BOVIDS AS PALAEOENVIRONMENTAL INDICATORS:
AN ECOMORPHOLOGICAL ANALYSIS OF BOVID POST-CRANIAL REMAINS FROM LAETOLI, TANZANIA

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ABSTRACT

This thesis reports on 1) a new method of palaeoenvironmental reconstruction using bovid ecomorphology and 2) the application of this methodology to fossil assemblages from the Plio-Pleistocene site of Laetoli, Tanzania.

A global sample of extant bovids (n=205), cervids (n=14) and tragulids (n=5) from seven known habitat types comprise the comparative dataset. All long bones, carpals, tarsals and phalanges are measured. These measurements are entered as predictor variables in discriminant function analyses (DFA) in order to evaluate the ability of each element to accurately predict habitat affiliation. The baseline of chance accuracy for DFAs (i.e. the percentage of correct predictions that can be expected when habitat assignments are randomised) is determined. This baseline serves as the cut-off point between good and bad habitat predictors. Analyses are conducted on non-size corrected and size corrected data. The results of both sets of analyses are similar. A total of 24 analyses of non-size corrected elements and 23 size corrected analyses yield percentages of correct classification over the baseline of accuracy. The non-size corrected analyses are extended to the Laetoli fossil assemblages.

DFAs are conducted on fossil assemblages from the Upper Laetolil Beds (3.50 – 3.80 mya) and the Upper Ndolanya Beds (2.66 mya). Summaries of the number of specimens predicted to belong to each habitat type and their associated probabilities of correct prediction are used to reconstruct the palaeoenvironment. The results indicate that at the time of the deposition of the Laetolil Beds the area had heavy woodland-bushland cover with some lighter tree and bush cover and grass available. This lends strong support to recent suggestions that the area was on the more wooded end of the habitat spectrum, contra initial conclusions that it represented a mosaic of more open habitats. It furthermore supports the theory that early australopithecines such as *Australopithecus afarensis* required a significant amount of tree cover for survival. The results also indicate that during the deposition of the Ndolanya Beds the environment had become more open and the grassland component of the environment had increased significantly. Light woodland-bushland and an abundance of grass cover dominated the landscape, although tracts of land with denser vegetation likely existed. This agrees with earlier suggestions that the area was a semi-arid bushland. It also supports the theory that *Paranthropus aethiopicus* was adapted to a lifestyle in a more open and arid environment than earlier species.

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Thus the universe and all things therein are without a single exception strange and wondrous when examined carefully.
~ Motoori Noringa ~

This is my attempt to examine one small part of the strange and wondrous universe.

Fire * Kovarovic
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1 INTRODUCTION

1.1 Hominid evolution and environment

One of the recent trends in palaeoanthropological research has focused on setting events in hominid evolution in an environmental context (Vrba, 1985b; Vrba *et al.*, 1989; Vrba, 1994; Bromage & Schrenk, 1995; Reed 1997; Potts, 1998; de Heinzelin *et al.*, 1999). This has been driven by the understanding that hominids are but one species in a larger mammalian community and that it is not only the individual species which respond and adapt to aspects of habitat, but entire communities of species (community is used here to mean the resident mammals in any one habitat). It has been suggested that environmental change has driven mammalian, and thus hominid, evolution (Vrba, 1985b; 1988; Vrba *et al.*, 1989; Foley, 1987; Hill & Ward, 1988; Potts, 1996a; Bobe *et al.*, 2002; Wynn, 2004). Attempts to understand past climatic changes, and the responses of mammalian communities to these changes, have been informed by research conducted in palynology, sedimentology, comparative anatomy, and palaeoecology. By combining various lines of evidence to provide a better picture of the environment at one locality at one point on the geological timeline, and then combining what we know about a number of sites at different points in time in the same area, we can build up an understanding of regional environmental change.

This is the backdrop against which we set the story of mammalian evolution, and the process through which we may better understand how environmental change and evolution interface to select for new adaptations, new species or, at the other extreme end, extinctions. Many novel adaptations and reconstructed behaviours in the hominid lineages including bipedalism (e.g. Laporte & Zihlman, 1983), the development of lithic tool industries (e.g. Washburn, 1960) and the megadontia of the robust australopithecines (e.g. Turner & Wood, 1993) that may have allowed for the processing of hard seeds (e.g. Jolly, 1970), in addition to the splitting of the *Homo* lineage (e.g. Vrba, 1988; Stanley, 1992), have all been attributed to environmental change.

Our earliest understanding of this change placed the narrative of evolution within the context of an expanding open and increasingly arid savanna, which our ancestors entered from the relative safety and abundance of the forests and woodlands (Dart, 1925, 1953; Bartholomew & Birdsell, 1953). Although the end of the Miocene did witness a marked shift towards environments that were more open and habitat diversity seems to have increased (Andrews, 1981; Retallack *et al.*, 1990; Cerling *et al.*, 1991), the picture is more complicated than a gradual and unidirectional shift from forest to open savanna and hence the setting for hominid evolution is ecologically complex. There is no doubt that aridification did occur and that it had some impact on evolution, but where and when and how it did so is still debated.

Proponents of the "turnover pulse" hypothesis (Vrba, 1980, 1985c, 1988) interpret synchronous speciation and extinction events – or "pulses" - as indicative of rapid environmental change. During the Pliocene and Pleistocene, such events are linked with evidence for global cooling indicated by changes in oxygen isotopes in deep-sea core samples (Prentice & Denton, 1988). This had the effect of shrinking the moister forest biome in Africa and replacing it with open, drier and more seasonal habitats. Appearances of open country grazing bovids (Vrba, 1985c, 1988, 1992, 1995) and the concomitant disappearance of forest-adapted micromammals (Wesselman, 1984) indicate that at approximately 2.5 Ma, when the robust australopithecines (i.e. *Paranthropus*) and the *Homo* lineage appeared, the environment went through such an alteration. Two additional pulses, again linked to trends in global cooling and African aridification, were further identified at 5Ma and .9Ma, when the Hominini appeared and when *Homo erectus* began migrating out of Africa, respectively (Vrba *et al.*, 1989).

Critics of the turnover pulse hypothesis point towards a pattern of climatic variability characterised by rapid fluctuations in temperature, aridity and localised remodelling of hydrology and floral communities as the most important selective force in hominid evolution (Potts, 1996a, 1998; Behrensmeyer *et al.,* 1997; Bobe *et al.,* 2002; deMenocal, 2004). Rapid oscillations in these conditions are hypothesised to have selected for biological and behavioural versatility and against species displaying habitat-specific characteristics or behaviour. Hominids throughout the Pliocene and Pleistocene were faced with rapid environmental change and those species that were more innovative in dealing with new habitats were more successful (Potts, 1996b). This "variability selection" hypothesis is supported by the correlation of periods of intense environmental fluctuation with the advent of adaptations in hominid species, which were presumably advantageous in novel habitats, including increased brain size, lithic tool use, symbolic communication and greater geographic ranges (van der Weil & Wijmstra, 1987; deMenocal *et al.*, 1993; Tiedemann *et al.*, 1994; Potts 1994, 1996a, 1996b).

1.1 Palaeoecological reconstruction

Our understanding of local and regional environments and the changes that occurred to them throughout hominid evolution will only be as good as the techniques that we have for revealing them. Providing a comprehensive picture across space and time is a multidisciplinary effort, but it is palaeoecology which uniquely informs us of both the physical environment and the living community which it supports.

Palaeoecological studies based on mammalian evidence seek to elucidate the relationships between faunal communities and the habitats in which they reside through analyses of fossils. Morphologies retained in skeletal remains, and distributions of body sizes inferred from regression formulae derived from measurements of post-cranial or dental features, provide clues as to habitat exploitation. Characteristics of skeletal anatomy can be related directly to habitat types; these features are known as ecomorphologies.

Phylogeny can be a potentially confounding factor in ecomorphological studies. The goal of such research is to identify characteristics that relate explicitly to habitat exploitation rather than shared ancestry. The assumption is that when two distantly related species live in similar habitats, the morphologies they have in common with one another, but which are not exhibited in more closely related species, are functional adaptations to their similar habitats. However, isolating ecomorphologies is hardly straightforward. Certain taxonomic groups prefer similar habitats; for instance, members of the bovid subfamily Caprinae favour rugged and usually mountainous terrain. Are caprine morphologies then phylogenetic or functional?

The answer in this case is likely that many of their characteristics indicate both habitat and phylogeny, perhaps in equal parts. Although there is no easy solution to this problem, it can be addressed by examining a diverse sample of species, both in terms of relatedness and known habitat preferences, and by rigorous testing of the morphologies in question to determine if they are better suited for discriminating taxonomic affiliation or habitat. It is also necessary to understand the myriad ways in which habitats can be utilised by mammals, the variables that differ between habitats and the resulting array of conditions presented to resident species.

A habitat can be defined on the basis of its biotic and abiotic parameters (Odum, 1983). The abiotic elements include such things as weather patterns, soil types, temperature, and geologic formations, and biotic elements consist of vegetation and resident animal and insect life. Individual species exist in a particular environment by filling both the spatial and trophic niches presented by the habitat in a unique way. Resource exploitation strategies may involve one or a combination of feeding preferences including herbivory, carnivory, insectivory or frugivory, and these may change throughout the year as seasonal changes affect the resource base. The spatial niche refers to the physical strata of the environment in which the species spends the majority of its time, and the distribution of cover presented by the habitat. An animal may therefore be terrestrial, arboreal, aquatic, or aerial, or it may combine locomotor patterns. Some have developed specialised forms of locomotion, such as fossorial rodents which burrow underground, scansorial felids which can climb efficiently up and down the vertical trunks and limbs of trees, and the "flying" squirrels which glide through the air.

A great number of ecomorphological studies have concentrated on analyses of Bovidae, an Artiodactyl family of ruminating mammals (a review of this work can be found in chapter 2), although they have also been conducted on carnivores (Van Valkenburgh, 1987), suids (Bishop, 1994) and cercopithecids (Elton, 2001). However, bovids are generally thought to be better for the task. Not only are their remains generally abundant at sites pertaining to hominid evolution in Africa, but they exist in many diverse forms across the world today, so that comparisons with fossils can easily be made. Bovid communities are potential tools for teasing out more specific environmental information. Especially in Africa, a great number of species may occupy the same general habitat, coexisting and avoiding competition through a complex system of resource partitioning.

This principle of coexistence has long interested ecologists who very early noted that several closely related species in one relatively stable environment can coexist along a set of dimensions that differentiate two environmental realities with which living communities are faced: resource availability across 1) space and 2) time (Hutchinson, 1957; Schoener, 1974). Some competition at the intersection of these dimensions creates a limit to each species' niche availability, however this competition contributes to the maintanance of population size and community stability (Hutchinson, 1957; May & MacArthur, 1972). For bovids, competition is characterised by an ability to partition herbivorous resources. Each species consumes a characteristic subset of the available grass and browse in varied proportions which may also change during the year as seasonal availability modifies the resource base (Underwood, 1983; McNaughton & Georgiadis, 1986). Furthermore, individual species may specialise in feeding on the different parts of a plant such as the leaf, stem, sheath, seed or fruit (Gwynne & Bell, 1968) or exploit different aspects of the soil catena in one area (Gwynne & Bell, 1968; Bell, 1970; 1971). This dietary diversification may have been the key to the successful radiations of bovids throughout the course of the family's evolutionary history.

Bovids have become an increasingly important aspect of current palaeoecological research as the scientific community has come to recognise their usefulness in habitat reconstruction. As we persist in refining our understanding of extant bovid resource partitioning, habitat selection and locomotor patterns, we will continue to apply this knowledge in greater detail to the fossil record so that we may produce more sensitive environmental reconstructions (Sponheimer *et al.*, 1999; Solounias & Semprebon, 2002; DeGusta & Vrba, 2003). This project seeks to add to this body of knowledge, and it will do so in two different ways.

Firstly, it explores the efficiency of bovid postcrania as habitat predictors by examining a number of extant bovid species from a variety of habitats around the world. Presently there exists a vast amount of research that has tackled the issue of the relationship between bovids and their habitats, and the research reported here contributes to what is already known. One of the most important contributions of this project is that it increases the number of skeletal elements that may be studied in an ecomorphological context. There is abundant literature pertaining to some of the long bones (Gentry, 1970; Scott, 1979, 1983, 1985; Kappelman, 1988, 1991; Köhler, 1993; Plummer & Bishop, 1994; Kappelman *et al.*, 1997), but the less conspicuous, smaller or more irregularly shaped elements have not received the same attention, with the single exception of one recent study of the talus (DeGusta & Vrba, 2003).

The dataset analysed in this project includes these hitherto ignored elements, allowing a great many more fossils to be studied than has previously been the case. In some cases, where the fossils from certain sites are quite fragmentary for a variety of taphonomic reasons (for instance, long-term weathering or carnivore damage prior to deposition), this may prove to be invaluable. Elements such as the carpals and tarsals are relatively small, but they often survive in situations where long bones would otherwise be destroyed. These elements are not only dense, but they are nutritionally unattractive to scavengers and, despite their proximity to the metapodials which are broken for their marrow, these are generally recovered intact.

The second aspect of this project is an improved palaeoenvironmental reconstruction of the important Plio-Pleistocene site of Laetoli in northern Tanzania using the efficient skeletal predictors identified in the analyses of the modern comparative dataset. Located just south of Olduvai Gorge, and initially surveyed in the 1940s (Kent, 1941; Kohl-Larsen, 1943), Laetoli has been extensively studied by a number of research teams for the past thirty years (Leakey & Harris, 1987; Ndessokia, 1990; Harrison, pers. comm.). Despite the site's prevalence in the literature, a closer look at the fossil bearing 3.5 – 3.8 mya Laetolil Beds and the younger 2.66 mya Upper Ndolanya Beds was warranted. Both of these beds have yielded hominid fossils; numerous remains of *Australopithecus afarensis*, including the holotype specimen, have been found in the Laetolil Beds deposits (Leakey & Harris, 1987) and two specimens attributed to *Paranthropus aethiopicus* have been found in the Ndolanya Beds, a recent discovery that has extended the known geographical range of this species further south from its previously known range in northern Kenya and southern Ethiopia (Harrison, 2002).

Recent palaeoecological analyses of the Laetolil Beds (Andrews, 1989; Reed, 1997; Andrews & Humphrey, 1999) have not supported earlier suggestions that a mosaic of open savanna habitats predominated at this time (Leakey & Harris, 1987). In fact, a number of analyses have suggested that the earlier australopithecines, like *Australopithecus afarensis*, preferred more wooded habitats than previously believed (e.g. Reed, 1997). Furthermore, the Ndolanya Beds have only received one in-depth palaeoecological analysis to date (Kovarovic, *et al.*, 2002). From the evidence presented therein, it appears that a significant change in environment occurred in the Laetoli area during the Plio-Pleistocene, from a predominantly wooded habitat represented by the Laetolil Beds, to a semi-arid bushland in the Ndolanya Beds. It is important to clarify the palaeoenvironmental conditions at Laetoli in order to understand the habitats that were exploited by the hominid species that inhabited the area.

A re-analysis of this site was facilitated by Terry Harrison's recent collections (from the 1997 – 2001 field seasons) from each fossil-bearing locality at the site and which are now available for study in the National Museums of Tanzania in Dar-es-Salaam. His collections were augmented by Mary Leakey's original Laetoli finds from excavations carried out between 1975 and 1981, although the majority of her bovid fossils have been previously dispersed to unspecified locations. Both the Harrison and Leakey material formed the fossil database.

1.2 Organisation of dissertation

Six chapters follow this introduction. In Chapter 2, the basic features and evolutionary history of the family Bovidae and the particulars of both past and present work at Laetoli all serve as a foundation for understanding and approaching the research reported in this dissertation. An account of previous work that has focused on bovids sets this project into the context of a large body of research aimed at palaeoenvironmental reconstruction utilising these fossils. This account, also found in Chapter 2, makes clear how the field has developed and how my work carries on from the contributions of others.

The bovid collections studied, the specific methods employed in gathering and coding the data and the statistical analyses applied to the final dataset are detailed in Chapter 3. This chapter also details the size correcting procedure and outlines the statistical considerations underlying discriminant function analyses. The point at which the analyses of individual elements may be discarded as inadequate habitat predictors is also determined.

Chapters 4 and 5 report on the results of the analyses conducted on the modern data. Chapter 4 focuses on the long bones and their distal and proximal ends, while Chapter 5 looks at the carpals, tarsals and phalanges. Analyses are conducted on both size corrected and non-size corrected data. The relative success rates of the analyses are compared and good to reasonable habitat predictors are identified. Examples of interpreting the cases of misclassified species are also provided, as is a description of the results as they compare to previous studies.

Nineteen good to reasonable predictor elements are carried forward to the fossil material from Laetoli in Chapter 6. Analyses are conducted on only non-size corrected data and the habitat predictions of the fossil material are compared between the Laetolil and Ndolanya Beds. An examination of the probabilities associated with the predictions is included in order to determine the confidence one can place in the predictions and subsequent conclusions drawn from the results.

Chapter 7 discusses the statistical considerations which relate to the analyses, specifically the affect of the composition of the modern comparative dataset on which the habitat predictions are based. An interpretation of the habitats present during the deposition of the Laetolil and Ndolanya Beds at Laetoli is then made. A brief outline of the palaeoenvironmental reconstructions of other Plio-Pleistocene East African sites is provided. The evolution of Plio-Pleistocene hominids dating to the timeframe which is bracketed by the Laetolil and Ndolanya Beds is discussed in light of the habitat types favoured by each species and the changing palaeoenvironmental conditions in East Africa.

2 LITERATURE REVIEW

2.1 Bovidae

2.1.1 Evolutionary history and diagnostic features

Bovidae is but one family in the order of even-toed mammals known as Artiodactyla, which in turn is one of seven extant orders comprising the mammalian superorder Ungulata, the hoofed mammals. These mammals arose approximately 65-70 million years ago, although there may be some evidence to suggest that the family Zhelestidae, which emerged twenty million years earlier, was the first ungulate taxa (Archibald, 1996; Kingdon, 1997). The extant orders of Ungulata are now believed to be Cetacea (whales and dolphins), Hyracoidea (hyraxes), Perissodactyla (odd-toed ungulates), Proboscidea (proboscids), Sirenia (sea cows) and Tubulidentata (aardvarks) in addition to Artiodactyla (Szalay, *et al.,* Eds, 1993). The composite taxa of Ungulata are summarised in Table 2.1.

Distinguishable artiodactyl features include their even numbered toes and paraxonic feet, the axis of which runs through the third and fourth digits, reduced partietals and enlarged frontals, generally absent clavicle, reduced ulna and fibula, simple premolars, diastema between the canine or incisors and the premolars, and a talus with an inferior pulley surface and a superior rolling articular surface, among others obvious characteristics (for a more in-depth summary of any of the artiodactyl family morphologies, see Romer, 1945 and Koopman, 1967). The order is divided into three suborders, the Suiformes (pigs, peccaries and hippopotamuses), Tylopoda (camels and llamas) and the Ruminantia, which are characterised by unique three or four chambered stomachs in which vegetation is efficiently and continuously digested (Romer, 1945). Both the living and fossil ruminants are also united by a skeletal

Table 2.1. Relationships of the taxa in the superorder Ungulata

SUPERORDER	ORDER	SUBORDER	INFRAORDER	FAMILY
Ungulata ⇒ hoofed mammals	**Cetacea** whales, dolphins			
	Hyracoidea hyraxes			
	Perissodactyla odd-toes ungulates			
	Proboscidea elephants			
	Sirenia sea-cows			
	Tubulidentata aardvarks			
	Artiodactyla ⇒ even-toed ungulates	**Suiformes** pigs, peccaries, hippos		
		Tylopoda camels, llamas		
		Ruminantia ⇒ ruminating mammals	**Tragulina** tragulids	
			Pecora ⇒ ruminants with cranial appendages	**Antilocapridae** **Giraffidae** **Moschidae (?)** **Cerivdae** **Bovidae**

apomorphy, the fusion of the navicular and the cuboid (Romer, 1945; Lavocat, 1955). Ruminants may further be subdivided into two infraorders, the basal Tragulina, which is comprised of only one living family, Tragulidae (chevrotain) and the Pecora, comprised of the remaining families: Cervidae (deer, which some believe is distinct from Moschidae, the musk deer), Antilocapridae (antilocaprids), Giraffidae (giraffe and okapi) and Bovidae (bovids) (Janis & Scott, 1987; Scott & Janis, 1993; Hassanin & Douzery, 2003).

Artiodactyls are first noticeable in the fossil record 55 million years ago at the beginning of the Eocene, when a drop in global sea level and a widespread mammalian radiation occurred concurrently (Gentry, 2000). Artiodactyls are known then from North America, where their remains are relatively abundant, and Europe and Asia, where they are scarcer. They appear to have been related to a diverse group of primitive, clawed herbivores known as condylarths. *Chriacus*, a small North American Arctocyonidae (a family of condylarths that superficially appear to be carnivores), closely resembles the earliest known artiodactyls (Rose, 1996). This indicates that artiodactyls may have evolved from arctocyonids, although others have suggested that Artiodactyla is a sister group to all other ungulates including the arctocyonids (Prothero *et al.*, 1988). Throughout the Eocene the artiodactyls were outnumbered by the Perissodactyla, their odd-toed ungulate cousins, until the Eocene-Oligocene transition when the feeding strategies of the specialised folivorous artiodactyls were better suited to increasingly more seasonal habitats (Janis, 1989, 1993).

Bovid roots lie in the tragulid lineage, the most primitive ruminant family which originated in the Old World tropics. These chevrotains are small ungulates possessing, among many other features, four toes, two metapodials (fusing in some species), complete fibula, and fused distal malleolus and tibia. Males have large upper canines which function as effective weapons. This once widespread family is now represented by only four species: three in the Asian genus, *Tragulus napu*, *Tragulus javanicus* and *Tragulus meminna*, and one in Africa, *Hyemoshcus aquaticus*. A common ancestor to both the cervids, deer, and the horned ungulates, or bovids, may have split from the traguloid line due to the evolution of a more advanced ruminating digestive system, which allowed these species to exploit a different vegetation base (Kingdon, 1982). The exact timing of this split is debated, but it may have occurred in the early Oligocene (Romer, 1945; Simpson, 1945).

Evidence for bovid and cervid evolution over the next several million years is scant, but it appears that cervids evolved in Eurasia from the early Miocene onwards, with bovids firmly established there by the middle Miocene (Gentry, 2000). The cervid-bovid split may have occurred when cervids took to the cooler regions at higher latitudes and primitive bovids adapted a better resistance to warmer temperatures, facilitating their later immigration into the African continent as the global climate warmed (Kingdon, 1982).

Extant cervid autapomorphies include small lateral toes and a fibula that has been reduced to only the unfused distal end (Koopman, 1967; Romer, 1945). Metapodials have also fused into one long bone, known as the cannon bone. Males annually grow and shed antlers that serve as defensive weapons (except in the genus *Rangifer*, where they are present in both sexes and *Hydropotes* where they are entirely absent). Cervidae is a non-African family, although in the past million years the red deer (*Cervus elaphus*) has immigrated to and successfully occupied North Africa (Kingdon, 1997). The greatest cervid diversity is found today in South America and Southeast Asia, but they are also found across all of Eurasia and the Americas. There is considerable ecological overlap between modern cervids and bovids, although it may have been along the temperature gradient that the two lines first divided.

Extant bovids are morphologically very similar to cervids but are unique in some characteristics. These include the loss of lateral digits (although they are occasionally present only as small vestigial bones), a reduced or absent upper canine, and a generally more hypsodont dentition (Romer, 1945). Bovids also possess a permanent sheath of keratin over a bony horn core in males and often in females, although often in a less developed form. The evolution of horns occurred in several separate artiodactyl lineages and was related to both reproductive strategies and ecological factors (Gentry, 2000; Janis, 1986; 1982; Geist, 1974). Janis (1982) argues that when climate changes occurred and ruminant artiodactyls evolved from small, forest and closed woodland dwelling frugivores into larger (>15 kg), more open woodland dwelling folivores, a selective advantage was conferred on those males that could adopt and maintain feeding and breeding territories. The development of horns as weapons played an important role in territory defence. Modern bovid species which are smaller than 15kg, or practice different feeding strategies than those viable within a woodland habitat, still retain and utilise their horns in dominance hierarchies and, as has been noted, horns also evolved in females of some species, most of which are larger open habitat feeders (Jarman, 1974).

Although some remains dating as far back as the Oligocene in Asia have been tentatively identified as bovid (Wang, 1992), the earliest true bovid that is well known from fossil evidence, *Eotragus*, appears approximately 18 million years ago during the Miocene. It was a brachyodont species possessing short, straight horns in males (Thenius, 1969). Early remains are found at Burdigalain d'Artenay, France (Ginsberg & Heintz, 1968), Bunyol, Spain (Moya Sola, 1983), Gebel Zelten, Libya (Hamilton,

1973) and in the Kamlial Formation, Pakistan (Solounias *et al.*, 1995a). However, before we have concrete evidence of the basal bovids such as *Eotragus* emerging in the fossil record, the Bovidae had evolved and differentiated into two main lineages, the Bovinae (bovines) and Antilopinae (antelopes, goats and sheep). *Eotragus* shares similarities with the Antilopinae, especially skull characteristics that resemble cephalophines, although it is too late in time and large-bodied to be a direct ancestor (Kingdon, 1982). The split had probably occurred by the time of the Oligocene-Miocene transition. The divergence may relate to a long period of continental separation, in which the Antilopinae would have evolved from Asian stock that migrated into Africa, where they initially specialised in drier habitats and were of a smaller size. Once in Africa they differentiated into tropical and arid types, some of which returned to Asia and gave rise to the goats and related species.

Bovinae is the more primitive of the two lineages (Gentry, 1978), and is distinct from the Antilopinae in a number of ways. The bovines are larger and possess smooth horns and two pairs of mammae in contrast to the antelope condition of annulated horns and one (although sometimes two) pair of mammae. The antelopes may also possess pedal glands for scent marking, which are always absent in the bovines. The most distinctive antilopine innovation, and one which lends credence to the theory that they were more arid adapted and thus able to successfully diversify in African environments, is their thermoregulation system in which nasal panting, rather than sweating, keeps them cool (Taylor, 1972; Johnson, 1977; Kingdon, 1982). In order to regulate body temperature through sweating, one needs a large body size and frequent intake of water. Smaller bovids would not be able to afford sweating away so much water, so therefore evaporation within the nasal passage is more economical in relation to their size. This adaptation also allowed them to inhabit drier habitats, because not only were they conservative with water loss, but their adaptation of nasal panting cools blood in the nasal linings, which is then circulated back into the body and towards the brain (Hayward, 1972).

Throughout bovid evolution there has been a high degree of parallel evolution in both bovine and antelope tribes in their dental morphology (especially in the premolars), development of horns, and ability to better digest and masticate grass, (Vrba, 1979). Further complicating the picture, radiations of species out of Eurasia and into Africa have occurred more than once (at the very least, three times), with the more arid adapted species being able to migrate more freely between the continents (Kingdon, 1997). Bovids diversified at an incredibly rapid pace during the Miocene, especially towards the end of the epoch, making their relationships difficult to trace in the fossil record. They eventually migrated into North America during the Pleistocene, but have not naturally colonised South America, Australia, or Antarctica (Simpson, 1945; Gentry, 1978; Savage & Russell, 1983).

2.1.2 Modern bovids

The exact evolutionary relationships of extant bovids are difficult to discern, and researchers have produced morphological, behavioural and molecular studies seeking to illuminate them. Such research is confounded by the apparent rapid radiation of bovid species (Vrba, 1985a) which, if assumed to be constant over evolutionary time, does not allow enough time for synapomorphic changes to accumulate, and the groupings in any tree are therefore less robust (Wyss *et al*, 1987; Gatesy *et al*, 1992). Most analyses highlight not only this confounding factor, but isolate four particular species that do not have a consistent taxonomic affiliation: the impala, *Aepyceros melampus*, Vaal rhebok, *Pelea capreolus*, chiru, *Pantholops hodgsonii*, and saiga, *Saiga tatarica*.

Traditional classifications of bovids, which include only Antilopinae and Bovidae as subfamilies, have been challenged by recent analyses that find evidence for further subdividing Antilopinae into several distinct subfamilies (Vrba & Schaller, 2000; Gentry pers. comm.). The taxonomic assignment of the twelve traditional tribes and their composite genera is outlined in Table 2.2, which has been modified from Gentry (1992; pers. comm.) and Vrba & Schaller (2000). These researchers generally agree with the subfamily divisions and tribal assignments, but differ on two main points: the placement of the indeterminate species and the position of the cephalophines. Gentry feels that Cephalophini should be assigned to either Bovinae or Antilopinae (Gentry, pers. comm.). However, Vrba and Schaller (2000) designate it as a separate subfamily, Cephalophinae, which is reminiscent of Schwarz's early revision of the Bovidae (Schwarz, 1937) in which he observed three main lineages, one of which included only the cephalophines. On the grounds that Vrba and Schaller's analysis only included one cephalophine species, I retain the more traditional classification in which the tribe is a member of the Antilopinae subfamily. Furthermore, I do not assign indeterminate species to a tribe or subfamily (but see discussion below). Thus, Table 2.2 does not represent an active contribution to bovid taxonomy, but it summarises the general state of our current understanding of bovid phylogenetic relationships.

A number of morphological studies sought to affiliate *Aepyceros*, *Pelea*, *Panthalops*, and *Saiga* with one of the extant tribes. Some workers originally placed *Aepyceros* in Antilopini (Simpson, 1945) while others later found it to be more closely affiliated to the alcelaphines (Gentry, 1978;1985; Vrba, 1979). Another school

Table 2.2. Extant bovid subfamilies, tribes and genera

Subfamily/Tribe	Genera
BOVINAE	
Tragelaphini	*Tragelaphus*, *Taurotragus*
Boselaphini	*Boselaphus*, *Tetracerus*
Bovini	*Bos*, *Bison*, *Syncerus*, *Bubalus*
ANTILOPINAE	
Cephalophini	*Cephalophus*, *Sylvicapra*
Neotragini	*Raphicerus*, *Dorcotragus*, *Neotragus*, *Madoqua*, *Oreotragus*, *Ourebia*
Antilopini	*Gazella*, *Antilope*, *Antidorcas*, *Litocranius*, *Ammodorcas*
REDUNCINAE	
Reduncini	*Kobus*, *Redunca*
HIPPOTRAGINAE	
Hippotragini	*Hippotragus*, *Oryx*, *Addax*
Alcelaphini	*Connochaetes*, *Alcelaphus*, *Damaliscus*
CAPRINAE	
Rupicaprini	*Rupicapra*, *Nemorhaedus*, *Oreamnos*, *Procapra*
Caprini	*Capra*, *Ovis*, *Pseudois*, *Hemitragus*
Ovibovini	*Ovibos*, *Budorcas*
INDETERMINATE	*Aepyceros*, *Pelea*, *Pantholops*, *Saiga*

Subfamilies are in capital letters, tribes in normal print and genera in italics of thought places it in a sister group, the tribe Aepycerotini (Vrba, 1984; Thomas, 1984), which is currently believed to have split during the early stages of antilopine evolution (Vrba & Schaller, 2000). *Pelea* was originally considered a reduncine (Schwarz, 1937), which is similar to the most recent cladistic analysis that indicates it is closely related to that tribe (Vrba & Schaller, 2000). It has alternatively been placed in Antilopini (Oboussier, 1970) or its own tribe, Peleini (Vrba, 1976, 1985). Gentry (1992) has suggested that it may be a neotragine, although affinities with *Aepyceros* can not be ignored. *Saiga* appears to be best affiliated with the Asian members of Antilopini and *Pantholops*, although proving the most difficult to place, is currently thought to be related to Caprini (Gentry, 1992; Vrba & Schaller, 2000).

Molecular studies on bovid relationships support the idea that several distinct subfamilies were mistakenly lumped under the original Antilopinae rubric. These studies complement the cladograms derived from analyses of morphological characteristics and have aimed not only to place the four controversial species firmly within a tribe, but to create a cladogram of the tribal relationships, and to sort out relationships within tribes, especially in regards to Reduncini, which has always presented difficulties (Gentry, 1992; Birungi & Arctander, 2001). A variety of methods have been utilised, including analyses of allozymes (Georgiadis *et al*, 1992), DNA sequences (Gatesy *et al.,* 1992, Chikuni *et al,* 1995; Groves & Shields, 1996), including mitochondrial DNA (Gatesy *et al.,* 1992, 1997; Hassanin & Douzery, 1999; Birungi & Arctander, 2001) and nuclear-ribosomal DNA (Wall *et al.,* 1992), immunodifficiency scores (Lowenstein, 1986), and protein sequences (Beintema *et al.,* 1986; Miyamoto & Goodman, 1986). Molecular data supports some of the morphological studies in acknowledging that *Saiga* is related to the Antilopini, but it has not resolved the placement of *Aepyceros* or *Pelea* which, in the case of an analysis of rDNA, finds *Pelea* related to the reduncines (in complete contradiction of Gentry's (1992) conclusion) and *Aepyceros* affiliating with the Caprini and other related species (Gatesy *et al.*, 1997). The same study finds that *Pantholops* is also likely to be related to Caprinae.

Despite the various tribal affiliations in contention, some generalisations can be made in regards to each tribe's physical features, habitat preference and geographical distribution (Gentry, 1978; Kingdon 1982, 1997; Lenstra & Bradley 1999; Geist, 2001):

Tragelaphini – medium to large African bovines with low crowned molars and twisted or spiral horns. They are adapted to very seasonal and unstable habitats and consume green and soft, often younger browse. They require a certain amount of cover and are only capable of swift locomotion in small spurts.

Boselaphini – a tribe now consisting of two species of large browsing bovines found only in India (the nilgai, *Boselaphus tragocamelus* and four-horned antelope, *Tetracerus quadricornis*), although a number of extinct species once inhabited Africa. Boselaphines live in a variety of habitats that are often found on hilly terrain, from open steppe to moderate cover woodlands, but they are never found in thick forests. They are dentally distinguishable by their long premolar rows and brachyodont cheek teeth. Temporal ridges are also very pronounced.

Bovini – A remarkably variable tribe comprised of two groups: buffaloes and cattle. Both are large bovines with smooth horns and low, wide skulls and short faces. Cheek teeth are fairly hypsodont with basal pillars. They require long periods for rumination. They have colonised a variety of habitats from open grasslands to forests in Africa, Eurasia and North America. Members of this tribe have been successfully domesticated throughout modern human history.

Cephalophini – small to medium sized antilopines adapted to a variety of forest conditions (except for the bush duiker, *Sylvicapra grimmia*, which prefers more open settings). They are browsers with large mouths and cheek teeth capable of cutting tougher fruits and seeds. Their small, backward projecting horns and relatively thick frontal bones are unique adaptations which may relate to fighting tactics which involve head butting.

Reduncini – a tribe of rather morphologically homogeneous medium to large water dependent bovids inhabiting unstable sumplands and valley grasslands in Africa. Hypsodont teeth reflect their grazing feeding habits. They have long bodies, thick necks, forward curling horns and basal pillars on cheek teeth.

Hippotragini - large, stocky, horse-like bovids possessing incredibly hypsodont teeth with characteristic basal pillars, and long slender horns that are equal in length in males and females. They are specially adapted to the arid, desert environments in Africa.

Alcelaphini – medium to large sized bovids adapted to running at great speeds in open environments. They possess long faces and legs, short thick necks and dense horn cores which support long, double curled, hollow horns. They are adapted to grazing in abundant but unstable grasslands and are found only in Africa.

Neotragini – a tribe of small browsing antilopines of diverse form and varied habitat preferences (from arid to moist, open to closed) reflecting their long evolutionary history. They have small straight horns, slender legs, round heads and small mouths. Flexible noses and reduced nasal bones relate to a system of nasal panting.

Antilopini – small to medium sized lightly-built antilopines adapted to more arid conditions and a generalised diet of grasses. They have long limbs and necks and very diverse horns and horn cores. Like the neotragines, they have flexible noses and small nasal bones. They have been successful in both Africa and Asia.

Rupicaprini – moderately small to medium sized browsing caprines adapted to extremely rugged conditions in Asia, the European Alps and North America. They require shrub or tree cover and are adapted to locomoting on steep and/or rocky mountainous terrain. They possess short sharp horns which they use to defend resource territories.

Ovibovini – today only represented by two species, the muskox (*Ovibos moschatus*) in the Arctic and the Tibetan takin (*Budorcas taxicolor*). They once flourished over a larger region of North America, Eurasia, and possibly Africa. They are medium to large sized caprines with short and divergent horn cores, a short premolar row and hypsodont cheek teeth.

Caprini – a diverse and specialised tribe of bovids inhabiting areas of difficult climate and terrain (often rocky or mountainous) in Eurasia, North Africa and North America, although introduced domesticated sheep and goats can survive in many environments in other regions. They are of medium build and possess hypsodont teeth, narrow skulls, and hollow horn cores.

These twelve bovid tribes are the legacy of millions of years of rapid speciation events and subsequent migrations. The family is comprised of members encompassing a very wide range of body sizes, feeding preferences and locomotor adaptations. They inhabit a variety of climates, from moist forests and dense thickets, to arid bush scrub and open floodplains. Bovids have successfully colonised nearly every continent, but remain the most diverse in Eurasia and Africa. Their greatest diversity can be seen in Africa, especially in the open country areas in the south and east (Bourlière & Verschuren, 1960; Lamprey, 1964; Field & Laws, 1970), where sites pertinent to early hominid evolution are located.

2.2 Bovids in palaeoenvironmental reconstruction

Herbivores in general are often believed to be good indicators of environment because they are dependent on various degrees and types of vegetation cover for both food and protection from predators (van Valkenburgh, 1994; Janis, 1995). However, frugivores and insectivores are the most climate and habitat sensitive mammalian species (Andrews & O'Brien, 2000). Problematically, they are generally small bodied and thus liable to taphonomic destruction. They are frequently conspicuously absent from or under-represented in palaeontological assemblages and hence of reduced value in palaeoenvironmental reconstruction. Conversely, bovids are the most common remains found in African Plio-Pleistocene fossil assemblages and appear to be the most prevalent large mammals that ranged during that time period (Vrba, 1976; Harris, 1978) and consequently their utility in palaeoecological reconstruction is clear.

Relative to other mammals, over the course of their evolution the initially browsing bovids developed adaptations that allowed for efficient grazing and they were able to quickly take over that aspect of niche exploitation when grazing environments became more widespread. Within the family, bovids have diversified in terms of feeding strategies to a great extent; some rely on grass, some on browse, and others on a complex combination of the two depending on a number of interrelated social and ecological variables (Gwynne & Bell, 1968; Estes, 1974; Jarman, 1974; Underwood, 1983; Sinclair, 2000).

Grass and dicots differ in their growth and development, nutritional status and dispersion. High quality foods are those that have a higher percentage of protein and a lower percentage of fibrous or lignified tissue, which are more difficult to digest (Jarman, 1974; Owen-Smith, 1997). Grasses are therefore of a relatively poor quality, being high in fibre and carbohydrates. A good source of proteins and other digestible nutrients are found in higher proportions in fruits, flowers, and leaves. In addition, younger fresh foliage is more palatable and higher in nutrients because as it ages the nutrient value falls as leaves are reinforced with fibre, and it drops significantly once photosynthesis stops (Jarman, 1974). Since browse grows from an apical meristem, a smaller proportion of the plant will be growing, and hence nutritious, at any given time. Once bitten, the leaf will also not regenerate, while grasses continue to grow from the base of an inter-calary meristem whilst alive. Although grasses are more evenly distributed through a habitat, they are not a completely homogenous resource because their nutrients vary by both part (leaf, sheath, stem) and season (McNaughton & Georgiadis, 1986; McNaughton, 1989). They tend to be highly seasonal and therefore only nutritious for a small amount time throughout the year.

Bovids have evolved over millions of years in response to the differences between grass and browse, and the high number of bovid species at single fossil localities indicates that they had successfully diversified into well-defined niches by the Plio-Pleistocene (Harris, 1978; Kingdon, 1982; Gentry, 1990). It is widely accepted that they have been able to successfully occupy the same geographic areas through resource partitioning, a system by which each species feeds on specific proportions of the two different types of vegetation and the various parts of the plants themselves, which may be achieved by feeding on them at different times of the year as seasons allow or stratifying themselves across the soil catena (Lamprey, 1963; Gwynne & Bell, 1968; Bell, 1970; Jarman, 1974; Hirst, 1975; Jarman & Sinclair, 1979; McNaughton & Georgiadis, 1986; McNaughton, 1989; Owen-Smith, 1997; Sinclair, 2000). There is also evidence to suggest that when a number of bovid species congregate in one area they are protected from predation, so that resource partitioning not only allows them to exploit the same habitat, but functions as an anti-predator adaptation as well (Sinclair 1985; 2000).

Bovid species possess digestive systems that specifically evolved to handle the different chemical and physicomechanical properties of their preferred forage types (there is a wealth of literature dealing with this subject: Hofmann's pioneering although recently criticised work, especially 1973, 1988, 1989; Hofmann & Stewart, 1972; Owen-Smith 1982; Gordon & Illius, 1994; overview in Clauss *et al.*, 2003 and excellent references therein), but it is their skeletal adaptations to these varying conditions and preferences that interest palaeoecologists. Craniodental morphologies functionally related to attaining and masticating varying proportions of grass and browse, and limb morphologies relating to movement within or between the habitats that provide the necessary vegetation patterns required by particular species' diets, underlie our ability to evaluate bovid communities and to relate fossil assemblages back to the environments in which they lived.

2.3 Analyses requiring taxonomic identification

A number of researchers have attempted palaeoecological reconstructions utilising bovid assemblages from a variety of sites in Africa, based on analogies with living relatives. These studies require a level of taxonomic identification to at least the tribe, as well as an inherent belief in uniformitarian principles. E.S. Vrba's research, based on the understanding that environmental norms exist for bovid tribes with very few exceptions (Vrba, 1984) and that bovids are, on the whole, ecologically consistent species (Vrba, 1980, 1987, 1988) originally noted a distinct correlation between bovid tribal affiliation and broad habitat preference. Alcelaphini and Antilopini have a preference for more open or grassland habitats, while other tribes favour more wooded and closed conditions depending on their dietary requirements and need for cover. Vrba began by analysing the environment at Sterkfontein, eventually including other South African sites (Vrba, 1974, 1975, 1976, 1982). Sterkfontein Member 4 was concluded to be a medium density woodland, changing to an open savanna by Member 5 times. Swartkrans appeared to be a moderately open savanna in Member 1 and 2 times, and both Kromdraai Members 1 and 2 were reconstructed to be an open savanna.

Vrba continued to refine her technique, and in some cases revised her earlier conclusions, as in the case of Sterkfontein which she deduced was a moderately open savanna in Member 4 times, rather than a medium density woodland (Vrba, 1985c). Her in-depth look at changes in species and tribal abundances of antelopes through time helped her to arrive at the Turnover Pulse Hypothesis, which seeks to account for those changes on the basis of a global cooling and drying trend which brought about the spread of more seasonal and grassland environments in Africa (Vrba, 1980, 1985, 1988, 1995). The increased incidence in grazing alcelaphines such as wildebeest and topi, and antilopines like the various gazelles, were taken to indicate that grassland habitats were becoming more common around 2.5 my, which was also when the *Homo* and robust australopithecine lineages originated. She further identified two more pulses in mammalian clades, one at the end of the Miocene at 5my and another at .9my, both dates that correlate with periods of global cooling according to other lines of evidence, including oxygen isotope and pollen records (Vrba 1985b; Vrba *et al.*, 1989). While her later work has tended to widen the time frame in which the climate change occurred and then became noticeable in the faunal record (Vrba, 1995), the general principles have remained the same. With only a few challenges to its authority (White, 1995; McKee 1996; Behrensmeyer *et al.*, 1997; Leakey 2001), it remains a relevant theory in current palaeoanthropology.

East African sites have yielded a significant number of bovid remains which lend themselves to analyses. Relying on the relative percentage of certain taxa, Gentry has made simple ecological conclusions about some of these sites, including Fort Ternan (1970), the Shungura Formation at Omo (1985), Olduvai (Gentry & Gentry, 1978a; 1978b) and Laetoli (Gentry, 1987). Although he identified four species of forest dwelling bovid including a tragelaphine, cephalophine and two extinct species, *Praedamalis deturi* and *Bravobus nanincisus*, 60% of the remaining bovids in the Laetolil Beds are comprised of Alcelaphini, Neotragini and Antilopini, indicating more open conditions (Gentry, 1987). This supported the original belief that Laetoli was a dry open woodland (Gentry, 1987).

Olduvai represents perhaps the best studied of the East African sites and many after Gentry and Gentry (1978a, 1978b) have looked at the vast bovid collections gathered from the various beds. Both Potts (1982, 1988) and Kappelman (1984) made use of Vrba's (1980) initial observation that members of the tribes Alcelaphini and Antilopini comprise more than 60% of the bovid community in modern open ecosystems, and less than 40% in areas of woodland or more closed habitats. They applied that statistic to Olduvai assemblages, Kappelman further considered the percentages of Reduncini, Tragelaphini, and Hippotragini as indicating more closed or moist conditions. These studies suggest that near the paleolake during the DK I depositional timeframe the habitats were mixed but included areas of grassland, trending towards a moist and closed habitat during the deposition of FLK NN I. The area grew increasingly arid through FLK I and FLK N I, when the region was quite arid and open.

Shipman and Harris (1988) took the proposed Alcelaphine/Antilopine relationship to habitat preference even further, investigating proportions of abundances of other tribes. They noted that in addition to Alcelaphini and Antilopini indicating open and dry conditions, Tragelaphini and Aepycerotini indicate closed and dry conditions, and Reduncini and Bovini point towards closed and wet habitats. On this basis they analysed a number of sites. All of the South African localities were open and arid, but there was a greater diversity of environments in East Africa. Olduvai appeared to host a wide range of habitats over the course of the deposition of Bed I, with FLK N I representing the most open and dry, and FLK NN I the most closed and wet, which agrees with both Potts (1982, 1988) and Kappelman (1984). Omo featured closed environments of varying degrees of wetness, Koobi Fora was mostly closed and wet with a few species indicating the existence of drier conditions at some points in time, and West Turkana was also closed and wet with some evidence for closed and dry surroundings. This is consistent with Walker *et al*'s (1986) assessment that the presence of reduncines indicated edaphic grasslands or marshy areas.

Using Shipman and Harris's tribal proportions, Schrenk *et al* (1995) analysed the local environments of a relatively new region to be studied palaeontologically, northern Malawi. Their analysis of the Chiwondo Beds reveals that the northern sections of the site ranged from open and arid to closed and wet, but that closed conditions dominated. The southern part of the area appears to have been a closed and dry habitat of either woodland or thicket. However, it should be noted that the fossils in this region are sparse and fragmented, and subject to a great deal of taphonomic bias. The sample sizes used in this study are small (89 in the northern and 60 in the southern portion) and potentially biased against smaller species.

Observations of specific proportions of bovid taxa led Harris (1991) to make some broad statements about the environmental conditions at a number of sites in East Africa, which he used in comparisons with Koobi Fora. The Tulu Bor Member at Koobi Fora are taken to indicate a flood plain with gallery forest, with edaphic grasslands to the south, and the overlying Burgi Member was much the same. Later in time, the KBS Member appeared more dry and open, returning to wetter conditions and edaphic grasslands during the deposition of the Okote Member. In contrast, the Denen Dora Member of Hadar seems to be represented by humid, open grassland species. Environmental change over time seems to be suggested at Laetoli, where Harris notes that in the Laetolil Beds 60% of the bovids were antelopes, indicating an open grassland, while the bovids from the younger Upper Ndolanya Beds are comprised of mostly alcelaphines, antilopines, and neotragines with a few reduncines. This would point to the development of a more permanent water source and lightly wooded savanna.

2.4 Taxon-free analyses and ecomorphology

All of the studies described above rely on taxonomic identifications of bovids to at least the tribal level, but genus and species identifications are often required. Due to the fragmentary and often taphonomically biased nature of the fossil record, this tends to limit the available sample size, thus biasing the sample (DeGusta & Vrba, 2003). A large body of research exists that seeks taxon-free approaches. This research seeks to correlate specific morphologies and characteristics to niche exploitation, and may involve post-crania or craniodental features, which relate to locomotion or feeding habits. These features are commonly known as ecovariables. They may be either metric or categorical and can be measured or scored without knowing the taxonomic affiliation of the specimen, which is a clear advantage when faced with a fossil assemblage.

A common criticism of this approach is that phylogeny may confound the analyses. It is often difficult to discern which variables are linked to evolutionary relatedness and which are linked to habitat exploitation. Often the reality is a confusing combination of the two circumstances. For instance, many bovid tribes are characterised by species that habitually favour particular habitats or species that do not vary greatly in size. Thus, any studies based on ecomorphology must aim to identify variables that relate more to habitat and not to phylogeny.

Body size, which is an important aspect of niche exploitation because it places limits on the physical strata in which a species can locomote, and determines energy requirements and hence dietary requirements, is sometimes used as an indicator of habitat (Scott, 1983; Damuth & McFadden, 1990). Body size may be determined through various regression formulae of long bone measurements or molar surface areas, with femur length being the best indicator in the case of bovids (Scott, 1983). However, despite the fact that body size is obviously related to locomotion, diet, and habitat preference (Leakey 2001), and it can be computed with fossil material by means of size regressions, the relationships are not well understood and there are exceptions to most rules (Ford & Davis, 1992). It can be seen that body size distributions are in fact similar across most tropical environments and so it is best not to use body size as a single line of evidence indicating environment (Andrews, 1996).

Gentry (1970) was the first to note that femur characteristics were related to locomotor patterns, but he did not systematically test which features were true habitat predictors or determine which were the best for such a task. It was much later that extensive studies of femoral morphologies as they relate to habitual locomotion within certain habitat types in extant bovids elucidated the role of the shape of the femoral head in creating a joint surface that is conducive to either fast running or manoeuvring around a range of obstacles (Kappelman, 1988, 1991; Köhler, 1993; Kappelman *et al.*, 1997). Bovids inhabiting environments with more closed canopies are faced with a number of fallen and upright trees, bushes, shrubs and roots, which limit long distance and high speed running. Their femoral heads are more rounded, indicating a mobile hip joint. Open country bovids on the other hand, have more elongated femoral heads that indicate the ability to run far and fast, as open country dwellers need to do when preyed upon. Furthermore, their femora also possess a larger moment arm for the extensor muscles. Species which live in habitats that are not as extreme as forest or grassland in terms of obstacles to locomotion, display intermediate morphologies.

This approach was applied to the Miocene sites of Fort Ternan and the Chinji Formation in Pakistan (Kappelman, 1991) as well as to Olduvai Gorge and Koobi Fora in East Africa (Kappelman *et al.*, 1997). In the latter case, the "intermediate cover" category was broken into "light" and "heavy" cover in order to construct a more sensitive picture of the palaeoenvironment. The small sample size (five for Koobi Fora and 22 for Olduvai) makes it difficult to conclude anything definitively, but the results tentatively indicate more closed conditions at Koobi Fora and more open habitats at Olduvai.

An ecomorphological analysis of the bovid metapodials from Olduvai Bed I (Plummer & Bishop, 1994) made use of the known relationships between metapodial functional anatomy, locomotor styles and habitat (Gentry, 1970; Scott, 1979, 1985; Köhler, 1993). The features observed related to joint stabilisation, diaphysis shape, and lever arm length and they discriminate well between open country, closed canopy and intermediate habitats. Over 300 metapodial fossils from Bed I were studied, and an overall trend towards increased aridity was noted from the middle to upper Bed I (Plummer & Bishop, 1994). This conclusion contradicts taxon-based bovid studies previously conducted and described earlier, but qualifies studies following other lines of evidence (Cerling *et al.*, 1977; Cerling & Hay, 1986). The study also indicated a higher proportion of intermediate to closed habitats bordering the palaeolake margin than previously thought, a conclusion supported with a high degree of precision by a study of small mammals (Fernandez-Jalvo *et al.*, 1996). Since many of the bovid assemblages included in this study may have been derived through hominid accumulation (DK I, FLK I and FLK N I) with the exception of FLK NN I level 2 which is thought to represent a carnivore accumulation (Potts, 1982), environmental interpretations of Olduvai have important implications for hominid behaviour. The fact that a number of metapodial adaptations for a variety of habitat types were noted in all levels indicates that hominids were foraging in and utilising the full range of habitats supported by the palaeolake Olduvai.

A third element that has been used to construct a picture of palaeoenvironment is the talus (DeGusta & Vrba, 2003). Long bones often provide the best habitat discrimination based on measurements of the complete element, but such fossils are rarely found in this state. Tali, as tarsals, are smaller irregular bones that are often found intact, thus conferring and obvious advantage over those studies focusing on long bones. Although a complete femur has a slightly higher predictive ability, the talus discriminated habitat types (forest, heavy cover, light cover, open) in 67% of the cases of known bovids. The eight features quantified were shown to be unrelated to body size or phylogeny; the best discriminators among the eight are superior-inferior length, medial-lateral width and anterior-posterior thickness. Compared to open country bovids, those residing in forests or habitats with light vegetation cover possess anterior-posteriorly compressed tali, in contrast to heavy cover bovids, which have anterior-posteriorly expanded tali. Superior-inferior compression is also characteristic of open country inhabitants. To date, this method has not been used to reconstruct the habitats of fossil assemblages.

2.5 Craniodental analyses

Ecomorphologies relating to trophic rather than locomotor adaptations naturally focus mainly on craniodental characteristics including molar shape and growth patterns, tooth wear due to attrition and abrasion, insertion points for masseter muscles and muzzle shape. It has long been suggested that these features correlate to the two basic patterns of bovid resource exploitation (Bell, 1971; Owen-Smith, 1982). Grazers possess features that allow them to tear off grass with head movements, bite off a greater quantity of food in one bite, and repetitively masticate one mouthful. They include a wide premaxilla, long face anterior to the tooth row, short premolar row separated from the molars by a long diastema, narrow palate, flexed braincase on the facial axis and a deep mandible (Solounias *et al.*, 1988; Solounias & Moelleken, 1993; Spencer, 1995, 1997). Conversely, browsers possess features that relate to their need for greater tongue and lip movement, ability to selectively bite at preferred plant parts, and to chew softer vegetation. Relative to grass feeders, they possess shallow mandibles, narrow premaxillae, short faces, broad palates, unflexed braincases, and longer premolar rows (Solounias *et al.*, 1995b; Spencer, 1995, 1997). Mixed feeders may possess some characteristics that indicate which type of plant material they prefer.

Janis and others have analysed hypsodonty in relation to diet (Janis, 1979, 1988, 1990a, 1990b; Janis & Ehrhardt, 1988; Solounias & Dawson-Saunders, 1988). The hypsodonty index is an expression of molar crown height and it is commonly measured by dividing the length of the lower second molar by the height of the unworn lower third molar (Janis, 1984). Molars designated hypsodont are those which possess a crown which is higher than their antero-posterior length, although Fortelius (1985) warns that the term is often used to describe the relative height of teeth in comparison to one another.

The low-crowned, or brachyodont, condition is related to a softer, browsing, dicot-based diet, while hypsodonty is one characteristic that has evolved along with the increased proportion of monocots in bovid diets. Hypsodont molars erupt over a long time period (in some ungulate species, continuously) during the individual's lifetime in order to prevent the teeth from wearing down to the point at which mastication is impeded or becomes impossible. The need for this functional adaptation in grazers may relate to either or both the incorporation of tough silica particles in grasses as a defence mechanism against overgrazing (Simpson, 1950; McNaughton *et al.*, 1984) or the increased amount of exogenous grit that may characterise a grass-based diet taken from close to ground level (Stirton, 1947; Healy & Ludwig, 1965; Kay & Covert, 1981, 1983). The abrasiveness of both of these particles puts the teeth under a great deal of stress and the surfaces tend to wear quickly. Natural dental attrition, or tooth-on-tooth wear (Butler, 1972), is also exacerbated by the need to repeatedly chew vast amounts of low-grade plant material in order to meet the energetic demands of grazers (Fortelius, 1985; Fortelius & Solounias, 2000). Conversely, browsers meet their own energetic demands by consuming smaller amounts of higher energy plant resources.

Comparisons of hypsodonty indices can distinguish between grazers, browsers and mixed feeders as well between those bovid communities favouring closed versus open habitats. The underlying assumption is that hyposdont grazers are found most often in open habitats and browsers in more wooded regions. However, recent research indicates that hypsodonty indices should not be used alone in palaeoecological considerations. The amount to which exogenous abrasives such as dust and grit influenced the adaptation's evolution is uncertain, but it appears that it may have played a greater role than inherent abrasives in the evolution of the trait (Williams & Kay, 2001). Furthermore, it appears that only common mammals evolved increasingly hypsodont molars during the European Miocene, while rare species retained their original molars sizes (Jernvall & Fortelius 2002). This infers that if a fossil assemblage is biased towards these rare mammals, an overall picture of a non-hysodont community may emerge and subsequently false ecological conclusions could be drawn. Finally, there may be a phylogenetic signal obscuring the function of the adaptation across mammalian families (Janis, 1988; William & Kay, 2001). All grazers do not share the same degree of hypsodonty, although within families it is more similar than between them (Mendoza *et al.*, 2002).

Seeking to tease more reliable environmental information out of bovid craniodental morphology, a number of studies took an in-depth look at distinctive craniodental features in extant bovids, often in conjunction with the hypsodonty index. A great deal of research in this area was applied to the Miocene fossil record in Greece (Solounias & Dawson-Saunders, 1988; Solounias *et al.*, 1988; Solounias & Moelleken, 1993; Solounias *et al*, 1994; Solounias *et al.*, 1995b). This work focused on a variety of characteristics including premaxillary shape and masseter muscle insertion points and also built upon previous microwear analyses in ruminants, extant primates, hominids and carnivores (Gordon, 1982; Teaford & Walker, 1984; Grine, 1986; Teaford, 1988; van Valkenburgh *et al.*, 1990; Solounias & Moelleken, 1992a, 1992b; Solounias & Moelleken, 1993).

Microwear patterns are valuable in that they reflect the recent diet of the individual prior to the time of death, but this can obviously cause problems in species that change their diet seasonally, as is the case with many bovids (Solounias *et al.*, 1994). Furthermore, if an entire population is forced to change its diet due to extreme climatic circumstances, so for instance if preferential browsers are forced to rely more on grazing in times of decreased rains and many of the community die off as a result, the assemblage as analysed will indicate that grassland is a more prevalent habitat than was really the case. However, premaxillary and masseter morphology will indicate long term evolutionary adaptations to dietary niche, rather than the most recent diet in an individual's life, and Solounias *et al.* has used microwear conclusions to support analyses of these cranial morphologies (1995b).

Premaxillary shape is highly correlated to dietary preference (Solounias *et al.*, 1988; Solounias & Moelleken, 1993; Spencer, 1995). Grazers display wider premaxillae that are squared off at the anterior margin, with a concomitantly straight lower incisor arcade. Browsing species, on the other hand, have more pointed premaxillae with a rounded lower incisor arch (Solounias & Moelleken, 1993).

Bovid masseter muscles are located in an anterior position on the skull and occupy a large area of the premaxilla (Zey, 1939; Turnbull, 1970; Vree & Gans, 1974). Grazers have a larger masseter muscle and more robust associated masseter features reflecting their tougher diets (Stockman, 1979; Axmacher & Hofmann, 1988), with a few exceptions such as the wildebeest and Indian chousingha (Solounias *et al.*, 1995b). Mixed feeders fall in between the two extremes. Five masseter related variables were analysed in a sample of extant bovids and giraffids, and the most discriminating feature was the height of the bony protrusion that is the origin of the masseter superficialis, which easily separates the grazers from the browsers from the mixed feeders (Solounias *et al.*, 1995b). Other suites of characteristics distinguish the browsers from the grazers, while the mixed feeders overlap substantially. Grazers possess a wide and deep maxillary fossa for the origin of the masseter profundus and a thick orbital rim under which the muscle attaches. The condition in browsers is more gracile.

On the basis of these features, and in conjunction with microwear studies, the habitat of the Miocene sites of Samos and Pikermi in Greece has been re-analysed (Solounias *et al.*, 1995b). It changes the picture of what was known of the range of habitats present in that region at that time. Unlike previous reconstructions, which have concluded that the area was an open grassland, Solounias *et al.* (1995b) find evidence that more wooded habitats must have existed to support the level of browsing indicated by the craniodental morphologies of the bovid species in the assemblages.

Spencer (1995, 1997) has reassessed known traits that have been long established as good indicators of the broad browser/grazer division in diet (Bell, 1970; Boue, 1970; Gordon & Illius, 1988), including microwear patterns (Walker *et al.*, 1978; Solounias *et al.*, 1994), masseter associated morphology (Solounias *et al.*, 1995b) and hypsodonty (Janis, 1988, 1990). She aimed to distinguish between grazers, mixed feeders preferring monocots, mixed feeders preferring dicots, and browsers. This is a slightly different dietary classification system than the one used traditionally by Janis, which attempts to distinguish between browsers, general grazers, fresh-grass grazers, mixed feeders and subsets within these groups (Mendoza *et al.*, 2002). Spencer identified the ratio of the depth of the mandible at M2/M3 to the total upper molar row length as a good discriminator between grazers, browsers and all mixed feeders, but failed to identify anything that could be concretely associated with the two categories of mixed feeders, although those favouring monocots tend to have a deeper mandibular body, wider premaxilla, and longer face (Spencer, 1995).

Spencer noted that African grasslands can be broadly divided into two types: edaphic, or those which result from impeded drainage of water from the soil, and secondary, or those which are arrested in a natural succession towards woody growth by fire or grazing pressure (Vesey-Fitzgerald 1963). Although the existence of edaphic grasslands can be traced to the Miocene (Retallack 1991), the emergence of secondary grasslands has not been identified. Spencer applied her analyses of extant bovid feeding morphologies to the fossil record in order to investigate the timing of the emergence of secondary grasslands in Africa (1997). This previously un-investigated event is important because although it is understood that later hominid evolution was occurring in the context of spreading grassland habitats in the Plio-Pleistocene, it is not known which type of grassland may have been the crucial scene for the evolution of novel hominid adaptations.

Principal components analyses were able to distinguish between bovids that ingest grass but inhabit edaphic versus secondary grasslands. Greater braincase flexion, wider mandibular bodies and shorter premolar rows are all associated with secondary grassland inhabitants. The first bovids considered to be adapted to secondary grasslands were *Connochaetes gentryi* and *Parmularius altidens* at 2 mya, which infers that this habitat type could not have played a role in the evolution of the Hominidae lineage, or in bipedality, both of which occurred much before 2 mya. However, this does roughly coincide with the emergence of *Homo erectus* and this species has been noted to possess characteristics which may be adaptive in a more open setting.

Both Spencer and Janis's craniodental indices provided Reed and her colleagues (Reed, 1996; Sponheimer *et al.*, 1999) with a tool for identifying the trophic adaptations of the bovids from Makapansgat. Her results indicated that there were limited edaphic grasslands during the time of the deposition of both Member 3 and Member 4. Furthermore, she identified evidence of climatic change between the two members. During Member 3 the habitat most closely resembles open woodland, and the Member 4 bovids are indicative of more closed woodland or bushland. However, Reed cautions basing any definitive conclusions on only the bovid sample, because the Member 4 fauna appears to have been derived from accumulations by birds of prey, and therefore would be biased against bovids and larger mammals (Reed, 1997).

A recent multivariate stepwise discriminant function analysis has combined the hypsodonty index with 22 other craniodental variables to obtain quadratic discriminant functions that successfully discriminate between feeding categories and habitat types that are ecologically meaningful (Mendoza *et al.*, 2002). Most of the research reported above (with the exception of Spencer's (1997) work which related bovid morphology to grassland types) has been based on univariate or bivariate analyses. These are able to differentiate between broad habitat categories, but there are a number of exceptions to the rule (i.e. that grazers inhabit grasslands and browsers closed habitats) which confound the analyses. However, the multivariate analysis provides a finer resolution in which general grazers, fresh grass grazers, mixed feeders in open habitats, mixed feeders in closed habitats, general browsers, high level browsers (those feeding in trees and bushes, but not near the ground) and frugivores cluster in their groups with very few misclassifications.

Multivariate analyses of craniodental variables, which appear to provide the best discrimination for these features are, however, unfortunately difficult to apply to the fossil record. The algorithms calculated in Mendoza *et al.*'s paper were used to reconstruct the diets and habitats of three extinct North American ungulates (none of which were bovid), although the conclusions are based on analyses that did not combine all of the possible categories in one single analysis. The authors reiterate the common lament that fossils are often so fragmentary that the measurements necessary for the best discrimination are unavailable.

Mesowear analysis, which requires only the teeth, may provide a solution to this problem (Fortelius & Solounias, 2000). Wear patterns create changes in cusp shape and relief which indicate the lifetime dietary affects of both abrasion (food-on-tooth) and attrition (tooth-on-tooth). The conclusion is that browsers' dentition displays wear caused more by attrition and that grazers are affected predominantly by abrasion. This technique draws attention away from both cumbersome and expensive microwear studies that only indicate the short-term diet of an individual prior to its death and analyses of adaptive features such as hypsodonty that relate to long-term evolutionary patterns that might not be completely indicative of the habitat the individual ranged in over its lifetime.

Fortelius and Solounias (2000) conducted cluster analyses of measurements of the buccal side of the upper molars that quantify and describe cusp relief, or the distance between the cusp tips and occlusal surface valleys, and cusp shape, which can be expressed as sharp, rounded or blunt. These measurements do not require special equipment and recording them is rapid process, thus allowing a large number of specimens to be studied (their dataset was comprised of 2200 individuals from 64 ungulate species). Their analyses were repeated with the addition of the hypsodonty index as a variable and the results indicate that their combined mesowear variables provide a slightly more robust dietary signature than hypsodonty alone. Their best dietary indicator was a percentage of sharp cusps, which easily discriminated between grazers, browsers and mixed feeders; the addition of their other variables further identified ecologically sound sub-groups within the major feeding categories.

This level of resolution can not be provided by any other craniodental method of analysis. In addition to this, mesowear patterns stabilise in a dataset of 30 individuals, and patterns are consistent throughout life, excluding the very youngest and very oldest age class, so obtaining a sample for this type of analysis is not difficult. Considering these circumstances, it may be that this type of analysis is the way forward with bovid dietary and habitat reconstruction. It was preliminarily used to look at a small sample of Greek and North American bovids and equids, although it would be interesting to see it used on a larger bovid sample.

2.6 Laetoli

Laetoli is located in northern Tanzania, 36 km south of Olduvai Gorge (Figure 2.1) in an environment now classified as a wooded and bushed grassland dominated by *Acacia* and *Commiphora* (Pratt & Gwynne, 1977). The first collections from the

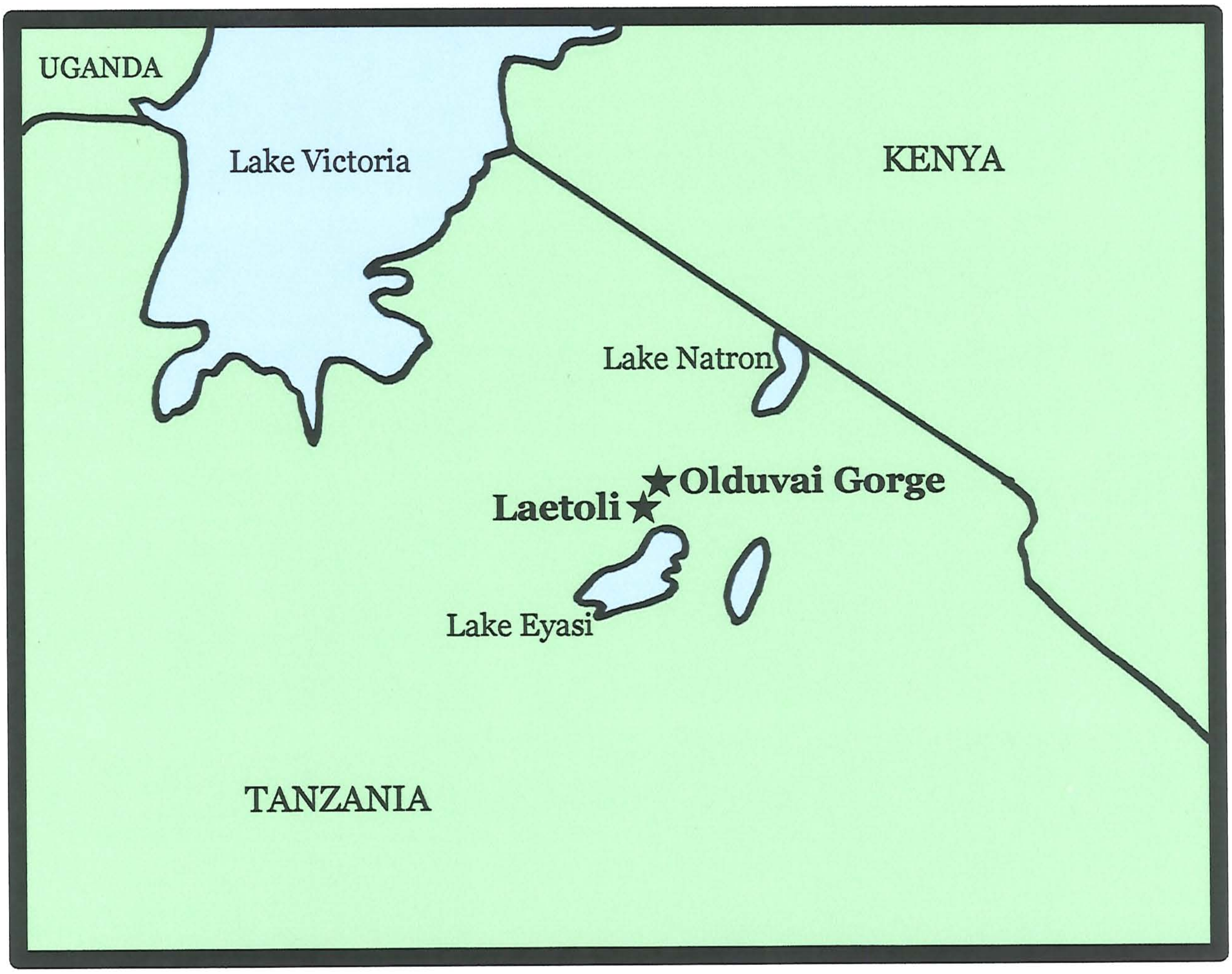


Figure 2.1. Location of Laetoli in relation to Olduvai Gorge

site were gathered by the mainly geological expedition lead by Kent (1941), followed shortly thereafter by the Kohl-Larsen expedition (Kohl-Larsen, 1943). Mary and Louis Leakey initially collected there in the1950s, but the majority of their work was supervised and conducted by Mary in the 1970s (Leakey & Harris, Eds, 1987). In the next decade the Institute of Human Origins, which was then at the University of California at Berkeley, organised a brief expedition and most of the work completed at that time is found in Prosper N.S. Ndessokia's unpublished PhD dissertation (1990). After that, the site was briefly visited by a handful of other researchers, but the finds have not thus far been published. The forthcoming publications by Professor Terry Harrison of New York University on the research conducted there over eight years (1997-2004) will contribute significantly to our knowledge of the site (Harrison, pers. comm.).

This site's geology has been analysed and a detailed stratigraphy produced by Hay (1987), presented in Figure 2.2. Although the site spans 4.3 to 0.12 mya, the majority of the fossils are found in the Laetolil Beds, which are exposed across the Laetoli area at more than thirty localities (Figure 2.3). These beds are divided into a lower unit, which only produces occasional fossils and an upper unit, from which the greatest number of fossils have been uncovered. A tuff in the lower part of the Lower Laetolil Beds has been K-Ar dated to 4.3 mya, and tuffs from both the base and upper part of the Upper Laetolil Beds have been K-Ar dated to 3.8 and 3.5 mya, respectively (Hay, 1987). The Laetolil Beds are overlaid by the younger Ndolanya Beds, which are also divided into a lower and upper unit. The lower unit bears no fossil remains. The Upper Ndolanya Beds have been dated to 2.66 ± 0.023 mya using the ^{40}Ar ^{39}Ar method (Ndessokia, 1990). They are exposed at a limited number of localities.

Upper Ngaloba Beds
Lower Ngaloba Beds
Olpiro Beds
Naibadad Beds
Ogol Lavas
Upper Ndolanya Beds
Lower Ndolanya Beds
Upper Laetolil Beds
Lower Laetolil Beds

Figure 2.2. Stratigraphy of Laetoli, Tanzania. See text for descriptions and ages of the strata.

Image removed due to third party copyright

Figure 2.3. Map of localities at Laetoli, Tanzania. Localities are listed by their number (original references and locality descriptions can be found in Leakey & Harris, 1987). Blue areas represent the Laetolil Beds and red areas represent the Ndolanya Beds. Broken lines are tracks. Kakesio and Endulen are nearby villages. *Courtesy of Professor Terry Harrison, New York University.*

A series of lava flows and tephra deposits known as the Ogol Lavas cap the Upper Ndolanya Beds and these are K-Ar dated to 2.4 mya (Hay, 1987). Above these lavas lie the Naibadad Beds, comprised of 95% tuffs and 5% claystone and conglomerate. Very few fossils have been discovered in the beds, which have been $^{40}Ar/^{39}Ar$ dated to 2.15 ± 0.022 mya (Ndessokia, 1990). The non-fossil bearing Olpiro Beds lie above the Naibadad Beds. Tuffs from the bottom of these beds date to 2.14 ± 0.018 using the $^{40}Ar/^{39}Ar$ method (Ndessokia, 1990). Fossils and artefacts have been recovered from the next youngest strata, the Ngaloba Beds. The lower unit has proved difficult to date because it does not possess datable tuffs or appropriate fossils for correlation. However, the Upper Ngaloba Beds have been estimated to between 1.2 and .12 mya on the basis of similarities with the Ndutu Beds at Olduvai Gorge (Hay, 1987). Black cotton soil is found over most of the Laetoli surface area.

Of particular interest is Tuff 7, the "footprint tuff", of the Upper Laetolil Beds. It has yielded invaluable information on the mammalian palaeocommunity in the form of tracks preserved in the ashfall from Sadiman, the nearby volcano, including those of early hominids (Leakey & Hay, 1979). Laetoli is perhaps best known for this fortuitous discovery, although the site has yielded a wealth of fossils and other remains. These include the brood cells and pupal cocoons of the solitary bee, Hymenoptera (Ritchie, 1987), termitaries and other evidence of soil-working invertebrates (Sands, 1987), and Acheulian and Middle Stone Age type artefacts (Hay, 1987). Hominids representing various stages in human evolutionary history have also been found there, including the holotype specimen for *Australopithecus afarensis* (Johanson, White & Coppens, 1978), a robust australopithecine (Harrison, 2002) and a very early individual of *Homo sapiens* (Day *et al*, 1980).

The palaeoenvironmental conclusions reached for Laetoli have been arrived at through a variety of analyses, but not all are in total agreement. Palynological studies have been unable to pinpoint a precise habitat, as pollen from a diverse variety of vegetation types across the entire floral spectrum, from open grassland to more closed woodland, have been observed in the Laetolil Beds (Bonnefille & Riollet, 1987; Bonnefille, 1994). This palynological signal is not atypical for habitats similar to the open types found in the Serengeti today, however. The difference is in the proportions of herbaceous and arboreal species, which differ between the palaeoflora and the modern Laetoli sample. Grasses dominate over other herbaceous species and the arboreal pollen is not high (Bonnefille & Riollet, 1987), suggesting that the climate was more arid in the past.

The footprint tuff also provides a snapshot of a fairly discrete moment in time, and gives some indication as to the associations of animals present in the area. The tracks of cercopithecids, which require tree cover for protection, and a number of browsing species such as rhinos, chalicotheres, and giraffids such as *Simatherium,* indicate that more closed woodland must have been available than previously thought (Andrews, 1989). This observation does not contradict the evidence from studies of stratified sediments and pollen, which suggest that the environmental conditions became moister above tuff 6 (Bonnefille & Riollet, 1987; Hay 1987), a condition necessary to support the woody growth exploited by browsers.

Other research has focused on faunal remains more directly. Some evaluations have simply relied on the presence or absence of so-called indicator species, such as the occurrence of the naked mole rat *Heterocephalus* (Hay, 1981), which points to warmer conditions. The complete absence of aquatic species or those known to require a nearby water source infers that the local Laetoli region was, like today, lacking a permanent source of water. Further brief environmental interpretations were provided by Hooijer (1987a, 1987b) and Guérin (1987a, 1987b), who were responsible for the analyses of Perissodactyla. The presence of quadrupedal chalicotheres, which appear to have hindlimbs indicative of occasional standing, presumably to feed on young leaves and shoots (Chavanon, 1962), infer that some shrub and tree cover was available. The two species of rhinoceros found in association indicate a dry bushland habitat (Guérin, 1987b). High proportions of the suid *Notochoerus* indicate that the Laetolil Beds were deposited when the habitat was more open, while the presence of *Kolpochoerus* in the Ndolanya fauna suggests that more humid conditions prevailed one million years later (Harris, 1987).

Relying on indicator species is not as informative or dependable as considering a number of taxa in conjunction, or the species composition of entire diverse taxonomic families. Therefore, attempts have been made to analyse a number of the mammalian families present in the palaeofauna. Associations of rodent species in the Laetolil and Ndolanya Beds, although they do not have exact modern analogues, are similar to other African communities. From rodent species lists and morphologies, Denys (1985, 1987) concluded that at approximately 3.5 mya Laetoli was a dry climate with *Acacia* dominating the arboreal component of the flora. She further believes that humid and potentially warmer conditions had developed by the time of the deposition of the Ndolanya Beds, a conclusion contested by others (Kovarovic *et al.*, 2002). Although rodents are good ecological indicators due to their sensitivity to climatic conditions, they are unfortunately also small and do not survive well in the fossil record, and are further known to be often transported far from their home range (Dodson, 1974).

Gentry has studied the identifiable specimens of Laetoli's Bovidae, which, while not being immune to taphonomical processes, are generally better preserved in the fossil record (Gentry, 1987). Percentages of remains assigned to Alcelaphini, Neotragini and Antilopini indicate an open non-woodland habitat during Laetolil Bed times, with the presence of some nearby vegetation cover indicated by a lesser number of genera such as *Tragelaphus* and a cephalophine. The incidence of alcelaphines, antilopines and neotragines increases in the Ndolanya Beds, perhaps indicating that the region had become more open, with the availability of tree cover decreasing.

Rodent and bovid communities are useful as environmental indicators because they are not only sensitive to variations in habitat, but a great many species co-exist within the same environment. Some environmental inferences can be drawn from other individual mammal communities, but may not be as reliable as those which are as diverse. For example, Petter (1987) and Barry (1987) identified and described the small and large carnivore samples, both of which are similar in diversity and species composition to modern East African communities. Some exceptions, such as the modern loss of saber-toothed forms and the relatively large body size of a number of the smaller carnivores in the Laetoli sample may relate more to the evolutionary history of the species in question than interpretable environmental differences.

Harris (1985), in summarising the analyses of the individual faunal families in conjunction with palaeofloral and sedimentological indicators, concluded that the biological community present during Laetolil Bed times is representative of an open grassland with some scattered but limited tree cover. In contrast, Andrews (1989; 1999) utilised a very different approach to understanding Laetoli's palaeoecology and came to a different conclusion. He used a novel taxon-free community analysis approach, focusing on the Laetolil Beds. His technique considers all of the mammalian families (excluding bats) and their adaptations in feeding preferences and locomotor patterns, as well as body size, and compares this community structure to those of well-defined modern habitats. The Laetoli structure bears greatest resemblance to the wooded end of extant Serengeti habitats. This conclusion is slightly different from the other simpler faunal analyses, that either indicated a drier and less wooded habitat, or could not pinpoint a more specific habitat within the open to closed woodland spectrum (Leakey & Harris, Eds, 1987). Kovarovic *et al.* (2002) followed a community technique similar to Andrews (1989; 1999). Their recent ecological diversity analysis indicates that at the time of the deposition of the Upper Ndolanya Beds the region was a semi-arid bushland. This is considerably drier and more open than the region is thought to have been one million years prior, according to the work of Andrews.

Laetoli serves as an excellent test of the bovid analysis technique reported herein for two reasons. Firstly, as the brief summaries above show, a great deal has been done to infer Laetoli's palaeoenvironment, but due to the nature of the material and taxa studied, most conclusions are, unfortunately, open to doubt. As reported, their conclusions are also often contradictory. Great advances have been made in recent years with the mammalian community work conducted by Andrews (1989; 1999) and Kovarovic *et al* (2002). However, while these studies considered the adaptations of the mammals in the Laetoli assemblages, the fossils themselves were not studied directly. It has become necessary to see if an in-depth ecomorphological analysis of the bovid material will give as good an indication of habitat as entire faunal community analyses.

Secondly, the Laetoli material, while rather fragmentary in nature, is comprised of a great deal of bovid remains. Not including the collections made by Harrison and the unpublished material gathered by the brief expeditions in the 1990s, of the 56 identifiable species in the Upper Laetolil Beds, 12 of them were bovid, and in the Upper Ndolanya Beds, 14 of the identifiable species were bovid out of a possible 33 (Ndessokia, 1990). This project further makes use of the bovid remains not identified to species level, and elements have been hitherto ignored, which greatly increases the number of fossils available for study.

3 MATERIALS AND METHODS

3.1 Data sample

Data were gathered on modern specimens in the collections of four museums between the summer of 2000 and the autumn of 2002: The Natural History Museum, London (NHM); Powell-Cotton Museum, Birchington-on-Sea, Kent (PC); the American Museum of Natural History, New York City, New York (AMNH) and the National Museum of Natural History, Smithsonian Institution, Washington, DC (NMNH). All specimens were adult and caught in their native habitats.

The species composition and geographic range of the modern sample is summarised in Table 3.1. The location and museum catalogue number of each specimen is provided in Appendix A. The sample includes 205 individuals of 70 species representing eleven of the twelve bovid tribes in the five subfamilies. In addition, the sample includes five tragulids (*Hyemoshcus aquaticus*) and 14 cervids (four *Alces alces,* four *Elaphodus cephalophus,* four *Odocoileus virginianus,* and two *Pudu mephisophiles*). The species sampled are known to exploit a wide range of habitats and are native to Africa, Asia, Europe and North America. Each species has been given a code derived from the first (and sometimes second) letter of its genus and species name in order to identify the individuals in subsequent analyses and graphs. These are also given in Table 3.1.

All relevant skeletal elements of each individual (see section 3.2 below) were measured, although not every specimen was complete. Smaller elements such as the carpals and phalanges were frequently absent or held together in articulation by dried soft tissue that could not be removed. In Chapter 4 and 5, where the results of the

Table 3.1. Sample size, species composition and geographical distribution of the modern sample

Species	Common name	Species Code	#	Tribe	Geographic Distribution
Subfamily BOVINAE (n = 40)					
Bison bison	bison	Bb	7	Bovini	North America
Bos javanicus	banteng	Bj	3	Bovini	Southeast Asia, Indochina
Bos sauveli	kouprey	Bs	2	Bovini	Indochina
Bubalus mindorensis	tamaraw	Bm	1	Bovini	Philippines
Syncerus caffer	African buffalo	Sc	3	Bovini	South of Sahara
Taurotragus derbianus	giant eland	Td	2	Tragelaphini	Senegal – Nile River
Taurotragus oryx	common eland	To	3	Tragelaphini	South, East Africa
Tragelaphus eurycerus	bongo	Te	3	Tragelaphini	Southwest Africa – East Africa
Tragelaphus scriptus	bushbuck	Ts	11	Tragelaphini	South of Sahara
Tragelaphus spekii	sitatunga	Tsp	1	Tragelaphini	South of Sahara
Tragelaphus strepsiceros	greater kudu	Tst	4	Tragelaphini	Northeast – South Africa
Subfamily ANTILOPINAE (n = 74)					
Antilope cervicapra	blackbuck	Ac	2	Antilopini	India
Gazella cuvieri	edmi gazelle	Gc	2	Antilopini	North Africa
Gazella granti	Grant's gazelle	Gg	4	Antilopini	East Africa
Gazella rurifrons	red-fronted gazelle	Gr	2	Antilopini	West, East Africa
Gazella soemmerringi	Soemmerring's gazelle	Gso	2	Antilopini	East Africa
Gazella speki	Speke's gazelle	Gso	2	Antilopini	Ethiopia, Somalia
Gazella subgutturosa	goitred gazelle	Gsu	2	Antilopini	Arabia - Mongolia
Gazella thomsonii	Thomson's gazelle	Gt	4	Antilopini	East Africa
Litocranius walleri	gerenuk	Lw	5	Antilopini	East Africa
Procapra picticaudata	Tibetan gazelle, goa	Pp	2	Antilopini	Tibetan Plateau
Cephalophus leucogaster	white-bellied duiker	Cl	2	Cephalophini	West Central Africa
Cephalophus monticola	blue duiker	Cm	5	Cephalophini	South, East, Southwest Africa
Cephalophus nigrifrons	black-fronted duiker	Cn	6	Cephalophini	South Central Africa
Sylvicapra grimmia	bush duiker	Sg	6	Cephalophini	South of Sahara
Madoqua guentheri	Guenther's dik dik	Mg	1	Neotragini	East Africa
Madoqua kirki	Kirk's dik dik	Mk	4	Neotragini	South, West and East Africa

Table 3.1, continued. Sample size, species composition and geographical distribution of the modern sample

Species	Common name	Species Code	#	Tribe	Geographic Distribution
Subfamily ANTILOPINAE (continued)					
Madoqua saltiana	Salt's dik dik	Ms	1	Neotragini	North, East Ethiopia and Somalia
Neotragus batesi	dwarf antelope	Nb	2	Neotragini	Southwest, West Central Africa
Neotragus moschatus	suni	Nm	1	Neotragini	East Africa, Eastern South Africa
Neotragus pygmaeus	royal antelope	Np	1	Neotragini	Sierra Leone - Ghana
Oreotragus oreotragus	klipspringer	Oo	4	Neotragini	South of Sahara
Ourebia ourebi	oribi	Ouo	5	Neotragini	South of Sahara
Raphicerus campestris	steinbok	Rc	6	Neotragini	South, East Africa
Raphicerus sharpei	Sharpe's grysbok	Rs	3	Neotragini	South, East Africa
Subfamily REDUNCINAE (n = 18)					
Kobus defassa	waterbuck	Kd	5	Reduncini	South of Sahara
Kobus kob	kob	Kk	5	Reduncini	Volta - Kenya
Kobus leche	lechwe	Kl	1	Reduncini	Northern South Africa
Redunca fulvorufula	mountain reedbuck	Rf	3	Reduncini	South, East, Central Africa
Redunca redunca	bohar reedbuck	Red	4	Reduncini	West - East Africa
Subfamily HIPPOTRAGINAE (n = 32)					
Alcelaphus buselaphus	hartebeest, kongoni	Ab	4	Alcelaphini	West, East, Southwest Africa
Aepyceros melampus	impala	Am	7	Alcelaphini	South, East Africa
Connochaetes gnou	black wildebeest	Cg	1	Alcelaphini	South Africa
Connochaetes taurinus	wildebeest	Ct	4	Alcelaphini	South, East Africa
Damaliscus dorcas	bontebok, blesbok	Dd	1	Alcelaphini	South Africa
Damaliscus hunteri	hirola	Dh	3	Alcelaphini	North Kenya - South Somalia
Damaliscus lunatus	topi, tiang	Dl	2	Alcelaphini	South of Sahara
Addax nasomaculatus	addax	An	1	Hippotragini	Sahara
Hippotragus equinus	roan antelope	He	2	Hippotragini	South of Sahara
Hippotragus niger	sable antelope	Hn	5	Hippotragini	South Africa - Kenya
Oryx beisa	gemsbok	Ob	2	Hippotragini	Southwest, East Africa

Table 3.1, continued. Sample size, species composition and geographical distribution of the modern sample

Species	Common name	Species Code	#	Tribe	Geographic Distribution
Subfamily CAPRINAE (n = 41)					
Capra sibirica	ibex	Cs	3	Caprini	Afghanistan, North India, Russia, China
Ovis ammon	argali	Oa	2	Caprini	West Mongolia - Himalayas
Ovis canadensis	mountain sheep	Oc	2	Caprini	Southwest Canada - Western US
Ovis dalli	dall, white sheep	Od	2	Caprini	Alaska - British Columbia
Ovis vignei	urial	Ov	3	Caprini	Kashmir - Iran
Pseudois nayaur	bharal	Pn	2	Caprini	Himalayas, West China
Budorcas taxicolor	takin	Bt	9	Ovibovini	East Himalayas, Southwest China
Ovibos moschatus	musk ox	Om	4	Ovibovini	Alaska - Greenland
Nemorhaedus crispus	Japanse serow	Nc	2	Rupicaprini	Japan
Nemorhaedus goral	common goral	Ng	3	Rupicaprini	North India, Pakistan, Nepal
Nemorhaedus sumatraensis	mainland serow	Ns	4	Rupicaprini	North India, Sumatra, China
Nemorhaedus swinhoei	Japanese serow	Nsw	1	Rupicaprini	Taiwan
Oreamnos americanus	mountain goat	Oa	2	Rupicaprini	Northwest US – South Alaska
Rupicapra rupicapra	alpine chamois	Rr	2	Rupicaprini	Alps - Caucasus
Family CERVIDAE (n = 14)					
Alces alces	moose	Aa	4		North Eurasia, North US, Canada, Alaska
Flaphodus cephalophus	tufted deer	Ec	4		Southern, Central China, Burma
Odocoileus virginianus	white-tailed deer	Odv	4		North, Central, South America
Pudu mephistophiles	Northern pudu	Pm	2		Andes Mountains
Family TRAGULIDAE (n = 5)					
Hyemoschus aquaticus	water chevrotain	Ha	5		West - Central Africa

analyses on the modern data are presented, total numbers of each element analysed are listed.

The Laetoli fossil bovid remains held at the National Museums of Tanzania, Dar-es-Salaam, Tanzania were studied between July and September 2002. The majority of the material is part of the collections accumulated during the 1998 – 2002 seasons of Terry Harrison's ongoing Eyasi Plateau Paleontological and Geological Project (NSF Grant Numbers: BCS-9903434 and BCS-0309513). A smaller number of the fossil specimens are part of the Mary Leakey collections that were originally held at the camp at Olduvai Gorge and in the Arusha Museum of Natural History, but were removed to the National Museums of Tanzania in the summer of 2002.

Table 3.2 summarises the fossil bovid data sample and lists the sample size for each element measured as well as a breakdown of the elements derived from the primary beds at Laetoli. Specimen numbers and field notes relating to the tuffs between which each fossil was found (where that information was available) can be found in Appendix B. The fossils derive from both the Upper Laetolil Beds (3.5 – 3.8 mya) and the younger Upper Ndolanya Beds (2.4 – 3.5 mya) and were collected from all of the localities visited by the Harrison and Leakey teams. Great care was taken to measure all observable features, although many elements were fragmentary or covered in matrix that could not be removed without damaging the specimen. Thus, because some measurements could not be taken on every fossil, not every specimen could be included in each analysis of that element. In Chapter 6, where the results of the Laetoli analyses are presented, the total sample size for each analysed element is given.

Table 3.2. Laetoli fossil sample summary

HUMERUS (N=153)	**DISTAL METAPODIAL (N=148)**	**SCAPHOID (N=37)**
Laetolil Beds (74)	Laetolil Beds (80)	Laetolil Beds (25)
Ndolanya Beds (79)	Ndolanya Beds (68)	Ndolanya Beds (12)
complete specimens (1)		complete specimens (34)
RADIUS (N=118)	**TALUS (N=186)**	**LUNAR (N=14)**
Laetolil Beds (35)	Laetolil Beds (155)	Laetolil Beds (9)
Ndolanya Beds (83)	Ndolanya Beds (31)	Ndolanya Beds (5)
complete specimens (1)	complete specimens (106)	complete specimens (9)
ULNA (N=21)	**CALCANEUS (N=54)**	**CUNEIFORM (N=20)**
Laetolil Beds (8)	Laetolil Beds (28)	Laetolil Beds (11)
Ndolanya Beds (13)	Ndolanya Beds (26)	Ndolanya Beds (9)
complete specimens (0)	complete specimens (6)	complete specimens (17)
METACARPAL (N=19)	**NAVICULO-CUBOID (N=48)**	**PISIFORM (N=1)**
Laetolil Beds (7)	Laetolil Beds (37)	Laetolil Beds (0)
Ndolanya Beds (12)	Ndolanya Beds (11)	Ndolanya Beds (1)
complete specimens (1)	complete specimens (20)	complete specimens (1)
FEMUR (N=52)	**EXTERNAL & MEDIAL CUNEIFORM (N=7)**	**PROXIMAL PHALANGES (N=173)**
Laetolil Beds (35)	Laetolil Beds (6)	Laetolil Beds (129)
Ndolanya Beds (17)	Ndolanya Beds (1)	Ndolanya Beds (44)
complete specimens (0)	complete specimens (6)	complete specimens (84)
TIBIA (N=80)	**MAGNUM (N=23)**	**INTERMEDIATE PHALANGES (N=115)**
Laetolil Beds (33)	Laetolil Beds (18)	Laetolil Beds (79)
Ndolanya Beds (47)	Ndolanya Beds (5)	Ndolanya Beds (36)
complete specimens (0)	complete specimens (19)	complete specimens (80)
METATARSAL (N=26)	**UNCIFORM (N=10)**	**DISTAL PHALANGES (N=71)**
Laetolil Beds (9)	Laetolil Beds (5)	Laetolil Beds (57)
Ndolanya Beds (17)	Ndolanya Beds (5)	Ndolanya Beds (14)
complete specimens (2)	complete specimens (8)	complete specimens (34)

3.2 Measurements

A total of 209 post-cranial measurements were taken on each complete individual. Measurements were taken on all long bones, tarsals, carpals, and phalanges, but the more irregular or variable elements such as ribs, innominates, vertebrae, and scapulae were not considered. Digital callipers recorded measurements up to 15 cm directly into an Excel spreadsheet. Measurements between 15 and 27 cm were taken using standard hand-held dial callipers and an osteometric board was used for long bone lengths greater than 27 cm. All measurements taken with callipers were recorded to the nearest hundredth of a millimetre; the osteometric board measured to the nearest millimetre.

All measurements have been given a code that was entered into subsequent analyses. The codes consist of one, two or three letters and a number according to the following system:

Long bones – the first letter of the element (i.e. "H" for humerus) capitalised and a number indicating the chronological order in which the measurement was taken. The metapodials are designated by two capital letters, "MC" for metacarpal and "MT" for metatarsal.

Other elements - the first letter of the generic category of the element (i.e. "C" for carpals, "T" for tarsals and "P" for phalanges) capitalised and a second lower-case letter (a – f) indicating in which order the elements within that group were measured, followed by a number indicating the chronological order in which the measurement was taken on that element. The talus and calcaneus are two exceptions to this system and are labelled "TA" and "C", respectively.

This system of coding was used rather than providing a series of acronyms or abbreviations for each measurement because of the large number of measurements analysed in this project. This would have created a cumbersome range of alphabetical notation. The codes for each element are listed in Table 3.3.

The measurements are defined in Table 3.4 where they are grouped by element and listed by their codes. They are also illustrated in accompanying Figures 3.1 – 3.20 which are referenced in Table 3.4.

A number of the measurements used are considered standard, and these relate in most cases to lengths, functional lengths, and diameters of distal and proximal ends of long bones and are often the same as or similar to those considered in the work of existing ecomorphological studies (Scott, 1983; Kappelman, 1988; Kohler, 1993; Plummer & Bishop, 1994; Hixson, 1998, DeGusta & Vrba, 2003). Table 3.5 lists measurements that are the same as, or similar to, that of another researcher. However, the majority of the measurements were devised specifically for the purposes of this project - especially in the case of carpals, tarsals and phalanges, which have not been previously studied, with the single exception of DeGusta & Vrba's (2003) study of the talus. Köhler (1993) looked at bovid phalanges, but her measurements are difficult to apply to phalanges found in isolation.

These new measurements were arrived at through an empirical method of direct comparison. Three specimens of different body sizes were studied in the Natural History Museum, London. Each element of the three specimens was examined and features that were observably different between them were noted. Landmarks that could be identified in the three test specimens which related to these features were used to orient the callipers so that the measurements could be repeated in all three individuals. An emphasis was placed on defining measurements of

Table 3.3. Element codes

ELEMENT	CODE
Long bones	
Humerus	H
Radius	R
Ulna	U
Metacarpal	MC
Femur	F
Tibia	T
Metatarsal	MT
Metapodial	MP
Carpals	
Magnum	Ca
Unciform	Cb
Scaphoid	Cc
Lunar	Cd
Cuneiform	Ce
Pisiform	Cf
Tarsals	
Talus	TA
Calcaneus	C
Naviculo-cuboid	Ta
External and middle cuneiform	Tb
Phalanges	
Proximal phalanges	Pa
Intermediate phalanges	Pb
Distal phalanges	Pc

Table 3.4. Measurement definitions and codes

Code	Definition
Humerus (see Figure 3.1):	
H1:	greatest length of the humerus
H2:	functional length of the humerus
H3:	height of the greater tuberosity, from the articular surface of the head to the tip of the tuberosity
H4:	measure of the most distal point of the deltoid crest to the tip of the greater tuberosity
H5:	width of the humeral head
H6:	anterior-posterior diameter of the proximal end
H7:	transverse diameter of the proximal end
H8:	width of the trochlea and capitulum
H9:	anterior-posterior diameter of the distal end
H10:	transverse diameter of the distal end
H11:	width of the trochlea in posterior view
H12:	length of trochlea in posterior view
H13:	anterior-posterior mid-shaft diameter
H14:	transverse mid-shaft diameter
Radius (see Figure 3.2):	
R1:	greatest length of the radius
R2:	functional length of the radius
R3:	anterior-poster diameter of the proximal end
R4:	transverse diameter of the proximal end
R5:	transverse width of the articular surface of the proximal end
R6:	anterior-posterior diameter of the distal end
R7:	transverse diameter of the distal end
R8:	anterior-poster mid-shaft diameter
R9:	transverse mid-shaft diameter
Ulna (see Figure 3.3):	
U1:	greatest length of the ulna
U2:	functional length of the ulna
U3:	measure of the length from the proximal tip of the ulna to the lateral extension of the radial articular surface
U4:	measure of the length from the proximal tip of the ulna to the proximal tip of the trochlear notch
U5:	measure of the shortest distance between the proximal tip of the ulna and the trochlear articular surface
U6:	greatest width of the radial articular surface
U7:	width of the articular surface for the olecranon
Metacarpal (see Figure 3.4):	
MC1:	greatest length of the metacarpal
MC2:	functional length of the metacarpal
MC3:	anterior-posterior diameter of the proximal end
MC4:	transverse diameter of the proximal end
MC5:	anterior-posterior diameter of the distal end
MC6:	transverse diameter of the distal end
MC7:	measure of the distance between the medial and lateral verticillus
MC8:	diameter of the lateral epicondyle
MC9:	transverse width of the lateral epicondyle

Table 3.4, continued. Measurement definitions and codes

Code	Definition
Metacarpal continued (see Figure 3.4):	
MC10:	measure of the distance between the medial and lateral epicondyle at the most proximal point
MC11:	measure of the distance between the medial and lateral epicondyle at the most distal point
MC12:	anterior-posterior mid-shaft diameter
MC13:	transverse mid-shaft diameter
Femur (see Figure 3.5):	
F1:	greatest length of femur
F2:	functional length of femur
F3:	anterior-posterior diameter of the proximal end
F4:	transverse diameter of the proximal end
F5:	measure of the distance between the tip of the greater trochanter and the tip of the lesser trochanter
F6:	measure of the distance between the tip of the lesser trochanter and the tip of the head
F7:	anterior-posterior diameter of the femoral head
F8:	transverse diameter of the femoral head
F9:	anterior-posterior diameter of the distal end
F10:	transverse diameter of the distal end
F11:	measure of the width of the anterior trochlea
F12:	measure of the width of the interior trochlea
F13:	anterior-posterior mid-shaft diameter
F14:	transverse mid-shaft diameter
Tibia (see Figure 3.6):	
T1:	greatest length of tibia
T2:	functional length of tibia
T3:	anterior-posterior diameter of the proximal end
T4:	transverse diameter of the proximal end
T5:	measure of the greatest anterior-posterior width of the lateral condyle
T6:	measure of the width of the articular surface of the lateral condyle
T7:	measure of the width of the articular surface of the medial condyle
T8:	measure of the distance between the articular surfaces of the lateral and medial condyles
T9:	anterior-posterior diameter of the distal end
T10:	transverse diameter of the distal end
T11:	anterior-posterior mid-shaft diameter
T12:	transverse mid-shaft diameter
Metatarsal (see Figure 3.7):	
MT1:	greatest length of the metatarsal
MT2:	functional length of the metatarsal
MT3:	anterior-posterior diameter of the proximal end
MT4:	transverse diameter of the proximal end
MT5:	anterior-posterior diameter of the distal end
MT6:	transverse diameter of the distal end
MT7:	measure of the distance between the medial and lateral verticillus
MT8:	diameter of the lateral epicondyle
MT9:	transverse width of the lateral epicondyle

Table 3.4, continued. Measurement definitions and codes

Code	Definition
Metatarsal continued (see Figure 3.7):	
MT10:	measure of the distance between the medial and lateral epicondyle at the most proximal point
MT11:	measure of the distance between the medial and lateral epicondyle at the most distal point
MT12:	anterior-posterior mid-shaft diameter
MT13:	transverse mid-shaft diameter
Magnum (see Figure 3.8):	
Ca1:	greatest transverse width of magnum
Ca2:	greatest dorsal-palmar length of magnum
Ca3:	greatest dorsal-palmar length of articular surface
Ca4:	greatest transverse width of articular surface
Ca5:	greatest dorsal-palmar length of the medial aspect of the proximal surface where it articulates with the scaphoid
Ca6:	dorsal-palmar length of the lateral margin of the proximal surface where it articulates with the lunar
Ca7:	width of the dorsal surface at the lateral edge
Ca7b:	width of the dorsal surface where it is joined by the proximal articular surface ridge
Ca8:	width of the dorsal surface at the medial edge
Unciform (see Figure 3.9):	
Cb1:	greatest transverse width of the unciform
Cb2:	greatest dorsal-palmar length of the unciform
Cb3:	greatest dorsal-palmar length of the distal articular surface
Cb4:	greatest transverse width of the distal articular surface
Cb5:	greatest dorsal-palmar length of the medial aspect of the proximal surface where it articulates with the lunar
Cb6:	dorsal-palmar length of the lateral aspect of the proximal surface where it articulates with the cuneiform
Cb7:	width of the dorsal surface at the lateral edge
Cb7b:	width of the dorsal surface where it is joined by the proximal articular surface ridge
Cb8:	width of the dorsal surface at the medial edge
Scaphoid (see Figure 3.10):	
Cc1:	greatest transverse width of the scaphoid
Cc2:	greatest dorsal-palmar length of the scaphoid
Cc3:	greatest dorsal-palmar length of the distal articular surface
Cc4:	dorsal-palmar length of the lateral surface where it articulates distally with the lunar
Lunar (see Figure 3.11):	
Cd1:	greatest transverse width of the lunar (in proximal view)
Cd2:	greatest dorsal-palmar length of the lunar (in proximal view)
Cd3:	dorsal-palmar length of the lateral margin of the distal surface where it articulates with the cuneiform
Cd4:	dorsal-palmar length of the distal surface where it articulates with the magnum and unciform
Cd5:	dorsal-palmar length of the medial margin of the distal surface
Cd6:	length of the lateral surface where it articulates distally with the cuneiform
Cd7:	length of the dorsal margin of the lateral surface
Cd8:	dorsal-palmar length of the medial surface where it articulates distally with the scaphoid
Cd9:	dorsal-palmar length of the medial surface where it articulates proximally with the scaphoid

Table 3.4, continued. Measurement definitions and codes

Code	Definition
Cuneiform (see Figure 3.12):	
Ce1:	greatest dorsal-palmar length of the cuneiform
Ce2:	length of the distal surface where it articulates with the unciform
Ce3:	length of the medial surface where it articulates distally with the lunar
Ce4:	length of the dorsal margin of the medial surface where it articulates with the lunar
Ce5:	length of the palmar articular surface
Pisiform (see Figure 3.13):	
Cf1:	greatest proximal-distal length of the pisiform
Cf2:	greatest dorsal-palmar length of the pisiform
Cf3:	length of the dorsal articular surface
Talus (see Figure 3.14):	
TA1:	greatest length of the talus
TA2:	measure of the distance from the distal base to the most inferior aspect of the medial articular surface
TA2b:	measure of the distance from the talar notch to the talar head, taken in medial view
TA3:	width of distal articular surface
TA4:	width of the proximal articular surface
TA5:	shortest length of the talus
TA6:	measure of the distance from the mid-point of the trochlear pit to the end of the proximal articular surface
TA7:	width of the inferior articular surface
TA8:	length of the inferior articular surface
Calcaneus (see Figure 3.15):	
C1:	greatest length of the calcaneus
C2:	length of the posterior extension from the end of the talar articular surface to the end of the calcaneus
C3:	greatest length of the articular surface for the medial malleolus of the tibia
C4:	greatest depth of the articular surface for the talus
C5:	length of the sustentaculum talus
C6:	greatest length of the articular surface for the naviculo-cuboid
C7:	anterior-poster mid-body diameter
C8:	transverse mid-body diameter
Naviculo-cuboid (see Figure 3.16):	
Ta1:	dorsal-palmar length of the naviculo-cuboid, taken in distal view
Ta2:	length of the larger lateral articular surface on the distal end
Ta3:	length of the smaller lateral articular surface on the distal end
Ta4:	length of the lateral aspect of the articular surface for the cuneiform
Ta5:	length of the adjoining articular surfaces for the cuneiform and metatarsal
Ta6:	length of the medial edge of the articular surface for the cuneiform
Ta7:	width of the medial articular surface on the distal end
Ta8:	width of the naviculo-cuboid, taken in proximal view
Ta9:	width of the talar articular surface
Ta10:	length of the articular surface for the calcaneus
Ta11:	length of the larger proximal "hook"
Ta12:	width of the medial surface

Table 3.4, continued. Measurement definitions and codes

Code	Definition
Naviculo-cuboid continued (see Figure 3.16):	
Ta13:	depth of the larger proximal "hook", from the articular surface to the tip
Ta14:	depth of the smaller proximal "hook", from the articular surface to the tip
Ta15:	width of the lateral surface
External and middle cuneiform (see Figure 3.17):	
Tb1:	length of the external and middle cuneiform
Tb2:	width of the external and middle cuneiform
Tb3:	length of the distal articular surface
Tb4:	width of the distal articular surface
Tb5:	width of the proximal articular surface
Tb6:	length of the medial aspect of the proximal articular surface
Tb7:	greatest length of the proximal articular surface
Tb8:	width of the medial surface
Proximal phalanges (see Figure 3.18):	
Pa1:	greatest length of the proximal phalanx
Pa2:	transverse diameter of distal end
Pa3:	transverse width of the distal articular surface
Pa3b:	dorsal-palmar length of the distal articular surface
Pa4:	transverse width of the proximal end
Pa5:	transverse width of the proximal articular surface
Pa5b:	dorsal-palmar length of the proximal articular surface
Pa6:	dorsal-palmar mid-shaft diameter
Pa7:	transverse mid-shaft diameter
Intermediate phalanges (see Figure 3.19):	
Pb1:	greatest length of the intermediate phalanx
Pb2:	transverse diameter of distal end
Pb3:	transverse width of the distal articular surface
Pb3b:	dorsal-palmar length of the distal articular surface
Pb4:	transverse width of the proximal end
Pb5:	transverse width of the proximal articular surface
Pb5b:	dorsal-palmar length of the proximal articular surface
Pb6:	dorsal-palmar mid-shaft diameter
Pb7:	transverse mid-shaft diameter
Distal phalanges (see Figure 3.20):	
Pc1:	greatest length of the distal phalanx
Pc2:	dorsal-palmar diameter of the proximal end
Pc3:	dorsal-palmar width of the proximal articular surface
Pc3b:	transverse width of the proximal articular surface
Pc4:	dorsal-palmar length at the mid-point
Pc5:	transverse width at the mid-point

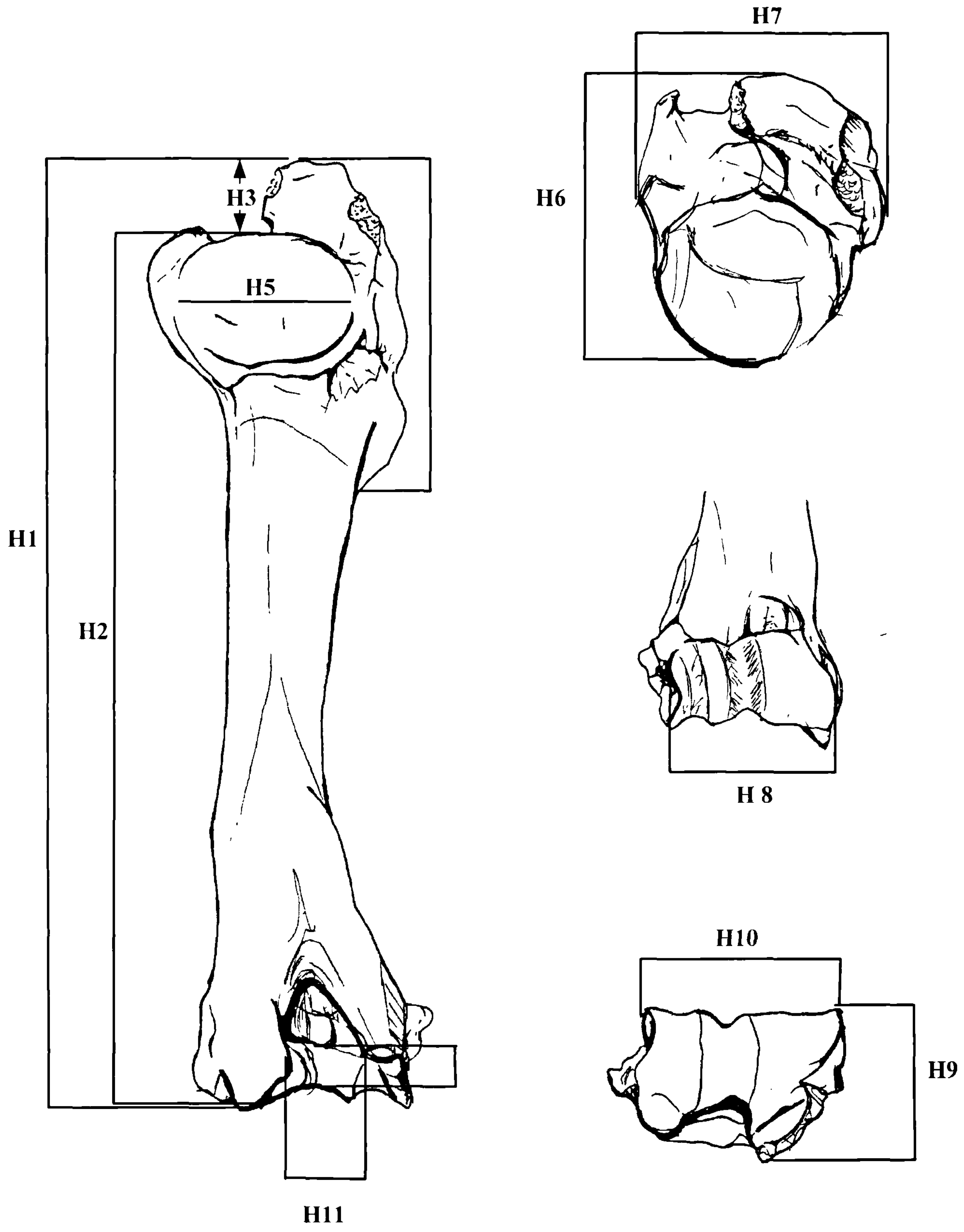


Figure 3.1. Measurements of the humerus. H13 (anterior-posterior mid-shaft diameter) and H14 (transverse mid-shaft diameter) are not shown. Measurement codes and definitions are in Table 3.4.

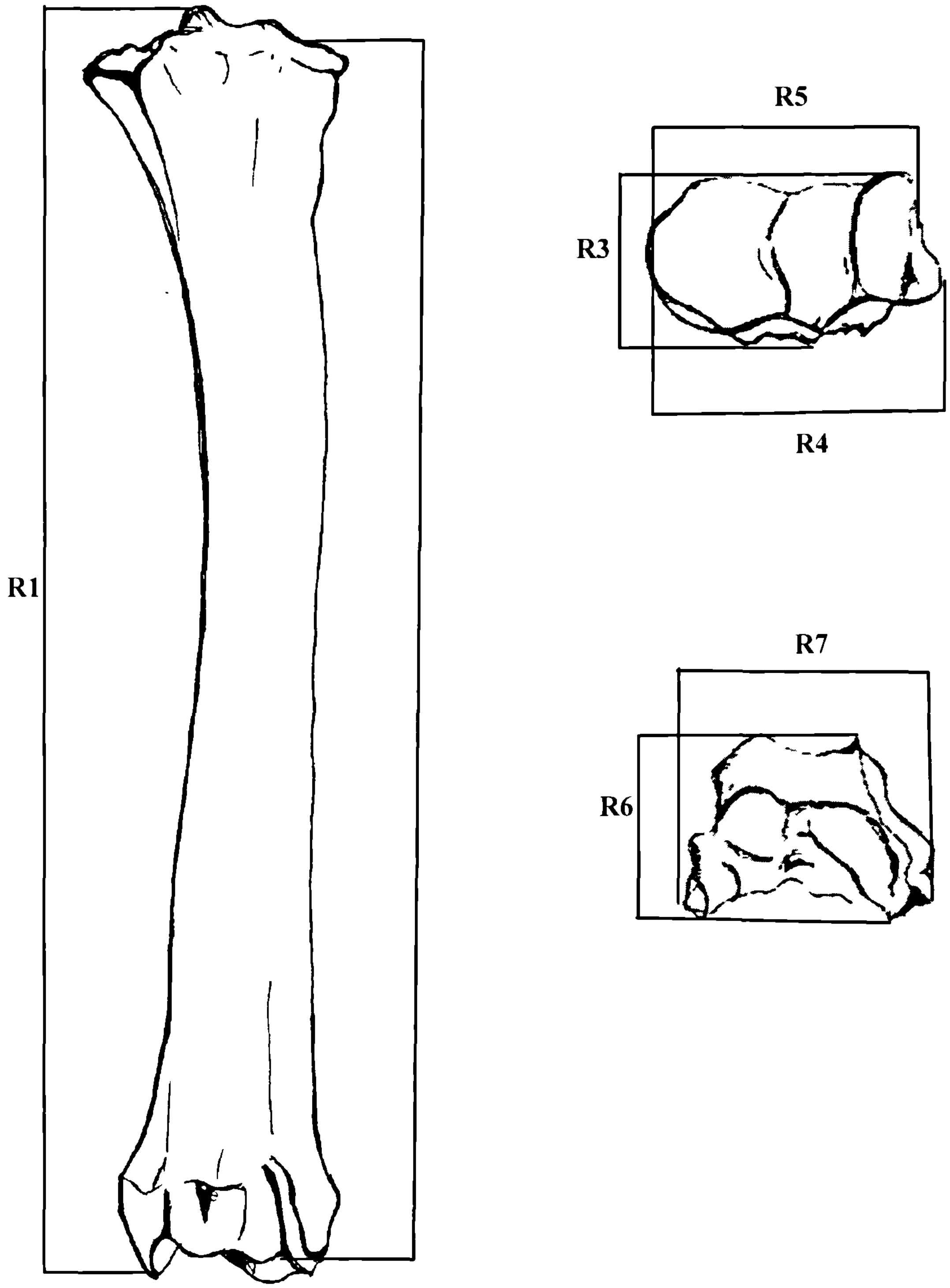


Figure 3.2. Measurements of the radius. R8 (anterior-posterior mid-shaft diameter) and R9 (transverse mid-shaft diameter) are not shown. Measurement codes and definitions are in Table 3.4.

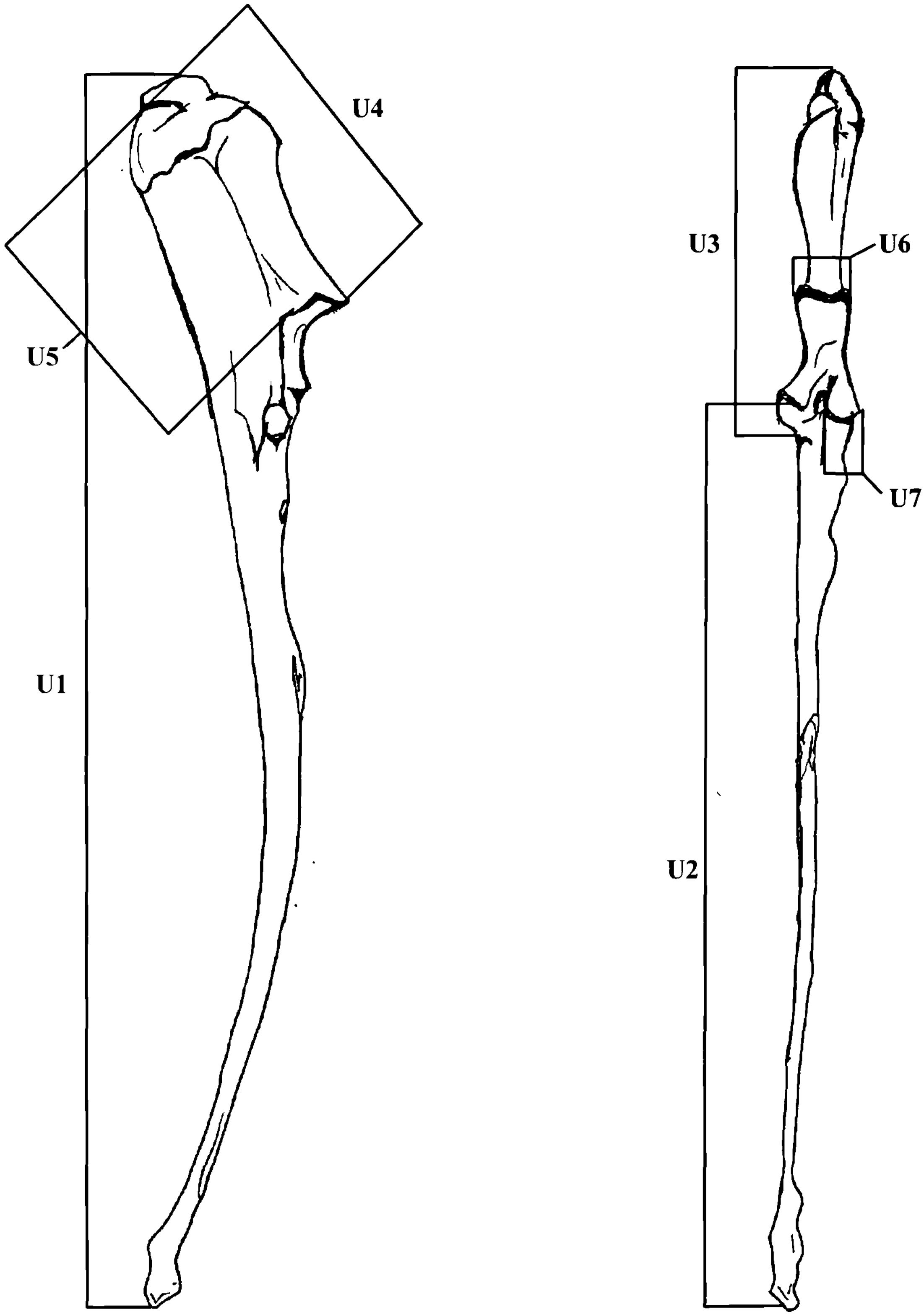


Figure 3.3. Measurements of the ulna. Measurement codes and definitions are in Table 3.4.

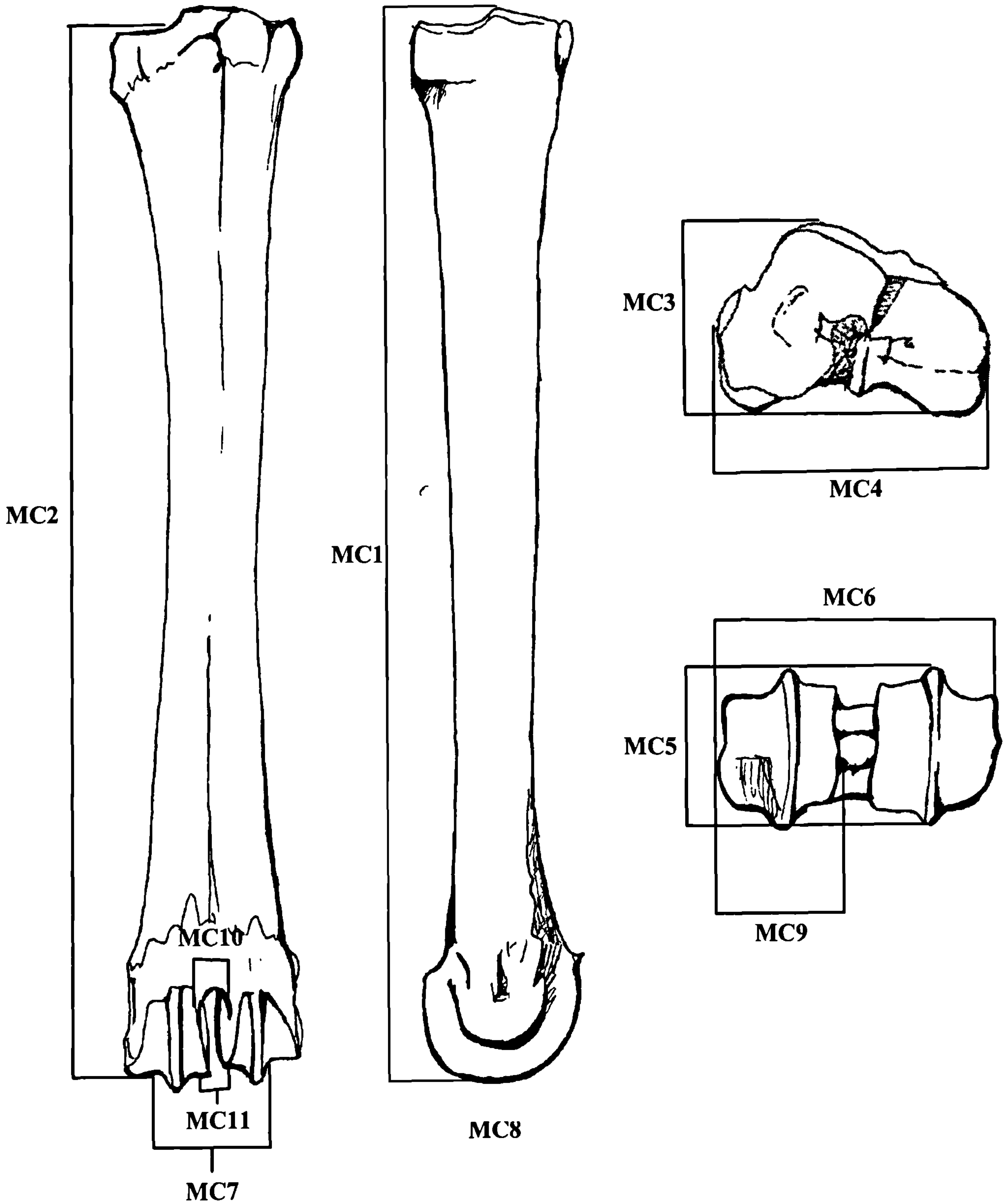


Figure 3.4. Measurements of the metacarpal. MC12 (anterior-posterior mid-shaft diameter) and MC13 (transverse mid-shaft diameter) are not shown. Measurement codes and definitions are in Table 3.4.

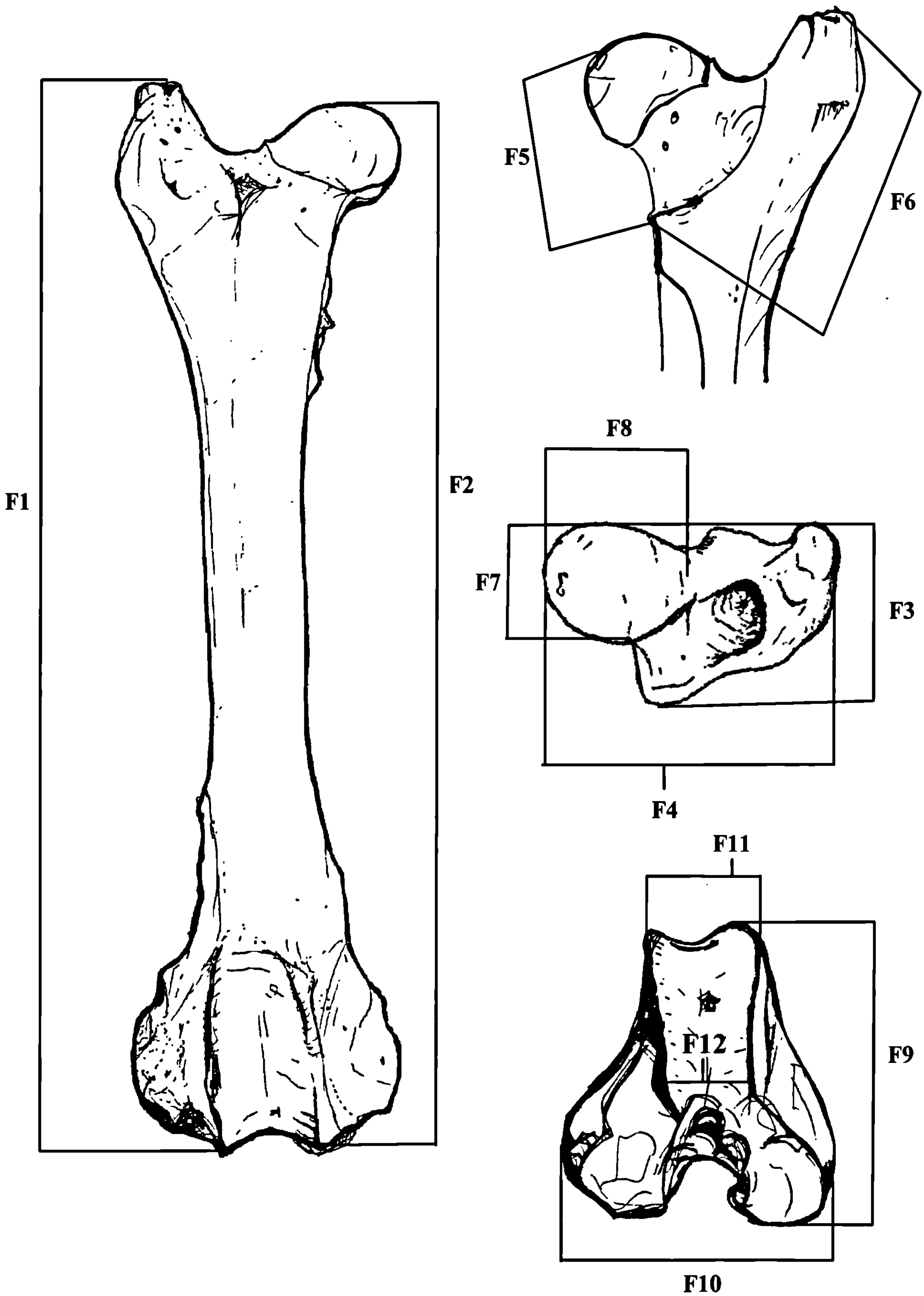


Figure 3.5. Measurements of the femur. F13 (anterior-posterior mid-shaft diameter) and F14 (transverse mid-shaft diameter) are not shown. Measurement codes and definitions are in Table 3.4.

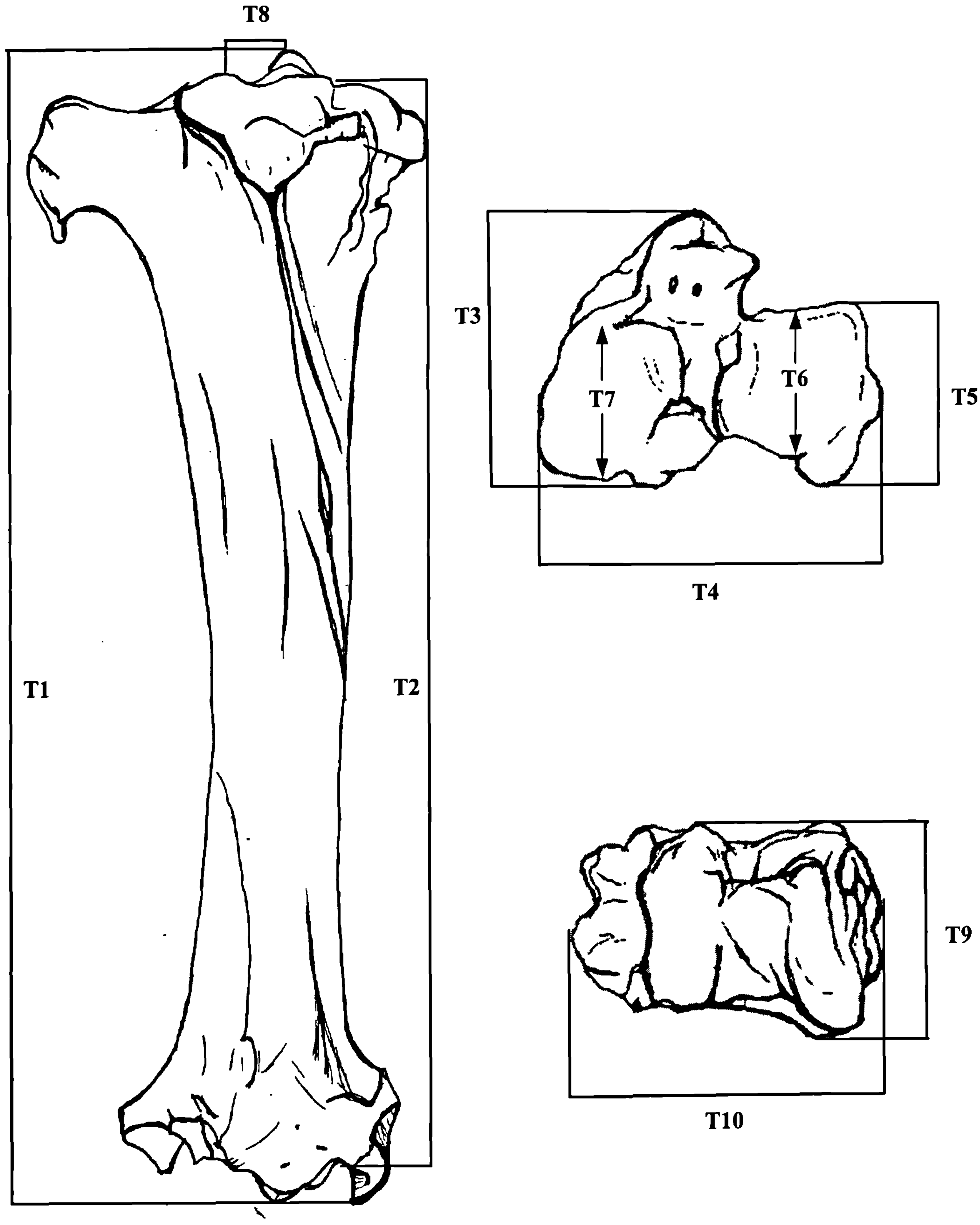


Figure 3.6. Measurements of the tibia. T11 (anterior-posterior mid-shaft diameter) and T12 (transverse mid-shaft diameter) are not shown. Measurement codes and definitions are in Table 3.4.

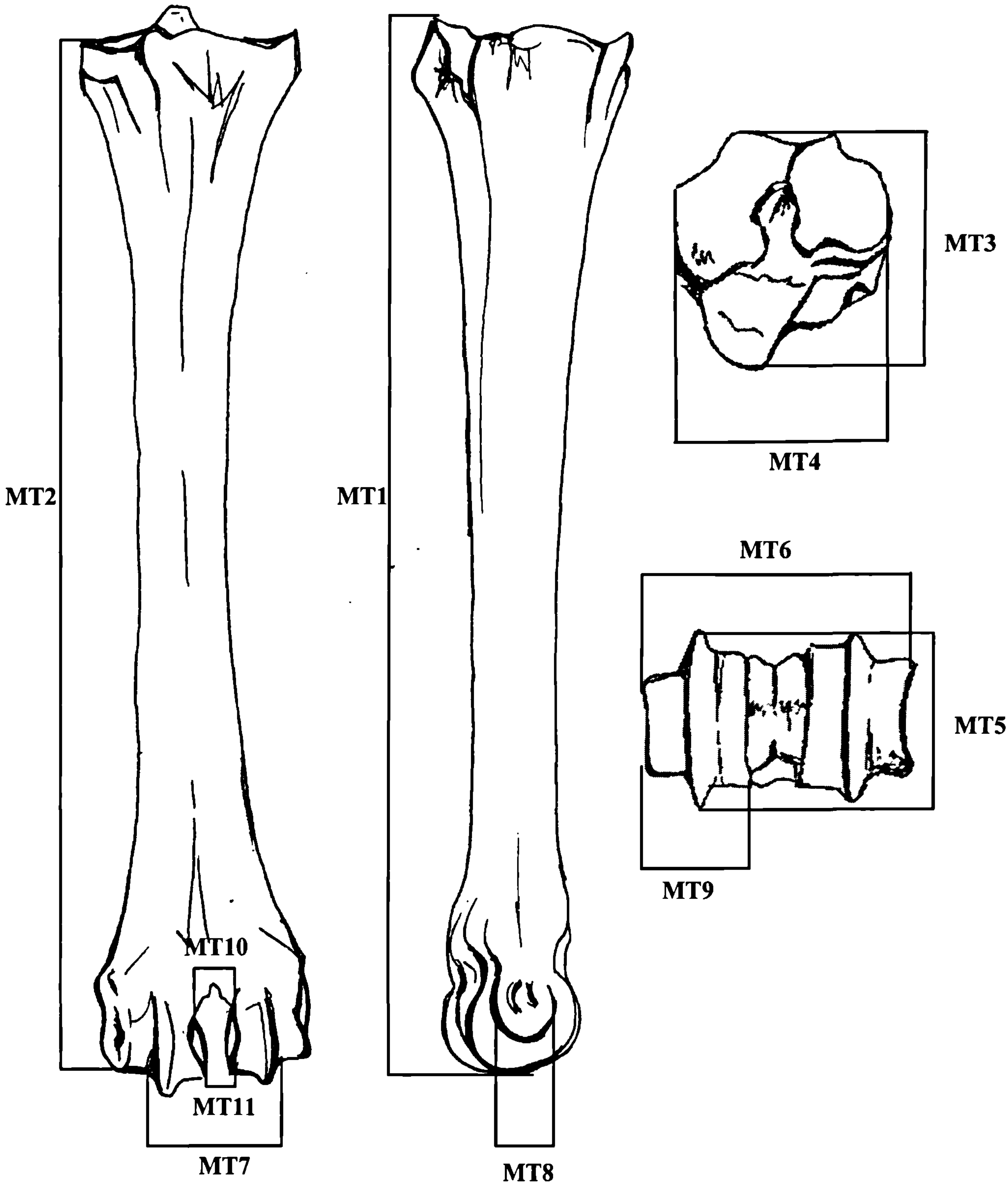


Figure 3.7. Measurements of the metatarsal. MT12 (anterior-posterior mid-shaft diameter) and MT13 (transverse mid-shaft diameter) are not shown. Measurement codes and definitions are in Table 3.4.

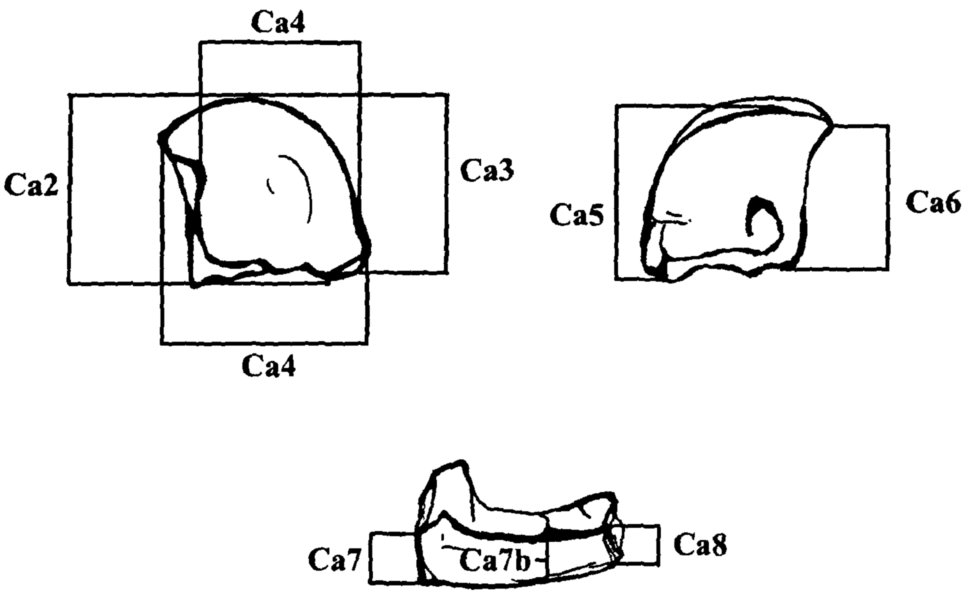


Figure 3.8. Measurements of the magnum. Measurement codes and definitions are in Table 3.4.

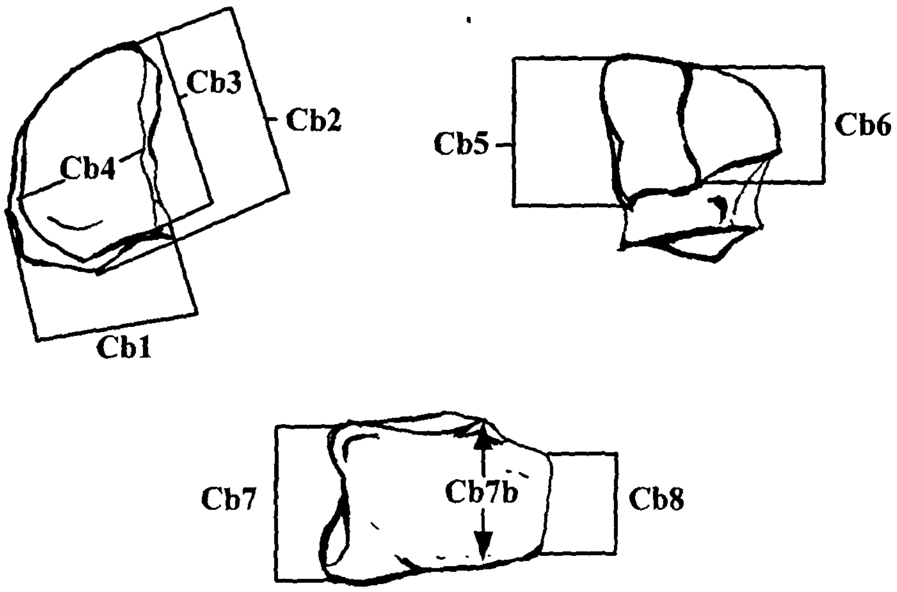


Figure 3.9. Measurements of the unciform. Measurement codes and definitions are in Table 3.4.

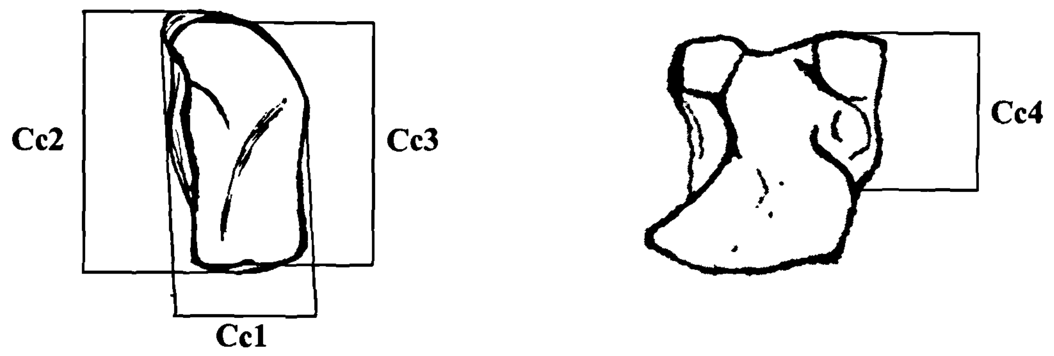


Figure 3.10. Measurements of the scaphoid. Measurement codes and definitions are in Table 3.4.

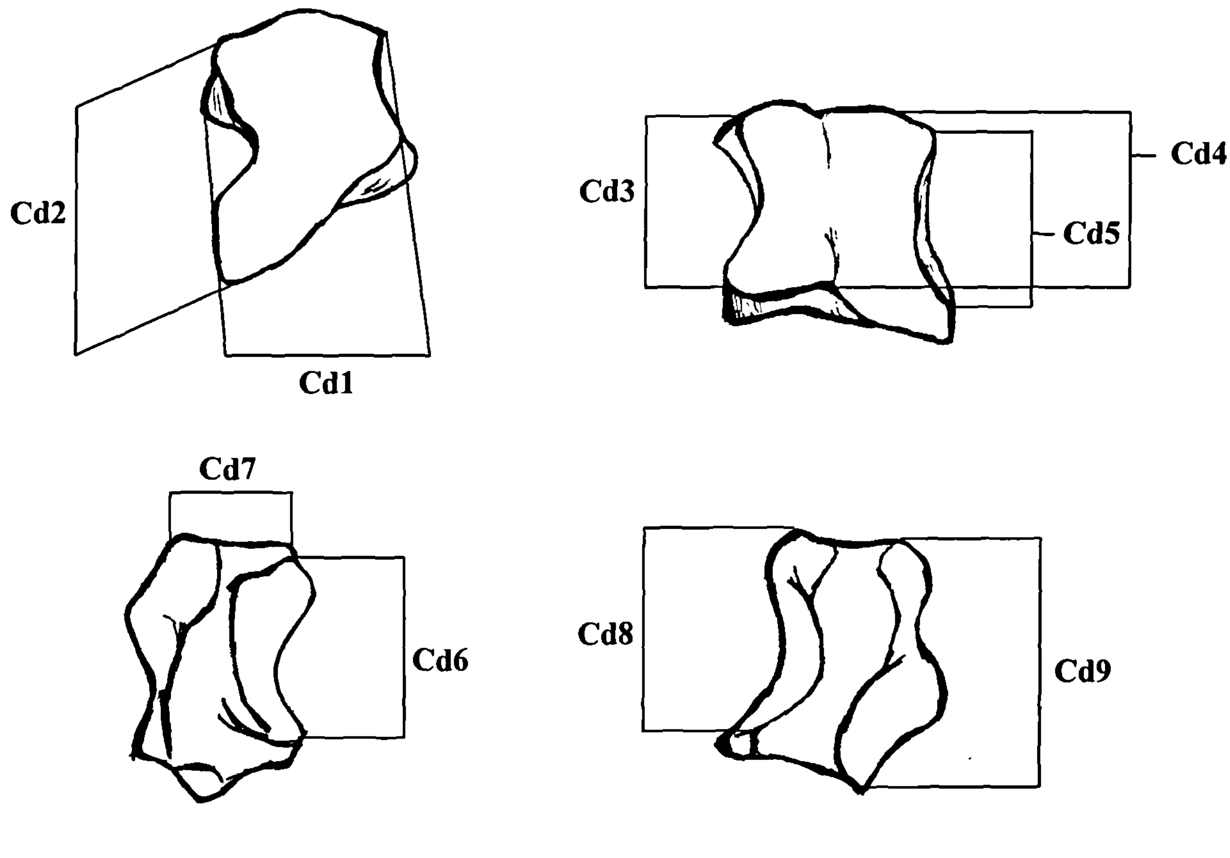


Figure 3.11. Measurements of the lunar. Measurement codes and definitions are in Table 3.4.

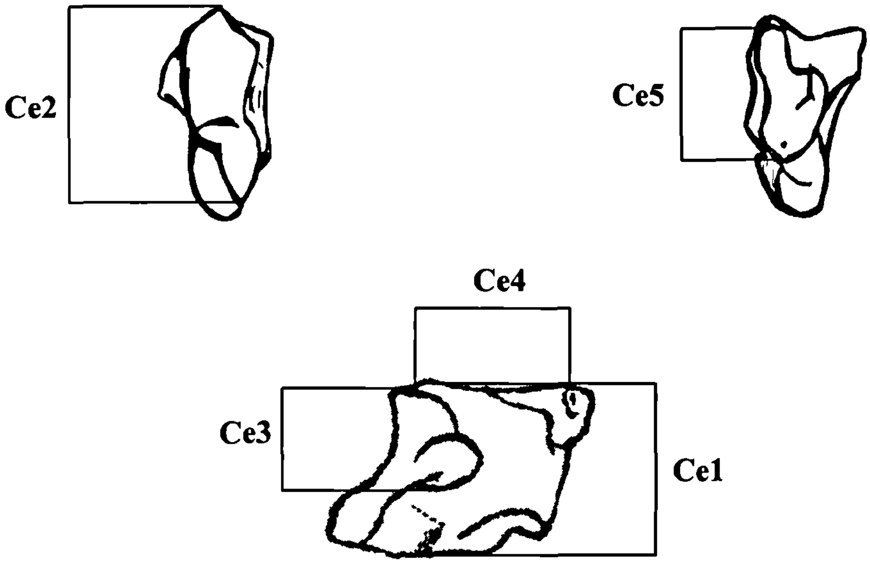


Figure 3.12. Measurements of the cuneiform. Measurement codes and definitions are in Table 3.4.

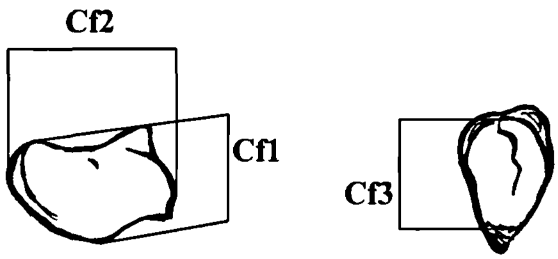


Figure 3.13. Measurements of the pisiform. Measurement codes and definitions are in Table 3.4.

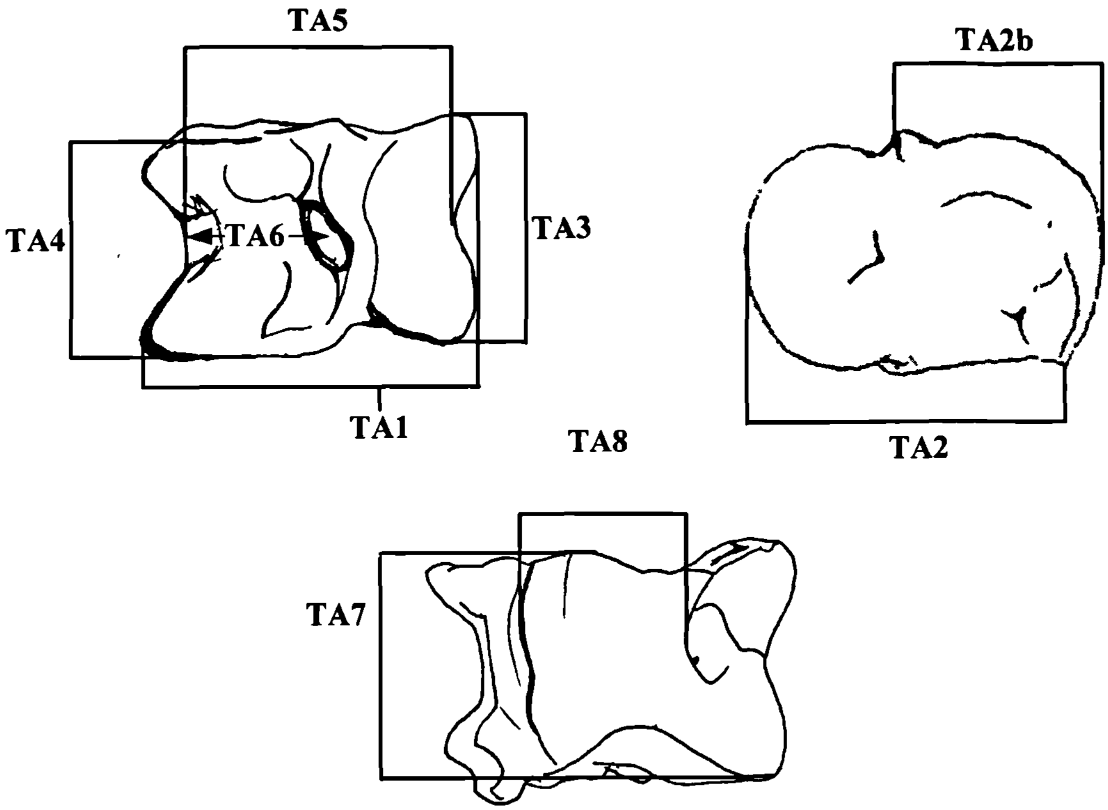


Figure 3.14. Measurements of the talus. Measurement codes and definitions are in Table 3.4.

