Hominin Landscapes and Co-Evolutionary Ecology: Accommodating Logical Incoherence and Complexity

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Abstract

Understanding primate (and human) evolutionary environments is a key goal of palaeoanthropology. The most recent contribution to this debate, the 'tectonic landscape model' (TLM) is the first to explicitly invoke either the spatial structure of environments generally or the physical landscape specifically as important to hominin evolution. It adds a layer of complexity to existing models and – if correct – has broader implications for the nature and analysis of evolutionary change. This thesis evaluates the TLM and its implications for palaeoanthropology. It explores the conceptual structure that surrounds the TLM to establish how this has so far impacted palaeoanthropology, then surveys the state-of-the-art in hominin landscape research to establish existing levels of knowledge. This suggests that little basic information is available about the structure of African landscapes themselves, their interactions with primates, or the possibility that complex cognition 'removes' humans from their influence. Three analytical designs are therefore developed which use landscape mapping techniques and a series of socioecological and anatomical case studies of *Papio* baboons and *Homo sapiens* to develop this baseline understanding. Although the landscape system is complex, it argues that it should be possible to explore the impacts of individual factors like topography and that there are interesting perspective-dependent relationships between landscapes and primate anatomy and socioecology, which persist in modern humans despite the considerable cultural 'filter' through which they view and interact with their surroundings. These insights are then used to extract three predictions from the TLM that are tested against existing knowledge of the fossil record and evolutionary pattern and process in the mammals. The key output is a new theory of human evolution, the 'complex topography hypothesis', which is shown to work at least as well as traditional explanations of the human evolutionary trajectory and the distinctive anatomies and ecologies of hominins including *Homo sapiens*.

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Author Declaration

The work presented here is my own, except where otherwise acknowledged, and has not been presented before.

Chapter One: Introduction and the Current State-of-the-Art

INTRODUCTION

Complaints that "everybody talks about the environment, but nobody does much about it" (Potts, 1998a, 94) notwithstanding, most current palaeoanthropological research places the context of hominin evolution at the centre of our understanding (see for example Elton, 2008, Rosenzweig, 1999, Kingston, 2007). Today, in fact, "[u]nraveling the context in which the evolution and diversification of early hominins occurred has become one of the core and highly debated subjects in paleoanthropology" (Alemseged et al., 2007, 159). As a result, palaeoanthropologists have begun to study the climate, vegetation, geology and ecology of the areas surrounding hominin findspots and to attempt to reconstruct conditions in these regions in the past through the rapidly expanding fields of palaeoenvironmental science and hominin palaeoecology. This work has focused particularly on elucidating and explaining the relationships between environments (and environmental change) and hominin evolution, with a number of hypotheses currently under debate in the literature (Potts, 1998a, 2007). These range from invoking simple, directional shifts in external conditions – like an increase in aridity which promoted the spread of savannah environments and changed the nature of selective pressures acting on hominins (Dart, 1925) – to more complicated models emphasising increased environmental variability (Potts, 1998b), seasonality (Foley, 1987a) and rapid environmental and consequently faunal turnover (Behrensmeyer et al., 1997).

The relationships between environment and evolutionary history promoted by these hypotheses may be generalised or context-specific. The recent suggestion that hominin encephalisation resulted from decreasing global temperatures and the consequent removal of thermoregulatory constraints on brain size (Kleidon, 2009), for instance, is part of a more general theory about the role of climate in life's history which attempts to explain the emergence of phototrophs, eukaryotes and metazoans as well as encephalisation in many disparate lineages (Schwartzman et al., 2009). Other hypotheses restrict attention to a subset of lineages like Plio-Pleistocene African mammals (Vrba, 1992, 2007), or even just the hominins (Dart, 1925, Morgan, 1982). This focus on explaining 'unique' human characteristics is perhaps more uncertain theoretically as it is difficult to test models of postulated one-off occurrences (Cartmill, 1990), but has been prominent in academic discussion. Whatever their level of applicability, environmental hypotheses of hominin evolution and consequent debates over their implications are ubiquitous in the palaeoanthropological literature (see, for example, Reed, 1997, Potts, 1998a, Kingston, 1999, Potts, 2007, Vrba, 2007, Winder, 2012).

The most recent environmental hypothesis of human evolution is the *tectonic landscape model* (TLM) proposed by King and Bailey (2006) following their observation that most fossil sites are located near to active volcanoes, faults, rifts or scarps (see Figure 1).

Figure 1: map showing the correlation between the distribution of major hominin fossil sites and volcanic activity in Africa; from King and Bailey (2006, their figure 1).

King and Bailey (2006) postulated that this pattern is neither coincidental nor wholly due to differential preservation (as suggested by Kullmer, 2007, among others) but results from tectonically active landscapes being somehow attractive to hominins. These landscapes are characterised by ‘complex’ topography; blocks of bedrock are lifted, faulted and downdropped to create scarps, boulder fields and fault lines at various scales and volcanic activity triggers lava flows which dissect the landscape and weather into jagged lava fields, often trapping sediment and water and modifying local habitats (King and Bailey, 2006, Bailey and King, 2011). They are thus typified by hilly, broken terrain which is ‘rough’ at various scales, and which might offer the hominins tactical advantages over their prey and predators, ready access to water, and habitat mosaics which provide a range of vegetation types and resources – including stone outcrops, shelters and refugia, as well as food – in a relatively small area (Bailey et al., 2011). The distribution of active landscapes can be mapped using measures of ‘roughness’, the simplest of which involves taking the slope of a hillslope map generated from digital elevation model (DEM) data to generate a variable which describes the variability in slopes and thus surface orientations. Roughness is even more closely correlated with hominin site distributions than volcanoes are, especially in South Africa where the landscape is tectonically active but not volcanic.

The TLM is unique in several ways. It allows that choice and behaviour might have been important in hominin evolution and treats landscapes as agents in the evolutionary process after Fletcher's (2004) concept of the built environment as an actor 'without intent' – capable of constraining and influencing humans and with which people must engage to negotiate their use of the environment (Bailey pers. comm.). Perhaps more importantly, however, the TLM is the first to link hominin history not just to temporal changes in environments, but also to their spatial configurations ('landscapes') and changes in these structures. To date, most studies of hominin sites have produced spatially-unresolved environmental parameters (single values or ranges denoting temperature, rainfall, dominant vegetation type etc.) and have largely ignored spatial heterogeneity. The recent publication of *Ardipithecus ramidus*, for example, was accompanied by several contextual papers (White et al., 2009a, White et al., 2009b, Louchart et al., 2009, WoldeGabriel et al., 2009) detailing the pollen, faunal remains and sediments found at the site but without explicit discussion of landscape patterning.

The TLM thus opens up an unexplored area of palaeoanthropology and forms the basis of this thesis, which aims to evaluate King and Bailey's claims. Before a research design can be developed to addres this aim, however, it is necessary to consider the conceptual framework within which the TLM must fit, as this model invokes several ideas – primarily of *landscape* (and environment more generally), but also of *agency* and (by implication in a system which incorporates spatially and temporally variable, interlinked elements and agents which can act in all sorts of ways) *complexity* – which all three require further exploration despite this thesis' overall focus on landscapes. In particular, it remains to be established what impact these ideas have had on palaeoanthropology to date, which has a bearing on the nature and extent of the baseline understanding(s) of key topics available for this thesis to build on. The focus of this chapter is therefore to survey the state-of-the-art in palaeoanthropological research into landscape (and environment), and consider the impacts and formulations of these three key concepts. It begins with a discussion of evolution, the broader theme which links them.

BACKGROUND: EVOLUTIONARY IDEAS AND PALAEOANTHROPOLOGY

Human origins hold particular interest for many people. Lectures and musem displays on our ancestors draw huge crowds, while new hominin fossils regularly occupy the front pages of magazines and journals that rarely feature other species (Harcourt-Smith, 2010). Stone chips and bone fragments which would be discarded were they without anthropocentric connections are instead discussed avidly (Alexander, 1990) and considerable time has been spent generating and defending lists of *Homo sapiens*' defining characters (Cartmill, 1990). For most organisms such description is important only for identification and classification, but for palaeoanthropologists the question of human uniqueness may remain central to subsequent study as well. Special interest is also manifest in academia, where the human past is the subject of three specialist fields (palaeoanthropology, archaeology and history) covering the full range from humanism to 'pure' natural science, while other species' histories fall into just two disciplines (evolutionary biology and palaeontology) with rather less breadth. The hominin fossil record has thus been intensively studied (Western, 1980) and has an almost unparalleled resolution of approximately one fossil find – although many are fragmentary – per millennium of the last four million years (Eckhardt, 2000).

For many, this interest results in part from an inherent desire to understand where we came from, but there are other motivations as well. Interpretations of our evolutionary past have been used to justify attitudes to race, sex and status in recent societies (Gould, 1981) and views presenting warfare, violence, cannibalism and other unpleasant traits as 'inherently human' and 'natural' have held some sway in the public imagination (De Waal, 2005). These views have been hotly contested, but the debates they embody remain subject to intense public scrutiny and ethical discussion. Such claims and their counterarguments continue to have political and social implications and, as narratives which appeal to our sense of story and can slip undetected into social debate (Landau, 1991), have been influential when only weakly supported or even after they have been falsified (Gould, 1981). More biologically oriented research into 'universal' human characters like large brains (Falk, 2007) or bipedalism (Harcourt-Smith, 2007) and more variable genetic or physiological states (like skin colour or lactose tolerance) may also have medical implications (Aiello and Dean, 1990). These studies advance our knowledge of how humans work as organisms (Aiello and Dean, 1990). This combination of inherent interest, relevance to modern concerns, increasingly abundant evidence and incomplete understanding ensures palaeoanthropology remains an active and exciting field of research.

However, palaeoanthropology has only a short history and much remains unknown. The field originated in two key events: the publication of the first functional evolutionary theory (Darwin and Wallace, 1858, and Darwin, 1859, reprinted 1960) and the discovery of the first hominin fossils – of *Homo neanderthalensis* – at about the same time (Henke, 2007). The modern approach, prioritising a view of fossils as once-living organisms forming part of complex ecosystems, rather than as 'missing links' in a chain leading inexorably to modern man, has dominated even less time – since as late as the mid-1940s (Gundling, 2010), when it appeared in parallel with major developments in a range of other neo-modern sciences at the shift between a period of pre-war empirical hypothesis testing and one of analytical and natural philosophical 'systems approaches' to society, ecology and archaeology. The decades since have seen many changes in prevailing paradigms and approaches to human evolution (though none has derailed this central emphasis) and more and more 'uniquely human' characters identified in our nearest relatives *Pan troglodytes* and *P. paniscus* (Russon and Begun, 2004, Lonsdorf et al., 2010). This has led to a shift toward viewing humans as just 'another unique species' with close ties to other animals and subject to many of the same processes (Foley, 1987a); a view which still underlies research today.

The Implications of an Evolutionary Perspective

The shift to a view of hominins as organisms occurred just after World War II (Gundling, 2010), during the solidification of the Modern Synthesis (MS) of evolutionary theory. Palaeoanthropological opinions vary on the impacts and benefits of the MS. Some researchers have claimed it was incorporated wholesale and was responsible for the post-war emphases on unilinealism, anagenesis and gradualism (Tattersall, 2000), while others suggest it had a more subtle impact and that these patterns resulted from the assumptions of researchers themselves rather than the imposition of evolutionary theories (Foley, 2001). It has even been suggested that it was palaeoanthropologists' *failure* to study or use evolutionary theory explicitly – with many instead cherry-picking concepts from the MS based on only a superficial understanding of the complexities involved – that caused these ideas to be so rigorously adopted and adhered to (Foley, 2001). There does, however, seem to be consensus that the MS was instrumental in bringing palaeoanthropological focus around to questions of hominin ecology and environmental context, and in fostering the perspectives described in the previous section (Gundling, 2010), perhaps with added impetus from the rise of popular environmentalism in the 1960s and 1970s following the publication and mass-media dissemination of Carson's *Silent Spring* and similar works (Kroll, 2001). The new evolutionary ideas of the MS, like their older counterparts in the writings of scientists like Lamarck and Saint-Hilaire (McBirney et al., 2009), made explicit reference to environment, typically as a driving force or control on change in lineages, although the precise nature of this environmental role remains the subject of research.

Another, more subtle, influence of an evolutionary perspective lies in the increasing palaeoanthropological recognition that events in our lineage's history are unique and unrepeateable, the result of a complex conjunction of spatio-temporally patterned factors (for example Nikitas and Nikita, 2005). The discussion at the start of this chapter noted that most hypotheses of hominin evolution which invoke changes in environments are focused on temporal change, but the most recent have begun to incorporate spatial elements as well, in parallel with a rise in general research interest in spatial patterning (e.g. Peters and Blumenschine, 1995, King and Bailey, 2006, Petraglia et al., 2009). The most obvious manifestation of this is the emergence of hominin dispersal research, which has taken off recently with the development of spatially-explicit computer simulations like STEPPINGOUT (Mithen and Reed, 2002, Hughes et al., 2007) and the palaeomap-based predictive model of Holmes (2007a, 2007b). Interest in spatial heterogeneity – 'landscape' pattern – has increased the attention paid to the biogeography of hominins (as mentioned above and in work by King and Bailey, 2006, and Kullmer, 2007) and the role of taphonomy in producing observed patterns of hominin findspots (Holmes et al., 2005, 2006). These investigations, although still in their early stages, are potentially important for understanding human evolution, especially as both landscapes (Hanski and Beverton, 1994) and ecological communities (Steele, 1991) are now known to be heterogeneous at a wide range of scales.

