

Hominin Paleoecology and Cervid Ecomorphology

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By

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Dedication

This dissertation is dedicated to my mother, Glenda Curran, whose constant friendship, hope, encouragement, and strength has always made burdens easier to bear.

Abstract

Homo erectus (sensu lato) was a remarkable hominin in that it was the first hominin to have a biogeographic distribution throughout the Old World. While there are many hypotheses regarding why *Homo erectus* dispersed into Eurasia when no other hominin before had, this dissertation focused on those hypotheses concerning extrinsic environmental influences. There were four main goals of this study: 1) to establish habitat reconstruction methods using ecomorphology for the family Cervidae (deer and relatives), 2) to introduce geometric morphometrics to studies of ecomorphology in paleoanthropology, 3) to expand ecomorphological methods that can be conducted upon incomplete bones, and 4) to apply the methods introduced here to four Eurasian fossil sites.

Ecomorphological methods have been established for the Bovidae, but methods for Cervidae, often the most abundant taxon in Eurasian paleoanthropological assemblages, are lacking. Cervid morphology as it relates to adaptations to habitats was analyzed here for four skeletal features using 3D geometric morphometrics (GM). GM was particularly suited to this study because it allowed for quantification of morphology that previously had been evaluated qualitatively. Further, shape variation associated with different habitats and substrates was visualized, allowing for recognition of subtle variations in morphology.

Two joints surfaces of extant cervid femora and tibiae, in addition to the entire calcaneus and the plantar morphology of the third phalanx, were analyzed here using canonical variates analysis. Morphology of the calcaneus was found to vary with habitat along a continuum from open to closed vegetational structure. The femoral and tibial

joint morphology was more discreet in variation, having closed and non-closed variants. Plantar morphology of the third phalanx was found to reflect substrate type and varied on a continuum from more dry to more wet substrates.

The methods introduced here were applied to four Plio-Pleistocene fossil sites. Though only one of the four sites ('Ubeidiya, Israel) contained hominin remains, all four were reconstructed to have been open to intermediate open habitats. These reconstructions are broadly similar to contemporaneous African and Eurasian hominin sites, and thus, habitat type did not preclude hominin occupation of Valea Graunceanului (Romania), and St. Vallier and Senèze (France).

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Chapter 1: Introduction

Accurate reconstructions of paleoenvironmental conditions are essential for building and testing hypotheses concerning human evolution since so many of the pressures of natural selection that shape evolution are environmentally controlled. A firm understanding of environmental conditions is necessary for addressing big questions such as the origins of bipedality, the role of hunting in hominin lifeways, and dispersals from Africa. This dissertation introduces new methods for reconstructing the habitats in which hominins lived. The question of how the first hominins dispersed from Africa into Eurasia is used here to frame and illustrate how the methods introduced here can be employed to better understand the ecological context of human evolution.

First appearing at the Plio-Pleistocene boundary, a time period marked by drastic climatic oscillations due to glacial cycling, *Homo erectus* rapidly dispersed throughout Africa and across Eurasia. What allowed *Homo erectus* to disperse so expansively when no other hominin had before? Was there something intrinsic to *Homo erectus* that provided the capacity for long-distance dispersal? Or, did extrinsic forces provide the impetus necessary for dispersal (Tappen 2007, 2008)? Intrinsic characteristics of *Homo erectus* that are proposed to have catalyzed its dispersal include increased body size and encephalization (Antón & Swisher 2004), homebase expansion (Antón *et al.* 2002), and increased carnivory (Shipman & Walker 1989, Foley 2001). Hypothesized extrinsic influences primarily relate to how climatic and environmental conditions impact dispersal, such as whether *Homo erectus* dispersed from Africa as a part of normal mammalian dispersals (Tchernov 1992c, Turner 1992) at the Plio-Pleistocene boundary perhaps due to a faunal turn-over pulse (Vrba 1995a, 1999) or whether *Homo erectus* had

evolved to be a habitat versatelist adapted to changing environmental conditions and could occupy a wide range of habitats (Potts 1998, 2001, 2007). Though it is understood that intrinsic and extrinsic factors are not truly dichotomous, since these factors influence each other, it is illustrative to examine aspects of each factor in order to understand their impacts on the system as a whole. This dissertation focuses on new evidence that can be used to address how much influence extrinsic (environmental) factors may have had on the dispersal of hominins from Africa by providing new proxies for paleohabitat reconstruction.

Paleoenvironments are reconstructed using several different proxies, each one of which can address specific aspects of the paleoenvironment. No single proxy can reconstruct all the ecological parameters of a site and thus several lines of evidence should be used in concert (such as stable isotopes, palynology, geomorphology, and faunal studies). Faunal remains are used in taxon-based reconstruction methods, community studies, and ecomorphological analyses. Taxon-based methods are founded on connections drawn between fossil taxa and their extant descendants, and assume behavioral stasis across time and space. Community studies (Reed 1997, 1998, 2002, 2008; Fleagle & Reed 1996; Kovarovic *et al.* 2002; Mendoza *et al.* 2005; Su & Harrison 2007) examine the mammalian compositions of site assemblages and compare them to compositions from modern habitats, using either taxon-based comparisons or ecomorphological analyses. Ecomorphology (as it is defined here) examines the functional morphology of organisms as it relates to adaptations to habitats, though in paleoanthropological studies, the main use of non-primate ecomorphological analysis is for habitat reconstructions. Several studies (Kappelman 1988, 1991, Plummer & Bishop

1994, Kappelman *et al.* 1997, Scott *et al.* 1999, Vrba & DeGusta 2003, 2005, Weinard 2007, Andrews & Kovorovic 2007, Plummer *et al.* 2008) have been performed on the ecomorphology of the family Bovidae (antelope and relatives), as bovids are generally the dominant taxa found in African paleoanthropological sites. However, in Eurasian paleoanthropological sites, the family Cervidae (deer and relatives) is usually the dominant taxon. This study introduces methods for habitat reconstructions of Eurasian hominin sites using cervid ecomorphology.

Ecomorphological analysis has several advantages. It does not depend on ancestor-descendant relationships (taxonomic uniformitarianism) for reconstructions. Instead, ecomorphological reconstructions are made using comparisons to groups of organisms that share similar adaptations. Though constrained to a certain extent by phylogeny, organisms in similar habitats often converge on similar morphological adaptations. Using specific functional hypotheses regarding how morphology reflects habitat, connections between shape and habitat can be extended to fossil specimens, even if they have no extant relatives. Further, ecomorphological studies are not dependent upon taxonomic identification of specimens to genus or species, which is often difficult with fossil specimens, especially post-cranial elements, and is subject to revision over time. Specimens need only to be identified to the taxonomic level that is the subject of the analysis, such as order or family, and these gross identifications are typically straightforward. Such specimens contribute little information to taxon-based methods but are easily incorporated into ecomorphological studies. Finally, ecomorphological studies of whole bones generally perform better than studies of incomplete bones (for example, only the proximal or distal portions, see Table 3-1). The methods introduced here are

designed to be conducted on specific features of skeletal elements, and thus whole bones are not necessary.

Though ecomorphological methods do offer an improved method for the utilization of mammalian remains in fossil assemblages for habitat reconstructions, they do have some limitations, which need to be explicitly elucidated. While ecomorphological analyses do not utilize taxonomic uniformitarianism, they do require that extant species be assigned to specific habitat types. This may be problematic in that many species make use of several habitat types, yet the statistics employed in ecomorphological methods (discriminant analysis) require each specimen to be assigned to a habitat type. A possible solution to this issue is to create a continuous variable along which specimens can be placed from closed to open habitats, such as Scott's (2004) Habitat Score (as described in Chapter 6).

Ecomorphological studies on bovid post-cranial remains (Kappelman 1988, 1991, Plummer & Bishop 1994, Kappelman *et al.* 1997, Scott *et al.* 1999, Vrba & DeGusta 2003, 2005, Weinard 2007, Andrews & Kovorovic 2007, Plummer *et al.* 2008) have been conducted on linear measurements across several skeletal elements. While linear measurements are easy to evaluate statistically, they are limited in their descriptive power because they do not maintain the position of the measurements relative to one another in space (Rohlf 2000). Though the goal of ecomorphological studies in paleoanthropology is to reconstruct habitats, information about the interrelationships of variables is valuable because it can better illustrate *how* variations in morphology are related to adaptations to habitats, and demonstrating how morphology varies with habitat provides deeper insight

into functional morphology. This study addresses this issue by quantifying morphology with geometric morphometrics methods.

Geometric morphometrics (GM) provides a better quantification of shape than linear measurements because it analyzes a region of interest as a whole unit. Data are collected as three-dimensional coordinates from across a region of interest and differences in positions of those coordinates across all specimens are analyzed. All geometric information about the relationships of the coordinates relative to each other is maintained (Zelditch *et al.* 2004). While GM analysis uses the same statistical tools as other multivariate studies, it has a further advantage in that differences in morphology can be visualized. In these ways, i.e. the analysis of morphology as a whole, the maintenance of coordinate interrelationships, and visualizations of morphological variability, GM is an improvement for analyses of ecomorphology.

Goals of this study

There are four main goals of this dissertation: 1) to establish ecomorphological methods for the family Cervidae, 2) to introduce geometric morphometrics to studies of ecomorphology in paleoanthropology, 3) to expand ecomorphological methods that can be conducted upon incomplete bones, and 4) to apply the methods introduced here to four Eurasian fossil sites.

The overarching theme of this study is the development of methods for using cervid skeletal remains as proxies for habitat reconstructions. Previous studies of cervid morphological variation with regard to ecological adaptation were either not explicitly ecomorphological (e.g. Scott 1987, which was a study of cervid post-cranial allometry) or included only a few cervid species (Köhler 1993, Kovarovic & Andrews 2007). No study

has examined all of Cervidae within an ecomorphological context. Thus, the methods introduced here expand the utility of cervid remains from fossil assemblages, which is especially important in Eurasian sites where Cervidae is often the dominant taxon. Adding cervids to the growing list of habitat proxies will help researchers to construct a more comprehensive understanding of Eurasia Plio-Pleistocene habitats and hominin sites.

This study also presents methods to improve the way ecomorphological studies are conducted. Geometric morphometrics provides a method of analysis that is rigorously quantitative yet also provides visualizations of variation in morphology. Quantitative methods allow for the categorization of cervid specimens into habitat types (or along a continuum). Visualizations of morphological variation are important to understand the direction of variation and to generate further hypotheses regarding how the variation is adaptive. Such endeavors deepen our understanding of functional morphology and allow for better hypothesis building and testing.

Ecomorphological analyses of whole skeletal elements have produced better results than those analyses conducted on just proximal or distal elements (Plummer & Bishop 1994, Kappelman *et al.* 1997, Scott *et al.* 1999). However, whole bones are the exception rather than the rule in fossil assemblages. By providing new methods that can be used on partial remains, this study will greatly enhance our ability to characterize habitats at important paleoanthropological sites.

Using the methods introduced here, habitats for four Eurasian sites are reconstructed. Three of these sites (Valea Graunceanului, Romania; St. Vallier, France; and Senèze, France) date to the Plio-Pleistocene boundary, but do not contain reliable

evidence of hominin occupation. The fourth site, ‘Ubeidiya, Israel, dates to approximately 1.4 Ma and contains *Homo* sp. remains as well as thousands of stone tools. Since all four sites contain several species of cervids, ecomorphological analysis of the cervid remains offers a unique perspective into the paleoecology of each of these sites.

Overview of this study

This dissertation begins in Chapter 2 with an illustration of the importance of paleoenvironmental reconstructions to the study of human evolution by reviewing several hypotheses regarding how *Homo erectus* became the first hominin to disperse through out the Old World. The second half of Chapter 2 reviews the paleohabitat reconstructions for Plio-Pleistocene Eurasian hominin sites in order to explore the range of habitats in which *Homo erectus* lived and to provide the context to which the sites included in this dissertation can be compared. Chapter 3 provides a review of bovid ecomorphological studies that inspired this research and discusses the advantages and limitations of ecomorphological methods in general. Possible solutions to the limitations of ecomorphological studies are discussed. Chapter 4 places the family Cervidae within an evolutionary context and reviews the ecology and behavior of extant species. Chapter 5 describes the selection criteria for the extant cervid specimens in this study and provides brief descriptions of the sites from which the fossil specimens included in this study are derived. Each of the four morphological units of analysis (the calcaneus, the medial margin of the patellar surface on the femur, the superior lateral condylar margin of the tibia, and the margin of the plantar surface of the 3rd phalanx) are discussed in terms of their functional significance and predictions of how their morphology varies with adaptations to specific habitats. Chapter 6 provides a description of analytical methods

used in this study, starting with a brief overview of geometric morphometric methodology and two multivariate analytical methods: principal components analysis and canonical variates analysis (and the formulation of the Habitat Score, which is based on the latter). The four habitat types used here are defined and compared to the habitat categories of previous studies. Several confounding variables are discussed, as are the analyses that were employed to test for their effects on the morphologies examined here. Chapter 7 provides the results for the analyses of the extant cervid sample and Chapter 8 provides results for the fossil samples and habitat reconstructions for each of the four sites. This dissertation concludes in Chapter 9 with a discussion of the results found here and suggestions for further research.

Chapter 2: Hominin dispersal into Eurasia

Introduction

Perhaps one of the most intriguing aspects of *Homo erectus*'s natural history is its biogeographical distribution. To date, it was the first hominin to be found in both Africa and Eurasia and its appearance in Eurasia occurred shortly after its first occurrence in the fossil record in Africa. *Homo erectus (sensu lato)* is first found at Koobi Fora, Kenya, dating to 1.88 million years (McDougall 1985, p. 159) and quickly developed a large biogeographical distribution, from Mojokerto in Java, by 1.81 Ma (Swisher *et al.* 1994) to Dmanisi in Georgia at 1.77 Ma (Gabunia *et al.* 2000a, Lordkipanidze *et al.* 2007). Several other hominin species existed contemporaneously with *Homo erectus*, including members of the same genus, *Homo habilis* and *H. rudolfensis*, and two robust australopiths, *Paranthropus boisei* in eastern Africa and *P. robustus*, in southern Africa. Why was *Homo erectus* the only hominin amongst them to disperse from the African continent? Does this dispersal represent a significant expansion of habitats to which *Homo erectus* was already adapted (Dennell 2003), or do the sites outside of Africa represent different habitats to which *Homo erectus* had to adapt? What factors limited the biogeographical distribution of *Homo erectus*? Were there significant environmental differences between contemporaneous Eurasian sites that contain evidence of hominin occupation and those that do not?

This chapter will explore these questions by reviewing hypotheses regarding how environments and climate affect the evolution and dispersal of species. The Plio-Pleistocene paleohabitats in which hominin remains and lithics are found will be briefly reviewed to elucidate the range of ecological conditions *Homo* could exploit and to

provide an ecological context to which the sites included in this dissertation can be compared. Only one site ('Ubeidiya, Israel) of the four analyzed in this dissertation contains hominin remains, however, the three other sites (Valea Graunceanului, Romania and St. Vallier and Senèze, France) provide Plio-Pleistocene examples of Eurasian sites *not* inhabited by hominins and may be illustrative of the limitations upon the types of habitats the earliest Eurasian hominins could occupy.

It should be noted that at several of the earliest Eurasian sites, hominin presence is represented only by archaeological remains (Xiaochangliang, Pirro Nord) or by hominin remains that are only assigned to *Homo* sp. ('Ubeidiya, Yuanmou), and thus may not be attributable to *Homo erectus*. Whether the hominins from Africa and Eurasia represent two species (*Homo ergaster* and *Homo erectus*) is also a question that is still being debated (Rightmire 1990, Wood 1994, Villmoare 2005, Terhune *et al.* 2007, Baab 2008), but for the purposes of simplicity, this study includes all African and Eurasian specimens in *Homo erectus (sensu lato)*. Specimens in the earliest site of Europe (Sima del Elefante, Atapuerca, Spain) are not recognized as *Homo erectus*, but instead are provisionally assigned to *Homo antecessor* (Carbonell *et al.* 2008) while other early European hominins are often attributed to *Homo heidelbergensis* (e.g. Gomez-Robles *et al.* 2008). Sites containing these species, which were likely the descendants of *Homo erectus*, are included in this review to further characterize the types of habitats found in Eurasia during the Pleistocene. The review of Eurasian habitats presented here focuses on the very earliest and well-documented hominin sites.

The significance of *Homo erectus*

Homo erectus represents a remarkable shift from earlier hominin species, including those attributed to the same genus (i.e. *Homo habilis* and *H. rudolfensis*) in several important ways. The average endocranial volume of early African *Homo erectus* specimens was 907 +/- 115 cm³, which is 200 cm³ larger than *Homo rudolfensis* (KNM-ER 1470) at 750 cm³ (Klein 1999, pp. 218, 276). Later Asian *Homo erectus* specimens again underwent encephalization with cranial capacities of 934 +/- 110 cm³ to 1151 +/- 99 cm³, the latter of which approaches the size of *Homo neanderthalensis* and *H. sapiens* (*ibid*, p. 276). Interestingly, an exception to this increase in encephalization in *Homo erectus* is found in the specimens from Dmanisi, which have cranial capacities in the early *Homo* range (600 to 775 cm³), though they are still more encephalized than *Homo habilis* (KNM-ER 1813) at 510 cm³ (Rightmire *et al.* 2006).

The Dmanisi hominins are also exceptional for their small body size (Gabunia *et al.* 2000b, p. 791; Lordkipanidze *et al.* 2007, p. 308) with height estimates of 144.9 to 166.2 cm and weight estimates of 40-50 kg (Lordkipanidze *et al.* 2007, p. 308). Though post-cranial remains of *Homo erectus* are rare, body size estimates on specimens from the sites of Nariokotome, Koobi Fora and Olduvai place these hominins at an average of 170 cm (Rightmire 1995, p. 486). This, again, represents a shift from earlier and even contemporaneous hominin species. The robust australopiths have stature estimates of 110-124 cm for females and 132-137 cm for males, while *Homo habilis* females averaged 125 cm and males reached an average of 157 cm (Klein 1999, p. 191). *Homo erectus* (especially WT 15000) is the first hominin to have human-like limb proportions, that is, its arms were significantly shorter than its legs (Reno *et al.* 2005). In sum, *Homo erectus*

was a dedicated terrestrial biped with human-like limb proportions and increased encephalization.

One of the most significant differences between *Homo erectus* and other previous and contemporary species of hominins was that *Homo erectus* had a biogeographic range that included not only Africa but also Eurasia. Shortly after the first appearance of *Homo erectus* at 1.88 Ma in Koobi Fora, Kenya, it is found in Mojokerto, Java at 1.81 million years (Swisher *et al.* 1994) and Dmanisi at 1.77 Ma (Lordkipanidze *et al.* 2007). By the end of the Early Pleistocene (780,000 years ago), *Homo erectus* remains and material culture are found through out eastern and southern Africa, across Europe, China, and Indonesia. What allowed *Homo erectus* to have such a large biogeographical distribution? How did this hominin disperse from the African continent when none other before had? Hypotheses put forward involve increases in body size, encephalization (Antón & Swisher 2004), a homebase expansion (Antón *et al.* 2002), and increased carnivory (Shipman & Walker 1989, Foley 2001). The goal of this chapter is to review and evaluate hypotheses relating to environmental impetuses. There are many hypotheses about how environmental factors may have influenced, perhaps even forced, the evolution and dispersal of *Homo erectus*, which is not surprising, since many of the pressures of natural selection come from the environment. While most of the following hypotheses specifically address the origin of new species, the ideas that are discussed are applicable to understanding why a population may disperse. Before turning to a discussion of the hypotheses, it will be useful to review how intercontinental dispersals may be facilitated.

Dispersal routes and mechanisms

Through out this work, “dispersal” is used to signify “a process whereby organisms are able to spread from their place of birth to another locality” (Tchernov 1992b, p. 21). Although “migration” and “dispersal” are often used interchangeably, here “migration” designates a movement of organisms that “recurs annually, with the same individuals participating in the return movement as well” (Tchernov 1992b, p. 23). Thus, the term “migration” does not suit the purposes of the questions that are being asked in this study, though it is often used in the *Homo erectus* “Out of Africa” literature.

In general, dispersal across large areas of space (and especially between continents) requires that there be corridors available through which fauna (including hominins) can disperse. Land-bridges are corridors between continents that may be semi-permanent, though more often they are intermittently available, such as at times of low sea levels during glaciation. According to Vrba’s (1995a) “Traffic Light” model of faunal exchange, not only must a land-bridge be present but the corridor must also contain a suitable habitat through which organisms can disperse. When climatic conditions become cooler, warm-adapted organisms disperse toward the equator, where it is warmer. When it begins to warm again, vegetational habitats expand to higher latitudes faster than the glacial ice melts and thus there is a brief period of time when there exists a land-bridge and climatic conditions are warm, which would facilitate the dispersal of warm-adapted species into higher latitudes. This model implies that dispersing taxa remain within habitats that are fairly homologous to their ancestral habitats. “Migration [dispersal] can not only be seen as the expansion of the geographic range of taxa, but also as the expansion of the environment where these taxa are able to survive. This means that the

values of the parameters describing the environment in this area are within the ranges that limit the niche of this taxon” (Van der Made 1992, p. 29). This statement provides a null hypothesis for this study: the habitats of Eurasian *Homo erectus* sites are broadly similar to those found in Africa.

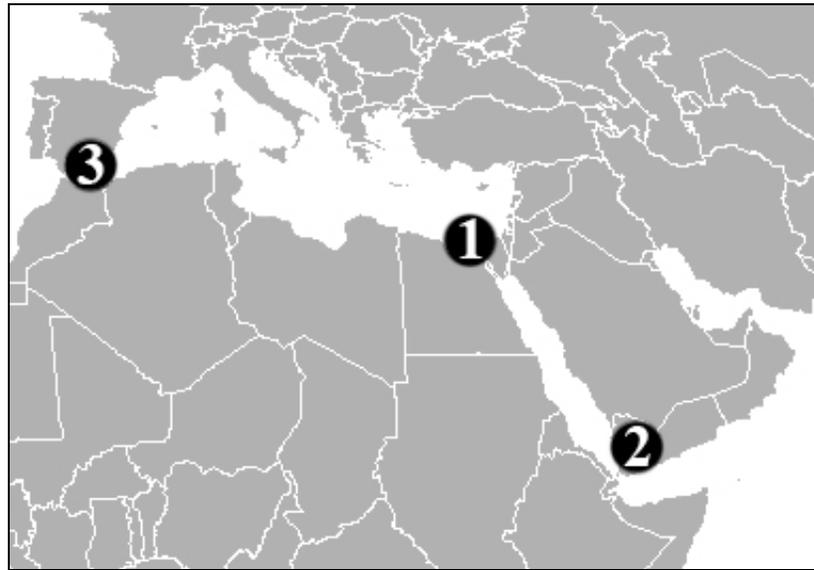


Figure 2-1: Possible dispersal routes into Eurasia from Africa. 1 = the Sinai Peninsula, 2 = Bab-el Mandab Straight, and 3 = Straight of Gibraltar.

There are three main dispersal routes out of Africa: 1) across the Sinai Peninsula and through the Levantine corridor, 2) across the Bab-el Mandab straight, and 3) across the straight of Gibraltar (see Figure 2-1). Access to Eurasia from Africa has been possible via the Sinai Peninsula (Tchernov 1992c, p. 150) since the Miocene, and is held by some researchers as the most likely dispersal route used by *Homo erectus* (Thomas 1985, Bar-Yosef 1999, Tchernov 1992c). This region, the Levantine Corridor, underwent drastic fluctuations in climatic regime with the onset of glacial cycling due to its proximity to two major bodies of water (Mediterranean Sea and Red Sea) and the Arabian Desert. Overall, however, it experienced a trend of increasing aridity (Tchernov 1992c, p. 150).

There is evidence of faunal exchanges going in both directions (i.e. south into Africa and north into Eurasia) during the Plio-Pleistocene, however, north-to-south dispersals became more rare throughout the Pleistocene, generally only occurring during colder phases (*ibid*, p. 151), as is predicted by Vrba's "Traffic Light" model (1995a).

Climatic oscillation likely affected another possible crossing point from Africa to Eurasia, the Bab-el Mandab strait, located at the south end of the Red Sea (Tchernov 1992a, p. 116). Presently, the strait is only 18 kilometers wide and has a sill, or a ridge on the sea floor, which currently lies 137 meters below the surface. A drop of 130 meters in sea level, as is estimated for the Last Glacial Maximum (Kump *et al.* 1999, p. 214) would put that sill close to sea level, though Sirocko (2003) claims that the sill would still have been 15 meters below sea level at that time. However, it would have likely been completely exposed during the Aullan event at 1.8-1.6 Ma, which caused a drop in sea levels by 200 meters (Arribas and Palmqvist 1999, p. 581). With a drop in sea level, waters in the Red Sea would have had a greater residence time and as a consequence experienced greater evaporation (Sirocko 2003, p. 813). Thus it is possible that during low sea level periods of glacial cycling of the Pleistocene there were times when the Bab-el Mandab was a land-bridge.

Currently, the Strait of Gibraltar separates Morocco and Spain by 14.5 kilometers, but this distance may have been as small as 6.5 kilometers during the Aullan event (Arribas and Palmqvist 1999, p. 581). Though it is unlikely that this region was ever a true land-bridge, crossings are currently possible using only very low-technological boats, as is evidenced by windsurfers from Tarifa, Spain being blown off course onto the shores of Morocco and crossings made by immigrants in small boats (Straus 2001, p. 91).

Artifacts attributed to *Homo erectus* are found on Flores, an island beyond the Wallace Line at 800,000 years ago (Morwood *et al.* 1998; but see Larh & Foley 2004), supporting the hypothesis that *H. erectus* was able to cross small bodies of water. Though other routes have been proposed, such as island hopping via northern Africa to islands of the Mediterranean (Arribas and Palmqvist 1999), most evidence points to one of the three above-described routes, with the crossing at the Sinai region the most likely (Bar-Yosef, 1999, p. 56).

The influence of climatic change

Climatic change is often proposed as an impetus for dispersal events as it creates shifts in environments that change the parameters of species niches. Here, again, some basic definitions are needed to clarify the usage of terms in this dissertation. “Climate” refers to the “ensemble of atmospheric conditions characteristic of a particular locality over a suitably long period ... Aspects considered include temperature, humidity, rainfall, solar radiation, cloud, wind, and atmospheric pressure” (Walker 1995, p. 205). When one speaks of “climatic change” they are referring to changes in these specific parameters, which are global in their influence. It is these parameters that influence what is found in an environment. “Environment” will be used to mean “the whole complex of climatic, edaphic, and biotic factors that act upon an organism or an ecological community and ultimately determine its form and survival” (“Environment”, Webster’s 1986, p. 760). Thus, the environment can be thought of as including climatic factors, but on the scale of organisms. “Climatic change” is often used interchangeably with “environmental change”, though climatic change is usually meant to imply large-scale, even global, change, while “environmental change” often is used to refer to more regional change.

This study will use these definitions, but will focus on more local reconstructions at the scale of habitats. Here, “habitat” will refer to “the specific set of environmental conditions under which an individual, species, or communities exists” (Brewer 1988, p. 858). “Habitat” is preferable to “environment” when reconstructing the parameters of a specific site. If one is able to look over a larger geographical area, “environment” may be more appropriate. Thus, habitats will be discussed for specific *Homo erectus* sites, environmental change will refer to change in the biotic and abiotic factors of a region and climatic change will refer to change on a global scale.

Discussions of climatic forcing of evolution or dispersal of a species are prevalent in anthropological literature. Indeed, Darwin even discussed this idea in *Origin of Species* (1859, p. 381):

“Change of climate must have had a powerful influence on migration. A region now impassable to certain organisms, from the nature of its climate, might have been a high road for migration when the climate was different... Where a sea now extends, land may at a former period have connected islands or possibly even continents together, and thus have allowed terrestrial productions to pass from one to another.”

This chapter reviews several hypotheses concerned with how environmental change influenced the evolution and dispersal of hominins into and throughout Eurasia in order to demonstrate the necessity of paleoenvironmental reconstruction for comprehensive understanding of hominin evolution and biogeography.

Climatic conditions prior to the evolution of Homo erectus

Several lines of evidence demonstrate a climatic shift to more arid conditions starting at 2.5 Ma. In East Africa, pollen records indicate that conditions were humid prior to 3.2 Ma (Bonnefille 1995) with a shift to more cool and dry adapted species

between 2.51 and 2.35 Ma (deMenocal & Bloemendal 1995). At 2.5 Ma, there was a shift from mesic (humid) to more arid conditions as recorded by oxygen isotope records (Prentice & Denton 1988). Aeolian dust records from East and West Africa show a similar pattern- from more wet and warm to cool and dry with increased seasonality and decreased precipitation, especially in East Africa (deMenocal 1995). The western Sahara desert began to develop at 2.8 Ma (Dupont and Leroy 1995, p. 291; Anton *et al.* 2002). This aridification may have been exacerbated in part by the one kilometer of tectonic uplift and rifting that East Africa experienced from 4-2 mya, creating one and then two rainshadows, and leaving East Africa very dry (deMenocal & Bloemendal 1995, Aguirre & Carbonell 2000). Mammalian evidence points to the same conclusion; there were many first appearance dates of arid-adapted bovid species from 2.7-2.5 Ma (Vrba 1995b) and micromammals indicate open conditions by 2.4 Ma (deMenocal & Bloemendal 1995). Stable carbon isotopes, pollen evidence, and $\delta^{18}\text{O}$ records all indicate a major expansion of grasslands and hot and dry conditions by 1.8 Ma, one of the most arid times the African continent has ever experienced (deMenocal & Bloemendal 1995, Bonnefille 1995, Cerling 1992). C_4 plants (tropical grasses and most sedges) increased in abundance dramatically by 1.7 Ma, with biomasses up to 60-80% (Cerling 1992). All these lines of evidence point to a true climatic change occurring in Africa starting during the Late Pliocene and Early Pliocene coincident with the first appearance of *Homo erectus*.

The Turnover Pulse Hypothesis

One of the most influential hypotheses concerning the climatic forcing of species evolution is Vrba's Turnover Pulse Hypothesis (1995a, 1999). "Turnover" is broadly defined as a concentration of first-appearance dates (FADs) and last-appearance dates

(LADs) of several lineages of organisms that correlate with climatic changes. This hypothesis specifically “posits that nearly all speciation and extinction events require initiation by climatic change that systematically concentrates these turnover events in time” (Vrba 1995b, p. 385). Environmental change forces evolution by fragmenting species’ habitats and causing vicariance. Vrba (1989, p. 29) points out that though “environmental change is *necessary* to precipitate significant evolutionary events [that] does not imply that it is *sufficient*” (italics original). Thus, climatic change and habitat fragmentation can have several outcomes other than speciation, such as dispersal or extinction. “The geographical distribution of species may respond to climatic changes by expansion, by contraction, by fragmentation, or simply by tracking habitats latitudinally” (Vrba 1995a, p. 27). Not all lineages need be affected in the same manner by a climatic change. Different species respond to different limiting parameters in their niche and change in one parameter may more drastically affect one group than another. Within (and between) lineages, those species that are more stenotopic (narrow habitat tolerance range, specialists) are more likely to experience turnover with smaller climatic changes than eurytopic (wide habitat tolerance, generalists) species (Vrba 1995a, p. 35). However, as the name of this model implies, it is predicted that several lineages undergo a “pulse” in turnovers at the time of a climatic shift (Vrba 1989, p. 30).

Vrba found that there are concentrations of FADs and LADs throughout the fossil record starting in the Miocene. The most pronounced concentration of bovid FADs is found at 2.6-2.4 Ma. There are concentrations at 2.0-1.8 Ma and again at 1.8-1.6Ma (Vrba 1989, p. 411), though these are not as pronounced as the 2.6-2.4 Ma event, which Vrba points to this as a true turnover event initiated by climatic change.

How well does the fossil record for the Hominini support the Turnover Pulse hypothesis? Vrba (1995b, p. 407) states that hominins, like bovids, show many FADs “distributed in the 2.7-1.8 Ma interval, especially between 2.7 and 2.5 Ma. These similar patterns suggest external causes, specifically that climate acted through vicariance and selection to influence speciation”.

Foley (1994) also examined the hominin (and baboon) fossil record to evaluate whether turnover pulses correlated with specific proxies for climatic change (deep sea core $\delta^{18}\text{O}$ values for temperature, stability and variability). He found that, unlike bovids, no significant correlation was found between hominin FADs and climatic change. However, hominin LADs do show significant correlations with minimum and modal temperatures. This, he states, is due to climatic change causing habitat loss and fragmentation and thus extinction (Foley 1994, p. 285). Frost (2007) found no significant turn-over pulse in cercopithecoid taxa at this time period, but instead found a fairly constant rate of species turn-over, with a general trend toward more open-adapted species. Frost also emphasized that forest fragmentation due to increasing aridity was likely to be a major component of cercopithecoid evolution (*ibid*).

In sum, the Turnover Pulse Hypothesis predicts that species’ FADs, LADs, and dispersal events should be concentrated in time corresponding to a climate change. Though a climatic shift does not necessarily guarantee a turnover event, one cannot happen without it. The fossil record should appear punctuated with many new species appearing at the same time as many are going extinct. Records from several lineages across wide geographical space should record species turnovers if a pulse has taken place. “The hypothesis predicts that patterns of speciation, extinction, and migration [dispersal]

within a biotic group should occur as nearly synchronous events in the geologic record rather than being randomly distributed through time. Further, turnover events of diverse biotic groups should occur as nearly synchronous pulses that correlate with climatically induced environmental changes determined independently from the geologic record” (Prentice & Denton 1988, pp. 385-7). The Turnover Pulse Hypothesis is significant to the study of the origin of *H. erectus* and its dispersal as this event was coincident with a turnover of bovid species around 1.8 Ma. Was *H. erectus* a product of a pulse of climatic change at the beginning of the Pleistocene? Other researchers, such as Potts (1998, 2001), suggest that instead of adapting to a single climatic change, hominins became adapted to climatic variability itself.

Variability Selection

“If climate had a role in determining hominid evolution, the most parsimonious interpretation of the available data is that it was a change in mode of subtropical climatic *variability* rather than wholesale, stepwise change in climate that prompted evolutionary responses” (deMenocal and Bloemendal 1995, p. 284).

Looking at FADs and LADs for all mammal groups in the late Pliocene Turkana Basin (Kenya and Ethiopia), Behrensmeyer *et al.* (1997) found a different pattern for the African bovids than had Vrba. While they found significant turnover between 3.0 and 1.8 Ma, they did not find the “pulse” at 2.8-2.5 Ma that Vrba had (*ibid*, p. 1591). Instead, Behrensmeyer *et al.* (1997) found a series of fluctuations in turnover. For example, in the period 2.4-2.2 Ma, 24-32% of all species experienced turnover (the former number based on minimized number of taxa, the latter on maximized) and from 2.0-1.8 Ma, the fauna experienced a turnover of 19-28% (*ibid*). While the entire time period of 3.0-2.0 Ma had a turnover rate of 41-59%, most of this change occurred between 2.5-2.0 Ma. By 1.8 Ma,

the number of FADs dropped, while LADs increased. It could be argued that each of the aforementioned events represents a “pulse”. According to the Turnover Pulse Hypothesis (Vrba 1995b), the proposed climatic change at 2.8-2.5 Ma was mainly in the direction of increasing open habitats, such as grasslands. While this is valid, it should be noted that open habitats existed before 2.8 Ma and that more closed habitats, such as woodland persisted even after 2.0 Ma (*ibid*, p. 1592). “We propose that a fluctuating but overall expansion of open habitats combined with the persistence of woodland and forest initially provided increased opportunities for mammals and led to a rise in diversity from 3.0-2.0 Ma, followed by a diversity decline as open habitats became dominant at the end of the Pliocene” (Behrensmeyer *et al.* 1997, p. 1593). Bobe and Behrensmeyer (2004, p. 416) state that it is likely that *fluctuations*, with more pronounced extremes (Feibel 2008), are more important to hominin evolution after 2.5 Ma rather than an overall change toward drier and more open habitats.

Potts (1998, 2001, 2007) points to increasing oscillation in climatic conditions, as seen in $\delta^{18}\text{O}$ isotope records and dust records, proxies for vegetative cover and rainfall, as being the driving force behind hominin evolution, with the glacial advances and retreats adding to the fluctuations (Prentice & Denton 1995, Gamble 1995). While most long-term records of climatic conditions indicate that there was an overall trend of increasing aridity and decreasing temperature, Potts states that *fluctuations* in climate during human evolution played a more important role for the selection of hominin phenotypes (and thus genotypes).

At 2.8 Ma, $\delta^{18}\text{O}$ isotope records show the start of the cooling trend that defines the Pleistocene, that is, the on-set of glaciation. As continental glaciers increased in size,

oceanic waters were sequestered into the ice sheets. This allowed for the formation of land-bridges and caused dramatic change in local vegetational regimes. The on-set of glacial cycling is not simply a step into colder temperatures, but a change toward dramatic climatic fluctuations, from glacial to interglacial time periods. “If this lineage faced inconsistency over a prolonged time, a genetic basis may be assembled underlying complex adaptations that promote versatility. These adaptations enable novel responses to the surroundings and augment the options available to the organism” (Potts 2001, p.19). A lineage can respond to climatic change in a variety of ways, such as dispersal into new areas that maintain a similar habitat or by evolving specialization to a specific resource. Under Potts’s Variability Selection Hypothesis, lineages can also adapt to climatic change by evolving “complex structures or behaviors that are designed to respond to novel and unpredictable adaptive settings” (Potts 1998, p. 85). Several adaptations in the early hominins may have been evolved in this way. Early australopiths’ positional repertoire allowed for a variety of locomotor behaviors, which, up until the evolution of *Homo* (and probably, more specifically, *Homo erectus*) included adaptations to arboreality in addition to bipedality. Encephalization has also been argued to allow for more flexible behavior (Potts 1998, p. 93), though, again, a major shift in encephalization does not occur until *Homo erectus* (Wood & Collard 1999). Beginning with early putative hominins (*Orrorin*, *Sahelanthropus*, *Ardipithecus*) at 6-7 Ma, and through the evolution of the australopiths, Potts’s proposed assemblage of a genetic basis promoting flexibility began to evolve. *Homo erectus* may represent an organism that is the product of a lineage specifically adapted to being flexible, that is, a versatelist.

The hominin lineage also shows evidence of organisms that were not versatilists. Species of *Paranthropus*, contemporaries of *Homo erectus*, show adaptations for specialization on hard vegetative matter, likely underground storage organs, as a fallback resource (Laden and Wrangham 2005, p. 493). While specialization allows an organism a competitive advantage over a versatelist in time periods when the resource the specialist is adapted to is plentiful, the versatelist has a competitive advantage when a shift in climate (and thus habitat) occurs. This is a possible explanation for why *Homo erectus*, and not *Paranthropus*, was able to disperse from the African continent. If a genetic basis for versatility had been accruing in a branch of the hominin lineage for six million years, by the time *Homo erectus* evolved, a decoupling from specific environments may have occurred (Potts 1998). Not only would *Homo erectus* persist through climatic oscillations, but it would also be able to exploit a variety of habitats. This decoupling may have been what allowed *Homo erectus* to disperse across land-bridges into Eurasia that were barriers to other species, such as the more specialized genus, *Paranthropus*.

The above review of how environmental conditions influence the evolution and dispersal of species illustrates that paleoenvironmental reconstructions are imperative to the study of human evolution. Whether the Turnover Pulse Hypothesis or the Variability Selection Hypothesis are sufficient explanations for the dispersal of hominins into Eurasia depends heavily upon accurate reconstructions of the earliest Eurasian hominin sites. The following section reviews the current understanding of the environmental conditions of the earliest Plio-Pleistocene sites.

Habitat Reconstructions of *Homo erectus* Sites

Much research has been conducted on reconstructing the environmental parameters of *Homo erectus* sites. There are many types of proxies from which paleoecological reconstructions can be made and each one records a specific aspect of the overall environment of a site. Thus, as many proxies as are available should be used to make a more comprehensive reconstruction. The geomorphology and depositional history of a site reveal information such as the former presence of lakes and streams, the deposition of glacial tills, or the existence of higher or lower sea levels. To understand the paleovegetative structure of a site, one can study plant macrofossils, palynology, and phytoliths. Isotopic studies provide insight into paleotemperatures, rainfall levels, and availability of different types of vegetation. Faunal remains can be studied to evaluate the taxonomic composition of a paleocommunity and the functional morphology of mammals demonstrates their adaptations to specific habitats.

The following is a review of paleohabitat reconstructions for selected Plio-Pleistocene hominin sites using the types of proxies mentioned above. This review starts with Koobi Fora, Kenya, which is the site with the earliest record of *Homo erectus*. It is assumed here that *Homo erectus* evolved in and dispersed from Africa, though it is recognized that some studies have hypothesized an Asian origin and origin and dispersal for Plio-Pleistocene hominins (Dennell & Roebroeks 2005, Martinon-Torres *et al.* 2007). As evidence of pre-*Homo erectus* hominin specimens from Eurasia is currently unavailable, this study will take the parsimonious view that *Homo erectus* originated in Africa. While Koobi Fora may provide a baseline for the type of habitat *Homo erectus* evolved in, but as this study is focused on Eurasian sites, and thus other African *Homo*

erectus sites are not reviewed in detail. Eurasian sites dating to 1.81-1.4 Ma are included here to illustrate the range of habitats that Eurasian hominins occupied during the Early Pleistocene.

Figure 2-2 shows the sites that will be discussed in the text and Table 2-1 is a list of all the sites reviewed here along with the paleohabitat reconstruction for each site. The sites in Figure 2-2 are numbered by the order they are discussed in the text below.

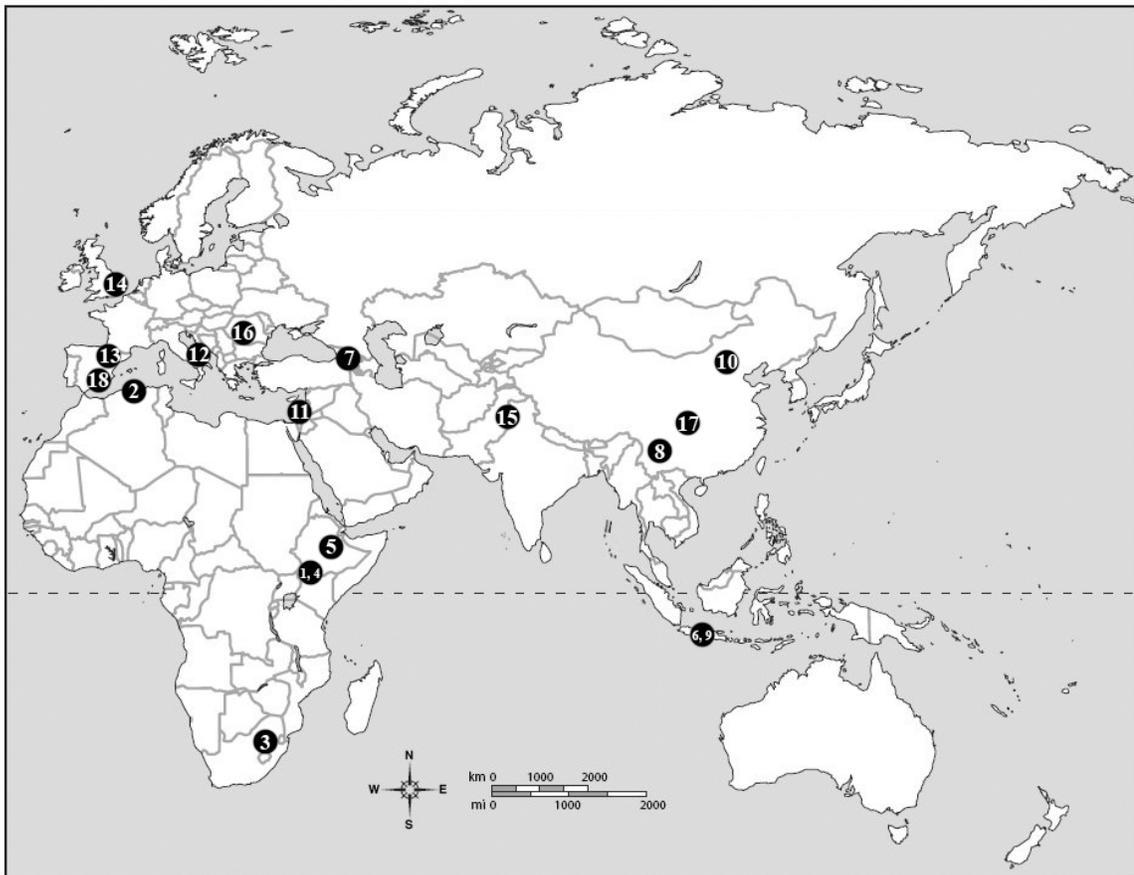


Figure 2-2 Map of the distribution of hominin sites discussed in the text. Each site is numbered in the order it appears in the text. 1=Koobi Fora, Kenya, 2=Ain Hanech, Algeria, 3=Swartkrans, South Africa, 4=Nariokotme, Kenya, 5=Gadeb, Ethiopia, 6=Mojokerto, Java, 7=Dmanisi, Georgia, 8=Yuanmou Basin, China, 9=Sangiran, Java, 10=Xiaochangliang, China, 11='Ubeidiya, Israel, 12=Pirro Nord, Italy, 13=Sima del Elefante, Atapuerca, Spain, 14=Pakefield, England, 15=Riwat, Pakistan, 16=Valea Grunceanului, Romania, 17=Longgupo, China, 18=Venta Micena, Orce, Spain

Koobi Fora, Kenya- 1.88 million years (Ma)

The earliest known representatives of *Homo erectus* are found in the Koobi Fora formation on the east side of Lake Turkana in Kenya. Many of the remains from this region were found just above the KBS Tuff, which dates to 1.88 Ma (McDougall 1985, p. 159, Rightmire 1990, p. 89). Geomorphological studies of the Koobi Fora Formation indicate that the depositional environment from 2.0- 1.88 Ma was lacustrine, followed by deltaic and fluvial deposition until 1.7 Ma (Feibel 1993, p. 69). Mammalian remains were deposited during the fluvial stage (*ibid*). The fluvial depositional environments were provided by the meandering Omo River, which, in this time period, would have supported thick gallery forests and seasonally flooded grasslands with drier thorn scrub away from the river (*ibid*, p. 67). Pedogenic carbonate isotopes indicate a woodland savanna habitat (Quinn *et al.* 2007).

Studies of the rodent community at Koobi Fora indicate that these micromammals inhabited “an arid environment with *Acacia* scrub and some riverine forest along intermittent stream channels” (Denys 1999, p. 247), a reconstruction that closely matches the geomorphological work by Feibel (1993). Work on the bovid community by Kappelman *et al.* (1997) found bovids with femoral adaptations to a wide variety of environments, though tending more towards the closed end of the spectrum (p. 250).

Other African sites

Homo erectus dispersed not only to Eurasia, but throughout Africa as well. Mode I artifacts were found in North Africa at Ain Hanech in Algeria, which date to 1.8 Ma (Sahnouni *et al.* 2002), though no hominin remains have been found. *Homo erectus* dispersed to South Africa by 1.7-1.5 Ma (Brain 1995, p. 453). These remains and

Acheulean tools were deposited in the cave site of Swartkrans during interglacial periods when the temperature was about 4-5°C higher than today (Brain 1981, p. 245; Brain 1995, pp. 456-7; Avery 1995, p. 467). The habitat surrounding Swartkrans has been reconstructed as open but with woodlands along a river (Avery 1995, p. 466; Reed 1997, pp. 306-7; Sillen *et al.* 1998, p. 2470). The most complete skeleton of *Homo erectus* (KNM-WT 15000) was found at the Nariokotome site on the west side of Lake Turkana dating to 1.53 Ma (Brown & McDougall 1993, p. 19). Nariokotome is reconstructed as a fluvial and palustrine (wetlands and swamps) system that had gallery forests along watercourses and open areas away from the Omo River (Harris & Leakey 1993, p. 58-60). “Developed” Oldowan and Acheulean tools, but no hominin remains are reported from 1.48 Ma site of Gadeb in the high Ethiopian plains located at 2300-2400 meters (Clark 1987, p. 809-10). The Gadeb artifacts were deposited in alluvial gravels and sands that resulted from the regression of the Pliocene Lake Gadeb (Williams *et al.* 1979). These sites represent a sample of the *Homo erectus* sites from Plio-Pleistocene of Africa. This review will now turn to the earliest evidence of Eurasian occupations.

Mojokerto, Java- 1.81 Ma

In 1936, a calvarium of a child (Mojokerto or Peking 1), later attributed to *Homo erectus*, was found on the Indonesian island of Java at the site of Mojokerto. Since its discovery, this specimen has caused quite a deal of controversy, specifically regarding whether the calvarium was found *in situ* or on the surface (Huffman *et al.* 2005). The current debate surrounding this fossil focuses on the dates assigned to the specimen. Swisher *et al.* (1994) dated sediment from near the original find site (Huffman 2001a) to 1.81 +/- 0.04 Ma, making it the oldest site outside of Africa. This date has been

contended for several reasons. First, the original provenience of the find is still contentious. However, Huffman *et al.* (2005) traced the chronology of the discovery via historic documents, relocated the original site and found evidence that the matrix inside the calvarium matches the matrix in the excavation (Huffman 2001a). Secondly, Langbroeks and Roebroeks (2000) question whether the samples Swisher *et al.* (1994) took for their dates can even be associated with the fossil. Huffman (2001a, p. 356) indicates that Swisher *et al.* took their samples from “the tuffaceous sandstone in the cliff below the commemorative monument at Pening”, which is near one of two previous relocations of the original site. As mentioned above, the original find site has almost certainly been relocated (Huffman *et al.* 2005) and this issue could be resolved if radiometric dates were taken from the original excavation unit. It remains ambiguous whether the sediments from which the specimen and dating samples were derived were reworked or not (Huffman 2001a, Langbroeks and Roebroeks 2000). Finally, evidence from magnetostratigraphy and a tektite-bearing stratum has led different research groups to different conclusions regarding the time depth of the Javan hominin fossils. Resolving these ambiguities has important implications for understanding the adaptive capacities of *Homo erectus*, since the site is very early and distant from the place of the origin of *Homo erectus*.

Java could have been accessed by a land-bridge that would have formed during the uptake of ocean waters into terrestrial ice sheets during glacial time periods. The exposed Sunda Shelf would have been a mosaic of “lowlands, rivers, lakes, lagoons, shorelines, estuaries, and bays” (Huffman 2001b, p. 5). The depositional environment of the Mojokerto site was that of a marine delta (Huffman *et al.* 2003, p. 3). From the

botanical remains, a fairly open, grassy environment is reconstructed for Mojokerto as pollen and phytoliths from grasses are dominant (*ibid*, pp. 16-17). Additionally, palynological remains indicate the presence of mangroves, rivers bordered by swamps, and forests in the mountains (*ibid*). Carbon isotopes from bovid and cervid teeth indicate that they consumed a C₄ diet, that is, mostly tropical grasses (Huffman & Zaim 2003, p. 15).

Sangiran, Java- 1.66 Ma

Homo erectus is first found at the central Javan site of Sangiran at 1.66 Ma (Semah *et al.* 2000) and has a fairly continuous record of habitation there until approximately 1.0 Ma (Anton 2003, p. 131). The species is represented by several skulls that, despite post-depositional deformation, indicate fairly large endocranial capacities (*ibid*, p. 142). The Sangiran hominins were buried in lacustrine and fluvial deposits (Bettis *et al.* 2004, p. 116). The paleohabitat of Sangiran was water-dominated with freshwater marshes and lake-margins at low elevations and wet grasslands and savanna at slightly higher elevations (Bettis *et al.* 2008).

Dmanisi, Georgia- 1.77 Ma

The site of Dmanisi in Georgia represents the first appearance (1.77 Ma; Gabunia *et al.* 2000a, Lordkipanidze *et al.* 2007, p. 305) of *Homo erectus* in temperate habitats. This site is remarkable for the completeness of the hominin finds, which include several almost complete crania and many complete long bones. Oldowan Mode-1 tools are found in association with these hominins (Gabunia *et al.* 2000a, p.1025). As described above, these hominins were small, with height estimates of 144.9 to 166.2 cm and weight estimates of 40-50 kg (Lordkipanidze 2007, p. 308), which falls into the range of early

Homo (*Homo rudolfensis*), but at the small end of the female scale for *Homo erectus* (Gabunia *et al* 2001, p. 168). This observation casts doubt upon the hypothesis that a significant increase in body size (as is seen with WT 15000) was an impetus for the initial dispersal of *Homo erectus*.

The fauna at Dmanisi was accumulated over a short period in a complicated series of depositions, which includes ash falls and hydraulic piping (Tappen *et al.* 2007, 132). Specimens from Dmanisi are remarkably well preserved with the majority showing little to no weathering, indicating rapid burial (Lordkipanidze 2007 Sup. Info., p. 6). One third of the bones are complete and the rest appear to have been broken prior to burial. Hominin-tool marks appear on only 1% of the bones, though the location of these marks indicates early access to the carcasses (Tappen *et al.* 2007). Carnivore toothmarks appear on 8-9% of the bones (and higher frequencies in certain locations within the site), though the carnivores do not appear to have consumed the hominins, as many of the skeletal elements that are readily consumed by carnivores are found in the Dmanisi assemblage (clavicles, patellae, ribs).

Several types of habitats are represented by the fauna at Dmanisi and indicate that there was likely a vertical zonation to the vegetative structure (Gabunia *et al.* 2000b, p. 795). Forest, forest-steppe, and steppe habitats are represented by various types of animal remains, predominantly cervids (*ibid*). The cervids found at Dmanisi include *Cervus abesalomi*, *Pseudodama* (= *Cervus*) *cf. nestii*, and *Eucladoceros aff. tugelensis*, which are stated to be indicative of “a flat and fairly wet river valley with gallery forests” (Lordkipanidze *et al.* 2007, Sup. Info., p. 6), though the latter genus is more likely to have lived in open habitats (as will be discussed in Chapter 8). The taxa represent a

Eurasian faunal assemblage, with *Homo* being the only certain African emigrant (Tappen *et al.* 2007, p. 124). Palynological evidence shows a wide variety in species representation from forest to more brush vegetation (Gabunia *et al.* 2000b, p. 797-8). Pollen remains also indicate an increase in aridity in this region at the time of deposition (Gabunia *et al.* 2001, p. 163-4). Using the composition of locomotor and trophic adaptations of the Dmanisi fauna, Palmqvist reconstructs Dmanisi as a much more open site, dominated by grasslands and shrublands, not unlike what is seen in modern African savannas, though he does acknowledge that forests likely existed on higher slopes (Palmqvist 2002, p. 4-5). Thus, Dmanisi can be reconstructed as having a warm climate with open vegetation found on the lower slopes of the region, where a lake and river formed an isthmus and with forests on higher slopes.

Yuanmou Basin, China- 1.7 Ma

Yuanmou Basin is located in southwestern China, near the southeastern margin of the Tibetan Plateau (Zhu *et al.* 2008). The dating of this site has been controversial as the hominin remains were removed from their original context prior to excavations (*ibid*). Excavations have revealed a rich mammalian assemblage, which is Villafranchian in nature, four stone tools, and two hominin central upper incisors (Zhu *et al.* 2008). Zhu *et al.* attribute the incisors to *Homo* sp., but state that “a provisional attribution to *Homo erectus* sensu lato is also defensible” (*ibid*). Of the taxa, 60% (n = 21/35) are assumed to be grazers based on taxonomic affiliation, though there are a few taxa associated with bushlands and forests. Deposition in a lacustrine or marsh habitat is evidenced by the presence of mollusks. Pollen indicates that the lake or swamp was surrounded by herbaceous vegetation with patches of forest (*ibid*). Yuanmou is thus reconstructed as

being a fairly open habitat around open water with patches of more closed cover away from the lake or swamp.

Xiaochangliang, China- 1.67-0.97 Ma

Xiaochangliang is situated at 41° N in the Nihewan Basin of northern China (Peterson *et al.* 2003). It is dated to between 1.67 and 0.97 Ma and includes only lithics and no hominin remains. The lithics and associated fauna are secondarily deposited and 90% of the faunal assemblage is very small fragments that cannot be identified to taxon or skeletal element (*ibid*). Hominins seem to have had little to do with the actual deposition of this site, but instead their tools were hydraulically transported along with the fauna to be deposited at the side of a paleolake. Looking at $\delta^{13}\text{C}$ values of equid tooth enamel, Wang *et al.* (1998) found that there was an increasing signal of C3 grasses being consumed throughout the Pleistocene, with the early Pleistocene showing evidence of grasses as being a large component in the equid diet.

‘Ubeidiya, Israel- 1.4 Ma

The site of ‘Ubeidiya, Israel is located in the Levantine corridor, the main dispersal route from Africa into Eurasia (see Figure 2-1). ‘Ubeidiya is dated to approximately 1.4 Ma based on a combination of biochronological dating and correlation with upper and lower date limits from radiometric dates on lava flows. The site contains several cycles of fluvial and lacustrine deposition with the majority of the lithic evidence and faunal (including hominin) remains deposited during the inferior fluvial (Fi) cycle (Belmaker 2006, p. 10). There have been few hominin specimens recovered from ‘Ubeidiya, which are assigned only to *Homo* sp., and only one specimen, a right lateral lower incisor (UB 335) has clear provenience (Belmaker *et al.* 2002). However, hominin

presence is firmly recorded in the thousands of lithics recovered from many different strata at 'Ubeidiya (Shea 1999).

The fauna at 'Ubeidiya is a mix of both African and Eurasian species. Though most strata are dominated by cervids (*Pseudodama* sp., *Capreolus* sp., and *Praemegaceros verticornis*), African taxa are represented by 11 species. It was found (Belmaker 2006, p. 67) that many of these African taxa were already present in the region by the time of 'Ubeidiya's deposition, thus weakening the argument that hominins dispersed with other African taxa. Dennell (2003, p. 427) states that the presence of African taxa indicates that 'Ubeidiya was open and arid. However, in an examination of all the taxa, Belmaker (2006) concludes that 'Ubeidiya was a closed Mediterranean biome.

'Ubeidiya is presented as a case study to test the methodology introduced in this dissertation, thus, the site will be discussed in further detail in Chapter 5, Materials.

Western Europe

It was previously thought (Anton & Swisher 2004, Dennell 2004) that hominins did not disperse into Western Europe until well after 1.0 Ma. Several recent finds have changed this view. Lithics (but no hominin remains) have been found at the site of Pirro Nord in Southern Italy that date to between 1.7 and 1.3 Ma (Arzarello *et al.* 2007). The lithics and fauna at Pirro Nord were accumulated in a natural trap in a karst system and likely have been displaced from their original context due to fluvial transport (*ibid*). The fauna assemblage includes African species and thus the authors reconstruct Pirro Nord and an open and arid habitat.

The oldest site in Spain, Sima del Elefante in Sierra de Atapuerca is also a karst in-filling and is dated to 1.2 Ma. Sima del Elefante contains 32 artifacts, faunal elements with hominin-processing marks, and a mandible fragment provisionally assigned to *Homo antecessor* (Carbonell *et al.* 2008). The insectivores of Sima del Elefante indicate “a general warm and humid paleoenvironment with warmer-cooler shifts” (*ibid*, p. 466).

Hominins are not found in Northern Europe until 700 kya at Pakefield in Suffolk, UK, a site that was formed during an interglacial period with a “warm seasonally dry Mediterranean climate” (Parfitt *et al.* 2005, p. 1010). Hominin presence at Pakefield is represented by 32 flint artifacts in various layers, but not by the hominins themselves. England, at the time of Pakefield’s deposition, was connected to mainland Europe by a land-bridge. The artifacts were deposited in riverine to marshy environments that had woodlands and open grasslands nearby (*ibid*).

Other early Eurasian sites

Claims of early hominin occupation have been made for several sites scattered across Eurasia, though these sites remain contentious due to reasons of uncertain provenience, dating, or ascription to hominin activity. Riwat, Pakistan is dated to 2.0 Ma by a combination of paleomagnetism and stratigraphic position below an ash layer dated to 1.6 Ma (Dennell *et al.* 1988, p. 498). Riwat contains no hominin remains and only 14 lithics that the authors (Dennell *et al.* 1988) consider to be hominin produced. Critics state that these artifacts are likely to have been produced by geological flaking due to fluvial transport (Stapert 1989, p. 318), and that the context of the finds is not robust enough to support a claim of hominin-made artifacts (Hemingway 1989, p. 317). Lithics have also been reported from Romania dating to late Pliocene (Radulescu *et al.* 2003) but

there is some doubt as to their association with the fauna used to report this date (Dobos, personal communication 2008). A site (Valea Graunceanului) closely associated with these lithics will be discussed in more detail in Chapter 5, as it is one of the case studies included in this dissertation. Longgupo Cave near the Sichuan Basin in China, dated to 1.96-1.78 Ma, contains primitive *Homo* dentition and Oldowan-like tools in association with open and woodland fauna (Huang *et al.* 1995, Wood & Turner 1995), though these dates and the status of the hominin remains are contested (Zhu *et al.* 2003). Claims have been made for an early presence (1.65 Ma, Gilbert *et al.* 1998) of hominins in Spain (Orce, Venta Micena). Remains from Venta Micena attributed to *Homo* sp. include two contentious humeral fragments and a skull fragment that was later attributed to a juvenile equid (Palmqvist 1997, but see also Gilbert *et al.* 1998). Venta Micena has been reconstructed as an open woodland (Mendoza *et al.* 2005).

Discussion

It is evident that *Homo erectus* represents an adaptive grade, both morphologically and behaviorally, away from all other hominins that preceded it. In fact, *Homo erectus* is sometimes referred to as the first true member of the genus *Homo* (Wood & Collard 1999). *Homo erectus* appears in the fossil record just after what can be considered a true climatic change. The shift from humid to cooler and more arid conditions is recorded in several climatic proxies and data are found throughout Africa and Eurasia that support this shift. There is little doubt that this climatic change is correlated with the onset of glacial cycling and that this was likely the “primary factor affecting African terrestrial climate after 2.8 Ma (deMenocal 1995, p. 57). Specifically, the growth of the Fennoscandian ice sheets commencing at 2.8 Ma would have started a

high pressure cell over the North Atlantic that would have forced cool, dry air out over Europe and Africa (deMenocal and Bloemendal 1995, p. 283). Temperatures continued to decline and aridity increased as the glacial ice sheets grew larger into the Pleistocene. One of the main effects of Northern Hemisphere glaciation was the fragmentation of habitats. It is known that during glacial times, forests retract and form refugia in which populations of species that used to have continuous distributions become isolated (Brown and Lomolino 1998, pp. 205-5), possibly resulting in allopatric speciation and certainly in dispersal. The onset of glacial cycling marked a significant change in climatic regime and would have affected local environmental conditions, causing more habitat heterogeneity than had been present before. This is perhaps the strongest impetus for the turnover pulse that Vrba found in African bovid fossil records. Much of the evidence that shows a climatic shift around 2.5 Ma also shows an increase in climatic oscillations (e.g. $\delta^{18}\text{O}$ and aeolian dust records, Denton 1999). To account for the appearance of *Homo erectus* in the fossil record at the Plio-Pleistocene boundary, two hypotheses may be appropriate: Vrba's Turnover Pulse Hypothesis and Potts's Variability Selection Hypothesis. While one hominin lineage (*Paranthropus*) responded to the climatic change commencing at 2.6 Ma by becoming dietary specialists, another lineage (*Homo*) continued to evolve adaptations for increased flexibility to oscillating climatic conditions. The adaptation to variability would have also allowed *Homo* to exploit a variety of habitats and possibly new niches. The initial evolution of *Homo erectus* may indeed have been due to the climatic change toward more arid conditions at the Plio-Pleistocene boundary, but the selection that acted upon *Homo erectus* continued to favor more versatile traits that allowed for occupation of a variety of habitats. In order to evaluate the latter statement,

we must first have an understanding of the range of habitats that *Homo erectus* was able to occupy.

In almost all reconstructions, *Homo erectus* is associated with aquatic resources, be they fluvial, lacustrine, palustrine, or marine. Like modern humans, water was a limiting resource for *Homo erectus*. Thus, it is not surprising that none of the reconstructions is desertic and even purely open grassland reconstructions are rare. However, some of the earliest sites are also some of the most open. Koobi Fora (1.88 Ma) is reconstructed as an *Acacia* savanna with gallery forests along a river (Denys 1999, p. 247, Feibel 1993, p. 67). Sites from Java are even more open, with the earliest site (Mojokerto, 1.81 Ma) reconstructed as being grassy, though with more closed habitats available (Huffman *et al.* 2003). The time period in which *Homo erectus* first appears in the fossil record, 1.8 Ma, has been documented as extremely arid by several proxies and across several continents (deMenocal & Bloemendal 1995, Bonnefille 1995, Cerling 1992, Wang *et al.* 1998). Shortly after this arid excursion, $\delta^{18}\text{O}$ records indicate a decrease in aridity and it is at this time that *Homo erectus* first appears in temperate habitats. Dmanisi (1.77 Ma) is reconstructed as having vertical zonation in vegetative types, with open areas on lower slopes, near a river, and forested habitats on upper slopes (Gabunia *et al.* 2000b). Yuanmou (1.7 Ma) is reconstructed as having a lake with open and closed vegetation nearby (Zhu *et al.* 2008). Sangiran (1.66 Ma) was likely a wet grassland with savanna regions available at higher elevations (Bettis *et al.* 2009). ‘Ubeidya is reported to have been more closed than previous sites (Belmaker 2006, Bar-Yosef & Tchernov 1972). Thus, the earliest sites from which *Homo erectus* remains are recovered (1.88 – 1.7 Ma), extending across all of the Old World, include open habitats

with areas of more closed vegetation available with an initial trend of increasing aridity followed by increasingly mesic conditions by 1.6 Ma. Regardless of which continent *Homo erectus* was living on, the paleoenvironmental evidence reviewed here indicates that *Homo erectus* inhabited mosaic environments, generally near a water source. Habitat reconstructions from Africa, temperate Eurasia, and even the more marine sites of Indonesia are all similar. *Homo erectus* does not appear to have been locked into the specific types of resources associated with each continent, but instead was adapted to exploit the variety of resources found in mosaic habitats.

Why, then, does *Homo erectus* not appear in western Europe until much later (1.2 Ma at Sima del Elefante)? Were mosaic habitats not available? Were there geographic features barring *Homo erectus*'s dispersal? Or is the evidence of absence simply the absence of evidence? Perhaps *Homo erectus* had very low population densities in its first dispersal into Eurasia and its remains are not represented in the fossil record due to taphonomic destruction. Increased and more thorough sampling may produce earlier evidence of hominin presence at the Plio-Pleistocene boundary in western Europe.

Geographic barriers have been proposed for the relatively late entry of *Homo erectus* into Europe (Rolland 1992). Mountains, such as the Taurus Mountains, running from the Mediterranean Sea to the Black Sea in Turkey may have delayed entry into Europe from the southeast while the Caucasus Mountains running along the border of Georgia and Russia would have been an effective barrier to dispersal from the central east. Further, the Black and Caspian Seas were connected by the Kura Strait of Akchagyl, adding a water barrier to the north of the Caucasus Mountains during the late Pliocene (Gabunia *et al.* 2001). Though there are passes through these mountains (through the

Turkish mountains more so than the Caucasus Mountains), it is possible that at the time of the initial dispersal of *Homo erectus* into Eurasia there were no suitable habitats in these passes and perhaps dispersal occurred only if and when such habitats were available. This hypothesis can only be tested with further sampling of sites in these regions at the Plio-Pleistocene boundary.

Evaluating the evidence of absence versus the absence of evidence is always difficult. Hominins (excluding *Homo sapiens*) are generally rare on the landscape and usually constitute a minority of the taxa found in fossil sites. Sites that have been thoroughly and extensively sampled and excavated (such as St. Vallier, France; Valli 2004b) yet have no evidence of hominin occupation in either skeletal remains, lithics, or hominin-modified bones, generally can be regarded as evidence of absence. Other sites that may have been sampled with less rigorous protocols during the earlier parts of the last century should be re-excavated with more exacting standards, as has recently begun for Senèze, France (Delson *et al.* 2006) and should be done for Valea Graunceanului, Romania. Excavations in the past five years have revealed that hominin occupation in Europe began earlier than previously thought (Carbonell *et al.* 2008, Arzarello *et al.* 2007, Parfitt *et al.* 2005). Only further such excavations can address the question of *Homo erectus*'s first appearance dates into Europe.

This dissertation examines three Plio-Pleistocene European sites that do not (currently) contain hominin remains. Habitat reconstructions of these sites provide insight into whether these sites were not occupied due to habitat intolerance of *Homo erectus*. That is, are the habitats of these sites remarkably different from those sites known to have been occupied by *Homo erectus*? If the reconstructions provided here for these sites are

not significantly different than other broadly contemporaneous sites, then alternative explanations must be sought for why these sites were not occupied.

	Site Name	Location	Date (Ma)	Paleohabitat Reconstruction
1	Koobi Fora	Kenya	1.95-1.78	arid <i>Acacia</i> scrub, some riverine forest, fluvially dominated with gallery forests, seasonally flooded grasslands
2	Ain Hanech	Algeria	1.8	NA
3	Swartkrans	South Africa	1.7-1.5	Warm and open but with woodlands along a river
4	Nariokotome	Kenya	1.53	gallery forests along watercourses and open areas away from the Omo river
5	Gadeb	Ethiopia	1.48	NA
6	Mojokerto	Java	1.81-1.1	fairly open, grassy marine delta with forest in the mountains
7	Dmanisi	Georgia	1.77	forest steppe, forested foothills, open, gallery forest with slightly warmer & drier than present mixed woodland to tall grass, shrubs, low bush/tree cover, unforested on lower slopes
8	Yuanmou Basin	China	1.7	fairly open habitat around open water with patches of more closed cover away from the lake or swamp
9	Sangiran	Java	1.66	freshwater marshes and lake-margins at low elevations and wet grasslands and savanna at slightly higher elevations
10	Xiaochangliang	China	1.67-0.97	lakeside with C3 and C4 plants available
11	Ubeidiya (Fi-layer)	Israel	1.4	delta & lake shore, Mediterranean climate, wetter than present
12	Pirro Nord	Italy	1.7-1.3	open and arid habitat
13	Sima del Elefante, Atapuerca	Spain	1.2	a general warm and humid paleoenvironment with warmer-cooler shifts
14	Pakefield	England	0.7	warm seasonally dry Mediterranean climate
15	Riwat	Pakistan	2	NA
16	Valea Graunceanului	Romania	late Pliocene	lacustrine delta
17	Longgupo	China	1.9-1.8	open & woodland fauna
18	Venta Micena, Orce	Spain	1.65	open woodland

Table 2-1 Summary of paleoenvironments for the hominin sites discussed (numbered to match the site order in Figure 2-2). For reference citations, please see the body of the text.

Chapter 3: Ecomorphology defined and critically examined

Introduction

For the purposes of this study, ecomorphology (ecological morphology) is defined as: *The study of functional morphology as it relates to adaptations to habitats*. This operational definition is understood to be a simplification of more complicated processes subsumed in the term “ecomorphology”. The concept of ecomorphology has been examined by biologists, ecologists, paleontologists, and anthropologists for many decades. “It is axiomatic in biology that phenotypic differences among individuals and species are related to differences in their ecology. Indeed, this notion is a cornerstone of our understanding of the nature of organismal diversity” (Wainwright 1994, p. 42). Ecomorphological studies are ultimately about fitness (expressed phenotypes and morphology) limit the way in which an organism can exploit resources, perform mate-attracting behaviors, and escape predators, which in turn directly affect that organism’s ability to pass on its alleles (Plummer *et al.* 2008).

The definition of ecomorphology used here may differ from those used in other studies but is provided to elucidate the purpose of this research: to introduce methods that utilize cervid remains as paleohabitat proxies. While cervid ecomorphology is interesting in its own right, most non-primate ecomorphological studies in anthropology (reviewed below) have explicit goals of reconstructing past habitats associated with hominin remains.

This study examines one specific feature of an organism’s behavioral repertoire that relates to its fitness- locomotion. “Locomotion adaptation is intimately associated with ecology, as it is likely to reflect habitat structure, and is an important component of

foraging and predator-avoidance strategies” (Plummer *et al.* 2008, p. 3017). In fact, it has been hypothesized (Geist 1998) that predator-escape behavior is the main selection pressure upon cervid post-cranial skeletal morphology. Kappelman (1988, p. 128) states that “differences in habitat structure encountered from closed canopy forest to open savanna appear to be primary determinants of bovid locomotion”, stressing that “the problem of predator avoidance may exert greater constraints on bovid behavior and locomotion” than food acquisition (p. 129). Geist (1998) hypothesizes the same is true for cervids.

Ecomorphology studies in paleoanthropology

Many paleoenvironmental reconstructions based on faunal remains rely on taxonomic uniformitarianism (Andrews 1995, p. 61), which draws behavioral correlations between fossil specimens and their extant relatives. Using such a method, one assumes niche stasis across space and through time, an assumption that has been shown to be invalid in several taxa, including fossil *Gazella*, caprines (*Pachytragus*), and Miocene hyaenids and hipparionines (Solounias and Dawson-Saunders 1988, p. 151). Here it is hypothesized that paleohabitat reconstructions based on the functional morphology of specimens are more likely to provide an accurate reconstruction of what past habitats looked like, since functional morphology asks *how* an organism moved through a habitat, not just *who* is represented. Vrba (1980) acknowledged that morphological features, such as those described by Gentry (1970), provide a way in which adaptations to (open) habitats can be evaluated, but notes, “unfortunately, an objective assessment of how these characters relate to environment is at present impossible. None of the four features [indicated by Gentry to be indicative of adaptations to habitats] has, to my knowledge,

been measured on adequate samples of modern bovid species” (Vrba 1980, p. 256).

Several studies in the 1980s began to address this issue, though the following review is limited to those studies on artiodactyls.

While not specifically researching ecomorphology (as defined here), K. Scott (1983, 1985, 1987) collected a large amount of data on bovid and cervid limb morphological characters in order to study body weight predictions and allometry. She found that most of her measurements scaled closely with body weight, except limb bone length, especially in more distal elements, such as metapodia. Metapodial length tends to vary with habitat: open-adapted species have long metapodia, species in montane habitats have short metapodia, with species inhabiting broken woodlands and rolling hills having intermediate-length metapodia (1985, p. 21).

Though K. Scott found little relation between her measurements of the femur and habitat, studies by Kappelman on bovid femora (1988, 1991, Kappelman *et al.* 1997, R. Scott *et al.* 1999) were able to separate bovids to their known habitats. Kappelman’s measurements were designed specifically to address questions of functional morphology of bovid femora. As the work by Kappelman is foundational to the approach used here, a brief description of the basic structure of such research is warranted.

An ecomorphological study of a taxonomic group, such as Bovidae, is conducted by correlating each member species with a preferred habitat type. Though ecomorphology is often referred to as being “taxon-free” (Plummer & Bishop 1994, Damuth 1992), this is not entirely accurate, as each species is associated with a specific habitat. Next, the known habitats for the extant species are condensed into three or four broad habitat groups, such as “Forest”, “Heavy Cover”, “Light Cover”, and “Open”

(Kappelman *et al.* 1997). Measurements, generally taken with calipers, flexible tape, and goniometers are then collected on variables that are designed to quantify aspects of functional morphology. Those measurements (here, referred to as “linear” measurements), often standardized for body size using ratios, are placed into a multivariate discriminant analysis, which produces linear recombinations of the original variables by maximizing group differences and minimizing within group variability (Mendoza *et al.* 2002). To estimate how well a data set will place fossil specimens into their most likely habitat, each specimen of the extant training set is reclassified into a habitat category using the discriminant functions. The percent of correct reclassifications, then, gives some indication of how well these functions can differentiate between habitat types. There are several ways in which these reclassifications can be accomplished, however. Most ecomorphological studies have reported their results as resubstitution values, which use the discriminant functions derived from all specimens in the training set (including the specimen being reclassified). Thus, the data for the specimen being reclassified is included in computations of discriminant functions, resulting in relatively high reclassification rates. Leave-one-out cross-validation, a jack-knife approach, instead reclassifies a specimen using the discriminant functions computed without that specimen’s data. Cross-validation is a better predictor for how well a data set will classify fossil specimens, since it does not include the specimen being reclassified in the algorithms used to make the reclassification (Sheets *et al.* 2006). This is similar to classifying “unknown” fossil specimens, except that the “unknown” extant specimens have known habitat types and the results returned with cross-validation can be evaluated for accuracy (see Chapter 6). The final step places measurements from fossil specimens

into the analysis as “unknowns” and uses discriminant analysis to place the unknown specimen into the category to which it is most similar.

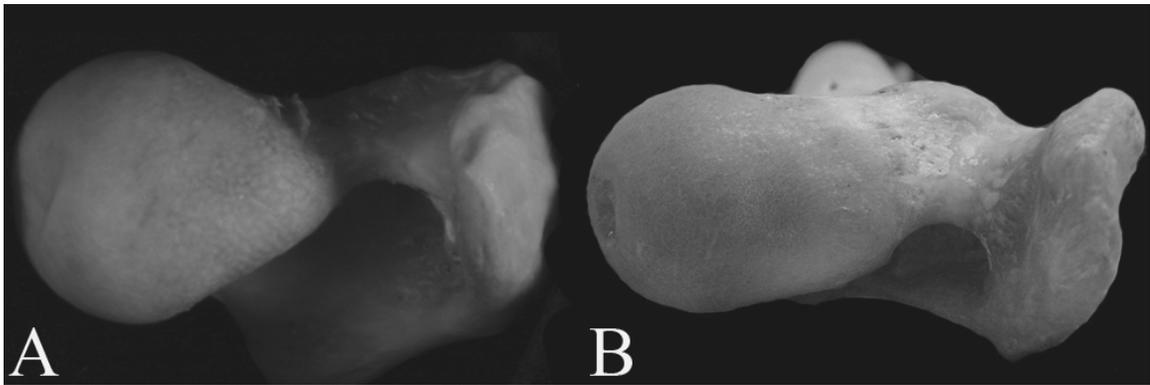


Figure 3-1 Femoral head shapes displaying the range in morphology from a closed-adapted cervid (A, *Pudu mephistophiles*, FM122523) and an open-adapted cervid (B, *Ozotoceros bezoarcticus*, NM270380). Closed-adapted cervids have femoral heads that taper laterally to allow for rotation away from the body while the femoral head of open-adapted cervids is wide laterally to limit rotation to the parasagittal plane.

Kappelman (1988, 1991 Kappelman *et al.* 1997, Scott *et al.* 1999) employed this methodology upon bovid femora using variables that have specific functional implications. Perhaps the most visually obvious morphological feature that varies with adaptations to different habitats is the Femoral Head Shape Score (Figure 3-1). For bovids living in closed habitats wherein they escape predators with saltatorial locomotion (bounding leaps) while placing obstacles between themselves and their predator, the femoral head must taper laterally (Figure 3-1a) to allow for movement of the leg away from the body and quick changes in direction. In open-adapted bovids that escape predators by flight, the femoral head needs to be wide in its lateral aspect (Figure 3-1b), which provides a more stable joint surface and restricts movement to the parasagittal plane. It should be noted that these basic patterns hold up for cervids also and in fact, the femoral heads in Figure 3-1 are those of cervids.

Kappelman's femoral variables perform well at reclassifying extant bovids into their known habitat categories. Using eight variables across the entire femur, 85% of the modern bovids reclassify (with resubstitution) into their correct habitats (Kappelman *et al.* 1997). When only four variables of the proximal femur are used in the analysis, 81% reclassify correctly (*ibid*), see Table 3-1. Unfortunately, femora, and especially complete femora, are rare in the fossil record, with sample sizes for paleoanthropological sites ranging from as low as four (Fort Ternan, complete data set, Kappelman 1991) to as high as 27 (various sites, reduced data set, Kappelman *et al.* 1997).

