download: Oglala National Grasslands, NE. DOI: usfs.maps.arcgis.com

- Van Valkenburgh, B. (1987). Skeletal Indicators of Locomotor Behavior in Living and Extinct Carnivores. *Journal of Vertebrate Paleontology*, 7(2):162-182.
- Vazquez, L.B., Medellin, R.A., & Cameron, G.N. (2000). Population and community ecology of small rodents in montane forest of western Mexico. *Journal of Mammalogy*, 81:77-85.
- Vieira, E.M., & Monteiro-Filho, E.L.A. (2003). Vertical Stratification of Small Mammals in the Atlantic Rain Forest of South-Eastern Brazil. *Journal of Tropical Ecology*, 19(5):501-507.
- Wada, N. (n.d.). Mammals' Locomotion: Swimming. Tokyo Zoological Park Society, Ueno, Japan. DOI: mammals-locomotion.com/swimming.html
- Warburton, N.M. & Prideaux, G.J. (2010). Functional pedal morphology of the extinct tree-kangaroo *Bohra* (Diprotodontia: Macropodineae). In: Coulson, G., and Eldridge, M. (eds.) *Macropods: The Biology of Kangaroos, Wallabies and Rat-Kangaroos*. Collingwood, Victoria, *CSIRO Publishing*, pp. 137-151.
- Webster, M., & Sheets, D.H. (2010). A Practical Introduction to Landmark-Based Geometric Morphometrics. In: *Quantitative Methods in Paleobiology*, pp. 163-188, Paleontological Society Short Course. The Paleontological Society Papers, *Volume 16*, John Alroy and Gene Hunt (eds.).
- Wheeler, E.A., & Landon, J. (1992). Late Eocene (Chadronian) dicotyledonous woods from Nebraska: evolutionary and ecological significance. *Review of Palaeobotany and Palynology*, 74:267-282.
- Whiting, E.T., & Hastings, A.K. (2015). First Fossil *Alligator* from the Late Eocene of Nebraska and the Late Paleogene Record of Alligators in the Great Plains. *Journal of Herpetology*, 49(4):560-569.

- Whiting, E.T. (2016). Constraining Neogene Temperature and Precipitation Histories in the Central Great Plains Using the Fossil Record of *Alligator*. Electronic Theses and Dissertations. DOI: <https://digitalcommons.unl.edu/cgi/viewcontent.cgi?referer=https://www.google.com/&httpsredir=1&article=1080&context=geoscidiss>
- World Weather and Climate Information. (2010-2016). DOI: <https://weather-and-climate.com>
- Wood, A.E. (1940). Lagomorpha. Part III in Scott, W.B., and Jepsen, G., The mammalian fauna of the White River Oligocene. *Trans. Amer. Phil. Soc.*, 28:271-362.
- Wood, A.E., Chaney, R.W., Clark, J., Colbert, E.H., Jepsen, G.L., Reeside, Jr., J.B. & Stock, C. (1941). Nomenclature and correlation of the North American continental Tertiary. *Geological Society of America Bulletin*, 52:1-48.
- Wood, A.E. (1969). Rodents and Lagomorphs from the “Chadronia Pocket,” Early Oligocene of Nebraska. American Museum of Natural History, New York, New York.
- Woodburne, M.O., Gunnell, G.F., Stucky, R.K. & Berggren, W.A. (2009). Climate Directly Influences Eocene Mammal Faunal Dynamics in North America. *Proceedings of the National Academy of Sciences of the United States of America*, 106(32):13399-13403.
- Wiles, G.J. (1981). Abundance and habitat preferences of small mammals in southwestern Thailand. *Nat. Hist. Bull. Siam Soc*, 29:44-54.
- Zanazzi, A., Kohn, M.J., MacFadden, B.J. & O’ Terry, Jr., D. (2007). Large temperature drop across the Eocene – Oligocene transition in central North America. *Nature*, 445:639-642.
- Zanazzi, A., & Kohn, Matthew J. (2008). Ecology and physiology of White River mammals based on stable isotope ratios of teeth. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 257:22-37.