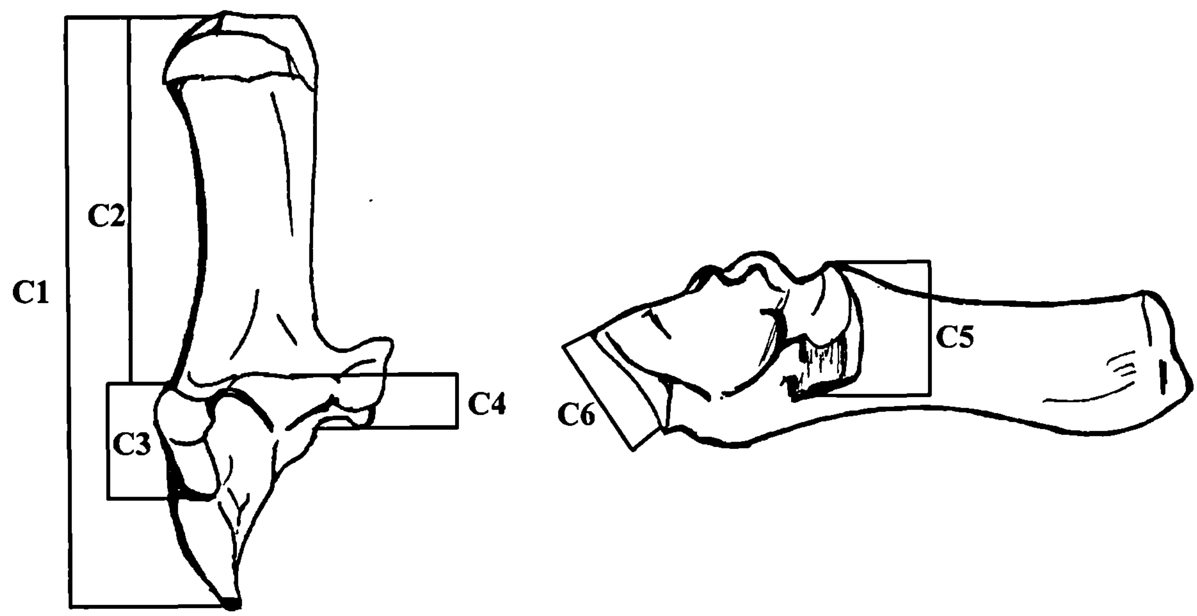


Figure 3.15. Measurements of the calcaneus. C7 (anterior-posterior mid-body diameter) and C8 (transverse mid-body diameter) are not shown. Measurement codes and definitions are in Table 3.4.

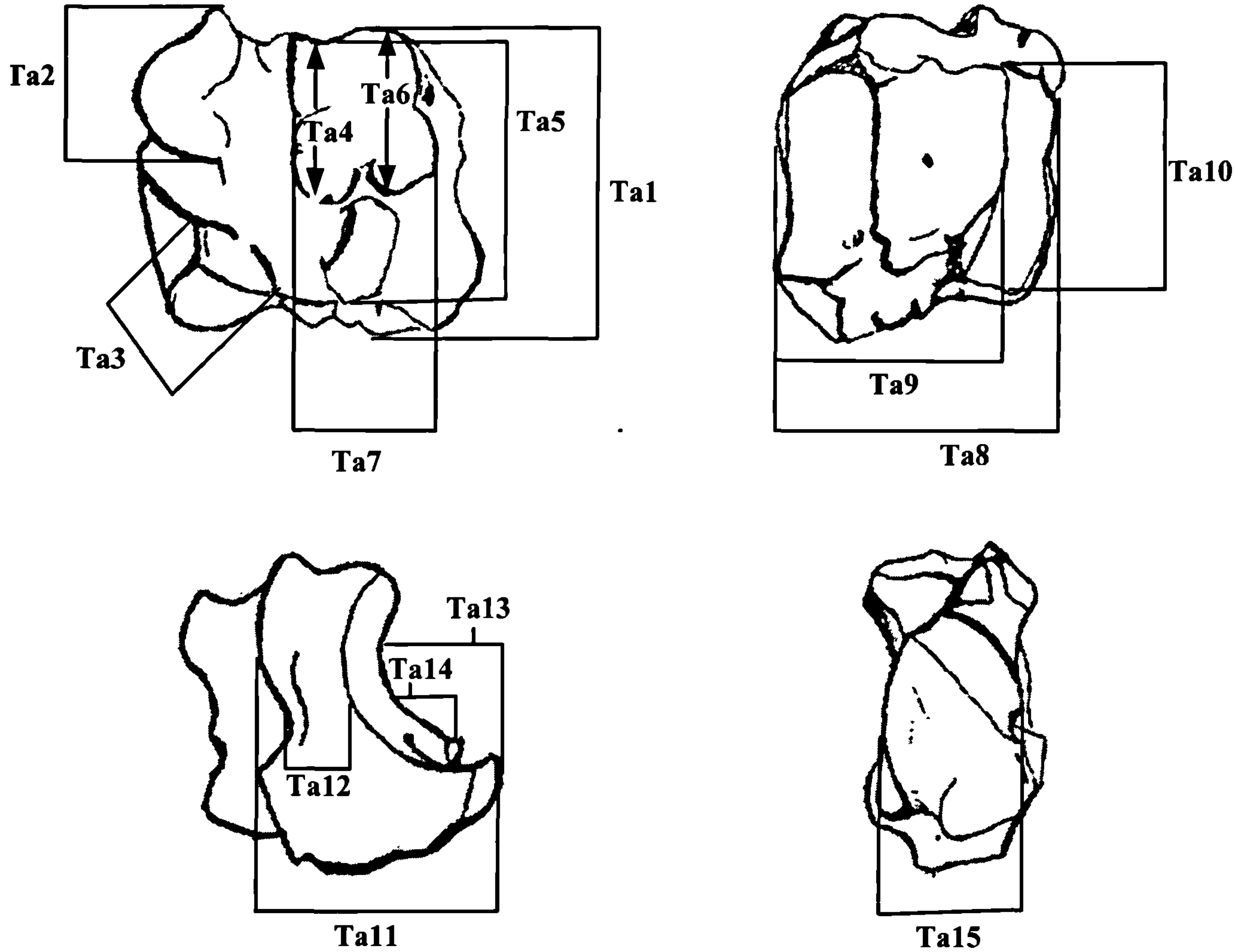


Figure 3.16. Measurements of the naviculo-cuboid. Measurement codes and definitions are in Table 3.4.

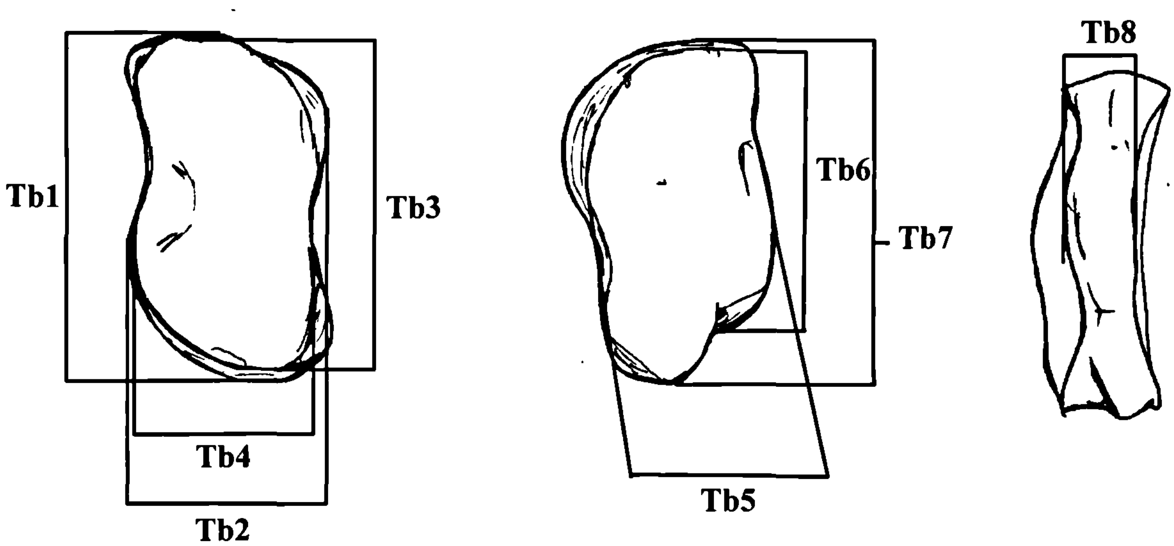


Figure 3.17. Measurements of the external and middle cuneiform. Measurement codes and definitions are in Table 3.4.

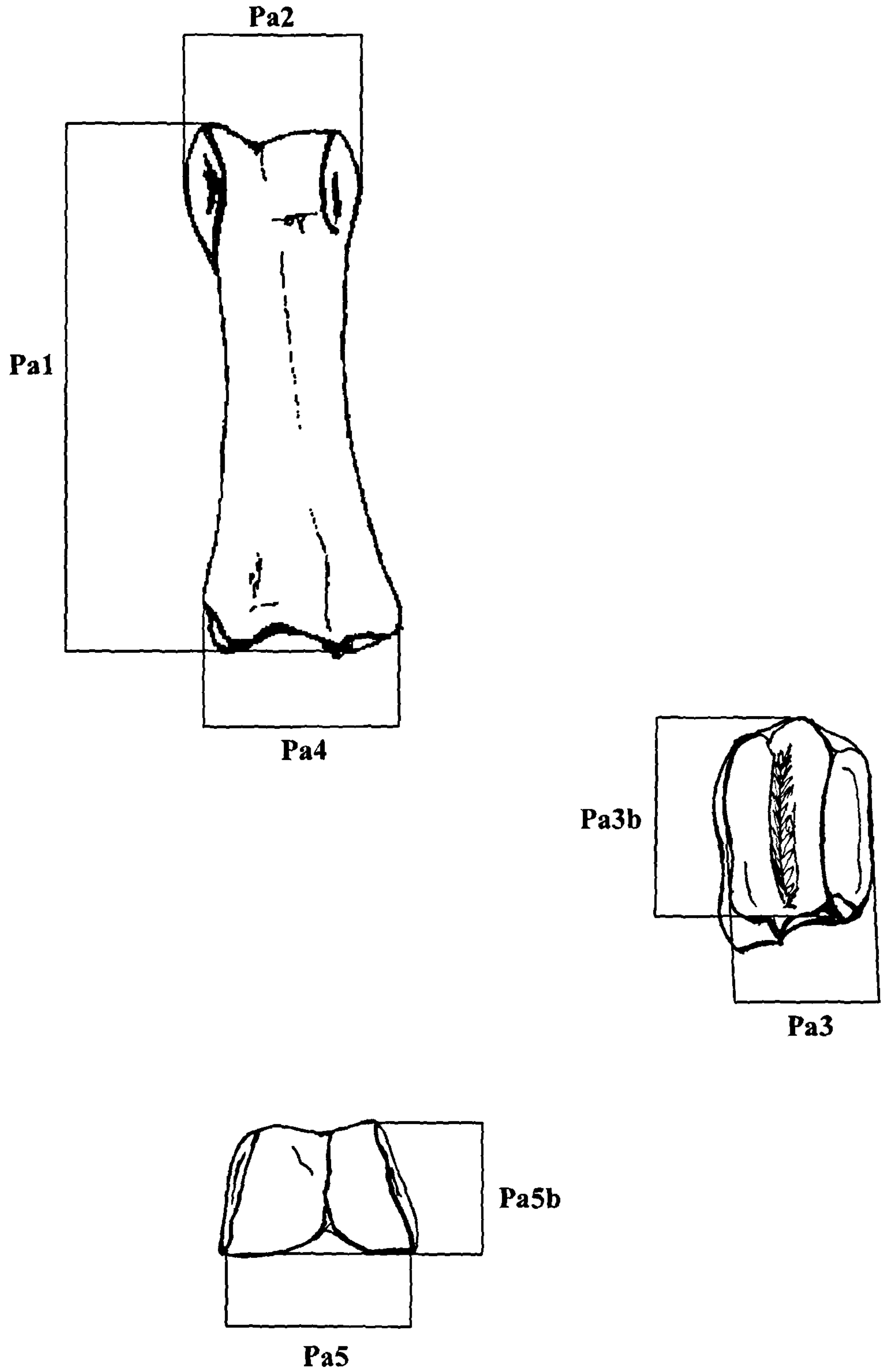


Figure 3.18. Measurements of the proximal phalanx. Pa6 (anterior-posterior mid-shaft diameter) and Pa7 (transverse mid-shaft diameter) are not shown. Measurement codes and definitions are in Table 3.4.

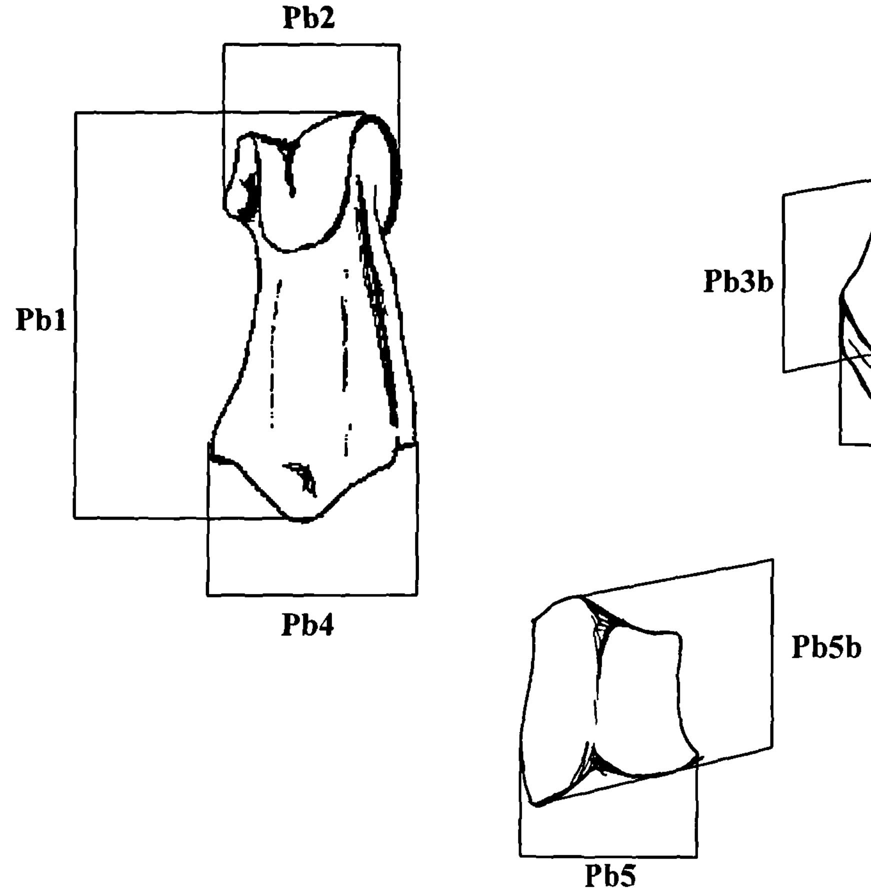


Figure 3.19. Measurements of the intermediate phalanx. Pb6 (anterior-posterior mid-shaft diameter) and Pb7 (transverse mid-shaft diameter) are not shown. Measurement codes and definitions are in Table 3.4.

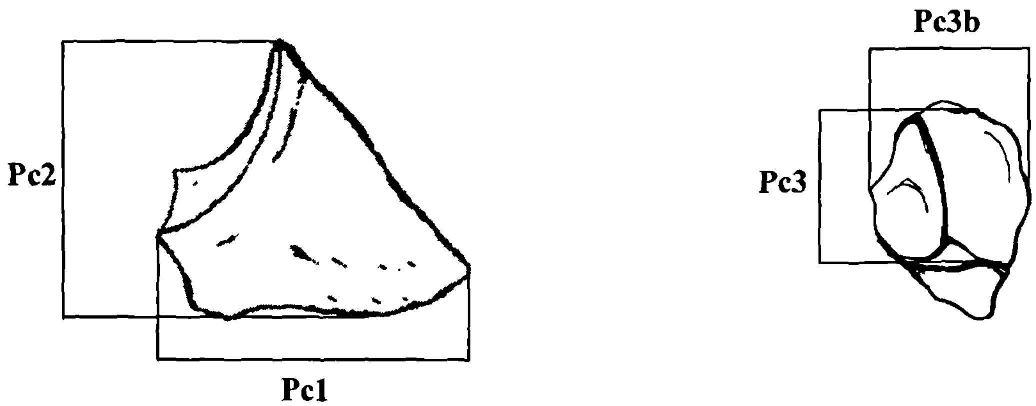


Figure 3.20. Measurements of the distal phalanx. Pc4 (anterior-posterior mid-body diameter) and Pc5 (transverse mid-body diameter) are not shown. Measurement codes and definitions are in Table 3.4.

Table 3.5. Sources of measurements

Measurement	Source	Measurement	Source	Measurement	Source
Humerus		***Femur***		***Calcaneus***	
H1	4	F1	4	C1	4
H2	1, 2	F2	1, 2	C2	4
H4	4	F3	2		
H5	1	F4	1, 2	***Proximal phalanx***	
H6	2	F5	1, 4	Pa1	4
H7	2	F6	1	Pa2	
H8	1, 4	F7	4	Pa3	
H9	2	F8	4	Pa3b	
H10	1, 2	F9	2	Pa4	
H11	1	F10	2, 4	Pa5	
		F11	4	Pa5b	
Radius		F12	1	Pa6	
R1	4			Pa7	
R2	1, 2	***Tibia***			
R3	1, 2	T1	4	***Intermediate phalanx***	
R4	1, 2	T2	1, 2	*Pb1*	
R5	1	T3	2, 4	Pb2	
R6	2	T4	1, 2, 4	Pb3	
R7	1, 2	T5	1	Pb3b	
		T9	1, 2	Pb4	
Ulna		T10	1, 2	Pb5	
U1	4			Pb5b	
U2	4	***Metatarsal***		Pb6	
U3	4	MT1	3, 4	Pb7	
U4	1	MT2	1, 2, 3		
U5	4	MT3	1, 3		
		MT4	1, 3		
Metacarpal		MT5	3		
MC1	3, 4	MT6	1, 3		
MC2	1, 2, 3	MT8	1, 3		
MC3	1, 3	MT9	3		
MC4	1, 3	MT12	3		
MC5	3	MT13	3		
MC6	1, 3				
MC8	1, 3	***Talus***			
MC9	3	TA1	4, 5		
MC12	3	TA2b	4		
MC13	3	TA3	5		
		TA5	5		

1 = Scott (1983)
2 = Kohler (1993)
3 = Plummer & Bishop (1994)
4 = Hixson (1998)
5 = DeGusta & Vrba (2003)

articular surfaces and the "mirror image" surface of adjoining bones. It was assumed that these joint features would be likely to relate to differences in locomoting within different habitat types and would thus be able to distinguish between them.

3.3 Error testing

The percentage error indicates the accuracy and repeatability of a particular measurement. A high percentage error indicates that a measurement is not repeatable and thus caution must be exercised when analysing an element that includes such measurements, especially if they are driving the analysis.

The measurements were repeated twice on the complete set of 209 variables for five specimens after the initial measurements were taken, for a total of three measurement trials. Two male and one female *Sylvicapra grimmia* (specimen numbers1966.9.26.1, 1966.9.22.1 and 1966.8.18.1), one male *Aepyceros melampus* (1932.6.6.3) and one female *Hippotragus niger* (1964.7.8.1) from the collections at The Natural History Museum, London were included in the error testing sample for all elements other than the phalanges. Five entirely complete specimens were not available and so three others substituted the *Sylvicapra grimmia* individuals which did not have all of their phalanges. They were a female *Oreotragus oreotragus* (1936.5.28.4), male *Kobus leche* (1969.1147) and male *Raphicerus campestris* (1936.5.28.3). Measurements of the phalanges of the forelimb and the hindlimb were taken separately for the error testing, although they are pooled in all subsequent analyses. In Table 3.6 the measurements of the phalanges of the limbs are distinguished by an "f" (forelimb) and "h" (hindlimb) added to their codes.

The species that were re-measured were chosen for two reasons. Firstly, they were selected to represent a range of bovid body sizes. Secondly, some specimens that

Table 3.6. Error testing percentages

Measurement	H1	H2	H3	H4	H5	H6	H7	H8	H9	H10	H11	H12	H13	H14	
% error	0.04	0.09	1.1	1.56	1.06	1.58	0.42	1.14	0.88	0.73	1.48	2.65	0.85	0.78	
Measurement	R1	R2	R3	R4	R5	R6	R7	R8	R9						
% error	0.15	0.16	1.21	0.28	0.36	1.46	0.86	0.94	0.48						
Measurement	U1	U2	U3	U4	U5	U6	U7								
% error	0.5	0.64	0.63	0.47	0.71	0.71	2.25								
Measurement	MC1	MC2	MC3	MC4	MC5	MC6	MC7	MC8	MC9	MC10	MC11	MC12	MC13		
% error	0.05	0.1	1.07	0.31	0.21	0.07	1.76	3.21	2.85	2.08	3.05	0.34	0.22		
Measurement	F1	F2	F3	F4	F5	F6	F7	F8	F9	F10	F11	F12	F13	F14	
% error	0.25	0.35	0.91	0.48	0.79	1.17	0.51	0.6	0.35	0.74	0.55	1.64	1.06	0.51	
Measurement	T1	T2	T3	T4	T5	T6	T7	T8	T9	T10	T11	T12			
% error	0.18	0.31	1.57	0.39	0.8	2.3	0.89	1.39	1.03	0.81	2.4	1.13			
Measurement	MT1	MT2	MT3	MT4	MT5	MT6	MT7	MT8	MT9	MT10	MT11	MT12	MT13		
% error	0.21	0.18	0.59	0.53	0.42	0.07	1.44	1.46	0.92	5.11	1.66	1.09	0.44		
Measurement	TA1	TA2	TA2b	TA3	TA4	TA5	TA6	TA7	TA8						
% error	0.1	1.79	0.8	0.56	1.2	0.15	2.02	3.26	0.47						
Measurement	C1	C2	C3	C4	C5	C6	C7	C8							
% error	0.23	0.69	1.34	2.04	0.91	0.91	0.93	1.19							
Measurement	Ta1	Ta2	Ta3	Ta4	Ta5	Ta6	Ta7	Ta8	Ta9	Ta10	Ta11	Ta12	Ta13	Ta14	Ta15
% error	0.35	0.91	2.6	2.17	0.51	1.88	1.54	0.45	0.9	2.03	1.05	4.18	4.08	4.92	0.86
Measurement	Tb1	Tb2	Tb3	Tb4	Tb5	Tb6	Tb7	Tb8							
% error	1.13	0.42	2.15	1.05	1.34	1.14	0.57	2.33							

Measurement definitions and codes can be found in Table 3.4. Measurements of the forelimb and hindlimb phalanges were taken separately and are denoted by an "f" for forelimb and "h" for hindlimb after their codes

Table 3.6, continued. Error testing percentages

Measurement	Ca1	Ca2	Ca3	Ca4	Ca5	Ca6	Ca7	Ca7b	Ca8
% error	0.63	0.36	1.25	1.96	1.18	1.11	2.69	0.79	1.4
Measurement	Cb1	Cb2	Cb3	Cb4	Cb5	Cb6	Cb7	Cb7b	Cb8
% error	1.83	0.89	1.38	1.48	2.07	1.06	1.49	0.71	3.04
Measurement	Cc1	Cc2	Cc3	Cc4					
% error	1.18	2.29	2.37	10.53					
Measurement	Cd1	Cd2	Cd3	Cd4	Cd5	Cd6	Cd7	Cd8	Cd9
% error	0.84	2.01	2.83	2.37	1.82	8.59	3.59	4.2	0.82
Measurement	Ce1	Ce2	Ce3	Ce4	Ce5				
% error	0.46	1.71	1.64	1.6	2.35				
Measurement	Cf1	Cf2	Cf3						
% error	0.36	0.65	0.7						
Measurement	Pa1f	Pa2f	Pa3f	Pa3bf	Pa4f	Pa5f	Pa5bf	Pa6f	Pa7f
% error	0.19	0.65	0.88	0.74	0.52	0.97	1.04	0.92	0.72
Measurement	Pb1f	Pb2f	Pb3f	Pb3bf	Pb4f	Pb5f	Pb5bf	Pb6f	Pb7f
% error	0.61	0.59	0.77	0.76	1.28	0.97	1.87	1.21	2.27
Measurement	Pc1f	Pc2f	Pc3f	Pc3bf	Pc4f	Pc5f			
% error	0.28	0.32	1.22	1.15	1.91	1.59			
Measurement	Pa1h	Pa2h	Pa3h	Pa3bh	Pa4h	Pa5h	Pa5bh	Pa6h	Pa7h
% error	0.16	0.48	0.96	0.44	0.71	0.87	0.96	1.2	0.47
Measurement	Pb1h	Pb2h	Pb3h	Pb3bh	Pb4h	Pb5h	Pb5bh	Pb6h	Pb7h
% error	0.67	0.81	0.77	0.99	1.91	1.81	1.17	0.89	1.62
Measurement	Pc1h	Pc2h	Pc3h	Pc3bh	Pc4h	Pc5h			
% error	0.5	0.33	1.67	0.7	0.95	1.72			

Measurement definitions and codes can be found in Table 3.4. Measurements of the forelimb and hindlimb phalanges were taken separately and are denoted by an "f" for forelimb and "h" for hindlimb after their codes were initially measured early in the data gathering process and others which were measured towards the end of the process were included in order to determine if the measuring protocol changed significantly as time went by, which could also be indicated by a high percentage error.

Five months passed before the specimens were measured for the second time and six weeks passed in between the second and third times. Thus any particularly anomalous feature of the specimen, or anything that might have influenced the way the first set of measurements were taken, were not influential in the subsequent sessions.

The percentage measurement error was estimated following the procedure set out by White (1991). It is illustrated in Table 3.7 using the three measurement trials for the variable H1, total humeral length, on the five individuals included in the sample.

The results are summarised in Table 3.6, which lists the percentage error calculated for each measurement. The results indicate that the measurements are accurately repeated and that the measuring protocol did not change significantly over time. The average percentage error for all of the measurements is 1.24%. The lowest percentage error was 0.04% for H1, total humeral length and the highest percentage error was 10.53% for Cc4, the dorsal-palmar length of the scaphoid where it articulates with the lunar. The six measurements with relatively high percentages of error (Cc4, Cd6, Cd8, Ta12, Ta13 and Ta14) are discussed below.

The variability that affects the percentage error in the bovid data here is attributed to the fact that different species will have slightly different muscle markings and features. Although the dataset is made up of bovids of vastly differing body sizes,

Table 3.7. Error testing procedure for H1, humeral length

			Step 1		**Step 2**
Sylvicapra grimmia	male	1966.9.26.1	Measurement A	121.55	(average-A)+(average-B)+(average-C)/3 = .013
			Measurement B	121.51	
			Measurement C	121.53	**Step 3**
			Average of A, B and C =	121.53	(.013 121.53)100 = .01%
			Step 1		**Step 2**
Sylvicapra grimmia	female	1966.9.22.1	Measurement A	124.39	(average-A)+(average-B)+(average-C)/3 = .027
			Measurement B	124.32	
			Measurement C	124.37	**Step 3**
			Average of A, B and C =	124.36	(.027/124.36)100 = .02%
			Step 1		**Step 2**
Sylvicapra grimmia	male	1966.8.18.1	Measurement A	123.97	(average-A)+(average-B)+(average-C)/3 = .009
			Measurement B	123.97	
			Measurement C	123.99	**Step 3**
			Average of A, B and C =	123.98	(.009/123.98)100 = .01%
			Step 1		**Step 2**
Aepyceros melampus	male	1932.6.6.3	Measurement A	191.60	(average-A)+(average-B)+(average-C)/3 = .033
			Measurement B	191.55	
			Measurement C	191.65	**Step 3**
			Average of A, B and C =	191.60	(.033/191.60)100 = .02%
Hippotragus niger	female	1964.7.8.1	**Step 1**		**Step 2**
			Measurement A	253.50	(average-A)+(average-B)+(average-C)/3 = .333
			Measurement B	253.00	
			Measurement C	254.00	**Step 3**
			Average of A, B and C =	253.50	(.333/253.50)100 = .13%
			Step 4		
			(.01+.02+.01+.02+.13)/5 = .04%		

that does not affect the percentage error calculation because the mean deviation calculated in step 2 is then divided by the average of the measurement trials in step 3, effectively cancelling out the size factor. However, the *measuring method* was slightly different for larger individuals, because a pair of callipers that could extend easily beyond 27 centimetres was not available and this did affect the calculations for larger individuals. In the case of a long bone length over that threshold, a basic osteometric board was used to take the measurement. The osteometric board was only capable of measuring to the nearest millimetre, while the callipers were more sensitive and could measure to the closest hundredth of a millimetre.

Table 3.7 illustrates this phenomenon quite well. The *Sylvicapra grimmia* and *Aepyceros melampus* specimens are small and medium sized and the callipers were able to record more accurate lengths on these individuals. *Hippotragus niger* on the other hand, is a large bodied species and the bone board was used to record the humeral length. In the three trials it was measured to be 253.5, 253 and 254. The average deviation is .333, which is a 0.13% error. Contrast this with the first male *Sylvicapra grimmia* specimen, with H1 measurements of 121.55, 121.51 and 121.53, an average deviation of .013 and a percentage error of only 0.01%. In fact, the other two *Sylvicapra grimmia* and *Aepyceros melampus* specimens did not yield a percentage error higher than .02% for this measurement. When all of the individuals' percentage errors were averaged, the *Hippotragus niger* value pulled this average up. However, it should be emphasised that this is attributable to the measuring protocol for larger specimens and that body size does not inherently affect percentage error.

Measurements of the carpals and tarsals had a generally higher percentage error than those taken on the long bones because they are more irregular and thus more difficult to consistently orient in order to take a measurement. Despite this, only six measurements had a percentage error high enough to warrant comment. The first, Cc4, the articular surface of the scaphoid where it adjoins the lunar distally, has a percentage error of 10.53%, the highest of any in the sample. This feature was sharply defined in some specimens and not in others, and this difference did not appear to be correlated with either species or sex. It was extremely difficult to determine the boundaries of the articular surface, especially the inferior margin.

Two lunar measurements, Cd6, the lateral surface where it articulates with the cuneiform distally, and Cd8, the dorsal-palmar length of the medial surface where it articulates with the scaphoid distally, had a percentage error of 8.59% and 4.20% respectively. These features were difficult to measure for the same reasons as Cc4. They were not always obvious articulations and quite frequently hard to discern at their inferior margins.

Three measurements on the naviculo-cuboid were problematic. Ta12, the width of the medial surface, has a high percentage error, 4.18%, for lack of an obvious associated landmark at which to place the callipers. The medial surface can be measured from several points and although it was intended that the measurement be taken at the midpoint of that particular edge, it is obviously not always possible to consistently judge where this is. Both Ta13 and Ta14, 4.08% and 4.92% respectively, are measurements of the two proximal hooks from their tips to the bases at the articular surface where the bone joins the talus. These measurements are both extremely difficult to obtain with a basic pair of callipers, which is clearly reflected in their percentage errors.

Finally, MT10, the distance between the medial and lateral halves of the distal end of the metatarsal at the most proximal point, has a calculated percentage error of 5.11%. This is somewhat surprising given that the same measurement on the metacarpal, MC10, only has a 2.08% percentage error and it is taken in the same way as MT10. A possible error could have been made in recording one or two of the measurement trials, or a particularly anomalous feature of my chosen specimens may have made it difficult to obtain the measurement. Dried soft tissues often posed a problem in taking certain measurements and this might have been the case in this instance.

3.4 Size-correcting the dataset

The bovid species included in the sample of modern data encompass a vast range of body sizes, from the African royal antelope *Neotragus pygmaeus*, which weighs on average 2.25 kilograms, to the Indochinese kouprey, *Bos sauveli*, which weighs an average of 800 kilograms. In order to illustrate the breadth of body sizes represented, each of the 70 modern bovid, cervid and tragulid species in the dataset have been classified according to a six group system of weight categories used in previous ecological analyses which investigated mammalian body weights in relation to habitat exploitation (Andrews & Humphrey, 1999; Kovarovic *et al*, 2002). The categories are as follows:

A: 1-10 kg
B: 11-45 kg
C: 46-90 kg
D: 91-180 kg
E: 181-360 kg
F: 360+ kg

Averages derived from body weight ranges in the literature (Kingdon, 1997; Nowak, 1999; MacDonald 2001) were calculated and each species was placed into one category according to the calculated average. Males and females were considered together. Table 3.8 summarises the weight classifications of each species and lists the number of individuals in each weight category.

Table 3.8. Body size categories of the species in this study

Species	Common name
CATEGORY A (1-10 kg)	
Total number of specimens = 20	
Cephalophus monticola	blue duiker
Madoqua guentheri	Gunther's dik dik
Madoqua kirki	Kirk's dik dik
Madoqua saltiana	Salt's dik dik
Neotragus batesi	dwarf antelope
Neotragus moschatus	suni
Neotragus pygmaeus	royal antelope
Pudu mephistophiles	Northern pudu
Raphicerus sharpei	Sharpe's grysbok
CATEGORY B (11-45 kg)	
Total number of specimens = 69	
Antilope cervicapra	blackbuck
Cephalophus leucogaster	white-bellied duiker
Cephalophus nigrifrons	black-fronted duiker
Elaphodus cephalophus	tufted deer
Gazella cuvieri	edmi gazelle
Gazella rufifrons	red fronted gazelle
Gazella soemmerringi	Soemmerring's gazelle
Gazella speki	Speke's gazelle
Gazella subgutturosa	goitred gazelle
Gazella thomsoni	Thomson's gazelle
Hyemoschus aquaticus	water chevrotain
Litocranius walleri	gerenuk
Nemorhaedus goral	common goral
Oreotragus oreotragus	klipspringer
Ourebia ourebi	oribi
Procapra picticaudata	Tibetan gazelle, goa
Raphicerus campestris	steinbuck
Redunca fulvorufula	mountain reedbuck
Rupicapra rupicapra	Alpine chamois
Sylvicapra grimmia	bush duiker
CATEGORY C (46-90 kg)	
Total number of specimens = 43	
Aepyceros melampus	impala
Capra sibirica	ibex
Damaliscus dorcas	bontebok, blesbok
Gazella granti	Grant's gazelle
Nemorhaedus crispus	Japanese serow
Nemorhaedus swinhoei	Taiwanese serow
Odocoileus virginianus	white-tailed deer
Ovis vignei	urial
Pseudois nayaur	bharal
CATEGORY C (46-90 kg) continued	
Redunca redunca	bohar reedbuck
Tragelaphus scriptus	bushbuck
Tragelaphus speki	sitatunga
CATEGORY D (91-180 kg)	
Total number of specimens = 31	
Addax nasomaculatus	addax
Alcelaphus buselaphus	hartebeest, kongoni
Connochaetes gnu	black wildebeest
Damaliscus hunteri	hirola
Damaliscus lunatus	topi, tiang
Kobus kob	kob
Kobus leche	lechwe
Nemorhaedus sumatraensis	mainland serow
Oreamnos americanus	mountain goat
Oryx beisa	gemsbok
Ovis ammon	argali
Ovis canadensis	mountain sheep
Ovis dalli	dall, whitesheep
CATEGORY E (181-360 kg)	
Total number of specimens = 37	
Bubalus mindorensis	tamaraw
Budorcas taxicolor	takin
Connochaetes taurinus	wildebeest
Hippotragus equinus	roan antelope
Hippotragus niger	sable antelope
Kobus defassa	waterbuck
Ovibos moschatus	musk ox
Tragelaphus eurycerus	bongo
Tragelaphus strepsiceros	greater kudu
CATEGORY F (360+ kg)	
Total number of specimens = 24	
Alces alces	moose
Bison bison	bison
Bos javanicus	banteng
Bos sauveli	kouprey
Syncerus caffer	African buffalo
Taurotragus derbianus	giant eland
Taurotragus oryx	common eland

Body size is an important ecological variable, and extant mammalian species in given habitats partition themselves both trophically and spatially according to size. Generally speaking for land mammals, larger species have a restricted range of locomotor repertoires to utilise. Small mammals may burrow in the ground, climb up trees and other obstacles, glide through the air and locomote terrestrially, but large mammals are mainly terrestrial. Likewise for feeding preferences there is an observable trend whereby insectivorous species are often small, frugivorous species small and medium sized but never large, and carnivorous and omnivorous species medium sized and never very small or very large (Andrews & O'Brien, 2000). It can also be observed that for a mammal of one size a tree or shrub may provide either shelter, shade or part of a meal for a temporally restricted period, while for a smaller mammal the same tree or shrub may provide all three on a much more permanent basis. Put another way, for a larger species it is one aspect of its habitat, for smaller species it *is* the habitat.

Body size has also been found to be correlated with a number of other life history and lifestyle variables including age at first reproduction (Wootton, 1987), frequency of grooming (Mooring *et al*, 2000), mating system (Jarman, 1974; Geist, 1977; Weckerly, 1998), the partitioning of resources (Hutchinson, 1959; Hutchsinson & MacArthur, 1959; Gwynne & Bell, 1968) and the size of the exploited home range (McNab, 1963; Mace & Harvey, 1983; Basset, 1995).

Although size is clearly an important ecological consideration, analyses of distributions of mammalian body sizes within habitats have not yet proved fruitful in identifying habitat types. Faunal communities found in widely differing modern habitat types show no statistically significant difference in their overall size distributions (Andrews *et al*, 1979; Andrews & Humphrey, 1999). However, in considering individual families rather than entire communities, it may be questioned if body size is informative in relation to habitat.

As Table 3.8 indicates, bovid species have average body sizes that range across the six weight classes. Stemming from the observation that browsing bovids are small-bodied and grazing bovids are larger, the Jarman-Bell principle (Bell, 1970, 1971; Geist, 1974; Jarman, 1974) proposes that this relationship relates to both the differing metabolic rates of the small and large bodied species and the varied energetic and nutritional packages provided by their preferred diets. Small bodied species which have low absolute energy requirements and high metabolic rates favour high quality food items, such as low-fibre protein-rich browse. As they require relatively lower amounts of food, they can spend more time searching for and selecting these more rare high quality items. Conversely, large bodied species with higher absolute energy requirements and lower metabolic rates must consume relatively greater amounts of food but cannot afford to be as selective in their provisioning. Thus they must eat widely available lower quality grasses with a high fibre component. This theory is also supported by evidence that in sexually dimorphic ungulate species the larger males consume more grass compared to females and they also have higher rates of dental attrition (Clutton-Brock *et al*, 1983; Mysterud, 2000; Loe *et al*, 2003).

Body mass has other implications for bovid lifestyles including predator avoidance strategies and group size (Jarman, 1974; Geist, 1977). Small bodied selective feeders sometimes form very small groups but more often exist in either monogamous pairs or as solitary individuals which hide from dangerous predators but usually engage in territory maintenance and defence against conspecifics. However, larger unselective feeders do congregate in groups and, when approached by predators, they either flee or counterattack. They seldom defend territories against access by their own species and group size often fluctuates depending on the season and availability of resources.

Establishing the negative relationship between diet quality and body size as a consistent or predictable trend, as well as firmly identifying correlations between body size and other variables, is confounded by phylogenetic factors. The early work that identified body size related variables was mostly qualitative in nature and little was done to support the theories with rigorous quantitative statistical analyses. Jarman's original hypotheses have recently been re-assessed by phylogenetically corrected analyses of variance at the taxonomic levels of subfamily and tribe (Brashares *et al*, 2000). Although body size and group size did vary predictably with dietary selectivity, and group size varied with antipredator behaviour, body size did not relate to antipredator defence. Furthermore, group size and body size were only shown to be related when the effects of phylogeny were not removed and there was only very weak support for that particular correlation at the level of subfamily but none at the level of tribe; in fact all of the relationships were weaker at the tribal level. This suggests that aspects of bovid behaviour may be the result of shared evolutionary histories within taxa rather than body size.

Size differences within the Bovidae certainly have ecological relevance, although there does not seem to be a consistently clear-cut relationship between body size and other aspects of niche exploitation (Williamson & Macho, unpublished manuscript). The ecological niche utilised by each species seems to be the result of a complex interaction between body size, phylogeny, locomotion and dietary preferences. From this it can be argued that it may not be desirable to reduce or eliminate the effects of body size in an analysis that seeks to link skeletal morphologies to habitat in order to investigate its effects. However, the problem remains that when samples including individuals across a wide range of body sizes are analysed, body size consistently accounts for the majority of the difference between the clusters of specimens and other relationships are obscured and their relevance downplayed.

The dataset analysed in this project was thus size corrected with the intention of investigating whether or not the size corrected or non-size corrected data yielded better results in terms of identifying clusters of extant species that correlated to the modern habitats to which they had been assigned. All data was $\log_{10}$ transformed, which does not correct for size, but satisfies assumptions about normality and homogeneity of variances within the dataset, issues especially concerning interspecific datasets (Harvey, 1982; LaBarbera, 1989). All non-size corrected data used in the analyses were log transformed in this way and there were no analyses conducted on the raw data itself. Where the results of the logged data are presented, all measurement codes are preceded by the prefix "LOG" to indicate that it is the non-size corrected dataset.

The size correcting procedure involved regressing the species logged average body weight against the log transformed data for each individual measurement and fitting a straight line through the cloud of points using the standard formula for a line: $y = ax+b$. The reduced major axis algorithm was chosen to calculate the line of best fit. This was done using version 1.19 of a freeware program called Palaeontological Statistics (or PAST, available at http://folk.iou.no/ohammer past) that has been tailor made for statistical analyses in palaeontological investigations (Hammer *et al*, 2001). PAST automatically uses the RMA fitting and standard error estimation procedures outlined in Miller & Kahn (1962). The resulting residual for each data point (i.e. the distance of the data point from the line of best fit) is understood to represent the variation of that individual from the baseline, or the expected value, with size now accounted for. The residuals were saved and recorded in the main database used in the ensuing analyses and comprised the size corrected dataset. The complete data from the regressions can be found in Appendix C.

Reduced major axis is not the only line of best fit that can be calculated in regression and the application of least squares (LS) and major axis (MA) regression techniques are debated (Jungers, 1984; 1985; Jungers *et al,* 1995; LaBarbera, 1989; Aiello, 1992). All three lines are calculated differently and produce very different results (Aiello, 1992). The advantage of using RMA, especially in allometric analyses, is that it is considered to be the most appropriate technique for describing functional relationships in the dataset. Although the aim of the regression in this instance was not to illuminate functional relationships but to simply reduce the effects of body size in the dataset for use in subsequent analyses, RMA was used because, unlike both MA and LS, this technique does not make a biased assumption about the error variance in the dataset, nor is it affected by the correlation coefficient. LS is preferred when it is intended to make predictions on the basis of the independent variable (Sokal & Rolf, 1981; Jungers, 1984; LaBarbera, 1989).

The above method of size correction using species average body weight and RMA regression was selected instead of the commonly employed technique of using the geometric mean of each measurement, because calculating the geometric mean corrects only for isometric size. The aim of size correction was to reduce the effects of all size relationships regardless of whether or not they are allometric or isometric.

Where the results of the size corrected data are presented, all measurement codes are preceded by the prefix "RES" (shorthand for residual) to indicate that it is the size corrected dataset.

3.5 Statistical analyses

Analyses of both the size corrected and non-size corrected modern data and the fossil data were conducted in order to investigate habitat prediction on the basis of the bovid skeletal material. Discriminant function analyses (DFA) were conducted with Version 11.0 of the Statistical Package for the Social Sciences (SPSS). This is the preferred statistical method in ecomorphological studies performed by other researchers (Kappelman, 1988; Plummer & Bishop, 1994; DeGusta & Vrba, 2003).

The purpose of DFA is twofold: firstly to determine the dimensions along which known groups differ and secondly to predict group membership on the basis of a set of variables (Tabachnick & Fidell, 2001). In this case the groups are habitat types and the variables are the anatomical measurements. The set of predictors which best separate the groups are called discriminant functions and the first discriminant function explains the most variation between the groups. The second function displays the second greatest amount of variation and the third function explains the third greatest amount, etc. (Manly, 1986). Not all of the functions will have true biological meaning, but generally the first two or three do.

Scatter plots of the discriminant functions are useful for illustrating the differences between the groups, but the meaning of the analyses is inherent in the variables and how highly they load on each of the discriminant functions. The researcher must interpret this meaning, which is naturally dependent upon the particular dataset being analysed. Groups are clustered around the centroid, or the mean discriminant score, for each group on a function. Ungrouped individuals can also be entered into the analysis in order to observe their likely affiliation to the groups and are clustered according to the centroids of the defined groups (Manly, 1986).

DFAs are advantageous because they report the cases that are correctly classified as a percentage of the total number entered into the analysis, which is a simple and easily understood statistic that is useful when making comparisons between the success rates of different DFAs that were based on the same defined groups. This type of analysis also indicates where misclassification has occurred and generally this technique tends to misclassify cases into groups with the most dispersion. This is an interesting point to the investigator if there are consistent patterns in misclassification that can be interpreted in a meaningful way. DFAs are also practical because unequal group sample sizes may be considered, so long as the number of variables entered into each analysis is less than the number of cases in the smallest group (Tabachnick & Fidell, 2001).

Unlike earlier ecomorphological works which utilised DFAs (Kappelman, 1988; Plummer & Bishop, 1994), the stepwise method was rejected in favour of the direct method which analyses all of the variables in the dataset rather than a reduced subset determined by the analysis. Stepwise methods are used in order to evaluate the relative importance of the predictor variables and discard those which do not contribute additional information to the observed variation between the groups. Each predictor variable is entered into the analysis one by one and if the subsequent addition of a new variable does not increase the amount of difference between the groups relative to the variables that are already included, it is discarded in favour of another variable further down the line which does. The order in which the variables are entered into the analysis may be manipulated in some programs, however most programs enter them in a forward fashion according to how they have been listed in the data spreadsheet. Statistical literature has stressed the faults inherent in both the method itself and the automatic procedures followed by common statistical packages (including SPSS) that offer the stepwise method (Huberty & Barton, 1989; Thompson, 1989; 1995; Snyder, 1991; Whitaker, 1997), but these cautions have only recently been heeded by palaeoecologists (DeGusta & Vrba, 2003).

Three problems with stepwise methods can be noted. Firstly, the incorrect degrees of freedom are used and the analysis is biased in favour of a falsely inflated level of statistical significance. Secondly, the technique also has the tendency to interpret sampling errors as meaningful differences in the dataset and thus it may exclude variables which do account for true variation and are worthy predictors. Finally, stepwise methods may not identify the best predictor variable set of a given size. All of these problems mean that the final subset of predictor variables that is chosen during the analysis may not be the subset which explains the most meaningful variation in the dataset. Researchers wishing to reduce their number of predictor variables are thus faced with the difficult problem of determining exactly how to select the most appropriate subset.

DeGusta & Vrba (2003) followed an empirical "trial and error" procedure of testing which variables provided the best discrimination in a variety of combinations. These tests were not reported in their work and one can only imagine how long and unwieldy such a method can be. Rather than employ such a procedure for every element included in this project, it was decided that all variables would be analysed. The common concern with this method is that the inclusion of correlated variables will reduce the discriminatory power of the analysis (Plummer & Bishop, 1994; Elton, 2001). However, DeGusta & Vrba (2003) also showed that this does not significantly affect the final percentage of correct classification. They replicated one of their variables and the measurement values for it so that their dataset then included two of the same, and hence perfectly correlated, variables. The results of that analysis did not differ from the previous analysis which did not include the duplicate. It is unclear as to why they then felt it necessary to reduce their predictor variable set and continued to empirically test a variety of combinations, although convenience may have played a large part in that decision. Regardless, the project reported in this thesis utilised direct DFAs and generally analysed all of the predictor variables, an equally convenient and statistically robust technique.

There were two infrequent conditions in which predictor variables were removed form the analyses. SPSS automatically conducts a tolerance test of the entered variables in order to determine how linearly related they are to one another (multicollinearity) and automatically discards those with a tolerance level less than .001. This occurred in relatively few circumstances and they are detailed in Chapter 4. Variables were intentionally removed when the number of predictors was greater than the number of individuals in the smallest habitat group, a condition which would have violated the statistical procedures, as stated above. This occurred in only one instance and it is addressed in Chapter 4.

All DFAs were conducted on complete elements, although long bones were subjected to further analyses in which they were divided into proximal and distal ends which were analysed separately. An additional analysis was conducted on all distal metapodials. Phalanges were not divided into those from the forelimb and hindlimb, but were combined in three separate analyses for the proximal, intermediate and distal phalanges. Obviously not every specimen or element was complete; therefore individuals missing a particular element or measurement were excluded from that analysis (where the results are reported in Chapter 4 and Chapter 5, the total number of elements that were analysed is provided).

Modern specimens were analysed twice; once with the log transformed data and once with the size corrected data. Each element was examined and the most useful elements for habitat prediction were identified as those which had a percentage of correct classification well above the baseline of accuracy outlined in Section 3.6 below. Those elements were selected for use in the fossil analyses. It was not possible to size correct the fossil data using an average species body mass and RMA regression and they were thus analysed only once, using the log-transformed measurements. Fossil specimens were entered as ungrouped cases in order to investigate the likelihood that they associated with one of the defined habitat groups and hence they provided a habitat prediction for the Upper Ndolanya and Upper Laetolil Beds at Laetoli. Consideration of both the numbers of specimens predicted to the habitat types as well as the probabilities associated with the predictions also informed the conclusions.

3.6 Establishing the "baseline of accuracy" for the discriminant function analyses

A particular caution for the use of discriminant function analyses is that given enough variables it is likely that some combination of them will result in the calculation of significant discriminant functions even without there being meaning inherent to them (Manly, 1986). Simply by chance one can expect that a number of cases will be properly assigned to their known groups (Whitaker, 1997). Discriminant function analyses are designed to emphasise the differences between the groups and thus do better than simple chance probability, or 1/n, where n = the number of defined groups in each analysis. This is a serious concern which is not often addressed.

For every dataset it is important to understand the point at which the reported correct percentage of classification reflects meaning in the predictor variable set rather than chance assignments. DeGusta & Vrba (2003) investigated this issue by assigning their individuals to incorrect habitat groups and re-running a DFA. This was repeated a number of times, with the resulting correct percentage of classification ranging from 40 – 50% with a median of 45% (the number of times this was carried out and the exact figures were not reported). When correctly assigned, their dataset yielded a figure of 67%. This is 2.7 times better than *true* chance (i.e. 2.7 x .25, or 2.7 times better than a one in four chance of assigning the individuals to their correct habitat category). It is 1.5 times better than the discriminant function analysis's baseline level of discrimination of 45% (i.e. 1.5 x .45).

However, using DeGusta & Vrba's 45% as a baseline of accuracy for the dataset in this project is not plausible. They divided their species into only four habitats and were using a set of nine predictor variables. The project reported here uses seven habitat categories (which are defined below in Section 3.8) and the number of predictor variables in each analysis range from 2 for many of the proximal or distal ends of long bones to 15 in the naviculo-cuboid. It was hypothesised that both of these factors would influence the baseline of accuracy. In order to determine the correct baseline of accuracy for this dataset, or the percentage of correct classification over which the analyses begin to reflect real biological meaning, a set of experiments similar to DeGusta & Vrba's was conducted.

For each element that was analysed in this experiment the entire dataset was re-assigned random habitat categories. In each instance the assignments were done empirically in an SPSS data spreadsheet in which four new variables were added. Each variable represented another random and incorrect habitat assignment. The proportion of individuals that were in each habitat category when correctly assigned was maintained for each new incorrect variable in order to make the results of the incorrect analyses comparable to the initial, correct analysis.

Eleven elements that reflected a range of predictor variable sets were chosen. The elements used and the number of predictor variables, or measurements taken on each element, are listed in Table 3.9. Discriminant function analyses were conducted with each element a total of eight times. Using the four incorrect habitat variables, the logged data were run through DFAs and this was repeated, again with the four incorrect variables, on the size corrected data. One exception was the humerus which was associated with fourteen measurements. All eight analyses were done on size corrected data with eight separate habitat variables. This was necessary because when the logged analyses were conducted the measurement H3 failed the tolerance test and was eliminated so that only thirteen predictor variables were used. The reported correct percentage of classification for each of the separate eight analyses on the eleven elements was recorded and these can be found in Table 3.10.

A cursory glance at Table 3.10 indicates that the percentages of correct classification range throughout the high twenties and thirties. Yet, it is not until the percentages are plotted against the number of predictor variables that an interesting pattern emerges. Figure 3.21a displays a scatter plot of this linear regression and Figure 3.21b presents a boxplot to illustrate the ranges of the percentages which result from the analyses with different numbers of predictor variables. There is a significant correlation ($r^2 = .6856$) between the number of predictor variables and the percentage of correct classification that results from a chance assignment to the seven habitat

Table 3.9. Number of predictor variables for the elements used in the analyses to establish the baseline of accuracy

ELEMENT	PREDICTOR VARIABLES
Proximal metapodial	2
Pisiform	3
Scaphoid	4
Cuneiform	5
Ulna	7
External and middle cuneiform	8
Lunar	9
Tibia	12
Femur	13
Humerus	14
Naviculo-cuboid	15

Table 3.10. Correct percentages of classification from the four DFA trials in which seven habitat categories were used and the individuals were randomly assigned to a habitat

Element	Number of predictor variables	Percentage of correct classification logged data	Percentage of correct classification size corrected data
PROXIMAL METATARSAL	2		
Incorrect DFA 1		25.6	29.3
Incorrect DFA 2		24.2	28.4
Incorrect DFA 3		25.1	25.6
Incorrect DFA 4		28.4	26.5
PISIFORM	3		
Incorrect DFA 1		30.0	27.6
Incorrect DFA 2		31.8	30.6
Incorrect DFA 3		23.5	25.9
Incorrect DFA 4		28.2	26.5
SCAPHOID	4		
Incorrect DFA 1		27.1	27.1
Incorrect DFA 2		30.4	29.0
Incorrect DFA 3		26.6	26.1
Incorrect DFA 4		30.0	31.9
CUNEIFORM	5		
Incorrect DFA 1		28.7	31.2
Incorrect DFA 2		30.2	29.2
Incorrect DFA 3		35.1	34.7
Incorrect DFA 4		28.7	28.7
ULNA	7		
Incorrect DFA 1		32.8	31.4
Incorrect DFA 2		28.4	29.4
Incorrect DFA 3		30.9	32.4
Incorrect DFA 4		30.9	28.4
EXTERNAL & MIDDLE CUNEIFORM	8		
Incorrect DFA 1		28.1	29.7
Incorrect DFA 2		34.4	33.9
Incorrect DFA 3		31.3	30.7
Incorrect DFA 4		31.3	29.7

Table 3.10, continued. Correct percentages of classification from the four DFA trials in which seven habitat categories were used and the individuals were randomly assigned to a habitat

Element	Number of predictor variables	Percentage of correct classification logged data	Percentage of correct classification size corrected data
LUNAR	9		
Incorrect DFA 1		31.0	31.5
Incorrect DFA 2		37.9	35.5
Incorrect DFA 3		31.5	29.6
Incorrect DFA 4		31.0	30.0
TIBIA	12		
Incorrect DFA 1		35.8	32.5
Incorrect DFA 2		32.1	33.0
Incorrect DFA 3		33.0	33.5
Incorrect DFA 4		35.4	32.1
FEMUR	13		
Incorrect DFA 1		30.9	33.8
Incorrect DFA 2		38.2	39.1
Incorrect DFA 3		30.9	34.8
Incorrect DFA 4		35.7	34.3
HUMERUS	14		
Incorrect DFA 1			38.4
Incorrect DFA 2			36.9
Incorrect DFA 3			38.9
Incorrect DFA 4			36.0
Incorrect DFA 5			38.9
Incorrect DFA 6			35.5
Incorrect DFA 7			37.4
Incorrect DFA 8			35.0
NAVOCULO-CUBOID	15		
Incorrect DFA 1		40.8	37.4
Incorrect DFA 2		37.9	39.3
Incorrect DFA 3		36.9	36.9
Incorrect DFA 4		34.5	35.0

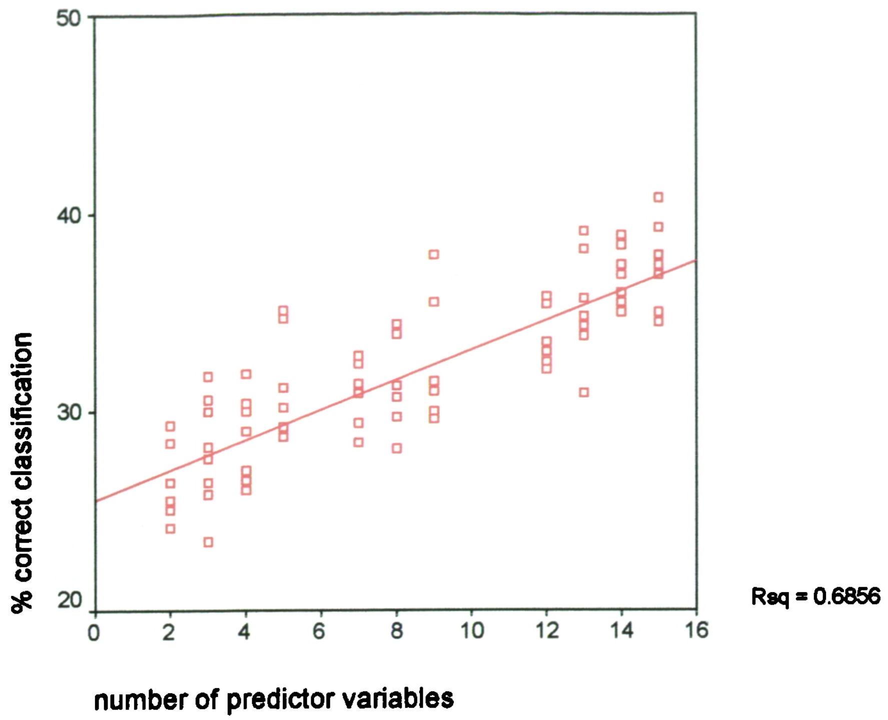


Figure 3.21a. Scatter plot of the linear regression of the number of predictor variables and percentages of correct classification from the four analyses using seven habitats

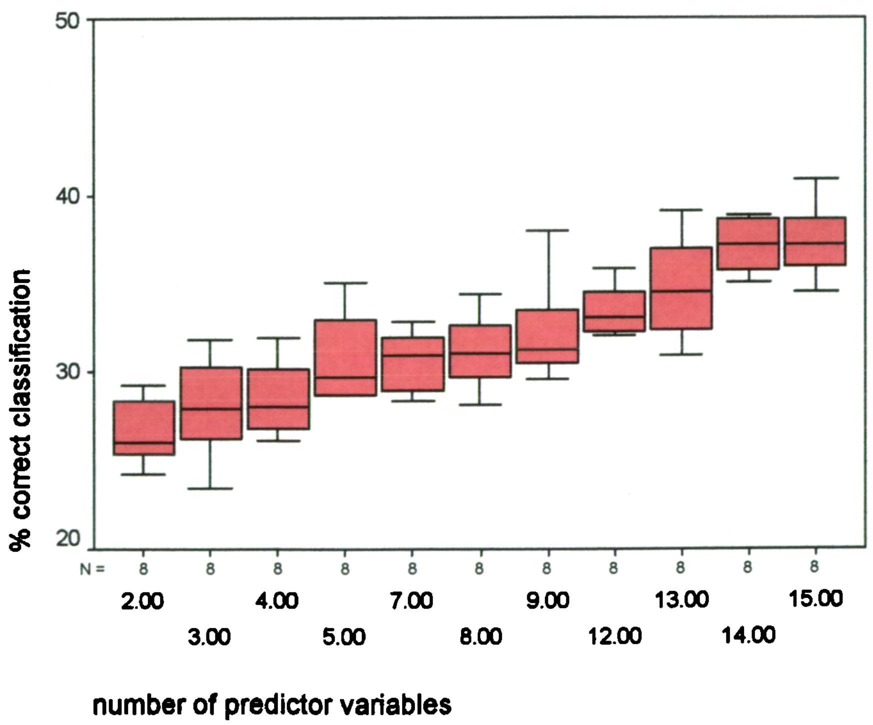


Figure 3.21b. Boxplot of the number of predictor variables and percentages of correct classification from the four analyses using seven habitats

categories. These analyses have shown that as the number of predictors increases, so does the baseline percentage of classification.

The baselines here established are significantly lower than the 45% found by DeGusta & Vrba (2003). The most apparent difference between their analyses and those subsequently conducted in this project relates to the number of habitat categories used. In order to determine if this also affects the baseline of accuracy a second experiment was conducted. The dataset comprised of the four incorrect habitat variables was amended to include only those individuals in four of the original seven habitat categories, reflecting the same number used by DeGusta & Vrba. Eight DFAs were again conducted for the same eleven elements, four times with the logged and four times with the size corrected data (although again the humerus analyses were conducted entirely on size corrected data). The correct percentage of classification was recorded for each analysis and these values are found in Table 3.11.

Figures 3.22a and 3.22b reveal a similar pattern to that discovered in the first trial of incorrect DFAs. As the number of predictor variables increases, so does the baseline of accuracy. There is an observed correlation between these two factors (r^2 = .4202), although it is weaker here than in the experiment which used seven habitat groups. A closer inspection of the four random and incorrect habitat variables showed that for certain elements, for instance the humerus with 14 predictor variables, the random habitat assignments for the individuals remaining in the four habitat categories was often the correct habitat preference of that species. The analysis was thus able to correctly extract some biological meaning from the dataset and relate that back to the habitat assignments which were, purely by chance, often correct. This accounts for an inflated percentage of correct classification in these analyses compared to that which could be expected if the habitat assignments had been entirely

Table 3.11. Correct percentages of classification from the four DFA trials in which four habitat categories were used and the individuals were randomly assigned to a habitat

Element	Number of predictor variables	Percentage of correct classification logged data	Percentage of correct classification size corrected data
PROXIMAL METATARSAL	2		
Incorrect DFA 1		36.9	40.4
Incorrect DFA 2		36.9	42.6
Incorrect DFA 3		39.0	37.6
Incorrect DFA 4		43.3	40.4
PISIFORM	3		
Incorrect DFA 1		40.5	40.5
Incorrect DFA 2		41.1	43.1
Incorrect DFA 3		34.5	37.1
Incorrect DFA 4		44.0	38.8
SCAPHOID	4		
Incorrect DFA 1		36.4	37.1
Incorrect DFA 2		41.3	43.4
Incorrect DFA 3		37.8	36.4
Incorrect DFA 4		43.4	42.7
CUNEIFORM	5		
Incorrect DFA 1		41.3	44.2
Incorrect DFA 2		43.5	42.3
Incorrect DFA 3		50.7	51.4
Incorrect DFA 4		40.6	44.9
ULNA	7		
Incorrect DFA 1		46.7	40.9
Incorrect DFA 2		40.1	40.1
Incorrect DFA 3		46.7	46.7
Incorrect DFA 4		44.5	40.9
EXTERNAL & MIDDLE CUNEIFORM	8		
Incorrect DFA 1		42.4	40.2
Incorrect DFA 2		52.3	48.5
Incorrect DFA 3		47.0	43.2
Incorrect DFA 4		43.2	43.2

Table 3.11, continued. Correct percentages of classification from the four DFA trials in which four habitat categories were used and the individuals were randomly assigned to a habitat

Element	Number of predictor variables	Percentage of correct classification logged data	Percentage of correct classification size corrected data
LUNAR	9		
Incorrect DFA 1		44.7	45.4
Incorrect DFA 2		48.9	46.1
Incorrect DFA 3		41.1	41.8
Incorrect DFA 4		46.8	46.1
TIBIA	12		
Incorrect DFA 1		45.4	45.4
Incorrect DFA 2		46.5	43.7
Incorrect DFA 3		45.4	48.2
Incorrect DFA 4		49.6	42.6
FEMUR	13		
Incorrect DFA 1		43.2	45.9
Incorrect DFA 2		44.5	47.3
Incorrect DFA 3		40.4	39.7
Incorrect DFA 4		48.6	51.4
HUMERUS	14		
Incorrect DFA 1			54.9
Incorrect DFA 2			50.7
Incorrect DFA 3			52.8
Incorrect DFA 4			47.9
Incorrect DFA 5			47.2
Incorrect DFA 6			49.3
Incorrect DFA 7			50.7
Incorrect DFA 8			47.9
NAVOCULO-CUBOID	15		
Incorrect DFA 1		53.5	53.5
Incorrect DFA 2		45.8	47.2
Incorrect DFA 3		51.4	47.9
Incorrect DFA 4		43.7	42.3

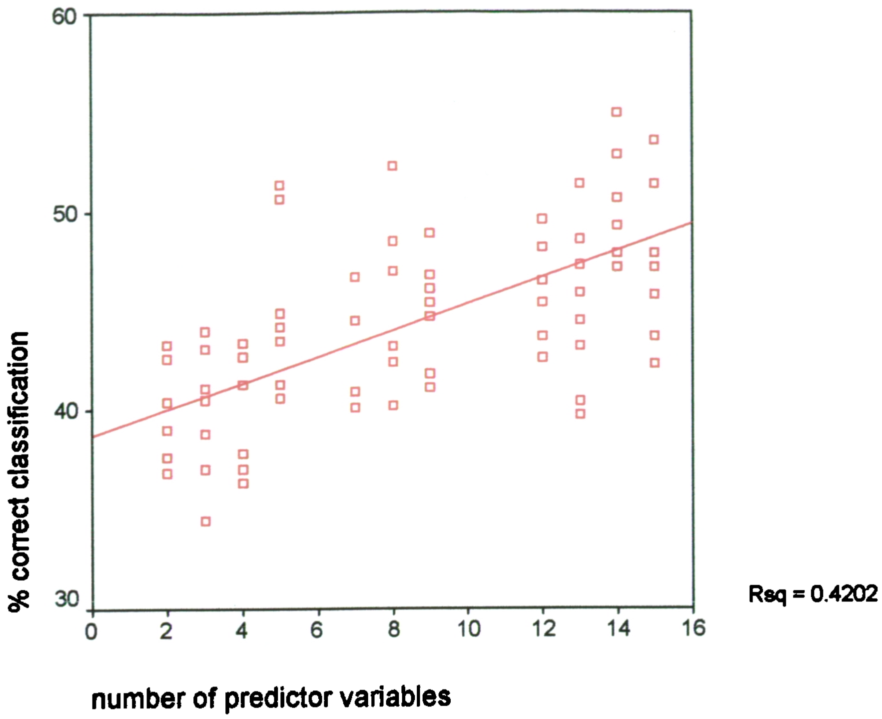


Figure 3.22a. Scatter plot of the linear regression of the number of predictor variables and percentages of correct classification from the four analyses using four habitats

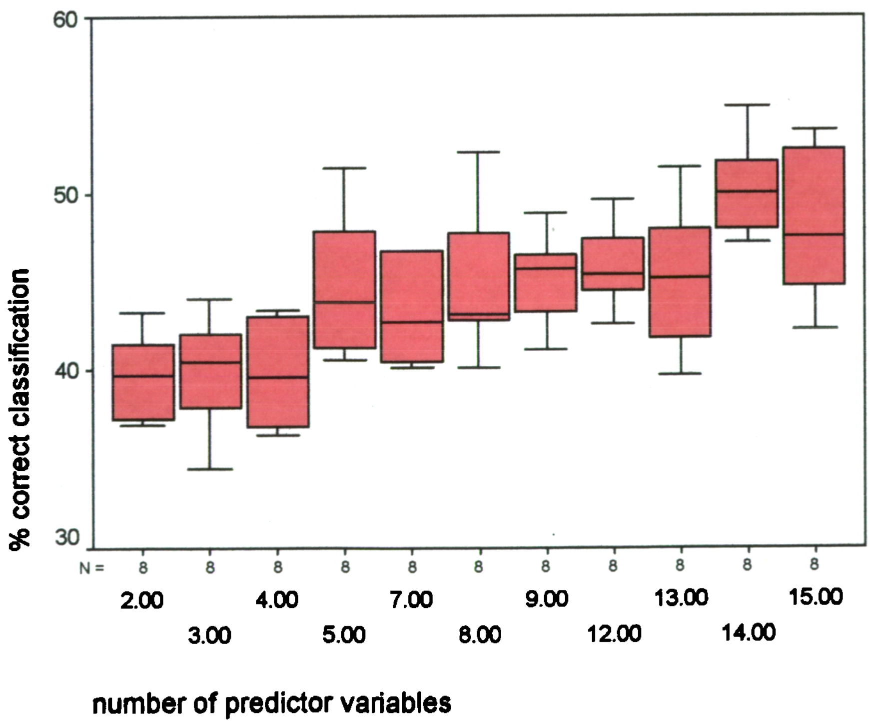


Figure 3.22b. Boxplot of the number of predictor variables and percentages of correct classification from the four analyses using four habitats

incorrect. The lower correlation coefficient for the analyses with four habitat groups relates in general to the greater spread of data within the sets of analyses conducted on each element. In all but one instance, the set of analyses with nine predictor variables, the standard deviation is greater for the analyses with four habitats (Table 3.12).

Figures 3.23a and 3.23b illustrate the results of this investigation into the baseline of accuracy for the discriminant function analyses. This boxplot displays the combined results of the correct percentages of classification for each of the two DFA trials using random and incorrect habitat assignments for the individuals analysed. In both cases, as the number of predictor variables increases so does the baseline of accuracy. Furthermore, it also demonstrates that the number of grouping variables affects the baseline of accuracy, such that when an analysis includes fewer groups, the baseline is higher than if more groups had been used. This makes a case for striving to refine the number and definitions of the grouping variables used in an analysis of this nature.

These results reflect those of DeGusta & Vrba (2003). The mean percentage of correct classification for *all* 88 of the analyses with four habitat groups is 44.26%, which is similar to the 45% which they reported (see Table 3.12). When utilising seven habitat categories, the mean percentage drops significantly to 31.87%. However, as DeGusta & Vrba (2003) were only analysing one element for which they had selected a total of nine measurements for analysis, they could not investigate the effect of the number of predictor variables on the baseline of accuracy, a factor that has been shown here to impact the baseline.

This exercise has highlighted the need to understand where the baseline lies for each particular dataset, in terms of the number of both the grouping and predictor variables. For the purposes of this project it was determined that two separate

Table 3.12. Descriptive statistics from the analyses using different numbers of predictor variables and four or seven habitat categories

Number of predictor variables	Number of habitats	Number of analyses	Minimum	Maximum	Mean	Standard deviation
2	4	8	36.90	43.30	39.64	2.48
2	7	8	24.20	29.30	26.64	1.84
3	4	8	34.50	44.00	39.95	3.10
3	7	8	23.50	31.80	28.01	2.73
4	4	8	36.40	43.40	39.81	3.18
4	7	8	26.10	31.90	28.53	2.10
5	4	8	40.60	51.40	44.74	4.18
5	7	8	28.70	35.10	30.81	2.67
7	4*	8	40.10	46.70	43.33	3.12
7	7	8	28.40	32.80	30.58	1.69
8	4	8	40.20	52.30	45.00	3.95
8	7	8	28.10	34.40	31.14	2.13
9	4	8	41.10	48.90	45.11	2.58
9	7	8	29.60	37.90	32.25	2.90
12	4	8	42.60	49.60	45.85	2.26
12	7	8	32.10	35.80	33.43	1.43
13	4	8	39.70	51.40	45.13	4.01
13	7	8	30.90	39.10	34.71	2.99
14	4	8	47.20	54.90	50.18	2.67
14	7	8	35.00	38.90	37.13	1.53
15	4	8	42.30	53.50	48.16	4.28
15	7	8	34.50	40.80	37.34	2.07
2 - 15	4	88	34.50	54.90	44.26	4.52
2 - 15	7	88	23.50	40.80	31.87	4.00
2 - 7	4	40	34.50	51.40	41.49	3.76
2 - 7	7	40	23.50	35.10	28.91	2.67
8 - 15	4	48	39.70	54.90	46.57	3.76
8 - 15	7	48	28.10	40.80	34.33	3.17

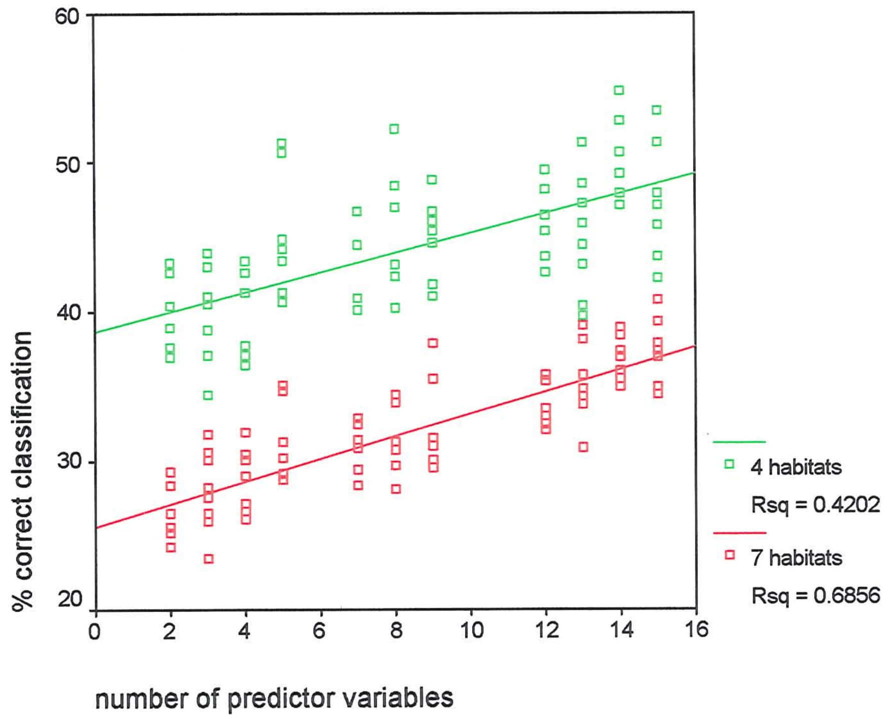


Figure 3.23a. Scatter plot of the linear regressions of the number of predictor variables and percentages of correct classification from the analyses using four (green) and seven (red) habitats

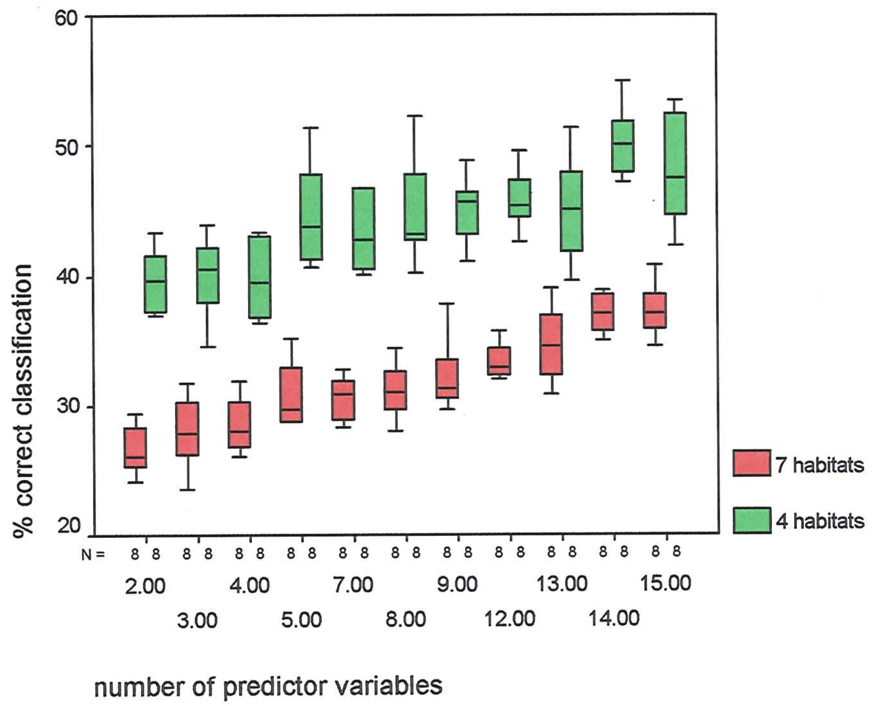


Figure 3.23b. Boxplot of the number of predictor variables and the percentages of correct classification from the analyses using four (green) and seven (red) habitats

baselines of accuracy should be established as cut-off points. Analyses with a percentage of correct classification over the baseline are assumed to have calculated discriminant functions that are able to predict the habitat category of the individuals on the basis of biological meaning inherent to the dataset. Analyses with percentages below or near the baseline are assumed to have made the habitat assignments based on chance alone. The mean percentage is not used here as the baseline, but the maximum.

Every analysis in this project seeks to affiliate the individuals into seven habitat categories, however the number of predictor variables changed according to the element analysed. The predictor variables range from 2 to 15, so there are fourteen possible sizes of the predictor variable set. This range was divided in half so that a baseline was calculated for analyses with 2 – 7 predictor variables and a different baseline for analyses with 8 – 15 variables. They are 35.10% and 40.80%, which are both rounded up to the nearest percentage for convenience to 36% and 41%, respectively.

3.7 Definition of habitats

Defining habitat categories is perhaps the greatest challenge in an analysis that uses modern environments as analogs for palaeoenvironments. This is an especially important consideration because discriminant function analyses are very sensitive to group definitions and work best when the groups are tightly defined (Tabachnick & Fidell, 2001). Thus, the analyses will only be as good as the habitat categories used, but the very process of confining the diverse array of global habitats to a typology of very few discrete categories is reductive and ignores the complexity of ecological reality. In general, most biological data is very difficult to order into distinct entities because it is more often representative of a continuous range of values along a spectrum.

Defining habitat types or broad environmental categories that are applicable to a worldwide sample is a necessary aspect of an ecomorphological study. Aside from the statistical considerations and conditions that must be fulfilled in order to conduct a DFA, are there ecologically sound reasons for doing this? It is well documented that, across geographically distant habitats, exact species compositions will differ. However, mammalian communities in similar habitats will share adaptive morphological characteristics which relate to aspects of niche exploitation, both in terms of dietary preference and locomotion within the various strata of cover provided by a particular environment (Cody & Mooney, 1978). Although there are certainly differences between, for example, forests in Africa and forests in Europe, ecomorphological studies do not necessarily tease out these more subtle distinctions as they consider gross skeletal adaptations to the habitat and terrain. Within a global ecomorphological context then, there are certainly grounds to assume that a forest is a forest is a forest.

In defining the habitat types and in interpreting the palaeoecology of Laetoli, the ambiguous and cumbersome term "savanna" has been avoided because there is no strict scientific definition in usage (although there have been many attempts to formalise a system of classification of savanna habitats – for example, see Conseil Scientifique pour l'Afrique, 1956; Hills, 1965). It has long been employed in Africa to denote any habitat in the transitory zone between forest and desert environments with continuous grasses and woody vegetation (Boulière & Hadley, 1970; 1983). However, its initial meaning most likely referred to a region of treeless land in South America where either short or long grasses dominate (Beard, 1953) and attempts to trace the etymology of the word also infer that it was first brought into usage in a non-African context (Boulière & Hadley, 1983). Its utility as a functional term has been questioned for some time by a number of researchers since the mid twentieth century because not only has its original meaning been largely ignored or forgotten, but as a result of that its application has become so broad as to render it nearly meaningless (Pratt, *et al.*, 1966; Greenway, 1973; Boulière, 1983; Owen-Smith, 1999). What may be referred to as savanna encompasses a vast range of habitat types and sub-types. Thus the term may only be colloquially useful, distinguishing between habitats in which trees and herbaceous vegetation co-exist, or the forest biome, and those savanna biome habitats which combine trees and grasses (Boulière, 1983).

Seven habitat categories were defined for this project. This is more than the number found in other bovid ecomorphological studies which have used a system of either three (open, closed and intermediate – e.g. Kappelman, 1988; 1991; Plummer & Bishop, 1994) or four (forest, open, light cover, heavy cover - e.g. Kappelman *et al.*, 1997; DeGusta & Vrba, 2003). The aim was to continue to refine the habitat distinctions that apply to Africa, where the sites of interest to early hominid palaeontologists (including of course, Laetoli) are located, and to encompass a broader spectrum of global habitats that have not previously been included in any datasets. The seven habitats are: grassland/tree-less, wooded-bushed grassland, light woodland-bushland, heavy woodland-bushland, forest, montane light cover and montane heavy cover. The first five relate to the amount of cover presented by the habitat or the horizontal terrain, and the montane categories also include and element of geographical vertical terrain.

In defining the following seven habitat categories, a number of sources were used. Many of them deal explicitly with African habitats, an artefact of the extremely varied environments found on one continent – a circumstance which has proved attractive to ecological researchers who have sought to investigate such diversity and create hierarchical or biologically meaningful systems of classification for the observed habitats. Individual sources relating to one or more of the habitat types are cited within the text below. More global sources that pertained to a variety of environments and informed the definitions are: Pratt, *et al.,* 1966; Greenway, 1973; White, 1983; Grunblatt, *et al.,* 1989; and Walter & Breckle, 2002. All percentages of canopy cover and height measurements of vegetation are not fixed figures. They were estimates and were to be used as guidelines for classification with some allowance for interpretation. In a sense these cut off points are arbitrary along a continuous gradient, but every effort was made to correspond to the classification systems of other workers.

Grassland/tree-less - This category encompasses all open plains and true grassland, tundra and steppe and desert habitats, which although they may be found in geographically distant areas, present resident bovids with a similar terrain over which to locomote and thus it can be expected that they share similar adaptations to moving over a landscape that is relatively free of obstacles.

Grasslands are difficult to define in an African context. Although they exist on a local basis, most grassland in Africa is interspersed by some form of woody vegetation and these areas are more appropriately assigned to the second habitat category, wooded-bushed grassland (Menaut, 1983). Furthermore, primary, or natural, grasslands in some parts of the world exist because of climatic reasons and in other areas, such as East Africa, they exist as the result of edaphic, or soil-related, features that are unfavourable for tree growth (Vesey-Fitzgerald, 1963; Menaut, 1983). Secondary grasslands are those which are caused when fire and grazing pressure arrest the natural process of woody growth taking over the landscape (Vesey-Fitzgerald, 1972). They are often present as the result of human activities. Pure grasslands are lands dominated by grasses not usually exceeding 1 metre in height, although occasionally a height of 2-3 can be obtained. Scattered woody cover does not exceed 2% of the canopy.

Tundras are distinctly seasonal regions of limited herbaceous vegetation cover of mosses and lichens and dwarf shrub which experience low temperatures and short growing seasons (Bliss *et al.*, 1973; Olson, *et al.*, 1983; Walter & Breckle, 1986; Matthews, 2004). In moister regions a thin layer resembling peat is often found (Walter, 1971) and the soil is underlain by a layer of permafrost in cooler areas (Matthews, 2004). Tundras are found in the high and low arctic as well as on montane slopes and plateaus. Steppes, like tundras, may occur in varied geographical areas and are similar to tundras in the amount and height of herbaceous and woody cover. However, they tend to display denser associations of herbs and are more likely found in tropical, subtropical and temperate regions (Menaut, 1983).

Deserts are habitats of low precipitation and high aridity which may occur from subtropical to arctic regions (Olson *et al.*, 1983). The vegetation is sparse due to the low and irregular rainfall and long dry season, and it therefore possesses adaptations related to water retention. Trees and bushes are small and often thorny, succulent climbers and ephemeral grasses are occasionally present, and ground cover is mostly comprised of annual grasses and herbs. Much of the ground is completely bare of vegetation and therefore the surface soil is the dominating aspect. It may be loose and sandy, hard and compacted, or stony.

Wooded-bushed grassland – These areas may be locally well-developed habitats or ecotonal areas between woodland and riverine or floodplain habitats (Vesey-

Fitzgerald, 1963). Grasses dominate the ground vegetation and may grow to a height of 1-3 metres. There is often some contribution of herbaceous growth to the extensive ground cover and lichens may be present, but epiphytes are uncommon (Greenway, 1973). There also exists an open canopy of trees and other woody vegetation including bushes and shrubs, which are scattered or grouped throughout the habitat, providing between 3-40% cover (White, 1983). The distinction between trees and bush/shrubland is one of crown height. Trees have a simple bole which generally exceeds 7m, while shrubs have short, low, multi-stemmed branches that do not often grow beyond 7m (Aubréville, 1963).

Where appropriate this category also includes semi-desert habitats, which present the same proportion of vegetation to open areas, but are generally found in more arid climates. These habitats may present dwarfed and thorny shrubs and trees that do not exceed 1 or 2m, as well as grasses and herbs which fluctuate with the season (Olson *et al.*, 1983). The soil is, like in more open desert environments, dry and often sandy or stony (Greenway, 1973).

Light woodland-bushland and **heavy woodland-bushland** - These categories combine woodland and bushland habitat types and are differentiated only in the degree of canopy cover presented by the woody vegetation. They represent, in effect, two gradients of the same habitat type. Light woodland-bushland has approximately 40-60% cover, the trees and bush tend to be shorter and grasses represent a more important part of the ground cover. Heavy woodland-bushland is denser and has approximately 61-75% canopy cover. It includes dense thickets as well as woodland and bushland, the trees and shrubs tend to be taller with grasses decreasing in importance and frequency in the ground cover.

A woodland has a closed tree canopy, providing approximately 40% or more ground cover and the canopy ranges between 8m and 20m (Menaut, 1983; White, 1983). Crowns may touch but are generally not interlocking and they are often leafless for a certain period throughout the year (Greenway, 1973). There may be an understorey of small trees or bushes, and the floor may be covered with grasses and herbs. A bushland presents an open to closed canopy, which also exceeds 40% (White, 1983). While it is dominated by woody plants, tall trees are not common and shrubs are typical. They generally do not exceed 6m in height. Herbs and grasses form the ground cover. In both woodland and bushland, epiphytes are rare (except in evergreen subtypes) but lichens may be present (Pratt *et al.,* 1966; Greenway, 1973).

Forest – Forest habitats provide the densest tree cover in the form of a continuous or nearly continuous canopy of interlocking crowns providing 76%-100% cover. They generally have more than one storey and, as grasses are generally prevented from growing beyond very localised small patches, the dominant ground cover is comprised of herbs and shrubs if it is not bare (Menaut, 1983; White, 1983). Lichens, lianes and epiphytic plants such as mosses and ferns are also common (Pratt *et al.,* 1966; Greenway, 1973). The uppermost canopy height ranges from 6 or 7.5m in dwarf forests to 40-50m in true forests (Pratt *et al.,* 1966; White, 1983; Grunblatt *et al.*, 1989).

Montane light cover and **montane heavy cover** – These two montane habitat categories have been included to encompass the broad spectrum of habitats that can be found in mountainous regions such as the Andes, Rockies or Himalayas. Light cover refers to habitats that are open, lightly covered by trees or other woody vegetation and includes alpine habitats above the tree-line. Heavy cover refers to denser woodland and forest habitats in the mountains. In both categories the vegetation is mixed but at higher latitudes where temperatures are low and snowfall may occur, it is generally comprised of hardier species that can withstand low temperatures and night-time frosts, including mosses, dwarf shrubs, and grass.

3.8 Habitat assignments

Each of the seventy bovid, cervid and tragulid species included in the dataset were assigned to one of the seven habitat categories defined in Section 3.7. Similar to the process of confining a diverse array of global habitats to a seven category typology, placing each species into one of them is a process which has the potential to obscure the breadth of behaviour exhibited by each species. Many of them do not restrict themselves to ranging in only one habitat type, yet they could not be assigned to more than one habitat group in order for the discriminant function analysis to be viable. Hence, the process is a necessary over-simplification of mammalian habitat preference and niche utilisation. As a result, the species habitat classifications represent the apparent best fit of species with habitat type. It is also expected that, in time when more is known about modern bovid ecology (especially the non-African species), these designations may be revised.

Habitat assignments are listed in Table 3.13. Species were assigned to a habitat type on the basis of accounts found in the published literature and not on direct observation in the field. A number of sources in particular were consulted for the majority of species. These are Kingdon (1982; 1997), Nowak (1999) and MacDonald (2001). There are also a number of excellent references online that summarise information from a diverse amount of scientific literature including the above sources. The online resources were never used as primary references, however the habitat assignments were often crosschecked with them. They are: Ultimate Ungulates

Table 3.13. Habitat assignments

Table removed due to third party copyright

Where no additional source is indicated, the following were consulted: Kingdon (1982; 1997), Nowak (1999) and MacDonald (2001)

Table 3.13, continued. Habitat assignments

Species	Common name	Species code	Source(s)
HEAVY WOODLAND-BUSHLAND			
Total number of specimens = 32			
Kobus defassa	waterbuck	Kd	
Madoqua kirki	Kirk's dik dik	Mk	
Madoqua saltiana	Salt's dik dik	Ms	
Neotragus batesi	dwarf antelope	Nb	
Neotragus moschatus	suni	Nm	
Neotragus pygmaeus	royal antelope	Np	
Taurotragus derbianus	giant eland	Td	
Tragelaphus scriptus	bushbuck	Ts	
Tragelaphus speki	sitatunga	Tsp	
Tragelaphus strepsiceros	greater kudu	Tst	
FOREST			
Total number of specimens = 35			
Alces alces	moose	Aa	
Bos javanicus	banteng	Bj	
Bos sauveli	kouprey	Bs	
Bubalus mindorensis	tamaraw	Bm	Kuehn (1986)
Cephalophus leucogaster	white-bellied duiker	Cl	
Cephalophus monticola	blue duiker	Cm	
Cephalophus nigrifrons	black-fronted duiker	Cn	
Hyemoschus aquaticus	water chevrotain	Ha	
Tragelaphus euryceros	bongo	Te	Klaus-Hugi *et al* (2000)
MONTANE LIGHT COVER			
Total number of specimens = 18			
Capra sibirica	ibex	Cs	
Oreamnos americanus	mountain goat	Ora	Dailey *et al* (1984)
Ovis ammon	argali	Oa	
Ovis canadensis	mountain sheep	Oc	
Ovis dalli	dall, whitesheep	Od	
Ovis vignei	urial	Ov	
Pseudois nayaur	bharal	Pn	Harris & Miller (1995)
Rupicapra rupicapra	Alpine chamois	Rr	Garcia-Gonzalez & Cuartas (1996)
MONTANE HEAVY COVER			
Total number of specimens = 21			
Budorcas taxicolor	takin	Bt	Groves & Shields (1997)
Elaphodus cephalophus	tufted deer	Ec	
Nemorhaedus crispus	Japanese serow	Nc	Deguchi *et al* (2001)
Nemorhaedus goral	common goral	Ng	
Nemorhaedus sumatraensis	mainland serow	Ns	
Nemorhaedus swinhoei	Taiwanese serow	Nsw	
Pudu mephistophiles	Northern pudu	Pm	

Where no additional source is indicated, the following were consulted: Kingdon (1982; 1997), Nowak (1999) and MacDonald (2001) (http://www.ultimateungulate.com), University of Michigan's Animal Diversity Web (http://animaldiversity.ummz.umich.edu) and AZA Antelope Taxon Advisory Group (http://www.csew.com).

Where individual sources specific to a particular species were consulted, they are listed in Table 3.13, otherwise it may be assumed that the four main text sources provided adequate information for a confident habitat assignment.

4 Results of the Analyses of the Extant Bovid Data: Long Bones

4.1 Introduction

This chapter reports on the results of the analyses of the modern bovid, cervid and tragulid long bone data. Discriminant function analyses in SPSS Version 11.0 were used to investigate the habitat affiliation of the species in this dataset based on measurements taken on the humerus, radius, ulna, metacarpal, femur, tibia and metatarsal. The dataset and all procedures and methods followed herein are outlined in Chapter 3.

Analyses of the logged (i.e. non size corrected) data and size corrected data are presented separately. Examples of the results of a "good" predictor element versus a "bad" predictor element are included in each section. A comparison of the logged and size corrected results is provided. The chapter is concluded with a summary of the selection of reliable habitat predictors. These elements are analysed in further palaeoenvironmental reconstructions of Laetoli in Chapter 6.

4.2 Utility of the long bones as accurate predictors of habitat

The aim of the analyses is to identify elements that have a percentage of correct classification over the baseline of accuracy determined in Section 3.6 in Chapter 3. For analyses with 2 – 7 predictor variables, the baseline is 36% and for analyses utilising 8 –15 predictor variables it is 41%. All of the long bones were analysed but, because complete elements in the fossil record are rare and are more often found as epiphyseal ends, the distal and proximal ends were analysed in addition to the complete element. A combined analysis was also conducted on all distal metapodials which is more appropriate for the fossil material, which can easily be identified as a metapodial but not as always as a metacarpal or metatarsal.

Every complete element and complete distal and proximal end of an element was analysed and incomplete specimens were excluded. Appendix D summarises the total number of each species in each habitat category that was included in the separate analyses. Table 4.1 summarises the sample size of each habitat category in the long bone analyses.

The intention was to analyse all of the measurements that were taken on the elements. However, in some cases this was not possible and it was necessary to remove some measurements. Table 4.2 documents the few occasions in which particular measurements were not used in the final analyses and the rationale for this in each instance.

There were two reasons for removing measurements. In the first case, an automatic tolerance test is performed as a part of the discriminant function analysis and it drops variables with a tolerance level less than .001. One variable was removed from the analysis of the logged humerus data, the height of the greater tuberosity of the humerus (H3) and one from the logged radius data, the functional length of the radius (R2). The analysis of the logged metacarpal data dropped all but three variables, leaving only the total length (MC1), functional length (MC2) and the distance between the medial and lateral epicondyle at the most proximal point (MC10). This was surprising considering that the morphologically similar metatarsal did not fare the same and that analyses of the size corrected data of both metapodials yielded similar results (these are reported below in Sections 4.2.1 and 4.2.2). Conducting an analysis of the raw metacarpal data resulted in the same significant

Table 4.1. Total number of specimens in each habitat group included in the long bone discriminant function analyses

Element	Total number	grassland/ tree-less	wooded-bushed grassland	light woodland-bushland	heavy woodland-bushland	forest	montane light cover	montane heavy cover
humerus	**203**	17	43	51	31	30	15	16
distal humerus	**203**	17	43	51	31	30	15	16
proximal humerus	**203**	17	43	51	31	30	15	16
radius	**207/205***	17	47/46	51/50	31	30	16	15
distal radius	**210/208**	17	48/47	51/50	31	30	17	16
proximal radius	**209**	17	47	52	31	30	17	15
ulna	**204**	13	44	49	31	27	17	23
proximal ulna	**209**	13	46	49	32	29	17	23
metacarpal	**211/210**	15	46	51	27	31	16/15	25
distal metacarpal	**211**	15	46	51	27	31	16	25
proximal metacarpal	**211**	15	46	51	27	31	16	25
femur	**207**	17	46	51	32	30	14	17
distal femur	**210**	17	46	52	32	30	16	17
proximal femur	**209**	17	46	52	32	30	15	17
tibia	**212**	13	46	50	32	30	17	24
distal tibia	**213**	13	46	50	32	30	17	25
proximal tibia	**213**	13	46	50	32	30	17	25
metatarsal	**215**	15	46	52	28	31	18	25
distal metatarsal	**215**	15	46	52	28	31	18	25
proximal metatarsal	**215**	15	46	52	28	31	18	25
distal metapodial	**426**	30	92	103	55	62	34	50

* Where the numbers differ between the logged and size corrected datasets, the logged total is given first and is separated from the size-corrected total by a slash

Table 4.2. Variables not included in the discriminant function analyses

Element	Measurement code	Definition	Reason for exclusion
Humerus			
	H3	height of greater tuberosity	tolerance*
Radius			
	R2	functional length of radius	tolerance
Metacarpal			
	MC3	anterior-posterior diameter of the proximal end	tolerance
	MC4	transverse diameter of the proximal end	tolerance
	MC5	anterior-posterior diameter of the distal end	tolerance
	MC6	transverse diameter of the distal end	tolerance
	MC7	measure of the distance between the medial and lateral verticillus	tolerance
	MC8	diameter of the lateral epicondyle	tolerance
	MC9	transverse width of the lateral epicondyle	tolerance
	MC11	measure of the distance between the medial and lateral epicondyle at the most distal point	tolerance
	MC12	anterior-posterior mid-shaft diameter	tolerance
	MC13	transverse mid-shaft diameter	tolerance
Femur			
	F1	greatest length of femur	too many predictors

* indicates that the variable has a tolerance value less than .001 and failed the automatic tolerance test – see section 3.5 for an explanation

loss of variables and returning to the original dataset prior to coding in preparation for the DFAs indicated that the data was sound.

The second reason for excluding a variable relates to the requirements of discriminant function analysis. In order for the results of a DFA to be statistically reliable, the predictor variables, or measurements, must be fewer than the number of cases in each group. This rule would have been violated in one case. Fourteen measurements were taken on the complete femur, but there were only fourteen individuals in the montane light cover category. Therefore, it was necessary to remove one measurement from both the logged and size corrected datasets.

Deciding which variable was appropriate to exclude was determined by a principal components analysis (PCA) with the logged and size corrected data in SPSS 11.0 in order to identify measurements that are correlated with one another and contribute the same information to the separation of the individuals in the dataset. Unlike a DFA, which uses a set of predictor variables to classify cases on the basis of prior group assignments, PCA is a data reduction technique that identifies a pattern in the relationships between variables which describes differences observed in the dataset. Correlated variables are combined into factors, or components, and variables that have the same factor loadings across the components are highly correlated and can be considered redundant (Manly, 1986; Tabachnick & Fidell, 2001).

It was desirable to not only exclude one redundant variable, but to select a variable that does not easily apply to the fossil material, or in the case of the long bones which are often found incomplete, a variable that relates to the entire element such as the total length or functional length. Tables 4.3a and 4.3b display the rotated component matrices for the logged and size corrected data and it can be observed that two measurements of the femur, LOGF1 and RESF1 and LOGF2 and RESF2

Table 4.3a. Rotated component matrix of the PCA of the logged femur data.

Rotated Component Matrix[a]

	Component							
	1	2	3	4	5	6	7	8
LOGF2	.726	.576	.290	.224				
LOGF1	.711	.595	.285	.220				
LOGF6	.684	.555	.301	.331			.106	
LOGF13	.671	.576	.268	.296	.233			
LOGF7	.650	.579	.311	.365				
LOGF10	.647	.607	.313	.294	.131			
LOGF3	.639	.591	.315	.362				
LOGF14	.628	.624	.297	.290	.129	.162		
LOGF11	.536	.751	.275	.243				
LOGF9	.589	.688	.284	.275	.122			
LOGF8	.586	.687	.261	.307	.112			
LOGF4	.583	.666	.319	.301	.115			
LOGF5	.612	.644	.306	.300	.130			
LOGF12	.580	.619	.445	.260	.110			

Extraction Method: Principal Component Analysis.
Rotation Method: Varimax with Kaiser Normalization.
a. Rotation converged in 7 iterations.

Table 4.3b. Rotated component matrix of the PCA of the size corrected femur data.

Rotated Component Matrix[a]

	Component							
	1	2	3	4	5	6	7	8
RESF11	.907	.205	.103		.204			
RESF9	.821	.264	.244	.205	.182			.250
RESF8	.809	.233	.348	.217		.135		.138
RESF4	.723	.217	.350	.200	.335	.171	.259	
RESF5	.650	.281	.324	.318	.293	.352	.128	
RESF10	.459	.397	.374	.325	.297	.236	.169	.423
RESF2	.231	.879	.267	.180	.155	.163	.105	
RESF1	.339	.847	.228	.220	.162	.150	.101	
RESF7	.323	.329	.774	.240	.209	.222	.133	
RESF3	.390	.317	.760	.225	.238	.188	.114	
RESF13	.286	.347	.303	.797	.107	.175	.133	
RESF12	.437	.253	.288	.109	.778	.123	.104	
RESF6	.198	.414	.449	.245	.158	.680	.138	
RESF14	499	.341	.316	.296	.211	.206	.589	

Extraction Method: Principal Component Analysis.
Rotation Method: Varimax with Kaiser Normalization.
a. Rotation converged in 6 iterations.

Total length (LOGF1; RESF1) and functional length (LOGF2; RESF2) are highlighted. Measurement definitions can be found in Table 3.4.

respectively, load similarly across the components. They are the highest loading variables on the first component in the logged analysis (Table 4.3a) and the highest loading variables on the second component in the size corrected analysis (Table 4.3b) and thus provide the same amount of information in the models.

It was decided that the total length (F1) should be removed from subsequent DFAs. Although both variables are measures of length and may be difficult to apply to the fossil material, the assumption was made that it is less likely that one will recover an entirely complete femur than one of which the greater trochanter, a projection that is prone to breakage or destruction in deposition, has been lost. Loss of the greater trochanter will result in the inability to quantify the total length (F1), but the functional length (F2) remains a viable measurement in this case.

4.2.1 Results of the analyses of the logged data

A total of 21 analyses were conducted on the logged long bone data. They yielded overall percentages of correct classification between 23.7 % (proximal metacarpal) and 68.0% (humerus). Table 4.4 displays the percentages of correct classification for each analysis conducted, as well as a breakdown of the percentage of individuals correctly identified within each habitat group in each analysis. The analyses are ordered according to their overall success rates and each cell in the table is colour coded according to how high or low the percentage of classification is.

Fourteen of the twenty-one analyses had an overall percentage of correct classification above the baseline of accuracy. These analyses are identified with an asterisk in Table 4.4. These fourteen elements and epiphyseal ends of elements are considered reasonable to good predictors of habitat in which the discriminant function

Table 4.4. Percentages of correct classification of the analyses of the logged long bone data, overall and within individual habitat categories

Element	# of meas	% correct overall	% correct grassland/ tree-less	% correct wooded-bushed grassland	% correct light woodland-bushland	% correct heavy woodland-bushland	% correct forest	% correct montane light cover	% correct montane heavy cover
humerus*	13[t]	**68.0**	76.5	62.8	72.5	67.7	43.3	93.3	81.3
femur*	13[t]	**66.7**	64.7	64.7	58.8	65.6	66.7	85.7	76.5
metatarsal*	13	**66.5**	80.0	69.6	61.5	50.0	64.5	66.7	84.0
radius*	8[t]	**58.0**	47.1	57.4	39.2	71.0	63.3	87.5	66.7
distal metacarpal*	7	**56.4**	66.7	56.5	51.0	29.6	51.6	75.0	84.0
proximal femur*	6	**52.6**	52.9	52.2	38.5	56.3	43.3	86.7	76.5
distal humerus*	5	**48.8**	52.9	46.5	58.8	35.5	36.7	66.7	50.0
distal metatarsal*	7	**48.4**	46.7	50.0	63.5	21.4	29.0	38.9	76.0
tibia*	12	**47.6**	7.7	60.9	62.0	28.1	56.7	41.2	33.3
distal metapodial*	7	**47.2**	50.0	46.7	51.5	20.0	45.2	47.1	70.0
distal femur*	4	**42.4**	23.5	58.7	50.0	28.1	20.0	56.3	47.1
proximal radius*	3	**41.1**	64.7	44.7	48.1	32.3	0.0	58.8	60.0
proximal tibia*	6	**37.6**	15.4	54.3	62.0	15.6	36.7	5.9	20.0
proximal humerus*	5	**37.4**	47.1	51.2	37.3	41.9	40.0	6.7	6.3
ulna	7	**35.8**	0.0	36.4	57.1	25.8	44.4	35.3	13.0
proximal metatarsal	2	**34.9**	33.3	4.3	75.0	0.0	29.0	0.0	80.0
proximal ulna	5	**32.5**	0.0	19.6	57.1	21.9	48.3	35.3	17.4
distal radius	2	**32.4**	41.2	39.6	47.1	19.4	33.3	11.8	0.0
metacarpal	3[t]	**32.2**	40.0	45.7	33.3	0.0	38.7	0.0	12.5
distal tibia	2	**31.5**	0.0	32.6	58.0	3.1	53.3	0.0	24.0
proximal metacarpal	2	**23.7**	46.7	34.8	31.4	0.0	35.5	0.0	0.0

cells are colour coded by percentage value: 0-30.0 = no colour; 30.1-40.0 = gray; 40.1-50.0 = pink; 50.1-60.0 = orange; 60.1-70.0 = yellow; 70.1-80.0 = green; 80.1-90.0 = blue; 90.1-100 = purple

[t] indicates that measurements were dropped from the analysis - see section 4.2 and Table 4.2 for a discussion.

* indicates that the percentage of correct classification is above the baseline of accuracy determined in Chapter 3.

analyses were able to detect a link between the quantified skeletal morphologies and habitat group.

The total relevant output of every analysis is not presented here but is included in Appendix E. The structure matrix, classification results table and a scatter plot of the first and second discriminant function are found therein. Here, in order to illustrate the differences between good and bad habitat predictors, only a select few analyses are discussed. All structure matrices presented display the pooled within-groups correlations between discriminating variables and standardised canonical discriminant functions.

The analysis of the complete humerus has the highest overall percentage of correct classification, 68.0% and as such can be considered the "best" habitat predictor in the logged analyses. Using thirteen of the original fourteen measurements (H3 was dropped in the tolerance test), six discriminant functions (DFs) were calculated (Table 4.5) the first four of which account for the majority of the variation between the groups; the first DF accounts for 52.1%, the second DF for 17.1%, the third DF for 15.6% and the fourth DF for 10.0%. The fifth and sixth DFs contribute very little to the model.

The scatter plot of the first two discriminant functions indicates that despite a success rate of 68.0%, there is some obvious overlap between the habitat clusters (Figure 4.1). Despite this overlap, some generalisations can be made in regards to the separation of the species. DF1 separates the montane species from the others whilst DF2 distinguishes between the amount of vegetation cover present in the environment, with the forest and heavy woodland-bushland species separating from the grassland/tree-less, wooded-bushed grassland and light woodland-bushland species.

Table 4.5. Structure matrix from an analysis of the logged humerus data

Structure Matrix

	Function					
	1 52.1%	2 17.1%	3 15.6%	4 10.0%	5 3.9%	6 1.3%
LOGH4	.039	.095	.342	.243	.065	.539
LOGH2	.080	.108	.382	.209	-.019	.535
LOGH1	.075	.109	.365	.217	-.032	.520
LOGH7	-.007	.167	.341	.286	-.007	.503
LOGH5	-.001	.174	.305	.266	-.002	.498
LOGH11	-.025	.200	.361	.194	.008	.495
LOGH9	-.050	.113	.386	.235	-.033	.495
LOGH6	.003	.118	.351	.281	-.001	.490
LOGH14	-.016	.155	.362	.231	.017	.486
LOGH10	.002	.151	.369	.219	.029	.482
LOGH8	.008	.161	.386	.244	-.010	.475
LOGH12	.023	.091	.356	.165	-.052	.471
LOGH13	.022	.122	.370	.291	.028	.458
LOGH3[a]	.039	.108	.228	.259	-.121	.388

a. This variable not used in the analysis.

The percentage of variance described by each function is provided. Measurement definitions can be found in Table 3.4.

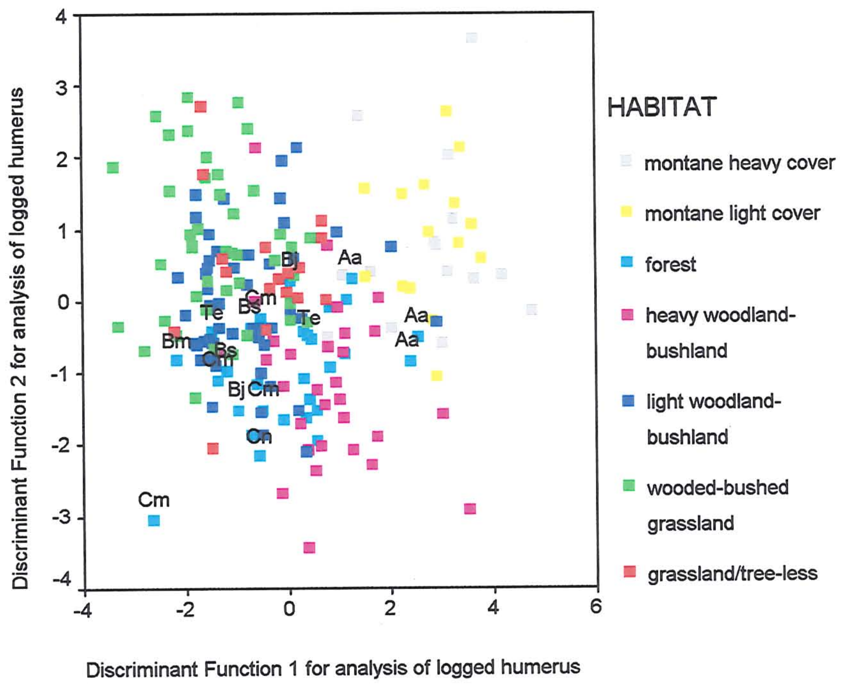


Figure 4.1. Scatter plot of the first and second discriminant functions from an analysis of the logged humerus data. Species codes are found in Table 3.1.

Table 4.6 presents the summary classification results of the logged humerus analysis. In addition to the overall success rate, the table provides details of the percentage of individuals in each habitat category that were both correctly and wrongly assigned. Success rates within each habitat group range from 43.4% in the forest category to 93.3% in montane light cover. All of the habitat categories have a high rate of correct classification, with the exception of the forest group in which 40.0% were misclassified as light woodland-bushland species and 16.7% as heavy woodland-bushland species. In DFAs it is common that the majority of misclassifications are found in the group with the greatest dispersion and largest sample size, in this case that is indeed the light woodland-bushland category with 51 individuals. The classification results in Table 4.6 show that in this instance, anywhere from 16.1 – 40.0% of the individuals in other habitat groups were wrongly predicted to belong to the light woodland-bushland group. However, this category has a very high success rate (72.5%) for it's own members.

In an analysis in which the individuals have been randomly and incorrectly assigned to a habitat group (such as those in which the baseline of accuracy was determined in Section 3.6), misclassifications are spread evenly among the habitat categories and have no biological meaning. However, misclassifications in an analysis which reliably predicts habitat affiliation, such as the humerus analysis above, are often centred on particular species which, for a variety of reasons (i.e. phylogeny, recent historical migrations out of their adaptive habitat), may resemble the morphology of species in other habitat groups.

The highest rate of misclassification was within the forest group in which seventeen of thirty forest individuals, or 57.7%, were misclassified as light (40.0%) and heavy (16.7%) woodland-bushland species. This case can be used as an example

Table 4.6. Classification results from an analysis of the logged humerus data

Classification Results[a]

		HABITAT	Predicted Group Membership							Total
			grassland/ tree-less	wooded-bushed grassland	light woodland-bushland	heavy woodland-bushland	forest	montane light cover	montane heavy cover	
Original	Count	grassland/tree-less	13	1	3	0	0	0	0	17
		wooded-bushed grassland	2	27	14	0	0	0	0	43
		light woodland-bushland	1	7	37	3	2	1	0	51
		heavy woodland-bushland	2	0	5	21	1	1	1	31
		forest	0	0	12	5	13	0	0	30
		montane light cover	0	0	0	0	0	14	1	15
		montane heavy cover	0	0	0	2	0	1	13	16
	%	grassland/tree-less	76.5	5.9	17.6	.0	.0	.0	.0	100.0
		wooded-bushed grassland	4.7	62.8	32.6	.0	.0	.0	.0	100.0
		light woodland-bushland	2.0	13.7	72.5	5.9	3.9	2.0	.0	100.0
		heavy woodland-bushland	6.5	.0	16.1	67.7	3.2	3.2	3.2	100.0
		forest	.0	.0	40.0	16.7	43.3	.0	.0	100.0
		montane light cover	.0	.0	.0	.0	.0	93.3	6.7	100.0
		montane heavy cover	.0	.0	.0	12.5	.0	6.3	81.3	100.0

a. 68.0% of original grouped cases correctly classified.

to illustrate the point above. A consideration of the forest misclassifications reveals that they occur only within seven species. Table 4.7 details these misclassifications. These species have also been identified on the scatter plot in Figure 4.1 by their assigned species code (species codes can be found in Table 3.1 in Chapter 3).

Four of the seven misclassified species, *Bos javanicus*, *Bos sauveli*, *Bubalus mindorensis* and *Tragelaphus eurycerus* are all large bodied Bovinae. With the exception of *Bison bison*, which is a grassland/tree-less species, the remaining Bovinae are classified as light or heavy woodland-bushland species and it may be that the shared phylogenetic relationship of these Bovinae dictates the humeral morphologies quantified by this analysis. The tamaraw, *Bubalus mindorensis*, also feeds in open fields and pastures and may possess humeral adaptations reflecting this pattern of resource exploitation. Furthermore, the bongo *Tragelaphus eurycerus,* may be only secondarily adapted to forest environments (Kingdon, 1997) and it is possible that their morphology reflects an adaptation to a less forested habitat, similar to that exploited by related tragelaphines, in the past.

The moose, *Alces alces*, was misclassified three times out of four and placed in the heavy woodland-bushland category. These species reside in temperate conifer forest and it may be that the amount of cover provided by their preferred environment is more similar to that provided by heavy woodland-bushland types, most of which are tropical African environments. It is unlikely that the six *Cephalophus* misclassifications relate to inappropriate habitat categorisation. It is more likely that they are the result of the fact that when handling ecological and biological data that can not easily be structured in discrete units, such as habitats and skeletal morphologies of closely related species, it is expected that there will be some overlap.

Table 4.7. Misclassifications of forest individuals from a discriminant function analysis of the logged humerus data

Species	Number misclassified	Total number in dataset	Predicted group
Alces alces	3	3	heavy woodland-bushland
Bos javanicus	2	3	light woodland-bushland
Bos sauveli	2	2	light woodland-bushland
Bubalus mindorensis	1	1	light woodland-bushland
Cephalophus monticola	5	5	light (4) and heavy (1) woodland-bushland
Cephalophus nigrifrons	1	6	light woodland-bushland
Tragelaphus eurycerus	3	3	light (2) and heavy (1) woodland-bushland
TOTALS	17	23	12 light woodland-bushland 5 heavy woodland bushland

This point in particular means that an overall percentage of correct classification of 68.0% in the logged humerus analysis represents a very high rate of success.

In contrast to the results of the analyses of good predictors such as the humerus, an example of a bad predictor will be illustrated. The logged proximal metacarpal analysis, with the lowest overall percentage of correct classification of 23.7% is more than 12% below the 36% baseline of accuracy for DFAs with 2 – 7 predictor variables.

There are only two measurements of the proximal metacarpal, the anterior-posterior diameter (MC3) and transversal diameter (MC4), thus two discriminant functions (DFs) were calculated (Table 4.8). They account for 62.8% and 37.2% of the variation between the habitat groups.

The scatter plot (Figure 4.2) of the two discriminant functions clearly displays that this element is not useful for discriminating on the basis of habitat. The individuals of each habitat type are scattered and habitat groups do not cluster together. The exception appears to be the montane light cover individuals which are restricted in space, however an examination of the classification results (Table 4.9) indicates that none of these individuals were correctly assigned. They overlap entirely with the wooded-bushed grassland and light woodland-bushland categories and have been assigned to those groups, 37.5% and 62.5%, respectively.

This is not surprising because these groups have the largest sample sizes (46 and 51, respectively) and, as explained above, the larger groups have a tendency to capture the majority of the incorrect classifications. Not only have the montane light cover species been assigned to these two groups, but the majority of the individuals in the remaining habitats have been assigned to them, as well. Interestingly, the

Table 4.8. Structure matrix from an analysis of the logged proximal metacarpal data

Structure Matrix

	Function	
	1 62.8%	2 37.2%
LOGMC4	.805	.593
LOGMC3	.721	.693

The percentage of variance described by each function is provided. Definitions of the measurements can be found in Table 3.4.

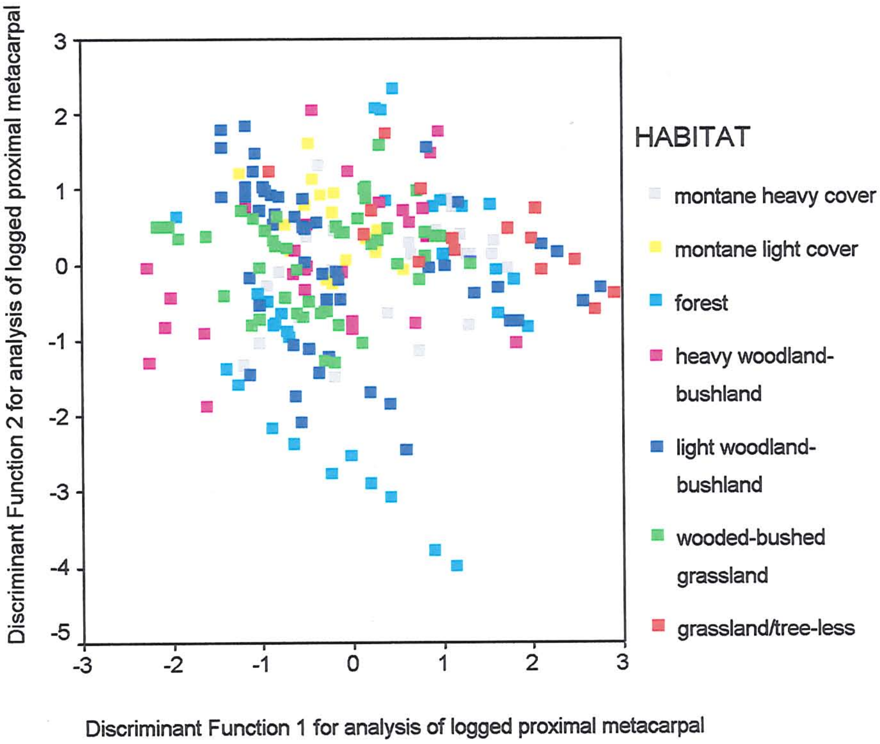


Figure 4.2. Scatter plot of the first and second discriminant functions from an analysis of the logged proximal metacarpal data.

Table 4.9. Classification results from an analysis of the logged proximal metacarpal data

Classification Results[a]

			Predicted Group Membership							
		HABITAT	grassland/ tree-less	wooded-bushed grassland	light woodland-bushland	heavy woodland-bushland	forest	montane light cover	montane heavy cover	Total
Original	Count	grassland/tree-less	7	1	7	0	0	0	0	15
		wooded-bushed grassland	0	16	27	0	3	0	0	46
		light woodland-bushland	4	21	16	0	10	0	0	51
		heavy woodland-bushland	0	8	17	0	2	0	0	27
		forest	3	6	11	0	11	0	0	31
		montane light cover	0	6	10	0	0	0	0	16
		montane heavy cover	3	5	14	0	3	0	0	25
	%	grassland/tree-less	46.7	6.7	46.7	.0	.0	.0	.0	100.0
		wooded-bushed grassland	.0	34.8	58.7	.0	6.5	.0	.0	100.0
		light woodland-bushland	7.8	41.2	31.4	.0	19.6	.0	.0	100.0
		heavy woodland-bushland	.0	29.6	63.0	.0	7.4	.0	.0	100.0
		forest	9.7	19.4	35.5	.0	35.5	.0	.0	100.0
		montane light cover	.0	37.5	62.5	.0	.0	.0	.0	100.0
		montane heavy cover	12.0	20.0	56.0	.0	12.0	.0	.0	100.0

a. 23.7% of original grouped cases correctly classified.

percentage of correct classifications *within* those groups were very low. Only 34.8% of wooded-bushed grassland individuals and 31.4% of light woodland-bushland individuals were properly assigned and a higher percentage of them were assigned to the *other* category. There were also no correct identifications in either of the two montane habitats or in the heavy woodland-bushland category.

The analysis of the logged proximal metacarpal data does not appear to have any biological basis and, in contrast to the humerus, is not a good habitat predictor. Bad predictors from the logged long bone analyses such as the proximal metacarpal, or those which fall under the baseline of accuracy, will not be considered in the palaeoenvironmental reconstruction of Laetoli.

4.2.2 Results of the analyses of the size corrected data

Discriminant function analyses of the size corrected data were conducted in order to ascertain if body size has a significant effect on habitat prediction using the elements and measurements utilised in this study. The good habitat predictors determined by this set of analyses will not used in the analyses of the Laetoli fossil material because it cannot be size corrected with the method followed herein. Rather, these analyses and their relative success rates are compared to the analyses of the logged data from the same elements. The total relevant output of every analysis, including the structure matrix, classification results table and a scatter plot of the first and second discriminant function is contained in Appendix E.

A total of 21 analyses were conducted on the size corrected long bone data. They yielded overall percentages of correct classification between 27.2 % (distal tibia) and 68.5% (humerus). Table 4.10 displays the percentages of correct classification for each analysis conducted, as well as a breakdown of the percentage of

Table 4.10. Percentages of correct classification of the analyses of the size corrected long bone data, overall and within individual habitat categories

Element	**# of meas**	**% correct overall**	**% correct grassland/ tree-less**	**% correct wooded-bushed grassland**	**% correct light woodland-bushland**	**% correct heavy woodland-bushland**	**% correct forest**	**% correct montane light cover**	**% correct montane heavy cover**
humerus*	14	**68.5**	76.5	67.4	64.7	67.7	50.0	93.3	87.5
metatarsal*	13	**67.9**	73.3	76.1	59.6	50.0	67.7	77.8	80.0
metacarpal*	13	**67.6**	60.0	73.9	60.8	51.9	74.2	93.3	68.0
femur*	13[t]	**66.2**	29.4	71.7	56.9	65.6	76.7	85.7	82.4
radius*	9	**61.0**	58.8	71.7	36.0	58.1	66.7	93.8	73.3
distal metacarpal*	7	**60.7**	20.0	69.6	56.9	44.4	67.7	68.8	80.0
proximal femur*	6	**54.1**	17.6	56.5	46.2	56.3	56.7	80.0	76.5
distal metatarsal*	7	**50.2**	0.0	65.2	55.8	35.7	48.4	27.8	76.0
distal humerus*	5	**47.8**	23.5	53.5	47.1	41.9	40.0	66.7	68.8
distal metapodial*	7	**47.2**	3.3	59.8	50.5	32.7	43.5	50.0	62.0
distal femur*	4	**46.7**	0.0	63.0	46.2	28.1	63.3	56.3	47.1
tibia*	12	**42.9**	7.7	60.9	60.0	31.3	36.7	35.3	20.8
proximal metatarsal*	2	**40.9**	0.0	63.0	55.8	0.0	35.5	5.6	72.0
proximal radius*	3	**39.2**	11.8	53.2	46.2	25.8	26.7	47.1	46.7
distal radius	2	**35.6**	0.0	57.4	42.0	29.0	46.7	17.6	0.0
proximal tibia	6	**35.2**	7.7	58.7	66.0	21.9	16.7	0.0	8.0
proximal humerus	5	**34.0**	17.6	51.2	41.2	29.0	40.0	6.7	6.3
ulna	7	**30.4**	0.0	36.4	51.0	25.8	14.8	29.4	17.4
proximal metacarpal	2	**28.6**	0.0	39.1	43.1	11.1	54.8	0.0	0.0
proximal ulna	5	**28.2**	0.0	21.7	42.9	34.4	34.5	29.4	8.7
distal tibia	2	**27.2**	0.0	50.0	70.0	0.0	0.0	0.0	0.0

cells are colour coded by percentage value: 0-30.0 = no colour; 30.1-40.0 = gray; 40.1-50.0 = pink; 50.1-60.0 = orange; 60.1-70.0 = yellow; 70.1-80.0 = green; 80.1-90.0 = blue; 90.1-100 = purple

[t] indicates that measurements were dropped from the analysis - see section 4.2 and Table 4.2 for a discussion.

* indicates that the percentage of correct classification is above the baseline of accuracy determined in Chapter 3.

individuals correctly identified within each habitat group in each analysis. The analyses are organised according to their overall success rates and each cell in the table is colour coded according to the percentage of classification, in increments of ten percent. Fourteen of the twenty-one analyses had an overall percentage of correct classification above the baseline of accuracy. These analyses are labelled with an asterisk in Table 4.10. These fourteen elements and epiphyseal ends of elements are considered good predictors of habitat.

The complete humerus is the best predictor with the highest overall percentage of correct classification, 68.5%. All of the habitat groups have a high rate of correct classification with the lowest, 50.0%, within the forest group. Analysing fourteen measurements, six discriminant functions (DFs) were calculated (Table 4.11) and the first four account for the majority (94.6%) of the variance between the habitat categories: DF1 for 57.1%, DF2 for 16.9%, DF3 for 11.9% and DF4 for 8.7%.

A scatter plot (Figure 4.3) of the first and second discriminant functions displays some overlap between the habitat groups. However, it can be said that generally DF 1 separates the montane species from those found in more open grassland, wooded-bushed grassland and light woodland-bushland environments. Forest and heavy woodland-bushland individuals fall in between. DF 2 is more difficult to interpret, although it appears that a number of forest and heavy woodland-bushland species load low on that function in comparison with the majority of those in the montane and more open cover categories.

The misclassifications that occurred with members of the forest category, which had the highest amount of incorrect classifications of any habitat group, can be examined more closely to reveal a pattern if mis-identification. The classification results in Table 4.12 indicate that although 50.0% were correctly assigned, the

Table 4.11. Structure matrix from an analysis of the size corrected humerus data

Structure Matrix

	Function					
	1 57.1%	2 16.1%	3 11.9%	4 8.7%	5 4.0%	6 1.4%
RESH5	.069	.492	.195	-.093	.145	.008
RESH11	.159	.465	-.148	.143	.073	.004
RESH7	.105	.438	.077	-.241	.153	-.048
RESH8	.045	.427	-.233	-.144	.217	.090
RESH10	.067	.380	-.152	.038	.029	.139
RESH14	.132	.324	-.071	-.004	.058	.072
RESH4	-.103	.103	.071	-.020	-.082	-.004
RESH13	-.031	.201	-.016	-.289	.036	.209
RESH6	.054	.218	.076	-.239	.176	.072
RESH3	-.059	.250	.295	-.042	.490	.336
RESH12	-.038	.077	-.079	.236	.395	.172
RESH9	.351	.143	-.142	-.043	.354	.018
RESH1	-.246	.172	-.095	.017	.333	-.010
RESH2	-.253	.141	-.167	.031	.261	-.055

The percentage of variance described by each function is provided. Definitions of the measurements can be found in Table 3.4.

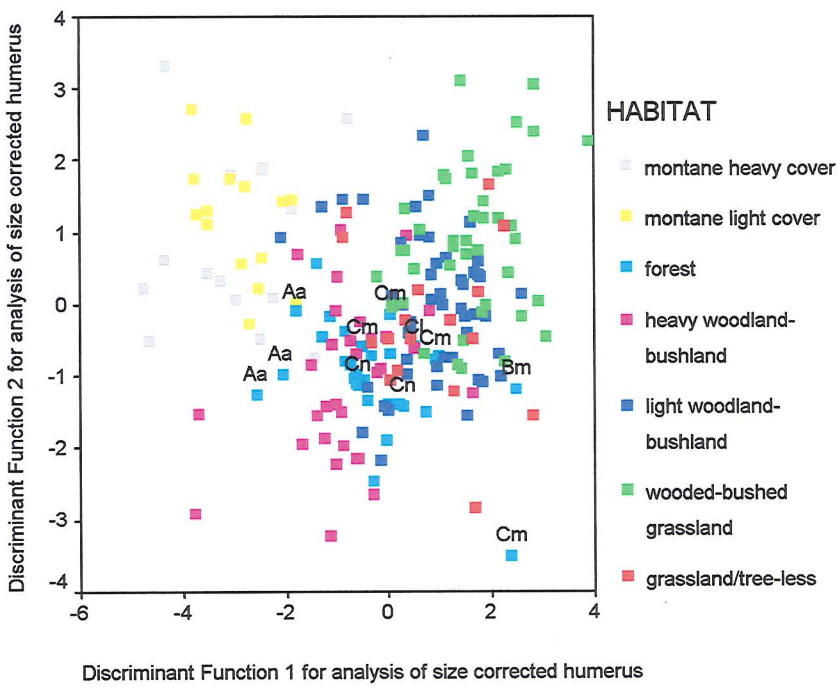


Figure 4.3. Scatter plot of the first and second discriminant functions from an analysis of the size corrected humerus data. Species codes are found in Table 3.1

Table 4.12. Classification results from an analysis of the size corrected humerus data

Classification Results[a]

		HABITAT	Predicted Group Membership: grassland/ tree-less	wooded-bushed grassland	light woodland-bushland	heavy woodland-bushland	forest	montane light cover	montane heavy cover	Total
Original	Count	grassland/tree-less	13	1	3	0	0	0	0	17
		wooded-bushed grassland	1	29	13	0	0	0	0	43
		light woodland-bushland	2	9	33	2	4	1	0	51
		heavy woodland-bushland	2	0	4	21	2	1	1	31
		forest	0	1	8	6	15	0	0	30
		montane light cover	0	0	0	0	0	14	1	15
		montane heavy cover	0	0	0	1	0	1	14	16
	%	grassland/tree-less	76.5	5.9	17.6	.0	.0	.0	.0	100.0
		wooded-bushed grassland	2.3	67.4	30.2	.0	.0	.0	.0	100.0
		light woodland-bushland	3.9	17.6	64.7	3.9	7.8	2.0	.0	100.0
		heavy woodland-bushland	6.5	.0	12.9	67.7	6.5	3.2	3.2	100.0
		forest	.0	3.3	26.7	20.0	50.0	.0	.0	100.0
		montane light cover	.0	.0	.0	.0	.0	93.3	6.7	100.0
		montane heavy cover	.0	.0	.0	6.3	.0	6.3	87.5	100.0

a. 68.5% of original grouped cases correctly classified.

remaining 50.0% were incorrectly assigned to wooded-bushed grassland (n=1, 3.3%), light woodland-bushland (n=6, 26.7%) and heavy woodland-bushland (n=5, 20.0%). The incorrect predictions occur only within six species and involve 15 individuals, which have been identified by their species code on the scatter plot of the first two DFs (Figure 4.3). Table 4.13 summarises the individual misclassifications.

The moose, *Alces alces*, was classified in this analysis as a heavy woodland-bushland species in three out of four cases, which could be the result of inappropriate habitat coding. *Alces* inhabits temperate conifer forests that may in fact be sparser than other forest environments and perhaps provide the same amount of cover as the heavy woodland-bushland environments.

Eight out of a possible 13 *Cephalophus* individuals were also misclassified, but it is unlikely that they were initially put in the wrong habitat category as cephalophines, with the exception of the common duiker *Sylvicapra grimmia*, are well known to reside in forested environments. The misclassifications could simply be the result of the fact that a certain degree of overlap in groups can be expected when dealing with biological data of this nature. However, cephalophines are also known to visit dense thickets and marshy areas and their humeral morphologies perhaps indicate this occasional preference for habitats which present less vegetation cover.

Tragelaphys eurycerus, the bongo, was most likely misclassified as a light or heavy woodland-bushland species on account of its original woodland adapted lifestyle. It most likely shares its humeral morphology with other related tragelaphines such as the bushbuck *Tragelaphus scriptus* and greater kudu *Tragelaphus strepsiceros*, which have remained in their ancestral heavy woodland-bushland habitats. *Bubalus mindorensis*, the rare Philippino tamaraw, was misclassified as a wooded-bushed grassland species. It inhabits dense forest regions, but also requires a

Table 4.13. Misclassifications of forest individuals from a discriminant function analysis of the size corrected humerus data

Species	**Number misclassified**	**Total number in dataset**	**Predicted group**
Alces alces	3	3	heavy woodland-bushland
Bubalus mindorensis	1	1	wooded-bushed grassland
Cephalophus leucogaster	1	2	light woodland-bushland
Cephalophus monticola	5	5	light (4) and heavy (1) woodland-bushland
Cephalophus nigrifrons	2	6	light (1) and heavy (1) woodland-bushland
Tragelaphus eurycerus	3	3	light (2) and heavy (1) woodland-bushland
TOTALS	15	20	1 wooded-bushed grassland 8 light woodland-bushland 6 heavy woodland bushland

significant amount of pasture and grassland for grazing. Humeral morphology may reflect an adaptation to this particular trophic constraint.

In contrast to the humerus, a bad predictor displays a very different set of results. The analysis of the distal tibia data resulted in the lowest overall percentage of classification of the size corrected analyses. At 27.2%, it is almost 9% lower than the baseline of accuracy for an analysis with two predictor variables. Two discriminant functions (DF) were calculated, accounting for 69.2% and 30.2% (Table 4.14) of the variance observed between the habitat groups.

The individuals in the dataset do not possess distinctive distal tibiae. The element is not an accurate habitat predictor and a scatter plot (Figure 4.4) of the two DFs illustrates this. There are no visibly isolated habitat clusters, but rather one large cluster surrounded by a number of scattered outliers that do not belong to any particular habitat type. A look at the classification results in Table 4.15 confirms that this element is a bad predictor. With the exception of one light woodland-bushland individual that was classified as heavy woodland-bushland, the remaining individuals were placed into the wooded-bushed grassland and light woodland-bushland categories. As the groups with the largest sample sizes (46 and 50, respectively) it is not surprising that they captured all of the misclassifications.

4.2.3 Comparison of the logged and size corrected analyses

Fourteen logged and fourteen size corrected analyses had overall percentages of correct classification above the baseline of accuracy. The elements used in these analyses are considered good habitat predictors. Table 4.16 lists these and compares their relative success rates.

Table 4.14. Structure matrix from an analysis of the size corrected distal tibia data

Structure Matrix

	Function	
	1 69.2%	2 30.8%
REST9	.054	.999
REST10	.608	.794

The percentage of variance described by each function is provided. Definitions of the measurements can be found in Table 3.4.

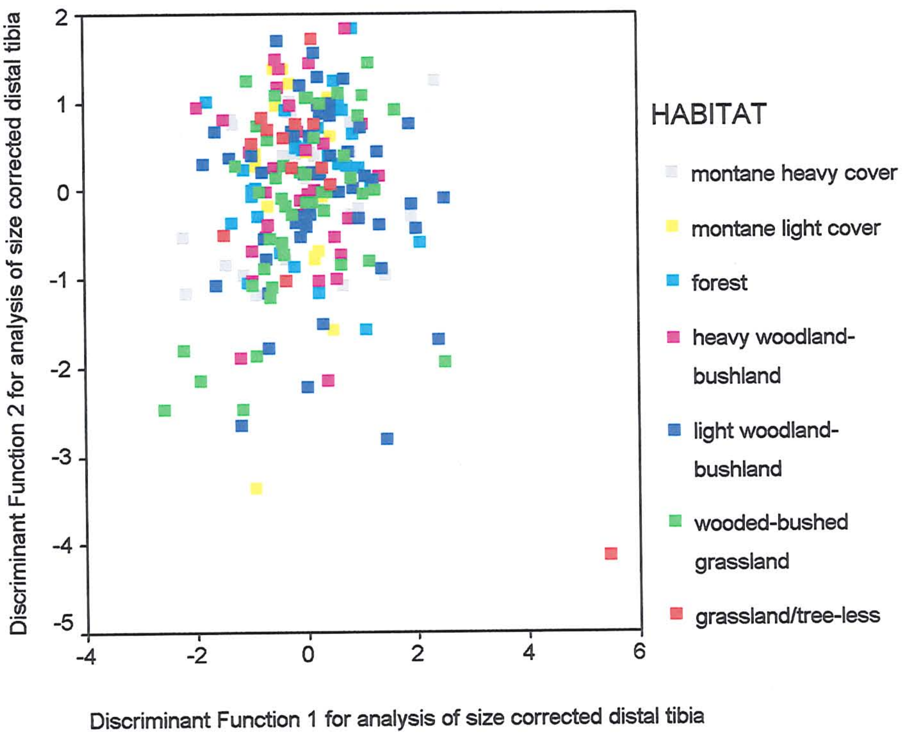


Figure 4.4. Scatter plot of the first and second discriminant functions from an analysis of the size corrected distal tibia data.

Table 4.15. Classification results from an analysis of the size corrected distal tibia data

Classification Results[a]

			Predicted Group Membership							
		HABITAT	grassland/ tree-less	wooded-bushed grassland	light woodland-bushland	heavy woodland-bushland	forest	montane light cover	montane heavy cover	Total
Original	Count	grassland/tree-less	0	6	7	0	0	0	0	13
		wooded-bushed grassland	0	23	23	0	0	0	0	46
		light woodland-bushland	0	14	35	1	0	0	0	50
		heavy woodland-bushland	0	11	21	0	0	0	0	32
		forest	0	11	19	0	0	0	0	30
		montane light cover	0	5	12	0	0	0	0	17
		montane heavy cover	0	9	16	0	0	0	0	25
	%	grassland/tree-less	.0	46.2	53.8	.0	.0	.0	.0	100.0
		wooded-bushed grassland	.0	50.0	50.0	.0	.0	.0	.0	100.0
		light woodland-bushland	.0	28.0	70.0	2.0	.0	.0	.0	100.0
		heavy woodland-bushland	.0	34.4	65.6	.0	.0	.0	.0	100.0
		forest	.0	36.7	63.3	.0	.0	.0	.0	100.0
		montane light cover	.0	29.4	70.6	.0	.0	.0	.0	100.0
		montane heavy cover	.0	36.0	64.0	.0	.0	.0	.0	100.0

a. 27.2% of original grouped cases correctly classified.

Table 4.16. Good predictors in the logged and size corrected discriminant function analyses of the long bones

Element	**Percentage of correct classification**	
	logged	***size corrected***
Humerus	68.0	68.5
Metacarpal	-	67.6
Femur	66.7	66.2
Metatarsal	66.5	67.9
Radius	58.0	61.0
Distal metacarpal	56.4	60.7
Proximal femur	52.6	54.1
Distal humerus	48.8	47.8
Distal metatarsal	48.4	50.2
Tibia	47.6	42.9
Distal metapodial	47.2	47.2
Distal femur	42.4	46.7
Proximal metatarsal	-	40.9
Proximal radius	41.1	39.2
Proximal tibia	37.6	-
Proximal humerus	37.4	-

Twelve of the elements were good predictors in both sets of analyses and had very similar overall percentages of classification. Amongst them, the greatest difference between the logged and size corrected results was found with the tibia which successfully predicted the habitat of 47.6% of the individuals in the logged analysis and 42.9% in the size corrected analysis, a difference of only 4.7%.

The proximal tibia and proximal humerus were good predictors in the logged analyses and not in the size corrected. However, as good predictors they only fell just above the 36% baseline of accuracy with 37.6% and 37.4% of the individuals correctly classified, respectively. When these data were size corrected and analysed they fell just below the baseline, with percentages of correct classification of 35.2% and 34.0% respectively.

One of the two elements which was a good predictor in the size corrected analysis and not in the logged, the proximal metatarsal, presented a similar situation. The logged data fell only 1.1% below the 36% baseline with a percentage of correct classification of 34.9%. When the data were size corrected they resulted in a success rate of 40.9%, only 4.9% over the baseline.

The complete metacarpal analyses presented a very different situation. In the logged analysis 10 of the 13 measurements were dropped because they failed the automatic tolerance test, leaving only three measurements to be used in the calculation of the discriminant functions. The result was only a 32.2% percentage of correct classification. However, when the size corrected data were analysed a very successful 67.6% of the individuals were correctly assigned to their true habitat category.

4.3 Comparison of the results with previous studies

It is difficult to make direct comparisons between the results presented here and the results of other studies. The femur (Kappelman, 1988, 1991; Kappelman *et al*, 1997) and the metapodials (Plummer & Bishop, 1994) have previously been analysed in an ecomorphological context, but the variables and the habitat types included in those analyses differed both in number and definition to those considered here.

Building on previous research (Kappelman, 1988, 1991), in an analysis of strictly African species, Kappelman *et al* (1997) obtained a percentage of correct classification of 85.1% for a non-size corrected analysis of the complete femur. In the study reported here, the complete femur was amongst the best habitat predictors in both the logged and size corrected analyses, yielding success rates of 66.7% and 66.2%, respectively. This discrepancy between the percentages obtained in the two studies may relate to the different measurements used, but most likely the reason lies within the composition of the habitat groups and the number of groups themselves. Kappelman *et al* (1997) did not consider non-African species and had only four habitat groups, thus there are no montane categories as there are no true mountain dwelling African bovids. They also removed any individuals from their study that had measurement values which fell several standard deviations away from the species mean, a practice not followed here in order to include the range variation each species is capable of displaying. It would have most likely decreased the potential for misclassification because the anomalous individuals would not have contributed anything to the model of prediction and DFAs are generally sensitive to the inclusion of outliers.

The conclusion of Kappelman *et al*'s (1997) study, however, does not contradict the findings here. It is apparent that the complete femur is an accurate habitat predictor, even when quantifying a different suite of characteristics and using a less sensitive range of habitats. This element was initially noted for displaying habitat-specific morphologies by Gentry (1970) and all subsequent research has upheld this conclusion (Kappelman, 1988, 1991; Kappelman *et al*, 1997).

More specifically, and very useful for the study of fragmentary fossils, the proximal femur has also shown itself to relate to habitat. Kappelman *et al* (1997) achieved an 81.4% success rate for a non-size corrected analysis of the proximal femur using the same dataset and habitat groups as in their complete femur analysis. However, the analyses reported here were less successful with an overall percentage of correct classification of 52.6% with the logged data and 54.1% with size corrected data. These results are well above the baseline of accuracy, but they are not as strong as those from Kappelman *et al*'s (1997) work.

Table 4.17 and Table 4.18 present the classification results from the logged and size corrected analyses of the femur in this study. The addition of two montane habitats in this study does not appear to negatively effect the habitat predictions. In both analyses these categories have very high rates of successful classification between 76.5% and 86.7%. The problems appear to be within the remaining five habitat groups and the ones which would indeed apply to African environments. The difference between the success of Kappelman *et al*'s (1997) study and the one presented here may be down to two factors. Firstly, the proximal femur may not be as sensitive to the finer partitioning of habitats in this study which used seven rather than four categories. Secondly, Kappelman *et al*'s (1997) four measurements were likely more relevant to locomotion within their four particular habitats categories. They used two ratios of shaft diameter at the proximal end, the area of the femoral head in superior view and a measure of femoral head shape. The six measurements used in

Table 4.17. Classification results from an analysis of the logged proximal femur data

Classification Results[a]

		HABITAT	Predicted Group Membership: grassland/ tree-less	wooded-bushed grassland	light woodland-bushland	heavy woodland-bushland	forest	montane light cover	montane heavy cover	Total
Original	Count	grassland/tree-less	9	2	2	1	0	0	3	17
		wooded-bushed grassland	0	24	16	5	1	0	0	46
		light woodland-bushland	2	16	20	9	4	0	1	52
		heavy woodland-bushland	0	3	9	18	2	0	0	32
		forest	3	0	3	8	13	2	1	30
		montane light cover	0	0	0	0	0	13	2	15
		montane heavy cover	0	0	0	1	3	0	13	17
	%	grassland/tree-less	52.9	11.8	11.8	5.9	.0	.0	17.6	100.0
		wooded-bushed grassland	.0	52.2	34.8	10.9	2.2	.0	.0	100.0
		light woodland-bushland	3.8	30.8	38.5	17.3	7.7	.0	1.9	100.0
		heavy woodland-bushland	.0	9.4	28.1	56.3	6.3	.0	.0	100.0
		forest	10.0	.0	10.0	26.7	43.3	6.7	3.3	100.0
		montane light cover	.0	.0	.0	.0	.0	86.7	13.3	100.0
		montane heavy cover	.0	.0	.0	5.9	17.6	.0	76 5	100.0

a 52 6% of original grouped cases correctly classified.

Table 4.18. Classification results from an analysis of the size corrected proximal femur data

Classification Results[a]

		HABITAT	Predicted Group Membership: grassland/ tree-less	wooded-bushed grassland	light woodland-bushland	heavy woodland-bushland	forest	montane light cover	montane heavy cover	Total
Original	Count	grassland/tree-less	3	3	5	1	2	0	3	17
		wooded-bushed grassland	2	26	15	3	0	0	0	46
		light woodland-bushland	1	15	24	8	4	0	0	52
		heavy woodland-bushland	4	1	6	18	3	0	0	32
		forest	3	0	2	6	17	1	1	30
		montane light cover	0	0	0	0	1	12	2	15
		montane heavy cover	0	0	0	1	3	0	13	17
	%	grassland/tree-less	17.6	17.6	29.4	5.9	11.8	.0	17.6	100.0
		wooded-bushed grassland	4.3	56.5	32.6	6.5	.0	.0	.0	100.0
		light woodland-bushland	1.9	28.8	46.2	15.4	7.7	.0	.0	100.0
		heavy woodland-bushland	12.5	3.1	18.8	56.3	9.4	.0	.0	100.0
		forest	10.0	.0	6.7	20.0	56.7	3.3	3.3	100.0
		montane light cover	.0	.0	.0	.0	6.7	80.0	13.3	100.0
		montane heavy cover	.0	.0	.0	5.9	17.6	.0	76.5	100.0

a. 54.1% of original grouped cases correctly classified.

this study were the transverse (F4) and anterior-posterior (F3) diameters of the proximal end, a measure of the diameter of the femoral head alone, both transverse (F8) and anterior-posterior (F7), and the distance between the tip of the lesser trochanter and greater trochanter (F5) and the head (F6).

The metacarpal and metatarsal have also been the subjects of previous ecomorphological studies. Plummer & Bishop (1994) undertook an exhaustive analysis of both metapodials and their distal and proximal ends. Their dataset was restricted to African bovid species and they utilised a scheme of three habitat types: closed, intermediate and open. Table 4.19 compares their results to those in this study. Their analyses obtained higher overall percentages of correct classification than any of the same in this study. However, in both studies the complete elements were better predictors than the ends and the distal ends were better than the proximal ends.

The measurements taken on the metapodials in Plummer & Bishop (1994) were more comprehensive then those included here and were converted into a series of dimensionless ratios entered into the analyses as predictor variables and selected as part of the stepwise function. These ratios may be more sensitive to the locomotor repertoire of the species in their dataset than the direct measurements utilised in this study. Plummer & Bishop's (1994) relatively low percentage of misclassifications may also be due to the fact they were careful to exclude any species which inhabit environments displaying anomalous features of the terrain such as cliffs or high plateaus or individuals weighing over 250kg. This variation in habitat type and body size was not avoided in this analysis and necessarily affects the rate of successful prediction.

An interesting consistency is found in the misclassifications that occurred the proximal metatarsal analyses in both studies. Plummer & Bishop (1994) found that

Table 4.19. Results of Plummer & Bishop's (1994) study of the metapodials compared to the results in this study.

Element	**Percentage of correct classification**		
	Plummer & Bishop (1994)	***Kovarovic (2004) logged***	***Kovarovic (2004) size corrected***
Metacarpal	84.0	32.2	67.6
Proximal metacarpal	60.0	23.7	28.6
Distal metacarpal	68.0	56.4	60.7
Metatarsal	89.0	66.5	67.9
Proximal metatarsal	62.0	34.9	40.9
Distal metatarsal	70.0	48.4	50.2

Results reported as an overall percentage of correct classification.

this element misclassified the open country alcelaphines *Alcelaphus buselaphus*, *Damaliscus lunatus*, *Connochaetes taurinus* and *Connochaetes gnou*, placing them into the intermediate cover category. These four species were also misclassified from grassland/tree-less or wooded-bushed grassland individuals to light woodland-bushland in the analyses reported in this thesis. This most likely results from the fact that these speed-adapted alcelaphines emphasise the use of their forelimbs over their hindlimbs, unlike other open country taxa such as the Antilopini, which do not emphasise either fore or hindlimb and were almost always correctly classified (Scott, 1979).

4.4 Summary of the long bone analyses

A total of 28 of the 42 long bone analyses (66.7%), successfully predicted the correct habitat of a percentage of the individuals which fell above the baseline of accuracy established in Section 3.6; 36% for analyses with 2 – 7 predictor variables and 41% for analyses with 8 – 15 predictor variables. Twelve elements were good predictors in both the logged and size corrected analyses (Table 4.16). Four elements were good predictors when only one set of data was used – two using logged data and two using size corrected data. In three instances (logged proximal tibia, logged proximal humerus and size corrected proximal metatarsal) it was shown that the percentages of correct classification fell just above the baseline and were relatively low compared to the other good predictors, and that in the analyses where they were bad predictors they fell just below the baseline.

