The Dietary Competitive Environment of the Origination and Early Diversification of Euprimates in North America

by

Laura Stroik

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Graduate Supervisory Committee:

Gary T. Schwartz, Chair
Kaye E. Reed
Christopher J. Campisano
Gregg F. Gunnell

ARIZONA STATE UNIVERSITY

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ABSTRACT

The earliest Eocene marked the appearance of the first North American euprimates (adapids, omomyids). Despite the fact that leading hypotheses assert that traits involved in food acquisition underlie euprimate origination and early diversification, the precise role that dietary competition played in establishing euprimates as successful members of mammalian communities is unclear. This is because the degree of niche overlap between euprimates and all likely mammalian dietary competitors ("the euprimate competitive guild") is unknown. This research determined which of three major competition hypotheses – non-competition, strong competition, and weak competition – characterized the late Paleocene-early Eocene euprimate competitive guild. Each of these hypotheses is defined by a unique temporal pattern of niche overlap between euprimates and their non-euprimate competitors, allowing an evaluation of the nature of dietary competitive interactions surrounding the earliest euprimates in North America.

Dietary niches were reconstructed for taxa within the fossil euprimate competitive guild using molar morphological measures determined to discriminate dietary regimes in two extant mammalian guilds. The degree of dietary niche separation among taxa was then evaluated across a series of fossil samples from the Bighorn Basin, Wyoming just prior to, during, and after euprimate origination. Statistical overlap between each pair of euprimate and non-euprimate dietary niches was determined using modified multivariate pairwise comparisons using distances in a multidimensional principal component "niche" space.

Results indicate that euprimate origination and diversification in North America was generally characterized by the absence of dietary competition. This lack of competition with non-euprimates is consistent with an increase in the abundance and diversity of euprimates during the early Eocene, signifying that the "success" of euprimates may not be the result of direct biotic interactions between euprimates and other mammals. An examination of the euprimate dietary niche itself determined that adapids and omomyids occupied distinct niches and did not engage in dietary competition during the early Eocene. Furthermore, changes in euprimate dietary niche size over time parallel major climatic shifts. Reconstructing how both biotic and abiotic mechanisms affected Eocene euprimates has the potential to enhance our understanding of these influences on modern primate communities.

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CHAPTER 1: INTRODUCTION

The onset of the Eocene (Wasatchian 0 or Wa0; ca. 55.8 Ma) (Fig. 1.1) marked the appearance of the first euprimates ("primates of modern aspect") in North America. At this point in their evolution, euprimates had already branched into two distinct clades, Adapidae and Omomyidae, but both euprimate families comprised only a single North American species: *Cantius torresi* and *Teilhardina brandti*, respectively (Gunnell, 2002; Smith et al., 2006; Rose et al., 2011, 2012).[1,2] These two clades differed in their dietary ecological adaptations, as adapids were larger-bodied and less insectivorous than omomyids (Rose et al., 1994; Gunnell, 2002). The radiation of each group during the Wasatchian consequently increased euprimate diversity, and the high relative diversity of omomyids as compared to adapids, which characterized their evolution throughout the Eocene, was already present in the early Wasatchian.

Throughout the early and middle parts of the Wasatchian (Wa0-Wa4), adapids were composed of a single anagenetic lineage, although the number of chronospecies referred to this lineage varies among studies (e.g., Gingerich and Schoeninger, 1977; O'Leary, 1997; Gunnell, 2002). In the Bighorn Basin, the site of this study, adapids

[1] Rose et al. (2011) and Rose et al. (2012) note that the origination of *Teilhardina* in North America likely slightly preceded that of *Cantius*.

[2] The objective of this study was not to evaluate the systematics of, or phylogenetic relationships among, adapid and omomyid species. As discussed in Chapter 4, taxonomic assignments of individual specimens included in the analyses herein were derived from museum collection labels and published specimen identifications. Although the specific classification of early euprimates varies among researchers (e.g., Bown and Rose, 1987; O'Leary, 1997; Gunnell, 1997; Gunnell, 2002), there is a consensus regarding general patterns, and these are discussed here.

underwent a cladogenetic event with the origination[3] of *Copelemur* in Wa5, postdating "Biohorizon B" (ca. 54 Ma; Wa4-Wa5 boundary).[4] It has been noted that adapids were less diverse, although more abundant, than omomyids during the early Eocene (Gunnell, 2002; Gunnell and Rose, 2002), as low adapid diversity has been attributed to the comparatively weak levels of interspecific competition typical of large primates with more generalized diets (Gunnell, 2002; Covert, 2004). Omomyidae also began as a single anagenetic lineage (species within *Teilhardina*), although omomyids quickly diversified to include several other genera in the early Wasatchian - *Anemorhysis*, *Tetonius*, and *Tetonoides* – and continually increased through Wa5 (Gunnell, 1997; Woodburne et al., 2009a). In addition, within Omomyidae, sub-NALMAs seem to be dominated by a single genus – *Teilhardina* (Wa0-Wa2), *Tetonius* (Wa3), *Pseudotetonius* (Wa4), and *Absarokius* (Wa5) (Gunnell, 1997; Fig. 1.1). Early Eocene adapids and omomyids are not likely candidates for the first euprimates, most significantly because they represent two, post-divergence euprimate lineages. However, because adapids and omomyids form the first known euprimate communities, and are thus much more abundant and skeletally complete than earlier, possibly ancestral euprimate species, they enable an assessment of the context in which early euprimates evolved.

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[3] The three fundamental processes of biogeography are extinction, dispersal (immigration and emigration), and speciation; these are alternative responses of a species to its biotic or abiotic environment that ultimately affect its biogeographic distribution (Hengeveld, 1990; Lieberman, 2005; Lomolino et al., 2006). Each of these processes either introduces a species to, or eliminates it from, an area, resulting in an origination or extinction, respectively – speciation and immigration cause originations, whereas species extinction and local extinction through emigration cause extinctions (Lieberman, 2005; Lomolino et al., 2006).

[4] The earliest *Copelemur* specimens in North America derive from southern Wyoming and northern Colorado and are dated to Wa4 (Maas and O'Leary, 1996; Gunnell, 2002).

Elucidating the adaptive and competitive conditions responsible for the origin and diversification of early euprimates is crucial for understanding the course of evolution of the entire euprimate clade, yet it is one of the most contested issues in primate paleobiology. The two leading euprimate origins hypotheses, the “grasping hypothesis” (Sussman, 1991; Bloch and Boyer, 2002) and the “visual predation hypothesis” (Cartmill, 1972, 1992), assert that “key innovations” involved in food acquisition (e.g., convergent orbits or grasping hands) were at the root of the initial euprimate radiation—that is, dietary niche was a primary driver of euprimate origination. Because key innovations are defined as novel traits that are adaptive (Gould, 1985; Benton, 1987; Erwin, 1992; Sudhaus, 2004), these hypotheses assume that euprimates first evolved in one of two scenarios: either through the exploitation of an open dietary niche ("absent competition") or through competitive exclusion of non-euprimate dietary competitors ("strong competition"). However, the role that diet played in establishing euprimates as successful members of early mammalian communities has not been explicitly addressed. On the other hand, if dietary competition between euprimates and non-euprimates was insubstantial ("weak competition"), diet was likely not a driving force in early euprimate evolution.

The Paleocene-Eocene Thermal Maximum, one of the most dramatic peaks in global temperatures in the whole of the Cenozoic, is associated with the Paleocene-Eocene boundary (Rea et al., 1990; Berggren et al., 1998; Fricke et al., 1998; Koch et al., 2003), and a correlation between this climatic event and mammalian taxonomic turnover is well-supported (e.g., Gingerich and Gunnell, 1995; Maas et al., 1995; Wing et al., 1995; Clyde and Gingerich, 1998; Bowen et al., 2001; Woodburne et al., 2009a).

Through the examination of first appearance dates (FADs) of taxa on different continents, many studies have suggested that this change in climate allowed a series of large-scale migrations, including a late Paleocene northern latitude dispersal of species to North America via Europe or Asia (McKenna, 1975; Beard, 1998; Alroy, 1999; Beard and Dawson, 1999; Smith et al., 2006; Silcox, 2008), which was likely responsible for the high incidence of faunal turnover of North American taxa, including euprimates, in the early Wasatchian (e.g., Maas and Krause, 1994; Wing, 1998a; Beard, 2002, 2006, 2008; Bowen et al., 2002; Clyde et al., 2005; Fleagle and Gilbert, 2006; Gunnell et al., 2008).

The Paleocene-Eocene boundary also coincides with the extinction or major decline of groups ecologically similar to euprimates, including carpolestids and plesiadapids (Krause, 1986; Gunnell, 1998; Maas et al., 1988; Woodburne et al., 2009b). However, other euprimate ecological vicars (e.g., microsyopids, paromomyids, didelphids, and rodents) persisted through this transition (Gunnell et al., 1995; Gunnell, 1998; Woodburne et al., 2009b). Shortly after their immigration to North America, euprimates greatly diversified, indicating an "invasion radiation" of this clade (Gingerich, 1981; Bown and Rose, 1987; Gunnell, 1997, 2002). As a result of the dramatic nature of the Paleocene-Eocene climatic change and the coincidence of euprimate origination and diversification with the decline of some likely euprimate dietary competitors but not others, the competitive environment into which these earliest euprimates arrived is not clear. Thus, the purpose of this study is to characterize the dietary competitive environment in which euprimates arose.

Competition is defined by niche overlap (Tokeshi, 1999; see Chapter 2); therefore, in order to discriminate among these three competitive scenarios (absence of competition,

strong competition, or weak competition), it is necessary to determine the degree of separation between the dietary niches of euprimates and those of their competitors: sympatric small-bodied, arboreal, insectivorous-frugivorous mammals (herein the "euprimate competitive guild"). To identify dental morphological variables that can be used to reconstruct dietary niches across the entire euprimate competitive guild in the late Paleocene and early Eocene, the relationships between dental measures, for which correlations with diet have the best empirical support in the literature, and known dietary regimes must first be examined within and across extant euprimate competitive guilds. Thus, this study has two objectives: The primary objective is to determine which of the three specific models of dietary competitive interaction defined the origination and early diversification of euprimates in North America. However, in order to complete this primary objective, a secondary objective – to identify phylogenetically independent, universal relationships between diet and molar morphology in extant euprimate competitive guilds – must first be addressed.

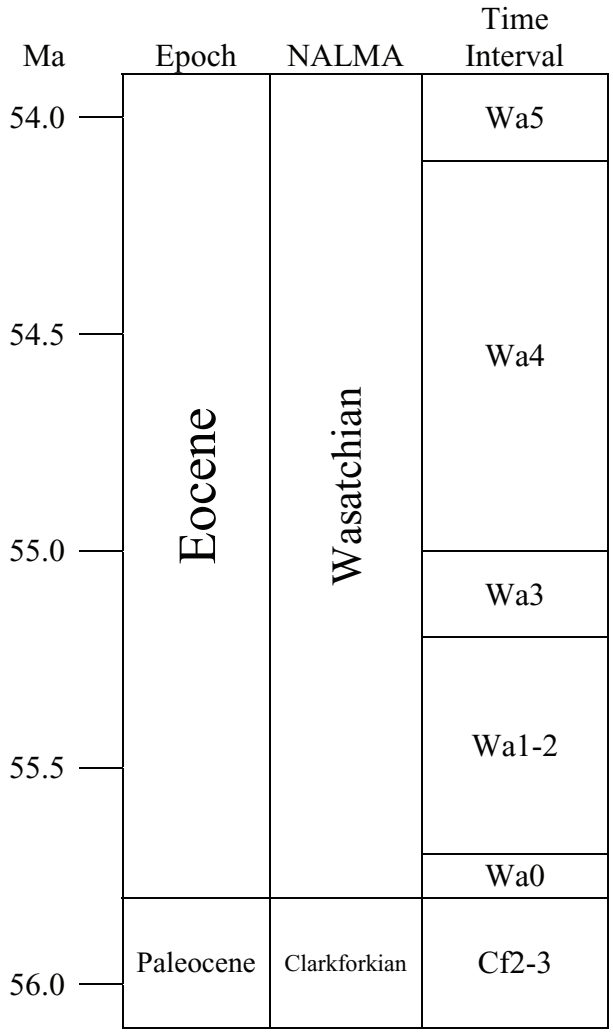


Fig. 1.1. Geologic timescale used in this study. NALMA = North American Land Mammal Age. "Time Interval" refers to the temporal unit of analysis used in this study. Time ranges follow Chew and Oheim (2013) and Woodburne (2004).

CHAPTER 2: BACKGROUND

As described in Chapter 1, the context of the origination of euprimates in North America in the earliest Eocene and their subsequent diversification in the early-middle Wasatchian is critical to understanding the course of euprimate evolution as a whole. This requires the evaluation of interactions between euprimates and the other members of the mammalian community in which they lived, specifically members of their guild, here defined as a group of species that exploit the same resources in a similar manner (Simberloff and Dayan, 1991). These biotic interactions include predation, competition, and mutualism; although, the latter is rarely found in mammalian communities[5] and will not be discussed further (Schoener, 1988). On the other hand, competitive interactions have the potential to significantly affect the structure of mammalian and primate communities (Connell, 1980; Arthur, 1987; Schoener, 1988; Tokeshi, 1997, 1999; Schemske, 2009; Chase and Myers, 2011), and from an evolutionary perspective, these effects of competition can impact speciation, extinction, changes in diversity and abundance, and morphological shifts (e.g., character displacement) in extinct groups (Arthur, 1982; Roughgarden, 1983; Janis and Damuth, 1990; Schluter, 1994; Vermeij, 1994; Sepkoski, 1996; Nosil and Harmon, 2009; Schemske, 2009; although see Benton, 1983, 1987; Masters and Rayner, 1993, Monroe, 2012).

For example, a relationship between extinction and diversity has been ascribed to the greater number of species interactions that accompanies heightened levels of diversity and leads to higher rates of competition (Hutchinson, 1959; Rosenzweig, 1995). Within a

[5] In addition, clear criteria for the identification of mutualistic interactions in the mammalian fossil record have not been established, and thus such interactions would likely not be detected.

geographic region, increased diversity reduces the number of individuals per species as competition for resources is increased, which can further increase the probability of species extinctions (Rosenzweig, 1995). As the onset of the Eocene is characterized by an overall increase in faunal diversity in North American sites, the greater occurrence of species interactions likely produced higher rates of speciation and extinction. However, species responses to both predation and abiotic changes can mimic patterns of competition (Janis, 1989; Abrams, 2000; Schweiger et al., 2008); thus, both the abiotic and biotic factors that can influence mammalian community structure and composition will be discussed.

ABIOTIC INFLUENCES ON THE EVOLUTION OF EARLY PALEOGENE MAMMALIAN COMMUNITIES

The abiotic, or physical, environment effects community change via mechanisms that are external to the fauna itself and thus not directly regulated by diversity (Brown, 1988). Climate is the most often cited determinant of biogeographic distributions and is inclusive of temperature, rainfall, and seasonality, which are most commonly used to reconstruct climatic change in the fossil record (Marshall, 1988; Lieberman, 2000; Darlington, 2004). Because many species are adapted to a relatively narrow range of environmental parameters, changes in climate force species to react, shifting conditions either away or towards species' optima (Cracraft, 1985; Brown, 1988). This can result in adaptation to the new environment (which can be coincident with speciation), dispersal (either local or global) to a different environment, or extinction (Rosenzweig, 1995).

The climate of the late Paleocene and early Eocene has been examined using a variety of data sources, including levels of carbon and oxygen isotopes in paleosols and

vertebrate fossils, floral morphology, and taxonomic similarity between extant and fossil faunal assemblages (Roehler, 1993; Wing and Greenwood, 1993; Fricke et al., 1998; Wilf et al., 1998; Wing, 1998a). Initial assessments of early Paleogene climate were based on deep-sea core data, but subsequent analyses of terrestrial data demonstrated that, although there are slight differences in the intensity and timing of reconstructed climatic patterns, the marine and non-marine records generally correlate with each another (Wing et al., 1991; Wing and Greenwood, 1993; Fricke et al., 1998; Koch et al., 2003). Together, these records have indicated that the global temperature was warmer than it is today and that mean temperature gradually increased from the onset of the Tiffanian in the Paleocene (ca. 60 Ma) through the early Eocene, where it peaked in Wa0 at the Paleocene-Eocene Thermal Maximum (PETM, or Eocene Thermal Maximum 1, ETM1) and reached a Cenozoic maximum at the Early Eocene Climatic Optimum (EECO) between 53 and 52 million years ago (Berggren et al., 1998; Woodburne et al., 2009a; Chew and Oheim, 2013; Fig. 2.1).

Studies of fossil plants and animals of the Western Interior of North America have suggested that this region was tropical to sub-tropical during the early Paleogene, reflected in the high abundance and diversity of small-bodied mammalian insectivores and frugivores and the prevalence of frost-intolerant plants, such as palms, cycads, and treeferns (Wing and Greenwood, 1993; Wing, 1998b). Specifically, analyses of isotopic ^{18}O values of soil carbonate, soil hematite, and enamel – a proxy for mean annual temperature – and leaf margin analyses have shown that temperature steadily increased from 60 Ma to 55.8 Ma (Wa0), decreased from the end of Wa0 to the end of Wa4 (ca. 54.3 Ma), and again rose to its highest point at the EECO, with suboptima at the Eocene

Thermal Maximum 2 (ETM2 or Hypothermal1, H1) and Hypothermal 2 (H2) in Wa5 (Alroy et al., 2000; Koch et al., 2003; Wing et al., 2005; Woodburne et al., 2009a; Secord et al., 2012; Chew and Oheim, 2013). Data on floral morphology, specifically leaf area, indicate that mean annual precipitation generally mirrors broad patterns of mean annual temperature in that aridity increased as temperature decreased from Wa0 to Wa4 (Wilf, 2000; Woodburne et al., 2009a).

Abrupt increases in mean annual temperature during this time have been linked to the depletion of levels of carbon stable isotope-13 (^{13}C) in the oceanic-atmospheric system, or negative carbon isotope excursion events (CIEs) (Yans et al., 2006; Secord et al., 2012). As such, $\delta^{13}C$-levels were relatively high throughout the early Paleogene but temporarily plummeted at the Paleocene-Eocene boundary, ETM2, and H2 (Abels et al., 2012). These dramatic declines in $\delta^{13}C$ have been attributed to the release of ^{13}C-poor (isotopically light) oceanic methane hydrate resulting from underwater volcanic activity or changes in oceanic circulation[6], which temporarily decrease $\delta^{13}C$ concentrations in marine environments (Rea et al., 1990; Corfield and Norris, 1998; Tripati and Elderfield, 2005; Abels et al., 2012). This influx of methane hydrate into the global carbon cycle increases overall levels of ^{13}C-depleted atmospheric CO_2[7], and it has been suggested that this mechanism may be responsible for initiating greenhouse effects and associated global warming (Rea, 1998; but see Tripati and Elderfield, 2005).

[6] However, Beck et al. (1998) suggest that the India-Asia collision and consequent Himalayan orogeny increased global carbon levels by decreasing the rate of organic carbon burial through the destruction of carbon sinks in continental margins and the erosion of organic carbon from marine strata.

[7] Evidence of an atmospheric link in $\delta^{13}C$ between marine systems and terrestrial soils, plants, and animals explains the detection of the CIE in both deep sea and terrestrial sediments (Koch et al., 2003).

The carbon isotope excursion at the Paleocene-Eocene boundary has thus been linked to the PETM, an increase in mean annual temperature of approximately 5-10°C in the span of less than 60 kya, concentrated poleward of 40˚ latitude (Beck et al., 1998; Berggren et al., 1998; Sloan and Thomas, 1998; Secord et al., 2012). The PETM has been associated with a reduction in latitudinal temperature gradients, a decrease in the intensity of atmospheric circulation (e.g., wind velocities), a more even latitudinal rainfall distribution, and increased continental precipitation (Clyde and Gingerich, 1998; Corfield and Norris, 1998; Rea, 1998; Sloan and Thomas, 1998; Wilf, 2000; Wing et al., 2005; Yans et al., 2006; McInerney and Wing, 2011; Abels et al., 2012; Secord et al., 2012; Kraus et al., 2013; Snell et al., 2013). Such a global climatic event would be expected to impact the biota, and the PETM has been correlated with marine planktonic and benthic foraminifera extinctions in several regions of the world as well as significant turnover in terrestrial faunas (Rea et al., 1990; Berggren et al., 1998; Clyde and Gingerich, 1998; Bowen et al., 2001; Gingerich, 2003; Tripati and Elderfield, 2005). In addition, studies have shown that mammalian body size was inversely related to temperature during the PETM, following the expectations of Bergmann's rule (Bown et al., 1994; Gingerich, 2003, 2004; Secord et al., 2012). As such, mammalian dwarfism occurred during Wa0, and as the circulation of carbon after its dispersal quickly restored the δ^{13}C-level to its previous value (accounting for the rapid nature of the excursion), body sizes subsequently increased (Clyde and Gingerich, 1998; Secord et al., 2012).

On the other hand, the carbon isotope excursions linked with ETM2 and H2 do not seem to have directly affected faunal turnover, as Biohorizon B, associated with a major mammalian turnover event, precedes these hyperthermals (Woodburne et al.,

2009a; Abels et al., 2012; Chew and Oheim, 2013). However, it has been suggested that diversity was lower and mean mammalian body mass was higher during the cooling and drying trend from Wa1 to Wa4, further supporting the link between climatic change and faunal community structure (Clyde and Gingerich, 1998; Chew and Oheim, 2013; although see Woodburne et al., 2009a).

Climatically driven shifts in the configuration of landmasses also affect species distributions, as barriers can be formed and removed through the rise and fall of sea levels. In addition, corridors composed of similar habitats can be created and dissolved by changes in local and global climatic variables (e.g., the latitudinal expansion of tropical habitats) (Lieberman, 2000; Lomolino et al., 2006). In fact, the continental structure at the end of the Paleocene and beginning of the Eocene had significant consequences for mammalian biogeography at this time, including the distribution of euprimates. For example, in addition to euprimates, the onset of the Eocene marked the appearance of perissodactyls, artiodactyls, and hyaenodontid creodonts in North America (Beard, 1998; Beard and Dawson, 1999; Alroy et al., 2000).

The early Paleogene was characterized by a remnant geographic division between the Laurasian (North America, Europe, and Asia) and Gondwanan (Australia, Africa, South America, and India) landmasses, and although the southern continents were largely separated from one another, this was not the case in the northern hemisphere (Adams, 1981; Holroyd and Maas, 1994; Miller et al., 2005; Smith et al., 2006). In fact, evidence has shown that mammalian dispersal between Holarctic continents was extensive (Russell, 1975; Adams, 1981; Holroyd and Maas, 1994; Miller et al., 2005). For example, late Paleocene-early Eocene Beringia has been denoted as a filter bridge, selectively

allowing passage of certain taxa but not others, and dispersals of a variety of mammals from Asia to North America are well-established (e.g., Simpson, 1968; Beard, 1998, 2006; Beard and Dawson, 1999). Furthermore, although the Turgai straits separated western and eastern Eurasia and there was not a continuous land bridge joining Europe and North America, there was enough connectivity among these northern landmasses for migrations to occur (McKenna, 1975; Russell, 1975; Adams, 1981; Smith et al., 2006). Thus, although it is unclear which circum-Holarctic route was used most frequently by early Paleogene mammals, dispersals to North America occurred via both eastern (through Beringia) and western (through Greenland) routes (Hooker, 1998; Beard and Dawson, 1999).

On the other hand, there is a growing consensus that euprimates originated in North America via a westward migration (Ni et al., 2005; Smith et al., 2006; Beard, 2008; although see Beard and Dawson, 1999; Beard, 2002; Beard, 2006). This stems from the biostratigraphic correlation of species of *Teilhardina* in Asia, Europe, and N. America, which has shown that Asian *T. asiatica* appeared earlier than European *T. belgica*, which itself originated before North American *T. brandti* and *T. magnoliana* (Smith et al., 2006; Beard, 2008; Rose et al., 2011). As *Teilhardina* is at the base of the omomyid clade, this chronology suggests that primate dispersal from Asia to North America progressed from east to west via Europe. A phylogenetic analysis of *Teilhardina* by Ni et al. (2005) further supports this conclusion by noting the affinity of *T. asiatica* to *T. belgica* and the sister species relationship of *T. americana* to the *T. asiatica*-*T. belgica* clade. This dispersal was presumably initiated by the PETM as well, as climatic warming, and the associated expansion of subtropical and tropical habitats to higher latitudes, would have

allowed dispersal along a Holarctic route from Asia to Europe across the Turgai Straits and from Europe to North America (McKenna, 1975; Russell, 1975; Maas and Krause, 1994; Clyde and Gingerich, 1998; Gunnell, 1998; Alroy et al., 2000; Smith et al. 2006). Thus, climatic change was ultimately responsible for the origination of adapids and omomyids in North America; however, the possible role that the biotic environment played in the evolution of euprimates after their arrival is the topic of the next section.

BIOTIC INFLUENCES ON THE EVOLUTION OF EARLY PALEOGENE MAMMALIAN COMMUNITIES

Competition, the focus of this section, is defined as a mutually negative interaction among species or populations due to the presence of a shared, limited resource (Tilman, 1982; Tokeshi, 1997, 1999; Holt, 2009). As such, competitive environments are defined by species interactions, and many models of interaction (which include "non-interactions") at the macroevolutionary level have been described (e.g., Van Valen, 1965; Cracraft, 1985; Benton, 1996, Schluter, 1996; Ricklefs, 2010). As noted in Chapter 1, competitive interactions in the fossil record are identified via niche overlap, and thus these models of interaction are characterized by specific patterns of niche separation or overlap between invasive (in this case, euprimate) and incumbent (non-euprimate potential competitor) taxa.

The Ecological Niche

The ecological niche, originally proposed by Grinnell (1917a,b), has evolved to include several different conceptualizations[8], and perhaps one of the most frequently

[8] McInerny and Etienne (2012a,b,c) provide an excellent discussion of the profusion of niche interpretations.

cited is that of the "functional (or Eltonian)" niche, which defines a niche as the ecological role, or place, of an organism (or taxon) within its community (Elton, 1927). This ecological role can be partitioned into various ecological axes, corresponding to particular limited resources in the physical world (i.e., Hutchinson's "biotope") (Hutchinson, 1978; Arthur, 1987; Colwell and Rangel, 2009; Nosil and Harmon, 2009; McInerny and Etienne, 2012b). If these ecological values are instead attributed to the taxa themselves, as Hutchinson proposed, and are thus reciprocal to the external environment in which they live, overlap of the values of taxa along their ecological axes is a precondition of resource competition (Hutchinson, 1959, 1965; Arthur, 1987; Colwell and Rangel, 2009; McInerny and Etienne, 2012b). In addition, niches have been described as inclusive of the entire range of ecological values and resources a taxon can theoretically express or use, respectively (the "fundamental niche") or as inclusive of the actual ecological values a taxon manifests (the "realized niche") (Patten and Auble, 1981). In this study, the concept of the Hutchinsonian, realized niche, which is intrinsic to a taxon, will be employed.

Extant mammalian niches have been modelled and characterized in a multitude of ways, both conceptually and in practice, and factors such as food resource and substrate use and availability, mechanisms of feeding and locomotion, habitat preferences and geographic distributions, physiological requirements, and seasonal patterning have been considered (Porter and Dueser, 1982; Fleagle and Reed, 1996; Ganzhorn, 1999; Ricklefs, 2010). The degree of similarity in single or multiple ecological factors has consequently been used to resolve the extent to which niche differentiation as a result of competitive interactions has influenced community composition.

In the mammalian fossil record, niches are defined almost exclusively by ecomorphological traits (morphological features closely correlated with ecological characteristics), representing the most fundamental elements of a mammalian ecological niche – diet, body mass, activity pattern, and locomotion (e.g., Van Valen and Sloan, 1966; Krause, 1986; Maas et al., 1988; Janis et al., 1994; Van Valkenburgh, 1994; Hunter, 1997; Dewar, 2008; Friscia and Van Valkenburgh, 2010). For example, ecomorphological characters of extant groups have also been used to generate ecological niche spaces, or ecospaces, in order to assign fossil specimens to specific niches (Morlo, 1999; Prevosti et al., 2013). However, these latter methods are not effective when the morphology of fossil species differs substantially from extant analogs or when related extant taxa are unknown.

Alternatively, ecomorphological traits can be used to represent a species' niche as a multidimensional hypervolume positioned within a larger "niche space," in which each dimension represents a particular ecomorphological characteristic (Hutchinson, 1957, 1965). Originally proposed in the primate communities literature by Fleagle and Reed (1996), previous studies have employed multivariate dimensionality reduction techniques, most commonly principal component or principal coordinates analysis, to reconstruct niches as multidimensional individually analyzable units (e.g., Van Valkenburgh, 1994; Fleagle and Reed, 1996, 1999; Gilbert, 2005; Friscia and Van Valkenburgh, 2010). The use of this niche concept in the evaluation of competitive interactions is discussed at the end of this chapter.

The dietary niche.

Teeth are the point of intersection between an organism and its dietary environment, and the identification of mammalian dietary niches in the fossil record requires (and almost always incorporates) an understanding of the relationships between dietary behavior and dental morphology in extant mammals (e.g. Butler, 1973; Krause, 1986; Maas et al., 1988; Hunter, 1997; Morlo, 1999; Dumont et al., 2000; Jernvall et al., 2000; Kirk and Simons, 2001; Strait, 2001; Dewar, 2003; White, 2006; Friscia and Van Valkenburgh, 2010). The association between tooth shape and general feeding habits is well-supported, and a great deal of attention has been paid to the congruence of postcanine, particularly molar, anatomy with dietary repertoire in the mammalian literature. As a result, and due to the abundance of these elements in fossil assemblages and their importance in fossil taxonomic identification, this study was conducted on first and second mandibular molars, which will be the focus of the following discussion.

Among mammals, a significant amount of variation in molar form can be explained by their functional demands, which relate to the material properties of dietary items and the corresponding manner in which these items are processed by the masticatory system (Kay and Hylander, 1978; Lucas 1979; Strait, 1991, 1997; Lucas and Cortlett, 1992; Strait and Vincent, 1998; Evans and Sanson, 2006). In a broad sense, crest-shearing, apposition of cusps and basins, and in some taxa, lateral movements along cusp tips, are most significant in maximizing the breakdown of food particles, the fundamental objective of chewing (Luke and Lucas, 1983; Lucas, 1979, 2006; Ungar, 2002; Evans, 2003; Evans and Sanson, 2003, 2005). Accordingly, the macroscopic structure of features related to these functions varies across the dietary spectrum.

For instance, longer, laterally concave, sharper crests, and high, pointed, angular, reciprocally concave cusps – i.e., high topographic relief – are thought to increase efficiency in piercing and shearing for crack initiation and propagation, respectively, in soft, tough diets, characteristic of insectivory (Kay, 1973, 1975b; Kay and Hiiemae, 1974; Butler, 1983; Kay and Covert, 1984; Lucas and Luke, 1984; Rensberger, 1986; Strait, 1991, 1993a,b, 1997; Popowics and Fortelius, 1997; Hiiemae, 2000; Lucas and Peters, 2000; Ungar, 2002; Evans, 2003; Evans and Sanson, 2003, 2005; Lucas, 2006; Berthaume et al., 2013). In contrast, round, flat, bulbous cusps and large, shallow basins – i.e., low topographic relief – are most effective in crushing and grinding either brittle, stiff plant material (e.g., seeds, nuts) or plastic, turgid ripe fruit (Butler, 1972, 1983; Rensberger, 1973; Kay and Hiiemae, 1974; Seligsohn, 1977; Kay and Covert, 1984; Maier, 1984; Yamashita, 1996; Hiiemae, 2000; Lucas and Peters, 2000; Ungar, 2002; Evans, 2006; White, 2009). Morphological parameters developed to quantify two- and three-dimensional functional aspects of molar form are diverse and have been conducted on samples of variable phylogenetic breadth and dietary specificity. Notably, the innovative metrics and models developed to characterize overall molar complexity without the use of landmarks, and thus reference to cusp and crest homologies (e.g., dental topographic analysis, geodesic distance analysis, orientation patch count, relief index, Dirichlet normal energy), exhibit significant potential in the ability to reconstruct diets in the fossil record (Ungar, 2007; Boyer, 2008; Boyer et al., 2010, 2011, 2012; Bunn et al., 2011; Joshi et al., 2011; Godfrey et al., 2012; Evans, 2013; Guy et al., 2013; Ledogar et al., 2013).

Still, none of these studies have employed dietary classifications that are sufficiently fine-grained to compare dietary regimes across entire communities. This is particularly important in evaluating dietary competition because dietary niche overlap occurs among species within major dietary categories (e.g., frugivory). It is possible that current methods are unable to detect associations between molar morphology and dietary niches at this level of precision; however, molar measurements designed to encompass functionally related aspects of molar form were evaluated in this study to determine if a relationship between finer dietary classifications and molar form could be discerned.

Models of Competitive Interactions

Much of the previous research on extant primate competition has focused on interactions or ecological partitioning within Primates as an isolated group (e.g., Dunbar and Dunbar, 1974; Schreier et al., 2009; Nijman and Nekaris, 2010; Ramdarshan et al., 2012), although primates almost certainly interact with non-primate species (Robinson and Redford, 1986; Ganzhorn, 1999). Relatively few studies have recognized the importance of examining interactions within guilds and mammalian communities, of which primates are only one component (e.g., Smythe, 1986; Shanahan and Compton, 2001; Sushma and Singh, 2006; Beaudrot et al., 2013b,c). In general, there is support for more intense or direct competition among related species, likely due to the effects of phylogenetic niche conservatism, or the tendency of closely related species to inhabit similar niches due to the shared inheritance of traits from a common ancestor (Wiens, 2011). However, the influence of competition is not limited to interactions within taxonomic groups (Losos, 2008). This is particularly relevant when considering the evolutionary history of living communities, during which primate diversity and

composition changed over the course of millions of years. Specifically, the ecological significance of interactions between primate and non-primate species was likely greater during time periods when primates were less diverse and primate communities were composed of fewer related species, namely at the origins of major clades (e.g., earliest Eocene adapids and omomyids, late Oligocene-early Miocene platyrrhines, European early-middle Miocene catarrhines).

Although competition as a biological process has a strong foundation in neoecological studies (e.g., Connor and Simberloff, 1979; Grant, 1986; Elton, 2004; Miljutin and Lehtonen, 2008; Calede et al., 2011; Esselstyn et al., 2011; Kamilar and Ledogar, 2011), the application of competition theory to fossil communities has been relatively limited (Abrams, 1990; Masters and Rayner, 1993). As discussed above, much of this disparity lies in the difficulty of defining niche overlap in extinct taxa, which, along with inverse patterns of diversity and abundance (the "double-wedge pattern") and similar biogeographical and temporal distributions, is necessary for determining the presence of competition in paleocommunities (Cifelli, 1981; Benton, 1990, 1996; Rosenzweig and McCord, 1991; Sepkoski, 1996; Van Valkenburgh, 1999, Butler et al., 2009a,b; see below). For an invasion radiation, such as the origination of euprimates in North America, only three main types of competitive interaction are possible: non-competition, competitive displacement, and competitive coexistence (Benton, 1990). It should be noted that the intensity of competition is affected by body size, trophic position, and the degree of niche separation between competitors. In this study, competitive interactions were examined within a single mammalian guild, minimizing or eliminating variation in – and thus the influence of – body mass and trophic position.

The first model, non-competition, refers to the absence of incumbent taxa, which, if they were present at the point of origination, would be in direct competition with the invasive taxon. As a result, the invasive taxon exploits an "empty niche" or "open ecospace," and this scenario can take two forms. Non-replacement ("expansion radiation"; Benton, 1990) occurs when an invasive taxon enters a niche that had been consistently unoccupied within the community. Post-extinction replacement (Benton, 1996) (variably referred to as "opportunistic replacement" (Krause, 1986), "incumbent replacement" (Rosenzweig and McCord, 1991)) is similar to the model of non-replacement except that the open niche is newly available due to recent extinctions in the community. In other words, ecologically similar incumbent taxa inhabited these niches just before the invasive taxon arrived.

The second model, competitive displacement (Krause, 1986) ("competitive replacement" (Benton, 1987), "taxonomic displacement" (Maas et al., 1988; Schluter and McPhail, 1993)), refers to strong competition among taxa. The most common criterion for the identification of competition between species in the fossil record is the demonstration of the "double-wedge pattern" of diversity or abundance. This pattern exhibits an inverse relationship in the diversity or abundance profiles of competing taxa (e.g., between invasive and incumbent taxa) (Benton, 1987; Sepkoski, 1996). Thus, if competitive displacement occurred between two fossil taxa, the diversity or abundance of the more "successful" competitor would have increased as the diversity or abundance of the less "successful" competitor decreased. It is also possible that competition may result in evolutionary niche divergence or "character displacement," in which the trait morphologies of species diverge in response to competition. In this scenario, temporal

morphological change (in this study, molar shape change over time) will occur in the invasive or incumbent taxon (or both) such that niche overlap decreases. Thus, competition will be reduced and may eventually cease over time (Brown and Wilson, 1956; Roughgarden and Diamond, 1986; Werdelin, 1996). Furthermore, niche divergence may occur in the absence of the double-wedge pattern.

Of course, competition can also occur within species, producing niche divergence between populations, a mechanism for taxonomic diversification (Schluter, 1994; Nosil and Harmon, 2009). This "competitive speciation" is a form of sympatric speciation in which competition among conspecifics results in disruptive selection (Rosenzweig, 1995; Pianka, 2004). In this scenario, diversification is driven by interactions among individuals in contrast to other forms of speciation (e.g., allopatric) that do not require mechanisms that rely on biotic interactions (Rosenzweig, 1995). This interaction requires that "ecological opportunities," or parts of a habitat that are potentially "useable" by species (i.e., open niches), be present in order for competitive speciation to occur (Rosenzweig, 1995). In addition, as the number of species becomes greater within a community, ecological opportunities will decrease, and competitive speciation will diminish. As a result, it has been suggested that the speciation rate per species will decrease as diversity increases (Rosenzweig, 1995). Rosenzweig (1995) also noted, however, that ecological opportunities for one species can derive from other species, predicting a positive feedback loop between diversity and speciation (also see Vermeij, 1994). Given the increase in euprimate diversity over the course of the Wasatchian within a single site (in this study, the Bighorn Basin), niche overlap, and subsequent reconstructions of competition, among euprimates will also be examined as a causal factor in their radiation.

As discussed earlier in this chapter, a taxon's response to predation or climatic changes can resemble patterns of competitive displacement in macroecological studies. For example, a decrease in the abundance of an incumbent taxon relative to an invasive taxon may be the result of the former's greater susceptibility to a new predation or climatic pressure (Janis, 1989; Benton, 1990; Sepkoski, 1996; Abrams, 2000; Schweiger et al., 2008). In this case, the observed diversity or abundance pattern or evolutionary niche divergence has no bearing on the interaction between the incumbent and invasive taxa. However, if it can be demonstrated that changes in the niches or abundance profiles of competitors are not correlated with climatic change or predator diversity or abundance, it can be concluded that niche shifts are the result of competitive displacement. Finally, it has been demonstrated in extant studies that competitive interactions can either be mediated or strengthened by an abiotic environmental change that affects both competitors (Northfield and Ives, 2013). In both scenarios, either character displacement or an inverse pattern of abundance will be evident; however, in the fossil record, the relative effects of climatic change on individual taxa that are adapted to similar environments (i.e., members of a mammalian guild) cannot be known. Thus, it was determined that the most conservative approach to the identification of competitive displacement was to consider it as an alternative to climate-induced changes. In other words, if climatic change is correlated with taxonomic niche divergence or a double-wedge pattern, competition was not immediately invoked as the causal mechanism.

The third model is competitive coexistence (Tokeshi, 1999) ("diffuse competition" (Van Valen, 1980)) in which the invasive and incumbent species occupy the same niche (and thus there is the potential for competitive displacement), but neither the

double-wedge pattern nor niche divergence is observed. Competitive coexistence has been documented in extant studies and has been ascribed to partial niche separation, the presence of only intermittent competition such that neither species is permanently affected, or sustained low-intensity competition (Van Valen and Sloan, 1966; Connell, 1980; Abrams, 1986, 1987).

Competitive Interactions Among Paleogene Mammals

Most research on competitive biotic interactions in the fossil record has relied solely on the detection of inverse patterns of diversity and abundance to infer competition over large geographic and temporal scales (e.g., Van Valen and Sloan, 1966; Gould and Calloway, 1980; Cifelli, 1981; Van Valkenburgh, 1999; Butler et al., 2009a,b). However, there are studies of competition among Paleogene mammals that have additionally included an examination of similar resource use and paleogeographic distributions (e.g., Krause, 1986; Maas et al., 1988; Hunter, 1997; Morlo, 1999; Dewar, 2003; Friscia and Van Valkenburgh, 2010).[9] These studies interpreted cases of high levels of ecomorphological similarity among fossil taxa, reconstructed via known relationships between ecological and morphological traits in related extant mammals, as evidence of shared resource use.

For example, body mass distributions and dental trait correlations have been compared among purported competitors to assess similarity in paleobiology, or niche

[9] Maas et al. (1988) note that identification of competitive displacement in the fossil record requires that competing taxa be geographically separated prior to competition. This is based on the supposition that resource limitation should prevent competitors from evolving sympatrically. Although changes in resource availability can alter the nature of the competitive interaction between sympatric taxa, the scenario required by Maas et al. (1998) certainly characterizes the origination of Wa0 adapids and omomyids in North America.

overlap (Krause, 1986; Maas et al., 1988). In subsequent studies, the representation of ecomorphological characteristics as dimensions of a multidimensional niche space, as discussed previously, was adopted as a means to identify niche overlap. Using values of ecomorphological features, taxa were plotted within a principal component, principal coordinate, or non-metric multidimensional scaling (NMDS) space. The occupation of similar regions of this space, or visual overlap of reconstructed two-dimensional "niche" polygons (akin to Hutchinsonian hypervolumes), among potential competitors was used as a proxy for niche overlap, a precondition of competition (Hunter, 1997; Morlo, 1999; Friscia and Van Valkenburgh, 2010; see McGowan and Dyke, 2007; Brusatte et al., 2008 for examples of this method in non-mammalian taxa). However, the lack of an associated statistical test makes the identification of niche overlap somewhat ambiguous in cases where two-dimensional coordinates or polygons are in close approximation, and this is often the case when examining likely competitors, as these are assumed to exhibit similar ecomorphologies. In addition, this approach rarely enables an analysis of the total amount of variation (i.e., all aspects of the ecological niche) present in the sample because only two, or perhaps three, dimensions can be considered simultaneously. A method for identifying niche overlap, and thus competitive interactions, that attempts to address these restrictions was used in this study and will be described in Chapter 5.

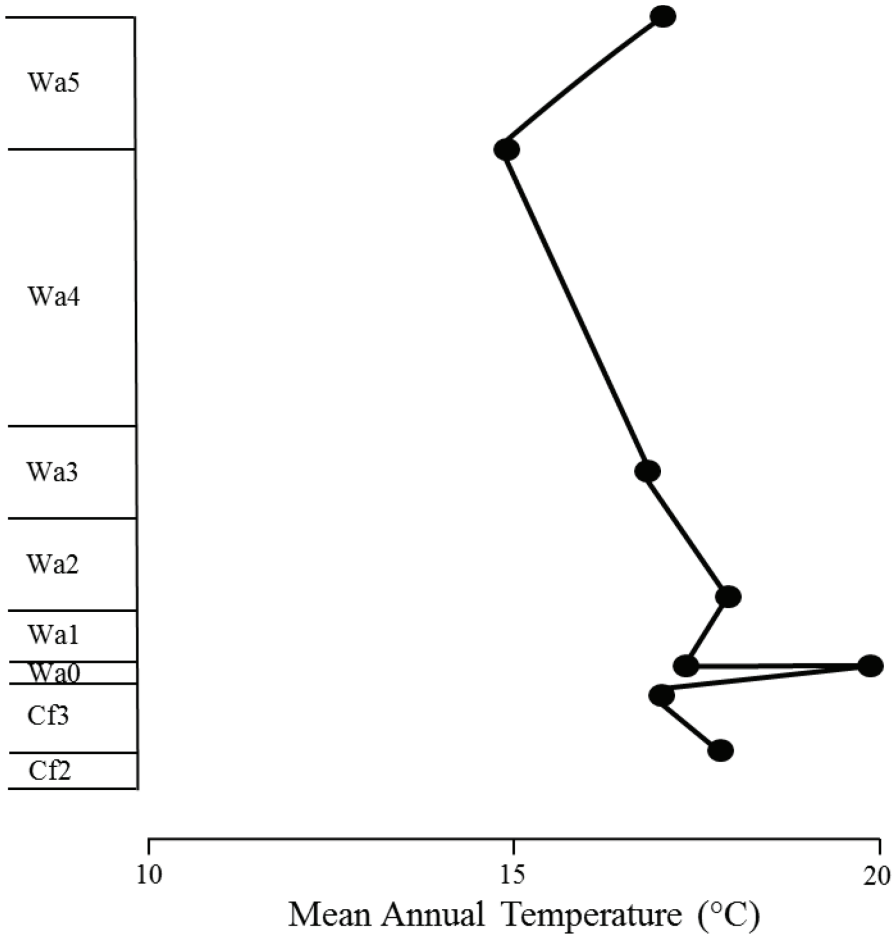


Fig. 2.1. Plot of mean annual paleotemperature across the time intervals examined in this study. Redrawn and modified from Woodburne et al. (2009a).

CHAPTER 3: HYPOTHESES AND PREDICTIONS FOR THE EARLY EUPRIMATE COMPETITIVE ENVIRONMENT

The primary objective of this study was to determine which of three models of dietary competitive interaction defined the origination and early diversification of euprimates in North America. These competition models are: (1) the absence of dietary competition ("non-competition"), (2) the presence of strong dietary competition ("competitive displacement"), and (3) the presence of weak, or diffuse, dietary competition ("competitive coexistence").

Each of these three hypotheses corresponds to a distinct model of competitive interaction (outlined in Chapter 2) between invasive (euprimate) and incumbent (non-euprimate) taxa and is characterized by a unique temporal pattern of dietary niche overlap between euprimates and their potential competitors (Fig. 3.1). As such, the following hypotheses are mutually exclusive and account for all possible patterns of dietary niche overlap over time. In addition to evaluating these hypotheses at the point of euprimate origination in North America in Wa0, the model of competitive interaction pertaining to the origination, or first appearance date (FAD), of each subsequent euprimate taxon can be assessed; thus, in the discussion below, "euprimate" refers to any euprimate taxon during the time period examined (Clarkforkian 2-Wasatchian 5; see Fig. 1.1). The hypotheses and predictions below are outlined in Table 3.1.

HYPOTHESIS 1: NON-COMPETITION

The first hypothesis of this study is that euprimate origination occurred in the absence of dietary competition, or non-competition. Non-competition can occur as the result of a longstanding absence of taxa occupying the original euprimate niche (non-

replacement) or as the result of recently available dietary niches due to the extinction of species that previously occupied the euprimate dietary niche (post-extinction replacement). Non-replacement predicts that during the time interval just prior to the euprimate first appearance date (FAD), no non-euprimate dietary niches will overlap the dietary niche of later euprimates. Furthermore, at the euprimate FAD, no non-euprimate dietary niches will overlap the euprimate dietary niche (i.e., the euprimate niche will be exclusive to euprimates). Post-extinction replacement, on the other hand, predicts that during the time interval just prior to the euprimate FAD, the dietary niches of one or more non-euprimates will overlap the dietary niche of later euprimates; however, at the point of the euprimate FAD, these non-euprimates will be absent, and their dietary niches will be vacant.

HYPOTHESIS 2: COMPETITIVE DISPLACEMENT

The second hypothesis, competitive displacement, states that euprimate origination occurred in the presence of direct, strong dietary competition with non-euprimates. This hypothesis predicts that during the time interval immediately preceding and including the euprimate FAD, the dietary niches of one or more non-euprimates will overlap the euprimate dietary niche. Following euprimate origination, competitive displacement can be identified by either an inverse relationship between euprimate and non-euprimate abundance or diversity profiles (the "double-wedge" pattern) or by the divergence of euprimate and non-euprimate dietary niches. Moreover, these changes in the abundance or diversity profiles or niche divergence will not be associated with changes in climate or an increase in predator origination rate or relative predator abundance.

HYPOTHESIS 3: COMPETITIVE COEXISTENCE

The third hypothesis is that euprimate origination occurred in the presence of dietary competition with non-euprimates, but this competition was weak and not sufficiently acute to cause competitive displacement, resulting instead in competitive coexistence. In this study, support of this hypothesis could also be evidence of ecological niche separation between euprimate and non-euprimate taxa along one or more non-dietary niche axes. This hypothesis predicts that during the time interval immediately preceding and including the euprimate FAD, the dietary niches of one or more non-euprimates will overlap the euprimate dietary niche. During the time intervals following the euprimate FAD, the dietary niches of euprimates and non-euprimates will not significantly diverge over time nor will there be a negative correlation between euprimate and non-euprimate abundance or diversity profiles. Finally, changes in the abundance profiles of euprimates and non-euprimates whose niches overlap will not be associated with changes in climate or an increase in predator origination rate or relative predator abundance.

Given that members of the Eocene euprimate competitive guild are at least partly arboreal and of generally similar body mass, it is unlikely that predation by a single taxon would affect one of these species exclusively. In other words, it would not be expected that a predator or group of predators would prey on some guild members and not others. However unlikely, this scenario cannot be excluded outright particularly if an increase in predator abundance or diversity is negatively correlated with the abundance or diversity of a non-euprimate taxon. Thus, predation will be considered post hoc in cases of niche overlap between euprimate and non-euprimate taxa.

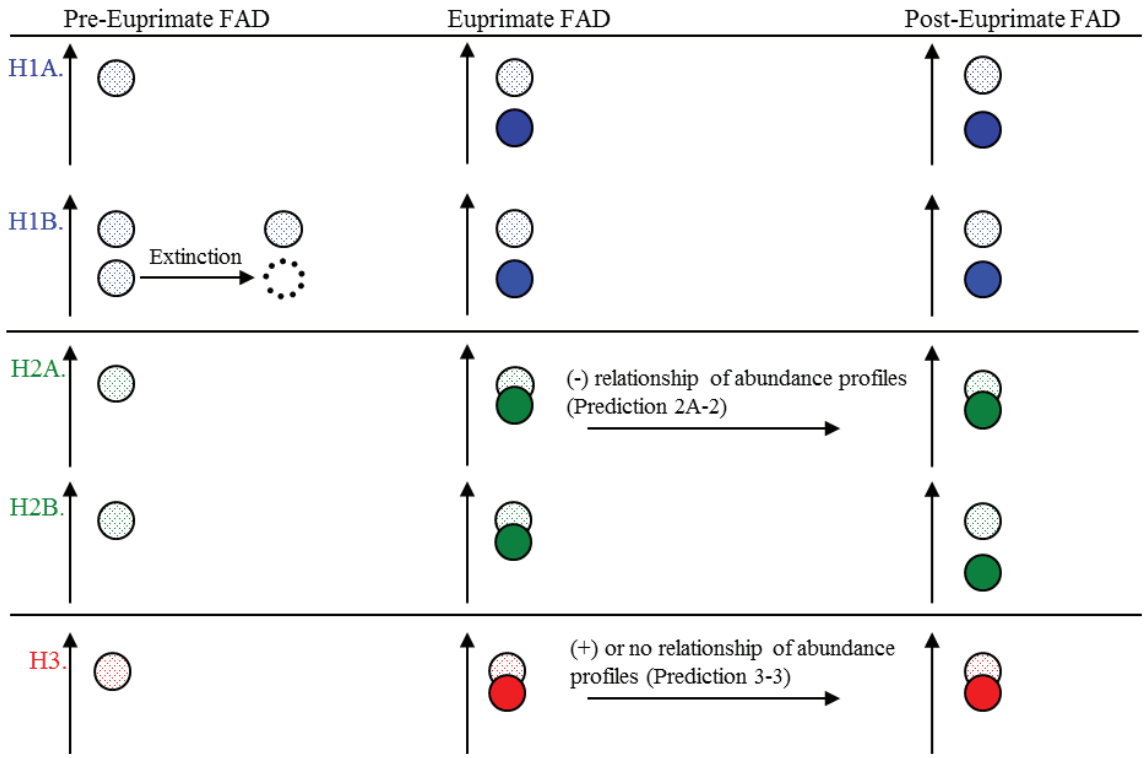


Figure 3.1. Models of hypotheses tested in this study. H1A. Non-replacement. H1B. Post-extinction replacement. H2A. Competitive displacement (in the absence of dietary niche divergence). H2B. Competitive displacement (with dietary niche divergence). H3. Competitive coexistence. Hatched circles: dietary niches of non-euprimates; solid circles: dietary niches of euprimates. Vertical distance (denoted by arrow) in all graphs is degree of dietary niche separation. FAD: first appearance date. Hypotheses and predictions refer to Table 3.1.

Table 3.1. Three competition hypotheses of euprimate origination and diversification to be tested in this study. Hypotheses will be evaluated for each time interval, and thus the terms "euprimate" or "non-euprimate" are used to indicate the applicability of these statements to the entire time range and taxonomic sample examined. Hypotheses 1-3 are mutually exclusive.

Hypothesis 1: Euprimate origination occurred in the absence of dietary competition. (Non-Competition)	
Hypothesis 1A: Euprimate origination occurred in the longstanding absence of taxa occupying the original euprimate dietary niche. (Non-Replacement)	**Prediction 1A-1:** During the time interval just prior to the euprimate first appearance date (FAD), no non-euprimate dietary niches will overlap the dietary niche of later euprimates. **Prediction 1A-2:** At the euprimate FAD, no non-euprimate dietary niches will overlap the euprimate dietary niche.
Hypothesis 1B: Euprimate origination occurred as the result of recently available dietary niches due to the extinction of taxa that previously occupied the euprimate dietary niche. (Post-Extinction Replacement)	**Prediction 1B-1:** During the time interval just prior to the euprimate FAD, the dietary niches of one or more non-euprimates will overlap the dietary niche of later euprimates. **Prediction 1B-2:** At the euprimate FAD, the non-euprimate(s) identified in Prediction 1B-1 will be absent, their dietary niches will be vacant, and no non-euprimate dietary niches will overlap the euprimate dietary niche.
Hypothesis 2: Euprimate origination occurred in the presence of direct, strong dietary competition with non-euprimates. (Competitive Displacement)	
Prediction 2-1: During the time interval immediately preceding and including the euprimate FAD, the dietary niches of one or more non-euprimates will overlap the euprimate dietary niche. **Prediction 2-2:** Changes in the abundance profiles or divergence of the dietary niches of euprimates and the non-euprimate(s) identified in Prediction 2-1 will not be associated with changes in climate or an increase in predator origination rate or relative predator abundance.	
Hypothesis 2A: Direct dietary competition between euprimates and non-euprimates occurred in the absence of dietary niche divergence.	**Prediction 2A-1:** During the time intervals following the euprimate FAD, the dietary niches of euprimates and the non-euprimate(s) identified in Prediction 2-1 will not significantly diverge over time. **Prediction 2A-2:** During the time intervals following the euprimate FAD, the abundance profiles of euprimates and the non-euprimate(s) identified in Prediction 2-1 will be negatively correlated.

Table 3.1, Cont'd.

Hypothesis 2B: Direct dietary competition between euprimates and non-euprimates resulted in dietary niche divergence.	**Prediction 2B-1:** During the time intervals following the euprimate FAD, the dietary niches of euprimates and the non-euprimate(s) identified in Prediction 2-1 will significantly diverge over time.
Hypothesis 3: Euprimate origination occurred in the presence of dietary competition with non-euprimates, but this competition was weak and not sufficiently acute to cause competitive displacement. (Competitive Coexistence)	
Prediction 3-1: During the time interval immediately preceding and including the euprimate FAD, the dietary niches of one or more non-euprimates will overlap the euprimate dietary niche.	
Prediction 3-2: During the time intervals following the euprimate FAD, the dietary niches of euprimates and the non-euprimate(s) identified in Prediction 3-1 will not significantly diverge over time.	
Prediction 3-3: During the time intervals following the euprimate FAD, the abundance profiles of euprimates and the non-euprimate(s) identified in Prediction 3-1 will not be negatively correlated.	
Prediction 3-4: Changes in the abundance profiles of euprimates and the non-euprimate(s) identified in Prediction 3-1 will not be associated with changes in climate or an increase in predator origination rate or relative predator abundance.	

CHAPTER 4: STUDY SAMPLES AND DATA COLLECTION

Before each of the competition hypotheses outlined in Chapter 3 could be evaluated in the early Paleogene euprimate fossil record, it was necessary to establish a clear and consistent relationship between molar morphology and diet across extant euprimate competitive guilds. Thus, the nature of the diet-dentition association was first examined using an extant sample comprising two distinct mammalian guilds, and these associations were then used in dietary niche reconstructions of taxa within the fossil mammalian sample. The composition of these two samples – extant and fossil – as well as the data collection methods applied to them are described here.

SAMPLE COMPOSITION

Extant Sample

The extant sample comprised first and second mandibular molars (m1 and m2, respectively[10]) of adult individuals derived from two mammalian communities: Balta, Peru and the island of Mindanao, Philippines. First mandibular molars were only included in a subset of the sample for the purpose of demonstrating the effectiveness of either molar in dietary reconstruction (see "Chapter 5, Comparison of First and Second Mandibular Molars"). In order to closely approximate natural guilds, and thus capture the dietary overlap among sympatric species, these samples were derived from either a small biogeographic region (Mindanao, Philippines) or a single locality (Balta, Peru). Both samples consisted of relatively small-bodied (less than 5 kg), at least partly arboreal species that have diets known to broadly overlap with the primates at these sites (i.e.,

[10] Herein, the permanent mandibular dentition will be denoted with a lower case letter (e.g., m1, m2), and the permanent maxillary dentition with an upper case letter (e.g., M1, M2).

frugivorous and insectivorous species[11]). Given the wide taxonomic range of species included in this study and the primary importance of creating a diverse sample (both taxonomically and dietarily), a minimum number of 6 individuals (3 male, 3 female) per species was deemed sufficient to accommodate intraspecies variation. This number is comparable to sample sizes used in similar studies of diet-dentition relationships across species (e.g., Strait, 1993a; Boyer, 2008; Bunn et al., 2011). However, the importance of comparing all possible species from these sites necessarily limited the number of specimens and resulted in the inclusion of fewer measured specimens for some species (see Appendix 1 and 2).

The Balta sample is composed of 67 species representing 12 families (*N*=263) (Table 4.1; see Appendix 1), and all specimens were housed at the Louisiana State University Museum of Natural Science (Baton Rouge, LA). The Mindanao sample comprised 46 species representing 12 families (*N*=202) (Table 4.2; see Appendix 2), and specimens were housed at the Field Museum of Natural History (Chicago, IL) and the National Museum of Natural History (Washington, DC). Alpha taxonomy of all specimens follows Wilson and Reeder (2005). Only wild-captured specimens with fully erupted, relatively unworn permanent dentitions were included.

[11] A single folivorous species, *Cynocephalus volans*, was included in the Mindanao sample. Dermopterans were not excluded from the study sample, as they constitute one of two mammalian orders that share a close phylogenetic relationship with primates (Euprimates, Scandentia, and Dermoptera compose the grandorder Euarchonta). In addition, their inclusion facilitates comparisons of the results presented here with those of previous studies of primate diet-dentition relationships, which also incorporated scandentians and dermopterans (e.g., Boyer, 2008; Bunn et al., 2011).

Fossil Sample

To best reconstruct true competitive guilds, the fossil sample comprised specimens collected from a common geological formation (Willwood Formation) at a single site, the Bighorn Basin, Wyoming. This sample was divided into six time intervals (see Fig. 1.1; Chapter 6), defined by sub-NALMAs, spanning the time period from Clarkforkian (Cf) 2 to Wastachian (Wa) 5 (56.10-53.91 Ma; Lofgren et al., 2004; Chew and Oheim, 2013). Communities and guilds cannot be known with absolute certainty in the fossil record, but the restriction of the units of analysis in this study to a single geological formation at a single site (a proxy for sympatry) and to narrow time intervals (a proxy for synchronism) minimizes the effects of time- and geographic-averaging, while maintaining adequate sample sizes necessary to test the hypotheses herein.

Only those taxa with habitat or substrate use similar to euprimates, as reconstructed in previous work, were included, as this factor affects the identification of direct dietary competition (Krause, 1986; Maas et al., 1988). For those taxa in which postcranial, incisor, canine, or premolar morphologies were known, highly derived structures previously shown to be indicative of specific dietary adaptations were considered. For example, if a taxon's incisor or postcranial morphology suggested a highly specialized diet or method of food procurement such that competition with euprimates for dietary resources was likely not substantial, this taxon was excluded as a potential significant euprimate competitor and its role in the euprimate dietary competitive environment was considered minimal (e.g., apatemyids; see Chapter 6). However, due to the fact that behavioral reconstructions of fossil species may be incomplete, this criterion was applied conservatively and evaluated post hoc.

Specimens were derived from the northern (specifically, the Polecat-Bench-Sand Coulee area) and central Bighorn Basin. Due to the geographic-geologic patterning of this area, the majority of specimens from Cf2 to Wa0 were derived from localities in the northern Bighorn Basin. Unfortunately, the point from which the stratigraphic sections of the northern and central Bighorn Basin have been measured (the K-T boundary and base of the Willwood Formation, respectively) differs, and as a result, specimens from different areas could not be assigned directly to common meter levels. Instead, specimens were each designated to a sub-NALMA based on the stratigraphy defined in Gingerich and Clyde (2001). For this reason, Wa1 and Wa2 faunas were combined into a single group (Wa1-2) to coincide with the stratigraphic correlations outlined in this source. It is noted that the biostratigraphy of the central Bighorn Basin has recently been reassessed, resulting in a reassignment of stratigraphic levels to sub-NALMAs and Biohorizons (Chew, 2005, 2009a). Ideally, analyses of the fossil sample would consider both the original and updated stratigraphy of the central Bighorn Basin, and this is a venue for future work. As a conservative measure, stratigraphic correlations to sub-NALMAs were derived from a single source, Gingerich and Clyde (2001), in an effort to minimize variation in stratigraphic comparisons between the northern and central Bighorn Basin (and thus between the Cf2-Wa0 and Wa1-Wa5 samples). Due to the scarcity of Cf3 specimens in the sample collections, Cf2 and Cf3 taxa were consolidated into a single Clarkforkian (Cf2-3) temporal group. Finally, although the fossil sample includes specimens from Wa5, the highest meter level represented is 490M, 35M below the Wa5-Wa6 boundary, and almost all Wa5 specimens originated from below 420M. Thus, fossil

patterns of niche overlap in Wa5 were interpreted as characteristic of only the first part of this sub-NALMA.

As sub-NALMAs represent varying amounts of time (see Fig. 1.1), one may question their use as the temporal unit of analysis (e.g., Alroy, 1996). The objective of this study was to understand changes in dietary competition in response to community dynamics (including faunal turnover), which are intrinsic to biochronologically defined time intervals, such as land mammal ages (Woodburne, 2004). Thus, this temporal framework is not inconsistent with the questions asked in this study, but it also does not dictate that patterns of niche overlap be associated with sub-NALMA transitions in a predictable way; i.e., defining time intervals in this manner is not inevitably circular in evaluating changes in competition. This is because sub-NALMAs in the Bighorn Basin have not been defined by taxa included in this study nor do they correlate with clear peaks in first or last appearance dates (FADs or LADs, respectively) of taxa within the euprimate competitive guild (Gingerich and Clyde, 2001; Woodburne, 2004). Furthemore, there is no clear association between climatic shifts (as measured by mean annual temperature and precipitation) and sub-NALMA transitions with the exception of the PETM (Woodburne et al., 2009a; Abels et al., 2012; Chew and Oheim, 2013). Finally, the analysis conducted on the fossil sample required the presence of at least three specimens per taxon per time interval (see Chapter 5), excluding the application of temporal binning at a finer scale. Therefore, the use of sub-NALMAs to differentiate mammalian communities was considered one of the broadest possible frameworks within which patterns of competition could be interpreted. The implications of the use of this temporal zonation will be discussed in Chapter 7.

The fossil sample comprised 710 mandibular molar specimens, representing 8 mammalian orders (Table 4.3; see Appendix 3). The Bighorn Basin sample was housed at Johns Hopkins University (Baltimore, MD), the National Museum of Natural History (Washington, DC), and the University of Michigan Museum of Paleontology (Ann Arbor, MI). Taxonomic assignment of individual specimens was determined from museum labels and the published literature, and the latter was preferred when the two sources conflicted (see Appendix 4 for references used in species- and genus-level assignments). Although species-level classifications were available for most specimens, the variability in species assignments across sources was considered too great to result in reliable comparisons among taxonomic groups across and within time intervals. This variability is not unexpected within fossil assemblages, as species identifications can be based only on skeletal or dental anatomy, and skeletal and dental elements are not equally represented among specimens. In addition, as extant species concepts cannot be directly applied to these fauna, criteria for the identification of fossil species differ among taxonomists (Chew, 2005; Rose and Bown, 1993). On the other hand, assignment of specimens to genera is generally more stable, and analyses were performed at this taxonomic level whenever sample size permitted. Furthermore, congeneric species are unlikely to differ in dietary regime; thus, the use of genera was deemed appropriate for this study. Familial and ordinal taxonomy follows Rose (2006).

Due to the limited representation of a selected dental (or skeletal) element in species across a fossil assemblage and the large sample necessary to conduct a community-wide study of this scale, both m1s and m2s were included in analyses of the Bighorn Basin specimens. Although m2s alone composed the extant sample, and thus

were the basis for subsequent analyses, the validity of using either molar in the discrimination of dietary groups is addressed in Chapter 5 (see "Comparison of First and Second Mandibular Molars").

MORPHOMETRIC DATA COLLECTION

Specimen Acquisition

The method of data collection using microCT scans required the initial molding and casting of all specimens. The postcanine mandibular dentition (left side preferred) of each extant specimen and either the first or second mandibular molar of each fossil specimen was molded using President Jet Affinis microsystem light-body silicone elastomer molding compound (Coltene-Whaledent). Before use of the molding applicator, this compound was first applied to the specimens using a soft-bristled, fine-point paintbrush in order to reduce air bubbles in the molds, particularly in the molar basins. The entire surface of each tooth crown was molded (i.e., molds extended onto the alveolar bone) to incorporate the cemento-enamel junction (CEJ) of each molar specimen.

The edges of each molded specimen (i.e., the most inferior aspects of the mold that were in contact with alveolar bone) were then trimmed using a scalpel and micro-dissecting scissors to eliminate excess molding material to facilitate cast-pouring. A polysiloxane molding putty support (Coltoflax, Coltene-Whaledent) was then built around each mold so that the base of each specimen was both flat and weighted. Before casting, canned air was sprayed into each mold to remove excess debris. Epoxy resin casts of each specimen were produced using Epo-Tek 301-1 and were stained gray to facilitate the assessment of specimen quality with a stereomicroscope before scanning. To

eliminate bubbles during the casting process, the smallest specimens (possessing molars that were less than approximately 1 mm^2) were first injected with epoxy using a 27-gauge needle. In addition, after the epoxy resin was added to the molds, all molds were spun at 3000 rpm for 2 minutes in an Allegra 21R, Beckman basket centrifuge.

Image Acquisition

To maximize the number of specimens scanned per session, most of the cast surrounding the tooth of interest (i.e., the mandible and the teeth positioned mesially and distally) was removed using a handheld rotary saw and burr. Individual molars were then glued to 18mm-diameter circular plastic discs, each including two diametrically opposed, vertically oriented struts. These discs were stacked 4-6 discs high, resulting in a maximum height of either 28mm (for the GE Locus scanner) or 40mm (for the Inveon scanner). Disc stacks were scanned using two microCT scanners housed at the University of Arizona Cancer Center (Tucson, AZ). Due to equipment availability, all extant specimens and Bighorn Basin specimens from sub-NALMAs Wa3-5 were scanned at a 27.35µm resolution using a Siemens Inveon microCT scanner (5000ms exposure time, 60kV, 300µA), whereas all Cf2-Wa2 Bighorn Basin specimens were scanned at a 10.4µm and reconstructed at a 20.8µm resolution using a GE Healthcare eXplore Locus SP microCT scanner (9000ms exposure time, 60kV, 90µA) (Fig. 4.1). The inclusion of images of different resolutions is addressed in "Measurement Error." Scan images were converted to sequences of 200-400 DICOM files (depending on the size and orientation of each disc stack) using Microview 2.1 (for the GE Locus scanner) and Inveon Research Workplace (for the Inveon scanner) software.

To reconstruct three-dimensional surfaces from the sequences of DICOM files for each scan, individual molars were first cropped from the image stack using ImageJ (Schneider et al., 2012). The resulting TIF image stack for each specimen was entered into Amira 5.2.0 for image segmentation and surface generation. The "LabelVoxel" function and "Image Segmentation Editor" were used to segment each tooth from the surrounding negative, or background, space. Optimal threshold values used for segmentation were defined as the minimum value of the distribution of voxel values for each scan, and these values consistently distinguished voxels of the dental cast from those of the surrounding air. Segmented scans were refined using the default values of the "Remove Islands" and "Smooth Labels" options. These latter functions do not significantly alter the resulting generated surface but remove small artifacts in order to recreate a "natural-looking" tooth surface. Three-dimensional volume renderings of each tooth were produced using the "SurfaceGen" function (see Fig. 4.2), to which landmarks were directly applied. Repeatability of this process is addressed in the section "Measurement Error." Overall, this process of image acquisition is similar to that used in previous work (e.g., Boyer, 2008; Bunn et al., 2011).

Data Acquisition

Three-dimensional coordinate landmarks were collected digitally on reconstructed molar surfaces in Amira using the "Landmarks" function. The number of landmarks differed among species due to variation in the presence or absence of molar cusps and crests. In other words, all resulting measurements were calculated for each tooth, but as molar structure differs somewhat among clades, the number of points digitized on each specimen corresponded to its specific morphology. The full complement of landmarks

and semilandmarks collected and the subsets of these landmarks that comprised each morphometric measure are outlined in Table 4.4 and illustrated in Fig. 4.3. Homologies of molar cusps and crests among species were assessed using published references prior to data collection. As the surfaces of all molars were not oriented in the same plane upon scanning, the resulting coordinate axes in Amira were independent of tooth orientation. That is, measurements that relied on the orientation of a molar in the occlusal plane could not be calculated directly. Thus, to create a plane of reference and facilitate consistency of landmark placement, a reconstructed occlusal plane was added to the surface image using the "ObliqueSlice" function of Amira.

Landmarks and semilandmarks corresponding to cusp tips and crest lengths, respectively, were generally collected in occlusal view, although specimens were rotated to ensure correct landmark placement. Landmarks corresponding to cusp height and angle measurements were collected in buccal and lingual views, defined by horizontal orientation of the occlusal plane. Eight linear, four angular, and two area measurements were obtained from the full landmark set (Table 4.5) although the absence of cusps resulted in fewer measurements for a subset of species (see Appendices 1 and 2). As discussed previously, these measurements are those for which correlations with diet have significant empirical support in previous studies (e.g., Kay, 1975b; Kay and Hylander, 1978; Rensberger, 1986; Janis and Fortelius, 1988; Strait 1993a,b, 2001; Maas and Krause, 1994; Gunnell et al., 1995; Hooker, 1998; Hunter, 1997; Seligsohn, 1997; Jernvall et al., 2000; Dewar, 2003; White, 2006). Linear and angular measurements[12]

[12] Angular measurements were converted to radians to minimize magnitude differences among variable values.

were calculated using three-dimensional Euclidean distances and vectors, respectively, whereas all area measurements were obtained by projecting the corresponding points onto either the occlusal or talonid plane (Table 4.5). However, as the occlusal and talonid planes were not aligned with the xyz coordinate system and thus were not parallel to the xy plane, it was not possible to directly calculate two-dimensional areas from these projected points. Thus, once projected onto the occlusal and talonid planes, the landmarks used to calculate area measurements were additionally rotated. This rotation moved all of these landmarks together within their coordinate framework such that the relationships of the points to one another were maintained. The end result of the rotation was a set of landmarks that all possessed equal z-values, which enabled the direct calculation of two-dimensional molar and talonid basin area from the x- and y-values of each coordinate, as the z-component no longer varied among landmarks. The rotation matrix used was:

$$\begin{bmatrix} \frac{b}{\sqrt{a^2+b^2}} & \frac{-a}{\sqrt{a^2+b^2}} & 0 \\ \frac{ac}{\sqrt{a^2+b^2}\sqrt{a^2+b^2+c^2}} & \frac{bc}{\sqrt{a^2+b^2}\sqrt{a^2+b^2+c^2}} & \frac{-a^2-b^2}{\sqrt{a^2+b^2}\sqrt{a^2+b^2+c^2}} \\ \frac{a}{\sqrt{a^2+b^2+c^2}} & \frac{b}{\sqrt{a^2+b^2+c^2}} & \frac{c}{\sqrt{a^2+b^2+c^2}} \end{bmatrix}$$

where the vector (a,b,c) was orthogonal to the occlusal plane (derived from the cross product of two vectors on the occlusal or talonid plane) (Foley et al., 1996). From these fourteen original measurements, an additional six summary measurements were derived (Table 4.6). All measurement calculations were performed in Excel.

Measurement Error

Measurement error was addressed in a sample of 10 specimens, including both fossil and extant species. Extant species included specimens from both the Mindanao and

Balta samples. Specimens ranged in two-dimensional molar area from 1.246 mm^2 (*Carollia perspicillata*) to 17.331 mm^2 (*Cebus albifrons*) and were chosen to encompass the variation in molar size represented in the full sample. In addition, the sample was selected without reference to the morphology of the specific specimen. For example, relative wear was not assessed prior to specimen selection such that the most unworn individuals were included in the measurement error analysis. A subset of measurements and their corresponding landmarks were re-digitized on each specimen 14 days after original data collection, and three-dimensional surface renderings were regenerated for each specimen prior to re-digitization. To assess the possibility that differences in image resolution and the corresponding microCT scanner affected three-dimensional molar reconstruction, original surface renderings of the fossil specimens were derived from 20.8µm scans (GE Locus scanner), and regenerated renderings were derived from 27.35µm scans (Inveon scanner). The measurements used for this analysis included examples of each type of measurement collected (linear, angular, and area): protoconid height, protoconid angle, protocristid length, and molar area.

Following White (2000), percent measurement error was calculated by first subtracting the mean difference of each trial measurement from the mean of both trials (in the case of two measurements, this is equivalent to the absolute value of the difference of either trial from the mean) and second, dividing this mean difference by the mean of both trials. Values were then converted to percentages to obtain a percent measurement error for the four variables. Percent measurement error values for each specimen are provided in Table 4.7. Mean percent measurement error for each variable and specimen were less than 3.5% and all individual percent measurement error values were less than

5%. In addition, percent measurement error does not seem related to size or image resolution. However, given that measurements were derived from up to 20 semilandmarks in the case of molar area (see Table 4.4), these levels of error should be noted.

DIETARY DATA COLLECTION

Reconstruction of dietary competition in the fossil record first requires an understanding of the extent to which competition occurs among extant species within broad dietary categories. In this study, an attempt was made to divide each of these general dietary groups (e.g., frugivory) into increasingly restricted subsets. Dietary parameters collected from the literature included the primary and secondary dietary components (i.e., fruit, insects), intake proportions of each significant food resource, considering seasonal variation, and specific dietary items (e.g., species of fruit or insect eaten). Species were classified into dietary categories based on natural groupings of dietary regimes, and quantitative studies, multiple, independent records of congruous dietary behavior, and data specific to the study sites were given greater weight in final dietary assignments.

When quantitative data were available for the proportions of dietary items consumed, dietary classification was based on primary and secondary dietary resources, or those that composed e 50% and 25-49% of the diet, respectively. For example, species classified as frugivore-insectivores eat primarily fruit (including nectar, pollen, flowers) (making up at least 50% of the diet) but also consume a considerable amount of insect material (constituting 25-49% of the diet). Similarly, the diets of insectivore-frugivores are characterized by at least 50% insect material and at least 25% (but less than 50%)

fruit products. Species lacking a dominant dietary component (i.e., no food resource contributed to greater than 50% of the diet and major resources comprised near-equal proportions of the dietary regime) were categorized as omnivores.

Although there are no published studies on direct dietary competition among all species included in this study, the dietary items consumed within a given dietary category significantly overlapped among taxa within each region. For example, ripe *Ficus* fruit is consumed by species of primates, didelphimorphian marsupials, and phyllostomid bats; *Astrocaryum* seeds are eaten by *Cebus* and *Sciurus*; and hymenopterans comprise the diets of primate, didelphimorphian, emballonurid, molossid, and phyllostomid species. Thus, the assigned dietary groups defined dietary overlap as precisely as possible and, as a result, comprised species that are most likely to directly compete for food resources.

Evaluating the precise dietary regimes of extant taxa can be problematic, as data collection methods and the variables recorded vary considerably among published studies. Furthermore, the categorical classification of diverse behaviors, such as feeding, is inherently oversimplistic. Thus, efforts were made to collate data from a multitude of sources. However, this still resulted in incongruent datasets among species, contrasting characterizations of diet for individual species among studies, and the lack of quantitative data for a portion of the dataset. As a result, categorization of diet is ultimately somewhat subjective. Furthermore, it should be noted that the amount of published behavioral research on Mindanao species is significantly less than that on species present at Balta. To alleviate the effects of these issues, at least in part, species were placed in two different dietary groupings: Dietary Group 1, which is the most specific grouping based on the data collected, and Dietary Group 2, which combined species with similar dietary

attributes into broader classes. Dietary group designations for each species are provided in Tables 4.1 and 4.2, and the references from which species data were collected are listed in Appendices 5 and 6.

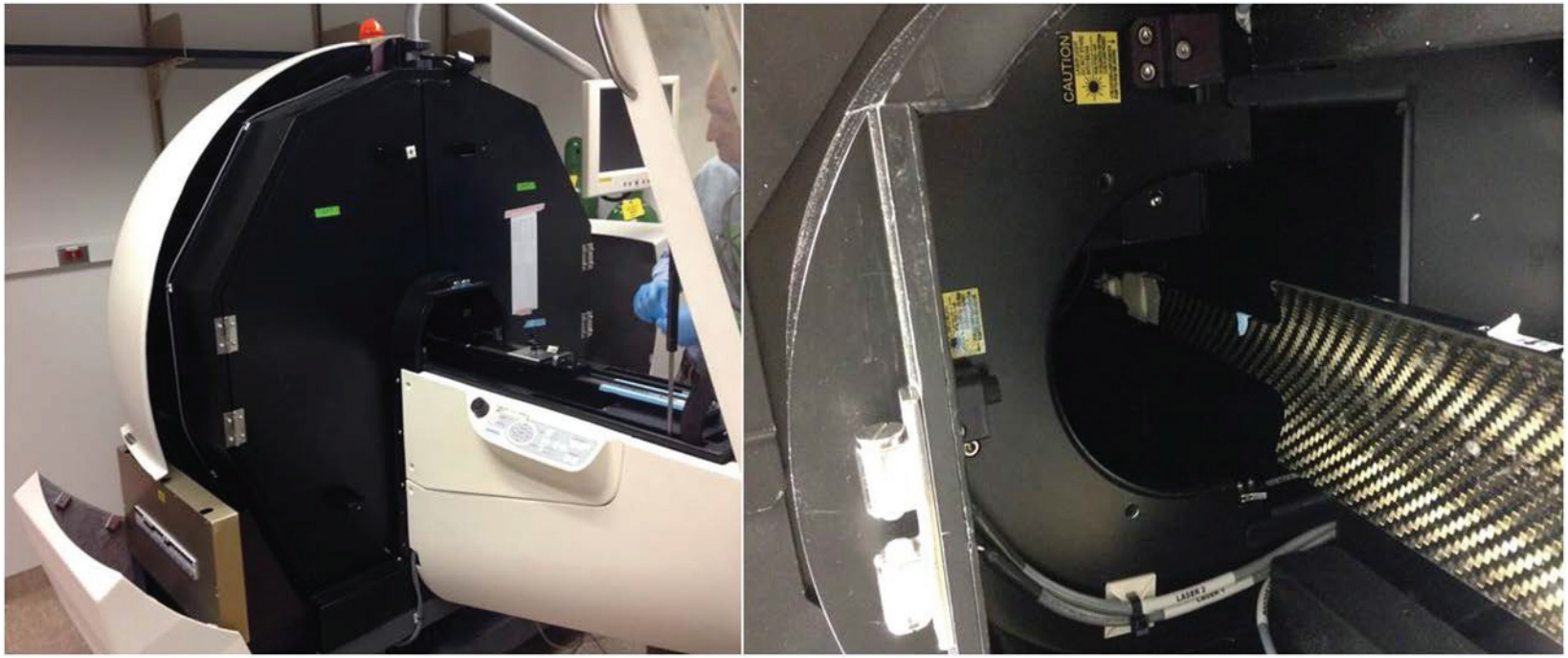


Fig. 4.1. Siemens Inveon microCT scanner housed at the University of Arizona Cancer Center (Tucson, AZ) used to acquire images on all extant and Wa3-5 Bighorn Basin specimens. Picture on the right is a closer view of the scanning chamber. Photo credited to G.T. Schwartz.