Appendix A: Trait Tables

Astragalus trait table

	A/T L	C	TG
Trochlear Symm.	Some > 0.731 but < 0.917	Symmetrical > 0.917 but ≤ 1	Some > 0.731 but < 0.917
HNLI	≥ 1 long	< 1 but > 0.50 intermediate	< 1 but > 0.50 intermediate
NA	< 25°	< 25°	< 35° but > 25°
Position of the Ectal Facet	Lateral	Lateral	Plantar
Trochlear Depth	deep	deep	moderate
Shape of the Navicular Facet	Round-AL < 1.1 Ovoid-TL ≥ 1.1 but ≤ 1.636 “Subcylindrical”- lagomorphs only	Ellipse > 1.636	Round < 1.1
P/A of a Squatting Facet: * “P”- species that utilize habitual squatting or hyperdorsiflexed postures			
Extension of the trochlear surface onto the dorsal surface of the astragalar neck * Present in arboreal leapers, arboreal climbers and scansorialists * Absence of this trait is not indicative of terrestriality.			

Astragalus Trait Table (continued)

	AC/SCAN	F	SA
Trochlear Symm.	Marked ≤ 0.731	Marked- medial rim not as short as in AC/SCAN ≤ 0.731	Symmetrical > 0.917 but ≤ 1
HNLI	< 1 but > 0.50 intermediate	< 1 but > 0.50 intermediate	≤ 0.50 short
NA	$> 35^\circ$	$> 35^\circ$	$< 35^\circ$ but $> 25^\circ$
Position of the Ectal Facet	Plantar	Plantar	Plantar
Trochlear Depth	Shallow-AC Moderate- SCAN	Shallow	Moderate
Shape of the Navicular Facet	Round-AC < 1.1 Ovoid-SCAN ≥ 1.1 but ≤ 1.636	Ellipse > 1.636	Ovoid ≥ 1.1 but ≤ 1.636
P/A of a Squatting Facet: * "P"- species that utilize habitual squatting or hyperdorsiflexed postures			
Extension of the trochlear surface onto the dorsal surface of the astragalar neck * Present in arboreal leapers, arboreal climbers and scansorialists * Absence of this trait is not indicative of terrestriality.			

Calcaneus trait table

	AL/TL	C	TG
AE (AL/TL)	$\geq 37\%$	$\geq 37\%$	$<37\%$ but $\geq 35\%$
PE (CNL/TL)	$\geq 38\%$	$\geq 38\%$	$< 38\%$
CTM (CTW/CTH)	> 0.657 but < 0.90	> 0.657 but < 0.90	> 0.657 but < 0.90
OEF (EFL/EFH)	< 2	< 2	≥ 2
Shape of the Cuboid Facet (CFW/CFH) CHECK ORIENTATION OF THE CRESCENT SHAPE (AL/TL AND C HAVE A DORSOPLANTAR MAIN AXIS ACCORDING TO (GINOT ET AL., 2016)	Crescent or bean-shaped * < 1 higher than wide * >1 wider than high	Crescent or bean-shaped * < 1 higher than wide * >1 wider than high	Crescent or bean-shaped * < 1 higher than wide * >1 wider than high
Development and Placement of the Peroneal Tubercle	Reduced, placed distally	Reduced, placed distally	Reduced, placed distally
Orientation of the Cuboid Facet	Oblique	Oblique	Perpendicular - If close to 90°
Orientation of the Ectal Facet	Oblique	Oblique	Anteroposterior $\leq 10^\circ$
Calcaneal Heel Inflection	Relatively straight	Relatively straight	Relatively straight
Cuboid Pivot (present in primates only)	- not well-defined, relatively shallow (VCL, generalized arboreal leapers)		

Calcaneus Trait Table (continued)

<p>Concavity of the cuboid facet</p> <p>* Present in arboreal leapers, arboreal climbers and scansorialists</p> <p>* Absence of this trait is not indicative of terrestriality.</p>			
<p>Articulation of the fibula on the lateral side of the ectal facet</p> <p>* Present in arboreal leapers, arboreal climbers and scansorialists</p> <p>* Absence of this trait is not indicative of terrestriality.</p>			
<p>Extension of the sustentacular facet beyond the sustentacular shelf</p> <p>* Present in arboreal leapers, arboreal climbers and scansorialists</p> <p>* Absence of this trait is not indicative of terrestriality.</p>			
<p>Development and length of the distal plantar tubercle</p>			