Metapodia, which are a commonly found skeletal element in the fossil record, were the subject of an ecomorphological study by Plummer and Bishop (1994). Though the authors state, "these [measurements] were used to generate dimensionless ratios reflecting shape and relative proportions of particular morphological features related to habitat preference" (1994, p. 52), they do not describe the functional implications of the variables they selected. Nevertheless, their variables do recover habitat with (resubstitution) accuracies ranging from 89% correct reclassification on entire metatarsals to 60% on proximal metatarsals (see Table 3-1). Plummer and Bishop applied their analysis to 319 metapodia from Olduvai Bed I and found that there were more open-adapted bovids in the assemblage than were found with taxon-based methods.

Ecomorphological studies of the past five years have not only increased the number of skeletal elements used for paleohabitat reconstruction, but also have expanded exploration of the multivariate analyses used to assign specimens to habitat categories. Building upon the work of Plummer and Bishop (1994), R. Scott (2004) expanded bovid metapodial ecomorphology to include more species and an extra habitat category

Element	Portion	n	# hab. types	# variables	Reclassification %			Reference
					Resub	Xval	J-K	
Metatarsal	Proximal	306	3	2	62	-	-	1
Metacarpal	Proximal	306	3	3	60	-	-	1
Metatarsal	Distal	306	3	5	70	-	-	1
Metacarpal	Distal	306	3	5	68	-	-	1
Metacarpal	Complete	306	3	8	84	-	-	1
Metatarsal	Complete	306	3	10	89	-	-	1
Femur	Proximal	188	4	4	81.4	-	-	2
Femur	Complete	188	4	8	85	-	-	2
Femur	Proximal	204	4	4	78.9	-	-	3
Femur	Complete	204	4	8	85.8	-	-	3
Astragalus	Complete	218	4	8	67	79.5	66.7	4
Phalanx 3	Complete	122	4	5	71.3	74	64	5
Phalanx 1	Complete	183	4	7	71	64	73	5
Phalanx 2	Complete	163	4	7	70.6	68	70	5
Metatarsal	Complete	339	5	9	81.7	-	70.5	6
Metacarpal	Complete	336	5	9	77.7	-	67.6	6
Metatarsal	Distal	340	5	9	77.6	-	66.2	6
Metacarpal	Distal	336	5	9	76.2	-	62.5	6
Astragalus	Complete	81	4	7	77.8	70.4	62.5	7
Phalanx 3	Complete	129	7	6	55.8	-	-	8
Cuneiform	Complete	202	7	5	40.6	-	-	8
Phalanx 1	Complete	303	7	9	57.1	-	-	8
Phalanx 2	Complete	181	7	9	51.9	-	-	8
Magnum	Complete	209	7	9	51.2	-	-	8
Unciform	Complete	206	7	9	51	-	-	8
Middle Cuboid	Complete	192	7	8	43.8	-	-	8
Radius	Complete	207	7	8	58	-	-	8
Lunar	Complete	203	7	9	53.2	-	-	8
Tibia	Complete	224	7	12	47.6	-	-	8
Metatarsal	Complete	215	7	13	66.5	-	-	8
Humerus	Complete	203	7	13	68	-	-	8
Femur	Complete	224	7	13	66.7	-	-	8
Cubonavicular	Complete	206	7	15	47.1	-	-	8
Femur	Proximal	224	7	6	52.6	-	-	8
Humerus	Distal	203	7	5	48.8	-	-	8
Medapodial	Distal	426	7	7	47.2	-	-	8
Femur	Distal	210	7	4	42.4	-	-	8
Radius	Proximal	209	7	8	41.1	-	-	8
Pisiform	Complete	170	7	3	39.4	-	-	8
Tibia	Proximal	213	7	12	37.6	-	-	8
Humerus	Proximal	203	7	5	37.4	-	-	8
Astragalus	Complete	286	4	11	92.7	91.7	87.1	9

Table 3-1 Reclassification rates for published bovid ecomorphological studies. Most studies used the resubstitution method for reclassification, though cross-validation rates are reported when available. Resub.

= resubstitution, Xval = cross-validation with subsets of specimens, J-K = Jackknife cross-validation (n-1).
1 = Plummer & Bishop 1994, 2 = Kappelman *et al.* 1997, 3 = Scott *et al.* 1999, 4 = DeGusta & Vrba 2003,
5 = Scott 2004, 6 = DeGusta & Vrba 2005, 7 = Weinand 2007, 8 = Kovarovic & Andrews 2007, 9 =
Plummer *et al.* 2008.

(“Mountain”) to better encompass the comparative descriptions of ruminant metapodia by Köhler (1993). Scott reported his reclassification results with both resubstitution and cross-validation. Reclassification results in Scott’s study ranged from 81.7% to 76.2% for the resubstitution method and 70.5% to 62.5% for cross-validation (see Table 3-1).

Additionally, Scott created a “Habitat Score” that allows specimens to be evaluated along a continuum from open to closed habitats, which will be described further in Chapter 6.

Using a four-habitat category system, DeGusta and Vrba obtained reclassification results of 67% for their study on the bovid astragalus (2003) and 64-73% for the phalanges (2005, see Table 3-1). DeGusta and Vrba (2003, 2005) also explored multiple reclassification methods, including resubstitution, several types of cross-validation, jackknifing, and tests I will refer to as the “confidence value threshold” and the “baseline of accuracy.” The confidence value threshold test asks, “what confidence value would we have to use as the cutoff value to obtain a misclassification rate of less than 5%?” (DeGusta & Vrba 2003, p. 1015). For each habitat category assigned to a specimen, a confidence value of it belonging to that group is given. For example, a specimen might be assigned to the “Forest” category, but may be given only a 57% likelihood (confidence value) of belonging to that category (and, maybe a 30% likelihood of belonging to “Light Cover” and a 13% likelihood of belonging to “Heavy Cover”). DeGusta and Vrba calculated the threshold at which these confidence values will return a correct reclassification result of 95%. While they state that those specimens scoring below the

confidence threshold are “accorded less weight”, it should be noted that those specimens still represent biological realities and their morphology should not be ignored. Instead, it would be illuminating to investigate why those specimens are not classifying correctly and then adjust methodologies appropriately (the specimen is assigned to the wrong habitat type, the habitat categories do not represent the variation in habitats, the variables do not reflect adaptations to habitats, etc.). Finally, DeGusta and Vrba advocate the use of a “baseline of accuracy” to test if the discriminant function is assigning specimens into categories simply by chance. They assigned incorrect habitat categories to each specimen and performed a discriminant analysis on these new, incorrect categories. These analyses did return lower reclassification rates (40-50%, 2003) than those with the correct categories. Weinand (2007) expanded upon DeGusta and Vrba’s astragalus methods by including bovids from Southeast Asia and by using recursive partitioning for reclassification. Weinand achieved rates between 74 and 79% for various reclassification methods.

The most recently published study of paleoanthropological ecomorphology continues investigations of the bovid astragalus and refinement of multivariate analyses. Plummer *et al.* (2008) specifically tested DeGusta and Vrba’s “confidence threshold” and found that “eliminating specimens with lower confidence of attribution may create more, rather than less, bias in the overall frequency of habitats represented” (*ibid.*, p. 3024), since the specimens with low confidence values tended to be from the same habitat types. Using 11 variables and four habitat categories, Plummer *et al.* (2008) obtained very high reclassification rates of 93% (resubstitution) and 87% (cross-validation). Further,

Plummer *et al.* (2008) offer *post hoc* functional interpretations for the variations found in morphology.

Kovarovic and Andrews (2007) performed a vast survey of all the appendicular elements (excluding scapulae) and included bovids, cervids, and tragulids in their sample. This is important to note, since all the ecomorphological studies described thus far, excepting Weinand (2007), had been conducted only on African bovid specimens. Further, Kovarovic and Andrews used seven habitat categories. Inclusion of many skeletal elements has the advantage of increasing the sample size of specimens available for paleohabitat reconstructions at fossil sites and more habitat types allows for more precise reconstructions. Reclassification results for all the skeletal elements ranged from 68% (4.76 times better than by chance alone in a seven-category system) for the complete humerus to 37.4% for the proximal humerus (see Table 3-1 for all results).

This dissertation starts, as Kappelman did, by selecting variables that are hypothesized to reflect aspects of locomotor morphology. Following the methodologies of ecomorphology studies published in the last five years, several multivariate analyses of the data are conducted, including resubstitution, cross-validation, and Scott's (2004) "Habitat Score." The continuum of habitats will be broken down into four categories, similar to Kappelman's (1991). Finally, functional interpretations of variations found in morphology as it relates to habitat will be proposed.

Advantages of ecomorphology

Ecomorphological studies of fossil specimens have three main advantages over taxon-based faunal list methods: A) they do not rely upon taxonomic identification in order to be useful, B) they can be used on specimens even if they have no extant

descendants, and C) they can be used on post-crania, which are often difficult to reliably identify to genus or species.

Perhaps the biggest advantage of ecomorphological methodologies is that they do not require specimens to be identified to the generic or specific level, which is often problematic and such identifications are often revised over time. Identifications become even more problematic for extinct species. Further, reliance on taxonomically identified specimens may limit sample sizes and introduce bias into the analysis (DeGusta & Vrba 2003, p. 1010).

Even if a positive identification can be made, taxon-based methods suffer from the assumption of stasis in habitat usage across geographic space and through time (*ibid*). Solounias and Dawson-Saunders (1988) refer to this as overmodernization or, the “tendency to over-extend analogies with modern species” (p. 151). They found this to be invalid in several examples; some *Hipparion* species were more ecologically similar to tapir than equids; Miocene hyaenids resembled civets, wolves, foxes, and felids more than modern hyaenids; and fossil *Gazella* species were more similar to *Litocranius* than to any extant gazelle (*ibid*).

Rather than taxonomic uniformitarianism, ecomorphological analyses rely upon morphological uniformitarianism. For example, the morphology of a joint surface restricts the range and type of motion possible at a joint and reflects the type of locomotion an organism performed. It is possible to make locomotor predictions from joint morphology not only within a single taxonomic group, such as cervids, but also between groups that have been phylogenetically separated for a very long time. “The antipredator behavior of ungulates probably influences predator locomotor morphology”

(Van Valkenburgh 1985, p. 417) and cursorial bovids and their predators are known to have homoplastic skeletal morphologies (Kappelman 1988, p. 128). Thus, by understanding how morphology relates to behavior, ecomorphological analyses can be used on specimens even when their genus or species is unknown or on specimens that have no extant descendants. Further, by understanding functional morphology, hypotheses can be made regarding what morphology would be most efficient for specific habitats and these hypotheses can be tested on extant specimens. Ultimately, the best way to test ecomorphological hypotheses would be to conduct performance experiments on living specimens (Wainwright 1994), but since these are difficult on organisms such as bovids and cervids, the current study is satisfied with finding correlations between skeletal morphology and known habitat preferences. Indeed, finding these correlations is the first step in formulating hypotheses regarding functional morphology that can be tested experimentally.

A final benefit to ecomorphological methods is that they are readily usable on post-cranial skeletal elements, which are often difficult to identify taxonomically. As long as a specimen is in the taxonomic group being investigated, it can be included in an ecomorphological analysis and this helps to increase the sample size of fossil specimens used to create a habitat reconstruction. Since sample sizes from paleoanthropological sites tend to be small, this in addition to independence of taxonomic identification, makes ecomorphological studies an important addition to taxon-based habitat reconstruction methods.

Limitations of ecomorphology

Since this study approaches ecomorphology as functional morphology with a goal of reconstructing habitats, it is important to understand the underlying functional implications of the variables being analyzed. “The success of ecomorphological analysis will depend to a large degree on selection of morphological characters based upon an understanding of their consequences for the functioning of the organism” (Ricklefs & Miles 1994, p. 20). After Kappelman’s (1988) study of the femur, few ecomorphology studies provided justification for why certain morphological variables were measured. Plummer & Bishop’s (1994) metapodial study recognized that “habitat-specific morphologies reflect the degree to which cursoriality is used as a predator avoidance strategy, and are mainly related to differences in joint stabilization, shaft shape, and lever arm length”, but do not offer interpretations of how these influences may be reflected in their results. R. Scott’s (2004) metapodial study used K. Scott’s (1985) and Köhler’s (1993) descriptions of metapodial biomechanical variation to choose variables and provided a good discussion of how the variation found reflects habitat adaptations. DeGusta and Vrba are explicit in not providing interpretations: “It is tempting to assert specific functional correlates of these differences, but rigorous analysis of the biomechanics involved is preferable to such speculation” (2003, p. 1018; 2005, p. 1109).

While it is true that: A) a more refined understanding of functional anatomy as it relates to the biomechanics of locomotion would likely provide deeper insight into the results from ecomorphological studies, B) biomechanical data would provide a direct test of the link between morphology and locomotion, strengthening inferences made in ecomorphological studies, and C) such data are not currently available in the literature

(paraphrased from DeGusta & Vrba 2003, p. 1021; 2005, p. 1111), this does not mean that such interpretations should not be made. In fact, there is a strong body of literature on functional morphology that can provide insights into morphological patterns that have been found, even if said literature does not directly concern bovids. This self-imposed limitation does little to further investigations of ecomorphology. Finding these patterns is the first step in creating biomechanical hypotheses (not “speculation”) to test the connection between functional morphology and adaptations to specific habitats in a more rigorous manner. Plummer *et al.* (2008) do exactly that in their astragalus study “in the hope they will encourage future lines of inquiry” (*ibid*, p. 3022).

A second issue in ecomorphological studies is the break-down of the reality of habitat continuum into categories. The discriminant analyses used in ecomorphological studies require the use of categories and thus some break-down is necessary. In a four-habitat system, much ecological variation is collapsed into a single category. For example, the category “Heavy Cover” contains bush, woodland, and swamp habitats (Kappelman *et al.* 1997), despite the fact that locomotion in woodlands, with generally firm substrates may be very different from locomotion in swamps, where the substrate can be yielding and slippery. A further break-down of the habitat continuum into more categories allows for more precise habitat reconstruction, but may reduce the ability of the discriminant analyses to place a specimen in its correct habitat type, since differences between habitat types on a smaller scale become more and more subtle. Considering all of the published bovid ecomorphological studies, I found a correlation ($R^2 = 0.58$, $p > 0.005$) between the number of habitat categories used and the success rate of reclassification (resubstitution, see Table 3-1).

A possible solution to this issue is to create a continuous scoring system, such as the “Habitat Score” developed by R. Scott (2004). To create this Habitat Score, Scott conducted a canonical variates analysis on the most open-adapted and the most closed-adapted bovids and then used the single resulting canonical variates axis to place the rest of the specimens along this continuum. This method provides a very different approach than categorical analyses and will be conducted here on cervids. A cautionary note with this type of analysis is that it assumes that habitats exist on a linear continuum (from closed to open) and that the morphology being investigated will reflect that. Some habitats, such as tundra, are unlikely to be fairly represented on this single dimension. While tundra is considered to be an “Open” habitat (that is, there is no tree cover), the substrate varies between hard, rocky, intermittently snow-covered permafrost to springy moss and lichen and locomotion on such substrates is unlikely to be directly comparable to locomotion in most hard-ground grassy open habitats.

In addition to breaking down the habitat continuum into categories, extant specimens analyzed must be placed into one of these categories. Generally, this is done by assigning a species to its most commonly preferred habitat. This is especially problematic for species with wide biogeographical distributions that are known to utilize several habitat types. This is probably a more significant problem for cervids than it is for bovids, which are reported to be more habitat-specific than cervids, as the latter are often characterized as being closed habitat dwellers (Kölher 1993, Mendoza *et al.* 2002, Christiansen & Adolfssen 2007). For a species like the white-tail deer (*Odocoileus virginianus*) that is found from Canada to South America, intraspecific variation is hypothesized to be great.

A final critique of ecomorphological studies in general is that they have all been conducted using linear measurements (length, width, depth, angles, etc.). While this method is inexpensive, expedient, and easy to conduct in the field, one must ask if it is the best way to investigate questions of functional morphology. This is related to the first critique in this section, but instead of asking how well the variables chosen reflect adaptations to habitats, this critique is asking, how well does the measurement system

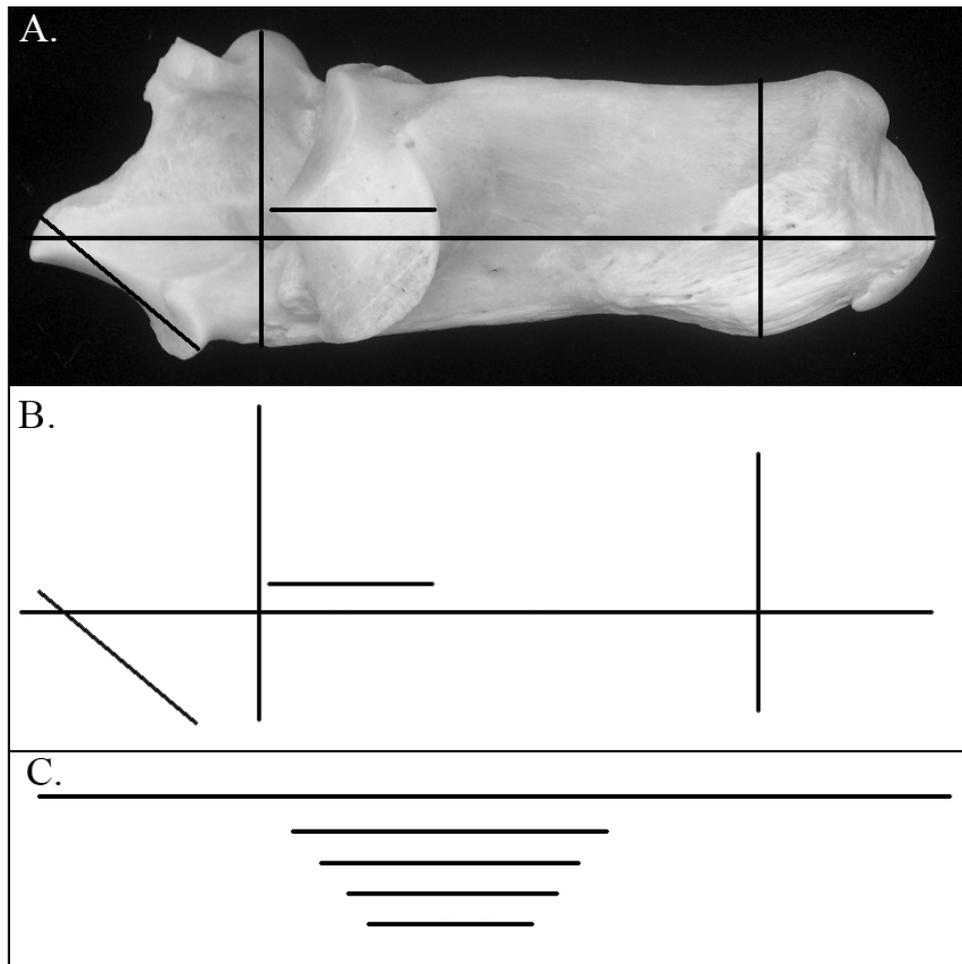


Figure 3-2 Some geometric information about a specimen is sacrificed with linear measurements. Once caliper measurements are entered into a spreadsheet, all information about their interrelationships is lost. 3-2A shows possible linear measurements on a calcaneus (MN 00-02, *Alces alces*, housed at the University of Minnesota's Anthropology Laboratories). 3-2B shows these measurements without the calcaneus. Since the location of the measurements is not recorded with traditional morphometrics, the variables could be arranged in any number of ways from the lines in 3-3C.

quantify the specific morphology? For example, if the unit of analysis is the calcaneus, do the linear dimensions in Figure 3-2A effectively quantify its shape? What do those measurements tell us about the shape of the bones once the data are entered into a database? Can we recreate what that bone looked like from those data? Figure 3-2B shows what the measurements look like without the calcaneus. Since linear methods do not record the *location* of these measurements, all information about how the measurements relate to one another is lost and the lines in Figure 3-2B could be arranged in any number of configurations from the lines in Figure 3-2C. In other words, while multivariate analyses might tell us how each of these lines varies in length relative to the other lines, we have lost information about how the lines might vary if their distances and angle from each other.

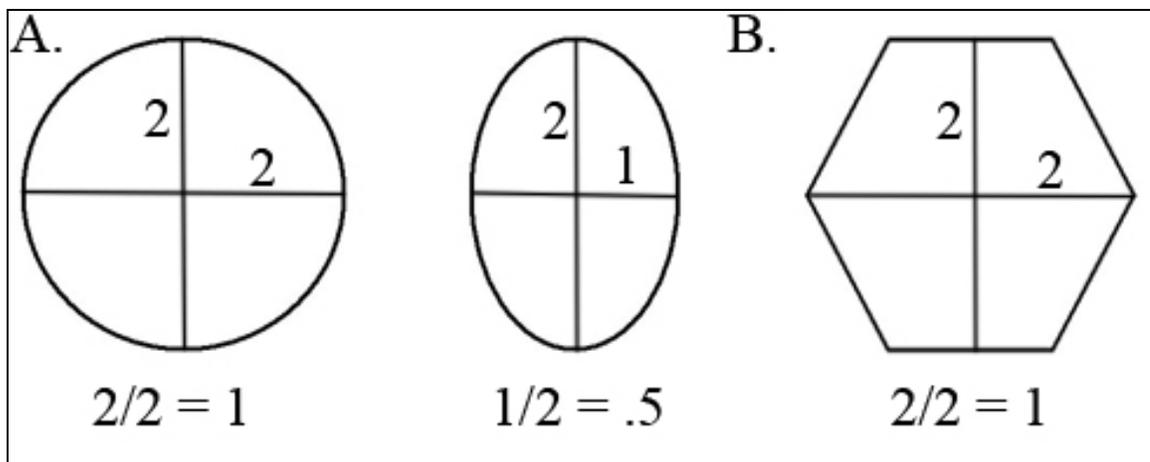


Figure 3-3 Ratios are used in a variety of morphometric studies, often to correct for body size. While a ratio can provide information about an object being more or less oblong, they lose detail about an object's shape. The three figures in 3-3 are different shapes, but when the aspect ratio of shape A. and B. are the same, thus information about an object's shape is lost with the use of ratios.

Using ratios of variables can retain some information about the interrelationships of variables, but ratios incur their own limitations. In figure 3-3a, two shapes are shown with measures of their length and width. A more round shape will have a higher ratio value than a more elliptical shape. However, ratios do not contain any information about the shape of the object's outline. That is, the ratio does not actually indicate "roundness" or "ellipticalness", but rather more or less "oblongness". In 3-3b, the hexagon, which is obviously a very different shape than the circle from 3-3a, will have the same ratio value as the circle. Clearly, even when ratios are used, information about shape is still lost.

Geometric morphometrics (GM), which will be described in detail in Chapter 6, is offered here as a suitable alternative to linear data in studies of functional morphology. GM provides a method to analyze the shape of an object *within its geometric and biological context* rather than as abstracted portions of the whole (linear dimensions). The basic data for a GM analysis are homologous landmark points on an object, such as suture intersections on bones. GM analysis maintains all information about how those landmark points vary relative to one another in space and no information about the original geometry of the object is lost during analysis. This is especially important for studies of functional morphology where the goal is not only to find correlations between shape and behavior but also to understand how and why certain morphologies are related to those behaviors and thereby understand the adaptations of animals that may no longer have living descendants.

Contributions of this study

There are three main contributions of this study: 1) ecomorphological methods for cervid skeletal remains are established, 2) geometric morphometrics methods are

introduced for paleoanthropological ecomorphology studies, and 3) ecomorphological methods designed specifically for incomplete bones are created.

Most of the ecomorphological studies conducted in anthropology have focused on the family Bovidae. These artiodactyls are often the dominant taxa in paleoanthropological assemblages in Plio-Pleistocene Africa. While there are bovids found in Eurasian paleoanthropological sites, the family Cervidae usually dominate these assemblages. To date there have been no systematic reviews of cervid ecomorphology. The aforementioned study by K. Scott (1987) was not strictly an ecomorphological study of the same nature as this dissertation. Köhler's (1993) influential study of ruminant morphology as it relates to habitat only included nine of the (approximately) forty extant cervid species and Kovarovic & Andrews (2007) only included four species. This study introduces ecomorphological methods for Cervidae using a four-habitat category system (detailed in Chapter 6). Additionally, this study introduces a Habitat Score for cervids, similar to that of R. Scott (2004). Thus, the current study fills a gap in the available habitat reconstruction methods for Eurasian sites.

This study also serves to introduce GM to studies of non-primate ecomorphology in paleoanthropology. Since ecomorphology is the study of functional morphology, analysis of shape as a whole unit is preferable to parsing out different aspects of an object's shape. Not only does GM analyze whole shapes, but it also maintains the original geometry of the objects being evaluated, which allows for more meaningful exploration of shape. Data exploration is a key benefit to employing GM, as it allows for innovative analyses that are impossible with linear measures (Bookstein *et al.* 2003, Gunz *et al.*

2005, McNulty *et al.* 2006, Harcourt-Smith *et al.* 2008). New insights into functional morphology are likely to arise from such data exploration methods.

Another advantage of using GM in an ecomorphological study of joint surfaces is that complete bones are not required. Ecomorphological analyses of whole bones, and especially long bones, incur the highest correct habitat reclassification rates (see Table 3-1). However, complete bones in the fossil record are the exception rather than the norm. For example, out of the >2000 bovid remains from Fort Ternan, Kappelman was only able to use his femoral methods on five specimens. Metapodial sample sizes were larger with up to 33 complete metacarpals from Olduvai FLK N1 (Plummer & Bishop 1994, p. 57). Kovarovic and Andrews (2007, p. 674) found the largest sample sizes with small, dense bones (74 1st phalanges, 62 2nd phalanges, etc.). All of these studies were able to increase their sample sizes by including broken bones. In order to do so, the analyses only included those measurements on the portion of unbroken bone (i.e. just the proximal or distal measurements). Since this study is conducted mainly on joint surfaces, the methods can be used upon whole or incomplete bones without losing any data.

Chapter 4: The Cervidae

Cervidae evolution and taxonomy

The Order Artiodactyla first appeared 55 Ma, at the start of the Eocene, most likely from a condylarth or arctocyonid ancestor (Gentry 2000, p. 11). Artiodactyla are part of the radiation of mammals that define the Eocene, which was a warm time period with extensive tropical forests (*ibid*, p. 20). The Artiodactyla are characterized by having ‘double-pulley’ astragalar morphology and by having paraxonic (axis of symmetry running between third and fourth digits) foot morphology (Janis and Scott 1987a, p. 4). Three suborders of Artiodactyla appeared in the Eocene: Suina, Tylopoda, and Ruminantia, with cervids belong to the latter (*ibid*). The first probable member of Ruminantia, *Archaeomeryx*, appeared in the Middle Eocene of Mongolia (Gentry 2000, p. 13). Ruminants are united by having fused cuboid and navicular bones (i.e. the cubonavicular), a general reduction in the metapodia and phalanges of the second, fifth and, especially, the first digits, a reduction in the ulna and fibula, and loss of upper incisors (Janis & Scott 1987b, p. 9; Gentry 2000, p.12). Ruminants experienced an adaptive radiation in the middle to late Eocene, when selenodont morphology is first seen (*ibid*). Selenodontology is likely to be an adaptation to the harsher climates and increased seasonality that began in the late Eocene (*ibid*, p. 20).

Of the Ruminantia, cervids are part of the infraorder Pecora, which is (currently) comprised of five families: Cervidae, Moscidae, Giraffidae, Bovidae, and Antilocapridae. A dramatic drop in world temperatures at the Eocene-Oligocene boundary shifted European faunal compositions and this is the time when pecorans first appear (*ibid*). Pecorans are characterized by having compact, parallel-sided astragali, loss of the

trapezium, fully selenodont but brachydont cheek teeth without a lingual cingulum, fused metapodia with a distal keel, and retention of metapodia II and V (Scott and Janis 1987a, 1987b, 1993). The earliest pecorans, such as *Gelocus* from the beginning of the Oligocene (Gentry 2000, p. 14), have elongated metapodia and reduced ulnae. Janis and Scott (1987b) found the 'Gelocidae' to be paraphyletic (p. 3) and state that "the higher pecora did not have a single common ancestry from within the "Gelocidae", but must have been derived from within the diversity of primitive pecoran taxa" (p. 75) during their late Neogene radiation. Cranial appendages (horns, antlers, and ossicones) are commonly found in pecorans but are independently derived in each family that has them and thus not homologous in this infraorder (Janis and Scott 1987b, pp. 10-19). Cranial appendages appeared in the early Miocene when pecorans became widespread (Gentry 2000, p. 20).

Eumeryx, an advanced pecoran of the East Asian Middle Oligocene, has a distal bridge across the anterior metatarsal gully (Gentry 2000, p. 14), the condition seen in all cervids, and may represent a possible ancestor for the Cervidae. Cervidae proper first appeared in the Late Oligocene to Early Miocene with *Dicrocerus* (Hamilton 1978, p. 496, Goss 1983, p. 85). *Dicrocerus* had 2-pronged antlers that stemmed from long pedicles with burrs and large canines and is a possible ancestor for the extant Muntiacini (Hamilton 1978, p. 496). However, Gentry (2000, p. 15) points to *Procervulus* from the Early Miocene as the first Cervidae in that it had antlers with a distal fork but lacked a burr. In either case, the Cervidae originated in the warm woodlands and forests of the Northern Temperate Zone in the Late Oligocene to Early Miocene (Hamilton 1978, p. 496).

With cooling during the Middle Miocene cervids underwent an adaptive radiation (Gentry 2000, p. 20). Many new genera appeared in the Middle Miocene, including *Ligeromeryx* (Gentry 2000, p. 15), *Lagomeryx* (Gilbert *et al.* 2006, p. 112), *Heteroprox* (Pitra *et al.* 2004, p. 880), *Stephanocemas*, which had up to seven-pronged palmate antlers (Goss 1983, p. 85-6), *Blastomeryx*, which dispersed to North America, though it is unlikely to have been ancestral to the cervids currently found in the Americas and may not be a cervid, but a musk deer (family Moscidae; Janis 2000, p. 26). Further, the Middle Miocene marks the evolution of two extant tribes of cervids: the Capreolini from *Procapreolus* (Groves 2007, p. 253) and the Muntiacini, which may have evolved from *Euprox* (Pitra *et al.* 2004, p. 880) though *Euprox* is also cited as the possible ancestor of all later deer (Gentry 2000, p. 15).

The three other extant cervid tribes- Cervini, Odocoileini, and Alceini- all appeared during the Late Miocene and Early Pliocene, which was a time of increasing aridity and harsh climatic conditions (Gentry 2000, 21). The megacerines (giant deer) evolved later in the Pliocene from a Cervini ancestor. The evolution and ecology of each of the cervid tribes will be reviewed separately below.

The Cervidae

For most of their evolution, cervids were restricted to Eurasia and are not found in the Mediterranean region, the Middle East, India, or Africa until the Pliocene. Cervids were likely restricted to a dispersal corridor defined to the north by the Alpine-Himalayan mountain ranges and to the south by the Taurus-Zagros-Beluchi ranges (Heintz *et al.* 1990, p. 81; DiStefano & Petronio 1998, p. 53). With increasing climatic cooling at the end of the Pliocene, cervids experienced higher diversity than they have today (Gentry

2000, p. 22). This increased diversity and population density in response to climatic conditions may have forced cervids to disperse into new regions (Heintz *et al.* 1990, p. 81). The Odocoileini dispersed into the Americas sometime before 5 Ma (Geist 1998). Cervids first appear in India after 3.0 Ma (Heintz *et al.* 1990, p. 80; DiStefano & Petronio 1998, p. 53; Gentry 2000, p. 22). This is likely the same time that cervids dispersed to Indonesia and the Philippines (Heintz *et al.* 1990, p. 80) and Africa (Hamilton 1978, p. 496-7), though dispersal to the Middle East does not occur until the Early Pleistocene ('Ubeidiya, Israel at 1.4 Ma). The details of these dispersals form the story of evolution in each of the cervid tribes.

The following review of cervid subfamilies, tribes, genera, and species is structured along the phylogeny presented by Gilbert *et al.* (2006, p. 112), which was based on both mitochondrial and nuclear DNA, and will be used throughout this dissertation (see Figure 4-1). Species with an asterisk (*) next to their name below are species for which specimens were available for study (see Appendix A for details). This review is not intended to be comprehensive but rather is an overview of the vast, albeit often obscurely published, literature that exists regarding cervid ecology and evolution and is specifically designed around the cervid taxa included in this study.

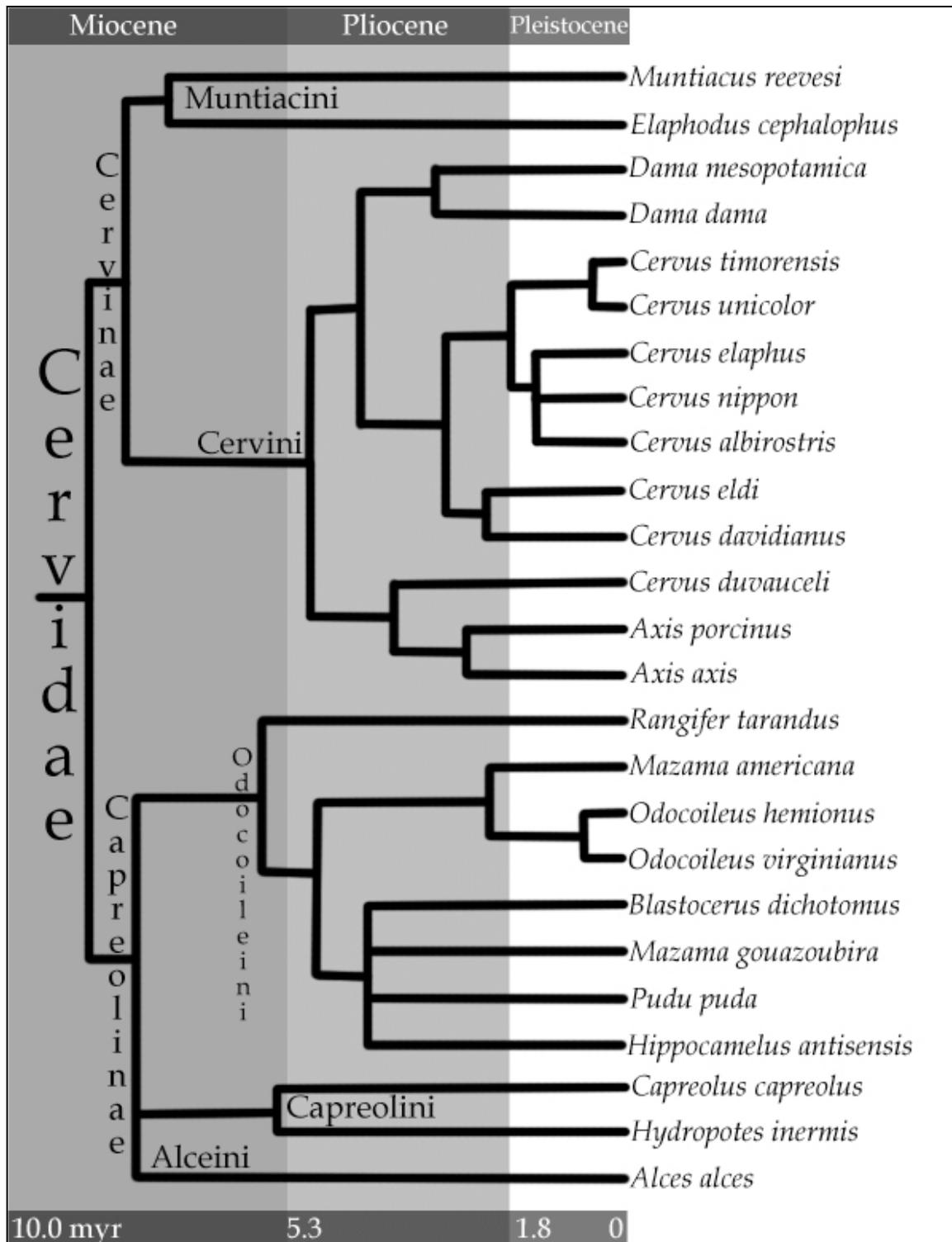


Figure 4-1 Phylogeny of the Cervidae, adapted from Gilbert *et al.* (2006, p. 112). This phylogeny will be used throughout this study.

Subfamily Cervinae

The subfamily Cervinae includes the tribes of Muntiacini (muntjaks) and Cervini (Old World Deer). The earliest Cervinae, such as *Eustylocerus*, were adapted to a subtropical temperate climate and exhibited moderate sexual dimorphism (Pitra *et al.* 2004, p. 881). Cervinae have the pleisometacarpalian condition wherein they have vestigial proximal metacarpals (II and V) with no distal remnants.

Tribe Muntiacini

*Elaphodus cephalophus**

*Muntiacus muntjak**

*M. reevesi**

M. feae

M. crinifrons

*M. atherodes**

Muntiacini evolved from primitive, two-pronged antlered deer in the mid-Miocene, possibly *Euprox* (Pitra *et al.* 2004, p. 880). *Eustyloceros* is the likely ancestor of the muntjaks as *Metacervulus* is for *Elaphodus* (Geist 1998, p. 44). The first species of the genus *Muntiacus*, *M. leilaoensis*, appeared in the late Miocene of Central Asia (Gilbert *et al.* 2005, p. 113). Extant muntjaks maintain many of the primitive morphologies of their ancestors and provide insight into the ecology and behavior of the earliest cervids.

The muntjaks (genus *Muntiacus*) and the tufted deer (genus *Elaphodus*) are the most primitive members of Cervidae, though there are several important differences between the two genera. Muntjaks (the ‘barking’ deer) are morphologically more primitive with very long pedicles and very small two-tined antlers that are shed

infrequently. Tufted deer have short pedicles and extremely small antlers that are rarely, if at all, shed (Geist 1998, p. 45). Tufted deer may be secondarily primitive, as is evidenced by their short pedicles (*ibid*, p. 47). *Elaphodus* is highly territorial with males and female of equal body size. It occupies montane scrub forests and escapes predators in a series of leaps (saltatorial locomotion), but never runs far from its territory (*ibid*). Three subspecies have been recognized, but they are more likely to be clinal variants across China (Groves & Grubb 1987, p. 38). Tufted deer have no lateral metacarpals or phalanges and extremely small lateral hooves while muntjaks have rather long proximal lateral metacarpals with no lateral phalanges, but lateral hooves are present (Geist 1998, p. 24). Both genera have fused cubonaviculars, external cuneiforms, and median cuneiforms (this condition is also present in *Pudu*, though it was independently acquired; *ibid*, p. 45). All Muntiacini possess large, curving upper canines used for combat (*ibid*, p. 46). Interestingly, muntjaks have a wide variety of chromosomal numbers- from 46 in *M. reevesi* to only 6-7 in *M. muntjak vaginalis*, the lowest number of any mammal (*ibid*, p. 45).

The main separation of *Muntiacus* and *Elaphodus* is their ecology. *Elaphodus* is a montane forest-dweller, living at 3,000 meters up to the tree line in China and Tibet and thrives in cooler habitats than muntjaks (Geist 1998, p. 46). Muntjaks are found in the warmer lower elevations across Asia and India. Where muntjaks are sympatric, they tend to be found in 'pairs' of species, usually with one larger-antlered species (*M. muntjak*- in Burma and Thailand, *M. reevesi*- in China, and *M. muntjak*- in Borneo) inhabiting more open habitats and the one smaller-antlered species (*M. fea*, *M. crinifrons*, and *M. atherodes*, respectively) inhabiting more closed habitats (Geist 1998, p. 48). It should be

noted that the difference between more open and closed is subtle; the difference between, say, seasonally dry monsoon forests and evergreen forests. The smaller-antlered species tend to be resource-defenders and use their antlers as weapons, while the larger antlered species use their antlers to spar for mating opportunities. The larger-antlered muntjaks are the phylogenetic older species while the smaller-antlered species are younger and secondarily primitive (*ibid*). Despite these subtle differences, muntjaks and tufted deer, as a tribe, can be characterized as small, primitive cervids that inhabit closed habitats.

Tribe Cervini

*Axis axis**

*A. porcinus**

Cervus albirostris

*C. duvauceli**

*C. elaphus**

*C. eldi**

*C. mariannus**

*C. nippon**

*C. timorensis**

*C. unicolor**

*Dama dama**

D. mesopotamica

*Elaphurus davidianus**

The tribe Cervini, or Old World Deer, is the second largest tribe of Cervidae, containing over one-third of all extant species of cervids (approximately 37%, depending on which taxonomy is used). The Cervini are a Pleistocene success story with descendants that spread across Eurasia and even into North America. They are currently found mainly in Asia with species occupying diverse habitats including ecotonal habitats, swamps, and forests. Though it is currently more conservative in ecological diversity than the largest cervid tribe, Odocoileini, during the Plio-Pleistocene, a great variety of

Cervini species evolved and flourished, many of which were open-adapted, but left no extant descendants. Two such groups are the megacerines and members of the genus *Eucladoceros*, the ‘bush-antlered’ deer. One megacerine, *Megaloceros giganteus*, will be included in this study and is described in detail below.

Cervocerus novorossiae of the Miocene-Pliocene boundary is referred to as the first member of the tribe Cervini (Gilbert *et al.* 2006, p. 113), though Groves and Grubb (1987, p. 24) point out that it had complete lateral metacarpals II and V, thus making it a candidate for the ancestor of both the plesiometacarpalian and telemetacarpalian cervids. *Cervocerus* had 3-pronged antlers, large canines, brachyodont dentition, and a very large lacrimal pit, making it very similar in morphology to the Muntiacini, excepting its antlers (*ibid*).

From a *Cervocerus*-like ancestor, the Cervini underwent several adaptive radiations, starting in the Pliocene with the primitive three-pronged forms that are represented today by the genera *Axis*, *Rusa*, and *Rucervus* (Geist 1998, p. 82). *Axis porcinus*, the extant hog deer, is the most primitive of the three-prong antlered deer as they retain small antlers grown from long pedicles and a small body size (Geist 1998, p. 55). Hog deer are widely distributed throughout Southeast Asia, but are ecologically restricted to areas with dense tall grass cover, upon which they can graze (*ibid*). Though they have a saltatorial body shape, they tend to escape predators by running along trails and diving under obstacles rather than leaping them. The other extant member of the same genus, *Axis axis*, the chital, has quite a different ecology, and may in fact not be as closely related to hog deer as previously thought (Groves & Grubb 1987, p. 41). The chital is a primitive ecotone deer that lives in herds all year and exhibits marked sexual

dimorphism (Geist 1998, p. 58-59). The chital has a much more cursorial body form than the hog deer, but it is not completely committed to cursoriality. It will run in a group away from predators and dive into cover as it tires (*ibid*). Chital feed on sprouting grasses and are dependent upon grass fires for renewal. It may have evolved as a savanna-succession grazer, exploiting the new growth that occurs after large bovines have grazed an area (Geist 1998, p. 59).

Species belonging to the subgenus *Rusa* (= *Cervus*) were widely dispersed in the Middle Pliocene and show adaptations to more open habitats (DiStefano & Petronio 2002, p. 313). The *Rusa* deer are morphologically similar to the *Pseudodama* of the Late Pliocene to Early Pleistocene, though the latter group evolved 4-pronged antlers (DiStefano & Petronio 1998, p. 4; 2002, p. 314-317). Extant *Rusa*-type Cervini are generally large, have 3-pronged antlers, and are found in warm habitats (Geist 1998, p. 73). Species include *Cervus unicolor* (the Indian sambar), *Cervus timorensis* (the Rusa deer), and *Cervus mariannus* (the Philippine sambar). These deer are course-vegetation grazers with subhypsodont dentition that inhabit tall grass and shrublands from the ocean up through subalpine zones (Geist 1998, p. 74). The sambar is generally a saltatorial runner, despite its large body size, but it is one of the few cervids that will turn and confront its predators directly (*ibid*, p. 75).

Members of the subgenus *Rucervus* (= *Cervus*) again show a different habitat adaptation - they are swamp specialists. *C. duvauceli* (the barasingha), *C. eldi* (Eld's deer), and *C. schomburgki* (not included in this study), all inhabit swamps, floodplains, and riverine and lacustrine areas and are specialist feeders of tall swamp grasses (Geist

1998, p. 78-79). They are large-bodied deer that have specialized legs and hooves for soft ground and escape predators in a manner similar to that of the chital (*ibid*).

The first representative of the most wide-spread genus in the Cervini, *Cervus*, appeared in the Early to Middle Pliocene. This species, *Cervus magnus*, had four-pronged antlers and is hypothesized to be ancestral to three lineages of deer; two that include boreal species (sika and red deer) and one that includes tropical species (the sambar, but see above) (DiStefano & Petronio 2002, p. 324). While the evolution of boreal forms from *Cervus magnus* seems probable, the evolution of the sambar and related species from *C. magnus* is suspect in that the extant species have 3-pronged antlers and are generally more primitive than what would be expected to have evolved from a common ancestor shared with the more advanced sika and red deer. It is more likely that *Axis*, *Rusa*, and *Rucerus* share a different, possibly older (*Cervocerus?*), common ancestor than *Cervus magnus*.

The first members of other extant genera also evolved during the Late Pliocene and include *Cervus nippon*, *C. albirostris*, and *Elaphurus davidanus* (Pitra *et al.* 2004, p. 892). *Elaphurus davidanus*, Père David's deer, is an old and primitive descendant of the 3-pronged deer that first appears in the Pliocene of China (Geist 1998, p. 101). It inhabits warm, moist riparian grasslands where it consumes grass and foliage. It is large with marked sexual dimorphism. Père David's deer has large hooves and is a slow runner (*ibid*). At the other end of the habitat spectrum is *Cervus (Przewalskium) albirostris*, the white-lipped deer, which is adapted to the cold, open, and rocky regions of the Tibetan alpine steppes at 3,500 to 5,000 meters (Geist 1998, p. 97-9). The white-lipped deer is large, gregarious, very sexually dimorphic, and has subhypsodont dentition. It inhabits

alpine shrublands where it consumes grasses, sedges, and forbs. To escape predators, the white-lipped deer runs rapidly into rocky ridges (*ibid*).

Cervus nippon, the sika, is the most primitive 4-pronged antler Cervini (Geist 1998, p. 87). Specimens of sika have been found dating to the Pliocene in China. Sika are warm-adapted and though somewhat ecologically flexible, prefer forested regions with dense understory (Feldhamer 1980, p. 4), however, Geist places them more as an ecotonal species (1998). Sika are saltatorial runners than hide in thickets when threatened (Geist 1998, p. 88) though they may stott (Feldhamer 1980, p. 5). They live in sexually segregated herds for most of the year and spend much time in ecotonal habitats. Sika consume a variety of vegetation, but prefer bamboo (*ibid*, p. 89).

Cervus elaphus, the red deer and wapiti, are one of the world's most iconic deer. In the European Middle Ages, they were closely associated with nobility, whose exclusive hunting rights were forcefully imposed (Cartmill 1996). *C. elaphus* has vexed biologists and taxonomists for well over a century in that it is unclear whether the species should be split into two different species- one the red deer of Eurasia and the other the wapiti of Siberia, China, and North America (Geist 1998, Pitra *et al.* 2004).

C. elaphus evolved from *Cervus perrieri*, which was similar to a large sika deer (Geist 1998, p. 89). The first *C. elaphus* are found in Europe at 900-700 kyr (*ibid*, p. 186). *C. elaphus acoronatus* is found extensively in mid-Pleistocene sites in England (Cromer Forest beds), Germany (Mauer, Mosbach), and Austria (Hundesheim fissure) (*ibid*) and may be ancestral to both red deer and wapiti (Groves and Grubb 1987, p. 48). There are three branches of *C. elaphus*- a primitive one found in China and Tibet, the red deer of Europe, and the wapiti of Siberia and North America, which may have been

separated for up to a million years (Geist 1998, p. 210). The most primitive *C. elaphus* inhabit montane forests to shrublands and are more dedicated browsers. They have 5-pronged antlers and are saltatorial. Though still more primitive than the wapiti, the European red deer are ecologically more plastic than the primitive *C. elaphus* of Asia, and inhabit a variety of habitats from forest to heaths (Geist 1998, p. 208). They also browse more than do wapiti. Red deer are enduring runners, which may take up to three relays of horses (2-5 hours) to bring down (*ibid*, p. 209). The most advanced *C. elaphus*, the wapiti, are the most open-adapted and evolved grazing adaptations.

“Formal classifications of deer have been inadequate, yet through repetition have become regarded as unquestioned primary sources of knowledge” (Groves & Grubb 1987, p. 22). This could not be any more true than it is for *Cervus elaphus*. Wapiti and red deer were regarded as different species until the two species were both placed in *Cervus elaphus* in 1940 by Heptner and repeated in the literature since (Geist 1998, p. 171). Recent studies have proven divisive. Groves and Grubb, in their morphological analysis state, “it is preferable to consider all elaphine deer as a single species” (1987, p. 46). Geist (1998, p. 171) also retains a single species but emphasizes the differences between the subgroups and points out that even in areas where primitive red deer and wapiti are geographically close they remain reproductively isolated as they exploit different habitats. The molecular study by Pitra *et al.* (2004, p. 890) indicates that not only are wapiti and red deer separated, but that *Cervus nippon* branches off of the wapiti line after the latter had split from the red deer. Pitra *et al.* (2004, p. 893) propose *Cervus canadensis* for the species name of the wapiti. In this study, the red deer will be referred

to as *C. elaphus* and the wapiti as *C. canadensis*. These groups can be collapsed if necessary.

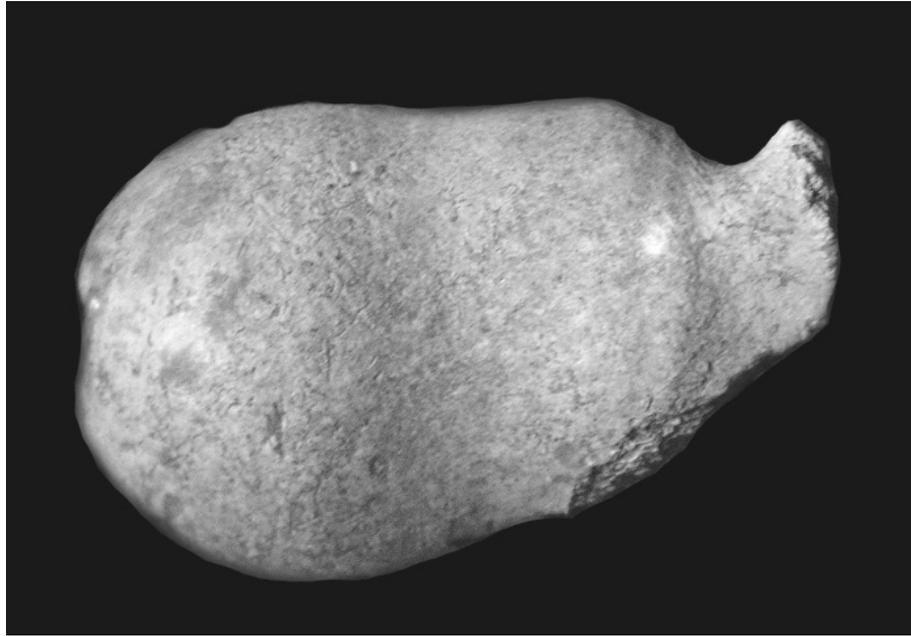


Figure 4-2 Superior view of the right femoral head of *Eucladoceros* from Valea Graunceanului (Specimen = “NoName”, housed at the “Emil Racovita” Institute of Speleology, Romania). The lateral (right hand side of the photo- the greater trochanter is missing) aspect of the femoral head is wide, giving the overall shape a rectangular appearance. This restricts the motion of the femur to the parasagittal plane, allowing for a stable joint surface during rapid locomotion.

The final group of open-adapted cervids belongs to genus *Eucladoceros*, all of which are now extinct (Geist 1998). They were, however, a major part of the Eurasian Pleistocene fauna. *Eucladoceros* first appears in the Early Pleistocene of Europe (Goss 1983, p. 87). *Eucladoceros ctenoides* was about the size of a modern red deer that had up to six tines on each antler (Kaiser & Croitor 2004, p. 664). *Eucladoceros* is found all across Europe and as far east as China (Geist 1998, p. 83). Adaptations to open habitats are reflected in their diet, as the mesowear signal of their dentition is similar to that of bovids in which grass makes up 80% of their diet (Kaiser & Croitor 2004, p. 669). Furthermore, the femoral head of *Eucladoceros* is wide in its lateral aspect, limiting

movement to the parasagittal plane, which is associated with adaptations to cursoriality (Kappelman 1988, see Figure 4-2). The post-crania of *Eucladoceros* tend to be more gracile than those of the megacerines, which were cold-adapted large deer (Van der Made 1999, p. 397).

Commonly (and erroneously) known as the Irish Elk, *Megaloceros giganteus* was neither an elk nor was it restricted to Ireland (Geist 1998, p. 122) and will be referred to here as the ‘giant deer’. *Megaloceros giganteus* belongs to the cervid subfamily Cervinae though they are sometimes placed into their own tribe, Megacerini (DiStefano & Petronio 2002, p. 313; Lister *et al.* 2005, p. 851). Phylogenies of the giant deer based on both morphological and molecular data (Lister *et al.* 2005) place it well within the Cervini as a sister taxon to *Dama dama*. Thus, placing *Megaloceros* and its relatives (including *Dama*) in their own tribe would render Cervini paraphyletic. To avoid this here, *Megaloceros* and *Dama* will remain in Cervini as a morphological grade (the megacerines), but not as a separate clade.

The megacerines likely evolved from a form similar to *Praemegaceros*, which is also included in this study, though the specimens from ‘Ubeidiya are assigned to species unknown. Though *Eucladoceros* sometimes has been considered a megacerine, it is more probable that *Megaloceros* and *Dama* form a group to the exclusion of *Eucladoceros* (Lister *et al.* 2005). Megacerines flourished throughout the Old World during the Pleistocene with species distributed from North Africa to Siberia and from Ireland to Japan (Geist 1998, p. 124). The megacerines, and *Megaloceros*, especially, are iconic of the Eurasian Pleistocene megafauna.

Though referred to as the ‘giant deer’, *Megaloceros giganteus* was not the largest deer to have existed, as that honor goes to *Cervalces latrifrons* (Geist 1998, p. 126; see below). In body size it was similar to the extant moose, *Alces alces*, but was more stoutly built with more robust limbs. The most remarkable feature of *M. giganteus* is its antler size, which reached up to 3.6 meters across (Stuart *et al.* 2004). These were the largest antlers ever carried by a cervid, both relatively and absolutely (Geist 1998). Having antlers of this size restricted the giant deer in several ways. First, these large antlers would have excluded males from closed habitats. Secondly, these deer would have to exploit very high quality food resources to invest in such large cranial appendages year after year. This would have precluded *M. giganteus* from inhabiting the tundra regions of the Eurasian Pleistocene (Stuart *et al.* 2004). This habitat preference is seen in the distribution of *M. giganteus* during glacial cycles. During interstadials, *M. giganteus* is widely distributed from Ireland to Siberia, while during glacial maxima, it is found only in refugia in southeastern Europe and south-central Asia until it finally goes extinct, last appearing in western Siberia at 6,816 years ago (Stuart *et al.* 2004).

Geist (1998) argues that *Megaloceros giganteus* was the most cursorial deer to have existed and this is the reason for its inclusion in this dissertation. While there are few extant cursorial deer species, it is likely that they were more common in the past and including them in this study allows for a broader definition of cervid cursoriality. Evidence for the extreme cursorial adaptation of *M. giganteus* can be found in a variety of morphological features. First, the size of a cervid’s antlers is an indication of adaptation to open habitats, as they are an honest signal of a male’s fitness (Geist 1998). In open habitats, cervid young must be able to run away from predators soon after they

are born and thus must be born large and precocious (*ibid*). Females select males with the best indication of fitness- very large antlers. A second indication of *M. giganteus* cursoriality is found in its limb portions. In comparing ratios of several limb and vertebral elements, Geist (1998, p. 140) found that *M. giganteus* clustered with short-legged cursorial bovid species such as the oryx, saiga, and eland, all of which are found in very open habitats. Further, Geist found that *M. giganteus* was likely an endurance runner with a thoracic cavity that had 1.75 times the volume of the similarly sized moose, which is indicative of a large heart and lungs; necessary features for long-distance cursor (Geist 1998, p. 142).

Megaloceros giganteus is included in this study as an open-adapted cervid, though this will be tested for each unit of analysis. Further details on the specimens included in this study can be found in Chapter 5 and Appendix B.

The fallow deer, *Dama dama*, is the last living relative of the giant deer. It is a striking deer with large, palmate antlers and a spotted coat. Though once widespread in Europe (and even into North Africa), fallow deer populations shrank during the cold glacial periods of the Pleistocene (Geist 1998, p. 126). This, in addition to hunting and placing these deer in royal parks during historic times, has made fallow deer almost extinct in their natural habitats during modern times (Novak 1999, p. 1099). Fallow deer have always been a favorite of kings and rulers, especially the Romans, Normans, and Phoenicians and even were transported to ancient Egypt, as they are proposed to be the deer that appears in Egyptian art (Goss 1983, p. 94-5; Novak 1999, p. 1099).

The evolution of the fallow deer may have its roots in *Pseudodama lyra* from the Italian Middle Pliocene, which had 3-pronged antlers (DiStefano & Petronio 1998, p. 41).

Several *Pseudodama* species are recognized through the Plio-Pleistocene, including *P. nestii*, which had 4-pronged antlers (*ibid*). This study includes *Pseudodama* sp. specimens from ‘Ubeidiya, Israel. DiStefano & Petronio (2002, p. 317) state that due to their close morphological affinity, *Pseudodama* should be referred to as genus *Rusa*. However, Groves and Grubb (1987, p. 40) and Geist (1998) are of the opinion that the fallow deer have ancestry in the megacerines. The first species with palmate antlers, the Clacton fallow deer is sometimes give its own genus (Groves & Grubb 1987, p. 40; DiStefano & Petronio 2002, p. 320) and it is sometimes referred to as a subspecies of the extant fallow deer (Feldhamer *et al.* 1988, p. 2). It appeared in the Middle Pleistocene (400 kyr) of Europe (Feldhamer *et al.* 1988, p. 2; DiStefano & Petronio 2002, p. 320). Specimens very similar to the extant fallow deer, *Dama dama*, appear at 250 kyr (Feldhamer *et al.* 1988, p. 2). Fallow deer have been successfully introduced to countries across the globe but their native habitats were warm, open regions in Europe. They are gregarious and are the most adapted to grazing of all the extant deer (Geist 1998, p. 96).

Cervini did disperse to northern Africa, though they are never the dominant taxon there, most likely due to competitive exclusion with the Bovidae (Goss 1983, p. 93). Three taxa are represented in African faunas. *Megaloceros algiricus* and *Cervus elaphus barbarus*, the latter of which still lives there, dispersed to Tunisia and Algeria in the late Pliocene through island hopping via Sicily (Hamilton 1978, p. 496-7) (though this date appears to be too early and the Middle Pleistocene seems more likely). *Dama dama* was also present in Africa from Egypt to Ethiopia, but went extinct by the late Pleistocene (*ibid*, p. 497). It is likely that bovids were better competitors than cervids in Africa. Bovids had been evolving on the African continent while cervids evolved in Eurasia.

Bovids have been noted for having stronger habitat-specificity than cervids, which are generally characterized as closed habitat dwellers (Mendoza *et al.* 2002, Christiansen & Adolfssen 2007). Cervids evolved to be more generalistic. Indeed, those cervid species that are the most widespread are either holarctic species (*Alces alces*, *Rangifer tarandus*) or are generalists (*Cervus elaphus*, *Odocoileus virginianus*). I hypothesize (after Geist 1998) that adaptation to highly seasonal environments requires a species to be a generalist. This is the reason for the success of the Cervidae in the glacial times. The consequence of being a generalist is that they are out-competed by specialists when conditions favor the specialists' adaptations. Perhaps this is why cervids were unsuccessful in Africa. Bovids occur in Eurasia and North America (but not South America) and they, like cervids, evolved in Asia. Eurasian and North American bovids are found in the tribes Bovini and Caprini. Though some cervid species became open-adapted, no species ever evolved the bauplan that is associated with the Bovini, which are generally very large, heavy, squat grazers with marked hypsodont dentition. *Bos* (cattle, yak), *Bison* (bison), and *Bubalus* (water buffalo) are examples of Eurasian Bovini, though many more exist. The Caprini were highly successful, again, in adaptations that cervids never evolved (except the *Hippocamelus* of South America and *Cervus albirostris*). The Caprini are the *Capra* (goats) and *Ovis* (sheep) that are generally specialists in extreme mountainous habitats, and the musk ox (*Ovibos*), which is adapted to extreme cold and are convergent with the Bovini bauplan.

Subfamily Capreolinae

Following the phylogeny of Gilbert *et al.* (2006), the subfamily Capreolinae includes the telemetacarpalian (retaining distal remnants of the lateral metacarpals) cervid

tribes Capreolini, Odocoileini, and Alceini. The molecular study by Gilbert *et al.* (2006) reported monophylogeny for the telemetacarpalian cervids. In the past, allying these tribes has been problematic due to the antlerless state of *Hydropotes*, which was often cited as a primitive cervid (Groves & Grubb 1987, p. 33, Janis & Scott 1987a, p. 14). However, *Hydropotes* has been shown (Gilbert *et al.* 2006) to be a sister taxon to *Capreolus*, placing it in the tribe Capreolini. In addition to being telemetacarpalian, the Capreolinae are united by the presence of a vomer septum that completely separates the choana (*ibid*, p. 102). There is little else to unite these tribes. The Capreolini are small-bodied with species that are cold-adapted generalists (*Capreolus*) and highly derived open-adapted specialists (*Hydropotes*). The extant Alceini (the moose) are closed-adapted cervids that evolved from open-adapted ancestors. The Odocoileini have species that have adapted to every ecological niche an herbivore can inhabit due to their successful adaptive radiation in South America. Each tribe will be reviewed in detail below.

Tribe Capreolini

*Capreolus capreolus**
C. pygargus
*Hydropotes inermis**

The Capreolini evolved in the Middle Miocene (Groves 2007, p. 253) in China and had primitive 3-pronged antlers (DiStefano & Petronio 2002, p. 329). They are part of the radiation of cervids into cold habitats (Geist 1998, p. 303). *Capreolus* probably has its origins in *Procapreolus* from the Pliocene, though the extant genus does not appear until the Middle Pleistocene (Sempere *et al.* 1996, p. 2; Whitehead 1993). The living species, *Capreolus capreolus*, the European roe deer, and *C. pygargus*, the Siberian roe deer, are separated geographically by the Caucasus Mountains, with the *C. capreolus*

found south of this mountain range and the latter to the north, living in latitudes up to 65° North (Geist 1998, p. 302-6). The Siberian roe deer is an extreme cold-adapted specialist and is intolerant of warmer conditions. *C. pygargus* is twice as large as *C. capreolus*, but is still a rather small deer at a maximum of 65 kg (*ibid*). The European roe deer averages about 25 kg with low sexual dimorphism (*ibid*). Like red deer and white-tailed deer, the European roe deer are habitat generalists due to inhabiting temperate regions with marked seasonality. *C. capreolus* can be found in habitats ranging from open meadows to forest-steppes (Sempere *et al.* 1996, p. 3). They tend to be solitary, territorial hidlers when in dense vegetation and form herds with less territoriality in more open habitats (Geist 1998, p. 305-308). European roe deer, like the chital, *Axis axis*, may be dependent upon succession-grazing, especially in the spring (*ibid*, p. 303). Unlike the chital, the European roe is a saltatorial runner with low endurance, and rely mainly on being cryptic to avoid predators (*ibid*, p. 308).

Hydropotes inermis, the water deer, is one of the most puzzling extant cervids. It is the only extant cervid with no antlers, though it does have very large saber-like canines. These characters alone have been cited as evidence of the water deer's primitiveness (Groves & Grubb 1987, p. 33, Janis & Scott 1987a, p. 14). However, it appears that this condition is likely secondarily derived (Randi *et al.* 1998, p. 799, Geist 1998, p. 21). The water deer is a temperate species that prefers hard ground near to alluvial deltas that have reeds and grasses (Geist 1998, p. 27-8). They are territorial resource defenders that feed on grass shoots. They are mainly cryptic but run with 'rabbitlike locomotion' (*ibid*, p. 28) when threatened.

Tribe Odocoileini

*Blastocerus dichotomus**
*Hippocamelus antisensis**
*H. bisculus**
*Mazama americana**
*M. chunyi**
*M. gouazoubira**
*M. rufina**
*Odocoileus hemionus**
*O. virginianus**
*Ozotoceros bezoarticus**
*Pudu mephistophiles**
*P. puda**
*Rangifer tarandus**

There is frustratingly little evidence of the origins of the Odocoileini, the New World deer. Molecular evidence points to a split from the pleisometacarpalian deer around 9.3-12.4 Ma in Eurasia (Miyamoto *et al.* 1990, p. 6131) but the fossil evidence to support this is lacking. Vislobokova (1980) has placed *Pavlodaria* from the early Pliocene of Kazakhstan as the earliest Odocoileini, but no other Eurasian paleontological evidence of the Odocoileini exists. The Odocoileini make a sudden appearance in North America at 5.0 Ma as *Eocoileus gentryorum* in Florida (Goss 1983, p. 95; Webb 2000). *Eocoileus* generally have relatively simple, 3-pronged antlers, though one specimen does show basal palmation (Webb 2000, p. 44). Also at 5.0 Ma, *Bretzia pseudoalces* is found in Nebraska and has palmated antlers (Webb 200, p. 53), which suggested adaptation to more open habitats (Geist 1998, p. 265). *Odocoileus brachyodontus* is found shortly thereafter at approximately 3.5 Ma in Kansas (Whitehead 1993) and later in California at 2.2 Ma (Geist 1998, p. 106). A remarkable cervid from the Pliocene (~3.0 Ma) of North America is *Navahoceros*, which was adapted to the mountainous terrain of the Rocky Mountains and had broad, short metapodia (Geist 1998, p. 111; Webb 200, p. 53). It is

around this same time (3.5-3.0 Ma) that the Great American Interchange of fauna between North and South America occurred (*ibid*, p. 38) and with it, deer dispersed to South America (as reviewed below).

White-tailed deer, *Odocoileus virginianus*, is the oldest species of extant deer, first appearing in the Late Pliocene (Geist 1998). They are true ecological opportunists and generalists. They occupy the largest latitudinal distance of any cervid- from 61° North to 18° South in Peru (Geist 1998, p. 112). It is thought that some white-tails dispersed to South America early, diversified regionally on that continent, and gave rise to the other species of South American deer. Indeed, South American white-tails are more genetically distant from North American white-tails than the latter is from black-tailed deer (*Odocoileus hemionus columbianus*) (*ibid*, p. 267). The South American white-tails are more primitive than their Northern relatives with smaller body sizes, smaller antlers, vestigial canines (*ibid*, p. 268) and no metatarsal gland (Groves and Grubb 1987, p. 37). White-tails are not prevalent in the paleontological record until after the Pleistocene megafaunal extinctions at 11,500 years ago. Before that, North America was populated by ecological specialists, with which it cannot compete (Geist 1998, p. 266). The extinctions reduced the numbers of large herbivores (competitors for resources) from 56 species to only 11 (*ibid*, p. 265) and then the already old species, *Odocoileus virginianus* flourished. There are currently 37 recognized subspecies of the white-tail (Geist 1998, p. 255), though Groves and Grubb (1987, p. 37) only accept two- *O. v. cariacou*, the primitive South American variety, and *O. v. virginianus*, the temperate white-tails. Much of the rest of white-tail variation is clinal. White-tail deer exist in almost every herbivorous niche in North America, except deserts and regions with very

deep snow (Geist 1998, p. 255-314). They inhabit forests, woodlands, swamps, but show a preference for ecotones and thrive in agricultural and disturbed areas. Across these varied landscapes, there are subtle differences in behaviors that are associated with more open or more closed habitats (as discussed below). White-tails are very plastic in their feeding behavior, which also varies with habitat, and will consume everything from graze to browse to carrion (*ibid*). White-tailed deer are swift runners, obtaining speeds of up to 65 km/h, but also retain the ability for saltatorial locomotion when necessary. White-tails run away from predators along series of well-known trails that are relatively free of ground obstacles yet curve enough to break visual contact with their predator (*ibid*). Geist (1998, p. 256) hypothesizes there to be a lack of fit between morphological adaptations and environment in white-tails, which is what one would expect of a generalist. Such a hypothesis is testable with the methods introduced in this study (though, due to the small size included here, these tests are preliminary).

Where white-tailed deer are the oldest extant cervid species, their close relative, the mule deer, *Odocoileus hemionus hemionus*, is the youngest (Geist 1998, p. 255-314). Mule deer evolved around 11 kyr from hybridization between white-tails and black-tailed deer (*O. h. columbianus* and *O. h. sitkensis*), the latter of which evolved from the white-tailed deer around 2 Ma (Geist 1998, p. 272) and has a much more constricted range (Alaska to British Columbia) than mule deer. Thus, the white-tails, black-tails, and mule deer form a distinct lineage. That they appeared shortly after the Pleistocene megafaunal extinctions is unlikely to be a coincidence. Mule deer, though a subspecies, are often treated as a separate species and are often referred to simply as *Odocoileus hemionus* (Anderson & Wallmo 1984, Whitehead 1993, Novak 1999, Eisenberg 2000, Gilbert *et al.*

2006, etc.), as they will be here. The ecology of white-tails and mule deer is very different. Though the two species are sometimes found in the same regions, mule deer are much more open-adapted. They can be found from Arizona to the Yukon Territory (Geist 1998, p. 273). Like white-tails, mule deer are opportunistic feeders, though mule deer include plants from more arid regions, such as prickly pear cactus, in their diets (*ibid*, p. 259). Mule deer are stotting-specialists and this explains their success in mountainous regions. While stotting, a deer lands with all four hooves on the ground at the same time, flexes the limbs after landing and springs forward again with the rearlimbs leaving the ground only slightly after the forelimbs. This is a costly form of locomotion, due to excessive body lift, but it is extremely efficient for bounding uphill, which is difficult to do in a gallop (Geist 1998, p. 288-289). By stotting, the mule deer can rapidly change directions, even in mid-stott, and can easily place obstacles between itself and its predator, which can include small gullies, as a stott can carry the mule deer 8 or more meters. Though effective for escaping predators in mountainous habitats, stotting is slower (30-50 km/h) and less efficient on flat land than a gallop (65 km/h). Mule deer do gallop, though mainly in social contexts (males chasing females) (*ibid*, p. 288). Though categorized here as an “Open” adapted species, mule deer are hypothesized to have unique morphology reflecting their stotting behavior. The mule deer leaves and returns to the ground at 25° to 30° angles while stotting, while a cursorial deer, such as *Rangifer*, has very little angular displacement (1°) while running. This should be reflected in mule deer joint surfaces in that they should be narrow in the medial-lateral direction to limit movement to the parasagittal plane but long in the anterior-posterior direction to provide more room for rotation.

The dispersal of cervids to South America after the Panama land-bridge closure of the Late Pliocene is one of the most remarkable examples of an adaptive radiation. From one, possibly two ancestors, cervids evolved to fill a huge variety of niches in South America- inhabiting dense tropical forests, mountain forests, open grasslands, swamps, and high, rocky mountains. Throughout the Pleistocene, many species evolved and went extinct, as is expected in an adaptive radiation. Some of the survivors include *Blastocerus* (the extant marsh deer), early specimens of which are dated to the Plio-Pleistocene of Argentina (Webb 2000, p. 55). The genera *Mazama* (the Brouzet deer) and *Ozotoceros* (the Pampas deer) are known from the late Pleistocene of Brazil (*ibid*, p. 56). Webb (2000, p. 56) claims an ancestor-descent relationship between *Rangifer* (reindeer/caribou) and *Pudu* (the smallest extant deer) and *Hippocamelus* (the Andean mountain deer). Geist (1998 p. 107) cites *Odocoileus* as the probable ancestor of all South American cervids, except the *Hippocamelus* species, which he claims to be more primitive and possibly descended from a '*Hippocamelus*-like deer' dating to the Pliocene of California. To further complicate things, molecular evidence suggests that the genus *Mazama* is paraphyletic, with *Mazama americana* linked to *Odocoileus* and the rest of *Mazama* species linked to the genera *Blastocerus*, *Hippocamelus*, and *Pudu* (Gilbert *et al.* 2006, p. 111). Interestingly, the former group includes the cervids that inhabit both North and South America while the latter group includes those cervids restricted to South America (*ibid*). Further studies are needed to test if this distinction is valid and if so, the species referred to as the Brouzet deer represent an extraordinary occurrence of convergence.

The South American deer are mainly saltatorial, which may be a result of having evolved in the absence of cursorial predators (Geist 1998, p. 110). While they are similar

in predator-escape behavior, other aspects of their ecology differ widely. *Blastocercus dichotomus*, the marsh deer, is the largest of the South American species with long, thin legs and large haunches (*ibid*, p. 117). It inhabits wetlands, riverine regions, and marshes with tall grass where it consumes grasses, reeds, and aquatic plants (Pinder & Grosse 1991, p. 3; Novak 1999, p. 1118). Its powerful rearlimbs and long, widely-splaying hooves allow it to produce powerful saltatorial leaps on marshy substrates (Geist 1998, p. 117). Marsh deer have heavy, 4-pronged antlers and are highly sexually dimorphic (*ibid*). *Ozotoceros bezoarticus*, the Pampas deer, is one of the few extant open-adapted deer. However, it is not cursorial, but rather escapes predators with a stiff-legged run or long saltatorial leaps (*ibid*, Novak 1999, p. 1120). It is a grassland specialist with subhysodont dentition (Geist 1998, p. 115) that feeds on new green growth (Jackson 1987, p. 3). Pampas deer are small, have 3-pronged antlers, are gregarious, have little sexual dimorphism, and are not territorial (Geist 1998, p. 115-6). Though the two species of *Hippocamelus* are mountain-adapted, they differ in their ecology. *Hippocamelus antisensis*, the taruka, is found in the high elevations (4,100-5,000 m) of the Andes from 12° to 28° South (*ibid*, p. 113). It is a short-legged rocky-outcrop specialist with small hooves. The taruka is sexually dimorphic though it has short antlers. The more open-adapted of the two species, *H. antisensis* feeds on forbs and grasses (*ibid*). The huemul, *Hippocamelus bisculus*, is found in lower elevations of the Andes (1,300-1,700 m; Novak 1999, p. 1122) at latitudes of 34° to 53° South, and is separated from the taruka by a desert (Geist 1998, p. 113). Like the taruka, the huemul inhabits steep and rocky terrain, but prefers more cover and feeds on more foliage and browse (Eisenberg 2000, p. 191).

The huemul will hide from predators and flee rapidly when spotted, placing obstacles between itself and its predator (*ibid*, p. 115).

In addition to open-adapted and mountain-adapted cervids, the South American radiation produced several forest-adapted species. The brocket deer (*Mazama*) are secondarily primitive, with small body sizes and small, dagger-like antlers that they use for defending resources (Geist 1998, p. 118). All brockets are saltatorial. The largest and most ubiquitous species, *M. americana*, the red brocket, is found in mountainous regions to plains from North America (southern Mexico) to Argentina and is rather ecologically plastic (*ibid*), though it does generally prefer dense thickets (Whitehead 1993) or moist forests (Eisenberg 2000, p. 193). *M. gouazoubria*, the gray brocket, is smaller and a faster runner (Geist 1998, p. 119) that prefers more open habitats, such as woodlands and savannas (Whitehead 1993; Eisenberg 2000, p. 193). *M. rufina*, the little red brocket, is an inhabitant of dense, cool, cloud forests from Venezuela to Ecuador (Geist 1998, p. 119). *M. chunyi*, the dwarf brocket, is a very small (8-12 kg) montane species, living at elevations up to 3,000 meters (*ibid*). It is outwardly similar to the pudu, to which the brockets are closely related and with which they can hybridize (*ibid*, p. 120). The pudu are the smallest extant cervids. They are very paedomorphic and duiker-like with small, spiky antlers and little sexual dimorphism. To escape predators, they run away in a zigzagging pattern sometimes even climbing inclined trees to cross streams (Novak 1999, p. 1126). The smaller species, *Pudu mephistophiles*, the northern pudu, weighs only 3.3-6 kg (Geist 1998, p. 120). It inhabits temperate forests at elevations of 2,000-4,000 meters (Novak 1999, p. 1126) and is a choosy browser. *Pudu puda*, the southern pudu, is larger- up to 13.4 kg- and inhabits humid forests of lower elevations (below 1,700 meters). The

two pudu species are widely separated, with 3,200 kilometers between them (Whitehead 1993).

Rangifer tarandus, the reindeer and caribou, is an old New World deer, specimens of which appear in Alaska around 2 Ma (Webb 2000, p. 58). *Rangifer* is different enough from the rest of the Odocoileini that it has often been placed in its own tribe, Rangiferini (Webb 2000), though molecular evidence suggests that it is within Odocoileini (Pitra *et al.* 2004; Gilbert *et al.* 2006). *Rangifer tarandus* is a deer of extremes: it migrates farther than any other terrestrial mammal- 5,055 km/yr (Novak 1999, p. 1129), it is the most cursorial extant deer (Geist 1998, p. 315), has the largest relative antler mass (p. 329), has the largest circumpolar distribution of any ungulate- from 14° West to 5° East, lives at latitudes up to 80° North (p. 319), and is the only cervid to ever have been domesticated (p. 315). *Rangifer* is adapted to the harshest of arctic environments, where it can stand temperatures down to -50° C and 280 days of snow (*ibid*, p. 318). There are two varieties of *Rangifer tarandus*- the barren ground and woodland forms, both of which have several subspecies. The barren ground reindeer evolved with wolves as predators and thus are gregarious and extremely cursorial runners on short limbs (*ibid*, p. 328). They do not hold territory and tend to be less sexually dimorphic than their woodland counterparts. They eat almost anything they come across, including animal carcasses and poisonous mushrooms, but are lichen specialists. Due to the large numbers in which they congregate, they can dramatically change the vegetation of an area by removing all the foliage (*ibid*, p. 330). The woodland forms practice more resource defense where males set up territories around females and fight to keep them. Woodland caribou tend to be

solitary hidlers (*ibid*, p. 328). *Rangifer tarandus* is probably one of the most important cervids in human evolution, as Neanderthals and early European *Homo sapiens* were highly dependant upon them as a resource (Gaudzinski & Roebroeks 2000, Mellars 2004). There are still reindeer herders in Sweden and Norway to this day (Suominen & Olofsson 2000).

Tribe Alceini

*Alces alces**

The Alceini are a product of the open-adapted radiation of cervids that began in the Late Pliocene. The first recognized Alceini is *Libralces (Cervalces) gallicus* from 2.0-1.6 Ma in Europe (Senèze, France) (Geist 1998, p. 223). *Libralces* had very unusual antlers that had small, spoon-shaped palms stemming from a very long beam (*ibid*, p. 247). It was a large, cold-adapted cursorial deer that had long legs adapted for reach rather than power (Geist 1998, p. 247). Though it was adapted to open habitats, it remained a browser, as indicated by its narrow muzzle (*ibid*). Species identified *Alces* sp. are included in this study and since they are from Senèze it is likely that they are *Libralces gallicus*. While most authors accept that *Libralces (Cervalces)* is ancestral to the Early Pleistocene *Cervalces*, Breda and Marchetti (2005, p. 777) state that they are a likely example of a chronospecies. From *Libralces* to *Cervalces* there was a dramatic increase in body size with a shortening of the antler beam (*ibid*). *Cervalces latifrons* was the largest cervid to have lived, estimated to have been twice as heavy as the extant moose and very robust with antlers widths approaching those of *Megaloceros* (Geist 1998, p. 248). *Cervalces* maintained a primitive dentition and may have consumed more woody matter than *Libralces* (*ibid*). *Cervalces* dispersed to North America during the

Rancholabrean (*Cervalces scotti*, the stag-moose) where it became fairly habitat specific, occupying marshy regions around proglacial lakes (Geist 1998, p. 251). While it resembled *Cervalces latifrons* cranially, post-cranially *C. scotti* was smaller with long legs and a short neck (*ibid*). Such morphology required it to be a foliage feeder. *Cervalces scotti* was replaced by the extant moose during the Younger Dryas, though *C. scotti* was probably not ancestral to *Alces alces* (Geist 1998, p. 253). *Alces alces* did not enter North America until a millennium after the terminal date of *Cervalces scotti* (*ibid*, p. 228), while the oldest fossils of *Alces alces* are from Europe, dating to 200-100 kyr (Franzmann 1981, p. 2).