These three elements, which straddled the baseline of accuracy depending on whether or not the size corrected or logged data were used, raise the question of how "good" a "good" predictor truly is. Arguably, a good predictor is one with not only a high rate of overall correct classification, but also high rates of classification *within* each individual habitat category. Misclassifications that occur are generally restricted to a few species or particularly anomalous individuals and can often be interpreted on the basis of unique morphologies that do not relate to their assigned known habitat type but do relate to specific ecological conditions or evolutionary relationships that can not be captured or explained by such a broad division of habitat types. The minutiae of the misclassifications are thus both ecologically and evolutionarily interesting in their own right.

Robust results are also associated with high probabilities of correct habitat prediction. Regardless of the overall percentage of correct classification, the probabilities must be high in order to place any amount of confidence in the predictions. This statistical consideration has been recently raised by DeGusta & Vrba (2003) and is taken up in this study.

For each specimen included in a discriminant function analysis, the probability that it affiliates with each of the habitat groups is automatically calculated. The probability is based on its proximity to the centroids for each of the habitat groups. The specimens are thus predicted to belong to the habitat with the highest associated probability. For instance, two elements included in the same analysis may both be predicted to belong to the grassland/tree-less habitat category, but Specimen A may have an associated probability of 90% while Specimen B may have a 40% probability. However, so long as 40% is the highest probability for Specimen B belonging to any of the habitats, it will be predicted to that group.

This issue can be illustrated by the scatter plot of the first two discriminant functions from the analysis of the logged humerus data (Figure 4.1). The misclassified forest species have been identified by their species codes (which can be found in

Table 3.1). A comparison of the habitat group predictions for each forest individual in the main SPSS data sheet with the individuals in the scatter plot that are on the edge of the forest habitat cluster or those that fall outside of the space in which the majority of the individuals in that habitat group lie, are those individuals which have been misclassified. Furthermore, the misclassified individuals have lower confidence values associated with their habitat predictions (Table 4.20). The correctly predicted individuals have an average probability of 75%, whereas those predicted to belong to the light woodland-bushland and heavy woodland-bushland categories have average probabilities of 51% and 47%, respectively.

Confidence values are considered in the analyses of the Laetoli material and in the evaluation of the results in Chapter 6. Size corrected analyses will not be used with the fossil material and thus only good predictors from the logged long bone analyses will be forwarded to the analyses of the Laetoli collection. The two exceptions are the distal metacarpal and distal metatarsal. The fossil material was not identified that specifically and all relevant specimens were grouped as distal metapodials. Table 4.21 lists the elements that will be used to reconstruct the habitat of Laetoli.

Table 4.20. Probabilities associated with the habitat predictions of the forest individuals in an analysis of the logged humerus data

Species	Species code	Predicted habitat	grassland/ tree-less	wooded-bushed grassland	light woodland-bushland	heavy woodland bushland	forest	montane light cover	montane heavy cover
Bos javanicus	Bj	light woodland-bushland	0.00888	0.08373	**0.39480**	0.28200	0.23055	0.00004	0.00000
Bos javanicus	Bj	light woodland-bushland	0.02171	0.19079	**0.48758**	0.11324	0.18262	0.00311	0.00095
Bos sauveli	Bs	light woodland-bushland	0.00582	0.22140	**0.44208**	0.06581	0.26436	0.00052	0.00001
Bos sauveli	Bs	light woodland-bushland	0.02834	0.15591	**0.49601**	0.10663	0.21308	0.00002	0.00000
Bubalus mindorensis	Bm	light woodland-bushland	0.07931	0.26121	**0.38684**	0.00994	0.26270	0.00000	0.00000
Cephalophus monticola	Cm	light woodland-bushland	0.00073	0.04347	**0.41950**	0.22265	0.31358	0.00002	0.00005
Cephalophus monticola	Cm	light woodland-bushland	0.00122	0.30341	**0.40356**	0.07769	0.21385	0.00013	0.00013
Cephalophus monticola	Cm	light woodland-bushland	0.00228	0.02125	**0.77057**	0.05604	0.14986	0.00000	0.00000
Cephalophus monticola	Cm	light woodland-bushland	0.00014	0.19723	**0.51411**	0.03120	0.25730	0.00000	0.00001
Cephalophus nigrifrons	Cn	light woodland-bushland	0.00002	0.01859	**0.42230**	0.14009	0.41886	0.00000	0.00014
Tragelaphus eurycerus	Te	light woodland-bushland	0.00089	0.07426	**0.81005**	0.05401	0.06068	0.00008	0.00003
Tragelaphus eurycerus	Te	light woodland-bushland	0.00184	0.20553	**0.56144**	0.00840	0.22278	0.00000	0.00001
Alces alces	Aa	heavy woodland-bushland	0.01496	0.00042	0.01664	**0.51415**	0.04117	0.05543	0.35723
Alces alces	Aa	heavy woodland-bushland	0.00126	0.00033	0.02470	**0.51322**	0.03000	0.00772	0.42276
Alces alces	Aa	heavy woodland-bushland	0.00506	0.04534	0.26843	**0.32287**	0.15041	0.01671	0.19117
Cephalophus monticola	Cm	heavy woodland-bushland	0.03707	0.03505	0.26958	**0.58438**	0.06127	0.00009	0.01256
Tragelaphus eurycerus	Te	heavy woodland-bushland	0.21993	0.02201	0.21466	**0.42390**	0.11182	0.00018	0.00751
Bos javanicus	Bj	forest	0.00126	0.07180	0.22554	0.10213	**0.59640**	0.00180	0.00107
Cephalophus leucogaster	Cl	forest	0.00038	0.03877	0.10239	0.09576	**0.76269**	0.00000	0.00002
Cephalophus leucogaster	Cl	forest	0.00040	0.15665	0.30261	0.20984	**0.33043**	0.00003	0.00005
Cephalophus nigrifrons	Cn	forest	0.00134	0.01160	0.09333	0.43706	**0.45456**	0.00012	0.00199
Cephalophus nigrifrons	Cn	forest	0.00121	0.03004	0.04606	0.10591	**0.80849**	0.00001	0.00827
Cephalophus nigrifrons	Cn	forest	0.00008	0.00884	0.08997	0.09967	**0.80098**	0.00011	0.00034
Cephalophus nigrifrons	Cn	forest	0.00105	0.01830	0.09562	0.29643	**0.58664**	0.00010	0.00185
Cephalophus nigrifrons	Cn	forest	0.00108	0.01882	0.05792	0.11534	**0.80610**	0.00000	0.00075
Hyemoschus aquaticus	Ha	forest	0.00024	0.02206	0.00845	0.00941	**0.94347**	0.01611	0.00026
Hyemoschus aquaticus	Ha	forest	0.00037	0.00689	0.01141	0.03354	**0.94230**	0.00385	0.00164
Hyemoschus aquaticus	Ha	forest	0.00127	0.00842	0.01201	0.04750	**0.92722**	0.00334	0.00023
Hyemoschus aquaticus	Ha	forest	0.00015	0.02298	0.01531	0.01939	**0.84351**	0.09780	0.00086
Hyemoschus aquaticus	Ha	forest	0.00010	0.00239	0.01138	0.05393	**0.93187**	0.00031	0.00003
AVERAGE PROBABILITY					**0.50907**	**0.47170**	**0.74882**		

The highest probabilities are in bold. For all of the specimens assigned to each category, the average probability has been calculated. The highest average is associated with the correctly assigned individuals.

Table 4.21. Long bones used in Laetoli analyses

Element
Humerus
Femur
Metatarsal
Radius
Proximal femur
Distal humerus
Tibia
Distal metapodial
Distal femur
Proximal radius
Proximal tibia
Proximal humerus

5 RESULTS OF THE ANALYSES OF THE EXTANT BOVID DATA: CARPALS, TARSALS AND PHALANGES

5.1 Introduction

This chapter reports on the results of the analyses of the data gathered on modern bovid, cervid and tragulid carpals, tarsals and phalanges. Discriminant function analyses in SPSS Version 11.0 were used to investigate the reliability of the following thirteen elements as accurate habitat predictors of the individuals in this dataset: magnum, unciform, scaphoid, lunar, cuneiform, pisiform (carpals), talus, calcaneus, naviculo-cuboid, external and middle cuneiform (tarsals) and the proximal, intermediate and distal phalanges. The dataset and all procedures and methods followed herein are outlined in Chapter 3.

The format of this chapter is the same as the chapter which reported the results of the long bone analyses; the logged (i.e. non size corrected) data and size corrected data are presented separately. Examples of the results of "good" predictor elements and "bad" predictor elements are included in each section. A comparison of the logged and size corrected results is also provided. The chapter concludes with a summary of the selection of reliable habitat predictors and these elements are analysed in further palaeoenvironmental reconstructions of Laetoli in Chapter 6.

5.2 Utility of the carpals, tarsals and phalanges as accurate predictors of habitat

The goal of the analyses is to establish which elements are able to correctly predict the habitats of a percentage of the specimens which is above the baseline of accuracy determined in Section 3.6 in Chapter 3. For analyses with 2 – 7 predictor variables, the baseline is 36% and for analyses utilising 8 –15 predictor variables it is

41%. Appendix D summarises the total number of each species in each habitat category that was included in the separate analyses. Table 5.1 summarises the sample size of each habitat category in the analyses of the carpals, tarsals and phalanges. All of the complete elements were analysed. Unlike the long bone analyses, none of the predictor variables (i.e. measurements) failed the automatic tolerance test or were intentionally excluded in order to maintain appropriate sample sizes within each habitat category.

In the case of the phalanges, which are not always identified as forelimb and hindlimb elements, they were combined into analyses of the proximal, intermediate and distal phalanges. Their measurements had initially been taken on them separately, and the error testing was conducted on these data. However, all subsequent DFAs were conducted on combined datasets.

The resulting dataset for the proximal phalanges has a total of 303 specimens (Table 5.1), which is larger than the others with the exception of the dataset for the combined metapodial analysis (Table 4.1), which has 426 specimens. However, the combined intermediate phalanges dataset has fewer (181 in the logged and 180 in the size corrected analysis) and a total of only 129 distal phalanges were analysed. In the museum collections these elements were simply not present for the majority of the species studied. The reduced number of the distal phalanges in the dataset was problematic in regards to the montane species represented. There are six measurements taken on each distal phalanx, but there were fewer than six individuals in one of the categories. Rather than remove measurements from the analysis in order to make the DFA viable, the specimens were combined into one overall montane habitat category.

Table 5.1. Total number of specimens in each habitat group included in the tarsal, carpal and phalanges discriminant function analyses

Element	Total number	grassland/ tree-less	wooded-bushed grassland	light woodland-bushland	heavy woodland-bushland	forest	montane light cover	montane heavy cover
talus	**206**	13	47	49	32	28	17	20
calcaneus	**208**	15	46	49	28	28	17	25
naviculo-cuboid	**206**	16	48	47	31	27	17	20
external & middle cuneiform	**192**	16	46	43	27	25	17	18
magnum	**209**	15	47	51	29	30	16	21
unciform	**206**	14	47	50	28	30	16	21
scaphoid	**207**	16	48	49	30	29	16	19
lunar	**203**	16	48	47	30	28	16	18
cuneiform	**202**	15	48	46	29	29	16	19
pisiform	**170**	13	40	37	26	24	14	16
proximal phalanges	**303**	27	46	83	39	53	21	34
intermediate phalanges	**181/180***	26	32	52/51	26	23	10	12
distal phalanges	**129**	22	23	33	24	14	13 (combined montane)	

* Where the numbers differ between the logged and size corrected datasets, the logged total is given first and is separated from the size-corrected total by a slash

However, this reduced the number of habitat categories by one and, as reported in Section 3.6, it is not only the number of predictor variables but the number of grouping variables which affects the baseline of accuracy, as well. As the number of grouping variables increases, the baseline of accuracy decreases (see Figure 3.23a and 3.23b). Therefore, it can be assumed that the baseline of accuracy for an analysis utilising six grouping variables would lie between the baseline for analyses with seven and the analyses with four.

A more specific baseline for the distal phalanges analysis is not established here for two reasons. Firstly, in Section 3.6 in which the issue of the baseline of accuracy is addressed, an analysis of randomly assigned specimens with six predictor variables was not conducted. The distal phalanx is the only element on which six measurements are taken, but it was not used in that experiment because the sample size (129) was much lower than the others which had approximately 200 individuals in the dataset. The potential effect of sample size on the baseline was not investigated, although it is assumed that 129 is an adequate number for a DFA of this nature.

Secondly, it can be inferred that the correct percentages of classification from the analyses of both the logged and size corrected distal phalanges datasets are high enough to be above the baseline of accuracy for an analysis of six predictors and six grouping variables. Table 5.2 summarises the baselines for analyses including four and seven habitat categories and five and seven predictor variables. The number of both the grouping and predictor variables for the distal phalanges analyses lie within those ranges and therefore it can be assumed that the baseline would also fall within those ranges. Table 5.2 also provides the percentages of correct classification from the logged and size corrected distal phalanges analyses (the results of all of the analyses are reported below in sections 5.2.1 and 5.2.2).

Table 5.2. Summary of the percentages of correct classification of analyses of the distal phalanges and the baselines of accuracy for analyses with 5 or 7 predictor variables and 4 or 7 habitat categories.

Number of predictor variables	**Number of habitats**	**Baseline of accuracy**
5	4	51.40%
	7	35.10%
7	4	46.70%
	7	32.80%
Distal phalanges analyses		
6	6	*Logged data* 55.80%
		Size corrected data 50.40%

The correct percentages of classification from the distal phalanges analyses are above the baselines for all of the analyses regardless of how many predictors or grouping variables were used with one exception. The size corrected analysis of the distal phalanges yields a percentage of correct classification, 50.40%, which is one percent *below* the baseline for an analysis including five predictors and four grouping variables, 51.40%. However, since the distal phalanges have a greater number of predictors and grouping variables (six of each), and the baseline of accuracy decreases as the numbers of both variable types increases, it can be inferred that the actual baseline of accuracy for the distal phalanges analysis would be lower than 51.40%.

5.2.1 Results of the analyses of the logged data

A total of 13 analyses were conducted on the logged carpal, tarsal and phalanges data. They yielded overall percentages of correct classification between 33.8 % (scaphoid) and 57.1% (proximal phalanges). Table 5.3 displays the percentages of correct classification for each analysis conducted, as well as a breakdown of the percentage of individuals correctly identified within each habitat group in each analysis. The analyses are ordered according to their overall success rates and each cell in the table is colour coded according to how high or low the percentage of classification is.

Ten of the thirteen analyses had an overall percentage of correct classification above the baseline of accuracy. These analyses are identified with an asterisk in Table 5.3. These ten elements are considered reasonable to good predictors of habitat in which the discriminant function analyses were able to detect a link between the quantified skeletal morphologies and habitat group.

Table 5.3. Percentages of correct classification for the analyses of the logged data of the carpals, tarsals and phalanges

Element	# of meas	% correct overall	% correct grassland/ tree-less	% correct wooded-bushed grassland	% correct light woodland-bushland	% correct heavy woodland-bushland	% correct forest	% correct montane light cover	% correct montane heavy cover
proximal phalanges*	9	**57.1**	59.3	17.4	68.7	38.5	66.0	81.0	73.5
distal phalanges*	6	**55.8**	72.7	34.8	72.7	62.5	35.7	30.8 (montane combined)	
lunar*	9	**53.2**	43.8	72.9	57.4	33.3	46.4	62.5	33.3
intermediate phalanges*	9	**51.9**	65.4	50.0	50.0	50.0	30.4	90.0	50.0
magnum*	9	**51.2**	73.3	51.1	51.0	51.7	53.3	62.5	23.8
unciform*	9	**51.0**	50.0	59.6	42.0	46.4	36.7	56.3	76.2
naviculo-cuboid*	15	**47.1**	12.5	52.1	59.6	51.6	44.4	29.4	45.0
external & middle cuneiform*	8	**43.8**	0.0	60.9	53.5	40.7	56.0	35.3	11.1
cuneiform*	5	**40.6**	66.7	47.9	41.3	62.1	13.8	37.5	10.5
calcaneus	8	**40.4**	6.7	54.3	42.9	35.7	42.9	23.5	44.0
pisiform*	3	**39.4**	53.8	80.0	32.4	46.2	12.5	0.0	6.3
talus	9	**37.9**	7.7	29.8	57.1	34.4	42.9	23.5	40.0
scaphoid	4	**33.8**	37.5	37.5	61.2	0.0	10.3	56.3	21.1

cells are colour coded by percentage value: 0-30.0 = no colour; 30.1-40.0 = gray; 40.1-50.0 = pink; 50.1-60.0 = orange; 60.1-70.0 = yellow; 70.1-80.0 = green; 80.1-90.0 = blue; 90.1-100 = purple

* indicates that the percentage of correct classification is above the baseline of accuracy determined in Chapter 3.

The total relevant output of every analysis is not presented here but is included in Appendix E. The structure matrix, classification results table and a scatter plot of the first and second discriminant function are found therein. Here, in order to illustrate the differences between good and bad habitat predictors, only a select few analyses are discussed. All structure matrices presented display the pooled within-groups correlations between discriminating variables and standardised canonical discriminant functions.

The analysis of the proximal phalanges has the highest overall percentage of correct classification, 57.1% and as such can be considered the "best" habitat predictor in the logged analyses. Using nine measurements of 303 individuals, six discriminant functions (DFs) were calculated (Table 5.4), the first three of which account for the majority of the variation between the groups; the first DF accounts for 55.3%, the second DF for 26.9%, the third DF for 9.9%. The fourth, fifth and sixth DFs contribute very little to the model.

The scatter plot of the first two discriminant functions indicates that despite a success rate of 57.1%, there is some obvious overlap between the habitat clusters (Figure 5.1). Despite this overlap, some generalisations can be made in regards to the separation of the species. DF1 separates the majority of the grassland/tree-less and montane species from the others whilst DF2 distinguishes between the light and heavy cover montane species and also appears to separate a number of the forest individuals.

Table 5.5 presents the summary classification results of the logged proximal phalanges analysis. In addition to the overall success rate, the table provides details of the percentage of individuals in each habitat category that were both correctly and wrongly assigned. Success rates within each habitat group range from 17.4% in the wooded-bushed grassland category to 81.0% in montane light cover. Five of the

Table 5.4. Structure matrix from an analysis of the logged proximal phalanges data

Structure Matrix

	Function					
	1 55.3%	2 26.9%	3 9.9%	4 5.3%	5 2.5%	6 0.1%
LOGPA6	.242	.193	.095	.880	.152	-.189
LOGPA5B	.265	.290	.099	.880	.133	-.159
LOGPA1	.114	.444	.054	.858	.063	-.098
LOGPA4	.375	.184	.033	.857	.057	-.096
LOGPA5	.387	.202	.044	.855	.075	-.090
LOGPA3B	.266	.304	.030	.847	.199	-.108
LOGPA7	.363	.140	.150	.836	.145	-.062
LOGPA2	.377	.235	.106	.819	.117	-.139
LOGPA3	.391	.241	.097	.819	.140	-.120

The percentage of variance described by each function is provided. Measurement definitions can be found in Table 3.4.

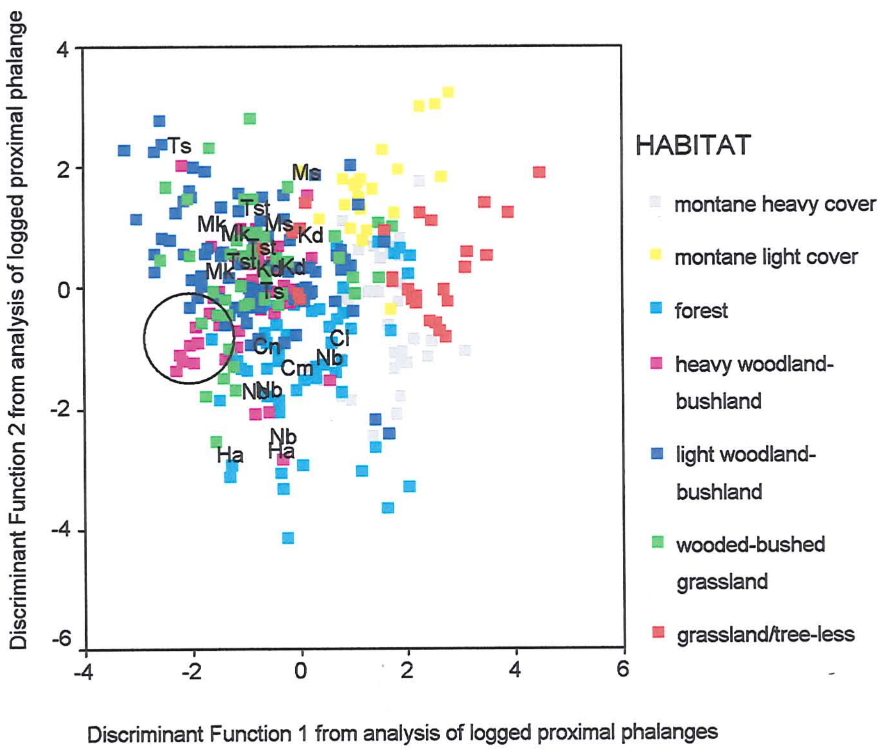


Figure 5.1. Scatter plot of the first and second discriminant functions from an analysis of the logged proximal phalanges data. Species codes are found in Table 3.1. The circled species consist of 12 *Tragelaphus scriptus*, 2 *Tragelaphus strespsiceros* and *Madoqua saltiana*, which were correctly predicted as heavy woodland-bushland species.

Table 5.5. Classification results from an analysis of the logged proximal phalanges data

Classification Results[a]

			Predicted Group Membership							
		HABITAT	grassland/ tree-less	wooded-bushed grassland	light woodland-bushland	heavy woodland-bushland	forest	montane light cover	montane heavy cover	Total
Original	Count	grassland/tree-less	16	2	4	0	0	3	2	27
		wooded-bushed grassland	2	8	27	6	1	0	2	46
		light woodland-bushland	2	12	57	5	4	3	0	83
		heavy woodland-bushland	0	3	15	15	5	1	0	39
		forest	5	0	6	3	35	0	4	53
		montane light cover	1	0	2	0	0	17	1	21
		montane heavy cover	4	0	1	0	2	2	25	34
	%	grassland/tree-less	59.3	7.4	14.8	.0	.0	11.1	7.4	100.0
		wooded-bushed grassland	4.3	17.4	58.7	13.0	2.2	.0	4.3	100.0
		light woodland-bushland	2.4	14.5	68.7	6.0	4.8	3.6	.0	100.0
		heavy woodland-bushland	.0	7.7	38.5	38.5	12.8	2.6	.0	100.0
		forest	9.4	.0	11.3	5.7	66.0	.0	7.5	100.0
		montane light cover	4.8	.0	9.5	.0	.0	81.0	4.8	100.0
		montane heavy cover	11.8	.0	2.9	.0	5.9	5.9	73.5	100.0

a. 57.1% of original grouped cases correctly classified.

habitat categories have a high rate of correct classification, while the wooded-bushed grassland and heavy woodland-bushland individuals were not successfully classified. The majority of the wooded-bushed grassland group (58.7%) were predicted to be light woodland-bushland species with the remaining misclassifications spread throughout the remaining habitats except for montane light cover. The heavy woodland-bushland species were correctly classified in 38.5% of the cases and the remaining were misclassified to all but the montane light cover and grassland/tree-less categories.

As it was explained in Chapter 4, it is common in DFAs to find that the majority of misclassifications are assigned to the group with the greatest dispersion and largest sample size. In this analysis that group is the light woodland-bushland category with 83 individuals, which is significantly greater than the next largest group, the forest category with 53 individuals. The classification results in Table 5.5 show that in this analysis, anywhere from 2.9 – 58.7% of the individuals in other habitat groups were wrongly predicted to be light woodland-bushland individuals. Furthermore, in each habitat category other than montane heavy cover, the largest percentage of misclassifications occurred in this category.

Although not displaying the highest rate of misclassification in this analysis, a look at the 24 wrongly predicted specimens within the sample of 39 heavy woodland-bushland individuals can illustrate several points about the nature of misclassifications. In analyses of accurate habitat predictors, misclassifications are focused on particular species and are often explained in terms of particularly unique morphologies or genetic relatedness between species which has a stronger signal than environmental adaptations. However, sampling may also create errors in classification.

Table 5.6 details the species composition and number of the misclassifications. They belong to all six of the heavy woodland-bushland species included in the analysis: *Kobus defassa, Madoqua kirki, Madoqua saltiana, Neotragus batesi, Tragelaphus scriptus* and *Tragelaphus strepsiceros*, although not in equal proportions. The misclassified individuals have also been identified on the scatter plot in Figure 5.1 by their assigned species code (species codes can be found in Table 3.1 in Chapter 3). The individuals which have been correctly identified, comprised of the remaining 12 *Tragelaphus scriptus*, 2 *Tragelphus strepsiceros* and 1 *Madoqua kirki,* have been circled in Figure 5.1.

The four *Neotragus batesi* individuals were all misclassified as forest species. This may reflect a number of factors. While this species prefers dense and low undergrowth, it often does visit forest environs. The individuals closest to *Neotragus batesi* in Figure 5.1 are clearly forest species including *Hyemoschus aquaticus* and the cephalophines (a few of which have been identified by their species codes for clarification), furthermore these forest species are small-bodied like *Neotragus batesi.* In addition to this, the cephalophines are, like *Neotragus*, members of the subfamily Antilopinae. The misclassification of this species can be explained in terms of environment, body size and phylogeny or a combination of these factors.

The misclassification of all but one of the *Madoqua* specimens may reflect a unique circumstance within either the Neotragini tribe (of which *Madoqua* and *Neotragus* are members) or the subfamily Antilopinae (of which *Madoqua*, *Neotragus* and *Cephalophus* are members). Although the two *Madoqua* species included in this analysis are small bodied like other members of the Neotragini tribe and indeed many other members of the genera and tribes comprising Antilopinae, they have a unique morphology that distinguishes them from both the cephalophines and neotragines.

Table 5.6. Misclassifications of heavy woodland-bushland individuals from a discriminant function analysis of the logged proximal phalanges data

Species	**Number misclassified**	**Total number in dataset**	**Predicted group**
Kobus defassa	6	6	wooded-bushed grassland (3) and light woodland-bushland (3)
Madoqua kirki	4	5	light woodland-bushland
Madoqua saltiana	2	2	light woodland-bushland (1) and montane light cover (1)
Neotragus batesi	4	4	forest
Tragelaphus scriptus	5	17	light woodland-bushland (4) and forest (1)
Tragelaphus strepsiceros	3	5	forest
TOTALS	24	39	3 wooded-bushed grassland 12 light woodland-bushland 8 forest 1 montane light cover

This may reflect the fact that as a genus, *Madoqua* is often found in more open environments than other neotragines. However, the two species here are unique within the genus in their preference for more closed habitats. Although every species of *Madoqua* requires cover for safety from predators, their overall environments tend to be more open than other species related at the subfamilial and tribal level. *Madoqua kirki* and *Madoqua saltiana* may possess morphologies which reflect the adaptations of the entire genus and not their unique habitat preferences *within* the genus.

The misclassification of the six *Kobus defassa* individuals into wooded-bushed grassland and light woodland-bushland may also be interpreted on the basis of phylogeny. *Kobus* is a water dependant genus often found in edaphic grasslands, floodplains and swamps near wooded areas. *Kobus defassa* is unique amongst the three *Kobus* species included in this analysis in that it prefers more heavily wooded areas. However, despite this habitat preference, it most likely retains the typical *Kobus* phalangeal morphology reflective of a locomotor pattern within a more open habitat.

Eight of 22 (36%) *Tragelaphus scriptus* and *Tragelaphus strepsiceros* individuals were misclassified, and the remainder were correct. The relatively high rate of success within this genus raises the issue of sampling. Just as a DFA is more likely to misclassify species into the group with the greatest dispersion and highest sample size, within each habitat group it takes the morphology represented by the greatest number of individuals as the defining morphology of the group itself. The sample size of the two tragelaphines was very great (22) compared to the other taxa and thus the highest rate of correct classification was likely to occur within this species.

Figure 5.1 clearly shows that the correctly identified individuals (which are circled), which are tragelaphines with the exception of one *Madoqua*, lie in a space distinct from and in between the forest group and a cluster of wooded-bushed grassland and light woodland-bushland individuals. This is a relatively tightly clustered group occupying a very small space; the misclassified individuals are clearly within the boundaries of their (mis)assigned groups and there is a great deal of overlap between the wooded-bushed grassland and light and heavy woodland-bushland categories.

In contrast to the results of the analyses of good predictors such as the proximal phalanges, an example of a bad predictor will be illustrated. The logged scaphoid analysis, with the lowest overall percentage of correct classification of 33.8%, is 2.2% below the 36% baseline of accuracy for DFAs with 2 – 7 predictor variables.

There are four measurements of the scaphoid, thus only four discriminant functions (DFs) were calculated (Table 5.7). The first DF accounts for 63.2%, the second DF for 24.6%, the third DF for 9.7% and the fourth for only 2.6% of the variation between the habitat groups. The scatter plot (Figure 5.2) of the two discriminant functions clearly displays that this element is not useful for discriminating on the basis of habitat. The individuals of each habitat type are scattered and habitat groups do not cluster together.

The summary classification results table (Table 5.8) further reveals that the scaphoid has not been effective in predicting the habitat affiliations of the species present in the dataset. The largest groups, which have a tendency to capture the majority of the incorrect classifications, are wooded-bushed grassland and light woodland-bushland with a total of 48 and 49 individuals, respectively. These groups do have a disproportionate number of individuals predicted to belong to them and the

Table 5.7. Structure matrix from an analysis of the logged scaphoid data

Structure Matrix

	Function			
	1 63.2%	2 24.6%	3 9.7%	4 2.6%
LOGCC4	.257	.914	.312	.026
LOGCC3	-.216	.842	.456	.194
LOGCC1	-.130	.838	.399	.350
LOGCC2	-.141	.792	.538	.250

The percentage of variance described by each function is provided. Measurement definitions can be found in Table 3.4.

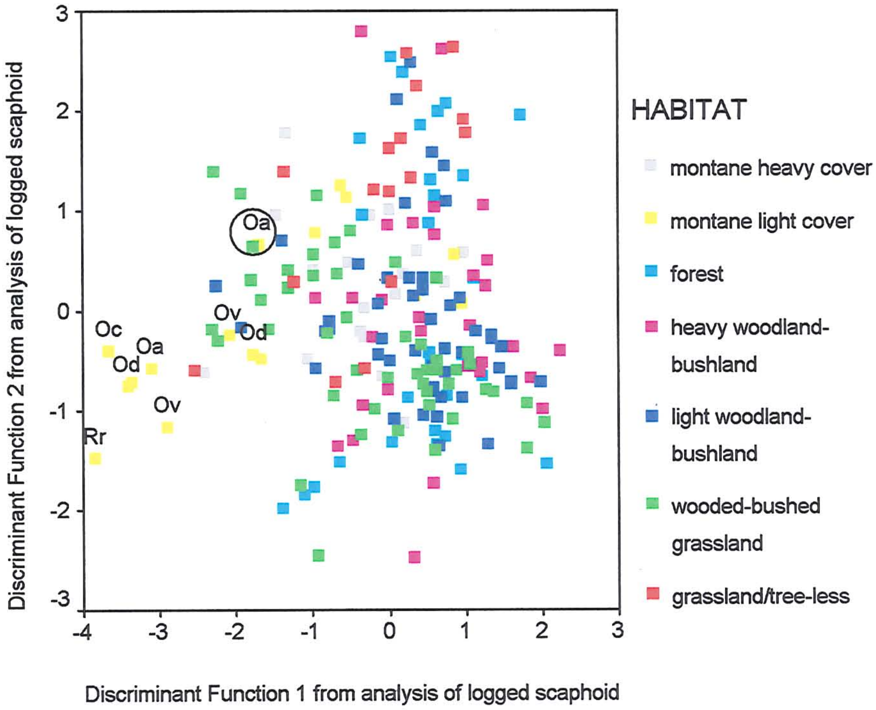


Figure 5.2. Scatter plot of the first and second discriminant functions from an analysis of the logged scaphoid data. The circled individual is the only misclassified *Ovis* specimen. Species codes can be found in Table 3.1.

Table 5.8. Classification results from an analysis of the logged scaphoid data

Classification Results[a]

			Predicted Group Membership							
		HABITAT	grassland/ tree-less	wooded-bushed grassland	light woodland-bushland	heavy woodland-bushland	forest	montane light cover	montane heavy cover	Total
Original	Count	grassland/tree-less	6	2	4	0	1	1	2	16
		wooded-bushed grassland	0	18	16	4	1	7	2	48
		light woodland-bushland	2	10	30	1	4	2	0	49
		heavy woodland-bushland	2	7	19	0	2	0	0	30
		forest	5	6	14	0	3	0	1	29
		montane light cover	1	1	3	0	1	9	1	16
		montane heavy cover	0	7	7	0	0	1	4	19
	%	grassland/tree-less	37.5	12.5	25.0	.0	6.3	6.3	12.5	100.0
		wooded-bushed grassland	.0	37.5	33.3	8.3	2.1	14.6	4.2	100.0
		light woodland-bushland	4.1	20.4	61.2	2.0	8.2	4.1	.0	100.0
		heavy woodland-bushland	6.7	23.3	63.3	.0	6.7	.0	.0	100.0
		forest	17.2	20.7	48.3	.0	10.3	.0	3.4	100.0
		montane light cover	6.3	6.3	18.8	.0	6.3	56.3	6.3	100.0
		montane heavy cover	.0	36.8	36.8	.0	.0	5.3	21.1	100.0

a. 33.8% of original grouped cases correctly classified.

high number of correct classifications within the light woodland-bushland group (61.2%) should not be interpreted as biologically meaningful. The only potentially unique morphology that this analysis has identified is found within the montane light cover category in which a total of nine individuals, or 56.3%, have been correctly identified. An examination of the species identifications of these individuals, which are labelled in Figure 5.2, indicates that they are all *Ovis* and one *Rupicapra rupicapra*. Only one *Ovis*, which is circled in Figure 5.2, is misclassified. This consistency in classification within this group alone indicates that this genus (and potentially *Rupicapra*) has a unique scaphoid morphology that distinguishes it from the remaining species in the analyses.

The analysis of the logged scaphoid data does not appear to have any biological basis and, in contrast to the proximal phalanx, is not a good habitat predictor. Bad predictors from the logged analyses of the carpals, tarsals and phalanges, such as the scaphoid reported above, or those which fall under the baseline of accuracy, will not be considered in the palaeoenvironmental reconstruction of Laetoli.

5.2.2 Results of the analyses of the size corrected data

Discriminant function analyses of the size corrected data were conducted in order to ascertain if body size effects the accuracy of the habitat predictions based on analyses of the elements and measurements utilised in this study. The good habitat predictors determined by this set of analyses will not used in the analyses of the Laetoli fossil material because it cannot be size corrected with the method followed herein. Rather, these analyses and their relative success rates are compared to the analyses of the logged data from the same elements. The total relevant output of every analysis, including the structure matrix, classification results table and a scatter plot of the first and second discriminant function is contained in Appendix E.

A total of 13 analyses were conducted on the size corrected data from the carpals, tarsals and phalanges. They yielded overall percentages of correct classification between 33.8 % (scaphoid) and 54.5% (proximal phalanges). Table 5.9 displays the percentages of correct classification for each analysis conducted, as well as a breakdown of the percentage of individuals correctly identified within each habitat group in each analysis. The analyses are organised according to their overall success rates and each cell in the table is colour coded according to the percentage of classification, in increments of ten percent. Nine of the fourteen analyses had an overall percentage of correct classification above the baseline of accuracy. These analyses are labelled with an asterisk in Table 5.9. These nine elements are considered reasonable to good predictors of habitat.

The proximal phalanx is the best predictor with the highest overall percentage of correct classification, 54.5%. Analysing nine measurements, six discriminant functions (DFs) were calculated (Table 5.10) and the first three account for the majority (94.2%) of the variance between the habitat categories: DF1 for 51.4%, DF2 for 27.5%, DF3 for 15.3%. The remaining three only account for a collective total of 5.8% of the variance.

A scatter plot (Figure 5.3) of the first and second discriminant functions displays some overlap between the habitat groups. However, it can be said that generally DF 1 separates the montane and grassland/tree-less species from the others, with the exception of a small number of overlapping forest individuals which include five of the ten tragulid specimens in the dataset (*Hyemoschus aquaticus* – Ha on the scatter plot) and the only two *Syncerus caffer* specimens included (Sc on the plot). Closer inspection of the data from the tragulid individuals reveals that *Hyemoshcus aquaticus* possesses proximal phalanges that differ greatly between the fore and

Table 5.9. Percentages of correct classification for the analyses of the size corrected data of the carpals, tarsals and phalanges

Element	# of meas	% correct overall	% correct grassland/ tree-less	% correct wooded-bushed grassland	% correct light woodland-bushland	% correct heavy woodland-bushland	% correct forest	% correct montane light cover	% correct montane heavy cover
proximal phalanges*	9	**54.5**	37.0	26.1	71.1	43.6	56.6	66.7	67.6
lunar*	9	**52.2**	18.8	72.9	55.3	36.7	50.0	56.3	44.4
intermediate phalanges*	9	**51.7**	53.8	59.4	54.9	50.0	21.7	70.0	58.3
magnum*	9	**50.7**	66.7	68.1	43.1	55.2	50.0	50.0	14.3
distal phalanges*	6	**50.4**	45.5	26.1	84.8	45.8	42.9	30.8 (montane combined)	
unciform*	9	**49.5**	7.1	68.1	42.0	50.0	43.3	43.8	66.7
naviculo-cuboid*	15	**46.6**	12.5	58.3	53.2	61.3	33.3	23.5	45.0
pisiform*	3	**44.1**	15.4	82.5	40.5	50.0	37.5	7.1	12.5
cuneiform*	5	**41.6**	6.7	58.3	39.1	62.1	27.6	25.0	36.8
external & middle cuneiform	8	**39.1**	6.3	65.2	48.8	33.3	32.0	29.4	5.6
talus	9	**37.9**	15.4	51.1	57.1	34.4	28.6	17.6	10.0
calcaneus	8	**35.6**	0.0	60.9	42.9	42.9	14.3	29.4	16.0
scaphoid	4	**33.8**	0.0	39.6	53.1	10.0	34.5	56.3	15.8

cells are colour coded by percentage value: 0-30.0 = no colour; 30.1-40.0 = gray; 40.1-50.0 = pink; 50.1-60.0 = orange; 60.1-70.0 = yellow; 70.1-80.0 = green; 80.1-90.0 = blue; 90.1-100 = purple

* indicates that the percentage of correct classification is above the baseline of accuracy determined in Chapter 3.

Table 5.10. Structure matrix from an analysis of the size corrected proximal phalanges data

Structure Matrix

	Function					
	1 51.4%	2 27.5%	3 15.3%	4 3.8%	5 1.9%	6 0.1%
RESPA1	.559	.666	.209	.286	.138	.171
RESPA3B	.197	.617	.433	.037	.435	.141
RESPA3	-.277	.470	.297	.312	.388	.130
RESPA2	-.231	.438	.292	.389	.358	.050
RESPA4	-.254	.301	.599	.453	.138	.217
RESPA5	-.281	.359	.532	.429	.225	.266
RESPA5B	.211	.533	.321	.379	.617	.169
RESPA6	.255	.210	.497	.271	.543	-.131
RESPA7	-.199	.043	.284	.302	.404	.282

The percentage of variance described by each function is provided. Definitions of the measurements can be found in Table 3.4.

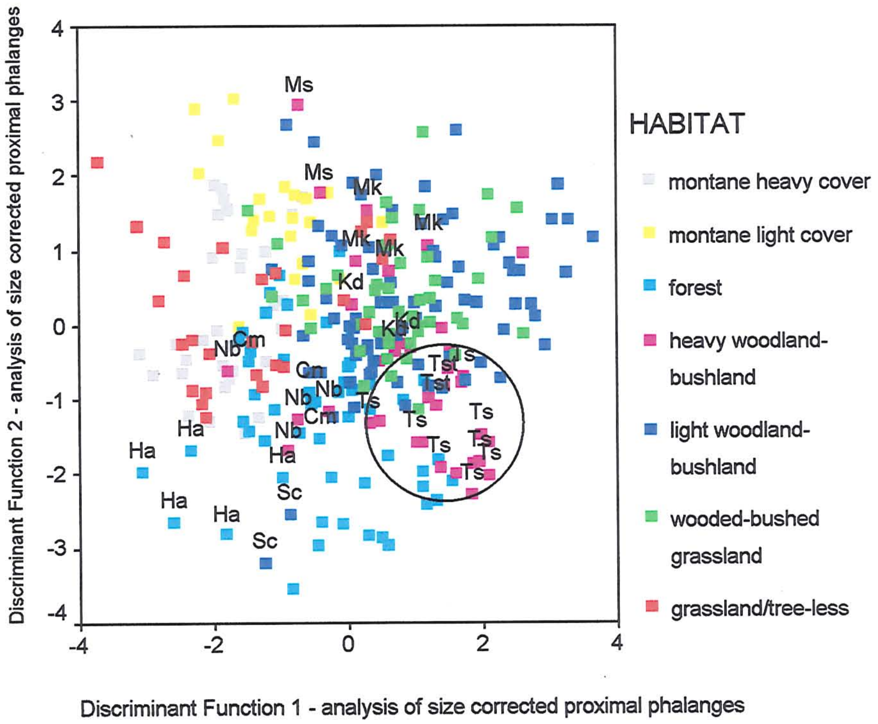


Figure 5.3. Scatter plot of the first and second discriminant functions from an analysis of the size corrected proximal phalanges. The circled individuals are correctly identified heavy woodland-bushland species. Species codes are found in Table 3.1.

hindlimb and the labelled specimens, which load the same on DF 1 as the montane and grassland/tree-less species, are from the forelimb. DF 2 separates both the forest species and a group of heavy woodland-bushland *Tragelaphus scriptus* from the other habitat groups.

Four of the habitat groups have a high rate of correct classification (Table 5.11) and are above 56%: light woodland-bushland (71.1%), forest (56.6%), montane light cover (66.7%) and montane heavy cover (67.6%). The remaining three habitat categories are much less successful: grassland/tree-less (37.0%), wooded-bushed grassland (26.1%) and heavy woodland-bushland (43.6%) and the majority of their members were misclassified.

The misclassifications within the heavy woodland-bushland group are consistent with the logged analysis reported above. The classification results in Table 5.11 indicate that although 17 individuals (43.6%) were correctly assigned, an almost equal number was assigned to light woodland-bushland (n=16, 41.0%) and the remaining individuals to forest (n=5, 12.8%) and montane light cover (n=1, 2.6%). The incorrect predictions, which are detailed in Table 5.12, occur within all of the species in that group but again are rare in the cases of *Tragelaphus scriptus* and *Tragelaphus strepsiceros* where only five of 22 tragelaphine individuals were misclassified. The correctly classified tragelaphines have been identified by their species code (Ts and Tst) and circled on the scatter plot of the first two DFs (Figure 5.3).

The correctly identified tragelaphines occupy a space between the light woodland-bushland and forest individuals, which is where they would be expected to fall on a continuum of vegetation cover in the habitat types. However, there is a great deal of overlap between these habitat clusters and the other heavy woodland-bushland

Table 5.11. Classification results from an analysis of the size corrected proximal phalanges data

Classification Results[a]

			Predicted Group Membership							
		HABITAT	grassland/ tree-less	wooded-bushed grassland	light woodland-bushland	heavy woodland-bushland	forest	montane light cover	montane heavy cover	Total
Original	Count	grassland/tree-less	10	5	1	0	4	4	3	27
		wooded-bushed grassland	1	12	31	0	0	0	2	46
		light woodland-bushland	2	9	59	3	8	2	0	83
		heavy woodland-bushland	0	0	16	17	5	1	0	39
		forest	4	0	5	8	30	0	6	53
		montane light cover	2	0	4	0	0	14	1	21
		montane heavy cover	3	0	2	0	4	2	23	34
	%	grassland/tree-less	37.0	18.5	3.7	.0	14.8	14.8	11.1	100.0
		wooded-bushed grassland	2.2	26.1	67.4	.0	.0	.0	4.3	100.0
		light woodland-bushland	2.4	10.8	71.1	3.6	9.6	2.4	.0	100.0
		heavy woodland-bushland	.0	.0	41.0	43.6	12.8	2.6	.0	100.0
		forest	7.5	.0	9.4	15.1	56.6	.0	11.3	100.0
		montane light cover	9.5	.0	19.0	.0	.0	66.7	4.8	100.0
		montane heavy cover	8.8	.0	5.9	.0	11.8	5.9	67.6	100.0

a. 54.5% of original grouped cases correctly classified.

Table 5.12. Misclassifications of heavy woodland-bushland individuals from a discriminant function analysis of the size corrected proximal phalanges data

Species	**Number misclassified**	**Total number in dataset**	**Predicted group**
Kobus defassa	6	6	light woodland-bushland
Madoqua kirki	5	5	light woodland-bushland
Madoqua saltiana	2	2	light woodland-bushland (1) and montane light cover (1)
Neotragus batesi	4	4	forest
Tragelaphus scriptus	3	17	light woodland-bushland (2) and forest (1)
Tragelaphus strepsiceros	2	5	light woodland-bushland
TOTALS	22	39	16 light woodland-bushland 5 forest 1 montane light cover

species in the dataset are incorrectly classified in every case. Again this phenomenon can also be explained by phylogenetic relationships and sampling. The greatest number of species pre-assigned to this habitat are the tragelaphines and as a result their phalangeal morphology defines the morphology for all heavy woodland-bushland individuals used in the analysis and on which the predictions are based. However, given their position between the light woodland-bushland and forest individuals, it may be that only these species represent a true heavy woodland-bushland adapted morphology and that the others have not yet evolved or not needed to evolve similar proximal phalanges.

The four *Neotragus batesi* individuals are found to cluster with the forest species, a possible reflection of their preference for sometimes visiting forest environments, but more likely related to their subfamilial relationship with forest dwelling cephalophines (three of which are labelled on Figure 5.3 with their species code). The seven misclassified *Madoqua* specimens, all but one of which were predicted to belong to the light woodland-bushland category, may reflect the fact that they possess a morphology similar to other member of their genus which inhabit more open environments. Likewise, there is a similar situation with the six misclassified *Kobus defassa* individuals. On Figure 5.3 they cluster with a number of light woodland-bushland and wooded-bushed grassland species (although they have been predicted to be light woodland-bushland species on account of their slightly closer proximity to the centroid of that habitat group). They apparently retain a morphology similar to others in the genus, which do inhabit these more open environments.

In contrast to the proximal phalanges, the analysis of the scaphoid yielded very different results. This analysis of the scaphoid data resulted in the lowest overall percentage of classification of the size corrected analyses, as it did in the logged analyses. At 33.8%, it is 2.2% lower than the baseline of accuracy for an analysis with two predictor variables. Four discriminant functions (DF) were calculated, the first two of which accounted for 66.9% and 28.0% of the variance between the habitat groups, respectively (Table 5.13). Together, DF3 and DF4 accounted for only 5.1% of the variance.

The individuals in the dataset do not possess distinctive scaphoids. The element is not an accurate habitat predictor and a scatter plot (Figure 5.4) of the two DFs illustrates this. There are no visibly isolated habitat clusters, with the one exception of montane light cover. A look at the classification results in Table 5.14 confirms that this element is a bad predictor overall, but that this particular habitat group has a relatively higher percentage of correct classification (56.3%). The identified individuals on Figure 5.4 were correctly classified as montane light cover and they belong to the genus *Ovis* and the one *Rupicapra rupicapra* specimen in this analysis. The consistency of classification infers that *Ovis* (and potentially *Rupicapra*) possesses a unique scaphoid morphology that is unlike the other species in the dataset.

The seemingly high percentage of correct classification within the light woodland-bushland category (53.1%) can not be concluded to relate to a unique morphology in that group. As one of the two groups with the largest sample sizes, wooded-bushed grassland (n=48) and light woodland-bushland (n=49), it is not surprising that it had a coincidentally high success rate. These two groups contain a very high proportion of the misclassifications overall and can not be said to relate to a unique morphology.

Table 5.13. Structure matrix from an analysis of the size corrected scaphoid data

Structure Matrix

	Function			
	1 66.9%	2 28.0%	3 4.0%	4 1.1%
RESCC2	-.269	.938	.085	.201
RESCC3	-.551	.580	.154	.580
RESCC1	-.175	.593	.760	.200
RESCC4	.629	.293	.114	.711

The percentage of variance described by each function is provided. Measurement definitions can be found in Table 3.4.

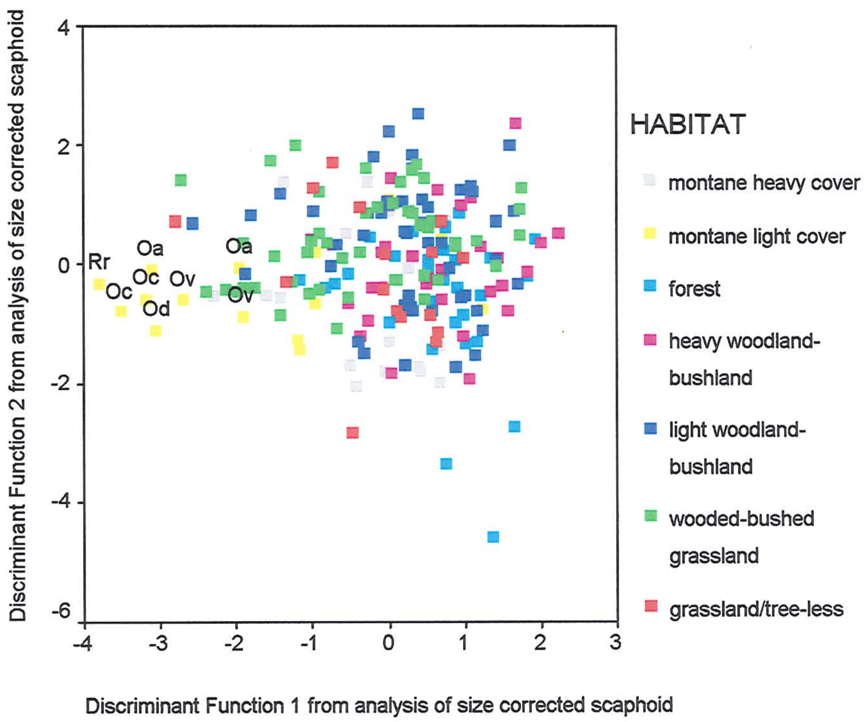


Figure 5.4. Scatter plot of the first and second discriminant functions from an analysis of the size corrected scaphoid data. Species codes can be found in Table 3.1.

Table 5.14. Classification results from an analysis of the size corrected scaphoid data

Classification Results[a]

			Predicted Group Membership							
		HABITAT	grassland/ tree-less	wooded-bushed grassland	light woodland-bushland	heavy woodland-bushland	forest	montane light cover	montane heavy cover	Total
Original	Count	grassland/tree-less	0	5	4	0	5	1	1	16
		wooded-bushed grassland	0	19	20	1	0	7	1	48
		light woodland-bushland	0	11	26	1	9	2	0	49
		heavy woodland-bushland	0	6	13	3	7	0	1	30
		forest	0	5	12	2	10	0	0	29
		montane light cover	0	5	1	0	1	9	0	16
		montane heavy cover	0	6	3	0	6	1	3	19
	%	grassland/tree-less	.0	31.3	25.0	.0	31.3	6.3	6.3	100.0
		wooded-bushed grassland	.0	39.6	41.7	2.1	.0	14.6	2.1	100.0
		light woodland-bushland	.0	22.4	53.1	2.0	18.4	4.1	.0	100.0
		heavy woodland-bushland	.0	20.0	43.3	10.0	23.3	.0	3.3	100.0
		forest	.0	17.2	41.4	6.9	34.5	.0	.0	100.0
		montane light cover	.0	31.3	6.3	.0	6.3	56.3	.0	100.0
		montane heavy cover	.0	31.6	15.8	.0	31.6	5.3	15.8	100.0

a. 33.8% of original grouped cases correctly classified.

5.2.3 Comparison of the logged and size corrected analyses

Ten logged and nine size corrected analyses had overall percentages of correct classification above the baseline of accuracy. The elements used in these analyses are considered reasonable to good habitat predictors. Table 5.15 lists these and compares their relative success rates.

Nine elements were good predictors in both sets of analyses and had very similar overall percentages of classification. Amongst them, the greatest difference between the logged and size corrected results occurred between the analyses of the distal phalanges, which successfully predicted the habitat of 55.8% of the individuals in the logged analysis and 50.4% in the size corrected analysis, which is a difference of only 5.4%.

The external and middle cuneiform was a good predictor in the logged analysis and not in the size corrected. As a good predictor it only fell 2.8% above the 41% baseline of accuracy, with 43.8% of the individuals correctly classified. In the size corrected analysis it correctly predicted the habitats of 39.1% of the individuals, which is only 1.9% below the cut-off. It does not appear that body size has significantly affected the success rates of the habitat predictions in the discriminant function analyses of the carpals, tarsals or phalanges.

This result is consistent with the long bone analyses reported in Chapter 4. When the analyses of the elements and their constituent epiphyseal ends were conducted, there was also little difference between the results of the analyses of the logged and size corrected data. The greatest difference between the analyses of the good predictor elements was found with the tibia. The logged analysis yielded a correct percentage of classification of 42.9% and an analysis of the size corrected data

Table 5.15. Good predictors in the logged and size corrected discriminant function analyses of the carpals, tarsals and phalanges

Element	**Percentage of correct classification**	
	logged	***size corrected***
Proximal phalanges	57.1	54.5
Distal phalanges	55.8	50.4
Lunar	53.2	52.2
Intermediate phalanges	51.9	51.7
Magnum	51.2	50.7
Unciform	51.0	49.5
Naviculo-cuboid	47.1	46.6
External and middle cuneiform	43.8	-
Cuneiform	40.6	41.6
Pisiform	39.4	44.1

correctly predicted the habitat of 47.6%. This is a difference of only 4.7% between the two success rates.

It appears that the wide range of body sizes displayed by the species included in the datasets analysed in this study does not affect the habitat predictions that are made possible by the good predictor elements. The logged data must be used from this point onwards in the analyses which include the Laetoli fossils, because this material can not be size corrected using the technique that was followed herein. However, in light of the comparison of the results of the analyses of the logged and size corrected data of the extant species, which do not differ significantly, body size should not be a concern in interpretation of the results of the fossil analyses.

5.3 Comparison of the results with previous studies

The talus has recently been analysed in an ecomorphological context (DeGusta & Vrba, 2003), but the variables, dataset and habitat types included in that study differ significantly to those considered here. DeGusta and Vrba (2003) measured a sample of 218 African bovids and assigned them according to a traditional habitat classification scheme of four types: forest, heavy cover, light cover and open environments. Their discriminant function analysis was conducted on non-size corrected and non log-transformed data using eight straight measurements and one ratio (intermediate length/intermediate width). Other measurements were initially taken but not reported or analysed, as their inclusion resulted in lower correct percentages of classification. They empirically selected variables out of their analyses by experimenting with various combinations of them, rather than by using the stepwise method previously employed by others (e.g. Plummer & Bishop, 1994; Kappelman *et al*, 1997).

Table 5.16 compares the overall success rates of the talus analyses conducted by DeGusta and Vrba (2003) and those conducted here and it is clear that DeGusta and Vrba (2003) have much stronger results with a percentage of correct classification 29.1% better than both the logged and size corrected analysis in this project. In fact, the talus analyses were both below the baseline of accuracy of 41% for analyses with 8 – 15 predictor variables and seven habitat groups and thus are not considered good habitat predictors. The reasons for this extreme discrepancy may relate to one or a combination of the following factors: the measurements used, the habitat scheme employed or the composition of the dataset.

Table 5.17 lists the measurements used in both studies which each included nine variables, although only three of which were in common: the greatest length (which is a measure of the length of the lateral side), the width of the distal articular surface and the shortest length. The eight straight (i.e. non-ratio) measurements used in DeGusta & Vrba's (2003) study appear to contrast the differing dimensions that can be observed between the medial and lateral halves of the talus and it may be in these types of differences where adaptations to locomotion within habitats of various amounts of cover occur. Indeed, they were able to graphically depict the general morphotype for each of their habitat categories and it is apparent that significant differences do lie in these dimensions.

Using four habitats, as DeGusta and Vrba (2003) do, rather than seven which are used in this project, has two effects on the outcome of the analysis. Firstly it increases the baseline of accuracy. Table 3.12 in Chapter 3 lists the maximum percentage of correct classification yielded by a trial of eight analyses of varying amounts of predictor variables and contrasts those figures for analyses considering schemes of both four and seven grouping variables. The maximum percentage (which

Table 5.16. Results of DuGusta & Vrba's (2003) study of the talus compared to the results in this study.

Element	Percentage of correct classification		
	DeGusta & Vrba (2003)	***Kovarovic (2004) logged***	***Kovarovic (2004) size corrected***
Talus	67.0	37.9	37.9

Results reported as an overall percentage of correct classification.

Table 5.17. Comparison of the measurements included in the analyses of the talus conducted by DeGusta & Vrba (2003) and Kovarovic (2004)

Measurement of the talus	Kovarovic (2004)	DeGusta & Vrba (2003)
greatest length	✓	✓
measure of the distance from the distal base to the most inferior aspect of the medial articular surface	✓	
measure of the distance from the talar notch to the talar head, taken in medial view	✓	
width of distal articular surface	✓	✓
width of the proximal articular surface	✓	
shortest length of the talus	✓	✓
measure of the distance from the mid-point of the trochlear pit to the end of the proximal articular surface	✓	
width of the inferior articular surface	✓	
length of the inferior articular surface	✓	
medial length		✓
distal thickness		✓
intermediate thickness		✓
proximal thickness		✓
intermediate width		✓
intermediate length/intermediate width (ratio)		✓

A check mark indicates that the measurement was included in the analysis was considered here to be the baseline of accuracy) for an analysis of nine predictor variables (like the talus analyses reported here and in DeGusta & Vrba, 2003) and seven grouping variables is 37.9% but is much higher, at 48.9%, with four grouping variables. However, DeGusta and Vrba's (2003) results are still 18.1% above this baseline and therefore it can be concluded that the analysis has distinguished some ecological meaning in the morphologies that relate to the four habitat categories.

However, and secondly, using only four habitat categories has the effect of broadening and homogenising the definitions of the morphologies that relate to each habitat group and makes it more likely that there will be a higher rate of success. So long as large sample sizes of potentially unique morphologies within each group are used, they contribute equally to the predictive model and can be included in the dataset as significant contributors. If their numbers were very small in relation to the overall number of individuals possessing more generalised morphologies within each group, they would act as outliers and most likely be misclassified.

Finally, the dataset composition of DeGusta & Vrba's (2003) study was comprised solely of African species. It may be that the addition of the montane species lowered the overall success rate, as they may not possess a particularly unique morphology but one which resembles that of species in different habitats. It is likely that the talus is less sensitive to a greater partitioning of habitat types and that it is only a good predictor when fewer habitat types are used and taxa found in non-African habitat are excluded.

5.1 Summary of the carpal, tarsal and phalanges analyses

A total of 19 of the 26 carpal, tarsal and phalanges analyses (73.1%), successfully predicted the correct habitat of a percentage of the individuals which fell above the baseline of accuracy established in Section 3.6; 36% for analyses with 2 – 7 predictor variables and 41% for analyses with 8 – 15 predictor variables. Nine elements were good predictors in both the logged and size corrected analyses (Table 5.15). One element, the external and middle cuneiform, was a good predictor when only the logged data was analysed. Its percentage of correct classification, 39.1%, fell just below the baseline of accuracy of 41% when the size corrected data was used.

This situation also occurred in the long bone analyses with the proximal tibia, proximal humerus and proximal metatarsal. In two cases they were good predictors only when the logged data were analysed (proximal tibia and proximal humerus) and in one instance (proximal metatarsal) only when the size corrected data were used. In addition to the external and middle cuneiform, these four elements, whose percentages of classification straddle the baseline of accuracy depending on which dataset is analysed, again raise the question of how "good" a "good" predictor truly is.

The discussion will not be repeated here (it can be found in section 4.4). In summary, a good predictor is one with both a high rate of overall correct classification and high rates of classification *within* each of the seven habitat categories. Misclassifications that occur are restricted to a few species or anomalous individuals and can be interpreted on the basis of idiosyncratic morphologies that do not relate to their assigned known habitat type but do relate to either specific ecological conditions or evolutionary relationships that can not be captured or explained by such a broad division of habitat types. In some cases, such as the proximal phalanges discussed above in section 5.2.1 and section 5.2.2, where the predictor is above the baseline of accuracy but the percentage of classification is in an "adequate" range (generally in the low to mid-fifties), sampling (in terms of both species composition and sample size) may explain certain misclassifications.

More importantly, reliable results are also associated with high probabilities, or confidence values, of correct habitat prediction. The probability that each specimen in the analysis belongs to each of the habitat groups is automatically calculated, a statistic that is based on the individuals' proximity to the centroids for each of the habitat groups. The highest probability determines the habitat prediction.

Confidence values are considered in the analyses of the Laetoli material and in the evaluation of the results in Chapter 6. Because misclassified individuals often have very low probabilities associated with their habitat predictions, and correctly predicted individuals have higher confidence values, this statistic needs to be considered when ungrouped cases - such as the Laetoli fossils - are entered into an analysis in order to determine their most likely habitat affiliations. More confidence can be placed in habitat predictions with associated high probabilities.

Size corrected analyses will not be used with the fossil material and thus only good predictors from the logged carpal, tarsal and phalanges analyses will be forwarded to the analyses of the Laetoli collection in addition to those long bones and epiphyseal ends reported in Chapter 4. Table 5.18 lists the carpals, tarsals and phalanges that will be used to reconstruct the habitat of Laetoli.

Table 5.18. Carpals, tarsals and phalanges used in Laetoli analyses

Element
Proximal phalanges
Distal phalanges
Lunar
Intermediate phalanges
Magnum
Unciform
Naviculo-cuboid
External and middle cuneiform
Cuneiform
Pisiform

6 Results of the Analyses of the Laetoli Data: Upper Laetolil and Upper Ndolanya Beds

6.1 Introduction

This chapter reports on the results of the analyses of the data gathered on the specimens from the Upper Laetolil Beds (3.5 – 4.3 mya) and Upper Ndolanya Beds (2.4 – 3.5 mya) at Laetoli, Tanzania. Although every available fossil was initially measured (see Appendix B and Table 3.2 for a summary), only the twenty-two elements that yielded percentages of correct classification over the baseline of accuracy determined in Chapter 3 when the modern data was analysed were chosen for use in the final fossil analyses (see Table 4.21 and Table 5.18). However, there were no complete tibiae, complete femora or proximal femora available in the Laetoli collection studied and thus only nineteen elements were analysed. They are listed alphabetically in Table 6.1.

All data were log-transformed and there were no analyses conducted on size corrected data. Using the method of size correction employed with the modern data, the fossil material could not be corrected because the species average body weights are unknown for these individuals. For each element, two separate analyses could be conducted; one on the data from the fossils derived from the Laetolil Beds and a second using the Ndolanya Bed fossils.

A total of 310 specimens from the Laetolil Beds were available while the Ndolanya Beds presented only 170. This is unsurprising considering that the Ndolanya Beds are exposed at fewer localities and the fossils deriving from them are often more fragmentary (Leakey and Harris, 1987). Thus, Ndolanya fossils are generally less well represented in the collection, regardless of the taxa. Furthermore,

Table 6.1. Alphabetical list of Laetoli fossil elements that were analysed

Element
Cuneiform
Distal femur
Distal humerus
Distal metapodial
Distal phalanges
External and middle cuneiform
Humerus
Intermediate phalanges
Lunar
Magnum
Metatarsal
Naviculo-cuboid
Proximal humerus
Proximal phalanges
Proximal radius
Proximal tibia
Radius
Pisiform
Unciform

not all elements were available from both beds. Sixteen analyses were conducted on the material from the Laetolil Beds and eighteen on Ndolanya material. A summary of the number of the Laetoli specimens from each bed compared to the number of modern specimens that were included in each analysis is presented in Table 6.2. In total, thirty-four discriminant function analyses were conducted in SPSS Version 11.0.

In contrast to the DFAs on modern data, which investigated whether a set of predictor variables (i.e. measurements) could identify the affiliation of each individual to its known group (i.e. habitat) in Chapter 4 and Chapter 5, the second function of a DFA has been used to predict the group membership of the fossil individuals of unknown affiliation. All fossils entered the analysis as "ungrouped cases" alongside the modern specimens of known habitat types. The analysis calculates the probability that each ungrouped individual belongs to each of the seven habitat groups and assigns them to the habitat with the highest associated probability in the same way that the "known group" (i.e. modern) individuals are classified. The habitat predictions of the ungrouped cases are reported in the classification results table as a percentage of the total number of cases. Essentially, the addition of the Laetoli material did not change the original analyses in which only the modern material was considered. The calculation of the discriminant functions was still based entirely on the modern data; the only difference to the output is the addition of the habitat prediction of the fossils based on the original discriminant functions. For this reason the total output from these analyses is not included as an appendix as it was for the analyses of the modern data (Appendix E).

Table 6.2. Laetoli dataset summary

Element	Percentage of correct classification	Number of modern specimens	Number from the Laetolil beds	Number from the Ndolanya Beds
Humerus	68.0	203	0	1
Metatarsal	66.5	215	2	0
Radius	58.0	207	1	1
Proximal phalanges	57.1	303	74	9
Distal phalanges	55.8	129	30	4
Lunar	53.2	203	6	3
Intermediate phalanges	51.9	181	62	18
Magnum	51.2	209	15	4
Unciform	51.0	206	5	4
Distal humerus	48.8	203	20	24
Distal metapodial	47.2	426	35	27
Naviculo-cuboid	47.1	206	16	5
External and middle cuneiform	43.8	192	5	1
Distal femur	42.4	210	8	3
Proximal radius	41.1	209	22	49
Cuneiform	40.6	202	8	9
Pisiform	39.4	170	0	1
Proximal tibia	37.6	213	1	6
Proximal humerus	37.4	203	0	1
TOTAL			**310** *(16 analyses)*	**170** *(18 analyses)*

The percentage of correct classification and the number of modern specimens refer to the analyses of the modern data reported in Chapters 4 and 5.

6.2 Results of the analyses of the Laetoli fossils

The first consideration in any DFA is the overall percentage of correct classification. While all of the analyses reported in this chapter have an overall percentage of correct classification over the established baseline of accuracy, they differ in their success rates - from the humerus analysis (68.0%) to the proximal humerus (37.4%). At what point should one begin to place less confidence in the results? For convenience, the results will be divided into two sets: those from analyses which correctly classify more than half of the modern individuals, i.e. those which have a percentage of correct classification over 50.0%, and those which classify less than half and yielded a percentage of correct classification under 50.0%.

Bearing this is mind, the results of these DFAs can be interpreted in a number of ways. The Laetoli habitat predictions are summarised in Table 6.3 (Laetolil Beds) and Table 6.4 (Ndolanya Beds), which tabulate the raw number and percentage of specimens in each analysis that are predicted to belong to each habitat group for both the Laetolil and Ndolanya Beds. The predictions are highlighted in yellow. In the Laetolil Beds analyses (Table 6.3) the best predictor with the highest number of specimens is the proximal phalanges, which yielded a success rate of 57.1%. A total of 74 fossil proximal phalanges were analysed and the majority were assigned firstly to the heavy woodland-bushland category (44.6%) and a lesser component in both the light woodland-bushland (33.8%) and forest (18.9%). The two other predictors which had both large samples sizes and percentages of correct classification over 50.0% are the distal phalanges (55.8%) and intermediate phalanges (51.9%). They paint a similar picture. The majority of both elements were predicted to the heavy woodland-bushland category; 73.3% of the distal phalanges and 61.3% of the intermediate phalanges.

Table 6.3. Habitat predictions of the Laetolil Beds specimens

Element	Percentage of correct classification	Total number		grassland/ tree-less	wooded-bushed grassland	light woodland-bushland	heavy woodland-bushland	forest	montane light cover	montane heavy cover
Metatarsal	66.5	2	#	0	0	0	0	1	0	1
			%	0.0	0.0	0.0	0.0	50.0	0.0	50.0
Radius	58.0	1	#	0	0	0	1	0	0	0
			%	0.0	0.0	0.0	100.0	0.0	0.0	0.0
Proximal phalanges	57.1	74	#	0	2	25	33	14	0	0
			%	0.0	2.7	33.8	44.6	18.9	0.0	0.0
Distal phalanges	55.8	30	#	0	3	3	22	2	0	(montane
			%	0.0	10.0	10.0	73.3	6.7	0.0	combined)
Lunar	53.2	6	#	0	1	2	2	0	0	1
			%	0.0	16.7	33.3	33.3	0.0	0.0	16.7
Intermediate phalanges	51.9	62	#	0	7	9	38	1	0	7
			%	0.0	11.3	14.5	61.3	1.6	0.0	11.3
Magnum	51.2	15	#	1	6	4	2	1	0	1
			%	6.7	40.0	26.7	13.3	6.7	0.0	6.7
Unciform	51.0	5	#	0	5	0	0	0	0	0
			%	0.0	100.0	0.0	0.0	0.0	0.0	0.0
Distal humerus	48.8	20	#	1	0	7	8	0	0	4
			%	5.0	0.0	35.0	40.0	0.0	0.0	20.0
Distal metapodial	47.2	35	#	1	6	16	0	7	3	2
			%	2.9	17.1	45.7	0.0	20.0	8.6	5.7
Naviculo-cuboid	47.1	16	#	2	1	4	0	4	1	4
			%	12.5	6.3	25.0	0.0	25.0	6.3	25.0
External and middle cuneiform	43.8	5	#	0	0	3	0	1	0	1
			%	0.0	0.0	60.0	0.0	20.0	0.0	20.0

All habit predictions have been highlighted. Both the raw numbers and percentage of the total number of specimens included in each analysis are listed.

Table 6.3, cont. Habitat predictions of the Laetolil Beds specimens

Element	Percentage of correct classification	Total number		grassland/ tree-less	wooded-bushed grassland	light woodland-bushland	heavy woodland-bushland	forest	montane light cover	montane heavy cover
Distal femur	42.4	8	#	0	2	0	3	0	3	0
			%	0.0	25.0	0.0	37.5	0.0	37.5	0.0
Proximal radius	41.1	22	#	0	5	14	2	1	0	0
			%	0.0	22.7	63.6	9.1	4.5	0.0	0.0
Cuneiform	40.6	8	#	0	4	0	1	0	3	0
			%	0.0	50.0	0.0	12.5	0.0	37.5	0.0
Proximal tibia	37.6	1	#	0	1	0	0	0	0	0
			%	0.0	100.0	0.0	0.0	0.0	0.0	0.0

All habit predictions have been highlighted. Both the raw numbers and percentage of the total number of specimens included in each analysis are listed.

The Ndolanya Beds analyses show that greater overall percentages of the specimens are predicted to belong to less wooded habitat categories, however this trend is harder to observe because the sample sizes are much smaller in these analyses (Table 6.4). The proximal phalanges and intermediate phalanges had the highest number of specimens for the analyses with overall success rates over 50.0%, 9 and 18 respectively. 44.0% of the proximal phalanges were predicted to belong to both the wooded-bushed grassland and light woodland-bushland category. The largest percentage of intermediate phalanges was predicted to belong to the wooded-bushed grassland, 44.4%. 33.3% were also predicted to heavy woodland-bushland and 16.7% to light woodland-bushland. Three predictors with lower overall success rates (less than 50.0%) had larger samples sizes – the distal humerus, distal metapodial and proximal radius. In all three cases the largest overall percentage of analysed specimens was predicted to belong to either wooded-bushed grassland (distal metapodial – 48.1% and proximal radius – 46.9%) or light woodland-bushland (distal humerus – 45.8%).

Small samples sizes may obscure patterns in the data. Combining the results of all of the analyses, the *total* number of predictions in each habitat group can be calculated for each bed in order to better observe a trend in habitat affiliation. Table 6.5 lists the combined number of specimens predicted for each habitat group, and divides this into analyses with a baseline of accuracy over 50% and under 50%. The greatest number of specimens in the Laetolil Beds (98) is predicted to belong to heavy woodland-bushland in analyses with success rates over 50.0%. Although the greatest number is predicted to belong to light woodland-bushland (44) in analyses with success rates under 50.0%, when all of the specimens are combined regardless of which set of analyses are considered, again the greatest number (112) is predicted to

Table 6.4. Habitat predictions of the Ndolanya Beds specimens

Element	Percentage of correct classification	Total number		grassland/ tree-less	wooded-bushed grassland	light woodland-bushland	heavy woodland-bushland	forest	montane light cover	montane heavy cover
Humerus	68.0	1	#	0	0	0	0	1	0	0
			%	0.0	0.0	0.0	0.0	100.0	0.0	0.0
Radius	58.0	1	#	0	1	0	0	0	0	0
			%	0.0	100.0	0.0	0.0	0.0	0.0	0.0
Proximal phalanges	57.1	9	#	0	4	4	0	1	0	0
			%	0.0	44.0	44.0	0.0	11.1	0.0	0.0
Distal phalanges	55.8	4	#	0	1	2	1	0	0	(montane
			%	0.0	25.0	50.0	25.0	0.0	0.0	combined)
Lunar	53.2	3	#	0	2	1	0	0	0	0
			%	0.0	66.7	33.3	0.0	0.0	0.0	0.0
Intermediate phalanges	51.9	18	#	1	8	3	6	0	0	0
			%	5.6	44.4	16.7	33.3	0.0	0.0	0.0
Magnum	51.2	4	#	0	1	2	1	0	0	0
			%	0.0	25.0	50.0	25.0	0.0	0.0	0.0
Unciform	51.0	4	#	0	2	1	0	0	1	0
			%	0.0	50.0	25.0	0.0	0.0	25.0	0.0
Distal humerus	48.8	24	#	0	1	11	7	0	1	4
			%	0.0	4.2	45.8	29.2	0.0	4.2	16.7
Distal metapodial	47.2	27	#	2	13	9	0	2	1	0
			%	7.4	48.1	33.3	0.0	7.4	3.7	0.0
Naviculo-cuboid	47.1	5	#	0	1	3	0	0	1	0
			%	0.0	20.0	60.0	0.0	0.0	20.0	0.0
External and middle cuneiform	43.8	1	#	0	0	1	0	0	0	0
			%	0.0	0.0	100.0	0.0	0.0	0.0	0.0

All habit predictions have been highlighted. Both the raw numbers and percentage of the total number of specimens included in each analysis are listed.

Table 6.4, cont. Habitat predictions of the Ndolanya Beds specimens

Element	Percentage of correct classification	Total number		grassland/ tree-less	wooded-bushed grassland	light woodland-bushland	heavy woodland-bushland	forest	montane light cover	montane heavy cover
Distal femur	42.4	3	#	0	3	0	0	0	0	0
			%	0.0	100.0	0.0	0.0	0.0	0.0	0.0
Proximal radius	41.1	49	#	5	23	18	1	2	0	0
			%	10.2	46.9	36.7	2.0	4.1	0.0	0.0
Cuneiform	40.6	9	#	0	3	1	0	0	5	0
			%	0.0	33.3	11.1	0.0	0.0	55.6	0.0
Pisiform	39.4	1	#	0	1	0	0	0	0	0
			%	0.0	100.0	0.0	0.0	0.0	0.0	0.0
Proximal tibia	37.6	6	#	0	1	4	0	1	0	0
			%	0.0	16.7	66.7	0.0	16.7	0.0	0.0
Proximal humerus	37.4	1	#	0	0	1	0	0	0	0
			%	0.0	0.0	100.0	0.0	0.0	0.0	0.0

All habit predictions have been highlighted. Both the raw numbers and percentage of the total number of specimens included in each analysis are listed.

Table 6.5. Number of Laetoli specimens predicted to belong to each habitat

	grassland/ tree-less	wooded-bushed grassland	light woodland-bushland	heavy woodland-bushland	forest	montane light cover	montane heavy cover
LAETOLIL BEDS							
Analyses with % of correct classification over 50%	1	24	43	98	19	0	3
Analyses with % of correct classification under 50%	4	19	44	14	13	10	18
All analyses	5	43	87	112	32	10	21
NDOLANYA BEDS							
Analyses with % of correct classification over 50%	1	19	13	8	2	1	0
Analyses with % of correct classification under 50%	7	46	48	8	5	8	4
All analyses	8	65	61	16	7	9	4

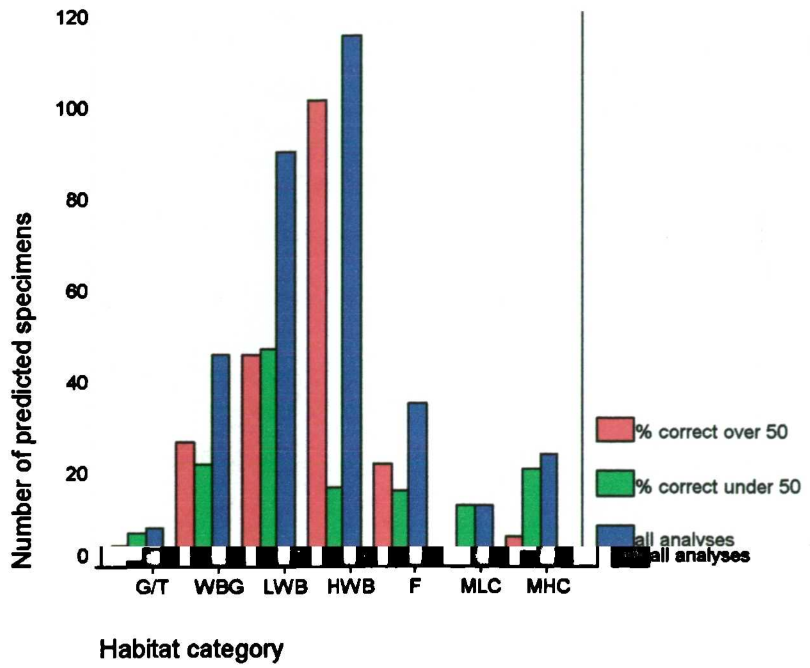
heavy woodland-bushland, with the next greatest number (87) to light woodland-bushland. Smaller numbers are predicted to both wooded-bushed grassland (43) and forest (32).

The greatest number of specimens in the Ndolanya Beds (19) which were included in analyses with success rates over 50.0% belongs to wooded-bushed grassland, with a lesser component belonging to light woodland-bushland (13). Nearly equal numbers are predicted to these same two categories (46 and 48, respectively) in analyses with success rates lower than 50.0% and in all of the analyses combined (65 and 61 respectively).

There is indeed a trend that can be best observed in Figures 6.1a and 6.1b. These figures display a bar chart for each bed which displays the number of specimens predicted to belong to each habitat category, with separate bars for the specimens from all of the analyses (blue bar), from analyses with a percentage of correct classification over 50% (red bar) and under 50% (green bar). Looking firstly at the trend observed from analyses with an overall percentage of correct classification over 50% (red bar), it is clear that the Laetolil Beds have a greater number of specimens predicted to belong to the heavy woodland-bushland category, while the Ndolanya Beds have a greatest number of specimens in the wooded-bushed grassland category followed closely by light woodland-bushland.

The addition of the specimens from analyses with percentages of correct classification under 50% does not significantly change the overall pattern observed, but contributes a greater proportion of specimens predicted to belong to the other habitat groups relative to the "peak" groups. The trends displayed by the numbers from all of the analyses (blue bar) still peak in the same habitat categories, although in

a) Laetolil Beds



b) Ndolanya Beds

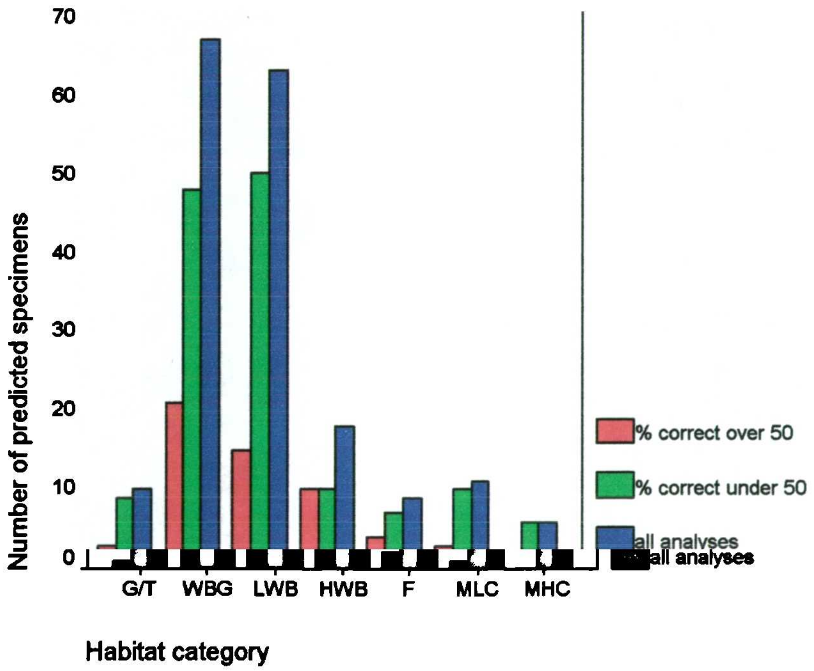


Figure 6.1. (a) Line graph of the number of Laetolil Beds specimens in each habitat category (b) Line graph of the number of Ndolanya Beds specimens in each habitat category. The number of specimens is presented as a total from all of the analyses and is also divided into those predicted in analyses with correct percentages of classification over 50% and under 50%. The Laetolil Beds have a peak in the heavy woodland-bushland category and the Ndolanya Beds peak between wooded-bushed grassland and light woodland-bushland. G/T = grassland/tree-less, WBG = wooded-bushed grassland, LWB = light woodland-bushland, HWB = heavy woodland-bushland, F = forest, MLC = montane light cover, MHC = montane heavy cover.

each bed there now appear to be more specimens in the light woodland-bushland category.

The advantage of surveying a number of elements in an ecomorphological analysis and summing the number of predicted specimens from all of the analyses, regardless of the element, is that it makes the trends clearer by increasing the sample size. For instance, these trends would not have been obvious if only the two best predictors had been used. For the Laetolil Beds, this would have only amounted to three specimens, two metatarsals and a radius (Table 6.3). For the Ndolanya Beds (Table 6.4), only a humerus and a radius would comprise the dataset. The best predictors are often complete elements; in fact the epiphyseal ends of long bones have relatively low rates of success (all under 50%) compared to complete long bones or other complete elements such as the phalanges, which have percentages of correct classification between 51.9% (intermediate phalanges) and 57.1% (proximal phalanges).

Complete long bone fossils are rare. To date, the smallest sample size of published bovid material that has been analysed in an ecomorphological context was four complete femora from the middle Miocene sites of Fort Ternan, Kenya and the Chinji Formation, Pakistan (Kappelman, 1991). Eight proximal femora were added to this analysis for a total of 12 individuals, five of which were from Fort Ternan, and seven from the Chinji Formation. They were used to build a picture of differing environments between the sites, with the Fort Ternan material indicating mixed woodland and forest and the Chinji material indicating a more forested condition. Five specimens from one site is arguably a very small sample on which to base any conclusions, but it is a common problem when dealing with fossil material. This can be ameliorated by conducting a survey of as many elements as possible, so long as they are relatively good predictors.

6.3 Probabilities

The question of the reliability of the habitat predictions is not related solely to the overall percentage of correct classification. The associated probabilities which are calculated for each specimen in the analysis, based on its proximity to the centroid for each habitat group, is another indicator. The highest probability dictates the habitat prediction for each specimen. However, each specimen will be given a habitat prediction even if that probability is relatively low, as long as it is the highest probability for that specimen in any given habitat group. This issue was recently given some attention in the literature (DeGusta & Vrba, 2003) and was raised in Chapter 4 and Chapter 5.

Good predictors have not only high overall percentages of classification, but high probabilities associated with the correct predictions in each group. Table 6.6 summarises the percentage of correctly predicted modern individuals falling within ten percent increments of probabilities for the nineteen elements that were also applied to the fossil material. It appears that the better predictors such as the humerus and metatarsal have greater numbers of specimens with high associated probabilities than do the less reliable predictors like the proximal tibia and proximal humerus.

For example, the humerus, which was the best overall predictor with a success rate of 68.0%, has just over half of the specimens (52.9%) predicted correctly with probabilities between 70% and 100%. This is in contrast to the worst overall predictor, the proximal humerus with a correct classification rate of 37.4%. This analysis yielded only 6.6% of its correctly predicted specimens with an associated

Table 6.6. Breakdown of probabilities for the correctly predicted modern individuals in the analyses of elements used to reconstruct the environment at Laetoli

Probability range	humerus (68.0)	metatarsal (66.5)	radius (58.0)	proximal phalanges (57.1)	distal phalanges (55.8)	lunar (53.2)	intermediate phalanges (51.9)	magnum (51.2)	unciform (51.0)
correct predictions/total	*138/203*	*143 215*	*120 207*	*173/303*	*72/129*	*108/203*	*94 181*	*107/209*	*105 206*
20.1-30.0	0.7	0.7	0.0	2.9	0.0	2.8	2.1	5.6	1.0
30.1-40.0	2.9	4.2	8.3	12.7	12.5	8.3	10.6	21.5	13.3
40.1-50.0	10.9	15.4	30.0	22.0	6.9	24.1	28.7	24.3	24.8
50.1-60.0	18.8	12.6	20.8	22.0	23.6	20.4	18.1	15.0	21.9
60.1-70.0	13.8	18.9	11.7	13.9	25.0	14.8	10.6	8.4	20.0
70.1-80.0	11.6	14.0	9.2	11.0	16.7	8.3	11.7	8.4	5.7
80.1-90.0	15.9	11.2	7.5	7.5	11.1	10.2	9.6	6.5	5.7
90.1-100.0	25.4	23.1	12.5	8.1	4.2	11.1	8.5	10.3	7.6

Probability range	distal humerus (48.8)	distal metapodial (47.2)	naviculo-cuboid (47.1)	external & middle cuneiform (43.8)	distal femur (42.4)	proximal radius (41.1)	cuneiform (40.6)	pisiform (39.4)	proximal tibia (37.6)	proximal humerus (37.4)
correct predictions/total	*99/203*	*201/426*	*97/206*	*84/192*	*89/210*	*86/209*	*82/202*	*67/170*	*80 213*	*76/203*
20.1-30.0	3.0	6.0	5.2	22.6	3.4	27.9	19.5	20.9	26.1	14.5
30.1-40.0	22.2	28.9	15.5	31.0	38.2	36.0	47.6	58.2	72.8	35.5
40.1-50.0	40.4	33.8	19.6	22.6	19.1	19.8	17.1	7.5	9.3	13.2
50.1-60.0	15.2	15.4	14.4	8.3	13.5	11.6	4.9	7.5	9.3	18.4
60.1-70.0	11.1	5.5	13.4	7.1	15.7	4.7	6.1	4.5	5.6	11.8
70.1-80.0	4.0	5.0	13.4	4.8	5.6	0.0	2.4	1.5	1.9	6.6
80.1-90.0	3.0	3.5	12.4	1.2	4.5	0.0	2.4	0.0	0.0	0.0
90.1-100.0	1.0	2.0	6.2	2.4	0.0	0.0	0.0	0.0	0.0	0.0

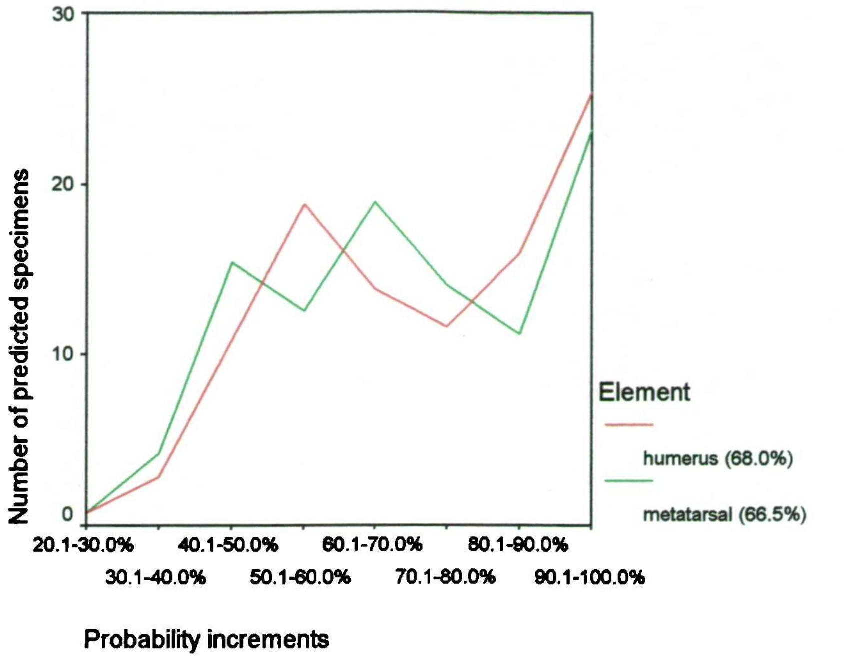
The overall percentage of correctly predicted individuals in each analysis is listed in parentheses under the name of the element. The value in each cell in the main body of the table is a percentage of the correctly predicted individuals with a probability falling within each increment.

probability between 70% and 100%, whereas exactly half of them fell in the lower range of probabilities between 20% and 40%.

Patterns of probabilities associated with the correctly predicted specimens are illustrated by the line graphs in Figures 6.2a – 6.2c. The two best predictor elements, the humerus and metatarsal, represent the good predictors with success rates in the range of 60 - 68%. They have a very small percentage of specimens predicted with low probabilities between 20% and 40%, an intermediate amount between 40% and 90% and the highest number with very high probabilities between 90% and 100% (Figure 6.2a). The lunar and intermediate phalanges (Figure 6.2b) represent the reasonable predictors with success rates between 50% and 60%. Although their success rates are only ten percent lower than the good predictor elements, their pattern of probabilities is very different. There are still few specimens with low probabilities between 20% and 40%, but the greater number of specimens peak in the range of 40 – 60% rather than 90-100%. An even greater contrast is provided by the poor predictors (Figure 6.2c), such as the proximal tibia and proximal humerus. None of their correctly predicted specimens have probabilities in the upper range between 80% and 100%, with a peak in the low range between 30% and 40%.

The overall percentage of correct classification and the associated probabilities are clearly related. This can also be illustrated by calculating the average and median probability for all of the correctly predicted specimens in each analysis and comparing that to the overall percentage of correct classification for each analysis. Figure 6.3 demonstrates that there is a linear relationship between these variables, such that as the probabilities become higher, the overall success rate also increases. This may relate to the fact that higher overall success rates indicate higher levels of predictive success within each individual habitat group.

a)



b)

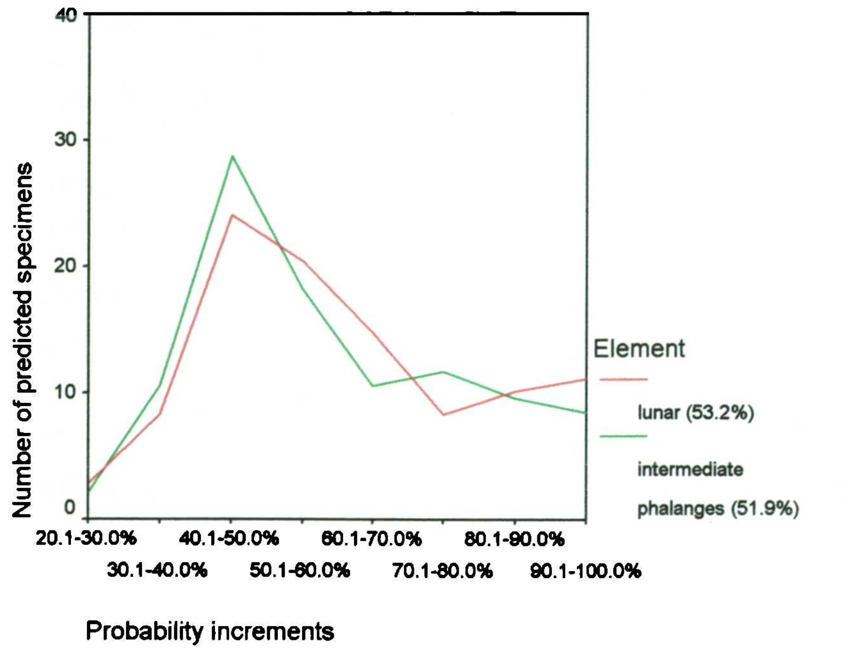


Figure 6.2. Patterns of probabilities associated with the correctly predicted modern specimens in the discriminant function analyses. Good predictors like the humerus and metatarsal (a) have a higher number of specimens predicted with high probabilities (60 – 100%). Reasonable predictors such as the lunar and intermediate phalanges (b) have more probabilities in the mid range (40 – 60%) while bad predictors like the proximal tibia and proximal humerus (c) have lower probabilities between 20 – 40%.

c)

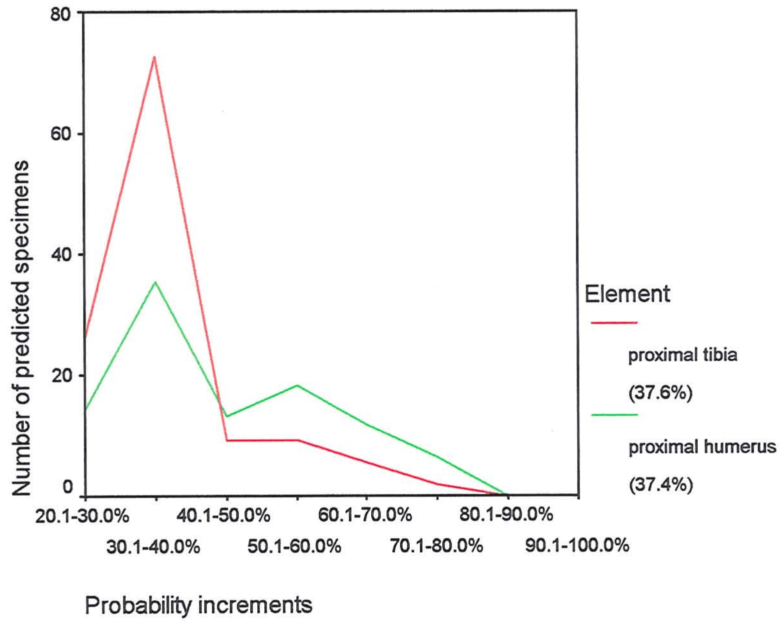


Figure 6.2, cont. Patterns of probabilities associated with the correctly predicted modern specimens in the discriminant function analyses. Good predictors like the humerus and metatarsal (a) have a higher number of specimens predicted with high probabilities (60 – 100%). Reasonable predictors such as the lunar and intermediate phalanges (b) have more probabilities in the mid range (40 – 60%) while bad predictors like the proximal tibia and proximal humerus (c) have lower probabilities between 20 – 40%.

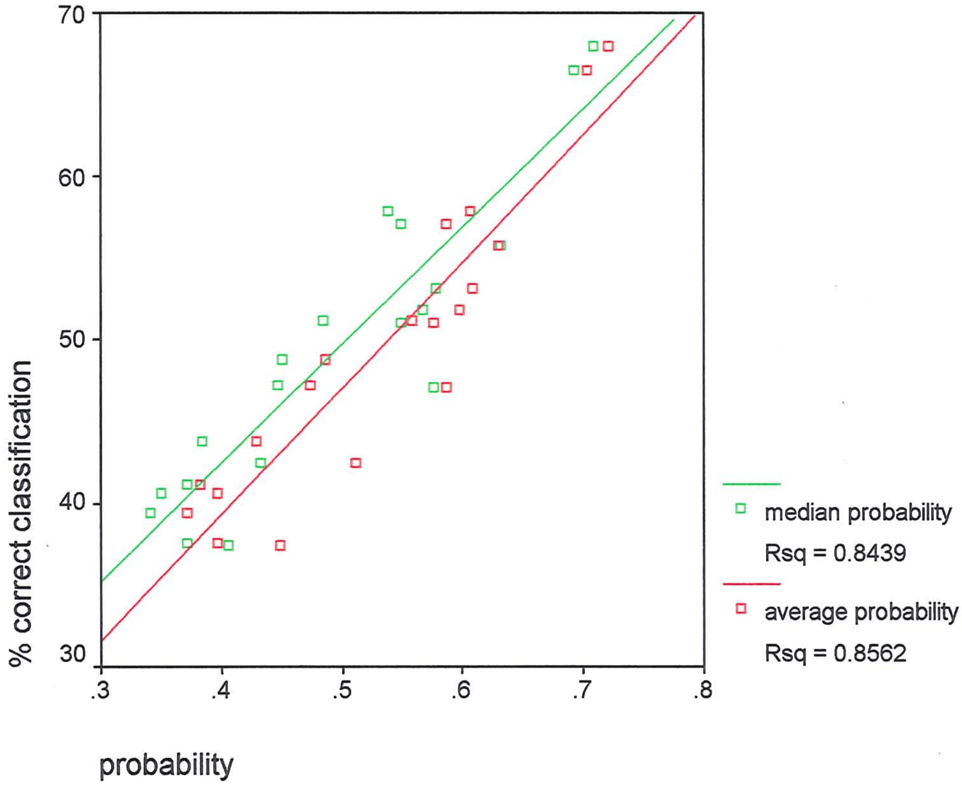


Figure 6.3. A scatter plot describing the relationship between the overall percentage of correct classification and probability of correct habitat prediction. Only the nineteen elements which were used with the fossil material are considered. Both the average and median probability for the correctly predicted modern specimens in each analysis is plotted against the percentage of correct classification for that analysis.

When the success rate is lower, the distinctions between the habitat categories are obscured by other factors (such as taxonomy and evolutionary history) and the analysis has a harder time predicting the specimens' habitat affiliation with any amount of "surety", i.e. the probabilities also drop because the differences between the groups are less obvious. This was described briefly in Section 4.4. Misclassified individuals have very low probabilities associated with their predictions and individuals that are correctly predicted but which lie on the edge of their habitat group's space (which can be observed in scatter plots of the discriminant functions), also have lower probabilities. In other words, these individuals are either anomalous for their habitat group or deviate somewhat from the norm of that group's morphology.

The probabilities and habitat predictions for every specimen that was analysed from both the Laetolil and Ndolanya Beds can be found in Appendix F. The *average* probability for all of the specimens predicted for each habitat group from each analysis is summarised for the Laetolil Beds in Table 6.7 and the Ndolanya Beds in Table 6.8. These tables also present the total number of specimens predicted to belong to each habitat group and the average probability of all specimens within the group regardless of their predictions (however, the value of most concern is the average probability of the specimens predicted to belong to each group).

For example, 74 proximal phalanges from the Laetolil Beds were analysed. None of them were predicted to belong to the grassland/tree-less, montane light cover or montane heavy cover habitat categories, exemplified by the low average probability for all 74 specimens belonging to them, which are calculated to be 0.00473, 0.01115 and 0.01948, respectively (Table 6.7). This contrasts to the higher average probabilities for the specimens in the habitat groups in which a number of

Table 6.7. Average probabilities for the habitat prediction of the specimens from the Laetolil Beds

Element	Probability grassland/ tree-less	Probability wooded-bushed grassland	Probability light woodland-bushland	Probability heavy woodland-bushland	Probability forest	Probability montane light cover	Probability montane heavy cover
METATARSAL (66.5%)							
number of predicted specimens	0	0	0	0	1	0	1
average probability of all specimens	0.00015	0.09049	0.16377	0.08700	0.28664	0.10285	0.26913
average probability of predicted specimens	n/a	n/a	n/a	n/a	0.46293	n/a	0.47306
RADIUS (58.0%)							
number of predicted specimens	0	0	0	1	0	0	0
average probability of all specimens	0.00153	0.02290	0.12373	0.69249	0.12991	0.00001	0.02943
average probability of predicted specimens	n/a	n/a	n/a	0.69249	n/a	n/a	n/a
PROXIMAL PHALANGES (57.1%)							
number of predicted specimens	0	2	25	33	14	0	0
average probability of all specimens	0.00473	0.16133	0.29984	0.32292	0.18056	0.01115	0.01948
average probability of predicted specimens	n/a	0.34334	0.42229	0.44130	0.41243	n/a	n/a
DISTAL PHALANGES (55.8%)							
number of predicted specimens	0	3	3	22	2	0	(combined
average probability of all specimens	0.01233	0.13564	0.07660	0.49748	0.13878	0.13916	montane)
average probability of predicted specimens	n/a	0.74265	0.41398	0.63227	0.35413	n/a	
LUNAR (53.2%)							
number of predicted specimens	0	1	2	2	0	0	1
average probability of all specimens	0.01496	0.17779	0.23818	0.22064	0.14869	0.06320	0.13654
average probability of predicted specimens	n/a	0.45199	0.45143	0.52603	n/a	n/a	0.58441

the percentage of correctly predicted modern individuals for each analysis is listed in parentheses next to the element

Table 6.7, cont. Average probabilities for the habitat prediction of the specimens from the Laetolil Beds

Element	Probability grassland/ tree-less	Probability wooded-bushed grassland	Probability light woodland-bushland	Probability heavy woodland-bushland	Probability forest	Probability montane light cover	Probability montane heavy cover
INTERMEDIATE PHALANGES (51.9%)							
number of predicted specimens	0	7	9	38	1	0	7
average probability of all specimens	0.02460	0.13853	0.12996	0.47133	0.03980	0.01083	0.18496
average probability of predicted specimens	n/a	0.53728	0.45435	0.64169	0.44382	n/a	0.57622
MAGNUM (51.2%)							
number of predicted specimens	1	6	4	2	1	0	1
average probability of all specimens	0.03087	0.26213	0.29011	0.17077	0.09996	0.03713	0.10902
average probability of predicted specimens	0.32435	0.42955	0.45274	0.45490	0.39213	n/a	0.38614
UNCIFORM (51.0%)							
number of predicted specimens	0	5	0	0	0	0	0
average probability of all specimens	0.00316	0.73743	0.18028	0.01758	0.01590	0.03286	0.01279
average probability of predicted specimens	n/a	0.73743	n/a	n/a	n/a	n/a	n/a
DISTAL HUMERUS (48.8%)							
number of predicted specimens	1	0	7	8	0	0	4
average probability of all specimens	0.05784	0.12284	0.25001	0.29139	0.05839	0.05355	0.16597
average probability of predicted specimens	0.34246	n/a	0.44724	0.47386	n/a	n/a	0.62454
DISTAL METAPODIAL (47.2%)							
number of predicted specimens	1	6	16	0	7	3	2
average probability of all specimens	0.04128	0.25741	0.25726	0.13595	0.15513	0.07986	0.07311
average probability of predicted specimens	0.39361	0.42411	0.40048	n/a	0.43233	0.30922	0.59290

the percentage of correctly predicted modern individuals for each analysis is listed in parentheses next to the element

Table 6.7, cont. Average probabilities for the habitat prediction of the specimens from the Laetolil Beds

Element	Probability grassland/ tree-less	Probability wooded-bushed grassland	Probability light woodland-bushland	Probability heavy woodland-bushland	Probability forest	Probability montane light cover	Probability montane heavy cover
NAVICULO-CUBOID (47.1%)							
number of predicted specimens	2	1	4	0	4	1	4
average probability of all specimens	0.12732	0.10640	0.23300	0.03639	0.16238	0.12075	0.21377
average probability of predicted specimens	0.37782	0.42465	0.32265	n/a	0.42483	0.63852	0.57122
EXTERNAL AND MIDDLE CUNEIFORM (43.8%)							
number of predicted specimens	0	0	3	0	1	0	1
average probability of all specimens	0.07901	0.09963	0.31613	0.10572	0.07197	0.14135	0.18618
average probability of predicted specimens	n/a	n/a	0.36113	n/a	0.26013	n/a	0.37718
DISTAL FEMUR (42.4%)							
number of predicted specimens	0	2	0	3	0	3	0
average probability of all specimens	0.00940	0.13438	0.16052	0.29244	0.11864	0.25190	0.03271
average probability of predicted specimens	n/a	0.40225	n/a	0.44620	n/a	0.59727	n/a
PROXIMAL RADIUS (41.1%)							
number of predicted specimens	0	5	14	2	1	0	0
average probability of all specimens	0.06441	0.24473	0.29370	0.14764	0.17107	0.03848	0.03998
average probability of predicted specimens	n/a	0.45413	0.30536	0.26201	0.25496	n/a	n/a
CUNEIFORM (40.6%)							
number of predicted specimens	0	4	0	1	0	3	0
average probability of all specimens	0.03199	0.27563	0.16507	0.16839	0.04437	0.23086	0.08369
average probability of predicted specimens	n/a	0.35486	n/a	0.72190	n/a	0.42246	n/a

the percentage of correctly predicted modern individuals for each analysis is listed in parentheses next to the element

Table 6.7, cont. Average probabilities for the habitat prediction of the specimens from the Laetolil Beds

Element	Probability grassland/ tree-less	Probability wooded-bushed grassland	Probability light woodland-bushland	Probability heavy woodland-bushland	Probability forest	Probability montane light cover	Probability montane heavy cover
PROXIMAL TIBIA (37.6%)							
number of predicted specimens	0	1	0	0	0	0	0
average probability of all specimens	0.06311	0.33577	0.08670	0.18774	0.19470	0.09278	0.03919
average probability of predicted specimens	n/a	0.33577	n/a	n/a	n/a	n/a	n/a

the percentage of correctly predicted modern individuals for each analysis is listed in parentheses next to the element

Table 6.8. Average probabilities for the habitat prediction of the specimens from the Ndolanya Beds

Element	Probability grassland/ tree-less	Probability wooded-bushed grassland	Probability light woodland-bushland	Probability heavy woodland-bushland	Probability forest	Probability montane light cover	Probability montane heavy cover
HUMERUS (68.0%)							
number of predicted specimens	0	0	0	0	1	0	0
average probability of all specimens	0.00182	0.10847	0.26018	0.12292	0.50646	0.00014	0.00000
average probability of predicted specimens	n/a	n/a	n/a	n/a	0.50646	n/a	n/a
RADIUS (58.0%)							
number of predicted specimens	0	1	0	0	0	0	0
average probability of all specimens	0.04824	0.58532	0.35477	0.00296	0.00506	0.00363	0.00002
average probability of predicted specimens	n/a	0.58532	n/a	n/a	n/a	n/a	n/a
PROXIMAL PHALANGES (57.1%)							
number of predicted specimens	0	4	4	0	1	0	0
average probability of all specimens	0.01278	0.36796	0.35717	0.08674	0.14073	0.00187	0.03275
average probability of predicted specimens	n/a	0.50695	0.47700	n/a	0.87618	n/a	n/a
DISTAL PHALANGES (55.8%)							
number of specimens	0	1	2	1	0	0	
average probability of all specimens	0.02691	0.38701	0.29092	0.09663	0.10281	0.09572	(combined
average probability of predicted specimens	n/a	0.86518	0.54780	0.32401	n/a	n/a	montane)
LUNAR (53.2%)							
number of predicted specimens	0	2	1	0	0	0	0
average probability of all specimens	0.05010	0.49297	0.28121	0.09639	0.04548	0.02739	0.00647
average probability of predicted specimens	n/a	0.55682	0.46004	n/a	n/a	n/a	n/a

the percentage of correctly predicted modern individuals for each analysis is listed in parentheses next to the element

Table 6.8, cont. Average probabilities for the habitat prediction of the specimens from the Ndolanya Beds

Element	Probability grassland/ tree-less	Probability wooded-bushed grassland	Probability light woodland-bushland	Probability heavy woodland-bushland	Probability forest	Probability montane light cover	Probability montane heavy cover
INTERMEDIATE PHALANGES (51.9%)							
number of predicted specimens	1	8	3	6	0	0	0
average probability of all specimens	0.05489	0.31378	0.22746	0.22758	0.08926	0.00433	0.08269
average probability of predicted specimens	0.37645	0.48936	0.36082	0.50174	n/a	n/a	n/a
MAGNUM (51.2%)							
number of predicted specimens	0	1	2	1	0	0	0
average probability of all specimens	0.00249	0.24841	0.30344	0.22634	0.07848	0.02764	0.11321
average probability of predicted specimens	n/a	0.42393	0.39525	0.28621	n/a	n/a	n/a
UNCIFORM (51.0%)							
number of predicted specimens	0	2	1	0	0	1	0
average probability of all specimens	0.01318	0.43518	0.30709	0.06004	0.03327	0.13190	0.01935
average probability of predicted specimens	n/a	0.57743	0.46277	n/a	n/a	0.32706	n/a
DISTAL HUMERUS (48.8%)							
number of predicted specimens	0	1	11	7	0	1	4
average probability of all specimens	0.04244	0.15612	0.31678	0.22509	0.07771	0.05185	0.13000
average probability of predicted specimens	n/a	0.41719	0.48341	0.41034	n/a	0.46723	0.57714
DISTAL METAPODIAL (47.2%)							
number of predicted specimens	2	13	9	0	2	1	0
average probability of all specimens	0.06021	0.31706	0.30358	0.12537	0.07932	0.06985	0.04460
average probability of predicted specimens	0.53065	0.42184	0.40316	n/a	0.39040	0.60179	n/a

the percentage of correctly predicted modern individuals for each analysis is listed in parentheses next to the element

Table 6.8, cont. Average probabilities for the habitat prediction of the specimens from the Ndolanya Beds

Element	Probability grassland/ tree-less	Probability wooded-bushed grassland	Probability light woodland-bushland	Probability heavy woodland-bushland	Probability forest	Probability montane light cover	Probability montane heavy cover
NAVICULO-CUBOID (47.1%)							
number of predicted specimens	0	1	3	0	0	1	0
average probability of all specimens	0.06257	0.19471	0.46534	0.05510	0.01899	0.10726	0.09604
average probability of predicted specimens	n/a	0.50525	0.60151	n/a	n/a	0.44972	n/a
EXTERNAL AND MIDDLE CUNEIFORM (43.8%)							
number of predicted specimens	0	0	1	0	0	0	0
average probability of all specimens	0.11618	0.16747	0.33544	0.09244	0.05181	0.07556	0.16110
average probability of predicted specimens	n/a	n/a	0.33544	n/a	n/a	n/a	n/a
DISTAL FEMUR (42.4%)							
number of predicted specimens	0	3	0	0	0	0	0
average probability of all specimens	0.03461	0.58529	0.29229	0.07437	0.01308	0.00028	0.00007
average probability of predicted specimens	n/a	0.58529	n/a	n/a	n/a	n/a	n/a
PROXIMAL RADIUS (41.1%)							
number of predicted specimens	5	23	18	1	2	0	0
average probability of all specimens	0.08360	0.29855	0.29632	0.11456	0.15186	0.02437	0.03074
average probability of predicted specimens	0.46959	0.41582	0.33461	0.28696	0.25934	n/a	n/a
CUNEIFORM (40.6%)							
number of predicted specimens	0	3	1	0	0	5	0
average probability of all specimens	0.05038	0.27181	0.20578	0.02953	0.04642	0.27910	0.11697
average probability of predicted specimens	n/a	0.31771	0.37301	n/a	n/a	0.37911	n/a

the percentage of correctly predicted modern individuals for each analysis is listed in parentheses next to the element

Table 6.8, cont. Average probabilities for the habitat prediction of the specimens from the Ndolanya Beds

Element	Probability grassland/ tree-less	Probability wooded-bushed grassland	Probability light woodland-bushland	Probability heavy woodland-bushland	Probability forest	Probability montane light cover	Probability montane heavy cover
PISIFORM (39.4%)							
number of predicted specimens	0	1	0	0	0	0	0
average probability of all specimens	0.04923	0.35696	0.22147	0.02251	0.04178	0.18687	0.12117
average probability of predicted specimens	n/a	0.35696	n/a	n/a	n/a	n/a	n/a
PROXIMAL TIBIA (37.6%)							
number of predicted specimens	0	1	4	0	1	0	0
average probability of all specimens	0.07745	0.15599	0.26928	0.11331	0.13299	0.10174	0.14925
average probability of predicted specimens	n/a	0.27512	0.34518	n/a	0.45518	n/a	n/a
PROXIMAL HUMERUS (37.4%)							
number of predicted specimens	0	0	1	0	0	0	0
average probability of all specimens	0.04003	0.13621	0.28215	0.15414	0.21965	0.06988	0.09795
average probability of predicted specimens	n/a	n/a	0.28215	n/a	n/a	n/a	n/a

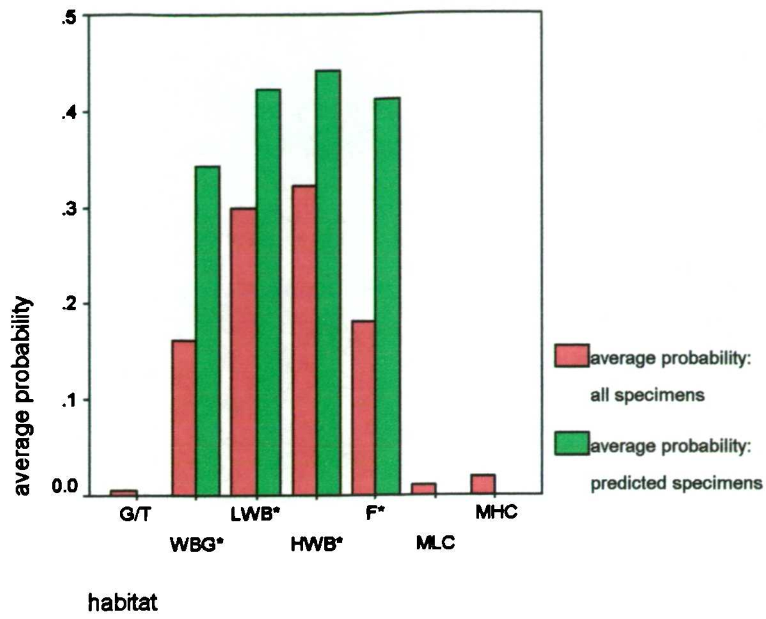
the percentage of correctly predicted modern individuals for each analysis is listed in parentheses next to the element

them were predicted to belong. For instance, there were 33 specimens predicted to belong to the heavy woodland-bushland category. The average probability for *all* 74 specimens belonging to heavy woodland-bushland is 0.32292, but higher, at 0.44130, for the 33 specimens which *were* predicted to belong.

Two of the better predictors from the Laetolil Beds with adequate sample sizes, the proximal (N=74) and intermediate phalanges (N=62), can be used to display this general pattern that can be observed in the probability data. Figures 6.4a and 6.4b present bar charts of the probabilities for all of the analysed specimens belonging to each habitat compared to the average probability for the specimens predicted to belong to each group. The average probability for all analysed specimens is low in groups in which none of the specimens have been predicted to belong, but higher in groups in which predictions have been made (which are denoted by a * in the figures). Within these groups the average probability of the predicted specimens is always higher than the average probability for all of the specimens combined.

The issue of sample size is again relevant. Although higher probabilities have been shown to be linked to overall success rates (Figure 6.3), one can not base any conclusion on an assessment of the probabilities associated with an analysis in which only a handful of individuals have been included. Probabilities are best considered a measure of the confidence one can place in the predictions. Combining the results of every analysis for each bed, the average probability for all of the specimens predicted to belong to each habitat category can be calculated and compared in the same way that the raw numbers were in Section 6.2 above. Table 6.9 lists this information and highlights the probabilities over 50.0%.

Importantly, when only the specimens from the analyses of elements that yielded percentages of correct classification over 50.0% are considered, the average a)



b)

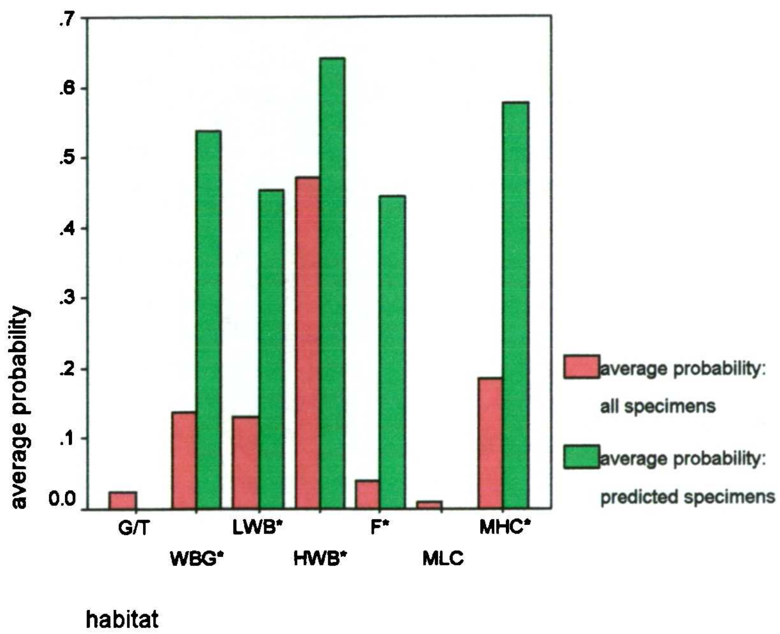


Figure 6.4. Bar charts of the average probability for all of the specimens within each habitat category (red) and for those predicted to belong to each category (green) in the analyses of the proximal phalanges (a) and intermediate phalanges (b) from the Laetolil Beds. G/T = grassland/tree-less, WBG = wooded-bushed grassland, LWB = light woodland-bushland, HWB = heavy woodland-bushland, F = forest, MLC = montane light cover, MHC = montane heavy cover. Specimens have been predicted to belong to habitats marked with a *. The average probability for all analysed specimens is low in groups in which none of the specimens have been predicted to belong, but generally higher in groups in which predictions have been made. Within these groups the average probability of the predicted specimens is always higher than the average probability for all of the specimens.

Table 6.9. Average probability of the Laetoli specimens predicted to belong to each habitat group

	grassland/ tree-less	wooded-bushed grassland	light woodland-bushland	heavy woodland-bushland	forest	montane light cover	montane heavy cover
LAETOLIL BEDS							
Analyses with % of correct classification over 50%	0.32435	**0.55800**	0.43261	**0.56850**	0.40954	n/a	**0.54772**
Analyses with % of correct classification under 50%	0.37293	0.41051	0.36789	0.45538	0.40313	0.46254	**0.57691**
All analyses	0.36321	0.49283	0.39988	**0.55436**	0.40694	0.46254	**0.56301**
NDOLANYA BEDS							
Analyses with % of correct classification over 50%	0.37645	**0.53082**	0.44610	0.45258	**0.69132**	0.32706	n/a
Analyses with % of correct classification under 50%	0.48704	0.41981	0.39885	0.39492	0.35093	0.42679	**0.57714**
All analyses	0.47321	0.45226	0.40892	0.42375	0.44819	0.41570	**0.57714**

Probabilities over 50.0% have been highlighted. N/A indicates that there were no specimens predicted to belong to the habitat category in that set of analyses and thus there is no associated probability.

probability for the peak habitat group from each bed, heavy woodland-bushland for the Laetolil Beds and wooded-bushed grassland for the Ndolanya Beds, is over 50.0%. A high probability is also associated with the wooded-bushed grassland individuals in the Laetolil Beds, which amount to 24 individuals or 12.8% of the sample for the analyses with success rates over 50.0%. The forest individuals also have a high probability in the Ndolanya Beds analyses, and there are two individuals in this category, or 4.5% of the specimens.

This does not change the interpretation of the habitats for these beds, but reinforces our understanding of the Laetoli area in the past representing a mosaic of habitats, much as it does today. Laetoli covers a large surface area and the fossils in these analyses have been pooled together by bed and not analysed by locality, for lack of an adequate sample size from the individual localities. Had this been done, there might be a way to build up a picture of more localised habitats, however on the scale addressed here we can expect that species preferring a number of habitats will be represented. The relevant point is the dominant habitat category for each bed and the probability associated with the predictions within that category. That other habitats are represented with some degree of confidence is unsurprising.

However, what *is* surprising is the number of predictions and the high probabilities associated with the specimens in the montane light cover and montane heavy cover categories. In the Laetolil Beds a total of 10 specimens were predicted as montane light cover and 21 as montane heavy cover; in the Ndolanya Beds 9 are predicted montane light cover and four as montane heavy cover. In every set of analyses, whether the success rate was above or below 50.0%, the probabilities associated with the montane heavy cover predictions are over .50, although in the more successful analyses there were very few specimens predicted to either of the montane groups (only three in the Laetolil Beds and one in the Ndolanya Beds).

The Laetoli region has never been associated with mountainous terrain, and the reason for these predictions may relate to the taxonomy of the comparative extant species in those two groups. They are comprised almost entirely of species in the subfamily Caprinae, which are known to inhabit a variety of montane environments in Europe, Asia and North America. These species are often easily distinguished from those inhabiting non-montane environments in the analyses, evidenced by the relatively high success rates within the two habitats (see Tables 4.4, 4.10, 5.3 and 5.9) and the high probabilities associated with the correct modern predictions (this data is not presented). Caprinae are known to possess a unique suite of morphologies which include such features as shortened metapodials, long tibiae, well-defined metapodial verticilli, spherical femoral heads and broad phalangeal epiphyses (Köhler, 1993).

Caprinae are no longer endemic to the African continent other than in the extreme northern region and other areas where they have been introduced in recent times. However, in the past they survived in both East Africa south of Ethiopia until the Pliocene-Pleistocene transition and in the southern parts of the continent until later in the Pleistocene (Gentry, personal communication). They have been found in deposits in East Africa including Bed I at Olduvai, Tanzania (Gentry & Gentry, 1978a), the Hadar Formation, Ethiopia (Gentry, 1996) and the Bouri Formation, Middle Awash, Ethiopia (Vrba, 1997) and a number of South African cave sites including Makapansgat, Swartkrans and Sterkfontein, where the ovibovine *Makapania broomi* (or "*Bos*" *makapaani*) is well known (Brink, 1999; de Ruiter, 2001).

However, caprines have never been described from the Laetoli fauna. Table 6.10 presents the list of bovid species which are currently known from the Laetolil and Ndolanya Beds. If the specimens predicted here to belong to the two montane categories are indeed affiliating on the basis of phylogeny, then this is the first potential evidence indicating they did range there during the time of the deposition of the Laetolil and Ndolanya Beds. Alternatively, these specimens may represent either extinct species for which there is no extant comparison, non-caprines with caprine-like adaptations or simple misclassifications in the analyses.

6.4 Comparison of the Laetolil and Ndolanya Beds

Nineteen elements which have been determined to reliably predict the preferred habitat of extant species were included in an ecomorphological survey of the fossil bovid remains from Laetoli, Tanzania. These analyses have constructed a picture of the environmental conditions that prevailed at the time of the deposition of the Upper Laetolil Beds and Upper Ndolanya Beds.

The earlier Laetolil Beds (3.5 – 4.3 mya) display a definite peak of specimens from all of the analyses which have success rates greater than 50.0% in the heavy woodland-bushland category. The average probability associated with these predictions infers that a high degree of confidence can be placed in the predictions. Slightly less successful analyses indicate that there was also a number of individuals preferring light woodland-bushland in the area. The combined results infer that there was a range of habitats present in the region but that the majority of the landscape was most likely dominated by medium to heavy cover woodland-bushland with some areas of more open grassland also present.

Table 6.10. Bovid species known from Laetoli

UPPER LAETOLIL BEDS	
Tragelaphus sp.	*Parmularius pandatus* sp. nov.
Simatherium kohllarseni	Alcelaphini sp. indet.
Bravobus nanincisus sp. nov.	*Madoqua avifluminis*
Cephalophini sp. indet.	?*Raphicerus* sp.
Praedamalis deturi	*Gazella janenschi*
?Hippotragini sp. nov.	*Pelea* aff. sp. indet.
UPPER NDOLANYA BEDS	
Tragelaphus sp.cf. *buxtoni*	Alcelaphini small sp.
Bovini sp. indet.	*Madoqua* ?*avifluminis*
Reduncini sp. indet.	?*Raphicerus* sp.
Hippotragini sp. indet.	*Antidorcas* sp.
Praedamalis deturi	*Gazella janenschi*
Parestigorgon gadjingeri	Antilopini sp. indet.
Alcelaphini medium sp.	?*Pelea* sp.

The material from the Ndolanya Beds, deposited between 3.5 and 2.5 million years ago (a recent estimate determined the average age of the beds to be 2.66 mya, Ndessokia, 1990) suggest that a different array of habitats was present in the Laetoli area one million years after Laetolil Beds times. The most successful predictor elements, supported by relatively high probabilities associated with the habitat predictions, indicate that a wooded-bushed grassland environment dominated the region. However, a greater number of specimens included in less successful analyses also indicate that there was a significant amount of light woodland-bushland nearby.

The evidence from the specimens predicted to the montane light cover and montane heavy cover categories may support these conclusions. Although caution must be exercised when using these particular data, as there are relatively few specimens to consider and it is unknown if they are affiliating with these groups on the basis of factors which do not relate to habitat per se (i.e. phylogeny of the Caprinae as described above), a potentially informative trend between the two beds can be noted here, as well. Of the montane predictions in the Laetolil Beds, of which there are 31 overall, 67.7% of them are predicted to belong to the montane heavy cover category and with a much stronger associated average confidence value (.56 as opposed to .46 for the ten montane light cover individuals). Although there were only 13 individuals in the Ndolanya Beds predicted to belong to either of the montane groups, 69.2% of them are predicted to belong to the light cover category. The remaining montane specimens in the heavy cover category have a higher associated probability (.58 compared to .42), but there are fewer of them and it appears that the light cover category is better represented. Laetoli was not mountainous in the past, but these montane predicted individuals may possess adaptations to the amount of vegetation cover, which are shared with non-montane species and the analyses have picked up on this fact.

During the roughly one million years separating the time of the deposition of the Upper Laetolil and Upper Ndolanya Beds, the Laetoli region underwent a significant environmental change. The *types* of habitats in the area had not altered, but their relative proportions to one another certainly did. The Laetolil Beds time period was characterised by heavy cover woodland-bushland interspersed by areas of lighter cover that included grassland, although not grassland that was completely free of trees and shrubs. By the time of the Ndolanya Beds era, heavy cover areas had given way to the spread of more lightly covered woodland-bushland and grassland areas. The Laetoli region had become less wooded, more open and most likely drier.

7 DISCUSSION

This project aimed to achieve two main goals: the development of an ecomorphological method for palaeoecological investigation and the use of this methodology in reconstructing the palaeoenvironment at Laetoli, Tanzania during the two time periods represented by the Laetolil Beds (3.5 – 3.8 mya) and the Ndolanya Beds (2.66 mya). The first section below discusses some of the statistical considerations that arise from the use of a discriminant function analysis for habitat prediction. The sections following that address the interpretation of the analyses of the Laetoli material and then provide a general picture of palaeoenvironmental conditions in East Africa as they relate to hominid evolution.

7.1 Statistical considerations

Discriminant function analyses have long been the favoured statistical technique for predicting the habitat affiliation of both extant and fossil bovid species in ecomorphological studies (Kappelman, 1991; Kappelman *et al.*, 1997; Plummer & Bishop, 1994; DeGusta & Vrba, 2003). The implicit assumptions of this type of analysis, the procedures for conducting it, and considerations of the baseline of accuracy as it changes with the amount of predictor and grouping variables was investigated in Chapter 3. The previous chapter addresses the relationship between the probabilities associated with the predictions for group affiliation and the overall rate of success of each analysis. These are aspects of the DFA which need to be considered when using this method regardless of the type of data to which the DFA is applied.

However, in using the kind of biological data included in this project, there is another set of concerns relating to both the taxonomic composition of the dataset and the body size range encompassed by it. Although the elements studied may also discriminate on the basis of taxonomy and body size using different combinations of predictor variables to calculate the appropriate discriminant functions, this was not the goal of the present study. However, it must be asked if these factors are influencing the habitat predictions.

The predictor variables are measurements of postcranial elements of a number of *evolutionarily related* species. They will share a complex evolutionary history and thus possess morphological adaptations that reflect their phylogenetic relationships. The aim of an ecomorphological analysis is to determine morphologies which relate to similar patterns of habitat exploitation rather than phylogeny, but bovids in particular are known to be relatively taxonomically consistent in terms of habitat exploitation (Vrba, 1980, 1984, 1987, 1988). Hence, the attractiveness of relying on bovid indicator species to indicate environmental conditions or the application of Vrba's alcelaphine-antilopine criteria, in which the underlying principle is the observation that these two tribes prefer more open settings compared to other tribes in Africa. A further consideration is that a discriminant function analysis uses the specimens in the dataset to define the morphology that represents each group, so that these definitions can change according to which species are included in each habitat category. It is worth asking how much the species composition of the dataset drives the habitat predictions.

Another major issue is the extent to which the range of body sizes represented by the species included in the dataset affect the results (a discussion of body size was included in Section 3.4, and Table 3.8 summarises the species average body weights for those included in the modern dataset). Habitat exploitation is conditioned by a combination of ecovariables including body size, phylogeny, dietary preferences and locomotor repertoire. Research conducted to date has not been able to discern consistent rules for identifying the relationships between these variables. However, the fact remains that size is a limiting factor for mammalian habitat use and is the most easily quantified ecological variable. Some of the measurements included in the analyses will certainly relate to and predict body size. Since this is a factor in habitat use and the most obvious difference between the modern species, it is wise to question if the analyses are predicting the body size of the specimens rather than their preferred habitats, so that the correct habitat predictions are merely a result of this overriding relationship.

The following two sections address these potentially confounding statistical considerations. Firstly, the taxonomic composition and sampling of the modern comparative dataset used in this project are discussed. Secondly, the issue of body size is examined.

7.1.1 Effect of taxonomy and sampling on discriminant function analyses

The dataset used in this project represents the full range of variation that is observed in extant bovids. Their geographical, trophic, body size, habitat and taxonomic differences are all encompassed in the sample, with only one exception. Of the twelve accepted bovid tribes (see Table 2.2), only one is missing from the present analysis (see Table 3.1). There was no methodological reason for not including members of the tribe Boselaphini in the subfamily Bovinae, but the material was simply not available in the museum collections where the specimens were measured.

However, despite the lack of boselaphines, Bovinae is well represented in relation to the other subfamilies.

The dataset also included 14 cervids and 5 tragulids. These related taxa share similar morphologies with bovids so that taking the same measurements did not require changes in the measuring protocol and they were easy to compare. These species inhabit similar diverse environments as bovids, and presumably adaptations to them, and they were included for this reason. In order to investigate if the inclusion of species from other mammalian families affected the predictive power of the analyses, a number of elements were analysed both with and without the cervids and tragulids (these analyses were not reported). The overall success rates varied by only a few percent in each case and thus it was assumed that their inclusion was informative and that they did not have a confounding effect on the model.

In gathering the dataset an attempt was made to represent all possible ranges of taxa, body sizes and habitats, but more specifically to have comparable numbers within each of these variables. However, group sizes did naturally vary as the result of availability of specimens. Historical interests in the fauna of particular areas and continents has biased the species compositions of many collections and furthermore, rare species are often under-represented or exist only as zoo specimens, which were not included in the dataset. So, for example, there was an abundance of *Tragelaphus scriptus* (11) and *Budorcas taxicolor* (9) but fewer of the other species. Taxa which range in Asia, such as the Caprinae, were especially difficult to locate.

This is an important consideration because the discriminant functions which are calculated to predict habitat affiliation are based on the exact modern sample that is entered into the model. The morphologies that the analysis uses to define the norm for each habitat will therefore rely more on the specimens that are over-represented. It is also expected that the inclusion or exclusion of particular species may have an effect, especially for those which are particularly distinct. To date, only DeGusta & Vrba (2003) have addressed the issue of taxonomic composition and they did so in two different ways.

Firstly, they "equalised" their dataset by either duplicating or deleting the specimens so that each species was represented by the same number of individuals. Their analysis was rerun with this modified dataset and the overall classification success rate was similar to their original analysis. The habitat predictions changed for less than 10% of the specimens and these were specimens which had low probabilities associated with their predictions in the original analysis and were therefore more likely to be misclassified when the dataset was modified and the calculated discriminant functions changed slightly.

Secondly, they removed each species in turn and ran the analysis again. Success rates varied between 63% and 70%, which fall only 3.7% on either side of the classification rate of their original analysis. The omitted specimens were then entered into the analysis as ungrouped cases. Misclassifications of these specimens were focused on four particular taxa: *Antidorcas marsupialis* (the South African springbok, not included in the dataset used here), *Cephalophus sylvicultor* (the yellow-backed duiker of central and southern Africa, also not included here), *Taurotragus oryx* and various *Gazella*. This suggests that the analysis is indeed sensitive to the inclusion of certain distinctive taxa but that it is generally robust.

Three of the species that DeGusta & Vrba (2003) found were misclassified were *Antidorcas marsupialis*, the springbok, *Cephalophus sylvicultor*, the yellow-backed duiker and *Taurotragus oryx*, the common eland. These are indeed unique in certain behaviours and possess morphologies that relate to them. The springbok is an antilopine which resembles related gazelle species. It has the peculiar habit of "pronking" when it is alarmed, a predator avoidance behaviour which involves leaping up to 3 or 4 meters into the air with a curved back and lowered head. The yellow-backed duiker is one of the largest cephalophines and is indeed much larger than the others included in their dataset. It spans the range of 45 – 80 kg compared to the next largest cephalophine, the black duiker, *Cephalophus niger*, which weights between 9 and 24 kg. The yellow-backed duiker is also known to climb termite mounds and other objects in order to observe its territory.

The common eland is a large-bodied Bovinae. Although its great size is not atypical for the bovines, it is by far the largest bovid included in their dataset by some 300 kg. If they had included other large-bodied forms it would not have been anomalously large and most likely would not have been misclassified to such an extent which, in fact, DeGusta & Vrba (2003) conclude. However, it is interesting that 75% of the elands were predicted to belong to the heavy cover habitat category rather than open. Considering that the majority of the remaining tragelaphines in DeGusta & Vrba's (2003) dataset belonged to the heavy cover and forest categories, it is more likely that phylogeny is at the root of the eland's misclassifications.

Based on the findings of DeGusta & Vrba (2003), the analyses conducted in this thesis were not repeated with the removal of individual species in order to investigate the varying success rates. It was assumed that the dataset was large and diverse enough that this would have had little impact on the overall classification results. However, the taxonomic composition of the individual habitat groups is biased in some of the habitat categories and this must be considered as a reason for certain species misclassifications.

This project involved the use of a dataset with an unequal number of specimens in each habitat group and unequal sample sizes of species within those groups. The numbers of species in each habitat group are listed in Table 7.1, although obviously these numbers changed somewhat according to the element that was analysed and its availability (dataset summaries for the individual analyses can be found in Appendix D). It is clear from this table that three of the groups had many fewer specimens overall – the grassland/tree-less, montane light cover and montane heavy cover categories with 17, 18 and 21 specimens, respectively. The grassland/tree-less category is taxonomically diverse, with four subfamilies represented, while the montane categories are composed almost entirely of the three tribes in the subfamily Caprinae with only an additional 6 cervids in the montane heavy cover group. This is an unavoidable circumstance as the caprines are the only true mountain dwelling extant bovids. Although taxonomic diversity in all of the habitat groups would support the conclusion that the analyses which yielded high success rates were truly predicting habitat and not deriving their successful predictions based on close taxonomic relationships within the group, if the species are not naturally inhabiting a wide range of ecological niches they can not be forced into other categories.

In simplifying the range and diversity of the habitats which bovids exploit by creating a seven category classification scheme, and in addition to the natural variation observed within and between bovids species, it is unlikely that the overall success rates of the analyses would be much higher than those yielded by the best predictors in this project, which were in the range of 60.7% (distal metacarpal, size corrected data) to 68.5% (humerus, size corrected data). This agrees with the 67% obtained by DeGusta & Vrba (2003). However, a closer look at the success rates

Table 7.1. Taxonomic composition of the habitat groups

Species	Subfamily	Tribe	Number
GRASSLAND			
Total number of specimens = 17			
Procapra picticaudata	Antilopinae	Antilopini	2
Bison bison	Bovinae	Bovini	7
Ovibos moschatus	Caprinae	Ovibovini	4
Damaliscus dorcas	Hippotraginae	Alcelaphini	1
Damaliscus lunatus	Hippotraginae	Alcelaphini	2
Addax nasomaculatus	Hippotraginae	Hippotragini	1
WOODED-BUSHED GRASSLAND			
Total number of specimens = 49			
Antilope cervicapra	Antilopinae	Antilopini	2
Gazella rufifrons	Antilopinae	Antilopini	2
Gazella soemmerringi	Antilopinae	Antilopini	2
Gazella speki	Antilopinae	Antilopini	2
Gazella subgutturosa	Antilopinae	Antilopini	2
Gazella thomsoni	Antilopinae	Antilopini	4
Madoqua guentheri	Antilopinae	Neotragini	1
Ourebia ourebi	Antilopinae	Neotragini	5
Raphicerus campestris	Antilopinae	Neotragini	6
Alcelaphus buselaphus	Hippotraginae	Alcelaphini	4
Connochaetes gnu	Hippotraginae	Alcelaphini	1
Connochaetes taurinus	Hippotraginae	Alcelaphini	4
Damaliscus hunteri	Hippotraginae	Alcelaphini	3
Hippotragus equinus	Hippotraginae	Hippotragini	2
Kobus kob	Reduncinae	Reduncini	5
Kobus leche	Reduncinae	Reduncini	1
Redunca fulvorufula	Reduncinae	Reduncini	3
LIGHT WOODLAND-BUSHLAND			
Total number of specimens = 52			
Gazella cuvieri	Antilopinae	Antilopini	2
Gazella granti	Antilopinae	Antilopini	4
Litocranius walleri	Antilopinae	Antilopini	5
Sylvicapra grimmia	Antilopinae	Cephalophini	6
Oreotragus oreotragus	Antilopinae	Neotragini	4
Raphicerus sharpei	Antilopinae	Neotragini	3
Syncerus caffer	Bovinae	Bovini	3
Taurotragus oryx	Bovinae	Tragelaphini	3
Odocoileus virginianus	Cervidae		4
Aepyceros melampus	Hippotraginae	Alcelaphini	7
Hippotragus niger	Hippotraginae	Hippotragini	5
Oryx beisa	Hippotraginae	Hippotragini	2
Redunca redunca	Reduncinae	Reduncini	4

Table 7.1, cont. Taxonomic composition of the habitat groups

Species	Subfamily	Tribe	Number
HEAVY WOODLAND-BUSHLAND			
Total number of specimens = 32			
Madoqua kirki	Antilopinae	Neotragini	4
Madoqua saltiana	Antilopinae	Neotragini	1
Neotragus batesi	Antilopinae	Neotragini	2
Neotragus moschatus	Antilopinae	Neotragini	1
Neotragus pygmaeus	Antilopinae	Neotragini	1
Kobus defassa	Reduncinae	Reduncini	5
Taurotragus derbianus	Bovinae	Tragelaphini	2
Tragelaphus scriptus	Bovinae	Tragelaphini	11
Tragelaphus speki	Bovinae	Tragelaphini	1
Tragelaphus strepsiceros	Bovinae	Tragelaphini	4
FOREST			
Total number of specimens = 35			
Cephalophus leucogaster	Antilopinae	Cephalophini	2
Cephalophus monticola	Antilopinae	Cephalophini	5
Cephalophus nigrifrons	Antilopinae	Cephalophini	6
Bos javanicus	Bovinae	Bovini	3
Bos sauveli	Bovinae	Bovini	2
Bubalus mindorensis	Bovinae	Bovini	1
Tragelaphus eurycerus	Bovinae	Tragelaphini	3
Alces alces	Cervidae		4
Hyemoschus aquaticus	Tragulidae		5
MONTANE LIGHT COVER			
Total number of specimens = 18			
Capra sibirica	Caprinae	Caprini	3
Ovis ammon	Caprinae	Caprini	2
Ovis canadensis	Caprinae	Caprini	2
Ovis dalli	Caprinae	Caprini	2
Ovis vignei	Caprinae	Caprini	3
Pseudois nayaur	Caprinae	Caprini	2
Oreamnos americanus	Caprinae	Rupicaprini	2
Rupicapra rupicapra	Caprinae	Rupicaprini	2
MONTANE HEAVY COVER			
Total number of specimens = 21			
Elaphodus cephalophus	Cervidae		4
Pudu mephistophiles	Cervidae		2
Budorcas taxicolor	Caprinae	Ovibovini	9
Nemorhaedus crispus	Caprinae	Rupicaprini	2
Nemorhaedus goral	Caprinae	Rupicaprini	3
Nemorhaedus sumatraensis	Caprinae	Rupicaprini	4
Nemorhaedus swinhoei	Caprinae	Rupicaprini	1

within the habitat categories further infers that the taxonomic sampling did have some affect on the predictive power of the analyses.

This is very clear when one compares the success rates between the three aforementioned habitat categories: grassland/tree-less, which is a small group that is taxonomically diverse and the two montane categories, which are both small and taxonomically homogenous. For instance, compare their percentages of correct classification from the analyses of the size corrected long bone data (which had success rates over the baseline of accuracy) in Table 7.2. The grassland/tree-less category has a success rate that is 50.0% or higher in only four analyses, compared to 10 for montane light cover and 11 in montane heavy cover. Thus, it appears that the specimens are generally predicted to belong to the montane categories more successfully than grassland/tree-less. The high success rate of the montane groups relates both to these species' unique morphologies (e.g. Köhler, 1993) and the taxonomic homogeneity in the two montane categories.

Figure 7.1 displays this trend in a line graph. For the analyses of the humerus, metacarpal, metatarsal, femur and radius, the success rates are relatively high in all three groups, with the one exception of the grassland/tree-less category in the femur analysis. However, after the radius analysis, which had an overall success rate of 61.0%, no more than 23.5% of the specimens are correctly predicted to the grassland/tree-less category, whereas the montane categories are markedly more successful until the tibia analysis at which point the percentages of correct classification decrease (with the exception of an anomalously high 72.0% in the montane heavy cover category in the proximal metatarsal analysis). This is most likely the double-effect of both the habitat *and* taxonomic similarities in the montane groups.

Table 7.2. Success rates within the grassland/tree-less and two montane categories from analyses of the size corrected long bone data that yielded overall percentages of correct classification over the baseline of accuracy

Element	% correct overall	% correct grassland/ tree-less	% correct montane light cover	% correct montane heavy cover
humerus	**68.5**	76.5	93.3	87.5
metatarsal	**67.9**	73.3	77.8	80.0
metacarpal	**67.6**	60.0	93.3	68.0
femur	**66.2**	29.4	85.7	82.4
radius	**61.0**	58.8	93.8	73.3
distal metacarpal	**60.7**	20.0	68.8	80.0
proximal femur	**54.1**	17.6	80.0	76.5
distal metatarsal	**50.2**	0.0	27.8	76.0
distal humerus	**47.8**	23.5	66.7	68.8
distal metapodial	**47.2**	3.3	50.0	62.0
distal femur	**46.7**	0.0	56.3	47.1
tibia	**42.9**	7.7	35.3	20.8
proximal metatarsal	**40.9**	0.0	5.6	72.0
proximal radius	**39.2**	11.8	47.1	46.7

Percentages of correct classification between 50.0 - 100.0% have been coloured yellow and 25.0 - 49.9% have been coloured orange. The two taxonomically homogenous montane categories have higher success rates than the taxonomically diverse grassland/ tree-less category.

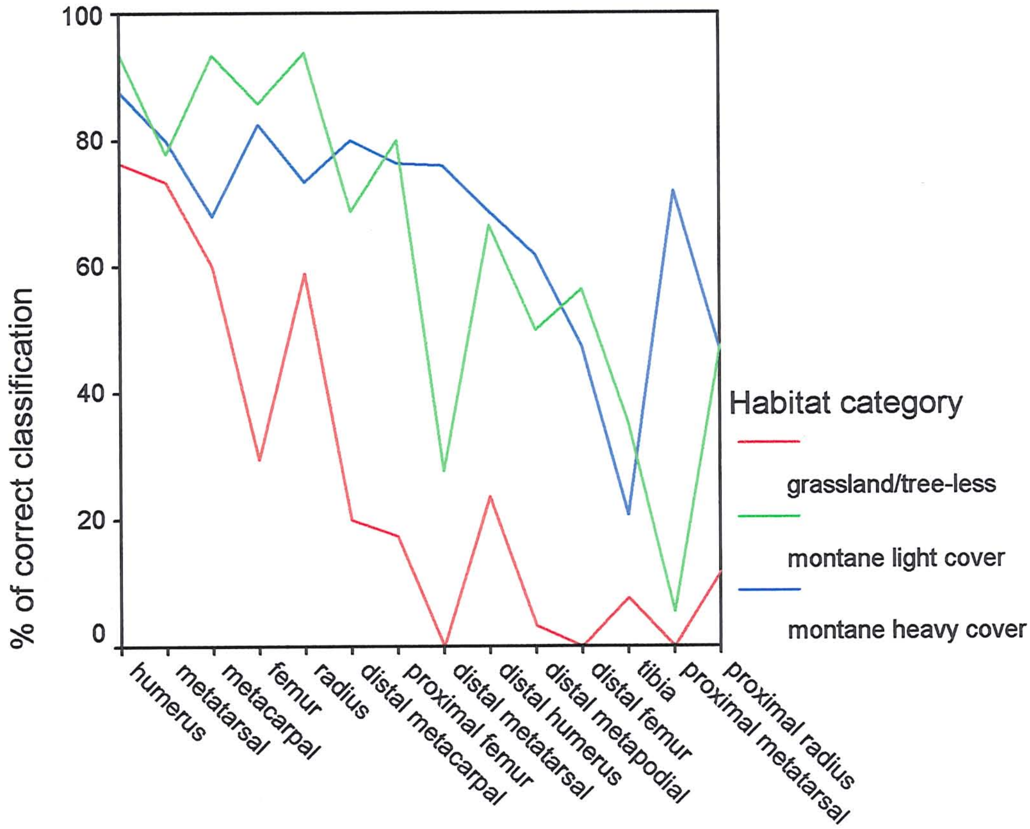


Figure 7.1. A comparison of the success rates within three habitats: the taxonomically diverse grassland/tree-less category and taxonomically homogenous montane light cover and montane heavy cover. The fourteen analyses displayed are those that yielded overall percentages of correct classification which were over the baseline of accuracy; they are presented as the best on the left to the worst on the right. The montane categories are consistently higher than grassland/tree-less, which never rises above 23.5% after the radius analysis, which had an overall success rate of 61.0%.

The misclassified grassland/tree-less species in the size corrected femur analysis further supports the point that taxonomic sampling can affect the outcome of the analyses. An anomalously low percentage of these specimens (29.4%) were correctly classified in an otherwise robust analysis which yielded an overall success rate of 66.2%. The classification results (Table 7.3) indicate that the 12 misclassified specimens were spread throughout four of the remaining six habitats. Table 7.4 lists the misclassified species and the incorrect habitat categories to which they were assigned. Four musk ox, *Ovibos moschatus*, have been wrongly assigned to the montane heavy cover category, most likely because this species is an ovibovine and it is affiliating with the other ovibovine (*Budorcas taxicolor*) within that category.

The remaining 8 misclassified specimens may also be affiliating with related taxa in other habitats, although this is less clear-cut than the case with the musk ox because the incorrect categories to which they were assigned are not as taxonomically consistent as the montane categories. None the less, these five species are assigned to categories comprised of ample numbers of members of their tribe (Table 7.1). Both the *Damaliscus dorcas* and *Damaliscus lunatus* specimens were assigned to wooded-bushed grassland, the habitat with the greatest number of alcelaphines, and *Addax nasomaculatus* was assigned to light woodland-bushland, where the majority of the hippotragines are placed. Two *Bison bison* were assigned to light woodland-bushland and another to forest, both categories with other bovines to which they likely bear morphological similarities. *Procapra picticaudata* may also be affiliating with related antilopini in the light woodland-bushland category, although there are also a number from this tribe in the wooded-bushed grassland category, as well.

Given the number of elements studied in this project, and the total number of analyses which were conducted, it was not possible to investigate the

Table 7.3. Classification results table from an analysis of the size corrected femur data

Classification Results[a]

			Predicted Group Membership							
		HABITAT	grassland/ tree-less	wooded-bushed grassland	light woodland-bushland	heavy woodland-bushland	forest	montane light cover	montane heavy cover	Total
Original	Count	grassland/tree-less	5	2	5	0	1	0	4	17
		wooded-bushed grassland	0	33	9	4	0	0	0	46
		light woodland-bushland	4	10	29	4	4	0	0	51
		heavy woodland-bushland	1	2	6	21	2	0	0	32
		forest	1	0	2	3	23	0	1	30
		montane light cover	0	0	0	0	0	12	2	14
		montane heavy cover	0	0	0	0	3	0	14	17
	%	grassland/tree-less	29.4	11.8	29.4	.0	5.9	.0	23.5	100.0
		wooded-bushed grassland	.0	71.7	19.6	8.7	.0	.0	.0	100.0
		light woodland-bushland	7.8	19.6	56.9	7.8	7.8	.0	.0	100.0
		heavy woodland-bushland	3.1	6.3	18.8	65.6	6.3	.0	.0	100.0
		forest	3.3	.0	6.7	10.0	76.7	.0	3.3	100.0
		montane light cover	.0	.0	.0	.0	.0	85.7	14.3	100.0
		montane heavy cover	.0	.0	.0	.0	17.6	.0	82.4	100 0

a. 66.2% of original grouped cases correctly classified.