Calcaneus Trait Table (continued)

	AC/SCAN	F	SA
AE (AL/TL)	< 35%	< 35%	< 35%
PE (CNL/TL)	< 38%	< 38%	≥ 38%
CTM (CTW/CTH)	≤ 0.657	≥ 0.90	> 0.657 but < 0.90

Calcaneus Trait Table (continued)

OEF (EFL/EFH)	≥ 2	< 2	< 2
<p>Shape of the Cuboid Facet (CFW/CFH)</p> <p>CHECK ORIENTATION OF THE CRESCENT SHAPE (AL/TL AND C HAVE A DORSOPLANTAR MAIN AXIS ACCORDING TO (GINOT ET AL., 2016)</p>	<p>Circular ~ = 1 ** high CFW and CFH values</p>	<p>Circular ~ = 1 ** high CFW and CFH values</p>	<p>Triangular? (in some species of Pantolestes) ** medium values (> .71 but < .83 CFW) (>.6 BUT < .8 CFH) This is just guess work based off of my current data</p>
<p>Development and Placement of the Peroneal Tubercle</p>	<p>Well-developed, placed proximally * Cruciform shape in scansorialists</p>	<p>Well-developed, placed distally</p>	<p>Well-developed, placed distally ** ALSO CHECK THE PLANTAR SURFACE OF THE SUS. FAC. (VERY DEEP AND WIDE GROOVE FOR FLEXOR FIBULARIS)</p>
Orientation of the Cuboid Facet	Perpendicular	Oblique	Oblique
Orientation of the Ectal Facet	Anteroposterior	Oblique	Oblique
Calcaneal Heel Inflection	Curved (medially and plantarly)	Relatively straight	Relatively straight

Calcaneus Trait Table (continued)

Cuboid Pivot (present in primates only)	- well-defined, relatively large, slightly deep (slow, cautious climbers; and generalized arboreal quadrupeds)		
<p>Concavity of the cuboid facet</p> <p>* Present in arboreal leapers, arboreal climbers and scansorialists</p> <p>* Absence of this trait is not indicative of terrestriality.</p>			
<p>Articulation of the fibula on the lateral side of the ectal facet</p> <p>* Present in arboreal leapers, arboreal climbers and scansorialists</p> <p>* Absence of this trait is not indicative of terrestriality.</p>			
<p>Extension of the sustentacular facet beyond the sustentacular shelf</p> <p>* Present in arboreal leapers, arboreal climbers and scansorialists</p> <p>* Absence of this trait is not indicative of terrestriality.</p>			
Development and length of the distal plantar tubercle	<p>* distal plantar tubercle is prominent and elongate (SCAN)</p> <p>* distal plantar tubercle is reduced (AC)</p>		

Appendix B: Thesis Data

Whitehead Creek astragalus sample. Specimen measurements. All measurements are in millimeters.

	TAL	LTL	MTL	MHW	MHH	HNL
UMPC - 19560	3.99	1.98	1.92	1.45	1.41	2.16
UMPC - 19561	2.84	1.76	1.31	1.29	0.77	1.3
UMPC - 19562	3.22	1.56	1.00	1.36	0.82	1.64
UMPC - 19563	3.13	1.71	1.30	1.40	0.97	1.43
UMPC - 19564	1.9	1.16	0.79	0.9	0.61	0.83
UMPC - 19565	4.89	2.61	2.03	2.13	1.59	2.27
UMPC - 19566	3.94	2.27	1.66	1.69	1.15	1.63
UMPC - 19567	3.6	2.13	1.48	1.3	0.93	1.65
UMPC - 19568	2.31	1.33	1.22	1.16	0.86	0.92
UMPC - 19569	3.57	2.25	1.54	1.34	1	1.52
UMPC - 19570	2.49	1.57	1.02	1.19	0.78	1.18
UMPC - 19571	5.12	2.82	2.01	2.44	1.66	2.21
UMPC - 19572	2.15	1.32	0.60	1.08	0.66	1.11
UMPC - 19573	2.69	1.49	0.77	0.95	0.71	1.32
UMPC - 19574	2.46	1.57	0.99	1.15	0.62	1.21
UMPC - 19575	2.42	1.29	0.84	0.87	0.72	1.03
UMPC - 19576	1.88	0.96	0.42	0.72	0.47	0.96
UMPC - 19577	2.15	1.73	1.19	1.15	0.73	1.32