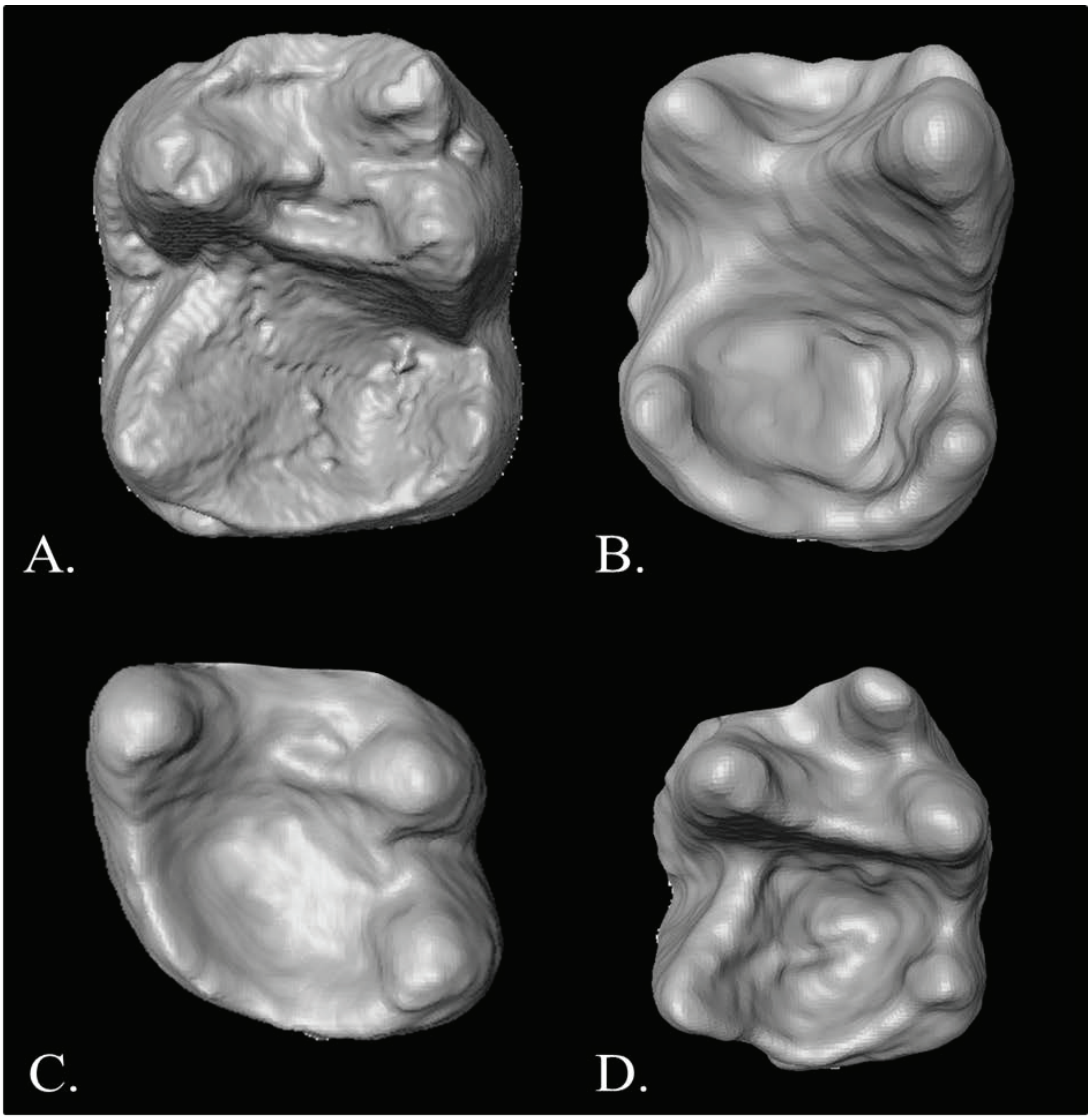


Fig. 4.2. Examples of three-dimensional surface renderings using protocol described in text. A. *Cantius ralstoni*. B. *Phenacolemur simonsi.* C. *Sundasciurus philippinensis*. D. *Tarsius syrichta*.

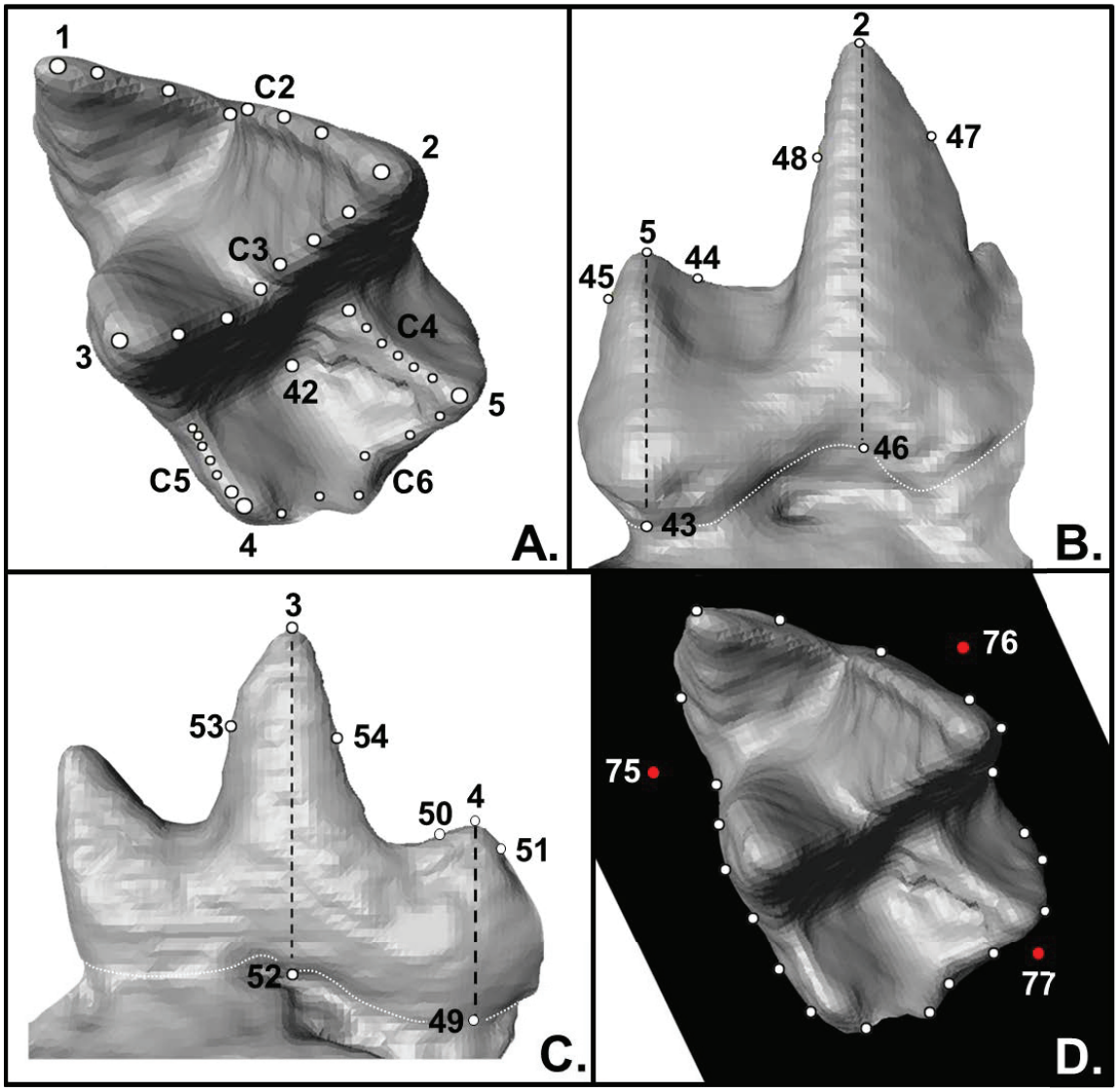


Fig. 4.3. Example of landmarks digitized in this study. Specimen illustrated is *Peradectes protinnominatus*. Landmark numbers and abbreviations correspond to those in Table 4.4 A. Cusp, crest, and talonid basin landmarks. Note that Crest 1 (C1) and the postmetacristid component of Crest 5 (C5) are not present in this specimen. B. Buccal cusp height and cusp angle landmarks. White dashed line is the estimated location of the cemento-enamel junction (CEJ). C. Lingual cusp height and cusp angle landmarks. White dashed line is the estimated location of the CEJ. D. Molar area and occlusal plane landmarks on specimen. Black plane is the reconstructed occlusal plane. Although not all molar area landmarks are on this plane upon landmark placement, allpoints are projected onto the occlusal plane prior to measurement calculation (see text).

Table 4.1. Balta, Peru specimens included in this study. Dietary group assignments are as follows: F=Frugivorous, FN=Frugivorous-nectarivorous, FI=Frugivorous-insectivorous, IF=Insectivorous-frugivorous, N=Nectarivorous, O=Omnivorous, I=Insectivorous, FH= Frugivorous(hard object feeder), FIFH=Frugivorous(hard object feeder)-insectivorous.

Species	Family	Subfamily	Tribe	*N*	Dietary Group 1	Dietary Group 2
CHIROPTERA						
Rhynchonycteris naso	Emballonuridae	Emballonurinae		3	I	I
Saccopteryx bilineata	Emballonuridae	Emballonurinae		6	I	I
Saccopteryx leptura	Emballonuridae	Emballonurinae		2	I	I
Molossops abrasus	Molossidae	Molossinae		1	I	I
Molossops greenhalli	Molossidae	Molossinae		1	I	I
Molossus molossus	Molossidae	Molossinae		2	I	I
Noctilio albiventris	Noctilionidae	Noctilioninae		5	I	I
Carollia brevicauda	Phyllostomidae	Carolliinae		6	F	F
Carollia castanea	Phyllostomidae	Carolliinae		6	F	F
Carollia perspicillata	Phyllostomidae	Carolliinae		6	F	F
Anoura caudifer	Phyllostomidae	Glossophaginae	Glossophagini	6	FN	FN
Anoura geoffroyi	Phyllostomidae	Glossophaginae	Glossophagini	2	FN	FN
Choeroniscus minor	Phyllostomidae	Glossophaginae	Glossophagini	2	N	FN
Glossophaga soricina	Phyllostomidae	Glossophaginae	Glossophagini	6	N	FN
Lonchophylla thomasi	Phyllostomidae	Glossophaginae	Lonchophyllini	6	N	FN
Lophostoma silvicolum	Phyllostomidae	Phyllostominae		5	IF	IF
Macrophyllum macrophyllum	Phyllostomidae	Phyllostominae		6	I	I
Micronycteris megalotis	Phyllostomidae	Phyllostominae		3	IF	IF
Micronycteris nicefori	Phyllostomidae	Phyllostominae		1	IF	IF
Mimon crenulatum	Phyllostomidae	Phyllostominae		4	I	I
Phyllostomus elongatus	Phyllostomidae	Phyllostominae		6	IF	IF

Table 4.1, Cont'd.

Species	Family	Subfamily	Tribe	*N*	Dietary Group 1	Dietary Group 2
Phyllostomus hastatus	Phyllostomidae	Phyllostominae		6	O	O
Tonatia minuta	Phyllostomidae	Phyllostominae		1	IF	IF
Tonatia saurophila	Phyllostomidae	Phyllostominae		5	IF	IF
Trachops cirrhosus	Phyllostomidae	Phyllostominae		6	I	I
Artibeus cinereus	Phyllostomidae	Stenodermatinae	Stenodermatini	6	F	F
Artibeus concolor	Phyllostomidae	Stenodermatinae	Stenodermatini	1	F	F
Artibeus literatus	Phyllostomidae	Stenodermatinae	Stenodermatini	5	F	F
Artibeus obscurus	Phyllostomidae	Stenodermatinae	Stenodermatini	5	F	F
Artibeus planirostris	Phyllostomidae	Stenodermatinae	Stenodermatini	6	F	F
Chiroderma villosum	Phyllostomidae	Stenodermatinae	Stenodermatini	6	F	F
Ectophylla macconnelli	Phyllostomidae	Stenodermatinae	Stenodermatini	6	F	F
Platyrrhinus brachycephalus	Phyllostomidae	Stenodermatinae	Stenodermatini	6	F	F
Platyrrhinus helleri	Phyllostomidae	Stenodermatinae	Stenodermatini	6	F	F
Platyrrhinus infuscus	Phyllostomidae	Stenodermatinae	Stenodermatini	2	F	F
Uroderma bilobatum	Phyllostomidae	Stenodermatinae	Stenodermatini	6	F	F
Uroderma magnirostrum	Phyllostomidae	Stenodermatinae	Stenodermatini	5	F	F
Vampyressa bidens	Phyllostomidae	Stenodermatinae	Stenodermatini	3	F	F
Vampyressa pusilla	Phyllostomidae	Stenodermatinae	Stenodermatini	5	F	F
Vampyrodes caraccioli	Phyllostomidae	Stenodermatinae	Stenodermatini	1	F	F
Sturnira lilium	Phyllostomidae	Stenodermatinae	Sturnirini	8	FN	FN
Sturnira tildae	Phyllostomidae	Stenodermatinae	Sturnirini	6	FN	FN
Myotis albescens	Vespertilionidae	Myotinae		6	I	I
Myotis riparius	Vespertilionidae	Myotinae		3	I	I
Myotis simus	Vespertilionidae	Myotinae		2	I	I
Eptesicus brasiliensis	Vespertilionidae	Vespertilioninae	Eptesicini	2	I	I

Table 4.1, Cont'd.

Species	Family	Subfamily	Tribe	*N*	Dietary Group 1	Dietary Group 2
Eptesicus furinalis	Vespertilionidae	Vespertilioninae	Eptesicini	2	I	I
Lasiurus borealis	Vespertilionidae	Vespertilioninae	Lasiurini	2	I	I
Lasiurus ega	Vespertilionidae	Vespertilioninae	Lasiurini	3	I	I
DIDELPHIMORPHIA						
Caluromys lanatus	Caluromyidae	Caluromyinae		1	F	F
Didelphis marsupialis	Didelphidae	Didelphinae		1	O	O
Gracilianus agilis	Didelphidae	Didelphinae		1	FI	FI
Philander mcilhennyi	Didelphidae	Didelphinae		2	O	O
Philander opossum	Didelphidae	Didelphinae		6	O	O
Marmosa murina	Marmosidae	Didelphinae		4	IF	IF
Marmosa quichua	Marmosidae	Didelphinae		2	IF	IF
Marmosops noctivagus	Marmosidae	Didelphinae		2	IF	IF
Metachirus nudicaudatus	Marmosidae	Didelphinae		3	IF	IF
Micoureus demerarae	Marmosidae	Didelphinae		6	IF	IF
PRIMATES						
Aotus trivirgatus	Aotidae	Aotinae		3	FI	FI
Saguinus imperator	Cebidae	Callitrichinae		6	FI	FI
Cebus albifrons	Cebidae	Cebinae		2	FIFH	FH
Saimiri boliviensis	Cebidae	Saimiriniiae		2	FI	FI
Callicebus moloch	Pitheciidae	Callicebinae		3	FH	FH
Pithecia monachus	Pitheciidae	Pitheciinae		3	FH	FH
RODENTIA						
Sciurus ignitus	Sciuridae	Sciurinae	Sciurini	4	FH	FH
Sciurus spadiceus	Sciuridae	Sciurinae	Sciurini	6	FH	FH

Table 4.2. Mindanao, Philippines specimens included in this study. Dietary group assignments are as follows: F=Frugivorous, FN=Frugivorous-nectarivorous, N=Nectarivorous, O=Omnivorous, I=Insectivorous, IB=Insectivorous (beetle specialist), Fa=Faunivorous, FH= Frugivorous(hard object feeder), FHFo=Frugivorous(hard object feeder)-folivorous.

Species	Family	Subfamily	Tribe	*N*	Dietary Group 1	Dietary Group 2
CHIROPTERA						
Emballonura alecto	Emballonuridae	Emballonurinae		5	I	I
Taphozous melanopogon	Emballonuridae	Taphozoinae		5	I	I
Coelops hirsutus	Hipposideridae			1	I	I
Hipposideros ater	Hipposideridae			1	IB	I
Hipposideros cervinus	Hipposideridae			2	IB	I
Hipposideros coronatus	Hipposideridae			1	IB	I
Hipposideros diadema griseus	Hipposideridae			8	IB	I
Hipposideros obscurus	Hipposideridae			5	IB	I
Megaderma spasma	Megadermatidae			3	Fa	I
Otomops formosus	Molossidae			2	I	I
Acerodon jubatus	Pteropodidae			8	F	F
Alionycteris paucidentata	Pteropodidae			6	F	F
Cynopterus brachyotis	Pteropodidae			8	FN	FN
Dyacopterus rickarti	Pteropodidae			1	F	F
Eonycteris robusta	Pteropodidae			2	N	FN
Haplonycteris fischeri	Pteropodidae			8	F	F
Harpyionycteris whiteheadi	Pteropodidae			5	FH	FH
Macroglossus minimus	Pteropodidae			5	NF	FN
Megaerops wetmorei	Pteropodidae			4	F	F
Ptenochirus jagori	Pteropodidae			5	F	F
Ptenochirus minor	Pteropodidae			2	F	F

Table 4.2, Cont'd.

Species	Family	Subfamily	Tribe	*N*	Dietary Group 1	Dietary Group 2
Pteropus hypomelanus	Pteropodidae			2	F	F
Pteropus pumilus	Pteropodidae			1	F	F
Pteropus speciosus	Pteropodidae			6	F	F
Pteropus vampyrus	Pteropodidae			5	F	F
Rousettus amplexicaudatus	Pteropodidae			4	FN	FN
Rhinolophus arcuatus	Rhinolophidae			5	I	I
Rhinolophus inops	Rhinolophidae			2	I	I
Rhinolophus rufus	Rhinolophidae			4	I	I
Rhinolophus virgo	Rhinolophidae			5	I	I
Kerivoula pellucida	Vespertilionidae	Kerivoulinae		1	I	I
Miniopterus australis	Vespertilionidae	Miniopterinae		6	I	I
Miniopterus schreibersii	Vespertilionidae	Miniopterinae		6	I	I
Miniopterus tristis	Vespertilionidae	Miniopterinae		5	I	I
Myotis macrotarsus	Vespertilionidae	Myotinae		1	I	I
Myotis muricola	Vespertilionidae	Myotinae		2	I	I
Scotophilus kuhlii	Vespertilionidae	Vespertilioninae	Nycticeiini	6	I	I
Pipistrellus javanicus	Vespertilionidae	Vespertilioninae	Pipistrellini	4	I	I
Philetor brachypterus	Vespertilionidae	Vespertilioninae	Vespertilionini	5	I	I
DERMOPTERA						
Cynocephalus volans	Cynocephalidae			9	Fo	Fo
LIPOTYPHLA						
Crocidura beatus	Soricidae			4	I	I
PRIMATES						
Tarsius syrichta	Tarsiidae			7	Fa	I

Table 4.2, Cont'd.

Species	Family	Subfamily	Tribe	*N*	Dietary Group 1	Dietary Group 2
RODENTIA						
Exilisciurus concinnus	Sciuridae	Callosciurinae		6	FHFo	FH
Sundasciurus philippinensis	Sciuridae	Callosciurinae		6	FHFo	FH
Petinomys crinitus	Sciuridae	Sciurinae		4	FHFo	FH
SCANDENTIA						
Urogale everetti	Tupaiidae			9	O	O

Table 4.3. Bighorn Basin genera included in this study. Familial and ordinal taxonomy follows Rose (2006). Assignment of sub-NALMAs follows Gingerich and Clyde (2001).

Order	Suborder	Family	Genus	Time Interval	*N*
Apatotheria		Apatemyidae	*Labidolemur*	Cf2-3	4
Dermoptera		Plagiomenidae	*Plagiomene*	Cf2-3	1
Dermoptera		Plagiomenidae	*Worlandia*	Cf2-3	6
Didelphimorphia		Peradectidae	*Peradectes*	Cf2-3	5
Didelphodonta		Palaeoryctidae	*Paleaeoryctes*	Cf2-3	1
Lipotyphla	Erinaceomorpha		*Diacocherus*	Cf2-3	3
Lipotyphla	Erinaceomorpha		*Leipsanolestes*	Cf2-3	2
Lipotyphla	Soricomorpha		*Leptacodon*	Cf2-3	4
Lipotyphla	Soricomorpha		*Nyctitherium*	Cf2-3	1
Lipotyphla	Soricomorpha		*Plagioctenodon*	Cf2-3	2
Lipotyphla	Soricomorpha		*Wyonycteris*	Cf2-3	2
Primates	Plesiadapiformes	Carpolestidae	*Carpolestes*	Cf2-3	9
Primates	Plesiadapiformes	Microsyopidae	*Arctodontomys*	Cf2-3	2
Primates	Plesiadapiformes	Paromomyidae	*Ignacius*	Cf2-3	3
Primates	Plesiadapiformes	Paromomyidae	*Phenacolemur*	Cf2-3	8
Primates	Plesiadapiformes	Plesiadapidae	*Plesiadapis*	Cf2-3	14
Rodentia		Paramyidae	*Acritoparamys*	Cf2-3	10
Rodentia		Paramyidae	*Microparamys*	Cf2-3	1
Rodentia		Paramyidae	*Paramys*	Cf2-3	5
Rodentia		Paramyidae	*Reithroparamys*	Cf2-3	1
Apatotheria		Apatemyidae	*Apatemys*	Wa0	4
Didelphimorphia		Peradectidae	*Mimoperadectes*	Wa0	5
Didelphimorphia		Peradectidae	*Peradectes*	Wa0	6
Didelphimorphia		Peradectidae	*Peratherium*	Wa0	5
Didelphodonta		Palaeoryctidae	*Didelphodus*	Wa0	3

Table 4.3, Cont'd.

Order	Suborder	Family	Genus	Time Interval	*N*
Leptictida		Leptictidae	*Prodiacodon*	Wa0	1
Lipotyphla	Erinaceomorpha		*Macrocranion*	Wa0	1
Lipotyphla	Erinaceomorpha		*Talpavoides*	Wa0	4
Lipotyphla	Soricomorpha		*Plagioctenoides*	Wa0	2
Lipotyphla	Soricomorpha		*Incertae sedis*	Wa0	3
Primates	Plesiadapiformes	Micromomyidae	*Chalicomomys*	Wa0	1
Primates	Plesiadapiformes	Microsyopidae	*Microsyops*	Wa0	1
Primates	Plesiadapiformes	Microsyopidae	*Niptomomys*	Wa0	7
Primates	Plesiadapiformes	Paromomyidae	*Ignacius*	Wa0	2
Primates	Plesiadapiformes	Paromomyidae	*Phenacolemur*	Wa0	4
Primates	Euprimates	Adapidae	*Cantius*	Wa0	20
Primates	Euprimates	Omomyidae	*Teilhardina*	Wa0	19
Primates	Euprimates	Cylindrodontidae	*Tuscahomys*	Wa0	4
Rodentia		Paramyidae	*Acritoparamys*	Wa0	3
Rodentia		Paramyidae	*Microparamys*	Wa0	1
Rodentia		Paramyidae	*Paramys*	Wa0	2
Rodentia		Paramyidae	*Reithroparamys*	Wa0	2
Rodentia		Paramyidae	*Incertae sedis*	Wa0	1
Apatotheria		Apatemyidae	*Apatemys*	Wa1-2	4
Apatotheria		Apatemyidae	*Labidolemur*	Wa1-2	6
Didelphimorphia		Peradectidae	*Peradectes*	Wa1-2	9
Didelphodonta		Palaeoryctidae	*Didelphodus*	Wa1-2	5
Didelphodonta		Palaeoryctidae	*Eoryctes*	Wa1-2	2
Didelphodonta		Palaeoryctidae	*Palaeoryctes*	Wa1-2	1
Leptictida		Leptictidae	*Palaeictops*	Wa1-2	2
Leptictida		Leptictidae	*Prodiacodon*	Wa1-2	3

Table 4.3, Cont'd.

Order	Suborder	Family	Genus	Time Interval	*N*
Leptictida		Leptictidae	*Prodiacodon*	Wa0	1
Lipotyphla	Erinaceomorpha		*Macrocranion*	Wa0	1
Lipotyphla	Erinaceomorpha		*Talpavoides*	Wa0	4
Lipotyphla	Soricomorpha		*Plagioctenoides*	Wa0	2
Lipotyphla	Soricomorpha		*Incertae sedis*	Wa0	3
Primates	Plesiadapiformes	Micromomyidae	*Chalicomomys*	Wa0	1
Primates	Plesiadapiformes	Microsyopidae	*Microsyops*	Wa0	1
Primates	Plesiadapiformes	Microsyopidae	*Niptomomys*	Wa0	7
Primates	Plesiadapiformes	Paromomyidae	*Ignacius*	Wa0	2
Primates	Plesiadapiformes	Paromomyidae	*Phenacolemur*	Wa0	4
Primates	Euprimates	Adapidae	*Cantius*	Wa0	20
Primates	Euprimates	Omomyidae	*Teilhardina*	Wa0	19
Rodentia		Cylindrodontidae	*Tuscahomys*	Wa0	4
Rodentia		Paramyidae	*Acritoparamys*	Wa0	3
Rodentia		Paramyidae	*Microparamys*	Wa0	1
Rodentia		Paramyidae	*Paramys*	Wa0	2
Rodentia		Paramyidae	*Reithroparamys*	Wa0	2
Rodentia		Paramyidae	*Incertae sedis*	Wa0	1
Apatotheria		Apatemyidae	*Apatemys*	Wa1-2	4
Apatotheria		Apatemyidae	*Labidolemur*	Wa1-2	6
Didelphimorphia		Peradectidae	*Peradectes*	Wa1-2	9
Didelphodonta		Palaeoryctidae	*Didelphodus*	Wa1-2	5
Didelphodonta		Palaeoryctidae	*Eoryctes*	Wa1-2	2
Didelphodonta		Palaeoryctidae	*Palaeoryctes*	Wa1-2	1
Leptictida		Leptictidae	*Palaeictops*	Wa1-2	2
Leptictida		Leptictidae	*Prodiacodon*	Wa1-2	3

Table 4.3, Cont'd.

Order	Suborder	Family	Genus	Time Interval	*N*
Lipotyphla	Erinaceomorpha		*Leipsanolestes*	Wa1-2	4
Lipotyphla	Erinaceomorpha		*Macrocranion*	Wa1-2	1
Lipotyphla	Erinaceomorpha		*Scenopagus*	Wa1-2	1
Lipotyphla	Erinaceomorpha		*Talpavus*	Wa1-2	1
Lipotyphla	Soricomorpha		*Leptacodon*	Wa1-2	1
Lipotyphla	Soricomorpha		*Plagioctenodon*	Wa1-2	6
Lipotyphla	Soricomorpha		*Wyonycteris*	Wa1-2	2
Lipotyphla	Soricomorpha		*Incertae sedis*	Wa1-2	2
Primates	Plesiadapiformes	Micromomyidae	*Tinimomys*	Wa1-2	1
Primates	Plesiadapiformes	Microsyopidae	*Arctodontomys*	Wa1-2	6
Primates	Plesiadapiformes	Microsyopidae	*Niptomomys*	Wa1-2	6
Primates	Plesiadapiformes	Paromomyidae	*Ignacius*	Wa1-2	6
Primates	Plesiadapiformes	Paromomyidae	*Phenacolemur*	Wa1-2	12
Primates	Euprimates	Adapidae	*Cantius*	Wa1-2	37
Primates	Euprimates	Omomyidae	*Anemorhysis*	Wa1-2	6
Primates	Euprimates	Omomyidae	*Teilhardina*	Wa1-2	8
Primates	Euprimates	Omomyidae	*Tetonius*	Wa1-2	5
Primates	Euprimates	Omomyidae	*Tetonoides*	Wa1-2	1
Rodentia		Paramyidae	*Acritoparamys*	Wa1-2	16
Rodentia		Paramyidae	*Microparamys*	Wa1-2	4
Rodentia		Paramyidae	*Paramys*	Wa1-2	14
Rodentia		Paramyidae	*Incertae sedis*	Wa1-2	2
Rodentia		Sciuravidae	*Knightomys*	Wa1-2	1
Apatotheria		Apatemyidae	*Apatemys*	Wa3	2
Apatotheria		Apatemyidae	*Labidolemur*	Wa3	4
Dermoptera		Plagiomenidae	*Plagiomene*	Wa3	8

Table 4.3, Cont'd.

Order	Suborder	Family	Genus	Time Interval	*N*
Didelphimorphia		Peradectidae	*Mimoperadectes*	Wa3	3
Didelphimorphia		Peradectidae	*Peradectes*	Wa3	2
Didelphimorphia		Peradectidae	*Peratherium*	Wa3	1
Didelphimorphia		Peradectidae	*Incertae sedis*	Wa3	1
Didelphodonta		Palaeoryctidae	*Didelphodus*	Wa3	1
Leptictida		Leptictidae	*Prodiacodon*	Wa3	1
Lipotyphla	Erinaceomorpha		*Auroralestes*	Wa3	1
Lipotyphla	Erinaceomorpha		*Macrocranion*	Wa3	1
Lipotyphla	Soricomorpha		*Centetodon*	Wa3	1
Lipotyphla	Soricomorpha		*Plagioctenodon*	Wa3	1
Lipotyphla	Soricomorpha		*Wyonycteris*	Wa3	1
Lipotyphla	Soricomorpha		*Incertae sedis*	Wa3	5
Primates	Plesiadapiformes	Microsyopidae	*Arctodontomys*	Wa3	2
Primates	Plesiadapiformes	Microsyopidae	*Microsyops*	Wa3	4
Primates	Plesiadapiformes	Microsyopidae	*Niptomomys*	Wa3	6
Primates	Plesiadapiformes	Paromomyidae	*Ignacius*	Wa3	3
Primates	Plesiadapiformes	Paromomyidae	*Phenacolemur*	Wa3	16
Primates	Euprimates	Adapidae	*Cantius*	Wa3	19
Primates	Euprimates	Omomyidae	*Anemorhysis*	Wa3	4
Primates	Euprimates	Omomyidae	*Teilhardina*	Wa3	16
Primates	Euprimates	Omomyidae	*Tetonius*	Wa3	19
Primates	Euprimates	Omomyidae	*Tetonius-Pseudotetonius*	Wa3	8
Primates	Euprimates	Omomyidae	*Tetonoides*	Wa3	2
Rodentia		Paramyidae	*Acritoparamys*	Wa3	3
Rodentia		Paramyidae	*Microparamys*	Wa3	1
Rodentia		Paramyidae	*Paramys*	Wa3	9

Table 4.3, Cont'd.

Order	Suborder	Family	Genus	Time Interval	*N*
Rodentia		Paramyidae	*Incertae sedis*	Wa3	1
Rodentia		Sciuravidae	*Knightomys*	Wa3	1
Apatotheria		Apatemyidae	*Apatemys*	Wa4	2
Dermoptera		Plagiomenidae	*Plagiomene*	Wa4	7
Didelphimorphia		Peradectidae	*Peradectes*	Wa4	2
Leptictida		Leptictidae	*Palaeictops*	Wa4	1
Leptictida		Leptictidae	*Incertae sedis*	Wa4	1
Lipotyphla	Erinaceomorpha		*Macrocranion*	Wa4	2
Primates	Plesiadapiformes	Microsyopidae	*Arctodontomys*	Wa4	3
Primates	Plesiadapiformes	Microsyopidae	*Microsyops*	Wa4	7
Primates	Plesiadapiformes	Microsyopidae	*Niptomomys*	Wa4	2
Primates	Plesiadapiformes	Paromomyidae	*Phenacolemur*	Wa4	10
Primates	Euprimates	Adapidae	*Cantius*	Wa4	14
Primates	Euprimates	Omomyidae	*Anemorhysis*	Wa4	2
Primates	Euprimates	Omomyidae	*Pseudotetonius*	Wa4	9
Primates	Euprimates	Omomyidae	*Tetonius*	Wa4	13
Primates	Euprimates	Omomyidae	*Tetonius-Pseudotetonius*	Wa4	10
Rodentia		Paramyidae	*Acritoparamys*	Wa4	3
Rodentia		Paramyidae	*Leptotomus*	Wa4	1
Rodentia		Paramyidae	*Microparamys*	Wa4	2
Rodentia		Paramyidae	*Paramys*	Wa4	13
Rodentia		Paramyidae	*Reithroparamys*	Wa4	1
Rodentia		Sciuravidae	*Knightomys*	Wa4	4
Apatotheria		Apatemyidae	*Apatemys*	Wa5	4
Didelphimorphia		Peradectidae	*Mimoperadectes*	Wa5	1
Didelphimorphia		Peradectidae	*Peradectes*	Wa5	1

Table 4.3, Cont'd.

Order	Suborder	Family	Genus	Time Interval	*N*
Didelphimorphia		Peradectidae	*Peratherium*	Wa5	2
Didelphodonta		Palaeoryctidae	*Didelphodus*	Wa5	2
Leptictida		Leptictidae	*Palaeictops*	Wa5	2
Lipotyphla	Erinaceomorpha		*Macrocranion*	Wa5	5
Lipotyphla	Erinaceomorpha		*Talpavoides*	Wa5	1
Primates	Plesiadapiformes	Microsyopidae	*Microsyops*	Wa5	3
Primates	Plesiadapiformes	Microsyopidae	*Niptomomys*	Wa5	3
Primates	Plesiadapiformes	Paromomyidae	*Phenacolemur*	Wa5	6
Primates	Plesiadapiformes	Picromomyidae	*Picromomys*	Wa5	1
Primates	Euprimates	Adapidae	*Cantius*	Wa5	24
Primates	Euprimates	Adapidae	*Copelemur*	Wa5	8
Primates	Euprimates	Omomyidae	*Absarokius*	Wa5	3
Primates	Euprimates	Omomyidae	*Anemorhysis*	Wa5	1
Primates	Euprimates	Omomyidae	*Arapahovius*	Wa5	2
Primates	Euprimates	Omomyidae	*Steinius*	Wa5	2
Rodentia		Paramyidae	*Acritoparamys*	Wa5	5
Rodentia		Paramyidae	*Leptotomus*	Wa5	1
Rodentia		Paramyidae	*Lophioparamys*	Wa5	1
Rodentia		Paramyidae	*Microparamys*	Wa5	1
Rodentia		Paramyidae	*Notoparamys*	Wa5	1
Rodentia		Paramyidae	*Paramys*	Wa5	12
Rodentia		Paramyidae	*Incertae sedis*	Wa5	2

Table 4.4. Three-dimensional landmarks used in this study. Note that landmarks are dependent on the presence of features; thus, not all landmarks were collected on every specimen.

Landmark No.	Landmark	Description
1	PARACONID	Apex of the paraconid
2	PROTOCONID	Apex of the protoconid
3	METACONID	Apex of the metaconid
4	ENTOCONID	Apex of the entoconid
5	HYPOCONID	Apex of the hypoconid
6-11	CREST 1 (C1)	6 semilandmarks along the premetacristid (Point 1 to Point 3)
12-17	CREST 2 (C2)	6 semilandmarks along the paracristid (Point 1 to Point 2)
18-23	CREST 3 (C3)	6 semilandmarks along the protocristid (Point 2 to Point 3)
24-29	CREST 4 (C4)	6 semilandmarks along the cristid obliqua (Point 5 to postvallid wall)
30-35	CREST 5 (C5)	6 semilandmarks along the combined postmetacristid and preentocristid length (Point 3 to Point 4, although this is variable depending on presence of either or both crests)
36-41	CREST 6 (C6)	6 semilandmarks along the combined postentocristid including the posthypocristid if present (Point 4 to Point 5)
42	TALONID BASIN	Most gingival point in the talonid basin
43	HYPOCONID BASE	Vertical projection of Point 5 onto the CEJ in buccal view
44	MESIAL HYPOCONID	Point on mesial aspect of hypoconid in buccal view
45	DISTAL HYPOCONID	Point on distal aspect of hypoconid in buccal view
46	PROTOCONID BASE	Vertical projection of Point 2 onto the CEJ in buccal view
47	MESIAL PROTOCONID	Point on mesial aspect of protoconid in buccal view
48	DISTAL PROTOCONID	Point on distal aspect of protoconid in buccal view
49	ENTOCONID BASE	Vertical projection of Point 4 onto the CEJ in lingual view
50	MESIAL ENTOCONID	Point on mesial aspect of entoconid in lingual view
51	DISTAL ENTOCONID	Point on distal aspect of entoconid in lingual view

Table 4.4., Cont'd.

Landmark No.	Landmark	Description
52	METACONID BASE	Vertical projection of Point 3 onto the CEJ in lingual view
53	MESIAL METACONID	Point on mesial aspect of metaconid in lingual view
54	DISTAL METACONID	Point on distal aspect of metaconid in lingual view
55-74	MOLAR AREA 1-20	20 semilandmarks around the perimeter of the molar in occlusal view
75-77	OCCLUSAL PLANE 1-3	3 points on the reconstructed occlusal plane

Table 4.5. Morphometric measurements used in this study. Total possible number of landmarks is 77, as some landmarks are used in more than one measurement. References indicate studies in which measurements were used to quantify diet, and from which the study measurements were derived. Asterisk (*) indicates measurement calculated for Pteropodidae, due to the non-tritubercular molar morphology of these specimens. Corresponding landmark numbers reference those in Table 4.4.

Measurement	Measurement Type	Corresponding Landmark Nos.	Definition
Protoconid height	Linear	2,46	Distance between the apex of the protoconid and the most gingival extent of the cemento-enamel junction at its base, measured perpendicular to the occlusal plane (Kay, 1975b).
Metaconid height	Linear	3,52	Distance between the apex of the metaconid and the most gingival extent of the cemento-enamel junction at its base, measured perpendicular to the occlusal plane (Kay, 1975b).
Entoconid height	Linear	4,49	Distance between the apex of the entoconid and the most gingival extent of the cemento-enamel junction at its base, measured perpendicular to the occlusal plane (Kay, 1975b).
Hypoconid height	Linear	5,43	Distance between the apex of the hypoconid and the most gingival extent of the cemento-enamel junction at its base, measured perpendicular to the occlusal plane (Kay, 1975b).
Crest length	Linear	6-41	Sum of the three-dimensional lengths of all crests, including associated cusp or cuspule apices. Each crest was represented by 6-8 semilandmarks, depending on the number of cusp apices included in the crest structure (Strait, 2001).
Protoconid angle	Angular	2,47,48	Angle at which the sides of each crest join at the protoconid apex in buccal view (Rensberger, 1986).
Metaconid angle	Angular	3,53,54	Angle at which the sides of each crest join at the metaconid apex in lingual view (Rensberger, 1986).
Entoconid angle	Angular	4,50,51	Angle at which the sides of each crest join at the entoconid apex in lingual view (Rensberger, 1986).

Table 4.5, Cont'd.

Measurement	Measurement Type	Corresponding Landmark Nos.	Definition
Hypoconid angle	Angular	5,44,45	Angle at which the sides of each crest join at the hypoconid apex in buccal view (Rensberger, 1986).
Talonid basin area	Area	4,5,24-29,30-35,36-41	Two-dimensional area of the talonid basin, defined by the borders of the postvallid wall, cristid obliqua, postentocristid, preentocristid, and postmetacristid (when present), projected onto the occlusal plane (Seligsohn, 1977).
Talonid basin depth	Linear	4,5,24,42	Orthogonal distance between the most gingival point in the talonid basin and a plane defined by the apex of the entoconid, apex of the hypoconid, and junction of the cristid obliqua to the postvallid wall ("talonid plane") (Seligsohn, 1977).
Talonid basin depth*	Linear	Variable	Orthogonal distance between the most gingival point in the molar basin and a plane defined by 3 points along the molar basin border; typically, the apex of the protoconid, apex of the metaconid, and most distal midline point (Seligsohn, 1977).
Trigonid-talonid relief	Linear	2,3,4,5,24	Mean of the orthogonal distances between the metaconid apex and the talonid plane and the protoconid apex and the "talonid plane" (Dewar, 2003).
Molar area	Area	55-77	Two-dimensional area calculated from semilandmarks placed along the molar occlusal outline and projected onto the occlusal plane (O'Leary, 1997).

Table 4.6. Morphometric measurements derived from mean values of measurements listed in Table 4.5.

Summary Variables	Definition
Mean cusp height	Mean of cusp height values for all cusps present
Mean cusp angle	Mean of cusp angle values for all cusps present
Mean trigonid cusp height	Mean of protoconid and metaconid cusp height
Mean trigonid cusp angle	Mean of protoconid and metaconid cusp angle
Mean talonid cusp height	Mean of hypoconid and entoconid cusp height
Mean talonid cusp angle	Mean of hypoconid and entoconid angle height

Table 4.7. Results of measurement error study.

Specimen	Species	Percent Measurement Error			
		Molar Area	Protocristid Length	Protoconid Height	Protoconid Angle
FMNH 56376	*Scotophilus kuhlii*	3.17%	3.47%	<1.00%	<1.00%
FMNH 56441	*Cynocephalus volans*	3.27%	1.24%	<1.00%	4.93%
FMNH 56740	*Tarsius syrichta*	<1.00%	1.23%	2.19%	1.68%
LSU 12028	*Noctilio albiventris*	4.20%	<1.00%	<1.00%	<1.00%
LSU 14340	*Cebus albifrons*	1.61%	<1.00%	<1.00%	4.8%
LSU 12501	*Carollia perspicillata*	2.72%	3.67%	2.82%	2.9%
UM 69979	*Labidolemur serus*	2.09%	<1.00%	<1.00%	3.36%
UM 82680	*Peradectes protinnominatus*	3.76%	2.82%	<1.00%	4.12%
UM 83021	*Carpolestes nigridens*	3.39%	<1.00%	3.33%	4.75%
USGS 27977	*Cantius ralstoni*	2.17%	1.04%	3.12%	2.77%
Mean		**2.67%**	**1.47%**	**1.47%**	**3.05%**

CHAPTER 5: RELATIONSHIP BETWEEN DIET AND MOLAR MORPHOLOGY IN EXTANT GUILDS

To reconstruct dietary niches in fossil taxa, the relationship between dietary regime and dental morphology in related extant species must be known. As previously discussed in Chapters 1 and 2, the associations between diet and specific aspects of molar morphology have been demonstrated for broad taxonomic groups of most mammals (e.g., Primates, Chiroptera) (e.g., Strait, 2001; Evans, 2005), but each group has been predominantly characterized independently (e.g., Kay, 1975b; Fortelius and Solounias, 2000; Jernvall et al., 2000; Lazzari et al., 2008; Teaford et al., 2008; White, 2009). Consequently, there is no common frame of reference with which to compare diet-dentition relationships of taxa across the extant euprimate competitive guild, a requisite for reconstructing dietary niches of species within the Eocene euprimate competitive guild. Thus, the objective of the extant component of this study was to identify phylogenetically independent, universal relationships between diet and molar morphology within extant euprimate competitive guilds. Specifically, the following questions were asked: (1) Do molar morphometrics significantly correlate with diet across extant euprimate competitive guilds? (2) If so, which molar measurements (or combinations thereof) best reconstruct dietary overlap among species composing extant euprimate competitive guilds?

Because two distinct extant samples were evaluated (see Chapter 4; Tables 4.1, 4.2), all analyses were performed on each sample separately as well as on the combined extant mammalian sample. As the analysis of all morphometric variables was not

possible for the Mindanao sample (see below), separate community analyses allowed for an examination of the full variable set in at least one sample.

For all multivariate analyses, measurement variables were analyzed in three sets (Table 5.1), and these sets will be referenced throughout this chapter. Differences among the variable sets were based predominantly on the inclusion of individual molar cusps, which by extension, influenced the inclusion of corresponding cusp height and angle measurements. Variable Set 1 comprised all individual molar measurements, including individual cusp heights and angles, from which it was possible to discern whether certain variations in cusp morphology within a given dentition corresponded with diet across taxa (e.g., whether metaconid height, specifically, was more highly correlated with diet than hypoconid height). However, due to the variable molar morphologies that characterized the extant sample, particularly the derived morphology of pteropodid bats, not all cusps were present in all specimens. Therefore, Variable Set 2, comprising only mean measurements, was constructed. In addition, because pteropodid bats do not have a clear trigonid-talonid distinction, inclusion of measures of talonid area and trigonid-talonid relief was not possible for any samples in which these species were incorporated (i.e., the Mindanao and combined Balta-Mindanao samples). Consequently, pteropodid talonid basin depth was calculated as the depth of the single molar basin. Although they possess a highly derived molar morphology, exclusion of the Pteropodidae was not possible, as species in this group were the only "frugivores" and "frugivore-nectarivores" in the Mindanao sample. Variable Set 3 was created to consider differences between trigonid and talonid morphology in those taxa for which a single cusp was absent (e.g., sturnirin chiropterans). This third variable set thus allowed the inclusion of taxa with

missing data in Variable Set 1 but encompassed morphological features that Variable Set 2 did not.

Unless otherwise stated, the ±-level for null hypothesis rejection for all analyses was 0.05 and analyses were performed in SAS 9.2.

ALLOMETRIC EFFECTS AND SIZE ADJUSTMENT

Differences in absolute values of molar measurements that are correlated with differences in absolute size of the dentition (and thus, the individual) must be considered in order to compare species of variable size within and across dietary regimes (Corrucini, 1987; Jungers et al., 1995). Previous studies of dental morphology have often used ratios of dental measures and dimensions of molar size (e.g., molar length and width, postcanine length and width, two-dimensional molar area) to scale individual measurements (e.g., Kay and Covert, 1984; Jernvall, 1995; Strait, 2001; Evans and Sanson, 2005; Boyer, 2008; Boyer et al., 2010, 2011, 2012; Bunn et al., 2011; Godfrey et al., 2012; Guy et al., 2013; Jones et al., 2014). However, this approach is only valid if proportionality is preserved across molar sizes; i.e., the dental measures (i.e., the ratio numerator) scale isometrically with the measure of molar size (i.e., the ratio denominator) (Smith, 2005).

To assess the isometric relationships among variables, logged values of each morphometric variable (see Table 4.5) were regressed against logged values of two-dimensional molar area for all species. There has been some debate as to whether ordinary least squares (OLS) or reduced major axis (RMA) regression is more (or equally) appropriate for analyses of allometry (e.g., Smith, 1999, 2009; Al-Wathiqui and Rodriguez, 2011), so to enable comparisons, both types of regression were performed. In

those cases in which isometry characterized the relationship between a variable and molar area, these morphometric measures could be confidently scaled using ratio calculations. As the goal was to analyze each of the three samples separately (Balta, Mindanao, and combined Balta-Mindanao), and considering that variable sets differed among samples, the relationship between each variable and molar area was assessed independently for the three sample groups. The software RMA 1.17 (Bohonak and van der Linde, 2004) was used to conduct reduced major axis regressions, and confidence intervals for the reduced major axis slope were derived from a bootstrapped distribution of 10,000 iterations. OLS regressions were performed in SAS 9.2.

The results of both OLS and RMA regressions for the Balta, Mindanao, and combined Balta-Mindanao samples are provided in Tables 5.2-5.4. All angular variables were uncorrelated with molar area (95% confidence intervals of slope include 0) and thus were not scaled for subsequent analyses. Almost all non-angular variables in all three samples scaled with isometry. The exceptions are total crest length (Balta and combined Balta-Mindanao samples), metaconid height (Balta sample), and talonid basin depth (all samples). The 95% confidence intervals of both total crest length and metaconid height were slightly positively allometric but approached isometry in at least one of the regression models. On the other hand, talonid basin depth was clearly positively allometric in all samples.

Because total crest length, metaconid height, and talonid basin depth scaled with positive allometry in at least one sample, a simple ratio of these variables to molar area will not yield equivalent size-corrected values. However, as the goal of the extant analyses is to identify molar variables that differentiate dietary groups, allometry is

problematic only if it exaggerates differences among groups, creating inflated discrimination (and thus, lower classification error rates). Thus, it may be more appropriate to examine whether allometric relationships differ among dietary groups (Kay, 1975a; Gingerich et al., 1982; Jernvall, 1995). For example, if talonid basin depth is negatively allometric only in frugivorous species, then for a given size, frugivores will have relatively shallower talonid basins than insectivores simply due to this allometric relationship. As talonid basin depth is greater in insectivores than frugivores (Butler, 1972; Kay and Hiiemae, 1974; Seligsohn, 1977; Yamashita, 1996; Evans, 2006; White, 2009; see Chapter 2), differentiation of these two groups based on a ratio of this trait to molar area would be more pronounced than if talonid basin depth was isometric. As a result, specimens were classified as "frugivores" and "insectivores" based on their primary dietary component (see Chapter 4), and regression analyses were performed on each of these two groups separately. True omnivores, for which no primary dietary component exists, were (1) classified as insectivores, (2) classified as frugivores, and (3) excluded from the analysis, and all three of these analyses produced the same pattern of allometric relationships among variables.

First, the outcomes of separate regression analyses of these two major dietary groups, insectivores and frugivores, indicated that the positive allometric signal for total crest length in all samples is driven solely by the frugivorous species (Tables 5.5-5.7; Figs. 5.1A, 5.2A, 5.3A)[13]. Based on known differences between insectivore and frugivore molar morphology (Butler, 1972; Kay and Hiiemae, 1974; Kay, 1975b; Seligsohn, 1977;

[13] This may be the result of the relatively smaller molars of frugivores at a given body size (Lucas, 2006).

Lucas and Luke, 1984; Strait, 1991, 1993a, 1997; Yamashita, 1996; Evans and Sanson, 2003, 2005; Evans, 2006; White, 2009; see Chapter 2), positive allometry in this trait is expected to produce greater similarity between insectivorous and frugivorous species, counter to the example of talonid basin depth described above. Thus, the use of ratios to scale this variable would likely not amplify, but instead diminish, the differences among dietary groups. This is also the case for the positive allometry characterizing mean cusp height in Mindanao frugivores (see Table 6; Fig. 5.2B). On the other hand, talonid basin depth is positively allometric in both insectivores and frugivores in the Balta and combined Balta-Mindanao samples and in frugivores in the Mindanao sample (Tables 5.5-5.7; Figs. 5.1C, 5.2C, 5.3B). As a result, talonid basin depth cannot be used in a simple ratio with molar area without further analysis of this allometric effect. Finally, the presence of positive allometry in metaconid height in the Balta sample is the result of its presence in insectivores only (Table 5.5; Fig. 5.1B). Metaconid height is likely the source of a positively allometric relationship in insectivore mean trigonid cusp height as well. Unlike total crest length, the use of metaconid height in a ratio has the potential to exaggerate group differences, as there is evidence that insectivores possess higher cusps than frugivores on average (Kay, 1973, 1975b; Rensberger, 1973; Butler, 1983; Kay and Covert, 1984; Maier, 1984; Rensberger, 1986; Ungar, 2002; Evans and Sanson, 2003, 2005; Berthaume et al., 2013). Nonetheless, mean cusp height is isometric with molar area, and thus allometry in cusp height should only influence analyses of Variable Set 1.

However, when allometric relationships are present, it is recommended that residual values from the OLS regression line be used to conduct subsequent analyses (Smith, 2009). To further evaluate the effects of allometry, the results of discriminant

analyses conducted using both residual and ratio data were compared. Species-level discriminant analyses for each possible variable set-sample combination were performed, and total misclassification (error) rates are provided in Table 5.8.[14]

Although a coarse comparison of these two methods of size-adjustment, this examination provides the most direct link between choice of scaling measure and implications for this study. From Table 5.8, it is clear that error rates are essentially unaffected by the scaling measure, and neither residual nor ratio data are consistently more effective at discriminating dietary groups. Given this similarity in discriminant analysis results, scaling using ratios of a given variable to molar area was preferred when the application of these measures to the fossil sample was considered. Because species assignments cannot be known with certainty in the fossil record, the products of species regression equations, i.e., residuals, cannot be employed in successive analyses of fossil taxa with the same confidence as in extant groups. This sample-specific aspect of regression residuals contrasts with the repeatability of ratio-scaling. In addition, most of the morphometric variables in the extant sample scale with isometry (see Tables 5.2-5.7), so it is reasonable to assume that these isometric relationships will be upheld in fossil taxa. Furthermore, the positive allometry for total crest length in frugivores will only lessen the detection of dietary differences among groups, producing conservative results. Finally, the significant positive allometry of talonid basin depth cannot be ignored. Discriminant analyses were conducted both including and excluding talonid basin depth to determine if the allometric effects of this variable strongly influenced dietary group separation. Although ratios will be used to scale all morphometric variables, the possible

[14] Discriminant analyses are discussed in more detail later in this chapter.

effects of positive allometry in certain variables are acknowledged and will be considered in the interpretation of the results.

COMPARISON OF FIRST AND SECOND MANDIBULAR MOLARS

Within a strict comparative framework, reconstructions of fossil behavior (e.g., diet) based on morphological structures are restricted to the relationships between behavior and the specific skeletal or dental elements examined in the comparative extant sample. In the case of the dentition, strong correlations between diet and both first and second mandibular molars have been demonstrated in extant mammals, and both m1s and m2s have been used in dietary reconstructions of fossil taxa. However, these two elements are not often combined in a single sample (e.g., Strait, 2001; Boyer, 2008; Bunn et al., 2011), and thus the extent to which m1s and m2s differ in their "dietary signal" within a single species or individual is not clear. Unfortunately, analyses of fossil communities necessitate large sample sizes, but specimen availability is often limited by sampling bias and the fragmentary nature of fossil material. In this study specifically, the analysis of dietary niche overlap required a minimum of three specimens per taxon per time interval (see "Modified MANOVA: Test Case of Fossil Analysis" below), and limiting the sample to second mandibular molars (to allow direct comparisons with the results of the extant sample) would have made comparisons impossible.

In order to determine if the inclusion of both first and second mandibular molars in the fossil sample was valid, possible variation in the efficacy of each molar in dietary discrimination was evaluated. For this purpose, first and second mandibular molars of 68 specimens, representing 40 (of the total 46) species from the Mindanao sample, were compared (Table 5.9). With the exception of *Acerodon jubatus*, the exclusion of species

from this subsample was based on availability. In the case of *Acerodon*, the m1 and m2 morphologies differ considerably, and the assumption that m1 and m2 morphometrics are comparable is only realistic when gross morphology is similar. For this reason, in fossil taxa exhibiting distinct m1 and m2 morphologies (e.g., carpolestids), only second mandibular molars were analyzed. Of the possible measurements described in Chapter 4, only four could be obtained from all specimens due to variable molar morphologies: total crest length, mean cusp height, mean cusp angle, and talonid basin depth, all of which were scaled by molar area (see discussion above).

First, paired t-tests were used to directly compare m1 and m2 measurements from the same individual. As not all differences between m1 and m2 values were normally distributed, the non-parametric Wilcoxon signed-rank test was used. It is known that first and second mandibular molars in any specimen are not identical structures (Gingerich and Schoeninger, 1979; Ribeiro et al., 2013); therefore, this was considered the most conservative approach in evaluating differences between these tooth types. A non-significant Wilcoxon signed-rank test indicated that m1s and m2s of a given specimen could be used interchangeably in further analyses. Although the null hypothesis of no difference between m1 and m2 values was not rejected for each of the four variables, the fact that results for mean cusp height and mean cusp angle approached significance indicated that these features may differ in first and second mandibular molars (Table 5.10). Differences in mean cusp height and mean cusp angle in m1s as compared to m2s were thus further investigated.

As stated above, the expectation that m1s and m2s are completely interchangeable is not entirely reasonable, as current inhibitory cascade models of dental development

demonstrate that the genetic and biochemical patterning of each tooth is not identical, although they are non-independent (Jernvall, 1995, 2000; Jernvall and Jung, 2000; Line, 2001; Kavanaugh et al., 2007; Polly, 2007; Salazar-Ciudad and Jernvall, 2010). In order to use a combined m1-m2 sample in dietary discrimination, it is instead only necessary for both molars to exhibit the same morphological signal (accounting for size) relating to dietary regime. Similarity in the pattern of dietary discrimination for m1s and m2s were assessed by contrasting the m1 and m2 results of non-parametric post-hoc Critchlow-Fligner comparisons of dietary categories for mean cusp angle and mean cusp height. If m1 and m2 measurements produced significant differences among the same dietary groups, this would suggest that both molars can be used as equivalent dietary indicators, validating the substitution of one molar with another in incomplete specimens. Dietary Group 2 was used for all pairwise comparisons, which were performed in SPSS v.22.

The results (Table 5.11) indicated that in both mean cusp height and mean cusp angle, the same pairings of dietary groups were found to be significantly different from one another regardless of whether m1 or m2 data were used.[15] Thus, combining m1 and m2 data to identify dietary niche differences appears justified, permitting the inclusion of both first and second mandibular molars in the fossil sample analyses.

PHYLOGENETIC EFFECTS

The nonindependence of species as the consequence of phylogenetic relatedness in statistical analyses is well-supported (e.g., Felsenstein, 1985; Nunn, 2011). This is of particular importance in large comparative samples where the objective is group

[15] As predicted by the results of the Wilcoxon signed-rank tests, the pairwise comparisons of total crest length and talonid basin depth showed similar findings using m1 and m2 data.

discrimination. In these analyses, genera represented by greater numbers of species (or families by greater numbers of genera), all of which may have derived a diet-dentition complex from a common ancestor, have an increased potential to impact discriminatory classification rules than those with fewer generic or familial representatives. Unfortunately, the nature of any community analysis is that one is limited by the evolutionary history and resulting phylogenetic structure of that community, in which phylogenetic niche conservatism – or the tendency of closely related species to inhabit similar niches due to the shared inheritance of traits from a common ancestor – may have played a considerable role in community composition (Losos, 2008; Wiens, 2011). In addition, diet, molar morphology, or both, may not vary greatly in some clades (e.g., rodents) and thus one might suggest that all species within that taxon be considered as a single statistical observation. This is particularly problematic for discriminatory analyses, as an analytical alternative that accounts for phylogenetic autocorrelation is not yet known. Thus, the effects of phylogenetic relatedness were evaluated in association with several of the analyses below.

UNIVARIATE AND MULTIVARIATE NORMALITY

Parametric statistical analyses require either univariate (e.g., for ANOVA) or multivariate (e.g., for discriminant analysis) normality of the sample data (counter to the regression analyses employed above, which require normality of sample residuals). Violations of these assumptions were assessed univariately for each morphometric variable using the Shapiro-Wilk test for normality and normal probability plots. As multivariate normality within groups is an assumption of discriminant analysis, a Mardia's multivariate normality test was performed on each dietary group present in the

Balta, Mindanao, and combined Balta-Mindanao samples using all possible variable datasets (see Table 5.1).

Univariate analyses indicated that not all morphological variables were normally distributed, and at least one dietary group in each sample exhibited non-normality in multivariate tests. Box-Cox transformations were performed to determine if normality could be attained; however, not all of these transformations resulted in normal distributions. In addition, the type of transformation (e.g., logarithmic, inverse) differed among variables, making it difficult to interpret results based on these transformed data. Thus, non-parametric alternatives to all statistical tests were used to analyze the extant samples.

PRINCIPAL COMPONENT ANALYSIS

Analytical Procedure

As a dimension-reduction technique, principal component analysis (PCA) can be used as an initial investigative tool to identify patterning within and among samples, in this case, dietary groups. Especially relevant to this study, one can examine the degree to which members of dietary groups cluster together in multidimensional principal component space. These results can then be compared directly to those of the fossil Bighorn Basin sample, as principal component analysis forms the basis of the fossil analyses. If patterning of species corresponds to diet, the principal component space can be viewed as a "dietary niche space" within which each species occupies a particular dietary niche (see Chapter 2). Furthermore, interpretation of eigenvectors can establish those morphological variables that may be most influential in explaining variation within the sample and guide the choice of variables to be applied to the fossil sample. Principal

component analyses were performed on all three variable sets of the Balta sample and on Variable Set 2* of both the Mindanao and combined Balta-Mindanao samples (see Table 5.1). To decrease the number of groups presented visually, all analyses were conducted using only Dietary Group 2.

Results

Balta sample.

Plots of the first and second principal components (PC1 and PC2) for Variable Sets 1-3 are shown in Figs. 5.4-5.6[16], and eigenvalue and eigenvector statistics are provided in Tables 5.12-5.14. Several important aspects of these results will be discussed. First, these plots demonstrate the same overall pattern: the first principal component, accounting for the majority (51-56%) of the variation in the sample, separates dietary groups from one another. In addition, specimens are not arranged along the first or second principal components by molar size (supporting the use of scaling ratios) or phylogenetic relatedness (see discussion below). This indicates that the morphological variables measured here are related to, and can likely be used to reconstruct, dietary regime. Variable loadings on each principal component are consistent among variable sets. Specifically, cusp height, cusp angle, talonid basin area, and trigonid-talonid relief contribute relatively equally to the first principal component, and loadings are in expected directions. For example, low cusp height, large (more obtuse) cusp angle, large talonid basin area, and low trigonid-talonid relief are correlated and have the potential to

[16] It should be noted that in these analyses, graphical representation of the third principal component (explaining ~10-12% of the variation in the sample) does not further clarify the general patterns discussed here, and thus are not depicted as part of this section. However, see "Modified MANOVA: Test Case of Fossil Analysis" for further discussion of PC3.

be viewed as a character complex of frugivorous taxa, whereas the opposite relationships characterize insectivorous species. This result is compatible with our current understanding of diet-dentition relationships; however, total crest length and talonid basin depth are relatively unimportant in explaining variation along this axis. Instead, these latter variables are most significant in creating separation along PC2, and thus are valuable in dietary discrimination, but perhaps less so than other measures.

Second, despite a general dietary pattern, there is significant overlap among some dietary categories. In particular, the insectivore-frugivore group is completely contained within, and therefore does not appear distinct from, the insectivores. Omnivorous taxa also do not form a distinct group, although they seem to partially bridge the gap between frugivorous and insectivorous species. However, the few omnivorous species examined here align most closely with insectivorous taxa, and this may be the result of phylogenetic relatedness (see Fig. 5.7 and discussion below). Distinctions between omnivores and other dietary groups will be explored further in the following analyses.

Third, the relative positions of groups generally fit a continuous dietary arrangement. In other words, the transition from negative to positive values of PC1 can be viewed as a gradation from insectivory to frugivory in the overall dietary niche space, matching the direction of variable loadings on this component (see above). For example, frugivore-insectivores trend towards the negative aspect ("insectivory end") of the non-carolliine frugivore spectrum (see Fig. 5.4). However, although they appear distinct from frugivore-insectivores, hard-object frugivores are also present in this general region, and frugivore-nectarivores span the principal component space between the insectivore and

frugivore groups. An examination of the variable loadings on the first two principal components provides some explanation for this pattern.

With regard to the hard-object frugivores (FH), their displacement within the frugivore group may relate to allometric relationships among the morphometric variables. All "FH" taxa have relatively large molars, and it is possible that the positive allometry of talonid basin depth and total crest length may exaggerate the magnitude of these traits such that they appear more "insectivore-like," although it is noted that these two variables have low loadings on PC1. Based on feeding habits, it might be expected that frugivore-nectarivores would possess the shortest and least angular molar cusps, but an examination of their morphology indicates that this is not always the case. All of the frugivore-nectarivores in this study are chiropterans, and it is possible that relatively taller and more angular cusps and greater trigonid-talonid relief in these nectarivorous taxa (Glossophagini and Lonchophyllini) are the result of inheritance from an insectivorous ancestor combined with the relaxation of constraints on chewing (Freeman, 1995). However, the published dietary accounts of these taxa conflict enormously, and the dominant categorization was chosen for these taxa (see Appendix 5 for reference list). This approach may have been inappropriate, and these species may best be classified as omnivorous, as some accounts indicated the presence of insect-feeding (see Appendix 5). In this case, the intermediate placement of these specimens within the "dietary niche space" is in accordance with their dietary habits. This highlights the continued need for more detailed and quantitative behavioral studies of many of the taxa included in this sample. Nonetheless, as no reconstructed nectarivorous taxa are included in the fossil sample, the relationship of this dietary group to others is not a major concern, although it

should be noted that, with the exception of sturnirins, the most frugivorous frugivore-nectarivores (see Fig. 5.5), the FN group is largely distinct in principal component space. Because the goal of this study is to best differentiate specific dietary regimes, these patterns of overlap will be further examined in subsequent analyses, designed to probe more precisely into morphological differences among dietary groups.

Mindanao sample.

In general, the patterning of dietary groups in the principal component plot and the variable loadings of the Mindanao sample are comparable to those of the Balta sample (Fig. 5.8; Table 5.15). However, there are a few notable exceptions. First, and almost certainly due in part to the inclusion of fewer variables, both total crest length and talonid basin depth have greater contributions to PC1. Second, frugivore-nectarivores are no longer positioned between the frugivore and insectivore groups but are instead embedded, in addition to hard-object frugivores, within the frugivore cluster. Thus, compared to the Balta sample, dietary niche differentiation within frugivory appears diminished, if not absent, in the Mindanao sample. Third, folivorous specimens, not present in the Balta sample, cluster with insectivores (particularly faunivores[17]), as might be expected given the similar, though not identical, food material properties of leaves and insect chitin (Hiiemae, 2000).

Finally, both the first and second principal components are involved in dietary separation. Although PC1 accounts for 68% of the variation, it seems that this variable mainly separates largely frugivorous and insectivorous (and to an extent, folivorous)

[17] It is not possible to discern whether the close proximity of faunivores (in this sample, tarsiers) to folivores (dermopterans) is the result of diets involving similar food material properties or phylogenetic relatedness.

groups. It is not possible to establish if this lack of dietary differentiation is related to the sample itself (e.g., perhaps these measurements are only applicable to tritubercular or quadricuspate molars, the dominant molar morphology of the Balta sample), but it is likely that differences between trigonid and talonid morphology, not captured in this analysis, are strongly related to dietary preference.

Combined Balta-Mindanao sample.

The results of the combined Balta-Mindanao sample (Table 5.16; Fig. 5.9) share aspects of both the individual Balta and Mindanao analyses. Again, this combined sample requires the use of a diminished variable set, which as discussed in the previous section, may decrease dietary group discrimination. First, it is important to recognize that the general dietary patterning demonstrated by each sample individually remains present, despite increased phylogenetic diversity within the combined sample. Second, both the first (on which total crest length, mean cusp angle, and talonid basin depth are most heavily loaded) and second (for which mean cusp height is most highly correlated) principal components affect dietary group separation. Third, the frugivore group clearly occupies the largest area of the principal component space, and a closer examination reveals a distinction between frugivorous pteropodid and phyllostomid chiropterans. If diet-dentition relationships are preserved in this study, it is posited that at least two types of frugivory may be represented in this sample. Although not conclusive, published studies seem to indicate the greater consumption of fruit juices than fruit pulp in pteropodids as compared to phyllostomids (see Appendix 6), and flat, rimmed pteropodid molars are particularly well-equipped to extract juice from fruit tissue (Lucas, 1979). This hypothesis certainly requires further study, and it is equally plausible that the highly

derived nature of pteropodid molars is unsuitable for morphological comparative studies of this kind. For this reason, highly derived molars (e.g., those of multituberculates) were excluded from the fossil sample, and this will be discussed further in Chapter 6.

Phylogenetic Patterning

Principal component analysis provides an additional opportunity to detect phylogenetic patterning if present among the data. For the sake of clarity, this will only be discussed for the Balta sample, but the Mindanao and combined Balta-Mindanao samples exhibit congruent patterns. Based on Fig. 5.7, which displays both taxonomic and dietary assignments of each specimen, it is clear that there is a relationship between evolutionary relatedness and diet within taxonomic groups; i.e., closely related taxa occupy similar dietary niches. As discussed previously in this chapter, this is not necessarily surprising if some degree of phylogenetic niche conservatism is present. However, the location of each taxonomic group within the larger "niche space" is compatible with its dietary regime. There are exceptions (e.g., frugivorous didelphimorphians, which are separated from other frugivores and are instead positioned near their more insectivorous relatives), but in the group that is most diverse in diet, the phyllostomids, the diet-dentition relationship eclipses dental similarity based on common phyllostomid ancestry. This, of course, does not eliminate the potential effects of multiple dependent statistical observations due to phylogenetic autocorrelation, as is evidenced by the fact that all carolliines cluster separately from other frugivores. However, it does indicate that if the morphological features examined here are used to reconstruct dietary niche overlap, taxonomic designations and phylogenetic relationships will not conceal the larger niche patterns.

Phylogenetic Principal Component Analysis

The method of phylogenetic principal component analysis (phylogenetic PCA) allows researchers to investigate relationships among multiple traits while accounting for the phylogenetic relationships among the taxa that possess them. Although this analysis is akin to a non-phylogenetic principal component analysis in that significance values cannot be attributed to the relationships among taxa or traits, they allow for comparison with the principal component analysis results presented above. Phylogenetic PCAs were conducted in R v.2.15 using the phytools package, and the species-level phylogenetic tree used in these analyses was obtained from Bininda-Emonds et al. (2007). Several species were excluded mainly due to unavailable phylogenetic data; however, congeneric species were used where possible (see Table 5.17 for these exceptions). Analyses were performed on the Balta, Mindanao, and combined Balta-Mindanao samples using species mean morphometric data, and plots of the first two principal components are shown in Figs. 5.10-5.12. Figures 5.10 and 5.11 illustrate that the phylogenetic PCA results for both the Balta and Mindanao samples generally resemble those of the non-phylogenetic PCAs. In both plots, a division between "frugivores" and "insectivores" (broadly defined) along the first principal component is still present, and omnivores remain closely aligned with insectivorous taxa. In the Balta sample, carolliines continue to form a distinct group in even greater association with insectivorous species, highlighting their unique molar morphology even when phylogenetic relatedness is considered. In addition, Balta frugivore-insectivores and insectivore-frugivores are positioned at the borders of the frugivore and insectivore groups, respectively, consistent with their mixed dietary regimes.

An examination of the combined Balta-Mindanao plot, on the other hand, demonstrates that a phylogenetic signal may be present in the data. Along the second principal component analysis, there is a separation along the x-axis between Balta and Mindanao species within the insectivore (I) and frugivore (F) groups (Fig. 5.12). As frugivores and insectivores in the Balta and Mindanao samples comprise species in mostly non-overlapping taxonomic groups (see Tables 4.1 and 4.2), this separation may be interpreted as phylogenetic in nature. However, an examination of the remaining dietary groups indicates that this pattern actually characterizes the entire combined sample, as the Balta and Mindanao specimens almost exclusively possess positive and negative values, respectively, along PC2. Given the variable phylogenetic relationships among taxa between these two communities, this division appears to supersede any phylogenetic distinction between the samples and instead seems to establish a difference between the mammalian guilds themselves. This result is surprising and certainly an area for further exploration. Nonetheless, for the purposes of this study, it is most notable that despite these community-level differences, even when both the Balta and Mindanao samples are considered together, there is still dietary distinction across the first principal component. Overall, this latter result is consistent with a non-phylogenetically autocorrelated relationship between molar form and diet and supports the use of the molar variables examined here as indicators of dietary regime across a diverse mammalian sample.

KRUSKAL-WALLIS TEST AND POST-HOC COMPARISONS

Analytical Procedure

Discriminant analysis is only appropriate when significant differences among groups have been demonstrated (Khattree and Naik, 2000). As Kruskal-Wallis one-way analysis of variance (ANOVA) tests the null hypothesis that at least two group means are different, this analysis was conducted on each variable in the Balta, Mindanao, and combined Balta-Mindanao samples for both dietary groupings. All variables significantly differentiated at least two groups for all three samples, even when a strict Bonferroni correction was applied (Tables 5.18-5.20).[18] Thus, discriminant analysis is an appropriate method to examine dietary differentiation. As the results of a Kruskal-Wallis test only indicate a difference between at least two (and not necessarily all) group means, Critchlow-Fligner non-parametric post-hoc comparisons were conducted. All pairwise comparisons were performed using Dietary Group 1 and Dietary Group 2, and these were performed in SPSS v.22. Finally, box plots of variable values for all dietary groups within each sample were used to provide visual representations of the results of these comparisons (Figs. 5.13-5.15).

Results

The principal results of the pairwise comparisons using both Dietary Group 1 and Dietary Group 2 categorizations correspond closely with one another in each sample and will be discussed together. Due to the number of pairwise comparisons involved, the

[18] The only exception is talonid basin depth in the Balta sample, which becomes non-significant when strict Bonferroni correction is applied.

combined Balta-Mindanao sample is not discussed, but the results mirror those of the individual samples.

Balta sample.

Overall, the pairs of dietary groups that differed consistently across variables contrasted an insectivorous and a frugivorous group (Tables 5.21 and 5.22). In other words, groups with low or no discrimination were members of the same larger "frugivore" or "insectivore" classes (e.g., FH and F within "frugivores"). Therefore, the further division of dietary categories within "frugivory" and "insectivory" in Dietary Group 1 did not provide additional discrimination, as this level of categorization appears too specific to capture the diet-dentition relationships studied here. Interestingly, however, this pattern is upheld in comparisons of frugivore-insectivores and insectivore-frugivores, which were significant in most cases.

All variables appeared to perform equally well at detecting group differences, with the exception of total crest length and talonid basin depth, which identified many fewer significant comparisons. However, these latter variables did identify significant differences between groups within the "frugivorous" class, and when additionally considering both the PCA and Kruskal-Wallis results, these two variables may still be important in the separation of dietary niches. Nonetheless, within this larger pattern, there is variation in the performance of individual variables. For instance, protoconid and metaconid height, the trigonid cusps, discriminated more pairs than entoconid and hypoconid height, the talonid cusps (Tables 5.21, 5.22; Figs. 5.13B-E). In addition, each of these variables, as well as the individual cusp angle variables, differentiated different sets of dietary groups such that, for every cusp, a ranking of groups based on variable

values would vary slightly (Tables 5.21, 5.22; Figs. 5.13B-E, G-J). Of note is the fact that the frugivore-insectivore group aligns with the other frugivorous groups when protoconid and hypoconid height, the buccal cusps, are examined but with the insectivorous groups in a comparison of metaconid and entoconid height (Figs. 5.13B-E). Thus, consideration of each cusp separately may lead to overall greater discrimination among dietary groups. Finally, for each morphometric variable, the range of values representing the frugivorous groups always exceeds that of the insectivorous groups, and in several variables (e.g., talonid basin area, total crest length), this variation is considerably greater in frugivores (Figs. 5.13A-R). This may indicate that the frugivore niche is also diverse and possibly comprises smaller niche components, in which species may or may not compete. Niche overlap within dietary categories, particularly frugivores, will be discussed further below.

Mindanao sample.

As in the Balta sample, only comparisons of a member of the "frugivore" class with a member of the "insectivore" or "folivore" class (Tables 5.23 and 5.24) were consistently significant across the variable set. With the exception of talonid basin depth, each variable demonstrates a clear distinction between these two groups (Figs. 5.14A-D). Furthermore, the morphometric variables were again unable to differentiate among the narrower dietary classifications of Dietary Group 1. In contrast to the discussion above, that the overall results of the Mindanao sample, with many fewer variables, are similar to those of the Balta sample suggests that a subset of the total variable set may be sufficient to reconstruct dietary niches at the level characterized by Dietary Group 2.

DISCRIMINANT ANALYSIS

Analytical Procedure

Discriminant analysis is a multivariate data reduction and discrimination technique that constructs classification rules designed to maximize group separation. This method additionally allows assessment of the efficacy of these classification rules, and thus ultimately the dataset, in group discrimination through the use of posterior probabilities, where individuals are assigned to groups based on the discriminant functions, and misclassification rates are calculated.[19] In the present study, this analysis can be applied to determine the strength of the diet-dentition relationship through the examination of error classification rates of each dietary group. If misclassification rates are low, these morphological variables (or a subset thereof) can be used to reconstruct distinct dietary niches.

Due to the multivariate non-normality of the dataset, the non-parametric k-nearest-neighbor method of discriminant analysis was used. Rather than formulating classification rules from the distance of observations to group means, this method establishes group assignment based on the distance of an observation to its nearest neighbors. Specifically, the group membership of each nearest neighbor is determined, and based on the prior probabilities of each of these groups, the posterior probability of the observation of interest is derived. In the case of a tie, the observation is assigned to "Other."

[19] Although error rates using posterior probabilities will always be biased downward, the use of unbiased cross-validation to estimate error rates is not recommended, as it requires exceptionally large datasets and eliminates a subset of the overall sample for use in constructing the discriminant functions (Khattree and Naik, 2000).

Discriminant analyses were conducted on both Dietary Groups 1 and 2 for Variable Sets 1-3 of the Balta sample and Variable Set 2* of the Mindanao and combined Balta-Mindanao samples. However, as demonstrated in the post-hoc comparisons, dietary discrimination at the resolution of Dietary Group 1 appears inaccessible to the morphological variable sets. Thus, the few additional dietary categories in Dietary Group 1 were those most commonly misclassified, and the error rate using this classification was slightly higher. Beyond this, however, the overall results using the two dietary groups were very similar, and these were compared for Variable Set 1 of the Balta sample to illustrate this point (Tables 5.25-5.28). Discriminant analyses were also run without the inclusion of talonid basin depth, as this variable was previously identified as significantly positively allometric (see Tables 5.33-5.35, 5.38, 5.41). Comparison of error rates and posterior probabilities in all samples and using all variable sets indicates that this variable does not greatly affect the outcomes of dietary group discrimination and thus can likely be used in further analyses without a substantial impact on the results. Finally, because there is no known standard of acceptable error rate in discriminant analysis, and akin to many other data reduction techniques, misclassification rates must be viewed in the context of other analyses (e.g., Kruskal-Wallis). For comparison of these results to other studies, see Semprebon et al. (2004), Wallace (2006), Pilbrow (2007), Boyer (2008), Deane (2009), Bunn et al. (2011), and Godfrey et al. (2012).[20]

[20] Published overall error rates and individual reclassification rates vary widely, but the results of the discriminant analyses presented here are within the range of previous studies.

Results

Balta sample.

Although the use of a greater number of variables in Variable Set 1 does provide the best discrimination (error rate of 0.09 for Dietary Group 1 and 0.06 for Dietary Group 2), overall error rates for the three variable sets are roughly alike (Tables 5.27, 5.29, 5.31). This lends further support for the use of a reduced, less autocorrelated variable set in the fossil sample analyses and demonstrates that the chosen morphometric variables are useful dietary discriminators. The posterior probabilities of each dietary group range from 83% to 98%; however, members of the omnivore group are consistently misclassified (Tables 5.27, 5.29, 5.31). As mentioned previously, the diet of this group is notoriously difficult to categorize based on its dental morphology. The highest omnivore reclassification rate is the result of using Variable Set 1, which might be cause to pursue the application of this set of variables in further analyses. The reason for the affinity of omnivorous taxa with insectivore-frugivores, the group into which they are most often misclassified, is unclear, and perhaps is sample-specific. Regardless, this indicates that dietary reconstructions based on these molar variables will likely omit the omnivore component of the dietary niche space.

On the other hand, when misclassified, specimens of each non-omnivore group align with groups of similar diets (Tables 5.28, 5.30, 5.32). For example, insectivores are most commonly misclassified into the insectivore-frugivore group and frugivores into the FH, FI, or FN categories, but these misclassifications are rare. Misclassified individuals span the range of molar size and represent equal proportions of the higher taxonomic groups; i.e., misclassification does not appear associated with size or phylogenetic

affinity. Species represented by few specimens (i.e., the larger didelphimorphians) are continually misclassified, but the molar morphology of this group also appears phylogenetically conserved (see Fig. 5.7).

Mindanao sample.

The overall error rate of this sample (0.08), which included only 4 variables, is comparable to that of the Balta sample in which Variable Set 1, the largest variable set, was employed (Table 5.36). However, a closer examination of the error rates of each dietary group shows that misclassification of frugivore-nectarivores and omnivores is significantly higher. In addition, it does not seem that the presence of the folivorous specimens in the Mindanao sample resulted in the misclassification of other group members as folivores. Still, as the dietary categories of these two groups do not completely overlap, it is difficult to determine how the absence of frugivore-insectivores and insectivore-frugivores may have influenced the Mindanao results.

Misclassified observations again span the sample molar size and phylogenetic spectrums, and as evidenced by the posterior probabilities, tree shrews, the sole omnivorous taxon in this sample, are most often allocated to the incorrect group (Table 5.37). Akin to the problematic dietary categorization of Balta frugivorous-nectarivous chiropterans, there is also evidence that insectivory may be dominant to frugivory in the feeding habits of "omnivorous" Philippine tree shrews (Heaney et al., 2006). However, even in this case, scandentians would likely be grouped with insectivores as no other insectivore-frugivores are present in the Mindanao sample. Alternatively, this may simply be another example of the complications involved in identifying omnivores from molar attributes.

Combined Balta-Mindanao sample.

Given the taxonomic and dietary diversity of the combined Balta-Mindanao sample, the similarity of these results to those of the individual samples, the low overall error rate (0.17), and the relatively high posterior probabilities of almost all dietary groups validate the strength of the molar morphometric variables as valuable discriminators of dietary regime within frugivorous and insectivorous niches (Table 5.39). In this combined sample, certain taxonomic and dietary groups are consistently misclassified, notably the folivorous dermopterans, omnivorous scandentians, omnivorous phyllostomids, and hard-object frugivorous Peruvian rodents (Table 5.40). The inability of the molar measures to correctly classify dermopterans may be a result of the dearth of folivorous taxa in the sample, as colugos are the only folivores included. As in almost all other analyses, omnivores pose a considerable problem and are rarely identified correctly. The interpretation and identification of the omnivorous niche with regard to the fossil analyses will be discussed below. The misclassification of the Peruvian sciurids is surprising, as they appear to occupy the central area of the FH niche, and this may demonstrate the ambiguity of dietary assignment in regions of partial overlap among the "frugivorous" niches.