The core of the MS, the theory of evolution by natural selection, proposes that organisms' phenotypes interact with their surroundings to determine which individuals in a population will have most success in survival and reproduction (Huneman, 2007). This differs from the views held by pre-evolutionary biologists in the recognition that this was not just a process which removed the less fit and maintained population equilibrium, but one which could drive a population in a new direction when the environment changed. Since the original publication of this theory (Darwin and Wallace, 1858), however, scientists have elaborated the list of conditions for natural selection and in so doing identified evolutionary systems which do not fit this model (Kimura, 1983) or are only partially encompassed within it (Jablonka and Lamb, 2005). Some have argued that *Homo sapiens* is particularly distinctive, with our sophisticated social, cultural and medical systems changing the situation "from the survival of the fittest to the survival of nearly everyone" (Balter, 2005, 234) and moving us beyond the reach of simple context-dependent evolution. More complex models, in which reciprocal environment-lineage links are invoked to explain evolution, are becoming ever more significant, for instance in the elaboration of 'niche construction' views of animal evolution that emphasise organisms' abilities to modify the selective environments of their offspring (Laland et al., 2001, Day et al., 2003). This is especially true where the subjects studied and the methods available for research are necessarily varied and multidisciplinary, as in palaeoanthropology and where particularly culturally invested groups are studied.

DEALING WITH THE HOMININS: CONCEPTS AND APPROACHES

Modern approaches to palaeoanthropology are grounded in several key debates about the identity and characteristics of the hominins, the nature of their interactions with the environment (particularly questions of agency, free will and the impact of behavioural adaptations on evolutionary ecology) and the implications of the choice of method for studying palaeoanthropological problems. As research continues to be shaped by evolutionary models, we are forced also to consider the mutability of species and the space-time 'fuzziness' of species boundaries. Evolution raises non-trivial problems for those studying the method, theory and philosophy of palaeoanthropology that merit consideration during the research design process.

Hominin Taxonomy and Palaeoanthropological Philosophy

Before hominin-landscape relationships can be studied directly or indirectly, a working taxonomy of the group is needed to place limits on the work to be done. The definition of the term 'hominin' determines how fossil specimens are classified and analysed and is important in selecting modern comparisons and theoretical paradigms, which can steer the choice of research method, specific questions, and interpretations of results. The philosophy of palaeoanthropology is actually quite distinct from that employed by other evolutionary and ecological sciences, as human uniqueness may play a central role in determining the theoretical bases, emphases and assumptions of researchers (Foley, 1987a), a situation which although natural, given that the discipline is motivated by a desire to understand our own species, may not be conducive to a balanced exploration of the group's biological character. Here, ways of defining and diagnosing the hominins – and the accompanying theoretical perspectives on our lineage – are therefore summarised and evaluated.

Defining and Diagnosing the Hominins

In modern palaeoanthropological writing, the term *hominin* denotes all taxa more closely related to modern humans than to the African apes (Harrison, 2010). This group constitutes a taxonomic tribe, the Hominini, nested successively within the African ape clade (subfamily Homininae), the 'great ape' group (family Hominidae, with the orang-utans) and the ape group (superfamily Hominoidea, including the hylobatids). This scheme, although common today, is relatively recent in origin and results from increasing recognition of the closeness of the panin-hominin relationship: the alternative, still seen in the literature, is to classify humans and their extinct relatives as a family in their own right with the name 'hominids' (Potts, 1998a), moving all subsequent groups up the taxonomic hierarchy. This model is typically favoured by those who believe that whatever their genetic similarity, panins and hominins remain sufficiently different ecologically and behaviourally to require a family-level separation (Tobias, 2003). This thesis uses the newer scheme, in recognition of the overall similarity between humans and panins.

One of the most fundamental unresolved questions in palaeoanthropology concerns how, in practice, members of the tribe Hominini are defined and distinguished from other hominids. Modern humans are undoubtedly unusual animals (Foley, 1987a) with highly flexible behaviour, language, upright bipedal locomotion, a brain much enlarged relative to other taxa, complex technology, and reduced dentition, all features cited in support of human uniqueness (Foley, 1987a, Aiello and Dean, 1990). Telling humans from non-human apes is simple even in the absence of behavioural data. The hominins, in contrast, are more variable. Early hominins display few if any "human" traits. In addition, many species are represented by incomplete fossils (especially in the earliest periods of hominin evolution) and are thus only partially characterised, and we remain wholly uncertain about the distribution of those distinctive human characters which do not fossilise. Diagnosis of the early hominins therefore rests on an assumption of early morphological differentiation after the hominin-panin split, and there is debate over the status of most early taxa as a result (Senut, 2007). The recent three-volume *Handbook of Paleoanthropology*, for instance, contains three chapters on defining respectively the hominins (called 'hominids' after the old convention), the genus *Homo* and *Homo erectus* specifically (Schwartz, 2007, Collard and Wood, 2007, Antón et al., 2007), as well as two on species concepts and taxonomic practice (Groves, 2007, Ohl, 2007).

This difficulty diagnosing the hominins is not helped by a disparity in definitions. For fossil taxa, only hard tissues – bones and teeth – are preserved. The anatomical definition of *Homo sapiens*, following work by authors like Le Gros Clark (1964), is based on the three functional complexes associated with erect bipedal locomotion, encephalisation and reduced dentition (Aiello and Dean, 1990). The latter two, unfortunately, do not appear until late in hominin history (Aiello and Dean, 1990), making them irrelevant for defining the hominins. Instead, palaeoanthropologists typically rely primarily on traits associated with bipedalism, with sources as diverse as popular science books (Johanson and Edey, 1981), scientific reference sources (Schwartz, 2007) and technical papers (Haile-Selassie et al., 2004) all relying on locomotor features to define the hominins. This tradition of employing bony characters linked to locomotion to define hominins is reminiscent of an eighteenth century definition of modern humans developed by Blumenbach (1795, as cited in Schwartz, 2007) that relied on the pelvic girdle and foot and of classical notions of man as a featherless biped (Cassidy, 1967).

The signature of bipedal locomotion is postcranial. Certain cranial features (like the orientation of the foramen magnum) *can* be indicative, but the emphasis on postcranial traits means that species like *Sahelanthropus tchadensis*, known only from cranial remains (Brunet et al., 2002, 2005), are harder to definitively classify (Harcourt-Smith, 2007). This is further complicated by the fact that the trait complex associated with bipedalism is highly complex, so fossils cannot be classified by the presence or absence of bipedal locomotion (Haile-Selassie et al., 2004). Instead, the number and predominance of bipedal adaptations increases from the origin of hominins to humans, with the former having only a few bipedal traits and likely to only occasionally engage in bipedalism (Senut, 2007) while the latter are obligate bipeds (Harcourt-Smith, 2007). The australopiths show a mosaic of adaptations to bipedalism and other (arboreal) locomotor strategies (Harcourt-Smith and Aiello, 2004) and are sometimes classed as habitual bipeds in terms of overall adaptation (Harcourt-Smith, 2007). Some bipedal characteristics, though, are arguably present in even the earliest putative hominin taxa, *Sahelanthropus tchadensis* (Brunet et al., 2002, 2005), *Orrorrin tugenesis* (Senut et al., 2001, Pickford et al., 2002) and *Ardipithecus ramidus* (Lovejoy et al., 2009c), having been used to classify all these taxa. The validity of this definition, especially given the recent discovery of *Oreopithecus bambolii*, an apparently bipedal non-hominin ape found in upper Miocene deposits in Tuscany and Sardinia (Kohler and Moya-Sola, 1997), is uncertain, but it remains our 'best guess' approach to classifying potential hominins.

Palaeoanthropological Philosophy: Are Hominins "Humans" or Animals?

Despite uncertainty over the precise characters defining humans and hominins, taxonomists have recognised the similarities between humans and the non-human apes for as long as these species have been known. Carl von Linné's *Systema Naturae* (1735, as described in Huxley, 1863) grouped humans and chimpanzees in a single genus, as *Homo sapiens* and *Homo troglodytes*. The first book specifically to treat humans in a (Darwinian) evolutionary framework, Huxley's *Evidence as to Man's Place in Nature*, identifies the first source on the "man-like apes" as a 1598 book derived from the sailor Eduardo Lopez' notes on the Congo, while the first reliable evidence is attributed to the writings of Andrew Battell in the early 17th century (Huxley, 1863). By the later 19th century, however, the implications of an evolutionary perspective were widely known and many scientists either denied the resemblance between humans and non-human apes or invoked some feature which set them apart despite anatomical similarity, like an immortal soul or the powers of reason and rationality (Corbey, 2005). This tendency to delineate "humans" from "animals", and the increasing recognition that there were several, superficially similar, species of non-human ape, led to these (chimpanzee, bonobo, gorilla and orang-utan) being placed in one family, the Pongidae, while humans went into Hominidae (Corbey, 2005). While genetic advances have since rearranged this phylogeny by moving humans into the African ape clade, the genetic difference between chimpanzees and humans (1.6%) remains less than between other pairs of sister species, like the hylobatids, placed within the same genus (Diamond, 1992).

Genetic similarities notwithstanding, there are clear differences between humans and other apes, primarily related to cognition, culture, language, locomotion and dentition (Foley, 1987a). Human behaviour is therefore placed within the social sciences in recognition of this difference, while animal behaviour is studied within the biological sciences as zoology, ecology or ethnology. Even the most biologically based of the anthropocentric disciplines concerned with behaviour therefore has close ties to social science and humanities research, and anthropology thus has a theoretical structure, philosophy, history and literature that is notably different in focus and style from those of the fields concerned with comparable studies of other apes. Palaeoanthropological and primatological studies are therefore not always comparable (or compatible) and certain questions – for instance about how 'special' humans really are – may not be addressed due to restrictions on the nature and scope of comparisons with other animals.

Corbey (2005) suggests that these differences between anthropocentric and non-human ape focused research result from these groups inhabiting different sides of a "human-animal boundary". This boundary is clearly defined when it comes to ethical and other perspectives concerning extant taxa (with humans typically occupying one side of the dichotomy and all other organisms the other, Diamond, 1992). It becomes much more complex when extinct hominins are included. Our lineage forms a continuum from the last common ancestor of hominins and panins (which most agree would fall among the animals) and modern humans which are by definition human. Any human-animal divide must thus separate a continuum into discrete groups, and researchers differ in their delineation of these classes. For some, hominins are not "human" until the emergence of modern behavioural patterns like language and art about forty thousand years ago (40Ka) (Diamond, 1992). Others argue that mid/late Pleistocene hominins like *Homo erectus* and later large-bodied large-brained species are too humanlike to be classed as "mere" animals. Many discussions of *Homo erectus*' dispersal out of Africa 1.8 million years ago (1.8Ma), for instance, centre upon that taxon's humanlike culture, anatomy and behaviour to explain its global expansion as the result of a cultural release from ecological/environmental constraints (Dennell and Roebroeks, 2005).

Whether the hominins, or specific hominin taxa, should be treated as "humans" (with human science paradigms) or "animals" (via biological perspectives) is thus largely decided by the judgement of individual scholars and may vary between studies. There are, however, some general patterns in the treatment of species successively more closely related to humans. Rees (2009) notes, for example, that the anthropological influence on early primatologists (especially in the USA) has led many modern researchers to justify their work through its relevance to understanding humans, and that this may lead to their methods, assumptions and standards differing from those of other biologists. Even the earliest hominins are typically grouped by palaeoanthropologists as closer to, and more informative about, humans than the non-human apes (Corbey, 2005). The hominins are usually assumed to be more complex cognitively and behaviourally and less subject to external controls on population, biogeography and dispersal than other apes. When specific elements of these assumptions are disproven, moreover, explanations of human "uniqueness" are modified or complexified rather than being discarded. The original justification for the inclusion of *Homo habilis* in that genus, for example, was its apparently unique use of tools. Despite more recent discoveries of tool-use in other hominins and hominoids, scientists have not reversed this judgement but have been led to re-define "human" or "sophisticated" tool use in ways that are then used to justify the taxon's status in place of the original evaluation (Corbey, 2005).

The feature most commonly associated with the human side of the animal-human boundary is the possession of complex culture. Stone tools emerged about 2.6Ma (Semaw et al., 2003), although earlier authors believed they had appeared at the emergence of *Homo* about 2-2.3Ma (Foley, 1987b). From this point onwards, the archaeological record is extensive and cultural studies of hominins begin to compete with palaeoanthropological ones for explanatory power. Even before they made stone tools, the hominins were probably relatively intelligent and behaviourally flexible taxa with the capacity to modify their environments (Laland et al., 2001), and may have engaged in cultural niche construction (Laland et al., 2000); they may also have been influenced by gene-culture co-evolution as a result (Laland et al., 2001). In many implicit models of hominin evolution, later taxa cease to adapt to new challenges morphologically and physiologically and, instead, absorb change through modifications to behaviour and culture. So ingrained has this model become that there have recently been several apparently controversial papers questioning whether *Homo sapiens* is actually evolving at all in the traditional sense (Balter, 2005). Simultaneously, evidence for tool use in non-human apes and monkeys, and recognition of the impact of predation, competition and environmental change on modern humans is accumulating. This suggests that a more balanced, less anthropocentric view of our evolution (in which human "uniqueness" is not assumed but allowed to emerge – or not – as the evidence dictates) might be more productive for understanding hominin history. This is the perspective which is adopted here, and requires that the evidence for a role for agency, choice and cognitive or cultural strategies for dealing with environments are explicitly evaluated in each case study.