Whitehead Creek Astragalus Measurements (continued)

UMPC – 19578	3.53	2.21	1.26	1.35	1.05	1.91
UMPC - 19579	2.37	1.02	0.76	0.74	0.51	1.25
UMPC – 19580	N/A	N/A	2.51	3.57	2.89	4.08
UMPC – 19581	1.59	1.07	N/A	N/A	0.56	N/A
UMPC – 19582	1.89	1.06	0.68	0.81	0.55	0.74
UMPC – 19583	3.63	2.32	1.33	1.7	1.25	1.69
UMPC – 19584	1.91	1.17	0.84	0.80	0.65	0.89
UMPC – 19585	2.01	1.29	1	0.74	0.58	0.9
UMPC – 19586	2.02	1.21	0.93	0.95	0.74	0.85
UMPC - 19587	2.8	1.61	1.39	1.18	1.03	1.38
UMPC – 19588	3.47	1.94	1.51	1.48	1.12	1.83
UMPC – 19589	3.17	1.94	N/A	1.20	1.11	1.70
UMPC – 19590	3.42	2.19	1.39	1.27	1.18	1.61
UMPC – 19591	2.68	1.63	1.29	0.95	0.78	1.21
UMPC – 19592	3.64	2.05	1.68	1.42	1.27	1.73
UMPC - 19593	2.61	1.57	1.22	1.1	0.77	1.44
UMPC – 19594	N/A	N/A	1.18	1.45	1.5	1.77
UMPC – 19595	N/A	N/A	N/A	1.44	1.29	1.62
UMPC - 19596	N/A	N/A	N/A	2.39	1.77	2.04
UMPC – 19597	2.54	1.53	N/A	N/A	N/A	1.26

Whitehead Creek Astragalus Measurements (continued)

UMPC – 19598	2.24	1.18	0.90	0.94	0.65	1.03
UMPC - 19599	3.82	2.24	2.72	1.6	1.68	1.4
UMPC – 19600	2.73	1.41	1.22	1.12	0.85	1.37
UMPC - 19601	2.08	1.21	0.92	0.89	0.67	0.97
UMPC - 19602	2.68	1.40	1.16	0.94	N/A	1.11
UMPC – 19603	1.94	1.10	N/A	0.81	0.57	0.92
UMPC – 19604	1.99	1.13	0.93	0.79	0.57	0.82
UMPC – 19605	2.83	1.35	1.68	1.23	0.95	1.42
UMPC – 19606	2.24	1.46	0.84	0.95	0.67	1.09
UMPC – 19607	2.78	1.28	1.04	0.95	0.73	1.13
UMPC – 19608	1.94	1.10	0.87	0.77	0.55	0.81
UMPC – 19609	2.69	1.64	1.20	0.95	0.76	1.40
UMPC – 19610	2.49	1.48	1.21	1.08	0.78	1.26
UMPC – 19611	3.32	1.90	1.42	1.27	1.11	1.73
UMPC – 19612	2.31	1.20	1.04	N/A	0.64	0.99
UMPC – 19613	2.88	1.72	1.10	1.12	0.76	1.39
UMPC – 19614	1.82	1.01	0.85	0.71	0.50	0.93
UMPC - 19615	2.21	1.14	0.75	0.83	0.69	1.33

Whitehead Creek calcaneus sample. Specimen measurements. All measurements are in millimeters.

	TL	MAX CALC. W	AL	CNL	CNW	CNH	EFL	EFH
UMPC - 19616	8.89	3.92	2.7	3.49	1.66	2.58	2.89	1.55
UMPC - 19617	3.72	1.68	1.39	1.67	0.64	0.95	0.97	0.57
UMPC - 19618	5.01	2.59	1.54	2.15	1.16	1.61	1.68	0.6
UMPC - 19619	5.75	3.04	2.04	N/A	1.55	N/A	1.66	1.03
UMPC - 19620	3.5	2.23	0.9	1.07	0.8	1.24	1.32	0.58
UMPC - 19621	5.12	2.14	1.44	1.95	0.99	1.49	1.56	0.95
UMPC - 19622	4.65	2.09	1.46	1.68	1.01	1.49	1.4	0.76
UMPC - 19623	N/A	2.9	1.3	N/A	N/A	N/A	1.11	0.67