Discriminant Analysis at Multiple Taxonomic Levels

To ascertain the effects of phylogeny on the primary analysis of the extant sample, discriminant analyses were performed at varying taxonomic levels. It should be noted that statistical analyses of samples of variable numbers of observations can alter results due to sample size alone, and the nature of this demonstration dictates that sample sizes will decrease as higher taxonomic levels are analyzed. However, if results are

generally consistent across hierarchical taxonomic groupings, this suggests that phylogenetic autocorrelation is not magnifying the relationship between molar morphology and dietary regime in more abundant higher taxa.

Alpha taxonomy of all species follows Wilson and Reeder (2005) and taxonomic groupings are listed in Table 5.42. All possible variable set-sample combinations were employed, and taxonomic groupings were as inclusive as each sample allowed. The main restriction regarding taxonomic groups was the requisite of discriminant analysis that all dietary groups include at least 2 observations. Thus, Dietary Group 2 (see Chapter 4), the broader of the two dietary categories was used, but even at the subfamilial level, only two dietary groups ("I" and "F") comprised more than two members in the Mindanao sample. As the objective of this exercise was to eliminate multiple observations evolutionarily derived from the same diet-dentition ancestral condition, taxa within a subfamily or family classified into different dietary groups were considered independent observations (e.g., insectivorous and frugivous phyllostomids were analyzed separately).

Although somewhat limited in number, the analyses for which sufficient data were available suggest that relationships between molar morphology and dietary regime are maintained when lower-level taxa are subsumed into more inclusive groups (Table 5.43). However, the significant reduction in error rate for certain higher taxonomic levels is concerning, suggesting that the consideration above, in which sample size may significantly affect results, is notable. In general, error rates increase in higher-level groups, although (with the exception of Variable Set 2 of the Balta sample) most rates are less than 0.25. In particular, Variable Set 3 performs rather consistently at all taxonomic levels. Despite the fact that this type of analysis of the effect of phylogeny is not

definitive, until a well-supported option that considers phylogenetic relationships in discriminant analysis is readily available, one can only consider the possible effects of phylogenetic relatedness post hoc on the results presented here.

MODIFIED MANOVA: TEST CASE OF FOSSIL ANALYSIS

As discussed in Chapter 2, a statistical test that can identify overlap among N-dimensional niches, as they have been defined and evaluated in previous ecological research, has the potential to produce more hypothesis-driven, probability-based assessments of ecological similarity across multiple niche axes, which can allow for a more complete and quantitative evaluation of competition in the fossil record. Furthermore, this analysis does not require knowledge of the nature of the dietary niche (i.e., the actual diet) of each group but only whether dietary niches overlap, which is particularly advantageous in the study of fossil taxa with no extant analogs. The method described below was used to analyze dietary niche overlap within the fossil sample, but it was additionally applied to a portion of the extant sample, the majority of the Balta species (Table 5.44), as a test case in which dietary regimes were known. Both the effect of dimensionality in testing overlap of niche hypervolumes and the interpretation of patterns of niche overlap among the Balta taxa, specifically the efficacy of specific molar measures in the reconstruction of dietary niche overlap within fossil communities, were explored.

Methodological Description

A principal component analysis (PCA) was first performed on all individual specimens using Variable Set 3 in order to reconstruct dietary niches; however, in general, the raw data for this method can consist of any unit of analysis (e.g., species

means). N principal components (PCs) can be used in the subsequent analysis of niche overlap, and the number of PCs varied among comparisons (see below). The resulting multidimensional principal component space is representative of a multidimensional niche space in which all possible niches represented in the sample are contained, and these niches are defined by the relationships among molar morphological variables. In this space, each specimen has a multidimensional point, or "niche coordinate." This model of niche reconstruction is most applicable to the evaluation of competition in fossil specimens, for which true niches are unknown, and therefore is dependent on previously demonstrated relationships between morphological characters and ecological niches of extant taxa.

The niche of any group of specimens (e.g., specimens contributing to a particular taxonomic group, site, or temporal unit) can be evaluated within this overall niche space, and these groupings are the basis for the analysis of niche overlap. These niches in principal component space can be represented visually as "hypervolumes": for example, convex hull polygons (in two dimensions) and confidence ellipsoids (in three dimensions) (Figs. 5.16 and 5.17). However, the subsequent test of niche overlap does not require that niches be circumscribed in this way, as it only considers the distribution of points in the predefined groups. Furthermore, although useful illustrative tools, graphical representations of niche space including fewer dimensions than the total number considered in the full analysis can be misleading, as they do not incorporate variation or separation along these additional, and potentially ecologically important, axes (see "Comparing Dimensionality in Patterns of Niche Overlap").

The method of dietary niche overlap described here is a modified non-parametric multiple analysis of variance (MANOVA) derived from Anderson (2001). This analysis constructs an *F*-statistic calculated using sums of squares of distances among "niche coordinates" in multidimensional principal component space. Specifically, SS_B (variance between groups), is the sum of squared distances between each niche coordinate and the centroid of the entire sample, and SS_W (variance within groups) is the sum of squared distances between each niche coordinate within a group and the centroid of that group. To simplify the resulting algorithm, the sums of squared interpoint distances (equivalent to the sums of squared distances between individual points and their centroids) and the consequent calculation of SS_B using SS_T (total variance within both groups combined) was preferred (Anderson, 2001) (Table 5.45).

Using this approach, the resulting value of the *F*-statistic will be higher when the variance between groups is greater than the variance within groups, indicating group separation. Thus, the null hypothesis of this analysis states that groups occupy statistically similar positions in the multivariate principal component space, the ecological interpretation of which is the presence of niche overlap, a requisite of competition. Consequently, rejection of the null hypothesis signifies the lack of overlap between niches. As the null distribution of this *F*-statistic is not identical to that of the parametric Fisher's *F*-statistic, a permutation test was used to calculate the *p*-value for each comparison. In this test, group identification is randomly reassigned to each individual, and the *F*-statistic is recalculated (*F**). Statistical significance was assessed by determining whether the observed *F*-value is within the upper 5% of the permuted distribution (Manly 1997; Anderson, 2001). Randomization also enables the application

of this method to small samples, as hypervolumes need only be defined by a minimum of three coordinates, a condition present in several reconstructed niche hypervolumes within the fossil sample (see Tables 4.3, 6.4-6.8). These analyses were performed in SAS 9.2 (see Appendix 7 for associated program).

Comparing Dimensionality in Patterns of Niche Overlap

Dietary niches were reconstructed for each of the seven dietary categories represented in the sample, and niche overlap among dietary groups using the first two, three, and five principal components, or niche axes, were contrasted. In this analysis, each niche axis represented a component of molar morphology, correlated with dietary differences, and thus was interpreted as an aspect of the dietary niche. The first two and three niche axes were examined to facilitate direct comparisons with previous studies, which have typically considered either two or three dimensions in niche reconstruction. Niches defined by five principal components were used to account for the vast majority, cumulatively contributing to 95%, of the variation in the study sample. Although the additive variation decreases with each subsequent principal component, variation left unaccounted for with two, or even three, dimensions can be considerable in some samples and therefore has the potential to contain important ecological information. The specific effects of dimensionality are sample-dependent, but an example of the degree to which additional niche axes can potentially influence patterns of niche overlap will be investigated here.

As discussed earlier in this chapter, a plot of the first and second principal components (Fig. 5.16) reveals: (1) clear separation among some groups (F-I, FH-I, F-O, FH-O, F-IF, and FH-IF), (2) clear overlap among other groups (I-O, I-IF), and (3) some

degree of overlap among the remaining dietary groups. If we assume then that the molar characters are sufficient proxies for aspects of the dietary niche, these results indicate that (1) the dietary niches of F and FH are distinct from those of O, IF, and I, (2) there is dietary niche overlap between the pairs I-O and I-IF (at least when considering these two niche axes), and (3) the rest of the dietary niches may or may not overlap. Thus, outside of an explicit statistical framework, it is difficult to determine the degree of overlap among the niches in (3). As mentioned previously, overlap is difficult to assess visually, and in fact, the results indicate that only the I, IF, and O groups and the FH and FI groups significantly overlap (Table 5.46).

Addition of the third dimension (Fig. 5.17) demonstrates that the orientation of the hypervolumes, and thus their three-dimensional shapes, differ along this third niche axis. For example, the F, O, and I niche spaces are more elongate along the third principal component (i.e., the ranges of third principal component values are greater) than the remaining niches. This is consistent with the variable loadings on the third principal component, which contrasts trigonid-talonid relief and crest length, on the one hand, with talonid basin depth on the other (see Table 5.14). These variations on the "typical" diet-dentition relationships seem to characterize subsets of specimens within each dietary group. For example, insectivorous noctilionid bats and certain genera of frugivorous phyllostomid bats exhibit relatively low trigonid-talonid relief and long crest lengths, respectively, compared to other species within their dietary groups. The values of PC3 also demonstrate niche separation in ways not evident from considering the first two principal components alone. For example, the FI group appears to occupy a higher position along the third niche axis as compared to the FH group, further defining the

nature of niche overlap, or lack thereof, between these three-dimensional niche spaces. The results of the MANOVAs indicate that this third dimension includes some information important in dietary niche differentiation, as *p*-values for the I-IF and I-O comparisons approach significance (p=0.09, p=0.14, respectively) (Table 5.46). However, separation among the I, IF, and O niches is not achieved even when three niche axes are considered. It is only when five dimensions are included in the analysis that all seven dietary niches are non-overlapping (Table 5.46). It should be noted that if significance levels are adjusted for multiple comparisons, the IF and O hypervolumes remain overlapping again highlighting the problematic nature of the "omnivorous" dietary category.

Overall, these analyses establish that the identification of niche overlap can be ambiguous and graphical representations can be misleading without an associated statistical test. Furthermore, the results of this study emphasize the importance of accounting for most, if not all, of the variation within a sample, as known dietary niches were not completely differentiated when only two or three dimensions were examined. Although it is possible that the first two or three niche axes will accommodate a large percentage of the variation within a sample, a thorough comparison of niche hypervolume overlap must investigate the complexity of the niche space in multiple dimensions. As indicated here, the variables (or variable combinations) critical to the separation of similar niches – the regions of ecospace in which competition may be especially prevalent – may only explain a small amount of variation in the entire multi-niche sample, and thus in the ecospace as a whole.

Comparing Patterns of Reconstructed Niche Overlap to Known Dietary Regimes

Five-dimensional niches were constructed for each genus, and analyses of hypervolume overlap were conducted. If the eight molar measurements of Variable Set 3 are appropriate indicators of diet, as the previous results of this chapter suggest, then overlap of hypervolumes will be restricted to those genera classified in the same dietary group. In other words, only comparisons of genera assigned to different dietary categories are expected to result in significant *F*-values. This result will support the use of genus-level hypervolumes in the reconstruction of frugivorous, frugivorous-nectarivorous, hard-object frugivorous, frugivorous-insectivorous, insectivorous, insectivorous-frugivorous, and omnivorous dietary niches in the fossil record. Accordingly, overlap of reconstructed hypervolumes of fossil genera would indicate dietary niche overlap as defined by occupation of the same dietary group. However, it should be noted that this is the strictest interpretation of this analysis, as true dietary niches of living species may be distinct even within these refined dietary classifications.

In accordance with the results discussed previously in this chapter, these analyses supported a strong relationship between the molar variables and diet, specifically demonstrating that there was a clear distinction between the "insectivorous" niche (comprising the I and IF niches) and the "frugivorous" niche (including the F, FH, FI, FN niches). It is within these larger groups that the morphological variables were less consistent at reconstructing expected niche overlap patterns – genera grouped in the same dietary category exhibited niche separation, while niches of genera grouped in different dietary categories were shown to overlap. This indicates that the mapping of molar

morphology onto dietary niches is more complex than the principal component analysis, ANOVA, and discriminant analysis results might suggest.

Overall, approximately 82% of all comparisons produced the expected outcome (niche overlap among genera of similar diets and niche separation among genera with different diets), but the results of the inter- and intra-dietary group comparisons contrasted significantly. Comparisons between genera from different dietary categories yielded a high number of outcomes in the expected direction; i.e., there were relatively few instances of niche overlap (~7%) (Table 5.47). However, niche overlap between genera within dietary categories was also low, particularly within frugivores, broadly defined; ~29% of comparisons yielded non-significant *F*-values (Table 5.47). Due to the high number of pairwise comparisons, significance levels were not adjusted for all analyses, but strict Bonferroni adjustment of intra-dietary group comparisons did reverse this pattern (~66% of comparisons were non-significant) (Table 5.47). Further adjustment would lead to extremely low alpha values, which was deemed inappropriate for an accurate interpretation of the results. The significance of these results is discussed below ("Reconstruction of Dietary Niche Overlap").

CONCLUSIONS

At the beginning of this chapter, two questions, designed to investigate the utility of extant diet-dentition relationships in reconstructing dietary niche overlap in the fossil euprimate competitive guild, were posed. Based on the preceding results, these questions will each be addressed in order to provide the context for the analysis of the fossil sample in Chapter 6.

Association of Molar Measurements with Diet

Overall, the results of the extant sample highlight the validity of the use of these molar measurements in dietary reconstruction, as they consistently identified dietary group differences and discriminated among dietary niches. Despite this identification of useful diet-dentition relationships, dental morphology was not an exact predictor of diet, particularly when considering the narrow dietary regimes examined here. In particular, the omnivore niche is especially problematic. Due to their variable dietary habits, the omnivore classification has presented issues in dietary categorization in previous studies (e.g., Boyer, 2008; White, 2009; Bunn et al., 2011; Godfrey et al., 2012), as it has been difficult to identify morphological features that are unique to this dietary class. This suggests that the term "omnivorous" may be a simple, uniform descriptor for diets that vary widely among taxa. Furthermore, the dentition of these species may be adapted to a dominant or more critical (e.g., scarce) dietary resource (Kay and Covert, 1984; Altmann, 2009). The similarity between omnivorous and insectivorous molar morphologies in this study is unclear, particularly as the omnivorous taxa span three mammalian orders. Thus, although possible, the difficulty in identifying a specific omnivorous niche does not appear to be sample-specific. This poses a significant problem for the analysis of fossil species, in which dietary niches are unknown. At this point, the only possible interpretation of the fossil analyses with regard to this issue is to acknowledge that some instances of niche overlap of taxa with an "insectivore-like" molar morphology may erroneously place non-competing species within the same dietary niche.

As discussed in Chapter 4, individual competitive guilds were chosen for this study because they closely approximate true community-level competition by including

species that are known to interact and whose fundamental niches overlap both spatially and temporally. However, the finite dietary and morphological breadth of individual communities incorporates only a portion of the variation exhibited in extant mammals, and thus different communities, with different taxonomic compositions and levels of diversity, may yield alternative conclusions. On the other hand, molar features have been demonstrated consistently as proxies of dietary behavior (see Chapter 2), and the congruence of the results of both communities analyzed here support the assumption that these morphological variables sufficiently capture the association between molar form and dietary regime across the euprimate competitive guild.

Reconstruction of Dietary Niche Overlap

Given that the diet-dentition relationship has been broadly established, the ability to reconstruct dietary niche overlap within communities must then be considered. The results of the modified MANOVA best speak to this issue and can be interpreted in three ways. First, it is possible that our ability to reconstruct dietary niches within broad dietary categories (i.e., insectivory or frugivory) using molar morphology needs further refinement. In general, this is undoubtedly so, but given the limitations of reconstructing diet in the fossil record, it is possible that this level of precision may not significantly increase with future research, at least of molar form alone. For example, consumption of different fruits (or insects) may be associated with subtle differences in molar morphology, as the six phyllostomid frugivorous bats studied here rely on figs to varying degrees. Nonetheless, within the general framework of known diet-dentition relationships, variation in the proportionality of different food items (with their accompanying potential diversity of material properties) is relatively unstudied and may

be inaccessible via dental macro-morphology (Ungar, 2004, 2009). Furthermore, this study does not account for the non-molar dentition, and the integration of the entire dental suite (in conjunction with cranial and postcranial anatomy) is certainly integral to the reconstruction of a complete account of dietary behavior.

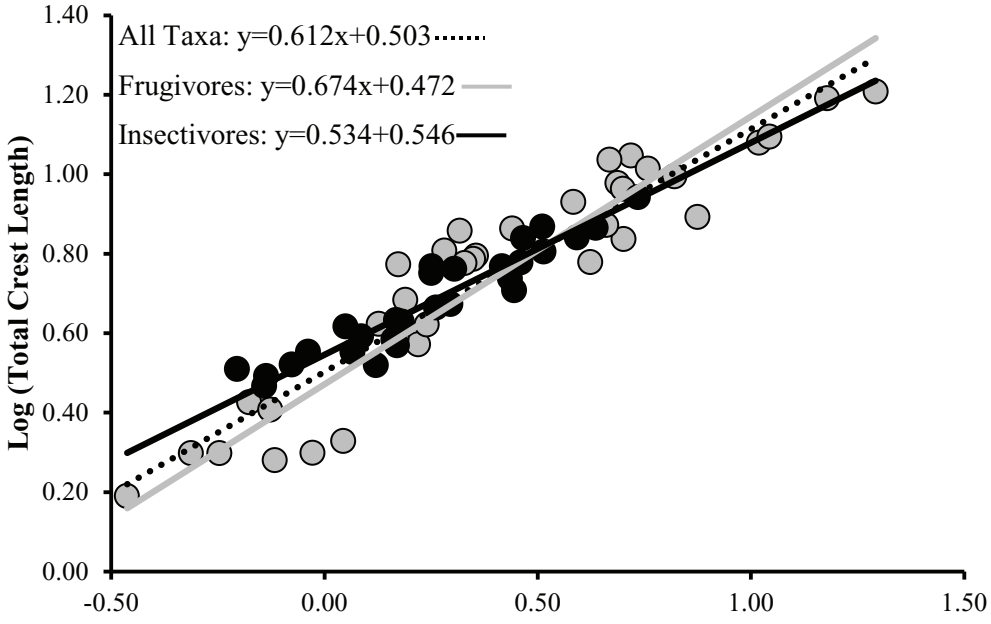
Second, however, if one accepts that the level of accuracy of these methods of dietary reconstruction are sufficient given the constraints of morphology-based analyses, then the results emphasize the importance of considering variation within larger dietary niches. In other words, there might be different ways for a "frugivore" to be a "frugivore." For instance, the frugivores included here supplement their diets with insects to different degrees, and within frugivory itself, variable amounts of ripe fruits, pollen, nectar, and flower parts may be eaten (see Appendix 4). This conclusion warrants further behavioral studies of the extent to which direct and indirect competition occurs among extant species sharing dietary resources and whether dental morphology reflects this process in any way. Additionally, increasing our knowledge of species' dietary niches within their communities, and how these niches are defined and classified, may resolve some of this disassociation. The difficulty in living communities, of course, is that we are observing the end results of millions of years of biotic interactions, culminating in possible equilibrium communities where competition and niche differentiation are at their minimum and maximum, respectively.

Third, as the value of dental morphology in the systematics of fossil taxa is well-known, by defining groups taxonomically in the genus-genus comparisons, the results may simply be reinforcing phylogenetic patterning within dietary categories when it is present. On the other hand, as the number of overlapping niches within dietary groups

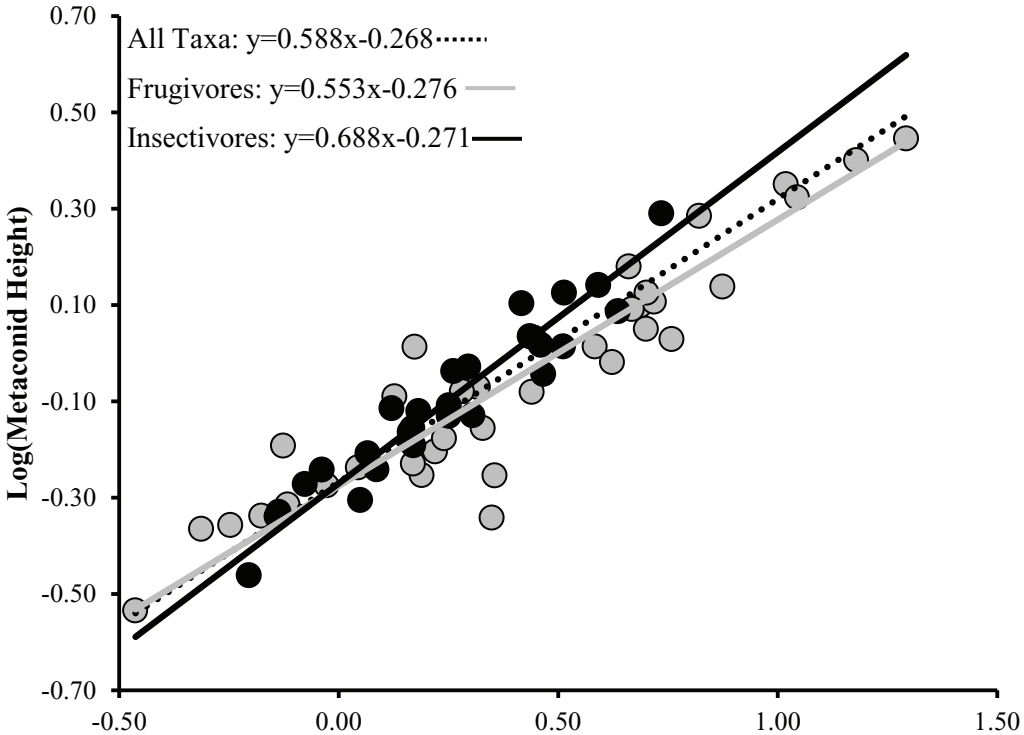
differs, these results may suggest that the strength of the phylogenetic, as compared to the ecological or functional, signal may be variable across dietary niches.

Therefore, one may ask if an examination of dental morphology at this level of detail is too specific to reconstruct dietary niches and their potential overlap in fossil taxa, and as a result, if we are constrained to general categories in defining shared food resource use among members of paleocommunities. Based on the results described above, it is clear that we can begin to make inferences of dietary niche overlap among taxa as long as we understand the limitations of doing so and take a conservative approach. Most importantly, if niche comparisons using the protocol presented here reveal very low significance values (i.e., high *p*-values), it is highly likely that niche overlap was present. These results can then be interpreted in conjunction with patterns of diversity and abundance and other aspects of the ecological niche (e.g., habitat use, activity pattern, substrate preference) to make the most informed decision regarding the likelihood (and impact) of competitive interactions among fossil species. These will all be considered in the subsequent chapters.

Finally, despite non-overlapping sets of dietary groups, the same morphological variables differentiated among dietary groups across both extant samples. However, when it could be used, Variable Sets 1 and 3 performed better overall than the reduced set of variables composing Variable Set 2. Although all taxa within the fossil sample possess molar morphologies that enable calculation of the variables in Variable Set 3, this is not true of Variable Set 1. Thus, to maximize the inclusion of multiple molar forms, Variable Set 3 was used in the analysis of the fossil sample.


All Taxa: y=0.612x+0.503
Frugivores: y=0.674x+0.472
Insectivores: y=0.534+0.546
Log (Total Crest Length)
1.40
1.20
1.00
0.80
0.60
0.40
0.20
0.00
-0.50
0.00
0.50
1.00
1.50
Log(Molar Area1/2)

A.


All Taxa: y=0.588x-0.268
Frugivores: y=0.553x-0.276
Insectivores: y=0.688x-0.271
Log(Metaconid Height)
0.70
0.50
0.30
0.10
-0.10
-0.30
-0.50
-0.70
-0.50
0.00
0.50
1.00
1.50
Log(Molar Area1/2)

B.

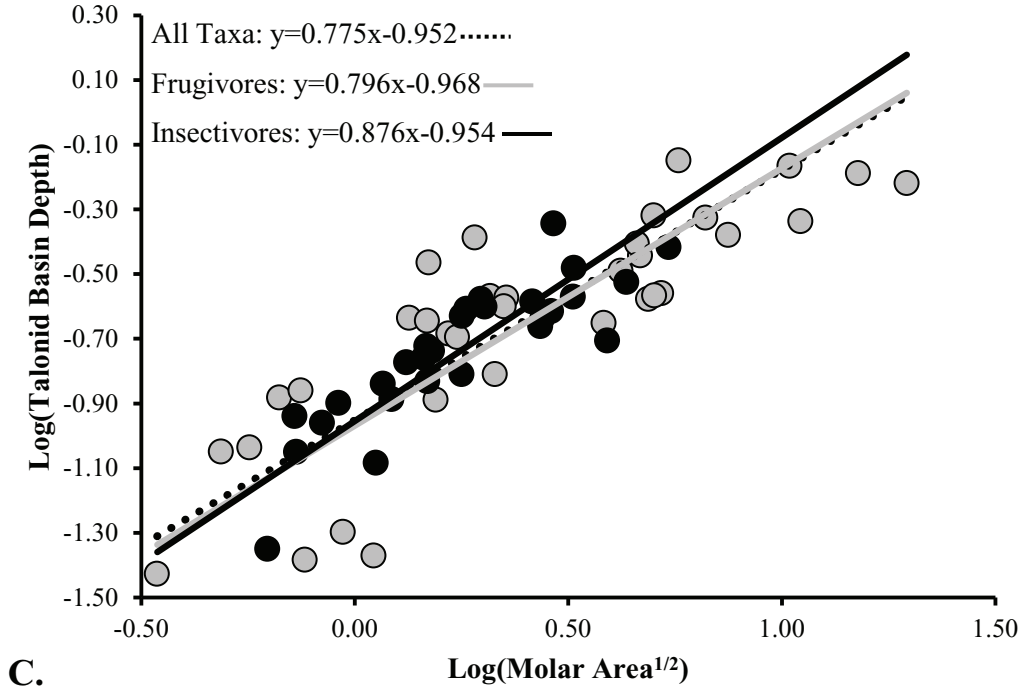
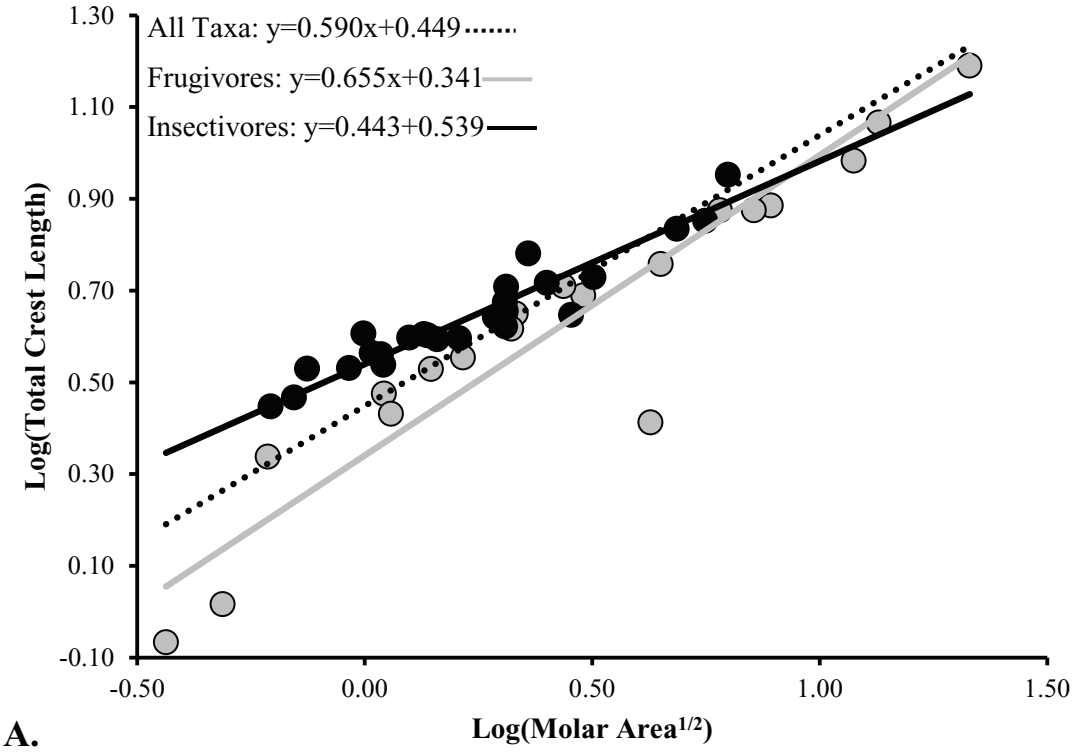
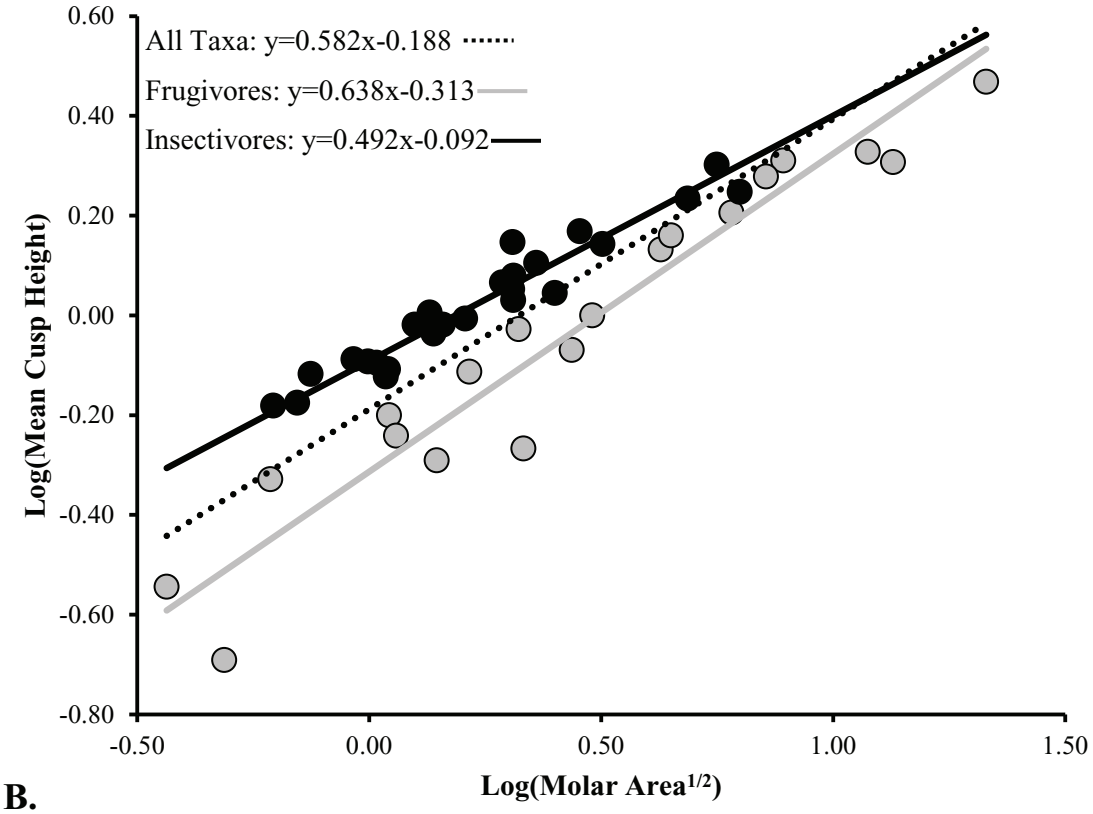


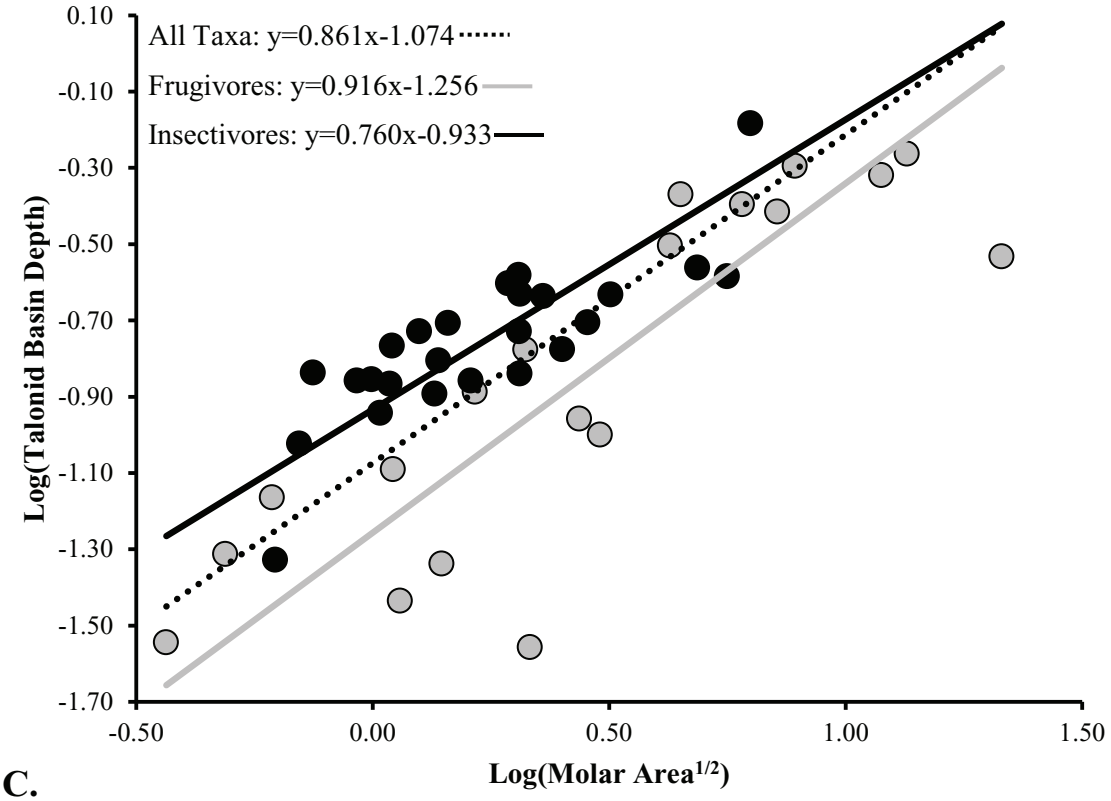
Figure 5.1. Scaling of variables identified as allometric in the Balta sample. Gray circles are "frugivore" individuals; gray line is the RMA regression line for frugivores only. Black circles are "insectivore" individuals; black line is the RMA regression line for insectivores only. Black dotted line is the RMA regression line for the entire sample ("frugivores" and "insectivores" combined). Slopes correspond to Tables 5.2 and 5.5.


All Taxa: y=0.590x+0.449
Frugivores: y=0.655x+0.341
Insectivores: y=0.443+0.539
Log(Total Crest Length)
Log(Molar Area1/2)
1.30
1.10
0.90
0.70
0.50
0.30
0.10
-0.10
-0.50
0.00
0.50
1.00
1.50

A.

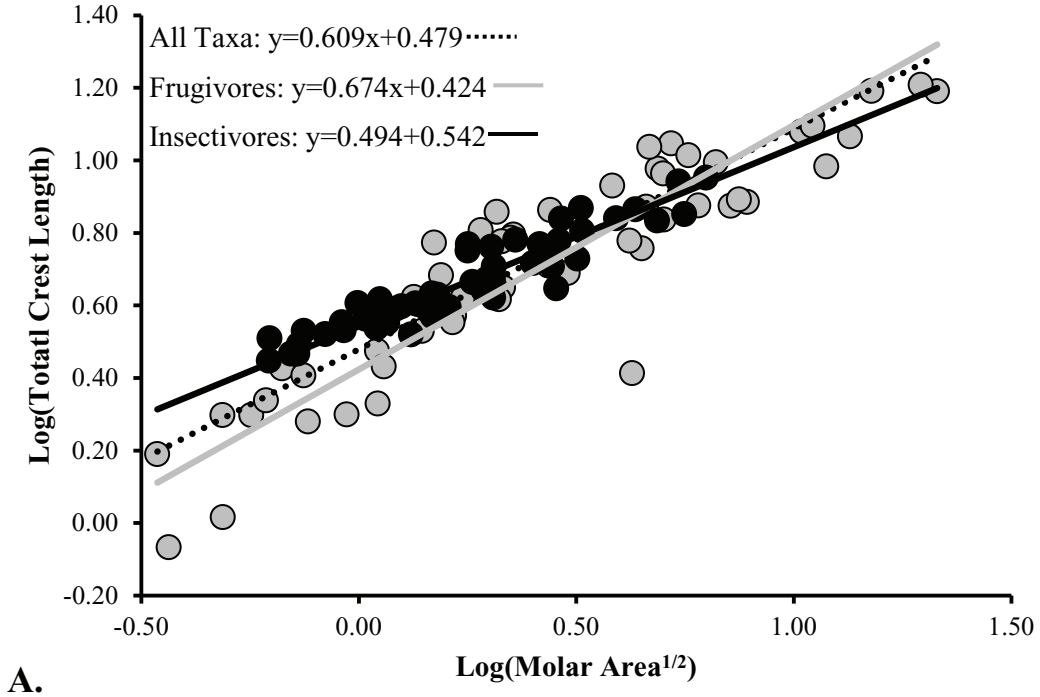

All Taxa: y=0.582x-0.188
Frugivores: y=0.638x-0.313
Insectivores: y=0.492x-0.092
Log(Mean Cusp Height)
Log(Molar Area1/2)
0.60
0.40
0.20
0.00
-0.20
-0.40
-0.60
-0.80
-0.50
0.00
0.50
1.00
1.50

B.

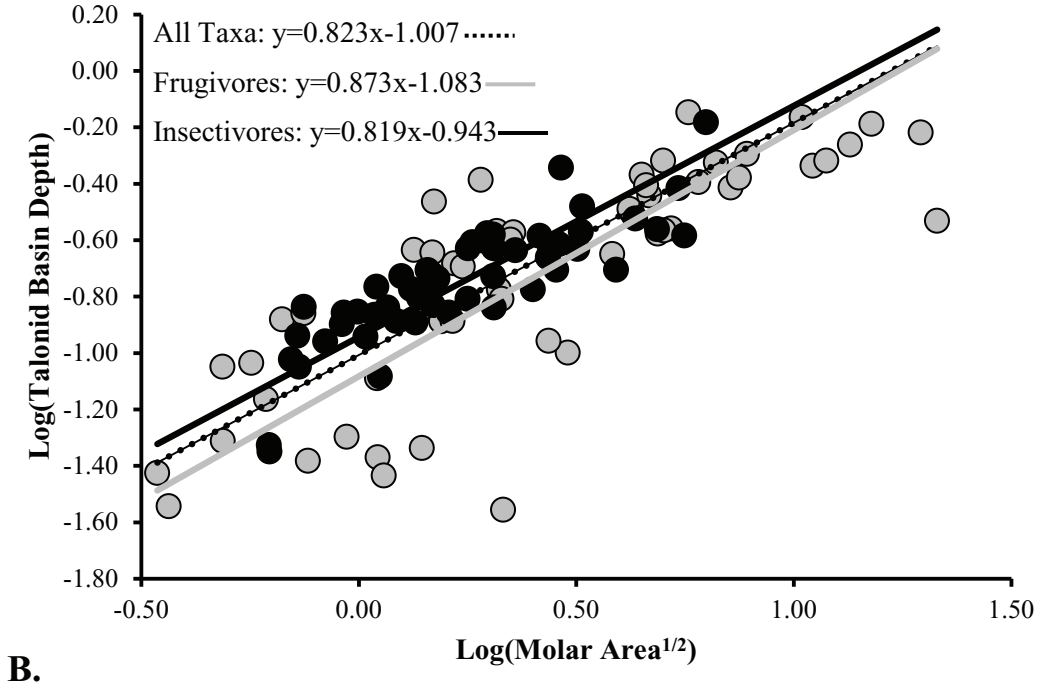


C.

Figure 5.2. Scaling of variables identified as allometric in the Mindanao sample. Gray circles are "frugivore" individuals; gray line is the RMA regression line for frugivores only. Black circles are "insectivore" individuals; black line is the RMA regression line for insectivores only. Black dotted line is the RMA regression line for the entire sample ("frugivores" and "insectivores" combined). Slopes correspond to Tables 5.3 and 5.6.



A.



B.

Figure 5.3. Scaling of variables identified as allometric in the combined Balta-Mindanao sample. Gray circles are "frugivore" individuals; gray line is the RMA regression line for frugivores only. Black circles are "insectivore" individuals; black line is the RMA regression line for insectivores only. Black dotted line is the RMA regression line for the entire sample ("frugivores" and "insectivores" combined). Slopes correspond to Tables 5.4 and 5.7.

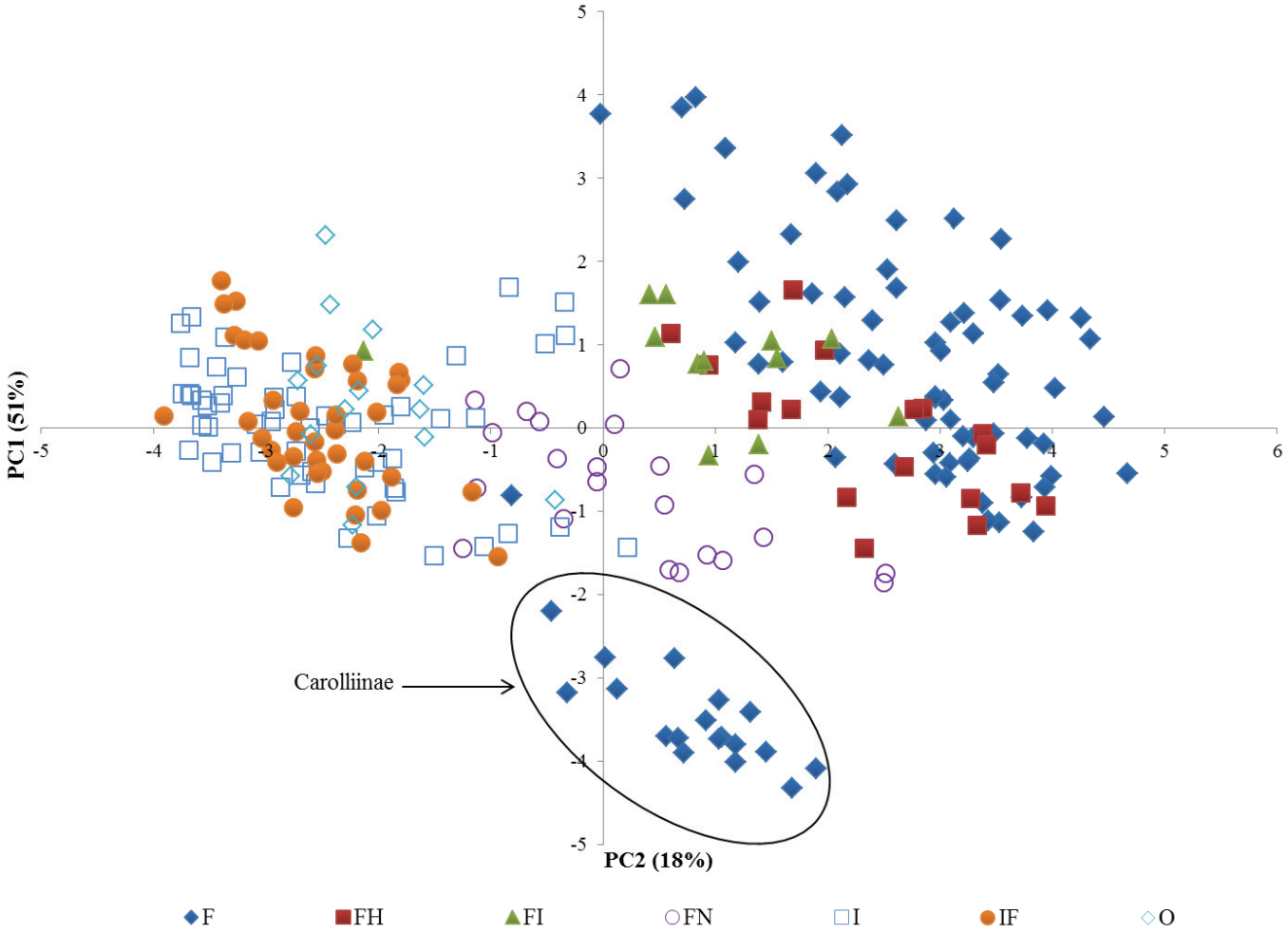


Figure 5.4. Plot of PC1 and PC2 for Variable Set 1 of the Balta sample. Each symbol corresponds to an individual specimen.

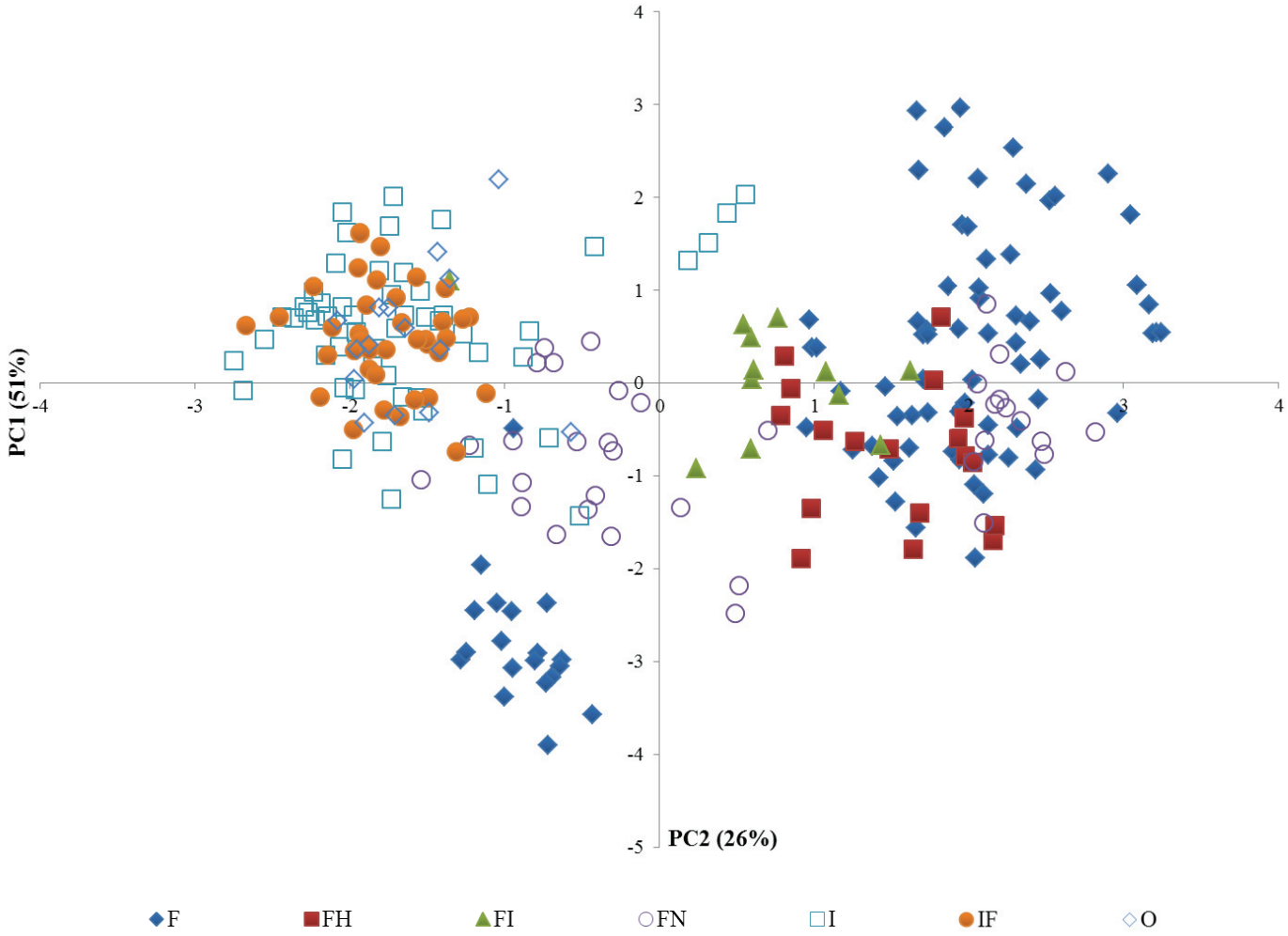


Figure 5.5. Plot of PC1 and PC2 for Variable Set 2 of the Balta sample. Note that the frugivore-nectarivores clustered within the frugivore group are sturnirins, comprising the least nectarivorous species within the frugivore-nectarivore group.

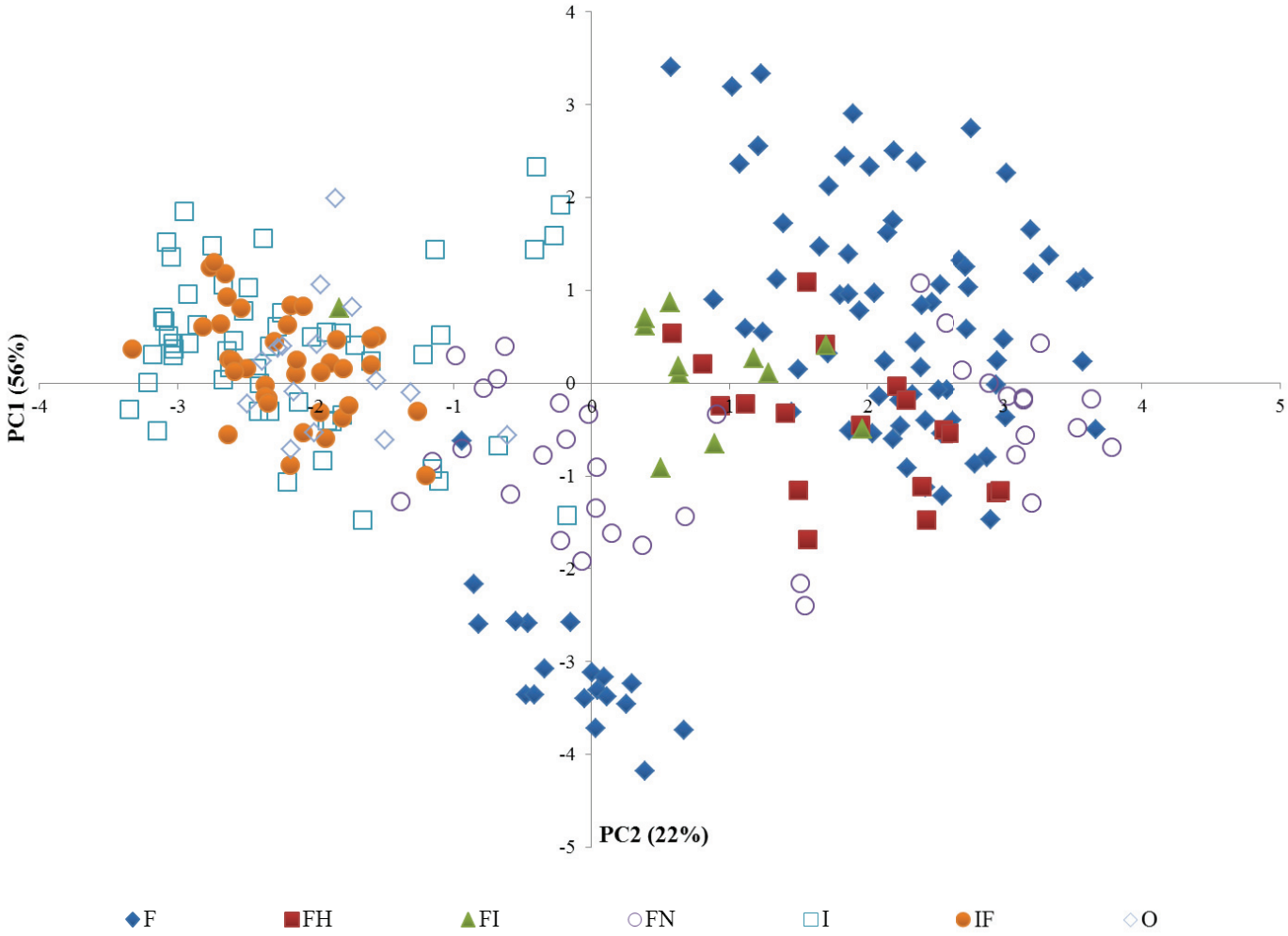


Figure 5.6. Plot of PC1 and PC2 for Variable Set 3 of the Balta sample.

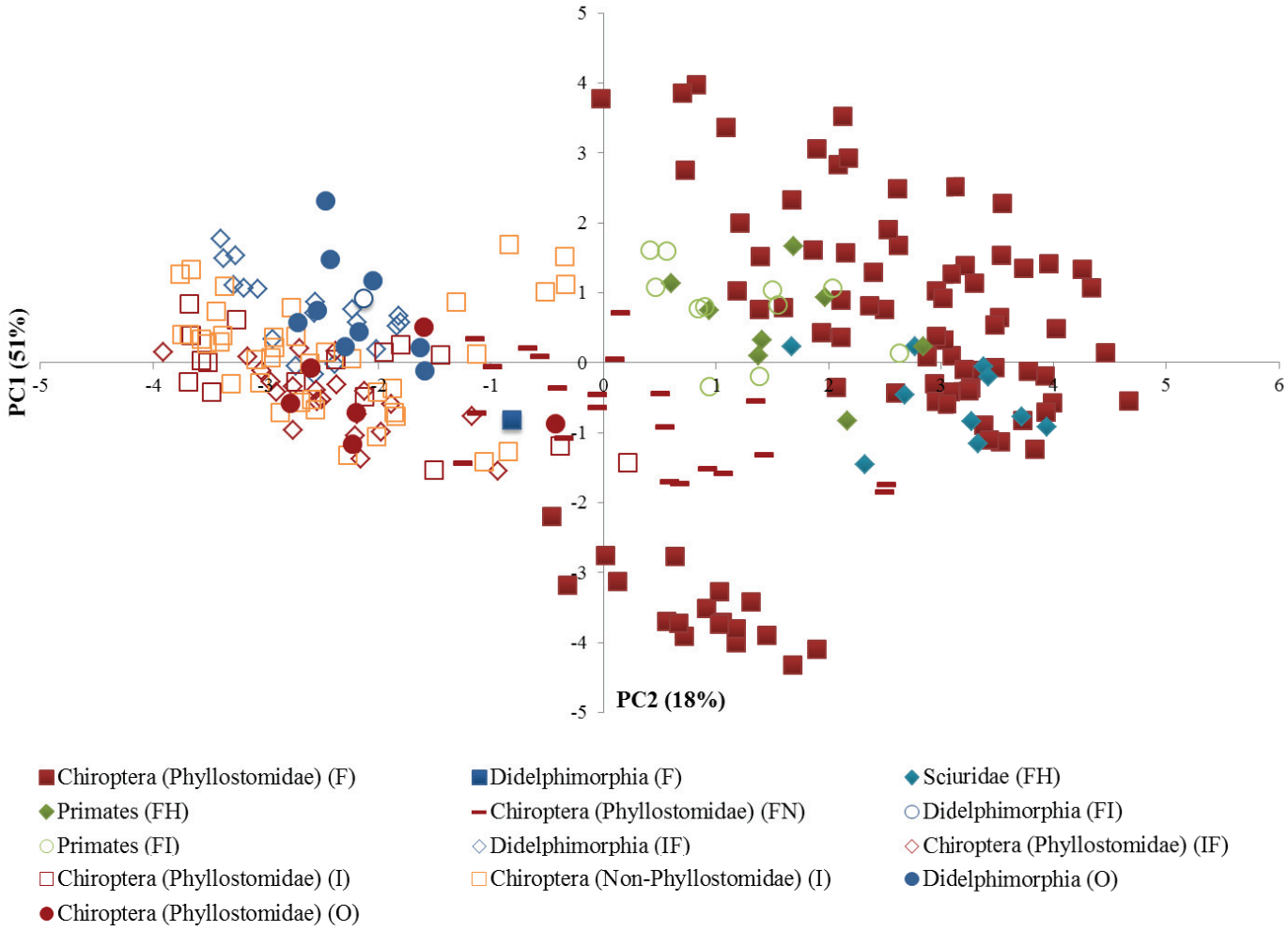


Figure 5.7. Plot of PC1 and PC2 for Variable Set 1 of the Balta sample, indicating phylogenetic affinity of each specimen.

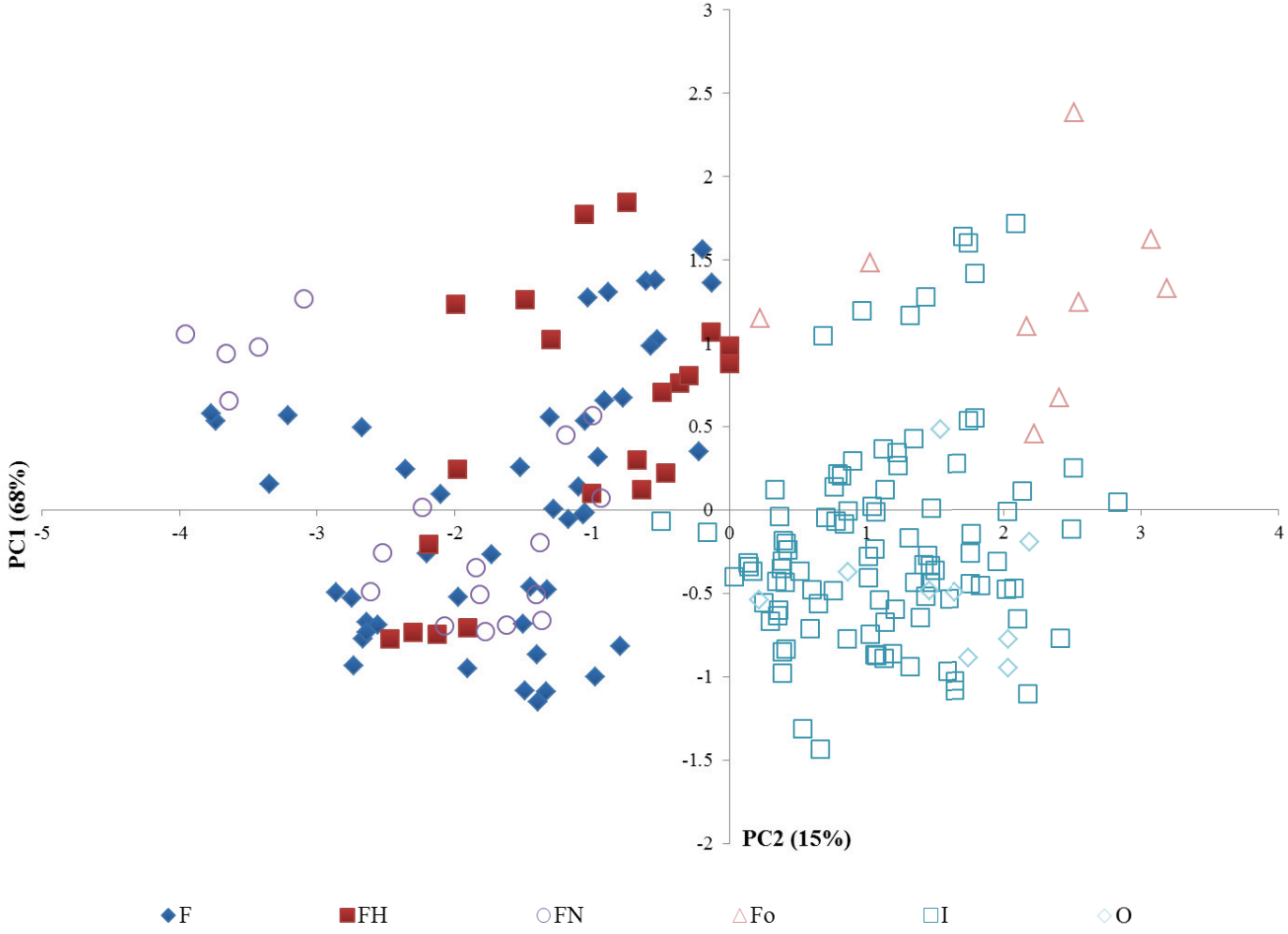


Figure 5.8. Plot of PC1 and PC2 for Variable Set 2* of the Mindanao sample.

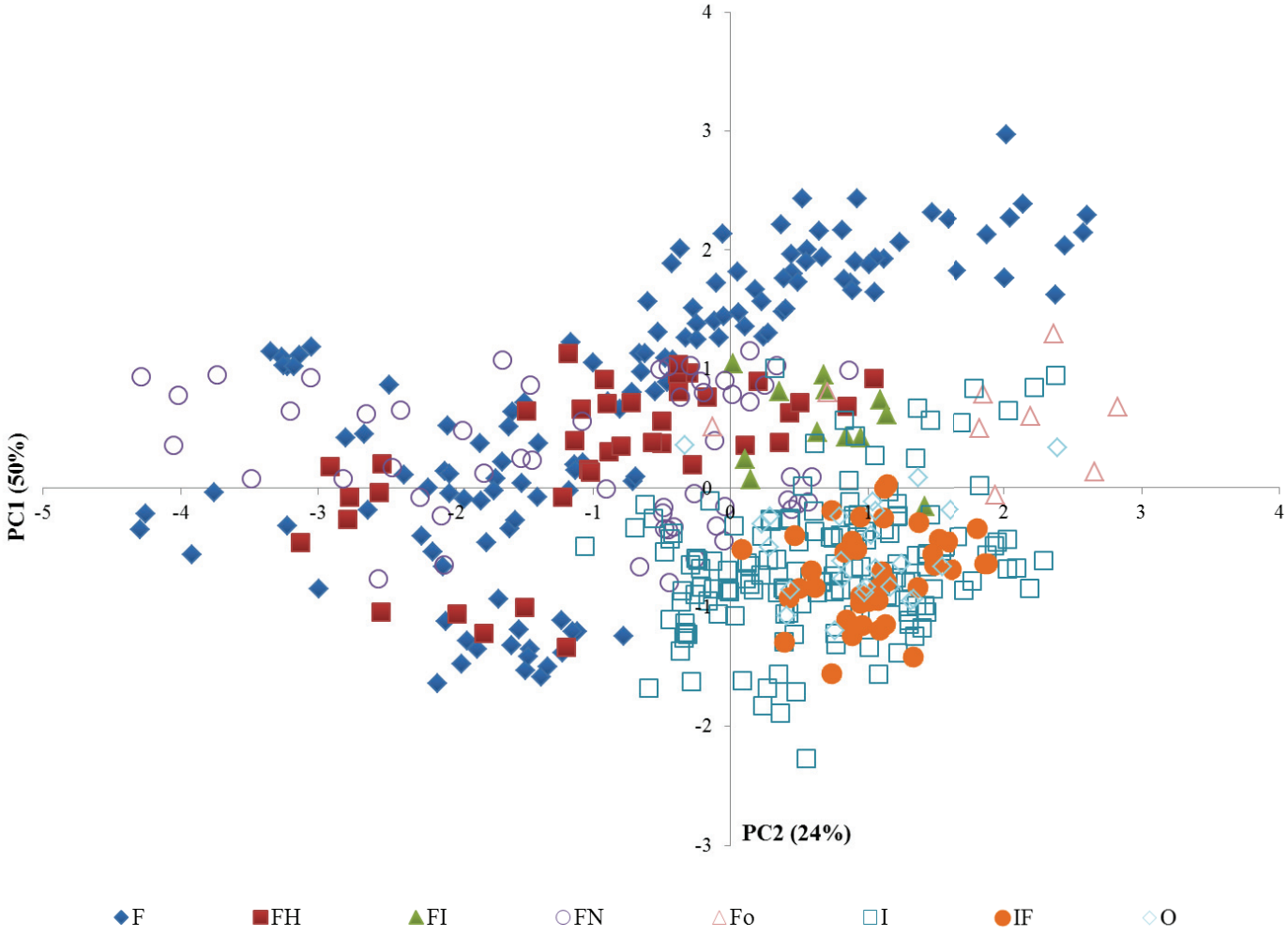


Figure 5.9. Plot of PC1 and PC2 for Variable Set 2* of the combined Balta-Mindanao sample.

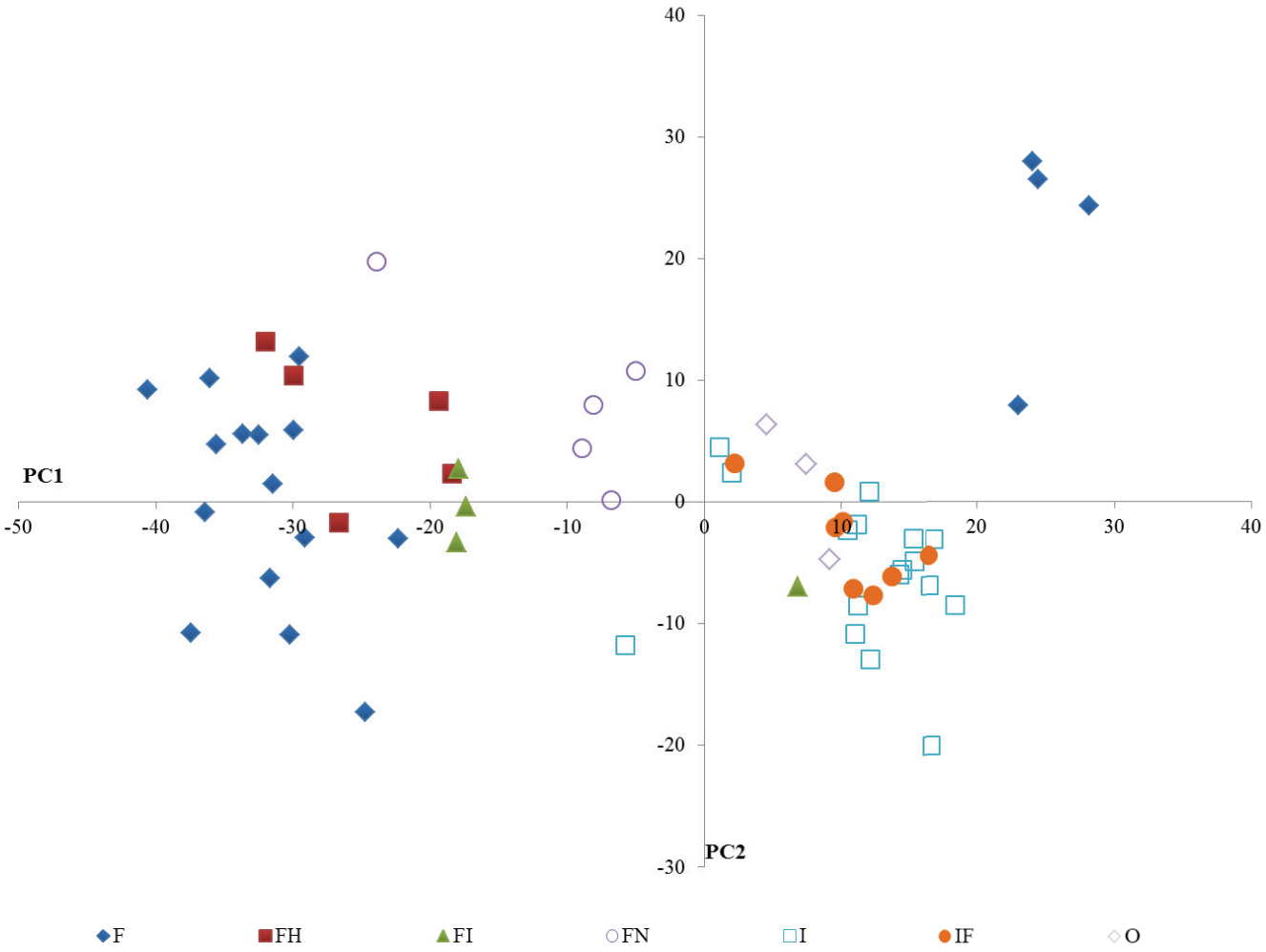


Figure 5.10. Plot of PC1 and PC2 for Variable Set 3 of the Balta sample using a phylogenetic principal component analysis.

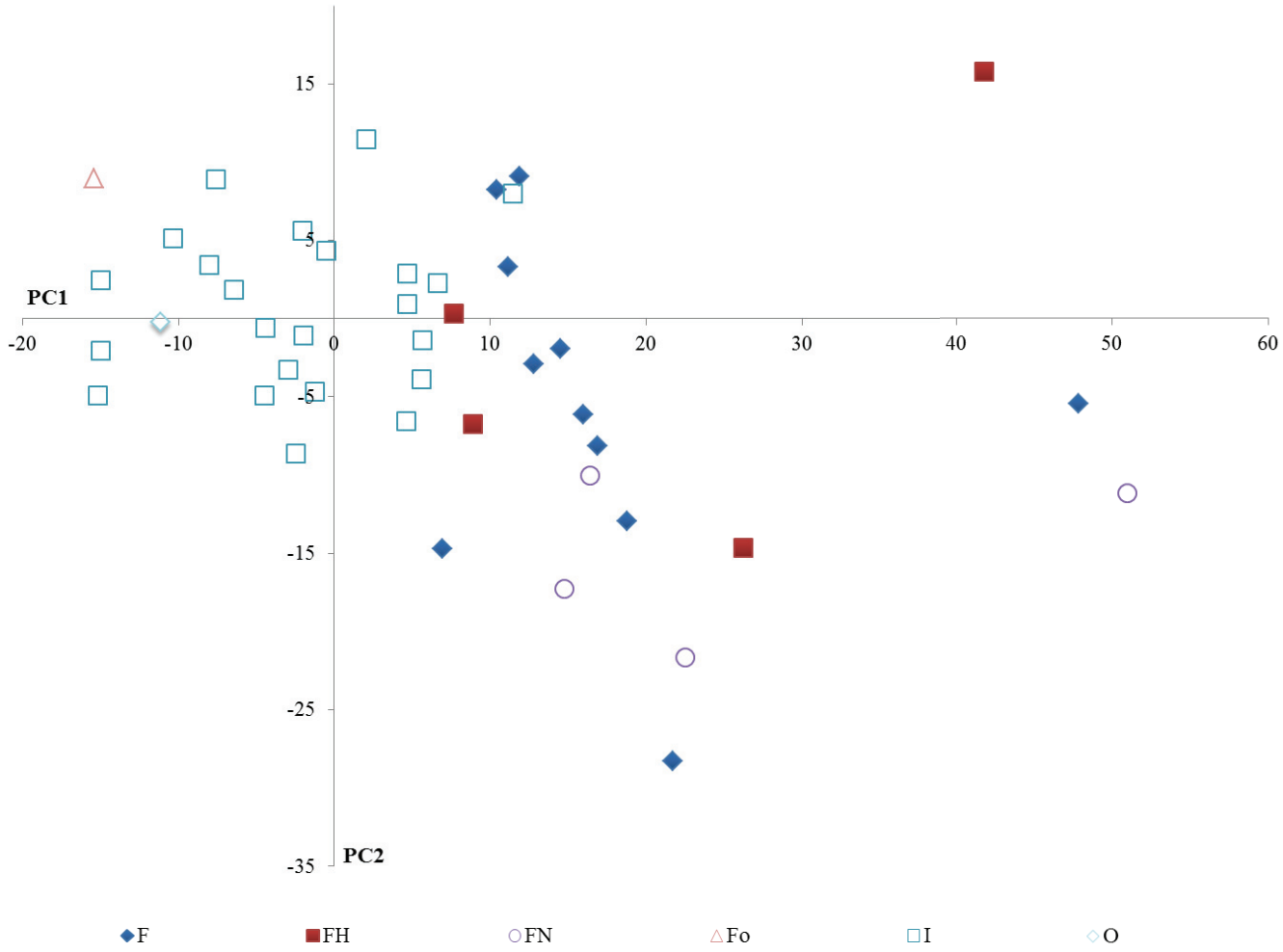


Figure 5.11. Plot of PC1 and PC2 for Variable Set 2* of the Mindanao sample using a phylogenetic principal component analysis.

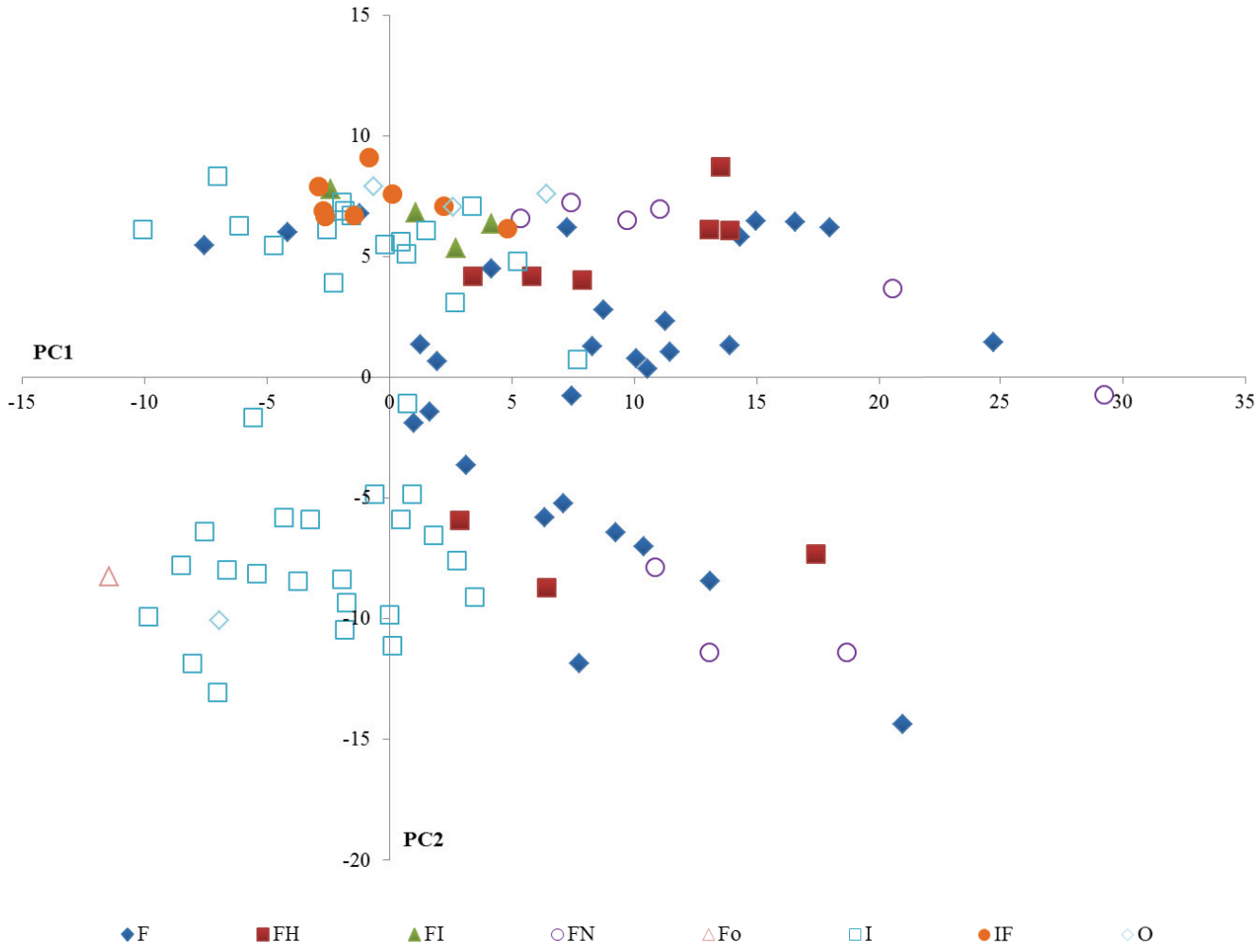
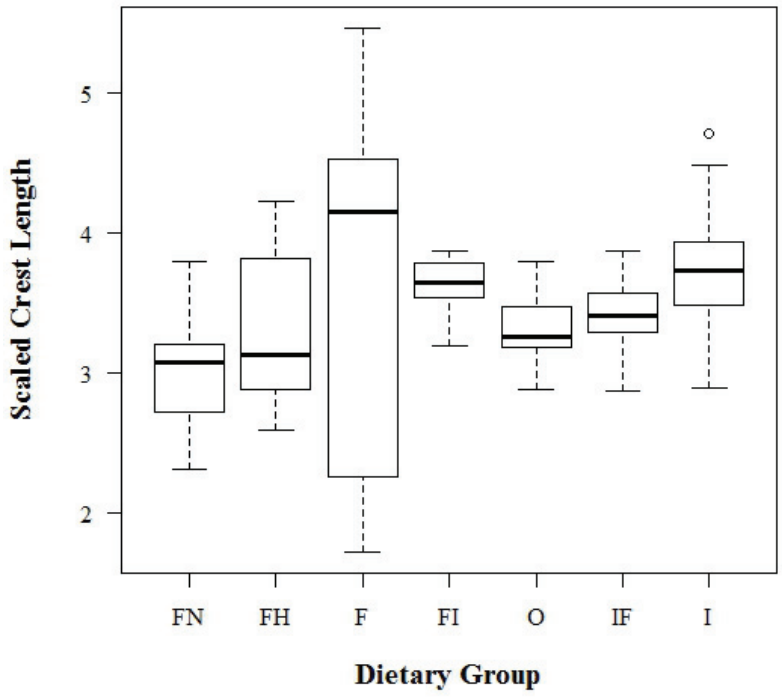
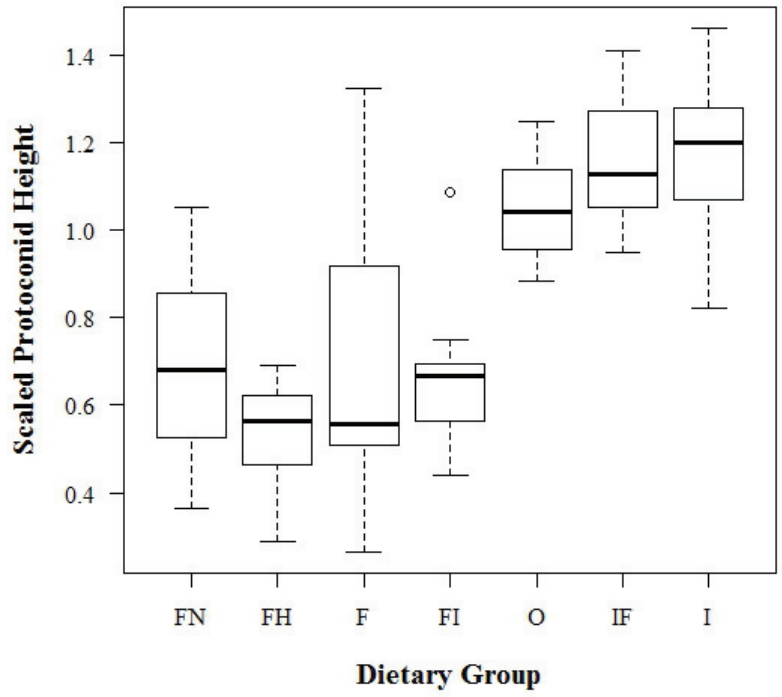


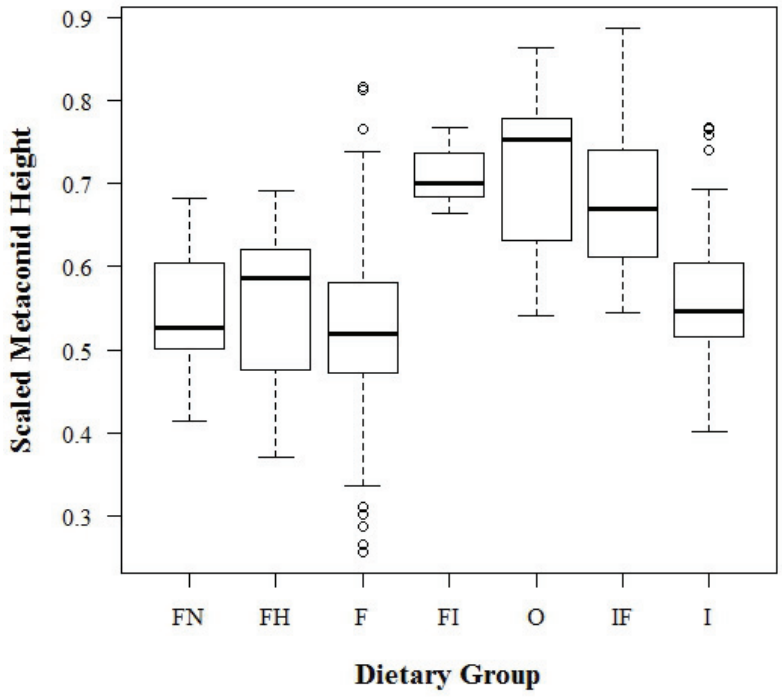
Figure 5.12. Plot of PC1 and PC2 for Variable Set 2* of the combined Balta-Mindanao sample using a phylogenetic principal component analysis.