Table 7.4. Misclassifications of grassland/tree-less individuals from a discriminant function analysis of the size corrected femur data

Species	**Number misclassified**	**Total number in dataset**	**Predicted group**
Addax nasomaculatus	1	1	light woodland-bushland
Bison bison	3	7	light woodland-bushland (2) and forest (1)
Damaliscus dorcas	1	1	wooded-bushed grassland
Damaliscus lunatus	1	2	wooded-bushed grassland
Procapra picticaudata	2	2	light woodland-bushland
Ovibos moschatus	4	4	montane heavy cover
TOTALS	12	17	2 wooded-bushed grassland 5 light woodland-bushland 1 forest 4 montane heavy cover

misclassifications in every instance. However, examples of the misclassifications of the forest taxa from the analyses of the humerus and of the heavy woodland-bushland taxa in the analyses of the proximal phalanges were also provided earlier in Sections 4.2.1, 4.2.2, 5.2.1 and 5.2.2. The reasons for these misclassifications also related to either the taxonomic sampling within the habitat groups or, in other cases, unique behaviours or ecological preferences (and thus the morphologies which relate to them) that are displayed by the misclassified taxa.

For example, in the first instance, sampling was posited as the reason for the misclassification of a number of the heavy woodland-bushland species in the proximal phalanges analyses. This category is dominated by tragelaphines and thus the majority of the misclassified taxa belonged to other tribes. In the second instance, unique ecological circumstances may account for the misclassification of the bongo, *Tragelaphus eurycerus*. The recent spread of forest environs possibly "trapped" the bongo, which has remained a relic woodland species in a predominantly forested habitat.

It is interesting to note than in many instances, the misclassified specimens have been placed into a category which is, if one considers the habitats to lie on a spectrum of vegetation cover, "next to" it's correct habitat on the spectrum. More specifically, the wooded-bushed grassland and light woodland-bushland category often experience a number of misclassifications between them and likewise for the heavy woodland-bushland and forest categories. It is likely that if these categories were combined, the success rates would increase. The habitat scheme in that case would include fewer categories and would thus resemble the schemes utilised by other ecomorphologists (Kappelman, 1991; Plummer & Bishop, 1994; DeGusta & Vrba, 2003). It has been shown that utilising fewer grouping variables has the double-effect of increasing both the baseline of accuracy and the overall percentage of correct classification. However, the seven-habitat scheme was retained here in order to increase the variety of habitat types that can be identified.

7.1.2 Effect of body size on discriminant function analyses

Previous ecomorphological work on bovid long bones has sought to minimise the potentially confounding effects of body weight on the analyses. This was accomplished in two ways. Firstly, species with average body weights above 250 kg were excluded because in the larger weight categories differences in size and shape scaling occur (Scott, 1979). Secondly, the measurements used were transformed into ratios (Kappelman, 1988; Plummer & Bishop, 1994; Kappelman, *et al.*, 1997). The relationship between the ratios and indices used to predict habitat and species body weight were investigated for the femur (Kappelman, 1991; Kappelman *et al.*, 1997) and the metapodials (Plummer & Bishop, 1994). Least squares regressions and reduced major axis regressions of measurements of the distal and proximal femur against body weight (or femoral length as a proxy for body weight) indicated that although the r^2 values were all generally low, a number of the correlations were statistically significant. The one exception was the relationship between femoral head area and body weight, which yielded an r-value of 0.988. Femoral head area can therefore be used to predict bovid body mass (Kappelman *et al*, 1997). Other quantifiable characteristics of the femoral head are also known to relate to body mass in other taxa (Ruff, 1988).

Plummer & Bishop (1994) followed a similar procedure in order to investigate the size dependence of their metatarsal and metacarpal ratios. The metapodial ratios of each individual were regressed against their calculated femoral lengths as a proxy for body size. The resulting correlation coefficients were also low. The highest r^2 value was 0.306 and related to the ratio describing the medio-lateral mid-shaft diameter and length of the metatarsal. Despite the weak correlations a number of them were also statistically significant, indicating that body size does explain some, but not a great deal, of the variance observed between the ratios.

The femoral measurements included in Kappelman's (1991) and Kappelman *et al.*'s (1997) studies were used to calculate discriminant functions which accurately predicted the habitat affiliation of a sample of bovids into a three and four habitat classification system with success rates between 73% and 85%. Plummer and Bishop (1994) also had high success rates between 60% and 89%. Although it was shown that the measurements used in these analyses were correlated to body weight, it was inferred that this factor was not driving the analyses and their habitat predictions because the correlations were weak.

However, Kappelman *et al.* (1997) do suggest that bovid body weights increase as the amount of vegetation cover decreases and therefore weight estimates from the femoral head area can be used to roughly sort fossil material into broad habitat types. There are some problems with this assumption and the data on which it was based. Firstly, there are a number of taxa which defy this rule, including certain tragelaphines and reduncines which inhabit closed woodland and forest conditions despite their large body size. Kappelman *et al.*'s (1997) analysis also did not investigate a truly representative sample of bovid body weights and morphologies present either on an African or a global scale. Finally, although a broad division of habitats was once useful, current palaeoecological investigations seek to go beyond a simple tripartite division of habitat categories in order to provide greater detail about the environmental conditions that prevailed at specific times and places.

DeGusta & Vrba (2003) approached the issue of body weight in two different ways. There was a highly statistically significant correlation between their eight raw measurements of the talus (they also included one ratio that was not investigated in this manner) and body weight ($r^2 = 0.91$). However, if body weight was driving the habitat predictions, one could expect that the habitats would correspond to a discrete range of body weights that could be predicted using their regression equation. DeGusta & Vrba (2003) found that this was not the case and that there was significant overlap between the ranges of predicted body weights compared to predicted habitat types.

Their second investigation utilised a principal components analysis. The first component is commonly understood to account for size differences when dealing with this sort of data, and indeed they found that the variables that scored highly on this component scaled tightly with both species body weights and talar length (which they also found to be highly correlated to body size). Using the remaining components as predictor variables, they entered these into a discriminant function analysis in order to see if they could predict habitat correctly once the size component had been removed. This analysis resulted in a total of 54% of the specimens being correctly predicted, a 13% difference from their original analysis. They interpret this to mean that 13% of the difference between the morphologies of their four habitat groups is accounted for by body size rather than shape.

The particular interpretation that body size accounts for 13% of the variation in the original discriminant function is interesting and a similar experiment was conducted with the dataset used for the project reported in this thesis. A predictor element with an overall success rate similar to that of DeGusta and Vrba's (2003) talus analysis was selected. The non-size corrected femur analysis yielded a percentage of correct classification that was 66.7%, exactly the same as that from DeGusta and Vrba (2003). All of the non-size corrected variables (F2 – F14, see Table 3.4 for measurement definitions) were entered into a principal component analysis and thirteen components were computed. These thirteen components, the same number of components as original quantitative variables, were then entered into a discriminant function analysis. It yielded the exact same overall success rate of 66.7%. However, when the first component was removed as a variable, effectively taking the size component out of the analysis, and the discriminant function analysis repeated, the success rate only dropped to 64.7%. This suggests that a much smaller amount of variance (2.0%) can be accounted for by size differences between the femora from the different habitat groups. As DeGusta and Vrba's (2003) findings indicate, the talus is an element that is more strongly linked to size compared to the femur. Although it was beyond the scope of this project, an interesting avenue for future study would be to look at the remaining individual bovid elements to determine how much of the variance between habitat types is related to size.

The relationship between body size and habitat preference in the species in the dataset used in this thesis was not investigated any further in the manner reported above or following the procedures outlined in other ecomorphology studies. Firstly, based on the wealth of research investigating this link in bovids and their positive conclusions, it was assumed that there would be a statistically significant link between average body weight and the measurements on all of the elements considered. However, simple confirmations in the form of two Kruskall-Wallis tests were performed. They tested the relationship between both the average species body weight and habitat and between the six size categories used here (see Table 3.8) and habitat.

For the test of size category, $p = 0.006$, and the test of average species body weight also yielded a highly significant p-value of 0.000.

Secondly, the issue was approached from another experimental angle in which the data were size corrected by performing reduced major axis regressions of the average species body weight against all of the measurements and utilising the resulting residuals as size corrected data. The discriminant function analyses were conducted firstly with the logged (i.e. non-size transformed) data and secondly with the size corrected data. Tables 4.16 and 5.15 in Section 4.2.3 and Section 5.2.3 present the overall success rates from these analyses of the good predictor elements. The difference between the success rates from the analyses of the logged and size corrected data was minimal and never exceeded 5.4%, which was the difference between the two analyses of the distal phalanges. This infers that size does not need to be removed from the data in order to accurately predict habitat based on the species and measurements used in this project. However, the discriminant functions that were calculated from both sets of data would have been different, with different combinations of variables accounting for the variation observed. Again another interesting avenue for further research would be to take an in-depth look at how the variables load on the functions from the different datasets in order to ascertain which measurements relate to size and which do not.

Although the analyses of the logged and size corrected data did not yield overall success rates that differed greatly between them, the success rates *within* the individual habitat groups did vary in some cases. An observation of these changes indicates that there is one habitat category for which there is a particularly strong link between body size and habitat. Table 7.5 presents the percentages of correct classification within the grassland tree-less category for every analysis that yielded a

Table 7.5. Percentages of correctly classified grassland/tree-less specimens in the logged and size corrected analyses

Element	% correct overall	% correct logged analyses	% correct size corrected analyses
LONG BONES			
humerus	**68.5**	76.5	67.7
femur	**67.9**	64.7	29.4
metatarsal	**67.6**	80.0	73.3
radius	**66.2**	47.1	58.8
distal metacarpal	**61.0**	66.7	20.0
proximal femur	**60.7**	52.9	17.6
distal humerus	**54.1**	52.9	23.5
distal metatarsal	**50.2**	46.7	0.0
tibia	**47.8**	7.7	7.7
distal metapodial	**47.2**	50.0	3.3
distal femur	**46.7**	23.5	0.0
proximal radius	**42.9**	64.7	11.8
CARPALS, TARSALS, PHALANGES			
proximal phalanges	**57.1**	59.3	37.0
distal phalanges	**55.8**	72.7	45.5
lunar	**53.2**	43.8	18.8
intermediate phalanges	**51.9**	65.4	53.8
magnum	**51.2**	73.3	66.7
unciform	**51.0**	50.0	7.1
naviculo-cuboid	**47.1**	12.5	12.5
cuneiform	**40.6**	66.7	6.7
pisiform	**39.4**	53.8	15.4

Percentages of correct classification over 60.0% have been coloured yellow and between 40.0 and 59.9% have been coloured orange. Only analyses with overall success rates over the baseline of accuracy and for which both sets of data were analysed for each element are listed. The logged analyses are consistently more successful, inferring that size is related to the exploitation of grassland/tree-less habitats.

success rate that was above the baseline of accuracy for both sets of data. The logged analyses are consistently better able to correctly predict the grassland/tree-less specimens, while the analyses which were conducted on the size corrected data fail to do so in all but the humerus, metatarsal, radius, intermediate phalanges and magnum analyses. From this it can be inferred that body size is the overriding similarity between these specimens and that when its effect is removed, the general morphologies of these specimens fail to resemble one another in any significant manner. It is likely that at this point the species bear a greater resemblance to those which are taxonomically related.

All of the evidence from both previous ecomorphological analyses and the ones reported herein indicates that there are undoubtedly relationships between bovid body weight and habitat exploitation. However, we are a long way from determining the particular circumstances that dictate the nature of these relationships or from even determining which morphologies relate more to one variable than the other or which measurements relate to them in equal parts. There is, as of yet, no sound reason to use bovid body size distributions to determine habitat types (indeed, when entire faunal communities from different habitats are analysed, they show no distinguishable difference between size distributions - Andrews, 1979), nor is there a reason to remove the effect of body size from ecomorphological analyses. The fact that correcting for size decreases the discriminating power within one of the habitat types (grassland/tree-less) further supports this. Furthermore, there is no evidence from any ecomorphological work conducted to date that body size drives habitat predictions.

7.2 Laetoli

Initial palaeoecological analyses of Laetoli focused purely on the Upper Laetolil Beds, which are more productive and cover a much greater area than the Ndolanya Beds or any other strata representing different depositional phases. The Upper Laetolil Beds produced a number of important finds including the "Footprint Tuff" (Leakey & Hay, 1979) and the type specimen of *Australopithecus afarensis* (Johanson, White & Coppens, 1978). Radiometric dating of these beds has bracketed them between 3.8 mya and 3.5 mya (Drake & Curtis, 1987). Until recently, there had been no hominid finds in other beds other than an early *Homo sapiens* from the Ngaloba Beds (Day *et al.*, 1980), although *Paranthropus aethiopicus* is now known during the Upper Ndolanya Beds times (Harrison, 2002). However, as the result of its high productivity, especially of early hominid fossils, the Upper Laetolil Beds remained the focus of most research for quite some time.

A wide range of evidence was used to support the initial conclusion that the Upper Laetolil Beds represented an arid to semi-arid grassland with some light bush and/or tree cover. The majority of this work was reported and synthesised to form this final conclusion in the Laetoli monograph in 1987 (Leakey & Harris, 1987). Pollen signatures pointed to a dominance of grassy vegetation over other herbaceous and arboreal types (Bonnefille & Roillet, 1987). The widespread wind transportation of large ash particles indicates there was a lack of vegetation capable of preventing it, and furthermore the mineral phillipsite is cemented to the ash particles, a situation that most likely occurred under alkaline conditions associated with seasonal semi-arid and arid environments (Hay, 1987).

The presence of particular species within individual mammalian families was also interpreted to suggest an open environment. Small and large carnivore communities indicated open and dry environs similar to those in the modern Serengeti (Barry, 1987; Petter, 1987) and the dominant presence of the hypsodont pig *Notochoerus euilus* (Harris, 1987) and the association of two rhinoceros (Guérin, 1987b) further infer a dry habitat. Taxonomic composition and ecomorphology of the rodent community indicated a dry climate with *Acacia* forming the main component of the arboreal vegetation (Denys, 1985; 1987). Bovids, too, seemed to point towards the existence of a more open non-woodland habitat, with the presence of Alcelaphini, Antilopini and Neotragini (Gentry, 1987). The evidence appeared unequivocal and the conclusion that the Laetolil Beds were deposited during a time when the area was dry and open was also qualified to some extent by the non-mammalian fauna (Watson, 1987).

However, even within the work reported in the original monograph (Leakey & Harris, 1987), there was some indication that the habitat of the Laetolil Beds may have been more wooded than was supposed. Quadrupedal chalicotheres, which are understood to have used their hindlegs for balance as they reached for and fed on young shoots and leaves (Chavanon, 1962) are present in the Laetolil Beds suggesting that tree and bush cover was available for their preferred feeding repertoire (Guérin, 1987a). The incidence of both tragelaphines and cephalophines also indicate more wooded habitats in the region and *Madoqua*, which is abundant at Laetoli, requires dense thicket and undergrowth to which they retreat when alarmed (Gentry, 1987). The diversity of the primate community, which includes a bushbaby, colobine and other cercopithecids, is indicative of a wooded habitat (Leakey & Delson, 1987; Walker, 1987). The presence of the woodland and forest suid *Potamochoerus*, the bush squirrel *Paraxerus* and the large elephant shrew *Rhynchocyon* further imply the availability of significantly wooded areas of land (Butler, 1987; Denys, 1987; Harris, 1987). There is also evidence from the invertebrates that there was thick vegetation or forest in the region (Verdcourt, 1987). Finally, the pollen signature presents a higher proportion of Afro-montane elements than is known in the modern pollen rain, indicating that wooded and/or forested regions were more important during the Laetolil time period (Bonnefille & Riollet, 1987).

A community ecology analysis was conducted on the Laetoli data in response to the monograph and its subtle indications that the presumed dry and open habitat prediction was too simple a scenario for the Upper Laetolil Beds (Andrews, 1989). Investigating the body size distributions, feeding preferences and locomotor repertoires exhibited by the identified mammalian species in the Laetolil community, this analysis found that the community bore a close resemblance to that which currently exploits the wooded end of the modern Serengeti habitat spectrum, observed to the west of the region today. Two similar analyses were conducted not long thereafter (Reed, 1997; Andrews & Humphrey, 1999). Both analyses concluded that the Laetolil Beds represent closed woodland habitats, probably more closed than any represented by the present day Serengeti types (Andrews & Humphrey, 1999). Although the Laetolil community is dominated by terrestrial species, the proportion of browsers to grazers and the percentages of both arboreal species and fruit eaters indicate that a significant number of species in the region relied on the tree component of the vegetation. This, in addition to the number of species which rely on tree cover or thicket for predator avoidance or sleeping (i.e. *Madoqua*), indicates that the open savanna interpretation of the Laetolil palaeoenvironment is incorrect.

Using the ^{40}Ar ^{39}Ar technique, the Upper Ndolanya Beds have been dated to 2.66 mya (Ndessokia, 1989) so the transition from the Upper Laetolil Beds lasted at least 850,000 years. This transition was marked by an observable change in both the taxonomic composition and structure of the mammalian community (Leakey & Harris, 1987). Mammal diversity was greater in the Laetolil Beds such that while bovids and lagomorphs comprise the greatest percentage of specimens found in the Laetolil Beds, bovids alone account for the greatest number of recovered fossils in the Ndolanya Beds.

It was previously suggested that aspects of the Ndolanya fauna indicate that the area had become more humid and possibly warmer, including the presence of the suid *Kolpochoerus* (Harris, 1987) and an association of rodents which includes the wetland species *Thryonomys* (Denys, 1987). However, at no time has there been standing water present in the Laetoli region (Hay, 1987) and the remaining rodents seem to infer arid conditions. The majority of the identified Ndolanya taxa do, in fact, seem to indicate more open and arid conditions than those implied by the fauna from the earlier deposits. The equid species present is remarkably more hypsodont than those found in the Laetolil Beds and the bovids are commonly open-country alcelaphines and antilopines (Harris, 1987).

More revealing is the mammal community structure, recently analysed by Kovarovic *et al.* (2002). Dominated by terrestrial species and a much greater proportion of grazers to browsers, it was reconstructed as a semi-arid bushland. This type of habitat provides abundant grass but also extensive bush and limited tree cover. The presence of a small number of arboreal and semi-arboreal species, including two primates and the rodent *Thallomys*, which is restricted to an arboreal existence in *Acacia* trees, further support this contention. Finally, allowing for some taphonomic loss of micromammals, the number of species present in the Ndolanya Beds, 44, approaches the number often found in tropical semi-arid bushlands that lack a permanent water source, and is greater than the average number of species found in more open grassland environments (Andrews *et al.*, 1979).

The results of the study reported in this thesis would agree with the interpretation of the Laetolil Beds as being closed woodland, which was also inferred by Andrews (1989), Andrews & Humphrey (1999) and Reed (1997). The results are summarised in Table 7.6. This table excludes the montane categories, which are discussed in Chapter 6 and, since it is not possible that Laetoli was a mountainous area and these predictions will not influence the interpretation of the palaeoecology, the discussion will not be repeated here. The majority of the specimens analysed from the Laetolil Beds were predicted to belong to the heavy woodland-bushland habitat category in the analyses with overall percentages of correct classification over 50%. A total of 98 specimens, or 52.1% of the total (N = 188) were predicted with an average associated probability of 56.9%. Smaller percentages were predicted to belong to three other habitats: 22.9% to light woodland-bushland, 12.8% to wooded-bushed grassland and 10.1% to forest.

The analyses which have overall percentages of correct classification under 50% present a slightly different trend. Only 14 individuals are predicted to belong to the heavy woodland bushland-category, which amounts to 11.5% of the total number of specimens included in these analyses (N = 122). A higher proportion is assigned to the light woodland-bushland category, 36.1%, while 15.6% are predicted to wooded-bushed grassland and 10.7% to forest. All of the predictions are supported with fairly weak probabilities, none of which are higher than the 45.5% in the heavy woodland-bushland category. The overall success rates of these analyses are lower, so the lower probabilities are unsurprising.

Table 7.6. Summary of the results from the Laetolil Beds

	grassland/ tree-less	wooded-bushed grassland	light woodland-bushland	heavy woodland-bushland	forest
Analyses with % of correct classification over 50%					
number (TOTAL = 188)	1	24	43	98	19
percentage of total	0.5	12.8	22.9	52.1	10.1
average probability	0.32435	0.55800	0.43261	0.56850	0.40954
Analyses with % of correct classification under 50%					
number (TOTAL = 122)	4	19	44	14	13
percentage of total	3.3	15.6	36.1	11.5	10.7
average probability	0.37293	0.41051	0.36789	0.45538	0.40313
All analyses					
number (TOTAL = 310)	5	43	87	112	32
percentage of total	1.6	13.9	28.1	36.1	10.3
average probability	0.36321	0.49283	0.39988	0.55436	0.40694

When all of the analyses are considered together, the predictive trend observed is similar to that from the more reliable analyses (those with percentages of correct classification over 50.0%), although the percentage of heavy woodland-bushland specimens drops to 36.1%. However, the associated probability for this habitat category is high, at 55.4%. 28.1% of the specimens are predicted to belong to light woodland-bushland, 13.9% to wooded-bushed grassland and 10.3% to forest. The highest average probability is always associated with the heavy woodland-bushland category, regardless of the set of analyses that are considered.

The strongest predictors and highest associated probabilities indicate that the Laetoli region was dominated by heavily wooded areas at the time of the deposition of the Laetolil Beds. This habitat type was most likely a permanent aspect of the landscape which was not associated with a riverine or lacustrine environment, as Laetoli has never possessed a permanent water source. The same is true of the area today. However, ephemeral streams may have supported greater amounts of dense growth on a seasonal basis. This conclusion is also supported by the wealth of other evidence described above and by the conclusions of community ecology analyses (Leakey & Harris, 1987; Andrews, 1989; Reed, 1997; Andrews & Humphrey, 1999). However, Laetoli was clearly not a homogenous environment. This is indicated by the remaining predictions in other habitat categories and the presence of particular taxa known to favour less wooded or grassier conditions. It is reasonable to assume that there were large tracts of land with fewer trees and that grass dominated the ground vegetation.

There has been less research conducted on the Ndolanya Beds, but the results from this project do not contradict the one major palaeoecological analysis completed to date (Kovarovic *et al.*, 2002) or any of the other inferences that have been based on pollen, fauna, or geography (Leakey & Harris, 1987). The results are summarised in Table 7.7. It is harder to base conclusions on the results of the analyses with overall success rates over 50.0% because there were very few specimens available for these analyses, a total of 44. However, the majority of the specimens were predicted to belong to the wooded-bushed grassland (43.2%) and light woodland-bushland (29.5%) category. A smaller proportion is assigned to heavy woodland-bushland (18.2%). The second highest probability, 53.1%, is associated with the wooded-bushed grassland habitat, the category to which the greatest number of specimens has been predicted. The highest probability, 69.1%, refers to only two specimens predicted to the forest habitat.

The trend in habitat prediction for the Ndolanya Beds is relatively consistent regardless of the set of analyses considered. The percentage of specimens predicted to the two dominant categories, wooded-bushed grassland and light woodland-bushland, is 36.5% and 38.1% in analyses with overall success rates under 50.0%, and 38.2% and 35.9% for all of the analyses combined. A much smaller number of specimens has been predicted to the grassland/tree-less, heavy woodland-bushland and forest habitats in each set of analyses. In fact, the highest probability is associated with the two forest specimens in the analyses with higher success rates (over 50%). This high probability infers that it is unlikely these specimens were misclassified. However, there is also no trouble conceiving that, despite the dominance of more open habitats, the Laetoli region during the Ndolanya Beds times was a mosaic of habitat types.

The results of these analyses are interpreted to infer that the Ndolanya Beds represent a time period in which the grass and scrub component of the environment had increased in importance since the Laetolil Beds had been deposited. Increasing aridty and seasonality most likely accompanied this change. Seasonal rains and

Table 7.7. Summary of the results from the Ndolanya Beds

	grassland/ tree-less	wooded-bushed grassland	light woodland-bushland	heavy woodland-bushland	forest
Analyses with % of correct classification over 50%					
number (TOTAL = 44)	1	19	13	8	2
percentage of total	2.3	43.2	29.5	18.2	4.5
average probability	0.37645	0.53082	0.44610	0.45258	0.69132
Analyses with % of correct classification under 50%					
number (TOTAL = 126)	7	46	48	8	5
percentage of total	5.6	36.5	38.1	6.3	4
average probability	0.48704	0.41981	0.39885	0.39492	0.35093
All analyses					
number (TOTAL = 170)	8	65	61	16	7
percentage of total	4.7	38.2	35.9	9.4	4.1
average probability	0.47321	0.45226	0.40892	0.42375	0.44819

resulting streams and rivers probably supported heavier growth, but this was likely to be an impermanent aspect of the landscape. However, its existence is supported by the presence of some heavy woodland-bushland and forest specimens in the Ndolanya community. These findings agree with Kovarovic *et al.*'s (2002) conclusion that Laetoli was a semi-arid bushland at this time.

In summary, the Laetoli region has displayed a great deal of ecological variability during the Pliocene. The region has always presented a mosaic of habitat types which were exploited by a wide variety of fauna, including hominids. Evidence from the bovid ecomorphology, supported by analyses of community ecology, pollen, and both non-mammalian and mammalian fauna, indicate that during the deposition of the Laetolil Beds 3.5 – 3.8 million years ago, the area was dominated by moderate to heavy woodland with a significant component of lighter tree cover and grass. In contrast, when the Ndolanya Beds were deposited 2.66 million years ago the area was dominated by both light woodland-bushland and more open grassy areas and the climate had most likely become drier and more seasonal.

7.3 Environment and evolution in East Africa

7.3.1 Palaeoenvironment at other East African sites

It is important to understand the environmental conditions at other East African sites in order to set hominid movements and evolution within a wider ecological framework. The palaeoecological reconstructions of sites of similar age to both the Upper Laetolil Beds (3.5 – 3.8 mya) and Upper Ndolanya Beds (2.66 mya) at Laetoli are provided below. Laetoli is the only site of its age in Tanzania, and the others are located in Chad, Ethiopia, Kenya and Malawi. All of the sites that are

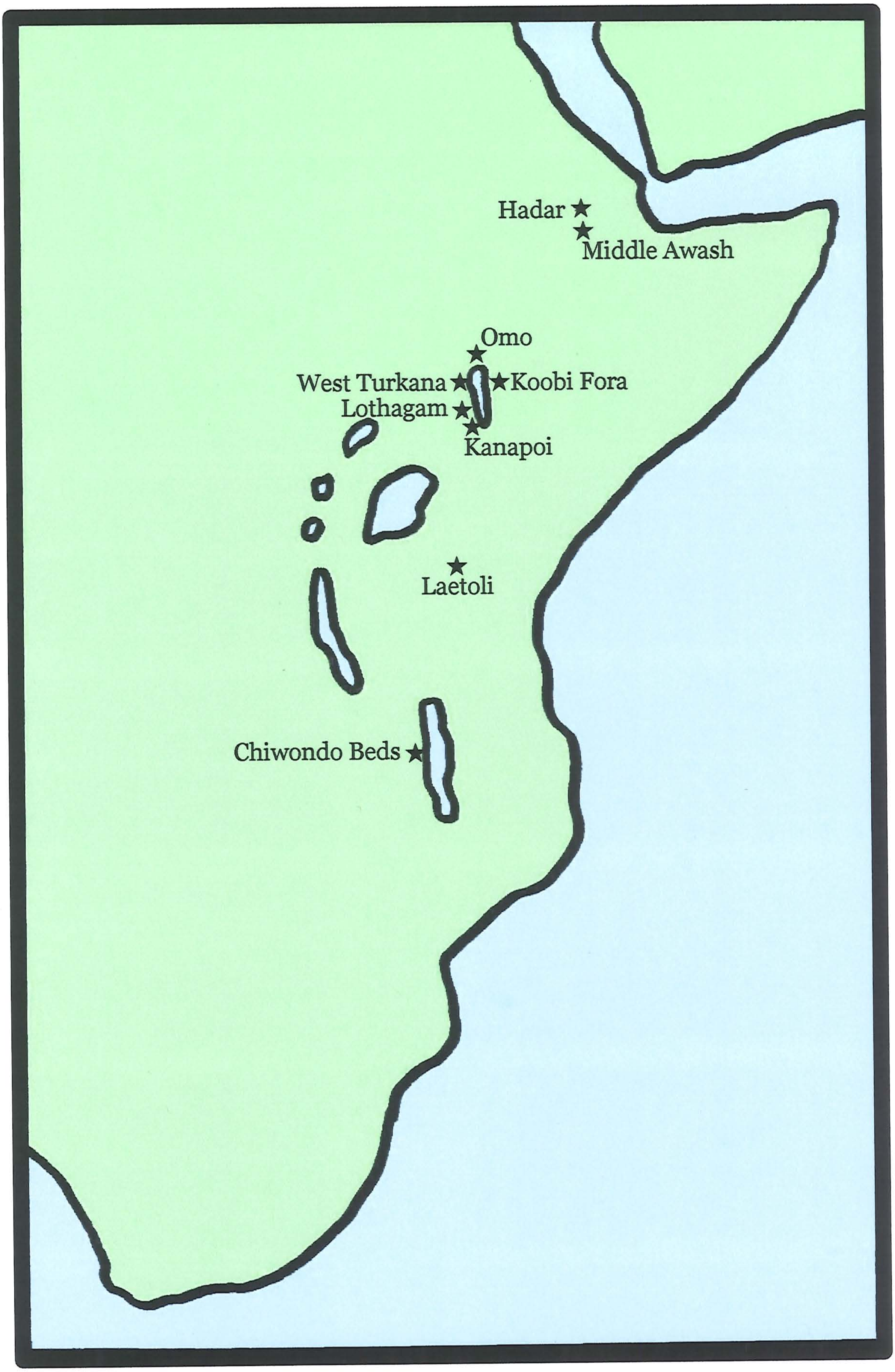


Figure7.2. Map of the East African Plio-Pleistocene sites mentioned in the text.

discussed are located on the map in Figure 7.2. They are listed below according to their geographical location, moving North to South along the Rift Valley system.

Hadar, Ethiopia (3.4 – 2.3 mya): Located in the Awash River Valley (but north of the sites located in what is commonly referred to as the Middle Awash), Hadar is a small site comprised of stream deposited sediments with some evidence for a lake that formed periodically and for only brief periods of time (Johansen *et al.*, 1982). There are four members, three of which bear hominid remains: the Sidi Hakoma Member (3.4 – 3.25 mya), Denen Dora Member (3.2 – 3.18 mya) and Kada Hadar Member (3.18 – 2.33 mya). Associated fauna have indicated that the palaeoenvironment fluctuated; during upper Kada Hadar times there was a lightly covered woodland with abundant grass, during the lower Kada Hadar and Sidi Hakoma times a dry woodland-bushland habitat predominated and a riverine forest in Denen Dora times was present (Kimbel *et al.*, 1996). However, palynological data (Bonnefille *et al.*, 1987; 2004) indicate that the vegetation communities prevalent in the Sidi Hakoma deposits were evergreen bushland and montane forest, replaced by grassland and associations of *Acacia* species by the Denen Dora Member. At approximately 2.9 mya the evergreen and montane communities returned (Bonnefille *et al.*, 1987). Community ecological analyses suggest a medium to open woodland was present during the Sidi Hakoma Member and that riparian woodland or forest may also have existed and furthermore that the Denen Dora Member was similarly wooded with forest regions near the water sources and edaphic grasslands (Reed, 1997). Bracketed between 3.4 and 2.9 mya, a great number of *Australopithecus afarensis* specimens have been derived from the Denen Dora deposits, the most well-known of which are the 40% complete "Lucy" skeleton and the remains of at least nine adults and four juveniles called the "First Family" (Johanson *et al.*, 1978; 1982;

Kimbel *et al.*, 1994). *Homo* specimens and associated lithic artefacts are found in the Kada Hadar Member beginning at 2.3 mya (Kimbel *et al.*, 1996).

Middle Awash, Ethiopia (4.4 – 0.6 mya): The Middle Awash region of Ethiopia is located along the Awash River, south of Hadar. The sediments which are older than 3.9 mya are lacustrine, while the sediments that post-date the palaeolake environment are riverine. The area encompasses a number of sites of various ages including Aramis, Maka, Gona, Bouri and Belohdelie, which have yielded hominid specimens from various species including *Ardipithecus ramidus*, *Australopithecus afarensis*, *Australopithecus garhi* and *Homo* (there are older Miocene sediments as well, but these deposits and their hominid remains are not discussed here). Recent stable isotope studies of the Middle Awash region suggest that the environment was gradually changing from a C3 vegetation signature, which indicates woodlands and forests, to C4 dominated vegetation, indicating a greater component of grassy areas (WoldeGabriel et al, 2001; Levin, 2004). The greatest shift in the signature occurs between 3 and 2 mya. The occurrence of numerous colobines and closed woodland adapted bovids in the earlier strata further supports the contention that a woodland habitat predominated in the area prior to the shift towards C4 vegetation. The mammalian community structure from Aramis indicates that at 4.5 mya the habitat was in the heavily wooded end of the vegetation cover spectrum, structurally similar to Miombo woodland (Andrews & Humphrey, 1999).

Shungura Formation (3.5 – 1.3 mya) **and Usno Formation** (3.36 – 3.0 mya) **Omo, Ethiopia**: These deposits are located in the lower basin of the Omo River where it enters Lake Turkana in Ethiopia. The fossiliferous Shungura Formation Members have been studied extensively for evidence of environmental change. Various lines of evidence including studies of fossil wood and pollen signatures and indicate that above Member C (2.95-2.6 mya) more open woodland and grassland communities replaced the more heavily covered woodland and riverine forest habitats (Bonnefille & Dechamps, 1983; Bonnefille, 1984; Eck & Jablonski, 1985). The faunal communities also point towards a shift towards drier and more open conditions throughout the members. Member B and C micromammals indicate a forest and humid wooded grassland mosaic with some evidence of drier wooded grassland present, but dry wooded grassland and steppe predominated by member F times (2.35 – 2.33 mya) (Wesselman, 1985). Bovids further support this change between Members B and G (Gentry, 1976). A comprehensive community analysis (Reed, 1997) indicates that Member B times were dominated by closed woodland and riverine forest and edaphic grassland but that between members C and F the closed woodland gave way to more open woodland-bushland. Much less material has derived from the Usno Formation deposits compared to the productive Shungura Formation members and therefore they have not been subjected to extensive palaeoecological analyses. However, Reed (1997) has suggested that the environment was a closed habitat with both bushland and thicket present, although an area of riverine forest also existed. Both formations have yielded hominid material, but the majority of it is derived from the Shungura Formation deposits between 2 and 3 mya. *Australopithecus afarensis* is known from both formations and dates to 3 mya, *Paranthropus aethiopicus* from 2.6 – 2.3 mya, *Paranthropus boisei* from 2.3 – 1.2 mya and fragmentary remains possibly attributable to *Homo habilis* from 2.3 – 1.3 mya (Howell *et al.*, 1987; Feibel *et al.*, 1989).

Koobi Fora Formation, Koobi Fora, East Turkana, Kenya (4.34 – 0.7 mya): Located on the northeastern shore of Lake Turkana in Kenya, the Koobi Fora Formation has a well-dated series of members which from 4.34 mya – 0.7 mya

(Brown & Fiebel, 1986). They comprise lacustrine, deltaic and fluvial deposits relating to the ebb and flow of the palaeolake's shoreline and the rivers and streams flowing to it, although after 2mya the lake has remained a permanent feature. Pollen and faunal studies have been used to determine the palaeoenvironment of the Plio-Pleistocene members. The Tulu Bor Member (3.33 – 3.0 mya) was most likely a flood plain with a gallery forest and the Burgi Member (3.0 – 2.0 mya) was a closed woodland that grew more open in the south (Harris, 1991). These interpretations were refined by Reed (1997) with an ecological community approach. She interpreted the community structure to infer a scrub woodland on a riverine floodplain for the Tulu Bor Member. However, in contrast to Harris' (1991) interpretation, she finds that the Burgi Member was more open than previously believed, with some evidence that edaphic grassland and riparian woodland were present in a predominantly open woodland environment (Reed, 1997). There are a number of hominids known from the Koobi Fora localities. Australopithecines and several species of *Homo* have been discovered in beds dating between 2.1 and 1.3 mya, including the *Homo* specimens KNM-ER 1470 (potentially *Homo rudolfensis*) and KNM-ER 1813 (potentially *Homo habilis*) from the Burgi Member, which many believe to show too much variation to be conspecific (e.g. Lieberman *et al.,* 1996).

Nachukui Formation, West Turkana, Kenya (4.3 – 0.7 mya): This is the same formation found at Lothagam, but further to the north along Lake Turkana. The most fossiliferous deposits are much younger than those to the south at Lothagam. The Plio-Pleistocene deposits have yielded many hominids, including a 3.2-3.2 mya *Australopithecus afarensis* and 3.5 mya *Kenyanthropus platyops* from the Lomekwi Member, the 2.5 – 2.4 mya Black Skull WT-17000, which is a *Paranthropus aethiopicus* cranium from the Lokalalei Member, a *Paranthropus boisei* in the later

2.3 – 1.6 mya Kaitio Member and fragmentary fossils that may represent *Homo habilis* in the Kalochoro member, which is slightly older than 2 mya (Feibel *et al.*, 1989). A basic palaeoecological model for the area proposes that the paranthropine localities represent closed and wet habitats and that the early *Homo* localities were more ecologically diverse and included both closed and wet and open and dry conditions (Shipman & Harris, 1988).

Lothagam, Kenya (5.0 - <3.9 mya): Located on the southwest edge of lake Turkana in Kenya, this site has yielded a mandibular fragment often thought to be the earliest hominid in East Africa (Patterson *et al.*, 1970), although faunal correlations indicate that it is earlier (approximately 5.6 mya) than the material yielded by the Apak Member, which has been dated to 5.0 – 4.22 mya and the Kaiyumung Member which is less than 3.9 mya. Oxygen isotope analyses have not pinpointed a specific habitat type in either member (Cerling *et al.*, 2003). However, the mammalian fauna indicate that a woodland with abundant grass and a river was present during the Apak times, and that an open habitat with bushland and abundant grass and a nearby lake was present during the later Kaiyamung times (Leakey & Harris, 2003).

Kanapoi, Kenya (4.2 – 3.9 mya): Kanapoi is located to the southwest of Lake Turkana in northern Kenya and slightly south of Lothagam. Lacustrine deposits, which are sandwiched between two units of fluvial deposits, have yielded a number of fossil hominid fragments that are now attributed to the species *Australopithecus anamensis* (Patterson & Howells, 1967; Leakey *at al.*, 1995; Ward *et al.*, 1997). Generally, the fauna is biased against small mammals and dominated by medium and large sized terrestrial browsers and grazers. This makes it difficult to apply a community approach, although based on this method Andrews & Humphrey (1999) have made the tentative conclusion that the site was a dry, open woodland with abundant grass. However, the presence of a Pliocene river has also been noted and particular taxa point to the exploitation of gallery forest, which certainly would have fringed the course of this permanent feature of the landscape (Leakey *et al.*, 1995). Ecotonal species, such as *Aepyceros* sp., which is similar to the extant impala, arboreal species such as the galago, *Galago senegalensis*, and water dependent species such as *Kobus* sp. are well known from the fauna.

Chiwondo Beds, Malawi (4.0 – 1.6 mya): This region in northern Malawi is known as the "corridor" area of Africa though which hominids and other fauna are thought to have travelled between South and East Africa. It comprises 145 fossil localities, approximately 2/3 of which are located in between the Mwangwabila and Remero Rivers near the town of Karonga in the northern section of the region and 1/3 are found in near Uraha Hill in the southern section (Bromage *et al.*, 1995). Age estimates are based on faunal correlation with radiometrically-dated units at other East African sites. Although the site is perhaps most well-known for Uraha specimens attributed to *Homo rudolfensis* in beds dated to 2.4 mya (Schrenk *et al.*, 1993), the majority of the fossils finds are fragmentary mammalian taxa with a heavy bias towards bovids, with a distinct lack of micromammals and carnivores (Schrenk, et al., 1995). The presence of a number of aquatic species (including fish, turtles and crocodiles) indicate the presence of an unstable lake, seasonal rivers and ephemeral streams, but the habitats outside of the gallery forest areas have been reconstructed based on the proportions of bovid tribes represented in the assemblages (Vrba, 1984; Shipman & Harris, 1988). Material from the Late Pliocene unit 3A was studied from the northern and southern collecting areas separately, although both areas are considered to have been relatively open. The southern assemblage possesses a relatively greater number of closed-dry taxa, while the northern collections possess more closed-wet taxa (Schrenk *et al.,* 1995). This has been interpreted to indicate that local geographical conditions in the south created a minor rain shadow which prevented moist habitats from forming as they did along the seasonal rivers in the north. Dry thicket and woodland with adjacent grass is thus the most likely reconstructions for the south.

7.1.1 Plio-Pleistocene hominids in East Africa

Our understanding of the few known Miocene hominid species which might be ancestral to those that lived during the East African Plio-Pleistocene is based on a limited number of recent fossil discoveries. *Sahelanthropus tchadensis*, known from a single skull found in the Djurab Desert in northern Chad, appears to possess a mosaic of both primitive ape-like and early hominid characteristics (Brunet *et al.,* 2002). It has been biochronologically dated to between 6 and 7 mya and both faunal and sedimentological indicators preliminarily point towards the existence of a lake and surrounding rich gallery forest with the present of a sandy desert nearby (Vignaud *et a.l,* 2002). A second possible ancestor is that of the 6 mya *Orrorin tugenensis* from the Tugen Hills, Kenya (Senut *et al.,* 2001). The remains are mostly postcranial and indicate both bipedal and arboreal adaptations. Associated fauna including colobines, indicate the presence of tree cover and the ecotonal bovid *Aepyceros*, the impala, indicates that the presence of less wooded areas in the vicinity. The palaeoenvironment is interpreted to be a marginal woodland.

It is difficult to compare *O. tugenensis* and *S. tchadensis* because of the lack of relevant material. Much more is known about the early Pliocene species *Ardipithecus ramidus* (and its possible subspecies or sister taxa, *Ardipithecus ramidus kadabba* or *Ardipithecus kadabba* – see Haile-Selassie 2001; Haile-Selassie *et al.,* 2004), which is known from Aramis, Ethiopia at 4.4 mya (White *et al.*, 1994; 1995) and possibly a mandible from Lothagam, Kenya at roughly 5 mya (White, 1986). The sudden change of its genus distinction from *Australopithecus* to *Ardipithecus* implies that the unpublished material appears more ape-like than initially reported. However, this species does appear to have been capable of bipedal locomotion, which is interesting in light of the palaeoecological conditions associated with it, which is heavy woodland at Aramis and possibly at Lothagam.

Sahelanthropus, *Orrorin* and *Ardipthecus* are species that existed during and just after the time period in which the hominid clade is understood to have diverged from the apes. They may well be a part of an early adaptive radiation of apes and early hominid ancestors in the African tropics, possibly following a migration from Asia. A second adaptive radiation involved the emergence of the early australopithecine clade in East Africa. These species expanded north as far as *Australopithecus bahrelghazali* in Chad and south as far as *Australopithecus africanus* in South Africa. The major adaptive complex of traits, which is associated with the ability to locomote bipedally, differentiates between these species. The earliest australopithecine, *Australopithecus anamensis*, appears to have been more adapted to an arboreal existence than its descendants although it could, as the other species that followed it, walk upright.

Bipedalism was long thought to have evolved in an open savanna environment, but the interpretations of the bipedal abilities of the early australopithecines and palaeoecological reconstructions of the sites where they are found has shattered that initial impression. *Australopithecus anamensis*, known from Kanapoi and Allia Bay, (on the east bank of Lake Turkana) between 4.2 and 3.9 mya (Leakey *et al.*, 1995; Ward *et al.*, 1997; 1999) displays a suite of characteristics of the lower limb which indicate bipedality. However, its upper limb retains more primitive, arboreal adapted features. The non-hominid fauna from both sites is comprised of an obvious forest and aquatic component. However, the few micromammal species represented and an ecotonal bovid, also indicate that woodland and bushland were within a close proximity of the river.

It has been suggested that the environment of *Australopithecus anamensis* was similar to that of *Australopithecus afarensis* (Ward *et al.,* 1999) (until more is known about the geographical and temporal range of *Australopithecus anamensis*, it can not be determined if they were contemporaries). This species, known best as the "Lucy" skeleton and "First Family" from Hadar (Johanson *et al.,* 1978; 1982; Kimbel *et al.,* 1994), existed between 3.9 and 2.9 mya. Abundant remains are known from the Denen Dora Member at Hadar, the Middle Awash, and the Usno and Shungura Formations of Omo (Ethiopian sites), West Turkana and Tulu Bor Member at Koobi Fora (Kenyan sites) and the Laetolil Beds at Laetoli, Tanzania, where the type specimen was unearthed. Facially this species resembles apes with its canine diastema, large anterior teeth and prognathism, but postcranially it continues a trend of developing bipedality. Although retaining the long forearms and curved phalanges of tree climbing species, inferring that this was still an important aspect of its lifestyle, a remodelled pelvis, human–like valgus angle and foot morphology indicate that it locomoted in an upright fashion. Further support for this are the tracks known from Tuff 7, the "Footprint Tuff" at Laetoli, which presumably were left in the damp ash by members of *A. afarensis*.

The majority of the palaeoecological evidence from *A. afarensis* sites indicates that this species frequented "edge" areas between the forests and dense woodlands that fringe rivers and lakes and the more open woodland and bushland beyond them. The only site that does not agree with this is Laetoli, which has no permanent water source, although it is expected that seasonal streams would have existed for short periods of time during the year. However, these beds have recently been interpreted (Andrews, 1989; Reed, 1997; Andrews & Humphrey, 1999; this thesis) to represent heavy woodland-bushland, thus indicating that the vegetation cover was the most important aspect of the habitat to *A. afarensis* and that their proximity to water was simply the result of the fact that denser growth occurs around water sources.

There are two hominid species which may have been contemporary with *Australopithecus afarensis*, but little is known of them and it is difficult to place them in an evolutionary scenario. The first is the northern-most australopithecine, *Australopithecus bahrelghazali,* which is known only from a small number of craniodental remains found in central Chad dating to 3.4 - 3.0 mya (Brunet *et al.*, 1995; 1996). The second is the only species at the time which has been given its own genus name, *Kenyanthropus platyops*, and may represent a second lineage of hominids during this time period (Leakey *et al.*, 2001). Discovered in deposits of the Nachukui Formation, West Turkana, it is dated to 3.5 mya and is known only from a single skull with a large flat face and small teeth. Both of these species appear to have inhabited environments similar to the other australopithecines. Both sites are reconstructed to have had a water source, closed forest surrounding it and more open woodland beyond. There is some evidence from the faunal community that the *Kenyanthropus* locality may have been much more heavily vegetated and wetter than contemporaneous *Australopithecus afarensis* localities at Hadar (Leakey *et al.*, 2001).

There are two later australopithecine species. The first is the south African *Australopithecus africanus*, which existed between 2.8 and 2.3 mya. Its habitat has been likened to those exploited by *Australopithecus afarensis*, but it was a more arid adapted species (Reed, 1997). *Australopithecus garhi* is a recently identified 2.5 mya hominid from the Middle Awash, Ethiopia (Asfaw *et al.*, 1999). The habitat of this species is a departure from the australopithecine species which preceded it. Although there was a lake, and most sites (with the exception of Laetoli) possess a permanent water source, the fauna at the site indicate that the surrounding area is much more open and grassy than earlier sites (de Heinzelin *et al.*, 1999).

A number of sites at the time period to which *Australopithecus garhi* dates indicate that a similar environmental change had occurred in other areas besides the Middle Awash. These localities relate to the so-called robust australopithecines, which are here included in a single genus, *Paranthropus*, and may represent a third possible adaptive radiation in hominid evolution. Dated to 2.7 – 2.3 mya, the earliest robust species is *Paranthropus aethiopicus* known from the Omo Shungura Formation, Nachukui Formation of West Turkana and most recently the Ndolanya Beds at Laetoli (Harrison, 2002). Its dish-shaped face and megadontia resemble later robust species, but other features link it to the earlier *Australopithecus afarensis*. There are no postcranial remains definitively assigned to this taxa and it has been difficult to interpret its relationship to later robust species. There is a possibility that the craniodental features may be convergent adaptations reflecting similarly coarse diets and that the robust species are not truly a part of the same clade.

Paranthropus aethiopicus sites are intermediate in vegetation cover between those of earlier australopithecines, which are moderately to densely covered, and those of later robust species, which are generally more open (Reed, 1997). Often found in deltaic environments with nearby woodland or bushland and edaphic grasslands, the exception is once again Laetoli which lacks a permanent water source.

However, this site is similar to other *P. aethiopicus* sites in terms of the amount of cover it provided. *Paranthropus boisei* is more robust than either *Paranthropus aethiopicus* or its southern, more arid-adapted and younger (1.8 – 1 mya) counterpart, *Paranthropus robustus*.

A number of East African localities between the ages of 2.3 and 1.2 mya have yielded *P. boisei* remains including those at Omo, West Turkana, Koobi Fora and Olduvai. At many sites, *P. boisei* appeared to have favoured relatively open habitats such as moderate to light woodland and scrub, but at Olduvai the type skull is associated with a fauna indicating a rich woodland habitat (Fernandez-Jalvo *et al.*, 1998). It is also generally associated with water sources and edaphic grasslands (Reed, 1997). Previous interpretations of the environment of paranthropines have varied, from dry and open habitats (Suwa *et al.*, 1997) to closed woodland (Shipman & Harris, 1988). However, it appears that they although they are linked to habitats that are more open, and most likely possess a greater amount of grassy ground cover than the preferred habitats of earlier australopithecines, they still required permanent water and tree cover. They can not be described as completely arid or open habitat adapted species. It is likely that increasing aridity in the Pleistocene caused a gradual shrinkage of their ecological niche and that the *Homo* lineage, which overlaps significantly with the paranthropine era, had an adaptive advantage over them in this environment. At 1 mya, when eolian dust records a drying event, the paranthropine clade may have been forced into extinction (deMenocal, 1995).

Much has been said about the influence of environmental change in Africa on the evolution of hominids. Although the narrative of evolution was originally set within the context of an open and arid savanna (Dart, 1925, 1953; Bartholomew & Birdsell, 1953), it has been suggested that the first truly open adapted species to appear was either *Homo habilis* (Fernandez-Jalvo *et al.*, 1998), which is associated with open woodland conditions at Olduvai Gorge, or *Homo erectus* slightly later in time (Stanley, 1992). The occurrence of open grassland environments did not arise until after the earlier hominid species had evolved and hence can not have conditioned their environmental adaptations and evolution (Cerling, 1992). This is supported by Reed's (1997) finding that percentages of grazing, arboreal and frugivorous species in East African mammal communities did not change to levels observed within modern shrubland and other open habitat types until the same time period.

Vrba's Turnover Pulse Hypothesis (1980; 1985c; 1988) was the first systematic attempt to link faunal turnover to environmental change. Parallel "pulses" in speciation and extinction events were inferred to have been driven by rapid climatic events and such pulses of various degrees in both bovid and hominid lineages in southern Africa were noted at approximately 5.0, 2.7 - 2.5, 1.8 and 0.7 mya. The first appearances of bovids during these pulses are grazing taxa and hence the underlying assumption was that grasslands and aridity were increasing in southern Africa. Evidence for global cooling in deep-sea core samples (Prentice & Denton, 1988) during these times and a decrease in forest-adapted micromammals in Africa at 2.5 mya further suggested that the African forest biome was rapidly shrinking and that this was linked to global climate change (Weselman, 1984). The hominid lineages appeared to respond to these changes.

However influential this early argument was, taxonomic turnover has not been identified in any other families at the times identified by Vrba's hypothesis (Kerr, 1996) nor has it been noted in tropical Africa (Behrensmeyer *et al.*, 1997). Furthermore, as stated above, there is no correspondence between overall faunal community change and the pulses observed in bovids (Reed, 1997), and it appears that C4 grasslands did not occur until much later than initially believed (Cerling, 1992), at approximately 1.8 mya when there is further supporting evidence that a drier and more seasonal climate had also developed (deMenocal, 1995; 2004).

A new synthesis of the palaeoenvironmental record and hominid evolution posits that a combination of long-term shifts in overall climate and extreme short-term fluctuations in climatic variability created an adaptive landscape of diverse habitats that varied rapidly and unpredictably (Potts, 1996a; 1998; Behrensmeyer *et al.,* 1997; Bobe *et al.,* 2002; deMenocal, 2004). The variability in habitat availability selected for both hominid biological and behavioural flexibility. Novel behaviours that are linked to the *Homo* lineage such as lithic tool use, increased social communication, expansion of the home range and diversification of the dietary repertoire, may have conferred an adaptive advantage over species tied to specific habitat types, such as the robust australopithecines. In the long term, Africa did become more arid and seasonal and there was a gradual decrease in forest and woodland habitats, but the faunal turnovers first noted by Vrba correspond not to sudden and temporally restricted environmental changes but the beginning of periods characterised by rapid and extreme climatic variability.

In light of our changed awareness of the evolutionary and environmental mechanisms that lie at the root of hominid evolution during the Plio-Pleistocene, it is necessary that we continue to refine the techniques employed in palaeoecological investigation. With the realisation that climatic variability was the chief influence on hominid evolution it has become more important than ever to reconstruct palaeoenvironments at specific places and at specific points in time, and to trace ecologically related variables through time on both a regional and local scale. The subtle differences between the preferred habitats of the hominid species described above become even more important in a scenario of environmental variability and future research should endeavour to expand on this theme.

7.4 And in conclusion...

The aims of this project were twofold: 1) to determine which bovid skeletal elements are effective predictors of habitat by using discriminant function analyses to investigate a large, diverse, and global dataset of extant species that exploit seven known habitat types and 2) to use these predictors to reconstruct the habitat present in the Laetoli region during the time of the deposition of the Laetolil Beds (3.5 – 3.8 mya) and the Ndolanya Beds (2.66 mya). In the process of successfully addressing these issues, some interesting points have emerged.

Discriminant function analysis is the preferred statistical technique for predicting the habitat affiliation of fossil specimens. Every effort was made to utilise a diverse dataset of extant species from which the discriminant functions are calculated, as well as one which was balanced both taxonomically and in terms of the body mass of the species included. Although it was shown that the measurements used in this project are able to discriminate habitat types regardless of whether or not the data are size corrected, and thus this factor was not overwhelming or driving the habitat predictions, there is some evidence that body size is relevant in the grassland/tree-less habitat category. When the effect of body size is removed from the dataset, the predictive success within this habitat decreases. This infers that size correcting the data is not necessary or desirable.

Discriminant function analysis assigns a percentage of specimens to their correct habitat groups simply by chance, and it was shown that this percentage varies according to both the number of grouping and predictor variables that are used. This so-called "baseline of accuracy" is the standard by which analyses are rejected or accepted as adequate habitat predictors. Good predictors have both high percentages of correct classification (over the baseline) and higher probabilities associated with the predictions. Furthermore, misclassifications are generally focused on particular taxa and can be explained in terms of biologically sound factors that may relate to unique behaviours, distinct morphologies or evolutionary history.

Several good habitat predictors were determined in the analyses of the modern material. They include a number of elements that have never been investigated in an ecomorphological context, such as the carpals, tarsals and phalanges. The importance of this finding is paramount to the study of fossil material. Previous studies of bovid postcrania have focused on the long bones, which are often fragmentary or few in number. Many of the elements which have now been recognised as accurate predictors are smaller, dense and often survive in greater quantities than complete long bones. Surveying a number of elements, including those that were previously ignored by palaeoecologists, not only increases the amount of material that is now available to us, but it increases the sample size of individual analyses and better allows patterns in the data to be observed.

Further analyses of the good habitat predictor elements that were available in the Laetoli assemblages illuminated a picture of the palaeoecological conditions that were present during the Laetolil and Ndolanya times. The Laetolil Beds appear to have been dominated by moderate to closed woodland with some lighter tree and bush cover and grass available. This conclusion strongly agrees with recent ecological diversity analyses of the mammalian fauna, which indicated that the area was heavily wooded (Andrews, 1989, Reed, 1997; Andrews & Humphrey, 1999). In contrast, initial research suggested that Laetoli was a mosaic of open, arid habitats at that time (e.g. Leakey & Harris, 1987), but this conclusion is now challenged. This sets the evolution of early australopithecines such as *Australopithecus afarensis*, the type site of which is Laetoli, in the context of a wooded habitat and infers that closed cover was of great importance to this species' survival in East Africa.

The Ndolanya Beds, which have received less attention in the literature, appear to represent a much more arid and open environment than that which existed in the region nearly a million years earlier. The majority of the specimens from this stratum affiliate equally with both the light woodland-bushland and wooded-bushed grassland category, inferring that the lighter cover and grassland component of the environment had developed significantly, most likely accompanied by a concomitant increase in aridity and seasonality. This agrees with an earlier ecological diversity analysis that indicated a semi-arid bushland community was present at the time (Kovarovic *et al.*, 2002). This corresponds to a certain extent with what is understood about the habitat exploitation of *Paranthropus aethiopicus*, which has recently been discovered in these beds (Harrison, 2002). However, the lack of permanent water at Laetoli is a unique and significant condition at that site and is interesting in light of the fact that all other robust species are found at sites where a permanent water source is in the vicinity, such as Koobi Fora, Omo, and West Turkana (Reed, 1997).

In light of our changing awareness of the relationship between the environment and evolution of hominids, it is imperative that we continue to refine and develop our techniques for reconstructing the palaeoecological conditions at sites where hominids are known to have ranged. If, as the variability selection hypothesis states (Potts, 1996a, 1998; Behrensmeyer *et al.*, 1997; Bobe *et al.*, 2002; deMenocal, 2004), rapid and extreme oscillations in the climate continuously re-modelled local conditions including hydrology and floral communities, thus selecting for traits relating to biological and behavioural flexibility, it is crucial that we understand the nature of the fluctuations in the habitats present in particular regions and at what times the changes occurred.

The major goal of palaeoanthropology should now be identifying conditions favoured by the various hominid species and situating these species within a framework of temporal and geographical environmental change. To this end, this project has made two contributions. Firstly, it refined a technique for palaeoenvironmental reconstruction that is applicable to any site with bovid remains. Secondly, it has demonstrated a trend of environmental change at Laetoli, Tanzania, from a habitat in which moderate to heavy woodland-bushland predominated between 3.5 and 3.8 mya to a more open and arid light woodland-bushland and grassland mosaic, similar to a semi-arid bushland at 2.66 mya. Future research using bovid ecomorphology may be able to identify the fluctuations that occurred within individual beds or even at particular localities at Laetoli or at other relevant sites.

Bibliography

Aiello, L.C. (1992). Allometry and the analysis of size and shape in human evolution. *Journal of Human Evolution* **22,** 127-147.

Andrews, P.J. (1989). Palaeoecology of Laetoli. *Journal of Human Evolution* **18,** 173-181.

Andrews, P.J. (1996). Palaeoecology and hominoid palaeoenvironments. *Biological Reviews* **71,** 257-300.

Andrews, P.J., Lord, J.M. & Nesbit Evans, E.M. (1979). Patterns of ecological diversity in fossil and modern mammalian faunas. *Biological Journal of the Linnean Society* **11,** 177-205.

Andrews, P.J. & Humphrey, L. (1999). African Miocene Environments and the transition to early hominines. In (T.G. Bromage & F. Schrenk, Eds) *African Biogeography, Climate Change, and Human Evolution*, pp. 282-300. Oxford: Oxford University Press.

Andrews, P.J. & O'Brien, E.M. (2000). Climate, vegetation, and predictive gradients in mammals species richness in southern Africa. *Journal of Zoology* **251,** 205-231.

Ansell, W.F.H. (1971). Artiodactyla. In (J. Meester & W.H. Setzer, Eds) *The Mammals of Africa,* pp. 1-93. Washington: Smithsonian Institution Press.

Anthony, R.G. & Smith, N. S. (1977). Ecological relationships between mule deer and white-tailed deer in southeastern Arizona. *Ecological Monographs* **47,** 255-277.

Archibald, J.D. (1996). Fossil evidence for a Late Cretaceous origin of "hoofed" mammals. *Science* **272,** 1150-1153.

Asfaw, B., White, T., Lovejoy, O., Latimer, B., Simpson, S. & Suwa, G. (1999). *Australopithecus garhi*: a new species of early hominid from Ethiopia. *Science* **284,** 629-635.

Aubréville, A. (1963). Classification des formes biologiques des plantes vasculaires en milieu tropical. *Adansonia* **3,** 221-226.

Axmacher, H. & Hofmann, R.R. (1988). Morphological characteristics of the masseter muscle of 22 ruminant species. *Journal of Zoology* **215,** 463-473.

Barry, J.C. (1987). Large carnivores (Canidae, Hyenidae, Felidae). In (M.D. Leakey & J.H. Harris, Eds) *The Pliocene Site of Laetoli, Northern Tanzania*, pp. 235-258. Oxford: Clarendon Press.

Bartholomew, G.A & Birdsell, J.B. (1953). Ecology and the protohominids. *American Anthropologist* **55,** 481-498.

Basset, A. (1995). Body size-related coexistence: an approach through allometric constraints on home range use. *Ecology* **76**(4), 1027-1035.

Beard, J.S. (1953). *Ecological Monographs* **23,** 149-215.

Behrensmeyer, A.K., Todd, N.E., Potts, R., & McBrinn, G.E. (1997). Late Pliocene faunal turnover in the Turkana Basin, Kenya, and Ethiopia. *Science* **278,** 1589-1594.

Beintema, J., Fitch, W.M. & Carsana, A. (1986). Molecular evolution of pancreatic-type ribonucleases. *Molecular Biology and Evolution* **3**(3), 262-275.

Bell, R.H.V. (1970). The use of the herb layer by grazing ungulates in the Serengeti. In (A. Watson, Ed) *Animal Populations in Relation to Their Food Resources*, pp. 111-123. Oxford: Blackwell Scientific Publications.

Bell, R.H.V. (1971). A grazing ecosystem in the Serengeti. *Scientific American* **224,** 86-93.

Birungi, J. & Arctander, P. (2001). Molecular systematics and phylogeny of the Reduncini (Artiodactyla: Bovidae) inferred from then analysis of Mitochondrial Cytochrome b gene sequences. *Journal of Mammalian Evolution* **8**(2), 125-147.

Bishop, L.C. (1994). *Pigs and the Ancestors: hominids, suids, and environments during the Plio-Pleistocene of East Africa*. PhD dissertation, Yale University.

Bliss, L.C., Courtin, G.M., Pattie, D.L., Riewe, R.R., Whitfield, D,W.A. & Widden, P. (1973). Arctic tundra ecosystems. *Annual Review of Ecology and Systematics* **4,** 359-399.

Bobe, R., Behrensmeyer, A.K. & Chapman, R.E. (2002). Faunal change, environmental variability and late Pliocene hominin evolution. *Journal of Human Evolution* **42,** 475-497.

Bonnefille, R. (1984). Cenozoic vegetation and environments of early hominids in east Africa. In (R.O. Whyte, Ed) *The Evolution of East African Environments, Volume II*. Paleobotany, Paleozoology, and Paleoanthropology, Centre of Asian Studies, University of Hong Kong.

Bonnefille, R. (1994). Palynology and paleoenvironments of East African hominid sites. In (R.S. Corruccini & R.L. Ciochon, Eds) *Integrative Paths to the Past,* pp. 415-427. Englewood Cliffs, New Jersey: Prentice-Hall.

Bonnefille, R. & DeChamps, R. (1983). Data on fossil flora. In (J. deHeinzelin, Ed) *The Omo Group: Archives of the International Omo Research Expedition, Annales, S. 8, Sciences Geologiques*, pp. 191-207. Tervuren: Musée de l'Afrique Centrale.

Bonnefille, R. & Riollet, G. (1987). Palynological spectra from the Upper Laetolil Beds. In (M.D. Leakey & J.H. Harris, Eds) *The Pliocene Site of Laetoli, Northern Tanzania*, pp. 52-61. Oxford: Clarendon Press.

Bonnefille, R., Vincens, A. & Buchet, G. (1987). Palynology and paleoenvironment of a Pliocene hominid site (2.9 – 3.3 Myr) at Hadar, Ethiopia. *Palaeogeography, Palaeoclimatology, Palaeoecology* **60,** 249-281.

Boue, C. (1970). Morphologie functionelle des dents labials chez les ruminants. *Mammalia* **34,** 696-711.

Boulière, F., Ed. (1983). *Ecosystems of the World: Tropical Savannas*. Amsterdam: Elsevier Scientific Publishing Company.

Boulière, F. & Hadley, M. (1970). The ecology of tropical savannas. *Annual Review of Ecology and Systematics* **1,** 125-152.

Boulière, F. & Hadley, M. (1983). Present-day savannas: an overview. In (F. Boulière, Ed) *Ecosystems of the World: Tropical Savannas*, pp. 1-17. Amsterdam: Elsevier Scientific Publishing Company.

Boulière, F. & Vershuren, J. (1960). Introduction à l'écologie des ongules de Parc National Albert. *Institut des Parcs Nationaux du Congo Belge Fasc.* **1,** 1-158.

Brain, C.K. (1981). The evolution of man in Africa: was it a consequence of Cainozoic cooling? *Annex. Trans. Geol. Soc. S. Afr. J. Sci.* **84,** 1-19.

Brashares, J.S., Garland, T., & Arcese, P. (2000). Phylogenetic analysis of coadaptaiton in beahvior, diet, and body size in the African antelope. *Behavioral Ecology* **4,** 452-463.

Brink, J. (1999). Preliminary report on a caprine from the Cape Mountains, South Africa. *Archaeozoologia* **10,** 11-25.

Bromage, T.G. & Schrenk, F. (1995). Biogeographic and climatic basis for a narrative of early hominid evolution. *Journal of Human Evolution* **28,** 109-114.

Bromage, T.G., Schrenk, F., & Juwayeyi, Y.M. (1995). Paleobiogeography of the Malawi Rift: age and vertebrate paleontology of the Chiwondo Beds, northern Malawi. *Journal of Human Evolution* **28,** 37 -57.

Brown, F.H. & Fiebel, C.S. (1986). Revision of the lithostratagraphic nomenclature in the Koobi Fora region, Kenya. *Journal of the Geologic Society, London* **143,** 297-310.

Brunet, M., Beauvilain, A., Coppens, Y., Heintz, E., Mouteye, A.H.E., & Pilbeam, D. (1995). The first australopithecine 2,500 kilometres west of the Rift Valley (Chad). *Nature* **378,** 273-275.

Brunet, M., Beauvilain, A., Coppens, Y., Heintz, E., Mouteye, A.H.E., & Pilbeam, D. (1996). *Australopithecus bahrelghazali*, une nouvelle espèce d'hominidé ancien de la région de Koro Toro (Tchad). *Comptes Rendus de l'Aadémie Sciences, Paris, serial 2A* **322,** 907-913.

Brunet, M., Guy, F., Pilbeam, D., Mackaye, H.T., Likius, A., Ahounta, D., Beauvilains, A., Blondel, C., Bocherens, H., Bousserie, J.R., de Bonis, L, Coppens, Y., Dejax, J., Denys, C., Duringer, P., Elsenmann, V., Fanone, G., Fronty, P., Geraads, D., Lehmann, T., Lihoreau, F., Louchart, A., Mahamat, A., Marceron, G., Mouchelin, G., Otero, O., Campomanes, P.P., de Leon, M.P., Rage, J.C., Sapenet, M., Schuster, M., Sudre, J., Tassy, P., Valentin, X., Vignaud, P., Virlot, P., Zazzao, A & Zollikofer, C. (2002). A new hominid from the Upper Miocene of Chad, Central Africa. *Nature* **418,** 145-151.

Butler, P.M. (1972). Some functional aspects of molar evolution. *Evolution* **26**(3), 474-483.

Butler, P.M. (1987). Fossil insectivores from Laetoli. In (M.D. Leakey & J.H. Harris, Eds) *The Pliocene Site of Laetoli, Northern Tanzania*, pp. 85-87. Oxford: Clarendon Press.

Cerling, T.E. (1992). Development of grasslands and savannas in East Africa during the Neogene. *Paleogeography, Paleoclimatology, Paleoecology* **97,** 241-247.

Cerling, T.E., Harris, J.M. & Leakey, M.G. (2003). Isotope palaeoecology of the Nawata and Nachukui Formations at Lothagam, Turkana Basin, Kenya. In (M.G. Leakey & J.M. Harris, Eds) *Lothagam: The Dawn of Humanity in Eastern Africa*, pp. 605-624. New York: Columbia University Press.

Cerling, T.E. & Hay, R.L. (1986). An isotopic study of paleosol carbonates from Olduvai Gorge. *Quaternary Research* **25,** 63-78.

Cerling, T.E., Hay, R.L., & O'Neil, J.R. (1977). Isotopic evidence for dramatic climatic changes in East Africa during the Pleistocene. *Nature* **267,** 137-138.

Cerling, T.E., Quade, J., Ambrose, S.H. & Sikes, N.E. (1991). Fossil soils, grasses and carbon isotopes from Fort Ternan, Kenya: grassland or woodland. *Journal of Human Evolution* **21,** 295-306.

Chavanon, S. (1962). Les Chalicotheriidae du Bassin Aquitain, Observation morphologiques, biométriques et éthologiques. PhD thesis. University of Bordeaux, France.

Chikuni, K., Mori, Y., Tabata, T., Saito, M., Monma, M & Kosugiyama, M. (1995). Molecular phylogeny based on the k-casein and cytochrome b sequences in the mammalian suborder Ruminantia. *Journal of Molecular Evolution* **41,** 859-866.

Clauss, M., Lechner-Doll, M. & Jurgen Streich, J. (2003). Ruminant diversification as an adaptation to the physicomechanical characteristics of forage. A reevaluation of an old debate and a new hypothesis. *Oikos* **102,** 253-262.

Clutton-Brock, T.H., Guinness, F.E., Albon, S.D. (1982). Red Deer: Behaviour and Ecology of Two Sexes. Edinburgh: Edinburgh University Press.

Cody, M.L. & Mooney, J.M. (1978). Convergence versus nonconvergence in Mediterranean-climate ecosystems. *Annual Review of Ecology and Systematics* **9,** 265-321.

Conseil Scientifique pour l'Afrique (CSA) (1956). *Réunion de Spécialistes du CSA en matière de Phytogéographie, Yangambi 1956, 28 July – 8 August.* London: CCTA/CSA Publications, No. 22.

Dailey, T.V., Hobbs, N.T., & Woodard, T.N. (1984). Experimental comparisons of diet selection by mountain goats and mountain sheep in Colorado. *Journal of Wildlife Management* **48**(3), 799-806.

Damuth, J & McFadden, B.J., Eds (1990). *Body Size in Mammalian Paleobiology: Estimation and Biological Implications.* Cambridge: Cambridge University Press.

Dart, R. (1925). *Australopithecus africanus*: the man-ape of South Africa. *Nature* **115,** 195-199.

Dart, R. (1953). The predatory transition from ape to man. *International Anthropological and Linguistics Review* **1,** 201-218.

Day, M.H., Leakey, M.D. & Magori, C. (1980). A new hominid fossil skull (L.H.18) from the Ngaloba Beds, Laetoli, northern Tanzania. *Nature* **284,** 55-56.

de Heinzelin, J., Clark, J.D., White, T., Hart, W., Renne, P., WoldeGabriel, G., Beyene, & Vrba, E.S. (1999). Environment and behavior of 2.5-million-year-old Bouri hominids. *Science* **284,** 625-629.

Deguchi, Y., Sato, S., & Sugawara, K. (2001). Relationship between some chemical components of herbage, dietary preference and fresh herbage intake rate by Japanese serow. *Applied Animal Behaviour Science* **73,** 69-79.

DeGusta, D. & Vrba, E.S. (2003). A method for inferring paleohabitats from the functional morphology of bovid astragali. *Journal of Archaeological Science* **30,** 1009-1022.

deMenocal, P.B. (2004). African climate change and faunal evolution during the Plio-Pleistocene. *Earth and Planetary Science Letters* **220,** 3-24.

deMenocal, P.B. (1995). Plio-Pleistocene African climate. *Science* **270,** 53-59.

deMenocal, P.B., Ruddiman, W., & Pokras, E. (1993). Influences of high- and low-latitude processes on African terrestrial climate: Pleistocene eolian records from equatorial Atlantic Ocean Drilling Program site 663. *Paleoceanography* 8(2), 209-242.

Denys, C. (1985). Laetoli: A Pliocene southern savanna fauna in the Eastern Rift Valley (Tanzania). Ecological implications. *Proceedings International Symposium of African Vertebrates,* Bonn. pp. 35-51.

Denys, C. (1987). Fossil rodents (other than Pedetidae) from Laetoli. In (M.D. Leakey & J.H. Harris, Eds) *The Pliocene Site of Laetoli, Northern Tanzania*, pp.118-170. Oxford: Clarendon Press.

De Ruiter, D.J. (2001). *A methodological analysis of the relative abundance of hominids and other macromammals from the site of Swartkrans, South Africa.* PhD dissertation, University of the Witwatersrand, Johannesburg.

Dodson, P. (1974). The significance of small bones in a palaeoecological interpretation. *Contributions to Geology/Special Papers, University of Wyoming* **No. 2**.

Drake, R.E. & Curtis, G.H. (1987). K-Ar geochronology of the Laetoli fossil localities. In (M.D. Leakey & J.H. Harris, Eds) *The Pliocene Site of Laetoli, Northern Tanzania*, pp.48-52. Oxford: Clarendon Press.

Eck, G.G. & Jablonski, N.G. (1985). The skull of *Theropithecus brumpti* compared with those of other species of the genus *Theropithecus*. In (Y. Coppens & F.C. Howell, Eds) *Les Faunes Plio-Pléistocene de la basse vallée de l'Omo (Éthiopie)*, pp. 18-122. Paris: Éditions du Centre National de la Recherche Scientifique.

Elton, S. (2001). Locomotor and habitat classifications of cercopithecoid postcranial material from Sterkfontein Member 4, Bolt's Farm and Swartkrans Members 1 and 2, South Africa. *Palaeontologica Africana* **37,** 115-126.

Estes, R.D. (1974). Social organization of the African Bovidae. *IUCN Publication* **24,** 166-205.

Feibel, C.S., Brown, F.H., & McDougall, I. (1989). Stratagraphic context of fossil hominids from the Omo Group deposits: Northern Turkana Basin, Kenya and Ethiopia. *American Journal of Physical Anthropology* **78,** 595-622.

Fernandez-Jalvo, Y., Denys, C., Andrews, P., Dauphin, Y., & Humphrey, L. (1998). Taphonomy and palaeoecology of Olduvai Bed-I (Pleistocene, Tanzania). *Journal of Human Evolution* **34,** 137-172.

Field, C.R. & Laws, R.M. (1970). The distribution of larger herbivores in the Queen Elizabeth National Park. *Journal of Applied Ecology* **7**(2), 273-294.

Foley, R. (1987). *Another Unique Species.* New York: Longman.

Ford, S.M. & Davis, L.C. (1992). Systematics and body size: implications for feeding adaptations in New World monkeys. *American Journal of Physical Anthropology* **88,** 415-468.

Fortelius, M. (1985). Ungulate cheek teeth: developmental, functional and evolutionary interrelations. *Acta Zoologica Fennica* **180,** 1-76.

Fortelius, M. & Solounias, N. (2000). Functional characterization of ungulate molars using the abrasion-attrition wear gradient: a new method for reconstructing paleodiets. *American Museum Novitates* **3301,** 1-36.

Gagnon, M. & Chew, A.E. (2000). Dietary preferences in extant African Bovidae. *Journal of Mammalogy* **81**(2), 490-511.

Garcia-Gonzalez, R. & Cuartas, P. (1996). Trophic utilization of a montane/subalpine forest by chamois (*Rupicapra rupicapra*) in the Central Pyrenees. *Forest Ecology and Management* **88,** 15-23.

Gatesy, J., Yelon, D., DeSalle, R., & Vrba, E.S. (1992). Phylogeny of the Bovidae (Artiodactyla, Mammalia), based on Mitochondrial Ribosomal DNA sequences. *Molecular Biology and Evolution* **9**(3), 433-446.

Geist, V. (1974). On the relationship of ecology and behaviour in the evolution of ungulates: theoretical considerations. In *The Behaviour of Ungulates and its Relation to Management*, pp. 235-246. Morges: IUCN Publications, New Series.

Geist, V. (1977). A comparison of social adaptations in relation to ecology in gallinaceous bird and ungulate societies. *Annual Review of Ecological Systematics* **8,** 193-207.

Geist, V. (2001). Goat antelopes. In (D. MacDonald, Ed) *The New Encyclopedia of Mammals*, pp. 570-575.

Gentry, A.W. (1970). The Bovidae (Mammalia) of the Fort Ternan fossil fauna. In (L.B.S. Leakey & R.G.J. Savage, Eds) *Fossil Vertebrates of Africa,* Vol. 2, pp. 243-323. London: Academic Press.

Gentry, A.W. (1976). Bovidae of the Omo Group deposits. In (Y. Coppens, F.C. Howell, G.L. Isaac & R.E. Leakey, Eds) *Earliest Man and Environments in the Lake Rudolf Basin*, pp. 275-292. Chicago: University of Chicago Press.

Gentry, A.W. (1978). Bovidae. In (Maglio, V.J. & Cooke, H.B.S., Eds) *Evolution of African Mammals*, pp. 540-572. Cambridge, Massachusetts: Harvard University Press.

Gentry, A.W. (1985). The Bovidae of the Omo Group deposits, Ethiopia. In *Les faunes Plio-Pleistocenes de la basse vallee de l'Omo (Ethiopie), Volume 1: Perrissodactyles-Artiodactyles (Bovidae). Cahiers de paleontologie-Travaux de Paleontologie est-africaine*, pp. 119-191. Paris: Editions du Centre National de la Recherche Scientifique.

Gentry, A.W. (1987). The bovids from Laetoli. In (M.D. Leakey & J.H. Harris, Eds) *The Pliocene Site of Laetoli, Northern Tanzania*, pp. 378-408. Oxford: Clarendon Press.

Gentry, A.W. (1990). Evolution and dispersal of African Bovidae. In (G.A. Bubenik and A.B. Bubenik, Eds) *Horns, Pronghorns, and Antlers,* pp. 195-227. New York: Springer-Verlag.

Gentry, A.W. (1992). The subfamilies and tribes of the family Bovidae. *Mammal Review* **22**(1), 1-32.

Gentry, A.W. (1996). In (K.M. Stewart & K.L. Seymour, Eds) *Palaeoecology and Palaeoenvironments of Late Cenozoic Mammals*, pp. 571-587. Toronto: University of Toronto Press.

Gentry, A.W. (2000). The ruminant radiation. In (E.S. Vrba & G.B. Schaller, Eds.) *Antelopes, Deer and Relatives: Fossil Record, Behavioral Ecology, Systematics and Conservation,* pp. 11-20. New Haven: Yale University Press.

Gentry, A. W. (2003). Personal Communication.

Gentry, A.W. & Gentry, A. (1978a). Fossil Bovidae (Mammalia) of Olduvai Gorge, Tanzania. Part I. *Bulletin of the British Museum (Natural History), Geology* **29,** 289-446.

Gentry, A.W. & Gentry, A. (1978b). Fossil Bovidae (Mammalia) of Olduvai Gorge, Tanzania. Part II. *Bulletin of the British Museum (Natural History), Geology* **30,** 1-83.

Gentry, A.W. & Hooker, J. (1988). The phylogeny of the Artiodactyla. In (M. Benton, Ed) *The Phylogeny and Classification of the Tetrapods, Volume 2: Mammals*, pp. 235-272. Oxford: Clarendon Press.

Georgiadis, N.J., Kat, P.W., Oketch, H., & Patton, J. (1991). Allozyme divergence within the Bovidae. *Evolution* **44**(8), 2135-2149.

Ginsberg, L. & Heintz, E. (1968). La plus ancienne antilope d'Europe, *Eotragus artenensis* du Burdigalain d'Artenay. *Bulletin du Museum National d'Histoire Naturelle, Paris* **40,** 837-842.

Gordon, I.J. & Illius, A. (1988). Incisor arcade structure and diet selection in ruminants. *Functional Ecology* **2,** 15-22.

Gordon, I.J. & Illius, A. (1994). The functional significance of the browser-grazer dichotomy in African ruminants. *Oecologia* **98,** 167-175.

Gordon, K.D. (1982). A study of microwear on chimpanzee molars: implications for dental microwear analysis. *American Journal of Physical Anthropology* **59,** 195-215.

Greenway, P.J. (1973). A classification of the vegetation of East Africa. *Kirkia* **9,** 1-68.

Grine, F.E. (1986). Dental evidence for dietary differences in *Australopithecus* and *Paranthropus*: a quantitative analysis of permanent molar microwear. *Journal of Human Evolution* **15,** 783-822.

Groves, P. & Shields, G. (1996). Phylogenetics of the Caprinae based on cytochrome b sequence. *Molecular Phylogenetics and Evolution* **5**(3), 467-476.

Groves, P. & Shields, G. (1997). Cytochrome b sequences suggest convergent evolution of the Asian takin and Arctic muskox. *Molecular Phylogenetics and Evolution* **8**(3), 363-374.

Grunblatt, J., Ottichilo, W.K. & Sinange, R.K. (1989). A hierarchical approach to vegetation classification in Kenya. *African Journal of Ecology* **27,** 45-51.

Guérin, C. (1987a). Chalicotheriidae (Mammalia, Perissodactyla) remains from Laetoli. In (M.D. Leakey & J.H. Harris, Eds) *The Pliocene Site of Laetoli, Northern Tanzania*, pp. 315-320. Oxford: Clarendon Press.

Guérin, C. (1987b) Fossil Rhinocerotidae (Mammalia, Perissodactyla) from Laetoli. In (M.D. Leakey & J.H. Harris, Eds) *The Pliocene Site of Laetoli, Northern Tanzania*, pp. 320-348. Oxford: Clarendon Press.

Gwynne, M.D. & Bell, R.H.V. (1968). Selection of vegetation components by grazing ungulates in the Serengeti National Park. *Nature* **220,** 390-393.

Haile-Selassie, Y. (2001). Late Miocene hominids from the Middle Awash, Ethiopia. *Nature* **412,** 178-181.

Haile-Selassie, Y., Suwa, G. & White, T.D. (2004). Late Miocene teeth from Middle Awash, Ethiopia, and early hominid dental evolution. *Science* **303,** 1503-1505.

Hamilton, W.R. (1973). The lower Miocene ruminants of Gebel Zelten, Libya. *Bulletin of the British Museum of Natural History* **21,** 75-150.

Hammer, Ø., Harper, D.A.T., & Ryan, P.D. (2001). PAST: Paleontological statistics software package for education and data analysis. *Palaeontologia Electronica* **4**(1), 1-9.

Harris, J.M. (1978). Paleontology. In (M.D. Leakey and R.E. Leakey, Eds) *Koobi For a Research Project, Vol 1: The Fossil Hominids and an Introduction to their Context, 1968-1974*, pp. 32-63. Oxford: Clarendon Press.

Harris, J.M. (1985). Age and palaeoecology of the Upper Laetolil Beds, Laetoli, Tanzania. In (E. Delson, Ed.) *Ancestors: The Hard Evidence,* pp. 76-81. New York: Alan R. Liss, Inc.

Harris, J.M. (1987). Fossil Suidae from Laetoli. In (M.D. Leakey & J.H. Harris, Eds) *The Pliocene Site of Laetoli, Northern Tanzania*, pp. 349-358. Oxford: Clarendon Press.

Harris, J.M. (1991). *Koobi Fora Research Project, Vol. 3: The Fossil Ungulates: Geology, Fossil Artiodactyls, and Paleoenvironments.* Oxford: Clarendon Press.

Harris, R.B. & Miller, D.J. (1995). Overlap in summer habitats and diets of Tibetan Plateau ungulates. *Mammalia* **59**(2), 197-212.

Harrison, T. (2002). Personal Communication.

Harrison, T. (2002). The first record of fossil hominines from the Ndolanya Beds, Laetoli, Tanzania. *American Journal of Physical Anthropology* **Supp 34,** 83.

Harvey, P.H. (1982). On rethinking allometry. *Journal of Theoretical Biology* **95,** 37-41.

Hassanin, A. & Douzery, E.J.P. (1999). The tribal radiation of the family Bovidae (Artiodactyla) and the evolution of the mitochondrial cytochrome b gene. *Molecular Phylogenetics and Evolution* **13**(2), 227-243.

Hassanin, A. & Douzery, E.J.P. (2003). Molecular and morphological phylogenies of Ruminantia and the alternative position of the Moschidae. *Systematic Biology* **52**(2), 206-228.

Hay, R.L. (1981). Paleoenvironments of the Laetolil Beds, Northern Tanzania. In (G. Rapp & C. Vondra, Eds) *Hominid Sites: Their Geologic Settings*, pp. 7-23. Boulder: Westview.

Hay, R.L. (1987). Geology of the Laetoli area. In (M.D. Leakey & J.H. Harris, Eds) *The Pliocene Site of Laetoli, Northern Tanzania*, pp. 23-47. Oxford: Clarendon Press.

Hayward, J.N. (1972). The anatomy of heat exchange: The pharmacology of thermoregulation. *Symp. San Fransisco* **1972,** 21-41.

Healy, W.B. & Ludwig, T.G. (1965). Wear of sheep's teeth. I. The role of ingested soil. *New Zealand Journal of Agricultural Research* **8,** 737-753.

Hill, A. & Ward, S. (1988). Origin of the Hominidae: the record of African large hominoid evolution between 14my and 4 my. *Yearbook of Physical Anthropology* **31,** 49-83.

Hills, T.L. (1965). Savannas: a review of a major research problem in tropical geography. *Canadian Geographer* **9,** 220-232.

Hirst, S.M. (1975). Ungulate habitat relationships in a South African woodland savanna ecosystem. *Wildlife Monographs* **44,** 1-60.

Hixson, S. (1998). *Paleohabitat Reconstruction of Fossil Hominoid Sites Using Modern Mammalian Community Analogs*. PhD dissertation, University of California, Berkeley.

Hofmann, R.R. (1973). The ruminant stomach. *East African Monographs in Biology Vol. II.* Nairobi: East African Literature Bureau.

Hofmann, R.R. (1988). Morphophysiological evolutionary adaptations of the ruminant digestive system. In (A. Dobson & M.J. Dobson, Eds) *Aspects of Digestive Physiology in Ruminants*, pp. 1-19. Ithica: Cornell University Press.

Hofmann, R.R. (1989). Evolutionary steps of ecophysiological adaptation and diversification in ruminants: a comparative view of their digestive system. *Oecologia* **87,** 443-457.

Hofmann, R.R. & Stewart, D.R.M. (1982). Grazer or browser: a classification based on stomach-structure and feeding habits of East African mammals. *Mammalia* **36,** 227-240.

Hooijer, D.A. (1987a). Hipparion teeth from the Ndolanya Beds. In (M.D. Leakey & J.H. Harris, Eds) *The Pliocene Site of Laetoli, Northern Tanzania*, pp. 312-315. Oxford: Clarendon Press.

Hooijer, D.A. (1987b). Hipparions of the Laetolil Beds, Tanzania. In (M.D. Leakey & J.H. Harris, Eds) *The Pliocene Site of Laetoli, Northern Tanzania*, pp. 301-312. Oxford: Clarendon Press.

Howell, F.C., Haesaerts, P. & de Heinzelin, J. (1987). Depositional environments, archaeological occurrences and hominids fro Members E and F of the Shungura Formation (Omo Basin, Ethiopia). *Journal of Human Evolution* **16,** 665-700.

Huberty, C.J. (1994). *Applied Discriminant Analysis*. New York: Wiley & Sons.

Huberty, C.J. & Barton, R.M. (1989). An introduction to discriminant analysis. *Measurement and Evaluation in Counseling and Development* **22,** 158-168.

Hutchinson, G.E. (1957). Concluding Remarks. *Cold Spring Harbor Symp. Quant. Biol.* **22,** 415-427.

Hutchinson, G.E. (1959). Homage to Santa Rosalia, or why are there so many kinds of animals. *American Naturalist* **93,** 145-159.

Hutchinson, G.E. & MacArthur, R.H. (1959). A theoretical ecological model of size distributions among species of animals. *American Naturalist* **93,** 117-125.

Janis, C.M. (1979). *Aspects of the Evolution of Herbivory in Ungulate Mammals.* PhD dissertation. Cambridge, Massachusetts: Harvard University.

Janis, C.M. (1982). Evolution of horns in ungulates: ecology and paleoecology. *Biological Reviews* **57,** 261-318.

Janis, C.M. (1984). The use of fossil ungulate communities as indicators of climate and environment. In (P. Benchley, Ed) *Fossils and Climate,* pp. 85-104. Chichester: John Wiley & Sons, Ltd.

Janis, C.M. (1986). Evolution of horns and related structures in hoofed animals. *Discover* **19,** 9-17.

Janis, C.M. (1988). An estimation of tooth volume and hypsodonty indices in ungulate animals, and the correlation of these factors with dietary preference. In (E. Russell, J.P. Santoro, & D. Signogneau-Russell, Eds) *Teeth Revisited: Proceedings of the VIIth International Symposium on Dental Morphology. Memoires du Museum national d'histoire Naturelle (Serie C) 53,* pp. 367-387. Paris: Editions du Museum.

Janis, C.M. (1989). A climatic explanation for patterns of evolutionary diversity in ungulate mammals. *Palaeontology* **32,** 463-81.

Janis, C.M. (1990a). Correlation of cranial and dental variables with body size in ungulates and macropodoids. In (J. Damuth & B. McFadden, Eds). *Body Size in Mammalian Paleobiology: Estimation and Biological Implications*, pp. 255-300. Cambridge: Cambridge University Press.

Janis, C.M. (1990b). Correlation of cranial and dental variables with dietary preferences in mammals: a comparison of macropodpoids and ungulates. *Memoirs of the Queensland Museum* **28,** 349-366.

Janis, C.M. (1993). Tertiary mammal evolution in the context of changing climates, vegetation, and tectonic events. *Annual Review of Ecological Systematics* **24,** 467-500.

Janis, C.M. (1995). Correlations between craniodental morphology and feeding behavior in fossil ungulates: reciprocal illumination between living and fossil taxa. In (J.J. Thompson, Ed) *Functional Morphology in Vertebrate Paleontology,* pp. 76-98. Cambridge: Cambridge University press.

Janis, C.M and Ehrhardt, D. (1988). Correlation of relative muzzle width and relative incisor width with dietary preference in ungulates. *Zoological Journal of the Linnean Society* **92,** 267-284.

Janis, C.M. and Scott, K.M. (1987). The interrelationships of higher ruminant families with special emphasis on the members of the Cervoidea. *American Museum Novitates* **2893,** 1-85.

Jarman, P.J. (1974). The social organisation of antelope in relation to their ecology. *Behaviour* **48,** 213-267.

Jarman, P.J. & Sinclair, A.R.E (1979). Feeding strategy and the pattern of resource partitioning in ungulates. In (A.R.E Sinclair and M. Norton-Griffiths, Eds) *Serengeti: Dynamics of an Ecosystem,* pp 130-163. Chicago: University of Chicago Press.

Jernvall, J. & Fortelius, M. (2002). Common mammals drive the evolutionary increase of hypsodonty in the Neogene. *Nature* **417,** 538-540.

Johanson, D.C., White, T.D. & Coppens, Y. (1978). A new species of the genus *Australopithecus* (Primates, Hominidae) from the Pliocene of eastern Africa. *Kirtlandia* **28,** 1-14.

Johanson, D.C., Taieb, M. & Coppens, Y. (1982). Pliocene hominids from the Hadar Formation, Ethiopia (1973-1977): stratigraphic, chronologic, and palaeoenvironmental contexts, with notes on hominid morphology and systematics. *American Journal of Physical Anthropology* **57,** 373-402.

Johnson, E. (1977). Seasonal changes in the skin of animals. In *Comparative Biology of the Skin. Symposia of the Zoological Society of London* **39,** 373-404. London: Academic Press.

Jolly, C. (1970). The seed-eaters: a new model of hominoid differentiation based on a baboon analogy. *Man* **5,** 5-26.

Jungers, W.L. (1984). Aspects of size and scaling in primate biology with special reference to the locomotor skeleton. *Yearbook of Physical Anthropology* **27,** 73-97.

Jungers, W.L., Ed (1985). *Size and Scaling in Primate Biology.* New York: Plenum Press.

Jungers, W.L., Falsetti, A.B., Wall, C.E. (1995). Shape, relative size, and size adjustments in morphometrics. *Yearbook of Physical Anthropology* **38,** 137-162.

Kappelman, J. (1984). Plio-Pleistocene environments of Bed I and Lower Bed II, Olduvai Gorge, Tanzania. *Palaeogeography, Palaeoclimatology, Palaeoecology* **48,** 171-196.

Kappelman, J. (1988). Morphology and locomotor adaptations of the bovid femur in relation to habitat. *Journal of Morphology* **198,** 119-130.

Kappelman, J. (1991). The paleoenvironment of *Kenyapithecus* at Fort Ternan. *Journal of Human Evolution* **20,** 95-129.

Kappelman, J., Plummer, T., Bishop, L., Duncan, A., & Appleton, S. (1997). Bovids as indicators of Plio-Pleistocene paleoenvironments in East Africa. *Journal of Human Evolution* **32,** 229-256.

Kay, R.F. & Covert, H.H. (1981). Dental microwear and diet: implications for determining the feeding behavior of extinct primates, with a comment on the dietary pattern of *Sivapithecus*. *American Journal of Physical Anthropology* **55,** 331-336.

Kay, R.F. & Covert, H.H. (1983). True grit: a microwear experiment. *American Journal of Physical Anthropology* **61,** 33-38.

Kent, P.E. (1941). The recent history and Pleistocene deposits of the plateau North of Lake Eyasi, Tanganyika. *Geological Magazine* **78,** 73-184.

Kerr, R.A. (1996). New mammal data challenge evolutionary pulse theory. *Science* **273,** 431-432.

Kimbel, W.H. Johanson, D.C., & Rak, Y. (1994). The first skull and other new discoveries of Australopithecus afarensis at Hadar, Ethiopia. *Nature* **368,** 449-451.

Kimbel, W.H., Walter, R.C., Johanson, D.C., Reed, K.E., Aronson, J.L., Assefa, Z., Marean, C..W., Eck, G.G., Bobe, R., Hovers, E., Rak, Y. Vondra, C., Yemane, T., York, D., Chen, Y. Evensen, N.M, & Smith, P.E. (1996). Late Pliocene *Homo* and Oldowan tools from the Hadar Formation (Kada Hadar Member), Ethiopia. *Journal of Human Evolution* **31,** 549-561.

Kingdon, J. (1982). *East African Mammals – Volume IIIC,D.* Chicago: University of Chicago Press.

Kingdon, J. (1997). *The Kingdon Field Guide to African Mammals.* San Diego: Academic Press.

Kohl-Larsen, L. (1943). *Auf den Spuren des Vormenschen.* Stuttgart: Stecker and Schroder.

Köhler, M. (1993). *Skeleton and Habitat of Recent and Fossil Ruminants.* München: Verlag Friedrich Pfeil.

Koopman, K.F. (1967). Artiodactyls. In (S. Andersen & J. Knox Jones Jr., Eds) *Recent Mammals of the World: A Synopsis of Families*, pp. 385-406. New York: The Ronald Press.

Kovarovic, K., Andrews, P., & Aiello, L. (2002). An ecological diversity analysis of the Upper Ndolanya Beds, Laetoli, Tanzania. *Journal of Human Evolution* **43,** 395 – 418.

Kuehn, D.W. (1986). Population and social characteristics of the tamarao (*Bubalus mindorensis*). *Biotropica* **18**(3), 263-266.

LaBarbera, M. (1989). Analyzing body size as a factor in ecology and evolution. *Annual Review of Ecology and Systematics* **20,** 97-117.

Lamprey, H.F. (1963). Ecological separation of the large mammals species in the Tangangire Game Reserve, Tanganyika. *East African Wildlife Journal* **13,** 297-304.

Lamprey, H.F. (1964). Estimation of the large animal densities, biomass and energy exchange in the Tarangire Game Reserve and the Masai Steppe in Tanganyika. *East African Wildlife Journal* **2,** 1-46.

Laporte, L.F. & Zihlman, A.L. (1983). Plates, climate and hominoid evolution. *South African Journal of Science* **79,** 96-110.

Lavocat, R. (1955). Ruminants fossiles. In *Traité de zoologie. Anatomie, systématique, biologie, Tome XVII, Premier fascicule. Mammifères. Les orders: Anatomie, éthologie, systématique*, pp. 668-693. Paris: P.P. Grassé, Masson & Cie, Eds

Leakey, L.N. (2001). *Body Weight Estimation of Bovidae and Plio-Pleistocene Faunal Change, Turkana Basin, Kenya.* PhD dissertation. University of London.

Leakey, M.D. & Delson, E. (1987). Fossil Cercopithecidae from the Laetolil Beds. In (M.D. Leakey & J.H. Harris, Eds) *The Pliocene Site of Laetoli, Northern Tanzania*, pp. 91-107. Oxford: Clarendon Press.

Leakey, M.D. & Hay, R.L (1979). Pliocene footprints in the Laetolil Beds, Northern Tanzania. *Nature* **278,** 317-323.

Leakey, M.D. & Harris, J.H., Eds (1987). *The Pliocene Site of Laetoli, Northern Tanzania*. Oxford: Clarendon Press.

Leakey, M.G., Fiebel, C.S., McDougall, I. & Walker, A. (1995). New four-million-year old hominid species from Kanapoi and Allia Bay, Kenya. *Nature* **376,** 565-571.

Leakey. M.G. & Harris, J.M., Eds. (2003). *Lothagam: The Dawn of Humanity in Eastern Africa*. New York: Columbia University Press.

Leakey, M.G., Spoor, F., Brown, F.H., Gathogo, P.N., Kiarie, C., Leakey, L.N. & McDougall, I. (2001). New hominin genus from eastern Africa shows diverse middle Pliocene lineages. *Nature* **410,** 433-440.

Lenstra, J.A., & Bradley, D.G. (1999). Systematics and phylogeny of cattle. In (R. Fries & A. Ruvinsky, Eds) *The Genetics of Cattle*, pp. 1-14. Germany: CABI Publishing.

Levin, N.L., Quade, J., Simpson, S.W., Semaw, S., & Rogers, M. (2004). Isotopic evidence for plio-Pleistocene environmental change at Gona, Ethiopia. *Earth and Planetary Science Letters* **219,** 93-110.

Lieberman, D,E., Wood, B.A. & Pilbeam, D.R. (1996). Homoplasy and early *Homo*: an analysis of the evolutionary relationships of *H. habilis* sensu stricto and *H. rudolfensis*. Journal of Human Evolution **30,** 97-120.

Loe, L.E., Mysterud, A., Langvatn, R., & Stenseth, N.C. (2003). Decelerating and sex-dependent tooth wear in Norwegian red deer. *Oecologia* **135,** 346-353.

Lowenstein, J. (1986). Bovid relations based on serum immunology. *South African Journal of Science* **82,** 77-78.

MacDonald, D., Ed (2001). *The New Encyclopedia of Mammals*. Oxford: Oxford University Press.

Mace, G.M. & Harvey, P.H. (1983). Energetic constraints on home-range size. *American Naturalist* **121,** 120-132.

Manly, B.F.J. (1986). *Multivariate Statistical methods: A Primer*. London: Chapman and Hall.

Matthews, J. (2004). Expedition research projects in tundra and periglacial regions. In (S. Winser, Ed) *Royal Geographical Society Handbook*, pp. 308-316. London: Royal Geographical Society.

May, R.M. & MacArthur, R.H. (1972). Niche overlap as a function of environmental variability. *Proceedings of the National Academy of Science U.S.A.* **69**(5), 1109-1113.

McKee, J.K. (1996). Faunal turnover patterns in the Pliocene and Pleistocene in southern Africa. *South African Journal of Science* **92,** 111-113.

McNab, B.K. (1963). Bioenergetics and the determination of home range size. *American Naturalist* **97,** 133-140.

McNaughton, S.J. (1989). Interactions of plants of the field layer with large herbivores. *Symposia of the Zoological Society of London* **61,** 15-29.

McNaughton, S.J. & Georgiadis, N.J. (1986). Ecology of African grazing and browsing mammals. *Annual Review of Ecological Systematics* **17,** 39-65.

McNaughton, S.J., Tarrants, J.L., McNaughton, M.M. & Davis, R.H. (1984). Silica as a defense against herbivory and a growth promotor in African grasses. *Ecology* **66,** 528-535.

Menaut, J. (1983). The vegetation of African savannas. In (F. Bouliére, Ed) *Ecosystems of the World: Tropical Savannas, Volume 13*, pp. 109-149. Amsterdam: Elsevier Scientific Publishing Co.

Mendoza, M. Janis, C.M. & Palmqvist, P. (2002). Characterising craniodental patterns related to feeding behaviour in ungulates: a multivariate approach. *Journal of Zoology: Proceedings of the Zoological Society of London* **258,** 223-246.

Meylan, P.A. (1987). Fossil snakes from Laetoli. In (M.D. Leakey & J.H. Harris, Eds) *The Pliocene Site of Laetoli, Northern Tanzania*, pp. 78-81. Oxford: Clarendon Press.

Miomoto, M. & Goodman, M. (1986). Biomolecular systematics of eutherian mammals: phylogenetic patterns and classification. *Systematic Zoology* **38,** 230-240.

Miller, R.L. & Kahn, J.S. (1962). *Statistical Analysis in the Geological Sciences*. New York: John Wiley & Sons.

Mooring, M.S., Benjamin, J.E., Harte, C.R. & Herzog, N.B. (2000). Testing the interspecific body size principle in ungulates: the smaller they come, the harder they groom. *Animal Behaviour* **60,** 35-45.

Moya Sola, S. (1983). Los Boselophini (Bovidae Mammalia) del neogeno de la peninsula Iberica. *Publicaciones de Geologia, Univeristat Autonoma de Barcelona.* **18,** 1-236.

Mysterud, A. (2000). The relationship between ecological segregation and sexual body-size dimorphism in large herbivores. *Oecologia* **124,** 40-54.

Ndessokia, P.N.S. (1990). *The Mammalian Fauna and Archaeology of the Ndolanya and Olpiro Beds, Laetoli, Tanzania.* PhD dissertation, University of California, Berkeley.

Nowak, R.M., Ed (1999). *Walker's Mammals of the World, 6th Edition.* Baltimore: Johns Hopkins University Press.

Oboussier, H. (1970). Beitrage sur Kenntnis der Pelea *(Pelea capreolus*, Bovidae, Mammalia), ein Vergleich mit etwa gleichgrossen anderen Bovinae (*Redunca fulorufula, Gazella thomsoni, Antidorcas marsupialis*). *Zeitschrift für Säugetierekunde* **35,** 342-353.

Odum, E.P. (1983). *Basic Ecology*. Philadelphia: W.B. Saunders.

Olson J.S., Watts J.A. & Allinson L.J. (1983). Carbon in live vegetation in major world ecosystems. *Environmental Sciences Division Publication* No. 1997. Oak Ridge National Laboratory, Tennessee.

Owen-Smith, N. (1982). Factors influencing the consumption of plant products by large herbivores. In (B.J. Huntley & B.H. Walker, Eds) *Ecology of Tropical Savannas,* pp. 359-404. New York: Springer.

Owen-Smith, N. (1997). Distinctive features of the nutritional ecology of browsing versus grazing ruminants. *Zeitschrift für Säugetierekunde* **62 Supp II,** 176-191.

Owen-Smith, N. (1999). Ecological links between African savanna environments, climate change, and early hominid evolution. In (T.G. Bromage & F. Schrenk, Eds) *African Biogeography, Climate Change, and Human Evolution*, pp. 138-149. Oxford: Oxford University Press.

Patterson, B., Behrensmeyer, A.K. & Sill, W.D. (1970). Geology and fauna of a new Pliocene locality in north-western Kenya. *Nature* **226,** 918.

Patterson, B. & Howells, W.W. (1967). Hominid humeral fragment from early Pleistocene of north-western Kenya. *Science* **156,** 64-66.

Petter, G. (1987). Small carnivores (Viverridae, Mustelidae, Canidae). In (M.D. Leakey & J.H. Harris, Eds) *The Pliocene Site of Laetoli, Northern Tanzania*, pp. 194-234. Oxford: Clarendon Press.

Plummer, T.W. & Bishop, L.C. (1994). Hominid paleoecology at Olduvai Gorge, Tanzania as indicated by antelope remains. *Journal of Human Evolution* **27,** 47-75.

Potts, R. (1982). Lower Pleistocene site formation and hominid activities at Olduvai Gorge, Tanzania. PhD dissertation, Harvard University. Cambridge, Massachusetts.

Potts, R. (1988). *Early Hominid Activities at Olduvai Gorge*. Hawthorne, New York: Aldine de Gruyter.

Potts. R. (1994). Variables versus models of early Pleistocene hominid land use. *Journal of Human Evolution* **27,** 7-24.

Potts, R. (1996a). Evolution and climate variability. *Science* **273,** 922-923.

Potts, R. (1996b). *Humanity's Descent: The Consequences of Ecological Instability.* New York: Morrow.

Potts, R. (1998). Environmental hypotheses of hominin evolution. *Yearbook of Physical Anthropology* **41,** 93-136.

Pratt, D., Greenway, P.J. & Gwynne, M.D. (1966). A classification of East African rangeland, with an appendix on terminology. *Journal of Applied Ecology* **3,** 369-382.

Pratt, D. & Gwynne, M.D. (1977). *Rangeland Management and Ecology in East Africa.* London: Hodder and Stoughton.

Prentice, M.L. & Denton, E.H. (1988). The deep-sea oxygen isotope record, the global ice sheet system and hominid evolution. In (F.E. Grine, Ed) *Evolutionary History of the Robust" Australopithecines*, pp. 383-403. New York: Aldine de Gruyter.

Prothero, D.R., Manning, E.M. & Fischer, M. (1988). The phylogeny of the ungulates. In (M.J. Benton, Ed) *The Phylogeny and Classification of Tetrapods,* Systematics Assoc. Spec. **35**(2), 201-234. Oxford: Clarendon Press.

Reed, K.E. (1996). The Paleoecology of Makapansgat and other African Pliocene Hominid Localities. PhD dissertation. New York: State University of New York at Stony Brook.

Reed, K.E. (1997). Early hominid evolution and ecological change through the African Plio-Pleistocene. *Journal of Human Evolution* **32,** 289-322.

Retallack, G.J. (1991). *Miocene Paleosols and Ape Habitats of Pakistan and Kenya.* New York: Oxford University Press.

Retallack, G.J., Dugas, D.P. &Bestland, E.A. (1990). Fossil soils and grasses of a middle Miocene East African grassland. *Science* **247,** 1325-1328.

Ritchie, J.M. (1987). Trace fossils of burrowing Hymenoptera from Laetoli. In (M.D. Leakey & J.H. Harris, Eds) *The Pliocene Site of Laetoli, Northern Tanzania*, pp. 433-438. Oxford: Clarendon Press.

Romer, A.S. (1945). *Vertebrate Paleontology.* Chicago: University of Chicago Press.

Ruff, C.B. (1988). Hindlimb articular surface allometry in Hominoidea and *Macaca*, with comparisons to diaphyseal scaling. Journal of Human Evolution **17,** 687-714.

Sands, W.A. (1987). Ichnocoenoses of probable termite origin from Laetoli. In (M.D. Leakey & J.H. Harris, Eds) *The Pliocene Site of Laetoli, Northern Tanzania*, pp. 409-433. Oxford: Clarendon Press.

Savage, D.E. & Russell, D.E. (1983). *Mammalian Paleofaunas of the World.* Reading, Massachusetts: Addison-Wesley.

Schoener, T.W. (1974). Resource portioning in ecological communities. *Science* **185,** 27-39.

Schrenk, F., Bromage, T.G., Betzler, C.G., Ring, U. & Juwayeyi, Y.M. (1993). Oldest *Homo* and Pliocene biogeography of the Malawi Rift. *Nature* **365,** 833-835.

Schrenk, F., Bromage, T.G., Gorthner, A., & Sandrock, O. (1995). Paleoecology of the Malawi Rift: vertebrate and invertebrate faunal contexts of the Chiwondo Beds, northern Malawi. *Journal of Human Evolution* **28,** 59-70.

Schwarz, E. (1937). Die fossilen Antilopen von Oldoway. *Wissenschaftliche Ergebnisse der Oldoway Expedition, Liepzig* **4,** 8-104.

Scott, K.M. (1979). Adaptation and allometry in bovid postcranial proportions. PhD dissertation. Yale University: New Haven, Connecticut.

Scott, K.M. (1983). Prediction of body weight of fossil Artiodactyla. *Zoological Journal of the Linnean Society* **77,** 199-215.

Scott, K.M. (1985). Allometric trends and locomotor adaptations in the Bovidae. *Bulletin of the American Museum of Natural History* **197,** 197-288.

Scott, K.M. & Janis, C.M. (1993). Relationships of the Ruminantia (Artiodactyla) and an analysis of the characters used in ruminant taxonomy. In (F.S. Szalay, M.J. Novacek, & M.C. McKenna, Eds). *Mammal Phylogeny: Placentals,* pp. 282-302. New York: Springer-Verlag.

Senut, B., Pickford, M., Gommery, D., Mein, P., Cheboi, K. & Coppens, Y. (2001). First hominid from the Miocene (Lukeino Formation, Kenya). *Comptes Rendus de l'Academie des Sciences, Series IIA - Earth and Planetary Science* **332**(2), 137-144.

Shipman, P. & Harris, J.M. (1988). Habitat preference and paleoecology of *Australopithecus boisei* in Eastern Africa. In (F.E. Grine, Ed) *The Evolutionary History of the "Robust" Australopithecines,* pp. 343-381. New York: Aldine de Gruyter.

Simpson, C.D. (1945). The principles of classification and a classification of mammals. *Bulletin of the American Museum of Natural History* **85,** 1-350.

Simpson, G.G. (1950). *Horses.* Oxford: Oxford University Press.

Sinclair, A.R.E (1985). Does interspecific competition or predation shape the African ungulate community? *Journal of Animal Ecology* **54,** 899-918.

Sinclair, A.R.E. (2000). Adaptation, niche partitioning, and coexistence of African Bovidae: clues to the past. In (E.S. Vrba & G.B. Schaller, Eds.) *Antelopes, Deer and Relatives: Fossil Record, Behavioral Ecology, Systematics and Conservation,* pp. 247-260. New Haven: Yale University Press.

Snyder, P. (1991). Three reasons why stepwise regression methods should not be used by researchers. In (B. Thompson, Ed.) *Advances in Educational Research: Substantive Findings, methodological Developments*, pp. 99-105. Greenwich, CT: JAI Press.

Sokal, R.R. & Rolf, F.J. (1981). *Biometry, 2nd Edition.* San Francisco: W.H. Freeman & Company.

Solounias, N., Barry, J.C., Bernor, R.L., Lindsay, E.H. & Raza, S.M. (1995a). The oldest bovid from the Siwaliks, Pakistan. *Journal of Vertebrate Paleontology* **15,** 806-814.

Solounias, N. & Dawson-Saunders, B. (1988). Dietary adaptations and palaeoecology of the late Miocene ruminants from Pikermi and Samos in Greece. *Palaeogeography, Palaeoclimatology, Palaeoecology* **65,** 149-172.

Solounias, N. & Moelleken, S. (1992a). Dietary interpretation of *Eotragus sansaniensis* (Mammalia, Ruminantia): tooth microwear analysis. *Journal of Vertebrate Paleontology* **12,** 250-255.

Solounias, N. & Moelleken, S. (1992b). Dietary adaptations of two goat ancestors and evolutionary considerations. *Geobios* **6,** 797-809.

Solounias, N. & Moelleken, S. (1993). Dietary adaptations of some extinct ruminants determined by premaxillary shape. *Journal of Mammalogy* **74,** 1059-1071.

Solounias, N. & Semprebon, G. (2002). Advances in the reconstruction of ungulate ecomorphology with application to early fossil equids. *American Museum Novitates* **3366,** 1-49.

Solounias, N., Teaford, M.F., & Walker, A.C. (1988). Interpreting the diet of extinct ruminants: the case of a non-browsing giraffid. *Paleobiology* **14,** 287-300.

Solounias, N., Fortelius, M., & Freeman, P. (1994). Molar wear rates in ruminants: a new approach. *Annales Zoologici Fennici, Helsinki* **31,** 219-227.

Solounias, N., Moelleken, M.C., & Plavcan, J.M. (1995b). Predicting the diet of extinct bovids using masseteric morphology. *Journal of Vertebrate Paleontology* **15**(4), 795-805.

Spencer, L.M. (1995). Morphological correlates of dietary resource partitioning in the African Bovidae. *Journal of Mammalogy* **76**(2), 448-471.

Spencer, L.M. (1997). Dietary adaptations of Plio-Pleistocene Bovidae: implications for hominid habitat use. *Journal of Human Evolution* **32,** 201-228.

Sponheimer, M., Reed, K.E. & Lee-Thorp, J.A. (1999). Combining isotopic and ecomorphological data to refine bovid paleodietary reconstruction: a case study from the Makapansgat Limeworks hominin locality. *Journal of Human Evolution* **36,** 705-718.

Stanley, S.M. (1992). An ecological theory for the origin in *Homo. Paleobiology* **18,** 237-257.

Stirton, R.A. (1947). Observations on evolutionary rates of hypsodonty. *Evolution* **1,** 32-41.

Stockman, von W. (1979). Differences in the shape of the mandibles in African Bovidae (Mammalia) in relation to food composition. *Zoologisches Jahrbuch der Systematik* **106,** 344-373.

Suwa, G., Asfaw, B., Beyene, Y., White, T.D., Katoh, S., Nagaoka, S., Nakaya, H., Uzawa, K., Renne, P., WoldeGabriel, G. (1997). The first skull of *Australopithecus boisei. Nature* **389,** 489-92.

Szalay, F.S., Novacek, M.J., & McKenna, M.C., Eds (1993). *Mammal Phylogeny: Placentals.* New York: Springer-Verlag.

Tabachnick, B.G. & Fidell, L.S. (2001). *Using Multivariate Statistics, 4th ed.* Boston, Massachusetts: Allyn and Bacon.

Taylor, C.R. (1972). The desert gazelle, a paradox resolved. In *Comparative Physiology of Desert Animals. Symposia of the Zoological Society of London* **31,** 215-227. London: Academic Press.

Teaford, M.F (1988). A review of dental microwear and diet in modern mammals. *Scanning Microscopy* **2,** 1149-1166.

Teaford, M.F. & Walker, A. (1984). Quantitative differences in dental microwear between primate species with different diets and a comment on the presumed diet of *Sivapithecus. American Journal of Physical Anthropology* **64,** 191-200.

Thenius, E. (1969). Stammesgeschichte der Säugetiere (einschliesslich der Hominiden). *Handbook of Zoology* **8**(470-48), 1-722.

Thomas, H. (1984). Le Bovide du Miocene du sous-continent Indien, de la pensinsule Arabique et de l'Afrique. *Palaeogeography, Palaeoclimatology, Palaeoecology* **45,** 251-299.

Thomas, H. (1994). Anatomie cranienne et relations phylogentetiques du nouveau bovide (*Pseudoryx nghetinhensis*) decouvert dans la cordillere annamatique au Vietnam. *Mammalia* **58**(3), 453-481.

Thompson, B. (1989). Why don't stepwise methods die? *Measurement and Evaluation in Counseling and Development* **21,** 146-148.

Thompson, B. (1995). Stepwise regression and stepwise discriminant analysis need not apply here: A guidelines editorial. *Educational and Psychological Measurement* **55,** 525-234.

Tiedemann, R., Sarnthein, M., & Shackleton, N.J. (1994). Astronomic timescale for the Pliocene Atlantic d18O and dust flux records of ODP Site 659. *Paleoceanography* **9,** 619-638. .

Turnbull, W.D. (1970). Mammalian masticatory apparatus. *Fieldiana, Geology* **18,** 147-356.

Turner, A. & Wood, B. (1993). Comparative palaeontological context for the evolution of the early hominid masticatory system. *Journal of Human Evolution* **24,** 301-318.

Underwood, R. (1983). The feeding behaviour of grazing African ungulates. *Behaviour* **84,** 201-243.

Van der Weil, A.M. & Wijmstra, T.A. (1987). Palynology of the lower part of the (78 – 120m) of the core Tenhagi Philippon II, Middle Pleistocene of Macedonia, Greece. *Review of Palaeobotany and Palynology* **52,** 73-88.

Van Valkenburgh, B. (1987). Skeletal indicators of locomotor behavior in living and extinct carnivores. *Journal of Vertebrate Paleontology* **7,** 162-182.

Van Valkenburgh, B. (1994). Ecomorphological analysis of fossil vertebrates and their fossil communities. In (P.C. Wainwright and S.M. Reilly, Eds) *Ecological Morphology: Integrative Organismal Biology,* pp. 140-166. Chicago: University of Chicago Press.

Van Valkenburgh, B., Teaford, M.F., & Walker, A. (1990). Molar microwear and diet in large carnivores: inferences concerning diet in the sabertooth cat, *Smilodon fatalis. Journal of Zoology* **222,** 319-340.

Verdocurt, B. (1987). Mollusca from the Laetolil and Upper Ndolanya Beds. In (M.D. Leakey & J.H. Harris, Eds) *The Pliocene Site of Laetoli, Northern Tanzania*, pp. 438-450. Oxford: Clarendon Press.

Vesey-Fitzgerald, D. (1963). Central African grasslands. *Journal of Ecology* **51,** 243-274.

Vesey-Fitzgerald, D. (1972). Fire and animal impact on vegetation in Tanzania's national parks. *Proceedings of the Tall Timbers Fire Ecology Conference* **11,** 297-317.

Vignaud, P., Duringer, P., Mackaye, H.T., Likius, A., Blondel, C., Boisserie, J.R., de Bonis, L., Eisenmann, V., Etienne, M.E., Geraads, D., Guy, F., Lehmann, T., Lihoreau, F., Lopez-Martinez, N., Mourer-Chauvire, C., Otero, O., Rage, J.C., Schuster, M., Viriot, L., Zazzo, A. & Brunet, M. (2002). Geology and paleontology of the Upper Miocene Torros-Menalla Locality, Chad. *Nature* **418,** 133-155.

Vrba, E.S. (1974). Chronological and ecological implications of the fossil Bovidae at the Sterkfontein australopithecine site. *Nature* **250,** 19-23.

Vrba, E.S. (1975). Some evidence of chronology and paleoecology of Sterkfontein, Swartkrans, and Kromdraai from the fossil Bovidae. *Nature* **254,** 301-304.

Vrba, E.S. (1976). The fossil Bovidae of Sterkfontein, Swartkrans and Kromdraai. *Transvaal Museum Memoirs* **21,** 1-166.

Vrba, E.S. (1979). Phylogenetic analysis and classification of fossil and recent Alcelaphini (Family Bovidae, Mammalia). *Zoological Journal of the Linnean Society* **11,** 207-228.

Vrba, E.S. (1980). The significance of bovid remains as indicators of environment and prediction patterns. In (A.K. Behrensmeyer & A. Hill, Eds) *Fossils in the Making, Vertebrate Taphonomy and Paleoecology,* pp. 247-271. Chicago: University of Chicago Press.

Vrba, E.S. (1982). Biostratigraphy and chronology, based partly on Bovidae, of southern African hominid-associated assemblages: Makapansgat, Sterkfontein, Taung, Kromdraai, Swartkrans; also Elandsfontein (Saldanha), Broken Hill (now Kabwe) and Cave of Hearths. In (H. de Lumley & M.A. de Lumley, Eds) *Proceedings of Congress International de Paleontologie Humaine,* Vol. 2., pp. 707-752. Nice: Union Internationale des Sciences Prehistoriques et Prohistoriques.

Vrba, E.S. (1984). Evolutionary pattern and process in the sister groups Alcelaphini-Aepycerotini. In (N. Eldredge & S.M. Stanley, Eds) *Living Fossils,* pp. 62-79. New York: Springer-Verlag.

Vrba, E.S. (1985a). African Bovidae: evolutionary events since the Miocene. *South African Journal of Science* **81,** 263-266.

Vrba, E.S. (1985b). Ecological and adaptive changes associated with early hominid evolution. In (E. Delson, Ed) *Ancestors: The Hard Evidence,* pp. 63-71. New York: Alan R. Liss, Inc.

Vrba, E.S. (1985c). Environment and evolution: alternative causes of the temporal distribution of evolutionary events. *South African Journal of Science* **81,** 229-236.

Vrba, E.S. (1987). A revision of the Bovini (Bovidae) and a preliminary revised checklist of Bovidae from Makapansgat. *Palaeont. Afr.* **26,** 33-46.

Vrba, E.S. (1988). Late Pliocene climatic events and hominid evolution. In (F.E. Grine, Ed) *The Evolutionary History of the "Robust" Australopithecines,* pp. 405-426. New York: Aldine de Gruyter.

Vrba, E.S. (1992). Mammals as a key to evolutionary theory. *Journal of Mammalogy* **73,** 1-28.

Vrba, E.S. (1994). An hypothesis of heterochrony in response to climatic cooling and its relevance to early hominid evolution. In (R.S. Corruccini, & R.L. Ciochon, Eds) *Integrative Paths to the Past*, pp. 345-376. New Jersey: Prentice Hall.

Vrba, E.S. (1995). The fossil record of African antelopes (Mammalia, Bovidae) in relation to human evolution and palaeoclimate. In (E.S. Vrba, G. Denton, L. Burckle & T. Partidge, Eds) *Paleoclimate and Evolution with an Emphasis on Human Origins,* pp. 385-424. New Haven: Yale University Press.

Vrba, E.S. (1997). New fossils of Alcelaphini and Caprinae (Bovidae, Mammalia) from Awash, Ethiopia, and phylogenetic analysis of living and extinct Alcelaphini. *Palaeontologia africana* **34,** 127-198.

Vrba, E.S., Denton, G.H., & Prentice, M.L. (1989). Climatic influences on early hominid behavior. *Ossa* **14,** 127-156.

Vrba, E.S. & Schaller, G.B. (2000). Phylogeny of Bovidae based on behavior, glands, skulls, and postcrania. In (E.S. Vrba & G.B. Schaller, Eds.) *Antelopes, Deer and Relatives: Fossil Record, Behavioral Ecology, Systematics and Conservation,* pp. 203-222. New Haven: Yale University Press.

Vree, F. de & Gans, C. (1974). Mastication in pygmy goats (*Capra hircus*). *Annales de la Societe Royale Zoologique de Belgique* **105,** 255-306.

Walker, A. (1987) Fossil Galaginae from Laetoli. In (M.D. Leakey & J.H. Harris, Eds) *The Pliocene Site of Laetoli, Northern Tanzania*, pp. 88-91. Oxford: Clarendon Press.

Walker, A., Hoeck, H.N., & Perez, L. (1978). Microwear of mammalian teeth as indicators of diet. *Science* **201,** 908-910.

Walker, A., Leakey, R.E., Harris, J.M. & Brown, F.H. (1986). 2.5 myr *Australopithecus boisei* from west of Lake Turkana. *Nature* **322,** 517-522.

Wall, D.A., Davis, S.K., & Read. B.M. (1992). Phylogenetic relationships in the subfamily Bovinae (Mammalia: Artiodactyla) based on ribosomal DNA. *Journal of Mammalogy* **73**(2), 262-275.

Walter, H. (1971). *Ecology of Tropical and Subtropical Vegetation.* Edinburgh: Oilver & Boyd.

Walter, H., Breckle, S. (2002). *Walter's Vegetation of the Earth: The Ecological Systems of the Geo-Biosphere, 4th edition.* New York: Springer-Verlag.

Wang, B. (1992). The Chinese Oligocene: a preliminary review of mammalian localities and local faunas. In (D.R. Prothero & W.A. Berggren, Eds.) *Eocene-*

Oligocene Climatic and Biotic Evolution, pp. 529-547. Princeton: Princeton University Press.

Ward, C.V., Leakey, M.G. & Walker, A. (1999). The new hominid species *Australopithecus anamensis. Evolutionary Anthropology* **7,** 197-205.

Ward, C.V., Walker, A.,& Leakey, M.G. (1997). New fossils of Australopithecus anamensis from Kanapoi and Allia Bay, Kenya. *American Journal of Physical Anthropology* **Supp 24,** 235.

Washburn, S.L. (1960). Tools and human evolution. *Scientific American* **203**(3), 63-75.

Watson, G.E. (1987). Pliocene bird fossils from Laetoli. In (M.D. Leakey & J.H. Harris, Eds) *The Pliocene Site of Laetoli, Northern Tanzania*, pp. 82-83. Oxford: Clarendon Press.

Weckerly, F.W. (1998). Sexual-size dimorphism: influence of mass and mating systems in the most dimorphic mammals. *Journal of Mammalogy* **79**(1), 33-52.

Wesselman, H.B. (1985). Fossil micromammals as indicators of climatic change about 2.4 Myr ago in the Omo Valley, Ethiopia. *South African Journal of Science* **81,** 260-261.

Wesselman, H.B. (1995). Of mice and almost-men: regional paleoecology and human evolution in the Turkana Basin. In (E.S Vrba, G.H. Denton, T.C. Partridge and L.H. Burckle, Eds) *Paleoclimate and Evolution, With Emphasis on Human Evolution*, pp. 356-368. New Haven: Yale University Press.

Whitaker, J.S. (1997). Use of stepwise methodology in discriminant analysis. Paper presented at the Annual Meeting of the Southwest Educational Research Association, Austin, Texas, January 1997.

White, F. (1983). *The Vegetation of Africa.* Switzerland: UNESCO.

White, T.D. (1995). African omnivores: global climatic change and Plio-Pleistocene hominids and suids. In (E.S. Vrba, G. Denton, L. Burckle & T. Partidge, Eds) *Paleoclimate and Evolution with an Emphasis on Human Origins,* pp. 369-384. New Haven: Yale University Press.

White, T.D. (1986). *Australopithecus afarensis* and the Lothagam mandible. *Anthropos* **23,** 79-90.

White, T.D. (1991). *Human Osteology*. San Diego: Academic Press.

White, T.D., Suwa, G. & Asfaw, B. (1994). *Australopithecus ramidus*, a new species of early hominid from Aramis, Ethiopia. *Nature* **371,** 305-312.

White, T.D., Suwa, G. & Asfaw, B. (1995). *Australopithecus ramidus*, a new species of early hominid from Aramis, Ethiopia. *Nature* **375,** 88.

Williams, S.H. & Kay, R.F. (2001). A comparative test of adaptive explanations for hypsodonty in ungulates and rodents. *Journal of Mammalian Evolution* **8,** 207-229.

Williamson, D. & Macho, G. (2001). Are body proportions a good indicator of habitat use and ecological niche? An example from the African bovids. Unpublished manuscript.

WoldeGabriel, G., Haile-Selassie, Y., Renne, P.R., Hart, H.K., Ambrose, S.H., Asfaw, B, Heiken, G., & White, T. (2001). Geology and paleontology of the Late Miocene Middle Awash valley, Afar Rift, Ethiopia. *Nature* **412,** 175-178.

Wootton, J.T. (1987). The effects of body mass, phylogeny, habitat and trophic level on mammalian age at first reproduction. *Evolution* **41**(4), 732-749.

Wynn, J.G. (2004). Influence of Plio-Pleistocene aridification on human evolution: evidence from paleosols of the Turkana Basin. *American Journal of Physical Anthropology* **123,** 106-118.

Wyss, A.R., Novacek, M.J., & McKenna, M.C. (1987). Amino acid sequence versus morphological data and the interordinal relationships of mammals. *Molecular Biology and Evolution* **4,** 99-116.

Zey, A. (1939). Funktion des Kauapparatus und Schadelgestaltung bei den Wiederkauern. Inaugurieren Dissertation, University of Frankfurt.