Whitehead Creek Calcaneus Measurements (continued)

UMPC - 19624	N/A	3.06	1.99	N/A	N/A	N/A	1.64	1.55
UMPC - 19625	4.75	2.37	1.36	1.84	1.13	1.46	1.39	0.85
UMPC - 19626	4.41	2.76	1.22	1.59	0.97	1.44	1.3	0.97
UMPC - 19627	3.61	1.35	0.94	1.22	0.67	0.95	1.2	0.58
UMPC - 19628	4.12	1.89	1.01	1.26	0.84	1.16	1.39	0.76
UMPC - 19629	5.68	N/A	1.87	1.66	1.18	1.87	1.93	1.19
UMPC - 19630	5.45	N/A	1.85	2.47	N/A	1.48	1.18	1
UMPC - 19631	N/A	1.92	1.15	N/A	N/A	N/A	1.66	0.63
UMPC - 19632	3.23	N/A	1.01	1.32	0.51	0.84	0.95	0.5

Whitehead Creek Calcaneus Measurements (continued)

UMPC - 19633	N/A	3.57	1.98	N/A	N/A	N/A	1.37	1.02
UMPC - 19634	N/A	N/A	1.63	N/A	N/A	N/A	1.27	0.48
UMPC - 19635	5.25	2.3	1.61	1.81	1.23	1.51	1.7	1.01
UMPC - 19636	4.5	2.33	1.25	1.74	0.89	1.34	1.29	0.7
UMPC - 19637	3.08	1.81	0.96	1.03	0.72	1.05	1.04	0.51
UMPC - 19638	3.3	1.92	1	1.22	0.74	1.13	0.95	0.53
UMPC - 19639	2.8	N/A	0.77	1.2	0.45	0.84	0.8	0.32
UMPC - 19640	4.87	N/A	1.21	2.01	0.95	1.49	1.62	0.78
UMPC - 19641	N/A	N/A	1.45	N/A	N/A	N/A	1.47	0.73

Whitehead Creek Calcaneus Measurements (continued)

UMPC - 19642	3.14	N/A	0.96	1.2	0.56	0.86	0.88	0.32
UMPC - 19643	4.8	N/A	1.48	1.97	1	1.75	1.33	0.67
UMPC - 19644	3.76	1.75	0.95	1.64	0.71	1.27	1.15	0.74
UMPC - 19645	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A
UMPC - 19646	4.4	N/A	N/A	1.65	0.87	1.47	1.47	1
UMPC - 19647	N/A	N/A	1.16	N/A	N/A	N/A	1.37	0.71
UMPC - 19648	N/A	N/A	1.02	N/A	N/A	N/A	1.52	0.93
UMPC - 19649	N/A	N/A	N/A	1.85	1.10	1.33	1.52	0.92
UMPC - 19650	3.91	N/A	1.30	1.61	0.71	1.18	1.13	0.65

Whitehead Creek Calcaneus Measurements (continued)

UMPC - 19651	N/A	N/A	N/A	2.05	1.19	1.46	1.54	0.95
UMPC - 19652	N/A	N/A	1.23	N/A	N/A	N/A	1.76	0.96
UMPC - 19653	3.78	N/A	1.01	1.56	0.87	1.2	1.10	0.71
UMPC - 19654	N/A	3.46	1.58	N/A	N/A	N/A	N/A	N/A
UMPC - 19655	N/A	N/A	1.57	N/A	N/A	N/A	N/A	0.64
UMPC - 19656	2.06	N/A	N/A	0.98	N/A	N/A	0.53	0.40
UMPC - 19657	4.3	2.10	1.31	1.78	0.95	1.43	1.24	0.72
UMPC - 19658	N/A	N/A	1.34	N/A	N/A	N/A	1.39	0.63
UMPC - 19659	N/A	N/A	1.14	N/A	N/A	N/A	1.41	1.12

Whitehead Creek Calcaneus Measurements (continued)