Alces alces likely evolved from *Cervalces latifrons* due to competition from *Megaloceros*. Both *Cervalces* and *Megaloceros* were cold-adapted deer that inhabited open and shrub habitats (Geist 1998, p. 249). Competition for resources forced these two deer to exploit different niches. *Megaloceros* remained cursorial and open-adapted while *Alces* evolved to be more closed-adapted and remained a browser in riparian and forest habitats (*ibid*). Extant moose are a holarctic species that inhabit almost all areas north of 40° latitude (*ibid*, p. 228). Though moose only dispersed to North America around 9,500 years ago, the American and European forms are different both behaviorally and ecologically. American moose (*A. alces gigas*, *A. a. shirasi*, *A. a. americanus*, amongst other subspecies) probably filled the niche that *Cervalces scotti* left open with its extinction and tend to be more open-adapted than the European moose with larger antlers and more ornate coloration (*ibid*, p. 231-3). European moose, having had *Megaloceros* to compete with, inhabit more closed areas. There is little difference in the body size of the European and America moose, as body size tends to vary more with latitude.

In general, *Alces alces* can be characterized as the largest extant cervid with palmate antlers, long limbs, and a browsing diet. It is a cold-adapted woodland to forest dweller that is intolerant of heat. Moose are most remarkable in their locomotor behavior. They are highly specialized trotters that use their long limbs to step over obstacles that their pursuers must leap over, tiring predators before they can catch the moose, which can trot at speeds up to 60 km/h (Geist 1998, p. 223-4). Moose are also one of the very few cervids that will turn and face and sometimes even attack predators (*ibid*, p. 225). Moose are a remnant of megafauna that characterize the Pleistocene and use their large size to their advantage.

General remarks on cervid ecology, evolution, and behavior

Cervid evolution can be generally characterized as the evolution of increasingly more open-adapted forms from primitive, closed-adapted forms (with the exception of the evolution of the secondarily primitive South American paedomorphs). Starting in the Miocene with small, saltatorial, resource-defending cervids, such as the muntjaks, there were several radiations into more open environments. Primitive 3-prong antlered cervids dispersed from closed forests into temperate forests, woodlands, and swamps. 4-prong antlered cervids moved out into ecotones and the open habitats of the Plio-Pleistocene boundary. Pleistocene megacervids evolved and dispersed throughout open habitats in Eurasia and even into North Africa. Larger-bodied cervids (excepting the Alceini) failed to evolve in the Americas due to the presence of its own endemic megafauna. Instead, a smaller opportunistic species held on through the Late Pliocene to Pleistocene and then, in the wake of Pleistocene extinction, spread across North America. With the closure of the Panama landbridge in the Pliocene, cervids radiated throughout South America,

filling every niche available to an herbivore. This is a gross simplification of the millions of years of cervid evolution, but it does serve to illustrate some generalities that can be drawn regarding adaptation and environment.

Throughout their evolutionary history, cervids have converged upon specific adaptations to habitats via natural and sexual selection. Figure 4-3 is a summary of some of the generalizations about cervid ecology and behavior that can be associated with habitat type. Cervids inhabiting forests tend to have smaller body sizes, as is exemplified by the genera *Pudu*, *Muntiacus*, and *Mazama*. *Alces* is an exception to this rule, but it evolved from open-adapted ancestors and its specialized predator-escape behavior requires a large body size. At the other end of the spectrum, the open-adapted cervids tend to be large, as is seen in the extinct *Megaloceros* and *Eucladoceros*, and the extant *Rangifer* and the *Rusa* and *Rucervus* subgenera. There are several exceptions to be noted: *Ozotoceros* and *Hydropotes* are both open-adapted, yet rather small. However, neither of the species is adapted to great areas of open expanses and instead they inhabit smaller pockets of open areas that are surrounded by more closed habitats. Accordingly, neither species is truly cursorial, as the other open-adapted cervids are, and instead they will run to cover when threatened. Another exception is the very large *Cervus elaphus/canadensis* group that generally requires some amount of cover. However, the wapiti is more open-adapted and is also much larger.

Though extant cervids are mostly saltatorial, which is associated with closed to ecotonal habitats, true cursors have evolved several times, including *Megaloceros*, *Eucladoceros*, and *Rangifer*. All three of these genera are open-habitat specialists. Other

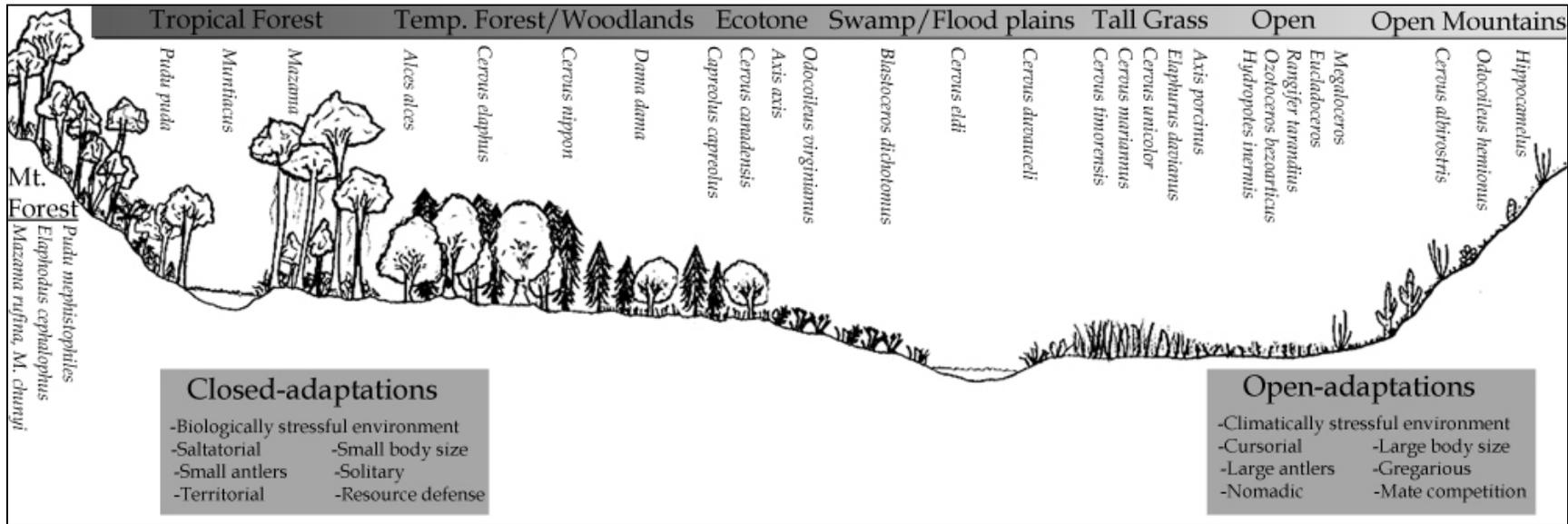


Figure 4-3 The continuous nature of habitat distribution. Though most cervid species can be identified with a particular habitat type, they may make use of different habitats throughout their range. Thus, the distribution of cervids forms a continuum from more closed to more open habitats. Suites of morphological and behavioral characteristics are associated with being closed-adapted or open-adapted (Geist 1998). These characteristics are reflected in cervid morphology, which can be placed along this continuum using a Habitat Score (Scott 2004).

predator-escape adaptations to open habitats have been evolved by cervids, such as the stott of the mule deer. Another adaptation to open habitats is the formation of selfish herds (Hamilton 1971). *Rangifer* and *Cervus canadensis* both became gregarious, as did several ecotonal species (*Axis axis*, *Cervus nippon*, and *Capreolus capreolus*, when they are found in open habitats).

Open-adapted cervids are less territorial than closed-adapted cervids. Life in forests is limited by fierce competition for limited resources. Antlers borne by closed-adapted cervids are generally small but they are used as weapons in territory defense rather than as advertisements of fitness, as in open-adapted deer. Further, resource-defending cervids in closed habitats often have large upper canines (except the secondarily primitive cervids of South America). Both canines and antlers may be used as weapons by small forest deer, which fight to injure rather than just as a contest. The largest and showiest antlers are borne by deer in open habitats. Geist (1998, p. 132-56) hypothesizes that the large antlers of the open-adapted deer are an honest advertisement of fitness. In open habitats, deer fawns must be able to run from predators and keep up with the herd soon after they are born. This requires calves to be born large and precocious. In order to meet such a demand, the female must have surplus energy to pass to her offspring via rich milk. This is matched by the males through the growth of large and ornate antlers. Females choose mates that display the highest fitness (antler size/symmetry) to ensure their offspring will also receive fit genes. Cervids throughout time and across space support this hypothesis, except, again, the moose with its open-adapted ancestry.

Interestingly, one feature that does not exist along this gradient is sexual dimorphism. Closed-adapted resource-defenders tend to be monomorphic. Open-adapted cervids also tend to be of similar sizes to better blend into the herd, which is taken to an extreme by the antler-bearing females of *Rangifer*. It is in ecotonal habitats that sexual dimorphism is most marked (Geist 1998, p. 52). In these species, such as *Axis axis*, males and females pursue different lifeways, only to come together for mating. Males invest energy in growing large body sizes and antlers while females invest in the security of their young. Male territories will often encompass the territory of several females and males fight to defend these territories.

It is hoped that from this brief review of cervid ecology, evolution, and behavior it is evident that the Cervidae are limited to closed habitats and browsing diets, as they are sometimes characterized (Mendoza *et al.* 2002, Christiansen & Adolfssen 2007). Cervids, though not as habitat-specific as bovids, have evolved diminutive tropical species through open-adapted giants, which were more numerous in the Pleistocene than they are currently. Cervids, however, do have more generalist species than bovids, which can complicate habitat reconstructions based on their morphology. For example, into which habitat category should *Odocoileus virginianus* or *Cervus elaphus* be placed? A more realistic evaluation of cervid ecomorphology would place them on a continuum such as is depicted in Figure 4-3. Thus, this study will include habitat reconstructions based on both a categorical and a continuous system.

Chapter 5: Materials

This dissertation includes analyses on specimens of extant and extinct cervid species. This chapter outlines how the specimens included in this study were chosen and provides brief overviews of the fossil sites from which the fossil specimens are derived. Discussion then turns to the morphological data collected and an overview of data collection techniques. Chapter 6 discusses the analytical techniques used here.

Extant Cervid Specimens

Table 5-1 provides summary totals of specimens from extant cervid species included in this analysis. Further details on specimens can be found in Appendix A. Data from extant specimens were collected from four museums: American Museum of Natural History (AM), New York, NY; National Museum of Natural History (NM), Washington, D.C.; Chicago Field Museum (FM), Chicago, IL; and the Museum of Vertebrate Zoology (MVZ), Berkeley, CA. Much of the composition of the sample (as shown in Table 5-1) was dependant upon which specimens were available for study at these institutions and the preservation of those specimens. Criteria for selecting specimens are described below.

Only adult specimens were included in this study. Adults were defined (minimally) as having all epiphyses completely fused or (preferably) as having all teeth in full occlusion, which is only possible to assess when skulls were associated with post-crania. Isolated elements were considered adult if the element's epiphyses were fused. Epiphyseal closure timing varies between cervid species and within cervid species between by sex, but little difference in timing has been found to be correlated with environment (Purdue 1983). Moreover, epiphyseal fusion is indicative of the cessation of

growth and as such signifies the appropriateness for treating that bone as “adult” regardless of the state of fusion of other skeletal elements.

Zoo specimens were avoided when possible, however, due to the scarcity of post-crania of some species (e.g. *Dama dama*, *Axis axis*, *Cervud eldi*- see Appendix A) in U.S. collections, some zoo specimens are included here. Since most phenotypic morphology is the result of interactions between genetic and epigenetic factors, the restricted living conditions of zoo animals is likely to affect morphology, though this assumption needs to be tested across a variety of skeletal features. Any zoo specimen with obvious pathology was not included. Osteoarthritis and bone spurs are especially prevalent amongst zoo specimens (personal observation) and specimens with these pathologies were not included in this study.

When possible, specimens were sampled evenly across the sexes. There tends to be a bias toward male cervids in museum collections, possibly due to trophy-hunted specimens that are later donated. Sexual dimorphism in cervids is correlated with their habitat preferences. Cervids from forest and open habitats tend to have less sexual dimorphism; while in ecotonal habitats sexual dimorphism is marked (Geist 1998, p. 52). Two species (*Odocoileus virgianus* and *O. hemionus*) are used to test for morphological differences due to sex.

Specimens were sampled from every taxon available. There are approximately forty extant cervid species (depending on which taxonomy is used), but some of these are so rare they do not exist in collections in the U.S., or if they do, they are only skull or

Species	# Individuals	Cal LMs	FemMed	TibLat	Phal3
<i>Alces alces</i>	7	6	6	6	3
<i>Axis axis</i>	2	2	2	2	2
<i>Axis porcinus</i>	4	2	3	3	0
<i>Blastocerus dichotomus</i>	3	3	3	3	2
<i>Capreolus capreolus</i>	7	7	7	7	6
<i>Cervus canadensis</i>	0	7	6	7	3
<i>Cervus duvaucelii</i>	1	1	1	1	0
<i>Cervus elaphus</i>	9	1	2	2	1
<i>Cervus eldii</i>	2	2	2	2	2
<i>Cervus mariannus</i>	3	4	4	4	3
<i>Cervus nippon</i>	5	4	4	4	2
<i>Cervus timorensis</i>	2	2	2	2	2
<i>Cervus unicolor</i>	2	2	2	2	0
<i>Dama dama</i>	5	2	5	4	4
<i>Elaphodus cephalophus</i>	6	6	7	6	1
<i>Elaphurus davidianus</i>	3	4	4	4	1
<i>Hippocamelus antisensis</i>	2	2	2	2	1
<i>Hippocamelus bisculus</i>	1	1	1	1	0
<i>Hydropotes inermis</i>	4	4	4	4	2
<i>Mazama americana</i>	2	2	0	0	0
<i>Mazama chunyi</i>	1	0	1	1	1
<i>Mazama gouazoubira</i>	3	2	2	3	1
<i>Mazama rufina</i>	2	2	1	2	0
<i>Muntiacus atherodes</i>	2	3	1	1	0
<i>Muntiacus muntjak</i>	3	1	1	3	0
<i>Muntiacus reevesi</i>	3	4	4	4	1
<i>Odocoileus hemionus</i>	17	15	17	17	7
<i>Odocoileus virginianus</i>	18	18	18	19	11
<i>Ozotoceros bezoarticus</i>	4	3	4	4	2
<i>Pudu mephistophiles</i>	3	3	4	4	0
<i>Pudu puda</i>	2	0	2	2	0
<i>Rangifer tarandus</i>	13	7	11	10	4
Totals	141	122	133	136	62

Table 5-1 Extant cervid specimen counts by species and unit of analysis. CalLMs = Calcaneus landmarks, FemMed = Femoral medial patellar margin, TibLat = Tibial lateral plateau margin, Phal3 = Third phalanx plantar margin. These four units of analysis are defined in detail in this chapter.

pelage specimens (*Axis kuhlii*, *Capreolus pygargus*, *Cervus albirostris*, *C. alfredi*, *Dama mesopotamica*, *Mazama chunyi*, *Muntiacus feae*, *Megamuntiacus*). This study includes (up to) 137 specimens from thirty species in the five cervid tribes (specimen counts vary for different skeletal elements).

Museum collections frequently have all the skeletal elements of a single individual and these were preferred over isolated elements. For more rare species, data for partial specimens were collected if they were available. Specimens with minimal post-processing or ‘drawer damage’ were selected over broken specimens. Finally, those specimens that had detailed catalog data (sex, collection location, etc.) were selected over specimens with unknown life history variables.

Fossil Cervid Specimens

Data for four fossil localities, as well as sub-fossil material from *Megaloceros*, were included in this study. Three of the four fossil sites (Valea Graunceanului, Romania and Saint Vallier and Senèze, France) are Plio-Pleistocene in age and do not contain hominin remains, though they do have large mammalian assemblages. These sites are contemporaneous with the earliest hominin sites in Eurasia and their lack of hominin fossils may be illustrative of the types of habitats that the earliest hominin dispersers did not occupy (though the reasons for non-occupation are certainly not limited to habitat type and could have been due to factors such as geographic/topographic barriers and predator pressures). The fourth site, ‘Ubeidiya, Israel, dating to approximately 1.4 Ma, contains hominin remains (*Homo* sp.), but is more recent than the aforementioned sites. Nevertheless, it is an extremely important site for understanding hominin dispersal from Africa as it stands at the crossroads of Africa and Eurasia.

Site Name	Country	Date (Ma)	Hominin/Primate presence at site	Paleohabitat/Depositional Environment
Grăunceanu	Romania	late Pliocene	<i>Paradolichopithecus</i> , possible lithics	open/wooded savanna, lacustrine delta
St. Vallier	France	MN 17 (2.4-1.9 Ma)	<i>Macaca sylvanus</i>	mosaic of warm open and wooded habitats along a lake or river
Senèze	France	MN 18 (2.2-1.5 Ma)	<i>Paradolichopithecus</i> , <i>M. sylvanus</i>	infilled Maar (lacustrine)
Ubeidiya	Israel	1.4 Ma	<i>Homo</i> sp., 8000+ lithics, <i>Theropithecus</i> cf. <i>oswaldi</i> , <i>M. sylvanus</i>	Mediterranean woodland/scrubland

Table 5-2 Summary information for the fossil sites included in this study (references in the text).

Site	Cervids Present	FemMed	TibLat	Cal LMs	Phal3	total/ species
Ireland (various)	<i>Megaloceros giganteus</i>	4	3	0	2	9
Saint Vallier, France	<i>Croizetoceros ramosus medius</i>	0	1	2	0	3
	<i>Eucladoceros ctenoides vireti</i>	0	0	3	0	3
	Cervidae (sp. + gen. unknown)	0	0	17	7	24
Senèze, France	<i>Alces (Libralces) sp.</i>	0	1	1	1	3
	<i>Eucladoceros ctenoides senezensis</i>	0	0	2	6	8
	<i>Cervus sp.</i>	0	1	1	1	3
	<i>Cervus philisi</i>	3	1	0	22	26
	Cervidae (sp. + gen. unknown)	3	3	4	9	19
Grăunceanu, Romania	<i>Eucladoceros sp.</i>	0	0	17	24	43
Ubeidiya, Israel	<i>Praemegaceros verticornis</i>	0	1	1	6	8
	<i>Pseudodama sp.</i>	0	0	3	10	13
	<i>Capreolus sp.</i>	1	0	0	0	1
	total per unit of analysis	11	13	51	88	163

Table 5-3 Fossil specimen counts by species, site, and unit of analysis (abbreviations as in Table 5-1).

The following review provides descriptions of each site, including information regarding dating methods, depositional and taphonomic histories, cervid species recovered, and previous paleoecological reconstructions when available. A summary of site information is provided in Table 5-2 and Table 5-3 indicates the cervid species and specimen counts from each locality.

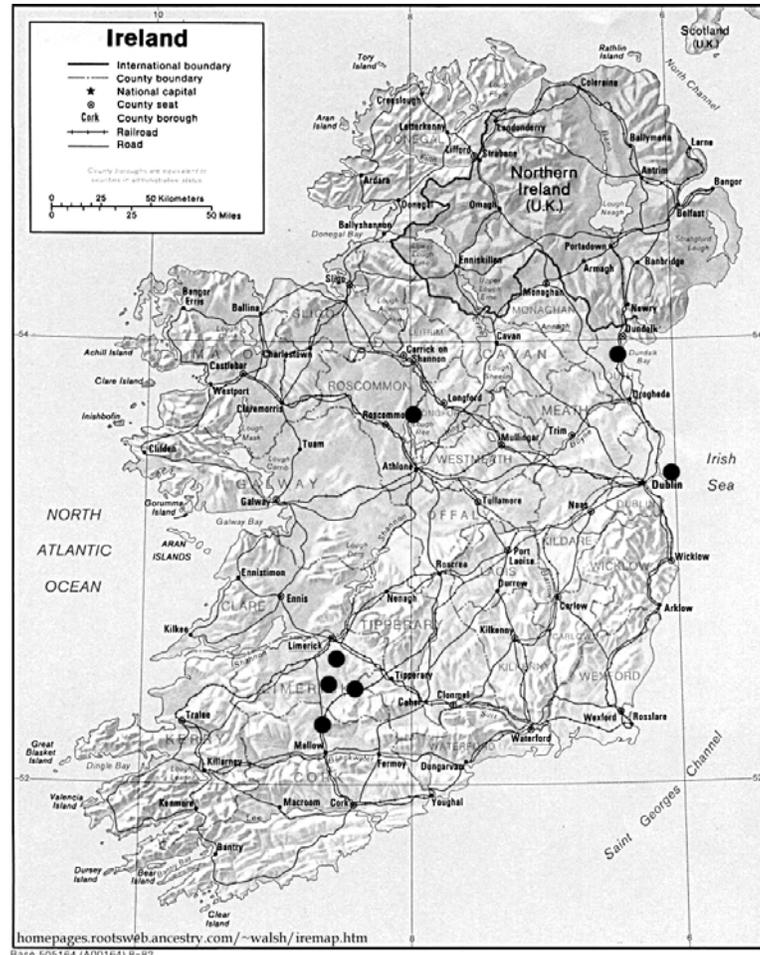


Figure 5-1 Location map for *Megaloceros giganteus* specimens (black dots) from Ireland.

Megaloceros giganteus specimens from Ireland

The *Megaloceros giganteus* specimens included in this study are housed at the National Museum of Ireland, Natural History Department in Dublin, Ireland. As these

specimens were preserved in peat bogs, they are in excellent, sometimes perfect, states of preservation. Most of these specimens were single finds from the first half of the 20th century in Ireland and date to approximately 11,000 years ago. Figure 5-1 is a map of the collection locations for specimens included in this study. Detailed information on specimens can be found in Appendix B and a discussion of *Megaloceros giganteus* ecology is included in Chapter 4.

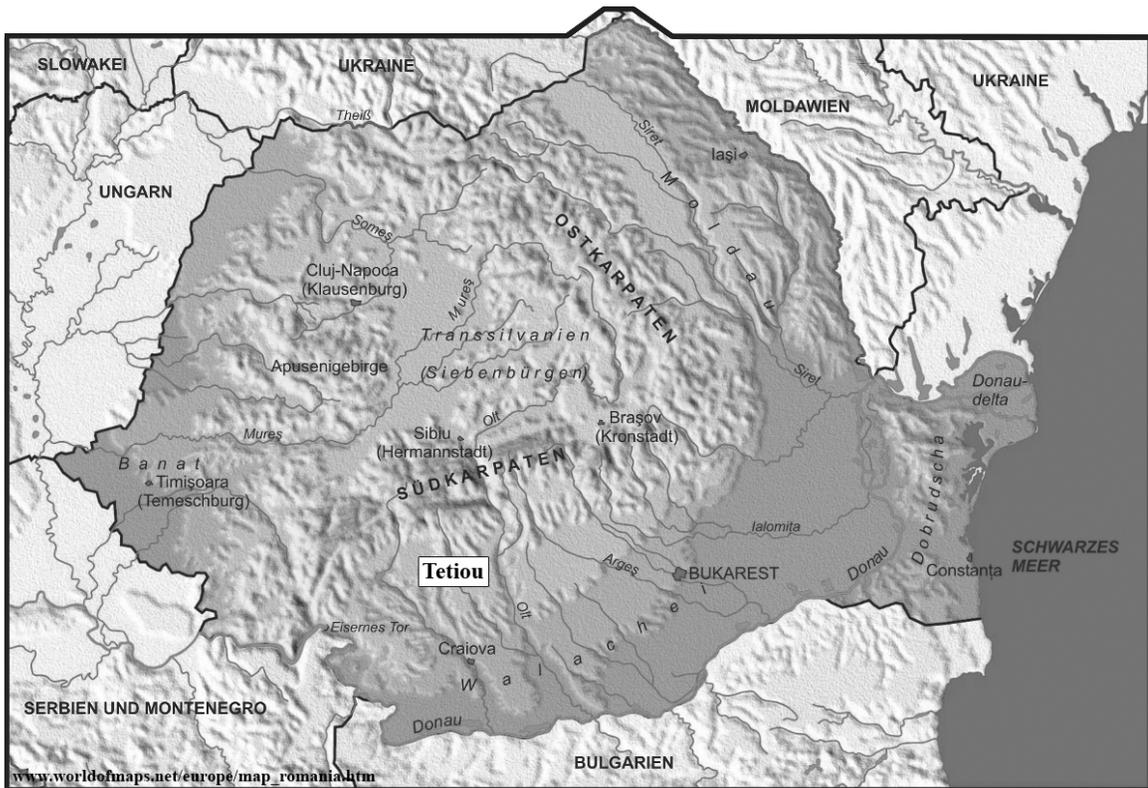


Figure 5-2 Location map for the site of Valea Graunceanului near Tetiou, Romania.

Valea Graunceanului, Romania

Specimens from Valea Graunceanului (Grăunceanu), Romania are housed in two museums: the ‘Emil Racovita’ Institute of Speleology in Bucharest, Romania, and the Museum of Oltenia in Craiova, Romania. The cervid assemblage is in very good

condition with little weathering. Small, dense bones (tarsals, phalanges, etc.) occur in much higher frequencies than do long bones, though metapodia are numerous. The collection itself appears to be divided between the two museums by skeletal element, with tarsals, metatarsals, and femora in Bucharest and phalanges and tibiae in Craiova. More detailed specimen information can be found in Appendix B.

Situated in the Oltet River valley near Tetiou, Romania (see Figure 5-2), Valea Graunceanului represents the most fossiliferous assemblage of the Tetiou I (Buguilesti) sequence (Rădulesco *et al.* 2003, p. 4). The mammalian remains of Tetiou I (Table 5-4) were accumulated in fluvial-lacustrine deposits (Samson & Rădulesco 1973, p. 202), with a lacustrine delta the most likely depositional environment for Valea Graunceanului (Necrasov *et al.* 1961, p. 402). This site is dated to the Late Pliocene (MN 17, Rădulesco *et al.* 2003) using biostratigraphy and paleomagnetism. Stone tools have been found from a near-by site (Dealul Mijlociu Hill) that dates to between the deposition of the Valea Graunceanului material and the assemblage deposited just prior, La Pietris (*ibid*), though there is some question of whether these tools are from a disturbed context (Dobos 2008).

Rădulesco *et al.* (2003) cite the abundance of cervids (*Eucladoceros* sp. and specimens from the *Cervus rhenanus/philisi* group) as evidence of a humid and warm environment, while Frost *et al.* (2005) suggest a savanna woodland habitat for Valea Graunceanului based on the functional morphology of *Paradolichopithecus*. Though it was similar in morphology to extant baboons and was a large, terrestrial cercopitheciine, *Paradolichopithecus* was actually more closely related to macaques (Delson & Frost 2004, Nishimura *et al.* 2007, 2008, Van der Geer 2002). A savanna ‘parkland’ (tall trees, shrubs, and grasses) is suggested by the presence of *Mammuthus meridionalis* (Ferretti &

Croitor 2001) in the fauna (see Table 5-4). Valea Graunceanului was likely to have been an open savanna with some wooded cover.

Primates	<i>Paradolichopithecus arvernensis geticus</i>
Proboscidea	<i>Mammuthus (Archidiskodon) meridionalis</i>
Perrisodactyla	<i>Stephanorhinus</i> sp.
	<i>Plesippus (Allohippus) athansiui</i>
Artiodactyla	<i>Eucladoceros</i> sp.
	<i>Cervus rhenanus/philisi</i> group
	<i>Pliotragus ardeus</i>
	<i>Gazellospira torticornis</i>
	<i>Mitilanotherium inexpectatum</i>
Carnivora	<i>Nyctereutes megamastoides</i>
	<i>Ursus etruscus</i>
	<i>Pliocrocuta perrieri</i>
	<i>Homotherium crenatidens</i>
	<i>Megantereon megantereon</i>
	<i>Lynx issiodorensis</i>
Pholidota	<i>Manis</i> cf. <i>hungarica</i>

Table 5-4 Faunal list for Valea Graunceanului, Romania (Rădulesco et al. 2003, pp. 552-554).

Saint Vallier, France

Specimens from Saint Vallier and Senèze, France included in this study are housed in two institutions; Claude Bernard University of Lyon 1 and Collection du Musée des Confluences, Lyon. Though the assemblages from both sites are split between both institutions, the majority of the data collected for Senèze was collected at Claude Bernard University of Lyon 1, while most Saint Vallier specimen data was collected at Collection du Musée des Confluences (details can be found in Appendix B).

St. Vallier is the reference locality for biozone MN17 (2.4 – 1.9 Ma) due to its rich and well-preserved fauna (Valli 2004b, p. 337). It is an open-air site south of Lyon, France to the east of the Rhone River (see Figure 5-3). The assemblage was likely

accumulated by moving water, though the remains have little weathering or abrasion, indicating that they probably were not transported very far and were quickly covered in sediment (*ibid*, pp. 343-5). The faunal assemblage (see Table 5-5) contains one primate species, *Macaca sylvanus* but no traces of hominin activity (*ibid*, pp. 338, 345).



Figure 5-3 Location of St. Vallier and Senèze, just south of Lyon, France.

Primates	<i>Macaca sylvana</i>
Proboscidea	<i>Ananucs arvernensis</i>
	<i>Mamuthus meridionalis</i>
Perrisodactyla	<i>Dicerorhinus etruscus etruscus</i>
	<i>Equus steninis vireti</i>
Artiodactyla	<i>Sus strozzii</i>
	<i>Croizetoceros ramosus medius</i>
	<i>Cervus philisi valliensis</i>
	<i>Eucladoceros ctenoides vireti</i>
	<i>Gazella borbonica</i>
	<i>Gazellospira torticornis</i>
	<i>Gallogoral meneghini</i>
	<i>Leptobos elatus merlai</i>
Carnivora	<i>Nyctereutes megamastoides</i>
	<i>Vulpes alopecoides</i>
	<i>Baranogale antiqua</i>
	<i>Enhydriactis ardea</i>
	<i>Aonyx bavardi</i>
	<i>Meles thoralis</i>
	<i>Ursus etruscus</i>
	<i>Pachycrocuta perrieri</i>
	<i>Chasmaporthetes lunensis</i>
	<i>Lynx issiodorensis</i>
	<i>Viretailurus schaubi</i>
	<i>Acinonyx pardinensis</i>
	<i>Homotherium crenatidens</i>
	<i>Megantereon cultridens</i>

Table 5-5 Faunal list for St. Vallier, France (Valli 2004a, 2004b, p. 338).

Previous paleoecological reconstructions using taxon-based methods indicate that St. Vallier had a mosaic of warm open and wooded habitats along a lake or river (Valli 2004b, pp. 337-338, see Table 5-5 for a faunal list). Cervids dominate the assemblage and include *Croizetoceros ramosus medius*, *Cervus philisi valliensis*, and *Eucladoceros ctenoides vireti*, with the first two species being the most prevalent. The latter two genera are also found at Valea Graunceanului, Romania, and Senèze, France.

Senèze, France

Senèze is younger than Saint Vallier (Delson *et al.* 2006) and faunally equivalent to Valea Graunceanului (Rădulesco *et al.* 2003). Though fossils have been recovered since the late 1800s, there is little published material about the site (Delson *et al.* 2006, p. 276). Recent efforts have been made to reopen the site and elucidate its taphonomic, paleoecological and depositional history, as well as to confidently assign Senèze a date (Delson *et al.* 2006). The latter goal is very important as Senèze was chosen as the biochronological reference for MN18, the Late Villafranchian (*ibid*).

The assemblage of Senèze was deposited in a depression formed by Pliocene maar that continued to infill throughout the Plio-Pleistocene (*ibid*). The Senèze lacustrine deposits were found to be mainly of reversed (Matuyama) polarity, except for a normal section at the top (Roger *et al.* 2000). Within these normal sediments, a tephra layer was dated to 2.1 Ma, placing the normal deposition in the Reunion event. Thus, the Senèze fauna, which is stratigraphically above the normal sediments, must be younger than 2.1 Ma (*ibid*). The fauna (see Table 5-6) contains four cervid species: *Eucladoceros ctenoides senèzensis*, *Cervus philisi philisi*, *Libralces gallicus*, and *Croizetoceros ramosus minor* (the latter species was not observed while collecting the data for this dissertation, but is mentioned in Delson *et al.* 2006, p. 277).

Primates	<i>Paradolichopithecus arvernensis</i>
	<i>Macaca sylvanus cf. florentina</i>
Proboscidea	<i>Mammuthus meridionalis</i>
Perissodactyla	<i>Dicerorhinus etruscus etruscus</i>
	<i>Allohippus stenois senezensis</i>
	<i>Equus bressanus</i>
	<i>Equus stehlini</i>
Artiodactyla	<i>Sus srtozzii</i>
	<i>Croizetoceros ramosus minor</i>
	<i>Cervus philisi philisi</i>
	<i>Eucladoceros ctenoides ctenoides</i>
	<i>Libralces gallicus</i>
	<i>Gazellospira torticornis</i>
	<i>Procamptoceras brivatense</i>
	<i>Megalovis latifrons</i>
	<i>Gallogoral menghinii</i>
	<i>Leptobos furtivus</i>
	<i>Leptobos etruscus</i>
	<i>Pliotragus ardeus</i>
Carnivora	<i>Nyctereutes megamastoides</i>
	<i>Vulpes alopecoides</i>
	<i>Canis senezensis</i>
	<i>Ursus etruscus</i>
	<i>Pachycrocuta perrieri</i>
	<i>Euryboas lunensis</i>
	<i>Acinonyx pardinensis</i>
	<i>Homotherium crenatidens</i>
	<i>Megantereon cultridens</i>

Table 5-6 Faunal list for Senèze, France (Delson et al. 2006, p. 277).



Figure 5-4 Location of the site of ‘Ubeidiya, just south of the Sea of Galilee in Israel.

‘Ubeidiya, Israel

Cervid specimens from ‘Ubeidiya, Israel are housed at the Hebrew University of Jerusalem, Israel. This assemblage has been described in great detail by Belmaker (2006) and the specimens included in this study are limited to those described in that thesis. The

site is located in the Jordan River Valley in Israel (Figure 5-4) and dates to approximately 1.4-1.6 Ma using a combination of magnetostratigraphy and biostratigraphy (Shea 1999, p. 194). Though the 'Ubeidiya sequence is known to span several different types of depositional stages, the specimens in this study are mostly derived from the inferior fluvial cycle, Fi. Belmaker (2006, p. 95) states that 'Ubeidiya was accumulated due to carnivore kills and was further modified by scavenger ravaging (*ibid*, p. 93). The assemblage shows very little weathering (mainly Stage 1) and little evidence of fluvial transport (*ibid*, p. 92). Hominins contributed little to the accumulation of 'Ubeidiya and may have just acted as scavengers upon the remains of carnivore kills (Belmaker 2006, p. 100). The hominins, attributed only to *Homo* sp., are represented by a large number of artifacts (almost 8,000 pieces (Bar-Yosef 1998)), including an assortment of cores, bifaces, flakes, and debitage (Shea 1999), a few cut-marked faunal elements (Belmaker 2006, p. 21) and by a few fragmentary hominin remains. Of the hominin remains (several cranial fragments and teeth), only one find, UB 335, an incisor, (Belmaker *et al.* 2002, Belmaker 2006) has uncontested provenience, having been found *in situ* while the other hominin remains were surface finds. UB 335 is assigned to *Homo* sp. and tentatively to *Homo erectus* (Belmaker *et al.* 2002).

'Ubeidiya has long been recognized as one of the first Eurasian hominin sites. It is located in the Levantine Corridor, which has been posited as the most probable route of dispersal for hominins from Africa (Thomas 1985, Bar-Yosef 1999, Tchernov 1992c). The fauna at 'Ubeidiya is a mixture between African and Eurasian species (Table 5-7). In addition to *Homo* sp., there are two other primates- *Theropithecus* cf. *osalwadi*, and *Macaca sylvana*. Though there are many African taxa (Tchernov 1992a), the assemblages

from ‘Ubeidiya tend to have cervids as the dominant taxon (Belmaker 2006, p. 52).

Cervid species from ‘Ubeidiya include *Pseudodama* sp., and *Capreolus* sp., and

Praemegaceros verticornis.

Primates	<i>Homo</i> sp.
	<i>Theropithecus</i> cf. <i>oswaldi</i>
	<i>Macaca sylvana</i>
Proboscidea	<i>Mammuthus</i> sp.
Perissodactyla	<i>Stephanorhinus etruscus</i>
	<i>Equus</i> sp.
	<i>Equus tabeti</i>
Artiodactyla	<i>Sus strozzi</i>
	<i>Kolpochoerus olduvaiensis</i>
	<i>Leptobos</i> sp.
	<i>Oryx</i> cf. <i>gazella</i>
	<i>Pelorovis oldowayensis</i>
	<i>Gazella</i> sp.
	Antilopini gen. Indet.
	<i>Giraffa</i> sp.
	<i>Camelus</i> sp.
	<i>Praemegaceros verticornis</i>
	<i>Pseudodama</i> sp.
	<i>Capreolus</i> sp.
Carnivora	<i>Crocuta crocuta</i>
	<i>Megantereon</i> sp.
	<i>Panthera gombaszoegensis</i>
	<i>Felis</i> cf. <i>chaus</i>
	<i>Lynx</i> sp.
	<i>Lycaon lycaonoides</i>
	<i>Canis mosbachensis</i>
	<i>Vulpes</i> sp.
	<i>Ursus etruscus</i>
	<i>Mellivora</i> sp.
	<i>Pannonictis pilgrimi</i>
	<i>Vormela peregusna</i>
	<i>Herpestes</i> sp.
<i>Lutra simplicidens</i>	

Table 5-7 Faunal list for ‘Ubeidiya, Israel (Belmaker 2006, p. 266).

Morphological units of analysis in this study

Four morphological units of analysis are examined in this study. A unit of analysis is defined here as a specific, discrete region of skeletal anatomy, such as a joint surface margin. This study includes analyses of: 1) the calcaneus as a whole, 2) the medial margin of the femoral patellar articular joint surface, 3) the margin of the lateral tibial condylar joint surface, and 4) the plantar margin of the third phalanx. These four morphological features are analyzed with different types of analyses (respectively): 1) landmark-based geometric morphometrics (GM), 2) open-curve outline GM of a joint surface, 3) closed-curve outline GM of a joint surface, and 4) closed-curve outline GM of a non-joint surface. The following is a description of each unit of analysis's functional importance, predictions of variations in morphology correlated with adaptations to specific habitat types, and data collection procedure. The methods of analysis (geometric morphometrics and multivariate analyses) are described in Chapter 6.

Unit of Analysis 1: Calcaneus Shape (CalLMs)

The hock (ankle) joint is a dynamic system of three main joints: tibia-astragalus, astragalus-calcaneus, and astragalus-cubonavicular. The calcaneus is a lever arm for the rear limb, providing propulsion when the gastrocnemius contracts by drawing the distal portion of the rear limb (metatarsal and phalanges) back in the parasagittal plane. The calcaneus slides along the surface of the astragalus during this contraction but its function is more complex than a simple extension of the lever arm for the distal limb. Several aspects of calcaneal morphology are hypothesized to affect its functionality in the hock joint, including its length and its rest position prior to distal limb extension as a function of the orientation of joint surfaces of the anterior process.

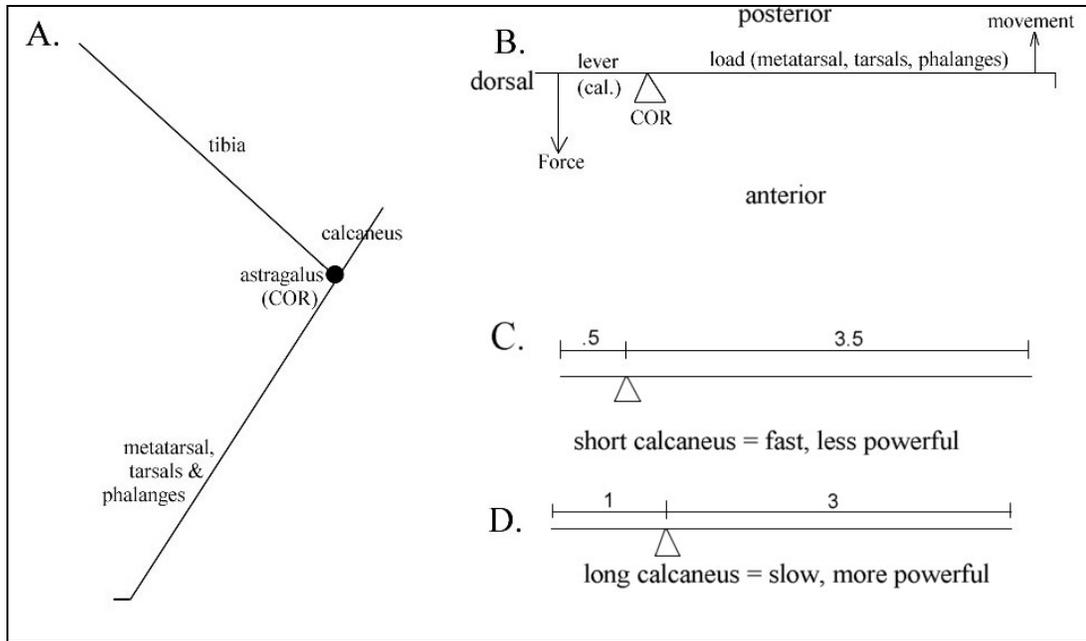


Figure 5-5 Representation of the calcaneus as the lever arm for the lower limb (tarsals, metatarsal, and phalanges). B: This system can be models as a type 1 lever, with the calcaneus as the lever arm, the lower limb as the load arm and the astragalus as the center of rotation (fulcrum). An increase in the length of the atragalus results in a lever with more power but less speed while a short calcaneus produces a lever with more speed and less power.



Figure 5-6 Landmarks on the calcaneus used in this study. The top image is taken from the medial view and the bottom is from the superior view.

Landmark	Location description
1	Anterior point of cubonavicular articular surface
2	Anteroinferior point of lateral astragular articular surface
3	Anteroposterior point of cubonavicular articular surface
4	Superomedial point of anterior astragular articular surface
5	Anterosuperior point of os malleous articular surface
6	Inferomedial point of sustentacular tali
7	Superomedial point of sustentacular tali
8	Posteroinferior point of gactronemius enthesis
9	Anterosuperior point of calceneal tuber
10	Posterosuperior point of caleanal tuber

Table 5-8 Anatomical descriptions of landmark locations on the calcaneus.

The length of the calcaneus affects how much effort is needed to move the distal limb (tarsals, metatarsal, and phalanges). In cervids, the astragalus-calcaneus joint acts as a Class 1 lever (Figure 5-5), with the joint surface as the fulcrum, the calcaneal body as the lever arm and the distal limb as the load arm. An increase in calcaneal length (keeping all else equal) will increase the lever arm and thus increases the mechanical advantage of the joint but creates a slower joint movement while a short calcaneus will provide less power but quicker movement (Figure 5-5d). Cervids that utilize saltatorial locomotion (bounding leaps) to escape predators (ecotone to closed habitats) are hypothesized to have longer calcanei than cervids that are cursorial in open habitats (Hildebrand 1985, p. 46) with cervids that stott (leaping with all four feet contacting the substrate at the same time; mostly found in open mountainous regions) having the longest calcanei. The length of the calcaneus is only one aspect of its overall shape and is recorded in this study as 3D (x,y,z) coordinates (#1 and #10 from Figure 5-6) from which

length data can be derived. The relative position of landmark #7 along the length of the calcaneus should be an indication of the length of calcaneal body.

The anterior process of the calcaneus articulates with three bones- anteriorly with the os malleus (landmark 5 in Figure 5-6), inferiorly with the cubonavicular (between landmarks 1 and 3 in Figure 5-6), and at several places with the astragalus, but most especially on the sustentaculum tali. Orientation of all of these joint surfaces affects the rest position of the calcaneus prior to lower limb extension, though motion at the hock joint is relatively restricted to the parasagittal plane in cervids. The rest position of the calcaneus determines how far the calcaneus moves along the astragalus when the gastrocnemius is contracted. If the calcaneus sits more vertically on the articulations with the cubonavicular and astragalus, then it moves a shorter distance, which allows for a quick but less powerful force to be generated. This morphology is associated with (open-adapted) cursors that increase speed by increasing the number of times the same foot strikes the ground per second (the pace cycle). A more horizontal rest position means that the calcaneus travels farther with the contraction of the gastrocnemius, which generates more power, but is slower. This morphology is associated with saltatorial runners that flee predators in a series of leaps that allow for maneuverability in more closed habitats.

To conduct an analysis on 3D coordinates with geometric morphometrics (GM, which is explained in greater detail in Chapter 6), one must first start with a set of homologous landmark points. Landmarks are defined as discrete points that can be located across all specimens and are of homologous biological origin. Post-cranial skeletal elements do not easily lend themselves to landmark-based GM studies, however, the calcaneus has several points that can be defined as mainly type II landmarks (maxima

of curvature or other local morphogenetic process (Bookstein 1991, p. 64). Though 16 landmarks were originally chosen for this analysis, six of these proved to be non-homologous or missing in some species. Ten landmarks were selected for the final analysis of the calcaneus as shown in Figure 5-6 and described in Table 5-8. Landmark data (x , y , z coordinates) were collected three times for each specimen with a Microscribe MLX and imported directly into an Excel (Microsoft Corp. 2000) spreadsheet. For each specimen, the mean of each of the ten landmarks was then submitted as the data for that specimen. Right-side specimens were preferentially selected, except where they were not available (such as in fossil specimens) and then landmarks from left calcanei were collected and reflected in Morphologika.

Unit of Analysis 2: Femoral Medial Patellar Articular Surface Margin (FemMed)

The extension of the hind limb provides the majority of propulsion in cervids, as it does in bovids (Kappelman 1988, p. 126). The patella is a sesamoid that rides along the patellar surface of the distal femur. It increases the moment arm of the quadriceps muscle group (major extensors of the knee joint) from the center of rotation in the knee (*ibid*). Given the same muscle power, a longer moment arm provides more torque at a joint, allowing greater movement on the load arm. Thus, the further the patella is from the center of rotation, the more torque is generated at the joint and this increases the ability to generate more distal limb propulsion.

Kappelman (1988, p. 127) found that bovids from open habitats have asymmetrical patellar joint surfaces, with the medial margin being much larger than the lateral margin. Further, the medial margin is elliptical in open-adapted bovids, while in closed-adapted bovids it is more circular. With an elliptically-shaped patellar surface, the

moment arm for the joint actually increases during knee extension, progressively increasing the torque provided at the joint (*ibid*). Though moment arm length is not the only factor contributing to strength of distal limb extension, it is one that is easily tested with morphological features. Open-adapted cervids are predicted to have more elliptically-shaped medial patellar margins, while more closed-adapted cervids should have more circular margins (Kappelman 1988).



Figure 5-7 Semilandmarks recorded on the femoral medial patellar articular surface margin. Image A is from the medial view and B is from the anterior view. The specimen is from the Anthropology Laboratories at the University of Minnesota (MN 00-02, *Alces alces*).

Medial patellar margin data were collected with a Microscribe as x , y , z coordinates in Rhinoceros (McNeal *et al.* 2002). A curve of 3D coordinates was collected along the most prominent ridge along the medial patellar surface, starting with the most anteriorly-projecting region of the ridge and running inferiorly along the margin (see Figure 5-7). Rhinoceros allows for visualization of 3D coordinate points as they are being collected and sufficient coordinates from each specimen were collected to completely represent the joint margin. The number of original coordinates varied between specimens as a factor of size (e.g. more points are required to sufficiently cover a moose medial

margin than one of a pudu). In Rhinoceros, a curve was fit to each set of coordinate points and the original data points were removed. Twenty-one evenly-spaced 3D coordinates were then extracted from this curve starting at the posterior end of the medial margin and proceeding anteriorly. These data are treated as landmarks in all future analyses. Data were exported as .txt files and data for each specimen were placed into a single .txt file to be analyzed with geometric morphometrics (Chapter 6).

Unit of Analysis 3: Tibial Lateral Condylar Surface Margin (TibLat)

Joint surface morphology restricts the type and range of motion possible at a joint. Different morphologies provide varying degrees of stability. The distal condyles of the femur rotate on the superior condyles of the tibial plateau to form the knee joint. In most mammals, the tibial condyles are flat to somewhat convex, though a concave joint surface, such as the acetabulum of the os-coxa, provides the highest joint stability (Hamrick 1996). This study analyzes the shape of the tibial lateral condylar joint surface margin.

Cervids that inhabit closed habitats are predicted to have rounded and convex condyles to allow for a greater range of movement at the knee joint. Since closed-adapted cervids bound away from predators in a zig-zag pattern, they must be able to quickly change direction. Joint surface stability is sacrificed for joint surface mobility. Cervids in open habitats are predicted to have condylar surfaces that are flat and narrow in the medial-lateral direction and long in the anterior-posterior direction. Stability is the primary concern for cursorial cervids (Hildebrand 1985, p. 35). Flatter joint surfaces provide a more stable surface during higher loadings (Organ and Ward 2006) and reduce

risk of dislocation while escaping predators in speedy flight while medial-lateral compression will serve to restrict motion to the parasagittal plane.

Data were collected in a similar manner to that described above for the medial patellar margin. Coordinates were collected around the margin of the lateral condyle with a Microscribe (Figure 5-8) and imported directly into Rhinoceros. The edge of this margin is readily discernable from the rest of the tibial plateau area as it often has a ridge or lip. In Rhinoceros, a curve was then fit to the original data and forty evenly-spaced 3D coordinates were then extracted from this curve starting at the superior-most projections of the intercondylar eminence and proceeding around the margin in a counter-clockwise direction. These coordinates were then exported as .txt files to become as data for GM analyses.

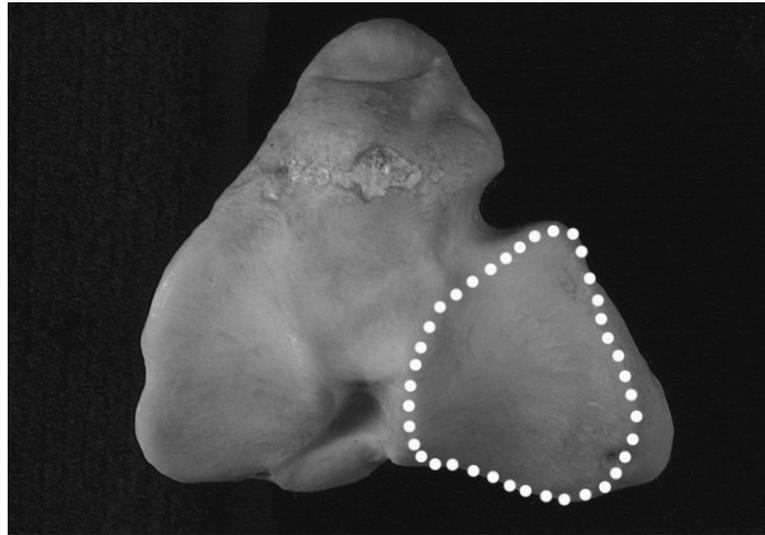


Figure 5-8 Semilandmarks recorded on the tibial lateral condylar surface margin. Specimen from the University of California, Berkeley, Museum of Vertebrate Zoology (*Pudu mephistophiles*, MVZ 122523).

Unit of Analysis 4: 3rd Phalanx Plantar Surface Margin (Phal3)

While not a joint surface, the plantar morphology of the 3rd phalanx does contain information about how a cervid is adapted to its habitat, since this phalanx is the place of contact between the animal and the substrate. Cervids in open habitats are predicted to have ‘blocky’ distal phalanx outlines while cervids adapted to habitats with difficult substrates (swamps, marshes, wetlands) have thinner phalanges that can be splayed during locomotion (Köhler 1993). Cervids adapted to snowy habitats that rely on speedy escape behavior (*Rangifer tarandus*) have short, wide, and curved phalanges to increase stability by increasing the contact surface with the ground (Hildebrand 1985, p. 43).

Coordinates were collected around the outer margin of the plantar surface of the 3rd phalanx, as shown in Figure 5-9. A curve was fit to the original points and thirty evenly spaced coordinates were exported from this curve as the data for future analyses.

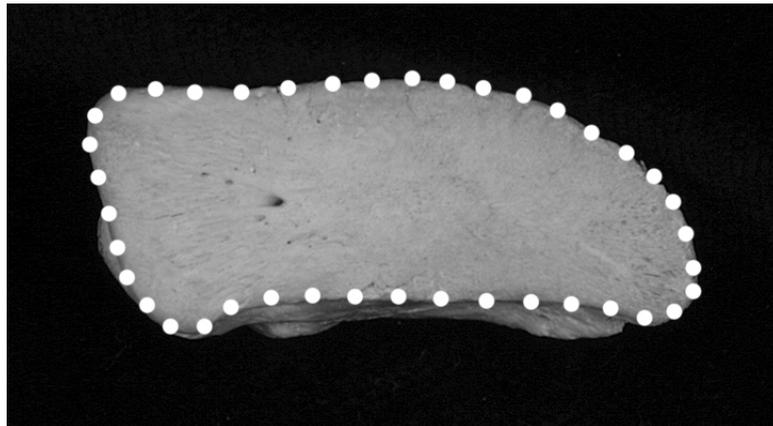


Figure 5-9 Semilandmarks recorded on the 3rd phalanx plantar surface margin. Specimen from the University of California, Berkeley, Museum of Vertebrate Zoology (*Rangifer tarandus*, MVZ 125629).

Summary

This dissertation investigates the ecomorphology of extant and extinct cervids using four morphological units of analysis. Coordinate data were collected on samples of 61-137 specimens (varies for each unit of analysis, see Table 5-1) of extant species to create a training set for multivariate analyses of fossil specimens (see Chapter 6). Data were then collected from four fossil localities from across Eurasia (see Table 5-2). Of these four sites, three (St. Vallier & Senèze, France and Valea Graunceanului, Romania) occur at the Plio-Pleistocene boundary, the time of the initial spread of hominins into Eurasia but contain no hominin remains, and one site ('Ubeidiya, Israel) contains the remains and material culture of hominins, but is dated to a later time period (1.4 Ma). These data constitute the beginning of a dataset for habitat reconstructions across Eurasia. Ultimately, the methods introduced in this dissertation will be applied to more Eurasian Plio-Pleistocene sites to form a picture of the range and types of sites occupied by the earliest hominin dispersers, and of those sites that were not occupied. Such data demonstrate the adaptive capabilities of the earliest Eurasian hominins.

Chapter 6: Methods

Introduction

Ecomorphological studies examine the complex interactions of morphology and behavior that result from the selective forces of evolution. In previous ecomorphological studies (Kappelman 1988, 1991, Plummer & Bishop 1994, Kappelman *et al.* 1997, Scott *et al.* 1999, Vrba & DeGusta 2003, 2005, Weinard 2007, Andrews & Kovorovic 2007, Plummer *et al.* 2008), researchers have analyzed this interaction by using qualitative descriptions or linear (caliper) measurements of morphological features. While qualitative analyses are often illustrative they suffer from issues of subjectivity and repeatability. Mammalian joint surfaces are typically simple, three-dimensional, smooth surfaces that are generally easily distinguished from non-articular areas. One could qualify the joint surface of the glenoid fossa, for example, as being more round or more tear-drop shaped, but this qualification is dependant upon the viewer's experience and fails to reflect more subtle aspects of shape variation. Linear measurements are inadequate for quantifying joint surface morphology, as length and width ratios indicate only more or less oblongness (Chapter 3), while areas or circumferences reflect size. As this study is concerned with quantifying variation in joint surfaces (in addition to non-joint surface morphologies), a descriptive yet rigorous shape quantification method is necessary.

Geometric Morphometrics

An increasingly common tool utilized to analyze shape variation is geometric morphometrics (GM). GM can be defined as “the suite of methods for the acquisition, processing, and analysis of shape variables that retain *all* of the geometric information

contained within the data” (Slice 2005, p. 5, italics original). Shape, in this context, is therefore defined as “all the geometric information that remains when location, scale, and rotational effects are filtered out from an object” (Zelditch *et al.* 2004, p. 11). GM is particularly appealing for studies of functional morphology due its ability to record and analyze the measurements of an object as a *whole* unit, rather divide them into a series of dissociated linear measurements. This is especially relevant to analyses of joint surfaces, which cannot be satisfactorily quantified with linear measures.

To conduct a GM analysis, one first starts with a configuration of homologous landmarks. Landmarks are specific anatomical loci that are recorded as *x*, *y*, and often, *z* coordinates in space. Analysis in GM is upon the entire set or configuration of landmarks rather than individual coordinates. Bookstein (1991, p. 63) divides landmarks into three types: Type I landmarks are discrete juxtapositions of tissues, such as a point where sutures intersect; Type II are “maxima of curvature or other local morphogenetic process” and include anatomical features such as the tip of an incisor or of the spinous process of vertebrae, and finally; Type III are extremal points that are “defined with respect to some distant structure” (Slice 2005, p. 9), such as the end points of a measurement of length. The landmark-based analysis of the calcaneus (see Chapter 5) is on mainly Type II landmarks.

Joint surfaces generally have few to no landmarks on them, but can be analyzed with semi-landmarks. Semi-landmarks are placed along curves or margins of specific anatomical regions forming an outline. The outline, itself, is considered to be the homologous feature (Bookstein 2006, personal communication). In this study, 3D coordinates were collected from the outlines of three anatomical margins (medial femoral

patellar margin, lateral tibial plateau margin, and the plantar margin of the 3rd phalanx). Curves were fit through the original data and then the curves were then resampled for semi-landmarks beginning with the same starting point across all specimens. This produced the same number of evenly spaced semi-landmarks across all specimens, which is necessary for all subsequent analyses. Several studies on 3D outlines (Bookstein *et al.* 1999, Gunz 2005, Gunz & Harvati 2006) have used sliding semi-landmarks, where semi-landmarks 'slide' along tangents to the curve they are derived from until they are as close as possible to the same semi-landmark of the reference specimen, and then are projected back down on to the original curve of the target specimen. An initial examination of the data used in this study by P. Gunz (2007, personal communication) indicated little change in the position of semi-landmarks resampled from curves after submitting them to a sliding procedure. Thus, the resampled coordinates were then submitted to all further analyses.

3D landmarks and semi-landmarks were collected using a Microscribe MLX (Immersion Corp.). The Microscribe MLX is a three-dimensional digitization device that rotates at six joints along an arm. The position of a stylus tip in space is then calculated from these rotations and transferred to a computer as x,y,z coordinates from a specified origin point. For this study, a 1 millimeter ruby ball tip was used as the interface between the stylus and the specimen so as to avoid damage to joint surfaces. To fix specimens in place during data collection, skeletal elements were braced with test-tube holders fixed to Bunsen burner test-tube stands, which were cinched to a table with a C-clamp (see Figure 6-1). 3D coordinates for the calcaneus landmarks were imported directly into an Excel

worksheet. 3D coordinates along anatomical margins were imported into Rhinoceros (McNeal *et al.* 2002), which allows data to be visualized as it is collected.



Figure 6-1 Set-up of the Microscribe MLX. Bunsen burner test tube clamps were used to keep specimens immobile. The Bunsen burner test tube holder was clamped to the table with a C-clamp. 3D coordinates were transferred from the Microscribe to the computer with a foot pedal.

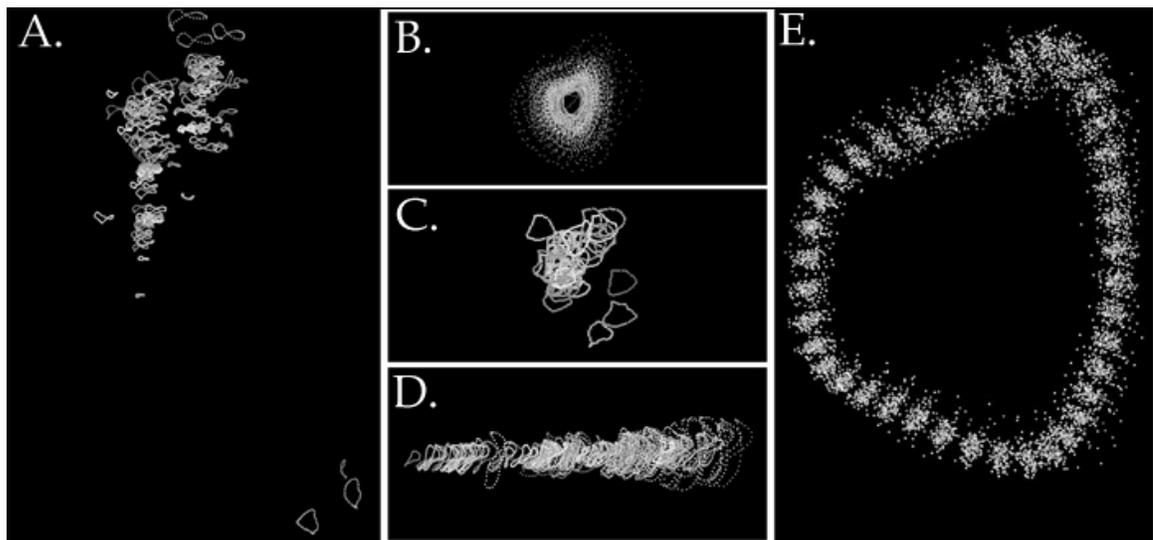


Figure 6-2 Steps in a Generalized Procrustes Analysis (GPA). A. shows the original scan data of all specimens (tibial lateral plateau) before GPA. Notice the variation in specimen location, orientation, and size. B. is all the specimens after they have been translated to a common location. C. shows specimens after they have been made the same size (centroid = 1). D. demonstrates all specimens optimally rotated. E. is the cumulative result from the GPA (steps B. through D. together).

Together, the 3D coordinates of a landmark or semi-landmark set comprise a configuration that captures the shape of the object under study. These raw coordinates have embedded in them information about their digitization location, orientation, and size (McNulty 2003, p. 60). In order to analyze “shape”, as defined above, information about location, orientation, and size was removed from the raw coordinates using a generalized Procrustes analysis (GPA) performed in Morphologika 2.4 (O’Higgins & Jones 2006). This process moves all specimens to a common origin, scales them to a unit centroid size, and rotates them according to a best least squares fit of all landmarks across all specimens (Slice 2005, Zelditch *et al.* 2004). Figure 6-2 illustrates the steps in a GPA using the lateral margins of the tibial plateau. Figure 6-2a shows the positions of tibia lateral plateau margins as they were scanned with the Microscribe. Notice the dispersion in space of each configuration (location), the different orientations of the outlines, and their range in size. To remove information about scan location, the centroid of each configuration was moved in space to a common origin. A specimen’s centroid is found by calculating the mean x , mean y , and mean z coordinate of every point in its configuration (the “center of gravity” for all the landmarks; McNulty 2003, p. 61). Subtracting the specimen’s mean x from all of its x -coordinates, the mean y from its y -coordinates, and the mean z from its z -coordinates translates the specimen to the origin; when applied to all specimens, this eliminates any differences due to location. Figure 6-2b demonstrates this translation. Next, the landmark configurations were scaled isometrically (Figure 6-2c). Size is a huge confounding factor in analyses of shape (as discussed in Chapter 3). GPA removes isometric size differences among specimens by dividing each coordinate of a specimen by that specimen’s centroid size, setting all

configurations to a centroid size of one (Zelditch *et al.* 2004, p. 79). Centroid size is a measure of size that has no correlation to shape and is defined as the square root of the sum of squared distances of a specimen's landmarks to its centroid (*ibid* p. 78). Note that setting specimens to the same centroid size does not eliminate the effects of allometry (shape change with size), and therefore size-correlated shape variation will remain in the coordinate configurations. Finally, coordinate configurations were rotated to minimize the distance between each specific landmark across all specimens (Figure 6-2d). This is an iterative least-squares process in which sum-of-squared distances between each landmark are minimized (Slice 2005, p. 18). In the first iteration, a mean configuration (reference configuration) of translated and scaled specimens is produced on to which all specimen configurations (target configurations) are then superimposed. A new mean configuration is then calculated and the process is repeated until further superimpositions produce negligible differences in distance minimization (*ibid*). Following a GPA, the aligned, scaled, and rotated coordinates are in a common coordinate system and can be used as shape variables (Slice 2005, p. 23), called Procrustes coordinates (see Figure 6-2e). These coordinates are the data that are submitted to multivariate analyses. Each x , y , z coordinate for each landmark is input as a variable, thus a configuration with 20 landmarks will have 60 variables for multivariate analysis.

Multivariate analyses

Several multivariate analyses were used in this study to create habitat reconstructions. Principal component analyses were performed on Procrustes coordinates in order to explore variation within the sample and summarize the original data into fewer variables for further analyses. A discriminant function analysis was performed on

principal component scores to assess the accuracy of each unit of analysis for correctly assigning cervids to their known habitat types and to assign fossil specimens to a habitat type. A continuous Habitat Score (after Scott 2004) that allows for specimens to be placed in a continuum from open to closed habitats was produced for cervids. Finally, several confounding variables (tribal membership, body size, and sex) were examined for their influence upon the skeletal morphologies analyzed here.

Principal Components Analysis

Principal components analysis (PCA) is a data exploration and dimensionality reduction technique. PCA can be thought of as a rigid rotation of the original data in multidimensional space to create axes that are orthogonal to each other (Neff & Marcus 1980, p. 51). In this study, the main reason for conducting PCA is to reduce the dimensionality of the data sets. 3D GM datasets usually contain a high number of variables (three for each landmark or semi-landmark), yet most statistical analyses require one to have more specimens than there are variables and having a high number of variables complicates canonical variates analysis (CVA), which is necessary for this study as it will be used to assign fossil cervid specimens to their most likely habitat category. PCA summarizes much of the variation found in a sample on a few axes and the PC scores of the specimens on those reduced axes are submitted to CVA as variables.

In this study, all statistical analyses were performed in SAS 9.1 (SAS Institute, Inc., 1999). PCAs were conducted on the covariance matrix of Procrustes coordinates and PCAs were run on the extant and fossil data sets together so that all specimens could be analyzed in the same multivariate (principal components) space.

Canonical Variates Analysis (CVA)

Unlike PCA, CVA starts with an *a priori* assignment of specimens to categories. CVA then transforms the multivariate space to maximize the variability among groups relative to the variability within groups (Neff & Marcus 1980, p. 145, Slice *et al.* 1996, p. 534). Like PCA, this produces linear recombinations (canonical variates) of the original variables (here, PC scores) that allow for groups to be separated. The number of canonical variates necessary to separate groups is dependent upon the number of groups or number of variables (Neff & Marcus 1980). For example, if there are three groups in the analysis, two canonical variates are necessary to separate them.

CVAs were conducted on PC scores for each of the four units of analysis described in Chapter 5 and were used to separate extant cervids into their known habitat types; discriminant applications in these canonical variates spaces (e.g., Neff and Marcus, 1980) were employed to categorize fossil specimens into a habitat type. The number of PCs submitted to a CVA was selected by determining the number of PCs that returned the highest mean correct leave-one-out cross-validation (cross-validation henceforth) reclassification percentage (after Sheets *et al.* 2006).

Cross-validation tests were used to evaluate how well the canonical variates performed at classifying extant specimens into their known habitat type. Cross-validation is hypothesized to be a predictor of how well the ecomorphological variable will perform at classifying fossil specimens of unknown habitat (Neff & Marcus 1980, p. 152). This process iteratively removed each specimen, re-computed the CVA, and then classified the removed specimen (treated as an “unknown”) into a habitat type. The “unknown” specimen was classified into the habitat group that had the smallest Mahalanobis squared

distance (D^2) from the group's centroid to the "unknown" specimen in canonical variates space (Neff & Marcus 1980, p. 147). Cross-validation returned correct reclassification percentages for the entire data sample (the mean cross-validation percentage across all habitat groups), the correct reclassification percentage for each of the habitat groups, the posterior probabilities (likelihoods) of group membership for individual specimens into each of the habitat groups, and D^2 for each specimen from the specimen to the centroid of the group into which the specimen was classified. It should be noted that the CVA *must* classify each specimen and it is possible that fossil specimens may be very different from cervid specimens in the extant training set. This can be evaluated by examining the posterior probabilities of group membership and D^2 .

In order to determine the best cross-validation results for each unit of analysis, CVAs were conducted starting with the first two PCs as variables and then iteratively adding each subsequent PC up to fifty. The CVA that returned the highest mean cross-validation percentage for all groups was selected for the results reported here. The possibility that better cross-validation results, and therefore potentially better fossil classifications, could be obtained from non-sequential combinations of PC variables was not tested in these analyses. Note that while using an incomplete set of PCs for CVAs will bias statistical inference, it is appropriate here as the goal of these analyses was to achieve the best possible classification not to estimate the probability of centroid equivalence.

Since most ecomorphological studies have published reclassification results using the resubstitution method, results for this method will be reported here also. Resubstitution differs from cross-validation reclassification in that it does not remove the

specimen to be reclassified from the CVA before calculating the canonical variates. Thus, the specimen that is being reclassified contributes to the calculation of the canonical variates. Resubstitution is likely to overestimate the classification power of the canonical variates, thus providing higher reclassification percentages (Sheets *et al.* 2006, p, 3). This is especially true when more principal components are used in the CVA as the data set becomes more specific to the original data submitted, that is, higher PCs are more likely to contain data idiosyncratic to the data set, which is less useful when classifying unknowns (fossils).

Pairwise non-parametric permutation tests were conducted to evaluate the statistical significance of D^2 between the centroids of each habitat group in canonical variates space. This test is analogous to Hotelling's T^2 but does not require the assumption of multivariate normality as do parametric procedures. The null-hypothesis of these pair-wise permutation tests is that the two groups are not significantly different (i.e., they share a multivariate centroid). Following that logic, if the groups are not different, then the distance between their centroids results merely from the random sampling of specimens into their respective groups. In that case, this distance should be reproducible from other random divisions of the sample. Accordingly, permutation tests started with the calculation of the Mahalanobis squared distance (D^2), the squared distance between group centroids (Neff & Marcus 1980, p. 150). Samples from both groups were pooled together and then randomly split into two new groups. If the D^2 between these new groups was at least as great as the D^2 between the original groups, then it constituted evidence that the original groups are not different. On the other hand, if the D^2 between randomly formed groups was less than the original distance then it was taken as evidence

that the two groups are different. In this study, each permutation was repeated 10,000 times, creating a probability distribution of the likelihood that the two groups share a common centroid. At an α -level of 0.05, if 5% or fewer of the permuted groups had D^2 values that were larger than the benchmark D^2 , then the null hypothesis was rejected and the difference between group centroids was considered significant.

Because a group with more specimens has a higher likelihood of being represented in *both* permuted groups, simple permutation tests that do not account for this difference will be biased toward finding significantly different groups (McNulty *et al.*, 2006, p. 280). Therefore, permutation tests performed here were based on equalized samples, created by randomly selecting specimens from the larger group until the number in that group equaled the number in the smaller group. For example, if the D^2 of “Open” (N=22) and “Closed” (N=36) habitat groups is being tested for significance, only 22 specimens would be randomly from each group *in each iteration of the permutation test*. This means that all 22 specimens in the “Open” sample would be ‘resampled’ while only 22 out of the original 36 specimens in the “Closed” habitat would be submitted to the permutation test.

In this study, permutation tests of pairwise differences between group centroids were conducted on the same number of PCs used in corresponding analyses of habitat or tribal affiliation. While the use of a reduced number of PCs may bias p-values in favor of finding significance (see Morphmet-Listserv (2009) for discussion), this bias is similar to that induced when choosing which variables to measure or, once data are collected, which variables to include in the analysis. With the goal of finding the best discriminators

for habitat and taxon groups, determining whether these groups are significantly different based on the same set of variables is appropriate.

Habitat types

As described above, in order to perform a CVA, training specimens must be placed into specific categories. A four-habitat category system, similar to that of Kappelman *et al.* (1997) and DeGusta & Vrba (2003, 2005), is used here, with slight modification for cervid-occupied habitats. “Open” habitats include grasslands, open mountainous regions, and tundra. “Intermediate Open” habitats include ecotonal habitats, areas with tall grass (versus the short grass of grasslands), and swamps. “Intermediate Closed” habitats include woodlands/shrublands and “Closed” includes temperate forests, tropical forests, and mountain forests. Obviously, much habitat variability is collapsed into single categories, but this is necessary in any such classification system.

It should be noted that these categories differ somewhat from other (bovid) ecomorphological studies, reflecting the behavioral difference between bovids and cervids. Kappelman (1988, 1991) included swamps in the “Intermediate Closed” category, while here swamps are placed in the “Intermediate Open” category. Many of the cervids that inhabit swamps also spend time in more open wet grasslands and floodplains (Nowak 1999, Geist 1998). While these habitats are more open than woodlands, they often contain tall grass and reeds, as opposed to the short grass of true grasslands. Kappelman included hilly areas in the “Intermediate Open” category while here these habitats are placed in the “Open” category. Cervids (e.g. *Odocoileus hemionus*) that are found in open mountainous habitats also spend time in the open in montane meadows and even on plains (Geist 1998). Finally, Kappelman placed ecotonal

habitats in the “Open” category while here they are placed in the “Intermediate Open” category. Cervids that live in ecotones usually feed in the open and run back to denser cover when threatened (Geist 1998). They are adapted for short bursts of speed, but still must be able to move quickly in denser cover. Selection pressure for cursoriality is not as strong for these cervids as it is for open-adapted cervids and this is hypothesized to be reflected in their skeletal morphology.

Habitat Scores

One solution to the restriction of having to place cervid specimens into habitat categories is using a continuous variable along which specimens can be placed from open to closed habitats. Scott (2004) created such an index for bovids and equids by conducting a CVA on two linear measurements of metapodia with two groups: plains and forest. The resulting axis was then used to place all other specimens along the continuum from most closed to most open habitats. A similar analysis was performed for cervids in this study.

A CVA was conducted on PC scores of selected cervid specimens from “Closed” and “Open” habitats in the same manner as described above for habitat categories. The specimens used in “Open” versus “Closed” training sets were then reclassified into their known habitat types for which cross-validation percentages are reported. A permutation test was run on each “Open”-versus-“Closed” set. All extant and fossil specimens were then treated as unknowns and classified using the “Open” versus “Closed” discriminant function. This produced a canonical variate score for each specimen, which were plotted in a scatterplot.

Visualizations

To demonstrate the differences in morphology between “Open” and “Closed” specimens, visualizations were created by adding and subtracting vectors of shape change to/from the consensus landmarks configurations (Frost *et al.* 2003, p. 1056). In the case of the Habitat Score, the vector representing shape differences was determined by multivariate regression of the training set’s Procrustes coordinates on their canonical variates scores for the single axis separating the two habitat groups (i.e. “Open” and “Closed” groups). The resulting vector of regression coefficients describes shape change for the entire configuration along the canonical variates axis (McNulty *et al.* 2006, p. 279). When this vector was added to and subtracted from the consensus configuration (for the entire data set), it produced two new configurations that demonstrated the differences between the two extremes (“Open” and “Closed”; Frost *et al.* 2003). In cases where shape differences were subtle, these vectors were multiplied by a scalar in order to better illustrate the morphology. This type of scaling affects only the magnitude of the vector rather than the direction of shape change. The resulting configurations were then visualized using Morpheus (Slice *et al.* 2002).

Possible confounding variables

Though the goal of this study is to provide methods that allow cervid morphological features to be used as proxies for habitats, it is understood that adaptation to habitat is not the only influence on skeletal morphology, and that age, sex, and pathology may influence morphology. Only adult specimens without obvious pathologies (such as breaks or arthritis) were sampled and zoo specimens were avoided. Specimens were sampled evenly between sexes and across all available species of Cervidae. In

addition, this study tested for the effect of other influences on morphology: taxonomy (tribal membership), body size, and sex. The following procedures do not control for the influence of the aforementioned confounding factors, but instead explore how the four units of analysis in this study vary with tribal membership, body size, and sex.

Taxonomy: tribal membership

Phylogeny will always constrain morphology, especially in highly related groups, such as the Cervidae. Thus, some of the morphological variation in each unit of analysis was likely due to phylogeny. Though it was not an expressed goal of this study, some of the features analyzed here performed well at categorizing cervids into their taxonomic tribes. As described in Chapter 4, there are five extant tribes of cervids: Alceini, Capreolini, Cervini, Muntiacini, and Odocoileini. When these tribes were selected as the class variable in a CVA, the analysis found the linear recombination of the PC scores that minimized the variability among the tribal groups relative to the variability within the groups. It should be noted that these linear recombination will not be the same as the linear recombinations for CVA of habitat types (DeGusta & Vrba 2003, p. 1020) as the specimens in each group will differ between the two analyses. Similar methods as described above for habitat categorization were used to test if cervids can be correctly reclassified to their known tribe. CVAs were run on the PC scores that returned the highest correct mean cross-validation percentages and permutation tests were conducted between all pairs of tribes.

The fossil specimens in this analysis were members of the tribes Cervini and one (possibly two) individual of Alceini, though many (n=43/173) are identified only as 'Cervidae.' No analyses of tribal membership were run on fossil specimens.

Body size

The influence of body size on skeletal morphology is a common concern in studies of functional morphology. Large and small body sizes place different demands and constraints on bone form and function. Scott (1987, p. 77) found that the length of cervid rear-limb elements scale with marked negative allometry while their diameters and midshaft areas scale with slightly positive allometry. That is, as body size increases, limb elements become shorter and wider to resist bending moments during locomotion. Thus, small cervids have relatively longer limb lengths than do larger cervids. Beyond this general pattern, Scott (1987, pp. 73-74) also found that more distal skeletal elements (tibia, metatarsal) tend to vary according to habitat with small cervids in closed habitats having shorter limbs than small cervids in open habitats while large and swamp-adapted cervids were found to have shorter limbs than expected for their body size.

While this study was not directly concerned with skeletal element length (except, to a certain degree, in the calcaneus), it was important to consider how body size influenced the morphologies under investigation. Joint surface areas have been found to be correlated to body size in humans (Eckstein *et al.* 2001), carnivores (Andersson 2004), and primates (Hamrick 1996) but not to joint curvature. As isometric size was eliminated by GPA, the data in this analysis related only to joint shape. To investigate if there was a correlation between joint shape and size, CV scores of the joint surface margins (and other units of analysis) were regressed against the natural log of centroid size (lnCS). Those canonical variates that were strongly influenced by size (allometric shape differences) had significant correlations. To test if the ln of centroid size was a good indicator of body size in cervids, ln of centroid size was also regressed against several

aspects of body size reported in the literature: body weight, body length, and body height at the shoulder. These data were typically represented as means and thus the results here should be considered estimates.