Agents and Actors: The Importance of Choice and Cognition

The above summary of hominins' intermediate position between apes and humans raises an additional question for palaeoanthropology: how much should be made of cognitive capacity? Modern archaeology recognises humans as *agents*, capable of making choices and actively changing their interactions with other humans, animals and environments, although specific definitions of agency are rare and there have been suggestions that the concept is sometimes over-used (Dobres and Robb, 2000). Much ecological work, in contrast, does not consider agency or "free will" as an important component in behaviour, preferring to consider an individual's actions as linked to ecological rules and predictable behaviour patterns. This conceptualises animal behaviour as at least partially predictable, while humans (and possibly other primates) may choose to act in certain, unpredictable ways. Agency theory was actually developed to counter a deterministic claim in the social sciences (Dornan, 2002), where it was later famously championed by Anthony Giddens (e.g. Giddens, 1979) – with hindsight, we can view this perspective as part of the natural philosophy-dominated processual phase in archaeology when the MS was introduced (see above), while the agency rebuttal is a component of post-processual theory that emerged in response to it. Like many other post-processual ideas, this one emphasises the social construction of present and past, and the importance of cognition.

Bailey and King's tectonic hypothesis implicitly adds another layer of complexity to palaeoanthropological studies of environment (Bailey pers. comm.). By framing their hypothesis within a framework which explicitly recognises hominin habitat *choice* as a key factor in the lineage's evolution (King and Bailey, 2006, Bailey et al., 2011), this model incorporates agency and sees hominins as capable of structuring their interactions with the environment. Agents are also typically conceived of as having a history which impacts their actions, and are thus situated in a spatiotemporal context in a way which mimics the view of lineages held by evolutionary biologists. This view, in which agents undergo historically constrained, *a priori* unpredictable and socially meaningful interactions with their environments has led Fletcher (1995, 2004) to propose that the material world can itself be thought of as an actor in this dialectic, constrained by its own history and acting to steer/constrain/facilitate human activity. The idea that individuals must engage with their surroundings to negotiate their way of life almost certainly also applies to cognitively complex hominins and potentially the non-human apes or other species too. Landscapes fulfil the requirements of agency in that they can be socially meaningful in a variety of ways, although unlike organismal agents they do not have intent or choice; they are a different type of agent, rather than a passive backdrop to hominin agency. This perspective, under which both hominins and their landscapes are agents (the former potentially with foresight and intent, the latter without), which may co-evolve with one another, provides another piece in a conceptual framework for the integrative analysis of landscape proposed above. The next step is to explore the analytical strategies available for this type of interdisciplinary, integrative, problem-driven research.

Analytical Approaches to Hominin-Environment Interaction

Palaeoanthropological investigations of environment require information on both the abiotic and the biotic components of hominin contexts. For some authors, this involves research in two distinct fields, palaeoecology (which focuses on the biotic, i.e. community structure and interactions between organisms, although this arguably cannot provide a complete picture of ecology in isolation) and palaeoenvironmental science (which typically emphasises abiotic climate and geology, supplemented with information about palaeovegetation). The two disciplines thus overlap and for the purposes of this thesis, a broad definition of 'environment' as including both biotic and abiotic components will be used. In palaeoanthropological research on the environment, three major research strategies can be identified which might produce information relevant to landscape research and the evaluation of King and Bailey's hypothesis:

- Direct studies of fossils and palaeoenvironmental records;
- Indirect environmental modelling, potentially drawing upon specific hypotheses of the hominin-environment relationship, and;
- Comparative work on extant species (like primates and humans).

Each strategy has its own advantages and disadvantages, which are discussed below.

Direct Palaeoecological and Palaeoenvironmental Reconstruction

Direct evidence for ecology and environment comes primarily from fossils and sedimentary records and may be extracted and analysed in several ways. Faunal assemblages are a well-known source of evidence, and although they never represent straightforward samples of past communities (Bennington and Bambach, 1996) are a key source of evidence on their structure (Reed, 1997, Bobe et al., 2002). Individual specimens' ecological niches may be reconstructed through assumptions of taxonomic uniformitarianism (using data on extant relatives to attribute characters to extinct species, Dodd and Stanton, 1990) or via analysis of adaptations (Kappelman et al., 1997), with or without taxonomic attribution. Analyses of the niches reconstructed for all or most specimens in a sample (Behrensmeyer et al., 2007) may be used to reconstruct communities and identify mixed assemblages, although the exact performance of these techniques remains uncertain (Reed, 1998, Rogers, 2000, Sponheimer et al., 2001) and we cannot be certain of taxonomy, attribution, or the validity of either anatomical interpretations or ecological comparisons (Reed, 1998). The same methods can also be used to reconstruct broader habitats and the basic trophic structure and character of communities (Fleming, 1973). Alternatively, analyses can focus at the multi-assemblage level, summarising diversity within a sample of sites (Rose, 1981), relating diversity to evolutionary patterns and environments (McKee, 2001), or using quantitative methods to compare samples (Simpson, 1960, Evans et al., 1981). Whether the assumptions used in interpreting patterns hold and whether modern comparisons are correctly chosen remains unclear, however, and such techniques sacrifice some detail in favour of quicker analysis and quantitative rather than qualitative techniques (Avery, 2007).

Palaeoanthropological reconstructions of environment have typically focused on geology, climate and vegetation. Geology is typically reconstructed to provide a taphonomic and sedimentary context for sites (Kullmer, 2007) rather than a picture of past topographies, or as a means of reconstructing the stratigraphic relationships between levels, finds and sites. Where geological studies are given with find reports, they typically serve to orient the reader and provide a background context for the fossil in these terms (e.g. Patterson et al., 1970, Vignaud et al., 2002, WoldeGabriel et al., 2009, Dirks et al., 2010). Sadly, work on specific palaeolandscape reconstruction has been sparse as it is hard to reconstruct small scales in the African Rift and this has put researchers off even where it is possible (Bailey et al., 2011).

The key direct evidence for climate comes from isotopic records. Various biological and physical processes preferentially incorporate specific isotopes of certain elements into sediments, and measuring their ratios can therefore inform on the state of those processes. Carbon and oxygen isotopes are fractionated during evaporation, condensation and freezing, while nitrogen and carbon can be informative about their respective nutrient cycles (Lee-Thorp and Sponheimer, 2007). This can provide data on vegetation, like the proportions of C_3 and C_4 plants at a site or in the diet of an organism (Cerling, 1992, Sponheimer and Lee-Thorp, 2007, Sponheimer and Dufour, 2009, Bocherens, 2009), or on climatic changes at various scales including the global long-term records from marine sediments and ice core samples (Lee-Thorp and Sponheimer, 2007). Additional information on vegetation can come from the direct study of plant macrofossils, which are relatively rare but informative (Birks and Birks, 2000), pollen and phytoliths, although these latter sources are both particularly influenced by problems associated with long-distance transport of remains (Sugita, 2007). Overall, the direct reconstruction of past conditions has the major advantage of exploiting any evidence which remains from that period, but suffers from problems of scale (Kingston, 2007), time-averaging (Fürsich and Aberhan, 1990), spatial mixing (Goodwin et al., 2004) and low resolution from the action of taphonomic processes (Kidwell and Flessa, 1996). In the absence of a substantial body of comparative research on palaeolandscapes which might be used to mitigate or at least identify these effects, attempts to directly reconstruct past conditions are likely to provide only partial success here.

Indirect Reconstruction (Modelling) of Past Conditions

In addition to reconstructions based on direct data, researchers are now beginning to model palaeoclimates and palaeoenvironments mathematically (e.g. Mithen and Reed, 2002, Holmes, 2007a, 2007b, Hughes et al., 2007). These models work on the same lines as models of current and future climates and environments, and may include a palaeoanthropological component that models hominin response to environmental patterning, for instance in the use of static frames from the PRISM2 Pliocene mapping project to drive a dispersal model in a geographical information system or GIS (Holmes, 2007a, Holmes, 2007b). More commonly, however, they simply model environments and their change through time, with some focusing on a single environmental component like climate (Haywood et al., 2000) and others coupling in models of other variables, like vegetation and/or ocean conditions (Haywood and Valdes, 2006). These models typically rely on direct palaeoenvironmental or environmental data to provide calibration and check results, making them subject to the same constraints as discussed in the section above plus others like limitations on resolution and increased uncertainty of local conditions introduced by the modelling process. They may be constructed at the regional (Sugita, 2007) or global scale (Haywood and Valdes, 2006, Salzmann et al., 2008), and are often sensitive both to the choice of initial conditions and the techniques employed to drive the model. In addition, constructing a model is a specialised process and must necessarily omit certain variables and make certain assumptions about patterns and processes of interest. Modelling is thus not a particularly attractive choice for the initial stages of an exploratory investigation of a potentially complex problem, like the research advocated in this thesis.

Comparative Approaches to Hominin-Environment Interactions

The final alternative is the comparative approach, i.e. studying other species to shed light on the hominins. Comparative data is important to palaeoanthropologists for several reasons. In living species characters not preserved in fossils, like life history features and physiology, can be studied and used to elucidate general rules about relationships between traits that can be tested for or extrapolated to fossils; analogous species can be sought, and a "baseline" for understanding our ancestors established (Harvey and Pagel, 1991, Nunn, 2011). Without a proper understanding of how modern animals work, as physiological and anatomical wholes, we cannot hope to extrapolate from sparse data how extinct ones functioned. Comparisons are also widely used in the development of taxonomies (Cosans and Frampton, 2001). This wide use ensures that even where a given study is not explicitly comparative itself, it will often cite comparative data in justifying and characterising interpretations of fossils. Previous explicitly comparative studies of the hominins have generally focused on one of two groups. Humans and the large non-human apes (*Pan*, *Gorilla* and *Pongo*) are the closest living relatives of the hominins, and are chosen for analysis by many as a means of characterising points which (presumably) bracket them (Corbey, 2005 and see above). Alternatively, some prefer to focus on potential *ecological* analogues for the hominins, with the best known being Jolly's "seed eater" model, based on baboons (Jolly, 1970, 2001). Other comparisons are drawn from across the primates (Elton, 2006) and beyond, with some studies for instance looking at the carnivore guild as a means of assessing hominin hunting and meat eating (Brantingham, 1998, Lewis and Werdelin, 2007). Comparative studies benefit from their disciplinary breadth and a wealth of existing data from other disciplines. Their drawbacks include a lack of *direct* data on the hominins, and the fact that we cannot always know how to select suitable comparators or analogues for particular projects.

For the purposes of this thesis, however, the identified lack of basic, broad knowledge of hominin interactions with spatially structured environments which could contextualise a study using the direct or indirect reconstructive approaches described above suggests that the comparative method, with judicious selection of comparators, is likely to be the most profitable approach. To develop a baseline understanding of primate-landscape interactions the papionins – which are well-known, may be ecologically analogous to the hominins, and occupy complex, tectonically active landscapes in areas where hominin finds abound – seem a logical first choice. Modern humans, the hominins' closest living relatives, are however probably a better choice for evaluating the role of agency and cultural 'buffering' against changes in external conditions, and will therefore also be included. Further comparisons, for example to evaluate King and Bailey's claim that tectonic landscapes offer hominins advantages over predators and prey species, will be selected and justified in the relevant chapters on the basis of individual groups' ecology and evidence from the fossil record. To accommodate the fact that each individual comparison is subject to bias and – potentially – inappropriate choice of comparators, the initial primate case studies will draw on two separate lines of evidence which can be cross-checked. Biogeography, or specifically the distribution of sites or species, has already been identified by King and Bailey (2006) as potentially informative. It will be supplemented by data from anatomical studies. Anatomy is chosen because it seems likely to show an influence from the environment – and potentially from landscape structures like 'rough' topographies – and because the preservation of hard tissues in the fossil record of the hominins suggests that, if it does prove informative, the results might be directly extrapolated to and tested on the hominins. Before this is begun, however, we need to establish how to deal with 'landscape' and increasingly complex models of human evolution within a comparative framework.

DEALING WITH EVOLUTIONARY AND ENVIRONMENTAL COMPLEXITY

The three approaches to palaeoanthropological studies of environment described above represent three different attempts to deal with problems of taxonomy, philosophy, cognition and complexity, and each intuitively recognise the fact that evolutionary systems (as described above) are ‘complex’ and may be difficult to simplify. In palaeoanthropology, researchers are constantly aware that their data do not conform to the ‘ideal’; taphonomic biases, gaps in the evidence and the assumptions required to deal with imperfect sources all combine to introduce error and uncertainty. There is, however, a tendency to assume that if all these biases or problems could somehow be mitigated, underneath it all there *would* be an ideal situation, in which data were available, complete and fully interpretable in their own right and problems which are traditionally dealt through simplification, exaggeration or ‘black box’ approaches would be transparent and directly accessible to logic. If the evolutionary system is genuinely complex, however (as suggested above), this may not be the case and facing up to these simplifications not just as ‘necessities’ imposed by the practicalities of the data but as analytical strategies which might influence the results we obtain becomes important.

Complexity is a concept which many people understand intuitively, but which often proves difficult to define (Gell-Mann, 1994, 27-28). There is, however, a rather old-fashioned understanding of complexity which is useful for this thesis – the idea that complexity is a state of spatial, temporal and ontological *ill-boundedness* accompanined by *logical incoherence*. This idea has a long history. The “one long argument” of Darwin’s *Origin* (Darwin, 1859, reprinted 1960, 426) is essentially that taxonomic categories are complex, i.e. ill-bounded, and come into and out of focus, even switching from species to other categories (subspecies or genera, for instance) as one moves from one space-time scale to another. This means that a category, for instance of ‘Galapagos finch’, is only meaningful at a specific space-time scale. This ill-boundedness creates an inconsistency between what can be known – or defined – about an evolutionary system *a priori* and what can be attributed to it *a posteriori*, specifically in Darwin’s recognition that while a species is clearly a species *today* (after the fact), before the speciation event which defined that species it would be impossible not only to describe it but also to infer the ontological boundaries around it (Darwin, 1859, reprinted 1960).