	CFW	CFH	CALC. TUB. W	CALC. TUB. H	SF MAX LENGTH	SFW	SF PROJECTING W
UMPC - 19616	2	2.41	1.89	2.85	2.32	1.19	1.52
UMPC - 19617	1.27	0.9	0.88	0.92	1.14	0.39	0.65
UMPC - 19618	1.78	1.15	1.16	1.54	1.34	0.63	0.91
UMPC - 19619	1.28	1.28	N/A	N/A	2.19	N/A	0.82
UMPC - 19620	0.95	0.95	0.88	1.34	0.82	0.49	0.7
UMPC - 19621	1.17	0.8	1.01	1.56	0.62	0.71	1.07
UMPC - 19622	1.15	1.47	1.26	1.62	0.7	0.85	1.03
UMPC - 19623	1.62	0.87	N/A	N/A	1.25	0.79	1.20

Whitehead Creek Calcaneus Measurements (continued)

UMPC - 19624	N/A	1.67	N/A	N/A	2.51	N/A	1.03
UMPC - 19625	N/A	1.2	1.15	1.73	1.29	0.72	0.94
UMPC - 19626	1.15	1.04	1	1.57	0.78	0.72	0.86
UMPC - 19627	0.95	0.68	0.96	1.14	1.02	0.43	0.51
UMPC - 19628	1.05	0.97	0.85	1.29	0.6	0.5	0.65
UMPC - 19629	1.12	1.66	1.14	1.99	1.44	N/A	1.22
UMPC - 19630	1.68	1.26	N/A	N/A	N/A	N/A	N/A
UMPC - 19631	N/A	N/A	N/A	N/A	0.93	0.44	0.49
UMPC - 19632	0.71	0.95	0.54	1.06	0.82	N/A	N/A

Whitehead Creek Calcaneus Measurements (continued)

UMPC - 19633	1.69	1.37	N/A	N/A	2.01	N/A	0.99
UMPC - 19634	1.08	1.51	N/A	N/A	1.17	0.61	0.90
UMPC - 19635	1.52	0.95	1	1.89	1.47	0.45	0.60
UMPC - 19636	N/A	N/A	0.95	1.49	1.26	0.66	0.81
UMPC - 19637	0.83	0.83	0.74	1.13	0.74	0.44	0.65
UMPC - 19638	0.78	0.82	0.86	1.14	1.2	0.4	0.53
UMPC - 19639	0.64	0.69	0.44	0.95	0.76	0.34	0.51
UMPC - 19640	N/A	1.24	1.07	1.6	1.23	0.64	0.91
UMPC - 19641	1.35	1.24	N/A	N/A	N/A	N/A	N/A

Whitehead Creek Calcaneus Measurements (continued)

UMPC - 19642	0.67	0.77	0.58	1.15	0.88	0.30	0.44
UMPC - 19643	1.35	1.46	1.07	1.56	1.25	0.65	0.93
UMPC - 19644	0.90	1.14	0.84	1.27	1.18	0.55	0.85
UMPC - 19645	1.41	1.28	N/A	N/A	1.27	0.70	0.84
UMPC - 19646	N/A	N/A	0.93	1.54	N/A	N/A	N/A
UMPC - 19647	0.86	0.77	N/A	N/A	1.15	0.63	0.78
UMPC - 19648	N/A	N/A	N/A	N/A	1.02	0.74	0.84
UMPC - 19649	N/A	N/A	1.19	1.47	1.16	0.88	0.95
UMPC - 19650	N/A	N/A	0.76	1.25	1.12	N/A	0.82

Whitehead Creek Calcaneus Measurements (continued)

UMPC - 19651	N/A	N/A	1.46	1.58	2.10	N/A	0.97
UMPC - 19652	N/A	N/A	N/A	N/A	1.15	0.78	0.92
UMPC - 19653	0.98	0.96	0.83	1.35	N/A	N/A	N/A
UMPC - 19654	1.40	1.49	N/A	N/A	1.66	0.96	1.35
UMPC - 19655	1.35	1.27	N/A	N/A	N/A	N/A	N/A
UMPC - 19656	N/A	N/A	N/A	0.7	0.67	0.38	0.45
UMPC - 19657	1.07	0.94	0.98	1.33	1.19	0.53	0.80
UMPC - 19658	N/A	N/A	N/A	N/A	1.41	N/A	0.85
UMPC - 19659	1.37	0.93	N/A	N/A	1.85	0.72	0.84