If significant correlations were found between shape and size, the question then became whether the influence of size on shape needed to be removed from an analysis such as this. Body size is, in itself, an ecological adaptation. Smaller cervids are often found in closed habitats where having a small body size allows for better hiding ability (*Pudu*, *Mazama*, *Muntiacus*). When confronted by predators, these cervids generally take flight in a series of rapid bounding hops (saltatorial locomotion). Cervids in ecotonal and woodland habitats are often medium-sized (Scott 1987) and are general low-stamina saltatorial runners (Geist 1998). Large cervids in closed habitats (*Alces alces*, *Cervus unicolor*) are remarkable in that they will confront predators, and thus body size in these cervids is a predator defense (Geist 1998). Large cervids in open habitats (*Rangifer tarandus*, *Cervus elaphus*) form selfish herds (Hamilton 1971) for protection from predators. Since body size is intimately tied to cervid predator-defense and locomotor behaviors, it may, in fact, be undesirable to eliminate body size from an analysis of cervid ecomorphology. Thus, when correlations were found between body size and morphology they are discussed, but allometric effects were not removed from this analysis.

Sex

Determining sex of post-cranial skeletal elements in a mixed fossil assemblage is problematic. However, sexual dimorphism does influence morphology. Sexual dimorphism is a result of differing selection pressures between the sexes and is strongly influenced by environmental conditions (Post *et al.* 1999, p. 4468). In cervids, sexual

dimorphism is strongest in ecotonal species, where males are territorial and fight for access to females (Geist 1998, p. 52). Larger body size, without regard to age, has been shown to be advantageous in competition for females (McElligott *et al.* 2001). Females in ecotone habitats invest in the protection of offspring and adopt more cryptic predator-avoidance behaviors incurring a smaller body size. These differing selection pressures result in high sexual dimorphism (*ibid*). In open habitats, where cervids are generally gregarious, females tend to look more like young males, which is most notable in the antler-carrying females of *Rangifer tarandus* (caribou/reindeer). Estes (1991) suggests that by looking like her son, a female increases her fitness because young males are less likely to be driven out of the herd by more dominant males. By being less dimorphic, females also blend into the herd and are less likely to be selected as prey due to a smaller body size. Further, in gregarious cervids, males and females spend much of the year together and have similar selection pressures. Cervids in closed habitats are monogamous resource-defenders and males and females tend to be of similar sizes (Geist 1998, p. 32). Thus, sexual dimorphism is hypothesized to be high in ecotonal species and low in open and closed species.

Variation in morphology due to sexual dimorphism was tested for the two species that had the largest samples: *Odocoileus hemionus*, the mule deer, and *Odocoileus virginianus*, the white-tail deer. Though *Odocoileus hemionus* is mainly an open country and open mountain inhabitant, males and females display behavior more like that of an ecotonal species. Males tend to inhabit areas high in rich resources while females tend to inhabit regions with higher canopy cover and with fewer predators, usually on mountain slopes (Main & Coblentz 1996). These differing selection pressures result in males that

are larger than females, thus sexual dimorphism is hypothesized to be marked in mule deer. *Odocoileus virginianus* is one of the most habitat-plastic cervids and is found in habitats from temperate forests of North America, to swamps of the Southern United States, and to the dense forests of South America. In the United States, the only habitat white-tail deer are not found in is the dry, open regions where mule deer are found.

Sexual dimorphism has been found to be plastic in response to environmental change. In a 32-year study of *Cervus elaphus* in Norway, Post *et al.* (1999) found that with increased warming during winter months, male red deer grew faster and larger, allowing them to compete for mates sooner, while females were able to invest earlier in reaching sexual maturity at the expense of increasing body size. As sexual dimorphism increased in three decades as a response to shifting environmental conditions, it is hypothesized that white-tail deer, one of the oldest species of extant deer (Geist 1998, p. 255), from different habitats are likely to show varying degrees of sexual dimorphism.

PCAs were performed on mule deer and white-tail deer as separate data sets. To examine if specimens can be assigned to the correct sex, CVAs were performed on the principal components scores for each data set in the manner described above but with sex as the class variable. Permutation tests were performed on each pair to test for significant differences between group centroids. If the species is sexually dimorphic in each unit of analysis investigated, then permutation tests should be significant and cross-validation rates high. If the species is monomorphic, then permutation tests should not show significant differences in centroids and cross-validations should not be able to sort specimens into the correct sex. This investigation only evaluates if there is a difference in *shape* between the sexes. To investigate if shape was correlated with size, canonical

variate scores were regressed against $\ln CS$. High correlations indicate that size is influencing shape and that there is an allometric signal in the shape data (McNulty 2003, p. 65).

As sex determination was not a goal of this study at the time of data collection, sample sizes for both mule deer and white-tail deer are small. The investigation of sexual differences in shape was an exploratory one and is reported here as a pilot study. The preliminary results indicate that such a study will be fruitful but testing this is dependant upon acquiring large samples. Further, the sample collected here was not able to distinguish if variation in white-tail deer along sex differs between habitats. Nonetheless, this research indicates that with a large enough sample size, it should be possible to differentiate fossil specimens into their sexes, which can be of value to studies of taphonomy and archaeology.

Chapter 7: Results- Extant cervid ecomorphology

Introduction

Results for extant cervid ecomorphological analyses are presented here by each unit of analysis (calcaneal landmarks, femoral medial patellar margin, tibial lateral plateau margin, and the plantar margin of the third phalanx). The following is a description of the layout for each subsection.

Analysis of Habitat

Principal Components Analysis

Results for principal components analysis (PCA) of extant cervid specimens are presented first for each unit of analysis. PCAs were conducted on the Procrustes aligned coordinates of all specimens (extant and fossils) for each unit of analysis. The extant data set included specimens of *Megaloceros* in the “Open” category, though the assumption of its membership in the “Open” group is tested for each unit of analysis. If distinctions were found in the plots of specimens in PCA space, those plots are provided and discussed.

Canonical Variates Analysis

For canonical variates analysis (CVA), each specimen was assigned to one of four habitat types: “Open”, “Intermediate Open”, “Intermediate Closed”, or “Closed”. Appendix A contains sex and collection location for all specimens (when available). Each extant species was assigned a general and specific habitat type, a tribal affiliation, a substrate type, and various measures of body size; these were drawn from published literature and can be found in Appendix C. The number of principal components (PCs) submitted to the CVA was chosen by iteratively performing CVAs starting with two PCs

and adding additional PCs up to fifty. The CVA with the highest correct mean cross-validation rate for the four habitat types was selected. Table 7-1 provides the numbers of PCs submitted to each CVA in addition to the cumulative eigenvalue for the PCs and the reclassification results (cross-validation and resubstitution) for each CVA. CVAs for habitat analysis of each morphological unit of analysis are then presented with correct reclassification percentages reported for both cross-validation and resubstitution. Percent variance summarized by each canonical variate (CV) and distributions of specimens along each CV axis are discussed. The results for permutation tests are also discussed.

When specimen distribution in principal component and canonical variates spaces are discussed, specimens are often described as scoring *positively* or *negatively* along the PC or CV axes. It should be noted that the use of these terms is specific to the figures provided and the visualization of these axes' directions is arbitrary.

Habitat analyses				
Unit of analysis	#PCs	PC cumulative variance %	Resub. %	Xval %
CalLMs	17	94.6	79.1	61.7
FemMed	44	100	71.8	42.1
Phal3	13	95.6	75.6	66.3
TibLat	26	98.2	75.1	49.8

Table 7-1: Summary of habitat analyses for the four units of analysis, including the number of principal components submitted to each canonical variates analysis (#PCs), the cumulative percent of variance summarized by the PCs (PC cumulative variance %), the mean correct reclassification for the extant data set using resubstitution (Resub. %) and Cross-validation (Xval %). CalLMs = calcaneus landmarks, FemMed = femoral medial patellar margin, Phal3 = third phalanx plantar margin, and TibLat = tibial lateral plateau margin.

Habitat Score

A habitat score was created for each unit of analysis by selecting the extant specimens that were exemplary of the most “Open” and most “Closed” habitats. PCA

was performed on these specimens and, like the analysis for the entire data set, iterative CVAs were run to find the number of PCs that had the highest correct mean cross-validation percentage for the two habitat types. CV scores were calculated for all specimens and plotted along the CV axis in a scatterplot.

Visualizations were created from the most open-adapted and the most closed-adapted specimens in the data sets. The specimens used to create the visualizations were the same as the ones used to create the habitat score. The visualizations to illustrate the difference between “Open” and “Closed” specimens followed the procedure described in Chapter 6. Occasionally, other visualizations are included for illustrative purposes. All visualizations were created in Morpheus *et al.* (Slice 2002).

Analysis of Tribal membership

The specimens included in the analysis of tribal membership were the same as those included in the analysis of habitat (see above). Since PCA is a rigid rotation of the original data with no *a priori* assignment of specimens to groups, the PCA presented for the analysis of habitat is the same as the PCA presented for the analysis of tribal membership. When PCA plots are provided, specimens were coded by tribe instead of by habitat (gray circles = Alceini, gray asterisks = Capreolini, black up-triangles = Cervini, gray crosses = Muntiacini, and gray down-triangles = Odocoileini).

CVA of tribal membership created linear combinations of the shape variables (PC scores) that maximized the variability among the tribes relative to the variability within tribes (Neff & Marcus 1980, p. 145, Slice *et al.* 1996, p. 534). These combinations were not the same as those of the CVA of habitat groups because they were based on entirely different class variables. The number of PCs submitted to the CVA, resubstitution and

cross-validation results, and CVA plots are presented for each unit of analysis. Table 7-2 provides a summary of the number of PCs submitted to the CVA, the cumulative percentage variation explained by those PCs, and cross-validation and resubstitution percentages for each unit of analysis.

Analyses by Tribe				
Unit of analysis	#PCs	PC cumulative variance %	Resub. %	Xval %
CalLMs	24	100	89.2	72.7
FemMed	2	78.8	50.3	50.3
Phal3	12	94.8	84.2	73.1
TibLat	29	98.6	58.6	83.7

Table 7-2: Summary data for analyses by tribe, using the abbreviations described for Table 7-1.

Analysis of Sex

To test if the units of analysis were able to distinguish the sex of cervid specimens, CVAs were run on PC scores for species of adequate sample sizes (*Odocoileus virginianus* and *O. hemionus*). Since these samples are small, this was an exploratory analysis. PCA was performed on Procrustes coordinates for both species independently. The number of PCs that returned the highest correct mean cross-validation percentage for two sexes was chosen for submission to CVA.

Since only one of the analyses of sex had significant results, the results for each study will not be discussed in detail (but see Table 7-3). Only the calcaneal landmarks for *Odocoileus hemionus* were able to distinguish between males and females. While several of the analyses had moderately high reclassification rates, the permutation tests indicated that the sexes were not significantly different. Sample sizes were too low to determine sex in this study.

Analyses of Sex							
Unit of Analysis	Species	# of PCs	Cross-validation	Resubstitution	Permutation test (p)	lnCS v. CV1	
						R ²	p-value
Calcaneus LMs	WT	2	61.9	69.1	0.0713	0.0336	0.5487
	MD	7	85.4	100	0.0008	0.1861	0.1236
Fem. Med. Margin	WT	2	79.2	79.2	0.0679	0.0014	0.9006
	MD	1	66.7	66.7	0.1234	0.1488	0.1556
Tib. Lat. Margin	WT	1	48.8	48.8	0.5368	0.1009	0.2903
	MD	2	65.1	65.1	0.1649	0.2085	0.0871
Phalanx 3 Margin	WT	3	83.3	100	0.0947	0.0556	0.6529
	MD	1	88	88	0.1654	0.0777	0.5927

Table 7-3 Summary data for analyses of sex for *Odocoileus virginianus* (WT) and *Odocoileus hemionus* (MD), with the number of PCs included in each analysis, the mean correct resubstitution and cross-validation percentages, results of the permutation test between group centroids (p = probability that the centroids were drawn from the same population), and regressions of canonical variate 1 (CV1) against the natural log of centroid size (lnCS) with R² and p-values.

Analysis of Body Size

As discussed in Chapter 6, body size affects morphology through allometric scaling. Generalized Procrustes analysis (GPA) removed the effects of isometric size differences, but not shape difference due to allometry. To test if size was correlated to shape as it relates to habitat, the natural log of centroid size (lnCS) was regressed against the first ten principal components and each of the canonical variates from the analysis of habitat (see above). Only the first ten PCs were included, as there was never a significant correlation to shape after ten PCs (and usually not after the first two PCs). There were only (maximally) three CVs for a CVA of four (habitat) categories. If significant correlations were found between the shape variables (PCs and CVs) and the lnCS, then the shape variables do vary with size and allometric effects must be taken into account. However, no attempt was made to remove allometric information from the shape

variables in this study, as size is an important component of cervid predator-defense behavior.

To test how well lnCS reflected different parameters of body size, bivariate regressions were computed between lnCS and the natural log of body weight (lnBW), natural log of body height (measured at the shoulder; lnBH) and natural log of body length (lnBL). Actual body size data for museum specimens are generally not provided and thus the data presented here are means from published reports (e.g. Whitehead 1993, Geist 1998, Nowak 1999, Eisenberg 2000). Cervids have a huge range in sizes (for example, from 3.3 - 825 kg in body weight, see Appendix C) and thus a natural log was taken of the means to normalize the data (Hammer & Harper 2006, p. 81). If significant correlations were found between lnCS and the various measures of body size, then lnCS can be taken as a good proxy for body size. Results are presented and discussed for each unit of analysis separately.

Unit of analysis 1: Calcaneal landmarks (CalLM)

Analysis of Habitat

Principal Components Analysis

Ten 3D landmarks were digitized for 122 extant and 54 fossil cervid specimens (details on each specimen can be found in Appendices A and B). Procrustes-aligned coordinates for the entire data set (extant + fossil) were submitted to a Principal Components Analysis (PCA). The PCA did not provide good visual distinction between the habitat groups, but some trends were evident. When PC1, which summarizes 22.1% of the total variance in the sample, is plotted with PC2, 13.2% of the variance (Figure 7-1), “Closed” habitat specimens scored positively on PC1 while “Open” and “Intermediate

Open” tended to score more negatively along PC1. Along PC2, specimens in the “Intermediate” categories tended to score more positively.

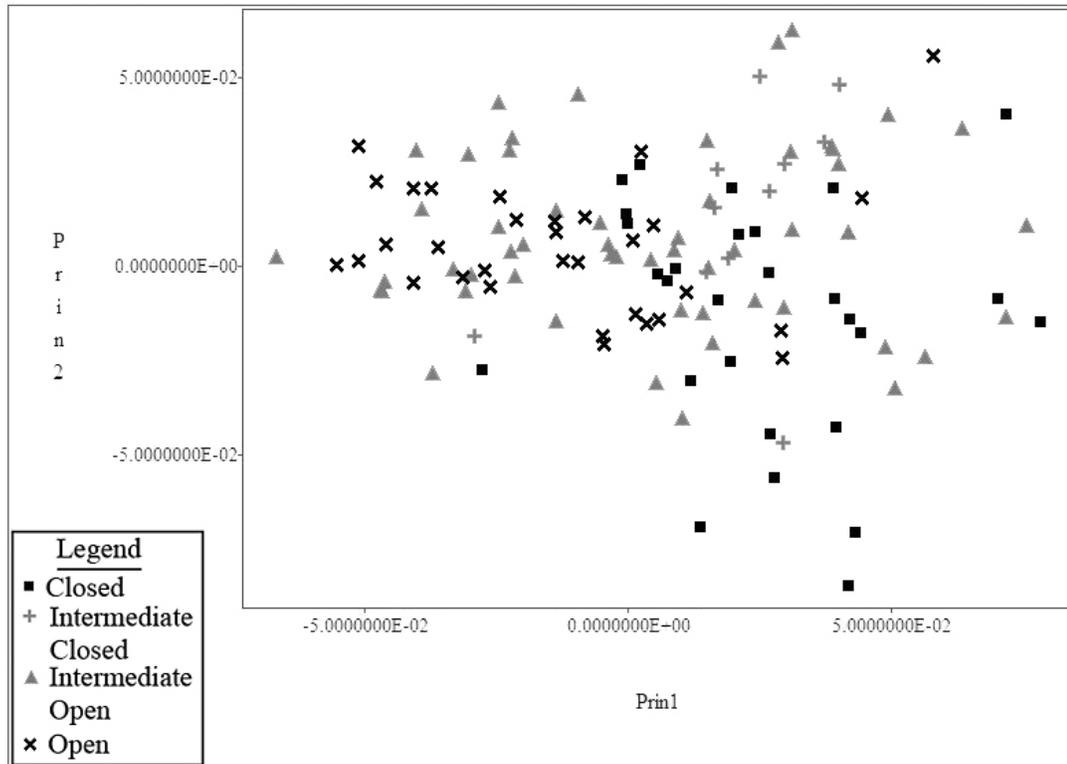


Figure 7-1 Plot of PC1 and PC2 for the habitat analysis of calcaneal landmarks. “Closed” habitat specimens tended to score positively along PC1 and “Open” specimens scored more negatively. “Intermediate” category specimens tended to score more positively along PC2.

Canonical Variates Analysis

The sample was split between the extant specimens and the fossil specimens. Only the results for the extant specimens are reported in this chapter. Fossil results can be found in Chapter 8. Three specimens belonging to *Megaloceros giganteus* were included in “Open” habitat category in the extant sample.

After iteratively submitting progressively higher numbers of PCs to CVA, the results for the CVA reported here are based on the number of PCs that returned the highest mean cross-validation result. Seventeen PCs, which summarized 94.6% of the

total variance in the sample in the PCA, were submitted to CVA. The CVA was able to correctly reclassify extant specimens to their known habitat groups 61.7% of the time with cross-validation and 79.1% of the time with resubstitution (Table 7-4).

Cross-validation					
	Closed	InterClosed	InterOpen	Open	Total
Closed	20 71.4	2 7.1	4 14.3	2 7.1	28 100
InterClosed	3 27.3	5 45.5	1 9.1	2 18.2	11 100
InterOpen	3 5.6	8 14.8	33 61.1	10 18.5	54 100
Open	0 0	4 12.5	6 18.8	22 68.8	32 100
Total	26 20.8	19 15.2	44 35.2	36 28.8	125 100
Resubstitution					
	Closed	InterClosed	InterOpen	Open	Total
Closed	26 92.9	0 0	0 0	2 7.1	28 100
InterClosed	0 0	9 81.8	1 9.1	1 9.1	11 100
InterOpen	3 5.6	6 11.1	36 66.7	9 16.7	54 100
Open	0 0	3 9.4	5 15.6	24 75	32 100
Total	29 23.2	18 14.4	42 33.6	36 28.8	125 100

Table 7-4 Cross-validation and resubstitution results for the habitat analysis of calcaneal landmarks, with specimen counts and mean correct reclassifications (shaded gray).

Specimens in the “Intermediate” habitat categories had lower cross-validation rates than did specimens from the “Open” and “Closed” habitat categories. Cross-validation correctly classified 71.4% of the “Closed” specimens, with two specimens

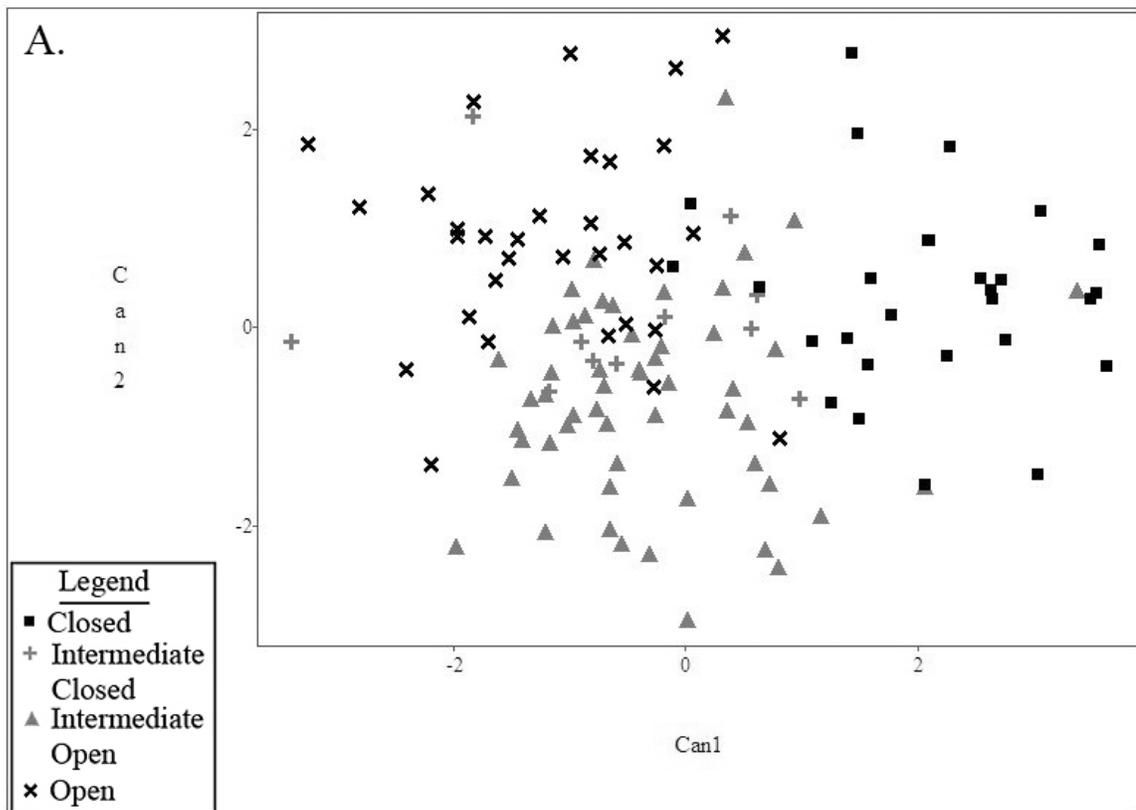
assigned to “Open”, two to “Intermediate Closed” and four to “Intermediate Open”, though there was little patterning amongst the species that were incorrectly classified. The lowest cross-validation result (45.5%) was for the “Intermediate Closed” category, with only *Capreolus capreolus* specimens and one *Rangifer tarandus* specimen correctly reclassified. Further, the posterior probabilities for these specimens were all rather low, indicating that the “Intermediate Closed” calcaneal morphology is poorly defined. “Intermediate Open” specimens were correctly reclassified 61.1% of the time and most incorrectly classified specimens were assigned to either “Intermediate Closed” (8/21) or “Open” (10/21). 68.8% of the “Open” specimens reclassified correctly with most incorrectly classified specimens placed into “Intermediate Open”. Interestingly, one of the *Megaloceros giganteus* (F21232) was assigned to “Intermediate Open” with a posterior probability of 50.4% (and to “Open” with 39.9% probability). This was the largest specimen in the data set (centroid size = 204.7, compared to the CS mean of 107), though it appears that the morphology of the calcaneus does not scale allometrically (see below).

Permutation tests also indicated that the “Intermediate” categories were the least different from each other. Though all pair-wise tests showed that the group centroids were significantly different (see Table 7-5), the test between the “Intermediate Open” and “Intermediate Closed” specimens had the highest p-value (0.0014).

	InterOpen	InterClosed	Closed
Open	<0.0001	0.0003	<0.0001
InterOpen		0.0014	<0.0001
InterClosed			<0.0001

Table 7-5 Results for permutation tests between each pair of habitat types in the analysis of calcaneal landmarks based on Mahalanobis distances between group centroids (see Chapter 6). The reported result is the probability that the two centroids were drawn from the same population.

The first canonical variates (CV) axis summarized 67.6% of the variation in the sample (Figure 7-2) and separated the “Closed” specimens from the other habitat categories. The second CV axis summarized 22.8% of the variation in the sample and separated the “Open” category from the “Intermediate Open” category. The third CV axis summarized the remaining 9.6% of the variation in the sample and separated the “Intermediate Closed” group from the other habitat groups (Figure 7-2), though there is much overlap.



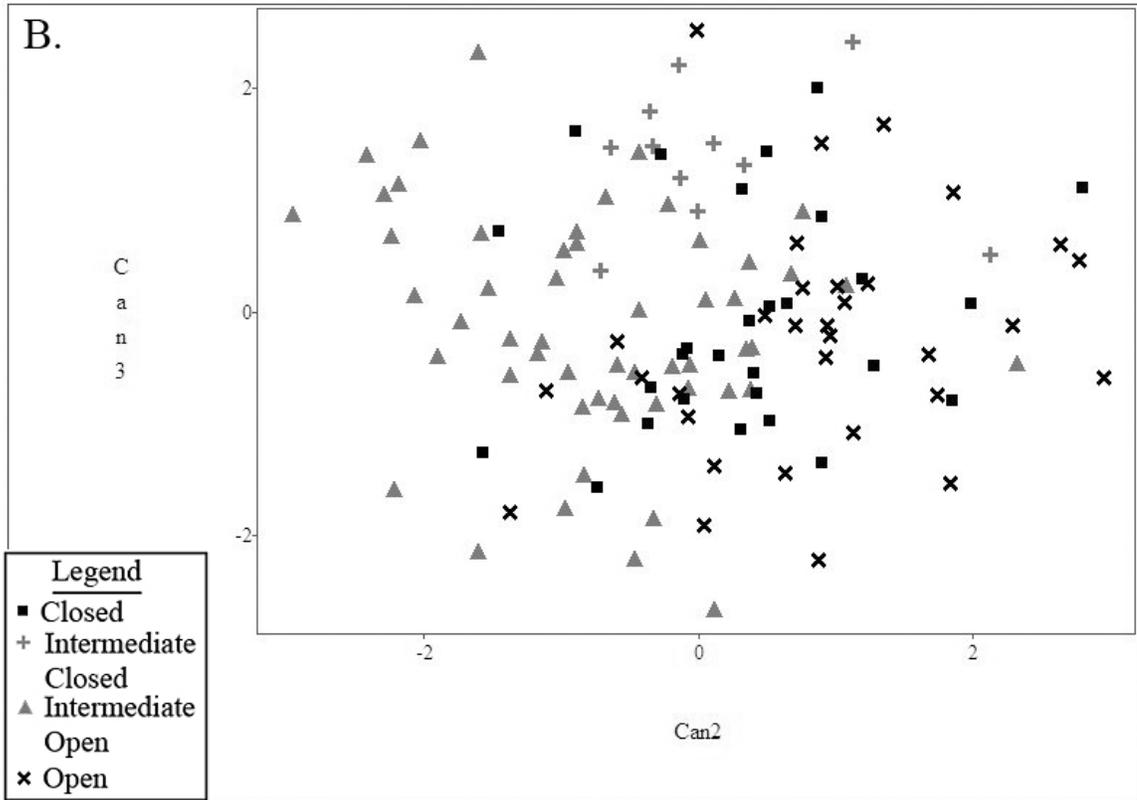


Figure 7-2 A: Plot of CV1 and CV2 for the habitat analysis of calcaneal landmarks. CV1 separated the “Closed” specimens from all other habitat types, CV2 separated “Open” specimens from “Intermediate Open” specimens. B: Plot of CV2 and CV3 for the calcaneal landmarks. CV3 separated the “Intermediate Closed” from the other habitat types, though there was much overlap.

Habitat Score

The habitat score for the calcaneus landmarks was created using ten specimens from the “Closed” category and ten specimens from the “Open” category. The permutation test reported significant difference in the group centroids ($p < 0.0001$ that they were drawn from the same population). However, cross-validation of the training specimens only returned a correct reclassification rate of 75% (resubstitution was 100% correct). Three “Closed” specimens and two “Open” specimens were incorrectly classified, with no distinct patterning amongst incorrectly classified specimens.

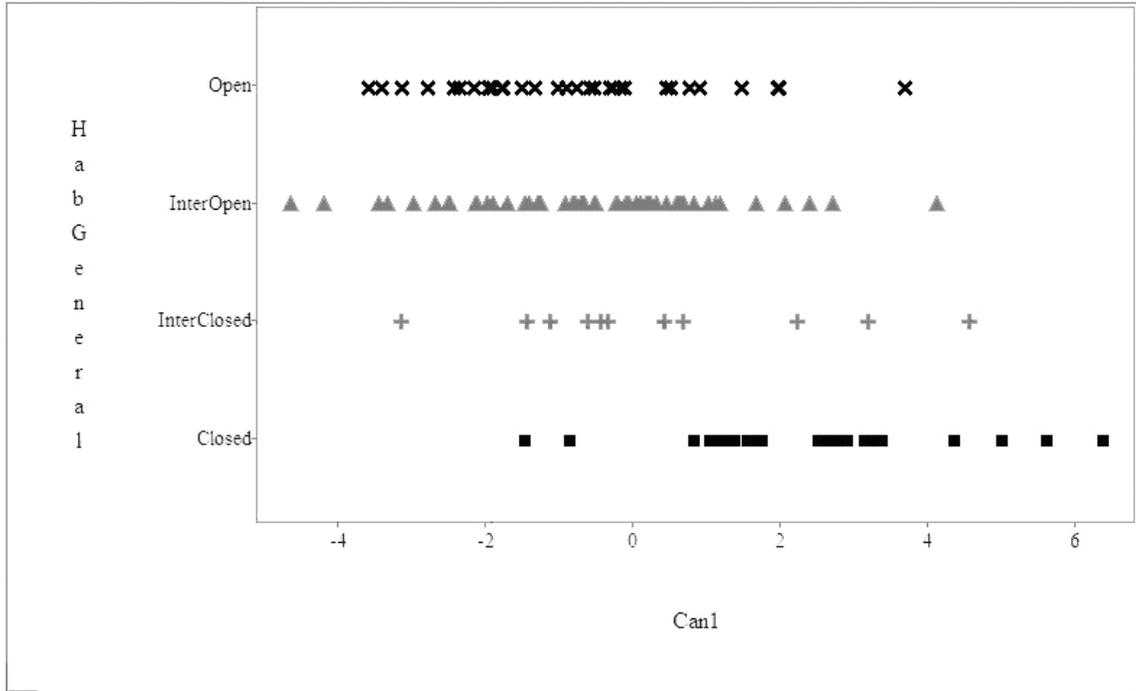


Figure 7-3 Habitat score plot for calcaneal landmark analysis of habitat. Specimen distribution along the canonical variate forms more an overlapping continuum from “Closed” to “Open”.

When all extant specimens were scored along the canonical variate produced with the training set, the four habitat categories did form a continuum from more “Closed” to more “Open” habitats, though there was substantial overlap between the groups (see Figure 7-3).

Visualizations were created using the habitat score training set specimens (the vector of shape change was multiplied by four in this case). In Figure 7-4, the top image in each subsection is the calcaneal landmark configuration from the medial view, the bottom image is the configuration from the superior view, and the right-side image is from the inferior-anterior view. The visualization of both extremes is shown superimposed in Figure 7-4A. “Closed” habitat specimens (Figure 7-4B) have an overall more blocky shape while “Open” specimens (Figure 7-4C) are more elongated. The

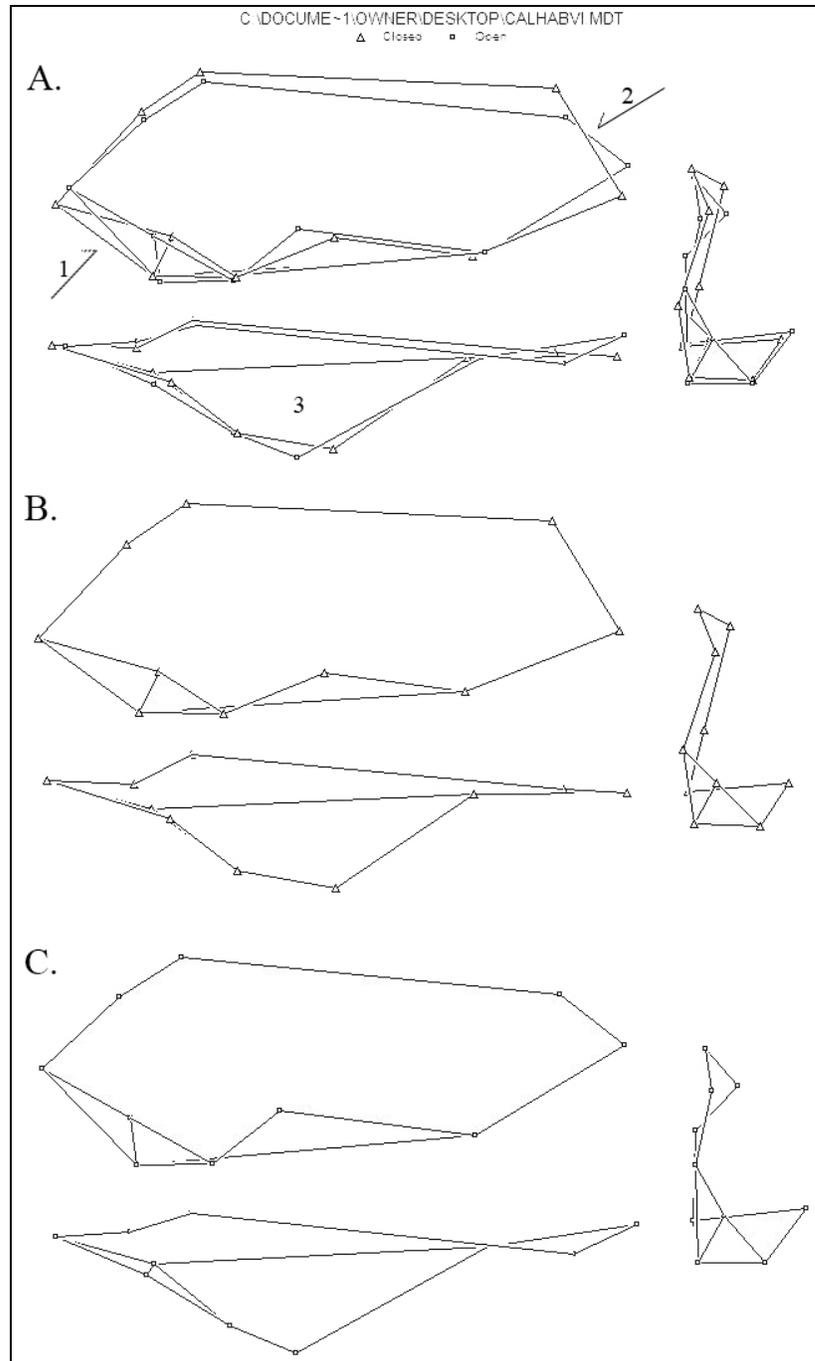


Figure 7-4 Visualizations of the shape change along the canonical variate from the calcaneal landmarks habitat score analysis, creating hypothetical "Closed" and "Open" specimens when the vector of shape change was applied to the mean configuration of all specimens. A = Overlaid "Open" and "Closed" specimens, B = "Closed" specimen, C = "Open" specimen. 1 = orientation of the cubonavicular articular surface, 2 = calcaneal tuber, 3 = sustentaculum tali. For each subsection, the top image is from medial, the bottom image is from anterior, and the right-side image is from antero-inferior.

articular surface for the cubonavicular (indicated by a “1” in Figure 7-4A) is more inferiorly oriented in the “Closed” habitat specimen, which gives the calcaneus a more oblique orientation to the rest of the lower limb in rest position. The cubonavicular articulation of the “Open” specimens is more anteriorly oriented, which gives the calcaneus a more vertical rest position. A more vertical rest position means that the calcaneus (as the lever arm for the lower limb) has a shorter distance to travel during limb extension, which provides a less powerful but quicker movement. A more powerful lever arm is necessary for closed-adapted cervids that use bounding leaps and rapid changes in direction to escape predators. A more oblique rest position of the calcaneus provides a more powerful but slower lever arm. “Closed” specimens have a large insertion area (calcaneal tuber) for the gastrocnemius muscle (“2” in Figure 7-4A) in the superior aspect than do “Open” specimens, which also may reflect the need for more power generation at the hock joint. The sustentaculum tali (“3” in Figure 7-4A) of “Closed” specimens is wider than that of “Open” specimens, which allows for more rotation and movement in the parasagittal plane between the calcaneus and astragalus. This allows for more flexibility at this joint, which is necessary for maneuvering through complex closed habitats. Open-adapted cervids restrict movement at the hock joint to the parasagittal plane to resist bending energies during rapid locomotion, reducing the risk of dislocation.

Analysis of Tribal membership

Figure 7-5 shows the same PCA plot illustrated above in Figure 7-1. In this case, however, specimens were labeled according to tribe rather than habitat. Now, it became evident that the species *Odocoileini* were separated from the other cervid tribes on PC1 (Figure 7-5). No further pattern was discernable from additional PCA plots.

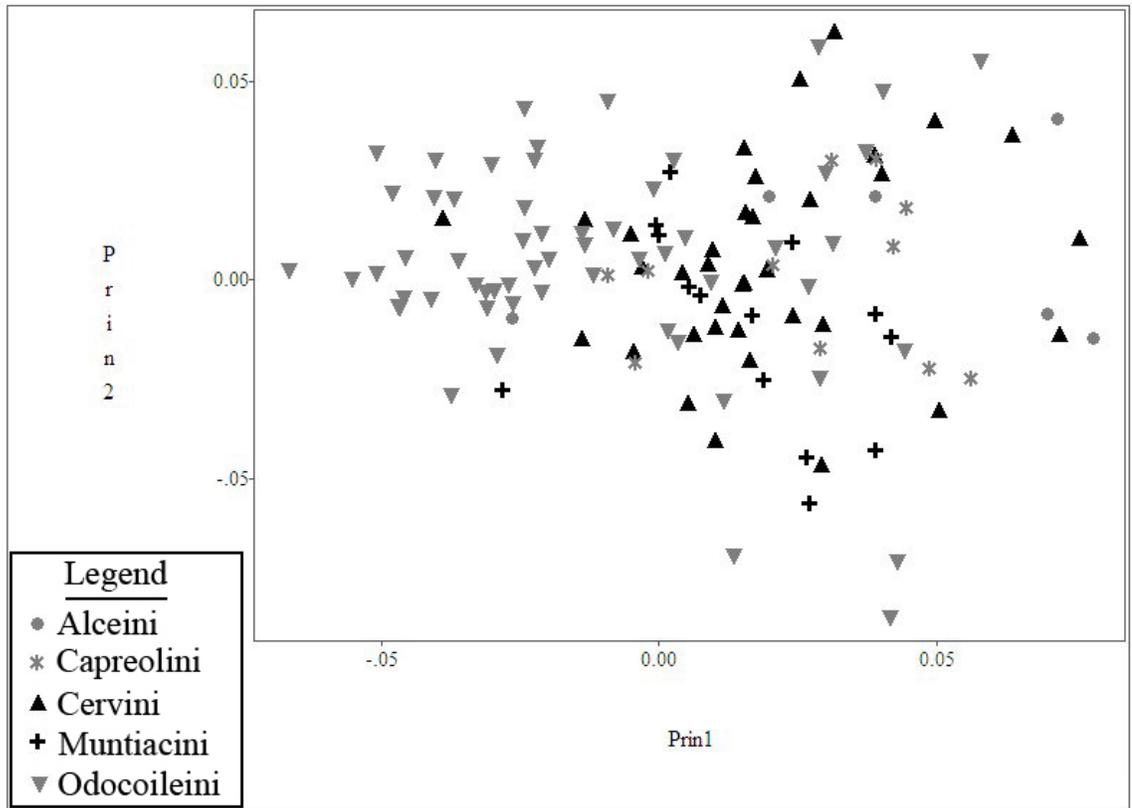


Figure 7-5 Plot of PC1 and PC2 for the tribal analysis of calcaneal landmarks. Odocoileini scored negatively along PC1. No other distinctions were evident amongst the tribes in principal components space.

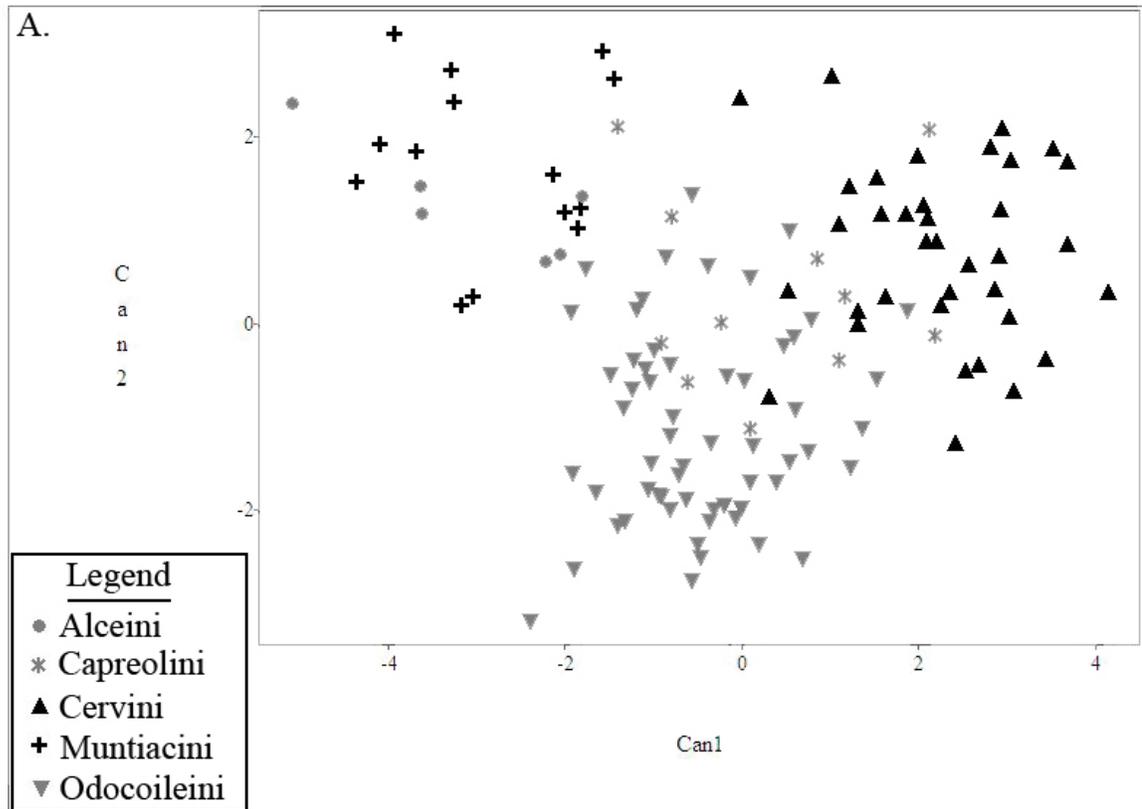
CVA was conducted on twenty-six PCs, which returned a mean correct cross-validation rate of 72.7% (89.2% for resubstitution) (Table 7-6). Permutation tests demonstrated that all group centroids were significantly different at (minimally) $p = 0.0015$ (Table 7-7). The Capreolini specimens had the lowest cross-validation rates (45.5%), though there was little patterning to their misclassification. CV1 (summarizing 54% of the total variance) separated the Cervini specimens from the Alceini + Muntiacini specimens, while CV2 (22.1% of the total variance) separated the Odocoileini from all other tribes. CV3 (14.9% of the variance) separated the Alceini specimens from all other tribes while CV4 (9.1% of the variance) weakly separated the Capreolini from the other tribes (Figure 7-6).

Cross-validation						
Tribe	Alceini	Capreolini	Cervini	Muntiacini	Odocoileini	Total
Alceini	5	0	0	1	0	6
	83.3	0	0	16.7	0	100
Capreolini	0	5	2	2	2	11
	0	45.5	18.2	18.2	18.2	100
Cervini	0	1	30	1	4	36
	0	2.8	83.3	2.8	11.1	100
Muntiacini	0	1	0	11	2	14
	0	7.1	0	78.6	14.3	100
Odocoileini	0	5	6	5	43	59
	0	8.5	10.2	8.5	72.9	100
Total	5	12	38	20	51	126
	4	9.5	30.2	15.9	40.5	100
Resubstitution						
Tribe	Alceini	Capreolini	Cervini	Muntiacini	Odocoileini	Total
Alceini	5	0	0	1	0	6
	83.3	0	0	16.7	0	100
Capreolini	0	9	0	1	1	11
	0	81.8	0	9.1	9.1	100
Cervini	0	1	34	0	1	36
	0	2.8	94.4	0	2.8	100
Muntiacini	0	0	0	14	0	14
	0	0	0	100	0	100
Odocoileini	0	3	3	2	51	59
	0	5.1	5.1	3.4	86.4	100
Total	5	13	37	18	53	126
	4	10.3	29.4	14.3	42.1	100

Table 7-6 Cross-validation and resubstitution results for the tribal analysis of calcaneal landmarks, with specimen counts and mean correct reclassifications (shaded gray).

	Capreolini	Cervini	Muntiacini	Odocoileini
Alceini	0.0015	0.001	0.0013	0.0013
Capreolini		<0.0001	<0.0001	0.0001
Cervini			<0.0001	<0.0001
Muntiacini				<0.0001

Table 7-7 Results for permutation tests between each pair of tribes in the tribal analysis of calcaneal landmarks based on Mahalanobis distances between group centroids. The reported result is the probability that the two centroids were drawn from the same population.



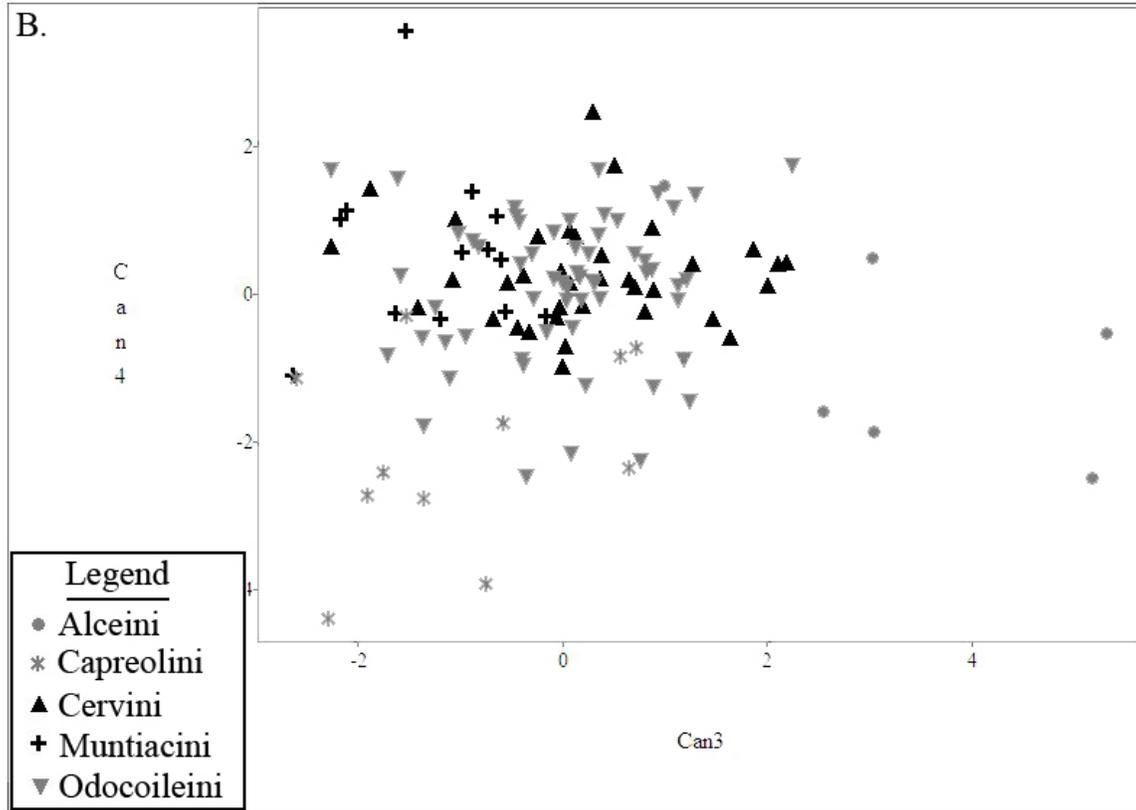


Figure 7-6 A: Plot of CV1 and CV2 for the tribal analysis of calcaneal landmarks. CV1 separated the Alceini + Muntiacini specimens from the Cervini specimens, CV2 separated Odocoileini specimens from all other tribes. B: Plot of CV3 and CV4 for the calcaneal landmarks by tribe. CV3 separated the Alceini from all other tribes and CV4 weakly separated the Capreolini from all other tribes.

Analysis of Body Size

For the calcaneus, the natural log of centroid size (lnCS) was highly correlated ($p < 0.0001$) to all body size parameters (Table 7-8) with R^2 values of 0.865 for body weight, 0.8133 for body height, and 0.8328 for body length. Thus, lnCS was taken as a good estimator of body size parameters.

No significant correlations were found between any of the first ten PCs and the lnCS, thus calcaneus shape does not vary with size. Though there was no allometric

Cal LMs: Extant Body Size		
Regression	R ²	p-value
lnBW	0.865	<0.0001
lnBH	0.8133	<0.0001
lnBL	0.8328	<0.0001
PC1	0.0003	0.8503
PC2	0.0255	0.075
PC3	0.0404	0.246
PC4	0.0072	0.3478
PC5	0.0698	0.0029
PC6	0.0038	0.4934
PC7	0.0063	0.3801
PC8	0.0312	0.0489
PC9	0.0032	0.5295
PC10	0.0054	0.4144
CV1	0.0743	0.0021
CV2	0.0021	0.6093
CV3	0.044	0.0189

Table 7-8 Regressions of the natural log of centroid size (lnCS) against several measures of body size (all natural logged) for extant species in the calcaneal landmark analysis of habitat: body weight (lnBW), body height at shoulder (lnBH), and body length (lnBL), the first ten principal component scores (PC1-PC10), and the three canonical variates (CV1-CV3). All measures of body size in extant cervids were highly correlated to the lnCS. None of the PCs or CVs was correlated to lnCS.

shape change associated with size, there was a patterning to the distribution of cervids from different habitats along lnCS. That is, “Closed” species tended to have the smallest body sizes (except for *Alces*), the “Intermediate” specimens tended to be of medium to large body size, and “Open” specimens had medium body sizes (except for *Megaloceros giganteus*, which had the largest body size of all the specimens in this analysis).

Regressions of the canonical variates against lnCS also showed no significant correlations. Though the regression of CV1 and lnCS did have a low p-value ($p = 0.0021$), the R² value was also quite low (0.0743). Calcaneal morphology did not scale allometrically.

Unit of analysis 2: Femoral Medial Patellar Articular Surface Margin (FemMed)

Analysis of Habitat

Principal Components Analysis

Twenty-one 3D semi-landmarks were digitized for 133 extant and eleven fossil cervid specimens. Four specimens of *Megaloceros giganteus* were included in the extant training set and thus results for 137 training specimens are reported. Procrustes-aligned coordinates for the entire data set (extant + fossil) were submitted to PCA. The “Closed” specimens formed a group away from the other habitat categories along PC1 (Figure 7-7), but no further differentiations were evident in other PCA plot.

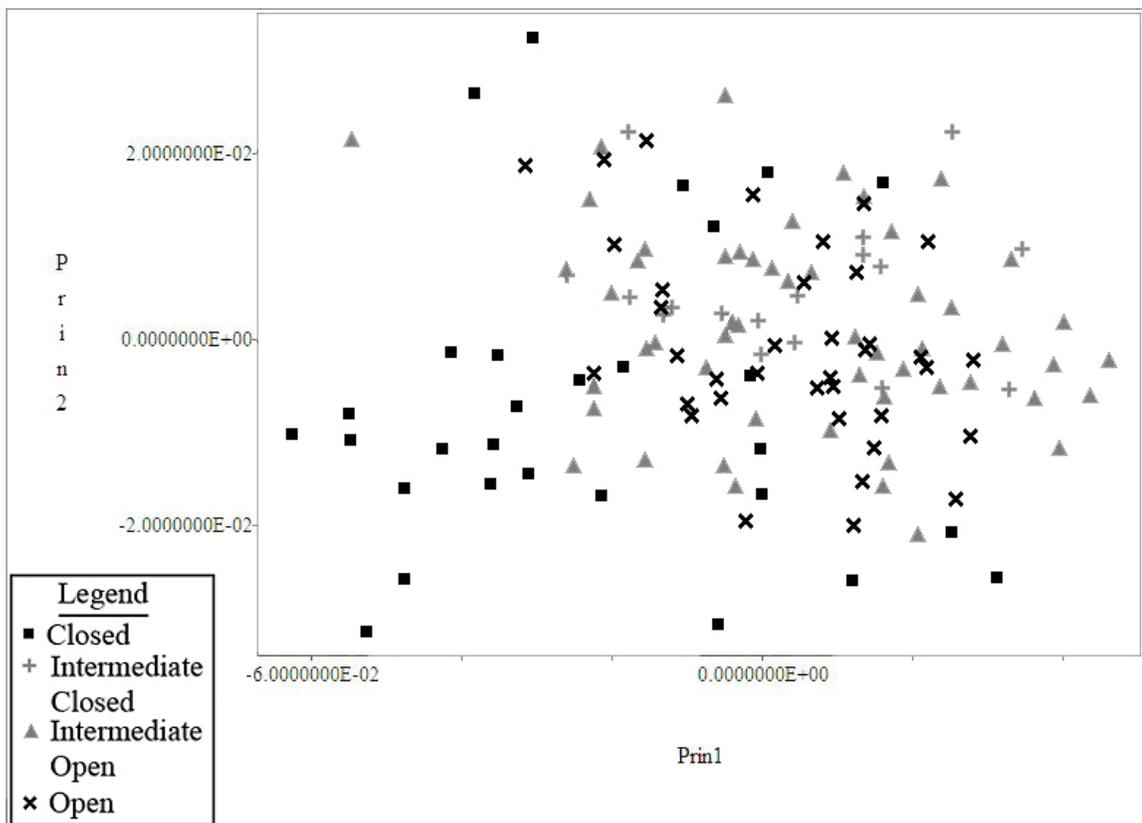


Figure 7-7 Plot of PC1 and PC2 for the habitat analysis of femoral medial patellar margin. “Closed” habitat specimens tended to score negatively along PC1. No other distinctions were evident among the habitat groups in principal components space.

Canonical Variates Analysis

When forty-four PCs were submitted to the CVA (100% of the total sample variance in the PCA), CV1 (summarizing 58.6% of the total sample variance) separated the “Closed” specimens from the other habitat categories, CV2 (22.3% of the variance) separated the “Open” specimens from the other categories, and CV3 (19.1% of the variance) separated the two intermediate categories (Figure 7-8). Mean correct cross-validation percentage for the four habitat groups was 42.1% (resubstitution = 71.8%) (Table 7-9). Permutation tests indicated that all group centroids were significantly different from each other (Table 7-10).

As can be seen in Figure 7-9, the differences in shape between open-adapted and closed-adapted cervids support Kappelman’s (1988, 1991) hypotheses regarding this unit of analysis. That is, closed-adapted cervids have a more circular medial patellar margin (B in Figure 7-9), while open-adapted cervids’ margins are more elliptical (C). A-C in Figure 7-9 were created using only the specimens included in the training set for the habitat score (see below). Interestingly, when visualizations were created for “Closed” specimens in one group versus all non-“Closed” specimens as a single group for the entire data set, the pattern of shape difference became more exaggerated rather than reduced, as demonstrated in Figure 7-9D. The antero-distal portion (to the left in the image) of the medial patellar margin has a distinct bulge in the non-“Closed” specimens.

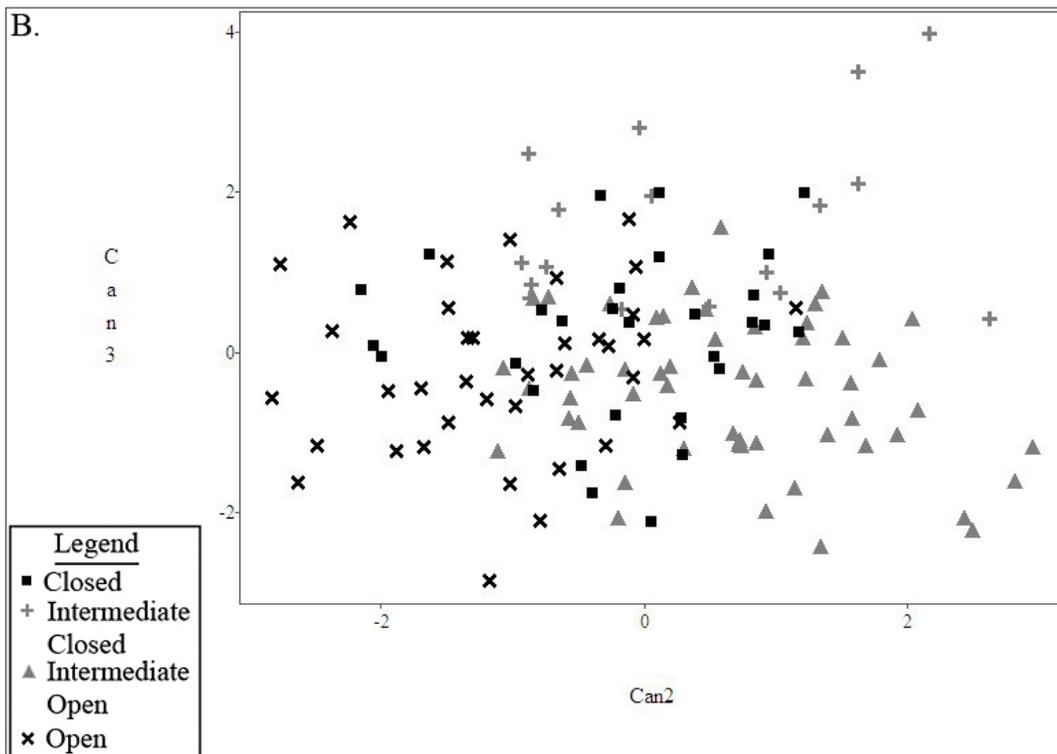
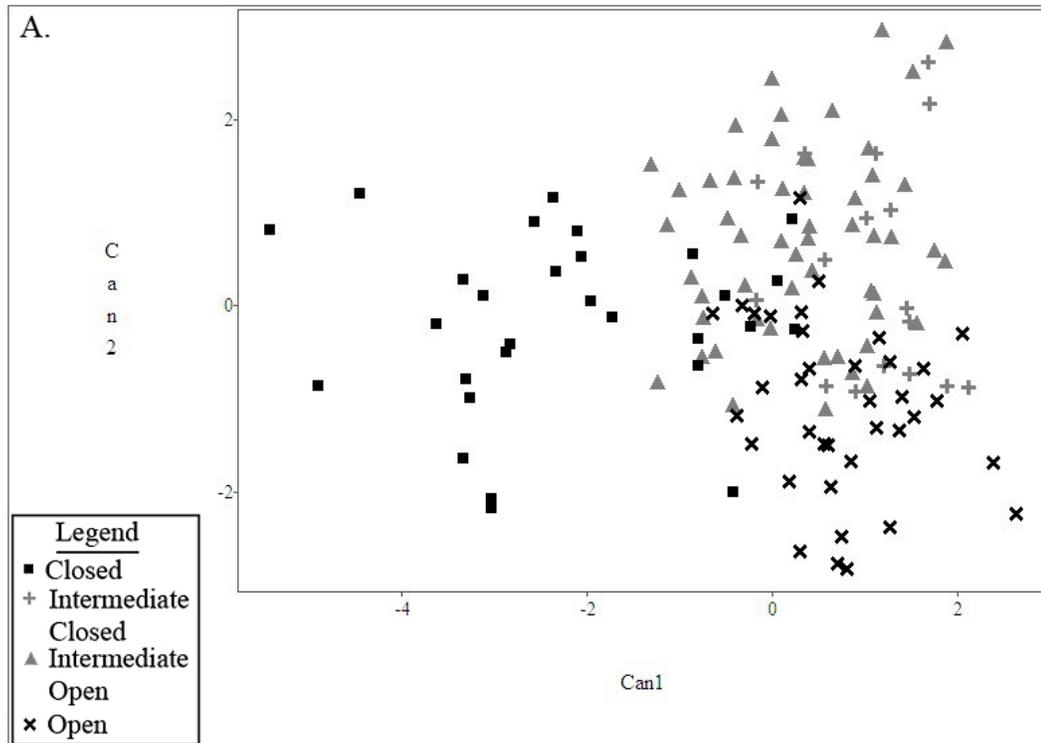


Figure 7-8 A: Plot of CV1 and CV2 for the habitat analysis of femoral medial patellar margin. CV1 separated the “Closed” specimens from all other habitat types, CV2 separated “Open” specimens from specimens of all other habitat types. B: Plot of CV2 and CV3 for the femoral medial patellar margin. CV3 separated the two “Intermediate” categories

Cross-validation					
	Closed	InterClosed	InterOpen	Open	Total
Closed	16 55.2	4 13.8	7 24.1	2 6.9	29 100
InterClosed	2 11.8	5 29.4	4 23.5	6 35.3	17 100
InterOpen	8 14.8	10 18.5	22 40.7	14 25.9	54 100
Open	1 2.7	9 24.3	11 29.7	16 43.2	37 100
Total	27 19.7	28 20.4	44 32.1	38 27.7	137 100
Resubstitution					
	Closed	InterClosed	InterOpen	Open	Total
Closed	21 72.4	3 10.3	3 10.3	2 6.9	29 100
InterClosed	0 0	12 70.6	2 11.8	3 17.7	17 100
InterOpen	3 5.6	5 9.3	37 68.5	9 16.7	54 100
Open	0 0	4 10.8	5 13.5	28 75.7	37 100
Total	24 17.5	24 17.5	47 34.3	42 30.7	137 100

Table 7-9 Cross-validation and resubstitution results for the habitat analysis of femoral medial patellar margin, with specimen counts and mean correct reclassifications (shaded gray).

	InterOpen	InterClosed	Closed
Open	<0.0001	<0.0001	<0.0001
InterOpen		<0.0001	<0.0001
InterClosed			<0.0001

Table 7-10 Results for permutation tests between each pair of habitat types for the femoral medial patellar margin based on Mahalanobis distances between group centroids. The reported result is the probability that the two centroids were drawn from the same population.

Thus, it appears that the medial patellar margin only reflects differences between closed-adapted and non-“Closed” adapted cervids (as was indicated by the permutation

tests). This can be clearly seen in Figure 7-10, which is a display of the mean configurations for the four habitat groups, the three non-“Closed” groups are almost identical. Variation in this trait does not appear to exist along a continuum from closed-adapted specimens to open-adapted specimens, but instead is an indication of “Closed” versus non-“Closed” adaptations.

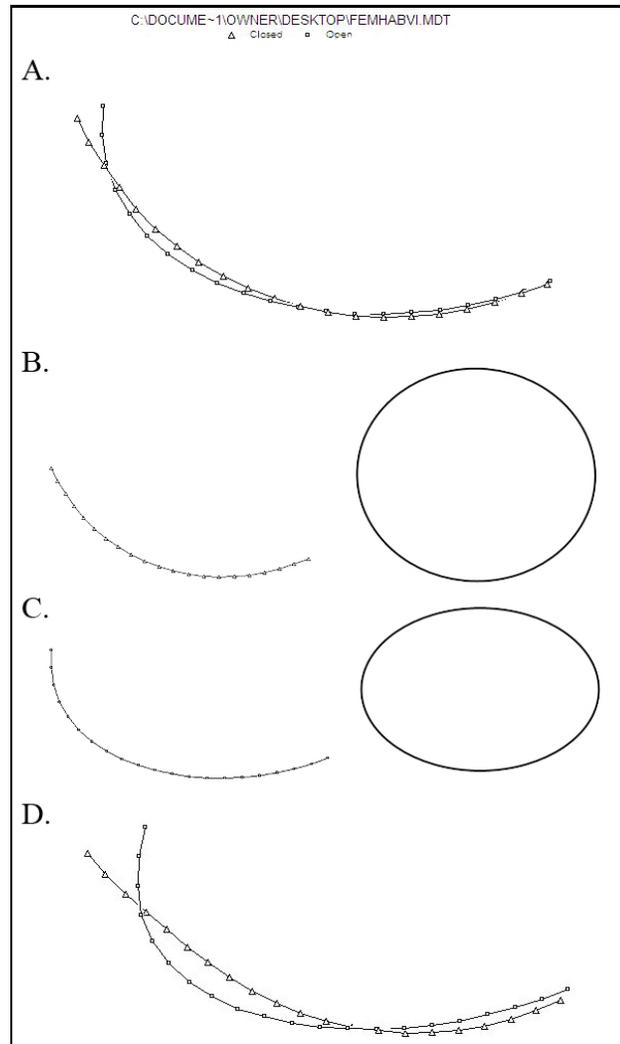


Figure 7-9 Visualizations of the shape change along the canonical variate from the habitat score analysis for the femoral medial patellar margin, creating hypothetical “Closed” and “Open” specimens when the vector of shape change was applied to the mean configuration of all specimens. A = overlaid “Open” and “Closed” specimens, B = “Closed” specimen, C = “Open” specimen, D = “Closed” and non-“Closed” specimens created from the vector of shape change defined by the two groups when applied to the consensus configuration.

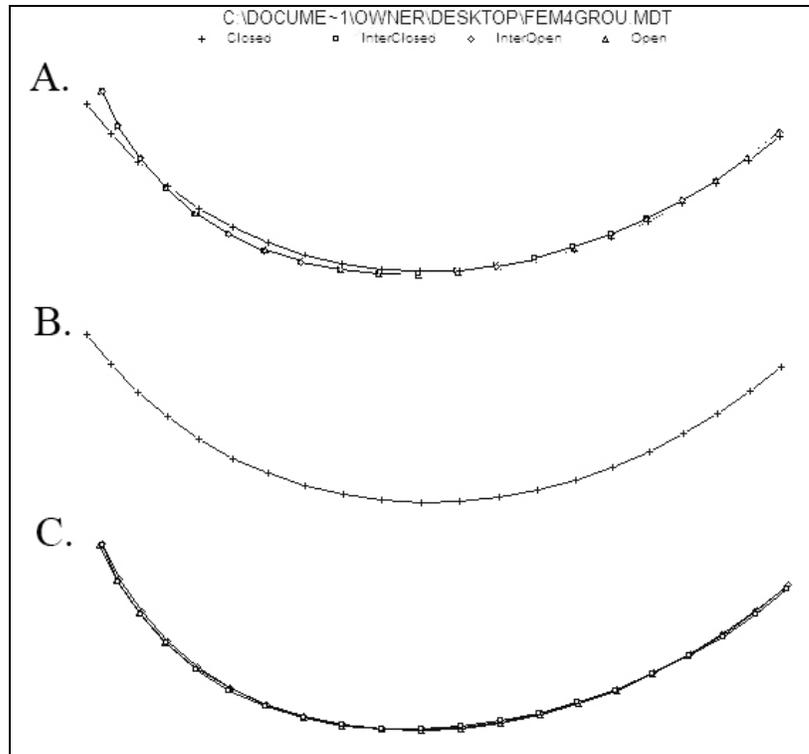


Figure 7-10 Visualization of the mean configuration of Procrustes coordinates for each habitat type in the femoral medial patellar margin analysis. A = all four mean configurations overlaid, B = “Closed” mean configuration, C = mean configurations for “Open”, “Intermediate Open” and “Intermediate Closed” categories.

Habitat Score

A single canonical variate was calculated to separate twelve “Open” and twelve “Closed” specimens. The first two PCs returned the highest correct cross-validation results when submitted to CVA (87.5%, with a resubstitution rate of 91.7%). All “Open” specimens reclassified correctly, but cross-validation reclassified three of the “Closed” specimens as “Open” specimens. These three specimens were *Muntiacus reevesi*, *Muntiacus atheroides*, and *Mazama rufina*. *Muntiacus reevesi* is known to be more plastic in its habitat preferences than other muntjaks (see Chapter 4), but the other two species are fairly committed to forests. Nevertheless, the permutation test returned a result of probability <0.0001 that the two samples were drawn from the same population.

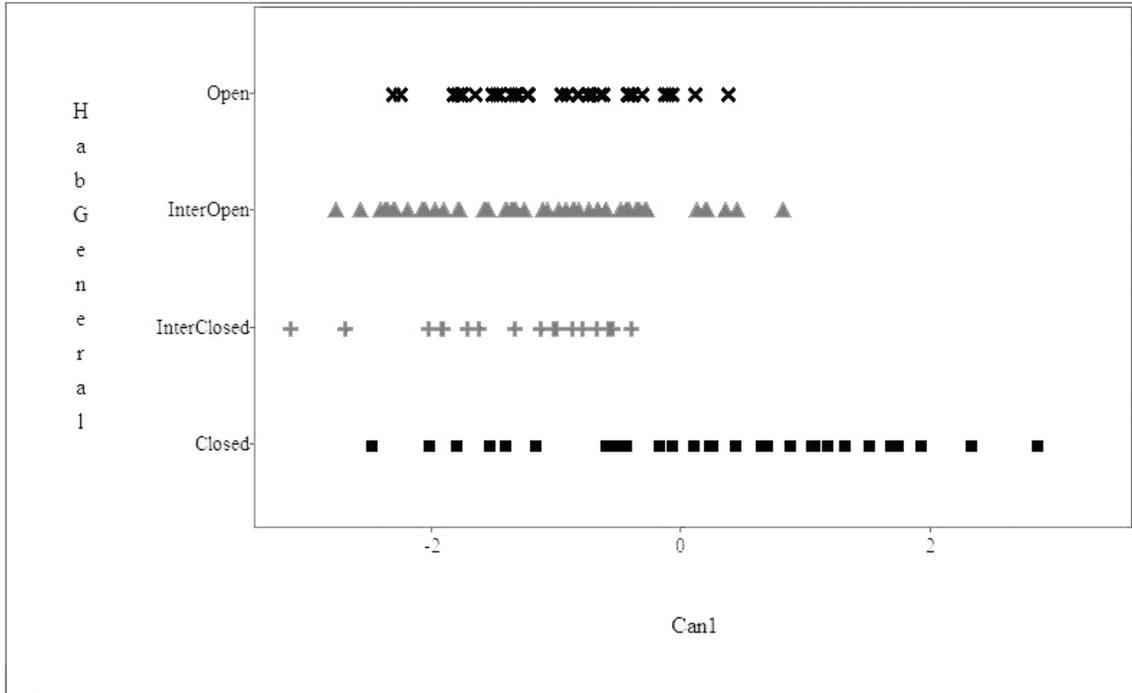


Figure 7-11 Habitat score plot for femoral medial patellar margin analysis of habitat. The specimens did not form a continuum along the canonical variate. Instead, the CV separates “Closed” from non-“Closed” specimens.

Canonical variates scores for all specimens were calculated and plotted (Figure 7-11). The specimens from the four habitats did not form a continuum from “Open” to Closed. Instead, the “Closed” specimens had negative scores along CV1 while the other three habitat categories had positive CV scores. There was much overlap between the three other categories, though the means of both the “Intermediate” categories were higher than the mean for the “Open” category. Since the non-continuous nature of this trait has been demonstrated, it was not surprising that the habitat score failed to form a continuum from “Closed” to “Open”.

Analysis of Tribal membership

When specimens were coded by their tribal affiliation rather than by habitat there was little evidence of the tribes sorting out in the PCA, except that Cervini specimens

scored more positively on PC1, Muntiacini specimens scored more positively along PC2, while Alceini specimens scored negatively along PC2 (Figure 7-12). No subsequent PC plots showed any further pattern.

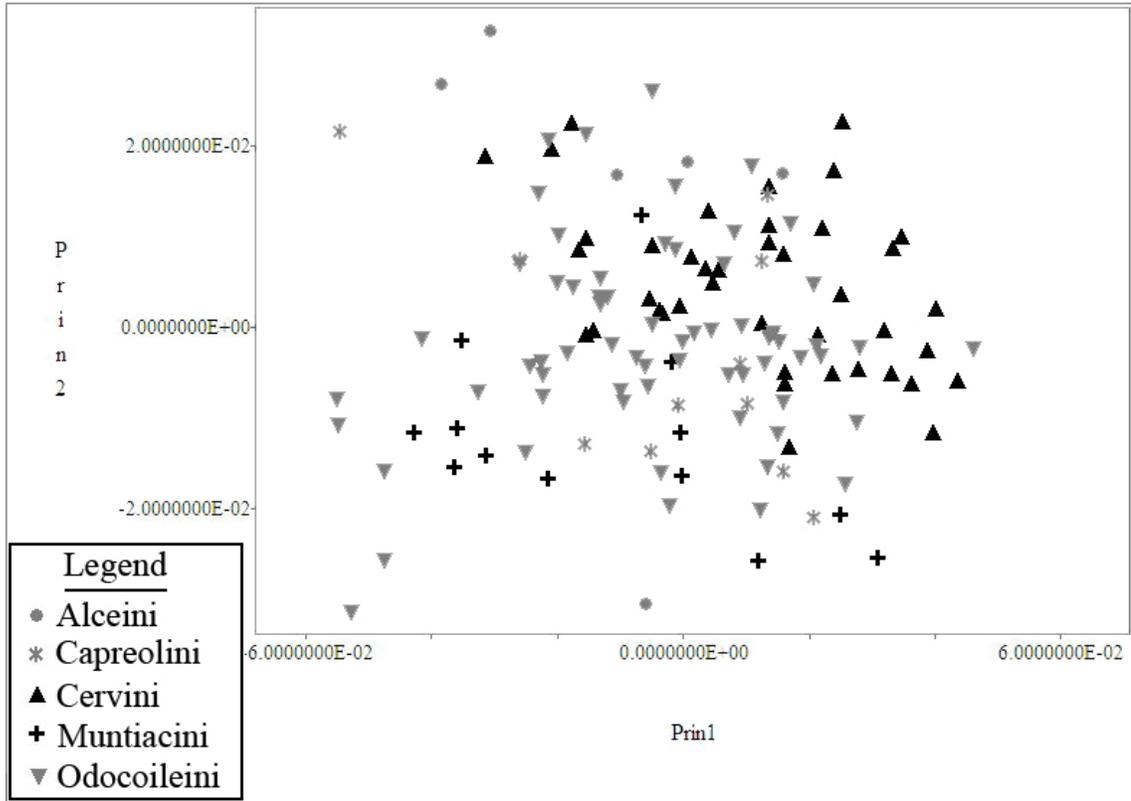


Figure 7-12 Plot of PC1 and PC2 for the tribal analysis of femoral medial patellar margin. Very little distinction is evident amongst the tribal groups, except that Alceini specimens scored negatively along PC2, while Muntiacini and Capreolini specimens scored positively.

Cross-validation						
Tribe	Alceini	Capreolini	Cervini	Muntiacini	Odocoileini	Total
Alceini	4	0	1	1	0	6
	66.7	0	16.7	16.7	0	100
Capreolini	2	3	2	4	0	11
	18.2	27.3	18.2	36.4	0	100
Cervini	7	3	25	0	6	41
	17.1	7.3	61	0	14.6	100
Muntiacini	1	1	0	10	1	13
	7.7	7.7	0	77	7.7	100
Odocoileini	10	12	14	17	13	66
	15.2	18.2	21.2	25.8	19.7	100
Total	24	19	42	32	20	137
	17.5	13.9	30.7	23.4	14.6	100
Resubstitution						
Tribe	Alceini	Capreolini	Cervini	Muntiacini	Odocoileini	Total
Alceini	4	0	1	1	0	6
	66.7	0	16.7	16.7	0	100
Capreolini	2	3	2	4	0	11
	18.2	27.3	18.2	36.4	0	100
Cervini	7	3	25	0	6	41
	17.1	7.3	61	0	14.6	100
Muntiacini	1	1	0	10	1	13
	7.7	7.7	0	76.9	7.7	100
Odocoileini	10	12	14	17	13	66
	15.2	18.2	21.2	25.8	19.7	100
Total	24	19	42	32	20	137
	17.5	13.9	30.7	23.4	14.6	100

Table 7-11 Cross-validation and resubstitution results for the tribal analysis of femoral medial patellar margin, with specimen counts and mean correct reclassifications (shaded gray).

After running iterative CVAs, two PCs submitted to CVA returned the highest correct cross-validation results (50.3%, resubstitution reported the same result, see Table 7-11). Odocoileini specimens had the lowest mean correct reclassification (19.7%- actually worse than would be expected by chance alone), though they showed no strong

affinity toward any other tribe. Capreolini specimens were also frequently classified incorrectly (72.7% of the time) and were assigned to Muntiacini 36.4% of the time. The other three tribes had correct reclassification rates of 61% to 76.9%. Only two permutation tests demonstrated significant differences between group centroids: Cervini from Muntiacini and Cervini from Odocoileini (Table 7-12).

	Capreolini	Cervini	Muntiacini	Odocoileini
Alceini	0.1808	0.2275	0.036	0.2206
Capreolini		0.0724	0.1075	0.9116
Cervini			<0.0001	<0.0001
Muntiacini				0.0543

Table 7-12 Results for permutation tests between each pair of tribes in the femoral medial patellar margin analysis based on Mahalanobis distances between group centroids. The reported result is the probability that the two centroids were drawn from the same population.

As only two PCs were submitted to the CVA, only two CVs were returned, which are shown plotted against each other in Figure 7-13. Along CV1, which summarized 92.2% of the total sample variance, Cervini specimens tended to score more positively and Muntiacini specimens more negatively. Along CV2 (7.8% of the variance) the Muntiacini specimens scored more negatively and Capreolini specimens scored positively. Though the Odocoileini and Cervini had a great deal of overlap along CV1, the Cervini tended to score more positively while the Odocoileini had more negative scores and they overlapped completely on CV2.

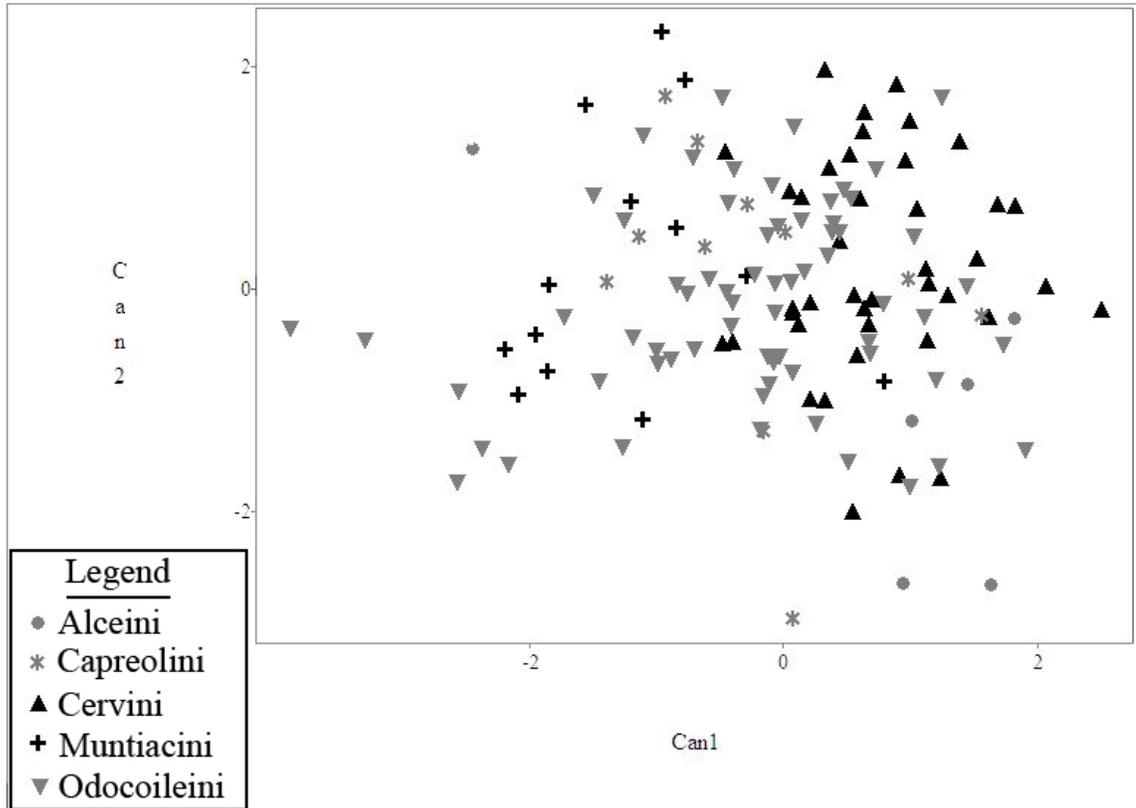


Figure 7-13 Plot of CV1 and CV2 for the tribal analysis of femoral medial patellar margin. CV1 separated the Cervini and Muntiacini specimens, while CV2 separated the Muntiacini and Capreolini specimens. Cervini and Odocoileini specimens occupied much of the same canonical variates space, though Cervini tended to score more positively along CV1, while Odocoileini score more negatively.