A more abstract version of the ill-boundedness concept of complexity is provided by Bertrand Russell in his work on set theory (Russell, 1959). A set is a defined group of objects, and any set – for instance, the ‘hominins’ – might reasonably be supposed to have a complement, or a set which comprises things which are ‘not hominins’. Sets, however, can represent groups of concrete things *and* groups of concepts – like the concept of a ‘set’ itself. This leads to a paradox as a complementary set must include the original set of objects. The set of things that are ‘not hominins’, for instance, must include the set of hominins, as this is a set and not a hominin. Russell showed that attempts to close a universe of discourse like this invariably generated logical paradoxes. One of the simplest of these is the barber paradox: if we characterise the barber as the man who shaves every man in the village who doesn’t shave himself, then it is impossible to decide who shaves the barber without engendering a logical contradiction. If the barber shaves himself, the definition is false. If the barber does not shave himself, the definition is false. The complementary set of men who do not shave themselves generates a paradox. The barber paradox deals with a special or local complement. More intractable paradoxes arise when we start to work with universal complements (the set of every non-hominin, for example).

The barber paradox can be resolved either by finding another definition of a barber, or by accepting that the set of men in the village who shave themselves is complex. It is possible to make logically coherent statements about the set of men who shave themselves, but not about the set of people who do not, just as it is possible to make logically coherent claims about the hominins but not about things that are 'not hominins' (which poses problems, for instance, for approaches to hominin evolution which emphasise contrasts to explain human uniqueness). According to this definition, evolutionary systems are irreducibly complex - the boundaries of categories (sets, e.g. species) are not only fuzzy but also changeable. This changeability may occur within a single set of boundary conditions, modifying the interactions within the system, or – under certain circumstances – may result in changes to those boundaries, and a change in the system itself. Speciation, for instance, changes the boundary conditions and thus the system itself, while smaller-scale changes might merely modify the appearance or behaviour of populations. The problem of complexity (and specifically of the ill-boundedness/logical incoherence type of complexity outlined above) is thus one which evolutionary biologists have had to deal with since the *Origin* was published. The strategies adopted have varied, but the three voyaging naturalists (Darwin, Huxley and Wallace) continue to represent the broad spectrum of solutions developed.

A Spectrum of Evolutionary Theories

The Modern Synthesis of evolutionary theory (MS) is referred to as 'neo-Darwinist' because although the initial presentation of natural selection was joint (Darwin and Wallace, 1858), Darwin rapidly became both a better known author – for *On the Origin of Species* (Darwin, 1859, reprinted 1960) and *The Descent of Man* (Darwin, 1872, reprinted 2004) – and a sort of figurehead for evolutionary ideas. The intellectual content of the synthesis, however, actually owes more to Wallace. Wallace considered himself a Darwinist (even going so far as to call his 1889 book 'Darwinism') despite the fact that his ideas differed in some significant respects from those of Darwin himself. In fact, certain modern concepts like punctuated equilibria or epigenetic inheritance (Eldredge and Gould, 1972, Jablonka and Lamb, 2005) which do not fit completely within the MS (Pigliucci and Muller, 2010) actually fit rather better with Darwin's own theories, especially as developed in his later life, than they do with the neo-Darwinian (Wallacean) equivalents. All of the three key early evolutionists – Darwin, Wallace and T.H. Huxley – had different conceptual models of evolution (Table 1), and most current debates can be traced back to their differences.

Table 1: the key characteristics of the evolutionary views of the three voyaging naturalists – Darwin, Huxley and Wallace.

	Darwin	**Wallace**	**Huxley**
Subject(s) of evolution	All organisms	All organisms *save humans*	All organisms
Model basis	Naturalistic	Vitalistic	Naturalistic
State	Disequilibrium (for organisms, but not contexts)	Near-equilibrium	Disequilibrium (for both organisms and contexts)
Pattern	Gradualistic	Gradualistic	Punctuated
Types of inheritance*	Pluralistic: genetic, epigenetic (including Lamarckian), ideational and cultural processes all accepted	Purely genetic	Materialistic: Huxley recognised both genetic and epigenetic processes, but the latter must be physically mediated

*This column uses modern terms, which may not have been in use at the time of the original texts.

As Table 1 shows, their disagreements span several areas. Wallace's model separates mind and body (a vitalistic system) and pertains to near-equilibrium systems in which both abiotic environments and biological systems were stable and changes were gradual and directional. Darwin saw abiotic environments as near to equilibrium but allowed for dynamism in the biological components, describing another gradualistic model but one which allowed for certain rapid environmental changes to cause quick biological turnover, extinction and adaptive radiation. Huxley, in contrast, emphasised disequilibrium dynamics and punctuated equilibrium patterns of evolution. The three also recognised different mechanisms of inheritance. Wallace, with his strict belief in natural selection and longer life – which spanned the period of Mendel's rediscovery in the early twentieth century – accepted only innate (genetic) inheritance (Wallace, 1889). Darwin was pluralistic and accepted a wide range of what we would call genetic, epigenetic, ideational and cultural inheritance mechanisms, which might act independently or in concert (Darwin, 1859, reprinted 1960, Darwin, 1872, reprinted 2004). Huxley, meanwhile, believed that both genetic and epigenetic processes might impact evolution, but did not recognise either ideational influences or the role of alternative agents of evolutionary change and believed that epigenetic processes must be biologically mediated and mechanistic (Huxley, 1879).

These differences are related to the different ways each naturalist dealt with complexity, a phenomenon they recognised to varying degrees. Wallace's vitalism and differing treatment of bodies and minds resulted in his proposing what we would call a 'god of the gaps' – a creator-agent beyond the natural rules who can be invoked to explain logically incoherent and complex problems. In *Darwinism*, Wallace states that:

> "[In] the case of man's intellectual and moral nature I propose to show that certain definite portions of it could not have been developed by variation and natural selection alone, and that, therefore, some other influence, law, or agency is required to account for them".
>
> Wallace (1889, 463-464).

He went even further in *The World of Life*, stating explicitly that "beyond all the phenomena of nature and their immediate cause and laws there is Mind and Purpose; and that the ultimate purpose is (so far as we can discern) the development of mankind for an enduring spiritual existence" (Wallace, 1914, 277-278). Huxley, in contrast, rejected the god argument and highlighted the role of empirical observation in resolving problems which are not accessible to logic. One of Huxley's most famous quotations is probably his definition of the "great tragedy of Science - the slaying of a beautiful hypothesis by an ugly fact - which is so constantly being enacted under the eyes of philosophers" (Huxley, 1870, no pagination), but he elaborated his position as follows:

> "[A]s to the logical consequences of this conviction of mine, I may be permitted to remark that logical consequences are the scarecrows of fools and the beacons of wise men. The only question which any wise man can ask himself, and which any honest man will ask himself, is whether a doctrine is true or false. Consequences will take care of themselves; at most their importance can only justify us in testing with extra care the reasoning process from which they result."
>
> Huxley (1874, no pagination).

Darwin, as usual, fitted between these two extremes of the spectrum, recognising complexity but advocating acceptance rather than a specific resolution of the associated problems – he believed that certain problems were logically inaccessible and certain categories could be bounded only at specific space-time scales, and that this was simply something the naturalist had to deal with – usually on a case-by-case basis – in the course of their work. Darwin wrote that:

> "[i]n short, we shall have to treat species in the same manner as those naturalists treat genera, who admit that genera are merely artificial combinations made for convenience. This may not be a cheering prospect; but we shall at least be free from the vain search for the undiscovered and undiscoverable essence of the term species."
>
> Darwin (1859, reprinted 1960, 447).

The MS reflects Darwin and Wallace's gradualism and incorporates Wallace's strict focus on near-equilibrium dynamics throughout the evolutionary system, as well as his proposal that natural selection was the only agent of change (Darwin preferred to recognise multiple processes). This was fused with Mendel's work on inheritance to produce a 'complete' evolutionary theory (Pigliucci, 2007), while other ideas from Darwin and Huxley formed an alternative in which both innate (genetic) and acquired (epigenetic) changes could be important – the MS recognised only innate change – and complex, non-reducible disequilibrium dynamics were expected. This paradigm deals more explicitly with logically incoherent, ill-bounded species than does the MS – which tends to assume that categories can relatively easily be simplified for scientific treatment. The MS, however, has remained the dominant paradigm despite calls for its extension to incorporate recent work on evolvability, phenotypic plasticity and development, epigenetic inheritance, complexity theory, genomics and highly-dimensional adaptive landscapes, among other ideas (Pigliucci, 2007, Carroll, 2008, Koonin, 2009) – calls which reflect a shift of opinion towards the Darwin-Huxley model and a broader conceptualisation of the evolutionary process (Pigliucci and Muller, 2010). Some envision this shift as requiring an incorporation of 'new' ideas without a major restructuring of the synthesis, while others propose a more complete reformulation of evolutionary theory (Arthur, 2002, 2004). For the purposes of this thesis, moreover, while Wallace's approach to evolutionary complexity and logical incoherence is unsuitable (as it effectively prevents any attempt to understand complex hominin landscapes), either Darwin's or Huxley's would be appropriate. The trick, and the focus within this text, is therefore to attempt to find means of simplifying 'complex' landscape system like that invoked by the tectonic landscape model which lay it open to empirical analysis (Huxley's stratagem) while remaining aware of the limitations imposed by those simplifications and the possibility that the resulting model of the system may not be 'accurate' with regards to reality (after Darwin). In this way, we can hope to improve understanding of the manifestations of this particular complex system while avoiding the pitfall of claiming to have 'the answer' to what is clearly a very complex problem.

Current Perspectives on the Role of Environment

Many current ideas on evolution and ecology can thus be traced to the work of naturalists in the 19th century, though they have been differently developed since. Table 1 provides only a very simplified view, however, and does not capture the multitude of modern understandings of organism/environment relationships that might be palaeoanthropologically relevant. As well as traditional evolutionary theories, these hypotheses may rely on advances in fields like genetics, developmental biology, ethnology, ecology and biochemistry to construct a picture of interaction dynamics that can be invoked in experiment or studies of the fossil record. Often, such models are used implicitly and are not subject to scrutiny in their own right, and while palaeoanthropology may or may not have effectively recognised their diversity, it seldom provides any justification (or even explanation) of those selected. Before palaeoanthropology can expand to effectively deal with the challenges of a spatially (as well as temporally) heterogeneous perspective on hominin environments, therefore, we need to understand more about these modern perspectives and their implementation.

This requires an effective definition of the scope of the term 'environment', which can be used to denote various concepts. The environmental hypotheses of hominin evolution focus mainly on climate and vegetation as key factors, and King and Bailey's model proposes that landscape also be included, but from Darwin onwards evolutionary biologists have recognised the interdependence of environment and ecosystem, and the close, irreducibly complex, relationships between the biotic (including animals as well as plants) and the abiotic. This leads back to the definition of environment already discussed in this thesis, as comprising all elements of an organisms' context, biotic and abiotic (including cultural). This therefore remains the definition used in the current work.

In broad terms, there are three possible conceptualisations of organism/environment relationships. Evolution could be independent of the environmental context, occurring via drift or other random processes. An older perspective, tracing back to Wallacean concepts, identifies environment as a control on evolution – a factor which determines the evolutionary trajectory or restricts the option space available. Finally, the more complex modern models (with links to the Darwin-Huxley synthesis) recognise more complicated organism-environment interactions which give rise to evolutionary trajectories as their emergent (explicably irreducible) and possible logically incoherent results. Each of these sets of processes includes many more nuanced views, may manifest themselves differently at different scales of enquiry and has been handled differently by researchers. In particular, the theory of context-independent evolution is based on theories of evolution in small samples, where stochastic processes and bias or the effects of slight differences in starting points can have significant influences. Wallace's model of evolution as controlled by the environment, in contrast, is a model of near-equilibrium dynamics in statistically robust (but not infinite) populations, while ideas of evolution as a control on context are Darwinistic and complex, and recognise a range of interacting processes at a range of scales.

Evolution in Small Samples: Drift and Neutral Processes

There are several ways populations can evolve without direct influence from their environment. The best known theories are the theory of genetic drift and the closely related model of neutral evolution (in which genes do not always drift but have no selective effect and hence can change independently of the environment). Under drift, selectively neutral genetic changes appear randomly and are fixed or lost according to the mathematical rules of population genetics. These changes may be neutral because they involve 'junk' DNA – non-coding and non-regulatory parts of the genome (Andolfatto, 2005, Bird et al., 2006) or because they simply have no noticeable impact. The genetic alphabet contains more letters than are needed to provide unique codes for individual amino acids, meaning that certain substitutions make no difference to the product. Neutral change may, however, be biased – producing non-random 'innovative' changes to the genome (Stoltzfus, 1999) – for instance where a neutral substitution predisposes the gene to certain future changes. Neutral change is accepted, but not granted a prominent role, by many neo-Darwinists, though other authors (e.g. Kimura, 1983) think it more integral and important.

Drift/neutral change is not the only mechanism for context-independent evolution. Alternatives to purely genetic inheritance – like epigenetic, behavioural and symbolic systems (Jablonka and Lamb, 2005) – may influence both developmental and evolutionary change. Some changes within each of these systems may, of course, be linked to changing environments despite their genetic independence (Jaenisch and Bird, 2003), but some do seem independent. One major epigenetic mechanism is DNA methylation, involved in the 'reprogramming' by adults of genes in gametes to ensure they compete for resources in a certain way (Reik et al., 2001). Fathers reprogram their gametes to grow faster and take more nutrient from the mother, while mothers imprint theirs to counter these trends (Reik et al., 2001). These changes are inherited, but are not linked to environment: the offspring will reprogram his/her gametes to suit their own reproductive strategy, and these seem likely to be largely environmentally independent as they are enacted in utero. It is difficult, however, to prove this conclusively. In humans (and other animals, particularly primates) inheritance may also take the form of (apparently) environmentally independent behavioural and symbolic changes fed back into the genome via genetic assimilation.