Scaled Crest Length
5
4
3
2
FN
FH
F
FI
O
IF
I
Dietary Group

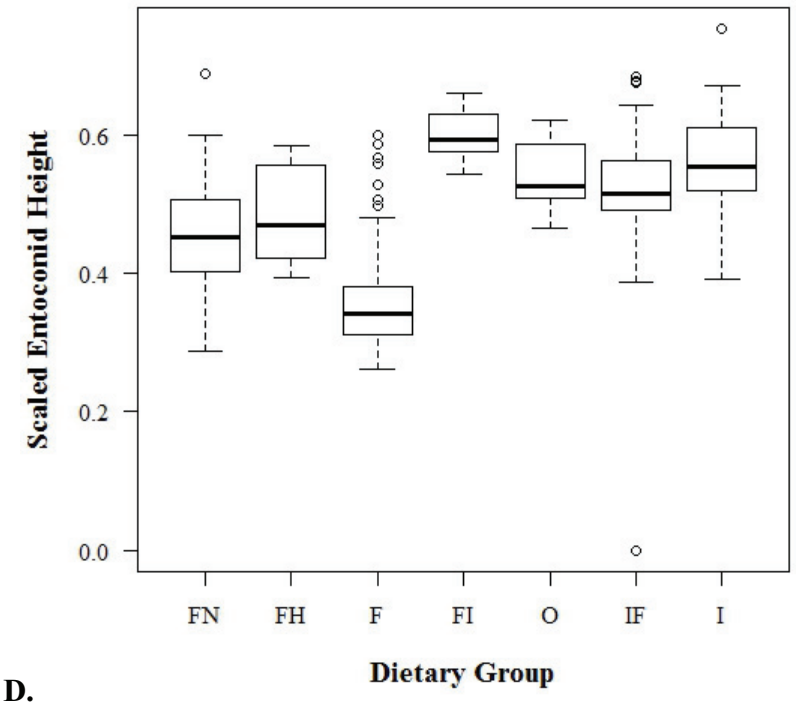
A.


Scaled Protoconid Height
1.4
1.2
1.0
0.8
0.6
0.4
FN
FH
F
FI
O
IF
I
Dietary Group

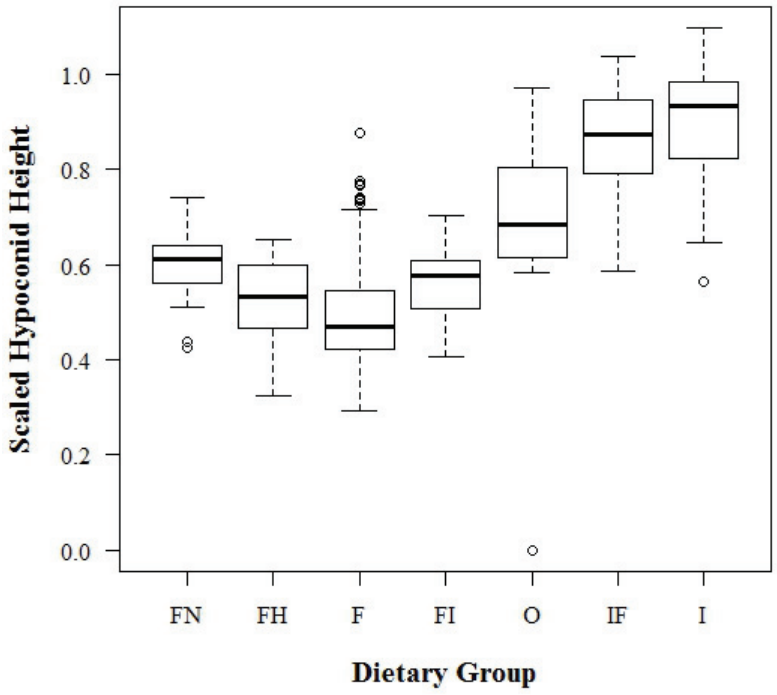
B.


Scaled Metaconid Height
0.9
0.8
0.7
0.6
0.5
0.4
0.3
FN
FH
F
FI
O
IF
I
Dietary Group

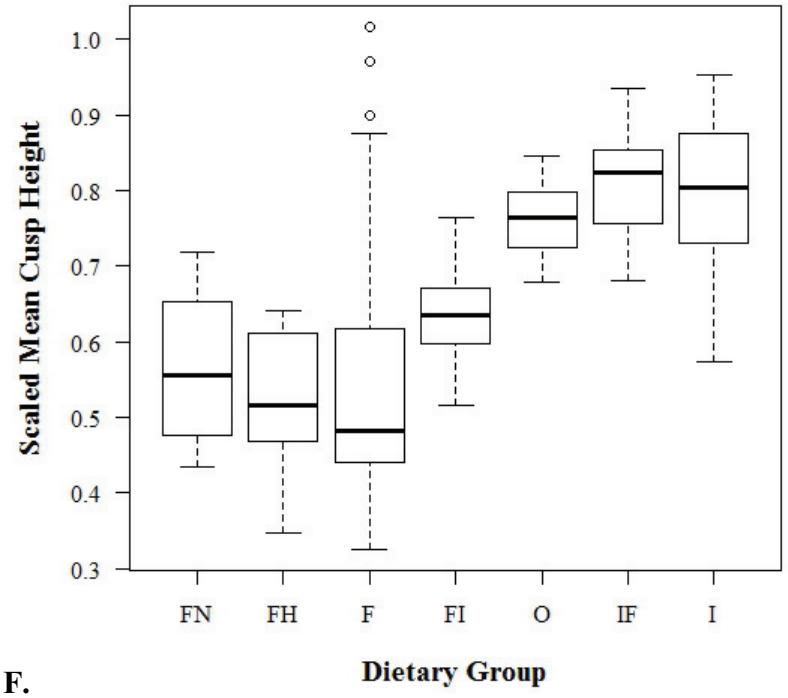
C.


Scaled Entoconid Height
0.6
0.4
0.2
0.0
FN
FH
F
FI
O
IF
I
Dietary Group

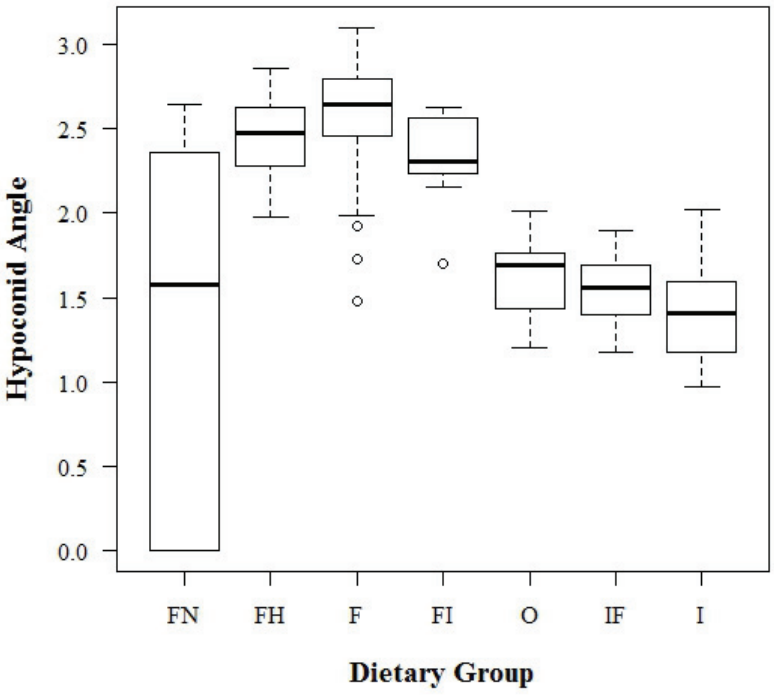
D.


Scaled Hypoconid Height
1.0
0.8
0.6
0.4
0.2
0.0
FN
FH
F
FI
O
IF
I
Dietary Group

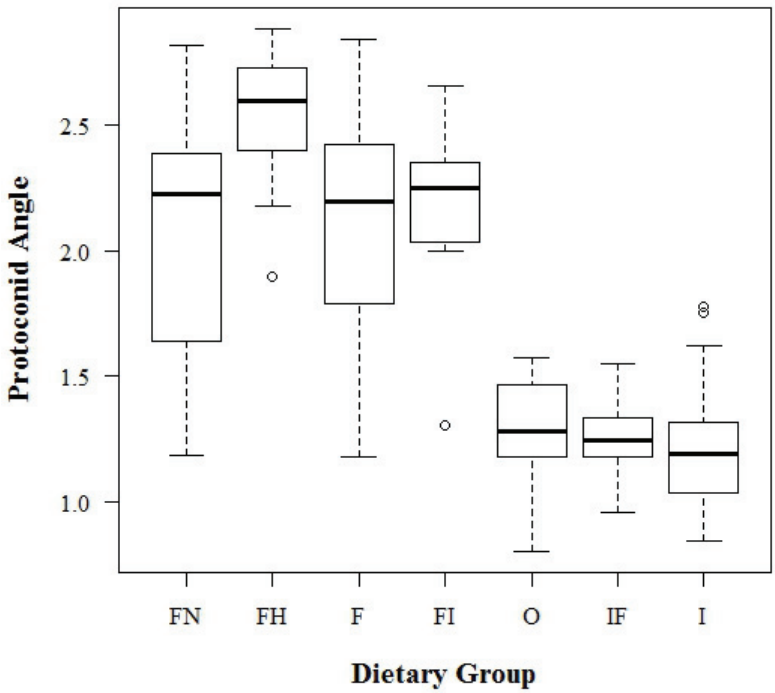
E.


Scaled Mean Cusp Height
1.0
0.9
0.8
0.7
0.6
0.5
0.4
0.3
FN
FH
F
FI
O
IF
I
Dietary Group

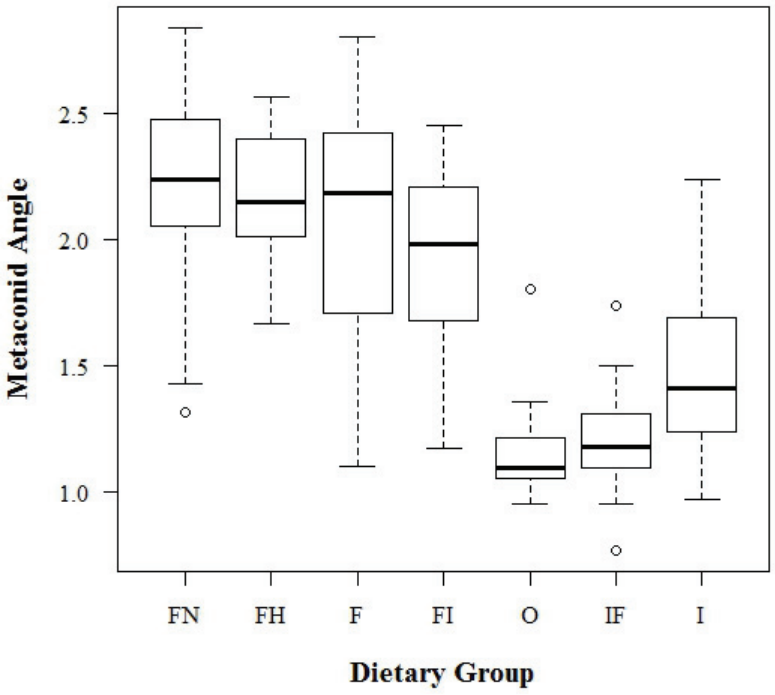
F.


Hypoconid Angle
3.0
2.5
2.0
1.5
1.0
0.5
0.0
FN
FH
F
FI
O
IF
I
Dietary Group

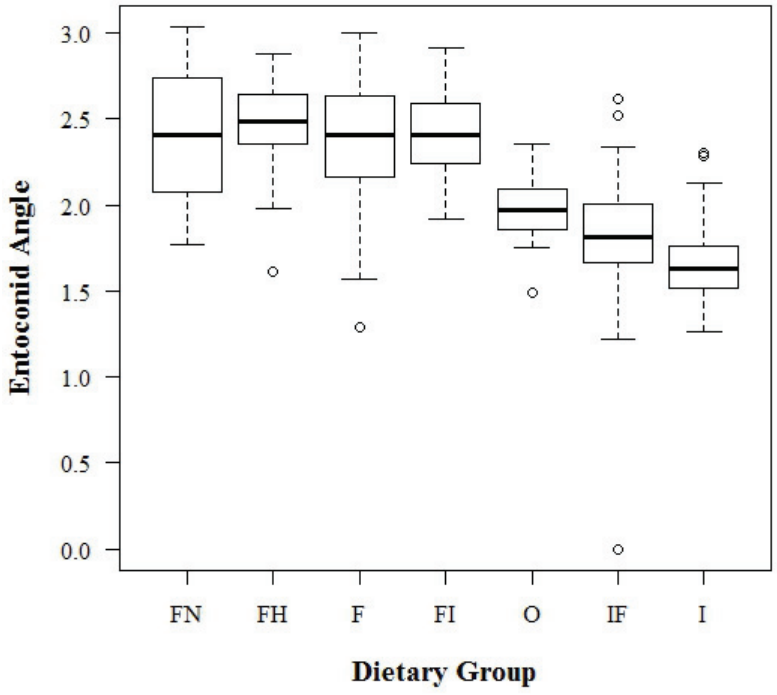
G.


Protoconid Angle
2.5
2.0
1.5
1.0
FN
FH
F
FI
O
IF
I
Dietary Group

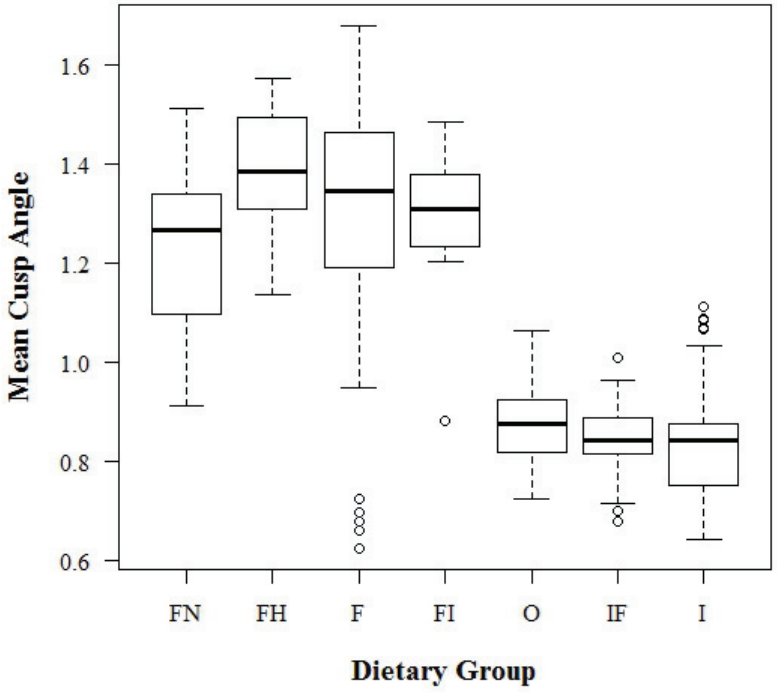
H.


Metaconid Angle
2.5
2.0
1.5
1.0
FN
FH
F
FI
O
IF
I
Dietary Group

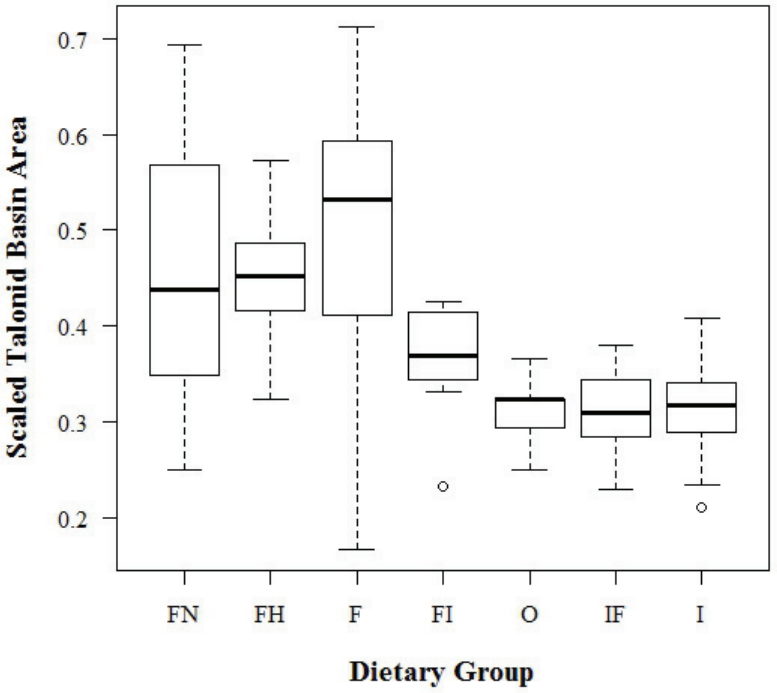
I.


Entoconid Angle
3.0
2.5
2.0
1.5
1.0
0.5
0.0
FN
FH
F
FI
O
IF
I
Dietary Group

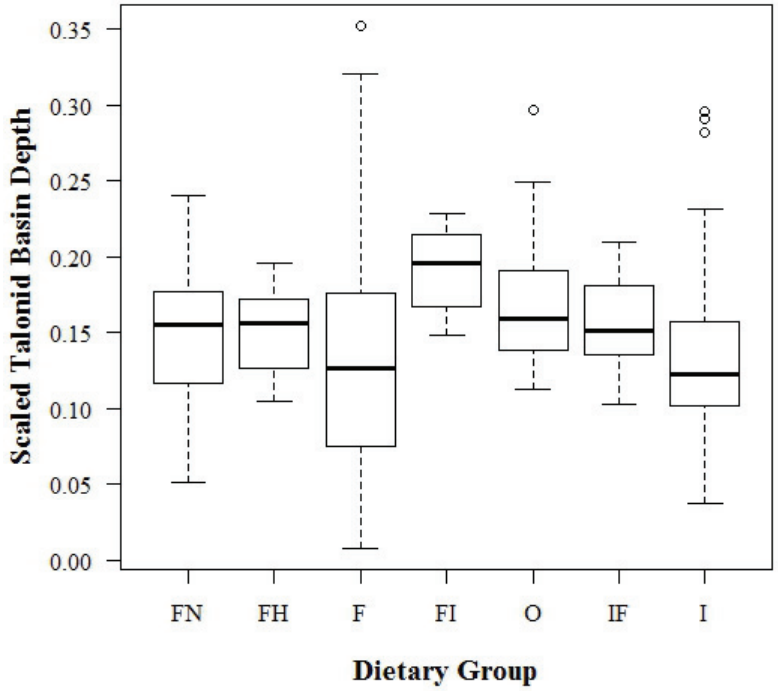
J.


Mean Cusp Angle
1.6
1.4
1.2
1.0
0.8
0.6
FN
FH
F
FI
O
IF
I
Dietary Group

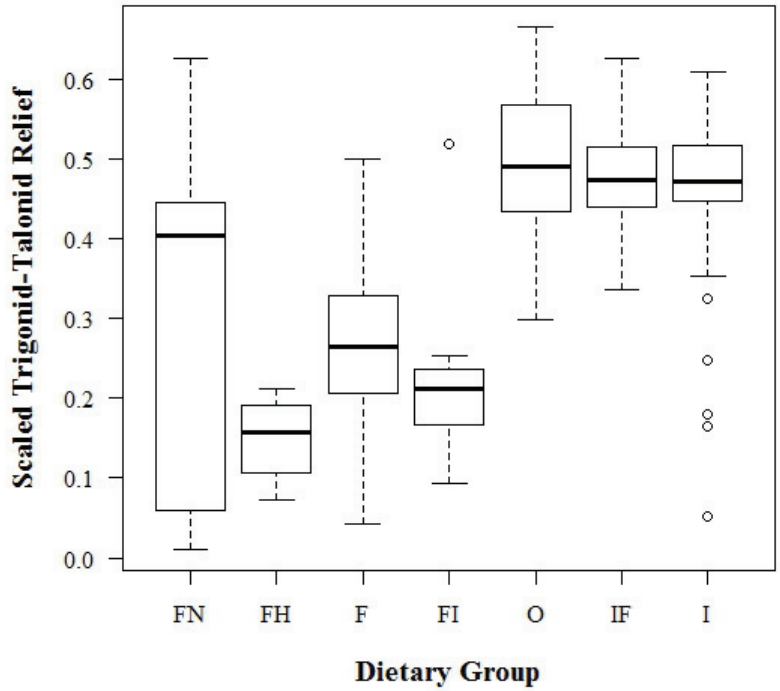
K.


Scaled Talonid Basin Area
0.7
0.6
0.5
0.4
0.3
0.2
FN
FH
F
FI
O
IF
I
Dietary Group

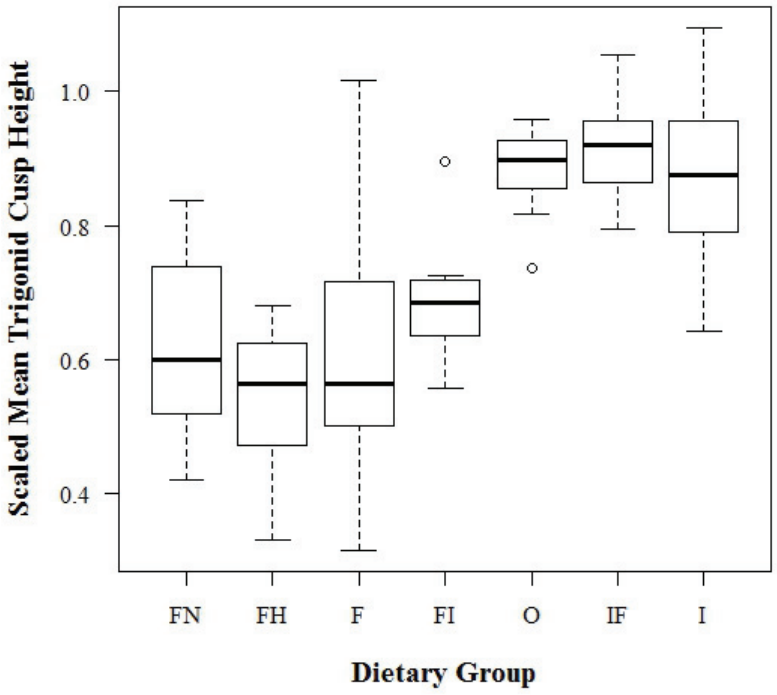
L.


Scaled Talonid Basin Depth
0.35
0.30
0.25
0.20
0.15
0.10
0.05
0.00
FN
FH
F
FI
O
IF
I
Dietary Group

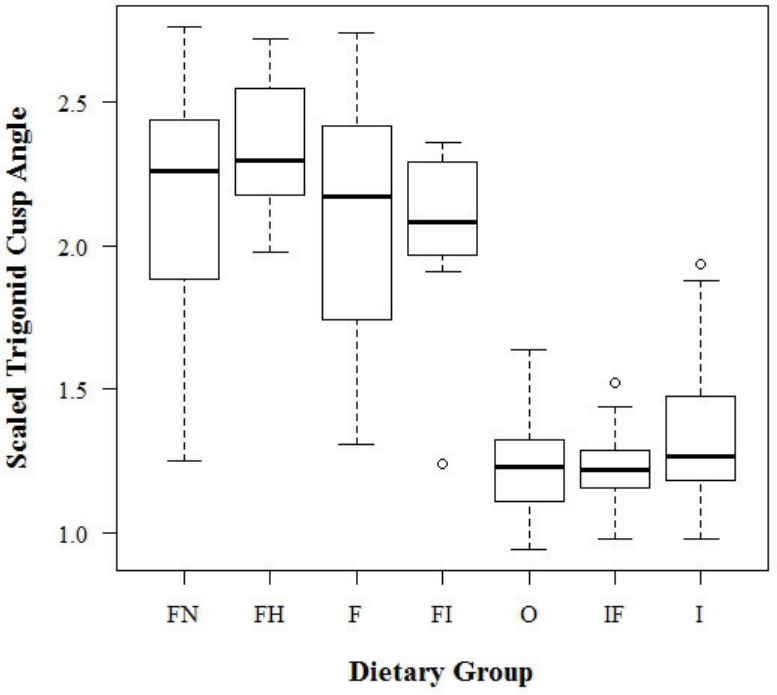
M.


Scaled Trigonid-Talonid Relief
0.6
0.5
0.4
0.3
0.2
0.1
0.0
FN
FH
F
FI
O
IF
I
Dietary Group

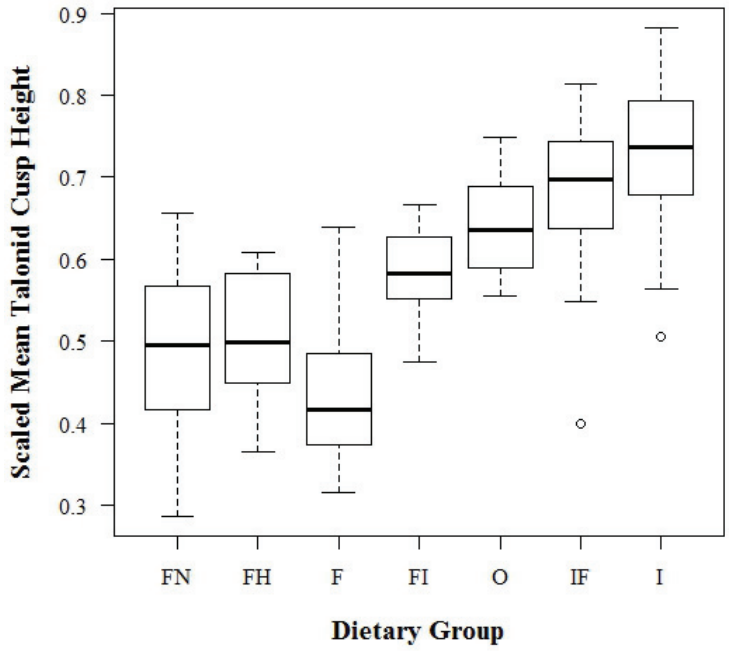
N.


Scaled Mean Trigonid Cusp Height
1.0
0.8
0.6
0.4
FN
FH
F
FI
O
IF
I
Dietary Group

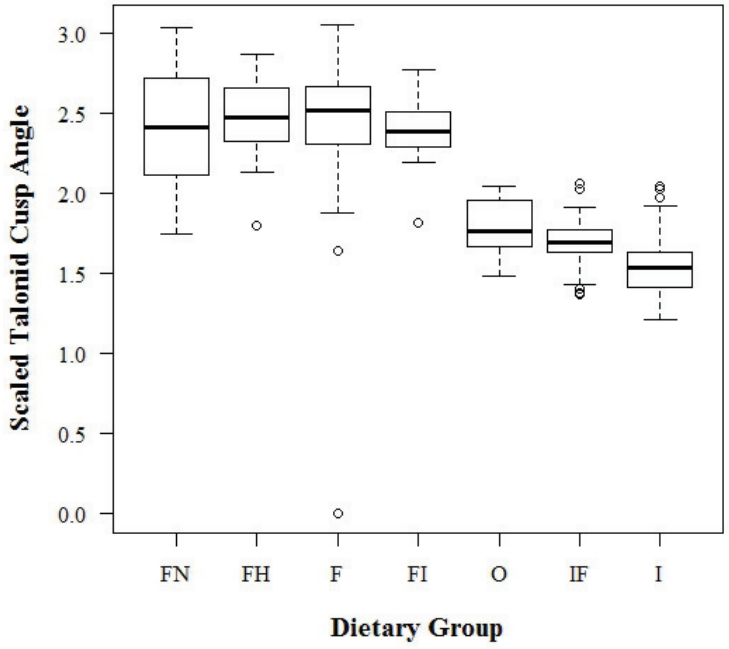
O.


Scaled Trigonid Cusp Angle
2.5
2.0
1.5
1.0
FN
FH
F
FI
O
IF
I
Dietary Group

P.

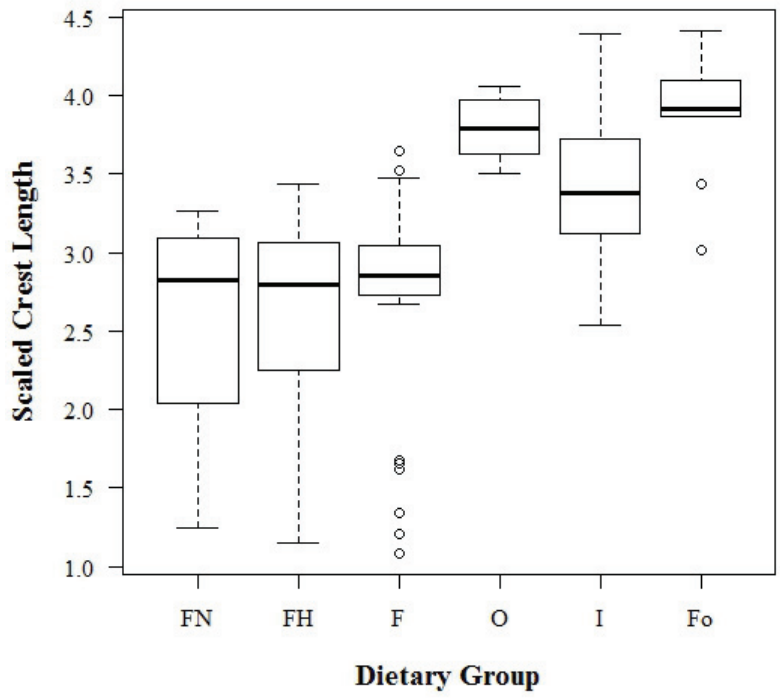


Q.

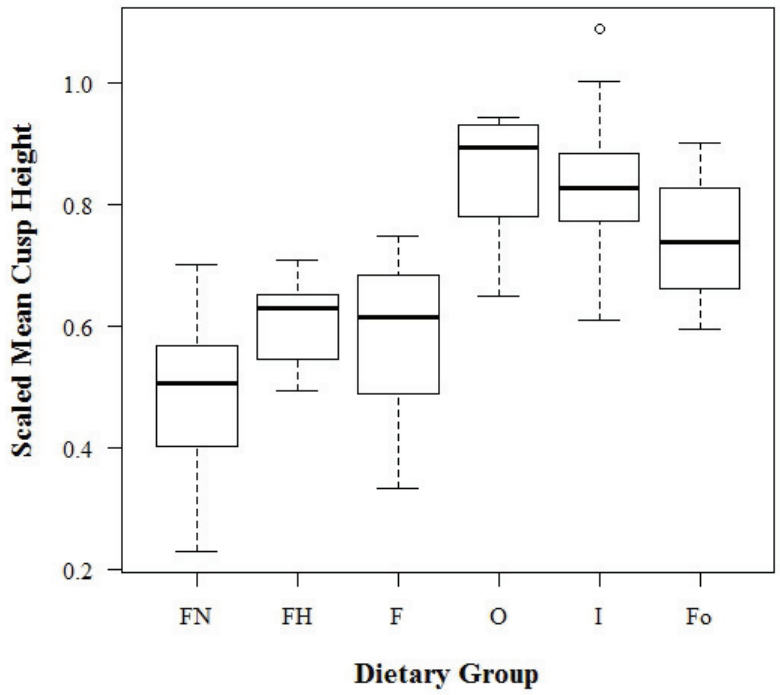


R.

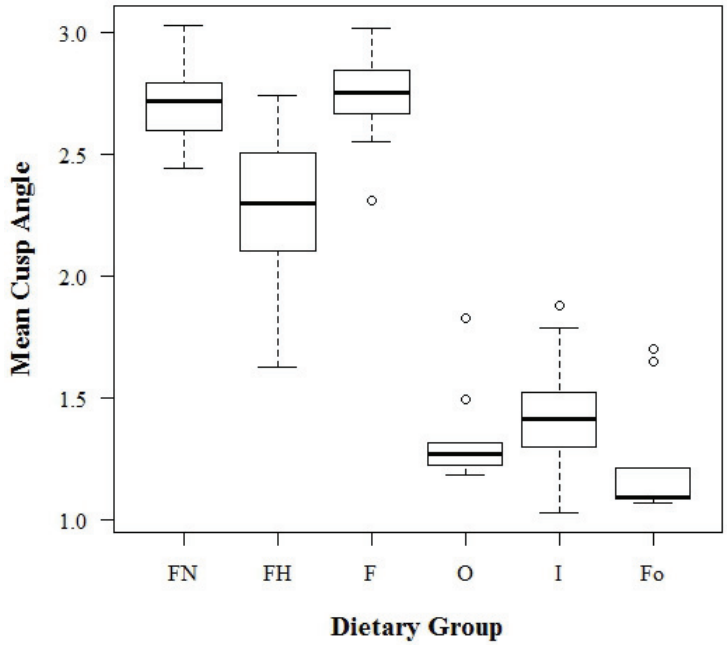
Figure 5.13. Box plots of each variable for Dietary Group 2 of the Balta sample. Angle values are in radians. Dietary codes are: FN=Frugivore-nectarivore, FH= Hard-object frugivore, F=Frugivore, FI=Frugivore-insectivore, O=Omnivore, IF=Insectivore-frugivore, I=Insectivore.


Scaled Crest Length
4.5
4.0
3.5
3.0
2.5
2.0
1.5
1.0
FN
FH
F
O
I
Fo
Dietary Group

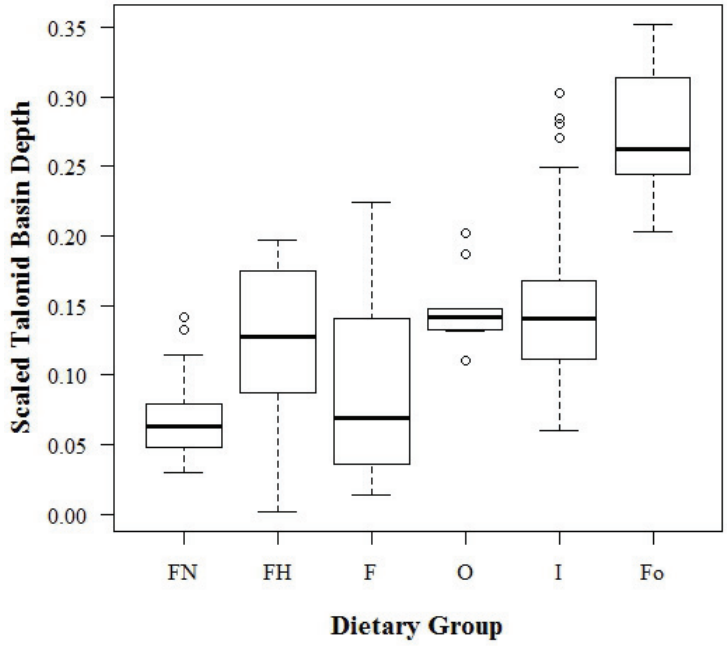
A.


Scaled Mean Cusp Height
1.0
0.8
0.6
0.4
0.2
FN
FH
F
O
I
Fo
Dietary Group

B.

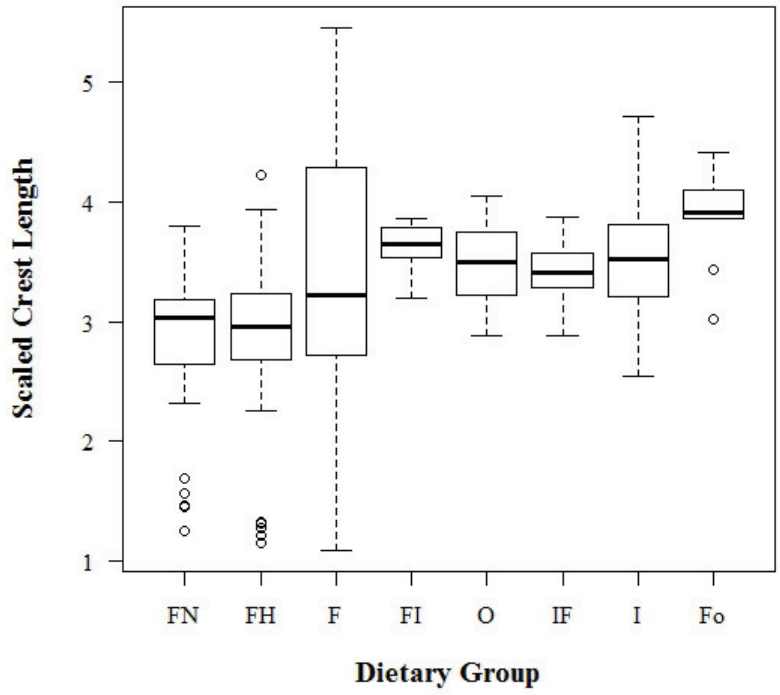


C.

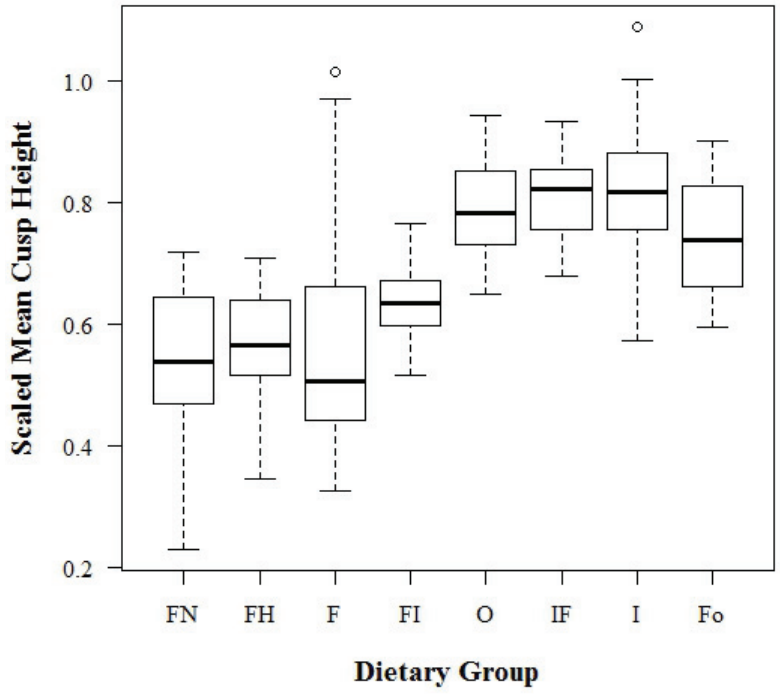


D.

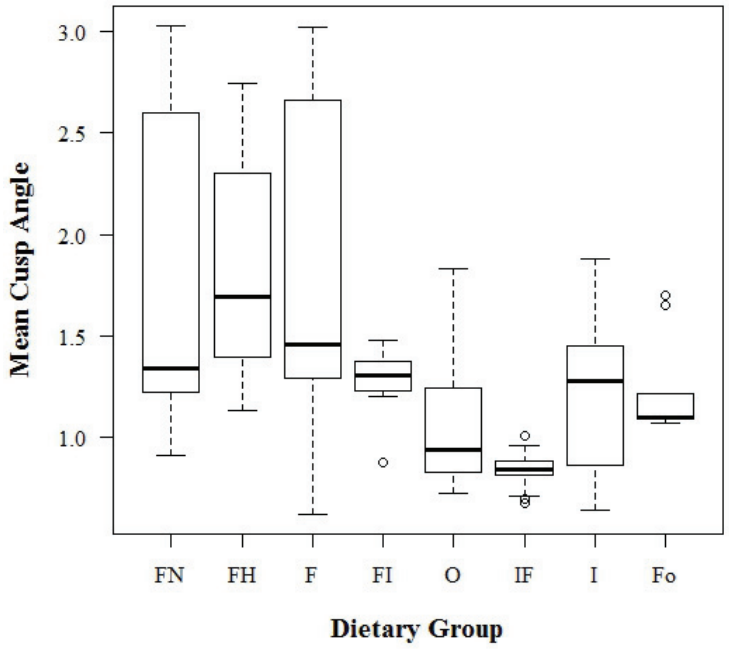
Figure 5.14. Box plots of each variable for Dietary Group 2 of the Mindanao sample. Angle values are in radians. Dietary codes are: FN=Frugivore-nectarivore, FH= Hard-object frugivore, F=Frugivore, O=Omnivore, I=Insectivore, Fo=Folivore.


Scaled Crest Length
5
4
3
2
1
FN
FH
F
FI
O
IF
I
Fo
Dietary Group

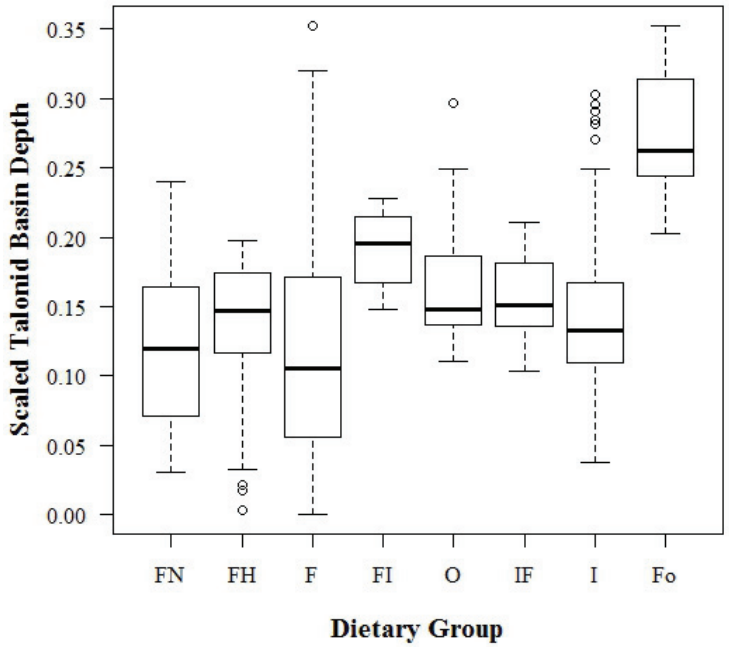
A.


Scaled Mean Cusp Height
1.0
0.8
0.6
0.4
0.2
FN
FH
F
FI
O
IF
I
Fo
Dietary Group

B.



C.



D.

Figure 5.15. Box plots of each variable for Dietary Group 2 of the combined Balta-Mindanao sample. Angle values are in radians. Dietary codes are: FN=Frugivore-nectarivore, FH= Hard-object frugivore, F=Frugivore, FI=Frugivore-insectivore, O=Omnivore, IF=Insectivore-frugivore, I=Insectivore, Fo=Folivore.

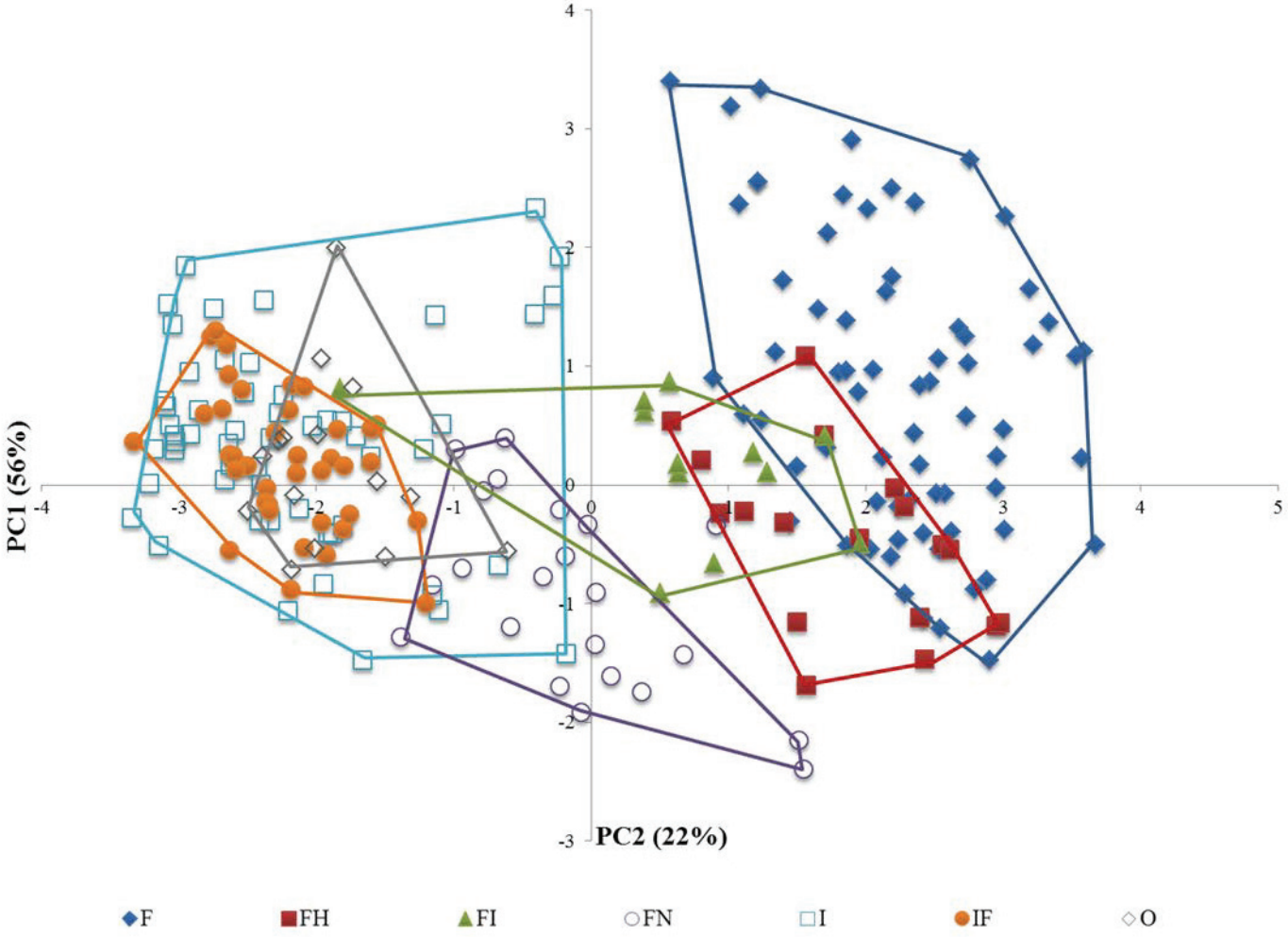


Figure 5.16. Graphical representation of dietary niches within a two-dimensional dietary niche space based on a plot of the first and second principal components for the seven dietary groups included in modified MANOVA.

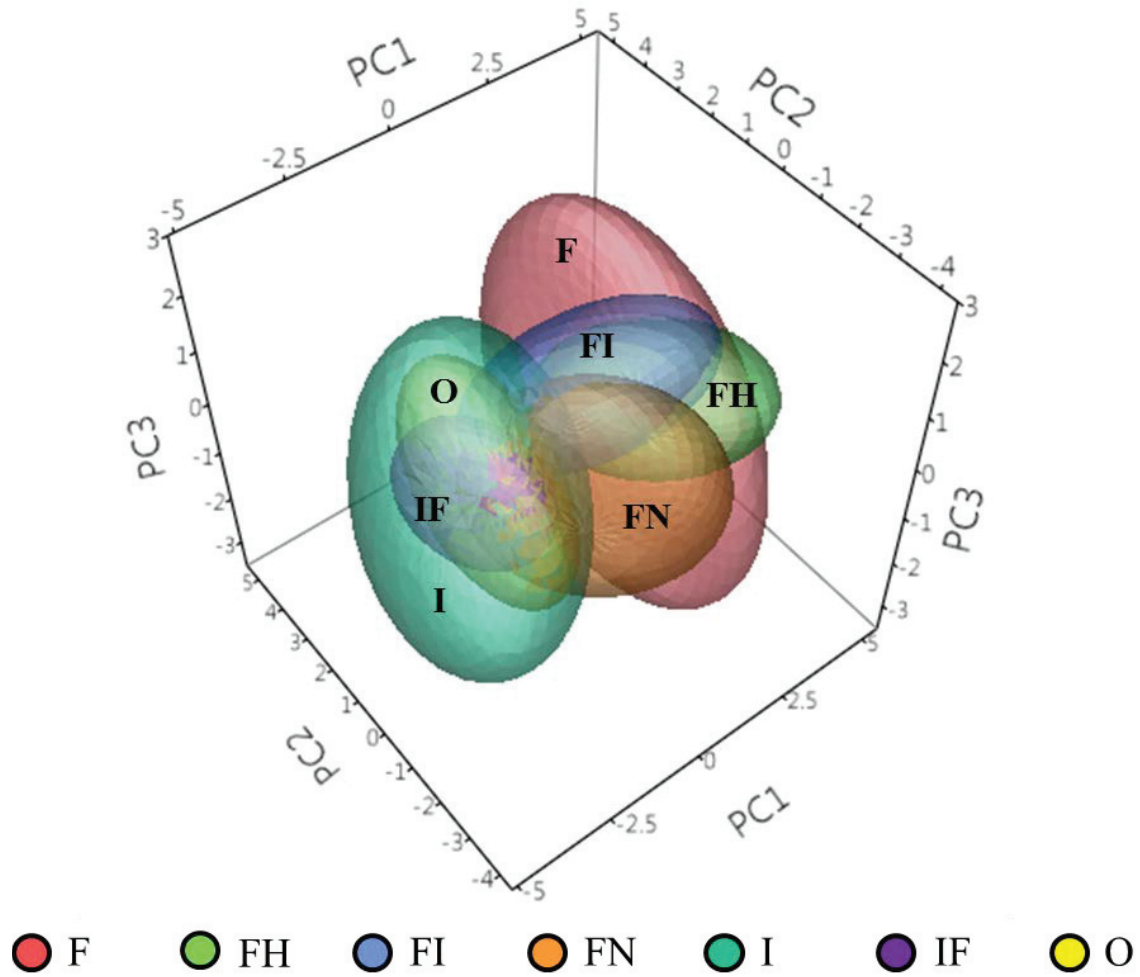


Figure 5.17. Graphical representation of dietary niches within a three-dimensional dietary niche space based on a plot of 95% confidence interval contour ellipsoids of the seven dietary groups. Note that the omnivore and insectivore-frugivore niches are contained within the insectivore niche.

Table 5.1. Variable sets used in analyses.

Variable Set 1	Variable Set 2	Variable Set 3
Total crest length	Total crest length*	Total crest length
Proconid height	Mean cusp height*	Mean trigonid cusp height
Metaconid height	Mean cusp angle*	Mean trigonid cusp angle
Entoconid height	Talonid basin area	Mean talonid cusp height
Hypoconid height	Talonid basin depth*	Mean talonid cusp angle
Protoconid angle	Trigonid-talonid relief	Talonid basin area
Metaconid angle		Talonid basin depth
Entoconid angle		Trigonid-talonid relief
Hypoconid angle		
Talonid basin area		
Talonid basin depth		
Trigonid-talonid relief		

Differences in variable sets relate to cusp height and angle measurements. Variable Set 1 includes individual cusp measurements. Variable Set 2 includes only mean values for all cusps. Variable Set 3 includes separate mean values for trigonid (protoconid, metaconid) and talonid (entoconid, hypoconid) cusps. Due to the derived nature of the pteropodid dentition, and in order to avoid exclusion of this group, only the measurements indicated by an asterisk(*) were included in analyses of the Mindanao sample and the combined Balta-Mindanao sample. This subset of Variable Set 2 will be referred to as Variable Set 2*.

Table 5.2. Ordinary least squares (OLS) and reduced major axis (RMA) regression of log(molar variable) against log(molar area) for the Balta, Peru sample. Slope of isometry for talonid area = 1.0. Slope of isometry for all other (non-angular) measures = 0.5. Slopes significantly different than isometry for both OLS and RMA regressions are bolded (angular measurements not included).

	OLS			RMA		
Measurement	Slope	95% CI	*r*	Slope	95% CI	*r*
Total crest length	**0.574**	**0.523, 0.626**	0.939	**0.612**	**0.552, 0.681**	0.939
Protoconid height	0.395	0.296, 0.493	0.704	0.562	0.476, 0.659	0.704
Metaconid height	**0.556**	**0.509, 0.603**	0.945	**0.588**	**0.553, 0.628**	0.945
Entoconid height	0.518	0.460, 0.577	0.909	0.570	0.525, 0.623	0.909
Hypoconid height	0.435	0.356, 0.514	0.811	0.536	0.478, 0.605	0.811
Mean cusp height	0.461	0.396, 0.526	0.867	0.531	0.484, 0.584	0.867
Hypoconid angle	0.073	-0.004, 0.149	0.233	0.311	-0.250, 0.389	0.233
Protoconid angle	0.074	-0.009, 0.157	0.215	0.344	-0.328, 0.414	0.215
Metaconid angle	-0.035	-0.107, 0.037	0.118	-0.296	-0.355, 0.329	0.118
Entoconid angle	0.025	-0.028, 0.077	0.116	0.214	-0.236, 0.270	0.116
Talonid area	1.073	0.996, 1.149	0.961	1.116	1.051, 1.198	0.961
Talonid basin depth	**0.672**	**0.577, 0.768**	0.867	**0.775**	**0.663, 0.905**	0.867
Trigonid-talonid relief	0.324	0.177, 0.471	0.479	0.676	0.489, 0.897	0.479
Trigonid cusp height	0.460	0.391, 0.528	0.731	0.538	0.481, 0.598	0.731
Trigonid cusp angle	0.019	-0.055, 0.092	0.062	0.302	-0.342, 0.358	0.060
Talonid cusp height	0.470	0.405, 0.536	0.761	0.539	0.498, 0.589	0.761
Talonid cusp angle	0.047	-0.013, 0.107	0.191	0.249	-0.220, 0.309	0.185

Table 5.3. Ordinary least squares (OLS) and reduced major axis (RMA) regression of log(molar variable) against log(molar area) for the Mindanao, Philippines sample. Slope of isometry for all (non-angular) measures = 0.5. Slopes significantly different than isometry for both OLS and RMA regressions are bolded (angular measurements not included).

	OLS			RMA		
Measurement	Slope	95% CI	*r*	Slope	95% CI	*r*
Total crest length	0.534	0.457, 0.610	0.904	0.590	0.484, 0.682	0.904
Mean cusp height	0.524	0.446, 0.601	0.899	0.582	0.487, 0.691	0.899
Mean cusp angle	0.049	-0.054, 0.153	0.143	0.344	-0.391, 0.424	0.143
Talonid basin depth	**0.681**	**0.521, 0.841**	0.791	**0.861**	**0.687, 1.052**	0.791

Table 5.4. Ordinary least squares (OLS) and reduced major axis (RMA) regression of log(molar variable) against log(molar area) for the combined Balta-Mindanao sample. Slope of isometry for all (non-angular) measures = 0.5. Slopes significantly different than isometry for both OLS and RMA regressions are bolded (angular measurements not included).

	OLS			RMA		
Measurement	Slope	95% CI	*r*	Slope	95% CI	*r*
Total crest length	**0.559**	**0.514, 0.604**	0.918	**0.609**	**0.554, 0.667**	0.918
Mean cusp height	0.486	0.436, 0.535	0.878	0.553	0.504, 0.606	0.878
Mean cusp angle	0.041	-0.014, 0.097	0.138	0.299	-0.309, 0.344	0.138
Talonid basin depth	**0.679**	**0.592, 0.767**	0.825	**0.823**	**0.722, 0.931**	0.825

Table 5.5. Ordinary least squares (OLS) and reduced major axis (RMA) regression of log(molar variable) against log(molar area) of frugivores and insectivores of the Balta, Peru sample. Slope of isometry for talonid area = 1.0. Slope of isometry for all other (non-angular) measures = 0.5. Slopes significantly different than isometry for both OLS and RMA regressions are bolded (angular measurements not included).

	OLS			RMA		
Measurement	Slope	95% CI	*r*	Slope	95% CI	*r*
FRUGIVORES						
Total crest length	**0.636**	**0.558, 0.714**	0.943	**0.674**	**0.604, 0.760**	0.943
Protoconid height	0.394	0.300, 0.489	0.823	0.479	0.390, 0.560	0.823
Metaconid height	0.518	0.451, 0.585	0.937	0.553	0.507, 0.605	0.937
Entoconid height	0.540	0.460, 0.621	0.922	0.586	0.516, 0.669	0.922
Hypoconid height	0.476	0.409, 0.542	0.934	0.509	0.445, 0.569	0.934
Mean cusp height	0.460	0.393, 0.526	0.924	0.498	0.436, 0.554	0.924
Hypoconid angle	0.018	-0.031, 0.067	0.132	0.135	-0.160, 0.190	0.132
Protoconid angle	0.051	-0.005, 0.108	0.301	0.171	-0.168, 0.231	0.301
Metaconid angle	-0.014	-0.070, 0.042	0.088	-0.160	-0.219, 0.221	0.088
Entoconid angle	-0.014	-0.051, 0.022	0.136	-0.104	-0.139, 0.120	0.136
Talonid area	1.093	0.991, 1.194	0.967	1.129	1.028, 1.231	0.967
Talonid basin depth	**0.672**	**0.522, 0.823**	0.845	**0.796**	**0.644, 0.947**	0.845
Trigonid-talonid relief	0.258	0.072, 0.445	0.442	0.586	0.333, 0.887	0.442
Trigonid cusp height	0.447	0.374, 0.520	0.906	0.493	0.427. 0.557	0.906
Trigonid cusp angle	0.019	-0.034, 0.072	0.125	0.153	-0.188, 0.219	0.125
Talonid cusp height	0.505	0.442, 0.568	0.944	0.535	0.472, 0.598	0.944
Talonid cusp angle	0.001	-0.034, 0.036	0.009	0.099	-0.122, 0.134	0.009

Table 5.5, Cont'd.

	OLS			RMA		
Measurement	Slope	95% CI	*r*	Slope	95% CI	*r*
INSECTIVORES						
Total crest length	0.503	0.431, 0.575	0.942	0.534	0.482, 0.604	0.942
Protoconid height	0.505	0.428, 0.583	0.934	0.541	0.463, 0.621	0.934
Metaconid height	**0.659**	**0.580, 0.739**	0.958	**0.688**	**0.603, 0.763**	0.958
Entoconid height	0.523	0.443, 0.603	0.935	0.559	0.482, 0.639	0.935
Hypoconid height	0.524	0.438, 0.609	0.927	0.565	0.493, 0.639	0.927
Mean cusp height	0.547	0.490, 0.604	0.969	0.565	0.510, 0.622	0.969
Hypoconid angle	0.092	-0.004, 0.180	0.387	0.237	-0.202, 0.315	0.387
Protoconid angle	0.091	-0.024, 0.158	0.482	0.189	-0.133, 0.260	0.482
Metaconid angle	-0.111	-0.228, 0.005	0.359	-0.310	-0.417, 0.289	0.359
Entoconid angle	0.025	-0.074, 0.124	0.102	0.246	-0.320, 0.343	0.102
Talonid area	1.020	0.947, 1.094	0.984	1.036	0.975, 1.099	0.984
Talonid basin depth	**0.758**	**0.582, 0.935**	0.866	**0.876**	**0.663, 1.090**	0.866
Trigonid-talonid relief	0.475	0.338, 0.612	0.813	0.584	0.488, 0.705	0.813
Trigonid cusp height	**0.559**	**0.503, 0.615**	0.971	**0.576**	**0.518, 0.636**	0.971
Trigonid cusp angle	-0.019	-0.090, 0.052	0.107	-0.178	-0.233, 0.237	0.107
Talonid cusp height	0.513	0.436, 0.590	0.937	0.547	0.491, 0.605	0.937
Talonid cusp angle	0.062	-0.014, 0.137	0.314	0.197	-0.106, 0.277	0.314

Table 5.6. Ordinary least squares (OLS) and reduced major axis (RMA) regression of log(molar variable) against log(molar area) of frugivores and insectivores of the Mindanao, Philippines sample. Slope of isometry for all (non-angular) measures = 0.5. Slopes significantly different than isometry for both OLS and RMA regressions are bolded (angular measurements not included).

	OLS			RMA		
Measurement	Slope	95% CI	*r*	Slope	95% CI	*r*
FRUGIVORES						
Total crest length	**0.617**	**0.506, 0.729**	0.943	**0.655**	**0.537, 0.728**	0.943
Mean cusp height	**0.615**	**0.529, 0.701**	0.964	**0.638**	**0.553, 0.741**	0.964
Mean cusp angle	-0.031	-0.080, 0.169	0.316	-0.100	-0.162, 0.034	0.316
Talonid basin depth	**0.777**	**0.528, 1.026**	0.847	**0.916**	**0.716, 1.229**	0.847
INSECTIVORES						
Total crest length	0.420	0.360, 0.480	0.949	0.443	0.383, 0.503	0.949
Mean cusp height	0.477	0.424, 0.529	0.969	0.492	0.447, 0.551	0.969
Mean cusp angle	0.064	-0.003, 0.131	0.383	0.168	-0.109, 0.254	0.383
Talonid basin depth	0.627	0.441, 0.812	0.824	0.760	0.488, 0.977	0.824

Table 5.7. Ordinary least squares (OLS) and reduced major axis (RMA) regression of log(molar variable) against log(molar area) for frugivores and insectivores of the combined Balta, Peru and Mindanao, Philippines sample. Slope of isometry for all (non-angular) measures = 0.5. Slopes significantly different than isometry for both OLS and RMA regressions are bolded (angular measurements not included).

	OLS			RMA		
Measurement	Slope	95% CI	*r*	Slope	95% CI	*r*
FRUGIVORES						
Total crest length	**0.620**	**0.547, 0.693**	0.920	**0.674**	**0.607, 0.743**	0.920
Mean cusp height	0.522	0.467, 0.576	0.935	0.558	0.506, 0.615	0.935
Mean cusp angle	0.003	-0.035, 0.040	0.019	0.136	-0.162, 0.172	0.019
Talonid basin depth	**0.704**	**0.561, 0.848**	0.807	**0.873**	**0.735, 1.034**	0.807
INSECTIVORES						
Total crest length	0.463	0.414, 0.512	0.936	0.494	0.452, 0.538	0.936
Mean cusp height	0.511	0.473, 0.549	0.966	0.529	0.490, 0.573	0.966
Mean cusp angle	0.044	-0.001, 0.089	0.272	0.163	-0.153, 0.233	0.272
Talonid basin depth	**0.692**	**0.568, 0.815**	0.844	**0.819**	**0.656, 0.972**	0.844

Table 5.8. Comparison of overall error rates derived from discriminant analyses using ratio and residual scaling methods.

Sample	Ratios	Residuals
Balta, Variable Set 1	0.078	0.108
Balta, Variable Set 2	0.197	0.149
Balta, Variable Set 3	0.136	0.105
Mindanao, Variable Set 2*	0.136	0.114
Combined, Variable Set 2*	0.232	0.205

Table 5.9. Specimens included in comparative analysis of m1 and m2 morphology.

Specimen	Species	Dietary Group 2
FMNH 147830	*Alionycteris paucidentata*	F
FMNH 148093	*Alionycteris paucidentata*	F
FMNH 166461	*Dyacopterus rickarti*	F
FMNH 146670	*Megaerops wetmorei*	F
FMNH 142602	*Ptenochirus jagori*	F
FMNH 146673	*Ptenochirus jagori*	F
FMNH 146688	*Ptenochirus minor*	F
FMNH 146689	*Ptenochirus minor*	F
FMNH 144748	*Pteropus hypomelanus*	F
NMNH 462182	*Pteropus hypomelanus*	F
FMNH 144759	*Pteropus pumilus*	F
FMNH 144745	*Pteropus speciosus*	F
FMNH 144747	*Pteropus speciosus*	F
FMNH 33701	*Pteropus vampyrus*	F
FMNH 87410	*Pteropus vampyrus*	F
FMNH 67747	*Exilisciurus concinnus*	FH
FMNH 92784	*Exilisciurus concinnus*	FH
FMNH 66302	*Harpyionycteris whiteheadi*	FH
FMNH 87440	*Petinomys crinitus*	FH
FMNH 87442	*Petinomys crinitus*	FH
FMNH 67750	*Sundasciurus philippinensis*	FH
FMNH 87455	*Sundasciurus philippinensis*	FH
FMNH 146608	*Cynopterus brachyotis*	FN
FMNH 146613	*Cynopterus brachyotis*	FN
FMNH 41354	*Eonycteris robusta*	FN
FMNH 56558	*Eonycteris robusta*	FN
FMNH 146653	*Macroglossus minimus*	FN
FMNH 56443	*Rousettus amplexicaudatus*	FN
FMNH 56446	*Rousettus amplexicaudatus*	FN
FMNH 56504	*Cynocephalus volans*	Fo
FMNH 56521	*Cynocephalus volans*	Fo
FMNH 146966	*Crocidura beatus*	I
FMNH 80360	*Crocidura beatus*	I
FMNH 60850	*Hipposideros cervinus*	I
FMNH 142613	*Hipposideros coronatus*	I
FMNH 80447	*Hipposideros diadema griseus*	I
FMNH 80452	*Hipposideros diadema griseus*	I
FMNH 190052	*Hipposideros obscurus*	I
FMNH 56689	*Hipposideros obscurus*	I

Table 5.9, Cont'd.

Specimen	Species	Dietary Group 2
FMNH 190112	*Kerivoula pellucida*	I
FMNH 168892	*Megaderma spasma*	I
FMNH 190036	*Megaderma spasma*	I
FMNH 166475	*Miniopterus australis*	I
FMNH 61086	*Miniopterus australis*	I
FMNH 61083	*Miniopterus schreibersii*	I
FMNH 61209	*Miniopterus schreibersii*	I
FMNH 168939	*Miniopterus tristis*	I
FMNH 145542	*Miniopterus tristis*	I
FMNH 113460	*Myotis macrotarsus*	I
FMNH 145546	*Myotis muricola*	I
FMNH 167382	*Otomops formosus*	I
FMNH 167240	*Otomops sp.*	I
FMNH 145548	*Philetor brachypterus*	I
FMNH 147068	*Philetor brachypterus*	I
FMNH 142614	*Pipistrellus javanicus*	I
FMNH 61230	*Rhinolophus arcuatus*	I
FMNH 61231	*Rhinolophus arcuatus*	I
FMNH 146701	*Rhinolophus inops*	I
FMNH 148122	*Rhinolophus inops*	I
FMNH 61222	*Rhinolophus rufus*	I
FMNH 1111	*Scotophilus kuhlii*	I
FMNH 56654	*Scotophilus kuhlii*	I
FMNH 56639	*Taphozous melanopogon*	I
FMNH 56642	*Taphozous melanopogon*	I
FMNH 56759	*Tarsius syrichta*	I
NMNH 282761	*Tarsius syrichta*	I
FMNH 166476	*Urogale everetti*	O
FMNH 61418	*Urogale everetti*	O

Table 5.10. Results of Wilcoxon signed-rank test comparing m1 and m2 measurements.

Measurement	Mean Difference	S Statistic	*p*-Value
Total crest length	-0.057	-85	0.599
Mean cusp height	-0.010	-287	0.073
Mean cusp angle	-0.038	-312	0.056
Talonid basin depth	0.003	39	0.810

Table 5.11. Results (*p*-values) of Critchlow-Fligner post-hoc multiple comparisons of Dietary Group 2 using m1 and m2. Significant results are bolded.

Groups Compared			Mean Cusp Height (m1)	Mean Cusp Height (m2)	Mean Cusp Angle (m1)	Mean Cusp Angle (m2)
F	vs	FH	1.000	1.000	1.000	1.000
F	vs	FN	1.000	1.000	1.000	1.000
F	vs	Fo	0.089	0.145	1.000	1.000
F	vs	I	**<0.001**	**<0.001**	**<0.001**	**<0.001**
F	vs	O	0.145	0.108	0.903	0.615
FH	vs	FN	1.000	1.000	1.000	1.000
FH	vs	Fo	1.000	1.000	1.000	1.000
FH	vs	I	0.052	0.056	**0.001**	**0.001**
FH	vs	O	1.000	1.000	0.924	0.406
FN	vs	Fo	0.178	0.253	1.000	1.000
FN	vs	I	**<0.001**	**<0.001**	**<0.001**	**<0.001**
FN	vs	O	0.271	0.196	0.216	0.075
Fo	vs	I	1.000	1.000	0.863	1.000
Fo	vs	O	1.000	1.000	1.000	1.000
I	vs	O	1.000	1.000	1.000	1.000

Table 5.12. Eigenvalues and eigenvectors of the principal component analysis of the Balta sample using Variable Set 1.

	Eigenvalue	Difference	Proportion	Cumulative		PC1	PC2	PC3	PC4	PC5
1	6.109	3.960	0.509	0.509	Total crest length	0.060	0.560	-0.320	0.093	0.416
2	2.149	0.990	0.179	0.688	Proconid height	-0.364	-0.191	-0.019	-0.135	0.073
3	1.159	0.474	0.097	0.785	Metaconid height	-0.201	0.202	0.608	0.480	-0.079
4	0.685	0.215	0.057	0.842	Entoconid height	-0.266	0.237	0.401	-0.112	0.533
5	0.470	0.115	0.039	0.881	Hypoconid height	-0.349	-0.106	-0.007	-0.339	0.261
6	0.355	0.053	0.030	0.911	Protoconid angle	0.370	-0.027	0.157	0.209	-0.037
7	0.302	0.044	0.025	0.936	Metaconid angle	0.353	-0.102	0.255	-0.019	0.158
8	0.258	0.083	0.022	0.957	Entoconid angle	0.332	-0.168	0.059	-0.159	0.527
9	0.175	0.014	0.015	0.972	Hypoconid angle	0.296	-0.226	0.343	-0.004	0.113
10	0.162	0.046	0.014	0.985	Talonid basin area	0.272	0.393	-0.238	0.194	0.064
11	0.115	0.056	0.010	0.995	Talonid basin depth	<0.001	0.539	0.296	-0.442	-0.342
12	0.060		0.005	1.000	Trigonid-talonid relief	-0.313	-0.082	-0.110	0.560	0.159

Table 5.13. Eigenvalues and eigenvectors of the principal component analysis of the Balta sample using Variable Set 2.

	Eigenvalue	Difference	Proportion	Cumulative		PC1	PC2	PC3	PC4	PC5
1	3.072	1.515	0.512	0.512	Total crest length	0.205	0.622	0.500	-0.470	0.312
2	1.557	0.835	0.260	0.772	Mean cusp height	-0.522	0.193	-0.164	-0.188	0.047
3	0.722	0.435	0.120	0.892	Mean cusp angle	0.451	-0.388	-0.023	0.095	0.708
4	0.286	0.045	0.048	0.940	Talonid basin area	0.483	0.243	0.266	0.466	-0.463
5	0.242	0.120	0.040	0.980	Talonid basin depth	0.157	0.590	-0.691	0.281	0.232
6	0.121		0.020	1.000	Trigonid-talonid relief	-0.473	0.131	0.418	0.662	0.362

Table 5.14. Eigenvalues and eigenvectors of the principal component analysis of the Balta sample using Variable Set 3.

	Eigenvalue	Difference	Proportion	Cumulative		PC1	PC2	PC3	PC4	PC5
1	4.508	2.778	0.564	0.564	Total crest length	0.087	0.641	-0.448	-0.442	0.256
2	1.730	0.974	0.216	0.780	Talonid basin area	0.363	0.360	-0.244	0.320	-0.021
3	0.756	0.435	0.095	0.874	Talonid basin depth	0.055	0.579	0.683	0.348	0.111
4	0.321	0.040	0.040	0.915	Trigonid-talonid relief	-0.386	-0.020	-0.420	0.608	0.456
5	0.281	0.098	0.035	0.950	Trigonid cusp height	-0.442	-0.027	0.141	-0.018	0.275
6	0.183	0.022	0.023	0.973	Trigonid cusp angle	0.406	-0.238	0.110	-0.212	0.571
7	0.161	0.101	0.020	0.993	Talonid cusp height	-0.421	0.107	0.233	-0.386	0.334
8	0.060		0.008	1.000	Talonid cusp angle	0.414	-0.233	0.103	0.131	0.448

Table 5.15. Eigenvalues and eigenvectors of the principal component analysis of the Mindanao sample using Variable Set 2*.

	Eigenvalue	Difference	Proportion	Cumulative		PC1	PC2	PC3	PC4
1	2.737	2.153	0.684	0.684	Total crest length	0.475	-0.378	0.794	0.025
2	0.584	0.110	0.146	0.830	Mean cusp height	0.529	-0.267	-0.465	0.658
3	0.474	0.269	0.119	0.949	Mean cusp angle	-0.546	0.124	0.362	0.746
4	0.205		0.051	1.000	Talonid basin depth	0.443	0.878	0.149	0.106

Table 5.16. Eigenvalues and eigenvectors of the principal component analysis of the combined Balta-Mindanao sample using Variable Set 2*.

	Eigenvalue	Difference	Proportion	Cumulative		PC1	PC2	PC3	PC4
1	1.999	1.021	0.500	0.500	Total crest length	0.512	0.488	-0.428	0.563
2	0.978	0.374	0.245	0.744	Mean cusp height	0.377	-0.795	0.142	0.454
3	0.604	0.185	0.151	0.895	Mean cusp angle	-0.579	0.187	0.412	0.678
4	0.419		0.105	1.000	Talonid basin depth	0.510	0.309	0.792	-0.130

Table 5.17. Species excluded or exchanged for congeners in the phylogenetic tree used in the phylogenetic principal component analyses.

Original Species	Species in Phylogeny
Dyacopterus rickarti	*Dyacopterus spadiceus*
Ectophylla macconnelli	*Ectophylla alba*
Eonycteris robusta	*Eonycteris spelaea*
Hipposideros ater	Excluded
Lophostoma silvicolum	Excluded
Marmosa quichua	Excluded
Philander mcilhennyi	Excluded
Rhinolophus arcuatus	Excluded
Sturnira lilium	Excluded
Sturnira tildae	Excluded
Tonatia minuta	*Tonatia bidens*
Tonatia saurophila	Excluded

Table 5.18. Results of Kruskal-Wallis analysis of each variable in the Balta, Peru sample. With strict Bonferroni correction, ±=0.002.

	Dietary Group 1		Dietary Group 2	
Variable	*F*-Value	*p*-Value	*F*-Value	*p*-Value
Total crest length	4.456	<.001	5.240	<.001
Protoconid height	49.068	<.001	64.396	<.001
Metaconid height	14.385	<.001	18.492	<.001
Entoconid height	34.330	<.001	45.237	<.001
Hypoconid height	48.620	<.001	64.938	<.001
Mean cusp height	47.817	<.001	62.680	<.001
Hypoconid angle	37.486	<.001	30.189	<.001
Protoconid angle	65.121	<.001	87.039	<.001
Metaconid angle	40.451	<.001	53.741	<.001
Entoconid angle	13.359	<.001	16.779	<.001
Mean cusp angle	62.345	<.001	82.451	<.001
Talonid basin area	13.583	<.001	12.980	<.001
Talonid basin depth	3.087	0.002	3.051	0.007
Trigonid-talonid relief	42.247	<.001	42.143	<.001
Trigonid cusp height	43.212	<.001	56.053	<.001
Trigonid cusp angle	63.781	<.001	85.226	<.001
Talonid cusp height	73.187	<.001	95.013	<.001
Talonid cusp angle	23.639	<.001	30.651	<.001

Table 5.19. Results of Kruskal-Wallis analysis of each variable in the Mindanao, Philippines sample. With strict Bonferroni correction, ±=0.013.

	Dietary Group 1		Dietary Group 2	
Variable	*F*-Value	*p*-Value	*F*-Value	*p*-Value
Total crest length	32.299	<.001	28.227	<.001
Mean cusp height	47.416	<.001	65.260	<.001
Mean cusp angle	324.107	<.001	443.700	<.001
Talonid basin depth	20.407	<.001	26.844	<.001

Table 5.20. Results of Kruskal-Wallis analysis of each variable in the combined Balta-Mindanao sample. With strict Bonferroni correction, ±=0.013.

	Dietary Group 1		Dietary Group 2	
Variable	*F*-Value	*p*-Value	*F*-Value	*p*-Value
Total crest length	7.257	<.001	8.989	<.001
Mean cusp height	58.145	<.001	98.370	<.001
Mean cusp angle	21.530	<.001	28.204	<.001
Talonid basin depth	9.819	<.001	11.710	<.001

Table 5.21. Results (*p*-values) of Critchlow-Fligner pairwise comparisons of all Balta dietary groups using Dietary Group 1. Significant results are bolded.

Groups Compared			Total Crest Length	Protoconid Height	Metaconid Height	Entoconid Height	Hypoconid Height
F	vs	FH	0.225	1.000	1.000	**0.003**	1.000
F	vs	FI	1.000	1.000	**<0.001**	**<0.001**	1.000
F	vs	FIFH	1.000	1.000	1.000	1.000	1.000
F	vs	FN	**0.002**	1.000	1.000	0.123	1.000
F	vs	I	1.000	**<0.001**	**<0.001**	**<0.001**	**<0.001**
F	vs	IF	0.188	**<0.001**	**<0.001**	**<0.001**	**<0.001**
F	vs	N	**<0.001**	1.000	0.839	**0.002**	1.000
F	vs	O	0.341	**0.004**	**<0.001**	**<0.001**	**0.003**
FH	vs	FI	1.000	1.000	**0.005**	0.103	1.000
FH	vs	FIFH	1.000	1.000	1.000	1.000	1.000
FH	vs	FN	1.000	1.000	1.000	1.000	1.000
FH	vs	I	0.253	**<0.001**	1.000	0.414	**<0.001**
FH	vs	IF	1.000	**<0.001**	**0.006**	1.000	**<0.001**
FH	vs	N	1.000	1.000	1.000	1.000	1.000
FH	vs	O	1.000	**0.001**	**0.010**	1.000	0.532
FI	vs	FIFH	1.000	1.000	1.000	1.000	1.000
FI	vs	FN	0.755	1.000	**<0.001**	**0.001**	1.000
FI	vs	I	1.000	**<0.001**	**0.001**	1.000	**<0.001**
FI	vs	IF	1.000	**0.001**	1.000	0.450	**0.002**
FI	vs	N	**0.014**	1.000	0.295	0.269	1.000
FI	vs	O	1.000	0.343	1.000	1.000	1.000
FIFH	vs	FN	1.000	1.000	1.000	1.000	1.000
FIFH	vs	I	1.000	1.000	1.000	1.000	1.000
FIFH	vs	IF	1.000	1.000	1.000	1.000	1.000
FIFH	vs	N	1.000	1.000	1.000	1.000	1.000
FIFH	vs	O	1.000	1.000	1.000	1.000	1.000
FN	vs	I	**0.004**	**<0.001**	1.000	**0.001**	0.118
FN	vs	IF	1.000	**<0.001**	**<0.001**	0.371	0.511
FN	vs	N	1.000	1.000	1.000	1.000	1.000
FN	vs	O	1.000	**0.012**	**<0.001**	0.200	1.000
I	vs	IF	0.276	1.000	**<0.001**	1.000	1.000
I	vs	N	**<0.001**	**0.001**	1.000	1.000	**<0.001**
I	vs	O	0.370	1.000	**0.001**	1.000	0.224
IF	vs	N	0.057	**0.004**	0.864	1.000	**0.002**
IF	vs	O	1.000	1.000	1.000	1.000	1.000
N	vs	O	1.000	0.918	0.588	1.000	1.000
No. Groups Discriminated			5	13	13	8	9

Table 5.21, Cont'd.

Groups Compared			Mean Cusp Height	Hypoconid Angle	Protoconid Angle	Metaconid Angle	Entoconid Angle
F	vs	FH	1.000	1.000	0.276	1.000	1.000
F	vs	FI	1.000	1.000	1.000	1.000	1.000
F	vs	FIFH	1.000	1.000	1.000	1.000	1.000
F	vs	FN	1.000	**<0.001**	1.000	1.000	1.000
F	vs	I	**<0.001**	**<0.001**	**<0.001**	**<0.001**	**<0.001**
F	vs	IF	**<0.001**	**<0.001**	**<0.001**	**<0.001**	**<0.001**
F	vs	N	1.000	1.000	1.000	1.000	1.000
F	vs	O	**<0.001**	**<0.001**	**<0.001**	**<0.001**	0.168
FH	vs	FI	1.000	1.000	1.000	1.000	1.000
FH	vs	FIFH	1.000	1.000	1.000	1.000	1.000
FH	vs	FN	1.000	0.000	0.463	1.000	1.000
FH	vs	I	**<0.001**	**<0.001**	**<0.001**	**<0.001**	**<0.001**
FH	vs	IF	**<0.001**	**<0.001**	**<0.001**	**<0.001**	**<0.001**
FH	vs	N	1.000	1.000	1.000	1.000	1.000
FH	vs	O	**0.001**	**0.015**	**<0.001**	**<0.001**	**0.015**
FI	vs	FIFH	1.000	1.000	1.000	1.000	1.000
FI	vs	FN	1.000	**0.001**	1.000	1.000	1.000
FI	vs	I	**0.028**	**0.001**	**<0.001**	0.304	**<0.001**
FI	vs	IF	**0.024**	**0.025**	**<0.001**	**0.001**	**0.002**
FI	vs	N	1.000	1.000	1.000	1.000	1.000
FI	vs	O	0.993	0.416	**0.007**	**0.003**	0.263
FIFH	vs	FN	1.000	1.000	1.000	1.000	1.000
FIFH	vs	I	1.000	1.000	0.267	1.000	1.000
FIFH	vs	IF	1.000	1.000	0.442	0.906	1.000
FIFH	vs	N	1.000	1.000	1.000	1.000	1.000
FIFH	vs	O	1.000	1.000	0.927	0.787	1.000
FN	vs	I	**<0.001**	1.000	**<0.001**	**<0.001**	**<0.001**
FN	vs	IF	**<0.001**	1.000	**<0.001**	**<0.001**	**<0.001**
FN	vs	N	1.000	**0.001**	1.000	1.000	1.000
FN	vs	O	**0.001**	1.000	**0.004**	**<0.001**	**0.015**
I	vs	IF	1.000	1.000	1.000	0.208	1.000
I	vs	N	**0.001**	**0.001**	**<0.001**	**0.004**	**<0.001**
I	vs	O	1.000	1.000	1.000	0.697	0.746
IF	vs	N	**0.001**	**0.040**	**<0.001**	**<0.001**	0.092
IF	vs	O	1.000	1.000	1.000	1.000	1.000
N	vs	O	0.208	0.661	**0.014**	**<0.001**	1.000
No. Groups Discriminated			13	13	15	14	11

Table 5.21, Cont'd.