Analysis of Body Size

All three measures of body size (body weight, body height, and body length) were found to be highly correlated to $\ln CS$ at $p < 0.0001$ and $R^2 = 0.834, 0.8381, \text{ and } 0.8242$, respectively. Of the first ten PCs, only the first two had significant ($p < 0.0001$) correlations with $\ln CS$ (see Table 7-13). However, both had small R^2 values, indicating that $\ln CS$ does not explain much of the variation along PC1 or PC2.

FemMed: Extant Body Size		
Regression	R ²	p-value
lnBW	0.0827	<0.0001
lnBH	0.8333	<0.0001
lnBL	0.8194	<0.0001
PC1	0.1283	<0.0001
PC2	0.1603	<0.0001
PC3	0.0038	0.4746
PC4	0.016	0.1407
PC5	0.0414	0.0171
PC6	0.0046	0.4297
PC7	0.0144	0.1624
PC8	0.0012	0.6827
PC9	0.0078	0.3063
PC10	0.0025	0.5586
CV1	0.2912	<0.0001
CV2	0.005	0.4129
CV3	0.0021	0.5948

Table 7-13 Regressions of the natural log of centroid size (lnCS) against several measures of body size (all natural logged) for extant species in the femoral medial patellar margin analysis of habitat: body weight (lnBW), body height at shoulder (lnBH), and body length (lnBL), the first ten principal component scores (PC1-PC10), and the three canonical variates (CV1-CV3). All measures of body size in extant cervids were highly correlated to the lnCS. The first two PCs were significantly correlated to lnCS, though R² values were small. The first CV was also correlated to lnCS; this correlation was mainly driven by the closed-adapted cervids.

Only the first canonical variate was correlated to lnCS ($R^2 = 0.2897$, $p < 0.0001$).

It appears that this correlation was greatly influenced by the distribution of the “Closed” specimens along CV1. The closed-habitat specimens tended to be very small (*Muntiacus*, *Elaphodus*, *Mazama*, *Pudu*) and very large (*Alces*). When these specimens were removed from the analysis of the entire extant data set, the R² dropped to 0.0509, $p = 0.0189$.

When regressions were calculated for each habitat type independently, only the “Closed” specimens showed a significant correlation ($R^2 = 0.4287$, $p < 0.0001$; Figure 7-15).

Though it might seem that this relationship may have been due to the gross size

differences between the small closed-adapted cervids and *Alces*, when the *Alces* specimens were removed from the analysis, the correlation still remained significant ($R^2 = 0.4906$, $p = 0.0002$). Thus, for the closed-adapted cervids, there was a correlation between the size and the shape of the medial patellar margin.

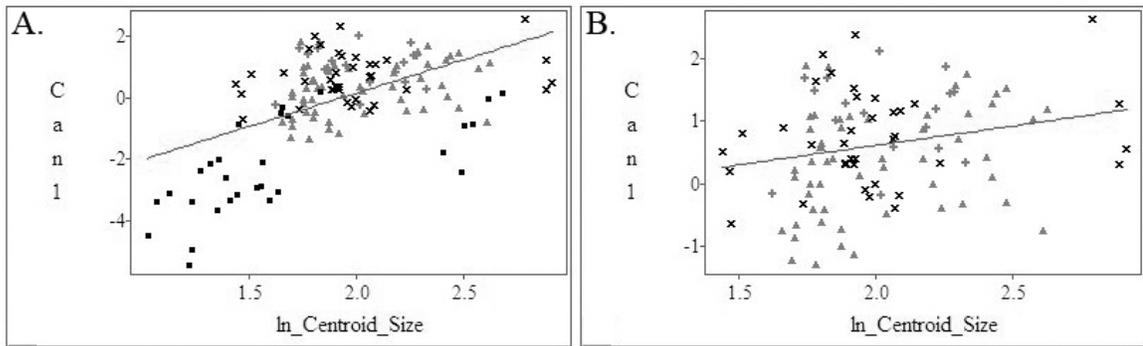


Figure 7-14 Plots of regressions of CV1 against lnCS in the femoral medial patellar margin analysis. A = all specimens in a linear regression, B = all non-“Closed” specimens in a linear regression.

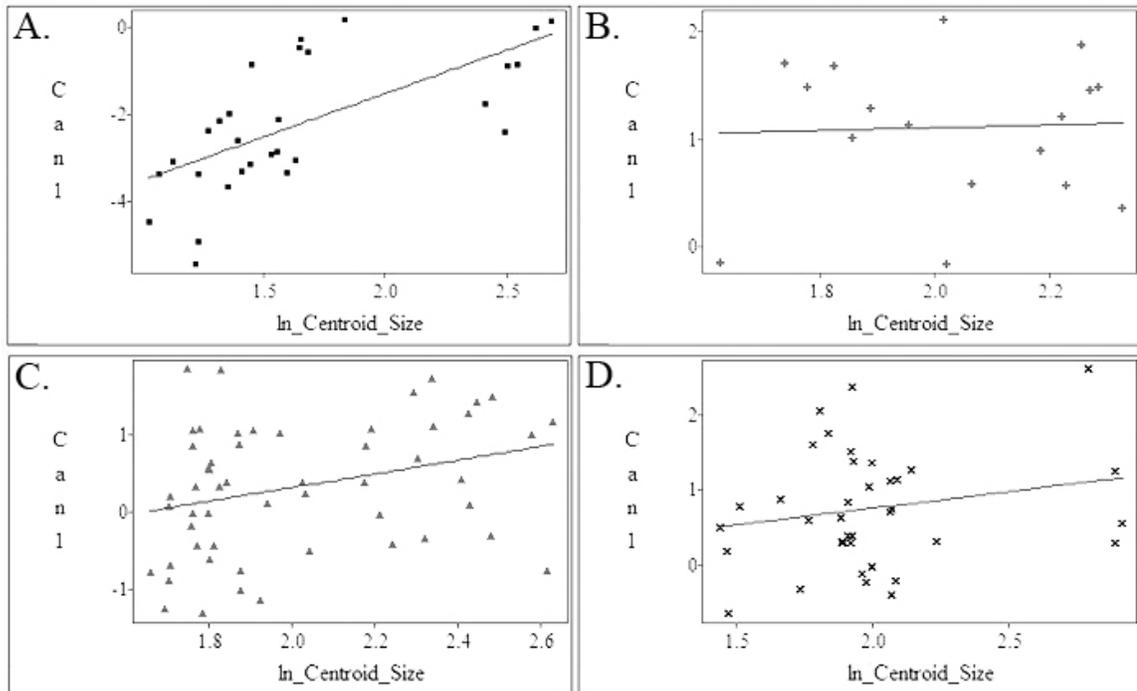


Figure 7-15 Plots of regressions of CV1 against lnCS for each of the habitat types in the femoral medial patellar margin analysis individually. A = “Closed”, B = “Intermediate Closed”, C = “Intermediate Open”, and D = “Open”. Only the “Closed” regression showed a significant correlation.

Unit of analysis 3: Tibial Lateral Condylar Surface Margin (TibLat)

Analysis of Habitat

Principal Components Analysis

140 specimens were submitted to the PCA, three of which were *Megaloceros giganteus*. Visual inspection of PCA plots did not yield any consistent patterning of the extant specimens, though “Closed” specimens tended to score more negatively along PC2 and “Open” specimens more positively (Figure 7-16). These two principal component axes summarized 29.6% and 19.5% of the total sample variation, respectively.

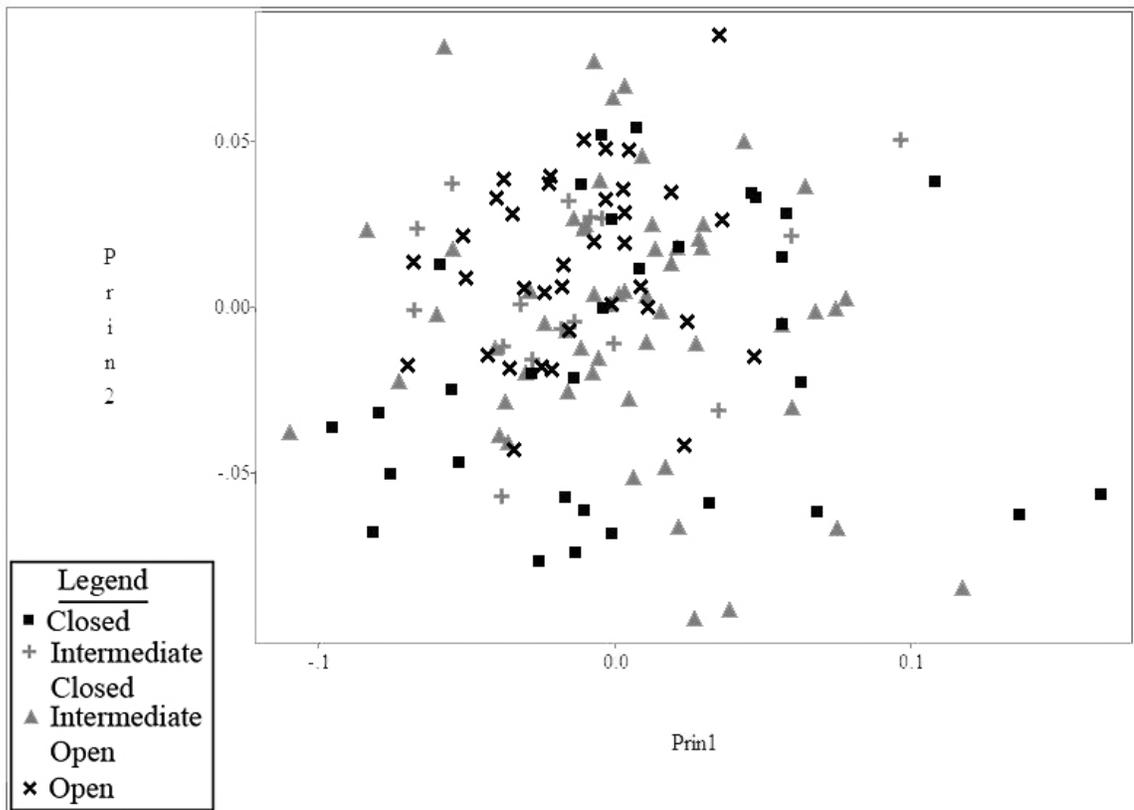


Figure 7-16 Plot of PC1 and PC2 for the habitat analysis of tibial lateral plateau margin. “Closed” habitat specimens tended to score negatively along PC2 and “Open” specimens scored more positively. No other distinctions were evident among the habitat groups in principal components space.

Canonical Variates Analysis

Twenty-six PCs, which summarized 98.2% of the total sample variance in the PCA, were submitted to the CVA. The mean correct cross-validation rate was 49.8% and the mean correct resubstitution rate was 75.1% (Table 7-14). With cross-validation, the “Closed” specimens had the highest mean correct reclassification rate (68.8%), the “Open” the second highest (50%), and the two “Intermediate” categories the lowest rates (“Intermediate Open” = 42.9% and “Intermediate “Closed” = 37.5%). This was supported by the permutation tests, as all group centroids had $p < 0.0001$ of having been drawn from the same population, except for the two “Intermediate” categories, though the permutation test was still significant at $p = 0.0005$ (Table 7-15). One of the *Megaloceros giganteus* specimens (F21174) was classified as “Intermediate Closed”, though the posterior probability was low (39.3% with 33% likelihood of being “Open” and 27.6% likelihood of being “Intermediate Open”). The other two *Megaloceros* specimens were classified as “Open”.

Cross-validation					
	Closed	InterClosed	InterOpen	Open	Total
Closed	22	1	4	5	32
	68.8	3.1	12.5	15.6	100
InterClosed	3	6	4	3	16
	18.8	37.5	25.0	18.8	100
InterOpen	4	13	24	15	56
	7.1	23.2	42.9	26.8	100
Open	4	8	6	18	36
	11.1	22.2	16.7	50.0	100
Total	33	28	38	41	140
	23.6	20.0	27.1	29.3	100

Resubstitution					
	Closed	InterClosed	InterOpen	Open	Total
Closed	26	1	2	3	32
	81.3	3.1	6.3	9.4	100
InterClosed	2	12	1	1	16
	12.5	75	6.3	6.3	100
InterOpen	3	9	34	10	56
	5.4	16.1	60.7	17.9	100
Open	0	2	4	30	36
	0	5.6	11.1	83.3	100
Total	30	25	39	46	140
	21.4	17.9	27.9	32.9	100

Table 7-14 Cross-validation and resubstitution results for the habitat analysis of tibial lateral plateau margin, with specimen counts and mean correct reclassifications (shaded gray).

	InterOpen	InterClosed	Closed
Open	<0.0001	<0.0001	<0.0001
InterOpen		0.0005	<0.0001
InterClosed			<0.0001

Table 7-15 Results for permutation tests between each pair of habitat types for the tibial lateral plateau margin based on Mahalanobis distances between group centroids. The reported result is the probability that the two centroids were drawn from the same population.

As with the other units of analysis discussed above, the first CV (summarizing 67.4% of the total sample variance) separated the “Closed” specimens from the other habitat groups. CV2 (20% of the variance) separated the “Open” specimens from the “Intermediate Open” specimens and CV3 (12.6% of the variance) separated the “Intermediate Closed” specimens from the other groups, though there is much overlap (Figure 7-17).

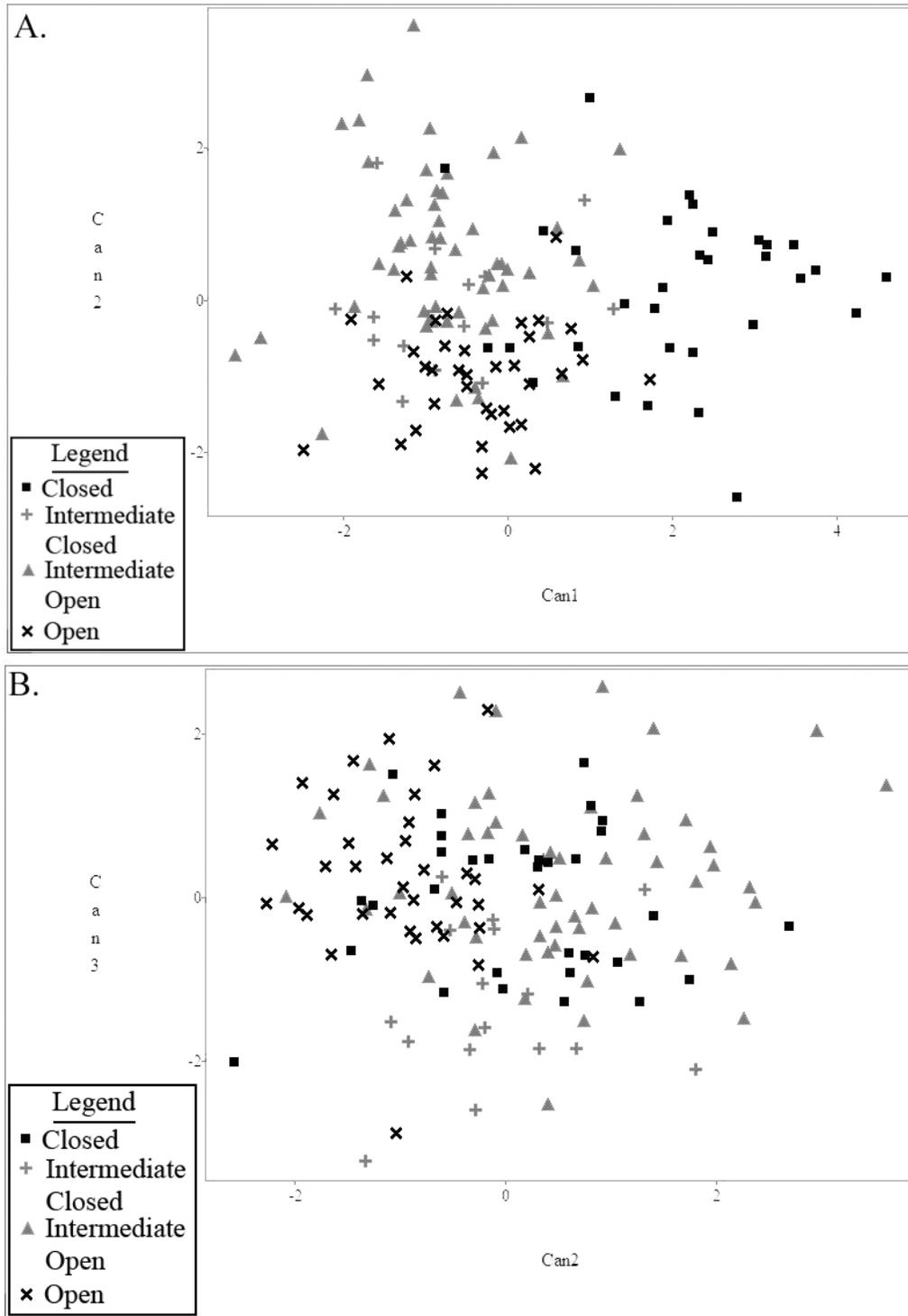


Figure 7-17 A: Plot of CV1 and CV2 for the habitat analysis of tibial lateral plateau margin. CV1 separated the “Closed” specimens from all other habitat types, CV2 separated “Open” specimens “Intermediate Open” specimens. B: Plot of CV2 and CV3 for the tibial lateral plateau margin. CV3 separated the two “Intermediate Closed” specimens from the other habitat groups, though there was much overlap.

Habitat Score

Eleven specimens were selected as representatives for each of the “Open” and “Closed” habitat categories for the training sample. Using four principal components in the CVA, all specimens were reclassified to their known habitat types 100% of the time with both cross-validation and resubstitution. The permutation test returned a probability of <0.0001 that the centroids of these groups were drawn from the same population. When the entire data sample was scored along the canonical variate created with the training sample, the habitat groups did not form a continuum. Instead, the specimens scored along the CV with a non-continuous distribution with “Closed” specimens on one side and the non-“Closed” specimens on the other (Figure 7-18), similar to what was found for the medial patellar margin of the femur.

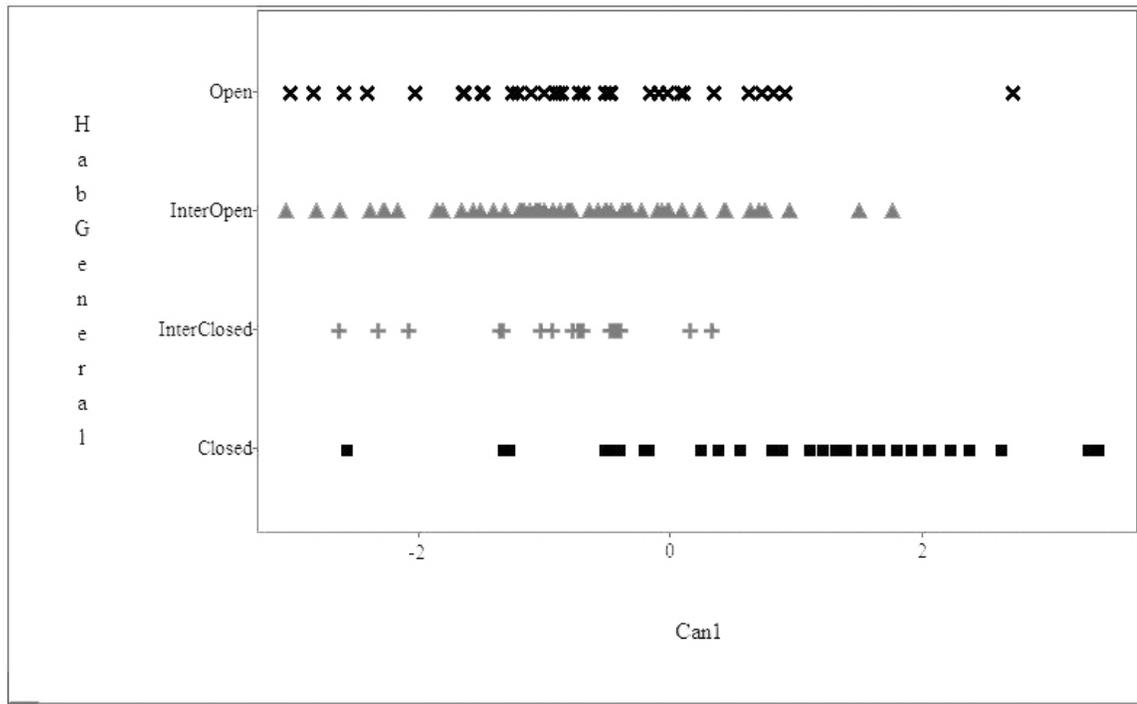


Figure 7-18 Habitat score plot for tibial lateral plateau margin analysis of habitat. As with the femoral medial patellar margin, the specimens did not form a continuum along the canonical variate. Instead, the CV separates “Closed” from non-“Closed” specimens.

Visualizations (with the vector of shape change multiplied by three) were created to explore the difference in morphology between “Open” and “Closed” specimens using the same specimens in the Habitat Score training set (Figure 7-19). The lateral tibial plateau of “Closed” specimens is more round when viewed superiorly, while the “Open” specimens are more compressed in the medial-lateral direction and have distinct tapering toward the intercondylar eminence. When viewed from the posterior and looking across the joint surface toward anterior, “Closed” specimens have a flatter and wider surface, while the “Open” specimens have a deeper and narrower surface. The “Closed” morphology allows for more movement at the knee joint, which is necessary for cervids that must rapidly change directions while fleeing predators. The “Open” morphology restricts the movement at the knee joint to the parasagittal plane and provides a more stable joint surface, which is necessary for cursoriality.

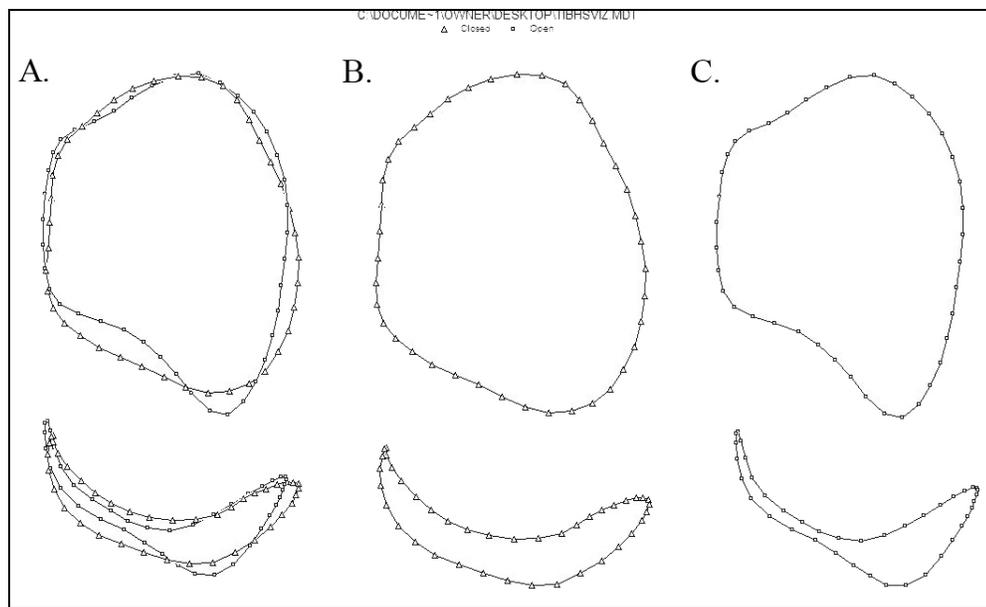


Figure 7-19 Visualizations of the shape change along the canonical variate from the tibial lateral plateau margin habitat score analysis, creating hypothetical “Closed” and “Open” specimens when the vector of shape change was applied to the mean configuration of all specimens. A = Overlaid “Open” and “Closed” specimens, B = “Closed” specimen, C = “Open” specimen. For each subsection, the top image is from the superior view and the bottom image is looking from posterior toward anterior.

Analysis of Tribal membership

When specimens were coded by tribe instead of habitat type in PCA plots, there was no obvious differentiation between the groups. Twenty-nine PCs were then submitted to CVA and returned a mean correct cross-validation rate of 58.6% and 83.7% with resubstitution (see Table 7-16). The two groups with the largest sample sizes also had the highest cross-validations: Cervini with 72.5% and Odocoileini with 68.1%. The other three tribes had mid-range cross-validation rates. Permutation tests indicated that tribal group centroids were all significantly different at (minimally) $p = 0.003$ (Table 7-17).

CV1 (summarizing 42.5% of the total sample variance) separated Cervini and Odocoileini specimens while CV2 (29.5% of the variance) separated these two groups from all other tribes (Figure 7-20). CV3 (16.4% of the variance) separated the Alceini specimens from all the other tribes and CV4 (11.6% of the variance) separated the Muntiacini from the Capreolini.

Cross-validation						
Tribe	Alceini	Capreolini	Cervini	Muntiacini	Odocoileini	Total
Alceini	3	0	1	1	1	6
	50	0	16.7	16.7	16.7	100
Capreolini	0	5	2	4	0	11
	0	45.5	18.2	36.4	0	100
Cervini	2	2	29	1	6	40
	5	5	72.5	2.5	15	100
Muntiacini	0	3	0	8	3	14
	0	21.4	0	57.1	21.4	100
Odocoileini	2	2	9	9	47	69
	2.9	2.9	13	13	68.1	100
Total	7	12	41	23	57	140
	5	8.6	29.3	16.4	40.7	100
Resubstitution						
Tribe	Alceini	Capreolini	Cervini	Muntiacini	Odocoileini	Total
Alceini	5	0	1	0	0	6
	83.3	0	16.7	0	0	100
Capreolini	0	10	1	0	0	11
	0	90.9	9.1	0	0	100
Cervini	1	0	36	1	2	40
	2.5	0	90	2.5	5	100
Muntiacini	0	2	0	10	2	14
	0	14.3	0	71.4	14.3	100
Odocoileini	0	2	5	5	57	69
	0	2.9	7.3	7.3	82.6	100
Total	6	14	43	16	61	140
	4.3	10	30.7	11.4	43.6	100

Table 7-16 Cross-validation and resubstitution results for the tribal analysis of tibial lateral plateau margin, with specimen counts and mean correct reclassifications (shaded gray).

	Capreolini	Cervini	Muntiacini	Odocoileini
Alceini	0.0014	0.003	0.0012	0.0014
Capreolini		<0.0001	<0.0001	<0.0001
Cervini			<0.0001	<0.0001
Muntiacini				<0.0001

Table 7-17 Results for permutation tests between each pair of habitat types for the tibial lateral plateau margin based on Mahalanobis distances between group centroids. The reported result is the probability that the two centroids were drawn from the same population.

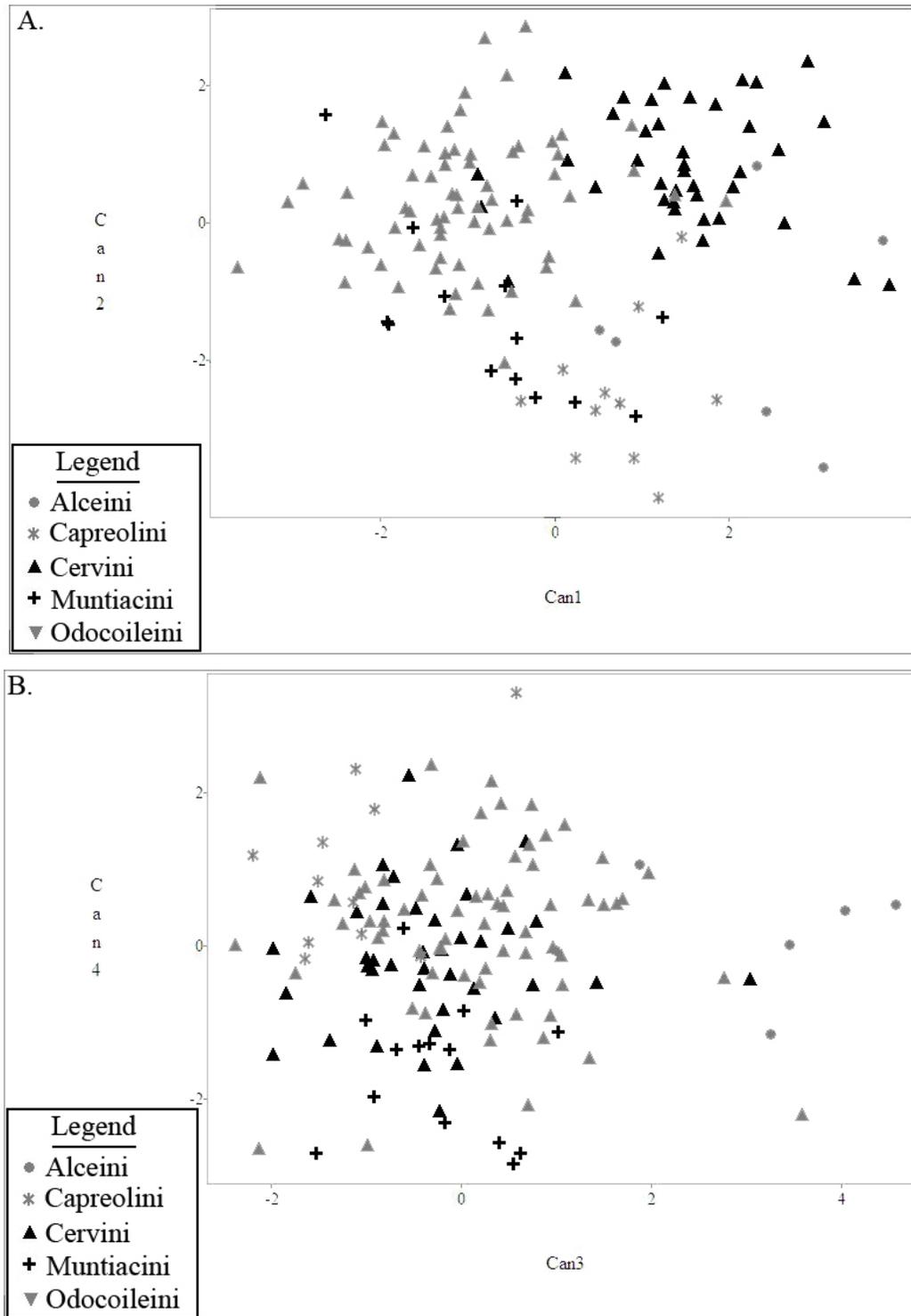


Figure 7-20 A: Plot of CV1 and CV2 for the tribal analysis of calcaneal landmarks for the tibial lateral plateau margin. CV1 separated the Odocoileini specimens from the Cervini specimens, CV2 separated these two groups from all other tribes. B: Plot of CV3 and CV4 for the calcaneal landmarks by tribe. CV3 separated the Alceini from all other tribes and CV4 weakly separated the Muntiacini from the Capreolini.

Analysis of Body Size

All three measures of body size were highly correlated with the natural log of centroid size (lnCS) at $p < 0.0001$ (Table 7-18). When the first ten principal component scores were regressed against lnCS, PC3 and PC4 were found to be significantly correlated ($p < 0.0001$, $R^2 = 0.1984$ and $R^2 = 0.228$, respectively). When the “Closed” specimens were removed and regressions were recalculated, the correlations were still significant ($p = 0.0009$ for PC3 and $p = 0.0006$ for PC4) but the R^2 values dropped ($R^2 = 0.0995$ for PC3 and $R^2 = 0.1056$ for PC4). Removing the *Alces* specimens did not change this result, indicating that the small “Closed” cervids were driving this correlation.

TibLat: Extant Body Size		
Regression	R^2	p-value
lnBW	0.847	<0.0001
lnBH	0.8247	<0.0001
lnBL	0.8198	<0.0001
PC1	0.00008	0.9186
PC2	0.0159	0.1377
PC3	0.1984	<0.0001
PC4	0.228	<0.0001
PC5	0.0003	0.8419
PC6	0.0051	0.4019
PC7	0.0043	0.4392
PC8	0.0158	0.1388
PC9	0.0189	0.1052
PC10	0.0015	0.6443
CV1	0.2554	<0.0001
CV2	0.0286	0.0457
CV3	0.0056	0.3785

Table 7-18 Regressions of the natural log of centroid size (lnCS) against several measures of body size (all natural logged) for extant species in the tibial lateral plateau margin analysis of habitat: body weight (lnBW), body height at shoulder (lnBH), and body length (lnBL), the first ten principal component scores (PC1-PC10), and the three canonical variates (CV1-CV3). All measures of body size in extant cervids were highly correlated to the lnCS. PCs 3 and 4 were significantly correlated to lnCS, though R^2 values were small. The first CV was also correlated to lnCS; this correlation was mainly driven by the small closed-adapted cervids.

When canonical variates were regressed against lnCS, only CV1 had a significant correlation ($p < 0.0001$, $R^2 = 0.2554$). As was found with the regressions of PC3 and PC4 with lnCS, the small “Closed” specimens were driving this correlation (Figure 7-21). When they were removed, R^2 dropped to 0.0643 with a p-value of 0.0078. The main species driving the correlation (that is, the specimens with the most negative scores along CV1 and the smallest lnCS values) were the two *Pudu* species, *Elaphodus*, *Mazama rufina*, and *Mazama chunyi*, many of which are mountain-forest species. These specimens are highlighted in Figure 7-21b, which also shows the regression line for the non-“Closed” specimens. “Closed” specimens with more positive scores along CV1 were the more behaviorally flexible species (as described in Chapter 4)- *Mazama gouazoubira*, *Muntjak muntjak*, and *Muntjak reevesi*, which exploit more open habitats than the other “Closed” species.

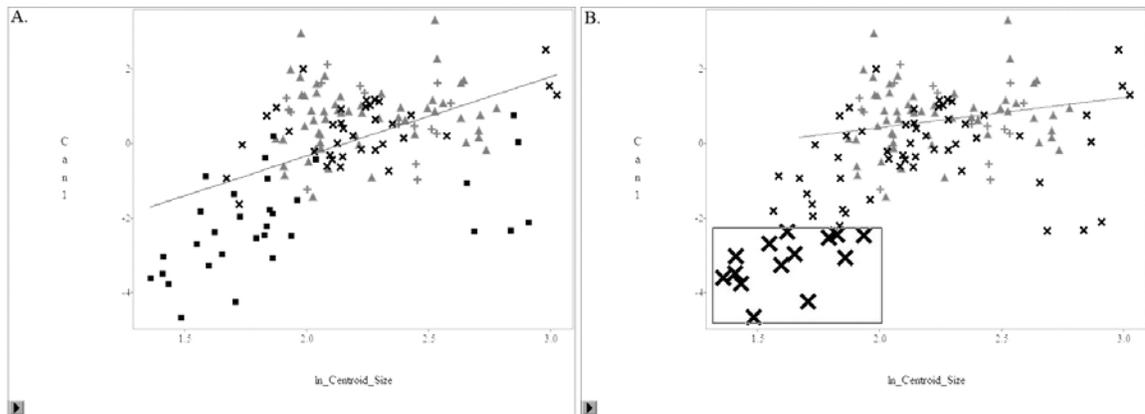


Figure 7-21 Plots of regressions of CV1 against lnCS for all specimens in the tibial lateral plateau margin analysis of habitat. A = regression line for all specimens, B = regression line for all non-“Closed” specimens with small “Closed” specimens highlighted.

Unit of analysis 4: 3rd Phalanx Plantar Surface Margin (Phal3)

Analysis of Habitat

With habitat type used as the *a priori* categorical variable in the CVA for the third phalanx plantar margin analysis of habitat, a low mean correct cross-validation result was returned (52%). The mean correct cross-validation rates for the “Open” and “Closed” groups were especially low (37.5% and 42.9%, respectively), though these two groups received the highest cross-validation rates in all other analyses of habitat. Further, specimens from the four habitat groups completely overlapped on the habitat score. As an exploratory exercise, the specimens were classified into nine habitat categories (Habitat Specific in Appendix C). Surprisingly, a mean correct cross-validation rate of 42.2% was returned for the nine habitat category analysis. When specimen scores on CV1 were plotted in a scatterplot, a continuum was formed, though not from “Open” to “Closed”, but along substrate moisture content. That is, the specimens from habitats with wet substrates (swamp, tropical forests, and montane (mist) forests) had more negative CV scores while specimens from habitats with dry substrates (open grasslands, areas with tall grasses, woodlands, and temporary forests) had more positive CV scores (see Figure 7-22). “Ecotone” and some “Tall Grass” and “Open Mountain” specimens scored in the middle. The sample sizes in some of the groups of the nine habitat types analysis were too small ($n = 2$) to perform any meaningful analysis. Instead, specimens were recategorized by substrate resistivity (how much ‘give’ a substrate allows) and CVAs were rerun. Results for the third phalanx are discussed in terms of the following substrate categories.

Species in the “Dry” substrate category live in habitats with a wide variety of vegetational cover- from open grasslands to temperate forests, all of which have hard, dry ground. These cervids have third phalanges that stay more or less in the same position while locomoting, in line with the metatarsals. Without the need to splay the phalanges, mobility of the phalanges away from the axis of the body is restricted, allowing for more stable joint surface (Köhler 1993). Species in the “Wet” substrate category are also found in a variety of habitats (swamps to tropical forests), which have more humid conditions and damper substrates. To move across a substrate that has more give and is slippery, cervids splay their third phalanges to get better support (Köhler 1993). All the phalanges are moved away from the axis of the foot at the metatarsal-proximal phalanx joint. Cervids in the “Mountain” category also splay their phalanges, but only at the intermediate phalanx-distal phalanx joint, while the rest of the phalanges are locked into a line with the metatarsal. This increases joint stability while splaying the third phalanx allows for a break on inclined slopes with loose gravel. Species in “Ecotone” habitats locomote across a variety of substrate types, therefore their third phalangeal morphology is a compromise between “Dry” and “Wet” morphologies.

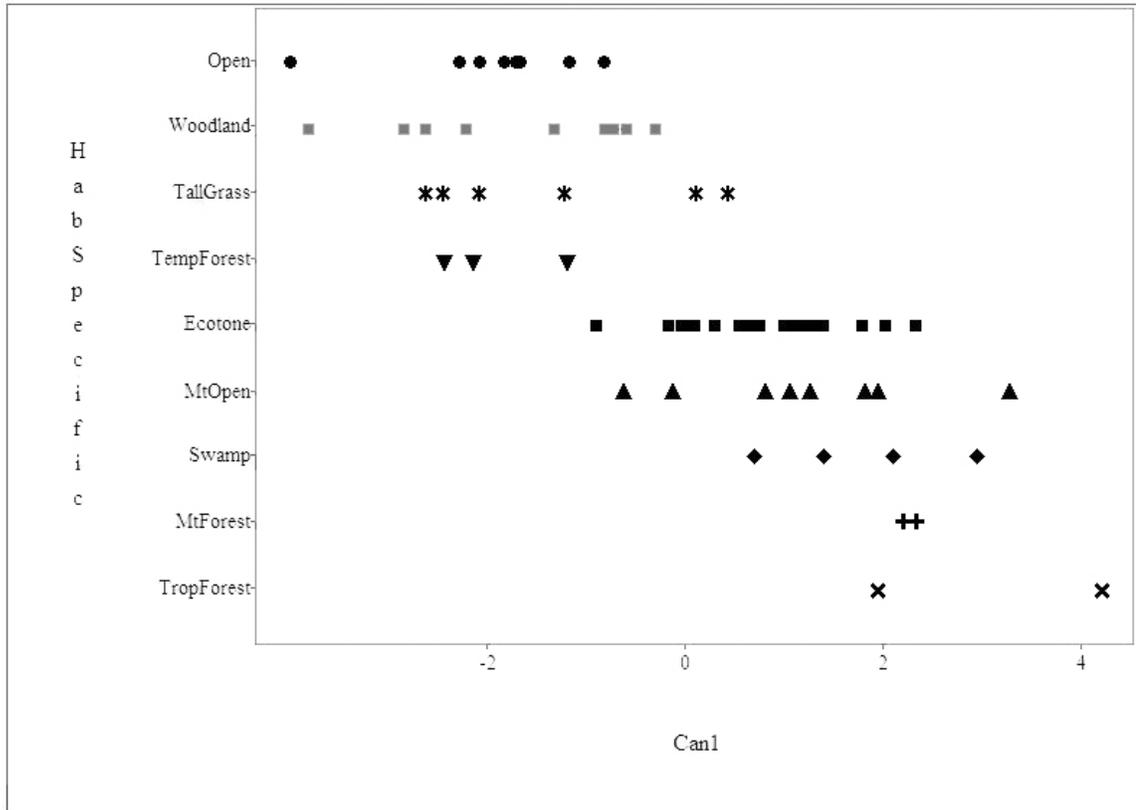


Figure 7-22 When specific habitats were used in a CVA of the PC scores, specimens formed a continuum from habitats with drier to wetter substrates along CV1.

Principal Components Analysis

Sixty-two extant cervid specimens and two *Megaloceros giganteus* were included in this analysis. Examinations of PCA plots did not reveal any obvious patterns, except that the *Megaloceros* and *Rangifer* specimens (and one *Elaphurus davidanus* specimen), all of which are large cervids in the “Dry” substrate category, scored the most negatively along PC1 (Figure 7-23).

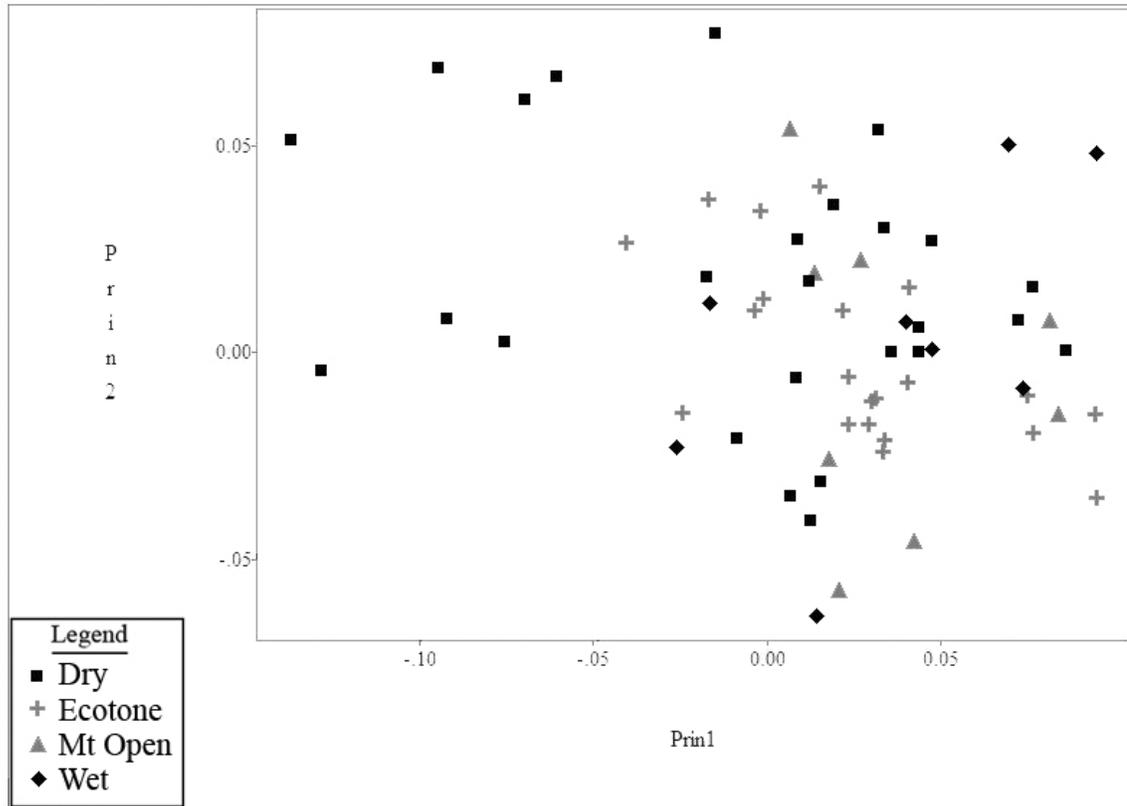


Figure 7-23 Plot of PC1 and PC2 for the habitat analysis of the third phalanx plantar margin. Specimens with very large body sizes scored negatively along PC1. No other distinctions were evident among the habitat groups in principal components space.

Canonical Variates Analysis

Thirteen PCs were submitted to CVA, which correctly classified specimens to their known substrate type 66.3% of the time (75.6% with resubstitution) (Table 7-19). Specimens in the “Dry” and “Wet” substrate categories had the highest mean correct cross-validation rates (73.1% and 75%, respectively). Specimens in the “Ecotone” substrate category had the lowest mean correct cross-validation rate (54.6%) and were mostly *Odocoileus virginianus* specimens incorrectly classified into “Mountain”. This may reflect the habitat plasticity of white-tail deer or the recent common ancestry (11 kyr) with *Odocoileus hemionus*, which was the most abundant species assigned to the

“Mountain” category. The “Mountain” category specimens also had lower mean correct cross-validation rates (62.5%) and were most incorrectly classified into “Wet”. The morphology of “Mountain” and “Wet” are very similar (see C. and D. in Figure 7-24), as species in both categories splay their phalanges. The permutation tests were significant for all groups (minimally) at $p = 0.005$, except for the pairs of “Wet” and “Mountain” and “Ecotone” and “Mountain”, likely due to the aforementioned reasons.

Resubstitution					
	Dry	Ecotone	Mt	Wet	Total
Dry	24 92.3	2 7.7	0 0	0 0	26 100
Ecotone	0 0	16 72.7	5 22.7	1 4.6	22 100
Mt	0 0	1 12.5	5 62.5	2 25	8 100
Wet	0 0	1 12.5	1 12.5	6 75	8 100
Total	24 37.5	20 31.3	11 17.2	9 14.1	64 100
Cross-validation					
	Dry	Ecotone	Mt	Wet	Total
Dry	19 73.1	6 23.1	1 3.9	0 0	26 100
Ecotone	1 4.6	12 54.6	6 27.3	3 13.6	22 100
Mt	1 12.5	0 0	5 62.5	2 25	8 100
Wet	0 0	1 12.5	1 12.5	6 75	8 100
Total	21 32.8	19 29.7	13 20.3	11 17.2	64 100

Table 7-19 Cross-validation and resubstitution results for the substrate analysis of the third phalanx plantar margin, with specimen counts and mean correct reclassifications (shaded gray).

	Ecotone	Mt.	Wet
Dry	<0.0001	0.001	0.0002
Ecotone		0.243	0.0027
Mt.			0.0075

Table 7-20 Results for permutation tests between each pair of habitat types for the third phalanx plantar margin based on Mahalanobis distances between group centroids. The reported result is the probability that the two centroids were drawn from the same population.

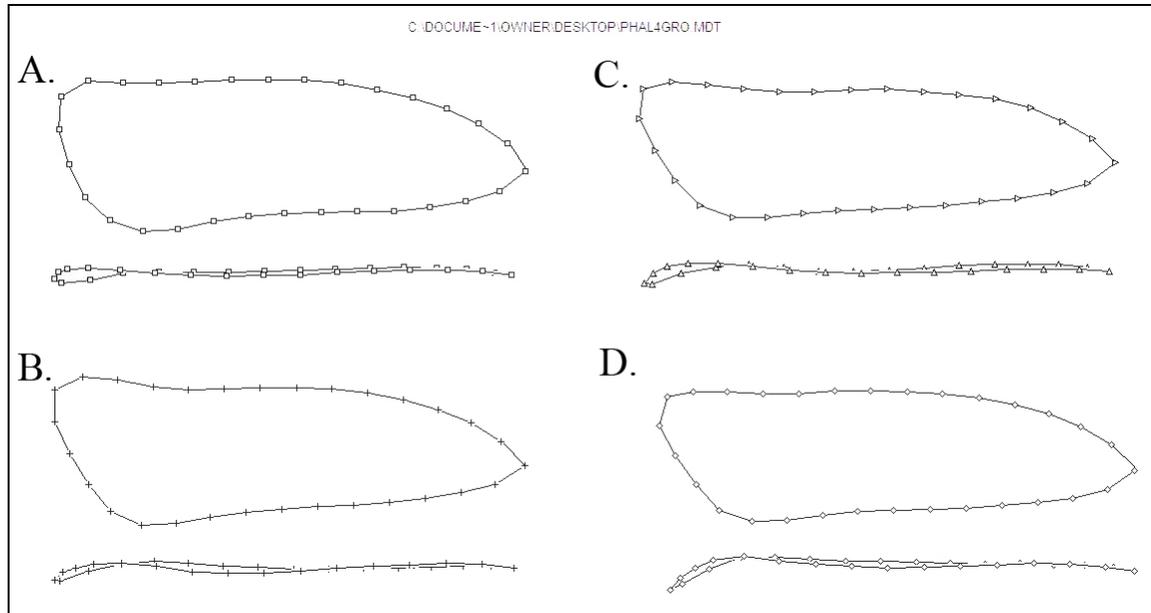


Figure 7-24 Visualizations of the mean configuration (based on Procrustes coordinates) for each substrate type. A= “Dry”, B= “Ecotone”, C= “Mountain”, and D= “Wet”.

In bivariate plots of the CVs (Figure 7-25), CV1 (summarizing 79.7% of the total sample variation) separated “Wet” from “Dry” specimens. CV2 (15.9% of the sample variation) weakly separated the “Wet” + “Dry” groups from the “Ecotone” + “Mountain” groups and CV3 (4.1% of the sample variation) separated the “Mountain” and “Ecotone” groups.

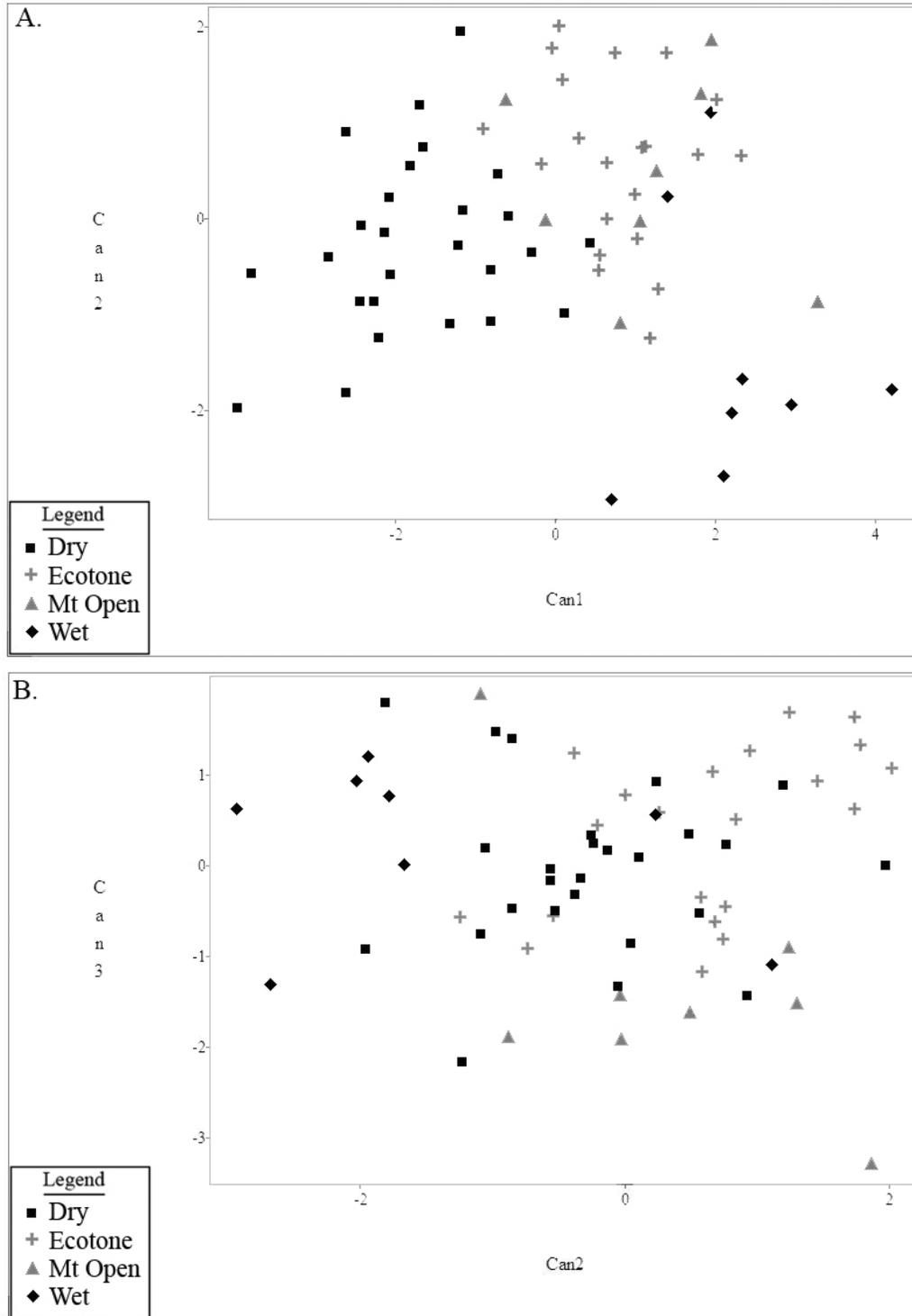


Figure 7-25 A: Plot of CV1 and CV2 for the substrate analysis of the third phalanx plantar margin. CV1 separated the “Wet” specimens from the “Dry” specimens, CV2 weakly separated “Wet” + “Dry” specimens “Ecotone” + “Mountain” specimens. B: Plot of CV2 and CV3 for the third phalanx plantar margin. CV3 separated the “Ecotone” specimens from the “Mountain” specimens.

Habitat Score

Eight specimens each from the “Wet” and “Dry” categories were used to create a habitat score for the third phalanx. These training specimens were correctly reclassified into the correct substrate category 93.8% of the time with cross-validation (100% with resubstitution). The permutation test indicated that there was <0.0001 probability that the two groups were drawn from the same population. The specimens formed a continuum from “Dry” to “Wet” in the habitat score plot (Figure 7-26).

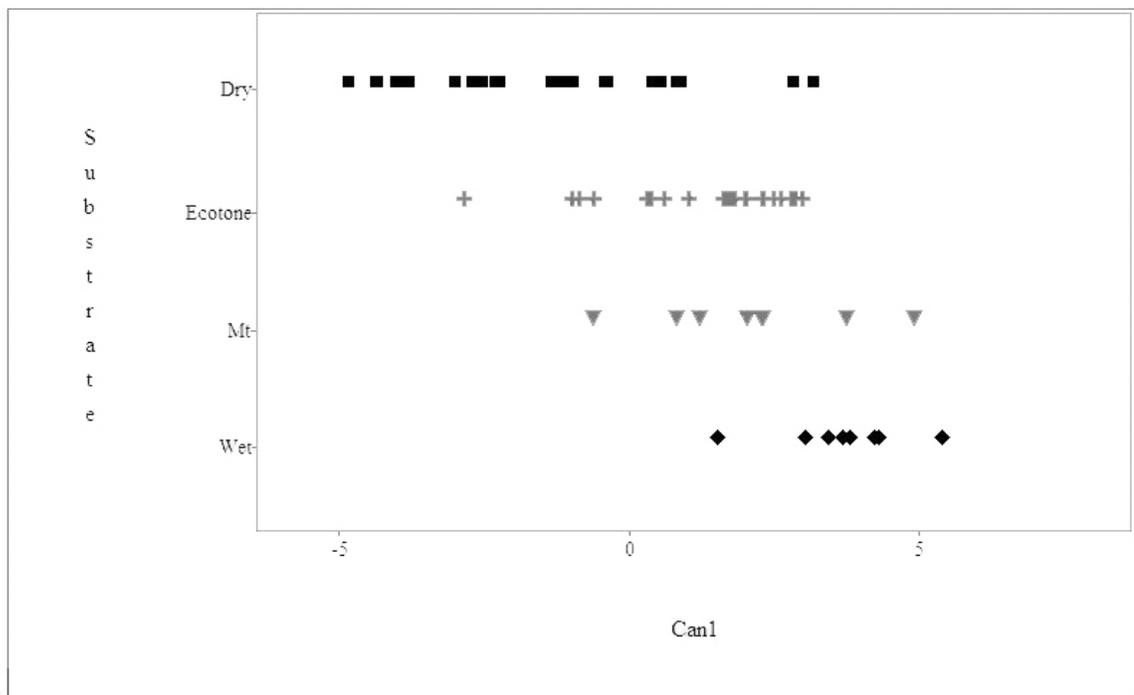


Figure 7-26 Habitat Score for the third phalanx plantar margin analysis of substrate. Specimens formed a continuum along CV1, though there is overlap.

Visualizations (with the vector of shape change multiplied by four) created using the habitat score training specimens demonstrated that the third phalanges of cervids moving across “Wet” substrates are thin and tapered anteriorly (Figure 7-27). This morphology is associated with the splaying of the third phalanx. Cervids that locomote on

hard and dry substrates have wider, flatter and less tapered third phalanges, which creates a more stable surface that reduces the risk of dislocation (Köhler 1993).

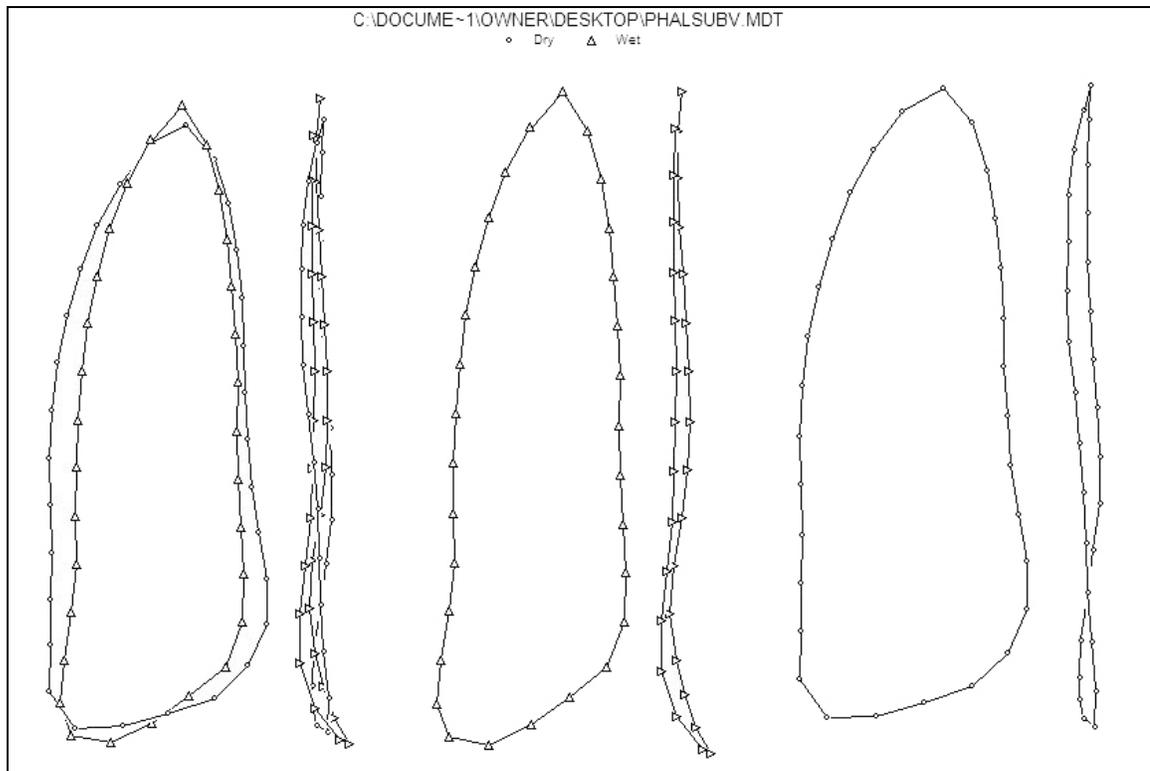


Figure 7-27 Visualizations of the shape change along the canonical variate from the third phalanx plantar margin analysis of substrate, creating hypothetical “Wet” and “Dry” specimens when the vector of shape change was applied to the mean configuration of all specimens. Left = “Dry” and “Wet” specimens overlapped with left-side image viewed from the plantar surface and the right-hand image viewed from the lateral edge. Middle = “Wet” specimen, show more tapering anteriorly, more bowing on the lateral side, and a deeper plantar surface. Right = “Dry” specimen, displaying a generally more broad and flat plantar surface.

Analysis of Tribal membership

While the CVA of third phalanges by tribe returned high mean correct cross-validation (73.1%) and resubstitution (84.2%) rates, this unit of morphology performed poorly at classifying Cervini and Odocoileini (the majority of the specimens) to their correct actual tribe. The three tribes with the smallest sample sizes (Alceini, Muntiacini, and Capreolini) had high correct reclassifications, which inflated the mean correct

reclassification percentages (Table 7-21). The permutation tests indicated that the tribal group centroids were not significantly different for any pair, except Odocoileini and Cervini ($p < 0.0001$) and Odocoileini and Capreolini ($p = 0.0017$) (Table 7-22). The significant differentiation of the centroids yet low reclassification rates for Odocoileini and Cervini was likely due to the wide distribution of these two tribes in the canonical variates space. While there was much overlap between the two tribes (Figure 7-28), their centroids were far enough apart that the permutation test was significant. However, the large region of overlap made it difficult for cross-validation to correctly reclassify specimens into their actual tribe. Cervini specimens were actually classified into Odocoileini (9/22) more often than into Cervini (7/22). Odocoileini specimens were also misclassified into Cervini more often than any other tribe.

Though Cervini and Odocoileini had much overlap, the other three tribes occupied fairly unique regions of canonical variates space (Figure 7-28). CV1 (summarizing 42.6% of the total sample variance) separated Muntiacini specimens from Alceini + Capreolini specimens, CV2 (26.7% of the variance) separated Alceini from Muntiacini + Capreolini, CV3 (21.4% of the variance) weakly separated Odocoileini and Cervini, and CV4 (9.2% of the variance) weakly separated Odocoileini from the other tribes.

Cross-validation						
Tribe	Alceini	Capreolini	Cervini	Muntiacini	Odocoileini	Total
Alceini	3	0	0	0	0	3
	100	0	0	0	0	100
Capreolini	0	6	1	0	1	8
	0	75	12.5	0	12.5	100
Cervini	2	3	7	1	9	22
	9.1	13.6	31.8	4.6	40.9	100
Muntiacini	0	0	0	2	0	2
	0	0	0	100	0	100
Odocoileini	2	3	6	1	17	29
	6.9	10.3	20.7	3.5	58.	100
Total	7	12	14	4	27	64
	10.9	18.8	21.9	6.3	42.2	100
Resubstitution						
Tribe	Alceini	Capreolini	Cervini	Muntiacini	Odocoileini	Total
Alceini	3	0	0	0	0	3
	100	0	0	0	0	100
Capreolini	0	7	1	0	0	8
	0	87.5	12.5	0	0	100
Cervini	1	1	15	1	4	22
	4.6	4.6	68.2	4.6	18.2	100
Muntiacini	0	0	0	2	0	2
	0	0	0	100	0	100
Odocoileini	1	3	5	1	19	29
	3.5	10.3	17.2	3.5	65.5	100
Total	5	11	21	4	23	64
	7.8	17.2	32.8	6.3	35.9	100

Table 7-21 Cross-validation and resubstitution results for the tribal analysis of the third phalanx plantar margin, with specimen counts and mean correct reclassifications (shaded gray).

	Capreolini	Cervini	Muntiacini	Odocoileini
Alceini	0.0649	0.0589	0.2237	0.0585
Capreolini		0.0724	0.1775	0.0017
Cervini			0.1972	<0.0001
Muntiacini				0.2153

Table 7-22 Results for permutation tests between each pair of tribes for the third phalanx plantar margin based on Mahalanobis distances between group centroids. The reported result is the probability that the two centroids were drawn from the same population.

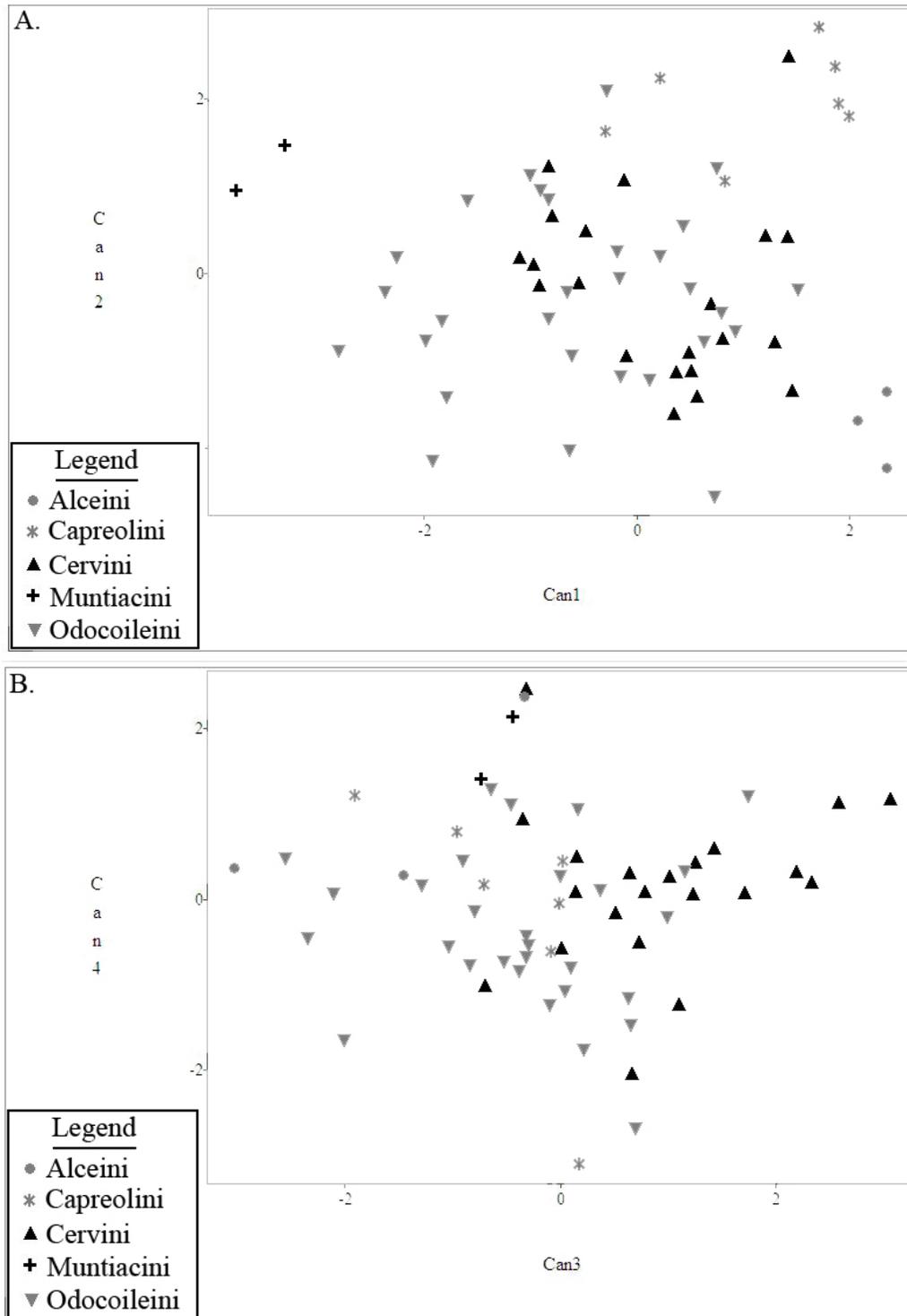


Figure 7-28 A: Plot of CV1 and CV2 for the tribal analysis of the third phalanx plantar margin for extant-only specimens. CV1 separated the Muntiacini specimens from the Alceini + Capreolini specimens, CV2 separated Alceini specimens from Muntiacini + Capreolini specimens. B: Plot of CV2 and CV3 for the third phalanx plantar margins. CV3 weakly separated the Odocoileini and Cervini specimens and CV4 weakly separated the Odocoileini from all other tribes.

Analysis of Body Size

All three measure of body size for extant cervids were highly correlated to the natural log of centroid size (lnCS), though the regression of the natural log of body height (at the shoulder) to lnCS had the lowest R^2 value of all the regressions of body size to lnCS in any unit of analysis ($p < 0.0001$, $R^2 = 0.6845$, see Table 7-23). Species with the largest deviations from the regression line were *Cervus marianus*, *Elaphurus davidanus*, *Rangifer tarandus*, and *Alces alces*, all of which had phalanges (lnCS) larger than expected for their body size, and *Axis axis*, *Cervus eldi*, *Capreolus capreolus*, and *Odocoileus virginianus*, which had smaller phalanges than expected. The species that had larger than expected third phalanges occupy fairly open habitats, such as open grasslands/tundra and regions with tall grasses, while the specimens with smaller than expected phalanges were ecotonal species, except for the swamp-dwelling *C. eldi*.

Of the first ten principal components, only the first two PCs, which together summarized 57.7% of the total sample variance, were significantly correlated to lnCS. These correlations were entirely driven by the largest cervid species- *Megaloceros giganteus*, *Alces alces*, *Cervus elaphus/canadensis*, *Rangifer tarandus* and *Elaphurus davidanus*. When these specimens were removed from the regressions, p-values were non-significant. Thus, for the first two principal components, size was a major source of shape variation. CV1 was also correlated to lnCS, though the R^2 value was small (0.1446), indicating that size did not account for much of the shape variation along CV1. CV2 and CV3 were not significantly correlated to lnCS.

Phalanx 3: Extant Body Size		
Regression	R ²	p-value
lnBW	0.8095	<0.0001
lnBH	0.6845	<0.0001
lnBL	0.8169	<0.0001
PC1	0.277	<0.0001
PC2	0.2369	<0.0001
PC3	0.0003	0.8847
PC4	0.0301	0.1703
PC5	0.0124	0.3803
PC6	0.0082	0.4761
PC7	0.0001	0.9315
PC8	0.0053	0.5683
PC9	0.0037	0.634
PC10	0.0009	0.8113
CV1	0.1446	0.0019
CV2	0.0135	0.3603
CV3	0.0196	0.2694

Table 7-23 Regressions of the natural log of centroid size (lnCS) against several measures of body size (all natural logged) for extant species in the third phalanx plantar margin analysis of habitat: body weight (lnBW), body height at shoulder (lnBH), and body length (lnBL), the first ten principal component scores (PC1-PC10), and the three canonical variates (CV1-CV3). All measures of body size in extant cervids were highly correlated to the lnCS, though lnBH had the weakest correlation of any of the extant measures of body size. Only PC1 was significantly correlated to lnCS and this correlation was mainly driven by specimens of large body size.

Chapter 8: Results- Fossil cervid ecomorphology

Introduction

This chapter presents results for the entire fossil sample as well as separate habitat reconstructions for each of the fossil sites. Results for each unit of analysis are discussed and an overall habitat reconstruction for each site is presented based on all of the units of analysis together. In PCA and CVA plots, all extant specimens are colored gray and fossil specimens are large black markers. Posterior probabilities of membership in each habitat type for all of the fossil specimens can be found in Appendix D.

Entire fossil sample

Analyses of habitat

Calcaneus landmarks

A canonical variates analysis (CVA) was performed on 125 specimens of known habitat type (122 extant species, plus three *Megaloceros giganteus* specimens) using seventeen principal components (PCs). Fifty-one fossil specimens were treated as habitat “unknown” and classified into one of four habitat types using discriminant functions produced from the extant training set. The CVA was able to correctly assign a mean of 61.7% of the extant training set specimens to their known habitats using cross-validation. High cross-validation rates were returned for “Closed” specimens (mean = 71.4%) and “Open” specimens (mean = 68.8%) and moderate rates were returned for the two intermediate habitat categories: “Intermediate Closed” (mean = 45.5%) and “Intermediate Open” (mean = 61.1%). Along CV1, which separated “Closed” specimens from all other habitat groups, all fossil specimens (asterisks in Figure 8-1) scored with the non-“Closed” specimens. CV2 separated “Open” and “Intermediate Open” specimens. Fossil specimens

were disbursed across CV2, though many scored positively with the “Open” extant group. CV3 separated the “Intermediate Closed” specimens from the other habitat groups. Most of the fossil specimens did not group with the “Intermediate Closed” specimens. Thirty fossil specimens were classified as “Open”, seventeen as “Intermediate Open”, and one specimen each as “Intermediate Closed” and “Closed”.

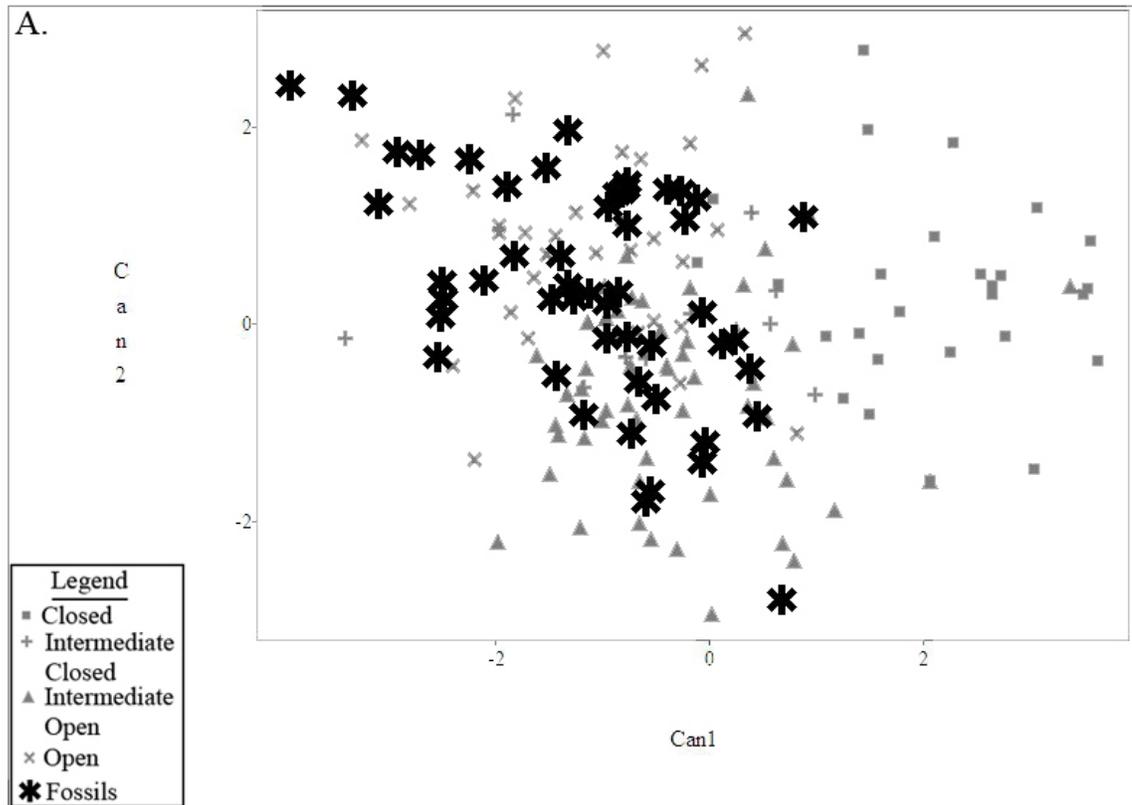
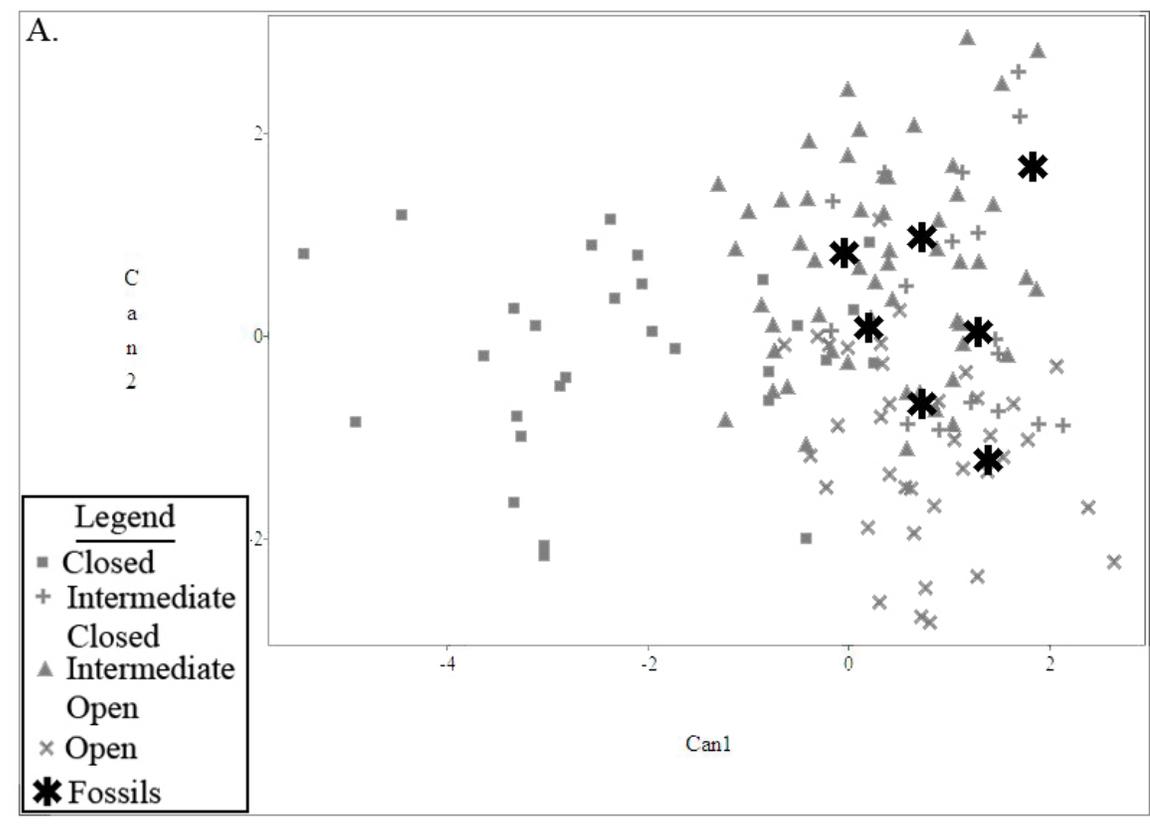


Figure 8-1 Plot of CV1 and CV2 for the habitat analysis of the calcaneus landmarks including all extant and fossil specimens.

Femoral medial patellar margin

Analyses were conducted on 137 specimens of known habitat type and seven fossil specimens (six from Senèze and one from ‘Ubeidiya). CVAs were conducted on forty-four PCs. Analyses of the medial patellar margin of extant specimens indicated that

this unit of analysis performed well at separating “Closed” from non-“Closed” specimens. The fossil specimens all fell within the non-“Closed” group (Figure 8-2). Further distinctions between the habitat types in the non-“Closed” group were more difficult, since the specimens overlapped substantially. In total, two fossil specimens were classified as “Open”, three as “Intermediate Open”, two as “Intermediate Closed”, and one as “Closed”.