Statistical Evolution: Adaptationism and the Role of Environment

Concepts of environment as a control on evolution are ubiquitous and span a spectrum from models which suggest that evolutionary trajectories are determined by the environment (environmental determinism), through to those which simply identify context-dependent natural selection as an important part of evolutionary processes. Environmental determinism has not been widely accepted for some decades, as the idea that natural selection might be able to narrow down the possibilities for an evolving species to just one (Coombes and Barber, 2005) has lost conviction with recent discoveries of the contrainsts other factors – like phylogeny, structure and development, among others – can place on selection and of the creative power of evolutionary processes. Constraints ensure that environment simply cannot produce certain changes in lineages (Gould, 1980), while creative forces like mutation (although themselves selectively neutral) may produce a range of equally adaptive types and thus overwhelm selection or introduce into a population recessive alleles which are hidden by their dominant equivalents. Determinism is now often accepted as disproven.

A softer version of this perspective can be called environmental possibilism and views environment as imposing constraints rather than determining evolutionary outcomes (Reitz and Wing, 2008). This model harks back to pre- and immediately post-Darwinian models which viewed selection not as a creative process but as one which acted to remove poorly adapted individuals. It was particularly well developed in the social sciences, like human geography and anthropology, where environment was seen as a passive backdrop to human activity – acting to place natural limits on possible strategies, but leaving it up to cultural and historical factors to determine which were ultimately selected (Moran, 1990). In many ways, environmental possibilism is the 'default' model for the role of context in evolution; it allows researchers to accept and explore the impacts of other factors but maintains the importance of context and natural selection, albeit more weakly than does adaptationism.

Neo-Darwinian adaptationism also fits this category of model, and overlaps with environmental possibilism, with the key difference that adherents believe natural selection is only minimally constrained by other factors and the majority of morphologies and physiologies can thus only be understood as adaptive reactions to specific contexts (Forber, 2009). Adaptationism as a paradigm is variable. Researchers may use the term differently, with some reserving 'adaptation' as a label for characters demonstrated to be subject to active selection while others use it more generally, making the empirical assumption that until active selection has been disproven, a feature is likely to be adaptive. It may also imply adherence to particular exploratory principles or preferred methodologies (Forber, 2009). Adaptationism has been extensively criticised (see for instance Gould and Lewontin, 1979), but various forms have proven informative and valid in certain settings, and critique typically focuses on the *a priori* use of assumption and the (unknown) frequency with which these settings occur. Overall, adaptationist and possibilist ideas – which in any case blend into one another – are both fairly widely used and form the basis, implicitly or explicitly, for many palaeoanthropological studies.

Complex Evolution: Co-evolution, Niche Construction and Symbiosis

Those dealing with complex evolution, in contrast, view the relationship between organism and environment (which includes other organisms) as much more complex, with interactions and influences flowing both ways. This perspective recognises the intimate connections between the biotic and the abiotic mentioned above and suggests that the outcomes of these interactions may be irreducibly complex and impossible to reduce to simple directional processes. This implies at least the possibility of logical incoherence, whereby we can empirically analyse the results of a process but cannot necessarily reconstruct or understand its causes and the way it works. There are several names for these theories. One of the most famous is the 'Gaia' theory, which likens the Earth (as a coherent whole including abiotic and biotic components) to a living organism, in which the component parts themselves act to regulate the whole and are wholly interdependent for their survival (Lovelock, 1979). The Gaia theory has been criticised for implying that the Earth is 'alive' or sentient in its own right, but is nonetheless popular and has formed the basis for Margulis' model of the symbiotic planet (Margulis, 1998) and other conceptualisations of the evolutionary system which view organisms and environment as complex and interlinked.

In mainstream biology, the concept of 'co-evolution' is another facet of the study of complex evolution. Co-evolution theory at its simplest suggests that changes in one evolutionary lineage can trigger or drive changes in another, for instance where predators and prey, or plants and pollinators, interact (Thompson, 1994). For the hominins, for example, co-evolution with the predator guild has been proposed as an explanation for certain changes in behaviour and biology through the lineage's history (Brantingham, 1998). Co-evolution can also involve cultures, with sociocultural co-evolution (where different societies or cultures co-evolve with one another, through trade or other interactions) and nature-culture co-evolution both widely recognised (Laland et al., 2001). Occasionally, the term 'co-evolution' is also used for phenotypic co-variation, for instance in discussions of the co-evolution of different – usually serially homologous – organs in a single body (e.g. in the discussion of human hands and feet given in Rolian et al., 2010), though this is more usually designated as a developmental rather than an evolutionary process. In this way, the term co-evolution acts as a shorthand for a whole range of processes variously involving interactions between organisms, cultures and environments or different combinations of these components. The nature-culture interaction is a special case of the intimate relationship between the biotic and the abiotic described above.

One particular type of co-evolution, coincident change in an organism and in its abiotic environment, has been given the label "niche construction theory" and developed into a theory of a new mode of inheritance through the modification of environments in which future generations may live (Day et al., 2003). Organisms may modify their environment simply by using up or generating resources, performing specific behaviours, moving things around and various other processes (Laland et al., 1999), many of which do not require active cognitive engagement with environmental modification and are not restricted to humans. Where these capacities are genetic, their expression in the environment introduces a genetic component to that environment which can co-evolve with the lineage and reciprocally influence trait evolution and expression (Donohue, 2009). Such influences can thus act with or against natural selection, driving evolutionary momentum or inertia, the fixation of otherwise deleterious alleles, the persistence of polymorphism where otherwise this would be unlikely, and population maintenance at disequilibrium (Laland et al., 1996).

Niche construction may also be cultural. Most of the processes by which an organism can modify its environment – for instance, through foraging – may have both genetic and cultural (or behavioural) components. In humans, for instance, niche construction has been invoked to explain the origins of social intelligence (Sterelny, 2007), language (Laland et al., 2000), and various other complex behaviours. In addition, human culture gives our species a vastly enhanced capacity for environmental modification – evidenced by *Homo sapiens* being one of just a few species to colonise all the continents and one of the most significant modern agents of environmental change at all scales (Alverson, 2007). Bearing this spectrum of conceptualisations of and interactions between environment and evolution in mind (rather than making *a priori* assumptions about which are most important), and particularly recognising the existence of complex evolution where processes at different scales and in different conceptual ‘systems’ (the genetic, the ecological, the symbolic…) can interact, we can now move on to defining the key term, “landscape”, which underlies subsequent chapters.

CONCEPTS OF “LANDSCAPE”

The final outstanding theoretical issue for this thesis concerns the definition of the term “landscape”. The word is widely used both in academia and among the general public, but has a multitude of meanings. For King and Bailey’s (2006) tectonic landscape model for instance the term landscape implies the three-dimensional structure of the land surface, but for a landscape ecologist the biotic components of the environment might also be included and for a landscape archaeologist what matters is not the physical but the cultural and conceptual. A brief survey of academic definitions of “landscape” is given in Table 2.

Table 2: a summary of the two key approaches to academic landscape study

	‘Natural’ landscape disciplines		**‘Cultural’ landscape disciplines**	
Emphasis	Landscapes are ‘real’ natural entities (independent of people) capable of changing themselves and of driving or responding to changes in human populations		Landscapes are culturally constructed and cannot be understood without recognition of spatially patterned behaviour and peoples’ conceptual maps of the areas in which they live	
Major Subdivisions	Biological	Physical	-	
Minor Subdivisions	-	-	Landscapes as ‘interfaces’	Purely conceptual fields
Examples	Biogeography, landscape ecology	Physical geography, geomorphology	Landscape archaeology, psychology, human geography	Art history, social science

All of these definitions are of relevance to palaeoanthropology. For much of hominin history, species’ dispersals and ecologies were probably shaped primarily by the environment (as suggested by Foley, 2002, and Carto et al., 2009 among others), and these factors remained important in the Middle and Late Pleistocene and Holocene too (Dennell et al., 2011). At the same time, assumptions that Plio-Pleistocene hominins were not to some extent actively modifying their environment seem implausible and cognitive patterns (perceptions and mental maps, for example) may also be relevant to understanding agency and behaviour in the primates (Laland et al., 2001, Willems and Hill, 2009a).

Bollig and Bubenzer (2009) proposed a general definition of a landscape which relied on three main characters, specifically *boundedness*, *integration* and *heterogeneity*. These concepts seem to underlie many of the academic definitions given above. For the physical and biological landscape disciplines – those focused on understanding the shape of the land surface (Hugget, 2003) and its interactions with the biosphere (Renschler et al., 2007) respectively – the dominant concept is one of heterogeneity. In landscape ecology, for instance, landscapes are explicitly defined as heterogeneous habitat mosaics (e.g. Wiens, 1995, 2001, Walsh et al., 1998), while physical geography emphasises land surface structure (Haines-Young and Chopping, 1996). This emphasis may be related to the scientific approaches which dominate the natural landscape fields and particularly to the use of mathematical models (e.g. Fahrig and Paloheimo, 1988, Dunning et al., 1995, Diffendorfer, 1998, Martin and Church, 2004, Elith and Leathwick, 2009). For the cultural landscape disciplines, in contrast, there is more emphasis on concepts of boundedness and integration. A cultural landscape can be thought of as a "material or tangible portion of a natural and cultural environment" (Muir, 1999, xiv), or alternatively as a unit "deliberately expressing a relationship between nature and humans" (Fowler, 2003, 16), both definitions which emphasise the interrelationships between nature and culture (integration) and a landscape as a *unit* (boundedness). In certain cases, concepts of cultural landscapes are even used in an attempt to bring about integration of culture and nature or between different occupants of a given area (see, for example, Fowler, 2003, or Pannell, 2006).

Bollig and Bubenzer's (2009) definition would thus seem to capture the essence of most current academic conceptualisations of landscape, with natural and cultural fields (and indeed different studies within fields) assigning different relative weightings to the three main concepts. However, looked at logically, this definition is not coherent in a sense that would allow analyses of complexity: it combines characteristics that emerge *a posteriori* from empirical studies of landscapes (like ideas of integration and heterogeneity) with those that are assumed *a priori* (boundedness). Ill-boundedness is one of the key characteristics of a complex system as defined in this thesis, and must be accommodated if the aim of opening up new problems and broadening research scope is to be achieved. The assumption of boundedness, therefore, while it may make analysis of certain specific questions easier also restricts access to other problems which cannot be addressed using well-bounded conceptual structures. In an analysis like this one, where the aim is to explore means of dealing explicitly with the complexity inherent in evolutionary systems, relaxing this assumption of boundedness is therefore a necessity. In addition, while many of these academic landscape disciplines *do* recognise the problem of scale and resolution, they tend to deal with it by parcelling fields up into subfields that apply specific methods and theories to all problems at the same space-time scale. For instance, biogeography is subdivided into three scale-defined subfields – historical biogeography, ecological biogeography and an intermediate scale of glacial-interglacial cycles (Avise, 2004), while Summerfield (2005) notes that entirely different paradigms prevail in small and large scale geomorphology. This approach ignores the complexity of scale-dependence in evolutionary systems by dealing with it again through *a priori* assumption rather than *a* *posteriori* following evaluations of the specifics of the problem and the scale of relevance. For this thesis, then, the term 'landscape' will denote spatially-structured environments containing (and composed of) a range of biotic and abiotic components which are interlinked but arrayed heterogeneously and are viewed through a 'lens' or 'filter' of cultural influences. These landscapes are probably structurally complex and dynamic in their own right (though this needs to be confirmed), and engage as 'agents without intent' in various interactions with primates. The distinct term 'physical landscape' will be retained for the topographic and land-surface concept of King and Bailey's tectonic landscape model (King and Bailey, 2006).

CONCLUSIONS: RESEARCH STRATEGY IN THIS THESIS

Most work on hominin environments to date has taken place within a 'neo-Darwinian' (Wallacean) statistical evolution paradigm, which does not recognise complexity in the sense of ill-boundedness and logical incoherence and may or may not be able to cope effectively with agency. The literature survey above, however, suggests that all three of the TLMs concepts of *landscape*, *agency* and *complexity* can be accommodated within modern evolutionary paradigms, even though they are rare – and even rarer in combination – in palaeoanthropology. This suggests that this thesis' key aim of **evaluating King and Bailey's suggestion that landscapes – and particularly the configurations of the land surfaces (topographies) associated with tectonically active regions – have played a key role in human evolution** can be addressed using a combination of existing conceptual frameworks from biology, complexity science, social science and archaeology. The fact that these concepts have not been employed together has, however, meant that we have little direct background knowledge of relevant landscape structures and their interactions with primates, and cannot yet judge the viability of different strategies for testing the TLM. In particular, it is not clear whether answers are likely to be scale-dependent or generalizable, and whether we can hope to access the problem of topography in the first place. The first priority of this thesis is therefore to fill in this knowledge gap by:

1. Mapping extant African landscapes and exploring the patterns visible at different scales and their implications for the interactions between different components (thus establishing whether there are correlations between factors like climate, vegetation and topography and how far we might hope to go in untangling their impacts on hominins and other primates), **Chapter Three**;
2. Exploring the relationships between primate anatomy, ecology and landscape via a series of case studies of *Papio* baboons focusing at different scales and on different lines of evidence, specifically the biogeographic distributions of different baboon groups and their locomotor anatomy (thus developing a baseline understanding of

primate-landscape interactions in a possible ecological analogue for the hominins), **Chapter Four**, and;

3. Evaluating the role of complex cognition and agency in modifying human-landscape interactions through two case studies, one of the type(s) of landscapes exploited by hominins and their biogeography (to see if they show preferences for or even are restricted to certain areas) and one of the links between anatomy and landscape (to establish whether humans are after all influenced by external conditions and traditional evolutionary processes), **Chapter Five**;

The results of these analyses will then inform the scope and structure of **Chapter Six**, which will focus on objective four:

4. Generating and testing a hypothesis of human evolution, the ‘complex topography hypothesis’, based on the TLM using appropriate comparisons and analyses.