Groups Compared			Mean Cusp Angle	Talonid Basin Area	Talonid Basin Depth	Trigonid-Talonid Relief	Trigonid Cusp Height
F	vs	FH	1.000	1.000	1.000	1.000	1.000
F	vs	FI	1.000	1.000	**0.001**	1.000	1.000
F	vs	FIFH	1.000	1.000	1.000	1.000	1.000
F	vs	FN	1.000	0.436	**0.015**	1.000	1.000
F	vs	I	**<0.001**	**<0.001**	1.000	**<0.001**	**<0.001**
F	vs	IF	**<0.001**	**<0.001**	0.104	**<0.001**	**<0.001**
F	vs	N	1.000	0.211	1.000	**0.003**	1.000
F	vs	O	**<0.001**	0.003	0.274	**<0.001**	**<0.001**
FH	vs	FI	1.000	1.000	1.000	1.000	1.000
FH	vs	FIFH	1.000	1.000	1.000	1.000	1.000
FH	vs	FN	0.471	1.000	1.000	1.000	1.000
FH	vs	I	**<0.001**	**0.001**	1.000	**<0.001**	**<0.001**
FH	vs	IF	**<0.001**	**<0.001**	1.000	**<0.001**	**<0.001**
FH	vs	N	1.000	0.196	0.931	**<0.001**	1.000
FH	vs	O	**<0.001**	**0.009**	1.000	**<0.001**	**<0.001**
FI	vs	FIFH	1.000	1.000	1.000	1.000	1.000
FI	vs	FN	1.000	0.177	1.000	1.000	1.000
FI	vs	I	**<0.001**	1.000	**0.005**	**<0.001**	0.069
FI	vs	IF	**<0.001**	1.000	1.000	**<0.001**	**0.004**
FI	vs	N	1.000	1.000	**0.003**	**0.024**	1.000
FI	vs	O	**0.015**	1.000	1.000	**<0.001**	0.188
FIFH	vs	FN	1.000	1.000	1.000	1.000	1.000
FIFH	vs	I	1.000	1.000	1.000	0.175	1.000
FIFH	vs	IF	1.000	1.000	1.000	0.111	1.000
FIFH	vs	N	1.000	1.000	1.000	0.572	1.000
FIFH	vs	O	1.000	1.000	1.000	0.120	1.000
FN	vs	I	**<0.001**	**<0.001**	0.080	**<0.001**	**<0.001**
FN	vs	IF	**<0.001**	**<0.001**	1.000	**<0.001**	**<0.001**
FN	vs	N	1.000	**0.002**	**0.046**	**0.005**	1.000
FN	vs	O	0.063	**<0.001**	1.000	**<0.001**	**<0.001**
I	vs	IF	1.000	1.000	0.580	1.000	1.000
I	vs	N	**<0.001**	1.000	1.000	1.000	**0.011**
I	vs	O	1.000	1.000	0.727	1.000	1.000
IF	vs	N	**<0.001**	1.000	0.270	1.000	**<0.001**
IF	vs	O	1.000	1.000	1.000	1.000	1.000
N	vs	O	**0.012**	1.000	0.245	1.000	0.064
No. Groups Discriminated			14	9	5	16	12

Table 5.21, Cont'd.

Groups Compared			Trigonid Cusp Angle	Talonid Cusp Height	Talonid Cusp Angle	No. Variables Resulting in Discrimination	% Variables Resulting in Discrimination
F	vs	FH	1.000	1.000	1.000	0	0.00
F	vs	FI	1.000	**0.016**	1.000	4	22.22
F	vs	FIFH	1.000	1.000	1.000	0	0.00
F	vs	FN	1.000	1.000	1.000	3	16.67
F	vs	I	**<0.001**	**<0.001**	**<0.001**	16	88.89
F	vs	IF	**<0.001**	**<0.001**	**<0.001**	16	88.89
F	vs	N	1.000	0.378	1.000	3	16.67
F	vs	O	**<0.001**	**<0.001**	**0.001**	14	77.78
FH	vs	FI	1.000	1.000	1.000	1	5.56
FH	vs	FIFH	1.000	1.000	1.000	0	0.00
FH	vs	FN	1.000	1.000	1.000	0	0.00
FH	vs	I	**<0.001**	**<0.001**	**<0.001**	14	77.78
FH	vs	IF	**<0.001**	**0.001**	**<0.001**	15	83.33
FH	vs	N	1.000	1.000	1.000	1	5.56
FH	vs	O	**<0.001**	1.000	**0.004**	13	72.22
FI	vs	FIFH	1.000	1.000	1.000	0	0.00
FI	vs	FN	1.000	0.732	1.000	3	16.67
FI	vs	I	**0.002**	0.119	**<0.001**	12	66.67
FI	vs	IF	**<0.001**	1.000	**0.003**	12	66.67
FI	vs	N	1.000	1.000	1.000	3	16.67
FI	vs	O	**0.002**	1.000	0.183	5	27.78
FIFH	vs	FN	1.000	1.000	1.000	0	0.00
FIFH	vs	I	1.000	1.000	1.000	0	0.00
FIFH	vs	IF	0.447	1.000	1.000	0	0.00
FIFH	vs	N	1.000	1.000	1.000	0	0.00
FIFH	vs	O	0.629	1.000	1.000	0	0.00
FN	vs	I	**<0.001**	**<0.001**	**<0.001**	14	77.78
FN	vs	IF	**<0.001**	**<0.001**	**<0.001**	13	72.22
FN	vs	N	1.000	1.000	1.000	4	22.22
FN	vs	O	**<0.001**	**0.046**	**0.002**	12	66.67
I	vs	IF	1.000	1.000	1.000	1	5.56
I	vs	N	**<0.001**	**0.001**	**<0.001**	13	72.22
I	vs	O	1.000	0.648	1.000	1	5.56
IF	vs	N	**<0.001**	**0.035**	**0.019**	11	61.11
IF	vs	O	1.000	1.000	1.000	0	0.00
N	vs	O	**<0.001**	1.000	0.745	4	22.22
No. Groups Discriminated			15	11	13		

Table 5.22. Results (*p*-values) of Critchlow-Fligner pairwise comparisons of all Balta dietary groups using Dietary Group 2. Significant results are bolded.

Groups Compared			Total Crest Length	Protoconid Height	Metaconid Height	Entoconid Height	Hypoconid Height	Mean Cusp Height	Hypoconid Angle
F	vs	FH	0.219	1.000	1.000	**0.001**	1.000	1.000	1.000
F	vs	FI	1.000	1.000	**<0.001**	**<0.001**	1.000	1.000	1.000
F	vs	FN	**<0.001**	1.000	1.000	**<0.001**	0.345	1.000	**<0.001**
F	vs	I	1.000	**<0.001**	1.000	**<0.001**	**<0.001**	**<0.001**	**<0.001**
F	vs	IF	0.110	**<0.001**	**<0.001**	**<0.001**	**<0.001**	**<0.001**	**<0.001**
F	vs	O	0.199	**0.002**	**<0.001**	**<0.001**	**0.002**	**<0.001**	**<0.001**
FH	vs	FI	1.000	1.000	**0.006**	**0.046**	1.000	1.000	1.000
FH	vs	FN	1.000	1.000	1.000	1.000	1.000	1.000	**0.001**
FH	vs	I	0.244	**<0.001**	1.000	0.167	**<0.001**	**<0.001**	**<0.001**
FH	vs	IF	1.000	**<0.001**	**0.007**	1.000	**<0.001**	**<0.001**	**<0.001**
FH	vs	O	1.000	**0.001**	**0.011**	**0.001**	0.292	**0.001**	**0.011**
FI	vs	FN	**0.034**	1.000	**<0.001**	1.000	1.000	1.000	0.075
FI	vs	I	1.000	**<0.001**	**<0.001**	0.263	**<0.001**	**0.016**	**0.001**
FI	vs	IF	1.000	**0.001**	1.000	1.000	**0.001**	**0.014**	**0.015**
FI	vs	O	1.000	0.200	1.000	**<0.001**	1.000	0.579	0.243
FN	vs	I	**<0.001**	**<0.001**	1.000	0.596	**<0.001**	**<0.001**	1.000
FN	vs	IF	0.124	**<0.001**	**<0.001**	1.000	**<0.001**	**<0.001**	1.000
FN	vs	O	1.000	**0.012**	**<0.001**	0.304	1.000	**0.001**	1.000
I	vs	IF	0.161	1.000	**<0.001**	1.000	1.000	1.000	1.000
I	vs	O	0.216	1.000	**0.001**	1.000	0.131	1.000	1.000
IF	vs	O	1.000	1.000	1.000	1.000	0.764	1.000	1.000
No. Groups Discriminated			3	11	12	9	9	11	10

Table 5.22, Cont'd.

Groups Compared			Protoconid Angle	Metaconid Angle	Entoconid Angle	Mean Cusp Angle	Talonid Basin Area	Talonid Basin Depth	Trigonid-Talonid Relief
F	vs	FH	0.187	1.000	1.000	1.000	1.000	0.972	0.442
F	vs	FI	1.000	1.000	1.000	1.000	1.000	**0.001**	1.000
F	vs	FN	1.000	1.000	1.000	1.000	1.000	0.777	1.000
F	vs	I	**<0.001**	**<0.001**	**<0.001**	**<0.001**	**<0.001**	1.000	**<0.001**
F	vs	IF	**<0.001**	**<0.001**	**<0.001**	**<0.001**	**<0.001**	0.059	**<0.001**
F	vs	O	**<0.001**	**<0.001**	0.098	**<0.001**	**0.002**	0.160	**<0.001**
FH	vs	FI	1.000	1.000	1.000	1.000	1.000	0.820	1.000
FH	vs	FN	0.180	1.000	1.000	0.596	1.000	1.000	**0.028**
FH	vs	I	**<0.001**	**<0.001**	**<0.001**	**<0.001**	**0.001**	1.000	**<0.001**
FH	vs	IF	**<0.001**	**<0.001**	**<0.001**	**<0.001**	**<0.001**	1.000	**<0.001**
FH	vs	O	**<0.001**	**<0.001**	**0.025**	**<0.001**	**0.009**	1.000	**<0.001**
FI	vs	FN	1.000	1.000	1.000	1.000	1.000	0.185	1.000
FI	vs	I	**<0.001**	0.178	**<0.001**	**<0.001**	1.000	**0.003**	**<0.001**
FI	vs	IF	**<0.001**	**<0.001**	**0.001**	**<0.001**	0.781	0.640	**<0.001**
FI	vs	O	**0.004**	**0.002**	0.153	**0.009**	1.000	1.000	**<0.001**
FN	vs	I	**<0.001**	**<0.001**	**<0.001**	**<0.001**	**<0.001**	1.000	**<0.001**
FN	vs	IF	**<0.001**	**<0.001**	**<0.001**	**<0.001**	**<0.001**	1.000	**<0.001**
FN	vs	O	**<0.001**	**<0.001**	**0.032**	**0.003**	**0.004**	1.000	**0.002**
I	vs	IF	1.000	0.121	1.000	1.000	1.000	0.338	1.000
I	vs	O	1.000	0.407	0.435	1.000	1.000	0.424	1.000
IF	vs	O	1.000	1.000	1.000	1.000	1.000	1.000	1.000
No. Groups Discriminated			12	11	10	12	9	2	13

Table 5.22, Cont'd.

Groups Compared	Trigonid Cusp Height	Trigonid Cusp Angle	Talonid Cusp Height	Talonid Cusp Angle	No. Variables Resulting in Discrimination	% Variables Resulting in Discrimination
F vs FH	1.000	1.000	0.775	1.000	1	5.56
F vs FI	1.000	1.000	**0.010**	1.000	4	22.22
F vs FN	1.000	1.000	0.575	1.000	3	16.67
F vs I	**<0.001**	**<0.001**	**<0.001**	**<0.001**	15	83.33
F vs IF	**<0.001**	**<0.001**	**<0.001**	**<0.001**	16	88.89
F vs O	**<0.001**	**<0.001**	**<0.001**	**<0.001**	15	83.33
FH vs FI	1.000	1.000	1.000	1.000	2	11.11
FH vs FN	1.000	1.000	1.000	1.000	2	11.11
FH vs I	**<0.001**	**<0.001**	**<0.001**	**<0.001**	14	77.78
FH vs IF	**<0.001**	**<0.001**	**<0.001**	**<0.001**	15	83.33
FH vs O	**<0.001**	**<0.001**	0.519	**0.005**	14	77.78
FI vs FN	1.000	1.000	1.000	1.000	2	11.11
FI vs I	**0.034**	**0.001**	0.070	**<0.001**	13	72.22
FI vs IF	**0.002**	**<0.001**	0.793	**0.002**	12	66.67
FI vs O	0.110	**0.001**	1.000	0.107	6	33.33
FN vs I	**<0.001**	**<0.001**	**<0.001**	**<0.001**	14	77.78
FN vs IF	**<0.001**	**<0.001**	**<0.001**	**<0.001**	14	77.78
FN vs O	**<0.001**	**<0.001**	0.081	**0.004**	12	66.67
I vs IF	1.000	1.000	1.000	1.000	1	5.56
I vs O	1.000	1.000	0.378	1.000	1	5.56
IF vs O	1.000	1.000	1.000	1.000	0	0.00
No. Groups Discriminated	11	12	8	11		

Table 5.23. Results (*p*-values) of Critchlow-Fligner pairwise comparisons of all Mindanao dietary groups using Dietary Group 1. Significant results are bolded.

Groups Compared			Total Crest Length	Mean Cusp Height	Mean Cusp Angle	Talonid Basin Depth	No. Variables Resulting in Discrimination
F	vs	FH	1.000	1.000	1.000	0.993	0
F	vs	FHFo	1.000	1.000	1.000	1.000	0
F	vs	FN	1.000	1.000	1.000	1.000	0
F	vs	Fo	**<0.001**	0.401	**<0.001**	**<0.001**	3
F	vs	I	**<0.001**	**<0.001**	**<0.001**	**<0.001**	4
F	vs	IFa	0.436	0.152	**0.002**	**<0.001**	2
F	vs	IH	0.944	**<0.001**	**<0.001**	1.000	2
F	vs	N	1.000	1.000	1.000	1.000	0
F	vs	O	**<0.001**	**<0.001**	**<0.001**	0.240	3
FH	vs	FHFo	1.000	1.000	1.000	1.000	0
FH	vs	FN	1.000	1.000	1.000	0.465	0
FH	vs	Fo	**<0.001**	1.000	0.424	1.000	1
FH	vs	I	**<0.001**	0.075	0.950	1.000	1
FH	vs	IFa	**0.030**	1.000	1.000	1.000	1
FH	vs	IH	0.066	1.000	1.000	1.000	0
FH	vs	N	1.000	1.000	1.000	0.302	0
FH	vs	O	**<0.001**	0.333	1.000	1.000	1
FHFo	vs	FN	1.000	1.000	1.000	1.000	0
FHFo	vs	Fo	**0.001**	0.437	**0.001**	**0.001**	3
FHFo	vs	I	**0.001**	**<0.001**	**<0.001**	1.000	3
FHFo	vs	IFa	1.000	0.204	1.000	0.144	0
FHFo	vs	IH	1.000	**0.001**	0.938	1.000	1
FHFo	vs	N	1.000	1.000	1.000	1.000	0
FHFo	vs	O	**0.001**	**<0.001**	**0.010**	1.000	3
FN	vs	Fo	**0.004**	0.545	**<0.001**	**<0.001**	3
FN	vs	I	**0.010**	**<0.001**	**<0.001**	**0.004**	4
FN	vs	IFa	1.000	0.273	0.296	**<0.001**	1
FN	vs	IH	1.000	**<0.001**	0.068	1.000	1
FN	vs	N	1.000	1.000	1.000	1.000	0
FN	vs	O	**0.003**	**0.001**	**0.001**	**0.142**	4
Fo	vs	I	1.000	1.000	1.000	**0.021**	1
Fo	vs	IFa	1.000	1.000	1.000	1.000	0
Fo	vs	IH	0.149	1.000	0.988	**<0.001**	1
Fo	vs	N	**<0.001**	**0.027**	**<0.001**	**<0.001**	4
Fo	vs	O	1.000	1.000	1.000	0.619	0

Table 5.23, Cont'd.

Groups Compared			Total Crest Length	Mean Cusp Height	Mean Cusp Angle	Talonid Basin Depth	No. Variables Resulting in Discrimination
I	vs	IFa	1.000	1.000	1.000	1.000	0
I	vs	IH	0.816	1.000	1.000	0.569	0
I	vs	N	**<0.001**	**<0.001**	**<0.001**	**0.012**	4
I	vs	O	1.000	1.000	1.000	1.000	0
IFa	vs	IH	1.000	1.000	1.000	**0.033**	1
IFa	vs	N	0.072	**0.012**	0.072	**0.001**	2
IFa	vs	O	1.000	1.000	1.000	1.000	0
IH	vs	N	0.161	**<0.001**	**0.018**	1.000	2
IH	vs	O	0.128	1.000	1.000	1.000	0
N	vs	O	**<0.001**	**<0.001**	**<0.001**	0.112	3
No. Groups Discriminated			17	14	15	14	

Table 5.24. Results (*p*-values) of Critchlow-Fligner pairwise comparisons of all Mindanao dietary groups using Dietary Group 2. Significant results are bolded.

Groups Compared			Total Crest Length	Mean Cusp Height	Mean Cusp Angle	Talonid Basin Depth	No. Variables Resulting in Discrimination
F	vs	FH	1.000	1.000	0.105	0.426	0
F	vs	FN	1.000	1.000	1.000	1.000	0
F	vs	Fo	**<0.001**	0.134	**<0.001**	**<0.001**	3
F	vs	I	**<0.001**	**<0.001**	**<0.001**	**<0.001**	4
F	vs	O	**<0.001**	**<0.001**	**<0.001**	0.080	3
FH	vs	FN	1.000	1.000	0.280	**0.042**	1
FH	vs	Fo	**<0.001**	0.193	**<0.001**	**0.001**	3
FH	vs	I	**<0.001**	**<0.001**	**<0.001**	1.000	3
FH	vs	O	**<0.001**	**<0.001**	**0.004**	1.000	3
FN	vs	Fo	**<0.001**	**0.015**	**<0.001**	**<0.001**	4
FN	vs	I	**<0.001**	**<0.001**	**<0.001**	**<0.001**	4
FN	vs	O	**<0.001**	**<0.001**	**<0.001**	**0.009**	4
Fo	vs	I	0.564	1.000	1.000	**0.003**	1
Fo	vs	O	1.000	1.000	1.000	0.206	0
I	vs	O	0.493	1.000	1.000	1.000	0
No. Groups Discriminated			9	7	9	8	

Table 5.25. K-nearest-neighbor discriminant analysis of Variable Set 1 of the Balta sample using Dietary Group 1 assignments. Correct reclassifications are bolded.

Original Group		Classified Group										
		F	FH	FI	FIFH	FN	I	IF	N	O	Other	Total
F	N	**86**	0	1	0	0	0	0	0	0	1	88
	%	**97.73**	0.00	1.14	0.00	0.00	0.00	0.00	0.00	0.00	1.14	100.00
FH	N	0	**14**	2	0	0	0	0	0	0	0	16
	%	0.00	**87.50**	12.50	0.00	0.00	0.00	0.00	0.00	0.00	0.00	100.00
FI	N	0	0	**11**	0	0	0	0	0	0	1	12
	%	0.00	0.00	**91.67**	0.00	0.00	0.00	0.00	0.00	0.00	8.33	100.00
FIFH	N	0	0	0	**0**	0	0	0	0	0	2	2
	%	0.00	0.00	0.00	**0.00**	0.00	0.00	0.00	0.00	0.00	100.00	100.00
FN	N	0	0	1	0	**2**	1	0	3	0	1	8
	%	0.00	0.00	12.50	0.00	**25.00**	12.50	0.00	37.50	0.00	12.50	100.00
I	N	0	0	0	0	0	**53**	1	0	1	0	55
	%	0.00	0.00	0.00	0.00	0.00	**96.36**	1.82	0.00	1.82	0.00	100.00
IF	N	0	0	0	0	0	2	**36**	0	1	0	39
	%	0.00	0.00	0.00	0.00	0.00	5.13	**92.31**	0.00	2.56	0.00	100.00
N	N	0	0	0	0	0	0	0	**13**	0	1	14
	%	0.00	0.00	0.00	0.00	0.00	0.00	0.00	**92.86**	0.00	7.14	100.00
O	N	0	0	0	0	0	0	4	0	**11**	0	15
	%	0.00	0.00	0.00	0.00	0.00	0.00	26.67	0.00	**73.33**	0.00	100.00
Total	N	86	14	15	0	2	56	41	16	13	**6**	249
	%	34.54	5.62	6.02	0.00	0.80	22.49	16.47	6.43	5.22	**2.41**	100.00
Priors		0.353	0.064	0.048	0.008	0.032	0.221	0.157	0.056	0.060		
Error Rate		0.023	0.125	0.083	1.000	0.750	0.036	0.077	0.071	0.267		**0.092**

Table 5.26. Misclassified individuals in the discriminant analysis of the Balta sample using Variable Set 1 and Dietary Group 1 classification.

Specimen	Species	Original Group	Assigned Group	Posterior Probabilities of Membership Into Each Dietary Group								
				F	FH	FI	FIFH	FN	I	IF	N	O
LSU 14127	*Anoura caudifer*	FN	Other	0.000	0.000	0.000	0.000	0.333	0.000	0.333	0.333	0.000
LSU 14130	*Anoura caudifer*	FN	N	0.000	0.000	0.000	0.000	0.333	0.000	0.000	0.667	0.000
LSU 14131	*Anoura caudifer*	FN	I	0.000	0.000	0.000	0.000	0.333	0.667	0.000	0.000	0.000
LSU 14132	*Anoura caudifer*	FN	N	0.000	0.000	0.000	0.000	0.333	0.000	0.000	0.667	0.000
LSU 16478	*Anoura caudifer*	FN	N	0.000	0.000	0.000	0.000	0.333	0.000	0.000	0.667	0.000
LSU 16468	*Anoura geoffroyi*	FN	FI	0.000	0.000	0.667	0.000	0.333	0.000	0.000	0.000	0.000
LSU 12290	*Callicebus moloch*	FH	FI	0.000	0.333	0.667	0.000	0.000	0.000	0.000	0.000	0.000
LSU 9267	*Callicebus moloch*	FH	FI	0.000	0.333	0.667	0.000	0.000	0.000	0.000	0.000	0.000
LSU 14025	*Caluromys lanatus*	F	Other	0.333	0.000	0.000	0.000	0.000	0.000	0.333	0.000	0.333
LSU 12296	*Cebus albifrons*	FIFH	Other	0.333	0.000	0.333	0.333	0.000	0.000	0.000	0.000	0.000
LSU 14340	*Cebus albifrons*	FIFH	Other	0.000	0.333	0.333	0.333	0.000	0.000	0.000	0.000	0.000
LSU 14001	*Didelphis marsupialis*	O	IF	0.000	0.000	0.000	0.000	0.000	0.000	0.667	0.000	0.333
LSU 16378	*Gracilianus agilis*	FI	Other	0.000	0.000	0.333	0.000	0.000	0.000	0.333	0.000	0.333
LSU 12100	*Lonchophylla thomasi*	N	Other	0.000	0.000	0.000	0.000	0.333	0.000	0.333	0.333	0.000
LSU 14079	*Lophostoma silvicolum*	IF	I	0.000	0.000	0.000	0.000	0.000	0.667	0.333	0.000	0.000
LSU 14075	*Macrophyllum macrophyllum*	I	O	0.000	0.000	0.000	0.000	0.000	0.333	0.000	0.000	0.667
LSU 16385	*Marmosa murina*	IF	O	0.000	0.000	0.000	0.000	0.000	0.000	0.333	0.000	0.667
LSU 16393	*Philander mcilhennyi*	O	IF	0.000	0.000	0.000	0.000	0.000	0.000	0.667	0.000	0.333
LSU 14103	*Phyllostomus elongatus*	IF	I	0.000	0.000	0.000	0.000	0.000	0.667	0.333	0.000	0.000
LSU 12071	*Phyllostomus hastatus*	O	IF	0.000	0.000	0.000	0.000	0.000	0.000	0.667	0.000	0.333
LSU 16455	*Phyllostomus hastatus*	O	IF	0.000	0.000	0.000	0.000	0.000	0.000	0.667	0.000	0.333
LSU 14033	*Saccopteryx bilineata*	I	IF	0.000	0.000	0.000	0.000	0.000	0.333	0.667	0.000	0.000
LSU 12526	*Vampyressa pusilla*	F	FI	0.333	0.000	0.667	0.000	0.000	0.000	0.000	0.000	0.000

Table 5.27. K-nearest-neighbor discriminant analysis of Variable Set 1 of the Balta sample using Dietary Group 2 assignments. Correct reclassifications are bolded.

Original Group		Classified Group								
		F	FH	FI	FN	I	IF	O	Other	Total
F	N	**86**	0	1	0	0	0	0	1	88
	%	**97.73**	0.00	1.14	0.00	0.00	0.00	0.00	1.14	100.00
FH	N	0	**17**	1	0	0	0	0	0	18
	%	0.00	**94.44**	5.56	0.00	0.00	0.00	0.00	0.00	100.00
FI	N	0	0	**11**	0	0	0	0	1	12
	%	0.00	0.00	**91.67**	0.00	0.00	0.00	0.00	8.33	100.00
FN	N	0	0	1	**20**	1	0	0	0	22
	%	0.00	0.00	4.55	**90.91**	4.55	0.00	0.00	0.00	100.00
I	N	0	0	0	0	**53**	1	1	0	55
	%	0.00	0.00	0.00	0.00	**96.36**	1.82	1.82	0.00	100.00
IF	N	0	0	0	0	2	**35**	1	0	39
	%	0.00	0.00	0.00	0.00	5.13	**92.31**	2.56	0.00	100.00
O	N	0	0	0	0	0	4	**11**	0	15
	%	0.00	0.00	0.00	0.00	0.00	26.67	**73.33**	0.00	100.00
Total	N	86	17	14	20	56	41	13	2	249
	%	34.54	6.83	5.62	8.03	22.49	16.47	5.22	0.80	100.00
Priors		0.353	0.072	0.048	0.088	0.221	0.157	0.060		
Error Rate		0.023	0.056	0.083	0.091	0.036	0.077	0.267		**0.060**

Table 5.28. Misclassified individuals in the discriminant analysis of the Balta sample using Variable Set 1 and Dietary Group 2 classification.

Specimen	Species	Original Group	Assigned Group	Posterior Probabilities of Membership Into Each Dietary Group						
				F	FH	FI	FN	I	IF	O
LSU 14131	*Anoura caudifer*	FN	I	0.000	0.000	0.000	0.333	0.667	0.000	0.000
LSU 16468	*Anoura geoffroyi*	FN	FI	0.000	0.000	0.667	0.333	0.000	0.000	0.000
LSU 9267	*Callicebus moloch*	FH	FI	0.000	0.333	0.667	0.000	0.000	0.000	0.000
LSU 14025	*Caluromys lanatus*	F	Other	0.333	0.000	0.000	0.000	0.000	0.333	0.333
LSU 14001	*Didelphis marsupialis*	O	IF	0.000	0.000	0.000	0.000	0.000	0.667	0.333
LSU 16378	*Gracilianus agilis*	FI	Other	0.000	0.000	0.333	0.000	0.000	0.333	0.333
LSU 14079	*Lophostoma silvicolum*	IF	I	0.000	0.000	0.000	0.000	0.667	0.333	0.000
LSU 14075	*Macrophyllum macrophyllum*	I	O	0.000	0.000	0.000	0.000	0.333	0.000	0.667
LSU 16385	*Marmosa murina*	IF	O	0.000	0.000	0.000	0.000	0.000	0.333	0.667
LSU 16393	*Philander mcilhennyi*	O	IF	0.000	0.000	0.000	0.000	0.000	0.667	0.333
LSU 14103	*Phyllostomus elongatus*	IF	I	0.000	0.000	0.000	0.000	0.667	0.333	0.000
LSU 12071	*Phyllostomus hastatus*	O	IF	0.000	0.000	0.000	0.000	0.000	0.667	0.333
LSU 16455	*Phyllostomus hastatus*	O	IF	0.000	0.000	0.000	0.000	0.000	0.667	0.333
LSU 14033	*Saccopteryx bilineata*	I	IF	0.000	0.000	0.000	0.000	0.333	0.667	0.000
LSU 12526	*Vampyressa pusilla*	F	FI	0.333	0.000	0.667	0.000	0.000	0.000	0.000

Table 5.29. K-nearest-neighbor discriminant analysis of Variable Set 2 of the Balta sample using Dietary Group 2 assignments. Correct reclassifications are bolded.

Original Group		Classified Group								
		F	FH	FI	FN	I	IF	O	Other	Total
F	N	**83**	1	1	2	0	0	0	1	88
	%	**94.32**	1.14	1.14	2.27	0.00	0.00	0.00	1.14	100.00
FH	N	1	**15**	1	1	0	0	0	0	18
	%	5.56	**83.33**	5.56	5.56	0.00	0.00	0.00	0.00	100.00
FI	N	0	1	**10**	0	0	0	0	1	12
	%	0.00	8.33	**83.33**	0.00	0.00	0.00	0.00	8.33	100.00
FN	N	0	0	0	**35**	0	0	0	1	36
	%	0.00	0.00	0.00	**97.22**	0.00	0.00	0.00	2.78	100.00
I	N	0	0	0	0	**48**	5	0	2	55
	%	0.00	0.00	0.00	0.00	**87.27**	9.09	0.00	3.64	100.00
IF	N	0	0	0	0	1	**35**	0	3	39
	%	0.00	0.00	0.00	0.00	2.56	**89.74**	0.00	7.69	100.00
O	N	0	0	0	0	1	4	**6**	4	15
	%	0.00	0.00	0.00	0.00	6.67	26.67	**40.00**	26.67	100.00
Total	N	84	17	12	38	50	44	6	12	263
	%	31.94	6.46	4.56	14.45	19.01	16.73	2.28	4.56	100.00
Priors		0.335	0.068	0.046	0.137	0.209	0.148	0.057		
Error Rate		0.057	0.167	0.167	0.028	0.127	0.103	0.600		**0.118**

Table 5.30. Misclassified individuals in the discriminant analysis of the Balta sample using Variable Set 2 and Dietary Group 2 classification.

Specimen	Species	Original Group	Assigned Group	Posterior Probabilities of Membership Into Each Dietary Group						
				F	FH	FI	FN	I	IF	O
LSU 9267	*Callicebus moloch*	FH	FI	0.000	0.333	0.667	0.000	0.000	0.000	0.000
LSU 14025	*Caluromys lanatus*	F	FN	0.333	0.000	0.000	0.667	0.000	0.000	0.000
LSU 14230	*Chiroderma villosum*	F	Other	0.333	0.333	0.000	0.000	0.333	0.000	0.000
LSU 14001	*Didelphis marsupialis*	O	IF	0.000	0.000	0.000	0.000	0.000	0.667	0.333
LSU 12184	*Ectophylla macconnelli*	F	FN	0.333	0.000	0.000	0.667	0.000	0.000	0.000
LSU 12280	*Eptesicus brasiliensis*	I	IF	0.000	0.000	0.000	0.000	0.333	0.667	0.000
LSU 12283	*Eptesicus furinalis*	I	IF	0.000	0.000	0.000	0.000	0.333	0.667	0.000
LSU 16378	*Gracilianus agilis*	FI	Other	0.000	0.000	0.333	0.000	0.000	0.333	0.333
LSU 14315	*Lasiurus ega*	I	IF	0.000	0.000	0.000	0.000	0.333	0.667	0.000
LSU 12098	*Lonchophylla thomasi*	FN	Other	0.333	0.000	0.000	0.333	0.000	0.333	0.000
LSU 16441	*Lophostoma silvicolum*	IF	Other	0.000	0.000	0.000	0.000	0.333	0.333	0.333
LSU 14074	*Macrophyllum macrophyllum*	I	IF	0.000	0.000	0.000	0.000	0.333	0.667	0.000
LSU 14075	*Macrophyllum macrophyllum*	I	Other	0.000	0.000	0.000	0.333	0.333	0.333	0.000
LSU 16380	*Marmosops noctivagus*	IF	I	0.000	0.000	0.000	0.000	0.667	0.333	0.000
LSU 14070	*Micronycteris megalotis*	IF	Other	0.000	0.000	0.000	0.000	0.333	0.333	0.333
LSU 14092	*Mimon crenulatum*	I	IF	0.000	0.000	0.000	0.000	0.333	0.667	0.000
LSU 16446	*Mimon crenulatum*	I	Other	0.000	0.000	0.000	0.000	0.333	0.333	0.333
LSU 16393	*Philander mcilhennyi*	O	IF	0.000	0.000	0.000	0.000	0.000	0.667	0.333
LSU 12009	*Philander opossum*	O	Other	0.000	0.000	0.333	0.000	0.000	0.333	0.333
LSU 12069	*Phyllostomus hastatus*	O	IF	0.000	0.000	0.000	0.000	0.000	0.667	0.333
LSU 12070	*Phyllostomus hastatus*	O	Other	0.000	0.000	0.000	0.000	0.333	0.333	0.333
LSU 12071	*Phyllostomus hastatus*	O	Other	0.000	0.000	0.000	0.000	0.333	0.333	0.333
LSU 14098	*Phyllostomus hastatus*	O	IF	0.000	0.000	0.000	0.000	0.000	0.667	0.333

Table 5.30, Cont'd.

Specimen	Species	Original Group	Assigned Group	Posterior Probabilities of Membership Into Each Dietary Group						
				F	FH	FI	FN	I	IF	O
LSU 16456	*Phyllostomus hastatus*	O	I	0.000	0.000	0.000	0.000	0.667	0.000	0.333
LSU 12177	*Platyrrhinus helleri*	F	FH	0.333	0.667	0.000	0.000	0.000	0.000	0.000
LSU 12298	*Saimiri boliviensis*	FI	FH	0.000	0.667	0.333	0.000	0.000	0.000	0.000
LSU 12312	*Sciurus ignitus*	FH	FN	0.000	0.333	0.000	0.667	0.000	0.000	0.000
LSU 12313	*Sciurus ignitus*	FH	F	0.667	0.333	0.000	0.000	0.000	0.000	0.000
LSU 14083	*Tonatia saurophila*	IF	Other	0.000	0.000	0.000	0.000	0.333	0.333	0.333
LSU 12526	*Vampyressa pusilla*	F	FI	0.333	0.000	0.667	0.000	0.000	0.000	0.000

Table 5.31. K-nearest-neighbor discriminant analysis of Variable Set 3 of the Balta sample using Dietary Group 2 assignments. Correct reclassifications are bolded.

Original Group		Classified Group								
		F	FH	FI	FN	I	IF	O	Other	Total
F	N	**87**	0	0	1	0	0	0	0	88
	%	**98.86**	0.00	0.00	1.14	0.00	0.00	0.00	0.00	100.00
FH	N	0	**15**	1	0	0	0	0	2	18
	%	0.00	**83.33**	5.56	0.00	0.00	0.00	0.00	11.11	100.00
FI	N	0	0	**11**	0	0	0	0	1	12
	%	0.00	0.00	**91.67**	0.00	0.00	0.00	0.00	8.33	100.00
FN	N	0	1	0	**33**	1	0	0	1	36
	%	0.00	2.78	0.00	**91.67**	2.78	0.00	0.00	2.78	100.00
I	N	0	0	0	0	**50**	2	0	3	55
	%	0.00	0.00	0.00	0.00	**90.91**	3.64	0.00	5.45	100.00
IF	N	0	0	0	0	3	**31**	3	2	39
	%	0.00	0.00	0.00	0.00	7.69	**79.49**	7.69	5.13	100.00
O	N	0	0	0	0	0	4	**7**	4	15
	%	0.00	0.00	0.00	0.00	0.00	26.67	**46.67**	26.67	100.00
Total	N	87	16	12	34	54	37	10	13	263
	%	33.08	6.08	4.56	12.93	20.53	14.07	3.80	4.94	100.00
Priors		0.335	0.068	0.046	0.137	0.209	0.148	0.057		
Error Rate		0.011	0.167	0.083	0.083	0.091	0.205	0.533		**0.110**

Table 5.32. Misclassified individuals in the discriminant analysis of the Balta sample using Variable Set 3 and Dietary Group 2 classification.

Specimen	Species	Original Group	Assigned Group	Posterior Probabilities of Membership Into Each Dietary Group						
				F	FH	FI	FN	I	IF	O
LSU 14130	*Anoura caudifer*	FN	FH	0.000	0.667	0.000	0.333	0.000	0.000	0.000
LSU 9267	*Callicebus moloch*	FH	FI	0.000	0.333	0.667	0.000	0.000	0.000	0.000
LSU 14025	*Caluromys lanatus*	F	FN	0.333	0.000	0.000	0.667	0.000	0.000	0.000
LSU 12296	*Cebus albifrons*	FH	Other	0.333	0.333	0.333	0.000	0.000	0.000	0.000
LSU 14340	*Cebus albifrons*	FH	Other	0.000	0.333	0.333	0.000	0.333	0.000	0.000
LSU 14001	*Didelphis marsupialis*	O	IF	0.000	0.000	0.000	0.000	0.000	0.667	0.333
LSU 16378	*Gracilianus agilis*	FI	Other	0.000	0.000	0.333	0.000	0.000	0.333	0.333
LSU 12098	*Lonchophylla thomasi*	FN	I	0.000	0.000	0.000	0.333	0.667	0.000	0.000
LSU 12100	*Lonchophylla thomasi*	FN	Other	0.000	0.000	0.000	0.333	0.333	0.333	0.000
LSU 14078	*Lophostoma silvicolum*	IF	O	0.000	0.000	0.000	0.000	0.000	0.333	0.667
LSU 14079	*Lophostoma silvicolum*	IF	I	0.000	0.000	0.000	0.000	0.667	0.333	0.000
LSU 16441	*Lophostoma silvicolum*	IF	Other	0.000	0.000	0.000	0.000	0.333	0.333	0.333
LSU 14075	*Macrophyllum macrophyllum*	I	Other	0.000	0.000	0.000	0.333	0.333	0.000	0.333
LSU 16385	*Marmosa murina*	IF	O	0.000	0.000	0.000	0.000	0.000	0.333	0.667
LSU 14068	*Micronycteris megalotis*	IF	O	0.000	0.000	0.000	0.000	0.000	0.333	0.667
LSU 14070	*Micronycteris megalotis*	IF	Other	0.000	0.000	0.000	0.000	0.333	0.333	0.333
LSU 14092	*Mimon crenulatum*	I	IF	0.000	0.000	0.000	0.000	0.333	0.667	0.000
LSU 12030	*Noctilio albiventris*	I	Other	0.000	0.000	0.333	0.000	0.333	0.333	0.000
LSU 16393	*Philander mcilhennyi*	O	IF	0.000	0.000	0.000	0.000	0.000	0.667	0.333
LSU 12009	*Philander opossum*	O	Other	0.000	0.000	0.333	0.000	0.000	0.333	0.333
LSU 14103	*Phyllostomus elongatus*	IF	I	0.000	0.000	0.000	0.000	0.667	0.333	0.000
LSU 14105	*Phyllostomus elongatus*	IF	I	0.000	0.000	0.000	0.000	0.667	0.333	0.000
LSU 12069	*Phyllostomus hastatus*	O	IF	0.000	0.000	0.000	0.000	0.000	0.667	0.333
LSU 12071	*Phyllostomus hastatus*	O	Other	0.000	0.000	0.000	0.000	0.333	0.333	0.333

Table 5.32, Cont'd.

Specimen	Species	Original Group	Assigned Group	Posterior Probabilities of Membership Into Each Dietary Group						
				F	FH	FI	FN	I	IF	O
LSU 14098	*Phyllostomus hastatus*	O	IF	0.000	0.000	0.000	0.000	0.000	0.667	0.333
LSU 16455	*Phyllostomus hastatus*	O	Other	0.000	0.000	0.000	0.000	0.333	0.333	0.333
LSU 16456	*Phyllostomus hastatus*	O	Other	0.000	0.000	0.000	0.000	0.333	0.333	0.333
LSU 12072	*Trachops cirrhosus*	I	Other	0.000	0.000	0.000	0.000	0.333	0.333	0.333
LSU 12074	*Trachops cirrhosus*	I	IF	0.000	0.000	0.000	0.000	0.333	0.667	0.000

Table 5.33. K-nearest-neighbor discriminant analysis of Variable Set 1 (excluding talonid basin depth) of the Balta sample using Dietary Group 2 assignments. Correct reclassifications are bolded.

Original Group		Classified Group								
		F	FH	FI	FN	I	IF	O	Other	Total
F	N	**92**	0	0	0	0	1	0	1	94
	%	**97.87**	0.00	0.00	0.00	0.00	1.06	0.00	1.06	100.00
FH	N	1	**16**	1	0	0	0	0	0	18
	%	5.56	**88.89**	5.56	0.00	0.00	0.00	0.00	0.00	100.00
FI	N	0	1	**10**	0	0	0	0	1	12
	%	0.00	8.33	**83.33**	0.00	0.00	0.00	0.00	8.33	100.00
FN	N	0	1	1	**18**	1	0	0	1	22
	%	0.00	4.55	4.55	**81.82**	4.55	0.00	0.00	4.55	100.00
I	N	0	0	0	0	**50**	3	1	1	55
	%	0.00	0.00	0.00	0.00	**90.91**	5.45	1.82	1.82	100.00
IF	N	0	0	0	0	1	**34**	1	3	39
	%	0.00	0.00	0.00	0.00	2.56	**87.18**	2.56	7.69	100.00
O	N	0	0	0	0	0	3	**12**	0	15
	%	0.00	0.00	0.00	0.00	0.00	20.00	**80.00**	0.00	100.00
Total	N	93	18	12	18	52	41	14	**7**	255
	%	36.47	7.06	4.71	7.06	20.39	16.08	5.49	**2.75**	100.00
Priors		0.369	0.071	0.047	0.086	0.216	0.153	0.059		
Error Rate		0.021	0.111	0.167	0.182	0.091	0.128	0.200		**0.090**

Table 5.34. K-nearest-neighbor discriminant analysis of Variable Set 2 (excluding talonid basin depth) of the Balta sample using Dietary Group 2 assignments. Correct reclassifications are bolded.

Original Group		Classified Group								
		F	FH	FI	FN	I	IF	O	Other	Total
F	N	**92**	1	0	1	0	0	0	0	94
	%	**97.87**	1.06	0.00	1.06	0.00	0.00	0.00	0.00	100.00
FH	N	1	**11**	2	1	0	0	0	3	18
	%	5.56	**61.11**	11.11	5.56	0.00	0.00	0.00	16.67	100.00
FI	N	1	1	**9**	0	1	0	0	0	12
	%	8.33	8.33	**75.00**	0.00	8.33	0.00	0.00	0.00	100.00
FN	N	0	2	1	**30**	0	0	0	3	36
	%	0.00	5.56	2.78	**83.33**	0.00	0.00	0.00	8.33	100.00
I	N	0	0	0	0	**43**	7	0	5	55
	%	0.00	0.00	0.00	0.00	**78.18**	12.73	0.00	9.09	100.00
IF	N	0	0	0	0	3	**29**	0	7	39
	%	0.00	0.00	0.00	0.00	7.69	**74.36**	0.00	17.95	100.00
O	N	0	0	0	0	4	2	**6**	3	15
	%	0.00	0.00	0.00	0.00	26.67	13.33	**40.00**	20.00	100.00
Total	N	94	15	12	32	51	38	6	**21**	269
	%	34.94	5.58	4.46	11.90	18.96	14.13	2.23	**7.81**	100.00
Priors		0.349	0.067	0.045	0.134	0.204	0.145	0.056		
Error Rate		0.021	0.389	0.250	0.167	0.218	0.256	0.600		**0.182**

Table 5.35. K-nearest-neighbor discriminant analysis of Variable Set 3 (excluding talonid basin depth) of the Balta sample using Dietary Group 2 assignments. Correct reclassifications are bolded.

Original Group		Classified Group								
		F	FH	FI	FN	I	IF	O	Other	Total
F	N	**86**	0	0	1	0	0	0	1	88
	%	**97.73**	0.00	0.00	1.14	0.00	0.00	0.00	1.14	100.00
FH	N	1	**12**	2	2	1	0	0	0	18
	%	5.56	**66.67**	11.11	11.11	5.56	0.00	0.00	0.00	100.00
FI	N	0	0	**11**	0	0	0	0	1	12
	%	0.00	0.00	**91.67**	0.00	0.00	0.00	0.00	8.33	100.00
FN	N	1	4	1	**26**	0	0	0	4	36
	%	2.78	11.11	2.78	**72.22**	0.00	0.00	0.00	11.11	100.00
I	N	0	0	0	0	**50**	3	0	2	55
	%	0.00	0.00	0.00	0.00	**90.91**	5.45	0.00	3.64	100.00
IF	N	0	0	0	0	3	**30**	4	2	39
	%	0.00	0.00	0.00	0.00	7.69	**76.92**	10.26	5.13	100.00
O	N	0	0	0	0	1	7	**6**	1	15
	%	0.00	0.00	0.00	0.00	6.67	46.67	**40.00**	6.67	100.00
Total	N	88	16	14	29	55	40	10	**11**	263
	%	33.46	6.08	5.32	11.03	20.91	15.21	3.80	**4.18**	100.00
Priors		0.335	0.068	0.046	0.137	0.209	0.148	0.057		
Error Rate		0.023	0.333	0.083	0.278	0.091	0.231	0.600		**0.160**

Table 5.36. K-nearest-neighbor discriminant analysis of Variable Set 2* of the Mindanao sample using Dietary Group 2 assignments. Correct reclassifications are bolded.

Original Group		Classified Group							
		F	FH	FN	Fo	I	O	Other	Total
F	N	**45**	0	1	0	0	0	1	47
	%	**95.74**	0.00	2.13	0.00	0.00	0.00	2.13	100.00
FH	N	0	**20**	0	0	0	0	1	21
	%	0.00	**95.24**	0.00	0.00	0.00	0.00	4.76	100.00
FN	N	3	0	**15**	0	0	0	1	19
	%	15.79	0.00	**78.95**	0.00	0.00	0.00	5.26	100.00
Fo	N	0	0	0	**7**	2	0	0	9
	%	0.00	0.00	0.00	**77.78**	22.22	0.00	0.00	100.00
I	N	0	0	0	0	**96**	1	0	97
	%	0.00	0.00	0.00	0.00	**98.97**	1.03	0.00	100.00
O	N	0	0	0	0	6	**3**	0	9
	%	0.00	0.00	0.00	0.00	66.67	**33.33**	0.00	100.00
Total	N	48	20	16	7	104	4	3	202
	%	23.76	9.90	7.92	3.47	51.49	1.98	1.49	100.00
Priors		0.233	0.104	0.094	0.045	0.480	0.045		
Error Rate		0.043	0.048	0.211	0.222	0.010	0.667		**0.079**

Table 5.37. Misclassified individuals in the discriminant analysis of the Mindanao sample using Variable Set 2* and Dietary Group 2 classification.

Specimen	Species	Original Group	Assigned Group	Posterior Probabilities of Membership Into Each Dietary Group					
				F	FH	FN	Fo	I	O
FMNH 56536	*Acerodon jubatus*	F	FN	0.333	0.000	0.667	0.000	0.000	0.000
FMNH 166461	*Dyacopterus rickarti*	F	Other	0.333	0.333	0.333	0.000	0.000	0.000
FMNH 67747	*Exilisciurus concinnus*	FH	Other	0.333	0.333	0.333	0.000	0.000	0.000
FMNH 146607	*Cynopterus brachyotis*	FN	F	0.667	0.000	0.333	0.000	0.000	0.000
FMNH 146610	*Cynopterus brachyotis*	FN	F	0.667	0.000	0.333	0.000	0.000	0.000
FMNH 146612	*Cynopterus brachyotis*	FN	F	0.667	0.000	0.333	0.000	0.000	0.000
FMNH 56444	*Rousettus amplexicaudatus*	FN	Other	0.333	0.333	0.333	0.000	0.000	0.000
FMNH 56441	*Cynocephalus volans*	Fo	I	0.000	0.000	0.000	0.333	0.667	0.000
NMNH 219056	*Cynocephalus volans*	Fo	I	0.000	0.000	0.000	0.333	0.667	0.000
FMNH 54923	*Pipistrellus javanicus*	I	O	0.000	0.000	0.000	0.000	0.333	0.667
FMNH 146590	*Urogale everetti*	O	I	0.000	0.000	0.000	0.000	0.667	0.333
FMNH 166479	*Urogale everetti*	O	I	0.000	0.000	0.000	0.000	0.667	0.333
FMNH 166480	*Urogale everetti*	O	I	0.000	0.000	0.000	0.000	0.667	0.333
FMNH 61079	*Urogale everetti*	O	I	0.000	0.000	0.000	0.000	0.667	0.333
FMNH 61418	*Urogale everetti*	O	I	0.000	0.000	0.000	0.000	0.667	0.333
FMNH 61419	*Urogale everetti*	O	I	0.000	0.000	0.000	0.000	0.667	0.333

Table 5.38. K-nearest-neighbor discriminant analysis of Variable Set 2* (excluding talonid basin depth) of the Mindanao sample using Dietary Group 2 assignments. Correct reclassifications are bolded.

Original Group		Classified Group							
		F	FH	FN	Fo	I	O	Other	Total
F	N	**43**	1	1	0	0	0	2	47
	%	**91.49**	2.13	2.13	0.00	0.00	0.00	4.26	100.00
FH	N	1	**19**	1	0	0	0	0	21
	%	4.76	**90.48**	4.76	0.00	0.00	0.00	0.00	100.00
FN	N	3	0	**13**	0	0	0	3	19
	%	15.79	0.00	**68.42**	0.00	0.00	0.00	15.79	100.00
Fo	N	0	0	0	**6**	3	0	0	9
	%	0.00	0.00	0.00	**66.67**	33.33	0.00	0.00	100.00
I	N	0	0	0	0	**94**	2	1	97
	%	0.00	0.00	0.00	0.00	**96.91**	2.06	1.03	100.00
O	N	0	0	0	0	4	**5**	0	9
	%	0.00	0.00	0.00	0.00	44.44	**55.56**	0.00	100.00
Total	N	47	20	15	6	101	7	**6**	202
	%	23.27	9.90	7.43	2.97	50.00	3.47	**2.97**	100.00
Priors		0.233	0.104	0.094	0.045	0.480	0.045		
Error Rate		0.085	0.095	0.316	0.333	0.031	0.444		**0.109**

Table 5.39. K-nearest-neighbor discriminant analysis of Variable Set 2* of the combined Balta-Mindanao sample using Dietary Group 2 assignments. Correct reclassifications are bolded.

Original Group		Classified Group									
		F	FH	FI	FN	Fo	I	IF	O	Other	Total
F	N	**126**	1	0	3	0	1	0	0	4	135
	%	**93.33**	0.74	0.00	2.22	0.00	0.74	0.00	0.00	2.96	100.00
FH	N	3	**29**	0	2	0	0	0	0	5	39
	%	7.69	**74.36**	0.00	5.13	0.00	0.00	0.00	0.00	12.82	100.00
FI	N	0	2	**9**	0	0	0	0	0	1	12
	%	0.00	16.67	**75.00**	0.00	0.00	0.00	0.00	0.00	8.33	100.00
FN	N	4	0	0	**44**	0	1	0	0	6	55
	%	7.27	0.00	0.00	**80.00**	0.00	1.82	0.00	0.00	10.91	100.00
Fo	N	0	0	0	0	**3**	4	0	0	2	9
	%	0.00	0.00	0.00	0.00	**33.33**	44.44	0.00	0.00	22.22	100.00
I	N	0	0	0	0	0	**139**	3	4	6	152
	%	0.00	0.00	0.00	0.00	0.00	**91.45**	1.97	2.63	3.95	100.00
IF	N	0	0	0	0	0	5	**31**	1	2	39
	%	0.00	0.00	0.00	0.00	0.00	12.82	**79.49**	2.56	5.13	100.00
O	N	0	0	0	0	0	7	5	**6**	6	24
	%	0.00	0.00	0.00	0.00	0.00	29.17	20.83	**25.00**	25.00	100.00
Total	N	133	32	9	49	3	157	39	11	**32**	465
	%	28.60	6.88	1.94	10.54	0.65	33.76	8.39	2.37	**6.88**	100.00
Priors		0.290	0.084	0.026	0.118	0.019	0.327	0.084	0.052		
Error Rate		0.067	0.256	0.250	0.200	0.667	0.086	0.205	0.750		**0.168**

Table 5.40. Misclassified individuals in the discriminant analysis of the combined Balta-Mindanao sample using Variable Set 2* and Dietary Group 2 classification.

Specimen	Species	Original Group	Assigned Group	Posterior Probabilities of Membership Into Each Dietary Group							
				F	FH	FI	FN	Fo	I	IF	O
FMNH 56536	*Acerodon jubatus*	F	FN	0.333	0.000	0.000	0.667	0.000	0.000	0.000	0.000
LSU 12103	*Anoura caudifer*	FN	Other	0.000	0.000	0.333	0.333	0.000	0.000	0.000	0.333
LSU 14131	*Anoura caudifer*	FN	I	0.000	0.000	0.000	0.333	0.000	0.667	0.000	0.000
LSU 14132	*Anoura caudifer*	FN	Other	0.000	0.000	0.000	0.333	0.000	0.000	0.333	0.333
LSU 14025	*Caluromys lanatus*	F	Other	0.333	0.000	0.000	0.333	0.000	0.000	0.000	0.333
LSU 12296	*Cebus albifrons*	FH	Other	0.333	0.333	0.000	0.333	0.000	0.000	0.000	0.000
FMNH 56441	*Cynocephalus volans*	Fo	I	0.000	0.000	0.000	0.000	0.333	0.667	0.000	0.000
FMNH 56503	*Cynocephalus volans*	Fo	I	0.000	0.000	0.000	0.000	0.333	0.667	0.000	0.000
FMNH 56504	*Cynocephalus volans*	Fo	Other	0.000	0.000	0.000	0.333	0.333	0.333	0.000	0.000
FMNH 56507	*Cynocephalus volans*	Fo	I	0.000	0.000	0.000	0.000	0.333	0.667	0.000	0.000
FMNH 56521	*Cynocephalus volans*	Fo	Other	0.000	0.000	0.333	0.000	0.333	0.333	0.000	0.000
NMNH 219056	*Cynocephalus volans*	Fo	I	0.000	0.000	0.000	0.000	0.333	0.667	0.000	0.000
FMNH 142647	*Cynopterus brachyotis*	FN	Other	0.333	0.333	0.000	0.333	0.000	0.000	0.000	0.000
FMNH 146607	*Cynopterus brachyotis*	FN	F	0.667	0.000	0.000	0.333	0.000	0.000	0.000	0.000
FMNH 146610	*Cynopterus brachyotis*	FN	F	0.667	0.000	0.000	0.333	0.000	0.000	0.000	0.000
FMNH 146612	*Cynopterus brachyotis*	FN	F	0.667	0.000	0.000	0.333	0.000	0.000	0.000	0.000
LSU 14001	*Didelphis marsupialis*	O	Other	0.000	0.000	0.000	0.000	0.000	0.333	0.333	0.333
FMNH 166461	*Dyacopterus rickarti*	F	Other	0.333	0.333	0.000	0.333	0.000	0.000	0.000	0.000
LSU 12182	*Ectophylla macconnelli*	F	FH	0.333	0.667	0.000	0.000	0.000	0.000	0.000	0.000
LSU 12184	*Ectophylla macconnelli*	F	Other	0.333	0.333	0.000	0.333	0.000	0.000	0.000	0.000
LSU 14238	*Ectophylla macconnelli*	F	FN	0.333	0.000	0.000	0.667	0.000	0.000	0.000	0.000
LSU 12280	*Eptesicus brasiliensis*	I	IF	0.000	0.000	0.000	0.000	0.000	0.333	0.667	0.000
LSU 12283	*Eptesicus furinalis*	I	IF	0.000	0.000	0.000	0.000	0.000	0.333	0.667	0.000
LSU 16463	*Glossophaga soricina*	FN	Other	0.000	0.333	0.000	0.333	0.000	0.333	0.000	0.000

Table 5.40, Cont'd.

Specimen	Species	Original Group	Assigned Group	Posterior Probabilities of Membership Into Each Dietary Group							
				F	FH	FI	FN	Fo	I	IF	O
LSU 16378	*Gracilianus agilis*	FI	Other	0.000	0.000	0.333	0.000	0.000	0.000	0.333	0.333
FMNH 146641	*Haplonycteris fischeri*	F	Other	0.333	0.333	0.000	0.333	0.000	0.000	0.000	0.000
LSU 12100	*Lonchophylla thomasi*	FN	Other	0.333	0.000	0.000	0.333	0.000	0.000	0.000	0.333
LSU 14079	*Lophostoma silvicolum*	IF	I	0.000	0.000	0.000	0.000	0.000	0.667	0.333	0.000
LSU 16441	*Lophostoma silvicolum*	IF	I	0.000	0.000	0.000	0.000	0.000	0.667	0.333	0.000
FMNH 146662	*Macroglossus macroglossus*	FN	F	0.667	0.000	0.000	0.333	0.000	0.000	0.000	0.000
LSU 14074	*Macrophyllum macrophyllum*	I	O	0.000	0.000	0.000	0.000	0.000	0.333	0.000	0.667
LSU 16380	*Marmosops noctivagus*	IF	I	0.000	0.000	0.000	0.000	0.000	0.667	0.333	0.000
LSU 16386	*Micoureus demerarae*	IF	Other	0.000	0.000	0.000	0.000	0.000	0.333	0.333	0.333
LSU 14071	*Micronycteris nicefori*	IF	I	0.000	0.000	0.000	0.000	0.000	0.667	0.333	0.000
FMNH 145520	*Miniopterus australis*	I	O	0.000	0.000	0.000	0.000	0.000	0.333	0.000	0.667
FMNH 61079	*Miniopterus schreibersii*	I	Other	0.000	0.000	0.000	0.000	0.000	0.333	0.333	0.333
FMNH 145541	*Miniopterus tristis*	I	O	0.000	0.000	0.000	0.000	0.000	0.333	0.000	0.667
LSU 12272	*Myotis albescens*	I	IF	0.000	0.000	0.000	0.000	0.000	0.333	0.667	0.000
LSU 12277	*Myotis albescens*	I	Other	0.333	0.000	0.000	0.000	0.000	0.333	0.333	0.000
LSU 12030	*Noctilio albiventris*	I	Other	0.000	0.000	0.000	0.000	0.333	0.333	0.000	0.333
LSU 12036	*Noctilio albiventris*	I	Other	0.000	0.000	0.333	0.000	0.333	0.333	0.000	0.000
FMNH 87440	*Petinomys crinitus*	FH	Other	0.333	0.333	0.000	0.333	0.000	0.000	0.000	0.000
LSU 16393	*Philander mcilhennyi*	O	Other	0.000	0.000	0.000	0.000	0.333	0.333	0.000	0.333
LSU 12007	*Philander opossum*	O	Other	0.000	0.000	0.333	0.000	0.000	0.000	0.333	0.333
LSU 14012	*Philander opossum*	O	IF	0.000	0.000	0.000	0.000	0.000	0.000	0.667	0.333
LSU 14016	*Philander opossum*	O	IF	0.000	0.000	0.000	0.000	0.000	0.000	0.667	0.333
LSU 14101	*Phyllostomus elongatus*	IF	I	0.000	0.000	0.000	0.000	0.000	0.667	0.333	0.000
LSU 12069	*Phyllostomus hastatus*	O	IF	0.000	0.000	0.000	0.000	0.000	0.000	0.667	0.333
LSU 12070	*Phyllostomus hastatus*	O	Other	0.000	0.000	0.000	0.000	0.000	0.333	0.333	0.333

Table 5.40, Cont'd.

Specimen	Species	Original Group	Assigned Group	Posterior Probabilities of Membership Into Each Dietary Group							
				F	FH	FI	FN	Fo	I	IF	O
LSU 12071	*Phyllostomus hastatus*	O	IF	0.000	0.000	0.000	0.000	0.000	0.000	0.667	0.333
LSU 14098	*Phyllostomus hastatus*	O	IF	0.000	0.000	0.000	0.000	0.000	0.000	0.667	0.333
LSU 16455	*Phyllostomus hastatus*	O	Other	0.000	0.000	0.000	0.000	0.000	0.333	0.333	0.333
LSU 16456	*Phyllostomus hastatus*	O	Other	0.333	0.000	0.000	0.333	0.000	0.000	0.000	0.333
FMNH 54923	*Pipistrellus javanicus*	I	O	0.000	0.000	0.000	0.000	0.000	0.333	0.000	0.667
FMNH 146673	*Ptenochirus jagori*	F	FN	0.333	0.000	0.000	0.667	0.000	0.000	0.000	0.000
FMNH 56444	*Rousettus amplexicaudatus*	FN	Other	0.333	0.333	0.000	0.333	0.000	0.000	0.000	0.000
LSU 14346	*Saguinus imperator*	FI	FH	0.000	0.667	0.333	0.000	0.000	0.000	0.000	0.000
LSU 12298	*Saimiri boliviensis*	FI	FH	0.000	0.667	0.333	0.000	0.000	0.000	0.000	0.000
LSU 12310	*Sciurus ignitus*	FH	F	0.667	0.333	0.000	0.000	0.000	0.000	0.000	0.000
LSU 12311	*Sciurus ignitus*	FH	FN	0.000	0.333	0.000	0.667	0.000	0.000	0.000	0.000
LSU 12312	*Sciurus ignitus*	FH	FN	0.000	0.333	0.000	0.667	0.000	0.000	0.000	0.000
LSU 12313	*Sciurus ignitus*	FH	Other	0.333	0.333	0.000	0.333	0.000	0.000	0.000	0.000
LSU 12314	*Sciurus spadiceus*	FH	Other	0.000	0.333	0.333	0.333	0.000	0.000	0.000	0.000
LSU 12315	*Sciurus spadiceus*	FH	F	0.667	0.333	0.000	0.000	0.000	0.000	0.000	0.000
LSU 12316	*Sciurus spadiceus*	FH	F	0.667	0.333	0.000	0.000	0.000	0.000	0.000	0.000
LSU 12317	*Sciurus spadiceus*	FH	Other	0.333	0.333	0.000	0.333	0.000	0.000	0.000	0.000
FMNH 56720	*Tarsius syrichta*	I	Other	0.000	0.333	0.000	0.000	0.333	0.333	0.000	0.000
LSU 14083	*Tonatia saurophila*	IF	Other	0.000	0.000	0.000	0.000	0.000	0.333	0.333	0.333
LSU 14086	*Tonatia saurophila*	IF	O	0.000	0.000	0.000	0.000	0.000	0.000	0.333	0.667
LSU 12072	*Trachops cirrhosus*	I	Other	0.000	0.000	0.000	0.000	0.000	0.333	0.333	0.333
FMNH 146590	*Urogale everetti*	O	I	0.000	0.000	0.000	0.000	0.000	0.667	0.000	0.333
FMNH 166479	*Urogale everetti*	O	I	0.000	0.000	0.000	0.000	0.000	0.667	0.000	0.333
FMNH 166480	*Urogale everetti*	O	I	0.000	0.000	0.000	0.000	0.000	0.667	0.000	0.333
FMNH 166481	*Urogale everetti*	O	I	0.000	0.000	0.000	0.000	0.000	0.667	0.000	0.333

Table 5.40, Cont'd.

Specimen	Species	Original Group	Assigned Group	Posterior Probabilities of Membership Into Each Dietary Group							
				F	FH	FI	FN	Fo	I	IF	O
FMNH 61079	*Urogale everetti*	O	I	0.000	0.000	0.000	0.000	0.000	0.667	0.000	0.333
FMNH 61418	*Urogale everetti*	O	I	0.000	0.000	0.000	0.000	0.000	0.667	0.000	0.333
FMNH 61419	*Urogale everetti*	O	I	0.000	0.000	0.000	0.000	0.000	0.667	0.000	0.333
LSU 12526	*Vampyressa pusilla*	F	I	0.333	0.000	0.000	0.000	0.000	0.667	0.000	0.000

Table 5.41. K-nearest-neighbor discriminant analysis of Variable Set 2* (excluding talonid basin depth) of the combined Balta-Mindanao sample using Dietary Group 2 assignments. Correct reclassifications are bolded.

Original Group		Classified Group									
		F	FH	FI	FN	Fo	I	IF	O	Other	Total
F	N	**133**	3	0	1	0	0	0	0	4	141
	%	**94.33**	2.13	0.00	0.71	0.00	0.00	0.00	0.00	2.84	100.00
FH	N	2	**29**	2	3	0	0	0	0	3	39
	%	5.13	**74.36**	5.13	7.69	0.00	0.00	0.00	0.00	7.69	100.00
FI	N	0	1	**8**	0	0	0	0	0	3	12
	%	0.00	8.33	**66.67**	0.00	0.00	0.00	0.00	0.00	25.00	100.00
FN	N	5	2	1	**41**	0	0	0	0	6	55
	%	9.09	3.64	1.82	**74.55**	0.00	0.00	0.00	0.00	10.91	100.00
Fo	N	0	0	1	0	**0**	5	0	0	3	9
	%	0.00	0.00	11.11	0.00	**0.00**	55.56	0.00	0.00	33.33	100.00
I	N	0	0	1	1	0	**129**	8	3	10	152
	%	0.00	0.00	0.66	0.66	0.00	**84.87**	5.26	1.97	6.58	100.00
IF	N	0	0	0	0	0	3	**32**	0	4	39
	%	0.00	0.00	0.00	0.00	0.00	7.69	**82.05**	0.00	10.26	100.00
O	N	0	0	0	0	0	8	3	**7**	6	24
	%	0.00	0.00	0.00	0.00	0.00	33.33	12.50	**29.17**	25.00	100.00
Total	N	140	35	13	46	0	145	43	10	**39**	471
	%	29.72	7.43	2.76	9.77	0.00	30.79	9.13	2.12	**8.28**	100.00
Priors		0.299	0.083	0.025	0.117	0.019	0.323	0.083	0.051		
Error Rate		0.057	0.256	0.333	0.255	1.000	0.151	0.180	0.708		**0.195**

Table 5.42. Composition of taxonomic groupings used in discriminant analysis to evaluate phylogenetic effects. For diet codes of species and genera, see Tables 4.1 and 4.2; all diet codes correspond to Dietary Group 2 in these tables. Diet codes in parentheses indicate subdivisions of subfamilies or families based on varying diets.

Taxonomic Level	BALTA		MINDANAO	COMBINED	
	Taxa	Diet	Taxa	Taxa	Diet
Taxonomic Group 1	All specimens		All specimens	All specimens	
Taxonomic Group 2	All species		All species	All species	
Taxonomic Group 3	All genera		All genera	All genera	
Taxonomic Group 4	Aotinae	FI		Aotinae	FI
	Callicebinae	FH		Callicebinae	FH
	Callitrichinae	FI		Callitrichinae	FI
	Calouromyinae	F		Callosciurinae	FH
	Carollinae	F		Calouromyinae	F
	Cebinae	O		Carollinae	F
	Didelphinae (IF)	IF		Cebinae	FIFH
	Didelphinae (O)	O		Crocidurinae	I
	Emballonurinae	FN		Didelphinae (IF)	IF
	Molossinae	I		Didelphinae (O)	O
	Myotinae	I		Emballonurinae	I
	Noctilioninae	I		Hipposiderinae	I
	Phyllostominae (I)	I		Kerivoulinae	I
	Phyllostominae (IF)	IF		Megadermatinae	I
	Phyllostominae (O)	O		Minopterinae	I
	Pitheciinae	FH		Molossinae	I
	Saimiriinae	FI		Myotinae	I
	Sciurinae	I		Noctilioninae	I
	Eptesicini	I		Phyllostominae (I)	I
	Glossophagaini	FN		Phyllostominae (IF)	IF
	Lasiurini	I		Phyllostominae (O)	O
	Lonchophyllini	FN		Pitheciinae	FH
	Stenodermatini	F		Pteropodinae (F)	F
	Sturiniri	FN		Pteropodinae (FN)	FN
				Rhinolophinae	I
				Saimiriinae	FI
				Sciurinae	FH
				Taphozoinae	I
				Tarsiinae	I
				Tupaiinae	O
				Vespertilioninae	I
				Eptesicini	I
				Glossophagaini	FN
				Lasiurini	I
				Lonchophyllini	FN
				Stenodermatini	F
				Sturiniri	FN

Table 5.42, Cont'd.

Taxonomic Level	BALTA		MINDANAO	COMBINED	
	Taxa	Diet	Taxa	Taxa	Diet
Taxonomic Group 5	Aotinae	FI		Aotinae	FI
	Callicebinae	FH		Callicebinae	FH
	Callitrichiniae	FI		Callitrichinae	FI
	Calouromyinae	F		Callosciurinae	F
	Carollinae	F		Calouromyinae	F
	Cebinae	FH		Carollinae	F
	Emballonurinae	I		Cebinae	FH
	Molossinae	I		Crocidurinae	I
	Myotinae	I		Didelphinae	O
	Noctilioninae	I		Emballonurinae	I
	Phyllostominae	I		Glossophaginae	FN
	Pitheciinae	FH		Hipposiderinae	I
	Saimiriinae	FI		Kerivoulinae	I
	Sciurinae	FH		Megadermatinae	I
	Stenodermatinae	F		Minopterinae	I
	Vespertilioninae	I		Molossinae	I
				Myotinae	I
				Noctilionininae	I
				Phyllostominae	I
				Pitheciinae	FH
				Pteropodinae	F
				Rhinolophinae	I
				Saimiriinae	FI
				Sciurinae	FH
				Stenodermatinae	F
				Taphozoinae	I
				Tarsiinae	I
				Tupaiinae	O
				Vespertilioninae	I

Table 5.12, Cont'd.

Taxonomic Level	BALTA		MINDANAO	COMBINED	
	Taxa	Diet	Taxa	Taxa	Diet
Taxonomic Group 6	Aotidae	FI		Aotidae	FI
	Cebidae (FH)	FH		Cebidae (FH)	FH
	Cebidae (FI)	FI		Cebidae (FI)	FI
	Didelphidae (F)	F		Didelphidae (F)	F
	Didelphidae (IF)	IF		Didelphidae (IF)	IF
	Didelphidae (O)	O		Didelphidae (O)	O
	Emballonuridae (I)	I		Emballonuridae	I
	Marmosidae	IF		Hipposideridae	I
	Molossidae	I		Marmosidae	IF
	Noctilionidae	I		Megadermatidae	I
	Phyllostomidae (F)	F		Molossidae	I
	Phyllostomidae (I)	I		Noctilionidae	I
	Phyllostomidae (IF)	IF		Phyllostomidae (F)	F
	Phyllostomidae (O)	O		Phyllostomidae (FN)	FN
	Pitheciidae	FH		Phyllostomidae (I)	I
	Sciuridae	FH		Phyllostomidae (IF)	IF
	Vespertilionidae	I		Phyllostomidae (O)	O
				Pitheciidae	FH
				Pteropodidae (F)	F
				Pteropodidae (FN)	FN
				Rhinolophidae	I
				Sciuridae	FH
				Soricidae	I
				Tarsiidae	I
				Tupaiidae	O
				Vespertilionidae	I

Table 5.43. Total misclassification rates of discriminant analyses at varying taxonomic levels. Composition of taxonomic groups is provided in Table 5.42. Inclusiveness of groups increases from Group 1 to Group 6.

	Taxonomic Level of Analysis					
Sample	Group 1	Group 2	Group 3	Group 4	Group 5	Group 6
Balta, Variable Set 1	0.060	0.078	0.171	<0.001		
Balta, Variable Set 2	0.118	0.197	0.357	0.333	0.333	0.529
Balta, Variable Set 3	0.110	0.136	0.238	0.167	<0.001	0.235
Mindanao, Variable Set 2*	0.079	0.136	0.167			
Combined, Variable Set 2*	0.168	0.232	0.343	0.244	0.121	0.393

Table 5.44. Species in the Balta sample used in the modified MANOVA. Dietary group assignments correspond to Dietary Group 2 (see Table 4.1).

Taxon	*N*	Dietary Group	Taxon	*N*	Dietary Group
CHIROPTERA			**CHIROPTERA, CONT'D.**		
Emballonuridae			**Phyllostomidae, Cont'd.**		
Rhynchonycteris naso	3	I	*Uroderma bilobatum*	6	F
Saccopteryx bilineata	6	I	*Uroderma magnirostrum*	5	F
Saccopteryx leptura	2	I	*Vampyressa bidens*	3	F
Molossidae			*Vampyressa pusilla*	5	F
Molossops abrasus	1	I	*Vampyrodes caraccioli*	1	F
Molossops greenhalli	1	I	**Vespertilionidae**		
Molossus molossus	2	I	*Eptesicus brasiliensis*	2	I
Noctilionidae			*Eptesicus furinalis*	2	I
Noctilio albiventris	5	I	*Lasiurus borealis*	2	I
Phyllostomidae			*Lasiurus ega*	3	I
Anoura caudifer	6	FN	*Myotis albescens*	6	I
Anoura geoffroyi	2	FN	*Myotis riparius*	3	I
Artibeus cinereus	6	F	*Myotis simus*	2	I
Artibeus concolor	1	F	**DIDELPHIMORPHIA**		
Artibeus literatus	5	F	**Didelphidae**		
Artibeus obscurus	5	F	*Didelphis marsupialis*	1	O
Artibeus planirostris	6	F	*Gracilianus agilis*	1	IF
Chiroderma villosum	6	F	*Philander mcilhennyi*	2	O
Choeroniscus minor	2	FN	*Philander opossum*	6	O
Ectophylla macconnelli	6	F	**Marmosidae**		
Glossophaga soricina	6	FN	*Marmosa murina*	4	IF
Lonchophylla thomasi	6	FN	*Marmosa quichua*	2	IF
Lophostoma silvicolum	5	IF	*Marmosops noctivagus*	2	IF
Macrophyllum macrophyllum	6	I	*Metachirus nudicaudatus*	3	IF
Micronycteris megalotis	3	IF	*Micoureus demerarae*	6	IF
Micronycteris nicefori	1	IF	**PRIMATES**		
Mimon crenulatum	4	I	*Aotus trivirgatus*	3	FI
Phyllostomus elongatus	6	IF	*Callicebus moloch*	3	FH
Phyllostomus hastatus	6	O	*Cebus albifrons*	2	FH
Platyrrhinus brachycephalus	6	F	*Pithecia monachus*	3	FH
Platyrrhinus helleri	6	F	*Saguinus imperator*	6	FI
Platyrrhinus infuscus	2	F	*Saimiri boliviensis*	2	FI
Tonatia minuta	1	IF	**RODENTIA**		
Tonatia saurophila	5	IF	*Sciurus ignitus*	4	FH
Trachops cirrhosus	6	I	*Sciurus spadiceus*	6	FH

Table 5.45. Formulae used in the non-parametric MANOVA employed to test for niche overlap.

(1) $SS_W = \sum_1^a \frac{1}{N_a} \sum_{k=1}^{N_a-1} \sum_{m=k+1}^{N_a} d_{ij}^2$

(2) $SS_T = \frac{1}{N} \sum_{i=1}^{N-1} \sum_{j=i+1}^{N} d_{ij}^2$

(3) $SS_B = SS_T - SS_W$

(4) $F = \frac{SS_T - SS_W / (a-1)}{SS_W / (N-2)}$

SS_W: variance within groups, SS_B: variance between groups, SS_T: total variance within both groups combined.
(1) d_{ij} is the distance between observations (or niche coordinates) k=1,…,N_a and observation m=1,…,N_a in group a, where N_a is the number of observations in group a.
(2),(4) N is the total number of observations in the group comparison (i.e., the total number of "niche coordinates" in both groups combined), d_{ij} is the distance between observation (or niche coordinate) i=1,…,N and observation j=1,…N, and a is the number of groups. Thus, this analysis can be applied to multiple groups, but only paired comparisons were considered here.

Table 5.46. Results (*p*-values) of pairwise MANOVAs of the seven dietary groups included in this study. Non-significant values (±=0.05), corresponding to niche overlap, are bolded.

	N	FI	IF	O	FN	I	FH
F	2	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001
	3	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001
	5	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001
FI	2		<0.001	<0.001	<0.001	<0.001	<0.001
	3		<0.001	<0.001	<0.001	<0.001	0.002
	5		<0.001	<0.001	<0.001	<0.001	<0.001
IF	2			**0.134**	<0.001	**0.508**	<0.001
	3			**0.180**	<0.001	**0.092**	<0.001
	5			0.026	<0.001	<0.001	<0.001
O	2				<0.001	**0.352**	<0.001
	3				<0.001	**0.140**	<0.001
	5				<0.001	<0.001	<0.001
FN	2					<0.001	<0.001
	3					<0.001	<0.001
	5					<0.001	<0.001
I	2						<0.001
	3						<0.001
	5						<0.001

Table 5.47. Results (*p*-values) of pairwise MANOVAs of all genera included in this study presented by dietary group.

	Intra-Group Comparisons					Intra-Group (Significance-Adjusted)					Inter-Group Comparisons					All Comparisons				
	Overlap		No Overlap		*N*	Overlap		No Overlap		*N*	Overlap		No Overlap		*N*	Expected		Not Expected		*N*
	No.	%	No.	%		No.	%	No.	%		No.	%	No.	%		No.	%	No.	%	
F	1	6.67	14	93.33	15	3	20.00	12	80.00	15	0	0.00	156	100.00	156	157	91.81	14	8.19	171
FH	0	0.00	3	100.00	3	0	0.00	3	100.00	3	0	0.00	87	100.00	87	87	96.67	3	3.33	90
FN	1	33.33	2	66.67	3	3	100.00	0	0.00	3	0	0.00	87	100.00	87	88	97.78	2	2.22	90
FI	1	100.00	0	0.00	1	1	100.00	0	0.00	1	1	1.67	59	98.33	60	60	98.36	1	1.64	61
I	14	38.89	22	61.11	36	29	80.56	7	19.44	36	24	14.04	147	85.96	171	161	77.78	46	22.22	207
IF	6	28.57	15	71.43	21	17	80.95	4	19.05	21	27	15.43	148	84.57	175	154	78.57	42	21.43	196
O	0	0.00	1	100.00	1	0	0.00	1	100.00	1	9	15.00	51	85.00	60	51	83.61	10	16.39	61
Total	23	28.75	57	71.25	80	53	66.25	27	33.75	80	31	7.45	385	92.55	416	408	82.26	88	17.74	496

N is the total number of comparisons within each category of comparisons. Intra- and inter-group comparisons refer to comparisons of genera within and between dietary categories, respectively. For example, within the F dietary category, only 1 genus-genus comparison resulted in niche overlap; all other comparisons within the F group indicated no overlap. For all comparisons, expected outcomes include "overlap" in intra-group comparisons and "no overlap" in inter-group comparisons. Note that the significance-adjusted intra-group comparisons are not included in the results for all comparisons. Total instances of overlap and non-overlap for inter-group and all comparisons are not sums of the columns above, as this would result in each comparison being counted twice, once for each group in the comparison.

CHAPTER 6: DIETARY NICHE OVERLAP OF EUPRIMATES AND NON-EUPRIMATES IN THE EARLY PALEOGENE OF NORTH AMERICA

The evaluation of the dietary competitive environment of the first euprimates in North America (and thus the test of the hypotheses outlined in Chapter 3) requires that the specific patterns of dietary niche overlap between euprimates and non-euprimates first be determined. The measurements associated with Variable Set 3 were collected on each euprimate and non-euprimate fossil specimen following the results of Chapter 5, and a single principal component analysis was then performed on the measurements associated with all specimens across the entire time range of the sample (Cf2 to Wa5). The resulting principal component space thus characterizes the multidimensional dietary niche space of the euprimate competitive guild from Cf2-3 to Wa5 and encompasses all euprimate and non-euprimate niches throughout this time. This allows dietary niches to be directly compared both within and across time intervals, as temporal patterns of niche overlap must be known to evaluate the three competition hypotheses of interest here (see Chapter 3). Thus, the modified MANOVA described in Chapter 5 was used, first, to assess whether the dietary niche of each euprimate taxon significantly overlapped those of each non-euprimate taxon within each of the six time intervals (Cf2-3, Wa0, Wa1-2, Wa3, Wa4, and Wa5), and second, to evaluate whether the dietary niche of each euprimate taxon overlapped those of the non-euprimate taxa present in the preceding time interval. For example, the dietary niche of Wa0 adapids was compared to other Wa0 non-euprimate taxa as well as all non-euprimate taxa present in Cf2-3. Patterns of overlap among the niches of euprimate genera and families were also reconstructed to examine the evolution of the euprimate dietary niche during the early Paleogene of North

America. Wherever possible (i.e., when at least three specimens per taxon per time interval were present; see Chapter 5), the genus was used as the taxonomic unit of analysis. However, genera were grouped into families if this "minimum number of specimens" requirement was not met, and families were grouped into orders or supraorders if familial groupings produced inadequate sample sizes.