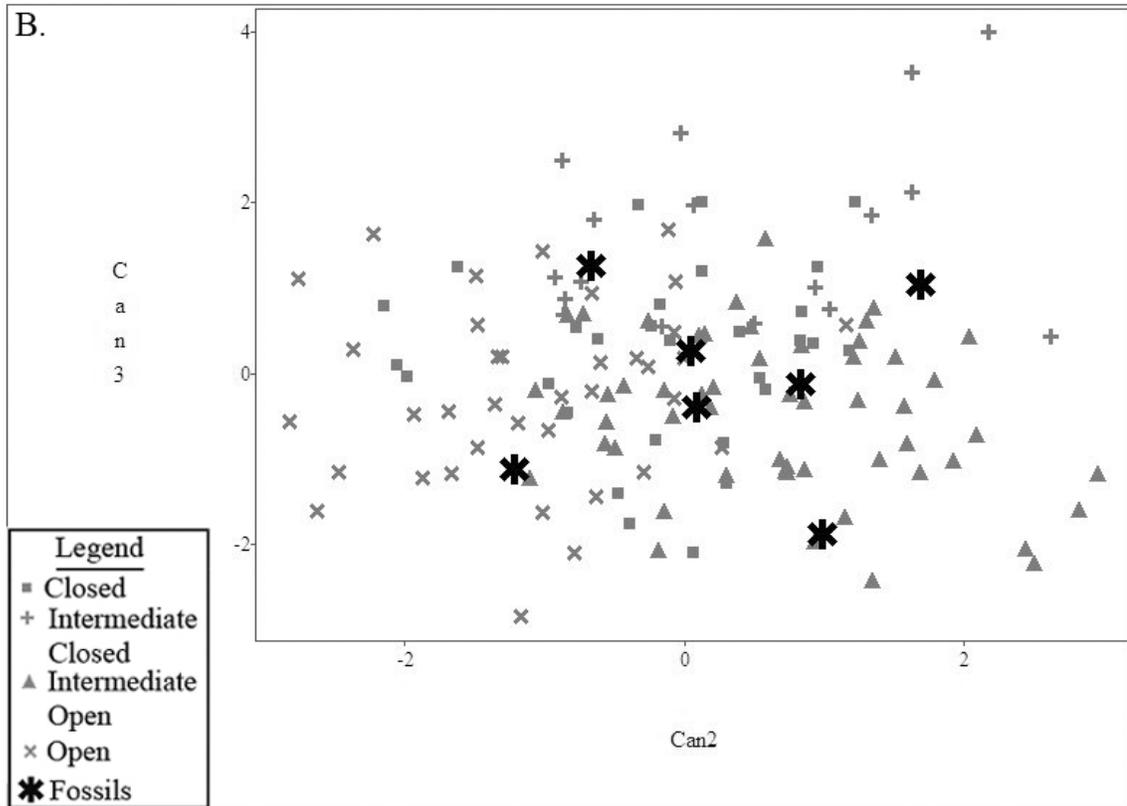


Figure 8-2 A: Plot of CV1 and CV2 for the habitat analysis of femoral medial patellar margin including all extant and fossil specimens. B: Plot of CV2 and CV3 for the femoral medial patellar margin for all extant and fossil specimens.

Tibial lateral plateau margin

One hundred and forty specimens of known habitat (137 extant plus three specimens of *Megaloceros*) and eight fossil specimens from three sites were included in this study. These specimens did not cluster in any obvious way when placed into the plot of PC1 and PC2. The fossil specimens scored with the non-“Closed” specimens along CV1, mostly with the “Intermediate Open” specimens along CV2, though several plotted with the “Intermediate Closed” specimens along CV3 (Figure 8-3). One specimen was classified as “Open”, five as “Intermediate Open”, and two as “Intermediate Closed”.

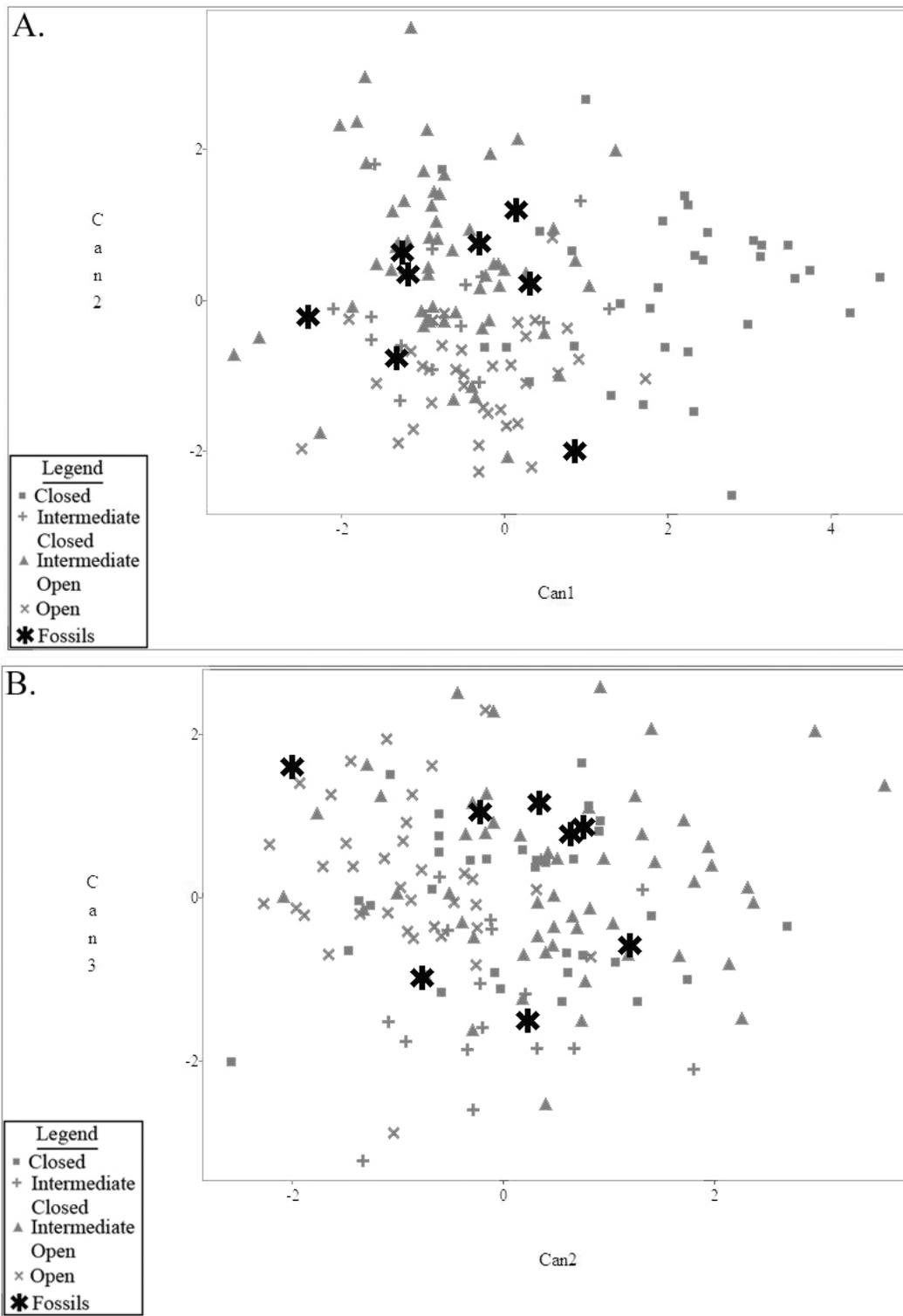
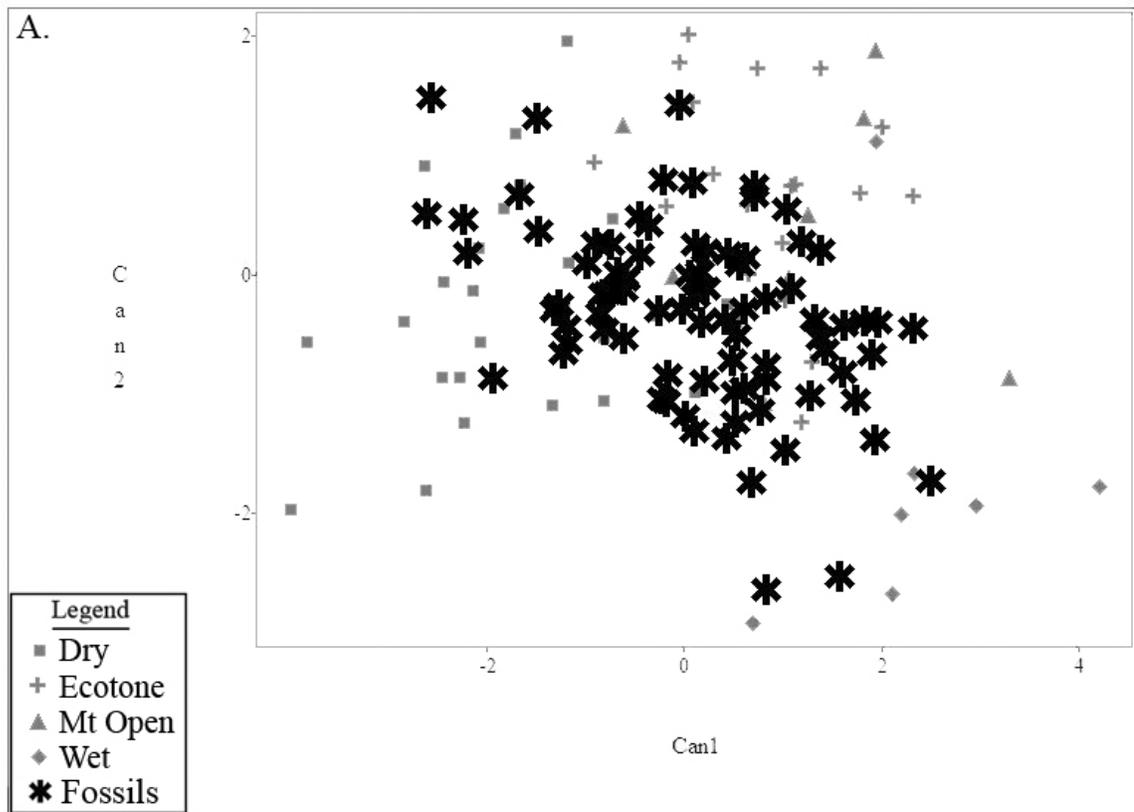


Figure 8-3 A: Plot of CV1 and CV2 for the habitat analysis of tibial lateral plateau margin including all extant and fossil specimens. B: Plot of CV2 and CV3 for the tibial lateral plateau margin for all extant and fossil specimens.

3rd phalanx plantar margin

Sixty-four specimens of known habitat type (sixty-two extant specimens plus two *Megaloceros* specimens) and eighty-six fossil specimens were included in this analysis. Fossil specimens were distributed throughout canonical variates space (Figure 8-4), though most were classified either as “Dry” (n = 31) or “Mountain” (n = 29). A further fifteen fossil specimens were classified into “Ecotone” and eleven into “Wet”. Fossil specimens ranged across all substrate types in the habitat score.



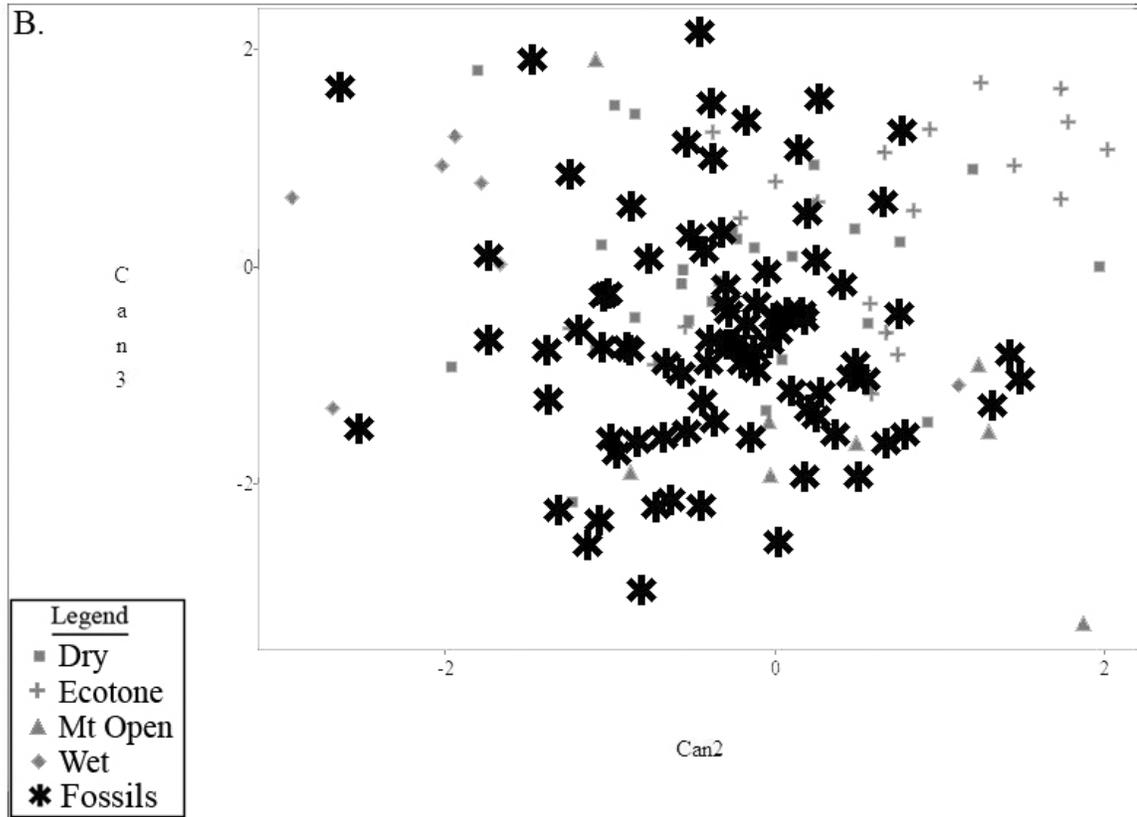


Figure 8-4 A: Plot of CV1 and CV2 for the substrate analysis of third phalanx plantar margin including all extant and fossil specimens. B: Plot of CV2 and CV3 for the third phalanx plantar margin for all extant and fossil specimens.

Analyses of body size

Calcaneus landmarks

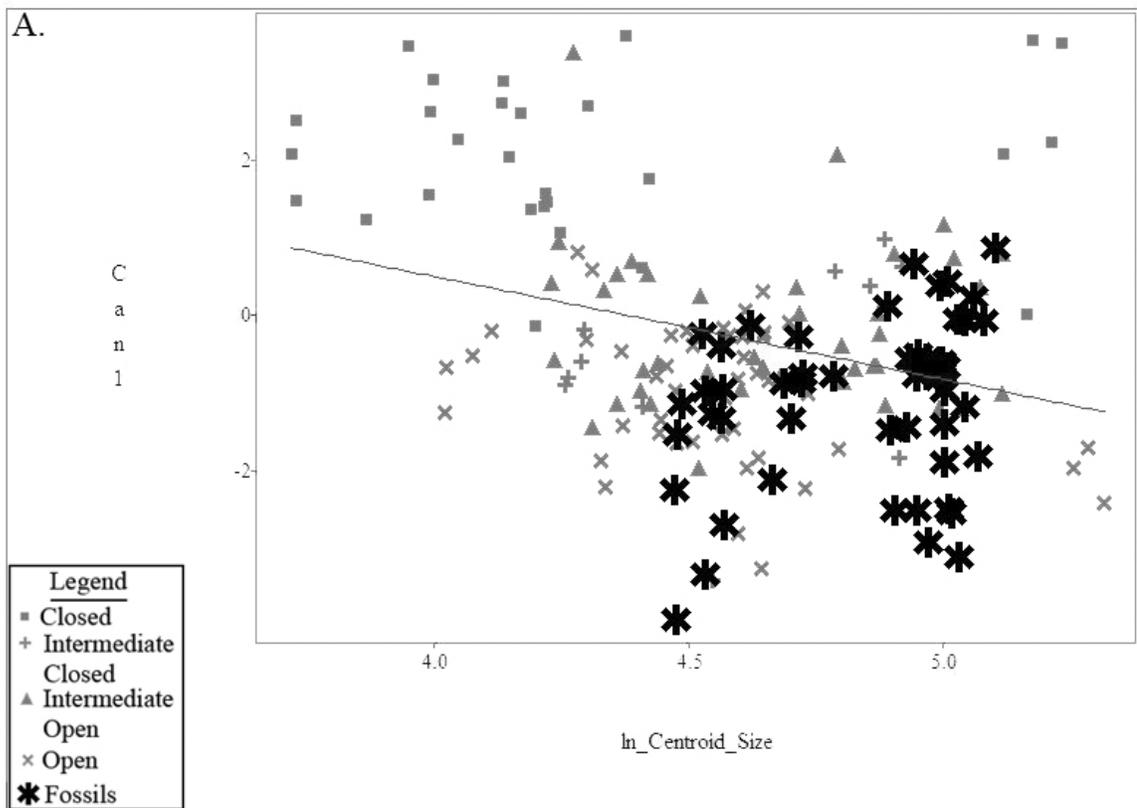
Adding the fossil specimens to the regression of natural log of centroid size (lnCS) and the principal component scores did not change the results remarkably from the regressions of just the extant specimens. No significant correlations were found (Table 8-1). In the regression of lnCS and the canonical variates, only CV1 had a significant correlation ($p < 0.0001$) to lnCS, though the R^2 value was small (0.092), indicating that the lnCS does not account for much of the variation along CV1.

Calcaneus Extant + Fossil Body Size		
Regression	R ²	p-value
PC1	0.0099	0.1883
PC2	0.0005	0.7725
PC3	0.0035	0.4362
PC4	0.0511	0.0217
PC5	0.0001	0.1009
PC6	0.0002	0.8411
PC7	0.0054	0.3311
PC8	0.0559	0.0016
PC9	0.0009	0.697
PC10	0.0005	0.7725
CV1	0.092	<0.0001
CV2	0.0041	0.3983
CV3	0.0023	0.531

Table 8-1 Regressions of the natural log of centroid size (lnCS) against the first ten principal component scores (PC1-PC10) and the three canonical variates (CV1-CV3) for all (extant + fossil) specimens in the calcaneus landmarks analysis of habitat. Only CV1 was found to be correlated to lnCS, though the value R² was low.

Though the calcaneal morphology of the fossil specimens did not show a strong correlation to lnCS, the fossil specimens did sort out into two size groups along lnCS, as can be seen in Figure 8-5A. When lnCS was plotted against CV1 for just the fossils (Figure 8-5B), the *Eucladoceros* specimens (black boxes = Valea Graunceanului, gray boxes = St. Vallier and Senèze) formed one cluster with *Praemegaceros* and *Alces* while *Pseudodama* and *Croizetoceros ramosus* formed another. Gray asterisks are specimens identified only to Cervidae, but several of these specimens (designated as Cervidae (1) in Appendix D) clustered within the *Eucladoceros* group. These specimens showed the same pattern in the plots of lnCS and the other two CVs. In fact, it is possible to discern three body sizes within Cervidae (species + genus unknown) specimens. Seven

specimens always grouped with the *Pseudodama + Croizetoceros* , eight specimens formed a group to themselves as medium-sized cervids (larger gray asterisks) and seven more specimens always clustered with the *Eucladoceros* group. Although taxonomic identification is not advisable with these data, they do present a line of inquiry that should be investigated (and will be discussed further below).



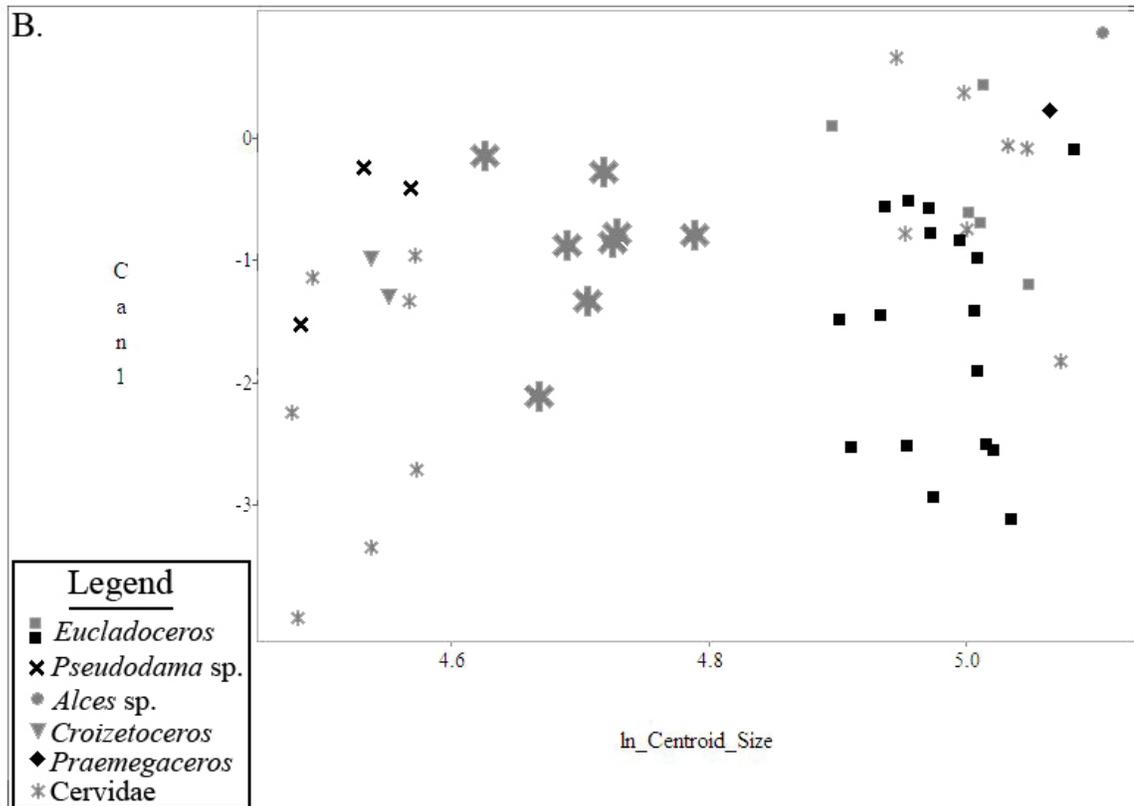


Figure 8-5 A: Plot of regressions of CV1 against lnCS in the calcaneus landmark analysis of habitat for all specimens. The fossil specimens fell into two size classes. B = Plot of CV1 and lnCS for just the fossil specimens (coded by species) showing that there may possibly be three size classes.

Femoral medial patellar margin

When the seven fossil specimens were added to the calcaneal data set for the regression of principal component scores on lnCS, only the first two PCs had significant correlations (Table 8-2). The R^2 for PC1 and lnCS was higher than for the sample of only extant species, but not by much ($r^2 = 0.1316$, $p < 0.0001$), while the R^2 for PC2 and lnCS fell ($r^2 = 0.1445$, $p < 0.0001$). Adding the fossil specimens to the regression of canonical variates scores against lnCS did not change the results from the extant-only regressions in any significant way.

Fem Med Extant + Fossil Body Size		
Regression	R ²	p-value
PC1	0.1316	<0.0001
PC2	0.1445	<0.0001
PC3	0.0021	0.5891
PC4	0.0127	0.1792
PC5	0.0438	0.0118
PC6	0.0041	0.4457
PC7	0.014	0.1579
PC8	0.0014	0.6575
PC9	0.0067	0.3299
PC10	0.002	0.5925
CV1	0.2925	<0.0001
CV2	0.0039	0.459
CV3	0.0017	0.6194

Table 8-2 Regressions of the natural log of centroid size (lnCS) against the first ten principal component scores (PC1-PC10) and the three canonical variates (CV1-CV3) for all (extant + fossil) specimens in the femoral medial patellar margin analysis of habitat. These results are roughly similar to those found for the extant-only specimens, with the correlations being driven by the “Closed” specimens.

Tibial lateral plateau margin

The addition of the eight tibial fossil samples to the extant sample did not produce significant differences in the results of regressions of either the first ten principal components or the three canonical variates against lnCS. In fact, for all regression found to be significant in the extant-only sample, R² values decreased marginally with the addition of the fossil specimens (Table 8-3).

Tib Lat Extant + Fossil Body Size		
Regression	R ²	p-value
PC1	0.0002	0.8756
PC2	0.0173	0.1082
PC3	0.1892	0.0001
PC4	0.198	0.0001
PC5	0.000006	0.9763
PC6	0.0051	0.3848
PC7	0.0053	0.3767
PC8	0.0177	0.1045
PC9	0.0298	0.0346
PC10	0.0049	0.3927
CV1	0.2512	<0.0001
CV2	0.0247	0.0549
CV3	0.0049	0.3927

Table 8-3 Regressions of the natural log of centroid size (lnCS) against the first ten principal component scores (PC1-PC10) and the three canonical variates (CV1-CV3) for all (extant + fossil) specimens in the tibial lateral plateau margin analysis of habitat. These results are roughly similar to those found for the extant-only specimens, with correlations being driven by the small “Closed” specimens.

3rd phalanx plantar margin

When the eighty-six fossil specimens were added to the regressions of lnCS with the principal components, only PC1 had a significant correlation at $p < 0.0001$ (Table 8-4). PC2 was found to be correlated at $p = 0.0017$, but the R^2 value dropped from the value found with the extant data set from 0.2369 to 0.0643. The regression of the canonical variates with lnCS changed with the addition of the fossil specimens in that all three CVs were more correlated to lnCS, though all had low R^2 values.

Phalanx 3 Extant + Fossil Body Size		
Regression	R ²	p-value
PC1	0.3311	<0.0001
PC2	0.0643	0.0017
PC3	0.005	0.3897
PC4	0.0668	0.0014
PC5	0.0152	0.1329
PC6	0.0034	0.4779
PC7	0.0002	0.1076
PC8	0.0006	0.7661
PC9	0.00001	0.9678
PC10	0.0002	0.863
CV1	0.1177	<0.0001
CV2	0.0218	0.0717
CV3	0.074	0.0008

Table 8-4 Regressions of the natural log of centroid size (lnCS) against the first ten principal component scores (PC1-PC10) and the three canonical variates (CV1-CV3) for all (extant + fossil) specimens in the third phalanx plantar margin analysis of substrate type. As with the extant-only sample, PC1 was significantly correlated to lnCS. The addition of fossil specimens to the analysis increased the correlations between the CVs and lnCS, though R² values were small.

As was found for the body size analyses of the calcaneus, two size classes were evident in the fossil data. In the scatterplot of lnCS and CV1 (Figure 8-6), the *Eucladoceros* + *Praemegaceros* (& *Libralces*) form one group and the *Cervus philisi* + *Pseudodama* + Cervidae (genus + species unknown) form a second. Two specimens labeled as *Cervus philisi* grouped with *Eucladoceros* and may have been mislabeled.

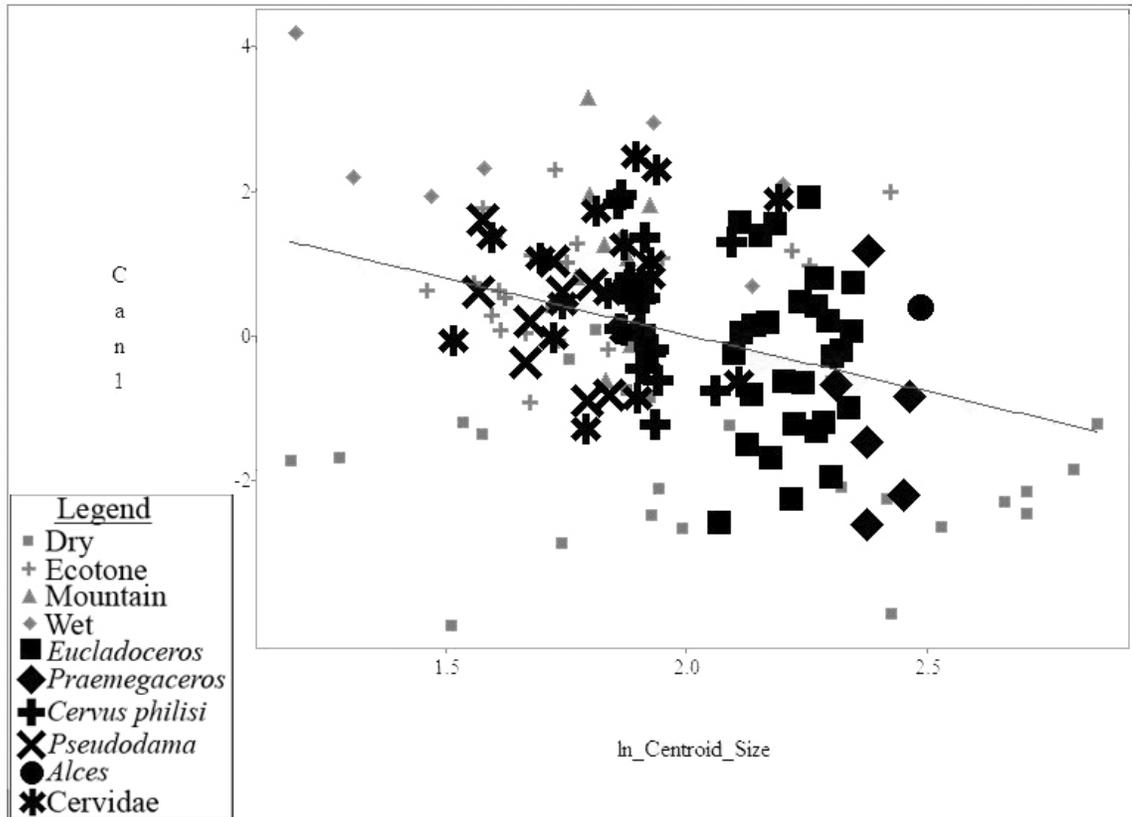


Figure 8-6 Plot of regressions of CV1 against lnCS in the third phalanx plantar margin analysis of substrate for all specimens. The fossil specimens fell into two, perhaps three, size classes.

Summary

Though it may be impractical or inadvisable to discuss the fossil habitat reconstructions as a single unit, some general patterns are worth mentioning. Only 3% of the fossil specimens were classified into the “Closed” habitat category, while 47.8% were classified as “Open”, 37.3% as “Intermediate Open” and 10.5% as “Intermediate Closed”. For the third phalanx, 35.6% of the fossil specimens were classified as “Dry”, 33.3% as “Mountain”, 17.2% as “Ecotone”, and only 12.6% as “Wet”. From these data it is clear that the fossil sites examined here mostly were not closed habitats. Indeed, most

can be characterized as being “Open” to “Intermediate Open” with “Dry” substrate and with mountainous terrain.

While the addition of fossil specimens to regressions of body size to shape generally did not change results found with the extant-only samples, these analyses indicated that the specimens in this analysis fall into two, and perhaps three size categories. Further, specimens identified only to Cervidae group with either the large species (*Eucladoceros* + *Praemegaceros*) or the medium/small species (*Cervus philisi*, *Pseudodama* sp., *Croizetoceros ramosus*). These two groups showed no overlap, except for two *Cervus philisi* third phalanges that were possibly misidentified and are hypothesized to belong to *Eucladoceros*.

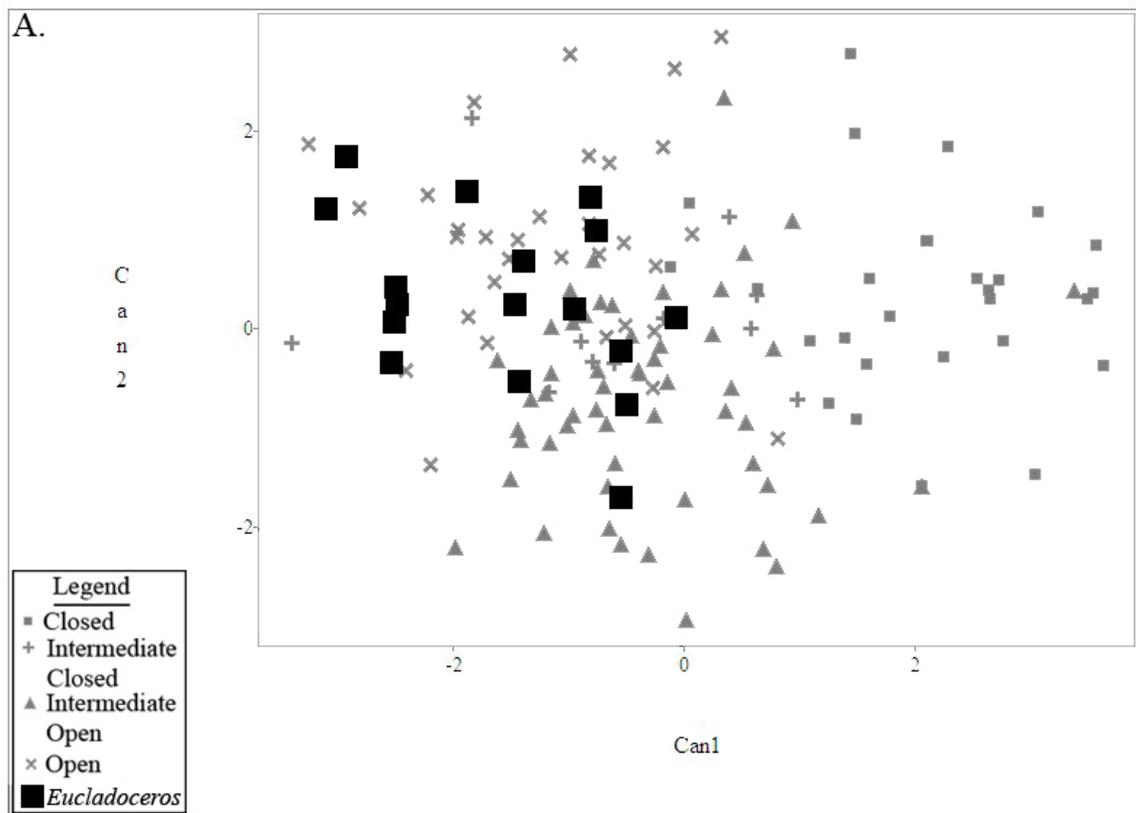
Valea Graunceanului, Romania

Analyses of habitat

Calcaneus landmarks

All seventeen calcaneus specimens from Valea Graunceanului, Romania were tentatively assigned to *Eucladoceros* (species unknown). Over half (9/17) of these specimens were classified (with cross-validation) into the “Open” habitat category with high posterior probabilities (mean = 82.2%). Five specimens were classified into the “Intermediate Open” category, though with lower posterior probabilities (mean = 52.2%). For all of the specimens classified into “Intermediate Open”, the “Open” category was the second most likely. Three specimens were classified into the “Intermediate Closed” category also with lower posterior probabilities (mean = 54.6%). The second most likely group for these specimens was also “Open”. These results are reflected in the CV plots (Figure 8-7). Along CV1, the Valea Graunceanului specimens group with the non-

“Closed” specimens. The specimens are spread across CV2, though they group more with the “Open” specimens than the “Intermediate Open” specimens. Along CV3, only three specimens group with the “Intermediate Closed” specimens. The *Eucladoceros* specimens were distributed on the “Open” end of the distribution in the habitat score with many specimens scoring as more “Open” than any of the extant specimens (Figure 8-8). These results indicate that the *Eucladoceros* specimens from Valea Graunceanului were mostly open-adapted.



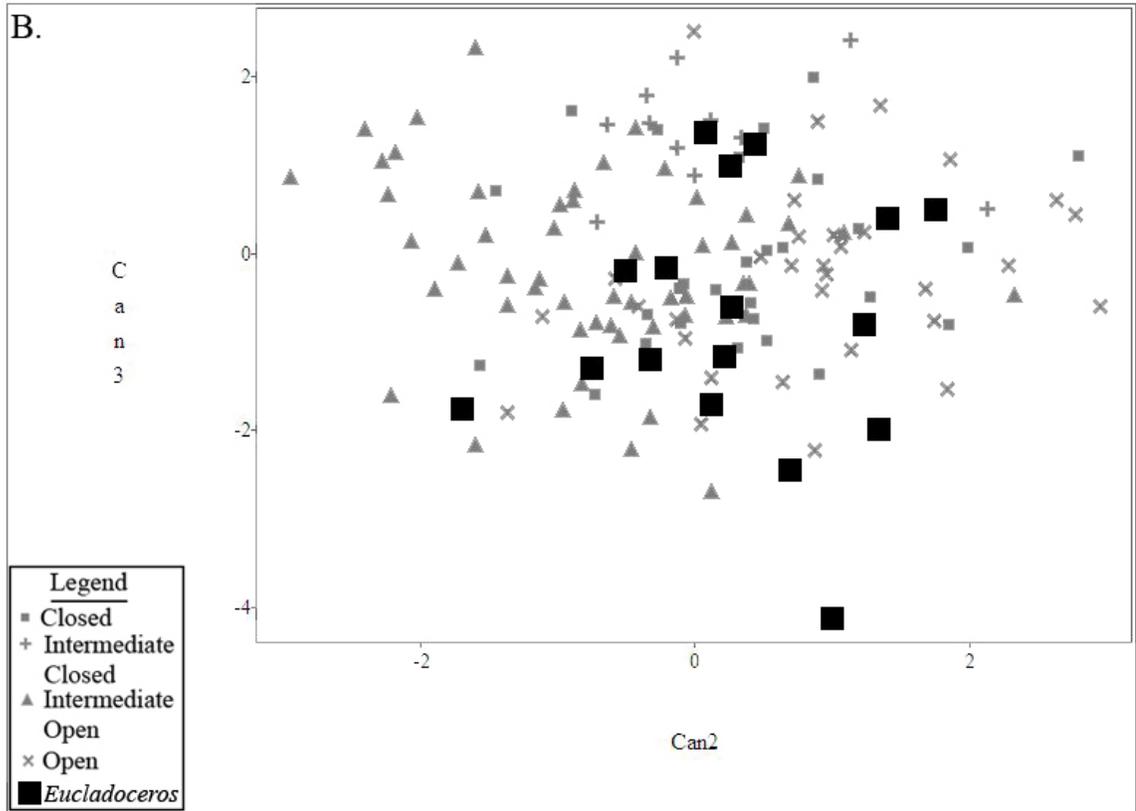


Figure 8-7 A: Plot of CV1 and CV2 for the habitat analysis of calcaneal landmarks including all extant and Valea Graunceanului specimens. B: Plot of CV2 and CV3 for the calcaneal landmarks for all extant and Valea Graunceanului specimens.

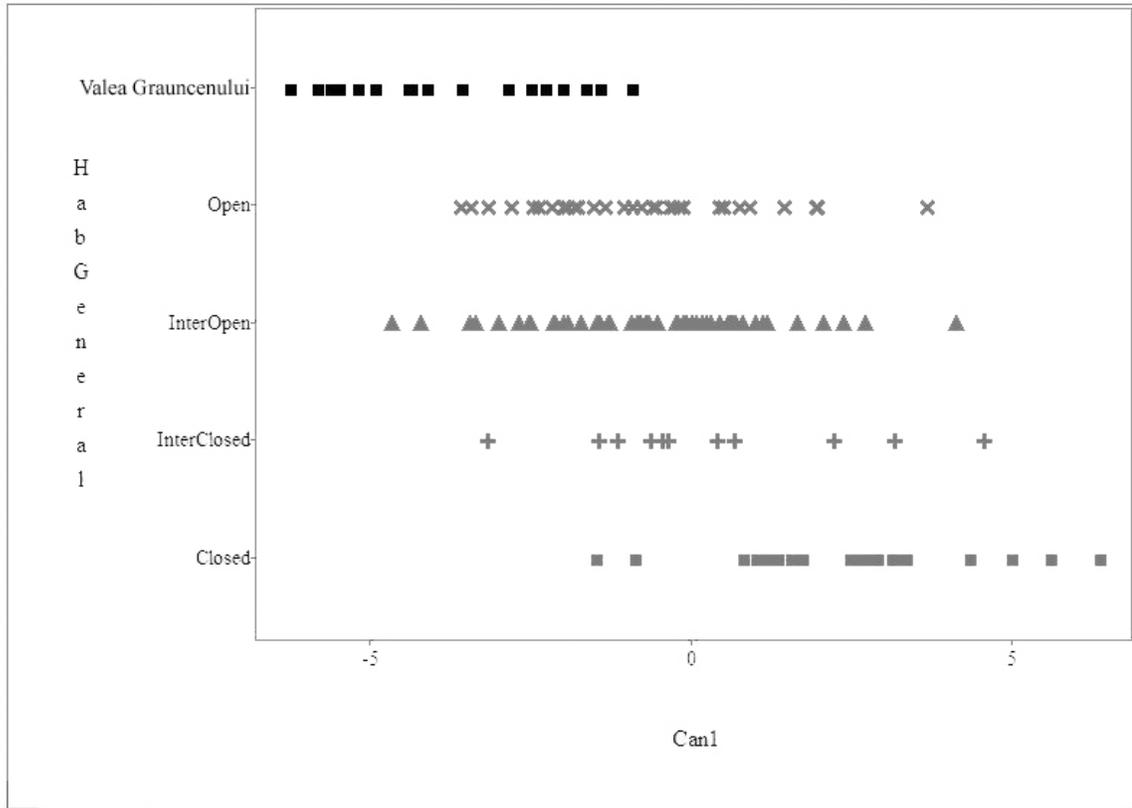


Figure 8-8 Habitat score plot for extant and Valea Graunceanului calcaneal specimens, indicating an “Open” adaptation for the *Eucladoceros* specimens.

3rd phalanx plantar margin

There were twenty-four specimens assigned to *Eucladoceros* included in this analysis. These specimens were classified fairly evenly into “Dry” and “Mountain” substrates; both with medium-high mean posterior probabilities (81.7% and 79%, respectively). One specimen was classified as “Ecotone” with low probability (43.2%) and one specimen was classified as “Wet” with medium-high probability (77.7%). The division of the *Eucladoceros* specimens into “Dry” or “Mountain” is perplexing and may possibly indicate that this species exhibits a morphology not well represented in the extant data set, which would not be surprising, as *Eucladoceros* went extinct without leaving any living descendants. This is further supported by the distribution of the

specimens in principal components space, in which the Romanian specimens occupy an area of the PC space that is not occupied by many extant specimens (Figure 8-11).

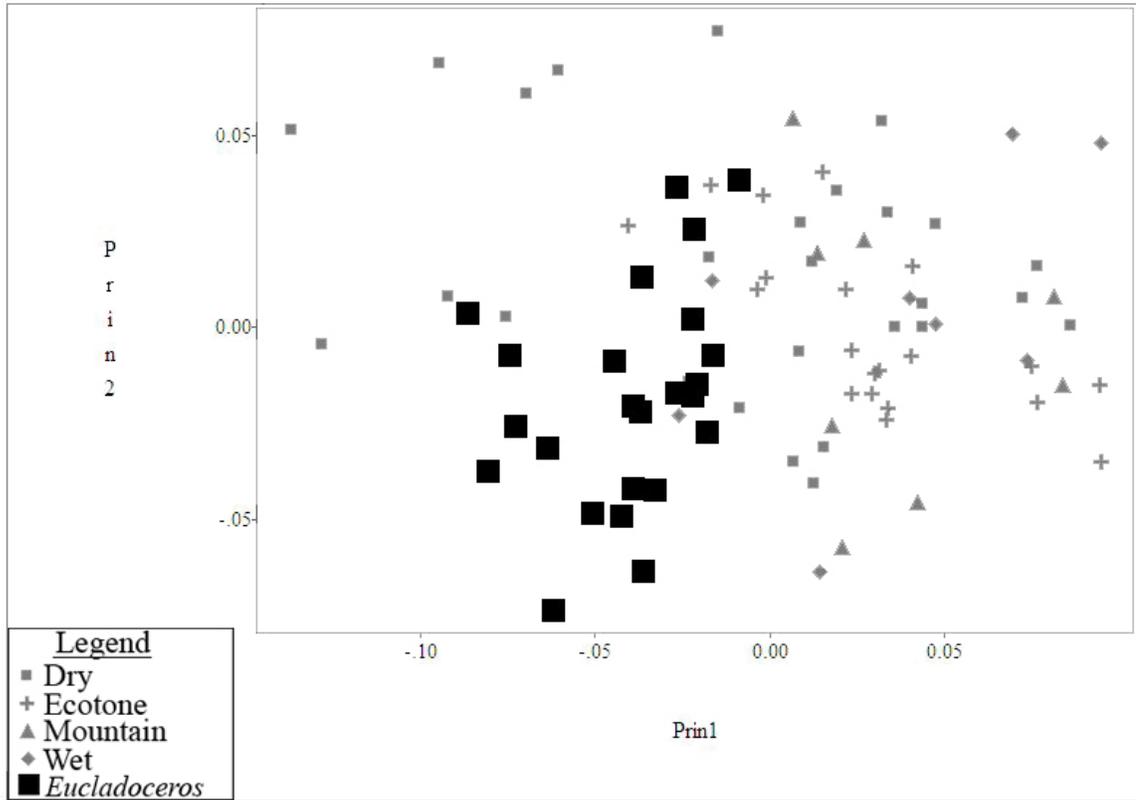


Figure 8-9 Plot of PC1 and PC2 for the substrate analysis of the third phalanx plantar margin including all extant and Valea Graunceanului specimens, with the *Eucladoceros* specimens occupying a region of PC space that few extant specimens occupied.

There was not much patterning to the distribution of the *Eucladoceros* specimens in canonical variates space, though they did not overlap with the “Ecotone” extant specimens much, as can be seen in Figure 8-12. They predominantly scored with the “Dry” specimens along CV1, opposite from the “Wet” specimens along CV2, and opposite of “Ecotone” specimens along CV3.

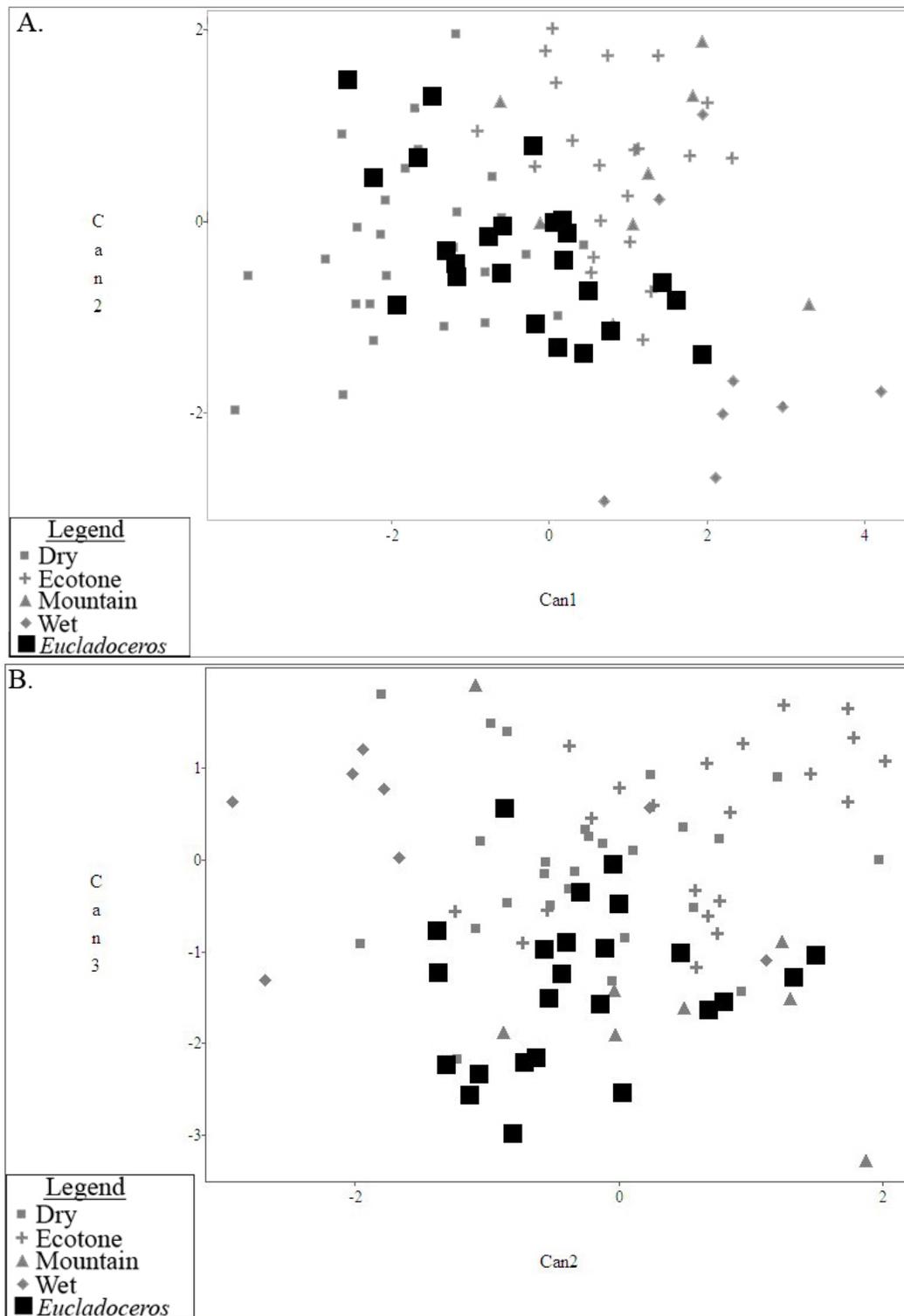


Figure 8-10 A: Plot of CV1 and CV2 for the substrate analysis of the third phalanx plantar margin including all extant and Valea Graunceanului specimens. B: Plot of CV2 and CV3 for the third phalanx plantar margin for all extant and Valea Graunceanului specimens. The *Eucladoceros* specimens were classified evenly into “Dry” and “Mountain”.

Summary

Since all of the Romanian specimens were *Eucladoceros* sp., this habitat reconstruction is limited to only what can be learned from this species. Analysis of calcaneal morphology indicated a mostly open adaptation for *Eucladoceros*. Over half of the specimens were classified to “Open” with high mean posterior probability. Specimens that were classified to other habitat categories usually had lower posterior probabilities for membership in those categories and “Open” was always the second most likely category. The twenty-four third phalanges were fairly evenly divided between “Dry” and “Mountain”. This, plus the unique distribution of the phalangeal specimens in PC space possibly indicates that the *Eucladoceros* specimens express morphology not well represented by any extant cervids. Further, though Valea Graunceanului sits at approximately 300 meters (~984 feet) in elevation, the region around the site is not particularly mountainous, with elevation changes of only ~100 feet between stream valleys. The closest mountains are the Carpathian Mountains (Transylvanian Alps), at ~20 miles to the north. It is possible that *Eucladoceros* migrated seasonally from summer habitats in the mountains to winter habitats at lower elevations to avoid dense snow cover, as some *Cervus elaphus* populations do (Luccarini *et al.* 2006).

The one femoral head from Valea Graunceanului (Figure 4-2), though not a part of the analyses here, was similar to bovids from open habitats, as discussed in Chapter 3. The calcanei also indicate mostly open-adaptation. The third phalanges indicated that *Eucladoceros* moved across dry and mountainous substrates. All these results point to an open adaptation for the Valea Graunceanului specimens.

St. Vallier, France

Analyses of habitat

Calcaneus landmarks

Of the twenty-two fossil calcaneal specimens from St. Vallier, three were identified as *Eucladoceros ctenoides*, two as *Croizetoceros ramosus*, and seventeen as Cervidae (genus + species unknown). Fourteen (63.6%) of these specimens were assigned to “Open” and eight (36.4%) to “Intermediate Open” with specimens in both groups having high posterior probabilities (mean = 81%). All *Eucladoceros ctenoides* specimens were assigned to “Intermediate Open” while the two *Croizetoceros ramosus* specimens were assigned to “Open”. Distribution of the St. Vallier specimens in canonical variates space is shown in Figure 8-13. Like the specimens from Valea Graunceanului, the St. Vallier fossil specimens scored toward the “Open” end of the calcaneus habitat score, with several specimens scoring as more “Open” than the extant training sample (Figure 8-14). These results suggest an “Open” habitat for St. Vallier, France.

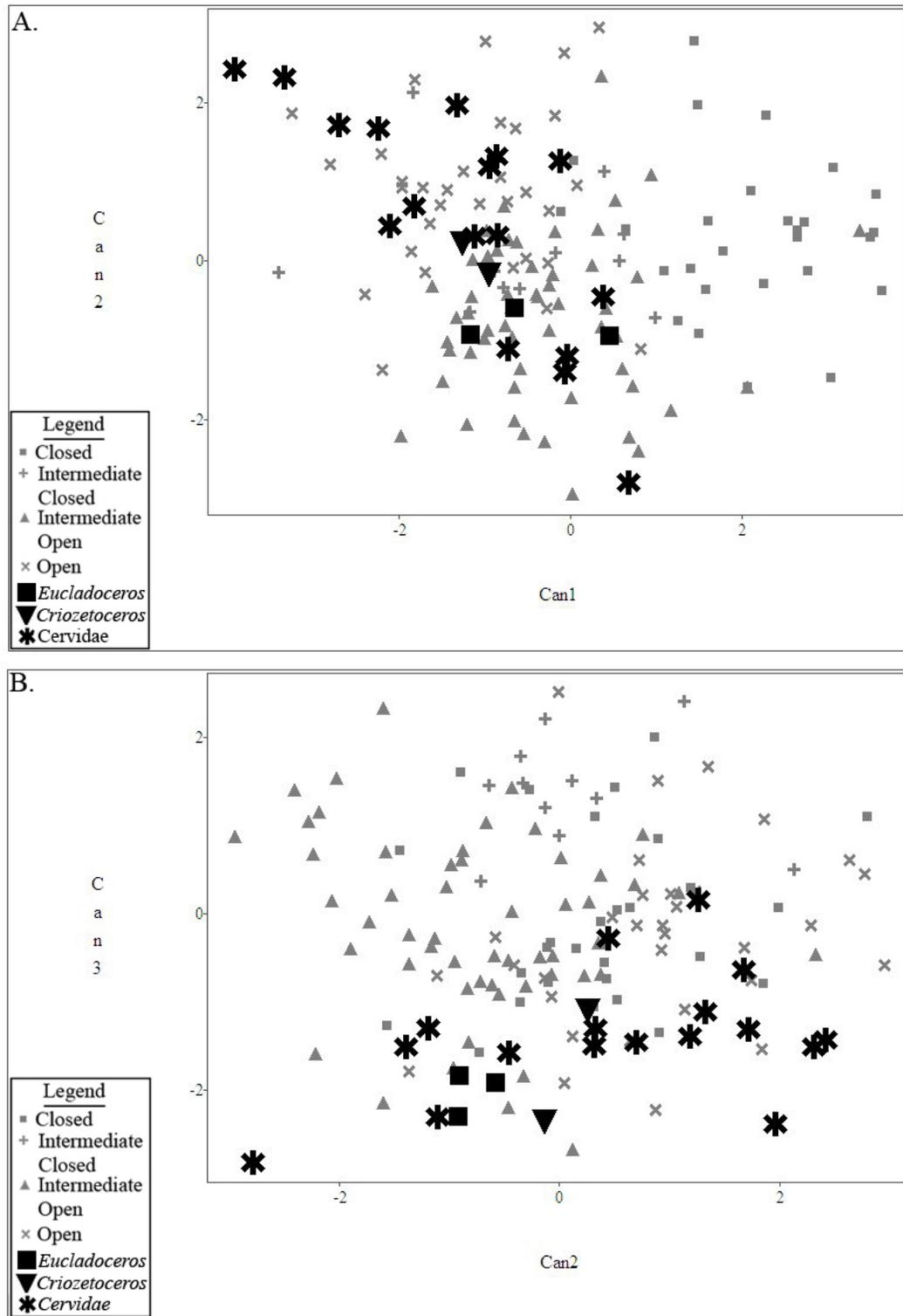


Figure 8-11 A: Plot of CV1 and CV2 for the habitat analysis of the calcanus landmarks including all extant and St. Vallier specimens. B: Plot of CV2 and CV3 for the calcanus landmarks for all extant and St. Vallier specimens. The St. Vallier specimens were classified as “Open” and “Intermediate Open”.

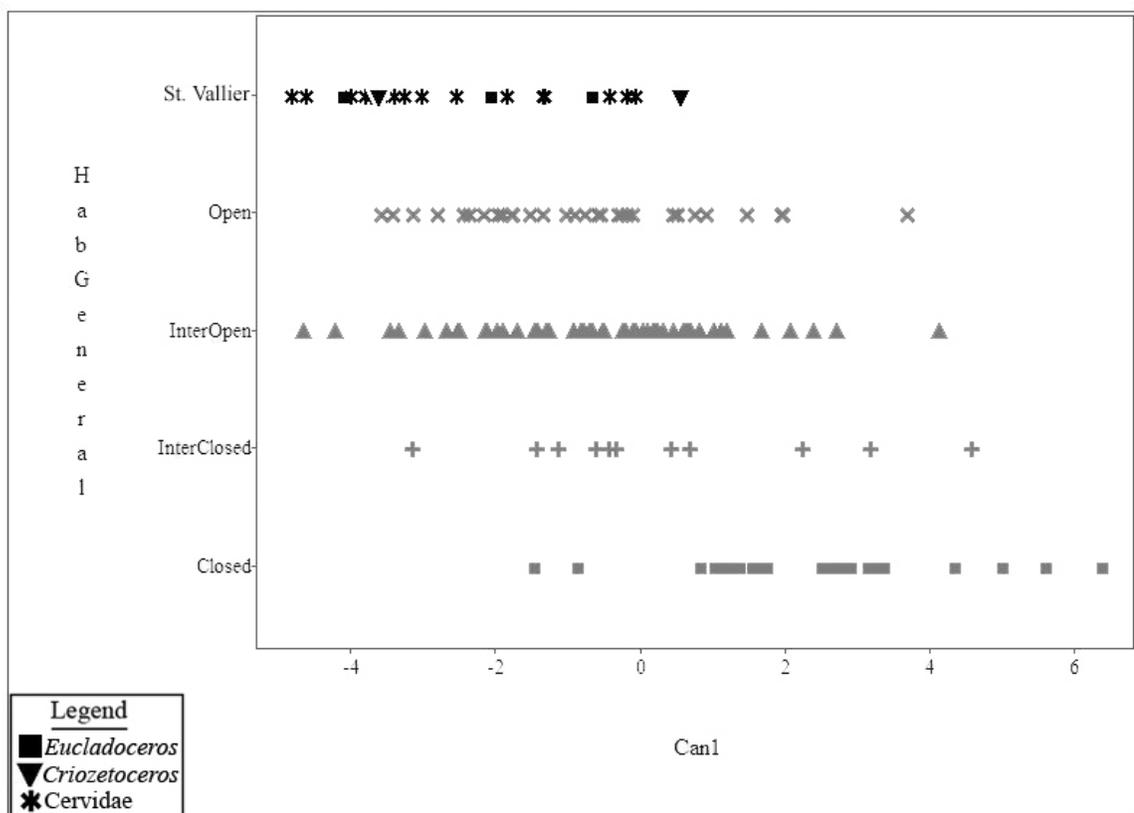


Figure 8-12 Habitat score plot for extant and St. Vallier calcaneal specimens, indicating a mostly “Open” adaptation, though slightly more closed than what was found for the Romanian specimens.

As was discussed above, when canonical variate scores are plotted against $\ln CS$, there is a distinction between large (*Eucladoceros*) and medium specimens (and a possible further division of the medium specimens into two more categories), as is shown in Figure 8-15. Of the Cervidae (genus + species unknown) specimens, six specimens (see Appendix D- Cervidae (l)), group close to the *Eucladoceros* specimens, four (Cervidae (m) in Appendix D) fall in the middle (large asterisks), and seven group closer to *Croizetoceros* (Cervidae (s)). Though this study did not attempt to provide taxonomic identification for the fossil specimens, there is a possibility that Cervidae (l) specimens belong to *Eucladoceros*, Cervidae (s) specimens to *Croizetoceros*, and Cervidae (m)

specimens to either *Croizetoceros* or another species, such as *Cervus philisi*, which is found at St. Vallier. These hypotheses need to be tested within a phylogenetic framework.

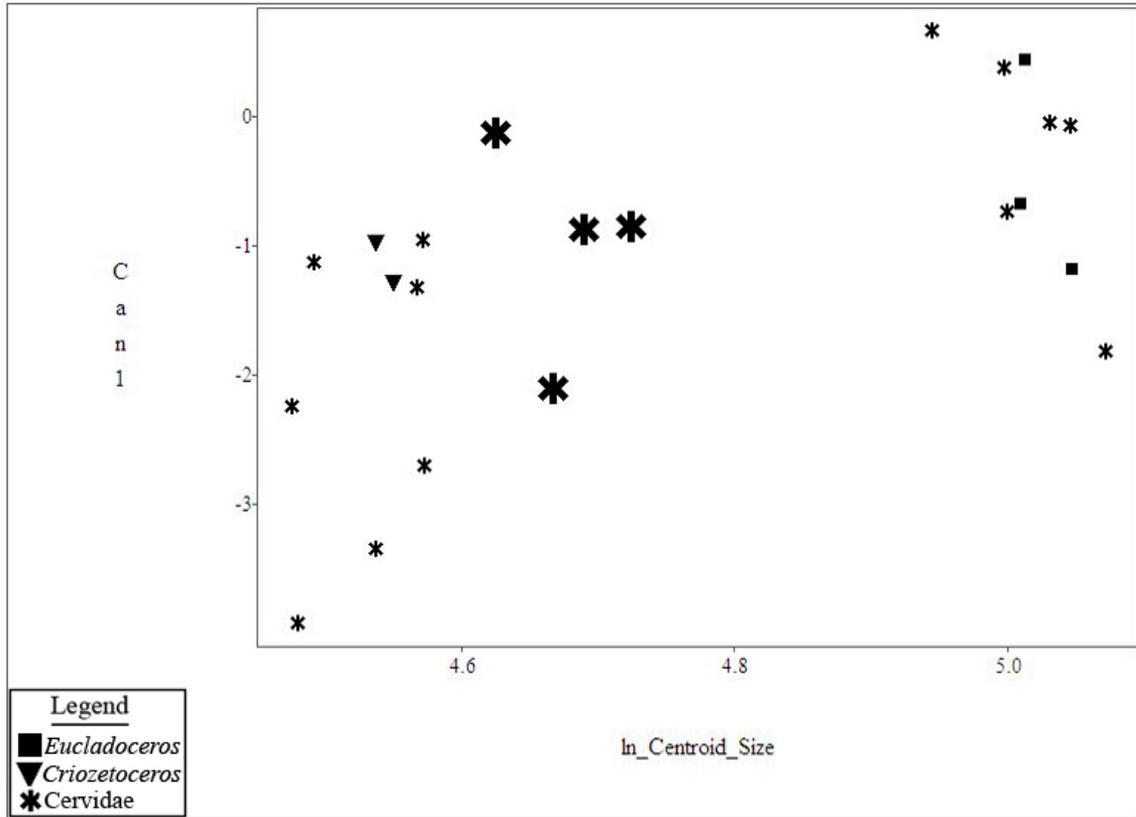


Figure 8-13 Plot of regressions of CV1 against lnCS in the calcaneus landmark analysis of habitat for the St. Vallier specimens, illustrating the two, and possibly, three sizes of cervids at this site.

Tibial lateral plateau margin

Only one tibia was available from St. Vallier, a specimen identified to *Croizetoceros ramosus medius*. This specimen classified as “Intermediate Open” with a 72.7% posterior probability and “Open” with a 18% probability (Figure 8-16).

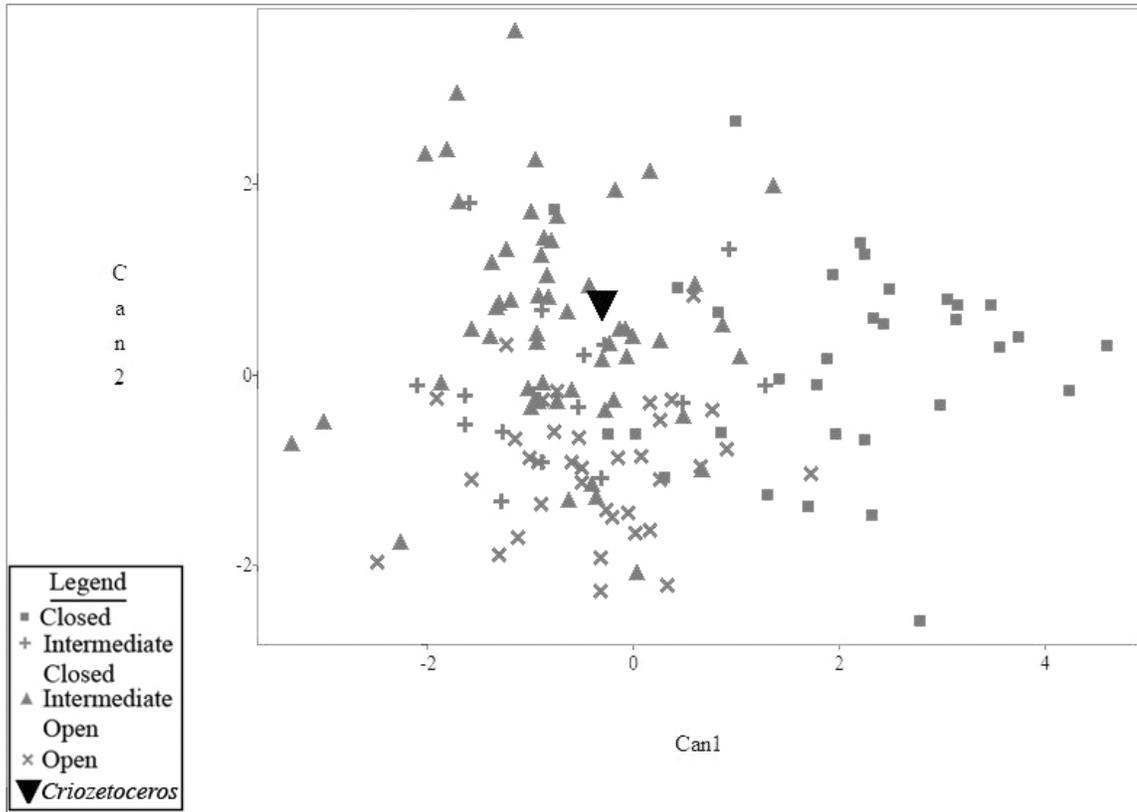


Figure 8-14 Plot of CV1 and CV2 for the habitat analysis of the tibial lateral plateau margin including all extant and the single St. Vallier specimen. This specimen, *Croizetoceros ramosus*, was classified as “Intermediate Open”.

3rd phalanx plantar margin

There were seven third phalanx specimens, all identified only to Cervidae, though they can probably be excluded from *Eucladoceros* based on their small size (Figure 8-17). Three specimens classified as “Mountain”, two as “Ecotone”, and one each as “Dry” and “Wet”, a distribution that can be seen in Figure 8-18. These results are not particularly conclusive, though they do suggest the presence of nearby mountains. St. Vallier is situated at ~200 meters (~656 feet) altitude in a non-mountainous area in the Massif Central of France. The closest mountains are the Monts du Vivarais, approximately 15 miles to the west/southwest, and the French Alps are located ~30 miles

to the east. Again, migrations between summer mountain habitats and winter habitats in lower, less snowy habitats are possible for these cervids, but this hypothesis requires more testing.

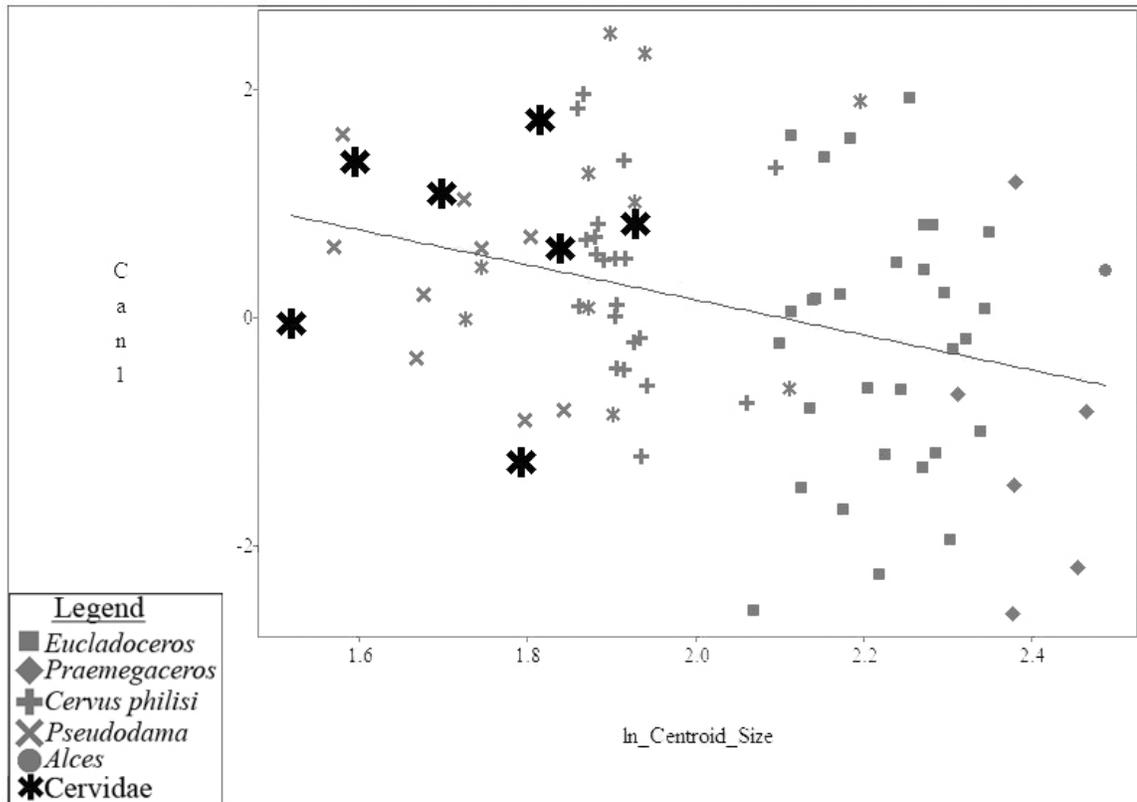


Figure 8-15 Plot of regressions of CV1 against lnCS in the third phalanx plantar margin analysis of habitat for the St. Vallier specimens. Though the specimens were identified only as Cervidae, they can likely be excluded from *Eucladoceros* due to their small size.

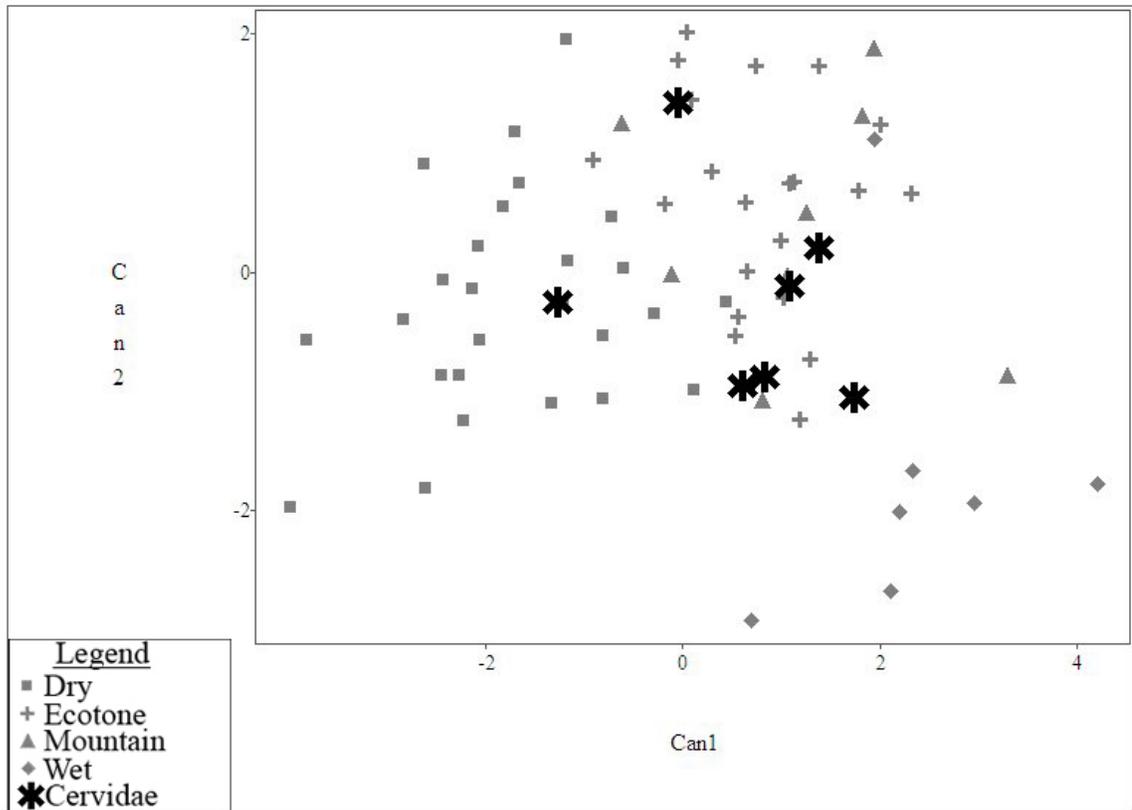


Figure 8-16 Plot of CV1 and CV2 for the substrate analysis of the third phalanx plantar margin including all extant and St. Vallier specimens. These specimens, identified only as Cervidae, were classified as all four substrate types.

Summary

Fossil specimens from three units of analysis (there were no femoral specimens) indicate that St. Vallier was mostly an open habitat. Interestingly, the *Eucladoceros ctenoides* specimens were almost always classified as “Intermediate Open”, thus differing from the more “Open” specimens from Valea Graunceanului, Romania.

This habitat reconstruction is consistent with previous studies, which have indicated a mosaic of warm open and wooded habitats along a lake or river (Valli 2004b, p. 337-8).

Senèze, France

Analyses of habitat

Calcaneus landmarks

Data for eight calcanei were collected from Senèze with one specimen labeled as *Alces* sp. (though it is likely *Libralces gallicus*, as the holotype of this species is from Senèze and the genus *Alces* did not appear until approximately 200 kyr), two specimens identified as *Eucladoceros ctenoides*, one specimen as *Cervus* sp., and four specimens as Cervidae (genus + species unknown). The four Cervidae specimens were classified into the “Open” habitat category with cross-validation, the *Cervus* sp. and the two *Eucladoceros* specimens were assigned to “Intermediate Open” and the *Alces* (*Libralces*) specimen to “Closed” (Figure 8-19). The latter result is surprising, as Geist (1998, p. 247) hypothesized that these deer were “fast runners in open, obstacle-strewn landscapes with firm ground”. Perhaps the operative phrase here is “obstacle-strewn”, which would require greater mobility at the hock joint than is selected for in more purely cursorial cervids. Similar to Valea Graunceanului and St. Vallier, the *Eucladoceros* specimens classified as “Intermediate Open”, and both had “Open” as their second most likely habitat category. All specimens scored toward the open end of the habitat score continuum, though as more closed than St. Vallier (Figure 8-20).

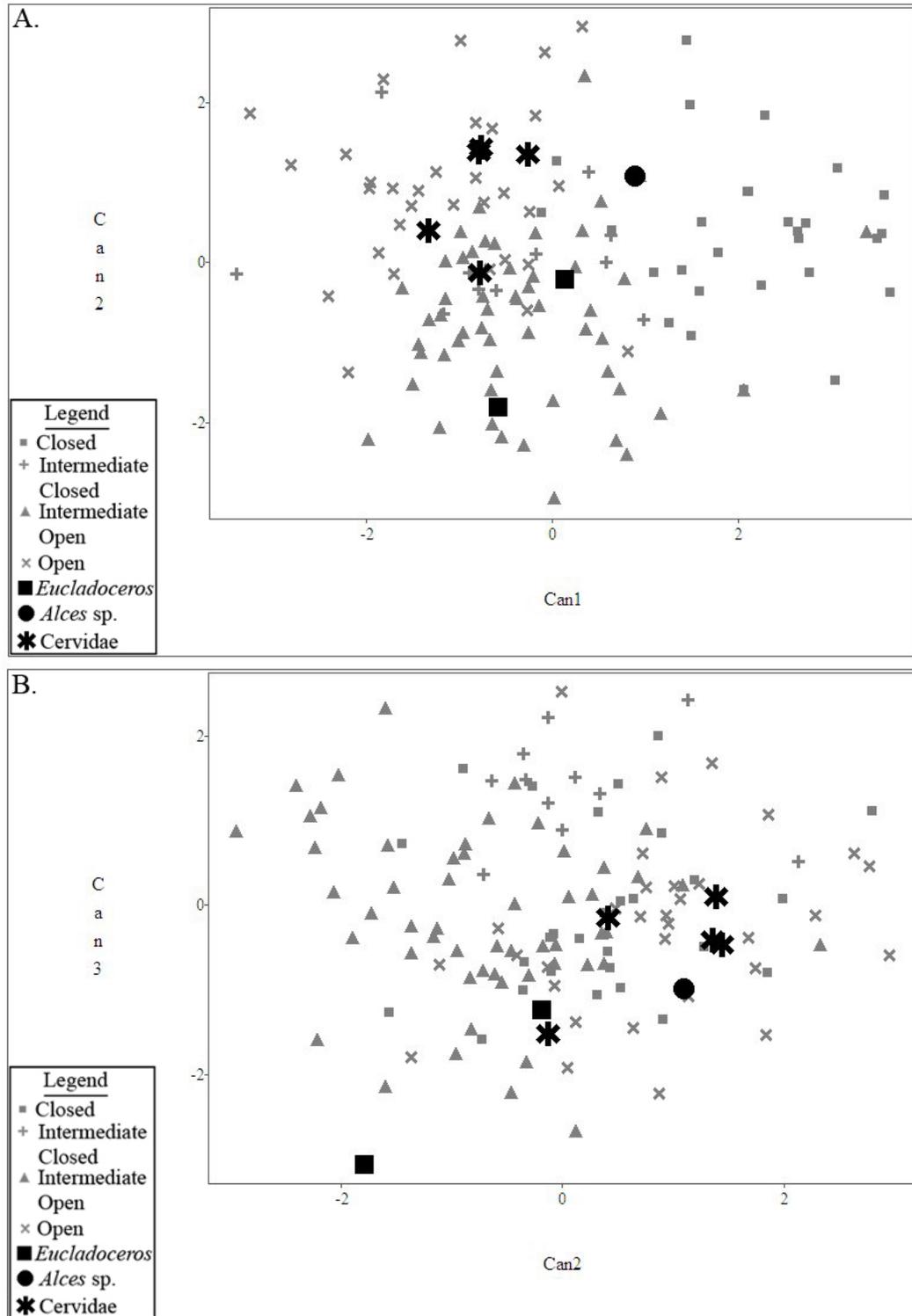


Figure 8-17 A: Plot of CV1 and CV2 for the habitat analysis of the calcaneus landmarks including all extant and Senèze specimens. B: Plot of CV2 and CV3 for the calcaneus landmarks for all extant and Senèze specimens. The Senèze specimens were classified as “Open” and “Intermediate Open”, except the *Alces* specimen, which was classified as “Closed”.