This final objective thus brings the focus of the thesis back to that originally set out in the aim.

The outcomes of this progressive build-up of analyses and the specific tests in Chapter Six in particular may have relevance for three major areas of palaeoanthropology, specifically through (a) theory development, both at the specific level of developing and evaluating a new theory of human evolution and (potentially) at the broader level in beginning to establish, for example, how important agency is to primate evolution and how landscapes and organisms interact; (b) methodology (in assessing the utility of the exploratory, comparative and interdisciplinary approach required to look at ecology-anatomy-landscape interactions and the role of agency) and (c) data, via the contribution of specific knowledge of the morphology and structure of African landscapes and the areas associated with *Papio* baboons, modern humans and hominins. Later chapters, and especially **Chapter Seven**, will return to these objectives and possibilities to see what progress has been made in addressing the overarching aim discussed.

Chapter Two: Materials and Methods

INTRODUCTION

This thesis, as Chapter One described, takes a broadly comparative approach to the question of hominin interactions with landscape and the potential of the TLM. The precise methods chosen fall into two groups, related to the use of biogeographical data (maps of landscape structures and species distributions) and anatomical evidence respectively. This chapter describes and develops these two methods.

The **biogeographical analyses** will use GIS techniques to identify patterns in landscape structures (including relevant cultural components) and explore the relationships between these patterns and the distributions of living *Papio* baboons and modern (i.e. present day or recent) *Homo sapiens*. Biogeography may be academically marginal (Avise, 2004), but it provides a perspective on evolutionary ecology which has no parallels in other approaches, especially for extinct organisms (MacDonald, 2006). There is already an extensive literature on primate biogeography (reviewed in Lehman and Fleagle, 2006a) which spans a range of scales and variables, while hominin distributions have also been studied biogeographically (for instance by Bromage and Schrenk, 1995, Strait and Wood, 1999, MacDonald, 2006, Marwick, 2009, and van der Made, 2011, among others), often using phylogeographic methods. Here, this focus is expanded to explicitly consider spatial structure in environments and explore links across scales, in accordance with the objectives outlined in Chapter One.

A**natomical analyses**, in contrast, are a mainstay of palaeoanthropology and medicine (Aiello and Dean, 1990). We know already that environment is just one influence on adult morphology (Macho, 2007), especially where complex morphological structures are concerned (Atchley and Hall, 1991). They don't come much more complex than the foot, the primary organ to interact with the landscape (particularly topography) in humans and hominins and therefore the structure chosen for detailed analysis here. The foot of *Homo sapiens* has no less than 26 bones and a correspondingly large number of joints, intrinsic and extrinsic muscles and ligaments (D'Aout and Aerts, 2008). Analyses of the interplay of various landscape components, and their influence on foot anatomy among living species will be used in establishing a baseline on baboon-landscape interactions and in exploring the scope and nature of biological effects of landscape choice in humans. The specific implications of these chosen approaches for choice of method, data, sampling strategy and analytical tools are the focus of this chapter. It begins with a discussion of the background principles and paradigms of each approach.

METHODOLOGICAL BACKGROUND: PRINCIPLES AND PARADIGMS

Although there has been less work on primate landscapes than on other aspects of these creatures' reliance on and interaction with the environment, and more on the general anatomy of the foot than on the influence of landscape specifically, understanding existing work on hominins and other species will be critical to the success of this thesis. This section therefore summarises the state of play in these disciplines.

Biogeography and Environmental Patterning

Foley (1987a, xx) identified palaeoanthropology's key aim as being to "locat[e] human origins in time and space" by "specifying the type of environment, both natural and social, in which the benefits of being human outweighed the costs". Understanding hominin distributions and their ecological meaning is thus important (as also argued by MacDonald, 2006). Spatial patterns are, however, typically only studied at large scales, with studies of dispersal within Africa (Bromage and Schrenk, 1995, Strait and Wood, 1999) less common than those focusing on intercontinental movement (Finlayson, 2005, Marwick, 2009, Dennell, 2004). Spatial heterogeneity is thus usually considered only at the scale of 'major features' like coastlines, land bridges, the Nile Delta and the Himalayas (as, for example, in Holmes, 2007a, which presents a predictive model of dispersal, and various dispersal models by Mithen and Reed, 2002, Field and Lahr, 2005, and Field et al., 2007). When more continuous, fine-grained variation is incorporated, it tends to be vegetation or climate based (e.g. Hughes et al., 2007) or to be substantially simplified (Field et al., 2007). While hominin distributions are known only from scattered findspots, however, primate biogeography and landscape use are better understood and have been studied at much smaller scales and finer resolutions.

Primate Biogeography

Some general rules for the links between species ranges and ecology have been formulated, though many – like Rapoport's proposed rule that average range size increases with latitude – only work for certain groups (MacDonald, 2006). Eeley and Foley's (1999) work on geographical patterning in catarrhine species ranges, for instance found adherence to this rule, but this seems only to hold under certain conditions (Cowlishaw and Hacker, 1997). Studies of primate biogeography are more variable than those on hominins, with spatiotemporal scales, time-depths, methods and study subjects all diverse. As just a few examples, Beard (2006) studies anthropoid phylogeography through a survey of placental mammal distributions, while Willems and Hill (2009b) study movements in two vervet troops across unique, small-scale landscapes and Gonder and Disotell (2006) study genetics in *Pan troglodytes* from Nigeria and Cameroon to explore which environmental features might have served to create subspecific groupings and distributions. Primate biogeography may focus at any scale from a single population up to studies of the entire order (e.g. Kamilar, 2009, Willems and Hill, 2009a, Heads, 2010, Lehman and Fleagle, 2006b). There has even been some work on the biogeography of extinct species, including studies of the papionins (Bettridge and Dunbar, In

Press) and Miocene apes (Folinsbee and Brooks, 2007) and a few models of extinct species' dispersal, for instance of the papionin *Theropithecus oswaldi* (Hughes et al., 2008).

Various sources of evidence are used to explore primate biogeography, from troop ecology (Kamilar, 2006) to genetics (Gonder and Disotell, 2006), plate tectonics and palaeoclimate (Fleagle and Gilbert, 2006) and even morphology (McGraw and Fleagle, 2006). These combinations offer further support for the approach adopted in this thesis, which combines biogeographical and anatomical analyses, as it suggests both forms of evidence can contribute to understanding each other as well as factors like ecology and landscape. For extant species, there is also an emphasis on corroborating patterns from one set of evidence with those from another. For Yoder and Heckman's study of mouse lemur biogeography (2006), the authors combined intensive field studies of environmental structures with mtDNA analysis to test phylogeographic hypotheses using data on Madagascan geology and history. These approaches – like that proposed here – not only synthesise different types of data, but work across scales with elements (like genetic or anatomical work) sampling single specimens, while others (on geomorphology and environment) focus at a much larger scale.

This broader evidence base allows primate biogeographers to study the links between distribution patterns and ecology in some detail. Kamilar's (2006, 169) work on savannah baboons for example aimed "to test Jolly's hypothesis [that, in terms of niche breadth at least, this group comprised a single species] and to examine how their ecological variation varied with geography" by looking at patterns in variables related not just to environment but also to diet, activity budget and social organisation. Similar links were the focus of work on primate distributions across different vegetation types, communities and suites of human influence in Guyana (Lehman et al., 2006). This suggests the integration of biogeographic and ecological patterns is both plausible and informative. Finally, studies of extinct primate species have benefited substantially from knowledge of their extant relatives, with Bettridge and Dunbar (In Press) for example, in their work on fossil papionins, using detailed evidence on living primates as well as fossil data.

Hominin Biogeography

Studies specifically addressing hominin biogeography are rather narrower, typically focusing on developing narratives of dispersal and vicariance in our history. This is because humans (whose evolution drives such studies) are distinctive among primates in their unique near-global distribution (Antón et al., 2002, Fleagle, 1998). Understanding how this range expansion took place across environmental conditions is thus of special interest to researchers (Aguirre and Carbonell, 2001, Abbate and Sagri, 2012, Garcea, 2012), especially as many existing hypotheses of human evolution (see Winder, 2012 and other chapters of this thesis) do not extend out of Africa and may rest on an unstated assumption that dispersing species were able to move precisely because they were no longer restricted to certain subsets of available global environments. Exceptions to this rule like Dennell's savannahstan model (Dennell and Roebroeks, 2005), King and Bailey's TLM (2006) and the coastal dispersal models favoured by some authors (e.g. Field and Lahr, 2005) have yet to be widely accepted as more than explanations of a transient phase of hominin history which subsequent species rapidly expanded beyond.

This may be because of the overriding emphasis on climate and vegetation, data on which come either from single sites (and thus cannot provide a comprehensive picture of conditions across the hominin range) or from low-resolution models. The climate data used in the STEPPINGOUT model, for instance, provides single values for climate and vegetation in each one degree square cell (Hughes et al., 2007), an area over 110 by 110km at the equator. The widespread use of biome maps testifies to the utility of this approach when the aim is simply to distinguish broad habitat types, largely because these follow predictable distribution patterns set up by the global circulation (Barry and Chorley, 2003). To develop a more nuanced approach to hominin landscapes, this continental or global scale is certainly not irrelevant (especially for wide ranging taxa like *Homo* and *Papio*), but it must be supplemented by work at smaller scales.

Existing smaller scale studies of hominin biogeography focus on the intracontinental scale, for instance of movements between East and South Africa (Bromage and Schrenk, 1995, Foley, 1999, Strait and Wood, 1999). These link hominin distributions with evolutionary patterns, as they reflect hypotheses of phylogeny projected onto geography. Such hypotheses can be checked against reconstructions from other taxonomic groups to identify common environmental influences (Arbogast and Kenagy, 2001) and the same methods can either serve to test phylogenies (Bromage and Schrenk, 1995) or to elucidate dispersal patterns (Strait and Wood, 1999). Research at even smaller scales is rare, and often focuses on single sites (e.g. Bromage et al., 1995 on the Malawi Rift). This suggests that we can use distributions in combination with *both* ecological and evolutionary data, and bodes well for this thesis' assessment of the TLM's success explaining our origins.

Landscape Use in Extant Primates

Although landscape is rarely incorporated into conventional biogeography, primate use of space has been studied separately. This is primarily for practical reasons, like enabling field workers to track cryptic and unhabituated groups and understand their subjects in more detail (Willems and Hill, 2009b). It is also important to conservation, which relies on primatologists understanding which elements of environment are vital to species preservation. Although it rarely incorporates topography explicitly, this research fills in the small scale end of the continuum of biogeographic and evolutionary ecological work and may help develop understanding of relationships between primates and their landscapes. Existing work has picked out two key factors in primate use of space: perceived risks from other species, and the distribution of resources like food, shelter and water (Schoener, 1971, Mangel and Clark, 1986). In combination, these factors work well to explain vervet monkey distributions (Willems and Hill, 2009b) and have been expanded to other species – at Yellowstone, for instance, moose birth sites have shifted to areas near human habitation, where people act to scare off predators (Berger, 2007).

The links between primate social organisation, behaviour and habitat use seem to be complex (Altmann, 1974). As a result, many traditional studies of the topic have focused on just one or two populations, and have used labour-intensive methods for obtaining data which is then compared with information on other troops (e.g. White, 1992 on bonobos, and Barton et al., 1996, and Whiten et al., 1987 on baboons, among many others). These approaches thus explicitly link ecology and environment, and invoke complex models of the primate-landscape system in that the different elements they recognise are dynamic and may be patterned at various spatiotemporal scales. They also invoke cognitive capacities in using *perception* of risk rather than its actual level, and the success of early studies of this type suggests that this type of approach is plausible, even if only used at certain scales to date. Resource distributions are also complex, but vary predictably. Primate use of resources thus also invokes cognition, but in a simpler fashion than usually assumed for humans, in tracking landscape changes through time and space. This requires that these species possess effective memory and processing abilities but does not necessarily invoke active thought or choice. Nonetheless, a cross-scalar approach like the chosen for this thesis would seem able to potentially benefit from the insights in several parts of biogeography. This also suggests that even for the *Papio* baboons, cognition – and perhaps agency – are worth including, especially at small scales.

Evolutionary Morphology and Morphometrics

The idea that anatomy can be interpreted to give insight into the ecology, evolution and function of the organism at hand has a long history (Macho, 2007). Modern research, however, has recognised that complex structures like the foot arise from a number of initial parts which may develop separately, co-ordinated by a complex sort of "developmental choreography" (Atchley and Hall, 1991, 102). Some important influences are genetic, while others are epigenetic and behavioural, or even – for some species – symbolic (Jablonka and Lamb, 2005 part two). Generating a body of theory which adequately treats the interplay of these forces with evolutionary dynamics and inherent phylogenetic, historical and functional constraints remains a growth area in modern biology, partly because of a diversity of views and problems of scale and complexity (see Chapter One). Adaptive processes occur over deep-time or at least conjunctural time scales (see Bintliff, 1991, introduction), while development is an individual process at the smallest scale, and all these processes may nonetheless interact across the hierarchy. Creatures with sophisticated cognitive systems may be particularly developmentally complex (Calabretta et al., 2003), though choice is rarely considered in summaries of factors influencing morphology like Figure 2 (Macho, 2007).

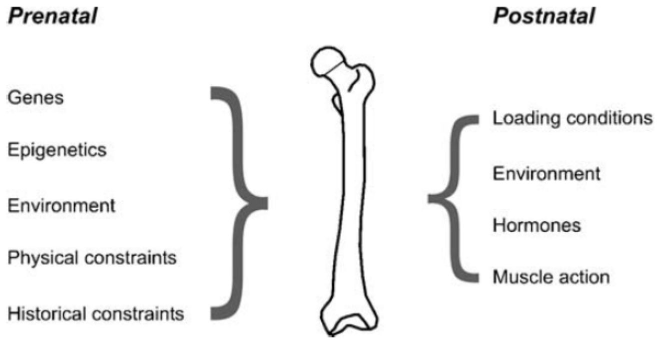


Figure 2: Macho's proposed system of factors influencing adult bone morphology; from Macho (2007, figure 26.1).