APPENDIX A

MODERN SPECIMENS

Museum	Museum Number	Species	Sex
ANTILOPINAE			
AMNH	35957	Antilope cervicapra	male
AMNH	54486	Antilope cervicapra	male
AMNH	34736	Cephalophus monticola musculoides	male
AMNH	52943	Cephalophus nigrifrons nigrifrons	male
AMNH	52930	Cephalophus nigrifrons nigrifrons	female
AMNH	52940	Cephalophus nigrifrons nigrifrons	female
AMNH	81170	Litocranius walleri sclateri	male
AMNH	88409	Litocranius walleri walleri	male
AMNH	187829	Litocranius walleri walleri	female
AMNH	82074	Oreotragus oreotragus schillingsi	female
AMNH	27827	Oreotragus oreotragus schillingsi	male
AMNH	80553	Oreotragus oreotragus tyleri	male
AMNH	82070	Ourebia ourebi cottoni	male
AMNH	34764	Ourebia ourebi cottoni	male
AMNH	53317	Ourebia ourebi goslingi	female
AMNH	216389	Raphicerus campestris capricornis	female
AMNH	80538	Raphicerus campestris kelleni	male
AMNH	233045	Raphicerus campestris steinhardti	male
NHM	1950.9.23.1	Cephalophus leucogaster	male
NHM	1936.10.28.28	Cephalophus monticola schultzei	male
NHM	1936.10.28.29	Cephalophus monticola schultzei	male
NHM	1936.10.28.30	Cephalophus monticola schultzei	female
NHM	1936.10.28.31	Cephalophus monticola schultzei	female
NHM	1939.2563	Gazella cuvieri	male
NHM	1936.9.5.2	Gazella granti	male
NHM	1935.12.14.2	Gazella granti	male
NHM	1936.3.28.10	Gazella granti petersi	male
NHM	1936.9.5.3	Gazella granti robertsi	female
NHM	1936.12.13.3	Gazella spekei	male
NHM	1896.10.6.1	Gazella spekei	?
NHM	1897.1.14.6	Gazella subgutturosa	male
NHM	1936.3.28.3	Litocranius walleri	male
NHM	1962.7.6.17	Litocranius walleri walleri	male
NHM	1962.10.18.1	Madoqua guentheri	female
NHM	1936.5.28.2	Madoqua kirki	male
NHM	1932.6.6.49	Madoqua kirki	female
NHM	1932.6.6.51	Madoqua kirki	female
NHM	1932.6.6.46	Madoqua kirki	female
NHM	1869.2.2.10	Madoqua saltiana	female
NHM	1937.8.4.26	Neotragus batesi	male
NHM	1937.8.4.27	Neotragus batesi	female
NHM	1962.12.14.5	Neotragus moschatus	male
NHM	1936.5.28.4	Oreotragus oreotragus	female
NHM	76.579	Raphicerus campestris	male
NHM	76.581	Raphicerus campestris	male
NHM	1936.5.28.3	Raphicerus campestris	male

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Museum	Museum Number	Species	Sex
ANTILOPINAE continued			
NHM	1966.7.28.1	Sylvicapra grimmia	female
NHM	1966.8.18.1	Sylvicapra grimmia	male
NHM	1966.9.22.1	Sylvicapra grimmia	female
NHM	1966.9.26.1	Sylvicapra grimmia	male
NHM	1966.8.5.1	Sylvicapra grimmia	male
NHM	1936.3.30.7	Sylvicapra grimmia grimmia	male
NMNH	USNM 252685	Gazella rufifrons laevipes	male
NMNH	USNM 252686	Gazella rufifrons laevipes	male
NMNH	USNM 240693	Gazella soemmerringi	male
NMNH	USNM 240691	Gazella soemmerringi	male
NMNH	USNM 062088	Gazella subgutturosa	male
NMNH	USNM 163048	Gazella thomsonii nasalis	male
NMNH	USNM 162005	Gazella thomsonii nasalis	female
NMNH	USNM 172903	Gazella thomsonii nasalis	male
NMNH	USNM 163053	Gazella thomsonii nasalis	male
NMNH	USNM 429835	Neotragus pygmaeus	male
NMNH	USNM 084084	Procapra picticaudata	female
NMNH	USNM 084085	Procapra picticaudata	male
NMNH	USNM 367433	Raphicerus sharpei	female
NMNH	USNM 367434	Raphicerus sharpei	male
NMNH	USNM 367445	Raphicerus sharpei	male
PC	MERFIELD 891	Cephalophus leucogaster	female
PC	MERFIELD 244	Cephalophus nigrifrons nigrifrons	male
PC	MERFIELD 342	Cephalophus nigrifrons nigrifrons	male
PC	MERFIELD 649	Cephalophus nigrifrons nigrifrons	male
PC	ALGERIA 4	Gazella cuvieri	female
PC	JUBALAND 101	Ourebia ourebi haggardi	male
PC	JUBALAND 40	Ourebia ourebi haggardi	male
BOVINAE			
AMNH	98957	Bison bison athabascae	female
AMNH	73615	Bison bison athabascae	male
AMNH	98953	Bison bison athabascae	male
AMNH	130211	Bison bison bison	female
AMNH	54551	Bos javanicus birmanicus	male
AMNH	53244	Tragelaphus scriptus	male
AMNH	216371	Tragelaphus scriptus	female
AMNH	187806	Tragelaphus scriptus	female
AMNH	53245	Tragelaphus scriptus	female
AMNH	36404	Tragelaphus scriptus delamerei	male
AMNH	34757	Tragelaphus scriptus delamerei	male
AMNH	34753	Tragelaphus scriptus delamerei	female
NHM	1960.11.10.3	Taurotragus oryx	?
NHM	1959.1.2.2	Tragelaphus eurycerus	female
NHM	1934.11.9.1	Tragelaphus eurycerus	female

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Museum	Museum Number	Species	Sex
BOVINAE continued			
NHM	1966.5.20.1	Tragelaphus scriptus	female
NHM	1966.5.20.2	Tragelaphus scriptus	female
NHM	1966.6.7.1	Tragelaphus scriptus	male
NHM	71.2115	Tragelaphus scriptus	female
NHM	1935.7.24.5	Tragelaphus strepsiceros	female
NHM	1935.12.12.4	Tragelaphus strepsiceros	male
NMNH	USNM 197705	Bison bison athabascae	female
NMNH	USNM A22377	Bison bison bison	male
NMNH	USNM A22375	Bison bison bison	male
NMNH	USNM 154385	Bos javanicus	female
NMNH	USNM 198317	Bos javanicus	male
NMNH	USNM 361392	Bos sauveli	female
NMNH	USNM 399379	Bos sauveli	female
NMNH	USNM 219049	Bubalus mindorensis	?
NMNH	USNM 161946	Syncerus caffer	female
NMNH	USNM 163311	Syncerus caffer	female
NMNH	USNM 164768	Syncerus caffer	male
NMNH	USNM 164645	Taurotragus derbianus	female
NMNH	USNM 164646	Taurotragus derbianus	male
NMNH	USNM 162984	Taurotragus oryx	male
NMNH	USNM 163308	Taurotragus oryx	male
NMNH	USNM 163226	Tragelaphus eurycerus	female
NMNH	USNM 164558	Tragelaphus spekii	male
NMNH	USNM 163320	Tragelaphus strepsiceros	male
NMNH	USNM A36881	Tragelaphus strepsiceros	female
CAPRINAE			
AMNH	165683	Naemorhedus crispus crispus	female
AMNH	43037	Naemorhedus sumatraensis montinus	male
AMNH	54614	Naemorhedus sumatraensis thar	female
AMNH	54865	Ovis ammon poli	male
AMNH	54870	Ovis ammon poli	male
AMNH	122673	Ovis canadensis canadensis	male
AMNH	164125	Ovis canadensis nelsoni	male
AMNH	123042	Ovis dalli dalli	female
AMNH	121817	Ovis dalli stonei	male
AMNH	54616	Ovis vignei vignei	male
AMNH	54615	Ovis vignei vignei	female
AMNH	119526	Ovis vignei vignei	male
AMNH	90234	Rupicapra rupicapra	male
AMNH	90235	Rupicapra rupicapra	male
NMNH	USNM 259079	Budorcas taxicolor tibetana	male
NMNH	USNM 258656	Budorcas taxicolor tibetana	female
NMNH	USNM 259078	Budorcas taxicolor tibetana	male
NMNH	USNM 258824	Budorcas taxicolor tibetana	male

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Museum	Museum Number	Species	Sex
CAPRINAE continued			
NMNH	USNM 258830	Budorcas taxicolor tibetana	male
NMNH	USNM 258652	Budorcas taxicolor tibetana	male
NMNH	USNM 252227	Budorcas taxicolor tibetana	female
NMNH	USNM 259024	Budorcas taxicolor tibetana	female
NMNH	USNM 259415	Budorcas taxicolor tibetana	male
NMNH	USNM 062092	Capra sibirica	female
NMNH	USNM 062093	Capra sibirica	male
NMNH	USNM 020409	Capra sibirica	male
NMNH	USNM 013829/A20934	Naemorhedus crispus	male
NMNH	USNM 259023	Naemorhedus goral griseus	female
NMNH	USNM 259398	Naemorhedus goral griseus	male
NMNH	USNM 259399	Naemorhedus goral griseus	female
NMNH	USNM 259025	Naemorhedus sumatraensis milneedwardii	female
NMNH	USNM 258670	Naemorhedus sumatraensis milneedwardii	male
NMNH	USNM 311229	Naemorhedus swinhoei	female
NMNH	USNM 174617	Oreamnos americanus missoulas	female
NMNH	USNM A20752	Oreamnos americanus missoulas	?
NMNH	USNM A49655	Ovibos moschatus wardi	female
NMNH	USNM 251592	Ovibos moschatus wardi	male
NMNH	USNM 288025	Ovibos moschatus wardi	male
NMNH	USNM 261803	Ovibos moschatus wardi	male
NMNH	USNM 240681	Pseudois nayaur szechuanensis	female
NMNH	USNM 259712	Pseudois nayaur szechuanensis	male
HIPOTRAGINAE			
AMNH	113812	Addax nasomaculatus addax	?
AMNH	88406	Damaliscus hunteri	male
AMNH	88408	Damaliscus hunteri	female
NHM	1967.11.8.1.	Aepyceros melampus	female
NHM	69.1142	Aepyceros melampus	female
NHM	1960.11.10.2	Aepyceros melampus	female
NHM	1932.6.6.32	Aepyceros melampus	male
NHM	1960.11.10.5	Aepyceros melampus	male
NHM	1960.11.10.2	Aepyceros melampus	female
NHM	1968.6.20.1	Aepyceros melampus	female
NHM	1932.6.6.55	Alcelaphus buselaphus cokei	male
NHM	1932.6.6.54	Alcelaphus buselaphus cokei	male
NHM	1960.11.10.9	Alcelaphus buselaphus cokei	male
NHM	1850.11.22.70 645d	Connochaetes gnu	female
NHM	36.3.30.15	Connochaetes taurinus	male
NHM	1932.6.6.27	Connochaetes taurinus	female
NHM	1935.12.14.3	Connochaetes taurinus albojubatus	male?
NHM	1940.83	Connochaetes taurinus johnstoni	male?
NHM	70.345	Damaliscus dorcas dorcas	male
NHM	1938.7.11.1	Damaliscus hunteri	male

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Museum	Museum Number	Species	Sex
HIPOTRAGINAE continued			
NHM	71.2500.	Damaliscus lunatus jimela	female
NHM	1964.7.8.1	Hippotragus niger	female
NHM	1935.5.8.1	Hippotragus niger variani	?
NHM	1936.3.11.1	Hippotragus niger variani	?
NHM	1936.3.28.2	Oryx beisa	male
NMNH	USNM 164705	Alcelaphus buselaphus lelwel	female
NMNH	USNM 163008	Damaliscus lunatus jimela	male
NMNH	USNM 163164	Hippotragus equinus langheldi	female
NMNH	USNM 163165	Hippotragus equinus langheldi	male
NMNH	USNM 163215	Oryx beisa annectens	male
PC	TANGANYIKA 34	Hippotragus niger kirki	male
PC	TANGANYIKA 51	Hippotragus niger kirki	male
REDUNCINAE			
AMNH	53494	Kobus defassa	female
AMNH	53515	Kobus defassa	female
NHM	61.1003	Kobus defassa	female
NHM	69.1147	Kobus leche	male
NHM	1936.3.30.9	Redunca fulvorufula fulvorufula	male
NHM	1962.12.14.7	Redunca redunca	female
NHM	1960.11.10.1	Redunca redunca wardi	female
NMNH	USNM 163182	Kobus defassa	male
NMNH	USNM 164689	Kobus defassa	male
NMNH	USNM 252689	Kobus kob leucotis	male
NMNH	USNM 163194	Kobus kob thomasi	male
NMNH	USNM 163195	Kobus kob thomasi	male
NMNH	USNM 163345	Kobus kob thomasi	female
NMNH	USNM 164499	Kobus kob thomasi	female
NMNH	USNM 161992	Redunca fulvorufula chanleri	female
NMNH	USNM 161994	Redunca fulvorufula chanleri	female
NMNH	USNM 163188	Redunca redunca wardi	male
NMNH	USNM 163190	Redunca redunca wardi	male
CERVIDAE			
AMNH	114551	Elaphodus cephalophus cephalophus	female
AMNH	115638	Elaphodus cephalophus cephalophus	male
AMNH	84462	Elaphodus cephalophus michianus	male
AMNH	84463	Elaphodus cephalophus michianus	male
NMNH	USNM 270013	Alces alces andersoni	male
NMNH	USNM 267290	Alces alces gigas	male
NMNH	USNM 267296	Alces alces gigas	female
NMNH	USNM 251053	Alces alces shirasi	female
NMNH	USNM 567252	Odocoileus virginianus clavium	male
NMNH	USNM 566616	Odocoileus virginianus ochronus	male

AMNH = American Museum of Natural History
NHM = Natural History Museum, London
NMNH = National Museum of Natural History (Smithsonian)
PC = Powell-Cotton Museum

Museum	Museum Number	Species	Sex
CERVIDAE continued			
NMNH	USNM 256055	Odocoileus virginianus venatorius	female
NMNH	USNM 396283	Odocoileus virginianus virginianus	female
NMNH	USNM 282141	Pudu mephistophiles	male
NMNH	USNM 309045	Pudu mephistophiles	female
TRAGULIDAE			
PC	MERFIELD 197	Hyemoschus aquaticus batesi	female
PC	MERFIELD 403	Hyemoschus aquaticus batesi	male
PC	MERFIELD 395	Hyemoschus aquaticus batesi	male
PC	MERFIELD 577	Hyemoschus aquaticus batesi	male
PC	CONGO 318	Hyemoschus aquaticus cottoni	female

AMNH = American Museum of Natural History
NHM = Natural History Museum, London
NMNH = National Museum of Natural History (Smithsonian)
PC = Powell-Cotton Museum

Appendix B

Fossil Specimens

Catalog number	Beds	Locality	Tuffs
HUMERUS			
EP 2976/00	Upper Laetolil Beds	1	between 6 & 8
EP 204/00	Upper Laetolil Beds	1	between 7 & Yellow Marker Tuff
LAET 75-752	Upper Laetolil Beds	1	
EP 640/00	Upper Laetolil Beds	2	between 5 & 7
EP 2630/00	Upper Laetolil Beds	2	between 5 & 7
EP 2631/00	Upper Laetolil Beds	2	between 5 & 7
LAET 75-2112	Upper Laetolil Beds	2	
LAET 75-2120	Upper Laetolil Beds	2	
EP 2726/00	Upper Laetolil Beds	3	between 7 & 8
LAET 75-2751	Upper Laetolil Beds	3	
LAET 74-158	Upper Laetolil Beds	4	
EP 1686/00	Upper Laetolil Beds	5	between 3 & 5
EP 3051/00	Upper Laetolil Beds	5	between 3 & 5
LAET 74-190	Upper Laetolil Beds	5	
LAET 75-3006	Upper Laetolil Beds	5	
EP 1323/00a	Upper Laetolil Beds	6	between 5 & 6
EP 1323/00b	Upper Laetolil Beds	6	between 5 & 6
EP 1323/00c	Upper Laetolil Beds	6	between 5 & 6
EP 3808/00	Upper Laetolil Beds	6	between 5 & 6
EP 101/01	Upper Laetolil Beds	6	between 5 & 6
EP 912/01	Upper Laetolil Beds	7	above 7
EP 950/01	Upper Laetolil Beds	7	above 7
EP 1499/00	Upper Laetolil Beds	7	
LAET 75-3215	Upper Laetolil Beds	7	
EP 246/00	Upper Laetolil Beds	8	above 8
EP 291/00	Upper Laetolil Beds	8	below 6
EP 344/00	Upper Laetolil Beds	8	between 7 & 8
EP 1128/98	Upper Laetolil Beds	9	below 6 & 7
EP 1129/98	Upper Laetolil Beds	9	below 6 & 7
EP 1130/98	Upper Laetolil Beds	9	below 6 & 7
EP 1507/98	Upper Laetolil Beds	9	below 6 & 7
EP 481/98	Upper Laetolil Beds	10	below 2
EP 544/98	Upper Laetolil Beds	10	below 2
EP 160/99	Upper Laetolil Beds	10	below 2
EP 621/01	Upper Laetolil Beds	10	below 3
EP 422/98	Upper Laetolil Beds	10	below 7
EP 2566/00	Upper Laetolil Beds	11	between 7 & 8
EP 4280/00	Upper Laetolil Beds	11	between 7 & 8
EP 2473/009	Upper Laetolil Beds	13	between 6 & 8
EP 413/01	Upper Laetolil Beds	13	between 6 & 8
EP 3342/00	Upper Laetolil Beds	15	between 6 & 7
EP 1104/01	Upper Laetolil Beds	15	Yellow Marker Tuff
LAET 75-2569	Upper Laetolil Beds	15	
EP 2393/00	Upper Laetolil Beds	16	between 7 & 2 metres above 8
EP 495/00a	Upper Laetolil Beds	21	between 5 & 8
EP 495/00b	Upper Laetolil Beds	21	between 5 & 8
LAET 75-3381	Upper Laetolil Beds	21	

EP indicates Harrison collection
LAET indicates Leakey collection

Catalog number	Beds	Locality	Tuffs
HUMERUS continued			
EP 3728/00	Upper Laetolil Beds	22	between 5 & 7
LAET 75-3626	Upper Laetolil Beds	22	
EP 049/99	Upper Laetolil Beds	10 E	below 6 & 7
EP 771/00	Upper Laetolil Beds	10 E	between 5 & 7
EP 774/00	Upper Laetolil Beds	10 E	between 5 & 7
EP 534/01a	Upper Laetolil Beds	10 E	between 5 & 7
EP 534/01b	Upper Laetolil Beds	10 E	between 5 & 7
EP 536/01	Upper Laetolil Beds	10 E	between 5 & 7
EP 539/01	Upper Laetolil Beds	10 E	between 5 & 7
EP 325/98	Upper Laetolil Beds	10 E	between 6 & 7
EP 585/98	Upper Laetolil Beds	10 W	below 2
EP 3158/00	Upper Laetolil Beds	10 W	below 3
EP 2445/00	Upper Laetolil Beds	13 E	between 5 & 8
EP 2446/00	Upper Laetolil Beds	13 E	between 5 & 8
EP 2112/00	Upper Laetolil Beds	13	between 6 & 7
EP 2113/00	Upper Laetolil Beds	13	between 6 & 7
EP 1837/00	Upper Laetolil Beds	2, NW gully	between 5 & 7
EP 1748/00	Upper Laetolil Beds	2, S gully	between 6 & 7
EP 1753/00	Upper Laetolil Beds	2, S gully	between 6 & 7
EP 1274/98	Upper Laetolil Beds	22 S	below 5
EP 1275/98	Upper Laetolil Beds	22 S	below 5
Ep 952/98	Upper Laetolil Beds	9 S	below 2
EP 953/98	Upper Laetolil Beds	9 S	below 2
EP 250/99	Upper Laetolil Beds	9 S	below 2
EP 1232/01	Upper Laetolil Beds	9 S	below 2
EP 1268/01	Upper Laetolil Beds	9 S	below 2
EP 1528/00	Upper Laetolil Beds	Emboremony 2	
EP 3033/00	Upper Ndolanya Beds	1	
EP 3391/00	Upper Ndolanya Beds	15	
EP 3392/00	Upper Ndolanya Beds	15	
EP 3394/00	Upper Ndolanya Beds	15	
EP 3395/00	Upper Ndolanya Beds	15	
EP 3372/00	Upper Ndolanya Beds	15	
EP 1034/01	Upper Ndolanya Beds	15	
EP 892/00	Upper Ndolanya Beds	18	
EP 898/00	Upper Ndolanya Beds	18	
EP 894/00	Upper Ndolanya Beds	18	
EP 896/00	Upper Ndolanya Beds	18	
EP 897/00	Upper Ndolanya Beds	18	
EP 899/00	Upper Ndolanya Beds	18	
EP 900/00	Upper Ndolanya Beds	18	
EP 901/00	Upper Ndolanya Beds	18	
EP 2348/00	Upper Ndolanya Beds	18	
EP 2354/00	Upper Ndolanya Beds	18	
EP 3240/00	Upper Ndolanya Beds	18	
EP 3252/00	Upper Ndolanya Beds	18	
EP 3254/00a	Upper Ndolanya Beds	18	

EP indicates Harrison collection
LAET indicates Leakey collection

Catalog number	Beds	Locality	Tuffs
HUMERUS continued			
EP 3254/00b	Upper Ndolanya Beds	18	
EP 3281/00	Upper Ndolanya Beds	18	
EP 3283/00	Upper Ndolanya Beds	18	
EP 748/01	Upper Ndolanya Beds	18	
EP 749/01	Upper Ndolanya Beds	18	
LAET 76-18-61	Upper Ndolanya Beds	18	
LAET 76-18-97	Upper Ndolanya Beds	18	
LAET 76-18-99	Upper Ndolanya Beds	18	
LAET 76-18-132	Upper Ndolanya Beds	18	
LAET 76-18-137	Upper Ndolanya Beds	18	
LAET 76-18-158	Upper Ndolanya Beds	18	
LAET 76-18-173	Upper Ndolanya Beds	18	
LAET 76-18-183	Upper Ndolanya Beds	18	
LAET 76-18-239	Upper Ndolanya Beds	18	
LAET 76-18-242	Upper Ndolanya Beds	18	
LAET 76-18-264	Upper Ndolanya Beds	18	
LAET 76-18-287	Upper Ndolanya Beds	18	
LAET 76-18-343	Upper Ndolanya Beds	18	
LAET 76-18-369	Upper Ndolanya Beds	18	
LAET 76-18-396	Upper Ndolanya Beds	18	
LAET 76-18-400	Upper Ndolanya Beds	18	
LAET 76-18-404	Upper Ndolanya Beds	18	
LAET 76-18-418	Upper Ndolanya Beds	18	
LAET 76-18-455	Upper Ndolanya Beds	18	
LAET 76-18-474	Upper Ndolanya Beds	18	
LAET 76-18-479	Upper Ndolanya Beds	18	
LAET 76-18-481	Upper Ndolanya Beds	18	
LAET 76-18-550	Upper Ndolanya Beds	18	
LAET 76-18-553	Upper Ndolanya Beds	18	
LAET 76-18-558	Upper Ndolanya Beds	18	
LAET 76-18-563	Upper Ndolanya Beds	18	
LAET 76-18-582	Upper Ndolanya Beds	18	
LAET 76-18-739	Upper Ndolanya Beds	18	
LAET 76-18-740	Upper Ndolanya Beds	18	
LAET 76-18-890B	Upper Ndolanya Beds	18	
LAET 76-18-913	Upper Ndolanya Beds	18	
LAET 78-4835	Upper Ndolanya Beds	18	
LAET 78-4880	Upper Ndolanya Beds	18	
EP 3759/00	Upper Ndolanya Beds	22 S	
EP 1466/00	Upper Ndolanya Beds	7 E	
EP 1486/00	Upper Ndolanya Beds	7 E	
EP 1486/00	Upper Ndolanya Beds	7 E	
EP 1486/00	Upper Ndolanya Beds	7 E	
EP 1486/00	Upper Ndolanya Beds	7 E	
EP 2185/00	Upper Ndolanya Beds	7 E	
EP 3974/00	Upper Ndolanya Beds	7 E	
EP 833/01	Upper Ndolanya Beds	7 E	

EP indicates Harrison collection
LAET indicates Leakey collection

Catalog number	Beds	Locality	Tuffs
HUMERUS continued			
LAET 76-7E-155	Upper Ndolanya Beds	7 E	
LAET 76-7E-157	Upper Ndolanya Beds	7 E	
LAET 76-7E-172	Upper Ndolanya Beds	7 E	
LAET 75-881	Upper Ndolanya Beds	7E	
LAET 75-1072	Upper Ndolanya Beds	7E	
unnumbered	Upper Ndolanya Beds	7E	
unnumbered	Upper Ndolanya Beds	7E	
LAET 75-885	Upper Ndolanya Beds	7E	
LAET 75-1026	Upper Ndolanya Beds	7E	
LAET 75-1048	Upper Ndolanya Beds	7E	
LAET 75-1071	Upper Ndolanya Beds	7E	
EP 1484/01	Upper Ndolanya Beds	Silal Artum	
RADIUS			
LAET 75-1470	Upper Laetolil Beds	9	
LAET 78-5417	Upper Laetolil Beds	10	10 inches below 3
LAET 78-4781	Upper Laetolil Beds	11	1 inch below 7B
EP 067/00	Upper Laetolil Beds	11	below 7
EP 068/00	Upper Laetolil Beds	11	below 7
EP 2035/00	Upper Laetolil Beds	13	between 5 & 7
EP 137/00	Upper Laetolil Beds	16	between 7 & 8
LAET 75-2969	Upper Laetolil Beds	16	
LAET 75-3192	Upper Laetolil Beds	20	
EP 051/99	Upper Laetolil Beds	10 E	below 6 & 7
EP 776/00	Upper Laetolil Beds	10 E	between 5 & 7
LAET 75-1802	Upper Laetolil Beds	10 W	
EP 1337/01	Upper Laetolil Beds	22 E	between 3 & 8
EP 957/98	Upper Laetolil Beds	9 S	below 2
EP 3659/00	Upper Laetolil Beds	9 S	below 2
EP 1217/01	Upper Laetolil Beds	9 S	below 2
EP 1233/01	Upper Laetolil Beds	9 S	below 2
EP 3923/00	Upper Laetolil Beds	Garusi River	
EP 3028/00	Upper Ndolanya Beds	1	
EP 1174/01	Upper Ndolanya Beds	1	
EP 3409/00	Upper Ndolanya Beds	15	
EP 3410/00	Upper Ndolanya Beds	15	
EP 4040/00	Upper Ndolanya Beds	15	
EP 4063/00	Upper Ndolanya Beds	15	
EP 3372/00	Upper Ndolanya Beds	15	
EP 1033/01a	Upper Ndolanya Beds	15	
EP 1033/01b	Upper Ndolanya Beds	15	
EP 903/00	Upper Ndolanya Beds	18	
EP 904/00	Upper Ndolanya Beds	18	
EP 905/00	Upper Ndolanya Beds	18	
EP 906/00	Upper Ndolanya Beds	18	
EP 907/00	Upper Ndolanya Beds	18	

EP indicates Harrison collection
LAET indicates Leakey collection

Catalog number	Beds	Locality	Tuffs
RADIUS continued			
EP 908/00	Upper Ndolanya Beds	18	
EP 909/00	Upper Ndolanya Beds	18	
EP 910/00	Upper Ndolanya Beds	18	
EP 970 00	Upper Ndolanya Beds	18	
EP 1026/00	Upper Ndolanya Beds	18	
EP 3226/00	Upper Ndolanya Beds	18	
EP 3227/00	Upper Ndolanya Beds	18	
EP 3228/00	Upper Ndolanya Beds	18	
EP 3229/00	Upper Ndolanya Beds	18	
EP 3231/00a	Upper Ndolanya Beds	18	
EP 3231/00b	Upper Ndolanya Beds	18	
EP 3232/00	Upper Ndolanya Beds	18	
EP 3283/00	Upper Ndolanya Beds	18	
EP 3287/00	Upper Ndolanya Beds	18	
EP 738/01	Upper Ndolanya Beds	18	
EP 773/01	Upper Ndolanya Beds	18	
LAET 76-18-46	Upper Ndolanya Beds	18	
LAET 76-18-54	Upper Ndolanya Beds	18	
LAET 76-18-60	Upper Ndolanya Beds	18	
LAET 76-18-149	Upper Ndolanya Beds	18	
LAET 76-18-179	Upper Ndolanya Beds	18	
LAET 76-18-210	Upper Ndolanya Beds	18	
LAET 76-18-240	Upper Ndolanya Beds	18	
LAET 76-18-251	Upper Ndolanya Beds	18	
LAET 76-18-276	Upper Ndolanya Beds	18	
LAET 76-18-298	Upper Ndolanya Beds	18	
LAET 76-18-351	Upper Ndolanya Beds	18	
LAET 76-18-370	Upper Ndolanya Beds	18	
LAET 76-18-408	Upper Ndolanya Beds	18	
LAET 76-18-420A	Upper Ndolanya Beds	18	
LAET 76-18-491A	Upper Ndolanya Beds	18	
LAET 76-18-520	Upper Ndolanya Beds	18	
LAET 76-18-538	Upper Ndolanya Beds	18	
LAET 76-18-571	Upper Ndolanya Beds	18	
LAET 76-18-583	Upper Ndolanya Beds	18	
LAET 76-18-697	Upper Ndolanya Beds	18	
LAET 78-4838	Upper Ndolanya Beds	18	
LAET 78-4839	Upper Ndolanya Beds	18	
LAET 78-4840	Upper Ndolanya Beds	18	
LAET 78-4856	Upper Ndolanya Beds	18	
LAET 78-4861	Upper Ndolanya Beds	18	
LAET 78-4865	Upper Ndolanya Beds	18	
LAET 76-18-826/827	Upper Ndolanya Beds	18	
LAET 78-4908	Upper Ndolanya Beds	22	
EP 3763/00	Upper Ndolanya Beds	22 S	
EP 1464/00a	Upper Ndolanya Beds	7 E	
EP 1464 00b	Upper Ndolanya Beds	7 E	

EP indicates Harrison collection
LAET indicates Leakey collection

Catalog number	Beds	Locality	Tuffs
RADIUS continued			
EP 1464/00c	Upper Ndolanya Beds	7 E	
EP 1465/00	Upper Ndolanya Beds	7 E	
EP 1485/00	Upper Ndolanya Beds	7 E	
EP 3958/00	Upper Ndolanya Beds	7 E	
EP 3959/00	Upper Ndolanya Beds	7 E	
EP 3960/00	Upper Ndolanya Beds	7 E	
EP 3965/00	Upper Ndolanya Beds	7 E	
EP 834/01	Upper Ndolanya Beds	7 E	
EP 835/01	Upper Ndolanya Beds	7 E	
LAET 75-932	Upper Ndolanya Beds	7 E	
EP 3964/00	Upper Ndolanya Beds	7E	
LAET 75-1028	Upper Ndolanya Beds	7E	
LAET 75-1074	Upper Ndolanya Beds	7E	
LAET 78-5096	Upper Ndolanya Beds	7E	
unnumbered	Upper Ndolanya Beds	7E	
unnumbered	Upper Ndolanya Beds	7E	
unnumbered	Upper Ndolanya Beds	7E	
LAET 75-1040	Upper Ndolanya Beds	7E	
EP 1498/01	Upper Ndolanya Beds	Silal Artum	
EP 1499/01	Upper Ndolanya Beds	Silal Artum	
EP 1501/01	Upper Ndolanya Beds	Silal Artum	
EP 1503/01	Upper Ndolanya Beds	Silal Artum	
ULNA			
LAET 75-1178	Upper Laetolil Beds	6	
EP 4108/00	Upper Laetolil Beds	8	between 5 & 7
EP 4277/00	Upper Laetolil Beds	11	between 7 & 8
LAET 75-1763	Upper Laetolil Beds	13	
EP 3344/00	Upper Laetolil Beds	15	between 6 & 7
LAET 75-1885	Upper Laetolil Beds	10 E	
EP 1283/98	Upper Laetolil Beds	22 S	below 5
EP 1047/00	Upper Laetolil Beds	9 S	below 2
EP 3402/00	Upper Ndolanya Beds	15	
EP 911/00	Upper Ndolanya Beds	18	
EP 912/00	Upper Ndolanya Beds	18	
EP 3267/00	Upper Ndolanya Beds	18	
EP 3268/00	Upper Ndolanya Beds	18	
EP 3269/00	Upper Ndolanya Beds	18	
LAET 76-18-181	Upper Ndolanya Beds	18	
LAET 76-18-371	Upper Ndolanya Beds	18	
LAET 76-18-772	Upper Ndolanya Beds	18	
EP 1485/00	Upper Ndolanya Beds	7 E	
LAET 75-1029	Upper Ndolanya Beds	7 E	
EP 1483/01a	Upper Ndolanya Beds	Silal Artum	
EP 1483/01b	Upper Ndolanya Beds	Silal Artum	

EP indicates Harrison collection
LAET indicates Leakey collection

Catalog number	Beds	Locality	Tuffs
METACARPAL			
EP 2629/00	Upper Laetolil Beds	2	between 5 & 7
EP 3815/00	Upper Laetolil Beds	6	between 5 & 6
EP 1142/98	Upper Laetolil Beds	9	below 6 & 7
EP 2856/00	Upper Laetolil Beds	10 E	between 5 & 7
EP 582/98	Upper Laetolil Beds	10 W	below 2
EP 3143/00	Upper Laetolil Beds	10 W	below 3
EP 958/98	Upper Laetolil Beds	9 S	below 2
EP 3043/00	Upper Ndolanya Beds	1	
EP 929/00	Upper Ndolanya Beds	18	
EP 930/00	Upper Ndolanya Beds	18	
EP 2345/00	Upper Ndolanya Beds	18	
EP 3270/00	Upper Ndolanya Beds	18	
EP 3272/00	Upper Ndolanya Beds	18	
EP 756/01	Upper Ndolanya Beds	18	
LAET 76-18-749	Upper Ndolanya Beds	18	
EP 1485/00	Upper Ndolanya Beds	7 E	
EP 3966/00	Upper Ndolanya Beds	7 E	
EP 3967/00	Upper Ndolanya Beds	7 E	
LAET 76-7E-151	Upper Ndolanya Beds	7 E	
FEMUR			
EP 1412/00	Upper Laetolil Beds	1	between 7 & Yellow Marker Tuff
EP 4252/00	Upper Laetolil Beds	2	between 5 & 7
EP 1589/00	Upper Laetolil Beds	3	between 7 & 8
EP 1917/00	Upper Laetolil Beds	5	between 3 & 5
EP 1998/00	Upper Laetolil Beds	5	between 3 & 5
EP 3810/00a	Upper Laetolil Beds	6	between 6 & 7
EP 3810/00b	Upper Laetolil Beds	6	between 6 & 7
LAET 79-5451	Upper Laetolil Beds	6	
EP 166/01	Upper Laetolil Beds	7	between 5 & 7
EP 3873/00	Upper Laetolil Beds	7	between 5 & 8
EP 2281/00	Upper Laetolil Beds	7	between 7 & 8
EP 4104/00	Upper Laetolil Beds	8	between 5 & 7
EP 2944/00	Upper Laetolil Beds	10	below 2
EP 963/01	Upper Laetolil Beds	11	above 7
EP 971/01	Upper Laetolil Beds	11	above 7
EP 4285/00	Upper Laetolil Beds	11	between 7 & 8
EP 1427/01	Upper Laetolil Beds	12	between 5 & 6
LAET 75-3159	Upper Laetolil Beds	12	
EP 412/01	Upper Laetolil Beds	13	between 6 & 8
EP 138/00	Upper Laetolil Beds	16	between 7 & 8
EP 355/00	Upper Laetolil Beds	19	between 5 & 6
EP 1549/98	Upper Laetolil Beds	10 E	below 6 & 7
EP 535/01	Upper Laetolil Beds	10 E	between 5 & 7
EP 409/98	Upper Laetolil Beds	10 NE	
EP 1603/98	Upper Laetolil Beds	10 W	below 2

EP indicates Harrison collection
LAET indicates Leakey collection

Catalog number	Beds	Locality	Tuffs
FEMUR continued			
EP 680/01	Upper Laetolil Beds	10 W	below 3
EP 386/00	Upper Laetolil Beds	12/12 E	between 5 & 7
EP 363/01	Upper Laetolil Beds	2 W	between 5 & 7
EP 1836/00	Upper Laetolil Beds	2, NW gully	between 5 & 7
EP 1743/00	Upper Laetolil Beds	2, S gully	between 6 & 7
EP 1264/98	Upper Laetolil Beds	22 S	below 5
EP 1266/98	Upper Laetolil Beds	22 S	below 5
EP 956/98	Upper Laetolil Beds	9 S	below 2
EP 1213/01a	Upper Laetolil Beds	9 S	below 2
EP 1213/01b	Upper Laetolil Beds	9 S	below 2
EP 3037/00	Upper Ndolanya Beds	1	
EP 3396/00	Upper Ndolanya Beds	15	
EP 3397/00	Upper Ndolanya Beds	15	
EP 3372/00	Upper Ndolanya Beds	15	
EP 1036/01	Upper Ndolanya Beds	15	
EP 921/00	Upper Ndolanya Beds	18	
EP 2361/00	Upper Ndolanya Beds	18	
EP 3251/00	Upper Ndolanya Beds	18	
EP 752/01	Upper Ndolanya Beds	18	
EP 3972/00	Upper Ndolanya Beds	7 E	
EP 3973/00	Upper Ndolanya Beds	7 E	
EP 832/01	Upper Ndolanya Beds	7 E	
LAET 76-7E-57	Upper Ndolanya Beds	7E	
LAET 76-7E-179	Upper Ndolanya Beds	7E	
LAET 78-5098	Upper Ndolanya Beds	7E	
EP 1481/01	Upper Ndolanya Beds	Silal Artum	
EP 1504/01	Upper Ndolanya Beds	Silal Artum	
TIBIA			
EP 2979/00	Upper Laetolil Beds	1	between 6 & 8
EP 641/00	Upper Laetolil Beds	2	between 5 & 7
EP 647/00	Upper Laetolil Beds	2	between 5 & 7
EP 2632/00	Upper Laetolil Beds	2	between 5 & 7
EP 2633/00	Upper Laetolil Beds	2	between 5 & 7
LAET 75-1739	Upper Laetolil Beds	2	
EP 016/00	Upper Laetolil Beds	4	below 6 & 7
EP 1941/00a	Upper Laetolil Beds	5	between 3 & 5
EP 1941/00b	Upper Laetolil Beds	5	between 3 & 5
EP 249/01	Upper Laetolil Beds	5	between 3 & 5
LAET 75-589	Upper Laetolil Beds	5	
LAET 78-5210	Upper Laetolil Beds	7	1-3 inches below 7B
LAET 78-5218	Upper Laetolil Beds	7	1-3 inches below 7B
EP 1068/00	Upper Laetolil Beds	8	between 5 & 7
EP 026/01	Upper Laetolil Beds	8	between 5 & 7
EP 1127/98	Upper Laetolil Beds	9	below 6 & 7
LAET 75-1410	Upper Laetolil Beds	9	

EP indicates Harrison collection
LAET indicates Leakey collection

Catalog number	Beds	Locality	Tuffs
TIBIA continued			
EP 423/98	Upper Laetolil Beds	10	below 7
EP 064/00	Upper Laetolil Beds	11	below 7
EP 2380/00	Upper Laetolil Beds	16	between 7 & 2 metres above 8
LAET 75-3171	Upper Laetolil Beds	19	
LAET 75-3400	Upper Laetolil Beds	21	
EP 3727/00	Upper Laetolil Beds	22	between 5 & 7
LAET 75-3659	Upper Laetolil Beds	22	
LAET 75-3660	Upper Laetolil Beds	22	
EP 537/01	Upper Laetolil Beds	10 E	between 5 & 7
EP 312/98	Upper Laetolil Beds	10 E	between 6 & 7
EP 332/98	Upper Laetolil Beds	10 E	between 6 & 7
LAET 75-2252	Upper Laetolil Beds	10 E	
EP 686/01	Upper Laetolil Beds	10 W	below 3
EP 1834/00	Upper Laetolil Beds	2, NW gully	between 5 & 7
EP 1267/98	Upper Laetolil Beds	22 S	below 5
EP 960/98	Upper Laetolil Beds	9 S	below 2
EP 3403/00	Upper Ndolanya Beds	15	
EP 3404/00	Upper Ndolanya Beds	15	
EP 3405/00	Upper Ndolanya Beds	15	
EP 3406/00	Upper Ndolanya Beds	15	
EP 3407/00	Upper Ndolanya Beds	15	
EP 1035/01	Upper Ndolanya Beds	15	
EP 914/00	Upper Ndolanya Beds	18	
EP 916/00	Upper Ndolanya Beds	18	
EP 917/00	Upper Ndolanya Beds	18	
EP 920/00	Upper Ndolanya Beds	18	
EP 2347/00	Upper Ndolanya Beds	18	
EP 3237/00	Upper Ndolanya Beds	18	
EP 3262/00	Upper Ndolanya Beds	18	
EP 3281/00	Upper Ndolanya Beds	18	
EP 3283/00	Upper Ndolanya Beds	18	
EP 737/01	Upper Ndolanya Beds	18	
EP 774/01	Upper Ndolanya Beds	18	
LAET 75-3068	Upper Ndolanya Beds	18	
LAET 76-18-87	Upper Ndolanya Beds	18	
LAET 76-18-135	Upper Ndolanya Beds	18	
LAET 76-18-152	Upper Ndolanya Beds	18	
LAET 76-18-216	Upper Ndolanya Beds	18	
LAET 76-18-288	Upper Ndolanya Beds	18	
LAET 76-18-292	Upper Ndolanya Beds	18	
LAET 76-18-352	Upper Ndolanya Beds	18	
LAET 76-18-401	Upper Ndolanya Beds	18	
LAET 76-18-405	Upper Ndolanya Beds	18	
LAET 76-18-406	Upper Ndolanya Beds	18	
LAET 76-18-496	Upper Ndolanya Beds	18	
LAET 76-18-529	Upper Ndolanya Beds	18	
LAET 76-18-565	Upper Ndolanya Beds	18	

EP indicates Harrison collection
LAET indicates Leakey collection

Catalog number	Beds	Locality	Tuffs
TIBIA continued			
LAET 76-18-781	Upper Ndolanya Beds	18	
LAET 76-18-800	Upper Ndolanya Beds	18	
LAET 78-4820	Upper Ndolanya Beds	18	
EP 2062/00	Upper Ndolanya Beds	13/14	
EP 3768/00	Upper Ndolanya Beds	22 S	
EP 1470/00a	Upper Ndolanya Beds	7 E	
EP 1470/00b	Upper Ndolanya Beds	7 E	
EP 1470/00c	Upper Ndolanya Beds	7 E	
EP 3971/00	Upper Ndolanya Beds	7 E	
LAET 75-913	Upper Ndolanya Beds	7E	
LAET 76-7E-133	Upper Ndolanya Beds	7E	
LAET 76-7E-159	Upper Ndolanya Beds	7E	
LAET 76-7E-179	Upper Ndolanya Beds	7E	
EP 1494/01	Upper Ndolanya Beds	Silal Artum	
EP 1495/01	Upper Ndolanya Beds	Silal Artum	
EP 1497/01	Upper Ndolanya Beds	Silal Artum	
METATARSAL			
EP 2981/00	Upper Laetolil Beds	1	between 6 & 8
EP 2982/00	Upper Laetolil Beds	1	between 6 & 8
EP 1067/00	Upper Laetolil Beds	8	between 5 & 7
EP 2378/00	Upper Laetolil Beds	16	between 7 & 2 metres above 8
EP 156/98	Upper Laetolil Beds	10 E	between 6 & 7
EP 332/98	Upper Laetolil Beds	10 E	between 6 & 7
EP 686/01	Upper Laetolil Beds	10 W	below 3
EP 959/98	Upper Laetolil Beds	9 S	below 2
EP 982/98	Upper Laetolil Beds	9 S	below 2
EP 3039/00	Upper Ndolanya Beds	1	
EP 1037/01	Upper Ndolanya Beds	15	
EP 924/00	Upper Ndolanya Beds	18	
EP 925/00	Upper Ndolanya Beds	18	
EP 928/00	Upper Ndolanya Beds	18	
EP 931/00	Upper Ndolanya Beds	18	
EP 2346/00	Upper Ndolanya Beds	18	
EP 3271/00	Upper Ndolanya Beds	18	
EP 3283/00	Upper Ndolanya Beds	18	
EP 754/01	Upper Ndolanya Beds	18	
EP 755/01	Upper Ndolanya Beds	18	
LAET 76-18-865	Upper Ndolanya Beds	18	
EP 1485/00	Upper Ndolanya Beds	7 E	
EP 1471/00	Upper Ndolanya Beds	7 E	
EP 1472/00	Upper Ndolanya Beds	7 E	
EP 2183/00	Upper Ndolanya Beds	7 E	
LAET 76-7E-70	Upper Ndolanya Beds	7E	

EP indicates Harrison collection
LAET indicates Leakey collection

Catalog number	Beds	Locality	Tuffs
DISTAL METAPODIAL			
EP 2977/00	Upper Laetolil Beds	1	between 6 & 8
EP 2983/00	Upper Laetolil Beds	1	between 6 & 8
EP 199/00a	Upper Laetolil Beds	1	between 7 & Yellow Marker Tuff
EP 199/00b	Upper Laetolil Beds	1	between 7 & Yellow Marker Tuff
EP 202/00	Upper Laetolil Beds	1	between 7 & Yellow Marker Tuff
EP 1413/00	Upper Laetolil Beds	1	between 7 & Yellow Marker Tuff
EP 1125/01	Upper Laetolil Beds	1	between 7 & Yellow Marker Tuff
EP 650/00a	Upper Laetolil Beds	2	between 5 & 7
EP 650/00b	Upper Laetolil Beds	2	between 5 & 7
EP 650/00c	Upper Laetolil Beds	2	between 5 & 7
EP 201/01	Upper Laetolil Beds	3	between 6 & 8
EP 1578/00a	Upper Laetolil Beds	3	between 7 & 8
EP 1578/00b	Upper Laetolil Beds	3	between 7 & 8
EP 1582/00a	Upper Laetolil Beds	3	between 7 & 8
EP 1582/00b	Upper Laetolil Beds	3	between 7 & 8
EP 1583/00	Upper Laetolil Beds	3	between 7 & 8
EP 1922/00	Upper Laetolil Beds	5	between 3 & 5
EP 1944/00a	Upper Laetolil Beds	5	between 3 & 5
EP 1944/00b	Upper Laetolil Beds	5	between 3 & 5
EP 909/01a	Upper Laetolil Beds	7	above 7
EP 909/01b	Upper Laetolil Beds	7	above 7
EP 3872/00	Upper Laetolil Beds	7	between 5 & 6
LAET 75-3563	Upper Laetolil Beds	7	
EP 1109/00	Upper Laetolil Beds	8	between 5 & 7
EP 1110/00	Upper Laetolil Beds	8	between 5 & 7
EP 1489/98	Upper Laetolil Beds	9	below 6 & 7
EP 1491/98	Upper Laetolil Beds	9	below 6 & 7
EP 1490/98	Upper Laetolil Beds	9	below 6 & 7
EP 198/99	Upper Laetolil Beds	9	below 6 & 7
EP 199/99	Upper Laetolil Beds	9	below 6 & 7
EP 2509/00	Upper Laetolil Beds	9	between 6 & 8
EP 486/98	Upper Laetolil Beds	10	below 2
EP 1056/00	Upper Laetolil Beds	10	below 2
EP 3517/00	Upper Laetolil Beds	10	below 3
EP 626/01	Upper Laetolil Beds	10	below 3
LAET 75-3315	Upper Laetolil Beds	10	
EP 4276/00	Upper Laetolil Beds	11	between 7 & 8
EP 4286/00	Upper Laetolil Beds	11	between 7 & 8
EP 1425/01	Upper Laetolil Beds	12	between 5 & 6
EP 2039/00	Upper Laetolil Beds	13	between 5 & 7
EP 3343/00	Upper Laetolil Beds	15	between 6 & 7
EP 134/00	Upper Laetolil Beds	16	between 7 & 8
EP 589/01	Upper Laetolil Beds	16	between 7 & just above 8
EP 448/00	Upper Laetolil Beds	20	between 5 & 7
EP 449/00	Upper Laetolil Beds	20	between 5 & 7
EP 3595/00	Upper Laetolil Beds	21	between 5 & 8
EP 1205/98	Upper Laetolil Beds	22	

EP indicates Harrison collection
LAET indicates Leakey collection

Catalog number	Beds	Locality	Tuffs
DISTAL METAPODIAL continued			
EP 1206/98	Upper Laetolil Beds	22	
EP 047/99	Upper Laetolil Beds	10 E	below 6 & 7
EP 777/00	Upper Laetolil Beds	10 E	between 5 & 7
EP 778/00	Upper Laetolil Beds	10 E	between 5 & 7
EP 2857/00a	Upper Laetolil Beds	10 E	between 5 & 7
EP 2857/00b	Upper Laetolil Beds	10 E	between 5 & 7
EP 2864/00	Upper Laetolil Beds	10 E	between 5 & 7
EP 197/98	Upper Laetolil Beds	10 E	between 6 & 7
EP 313/98	Upper Laetolil Beds	10 E	between 6 & 7
EP 595/98	Upper Laetolil Beds	10 W	below 2
EP 710/98	Upper Laetolil Beds	10 W	below 2
EP 711/98	Upper Laetolil Beds	10 W	below 2
EP 774/98	Upper Laetolil Beds	10 W	below 2
EP 775/98	Upper Laetolil Beds	10 W	below 2
EP 840/00	Upper Laetolil Beds	10 W	below 2
EP 2115/00	Upper Laetolil Beds	13	between 6 & 7
EP 1826/00	Upper Laetolil Beds	2, NW gully	between 5 & 7
EP 1835/00	Upper Laetolil Beds	2, NW gully	between 5 & 7
EP 1746/00	Upper Laetolil Beds	2, S gully	between 6 & 7
EP 1336/01	Upper Laetolil Beds	22 E	between 3 & 8
EP 1255/98	Upper Laetolil Beds	22 S	below 5
EP 1256/98	Upper Laetolil Beds	22 S	below 5
EP 1257/98	Upper Laetolil Beds	22 S	below 5
EP 1258/98	Upper Laetolil Beds	22 S	below 5
EP 1259/98	Upper Laetolil Beds	22 S	below 5
EP1260/98	Upper Laetolil Beds	22 S	below 5
EP 1262/98	Upper Laetolil Beds	22 S	below 5
EP 975/98	Upper Laetolil Beds	9 S	below 2
EP 976/98	Upper Laetolil Beds	9 S	below 2
EP 1216/01a	Upper Laetolil Beds	9 S	below 2
EP 1216/01b	Upper Laetolil Beds	9 S	below 2
EP 1216/01c	Upper Laetolil Beds	9 S	below 2
EP 1229/01	Upper Laetolil Beds	9 S	below 2
EP 3040/00	Upper Ndolanya Beds	1	
EP 3041/00	Upper Ndolanya Beds	1	
EP 1175/01	Upper Ndolanya Beds	1	
EP 1176/01	Upper Ndolanya Beds	1	
EP 3415/00	Upper Ndolanya Beds	15	
EP 3418/00	Upper Ndolanya Beds	15	
EP 3419/00	Upper Ndolanya Beds	15	
EP 3420/00	Upper Ndolanya Beds	15	
EP 3459/00a	Upper Ndolanya Beds	15	
EP 3459/00b	Upper Ndolanya Beds	15	
EP 4044/00	Upper Ndolanya Beds	15	
EP 1039/01	Upper Ndolanya Beds	15	
EP 1040/01	Upper Ndolanya Beds	15	
EP 932/00a	Upper Ndolanya Beds	18	

EP indicates Harrison collection
LAET indicates Leakey collection

Catalog number	Beds	Locality	Tuffs
DISTAL METAPODIAL continued			
EP 932/00b	Upper Ndolanya Beds	18	
EP 932/00c	Upper Ndolanya Beds	18	
EP 932/00d	Upper Ndolanya Beds	18	
EP 932/00e	Upper Ndolanya Beds	18	
EP 932/00f	Upper Ndolanya Beds	18	
EP 933/00	Upper Ndolanya Beds	18	
EP 934/00	Upper Ndolanya Beds	18	
EP 935/00	Upper Ndolanya Beds	18	
EP 936/00a	Upper Ndolanya Beds	18	
EP 936/00b	Upper Ndolanya Beds	18	
EP 936/00c	Upper Ndolanya Beds	18	
EP 936/00d	Upper Ndolanya Beds	18	
EP 936/00e	Upper Ndolanya Beds	18	
EP 936/00f	Upper Ndolanya Beds	18	
EP 936/00g	Upper Ndolanya Beds	18	
EP 936/00h	Upper Ndolanya Beds	18	
EP 1029/00	Upper Ndolanya Beds	18	
EP 1030/00	Upper Ndolanya Beds	18	
EP 2349/00	Upper Ndolanya Beds	18	
EP 3258/00	Upper Ndolanya Beds	18	
EP 3259/00a	Upper Ndolanya Beds	18	
EP 3259/00b	Upper Ndolanya Beds	18	
EP 3259/00c	Upper Ndolanya Beds	18	
EP 3282/00	Upper Ndolanya Beds	18	
EP 731/01	Upper Ndolanya Beds	18	
EP 732/01	Upper Ndolanya Beds	18	
EP 739/01	Upper Ndolanya Beds	18	
EP 747/01	Upper Ndolanya Beds	18	
LAET 76-18-893B	Upper Ndolanya Beds	18	
LAET 76-18-842	Upper Ndolanya Beds	18	
EP 3767/00	Upper Ndolanya Beds	22 S	
EP 1288/01	Upper Ndolanya Beds	22 S	
EP 1474/00a	Upper Ndolanya Beds	7 E	
EP 1474/00b	Upper Ndolanya Beds	7 E	
EP 1474/00c	Upper Ndolanya Beds	7 E	
EP 2187/00	Upper Ndolanya Beds	7 E	
EP 3968/00	Upper Ndolanya Beds	7 E	
EP 3994/00a	Upper Ndolanya Beds	7 E	
EP 3994/00b	Upper Ndolanya Beds	7 E	
EP 3994/00c	Upper Ndolanya Beds	7 E	
EP 3995/00	Upper Ndolanya Beds	7 E	
EP 840/01a	Upper Ndolanya Beds	7 E	
EP 840/01b	Upper Ndolanya Beds	7 E	
LAET 76-7E-9	Upper Ndolanya Beds	7E	
LAET 76-7E-55	Upper Ndolanya Beds	7E	
LAET 76-7E-69	Upper Ndolanya Beds	7E	
EP 1469/01	Upper Ndolanya Beds	Silal Artum	

EP indicates Harrison collection
LAET indicates Leakey collection

Catalog number	Beds	Locality	Tuffs
DISTAL METAPODIAL continued			
EP 1470/01	Upper Ndolanya Beds	Silal Artum	
EP 1471/01	Upper Ndolanya Beds	Silal Artum	
EP 1472/01	Upper Ndolanya Beds	Silal Artum	
EP 1474/01	Upper Ndolanya Beds	Silal Artum	
EP 1475/01	Upper Ndolanya Beds	Silal Artum	
EP 1486/01a	Upper Ndolanya Beds	Silal Artum	
EP 1486/01b	Upper Ndolanya Beds	Silal Artum	
TALUS			
EP 2986/00a	Upper Laetolil Beds	1	between 6 & 8
EP 2986/00b	Upper Laetolil Beds	1	between 6 & 8
EP 198/00	Upper Laetolil Beds	1	between 7 & Yellow Marker Tuff
EP 1127/01	Upper Laetolil Beds	1	between 7 & Yellow Marker Tuff
EP 1128/01	Upper Laetolil Beds	1	between 7 & Yellow Marker Tuff
LAET 75-681	Upper Laetolil Beds	1	
EP 642/00	Upper Laetolil Beds	2	between 5 & 7
EP 643/00	Upper Laetolil Beds	2	between 5 & 7
EP 644/00	Upper Laetolil Beds	2	between 5 & 7
EP 657/00	Upper Laetolil Beds	2	between 5 & 7
EP 2628/00a	Upper Laetolil Beds	2	between 5 & 7
EP 2628/00b	Upper Laetolil Beds	2	between 5 & 7
LAET 75-2111	Upper Laetolil Beds	2	
EP 1577/00a	Upper Laetolil Beds	3	between 7 & 8
EP 1577/00b	Upper Laetolil Beds	3	between 7 & 8
LAET 75-3459	Upper Laetolil Beds	3	
EP 1682/00	Upper Laetolil Beds	5	between 3 & 5
EP 1919/00	Upper Laetolil Beds	5	between 3 & 5
EP 1943/00a	Upper Laetolil Beds	5	between 3 & 5
EP 1943/00b	Upper Laetolil Beds	5	between 3 & 5
EP 1943/00c	Upper Laetolil Beds	5	between 3 & 5
EP 1943/00d	Upper Laetolil Beds	5	between 3 & 5
EP 1943/00e	Upper Laetolil Beds	5	between 3 & 5
EP 1943/00f	Upper Laetolil Beds	5	between 3 & 5
EP 1943/00g	Upper Laetolil Beds	5	between 3 & 5
LAET 75-2677	Upper Laetolil Beds	5	
LAET 75-2801	Upper Laetolil Beds	5	
EP 1319/00a	Upper Laetolil Beds	6	between 5 & 6
EP 1319/00b	Upper Laetolil Beds	6	between 5 & 6
EP 1319/00c	Upper Laetolil Beds	6	between 5 & 6
EP 103/01	Upper Laetolil Beds	6	between 5 & 6
EP 104/01	Upper Laetolil Beds	6	between 5 & 6
EP 105/01	Upper Laetolil Beds	6	between 5 & 6
EP 903/01	Upper Laetolil Beds	7	above 7
EP 165/01a	Upper Laetolil Beds	7	between 5 & 7
EP 165/01b	Upper Laetolil Beds	7	between 5 & 7
EP 2215/00	Upper Laetolil Beds	7	between 5 & 7

EP indicates Harrison collection
LAET indicates Leakey collection

Catalog number	Beds	Locality	Tuffs
TALUS continued			
EP 2216/00	Upper Laetolil Beds	7	between 5 & 7
EP 3874/00	Upper Laetolil Beds	7	between 5 & 8
EP 287/00	Upper Laetolil Beds	8	below 6
EP 1066/00a	Upper Laetolil Beds	8	between 5 & 7
EP 1066/00b	Upper Laetolil Beds	8	between 5 & 7
EP 1066/00c	Upper Laetolil Beds	8	between 5 & 7
EP 1119/00a	Upper Laetolil Beds	8	between 5 & 7
EP 1119/00b	Upper Laetolil Beds	8	between 5 & 7
EP 4097/00	Upper Laetolil Beds	8	between 5 & 7
EP 025/01a	Upper Laetolil Beds	8	between 5 & 7
EP 025/01b	Upper Laetolil Beds	8	between 5 & 7
EP 1135/98	Upper Laetolil Beds	9	below 6 & 7
EP 1136/98	Upper Laetolil Beds	9	below 6 & 7
EP 1137/98	Upper Laetolil Beds	9	below 6 & 7
EP 1646/98	Upper Laetolil Beds	9	below 6 & 7
EP 201/99	Upper Laetolil Beds	9	below 6 & 7
EP 202/99	Upper Laetolil Beds	9	below 6 & 7
EP 2506/00	Upper Laetolil Beds	9	between 6 & 8
EP 474/98	Upper Laetolil Beds	10	below 2
EP 475/98	Upper Laetolil Beds	10	below 2
EP 476/98	Upper Laetolil Beds	10	below 2
EP 477/98	Upper Laetolil Beds	10	below 2
EP 478/98	Upper Laetolil Beds	10	below 2
EP 479/98	Upper Laetolil Beds	10	below 2
EP 484/98	Upper Laetolil Beds	10	below 2
EP 849/98	Upper Laetolil Beds	10	below 2
EP 850/98	Upper Laetolil Beds	10	below 2
EP 161/99	Upper Laetolil Beds	10	below 2
EP 824/00	Upper Laetolil Beds	10	below 2
EP 2945/00	Upper Laetolil Beds	10	below 2
EP 625/01	Upper Laetolil Beds	10	below 3
LAET 75-2011	Upper Laetolil Beds	10	
EP 961/01a	Upper Laetolil Beds	11	above 7
EP 961/01b	Upper Laetolil Beds	11	above 7
EP 970/01	Upper Laetolil Beds	11	above 7
EP 070/00	Upper Laetolil Beds	11	below 7
EP 073/00	Upper Laetolil Beds	11	below 7
EP 065/00	Upper Laetolil Beds	11	below 7
EP 4282/00	Upper Laetolil Beds	11	between 7 & 8
EP 3554/00	Upper Laetolil Beds	12	between 5 & 6
EP 1426/01	Upper Laetolil Beds	12	between 5 & 6
LAET 75-3158	Upper Laetolil Beds	12	
EP 2034/00	Upper Laetolil Beds	13	between 5 & 7
EP 2147/00	Upper Laetolil Beds	13	between 7& 8
EP 1422/98	Upper Laetolil Beds	15	below 7 & 8
EP 1085/01	Upper Laetolil Beds	15	between 6 & 8
LAET 75-2571	Upper Laetolil Beds	15	

EP indicates Harrison collection
LAET indicates Leakey collection

Catalog number	Beds	Locality	Tuffs
TALUS continued			
EP 2379/00	Upper Laetolil Beds	16	between 7 & 2 metres above 8
EP 124/00	Upper Laetolil Beds	16	between 7 & 8
EP 606/01	Upper Laetolil Beds	16	between 7 & just above 8
EP 2308/00	Upper Laetolil Beds	17	between 7 & Yellow Marker Tuff
EP 356/00a	Upper Laetolil Beds	19	between 5 & 6
EP 356/00b	Upper Laetolil Beds	19	between 5 & 6
EP 356/00c	Upper Laetolil Beds	19	between 5 & 6
EP 356/00d	Upper Laetolil Beds	19	between 5 & 6
EP 454/00	Upper Laetolil Beds	20	between 5 & 7
EP 484/00	Upper Laetolil Beds	21	between 5 & 8
EP 493/00	Upper Laetolil Beds	21	between 5 & 8
EP 3619/00	Upper Laetolil Beds	21	between 5 & 8
EP 1437/01a	Upper Laetolil Beds	21	between 5 & 8
EP 1437/01b	Upper Laetolil Beds	21	between 5 & 8
EP 1439/01	Upper Laetolil Beds	21	between 5 & 8
LAET 78-4894	Upper Laetolil Beds	22	below 6
EP 547/00	Upper Laetolil Beds	22	between 5 & 7
EP 1208/98	Upper Laetolil Beds	22	
EP 1234/98	Upper Laetolil Beds	22	
EP 1552/98	Upper Laetolil Beds	10 E	below 6 & 7
EP 052/99a	Upper Laetolil Beds	10 E	below 6 & 7
EP 052/99b	Upper Laetolil Beds	10 E	below 6 & 7
EP 772/00a	Upper Laetolil Beds	10 E	between 5 & 7
EP 772/00b	Upper Laetolil Beds	10 E	between 5 & 7
EP 2858/00	Upper Laetolil Beds	10 E	between 5 & 7
EP 133/98	Upper Laetolil Beds	10 E	between 6 & 7
EP 190/98	Upper Laetolil Beds	10 E	between 6 & 7
EP 192/98a	Upper Laetolil Beds	10 E	between 6 & 7
EP 192/98b	Upper Laetolil Beds	10 E	between 6 & 7
EP 192/98c	Upper Laetolil Beds	10 E	between 6 & 7
EP 313/98	Upper Laetolil Beds	10 E	between 6 & 7
EP 315/98	Upper Laetolil Beds	10 E	between 6 & 7
EP 316/98	Upper Laetolil Beds	10 E	between 6 & 7
EP 317/98	Upper Laetolil Beds	10 E	between 6 & 7
EP 318/98	Upper Laetolil Beds	10 E	between 6 & 7
EP 319/98	Upper Laetolil Beds	10 E	between 6 & 7
EP 320/98	Upper Laetolil Beds	10 E	between 6 & 7
EP 332/98	Upper Laetolil Beds	10 E	between 6 & 7
LAET 75-1981	Upper Laetolil Beds	10 E	
EP 587/98	Upper Laetolil Beds	10 W	below 2
EP 588/98	Upper Laetolil Beds	10 W	below 2
EP 589/98	Upper Laetolil Beds	10 W	below 2
EP 590/98	Upper Laetolil Beds	10 W	below 2
EP 715/98	Upper Laetolil Beds	10 W	below 2
EP 716/98	Upper Laetolil Beds	10 W	below 2
EP 1601/98a	Upper Laetolil Beds	10 W	below 2
EP 1601/98b	Upper Laetolil Beds	10 W	below 2

EP indicates Harrison collection
LAET indicates Leakey collection

Catalog number	Beds	Locality	Tuffs
TALUS continued			
EP 139/99	Upper Laetolil Beds	10 W	below 2
EP 3155/00a	Upper Laetolil Beds	10 W	below 3
EP 3155/00b	Upper Laetolil Beds	10 W	below 3
EP 3190/00	Upper Laetolil Beds	10 W	below 3
EP 672/01	Upper Laetolil Beds	10 W	below 3
EP 682/01	Upper Laetolil Beds	10 W	below 3
EP 1410/01	Upper Laetolil Beds	12 E	between 5 & 7
EP 392/00	Upper Laetolil Beds	12/12 E	between 5 & 7
EP 400/00	Upper Laetolil Beds	12/12 E	between 5 & 7
EP 2109/00	Upper Laetolil Beds	13	between 6 & 7
EP 1829/00	Upper Laetolil Beds	2, NW gully	between 5 & 7
EP 1741/00	Upper Laetolil Beds	2, S gully	between 6 & 7
EP 1276/98	Upper Laetolil Beds	22 S	below 5
EP 965/98	Upper Laetolil Beds	9 S	below 2
EP 966/98	Upper Laetolil Beds	9 S	below 2
EP 967/98	Upper Laetolil Beds	9 S	below 2
EP 969/98	Upper Laetolil Beds	9 S	below 2
EP 970/98	Upper Laetolil Beds	9 S	below 2
EP 971/98	Upper Laetolil Beds	9 S	below 2
EP 972/98	Upper Laetolil Beds	9 S	below 2
EP 973/98	Upper Laetolil Beds	9 S	below 2
EP 1211/01a	Upper Laetolil Beds	9 S	below 2
EP 1211/01b	Upper Laetolil Beds	9 S	below 2
EP 3657/00	Upper Laetolil Beds	9 S	below 3
EP 1441/00	Upper Ndolanya Beds	1	
EP 3030/00	Upper Ndolanya Beds	1	
EP 3413/00	Upper Ndolanya Beds	15	
EP 4045/00	Upper Ndolanya Beds	15	
EP 1044/01	Upper Ndolanya Beds	15	
EP 948/00a	Upper Ndolanya Beds	18	
EP 948/00b	Upper Ndolanya Beds	18	
EP 948/00c	Upper Ndolanya Beds	18	
EP 948/00d	Upper Ndolanya Beds	18	
EP 949/00	Upper Ndolanya Beds	18	
EP 950/00	Upper Ndolanya Beds	18	
EP 952/00	Upper Ndolanya Beds	18	
EP 953/00	Upper Ndolanya Beds	18	
EP 3222/00a	Upper Ndolanya Beds	18	
EP 3222/00b	Upper Ndolanya Beds	18	
EP 3222/00c	Upper Ndolanya Beds	18	
EP 3222/00d	Upper Ndolanya Beds	18	
EP 3222/00e	Upper Ndolanya Beds	18	
EP 3283/00	Upper Ndolanya Beds	18	
EP 740/01	Upper Ndolanya Beds	18	
EP 741/01	Upper Ndolanya Beds	18	
LAET 76-18-837	Upper Ndolanya Beds	18	
EP 3764/00	Upper Ndolanya Beds	22 S	

EP indicates Harrison collection
LAET indicates Leakey collection

Catalog number	Beds	Locality	Tuffs
TALUS continued			
EP 1285/01	Upper Ndolanya Beds	22 S	
EP 1468/00	Upper Ndolanya Beds	7 E	
EP 1469/00	Upper Ndolanya Beds	7 E	
EP 1488/00a	Upper Ndolanya Beds	7 E	
EP 1488/00b	Upper Ndolanya Beds	7 E	
EP 2177/00	Upper Ndolanya Beds	7 E	
EP 3989/00	Upper Ndolanya Beds	7 E	
EP 3990/00	Upper Ndolanya Beds	7 E	
CALCANEUS			
EP 1416/00	Upper Laetolil Beds	1	between 7 & Yellow Marker Tuff
EP 1122/01	Upper Laetolil Beds	1	between 7 & Yellow Marker Tuff
EP 657/00	Upper Laetolil Beds	2	between 5 & 7
EP 663/00	Upper Laetolil Beds	2	between 5 & 7
EP 2727/00	Upper Laetolil Beds	3	between 7 & 8
EP 1940/00	Upper Laetolil Beds	5	between 3 & 5
EP 911/01	Upper Laetolil Beds	7	above 7
EP 4078/00	Upper Laetolil Beds	8	between 5 & 7
EP 4079/00	Upper Laetolil Beds	8	between 5 & 7
EP 1488/98	Upper Laetolil Beds	9	below 6 & 7
EP 483/98	Upper Laetolil Beds	10	below 2
EP 3107/00	Upper Laetolil Beds	10	below 3
EP 069/00	Upper Laetolil Beds	11	below 7
EP 073/00	Upper Laetolil Beds	11	below 7
EP 137/00	Upper Laetolil Beds	16	between 7 & 8
LAET 75-3171	Upper Laetolil Beds	19	
EP 550/00	Upper Laetolil Beds	22	between 5 & 7
EP 1233/98	Upper Laetolil Beds	22	
EP 332/98	Upper Laetolil Beds	10 E	between 6 & 7
EP 714/98	Upper Laetolil Beds	10 W	below 2
EP 3156/00	Upper Laetolil Beds	10 W	below 3
EP 684/01	Upper Laetolil Beds	10 W	below 3
EP 1282/98	Upper Laetolil Beds	22 S	below 5
EP 1284/98	Upper Laetolil Beds	22 S	below 5
EP 962/98	Upper Laetolil Beds	9 S	below 2
EP 963/98	Upper Laetolil Beds	9 S	below 2
EP 1045/00	Upper Laetolil Beds	9 S	below 2
EP 1046/00	Upper Laetolil Beds	9 S	below 2
EP 3411/00	Upper Ndolanya Beds	15	
EP 3412/00	Upper Ndolanya Beds	15	
EP 3456/00	Upper Ndolanya Beds	15	
EP 4046/00	Upper Ndolanya Beds	15	
EP 937/00	Upper Ndolanya Beds	18	
EP 938/00	Upper Ndolanya Beds	18	
EP 939/00	Upper Ndolanya Beds	18	
EP 940/00	Upper Ndolanya Beds	18	

EP indicates Harrison collection
LAET indicates Leakey collection

Catalog number	Beds	Locality	Tuffs
CALCANEUS continued			
EP 941/00	Upper Ndolanya Beds	18	
EP 1028/00	Upper Ndolanya Beds	18	
EP 3223/00	Upper Ndolanya Beds	18	
EP 3225/00	Upper Ndolanya Beds	18	
EP 3233/00	Upper Ndolanya Beds	18	
EP 3283/00	Upper Ndolanya Beds	18	
EP 742/01	Upper Ndolanya Beds	18	
EP 743/01	Upper Ndolanya Beds	18	
LAET 76-18-779	Upper Ndolanya Beds	18	
LAET 76-18-840	Upper Ndolanya Beds	18	
EP 2179/00	Upper Ndolanya Beds	7 E	
EP 2180/00	Upper Ndolanya Beds	7 E	
EP 3981/00	Upper Ndolanya Beds	7 E	
EP 3983/00	Upper Ndolanya Beds	7 E	
EP 3984/00	Upper Ndolanya Beds	7 E	
EP 837/01	Upper Ndolanya Beds	7 E	
LAET 76-7E-179	Upper Ndolanya Beds	7 E	
EP 1526/00	Upper Ndolanya Beds	Emboremony 2	
NAVICULO-CUBOID			
EP 655/00	Upper Laetolil Beds	2	between 5 & 7
EP 2625/00	Upper Laetolil Beds	2	between 5 & 7
EP 4204/00	Upper Laetolil Beds	2	between 5 & 7
EP 1579/00	Upper Laetolil Beds	3	between 7 & 8
EP 2728/00	Upper Laetolil Beds	3	between 7 & 8
EP 1916/00	Upper Laetolil Beds	5	between 3 & 5
EP 1942/00	Upper Laetolil Beds	5	between 3 & 5
EP 2798/00	Upper Laetolil Beds	5	between 3 & 5
LAET 75-1115	Upper Laetolil Beds	6	
LAET 75-1136	Upper Laetolil Beds	6	
LAET 75-2849	Upper Laetolil Beds	6	
LAET 78-5211	Upper Laetolil Beds	7	1-3 inches below 7B
EP 2216/00	Upper Laetolil Beds	7	between 5 & 7
LAET 78-5073	Upper Laetolil Beds	8	5 inches above 7B
EP 4077/00	Upper Laetolil Beds	8	between 5 & 7
EP 4096/00a	Upper Laetolil Beds	8	between 5 & 7
EP 4096/00b	Upper Laetolil Beds	8	between 5 & 7
LAET 75-1347	Upper Laetolil Beds	8	
EP 1516/98	Upper Laetolil Beds	9	between 6 & 7
EP 459/01	Upper Laetolil Beds	9	between 6 & 8
LAET 75-1501	Upper Laetolil Beds	9	
LAET 78-5310	Upper Laetolil Beds	10	4 inches below 7
EP 827/00	Upper Laetolil Beds	10	below 2
EP 3106/00	Upper Laetolil Beds	10	below 3
LAET 78-4781	Upper Laetolil Beds	11	1 inch below 7B
EP 586/01	Upper Laetolil Beds	16	between 7 and just above 8

EP indicates Harrison collection
LAET indicates Leakey collection

Catalog number	Beds	Locality	Tuffs
NAVICULO-CUBOID continued			
EP 1209/98	Upper Laetolil Beds	22	
EP 531/01	Upper Laetolil Beds	10 E	between 5 & 7
EP 191/98	Upper Laetolil Beds	10 E	between 6 & 7
EP 324/98	Upper Laetolil Beds	10 E	between 6 & 7
EP 332/98	Upper Laetolil Beds	10 E	between 6 & 7
EP 1601/98	Upper Laetolil Beds	10 W	below 2
EP 3157/00	Upper Laetolil Beds	10 W	below 3
EP 1279/98	Upper Laetolil Beds	22 S	below 5
EP 1280/98	Upper Laetolil Beds	22 S	below 5
EP 1281/98	Upper Laetolil Beds	22 S	below 5
EP 1222/01	Upper Laetolil Beds	9 S	below 2
EP 3372/00	Upper Ndolanya Beds	15	
EP 942/00	Upper Ndolanya Beds	18	
EP 943/00	Upper Ndolanya Beds	18	
EP 2342/00	Upper Ndolanya Beds	18	
EP 3236/00	Upper Ndolanya Beds	18	
EP 3283/00	Upper Ndolanya Beds	18	
EP 733/01	Upper Ndolanya Beds	18	
LAET 76-18-863	Upper Ndolanya Beds	18	
EP 2176/00	Upper Ndolanya Beds	7 E	
EP 3961/00	Upper Ndolanya Beds	7 E	
EP 3962/00	Upper Ndolanya Beds	7 E	
EXTERNAL & MIDDLE CUNEIFORM			
EP 1130/01	Upper Laetolil Beds	1	between 7 & Yellow Marker Tuff
EP 1591/00	Upper Laetolil Beds	3	between 7 & 8
EP 586/01	Upper Laetolil Beds	16	between 7 & just above 8
EP 2111/00	Upper Laetolil Beds	13	between 6 & 7
EP 332/01	Upper Laetolil Beds	2 S	
EP 1293/98	Upper Laetolil Beds	22 S	below 5
EP 954/00	Upper Ndolanya Beds	18	
MAGNUM			
LAET 74-108	Upper Laetolil Beds	1	
LAET 74-179	Upper Laetolil Beds	4	
LAET 75-2803	Upper Laetolil Beds	5	
EP 867/01	Upper Laetolil Beds	7	above 7
EP 3870/00	Upper Laetolil Beds	7	between 5 & 8
LAET 75-1314	Upper Laetolil Beds	8	
EP 3516/00	Upper Laetolil Beds	9	between 6 & 8
LAET 75-3107	Upper Laetolil Beds	12	
EP 2391/00	Upper Laetolil Beds	16	between 7 & 2 metres above 8
LAET 75-3638	Upper Laetolil Beds	22	
EP 326/98	Upper Laetolil Beds	10 E	between 6 & 7
LAET 75-1882	Upper Laetolil Beds	10 E	

EP indicates Harrison collection
LAET indicates Leakey collection

Catalog number	Beds	Locality	Tuffs
MAGNUM continued			
EP 728/98	Upper Laetolil Beds	10 W	below 2
EP 729/98	Upper Laetolil Beds	10 W	below 2
EP 3142/00	Upper Laetolil Beds	10 W	below 3
EP 252/99	Upper Laetolil Beds	9 S	below 2
EP 252/99	Upper Laetolil Beds	9 S	below 2
EP 1224/01	Upper Laetolil Beds	9 S	below 2
EP 3455/00	Upper Ndolanya Beds	15	
EP 3234/00	Upper Ndolanya Beds	18	
EP 3774/00	Upper Ndolanya Beds	22 S	
LAET 76-7E-96	Upper Ndolanya Beds	7E	
LAET 76-7E-171	Upper Ndolanya Beds	7E	
UNCIFORM			
LAET 78-4728	Upper Laetolil Beds	6	5 inches below 6
LAET 78-5216	Upper Laetolil Beds	7	1-3 inches below 7B
EP 2391/00	Upper Laetolil Beds	16	between 7 & 2 metres above 8
EP 2865/00	Upper Laetolil Beds	10 E	between 5 & 7
EP 727/98	Upper Laetolil Beds	10 W	below 2
EP 734/01	Upper Ndolanya Beds	18	
EP 734/01	Upper Ndolanya Beds	18	
LAET 75-1088	Upper Ndolanya Beds	7E	
LAET 75-3777	Upper Ndolanya Beds	7E	
LAET 76-7E-167	Upper Ndolanya Beds	7E	
SCAPHOID			
EP 2980/00	Upper Laetolil Beds	1	between 6 & 8
EP 4205/00	Upper Laetolil Beds	2	between 5 & 7
EP 2734/00	Upper Laetolil Beds	3	between 7 & 8
LAET 75-2804	Upper Laetolil Beds	5	
EP 171/01	Upper Laetolil Beds	7	between 5 & 7
EP 4081/00	Upper Laetolil Beds	8	between 5 & 7
EP 4106/00a	Upper Laetolil Beds	8	between 5 & 7
EP 4106/00b	Upper Laetolil Beds	8	between 5 & 7
LAET 75-1313	Upper Laetolil Beds	8	
EP 1139/98	Upper Laetolil Beds	9	below 6 & 7
LAET 78-5159	Upper Laetolil Beds	9	
EP 852/98	Upper Laetolil Beds	10	below 2
EP 066/00	Upper Laetolil Beds	11	below 7
EP 2566/00	Upper Laetolil Beds	11	between 7 & 8
EP 4287/00	Upper Laetolil Beds	11	between 7 & 8
EP 607/01	Upper Laetolil Beds	16	between 7 & just above 8
EP 1210/98	Upper Laetolil Beds	22	below 6 & 7
EP 196/98	Upper Laetolil Beds	10 E	between 6 & 7
LAET 75-1860	Upper Laetolil Beds	10 E	
EP 817/98	Upper Laetolil Beds	10 W	below 2

EP indicates Harrison collection
LAET indicates Leakey collection

Catalog number	Beds	Locality	Tuffs

SCAPHOID continued

LAET 78-5247	Upper Laetolil Beds	2 S	1 inch above 7B
EP 329/01a	Upper Laetolil Beds	2 S	
EP 329/01b	Upper Laetolil Beds	2 S	
EP 362/01	Upper Laetolil Beds	2 W	between 5 & 7
EP1273/98	Upper Laetolil Beds	22 S	below 5
EP 944/00	Upper Ndolanya Beds	18	
EP 945/00	Upper Ndolanya Beds	18	
EP 946/00	Upper Ndolanya Beds	18	
EP 3235/00a	Upper Ndolanya Beds	18	
EP 3235/00b	Upper Ndolanya Beds	18	
EP 3235/00c	Upper Ndolanya Beds	18	
EP 735/01	Upper Ndolanya Beds	18	
LAET 76-18-754	Upper Ndolanya Beds	18	
LAET 76-18-914	Upper Ndolanya Beds	18	
EP 3754/00	Upper Ndolanya Beds	22 S	
EP 3755/00	Upper Ndolanya Beds	22 S	
EP 3980/00	Upper Ndolanya Beds	7 E	

LUNAR

EP 120/99	LB, LU	Esere 2	
EP 1417/00	Upper Laetolil Beds	1	between 7 & Yellow Marker Tuff
LAET 75-673	Upper Laetolil Beds	1	
LAET 75-3008	Upper Laetolil Beds	3	
EP 1921/00	Upper Laetolil Beds	5	between 3 & 5
EP 255/00	Upper Laetolil Beds	8	between 7 & 8
EP 967/01	Upper Laetolil Beds	11	above 7
EP 364/01	Upper Laetolil Beds	2 W	between 5 & 7
EP 1221/01	Upper Laetolil Beds	9 S	below 2
EP 3460/00	Upper Ndolanya Beds	15	
EP 3758/00	Upper Ndolanya Beds	22 S	
EP 1485/00	Upper Ndolanya Beds	7 E	
EP 3979/00	Upper Ndolanya Beds	7 E	
LAET 76-18-916	Upper Ndolanya Beds	18	

CUNEIFORM

LAET 75-673	Upper Laetolil Beds	1	
EP 2629/00	Upper Laetolil Beds	2	between 5 & 7
EP 1335/00	Upper Laetolil Beds	6	between 5 & 6
EP 3869/00	Upper Laetolil Beds	7	between 5 & 8
EP 4107/00	Upper Laetolil Beds	8	between 5 & 7
EP 4110/00	Upper Laetolil Beds	8	between 5 & 7
EP 1174/98	Upper Laetolil Beds	9	below 6 & 7
EP 853/98	Upper Laetolil Beds	10	below 2
EP 2392/00	Upper Laetolil Beds	16	between 7 & 2 metres above 8
LAET 75-2941	Upper Laetolil Beds	16	

EP indicates Harrison collection
LAET indicates Leakey collection

Catalog number	Beds	Locality	Tuffs
CUNEIFORM continued			
LAET 75-2281	Upper Laetolil Beds	10 E	
EP 3756/00	Upper Ndolanya Beds	22 S	
EP 3757/00	Upper Ndolanya Beds	22 S	
EP 2178/00	Upper Ndolanya Beds	7 E	
EP 3976/00	Upper Ndolanya Beds	7 E	
EP 3977/00	Upper Ndolanya Beds	7 E	
EP 3978/00	Upper Ndolanya Beds	7 E	
LAET 76-7E-97	Upper Ndolanya Beds	7 E	
LAET 75-3772	Upper Ndolanya Beds	7 E	
LAET 76-18-915	Upper Ndolanya Beds	18	
PISIFORM			
EP 1485/00	Upper Ndolanya Beds	7 E	
PROXIMAL PHALANGES			
LAET 78-5562	Upper Laetolil Beds	1	below 3
EP 1117/01a	Upper Laetolil Beds	1	between 7 & Yellow Marker Tuff
EP 1117/01b	Upper Laetolil Beds	1	between 7 & Yellow Marker Tuff
EP 1124/01	Upper Laetolil Beds	1	between 7 & Yellow Marker Tuff
LAET 75-677	Upper Laetolil Beds	1	
LAET 78-5014	Upper Laetolil Beds	2	above 6
LAET 75-1726	Upper Laetolil Beds	2	
LAET 81-20	Upper Laetolil Beds	2	
LAET 75- 2091	Upper Laetolil Beds	2	
LAET 75-2494	Upper Laetolil Beds	2	
EP 204/01a	Upper Laetolil Beds	3	between 6 & 8
EP 204/01b	Upper Laetolil Beds	3	between 6 & 8
EP 205/01	Upper Laetolil Beds	3	between 6 & 8
EP 1576/00a	Upper Laetolil Beds	3	between 7 & 8
EP 1587/00b	Upper Laetolil Beds	3	between 7 & 8
EP 2730/00	Upper Laetolil Beds	3	between 7 & 8
LAET 75-2702	Upper Laetolil Beds	3	
LAET 75-2735	Upper Laetolil Beds	3	
EP 014/00a	Upper Laetolil Beds	4	below 6 & 7
EP 014/00b	Upper Laetolil Beds	4	below 6 & 7
EP 015/00	Upper Laetolil Beds	4	below 6 & 7
EP 1263/00a	Upper Laetolil Beds	4	below 6 & 7
EP 1263/00b	Upper Laetolil Beds	4	below 6 & 7
LAET 74-172	Upper Laetolil Beds	4	
EP 1935/00	Upper Laetolil Beds	5	between 3 & 5
EP 248/01	Upper Laetolil Beds	5	between 3 & 5
LAET 75-2639	Upper Laetolil Beds	5	
EP 1320/00	Upper Laetolil Beds	6	between 5 & 6
EP 3813/00	Upper Laetolil Beds	6	between 5 & 6
EP 097/01	Upper Laetolil Beds	6	between 5 & 6

EP indicates Harrison collection
LAET indicates Leakey collection

Catalog number	Beds	Locality	Tuffs
PROXIMAL PHALANGES continued			
EP 868/01	Upper Laetolil Beds	7	above 7
EP 869/01	Upper Laetolil Beds	7	above 7
EP 904/01	Upper Laetolil Beds	7	above 7
EP 905/01	Upper Laetolil Beds	7	above 7
EP 168/01	Upper Laetolil Beds	7	between 5 & 7
EP 3876/00	Upper Laetolil Beds	7	between 5 & 8
LAET 75-3216	Upper Laetolil Beds	7	
LAET 75-835	Upper Laetolil Beds	7	
LAET 75-857	Upper Laetolil Beds	7	
EP 290/00	Upper Laetolil Beds	8	below 6 & 7
EP 021/01	Upper Laetolil Beds	8	between 5 & 7
LAET 78-5181	Upper Laetolil Beds	9	below 1
EP 1140/98	Upper Laetolil Beds	9	below 6 & 7
EP 1480/98	Upper Laetolil Beds	9	below 6 & 7
EP 1481/98	Upper Laetolil Beds	9	below 6 & 7
EP 458/01	Upper Laetolil Beds	9	between 6 & 8
EP 490/98	Upper Laetolil Beds	10	below 2
EP 491/98	Upper Laetolil Beds	10	below 2
EP 492/98	Upper Laetolil Beds	10	below 2
EP 859/98	Upper Laetolil Beds	10	below 2
EP 162/99	Upper Laetolil Beds	10	below 2
EP 823/00	Upper Laetolil Beds	10	below 2
EP 825/00	Upper Laetolil Beds	10	below 2
EP 3108/00a	Upper Laetolil Beds	10	below 3
EP 3108/00b	Upper Laetolil Beds	10	below 3
EP 3108/00c	Upper Laetolil Beds	10	below 3
EP 643/01	Upper Laetolil Beds	10	below 3
LAET 75-2316	Upper Laetolil Beds	10	
LAET 75-2388	Upper Laetolil Beds	10	
LAET 75-2017	Upper Laetolil Beds	10	
LAET 75-2327	Upper Laetolil Beds	10	
LAET 75-2355	Upper Laetolil Beds	10	
LAET 75-2446	Upper Laetolil Beds	10	
LAET 75-2447	Upper Laetolil Beds	10	
EP 966/01	Upper Laetolil Beds	11	above 7
EP 071/00	Upper Laetolil Beds	11	below 7
EP 4291/00	Upper Laetolil Beds	11	between 7 & 8
EP 4292/00a	Upper Laetolil Beds	11	between 7 & 8
EP 4292/00b	Upper Laetolil Beds	11	between 7 & 8
LAET 76-4135	Upper Laetolil Beds	11	
EP 416/01	Upper Laetolil Beds	13	between 6 & 8
EP 2384/00	Upper Laetolil Beds	16	between 7 & 2 metres above 8
EP 135/00a	Upper Laetolil Beds	16	between 7 & 8
EP 135/00b	Upper Laetolil Beds	16	between 7 & 8
EP 137/00	Upper Laetolil Beds	16	between 7 & 8
LAET 75-2950	Upper Laetolil Beds	16	
EP 084/01	Upper Laetolil Beds	17	between 7 & Yellow Marker Tuff

EP indicates Harrison collection
LAET indicates Leakey collection

Catalog number	Beds	Locality	Tuffs
PROXIMAL PHALANGES continued			
EP 357/00	Upper Laetolil Beds	19	between 5 & 6
EP 1438/01	Upper Laetolil Beds	21	between 5 & 8
EP 549/00	Upper Laetolil Beds	22	between 5 & 7
EP 1211/98	Upper Laetolil Beds	22	
EP 529/01	Upper Laetolil Beds	10 E	between 5 & 7
EP 541/01	Upper Laetolil Beds	10 E	between 5 & 7
EP 542/01	Upper Laetolil Beds	10 E	between 5 & 7
EP 323/98	Upper Laetolil Beds	10 E	between 6 & 7
EP 329/98	Upper Laetolil Beds	10 E	between 6 & 7
EP 332/98	Upper Laetolil Beds	10 E	between 6 & 7
LAET 75-2277	Upper Laetolil Beds	10 E	
LAET 75-1840	Upper Laetolil Beds	10 E	
LAET 75-2254	Upper Laetolil Beds	10 E	
EP 722/98	Upper Laetolil Beds	10 W	below 2
EP 730/98	Upper Laetolil Beds	10 W	below 2
EP 778/98	Upper Laetolil Beds	10 W	below 2
EP 779/98	Upper Laetolil Beds	10 W	below 2
EP 780/98	Upper Laetolil Beds	10 W	below 2
EP 1606/98	Upper Laetolil Beds	10 W	below 2
EP 3160/00a	Upper Laetolil Beds	10 W	below 3
EP 3160/00b	Upper Laetolil Beds	10 W	below 3
EP 3160/00c	Upper Laetolil Beds	10 W	below 3
EP 685/01	Upper Laetolil Beds	10 W	below 3
LAET 75-1785	Upper Laetolil Beds	10 W	
LAET 75-2609	Upper Laetolil Beds	10 W	
LAET 75-2640	Upper Laetolil Beds	10 W	
LAET 75-3508	Upper Laetolil Beds	10 W	
EP 1408/01	Upper Laetolil Beds	12 E	between 5 & 7
EP 2154/00	Upper Laetolil Beds	2 NW	between 5 & 7
EP 1833/00	Upper Laetolil Beds	2. NW gully	between 5 & 7
EP 1747/00	Upper Laetolil Beds	2, S gully	between 6 & 7
EP 1752/00	Upper Laetolil Beds	2, S gully	between 6 & 7
EP 1285/98	Upper Laetolil Beds	22 S	below 5
EP 1288/98	Upper Laetolil Beds	22 S	below 5
EP 984/98	Upper Laetolil Beds	9 S	below 2
EP 985/98	Upper Laetolil Beds	9 S	below 2
EP 986/98	Upper Laetolil Beds	9 S	below 2
EP 987/98	Upper Laetolil Beds	9 S	below 2
EP 988/98	Upper Laetolil Beds	9 S	below 2
EP 989/98	Upper Laetolil Beds	9 S	below 2
EP 990/98	Upper Laetolil Beds	9 S	below 2
EP 991/98	Upper Laetolil Beds	9 S	below 2
EP 246/99	Upper Laetolil Beds	9 S	below 2
EP 248/99	Upper Laetolil Beds	9 S	below 2
EP 3660/00	Upper Laetolil Beds	9 S	below 2
EP 1218/01a	Upper Laetolil Beds	9 S	below 2
EP 1218/01b	Upper Laetolil Beds	9 S	below 2

EP indicates Harrison collection
LAET indicates Leakey collection

Catalog number	Beds	Locality	Tuffs
PROXIMAL PHALANGES continued			
EP 1218/01c	Upper Laetolil Beds	9 S	below 2
EP 1218/01d	Upper Laetolil Beds	9 S	below 2
EP 1225/01	Upper Laetolil Beds	9 S	below 2
EP 1226/01	Upper Laetolil Beds	9 S	below 2
LAET 75-1433	Upper Laetolil Beds	9 S	
EP 3461/00	Upper Ndolanya Beds	15	
EP 3462/00	Upper Ndolanya Beds	15	
EP 4043/00	Upper Ndolanya Beds	15	
EP 1048/01a	Upper Ndolanya Beds	15	
EP 1048/01b	Upper Ndolanya Beds	15	
EP 955/00a	Upper Ndolanya Beds	18	
EP 955/00b	Upper Ndolanya Beds	18	
EP 955/00c	Upper Ndolanya Beds	18	
EP 955/00d	Upper Ndolanya Beds	18	
EP 955/00e	Upper Ndolanya Beds	18	
EP 955/00f	Upper Ndolanya Beds	18	
EP 956/00a	Upper Ndolanya Beds	18	
EP 956/00b	Upper Ndolanya Beds	18	
EP 956/00c	Upper Ndolanya Beds	18	
EP 956/00d	Upper Ndolanya Beds	18	
EP 2344/00	Upper Ndolanya Beds	18	
EP 3273/00	Upper Ndolanya Beds	18	
EP 3274/00a	Upper Ndolanya Beds	18	
EP 3274/00b	Upper Ndolanya Beds	18	
EP 3275/00a	Upper Ndolanya Beds	18	
EP 3275/00b	Upper Ndolanya Beds	18	
EP 3282/00	Upper Ndolanya Beds	18	
EP 3282/00	Upper Ndolanya Beds	18	
EP 758/01a	Upper Ndolanya Beds	18	
EP 758/01b	Upper Ndolanya Beds	18	
EP 758/01c	Upper Ndolanya Beds	18	
EP 759/01	Upper Ndolanya Beds	18	
EP 760/01	Upper Ndolanya Beds	18	
EP 761/01	Upper Ndolanya Beds	18	
EP 762/01	Upper Ndolanya Beds	18	
LAET 76-18-748	Upper Ndolanya Beds	18	
LAET 76-18-823	Upper Ndolanya Beds	18	
LAET 76-18-908	Upper Ndolanya Beds	18	
EP 1485/00	Upper Ndolanya Beds	7 E	
EP 1485/00	Upper Ndolanya Beds	7 E	
EP 1490/00	Upper Ndolanya Beds	7 E	
EP 1491/00	Upper Ndolanya Beds	7 E	
EP 2193/00	Upper Ndolanya Beds	7 E	
EP 3997/00a	Upper Ndolanya Beds	7 E	
EP 3997/00b	Upper Ndolanya Beds	7 E	
EP 841/01	Upper Ndolanya Beds	7 E	
LAET 76-7E-173	Upper Ndolanya Beds	7 E	

EP indicates Harrison collection
LAET indicates Leakey collection

Catalog number	Beds	Locality	Tuffs
PROXIMAL PHALANGES continued			
LAET 76-7E-179	Upper Ndolanya Beds	7 E	
EP 1477/01	Upper Ndolanya Beds	Silal Artum	
INTERMEDIATE PHALANGES			
EP 127/00a	Upper Laetolil Beds	1	between 7 & Yellow Marker Tuff
EP 127/00b	Upper Laetolil Beds	1	between 7 & Yellow Marker Tuff
EP 127/00c	Upper Laetolil Beds	1	between 7 & Yellow Marker Tuff
EP 201/00	Upper Laetolil Beds	1	between 7 & Yellow Marker Tuff
EP 203/00	Upper Laetolil Beds	1	between 7 & Yellow Marker Tuff
EP 1118/01	Upper Laetolil Beds	1	between 7 & Yellow Marker Tuff
EP 1124/01	Upper Laetolil Beds	1	between 7 & Yellow Marker Tuff
EP 645/00	Upper Laetolil Beds	2	between 5 & 7
EP 646/00	Upper Laetolil Beds	2	between 5 & 7
EP 2627/00	Upper Laetolil Beds	2	between 5 & 7
EP 2634/00	Upper Laetolil Beds	2	between 5 & 7
EP 4209/00	Upper Laetolil Beds	2	between 5 & 7
EP 1575/00a	Upper Laetolil Beds	3	between 7 & 8
EP 1575/00b	Upper Laetolil Beds	3	between 7 & 8
EP 1575/00c	Upper Laetolil Beds	3	between 7 & 8
EP 1575/00d	Upper Laetolil Beds	3	between 7 & 8
EP 1575/00e	Upper Laetolil Beds	3	between 7 & 8
EP 2731/00	Upper Laetolil Beds	3	between 7 & 8
LAET 75-2736	Upper Laetolil Beds	3	
EP 2540/00	Upper Laetolil Beds	4	between 5 & 7
EP 1683/00	Upper Laetolil Beds	5	between 3 & 5
EP 1936/00a	Upper Laetolil Beds	5	between 3 & 5
EP 1936/00b	Upper Laetolil Beds	5	between 3 & 5
EP 1936/00c	Upper Laetolil Beds	5	between 3 & 5
EP 1936/00d	Upper Laetolil Beds	5	between 3 & 5
EP 1938/00	Upper Laetolil Beds	5	between 3 & 5
EP 1946/00	Upper Laetolil Beds	5	between 3 & 5
EP 1321/00	Upper Laetolil Beds	6	between 5 & 6
EP 3806/00	Upper Laetolil Beds	6	between 5 & 6
EP 098/01	Upper Laetolil Beds	6	between 5 & 6
LAET 75-1103	Upper Laetolil Beds	6	
EP 870/01	Upper Laetolil Beds	7	above 7
EP 907/01	Upper Laetolil Beds	7	above 7
EP 3875/00	Upper Laetolil Beds	7	between 5 & 8
LAET 75-351	Upper Laetolil Beds	7	
LAET 75-3216	Upper Laetolil Beds	7	
EP 288/00	Upper Laetolil Beds	8	below 6
EP 4101/00	Upper Laetolil Beds	8	between 5 & 7
EP 4109/00	Upper Laetolil Beds	8	between 5 & 7
EP 1479/98	Upper Laetolil Beds	9	below 6 & 7
EP 494/98	Upper Laetolil Beds	10	below 2
EP 860/98	Upper Laetolil Beds	10	below 2

EP indicates Harrison collection
LAET indicates Leakey collection

Catalog number	Beds	Locality	Tuffs
INTERMEDIATE PHALANGES continued			
Ep 886/98	Upper Laetolil Beds	10	below 2
EP 3109/00	Upper Laetolil Beds	10	below 3
EP 3518/00	Upper Laetolil Beds	10	below 3
EP 644/01	Upper Laetolil Beds	10	below 3
LAET 75-2356	Upper Laetolil Beds	10	
EP 072/00	Upper Laetolil Beds	11	below 7
EP 4293/00	Upper Laetolil Beds	11	between 7 & 8
EP 1357/98	Upper Laetolil Beds	13	
EP 2386/00	Upper Laetolil Beds	16	between 7 & 2 metres above 8
LAET 75-3051	Upper Laetolil Beds	17	
EP 455/00	Upper Laetolil Beds	20	between 5 & 7
EP 486/00	Upper Laetolil Beds	21	between 5 & 8
LAET 75-3401	Upper Laetolil Beds	21	
EP 1212/98	Upper Laetolil Beds	22	
EP 2859/00	Upper Laetolil Beds	10 E	between 5 & 7
EP 193/98	Upper Laetolil Beds	10 E	between 6 & 7
EP 195/98	Upper Laetolil Beds	10 E	between 6 & 7
EP 322/98	Upper Laetolil Beds	10 E	between 6 & 7
EP 332/98	Upper Laetolil Beds	10 E	between 6 & 7
EP 375/98	Upper Laetolil Beds	10 E	between 6 & 7
LAET 75-3322	Upper Laetolil Beds	10 E	
EP 781/98	Upper Laetolil Beds	10 W	below 2
EP 782/98	Upper Laetolil Beds	10 W	below 2
EP 1605/98	Upper Laetolil Beds	10 W	below 2
EP 1407/01	Upper Laetolil Beds	12 E	between 5 & 7
EP 391/00	Upper Laetolil Beds	12/12 E	between 5 & 7
EP 2110/00	Upper Laetolil Beds	13	between 6 & 7
EP 2155/00	Upper Laetolil Beds	2 NW	between 5 & 7
EP 1831/00	Upper Laetolil Beds	2, NW gully	between 5 & 7
EP 1832/00	Upper Laetolil Beds	2, NW gully	between 5 & 7
EP 1290/98	Upper Laetolil Beds	22 S	below 5
EP 1291/98	Upper Laetolil Beds	22 S	below 5
EP 993/98	Upper Laetolil Beds	9 S	below 2
EP 994/98	Upper Laetolil Beds	9 S	below 2
EP 247/99	Upper Laetolil Beds	9 S	below 2
EP 1219/01a	Upper Laetolil Beds	9 S	below 2
EP 1219/01b	Upper Laetolil Beds	9 S	below 2
EP 3417/00	Upper Ndolanya Beds	15	
EP 3463/00	Upper Ndolanya Beds	15	
EP 3464/00	Upper Ndolanya Beds	15	
EP 1046/01	Upper Ndolanya Beds	15	
EP 1047/01a	Upper Ndolanya Beds	15	
EP 1047/01b	Upper Ndolanya Beds	15	
EP 957/00	Upper Ndolanya Beds	18	
EP 958/00	Upper Ndolanya Beds	18	
EP 959/00	Upper Ndolanya Beds	18	
EP 961/00	Upper Ndolanya Beds	18	

EP indicates Harrison collection
LAET indicates Leakey collection

Catalog number	Beds	Locality	Tuffs
INTERMEDIATE PHALANGES continued			
EP 3276/00	Upper Ndolanya Beds	18	
EP 3282/00	Upper Ndolanya Beds	18	
EP 3282/00	Upper Ndolanya Beds	18	
EP 3283/00	Upper Ndolanya Beds	18	
EP 763/01	Upper Ndolanya Beds	18	
EP 764/01	Upper Ndolanya Beds	18	
EP 765/01a	Upper Ndolanya Beds	18	
EP 765/01b	Upper Ndolanya Beds	18	
EP 766/01a	Upper Ndolanya Beds	18	
EP 766/01b	Upper Ndolanya Beds	18	
LAET 76-18-742	Upper Ndolanya Beds	18	
LAET 76-18-752	Upper Ndolanya Beds	18	
EP 3769/00	Upper Ndolanya Beds	22 S	
EP 3771/00	Upper Ndolanya Beds	22 S	
EP 3772/00	Upper Ndolanya Beds	22 S	
EP 1485/00	Upper Ndolanya Beds	7 E	
EP 1485/00	Upper Ndolanya Beds	7 E	
EP 1475/00a	Upper Ndolanya Beds	7 E	
EP 1475/00b	Upper Ndolanya Beds	7 E	
EP 1475/00c	Upper Ndolanya Beds	7 E	
EP 3998/00	Upper Ndolanya Beds	7 E	
EP 3999/00	Upper Ndolanya Beds	7 E	
EP 843/01	Upper Ndolanya Beds	7 E	
EP 844/01	Upper Ndolanya Beds	7 E	
LAET 76-7E-179	Upper Ndolanya Beds	7 E	
EP 1478/01	Upper Ndolanya Beds	Silal Artum	
DISTAL PHALANGES			
EP 2988/00	Upper Laetolil Beds	1	between 6 & 8
EP 1409/00	Upper Laetolil Beds	1	between 7 & Yellow Marker Tuff
LAET 74-99	Upper Laetolil Beds	1	
LAET 75-678	Upper Laetolil Beds	1	
LAET 75-679	Upper Laetolil Beds	1	
LAET 75-680	Upper Laetolil Beds	1	
EP 2624/00	Upper Laetolil Beds	2	between 5 & 7
EP 4206/00	Upper Laetolil Beds	2	between 5 & 7
EP 4207a/00	Upper Laetolil Beds	2	between 5 & 7
EP 1574/00	Upper Laetolil Beds	3	between 7 & 8
EP 2729/00	Upper Laetolil Beds	3	between 7 & 8
LAET 75-3472	Upper Laetolil Beds	3	
EP 2541/00	Upper Laetolil Beds	4	between 5 & 7
EP 1937/00a	Upper Laetolil Beds	5	between 3 & 5
EP 1937/00b	Upper Laetolil Beds	5	between 3 & 5
EP 1937/00c	Upper Laetolil Beds	5	between 3 & 5
EP 1322/00d	Upper Laetolil Beds	6	between 5 & 6
EP 3805/00a	Upper Laetolil Beds	6	between 5 & 6

EP indicates Harrison collection
LAET indicates Leakey collection

Catalog number	Beds	Locality	Tuffs
DISTAL PHALANGES continued			
EP 3805/00b	Upper Laetolil Beds	6	between 5 & 6
EP 3814/00	Upper Laetolil Beds	6	between 5 & 6
EP 167/01	Upper Laetolil Beds	7	between 5 & 7
EP 2298/00	Upper Laetolil Beds	7	between 7 & 8
EP 249/00	Upper Laetolil Beds	8	above 8
EP 288/00	Upper Laetolil Beds	8	below 6
EP 027/01	Upper Laetolil Beds	8	between 5 & 7
EP 1478/98	Upper Laetolil Beds	9	below 6 & 7
EP 3104/00	Upper Laetolil Beds	10	below 3
LAET 79-5460	Upper Laetolil Beds	10	below 3
LAET 75-2452	Upper Laetolil Beds	10	
EP 4294/00	Upper Laetolil Beds	11	between 7 & 8
EP 2037/00	Upper Laetolil Beds	13	between 5 & 7
EP 417/01	Upper Laetolil Beds	13	between 6 & 8
EP 1421/98	Upper Laetolil Beds	15	below 7 & 8
EP 2383/00	Upper Laetolil Beds	16	between 7 & 2 metres above 8
EP 2385/00	Upper Laetolil Beds	16	between 7 & 2 metres above 8
EP 136/00	Upper Laetolil Beds	16	between 7 & 8
EP 358/00a	Upper Laetolil Beds	19	between 5 & 6
EP 358/00b	Upper Laetolil Beds	19	between 5 & 6
EP 358/00c	Upper Laetolil Beds	19	between 5 & 6
EP 3565/00	Upper Laetolil Beds	20	between 5 & 7
EP 054/99	Upper Laetolil Beds	10 E	below 6 & 7
EP 2862/00a	Upper Laetolil Beds	10 E	between 5 & 7
EP 2862/00b	Upper Laetolil Beds	10 E	between 5 & 7
EP 2862/00c	Upper Laetolil Beds	10 E	between 5 & 7
EP 2862/00	Upper Laetolil Beds	10 E	between 5 & 7
EP 194/98	Upper Laetolil Beds	10 E	between 6 & 7
EP 332/98	Upper Laetolil Beds	10 E	between 6 & 7
EP 374/98	Upper Laetolil Beds	10 E	between 6 & 7
LAET 75-2251	Upper Laetolil Beds	10 E	
EP 1604/98	Upper Laetolil Beds	10 W	below 2
EP 3161/00	Upper Laetolil Beds	10 W	below 3
EP 387/00	Upper Laetolil Beds	12/12 E	between 5 & 7
EP 332/01	Upper Laetolil Beds	2 S	
EP 1292/98	Upper Laetolil Beds	22 S	below 5
EP 1049/00	Upper Laetolil Beds	9 S	below 2
EP 1220/01a	Upper Laetolil Beds	9 S	below 2
EP 1220/01b	Upper Laetolil Beds	9 S	below 2
EP 3465/00a	Upper Ndolanya Beds	15	
EP 3465/00b	Upper Ndolanya Beds	15	
EP 1050/01	Upper Ndolanya Beds	15	
EP 1051/01	Upper Ndolanya Beds	15	
EP 3277/00	Upper Ndolanya Beds	18	
EP 3278/00	Upper Ndolanya Beds	18	
EP 3282/00	Upper Ndolanya Beds	18	
LAET 76-18-743	Upper Ndolanya Beds	18	

EP indicates Harrison collection
LAET indicates Leakey collection

Catalog number	Beds	Locality	Tuffs
DISTAL PHALANGES continued			
LAET 76-18-868	Upper Ndolanya Beds	18	
EP 3761/00a	Upper Ndolanya Beds	22 S	
EP 3761/00b	Upper Ndolanya Beds	22 S	
EP 3761/00c	Upper Ndolanya Beds	22 S	
EP 1485/00	Upper Ndolanya Beds	7 E	
EP 845/01	Upper Ndolanya Beds	7 E	

EP indicates Harrison collection
LAET indicates Leakey collection

APPENDIX C

SIZE CORRECTING DATA

Measurement	# of specimens	a (slope)	b (intercept)	error a	error b	r	95% on a		95% on b	
HUMERUS										
H1	203	0.29282	1.7389	0.004749	0.008945	0.97294	0.2834	0.3027	1.722	1.754
H2	203	0.28577	1.706	0.00486	0.009154	0.9702	0.2757	0.2964	1.688	1.723
H3	203	0.37945	0.57295	0.018177	0.018177	0.93204	0.3589	0.3992	0.5384	0.6097
H4	204	0.36018	1.2091	0.00591	0.01112	0.97215	0.3484	0.373	1.187	1.23
H5	204	0.36091	0.89495	0.005611	0.010558	0.97503	0.3496	0.3724	0.8745	0.9153
H6	204	0.37799	1.0351	0.004972	0.009355	0.98219	0.3681	0.3877	1.018	1.053
H7	204	0.3986	0.94715	0.005778	0.010871	0.97834	0.3877	0.4091	0.9273	0.9663
H8	203	0.38755	0.84158	0.004808	0.009057	0.98425	0.3781	0.397	0.8243	0.8586
H9	203	0.40293	0.79694	0.005123	0.00965	0.98345	0.3928	0.4128	0.7791	0.8141
H10	203	0.37392	0.89823	0.004694	0.008842	0.98387	0.3646	0.3826	0.8828	0.9142
H11	203	0.35247	0.49309	0.006171	0.011623	0.96839	0.341	0.3636	0.4731	0.5135
H12	203	0.34057	0.50908	0.005813	0.010949	0.96998	0.3273	0.3536	0.4866	0.531
H13	203	0.38573	0.6536	0.005722	0.010777	0.97741	0.3749	0.3968	0.6341	0.6718
H14	203	0.39838	0.54995	0.006126	0.011539	0.9757	0.3862	0.4108	0.5288	0.5699
RADIUS										
R1	209	0.31154	1.7232	0.007949	0.014942	0.92949	0.2941	0.3294	1.692	1.754
R2	209	0.30742	1.7078	0.008219	0.01545	0.92229	0.289	0.3261	1.674	1.74
R3	209	0.38011	0.60839	0.005603	0.010532	0.97703	0.3685	0.3915	0.5877	0.6295
R4	209	0.40804	0.82387	0.005381	0.010115	0.98166	0.3979	0.4183	0.8052	0.8424
R5	209	0.40072	0.8047	0.007939	0.014923	0.95811	0.3897	0.4115	0.7866	0.8224
R6	210	0.3737	0.7088	0.005784	0.010849	0.97453	0.362	0.3857	0.687	0.7293
R7	210	0.40026	0.79553	0.005562	0.010434	0.97952	0.3886	0.4115	0.776	0.8159
R8	211	0.38056	0.42264	0.006309	0.011819	0.97057	0.3678	0.3939	0.3999	0.4442
R9	211	0.38129	0.64763	0.005917	0.011084	0.97426	0.369	0.3931	0.6273	0.6683
ULNA										
U1	205	0.30977	1.7936	0.007254	0.01363	0.94212	0.294	0.3254	1.768	1.821
U2	204	0.30868	1.7033	0.00812	0.015253	0.92674	0.2914	0.3267	1.673	1.735
U3	206	0.36054	1.1423	0.005717	0.010702	0.97375	0.3484	0.3717	1.123	1.164
U4	209	0.38435	0.99517	0.006601	0.012375	0.96869	0.3714	0.3989	0.9691	1.018
U5	209	0.38352	0.93163	0.006933	0.012997	0.96525	0.3694	0.3976	0.9055	0.9577
U6	210	0.36109	0.43094	0.006232	0.011673	0.96822	0.3498	0.3722	0.4103	0.4513
U7	210	0.37542	0.20441	0.010365	0.019412	0.91648	0.3544	0.3973	0.1635	0.242
METACARPAL										
MC1	211	0.30497	1.6606	0.015037	0.02884	0.69786	0.2714	0.3379	1.598	1.725
MC2	211	0.31144	1.6338	0.015935	0.030562	0.66901	0.2755	0.3464	1.566	1.706
MC3	211	0.35461	0.65426	0.00607	0.011642	0.96863	0.3425	0.3672	0.6305	0.6786
MC4	211	0.36072	0.76802	0.005409	0.010374	0.97847	0.3698	0.3916	0.7491	0.7879
MC5	211	0.34932	0.64898	0.006581	0.012622	0.96182	0.3357	0.3632	0.6219	0.6769
MC6	211	0.4034	0.73006	0.007702	0.014772	0.96077	0.3886	0.4195	0.7013	0.7566
MC7	211	0.4011	0.52074	0.008234	0.015792	0.9545	0.3849	0.4165	0.4902	0.5507

Measurement	# of specimens	a (slope)	b (intercept)	error a	error b	r	95% on a		95% on b	
METACARPAL continued										
MC8	211	0.36915	0.4807	0.0086	0.016494	0.941	0.3491	0.3892	0.4398	0.5211
MC9	211	0.40543	0.38911	0.007386	0.014168	0.96435	0.3909	0.4196	0.3627	0.4161
MC10	211	0.39614	-0.23921	0.012315	0.023618	0.89225	0.3737	0.4207	-0.286	-0.199
MC11	211	0.39622	-0.36168	0.013413	0.025724	0.87076	0.373	0.422	-0.414	-0.3154
MC12	211	0.36527	0.47807	0.007099	0.013616	0.95932	0.35	0.3797	0.4513	0.5073
MC13	211	0.39111	0.53766	0.008922	0.017112	0.9435	0.3723	0.4099	0.5043	0.5718
FEMUR										
F1	207	0.27812	1.8596	0.004241	0.007944	0.97563	0.2693	0.2868	1.845	1.875
F2	207	0.2709	1.8531	0.004168	0.007806	0.97519	0.2623	0.2789	1.84	1.867
F3	209	0.33076	0.80917	0.004833	0.009052	0.97744	0.3214	0.3397	0.7925	0.8255
F4	209	0.37254	1.0927	0.005957	0.011158	0.97291	0.3619	0.3834	1.072	1.111
F5	209	0.36801	1.1047	0.00567	0.010621	0.97488	0.3569	0.3786	1.084	1.125
F6	209	0.32791	1.0579	0.004913	0.009203	0.97626	0.3177	0.3377	1.041	1.075
F7	209	0.33246	0.80074	0.004673	0.008754	0.97913	0.3229	0.3424	0.7827	0.8168
F8	209	0.34988	0.08285	0.005917	0.011083	0.96965	0.3391	0.36	0.8645	0.9023
F9	210	0.34613	1.1692	0.005405	0.010124	0.97407	0.3362	0.3559	1.151	1.187
F10	210	0.33514	1.0768	0.004332	0.008115	0.9823	0.3261	0.3441	1.06	1.093
F11	210	0.36934	0.73723	0.007373	0.013813	0.95724	0.3572	0.3816	0.7132	0.7596
F12	210	0.32034	0.72949	0.005722	0.010718	0.96592	0.3094	0.3315	0.709	0.7508
F13	207	0.34949	0.6979	0.00547	0.010245	0.97432	0.3386	0.3595	0.6794	0.7173
F14	207	0.32649	0.71561	0.005322	0.009972	0.97198	0.3155	0.337	0.6959	0.7353
TIBIA										
T1	212	0.2488	1.9676	0.005974	0.01118	0.9369	0.2359	0.2617	1.945	1.991
T2	212	0.24278	1.9516	0.006389	0.011957	0.92369	0.0229	0.2572	1.928	1.977
T3	213	0.3065	1.1661	0.005584	0.01403	0.96401	0.2941	0.3185	1.144	1.189
T4	213	0.33169	1.1192	0.004187	0.007821	0.98288	0.3231	0.3401	1.104	1.134
T5	213	0.30284	0.97658	0.006188	0.011558	0.9545	0.2889	0.3173	0.9494	1.002
T6	213	0.29409	0.84925	0.005066	0.009462	0.96789	0.2841	0.3044	0.8297	0.8675
T7	213	0.34725	0.85976	0.006081	0.011359	0.96679	0.3348	0.3594	0.8381	0.8821
T8	213	0.2779	0.5065	0.006067	0.011333	0.94788	0.2662	0.2893	0.4836	0.5287
T9	213	0.33803	0.80192	0.004912	0.009174	0.97726	0.3291	0.3472	0.7862	0.8175
T10	213	0.33727	0.90338	0.004582	0.008558	0.98015	0.3279	0.3462	0.8871	0.92
T11	212	0.30911	0.70795	0.005963	0.011159	0.95975	0.2964	0.3216	0.6833	0.7292
T12	212	0.34045	0.71219	0.005578	0.01044	0.97113	0.3303	0.351	0.6914	0.7313
METATARSAL										
MT1	215	0.26727	1.7691	0.013117	0.025067	0.69439	0.2411	0.2951	1.711	1.822
MT2	215	0.26628	1.7544	0.012603	0.024086	0.71996	0.241	0.2911	1.707	1.804
MT3	215	0.32134	0.84727	0.005881	0.01124	0.96332	0.3091	0.3323	0.826	0.8705
MT4	215	0.32767	0.82747	0.004821	0.009214	0.97645	0.3182	0.3374	0.8099	0.8459
MT5	215	0.30858	0.74472	0.056794	0.010854	0.9629	0.2963	0.3217	0.7193	0.7698

Measurement	# of specimens	a (slope)	b (intercept)	error a	error b	r	95% on a		95% on b	
METATARSAL continued										
MT6	215	0.35341	0.82623	0.006438	0.012304	0.96366	0.34	0.3676	0.7985	0.8515
MT7	215	0.36168	0.59764	0.007458	0.014254	0.95319	0.3456	0.3782	0.5643	0.6303
MT8	215	0.33452	0.54841	0.007394	0.014131	0.94602	0.3169	0.3526	0.5117	0.5839
MT9	215	0.35943	0.4785	0.006823	0.01304	0.96048	0.3436	0.3752	0.4495	0.5079
MT10	215	0.34304	-0.0553	0.008305	0.015871	0.93487	0.3273	0.3589	-0.085	-0.028
MT11	215	0.34896	-0.20996	0.010614	0.020285	0.89503	0.3272	0.3713	-0.258	-0.1631
MT12	215	0.32606	0.63896	0.006869	0.013127	0.95171	0.3148	0.3406	0.6046	0.6563
MT13	215	0.33833	0.60341	0.007069	0.01351	0.95191	0.3243	0.3536	0.5756	0.6294
MAGNUM										
Ca1	209	0.38496	0.53624	0.00633	0.012079	0.97133	0.3729	0.3971	0.5151	0.5587
Ca2	211	0.36507	0.59496	0.005762	0.01065	0.97336	0.3539	0.376	0.5757	0.616
Ca3	210	0.36021	0.56138	0.005852	0.011155	0.97189	0.3494	0.3706	0.5417	0.5815
Ca4	210	0.3608	0.46451	0.006917	0.013185	0.96474	0.3688	0.3935	0.441	0.4865
Ca5	211	0.36322	0.56529	0.005918	0.011263	0.97159	0.3512	0.3744	0.5455	0.5876
Ca6	210	0.34313	0.4822	0.007825	0.014916	0.94382	0.3257	0.3611	0.4488	0.5148
Ca7	210	0.38455	0.10257	0.008547	0.016292	0.94671	0.3667	0.4031	0.0674	0.1374
Ca7b	211	0.37667	0.25666	0.006166	0.011734	0.97135	0.3637	0.3898	0.2329	0.2816
Ca8	211	0.3864	0.17574	0.007059	0.013434	0.96414	0.3731	0.3994	0.1512	0.202
UNCIFORM										
Cb1	207	0.37884	0.42941	0.006017	0.011488	0.97354	0.3648	0.3923	0.4054	0.4543
Cb2	208	0.37428	0.52654	0.0061	0.011623	0.97198	0.3608	0.387	0.5023	0.5522
Cb3	207	0.36712	0.49378	0.006477	0.012362	0.96724	0.3542	0.381	0.4676	0.5196
Cb4	208	0.40047	0.28441	0.006799	0.012967	0.96956	0.3871	0.4134	0.2607	0.3074
Cb5	208	0.36106	0.41369	0.013527	0.0258	0.84145	0.3388	0.3838	0.3678	0.4589
Cb6	208	0.37889	0.33846	0.013432	0.025618	0.85941	0.3581	0.3991	0.3	0.3787
Cb7	209	0.35089	0.40436	0.006397	0.01218	0.96464	0.3376	0.3642	0.3806	0.4287
Cb7b	209	0.37617	0.36969	0.00668	0.012719	0.96648	0.3607	0.3909	0.3422	0.3987
Cb8	209	0.33912	0.24793	0.008178	0.015571	0.93726	0.3238	0.3541	0.2199	0.2756
SCAPHOID										
Cc1	208	0.38698	0.39461	0.006238	0.011887	0.9726	0.375	0.3994	0.3709	0.4167
Cc2	209	0.37131	0.63443	0.005893	0.011227	0.97332	0.3587	0.383	0.6134	0.6566
Cc3	210	0.3745	0.53066	0.005844	0.011125	0.9741	0.3625	0.3865	0.5089	0.5517
Cc4	207	0.36125	0.39508	0.013167	0.02513	0.85146	0.3387	0.384	0.3471	0.4394
LUNAR										
Cd1	203	0.3731	0.46368	0.006356	0.012179	0.97009	0.36	0.3864	0.4396	0.4873
Cd2	208	0.36953	0.61337	0.005706	0.010875	0.97489	0.3582	0.3809	0.5928	0.6336
Cd3	208	0.381231	0.32677	0.006667	0.012706	0.96766	0.3683	0.3942	0.3043	0.349
Cd4	208	0.35254	0.44936	0.007404	0.01411	0.95302	0.3362	0.3682	0.4216	0.4789

Measurement	# of specimens	a (slope)	b (intercept)	error a	error b	r	95% on a		95% on b	
LUNAR continued										
Cd5	207	0.35849	0.5396	0.00693	0.013222	0.96054	0.3446	0.3709	0.5169	0.5655
Cd6	206	0.36801	0.38813	0.007018	0.013409	0.96181	0.355	0.3807	0.3624	0.413
Cd7	206	0.32725	0.50198	0.006447	0.012318	0.95919	0.3137	0.3408	0.4779	0.5242
Cd8	205	0.42069	0.33733	0.017276	0.033031	0.80887	0.3938	0.4462	0.2787	0.3946
Cd9	205	0.37341	0.56847	0.007441	0.014227	0.95843	0.3565	0.3921	0.5291	0.602
CUNEIFORM										
Ce1	203	0.38678	0.51042	0.00556	0.010551	0.9788	0.3748	0.3981	0.4901	0.5314
Ce2	204	0.38899	0.45328	0.006271	0.011887	0.97313	0.3757	0.4015	0.4304	0.4753
Ce3	202	0.3647	0.31275	0.006164	0.011714	0.97073	0.3533	0.3764	0.291	0.3341
Ce4	202	0.33774	0.50338	0.005881	0.011178	0.96889	0.3238	0.3515	0.4805	0.5258
Ce5	204	0.35367	0.42264	0.006933	0.013143	0.96	0.34	0.3673	0.3975	0.4479
PISIFORM										
Cf1	170	0.3676	0.42822	0.00682	0.013031	0.9703	0.3532	0.3821	0.4041	0.4523
Cf2	170	0.34216	0.60503	0.007685	0.014682	0.95616	0.3265	0.359	0.5768	0.6328
Cf3	170	0.37122	0.34829	0.008844	0.016898	0.9505	0.3521	0.3898	0.3148	0.3829
TALUS										
TA1	206	0.31821	0.99842	0.004746	0.009005	0.97682	0.3091	0.3274	0.981	1.016
TA2	206	0.30559	0.90965	0.004808	0.009123	0.97417	0.2971	0.3142	0.8935	0.9255
TA2b	206	0.31686	0.76122	0.004913	0.009323	0.97492	0.3069	0.3257	0.7449	0.7796
TA3	206	0.3393	0.74777	0.004696	0.00891	0.98007	0.3298	0.3485	0.732	0.7645
TA4	206	0.34086	0.73096	0.004732	0.008973	0.97995	0.3317	0.3497	0.7145	0.7479
TA5	206	0.31129	0.90886	0.004838	0.00918	0.9748	0.3021	0.3206	0.8913	0.9259
TA6	206	0.3128	0.55914	0.005784	0.010974	0.96414	0.3005	0.3248	0.5358	0.5826
TA7	206	0.32406	0.66884	0.005375	0.010199	0.97125	0.3139	0.3344	0.6502	0.6867
TA8	206	0.31835	0.75311	0.004902	0.009301	0.97527	0.3092	0.3277	0.7358	0.7696
CUNEIFORM										
C1	209	0.30953	1.3287	0.004762	0.009009	0.97496	0.2997	0.3191	1.311	1.347
C2	210	0.31043	1.1513	0.005021	0.009485	0.97214	0.3005	0.3205	1.133	1.17
C3	211	0.33897	0.58854	0.006152	0.011635	0.96463	0.3256	0.3531	0.5613	0.6153
C4	212	0.34234	0.59535	0.006672	0.012601	0.95889	0.3286	0.3553	0.5721	0.6185
C5	212	0.34748	0.74875	0.004646	0.008774	0.98087	0.3367	0.3576	0.7297	0.7684
C6	210	0.34277	0.66499	0.006268	0.011861	0.96425	0.3299	0.3553	0.6411	0.6894
C7	212	0.32478	0.72154	0.00506	0.009555	0.97394	0.3147	0.3342	0.7042	0.7398
C8	212	0.32744	0.43342	0.00676	0.012767	0.95375	0.3143	0.3403	0.4076	0.4592
CALCANEUS										
Ta1	210	0.33398	0.83201	0.00525	0.010056	0.97371	0.3231	0.3441	0.8125	0.8535

Measurement	# of specimens	a (slope)	b (intercept)	error a	error b	r	95% on a		95% on b	
CALCANEUS continued										
Ta2	211	0.35138	0.55344	0.005795	0.011092	0.97088	0.3397	0.3631	0.5316	0.5754
Ta3	210	0.31912	0.40678	0.01018	0.019499	0.88674	0.2944	0.3444	0.3578	0.4507
Ta4	207	0.38111	0.39571	0.008616	0.016595	0.94562	0.3638	0.3988	0.3639	0.4268
Ta5	207	0.31037	0.81045	0.005933	0.011428	0.96143	0.2993	0.3213	0.7889	0.8317
Ta6	207	0.33517	0.60336	0.006215	0.011969	0.96376	0.3231	0.3469	0.58	0.6269
Ta7	207	0.32487	0.48661	0.006238	0.012015	0.96108	0.3122	0.3373	0.4615	0.5125
Ta8	213	0.33605	0.86169	0.00465	0.008867	0.9794	0.3271	0.3452	0.8446	0.8777
Ta9	213	0.33452	0.77525	0.004585	0.008744	0.97979	0.3254	0.3427	0.7593	0.792
Ta10	213	0.35563	0.66712	0.0064	0.012205	0.96489	0.3408	0.3695	0.6402	0.6951
Ta11	210	0.33993	0.69131	0.005649	0.010816	0.97057	0.3295	0.3507	0.6706	0.7113
Ta12	210	0.33981	0.24898	0.00748	0.014323	0.94775	0.3245	0.3546	0.2192	0.2791
Ta13	211	0.37478	0.34928	0.007567	0.014479	0.95602	0.3584	0.3898	0.3179	0.3817
Ta14	211	0.33594	0.21724	0.00954	0.018253	0.91096	0.3181	0.353	0.1814	0.2529
Ta15	211	0.29075	0.56941	0.007913	0.015141	0.91853	0.2731	0.3087	0.535	0.6026
NAVICULO-CUBOID										
Tb1	193	0.31396	0.67102	0.010505	0.020529	0.8854	0.2959	0.3303	0.6394	0.7035
Tb2	192	0.36913	0.40355	0.010769	0.021073	0.92355	0.3675	0.4115	0.3644	0.44
Tb3	196	0.32948	0.64309	0.006403	0.012436	0.96226	0.3154	0.3427	0.619	0.6693
Tb4	196	0.33723	0.40062	0.006586	0.012792	0.9619	0.3253	0.3489	0.378	0.4231
Tb5	193	0.32307	0.4744	0.007704	0.015054	0.94352	0.3092	0.3369	0.447	0.5005
Tb6	193	0.33605	0.55996	0.007061	0.013797	0.95644	0.3215	0.3496	0.5323	0.5884
Tb7	193	0.32742	0.64035	0.007064	0.013802	0.95403	0.3094	0.3484	0.5972	0.6765
Tb8	194	0.33212	0.22264	0.010148	0.019804	0.90492	0.3063	0.3609	0.1705	0.2704
PROXIMAL PHALANX (Forelimb)										
Pa1f	149	0.32812	1.0558	0.013729	0.025612	0.85972	0.2979	0.3618	0.9964	1.117
Pa2f	149	0.40191	0.38888	0.008623	0.016086	0.9651	0.3845	0.4179	0.3602	0.4191
Pa3f	149	0.40127	0.38006	0.008847	0.016504	0.9631	0.3832	0.4179	0.35	0.4101
Pa3fb	149	0.36138	0.43459	0.0092	0.017162	0.95049	0.3419	0.3809	0.3973	0.4737
Pa4f	149	0.39061	0.45397	0.008366	0.015606	0.96522	0.3741	0.4083	0.4232	0.4835
Pa5f	149	0.38288	0.44572	0.008361	0.015597	0.96382	0.3661	0.3995	0.4173	0.4746
Pa5fb	149	0.34661	0.53025	0.008308	0.015498	0.95624	0.3285	0.365	0.4958	0.5627
Pa6f	149	0.36161	0.45067	0.00765	0.014271	0.96612	0.3465	0.3772	0.4238	0.4794
Pa7f	149	0.40332	0.32918	0.008945	0.016687	0.96266	0.3864	0.4213	0.2976	0.3595
INTERMEDIATE PHALANX (Forelimb)										
Pb1f	90	0.2583	0.97981	0.009575	0.019097	0.93613	0.2377	0.2766	0.9416	1.024
Pb2f	90	0.40546	0.31364	0.010657	0.021255	0.96842	0.3865	0.4286	0.2679	0.3498
Pb3f	90	0.40396	0.31161	0.010885	0.021709	0.96678	0.3834	0.4258	0.2675	0.3502
Pb3fb	90	0.38069	0.46993	0.008396	0.016746	0.97787	0.3647	0.3994	0.431	0.5033
Pb4f	94	0.38922	0.4208	0.009253	0.018281	0.97307	0.3718	0.4092	0.3797	0.455
Pb5f	94	0.38899	0.40715	0.009253	0.018281	0.97304	0.3715	0.4097	0.3652	0.4418

Measurement	# of specimens	a (slope)	b (intercept)	error a	error b	r	95% on a		95% on b	
INTERMEDIATE PHALANX (Forelimb) continued										
Pb5fb	94	0.33871	0.49802	0.007605	0.015025	0.97602	0.3238	0.356	0.4632	0.5278
Pb6f	94									
Pb7f	94	0.40974	0.25972	0.00945	0.01867	0.97468	0.3916	0.4289	0.2218	0.2938
DISTAL PHALANX (Forelimb)										
Pc1f	64	0.36461	0.8817	0.00955	0.019448	0.9778	0.3516	0.3799	0.8502	0.9084
Pc2f	64	0.38108	0.60469	0.011547	0.023547	0.97017	0.3598	0.4057	0.5506	0.6496
Pc3f	64	0.36099	0.50323	0.010605	0.021596	0.97199	0.3393	0.3849	0.4532	0.5459
Pc3fb	65	0.38916	0.32706	0.012462	0.025302	0.9661	0.3679	0.4143	0.2714	0.3707
Pc4f	64	0.41718	0.39471	0.016114	0.032814	0.95106	0.3891	0.4465	0.3253	0.462
Pc5f	64	0.40888	0.15343	0.012407	0.025265	0.97009	0.3842	0.4359	0.0982	0.2001
PROXIMAL PHALANX (Hindlimb)										
Pa1h	154	0.28031	1.1446	0.009042	0.01689	0.91639	0.2586	0.3013	1.106	1.187
Pa2h	154	0.36354	0.46046	0.006953	0.012987	0.97143	0.3497	0.3771	0.4351	0.4852
Pa3h	154	0.36427	0.44621	0.007	0.013075	0.97115	0.3499	0.3783	0.4211	0.4716
Pa3hb	154	0.32056	0.49604	0.007027	0.013125	0.96229	0.3052	0.335	0.4667	0.5272
Pa4h	154	0.35062	0.53123	0.007315	0.013663	0.96595	0.3355	0.366	0.5031	0.5589
Pa5h	154	0.33986	0.5207	0.007065	0.013196	0.96616	0.3251	0.354	0.4943	0.5473
Pah5b	154	0.31265	0.60835	0.006815	0.01273	0.96272	0.2983	0.3274	0.5799	0.6365
Pa6h	154	0.32184	0.53314	0.006834	0.012766	0.96465	0.3082	0.3358	0.506	0.5592
Pa7h	154									
INTERMEDIATE PHALANX (Hindlimb)										
Pb1h	91	0.24163	1.0204	0.009025	0.018151	0.93438	0.2219	0.2611	0.9805	1.061
Pb2h	90	0.36963	0.37003	0.009546	0.019206	0.96952	0.3527	0.3889	0.3304	0.4025
Pb3h	91	0.37308	0.359	0.009812	0.019734	0.96802	0.3548	0.3939	0.3133	0.3933
Pb3hb	91	0.36275	0.48115	0.009568	0.019244	0.96783	0.3433	0.3838	0.4401	0.5178
Pb4h	96	0.3585	0.47536	0.008275	0.016431	0.97409	0.3414	0.3778	0.4353	0.51
Pb5h	96	0.35806	0.45625	0.008442	0.016761	0.97296	0.3405	0.3765	0.418	0.49
Pb5hb	96	0.30781	0.53983	0.008145	0.016173	0.96581	0.2921	0.3245	0.5048	0.5702
Pb6h	96	0.35194	0.40247	0.009011	0.017892	0.96803	0.333	0.3716	0.3634	0.4381
Pb7h	96	0.3666	0.33344	0.008973	0.017816	0.97082	0.3492	0.3837	0.2966	0.3693
DISTAL PHALANX (Hindlimb)										
Pc1h	65	0.32147	0.95612	0.009716	0.019741	0.96986	0.3057	0.3414	0.9138	0.9878
Pc2h	65	0.34213	0.67584	0.011114	0.02258	0.9651	0.3228	0.3651	0.6228	0.7182
Pc3h	66	0.32289	0.55663	0.010527	0.021327	0.96429	0.2999	0.3481	0.5011	0.6036
Pc3hb	66	0.36516	0.36191	0.012797	0.025925	0.95862	0.3429	0.3933	0.3002	0.4077
Pc4h	65	0.38456	0.4406	0.015913	0.032331	0.94271	0.3577	0.4134	0.3719	0.5025
Pc5h	65	0.38242	0.19452	0.011033	0.022416	0.97257	0.3605	0.4069	0.1421	0.236

APPENDIX D

DATASET SUMMARY AND SPECIES BREAKDOWN FOR DISCRIMINANT FUNCTION ANALYSES OF THE MODERN DATA

Note: All species codes are given in Table 3.1 in Chapter 3. Where the total number of analysed specimens differed between the analyses of the logged and size corrected data, this is indicated in the "Number" column. In these few instances the number of elements in the logged analysis is listed first and separated by a forward slash from the number of elements in the size corrected analysis.

Appendix D, Table A. Species breakdown of the calcaneus dataset

Species	Species code	Number
TOTAL = 208		
GRASSLAND		
Total number of specimens = 15		
Addax nasomaculatus	An	1
Bison bison	Bb	7
Damaliscus dorcas	Dd	1
Damaliscus lunatus	Dl	2
Ovibos moschatus	Om	2
Procapra picticaudata	Pp	2
WOODED-BUSHED GRASSLAND		
Total number of specimens = 46		
Alcelaphus buselaphus	Ab	4
Antilope cervicapra	Ac	2
Connochaetes gnu	Cg	1
Connochaetes taurinus	Ct	4
Damaliscus hunteri	Dh	2
Gazella rufifrons	Gr	2
Gazella soemmerringi	Gso	2
Gazella speki	Gs	2
Gazella subgutturosa	Gsu	2
Gazella thomsoni	Gt	4
Hippotragus equinus	He	2
Kobus kob	Kk	5
Kobus leche	Kl	1
Madoqua guentheri	Mg	1
Ourebia ourebi	Ouo	3
Raphicerus campestris	Rc	6
Redunca fulvorufula	Rf	3
LIGHT WOODLAND-BUSHLAND		
Total number of specimens = 49		
Aepyceros melampus	Am	7
Gazella cuvieri	Gc	2
Gazella granti	Gg	4
Hippotragus niger	Hn	5
Litocranius walleri	Lw	5
Odocoileus virginianus	Odv	4
Oreotragus oreotragus	Oo	4
Oryx beisa	Ob	1
Raphicerus sharpei	Rs	3
Redunca redunca	Red	4
Sylvicapra grimmia	Sg	4
Syncerus caffer	Sc	3
Taurotragus oryx	To	3
HEAVY WOODLAND-BUSHLAND		
Total number of specimens = 28		
Kobus defassa	Kd	5
Madoqua kirki	Mk	4
Madoqua saltiana	Ms	0
Neotragus batesi	Nb	1
Neotragus moschatus	Nm	0
Neotragus pygmaeus	Np	1
Taurotragus derbianus	Td	2
Tragelaphus scriptus	Ts	10
Tragelaphus speki	Tsp	1
Tragelaphus strepsiceros	Tst	4
FOREST		
Total number of specimens = 28		
Alces alces	Aa	4
Bos javanicus	Bj	3
Bos sauveli	Bs	2
Bubalus mindorensis	Bm	1
Cephalophus leucogaster	Cl	2
Cephalophus monticola	Cm	3
Cephalophus nigrifrons	Cn	6
Hyemoschus aquaticus	Ha	4
Tragelaphus eurycerus	Te	3
MONTANE LIGHT COVER		
Total number of specimens = 17		
Capra sibirica	Cs	3
Oreamnos americanus	Ora	2
Ovis ammon	Oa	2
Ovis canadensis	Oc	2
Ovis dalli	Od	2
Ovis vignei	Ov	3
Pseudois nayaur	Pn	1
Rupicapra rupicapra	Rr	2
MONTANE HEAVY COVER		
Total number of specimens = 25		
Budorcas taxicolor	Bt	9
Elaphodus cephalophus	Ec	4
Nemorhaedus crispus	Nc	2
Nemorhaedus goral	Ng	3
Nemorhaedus sumatraensis	Ns	4
Nemorhaedus swinhoei	Nsw	1
Pudu mephistophiles	Pm	2

Appendix D, Table B. Species breakdown of the cuneiform dataset

Species	Species code	Number	Species	Species code	Number
TOTAL = 202			**HEAVY WOODLAND-BUSHLAND**		
			Total number of specimens = 29		
GRASSLAND					
Total number of specimens = 15			Kobus defassa	Kd	4
			Madoqua kirki	Mk	2
Addax nasomaculatus	An	1	Madoqua saltiana	Ms	1
Bison bison	Bb	7	Neotragus batesi	Nb	2
Damaliscus dorcas	Dd	1	Neotragus moschatus	Nm	1
Damaliscus lunatus	Dl	2	Neotragus pygmaeus	Np	1
Ovibos moschatus	Om	3	Taurotragus derbianus	Td	2
Procapra picticaudata	Pp	1	Tragelaphus scriptus	Ts	11
			Tragelaphus speki	Tsp	1
WOODED-BUSHED GRASSLAND			Tragelaphus strepsiceros	Tst	4
Total number of specimens = 48					
			FOREST		
Alcelaphus buselaphus	Ab	4	**Total number of specimens = 29**		
Antilope cervicapra	Ac	2			
Connochaetes gnu	Cg	1	Alces alces	Aa	4
Connochaetes taurinus	Ct	4	Bos javanicus	Bj	3
Damaliscus hunteri	Dh	3	Bos sauveli	Bs	2
Gazella rufifrons	Gr	2	Bubalus mindorensis	Bm	1
Gazella soemmerringi	Gso	2	Cephalophus leucogaster	Cl	2
Gazella speki	Gs	2	Cephalophus monticola	Cm	5
Gazella subgutturosa	Gsu	2	Cephalophus nigrifrons	Cn	5
Gazella thomsoni	Gt	4	Hyemoschus aquaticus	Ha	4
Hippotragus equinus	He	2	Tragelaphus eurycerus	Te	3
Kobus kob	Kk	4			
Kobus leche	Kl	1	**MONTANE LIGHT COVER**		
Madoqua guentheri	Mg	1	**Total number of specimens = 16**		
Ourebia ourebi	Ouo	5			
Raphicerus campestris	Rc	6	Capra sibirica	Cs	3
Redunca fulvorufula	Rf	3	Oreamnos americanus	Ora	1
			Ovis ammon	Oa	2
LIGHT WOODLAND-BUSHLAND			Ovis canadensis	Oc	2
Total number of specimens = 46			Ovis dalli	Od	2
			Ovis vignei	Ov	3
Aepyceros melampus	Am	5	Pseudois nayaur	Pn	2
Gazella cuvieri	Gc	1	Rupicapra rupicapra	Rr	1
Gazella granti	Gg	4			
Hippotragus niger	Hn	5	**MONTANE HEAVY COVER**		
Litocranius walleri	Lw	4	**Total number of specimens = 19**		
Odocoileus virginianus	Odv	4			
Oreotragus oreotragus	Oo	4	Budorcas taxicolor	Bt	5
Oryx beisa	Ob	2	Elaphodus cephalophus	Ec	4
Raphicerus sharpei	Rs	3	Nemorhaedus crispus	Nc	2
Redunca redunca	Red	4	Nemorhaedus goral	Ng	1
Sylvicapra grimmia	Sg	5	Nemorhaedus sumatraensis	Ns	4
Syncerus caffer	Sc	2	Nemorhaedus swinhoei	Nsw	1
Taurotragus oryx	To	3	Pudu mephistophiles	Pm	2

Appendix D, Table C. Species breakdown of the external and middle cuneiform dataset

Species	Species code	Number	Species	Species code	Number
TOTAL = 192			**HEAVY WOODLAND-BUSHLAND**		
			Total number of specimens = 27		
GRASSLAND					
Total number of specimens = 16			Kobus defassa	Kd	1
			Madoqua kirki	Mk	4
Addax nasomaculatus	An	1	Madoqua saltiana	Ms	0
Bison bison	Bb	7	Neotragus batesi	Nb	2
Damaliscus dorcas	Dd	1	Neotragus moschatus	Nm	1
Damaliscus lunatus	Dl	2	Neotragus pygmaeus	Np	1
Ovibos moschatus	Om	3	Taurotragus derbianus	Td	2
Procapra picticaudata	Pp	2	Tragelaphus scriptus	Ts	11
			Tragelaphus speki	Tsp	1
WOODED-BUSHED GRASSLAND			Tragelaphus strepsiceros	Tst	4
Total number of specimens = 46					
			FOREST		
Alcelaphus buselaphus	Ab	4	**Total number of specimens = 25**		
Antilope cervicapra	Ac	2			
Connochaetes gnu	Cg	1	Alces alces	Aa	4
Connochaetes taurinus	Ct	4	Bos javanicus	Bj	2
Damaliscus hunteri	Dh	3	Bos sauveli	Bs	2
Gazella rufifrons	Gr	2	Bubalus mindorensis	Bm	1
Gazella soemmerringi	Gso	2	Cephalophus leucogaster	Cl	1
Gazella speki	Gs	2	Cephalophus monticola	Cm	3
Gazella subgutturosa	Gsu	2	Cephalophus nigrifrons	Cn	6
Gazella thomsoni	Gt	4	Hyemoschus aquaticus	Ha	4
Hippotragus equinus	He	2	Tragelaphus euryceros	Te	2
Kobus kob	Kk	3			
Kobus leche	Kl	0	**MONTANE LIGHT COVER**		
Madoqua guentheri	Mg	1	**Total number of specimens = 17**		
Ourebia ourebi	Ouo	5			
Raphicerus campestris	Rc	6	Capra sibirica	Cs	3
Redunca fulvorufula	Rf	3	Oreamnos americanus	Ora	2
			Ovis ammon	Oa	2
LIGHT WOODLAND-BUSHLAND			Ovis canadensis	Oc	2
Total number of specimens = 43			Ovis dalli	Od	2
			Ovis vignei	Ov	3
Aepyceros melampus	Am	7	Pseudois nayaur	Pn	1
Gazella cuvieri	Gc	2	Rupicapra rupicapra	Rr	2
Gazella granti	Gg	4			
Hippotragus niger	Hn	5	**MONTANE HEAVY COVER**		
Litocranius walleri	Lw	5	**Total number of specimens = 18**		
Odocoileus virginianus	Odv	4			
Oreotragus oreotragus	Oo	4	Budorcas taxicolor	Bt	7
Oryx beisa	Ob	2	Elaphodus cephalophus	Ec	4
Raphicerus sharpei	Rs	2	Nemorhaedus crispus	Nc	2
Redunca redunca	Red	3	Nemorhaedus goral	Ng	2
Sylvicapra grimmia	Sg	2	Nemorhaedus sumatraensis	Ns	0
Syncerus caffer	Sc	0	Nemorhaedus swinhoei	Nsw	1
Taurotragus oryx	To	3	Pudu mephistophiles	Pm	2

Appendix D, Table D. Species breakdown of the femur dataset

Species	Species code	Number
TOTAL = 207		
GRASSLAND		
Total number of specimens = 17		
Addax nasomaculatus	An	1
Bison bison	Bb	7
Damaliscus dorcas	Dd	1
Damaliscus lunatus	Dl	2
Ovibos moschatus	Om	4
Procapra picticaudata	Pp	2
WOODED-BUSHED GRASSLAND		
Total number of specimens = 46		
Alcelaphus buselaphus	Ab	4
Antilope cervicapra	Ac	2
Connochaetes gnu	Cg	1
Connochaetes taurinus	Ct	4
Damaliscus hunteri	Dh	3
Gazella rufifrons	Gr	2
Gazella soemmerringi	Gso	0
Gazella speki	Gs	2
Gazella subgutturosa	Gsu	2
Gazella thomsoni	Gt	3
Hippotragus equinus	He	2
Kobus kob	Kk	5
Kobus leche	Kl	1
Madoqua guentheri	Mg	1
Ourebia ourebi	Ouo	5
Raphicerus campestris	Rc	6
Redunca fulvorufula	Rf	3
LIGHT WOODLAND-BUSHLAND		
Total number of specimens = 51		
Aepyceros melampus	Am	7
Gazella cuvieri	Gc	2
Gazella granti	Gg	4
Hippotragus niger	Hn	5
Litocranius walleri	Lw	5
Odocoileus virginianus	Odv	4
Oreotragus oreotragus	Oo	4
Oryx beisa	Ob	2
Raphicerus sharpei	Rs	3
Redunca redunca	Red	3
Sylvicapra grimmia	Sg	6
Syncerus caffer	Sc	3
Taurotragus oryx	To	3
HEAVY WOODLAND-BUSHLAND		
Total number of specimens = 32		
Kobus defassa	Kd	5
Madoqua kirki	Mk	4
Madoqua saltiana	Ms	1
Neotragus batesi	Nb	2
Neotragus moschatus	Nm	1
Neotragus pygmaeus	Np	1
Taurotragus derbianus	Td	2
Tragelaphus scriptus	Ts	11
Tragelaphus speki	Tsp	1
Tragelaphus strepsiceros	Tst	4
FOREST		
Total number of specimens = 30		
Alces alces	Aa	3
Bos javanicus	Bj	3
Bos sauveli	Bs	2
Bubalus mindorensis	Bm	1
Cephalophus leucogaster	Cl	2
Cephalophus monticola	Cm	5
Cephalophus nigrifrons	Cn	6
Hyemoschus aquaticus	Ha	5
Tragelaphus eurycerus	Te	3
MONTANE LIGHT COVER		
Total number of specimens = 14		
Capra sibirica	Cs	2
Oreamnos americanus	Ora	1
Ovis ammon	Oa	1
Ovis canadensis	Oc	2
Ovis dalli	Od	2
Ovis vignei	Ov	3
Pseudois nayaur	Pn	1
Rupicapra rupicapra	Rr	2
MONTANE HEAVY COVER		
Total number of specimens = 17		
Budorcas taxicolor	Bt	1
Elaphodus cephalophus	Ec	4
Nemorhaedus crispus	Nc	2
Nemorhaedus goral	Ng	3
Nemorhaedus sumatraensis	Ns	4
Nemorhaedus swinhoei	Nsw	1
Pudu mephistophiles	Pm	2

Appendix D, Table E. Species breakdown of the distal femur dataset

Species	Species code	Number	Species	Species code	Number
TOTAL = 210			**HEAVY WOODLAND-BUSHLAND**		
			Total number of specimens = 32		
GRASSLAND					
Total number of specimens = 17			Kobus defassa	Kd	5
			Madoqua kirki	Mk	4
Addax nasomaculatus	An	1	Madoqua saltiana	Ms	1
Bison bison	Bb	7	Neotragus batesi	Nb	2
Damaliscus dorcas	Dd	1	Neotragus moschatus	Nm	1
Damaliscus lunatus	Dl	2	Neotragus pygmaeus	Np	1
Ovibos moschatus	Om	4	Taurotragus derbianus	Td	2
Procapra picticaudata	Pp	2	Tragelaphus scriptus	Ts	11
			Tragelaphus speki	Tsp	1
WOODED-BUSHED GRASSLAND			Tragelaphus strepsiceros	Tst	4
Total number of specimens = 46					
			FOREST		
Alcelaphus buselaphus	Ab	4	**Total number of specimens = 30**		
Antilope cervicapra	Ac	2			
Connochaetes gnu	Cg	1	Alces alces	Aa	3
Connochaetes taurinus	Ct	4	Bos javanicus	Bj	3
Damaliscus hunteri	Dh	3	Bos sauveli	Bs	2
Gazella rufifrons	Gr	2	Bubalus mindorensis	Bm	1
Gazella soemmerringi	Gso	0	Cephalophus leucogaster	Cl	2
Gazella speki	Gs	2	Cephalophus monticola	Cm	5
Gazella subgutturosa	Gsu	2	Cephalophus nigrifrons	Cn	6
Gazella thomsoni	Gt	3	Hyemoschus aquaticus	Ha	5
Hippotragus equinus	He	2	Tragelaphus eurycerus	Te	3
Kobus kob	Kk	5			
Kobus leche	Kl	1	**MONTANE LIGHT COVER**		
Madoqua guentheri	Mg	1	**Total number of specimens = 16**		
Ourebia ourebi	Ouo	5			
Raphicerus campestris	Rc	6	Capra sibirica	Cs	3
Redunca fulvorufula	Rf	3	Oreamnos americanus	Ora	1
			Ovis ammon	Oa	2
LIGHT WOODLAND-BUSHLAND			Ovis canadensis	Oc	2
Total number of specimens = 52			Ovis dalli	Od	2
			Ovis vignei	Ov	3
Aepyceros melampus	Am	7	Pseudois nayaur	Pn	1
Gazella cuvieri	Gc	2	Rupicapra rupicapra	Rr	2
Gazella granti	Gg	4			
Hippotragus niger	Hn	5	**MONTANE HEAVY COVER**		
Litocranius walleri	Lw	5	**Total number of specimens = 17**		
Odocoileus virginianus	Odv	4			
Oreotragus oreotragus	Oo	4	Budorcas taxicolor	Bt	1
Oryx beisa	Ob	2	Elaphodus cephalophus	Ec	4
Raphicerus sharpei	Rs	3	Nemorhaedus crispus	Nc	2
Redunca redunca	Red	4	Nemorhaedus goral	Ng	3
Sylvicapra grimmia	Sg	6	Nemorhaedus sumatraensis	Ns	4
Syncerus caffer	Sc	3	Nemorhaedus swinhoei	Nsw	1
Taurotragus oryx	To	3	Pudu mephistophiles	Pm	2

Appendix D, Table F. Species breakdown of the proximal humerus dataset

Species	Species code	Number	Species	Species code	Number
TOTAL = 209			**HEAVY WOODLAND-BUSHLAND**		
			Total number of specimens = 32		
GRASSLAND					
Total number of specimens = 17			Kobus defassa	Kd	5
			Madoqua kirki	Mk	4
Addax nasomaculatus	An	1	Madoqua saltiana	Ms	1
Bison bison	Bb	7	Neotragus batesi	Nb	2
Damaliscus dorcas	Dd	1	Neotragus moschatus	Nm	1
Damaliscus lunatus	Dl	2	Neotragus pygmaeus	Np	1
Ovibos moschatus	Om	4	Taurotragus derbianus	Td	2
Procapra picticaudata	Pp	2	Tragelaphus scriptus	Ts	11
			Tragelaphus speki	Tsp	1
WOODED-BUSHED GRASSLAND			Tragelaphus strepsiceros	Tst	4
Total number of specimens = 46					
			FOREST		
Alcelaphus buselaphus	Ab	4	**Total number of specimens = 30**		
Antilope cervicapra	Ac	2			
Connochaetes gnu	Cg	1	Alces alces	Aa	3
Connochaetes taurinus	Ct	4	Bos javanicus	Bj	3
Damaliscus hunteri	Dh	3	Bos sauveli	Bs	2
Gazella rufifrons	Gr	2	Bubalus mindorensis	Bm	1
Gazella soemmerringi	Gso	0	Cephalophus leucogaster	Cl	2
Gazella speki	Gs	2	Cephalophus monticola	Cm	5
Gazella subgutturosa	Gsu	2	Cephalophus nigrifrons	Cn	6
Gazella thomsoni	Gt	3	Hyemoschus aquaticus	Ha	5
Hippotragus equinus	He	2	Tragelaphus eurycerus	Te	3
Kobus kob	Kk	5			
Kobus leche	Kl	1	**MONTANE LIGHT COVER**		
Madoqua guentheri	Mg	1	**Total number of specimens = 15**		
Ourebia ourebi	Ouo	5			
Raphicerus campestris	Rc	6	Capra sibirica	Cs	2
Redunca fulvorufula	Rf	3	Oreamnos americanus	Ora	1
			Ovis ammon	Oa	2
LIGHT WOODLAND-BUSHLAND			Ovis canadensis	Oc	2
Total number of specimens = 52			Ovis dalli	Od	2
			Ovis vignei	Ov	3
Aepyceros melampus	Am	7	Pseudois nayaur	Pn	1
Gazella cuvieri	Gc	2	Rupicapra rupicapra	Rr	2
Gazella granti	Gg	4			
Hippotragus niger	Hn	5	**MONTANE HEAVY COVER**		
Litocranius walleri	Lw	5	**Total number of specimens = 17**		
Odocoileus virginianus	Odv	4			
Oreotragus oreotragus	Oo	4	Budorcas taxicolor	Bt	1
Oryx beisa	Ob	2	Elaphodus cephalophus	Ec	4
Raphicerus sharpei	Rs	3	Nemorhaedus crispus	Nc	2
Redunca redunca	Red	4	Nemorhaedus goral	Ng	3
Sylvicapra grimmia	Sg	6	Nemorhaedus sumatraensis	Ns	4
Syncerus caffer	Sc	3	Nemorhaedus swinhoei	Nsw	1
Taurotragus oryx	To	3	Pudu mephistophiles	Pm	2

Appendix D, Table G. Species breakdown of the humerus dataset

Species	Species code	Number
TOTAL = 203		
GRASSLAND		
Total number of specimens = 17		
Addax nasomaculatus	An	1
Bison bison	Bb	7
Damaliscus dorcas	Dd	1
Damaliscus lunatus	Dl	2
Ovibos moschatus	Om	4
Procapra picticaudata	Pp	2
WOODED-BUSHED GRASSLAND		
Total number of specimens = 43		
Alcelaphus buselaphus	Ab	4
Antilope cervicapra	Ac	2
Connochaetes gnu	Cg	1
Connochaetes taurinus	Ct	4
Damaliscus hunteri	Dh	3
Gazella rufifrons	Gr	2
Gazella soemmerringi	Gso	0
Gazella speki	Gs	2
Gazella subgutturosa	Gsu	1
Gazella thomsoni	Gt	3
Hippotragus equinus	He	2
Kobus kob	Kk	3
Kobus leche	Kl	1
Madoqua guentheri	Mg	1
Ourebia ourebi	Ouo	5
Raphicerus campestris	Rc	6
Redunca fulvorufula	Rf	3
LIGHT WOODLAND-BUSHLAND		
Total number of specimens = 51		
Aepyceros melampus	Am	7
Gazella cuvieri	Gc	2
Gazella granti	Gg	4
Hippotragus niger	Hn	5
Litocranius walleri	Lw	5
Odocoileus virginianus	Odv	4
Oreotragus oreotragus	Oo	3
Oryx beisa	Ob	2
Raphicerus sharpei	Rs	3
Redunca redunca	Red	4
Sylvicapra grimmia	Sg	6
Syncerus caffer	Sc	3
Taurotragus oryx	To	3
HEAVY WOODLAND-BUSHLAND		
Total number of specimens = 31		
Kobus defassa	Kd	5
Madoqua kirki	Mk	3
Madoqua saltiana	Ms	1
Neotragus batesi	Nb	2
Neotragus moschatus	Nm	1
Neotragus pygmaeus	Np	1
Taurotragus derbianus	Td	2
Tragelaphus scriptus	Ts	11
Tragelaphus speki	Tsp	1
Tragelaphus strepsiceros	Tst	4
FOREST		
Total number of specimens = 30		
Alces alces	Aa	3
Bos javanicus	Bj	3
Bos sauveli	Bs	2
Bubalus mindorensis	Bm	1
Cephalophus leucogaster	Cl	2
Cephalophus monticola	Cm	5
Cephalophus nigrifrons	Cn	6
Hyemoschus aquaticus	Ha	5
Tragelaphus eurycerus	Te	3
MONTANE LIGHT COVER		
Total number of specimens = 15		
Capra sibirica	Cs	3
Oreamnos americanus	Ora	1
Ovis ammon	Oa	2
Ovis canadensis	Oc	2
Ovis dalli	Od	2
Ovis vignei	Ov	2
Pseudois nayaur	Pn	1
Rupicapra rupicapra	Rr	2
MONTANE HEAVY COVER		
Total number of specimens = 16		
Budorcas taxicolor	Bt	1
Elaphodus cephalophus	Ec	4
Nemorhaedus crispus	Nc	2
Nemorhaedus goral	Ng	2
Nemorhaedus sumatraensis	Ns	4
Nemorhaedus swinhoei	Nsw	1
Pudu mephistophiles	Pm	2

Appendix D, Table H. Species breakdown of the distal humerus dataset

Species	Species code	Number	Species	Species code	Number
TOTAL = 203			**HEAVY WOODLAND-BUSHLAND**		
			Total number of specimens = 31		
GRASSLAND					
Total number of specimens = 17			Kobus defassa	Kd	5
			Madoqua kirki	Mk	3
Addax nasomaculatus	An	1	Madoqua saltiana	Ms	1
Bison bison	Bb	7	Neotragus batesi	Nb	2
Damaliscus dorcas	Dd	1	Neotragus moschatus	Nm	1
Damaliscus lunatus	Dl	2	Neotragus pygmaeus	Np	1
Ovibos moschatus	Om	4	Taurotragus derbianus	Td	2
Procapra picticaudata	Pp	2	Tragelaphus scriptus	Ts	11
			Tragelaphus speki	Tsp	1
WOODED-BUSHED GRASSLAND			Tragelaphus strepsiceros	Tst	4
Total number of specimens = 43					
			FOREST		
Alcelaphus buselaphus	Ab	4	**Total number of specimens = 30**		
Antilope cervicapra	Ac	2			
Connochaetes gnu	Cg	1	Alces alces	Aa	3
Connochaetes taurinus	Ct	4	Bos javanicus	Bj	3
Damaliscus hunteri	Dh	3	Bos sauveli	Bs	2
Gazella rufifrons	Gr	2	Bubalus mindorensis	Bm	1
Gazella soemmerringi	Gso	0	Cephalophus leucogaster	Cl	2
Gazella speki	Gs	2	Cephalophus monticola	Cm	5
Gazella subgutturosa	Gsu	1	Cephalophus nigrifrons	Cn	6
Gazella thomsoni	Gt	3	Hyemoschus aquaticus	Ha	5
Hippotragus equinus	He	2	Tragelaphus eurycerus	Te	3
Kobus kob	Kk	3			
Kobus leche	Kl	1	**MONTANE LIGHT COVER**		
Madoqua guentheri	Mg	1	**Total number of specimens = 15**		
Ourebia ourebi	Ouo	5			
Raphicerus campestris	Rc	6	Capra sibirica	Cs	3
Redunca fulvorufula	Rf	3	Oreamnos americanus	Ora	1
			Ovis ammon	Oa	2
LIGHT WOODLAND-BUSHLAND			Ovis canadensis	Oc	2
Total number of specimens = 51			Ovis dalli	Od	2
			Ovis vignei	Ov	2
Aepyceros melampus	Am	7	Pseudois nayaur	Pn	1
Gazella cuvieri	Gc	2	Rupicapra rupicapra	Rr	2
Gazella granti	Gg	4			
Hippotragus niger	Hn	5	**MONTANE HEAVY COVER**		
Litocranius walleri	Lw	5	**Total number of specimens = 16**		
Odocoileus virginianus	Odv	4			
Oreotragus oreotragus	Oo	3	Budorcas taxicolor	Bt	1
Oryx beisa	Ob	2	Elaphodus cephalophus	Ec	4
Raphicerus sharpei	Rs	3	Nemorhaedus crispus	Nc	2
Redunca redunca	Rcd	4	Nemorhaedus goral	Ng	2
Sylvicapra grimmia	Sg	6	Nemorhaedus sumatraensis	Ns	4
Syncerus caffer	Sc	3	Nemorhaedus swinhoei	Nsw	1
Taurotragus oryx	To	3	Pudu mephistophiles	Pm	2

Appendix D, Table I. Species breakdown of the proximal humerus dataset

Species	Species code	Number
TOTAL = 203		
GRASSLAND		
Total number of specimens = 17		
Addax nasomaculatus	An	1
Bison bison	Bb	7
Damaliscus dorcas	Dd	1
Damaliscus lunatus	Dl	2
Ovibos moschatus	Om	4
Procapra picticaudata	Pp	2
WOODED-BUSHED GRASSLAND		
Total number of specimens = 43		
Alcelaphus buselaphus	Ab	4
Antilope cervicapra	Ac	2
Connochaetes gnu	Cg	1
Connochaetes taurinus	Ct	4
Damaliscus hunteri	Dh	3
Gazella rufifrons	Gr	2
Gazella soemmerringi	Gso	0
Gazella speki	Gs	2
Gazella subgutturosa	Gsu	1
Gazella thomsoni	Gt	3
Hippotragus equinus	He	2
Kobus kob	Kk	3
Kobus leche	Kl	1
Madoqua guentheri	Mg	1
Ourebia ourebi	Ouo	5
Raphicerus campestris	Rc	6
Redunca fulvorufula	Rf	3
LIGHT WOODLAND-BUSHLAND		
Total number of specimens = 51		
Aepyceros melampus	Am	7
Gazella cuvieri	Gc	2
Gazella granti	Gg	4
Hippotragus niger	Hn	5
Litocranius walleri	Lw	5
Odocoileus virginianus	Odv	4
Oreotragus oreotragus	Oo	3
Oryx beisa	Ob	2
Raphicerus sharpei	Rs	3
Redunca redunca	Red	4
Sylvicapra grimmia	Sg	6
Syncerus caffer	Sc	3
Taurotragus oryx	To	3
HEAVY WOODLAND-BUSHLAND		
Total number of specimens = 31		
Kobus defassa	Kd	5
Madoqua kirki	Mk	3
Madoqua saltiana	Ms	1
Neotragus batesi	Nb	2
Neotragus moschatus	Nm	1
Neotragus pygmaeus	Np	1
Taurotragus derbianus	Td	2
Tragelaphus scriptus	Ts	11
Tragelaphus speki	Tsp	1
Tragelaphus strepsiceros	Tst	4
FOREST		
Total number of specimens = 30		
Alces alces	Aa	3
Bos javanicus	Bj	3
Bos sauveli	Bs	2
Bubalus mindorensis	Bm	1
Cephalophus leucogaster	Cl	2
Cephalophus monticola	Cm	5
Cephalophus nigrifrons	Cn	6
Hyemoschus aquaticus	Ha	5
Tragelaphus eurycerus	Te	3
MONTANE LIGHT COVER		
Total number of specimens = 15		
Capra sibirica	Cs	3
Oreamnos americanus	Ora	1
Ovis ammon	Oa	2
Ovis canadensis	Oc	2
Ovis dalli	Od	2
Ovis vignei	Ov	2
Pseudois nayaur	Pn	1
Rupicapra rupicapra	Rr	2
MONTANE HEAVY COVER		
Total number of specimens = 16		
Budorcas taxicolor	Bt	1
Elaphodus cephalophus	Ec	4
Nemorhaedus crispus	Nc	2
Nemorhaedus goral	Ng	2
Nemorhaedus sumatraensis	Ns	4
Nemorhaedus swinhoei	Nsw	1
Pudu mephistophiles	Pm	2

Appendix D, Table J. Species breakdown of the lunar dataset

TOTAL = 203

GRASSLAND
Total number of specimens = 16

Species	Species code	Number
Addax nasomaculatus	An	1
Bison bison	Bb	7
Damaliscus dorcas	Dd	1
Damaliscus lunatus	Dl	2
Ovibos moschatus	Om	4
Procapra picticaudata	Pp	1

WOODED-BUSHED GRASSLAND
Total number of specimens = 48

Species	Species code	Number
Alcelaphus buselaphus	Ab	4
Antilope cervicapra	Ac	2
Connochaetes gnu	Cg	1
Connochaetes taurinus	Ct	4
Damaliscus hunteri	Dh	3
Gazella rufifrons	Gr	2
Gazella soemmerringi	Gso	2
Gazella speki	Gs	2
Gazella subgutturosa	Gsu	2
Gazella thomsoni	Gt	4
Hippotragus equinus	He	2
Kobus kob	Kk	4
Kobus leche	Kl	1
Madoqua guentheri	Mg	1
Ourebia ourebi	Ouo	5
Raphicerus campestris	Rc	6
Redunca fulvorufula	Rf	3

LIGHT WOODLAND-BUSHLAND
Total number of specimens = 47

Species	Species code	Number
Aepyceros melampus	Am	5
Gazella cuvieri	Gc	1
Gazella granti	Gg	4
Hippotragus niger	Hn	5
Litocranius walleri	Lw	4
Odocoileus virginianus	Odv	4
Oreotragus oreotragus	Oo	4
Oryx beisa	Ob	2
Raphicerus sharpei	Rs	3
Redunca redunca	Red	4
Sylvicapra grimmia	Sg	5
Syncerus caffer	Sc	3
Taurotragus oryx	To	3

HEAVY WOODLAND-BUSHLAND
Total number of specimens = 30

Species	Species code	Number
Kobus defassa	Kd	5
Madoqua kirki	Mk	2
Madoqua saltiana	Ms	1
Neotragus batesi	Nb	2
Neotragus moschatus	Nm	1
Neotragus pygmaeus	Np	1
Taurotragus derbianus	Td	2
Tragelaphus scriptus	Ts	11
Tragelaphus speki	Tsp	1
Tragelaphus strepsiceros	Tst	4

FOREST
Total number of specimens = 28

Species	Species code	Number
Alces alces	Aa	4
Bos javanicus	Bj	3
Bos sauveli	Bs	2
Bubalus mindorensis	Bm	1
Cephalophus leucogaster	Cl	2
Cephalophus monticola	Cm	5
Cephalophus nigrifrons	Cn	4
Hyemoschus aquaticus	Ha	4
Tragelaphus eurycerus	Te	3