As discussed in Chapters 2 and 3, niche divergence – the product of a shift (or shifts) in niche position and overlap – may be the result of changes in the physical environment or selective predation rather than competitive interactions (Janis, 1989; Morgan et al., 1995; Abrams, 2000; Schweiger et al., 2008). Because each time interval is associated with 1-2 sub-NALMAs in this study, each temporal bin encompasses tens, or hundreds, of thousands of years. Consequently, specimens considered coeval in the following analyses (i.e., assigned to the same time interval), fall within a range of stratigraphic levels and thus vary in absolute age. For this reason, associations between niche shifts and environmental change can be difficult to evaluate, as current climatic reconstructions show fluctuations in mean annual temperature and precipitation within sub-NALMAs (e.g., Koch et al., 2003; Secord et al., 2012). Furthermore, habitat variability (e.g., distance from basin centers) can be present even within single stratigraphic units, thus increasing the heterogeneity of abiotic variables even in highly temporally controlled samples (Gunnell, 1997; Gunnell and Bartels, 2001). In addition, these reconstructions vary depending on the evidence from which they are derived (e.g., isotopic signatures obtained from fossil material or paleosols) (Fricke et al., 1998; Koch et al., 2003; see Chapter 2). Thus, the association of climatic variables with niche shifts will be based mainly on reconstructed large-scale climate change, for example, those

attributed to carbon isotope excursions, and general climatic trends based on data gathered from the Bighorn Basin and surrounding areas. As a result of data availability, trends in taxonomic diversity and abundance of both euprimate competitive guild members and their potential predators are instead based on cumulative data from sites across the Western Interior. As described in Chapter 3, predation will only be considered as an alternative to competition or climatic change when patterns of niche overlap coincide with a significant change in the diversity or composition of the predator guild.

OVERALL PATTERN OF DIETARY NICHE OVERLAP BETWEEN EUPRIMATES AND NON-EUPRIMATES

The results of the principal component analysis of all specimens across all time periods are provided in Table 6.1, and specimen values on the first two principal components for each time interval are plotted in Figs. 6.1-6.6. An examination of the eigenvalues indicates that the first six principal components cumulatively contribute to approximately 94% of the variation, and thus, the values of PC1-PC6 were used in the subsequent MANOVA comparisons (as per Chapter 5). For the fossil sample as a whole, the first eigenvector demonstrates that variables related to the trigonid, particularly trigonid cusp angle, have the greatest weight, although both talonid cusp height and angle also possess high loadings on PC1. As predicted, cusp height and angle variables are inversely related; i.e., "sharper," more acute cusps are associated with greater cusp heights, and "duller" cusps are associated with lower cusp heights. Unlike the extant Balta sample (the only sample in which Variable Set 3 was analyzed and thus the only sample which can be directly compared with the fossil sample), in which total crest length had a minimal influence on PC1, this variable is more significant in the fossil

analysis. However, similar to the Balta sample, talonid basin depth (in addition to talonid basin area) has the least effect on the first principal component.

The second principal component reveals a relationship between long crests and large, deep talonid basins, on the one hand, and a short trigonid coupled with low trigonid-talonid relief, on the other. Eigenvectors are consistent with the distribution of dietary niches within the two-dimensional principal component (dietary niche) space, as there is a morphological gradation from the top left to the bottom right quadrants of the plot. In other words, taxa with tall, sharp cusps, small basins, short crest lengths, and high trigonid-talonid relief (e.g., peradectids and palaeoryctids) are located in the bottom right quadrant, whereas taxa with low, bulbous cusps, large basins, long crest lengths, and low trigonid-talonid relief (e.g., rodents), are positioned in the top left quadrant of the principal component space. Those taxa located in the central area of the plot indicate more generalized molar morphologies and include euprimates and most plesiadapiforms.

Changes in the position of the guild-wide niche hypervolume (i.e., the niche including all specimens) through time were examined by calculating distances between niche centroids in adjacent time intervals (Table 6.2). These calculations indicate that the position of the guild-wide dietary niche does shift slightly among time intervals. The greatest displacement in centroid location is between the Wa1-2 and Wa3 time intervals and involves a major shift in the dietary niches of many taxonomic groups, particularly rodents, plesiadapiforms, peradectids, and omomyids (Table 6.2). Conversely, the positions of the soricomorphan and leptictid niches change the least during this transition. The boundary between Wa1-2 and Wa3 is not clearly linked to a specific climatic event or increase in predator diversity (Wilf, 2000; Woodburne, 2009a; Chew and Oheim,

2013), and thus the reason for this guild-wide displacement is not clear. However, this transition will be discussed within the context of the euprimate niche and euprimate competitive interactions in this and the subsequent chapter. In addition, although the positions of individual dietary niches relative to one another and within the overall dietary niche space do not vary considerably over the time period examined, there are slight positional shifts among taxa, indicating evolutionary change in the dietary niches of this mammalian guild.

Temporal changes in the size of the guild-wide, six-dimensional dietary niche were evaluated using three measures: (1) absolute "hypervolumetric size," or the "volume" of the multi-dimensional "space" occupied by each niche, (2) relative hypervolumetric size, or the percentage of the total niche space (including all time intervals) filled by the niche from a single time period, and (3) mean distance of individuals from niche centroids (see Tables 6.3, 6.15). Calculations of hypervolumetric size were performed in MATLAB R2012a. The strength of the association of niche size with time, where each time interval was defined by the midpoint of its range in millions of years, was evaluated using non-parametric Spearman rank correlation coefficients; these analyses were conducted in SPSS v.22. As the absolute hypervolumetric sizes of the multidimensional niches for each time interval appeared to be positively correlated with sample size, relative size was assessed using a weighted percentage, designed to account for sample size variation (Table 6.3). Results of two-tailed correlation analyses indicate a near-significant decrease in relative hypervolumetric niche size (r=0.771, p=0.072) and mean distance from niche centroid (r=0.771, p=0.072) across time intervals, which suggests a "narrowing" of the guild-wide niche space through time,

particularly from Wa1-2 to Wa5 (Table 6.3). Because the ordinal and familial diversities are near-equal for all time periods[21], it is unclear whether this collapse in niche size is the result of increased similarity among taxa or a consequence of decreased diversity or morphological (and presumably dietary) variation within higher-level taxa.[22] However, it is interesting to note that the niche expansion from Cf2-3 to Wa0 and its subsequent contraction from Wa1-2 to Wa5 broadly parallels reconstructions of mean annual temperature and precipitation during this time, if adjusted for a slight temporal lag in the faunal response to this change (see Chapter 2; Alroy et al., 2000). A more detailed exploration of this phenomenon as it relates to the euprimate clade is discussed in the last section of this chapter as well as in Chapter 7.

The results of the pairwise MANOVAs are presented in Tables 6.4-6.13. Overall, the consistently low *p*-values between euprimate and non-euprimate taxa reveal that euprimate niches rarely overlapped with those of other groups, suggesting that Paleogene euprimates in North America engaged in minimal dietary competition. Those instances of potential competition between euprimates and specific non-euprimate taxa are illustrated in Fig. 6.7 and are discussed in detail in the next section. However, it is important to note that the results of the test case of the modified MANOVA using the extant Balta sample described in the previous chapter suggest this analysis might not accurately detect dietary competition among taxa whose reconstructed niche hypervolumes do not statistically

[21] Although generic diversity changes among time intervals, it does not decrease from Cf2-Wa5. Sample diversity is greatest during Wa1-2 and Wa3 (31 genera) and includes 20-23 genera during the remaining time intervals.

[22] The calculation of a six-dimensional niche volume requires at least six six-dimensional points; thus, the hypervolume of the niches of individual taxa within a time interval could not be calculated in most cases.

overlap. In other words, some niche comparisons may represent "false negatives" such that a significant test statistic (indicating a lack of overlap) may mask true niche overlap and possible competition between taxa; i.e., there may be a high level of type I error in the analysis. Thus, although occurrences of niche overlap (non-significant results) between euprimates and non-euprimates likely characterized true dietary competition in the past, it is possible that those non-euprimate taxa whose niches do not overlap with euprimates (and thus are not considered below) also played a role in the dietary competitive environment of the earliest euprimates. The implications of these "false negatives" will be considered in Chapter 7.

INSTANCES OF NICHE OVERLAP BETWEEN EUPRIMATES AND NON-EUPRIMATES

Euprimate Origination (Cf2-3 to Wa1-2)

The following sections describe instances of dietary niche overlap between Wa0 and Wa1-2 euprimates and Cf2-3 to Wa1-2 non-euprimate taxa. As described above, both niche overlap between euprimates and non-euprimates in preceding time intervals and overlap between euprimates and non-euprimates within coincident time intervals are considered (see Chapter 3). At the point of euprimate origination (Wa0), both adapids and omomyids consist of a single genus: *Cantius* and *Teilhardina*, respectively. Although Wa1-2 does mark the initial divergence of the omomyid lineage, this time interval is included in this section because overlap between Wa1-2 omomyids and soricomorphans spans both Wa0 and Wa1-2.

Wa0 Adapidae-Cf2-3 Plesiadapidae.

Although plesiadapids and adapids are not present during the same time interval, their dietary niches overlap asynchronously: the Cf2-3 plesiadapid niche occupies a statistically similar position to that of Wa0 adapids (p=0.096; Table 6.4). The consequent ecological interpretation of this pattern is that during Cf2-3, plesiadapids occupied the same dietary niche that adapids would subsequently inhabit upon their arrival in North America in the earliest Wasatchian. However, it is not possible to examine coeval overlap between these two taxa because plesiadapids essentially become extinct in the Bighorn Basin at the end of the Clarkforkian (Gunnell et al., 1993; Maas et al., 1995; Gingerich, 2003, 2004). Thus, at the temporal resolution employed herein, this scenario is consistent with non-competition between adapids and plesiadapids; i.e., adapids entered the Bighorn Basin mammalian community in the absence of their potential plesiadapid dietary competitor and invaded the resultant open dietary niche. Despite the fact that, based on the analysis of niche overlap alone, it is not possible to discriminate between this latter scenario and a situation in which adapids outcompeted plesiadapids over a very short period of time at the onset of the Wasatchian, prior studies of plesiadapid abundance and diversity demonstrate that this taxon had long been in decline prior to euprimate origination (Maas et al., 1988; Gunnell, 1998; Woodburne et al., 2009a). Of course, it is possible that an already waning plesiadapid population was driven to extinction by the appearance of adapids, but previous research has suggested that this outcome was inevitable despite euprimate invasion[23] (Maas et al., 1988). Thus, in accordance with

[23] Euprimate origination is also coincident with the onset of the Paleocene-Eocene Thermal Maximum, which may have played a role in plesiadapid extinction.

previous conclusions, competition between plesiadapids and euprimates was likely either absent or of minimal consequence to either group (Maas et al., 1988). The results of this study further demonstrate the significance of the plesiadapid decline to euprimate origination, as these two groups likely would have engaged in dietary competition had plesiadapids been abundant in the earliest Wasatchian.

Wa0 Omomyidae-Cf2-3 Apatemyidae

Like adapids and plesiadapids, dietary niche overlap between omomyids and apatemyids is not coincident, as the dietary niches of Wa0 omomyids overlap those of only Clarkforkian, and not Wa0, apatemyids (p=0.069; Table 6.4). From Cf2-3 to Wa0, there was a shift in the dietary niche of apatemyids such that niche overlap, and thus competition, with omomyids did not occur in the earliest Wasatchian or at any point thereafter. An examination of the distance between the centroids of the apatemyid and omomyid niche hypervolumes over time reveals that niche separation is lowest between Cf2-3 apatemyids and Wa0 omomyids, increases between Wa0 apatemyids and omomyids, and does not decrease to the original level at any point thereafter (Table 6.4). Again, it is possible that omomyids and apatemyids were briefly in competition in the earliest Wasatchian; however, a consideration of the overall biology of these two groups and their broader ecological niches suggests that significant dietary competition did not occur. For instance, the autapomorphies of apatemyids include enlarged incisors, the lower of which are procumbent, and elongated second and third manual digits (McKenna, 1963; Gingerich and Rose, 1982; von Koenigswald et al., 2005; Gunnell et al., 2008). The dietary behavioral reconstructions based on these traits suggest that apatemyids engaged in bark-gnawing and insect-probing, using their large incisors and long, thin

fingers, respectively, as do extant aye-ayes and the phalangeroid marsupial, *Dactylopsila*, with which they are convergent (McKenna, 1963; von Koenigswald et al., 2005; Silcox et al., 2011). Given this highly specialized dietary behavior, a significant difference in the method of food procurement between apatemyids and euprimates greatly reduces the probability that these two groups competed for the same limited resources. Thus, although it is possible that apatemyids and omomyids consumed similar food items and consequently evolved similar molar morphologies, they likely occupied distinct realized dietary niches and consequently did not engage in a strong competitive interaction.

In the absence of competition with omomyids, several other factors may have caused a shift in the apatemyid niche at the Clarkforkian-Wasatchian boundary. First, because the majority of Cf2-3 apatemyid specimens are derived from Cf2, combining the Cf2 and Cf3 sub-NALMAs into a single time interval may have conflated a more gradual niche shift across the Clarkforkian, creating the appearance of a single, abrupt change. On the other hand, molar morphological variation between the two apatemyid genera represented in the sample may explain the difference in apatemyid niche position, as the generic composition of the apatemyid sample changes from Cf2-3 (in which only *Labidolemur* is present) to Wa0 (in which only *Apatemys* is present).[24] However, it is possible that this shift instead indicates true biological change; for example, competition between apatemyids and another taxon or taxa could have resulted in niche divergence, which subsequently altered the position of the apatemyid dietary niche. Alternatively, perhaps the increase in carnivorans, specifically miacids, influenced apatemyid evolution

[24] Although *Apatemys* originates in the Bighorn Basin in Wa0 (Gingerich, 1982; Woodburne, 2009a), *Labidolemur* does not become extinct at the end of the Clarkforkian; it is simply absent from the Wa0 time period in this sample.

either through direct predation or predation on apatemyid competitors (Gunnell et al., 1995; Maas et al., 1995; Abrams, 2000; Woodburne, 2009a). Finally, the Clarkforkian-Wasatchian boundary was also coincident with the onset of the Paleocene-Eocene Thermal Maximum (PETM or Eocene Thermal Maximum 1, ETM1) and associated Carbon Isotope Excursion (CIE), which involved a rapid fluctuation in mean annual temperature, mean annual precipitation, and soil aridity (Clyde and Gingerich, 1998; Wing et al., 2005; Yans et al., 2006; McInerney and Wing, 2011; Abels et al., 2012; Secord et al., 2012; Kraus et al., 2013; Snell et al., 2013; see Chapter 2). Thus, this dramatic climatic change may have caused a transition in the dietary behavior, dental morphology, or both, of apatemyids during that interval of time.[25] Regardless, the presence of a new apatemyid genus in the Wasatchian (Gingerich, 1982; Woodburne et al., 2009a), and the correlated increase in the diversity of apatemyids at the Cf3-Wa0 boundary (Woodburne et al., 2009a), support the association of this time period with evolutionary transition in this group.

Wa0 Omomyidae-Cf2-3 Erinaceomorpha.

The dietary niche of Wa0 omomyids also overlaps that of Clarkforkian erinaceomorphans (p=0.339; Table 6.4). The centroid distance between the niches of these two groups is at its minimum when the niches of Cf2-3 erinaceomorphans and Wa0 omomyids are compared, and the distance between erinaceomorphans and omomyids within each time interval increases from Wa0 to Wa4 (although results of the correlation analyses are non-significant; r=-0.800, p=0.200; Table 6.14). Given the lack of dietary

[25] Gingerich (1982) notes that the appearance of *Apatemys chardini* in Wa0 may be the result of an immigration event, possibly from Europe, linked to climatic change at the Paleocene-Eocene boundary.

niche overlap and increased niche divergence between omomyids and erinaceomorphans from Wa0 to Wa4, it is unlikely that erinaceomorphans competed with euprimates at the time of the euprimate origination. However, the decreased centroid distance and presence of niche overlap between omomyids and erinaceomorphans in Wa5 suggests that competition with erinaceomorphans may have had an impact on early euprimate evolution, and this will be discussed further below.

As was the case with Wa0 apatemyids, the shift in the erinaceomorphan dietary niche in the earliest Wasatchian, if not the result of competition with euprimates, could be dependent solely on sample composition, as in this sample, the generic composition of Clarkforkian and Wa0 erinaceomorphans is non-overlapping (e.g., *Macrocranion* originated in Wa0). In addition, although there is no clear change in erinaceomorphan diversity at the Paleocene-Eocene boundary (Woodburne et al., 2009a), it is again possible that interspecific competition with non-euprimate taxa, an increase in predator diversity, or climatic change in the earliest Wasatchian caused displacement of the erinaceomorphan dietary niche.

Wa0-Wa1-2 Omomyidae-Wa0 Soricomorpha.

The dietary niche of Wa0 soricomorphans overlaps both the niche of the single Wa0 omomyid genus (*Teilhardina*) (p=0.055) and the niches of each Wa1-2 omomyid genus (*Anemorhysis*: p=0.205, *Tetonius*: p=0.057, *Teilhardina*: p=0.101; Tables 6.4-6.5). However, (1) the lack of overlap between Wa1-2 Omomyidae as a whole and Wa0 soricomorphans and (2) the variation in p-values among comparisons of individual Wa1-2 omomyid genera and Wa0 soricomorphans suggest that overlap with soricomorphans occurs within a specific part of the Wa1-2 omomyid niche hypervolume. In other words,

when all omomyids are considered, there are likely a substantial number of omomyid individuals distanced from the soricorphan specimens such that the value of SS_B is larger in the Omomyidae-Soricomorpha comparison than in comparisons of soricomorphans and individual omomyid genera. Because *Tetonius* and *Anemorhysis* are not present before Wa1-2, divergence between the centroids of the omomyid and soricomorphan niches can only be assessed for all omomyids combined. These results show increased niche divergence between soricomorphans and omomyids from Wa0 to Wa3; i.e., from the point of euprimate origination through the last time interval for which comparisons can be made (Table 6.14).[26] A comparison of the displacement of soricomorphan and omomyid niche centroids through time reveals that the shift in the soricomorphan niche was greater than that of omomyids from Wa0 to Wa1-2 (see Table 6.2). In addition, the results of the modified MANOVA indicate that the niches of Wa0 and Wa1-2 omomyids overlap and that the niches of Wa1-2 omomyids overlap with those of Wa0 but not Wa1-2 soricomorphans (Tables 6.5, 6.9); this is consistent with minimal euprimate niche positional change across the Wa0-Wa1-2 boundary. Thus, the niche divergence between omomyids and soricomorphans from Wa0 to Wa1-2 seems to be due mainly to a shift in the soricomorphan niche.

Although the dietary niches of Clarkforkian soricomorphans and Wa0 euprimates do not overlap, this pattern of initial niche overlap between euprimates and soricomorphans at the time of euprimate origination (i.e., Wa0) and subsequent niche divergence in successive time intervals is generally consistent with the presence of strong

[26] No soricomorphans are represented in the study sample after Wa3.

competition between these two groups. However, it is possible that changes in the abiotic environment were responsible for this niche divergence rather than competitive interaction. The end of the Wa0 sub-NALMA is associated with the termination of the Carbon Isotope Excursion such that mean annual precipitation increased and mean annual temperature decreased across the Wa0-Wa1-2 boundary (Fricke et al., 1998; Wilf, 2000; Wing et al., 2005; Woodburne et al., 2009b; Abels et al., 2012; Chew and Oheim, 2013). Thus, rather than strong competition, the initial divergence in soricomorphan and omomyid niches may have been the result of a soricomorphan response to a shift in climate associated with the end of the Paleocene-Eocene Thermal Maximum (PETM). Alternatively, the fact that only the niche of Wa0 (rather than later) soricomorphans overlaps that of euprimates might indicate that the occupation of the euprimate niche by soricomorphans in Wa0 was the consequence of the warmer, drier climate present during that specific sub-NALMA, i.e., the PETM. This same time period has also been associated with molar morphological change, specifically size, in other Bighorn Basin mammals (Bown et al., 1994; Gingerich, 2003, 2004; Yans et al., 2006; Chew, 2009b; Secord et al., 2012), demonstrating the effects that this climatic event likely had on mammalian biology (see Chapter 2).

Finally, soricomorphans are typically reconstructed as terrestrial mammals, as this group includes shrews, moles, and their relatives, and thus it is possible that a difference in substrate use greatly minimized, if not precluded, instances of shared food resource use by euprimates and soricomorphans. Consequently, even if climatic change was not responsible for the shift in the soricomorphan niche after Wa0, dietary competition with euprimates may yet have been absent.

Euprimate Radiation (Wa3 to Wa5)

The following sections detail instances of dietary niche overlap between euprimate genera and families and non-euprimate groups in Wa3, Wa4, and Wa5. For those occurrences of niche overlap within the Wa5 time interval, further evidence is needed to support either the hypothesis of strong or weak competition, as these models require that patterns of niche overlap be examined after the point of initial overlap. Therefore, as discussed below, it is necessary to extend these analyses into later time intervals (e.g., Wa6, Wa7) in order to fully evaluate some of the instances of possible euprimate-non-euprimate competition described in the following sections.[27]

Wa3 *Anemorhysis*-Wa3 Microsyopidae.

The dietary niches of a single genus of omomyid, *Anemorhysis*, and microsyopids overlap within a single sub-NALMA, Wa3 (p=0.065; Table 6.6). This result is unexpected, as overlap occurs only during this time interval, and the composition of the microsyopid sample does not change markedly from Wa1-2 to Wa3.[28] If dietary niche overlap between *Anemorhysis* and microsyopids truly occurred (although see below), then it appears to be the result of niche convergence. As discussed above, the transition from Wa1-2 to Wa3 is correlated with the greatest displacement of both the microsyopid and omomyid niche centroids, resulting in a minimum distance between the centroids of

[27] Although *Tetonius*, *Tetonius-Pseudotetonius*, and *Pseudotetonius* compose a single anagenetic lineage, these three "genera" are considered separately in the following analyses. This was done in an attempt to minimize variation within the operational taxonomic units (OTUs). As demonstrated in the last section of this chapter, this division of the *Tetonius-Pseudotetonius* lineage does not affect the resulting pattern of niche overlap either among euprimate genera or between euprimate and non-euprimate groups.
[28] The major difference in sample composition between Wa1-2 and Wa3 Microsyopidae is the presence of a greater number of *Microsyops* specimens in Wa3.

microsyopids and *Anemorhysis* in Wa3. This distance then increases in Wa4 (see Table 6.14). Although no major climatic event (e.g., rapid spike or drop in temperature) is associated with the Wa2-Wa3 or Wa3-Wa4 boundaries, perhaps the overall increase in aridity and decline in mean annual temperature during this time limited food resources and restricted microsyopids and *Anemorhysis* to a similar region of the dietary niche space in Wa3 (Fricke et al., 1998; Wilf, 2000; Woodburne et al., 2009a, 2009b; Chew and Oheim, 2013). Consequently, this niche space co-occupation could have resulted in competition between these two taxa, thus driving their niches apart.[29] Although this pattern of niche convergence followed by divergence does not directly coincide with any of the three models of competitive interactions described in Chapter 3, the increase in centroid distance between the *Anemorhysis* and microsyopid niches and the decrease in microsyopid diversity between Wa3 and Wa4 (the "double-wedge pattern") (Woodburne et al., 2009a) could be indicative of strong competition between these taxa.

However, if the Wa3 microsyopids are divided into two groups of genera (the larger microsyopids, *Arctodontomys* and *Microsyops*, and the diminutive genus, *Niptomomys*), the niches of these groups do not overlap with the niche of *Anemorhysis* (or any other omomyid) (*Anemorhysis*-*Arctodontomys*+*Microsyops*: $p<0.001$; *Anemorhysis*-*Niptomomys*: $p=0.014$; Table 6.6). As a result, it seems that the dietary niche of *Anemorhysis* is positioned between these two groups of microsyopids such that the *Anemorhysis* niche is encompassed by (and in a relatively vacant region of) the total

[29] Although the stratigraphic range of *Anemorhysis* extends into Wa6, it is only represented through Wa4 in this sample (Bown and Rose, 1987; Chew, 2005). Unfortunately, only two Wa4 specimens of *Anemorhysis* are present in the sample and thus can only be included in analyses of niche divergence and not of niche overlap.

bimodal microsyopid niche space. This lack of niche overlap at the genus level highlights potential issues that can arise from using varying taxonomic groupings in niche comparisons, and this will be considered in Chapter 7.

Wa5 *Copelemur*-Wa4 Plagiomenidae.

The adapid genus, *Copelemur*, originates in the Wa5 time interval, and its reconstructed dietary niche overlaps that of Wa4 plagiomenids (p=0.078; Table 6.8). However Wa4 is the last time period during which plagiomenids are present in the Bighorn Basin and surrounding areas until the middle Eocene, when a new plagiomenid genus appears in the Uintan (Maas et al. 1995; Gingerich and Clyde, 2001; Gingerich, 2003; Chew, 2009a; Woodburne et al., 2009a). As such, plagiomenids and *Copelemur* were asynchronous and could not have occupied the same dietary niche concurrently, eliminating the possibility of dietary competition between these groups. In fact, this pattern of niche overlap between a non-euprimate and a euprimate taxon, in which the extinction of the non-euprimate precedes the euprimate origination event, closely resembles that of Cf2-3 plesiadapids and Wa0 adapids. Due to the sparse plagiomenid sample throughout the early part of the Wasatchian, changes in the distances between the adapid and plagiomenid niches over time cannot be established. For example, it is unclear whether the dietary niches of adapids and plagiomenids converged from Wa0 to Wa4, or whether this allochronic overlap was simply the result of the dramatic shift in the location of the adapid niche centroid between Wa4 and Wa5 (Table 6.2). However, similar to the decrease in abundance and diversity of plesiadapids before the arrival of adapids in North America in Wa0, plagiomenid diversity had also been declining since the Clarkforkian (i.e., prior to the origination of *Copelemur*) (Woodburne et al., 2009a). Thus, these results

are most consistent with euprimates moving into the recently vacated dietary niche of plagiomenids following their extinction; i.e., the model of non-competition.

Wa5 *Copelemur*-Wa4-5 Paromomyidae.

The dietary niche of *Copelemur* overlaps that of both Wa4 and Wa5 paromomyids (p=0.053 and p=0.100, respectively; Table 6.8). Although the niche of *Copelemur* does overlap that of Wa5 *Cantius* (p=0.403; Table 6.12), there is no niche overlap between Wa4 or Wa5 paromomyids and either the niches of Wa5 *Cantius* or all Wa5 adapids combined (Wa4 Paromomyidae-Wa5 *Cantius*: p<0.001; Wa5 Paromomyidae-Wa5 *Cantius*: p=0.002; Wa4 Paromomyidae-Wa5 Adapidae: p<0.001; Wa5 Paromomyidae-Wa5 Adapidae: p<0.001; Table 6.8). In conjunction with the fact that the niches of Wa5 adapids (including *Copelemur*) do not overlap the niche of Wa4 adapids (Table 6.12), this indicates that the *Copelemur* niche is uniquely positioned within both the Wa4 and Wa5 adapid dietary niche spaces. Furthermore, this suggests that the paromomyid dietary niche overlaps with only a portion of the overall adapid niche, coincident with the niche of *Copelemur* specifically. A consideration of Figs. 6.6 and 6.12 illustrates that even in two dimensions, within Adapidae, there are a greater number of *Copelemur* than *Cantius* specimens in close proximity to paromomyids.

Over the course of the Wasatchian, the distance between the centroids of the paromomyid and adapid niches generally decreases, indicating that the niches of these taxa slowly converged during this time. As mean annual temperature and mean annual precipitation decreased during this period (Fricke et al., 1998; Wilf, 2000; Woodburne et al., 2009a,b; Chew and Oheim, 2013), it is possible that this convergence was the result of a gradual decline in food resources. Paromomyid species diversity remained

essentially unchanged throughout the Wasatchian (Gunnell, 1998; Woodburne et al., 2009a), but *Ignacius*, one of only two genera in the paromomyid sample, becomes extinct at around 240M in the central Bighorn Basin (corresponding to Wa3 in this study) (Maas et al., 1995; Silcox et al., 2008), which may have altered the overall niche space inhabited by paromomyids in Wa4 and Wa5. However, statistically significant niche overlap between euprimates and paromomyids was not detected until the major shift in adapid niche position between Wa4 and Wa5, coincident with the emergence of *Copelemur*. As a result, niche overlap between *Copelemur* and paromomyids does seem to indicate dietary competition between these two taxa. On the other hand, it is important to note that paromomyids and adapids differed substantially in size, as reconstructed body masses indicate that *Copelemur* may have been at least four times as large as the largest paromomyid (Bloch et al., 2007; Fleagle, 1999). Thus, this high degree of body size separation may be inconsistent with the presence of a strong competitive interaction between these taxa (Krause, 1986; Maas et al., 1988). Regardless, because the fossil sample only incorporates specimens from Cf2 to Wa5, an examination of the results of this overlap, and thus the associated competitive model, requires niche reconstructions of both taxa in Wa6. Therefore, given the available data, it is not possible to determine the extent to which dietary niche overlap or competition occurred between adapids and paromomyids.

Wa5 Adapidae-Wa5 Microsyopidae.

The dietary niche of Wa5 Microsyopidae overlaps that of Wa5 *Copelemur* (p=0.273) as well as all Wa5 adapids combined (*Copelemur* and *Cantius*) (p=0.055; Table 6.8). However, the niches of *Copelemur*, *Cantius*, and both genera combined

(Adapidae) do not overlap those of the individual microsyopid genera (*Niptomomys* and *Microsyops*) when each is considered separately (*Copelemur*-*Niptomomys*: p=0.006; *Copelemur*-*Microsyops*: p=0.018; Adapidae-*Niptomomys*: p<0.001, Adapidae-*Microsyops*: p=0.001; Table 6.8). This incidence of overlap between euprimates and non-euprimates, as was also the case for Wa3 *Anemorhysis* and Microsyopidae, appears to be the result of combining the niches of two distinct lineages of microsyopids (Gunnell, 1985), neither of which individually overlaps with adapids, into a single dietary niche that spans the adapid niche space. The distribution of Wa5 microsyopids in two dimensions illustrates that specimens of *Niptomomys* (with relatively low values on PC1) form a cluster distinct from that of *Microsyops* (with relatively high values on PC1), each of which is positioned on either side of the adapid niche (Fig 6.6). In addition, given the relative size differences between Wa5 adapids and *Niptomomys* (Gingerich, 1986; Gunnell, 1989; Rose et al., 1993; Jones et al., 2014) as well as the derived anterior microsyopid dentition (Gunnell 1985, 1989), competition between these taxa is not likely. However, even if one assumes that adapids and the larger microsyopids did compete for dietary resources, it is not possible to test whether niche overlap is the result of strong or weak competition (or possible climatic change; see "Wa5 Omomyidae-Wa5 Erinaceomorpha") without evaluating the dietary niches of these taxa in Wa6 (and later).

Wa5 Omomyidae-Wa5 Erinaceomorpha.

The dietary niche of Wa5 omomyids overlaps that of Wa5 erinaceomorphans p=0.060; Table 6.8). Because so few specimens represent each of the four Wa5 omomyid genera (*Absarokius*, *Anemorhysis*, *Steinius*, and *Arapahovius*), it is not possible to determine if the Wa5 erinaceomorphan niche overlaps all or merely a subset of the

omomyid genera included in this time period. Furthermore, given the high species and generic diversity of erinaceomorphans, the taxonomic instability of species, genera, families, and even the group "Erinaceomorpha" (Novacek et al., 1985; Rose, 2006; Gunnell and Bloch, 2008), and the relatively low representation of each erinaceomorphan genus in the fossil sample, it is difficult to ascertain if niche overlap between erinaceomorphans and omomyids is the result of overlap involving a single erinaceomorphan genus, family, or the group as a whole.

The distance between the erinaceomorphan and omomyid niche centroids increases from Wa0 to Wa4, but sharply decreases between Wa4 and Wa5. The Wa5 omomyid niche overlaps with that of Wa4 omomyids, but the generic composition of Omomyidae changes significantly from Wa4 to Wa5, as the *Tetonius-Pseudotetonius* lineage is replaced by several new omomyid genera (Bown and Rose, 1987). There is evidence that the mean annual temperature began to increase at the end of Wa4 or beginning of Wa5, as temperatures continued to climb, culminating in the Early Eocene Climatic Optimum in Wa7 (Bown et al., 1994; Fricke et al., 1998; Wilf, 2000; Woodburne et al., 2009a,b; Chew and Oheim, 2013). In addition, Wa5 is associated with Eocene Thermal Maximum 2 (ETM2) (Abels et al., 2012; Chew and Oheim, 2013), although most Wa5 specimens included in this sample correspond to the earlier part of Wa5, preceding this hypothermal event. Thus, erinacemorphan-omomyid niche overlap in Wa5 may have either resulted in competition or may be an indirect effect of associated climatic change. Furthermore, it should be noted that too few erinaceomorphan specimens are present in both the Wa3 and Wa4 samples to evaluate niche overlap. This allows for the possibility that omomyids and erinaceomorphans competed prior to Wa5,

suggesting that erinaceomorphans may have been a significant omomyid dietary competitor during the early Paleogene. To evaluate any of these possibilities, however, the erinaceomorphan sample must be expanded to examine niche overlap in time intervals both prior and subsequent to Wa5, which the current sample does not allow.

Finally, it is important to consider that the relatively few postcranial specimens assigned to erinaceomorphan taxa suggest that many of these taxa may have been predominantly terrestrial (von Koenigswald et al., 1992; Storch, 1996; Smith et al., 2002; Gunnell and Bloch, 2008). If further evidence of substrate use in erinaceomorphans indicates high levels of terrestriality, this may diminish the likelihood of dietary competition between erinaceomorphans and euprimates regardless of whether niche overlap is identified in later time intervals (i.e., Wa6 and later). As was the case for the other instances of dietary niche overlap between euprimates and non-euprimates in Wa5, erinaceomorphan-omomyid overlap during this final time period is likewise identified as a potentially important interaction, necessitating further consideration, in the reconstruction of early euprimate dietary competition.

THE EUPRIMATE DIETARY NICHE

From Wa0 to Wa5, the dietary niches of adapids and omomyids remain distinct with the distance between the adapid and omomyid niche centroids reaching a maximum in Wa4 (Tables 6.9-6.12). In addition, adapids and omomyids do not concurrently overlap the niche of a non-euprimate group (Fig. 6.7). Even in the case of microsyopids, with whom omomyids and adapids potentially competed in Wa3 and Wa5, respectively, these events were separated by several hundred thousand years. As such, the patterns of overlap between both adapid and omomyid niches and those of non-euprimates, and thus

the potential competitive interactions that each euprimate clade encountered, also differ. Consequently, not only was the euprimate dietary niche heterogeneous within each time interval, but it also changed throughout the course of the earliest Paleogene.

Both in terms of absolute (all euprimates only) and relative (all euprimates and omomyids) hypervolumetric size (see explanation in "Overall Pattern of Dietary Niche Overlap Between Euprimates and Non-Euprimates"), dietary niche sizes of omomyids and euprimates as a whole decrease from Wa0 to Wa5 (Euprimates(absolute size): r=0.900, p=0.037; Euprimates(relative size): r=1.000, p<0.001; Omomyidae(absolute size): r=0.800, p=0.119; Omomyidae(relative size): r=1.000, p<0.001; Table 6.3; Figs. 6.8-6.15). The adapid niche also decreases in size from Wa0 to Wa4 but subsequently broadens in Wa5, although this pattern is not statistically significant (r=0.800, p=0.200; Table 6.3; Figs. 6.14-6.15). This signifies that euprimates occupied a much larger percentage of the guild-wide dietary niche space upon their origination in North America than during almost all subsequent time intervals examined; i.e., the euprimate dietary niche generally contracted over time. Furthermore, the mean distances of omomyid and adapid specimens from their niche centroids similarly decrease from Wa0 to Wa4 (Adapidae: r=1.000, p<0.001; Omomyidae: r=0.800, p=0.200) and increase from Wa4 to Wa5 (although mean centroid distances of all euprimate specimens combined decreases from Wa0 to Wa5 (r=0.900, p=0.037)) (Table 6.15; Fig. 6.16). With the exception of the peak of the Carbon Isotope Excursion (CIE) in Wa0, mean annual precipitation and temperature decreased from Wa0 to Wa4 and increased from Wa4 to Wa5 (Wilf, 2000; Woodburne et al., 2009a,b; Chew and Oheim, 2013; see Fig. 2.1).

This near-parallel pattern between niche expansion and contraction, on the one hand, and changes in temperature, on the other, suggests that there may be a link between early Paleogene climate and the euprimate (at least adapid) dietary niche. On the other hand, dietary niche sizes of euprimates may have changed in response to competition (or the lack thereof) with non-euprimates, and this will be discussed further in Chapter 7.

In addition to an overall decrease in the size of euprimate niches, the patterns of niche overlap among euprimate genera and comparisons of distances between niche centroids in adjacent time intervals suggest that the position of the euprimate dietary niche within the guild-wide niche space also shifted through time. First, if one simply considers the first two niche axes, it appears that the niches of both adapids and omomyids are shifting in a similar direction, away from the original (Wa0) niche (at least from Wa0 to Wa3) (Figs. 6.17-6.21; see Fig 6.13). In fact, the distance between the overall euprimate Wa0 niche centroid and the centroid of the niche in each subsequent time interval is greatest in Wa3 (although the distance between the Wa0 and Wa4 centroids is almost equivalent) (Table 6.15; Figs. 6.17-6.21). Relative to their corresponding Wa0 dietary niche centroids, the niche centroids of both adapids and omomyids are furthest from their Wa0 starting points in Wa4, at which time the niches of both adapids and omomyids move towards the Wa0 niche position in Wa5 (Table 6.15; Figs. 6.17-6.21). Results indicate that the greatest shift in the adapid niche occurred between Wa4 and Wa5, whereas that of the omomyid niche was coincident with the transition from Wa1-2 to Wa3 (see Table 6.2). This asynchronicity is consistent with separate evolutionary trajectories for the adapid and omomyid niches. An examination of the distance between the adapid and omomyid niche centroids for each time interval, a

proxy for the degree of niche separation, demonstrates that this distance remains fairly constant from Wa0 to Wa3, dramatically increases in Wa4, and subsequently drops to its minimum value in Wa5 (Table 6.15; Fig. 6.22).

The analyses of niche overlap among adapid and omomyid genera provide further detail regarding the above patterns. First, within the adapid and omomyid niches, almost all synchronous omomyid or adapid genera overlap with one another; the sole exception is the lack of niche overlap between *Tetonius* and *Teilhardina* in Wa1-2 (see Tables 6.9-6.12). Perhaps not surprisingly, this indicates that although the euprimate niche is heterogenous, the dietary niches of each major group of euprimates (adapids and omomyids) are much less so. Second, there is much greater overlap among omomyid niches across time intervals than among adapid niches. In omomyids, the dietary niches corresponding to the Wa0 and Wa1-2 time intervals overlap one another as do the three niches from Wa3 to Wa5 (see Table 6.13). In other words, there appears to be a distinction between the early (Wa0 and Wa1-2) and later (Wa3-Wa5) omomyid niches. This is consistent with the shift in omomyid niche centroid location between Wa1-2 and Wa3, as discussed above, as well the reduced number of instances of overlap among Wa3 and Wa1-2 omomyid genera (see Table 6.2, 6.10; Figs. 6.9, 6.10, 6.13). In contrast, only the adapid niches of Wa0 and Wa1-2 and those of Wa3 and Wa5 significantly overlap (Table 6.15). Taken together with the patterns of centroid location discussed previously, the adapid niche seems to shift in one direction from Wa1-2 to Wa3 and from Wa3 to Wa4 but reverses direction between Wa4 and Wa5, such that the location of the Wa5 adapid niche is similar to that of the niche in Wa3 (see Table 6.2; Figs. 6.8-6.13).

Altogether, these results indicate that the evolutionary course of the euprimate dietary niche is the consequence of distinct patterns, and likely distinct processes, that were occurring within each of the two main euprimate groups: adapids and omomyids. Possible explanations for the changes in the adapid and omomyid, and thus euprimate, dietary niches discussed above will be examined within the context of the euprimate dietary competitive environment in the following chapter.

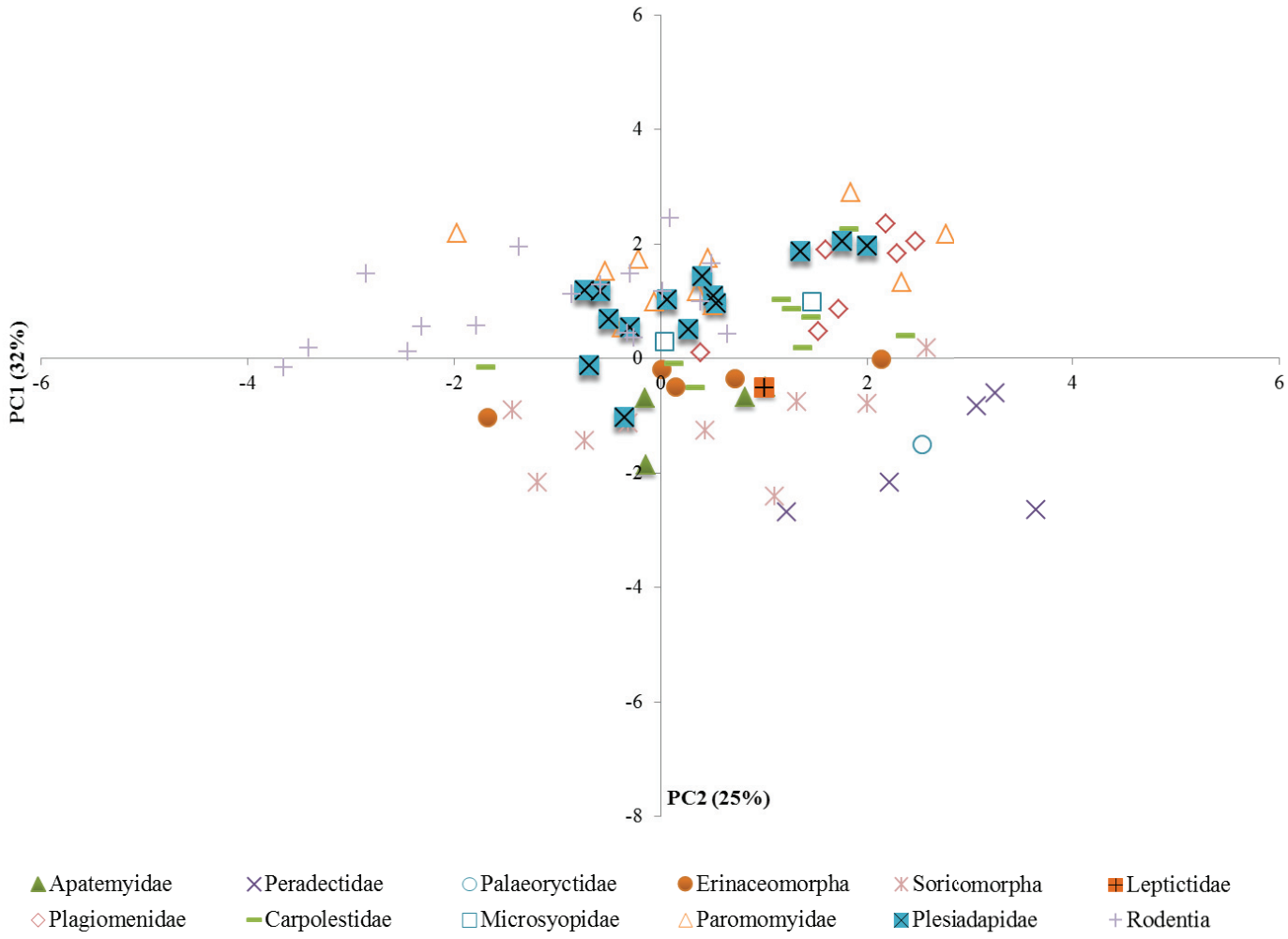


Figure 6.1. Plot of PC1 and PC2 for all fossil specimens in Cf2-3. Each symbol corresponds to an individual specimen.

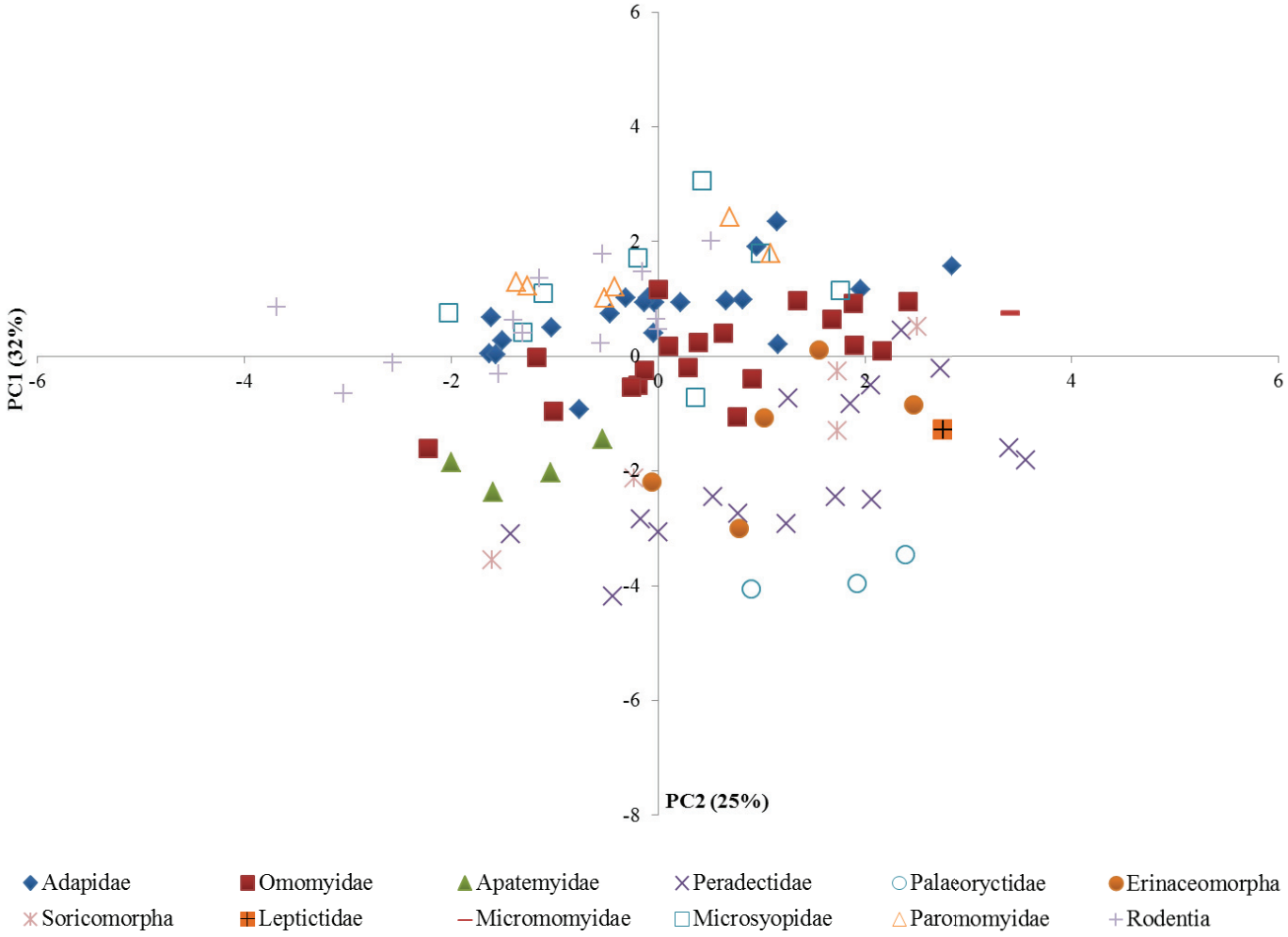


Figure 6.2. Plot of PC1 and PC2 for all fossil specimens in Wa0. Each symbol corresponds to an individual specimen.

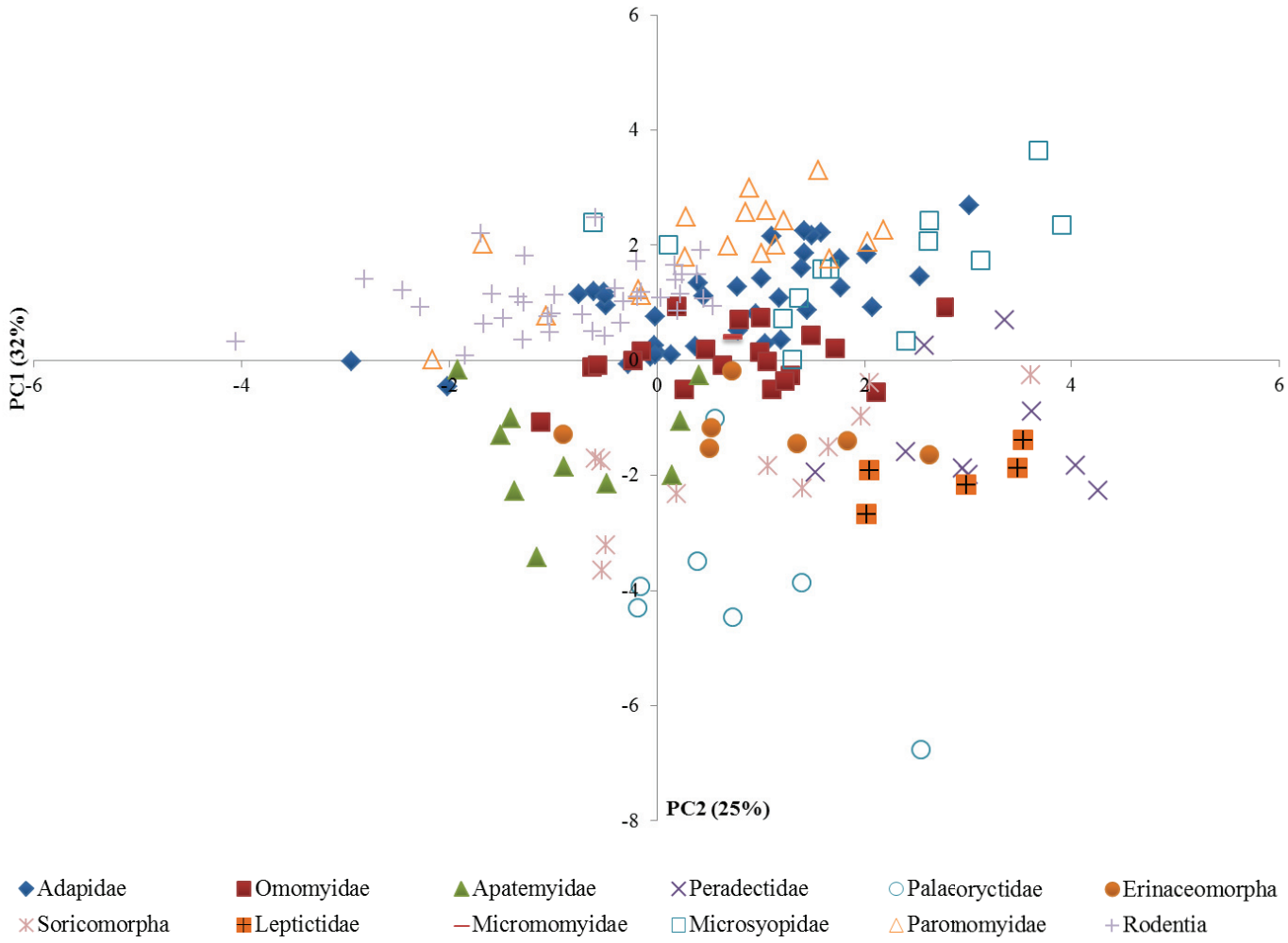


Figure 6.3. Plot of PC1 and PC2 for all fossil specimens in Wa1-2. Each symbol corresponds to an individual specimen.

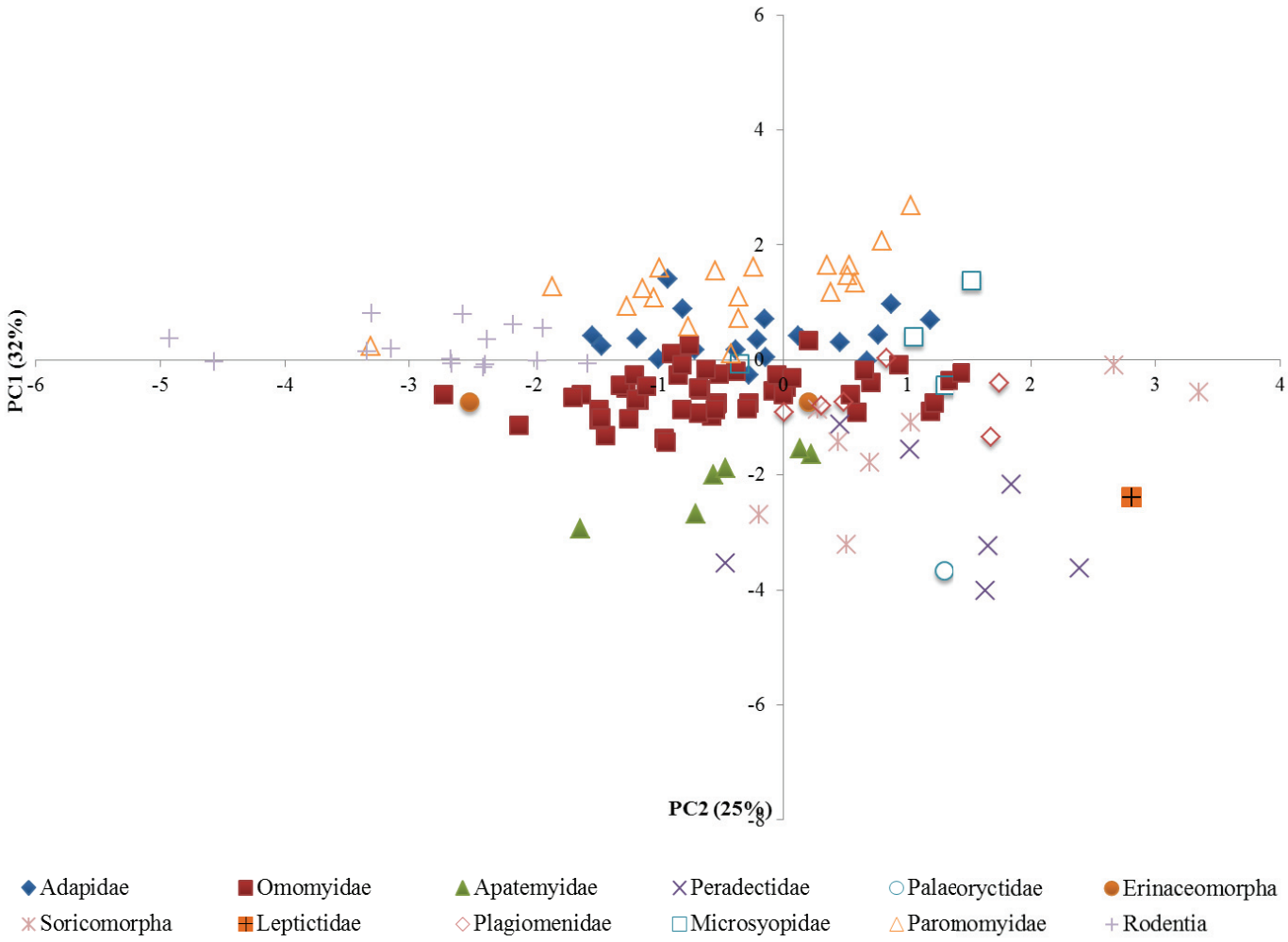


Figure 6.4. Plot of PC1 and PC2 for all fossil specimens in Wa3. Each symbol corresponds to an individual specimen.

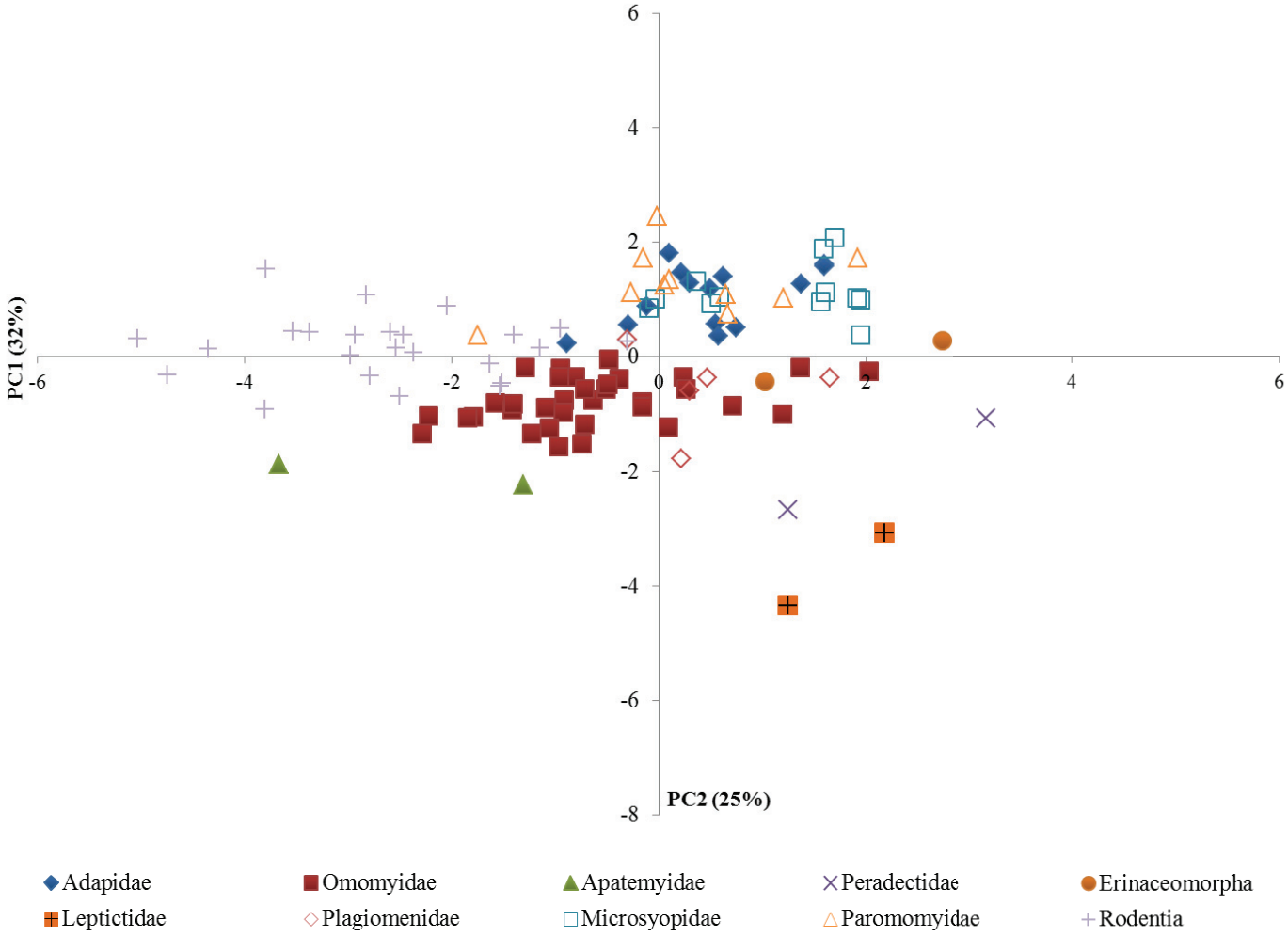


Figure 6.5. Plot of PC1 and PC2 for all fossil specimens in Wa4. Each symbol corresponds to an individual specimen.

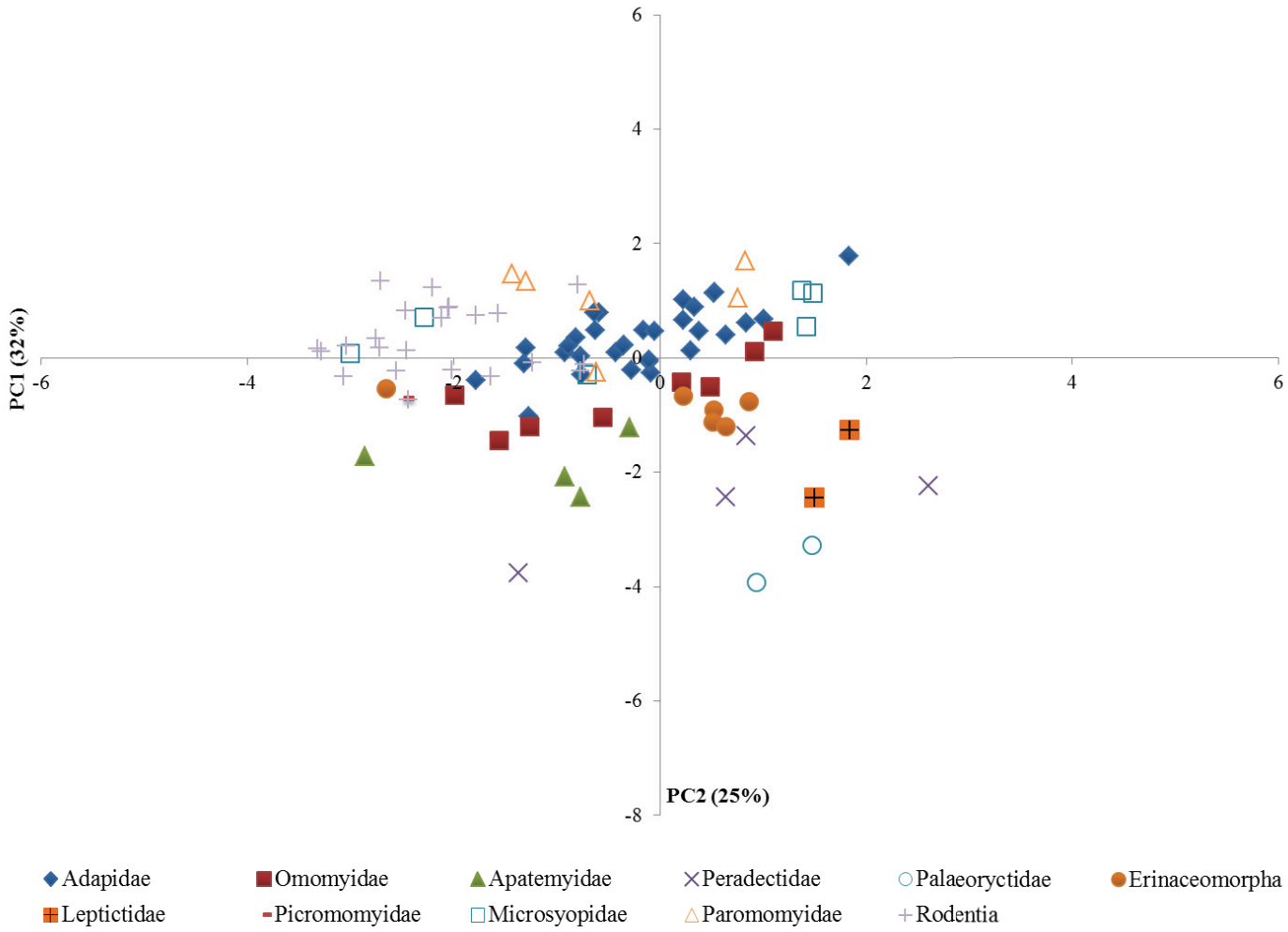


Figure 6.6. Plot of PC1 and PC2 for all fossil specimens in Wa5. Each symbol corresponds to an individual specimen.

		Wa0	Wa1-2	Wa3	Wa4	Wa5
Non-Euprimate Dietary Niche Space		Cf2-3 Plagiomenidae Cf2-3 Didelphidae Cf2-3 Soricomorpha Cf2-3 Carpolestidae Cf2-3 Paromomyidae Cf2-3 Paramyidae Wa0 Apatemyidae Wa0 Peradectidae Wa0 Palaeoryctidae Wa0 Erinaceomorpha Wa0 Microsyopidae Wa0 Paromomyidae Wa0 Paramyidae Wa0 Cylindrodontidae	Wa0 Apatemyidae Wa0 Peradectidae Wa0 Palaeoryctidae Wa0 Erinaceomorpha Wa0 Microsyopidae Wa0 Paromomyidae Wa0 Paramyidae Wa0 Cylindrodontidae Wa1-2 Apatemyidae Wa1-2 Palaeoryctidae Wa1-2 Leptictida Wa1-2 Erinaceomorpha Wa1-2 Soricomorpha Wa1-2 Peradectidae Wa1-2 Microsyopidae Wa1-2 Paromomyidae Wa1-2 Paramyidae	Wa1-2 Apatemyidae Wa1-2 Palaeoryctidae Wa1-2 Leptictida Wa1-2 Erinaceomorpha Wa1-2 Soricomorpha Wa1-2 Peradectidae Wa1-2 Microsyopidae Wa1-2 Paromomyidae Wa1-2 Paramyidae Wa3 Apatemyidae Wa3 Lipotyphla Wa3 Peradectidae Wa3 *Niptomomys* Wa3 Paromomyidae Wa3 Paramyidae Wa3 Plagiomenidae Wa3 *Arctodontomys* +*Microsyops*	Wa3 Apatemyidae Wa3 Plagiomenidae Wa3 Lipotyphla Wa3 Peradectidae Wa3 Microsyopidae Wa3 Paromomyidae Wa3 Paramyidae Wa4 Plagiomenidae Wa4 Lipotyphla + Leptictida Wa4 Microsyopidae Wa4 Paromomyidae Wa4 Paramyidae Wa4 Sciuravidae	Wa4 Lipotyphla + Leptictida Wa4 Microsyopidae Wa4 Paramyidae Wa4 Sciuravidae Wa5 Apatemyidae Wa5 Lipotyphla + Leptictida Wa5 Didelphidae Wa5 Paramyidae
Euprimate Dietary Niche	Adapid Niche	Cf2-3 Plesiadapidae				Wa4 Plagiomenidae Wa4 Paromomyidae Wa5 Microsyopidae Wa5 Paromomyidae
	Omomyid Niche	Cf2-3 Apatemyidae Cf2-3 Erinaceomorpha Wa0 Soricomorpha	Wa0 Soricomorpha	Wa3 Microsyopidae		Wa5 Erinaceomorpha

Fig 6.7. Schematic of the occupation of the guild-wide dietary niche space from Wa0 to Wa5. Each column represents a time interval within this study, and each time interval is divided into two sections: the top section denotes the dietary niche space that does not significantly overlap that of euprimates, and the bottom two sections represent the euprimate dietary niche spaces of adapids and omomyids, respectively. The location of each non-euprimate taxon signifies its presence either "outside" the euprimate dietary niche (i.e., taxa whose niches did not overlap with those of euprimates) or "inside" the euprimate dietary niche (i.e., taxa whose niches overlapped the euprimate niche) in each time period.

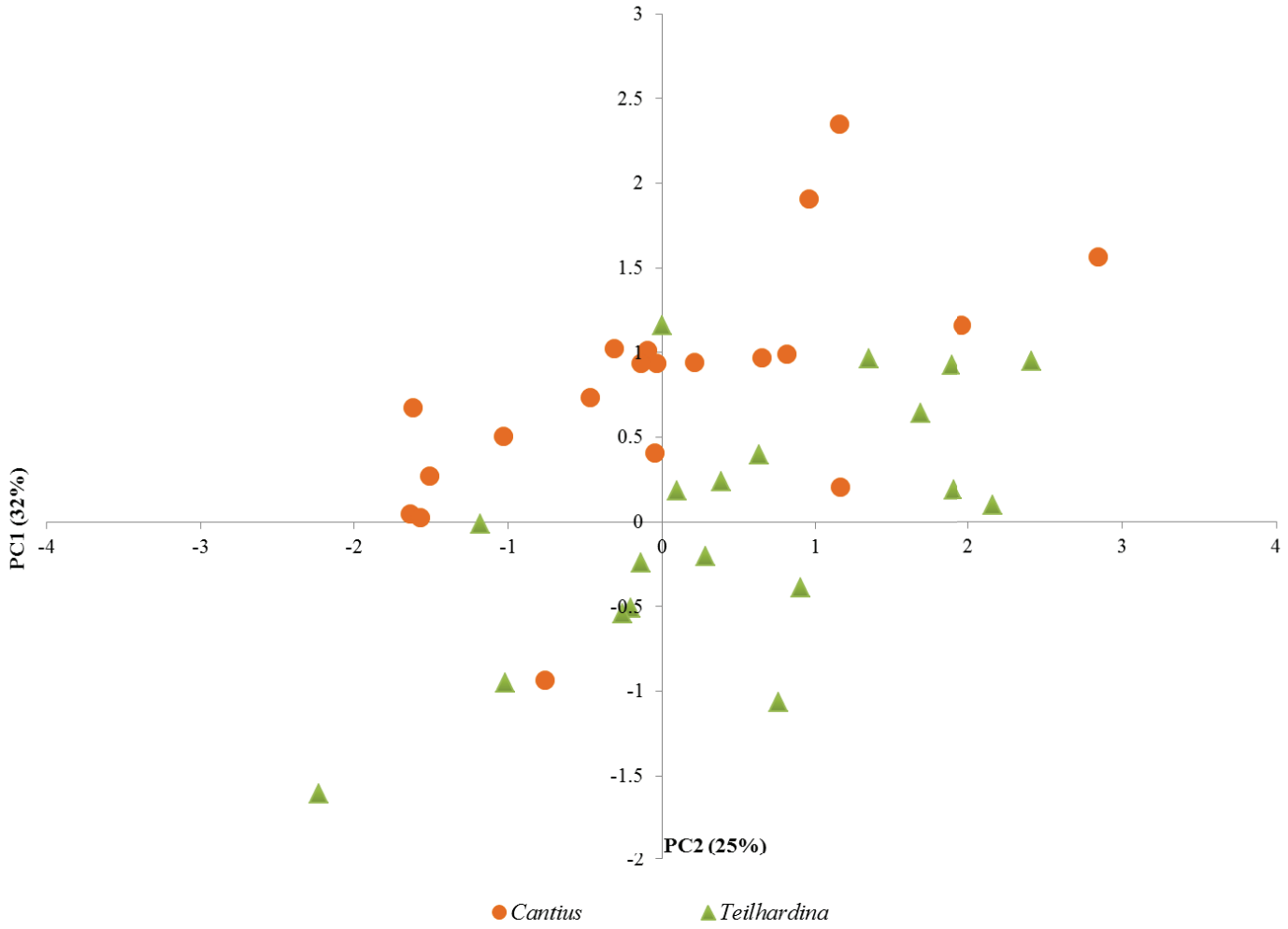


Figure 6.8. Plot of PC1 and PC2 for all euprimate specimens in Wa0. Each symbol corresponds to an individual specimen.

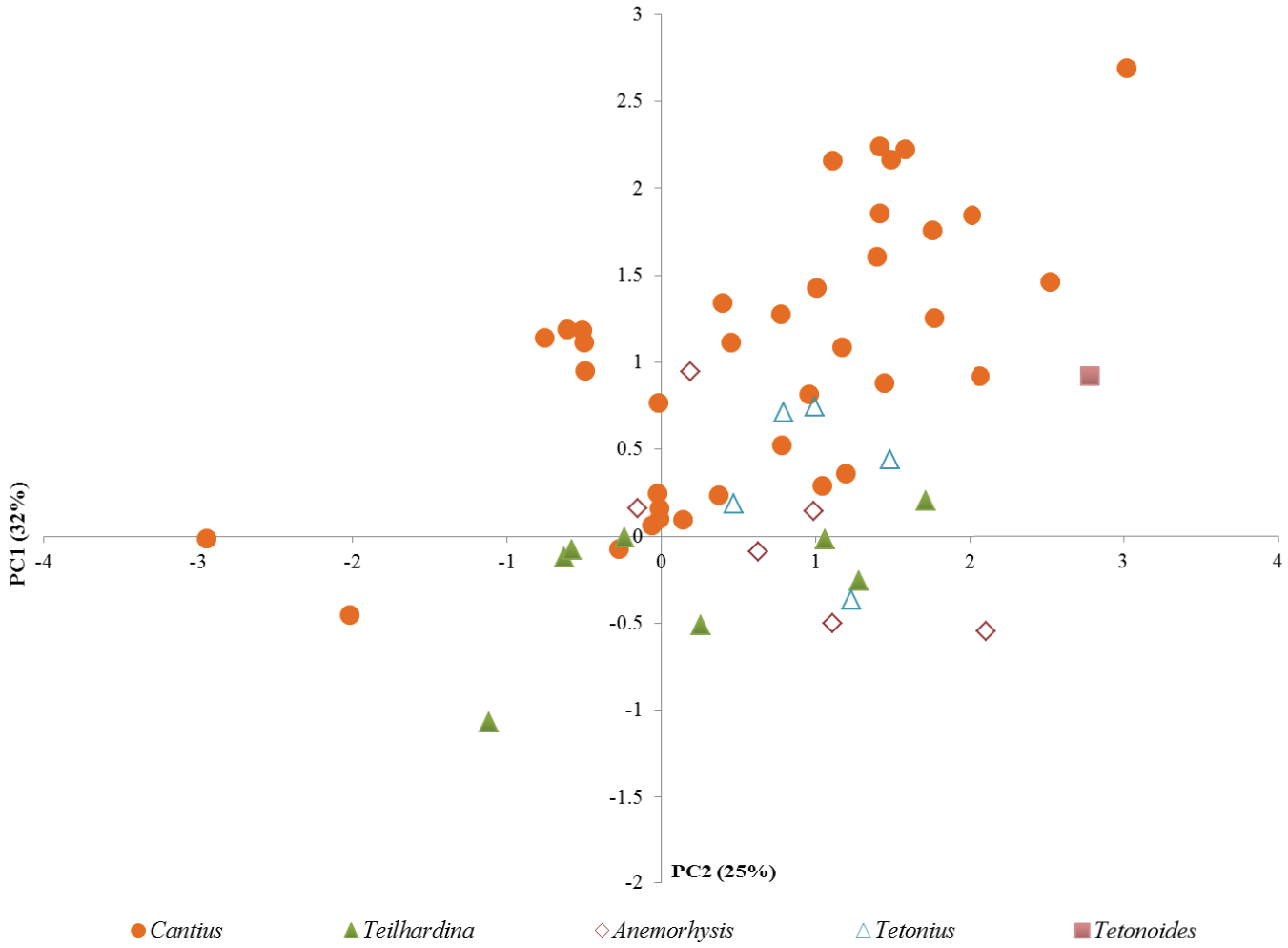


Figure 6.9. Plot of PC1 and PC2 for all euprimate specimens in Wa1-2. Each symbol corresponds to an individual specimen.

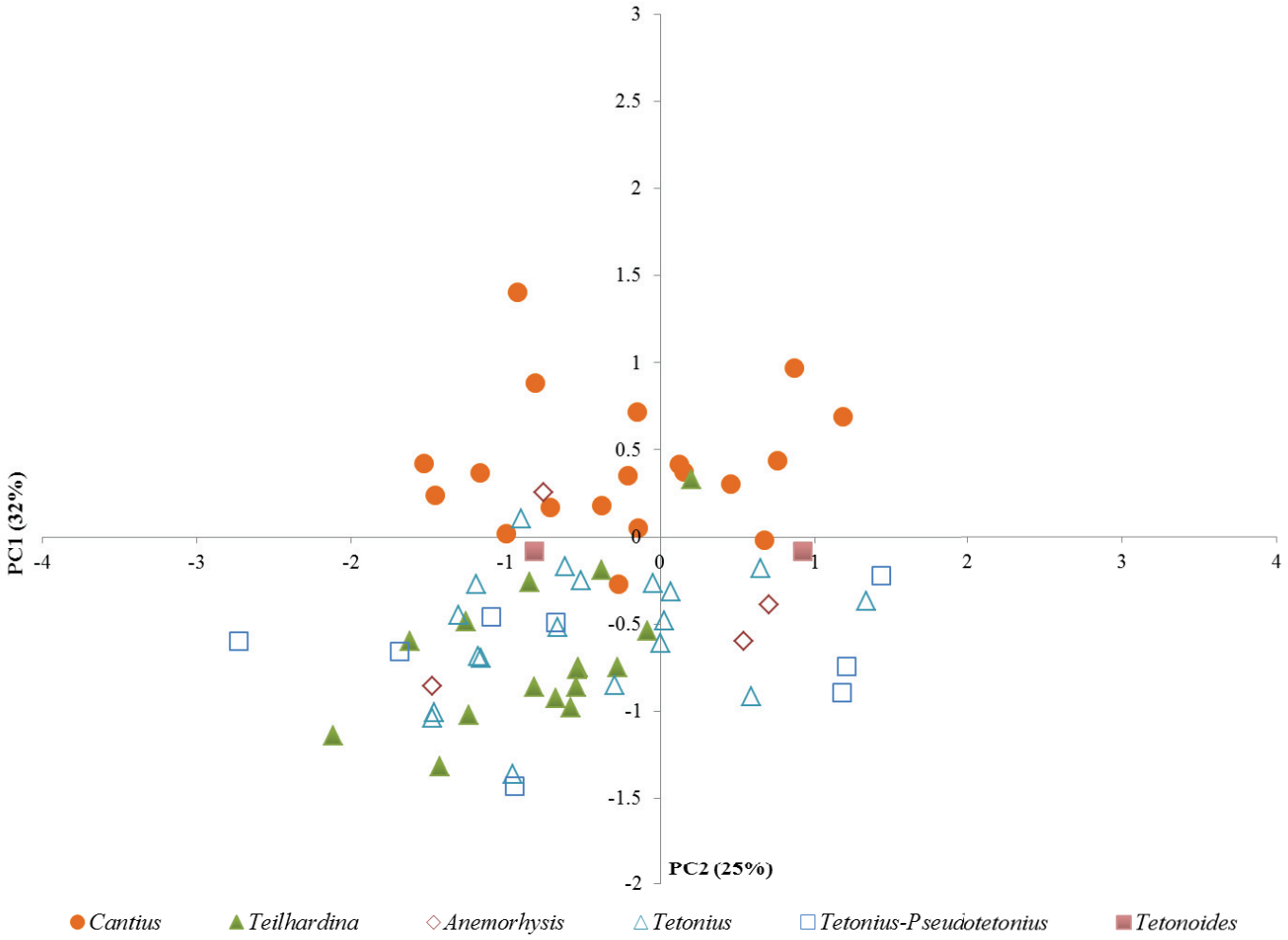


Figure 6.10. Plot of PC1 and PC2 for all euprimate specimens in Wa3. Each symbol corresponds to an individual specimen.

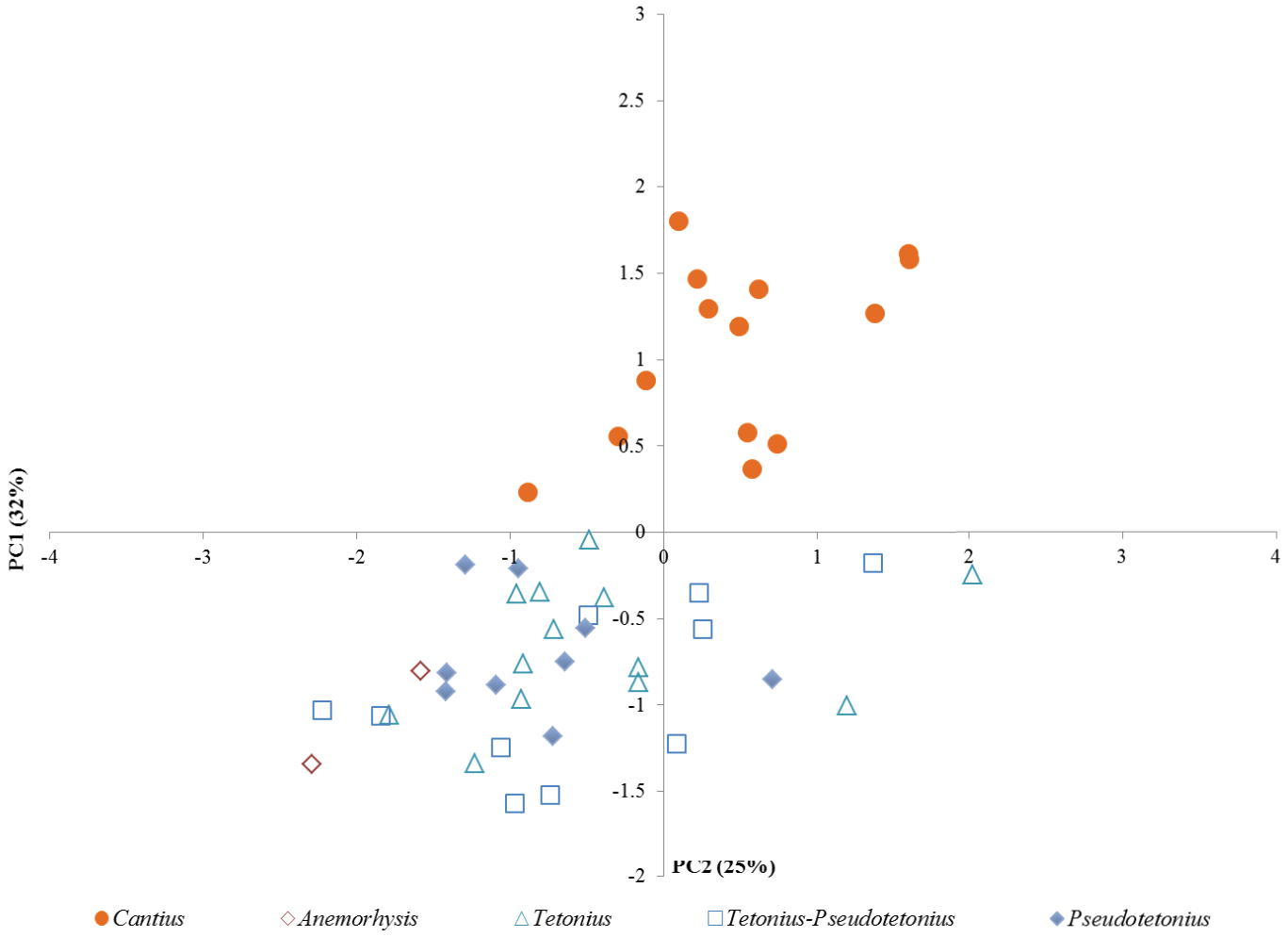


Figure 6.11. Plot of PC1 and PC2 for all euprimate specimens in Wa4. Each symbol corresponds to an individual specimen.