If we look for areas in these models where landscape might be important, we find no single component which encompasses all its influences. Landscapes probably contribute to several of the factors in Figure 2, for example, including postnatal loading conditions, environment and prenatal genetics, epigenetics and constraints on evolutionary change. Whether these different influences can be unpicked, however, depends upon the evolutionary dynamics of the system. By a neo-Darwinian perspective some signals (like constraint) would be expected to be minor and others (like environment) more centrally important, and those which play a key role ought to be resolvable by virtue of the system's near-equilibrium dynamical status. However, if the Darwin-Huxley synthesis is preferred, both biology *and* context may be highly dynamic and there is no way of predicting *a priori* which factors are more influential (see Chapter One). Equifinality of different factors and their complex interactions might also complicate attempts to unpick the results of different groups of factors. An alternative model of evolutionary-developmental biology helps clarify things somewhat. Lewontin (1974, as cited in Atchley and Hall, 1991) saw the evolutionary morphological system as a series of interactions which moved lineages from genotypic to phenotypic space and back each generation, and sorted their activities within each zone (see Figure 3). This model subsumes components like genetics and epigenetics under four main processes (development, selection, gamete formation and fertilisation) and recognises equifinality among factors from Figure 2 by combining them into several major life history transformations which may not be reducible to simpler components.

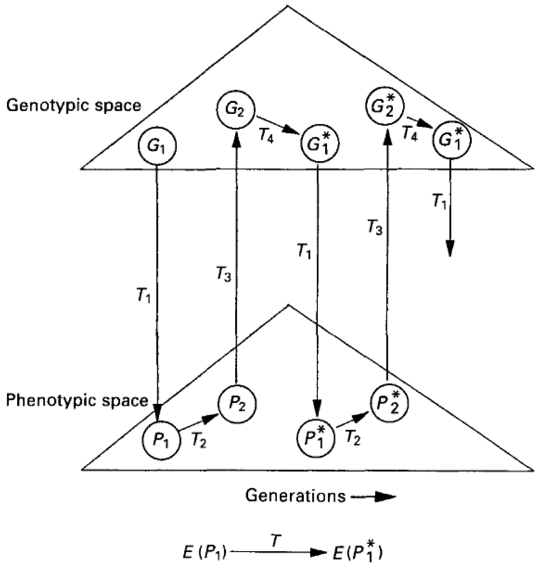


Figure 3: Lewontin's model of changes in morphology as produced by various processes in development and genetic transmission. Processes T1, T2, T3 and T4 represent development, population biology, gamete formation and fertilisation respectively; from Atchley and Hall (1991, figure 1).

Morphology is just one product of this life cycle, suggesting that evolution is a system in which many cause-effect relationships are possible. This suggests that evaluating the TLM in this way will involve grappling with a complex system, just as King and Bailey's model initially seemed to imply. This will have to be taken into account in the design and interpretation of the anatomical case studies.

Studying Morphology: Evolutionary Explanations

Lauder (1981) identifies two types of evolutionary explanation – *transformational models* which relate pathways from "primitive" to "derived", and *relational models* which focus on morphological diversity and pattern among extant branch taxa as analogues for adaptive patterns in history. Palaeoanthropologists can choose either technique, but despite the recent increase in the hominin fossil record – with new foot fossils from Dmanisi (Pontzer et al., 2010), Flores (Jungers et al., 2009), Aramis (Lovejoy et al., 2009a), and Malapa (Berger et al., 2010), new finds from older taxa (like the australopith fourth metatarsal described by Ward et al., 2011) and new analyses of old bones like the OH8 foot (e.g. DeSilva et al., 2010, and Susman et al., 2011) all contributing to the increase – sample sizes remain small and poor preservation coupled with taxonomic uncertainty means we cannot establish reliable ancestor-descendent relationships except possibly for a few taxa in the middle of the tree (Ackermann and Smith, 2007). A transitional study would thus be forced to rely on an incomplete reconstruction of the lineage and one for which taxonomies remain only 'working hypotheses' (Dunsworth, 2011). A relational model is thus preferred, providing additional support for this thesis' choice of a comparative methodology. Such models are typical in palaeoanthropology.

Prior studies of fossil foot bones like OH8 (Kidd et al., 1996), Stw573 (Kidd and Oxnard, 2005) and the Dmanisi fossils (Pontzer et al., 2010) for instance, typically interpret these through comparisons with the bones of humans and the non-human great apes rather than through comparisons with earlier or later hominins. Here, rather than focusing on interpreting one or two specimens in this way, the focus will be on developing a broad understanding of the potential of anatomy as a source of evidence to evaluate the TLM.

Traditional and Geometric Morphometrics

Traditional comparative anatomy is descriptive and pictorial (Cosans and Frampton, 2001). In the early twentieth century, however, there was a shift towards the use of quantitative rather than qualitative data (Reyment, 1996) and morphometric analysis was begun. The earliest morphometric techniques involved simple statistical analyses of groups of variables, with more complex specialist techniques developed later (Adams et al., 2004). The most substantial analytical change, called the 'morphometric revolution', took place in the 1980s-1990s (Rohlf and Marcus, 1993, Zelditch et al., 2004) with the introduction of geometric morphometric (GMM) techniqes for analysing 3D shape data and co-ordinates rather than 2D metric measures. This allows more analysis based on a single dataset, as co-ordinates can be recorded for all anatomical landmarks and measurements generated later as required, and permitted results to be visualised in the same 3D space as the original specimens. Changing attitudes to 3D data, and advances in multivariate statistics and shape theory made GMM methods popular (Marcus and Corti, 1996), but they did not completely replace traditional measurements because they require more specialist knowledge and equipment and may produce results that cannot be compared with older data.

GMM techniques have not yet been widely applied to the foot (the work of Jungers et al., 2009, and Tocheri et al., 2011 published during this PhD being notable exceptions), and most prior work (e.g. Lisowski et al., 1974, 1976, Kidd and Oxnard, 2002, Harris, 2009) has been traditional in approach. Traditional techniques (TMM) also have advantages in their simplicity and flexibility in the selection of analytical techniques and data adjustments, especially when – as in this thesis – the purpose at least initially is to explore a new set of concepts and factors rather than to resolve specific competing hypotheses about the form or function of individual features. There is also a difference of focus between GMM and TMM methods, with TMM capable of producing detailed information about structures, proportions and relative shapes, while GMM works by comparing specimens rather than describing individuals or single species, such that results change depending upon the comparators chosen (Jungers et al., 1995). For the quantitative analyses of foot bone anatomy in this thesis, a traditional technique is ultimately selected as it is more comparable to existing datasets and likely to place fewer restrictions on the intended fairly complex, exploratory style analyses than the more refined GMM methods. To make comparisons even easier, and ensure effective data capture, a scheme of measurements based on existing work by the Oxnard research group (Oxnard, 1972, Lisowski et al., 1974, Lisowski et al., 1976, Oxnard and Lisowski, 1980, Kidd et al., 1996, Kidd and Oxnard, 2002, Kidd and Oxnard, 2005) was chosen rather than a new suite of measures.

MATERIALS AND DATA COLLECTION

This synthetic focus on landscape and co-evolutionary ecology requires a range of different types of data. Maps of species distributions and environments were obtained from the literature and internet repositories for manipulation in GIS programmes. Anatomical information was collected directly from skeletons in museum collections for statistical analysis.

Environmental Data

Maps of African environments and primate distributions are integral to Chapter Three on landscape structure and to the biogeographic case studies in Chapters Four and Five. The literature review in Chapter One led to the selection of three main groups of variables to be studied – climatic, biotic and physical landscape related, respectively the mainstays of traditional hypotheses of human evolution and the TLM – and these were projected onto basemaps of rivers, coastlines and political boundaries. An ideal resolution of about 30 arc seconds (~1km at the equator) was selected as a compromise between the added detail available at finer resolutions and the processing costs of larger datasets. For finer scale work, on regional or local areas, finer-grained maps were located where possible. The sections below summarise the sources and natures of key materials used throughout.

Basemaps: Coasts, Rivers and Political Boundaries

Maps of rivers, coastlines, inland water bodies and political boundaries came from the CIA World DataBank II website at http://www.evl.uic.edu/pape/data/WDB/ in vector files with a high resolution (approximately equivalent to 30 arc second rasters) and tar.gz format. They were georeferenced in a WGS 84 projection, which was adopted for all further analyses.

Landscape Variables: Topography, Roughness, Soils and Surface Geology

Continental topography data from GTOPO and GDEM maps and SRTM30 tiles, together with slope and roughness maps derived from them, were provided by Geoffrey King (pers. comm.) from prior work by King and Bailey (2006), Bailey et al. (2011) and Reynolds et al. (2011). These were provided as raster maps with 30 arc second resolution, in geotiff format and WGS 84 projection like the basemaps. More detailed topographic data was obtained as 5x5 degree tiles from the SRTM Digital Elevation Database version 4.1. It was stored in referenced .geotiff format and was mosaicked together in Global Mapper, while slope and roughness were derived using the ArcGIS ‘slope’ tool once for hillslopes and twice for roughness. Slope is a measure of the difference in altitude between adjacent pixels, while roughness measures thus capture information on the slope of the slope, or the *variability* in slopes. This fits with the definition of roughness, as variation in slope, given in Chapter One.

Continental soil distributions were obtained from the Harmonised World Soil Database, version 1.2 (available from http://www.iiasa.ac.at/Research/LUC/External-World-soil-database/HTML/index.html). The resolution of this raster was 30 arc seconds, although this varies locally as the database comprises a synthesis of data from a wide range of sources (FAO/IIASA/ISS-CAS/JRC, 2009). It came as a .geotiff map and was re-registered and cut down for analyses at the regional or local scale as more detailed data could not be found.

Surficial geology at the continental scale was downloaded as a vector shapefile from the USGS Geological Survey Central Energy Resources Team website (available from http://certmapper.cr.usgs.gov/erp_datafinder_v1.1/details.jsp?goTo=details&docId={C7E34C48-9BD9-45C6-AD08-E549CFB3715A}&mode=ME&loggedIn=false). This data is scaled at 1:5,000,000 and came ready georeferenced in WGS 84. This too was cut down for local and regional analyses where necessary.

Climate Variables – Temperature, Rainfall and Seasonality

Climate data came from the WorldClim website (www.worldclim.org) as a suite of bioclimate variables from which mean annual temperature, mean annual rainfall, mean annual temperature seasonality and mean annual rainfall seasonality were extracted. These variables are known to be important to primates (Hill and Dunbar, 2002). All maps were georeferenced .bil files at 30 arc second resolution (Hijmans et al., 2005) and were manipulated in Global Mapper to get them into a format for ArcGIS. They were cut down for small scale analyses, and compared with local data from the literature.

Biological Variables – Vegetation, Land Cover and Species Distributions

The two-part 'Vegetation Map of Africa' (based on work by White, 1983) was obtained from the World Agroforestery Centre website (www.worldagroforestery.org). The layer on physiognomy was selected and exported as a georeferenced vector polygon map at a scale of 1:500,000 and is only a little modified from the original 1980s map (changes are detailed in Kindt et al., 2011). The low resolution was a drawback, but finer scale information was patchy and not available for relevant areas of Africa.

The WWF terrestrial ecoregion map was downloaded from the WWF website at http://www.worldwildlife.org/science/ecoregions/item1267.html as a georeferenced WGS 84 shapefile of vector polygons. This data summarises vegetation and the distribution of broader biodiversity and specific endemic species (Olson et al., 2001). Like the vegetation map, it was already in a suitable format, although resolution remains uncertain and locally variable (Olson et al., 2001).

In addition to downscaling continental maps of vegetation and ecoregions, further data on land cover at the smaller scale were obtained from LANDSAT legacy mosaic tiles (http://glovis.usgs.gov/). For this study, LANDSAT Legacy collection ETM+ Pan Mosaic data were used wherever possible, with South Africa being a notable exception as there are gaps in the dataset over that region. This data was already georeferenced.

Primate range data came from the IUCN Red List database as a single terrestrial mammal dataset (http://www.iucnredlist.org/technical-documents/spatial-data). The biogeography of each species is recorded at a 1:1,000,000 scale and is a vector shapefile in the WGS 84 projection. Key species like the *Papio* baboons and their major predators, including *Panthera leo*, *Panthera pardus*, *Hyaena hyaena*, *Crocuta crocuta* and *Hyaena brunnea*, were extracted and saved separately.

Data on the distribution of modern *Homo sapiens* were obtained from the UNEP/GRID Sioux Falls data centre (http://na.unep.net/siouxfalls/datasets/datalist.php). This site stores data on population densities across Africa for 1960, 1970, 1980, 1990 and 2000 as georeferenced raster (.tif) files, which were downloaded and imported into ArcGIS. The resolution was uneven, but better for the more recent data: the continent was divided into administrative regions of various sizes using the census information.

GIS Display Conventions

Once all of these datasets had been imported into ArcGIS, they had to be displayed for exploration and analysis. Table 3 summarises the display parameters used throughout the remainder of the thesis. Measurement follows standard scales (e.g. metres or degrees Centigrade) where possible, but arbitrary units are used for a few variables. The map of continental roughness provided by Geoffrey King, for example, records roughness on a scale of 0-255 arbitrary units as this is easier to display as a colourmap than the original values which included three or four decimal places. The conversion simply involved splitting the original range into 255 equal categories. The other two maps using non-standard units both employ measures of climatic variability. The units for temperature seasonality represent the standard deviation of annual temperature multiplied by a hundred and those for rainfall seasonality represent the coefficient of variation on annual rainfall (Hijmans et al., 2005).