MONTANE LIGHT COVER
Total number of specimens = 16

Species	Species code	Number
Capra sibirica	Cs	3
Oreamnos americanus	Ora	1
Ovis ammon	Oa	2
Ovis canadensis	Oc	2
Ovis dalli	Od	2
Ovis vignei	Ov	3
Pseudois nayaur	Pn	2
Rupicapra rupicapra	Rr	1

MONTANE HEAVY COVER
Total number of specimens = 18

Species	Species code	Number
Budorcas taxicolor	Bt	5
Elaphodus cephalophus	Ec	4
Nemorhaedus crispus	Nc	2
Nemorhaedus goral	Ng	0
Nemorhaedus sumatraensis	Ns	4
Nemorhaedus swinhoei	Nsw	1
Pudu mephistophiles	Pm	2

Appendix D, Table K. Species breakdown of the magnum dataset

Species	Species code	Number
TOTAL = 209		
GRASSLAND		
Total number of specimens = 15		
Addax nasomaculatus	An	1
Bison bison	Bb	7
Damaliscus dorcas	Dd	1
Damaliscus lunatus	Dl	2
Ovibos moschatus	Om	4
Procapra picticaudata	Pp	0
WOODED-BUSHED GRASSLAND		
Total number of specimens = 47		
Alcelaphus buselaphus	Ab	4
Antilope cervicapra	Ac	2
Connochaetes gnu	Cg	1
Connochaetes taurinus	Ct	4
Damaliscus hunteri	Dh	3
Gazella rufifrons	Gr	2
Gazella soemmerringi	Gso	2
Gazella speki	Gs	2
Gazella subgutturosa	Gsu	2
Gazella thomsoni	Gt	4
Hippotragus equinus	He	2
Kobus kob	Kk	4
Kobus leche	Kl	1
Madoqua guentheri	Mg	0
Ourebia ourebi	Ouo	5
Raphicerus campestris	Rc	6
Redunca fulvorufula	Rf	3
LIGHT WOODLAND-BUSHLAND		
Total number of specimens = 51		
Aepyceros melampus	Am	7
Gazella cuvieri	Gc	2
Gazella granti	Gg	4
Hippotragus niger	Hn	5
Litocranius walleri	Lw	5
Odocoileus virginianus	Odv	4
Oreotragus oreotragus	Oo	4
Oryx beisa	Ob	2
Raphicerus sharpei	Rs	3
Redunca redunca	Rcd	4
Sylvicapra grimmia	Sg	5
Syncerus caffer	Sc	3
Taurotragus oryx	To	3
HEAVY WOODLAND-BUSHLAND		
Total number of specimens = 29		
Kobus defassa	Kd	4
Madoqua kirki	Mk	2
Madoqua saltiana	Ms	1
Neotragus batesi	Nb	2
Neotragus moschatus	Nm	1
Neotragus pygmaeus	Np	1
Taurotragus derbianus	Td	2
Tragelaphus scriptus	Ts	11
Tragelaphus speki	Tsp	1
Tragelaphus strepsiceros	Tst	4
FOREST		
Total number of specimens = 30		
Alces alces	Aa	4
Bos javanicus	Bj	3
Bos sauveli	Bs	2
Bubalus mindorensis	Bm	1
Cephalophus leucogaster	Cl	2
Cephalophus monticola	Cm	5
Cephalophus nigrifrons	Cn	6
Hyemoschus aquaticus	Ha	4
Tragelaphus eurycerus	Te	3
MONTANE LIGHT COVER		
Total number of specimens = 16		
Capra sibirica	Cs	3
Oreamnos americanus	Ora	1
Ovis ammon	Oa	2
Ovis canadensis	Oc	2
Ovis dalli	Od	2
Ovis vignei	Ov	3
Pseudois nayaur	Pn	2
Rupicapra rupicapra	Rr	1
MONTANE HEAVY COVER		
Total number of specimens = 21		
Budorcas taxicolor	Bt	6
Elaphodus cephalophus	Ec	4
Nemorhaedus crispus	Nc	2
Nemorhaedus goral	Ng	2
Nemorhaedus sumatraensis	Ns	4
Nemorhaedus swinhoei	Nsw	1
Pudu mephistophiles	Pm	2

Appendix D, Table L. Species breakdown of the metacarpal dataset

Species	Species code	Number	Species	Species code	Number
TOTAL = 211 logged; 210 size corrected			**HEAVY WOODLAND-BUSHLAND**		
			Total number of specimens = 27		
GRASSLAND					
Total number of specimens = 15			Kobus defassa	Kd	5
			Madoqua kirki	Mk	3
Addax nasomaculatus	An	1	Madoqua saltiana	Ms	1
Bison bison	Bb	7	Neotragus batesi	Nb	2
Damaliscus dorcas	Dd	1	Neotragus moschatus	Nm	0
Damaliscus lunatus	Dl	2	Neotragus pygmaeus	Np	0
Ovibos moschatus	Om	4	Taurotragus derbianus	Td	2
Procapra picticaudata	Pp	0	Tragelaphus scriptus	Ts	10
			Tragelaphus speki	Tsp	1
WOODED-BUSHED GRASSLAND			Tragelaphus strepsiceros	Tst	3
Total number of specimens = 46					
			FOREST		
Alcelaphus buselaphus	Ab	4	**Total number of specimens = 31**		
Antilope cervicapra	Ac	2			
Connochaetes gnu	Cg	1	Alces alces	Aa	4
Connochaetes taurinus	Ct	4	Bos javanicus	Bj	3
Damaliscus hunteri	Dh	3	Bos sauveli	Bs	2
Gazella rufifrons	Gr	2	Bubalus mindorensis	Bm	1
Gazella soemmerringi	Gso	2	Cephalophus leucogaster	Cl	2
Gazella speki	Gs	1	Cephalophus monticola	Cm	5
Gazella subgutturosa	Gsu	2	Cephalophus nigrifrons	Cn	6
Gazella thomsoni	Gt	4	Hyemoschus aquaticus	Ha	5
Hippotragus equinus	He	2	Tragelaphus eurycerus	Te	3
Kobus kob	Kk	4			
Kobus leche	Kl	1	**MONTANE LIGHT COVER**		
Madoqua guentheri	Mg	0	**Total number of specimens = 16/15**		
Ourebia ourebi	Ouo	5			
Raphicerus campestris	Rc	6	Capra sibirica	Cs	3/2
Redunca fulvorufula	Rf	3	Oreamnos americanus	Ora	1
			Ovis ammon	Oa	2
LIGHT WOODLAND-BUSHLAND			Ovis canadensis	Oc	2
Total number of specimens = 51			Ovis dalli	Od	2
			Ovis vignei	Ov	2
Aepyceros melampus	Am	7	Pseudois nayaur	Pn	2
Gazella cuvieri	Gc	2	Rupicapra rupicapra	Rr	2
Gazella granti	Gg	4			
Hippotragus niger	Hn	5	**MONTANE HEAVY COVER**		
Litocranius walleri	Lw	5	**Total number of specimens = 25**		
Odocoileus virginianus	Odv	4			
Oreotragus oreotragus	Oo	4	Budorcas taxicolor	Bt	9
Oryx beisa	Ob	2	Elaphodus cephalophus	Ec	4
Raphicerus sharpei	Rs	3	Nemorhaedus crispus	Nc	2
Redunca redunca	Rcd	4	Nemorhaedus goral	Ng	3
Sylvicapra grimmia	Sg	5	Nemorhaedus sumatraensis	Ns	4
Syncerus caffer	Sc	3	Nemorhaedus swinhoei	Nsw	1
Taurotragus oryx	To	3	Pudu mephistophiles	Pm	2

Appendix D, Table M. Species breakdown of the distal metacarpal dataset

Species	Species code	Number
TOTAL = 211		
GRASSLAND		
Total number of specimens = 15		
Addax nasomaculatus	An	1
Bison bison	Bb	7
Damaliscus dorcas	Dd	1
Damaliscus lunatus	Dl	2
Ovibos moschatus	Om	4
Procapra picticaudata	Pp	0
WOODED-BUSHED GRASSLAND		
Total number of specimens = 46		
Alcelaphus buselaphus	Ab	4
Antilope cervicapra	Ac	2
Connochaetes gnu	Cg	1
Connochaetes taurinus	Ct	4
Damaliscus hunteri	Dh	3
Gazella rufifrons	Gr	2
Gazella soemmerringi	Gso	2
Gazella speki	Gs	1
Gazella subgutturosa	Gsu	2
Gazella thomsoni	Gt	4
Hippotragus equinus	He	2
Kobus kob	Kk	4
Kobus leche	Kl	1
Madoqua guentheri	Mg	0
Ourebia ourebi	Ouo	5
Raphicerus campestris	Rc	6
Redunca fulvorufula	Rf	3
LIGHT WOODLAND-BUSHLAND		
Total number of specimens = 51		
Aepyceros melampus	Am	7
Gazella cuvieri	Gc	2
Gazella granti	Gg	4
Hippotragus niger	Hn	5
Litocranius walleri	Lw	5
Odocoileus virginianus	Odv	4
Oreotragus oreotragus	Oo	4
Oryx beisa	Ob	2
Raphicerus sharpei	Rs	3
Redunca redunca	Rcd	4
Sylvicapra grimmia	Sg	5
Syncerus caffer	Sc	3
Taurotragus oryx	To	3
HEAVY WOODLAND-BUSHLAND		
Total number of specimens = 27		
Kobus defassa	Kd	5
Madoqua kirki	Mk	3
Madoqua saltiana	Ms	1
Neotragus batesi	Nb	2
Neotragus moschatus	Nm	0
Neotragus pygmaeus	Np	0
Taurotragus derbianus	Td	2
Tragelaphus scriptus	Ts	10
Tragelaphus speki	Tsp	1
Tragelaphus strepsiceros	Tst	3
FOREST		
Total number of specimens = 31		
Alces alces	Aa	4
Bos javanicus	Bj	3
Bos sauveli	Bs	2
Bubalus mindorensis	Bm	1
Cephalophus leucogaster	Cl	2
Cephalophus monticola	Cm	5
Cephalophus nigrifrons	Cn	6
Hyemoschus aquaticus	Ha	5
Tragelaphus eurycerus	Te	3
MONTANE LIGHT COVER		
Total number of specimens = 16		
Capra sibirica	Cs	3
Oreamnos americanus	Ora	1
Ovis ammon	Oa	2
Ovis canadensis	Oc	2
Ovis dalli	Od	2
Ovis vignei	Ov	2
Pseudois nayaur	Pn	2
Rupicapra rupicapra	Rr	2
MONTANE HEAVY COVER		
Total number of specimens = 25		
Budorcas taxicolor	Bt	9
Elaphodus cephalophus	Ec	4
Nemorhaedus crispus	Nc	2
Nemorhaedus goral	Ng	3
Nemorhaedus sumatraensis	Ns	4
Nemorhaedus swinhoei	Nsw	1
Pudu mephistophiles	Pm	2

Appendix D, Table N. Species breakdown of the proximal metacarpal dataset

Species	Species code	Number
TOTAL = 211		
GRASSLAND		
Total number of specimens = 15		
Addax nasomaculatus	An	1
Bison bison	Bb	7
Damaliscus dorcas	Dd	1
Damaliscus lunatus	Dl	2
Ovibos moschatus	Om	4
Procapra picticaudata	Pp	0
WOODED-BUSHED GRASSLAND		
Total number of specimens = 46		
Alcelaphus buselaphus	Ab	4
Antilope cervicapra	Ac	2
Connochaetes gnu	Cg	1
Connochaetes taurinus	Ct	4
Damaliscus hunteri	Dh	3
Gazella rufifrons	Gr	2
Gazella soemmerringi	Gso	2
Gazella speki	Gs	1
Gazella subgutturosa	Gsu	2
Gazella thomsoni	Gt	4
Hippotragus equinus	He	2
Kobus kob	Kk	4
Kobus leche	Kl	1
Madoqua guentheri	Mg	0
Ourebia ourebi	Ouo	5
Raphicerus campestris	Rc	6
Redunca fulvorufula	Rf	3
LIGHT WOODLAND-BUSHLAND		
Total number of specimens = 51		
Aepyceros melampus	Am	7
Gazella cuvieri	Gc	2
Gazella granti	Gg	4
Hippotragus niger	Hn	5
Litocranius walleri	Lw	5
Odocoileus virginianus	Odv	4
Oreotragus oreotragus	Oo	4
Oryx beisa	Ob	2
Raphicerus sharpei	Rs	3
Redunca redunca	Rcd	4
Sylvicapra grimmia	Sg	5
Syncerus caffer	Sc	3
Taurotragus oryx	To	3
HEAVY WOODLAND-BUSHLAND		
Total number of specimens = 27		
Kobus defassa	Kd	5
Madoqua kirki	Mk	3
Madoqua saltiana	Ms	1
Neotragus batesi	Nb	2
Neotragus moschatus	Nm	0
Neotragus pygmaeus	Np	0
Taurotragus derbianus	Td	2
Tragelaphus scriptus	Ts	10
Tragelaphus speki	Tsp	1
Tragelaphus strepsiceros	Tst	3
FOREST		
Total number of specimens = 31		
Alces alces	Aa	4
Bos javanicus	Bj	3
Bos sauveli	Bs	2
Bubalus mindorensis	Bm	1
Cephalophus leucogaster	Cl	2
Cephalophus monticola	Cm	5
Cephalophus nigrifrons	Cn	6
Hyemoschus aquaticus	Ha	5
Tragelaphus euryceros	Te	3
MONTANE LIGHT COVER		
Total number of specimens = 16		
Capra sibirica	Cs	3
Oreamnos americanus	Ora	1
Ovis ammon	Oa	2
Ovis canadensis	Oc	2
Ovis dalli	Od	2
Ovis vignei	Ov	2
Pseudois nayaur	Pn	2
Rupicapra rupicapra	Rr	2
MONTANE HEAVY COVER		
Total number of specimens = 25		
Budorcas taxicolor	Bt	9
Elaphodus cephalophus	Ec	4
Nemorhaedus crispus	Nc	2
Nemorhaedus goral	Ng	3
Nemorhaedus sumatraensis	Ns	4
Nemorhaedus swinhoei	Nsw	1
Pudu mephistophiles	Pm	2

Appendix D, Table O. Species breakdown of the metatarsal dataset

TOTAL = 215

GRASSLAND
Total number of specimens = 15

Species	Species code	Number
Addax nasomaculatus	An	1
Bison bison	Bb	7
Damaliscus dorcas	Dd	1
Damaliscus lunatus	Dl	2
Ovibos moschatus	Om	4
Procapra picticaudata	Pp	0

WOODED-BUSHED GRASSLAND
Total number of specimens = 46

Species	Species code	Number
Alcelaphus buselaphus	Ab	4
Antilope cervicapra	Ac	2
Connochaetes gnu	Cg	1
Connochaetes taurinus	Ct	4
Damaliscus hunteri	Dh	3
Gazella rufifrons	Gr	2
Gazella soemmerringi	Gso	2
Gazella speki	Gs	1
Gazella subgutturosa	Gsu	2
Gazella thomsoni	Gt	4
Hippotragus equinus	He	2
Kobus kob	Kk	4
Kobus leche	Kl	1
Madoqua guentheri	Mg	0
Ourebia ourebi	Ouo	5
Raphicerus campestris	Rc	6
Redunca fulvorufula	Rf	3

LIGHT WOODLAND-BUSHLAND
Total number of specimens = 52

Species	Species code	Number
Aepyceros melampus	Am	7
Gazella cuvieri	Gc	2
Gazella granti	Gg	4
Hippotragus niger	Hn	5
Litocranius walleri	Lw	5
Odocoileus virginianus	Odv	4
Oreotragus oreotragus	Oo	4
Oryx beisa	Ob	2
Raphicerus sharpei	Rs	3
Redunca redunca	Red	4
Sylvicapra grimmia	Sg	6
Syncerus caffer	Sc	3
Taurotragus oryx	To	3

HEAVY WOODLAND-BUSHLAND
Total number of specimens = 28

Species	Species code	Number
Kobus defassa	Kd	5
Madoqua kirki	Mk	4
Madoqua saltiana	Ms	1
Neotragus batesi	Nb	2
Neotragus moschatus	Nm	0
Neotragus pygmaeus	Np	0
Taurotragus derbianus	Td	2
Tragelaphus scriptus	Ts	10
Tragelaphus speki	Tsp	1
Tragelaphus strepsiceros	Tst	3

FOREST
Total number of specimens = 31

Species	Species code	Number
Alces alces	Aa	4
Bos javanicus	Bj	3
Bos sauveli	Bs	2
Bubalus mindorensis	Bm	1
Cephalophus leucogaster	Cl	2
Cephalophus monticola	Cm	5
Cephalophus nigrifrons	Cn	6
Hyemoschus aquaticus	Ha	5
Tragelaphus eurycerus	Te	3

MONTANE LIGHT COVER
Total number of specimens = 18

Species	Species code	Number
Capra sibirica	Cs	3
Oreamnos americanus	Ora	2
Ovis ammon	Oa	2
Ovis canadensis	Oc	2
Ovis dalli	Od	2
Ovis vignei	Ov	3
Pseudois nayaur	Pn	2
Rupicapra rupicapra	Rr	2

MONTANE HEAVY COVER
Total number of specimens = 25

Species	Species code	Number
Budorcas taxicolor	Bt	9
Elaphodus cephalophus	Ec	4
Nemorhaedus crispus	Nc	2
Nemorhaedus goral	Ng	3
Nemorhaedus sumatraensis	Ns	4
Nemorhaedus swinhoei	Nsw	1
Pudu mephistophiles	Pm	2

Appendix D, Table P. Species breakdown of the distal metatarsal dataset

Species	Species code	Number	Species	Species code	Number
TOTAL = 215			**HEAVY WOODLAND-BUSHLAND**		
			Total number of specimens = 28		
GRASSLAND					
Total number of specimens = 15			Kobus defassa	Kd	5
			Madoqua kirki	Mk	4
Addax nasomaculatus	An	1	Madoqua saltiana	Ms	1
Bison bison	Bb	7	Neotragus batesi	Nb	2
Damaliscus dorcas	Dd	1	Neotragus moschatus	Nm	0
Damaliscus lunatus	Dl	2	Neotragus pygmaeus	Np	0
Ovibos moschatus	Om	4	Taurotragus derbianus	Td	2
Procapra picticaudata	Pp	0	Tragelaphus scriptus	Ts	10
			Tragelaphus speki	Tsp	1
WOODED-BUSHED GRASSLAND			Tragelaphus strepsiceros	Tst	3
Total number of specimens = 46					
			FOREST		
Alcelaphus buselaphus	Ab	4	**Total number of specimens = 31**		
Antilope cervicapra	Ac	2			
Connochaetes gnu	Cg	1	Alces alces	Aa	4
Connochaetes taurinus	Ct	4	Bos javanicus	Bj	3
Damaliscus hunteri	Dh	3	Bos sauveli	Bs	2
Gazella rufifrons	Gr	2	Bubalus mindorensis	Bm	1
Gazella soemmerringi	Gso	2	Cephalophus leucogaster	Cl	2
Gazella speki	Gs	1	Cephalophus monticola	Cm	5
Gazella subgutturosa	Gsu	2	Cephalophus nigrifrons	Cn	6
Gazella thomsoni	Gt	4	Hyemoschus aquaticus	Ha	5
Hippotragus equinus	He	2	Tragelaphus eurycerus	Te	3
Kobus kob	Kk	4			
Kobus leche	Kl	1	**MONTANE LIGHT COVER**		
Madoqua guentheri	Mg	0	**Total number of specimens = 18**		
Ourebia ourebi	Ouo	5			
Raphicerus campestris	Rc	6	Capra sibirica	Cs	3
Redunca fulvorufula	Rf	3	Oreamnos americanus	Ora	2
			Ovis ammon	Oa	2
LIGHT WOODLAND-BUSHLAND			Ovis canadensis	Oc	2
Total number of specimens = 52			Ovis dalli	Od	2
			Ovis vignei	Ov	3
Aepyceros melampus	Am	7	Pseudois nayaur	Pn	2
Gazella cuvieri	Gc	2	Rupicapra rupicapra	Rr	2
Gazella granti	Gg	4			
Hippotragus niger	Hn	5	**MONTANE HEAVY COVER**		
Litocranius walleri	Lw	5	**Total number of specimens = 25**		
Odocoileus virginianus	Odv	4			
Oreotragus oreotragus	Oo	4	Budorcas taxicolor	Bt	9
Oryx beisa	Ob	2	Elaphodus cephalophus	Ec	4
Raphicerus sharpei	Rs	3	Nemorhaedus crispus	Nc	2
Redunca redunca	Red	4	Nemorhaedus goral	Ng	3
Sylvicapra grimmia	Sg	6	Nemorhaedus sumatraensis	Ns	4
Syncerus caffer	Sc	3	Nemorhaedus swinhoei	Nsw	1
Taurotragus oryx	To	3	Pudu mephistophiles	Pm	2

Appendix D. Table Q. Species breakdown of the proximal metatarsal dataset

TOTAL = 215

GRASSLAND
Total number of specimens = 15

Species	Species code	Number
Addax nasomaculatus	An	1
Bison bison	Bb	7
Damaliscus dorcas	Dd	1
Damaliscus lunatus	Dl	2
Ovibos moschatus	Om	4
Procapra picticaudata	Pp	0

WOODED-BUSHED GRASSLAND
Total number of specimens = 46

Species	Species code	Number
Alcelaphus buselaphus	Ab	4
Antilope cervicapra	Ac	2
Connochaetes gnu	Cg	1
Connochaetes taurinus	Ct	4
Damaliscus hunteri	Dh	3
Gazella rufifrons	Gr	2
Gazella soemmerringi	Gso	2
Gazella speki	Gs	1
Gazella subgutturosa	Gsu	2
Gazella thomsoni	Gt	4
Hippotragus equinus	He	2
Kobus kob	Kk	4
Kobus leche	Kl	1
Madoqua guentheri	Mg	0
Ourebia ourebi	Ouo	5
Raphicerus campestris	Rc	6
Redunca fulvorufula	Rf	3

LIGHT WOODLAND-BUSHLAND
Total number of specimens = 52

Species	Species code	Number
Aepyceros melampus	Am	7
Gazella cuvieri	Gc	2
Gazella granti	Gg	4
Hippotragus niger	Hn	5
Litocranius walleri	Lw	5
Odocoileus virginianus	Odv	4
Oreotragus oreotragus	Oo	4
Oryx beisa	Ob	2
Raphicerus sharpei	Rs	3
Redunca redunca	Red	4
Sylvicapra grimmia	Sg	6
Syncerus caffer	Sc	3
Taurotragus oryx	To	3

HEAVY WOODLAND-BUSHLAND
Total number of specimens = 28

Species	Species code	Number
Kobus defassa	Kd	5
Madoqua kirki	Mk	4
Madoqua saltiana	Ms	1
Neotragus batesi	Nb	2
Neotragus moschatus	Nm	0
Neotragus pygmaeus	Np	0
Taurotragus derbianus	Td	2
Tragelaphus scriptus	Ts	10
Tragelaphus speki	Tsp	1
Tragelaphus strepsiceros	Tst	3

FOREST
Total number of specimens = 31

Species	Species code	Number
Alces alces	Aa	4
Bos javanicus	Bj	3
Bos sauveli	Bs	2
Bubalus mindorensis	Bm	1
Cephalophus leucogaster	Cl	2
Cephalophus monticola	Cm	5
Cephalophus nigrifrons	Cn	6
Hyemoschus aquaticus	Ha	5
Tragelaphus eurycerus	Te	3

MONTANE LIGHT COVER
Total number of specimens = 18

Species	Species code	Number
Capra sibirica	Cs	3
Oreamnos americanus	Ora	2
Ovis ammon	Oa	2
Ovis canadensis	Oc	2
Ovis dalli	Od	2
Ovis vignei	Ov	3
Pseudois nayaur	Pn	2
Rupicapra rupicapra	Rr	2

MONTANE HEAVY COVER
Total number of specimens = 25

Species	Species code	Number
Budorcas taxicolor	Bt	9
Elaphodus cephalophus	Ec	4
Nemorhaedus crispus	Nc	2
Nemorhaedus goral	Ng	3
Nemorhaedus sumatraensis	Ns	4
Nemorhaedus swinhoei	Nsw	1
Pudu mephistophiles	Pm	2

Appendix D, Table R. Species breakdown of the distal metapodial dataset

Species	Species code	Number
TOTAL = 426		
GRASSLAND		
Total number of specimens = 30		
Addax nasomaculatus	An	2
Bison bison	Bb	14
Damaliscus dorcas	Dd	2
Damaliscus lunatus	Dl	4
Ovibos moschatus	Om	8
Procapra picticaudata	Pp	0
WOODED-BUSHED GRASSLAND		
Total number of specimens = 92		
Alcelaphus buselaphus	Ab	8
Antilope cervicapra	Ac	4
Connochaetes gnu	Cg	2
Connochaetes taurinus	Ct	8
Damaliscus hunteri	Dh	6
Gazella rufifrons	Gr	4
Gazella soemmerringi	Gso	4
Gazella speki	Gs	2
Gazella subgutturosa	Gsu	4
Gazella thomsoni	Gt	8
Hippotragus equinus	He	4
Kobus kob	Kk	8
Kobus leche	Kl	2
Madoqua guentheri	Mg	0
Ourebia ourebi	Ouo	10
Raphicerus campestris	Rc	12
Redunca fulvorufula	Rf	6
LIGHT WOODLAND-BUSHLAND		
Total number of specimens = 103		
Aepyceros melampus	Am	14
Gazella cuvieri	Gc	4
Gazella granti	Gg	8
Hippotragus niger	Hn	10
Litocranius walleri	Lw	10
Odocoileus virginianus	Odv	8
Oreotragus oreotragus	Oo	8
Oryx beisa	Ob	4
Raphicerus sharpei	Rs	6
Redunca redunca	Red	8
Sylvicapra grimmia	Sg	11
Syncerus caffer	Sc	6
Taurotragus oryx	To	6
HEAVY WOODLAND-BUSHLAND		
Total number of specimens = 55		
Kobus defassa	Kd	10
Madoqua kirki	Mk	7
Madoqua saltiana	Ms	2
Neotragus batesi	Nb	4
Neotragus moschatus	Nm	0
Neotragus pygmaeus	Np	0
Taurotragus derbianus	Td	4
Tragelaphus scriptus	Ts	20
Tragelaphus speki	Tsp	2
Tragelaphus strepsiceros	Tst	6
FOREST		
Total number of specimens = 62		
Alces alces	Aa	8
Bos javanicus	Bj	6
Bos sauveli	Bs	4
Bubalus mindorensis	Bm	2
Cephalophus leucogaster	Cl	4
Cephalophus monticola	Cm	10
Cephalophus nigrifrons	Cn	12
Hyemoschus aquaticus	Ha	10
Tragelaphus eurycerus	Te	6
MONTANE LIGHT COVER		
Total number of specimens = 34		
Capra sibirica	Cs	6
Oreamnos americanus	Ora	3
Ovis ammon	Oa	4
Ovis canadensis	Oc	4
Ovis dalli	Od	4
Ovis vignei	Ov	5
Pseudois nayaur	Pn	4
Rupicapra rupicapra	Rr	4
MONTANE HEAVY COVER		
Total number of specimens = 50		
Budorcas taxicolor	Bt	18
Elaphodus cephalophus	Ec	8
Nemorhaedus crispus	Nc	4
Nemorhaedus goral	Ng	6
Nemorhaedus sumatraensis	Ns	8
Nemorhaedus swinhoei	Nsw	2
Pudu mephistophiles	Pm	4

Appendix D, Table S. Species breakdown of the naviculo-cuboid dataset

Species	Species code	Number
TOTAL = 206		
GRASSLAND		
Total number of specimens = 16		
Addax nasomaculatus	An	1
Bison bison	Bb	7
Damaliscus dorcas	Dd	1
Damaliscus lunatus	Dl	2
Ovibos moschatus	Om	3
Procapra picticaudata	Pp	2
WOODED-BUSHED GRASSLAND		
Total number of specimens = 48		
Alcelaphus buselaphus	Ab	4
Antilope cervicapra	Ac	2
Connochaetes gnu	Cg	1
Connochaetes taurinus	Ct	4
Damaliscus hunteri	Dh	3
Gazella rufifrons	Gr	2
Gazella soemmerringi	Gso	2
Gazella speki	Gs	2
Gazella subgutturosa	Gsu	2
Gazella thomsoni	Gt	4
Hippotragus equinus	He	2
Kobus kob	Kk	4
Kobus leche	Kl	1
Madoqua guentheri	Mg	1
Ourebia ourebi	Ouo	5
Raphicerus campestris	Rc	6
Redunca fulvorufula	Rf	3
LIGHT WOODLAND-BUSHLAND		
Total number of specimens = 47		
Aepyceros melampus	Am	6
Gazella cuvieri	Gc	2
Gazella granti	Gg	4
Hippotragus niger	Hn	5
Litocranius walleri	Lw	5
Odocoileus virginianus	Odv	4
Oreotragus oreotragus	Oo	4
Oryx beisa	Ob	2
Raphicerus sharpei	Rs	3
Redunca redunca	Red	3
Sylvicapra grimmia	Sg	4
Syncerus caffer	Sc	2
Taurotragus oryx	To	3

Species	Species code	Number
HEAVY WOODLAND-BUSHLAND		
Total number of specimens = 31		
Kobus defassa	Kd	5
Madoqua kirki	Mk	4
Madoqua saltiana	Ms	0
Neotragus batesi	Nb	2
Neotragus moschatus	Nm	1
Neotragus pygmaeus	Np	1
Taurotragus derbianus	Td	2
Tragelaphus scriptus	Ts	11
Tragelaphus speki	Tsp	1
Tragelaphus strepsiceros	Tst	4
FOREST		
Total number of specimens = 27		
Alces alces	Aa	4
Bos javanicus	Bj	2
Bos sauveli	Bs	2
Bubalus mindorensis	Bm	1
Cephalophus leucogaster	Cl	1
Cephalophus monticola	Cm	3
Cephalophus nigrifrons	Cn	6
Hyemoschus aquaticus	Ha	5
Tragelaphus eurycerus	Te	3
MONTANE LIGHT COVER		
Total number of specimens = 17		
Capra sibirica	Cs	3
Oreamnos americanus	Ora	2
Ovis ammon	Oa	2
Ovis canadensis	Oc	2
Ovis dalli	Od	2
Ovis vignei	Ov	3
Pseudois nayaur	Pn	1
Rupicapra rupicapra	Rr	2
MONTANE HEAVY COVER		
Total number of specimens = 20		
Budorcas taxicolor	Bt	8
Elaphodus cephalophus	Ec	4
Nemorhaedus crispus	Nc	2
Nemorhaedus goral	Ng	3
Nemorhaedus sumatraensis	Ns	0
Nemorhaedus swinhoei	Nsw	1
Pudu mephistophiles	Pm	2

Appendix D, Table T. Species breakdown of the distal phalanges dataset

Species	Species code	Number	Species	Species code	Number
TOTAL = 129			**HEAVY WOODLAND-BUSHLAND**		
			Total number of specimens = 24		
GRASSLAND					
Total number of specimens = 22			Kobus defassa	Kd	5
			Madoqua kirki	Mk	5
Addax nasomaculatus	An	2	Madoqua saltiana	Ms	2
Bison bison	Bb	13	Neotragus batesi	Nb	0
Damaliscus dorcas	Dd	1	Neotragus moschatus	Nm	0
Damaliscus lunatus	Dl	2	Neotragus pygmaeus	Np	1
Ovibos moschatus	Om	4	Taurotragus derbianus	Td	0
Procapra picticaudata	Pp	0	Tragelaphus scriptus	Ts	6
			Tragelaphus speki	Tsp	1
WOODED-BUSHED GRASSLAND			Tragelaphus strepsiceros	Tst	4
Total number of specimens = 23					
			FOREST		
Alcelaphus buselaphus	Ab	4	**Total number of specimens = 14**		
Antilope cervicapra	Ac	4			
Connochaetes gnu	Cg	1	Alces alces	Aa	5
Connochaetes taurinus	Ct	2	Bos javanicus	Bj	0
Damaliscus hunteri	Dh	1	Bos sauveli	Bs	0
Gazella rufifrons	Gr	0	Bubalus mindorensis	Bm	0
Gazella soemmerringi	Gso	0	Cephalophus leucogaster	Cl	0
Gazella speki	Gs	0	Cephalophus monticola	Cm	0
Gazella subgutturosa	Gsu	0	Cephalophus nigrifrons	Cn	7
Gazella thomsoni	Gt	0	Hyemoschus aquaticus	Ha	1
Hippotragus equinus	He	1	Tragelaphus eurycerus	Te	1
Kobus kob	Kk	1			
Kobus leche	Kl	1	**MONTANE**		
Madoqua guentheri	Mg	0	**Total number of specimens = 13**		
Ourebia ourebi	Ouo	4			
Raphicerus campestris	Rc	4	Budorcas taxicolor	Bt	0
Redunca fulvorufula	Rf	0	Capra sibirica	Cs	0
			Elaphodus cephalophus	Ec	4
LIGHT WOODLAND-BUSHLAND			Nemorhaedus crispus	Nc	1
Total number of specimens = 33			Nemorhaedus goral	Ng	0
			Nemorhaedus sumatraensis	Ns	1
Aepyceros melampus	Am	7	Nemorhaedus swinhoei	Nsw	1
Gazella cuvieri	Gc	0	Oreamnos americanus	Ora	1
Gazella granti	Gg	4	Ovis ammon	Oa	3
Hippotragus niger	Hn	5	Ovis canadensis	Oc	2
Litocranius walleri	Lw	0	Ovis dalli	Od	0
Odocoileus virginianus	Odv	5	Ovis vignei	Ov	0
Oreotragus oreotragus	Oo	5	Pseudois nayaur	Pn	0
Oryx beisa	Ob	1	Pudu mephistophiles	Pm	0
Raphicerus sharpei	Rs	0	Rupicapra rupicapra	Rr	0
Redunca redunca	Red	2			
Sylvicapra grimmia	Sg	0			
Syncerus caffer	Sc	2			
Taurotragus oryx	To	2			

Appendix D, Table U. Species breakdown of the intermediate phalanges dataset

Species	Species code	Number	Species	Species code	Number
TOTAL = 181 logged/180 size corrected			**HEAVY WOODLAND-BUSHLAND**		
			Total number of specimens = 26		
GRASSLAND					
Total number of specimens = 26			Kobus defassa	Kd	5
			Madoqua kirki	Mk	4
Addax nasomaculatus	An	2	Madoqua saltiana	Ms	2
Bison bison	Bb	13	Neotragus batesi	Nb	0
Damaliscus dorcas	Dd	2	Neotragus moschatus	Nm	0
Damaliscus lunatus	Dl	4	Neotragus pygmaeus	Np	1
Ovibos moschatus	Om	5	Taurotragus derbianus	Td	0
Procapra picticaudata	Pp	0	Tragelaphus scriptus	Ts	9
			Tragelaphus speki	Tsp	1
WOODED-BUSHED GRASSLAND			Tragelaphus strepsiceros	Tst	4
Total number of specimens = 32					
			FOREST		
Alcelaphus buselaphus	Ab	5	**Total number of specimens = 23**		
Antilope cervicapra	Ac	4			
Connochaetes gnu	Cg	1	Alces alces	Aa	6
Connochaetes taurinus	Ct	5	Bos javanicus	Bj	4
Damaliscus hunteri	Dh	4	Bos sauveli	Bs	0
Gazella rufifrons	Gr	0	Bubalus mindorensis	Bm	0
Gazella soemmerringi	Gso	1	Cephalophus leucogaster	Cl	0
Gazella speki	Gs	1	Cephalophus monticola	Cm	0
Gazella subgutturosa	Gsu	0	Cephalophus nigrifrons	Cn	7
Gazella thomsoni	Gt	0	Hyemoschus aquaticus	Ha	3
Hippotragus equinus	He	1	Tragelaphus eurycerus	Te	3
Kobus kob	Kk	1			
Kobus leche	Kl	1	**MONTANE LIGHT COVER**		
Madoqua guentheri	Mg	0	**Total number of specimens = 10**		
Ourebia ourebi	Ouo	4			
Raphicerus campestris	Rc	4	Capra sibirica	Cs	0
Redunca fulvorufula	Rf	0	Oreamnos americanus	Ora	1
			Ovis ammon	Oa	4
LIGHT WOODLAND-BUSHLAND			Ovis canadensis	Oc	3
Total number of specimens = 52/51			Ovis dalli	Od	0
			Ovis vignei	Ov	2
Aepyceros melampus	Am	7	Pseudois nayaur	Pn	0
Gazella cuvieri	Gc	3	Rupicapra rupicapra	Rr	0
Gazella granti	Gg	5			
Hippotragus niger	Hn	9	**MONTANE HEAVY COVER**		
Litocranius walleri	Lw	4	**Total number of specimens = 12**		
Odocoileus virginianus	Odv	5/4			
Oreotragus oreotragus	Oo	7	Budorcas taxicolor	Bt	0
Oryx beisa	Ob	1	Elaphodus cephalophus	Ec	7
Raphicerus sharpei	Rs	0	Nemorhaedus crispus	Nc	1
Redunca redunca	Red	2	Nemorhaedus goral	Ng	0
Sylvicapra grimmia	Sg	5	Nemorhaedus sumatraensis	Ns	1
Syncerus caffer	Sc	2	Nemorhaedus swinhoei	Nsw	1
Taurotragus oryx	To	2	Pudu mephistophiles	Pm	2

Appendix D, Table V. Species breakdown of the proximal phalanges dataset

Species	Species code	Number	Species	Species code	Number
TOTAL = 303			**HEAVY WOODLAND-BUSHLAND**		
			Total number of specimens = 39		
GRASSLAND					
Total number of specimens = 27			Kobus defassa	Kd	6
			Madoqua kirki	Mk	5
Addax nasomaculatus	An	2	Madoqua saltiana	Ms	2
Bison bison	Bb	14	Neotragus batesi	Nb	4
Damaliscus dorcas	Dd	2	Neotragus moschatus	Nm	0
Damaliscus lunatus	Dl	4	Neotragus pygmaeus	Np	0
Ovibos moschatus	Om	5	Taurotragus derbianus	Td	0
Procapra picticaudata	Pp	0	Tragelaphus scriptus	Ts	17
			Tragelaphus speki	Tsp	0
WOODED-BUSHED GRASSLAND			Tragelaphus strepsiceros	Tst	5
Total number of specimens = 46					
			FOREST		
Alcelaphus buselaphus	Ab	4	**Total number of specimens = 53**		
Antilope cervicapra	Ac	4			
Connochaetes gnu	Cg	2	Alces alces	Aa	6
Connochaetes taurinus	Ct	6	Bos javanicus	Bj	6
Damaliscus hunteri	Dh	6	Bos sauveli	Bs	4
Gazella rufifrons	Gr	0	Bubalus mindorensis	Bm	0
Gazella soemmerringi	Gso	0	Cephalophus leucogaster	Cl	4
Gazella speki	Gs	2	Cephalophus monticola	Cm	8
Gazella subgutturosa	Gsu	2	Cephalophus nigrifrons	Cn	12
Gazella thomsoni	Gt	0	Hyemoschus aquaticus	Ha	10
Hippotragus equinus	He	0	Tragelaphus eurycerus	Te	3
Kobus kob	Kk	0			
Kobus leche	Kl	2	**MONTANE LIGHT COVER**		
Madoqua guentheri	Mg	0	**Total number of specimens = 21**		
Ourebia ourebi	Ouo	8			
Raphicerus campestris	Rc	8	Capra sibirica	Cs	0
Redunca fulvorufula	Rf	2	Oreamnos americanus	Ora	1
			Ovis ammon	Oa	4
LIGHT WOODLAND-BUSHLAND			Ovis canadensis	Oc	4
Total number of specimens = 83			Ovis dalli	Od	2
			Ovis vignei	Ov	6
Aepyceros melampus	Am	10	Pseudois nayaur	Pn	2
Gazella cuvieri	Gc	4	Rupicapra rupicapra	Rr	2
Gazella granti	Gg	8			
Hippotragus niger	Hn	10	**MONTANE HEAVY COVER**		
Litocranius walleri	Lw	10	**Total number of specimens = 34**		
Odocoileus virginianus	Odv	6			
Oreotragus oreotragus	Oo	8	Budorcas taxicolor	Bt	8
Oryx beisa	Ob	2	Elaphodus cephalophus	Ec	6
Raphicerus sharpei	Rs	5	Nemorhaedus crispus	Nc	4
Redunca redunca	Red	4	Nemorhaedus goral	Ng	6
Sylvicapra grimmia	Sg	12	Nemorhaedus sumatraensis	Ns	4
Syncerus caffer	Sc	2	Nemorhaedus swinhoei	Nsw	2
Taurotragus oryx	To	2	Pudu mephistophiles	Pm	4

Appendix D, Table W. Species breakdown of the pisiform dataset

Species	Species code	Number
TOTAL = 170		
GRASSLAND		
Total number of specimens = 13		
Addax nasomaculatus	An	1
Bison bison	Bb	7
Damaliscus dorcas	Dd	0
Damaliscus lunatus	Dl	2
Ovibos moschatus	Om	3
Procapra picticaudata	Pp	0
WOODED-BUSHED GRASSLAND		
Total number of specimens = 40		
Alcelaphus buselaphus	Ab	4
Antilope cervicapra	Ac	2
Connochaetes gnu	Cg	1
Connochaetes taurinus	Ct	4
Damaliscus hunteri	Dh	2
Gazella rufifrons	Gr	2
Gazella soemmerringi	Gso	1
Gazella speki	Gs	1
Gazella subgutturosa	Gsu	1
Gazella thomsoni	Gt	4
Hippotragus equinus	He	2
Kobus kob	Kk	4
Kobus leche	Kl	1
Madoqua guentheri	Mg	0
Ourebia ourebi	Ouo	3
Raphicerus campestris	Rc	5
Redunca fulvorufula	Rf	3
LIGHT WOODLAND-BUSHLAND		
Total number of specimens = 37		
Aepyceros melampus	Am	4
Gazella cuvieri	Gc	1
Gazella granti	Gg	2
Hippotragus niger	Hn	4
Litocranius walleri	Lw	2
Odocoileus virginianus	Odv	4
Oreotragus oreotragus	Oo	3
Oryx beisa	Ob	1
Raphicerus sharpei	Rs	3
Redunca redunca	Rcd	4
Sylvicapra grimmia	Sg	5
Syncerus caffer	Sc	1
Taurotragus oryx	To	3
HEAVY WOODLAND-BUSHLAND		
Total number of specimens = 26		
Kobus defassa	Kd	3
Madoqua kirki	Mk	2
Madoqua saltiana	Ms	0
Neotragus batesi	Nb	2
Neotragus moschatus	Nm	0
Neotragus pygmaeus	Np	1
Taurotragus derbianus	Td	2
Tragelaphus scriptus	Ts	11
Tragelaphus speki	Tsp	1
Tragelaphus strepsiceros	Tst	4
FOREST		
Total number of specimens = 24		
Alces alces	Aa	1
Bos javanicus	Bj	3
Bos sauveli	Bs	2
Bubalus mindorensis	Bm	1
Cephalophus leucogaster	Cl	2
Cephalophus monticola	Cm	4
Cephalophus nigrifrons	Cn	5
Hyemoschus aquaticus	Ha	4
Tragelaphus eurycerus	Te	2
MONTANE LIGHT COVER		
Total number of specimens = 14		
Capra sibirica	Cs	3
Oreamnos americanus	Ora	1
Ovis ammon	Oa	2
Ovis canadensis	Oc	2
Ovis dalli	Od	2
Ovis vignei	Ov	2
Pseudois nayaur	Pn	1
Rupicapra rupicapra	Rr	1
MONTANE HEAVY COVER		
Total number of specimens = 16		
Budorcas taxicolor	Bt	3
Elaphodus cephalophus	Ec	4
Nemorhaedus crispus	Nc	2
Nemorhaedus goral	Ng	0
Nemorhaedus sumatraensis	Ns	4
Nemorhaedus swinhoei	Nsw	1
Pudu mephistophiles	Pm	2

Appendix D, Table X. Species breakdown of the radius dataset

Species	Species code	Number	Species	Species code	Number
TOTAL = 207 logged/205 size corrected			**HEAVY WOODLAND-BUSHLAND**		
			Total number of specimens = 31		
GRASSLAND					
Total number of specimens = 17			Kobus defassa	Kd	5
			Madoqua kirki	Mk	3
Addax nasomaculatus	An	1	Madoqua saltiana	Ms	1
Bison bison	Bb	7	Neotragus batesi	Nb	2
Damaliscus dorcas	Dd	1	Neotragus moschatus	Nm	1
Damaliscus lunatus	Dl	2	Neotragus pygmaeus	Np	1
Ovibos moschatus	Om	4	Taurotragus derbianus	Td	2
Procapra picticaudata	Pp	2	Tragelaphus scriptus	Ts	11
			Tragelaphus speki	Tsp	1
WOODED-BUSHED GRASSLAND			Tragelaphus strepsiceros	Tst	4
Total number of specimens = 47/46					
			FOREST		
Alcelaphus buselaphus	Ab	4	**Total number of specimens = 30**		
Antilope cervicapra	Ac	2			
Connochaetes gnu	Cg	1	Alces alces	Aa	3
Connochaetes taurinus	Ct	4	Bos javanicus	Bj	3
Damaliscus hunteri	Dh	3	Bos sauveli	Bs	2
Gazella rufifrons	Gr	2	Bubalus mindorensis	Bm	1
Gazella soemmerringi	Gso	2	Cephalophus leucogaster	Cl	2
Gazella speki	Gs	2	Cephalophus monticola	Cm	5
Gazella subgutturosa	Gsu	2	Cephalophus nigrifrons	Cn	6
Gazella thomsoni	Gt	4	Hyemoschus aquaticus	Ha	5
Hippotragus equinus	He	2	Tragelaphus eurycerus	Te	3
Kobus kob	Kk	4			
Kobus leche	Kl	1	**MONTANE LIGHT COVER**		
Madoqua guentheri	Mg	0	**Total number of specimens = 16**		
Ourebia ourebi	Ouo	5			
Raphicerus campestris	Rc	6/5	Capra sibirica	Cs	3
Redunca fulvorufula	Rf	3	Oreamnos americanus	Ora	1
			Ovis ammon	Oa	1
LIGHT WOODLAND-BUSHLAND			Ovis canadensis	Oc	2
Total number of specimens = 51/50			Ovis dalli	Od	2
			Ovis vignei	Ov	3
Aepyceros melampus	Am	7	Pseudois nayaur	Pn	2
Gazella cuvieri	Gc	2	Rupicapra rupicapra	Rr	2
Gazella granti	Gg	4			
Hippotragus niger	Hn	5	**MONTANE HEAVY COVER**		
Litocranius walleri	Lw	5/4	**Total number of specimens = 15**		
Odocoileus virginianus	Odv	4			
Oreotragus oreotragus	Oo	4	Budorcas taxicolor	Bt	1
Oryx beisa	Ob	2	Elaphodus cephalophus	Ec	3
Raphicerus sharpei	Rs	3	Nemorhaedus crispus	Nc	2
Redunca redunca	Red	4	Nemorhaedus goral	Ng	2
Sylvicapra grimmia	Sg	5	Nemorhaedus sumatraensis	Ns	4
Syncerus caffer	Sc	3	Nemorhaedus swinhoei	Nsw	1
Taurotragus oryx	To	3	Pudu mephistophiles	Pm	2

Appendix D, Table Y. Species breakdown of the distal radius dataset

Species	Species code	Number	Species	Species code	Number
TOTAL = 210 logged/208 size corrected			**HEAVY WOODLAND-BUSHLAND**		
			Total number of specimens = 31		
GRASSLAND					
Total number of specimens = 17			Kobus defassa	Kd	5
			Madoqua kirki	Mk	3
Addax nasomaculatus	An	1	Madoqua saltiana	Ms	1
Bison bison	Bb	7	Neotragus batesi	Nb	2
Damaliscus dorcas	Dd	1	Neotragus moschatus	Nm	1
Damaliscus lunatus	Dl	2	Neotragus pygmaeus	Np	1
Ovibos moschatus	Om	4	Taurotragus derbianus	Td	2
Procapra picticaudata	Pp	2	Tragelaphus scriptus	Ts	11
			Tragelaphus speki	Tsp	1
WOODED-BUSHED GRASSLAND			Tragelaphus strepsiceros	Tst	4
Total number of specimens = 48/47					
			FOREST		
Alcelaphus buselaphus	Ab	4	**Total number of specimens = 30**		
Antilope cervicapra	Ac	2			
Connochaetes gnu	Cg	1	Alces alces	Aa	3
Connochaetes taurinus	Ct	4	Bos javanicus	Bj	3
Damaliscus hunteri	Dh	3	Bos sauveli	Bs	2
Gazella rufifrons	Gr	2	Bubalus mindorensis	Bm	1
Gazella soemmerringi	Gso	2	Cephalophus leucogaster	Cl	2
Gazella speki	Gs	2	Cephalophus monticola	Cm	5
Gazella subgutturosa	Gsu	2	Cephalophus nigrifrons	Cn	6
Gazella thomsoni	Gt	4	Hyemoschus aquaticus	Ha	5
Hippotragus equinus	He	2	Tragelaphus eurycerus	Te	3
Kobus kob	Kk	4			
Kobus leche	Kl	1	**MONTANE LIGHT COVER**		
Madoqua guentheri	Mg	1	**Total number of specimens = 17**		
Ourebia ourebi	Ouo	5			
Raphicerus campestris	Rc	6/5	Capra sibirica	Cs	3
Redunca fulvorufula	Rf	3	Oreamnos americanus	Ora	1
			Ovis ammon	Oa	2
LIGHT WOODLAND-BUSHLAND			Ovis canadensis	Oc	2
Total number of specimens = 51/50			Ovis dalli	Od	2
			Ovis vignei	Ov	3
Aepyceros melampus	Am	7	Pseudois nayaur	Pn	2
Gazella cuvieri	Gc	2	Rupicapra rupicapra	Rr	2
Gazella granti	Gg	4			
Hippotragus niger	Hn	5	**MONTANE HEAVY COVER**		
Litocranius walleri	Lw	5/4	**Total number of specimens = 16**		16
Odocoileus virginianus	Odv	4			
Oreotragus oreotragus	Oo	4	Budorcas taxicolor	Bt	1
Oryx beisa	Ob	2	Elaphodus cephalophus	Ec	4
Raphicerus sharpei	Rs	3	Nemorhaedus crispus	Nc	2
Redunca redunca	Red	4	Nemorhaedus goral	Ng	2
Sylvicapra grimmia	Sg	5	Nemorhaedus sumatraensis	Ns	4
Syncerus caffer	Sc	3	Nemorhaedus swinhoei	Nsw	1
Taurotragus oryx	To	3	Pudu mephistophiles	Pm	2

Appendix D, Table Z. Species breakdown of the proximal radius dataset

Species	Species code	Number
TOTAL = 209		
GRASSLAND		
Total number of specimens = 17		
Addax nasomaculatus	An	1
Bison bison	Bb	7
Damaliscus dorcas	Dd	1
Damaliscus lunatus	Dl	2
Ovibos moschatus	Om	4
Procapra picticaudata	Pp	2
WOODED-BUSHED GRASSLAND		
Total number of specimens = 47		
Alcelaphus buselaphus	Ab	4
Antilope cervicapra	Ac	2
Connochaetes gnu	Cg	1
Connochaetes taurinus	Ct	4
Damaliscus hunteri	Dh	3
Gazella rufifrons	Gr	2
Gazella soemmerringi	Gso	2
Gazella speki	Gs	2
Gazella subgutturosa	Gsu	2
Gazella thomsoni	Gt	4
Hippotragus equinus	He	2
Kobus kob	Kk	4
Kobus leche	Kl	1
Madoqua guentheri	Mg	0
Ourebia ourebi	Ouo	5
Raphicerus campestris	Rc	6
Redunca fulvorufula	Rf	3
LIGHT WOODLAND-BUSHLAND		
Total number of specimens = 52		
Aepyceros melampus	Am	7
Gazella cuvieri	Gc	2
Gazella granti	Gg	4
Hippotragus niger	Hn	5
Litocranius walleri	Lw	5
Odocoileus virginianus	Odv	4
Oreotragus oreotragus	Oo	4
Oryx beisa	Ob	2
Raphicerus sharpei	Rs	3
Redunca redunca	Red	4
Sylvicapra grimmia	Sg	6
Syncerus caffer	Sc	3
Taurotragus oryx	To	3
HEAVY WOODLAND-BUSHLAND		
Total number of specimens = 31		
Kobus defassa	Kd	5
Madoqua kirki	Mk	3
Madoqua saltiana	Ms	1
Neotragus batesi	Nb	2
Neotragus moschatus	Nm	1
Neotragus pygmaeus	Np	1
Taurotragus derbianus	Td	2
Tragelaphus scriptus	Ts	11
Tragelaphus speki	Tsp	1
Tragelaphus strepsiceros	Tst	4
FOREST		
Total number of specimens = 30		
Alces alces	Aa	3
Bos javanicus	Bj	3
Bos sauveli	Bs	2
Bubalus mindorensis	Bm	1
Cephalophus leucogaster	Cl	2
Cephalophus monticola	Cm	5
Cephalophus nigrifrons	Cn	6
Hyemoschus aquaticus	Ha	5
Tragelaphus eurycerus	Te	3
MONTANE LIGHT COVER		
Total number of specimens = 17		
Capra sibirica	Cs	3
Oreamnos americanus	Ora	1
Ovis ammon	Oa	2
Ovis canadensis	Oc	2
Ovis dalli	Od	2
Ovis vignei	Ov	3
Pseudois nayaur	Pn	2
Rupicapra rupicapra	Rr	2
MONTANE HEAVY COVER		
Total number of specimens = 15		
Budorcas taxicolor	Bt	1
Elaphodus cephalophus	Ec	3
Nemorhaedus crispus	Nc	2
Nemorhaedus goral	Ng	2
Nemorhaedus sumatraensis	Ns	4
Nemorhaedus swinhoei	Nsw	1
Pudu mephistophiles	Pm	2

Appendix D, Table AA. Species breakdown of the scaphoid dataset

Species	Species code	Number
TOTAL = 207		
GRASSLAND		
Total number of specimens = 16		
Addax nasomaculatus	An	1
Bison bison	Bb	7
Damaliscus dorcas	Dd	1
Damaliscus lunatus	Dl	2
Ovibos moschatus	Om	4
Procapra picticaudata	Pp	1
WOODED-BUSHED GRASSLAND		
Total number of specimens = 48		
Alcelaphus buselaphus	Ab	4
Antilope cervicapra	Ac	2
Connochaetes gnu	Cg	1
Connochaetes taurinus	Ct	4
Damaliscus hunteri	Dh	3
Gazella rufifrons	Gr	2
Gazella soemmerringi	Gso	2
Gazella speki	Gs	2
Gazella subgutturosa	Gsu	2
Gazella thomsoni	Gt	4
Hippotragus equinus	He	2
Kobus kob	Kk	4
Kobus leche	Kl	1
Madoqua guentheri	Mg	1
Ourebia ourebi	Ouo	5
Raphicerus campestris	Rc	6
Redunca fulvorufula	Rf	3
LIGHT WOODLAND-BUSHLAND		
Total number of specimens = 49		
Aepyceros melampus	Am	6
Gazella cuvieri	Gc	2
Gazella granti	Gg	4
Hippotragus niger	Hn	5
Litocranius walleri	Lw	4
Odocoileus virginianus	Odv	4
Oreotragus oreotragus	Oo	4
Oryx beisa	Ob	2
Raphicerus sharpei	Rs	3
Redunca redunca	Red	4
Sylvicapra grimmia	Sg	5
Syncerus caffer	Sc	3
Taurotragus oryx	To	3
HEAVY WOODLAND-BUSHLAND		
Total number of specimens = 30		
Kobus defassa	Kd	5
Madoqua kirki	Mk	2
Madoqua saltiana	Ms	1
Neotragus batesi	Nb	2
Neotragus moschatus	Nm	1
Neotragus pygmaeus	Np	1
Taurotragus derbianus	Td	2
Tragelaphus scriptus	Ts	11
Tragelaphus speki	Tsp	1
Tragelaphus strepsiceros	Tst	4
FOREST		
Total number of specimens = 29		
Alces alces	Aa	4
Bos javanicus	Bj	3
Bos sauveli	Bs	2
Bubalus mindorensis	Bm	1
Cephalophus leucogaster	Cl	2
Cephalophus monticola	Cm	5
Cephalophus nigrifrons	Cn	5
Hyemoschus aquaticus	Ha	4
Tragelaphus eurycerus	Te	3
MONTANE LIGHT COVER		
Total number of specimens = 16		
Capra sibirica	Cs	3
Oreamnos americanus	Ora	1
Ovis ammon	Oa	2
Ovis canadensis	Oc	2
Ovis dalli	Od	2
Ovis vignei	Ov	3
Pseudois nayaur	Pn	2
Rupicapra rupicapra	Rr	1
MONTANE HEAVY COVER		
Total number of specimens = 19		
Budorcas taxicolor	Bt	5
Elaphodus cephalophus	Ec	4
Nemorhaedus crispus	Nc	2
Nemorhaedus goral	Ng	1
Nemorhaedus sumatraensis	Ns	4
Nemorhaedus swinhoei	Nsw	1
Pudu mephistophiles	Pm	2

Appendix D, Table BB. Species breakdown of the talus dataset

Species	Species code	Number
TOTAL = 206		
GRASSLAND		
Total number of specimens = 13		
Addax nasomaculatus	An	1
Bison bison	Bb	7
Damaliscus dorcas	Dd	1
Damaliscus lunatus	Dl	2
Ovibos moschatus	Om	0
Procapra picticaudata	Pp	2
WOODED-BUSHED GRASSLAND		
Total number of specimens = 47		
Alcelaphus buselaphus	Ab	4
Antilope cervicapra	Ac	2
Connochaetes gnu	Cg	1
Connochaetes taurinus	Ct	4
Damaliscus hunteri	Dh	3
Gazella rufifrons	Gr	2
Gazella soemmerringi	Gso	2
Gazella speki	Gs	2
Gazella subgutturosa	Gsu	2
Gazella thomsoni	Gt	4
Hippotragus equinus	He	2
Kobus kob	Kk	5
Kobus leche	Kl	1
Madoqua guentheri	Mg	1
Ourebia ourebi	Ouo	3
Raphicerus campestris	Rc	6
Redunca fulvorufula	Rf	3
LIGHT WOODLAND-BUSHLAND		
Total number of specimens = 49		
Aepyceros melampus	Am	7
Gazella cuvieri	Gc	2
Gazella granti	Gg	4
Hippotragus niger	Hn	5
Litocranius walleri	Lw	5
Odocoileus virginianus	Odv	4
Oreotragus oreotragus	Oo	3
Oryx beisa	Ob	2
Raphicerus sharpei	Rs	3
Redunca redunca	Red	4
Sylvicapra grimmia	Sg	4
Syncerus caffer	Sc	3
Taurotragus oryx	To	3
HEAVY WOODLAND-BUSHLAND		
Total number of specimens = 32		
Kobus defassa	Kd	5
Madoqua kirki	Mk	4
Madoqua saltiana	Ms	1
Neotragus batesi	Nb	2
Neotragus moschatus	Nm	1
Neotragus pygmaeus	Np	1
Taurotragus derbianus	Td	2
Tragelaphus scriptus	Ts	11
Tragelaphus speki	Tsp	1
Tragelaphus strepsiceros	Tst	4
FOREST		
Total number of specimens = 28		
Alces alces	Aa	4
Bos javanicus	Bj	3
Bos sauveli	Bs	2
Bubalus mindorensis	Bm	1
Cephalophus leucogaster	Cl	2
Cephalophus monticola	Cm	3
Cephalophus nigrifrons	Cn	6
Hyemoschus aquaticus	Ha	4
Tragelaphus eurycerus	Te	3
MONTANE LIGHT COVER		
Total number of specimens = 17		
Capra sibirica	Cs	3
Oreamnos americanus	Ora	2
Ovis ammon	Oa	1
Ovis canadensis	Oc	2
Ovis dalli	Od	2
Ovis vignei	Ov	3
Pseudois nayaur	Pn	2
Rupicapra rupicapra	Rr	2
MONTANE HEAVY COVER		
Total number of specimens = 20		
Budorcas taxicolor	Bt	9
Elaphodus cephalophus	Ec	4
Nemorhaedus crispus	Nc	0
Nemorhaedus goral	Ng	1
Nemorhaedus sumatraensis	Ns	4
Nemorhaedus swinhoei	Nsw	0
Pudu mephistophiles	Pm	2

Appendix D, Table CC. Species breakdown of the tibia dataset

Species	Species code	Number
TOTAL = 212		
GRASSLAND		
Total number of specimens = 13		
Addax nasomaculatus	An	1
Bison bison	Bb	7
Damaliscus dorcas	Dd	1
Damaliscus lunatus	Dl	2
Ovibos moschatus	Om	0
Procapra picticaudata	Pp	2
WOODED-BUSHED GRASSLAND		
Total number of specimens = 46		
Alcelaphus buselaphus	Ab	4
Antilope cervicapra	Ac	2
Connochaetes gnu	Cg	1
Connochaetes taurinus	Ct	4
Damaliscus hunteri	Dh	3
Gazella rufifrons	Gr	2
Gazella soemmerringi	Gso	2
Gazella speki	Gs	2
Gazella subgutturosa	Gsu	2
Gazella thomsoni	Gt	4
Hippotragus equinus	He	2
Kobus kob	Kk	5
Kobus leche	Kl	1
Madoqua guentheri	Mg	1
Ourebia ourebi	Ouo	2
Raphicerus campestris	Rc	6
Redunca fulvorufula	Rf	3
LIGHT WOODLAND-BUSHLAND		
Total number of specimens = 50		
Aepyceros melampus	Am	7
Gazella cuvieri	Gc	2
Gazella granti	Gg	4
Hippotragus niger	Hn	5
Litocranius walleri	Lw	5
Odocoileus virginianus	Odv	4
Oreotragus oreotragus	Oo	4
Oryx beisa	Ob	2
Raphicerus sharpei	Rs	3
Redunca redunca	Red	4
Sylvicapra grimmia	Sg	4
Syncerus caffer	Sc	3
Taurotragus oryx	To	3
HEAVY WOODLAND-BUSHLAND		
Total number of specimens = 32		
Kobus defassa	Kd	5
Madoqua kirki	Mk	4
Madoqua saltiana	Ms	1
Neotragus batesi	Nb	2
Neotragus moschatus	Nm	1
Neotragus pygmaeus	Np	1
Taurotragus derbianus	Td	2
Tragelaphus scriptus	Ts	11
Tragelaphus speki	Tsp	1
Tragelaphus strepsiceros	Tst	4
FOREST		
Total number of specimens = 30		
Alces alces	Aa	4
Bos javanicus	Bj	3
Bos sauveli	Bs	2
Bubalus mindorensis	Bm	1
Cephalophus leucogaster	Cl	2
Cephalophus monticola	Cm	5
Cephalophus nigrifrons	Cn	6
Hyemoschus aquaticus	Ha	4
Tragelaphus eurycerus	Te	3
MONTANE LIGHT COVER		
Total number of specimens = 17		
Capra sibirica	Cs	3
Oreamnos americanus	Ora	2
Ovis ammon	Oa	1
Ovis canadensis	Oc	2
Ovis dalli	Od	2
Ovis vignei	Ov	3
Pseudois nayaur	Pn	2
Rupicapra rupicapra	Rr	2
MONTANE HEAVY COVER		
Total number of specimens = 24		
Budorcas taxicolor	Bt	9
Elaphodus cephalophus	Ec	4
Nemorhaedus crispus	Nc	2
Nemorhaedus goral	Ng	2
Nemorhaedus sumatraensis	Ns	4
Nemorhaedus swinhoei	Nsw	1
Pudu mephistophiles	Pm	2

Appendix D, Table DD. Species breakdown of the distal tibia dataset

Species	Species code	Number
TOTAL = 213		
GRASSLAND		
Total number of specimens = 13		
Addax nasomaculatus	An	1
Bison bison	Bb	7
Damaliscus dorcas	Dd	1
Damaliscus lunatus	Dl	2
Ovibos moschatus	Om	0
Procapra picticaudata	Pp	2
WOODED-BUSHED GRASSLAND		
Total number of specimens = 46		
Alcelaphus buselaphus	Ab	4
Antilope cervicapra	Ac	2
Connochaetes gnu	Cg	1
Connochaetes taurinus	Ct	4
Damaliscus hunteri	Dh	3
Gazella rufifrons	Gr	2
Gazella soemmerringi	Gso	2
Gazella speki	Gs	2
Gazella subgutturosa	Gsu	2
Gazella thomsoni	Gt	4
Hippotragus equinus	He	2
Kobus kob	Kk	5
Kobus leche	Kl	1
Madoqua guentheri	Mg	1
Ourebia ourebi	Ouo	2
Raphicerus campestris	Rc	6
Redunca fulvorufula	Rf	3
LIGHT WOODLAND-BUSHLAND		
Total number of specimens = 50		
Aepyceros melampus	Am	7
Gazella cuvieri	Gc	2
Gazella granti	Gg	4
Hippotragus niger	Hn	5
Litocranius walleri	Lw	5
Odocoileus virginianus	Odv	4
Oreotragus oreotragus	Oo	4
Oryx beisa	Ob	2
Raphicerus sharpei	Rs	3
Redunca redunca	Rcd	4
Sylvicapra grimmia	Sg	4
Syncerus caffer	Sc	3
Taurotragus oryx	To	3
HEAVY WOODLAND-BUSHLAND		
Total number of specimens = 32		
Kobus defassa	Kd	5
Madoqua kirki	Mk	4
Madoqua saltiana	Ms	1
Neotragus batesi	Nb	2
Neotragus moschatus	Nm	1
Neotragus pygmaeus	Np	1
Taurotragus derbianus	Td	2
Tragelaphus scriptus	Ts	11
Tragelaphus speki	Tsp	1
Tragelaphus strepsiceros	Tst	4
FOREST		
Total number of specimens = 30		
Alces alces	Aa	4
Bos javanicus	Bj	3
Bos sauveli	Bs	2
Bubalus mindorensis	Bm	1
Cephalophus leucogaster	Cl	2
Cephalophus monticola	Cm	5
Cephalophus nigrifrons	Cn	6
Hyemoschus aquaticus	Ha	4
Tragelaphus eurycerus	Te	3
MONTANE LIGHT COVER		
Total number of specimens = 17		
Capra sibirica	Cs	3
Oreamnos americanus	Ora	2
Ovis ammon	Oa	1
Ovis canadensis	Oc	2
Ovis dalli	Od	2
Ovis vignei	Ov	3
Pseudois nayaur	Pn	2
Rupicapra rupicapra	Rr	2
MONTANE HEAVY COVER		
Total number of specimens = 25		
Budorcas taxicolor	Bt	9
Elaphodus cephalophus	Ec	4
Nemorhaedus crispus	Nc	2
Nemorhaedus goral	Ng	3
Nemorhaedus sumatraensis	Ns	4
Nemorhaedus swinhoei	Nsw	1
Pudu mephistophiles	Pm	2

Appendix D, Table EE. Species breakdown of the proximal tibia dataset

Species	Species code	Number
TOTAL = 213		
GRASSLAND		
Total number of specimens = 13		
Addax nasomaculatus	An	1
Bison bison	Bb	7
Damaliscus dorcas	Dd	1
Damaliscus lunatus	Dl	2
Ovibos moschatus	Om	0
Procapra picticaudata	Pp	2
WOODED-BUSHED GRASSLAND		
Total number of specimens = 46		
Alcelaphus buselaphus	Ab	4
Antilope cervicapra	Ac	2
Connochaetes gnu	Cg	1
Connochaetes taurinus	Ct	4
Damaliscus hunteri	Dh	3
Gazella rufifrons	Gr	2
Gazella soemmerringi	Gso	2
Gazella speki	Gs	2
Gazella subgutturosa	Gsu	2
Gazella thomsoni	Gt	4
Hippotragus equinus	He	2
Kobus kob	Kk	5
Kobus leche	Kl	1
Madoqua guentheri	Mg	1
Ourebia ourebi	Ouo	2
Raphicerus campestris	Rc	6
Redunca fulvorufula	Rf	3
LIGHT WOODLAND-BUSHLAND		
Total number of specimens = 50		
Aepyceros melampus	Am	7
Gazella cuvieri	Gc	2
Gazella granti	Gg	4
Hippotragus niger	Hn	5
Litocranius walleri	Lw	5
Odocoileus virginianus	Odv	4
Oreotragus oreotragus	Oo	4
Oryx beisa	Ob	2
Raphicerus sharpei	Rs	3
Redunca redunca	Red	4
Sylvicapra grimmia	Sg	4
Syncerus caffer	Sc	3
Taurotragus oryx	To	3
HEAVY WOODLAND-BUSHLAND		
Total number of specimens = 32		
Kobus defassa	Kd	5
Madoqua kirki	Mk	4
Madoqua saltiana	Ms	1
Neotragus batesi	Nb	2
Neotragus moschatus	Nm	1
Neotragus pygmaeus	Np	1
Taurotragus derbianus	Td	2
Tragelaphus scriptus	Ts	11
Tragelaphus speki	Tsp	1
Tragelaphus strepsiceros	Tst	4
FOREST		
Total number of specimens = 30		
Alces alces	Aa	4
Bos javanicus	Bj	3
Bos sauveli	Bs	2
Bubalus mindorensis	Bm	1
Cephalophus leucogaster	Cl	2
Cephalophus monticola	Cm	5
Cephalophus nigrifrons	Cn	6
Hyemoschus aquaticus	Ha	4
Tragelaphus eurycerus	Te	3
MONTANE LIGHT COVER		
Total number of specimens = 17		
Capra sibirica	Cs	3
Oreamnos americanus	Ora	2
Ovis ammon	Oa	1
Ovis canadensis	Oc	2
Ovis dalli	Od	2
Ovis vignei	Ov	3
Pseudois nayaur	Pn	2
Rupicapra rupicapra	Rr	2
MONTANE HEAVY COVER		
Total number of specimens = 25		
Budorcas taxicolor	Bt	9
Elaphodus cephalophus	Ec	4
Nemorhaedus crispus	Nc	2
Nemorhaedus goral	Ng	3
Nemorhaedus sumatraensis	Ns	4
Nemorhaedus swinhoei	Nsw	1
Pudu mephistophiles	Pm	2

Appendix D, Table FF. Species breakdown of the ulna dataset

Species	Species code	Number	Species	Species code	Number
TOTAL = 204			**HEAVY WOODLAND-BUSHLAND**		
			Total number of specimens = 31		
GRASSLAND					
Total number of specimens = 13			Kobus defassa	Kd	5
			Madoqua kirki	Mk	4
Addax nasomaculatus	An	1	Madoqua saltiana	Ms	0
Bison bison	Bb	7	Neotragus batesi	Nb	2
Damaliscus dorcas	Dd	1	Neotragus moschatus	Nm	1
Damaliscus lunatus	Dl	2	Neotragus pygmaeus	Np	1
Ovibos moschatus	Om	0	Taurotragus derbianus	Td	2
Procapra picticaudata	Pp	2	Tragelaphus scriptus	Ts	11
			Tragelaphus speki	Tsp	1
WOODED-BUSHED GRASSLAND			Tragelaphus strepsiceros	Tst	4
Total number of specimens = 44					
			FOREST		
Alcelaphus buselaphus	Ab	4	**Total number of specimens = 27**		
Antilope cervicapra	Ac	0			
Connochaetes gnu	Cg	1	Alces alces	Aa	3
Connochaetes taurinus	Ct	4	Bos javanicus	Bj	3
Damaliscus hunteri	Dh	3	Bos sauveli	Bs	2
Gazella rufifrons	Gr	2	Bubalus mindorensis	Bm	1
Gazella soemmerringi	Gso	2	Cephalophus leucogaster	Cl	2
Gazella speki	Gs	2	Cephalophus monticola	Cm	4
Gazella subgutturosa	Gsu	2	Cephalophus nigrifrons	Cn	6
Gazella thomsoni	Gt	4	Hyemoschus aquaticus	Ha	3
Hippotragus equinus	He	2	Tragelaphus eurycerus	Te	3
Kobus kob	Kk	5			
Kobus leche	Kl	1	**MONTANE LIGHT COVER**		
Madoqua guentheri	Mg	1	**Total number of specimens = 17**		
Ourebia ourebi	Ouo	2			
Raphicerus campestris	Rc	6	Capra sibirica	Cs	3
Redunca fulvorufula	Rf	3	Oreamnos americanus	Ora	2
			Ovis ammon	Oa	1
LIGHT WOODLAND-BUSHLAND			Ovis canadensis	Oc	2
Total number of specimens = 49			Ovis dalli	Od	2
			Ovis vignei	Ov	3
Aepyceros melampus	Am	7	Pseudois nayaur	Pn	2
Gazella cuvieri	Gc	2	Rupicapra rupicapra	Rr	2
Gazella granti	Gg	4			
Hippotragus niger	Hn	5	**MONTANE HEAVY COVER**		
Litocranius walleri	Lw	5	**Total number of specimens = 23**		
Odocoileus virginianus	Odv	4			
Oreotragus oreotragus	Oo	4	Budorcas taxicolor	Bt	9
Oryx beisa	Ob	2	Elaphodus cephalophus	Ec	4
Raphicerus sharpei	Rs	3	Nemorhaedus crispus	Nc	1
Redunca redunca	Red	3	Nemorhaedus goral	Ng	3
Sylvicapra grimmia	Sg	4	Nemorhaedus sumatraensis	Ns	4
Syncerus caffer	Sc	3	Nemorhaedus swinhoei	Nsw	1
Taurotragus oryx	To	3	Pudu mephistophiles	Pm	1

Appendix D, Table GG. Species breakdown of the proximal dataset

Species	Species code	Number
TOTAL = 209		
GRASSLAND		
Total number of specimens = 13		
Addax nasomaculatus	An	1
Bison bison	Bb	7
Damaliscus dorcas	Dd	1
Damaliscus lunatus	Dl	2
Ovibos moschatus	Om	0
Procapra picticaudata	Pp	2
WOODED-BUSHED GRASSLAND		
Total number of specimens = 46		
Alcelaphus buselaphus	Ab	4
Antilope cervicapra	Ac	2
Connochaetes gnu	Cg	1
Connochaetes taurinus	Ct	4
Damaliscus hunteri	Dh	3
Gazella rufifrons	Gr	2
Gazella soemmerringi	Gso	2
Gazella speki	Gs	2
Gazella subgutturosa	Gsu	2
Gazella thomsoni	Gt	4
Hippotragus equinus	He	2
Kobus kob	Kk	5
Kobus leche	Kl	1
Madoqua guentheri	Mg	1
Ourebia ourebi	Ouo	2
Raphicerus campestris	Rc	6
Redunca fulvorufula	Rf	3
LIGHT WOODLAND-BUSHLAND		
Total number of specimens = 49		
Aepyceros melampus	Am	7
Gazella cuvieri	Gc	2
Gazella granti	Gg	4
Hippotragus niger	Hn	5
Litocranius walleri	Lw	5
Odocoileus virginianus	Odv	4
Oreotragus oreotragus	Oo	4
Oryx beisa	Ob	2
Raphicerus sharpei	Rs	3
Redunca redunca	Red	3
Sylvicapra grimmia	Sg	4
Syncerus caffer	Sc	3
Taurotragus oryx	To	3
HEAVY WOODLAND-BUSHLAND		
Total number of specimens = 32		
Kobus defassa	Kd	5
Madoqua kirki	Mk	4
Madoqua saltiana	Ms	1
Neotragus batesi	Nb	2
Neotragus moschatus	Nm	1
Neotragus pygmaeus	Np	1
Taurotragus derbianus	Td	2
Tragelaphus scriptus	Ts	11
Tragelaphus speki	Tsp	1
Tragelaphus strepsiceros	Tst	4
FOREST		
Total number of specimens = 29		
Alces alces	Aa	4
Bos javanicus	Bj	3
Bos sauveli	Bs	2
Bubalus mindorensis	Bm	1
Cephalophus leucogaster	Cl	2
Cephalophus monticola	Cm	4
Cephalophus nigrifrons	Cn	6
Hyemoschus aquaticus	Ha	4
Tragelaphus eurycerus	Te	3
MONTANE LIGHT COVER		
Total number of specimens = 17		
Capra sibirica	Cs	3
Oreamnos americanus	Ora	2
Ovis ammon	Oa	1
Ovis canadensis	Oc	2
Ovis dalli	Od	2
Ovis vignei	Ov	3
Pseudois nayaur	Pn	2
Rupicapra rupicapra	Rr	2
MONTANE HEAVY COVER		
Total number of specimens = 23		
Budorcas taxicolor	Bt	9
Elaphodus cephalophus	Ec	4
Nemorhaedus crispus	Nc	1
Nemorhaedus goral	Ng	3
Nemorhaedus sumatraensis	Ns	4
Nemorhaedus swinhoei	Nsw	1
Pudu mephistophiles	Pm	1

Appendix D, Table HH. Species breakdown of the unciform dataset

Species	Species code	Number	Species	Species code	Number
TOTAL = 206			**HEAVY WOODLAND-BUSHLAND**		
			Total number of specimens = 28		
GRASSLAND					
Total number of specimens = 14			Kobus defassa	Kd	4
			Madoqua kirki	Mk	2
Addax nasomaculatus	An	1	Madoqua saltiana	Ms	1
Bison bison	Bb	7	Neotragus batesi	Nb	2
Damaliscus dorcas	Dd	1	Neotragus moschatus	Nm	0
Damaliscus lunatus	Dl	2	Neotragus pygmaeus	Np	1
Ovibos moschatus	Om	3	Taurotragus derbianus	Td	2
Procapra picticaudata	Pp	0	Tragelaphus scriptus	Ts	11
			Tragelaphus speki	Tsp	1
WOODED-BUSHED GRASSLAND			Tragelaphus strepsiceros	Tst	4
Total number of specimens = 47					
			FOREST		
Alcelaphus buselaphus	Ab	4	**Total number of specimens = 30**		
Antilope cervicapra	Ac	2			
Connochaetes gnu	Cg	1	Alces alces	Aa	4
Connochaetes taurinus	Ct	4	Bos javanicus	Bj	3
Damaliscus hunteri	Dh	3	Bos sauveli	Bs	2
Gazella rufifrons	Gr	2	Bubalus mindorensis	Bm	1
Gazella soemmerringi	Gso	2	Cephalophus leucogaster	Cl	2
Gazella speki	Gs	2	Cephalophus monticola	Cm	5
Gazella subgutturosa	Gsu	2	Cephalophus nigrifrons	Cn	6
Gazella thomsoni	Gt	4	Hyemoschus aquaticus	Ha	4
Hippotragus equinus	He	2	Tragelaphus eurycerus	Te	3
Kobus kob	Kk	4			
Kobus leche	Kl	1	**MONTANE LIGHT COVER**		
Madoqua guentheri	Mg	0	**Total number of specimens = 16**		
Ourebia ourebi	Ouo	5			
Raphicerus campestris	Rc	6	Capra sibirica	Cs	3
Redunca fulvorufula	Rf	3	Oreamnos americanus	Ora	1
			Ovis ammon	Oa	2
LIGHT WOODLAND-BUSHLAND			Ovis canadensis	Oc	2
Total number of specimens = 50			Ovis dalli	Od	2
			Ovis vignei	Ov	3
Aepyceros melampus	Am	7	Pseudois nayaur	Pn	2
Gazella cuvieri	Gc	2	Rupicapra rupicapra	Rr	1
Gazella granti	Gg	4			
Hippotragus niger	Hn	5	**MONTANE HEAVY COVER**		
Litocranius walleri	Lw	4	**Total number of specimens = 21**		
Odocoileus virginianus	Odv	4			
Oreotragus oreotragus	Oo	4	Budorcas taxicolor	Bt	6
Oryx beisa	Ob	2	Elaphodus cephalophus	Ec	4
Raphicerus sharpei	Rs	3	Nemorhaedus crispus	Nc	2
Redunca redunca	Red	4	Nemorhaedus goral	Ng	2
Sylvicapra grimmia	Sg	5	Nemorhaedus sumatraensis	Ns	4
Syncerus caffer	Sc	3	Nemorhaedus swinhoei	Nsw	1
Taurotragus oryx	To	3	Pudu mephistophiles	Pm	2

APPENDIX E

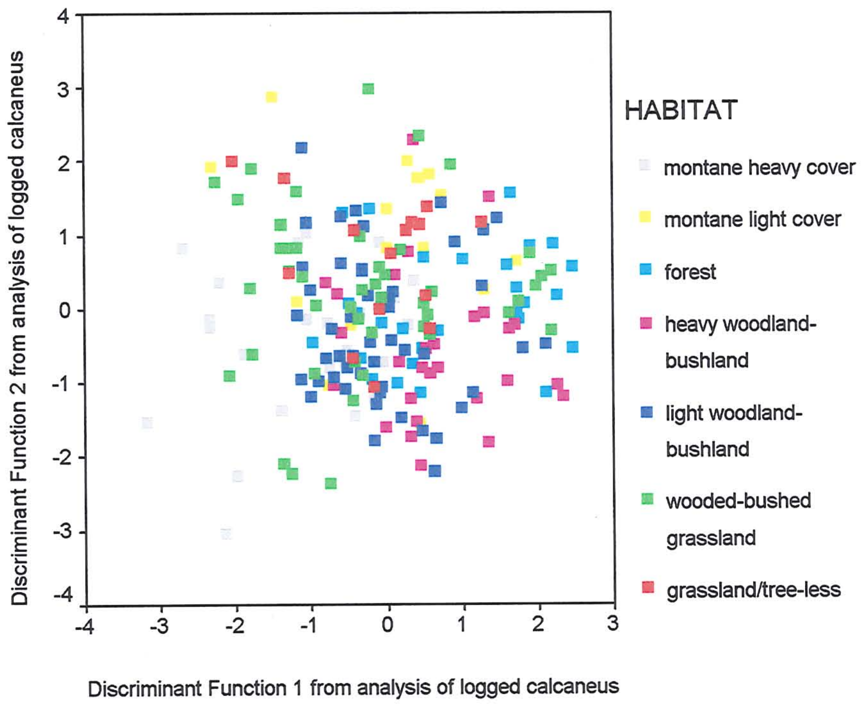
COMPLETE RESULTS OF THE DISCRIMINANT FUNCTION ANALYSES: STRUCTURE MATRICES, CLASSIFICATION RESULTS TABLES AND SCATTER PLOTS OF THE FIRST AND SECOND DISCRIMINANT FUNCTION FOR EVERY ANALYSIS CONDUCTED ON THE MODERN DATA

Note: All structure matrices present pooled within-groups correlations between discriminating variables and standardised canonical discriminant functions. The percentage of variance described by each function is provided. Where the logged data has been analysed, the measurement is preceded by the prefix "LOG" and the size corrected analyses use the prefix "RES". Measurement definitions and codes can be found in Table 3.4 in Chapter 3.

Appendix E, Table A1. Structure matrix from an analysis of the logged calcaneus data

Structure Matrix

	Function					
	1 45.8%	2 27.9%	3 12.9%	4 8.3%	5 2.9%	6 2.1%
LOGC5	.816	.451	.131	.070	.273	.016
LOGC7	.803	.411	.177	.240	.261	.000
LOGC1	.799	.428	.138	.190	.295	.103
LOGC2	.788	.418	.124	.193	.302	.122
LOGC8	.777	.502	.153	.131	.209	-.101
LOGC3	.754	.493	.273	.194	.225	.119
LOGC6	.750	.435	.284	.140	.359	.060
LOGC4	.691	.590	.073	.119	.348	-.048



Appendix E, Figure A1. Scatter plot of the first and second discriminant functions from an analysis of the logged calcaneus data

Appendix E, Tale A2. Classification results table from an analysis of the logged calcaneus data

Classification Results[a]

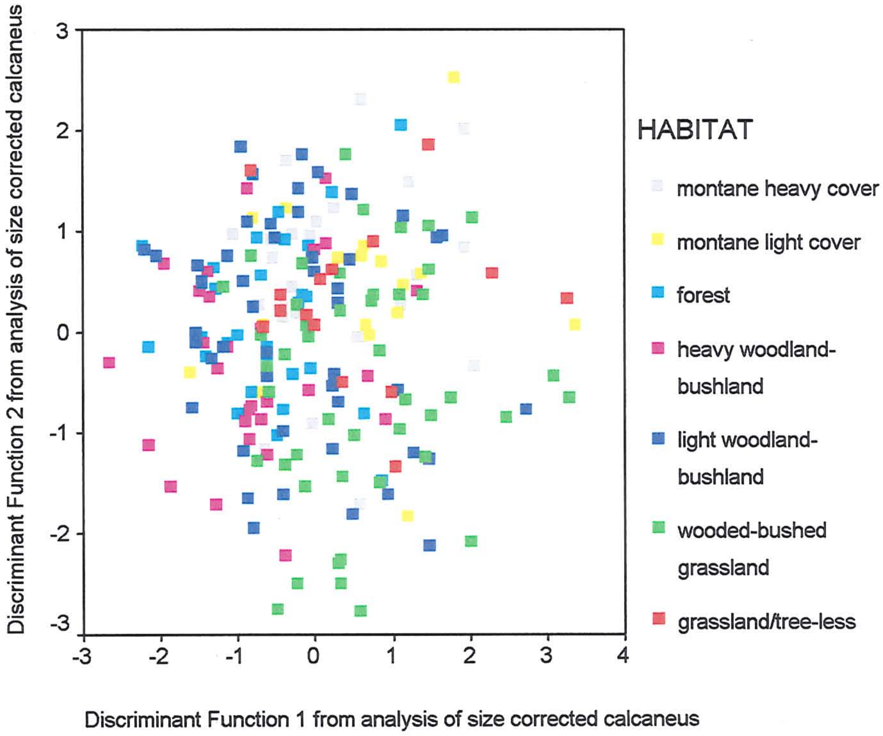
		HABITAT	Predicted Group Membership: grassland/ tree-less	wooded-bushed grassland	light woodland-bushland	heavy woodland-bushland	forest	montane light cover	montane heavy cover	Total
Original	Count	grassland/tree-less	1	7	4	0	2	1	0	15
		wooded-bushed grassland	2	25	7	1	7	1	3	46
		light woodland-bushland	1	13	21	4	6	0	4	49
		heavy woodland-bushland	0	5	11	10	2	0	0	28
		forest	1	3	10	2	12	0	0	28
		montane light cover	1	2	3	1	4	4	2	17
		montane heavy cover	1	4	9	0	0	0	11	25
	%	grassland/tree-less	6.7	46.7	26.7	.0	13.3	6.7	.0	100.0
		wooded-bushed grassland	4.3	54.3	15.2	2.2	15.2	2.2	6.5	100.0
		light woodland-bushland	2.0	26.5	42.9	8.2	12.2	.0	8.2	100.0
		heavy woodland-bushland	.0	17.9	39.3	35.7	7.1	.0	.0	100.0
		forest	3.6	10.7	35.7	7.1	42.9	.0	.0	100.0
		montane light cover	5.9	11.8	17.6	5.9	23.5	23.5	11.8	100.0
		montane heavy cover	4.0	16.0	36.0	.0	.0	.0	44.0	100.0

a. 40.4% of original grouped cases correctly classified.

Appendix E, Table A3. Structure matrix from an analysis of the size corrected calcaneus data

Structure Matrix

	Function					
	1 51.1%	2 23.9%	3 12.0%	4 6.8%	5 4.5%	6 1.7%
RESC6	-.235	.781	.058	-.078	.265	.377
RESC3	-.112	.729	.061	.396	-.017	.464
RESC7	-.428	.486	.372	.382	.410	.124
RESC4	.288	.302	-.106	.148	.811	.211
RESC5	-.402	.350	-.329	.153	.561	.203
RESC8	-.100	.338	-.128	.387	.484	-.147
RESC1	-.353	.352	.217	.179	.308	.503
RESC2	-.318	.302	.276	.062	.262	.416



Appendix E, Figure A2. Scatter plot of the first and second discriminant functions from an analysis of the size corrected calcaneus data

Appendix E, Table A4. Classification results table from an analysis of the size corrected calcaneus data

Classification Results[a]

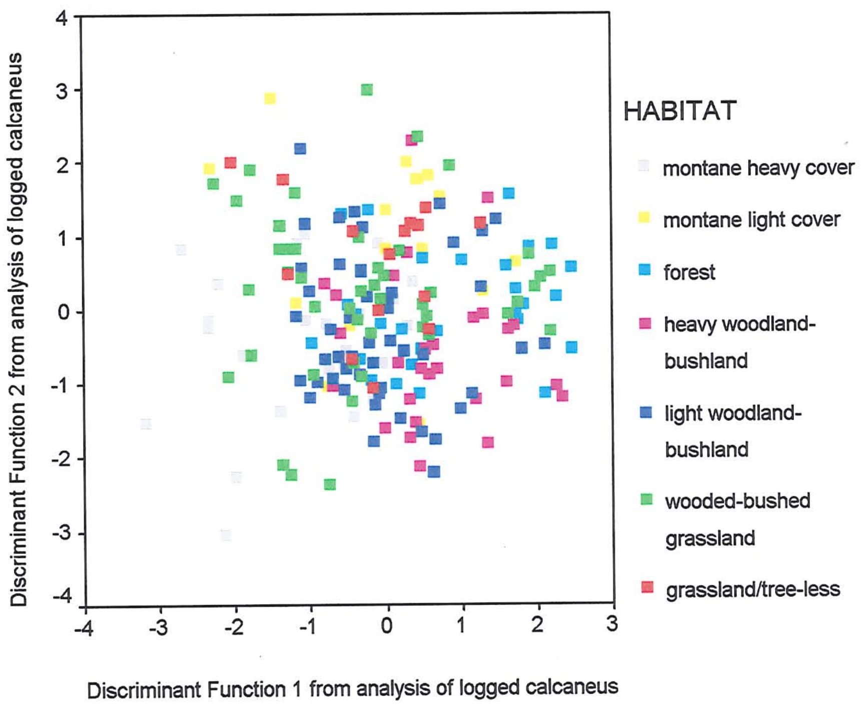
		HABITAT	Predicted Group Membership							Total
			grassland/ tree-less	wooded-bushed grassland	light woodland-bushland	heavy woodland-bushland	forest	montane light cover	montane heavy cover	
Original	Count	grassland/tree-less	0	4	7	0	1	0	3	15
		wooded-bushed grassland	1	28	11	2	0	1	3	46
		light woodland-bushland	0	11	21	4	5	2	6	49
		heavy woodland-bushland	0	4	10	12	0	1	1	28
		forest	0	4	17	2	4	0	1	28
		montane light cover	1	3	5	1	1	5	1	17
		montane heavy cover	1	5	10	0	3	2	4	25
	%	grassland/tree-less	.0	26.7	46.7	.0	6.7	.0	20.0	100.0
		wooded-bushed grassland	2.2	60.9	23.9	4.3	.0	2.2	6.5	100.0
		light woodland-bushland	.0	22.4	42.9	8.2	10.2	4.1	12.2	100.0
		heavy woodland-bushland	.0	14.3	35.7	42.9	.0	3.6	3.6	100.0
		forest	.0	14.3	60.7	7.1	14.3	.0	3.6	100.0
		montane light cover	5.9	17.6	29.4	5.9	5.9	29.4	5.9	100.0
		montane heavy cover	4.0	20.0	40.0	.0	12.0	8.0	16.0	100.0

a. 35.6% of original grouped cases correctly classified.

Appendix E, Table B1. Structure matrix from an analysis of the logged cuneiform data

Structure Matrix

	Function				
	1 65.4%	2 23.4%	3 7.9%	4 3.1%	5 0.2%
LOGCE1	.400	.088	.606	.544	.411
LOGCE5	.460	-.001	.460	.654	.386
LOGCE4	.287	.152	.500	.648	.474
LOGCE3	.348	.064	.623	.637	.287
LOGCE2	.444	.180	.567	.575	.345



Appendix E, Figure B1. Scatter plot of the first and second discriminant functions from an analysis of the logged cuneiform data

Appendix A, Table B2. Classification results table from an analysis of the logged cuneiform data

Classification Results[a]

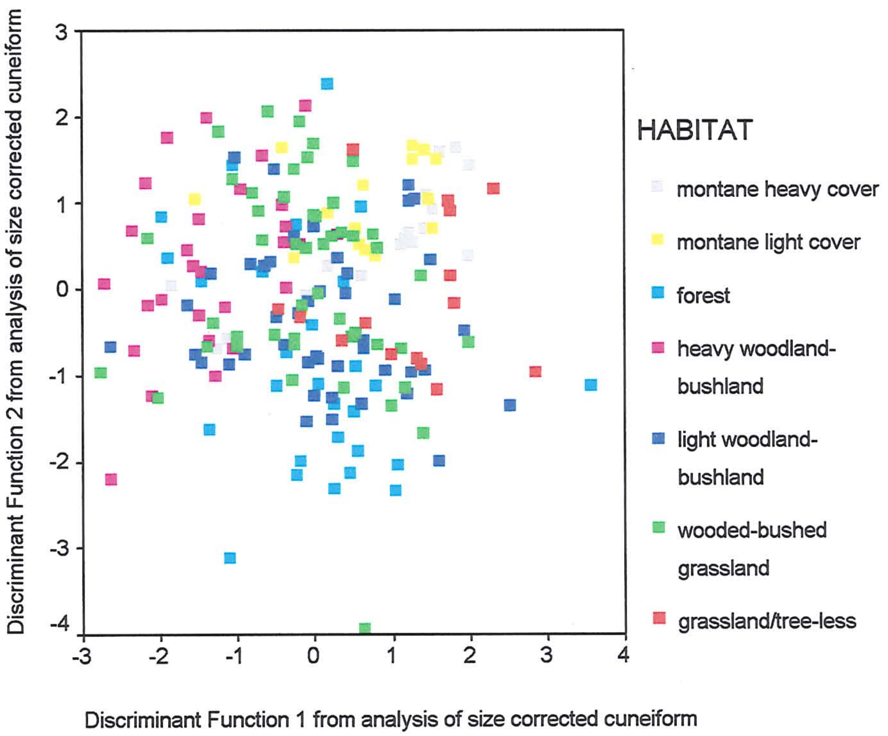
		HABITAT	Predicted Group Membership: grassland/ tree-less	wooded-bushed grassland	light woodland-bushland	heavy woodland-bushland	forest	montane light cover	montane heavy cover	Total
Original	Count	grassland/tree-less	10	1	1	0	0	2	1	15
		wooded-bushed grassland	0	23	13	7	4	1	0	48
		light woodland-bushland	2	20	19	4	1	0	0	46
		heavy woodland-bushland	0	9	1	18	1	0	0	29
		forest	2	5	12	3	4	2	1	29
		montane light cover	1	6	2	1	0	6	0	16
		montane heavy cover	6	3	3	4	0	1	2	19
	%	grassland/tree-less	66.7	6.7	6.7	.0	.0	13.3	6.7	100.0
		wooded-bushed grassland	.0	47.9	27.1	14.6	8.3	2.1	.0	100.0
		light woodland-bushland	4.3	43.5	41.3	8.7	2.2	.0	.0	100.0
		heavy woodland-bushland	.0	31.0	3.4	62.1	3.4	.0	.0	100.0
		forest	6.9	17.2	41.4	10.3	13.8	6.9	3.4	100.0
		montane light cover	6.3	37.5	12.5	6.3	.0	37.5	.0	100.0
		montane heavy cover	31.6	15.8	15.8	21.1	.0	5.3	10.5	100.0

a. 40.6% of original grouped cases correctly classified.

Appendix E, Table B3. Structure matrix from an analysis of the size corrected cuneiform data

Structure Matrix

	Function				
	1 54.2%	2 28.3%	3 11.9%	4 4.8%	5 0.8%
RESCE2	.364	.583	.493	.429	.317
RESCE5	.415	-.071	.889	.028	.179
RESCE4	-.332	.439	.822	.064	-.130
RESCE1	.196	.207	.630	.722	.037
RESCE3	-.069	.059	.595	.492	.629



Appendix E, Figure B2. Scatter plot of the first and second discriminant functions from an analysis of the size corrected cuneiform data

Appendix E, Table B4. Classification results table from an analysis of the size corrected cuneiform data

Classification Results[a]

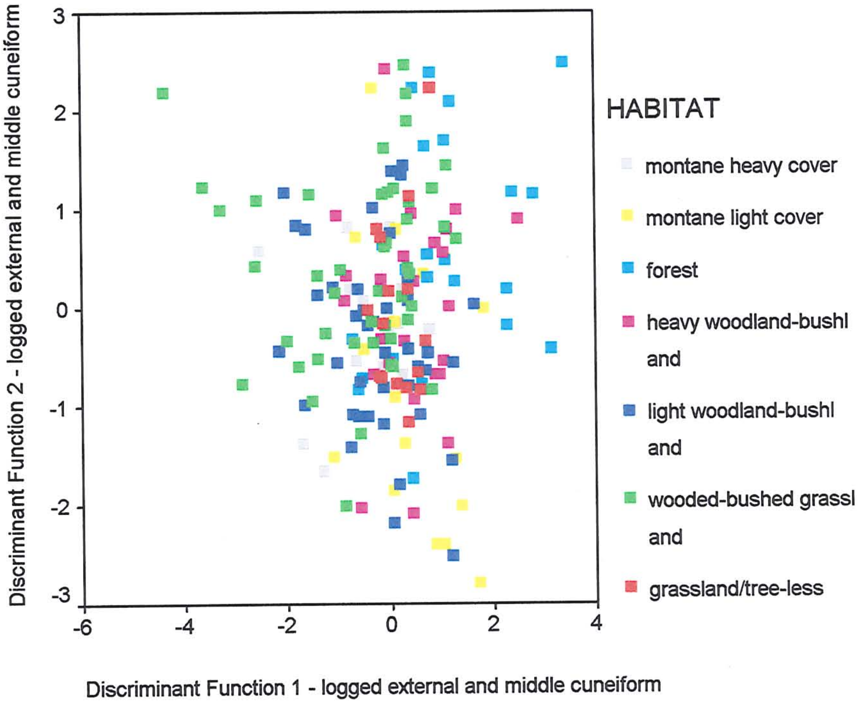
			Predicted Group Membership							
		HABITAT	grassland/ tree-less	wooded-bushed grassland	light woodland-bushland	heavy woodland-bushland	forest	montane light cover	montane heavy cover	Total
Original	Count	grassland/tree-less	1	1	8	0	2	2	1	15
		wooded-bushed grassland	0	28	14	5	1	0	0	48
		light woodland-bushland	3	15	18	5	3	1	1	46
		heavy woodland-bushland	0	8	1	18	0	1	1	29
		forest	1	4	10	2	8	2	2	29
		montane light cover	1	4	3	1	0	4	3	16
		montane heavy cover	0	6	1	3	1	1	7	19
	%	grassland/tree-less	6.7	6.7	53.3	.0	13.3	13.3	6.7	100.0
		wooded-bushed grassland	.0	58.3	29.2	10.4	2.1	.0	.0	100.0
		light woodland-bushland	6.5	32.6	39.1	10.9	6.5	2.2	2.2	100.0
		heavy woodland-bushland	.0	27.6	3.4	62.1	.0	3.4	3.4	100.0
		forest	3.4	13.8	34.5	6.9	27.6	6.9	6.9	100.0
		montane light cover	6.3	25.0	18.8	6.3	.0	25.0	18.8	100.0
		montane heavy cover	.0	31.6	5.3	15.8	5.3	5.3	36.8	100.0

a. 41.6% of original grouped cases correctly classified.

Appendix E, Table C1. Structure matrix from an analysis of the logged external and middle cuneiform data

Structure Matrix

	Function					
	1 44.1%	2 24.2%	3 16.7%	4 9.7%	5 4.5%	6 0.8%
LOGTB1	.730	.389	.249	.061	-.239	.434
LOGTB8	.714	.239	.423	.130	.024	.334
LOGTB3	.669	.227	.517	-.053	-.154	.399
LOGTB7	.655	.259	.451	-.144	-.050	.471
LOGTB6	.642	.301	.438	-.215	-.042	.342
LOGTB5	.609	.215	.460	-.014	-.053	.493
LOGTB4	.579	.340	.524	.008	-.028	.437
LOGTB2	.545	.129	.646	-.119	.127	.355



Appendix E, Figure C1. Scatter plot if the first and second discriminant functions from an analysis of the logged external and middle cuneiform data

Appendix E, Table C2. Classification results table from an analysis of the logged external and middle cuneiform data

Classification Results[a]

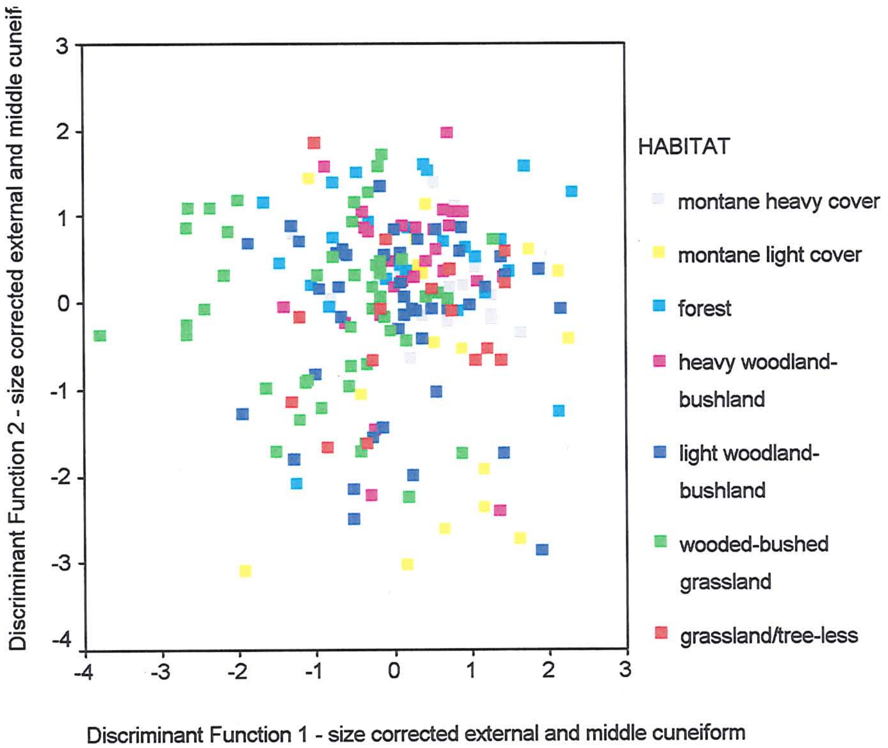
			Predicted Group Membership							
		HABITAT	grassland/ tree-less	wooded-bushed grassland	light woodland-bushland	heavy woodland-bushland	forest	montane light cover	montane heavy cover	Total
Original	Count	grassland/tree-less	0	6	8	1	0	1	0	16
		wooded-bushed grassland	0	28	9	5	3	1	0	46
		light woodland-bushland	0	9	23	3	1	7	0	43
		heavy woodland-bushland	0	6	5	11	4	1	0	27
		forest	0	3	5	3	14	0	0	25
		montane light cover	0	4	4	2	1	6	0	17
		montane heavy cover	2	3	11	0	0	0	2	18
	%	grassland/tree-less	.0	37.5	50.0	6.3	.0	6.3	.0	100.0
		wooded-bushed grassland	.0	60.9	19.6	10.9	6.5	2.2	.0	100.0
		light woodland-bushland	.0	20.9	53.5	7.0	2.3	16.3	.0	100.0
		heavy woodland-bushland	.0	22.2	18.5	40.7	14.8	3.7	.0	100.0
		forest	.0	12.0	20.0	12.0	56.0	.0	.0	100.0
		montane light cover	.0	23.5	23.5	11.8	5.9	35.3	.0	100.0
		montane heavy cover	11.1	16.7	61.1	.0	.0	.0	11.1	100.0

a. 43 8% of original grouped cases correctly classified.

Appendix E, Table C3. Structure matrix from an analysis of the size corrected external and middle cuneiform data

Structure Matrix

	Function					
	1 44.9%	2 25.5%	3 16.1%	4 9.0%	5 3.2%	6 1.3%
RESTB3	.686	-.087	.490	-.305	.104	.241
RESTB8	.613	.157	.535	.254	.157	-.393
RESTB7	.578	.069	.152	-.047	.318	.328
RESTB5	.498	-.080	.386	.194	.032	.491
RESTB2	.290	-.600	.234	.167	.564	-.040
RESTB1	.442	.584	.347	-.020	-.167	.475
RESTB4	.245	.029	.734	.103	.270	.222
RESTB6	.422	.177	.027	-.239	.619	.179



Appendix E, Figure C2. Scatter plot of the first and second discriminant functions from an analysis of the size corrected external and middle cuneiform data

Appendix E, Table C4. Classification results table from an analysis of the size corrected external and middle cuneiform data

Classification Results[a]

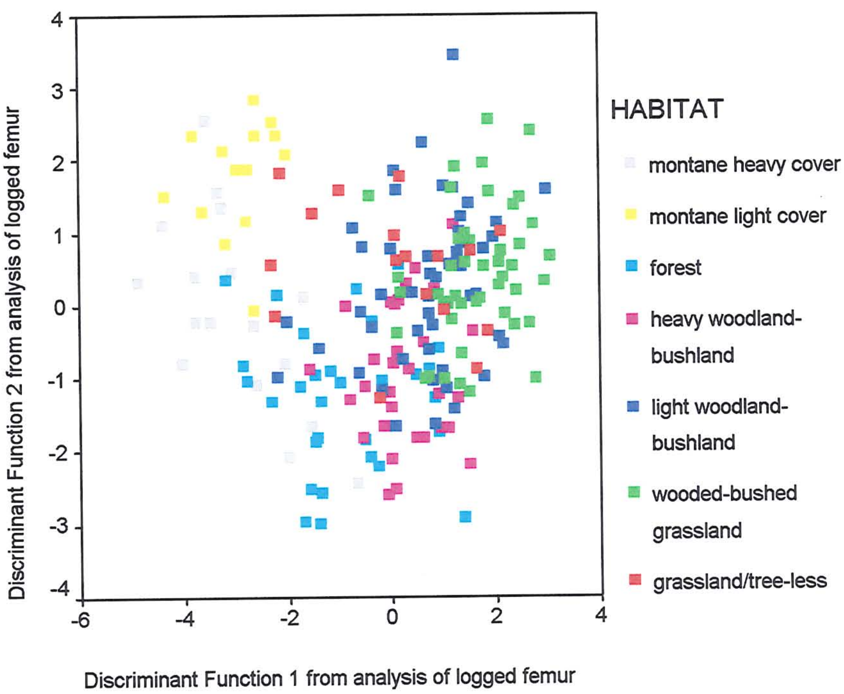
		HABITAT	Predicted Group Membership							Total
			grassland/ tree-less	wooded-bushed grassland	light woodland-bushland	heavy woodland-bushland	forest	montane light cover	montane heavy cover	
Original	Count	grassland/tree-less	1	6	7	1	1	0	0	16
		wooded-bushed grassland	0	30	8	5	2	1	0	46
		light woodland-bushland	1	13	21	3	2	3	0	43
		heavy woodland-bushland	0	9	5	9	3	1	0	27
		forest	2	6	3	6	8	0	0	25
		montane light cover	0	3	6	1	1	5	1	17
		montane heavy cover	3	3	7	2	2	0	1	18
	%	grassland/tree-less	6.3	37.5	43.8	6.3	6.3	.0	.0	100.0
		wooded-bushed grassland	.0	65.2	17.4	10.9	4.3	2.2	.0	100.0
		light woodland-bushland	2.3	30.2	48.8	7.0	4.7	7.0	.0	100.0
		heavy woodland-bushland	.0	33.3	18.5	33.3	11.1	3.7	.0	100.0
		forest	8.0	24.0	12.0	24.0	32.0	.0	.0	100.0
		montane light cover	.0	17.6	35.3	5.9	5.9	29.4	5.9	100.0
		montane heavy cover	16.7	16.7	38.9	11.1	11.1	.0	5.6	100.0

a. 39.1% of original grouped cases correctly classified.

Appendix E, Table D1. Structure matrix from an analysis of the logged femur data

Structure Matrix

	Function					
	1 56.1%	2 17.2%	3 12.3%	4 9.3%	5 3.0%	6 2.2%
LOGF8	.084	.126	.321	.086	.247	.614
LOGF2	-.013	.162	.240	.106	.259	.612
LOGF5	.038	.170	.327	.026	.246	.599
LOGF7	-.007	.151	.353	.097	.254	.598
LOGF11	.114	.171	.288	.050	.256	.592
LOGF4	.058	.204	.339	.046	.266	.591
LOGF9	.075	.156	.338	.066	.216	.590
LOGF3	.004	.159	.349	.094	.238	.588
LOGF13	-.006	.096	.314	.000	.254	.587
LOGF10	.009	.154	.323	.074	.218	.586
LOGF6	-.019	.127	.342	.096	.287	.569
LOGF14	.030	.162	.310	.041	.317	.550
LOGF12	.037	.223	.324	.096	.242	.500



Appendix E, Figure D1. Scatter plot of the first and second discriminant functions from an analysis of the logged femur

Appendix E, Table D2. Classification results table from an analysis of the logged femur data

Classification Results[a]

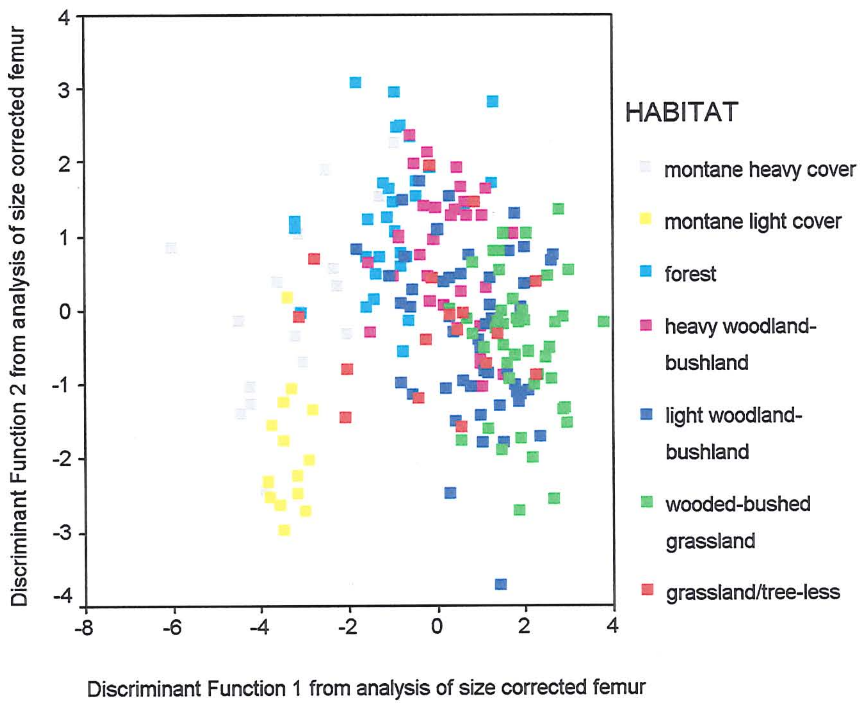
			Predicted Group Membership							
		HABITAT	grassland/ tree-less	wooded-bushed grassland	light woodland-bushland	heavy woodland-bushland	forest	montane light cover	montane heavy cover	Total
Original	Count	grassland/tree-less	11	3	1	0	0	0	2	17
		wooded-bushed grassland	0	31	10	5	0	0	0	46
		light woodland-bushland	4	9	30	5	2	0	1	51
		heavy woodland-bushland	0	3	6	21	2	0	0	32
		forest	2	0	5	2	20	1	0	30
		montane light cover	0	0	0	0	0	12	2	14
		montane heavy cover	0	0	1	0	3	0	13	17
	%	grassland/tree-less	64.7	17.6	5.9	.0	.0	.0	11.8	100.0
		wooded-bushed grassland	.0	67.4	21.7	10.9	.0	.0	.0	100.0
		light woodland-bushland	7.8	17.6	58.8	9.8	3.9	.0	2.0	100.0
		heavy woodland-bushland	.0	9.4	18.8	65.6	6.3	.0	.0	100.0
		forest	6.7	.0	16.7	6.7	66.7	3.3	.0	100.0
		montane light cover	.0	.0	.0	.0	.0	85.7	14.3	100.0
		montane heavy cover	.0	.0	5.9	.0	17.6	.0	76.5	100.0

a. 66.7% of original grouped cases correctly classified.

Appendix E, Table D3. Structure matrix from an analysis of the size corrected femur data

Structure Matrix

	Function					
	1 63.6%	2 15.0%	3 9.6%	4 8.2%	5 2.6%	6 1.1%
RESF11	.584	-.153	.103	.161	.059	.204
RESF9	.524	-.072	-.144	.029	-.122	.277
RESF8	.522	.082	.018	-.028	-.004	.076
RESF4	.392	-.299	-.179	.115	.130	.127
RESF5	.293	-.139	-.126	.226	-.003	.186
RESF2	.066	-.140	.355	-.037	-.014	.238
RESF13	.094	.187	-.050	.351	.005	.346
RESF14	.237	-.103	-.018	.164	.350	.317
RESF12	.252	-.337	-.083	-.115	.115	.597
RESF10	.188	-.073	-.066	-.001	-.133	.375
RESF6	.047	.073	-.083	-.102	.200	.273
RESF3	.144	-.066	-.148	-.117	-.014	.227
RESF7	.100	-.026	-.153	-.136	.038	.154



Appendix E, Figure D2. Scatter plot of the first and second discriminant functions from an analysis of the size corrected femur data

Appendix E, Table D4. Classification results table from an analysis of the size corrected femur data

Classification Results[a]

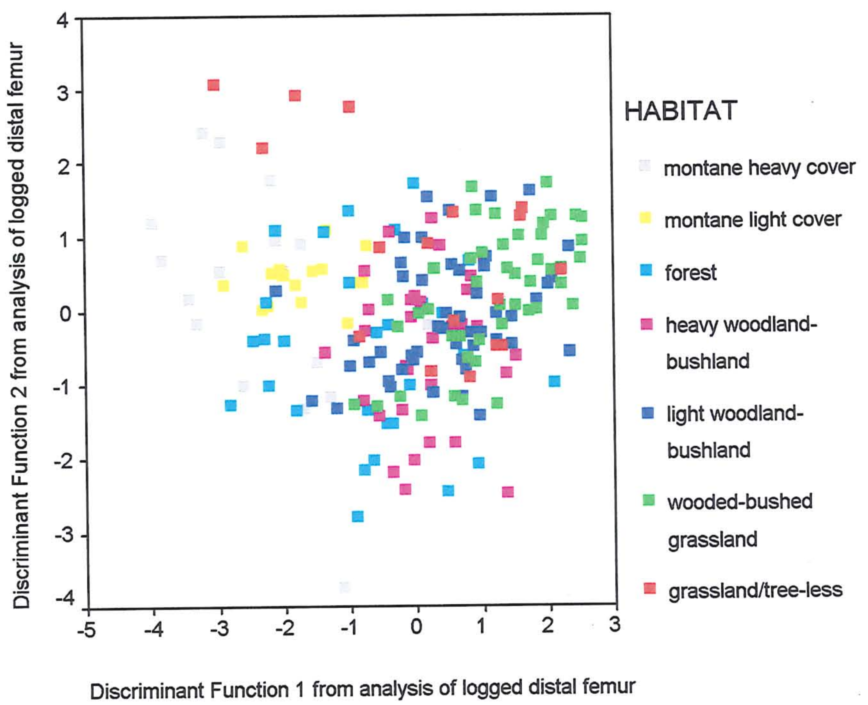
			Predicted Group Membership							
		HABITAT	grassland/ tree-less	wooded-bushed grassland	light woodland-bushland	heavy woodland-bushland	forest	montane light cover	montane heavy cover	Total
Original	Count	grassland/tree-less	5	2	5	0	1	0	4	17
		wooded-bushed grassland	0	33	9	4	0	0	0	46
		light woodland-bushland	4	10	29	4	4	0	0	51
		heavy woodland-bushland	1	2	6	21	2	0	0	32
		forest	1	0	2	3	23	0	1	30
		montane light cover	0	0	0	0	0	12	2	14
		montane heavy cover	0	0	0	0	3	0	14	17
	%	grassland/tree-less	29.4	11.8	29.4	.0	5.9	.0	23.5	100.0
		wooded-bushed grassland	.0	71.7	19.6	8.7	.0	.0	.0	100.0
		light woodland-bushland	7.8	19.6	56.9	7.8	7.8	.0	.0	100.0
		heavy woodland-bushland	3.1	6.3	18.8	65.6	6.3	.0	.0	100.0
		forest	3.3	.0	6.7	10.0	76.7	.0	3.3	100.0
		montane light cover	.0	.0	.0	.0	.0	85.7	14.3	100.0
		montane heavy cover	.0	.0	.0	.0	17.6	.0	82.4	100.0

a. 66.2% of original grouped cases correctly classified.

Appendix E, Table E1. Structure matrix from an analysis of the logged distal femur data

Structure Matrix

	Function			
	1 77.8%	2 11.9%	3 7.7%	4 2.7%
LOGF12	.060	.664	.502	.551
LOGF9	.111	.540	.632	.545
LOGF10	.018	.539	.603	.588
LOGF11	.167	.517	.540	.643



Appendix E, Figure E1. Scatter plot of the first and second discriminant functions from an analysis of the logged distal femur data

Appendix E, Table E2. Classification results table from an analysis of the logged distal femur data

Classification Results[a]

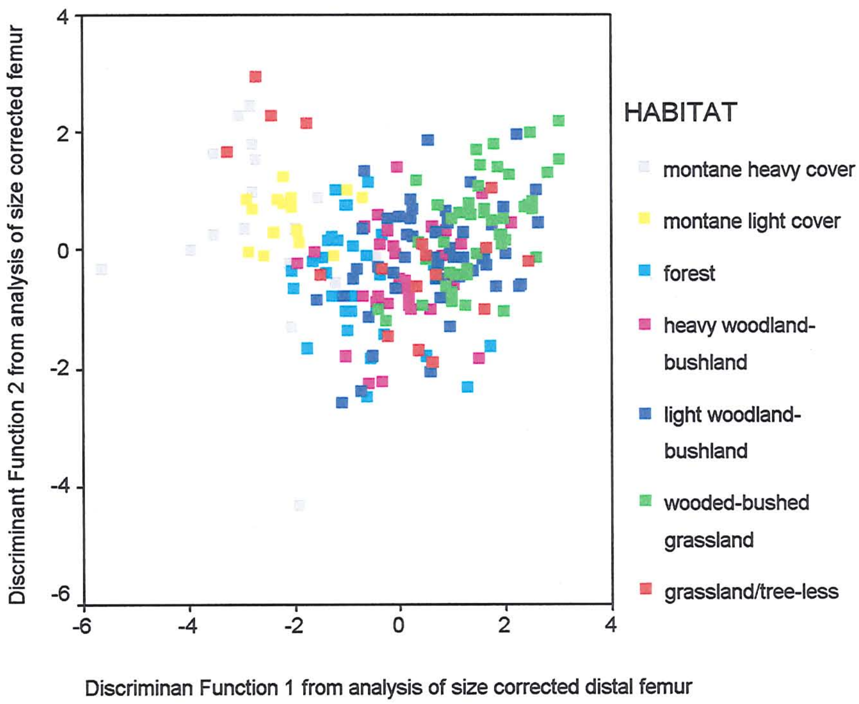
			Predicted Group Membership							
		HABITAT	grassland/ tree-less	wooded-bushed grassland	light woodland-bushland	heavy woodland-bushland	forest	montane light cover	montane heavy cover	Total
Original	Count	grassland/tree-less	4	5	4	0	1	1	2	17
		wooded-bushed grassland	0	27	15	2	2	0	0	46
		light woodland-bushland	1	15	26	3	6	0	1	52
		heavy woodland-bushland	0	5	14	9	3	1	0	32
		forest	3	0	8	5	6	2	6	30
		montane light cover	0	0	1	1	1	9	4	16
		montane heavy cover	0	0	1	0	4	4	8	17
	%	grassland/tree-less	23.5	29.4	23.5	.0	5.9	5.9	11.8	100.0
		wooded-bushed grassland	.0	58.7	32.6	4.3	4.3	.0	.0	100.0
		light woodland-bushland	1.9	28.8	50.0	5.8	11.5	.0	1.9	100.0
		heavy woodland-bushland	.0	15.6	43.8	28.1	9.4	3.1	.0	100.0
		forest	10.0	.0	26.7	16.7	20.0	6.7	20.0	100.0
		montane light cover	.0	.0	6.3	6.3	6.3	56.3	25.0	100.0
		montane heavy cover	.0	.0	5.9	.0	23.5	23.5	47.1	100.0

a. 42.4% of original grouped cases correctly classified.

Appendix E, Table E3. Structure matrix from an analysis of the size corrected distal femur data

Structure Matrix

	Function			
	1 87.8%	2 7.9%	3 3.9%	4 0.4%
RESF11	.769	.124	.351	.519
RESF9	.679	.099	-.348	.639
RESF12	.333	.788	-.045	.516
RESF10	.239	.185	-.138	.943



Appendix E, Figure E2. Scatter plot of the first and second discriminant functions from an analysis of the size corrected distal femur data

Appendix E, Table E4. Classification results table from an analysis of the size corrected distal femur data

Classification Results[a]

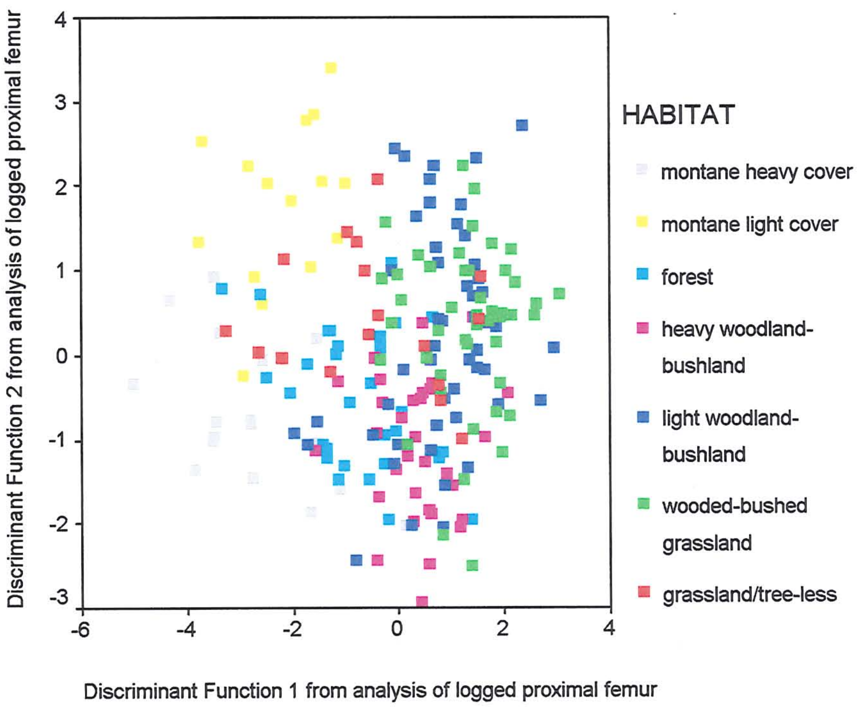
		HABITAT	Predicted Group Membership: grassland/tree-less	wooded-bushed grassland	light woodland-bushland	heavy woodland-bushland	forest	montane light cover	montane heavy cover	Total
Original	Count	grassland/tree-less	0	3	7	1	2	0	4	17
		wooded-bushed grassland	0	29	15	0	2	0	0	46
		light woodland-bushland	0	16	24	4	8	0	0	52
		heavy woodland-bushland	0	2	17	9	3	1	0	32
		forest	0	0	4	6	19	1	0	30
		montane light cover	0	0	1	1	1	9	4	16
		montane heavy cover	0	0	1	0	3	5	8	17
	%	grassland/tree-less	.0	17.6	41.2	5.9	11.8	.0	23.5	100.0
		wooded-bushed grassland	.0	63.0	32.6	.0	4.3	.0	.0	100.0
		light woodland-bushland	.0	30.8	46.2	7.7	15.4	.0	.0	100.0
		heavy woodland-bushland	.0	6.3	53.1	28.1	9.4	3.1	.0	100.0
		forest	.0	.0	13.3	20.0	63.3	3.3	.0	100.0
		montane light cover	.0	.0	6.3	6.3	6.3	56.3	25.0	100.0
		montane heavy cover	.0	.0	5.9	.0	17.6	29.4	47.1	100.0

a. 46.7% of original grouped cases correctly classified.

Appendix E, Table F1. Structure matrix from an analysis of the logged proximal femur data

Structure Matrix

	Function					
	1 67.8%	2 22.8%	3 6.3%	4 2.3%	5 0.8%	6 0.0%
LOGF7	-.041	.178	.710	.573	.130	.341
LOGF8	.066	.150	.708	.587	.096	.343
LOGF3	-.029	.188	.704	.553	.148	.376
LOGF4	.036	.244	.703	.566	.069	.346
LOGF6	-.054	.154	.684	.578	.024	.413
LOGF5	.014	.216	.641	.626	.084	.377



Appendix E, Figure F1. Scatter plot of the first and second discriminant functions from an analysis of the logged proximal femur

Appendix E, Table F2. Classification results table from an analysis of the logged proximal femur data

Classification Results[a]

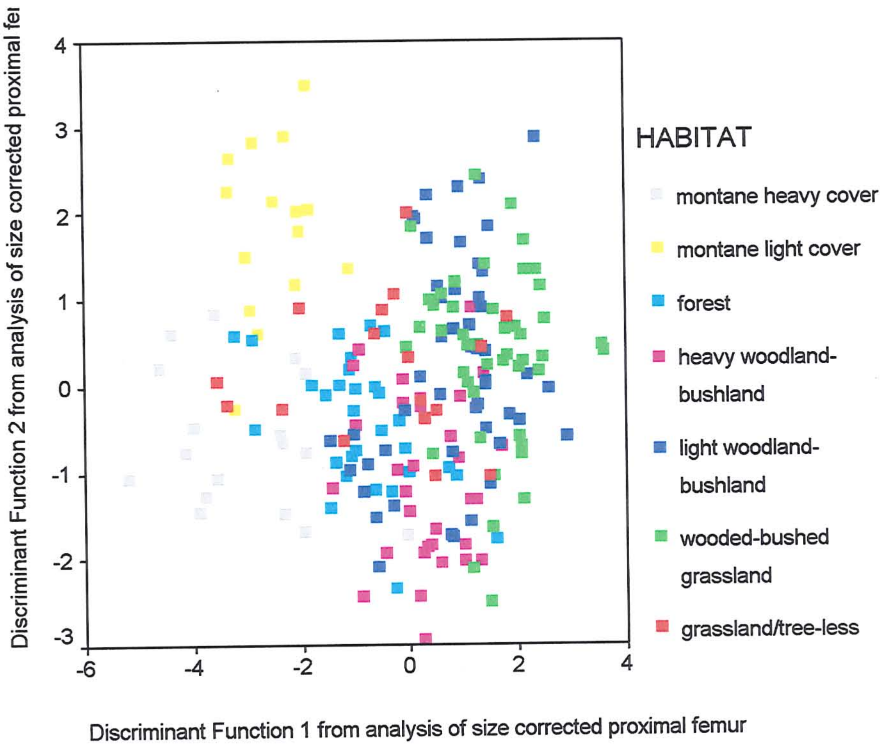
		HABITAT	Predicted Group Membership							Total
			grassland/ tree-less	wooded-bushed grassland	light woodland-bushland	heavy woodland-bushland	forest	montane light cover	montane heavy cover	
Original	Count	grassland/tree-less	9	2	2	1	0	0	3	17
		wooded-bushed grassland	0	24	16	5	1	0	0	46
		light woodland-bushland	2	16	20	9	4	0	1	52
		heavy woodland-bushland	0	3	9	18	2	0	0	32
		forest	3	0	3	8	13	2	1	30
		montane light cover	0	0	0	0	0	13	2	15
		montane heavy cover	0	0	0	1	3	0	13	17
	%	grassland/tree-less	52.9	11.8	11.8	5.9	.0	.0	17.6	100.0
		wooded-bushed grassland	.0	52.2	34.8	10.9	2.2	.0	.0	100.0
		light woodland-bushland	3.8	30.8	38.5	17.3	7.7	.0	1.9	100.0
		heavy woodland-bushland	.0	9.4	28.1	56.3	6.3	.0	.0	100.0
		forest	10.0	.0	10.0	26.7	43.3	6.7	3.3	100.0
		montane light cover	.0	.0	.0	.0	.0	86.7	13.3	100.0
		montane heavy cover	.0	.0	.0	5.9	17.6	.0	76.5	100.0

a 52.6% of original grouped cases correctly classified.

Appendix E, Table F3. Structure matrix from an analysis of the size corrected proximal femur data

Structure Matrix

	Function					
	1 75.4%	2 19.3%	3 3.8%	4 0.8%	5 0.4%	6 0.3%
RESF7	.098	.034	.372	.051	.300	.870
RESF3	.146	.079	.371	-.060	.455	.790
RESF5	.333	.225	-.060	.270	.416	.767
RESF8	.591	-.127	.265	.152	.241	.696
RESF4	.447	.353	.346	.267	.288	.634
RESF6	.039	-.069	.240	.477	.586	.604



Appendix E, Figure F2. Scatter plot of the first and second discriminant functions from an analysis of the size corrected proximal femur data

Appendix E, Table F4. Classification results table from an analysis of the size corrected proximal femur data

Classification Results[a]

			Predicted Group Membership							
		HABITAT	grassland/tree-less	wooded-bushed grassland	light woodland-bushland	heavy woodland-bushland	forest	montane light cover	montane heavy cover	Total
Original	Count	grassland/tree-less	3	3	5	1	2	0	3	17
		wooded-bushed grassland	2	26	15	3	0	0	0	46
		light woodland-bushland	1	15	24	8	4	0	0	52
		heavy woodland-bushland	4	1	6	18	3	0	0	32
		forest	3	0	2	6	17	1	1	30
		montane light cover	0	0	0	0	1	12	2	15
		montane heavy cover	0	0	0	1	3	0	13	17
	%	grassland/tree-less	17.6	17.6	29.4	5.9	11.8	.0	17.6	100.0
		wooded-bushed grassland	4.3	56.5	32.6	6.5	.0	.0	.0	100.0
		light woodland-bushland	1.9	28.8	46.2	15.4	7.7	.0	.0	100.0
		heavy woodland-bushland	12.5	3.1	18.8	56.3	9.4	.0	.0	100.0
		forest	10.0	.0	6.7	20.0	56.7	3.3	3.3	100.0
		montane light cover	.0	.0	.0	.0	6.7	80.0	13.3	100.0
		montane heavy cover	.0	.0	.0	5.9	17.6	.0	76.5	100.0

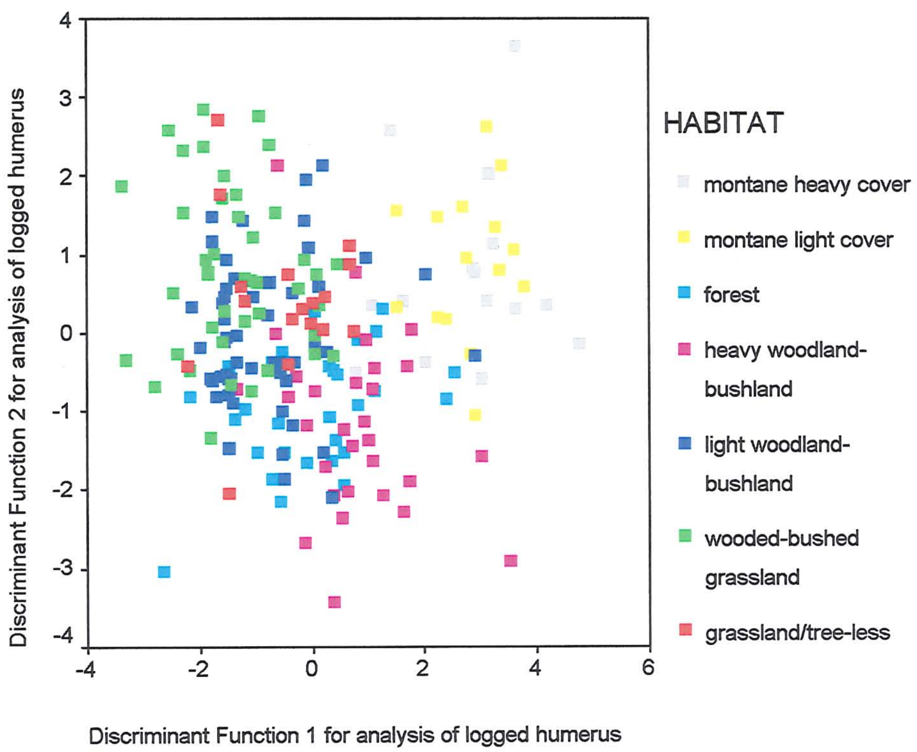
a. 54.1% of original grouped cases correctly classified.

Appendix E. Table G1. Structure matrix from an analysis of the logged humerus data

Structure Matrix

	Function					
	1 52.1%	2 17.1%	3 15.6%	4 10.0%	5 3.9%	6 1.3%
LOGH4	.039	.095	.342	.243	.065	.539
LOGH2	.080	.108	.382	.209	-.019	.535
LOGH1	.075	.109	.365	.217	-.032	.520
LOGH7	-.007	.167	.341	.286	-.007	.503
LOGH5	-.001	.174	.305	.266	-.002	.498
LOGH11	-.025	.200	.361	.194	.008	.495
LOGH9	-.050	.113	.386	.235	-.033	.495
LOGH6	.003	.118	.351	.281	-.001	.490
LOGH14	-.016	.155	.362	.231	.017	.486
LOGH10	.002	.151	.369	.219	.029	.482
LOGH8	.008	.161	.386	.244	-.010	.475
LOGH12	.023	.091	.356	.165	-.052	.471
LOGH13	.022	.122	.370	.291	.028	.458
LOGH3[a]	.039	.108	.228	.259	-.121	.388

a. This variable not used in the analysis.



Appendix E, Figure G1. Scatter plot of the first and second discriminant function from an analysis of the logged humerus

Appendix E, Table G2. Classification results table from an analysis of the logged humerus data

Classification Results[a]

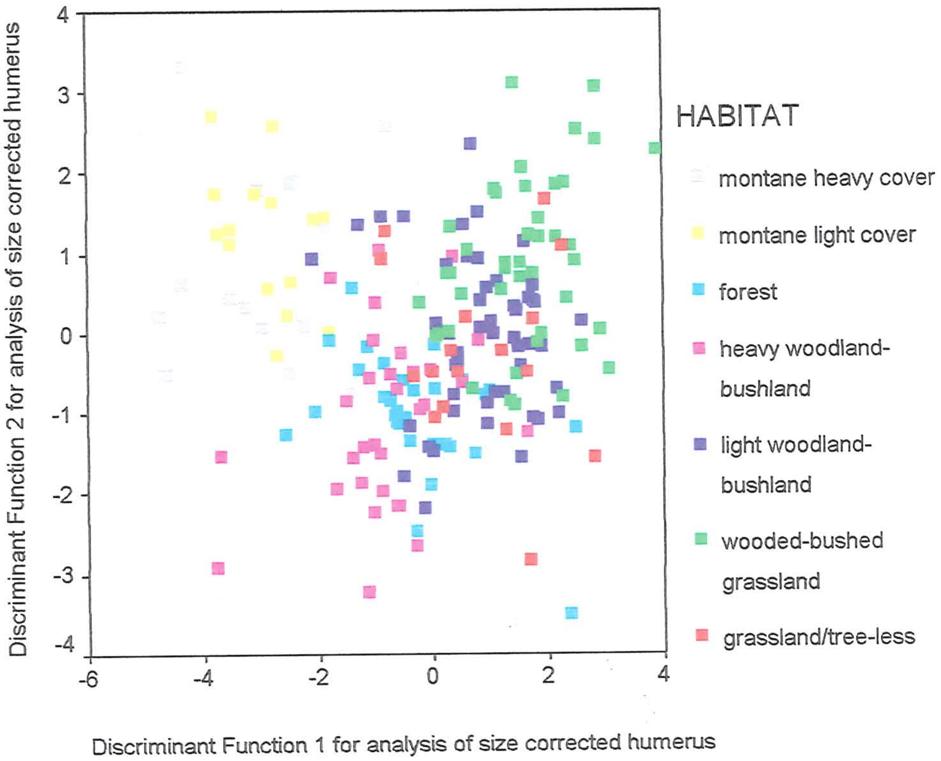
		HABITAT	Predicted Group Membership: grassland/tree-less	wooded-bushed grassland	light woodland-bushland	heavy woodland-bushland	forest	montane light cover	montane heavy cover	Total
Original	Count	grassland/tree-less	13	1	3	0	0	0	0	17
		wooded-bushed grassland	2	27	14	0	0	0	0	43
		light woodland-bushland	1	7	37	3	2	1	0	51
		heavy woodland-bushland	2	0	5	21	1	1	1	31
		forest	0	0	12	5	13	0	0	30
		montane light cover	0	0	0	0	0	14	1	15
		montane heavy cover	0	0	0	2	0	1	13	16
	%	grassland/tree-less	76.5	5.9	17.6	.0	.0	.0	.0	100.0
		wooded-bushed grassland	4.7	62.8	32.6	.0	.0	.0	.0	100.0
		light woodland-bushland	2.0	13.7	72.5	5.9	3.9	2.0	.0	100.0
		heavy woodland-bushland	6.5	.0	16.1	67.7	3.2	3.2	3.2	100.0
		forest	.0	.0	40.0	16.7	43.3	.0	.0	100.0
		montane light cover	.0	.0	.0	.0	.0	93.3	6.7	100.0
		montane heavy cover	.0	.0	.0	12.5	.0	6.3	81.3	100.0

a. 68.0% of original grouped cases correctly classified.

Appendix E, Table G3. Structure matrix from an analysis of the size corrected humerus data

Structure Matrix

	Function					
	1 57.1%	2 16.1%	3 11.9%	4 8.7%	5 4.0%	6 1.4%
RESH5	.069	.492	.195	-.093	.145	.008
RESH11	.159	.465	-.148	.143	.073	.004
RESH7	.105	.438	.077	-.241	.153	-.048
RESH8	.045	.427	-.233	-.144	.217	.090
RESH10	.067	.380	-.152	.038	.029	.139
RESH14	.132	.324	-.071	-.004	.058	.072
RESH4	-.103	.103	.071	-.020	-.082	-.004
RESH13	-.031	.201	-.016	-.289	.036	.209
RESH6	.054	.218	.076	-.239	.176	.072
RESH3	-.059	.250	.295	-.042	.490	.336
RESH12	-.038	.077	-.079	.236	.395	.172
RESH9	.351	.143	-.142	-.043	.354	.018
RESH1	-.246	.172	-.095	.017	.333	-.010
RESH2	-.253	.141	-.167	.031	.261	-.055



Appendix E, Figure G2. Scatter plot of the first and second discriminant function from an analysis of the size corrected humerus

Appendix E, Table G4. Classification results table from an analysis of the size corrected humerus data

Classification Results[a]

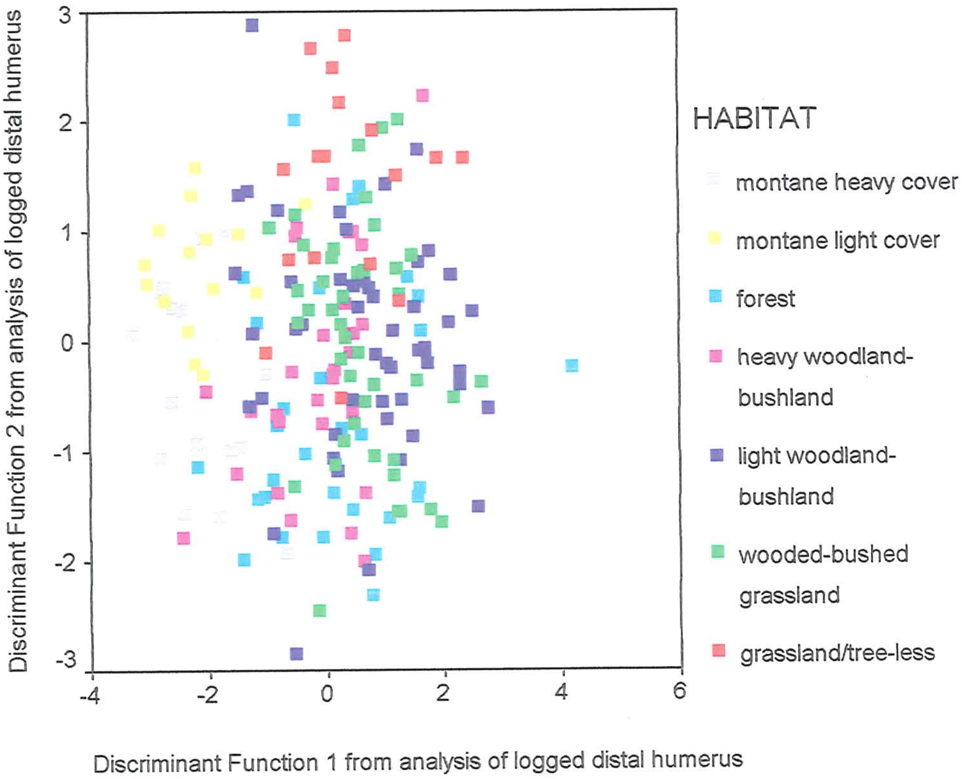
			Predicted Group Membership							
		HABITAT	grassland/ tree-less	wooded-bushed grassland	light woodland-bushland	heavy woodland-bushland	forest	montane light cover	montane heavy cover	Total
Original	Count	grassland/tree-less	13	1	3	0	0	0	0	17
		wooded-bushed grassland	1	29	13	0	0	0	0	43
		light woodland-bushland	2	9	33	2	4	1	0	51
		heavy woodland-bushland	2	0	4	21	2	1	1	31
		forest	0	1	8	6	15	0	0	30
		montane light cover	0	0	0	0	0	14	1	15
		montane heavy cover	0	0	0	1	0	1	14	16
	%	grassland/tree-less	76.5	5.9	17.6	.0	.0	.0	.0	100.0
		wooded-bushed grassland	2.3	67.4	30.2	.0	.0	.0	.0	100.0
		light woodland-bushland	3.9	17.6	64.7	3.9	7.8	2.0	.0	100.0
		heavy woodland-bushland	6.5	.0	12.9	67.7	6.5	3.2	3.2	100.0
		forest	.0	3.3	26.7	20.0	50.0	.0	.0	100.0
		montane light cover	.0	.0	.0	.0	.0	93.3	6.7	100.0
		montane heavy cover	.0	.0	.0	6.3	.0	6.3	87.5	100.0

a. 68.5% of original grouped cases correctly classified.

Appendix E, Table H1. Structure matrix from an analysis of the logged distal humerus data

Structure Matrix

	Function				
	1 63.3%	2 20.0%	3 10.9%	4 3.7%	5 2.1%
LOGH12	-.023	.490	.166	.023	.855
LOGH10	-.005	.578	.055	.127	.804
LOGH11	.024	.594	-.046	.014	.802
LOGH9	.076	.587	.115	.091	.793
LOGH8	-.013	.618	.082	.092	.777



Appendix E, Figure H1. Scatter plot of the first and second discriminant function from an analysis of the logged distal humerus data

Appendix E, Table H2. Classification results table from an analysis of the logged distal humerus data

Classification Results[a]

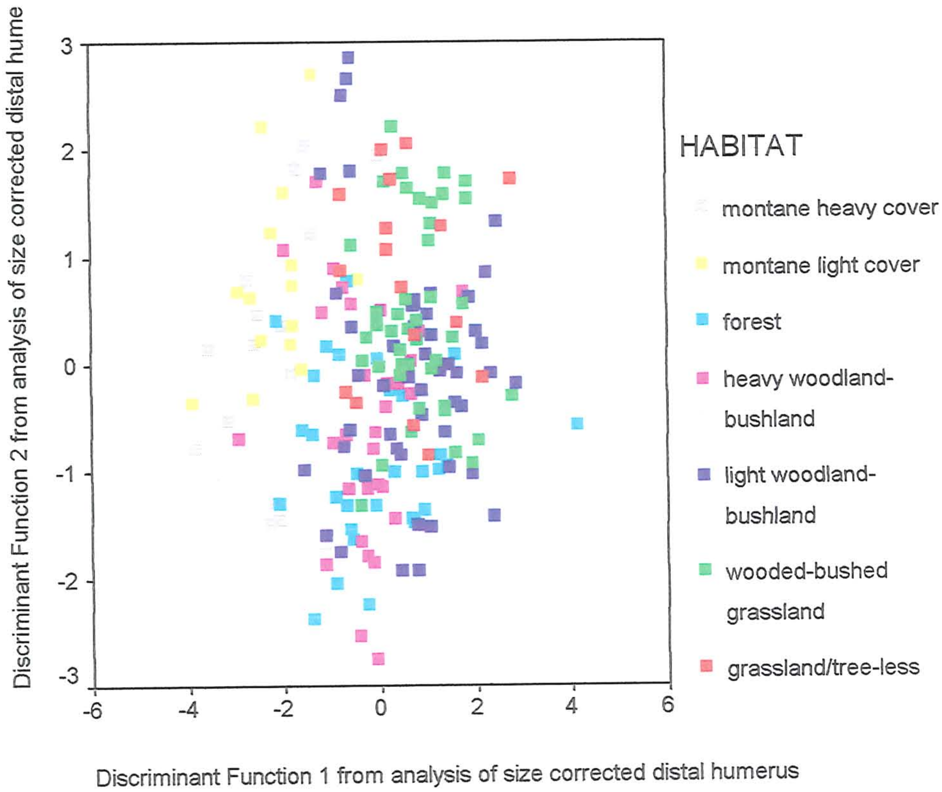
			Predicted Group Membership							
		HABITAT	grassland/ tree-less	wooded-bushed grassland	light woodland-bushland	heavy woodland-bushland	forest	montane light cover	montane heavy cover	Total
Original	Count	grassland/tree-less	9	3	3	0	2	0	0	17
		wooded-bushed grassland	2	20	15	2	4	0	0	43
		light woodland-bushland	2	7	30	7	2	3	0	51
		heavy woodland-bushland	2	0	11	11	3	1	3	31
		forest	2	3	7	6	11	0	1	30
		montane light cover	0	1	0	0	0	10	4	15
		montane heavy cover	0	1	0	2	1	4	8	16
	%	grassland/tree-less	52.9	17.6	17.6	.0	11.8	.0	.0	100.0
		wooded-bushed grassland	4.7	46.5	34.9	4.7	9.3	.0	.0	100.0
		light woodland-bushland	3.9	13.7	58.8	13.7	3.9	5.9	.0	100.0
		heavy woodland-bushland	6.5	.0	35.5	35.5	9.7	3.2	9.7	100.0
		forest	6.7	10.0	23.3	20.0	36.7	.0	3.3	100.0
		montane light cover	.0	6.7	.0	.0	.0	66.7	26.7	100.0
		montane heavy cover	.0	6.3	.0	12.5	6.3	25.0	50.0	100.0

a. 48.8% of original grouped cases correctly classified.