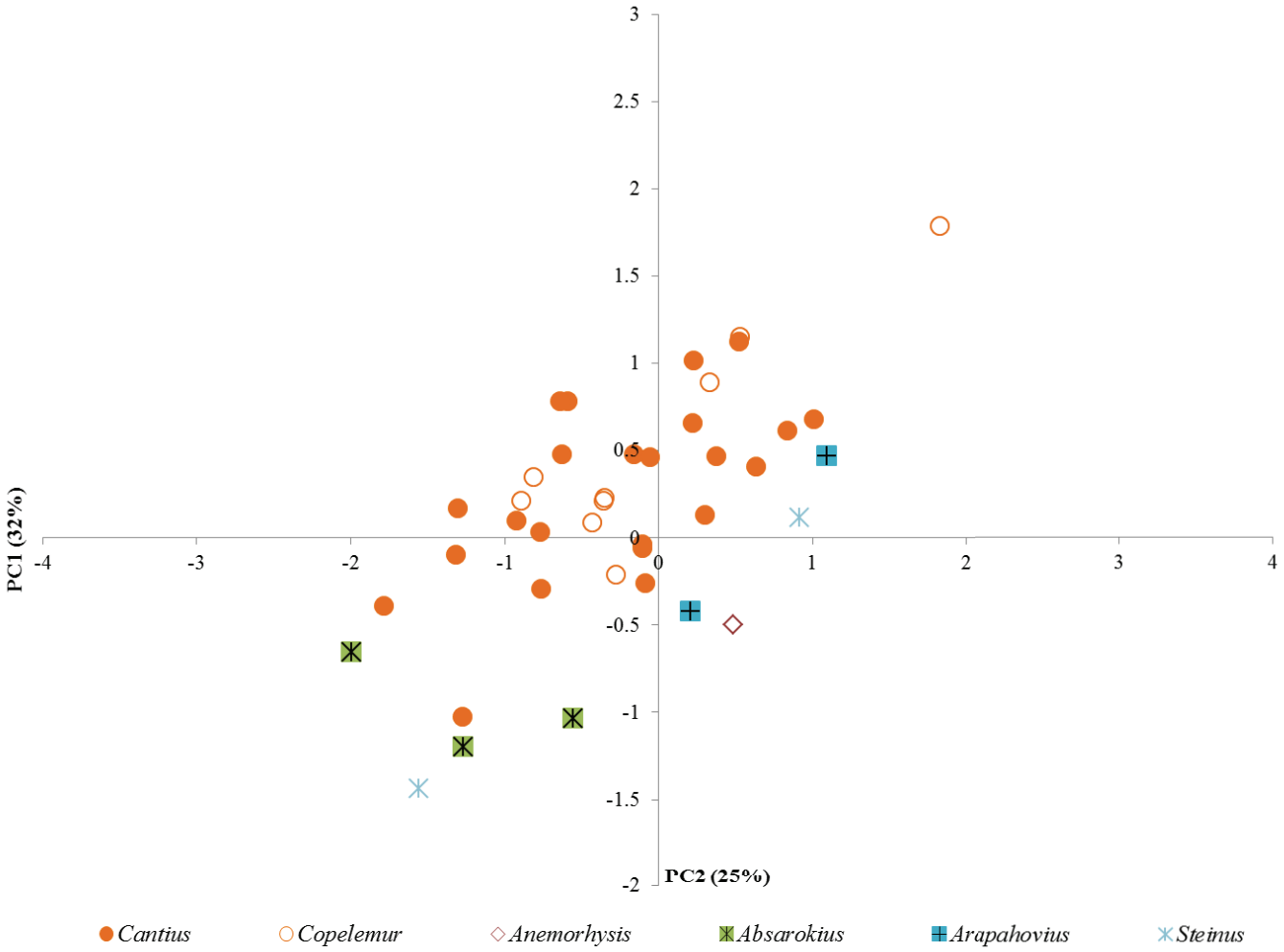


Figure 6.12. Plot of PC1 and PC2 for all euprimate specimens in Wa5. Each symbol corresponds to an individual specimen.

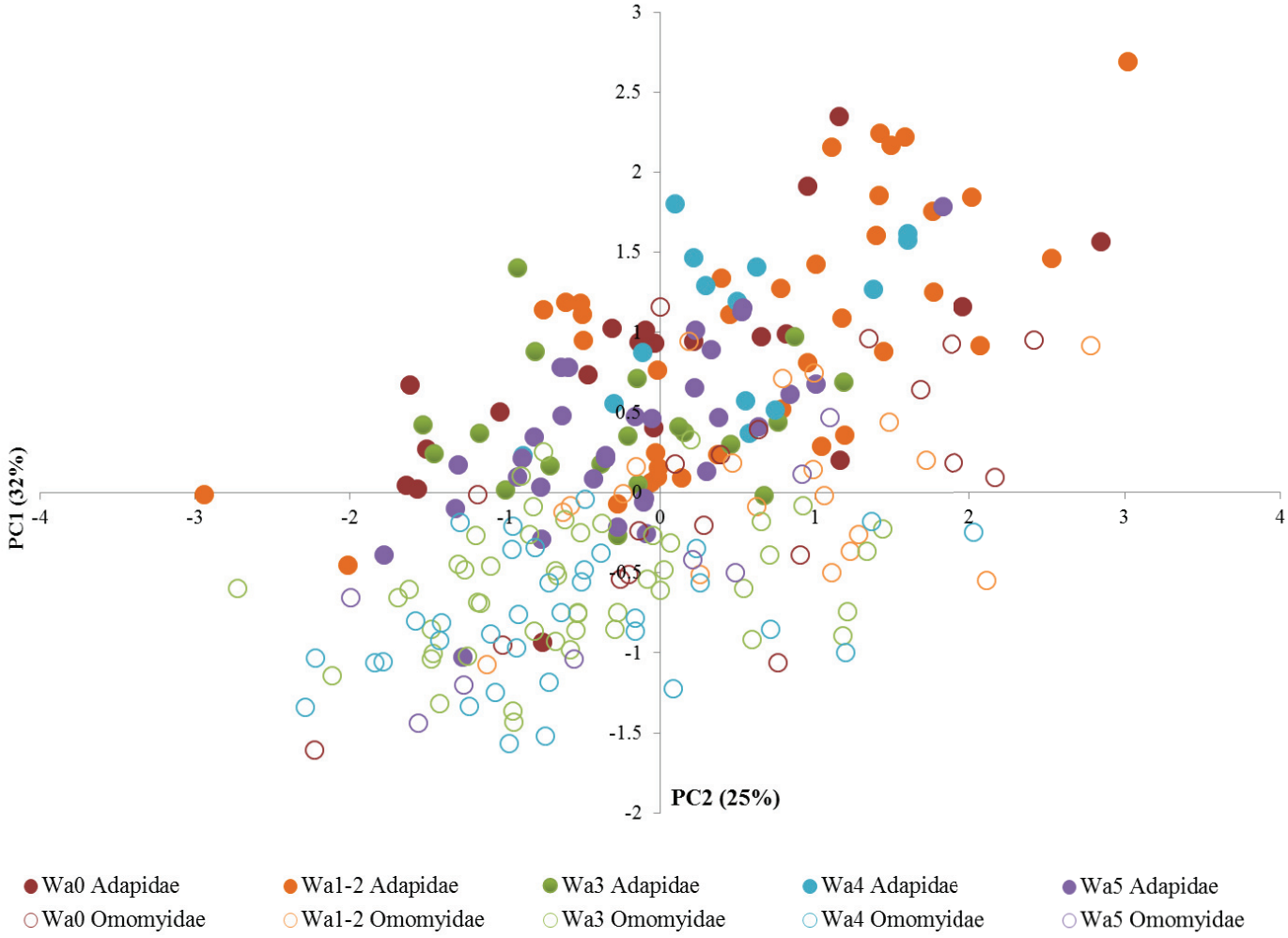


Figure 6.13. Plot of PC1 and PC2 for all euprimate specimens from Wa0 to Wa5. Each symbol corresponds to an individual specimen.

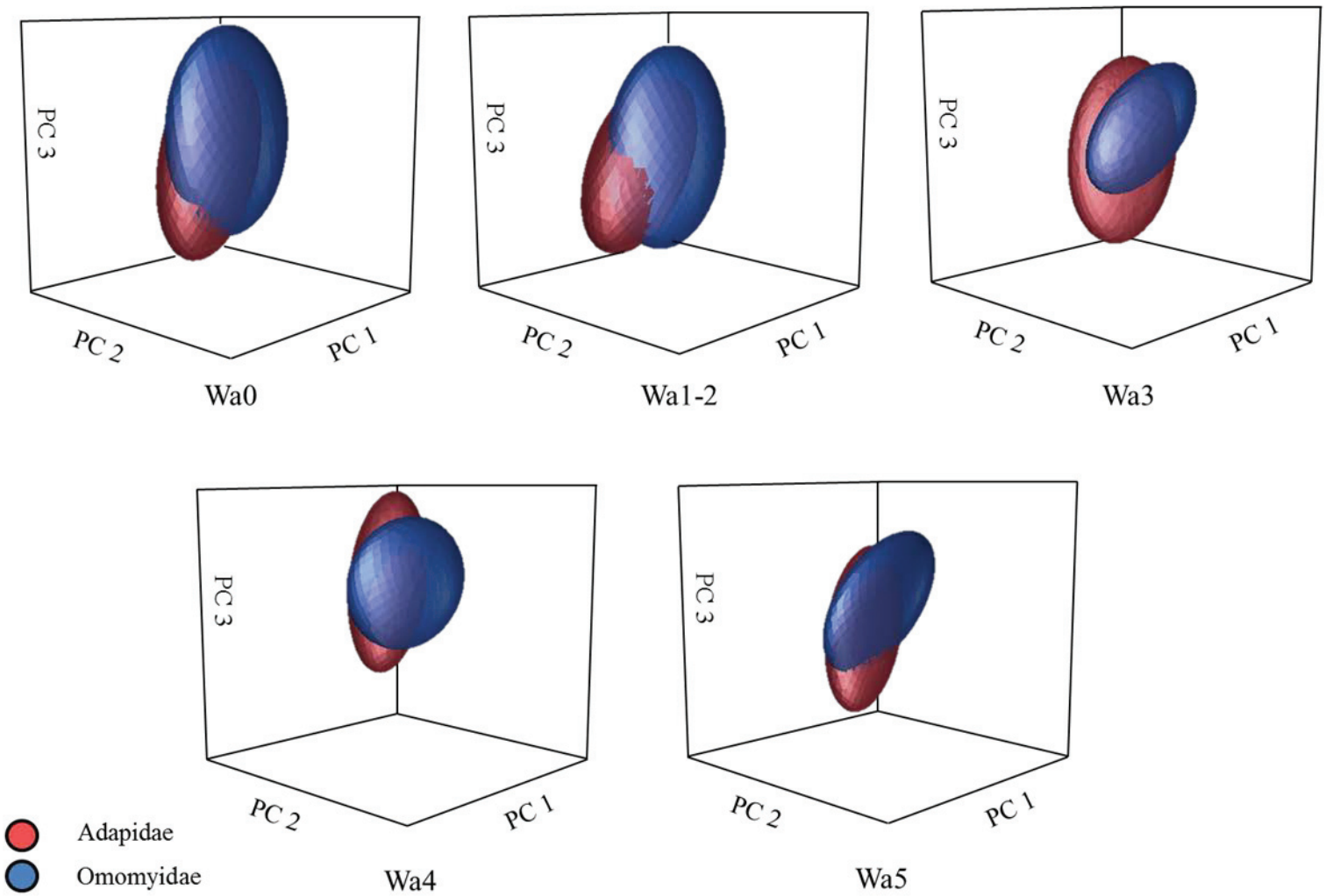


Fig. 6.14. Three-dimensional 95% confidence ellipsoids ("hypervolumes") of adapid and omomyid niches from Wa0 to Wa5.

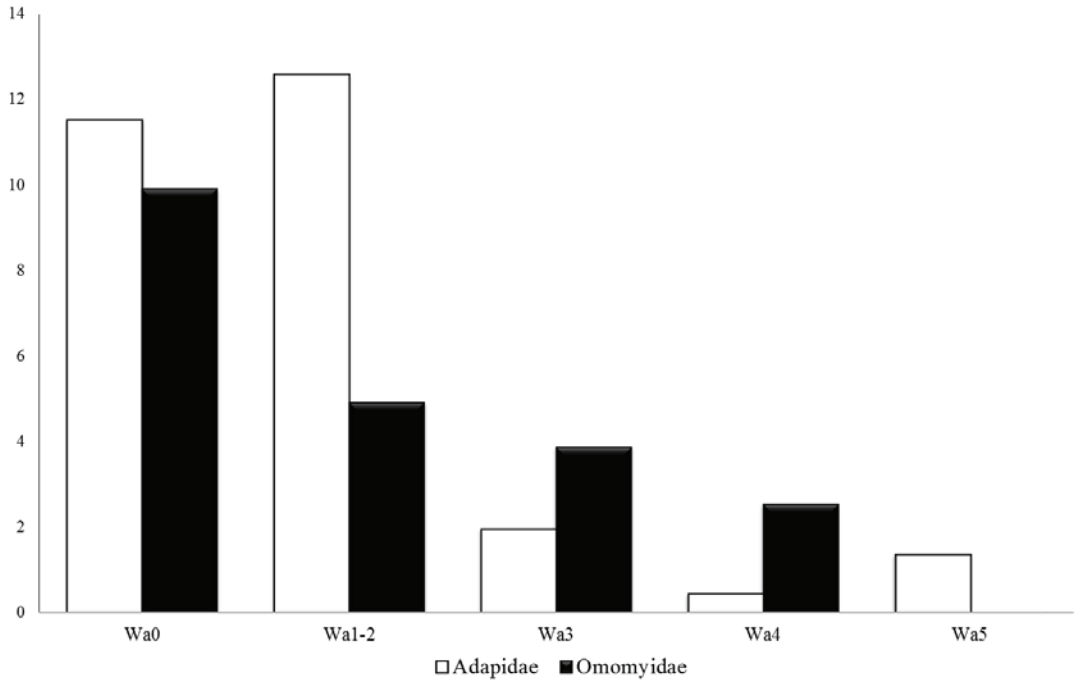


Fig. 6.15. Plot of the relative hypervolumetric size of adapid and omomyid six-dimensional niches for each time interval. Values on the y-axis represent percentage of the total guild-wide niche space.

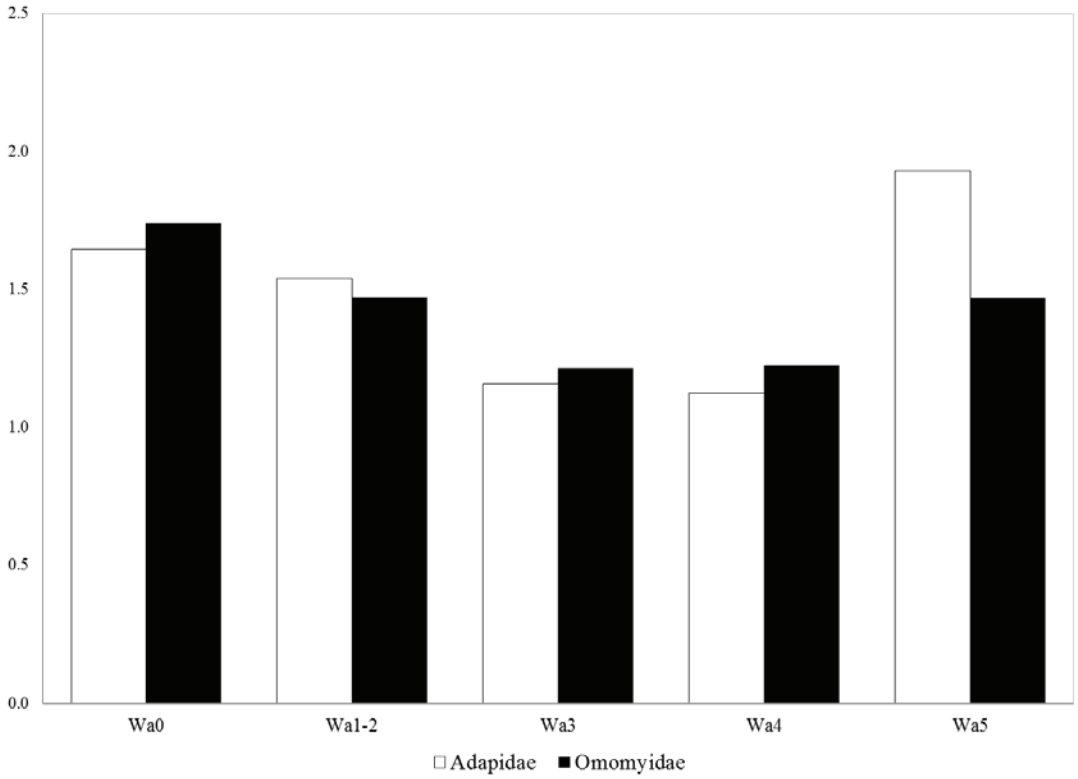


Fig. 6.16. Plot of the mean distances of adapid and omomyid individuals from their respective group centroids for each time interval.

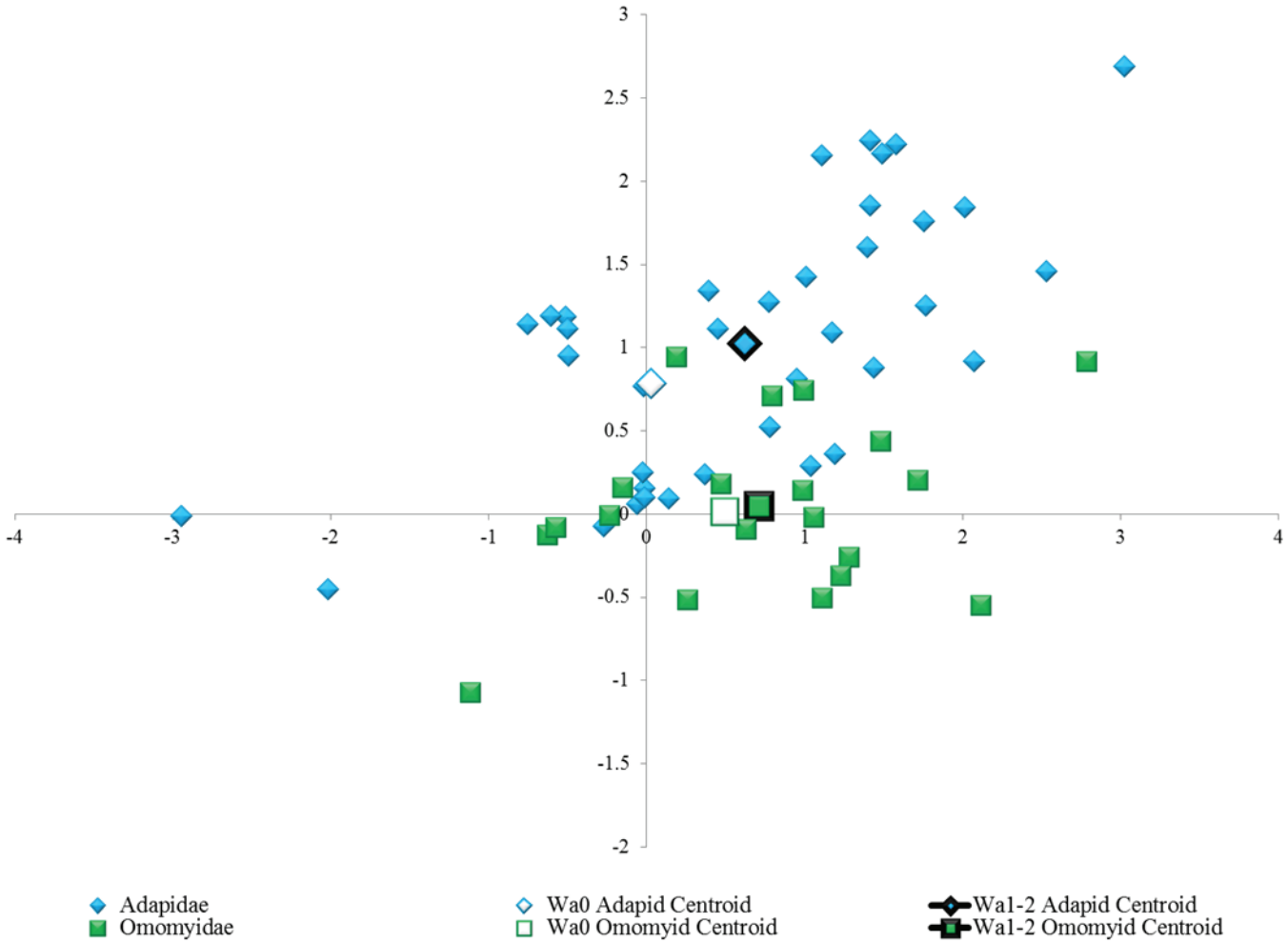


Fig. 6.17. Plot of PC1 and PC2 for all Wa1-2 euprimate specimens including Wa0 and Wa1-2 hypervolume centroids. Note the distance between the Wa0 and Wa1-2 centroids of adapids and omomyids. Each symbol corresponds to an individual specimen.

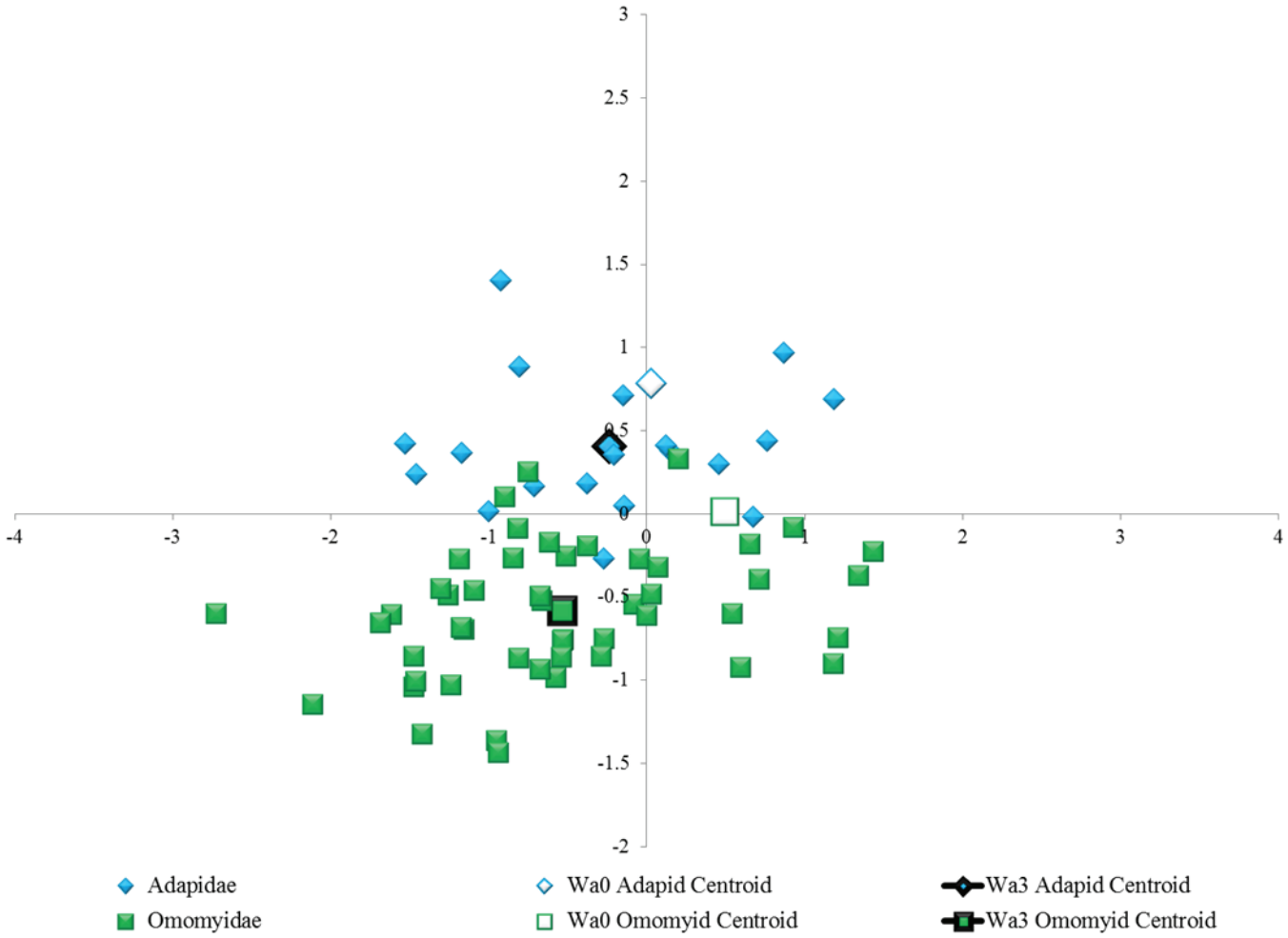


Fig. 6.18. Plot of PC1 and PC2 for all Wa3 euprimate specimens including Wa0 and Wa3 hypervolume centroids. Note the distance between the Wa0 and Wa3 centroids of adapids and omomyids. Each symbol corresponds to an individual specimen.

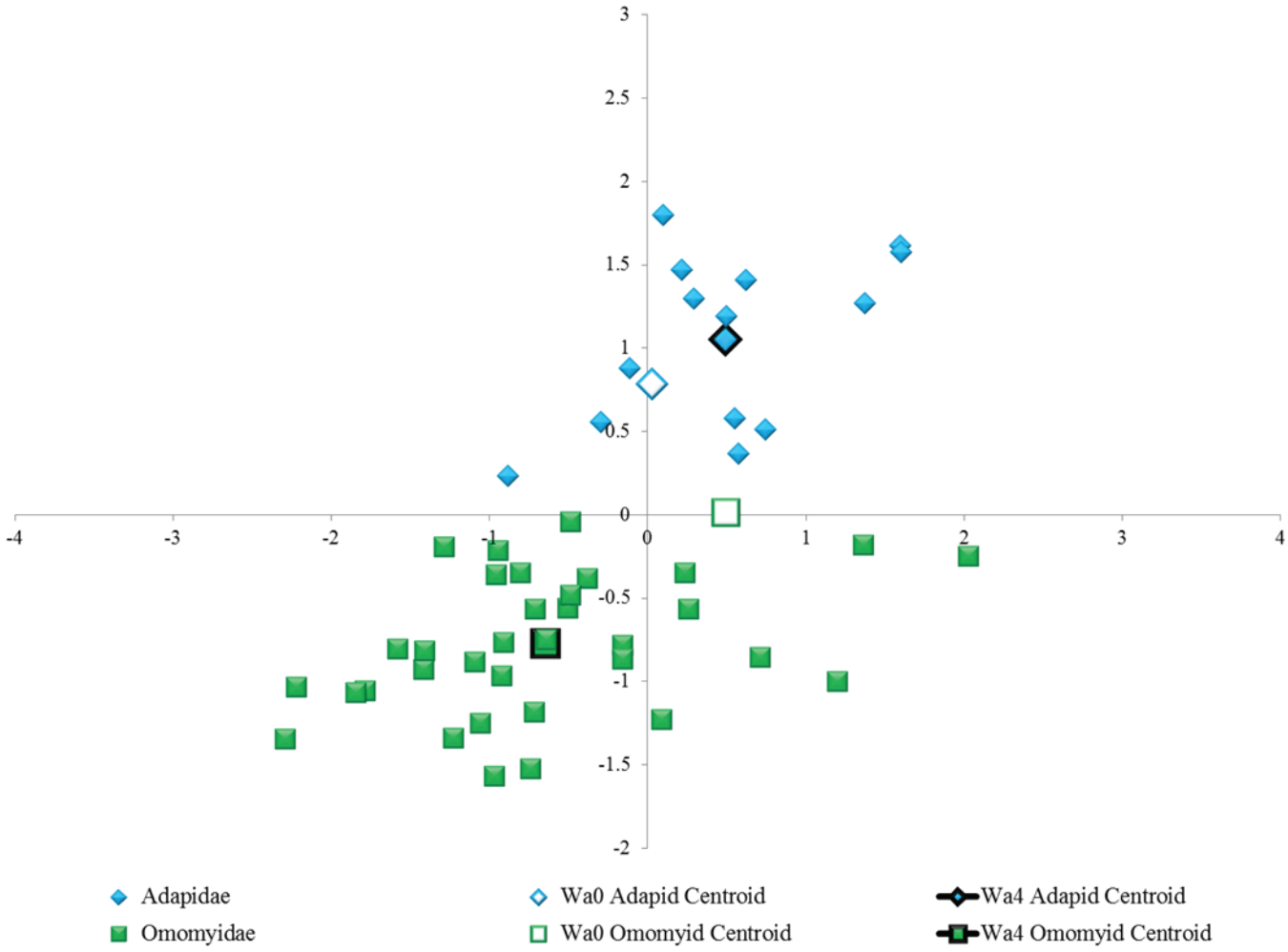


Fig. 6.19. Plot of PC1 and PC2 for all Wa4 euprimate specimens including Wa0 and Wa4 hypervolume centroids. Note the distance between the Wa0 and Wa4 centroids of adapids and omomyids. Each symbol corresponds to an individual specimen.

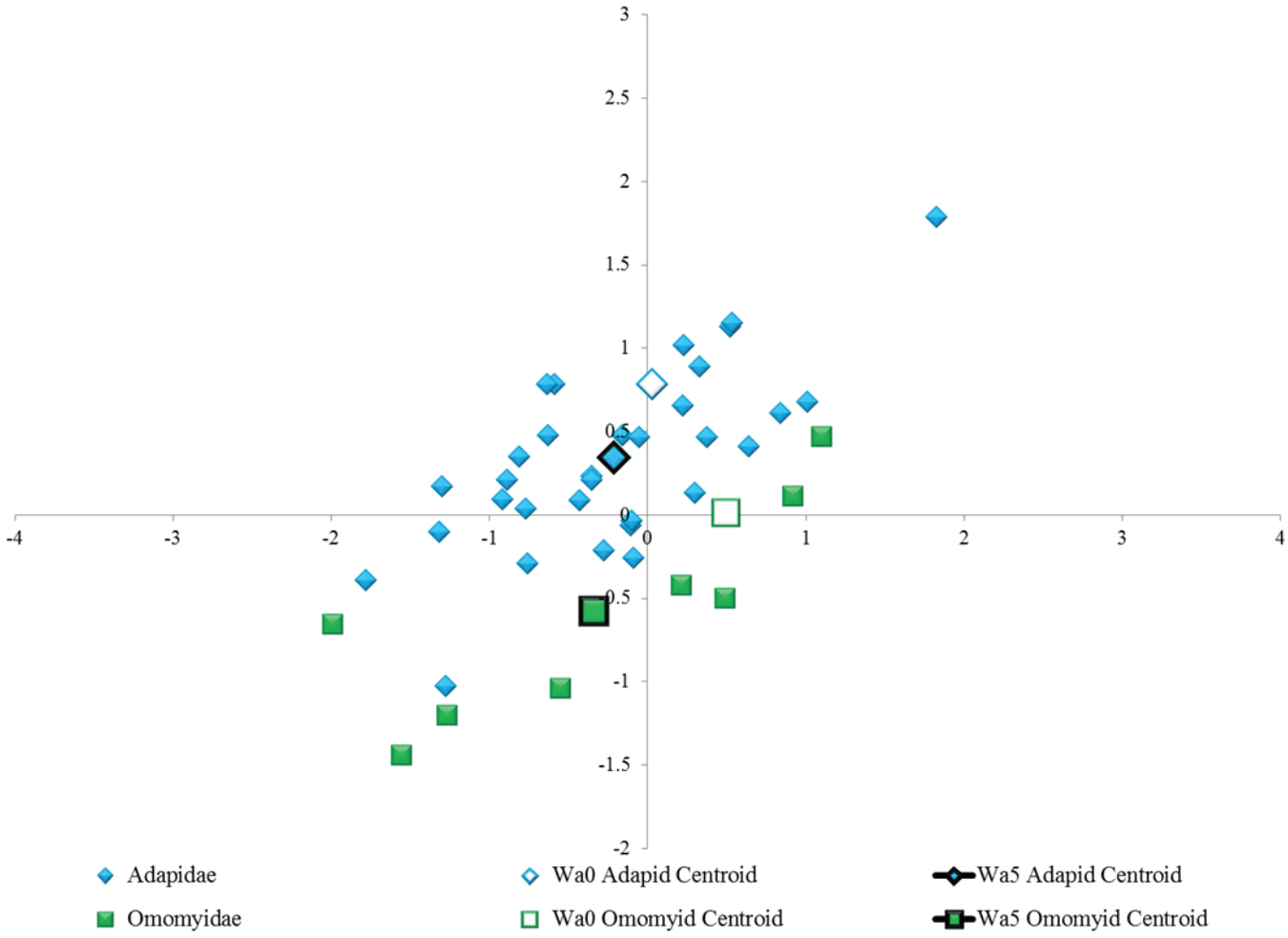


Fig. 6.20. Plot of PC1 and PC2 for all Wa5 euprimate specimens including Wa0 and Wa5 hypervolume centroids. Note the distance between the Wa0 and Wa5 centroids of adapids and omomyids. Each symbol corresponds to an individual specimen.

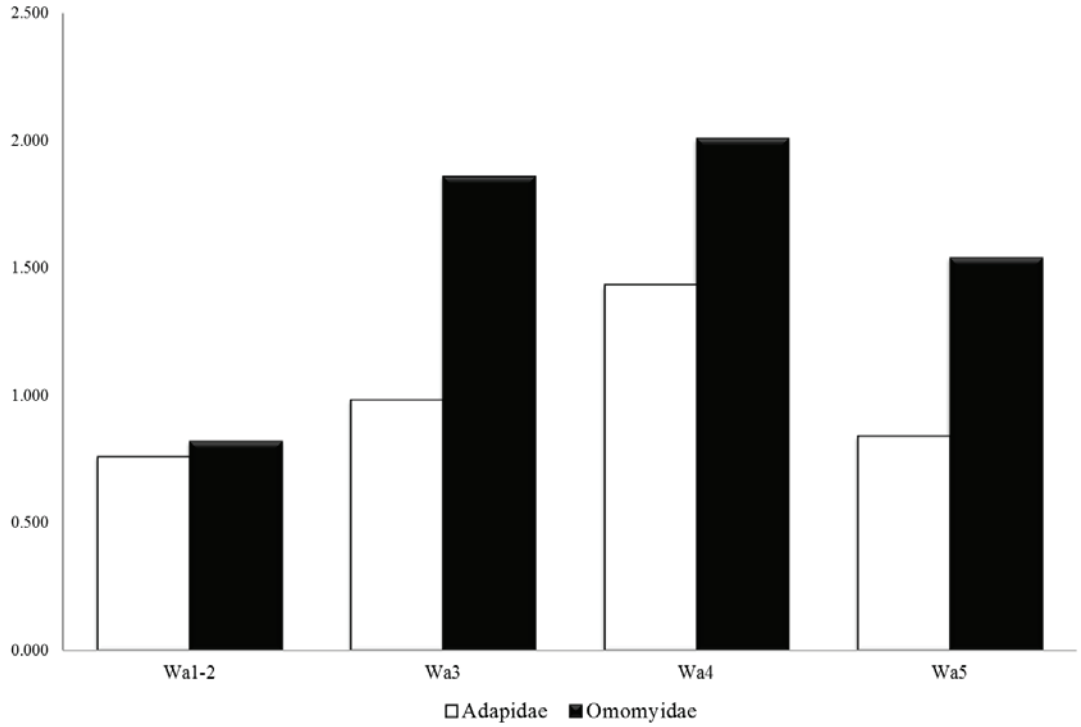


Fig. 6.21. Plot of the six-dimensional distances between the Wa0 hypervolume centroids of adapids and omomyids and the centroids of each subsequent time interval .

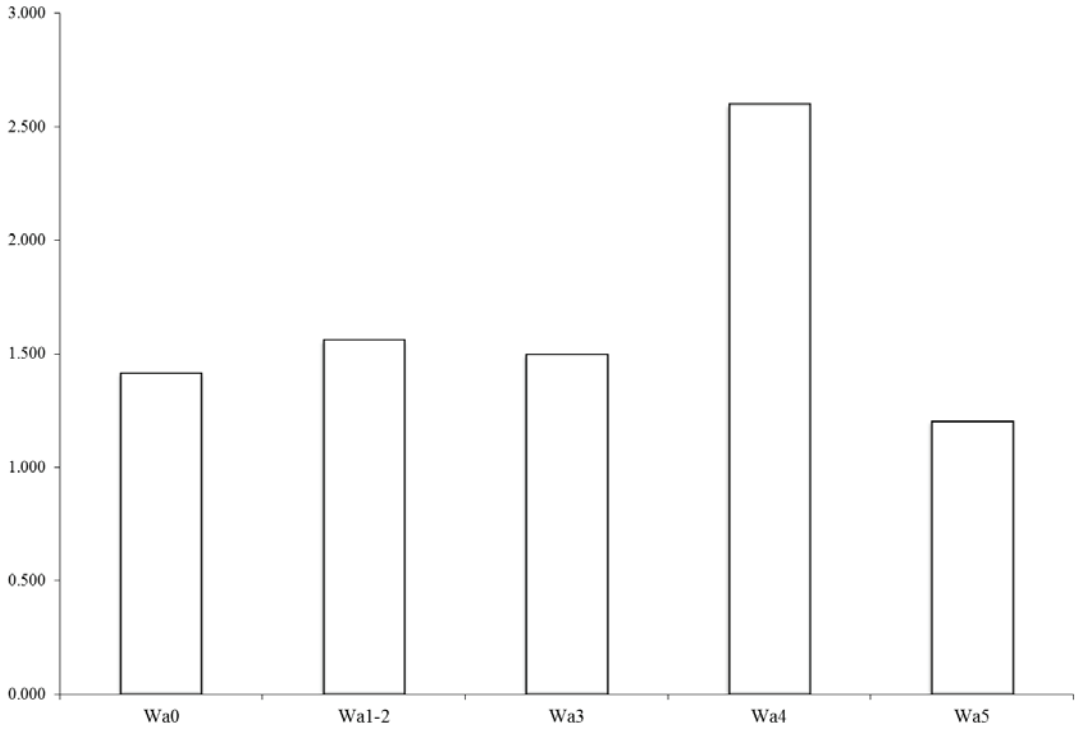


Fig. 6.22. Plot of the six-dimensional distances between the hypervolume centroids of adapids and omomyids for each time interval.

Table 6.1. Eigenvalues and eigenvectors of the principal component analysis of the entire fossil sample (including all specimens for all time intervals) using Variable Set 3.

	Eigenvalue	Difference	Proportion	Cumulative		PC1	PC2	PC3	PC4	PC5	PC6
1	2.544	0.530	0.318	0.318	Total crest length	0.304	0.406	-0.100	0.468	0.084	0.675
2	2.014	0.960	0.252	0.570	Talonid basin area	-0.129	0.444	-0.609	-0.006	0.363	-0.218
3	1.054	0.237	0.132	0.702	Talonid basin depth	0.179	0.423	0.461	0.404	0.160	-0.605
4	0.817	0.246	0.102	0.804	Trigonid-talonid relief	0.314	-0.399	-0.417	0.064	0.491	-0.202
5	0.572	0.081	0.071	0.875	Trigonid cusp height	0.426	-0.412	0.177	0.173	0.159	-0.009
6	0.490	0.173	0.061	0.937	Trigonid cusp angle	-0.519	0.070	0.228	-0.187	0.442	0.114
7	0.317	0.127	0.040	0.976	Talonid cusp height	0.376	0.196	0.331	-0.587	0.451	0.206
8	0.190		0.024	1.000	Talonid cusp angle	-0.411	-0.294	0.198	0.452	0.413	0.185

Table 6.2. Distances between dietary niche centroids of adjacent time intervals for each major taxonomic group. Bolded values represent the largest change in centroid location (i.e., the greatest distance between centroids) for each taxon.

	Cf2-3-Wa0	Wa0-Wa1-2	Wa1-2-Wa3	Wa3-Wa4	Wa4-Wa5
ALL TAXA	0.690	0.537	**1.393**	0.395	0.471
Adapidae	---	0.761	1.160	1.184	**1.453**
Omomyidae	---	0.820	**1.592**	0.224	0.575
Euprimates	---	0.674	**1.675**	0.263	0.808
Apatemyidae	**2.555**	1.316	1.161	2.345	1.682
Peradectidae	1.574	2.075	**2.675**	1.947	2.065
Paleoryctidae	**4.116**	1.806	2.409	---	---
Erinaceomorpha	1.981	1.033	2.969	**3.488**	2.090
Soricomorpha	0.824	**1.040**	0.829	---	---
Leptictidae	**2.737**	1.124	0.802	2.520	2.545
Microsyopidae	1.683	2.060	**2.536**	1.453	1.688
Paromomyidae	1.232	1.317	**1.375**	0.833	1.049
Plagiomenidae	---	---	---	1.349	---
Rodentia	0.350	0.607	**2.480**	0.399	0.623

Table 6.3. Hypervolumetric size and Spearman rank correlation coefficients of niche size with time for all taxa within the euprimate competitive guild, euprimates, adapids, and omomyids. Correlations of adapid absolute and relative niche sizes with time include only Wa0 to Wa4 values.

		Guild	Euprimates	Adapids	Omomyids
Cf2-3	Abs. Vol. Size	310.022	--	--	--
	Rel. Vol. Size	9.192			
	Wtd. Rel. Size	12.814			
	N	85			
Wa0	Abs. Vol. Size	433.545	7.75	0.934	0.873
	Rel. Vol. Size	12.854	14.82	8.237	6.565
	Wtd. Rel. Size	15.081	21.53	11.532	9.905
	N	101	39	20	19
Wa1-2	Abs. Vol. Size	792.249	7.89	1.887	0.456
	Rel. Vol. Size	23.489	15.09	16.647	3.428
	Wtd. Rel. Size	15.905	15.00	12.598	4.913
	N	175	57	37	20
Wa3	Abs. Vol. Size	409.069	3.68	0.151	0.883
	Rel. Vol. Size	12.128	7.04	1.334	6.639
	Wtd. Rel. Size	9.777	5.87	1.966	3.884
	N	147	68	19	49
Wa4	Abs. Vol. Size	232.337	2.04	0.025	0.402
	Rel. Vol. Size	6.888	3.91	0.223	3.022
	Wtd. Rel. Size	7.489	4.61	0.446	2.548
	N	109	48	14	34
Wa5	Abs. Vol. Size	76.768	0.62	0.178	0.002
	Rel. Vol. Size	2.276	1.19	1.570	0.011
	Wtd. Rel. Size	2.869	1.69	1.373	0.040
	N	94	40	32	8
TOTAL	Abs. Vol. Size	3372.900	52.273	11.334	13.301
	N	711	252	122	130
	Mean *N*	118.500	56.667	28.000	28.667
r (Abs.)		0.600	0.900	0.800	0.700
p (Abs.)		0.208	0.037	0.200	0.118
r (Rel.)		0.771	1.000	0.800	1.000
p (Rel.)		0.072	<0.001	0.200	<0.001

Abbreviations are as follows: Abs. Vol. Size.=Absolute volumetric size, Rel. Vol. Size=Relative volumetric size as a percentage, Wtd. Rel. Size=Relative volumetric size weighted by sample size, *N*=sample size, Mean *N*=mean sample size across all time intervals, *r,p*(Abs.)=Spearman rank correlation coefficient and p-value of Abs. Vol. Size with the midpoint of each time interval (following Woodburne (2004) and Chew and Oheim (2013); see Fig. 1.1), *r,p*(Rel.)=Spearman rank correlation coefficient and *p*-value of Wtd. Rel. Size with the midpoint of each time interval. Relative volumetric size was calculated as the percentage of the absolute volumetric size across all time intervals that is occupied by the niche within a given time interval for each taxonomic group (e.g., euprimates): e.g., [(Cf2-3 Abs. Vol. Size)/(Total Abs. Vol. Size)]*100. Wtd. Rel. Size was calculated as follows: [((Abs. Vol. Size)*(Mean *N*/*N*))/(Total Abs. Vol. Size)]*100.

Table 6.4. Significance (*p*-values) of pairwise comparisons of the niches of Wa0 euprimates and those of Cf2-3 and Wa0 non-euprimates using the modified MANOVA. Non-significant values (i.e., those that indicate niche overlap) are bolded. For those higher taxa that include genera with greater than 3 specimens, comparisons were made at both the familial and generic levels.

	Wa0 Adapidae (*Cantius*)	Wa0 Omomyidae (*Teilhardina*)
Cf2-3 Apatemyidae	0.008	**0.069**
Cf2-3 Plagiomenidae	<0.001	<0.001
Cf2-3 Peradectidae	<0.001	<0.001
Cf2-3 Erinaceomorpha	0.001	**0.339**
Cf2-3 Soricomorpha	<0.001	0.036
Cf2-3 Carpolestidae	<0.001	0.009
Cf2-3 *Ignacius*	0.004	<0.001
Cf2-3 *Phenacolemur*	0.005	0.001
Cf2-3 Paromomyidae	0.002	<0.001
Cf2-3 Plesiadapidae	**0.096**	<0.001
Cf2-3 *Acritoparamys*	<0.001	<0.001
Cf2-3 *Paramys*	<0.001	<0.001
Cf2-3 Paramyidae	<0.001	<0.001
Wa0 Apatemyidae	<0.001	<0.001
Wa0 *Mimoperadectes*	<0.001	<0.001
Wa0 *Peradectes*	<0.001	0.002
Wa0 *Peratherium*	<0.001	0.002
Wa0 Peradectidae	<0.001	<0.001
Wa0 Palaeoryctidae	<0.001	<0.001
Wa0 Erinaceomorpha	<0.001	0.010
Wa0 Soricomorpha	<0.001	**0.055**
Wa0 Microsyopidae	0.002	0.003
Wa0 *Ignacius*	0.006	<0.001
Wa0 *Phenacolemur*	0.025	0.001
Wa0 Paromomyidae	0.004	<0.001
Wa0 Paramyidae	<0.001	<0.001
Wa0 Cylindrodontidae	0.004	0.005

Table 6.5. Significance (*p*-values) of pairwise comparisons of the niches of Wa1-2 euprimates and those of Wa0 and Wa1-2 non-euprimates using the modified MANOVA. Non-significant values (i.e., those that indicate niche overlap) are bolded.

	Wa1-2 Adapidae (*Cantius*)	Wa1-2 Omomyidae (*Anemorhysis*)	Wa1-2 Omomyidae (*Teilhardina*)	Wa1-2 Omomyidae (*Tetonius*)	Wa1-2 Omomyidae
Wa0 Apatemyidae	<0.001	0.006	<0.001	<0.001	<0.001
Wa0 *Mimoperadectes*	<0.001	<0.001	<0.001	<0.001	<0.001
Wa0 *Peradectes*	<0.001	0.009	<0.001	0.012	<0.001
Wa0 *Peratherium*	<0.001	<0.001	<0.001	0.008	<0.001
Wa0 Peradectidae	<0.001	0.003	0.001	0.001	<0.001
Wa0 Palaeoryctidae	<0.001	0.012	<0.001	<0.001	0.001
Wa0 Erinaceomorpha	<0.001	0.010	<0.001	0.008	<0.001
Wa0 Soricomorpha	<0.001	**0.205**	**0.101**	**0.057**	0.017
Wa0 Microsyopidae	<0.001	0.001	0.001	<0.001	<0.001
Wa0 *Ignacius*	0.001	0.040	<0.001	<0.001	0.005
Wa0 *Phenacolemur*	0.004	0.007	<0.001	<0.001	<0.001
Wa0 Paromomyidae	<0.001	0.002	<0.001	0.003	<0.001
Wa0 Paramyidae	<0.001	<0.001	<0.001	<0.001	<0.001
Wa0 Cylindrodontidae	<0.001	<0.001	0.003	<0.001	<0.001
Wa1-2 *Apatemys*	<0.001	<0.001	0.004	0.009	<0.001
Wa1-2 *Labidolemur*	<0.001	0.003	0.003	0.006	<0.001
Wa1-2 Apatemyidae	<0.001	<0.001	0.001	<0.001	<0.001
Wa1-2 Palaeoryctidae	<0.001	0.002	<0.001	0.002	<0.001
Wa1-2 Leptictidae	<0.001	<0.001	<0.001	<0.001	<0.001
Wa1-2 Erinaceomorpha	<0.001	0.023	0.033	0.001	<0.001
Wa1-2 Soricomorpha	<0.001	0.002	<0.001	0.003	<0.001
Wa1-2 Peradectidae	<0.001	<0.001	<0.001	<0.001	<0.001

Table 6.5, Cont'd.

	Wa1-2 Adapidae (*Cantius*)	Wa1-2 Omomyidae (*Anemorhysis*)	Wa1-2 Omomyidae (*Teilhardina*)	Wa1-2 Omomyidae (*Tetonius*)	Wa1-2 Omomyidae
Wa1-2 *Arctodontomys*	<0.001	<0.001	<0.001	0.003	<0.001
Wa1-2 *Niptomomys*	<0.001	<0.001	<0.001	0.010	<0.001
Wa1-2 Microsyopidae	<0.001	0.001	<0.001	0.007	<0.001
Wa1-2 *Ignacius*	0.010	<0.001	<0.001	0.007	<0.001
Wa1-2 *Phenacolemur*	<0.001	<0.001	<0.001	<0.001	<0.001
Wa1-2 Paromomyidae	<0.001	<0.001	<0.001	<0.001	<0.001
Wa1-2 *Acritoparamys*	<0.001	<0.001	<0.001	<0.001	<0.001
Wa1-2 *Paramys*	<0.001	<0.001	<0.001	<0.001	<0.001
Wa1-2 *Microparamys*	<0.001	<0.001	<0.001	<0.001	<0.001
Wa1-2 Paramyidae	<0.001	<0.001	<0.001	<0.001	<0.001

Table 6.6. Significance (*p*-values) of pairwise comparisons of the niches of Wa3 euprimates and those of Wa1-2 and Wa3 non-euprimates using the modified MANOVA. Non-significant values (i.e., those that indicate niche overlap) are bolded.

	Wa3 Adapidae (*Cantius*)	Wa3 Omomyidae (*Anemorhysis*)	Wa3 Omomyidae (*Teilhardina*)	Wa3 Omomyidae (*Tetonius-Pseudotetonius*)	Wa3 Omomyidae (*Tetonius*)	Wa3 Omomyidae
Wa1-2 *Apatemys*	<0.001	0.026	0.001	0.003	<0.001	<0.001
Wa1-2 *Labidolemur*	<0.001	0.041	0.001	0.004	<0.001	<0.001
Wa1-2 Apatemyidae	<0.001	0.004	<0.001	<0.001	<0.001	<0.001
Wa1-2 Palaeoryctidae	<0.001	0.006	<0.001	<0.001	<0.001	<0.001
Wa1-2 Leptictidae	<0.001	0.006	<0.001	<0.001	<0.001	<0.001
Wa1-2 Erinaceomorpha	<0.001	0.018	<0.001	<0.001	<0.001	<0.001
Wa1-2 Soricomorpha	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001
Wa1-2 Peradectidae	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001
Wa1-2 *Arctodontomys*	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001
Wa1-2 *Niptomomys*	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001
Wa1-2 Microsyopidae	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001
Wa1-2 *Ignacius*	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001
Wa1-2 *Phenacolemur*	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001
Wa1-2 Paromomyidae	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001
Wa1-2 *Acritoparamys*	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001
Wa1-2 *Paramys*	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001
Wa1-2 *Microparamys*	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001
Wa1-2 Paramyidae	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001

Table 6.6, Cont'd.

	Wa3 Adapidae (*Cantius*)	Wa3 Omomyidae (*Anemorhysis*)	Wa3 Omomyidae (*Teilhardina*)	Wa3 Omomyidae (*Tetonius-Pseudotetonius*)	Wa3 Omomyidae (*Tetonius*)	Wa3 Omomyidae
Wa3 Apatemyidae	<0.001	0.006	0.000	<0.001	<0.001	<0.001
Wa3 Plagiomenidae	<0.001	0.016	<0.001	0.003	<0.001	<0.001
Wa3 Lipotyphla	<0.001	0.042	<0.001	0.005	<0.001	<0.001
Wa3 Peradectidae	<0.001	0.003	<0.001	<0.001	<0.001	<0.001
Wa3 *Arctodontomys+Microsyops*	<0.001	<0.001	<0.001	<0.001	0.001	<0.001
Wa3 *Niptomomys*	<0.001	0.014	<0.001	0.031	<0.001	<0.001
Wa3 Microsyopidae	0.043	**0.065**	<0.001	0.007	<0.001	<0.001
Wa3 *Ignacius*	0.026	0.039	<0.001	0.041	<0.001	<0.001
Wa3 *Phenacolemur*	<0.001	0.001	<0.001	<0.001	<0.001	<0.001
Wa3 Paromomyidae	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001
Wa3 *Acritoparamys*	<0.001	<0.001	<0.001	0.008	<0.001	<0.001
Wa3 *Paramys*	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001
Wa3 Paramyidae	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001

Table 6.7. Significance (*p*-values) of pairwise comparisons of the niches of Wa4 euprimates and those of Wa3 and Wa4 non-euprimates using the modified MANOVA. Non-significant values (i.e., those that indicate niche overlap) are bolded.

	Wa4 Adapidae (*Cantius*)	Wa4 Omomyidae (*Tetonius*)	Wa4 Omomyidae (*Tetonius*-*Pseudotetonius*)	Wa4 Omomyidae (*Pseudotetonius*)	Wa4 Omomyidae
Wa3 Apatemyidae	<0.001	<0.001	<0.001	<0.001	<0.001
Wa3 Plagiomenidae	<0.001	<0.001	<0.001	<0.001	<0.001
Wa3 Lipotyphla	<0.001	<0.001	<0.001	<0.001	<0.001
Wa3 Peradectidae	<0.001	<0.001	<0.001	<0.001	<0.001
Wa3 *Arctodontomys*+*Microsyops*	<0.001	<0.001	0.002	<0.001	<0.001
Wa3 *Niptomomys*	<0.001	<0.001	<0.001	<0.001	<0.001
Wa3 Microsyopidae	<0.001	0.006	<0.001	0.001	<0.001
Wa3 *Ignacius*	0.001	0.003	<0.001	<0.001	<0.001
Wa3 *Phenacolemur*	<0.001	<0.001	<0.001	<0.001	<0.001
Wa3 Paromomyidae	<0.001	<0.001	<0.001	<0.001	<0.001
Wa3 *Acritoparamys*	<0.001	<0.001	0.002	0.007	<0.001
Wa3 *Paramys*	<0.001	<0.001	<0.001	<0.001	<0.001
Wa3 Paramyidae	<0.001	<0.001	<0.001	<0.001	<0.001
Wa4 Plagiomenidae	0.002	<0.001	<0.001	<0.001	<0.001
Wa4 Lipotyphla+Leptictida	<0.001	0.001	0.003	0.001	<0.001
Wa4 Microsyopidae	<0.001	<0.001	<0.001	<0.001	<0.001
Wa4 Paromomyidae	0.007	<0.001	<0.001	<0.001	<0.001
Wa4 *Acritoparamys*	0.001	<0.001	0.001	<0.001	<0.001
Wa4 *Paramys*	<0.001	<0.001	<0.001	<0.001	<0.001
Wa4 Paramyidae	<0.001	<0.001	<0.001	<0.001	<0.001
Wa4 Sciuravidae	<0.001	<0.001	<0.001	<0.001	<0.001

Table 6.8. Significance (*p*-values) of pairwise comparisons of the niches of Wa5 euprimates and those of Wa4 and Wa5 non-euprimates using the modified MANOVA. Non-significant values (i.e., those that indicate niche overlap) are bolded.

	Wa5 Adapidae (*Cantius*)	Wa5 Adapidae (*Copelemur*)	Wa5 Adapidae	Wa5 Omomyidae
Wa4 Plagiomenidae	0.002	**0.078**	0.001	0.010
Wa4 Lipotyphla+Leptictida	<0.001	0.001	<0.001	0.001
Wa4 Microsyopidae	<0.001	0.003	<0.001	<0.001
Wa4 Paromomyidae	<0.001	**0.053**	<0.001	<0.001
Wa4 *Acritoparamys*	<0.001	0.007	<0.001	0.015
Wa4 *Paramys*	<0.001	<0.001	<0.001	<0.001
Wa4 Paramyidae	<0.001	<0.001	<0.001	<0.001
Wa4 Sciuravidae	<0.001	<0.001	<0.001	<0.001
Wa5 Apatemyidae	<0.001	0.003	<0.001	0.005
Wa5 Erinaceomorpha	<0.001	<0.001	<0.001	**0.060**
Wa5 Lipotyphla + Leptictida	<0.001	<0.001	<0.001	0.015
Wa5 Peradectidae	<0.001	0.001	<0.001	0.004
Wa5 *Niptomomys*	0.001	0.006	<0.001	0.023
Wa5 *Microsyops*	0.001	0.018	0.001	0.014
Wa5 Microsyopidae	0.049	**0.273**	**0.055**	0.040
Wa5 Paromomyidae	0.002	**0.100**	<0.001	<0.001
Wa5 *Acritoparamys*	<0.001	<0.001	<0.001	<0.001
Wa5 *Paramys*	<0.001	<0.001	<0.001	<0.001
Wa5 Paramyidae	<0.001	<0.001	<0.001	<0.001

Table 6.9. Significance (*p*-values) of pairwise comparisons of the niches of euprimates within the Wa0 and Wa1-2 time intervals and between the niches of Wa0 and Wa1-2 euprimates using the modified MANOVA. Non-significant values (i.e., those that indicate niche overlap) are bolded.

	Wa0 Omomyidae (*Teilhardina*)	Wa1-2 Adapidae (*Cantius*)	Wa1-2 *Anemorhysis*	Wa1-2 *Teilhardina*	Wa1-2 *Tetonius*	Wa1-2 Omomyidae
Wa0 Adapidae (*Cantius*)	<0.001	**0.080**	0.001	0.003	0.025	<0.001
Wa0 *Teilhardina*		0.001	**0.169**	**0.332**	**0.200**	**0.071**
Wa1-2 Adapidae (*Cantius*)			<0.001	0.004	0.048	<0.001
Wa1-2 *Anemorhysis*				**0.315**	**0.287**	
Wa1-2 *Teilhardina*					0.038	
Wa1-2 *Tetonius*						
Wa1-2 Omomyidae						

Table 6.10. Significance (*p*-values) of pairwise comparisons of the niches of euprimates within the Wa3 time interval and between the niches of Wa1-2 and Wa3 euprimates using the modified MANOVA. Non-significant values (i.e., those that indicate niche overlap) are bolded.

	Wa3 Adapidae (*Cantius*)	Wa3 *Anemorhysis*	Wa3 *Teilhardina*	Wa3 *Tetonius-Pseudotetonius*	Wa3 *Tetonius*	Wa3 Omomyidae
Wa1-2 Adapidae (*Cantius*)	<0.001	0.001	<0.001	<0.001	<0.001	<0.001
Wa1-2 *Anemorhysis*	<0.001	**0.066**	<0.001	0.036	<0.001	<0.001
Wa1-2 *Teilhardina*	0.007	**0.196**	0.001	**0.104**	0.021	<0.001
Wa1-2 *Tetonius*	<0.001	0.029	<0.001	0.025	<0.001	<0.001
Wa1-2 Omomyidae	<0.001	**0.057**	<0.001	0.004	<0.001	<0.001
Wa3 Adapidae (*Cantius*)		0.005	<0.001	<0.001	<0.001	<0.001
Wa3 *Anemorhysis*			**0.343**	**0.771**	**0.221**	
Wa3 *Teilhardina*				**0.562**	**0.103**	
Wa3 *Tetonius-Pseudotetonius*					**0.544**	
Wa3 *Tetonius*						
Wa3 Omomyidae						

Table 6.11. Significance (*p*-values) of pairwise comparisons of the niches of euprimates within the Wa4 time interval and between the niches of Wa3 and Wa4 euprimates using the modified MANOVA. Non-significant values (i.e., those that indicate niche overlap) are bolded.

	Wa4 Adapidae (*Cantius)*	Wa4 *Tetonius*	Wa4 *Tetonius-Pseudotetonius*	Wa4 *Pseudotetonius*	Wa4 Omomyidae
Wa3 Adapidae (*Cantius*)	0.003	<0.001	<0.001	<0.001	<0.001
Wa3 *Anemorhysis*	<0.001	**0.730**	**0.424**	**0.234**	**0.353**
Wa3 *Teilhardina*	<0.001	**0.248**	**0.603**	**0.960**	**0.824**
Wa3 *Tetonius-Pseudotetonius*	<0.001	**0.937**	**0.805**	**0.540**	**0.807**
Wa3 *Tetonius*	<0.001	**0.199**	**0.193**	**0.324**	**0.291**
Wa3 Omomyidae	<0.001	**0.651**	**0.464**	**0.629**	**0.670**
Wa4 Adapidae (*Cantius)*		<0.001	<0.001	<0.001	<0.001
Wa4 *Tetonius*			**0.380**	**0.264**	
Wa4 *Tetonius-Pseudotetonius*				**0.735**	
Wa4 *Pseudotetonius*					
Wa4 Omomyidae					

Table 6.12. Significance (*p*-values) of pairwise comparisons of the niches of euprimates within the Wa5 time interval and between the niches of Wa4 and Wa5 euprimates using the modified MANOVA. Non-significant values (i.e., those that indicate niche overlap) are bolded.

	Wa5 *Cantius*	Wa5 *Copelemur*	Wa5 Adapidae	Wa5 Omomyidae
Wa4 Adapidae (*Cantius)*	<0.001	0.016	<0.001	<0.001
Wa4 *Tetonius*	<0.001	0.001	<0.001	**0.599**
Wa4 *Tetonius-Pseudotetonius*	<0.001	<0.001	<0.001	**0.348**
Wa4 *Pseudotetonius*	<0.001	<0.001	<0.001	**0.383**
Wa4 Omomyidae	<0.001	<0.001	<0.001	**0.316**
Wa5 *Cantius*		**0.403**		0.003
Wa5 *Copelemur*				0.027
Wa5 Adapidae				0.002
Wa5 Omomyidae				

Table 6.13. Significance (*p*-values) of pairwise comparisons of the niches of adapids and omomyids across time intervals using the modified MANOVA. Non-significant values (i.e., those that indicate niche overlap) are bolded.

ADAPIDAE	Wa1-2	Wa3	Wa4	Wa5
Wa0	**0.080**	0.014	0.001	0.012
Wa1-2		<0.001	0.014	<0.001
Wa3			0.003	**0.205**
Wa4				<0.001
OMOMYIDAE	Wa1-2	Wa3	Wa4	Wa5
Wa0	**0.071**	<0.001	<0.001	0.012
Wa1-2		<0.001	<0.001	0.008
Wa3			**0.670**	**0.477**
Wa4				**0.316**

Table 6.14. Distances between dietary niche centroids of overlapping euprimate and non-euprimate taxa for each time period and Spearman rank correlation coefficients of centroid distance with time (in millions of years). Beginning and end dates of each sub-NALMA are from Woodburne (2004) and Chew and Oheim (2013), and midpoints of each time interval were used for correlation analyses. Note that negative correlations indicate that centroid distance (and niche separation) increased through time; positive correlations indicate niche convergence through time. Distances between the centroid of Cf2-3 non-euprimates and Wa0 euprimates (Cf2-3-Wa0) were not included in correlation analyses. The correlation for the comparison of microsyopid-omomyid centroid distances includes only Wa3-Wa5, as Wa3 is the point at which niche overlap was detected. The correlation for the comparison of erinaceomorphan and omomyid centroid distances includes only Wa0-Wa4, as niche overlap is reestablished in Wa5. Plagiomenids were excluded, as they are absent in several time intervals. All correlations are non-significant, likely due to the small sample sizes involved. Thus, the general patterns of centroid distances over time are used simply to further describe patterns of niche overlap discussed in the text.

	Start (Ma)	End (Ma)	Midpoint (Ma)	Soricomorpha-Omomyidae	Paromomyidae-Adapidae	Apatemyidae-Omomyidae	Erinaceomorpha-Omomyidae	Microsyopidae-Omomyidae	Microsyopidae-Adapidae
Cf2-3-Wa0				1.395	1.836	1.578	0.959	1.014	1.479
Wa0	55.80	55.75	55.78	1.618	1.966	3.753	1.885	1.808	1.964
Wa1-2	55.75	55.20	55.48	2.509	1.637	3.178	1.615	2.517	2.057
Wa3	55.20	54.98	55.09	2.482	1.317	2.718	2.355	1.573	0.854
Wa4	54.98	54.60	54.79	NA	1.118	3.764	2.939	2.884	1.717
Wa5	54.60	53.91	54.26	NA	1.357	2.503	1.470	1.802	1.065
r				-0.800	0.700	0.400	-0.800	-0.500	0.600
p-value				0.200	0.188	0.505	0.200	0.667	0.285

Table 6.15. Summary statistics for the euprimate dietary niche. Correlation statistics at the bottom of the table relate to the Spearman's rank correlation coefficients of centroid distance with time and follow Table 6.14. Correlations between adapid and omomyid mean distance from centroid and time include only Wa0 to Wa4 values. Mean distance from centroid is the mean of the distances of individual specimens from their respective niche centroids. "Guild" refers to all specimens within the euprimate competitive guild (including euprimates) for each time interval. Distance from Wa0 niche centroid is the distance between the centroid of the Wa0 niche and the centroid of the niche corresponding to each subsequent time interval. The highest distance value for each column is bolded.

		Distance Between Niche Centroids	Mean Distance From Centroid				Distance from Wa0 Niche Centroid		
	Midpoint (Ma)	Adapidae-Omomyidae	Adapidae	Omomyidae	Euprimates	Guild	Adapidae	Omomyidae	Euprimates
Cf2-3	55.95					2.553			
Wa0	55.78	1.416	1.644	**1.741**	**1.845**	**2.646**	--	--	--
Wa1-2	55.48	1.561	1.540	1.470	1.666	2.645	0.761	0.820	0.674
Wa3	55.09	1.499	1.158	1.214	1.367	2.221	0.983	1.860	**1.582**
Wa4	54.79	**2.600**	1.122	1.226	1.648	2.433	**1.432**	**2.008**	1.558
Wa5	54.26	1.203	**1.929**	1.469	1.243	2.041	0.840	1.540	0.873
r		0.100	1.000	0.800	0.900	0.771			
p-value		0.873	0.000	0.200	0.037	0.072			

CHAPTER 7: THE EARLY EUPRIMATE DIETARY COMPETITIVE ENVIRONMENT OF NORTH AMERICA

The primary objective of this study was to determine which of three specific models of dietary competitive interaction, as outlined in Chapter 3, characterized the origination and early diversification of euprimates in North America, as defined by patterns derived from the Bighorn Basin, Wyoming. These competitive models are: (1) the absence of dietary competition (non-competition), (2) the presence of strong dietary competition (competitive displacement), and (3) the presence of weak, or diffuse, dietary competition (competitive coexistence). Overall, the results of this study suggest that, within the "euprimate competitive guild," there was minimal dietary niche overlap between euprimates and non-euprimates. Specifically, few pairwise comparisons using the modified MANOVA resulted in non-significant *p*-values, indicating potential competition. At face value, this reveals that dietary competition was not ubiquitous during early adapid and omomyid evolution in North America. However, the euprimate dietary niche was not unique within this mammalian community, as nine instances of niche overlap between euprimates and non-euprimates were identified and described in Chapter 6. These periods of overlap – clustered around the origination of euprimates in North America, at the onset of the Eocene, and towards the end of the time period examined, in the middle Wasatchian – will be discussed separately below.

Euprimate Origination (Wa0 to Wa1-2)

Of the four identified cases of niche overlap between euprimates and non-euprimates during the early Wastachian, three can be excluded from a discussion of the euprimate dietary competitive environment. First, as the dietary niches of Wa0 omomyids

and Cf2-3 erinaceomorphans do not concurrently overlap, a competitive interaction between these taxa at the point of euprimate origination can be ruled out. Second, as discussed in Chapter 6, apatemyids likely did not directly compete for dietary resources with euprimates, or at least not to a significant extent. For example, interspecies competition with aye-ayes, with which apatemyids are convergent, is expected to be low as a result of the aye-aye's unique set of morphological dietary adaptations and resulting distinct niche within its community (Petter, 1977; Grime and Pierce, 2012). Given the similar molar morphologies of apatemyids and omomyids, as found in this study, and thus an inferred similarity in consumed food items, generally speaking, it is possible that the highly adaptive behavior and morphology of apatemyids excluded omomyids from certain dietary resources (e.g., invertebrates located in the trunks or larger branches of trees), thereby influencing the evolution of the omomyid dietary niche, perhaps towards a greater reliance on terminal branch feeding (of insects, flowers and fruit, or both) (Rasmussen, 1990; Sussman, 1991, 2013; Bloch and Boyer, 2002; Ravosa and Savakova, 2004; Orkin and Pontzer, 2011). Unfortunately, the precise impact of such a scenario on either taxon is unknowable in the fossil record (barring the discovery of stomach contents), if it was present at all. Apatemyids have been previously suggested as potential omomyid competitors (Gunnell, 2002), and the results of this study highlight that the dietary ecospaces of these taxa may only have been separated by a single (albeit critical) niche dimension: method of food procurement. Third, although the pattern of niche overlap between omomyids and soricomorphans from Wa0 to Wa3 is consistent with a hypothesis of strong competition via niche divergence, this divergence is associated with a period of directional climatic change. Consequently, strong competition between these

taxa cannot be exclusively supported. On the other hand, niche overlap between Clarkforkian plesiadapids and adapids is a clear example of non-competition, specifically post-extinction replacement. Thus, the arrival of adapids in North America occurred in the absence of dietary competition, and this niche was occupied exclusively by a single anagenetic adapid lineage until the diversification of adapids in the middle Wasatchian.

Based on the results of this study as they correspond to the competition models outlined in Chapter 3, euprimate origination in North America was generally characterized by the absence of dietary competition with non-euprimate members of their guild. In addition, adapids and omomyids did not engage in dietary competition (as supported by the lack of adapid-omomyid niche overlap) during this time. This has several implications for the evolution of euprimates and their mammalian dietary guild as a whole. First, it indicates, at least in terms of dietary competition, that euprimates did not competitively exclude non-euprimate taxa within their guild. In other words, the presence of euprimates did not negatively impact the abundance or diversity or drive shifts in the niche spaces of non-euprimate taxa. Conversely, a lack of competition with non-euprimates is consistent with an increase in the abundance and diversity of euprimates themselves, signifying that the "success" of euprimates does not appear to be the result of a direct biotic interaction between euprimates and other mammals. As such, the suite of key anatomical features possessed by adapids and omomyids upon their origination in North America conferred an advantage insofar as they helped to reduce the potential negative effects of competition (e.g., decreased abundance and diversity, increased likelihood of extinction) with incumbent species, interactions which typically result in the

extinction or decline of the invasive species (in this case, euprimates) (the "incumbent advantage"; Alroy, 1996; Ivany, 1996).

Euprimate Radiation (Wa3 to Wa5)

From Wa1-2 through Wa4, there is only one example of synchronous niche overlap between a euprimate and non-euprimate taxon: Wa3 *Anemorhysis* and Wa3 Microsyopidae. However, the lack of overlap between *Anemorhysis* and individual microsyopid genera significantly diminishes the likelihood of, if not rejects, a true competitive interaction. Thus, a lack of competition between euprimates and non-euprimates appears to extend from the early Wasatchian (Wa0) to the late middle Wasatchian (end of Wa4), at which point the incidence of niche overlap between euprimates and non-euprimates increases.

The transition from Wa4 to Wa5 is not associated with a major shift in the guild-wide niche as whole (for instance, the greatest change in the centroid location of this niche is between Wa1-2 and Wa3); however, the overall size of this niche (as measured by weighted relative hypervolumetric size and mean distance of individuals from the niche centroid; see Chapter 6) is at its minimum in Wa5. As described in Chapter 6, this decrease in niche size is possibly linked to the decrease in mean annual temperature and precipitation from Wa1-2 to Wa4, granting a slight time lag in the faunal response to this abiotic change. In this scenario, limited food availability associated with the climatic shift may have resulted in niche contraction within the guild through Wa4. When the euprimate dietary niche subsequently expanded in Wa5, the prior guild-wide contraction increased the likelihood of euprimate-non-euprimate niche overlap, specifically between omomyids and erinaceomorphans, on the one hand, and adapids and paromomyids on the

other (MacArthur and Levins, 1967; Giller, 1984; Grant, 1986; Keddy, 2001; Van der Putten et al., 2010; Nakazawa, 2013).[30] However, as discussed in Chapter 6, the inadequate erinaceomorphan sample sizes in Wa3 and Wa4 prevent an identification of the specific point at which these niches began to overlap, suggesting the time of overlap may have been earlier. In contrast, the increase in niche overlap between adapids and paromomyids in Wa5 is due exclusively to the diversification of adapids. In fact, in this study, the only example of coincident adapid-non-euprimate niche overlap involves the single non-*Cantius* genus, *Copelemur* (if the Wa5 Adapidae-Wa5 Microsyopidae interaction is excluded; see Chapter 6). Specifically, the origination of *Copelemur*[31] in the Bighorn Basin (either through dispersal from the south or via cladogenesis; O'Leary, 1997; Gunnell, 2002) is associated with both non-competition (with plagiomenids) and possible strong competition (with paromomyids). However, as noted in Chapter 6, the difference in reconstructed body size between paromomyids and the much larger adapid, *Copelemur*, may have diminished competition between these taxa (Fleagle, 1999; Bloch et al., 2007).

[30] The association between niche contraction and resource limitation is well-documented within species; however, the extent to which this concept can be applied to entire guilds is less clear (although see Grossnickle and Polly, 2013). Thus, it is possible that the guild-wide niche contraction was the result of an alternate mechanism.

[31] It is recognized that some researchers have excluded the Bighorn Basin specimens identified as *Copelemur feretutus* from the genus *Copelemur* (e.g., Gunnell, 2002; Gunnell et al., 2008). If these specimens are members of a distinct, non-*Cantius* genus, then the impact on this study is simply a matter of nomenclature. However, if these specimens belong to an additional species of *Cantius*, then the analyses herein have identified an instance of overlap involving an adapid species (rather than genus), albeit a species not included in the anagenetic *Cantius* lineage of Wa0-Wa4. In either case, adapid-non-euprimate niche overlap was identified, and the resulting potential for competition between these taxa is the subject of this discussion.

Still, if erinaceomorphans and omomyids, on the one hand, and paromomyids and *Copelemur*, on the other, are true examples of competition (and if erinaceomorphan-omomyid competition does not begin prior to Wa5), it is interesting that the competitive environments of both adapids and omomyids changed at the same time, coincident with a niche expansion in both groups (see below for further discussion). Our current understanding of competition theory and evidence that these competitive interactions took place so long after the origination and establishment of euprimates within their communities (i.e., the lack of niche overlap until Wa5) propose that: (1) taxa within the euprimate competitive guild were forced to narrow their niches in response to climatic change and associated limitation of food resources from Wa0 to Wa4 and (2) upon a change in climate in Wa5, euprimates responded by expanding their dietary niche to exploit newly available resources, resulting in niche overlap with non-euprimates (MacArthur and Levins, 1967; Giller, 1984; Abrams, 1986, 1987; Grant, 1986; Keddy, 2001; Chase and Liebold, 2003). Unfortunately, the hypotheses of competition examined here require that patterns of niche overlap be evaluated in time intervals following the original point of overlap and thus cannot be explored fully here (see Chapter 3). As such, these new instances of niche overlap between euprimates and non-euprimates in Wa5 either led to strong competitive interactions, whose effects are not yet observable so close to the onset of competition, or they resulted in weak dietary competition, allowing taxa to remain in the same dietary niche space over time. The effect that either scenario may have had on euprimate evolution in the late Wasatchian and Bridgerian is certainly an area for future study.

The Euprimate Dietary Niche

The results presented here demonstrate the differentiation of the euprimate dietary niche between adapids and omomyids, consistent with previous dietary reconstructions of these taxa (e.g., Covert, 1985; Rose, 1995; Gunnell, 2002; Jones et al., 2014). Although the specific changes (e.g., changes in niche size and centroid locations) within the adapid and omomyid niches over time are not identical, the dietary niches of adapids and omomyids exhibit two major patterns of change that broadly mirror one another and, in part, the guild as a whole (Table 7.1; see Tables 6.4; 6.15). First, the sizes of the adapid and omomyid dietary niches decreased from Wa0 to Wa4 and increased from Wa4 to Wa5.[32,33] The contraction of the euprimate dietary niche from Wa0 to Wa4 (possibly linked to niche specialization in a limited resource environment[34]) runs counter to the expectations of a successful invasion radiation, particularly one that is shortly followed by diversification, as occurred in omomyids (Schluter, 2000; Ricklefs, 2010; although see Erwin, 1992; Bailey et al., 2013). However, as discussed above, this niche contraction, in concert with the subsequent expansion in Wa5, tracks climatic reconstructions during this time, as mean annual temperature and precipitation decreased from Wa0 to Wa4 and temperature increased from Wa4 to Wa5 (Wilf, 2000; Woodburne et al., 2009a,b; Chew

[32] Statistical tests were not performed on differences between adapid and omomyid niche sizes and not all correlations between niche size and time were significant (although most were), likely as a result of the low number of niches included (i.e., the presence of relatively few data points for analysis). Thus, the discussion here considers only general trends in niche size over time, and it is granted that subsequent analyses may alter these conclusions.

[33] However, the relative weighted hypervolumetric size (but not mean distance of individuals from the mean centroid) of omomyids decreased from Wa4 to Wa5.

[34] However, this would not explain the contraction of the guild-wide niche, as it would not be expected that niche specialization would result in niche convergence among taxa (Grime and Pierce, 2012; Pfennig and Pfennig, 2012).

and Oheim, 2013). This is somewhat distinct from the guild-wide pattern of niche size, in which niche contraction extended into Wa5, and euprimates may have been better able and quicker to respond to periods of climatic change than the other taxa included in this study (yet this seems unlikely among taxa within a mammalian guild). Alternatively, specific non-euprimate taxa could be driving the contraction of the guild-wide niche from Wa4 to Wa5, masking a niche expansion across the remaining taxa, including euprimates.

An increase in temperature in Wa5 is further associated with an increase in adapid diversity and a shift in omomyid generic composition, which may have proximately caused the niche expansion from Wa4 to Wa5. On the other hand, climatic change may ultimately still be responsible, as new adapid and omomyid species could have derived from allopatric speciation events associated with colder, drier climates prior to Wa5 (e.g., increased habitat patchiness) or as the result of newly opened portions of the ecological niche space (dietary or non-dietary) in Wa5. In either case, overall, these temporal changes in euprimate niche size are best fit to climatic patterns; thus, perhaps an abiotic mechanism (rather than a response to non-euprimate biotic interactions[35]) is responsible for these shifts in the size of the euprimate dietary niche in the early-middle Wasatchian.

Second, there is a distinction between the position of the early (Wa0-2) and later (Wa3-5) dietary niches of both adapids and omomyids. For omomyids, this transition is

[35] The response of euprimates to biotic interactions was considered less likely as there were no instances of niche overlap between euprimate and non-euprimate taxa during the period of niche contraction. In addition, the expansion of the omomyid and adapid niches in Wa5 is only correlated with the extinction of plagiomenids, which should not have affected omomyids (although see Footnote 33). To further evaluate this hypothesis, the relative sizes of non-euprimate niches within the guild would need to be compared with those of euprimate niches through time. In this analysis, an inverse relationship between euprimate and non-euprimate niche size would be expected.

clear cut: the niches of Wa0 and Wa1-2 are distinct from those of Wa3-5. As no climatic event or significant change in guild composition coincides with the transition between Wa2 and Wa3, the cause of this distinction is unclear. Moreover, the separation among the (Wa0 and Wa1-2), Wa4, and (Wa3 and Wa5) niches of adapids, also does not appear to be patterned with any variables examined in this study. It is possible that these patterns of niche position: (1) relate to the movement of niches of specific non-euprimate taxa, (2) are associated with other (non-dietary) aspects of the euprimate ecological niche, or (3) are the result of changes in the sample size and composition of euprimates within each time interval. Regardless, the shifts in euprimate niche position and lack of detected competition associated with these shifts suggest that the euprimate niche changed its position within a specific, limited region of the guild-wide niche space. Furthermore, as this space was exclusive to euprimates during each time interval (excepting Wa5), the corresponding lack of niche overlap with non-euprimates may have allowed for greater variance in niche location within this limited region (Giller, 1984; Keddy, 2001; Bolnick et al., 2007; Pfennig and Pfennig, 2012).