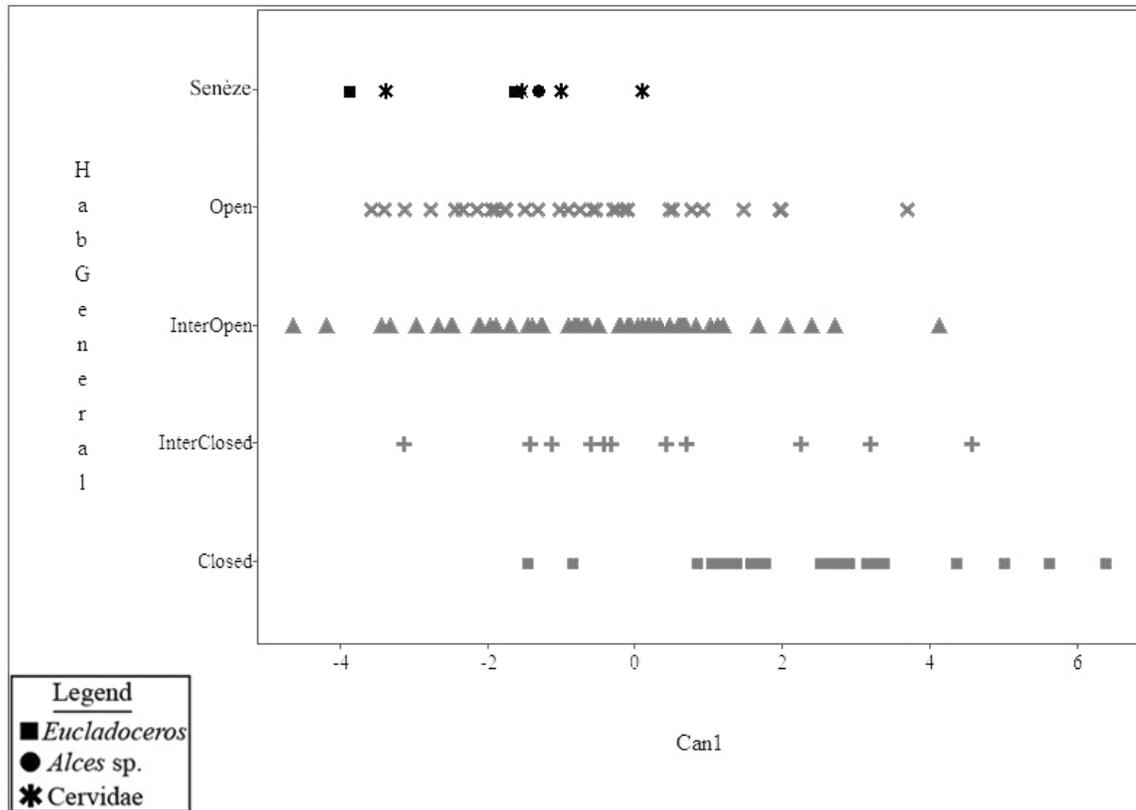


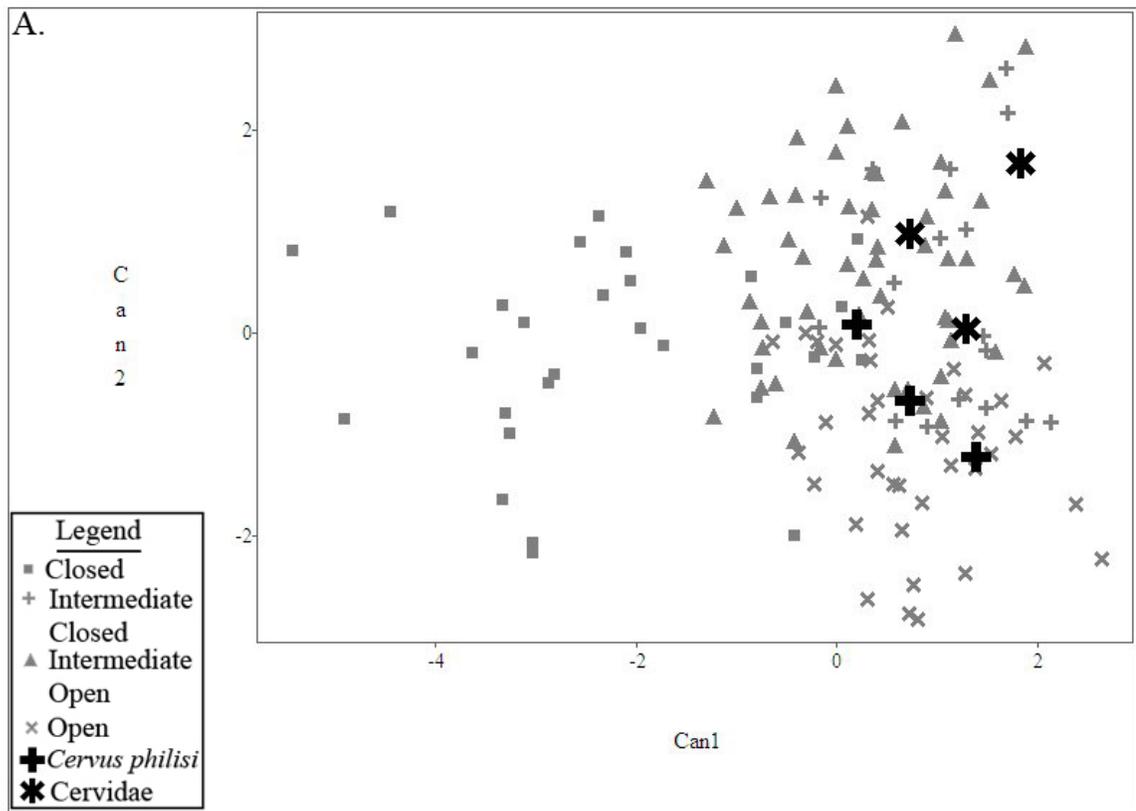
Figure 8-18 Habitat score plot for extant and Senèze calcaneal specimens, indicating a mostly “Open” adaptation.

When the canonical variates were plotted against lnCS, the specimen labeled as *Cervus* sp. grouped well within the *Eucladoceros* cluster, while the four Cervidae specimens formed a group with four other Cervidae specimens from St. Vallier and are labeled as Cervidae (m) in Appendix D. As was hypothesized for the specimens from St. Vallier, these specimens may belong to *Cervus philisi*.

Femoral medial patellar margin

In the CVA of extant cervid specimens, the first canonical variate separated the “Closed” specimens from non-“Closed” habitat groups. All six fossil specimens from Senèze cluster with the non-“Closed” groups. CV2 separated Intermediate “Open”

specimens from “Open” specimens, while CV3 separated the “Intermediate Closed” specimens from the other habitat types (see Figure 8-21). Along CV2, specimens of *Cervus philisi* and one Cervidae unknown specimen (FR655c) scored negatively and grouped with the “Open” specimens, while two Cervidae unknown specimens grouped with the “Intermediate Open” specimens. Along CV3, one Cervidae unknown (FR293) specimen and *Cervus philisi* specimen (FR654) grouped close to the “Intermediate Closed” specimens. Two specimens were classified into each non-“Closed” group; each category has one specimen of *Cervus philisi* and one of Cervidae unknown. With such a distribution, the only habitat reconstruction that can be made with this unit of analysis is that it was not “Closed”. This was also readily apparent with the distribution of specimens along the habitat score (Figure 8-22).



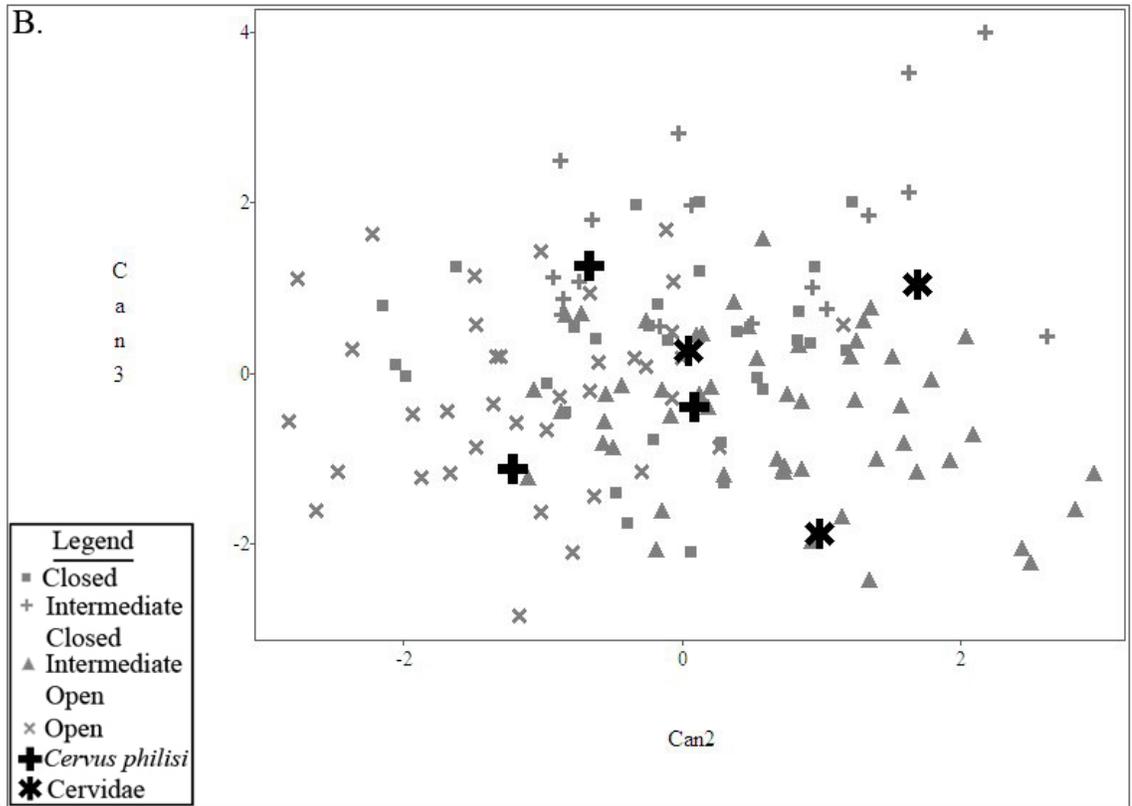


Figure 8-19 A: Plot of CV1 and CV2 for the habitat analysis of the femoral medial patellar margin including all extant and Senèze specimens. B: Plot of CV2 and CV3 for the femoral medial patellar margin for all extant and Senèze specimens. The Senèze specimens were classified as non-“Closed”.

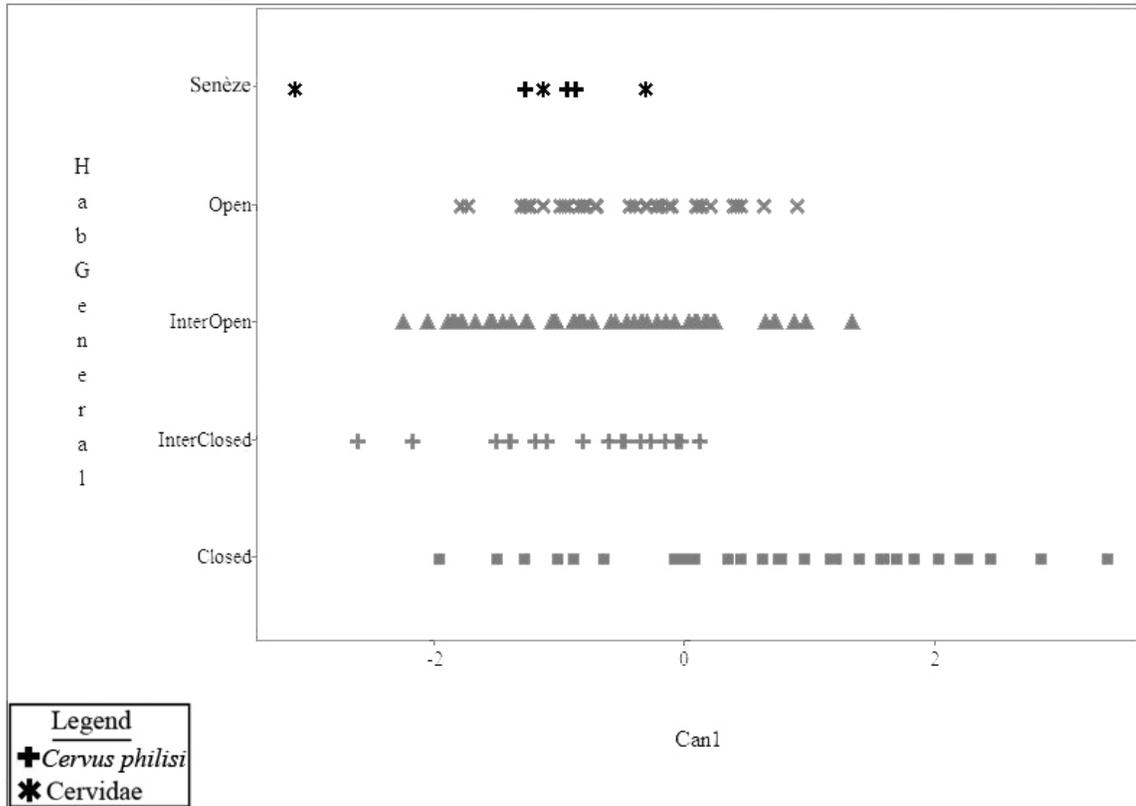


Figure 8-20 Habitat score plot for extant and Senèze femoral medial patellar margin specimens. All specimens fell within the non-“Closed” range along CV1.

Tibial lateral plateau margin

Five tibial specimens were available from Senèze; one identified as *Alces* (probably *Libralces gallicus*), one as *Cervus philisi*, and three as Cervidae (genus + species unknown). The *C. philisi* specimen was classified as “Open” with a high posterior probability (86%). All other specimens were classified as “Intermediate Open”, except one Cervidae specimen, which was classified as “Intermediate Closed” (Figure 8-23). These specimens had posterior probabilities of group membership ranging from 62-77%. All specimens scored with the non-“Closed” specimens in the habitat score (Figure 8-24).

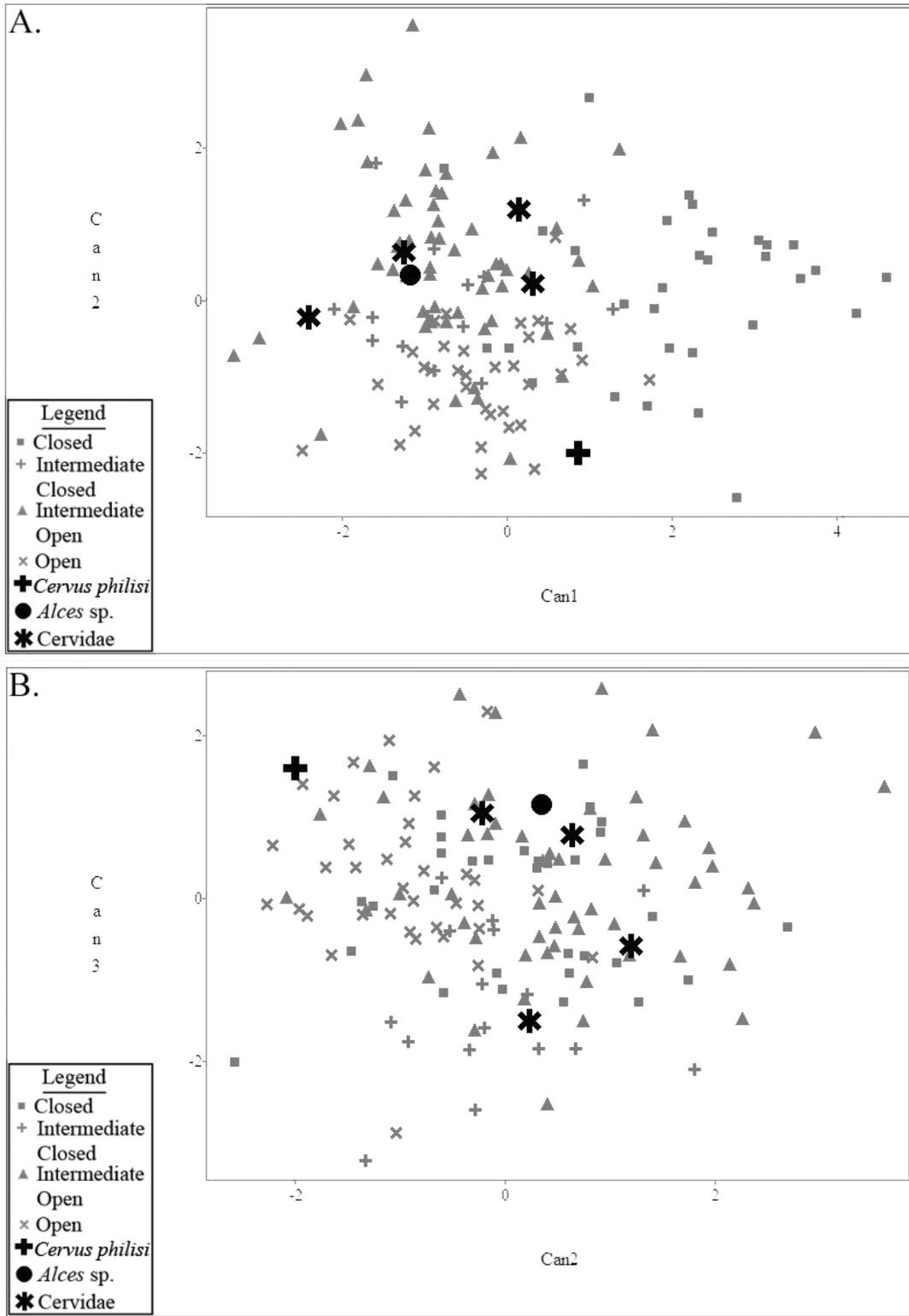


Figure 8-21 Plot of CV1 and CV2 for the habitat analysis of the tibial lateral plateau margin including all extant and Senèze specimens. All Senèze specimens were classified as non-“Closed”.

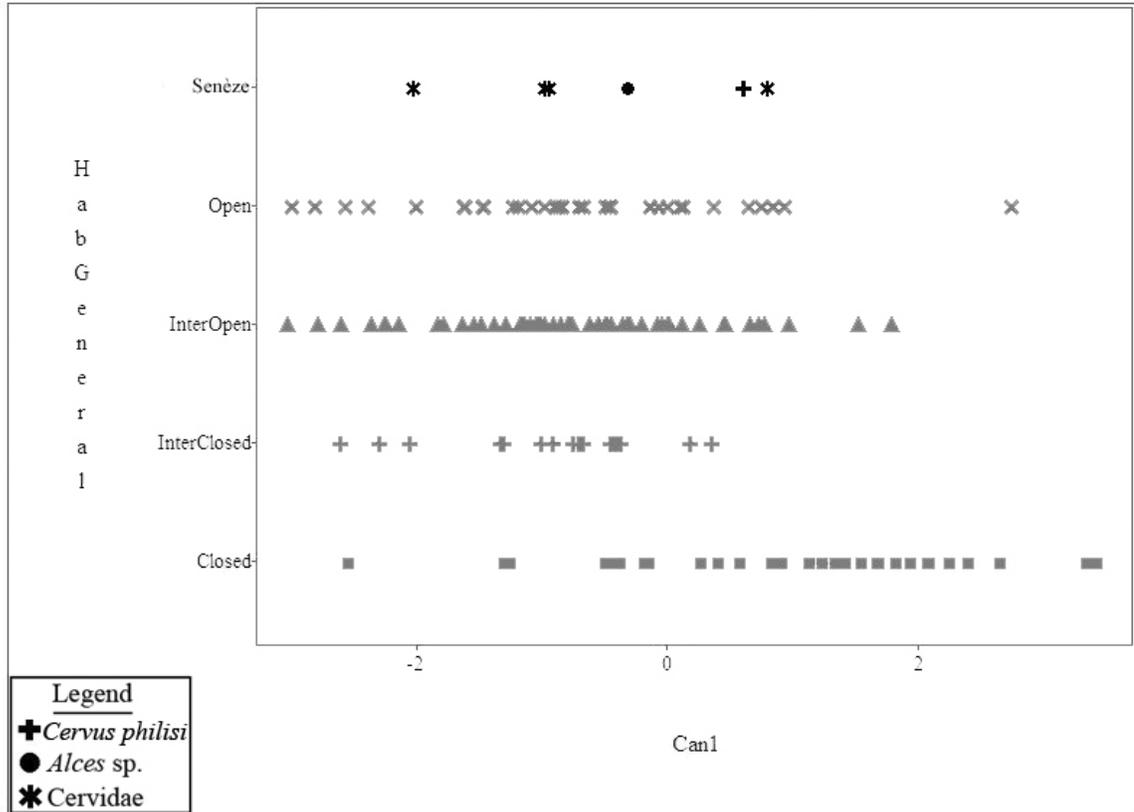


Figure 8-22 Habitat score plot for extant and Senèze tibial lateral plateau margin specimens. All specimens fell within the non-“Closed” range along CV1.

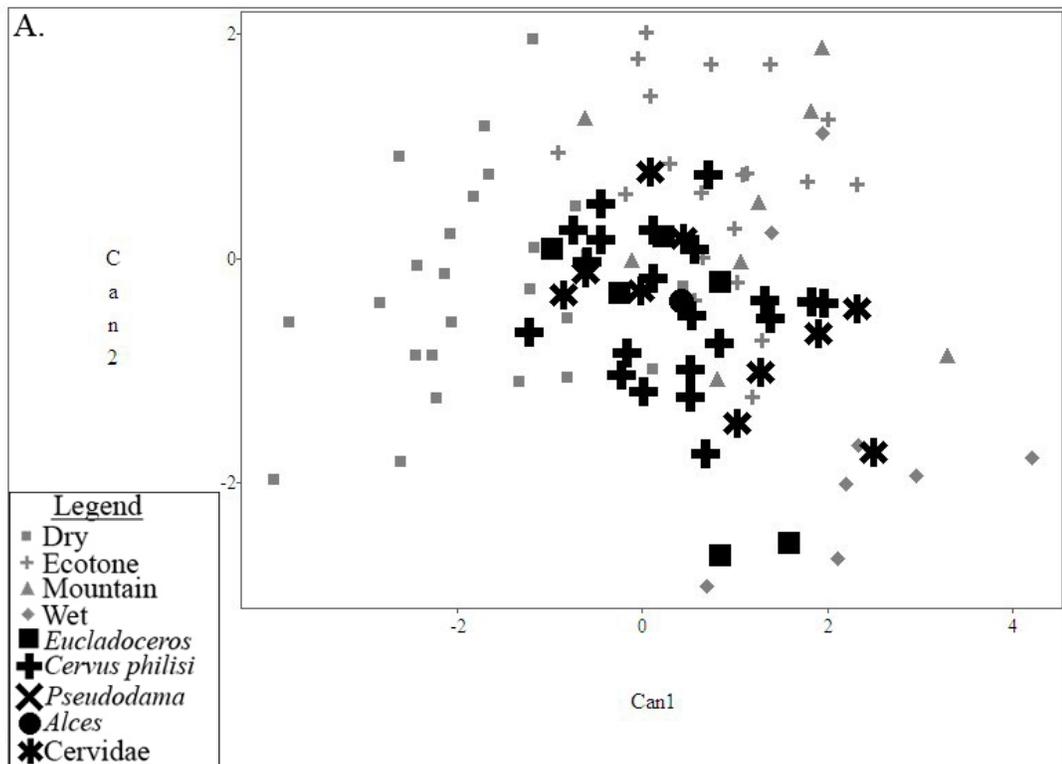
3rd phalanx plantar margin

Thirty-nine third phalangeal specimens were analyzed for Senèze: six were identified as *Eucladoceros ctenoides*, twenty-one as *Cervus philisi*, one as *Alces* (*Libralces*), one as *Cervus sp.*, and nine only as Cervidae. Eleven specimens were classified as “Open”, nine as “Ecotone”, eleven as “Mountain” and eight as “Wet”. Surprisingly, the group with the highest mean posterior probability was the “Wet” group (71.7%), means for the other substrate types ranged from 55.2% (“Dry”) to 66.2% (“Mountain”). Even more surprising is that two of the specimens classified as “Wet” were *Eucladoceros*, indicating that the French *Eucladoceros* specimens possibly

occupied a wetter habitat than the Romanian specimens, though it is still doubtful that they occupied closed habitats. Further, due to the similarity in shape between “Wet” and “Mountainous” morphotypes, it is possible that these specimens were misclassified.

Like St. Vallier, Senèze is in the Massif Central of France, but is located at a much higher elevation than St. Vallier (~600 meters or ~1980 feet). There are few nearby mountain ranges, though the Cantal Mountains are approximately 40 miles to the west/southwest and the Monts du Vivarais are found ~50 miles to east/southeast. These distances are likely to be too large to consider seasonal migrations of the cervids as an explanation for the presence of “Mountain” third phalanx morphotypes, which, in this context, are more likely reflect the local topography.

Figure 8-57 shows the distribution of Senèze specimens in canonical variates space.



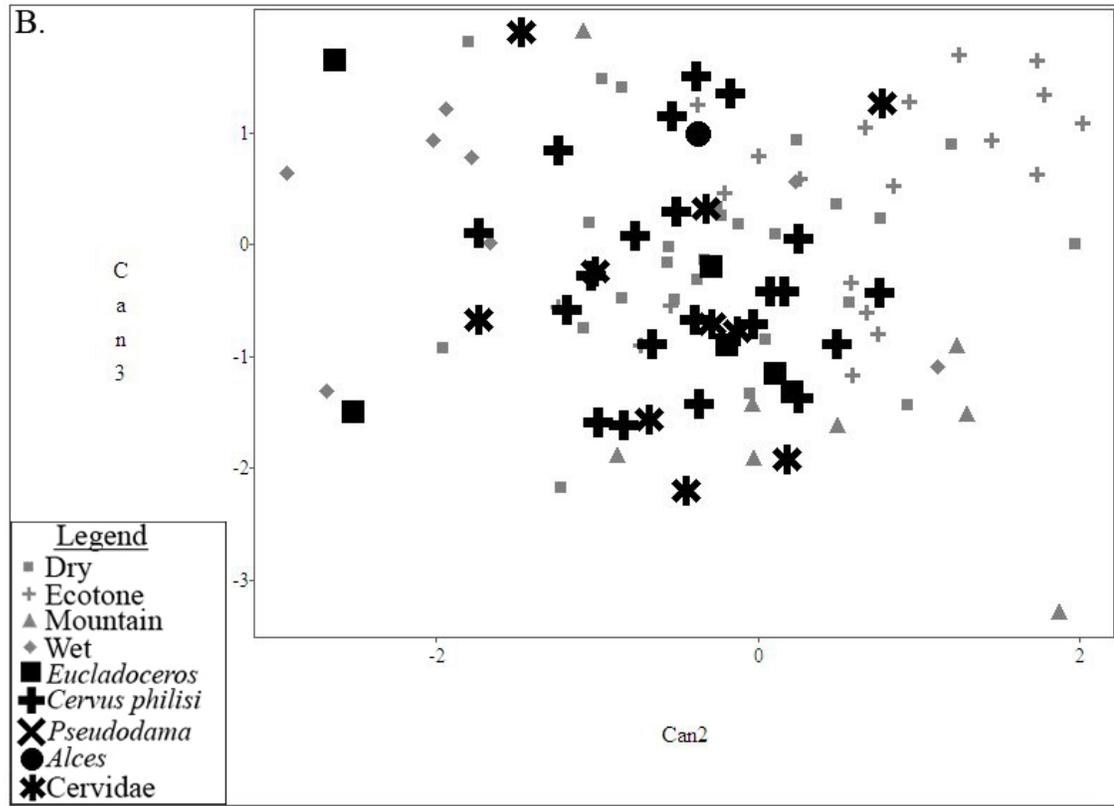


Figure 8-23 A: Plot of CV1 and CV2 for the substrate analysis of third phalanx plantar margin including all extant and Senèze specimens. B: Plot of CV2 and CV3 for the third phalanx plantar margin for all extant and Senèze specimens.

Two each of the *Eucladoceros ctenoides* third phalanx specimens were classified into “Dry”, “Mountain”, and “Wet” substrate categories. The twenty-one *Cervus philisi* specimens were classified to all four substrate groups (seven as “Dry”, seven to “Ecotone”, five to “Mountain”, and three to “Wet”). It should be noted that two specimens (FR694a and FR694h) identified as *Cervus philisi* more likely belong to *Eucladoceros*, as do the *Cervus* sp. (FR662a) and Cervidae (FRSenèze1) specimens. *Cervus philisi* specimens have a very narrow size range (Figure 8-26), and the four aforementioned specimens exceed this, falling more into the range of *Eucladoceros*. The two misidentified *Cervus philisi* specimens and FRSenèze1 all classified as “Dry”, while

FR662a was classified as “Mountain”. Most of the Cervidae (genus + species unknown) specimens grouped with *Cervus philisi* according to size, though two specimens were smaller (FR690b and FR697b). The Cervidae specimens also were classified at all four habitat types: two to “Dry”, one to “Ecotone”, four to “Mountain”, and three to “Wet”. The *Libralces* specimen was classified as “Ecotone”. These results suggest that Senèze mostly was not “Wet”, though specimens were fairly evenly distributed across all the other substrate categories, making a more specific habitat reconstruction based on the third phalanx plantar margin difficult.

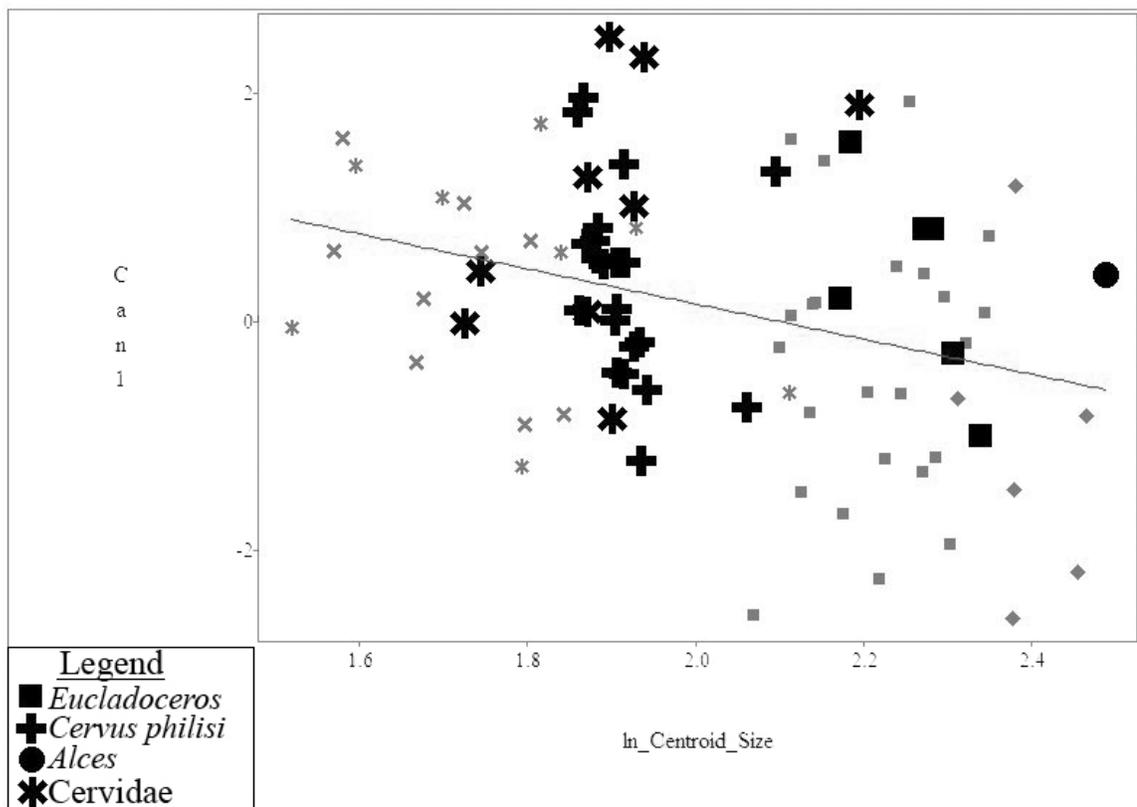


Figure 8-24 Plots of regressions of CV1 against lnCS for all extant and Senèze fossil specimens in the in the third phalanx analysis of substrate. *Eucladoceros* and *Cervus philisi* specimens are well separated along lnCS, indicating that the two specimens of *Cervus philisi* grouping closer to the *Eucladoceros* specimens may have been misidentified.

Summary

The habitat reconstruction for Senèze is broadly similar to that of St. Vallier. The calcanei indicated an open to intermediate open habitat. The femora indicate that the site was not closed. The tibiae were mostly “Intermediate Open”. Third phalangeal specimens were classified mostly to non-“Wet” substrate types, though many were either “Dry” or “Mountain”. Thus, the habitat of Senèze can be reconstructed as being similar to St. Vallier, though probably more closed.

‘Ubeidiya, Israel

Analyses of habitat

Calcaneus landmarks

Two specimens Belmaker’s (2006) pooled stratum II 23-25 were identified as *Pseudodama* sp. and *Praemegaceros verticornis*. The *Praemegaceros* specimen was classified as “Intermediate Open” by cross-validation and the *Pseudodama* specimen was classified as “Open”. Two other *Pseudodama* specimens, one each from pooled strata II 26-27 and III 11-13, also classified as “Open” specimens (Figure 8-27). All specimens scored at the “open” end of the habitat score.

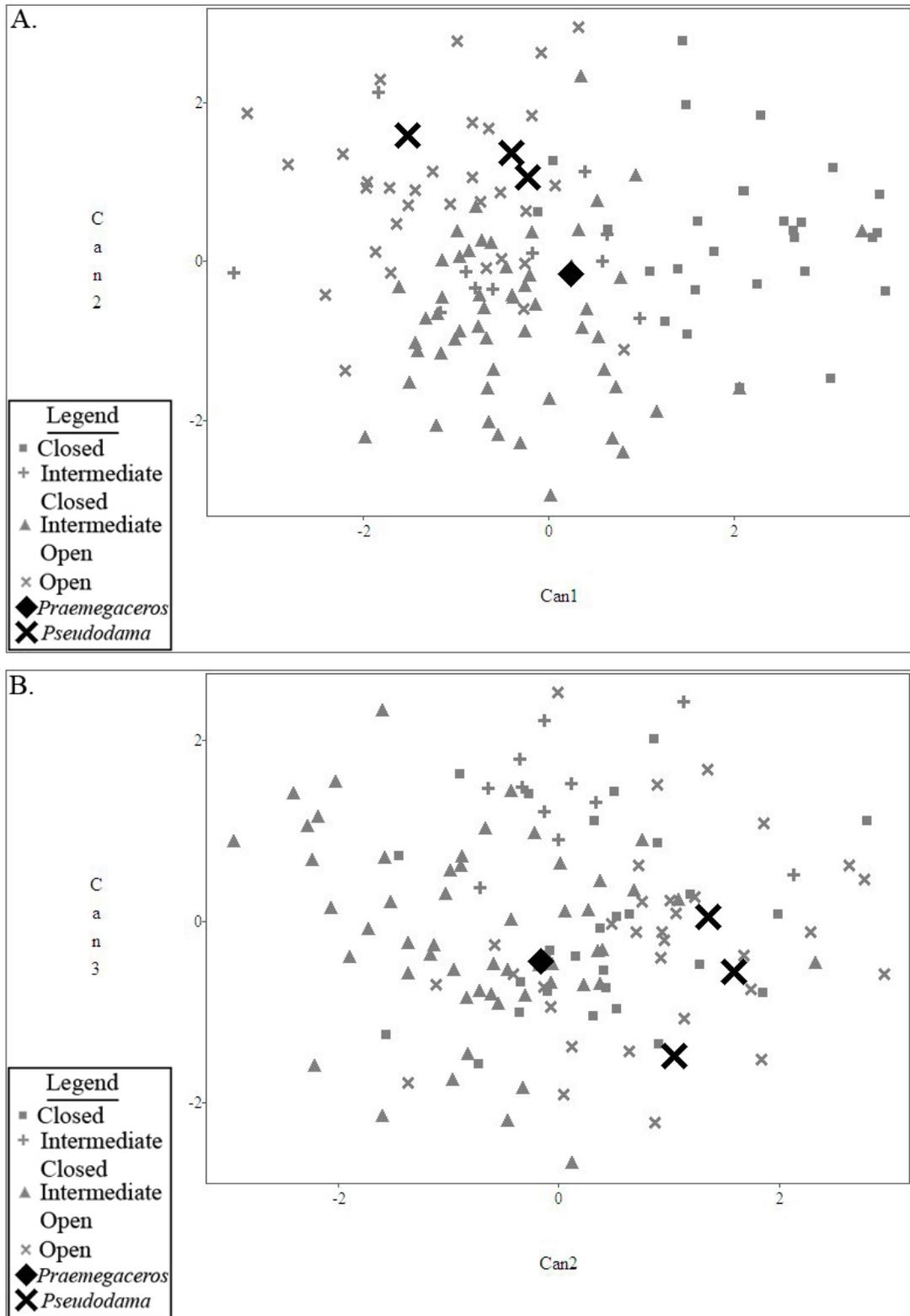


Figure 8-25 Plot of CV1 and CV2 for the habitat analysis of the calcaneus landmarks including all extant and ‘Ubeidiya specimens. The ‘Ubeidiya specimens were classified into “Open” and “Intermediate Open”.

Femoral medial patellar margin

The one femoral specimen from ‘Ubeidiya (pooled stratum II 26-27) included in this analysis was identified as *Capreolus* sp. This specimen was classified as an “Intermediate Open” specimen with 76.4% posterior probability (and probabilities of 10.1% for “Open”, 9% for “Intermediate Closed”, and 4.6% for “Closed”). This specimen groups in the middle of the distributions for “Intermediate Open” and *Capreolus capreolus* specimens, which are marked with black asterisks in Figure 8-28.

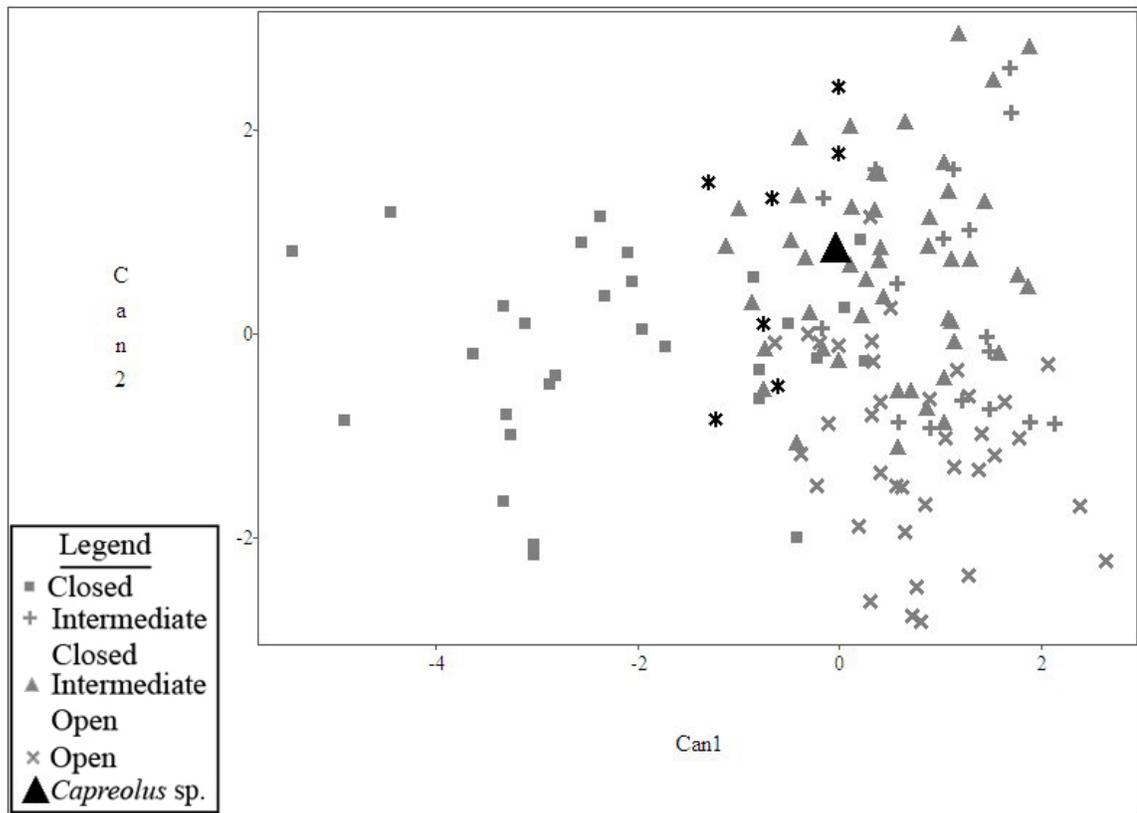


Figure 8-26 Plot of CV1 and CV2 for the habitat analysis of the medial femoral patellar margin including all extant and the single *Capreolus* sp. Specimen from ‘Ubeidiya. This specimen was classified as “Intermediate Open” and plots in the middle of the distribution of extant specimens of *Capreolus capreolus* (black asterisks).

Tibial lateral plateau margin

One tibial specimen was available from pooled stratum III 11-13, which was identified as *Praemegaceros verticornis*. This specimen was classified as “Intermediate Closed” with 56.5% likelihood, “Open” with 27.3% likelihood, and “Intermediate Open” with 16% likelihood (Figure 8-29).

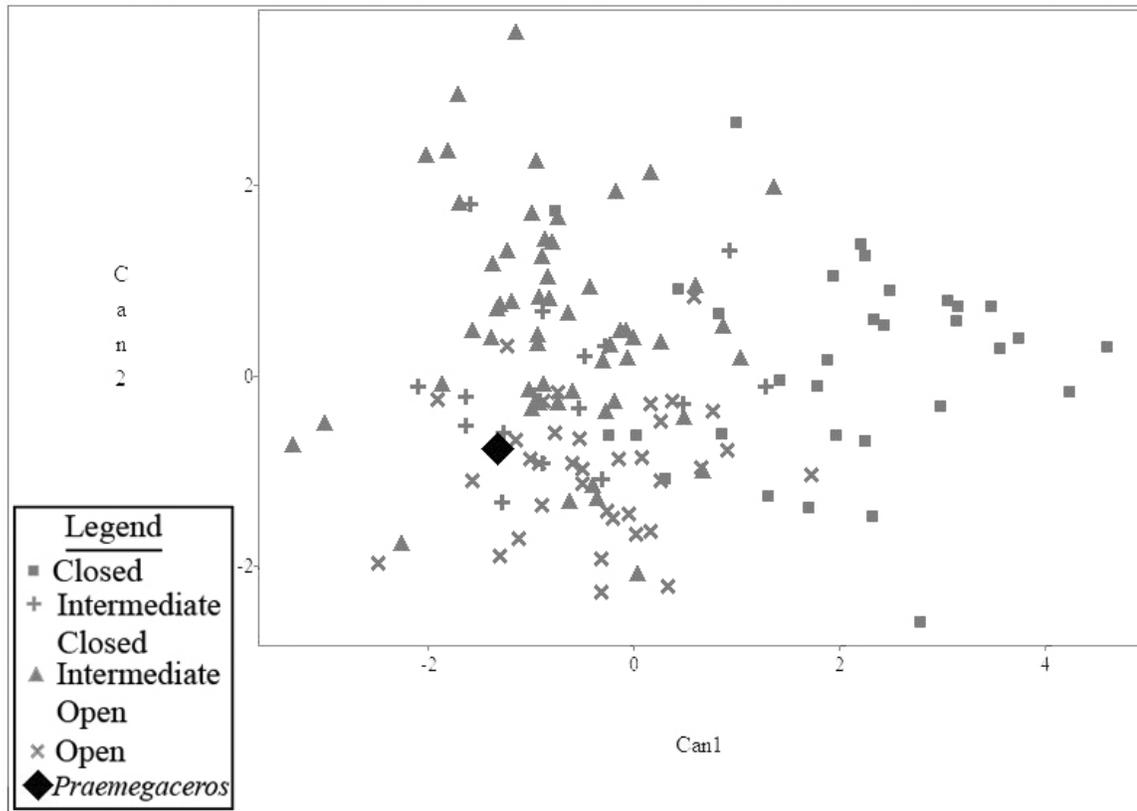
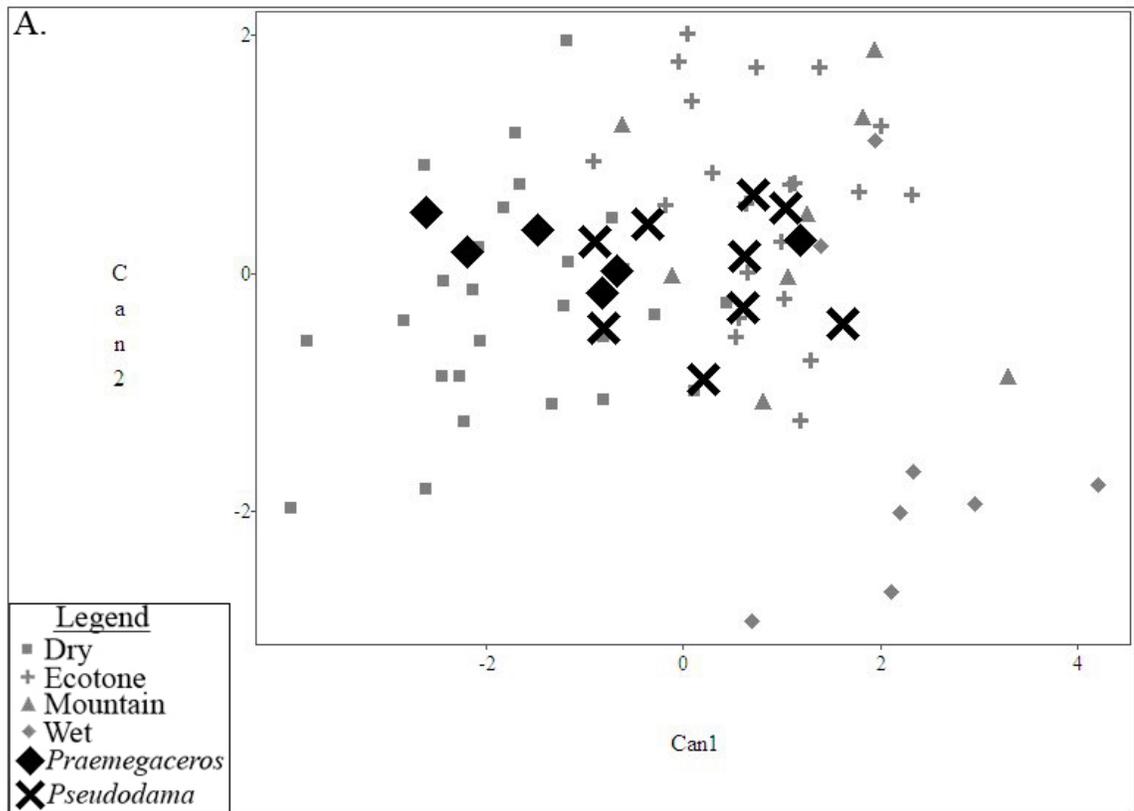


Figure 8-27 Plot of CV1 and CV2 for the habitat analysis of the tibial lateral plateau margin including all extant and the single *Praemegaceros* specimen from ‘Ubeidiya. This specimen was classified into “Intermediate Closed”.

3rd phalanx plantar margin

Sixteen third phalanx specimens were available from ‘Ubeidiya, including ten specimens identified as *Pseudodama* sp. and six as *Praemegoceros verticornis*. All *Praemegoceros* specimens classified as “Dry”, except one that classified as “Mountain”.

The *Pseudodama* specimens classified evenly across the substrate types (three specimens each), except “Wet”, to which only one *Pseudodama* specimen was classified. Specimen distribution in canonical variates space is illustrated in Figure 8-30.



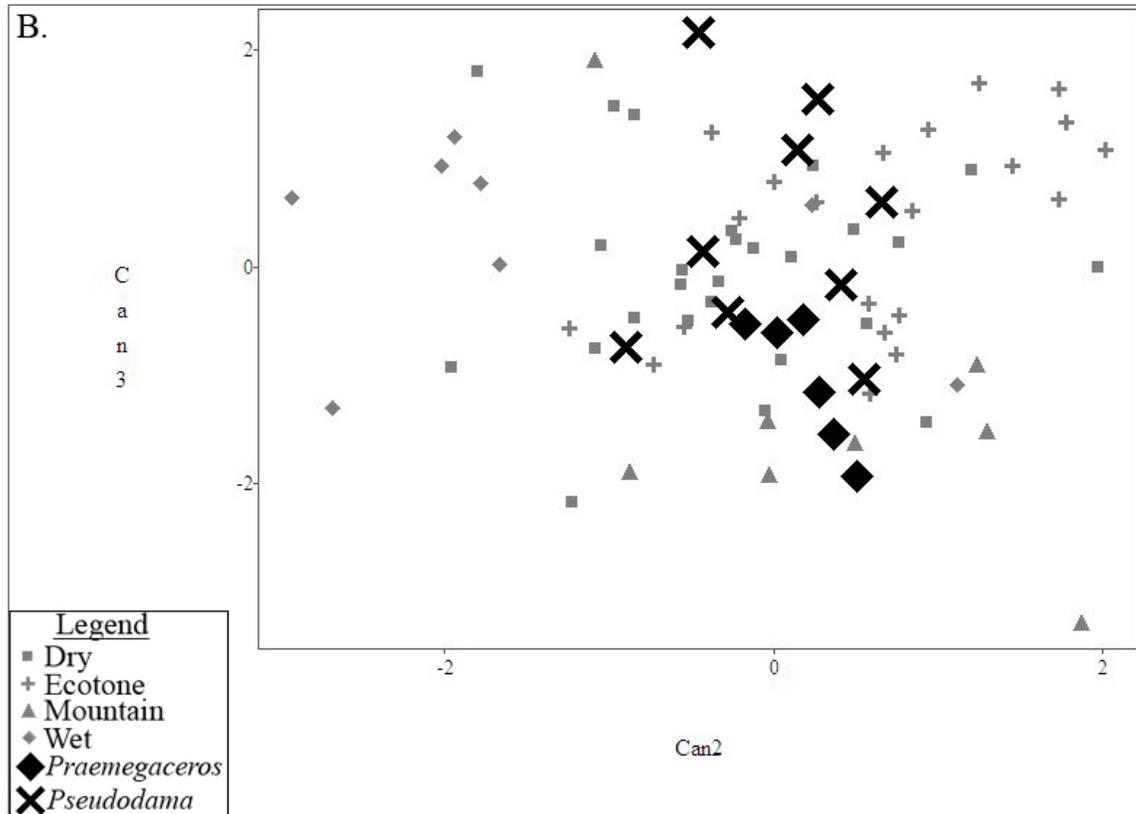


Figure 8-28 A: Plot of CV1 and CV2 for the substrate analysis of third phalanx plantar margin including all extant and ‘Ubeidiya specimens. B: Plot of CV2 and CV3 for the third phalanx plantar margin for all extant and ‘Ubeidiya specimens. The *Praemegaceros* specimens were classified into “Dry”, except one specimen, while the *Pseudodama* specimens were classified into all substrate types.

Summary

Sample sizes from each of the pooled strata were not large enough to make robust habitat reconstructions. However, Belmaker (2006) found that the fauna from ‘Ubeidiya fall into two faunal units: A, which includes pooled stratum III 11-13, and B, which includes all other pooled strata in this analysis. B was further broken down into B1, which includes II 23-25, III 21-22, and II 26-27, and B2, which includes II 37. Results are summarized here by these faunal units.

Specimens from faunal unit A were mostly classified as “Open” or “Intermediate Open”. The *Pseudodama* sp. specimens were classified as “Open” (calcaneus) and “Intermediate Open” (lateral tibial margin). There were three third phalanges; two classified as “Dry” (one each of *Pseudodama* sp. and *Praemegaceros verticornis*,) and one *Pseudodama* specimen classified as “Ecotone”. These results point to a dry and “Open” to “Intermediate Open” habitat for faunal unit A.

Specimens from faunal unit B1 included three cervid species: *Pseudodama* sp., *Capreolus* sp., and *Praemegaceros verticornis*. Two calcanei of *Pseudodama* sp. were classified as “Open”, while the single calcaneus of *Praemegaceros* classified as “Intermediate Open”. The one medial femoral margin of *Capreolus* sp. was also classified as “Intermediate Open”. Of the eight third phalanges of *Pseudodama*, three were classified as “Mountain”, two each as “Dry” and “Ecotone” and one as “Wet”. One of each of the two *Praemegaceros* specimens were classified into the “Mountain” and “Dry” categories. Like *Eucladoceros*, *Pseudodama* presented a mosaic of open and closed morphologies- its calcanei classified as “Open” while its third phalanges classified across all substrate types. *Praemegaceros* and *Capreolus* both fall into the “Intermediate” categories, with *Praemegaceros* further indicating a “Dry” substrate. Faunal unit B2 was only represented by two third phalangeal specimens, both identified as *Praemegaceros*, and both classified as “Dry”. Results for faunal unit B are broadly similar to those for faunal unit A, that is, “Open” to “Intermediate Open”.

Chapter 9: Discussion and conclusion

Introduction

There were four main goals in this dissertation: 1) to establish ecomorphological methods for the family Cervidae, 2) to introduce geometric morphometrics to studies of ecomorphology in paleoanthropology, 3) to expand ecomorphological methods that can be conducted upon incomplete bones, and 4) to apply the methods introduced here to four Eurasian fossil sites. This chapter discusses the success of these goals, evaluates the classification power of each unit of analysis, and relates the results found here to other ecomorphological studies. Variation in the units of analysis examined here is examined in terms of how they reflect cervid locomotor behavior. The contributions of the habitat reconstructions produced here are discussed for the four fossil sites examined. Finally, future directions for this analysis are discussed.

Extant results

Since the main goal of this dissertation was to provide ecomorphological methods to reconstruct past habitats using Cervidae remains, it is important to consider how successful these methods were on specimens of known habitat before discussing the implications for fossil specimens. The main way to assess how well a unit of analysis will perform at classifying *fossils* into habitat types is to examine how well the predictor variables perform at reclassifying *extant* specimens of known habitat type into that habitat type. There are several ways in which to do this, such as resubstitution and cross-validation (as discussed in Chapters 3 and 6). In evaluating each of the units of analysis for effectiveness in this section, only cross-validation results are discussed, as they are hypothesized to be better predictions of how well the analysis will place fossil specimens

since they are calculated by removing each specimen from the analysis before the canonical variates are calculated. Resubstitution results will only be discussed in comparisons to other ecomorphological studies, as this is the method of reclassification reported for most studies.

Of the four units of analysis in this study, the calcaneus landmarks provided the best proxy for habitat type with 61.1% mean correct cross-validation. Permutation tests indicated that the habitat group centroids were significantly different at (minimally) $p = 0.005$. The discriminant functions were better at reclassifying specimens into the “Closed” and “Open” habitat categories than into the two “Intermediate” categories, though this result was not surprising, since cervids in the “Intermediate” categories have to maintain adaptations to both more open and more closed habitats. The calcaneus landmarks analysis was the only unit of analysis for which the extant specimens scored along a continuum from “Open” to “Closed” with the habitat score. Calcaneal morphology provides a good proxy for reconstructing past habitats.

Habitat analyses of the femoral medial patellar margin and the tibial lateral plateau margin were broadly similar in that they both performed well at separating “Closed” specimens from non-“Closed” specimens, though the tibial lateral plateau margin had a higher mean correct cross-validation rate (49.8% versus 42.1%). The habitat score for both units of analysis performed well at reclassifying the training specimens, but when the rest of the specimens were scored, specimens from the two “Intermediate” habitat categories completely overlapped with the “Open” specimens (Figures 7-11, 7-18). Kappelman (1991, p. 114) found a similar pattern in his study of the femur in that intermediate specimens were more similar to open-adapted bovids than

closed-adapted bovids. Morphological variation in these two units of analysis is more discrete than continuous.

As discussed in Chapter 7, the third phalanx is a proxy for substrate resistivity rather than vegetational (habitat) structure. With substrate type as the classifying variable, the correct mean cross-validation rate for the four groups was 66.3%. Specimens in the “Dry” and “Wet” categories had the highest cross-validation rates (73.1% and 75%, respectively), while the “Ecotone” and “Mountain” specimens were lower (54.6% and 62.5%, respectively). Specimens misclassified in the “Ecotone” category were mainly *Odocoileus virginianus*, which was often classified into “Mountain”, perhaps reflecting its habitat plasticity or recent shared ancestry with *Odocoileus hemionus*. Specimens in the four substrate groups formed a continuum from “Dry” to “Wet”. Thus, the third phalanx can be considered a good proxy for substrate type.

The results found here are comparable to results found in other (bovid) ecomorphological studies. Since most of these studies reported results for mean correct reclassification with resubstitution, results for this study will also be discussed in terms of this reclassification method in this section. The mean correct resubstitution results for the habitat analyses were fairly high for all units of analysis (71.8-79.1%). However, DeGusta & Vrba (2005, p. 1110) suggest that “the accuracy of a discriminant function must be considered relative to the number of groups it is attempting to discriminate between” and recommend examining the accuracy of the function relative to random assignment to a habitat category. In other words, they ask, how much better does the analysis perform at assigning a specimen to the correct habitat category than could be achieved by chance alone? To calculate this, the resubstitution result is divided by the

prior probability of group membership, or the random chance of classification into the correct habitat (henceforth referred to as ‘better than chance’). For example, in a four-group classification system, the prior probability of classifying a specimen into the correct habitat by chance alone is one out of four or 0.25. While it is instructive to know how much better the function performs than by random chance, it is not clear that this is the best way in which to report results. For all of the published ecomorphological studies to date, the number of habitat categories used was found to be significantly correlated to both the mean correct resubstitution percentage and the ‘better than chance’ result (see Table 9-1). Specifically, higher numbers of habitat categories incurred lower mean correct resubstitution results, but higher ‘better than chance’ results. However, only the ‘better than chance’ results were correlated to the number of variables used in the study. With higher numbers of variables, the ‘better than chance’ results increased. Thus, resubstitution is considered here to be a better way to report results, since it is not correlated to the number of variables used. Neither resubstitution nor ‘better than chance’ were correlated to the number of specimens in the study across the published ecomorphological studies.

Published Studies				Published studies + this study			
Response	Predictor	R ²	p-value	Response	Predictor	R ²	p-value
Resub	# Hab. Types	0.5803	< 0.0001	Resub	# Hab. Types	0.6004	< 0.0001
	n	0.0474	0.166		n	0.0067	0.5879
	# Variables	0.0007	0.598		# Variables	0.0329	0.2277
	x BTC	0.0149	0.4406		x BTC	0.0092	0.5269
x BTC	# Hab. Types	0.2846	0.0003	x BTC	# Hab. Types	0.2908	0.0002
	n	0.0042	0.6842		n	0.00009	0.9501
	# Variables	0.3783	< 0.0001		# Variables	0.0272	0.2732

Table 9-1 Regression results for mean correct resubstitution percentages and ‘better than chance’ (x BTC) against the number of habitat type categories (# Hab. Types), sample size (n), and the number of variables (# Variables) in published studies and for published studies plus this study. Significant correlations are highlighted in gray.

When the results for this study were included in the regressions discussed above for published ecomorphological studies, the number of habitat categories was still found to be significantly correlated to mean correct resubstitution and ‘better than chance’ results, but the correlation between the number of variables used in the study and the ‘better than chance’ result became non-significant. This was due to the high number of variables in this study, which represents the difference between using linear measurements (2-15 measurements in the published studies) and geometric morphometric data (13-44 PCs used for various units of analysis). Correct mean resubstitution results were not significantly correlated to the number of variables used in the study, despite the high number of variables used here.

An advantage of using geometric morphometric data in an ecomorphological analysis is that all the interrelationships of data (coordinates) are maintained and can be used to create visualizations of the differences between habitat types. Visualizing the differences in adaptations led to a better understanding of the nature of variation in each of the units of analysis. For example, in the habitat analysis of the femoral medial patellar margin, based on the low cross-validation rates for each non-“Closed” habitat type, one might just accept that this unit of analysis simply performs poorly at reclassifying specimens into known habitat type and is thus a poor proxy for paleohabitats. Instead, by visualizing the mean configurations for each habitat type (Figure 7-10), it was learned that variation in shape for the medial patellar margin is discontinuous in nature. That is, “Closed” specimens have a more circular margin and non-“Closed” specimens have a more elliptical margin. Indeed, when CVA was performed on “Closed” versus non-“Closed” specimens, the reclassification rates (for both methods) were high- 69% for

“Closed” and 82.4% for the non-“Closed” group. Further, the GM data in this study can be used to create visualization of the shape differences associated with adaptations to different habitats. The vector of shape change along the canonical variate that separated “Open” and “Closed” specimens in the habitat scores analyses, for example, was multiplied several times before being added to and subtracted from the consensus configuration for all specimens. This permitted the differences between these two habitat types to be more easily identified, allowing for better understanding of how shape varies with habitat and better hypothesis generation. The following is a series of hypotheses regarding what the morphological variation in the units of analysis in this study imply for cervid locomotion.

Implications for cervid locomotor behavior

Visualizations indicated that the rest angle of the calcaneus prior to limb extension and mobility at the hock joint are two main differentiations between “Open” and “Closed” specimens (Figure 7-3). The visualizations for “Open” and “Closed” specimens are shown in Figure 9-1 in their approximate rest orientations. In “Open” specimens (Figure 9-1A), the cubonavicular articular facet of the calcaneus is oriented more anteriorly, which creates a more vertically-oriented calcaneus, while the cubonavicular articular facet in “Closed” specimens (Figure 9-1B) is more inferiorly-oriented, creating a more obliquely-oriented calcaneus. A more vertically oriented calcaneus shortens the distance that the calcaneus travels when the gastrocnemius is contracted, providing a quicker, but less powerful force. Cursorial (open-adapted) cervids place more emphasis on moving quickly through each pace cycle than creating powerful forces with each cycle. This is what is seen in *Rangifer tarandus*, the most cursorial

extant cervid, which has four or five pace cycles per second during its gallop (Geist 1998, p. 289). The more obliquely oriented calcaneus of closed-adapted cervids moves the insertion of the gastrocnemius away from its origin on the femur and thus enables a more powerful but slower movement. This is advantageous for saltatorial (closed-adapted) cervids that escape predators. Saltatorial locomotion reduces the number of pace cycles per second, but the cervid is propelled further with each pace cycle than it is in a gallop. Saltatorial locomotion also allows for rapid changes in direction, which is necessary for closed-adapted cervids that place obstacles between themselves and their predators while being pursued. Rapidly changing direction requires more mobility at the hock joint, and closed-adapted cervids have wider sustentaculum tali than open-adapted cervids, which allows for more mobility between the calcaneus and astragalus.

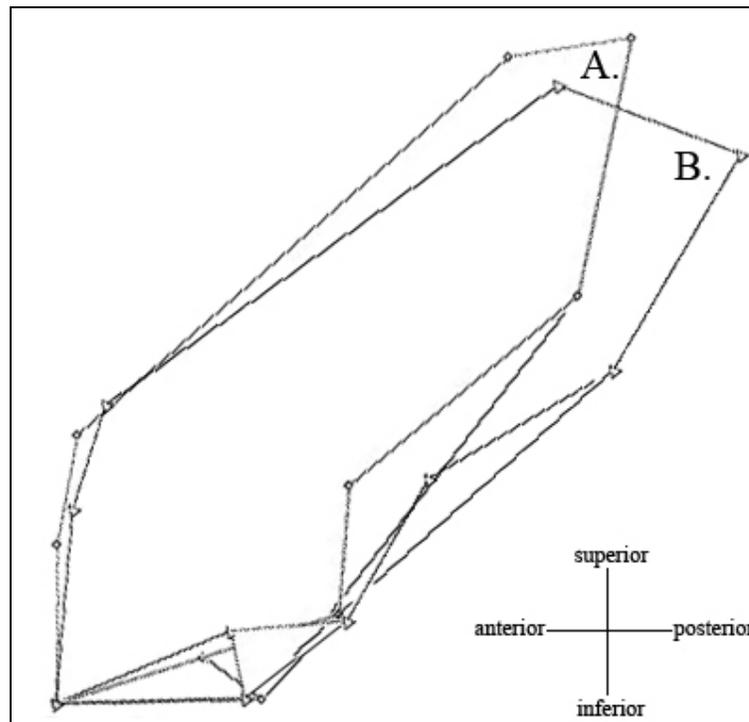


Figure 9-1 Visualizations for the calcaneus of “Open” (A) and “Closed” cervids in the rest position (viewed medially) prior to the contraction of the gastrocnemius, demonstrating the more vertical position for “Open” specimens and the more oblique position for “Closed” specimens.

In the case of the tibial lateral plateau, “Closed” cervids have a more rounded and flatter joint surface, which allows for greater mobility. Cervids from the other habitat types have more narrow and deeper joint surfaces, which restrict movement to the parasagittal plane and provide a more stable joint surface. The femoral medial patellar margins of “Open” cervids are more elliptical than those of “Closed” cervids, which provides a greater lever arm for the quadriceps muscles (Kappelman 1988, p. 127). For both of these units of analysis, morphological variation is not continuous from “Open” to “Closed”, as was found for the calcaneus. Instead, variation in the tibial lateral plateau margin and the femoral medial patellar margin is of a discrete nature, with “Closed” species expressing one variant and non-“Closed” species another. Knee morphology associated with “Closed” species is specific to closed habitats, while the morphology associated with non-“Closed” species is similar across species adapted to habitats ranging from woodlands to open grasslands. That is, cervid species in “Closed” habitats are ‘locked’ into closed habitats, while species in non-“Closed” habitats express morphology that is applicable to a wider range of habitats. This implies that “Closed” species rarely venture into more open habitats, as their morphology makes escaping predators in more open habitats very difficult. Thus, the presence of “Closed” specimens in an assemblage is a very good indicator of closed conditions.

Unlike the other units of analysis in this study, the plantar margin of the third phalanx does not reflect vegetation structure, but instead is a proxy for the resistivity of the substrate (how much ‘give’ it has). Cervids that locomote on dry substrates (including open, woodland, temperate forest, and tall grass habitats) have wide, blocky third phalanges with little anterior tapering (Figure 7-28). The third phalanges of the

“Mountain” and “Wet” species are similar in morphology (Figure 7-24), which reflects locomotion on “difficult ground” (Köhler 1993, p. 22). Cervids in “Wet” habitats splay their phalanges at the metatarsal-phalangeal joints to increase the support area while moving across wet and slippery substrates (Köhler 1993). Cervids in rocky and mountainous habitats also splay their third phalanges, though they do so at the joint of the second and third phalanges. Splaying only the distal phalanges allows these cervids to increase stability at the metatarsal-phalangeal joint, but still use the splayed third phalanges as a brake on inclined surfaces (Köhler 1993). Species living in ecotonal habitats have moderately tapered third phalanges, which are wide in the posterior aspect. This morphology is likely a compromise between locomoting on wet and dry substrates.

Putting together the biomechanical implications of the units of analysis discussed above (summarized in Table 9-2), “Open” cervids have a calcaneus that allows for rapid movement through each pace cycle, a tibial lateral plateau surface that restricts movement to the parasagittal plane, and a femoral medial patellar margin that allows for greater torque at the knee. These observations fit what would be expected of a cursorial animal: rapid pace cycling, joint stability, and enhanced power generation. “Closed” cervids have a calcaneus that allows for more powerful extension of the lower limb, but slower pace cycling, a tibial lateral plateau that allows for enhanced mobility, and femoral medial patellar margin without enhanced increased torque at the knee but that allows for quicker recovery time between flexion and extension. Powerful extension of the lower limb and joint mobility are necessary for closed-adapted cervids (as described above), and quicker recovery time between flexion and extension allows the “Closed”

cervids to quickly bring their rearlimbs back underneath their body after the long extended suspension phase that is typical of saltatorial locomotion (Hildebrand 1985).

In the third phalanx, morphology does not vary on the “Open” versus “Closed” spectrum described above, but instead varies with how wet or dry the substrate is. Cervids living on hard ground have wide and non-tapering third phalanges that do not splay. Cervids living on wet or rocky substrates splay their third phalanges, which are thinner and more tapered, in order to increase stability and to act as a brake. The substrate categories for the third phalanx do not directly coincide with the divisions by habitat categories for the other three units of analysis, but instead can provide more specificity to the overall habitat reconstruction for a site when used in concert with the other ecomorphological proxies introduced here.

The combination of the four morphological units of analysis introduced here allow for a better understanding of cervid locomotion associated with habitat types, and thus for the habitat type, itself. The femoral medial patellar margin and the tibial lateral plateau margin are indicative of the presence of either “Closed” or non-“Closed” conditions. Calcaneal morphology allows for further distinction into four habitat types- “Closed”, “Intermediate Closed”, “Intermediate Open”, and “Open”. Finally, the third phalanx plantar margin adds another layer of detail by reflecting the moisture content and ‘difficulty’ of the substrate, that is, whether the substrate was “Wet”, “Dry”, “Mountainous”, or in between (“Ecotone”). Used in concert, these four ecomorphological proxies allow for reliable habitat reconstructions.

Open	Closed
<p>Calcaneus:</p> <ul style="list-style-type: none"> -anteriorly-oriented cubonavicular articular facet -vertically-oriented calcaneus for quick but less powerful force (cursorial) -narrow sustentaculum tali, restricting movement to the parasagittal plane, increasing joint stability -small enthesis on calcaneal tuber 	<p>Calcaneus:</p> <ul style="list-style-type: none"> -inferiorly-oriented cubonavicular facet -obliquely-oriented calcaneus for powerful but less rapid movement (saltatorial) -wide sustentaculum tali allows for increased movement at hock joint -large enthesis on calcaneal tuber
<p>Femoral medial patellar margin:</p> <ul style="list-style-type: none"> -long anterior-posteriorly, more elliptical in shape -increases torque generated at knee 	<p>Femoral medial patellar margin:</p> <ul style="list-style-type: none"> -short anterior-posteriorly, more circular in shape -quicker recovery time after suspended extension
<p>Tibial lateral plateau margin:</p> <ul style="list-style-type: none"> -narrow and deeper with marked tapering medially -limits motion to parasagittal plane, increasing joint stability 	<p>Tibial lateral plateau margin:</p> <ul style="list-style-type: none"> -wide, flatter, and more round in shape -allows for increased movement at knee joint
Dry	Wet
<p>Third phalanx plantar margin:</p> <ul style="list-style-type: none"> -wide and flat with little anterior tapering -increases substrate contact surface without splaying the phalanges (stable joint surface) 	<p>Third phalanx plantar margin:</p> <ul style="list-style-type: none"> -narrow and concaved on the plantar surface with marked anterior tapering -the phalanges are splayed to increase contact with slippery substrates

Table 9-2: Summary of the morphological characters and functional significance associated with adaptations to “Open” and “Closed” habitat types and “Dry” and “Wet” substrates for the four units of analysis in this study.

Fossil results

Valea Graunceanului, Romania

All specimens from Valea Graunceanului, Romania included in this analysis were assigned to *Eucladoceros* sp. (Rădulescu *et al.* 2003). *Eucladoceros* had several features that indicate it was open-adapted, including large and ornate antlers (Geist 1998, p. 85), a mesowear signal indicative of grazing (Kaiser & Croitor 2004, p. 669), and a laterally-expanded femoral head (see Figure 4-2). The calcaneus landmarks analysis of *Eucladoceros* specimens from Valea Graunceanului indicated an “Open” habitat. The third phalanges in the Valea Graunceanului assemblage were classified evenly into “Dry” and “Mountain” substrates; both with medium-high mean posterior probabilities (81.7% and 79%, respectively).. The Romanian *Eucladoceros* were adapted to open habitats.

These results, in addition to the lacustrine depositional environment of this assemblage (Samson & Rădulescu 1973, Necrasov *et al.* 1961), indicate that the area around Valea Graunceanului was open with near-by water resources and possibly mountains.

St. Vallier, France

There were two species identified for St. Vallier, *Eucladoceros ctenoides* and *Croizetoceros ramosus medius*, in addition to several specimens labeled only as Cervidae. As discussed above, *Eucladoceros* displayed a mosaic of morphological features, most of which indicated an open adaptation. *Eucladoceros ctenoides* appears to have been slightly more closed-adapted than the *Eucladoceros* sp. specimens from Valea Graunceanului, Romania, which is broadly contemporaneous with St. Vallier (Late Pliocene). The calcaneus landmark analysis of habitat classified all three *E. ctenoides*

specimens as “Intermediate Open”, as were the six large calcanei identified only as Cervidae, which may belong to *E. ctenoides*.

Mesowear studies of *Croizetoceros ramosus* from Sésκλο, Greece (Rivals & Athanassiou 2008) indicate that this species was a browser and suggest that *C. ramosus* perhaps browsed in non-forested areas. The *C. ramosus* specimens in this study support this hypothesis in that they were classified as “Open” (two calcanei) and “Intermediate Open” (a single lateral tibial plateau margin). Seven additional calcanei, identified only as Cervidae, may belong to *C. ramosus*, but this interpretation is based only on their small size and thus is not particularly robust. These seven specimens all classified as “Open”. There were four medium-sized calcanei (possibly *Cervus philisi*) that were all classified into “Open”.

The third phalanx specimens from St. Vallier were only identified as Cervidae, though they were all small and can thus be excluded from *Eucladoceros*. These specimens were classified into all substrate types, though few had very high posterior probabilities of group membership. Three specimens were classified as “Mountain”, two as “Ecotone” and one each as “Dry” and “Wet”. Though no definitive habitat reconstruction is possible from the third phalanx results, they do suggest that mountainous terrain was near St. Vallier.

Combined, these results point to an “Open” to “Intermediate Open” paleohabitat with nearby mountains for St. Vallier and thus is broadly similar to Valea Graunceanului, Romania.

Senèze, France

Three cervid species are recognized from Senèze: *Eucladoceros ctenoides*, *Cervus philisi*, *Alces (Libralces gallicus)*, and several specimens labeled as only *Cervus* sp. or Cervidae. As with specimens from St. Vallier, the *Eucladoceros ctenoides* calcanei specimens indicated an “Intermediate Open” habitat, as did a specimen labeled as *Cervus* sp., though this specimen (FR662a) can be tentatively assigned to *Eucladoceros*. Four other calcanei labeled only as Cervidae (possibly *Cervus philisi*) were all classified as “Open”. One *Alces (Libralces)* specimen classified as “Closed”. As discussed in Chapter 8, the “Closed” morphology of the *Libralces* specimen may reflect a need for increased maneuverability in “obstacle-strewn landscapes” (Geist 1998, p. 247). Geist (*ibid*) further states that these cervids were adapted more for reach than speed. Extant *Alces alces* are highly specialized trotters that lift their limbs over obstacles rather than moving around them. Perhaps the *Libralces* calcaneal morphology found in this study reflects this need for increased maneuverability, rather than a “Closed” habitat. The very long antler beams (one meter on each side) would certainly have made locomotion in closed habitats difficult.

There were six fossil femora from Senèze, three identified as *Cervus philisi* and three as Cervidae. One specimen from each of these taxa was classified into the three non-“Closed” habitat categories. The medial femoral patellar margin performed well at separating “Closed” specimens from non-“Closed” specimens, but further distinctions in the non-“Closed” groups were problematic. Thus, it is only safe to say that the femoral specimens from Senèze were not from “Closed” habitats. The analysis of the lateral tibial plateau was similar to the femoral analysis in that it performed well at distinguishing

between only “Closed” and non-“Closed” specimens. Five Senèze specimens (one identified as *Alces (Libralces)*, one as *Cervus* sp., and three as Cervidae) were classified as “Intermediate Open”, while one specimen of *Cervus philisi* was classified into “Open”. These specimens were more toward the “Open” end of the non-“Closed” specimens in the habitat score analysis.

The results for the third phalanx plantar margin were broadly similar to those for St. Vallier in that specimens were classified into all four substrate types, though “Dry” and “Mountainous” types were dominant. However, more specimens were classified as “Wet” for the Senèze assemblage than for St. Vallier, indicating more water resources or more closed conditions.

The paleohabitat of Senèze can thus be reconstructed as being an “Open” to “Intermediate Open” region with some mountainous relief and nearby water resources (a maar (Delson *et al.* 2006)).

‘Ubeidiya, Israel

The fossil sample from ‘Ubeidiya examined in this dissertation can be divided into two faunal units, as defined by Belmaker (2006). Faunal Unit A (containing pooled stratum III 11-13), which was deposited during the inferior limnic cycle (Li), and Faunal Unit B (containing pooled strata II 23-25, III 21-22, II 26-27, and II 37), which was deposited during the inferior fluvial cycle (Fi). Belmaker (2006) reconstructed the habitats of both depositional events as being Mediterranean biomes, with increasing desiccation through time.

The analyses of habitat here support an “Open” to “Intermediate Open” habitat for both faunal units, though the cervids do not indicate increasing aridity. Specimens from

Faunal Unit A included a calcaneus of *Pseudodama* sp. (classified as “Open”), a lateral tibial plateau of *Pseudodama* (classified as “Intermediate Open”) and two third phalanges, one from *Pseudodama* (classified as “Ecotone”) and one of *Praemegaceros verticornis* (classified as “Dry”). These results indicate an “Open” to “Intermediate Open” habitat from Faunal Unit A.

Faunal Unit B contained the remains of *Pseudodama* sp., *Capreolus* sp., and *Praemegaceros verticornis*. The *Pseudodama* calcanei were classified as being “Open”, while their third phalanges were classified into all substrate types except “Wet”. The *Praemegaceros* calcaneus specimen was classified as “Intermediate Open”, while the phalangeal specimens were classified as “Dry” and “Mountain”. The *Capreolus* sp. femoral medial patellar margin was classified as “Intermediate Open”. These results indicated an “Intermediate” habitat for the cervids of Faunal Unit B.

Pseudodama has been hypothesized to be a forest dweller (Belmaker 2006) with montane adaptations (Croitor 2001) and a mixed-feeding diet with little dependence on water resources (Palmqvist *et al.* 2008). The results here suggest that this species inhabited more open habitats. The combination of all these lines of evidence might suggest that *Pseudodama* spent time feeding in the open and ran to more closed cover when threatened. The “Intermediate Open” habitat suggested for *Praemegaceros* based on the data in this study is also at odds with what has been found by other researchers. Belmaker (2006) states that *Praemegaceros* was a mixed-feeder in an open landscape, which is supported by Geist (1998), who suggests it was a moist savanna inhabitant. Palmqvist *et al.* (2008) state that *Praemegaceros* was a closed-habitat mixed-feeder or

browser with dependence on water resources. The results here suggest a dry and open habitat adaptation for *Praemegaceros*.

To briefly summarize, based on the data analyzed here, the habitat reconstructions for both faunal units at 'Ubeidiya suggest an "Intermediate Open" habitat with a mixture of more open and more closed regions and near-by water resources.

Conclusion

This dissertation has demonstrated that Cervidae remains can be used as paleohabitat proxies. Paleohabitat reconstructions based on the functional morphology of cervids offer an enriched utilization of these remains, which are often the dominant taxon in Eurasian paleoanthropological assemblages. This is an improvement on taxon-based methods, especially in cases where ancestry is unknown, taxonomic identification is lacking, or for species that have no extant relatives, such as *Eucladoceros*.

This dissertation further demonstrated that ecomorphological studies conducted with geometric morphometrics allow for quantification of morphology that previously had been evaluated qualitatively, such as outlines of joint surfaces. As the interrelationships of coordinates are maintained with geometric morphometrics, shape as a whole unit was analyzed, rather than being broken into a series of linear measurements for which geometric interrelationships are lost. Further, shape variation associated with different habitats and substrates was visualized, which allowed for recognition of subtle variations in morphology. Geometric morphometrics opens up new directions for ecomorphology to move in, including the quantification of previously qualified morphology and visualizations of subtle variations in morphology that may be missed with linear measurements.

The methods introduced in this dissertation were designed to be used on incomplete skeletal elements (proximal tibia and distal femur), as complete bones are rare in the fossil record. The incorporation of incomplete bones in an ecomorphological analysis increases the sample size upon which habitat reconstructions are based. This dissertation also introduced ecomorphological methods for small, dense bones that are commonly found in fossil assemblages (calcaneus and third phalanx). By combining the ecomorphological results from several units of analysis in this study, a suite of functional morphological hypotheses for cervid locomotion was created and applied to fossil cervid specimens, thus increasing the utility of the abundant cervid remains found in Eurasian sites.