Appendix E, Table H3. Structure matrix from an analysis of the size corrected distal humerus data

Structure Matrix

	Function				
	1 66.4%	2 18.7%	3 10.2%	4 4.6%	5 0.2%
RESH8	.014	.711	.129	.422	.547
RESH11	.169	.621	.614	.451	.078
RESH12	-.061	.007	.148	.808	.567
RESH10	.045	.535	.393	.286	.690
RESH9	.495	.386	.072	.501	.592



Appendix E, Table H2. Scatter plot of the first and second discriminant functions from an analysis of the size corrected distal humerus data

Appendix E, Table H4. Classification results table from an analysis of the size corrected distal humerus data

Classification Results[a]

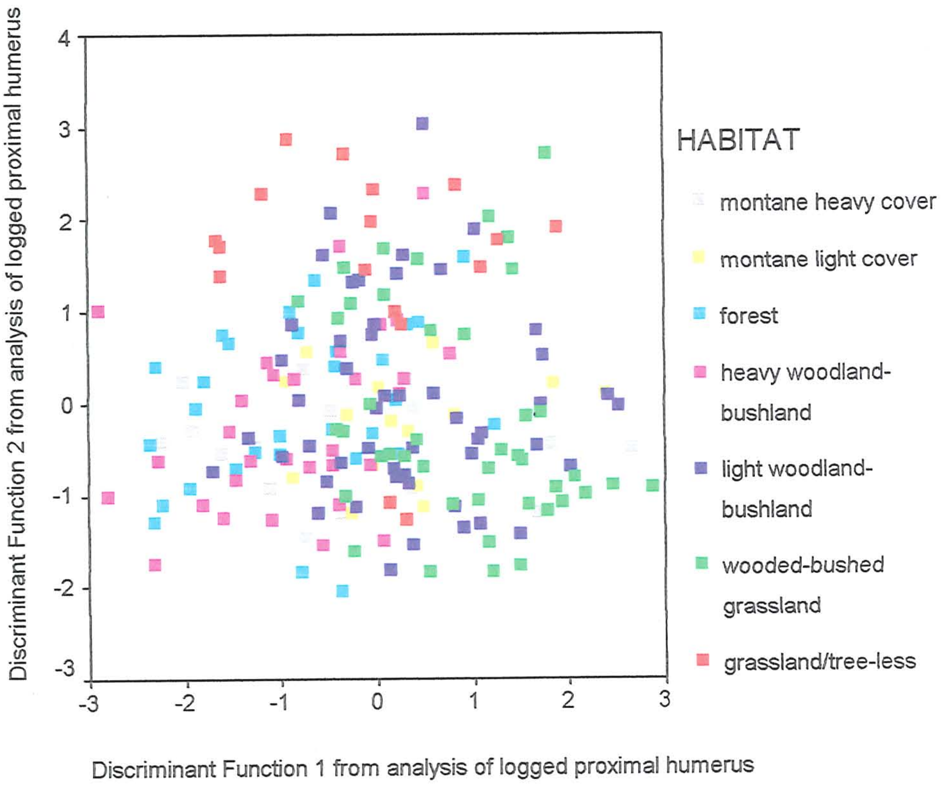
		HABITAT	Predicted Group Membership							Total
			grassland/ tree-less	wooded-bushed grassland	light woodland-bushland	heavy woodland-bushland	forest	montane light cover	montane heavy cover	
Original	Count	grassland/tree-less	4	5	5	2	1	0	0	17
		wooded-bushed grassland	2	23	15	1	2	0	0	43
		light woodland-bushland	3	13	24	7	3	1	0	51
		heavy woodland-bushland	0	2	9	13	3	2	2	31
		forest	0	2	9	5	12	0	2	30
		montane light cover	0	0	1	0	0	10	4	15
		montane heavy cover	0	1	0	0	1	3	11	16
	%	grassland/tree-less	23.5	29.4	29.4	11.8	5.9	.0	.0	100.0
		wooded-bushed grassland	4.7	53.5	34.9	2.3	4.7	.0	.0	100.0
		light woodland-bushland	5.9	25.5	47.1	13.7	5.9	2.0	.0	100.0
		heavy woodland-bushland	.0	6.5	29.0	41.9	9.7	6.5	6.5	100.0
		forest	.0	6.7	30.0	16.7	40.0	.0	6.7	100.0
		montane light cover	.0	.0	6.7	.0	.0	66.7	26.7	100.0
		montane heavy cover	.0	6.3	.0	.0	6.3	18.8	68.8	100.0

a. 47.8% of original grouped cases correctly classified.

Appendix E, Table I1. Structure matrix from an analysis of the logged proximal humerus data

Structure Matrix

	Function				
	1 53.6%	2 29.5%	3 11.0%	4 5.8%	5 0.1%
LOGH3	.059	.440	.007	.862	.244
LOGH4	-.031	.599	.212	.708	.308
LOGH7	.099	.652	.115	.678	.305
LOGH5	.108	.590	.150	.677	.398
LOGH6	.037	.648	.083	.656	.375



Appendix E, Figure I1. Scatter plot of the first and second discriminant functions from an analysis of the logged proximal humerus data

Appendix E, Table I2. Classification results table from an analysis of the logged proximal humerus data

Classification Results[a]

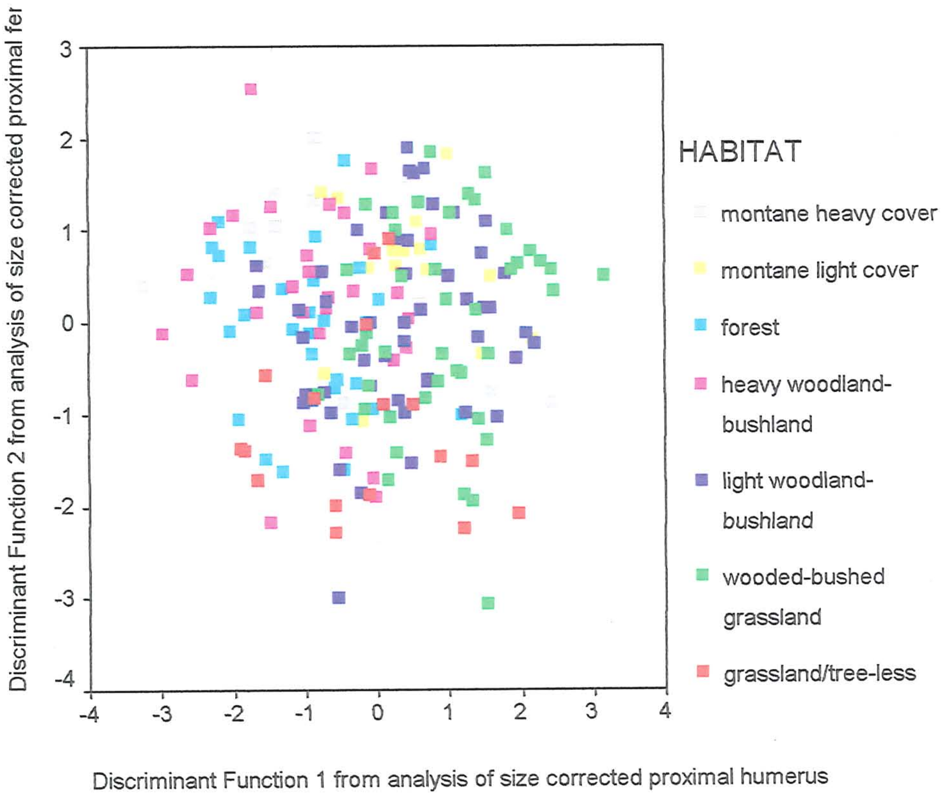
		HABITAT	Predicted Group Membership: grassland/ tree-less	wooded-bushed grassland	light woodland-bushland	heavy woodland-bushland	forest	light woodland-bushland	heavy woodland-bushland	Total
Original	Count	grassland/tree-less	8	2	5	1	1	0	0	17
		wooded-bushed grassland	5	22	12	3	0	0	1	43
		light woodland-bushland	5	13	19	6	4	2	2	51
		heavy woodland-bushland	2	0	11	13	5	0	0	31
		forest	1	0	10	7	12	0	0	30
		montane light cover	0	3	8	1	1	1	1	15
		montane heavy cover	0	3	2	3	7	0	1	16
	%	grassland/tree-less	47.1	11.8	29.4	5.9	5.9	.0	.0	100.0
		wooded-bushed grassland	11.6	51.2	27.9	7.0	.0	.0	2.3	100.0
		light woodland-bushland	9.8	25.5	37.3	11.8	7.8	3.9	3.9	100.0
		heavy woodland-bushland	6.5	.0	35.5	41.9	16.1	.0	.0	100.0
		forest	3.3	.0	33.3	23.3	40.0	.0	.0	100.0
		montane light cover	.0	20.0	53.3	6.7	6.7	6.7	6.7	100.0
		montane heavy cover	.0	18.8	12.5	18.8	43.8	.0	6.3	100.0

a. 37.4% of original grouped cases correctly classified.

Appendix E, Table I3. Structure matrix from an analysis of the size corrected proximal humerus data

Structure Matrix

	Function				
	1 64.3%	2 21.4%	3 11.8%	4 2.2%	5 0.2%
RESH5	.598	.301	-.069	.503	.543
RESH3	.257	.715	.400	.472	-.196
RESH4	-.006	.313	-.236	.878	.273
RESH7	.583	.001	.106	.780	.201
RESH6	.315	.018	.295	.686	.585



Appendix E, Figure I2. Scatter plot of the first and second discriminant functions from an analysis of the size corrected proximal humerus data

Appendix E, Table I4. Classification results table from an analysis of the size corrected proximal humerus data

Classification Results[a]

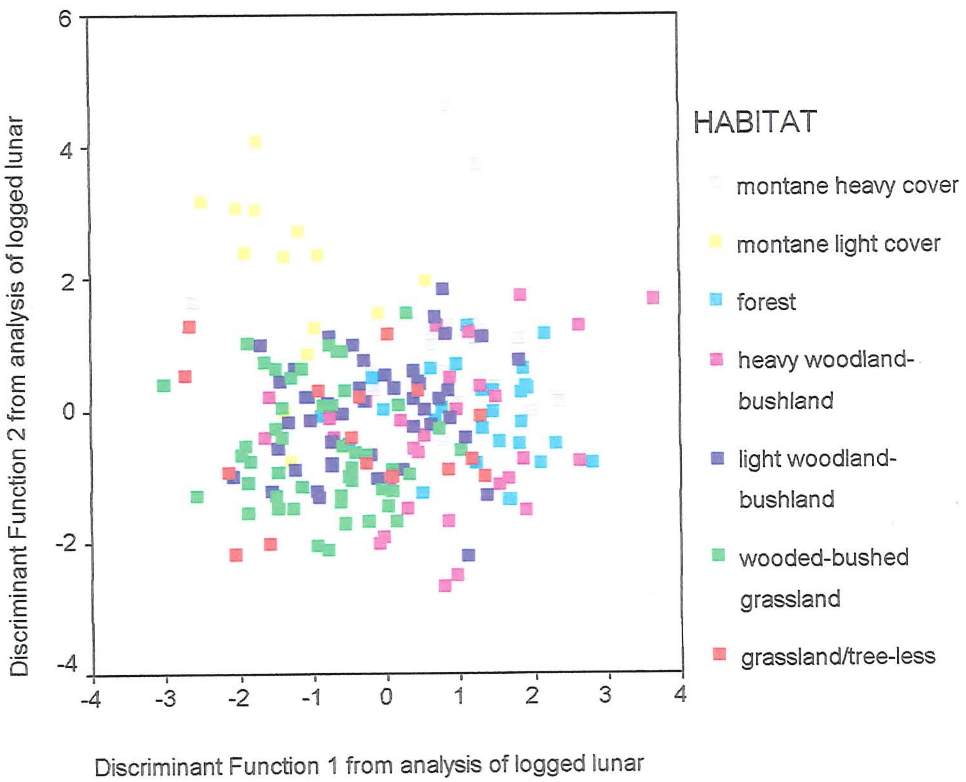
		HABITAT	Predicted Group Membership							Total
			grassland/ tree-less	wooded-bushed grassland	light woodland-bushland	heavy woodland-bushland	forest	light woodland-bushland	heavy woodland-bushland	
Original	Count	grassland/tree-less	3	3	6	3	2	0	0	17
		wooded-bushed grassland	2	22	17	1	0	0	1	43
		light woodland-bushland	2	15	21	5	5	2	1	51
		heavy woodland-bushland	3	0	12	9	7	0	0	31
		forest	1	1	8	8	12	0	0	30
		montane light cover	0	3	8	0	1	1	2	15
		montane heavy cover	0	3	4	2	5	1	1	16
	%	grassland/tree-less	17.6	17.6	35.3	17.6	11.8	.0	.0	100.0
		wooded-bushed grassland	4.7	51.2	39.5	2.3	.0	.0	2.3	100.0
		light woodland-bushland	3.9	29.4	41.2	9.8	9.8	3.9	2.0	100.0
		heavy woodland-bushland	9.7	.0	38.7	29.0	22.6	.0	.0	100.0
		forest	3.3	3.3	26.7	26.7	40.0	.0	.0	100.0
		montane light cover	.0	20.0	53.3	.0	6.7	6.7	13.3	100.0
		montane heavy cover	.0	18.8	25.0	12.5	31.3	6.3	6.3	100.0

a. 34.0% of original grouped cases correctly classified.

Appendix E, Table J1. Structure matrix from an analysis of the logged lunar data

Structure Matrix

	Function					
	1 39.2%	2 27.7%	3 16.0%	4 11.3%	5 5.3%	6 0.6%
LOGCD6	-.064	.062	.585	.172	.444	.566
LOGCD1	-.109	.124	.549	.297	.511	.484
LOGCD9	-.138	.093	.494	.302	.488	.457
LOGCD2	-.110	.089	.519	.257	.598	.451
LOGCD7	-.035	.055	.404	.254	.564	.547
LOGCD3	-.060	.155	.477	.286	.553	.488
LOGCD5	-.180	.012	.496	.272	.536	.525
LOGCD4	-.162	.171	.424	.259	.544	.566
LOGCD8	.127	-.143	.494	.493	.349	.503



Appendix E, Figure J1. Scatter plot of the first and second discriminant functions from an analysis of the logged lunar data

Appendix E, Table J2. Classification results table from an analysis of the logged lunar data

Classification Results[a]

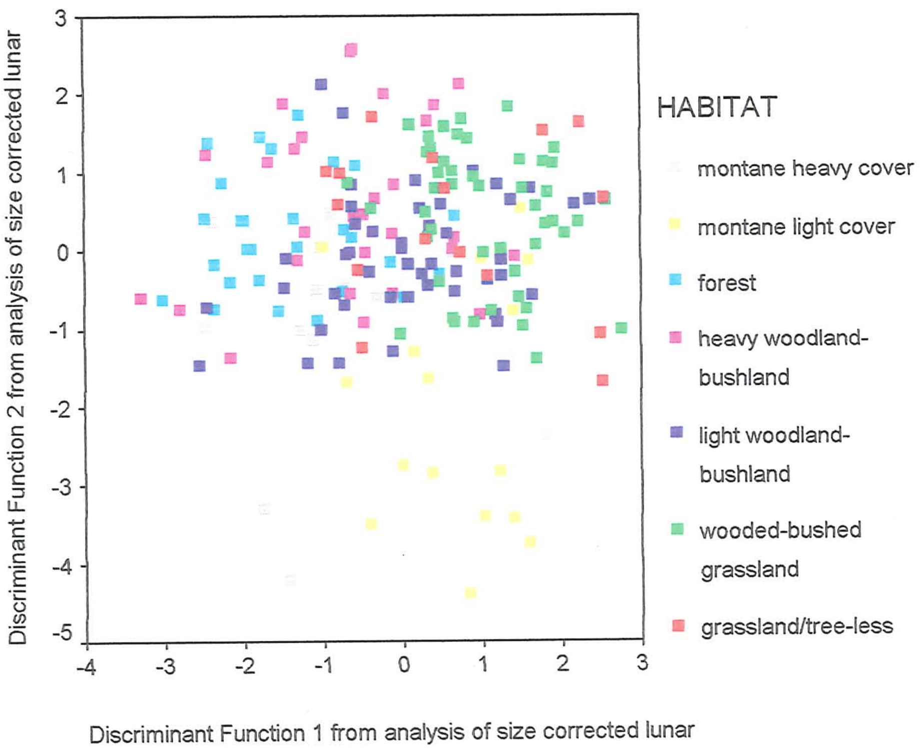
			Predicted Group Membership							
		HABITAT	grassland/ tree-less	wooded-bushed grassland	light woodland-bushland	heavy woodland-bushland	forest	montane light cover	montane heavy cover	Total
Original	Count	grassland/tree-less	7	4	4	0	0	1	0	16
		wooded-bushed grassland	0	35	10	1	0	1	1	48
		light woodland-bushland	2	8	27	5	3	1	1	47
		heavy woodland-bushland	1	3	6	10	8	0	2	30
		forest	1	1	7	4	13	0	2	28
		montane light cover	1	1	3	0	0	10	1	16
		montane heavy cover	0	4	3	2	3	0	6	18
	%	grassland/tree-less	43.8	25.0	25.0	.0	.0	6.3	.0	100.0
		wooded-bushed grassland	.0	72.9	20.8	2.1	.0	2.1	2.1	100.0
		light woodland-bushland	4.3	17.0	57.4	10.6	6.4	2.1	2.1	100.0
		heavy woodland-bushland	3.3	10.0	20.0	33.3	26.7	.0	6.7	100.0
		forest	3.6	3.6	25.0	14.3	46.4	.0	7.1	100.0
		montane light cover	6.3	6.3	18.8	.0	.0	62.5	6.3	100.0
		montane heavy cover	.0	22.2	16.7	11.1	16.7	.0	33.3	100.0

a. 53.2% of original grouped cases correctly classified.

Appendix E, Table J3. Structure matrix from an analysis of the size corrected lunar data

Structure Matrix

	Function					
	1 43.1%	2 28.7%	3 14.3%	4 9.6%	5 3.2%	6 1.3%
RESCD5	.770	.235	.107	.174	.261	.486
RESCD4	.523	-.327	.245	.415	.368	.475
RESCD9	.481	-.047	.110	.046	.311	.436
RESCD7	.163	.162	.284	.482	.280	.480
RESC6	.278	.143	-.429	.219	.646	.397
RESCD1	.431	-.141	-.096	.020	.194	.780
RESCD3	.212	-.211	.112	.294	.144	.724
RESCD2	.530	.000	-.053	.363	-.092	.692
RESCD8	-.137	.428	.193	-.275	.255	.449



Appendix E, Table J2. Scatter plot of the first and second discriminant functions from an analysis of the size corrected lunar data

Appendix E, Table J4. Classification results table from an analysis of the size corrected lunar data

Classification Results[a]

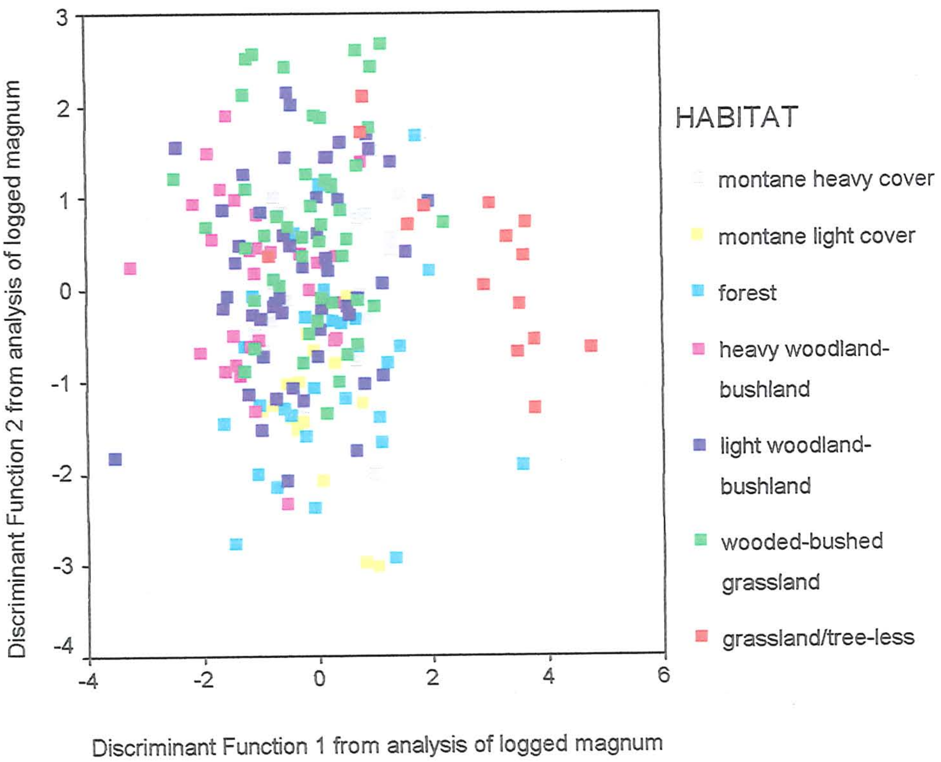
			Predicted Group Membership							
		HABITAT	grassland/ tree-less	wooded-bushed grassland	light woodland-bushland	heavy woodland-bushland	forest	montane light cover	montane heavy cover	Total
Original	Count	grassland/tree-less	3	6	2	4	0	1	0	16
		wooded-bushed grassland	1	35	9	2	0	0	1	48
		light woodland-bushland	2	10	26	4	4	0	1	47
		heavy woodland-bushland	3	3	7	11	5	0	1	30
		forest	1	1	5	6	14	0	1	28
		montane light cover	1	2	3	0	0	9	1	16
		montane heavy cover	0	1	2	4	2	1	8	18
	%	grassland/tree-less	18.8	37.5	12.5	25.0	.0	6.3	.0	100.0
		wooded-bushed grassland	2.1	72.9	18.8	4.2	.0	.0	2.1	100.0
		light woodland-bushland	4.3	21.3	55.3	8.5	8.5	.0	2.1	100.0
		heavy woodland-bushland	10.0	10.0	23.3	36.7	16.7	.0	3.3	100.0
		forest	3.6	3.6	17.9	21.4	50.0	.0	3.6	100.0
		montane light cover	6.3	12.5	18.8	.0	.0	56.3	6.3	100.0
		montane heavy cover	.0	5.6	11.1	22.2	11.1	5.6	44.4	100.0

a. 52.2% of original grouped cases correctly classified.

Appendix E, Table K1. Structure matrix from an analysis of the logged magnum data

Structure Matrix

	Function					
	1 45.2%	2 26.2%	3 17.2%	4 6.6%	5 3.7%	6 1.0%
LOGCA4	.476	.074	.243	.132	.352	.403
LOGCA1	.475	.065	.228	.104	.374	.466
LOGCA8	.401	.160	.146	.038	.363	.560
LOGCA7B	.365	.080	.210	.022	.362	.526
LOGCA3	.400	.018	.237	.122	.439	.515
LOGCA6	.311	.098	.262	.223	.413	.500
LOGCA2	.397	.050	.175	.119	.435	.479
LOGCA5	.404	.088	.199	.114	.459	.472
LOGCA7	.292	.143	.258	-.045	.416	.468



Appendix E, Figure K1. Scatter plot of the first and second discriminant functions from an analysis of the logged magnum

Appendix E, Table K2. Classification results table from an analysis of the logged magnum data

Classification Results[a]

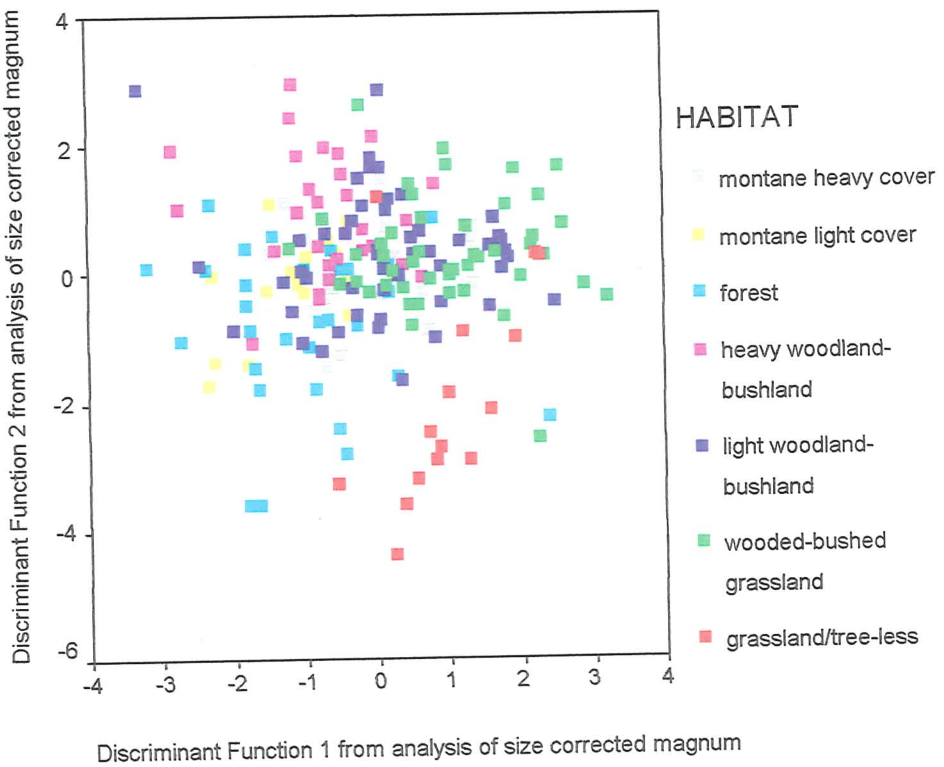
			Predicted Group Membership							
		HABITAT	grassland/ tree-less	wooded-bushed grassland	light woodland-bushland	heavy woodland-bushland	forest	montane light cover	montane heavy cover	Total
Original	Count	grassland/tree-less	11	3	1	0	0	0	0	15
		wooded-bushed grassland	1	24	12	8	0	1	1	47
		light woodland-bushland	1	9	26	5	5	4	1	51
		heavy woodland-bushland	0	4	7	15	3	0	0	29
		forest	2	4	5	1	16	1	1	30
		montane light cover	0	2	3	0	1	10	0	16
		montane heavy cover	1	2	8	3	1	1	5	21
	%	grassland/tree-less	73.3	20.0	6.7	.0	.0	.0	.0	100.0
		wooded-bushed grassland	2.1	51.1	25.5	17.0	.0	2.1	2.1	100.0
		light woodland-bushland	2.0	17.6	51.0	9.8	9.8	7.8	2.0	100.0
		heavy woodland-bushland	.0	13.8	24.1	51.7	10.3	.0	.0	100.0
		forest	6.7	13.3	16.7	3.3	53.3	3.3	3.3	100.0
		montane light cover	.0	12.5	18.8	.0	6.3	62.5	.0	100.0
		montane heavy cover	4.8	9.5	38.1	14.3	4.8	4.8	23.8	100.0

a. 51.2% of original grouped cases correctly classified.

Appendix E, Table K3. Structure matrix from an analysis of the size corrected magnum data

Structure Matrix

	Function					
	1 38.2%	2 33.7%	3 14.7%	4 8.3%	5 3.9%	6 1.2%
RESCA8	.739	.234	-.100	.195	.377	.293
RESCA1	.597	-.123	.401	.405	.062	.193
RESCA4	.573	-.096	.427	.409	-.036	-.093
RESCA5	.554	.185	.156	.414	-.141	.451
RESCA7	.400	.572	.181	-.117	.288	.216
RESCA6	.364	.469	.285	.591	-.175	.193
RESCA2	.438	.147	.090	.562	.017	.370
RESCA7B	.484	.341	.201	.253	.498	.276
RESCA3	.332	.135	.380	.556	.001	.562



Appendix E, Table K2. Scatter plot of the first and second discriminant functions from an analysis of the size corrected magnum data

Appendix E, Table K4. Classification results table from an analysis of the size corrected magnum data

Classification Results[a]

			Predicted Group Membership							
		HABITAT	grassland/ tree-less	wooded-bushed grassland	light woodland-bushland	heavy woodland-bushland	forest	montane light cover	montane heavy cover	Total
Original	Count	grassland/tree-less	10	3	2	0	0	0	0	15
		wooded-bushed grassland	1	32	10	2	0	1	1	47
		light woodland-bushland	0	14	22	4	6	5	0	51
		heavy woodland-bushland	0	4	7	16	1	1	0	29
		forest	2	2	4	5	15	2	0	30
		montane light cover	0	0	5	0	3	8	0	16
		montane heavy cover	1	4	7	2	3	1	3	21
	%	grassland/tree-less	66.7	20.0	13.3	.0	.0	.0	.0	100.0
		wooded-bushed grassland	2.1	68.1	21.3	4.3	.0	2.1	2.1	100.0
		light woodland-bushland	.0	27.5	43.1	7.8	11.8	9.8	.0	100.0
		heavy woodland-bushland	.0	13.8	24.1	55.2	3.4	3.4	.0	100.0
		forest	6.7	6.7	13.3	16.7	50.0	6.7	.0	100.0
		montane light cover	.0	.0	31.3	.0	18.8	50.0	.0	100.0
		montane heavy cover	4.8	19.0	33.3	9.5	14.3	4.8	14.3	100.0

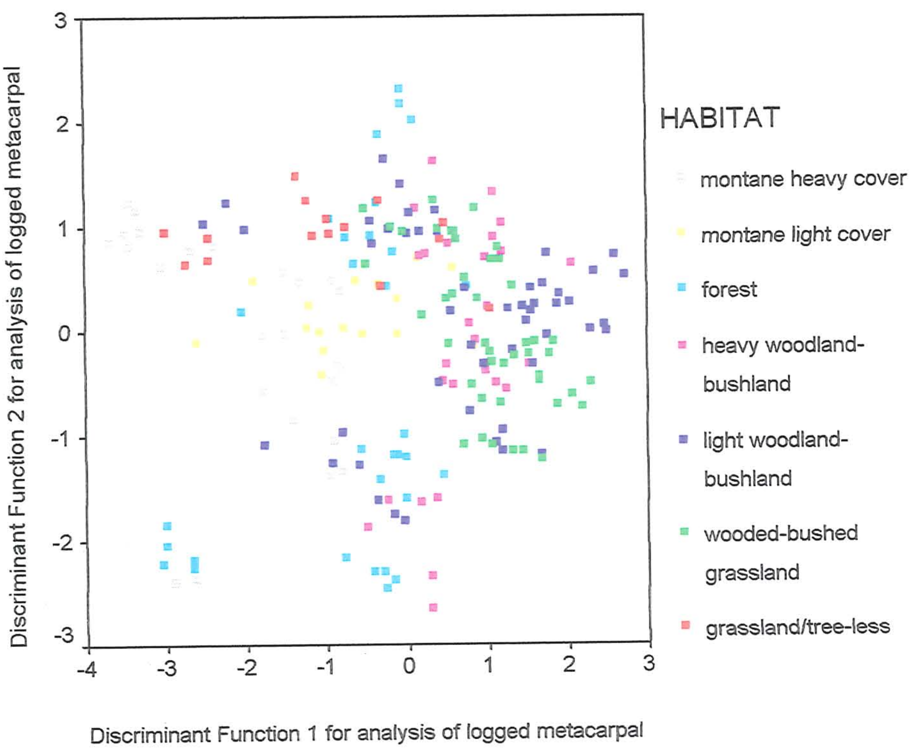
a. 50.7% of original grouped cases correctly classified.

Appendix E, Table L1. Structure matrix from an analysis of the logged metacarpal data

Structure Matrix

	Function		
	1 87.4%	2 8.9%	3 3.7%
LOGMC5[a]	-.098	.976	-.018
LOGMC8[a]	.003	.975	.065
LOGMC12[a]	-.032	.971	-.005
LOGMC3[a]	-.107	.967	.003
LOGMC4[a]	-.179	.952	.000
LOGMC6[a]	-.246	.940	-.019
LOGMC9[a]	-.242	.939	-.015
LOGMC7[a]	-.252	.937	-.043
LOGMC1	.360	.927	.102
LOGMC13[a]	-.284	.916	-.113
LOGMC2	.391	.911	.129
LOGMC10	-.360	.897	.257
LOGMC11[a]	-.307	.871	.041

a. This variable not used in the analysis.



Appendix E, Figure L1. Scatter plot of the first and second discriminant functions from an analysis of the logged metacarpal

Appendix E, Table L2. Classification results table from an anlysis of the logged metacarpal data

Classification Results[a]

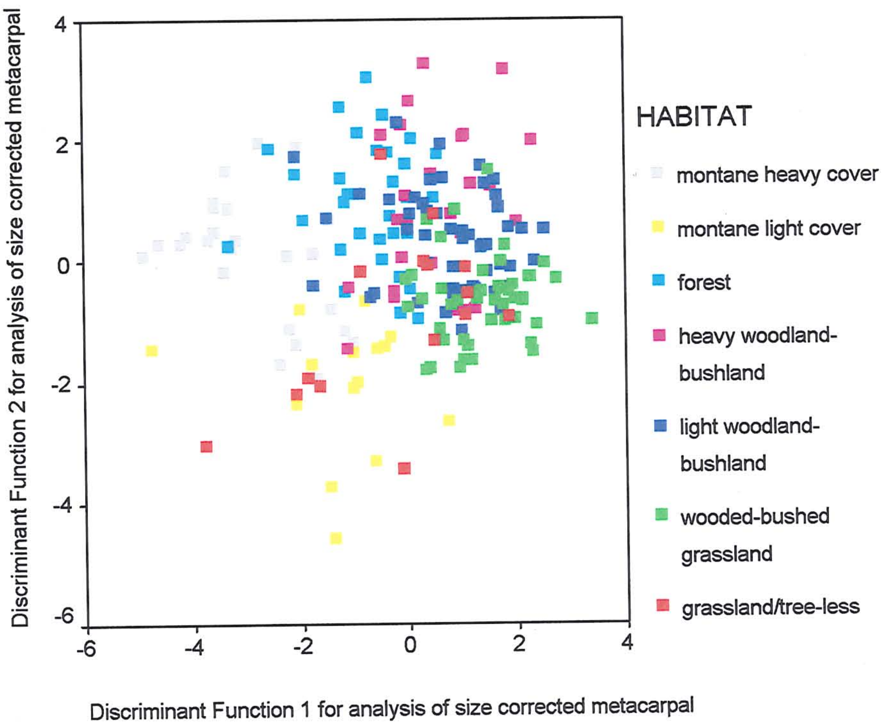
		HABITAT	Predicted Group Membership							Total
			grassland/ tree-less	wooded-bushed grassland	light woodland-bushland	heavy woodland-bushland	forest	montane light cover	montane heavy cover	
Original	Count	grassland/tree-less	6	0	5	0	0	0	4	15
		wooded-bushed grassland	0	21	23	0	0	2	0	46
		light woodland-bushland	0	24	17	0	7	0	3	51
		heavy woodland-bushland	0	4	18	0	5	0	0	27
		forest	3	0	8	0	12	2	6	31
		montane light cover	0	0	7	0	7	0	2	16
		montane heavy cover	0	0	0	0	9	4	12	25
	%	grassland/tree-less	40.0	.0	33.3	.0	.0	.0	26.7	100.0
		wooded-bushed grassland	.0	45.7	50.0	.0	.0	4.3	.0	100.0
		light woodland-bushland	.0	47.1	33.3	.0	13.7	.0	5.9	100.0
		heavy woodland-bushland	.0	14.8	66.7	.0	18.5	.0	.0	100.0
		forest	9.7	.0	25.8	.0	38.7	6.5	19.4	100.0
		montane light cover	.0	.0	43.8	.0	43.8	.0	12.5	100.0
		montane heavy cover	.0	.0	.0	.0	36.0	16.0	48.0	100.0

a. 32.2% of original grouped cases correctly classified.

Appendix E, Table L3. Structure matrix from an analysis of the size corrected metacarpal data

Structure Matrix

	Function					
	1 48.3%	2 19.4%	3 16.5%	4 10.0%	5 4.6%	6 1.1%
RESMC2	.668	-.115	.324	.510	.051	.187
RESMC1	.667	-.130	.309	.529	.043	.190
RESMC10	-.288	-.242	.050	.198	.122	-.035
RESMC11	-.226	-.507	-.081	.424	.048	.054
RESMC7	-.159	-.495	-.235	.394	.125	-.251
RESMC6	-.209	-.493	-.301	.417	.194	-.214
RESMC9	-.127	-.472	-.367	.335	.240	-.210
RESMC12	.335	-.176	.078	.646	-.161	-.058
RESMC8	.485	-.159	-.166	.566	-.202	.083
RESMC5	.252	-.413	-.090	.516	-.089	-.037
RESMC3	.098	-.407	-.116	.496	-.130	.262
RESMC13	-.306	-.094	-.217	.412	.218	-.118
RESMC4	.023	-.322	-.296	.397	-.056	-.029



Appendix E, Figure L2. Scatter plot of the first and second discriminant functions from an analysis of the size corrected metacarpal

Appendix E, Table L4. Classification results table from an analysis of the size corrected metacarpal data

Classification Results[a]

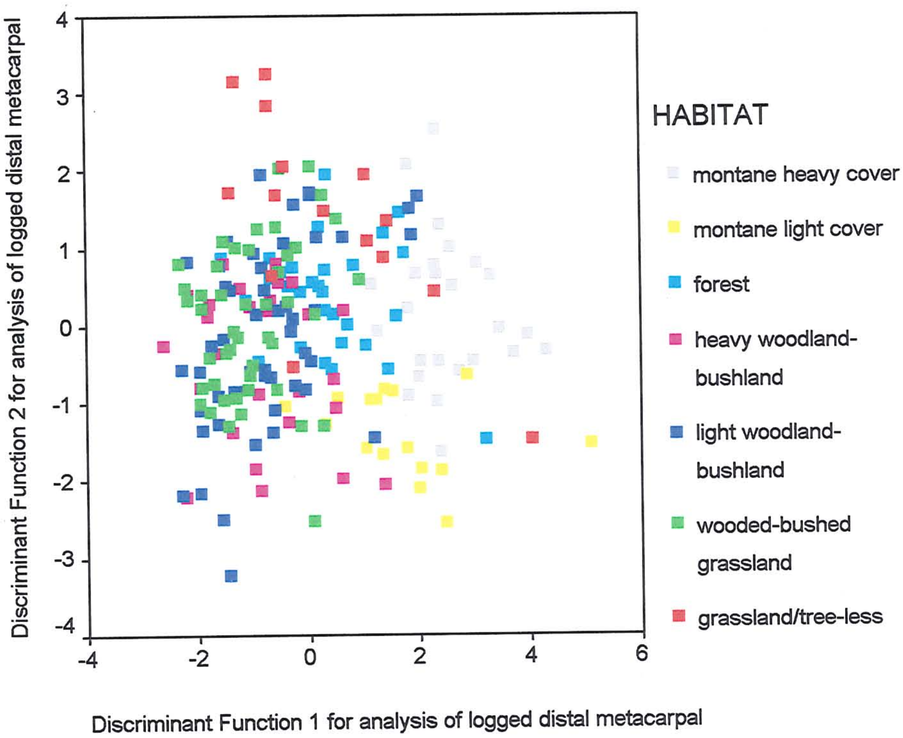
		HABITAT	Predicted Group Membership: grassland/ tree-less	wooded-bushed grassland	light woodland-bushland	heavy woodland-bushland	forest	montane light cover	montane heavy cover	Total
Original	Count	grassland/tree-less	9	2	1	0	1	2	0	15
		wooded-bushed grassland	0	34	12	0	0	0	0	46
		light woodland-bushland	2	10	31	4	3	0	1	51
		heavy woodland-bushland	1	2	6	14	2	2	0	27
		forest	0	1	4	2	23	1	0	31
		montane light cover	0	0	0	0	0	14	1	15
		montane heavy cover	0	0	1	0	4	3	17	25
	%	grassland/tree-less	60.0	13.3	6.7	.0	6.7	13.3	.0	100.0
		wooded-bushed grassland	.0	73.9	26.1	.0	.0	.0	.0	100 0
		light woodland-bushland	3.9	19.6	60.8	7.8	5.9	.0	2.0	100.0
		heavy woodland-bushland	3.7	7.4	22.2	51.9	7.4	7.4	.0	100.0
		forest	.0	3.2	12.9	6.5	74.2	3.2	.0	100.0
		montane light cover	.0	.0	.0	.0	.0	93.3	6.7	100 0
		montane heavy cover	.0	.0	4.0	.0	16 0	12 0	68 0	100 0

a 67 6% of original grouped cases correctly classified.

Appendix E, Table M1. Structure matrix from an analysis of the logged distal metacarpal data

Structure Matrix

	Function					
	1 64.1%	2 15.3%	3 10.8%	4 7.8%	5 1.8%	6 0.3%
LOGMC11	.300	.256	.759	.260	.407	.096
LOGMC7	.203	.338	.604	.242	.577	-.031
LOGMC6	.211	.359	.583	.229	.573	.032
LOGMC10	.299	.250	.475	.246	.713	.217
LOGMC8	-.020	.288	.598	.107	.629	.174
LOGMC5	.074	.260	.597	.207	.613	.075
LOGMC9	.184	.385	.572	.249	.573	.035



Appendix E, Figure M1. Scatter plot of the first and second discriminant functions from an analysis of the logged distal metacarpal data

Appendix E, Table M2. Classification results table from an analysis of the logged distal metacarpal data

Classification Results[a]

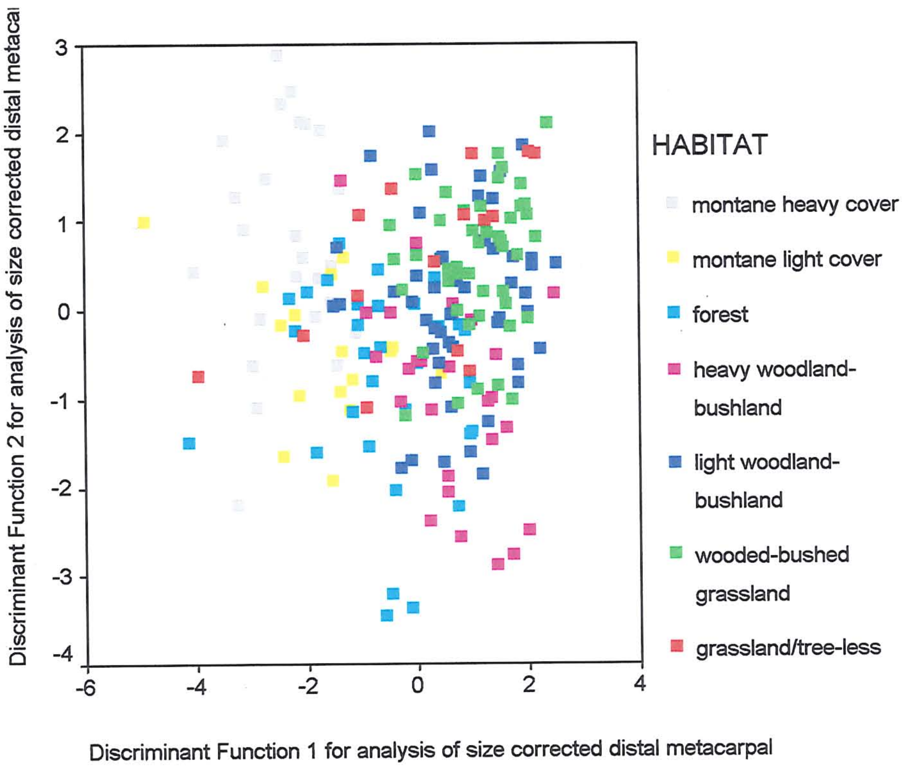
			Predicted Group Membership							
		HABITAT	grassland/ tree-less	wooded-bushed grassland	light woodland-bushland	heavy woodland-bushland	forest	montane light cover	montane heavy cover	Total
Original	Count	grassland/tree-less	10	1	2	0	0	1	1	15
		wooded-bushed grassland	4	26	15	1	0	0	0	46
		light woodland-bushland	2	12	26	4	4	1	2	51
		heavy woodland-bushland	0	7	10	8	0	2	0	27
		forest	3	1	9	0	16	1	1	31
		montane light cover	0	1	1	0	0	12	2	16
		montane heavy cover	0	0	0	0	1	3	21	25
	%	grassland/tree-less	66.7	6.7	13.3	.0	.0	6.7	6.7	100.0
		wooded-bushed grassland	8.7	56.5	32.6	2.2	.0	.0	.0	100.0
		light woodland-bushland	3.9	23.5	51.0	7.8	7.8	2.0	3.9	100.0
		heavy woodland-bushland	.0	25.9	37.0	29.6	.0	7.4	.0	100.0
		forest	9.7	3.2	29.0	.0	51.6	3.2	3.2	100.0
		montane light cover	.0	6.3	6.3	.0	.0	75.0	12.5	100.0
		montane heavy cover	.0	.0	.0	.0	4.0	12.0	84.0	100.0

a. 56.4% of original grouped cases correctly classified.

Appendix E, Table M3. Structure matrix from an analysis of the size corrected distal metacarpal data

Structure Matrix

	Function					
	1 60.8%	2 17.1%	3 14.3%	4 7.3%	5 0.4%	6 0.1%
RESMC8	.545	.499	.428	-.164	-.154	.468
RESMC6	-.260	.807	.223	.357	.220	.205
RESMC9	-.163	.804	.117	.441	.223	.216
RESMC7	-.208	.735	.295	.374	.390	.054
RESMC11	-.292	.624	.458	.323	-.181	-.187
RESMC5	.250	.583	.586	.230	.154	.409
RESMC10	-.357	.229	.255	.154	-.026	.514



Appendix E, Figure M2. Scatter plot of the first and second discriminant functions from an analysis of the size corrected distal metacarpal data

Appendix E, Table M4. Classification results table from an analysis of the size corrected distal metacarpal data

Classification Results[a]

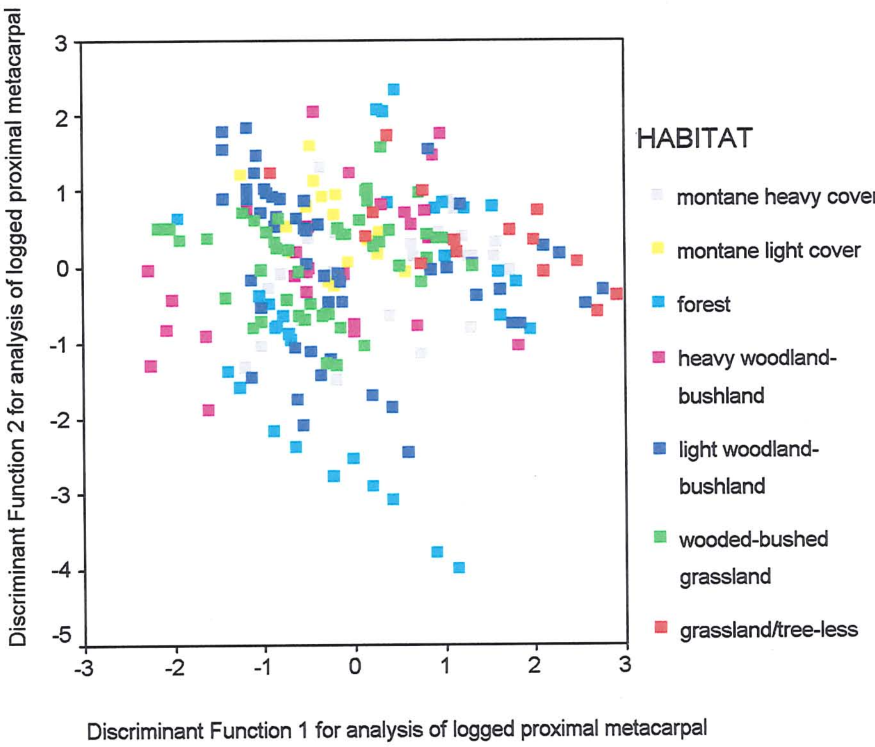
			Predicted Group Membership							
		HABITAT	grassland/ tree-less	wooded-bushed grassland	light woodland-bushland	heavy woodland-bushland	forest	montane light cover	montane heavy cover	Total
Original	Count	grassland/tree-less	3	5	3	0	3	1	0	15
		wooded-bushed grassland	0	32	13	1	0	0	0	46
		light woodland-bushland	0	12	29	4	5	1	0	51
		heavy woodland-bushland	0	3	9	12	1	1	1	27
		forest	0	1	5	2	21	1	1	31
		montane light cover	0	1	1	0	1	11	2	16
		montane heavy cover	0	0	0	0	2	3	20	25
	%	grassland/tree-less	20.0	33.3	20.0	.0	20.0	6.7	.0	100.0
		wooded-bushed grassland	.0	69.6	28.3	2.2	.0	.0	.0	100.0
		light woodland-bushland	.0	23.5	56.9	7.8	9.8	2.0	.0	100.0
		heavy woodland-bushland	.0	11.1	33.3	44.4	3.7	3.7	3.7	100.0
		forest	.0	3.2	16.1	6.5	67.7	3.2	3.2	100.0
		montane light cover	.0	6.3	6.3	.0	6.3	68.8	12.5	100.0
		montane heavy cover	.0	.0	.0	.0	8.0	12.0	80.0	100.0

a. 60.7% of original grouped cases correctly classified.

Appendix E, Table N1. Structure matrix from an analysis of the logged proximal metacarpal data

Structure Matrix

	Function	
	1 62.8%	2 37.2%
LOGMC4	.805	.593
LOGMC3	.721	.693



Appendix E, Figure N1. Scatter plot of the first and second discriminant functions from an analysis of the logged proximal metacarpal data

Appendix E, Table N2. Classification results table from an anlysis of the logged proximal metacarpal data

Classification Results[a]

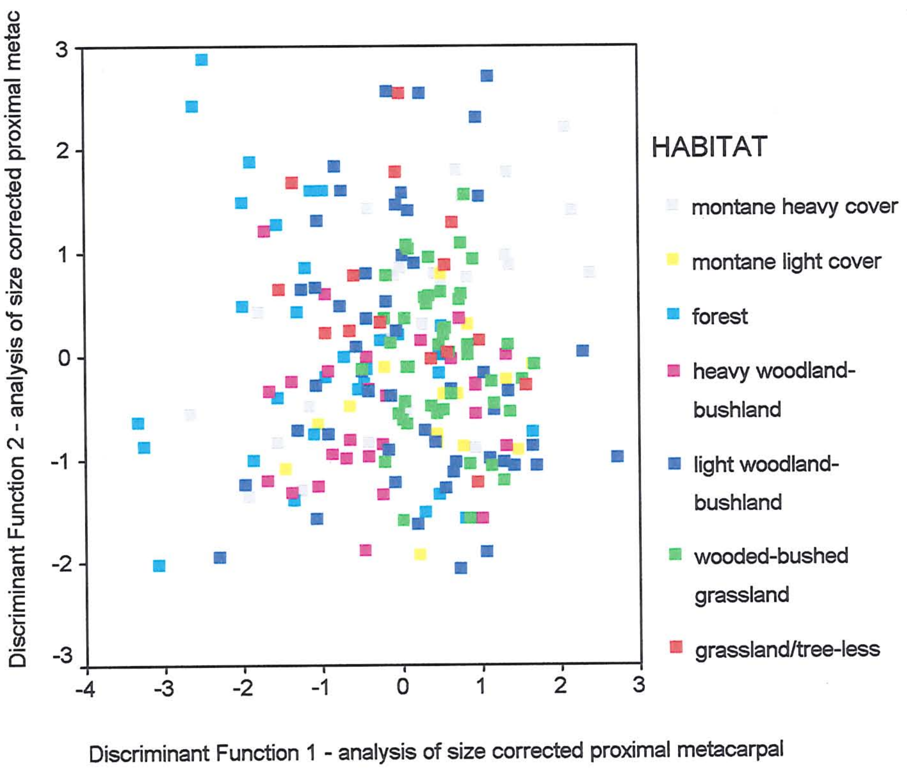
			Predicted Group Membership							
		HABITAT	grassland/ tree-less	wooded-bushed grassland	light woodland-bushland	heavy woodland-bushland	forest	montane light cover	montane heavy cover	Total
Original	Count	grassland/tree-less	7	1	7	0	0	0	0	15
		wooded-bushed grassland	0	16	27	0	3	0	0	46
		light woodland-bushland	4	21	16	0	10	0	0	51
		heavy woodland-bushland	0	8	17	0	2	0	0	27
		forest	3	6	11	0	11	0	0	31
		montane light cover	0	6	10	0	0	0	0	16
		montane heavy cover	3	5	14	0	3	0	0	25
	%	grassland/tree-less	46.7	6.7	46.7	.0	.0	.0	.0	100.0
		wooded-bushed grassland	.0	34.8	58.7	.0	6.5	.0	.0	100.0
		light woodland-bushland	7.8	41.2	31.4	.0	19.6	.0	.0	100.0
		heavy woodland-bushland	.0	29.6	63.0	.0	7.4	.0	.0	100.0
		forest	9.7	19.4	35.5	.0	35.5	.0	.0	100.0
		montane light cover	.0	37.5	62.5	.0	.0	.0	.0	100.0
		montane heavy cover	12.0	20.0	56.0	.0	12.0	.0	0	100.0

a 23.7% of original grouped cases correctly classified.

Appendix E, Table N3. Structure matrix from an analysis of the size corrected proximal metacarpal data

Structure Matrix

	Function	
	1 69.8%	2 30.2%
RESMC3	.997	.080
RESMC4	.778	.628



Appendix E, Figure N2. Scatter plot of the first and second discriminant functions from an analysis of the size corrected proximal metacarpal data

Appendix E, Table N4. Classification results table from an analysis of the size corrected proximal metacarpal data

Classification Results[a]

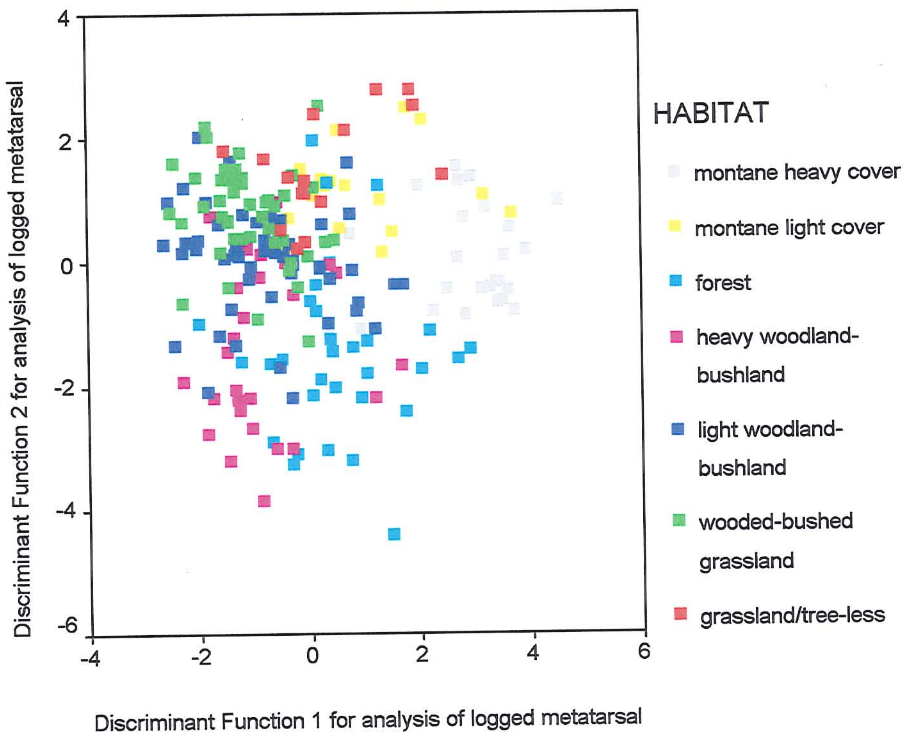
			Predicted Group Membership							
		HABITAT	grassland/ tree-less	wooded-bushed grassland	light woodland-bushland	heavy woodland-bushland	forest	montane light cover	montane heavy cover	Total
Original	Count	grassland/tree-less	0	4	7	0	3	0	1	15
		wooded-bushed grassland	0	18	28	0	0	0	0	46
		light woodland-bushland	0	16	22	1	8	0	4	51
		heavy woodland-bushland	0	8	9	3	7	0	0	27
		forest	0	2	11	1	17	0	0	31
		montane light cover	0	6	6	1	2	0	0	15
		montane heavy cover	0	10	9	1	5	0	0	25
	%	grassland/tree-less	.0	26.7	46.7	.0	20.0	.0	6.7	100.0
		wooded-bushed grassland	.0	39.1	60.9	.0	.0	.0	.0	100.0
		light woodland-bushland	.0	31.4	43.1	2.0	15.7	.0	7.8	100.0
		heavy woodland-bushland	.0	29.6	33.3	11.1	25.9	.0	.0	100.0
		forest	.0	6.5	35.5	3.2	54.8	.0	.0	100.0
		montane light cover	.0	40.0	40.0	6.7	13.3	.0	.0	100.0
		montane heavy cover	.0	40.0	36.0	4.0	20.0	.0	.0	100.0

a. 28.6% of original grouped cases correctly classified.

Appendix E, Table O1. Structure matrix from an analysis of the logged metatarsal data

Structure Matrix

	Function					
	1 48.9%	2 30.9%	3 12.4%	4 5.1%	5 1.6%	6 1.1%
LOGMT3	-.011	.222	.407	.176	.390	.272
LOGMT9	.146	.264	.403	.112	.338	.245
LOGMT4	.086	.196	.400	.156	.379	.199
LOGMT6	.162	.277	.388	.140	.359	.256
LOGMT8	-.016	.230	.380	.311	.338	.214
LOGMT11	.207	.365	.376	.032	.375	.179
LOGMT12	-.034	.199	.368	.206	.321	.289
LOGMT1	-.267	.271	.128	.361	.329	.106
LOGMT10	.242	.245	.408	.143	.461	.198
LOGMT5	.052	.255	.336	.198	.398	.270
LOGMT7	.168	.294	.376	.103	.386	.269
LOGMT13	.182	.135	.370	.152	.378	.324
LOGMT2	-.285	.211	.146	.230	.296	.255



Appendix E, Figure O1. Scatter plot of the first and second discriminant functions from an analysis of the logged metatarsal data

Appendix E, Table O2. Classification results table from an analysis of the logged metatarsal data

Classification Results[a]

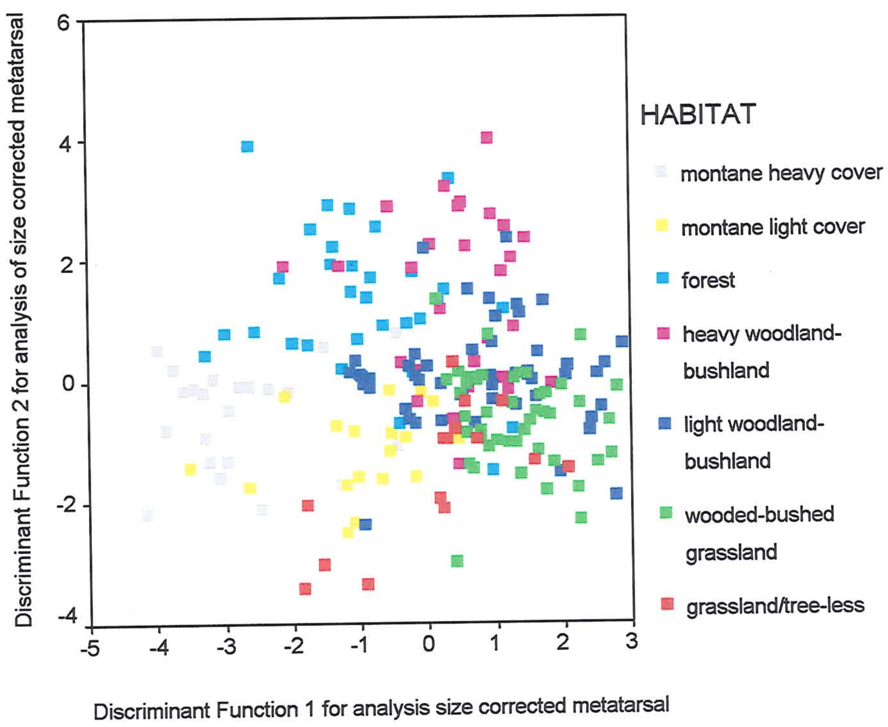
			Predicted Group Membership							
		HABITAT	grassland/ tree-less	wooded-bushed grassland	light woodland-bushland	heavy woodland-bushland	forest	montane light cover	montane heavy cover	Total
Original	Count	grassland/tree-less	12	2	1	0	0	0	0	15
		wooded-bushed grassland	3	32	11	0	0	0	0	46
		light woodland-bushland	1	9	32	4	3	0	3	52
		heavy woodland-bushland	0	7	5	14	1	0	1	28
		forest	1	0	3	5	20	1	1	31
		montane light cover	0	2	2	0	0	12	2	18
		montane heavy cover	0	0	1	0	2	1	21	25
	%	grassland/tree-less	80.0	13.3	6.7	.0	.0	.0	.0	100.0
		wooded-bushed grassland	6.5	69.6	23.9	.0	.0	.0	.0	100.0
		light woodland-bushland	1.9	17.3	61.5	7.7	5.8	.0	5.8	100.0
		heavy woodland-bushland	.0	25.0	17.9	50.0	3.6	.0	3.6	100.0
		forest	3.2	.0	9.7	16.1	64.5	3.2	3.2	100.0
		montane light cover	.0	11.1	11.1	.0	.0	66.7	11.1	100.0
		montane heavy cover	.0	.0	4.0	.0	8.0	4.0	84.0	100.0

a. 66.5% of original grouped cases correctly classified.

Appendix E, Table O3. Structure matrix from an analysis of the size corrected metatarsal data

Structure Matrix

	Function					
	1 49.9%	2 27.9%	3 12.3%	4 5.6%	5 3.2%	6 1.1%
RESMT2	.647	.104	.445	.184	.209	-.026
RESMT3	.618	-.115	-.054	.263	.380	-.126
RESMT12	.613	.006	.082	.396	.428	-.234
RESMT1	.580	.000	.432	.330	.064	.190
RESMT8	.518	-.114	.032	.661	.156	.037
RESMT5	.319	-.293	.210	.375	.308	-.112
RESMT9	-.013	-.375	-.041	.179	.636	-.033
RESMT6	-.065	-.463	.013	.276	.586	-.067
RESMT4	.190	-.113	-.069	.319	.575	.196
RESMT7	-.069	-.461	.065	.127	.530	-.077
RESMT11	-.097	-.468	.065	-.017	.482	.148
RESMT13	-.190	.044	.024	.277	.462	-.247
RESMT10	-.267	-.289	-.037	.193	.322	.172



Appendix E, Figure O2. Scatter plot of the first and second discriminant functions from an analysis of the size corrected metatarsal data

Appendix E, Table O4. Classification results table from an analysis of the size corrected metatarsal data

Classification Results[a]

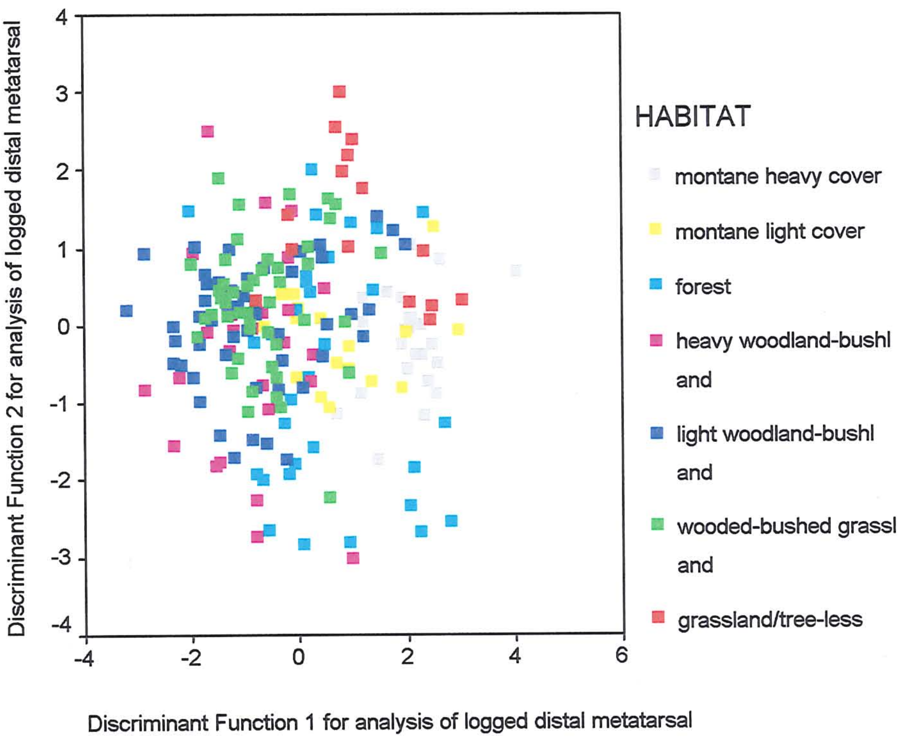
			Predicted Group Membership							
		HABITAT	grassland/ tree-less	wooded-bushed grassland	light woodland-bushland	heavy woodland-bushland	forest	montane light cover	montane heavy cover	Total
Original	Count	grassland/tree-less	11	3	1	0	0	0	0	15
		wooded-bushed grassland	1	35	9	0	0	1	0	46
		light woodland-bushland	1	9	31	5	3	2	1	52
		heavy woodland-bushland	0	5	7	14	2	0	0	28
		forest	0	0	4	6	21	0	0	31
		montane light cover	0	0	2	0	0	14	2	18
		montane heavy cover	0	1	0	0	3	1	20	25
	%	grassland/tree-less	73.3	20.0	6.7	.0	.0	.0	.0	100.0
		wooded-bushed grassland	2.2	76.1	19.6	.0	.0	2.2	.0	100.0
		light woodland-bushland	1.9	17.3	59.6	9.6	5.8	3.8	1.9	100.0
		heavy woodland-bushland	.0	17.9	25.0	50.0	7.1	.0	.0	100.0
		forest	.0	.0	12.9	19.4	67.7	.0	.0	100.0
		montane light cover	.0	.0	11.1	.0	.0	77.8	11.1	100.0
		montane heavy cover	.0	4.0	.0	.0	12.0	4.0	80.0	100.0

a 67.9% of original grouped cases correctly classified.

Appendix E, Table P1. Structure matrix from an analysis of the logged metatarsal data

Structure Matrix

	Function					
	1 71.8%	2 15.0%	3 8.6%	4 2.9%	5 1.2%	6 0.4%
LOGMT11	.339	.768	-.100	.350	.298	.117
LOGMT8	.046	.708	.247	.461	.327	.199
LOGMT7	.280	.679	.036	.421	.374	.321
LOGMT6	.270	.667	.097	.424	.339	.323
LOGMT5	.130	.665	.091	.474	.371	.280
LOGMT9	.252	.659	.120	.350	.438	.300
LOGMT10	.361	.580	.164	.540	.371	.114



Appendix E, Figure P1. Scatter plot of the first and second discriminant functions from an analysis of the logged distal metatarsal data

Appendix E, Table P2. Classification results table from an analysis of the logged distal metatarsal data

Classification Results[a]

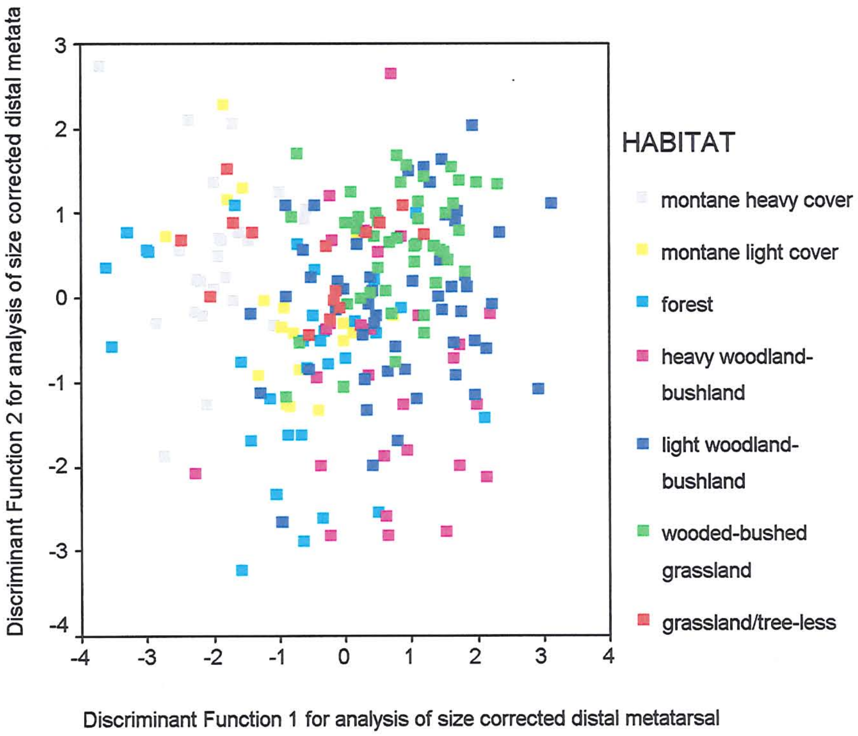
		HABITAT	Predicted Group Membership: grassland/ tree-less	wooded-bushed grassland	light woodland-bushland	heavy woodland-bushland	forest	montane light cover	montane heavy cover	Total
Original	Count	grassland/tree-less	7	2	1	0	0	0	5	15
		wooded-bushed grassland	4	23	16	0	3	0	0	46
		light woodland-bushland	3	8	33	4	2	1	1	52
		heavy woodland-bushland	0	8	11	6	3	0	0	28
		forest	5	4	5	3	9	5	0	31
		montane light cover	0	4	2	0	2	7	3	18
		montane heavy cover	0	0	0	0	3	3	19	25
	%	grassland/tree-less	46.7	13.3	6.7	.0	.0	.0	33.3	100.0
		wooded-bushed grassland	8.7	50.0	34.8	.0	6.5	.0	.0	100.0
		light woodland-bushland	5.8	15.4	63.5	7.7	3.8	1.9	1.9	100.0
		heavy woodland-bushland	.0	28.6	39.3	21.4	10.7	.0	.0	100.0
		forest	16.1	12.9	16.1	9.7	29.0	16.1	.0	100.0
		montane light cover	.0	22.2	11.1	.0	11.1	38.9	16.7	100.0
		montane heavy cover	.0	.0	.0	.0	12.0	12.0	76.0	100.0

a 48.4% of original grouped cases correctly classified.

Appendix E, Table P3. Structure matrix from an analysis of the size corrected metatarsal data

Structure Matrix

	Function					
	1 67.8%	2 20.6%	3 8.2%	4 2.6%	5 0.5%	6 0.2%
RESMT8	.678	.497	.305	.234	.011	.344
RESMT6	-.136	.882	-.160	.160	-.353	.083
RESMT7	-.144	.825	-.343	.054	-.250	-.034
RESMT11	-.191	.784	-.449	-.112	.258	.249
RESMT9	-.072	.755	-.077	-.202	-.478	.277
RESMT5	.399	.667	-.274	.266	-.366	.299
RESMT10	-.370	.492	.001	.403	.049	.530



Appendix E, Figure P2. Scatter plot of the first and second discriminant functions from an analysis of the size corrected distal metatarsal data

Appendix E, Table P4. Classification results table from an analysis of the size corrected distal metatarsal data

Classification Results[a]

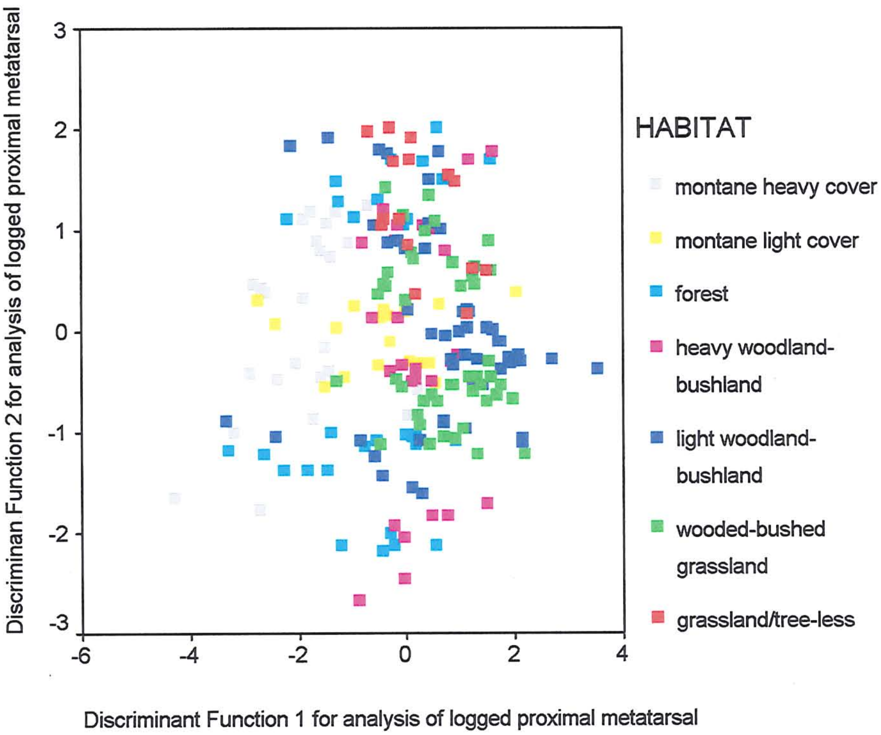
		HABITAT	Predicted Group Membership							Total
			grassland/ tree-less	wooded-bushed grassland	light woodland-bushland	heavy woodland-bushland	forest	montane light cover	montane heavy cover	
Original	Count	grassland/tree-less	0	5	2	0	3	0	5	15
		wooded-bushed grassland	1	30	12	0	2	1	0	46
		light woodland-bushland	0	14	29	3	5	0	1	52
		heavy woodland-bushland	0	6	9	10	3	0	0	28
		forest	1	1	6	1	15	4	3	31
		montane light cover	0	1	3	0	5	5	4	18
		montane heavy cover	0	2	0	0	3	1	19	25
	%	grassland/tree-less	.0	33.3	13.3	.0	20.0	.0	33.3	100.0
		wooded-bushed grassland	2.2	65.2	26.1	.0	4.3	2.2	.0	100.0
		light woodland-bushland	.0	26.9	55.8	5.8	9.6	.0	1.9	100.0
		heavy woodland-bushland	.0	21.4	32.1	35.7	10.7	.0	.0	100.0
		forest	3.2	3.2	19.4	3.2	48.4	12.9	9.7	100.0
		montane light cover	.0	5.6	16.7	.0	27.8	27.8	22.2	100.0
		montane heavy cover	.0	8.0	.0	.0	12.0	4.0	76.0	100.0

a. 50.2% of original grouped cases correctly classified.

Appendix E, Table Q1. Structure matrix from an analysis of the logged proximal metatarsal data

Structure Matrix

	Function	
	1 84.9%	2 15.1%
LOGMT4	-.046	.999
LOGMT3	.104	.995



Appendix E, Figure Q1. Scatter plot of the first and second discriminant functions from an analysis of the logged proximal metatarsal data

Appendix E, Table Q2. Classification results table from an analysis of the logged proximal metatarsal data

Classification Results[a]

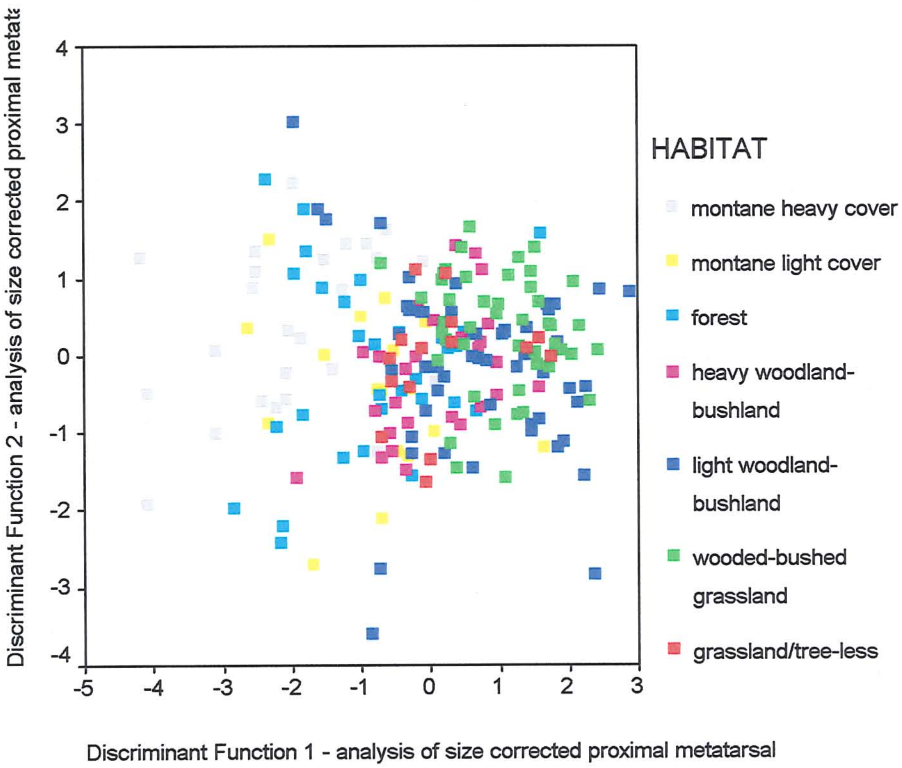
			Predicted Group Membership							
		HABITAT	grassland/ tree-less	wooded-bushed grassland	light woodland-bushland	heavy woodland-bushland	forest	montane light cover	montane heavy cover	Total
Original	Count	grassland/tree-less	5	0	10	0	0	0	0	15
		wooded-bushed grassland	1	2	40	0	3	0	0	46
		light woodland-bushland	3	3	39	0	3	0	4	52
		heavy woodland-bushland	0	4	19	0	5	0	0	28
		forest	4	1	10	0	9	0	7	31
		montane light cover	0	0	10	0	6	0	2	18
		montane heavy cover	0	0	2	0	3	0	20	25
	%	grassland/tree-less	33.3	.0	66.7	.0	.0	.0	.0	100.0
		wooded-bushed grassland	2.2	4.3	87.0	.0	6.5	.0	.0	100.0
		light woodland-bushland	5.8	5.8	75.0	.0	5.8	.0	7.7	100.0
		heavy woodland-bushland	.0	14.3	67.9	.0	17.9	.0	.0	100.0
		forest	12.9	3.2	32.3	.0	29.0	.0	22.6	100.0
		montane light cover	.0	.0	55.6	.0	33.3	.0	11.1	100.0
		montane heavy cover	.0	.0	8.0	.0	12.0	.0	80.0	100.0

a 34 9% of original grouped cases correctly classified.

Appendix E, Table Q3. Structure matrix from an analysis of the size corrected proximal metatarsal data

Structure Matrix

	Function	
	1 93.5%	2 6.5%
RESMT3	.821	.571
RESMT4	.264	.965



Appendix E, Figure Q2. Scatter plot of the first and second discriminant functions from an analysis of the size corrected proximal metatarsal data

Appendix E, Table Q4. Classification results table from an analysis of the size corrected proximal metatarsal data

Classification Results[a]

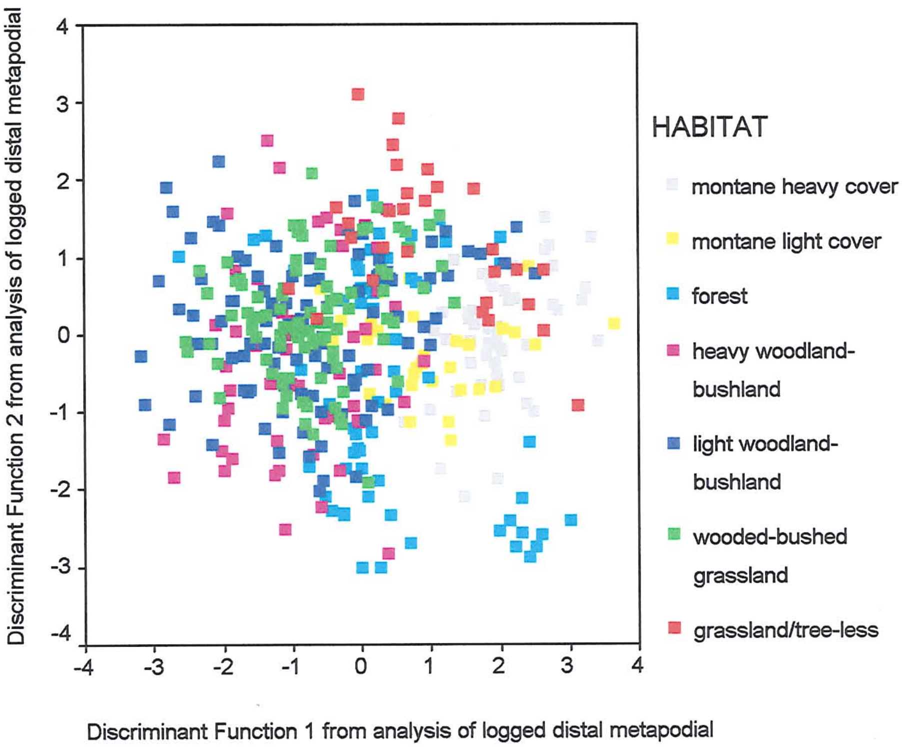
			Predicted Group Membership							
		HABITAT	grassland/ tree-less	wooded-bushed grassland	light woodland-bushland	heavy woodland-bushland	forest	montane light cover	montane heavy cover	Total
Original	Count	grassland/tree-less	0	4	8	0	3	0	0	15
		wooded-bushed grassland	0	29	16	0	1	0	0	46
		light woodland-bushland	0	15	29	0	3	2	3	52
		heavy woodland-bushland	0	5	15	0	8	0	0	28
		forest	0	2	9	0	11	2	7	31
		montane light cover	0	0	6	0	8	1	3	18
		montane heavy cover	0	1	1	0	5	0	18	25
	%	grassland/tree-less	.0	26.7	53.3	.0	20.0	.0	.0	100.0
		wooded-bushed grassland	.0	63.0	34.8	.0	2.2	.0	.0	100.0
		light woodland-bushland	.0	28.8	55.8	.0	5.8	3.8	5.8	100.0
		heavy woodland-bushland	.0	17.9	53.6	.0	28.6	.0	.0	100.0
		forest	.0	6.5	29.0	.0	35.5	6.5	22.6	100.0
		montane light cover	.0	.0	33.3	.0	44.4	5.6	16.7	100.0
		montane heavy cover	.0	4.0	4.0	.0	20.0	.0	72.0	100.0

a. 40.9% of original grouped cases correctly classified.

Appendix E, Table R1. Structure matrix from an analysis of the logged distal metapodial data

Structure Matrix

	Function					
	1 68.6%	2 15.5%	3 9.9%	4 3.2%	5 2.5%	6 0.3%
LOGMP11	.367	.758	-.184	-.010	.454	.100
LOGMP8	.029	.725	.112	.130	.592	-.007
LOGMP7	.289	.696	-.002	-.016	.589	-.136
LOGMP9	.266	.688	.083	-.056	.591	-.069
LOGMP6	.290	.686	.042	.016	.576	-.101
LOGMP5	.130	.681	-.006	.042	.629	-.055
LOGMP10	.372	.539	-.001	.143	.700	.172



Appendix E, Figure R1. Scatter plot of the first and second discriminant functions from an analysis of the logged distal metapodial

Appendix E, Table R2. Classification results table from an analysis of the logged distal metapodial data

Classification Results[a]

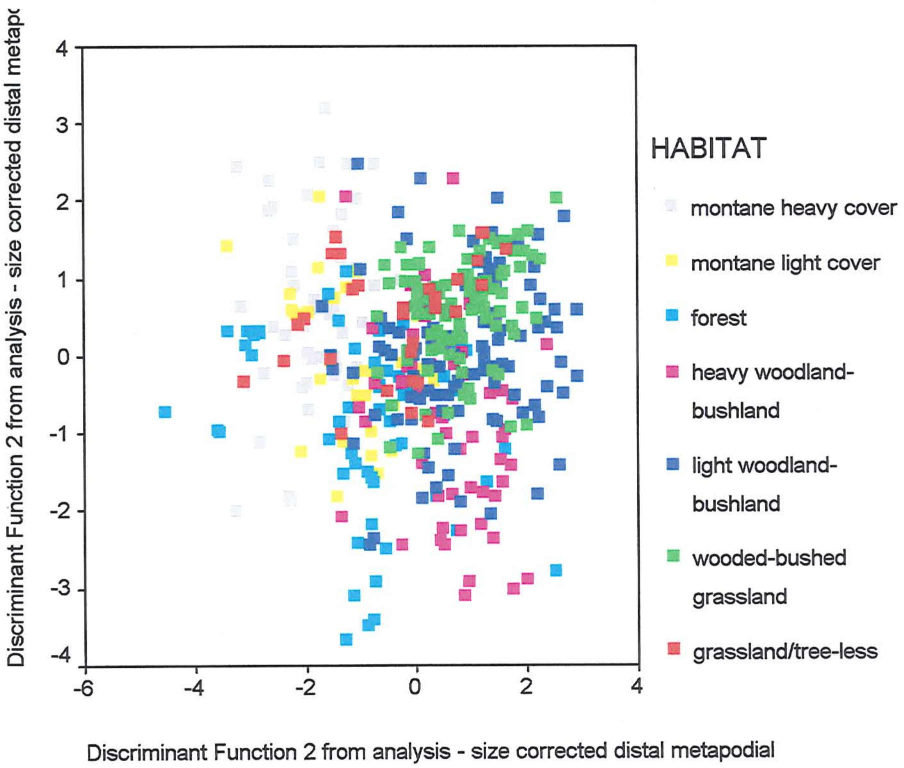
			Predicted Group Membership							
		HABITAT	grassland/ tree-less	wooded-bushed grassland	light woodland-bushland	heavy woodland-bushland	forest	montane light cover	montane heavy cover	Total
Original	Count	grassland/tree-less	15	0	6	0	0	0	9	30
		wooded-bushed grassland	9	43	38	0	2	0	0	92
		light woodland-bushland	5	24	53	6	9	1	5	103
		heavy woodland-bushland	0	17	19	11	6	1	1	55
		forest	4	6	14	0	28	7	3	62
		montane light cover	0	5	5	0	3	16	5	34
		montane heavy cover	0	0	0	0	6	9	35	50
	%	grassland/tree-less	50.0	.0	20.0	.0	.0	.0	30.0	100.0
		wooded-bushed grassland	9.8	46.7	41.3	.0	2.2	.0	.0	100.0
		light woodland-bushland	4.9	23.3	51.5	5.8	8.7	1.0	4.9	100.0
		heavy woodland-bushland	.0	30.9	34.5	20.0	10.9	1.8	1.8	100.0
		forest	6.5	9.7	22.6	.0	45.2	11.3	4.8	100.0
		montane light cover	.0	14.7	14.7	.0	8.8	47.1	14.7	100.0
		montane heavy cover	.0	.0	.0	.0	12.0	18.0	70.0	100.0

a. 47.2% of original grouped cases correctly classified.

Appendix E, Table R3. Structure matrix from an analysis of the size corrected distal metapodial data

Structure Matrix

	Function					
	1 62.5%	2 21.8%	3 12.0%	4 3.1%	5 0.5%	6 0.2%
RESMP8	.700	.500	.061	.266	.188	.356
RESMP6	-.213	.880	.213	-.110	-.146	.300
RESMP7	-.184	.819	.318	-.214	-.265	.130
RESMP9	-.126	.808	.087	-.381	-.044	.375
RESMP11	-.250	.736	.471	-.113	.318	-.148
RESMP5	.377	.656	.447	-.039	-.106	.461
RESMP10	-.376	.370	.257	.245	.239	.445



Appendix E, Figure R2. Scatter plot of the first and second discriminant functions from an analysis of the size corrected distal metapodial data

Appendix E, Table R4. Classification results table from an analysis of the size corrected distal metapodial data

Classification Results[a]

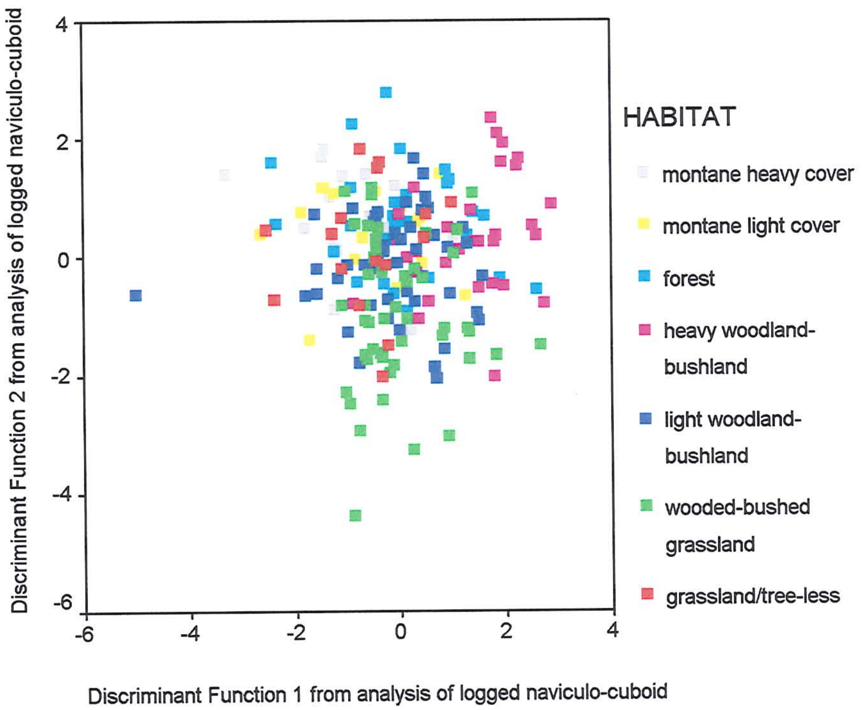
			Predicted Group Membership							
		HABITAT	grassland/ tree-less	wooded-bushed grassland	light woodland-bushland	heavy woodland-bushland	forest	montane light cover	montane heavy cover	Total
Original	Count	grassland/tree-less	1	10	5	0	5	1	8	30
		wooded-bushed grassland	1	55	31	1	3	0	1	92
		light woodland-bushland	0	27	52	8	12	0	4	103
		heavy woodland-bushland	0	9	19	18	6	2	1	55
		forest	0	1	13	6	27	8	7	62
		montane light cover	0	1	3	1	6	17	6	34
		montane heavy cover	1	2	0	0	11	5	31	50
	%	grassland/tree-less	3.3	33.3	16.7	.0	16.7	3.3	26.7	100.0
		wooded-bushed grassland	1.1	59.8	33.7	1.1	3.3	.0	1.1	100.0
		light woodland-bushland	.0	26.2	50.5	7.8	11.7	.0	3.9	100.0
		heavy woodland-bushland	.0	16.4	34.5	32.7	10.9	3.6	1.8	100.0
		forest	.0	1.6	21.0	9.7	43.5	12.9	11.3	100.0
		montane light cover	.0	2.9	8.8	2.9	17.6	50.0	17.6	100.0
		montane heavy cover	2.0	4.0	.0	.0	22.0	10.0	62.0	100.0

a. 47.2% of original grouped cases correctly classified.

Appendix E, Table S1. Structure matrix from an analysis of the logged naviculo-cuboid data.

Structure Matrix

	Function					
	1 33.2%	2 28.8%	3 18.3%	4 11.6%	5 6.3%	6 1.7%
LOGTA3	.373	.221	.800	.193	.034	-.136
LOGTA9	.132	.195	.784	.448	-.087	-.053
LOGTA11	.130	.244	.775	.460	-.009	.003
LOGTA1	.118	.272	.774	.459	-.041	-.067
LOGTA8	.133	.206	.772	.453	-.081	-.076
LOGTA13	.132	.232	.750	.396	-.046	.036
LOGTA5	.121	.322	.745	.445	-.054	-.057
LOGTA4	.152	.289	.744	.313	-.202	-.031
LOGTA15	.001	.326	.731	.412	.120	-.034
LOGTA6	.145	.298	.729	.454	-.073	.005
LOGTA2	.111	.193	.726	.465	-.051	-.080
LOGTA7	.099	.270	.719	.489	-.110	-.065
LOGTA12	.209	.259	.698	.497	-.038	-.053
LOGTA10	.145	.296	.692	.471	-.009	-.111
LOGTA14	.339	.181	.682	.433	-.058	.094



Appendix E, Figure S1. Scatter plot of the first and second discriminant functions from an analysis of the logged naviculo-cuboid data

Appendix E, Table S2. Classification results table from an analysis of the logged naviculo-cuboid data

Classification Results[a]

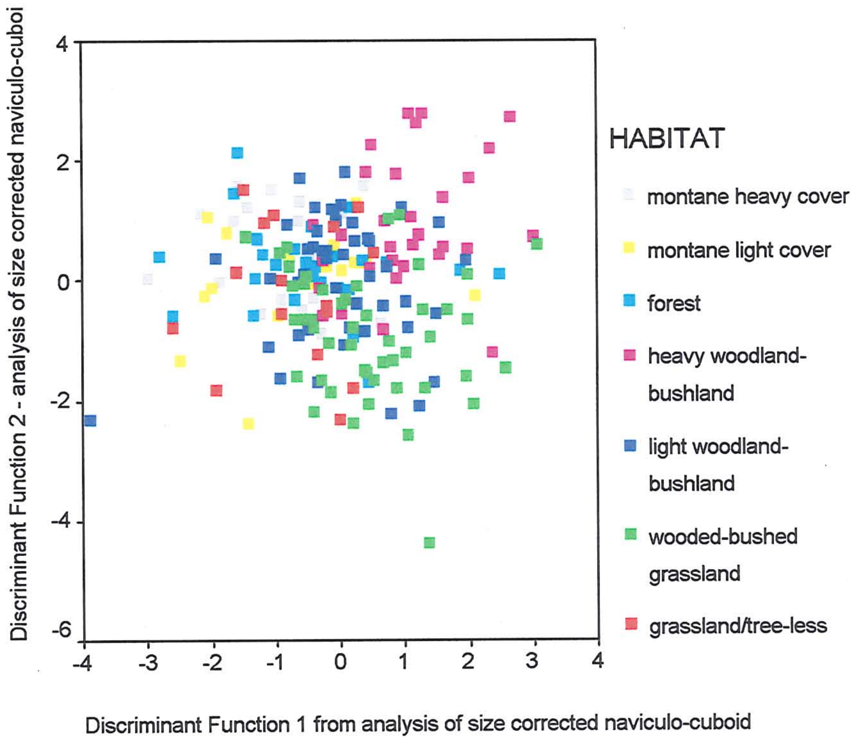
			Predicted Group Membership							
		HABITAT	grassland/ tree-less	wooded-bushed grassland	light woodland-bushland	heavy woodland-bushland	forest	montane light cover	montane heavy cover	Total
Original	Count	grassland/tree-less	2	3	5	1	0	2	3	16
		wooded-bushed grassland	0	25	12	2	5	3	1	48
		light woodland-bushland	0	11	28	2	2	1	3	47
		heavy woodland-bushland	0	2	6	16	5	1	1	31
		forest	1	3	3	3	12	2	3	27
		montane light cover	0	2	4	1	2	5	3	17
		montane heavy cover	0	1	4	1	1	4	9	20
	%	grassland/tree-less	12.5	18.8	31.3	6.3	.0	12.5	18.8	100.0
		wooded-bushed grassland	.0	52.1	25.0	4.2	10.4	6.3	2.1	100.0
		light woodland-bushland	.0	23.4	59.6	4.3	4.3	2.1	6.4	100.0
		heavy woodland-bushland	.0	6.5	19.4	51.6	16.1	3.2	3.2	100.0
		forest	3.7	11.1	11.1	11.1	44.4	7.4	11.1	100.0
		montane light cover	.0	11.8	23.5	5.9	11.8	29.4	17.6	100.0
		montane heavy cover	.0	5.0	20.0	5.0	5.0	20.0	45.0	100.0

a. 47.1% of original grouped cases correctly classified.

Appendix E, Table S3. Structure matrix from an analysis of the size corrected naviculo-cuboid data

Structure Matrix

	Function					
	1 39.0%	2 31.9%	3 14.8%	4 7.5%	5 4.8%	6 2.0%
RESTA7	-.344	.246	-.163	-.007	-.066	-.058
RESTA14	.336	.263	-.026	.153	-.031	.316
RESTA10	-.253	.435	-.156	.367	-.044	-.220
RESTA5	-.374	.429	.039	.166	-.246	.000
RESTA6	-.263	.414	-.017	.114	-.184	.211
RESTA12	.000	.345	-.163	.185	-.254	.009
RESTA3	.307	.289	.513	.330	-.118	-.161
RESTA4	-.176	.328	.350	-.200	.203	.022
RESTA15	-.506	.180	.024	.563	.073	.029
RESTA2	-.220	.038	-.132	.254	.036	-.140
RESTA1	-.373	.287	.040	.244	-.395	-.031
RESTA11	-.254	.192	.024	.342	-.365	.236
RESTA9	-.194	.034	.075	.093	-.290	.002
RESTA8	-.207	.088	.033	.123	-.251	-.108
RESTA13	-.179	.160	.137	.229	-.004	.261



Appendix E, Figure S2. Scatter plot of the first and second discriminant functions from an analysis of the size corrected naviculo-cuboid data

Appendix E, Table S4. Classification results table from an analysis of the size corrected naviculo-cuboid data

Classification Results[a]

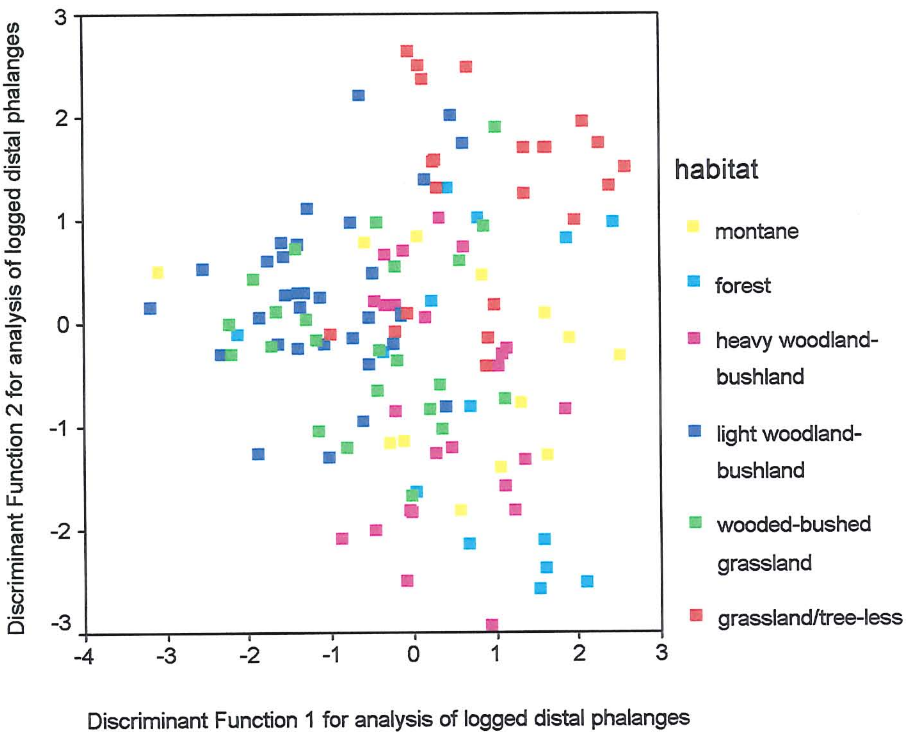
			Predicted Group Membership							
		HABITAT	grassland/ tree-less	wooded-bushed grassland	light woodland-bushland	heavy woodland-bushland	forest	montane light cover	montane heavy cover	Total
Original	Count	grassland/tree-less	2	3	6	0	0	2	3	16
		wooded-bushed grassland	0	28	11	3	2	3	1	48
		light woodland-bushland	1	11	25	4	3	0	3	47
		heavy woodland-bushland	0	4	6	19	1	1	0	31
		forest	2	3	7	2	9	0	4	27
		montane light cover	0	2	6	0	3	4	2	17
		montane heavy cover	0	1	3	0	4	3	9	20
	%	grassland/tree-less	12.5	18.8	37.5	.0	.0	12.5	18.8	100.0
		wooded-bushed grassland	.0	58.3	22.9	6.3	4.2	6.3	2.1	100.0
		light woodland-bushland	2.1	23.4	53.2	8.5	6.4	.0	6.4	100.0
		heavy woodland-bushland	.0	12.9	19.4	61.3	3.2	3.2	.0	100.0
		forest	7.4	11.1	25.9	7.4	33.3	.0	14.8	100.0
		montane light cover	.0	11.8	35.3	.0	17.6	23.5	11.8	100.0
		montane heavy cover	.0	5.0	15.0	.0	20.0	15.0	45.0	100.0

a. 46.6% of original grouped cases correctly classified.

Appendix E, Table T1. Structure matrix from an analysis of the logged distal phalnges data

Structure Matrix

	Function				
	1 44.0%	2 35.4%	3 16.1%	4 4.1%	5 0.4%
LOGPC4	.293	.816	.076	.214	.250
LOGPC2	.244	.786	.046	.400	.203
LOGPC5	.407	.770	.151	.393	.187
LOGPC3	.345	.743	-.086	.399	.284
LOGPC3B	.318	.736	.174	.393	.351
LOGPC1	.368	.661	.086	.472	.201



Appendix E, Figure T1. Scatter plot of the first and second discriminant function from an analysis of the logged distal phalanges data

Appendix E, Table T2. Classification results table from an anlysis of the logged distal phalanges data

Classification Results[a]

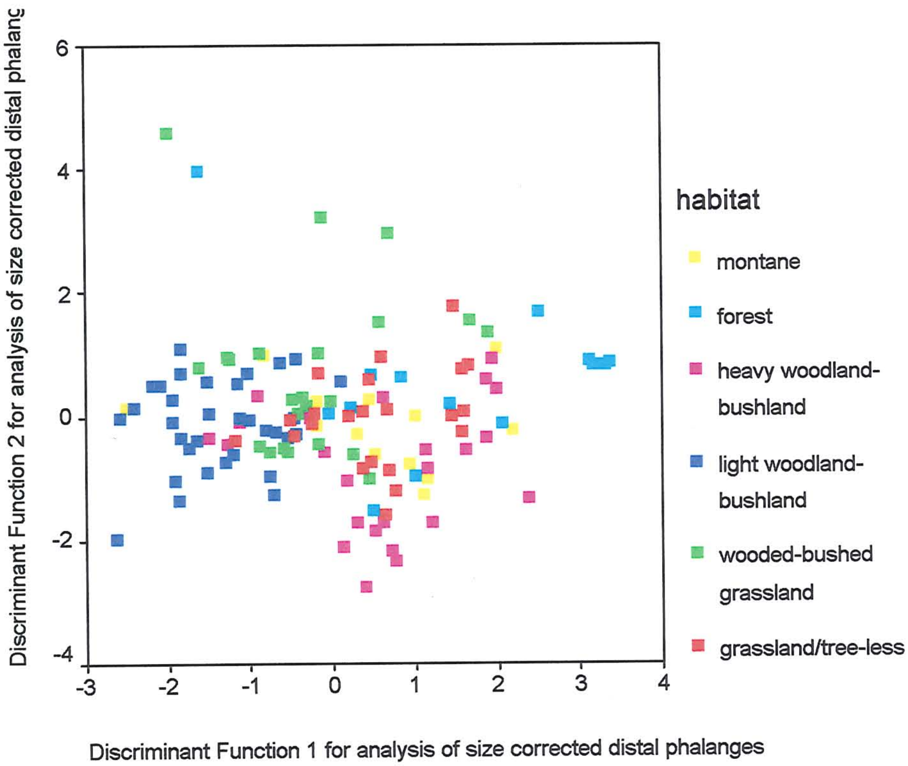
			Predicted Group Membership						
		habitat	grassland/ tree-less	wooded-bushed grassland	light woodland-bushland	heavy woodland-bushland	forest	montane light cover	Total
Original	Count	grassland/tree-less	16	1	2	1	1	1	22
		wooded-bushed grassland	2	8	9	2	2	0	23
		light woodland-bushland	3	3	24	2	1	0	33
		heavy woodland-bushland	1	0	5	15	2	1	24
		forest	4	2	1	2	5	0	14
		montane	0	0	3	5	1	4	13
	%	grassland/tree-less	72.7	4.5	9.1	4.5	4.5	4.5	100.0
		wooded-bushed grassland	8.7	34.8	39.1	8.7	8.7	.0	100.0
		light woodland-bushland	9.1	9.1	72.7	6.1	3.0	.0	100.0
		heavy woodland-bushland	4.2	.0	20.8	62.5	8.3	4.2	100.0
		forest	28.6	14.3	7.1	14.3	35.7	.0	100.0
		montane	.0	.0	23.1	38.5	7.7	30.8	100.0

a. 55.8% of original grouped cases correctly classified.

Appendix E, Table T3. Structure matrix from an analysis of the size corrected distal phalanges data

Structure Matrix

	Function				
	1 64.0%	2 19.6%	3 8.5%	4 7.3%	5 0.6%
RESPC5	.373	.589	.605	.290	.223
RESPC2	-.155	.350	.305	.549	.479
RESPC1	.375	.389	-.186	.441	.336
RESPC3B	.125	.615	.180	.229	.707
RESPC3	.141	-.158	.289	.629	.660
RESPC4	-.040	.273	.534	.087	.643



Appendix E, Figure T2. Scatter plot of the first and second discriminant functions from an analysis of the size corrected distal phalanges data

Appendix E, Table T4. Classification results table from an analysis of the size corrected naviculo-cuboid data

Classification Results[a]

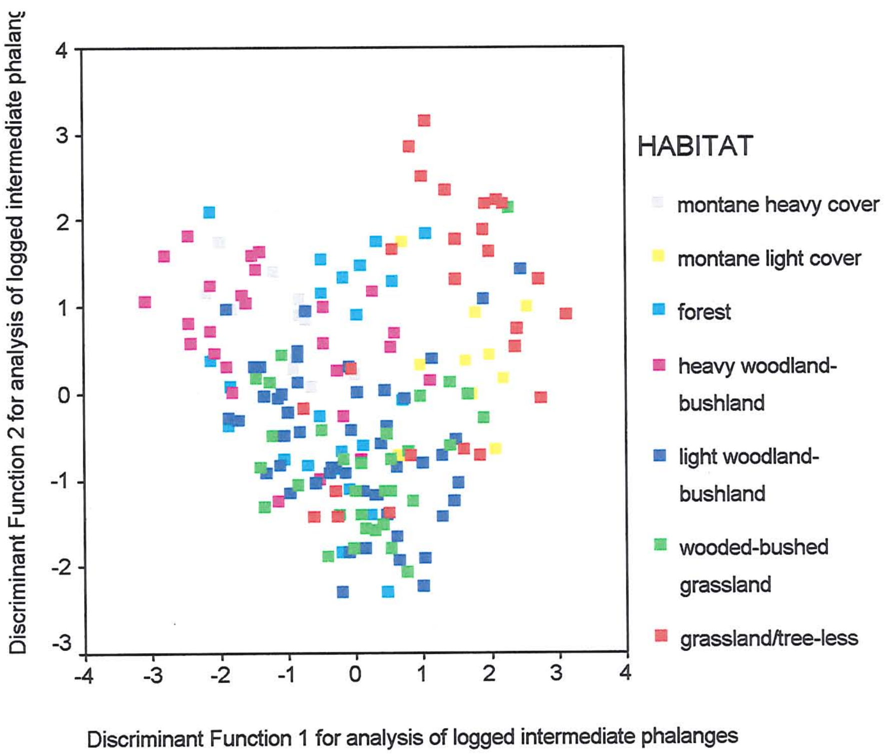
			Predicted Group Membership						
		habitat	grassland/ tree-less	wooded-bushed grassland	light woodland-bushland	heavy woodland-bushland	forest	montane	Total
Original	Count	grassland/tree-less	10	2	2	3	1	4	22
		wooded-bushed grassland	2	6	8	4	2	1	23
		light woodland-bushland	2	1	28	2	0	0	33
		heavy woodland-bushland	4	1	4	11	3	1	24
		forest	2	3	0	3	6	0	14
		montane	1	0	3	4	1	4	13
	%	grassland/tree-less	45.5	9.1	9.1	13.6	4.5	18.2	100.0
		wooded-bushed grassland	8.7	26.1	34.8	17.4	8.7	4.3	100.0
		light woodland-bushland	6.1	3.0	84.8	6.1	.0	.0	100.0
		heavy woodland-bushland	16.7	4.2	16.7	45.8	12.5	4.2	100.0
		forest	14.3	21.4	.0	21.4	42.9	.0	100.0
		montane	7.7	.0	23.1	30.8	7.7	30.8	100.0

a. 50 4% of original grouped cases correctly classified

Appendix E, Table U1. Structure matrix from an analysis of the logged intermediate phalanges data

Structure Matrix

	Function					
	1 41.4%	2 25.3%	3 17.1%	4 13.1%	5 3.0%	6 0.2%
LOGPB5	.544	.301	.511	.316	.155	.084
LOGPB4	.542	.295	.506	.322	.135	.080
LOGPB1	.501	.084	.420	.400	.304	.058
LOGPB3B	.424	.211	.628	.296	.181	.023
LOGPB5B	.443	.229	.593	.324	.275	.068
LOGPB3	.571	.231	.581	.315	.113	.049
LOGPB6	.403	.239	.580	.409	.175	.096
LOGPB2	.566	.214	.567	.317	.151	.231
LOGPB7	.505	.321	.560	.379	.160	.050



Appendix E, Figure U1. Scatter plot of the first and second discriminant functions from an analysis of the logged intermediate phalanges data

Appendix E, Table U2. Classification results table from an analysis of the logegd intermediate phalanges data

Classification Results[a]

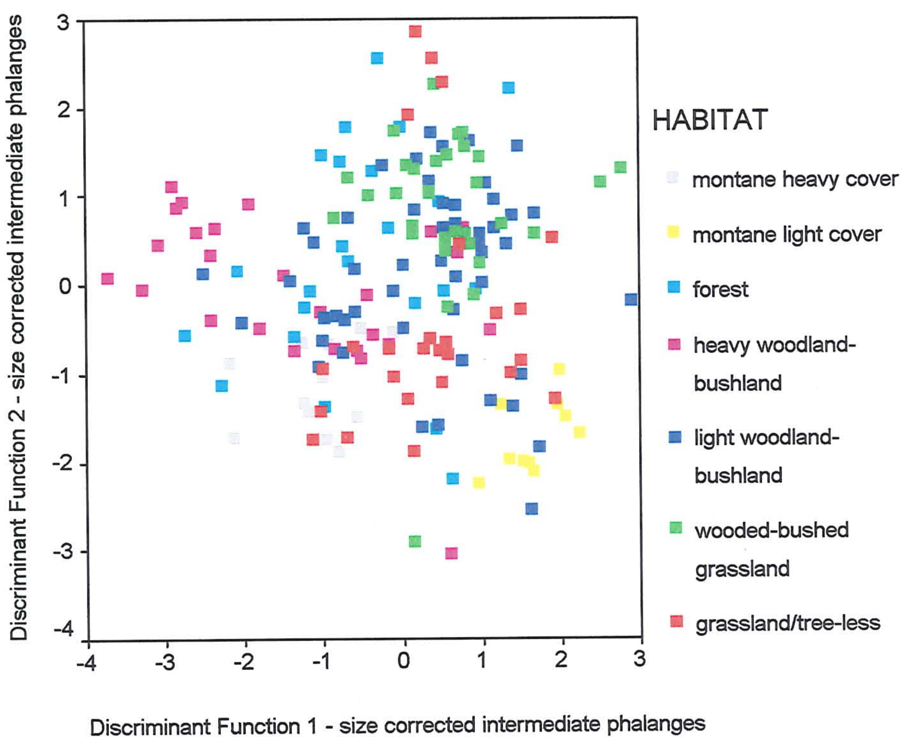
		HABITAT	Predicted Group Membership							Total
			grassland/ tree-less	wooded-bushed grassland	light woodland-bushland	heavy woodland-bushland	forest	montane light cover	montane heavy cover	
Original	Count	grassland/tree-less	17	5	3	0	0	1	0	26
		wooded-bushed grassland	4	16	8	4	0	0	0	32
		light woodland-bushland	3	14	26	3	3	3	0	52
		heavy woodland-bushland	2	2	4	13	1	1	3	26
		forest	3	3	6	3	7	0	1	23
		montane light cover	1	0	0	0	0	9	0	10
		montane heavy cover	0	0	4	2	0	0	6	12
	%	grassland/tree-less	65.4	19.2	11.5	.0	.0	3.8	.0	100 0
		wooded-bushed grassland	12.5	50.0	25.0	12.5	.0	.0	.0	100.0
		light woodland-bushland	5.8	26.9	50.0	5.8	5.8	5.8	.0	100.0
		heavy woodland-bushland	7.7	7.7	15.4	50.0	3.8	3.8	11.5	100.0
		forest	13.0	13.0	26.1	13.0	30.4	.0	4.3	100.0
		montane light cover	10.0	.0	.0	.0	.0	90.0	.0	100.0
		montane heavy cover	.0	.0	33.3	16.7	.0	.0	50.0	100 0

a. 51.9% of original grouped cases correctly classified.

Appendix E, Table U3. Structure matrix from an analysis of the size corrected intermediate phalanges data

Structure Matrix

	Function					
	1 40.6%	2 26.4%	3 18.8%	4 10.7%	5 3.1%	6 0.4%
RESPB2	.594	.221	.457	.408	.018	.317
RESPB3	.570	.209	.388	.375	-.050	.444
RESPB1	.452	.220	-.362	.127	.449	.156
RESPB4	.445	-.105	.326	.388	.049	.227
RESPB5	.427	-.105	.360	.378	.137	.278
RESPB3B	.125	.595	.262	.112	.218	.242
RESPB7	.220	.020	.354	.640	.168	.369
RESPB6	-.009	.434	.018	.546	.220	.149
RESPB5B	.143	.394	.208	.197	.539	.335



Appendix E, Figure U2. Scatter plot of the first and second discriminant functions from an analysis of the size corrected intermediate phalanges data

Appendix E, Table U4. Classification results table from an analysis of the size corrected intermediate phalanges data

Classification Results[a]

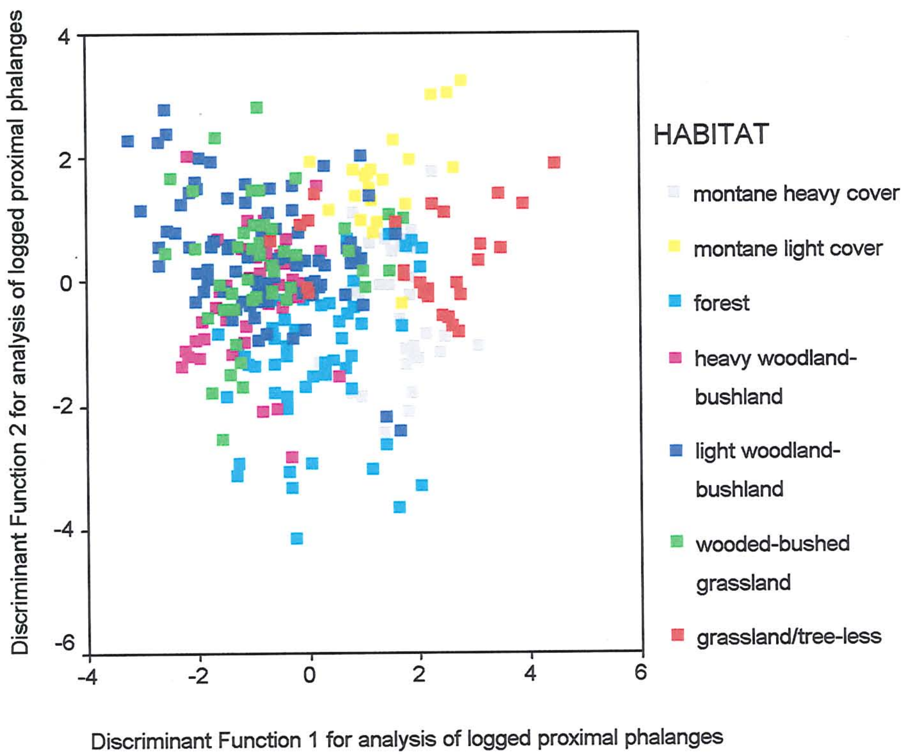
		HABITAT	Predicted Group Membership: grassland/ tree-less	wooded-bushed grassland	light woodland-bushland	heavy woodland-bushland	forest	montane light cover	montane heavy cover	Total
Original	Count	grassland/tree-less	14	5	4	2	0	1	0	26
		wooded-bushed grassland	0	19	9	3	0	0	1	32
		light woodland-bushland	3	10	28	2	5	1	2	51
		heavy woodland-bushland	4	2	4	13	1	1	1	26
		forest	3	3	6	6	5	0	0	23
		montane light cover	1	0	2	0	0	7	0	10
		montane heavy cover	1	0	3	0	1	0	7	12
	%	grassland/tree-less	53.8	19.2	15.4	7.7	.0	3.8	.0	100.0
		wooded-bushed grassland	.0	59.4	28.1	9.4	.0	.0	3.1	100.0
		light woodland-bushland	5.9	19.6	54.9	3.9	9.8	2.0	3.9	100.0
		heavy woodland-bushland	15.4	7.7	15.4	50.0	3.8	3.8	3.8	100.0
		forest	13.0	13.0	26.1	26.1	21.7	.0	.0	100.0
		montane light cover	10.0	.0	20.0	.0	.0	70.0	.0	100.0
		montane heavy cover	8.3	.0	25.0	.0	8.3	.0	58.3	100.0

a. 51.7% of original grouped cases correctly classified.

Appendix E, Table V1. Structure matrix from an analysis of the logged proximal phalanges data

Structure Matrix

	Function					
	1 55.3%	2 26.9%	3 9.9%	4 5.3%	5 2.5%	6 0.1%
LOGPA6	.242	.193	.095	.880	.152	-.189
LOGPA5B	.265	.290	.099	.880	.133	-.159
LOGPA1	.114	.444	.054	.858	.063	-.098
LOGPA4	.375	.184	.033	.857	.057	-.096
LOGPA5	.387	.202	.044	.855	.075	-.090
LOGPA3B	.266	.304	.030	.847	.199	-.108
LOGPA7	.363	.140	.150	.836	.145	-.062
LOGPA2	.377	.235	.106	.819	.117	-.139
LOGPA3	.391	.241	.097	.819	.140	-.120



Appendix E, Figure V1. Scatter plot of the first and second discriminant functions from an analysis of the logged proximal phalanges data

Appendix E, Table V2. Classification results table from an analysis of the logged proximal phalanges data

Classification Results[a]

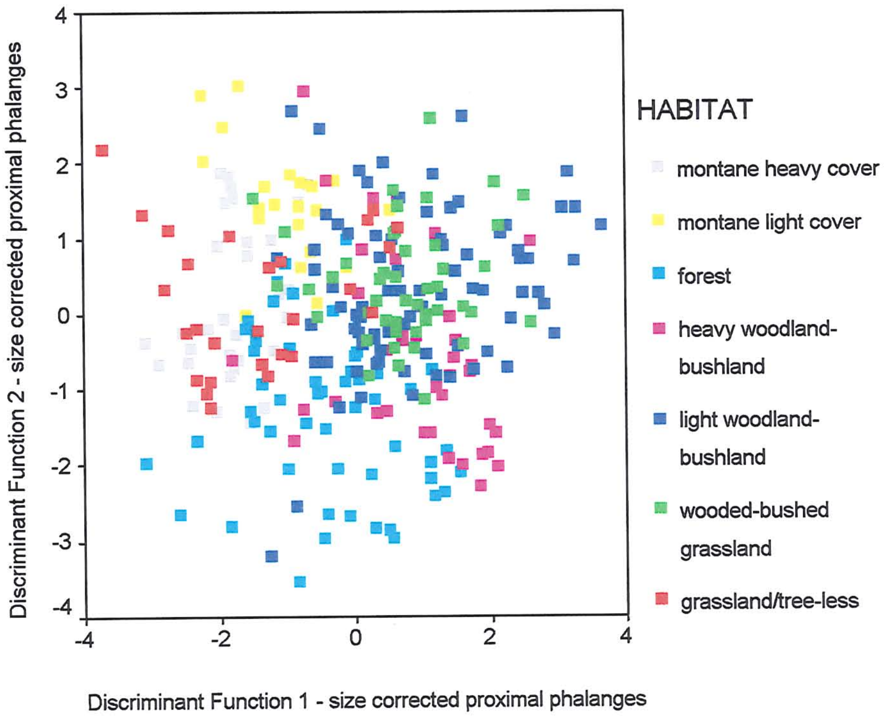
			Predicted Group Membership							
		HABITAT	grassland/ tree-less	wooded-bushed grassland	light woodland-bushland	heavy woodland-bushland	forest	montane light cover	montane heavy cover	Total
Original	Count	grassland/tree-less	16	2	4	0	0	3	2	27
		wooded-bushed grassland	2	8	27	6	1	0	2	46
		light woodland-bushland	2	12	57	5	4	3	0	83
		heavy woodland-bushland	0	3	15	15	5	1	0	39
		forest	5	0	6	3	35	0	4	53
		montane light cover	1	0	2	0	0	17	1	21
		montane heavy cover	4	0	1	0	2	2	25	34
	%	grassland/tree-less	59.3	7.4	14.8	.0	.0	11.1	7.4	100.0
		wooded-bushed grassland	4.3	17.4	58.7	13.0	2.2	.0	4.3	100.0
		light woodland-bushland	2.4	14.5	68.7	6.0	4.8	3.6	.0	100.0
		heavy woodland-bushland	.0	7.7	38.5	38.5	12.8	2.6	.0	100.0
		forest	9.4	.0	11.3	5.7	66.0	.0	7.5	100.0
		montane light cover	4.8	.0	9.5	.0	.0	81.0	4.8	100.0
		montane heavy cover	11.8	.0	2.9	.0	5.9	5.9	73.5	100.0

a. 57.1% of original grouped cases correctly classified.

Appendix E, Table V3. Structure matrix from an analysis of the size corrected proximal phalanges data

Structure Matrix

	Function					
	1 51.4%	2 27.5%	3 15.3%	4 3.8%	5 1.9%	6 0.1%
RESPA1	.559	.666	.209	.286	.138	.171
RESPA3B	.197	.617	.433	.037	.435	.141
RESPA3	-.277	.470	.297	.312	.388	.130
RESPA2	-.231	.438	.292	.389	.358	.050
RESPA4	-.254	.301	.599	.453	.138	.217
RESPA5	-.281	.359	.532	.429	.225	.266
RESPA5B	.211	.533	.321	.379	.617	.169
RESPA6	.255	.210	.497	.271	.543	-.131
RESPA7	-.199	.043	.284	.302	.404	.282



Appendix E, Figure V2. Scatter plot of the first and second discriminant functions from an analysis of the size corrected proximal phalanges data

Appendix E, Table V4. Classification results table from an analysis of the size corrected proximal phalanges data

Classification Results[a]

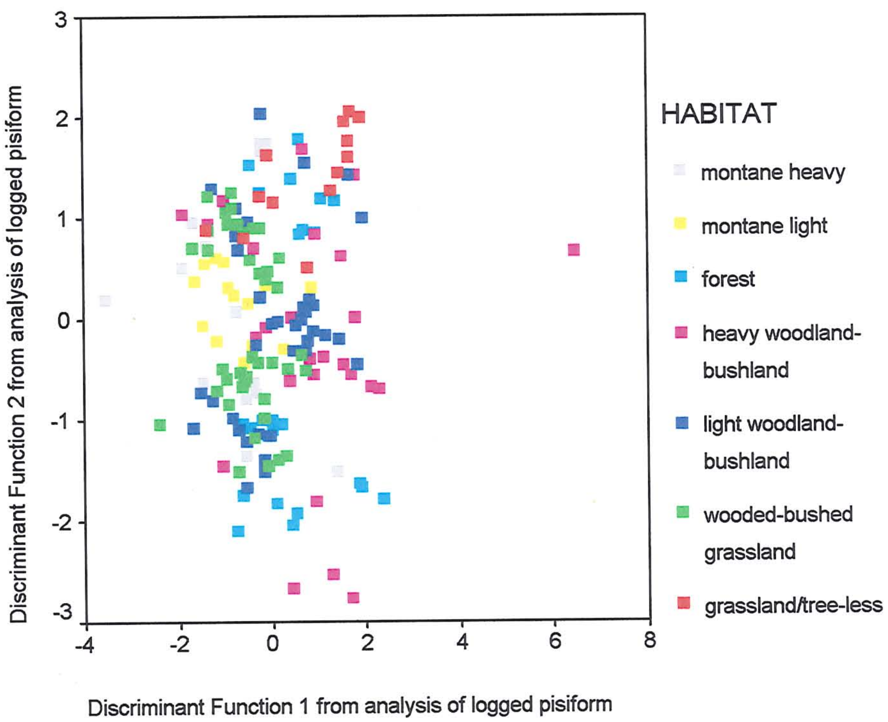
		HABITAT	Predicted Group Membership: grassland/ tree-less	wooded-bushed grassland	light woodland-bushland	heavy woodland-bushland	forest	montane light cover	montane heavy cover	Total
Original	Count	grassland/tree-less	10	5	1	0	4	4	3	27
		wooded-bushed grassland	1	12	31	0	0	0	2	46
		light woodland-bushland	2	9	59	3	8	2	0	83
		heavy woodland-bushland	0	0	16	17	5	1	0	39
		forest	4	0	5	8	30	0	6	53
		montane light cover	2	0	4	0	0	14	1	21
		montane heavy cover	3	0	2	0	4	2	23	34
	%	grassland/tree-less	37.0	18.5	3.7	.0	14.8	14.8	11.1	100.0
		wooded-bushed grassland	2.2	26.1	67.4	.0	.0	.0	4.3	100.0
		light woodland-bushland	2.4	10.8	71.1	3.6	9.6	2.4	.0	100.0
		heavy woodland-bushland	.0	.0	41.0	43.6	12.8	2.6	.0	100.0
		forest	7.5	.0	9.4	15.1	56.6	.0	11.3	100.0
		montane light cover	9.5	.0	19.0	.0	.0	66.7	4.8	100.0
		montane heavy cover	8.8	.0	5.9	.0	11.8	5.9	67.6	100.0

a 54.5% of original grouped cases correctly classified.

Appendix E, Table W1. Structure matrix from an analysis of the logged pisiform data

Structure Matrix

	Function		
	1 58.6%	2 33.3%	3 8.0%
LOGCF2	-.061	.998	-.029
LOGCF1	.178	.984	.016
LOGCF3	.056	.982	.180



Appendix E, Table W1. Scatter plot of the first and second discriminant functions from an analysis of the logged pisiform data

Appendix E, Table W2. Classification results table from an analysis of the logged pisiform data

Classification Results[a]

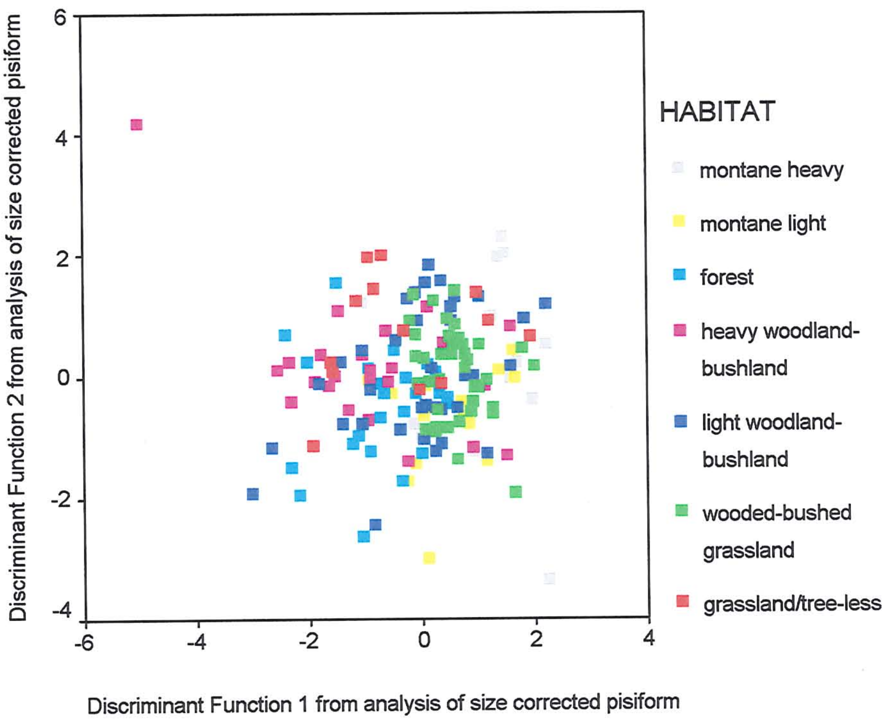
			Predicted Group Membership							
		HABITAT	grassland/ tree-less	wooded-bushed grassland	light woodland-bushland	heavy woodland-bushland	forest	montane light	montane heavy	Total
Original	Count	grassland/tree-less	7	3	3	0	0	0	0	13
		wooded-bushed grassland	0	32	4	2	2	0	0	40
		light woodland-bushland	4	18	12	3	0	0	0	37
		heavy woodland-bushland	2	6	4	12	1	0	1	26
		forest	3	6	7	5	3	0	0	24
		montane light	0	10	3	1	0	0	0	14
		montane heavy	1	12	1	1	0	0	1	16
	%	grassland/tree-less	53.8	23.1	23.1	.0	.0	.0	.0	100.0
		wooded-bushed grassland	.0	80.0	10.0	5.0	5.0	.0	.0	100.0
		light woodland-bushland	10.8	48.6	32.4	8.1	.0	.0	.0	100.0
		heavy woodland-bushland	7.7	23.1	15.4	46.2	3.8	.0	3.8	100.0
		forest	12.5	25.0	29.2	20.8	12.5	.0	.0	100.0
		montane light	.0	71.4	21.4	7.1	.0	.0	.0	100.0
		montane heavy	6.3	75.0	6.3	6.3	.0	.0	6.3	100.0

a. 39.4% of original grouped cases correctly classified.

Appendix E, Table W3. Structure matrix from an analysis of the size corrected pisiform data

Structure Matrix

	Function		
	1 70.7%	2 21.1%	3 8.2%
RESCF2	.877	.468	.107
RESCF1	.126	.935	.330
RESCF3	.424	.506	.751



Appendix E, Figure W2. Scatter plot of the first and second discriminant functions from an analysis of the size corrected pisiform data

Appendix E, Table W4. Classification results table from an analysis of the size corrected pisiform data

Classification Results[a]

		HABITAT	Predicted Group Membership: grassland/ tree-less	wooded-bushed grassland	light woodland-bushland	heavy woodland-bushland	forest	montane light	montane heavy	Total
Original	Count	grassland/tree-less	2	4	3	3	1	0	0	13
		wooded-bushed grassland	0	33	7	0	0	0	0	40
		light woodland-bushland	0	16	15	1	4	0	1	37
		heavy woodland-bushland	0	5	5	13	2	0	1	26
		forest	0	2	7	6	9	0	0	24
		montane light	0	8	3	1	1	1	0	14
		montane heavy	0	10	0	1	2	1	2	16
	%	grassland/tree-less	15.4	30.8	23.1	23.1	7.7	.0	.0	100.0
		wooded-bushed grassland	.0	82.5	17.5	.0	.0	.0	.0	100.0
		light woodland-bushland	.0	43.2	40.5	2.7	10.8	.0	2.7	100.0
		heavy woodland-bushland	.0	19.2	19.2	50.0	7.7	.0	3.8	100.0
		forest	.0	8.3	29.2	25.0	37.5	.0	.0	100 0
		montane light	.0	57.1	21.4	7.1	7.1	7.1	.0	100 0
		montane heavy	.0	62.5	.0	6.3	12.5	6.3	12.5	100.0

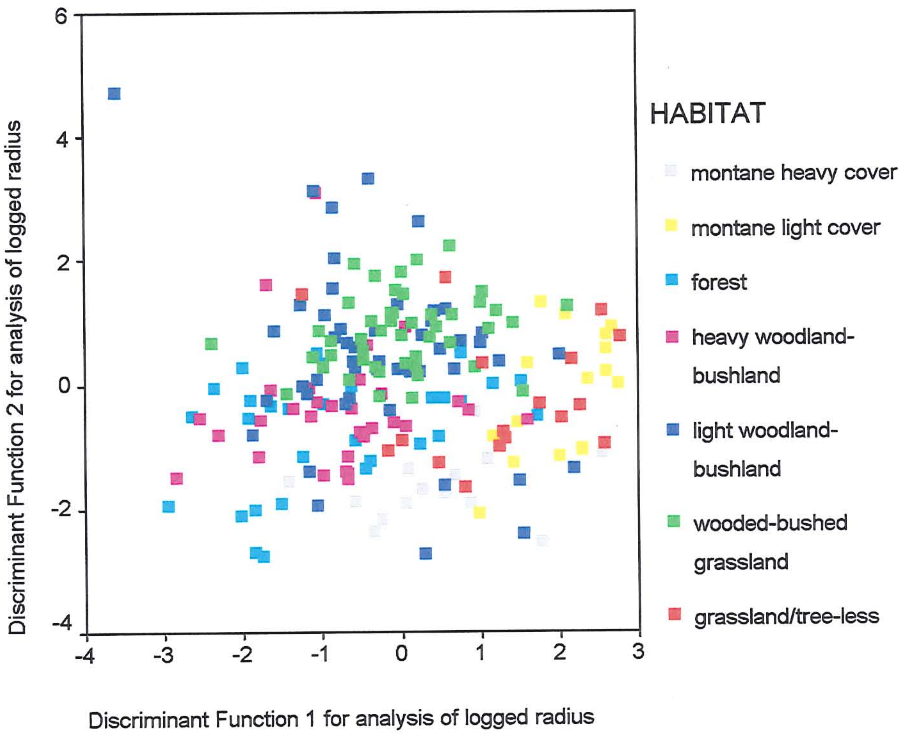
a. 44 1% of original grouped cases correctly classified.

Appendix E, Table X1. Structure matrix from an analysis of the logged radius data

Structure Matrix

	Function					
	1 36.3%	2 27.4%	3 19.3%	4 10.3%	5 5.7%	6 0.9%
LOGR2[a]	.276	.216	.158	.419	.201	.075
LOGR1	.280	.206	.172	.413	.204	.070
LOGR6	.258	.034	.294	.409	.199	.039
LOGR3	.254	.056	.382	.386	.235	.054
LOGR5	.298	.000	.317	.374	.276	.013
LOGR8	.213	-.007	.311	.365	.193	.011
LOGR4	.281	.038	.318	.349	.279	-.009
LOGR7	.306	.003	.331	.334	.213	.037
LOGR9	.226	.027	.288	.334	.274	.117

a. This variable not used in the analysis.



Appendix E, Figure X1. Scatter plot of the first and second discriminant functions from an analysis of the logged radius data

Appendix E, Table X2. Classification results table from an analysis of the logged radius data

Classification Results[a]

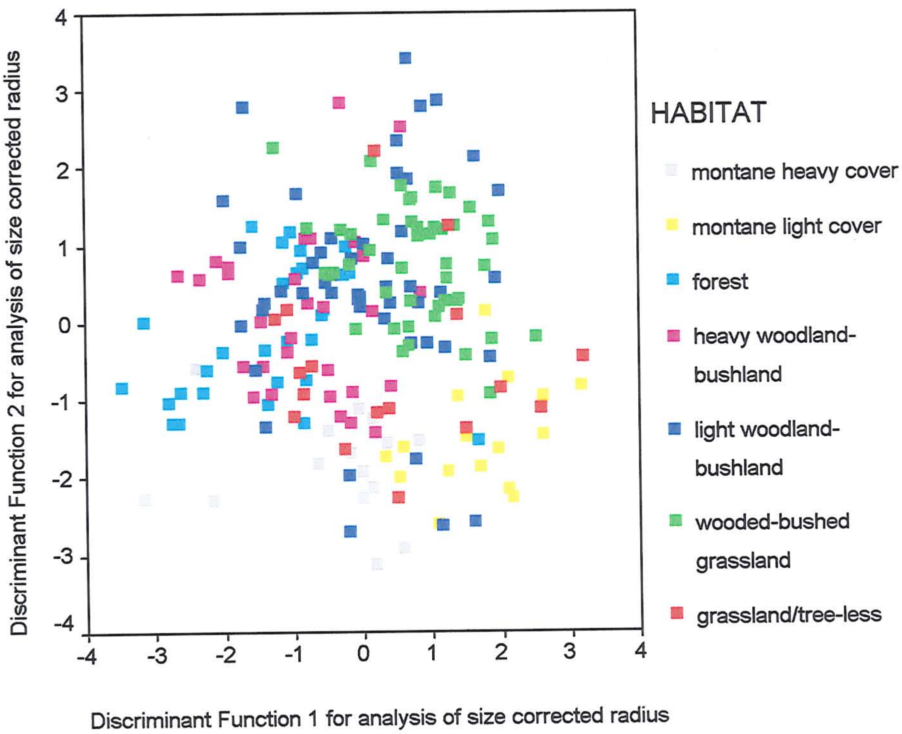
		HABITAT	Predicted Group Membership							Total
			grassland/ tree-less	wooded-bushed grassland	light woodland-bushland	heavy woodland-bushland	forest	montane light cover	montane heavy cover	
Original	Count	grassland/tree-less	8	2	1	0	2	3	1	17
		wooded-bushed grassland	0	27	17	3	0	0	0	47
		light woodland-bushland	3	13	20	4	7	1	3	51
		heavy woodland-bushland	1	3	4	22	1	0	0	31
		forest	2	1	3	4	19	1	0	30
		montane light cover	0	1	0	1	0	14	0	16
		montane heavy cover	0	0	0	1	2	2	10	15
	%	grassland/tree-less	47.1	11.8	5.9	.0	11.8	17.6	5.9	100.0
		wooded-bushed grassland	.0	57.4	36.2	6.4	.0	.0	.0	100.0
		light woodland-bushland	5.9	25.5	39.2	7.8	13.7	2.0	5.9	100.0
		heavy woodland-bushland	3.2	9.7	12.9	71.0	3.2	.0	.0	100.0
		forest	6.7	3.3	10.0	13.3	63.3	3.3	.0	100.0
		montane light cover	.0	6.3	.0	6.3	.0	87.5	.0	100.0
		montane heavy cover	.0	.0	.0	6.7	13.3	13.3	66.7	100.0

a. 58.0% of original grouped cases correctly classified.

Appendix E, Table X3. Structure matrix from an analysis of the size corrected radius data

Structure Matrix

	Function					
	1 34.8%	2 30.5%	3 15.8%	4 12.9%	5 4.7%	6 1.2%
RESR1	.582	.452	.321	.358	.319	-.030
RESR2	.577	.453	.359	.344	.317	-.027
RESR7	.436	.007	-.190	.078	.429	.264
RESR9	.190	.256	.114	.109	.222	-.007
RESR3	.318	.363	-.392	.169	.283	.255
RESR8	.066	.184	-.013	.208	.497	.423
RESR6	.338	.234	-.041	.423	.458	.263
RESR4	.465	.217	-.087	.125	.112	.467
RESR5	.433	.023	-.132	.255	.084	.438



Appendix E, Figure X2. Scatter plot of the first and second discriminant functions from an analysis of the size corrected radius data

Appendix E, Table X4. Classification results table from an analysis of the size corrected radius data

Classification Results[a]

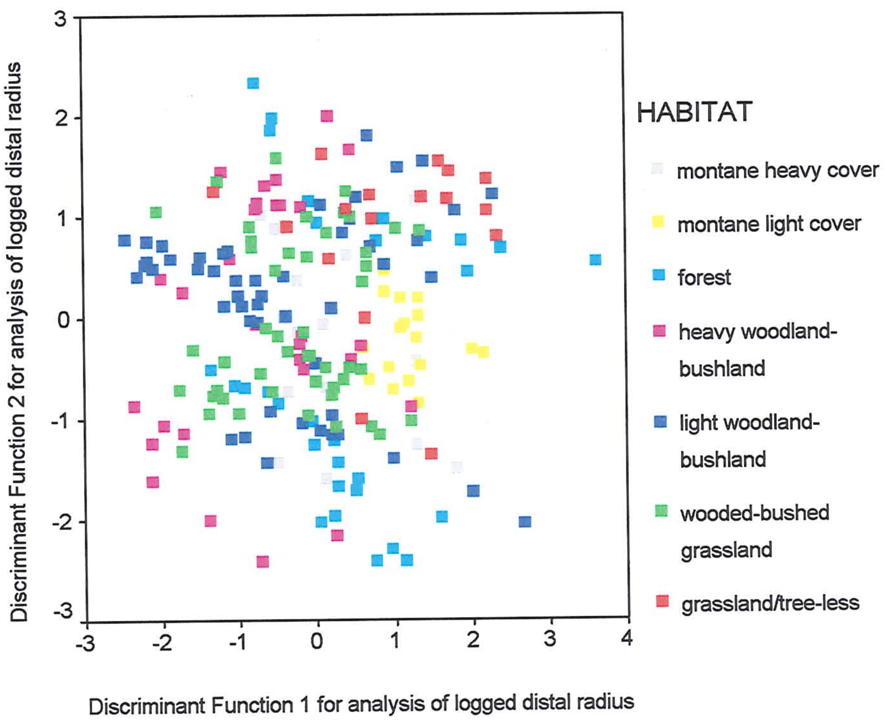
		HABITAT	Predicted Group Membership							Total
			grassland/ tree-less	wooded-bushed grassland	light woodland-bushland	heavy woodland-bushland	forest	montane light cover	montane heavy cover	
Original	Count	grassland/tree-less	10	3	0	0	1	3	0	17
		wooded-bushed grassland	0	33	11	2	0	0	0	46
		light woodland-bushland	2	15	18	6	5	2	2	50
		heavy woodland-bushland	0	2	8	18	2	0	1	31
		forest	1	0	6	2	20	1	0	30
		montane light cover	0	1	0	0	0	15	0	16
		montane heavy cover	2	0	0	0	2	0	11	15
	%	grassland/tree-less	58.8	17.6	.0	.0	5.9	17.6	.0	100.0
		wooded-bushed grassland	.0	71.7	23.9	4.3	.0	.0	.0	100.0
		light woodland-bushland	4.0	30.0	36.0	12.0	10.0	4.0	4.0	100.0
		heavy woodland-bushland	.0	6.5	25.8	58.1	6.5	.0	3.2	100.0
		forest	3.3	.0	20.0	6.7	66.7	3.3	.0	100.0
		montane light cover	.0	6.3	.0	.0	.0	93.8	.0	100.0
		montane heavy cover	13.3	.0	.0	.0	13.3	.0	73.3	100.0

a. 61.0% of original grouped cases correctly classified.

Appendix E, Table Y1. Structure matrix from an analysis of the logged distal radius data

Structure Matrix

	Function	
	1 78.2%	2 21.8%
LOGR6	.289	.957
LOGR7	.391	.920



Appendix E, Figure Y1. Scatter plot of the first and second discriminant functions from an analysis of the logged distal radius data

Appendix E, Table Y2. Classification results table from an analysis of the logged distal radius data

Classification Results[a]

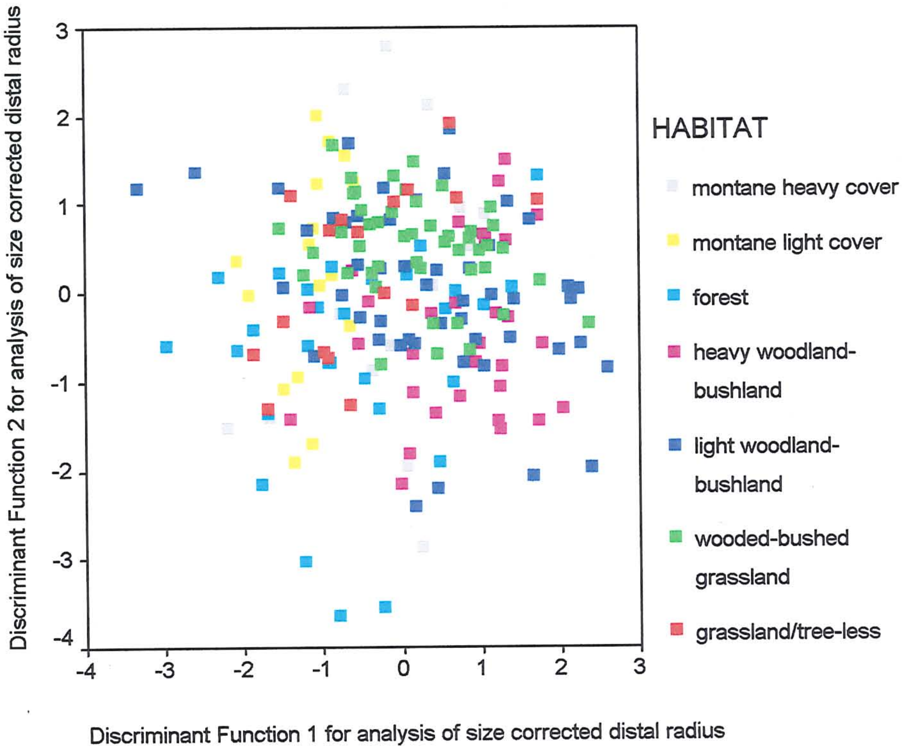
			Predicted Group Membership							
		HABITAT	grassland/ tree-less	wooded-bushed grassland	light woodland-bushland	heavy woodland-bushland	forest	montane light cover	montane heavy cover	Total
Original	Count	grassland/tree-less	7	1	7	0	2	0	0	17
		wooded-bushed grassland	2	19	21	3	3	0	0	48
		light woodland-bushland	6	9	24	7	2	3	0	51
		heavy woodland-bushland	0	7	16	6	2	0	0	31
		forest	3	7	8	0	10	2	0	30
		montane light cover	0	1	2	0	12	2	0	17
		montane heavy cover	1	3	8	0	4	0	0	16
	%	grassland/tree-less	41.2	5.9	41.2	.0	11.8	.0	.0	100.0
		wooded-bushed grassland	4.2	39.6	43.8	6.3	6.3	.0	.0	100.0
		light woodland-bushland	11.8	17.6	47.1	13.7	3.9	5.9	.0	100.0
		heavy woodland-bushland	.0	22.6	51.6	19.4	6.5	.0	.0	100.0
		forest	10.0	23.3	26.7	.0	33.3	6.7	.0	100.0
		montane light cover	.0	5.9	11.8	.0	70.6	11.8	.0	100.0
		montane heavy cover	6.3	18.8	50.0	.0	25.0	.0	.0	100.0

a. 32.4% of original grouped cases correctly classified.

Appendix E, Table Y3. Structure matrix from an analysis of the size corrected distal radius data

Structure Matrix

	Function	
	1 62.4%	2 37.6%
RESR7	-.166	.986
RESR6	.362	.932



Appendix E, Figure Y2. Scatter plot of the first and second discriminant functions from an analysis of the size corrected distal radius data

Appendix E, Table Y4. Classification results table from an analysis of the size corrected distal radius data

Classification Results[a]

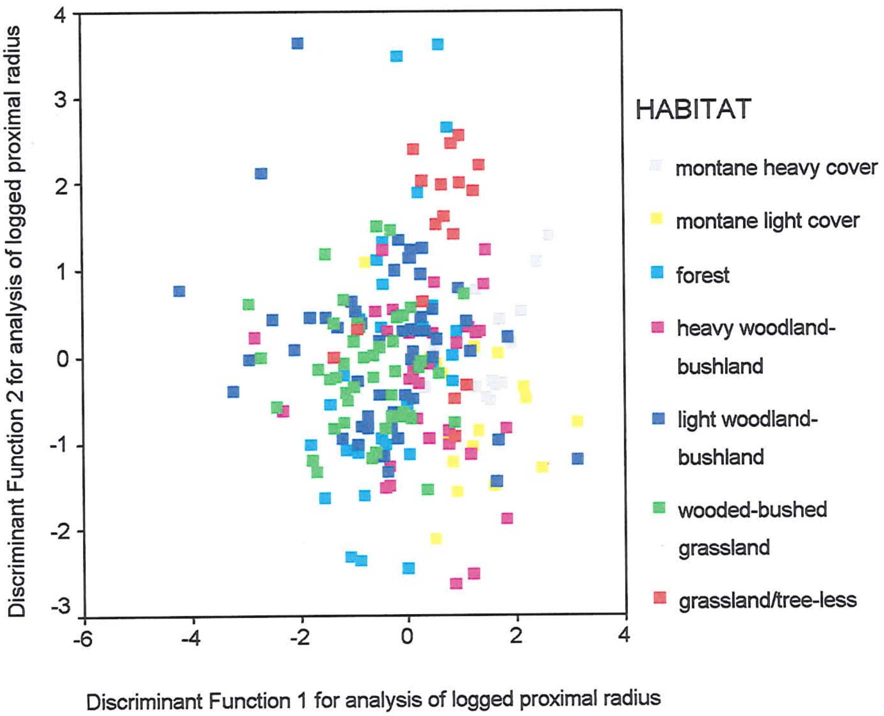
			Predicted Group Membership							
		HABITAT	grassland/ tree-less	wooded-bushed grassland	light woodland-bushland	heavy woodland-bushland	forest	montane light cover	montane heavy cover	Total
Original	Count	grassland/tree-less	0	8	2	0	6	1	0	17
		wooded-bushed grassland	0	27	17	1	0	2	0	47
		light woodland-bushland	0	14	21	9	2	4	0	50
		heavy woodland-bushland	0	7	10	9	5	0	0	31
		forest	0	3	9	1	14	3	0	30
		montane light cover	0	9	1	0	4	3	0	17
		montane heavy cover	0	6	3	0	7	0	0	16
	%	grassland/tree-less	.0	47.1	11.8	.0	35.3	5.9	.0	100.0
		wooded-bushed grassland	.0	57.4	36.2	2.1	.0	4.3	.0	100.0
		light woodland-bushland	.0	28.0	42.0	18.0	4.0	8.0	.0	100.0
		heavy woodland-bushland	.0	22.6	32.3	29.0	16.1	.0	.0	100.0
		forest	.0	10.0	30.0	3.3	46.7	10.0	.0	100.0
		montane light cover	.0	52.9	5.9	.0	23.5	17.6	.0	100.0
		montane heavy cover	.0	37.5	18.8	.0	43.8	.0	.0	100.0

a. 35.6% of original grouped cases correctly classified.