Within the adapid and omomyid dietary niches, the niches of almost all coeval genera overlap. This suggests that adapid and omomyid diversification was not driven by dietary differentiation or changes in molar morphology. However, if early-middle Wasatchian euprimate genera within their respective families had similar diets, as suggested in previous research (e.g., Covert, 1985, 1986; Maas and O'Leary, 1996; Strait, 2001; Gunnell, 2002), this observation contrasts with the results presented in Chapter 5, in which dietary niche overlap was examined within an extant mammalian guild. Comparisons of the reconstructed niches of extant genera indicated that most of the

niches within dietary groups did not overlap. This suggests that either the modified MANOVA used has a high type I error rate or that the molar morphological measures included do not closely align with dietary regime (discussed further below). However, the niche overlap structure of an extant community is the product of millions of years of species interactions, including competitive exclusion, the result of which is minimal niche overlap even among members of the same dietary group (Grant, 1972; Connell, 1980; Grant and Schluter, 1984; Roughgarden and Diamond, 1986; Schoener, 1988; Dayan and Simberloff, 1989, 1994, 2005; Schluter, 2000; although see Connor and Simberloff, 1979). This latter interpretation may explain the greater amount of overlap among the niches of adapid and omomyid genera in the early Eocene, a time when euprimates had recently joined the mammalian community in North America and when euprimate diversification had just begun.

Finally, adapids and omomyids seem to have divided up their respective niche spaces to different degrees. The weighted relative hypervolumetric size of adapids is greater than that of omomyids in Wa0, Wa1-2, and Wa5, and the mean distance of individuals from the adapid niche centroid is greater than that of omomyids in Wa1-2 and Wa5. In these latter two time intervals, the number of omomyid genera was greater than the number of adapid genera despite the smaller size of the omomyid niche. This indicates that during these times, the dietary niches of individual omomyid genera were likely smaller than those of adapid genera and may have been associated with a greater

degree of dietary niche specialization (Gunnell, 2002; Bolnick et al., 2007, 2010; Agashe and Bolnick, 2010; Pfennig and Pfennig, 2012; although see Giller, 1984).[36,37]

FUTURE RESEARCH

These results naturally lead to many further lines of inquiry, and several avenues for future research will be discussed here. First, the application of alternative methods of capturing diet-related variation in molar form across extant mammalian guilds has the potential to demonstrate a closer association between molar morphology and dietary regimes than the measures employed here. Use of these methods could thus produce different reconstructions of dietary niche structure within the Eocene euprimate competitive guild. For instance, as discussed in Chapter 2, recent quantitative measures such as dental topographic variables (slope, relief, angularity), orientation patch count, and Dirichlet normal energy (Ungar, 2007; Boyer, 2008; Boyer et al., 2010, 2011, 2012; Bunn et al., 2011; Joshi et al., 2011; Godfrey et al., 2012; Evans, 2013; Guy et al., 2013; Ledogar et al., 2013), may exhibit a greater ability (either individually or jointly) to reconstruct diets among species in fossil communities.

Second, in this study, dietary niches were reconstructed using only molar measures, whereas incisor, canine, and premolar morphologies are certainly informative regarding dietary behavior among fossil taxa. The inclusion of additional tooth types, as well as other aspects of a taxon's ecological niche (e.g., feeding and locomotor behaviors, substrate preferences, activity pattern), will enable a more complete evaluation of niche

[36] See Whitlock (1996) for an alternative explanation of inverse relationships between diversity and niche size.
[37] As stated in Chapter 6, the calculation of hypervolumetric size was not possible for individual genera, as this calculation required at least six individuals per genus.

overlap and competitive interactions. These expanded niche reconstructions have the potential to either preclude competition between taxa whose dietary niches overlap or to identify niche overlap along other ecological niche axes between taxa whose dietary niches did not overlap (see Jones et al., 2014).

Third, as in any fossil analysis, these results are dependent on the sample composition and size and the unit of time employed. Although competitive interactions occur at the level of the population (whose best approximation in the fossil record is the species), species-species comparisons were not possible in the fossil sample due in part to small sample sizes. As a result, the patterns observed herein potentially (1) veil competitive interactions within higher taxa (genus or family) and (2) conflate competitive interactions among species within genera or families due to the combined inclusion of species in a single niche. Only increased numbers of specimens can alleviate these issues, but, given the relative rarity of certain groups within North American Eocene fossil assemblages, it may not be possible to substantially increase the specimen numbers for each taxon within the euprimate competitive guild.[38] Similarly, it is unlikely that shorter, more refined temporal units can be used, as the length of the time interval in these analyses is also dependent on sample size (see Chapter 5). However, different classifications of time (e.g., equal time bins, the sub-NALMA revision of Chew (2005)) may affect observed patterns of niche overlap and thus the identification of taxa which may have engaged in competitive interactions during this time.

[38] Nonetheless, even a small increase in the sample sizes of certain taxa excluded in these analyses (but known to be present during the time intervals evaluated) (e.g., picrodontids, micromomyids) would allow the evaluation of niche overlap using the modified MANOVA.

Fourth, species outside the euprimate competitive guild (as defined here) certainly affected taxa within the guild. Communities are comprised of numerous, interacting guilds, and a complete characterization of the euprimate competitive environment will include all (mammalian and non-mammalian) community members. For instance, although likely less significant, dietary competition between euprimates and non-guild members (e.g., arctocyonids) could still have influenced the structure and position of dietary niches within the community-wide and guild-wide niche spaces. Furthermore, non-mammalian predators were not considered in the evaluation of the effects of predation on changes in the positions of niches or the abundance and diversity of euprimate and non-euprimate taxa. Yet, avian predators surely influenced the structure of the small-bodied, arboreal mammals that comprised the euprimate competitive guild, as studies of similar extant guilds suggest (e.g., Goodman et al., 1993; Mitani et al., 2001; Granzinolli and Motta-Junior, 2006). Thus, the inclusion of these taxa is critical to a full understanding of euprimate competition in the early Eocene.

Fifth, if the analysis of extant dietary niches using the modified MANOVA outlined in Chapter 5 demonstrates a bias towards low, significant *p*-values (indicative of niche differentiation), then competitive interactions between early Eocene euprimates and non-euprimates may have been more frequent than the present results suggest. In other words, some of the numerous significant *p*-values identified in euprimate-non-euprimate niche comparisons may be false negatives (see Chapter 5), masking niche overlap (and competition) in the fossil sample. A further examination of niche overlap patterns in living communities is needed in order to determine the extent to which the observed extant niche structure (i.e., minimal overlap among niches within a dietary group) holds.

On the other hand, the extant analysis consequently demonstrated that non-significant MANOVA results were highly indicative of actual niche overlap between taxa. Thus, it is reasonable to assume that the instances of niche overlap identified and evaluated here are true examples of competitive interactions within the Eocene euprimate guild.

Finally, this study only included members of the euprimate competitive guild at a single site in North America, the Bighorn Basin. This site was chosen for its taxonomic diversity, abundant euprimate sample, and high stratigraphic resolution; however, the inclusion of non-Bighorn Basin fossil material will enable an assessment of the universality of the patterns identified in this study. Furthermore, complementing the fossil sample herein with specimens from additional sites in the Western Interior has the ability to produce a regional assessment of the euprimate competitive environment as it changed through the middle Eocene.

Overall, the major results of this study can be summarized as follows: (1) a lack of dietary competition characterized the origination and early diversification of the earliest euprimates in North America (consistent with current prevailing hypotheses of euprimate origins); (2) the dietary niches of adapids and omomyids remained distinct throughout the early-middle Wasatchian; (3) changes in euprimate dietary niche size over time parallel major climatic shifts from Wa0 to Wa5; and (4) the dietary niches of euprimate genera within a given time interval consistently overlap within each family (Adapidae and Omomyidae), contrasting with the niche structure observed in a living community and underscoring that the pattern of dietary niches in this Eocene euprimate competitive guild may represent only the beginnings of a dynamic process that altered the structure of this "species assemblage" for millions of years. It is these same abiotic and

biotic processes that still influence, and will continue to influence, the composition and structure of mammalian guilds and communities of both the present and future.

Table 7.1. Summary of changes in niche position and size of adapid and omomyid niches for each transition between time intervals. Measures of niche position and size are those discussed in Chapter 6. For the MANOVA pairwise comparisons, "NE," or "not equal," indicates a shift in the adapid or omomyid niche. For all other measures, a directional shift (i.e., the change from a '+' to a '-' in subsequent transition points) indicates the presence of a shift in niche position or size. Parentheses indicate weak changes between time intervals. Note that the majority of shifts in niche size and position in both adapids and omomyids are coincident with the transition between Wa4 and Wa5 (Wa4-Wa5).

			Wa0-Wa1-2	Wa1-2-Wa3	Wa3-Wa4	Wa4-Wa5
NICHE POSITION	MANOVA Pairwise Comparisons	Adapidae	=	NE	NE	NE
		Omomyidae	=	NE	=	=
	Adapid-Omomyid Centroid Distance		=	=	+	—
	Distance From Wa0 Centroid	Adapidae		+	+	—
		Omomyidae		+	+	—
NICHE SIZE	Relative Hypervolumetric Size	Adapidae	(+)	—	—	+
		Omomyidae	—	—	—	—
	Mean Distance from Centroid	Adapidae	(—)	—	=	+
		Omomyidae	—	—	=	+

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APPENDIX A

MEAN VALUES OF UNSCALED MORPHOMETRIC MEASURES OF BALTA, PERU SPECIES.

Linear measures are in mm, area measures are in mm^2, and angular measures are in radians. Measurements that could not be taken due to the lack of a feature in a species (e.g., absence the hypoconid) are denoted by '---.'

Species	Molar Area	Protoconid Height	Metaconid Height	Entoconid Height
Anoura caudifer	0.666	0.729	0.459	0.398
Anoura geoffroyi	0.747	0.548	0.642	0.491
Aotus trivirgatus	10.439	1.976	2.243	1.982
Artibeus cinereus	1.547	0.590	0.558	0.409
Artibeus concolor	2.077	0.820	0.850	0.559
Artibeus literatus	4.867	1.021	1.256	0.753
Artibeus obscurus	3.832	0.999	1.032	0.635
Artibeus planirostris	5.229	1.210	1.279	0.743
Callicebus moloch	11.062	2.095	2.106	1.901
Caluromys lanatus	5.028	2.001	1.334	1.140
Carollia brevicauda	0.938	1.030	0.531	0.337
Carollia castanea	0.765	1.024	0.485	0.286
Carollia perspicillata	1.107	1.116	0.579	0.302
Cebus albifrons	19.614	2.730	2.790	2.081
Chiroderma villosum	4.660	1.362	1.235	1.016
Choeroniscus minor	0.344	0.238	0.292	0.295
Didelphis marsupialis	24.013	4.325	3.688	2.582
Ectophylla macconnelli	1.659	0.686	0.625	0.421
Eptesicus brasiliensis	1.520	1.540	0.757	0.737
Eptesicus furinalis	1.479	1.412	0.643	0.677
Glossophaga soricina	0.567	0.670	0.439	0.347
Gracilianus agilis	1.340	1.259	0.813	0.665
Lasiurus borealis	0.730	1.095	0.468	0.455
Lasiurus ega	1.473	1.491	0.698	0.739
Lonchophylla thomasi	0.486	0.539	0.431	0.366
Lophostoma silvicolum	2.724	2.006	1.085	0.843
Macrophyllum macrophyllum	1.220	1.084	0.574	0.556
Marmosa murina	1.826	1.417	0.918	0.738
Marmosa quichua	1.974	1.374	0.938	0.708
Marmosops noctivagus	2.609	1.677	1.269	0.888
Metachirus nudicaudatus	5.437	2.409	1.951	1.447
Micoureus demerarae	3.264	1.984	1.335	1.072
Micronycteris megalotis	1.452	1.410	0.686	0.577
Micronycteris nicefori	1.165	1.179	0.619	0.419
Mimon crenulatum	2.884	2.110	1.040	0.925

Species	Molar Area	Protoconid Height	Metaconid Height	Entoconid Height
Molossops abrasus	3.245	2.356	1.031	1.005
Molossops greenhalli	1.783	1.841	0.779	0.888
Molossus molossus	2.017	1.886	0.743	0.747
Myotis albescens	0.723	0.998	0.458	0.475
Myotis riparius	0.838	1.114	0.535	0.583
Myotis simus	0.916	1.225	0.572	0.596
Noctilio albiventris	2.923	1.714	0.905	0.895
Philander mcilhennyi	9.922	2.939	2.471	1.759
Philander opossum	7.222	2.756	2.085	1.520
Phyllostomus elongatus	4.328	2.652	1.222	1.074
Phyllostomus hastatus	6.155	2.831	1.499	1.265
Pithecia monachus	15.103	2.428	2.514	2.081
Platyrrhinus brachycephalus	2.267	0.736	0.557	0.506
Platyrrhinus helleri	2.234	0.610	0.455	0.462
Platyrrhinus infuscus	5.731	1.294	1.070	1.047
Rhynchonycteris naso	0.624	0.730	0.346	0.375
Saccopteryx bilineata	1.782	1.657	0.741	0.746
Saccopteryx leptura	1.121	1.313	0.495	0.597
Saguinus imperator	4.581	1.361	1.513	1.275
Saimiri boliviensis	6.624	1.550	1.926	1.587
Sciurus ignitus	4.199	0.957	0.957	0.938
Sciurus spadiceus	7.490	1.274	1.374	1.163
Sturnira lilium	1.478	0.664	0.590	0.525
Sturnira tildae	1.738	0.697	0.665	0.487
Tonatia minuta	1.321	1.591	0.768	0.600
Tonatia saurophila	2.787	2.088	1.076	0.753
Trachops cirrhosus	3.905	2.490	1.385	1.203
Uroderma bilobatum	2.756	0.941	0.830	0.565
Uroderma magnirostrum	2.131	0.859	0.699	0.503
Vampyressa bidens	1.911	0.790	0.833	0.616
Vampyressa pusilla	1.491	0.662	1.030	0.709
Vampyrodes caraccioli	5.015	1.172	1.122	0.886

Species	Hypoconid Height	Mean Cusp Height	Crest Length	Hypoconid Angle
Anoura caudifer	0.537	0.531	2.665	1.939
Anoura geoffroyi	0.502	0.546	2.551	1.924
Aotus trivirgatus	1.971	2.043	11.989	2.313
Artibeus cinereus	0.555	0.528	4.821	2.686
Artibeus concolor	0.699	0.732	7.200	2.926
Artibeus literatus	0.976	1.001	9.482	2.751
Artibeus obscurus	0.823	0.872	8.504	2.700
Artibeus planirostris	0.951	1.046	11.135	2.729
Callicebus moloch	2.081	2.046	12.430	2.274
Caluromys lanatus	1.727	1.551	6.857	1.724
Carollia brevicauda	0.674	0.643	1.989	2.576
Carollia castanea	0.667	0.615	1.905	2.411
Carollia perspicillata	0.729	0.681	2.131	2.372
Cebus albifrons	2.397	2.500	16.144	2.202
Chiroderma villosum	1.086	1.119	10.872	2.137
Choeroniscus minor	0.253	0.269	1.548	2.504
Didelphis marsupialis	2.865	3.365	14.099	2.017
Ectophylla macconnelli	0.521	0.563	3.729	2.872
Eptesicus brasiliensis	1.202	1.059	4.253	1.386
Eptesicus furinalis	1.147	0.970	3.706	1.436
Glossophaga soricina	0.447	0.476	1.983	2.042
Gracilianus agilis	0.805	0.886	4.197	1.700
Lasiurus borealis	0.763	0.695	3.104	1.441
Lasiurus ega	1.106	1.009	4.289	1.400
Lonchophylla thomasi	0.421	0.440	1.982	2.367
Lophostoma silvicolum	1.502	1.359	5.460	1.356
Macrophyllum macrophyllum	0.837	0.763	3.902	1.508
Marmosa murina	0.959	1.008	4.613	1.572
Marmosa quichua	0.937	0.989	4.711	1.671
Marmosops noctivagus	1.346	1.356	5.860	1.615
Metachirus nudicaudatus	1.781	1.897	8.743	1.816
Micoureus demerarae	1.511	1.476	6.387	1.652
Micronycteris megalotis	1.059	0.933	3.833	1.339
Micronycteris nicefori	0.845	0.765	3.565	1.796
Mimon crenulatum	1.667	1.435	5.994	1.360

Species	Hypoconid Height	Mean Cusp Height	Crest Length	Hypoconid Angle
Molossops abrasus	1.794	1.547	7.379	1.403
Molossops greenhalli	1.467	1.244	5.865	1.075
Molossus molossus	1.459	1.209	5.768	1.293
Myotis albescens	0.703	0.658	2.929	1.370
Myotis riparius	0.822	0.763	3.313	1.251
Myotis simus	0.946	0.835	3.572	1.169
Noctilio albiventris	1.516	1.258	6.903	1.590
Philander mcilhennyi	2.230	2.350	11.335	1.710
Philander opossum	1.742	2.026	9.187	1.740
Phyllostomus elongatus	2.068	1.754	7.320	1.316
Phyllostomus hastatus	2.198	1.937	7.825	1.402
Pithecia monachus	2.367	2.348	15.517	2.393
Platyrrhinus brachycephalus	0.673	0.618	6.229	2.699
Platyrrhinus helleri	0.625	0.538	6.110	2.759
Platyrrhinus infuscus	1.172	1.146	10.321	2.626
Rhynchonycteris naso	0.571	0.505	3.230	1.157
Saccopteryx bilineata	1.252	1.099	5.634	1.271
Saccopteryx leptura	0.939	0.836	4.136	1.528
Saguinus imperator	1.151	1.325	7.443	2.362
Saimiri boliviensis	1.306	1.592	9.874	2.589
Sciurus ignitus	0.990	0.961	6.004	2.547
Sciurus spadiceus	1.288	1.275	7.797	2.607
Sturnira lilium	---	0.593	3.865	---
Sturnira tildae	---	0.616	4.179	---
Tonatia minuta	1.193	1.038	3.304	1.717
Tonatia saurophila	1.492	1.352	5.103	1.512
Trachops cirrhosus	1.735	1.703	6.921	1.744
Uroderma bilobatum	0.744	0.770	7.288	2.534
Uroderma magnirostrum	0.648	0.677	5.973	2.807
Vampyressa bidens	0.637	0.719	6.414	2.563
Vampyressa pusilla	0.618	0.755	5.928	2.393
Vampyrodes caraccioli	1.197	1.095	9.186	2.738

Species	Protoconid Angle	Metaconid Angle	Entoconid Angle	Mean Cusp Angle
Anoura caudifer	1.617	1.963	2.074	1.898
Anoura geoffroyi	1.679	2.200	2.223	2.007
Aotus trivirgatus	2.271	1.851	2.354	2.197
Artibeus cinereus	2.285	2.140	2.502	2.403
Artibeus concolor	2.347	2.308	2.412	2.498
Artibeus literatus	2.344	2.157	2.418	2.418
Artibeus obscurus	2.009	1.973	2.312	2.248
Artibeus planirostris	2.106	2.332	2.243	2.352
Callicebus moloch	2.369	1.963	2.300	2.227
Caluromys lanatus	1.403	1.492	2.615	1.808
Carollia brevicauda	2.275	1.989	2.506	2.336
Carollia castanea	2.133	2.356	2.732	2.408
Carollia perspicillata	2.033	2.049	2.697	2.288
Cebus albifrons	2.328	2.073	1.987	2.147
Chiroderma villosum	1.688	1.535	1.823	1.771
Choeroniscus minor	2.804	2.480	2.518	2.577
Didelphis marsupialis	1.357	1.112	1.966	1.613
Ectophylla macconnelli	2.150	2.238	2.484	2.436
Eptesicus brasiliensis	1.186	1.200	1.469	1.310
Eptesicus furinalis	1.363	1.539	1.739	1.519
Glossophaga soricina	1.935	1.981	2.178	2.034
Gracilianus agilis	1.305	1.173	1.919	1.524
Lasiurus borealis	1.097	1.309	1.660	1.377
Lasiurus ega	1.192	1.479	1.513	1.396
Lonchophylla thomasi	1.973	2.111	2.206	2.164
Lophostoma silvicolum	1.274	1.258	1.844	1.433
Macrophyllum macrophyllum	1.355	1.595	1.706	1.541
Marmosa murina	1.196	1.020	1.807	1.399
Marmosa quichua	1.286	1.127	1.779	1.466
Marmosops noctivagus	1.234	0.959	1.215	1.271
Metachirus nudicaudatus	1.293	1.133	1.626	1.467
Micoureus demerarae	1.215	1.101	1.778	1.437
Micronycteris megalotis	1.258	1.264	1.991	1.463
Micronycteris nicefori	1.103	1.739	2.014	1.663
Mimon crenulatum	1.141	1.297	1.528	1.331

Species	Protoconid Angle	Metaconid Angle	Entoconid Angle	Mean Cusp Angle
Molossops abrasus	1.264	1.691	1.818	1.544
Molossops greenhalli	1.021	1.378	1.425	1.225
Molossus molossus	1.191	1.389	1.528	1.350
Myotis albescens	1.225	1.395	1.573	1.391
Myotis riparius	1.017	1.443	1.536	1.312
Myotis simus	0.893	1.276	1.304	1.160
Noctilio albiventris	1.316	1.990	2.079	1.744
Philander mcilhennyi	1.349	1.047	2.068	1.543
Philander opossum	1.256	1.106	1.934	1.509
Phyllostomus elongatus	1.147	1.221	1.769	1.363
Phyllostomus hastatus	1.307	1.267	1.976	1.488
Pithecia monachus	2.535	2.126	2.477	2.383
Platyrrhinus brachycephalus	2.133	2.207	2.263	2.326
Platyrrhinus helleri	2.560	2.350	2.305	2.494
Platyrrhinus infuscus	2.615	2.232	2.163	2.409
Rhynchonycteris naso	1.031	2.005	1.739	1.483
Saccopteryx bilineata	1.139	1.456	1.786	1.413
Saccopteryx leptura	1.062	1.503	1.876	1.492
Saguinus imperator	2.266	2.209	2.619	2.364
Saimiri boliviensis	2.200	1.679	2.170	2.159
Sciurus ignitus	2.444	1.934	2.539	2.366
Sciurus spadiceus	2.761	2.464	2.627	2.615
Sturnira lilium	2.213	2.382	2.712	2.436
Sturnira tildae	2.425	2.404	2.753	2.528
Tonatia minuta	1.414	1.257	2.069	1.614
Tonatia saurophila	1.333	1.370	2.246	1.615
Trachops cirrhosus	1.377	1.224	1.589	1.483
Uroderma bilobatum	2.137	2.196	2.309	2.294
Uroderma magnirostrum	2.321	2.501	2.559	2.547
Vampyressa bidens	2.072	1.743	2.109	2.122
Vampyressa pusilla	2.029	1.666	2.281	2.093
Vampyrodes caraccioli	2.117	1.782	1.998	2.159

Species	Talonid Basin Area	Talonid Basin Depth	Trigonid-Talonid Relief
Anoura caudifer	0.290	0.131	0.389
Anoura geoffroyi	0.293	0.138	0.344
Aotus trivirgatus	4.347	0.683	0.616
Artibeus cinereus	0.692	0.129	0.366
Artibeus concolor	1.149	0.270	0.399
Artibeus literatus	2.522	0.265	0.641
Artibeus obscurus	2.060	0.223	0.626
Artibeus planirostris	3.469	0.276	0.633
Callicebus moloch	4.562	0.460	0.606
Caluromys lanatus	1.835	0.272	1.016
Carollia brevicauda	0.212	0.050	0.252
Carollia castanea	0.153	0.041	0.271
Carollia perspicillata	0.258	0.043	0.309
Cebus albifrons	6.769	0.603	0.563
Chiroderma villosum	2.215	0.361	0.288
Choeroniscus minor	0.132	0.037	0.238
Didelphis marsupialis	6.836	0.740	2.401
Ectophylla macconnelli	1.050	0.207	0.264
Eptesicus brasiliensis	0.468	0.183	0.607
Eptesicus furinalis	0.392	0.147	0.561
Glossophaga soricina	0.180	0.092	0.350
Gracilianus agilis	0.462	0.232	0.600
Lasiurus borealis	0.204	0.089	0.439
Lasiurus ega	0.415	0.190	0.598
Lonchophylla thomasi	0.161	0.089	0.301
Lophostoma silvicolum	0.833	0.218	0.746
Macrophyllum macrophyllum	0.422	0.130	0.470
Marmosa murina	0.526	0.247	0.688
Marmosa quichua	0.547	0.265	0.634
Marmosops noctivagus	0.871	0.260	0.970
Metachirus nudicaudatus	1.909	0.383	1.408
Micoureus demerarae	1.013	0.330	0.933
Micronycteris megalotis	0.370	0.174	0.447
Micronycteris nicefori	0.378	0.145	0.466
Mimon crenulatum	0.876	0.243	0.750

Species	Talonid Basin Area	Talonid Basin Depth	Trigonid-Talonid Relief
Molossops abrasus	1.028	0.269	0.812
Molossops greenhalli	0.700	0.235	0.630
Molossus molossus	0.695	0.251	0.641
Myotis albescens	0.217	0.115	0.416
Myotis riparius	0.258	0.110	0.459
Myotis simus	0.305	0.126	0.486
Noctilio albiventris	1.043	0.453	0.335
Philander mcilhennyi	3.208	0.699	1.570
Philander opossum	2.374	0.507	1.614
Phyllostomus elongatus	1.411	0.299	0.958
Phyllostomus hastatus	1.761	0.342	1.000
Pithecia monachus	7.503	0.648	0.312
Platyrrhinus brachycephalus	1.198	0.267	0.307
Platyrrhinus helleri	1.102	0.251	0.196
Platyrrhinus infuscus	3.697	0.710	0.586
Rhynchonycteris naso	0.212	0.045	0.376
Saccopteryx bilineata	0.607	0.155	0.645
Saccopteryx leptura	0.339	0.082	0.551
Saguinus imperator	1.515	0.393	0.408
Saimiri boliviensis	2.624	0.472	0.537
Sciurus ignitus	2.111	0.323	0.350
Sciurus spadiceus	3.268	0.417	0.423
Sturnira lilium	0.872	0.227	0.045
Sturnira tildae	1.027	0.202	0.083
Tonatia minuta	0.359	0.168	0.538
Tonatia saurophila	0.808	0.237	0.731
Trachops cirrhosus	1.022	0.197	1.023
Uroderma bilobatum	1.638	0.231	0.556
Uroderma magnirostrum	1.213	0.155	0.462
Vampyressa bidens	1.052	0.410	0.246
Vampyressa pusilla	0.850	0.343	0.298
Vampyrodes caraccioli	2.917	0.480	0.657

APPENDIX B

MEAN VALUES OF UNSCALED MORPHOMETRIC MEASURES OF MINDANAO, PHILIPPINES SPECIES.

Linear measures are in mm, area measures are in mm^2, and angular measures are in radians. Measurements that could not be taken due to the lack of a feature in a species (e.g., absence the hypoconid) are denoted by '---.'

Species	Molar Area	Protoconid Height	Metaconid Height	Entoconid Height
Acerodon jubatus	21.365	3.003	2.870	---
Alionycteris paucidentata	0.366	0.286	---	---
Coelops hirsutus	0.622	1.080	0.382	0.378
Crocidura beatus	1.351	1.462	0.816	0.680
Cynocephalus volans	13.255	3.102	2.739	2.117
Cynopterus brachyotis	1.103	0.632	0.628	---
Dyacopterus rickarti	3.024	1.002	0.997	---
Emballonura alecto	1.037	1.182	0.537	0.594
Eonycteris robusta	1.398	0.536	0.487	---
Exilisciurus concinnus	1.143	0.540	0.597	0.532
Haplonycteris fischeri	2.150	0.557	0.523	---
Harpyionycteris whiteheadi	4.253	1.504	1.367	---
Hipposideros ater	1.099	1.267	0.606	0.529
Hipposideros cervinus	1.377	1.414	0.717	0.540
Hipposideros coronatus	2.515	1.956	0.897	0.675
Hipposideros diadema griseus	5.610	3.096	1.510	1.109
Hipposideros obscurus	2.045	1.732	0.752	0.632
Kerivoula pellucida	1.087	1.108	0.496	0.561
Macroglossus minimus	0.488	0.203	---	---
Megaderma spasma	2.846	2.212	1.299	0.843
Megaerops wetmorei	0.613	0.494	0.443	---
Miniopterus australis	0.748	1.156	0.497	0.514
Miniopterus schreibersii	1.253	1.467	0.615	0.616
Miniopterus tristis	2.047	1.879	0.771	0.751
Myotis macrotarsus	1.613	1.427	0.696	0.715
Myotis muricola	0.700	1.016	0.472	0.518
Otomops formosus	2.036	1.616	0.837	0.828
Petinomys crinitus	13.472	2.098	2.182	1.683
Philetor brachypterus	0.994	1.188	0.528	0.607
Pipistrellus javanicus	0.925	1.150	0.548	0.661
Ptenochirus jagori	2.102	1.011	0.865	---
Ptenochirus minor	1.644	0.777	0.762	---
Pteropus hypomelanus	7.808	2.147	1.939	---
Pteropus pumilus	4.475	1.421	1.469	---

Species	Molar Area	Protoconid Height	Metaconid Height	Entoconid Height
Pteropus speciosus	7.165	2.024	1.769	---
Pteropus vampyrus	11.884	2.224	2.025	---
Rhinolophus arcuatus	1.935	1.722	0.923	0.705
Rhinolophus inops	3.185	2.092	1.040	0.797
Rhinolophus rufus	4.857	2.631	1.340	0.949
Rhinolophus virgo	1.442	1.423	0.721	0.609
Rousettus amplexicaudatus	2.734	0.857	0.845	---
Scotophilus kuhlii	2.038	2.195	1.046	0.820
Sundasciurus philippinensis	6.036	1.577	1.953	1.374
Taphozous melanopogon	2.291	1.844	0.947	0.847
Tarsius syrichta	6.290	2.216	1.831	1.165
Urogale everetti	6.856	2.976	2.039	1.434

Species	Hypoconid Height	Mean Cusp Height	Crest Length	Hypoconid Angle
Acerodon jubatus	---	2.937	15.483	---
Alionycteris paucidentata	---	0.286	0.856	---
Coelops hirsutus	0.795	0.659	2.799	1.273
Crocidura beatus	1.092	1.012	4.027	1.462
Cynocephalus volans	2.876	2.708	14.151	1.475
Cynopterus brachyotis	---	0.630	2.985	---
Dyacopterus rickarti	---	1.000	4.884	---
Emballonura alecto	0.899	0.803	3.658	1.319
Eonycteris robusta	---	0.512	3.379	---
Exilisciurus concinnus	0.625	0.574	2.697	2.595
Haplonycteris fischeri	---	0.540	4.460	---
Harpyionycteris whiteheadi	---	1.355	2.584	---
Hipposideros ater	0.716	0.780	3.448	1.794
Hipposideros cervinus	1.004	0.919	4.001	1.475
Hipposideros coronatus	0.905	1.108	5.201	2.119
Hipposideros diadema griseus	2.299	2.004	7.100	1.596
Hipposideros obscurus	1.175	1.073	4.519	1.541
Kerivoula pellucida	0.847	0.753	3.639	1.341
Macroglossus minimus	---	0.203	1.037	---
Megaderma spasma	1.537	1.473	4.429	1.747
Megaerops wetmorei	---	0.469	2.174	---
Miniopterus australis	0.885	0.763	3.383	1.149
Miniopterus schreibersii	1.129	0.957	3.956	1.105
Miniopterus tristis	1.396	1.199	5.103	1.267
Myotis macrotarsus	1.099	0.985	3.940	1.065
Myotis muricola	0.665	0.668	2.930	1.185
Otomops formosus	1.227	1.127	4.729	1.152
Petinomys crinitus	2.150	2.028	11.639	1.953
Philetor brachypterus	0.908	0.808	4.037	1.248
Pipistrellus javanicus	0.903	0.816	3.393	1.451
Ptenochirus jagori	---	0.938	4.137	---
Ptenochirus minor	---	0.770	3.577	---
Pteropus hypomelanus	---	2.043	7.672	---
Pteropus pumilus	---	1.445	5.719	---

Species	Hypoconid Height	Mean Cusp Height	Crest Length	Hypoconid Angle
Pteropus speciosus	---	1.896	7.488	---
Pteropus vampyrus	---	2.124	9.604	---
Rhinolophus arcuatus	1.301	1.163	4.383	1.484
Rhinolophus inops	1.628	1.389	5.353	1.434
Rhinolophus rufus	1.932	1.713	6.824	1.557
Rhinolophus virgo	1.079	0.958	3.923	1.545
Rousettus amplexicaudatus	---	0.851	5.117	---
Scotophilus kuhlii	1.541	1.400	4.179	1.636
Sundasciurus philippinensis	1.520	1.606	7.497	2.223
Taphozous melanopogon	1.452	1.272	6.029	1.292
Tarsius syrichta	1.850	1.766	8.948	1.862
Urogale everetti	2.369	2.205	9.930	1.444

Species	Protoconid Angle	Metaconid Angle	Entoconid Angle	Mean Cusp Angle
Acerodon jubatus	2.709	2.646	---	2.677
Alionycteris paucidentata	2.794	---	---	2.794
Coelops hirsutus	1.086	1.446	1.847	1.413
Crocidura beatus	1.136	1.310	1.831	1.435
Cynocephalus volans	1.191	1.061	1.245	1.243
Cynopterus brachyotis	2.617	2.685	---	2.651
Dyacopterus rickarti	2.693	1.936	---	2.314
Emballonura alecto	1.044	1.497	1.736	1.399
Eonycteris robusta	3.019	3.001	---	3.010
Exilisciurus concinnus	2.451	2.643	2.720	2.602
Haplonycteris fischeri	2.803	2.811	---	2.807
Harpyionycteris whiteheadi	1.882	1.771	---	1.912
Hipposideros ater	1.235	1.447	1.395	1.468
Hipposideros cervinus	1.253	1.420	1.764	1.478
Hipposideros coronatus	1.223	1.798	1.976	1.779
Hipposideros diadema griseus	1.250	1.426	1.852	1.531
Hipposideros obscurus	1.288	1.399	2.020	1.562
Kerivoula pellucida	1.761	2.147	1.827	1.769
Macroglossus minimus	2.761	---	---	2.761
Megaderma spasma	1.473	1.293	2.048	1.640
Megaerops wetmorei	2.727	2.764	---	2.746
Miniopterus australis	1.060	1.414	1.466	1.273
Miniopterus schreibersii	1.003	1.244	1.293	1.161
Miniopterus tristis	1.135	1.354	1.454	1.302
Myotis macrotarsus	1.530	1.152	1.330	1.269
Myotis muricola	0.899	1.626	1.407	1.279
Otomops formosus	1.192	1.246	1.470	1.265
Petinomys crinitus	2.296	2.019	2.368	2.159
Philetor brachypterus	1.208	1.590	1.387	1.358
Pipistrellus javanicus	1.090	1.380	1.420	1.335
Ptenochirus jagori	2.763	2.843	---	2.803
Ptenochirus minor	2.812	2.893	---	2.852
Pteropus hypomelanus	2.858	3.032	---	2.945
Pteropus pumilus	2.763	2.734	---	2.749

Species	Protoconid Angle	Metaconid Angle	Entoconid Angle	Mean Cusp Angle
Pteropus speciosus	2.642	2.698	---	2.670
Pteropus vampyrus	2.712	2.813	---	2.762
Rhinolophus arcuatus	1.104	1.204	1.824	1.404
Rhinolophus inops	1.201	1.313	1.802	1.438
Rhinolophus rufus	1.289	1.432	1.784	1.515
Rhinolophus virgo	1.095	1.457	1.832	1.482
Rousettus amplexicaudatus	2.705	2.612	---	2.658
Scotophilus kuhlii	1.239	1.266	1.736	1.469
Sundasciurus philippinensis	2.228	2.083	2.635	2.292
Taphozous melanopogon	1.071	1.288	1.603	1.314
Tarsius syrichta	1.178	1.311	1.839	1.547
Urogale everetti	1.215	1.113	1.591	1.341

Species	Talonid Basin Area	Talonid Basin Depth	Trigonid-Talonid Relief
Acerodon jubatus	---	0.293	---
Alionycteris paucidentata	---	0.029	---
Coelops hirsutus	0.200	0.047	0.368
Crocidura beatus	0.436	0.128	0.603
Cynocephalus volans	5.729	1.001	1.564
Cynopterus brachyotis	---	0.081	---
Dyacopterus rickarti	---	0.100	---
Emballonura alecto	0.303	0.114	0.522
Eonycteris robusta	---	0.046	---
Exilisciurus concinnus	0.401	0.037	0.285
Haplonycteris fischeri	---	0.028	---
Harpyionycteris whiteheadi	---	0.313	---
Hipposideros ater	0.260	0.171	0.446
Hipposideros cervinus	0.343	0.157	0.476
Hipposideros coronatus	0.611	0.168	0.618
Hipposideros diadema griseus	1.073	0.260	1.026
Hipposideros obscurus	0.491	0.145	0.615
Kerivoula pellucida	0.299	0.136	0.456
Macroglossus minimus	---	0.049	---
Megaderma spasma	0.436	0.197	0.561
Megaerops wetmorei	---	0.068	---
Miniopterus australis	0.288	0.145	0.465
Miniopterus schreibersii	0.373	0.187	0.527
Miniopterus tristis	0.663	0.234	0.724
Myotis macrotarsus	0.371	0.139	0.558
Myotis muricola	0.217	0.095	0.420
Otomops formosus	0.583	0.262	0.559
Petinomys crinitus	6.447	0.546	0.775
Philetor brachypterus	0.324	0.140	0.474
Pipistrellus javanicus	0.270	0.139	0.435
Ptenochirus jagori	---	0.167	---
Ptenochirus minor	---	0.130	---
Pteropus hypomelanus	---	0.507	---
Pteropus pumilus	---	0.427	---

Species	Talonid Basin Area	Talonid Basin Depth	Trigonid-Talonid Relief
Pteropus speciosus	---	0.385	---
Pteropus vampyrus	---	0.479	---
Rhinolophus arcuatus	0.603	0.249	0.592
Rhinolophus inops	0.835	0.233	0.722
Rhinolophus rufus	1.346	0.274	0.934
Rhinolophus virgo	0.425	0.196	0.497
Rousettus amplexicaudatus	---	0.110	---
Scotophilus kuhlii	0.443	0.187	0.714
Sundasciurus philippinensis	2.974	0.402	0.688
Taphozous melanopogon	0.705	0.231	0.789
Tarsius syrichta	2.300	0.655	1.086
Urogale everetti	2.481	0.387	1.328

APPENDIX C

BIGHORN BASIN SPECIMENS INCLUDED IN THIS STUDY.

Abbreviations are as follows: UM=University of Michigan, USGS=United States Geological Survey, USNM=United States National Museum, UW=University of Wyoming, YPM=Yale Peabody Museum, Uncat.=Uncatalogued. USGS and USNM specimens are housed at Johns Hopkins University (Baltimore, MD) and the National Museum of Natural History (Washington, DC). UM specimens are housed at the University of Michigan Museum of Paleontology (Ann Arbor, MI). Parentheses denote number of specimens included in the analyses that share the same specimen number. All holotype, UW, and YPM specimens were molded from casts.

	Cf2-3	Wa0	Wa1-2	Wa3	Wa4	Wa5
APATOTHERIA						
Apatemyidae						
Apatemys		USGS 23821	UM 76834	USNM 527699	UM 67310	USGS 17633
		USGS 26548	USGS 9614	USNM 533453	USGS 9873	USNM 487861
		USGS 9038	USGS 9742			USNM 491812
		UW 9571	UW 8999			USNM 491813
Labidolemur	UM 71012		UM 69979	UM 68588		
	UM 71481		UM 77399	UM 68590		
	UM 73500		UM 81465	UM 71525		
	UM 73501		UM 81474	UM 79278		
			UM 81567			
			UM 82152			
DIDELPHIMORPHIA						
Peradectidae						
Mimoperadectes		UM 93381		USGS 14724		YPM 35149
		USNM 533571		USGS 15890		
		USNM 538265		UW 9826		
		USNM 538266				
		USNM 538314				
Peradectes	UM 109746	USGS 2715	UM 68867	UM 73884	USGS 17625	
	UM 65001	USGS 3932	UM 75143	YPM 30594	Uncat. (1)	
	UM 73606	USNM 493839	UM 81573			
	UM 82390	UW 9605	UM 95353			
	UM 82680		UM 95384			
			USGS 2530			

	Cf2-3	Wa0	Wa1-2	Wa3	Wa4	Wa5
Peradectes			USGS 2569 (2) USGS 2885			
Peratherium		USGS 2717 (3) USNM 527686 UW 9564		YPM 30644		USGS 9850 USNM 495252
Incertae sedis			UM 71724			
DIDELPHODONTA Palaeoryctidae *Didelphodus*		USNM 533578 USNM 533580 USNM 540166	UM 66988 UM 69850 USGS 9617 USGS 9652	Uncat. (1)		USGS 9107 USNM 491894
Eoryctes			UM 81544 UM 81555			
Palaeoryctes	UM 82674		UM 79657			
ERINACEOMORPHA *Auroralestes*				USNM 527511		
Diacocherus	UM 109739 UM 71685 UM 87803					
Leipsanolestes	UM 71660 UM 77572		UM 69475 UM 71133 UW 9568 UW 9672			
Macrocranion		USGS 8098	UW 9640	USNM 542092	USNM 494902 USNM 495193	USNM 495026 USNM 495031 USNM 495037 USNM 495319
Scenopagus			UW 8998			
Talpavoides	USGS 2729 UW 6999					

	Cf2-3	Wa0	Wa1-2	Wa3	Wa4	Wa5
Talpavoides (Cont'd.)	UW 9623					
	UW 9624					
Talpavus			UM 72269			
EUPRIMATES						
Adapidae						
Cantius		UM 101958	UM 115572	UM 71533	USGS 13749	UM 75288
		UM 87341	UM 64613	UM 83032	USGS 1679	UM 75569
		UM 87852	UM 64689	USGS 13578	USGS 25987 (2)	USGS 18366
		UM 95305	UM 64699	USGS 13634	USGS 30045	USGS 25244
		USGS 10507	UM 64703	USGS 13645	USGS 30237	USGS 25818
		USGS 13650	UM 64822	USGS 1815	USGS 3670	USGS 25862
		USGS 13746	UM 64891	USGS 1911	USGS 4454	USGS 27670
		USGS 16503	UM 64964	USGS 2133	USGS 4700	USGS 27723
		USGS 23705	UM 64988	USGS 2384	USGS 7360	USGS 27726
		USGS 23725	UM 65324	USGS 2492	USGS 7385	USGS 28000
		USGS 23727	UM 67497	USGS 27599	USGS 9755	USGS 28001
		USGS 25850	UM 67513	USGS 27679	USGS 9933	USGS 28010
		USGS 27210	UM 68160	USGS 30095	USNM 522181	USGS 28051
		USGS 27977	UM 68313	USGS 38507		USGS 30222
		USGS 30218	UM 69865	USGS 4497		USGS 4564
		USGS 38057	UM 69982	USGS 7947		USGS 4567
		USGS 4695	UM 75299	USGS 8071		USGS 4719
		USGS 4709	UM 75968	USGS 9663		USGS 6990
		USGS 8869	UM 76250	USNM 522172		USGS 8015
		USGS 9035	UM 76364			USGS 8581
			UM 78929			USGS 9954
			UM 80029			USGS 27714
			UM 80169			USNM 495344
			UM 80477			USNM 495489
			UM 80482			
			UM 80484			

	Cf2-3	Wa0	Wa1-2	Wa3	Wa4	Wa5
Cantius (Cont'd.)			UM 80835			
			UM 81934			
			UM 82208			
			UM 99041			
			USGS 13727			
			USGS 2558			
			USGS 8159			
			USGS 9024			
			USGS 9322			
			USGS 9599			
			USGS 9738			
Copelemur						USGS 27662
						USGS 27733
						USGS 30189
						USGS 4655
						USGS 7120
						USGS 9955
						USNM 495376
						USNM 511281
Omomyidae						
Absarokius						UM 91756
						UM 91795
						UM 91970
Anemorhysis			UM 69991	UM 69198	USGS 27425	USGS 15403
			UM 71288	UM 69646	YPM 24984	
			UM 76492	UM 78965		
			UM 80836	UM 79218		
			UM 82209			
Arapahovius						USNM 491904
						USNM 491907

	Cf2-3	Wa0	Wa1-2	Wa3	Wa4	Wa5
Pseudotetonius					JHU 66	
					UM 73453	
					UM 73462	
					USGS 26183	
					USGS 26527	
					USGS 27849	
					USGS 3867	
					USGS 5973	
					USGS 9155	
Steinius						USNM 491941
						USNM 491951
Teilhardina		UM 99031	UM 67424	UM 69147		
		USGS 12193	UM 71386	UM 73876		
		USGS 15406	UM 71398	UM 73908		
		USGS 2428	UM 72105	UM 75005		
		USGS 25324	UM 72251	USGS 12192		
		USGS 3864	UM 76600	USGS 14730		
		USGS 5991	USGS 8819	USGS 23917		
		USGS 7195	USGS 9156	USGS 23918		
		USNM 493913		USGS 477		
		USNM 493914		USGS 512		
		USNM 521795		USNM 488359		
		USNM 525543		YPM 30705		
		USNM 525546		YPM 30720		
		USNM 525622		YPM 30721		
		USNM 533505		YPM 30731		
		USNM 533554		YPM-PU 17418		
		USNM 538082				
		UW 6896				
		UW 7165				
Tetonius			UM 76501	UM 69108	UM 73204	
			UM 83122	UM 69124	UM 73294	

	Cf2-3	Wa0	Wa1-2	Wa3	Wa4	Wa5
Tetonius (Cont'd.)			UM 83394	UM 69204	UM 75681	
			USGS 9154	UM 69610	UM 77247	
			USGS 9225	UM 69637	UM 77248	
				UM 73951	UM 80129	
				UM 83037	UM 92574	
				USGS 15408	USGS 21664	
				USGS 1643	USGS 25360	
				USGS 3856	USGS 26934	
				USGS 495	USGS 27457	
				USGS 6634	USGS 27464	
				USGS 7198	USNM 542093	
				USGS 7205		
				USNM 487864		
				USNM 527712		
				USNM 527713		
				USNM 533455		
				YPM 35016		
Tetonius-Pseudotetonius				USGS 15407	USGS 21729	
				USGS 3840	USGS 27451	
				USGS 3842	USGS 3876 (2)	
				USGS 3843	USGS 510	
				USGS 3879	USGS 9140	
				USGS 7201	USGS 9148 (2)	
				USGS 7202	USGS 9202	
				USNM 511302	UW 10212	
Tetonoides			UM 81485	UM 69197		
				UM 71513		
LEPTICTIDA						
Leptictidae						
Diacodon	UM 71232					
Palaeictops			UM 80036		UM 73130	USGS 308
			UM 80508			USNM 491876

	Cf2-3	Wa0	Wa1-2	Wa3	Wa4	Wa5
Prodiacodon		USGS 6275	USGS 2566 USGS 9311 USGS 9743	USGS 9670		
Incertae sedis					UM 73068	
PLESIADAPIFORMES						
Carpolestidae						
Carpolestes	UM 109908 UM 71004 UM 80562 UM 82615 UM 82672 UM 82673 UM 83021 UM 86544 UM 98199					
Micromomyidae						
Chalicomomys		USGS 25025				
Tinimomys			USGS 366			
Microsyopidae						
Arctodontomys	UM 83015 UM 83019		UM 64809 UM 67440 UM 68598 UM 74122 UM 76617 UM 82279	UM 85689 UM 85968	UM 66780 UM 66798	
Microsyops		USNM 540292		UM 92809 USNM 540227 USNM 540282 USNM 540301	UM 73099 UM 73140 UM 73177 UM 73197 UM 73284 UM 80137	UM 74015 UM 75637 UM 96622

	Cf2-3	Wa0	Wa1-2	Wa3	Wa4	Wa5
Microsyops (Cont'd.)					UM 80153 UM 80864	
Niptomomys		USGS 10520 USGS 25496 USGS 26546 USGS 3831 USGS 8883 USGS 8884 USGS 8887	UM 81476 UM 81478 UM 82190 USGS 27867 USGS 28475 USGS 9306 USGS 9621	UM 96341 USGS 23920 USNM 525552 USNM 527509 USNM 542099 USNM 542102	UM 74056 USNM 542014	UM 88346 USGS 6703 USNM 494958
Paromomyidae						
Ignacius	UM 115600 UM 69877 UM 88182	USNM 538360 UW 7116	UM 114794 UM 83365 UM 86538 USGS 25375 (2) USNM 493883	UM 96974 USNM 511224 USNM 525603		
Phenacolemur	UM 109684 UM 109688 UM 66908 UM 69269 UM 71023 UM 71026 UM 73402 UM 81428	USGS 25323 USGS 27394 USGS 9016 USNM 540232	UM 65773 UM 68810 UM 75313 UM 75972 UM 81492 UM 95364 USGS 25371 USGS 25379 USGS 2560 USGS 28354 USGS 9606 USNM 521598	USGS 12912 USGS 14722 USGS 2136 USGS 2347 USGS 3614 USNM 488331 USNM 488358 USNM 493867 USNM 493872 USNM 509590 USNM 511212 USNM 511220 USNM 511245 USNM 521596 USNM 533500 YPM 24429	UM 67333 UM 73042 UM 73138 USGS 12751 USGS 21728 USGS 28350 USGS 28352 USGS 3892 USGS 3901 USNM 511237	USGS 12807 USGS 21712 USGS 2349 USGS 27124 USGS 27407 USGS 9693
Picromomyidae						
Picromomys						USGS 28476

	Cf2-3	Wa0	Wa1-2	Wa3	Wa4	Wa5
Plesiadapidae						
Plesiadapis	UM 109682					
	UM 109907					
	UM 63289					
	UM 67244					
	UM 68357					
	UM 69175					
	UM 69313					
	UM 71332					
	UM 77562					
	UM 85995					
	UM 86546					
	UM 95858					
	UM 98075					
	UM 98094					
RODENTIA						
Cylindrodontidae						
Tuscahomys		USNM 540625				
		USNM 540626				
		USNM 540627				
		USNM 541961				
Paramyidae						
Acritoparamys	UM 69871	UM 82383	UM 110355	UM 71228	UM 73077	USGS 38278
	UM 71173	UM 86564	UM 46129	UM 78963	UM 77816	USGS 5295 1
	UM 71177	USGS 8873	UM 72177	USGS 38256	USNM 525117	USGS 9114
	UM 77705		UM 72865			Uncat. (2)
	UM 77716		UM 75881			
	UM 77741		UM 76626			
	UM 77752		UM 77515			
	UM 77755		UM 77800			
	UM 77797		UM 77808			
	UM 85996		UM 77810			
			UM 77813			

	Cf2-3	Wa0	Wa1-2	Wa3	Wa4	Wa5
Acritoparamys (Cont'd.)			UM 77817			
			UM 77827			
			UM 77839			
			UM 82770			
			UM 85891			
Leptotomus					USNM 495329	USNM 525128
Lophioparamys						USGS 27098
Microparamys	UM 77719	USNM 488360	UM 102476	UM 85706	UM 81390	USGS 6740
			UM 103102		UM 81392	
			UM 77785			
			UM 85624			
Notoparamys						Uncat. (1)
Paramys	UM 65120	USNM 525634	UM 65203	UM 73020	UM 115376	UM 92045
	UM 73569	USNM 540591	UM 65275	UM 78970	UM 77794	UM 96619
	UM 77727		UM 69821	UM 79227	UM 77814	UM 97093
	UM 77834		UM 76229	UM 79324	UM 77830	USGS 38292
	UM 78877		UM 76575	UM 83031	UM 77838	USGS 38298
			UM 76839	USGS 38230	UM 77840	USGS 514
			UM 77787	USGS 8074	UM 79920	USGS 8659
			UM 77823	USNM 511177	UM 79955	USNM 491852
			UM 77848	USNM 525113	UM 88099	USNM 491864
						USNM 491875
			UM 81618		USGS 13702	(2)
			UM 82270		USGS 4066	USNM 527697
			UM 85884		USGS 8355	
			USNM 525101		USGS 8362	
			USNM 525104			
Reithroparamys	UM 77742	UM 114570			UM 77853	
		USNM 525635				
Incertae sedis		UM 99626	UM 113261	USNM 511178		Uncat. (2)
			UM 98149			

	Cf2-3	Wa0	Wa1-2	Wa3	Wa4	Wa5
Sciuravidae						
Knightomys			UM 78889	USNM 525109	UM 72967 UM 77245 USNM 495274 USNM 495275	
SORICOMORPHA						
Centetodon				USNM 527505		
Leptacodon	UM 68866 UM 71661 UM 82389 UM 99032		UM 98356			
Nyctitherium	UM 92846					
Plagioctenodon	UM 71686 UM 71689		UM 75227 UM 82203 USGS 17626 USGS 2563 USGS 2574	YPM 34257		
Plagioctenoides		USGS 23805 USNM 488363	USGS 2573			
Wyonycteris	UM 68288 UM 80257		UM 80615 UM 95373	UM 83049		
Nyctitheriidae (*Incertae sedis*)		USGS 23815 USGS 8879 USNM 539487	UM 95390 USGS 2531	USNM 527513 USNM 527518 USNM 527519 USNM 527520 USNM 527521		

	Cf2-3	Wa0	Wa1-2	Wa3	Wa4	Wa5
INCERTAE SEDIS						
Plagiomenidae						
Plagiomene	UM 65472			USGS 6266	UM 66800	
				USNM 511124	UM 73227	
				USNM 521778	UM 79923	
				USNM 527689	USGS 3937	
				Uncat. (2)	USGS 3944	
					USNM 527645	
					YPM 24971	
Worlandia	UM 109708					
	UM 109777					
	UM 109797					
	UM 69601					
	UM 69602					
	UM 71042					

APPENDIX D

REFERENCES USED IN GENUS-LEVEL DESIGNATIONS OF BIGHORN BASIN SPECIMENS.

Taxon	References
Apatotheria	4,7,8
Didelphimorphia	4,5,6,12,17,30
Didelphodonta	30
Erinaceomorpha	4,6,7
Leptictida	4,6,7,23
Dermoptera	1,5,6
Plesiadapiformes	2,4,6,9,10,15,20,22,27,30
Rodentia	6,12,13,25
Euprimates	3,11,12,14,16,17,18,19,21,24,26,28,29,30

[1]Rose (1973), [2]Bown and Rose (1976), [3]Gingerich and Simons (1977), [4]Bown (1979), [5]Bown and Rose (1979), [6]Rose (1981), [7]Bown and Schankler (1982), [8]Gingerich (1982), [9]Rose and Bown (1982), [10]Gunnell (1985), [11]Bown and Rose (1987), [12]Gingerich (1989), [13]Ivy (1990), [14]Bown and Rose (1991), [15]Rose et al. (1993), [16]Gingerich (1993), [17]Bown et al. (1994), [18]Gingerich (1995), [19]Rose (1995), [20]Rose and Bown (1996), [21]O'Leary (1997), [22]Bloch and Gingerich (1998), [23]Rose (2001), [24]Strait (2001), [25]Rose and Chinnery (2004), [26]Smith et al. (2006), [27]Silcox et al. (2008), [28]Tornow (2008), [29]Rose et al. (2011), [30]Rose et al. (2012)

APPENDIX E

REFERENCES FROM WHICH DIETARY DATA WERE COLLECTED FOR THE BALTA, PERU SAMPLE.

Species	References
CHIROPTERA	
Emballonuridae	
Rhynchonycteris naso	3,7,8,9,11,13,16,42,46,51
Saccopteryx bilineata	2,3,8,9,13,16,17,26,28,30,34,36,42,46
Saccopteryx leptura	2,3,7,8,16,17,21,26,28,30,34,36,42,51
Molossidae	
Molossops abrasus	2,3,11,24,28,36
Molossops greenhalli	2,3,11,28,36
Molossus molossus	3,7,9,11,14,24,30,34,42,51
Noctilionidae	
Noctilio albiventris	3,7,8,9,11,13,14,24,30,34,36,42,51
Phyllostomidae	
Anoura caudifer	3,7,8,9,12,30,34,36
Anoura geoffroyi	3,8,9,11,12,13,17,36
Artibeus cinereus	2,3,7,8,9,12,17,19,28,34,36
Artibeus concolor	1,2,3,7,8,9,17,19,28,30,34,36,42
Artibeus literatus	1,2,3,7,8,9,11,12,14,15,16,19,23,24,26,28,30,36,42,46,51,61
Artibeus obscurus	2,3,7,8,9,16,17,19,23,28,30,36,42,46
Artibeus planirostris	3,7,8,9,17,19,27,36,42
Carollia brevicauda	2,3,7,9,11,12,16,17,28,30,36,42,46,47,51,61
Carollia castanea	3,7,9,11,12,17,26,30,36,42,46,47,51,61
Carollia perspicillata	2,3,7,9,11,12,13,14,16,17,23,24,25,26,27,28,30,34,36,42,46,47,51,52,61
Chiroderma villosum	2,3,7,9,12,16,17,26,28,30,36,42,51,61
Choeroniscus minor	2,28,36,42
Ectophylla macconnelli	2,9,13,36,42,51
Glossophaga soricina	2,3,7,9,11,12,13,14,17,23,24,26,28,30,34,35,36,42,46,51,52,61
Lonchophylla thomasi	2,3,7,8,9,17,28,30,36,42,46

Species	References
Lophostoma silvicolum	7,42
Macrophyllum macrophyllum	3,7,9,11,12,14,17,24,36,51,52,61
Micronycteris megalotis	2,3,7,8,12,13,16,17,26,28,30,36,39,42,51,61
Micronycteris nicefori	9,12,28,30,36,51
Mimon crenulatum	2,7,8,9,11,12,17,26,28,30,36,39,42,46,51,61
Phyllostomus elongatus	2,3,7,8,9,13,17,28,30,34,36,42,46
Phyllostomus hastatus	2,3,7,8,9,11,12,13,14,26,28,30,32,36,39,42,46,51,52,61
Platyrrhinus brachycephalus	3,7,8,17,30,42
Platyrrhinus helleri	3,7,8,11,12,13,16,17,26,30,42,46,51,61
Platyrrhinus infuscus	3,17,42
Sturnira lilium	2,3,7,8,9,11,12,13,14,16,17,23,24,28,30,34,36,42,46
Sturnira tildae	2,3,7,8,9,12,16,17,28,30,34,36,42
Tonatia minuta	8,9,36
Tonatia saurophila	2,7,8,9,11,17,28,36,42,61
Trachops cirrhosus	2,3,7,8,9,11,12,13,17,19,26,28,30,36,39,42,51,61
Uroderma bilobatum	2,3,7,11,12,13,16,17,23,28,30,34,36,42,46,51,61
Uroderma magnirostrum	7,11,16,17,22,23,30,36,42,46,51
Vampyressa bidens	2,3,7,8,9,16,17,28,36,42
Vampyressa pusilla	3,7,8,9,11,12,14,24,26,30,34,36,42,46,51,61
Vampyrodes caraccioli	8,7,11,12,13,16,17,26,36,42,51,61
Vespertilionidae	
Eptesicus brasiliensis	2,3,8,9,24,28,30,36,42
Eptesicus furinalis	3,9,24,36,51
Lasiurus borealis	3,9,13,14,17,36
Lasiurus ega	3,9,24,36,42
Myotis albescens	3,11,17,24,36,42,46,51

Species	References
Myotis riparius	2,3,8,17,24,28,30,36,42,46,51
Myotis simus	3,8,24,30,36,42
DIDELPHIMORPHIA	
Caluromyidae	
Caluromys lanatus	3,7,17,49,57,60,62
Didelphidae	
Didelphis marsupialis	6,7,8,11,13,38,43,49,53,56,57,59,62
Gracilianus agilis	50,62
Philander mcilhennyi	7
Philander opossum	3,6,7,8,11,38,43,53,57,59
Marmosidae	
Marmosa murina	3,6,8,13,17,38,43,49,50,62
Marmosa quichua	3,49,62
Marmosops noctivagus	8,17,50,53,62
Metachirus nudicaudatus	3,6,7,11,13,14,17,29,44,53,59,62
Micoureus demerarae	3,17,20,44,62
PRIMATES	
Callitrichidae	
Saguinus imperator	6,8,13,17,31,48,53,54,55,57,63,64,65
Cebidae	
Aotus trivirgatus	6,8,10,13,17,31,37,48,53,54,55,57,63,64,65
Callicebus moloch	6,8,10,13,14,17,31,37,48,53,54,55,63,64
Cebus albifrons	6,8,10,13,17,31,37,40,48,49,53,54,55,57,63,64,65
Pithecia monachus	6,8,10,37,40,48,53,54,64,65
Saimiri boliviensis	6,10,17,37,48,54,55,64,65

Species	References
RODENTIA	
Sciuridae	
Sciurus ignitus	3,6,8,13,53,57,58
Sciurus spadiceus	3,6,8,13,17,49,53,57,58

[1]Bernard (1997), [2]Bernard (2002), [3]Eisenberg and Redford (1989), [4]Patton et al. (2000), [5]Handley (1989), [6]Robinson and Redford (1989), [7]Gardner (2007), [8]Emmons and Feer (1997), [9]Nowak (1994), [10]Napier (1976), [11]Reid (1997), [12]Baker et al. (1977), [13]Eisenberg (1989), [14]Redford and Eisenberg (1989), [15]Marchan-Rivadeneira et al. (2012), [16]Voss and Emmons (1996), [17]IUCN (2013), [18]Geiselman et al. (2002), [19]Merritt (2010), [20]Caceres et al. (2002), [21]Noguiera et al. (2002), [22]Noguiera et al. (2003), [23]Munoz-Saba et al. (1997), [24]Lopez-Gonzalez (2004), [25]Fleming and Heithaus (1986), [26]Bonaccorso (1978), [27]Ascorra et al. (1993), [28]Bernard (2001), [29]Caceres (2004), [30]Gorchov et al. (1995), [31]Reed (1999), [32]Fleming and Eby (2003), [33]Swartz et al. (2003), [34]Speakman and Thomas (2003), [35]Simmons and Conway (2003), [36]Wilson (1973), [37]Campbell et al. (2011), [38]Charles-Dominique et al. (1981), [39]Humphrey et al. (1983), [40]Youlatos (2004), [41]Smith et al. (2003), [42]Hice et al. (2004), [43]Guillotin (1982), [44]de Carvalho et al. (1999), [45]Anapol and Lee (1994), [46]Ascorra and Wilson (1992), [47]Bonaccorso et al. (2006), [48]Rosenberger (1992), [49]Smythe (1986), [50]Pacheco and Vivar (1996), [51]Kalko et al. (1996), [52]Fleming (1988), [53]Janson and Emmons (1990), [54]Kinzey (1997), [55]Smuts et al. (1987), [56]O'Connell (1979), [57]Glanz (1982), [58]O'Connell (1982), [59]Streilein (1982), [60]Marshall (1982), [61]Giannini and Kalko (2004), [62]Nowak (2005), [63]Terborgh (1983), [64]Peres and Janson (1999), [65]Nowak (1999a,b)

APPENDIX F

REFERENCES FROM WHICH DIETARY DATA WERE COLLECTED FOR THE MINDANAO, PHILIPPINES SAMPLE.

Species	References
CHIROPTERA	
Emballonuridae	
Emballonura alecto	1,2,10,15,17,22,31
Taphozous melanopogon	1,15,22,23,26,28,29,31
Hipposideridae	
Coelops hirsutus	2,10,15,22
Hipposideros ater	1,7,15,20,29,31,33
Hipposideros cervinus	1,15,20,31,33
Hipposideros coronatus	1,15,31
Hipposideros diadema	1,6,7,9,12,15,17,18,20,31,33,34,39,40,49,56,57,60
Hipposideros obscurus	1,15,31
Megadermatidae	
Megaderma spasma	1,2,6,7,9,15,17,18,19,22,23,26,27,28,29,31,35,40,41,48,49,56,59,61
Molossidae	
Otomops formosus	15
Pteropodidae	
Acerodon jubatus	1,11,15,17,32,34
Alionycteris paucidentata	1,31
Cynopterus brachyotis	1,6,8,14,15,18,21,23,23,26,29,30,31,32,41,42,43,45,49,56
Dyacopterus rickarti	15,32
Eonycteris robusta	1,6,9,15,31,32,56
Haplonycteris fischeri	15,31,32,34
Harpyionycteris whiteheadi	1,7,8,15,17,26,31,32,37,40,42,45,56
Macroglossus minimus	1,2,6,8,9,14,15,18,19,20,22,23,26,27,28,31,32,33,42,45,49,56
Megaerops wetmorei	15
Ptenochirus jagori	1,6,8,9,15,25,31,32,40,42,45,46,49,51,56

Species	References
Pteropus hypomelanus	1,4,6,7,13,14,15,17,20,29,31,32,34,56,63
Pteropus pumilus	1,13,14,15,31,32,34,34
Pteropus speciosus	1,13,15,17,31,34
Pteropus vampyrus	1,5,6,8,11,13,15,17,21,23,25,26,28,31,32,34,48,50,55,56,58
Rousettus amplexicaudatus	1,6,7,8,14,15,17,20,21,23,25,26,28,32,40,41,42,44,45,49,56
Rhinolophus arcuatus	1,7,15,17,20,22,31,34
Rhinolophus inops	1,2,9,10,15,19,22,31,34
Rhinolophus rufus	1,2,9,10,15,19,22,31,34
Rhinolophus virgo	1,2,9,10,15,19,22,31,34
Kerivoula pellucida	15
Miniopterus australis	1,7,10,15,18,20,23,31
Miniopterus schreibersii	1,7,10,12,15,17,20,23,29,31,33,34
Miniopterus tristis	1,7,10,15,31
Myotis macrotarsus	1,6,15,31
Myotis muricola	1,15,31
Philetor brachypterus	1,15,20,31
Pipistrellus javanicus	1,7,15,31
Scotophilus kuhlii	1,7,15,23,26,28,29,31,34
DERMOPTERA	
Cynocephalidae	
Cynocephalus volans	2,6,7,8,17,19,22,23,25,27,30,31,34,54,56
LIPOTYPHLA	
Soricidae	
Crocidura beatus	2,6,8,31,42,56
PRIMATES	
Tarsiidae	
Tarsius syrichta	2,3,6,7,16,17,24,25,47,53,56,62

Species	References
RODENTIA	
Sciuridae	
Exilisciurus concinnus	8,31
Petinomys crinitus	31,38
Sundasciurus philippinensis	31
SCANDENTIA	
Tupaiidae	
Urogale everetti	2,6,8,17,22,31,34,52,57

[1]Nowak (1994), [2]Feldhamer et al. (2007), [3]Dagosto et al. (2003), [4]Jones and Kunz (2000), [5]Kunz and Jones (2000), [6]Esselstyn et al. (2004), [7]IUCN (2013), [8]Heaney et al. (2006), [9]Ingle and Heaney (1992), [10]Srinivasulu et al. (2010), [11]Stier and Mildenstein (2005), [12]Evans (2003), [13]Dumont (2003), [14]Speakman and Thomas (2003), [15]Wilson (1973), [16]Smuts et al. (1987), [17]Rabor (1986), [18]Flannery (1995), [19]Harrison (1966), [20]Bonaccorso (1998), [21]Cranbook (1969), [22]Corbet and Hill (1992), [23]Lekagul and McNeely (1977), [24]Nowak (1999b), [25]Rabor (1977), [26]Francis (2008), [27]Wischusen et al. (1992), [28]Bennett et al. (1997), [29]Bates and Harrison (1997), [30]Wischusen et al. (1994), [31]Nowak (1999a), [32]Mickleburgh et al. (1992), [33]Strahan (1995), [34]Hutchins et al. (2003), [35]Ferrarezzi and Gimenez (1996), [36]Balete et al. (2008), [37]Heaney (1984), [38]Heaney and Tabaranza (2006a), [39]Heaney and Tabaranza (2006b), [40]Heaney et al. (1999), [41]Heaney et al. (1991), [42]Heaney et al. (1989), [43]Heideman (1989), [44]Heideman and Utzurrum (2003), [45]Heideman and Heaney (1989), [46]Heidemen and Powell (1998), [47]Hoogstraal (1951), [48]Lawrence (1939), [49]Lepiten (1995), [50]Mildenstein et al. (2005), [51]Mudar and Allen (1986), [52]Musser and Heaney (1992), [53]Neri-Arboleda and Arboleda (2002), [54]Wischusen and Richmond (1989), [55]Rabor (1955), [56]Rickart et al. (1993), [57]Sanborn (1952), [58]Sanborn (1953), [59]Sedlock (2001), [60]Sedlock et al. (2008), [61]Taylor (1934), [62]Thomas (1898), [63]Utzurrum (1992)

APPENDIX G

SAS CODE FOR THE MODIFIED MANOVA PAIRWISE COMPARISONS.

The example below is for the comparison of two fossil groups. The imported file has the following columns: taxonomic group(s), time interval, eigenvectors from principal component analysis. “Taxon_level” references columns of the import file that pertain to different hierarchical taxonomic levels such that a specimen is assigned to a species, genus, family, order, etc. This allows analyses using variable taxonomic groupings. “Taxon1” and “taxon2” are the groups to be compared in the analysis (e.g., taxon1=Carpolestidae, taxon2=Adapidae). In this analysis, “time_interval”s correspond to the time intervals illustrated in Fig. 1.1. “b” is the number of iterations of the randomization procedure. The following code includes six principal components but can easily be modified for fewer or greater principal components by deletion or insertion of “pc”s. The last line of the code provides examples of the variable values included. The output file provides the *F*-statistic and associated *p*-value for the comparison.

```
%macro distance (taxon1, taxon2, taxon_level1, taxon_level2, time_interval1, time_interval2,
file, b);
data data2;
set data1;
if ((&taxon_level1 eq &taxon1) and (time_interval eq &time_interval1)) then do;
group = 1;
end;
if ((&taxon_level2 eq &taxon2) and (time_interval eq &time_interval2)) then do;
group = 2;
end;
if group = '.' then delete;
run;

/*Both groups*/
data data3;
set data2 end = eof;
count+1;
if eof then call symput ("nobs",count);
run;

data data4;
set data3;
drop pc1 pc2 pc3 pc4 pc5 pc6;
%do i = 1 %to &nobs;
retain pc1-pc1&i pc2-pc2&i pc3-pc3&i pc4-pc4&i pc5-pc5&i pc6-pc6&i;
if _N_ eq &i then do;
pc1&i = pc1;
pc2&i = pc2;
pc3&i = pc3;
pc4&i = pc4;
pc5&i = pc5;
pc6&i = pc6;
end;
%end;
if _N_ ne &nobs then delete;
run;

data data5;
```

```
set data4;
%let nobs2 = %eval(&nobs - 1);
%do i = 1 %to &nobs2;
%let i2 = %eval(&i + 1);
%do i3 = &i2 %to &nobs;
interdist&i3 = (pc1&i - pc1&i3)**2 + (pc2&i - pc2&i3)**2 + (pc3&i - pc3&i3)**2 + (pc4&i -
pc4&i3)**2 + (pc5&i - pc5&i3)**2 + (pc6&i- pc6&i3)**2;
%end;
inter_dist&i = sum(of interdist&i2-interdist&i3);
%end;
run;

data data6;
set data5;
%let i = &nobs;
interdist_final_sum = sum(of inter_dist1-inter_dist&i);
interdist = interdist_final_sum/&nobs;
run;

/*Group 1*/
data group1;
set data2;
if group ne 1 then delete;
run;

data nobs1;
set group1 end = eof;
count+1;
if eof then call symput ("nobs_gr1",count);
run;

data group1_2;
set group1;
drop pc1 pc2 pc3 pc4 pc5 pc6;
%do i = 1 %to &nobs_gr1;
retain pc1-pc1&i pc2-pc2&i pc3-pc3&i pc4-pc4&i pc5-pc5&i pc6-pc6&i;
if _N_ eq &i then do;
pc1&i = pc1;
pc2&i = pc2;
pc3&i = pc3;
pc4&i = pc4;
pc5&i = pc5;
pc6&i = pc6;
end;
%end;
if _N_ ne &nobs_gr1 then delete;
run;

data group1_3;
set group1_2;
```

```
%let nobs2_gr1 = %eval(&nobs_gr1 - 1);
%do i = 1 %to &nobs2_gr1;
%let i2 = %eval(&i + 1);
%do i3 = &i2 %to &nobs_gr1;
interdist&i3 = (pc1&i - pc1&i3)**2 + (pc2&i - pc2&i3)**2 + (pc3&i - pc3&i3)**2 + (pc4&i -
pc4&i3)**2 + (pc5&i - pc5&i3)**2 + (pc6&i - pc6&i3)**2;
%end;
inter_dist&i = sum(of interdist&i2-interdist&i3);
%end;
run;

data group1_4;
set group1_3;
%let i = &nobs_gr1;
interdist_final_sum = sum(of inter_dist1-inter_dist&i);
interdist = interdist_final_sum/&nobs_gr1;
run;

/*Group 2*/
data group2;
set data2;
if group ne 2 then delete;
run;

data nobs2;
set group2 end = eof;
count+1;
if eof then call symput ("nobs_gr2",count);
run;

data group2_2;
set group2;
drop pc1 pc2 pc3 pc4 pc5 pc6;
%do i = 1 %to &nobs_gr2;
retain pc1-pc1&i pc2-pc2&i pc3-pc3&i pc4-pc4&i pc5-pc5&i pc6-pc6&i;
if _N_ eq &i then do;
pc1&i = pc1;
pc2&i = pc2;
pc3&i = pc3;
pc4&i = pc4;
pc5&i = pc5;
pc6&i = pc6;
end;
%end;
if _N_ ne &nobs_gr2 then delete;
run;

data group2_3;
set group2_2;
%let nobs2_gr2 = %eval(&nobs_gr2 - 1);
```

```
%do i = 1 %to &nobs2_gr2;
%let i2 = %eval(&i + 1);
%do i3 = &i2 %to &nobs_gr2;
interdist&i3 = (pc1&i - pc1&i3)**2 + (pc2&i - pc2&i3)**2 + (pc3&i - pc3&i3)**2 + (pc4&i -
pc4&i3)**2 + (pc5&i - pc5&i3)**2 + (pc6&i - pc6&i3)**2;
%end;
inter_dist&i = sum(of interdist&i2-interdist&i3);
%end;
run;

data group2_4;
set group2_3;
%let i = &nobs_gr2;
interdist_final_sum = sum(of inter_dist1-inter_dist&i);
interdist = interdist_final_sum/&nobs_gr2;
run;

/*F Statistic*/
data fstat;
set data6 group1_4 group2_4;
keep interdist;
run;

proc transpose data = fstat out = fstat2;
run;

data fstat3;
set fstat2;
fstat_orig = (col1-(col2+col3))/((col2+col3)/(&nobs-2));
run;

/*Randomization*/
%do i4 = 1 %to &b;
data permutation;
set data2;
select = rannor(-1);
run;

proc sort data = permutation;
by select;
run;

data random;
set permutation end = eof;
count+1;
if eof then call symput ("nobs",count);
run;

data random2;
set random;
```

```
drop pc1 pc2 pc3 pc4 pc5 pc6;
%do i = 1 %to &nobs;
retain pc1-pc1&i pc2-pc2&i pc3-pc3&i pc4-pc4&i pc5-pc5&i pc6-pc6&i;
if _N_ eq &i then do;
pc1&i = pc1;
pc2&i = pc2;
pc3&i = pc3;
pc4&i = pc4;
pc5&i = pc5;
pc6&i = pc6;
end;
%end;
if _N_ ne &nobs then delete;
run;

data random3;
set random2;
%let nobs2 = %eval(&nobs - 1);
%do i = 1 %to &nobs2;
%let i2 = %eval(&i + 1);
%do i3 = &i2 %to &nobs;
interdist&i3 = (pc1&i - pc1&i3)**2 + (pc2&i - pc2&i3)**2 + (pc3&i - pc3&i3)**2 + (pc4&i -
pc4&i3)**2 + (pc5&i - pc5&i3)**2 +
(pc6&i - pc6&i3)**2;
%end;
inter_dist&i = sum(of interdist&i2-interdist&i3);
%end;
run;

data random4;
set random3;
%let i = &nobs;
interdist_final_sum = sum(of inter_dist1-inter_dist&i);
interdist = interdist_final_sum/&nobs;
run;

data assign;
set permutation;
if _N_ le &nobs_gr1 then group = 1;
else group = 2;
run;

/*Group 1 Random*/
data group1;
set assign;
if group ne 1 then delete;
run;

data group1_2;
set group1;
```

```
drop pc1 pc2 pc3 pc4 pc5 pc6;
%do i = 1 %to &nobs_gr1;
retain pc1-pc1&i pc2-pc2&i pc3-pc3&i pc4-pc4&i pc5-pc5&i pc6-pc6&i;
if _N_ eq &i then do;
pc1&i = pc1;
pc2&i = pc2;
pc3&i = pc3;
pc4&i = pc4;
pc5&i = pc5;
pc6&i = pc6;
end;
%end;
if _N_ ne &nobs_gr1 then delete;
run;

data group1_3;
set group1_2;
%let nobs2_gr1 = %eval(&nobs_gr1 - 1);
%do i = 1 %to &nobs2_gr1;
%let i2 = %eval(&i + 1);
%do i3 = &i2 %to &nobs_gr1;
interdist&i3 = (pc1&i - pc1&i3)**2 + (pc2&i - pc2&i3)**2 + (pc3&i - pc3&i3)**2 + (pc4&i -
pc4&i3)**2 + (pc5&i - pc5&i3)**2 + (pc6&i - pc6&i3)**2;
%end;
inter_dist&i = sum(of interdist&i2-interdist&i3);
%end;
run;

data group1_4;
set group1_3;
%let i = &nobs_gr1;
interdist_final_sum = sum(of inter_dist1-inter_dist&i);
interdist = interdist_final_sum/&nobs_gr1;
run;

/*Group 2 Random*/
data group2;
set assign;
if group ne 2 then delete;
run;

data group2_2;
set group2;
drop pc1 pc2 pc3 pc4 pc5 pc6;
%do i = 1 %to &nobs_gr2;
retain pc1-pc1&i pc2-pc2&i pc3-pc3&i pc4-pc4&i pc5-pc5&i pc6-pc6&i;
if _N_ eq &i then do;
pc1&i = pc1;
pc2&i = pc2;
pc3&i = pc3;
```

```
pc4&i = pc4;
pc5&i = pc5;
pc6&i = pc6;
end;
%end;
if _N_ ne &nobs_gr2 then delete;
run;

data group2_3;
set group2_2;
%let nobs2_gr2 = %eval(&nobs_gr2 - 1);
%do i = 1 %to &nobs2_gr2;
%let i2 = %eval(&i + 1);
%do i3 = &i2 %to &nobs_gr2;
interdist&i3 = (pc1&i - pc1&i3)**2 + (pc2&i - pc2&i3)**2 + (pc3&i - pc3&i3)**2 + (pc4&i -
pc4&i3)**2 + (pc5&i - pc5&i3)**2 + (pc6&i - pc6&i3)**2;
%end;
inter_dist&i = sum(of interdist&i2-interdist&i3);
%end;
run;

data group2_4;
set group2_3;
%let i = &nobs_gr2;
interdist_final_sum = sum(of inter_dist1-inter_dist&i);
interdist = interdist_final_sum/&nobs_gr2;
run;

/*F Statistic Random*/
data fstat_ran;
set data6 group1_4 group2_4;
keep interdist;
run;

proc transpose data = fstat_ran out = fstat2_ran;
run;

data fstat3_ran;
set fstat2_ran;
fstat_ran = (col1-(col2+col3))/((col2+col3)/(&nobs-2));
run;

data write_difference;
set fstat3_ran;
file 'fisherout.txt' mod;
put @1 fstat_ran 6.4;
run;

%end;
```

```
data asl;
infile 'fisherout.txt';
input @1 fstat_ran 6.4;
run;

data asl_perm;
merge asl fstat3
end = last;
retain fstat_orig2 count_n;
drop _name_ col1 col2 col3;
if _N_ eq 1 then do;
fstat_orig2 = fstat_orig;
count_n = 0;
end;
if fstat_ran ge fstat_orig2 then count_n = count_n + 1;
if last then do;
p_value = count_n / &b;
output;
end;
run;

data p_value;
set asl_perm;
set fstat3;
file &file;
put @1 p_value 6.4
@20 fstat_orig 6.4;
run;

filename newlog 'fisher.log';
proc printto log = newlog;
run;

%mend distance;

%distance ('Tetonius-Pseudotetonius', 'Paramys', genus, genus, 'Wa4', 'Wa4', 'Wa4Tetonius-
Pseudotetonius_Wa4Paramys.txt', 1000)
```