The nature of morphological variation associated with habitat types was also investigated in this study. Only one of the four units of analysis examined here (the calcaneal landmarks) varied along a continuum from more open to more closed vegetation structure. Two other units of analysis (the lateral tibial plateau margin and the femoral medial patellar margin) were found to have more discrete variation, that is, “Closed” and non-“Closed”. Finally, the plantar margin of the third phalanx was found not to vary by habitat (vegetational) structure, but by substrate resistivity, or how wet, dry, or rocky/inclined a substrate is. Used in concert, these four units of analysis allowed for a more nuanced reconstruction of the four fossil sites than would have been afforded by a single unit of analysis.

Three of the four fossil sites included in this study date to the late Pliocene to early Pleistocene, coincident with the first appearance of *Homo erectus* in Eurasia, though they do not contain any hominin remains. However, stone tools have been

associated with Valea Graunceanului, Romania, though the nature of this association is not yet clear. Previous habitat reconstructions indicated a warm/humid environment based on the abundance of cervids (Rădulesco *et al.* 2003) and a wooded savanna, as indicated by *Paradolichopithecus* (Frost *et al.* 2005) and *Mammuthus meridionalis* (Ferretti & Croitor 2001). Valea Graunceanului was reconstructed here as being mostly open and dry with nearby mountains and water resources. This reconstruction was based only on *Eucladoceros* specimens, though *Cervus rhenus/philisi* is also reported from this site (Rădulesco *et al.* 2003; though I did not locate any post-cranial remains of this species in the collections). That *Eucladoceros* was open-adapted is supported by several other lines of evidence in addition to the data provided by this study. The femoral head of *Eucladoceros* from Valea Graunceanului was wide in its lateral aspect, limiting movement to the parasagittal plane. This is the condition seen in open-adapted bovids (Kappelman 1988). Further, the mesowear signal from *Eucladoceros* is similar to that of bovids that consume up to 80% grass in their diet (Kaiser & Croitor 2004, p. 669). Thus, it appears that Valea Graunceanului was likely an open habitat surrounding a lacustrine delta (Necrasov *et al.* 1961, p. 402) with more wooded areas available. Interestingly, it is likely that the open regions were occupied by *Eucladoceros* while the more closed regions

St. Vallier, France, was reconstructed as being “Open” to “Intermediate Open”; slightly more closed than Valea Graunceanului, with which it is roughly contemporaneous. Senèze, France, which is slightly younger than St. Vallier, was also reconstructed as being “Open” to “Intermediate Open” with nearby mountains and water resources. The fourth site included in this study, ‘Ubeidiya, Israel, is dated to

approximately 1.4 Ma and contains the remains of *Homo* sp. in addition to thousands of stone tools. ‘Ubeidiya was reconstructed here as being “Intermediate Open” with more closed areas available, which supports Belmaker’s (2006) paleohabitat reconstruction as having various gradients within a Mediterranean biome.

These results support what has been previously described for the Plio-Pleistocene African climate. Stable carbon isotopes, pollen evidence, and $\delta^{18}\text{O}$ records all indicate a major expansion of grasslands and hot and dry conditions by 1.8 Ma, making the Plio-Pleistocene boundary one of the most arid times the African continent had ever experienced (deMenocal & Bloemendal 1995, Bonnefille 1995, Cerling 1992). The reconstructions presented here for late Pliocene Eurasian sites indicate that they were open to intermediate open. That this result was found with Cervidae remains is particularly remarkable, since they have previously been considered to be mostly indicative of more closed habitats (Mendoza *et al.* 2002, Palmqvist *et al.* 2008). The reconstruction for ‘Ubeidiya presented here (intermediate open with closed habitats available) further supports what has been found in Africa, in that C_4 plants increased in abundance by 1.7 Ma, with biomasses up to 60-80%, but decreased in abundance from 1.6-1.4 (Cerling 1992). Cervid ecomorphology is thus considered a good indicator of paleohabitat.

In terms of the dispersal of *Homo erectus* from Africa, the paleohabitat reconstructions presented here for the fossil sites without associated hominin all indicate fairly open to intermediate open habitats. Since these reconstructions are broadly similar to those for roughly contemporaneous sites that contain hominin remains (Koobi Fora and Mojokerto), it does not appear that hominins were precluded from occupying the

Plio-Pleistocene sites examined here due to environmental reasons. Indeed, from the habitat reconstructions presented in Chapter 2 for various *Homo erectus* sites dating to this time period, it is apparent that this hominin was able to exploit a wide variety of habitats. Distance also does not seem to have been a determining factor in *Homo erectus* biogeography for this time period, as Mojokerto, Java is farther from any dispersal point out of Africa than are any of the sites examined here. Perhaps dispersal into Western Europe was delayed due to geographic barriers, such as the Taurus and Zagros Mountains (Rolland 1992), though Dmanisi in Georgia is north of these mountains and was occupied at 1.77 Ma (Lordkipanidze *et al.* 2007). Though this dissertation cannot address why hominins are *not* found at the Plio-Pleistocene sites examined here, it does suggest that hominins could have occupied these sites. However, all three Plio-Pleistocene sites have extensive faunal assemblages with no hominin remains, which indicates that the absence of hominins at these sites is not due to an absence of evidence. Continued excavations at these sites will help to resolve this issue, while the application of the methods introduced here to further Eurasian Plio-Pleistocene sites will help address questions of hominin dispersal from Africa by elucidating the range of habitats *Homo erectus* was able to occupy.

Future directions

There are many directions in which this research can be taken. The possibility that better cross-validation results, and therefore potentially better fossil classifications, could be obtained from non-sequential combinations of PC variables will be examined. Phylogenetic influences on morphology in the units of analysis in this study will be controlled for using independent contrasts (Felsenstein 1985). As with any study,

increased sample sizes would allow for more robust results, especially in the case of the third phalanx. Though it might be possible to improve the specificity of the habitat reconstructions by increasing the number of habitat categories specimens are classified into, this may be inadvisable, since the number of habitat categories used in an ecomorphological analysis was found to be negatively correlated to the mean correct resubstitution rate. Instead, it may be possible to find correlations between the shape variables used here and specific ecological and climatic aspects of habitat. Museum specimen catalogs provide collection locations for each specimen, which, when enough location data are provided, can be georeferenced, producing approximate GPS coordinates. Using GPS coordinates, a huge variety of climatic databases (e.g. <http://edcimswww.cr.usgs.gov/pub/imswelcome/>) can provide very specific climatic and ecological data, such as temperature, rainfall, seasonality, day length, percent tree cover (Kozak *et al.* 2008). These data can be regressed against shape variables (PCs or CVs) to test for correlations. Further, these climatic and ecological data can provide for more accurate assignment of individual specimens to habitat types, which would be especially valuable for species with wide habitat tolerances, such as *Odocoileus virginianus*.

Results for four units of analysis were presented in this study, however, data for twenty-five units of analysis were collected from across the entire rearlimb, including several joint surfaces (femoral head, patellar surface, medial tibial plateau, etc.), open and closed outlines, 3D coordinates from which linear measurements can be derived, and impressions of several muscle entheses. The surface and outline data will be examined with methods similar to those described here. The 3D coordinates for linear measurements can possibly be treated as landmarks, though they were not collected as

such. Minimally these linear measurements can be directly compared to published ecomorphological studies for bovids. The muscle scar impressions can be analyzed with several techniques, including GM of general outline shape, analyses of standard metrological parameters of roughness (R_A , R_Z , and R_{PM}/R_Z) for transect across the entheses, and area-scale fractal complexity for rugosity.

The methods introduced in this dissertation will be applied to the family Bovidae. Since bovids are generally the most abundant taxa in African paleoanthropological sites and cervids are the most abundant taxa in Eurasian sites, habitat reconstructions can be made for virtually all hominin sites with a single methodology. Whether the cervid and bovid data sets will be able to be treated as a single data set is not yet clear. The bovid data will be examined to see if they are more habitat-specific in the units of analysis in this study than cervids. Habitat analyses for forelimb elements can also be created using similar methods to the ones introduced here.

Finally, these methods can be applied to any hominin site containing cervid (or bovid) remains. This study marks the first step toward creating habitat reconstructions (using the methods introduced here) for paleontological and paleoanthropological sites across Africa and Eurasia from the Plio-Pleistocene boundary in order to examine patterns of *Homo erectus* habitat use and dispersal. These methods, when used in concert with other paleoecological proxies, provide a comprehensive reconstruction of past habitats.

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Appendix A- Extant specimen information

ID#	Taxon	Sex	Collection location
AM113759	<i>Axis porcinus annamiticus</i>	m	Vietnam, Cochin China, Lagna River
AM113761	<i>Axis porcinus annamiticus</i>		Vietnam, Cochin China, Lagna River
AM114550	<i>Muntiacus muntjak raginalis</i>		North Burma, Hpare, 6000'
AM115638	<i>Elaphodus cephalophus</i>	m	China: Szechuan, Mao Mo Gou, 30 mi W Wenchwan, 8600'
AM122668	<i>Rangifer tarandus caribou</i>		Canada, Alberta; Thoral Creek, 50 mi NE Jasper, 7000 ft
AM122674	<i>Alces alces americana</i>		Canada, Alberta; Entrance, 3000 ft
AM130202	<i>Odocoileus virginianus borealis</i>		USA, Nehasane, Hamilton Co., N.Y.
AM130203	<i>Odocoileus virginianus borealis</i>		USA, Nehasane, Hamilton Co., N.Y.
AM135051	<i>Odocoileus hemionus hemionus</i>		USA, AZ: Kaibab Forest, Buckridge
AM139685	<i>Rangifer tarandus caribou</i>		Canada, Alberta: North of Jasper Park, Little Smoky River
AM14093	<i>Dama dama</i>	m	Zoo
AM147434	<i>Hydropotes inermis</i>	m	Zoo
AM163843	<i>Capreolus capreolus canus</i>	m	Spain, Mots de Toledo Vebes Robledo
AM165672	<i>Elaphurus davidianus</i>		Zoo
AM182563	<i>Hydropotes inermis</i>		Zoo
AM22851	<i>Hydropotes inermis</i>	f	Zoo
AM22936	<i>Rangifer tarandus groenlandicus</i>		Wajer River, NW coast of Hudson Bay.
AM245629	<i>Odocoileus virginianus</i>		USA, GA: Liberty Co, St C
AM35365	<i>Dama dama</i>		Zoo
AM35704	<i>Cervus eldi</i>		Zoo
AM54497	<i>Cervus duvauceli duvauceli</i>		No. Kheri Forest, India
AM54916	<i>Capreolus capreolus</i>		Russia, Thian Shan Mts.
AM54917	<i>Capreolus capreolus pygargus</i>		Russia, Thian Shan Mts.

ID#	Taxon	Sex	Collection location
AM54923	<i>Capreolus capreolus pygargus</i>	m	Russia, Thian Shan Mts.
AM54924	<i>Capreolus capreolus pygargus</i>		Russia, Thian Shan Mts.
AM90409	<i>Dama dama</i>		Zoo
FM10933	<i>Rangifer tarandus caribou</i>	m	Newfoundland
FM125122	<i>Mazama rufina bricenii</i>	f	Ecuador, Napo, San Jose de Payamino
FM15572	<i>Rangifer tarandus caribou</i>		USA., ME
FM15574	<i>Odocoileus virginianus borealis</i>		USA, WI
FM188613	<i>Cervus mariannus</i>	f	Mariana Island, Guam, Anderson Airforce Base, northwest field
FM20336	<i>Alces alces gigas</i>	f	USA, AK, Kenai Peninsula, Kelley River
FM20338	<i>Alces alces gigas</i>	m	USA, AK, Kenai Peninsula, Kelley River
FM24363	<i>Pudu puda</i>	m	Chile, Los Lagos, Chiloe I, Quellon
FM25178	<i>Odocoileus hemionus columbianus</i>	m	British Columbia, Elk Creek, 20 mi from White Swan Lake
FM25665	<i>Cervus elaphus songaricus</i>	m	China, Xinjiang Uygur, Ili Kazak Pref, Upper Kooksu R
FM25700	<i>Axis porcinus porcinus</i>	m	India, Uttar Pradesh, Kheri, Oudh, Palia
FM25701	<i>Axis porcinus porcinus</i>	f	India, Uttar Pradesh, Kheri, Oudh, Palia
FM27448	<i>Axis porcinus porcinus</i>	f	India, Uttar Pradesh, North Kheri
FM27455	<i>Cervus unicolor niger</i>	m	India, Uttar Pradesh, Kheri
FM28280	<i>Blastocerus dichotomus</i>		Brazil, Mato Graso, Descalvado (=Descalvados Ranch)
FM28290	<i>Ozotoceros bezoarticus campestris</i>	f	Brazil, Mato Graso, Descalvado (=Descalvados Ranch)
FM28305	<i>Mazama gouazoubria nana</i>	f	Brazil, Mato Graso, Descalvado (=Descalvados Ranch)
FM29184	<i>Ozotoceros bezoarticus campestris</i>	m	Brazil, Mato Graso, Descalvado (=Descalvados Ranch)
FM29918	<i>Odocoileus hemionus hemionus</i>	m	USA, AZ, Coconino Co, Kaibab Forest
FM34420	<i>Cervus elaphus scoticus</i>	m	UK-Scotland, Highland Reg, Affaric Estate, Aultbea* Beat
FM36780	<i>Elaphodus cephalophus</i>	m	China, Sichuan, Yaan Pref, Dun Shih Goh, above Baoxing
FM39491	<i>Elaphodus cephalophus</i>	m	China, Sichuan, Chung Chiang Miao, 30 mi W Mapienting

ID#	Taxon	Sex	Collection location
FM39493	<i>Elaphodus cephalophus</i>	m	China, Sichuan, Chung Chiang Miao, 30 mi W Mapienting
FM39497	<i>Muntiacus reevesi</i>	m	China, Sichuan, Chung Chiang Miao, 30 mi W Mapienting
FM39516	<i>Muntiacus reevesi</i>	f	China, Sichuan
FM44335	<i>Mazama rufina</i>	f	Ecuador, Pichincha, Volcan Pichincha, occidente
FM46955	<i>Odocoileus virginianus carminis</i>	f	USA, TX, Brewster Co, Chisos Mts, the Basin
FM57222	<i>Odocoileus hemionus</i>	m	Zoo
FM57615	<i>Elaphurus davidianus</i>		Zoo
FM60207	<i>Elaphurus davidianus</i>		Zoo
FM60771	<i>Dama dama</i>	m	Zoo
FM60772	<i>Odocoileus virginianus</i>	f	Zoo
FM61007	<i>Cervus mariannus aponensis</i>	f	Philippine Is, Mindanao I, Davao del Sur Prov, Mt Apo, east skull onlype, Meran
FM65360	<i>Capreolus capreolus</i>	f	Bavaria, Bavarian Forest, Waldmuchen
FM65571	<i>Capreolus capreolus</i>	f	Bavaria, Bavarian Forest, Waldmuchen
FM65802	<i>Axis axis axis</i>	f	Zoo
FM68761	<i>Muntiacus atherodes pleiharicus</i>	m	Malaysia, Sabah, East Coast Residency, Sandakan Dist, SApagaya Forest Reserve
FM68763	<i>Muntiacus atherodes pleiharicus</i>	m	Malaysia, Sabah, East Coast Residency, Kinabatangan Dist, Little Kretam River
FM68764	<i>Muntiacus atherodes pleiharicus</i>	f	Malaysia, Sabah, East Coast Residency, Sandakan Dist, SApagaya Forest Reserve
FM70559	<i>Mazama gouzoubira nemorivaga</i>	f	Colombia, Putumayo, Rio Mecaya
FM78657	<i>Mazama americana temama</i>	f	Peru, Cuzco, Quispicanchi, Huajyumbe
FM78658	<i>Mazama americana</i>	m	Peru, Cuzco, Quispicanchi, Quincemil
FM79912	<i>Mazama chunyi</i>	f	Peru, Puno, Sandia, San Juan
FM86846	<i>Pudu mephistopheles</i>	m	Columbia, Cauca, Malvasa
FM88785	<i>Muntiacus muntjak pleiharicus</i>	m	Malaysia, Sarawak, Fourth Division, Ulu Selio
FM88786	<i>Muntiacus muntjak pleiharicus</i>	f	Malaysia, Sarawak, Fourth Division, Ulu Selio
FM97893	<i>Cervus elaphus maral</i>	f	Iran, Mazandaran, Sama, 9 km SSW

ID#	Taxon	Sex	Collection location
MVZ101379	<i>Alces alces shirasi</i>	m	USA, MO, Ravalli Co., E Fork, Bitterroot River
MVZ105681	<i>Odocoileus hemionus hemionus</i>	f	USA, CA, Mono Co., Deep Creek, Sweetwater Mts.
MVZ116326	<i>Hippocamelus antisensis</i>	m	Peru, Depto. Tacna, 4 km N Tarata
MVZ119372	<i>Odocoileus hemionus inyoensis</i>	f	USA, CA., Inyo Co., Wyman Creek
MVZ121091	<i>Odocoileus hemionus hemionus</i>	f	USA, CA, Sierra Co., Bickford Meadow, Little Truckee River, 10.5 mi SE Sierraville
MVZ121107	<i>Odocoileus virginianus couesi</i>		USA, AZ, Cochise Co., AMNH Southwestern Research Station, Chiricahua Mts
MVZ122523	<i>Pudu mephistophiles</i>	f	Columbia, Depto. Cauca, Paramo de Purace, 18 km E Purace
MVZ124024	<i>Rangifer tarandus intergrade</i>	f	USA, AK, Kaolak River, Latitude 70 degrees N
MVZ132244	<i>Cervus elaphus nannodes</i>	f	USA, CA, Inyo Co., 4 mi SE Bishop
MVZ152833	<i>Hippocamelus antisensis</i>	f	Peru, Depto. Cuzco, above La Raya Pass
MVZ158479	<i>Pudu puda</i>	f	Chile, Region de Los Lagos, Isla Chiloé
MVZ16327	<i>Odocoileus hemionus californicus</i>	f	USA, CA, Tulare Co., Taylor Meadow
MVZ184222	<i>Rangifer tarandus granti</i>	m	USA, AK, Borough, vicinity of McKinley Park
MVZ22977	<i>Odocoileus hemionus californicus</i>		USA, CA, Mariposa Co., Chinquipin, Yosemite National Park
MVZ2338	<i>Odocoileus hemionus fuliginatus</i>	f	USA, CA, Riverside Co., Tahquitz Valley, San Jacinto Mts.
MVZ31118	<i>Odocoileus virginianus couesi</i>	m	USA, AZ, Cohise Co., floor of Pinery Canyon, Chiricahua Mts
MVZ32031	<i>Odocoileus virginianus couesi</i>	f	USA, AZ, Cohise Co., Chiricahua Mts.
MVZ42615	<i>Rangifer tarandus caribou</i>	m	British Columbia, Indianpoint Lake, vicinity of NE Barkerville
MVZ42616	<i>Rangifer tarandus caribou</i>	m	British Columbia, Indianpoint Ranch, vicinity of NE Barkerville
MVZ43222	<i>Odocoileus hemionus peninsulae</i>	m	Mexico, Baja California Sur, El Sauce, Victoria Mts.
MVZ44124	<i>Cervus elaphus nannodes</i>	f	Montana, Madison Co., Mammoth
MVZ57121	<i>Cervus elaphus nannodes</i>	m	USA, CA, Kern Co., 6 mi SW Buttonwillow
MVZ59929	<i>Odocoileus hemionus columbianus</i>	f	USA, CA, Butte CO., 10 mi S, 6 mi W Chico
MVZ59938	<i>Odocoileus hemionus columbianus</i>	m	USA, CA, Butte Co., 11.5 mi S, 7.5 mi W Chic
MVZ63307	<i>Axis axis</i>	m	Zoo

ID#	Taxon	Sex	Collection location
MVZ68800	<i>Odocoileus hemionus californicus</i>	f	USA, CA, Santa Barbara Co., 4.5 mi W, 2.5 mi S Las Cruces
MVZ74388	<i>Odocoileus virginianus couesi</i>		USA, AZ, Cochise Co., Bar foot Park, Chiricahua Mts
MVZ81524	<i>Cervus elaphus roosevelti</i>	m	USA, CA, Humboldt Co., Gold Bluff, 4.5 mi N Oric
MVZ86082	<i>Odocoileus virginianus couesi</i>	f	Mexico, Sonora, 0.5 mi W Guasima
MVZ8961	<i>Odocoileus hemionus columbianus</i>	f	USA, CA, Marin Co., Mailliard
MVZ90596	<i>Odocoileus hemionus columbianus</i>	m	USA, CA, Santa Clara Co., Skunk Creek
MVZ93840	<i>Odocoileus hemionus hemionus</i>	m	USA, CA, Siskiyou Co., near Medicine Lake
MVZ94762	<i>Cervus elaphus nelsoni</i>	f	USA, CO, Larimer Co., Beaver Meadows, Estes Park
MVZ97800	<i>Odocoileus hemionus sheldoni</i>	m	Mexico, Sonora, 3 mi NE Ensenada del Perro, Isla Tiburón; Gulf of California Islands
MVZ98889	<i>Odocoileus virginianus truei</i>	m	El Salvador, Miguel, Lake Olomega
NM092167	<i>Hippocamelus bisulcus</i>	f	Argentina, Santa Cruz,
NM122612	<i>Cervus mariannus</i>	f	Zoo
NM12758	<i>Alces alces americana</i>	m	Nova Soctia
NM13973	<i>Cervus elaphus canadensis</i>	m	USA, ND, Fort Bufort, White Earth River
NM151859	<i>Cervus unicolor brookei</i>	f	Indonesia, Saratok River
NM151862	<i>Muntiacus muntjak peninsulae</i>	m	Indonesia, Klumpang Bay
NM154383	<i>Muntiacus muntjak peninsulae</i>	f	Indonesia, Siri Island, Mata
NM197040	<i>Dama dama</i>	m	Zoo
NM199847	<i>Cervus timorensis</i>	f	Indonesia, Toli Toli
NM22454	<i>Odocoileus virginianus gymnotis</i>	f	South America
NM238130	<i>Odocoileus virginianus borealis</i>	f	USA, NJ, Atlantic County, Newtonville, 2 1/2 Mi S
NM239596	<i>Muntiacus reevesi</i>	f	China, Hunan, Yochow
NM239609	<i>Hydropotes inermis</i>		China, Hunan, Yochow
NM241581	<i>Rangifer tarandus granti</i>	m	USA, AK
NM249425	<i>Odocoileus hemionus sitkensis</i>	f	USA, AK, Alexander Archipelago, Prince of Wales Island, S End

ID#	Taxon	Sex	Collection location
NM251054	<i>Cervus elaphus nelsoni</i>	m	USA, Wyoming, Jackson
NM251087	<i>Rangifer tarandus caribou</i>	f	USA, MN, Red Lakes, 2 Mi W And 5 Mi N Of Heulin
NM256018	<i>Odocoileus virginianus hiltonensis</i>	f	USA, SC, Beauford Co., Hilton Head Island
NM256019	<i>Odocoileus virginianus hiltonensis</i>	f	USA, SC, Beauford Co., Hilton Head Island
NM256055	<i>Odocoileus virginianus venatorius</i>	m	USA, SC, Beauford Co., Hunting Island
NM256056	<i>Odocoileus virginianus venatorius</i>	m	USA, SC, Beauford Co., Hunting Island
NM256107	<i>Elaphodus cephalophus cephalophus</i>	m	China, Sichuan, Mupin
NM258680	<i>Elaphodus cephalophus cephalophus</i>	m	China, Sichuan, Mupin
NM258681	<i>Elaphodus cephalophus cephalophus</i>	m	China, Sichuan, Mupin
NM259386	<i>Elaphodus cephalophus cephalophus</i>	m	China, Sichuan, Wes Chuan
NM259387	<i>Elaphodus cephalophus cephalophus</i>	m	China, Sichuan, Wes Chuan
NM259465	<i>Muntiacus reevesi</i>	m	China, Sichuan, Wes Chuan
NM261017	<i>Blastocerus dichotomus</i>	m	Bolivia, Curichi Grande, Bolivian Brazilian Border
NM261018	<i>Blastocerus dichotomus</i>	f	Bolivia, Curichi Grande, 50 Miles North
NM261021	<i>Mazama gouazoupira superciliaris</i>	f	Brazil, Bolivian Border, 100 Mi. East At 15 Degrees Latitude
NM270379	<i>Ozotoceros bezoarcticus</i>	f	Brazil, Sao Luiz De Caceres, 100 Mi
NM270380	<i>Ozotoceros bezoarcticus</i>	m	Brazil, Sao Luiz De Caceres, 100 Mi
NM271660	<i>Odocoileus hemionus hemionus</i>	f	USA, OR, Hart Mountain Refuge, T37s, R26e, Sec 18
NM272845	<i>Odocoileus hemionus hemionus</i>	m	USA, WY, Jackson, Huback Canyon
NM275127	<i>Alces alces gigas</i>	m	USA, AK, Coleville River, 5 Mi From Navy Camp, 20 Mi Above Anaktonak Junction
NM282141	<i>Pudu mephistophiles</i>	m	Columbia, Cauca, Paramo De Purall
NM282815	<i>Rangifer tarandus pearyi</i>	m	Canada, NW Territories, Franklin District, Ellesmere Island, Goose Fjord, SW
NM301941	<i>Cervus nippon</i>	f	USA, MD, Dorchester Co., James Island
NM307612	<i>Elaphurus davidianus</i>		Zoo
NM309045	<i>Pudu mephistophiles</i>	f	Columbia, Cauca, Malvasa

ID#	Taxon	Sex	Collection location
NM330791	<i>Muntiacus reevesi micrurus</i>		Taiwan, I-Lan, Chine-Chi
NM35261	<i>Cervus mariannus</i>	m	Philippines
NM395181	<i>Cervus nippon</i>	f	USA, VA, Accomack Co., Assateague Island
NM396283	<i>Odocoileus virginianus virginianus</i>	f	USA, WV, Hardy Co., Moorefield, 15 Mi E
NM538381	<i>Cervus eldi</i>	f	Zoo
NM538456	<i>Cervus timorensis</i>	f	Indonesia, Maluku Province, Halmahera, Wasile District; Kampung Loleba
NM545015	<i>Cervus eldi</i>	m	Zoo
NM566616	<i>Odocoileus virginianus ochrourus</i>	m	USA, MO, Ravalli Co., Metcalf Refuge, Bitterroot River, 25 Mi S Of Missoula
NM567252	<i>Odocoileus virginianus clavium</i>	m	USA, FL, Monroe Co., Key Deer National Wildlife Refuge
NM567255	<i>Odocoileus virginianus clavium</i>	m	USA, FL, Monroe Co., Key Deer National Wildlife Refuge
NM588564	<i>Cervus nippon</i>	m	USA, MD, Dorchester Co., Tudor Farms
NM588747	<i>Cervus nippon</i>	f	USA, MD, Dorchester Co., Fishing Bay Wildlife Management Area
NM588757	<i>Cervus nippon</i>	f	USA, MD, Dorchester Co., Blackwater National Wildlife Refuge
NM588790	<i>Cervus nippon</i>	f	USA, MD, Dorchester Co., Blackwater Road
NM092167	<i>Hippocamelus bisulcus</i>	f	Argentina, Santa Cruz, Cordilleras, Rio Chico

Abbreviations: AM= American Museum of Natural History (New York, NY, USA), FM = Chicago Field Museum (Chicago, IL, USA), MVZ = Museum of Vertebrate Zoology, University of California at Berkeley (Berkeley, CA, USA), NM = National Museum of Natural History, Smithsonian (Washington, DC, USA)

Appendix B- Fossil specimen information

Storage location & museum ID #	Assigned ID#	Country	Site	Taxon	Element	Side
NMING:F21232	F21174	Ireland	Buttevant, Co. Cork	<i>Megaloceros giganteus</i>	Calcaneus	L
NMING:F21174	F21232	Ireland	Howth, Co. Dublin	<i>Megaloceros giganteus</i>	Calcaneus	R
NMING:F21306	F21306	Ireland	Ardpatrick, Co. Limerick	<i>Megaloceros giganteus</i>	Calcaneus	L
NMING:F21244	F21232	Ireland	Howth, Co. Dublin	<i>Megaloceros giganteus</i>	Femur	R
NMING:F21648	F21244	Ireland	Castlebellingham, Co. Louth	<i>Megaloceros giganteus</i>	Femur	L
NMING:F21232	F21245	Ireland	Lanesboro, Co. Longford	<i>Megaloceros giganteus</i>	Femur	R
NMING:F21232	F21648	Ireland	Lough Gur, Co. Limerick	<i>Megaloceros giganteus</i>	Femur	L
NMING:F21174	F21174	Ireland	Buttevant, Co. Cork	<i>Megaloceros giganteus</i>	Phalanx 3	NA
NMING:F21232	F21232	Ireland	Howth, Co. Dublin	<i>Megaloceros giganteus</i>	Phalanx 3	NA
NMING:F21232	F21174	Ireland	Buttevant, Co. Cork	<i>Megaloceros giganteus</i>	Tibia	L
NMING:F21174	F21232	Ireland	Howth, Co. Dublin	<i>Megaloceros giganteus</i>	Tibia	R
NMING:F21232	F21245	Ireland	Lanesboro, Co. Longford	<i>Megaloceros giganteus</i>	Tibia	R
UCBL1: 210537a	FR537a	France	Senèze	<i>Alces</i>	Calcaneus	R
UCBL1: 210683a	FR683a	France	Senèze	Cervidae	Calcaneus	R
UCBL1: 210684a	FR684a	France	Senèze	Cervidae	Calcaneus	R
UCBL1: 210684b	FR684b	France	Senèze	Cervidae	Calcaneus	L
UCBL1: 210684c	FR684c	France	Senèze	Cervidae	Calcaneus	L
UCBL1: 210662a	FR662a	France	Senèze	<i>Cervus</i> sp	Calcaneus	R
UCBL1: 210574a	FR574a	France	Senèze	<i>Eucladoceros ctenoides</i>	Calcaneus	R
UCBL1: 210608a	FR608a	France	Senèze	<i>Eucladoceros ctenoides</i>	Calcaneus	R
UCBL1: 210293	FR293	France	Senèze	Cervidae	Femur	L
UCBL1: 210643	FR643	France	Senèze	Cervidae	Femur	L
UCBL1: 210655c	FR655c	France	Senèze	Cervidae	Femur	R
UCBL1: 210654	FR654	France	Senèze	<i>Cervus philisi</i>	Femur	R
UCBL1: 210739	FR739	France	Senèze	<i>Cervus philisi</i>	Femur	R
UCBL1: FSL495789	FR789	France	Senèze	<i>Cervus philisi</i>	Femur	L

Storage location & museum ID #	Assigned ID#	Country	Site	Taxon	Element	Side
UCBL1: 210548a	FR548a	France	Senèze	<i>Alces</i>	Phalanx 3	NA
MdIC: Senèze1	FRSenèze1	France	Senèze	Cervidae	Phalanx 3	NA
UCBL1: 210690a	FR690a	France	Senèze	Cervidae	Phalanx 3	NA
UCBL1: 210690b	FR690b	France	Senèze	Cervidae	Phalanx 3	NA
UCBL1: 210690c	FR690c	France	Senèze	Cervidae	Phalanx 3	NA
UCBL1: 210690d	FR690d	France	Senèze	Cervidae	Phalanx 3	NA
UCBL1: 210691a	FR691a	France	Senèze	Cervidae	Phalanx 3	NA
UCBL1: 210693a	FR693a	France	Senèze	Cervidae	Phalanx 3	NA
UCBL1: 210697a	FR697a	France	Senèze	Cervidae	Phalanx 3	NA
UCBL1: 210697b	FR697b	France	Senèze	Cervidae	Phalanx 3	NA
UCBL1: 210694a	FR694a	France	Senèze	<i>Cervus philisi</i>	Phalanx 3	NA
UCBL1: 210694b	FR694b	France	Senèze	<i>Cervus philisi</i>	Phalanx 3	NA
UCBL1: 210694c	FR694c	France	Senèze	<i>Cervus philisi</i>	Phalanx 3	NA
UCBL1: 210694d	FR694d	France	Senèze	<i>Cervus philisi</i>	Phalanx 3	NA
UCBL1: 210694e	FR694e	France	Senèze	<i>Cervus philisi</i>	Phalanx 3	NA
UCBL1: 210694f	FR694f	France	Senèze	<i>Cervus philisi</i>	Phalanx 3	NA
UCBL1: 210694g	FR694g	France	Senèze	<i>Cervus philisi</i>	Phalanx 3	NA
UCBL1: 210694h	FR694h	France	Senèze	<i>Cervus philisi</i>	Phalanx 3	NA
UCBL1: 210698a	FR698a	France	Senèze	<i>Cervus philisi</i>	Phalanx 3	NA
UCBL1: 210698b	FR698b	France	Senèze	<i>Cervus philisi</i>	Phalanx 3	NA
UCBL1: 210700a	FR700a	France	Senèze	<i>Cervus philisi</i>	Phalanx 3	NA
UCBL1: 210723a	FR723a	France	Senèze	<i>Cervus philisi</i>	Phalanx 3	NA
UCBL1: 210723b	FR723b	France	Senèze	<i>Cervus philisi</i>	Phalanx 3	NA
UCBL1: 210723c	FR723c	France	Senèze	<i>Cervus philisi</i>	Phalanx 3	NA
UCBL1: 210725a	FR725a	France	Senèze	<i>Cervus philisi</i>	Phalanx 3	NA
UCBL1: 210725b	FR725b	France	Senèze	<i>Cervus philisi</i>	Phalanx 3	NA
UCBL1: 210725c	FR725c	France	Senèze	<i>Cervus philisi</i>	Phalanx 3	NA
UCBL1: 210725d	FR725d	France	Senèze	<i>Cervus philisi</i>	Phalanx 3	NA
UCBL1: 210725e	FR725e	France	Senèze	<i>Cervus philisi</i>	Phalanx 3	NA

Storage location & museum ID #	Assigned ID#	Country	Site	Taxon	Element	Side
UCBL1: 210725f	FR725f	France	Senèze	<i>Cervus philisi</i>	Phalanx 3	NA
UCBL1: 210729a	FR729a	France	Senèze	<i>Cervus philisi</i>	Phalanx 3	NA
UCBL1: 210729b	FR729b	France	Senèze	<i>Cervus philisi</i>	Phalanx 3	NA
UCBL1: 210662a	FR662a	France	Senèze	<i>Cervus</i> sp.	Phalanx 3	NA
UCBL1: 210580a	FR580a	France	Senèze	<i>Eucladoceros ctenoides</i>	Phalanx 3	NA
UCBL1: 210581a	FR581a	France	Senèze	<i>Eucladoceros ctenoides</i>	Phalanx 3	NA
UCBL1: 210581b	FR581b	France	Senèze	<i>Eucladoceros ctenoides</i>	Phalanx 3	NA
UCBL1: 210581c	FR581c	France	Senèze	<i>Eucladoceros ctenoides</i>	Phalanx 3	NA
UCBL1: 210581d	FR581d	France	Senèze	<i>Eucladoceros ctenoides</i>	Phalanx 3	NA
UCBL1: 210581e	FR581e	France	Senèze	<i>Eucladoceros ctenoides</i>	Phalanx 3	NA
UCBL1: 210525	FR525	France	Senèze	<i>Alces</i>	Tibia	R
UCBL1: 210651	FR651	France	Senèze	Cervidae	Tibia	L
UCBL1: 210655a	FR655a	France	Senèze	Cervidae	Tibia	R
UCBL1: 210655b	FR655b	France	Senèze	Cervidae	Tibia	L
UCBL1: 210652	FR652	France	Senèze	<i>Cervus philisi</i>	Tibia	R
UCBL1: 210653	FR653	France	Senèze	<i>Cervus</i> sp.	Tibia	L
MdIC: 21062792	FR2792	France	St. Vallier	Cervidae	Calcaneus	R
MdIC: 21062795	FR2795	France	St. Vallier	Cervidae	Calcaneus	L
MdIC: 21062796	FR2796	France	St. Vallier	Cervidae	Calcaneus	L
MdIC: 21062797	FR2797	France	St. Vallier	Cervidae	Calcaneus	R
MdIC: 21062798	FR2798	France	St. Vallier	Cervidae	Calcaneus	L
MdIC: 21062805	FR2805	France	St. Vallier	Cervidae	Calcaneus	L
MdIC: 21062808	FR2808	France	St. Vallier	Cervidae	Calcaneus	R
MdIC: 21062809	FR2809	France	St. Vallier	Cervidae	Calcaneus	L
MdIC: 21062810	FR2810	France	St. Vallier	Cervidae	Calcaneus	R
MdIC: 21062813	FR2813	France	St. Vallier	Cervidae	Calcaneus	L
MdIC: 21062816	FR2816	France	St. Vallier	Cervidae	Calcaneus	R
MdIC: 21062817	FR2817	France	St. Vallier	Cervidae	Calcaneus	R
MdIC: 21062818	FR2818	France	St. Vallier	Cervidae	Calcaneus	R

Storage location & museum ID #	Assigned ID#	Country	Site	Taxon	Element	Side
MdIC: 21062819	FR2819	France	St. Vallier	Cervidae	Calcaneus	R
MdIC: 21062821	FR2821	France	St. Vallier	Cervidae	Calcaneus	L
MdIC: 21062823	FR2823	France	St. Vallier	Cervidae	Calcaneus	R
UCBL1: FSL497661	FR497661	France	St. Vallier	<i>Croizetoceros ramosus</i>	Calcaneus	R
UCBL1: FSL497716	FR497716	France	St. Vallier	<i>Croizetoceros ramosus</i>	Calcaneus	R
MdIC: 21062120	FR2120	France	St. Vallier	<i>Eucladoceros ctenoides</i>	Calcaneus	R
MdIC: 21062130	FR2130	France	St. Vallier	<i>Eucladoceros ctenoides</i>	Calcaneus	L
MdIC: 21062131	FR2131	France	St. Vallier	<i>Eucladoceros ctenoides</i>	Calcaneus	L
MdIC: 21063203	FR3203	France	St. Vallier	Cervidae	Phalanx 3	NA
MdIC: 21063204	FR3204	France	St. Vallier	Cervidae	Phalanx 3	NA
MdIC: 21063205	FR3205	France	St. Vallier	Cervidae	Phalanx 3	NA
MdIC: 21063206	FR3206	France	St. Vallier	Cervidae	Phalanx 3	NA
MdIC: 21063210	FR3210	France	St. Vallier	Cervidae	Phalanx 3	NA
MdIC: 21063212	FR3212	France	St. Vallier	Cervidae	Phalanx 3	NA
MdIC: 21063214	FR3214	France	St. Vallier	Cervidae	Phalanx 3	NA
UCBL1: 21062073	FR62073	France	St. Vallier	<i>Croizetoceros ramosus medius</i>	Tibia	R
HUJGR: UB2086	UB2086	Israel	Ubeidiya II23-25	<i>Praemegaceros verticornis</i>	Calcaneus	L
HUJGR: UB929	UB929	Israel	Ubeidiya II23-25	<i>Pseudodama</i> sp.	Calcaneus	L
HUJGR: UB503	UB503	Israel	Ubeidiya II26-27	<i>Pseudodama</i> sp.	Calcaneus	R
HUJGR: UB1077	UB1077	Israel	Ubeidiya III11-13	<i>Pseudodama</i> sp.	Calcaneus	R
HUJGR: UB9427	UB9427	Israel	Ubeidiya II26-27	<i>Capreolus</i> sp.	Femur	R
HUJGR: UB856	UB856	Israel	Ubeidiya II23-25	<i>Praemegaceros verticornis</i>	Phalanx 3	NA
HUJGR: UB860	UB860	Israel	Ubeidiya II23-25	<i>Praemegaceros verticornis</i>	Phalanx 3	NA
HUJGR: UB1756	UB1756	Israel	Ubeidiya II23-25	<i>Pseudodama</i> sp.	Phalanx 3	NA
HUJGR: UB933	UB933	Israel	Ubeidiya II23-25	<i>Pseudodama</i> sp.	Phalanx 3	NA
HUJGR: UB935	UB935	Israel	Ubeidiya II23-25	<i>Pseudodama</i> sp.	Phalanx 3	NA
HUJGR: UB992	UB992	Israel	Ubeidiya II23-25	<i>Pseudodama</i> sp.	Phalanx 3	NA
HUJGR: UB2477	UB2477	Israel	Ubeidiya II26-27	<i>Pseudodama</i> sp.	Phalanx 3	NA
HUJGR: UB2481	UB2481	Israel	Ubeidiya II26-27	<i>Pseudodama</i> sp.	Phalanx 3	NA

Storage location & museum ID #	Assigned ID#	Country	Site	Taxon	Element	Side
HUJGR: UB691a	UB691a	Israel	Ubeidiya II37	<i>Praemegaceros verticornis</i>	Phalanx 3	NA
HUJGR: UB691b	UB691b	Israel	Ubeidiya II37	<i>Praemegaceros verticornis</i>	Phalanx 3	NA
HUJGR: UB1068	UB1068	Israel	Ubeidiya III11-13	<i>Praemegaceros verticornis</i>	Phalanx 3	NA
HUJGR: UB1017	UB1017	Israel	Ubeidiya III11-13	<i>Pseudodama</i> sp.	Phalanx 3	NA
HUJGR: UB2212	UB2212	Israel	Ubeidiya III21-22	<i>Pseudodama</i> sp.	Phalanx 3	NA
HUJGR: UB2281	UB2281	Israel	Ubeidiya III21-22	<i>Pseudodama</i> sp.	Phalanx 3	NA
HUJGR: UB2460	UB2460	Israel	Ubeidiya III21-22	<i>Pseudodama</i> sp.	Phalanx 3	NA
HUJGR: UB2474	UB2474	Israel	Ubeidiya K39-42	<i>Praemegaceros verticornis</i>	Phalanx 3	NA
HUJGR: UB435	UB435	Israel	Ubeidiya III11-13	<i>Praemegaceros verticornis</i>	Tibia	L
ERIoS: GrV963 C5-6 (1)	ROIV-V.1	Romania	Valea Graunceanului	<i>Eucladoceros</i> sp.	Calcaneus	L
ERIoS: Bug 1962 Gr Comp IV 247	RO247	Romania	Valea Graunceanului	<i>Eucladoceros</i> sp.	Calcaneus	L
ERIoS: Bug 1962 Gr Comp IV 404	RO404	Romania	Valea Graunceanului	<i>Eucladoceros</i> sp.	Calcaneus	L
ERIoS: Bug 62 Gr Comp IV (1)	ROIV.1	Romania	Valea Graunceanului	<i>Eucladoceros</i> sp.	Calcaneus	L
ERIoS: Bug 1962 Gr Comp III (1)	ROIII.1	Romania	Valea Graunceanului	<i>Eucladoceros</i> sp.	Calcaneus	L
ERIoS: Bug 1962 Gr Comp III (2)	ROIII.2	Romania	Valea Graunceanului	<i>Eucladoceros</i> sp.	Calcaneus	L
ERIoS: Bug 62 Gr C2 (1)	ROII.1a	Romania	Valea Graunceanului	<i>Eucladoceros</i> sp.	Calcaneus	L
ERIoS: Bug 62 GrV Comp II (1)	ROII.1b	Romania	Valea Graunceanului	<i>Eucladoceros</i> sp.	Calcaneus	L
ERIoS: Bug 1962 Gr Comp IV (2)	ROIV.2	Romania	Valea Graunceanului	<i>Eucladoceros</i> sp.	Calcaneus	L
ERIoS: Bug 62 Gr Comp IV (3)	ROIV.3	Romania	Valea Graunceanului	<i>Eucladoceros</i> sp.	Calcaneus	R
ERIoS: Bug 1962 Gr Comp IV 356	RO356	Romania	Valea Graunceanului	<i>Eucladoceros</i> sp.	Calcaneus	R
ERIoS: Bug 62 VGr Comp IV (4)	ROIV.4	Romania	Valea Graunceanului	<i>Eucladoceros</i> sp.	Calcaneus	R
ERIoS: Bug 1962 Gr Comp IV 24	RO24	Romania	Valea Graunceanului	<i>Eucladoceros</i> sp.	Calcaneus	R
ERIoS: Bug 1961 Gr 22	RO22	Romania	Valea Graunceanului	<i>Eucladoceros</i> sp.	Calcaneus	R
ERIoS: Bug 62 VGr Comp III (3)	ROIII.3	Romania	Valea Graunceanului	<i>Eucladoceros</i> sp.	Calcaneus	R
MoO: Gr 1965 9272	RO9272	Romania	Valea Graunceanului	<i>Eucladoceros</i> sp.	Calcaneus	L
MoO: Bug 1962 Gr IV 9243	RO9243	Romania	Valea Graunceanului	<i>Eucladoceros</i> sp.	Calcaneus	R
MoO: Bug 1962 Gr I 9787	RO9787	Romania	Valea Graunceanului	<i>Eucladoceros</i> sp.	Calcaneus	L
MoO: Bug961 Gr 22 9271	RO9271	Romania	Valea Graunceanului	<i>Eucladoceros</i> sp.	Calcaneus	L
ERIoS: Gr963 C10 9341	RO9341	Romania	Valea Graunceanului	<i>Eucladoceros</i> sp.	Phalanx 3	NA

Storage location & museum ID #	Assigned ID#	Country	Site	Taxon	Element	Side
ERIoS: Gr963 C8 9372	RO9372	Romania	Valea Graunceanului	<i>Eucladoceros</i> sp.	Phalanx 3	NA
MoO: Gr963 C8 9337	RO9337	Romania	Valea Graunceanului	<i>Eucladoceros</i> sp.	Phalanx 3	NA
MoO: Gr964 C7 516 9355	RO9355	Romania	Valea Graunceanului	<i>Eucladoceros</i> sp.	Phalanx 3	NA
MoO: Bug 62 VGr Comp IV 9351	RO9351	Romania	Valea Graunceanului	<i>Eucladoceros</i> sp.	Phalanx 3	NA
MoO: Gr963 C8 9349	RO9349	Romania	Valea Graunceanului	<i>Eucladoceros</i> sp.	Phalanx 3	NA
MoO: Gr963 C8 9369	RO9369	Romania	Valea Graunceanului	<i>Eucladoceros</i> sp.	Phalanx 3	NA
MoO: Gr963 C11-12 NII 9358	RO9358	Romania	Valea Graunceanului	<i>Eucladoceros</i> sp.	Phalanx 3	NA
MoO: Gr963 C8 9361	RO9361	Romania	Valea Graunceanului	<i>Eucladoceros</i> sp.	Phalanx 3	NA
MoO: Gr963 C11 9368	RO9368	Romania	Valea Graunceanului	<i>Eucladoceros</i> sp.	Phalanx 3	NA
MoO: Gr963 C8 9333	RO9333	Romania	Valea Graunceanului	<i>Eucladoceros</i> sp.	Phalanx 3	NA
MoO: Gr963 C6 9343	RO9343	Romania	Valea Graunceanului	<i>Eucladoceros</i> sp.	Phalanx 3	NA
MoO: Gr963 C5 9371	RO9371	Romania	Valea Graunceanului	<i>Eucladoceros</i> sp.	Phalanx 3	NA
MoO: Gr 1964 C13 9357	RO9357	Romania	Valea Graunceanului	<i>Eucladoceros</i> sp.	Phalanx 3	NA
MoO: Gr 1964 C13 9353	RO9353	Romania	Valea Graunceanului	<i>Eucladoceros</i> sp.	Phalanx 3	NA
MoO: Gr963 C8 9366	RO9366	Romania	Valea Graunceanului	<i>Eucladoceros</i> sp.	Phalanx 3	NA
MoO: Gr 1964 C7 51F 9342	RO9342	Romania	Valea Graunceanului	<i>Eucladoceros</i> sp.	Phalanx 3	NA
MoO: Gr 1964 C10 9336	RO9336	Romania	Valea Graunceanului	<i>Eucladoceros</i> sp.	Phalanx 3	NA
MoO: Gr 1964 C10 9335	RO9335	Romania	Valea Graunceanului	<i>Eucladoceros</i> sp.	Phalanx 3	NA
MoO: Gr 1964 C10 9354	RO9354	Romania	Valea Graunceanului	<i>Eucladoceros</i> sp.	Phalanx 3	NA
MoO: Bug 62 VGr Comp IV 9346	RO9346	Romania	Valea Graunceanului	<i>Eucladoceros</i> sp.	Phalanx 3	NA
MoO: Gr963 C9 9356	RO9356	Romania	Valea Graunceanului	<i>Eucladoceros</i> sp.	Phalanx 3	NA
MoO: Bug 1962 Gr Comp III 371 9334	RO9334	Romania	Valea Graunceanului	<i>Eucladoceros</i> sp.	Phalanx 3	NA
MoO: Bug 1962 Gr Comp IV 371 9362	RO9362	Romania	Valea Graunceanului	<i>Eucladoceros</i> sp.	Phalanx 3	NA

Abbreviations: NMING = National Museum of Ireland, Natural History Division; UCBL1 = Claude Bernard University of Lyon 1; MdIC: Collection du Musée des Confluences, Lyon; HJGR = Hebrew University of Jerusalem, Givat Ram; ERIoS = 'Emil Racovita' Institute of Speleology; MoO = Museum of Oltenia.

Appendix C- Extant species information

Species	Common name	Tribe	Habitat (specific)	Habitat (general)	Substrate type
<i>Alces alces</i>	Moose, European Elk	Alceini	TempForest	Closed	Dry
<i>Axis axis</i>	Chital	Cervini	Ecotone	InterOpen	Ecotone
<i>Axis porcinus</i>	Hog deer	Cervini	TallGrass	InterOpen	Dry
<i>Blastocerus dichotomus</i>	Marsh deer	Odocoileini	Swamp	InterOpen	Wet
<i>Capreolus capreolus</i>	Roe deer	Capreolini	Ecotone	InterOpen	Ecotone
<i>Cervus duvauceli</i>	Barasingha	Cervini	Swamp	InterOpen	Wet
<i>Cervus canadensis</i>	Wapiti	Cervini	Ecotone	InterOpen	Ecotone
<i>Cervus elaphus</i>	Red deer	Cervini	Woodland	InterClosed	Dry
<i>Cervus eldii</i>	Eld's deer	Cervini	Swamp	InterOpen	Wet
<i>Cervus marianus</i>	Philippine sambar	Cervini	TallGrass	InterOpen	Dry
<i>Cervus nippon</i>	Sika	Cervini	Woodland	InterClosed	Dry
<i>Cervus timorensis</i>	Rusa deer	Cervini	TallGrass	InterOpen	Dry
<i>Cervus unicolor</i>	Sambar	Cervini	TallGrass	InterClosed	Dry
<i>Dama dama</i>	Fallow deer	Cervini	Woodland	InterClosed	Dry
<i>Elaphodus cephalophus</i>	Tufted deer	Muntiacini	MtForest	Closed	Wet
<i>Elaphurus davidianus</i>	Pere David's deer	Cervini	TallGrass	InterOpen	Dry
<i>Hippocamelus antisensis</i>	Taruka	Odocoileini	MtOpen	Open	Mountain
<i>Hippocamelus bisculus</i>	Huemul	Odocoileini	MtOpen	Open	Mountain
<i>Hydropotes inermis</i>	Chinese Water deer	Capreolini	Open	Open	Dry
<i>Mazama americana</i>	Red brocket	Odocoileini	MtForest	Closed	Wet
<i>Mazama chunyi</i>	Dwarf brocket	Odocoileini	MtForest	Closed	Wet
<i>Mazama gouazoubira</i>	Brown brocket	Odocoileini	TropForest	Closed	Wet

Species	Common name	Tribe	Habitat (specific)	Habitat (general)	Substrate type
<i>Mazama rufina</i>	Little red brocket	Odocoileini	MtForest	Closed	Wet
<i>Muntiacus atherodes</i>	Bornean yellow muntjak	Muntiacini	TropForest	Closed	Wet
<i>Muntiacus muntjak</i>	Indian muntjac	Muntiacini	TropForest	Closed	Wet
<i>Muntiacus reevesi</i>	Reeve's deer	Muntiacini	TropForest	Closed	Wet
<i>Odocoileus hemionus</i>	Mule deer	Odocoileini	MtOpen	Open	Mountain
<i>Odocoileus virginianus</i>	White-tailed deer	Odocoileini	Ecotone	InterOpen	Ecotone
<i>Ozotoceros bezoarticus</i>	Pampas deer	Odocoileini	Open	Open	Dry
<i>Pudu mephistophiles</i>	Northern pudu	Odocoileini	MtForest	Closed	Wet
<i>Pudu puda</i>	Southern pudu	Odocoileini	TempForest	Closed	Wet
<i>Rangifer tarandus</i>	Barren-ground caribou/reindeer	Odocoileini	Open	Open	Dry
<i>Rangifer tarandus caribou</i>	Woodland Caribou	Odocoileini	Woodland	InterClosed	Dry

Appendix C- Extant species information (continued)

Species	Body length (cm)			Height at shoulder (cm)			Body weight (kg)			Geographic location
	Min	Max	Mean	Min	Max	Mean	Min	Max	Mean	
<i>Alces alces</i>	240	310	275	140	235	187.5	200	825	512.5	northern hemisphere
<i>Axis axis</i>	100	170	135	60	200	130	27	110	68.5	India, Nepal, Sikkim, Sri Lanka
<i>Axis porcinus</i>	100	170	135	60	100	80	27	110	68.5	N. India, SE Asia
<i>Blastocerus dichotomus</i>	153	195	174	110	127	118.5	80	150	115	central Southern America
<i>Capreolus capreolus</i>	95	151	123	65	100	82.5	15	50	32.5	UK, Spain to Iran
<i>Cervus duvauceli</i>	NA	NA	NA	119	124	121.5	172	181	176.5	Northern India, Assam, Nepal
<i>Cervus canadensis</i>	95	151	123	65	100	82.5	125	204	230	North America, China
<i>Cervus elaphus</i>	95	151	123	65	100	82.5	125	204	230	Northern Hemisphere
<i>Cervus eldii</i>	130	170	150	120	130	125	95	150	122.5	Assam to Indochina, Hainan
<i>Cervus marianus</i>	100	150	125	55	70	62.5	40	60	50	Luzon, Mindoro, Mindanao, Basilan Islands
<i>Cervus nippon</i>	95	140	117.5	64	81	72.5	26	33	29.5	Eastern Asia, Japan
<i>Cervus timorensis</i>	142	185	163.5	83	110	96.5	50	115	82.5	southern Indonesia
<i>Cervus unicolor</i>	162	246	204	102	160	131	109	260	184.5	Asia, Indonesia
<i>Dama dama</i>	130	175	152.5	80	105	92.5	40	100	70	British Isles, "mediterranean" Europe
<i>Elaphodus cephalophus</i>	110	160	135	50	70	60	17	50	33.5	China, northern Burma
<i>Elaphurus davidianus</i>	183	216	199.5	122	137	129.5	159	214	186.5	Northeast China
<i>Hippocamelus antisensis</i>	140	165	152.5	77	90	83.5	45	65	55	Peru, N. Andes
<i>Hippocamelus bisculus</i>	140	165	152.5	77	90	83.5	70	100	85	Chile, Argentina
<i>Hydropotes inermis</i>	77	100	88.5	45	55	50	11	14	12.5	China, Korea
<i>Mazama americana</i>	72	135	103.5	60	70	65	29	35	32	Central and South America
<i>Mazama chunyi</i>	72	135	103.5	35	75	55	8	16	12	S. Peru and Bolivia
<i>Mazama gouazoubira</i>	72	135	103.5	55	60	57.5	17	23	20	central South America

Species	Body length (cm)			Height at shoulder (cm)			Body weight (kg)			Geographic location
	Min	Max	Mean	Min	Max	Mean	Min	Max	Mean	
<i>Mazama rufina</i>	72	135	103.5	35	75	55	8	25	16.5	central South America
<i>Muntiacus atherodes</i>	64	135	99.5	41	78	59.5	14	33	23.5	Borneo
<i>Muntiacus muntjak</i>	64	135	99.5	50	58	54	14	18	16	Asia, Indonesia
<i>Muntiacus reevesi</i>	64	135	99.5	45	50	47.5	12	17	14.5	Southern China and Taiwan
<i>Odocoileus hemionus</i>	85	210	147.5	55	110	82.5	56	94	75	Southern Yukon to Baja California
<i>Odocoileus virginianus</i>	85	210	147.5	55	110	82.5	50	120	85	Southern Canada to Brazil
<i>Ozotoceros bezoarticus</i>	110	140	125	70	75	72.5	25	40	32.5	Brazil south of the Amazon to central Argentina
<i>Pudu mephistophiles</i>	60	83	71.5	32	35	33.5	3.3	6	4.65	Columbia, Ecuador, central Peru
<i>Pudu puda</i>	60	83	71.5	37	41	39	4	13.4	8.7	S. Chile and Argentina
<i>Rangifer tarandus</i>	120	220	170	87	140	113.5	120	180	150	N. America, Greenland, Eurasia
<i>Rangifer tarandus caribou</i>	120	220	170	87	140	113.5	120	180	150	N. America

References: Anderson & Wallmo 1984, Caro *et al.* 2004, Eisenberg 2000, Feldhamer 1980, Feldhamer *et al.* 1988, Franzmann 1981, Geist 1998, Jackman 1987, Janis 1986, Kovarovic & Andrews 2007, Lister 1996, Mendoza *et al.* 2002, Nowak 1999, Pinder & Grosse 1991, Putnam 1988, Sempre *et al.* 1996, Smith 1991, Whitehead 1993

Appendix D- Posterior probabilities of group membership for fossil specimens

ID	Species	Site	Element	Assigned Hab.	Closed	InterClosed	InterOpen	Open
FR537a	<i>Alces</i>	Senèze	Calcaneus	Closed	0.5834	0.0318	0.1544	0.2305
FR683a	Cervidae (m)	Senèze	Calcaneus	Open	0.0022	0.1576	0.2168	0.6235
FR684c	Cervidae (m)	Senèze	Calcaneus	Open	0.0439	0.1076	0.1281	0.7204
FR684b	Cervidae (m)	Senèze	Calcaneus	Open	0.0091	0.1811	0.0838	0.726
FR684a	Cervidae (m)	Senèze	Calcaneus	Open	0.0096	0.0792	0.0839	0.8273
FR662a	<i>Cervus</i> (l)	Senèze	Calcaneus	InterOpen	0.0094	0.0248	0.5111	0.4547
FR574a	<i>Eucladoceros ctenoides</i>	Senèze	Calcaneus	InterOpen	0.0037	0.001	0.9376	0.0577
FR608a	<i>Eucladoceros ctenoides</i>	Senèze	Calcaneus	InterOpen	0.0938	0.036	0.6379	0.2323
FR293	Cervidae	Senèze	Femur	InterClosed	0.0001	0.8174	0.1675	0.015
FR643	Cervidae	Senèze	Femur	InterOpen	0.0017	0.0045	0.9163	0.0775
FR655c	Cervidae	Senèze	Femur	Open	0.0017	0.3203	0.3309	0.347
FR739	<i>Cervus philisi</i>	Senèze	Femur	InterOpen	0.029	0.0598	0.6012	0.31
FR654	<i>Cervus philisi</i>	Senèze	Femur	InterClosed	0.0073	0.5563	0.0883	0.3481
FR789	<i>Cervus philisi</i>	Senèze	Femur	Open	0.0005	0.0095	0.1231	0.867
FR525	<i>Alces (Libralces)</i>	Senèze	Tibia	InterOpen	0.0032	0.0443	0.7103	0.2422
FR655a	Cervidae	Senèze	Tibia	InterClosed	0.091	0.6683	0.143	0.0976
FR655b	Cervidae	Senèze	Tibia	InterOpen	0.0029	0.0719	0.7654	0.1598
FR651	Cervidae	Senèze	Tibia	InterOpen	0.0001	0.0625	0.6247	0.3127
FR652	<i>Cervus philisi</i>	Senèze	Tibia	Open	0.1033	0.0049	0.0314	0.8604
FR2798	Cervidae (l)	St. Vallier	Calcaneus	InterOpen	0.0267	0.0004	0.9689	0.004
FR2797	Cervidae (l)	St. Vallier	Calcaneus	InterOpen	0.0221	0.0124	0.9081	0.0575
FR2795	Cervidae (l)	St. Vallier	Calcaneus	InterOpen	0.0288	0.0193	0.878	0.0739
FR2796	Cervidae (l)	St. Vallier	Calcaneus	InterOpen	0.1394	0.0171	0.7031	0.1405

ID	Species	Site	Element	Assigned Hab.	Closed	InterClosed	InterOpen	Open
FR2792	Cervidae (l)	St. Vallier	Calcaneus	InterOpen	0.0053	0.0051	0.8284	0.1612
FR2791	Cervidae (l)	St. Vallier	Calcaneus	Open	0.0004	0.0157	0.1087	0.8752
FR2809	Cervidae (m)	St. Vallier	Calcaneus	Open	0.0627	0.2448	0.137	0.5555
FR2823	Cervidae (m)	St. Vallier	Calcaneus	Open	0.0085	0.0337	0.3265	0.6314
FR2805	Cervidae (m)	St. Vallier	Calcaneus	Open	0.0002	0.0995	0.1293	0.771
FR2808	Cervidae (m)	St. Vallier	Calcaneus	Open	0.0067	0.03	0.0906	0.8727
FR2813	Cervidae (s)	St. Vallier	Calcaneus	Open	0.0036	0.0231	0.2835	0.6898
FR2810	Cervidae (s)	St. Vallier	Calcaneus	Open	0.0052	0.0199	0.1021	0.8727
FR2818	Cervidae (s)	St. Vallier	Calcaneus	Open	0.0001	0.0254	0.0189	0.9556
FR2819	Cervidae (s)	St. Vallier	Calcaneus	Open	0.001	0.002	0.0212	0.9758
FR2816	Cervidae (s)	St. Vallier	Calcaneus	Open	0	0.0063	0.0112	0.9825
FR2821	Cervidae (s)	St. Vallier	Calcaneus	Open	0	0.0021	0.0025	0.9954
FR2817	Cervidae (s)	St. Vallier	Calcaneus	Open	0	0.0015	0.0013	0.9972
FR497661	<i>Croizetoceros ramosus</i>	St. Vallier	Calcaneus	Open	0.005	0.0068	0.4675	0.5207
FR497716	<i>Croizetoceros ramosus</i>	St. Vallier	Calcaneus	Open	0.0025	0.0437	0.2825	0.6713
FR2131	<i>Eucladoceros ctenoides</i>	St. Vallier	Calcaneus	InterOpen	0.1063	0.0043	0.8121	0.0772
FR2120	<i>Eucladoceros ctenoides</i>	St. Vallier	Calcaneus	InterOpen	0.0021	0.0123	0.7241	0.2616
FR2130	<i>Eucladoceros ctenoides</i>	St. Vallier	Calcaneus	InterOpen	0.0096	0.0123	0.696	0.2821
FR62073	<i>Croizetoceros ramosus</i>	St. Vallier	Tibia	InterOpen	0.0353	0.0583	0.7266	0.1798
UB2086	<i>Pseudodama</i> sp.	Ubeidiya II23-25	Calcaneus	InterOpen	0.1252	0.1088	0.5812	0.1848
UB929	<i>Pseudodama</i> sp.	Ubeidiya II23-25	Calcaneus	Open	0.0481	0.0239	0.1946	0.7334
UB503	<i>Pseudodama</i> sp.	Ubeidiya II26-27	Calcaneus	Open	0.0008	0.0438	0.0382	0.9171
UB9427	<i>Capreolus</i> sp.	Ubeidiya II26-27	Femur	InterOpen	0.0458	0.0898	0.7635	0.1008
UB1077	<i>Pseudodama</i> sp.	Ubeidiya III11-13	Calcaneus	Open	0.0294	0.1933	0.1107	0.6666
UB435	<i>Praemegoceros verticornis</i>	Ubeidiya III11-13	Tibia	InterClosed	0.0014	0.5654	0.1598	0.2734

ID	Species	Site	Element	Assigned Hab.	Closed	InterClosed	InterOpen	Open
ROIV.4	<i>Eucladoceros</i> sp.	Valea Graunceanului	Calcaneus	InterOpen	0.0051	0.0078	0.9313	0.0559
RO9243	<i>Eucladoceros</i> sp.	Valea Graunceanului	Calcaneus	InterOpen	0.0139	0.0288	0.7652	0.1921
RO247	<i>Eucladoceros</i> sp.	Valea Graunceanului	Calcaneus	InterOpen	0.0168	0.179	0.5216	0.2826
ROIV.1	<i>Eucladoceros</i> sp.	Valea Graunceanului	Calcaneus	InterClosed	0	0.6203	0.0786	0.3011
RO404	<i>Eucladoceros</i> sp.	Valea Graunceanului	Calcaneus	InterClosed	0.0009	0.5458	0.1419	0.3113
ROIII.1	<i>Eucladoceros</i> sp.	Valea Graunceanului	Calcaneus	InterOpen	0.0014	0.158	0.4917	0.3489
RO9272	<i>Eucladoceros</i> sp.	Valea Graunceanului	Calcaneus	InterOpen	0.0657	0.0203	0.5235	0.3905
ROIV.2	<i>Eucladoceros</i> sp.	Valea Graunceanului	Calcaneus	InterClosed	0	0.5296	0.0602	0.4101
ROIII.3	<i>Eucladoceros</i> sp.	Valea Graunceanului	Calcaneus	Open	0.0062	0.0422	0.3503	0.6013
ROIII.2	<i>Eucladoceros</i> sp.	Valea Graunceanului	Calcaneus	Open	0.0001	0.029	0.2595	0.7114
ROII.1a	<i>Eucladoceros</i> sp.	Valea Graunceanului	Calcaneus	Open	0.0003	0.1755	0.0365	0.7877
RO24	<i>Eucladoceros</i> sp.	Valea Graunceanului	Calcaneus	Open	0.0001	0.0571	0.1281	0.8148
RO22	<i>Eucladoceros</i> sp.	Valea Graunceanului	Calcaneus	Open	0.0013	0.0041	0.1387	0.8559
RO9277	<i>Eucladoceros</i> sp.	Valea Graunceanului	Calcaneus	Open	0.0061	0.0003	0.1192	0.8745
ROII.1b	<i>Eucladoceros</i> sp.	Valea Graunceanului	Calcaneus	Open	0	0.0994	0.01	0.8905
RO9787	<i>Eucladoceros</i> sp.	Valea Graunceanului	Calcaneus	Open	0.0068	0.0077	0.0869	0.8986
ROIV-V.1	<i>Eucladoceros</i> sp.	Valea Graunceanului	Calcaneus	Open	0	0.017	0.0187	0.9642
ID	Species	Site	Element	Assigned Sub.	Dry	Ecotone	Mountain	Wet
FR548a	<i>Alces (Libralces)</i>	Senèze	Phalanx 3	Ecotone	0.0946	0.7225	0.0581	0.1247
FRSeneze1	Cervidae (l)	Senèze	Phalanx 3	Dry	0.5859	0.195	0.213	0.0061
FR697a	Cervidae (m)	Senèze	Phalanx 3	Dry	0.7666	0.1978	0.0304	0.0053
FR693a	Cervidae (m)	Senèze	Phalanx 3	Ecotone	0.0799	0.8854	0.0271	0.0076
FR691a	Cervidae (m)	Senèze	Phalanx 3	Mountain	0.0001	0.0172	0.8763	0.1065
FR690a	Cervidae (m)	Senèze	Phalanx 3	Wet	0.0094	0.187	0.2337	0.5698
FR690c	Cervidae (m)	Senèze	Phalanx 3	Wet	0.0001	0.0097	0.0555	0.9348

ID	Species	Site	Element	Assigned Sub.	Dry	Ecotone	Mountain	Wet
FR690d	Cervidae (m)	Senèze	Phalanx 3	Wet	0.0114	0.2072	0.0062	0.7752
FR690b	Cervidae (s)	Senèze	Phalanx 3	Mountain	0.2379	0.3125	0.4172	0.0324
FR697b	Cervidae (s)	Senèze	Phalanx 3	Mountain	0.0207	0.0765	0.8954	0.0074
FR694c	<i>Cervus philisi</i>	Senèze	Phalanx 3	Dry	0.4465	0.3496	0.1971	0.0069
FR694f	<i>Cervus philisi</i>	Senèze	Phalanx 3	Dry	0.563	0.2218	0.2096	0.0056
FR694h	<i>Cervus philisi</i>	Senèze	Phalanx 3	Dry	0.5089	0.1345	0.3549	0.0017
FR723a	<i>Cervus philisi</i>	Senèze	Phalanx 3	Dry	0.9096	0.0395	0.0493	0.0016
FR723c	<i>Cervus philisi</i>	Senèze	Phalanx 3	Dry	0.5027	0.2394	0.1728	0.0851
FR725a	<i>Cervus philisi</i>	Senèze	Phalanx 3	Dry	0.3315	0.2106	0.303	0.1549
FR725c	<i>Cervus philisi</i>	Senèze	Phalanx 3	Dry	0.5027	0.2394	0.1728	0.0851
FR698a	<i>Cervus philisi</i>	Senèze	Phalanx 3	Ecotone	0.0543	0.4744	0.4212	0.0501
FR698b	<i>Cervus philisi</i>	Senèze	Phalanx 3	Ecotone	0.0412	0.3971	0.2188	0.343
FR700a	<i>Cervus philisi</i>	Senèze	Phalanx 3	Ecotone	0.0877	0.5655	0.1727	0.174
FR725b	<i>Cervus philisi</i>	Senèze	Phalanx 3	Ecotone	0.1513	0.7694	0.0275	0.0518
FR725d	<i>Cervus philisi</i>	Senèze	Phalanx 3	Ecotone	0.0063	0.4795	0.0469	0.4673
FR729a	<i>Cervus philisi</i>	Senèze	Phalanx 3	Ecotone	0.1514	0.6351	0.1919	0.0216
FR729b	<i>Cervus philisi</i>	Senèze	Phalanx 3	Ecotone	0.0224	0.5417	0.4189	0.017
FR694a	<i>Cervus philisi</i>	Senèze	Phalanx 3	Mountain	0.0041	0.0969	0.8	0.099
FR694d	<i>Cervus philisi</i>	Senèze	Phalanx 3	Mountain	0.346	0.3005	0.3503	0.0032
FR694e	<i>Cervus philisi</i>	Senèze	Phalanx 3	Mountain	0.0474	0.0803	0.774	0.0983
FR723b	<i>Cervus philisi</i>	Senèze	Phalanx 3	Mountain	0.2484	0.0878	0.6357	0.0281
FR725f	<i>Cervus philisi</i>	Senèze	Phalanx 3	Mountain	0.001	0.157	0.4555	0.3865
FR694b	<i>Cervus philisi</i>	Senèze	Phalanx 3	Wet	0.0903	0.3686	0.0536	0.4875
FR694g	<i>Cervus philisi</i>	Senèze	Phalanx 3	Wet	0.0013	0.4214	0.0252	0.5521
FR725e	<i>Cervus philisi</i>	Senèze	Phalanx 3	Wet	0.0476	0.1302	0.0884	0.7339

ID	Species	Site	Element	Assigned Sub.	Dry	Ecotone	Mountain	Wet
FR662a	<i>Cervus sp. (l)</i>	Senèze	Phalanx 3	Mountain	0.0007	0.0476	0.7209	0.2308
FR580a	<i>Eucladoceros ctenoides</i>	Senèze	Phalanx 3	Dry	0.7244	0.1024	0.172	0.0012
FR581a	<i>Eucladoceros ctenoides</i>	Senèze	Phalanx 3	Dry	0.4184	0.3772	0.1789	0.0255
FR581b	<i>Eucladoceros ctenoides</i>	Senèze	Phalanx 3	Mountain	0.0715	0.2004	0.7166	0.0115
FR581d	<i>Eucladoceros ctenoides</i>	Senèze	Phalanx 3	Mountain	0.0241	0.2561	0.64	0.0798
FR581c	<i>Eucladoceros ctenoides</i>	Senèze	Phalanx 3	Wet	0.0078	0.0267	0.0017	0.9638
FR3205	Cervidae (m)	St. Vallier	Phalanx 3	Mountain	0.0342	0.2012	0.5031	0.2616
FR3204	Cervidae (s)	St. Vallier	Phalanx 3	Dry	0.9014	0.0551	0.0427	0.0008
FR3210	Cervidae (s)	St. Vallier	Phalanx 3	Ecotone	0.006	0.6752	0.1643	0.1545
FR3212	Cervidae (s)	St. Vallier	Phalanx 3	Ecotone	0.0844	0.4874	0.427	0.0012
FR3206	Cervidae (s)	St. Vallier	Phalanx 3	Mountain	0.0317	0.0655	0.8158	0.0869
FR3214	Cervidae (s)	St. Vallier	Phalanx 3	Mountain	0.0147	0.4177	0.4247	0.1429
FR3203	Cervidae (s)	St. Vallier	Phalanx 3	Wet	0.0017	0.0832	0.312	0.6031
FR581e	<i>Eucladoceros ctenoides</i>	St. Vallier	Phalanx 3	Wet	0.0009	0.0056	0.1168	0.8766
UB2474	<i>Praemegoceros verticornis</i>	Ubeidiya δK39-42	Phalanx 3	Dry	0.9867	0.0101	0.0031	0
UB860	<i>Praemegoceros verticornis</i>	Ubeidiya II23-25	Phalanx 3	Dry	0.7346	0.1583	0.1033	0.0038
UB856	<i>Praemegoceros verticornis</i>	Ubeidiya II23-25	Phalanx 3	Mountain	0.0053	0.1923	0.7635	0.0389
UB1756	<i>Pseudodama sp.</i>	Ubeidiya II23-25	Phalanx 3	Dry	0.5877	0.4042	0.0058	0.0023
UB933	<i>Pseudodama sp.</i>	Ubeidiya II23-25	Phalanx 3	Dry	0.6267	0.3613	0.0023	0.0098
UB935	<i>Pseudodama sp.</i>	Ubeidiya II23-25	Phalanx 3	Dry	0.6267	0.3613	0.0023	0.0098
UB992	<i>Pseudodama sp.</i>	Ubeidiya II23-25	Phalanx 3	Mountain	0.1882	0.2397	0.4435	0.1286
UB2481	<i>Pseudodama sp.</i>	Ubeidiya II26-27	Phalanx 3	Mountain	0.0077	0.2582	0.7115	0.0227
UB2477	<i>Pseudodama sp.</i>	Ubeidiya II26-27	Phalanx 3	Wet	0.0035	0.3382	0.2046	0.4537
UB691a	<i>Praemegoceros verticornis</i>	Ubeidiya II37	Phalanx 3	Dry	0.9896	0.0026	0.0078	0
UB691b	<i>Praemegoceros verticornis</i>	Ubeidiya II37	Phalanx 3	Dry	0.8621	0.039	0.0987	0.0001

ID	Species	Site	Element	Assigned Sub.	Dry	Ecotone	Mountain	Wet
UB1068	<i>Praemegoceros verticornis</i>	Ubeidiya III11-13	Phalanx 3	Dry	0.606	0.2224	0.167	0.0045
UB1017	<i>Pseudodama</i> sp.	Ubeidiya III11-13	Phalanx 3	Ecotone	0.0392	0.8433	0.0541	0.0633
UB2212	<i>Pseudodama</i> sp.	Ubeidiya III21-22	Phalanx 3	Ecotone	0.3458	0.4806	0.1675	0.0061
UB2460	<i>Pseudodama</i> sp.	Ubeidiya III21-22	Phalanx 3	Ecotone	0.024	0.8393	0.1104	0.0263
UB2281	<i>Pseudodama</i> sp.	Ubeidiya III21-22	Phalanx 3	Mountain	0.0584	0.4143	0.4248	0.1024
RO9362	<i>Eucladoceros</i> sp.	Valea Graunceanului	Phalanx 3	Dry	0.5203	0.0851	0.3874	0.0072
RO9335	<i>Eucladoceros</i> sp.	Valea Graunceanului	Phalanx 3	Dry	0.5616	0.0851	0.3508	0.0025
RO9368	<i>Eucladoceros</i> sp.	Valea Graunceanului	Phalanx 3	Dry	0.5926	0.3093	0.091	0.0071
RO9358	<i>Eucladoceros</i> sp.	Valea Graunceanului	Phalanx 3	Dry	0.7938	0.0955	0.1107	0
RO9342	<i>Eucladoceros</i> sp.	Valea Graunceanului	Phalanx 3	Dry	0.8678	0.0418	0.0893	0.0012
RO9341	<i>Eucladoceros</i> sp.	Valea Graunceanului	Phalanx 3	Dry	0.8897	0.0448	0.0639	0.0016
RO9369	<i>Eucladoceros</i> sp.	Valea Graunceanului	Phalanx 3	Dry	0.8915	0.0316	0.0768	0
RO9333	<i>Eucladoceros</i> sp.	Valea Graunceanului	Phalanx 3	Dry	0.9181	0.0576	0.0234	0.0009
RO9372	<i>Eucladoceros</i> sp.	Valea Graunceanului	Phalanx 3	Dry	0.9841	0.0109	0.005	0
RO9355	<i>Eucladoceros</i> sp.	Valea Graunceanului	Phalanx 3	Dry	0.9845	0.0092	0.0063	0
RO9337	<i>Eucladoceros</i> sp.	Valea Graunceanului	Phalanx 3	Dry	0.9873	0.0116	0.0009	0.0002
RO9343	<i>Eucladoceros</i> sp.	Valea Graunceanului	Phalanx 3	Ecotone	0.1866	0.4323	0.3546	0.0264
RO9361	<i>Eucladoceros</i> sp.	Valea Graunceanului	Phalanx 3	Mountain	0.0004	0.0058	0.9621	0.0317
RO9366	<i>Eucladoceros</i> sp.	Valea Graunceanului	Phalanx 3	Mountain	0.0015	0.0268	0.907	0.0647
RO9334	<i>Eucladoceros</i> sp.	Valea Graunceanului	Phalanx 3	Mountain	0.0085	0.0151	0.9325	0.0439
RO9357	<i>Eucladoceros</i> sp.	Valea Graunceanului	Phalanx 3	Mountain	0.0223	0.035	0.9165	0.0262
RO9371	<i>Eucladoceros</i> sp.	Valea Graunceanului	Phalanx 3	Mountain	0.025	0.0299	0.9422	0.0029
RO9346	<i>Eucladoceros</i> sp.	Valea Graunceanului	Phalanx 3	Mountain	0.09	0.0297	0.8363	0.044
RO9356	<i>Eucladoceros</i> sp.	Valea Graunceanului	Phalanx 3	Mountain	0.0911	0.1023	0.573	0.2336
RO9336	<i>Eucladoceros</i> sp.	Valea Graunceanului	Phalanx 3	Mountain	0.1098	0.2744	0.5863	0.0295

ID	Species	Site	Element	Assigned Sub.	Dry	Ecotone	Mountain	Wet
RO9349	<i>Eucladoceros</i> sp.	Valea Graunceanului	Phalanx 3	Mountain	0.124	0.1863	0.6881	0.0017
RO9351	<i>Eucladoceros</i> sp.	Valea Graunceanului	Phalanx 3	Mountain	0.1456	0.0295	0.8073	0.0176
RO9354	<i>Eucladoceros</i> sp.	Valea Graunceanului	Phalanx 3	Mountain	0.1507	0.2627	0.5384	0.0482
RO9353	<i>Eucladoceros</i> sp.	Valea Graunceanului	Phalanx 3	Wet	0.0007	0.0392	0.1836	0.7765

Abbreviations: Assigned Hab. = Habitat assigned to specimen based on cross-validation, Assigned Sub. – Substrate assigned to specimen based on cross-validation, InterOpen = Intermediate Open, InterClosed = Intermediate Closed, (s) = small-sized Cervidae specimen, (m) = medium-sized Cervidae specimen, (l) = large-sized Cervidae specimen, sp. = Species unknown or unidentified.