Appendix E, Table Z1. Structure matrix from an analysis of the logged proximal radius data

Structure Matrix

	Function		
	1 64.8%	2 25.8%	3 9.4%
LOGR4	.142	.602	.786
LOGR5	.184	.626	.758
LOGR3	.095	.686	.722



Appendix E, Figure Z1. Scatter plot of the first and second discriminant functions from an analysis of the logged proximal radius data

Appendix E, Table Z2. Classification results table from an analysis of the logged proximal radius data

Classification Results[a]

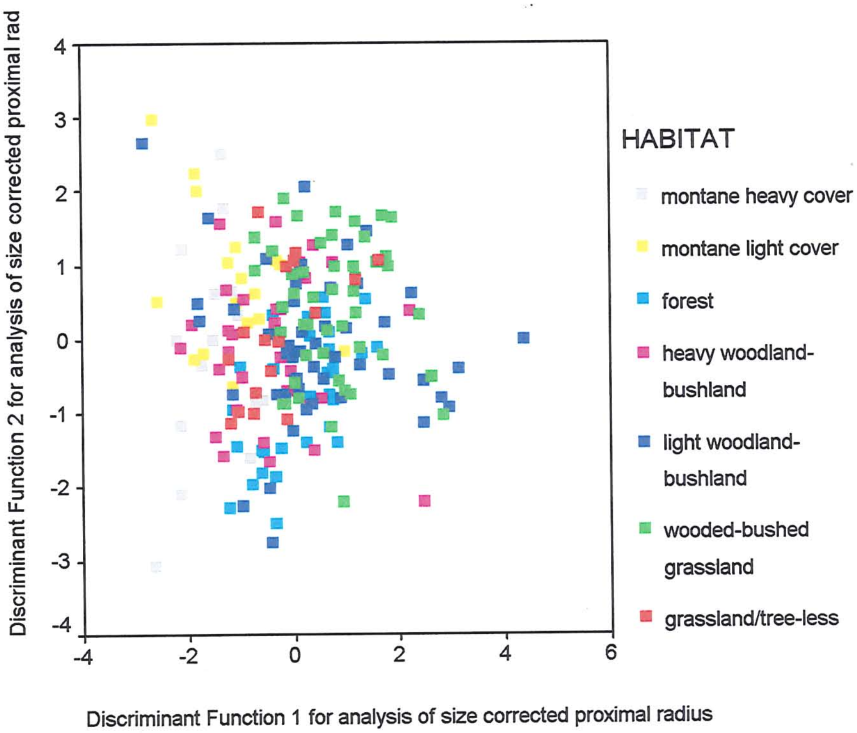
			Predicted Group Membership							
		HABITAT	grassland/ tree-less	wooded-bushed grassland	light woodland-bushland	heavy woodland-bushland	forest	montane light cover	montane heavy cover	Total
Original	Count	grassland/tree-less	11	2	1	2	0	1	0	17
		wooded-bushed grassland	0	21	24	1	0	1	0	47
		light woodland-bushland	2	19	25	1	0	2	3	52
		heavy woodland-bushland	2	5	11	10	1	2	0	31
		forest	4	11	10	3	0	2	0	30
		montane light cover	0	0	3	3	0	10	1	17
		montane heavy cover	1	0	3	1	0	1	9	15
	%	grassland/tree-less	64.7	11.8	5.9	11.8	.0	5.9	.0	100.0
		wooded-bushed grassland	.0	44.7	51.1	2.1	.0	2.1	.0	100.0
		light woodland-bushland	3.8	36.5	48.1	1.9	.0	3.8	5.8	100.0
		heavy woodland-bushland	6.5	16.1	35.5	32.3	3.2	6.5	.0	100.0
		forest	13.3	36.7	33.3	10.0	.0	6.7	.0	100.0
		montane light cover	.0	.0	17.6	17.6	.0	58.8	5.9	100.0
		montane heavy cover	6.7	.0	20.0	6.7	.0	6.7	60.0	100.0

a 41.1% of original grouped cases correctly classified.

Appendix E, Table Z3. Structure matrix from an analysis of the size corrected proximal radius data

Structure Matrix

	Function		
	1 61.5%	2 23.3%	3 15.1%
RESR4	.271	.920	.282
RESR5	.046	.872	.488
RESR3	.482	.547	.685



Appendix E, Figure Z2. Scatter plot of the first and second discriminant functions from an analysis of the size corrected proximal radius data

Appendix E, Table Z4. Classification results table from an analysis of the size corrected proximal radius data

Classification Results[a]

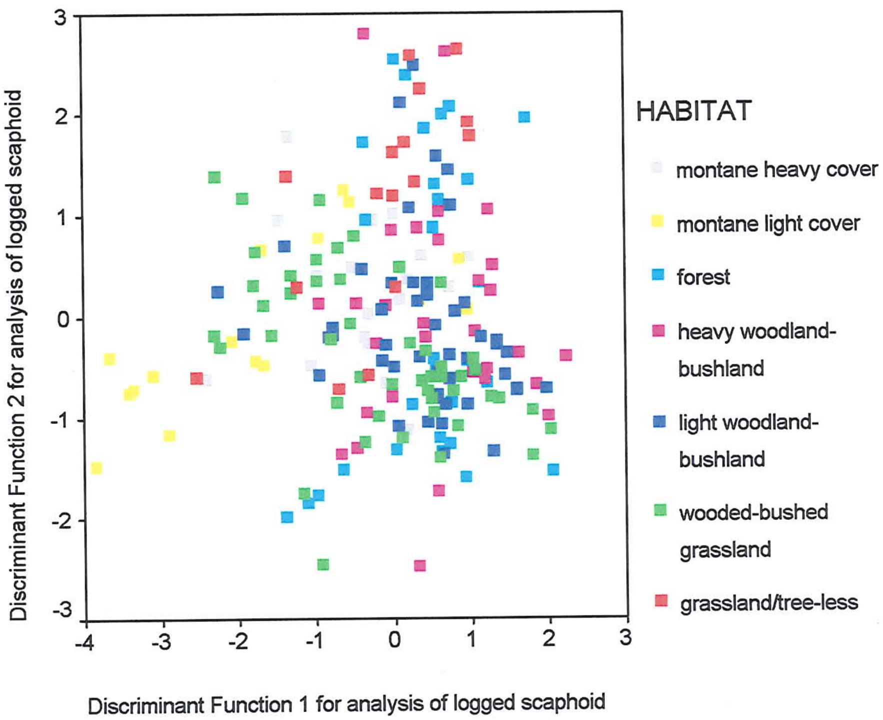
		HABITAT	Predicted Group Membership: grassland/ tree-less	wooded-bushed grassland	light woodland-bushland	heavy woodland-bushland	forest	montane light cover	montane heavy cover	Total
Original	Count	grassland/tree-less	2	4	5	3	1	1	1	17
		wooded-bushed grassland	1	25	17	0	2	2	0	47
		light woodland-bushland	1	17	24	1	5	3	1	52
		heavy woodland-bushland	1	5	7	8	5	4	1	31
		forest	2	5	12	3	8	0	0	30
		montane light cover	0	1	3	4	0	8	1	17
		montane heavy cover	1	0	1	3	1	2	7	15
	%	grassland/tree-less	11.8	23.5	29.4	17.6	5.9	5.9	5.9	100.0
		wooded-bushed grassland	2.1	53.2	36.2	.0	4.3	4.3	.0	100.0
		light woodland-bushland	1.9	32.7	46.2	1.9	9.6	5.8	1.9	100.0
		heavy woodland-bushland	3.2	16.1	22.6	25.8	16.1	12.9	3.2	100.0
		forest	6.7	16.7	40.0	10.0	26.7	.0	.0	100.0
		montane light cover	.0	5.9	17.6	23.5	.0	47.1	5.9	100.0
		montane heavy cover	6.7	.0	6.7	20.0	6.7	13.3	46.7	100.0

a. 39.2% of original grouped cases correctly classified.

Appendix E, Table AA1. Structure matrix from an analysis of the logged scaphoid data

Structure Matrix

	Function			
	1 63.2%	2 24.6%	3 9.7%	4 2.6%
LOGCC4	.257	.914	.312	.026
LOGCC3	-.216	.842	.456	.194
LOGCC1	-.130	.838	.399	.350
LOGCC2	-.141	.792	.538	.250



Appendix E, Figure AA1. Scatter plot of the first and second discriminant functions from an analysis of the logged scaphoid data

Appendix E, Table AA2. Classification results table from an analysis of the logged scaphoid data

Classification Results[a]

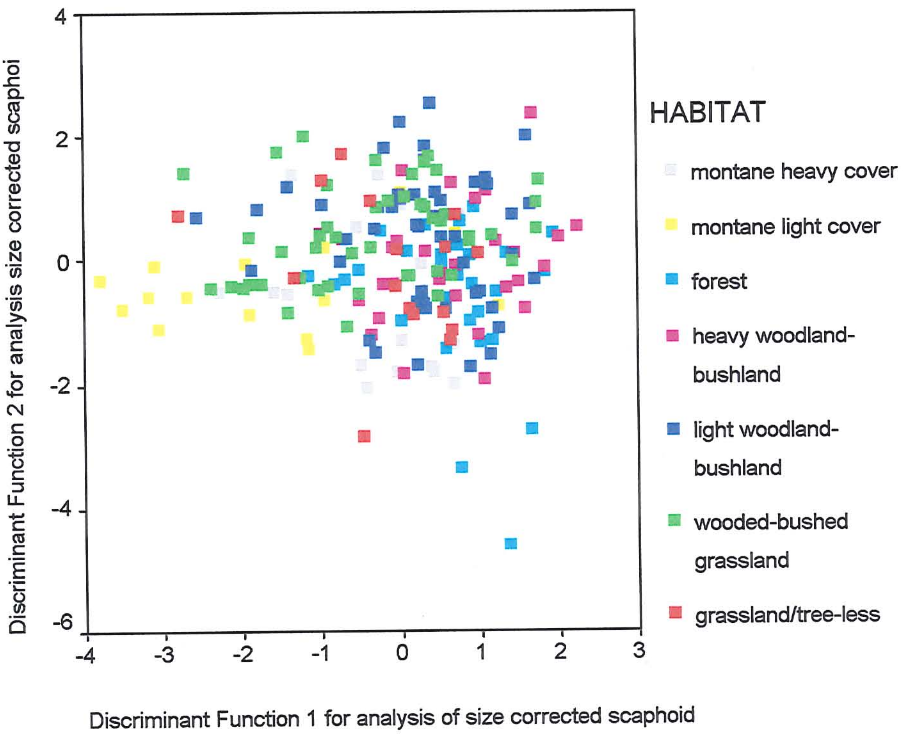
			Predicted Group Membership							
		HABITAT	grassland/ tree-less	wooded-bushed grassland	light woodland-bushland	heavy woodland-bushland	forest	montane light cover	montane heavy cover	Total
Original	Count	grassland/tree-less	6	2	4	0	1	1	2	16
		wooded-bushed grassland	0	18	16	4	1	7	2	48
		light woodland-bushland	2	10	30	1	4	2	0	49
		heavy woodland-bushland	2	7	19	0	2	0	0	30
		forest	5	6	14	0	3	0	1	29
		montane light cover	1	1	3	0	1	9	1	16
		montane heavy cover	0	7	7	0	0	1	4	19
	%	grassland/tree-less	37.5	12.5	25.0	.0	6.3	6.3	12.5	100.0
		wooded-bushed grassland	.0	37.5	33.3	8.3	2.1	14.6	4.2	100.0
		light woodland-bushland	4.1	20.4	61.2	2.0	8.2	4.1	.0	100 0
		heavy woodland-bushland	6.7	23.3	63.3	.0	6.7	.0	.0	100.0
		forest	17.2	20.7	48.3	.0	10.3	.0	3.4	100.0
		montane light cover	6.3	6.3	18.8	.0	6.3	56.3	6.3	100 0
		montane heavy cover	.0	36.8	36.8	.0	.0	5.3	21 1	100 0

a 33 8% of original grouped cases correctly classified.

Appendix E, Table AA3. Structure matrix from an analysis of the size corrected scaphoid data

Structure Matrix

	Function			
	1 66.9%	2 28.0%	3 4.0%	4 1.1%
RESCC2	-.269	.938	.085	.201
RESCC3	-.551	.580	.154	.580
RESCC1	-.175	.593	.760	.200
RESCC4	.629	.293	.114	.711



Appendix E, Figure AA2. Scatter plot of the first and second discriminant functions from an analysis of the size corrected scaphoid data

Appendix E, AA4. Classification results table from an analysis of the size corrected scaphoid data

Classification Results[a]

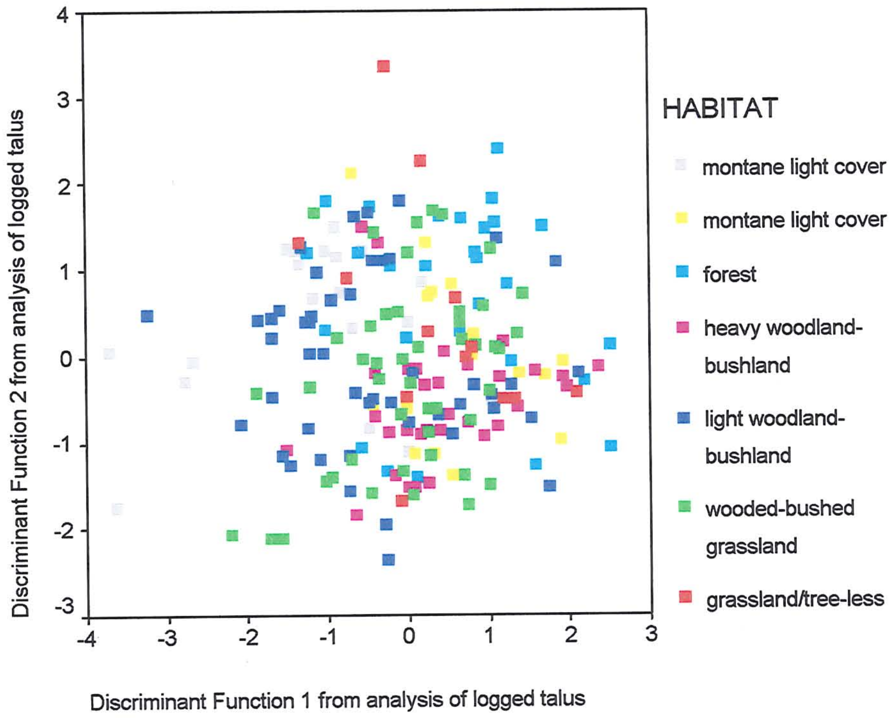
			Predicted Group Membership							
		HABITAT	grassland/ tree-less	wooded-bushed grassland	light woodland-bushland	heavy woodland-bushland	forest	montane light cover	montane heavy cover	Total
Original	Count	grassland/tree-less	0	5	4	0	5	1	1	16
		wooded-bushed grassland	0	19	20	1	0	7	1	48
		light woodland-bushland	0	11	26	1	9	2	0	49
		heavy woodland-bushland	0	6	13	3	7	0	1	30
		forest	0	5	12	2	10	0	0	29
		montane light cover	0	5	1	0	1	9	0	16
		montane heavy cover	0	6	3	0	6	1	3	19
	%	grassland/tree-less	.0	31.3	25.0	.0	31.3	6.3	6.3	100.0
		wooded-bushed grassland	.0	39.6	41.7	2.1	.0	14.6	2.1	100.0
		light woodland-bushland	.0	22.4	53.1	2.0	18.4	4.1	.0	100.0
		heavy woodland-bushland	.0	20.0	43.3	10.0	23.3	.0	3.3	100.0
		forest	.0	17.2	41.4	6.9	34.5	.0	.0	100.0
		montane light cover	.0	31.3	6.3	.0	6.3	56.3	.0	100.0
		montane heavy cover	.0	31.6	15.8	.0	31.6	5.3	15.8	100.0

a 33.8% of original grouped cases correctly classified.

Appendix E, Table BB1. Structure matrix from an analysis of the logged talus data

Structure Matrix

	Function					
	1 46.7%	2 22.6%	3 17.2%	4 7.8%	5 5.2%	6 0.4%
LOGTA2B	.739	.336	.204	.155	-.033	.219
LOGTA6	.727	.299	.219	.294	.031	.158
LOGTA5	.723	.282	.277	.184	-.031	.187
LOGTA1	.702	.332	.285	.206	-.056	.188
LOGTA7	.696	.411	.241	.143	.073	.171
LOGTA2	.690	.303	.327	.175	-.034	.276
LOGTA3	.675	.342	.262	.211	.004	.160
LOGTA4	.667	.375	.285	.174	-.069	.155
LOGTA8	.663	.346	.218	.194	-.028	.237



Appendix E, Figure BB1. Scatter plot of the first and second discriminant functions from an analysis of the logged talus data

Appendix E, Table BB2. Classification results table from an analysis of the talus data

Classification Results[a]

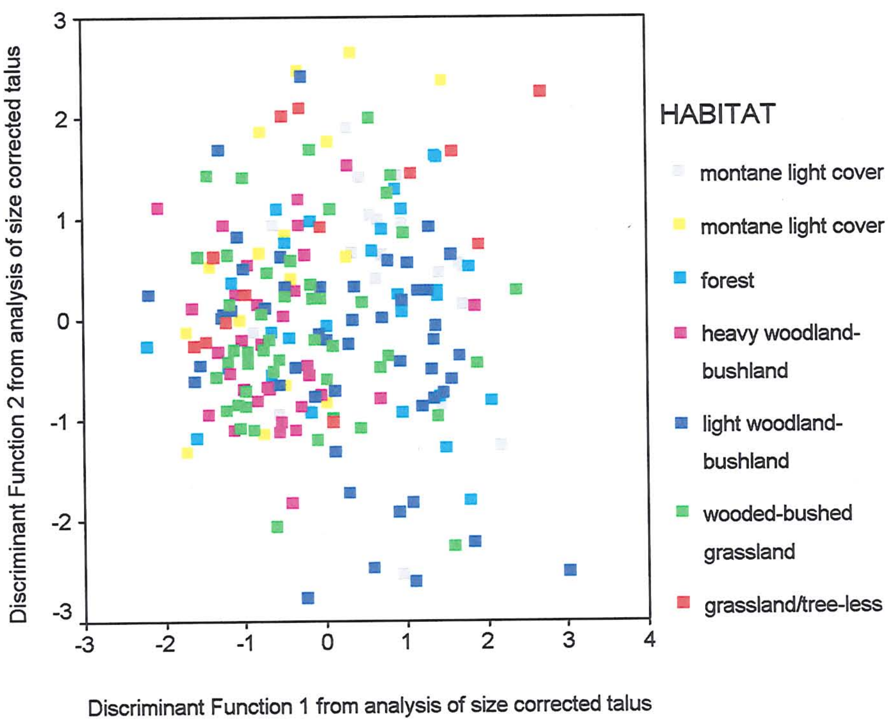
			Predicted Group Membership							
		HABITAT	grassland/ tree-less	wooded-bushed grassland	light woodland-bushland	heavy woodland-bushland	forest	montane light cover	montane light cover	Total
Original	Count	grassland/tree-less	1	1	4	3	3	1	0	13
		wooded-bushed grassland	1	14	15	5	6	4	2	47
		light woodland-bushland	2	8	28	7	2	0	2	49
		heavy woodland-bushland	1	13	3	11	4	0	0	32
		forest	0	3	8	3	12	1	1	28
		montane light cover	1	6	0	3	3	4	0	17
		montane light cover	0	5	7	0	0	0	8	20
	%	grassland/tree-less	7.7	7.7	30.8	23.1	23.1	7.7	.0	100.0
		wooded-bushed grassland	2.1	29.8	31.9	10.6	12.8	8.5	4.3	100.0
		light woodland-bushland	4.1	16.3	57.1	14.3	4.1	.0	4.1	100.0
		heavy woodland-bushland	3.1	40.6	9.4	34.4	12.5	.0	.0	100.0
		forest	.0	10.7	28.6	10.7	42.9	3.6	3.6	100.0
		montane light cover	5.9	35.3	.0	17.6	17.6	23.5	.0	100.0
		montane light cover	.0	25.0	35.0	.0	.0	.0	40.0	100.0

a. 37.9% of original grouped cases correctly classified.

Appendix E, Table BB3. Structure matrix from an analysis of the size corrected talus data

Structure Matrix

	Function					
	1 41.5%	2 25.2%	3 17.1%	4 9.1%	5 6.6%	6 0.7%
RESTA4	.295	.068	.524	.416	-.103	.510
RESTA2B	-.135	.345	.507	.292	.012	.267
RESTA2	.031	-.210	.485	.300	.013	.076
RESTA5	-.166	-.051	.466	.364	.039	.420
RESTA7	.201	.312	.448	-.025	.358	.390
RESTA1	.042	.011	.492	.505	.071	.308
RESTA6	-.152	.133	.139	.488	.378	.442
RESTA3	.135	.066	.309	.356	.161	.631
RESTA8	.136	.193	.180	.303	-.125	.401



Appendix E, Figure BB2. Scatter plot of the first and second discriminant functions from an analysis of the size corrected talus data

Appendix E, Table BB4. Classification results table from an analysis of the size corrected talus data

Classification Results[a]

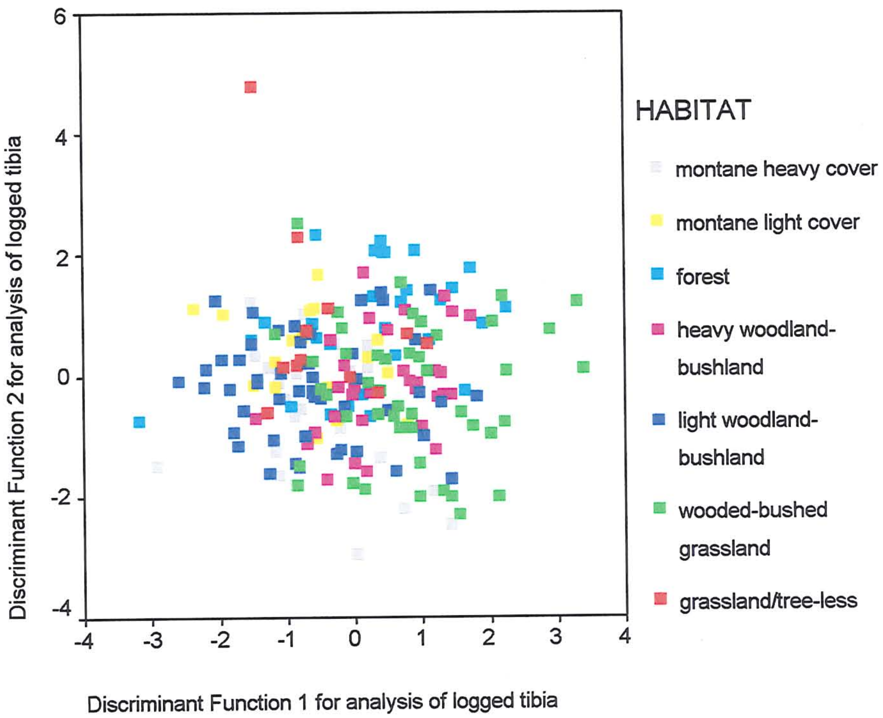
			Predicted Group Membership							
		HABITAT	grassland/ tree-less	wooded-bushed grassland	light woodland-bushland	heavy woodland-bushland	forest	montane light cover	montane light cover	Total
Original	Count	grassland/tree-less	2	3	3	2	2	0	1	13
		wooded-bushed grassland	0	24	9	5	4	3	2	47
		light woodland-bushland	2	6	28	6	4	0	3	49
		heavy woodland-bushland	1	12	7	11	1	0	0	32
		forest	0	7	9	3	8	0	1	28
		montane light cover	1	5	3	3	2	3	0	17
		montane light cover	0	7	8	0	3	0	2	20
	%	grassland/tree-less	15.4	23.1	23.1	15.4	15.4	.0	7.7	100.0
		wooded-bushed grassland	.0	51.1	19.1	10.6	8.5	6.4	4.3	100.0
		light woodland-bushland	4.1	12.2	57.1	12.2	8.2	.0	6.1	100.0
		heavy woodland-bushland	3.1	37.5	21.9	34.4	3.1	.0	.0	100.0
		forest	.0	25.0	32.1	10.7	28.6	.0	3.6	100.0
		montane light cover	5.9	29.4	17.6	17.6	11.8	17.6	.0	100.0
		montane light cover	.0	35.0	40.0	.0	15.0	.0	10.0	100.0

a. 37.9% of original grouped cases correctly classified.

Appendix E, Table CC1. Structure matrix from an analysis of the logged tibia data

Structure Matrix

	Function					
	1 39.5%	2 25.6%	3 14.8%	4 10.4%	5 5.8%	6 3.8%
LOGT3	.142	.837	.303	.082	.110	.248
LOGT7	.168	.831	.284	.028	.008	.243
LOGT12	.194	.823	.275	.062	-.045	.263
LOGT11	.149	.806	.327	.045	-.006	.343
LOGT5	.117	.805	.265	.029	.087	.285
LOGT6	.099	.802	.337	.037	.010	.302
LOGT4	.210	.793	.336	.004	.019	.295
LOGT9	.228	.784	.353	.026	.054	.268
LOGT10	.211	.782	.351	-.005	-.008	.306
LOGT2	.107	.769	.186	.034	.220	.379
LOGT8	.235	.765	.296	.141	.046	.409
LOGT1	.128	.759	.221	.079	.192	.366



Scatter plot of the first and second discriminant functions from an analysis of the logged tibia data

Appendix E, Table CC2. Classificaiton results table from an analysis of the logged tibia data

Classification Results[a]

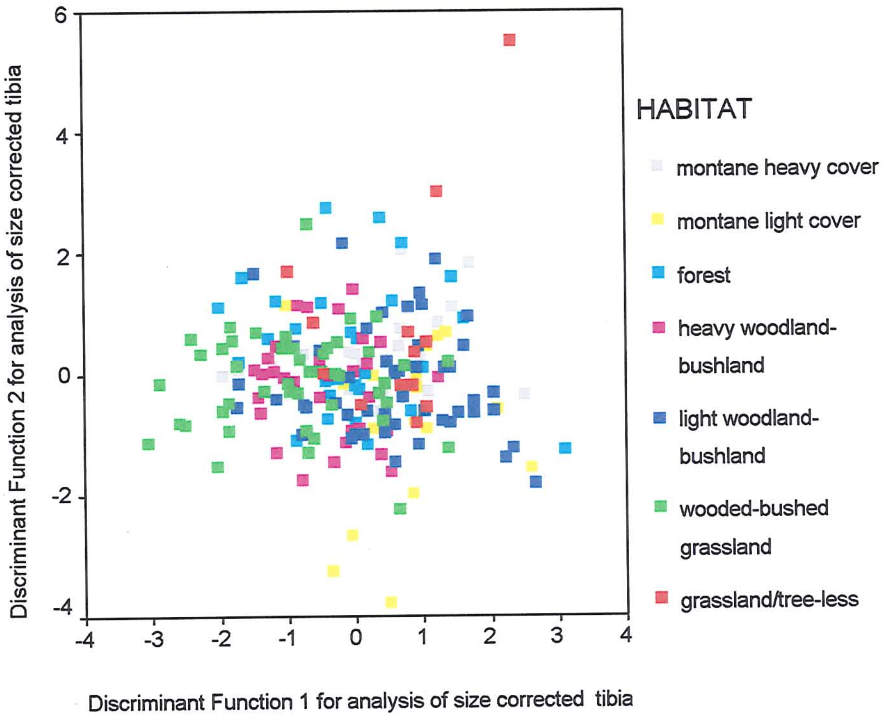
			Predicted Group Membership							Total
		HABITAT	grassland/ tree-less	wooded-bushed grassland	light woodland-bushland	heavy woodland-bushland	forest	montane light cover	montane heavy cover]	
Original	Count	grassland/tree-less	1	2	5	2	2	1	0	13
		wooded-bushed grassland	0	28	9	4	4	1	0	46
		light woodland-bushland	2	6	31	2	4	2	3	50
		heavy woodland-bushland	0	10	9	9	2	0	2	32
		forest	1	4	4	2	17	1	1	30
		montane light cover	0	1	6	1	1	7	1	17
		montane heavy cover	1	3	10	2	0	0	8	24
	%	grassland/tree-less	7.7	15.4	38.5	15.4	15.4	7.7	.0	100.0
		wooded-bushed grassland	.0	60.9	19.6	8.7	8.7	2.2	.0	100.0
		light woodland-bushland	4.0	12.0	62.0	4.0	8.0	4.0	6.0	100.0
		heavy woodland-bushland	.0	31.3	28.1	28.1	6.3	.0	6.3	100.0
		forest	3.3	13.3	13.3	6.7	56.7	3.3	3.3	100.0
		montane light cover	.0	5.9	35.3	5.9	5.9	41.2	5.9	100.0
		montane heavy cover	4.2	12.5	41.7	8.3	.0	.0	33.3	100.0

a 47.6% of original grouped cases correctly classified.

Appendix E, table CC3. Structure matrix from an analysis of the size corrected tibia data

Structure Matrix

	Function					
	1 48.3%	2 20.0%	3 13.1%	4 9.5%	5 7.1%	6 1.9%
REST6	.553	.173	.197	.062	.059	.447
REST5	.399	.355	.121	.140	-.191	.284
REST12	.205	.463	.272	-.128	.217	.389
REST7	.289	.404	.132	-.133	-.002	.352
REST2	.319	.405	.103	.468	-.393	.262
REST1	.291	.356	.238	.457	-.366	.250
REST4	.163	.240	.086	.004	.008	.709
REST10	.140	.134	.048	.022	.146	.659
REST11	.316	.199	.194	.057	.119	.620
REST8	.010	.224	.444	.262	.009	.619
REST9	.061	.134	.170	-.014	-.160	.485
REST3	.376	.342	.324	-.082	-.357	.464



Appendix E, Figure CC3. Scatter plot of the first and second discriminant functions from an analysis of the size corrected tibia data

Appendix E, Table CC4. Classification results table from an analysis of the size corrected tibia data

Classification Results[a]

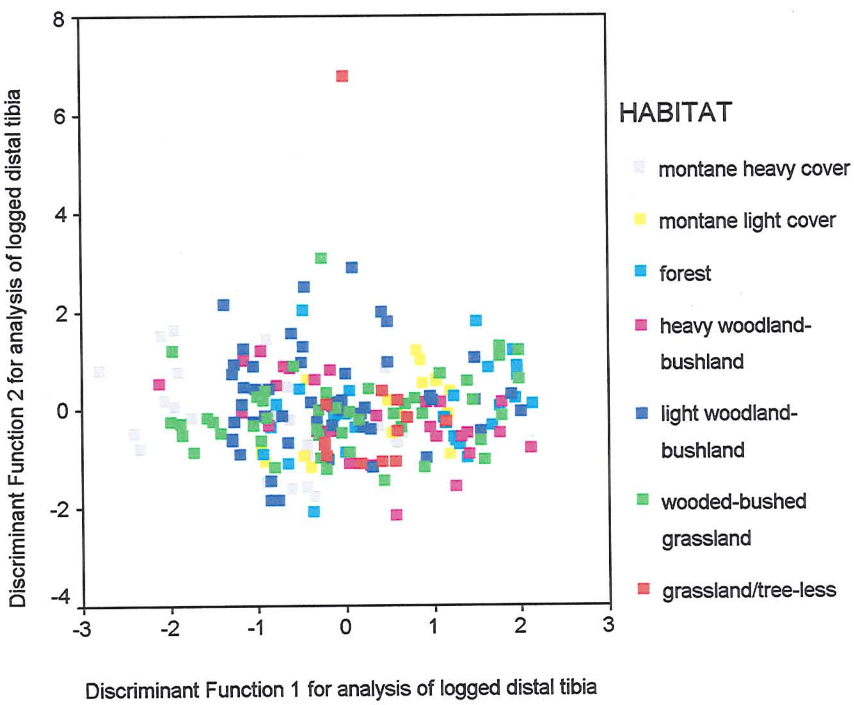
		HABITAT	Predicted Group Membership							Total
			grassland/ tree-less	wooded-bushed grassland	light woodland-bushland	heavy woodland-bushland	forest	montane light cover	montane heavy cover]	
Original	Count	grassland/tree-less	1	2	6	2	1	1	0	13
		wooded-bushed grassland	0	28	9	5	2	1	1	46
		light woodland-bushland	2	9	30	3	2	1	3	50
		heavy woodland-bushland	0	10	8	10	2	0	2	32
		forest	1	9	4	1	11	1	3	30
		montane light cover	0	1	9	0	0	6	1	17
		montane heavy cover	1	4	10	2	2	0	5	24
	%	grassland/tree-less	7.7	15.4	46.2	15.4	7.7	7.7	.0	100.0
		wooded-bushed grassland	.0	60.9	19.6	10.9	4.3	2.2	2.2	100.0
		light woodland-bushland	4.0	18.0	60.0	6.0	4.0	2.0	6.0	100.0
		heavy woodland-bushland	.0	31.3	25.0	31.3	6.3	.0	6.3	100.0
		forest	3.3	30.0	13.3	3.3	36.7	3.3	10.0	100.0
		montane light cover	.0	5.9	52.9	.0	.0	35.3	5.9	100.0
		montane heavy cover	4.2	16.7	41.7	8.3	8.3	.0	20.8	100.0

a. 42.9% of original grouped cases correctly classified.

Appendix E, Table DD1. Structure matrix from an analysis of the logged distal tibia data

Structure Matrix

	Function	
	1 90.2%	2 9.8%
LOGT9	.999	.036
LOGT10	.986	.169



Appendix E, Figure DD 1. Scatter plot of the first and second discriminant functions from an analysis of the logged distal tibia data

Appendix E, Table DD2. Classification results table from an analysis of the logged distal tibia data

Classification Results[a]

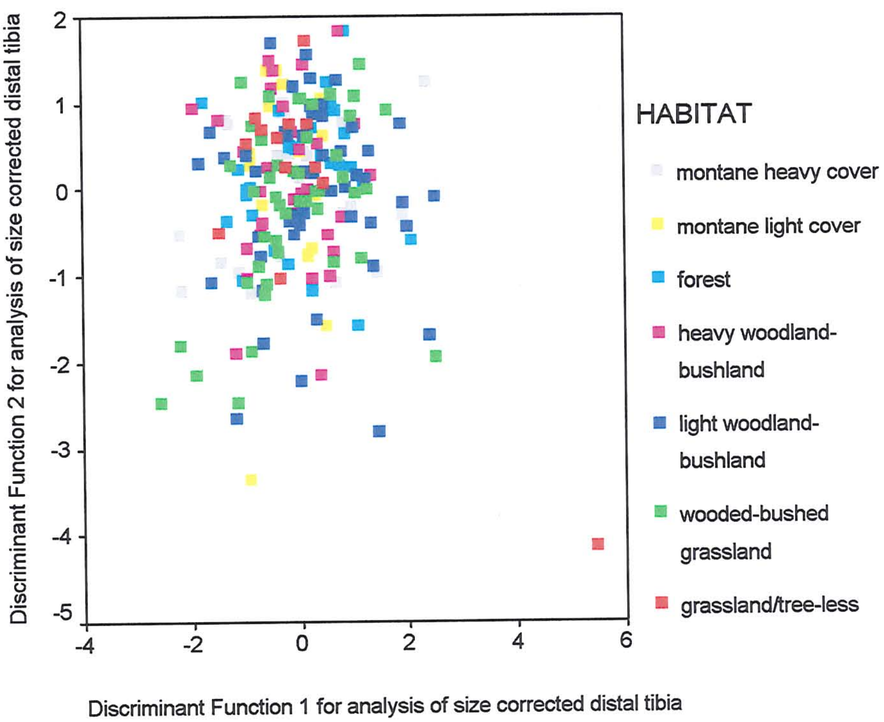
			Predicted Group Membership							
		HABITAT	grassland/ tree-less	wooded-bushed grassland	light woodland-bushland	heavy woodland-bushland	forest	montane light cover	montane heavy cover	Total
Original	Count	grassland/tree-less	0	9	3	0	1	0	0	13
		wooded-bushed grassland	0	15	14	0	10	0	7	46
		light woodland-bushland	0	11	29	0	7	0	3	50
		heavy woodland-bushland	0	8	12	1	10	0	1	32
		forest	0	5	9	0	16	0	0	30
		montane light cover	0	8	4	0	5	0	0	17
		montane heavy cover	0	10	9	0	0	0	6	25
	%	grassland/tree-less	.0	69.2	23.1	.0	7.7	.0	.0	100.0
		wooded-bushed grassland	.0	32.6	30.4	.0	21.7	.0	15.2	100.0
		light woodland-bushland	.0	22.0	58.0	.0	14.0	.0	6.0	100.0
		heavy woodland-bushland	.0	25.0	37.5	3.1	31.3	.0	3.1	100.0
		forest	.0	16.7	30.0	.0	53.3	.0	.0	100.0
		montane light cover	.0	47.1	23.5	.0	29.4	.0	.0	100.0
		montane heavy cover	.0	40.0	36.0	.0	.0	.0	24.0	100.0

a. 31.5% of original grouped cases correctly classified.

Appendix E. Table DD3. Structure matrix from an analysis of the size corrected distal tibia data

Structure Matrix

	Function	
	1 69.2%	2 30.8%
REST9	.054	.999
REST10	.608	.794



Appendix E, Figure DD2. Scatter plot of the first and second discriminant functions from an analysis of the size corrected distal tibia data

Appendix E, Table DD4. Classification results table from an analysis of the size corrected distal tibia data

Classification Results[a]

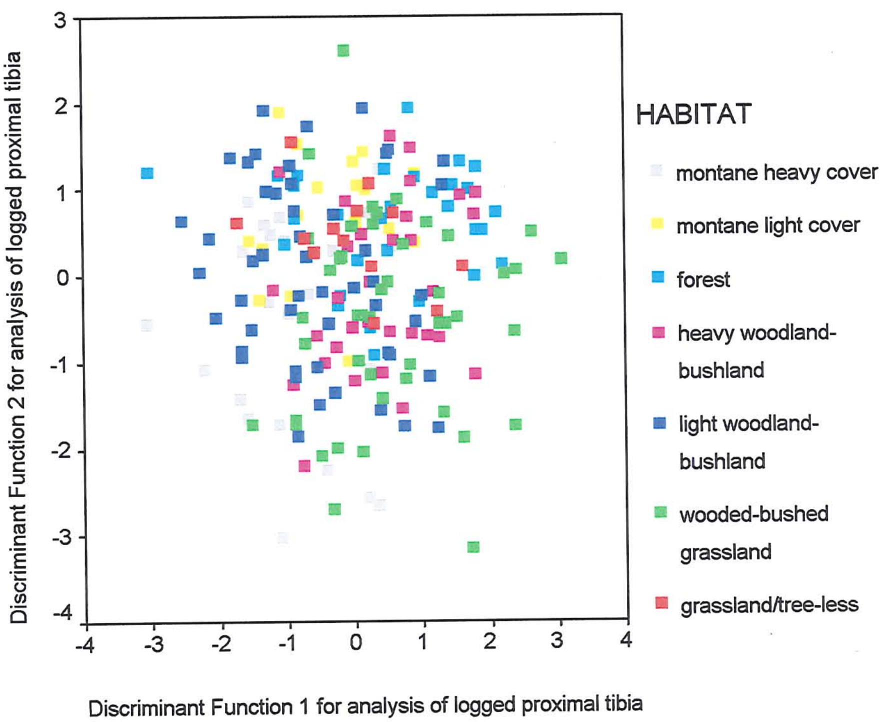
		HABITAT	Predicted Group Membership: grassland/ tree-less	wooded-bushed grassland	light woodland-bushland	heavy woodland-bushland	forest	montane light cover	montane heavy cover	Total
Original	Count	grassland/tree-less	0	6	7	0	0	0	0	13
		wooded-bushed grassland	0	23	23	0	0	0	0	46
		light woodland-bushland	0	14	35	1	0	0	0	50
		heavy woodland-bushland	0	11	21	0	0	0	0	32
		forest	0	11	19	0	0	0	0	30
		montane light cover	0	5	12	0	0	0	0	17
		montane heavy cover	0	9	16	0	0	0	0	25
	%	grassland/tree-less	.0	46.2	53.8	.0	.0	.0	.0	100.0
		wooded-bushed grassland	.0	50.0	50.0	.0	.0	.0	.0	100.0
		light woodland-bushland	.0	28.0	70.0	2.0	.0	.0	.0	100.0
		heavy woodland-bushland	.0	34.4	65.6	.0	.0	.0	.0	100.0
		forest	.0	36.7	63.3	.0	.0	.0	.0	100.0
		montane light cover	.0	29.4	70.6	.0	.0	.0	.0	100.0
		montane heavy cover	.0	36.0	64.0	.0	.0	.0	.0	100.0

a. 27.2% of original grouped cases correctly classified.

Appendix E, Table EE1. Structure matrix from an analysis of the logged proximal tibia data

Structure Matrix

	Function					
	1 48.8%	2 31.9%	3 9.1%	4 6.1%	5 2.5%	6 1.7%
LOGT3	.476	.825	.114	.016	.014	.282
LOGT6	.421	.816	.245	.022	.099	.295
LOGT7	.502	.796	.189	-.063	.152	.227
LOGT5	.437	.793	.127	-.052	.098	.390
LOGT4	.533	.744	.265	.009	.055	.297
LOGT8	.545	.710	.134	.211	.186	.317



Appendix E, Figure EE1. Scatter plot of the first and second discriminant functions from an analysis of the logged proximal tibia data

Appendix E, Table EE2. Classification results table from an analysis of the logged proximal tibia data

Classification Results[a]

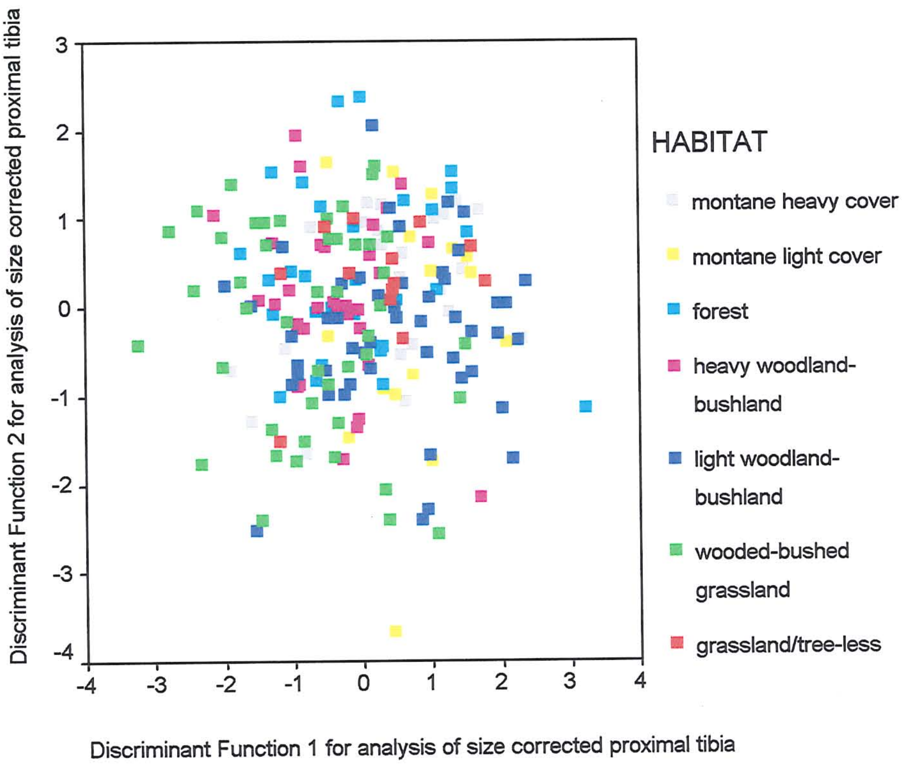
		HABITAT	Predicted Group Membership: grassland/ tree-less	wooded-bushed grassland	light woodland-bushland	heavy woodland-bushland	forest	montane light cover	montane heavy cover	Total
Original	Count	grassland/tree-less	2	3	5	0	3	0	0	13
		wooded-bushed grassland	1	25	10	3	5	1	1	46
		light woodland-bushland	0	10	31	2	4	0	3	50
		heavy woodland-bushland	1	10	8	5	7	0	1	32
		forest	1	6	10	1	11	1	0	30
		montane light cover	0	1	10	1	3	1	1	17
		montane heavy cover	0	6	11	0	3	0	5	25
	%	grassland/tree-less	15.4	23.1	38.5	.0	23.1	.0	.0	100.0
		wooded-bushed grassland	2.2	54.3	21.7	6.5	10.9	2.2	2.2	100.0
		light woodland-bushland	.0	20.0	62.0	4.0	8.0	.0	6.0	100.0
		heavy woodland-bushland	3.1	31.3	25.0	15.6	21.9	.0	3.1	100.0
		forest	3.3	20.0	33.3	3.3	36.7	3.3	.0	100.0
		montane light cover	.0	5.9	58.8	5.9	17.6	5.9	5.9	100.0
		montane heavy cover	.0	24.0	44.0	.0	12.0	.0	20.0	100.0

a. 37.6% of original grouped cases correctly classified.

Appendix E, Table EE3. Structure matrix from an analysis of the size corrected proximal tibia data

Structure Matrix

	Function					
	1 62.6%	2 15.8%	3 9.1%	4 6.6%	5 4.3%	6 1.6%
REST6	.645	.336	.070	.192	.501	.421
REST3	.431	.781	.053	.075	.160	.412
REST5	.456	.562	-.041	.546	.197	.371
REST8	.027	.461	.683	.259	.474	.166
REST7	.313	.579	-.230	.216	.660	.180
REST4	.175	.360	.005	.174	.544	.716



Appendix E, Figure EE2. Scatter plot of the first and second discriminant functions from an analysis of the size corrected proximal tibia data

Appendix E, Table EE4. Classification results table from an analysis of the size corrected proximal tibia data

Classification Results[a]

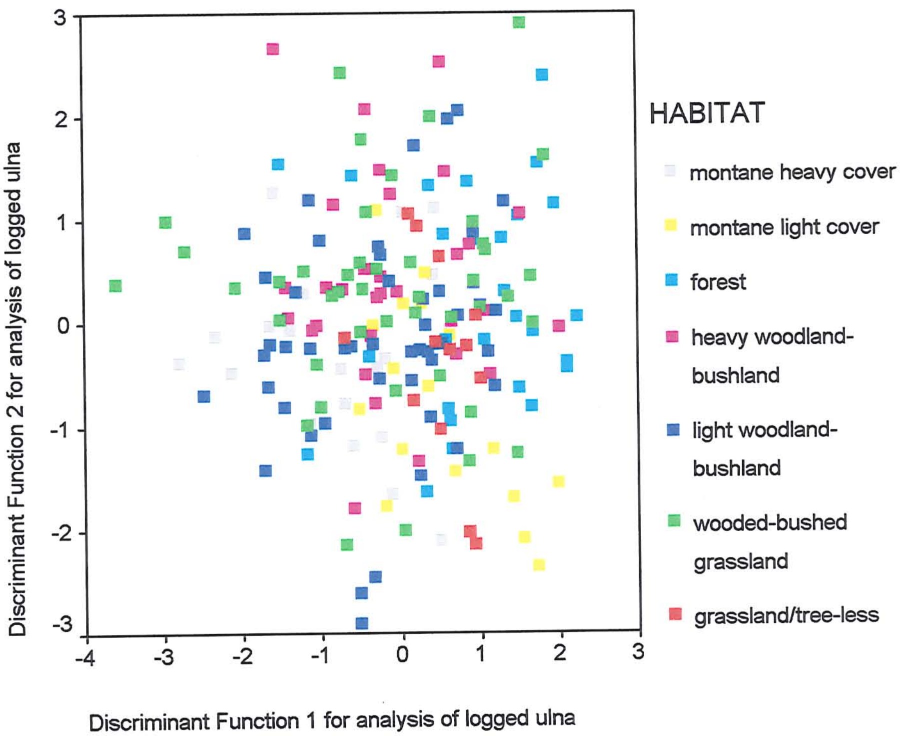
		HABITAT	Predicted Group Membership: grassland/ tree-less	wooded-bushed grassland	light woodland-bushland	heavy woodland-bushland	forest	montane light cover	montane heavy cover	Total
Original	Count	grassland/tree-less	1	2	8	1	1	0	0	13
		wooded-bushed grassland	2	27	10	1	4	1	1	46
		light woodland-bushland	1	12	33	1	1	1	1	50
		heavy woodland-bushland	1	13	6	7	5	0	0	32
		forest	0	13	11	1	5	0	0	30
		montane light cover	0	2	11	0	3	0	1	17
		montane heavy cover	0	5	15	1	2	0	2	25
	%	grassland/tree-less	7.7	15.4	61.5	7.7	7.7	.0	.0	100.0
		wooded-bushed grassland	4.3	58.7	21.7	2.2	8.7	2.2	2.2	100.0
		light woodland-bushland	2.0	24.0	66.0	2.0	2.0	2.0	2.0	100.0
		heavy woodland-bushland	3.1	40.6	18.8	21.9	15.6	.0	.0	100.0
		forest	.0	43.3	36.7	3.3	16.7	.0	.0	100.0
		montane light cover	.0	11.8	64.7	.0	17.6	.0	5.9	100.0
		montane heavy cover	.0	20.0	60.0	4.0	8.0	.0	8.0	100.0

a. 35.2% of original grouped cases correctly classified.

Appendix E, Table FF1. Structure matrix from an analysis of the logged ulna data

Structure Matrix

	Function					
	1 46.6%	2 23.5%	3 15.7%	4 10.6%	5 3.3%	6 0.2%
LOGU1	.849	.186	.222	.164	.188	-.109
LOGU2	.846	.154	.206	.237	.184	-.088
LOGU4	.844	.204	.129	-.031	.248	.005
LOGU5	.841	.190	.101	-.021	.226	-.036
LOGU6	.838	.084	.254	-.118	.187	.039
LOGU3	.807	.216	.200	-.034	.246	-.002
LOGU7	.775	.374	.246	-.024	-.118	.111



Appendix E, Figure FF1. Scatter plot of the first and second discriminant functions from an analysis of the logged ulna data

Appendix E, Table FF2. Classification results table from an analysis of the logged ulna data

Classification Results[a]

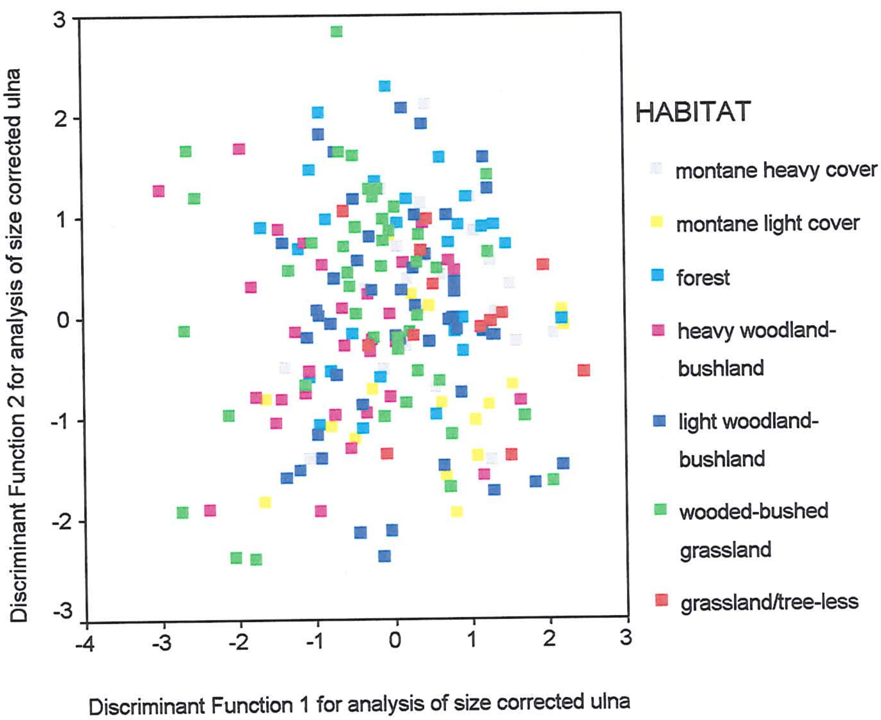
			Predicted Group Membership							
		HABITAT	grassland/ tree-less	wooded-bushed grassland	light woodland-bushland	heavy woodland-bushland	forest	montane light cover	montane heavy cover	Total
Original	Count	grassland/tree-less	0	2	6	3	0	2	0	13
		wooded-bushed grassland	1	16	13	5	5	1	3	44
		light woodland-bushland	0	9	28	5	5	0	2	49
		heavy woodland-bushland	0	11	8	8	3	0	1	31
		forest	0	4	6	3	12	1	1	27
		montane light cover	0	2	8	1	0	6	0	17
		montane heavy cover	0	4	15	0	0	1	3	23
	%	grassland/tree-less	.0	15.4	46.2	23.1	.0	15.4	.0	100.0
		wooded-bushed grassland	2.3	36.4	29.5	11.4	11.4	2.3	6.8	100.0
		light woodland-bushland	.0	18.4	57.1	10.2	10.2	.0	4.1	100.0
		heavy woodland-bushland	.0	35.5	25.8	25.8	9.7	.0	3.2	100.0
		forest	.0	14.8	22.2	11.1	44.4	3.7	3.7	100.0
		montane light cover	.0	11.8	47.1	5.9	.0	35.3	.0	100 0
		montane heavy cover	.0	17.4	65.2	.0	.0	4.3	13 0	100 0

a. 35 8% of original grouped cases correctly classified.

Appendix E, Table FF3. Structure matrix from an analysis of the size corrected ulna data

Structure Matrix

	Function					
	1 44.0%	2 23.1%	3 18.1%	4 8.5%	5 4.6%	6 1.6%
RESU6	.778	-.151	.025	-.303	-.165	.490
RESU5	.698	.564	.188	-.120	-.187	.145
RESU4	.664	.539	.197	-.118	-.338	.274
RESU3	.569	.356	.414	-.280	-.360	.317
RESU1	.508	.222	.504	.457	-.163	.211
RESU2	.538	.203	.549	.519	-.099	.119
RESU7	.002	.295	.343	-.076	.448	.766



Appendix E, Figure FF2. Scatter plot of the first and second discriminant functions from an analysis of the size corrected ulna data

Appendix E, Table FF4. Classification results table from an analysis of the size corrected ulna data

Classification Results[a]

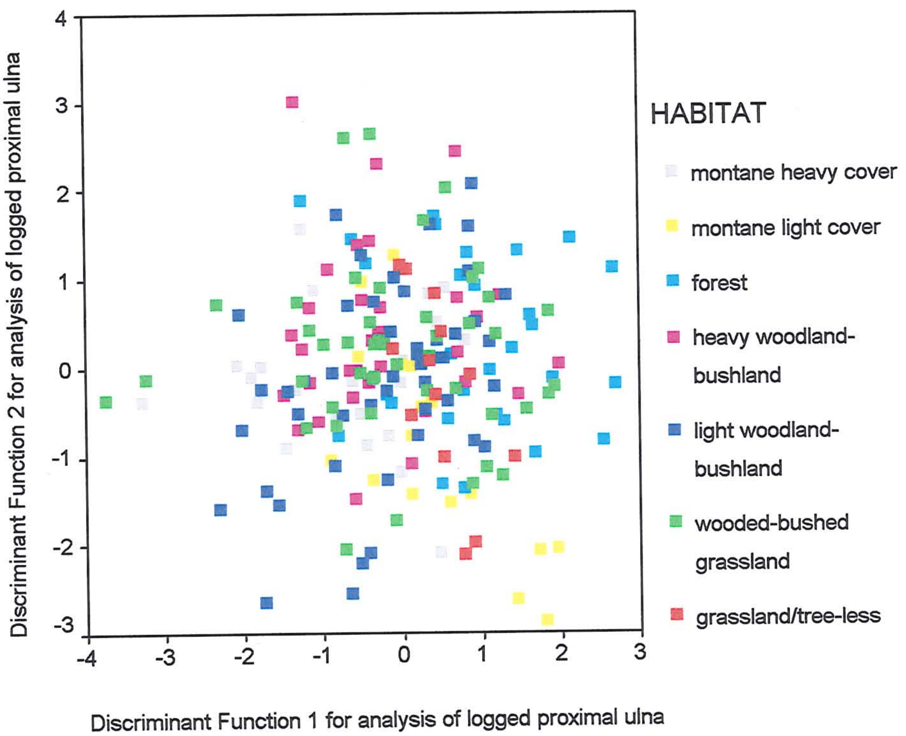
			Predicted Group Membership							
		HABITAT	grassland/ tree-less	wooded-bushed grassland	light woodland-bushland	heavy woodland-bushland	forest	montane light cover	montane heavy cover	Total
Original	Count	grassland/tree-less	0	2	7	1	1	2	0	13
		wooded-bushed grassland	0	16	15	5	6	0	2	44
		light woodland-bushland	0	12	25	4	2	4	2	49
		heavy woodland-bushland	0	9	13	8	1	0	0	31
		forest	1	10	8	3	4	0	1	27
		montane light cover	0	1	8	1	1	5	1	17
		montane heavy cover	0	3	12	2	1	1	4	23
	%	grassland/tree-less	.0	15.4	53.8	7.7	7.7	15.4	.0	100.0
		wooded-bushed grassland	.0	36.4	34.1	11.4	13.6	.0	4.5	100.0
		light woodland-bushland	.0	24.5	51.0	8.2	4.1	8.2	4.1	100.0
		heavy woodland-bushland	.0	29.0	41.9	25.8	3.2	.0	.0	100.0
		forest	3.7	37.0	29.6	11.1	14.8	.0	3.7	100.0
		montane light cover	.0	5.9	47.1	5.9	5.9	29.4	5.9	100.0
		montane heavy cover	.0	13.0	52.2	8.7	4.3	4.3	17.4	100.0

a. 30.4% of original grouped cases correctly classified.

Appendix E, Table GG1. Structure matrix from an analysis of the logged proximal ulna data

Structure Matrix

	Function				
	1 53.0%	2 27.3%	3 16.1%	4 3.4%	5 0.2%
LOGU5	.859	.144	.312	-.140	.351
LOGU4	.859	.153	.348	-.159	.303
LOGU6	.830	-.005	.466	-.102	.288
LOGU3	.813	.156	.415	-.164	.342
LOGU7	.741	.290	.506	.203	.264



Appendix E, Figure GG1. Scatter plot of the first and second discriminant functions from an analysis of the logged proximal ulna data

Appendix E, Table GG2. Classification results from an analysis of the logged proximal ulna data

Classification Results[a]

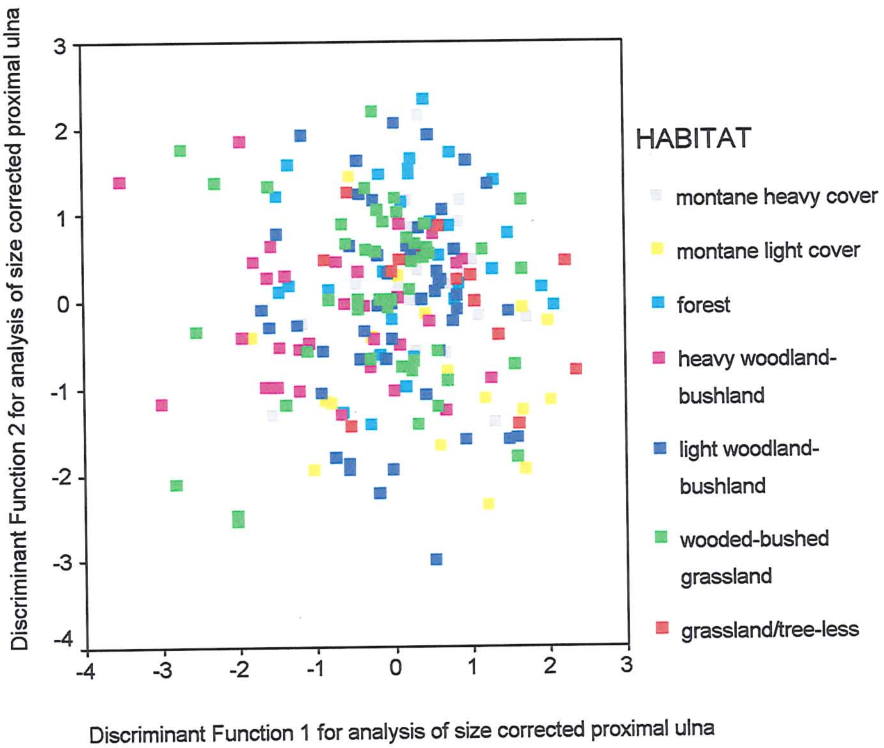
			Predicted Group Membership							
		HABITAT	grassland/ tree-less	wooded-bushed grassland	light woodland-bushland	heavy woodland-bushland	forest	montane light cover	montane heavy cover	Total
Original	Count	grassland/tree-less	0	5	5	1	0	2	0	13
		wooded-bushed grassland	0	9	18	6	7	2	4	46
		light woodland-bushland	0	10	28	5	6	0	0	49
		heavy woodland-bushland	0	8	12	7	4	0	1	32
		forest	0	4	7	2	14	2	0	29
		montane light cover	0	4	6	1	0	6	0	17
		montane heavy cover	0	3	14	1	1	0	4	23
	%	grassland/tree-less	.0	38.5	38.5	7.7	.0	15.4	.0	100.0
		wooded-bushed grassland	.0	19.6	39.1	13.0	15.2	4.3	8.7	100.0
		light woodland-bushland	.0	20.4	57.1	10.2	12.2	.0	.0	100.0
		heavy woodland-bushland	.0	25.0	37.5	21.9	12.5	.0	3.1	100.0
		forest	.0	13.8	24.1	6.9	48.3	6.9	.0	100.0
		montane light cover	.0	23.5	35.3	5.9	.0	35.3	.0	100.0
		montane heavy cover	.0	13.0	60.9	4.3	4.3	.0	17.4	100.0

a. 32.5% of original grouped cases correctly classified.

Appendix E, Figure GG3. Structure matrix from an analysis of the size corrected proximal ulna data

Structure Matrix

	Function				
	1 49.6%	2 30.5%	3 13.3%	4 5.0%	5 1.5%
RESU6	.792	-.204	.463	-.062	.335
RESU5	.706	.572	.414	-.040	-.029
RESU4	.670	.554	.428	-.199	.145
RESU3	.534	.393	.711	-.217	.095
RESU7	-.062	.268	.487	.561	.610



Appendix E, Figure GG2. Scatter plot of the first and second discriminant functions from an analysis of the size corrected proximal ulna data

Appendix E, Table GG4. Classification results table from an analysis of the size corrected proximal ulna data

Classification Results[a]

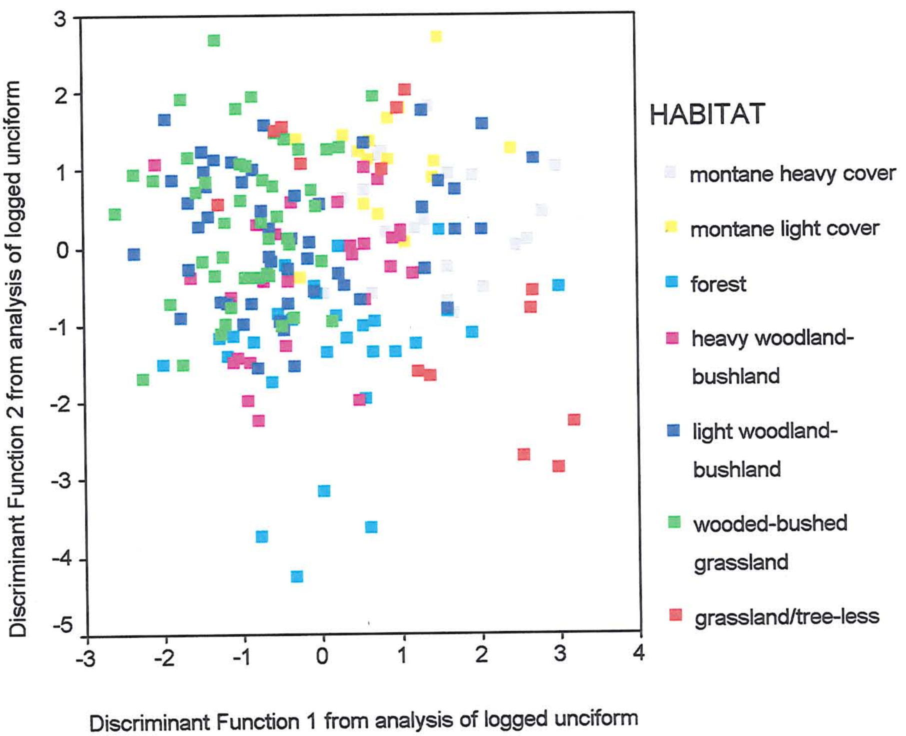
			Predicted Group Membership							
		HABITAT	grassland/ tree-less	wooded-bushed grassland	light woodland-bushland	heavy woodland-bushland	forest	montane light cover	montane heavy cover	Total
Original	Count	grassland/tree-less	0	3	7	1	0	2	0	13
		wooded-bushed grassland	1	10	16	7	7	1	4	46
		light woodland-bushland	0	11	21	6	6	4	1	49
		heavy woodland-bushland	0	8	12	11	1	0	0	32
		forest	1	5	11	2	10	0	0	29
		montane light cover	0	2	8	1	0	5	1	17
		montane heavy cover	0	4	14	1	2	0	2	23
	%	grassland/tree-less	.0	23.1	53.8	7.7	.0	15.4	.0	100.0
		wooded-bushed grassland	2.2	21.7	34.8	15.2	15.2	2.2	8.7	100.0
		light woodland-bushland	.0	22.4	42.9	12.2	12.2	8.2	2.0	100.0
		heavy woodland-bushland	.0	25.0	37.5	34.4	3.1	.0	.0	100.0
		forest	3.4	17.2	37.9	6.9	34.5	.0	.0	100.0
		montane light cover	.0	11.8	47.1	5.9	.0	29.4	5.9	100.0
		montane heavy cover	.0	17.4	60.9	4.3	8.7	.0	8.7	100.0

a. 28.2% of original grouped cases correctly classified.

Appendix E, Table HH1. Structure matrix from an analysis of the logged unciform data

Structure Matrix

	Function					
	1 36.0%	2 26.6%	3 16.2%	4 12.3%	5 6.1%	6 2.8%
LOGCB6	.361	.074	.244	.086	.641	.487
LOGCB5	.265	.255	.244	.050	.618	.534
LOGCB8	.205	.093	.350	.114	.613	.562
LOGCB3	.310	.161	.374	.085	.573	.531
LOGCB2	.296	.143	.349	.065	.554	.519
LOGCB7	.216	.067	.258	.106	.589	.610
LOGCB1	.345	.071	.265	.076	.538	.569
LOGCB7B	.272	.095	.293	.219	.551	.569
LOGCB4	.388	.111	.298	.109	.504	.568



Appendix E, Figure HH1. Scatter plot of the first and second discriminant functions from an analysis of the logged unciform data

Appendix E, Table HH2. Classification results table from an analysis of the logged unciform data

Classification Results[a]

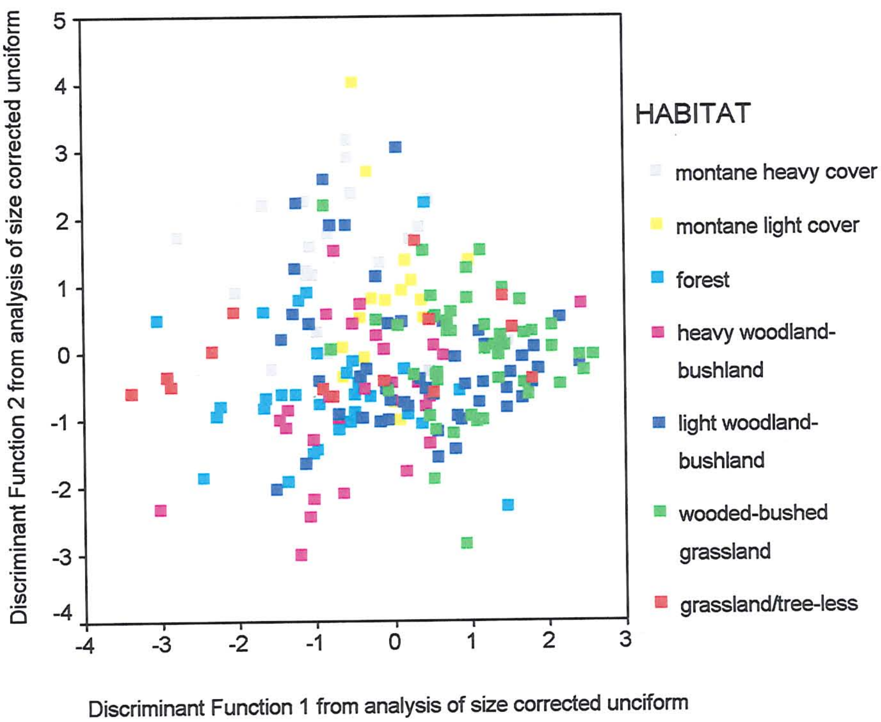
			Predicted Group Membership							
		HABITAT	grassland/ tree-less	wooded-bushed grassland	light woodland-bushland	heavy woodland-bushland	forest	montane light cover	montane heavy cover	Total
Original	Count	grassland/tree-less	7	1	4	0	0	1	1	14
		wooded-bushed grassland	0	28	13	3	0	2	1	47
		light woodland-bushland	1	12	21	4	3	4	5	50
		heavy woodland-bushland	0	2	6	13	3	2	2	28
		forest	5	2	4	7	11	0	1	30
		montane light cover	0	1	4	0	0	9	2	16
		montane heavy cover	0	0	4	0	1	0	16	21
	%	grassland/tree-less	50.0	7.1	28.6	.0	.0	7.1	7.1	100.0
		wooded-bushed grassland	.0	59.6	27.7	6.4	.0	4.3	2.1	100.0
		light woodland-bushland	2.0	24.0	42.0	8.0	6.0	8.0	10.0	100.0
		heavy woodland-bushland	.0	7.1	21.4	46.4	10.7	7.1	7.1	100.0
		forest	16.7	6.7	13.3	23.3	36.7	.0	3.3	100.0
		montane light cover	.0	6.3	25.0	.0	.0	56.3	12.5	100.0
		montane heavy cover	.0	.0	19.0	.0	4.8	.0	76.2	100.0

a. 51.0% of original grouped cases correctly classified.

Appendix E, Table HH3. Structure matrix from an analysis of the size corrected unciform data

Structure Matrix

	Function					
	1 36.8%	2 29.3%	3 15.2%	4 12.2%	5 5.9%	6 0.6%
RESCB7	.561	.006	-.306	-.196	.271	.548
RESCB8	.479	-.048	.028	.042	.294	.271
RESCB3	.386	.332	.205	.409	.309	.310
RESCB6	.029	.178	.127	-.170	.800	.448
RESCB5	.342	.266	.082	.001	.709	.356
RESCB2	.180	.117	.249	.009	.650	.560
RESCB1	.132	.368	-.247	.088	.215	.658
RESCB4	.050	.506	.042	.147	.069	.591
RESCB7B	.505	.301	.153	-.316	.124	.512



Appendix E, Figure HH2. Scatter plot of the first and second discriminant functions from an analysis of the size corrected unciform data

Appendix E, Table HH4. Classification results table from an analysis of the size corrected unciform data

Classification Results[a]

			Predicted Group Membership							
		HABITAT	grassland/ tree-less	wooded-bushed grassland	light woodland-bushland	heavy woodland-bushland	forest	montane light cover	montane heavy cover	Total
Original	Count	grassland/tree-less	1	2	6	1	4	0	0	14
		wooded-bushed grassland	0	32	11	3	0	0	1	47
		light woodland-bushland	0	14	21	4	3	3	5	50
		heavy woodland-bushland	0	2	9	14	2	0	1	28
		forest	0	3	6	7	13	1	0	30
		montane light cover	0	2	5	0	1	7	1	16
		montane heavy cover	1	2	1	1	2	0	14	21
	%	grassland/tree-less	7.1	14.3	42.9	7.1	28.6	.0	.0	100.0
		wooded-bushed grassland	.0	68.1	23.4	6.4	.0	.0	2.1	100.0
		light woodland-bushland	.0	28.0	42.0	8.0	6.0	6.0	10.0	100.0
		heavy woodland-bushland	.0	7.1	32.1	50.0	7.1	.0	3.6	100.0
		forest	.0	10.0	20.0	23.3	43.3	3.3	.0	100.0
		montane light cover	.0	12.5	31.3	.0	6.3	43.8	6.3	100.0
		montane heavy cover	4.8	9.5	4.8	4.8	9.5	0	66.7	100.0

a. 49.5% of original grouped cases correctly classified.

APPENDIX F

PROBABILITIES AND HABITAT PREDICTIONS FOR LAETOLI SPECIMENS

Note: Elements are listed in order of their percentages of correct classification from the modern analyses. This figure is listed in parentheses next to the element name. Each specimen from Laetoli is presented according to the beds from which it derived and all associated probabilities for habitat prediction are listed. The highest probability is highlighted and predicted habitat noted. The average probability for all specimens within each habitat group and for all individuals predicted to belong to each group within the individual analyses have been calculated.

Element	Predicted habitat	Probability grassland/ tree-less	Probability wooded-bushed grassland	Probability light woodland-bushland	Probability heavy woodland-bushland	Probability forest	Probability montane light cover	Probability montane heavy cover	Identification
HUMERUS (68.0%)									
Ndolanya Beds									
	forest	0.00182	0.10847	0.26018	0.12292	**0.50646**	0.00014	0.00000	
number of specimens		0	0	0	0	1	0	0	
average probability of all specimens		0.00182	0.10847	0.26018	0.12292	0.50646	0.00014	0.00000	
average probability of predicted specimens		n/a	n/a	n/a	n/a	0.50646	n/a	n/a	
METATARSAL (66.5%)									
Laetolil Beds									
	montane heavy cover	0.00026	0.10944	0.12947	0.02531	0.11035	0.15211	**0.47306**	*Madoqua*
	forest	0.00003	0.07154	0.19806	0.14868	**0.46293**	0.05358	0.06519	*Madoqua*
number of specimens		0	0	0	0	1	0	1	
average probability of all specimens		0.00015	0.09049	0.16377	0.08700	0.28664	0.10285	0.26913	
average probability of predicted specimens		n/a	n/a	n/a	n/a	0.46293	n/a	0.47306	
RADIUS (58.0%)									
Ndolanya Beds									
	wooded-bushed grassland	0.04824	**0.58532**	0.35477	0.00296	0.00506	0.00363	0.00002	
number of specimens		0	1	0	0	0	0	0	
average probability of all specimens		0.04824	0.58532	0.35477	0.00296	0.00506	0.00363	0.00002	
average probability of predicted specimens		n/a	0.58532	n/a	n/a	n/a	n/a	n/a	
Laetolil Beds									
	heavy woodland-bushland	0.00153	0.02290	0.12373	**0.69249**	0 12991	0.00001	0.02943	
number of specimens		0	0	0	1	0	0	0	
average probability of all specimens		0.00153	0.02290	0.12373	0.69249	0.12991	0.00001	0.02943	
average probability of predicted specimens		n/a	n/a	n/a	0.69249	n/a	n/a	n/a	

Element	Predicted habitat	Probability grassland/ tree-less	Probability wooded-bushed grassland	Probability light woodland-bushland	Probability heavy woodland-bushland	Probability forest	Probability montane light cover	Probability montane heavy cover	Identification
PROXIMAL PHALANGES (57.1%)									
Ndolanya Beds									
	light woodland-bushland	0.00247	0.14898	**0.43597**	0.22762	0.17502	0.00452	0.00542	
	light woodland-bushland	0.00001	0.44447	**0.47649**	0.07540	0.00321	0.00011	0.00031	
	wooded-bushed grassland	0.00043	**0.55765**	0.37707	0.04752	0.00638	0.00019	0.01077	
	wooded-bushed grassland	0.00018	**0.59286**	0.37129	0.02111	0.00708	0.00030	0.00719	
	light woodland-bushland	0.00010	0.35827	**0.48779**	0.14120	0.01119	0.00063	0.00082	
	wooded-bushed grassland	0.03159	**0.52591**	0.26138	0.01083	0.00487	0.00478	0.16063	
	wooded-bushed grassland	0.07824	**0.35136**	0.27083	0.06751	0.14696	0.00065	0.08446	
	forest	0.00001	0.01040	0.02598	0.08742	**0.87618**	0.00000	0.00001	
	light woodland-bushland	0.00202	0.32177	**0.50773**	0.10201	0.03565	0.00563	0.02518	
number of specimens		0	4	4	0	1	0	0	
average probability of all specimens		0.01278	0.36796	0.35717	0.08674	0.14073	0.00187	0.03275	
average probability of predicted specimens		n/a	0.50695	0.47700	n/a	0.87618	n/a	n/a	
Laetolil Beds									
	forest	0.00008	0.07089	0.12543	0.31570	**0.48577**	0.00001	0.00211	*Madoqua*
	forest	0.00046	0.18479	0.19743	0.20088	**0.39462**	0.00013	0.02170	*Madoqua*
	light woodland-bushland	0.06353	0.11092	**0.54023**	0.05263	0.07071	0.15918	0.00279	
	heavy woodland-bushland	0.00125	0.14384	0.29429	**0.33449**	0.15732	0.00329	0.06552	
	light woodland-bushland	0.00216	0.13032	**0.46337**	0.32575	0.05508	0.01146	0.01186	
	light woodland-bushland	0.00017	0.13299	**0.49939**	0.25763	0.10946	0.00030	0.00006	
	light woodland-bushland	0.00010	0.35626	**0.52698**	0.11111	0.00433	0.00079	0.00044	
	light woodland-bushland	0.00039	0.12460	**0.45279**	0.37877	0.02341	0.00956	0.01047	*Madoqua*
	wooded-bushed grassland	0.00036	**0.29461**	0.27207	0.27151	0.06506	0.00095	0.09543	*Madoqua*
	heavy woodland-bushland	0.00014	0.17984	0.26285	**0.33128**	0.22231	0.00015	0.00342	
	light woodland-bushland	0.00058	0.15968	**0.30040**	0.25775	0.15540	0.00735	0.11884	*Madoqua*
	heavy woodland-bushland	0.00055	0.07121	0.31086	**0.51580**	0.07708	0.00951	0.01499	*Madoqua*
	light woodland-bushland	0.00217	0.15471	**0.38959**	0.22339	0.20719	0.01005	0.01289	
	heavy woodland-bushland	0.00018	0.25044	0.29485	**0.32267**	0.07239	0.00055	0.05893	
	heavy woodland-bushland	0.00014	0.21556	0.29880	**0.41765**	0.04671	0.00147	0.01966	
	light woodland-bushland	0.00072	0.19624	**0.28405**	0.27743	0.22859	0.00094	0.01203	

Element	Predicted habitat	Probability grassland/ tree-less	Probability wooded-bushed grassland	Probability light woodland-bushland	Probability heavy woodland-bushland	Probability forest	Probability montane light cover	Probability montane heavy cover	Identification
PROXIMAL PHALANGES (57.1%), cont.									
Laetolil Beds, cont.									
	light woodland-bushland	0.00032	0.24749	**0.54453**	0.19279	0.01417	0.00033	0.00038	
	light woodland-bushland	0.00144	0.09958	**0.39323**	0.25021	0.13595	0.08490	0.03468	*Madoqua*
	forest	0.00045	0.14633	0.20082	0.26237	**0.38298**	0.00014	0.00691	
	heavy woodland-bushland	0.00011	0.09045	0.19261	**0.42565**	0.29029	0.00005	0.00085	*Madoqua*
	heavy woodland-bushland	0.00031	0.09032	0.20190	**0.56049**	0.13340	0.00051	0.01308	
	heavy woodland-bushland	0.00012	0.18546	0.29915	**0.37412**	0.13409	0.00025	0.00681	
	heavy woodland-bushland	0.00033	0.13126	0.35776	**0.42918**	0.04616	0.00444	0.03087	
	heavy woodland-bushland	0.00019	0.14436	0.32798	**0.44976**	0.06903	0.00127	0.00741	
	heavy woodland-bushland	0.00002	0.26993	0.20798	**0.39360**	0.11410	0.00001	0.01438	*Madoqua*
	light woodland-bushland	0.00469	0.22098	**0.24929**	0.18546	0.16180	0.00481	0.17297	*Madoqua*
	heavy woodland-bushland	0.00097	0.14921	0.33761	**0.35019**	0.14134	0.00492	0.01576	*Madoqua*
	light woodland-bushland	0.00131	0.15888	**0.41302**	0.30176	0.05967	0.01953	0.04583	*Madoqua*
	heavy woodland-bushland	0.00021	0.18964	0.28281	**0.36703**	0.15321	0.00034	0.00677	*Madoqua*
	heavy woodland-bushland	0.00041	0.23916	0.24645	**0.29196**	0.16906	0.00073	0.05222	*Madoqua*
	light woodland-bushland	0.00018	0.25526	**0.45238**	0.24689	0.03381	0.00429	0.00719	
	heavy woodland-bushland	0.00002	0.11962	0.16419	**0.45650**	0.25745	0.00001	0.00220	
	heavy woodland-bushland	0.00001	0.19990	0.24823	**0.39268**	0.15889	0.00001	0.00028	
	forest	0.00018	0.11179	0.18795	0.32712	**0.37003**	0.00010	0.00283	
	heavy woodland-bushland	0.00018	0.10489	0.21558	**0.40955**	0.26710	0.00019	0.00252	
	forest	0.00014	0.18366	0.21991	0.27946	**0.31151**	0.00006	0.00525	
	light woodland-bushland	0.00268	0.16309	**0.25682**	0.21556	0.17938	0.00667	0.17580	*Madoqua*
	forest	0.00342	0.07933	0.27500	0.17306	**0.45241**	0.00696	0.00982	*Madoqua*
	light woodland-bushland	0.00000	0.39088	**0.45073**	0.15584	0.00231	0.00002	0.00021	
	light woodland-bushland	0.00003	0.23129	**0.29333**	0.25817	0.21564	0.00003	0.00151	*Madoqua*
	light woodland-bushland	0.00092	0.13216	**0.51158**	0.17219	0.03346	0.13377	0.01592	*Madoqua*
	forest	0.00043	0.11434	0.25837	0.28846	**0.33370**	0.00068	0.00402	*Madoqua*
	heavy woodland-bushland	0.00012	0.14517	0.31796	**0.41619**	0.10959	0.00099	0.00997	
	heavy woodland-bushland	0.00003	0.09517	0.22687	**0.60494**	0.07081	0.00006	0.00213	*Madoqua*
	heavy woodland-bushland	0.00009	0.09540	0.23389	**0.35694**	0.31220	0.00011	0.00137	*Madoqua*
	heavy woodland-bushland	0.00043	0.08585	0.29469	**0.55463**	0.05119	0.00302	0.01019	

Element	Predicted habitat	Probability grassland/ tree-less	Probability wooded-bushed grassland	Probability light woodland-bushland	Probability heavy woodland-bushland	Probability forest	Probability montane light cover	Probability montane heavy cover	Identification
PROXIMAL PHALANGES (57.1%), cont.									
Laetolil Beds, cont.									
	heavy woodland-bushland	0.00016	0.19483	0.23725	**0.32383**	0.23201	0.00010	0.01183	*Madoqua*
	light woodland-bushland	0.00052	0.11127	**0.56578**	0.20498	0.00892	0.10656	0.00197	
	heavy woodland-bushland	0.00003	0.11591	0.22123	**0.62151**	0.02783	0.00014	0.01334	
	forest	0.00037	0.27175	0.14614	0.13536	**0.38141**	0.00006	0.06491	
	light woodland-bushland	0.00680	0.38213	**0.42822**	0.12085	0.05591	0.00103	0.00506	
	heavy woodland-bushland	0.00003	0.06108	0.24887	**0.66093**	0.02816	0.00038	0.00056	*Madoqua*
	forest	0.00024	0.07208	0.16930	0.35646	**0.39897**	0.00012	0.00283	*Madoqua*
	wooded-bushed grassland	0.00001	**0.39207**	0.33321	0.19601	0.07788	0.00003	0.00077	*Madoqua*
	heavy woodland-bushland	0.00136	0.11500	0.35244	**0.39482**	0.10255	0.00904	0.02479	*Madoqua*
	light woodland-bushland	0.00033	0.22941	**0.31266**	0.21665	0.23644	0.00113	0.00339	*Madoqua*
	heavy woodland-bushland	0.00012	0.05392	0.22861	**0.55406**	0.16232	0.00026	0.00072	
	heavy woodland-bushland	0.00002	0.08524	0.29079	**0.52566**	0.09764	0.00025	0.00039	
	forest	0.00006	0.14276	0.22749	0.30372	**0.32430**	0.00006	0.00160	
	forest	0.00111	0.07809	0.21056	0.32882	**0.37495**	0.00087	0.00559	
	forest	0.23489	0.04295	0.08116	0.08931	**0.49370**	0.00061	0.05738	*Simatherium*
	light woodland-bushland	0.00167	0.13845	**0.34745**	0.19456	0.31293	0.00167	0.00327	
	heavy woodland-bushland	0.00001	0.03618	0.12428	**0.46181**	0.37764	0.00000	0.00007	
	light woodland-bushland	0.00036	0.19217	**0.39971**	0.30568	0.08386	0.00714	0.01109	*Madoqua*
	heavy woodland-bushland	0.00007	0.10596	0.19531	**0.41736**	0.27965	0.00002	0.00162	
	forest	0.00005	0.04925	0.12198	0.32012	**0.50816**	0.00001	0.00043	*Madoqua*
	light woodland-bushland	0.00678	0.13942	**0.35533**	0.11593	0.13530	0.17674	0.07050	*Madoqua*
	light woodland-bushland	0.00013	0.31884	**0.52915**	0.14401	0.00600	0.00131	0.00056	
	heavy woodland-bushland	0.00003	0.13264	0.20968	**0.40516**	0.25177	0.00001	0.00070	*Madoqua*
	heavy woodland-bushland	0.00006	0.23463	0.25028	**0.45134**	0.04981	0.00011	0.01377	*Madoqua*
	heavy woodland-bushland	0.00051	0.08329	0.31818	**0.50530**	0.08291	0 00391	0.00591	*Madoqua*
	heavy woodland-bushland	0.00002	0.14470	0.20403	**0.48589**	0.16435	0.00002	0.00099	*Madoqua*
	light woodland-bushland	0.00031	0.30130	**0.59733**	0.07672	0.00441	0.01846	0.00147	
	forest	0.00093	0.06533	0.10564	0.24193	**0.56156**	0.00020	0.02440	
number of specimens		0	2	25	33	14	0	0	
average probability of all specimens		0.00473	0.16133	0.29984	0.32292	0.18056	0.01115	0.01948	
average probability of predicted specimens		n/a	0.34334	0.42229	0.44130	0.41243	n/a	n/a	

Element	Predicted habitat	Probability grassland/ tree-less	Probability wooded-bushed grassland	Probability light woodland-bushland	Probability heavy woodland-bushland	Probability forest	Probability montane light cover	Probability montane heavy cover	Identification
DISTAL PHALANGES (55.8%)									
Ndolanya Beds									
	heavy woodland-bushland	0.04206	0.06583	0.01652	**0.32401**	0.28331	0.26827	(combined montane)	
	light woodland-bushland	0.06409	0.32794	**0.40469**	0.04856	0.04851	0.10622		
	light woodland-bushland	0.00068	0.28910	**0.69091**	0.01080	0.00588	0.00264		
	wooded-bushed grassland	0.00082	**0.86518**	0.05156	0.00314	0.07354	0.00575		
number of specimens		0	1	2	1	0	0		
average probability of all specimens		0.02691	0.38701	0.29092	0.09663	0.10281	0.09572		
average probability of predicted specimens		n/a	0.86518	0.54780	0.32401	n/a	n/a		
Laetolil Beds									
	heavy woodland-bushland	0.00108	0.02328	0.02313	**0.85995**	0.05346	0.03911	(combined montane)	
	wooded-bushed grassland	0.00001	**0.86307**	0.01040	0.00068	0.10809	0.01776		
	heavy woodland-bushland	0.00109	0.06461	0.03484	**0.66922**	0.14945	0.08080		
	heavy woodland-bushland	0.01020	0.03321	0.06156	**0.58978**	0.03769	0.26756		
	wooded-bushed grassland	0.00000	**0.98182**	0.00644	0.00001	0.01108	0.00064		
	heavy woodland-bushland	0.00144	0.08780	0.05773	**0.60413**	0.10538	0.14351		
	light woodland-bushland	0.00190	0.26491	**0.59726**	0.10183	0.01596	0.01815		
	heavy woodland-bushland	0.00096	0.00062	0.00012	**0.69757**	0.17766	0.12306		
	heavy woodland-bushland	0.00325	0.14768	0.06703	**0.38626**	0.20431	0.19147		
	heavy woodland-bushland	0.00549	0.08298	0.10894	**0.57517**	0.06526	0.16216		
	heavy woodland-bushland	0.00175	0.01409	0.00819	**0.78267**	0.13424	0.05907		
	heavy woodland-bushland	0.01057	0.01445	0.01238	**0.56130**	0.14475	0.25655		
	forest	0.00208	0.01058	0.00158	0.23116	**0.38134**	0.37325		
	heavy woodland-bushland	0.00284	0.01777	0.03280	**0.83180**	0.03392	0.08087		
	light woodland-bushland	0.12996	0.23035	**0.30606**	0.10183	0.09594	0.13585		
	heavy woodland-bushland	0.00429	0.08062	0.04720	**0.44860**	0.16278	0.25650		
	heavy woodland-bushland	0.00514	0.00770	0.00462	**0.68244**	0.08223	0.21787		
	light woodland-bushland	0.12659	0.22758	**0.33861**	0.10544	0.05904	0.14275		
	heavy woodland-bushland	0.00067	0.00148	0.00157	**0.92593**	0.03095	0.03941		
	heavy woodland-bushland	0.00124	0.03670	0.03809	**0.80189**	0.07394	0.04813		

Element	Predicted habitat	Probability grassland/ tree-less	Probability wooded-bushed grassland	Probability light woodland-bushland	Probability heavy woodland-bushland	Probability forest	Probability montane light cover	Probability montane heavy cover	Identification
DISTAL PHALANGES (55.8%), cont.									
Laetolil Beds, cont.									
	heavy woodland-bushland	0.00103	0.01632	0.00292	**0.47093**	0.30714	0.20165		
	heavy woodland-bushland	0.00125	0.08196	0.02389	**0.45029**	0.33689	0.10571		
	heavy woodland-bushland	0.00042	0.00869	0.00239	**0.83174**	0.06896	0.08781		
	heavy woodland-bushland	0.00168	0.03239	0.01166	**0.54282**	0.26045	0.15099		
	forest	0.00141	0.08306	0.01372	0.30409	**0.32691**	0.27081		
	heavy woodland-bushland	0.00103	0.03051	0.00858	**0.64035**	0.19227	0.12726		
	heavy woodland-bushland	0.00210	0.02989	0.01584	**0.68581**	0.17007	0.09630		
	heavy woodland-bushland	0.04292	0.17805	0.20690	**0.45724**	0.07222	0.04266		
	wooded-bushed grassland	0.00395	**0.38307**	0.24318	0.16944	0.12596	0.07440		
	heavy woodland-bushland	0.00343	0.03399	0.01048	**0.41405**	0.17520	0.36285		
number of specimens		0	3	3	22	2	0		
average probability of all specimens		0.01233	0.13564	0.07660	0.49748	0.13878	0.13916		
average probability of predicted specimens		n/a	0.74265	0.41398	0.63227	0.35413	n/a		
LUNAR (53.2%)									
Ndolanya Beds									
	light woodland-bushland	0.05243	0.36528	**0.46004**	0.05356	0.01950	0.04377	0.00543	
	wooded-bushed grassland	0.08072	**0.50296**	0.35954	0.01506	0.00271	0.03799	0.00102	
	wooded-bushed grassland	0.01716	**0.61068**	0.02405	0.22056	0.11422	0.00040	0.01295	
number of specimens		0	2	1	0	0	0	0	
average probability of all specimens		0.05010	0.49297	0.28121	0.09639	0.04548	0.02739	0.00647	
average probability of predicted specimens		n/a	0.55682	0.46004	n/a	n/a	n/a	n/a	
Laetolil Beds									
	heavy woodland-bushland	0.00457	0.24179	0.09193	**0.41033**	0.16146	0.00726	0.08266	
	wooded-bushed grassland	0.03493	**0.45199**	0.39870	0.04397	0.02285	0.03001	0.01755	
	montane heavy cover	0.00012	0.00614	0.03264	0.07360	0.30287	0.00021	**0.58441**	
	light woodland-bushland	0.03882	0.31425	**0.34454**	0.07095	0.04581	0.10146	0.08418	

Element	Predicted habitat	Probability grassland/ tree-less	Probability wooded-bushed grassland	Probability light woodland-bushland	Probability heavy woodland-bushland	Probability forest	Probability montane light cover	Probability montane heavy cover	Identification
LUNAR (53.2%), cont.									
Laetolil Beds, cont.									
	light woodland-bushland	0.00652	0.02930	**0.55832**	0.08329	0.03486	0.23996	0.04775	
	heavy woodland-bushland	0.00482	0.02327	0.00296	**0.64172**	0.32426	0.00030	0.00267	*Madoqua*
number of specimens		0	1	2	2	0	0	1	
average probability of all specimens		0.01496	0.17779	0.23818	0.22064	0.14869	0.06320	0.13654	
average probability of predicted specimens		n/a	0.45199	0.45143	0.52603	n/a	n/a	0.58441	
INTERMEDIATE PHALANGES (51.9%)									
Ndolanya Beds									
	light woodland-bushland	0.04195	0.16794	**0.31502**	0.26322	0.19216	0.00093	0.01879	
	wooded-bushed grassland	0.04348	**0.49023**	0.23675	0.15815	0.00918	0.01465	0.04756	
	light woodland-bushland	0.00709	0.14206	**0.42174**	0.06317	0.24363	0.00047	0.12185	
	wooded-bushed grassland	0.11454	**0.44998**	0.38057	0.00973	0.02927	0.01554	0.00038	
	wooded-bushed grassland	0.03917	**0.31957**	0.25119	0.05910	0.29861	0.00011	0.03224	
	heavy woodland-bushland	0.00407	0.02248	0.04604	**0.49362**	0.00317	0.00615	0.42447	
	heavy woodland-bushland	0.01698	0.32709	0.19826	**0.35370**	0.02034	0.00161	0.08202	
	heavy woodland-bushland	0.00122	0.01631	0.02399	**0.71916**	0.00113	0.00123	0.23695	*Madoqua*
	wooded-bushed grassland	0.02953	**0.51079**	0.23083	0.08268	0.11973	0.00011	0.02633	
	wooded-bushed grassland	0.01981	**0.70591**	0.19135	0.03276	0.04384	0.00011	0.00623	
	wooded-bushed grassland	0.01830	**0.42646**	0.20698	0.12900	0.19329	0.00003	0.02594	
	grassland/tree-less	**0.37645**	0.29707	0.25100	0.01441	0.04718	0.01304	0.00084	
	wooded-bushed grassland	0.15631	**0.44661**	0.33143	0.00578	0.05033	0.00874	0.00079	
	wooded-bushed grassland	0.00941	**0.56531**	0.27438	0.07921	0.04746	0.00014	0.02409	
	heavy woodland-bushland	0.04809	0.04466	0.05334	**0.77158**	0.00595	0.01158	0.06479	
	light woodland-bushland	0.01331	0.19391	**0.34569**	0.18875	0.10146	0.00116	0.15573	
	heavy woodland-bushland	0.01719	0.25653	0.16880	**0.34164**	0.01642	0.00236	0.19705	
	heavy woodland-bushland	0.03105	0.26521	0.16696	**0.33071**	0.18357	0.00005	0.02244	
number of specimens		1	8	3	6	0	0	0	
average probability of all specimens		0.05489	0.31378	0.22746	0.22758	0.08926	0.00433	0.08269	
average probability of predicted specimens		0.37645	0.48936	0.36082	0.50174	n/a	n/a	n/a	

Element	Predicted habitat	Probability grassland/ tree-less	Probability wooded-bushed grassland	Probability light woodland-bushland	Probability heavy woodland-bushland	Probability forest	Probability montane light cover	Probability montane heavy cover	Identification
INTERMEDIATE PHALANGES (51.9%), cont.									
Laetolil Beds									
	heavy woodland-bushland	0.01441	0.06401	0.11688	**0.52816**	0.00294	0.06946	0.20415	*Madoqua*
	heavy woodland-bushland	0.01624	0.10704	0.16310	**0.61042**	0.00880	0.01879	0.07561	*Madoqua*
	heavy woodland-bushland	0.00456	0.04056	0.03925	**0.53338**	0.00119	0.00769	0.37339	*Madoqua*
	heavy woodland-bushland	0.05146	0.23982	0.20931	**0.27832**	0.11725	0.00067	0.10317	
	light woodland-bushland	0.03031	0.22597	**0.62890**	0.01170	0.06087	0.02906	0.01319	
	montane heavy cover	0.00190	0.00050	0.00219	0.42405	0.00018	0.01130	**0.55987**	
	heavy woodland-bushland	0.00541	0.09177	0.04804	**0.81332**	0.00179	0.00135	0.03831	*Madoqua*
	heavy woodland-bushland	0.00358	0.02163	0.06498	**0.68452**	0.01351	0.00096	0.21083	*Madoqua*
	heavy woodland-bushland	0.02432	0.33884	0.16843	**0.39986**	0.00173	0.04642	0.02040	*Madoqua*
	wooded-bushed grassland	0.00112	**0.83531**	0.04490	0.11673	0.00053	0.00002	0.00139	*Madoqua*
	heavy woodland-bushland	0.00288	0.05346	0.02867	**0.74161**	0.00349	0.00017	0.16972	*Madoqua*
	light woodland-bushland	0.00710	0.22698	**0.38318**	0.23785	0.03402	0.00281	0.10804	
	heavy woodland-bushland	0.00102	0.00598	0.00449	**0.65311**	0.00040	0.00023	0.33477	*Madoqua*
	heavy woodland-bushland	0.00281	0.01652	0.01333	**0.58329**	0.00386	0.00013	0.38005	*Madoqua*
	heavy woodland-bushland	0.00176	0.05785	0.01272	**0.87768**	0.00100	0.00005	0.04893	*Madoqua*
	heavy woodland-bushland	0.00010	0.04247	0.01735	**0.68229**	0.00165	0.00000	0.25613	*Madoqua*
	heavy woodland-bushland	0.03380	0.27776	0.15029	**0.28309**	0.00111	0.17123	0.08271	*Madoqua*
	heavy woodland-bushland	0.00611	0.01899	0.04019	**0.56265**	0.00490	0.00447	0.36270	*Madoqua*
	heavy woodland-bushland	0.00004	0.00001	0.00004	**0.82639**	0.00000	0.00008	0.17344	*Madoqua*
	heavy woodland-bushland	0.00519	0.17238	0.03272	**0.58345**	0.00090	0.00084	0.20452	*Madoqua*
	light woodland-bushland	0.03405	0.17908	**0.43598**	0.10910	0.23391	0.00101	0.00688	
	light woodland-bushland	0.08236	0.06081	**0.45105**	0.17551	0.15584	0.04576	0.02866	
	heavy woodland-bushland	0.00395	0.11914	0.04714	**0.59840**	0.00408	0.00027	0.22702	*Madoqua*
	heavy woodland-bushland	0.00075	0.00379	0.00814	**0.66012**	0.00091	0.00076	0.32552	*Madoqua*
	heavy woodland-bushland	0.00857	0.20001	0.31664	**0.36846**	0.01763	0.00526	0.08343	
	heavy woodland-bushland	0.00090	0.01245	0.00414	**0.92010**	0.00127	0.00001	0.06114	
	montane heavy cover	0.00409	0.00788	0.02330	0.40790	0.00457	0.00262	**0.54965**	*Madoqua*
	heavy woodland-bushland	0.01427	0.03337	0.05936	**0.46438**	0.00674	0.00921	0.41267	*Madoqua*
	heavy woodland-bushland	0.00727	0.05520	0.03429	**0.84347**	0.00081	0.00637	0.05259	
	wooded-bushed grassland	0.01404	**0.59300**	0.09634	0.16437	0.00198	0.00248	0.12780	*Madoqua*

Element	Predicted habitat	Probability grassland/ tree-less	Probability wooded-bushed grassland	Probability light woodland-bushland	Probability heavy woodland-bushland	Probability forest	Probability montane light cover	Probability montane heavy cover	Identification
INTERMEDIATE PHALANGES (51.9%), cont.									
Laetolil Beds, cont.									
	light woodland-bushland	0.03558	0.11968	**0.41199**	0.11346	0.30259	0.00122	0.01547	
	heavy woodland-bushland	0.00788	0.34630	0.13273	**0.46950**	0.00487	0.00139	0.03732	*Madoqua*
	heavy woodland-bushland	0.00377	0.02756	0.03917	**0.73748**	0.00061	0.01952	0.17189	*Madoqua*
	montane heavy cover	0.00199	0.00027	0.00133	0.32492	0.00036	0.00265	**0.66848**	*Madoqua*
	heavy woodland-bushland	0.00380	0.01665	0.02855	**0.79100**	0.00100	0.00952	0.14949	
	heavy woodland-bushland	0.00090	0.00621	0.01232	**0.70577**	0.00118	0.00060	0.27302	
	heavy woodland-bushland	0.00005	0.00285	0.01448	**0.85347**	0.00211	0.00004	0.12700	*Madoqua*
	heavy woodland-bushland	0.00800	0.06622	0.03593	**0.80017**	0.00679	0.00020	0.08269	*Madoqua*
	heavy woodland-bushland	0.00272	0.00285	0.01041	**0.67940**	0.00189	0.00205	0.30069	*Madoqua*
	wooded-bushed grassland	0.15556	**0.33598**	0.20304	0.21965	0.03714	0.00666	0.04197	
	montane heavy cover	0.00091	0.00249	0.00312	0.43323	0.00067	0.00015	**0.55944**	*Madoqua*
	light woodland-bushland	0.12803	0.26469	**0.47250**	0.01772	0.10507	0.01077	0.00121	
	forest	0.27472	0.05125	0.22084	0.00138	**0.44382**	0.00664	0.00135	
	wooded-bushed grassland	0.01311	**0.52616**	0.23047	0.18213	0.02765	0.00039	0.02009	*Madoqua*
	light woodland-bushland	0.03162	0.26370	**0.37604**	0.20804	0.08899	0.00219	0.02942	
	wooded-bushed grassland	0.00474	**0.72220**	0.19344	0.06142	0.00227	0.00297	0.01295	
	light woodland-bushland	0.10892	0.09757	**0.43526**	0.03598	0.29658	0.00974	0.01596	
	heavy woodland-bushland	0.01327	0.01571	0.04309	**0.65143**	0.00308	0.03070	0.24272	*Madoqua*
	heavy woodland-bushland	0.00608	0.11264	0.05594	**0.64805**	0.00464	0.00065	0.17200	*Madoqua*
	light woodland-bushland	0.10191	0.21420	**0.49422**	0.07547	0.07113	0.02900	0.01408	
	heavy woodland-bushland	0.00042	0.01644	0.02573	**0.55455**	0.02164	0.00001	0.38121	*Madoqua*
	montane heavy cover	0.00295	0.01945	0.05184	0.39525	0.00875	0.00174	**0.52001**	*Madoqua*
	heavy woodland-bushland	0.00437	0.21033	0.06972	**0.64292**	0.00099	0.00272	0.06895	*Madoqua*
	wooded-bushed grassland	0.05669	**0.40447**	0.31520	0.00756	0.21347	0.00035	0.00226	
	montane heavy cover	0.00366	0.00246	0.00875	0.20637	0.00198	0.00369	**0.77308**	*Madoqua*
	heavy woodland-bushland	0.00076	0.00410	0.00112	**0.96580**	0.00001	0.00046	0.02775	*Madoqua avifluminis*
	montane heavy cover	0.13062	0.03215	0.03286	0.37107	0.00643	0.02383	**0.40304**	
	wooded-bushed grassland	0.01051	**0.34386**	0.20916	0.33587	0.09082	0.00005	0.00974	
	heavy woodland-bushland	0.00319	0.02761	0.06269	**0.57840**	0.02574	0.00033	0.30203	*Madoqua*
	heavy woodland-bushland	0.00026	0.00891	0.01014	**0.85116**	0.00267	0.00001	0.12685	*Madoqua*

Element	Predicted habitat	Probability grassland/ tree-less	Probability wooded-bushed grassland	Probability light woodland-bushland	Probability heavy woodland-bushland	Probability forest	Probability montane light cover	Probability montane heavy cover	Identification
INTERMEDIATE PHALANGES (51.9%), cont.									
Laetolil Beds, cont.									
	heavy woodland-bushland	0.00755	0.07583	0.11099	**0.55773**	0.00295	0.02495	0.21999	*Madoqua*
	heavy woodland-bushland	0.01602	0.14559	0.09884	**0.60259**	0.00160	0.03667	0.09869	*Madoqua*
number of specimens		0	7	9	38	1	0	7	
average probability of all specimens		0.02460	0.13853	0.12996	0.47133	0.03980	0.01083	0.18496	
average probability of predicted specimens		n/a	0.53728	0.45435	0.64169	0.44382	n/a	0.57622	
MAGNUM (51.2%)									
Ndolanya Beds	wooded-bushed grassland	0.00151	**0.42393**	0.15601	0.26609	0.00551	0.00389	0.14306	
	light woodland-bushland	0.00548	0.09805	**0.30643**	0.24207	0.04899	0.09163	0.20735	
	heavy woodland-bushland	0.00238	0.22695	0.26724	**0.28621**	0.16495	0.00668	0.04559	*Madoqua*
	light woodland-bushland	0.00059	0.24469	**0.48406**	0.11100	0.09447	0.00835	0.05685	
number of specimens		0	1	2	1	0	0	0	
average probability of all specimens		0.00249	0.24841	0.30344	0.22634	0.07848	0.02764	0.11321	
average probability of predicted specimens		n/a	0.42393	0.39525	0.28621	n/a	n/a	n/a	
Laetolil Beds									
	wooded-bushed grassland	0.00336	**0.48548**	0.34542	0.08807	0.02046	0.00218	0.05502	
	light woodland-bushland	0.02191	0.28580	**0.30971**	0.13123	0.13837	0.01762	0.09535	
	wooded-bushed grassland	0.00004	**0.47581**	0.28001	0.10574	0.01355	0.02311	0.10174	
	wooded-bushed grassland	0.00129	**0.48739**	0.33884	0.05177	0.03916	0.00895	0.07261	
	grassland/tree-less	**0.32435**	0.19108	0.14682	0.04585	0.04891	0.02458	0.21842	
	montane heavy cover	0.00149	0.16826	0.20425	0.14423	0.01632	0.07931	**0.38614**	
	heavy woodland-bushland	0.03963	0.25372	0.10945	**0.32013**	0.24238	0.00528	0.02941	
	light woodland-bushland	0.00237	0.15968	**0.53307**	0.13548	0.01383	0.00947	0.14610	
	wooded-bushed grassland	0.00010	**0.36296**	0.29628	0.26910	0.03453	0.00256	0.03447	*Madoqua*
	heavy woodland-bushland	0.00001	0.03478	0.23515	**0.58967**	0.06458	0.04795	0.02786	
	wooded-bushed grassland	0.04440	**0.25673**	0.22835	0.22811	0.06910	0.02664	0.14666	
	forest	0.00043	0.01816	0.19546	0.06778	**0.39213**	0.26200	0.06404	
	light woodland-bushland	0.00015	0.16746	**0.56346**	0.12170	0.09603	0.00974	0.04146	

Element	Predicted habitat	Probability grassland/ tree-less	Probability wooded-bushed grassland	Probability light woodland-bushland	Probability heavy woodland-bushland	Probability forest	Probability montane light cover	Probability montane heavy cover	Identification
MAGNUM (51.2%), cont.									
Laetolil Beds, cont.									
	wooded-bushed grassland	0.02317	**0.50890**	0.16066	0.13564	0.02244	0.00516	0.14404	
	light woodland-bushland	0.00029	0.07581	**0.40471**	0.12704	0.28768	0.03247	0.07200	*Madoqua*
number of specimens		1	6	4	2	1	0	1	
average probability of all specimens		0.03087	0.26213	0.29011	0.17077	0.09996	0.03713	0.10902	
average probability of predicted specimens		0.32435	0.42955	0.45274	0.45490	0.39213	n/a	0.38614	
UNCIFORM (51.0%)									
Ndolanya Beds									
	montane light cover	0.04096	0.22493	0.27188	0.08647	0.04377	**0.32706**	0.00492	
	light woodland-bushland	0.00407	0.36092	**0.46277**	0.00504	0.00831	0.15822	0.00067	
	wooded-bushed grassland	0.00636	**0.43913**	0.28981	0.11272	0.05917	0.02630	0.06652	
	wooded-bushed grassland	0.00133	**0.71572**	0.20389	0.03593	0.02183	0.01603	0.00527	*Madoqua*
number of specimens		0	2	1	0	0	1	0	
average probability of all specimens		0.01318	0.43518	0.30709	0.06004	0.03327	0.13190	0.01935	
average probability of predicted specimens		n/a	0.57743	0.46277	n/a	n/a	0.32706	n/a	
Laetolil Beds									
	wooded-bushed grassland	0.00269	**0.77250**	0.18346	0.00735	0.00832	0.01626	0.00941	
	wooded-bushed grassland	0.00425	**0.64066**	0.24091	0.04674	0.00581	0.03713	0.02450	
	wooded-bushed grassland	0.00003	**0.88528**	0.06051	0.01645	0.03704	0.00046	0.00023	*Madoqua*
	wooded-bushed grassland	0.00223	**0.67186**	0.27905	0.00538	0.01150	0.00877	0.02120	
	wooded-bushed grassland	0.00661	**0.71687**	0.13746	0.01199	0.01682	0.10166	0.00860	
number of specimens		0	5	0	0	0	0	0	
average probability of all specimens		0.00316	0.73743	0.18028	0.01758	0.01590	0.03286	0.01279	
average probability of predicted specimens		n/a	0.73743	n/a	n/a	n/a	n/a	n/a	

Element	Predicted habitat	Probability grassland/ tree-less	Probability wooded-bushed grassland	Probability light woodland-bushland	Probability heavy woodland-bushland	Probability forest	Probability montane light cover	Probability montane heavy cover	Identification
DISTAL HUMERUS (48.8%)									
Ndolanya Beds									
	montane heavy cover	0.00185	0.06594	0.06187	0.25568	0.14232	0.14654	**0.32580**	
	montane light cover	0.00347	0.03496	0.03220	0.19169	0.05206	**0.46723**	0.21838	
	light woodland-bushland	0.00306	0.17039	**0.54400**	0.13660	0.14586	0.00001	0.00008	
	montane heavy cover	0.00002	0.00006	0.00008	0.00137	0.00012	0.15907	**0.83929**	
	light woodland-bushland	0.05956	0.30894	**0.33945**	0.14569	0.12953	0.01008	0.00676	
	light woodland-bushland	0.32128	0.18441	**0.44712**	0.03471	0.01242	0.00005	0.00001	
	light woodland-bushland	0.01985	0.23220	**0.46271**	0.19699	0.08200	0.00133	0.00492	
	wooded-bushed grassland	0.01835	**0.41719**	0.40662	0.07118	0.08317	0.00097	0.00252	
	light woodland-bushland	0.01460	0.20210	**0.39483**	0.21083	0.06320	0.00748	0.10696	
	light woodland-bushland	0.06332	0.30468	**0.58353**	0.03300	0.01546	0.00001	0.00001	
	heavy woodland-bushland	0.01112	0.03913	0.09205	**0.39033**	0.09642	0.10977	0.26118	
	heavy woodland-bushland	0.15170	0.05383	0.28306	**0.45805**	0.04599	0.00535	0.00202	
	light woodland-bushland	0.01813	0.17885	**0.55951**	0.19486	0.04802	0.00015	0.00049	
	montane heavy cover	0.00219	0.00385	0.01139	0.14543	0.01178	0.25848	**0.56688**	
	light woodland-bushland	0.05718	0.38872	**0.47673**	0.04968	0.02658	0.00051	0.00060	
	light woodland-bushland	0.00969	0.11631	**0.52911**	0.30492	0.03621	0.00026	0.00350	
	heavy woodland-bushland	0.02771	0.10607	0.24609	**0.39235**	0.20181	0.01109	0.01488	
	heavy woodland-bushland	0.01719	0.04521	0.16209	**0.57275**	0.09288	0.03020	0.07967	
	light woodland-bushland	0.02522	0.23609	**0.46142**	0.19262	0.05979	0.00369	0.02116	
	montane heavy cover	0.00019	0.02480	0.08950	0.28102	0.02501	0.00288	**0.57659**	*Madoqua avifluminis*
	heavy woodland-bushland	0.01321	0.14549	0.25809	**0.33756**	0.20333	0.01121	0.03112	
	light woodland-bushland	0.13404	0.22318	**0.51911**	0.08360	0.03923	0.00041	0.00043	
	heavy woodland-bushland	0.02545	0.11638	0.36138	**0.40677**	0.08342	0.00252	0.00408	
	heavy woodland-bushland	0.02008	0.14820	0.28083	**0.31455**	0.16847	0.01518	0.05268	
number of specimens		0	1	11	7	0	1	4	
average probability of all specimens		0.04244	0.15612	0.31678	0.22509	0.07771	0.05185	0.13000	
average probability of predicted specimens		n/a	0.41719	0.48341	0.41034	n/a	0.46723	0.57714	

Element	Predicted habitat	Probability grassland/ tree-less	Probability wooded-bushed grassland	Probability light woodland-bushland	Probability heavy woodland-bushland	Probability forest	Probability montane light cover	Probability montane heavy cover	Identification
DISTAL METAPODIAL (47.2%), cont.									
Ndolanya Beds, cont.									
	light woodland-bushland	0.02414	0.40986	**0.41035**	0.09834	0.01921	0.02316	0.01493	
	wooded-bushed grassland	0.01179	**0.44667**	0.33282	0.14969	0.05304	0.00436	0.00164	
	wooded-bushed grassland	0.07694	**0.44323**	0.15323	0.06228	0.16204	0.04061	0.06168	
	light woodland-bushland	0.00529	0.24234	**0.48364**	0.18131	0.00855	0.07451	0.00435	
	light woodland-bushland	0.00177	0.13967	**0.41724**	0.29705	0.07635	0.06170	0.00622	
	wooded-bushed grassland	0.00140	**0.39270**	0.39258	0.18201	0.02756	0.00353	0.00022	
	light woodland-bushland	0.00317	0.35179	**0.45192**	0.15453	0.02094	0.01562	0.00204	
	wooded-bushed grassland	0.03730	**0.46339**	0.36241	0.11258	0.02129	0.00227	0.00076	
	forest	0.00643	0.19837	0.12986	0.07219	**0.38677**	0.06006	0.14631	*Madoqua*
	light woodland-bushland	0.01120	0.28912	**0.29519**	0.18168	0.12100	0.07813	0.02368	
	wooded-bushed grassland	0.00409	**0.40852**	0.38715	0.14649	0.04473	0.00775	0.00128	
	wooded-bushed grassland	0.00340	**0.46711**	0.36455	0.12108	0.03428	0.00822	0.00136	
	light woodland-bushland	0.00112	0.28659	**0.34089**	0.17882	0.05077	0.13987	0.00194	
	wooded-bushed grassland	0.00614	**0.30798**	0.30342	0.16205	0.12520	0.08419	0.01103	*Gazella janenschi*
	forest	0.00476	0.17389	0.08150	0.05085	**0.39403**	0.15251	0.14245	*Madoqua*
	montane light cover	0.00252	0.07598	0.05596	0.02043	0.03390	**0.60179**	0.20942	*Madoqua*
	wooded-bushed grassland	0.09076	**0.47724**	0.23186	0.07424	0.10482	0.00345	0.01764	
	light woodland-bushland	0.00862	0.18273	**0.33962**	0.18079	0.12223	0.13136	0.03465	
	wooded-bushed grassland	0.02219	**0.49146**	0.36228	0.08442	0.02567	0.00787	0.00612	
	wooded-bushed grassland	0.00169	**0.45671**	0.39992	0.12537	0.01245	0.00372	0.00015	
	light woodland-bushland	0.00089	0.25095	**0.37236**	0.20591	0.05069	0.11530	0.00391	
	wooded-bushed grassland	0.02230	**0.40411**	0.31500	0.15566	0.08898	0.00642	0.00753	
	wooded-bushed grassland	0.00556	**0.44729**	0.34669	0.13029	0.02933	0.03738	0.00347	
	wooded-bushed grassland	0.19150	**0.27750**	0.24076	0.07195	0.07775	0.07680	0.06374	
number of specimens		2	13	9	0	2	1	0	
average probability of all specimens		0.06021	0.31706	0.30358	0.12537	0.07932	0.06985	0.04460	
average probability of predicted specimens		0.53065	0.42184	0.40316	n/a	0.39040	0.60179	n/a	

Element	Predicted habitat	Probability grassland/ tree-less	Probability wooded-bushed grassland	Probability light woodland-bushland	Probability heavy woodland-bushland	Probability forest	Probability montane light cover	Probability montane heavy cover	Identification
DISTAL METAPODIAL (47.2%), cont.									
Ndolanya Beds, cont.									
	light woodland-bushland	0.02414	0.40986	**0.41035**	0.09834	0.01921	0.02316	0.01493	
	wooded-bushed grassland	0.01179	**0.44667**	0.33282	0.14969	0.05304	0.00436	0.00164	
	wooded-bushed grassland	0.07694	**0.44323**	0.15323	0.06228	0.16204	0.04061	0.06168	
	light woodland-bushland	0.00529	0.24234	**0.48364**	0.18131	0.00855	0.07451	0.00435	
	light woodland-bushland	0.00177	0.13967	**0.41724**	0.29705	0.07635	0.06170	0.00622	
	wooded-bushed grassland	0.00140	**0.39270**	0.39258	0.18201	0.02756	0.00353	0.00022	
	light woodland-bushland	0.00317	0.35179	**0.45192**	0.15453	0.02094	0.01562	0.00204	
	wooded-bushed grassland	0.03730	**0.46339**	0.36241	0.11258	0.02129	0.00227	0.00076	
	forest	0.00643	0.19837	0.12986	0.07219	**0.38677**	0.06006	0.14631	*Madoqua*
	light woodland-bushland	0.01120	0.28912	**0.29519**	0.18168	0.12100	0.07813	0.02368	
	wooded-bushed grassland	0.00409	**0.40852**	0.38715	0.14649	0.04473	0.00775	0.00128	
	wooded-bushed grassland	0.00340	**0.46711**	0.36455	0.12108	0.03428	0.00822	0.00136	
	light woodland-bushland	0.00112	0.28659	**0.34089**	0.17882	0.05077	0.13987	0.00194	
	wooded-bushed grassland	0.00614	**0.30798**	0.30342	0.16205	0.12520	0.08419	0.01103	*Gazella janenschi*
	forest	0.00476	0.17389	0.08150	0.05085	**0.39403**	0.15251	0.14245	*Madoqua*
	montane light cover	0.00252	0.07598	0.05596	0.02043	0.03390	**0.60179**	0.20942	*Madoqua*
	wooded-bushed grassland	0.09076	**0.47724**	0.23186	0.07424	0.10482	0.00345	0.01764	
	light woodland-bushland	0.00862	0.18273	**0.33962**	0.18079	0.12223	0.13136	0.03465	
	wooded-bushed grassland	0.02219	**0.49146**	0.36228	0.08442	0.02567	0.00787	0.00612	
	wooded-bushed grassland	0.00169	**0.45671**	0.39992	0.12537	0.01245	0.00372	0.00015	
	light woodland-bushland	0.00089	0.25095	**0.37236**	0.20591	0.05069	0.11530	0.00391	
	wooded-bushed grassland	0.02230	**0.40411**	0.31500	0.15566	0.08898	0.00642	0.00753	
	wooded-bushed grassland	0.00556	**0.44729**	0.34669	0.13029	0.02933	0.03738	0.00347	
	wooded-bushed grassland	0.19150	**0.27750**	0.24076	0.07195	0.07775	0.07680	0.06374	
number of specimens		2	13	9	0	2	1	0	
average probability of all specimens		0.06021	0.31706	0.30358	0.12537	0.07932	0.06985	0.04460	
average probability of predicted specimens		0.53065	0.42184	0.40316	n/a	0.39040	0.60179	n/a	

Element	Predicted habitat	Probability grassland/ tree-less	Probability wooded-bushed grassland	Probability light woodland-bushland	Probability heavy woodland-bushland	Probability forest	Probability montane light cover	Probability montane heavy cover	Identification
DISTAL METAPODIAL (47.2%), cont.									
Laetolil Beds									
	light woodland-bushland	0.00241	0.31484	**0.43727**	0.22307	0.01753	0.00470	0.00018	
	montane heavy cover	0.01198	0.05721	0.03718	0.01089	0.03579	0.09509	**0.75185**	*Madoqua*
	forest	0.00438	0.22529	0.09902	0.10709	**0.51601**	0.02665	0.02157	*Madoqua*
	light woodland-bushland	0.00969	0.34057	**0.39505**	0.19042	0.04595	0.01654	0.00177	
	light woodland-bushland	0.02088	0.23504	**0.48019**	0.18537	0.06229	0.01117	0.00505	
	light woodland-bushland	0.02289	0.24627	**0.53566**	0.15850	0.03070	0.00315	0.00282	
	montane light cover	0.00124	0.18827	0.16036	0.11521	0.14557	**0.36481**	0.02453	*Madoqua*
	montane light cover	0.00860	0.22124	0.14742	0.07680	0.15564	**0.25948**	0.13082	*Madoqua*
	montane heavy cover	0.15260	0.05748	0.05947	0.01203	0.04982	0.23466	**0.43394**	
	light woodland-bushland	0.32985	0.15380	**0.33260**	0.04949	0.03526	0.02052	0.07847	
	light woodland-bushland	0.02941	0.35100	**0.36946**	0.17623	0.05039	0.01768	0.00582	
	montane light cover	0.01239	0.24938	0.13106	0.07053	0.13659	**0.30336**	0.09668	
	wooded-bushed grassland	0.21748	**0.37239**	0.29080	0.05084	0.03344	0.00991	0.02515	
	grassland/tree-less	**0.39361**	0.06737	0.11976	0.02735	0.06909	0.12765	0.19518	Bovidae?
	wooded-bushed grassland	0.00526	**0.28660**	0.19950	0.15189	0.18481	0.08471	0.08722	*Madoqua*
	light woodland-bushland	0.00486	0.34760	**0.46173**	0.16487	0.01501	0.00529	0.00064	
	forest	0.00278	0.26583	0.12259	0.07151	**0.46837**	0.02684	0.04208	*Madoqua*
	forest	0.00181	0.28296	0.10411	0.08633	**0.44822**	0.05248	0.02409	*Madoqua*
	light woodland-bushland	0.00254	0.27122	**0.34303**	0.22516	0.11068	0.04300	0.00437	
	forest	0.00473	0.07662	0.03659	0.03953	**0.59131**	0.04323	0.20798	
	light woodland-bushland	0.00721	0.19663	**0.30897**	0.28305	0.14828	0.04959	0.00628	*Gazella janenschi*
	light woodland-bushland	0.00534	0.28123	**0.35252**	0.17918	0.09977	0.06970	0.01225	
	light woodland-bushland	0.05252	0.20046	**0.33325**	0.17155	0.17965	0.01528	0.04729	
	light woodland-bushland	0.07169	0.25565	**0.38443**	0.15453	0.12613	0.00134	0.00623	
	light woodland-bushland	0.00216	0.27222	**0.35577**	0.24575	0.09342	0.02915	0.00152	
	light woodland-bushland	0.00646	0.33516	**0.40119**	0.15214	0.05283	0.04330	0.00892	
	forest	0.00282	0.12242	0.19074	0.11253	**0.23749**	0.21485	0.11915	
	light woodland-bushland	0.00774	0.25704	**0.49609**	0.19925	0.03628	0.00220	0.00140	
	wooded-bushed grassland	0.00000	**0.53883**	0.08025	0.30735	0.00128	0.07228	0.00000	*Madoqua*
	light woodland-bushland	0.02682	0.35539	**0.42048**	0.13842	0.04315	0.01239	0.00335	

Element	Predicted habitat	Probability grassland/ tree-less	Probability wooded-bushed grassland	Probability light woodland-bushland	Probability heavy woodland-bushland	Probability forest	Probability montane light cover	Probability montane heavy cover	Identification
DISTAL METAPODIAL (47.2%), cont.									
Laetolil Beds, cont.									
	forest	0.00067	0.09619	0.22397	0.25656	**0.27757**	0.14027	0.00477	
	forest	0.00609	0.14015	0.05226	0.02728	**0.48736**	0.11949	0.16737	
	wooded-bushed grassland	0.00145	**0.29629**	0.13963	0.12199	0.23562	0.19407	0.01094	*Madoqua*
	wooded-bushed grassland	0.01270	**0.55142**	0.19104	0.07414	0.08317	0.06183	0.02568	*Madoqua*
	wooded-bushed grassland	0.00187	**0.49915**	0.21049	0.14145	0.12493	0.01851	0.00361	*Madoqua*
number of specimens		1	6	16	0	7	3	2	
average probability of all specimens		0.04128	0.25741	0.25726	0.13595	0.15513	0.07986	0.07311	
average probability of predicted specimens		0.39361	0.42411	0.40048	n/a	0.43233	0.30922	0.59290	
NAVICULO-CUBOID (47.1%)									
Ndolanya Beds									
	montane light cover	0.08891	0.01687	0.18483	0.00555	0.00864	**0.44972**	0.24549	
	wooded-bushed grassland	0.01160	**0.50525**	0.33732	0.07976	0.00446	0.01191	0.04970	*Madoqua*
	light woodland-bushland	0.09602	0.10170	**0.64773**	0.01370	0.00570	0.01983	0.11532	*Madoqua*
	light woodland-bushland	0.04014	0.12784	**0.58563**	0.14414	0.05742	0.02038	0.02445	
	light woodland-bushland	0.07617	0.22189	**0.57117**	0.03233	0.01871	0.03447	0.04526	
number of specimens		0	1	3	0	0	1	0	
average probability of all specimens		0.06257	0.19471	0.46534	0.05510	0.01899	0.10726	0.09604	
average probability of predicted specimens		n/a	0.50525	0.60151	n/a	n/a	0.44972	n/a	
Laetolil Beds									
	montane heavy cover	0.13090	0.03787	0.05429	0.00210	0.00598	0.18607	**0.58278**	
	forest	0.13046	0.05449	0.12314	0.05086	**0.28139**	0.24086	0.11879	*Madoqua*
	montane heavy cover	0.06751	0.06495	0.24623	0.02821	0.04269	0.00863	**0.54178**	
	light woodland-bushland	0.12563	0.03684	**0.25857**	0.05060	0.21756	0.22082	0.08999	*Madoqua*
	grassland/tree-less	**0.45328**	0.01908	0.36997	0.01826	0.06411	0.02291	0.05240	*Madoqua*
	forest	0.08823	0.14440	0.01575	0.02637	**0.63417**	0.06059	0.03049	
	light woodland-bushland	0.04708	0.30402	**0.34223**	0.13333	0.10012	0.02394	0.04930	
	montane light cover	0.01078	0.04771	0.01905	0.00342	0.00193	**0.63852**	0.27860	

Element	Predicted habitat	Probability grassland/ tree-less	Probability wooded-bushed grassland	Probability light woodland-bushland	Probability heavy woodland-bushland	Probability forest	Probability montane light cover	Probability montane heavy cover	Identification
NAVICULO-CUBOID (47.1%), cont.									
Laetolil Beds, cont.									
	forest	0.07306	0.07476	0.16639	0.10802	**0.43609**	0.07732	0.06438	
	forest	0.04749	0.14792	0.30383	0.01719	**0.34767**	0.03004	0.10587	
	wooded-bushed grassland	0.10423	**0.42465**	0.26999	0.03273	0.00655	0.01285	0.14900	
	light woodland-bushland	0.07171	0.05234	**0.32279**	0.03109	0.22239	0.21436	0.08532	*Madoqua*
	montane heavy cover	0.03207	0.01815	0.26432	0.00854	0.01943	0.00902	**0.64845**	
	light woodland-bushland	0.29161	0.20088	**0.36699**	0.04773	0.05219	0.02576	0.01485	*Madoqua*
	montane heavy cover	0.06074	0.01728	0.37200	0.01190	0.00394	0.02227	**0.51187**	
	grassland/tree-less	**0.30235**	0.05702	0.23238	0.01194	0.16181	0.13803	0.09647	
number of specimens		2	1	4	0	4	1	4	
average probability of all specimens		0.12732	0.10640	0.23300	0.03639	0.16238	0.12075	0.21377	
average probability of predicted specimens		0.37782	0.42465	0.32265	n/a	0.42483	0.63852	0.57122	
EXTERNAL AND MIDDLE CUNEIFORM (43.8%)									
Ndolanya Beds									
	light woodland-bushland	0.11618	0.16747	**0.33544**	0.09244	0.05181	0.07556	0.16110	
number of specimens		0	0	1	0	0	0	0	
average probability of all specimens		0.11618	0.16747	0.33544	0.09244	0.05181	0.07556	0.16110	
average probability of predicted specimens		n/a	n/a	0.33544	n/a	n/a	n/a	n/a	
Laetolil Beds									
	light woodland-bushland	0.06672	0.06349	**0.36664**	0.07175	0.01562	0.35000	0.06579	
	forest	0.13152	0.04026	0.16597	0.17771	**0.26013**	0.15304	0.07137	
	montane heavy cover	0.03344	0.07121	0.33132	0.11507	0.01728	0.05450	**0.37718**	
	light woodland-bushland	0.04159	0.13291	**0.32356**	0.11640	0.03091	0.08995	0.26467	*Madoqua*
	light woodland-bushland	0.12176	0.19030	**0.39318**	0.04768	0.03592	0.05925	0.15191	
number of specimens		0	0	3	0	1	0	1	
average probability of all specimens		0.07901	0.09963	0.31613	0.10572	0.07197	0.14135	0.18618	
average probability of predicted specimens		n/a	n/a	0.36113	n/a	0.26013	n/a	0.37718	

Element	Predicted habitat	Probability grassland/ tree-less	Probability wooded-bushed grassland	Probability light woodland-bushland	Probability heavy woodland-bushland	Probability forest	Probability montane light cover	Probability montane heavy cover	Identification
DISTAL FEMUR (42.4%)									
Ndolanya Beds									
	wooded-bushed grassland	0.01287	**0.62989**	0.26396	0.08489	0.00823	0.00015	0.00001	
	wooded-bushed grassland	0.05386	**0.62867**	0.25863	0.04331	0.01477	0.00058	0.00018	
	wooded-bushed grassland	0.03711	**0.49731**	0.35428	0.09491	0.01625	0.00012	0.00002	
number of specimens		0	3	0	0	0	0	0	
average probability of all specimens		0.03461	0.58529	0.29229	0.07437	0.01308	0.00028	0.00007	
average probability of predicted specimens		n/a	0.58529	n/a	n/a	n/a	n/a	n/a	
Laetolil Beds									
	heavy woodland-bushland	0.00493	0.15081	0.27366	**0.41961**	0.13435	0.01297	0.00367	
	montane light cover	0.00000	0.00008	0.00014	0.00287	0.00012	**0.99078**	0.00601	
	montane light cover	0.00003	0.00101	0.01265	0.37764	0.07789	**0.49266**	0.03812	*Madoqua*
	montane light cover	0.00012	0.00139	0.01981	0.26691	0.24395	**0.30838**	0.15946	*Madoqua*
	wooded-bushed grassland	0.05743	**0.45447**	0.36090	0.09871	0.02775	0.00062	0.00013	
	heavy woodland-bushland	0.00399	0.09831	0.19746	**0.42796**	0.14128	0.10800	0.02300	
	wooded-bushed grassland	0.00727	**0.35002**	0.31034	0.25481	0.07078	0.00520	0.00158	
	heavy woodland-bushland	0.00146	0.01897	0.10918	**0.49103**	0.25303	0.09659	0.02974	
number of specimens		0	2	0	3	0	3	0	
average probability of all specimens		0.00940	0.13438	0.16052	0.29244	0.11864	0.25190	0.03271	
average probability of predicted specimens		n/a	0.40225	n/a	0.44620	n/a	0.59727	n/a	
PROXIMAL RADIUS (41.1%)									
Ndolanya Beds									
	light woodland-bushland	0.11018	0.16776	**0.24749**	0.19509	0.11988	0.11969	0.03992	
	light woodland-bushland	0.21879	0.19373	**0.36316**	0.06324	0.14454	0.00539	0.01115	
	wooded-bushed grassland	0.00282	**0.64866**	0.24877	0.02511	0.07268	0.00190	0.00005	
	light woodland-bushland	0.02868	0.24603	**0.36855**	0.09677	0.24085	0.00378	0.01534	
	light woodland-bushland	0.01635	0.26238	**0.31232**	0.15839	0.21578	0.01585	0.01894	
	light woodland-bushland	0.07455	0.30366	**0.38758**	0.06848	0.15558	0.00569	0.00446	
	wooded-bushed grassland	0.02779	**0.38025**	0.34082	0.09232	0.14200	0.01389	0.00293	

Element	Predicted habitat	Probability grassland/ tree-less	Probability wooded-bushed grassland	Probability light woodland-bushland	Probability heavy woodland-bushland	Probability forest	Probability montane light cover	Probability montane heavy cover	Identification
PROXIMAL RADIUS (41.1%), cont.									
Ndolanya Beds, cont.									
	light woodland-bushland	0.10174	0.26863	**0.34542**	0.11053	0.13922	0.02493	0.00953	
	light woodland-bushland	0.07683	0.15483	**0.28192**	0.18989	0.18316	0.03796	0.07542	
	light woodland-bushland	0.02717	0.29655	**0.30449**	0.16168	0.15973	0.03907	0.01131	
	wooded-bushed grassland	0.02449	**0.41614**	0.36549	0.05119	0.13827	0.00333	0.00109	
	forest	0.01135	0.17035	0.27147	0.18974	**0.27547**	0.01073	0.07090	*Madoqua*
	wooded-bushed grassland	0.02108	**0.42351**	0.31617	0.09457	0.12189	0.02093	0.00185	
	light woodland-bushland	0.05436	0.17906	**0.31956**	0.15774	0.21984	0.01567	0.05377	
	light woodland-bushland	0.01042	0.29407	**0.31081**	0.14379	0.21690	0.01185	0.01217	
	wooded-bushed grassland	0.01783	**0.36461**	0.27159	0.15397	0.11989	0.06782	0.00430	
	wooded-bushed grassland	0.01867	**0.35988**	0.27116	0.15576	0.11954	0.07050	0.00450	
	forest	0.01214	0.13369	0.22583	0.23596	**0.24321**	0.02227	0.12689	
	wooded-bushed grassland	0.03007	**0.33271**	0.30612	0.14322	0.13834	0.04305	0.00649	
	grassland/tree-less	**0.27504**	0.12314	0.26175	0.12637	0.12177	0.03882	0.05311	
	wooded-bushed grassland	0.03159	**0.31014**	0.28072	0.16690	0.12629	0.07635	0.00802	
	wooded-bushed grassland	0.02370	**0.41275**	0.33838	0.07956	0.13259	0.01121	0.00181	
	wooded-bushed grassland	0.00533	**0.45093**	0.33319	0.04452	0.16412	0.00121	0.00069	
	wooded-bushed grassland	0.00695	**0.38723**	0.24741	0.16606	0.12733	0.06136	0.00366	
	wooded-bushed grassland	0.00969	**0.41779**	0.31650	0.09054	0.15405	0.00934	0.00208	
	light woodland-bushland	0.02425	0.28572	**0.38726**	0.06733	0.22724	0.00178	0.00643	
	wooded-bushed grassland	0.00970	**0.26680**	0.24840	0.22547	0.17087	0.06058	0.01818	
	heavy woodland-bushland	0.00959	0.07796	0.13907	**0.28696**	0.16801	0.06164	0.25676	
	light woodland-bushland	0.16285	0.17984	**0.29872**	0.14445	0.13641	0.04627	0.03146	
	light woodland-bushland	0.01852	0.24968	**0.30476**	0.17249	0.21063	0.02081	0.02311	
	wooded-bushed grassland	0.02322	**0.34510**	0.28083	0.15549	0.12438	0.06554	0.00543	
	light woodland-bushland	0.03334	0.26437	**0.36713**	0.10043	0.21659	0.00566	0.01249	
	wooded-bushed grassland	0.00392	**0.54915**	0.28651	0.04434	0.11289	0.00293	0.00026	
	wooded-bushed grassland	0.02483	**0.41731**	0.33058	0.08482	0.12544	0.01521	0.00180	
	grassland/tree-less	**0.57354**	0.04933	0.17080	0.05333	0.07846	0.00836	0.06617	
	wooded-bushed grassland	0.00786	**0.56147**	0.29817	0.03593	0.09333	0.00307	0.00017	
	grassland/tree-less	**0.46041**	0.05056	0.23747	0.03337	0.14133	0.00064	0.07622	

Element	Predicted habitat	Probability grassland/ tree-less	Probability wooded-bushed grassland	Probability light woodland-bushland	Probability heavy woodland-bushland	Probability forest	Probability montane light cover	Probability montane heavy cover	Identification
PROXIMAL RADIUS (41.1%), cont.									
Ndolanya Beds, cont.									
	wooded-bushed grassland	0.03880	**0.43866**	0.37963	0.02988	0.11107	0.00155	0.00041	
	grassland/tree-less	**0.55019**	0.00645	0.03782	0.03555	0.02230	0.01799	0.32969	
	wooded-bushed grassland	0.00829	**0.42013**	0.29570	0.11020	0.14644	0.01687	0.00237	
	light woodland-bushland	0.01722	0.27013	**0.32283**	0.14420	0.21678	0.01265	0.01620	
	light woodland-bushland	0.05890	0.38805	**0.38887**	0.03944	0.12117	0.00265	0.00092	Alcelaphini
	wooded-bushed grassland	0.01142	**0.43078**	0.28201	0.11877	0.12075	0.03423	0.00204	
	wooded-bushed grassland	0.01939	**0.43651**	0.32045	0.08448	0.12207	0.01561	0.00149	
	light woodland-bushland	0.05701	0.19533	**0.36999**	0.10015	0.24352	0.00409	0.02991	
	grassland/tree-less	**0.48878**	0.06524	0.21867	0.05596	0.10567	0.00537	0.06030	
	wooded-bushed grassland	0.00580	**0.47936**	0.29448	0.07725	0.13386	0.00830	0.00095	
	wooded-bushed grassland	0.01248	**0.31395**	0.28061	0.17702	0.16626	0.03968	0.00999	
	light woodland-bushland	0.23872	0.18849	**0.34205**	0.07470	0.13287	0.01003	0.01315	
number of specimens		5	23	18	1	2	0	0	
average probability of all specimens		0.08360	0.29855	0.29632	0.11456	0.15186	0.02437	0.03074	
average probability of predicted specimens		0.46959	0.41582	0.33461	0.28696	0.25934	n/a	n/a	
Laetolil Beds									
	heavy woodland-bushland	0.01146	0.12222	0.19818	**0.26944**	0.21300	0.03994	0.14576	*Madoqua*
	light woodland-bushland	0.00762	0.27280	**0.33191**	0.10366	0.26946	0.00283	0.01173	*Madoqua*
	light woodland-bushland	0.05017	0.21626	**0.32303**	0.15999	0.19594	0.02291	0.03171	
	light woodland-bushland	0.16626	0.14837	**0.31917**	0.12203	0.17582	0.01531	0.05303	
	light woodland-bushland	0.02261	0.24690	**0.31938**	0.15694	0.21543	0.01606	0.02268	
	heavy woodland-bushland	0.02810	0.16581	0.18587	**0.25457**	0.10961	0.21968	0.03636	
	wooded-bushed grassland	0.01192	**0.44942**	0.27810	0.11165	0.11046	0.03690	0.00155	
	wooded-bushed grassland	0.02243	**0.37693**	0.34743	0.08563	0.15580	0.00885	0.00294	
	light woodland-bushland	0.07538	0.15713	**0.23066**	0.22348	0.12722	0.13267	0.05346	
	light woodland-bushland	0.12324	0.15197	**0.31924**	0.13594	0.19246	0.01567	0.06146	
	wooded-bushed grassland	0.01568	**0.46127**	0.34442	0.04790	0.12677	0.00330	0.00065	
	wooded-bushed grassland	0.00410	**0.47720**	0.27908	0.08970	0.13829	0.01053	0.00111	
	light woodland-bushland	0.07010	0.22262	**0.27649**	0.18616	0.13194	0.09026	0.02244	

Element	Predicted habitat	Probability grassland/ tree-less	Probability wooded-bushed grassland	Probability light woodland-bushland	Probability heavy woodland-bushland	Probability forest	Probability montane light cover	Probability montane heavy cover	Identification
PROXIMAL RADIUS (41.1%), cont.									
Laetolil Beds, cont.									
	light woodland-bushland	0.17959	0.13390	**0.28807**	0.14258	0.15878	0.02771	0.06936	
	light woodland-bushland	0.09392	0.17072	**0.29682**	0.17413	0.17231	0.03825	0.05385	
	light woodland-bushland	0.06945	0.18240	**0.28781**	0.19164	0.17091	0.04854	0.04924	
	wooded-bushed grassland	0.00689	**0.50584**	0.31418	0.04609	0.12378	0.00281	0.00041	
	light woodland-bushland	0.09521	0.20595	**0.37179**	0.09730	0.20067	0.00672	0.02236	
	light woodland-bushland	0.27879	0.17664	**0.33442**	0.06521	0.12488	0.00813	0.01192	
	light woodland-bushland	0.01840	0.23625	**0.31446**	0.15951	0.23148	0.01333	0.02657	
	forest	0.01827	0.12063	0.23901	0.20275	**0.25496**	0.01395	0.15042	
	light woodland-bushland	0.04733	0.18283	**0.26178**	0.22167	0.16364	0.07218	0.05057	
number of specimens		0	5	14	2	1	0	0	
average probability of all specimens		0.06441	0.24473	0.29370	0.14764	0.17107	0.03848	0.03998	
average probability of predicted specimens		n/a	0.45413	0.30536	0.26201	0.25496	n/a	n/a	
CUNEIFORM (40.6%)									
Ndolanya Beds									
	montane light cover	0.00963	0.24173	0.11081	0.08956	0.02031	**0.41460**	0.11337	
	montane light cover	0.00885	0.26735	0.14467	0.02043	0.01982	**0.42211**	0.11678	
	montane light cover	0.07951	0.23806	0.22736	0.01022	0.03504	**0.24875**	0.16106	
	montane light cover	0.12863	0.18171	0.13081	0.00814	0.01634	**0.41117**	0.12320	
	montane light cover	0.06021	0.20259	0.15640	0.01159	0.01828	**0.39891**	0.15201	
	wooded-bushed grassland	0.07067	**0.32683**	0.28069	0.03295	0.05355	0.12957	0.10574	
	light woodland-bushland	0.01562	0.36174	**0.37301**	0.02416	0.16323	0.01886	0.04338	*Madoqua*
	wooded-bushed grassland	0.05674	**0.33925**	0.24641	0.01886	0.05038	0.18726	0.10110	
	wooded-bushed grassland	0.02358	**0.28705**	0.18189	0.04982	0.04086	0.28068	0.13613	
number of specimens		0	3	1	0	0	5	0	
average probability of all specimens		0.05038	0.27181	0.20578	0.02953	0.04642	0.27910	0.11697	
average probability of predicted specimens		n/a	0.31771	0.37301	n/a	n/a	0.37911	n/a	

Element	Predicted habitat	Probability grassland/ tree-less	Probability wooded-bushed grassland	Probability light woodland-bushland	Probability heavy woodland-bushland	Probability forest	Probability montane light cover	Probability montane heavy cover	Identification
CUNEIFORM (40.6%), cont.									
Laetolil Beds									
	montane light cover	0.06654	0.22005	0.17563	0.01263	0.02946	**0.33742**	0.15829	
	wooded-bushed grassland	0.00210	**0.32491**	0.08178	0.25963	0.02402	0.26446	0.04309	*Madoqua*
	wooded-bushed grassland	0.09410	**0.29046**	0.26366	0.01260	0.04056	0.17974	0.11888	
	wooded-bushed grassland	0.00134	**0.42085**	0.17438	0.19677	0.07930	0.08039	0.04697	*Madoqua*
	heavy woodland-bushland	0.00017	0.14170	0.05045	**0.72190**	0.03442	0.02923	0.02212	
	montane light cover	0.02377	0.12951	0.07380	0.01278	0.00857	**0.62183**	0.12974	
	wooded-bushed grassland	0.01019	**0.38322**	0.32160	0.09719	0.11534	0.02568	0.04678	
	montane light cover	0.05774	0.29431	0.17924	0.03360	0.02331	**0.30813**	0.10367	
number of specimens		0	4	0	1	0	3	0	
average probability of all specimens		0.03199	0.27563	0.16507	0.16839	0.04437	0.23086	0.08369	
average probability of predicted specimens		n/a	0.35486	n/a	0.72190	n/a	0.42246	n/a	
PISIFORM (39.4%)									
Ndolanya Beds									
	wooded-bushed grassland	0.04923	**0.35696**	0.22147	0.02251	0.04178	0.18687	0.12117	
number of specimens		0	1	0	0	0	0	0	
average probability of all specimens		0.04923	0.35696	0.22147	0.02251	0.04178	0.18687	0.12117	
average probability of predicted specimens		n/a	0.35696	n/a	n/a	n/a	n/a	n/a	
PROXIMAL TIBIA (37.6%)									
Ndolanya Beds									
	light woodland-bushland	0.02451	0.11073	**0.43339**	0.12115	0.05246	0.12301	0.13475	
	light woodland-bushland	0.04058	0.04436	**0.41672**	0.07393	0.03351	0.08523	0.30567	
	forest	0.01658	0.21553	0.03085	0.20877	**0.45518**	0.01995	0.05313	
	light woodland-bushland	0.10316	0.20981	**0.23591**	0.11761	0.11743	0.03578	0.18030	
	wooded-bushed grassland	0.18169	**0.27512**	0.20409	0.07845	0.09324	0.10848	0.05892	
	light woodland-bushland	0.09815	0.08038	**0.29470**	0.07997	0.04609	0.23797	0.16275	

Element	Predicted habitat	Probability grassland/ tree-less	Probability wooded-bushed grassland	Probability light woodland-bushland	Probability heavy woodland-bushland	Probability forest	Probability montane light cover	Probability montane heavy cover	Identification
PROXIMAL TIBIA (37.6%), cont.									
Ndolanya Beds, cont.									
number of specimens		0	1	4	0	1	0	0	
average probability of all specimens		0.07745	0.15599	0.26928	0.11331	0.13299	0.10174	0.14925	
average probability of predicted specimens		n/a	0.27512	0.34518	n/a	0.45518	n/a	n/a	
Laetolil Beds									
	wooded-bushed grassland	0.06311	**0.33577**	0.08670	0.18774	0.19470	0.09278	0.03919	*Madoqua*
number of specimens		0	1	0	0	0	0	0	
average probability of all specimens		0.06311	0.33577	0.08670	0.18774	0.19470	0.09278	0.03919	
average probability of predicted specimens		n/a	0.33577	n/a	n/a	n/a	n/a	n/a	
PROXIMAL HUMERUS (37.4%)									
Ndolanya Beds									
	light woodland-bushland	0.04003	0.13621	**0.28215**	0.15414	0.21965	0.06988	0.09795	
number of specimens		0	0	1	0	0	0	0	
average probability of all specimens		0.04003	0.13621	0.28215	0.15414	0.21965	0.06988	0.09795	
average probability of predicted specimens		n/a	n/a	0.28215	n/a	n/a	n/a	n/a	

The findings of the project reported in this thesis support the earlier contention (Kappelman *et al.*, 1997) that bovids are way cool.