Table 3: format, symbols and display information for the datasets used in Chapters Three-Five.

Variable[+]	File types	Symbology	Range	Display
Topography (C)	Raster	Continuous spectrum*	0 to 5895m	Standard deviations (3)
Roughness (C)	Raster	Colormap (pre-defined with full spectrum range)	0 to 255 units	-
Vegetation (C)	Vector polygon	Classified into 'open', 'semi-open', 'closed', 'aquatic' and 'arid/semi-arid'	-	Coloured by category
Soils (C)	Raster	Classified by unique values	-	Coloured by category
Geology (C)	Vector polygon	Classified by unique values	-	Coloured by category
Rivers (C)	Vector line	Single colour	-	Blue
Coastlines (C)	Vector line	Single colour	-	Black
Political boundaries (C)	Vector line	Single colour	-	Purple
Annual mean temperature (C)	Raster	Continuous spectrum**	0 to 32°C	Minimum-maximum
Temperature seasonality (C)	Raster	Continuous spectrum**	62 to 22,500 units	Minimum-maximum
Annual mean precipitation (C)	Raster	Continuous spectrum***	0 to 4560 mm	Minimum-maximum
Precipitation seasonality (C)	Raster	Continuous spectrum**	0 to 206 units	Minimum-maximum
Ecoregions (C)	Vector polygon	Classified by ecoregion	-	Coloured by category
Human population density (C)	Raster	Continuous spectrum from white to dark red	0 to c. 89,000 per unit area	Standard deviations (2)
Papio distributions (C)	Vector polygon	Classified by species/subspecies	-	Coloured by category
Other species distributions (C)	Vector polygon	Classified by species	-	Coloured by category
Topography (R)	Raster	Continuous spectrum*	Area dependent	Standard deviations (2)
Slope (R)	Raster	Continuous spectrum**	0 to 90 degrees	Standard deviations (2)
Roughness (R)	Raster	Continuous spectrum**	Area dependent	Standard deviations (2)

[+]codes following variable names denote map scale: C = continental (may also be used cut down with the same symbology), R = regional; *full (purple-red) spectrum used to display all variables with this symbol; **near-full (blue-red) spectrum used to display all variables with this symbol; ***half (blue-green) spectrum used to display all variables with this symbol.

Anatomical Data

Following the decision to develop the Oxnard group's measurements (see above), research design for the anatomical components became relatively straightforward. The human (and primate) foot is an extremely complex structure, as Figure 4 shows. It comprises seven tarsals, five metatarsals and fourteen phalanges, and studying all of these bones was not practical for this project. The functional literature was used to choose a subsample.

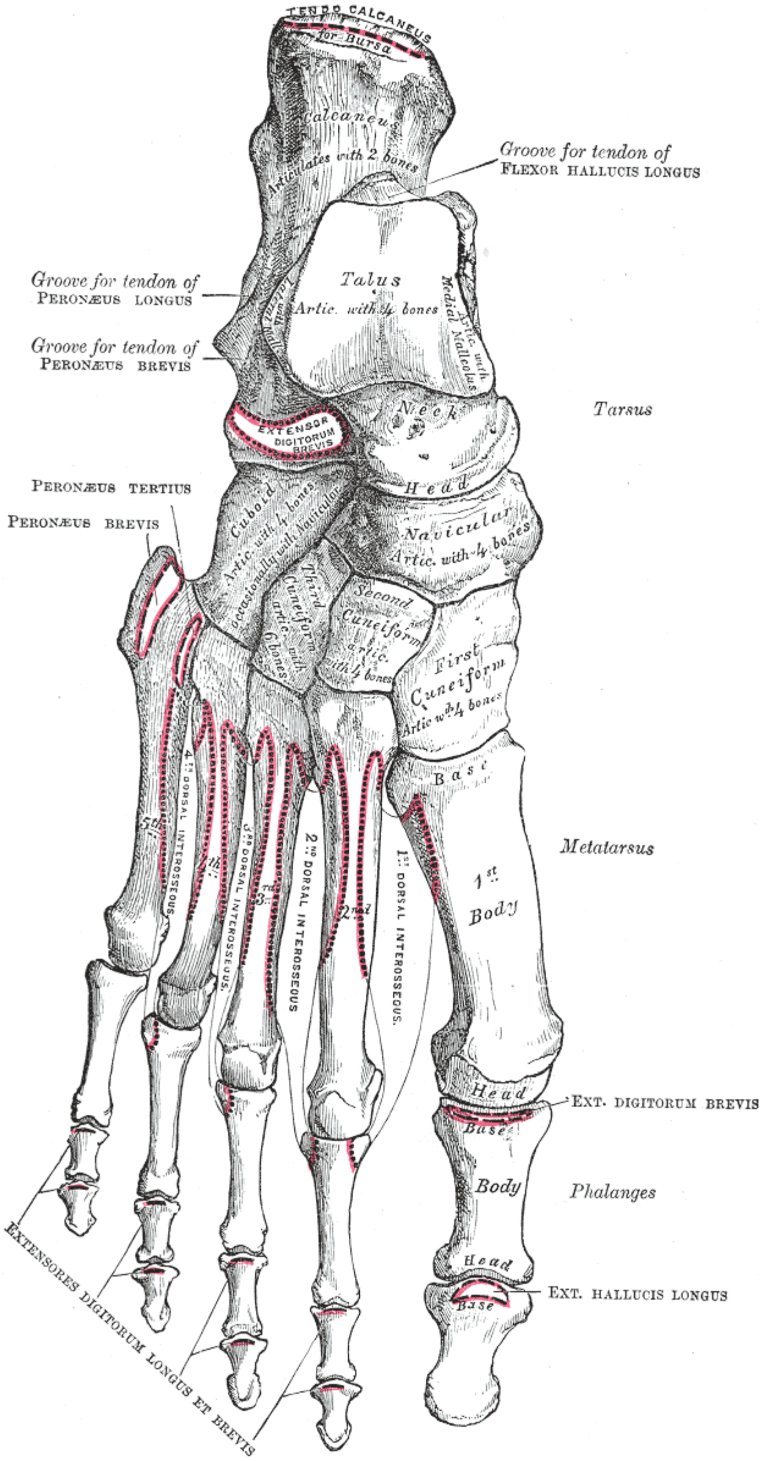


Figure 4: the skeleton of the human foot, showing some key muscle attachments and features; from Gray (1918, figure 268), available at http://www.bartleby.com/107/illus268.html.

For the primates, two major functional units (the medial and lateral columns, see Wood-Jones, 1944) have been identified. The talus, navicular, calcaneus, and cuboid form the bases for the medial and lateral columns respectively, and are also involved in other key joints of the foot, making them logical choices. To incorporate more of the rest of the foot, including some of the digits, the respective columns' key metatarsals – first and fifth – were also selected, along with the medial cuneiform (to connect first metatarsal with medial column tarsals), as was the third metatarsal, to enable comparisons of digit lengths across the foot. The phalanges, however, are less functionally important (Aiello and Dean, 1990) and were excluded, together with the intermediate and lateral cuneiforms, after preliminary examination of *Papio hamadryas* bones suggested that they would not be accurately measurable in that species. The measurements were trialled on a sample from York which was blind re-sampled three times over six months; no significant differences (p values between 0.998 and 1) were found in comparisons of these three measurement periods and results were comparable to those of earlier works.

Skeletal Materials: Baboons and Humans

The primate sample used in the analysis of *Papio* baboons came from the Florida Museum of Natural History, Gainesville, and comprised 38 male baboons collected by Maples (1967). These specimens included 17 yellow baboons, 15 olive baboons and 6 apparent hybrids sampled from known locations across southern Kenya. All individuals were adult by dental and skeletal reckonings, and all skeletons were complete (Maples, 1967).

Human samples were obtained from the Duckworth Laboratory (University of Cambridge) and the University of Sheffield collections. Three archaeological samples were chosen, from Jebel Moya in Neolithic Africa and from more recent British cemeteries at the Blackgate and the Barbican, with details of the selection process given in Chapter Five. In brief, the Jebel Moyan sample is of broadly Neolithic age, and comes from a settlement and cemetery in south-central Sudan, excavated in 1911-1914 by Sir Henry Wellcome. The Blackgate sample comes from the early medieval period in Newcastle Upon Tyne, and the Barbican sample from medieval York. This implies that the latter two samples would have moved across man-made surfaces and, while we have no way of knowing which (if any) individuals would have worn shoes, their locomotion would not have been purely 'naturalistic'. The Jebel Moyan group in contrast would have moved on natural surfaces, and if they wore shoes, would have favoured unrestrictive sandals. The archaeological nature of all three human samples meant they were not as complete as the primate skeletons and rather than being able to sample a given number of specimens and obtain equally sized samples, the human skeletons were simply sampled until individual element totals were sufficiently high to permit statistical testing of inter-sample differences (see Table 4). To this end, an ideal sample size of about 50 of each bone per sample was chosen, although in some cases it was hard to move beyond about 40. Obtaining samples of 40-50 examples of each element involved sampling upwards of 250 labelled individuals.

Table 4: the skeletal samples used to explore variation in the human foot skeleton.

Population	**Bone**	**Male**	**Female**	**Unknown**	**Total**
Jebel Moya (African Neolithic)	Talus	33	12	8	**53**
	Calcaneus	28	14	7	**49**
	Cuboid	14	6	7	**27**
	Navicular	19	6	6	**31**
	Medial cuneiform	17	7	6	**30**
	First metatarsal	28	14	9	**51**
	Third metatarsal	8	5	5	**18**
	Fifth metatarsal	23	13	7	**43**
Blackgate	Talus	18	19	16	**53**
	Calcaneus	14	21	14	**49**
	Cuboid	15	19	13	**47**
	Navicular	15	15	13	**43**
	Medial cuneiform	14	18	12	**44**
	First metatarsal	16	17	14	**47**
	Third metatarsal	11	15	9	**35**
	Fifth metatarsal	14	17	11	**42**
The Barbican	Talus	20	19	10	**49**
	Calcaneus	20	19	11	**50**
	Cuboid	19	19	10	**48**
	Navicular	18	18	9	**45**
	Medial cuneiform	20	19	9	**48**
	First metatarsal	20	19	10	**49**
	Third metatarsal	19	16	11	**46**
	Fifth metatarsal	19	19	10	**48**
Total bones*	-	**442**	**366**	**237**	**1045**

*Total numbers of individuals are not given because the sampling strategy (described above) does not imply a uniform number for each bone.

Measurements of the Talus

The talus participates in three joints at the ankle, the subtalar joint and the midtarsal (or transverse tarsal) joint. Most of its morphology is thus linked to joint function. Metric and non-metric measurements (see Table 5 and Table 6) were adapted from Lisowski et al. (1974) and Finnegan (1978), Oygucu et al. (1998) and Aiello and Dean (1990) respectively. The system adopted here reduces the number of metric variables from those taken by Lisowski et al. (1974) on the grounds that (a) several duplicate very similar information and (b) for the purposes of this study, it is the function of the joint complexes – and hence the articular surfaces – and the relative sizes of the bones which are key, and some of the original series of measurements do not reflect any of these properties.

Table 5: metric measurements of the talus, adapted from Lisowski et al. (1974).

Measurement (no).	Definition
Maximum medial height (MMH)	Height of the highest point on the medial margin of the trochlear facet, measured with the bone on a sheet of glass of known thickness.
Maximum lateral height (MLH)	Height of the highest point on the lateral margin of the trochlear facet. Measured as above.
Anterior trochlear breadth (ATB)	The *maximum* distance between the medial and lateral margins of the trochlear facet, taken perpendicular to the lateral trochlear margin.
Posterior trochlear breadth (PTB)	The *minumim* distance between the medial and lateral margins of the trochlear facet, taken parallel to the above.
Maximum breadth (MB)	The maximum talar breath, from the lateral prominence and measured at right angles to the lateral trochlear margin.
Long dimension of the head (LDH)	The length of the long dimension of the talonavicular articulation of the head, measured obliquely along the long axis from the facet margins. Not taken in STBP.
Short dimension of the head (SDH)	The maximum value of the short dimension of the talonavicular articulation of the head, measured at right angles to the above, including the facet for the spring ligament where relevant. Not measured in STBP.
Maximum functional length (MFL)	Length from the groove for the tendon of flexor hallucis longus to the most posterior point of the talonavicular facet edge.
Trochlear length (TL)	Length of the trochlear surface, taken between the most anterior and posterior points of the central trough or break of slope.
Medial facet length (MeFL)	The maximum distance between the anterior border and posterior tip of the medial facet, measured parallel to the STBP.
Lateral facet length (LFL)	The maximum distance between the anterior and posterior borders of the lateral facet, measured parallel to the STBP.
Posterior facet length (PFL)	The maximum length of the posterior calcaneal facet, taken along the long axis from edge to edge. Not measured in STBP.
Posterior facet breadth (PFB)	The maximum breadth of the posterior calcaneal facet, taken perpendicular to the above. Not measured in STBP.
Anterior facet length (AFL)*	The maximum length of the anterior calcaneal facet, taken along the long axis from edge to edge. Not measured in STBP.
Anterior facet breadth (AFB)*	The maximum breadth of the anterior calcaneal facet, taken perpendicular to the above. Not measured in STBP.
Medial facet length (MeFL2)*	The maximum length of the medial calcaneal facet, taken along the long axis from edge to edge. Not measured in STBP.
Medial facet breadth (MeFB)*	The maximum breadth of the medial calcaneal facet, taken perpendicular to the above. Not measured in STBP.

*NB. Where the two facets are fused and indistinguishable (i.e. not subdivided by a marked line), the measurements will be entered in anterior facet length/breadth only.

Table 6: non-metric measurements on the talus, adapted from Finnegan (1978), Oygucu et al. (1998) and Aiello and Dean (1990).

Variable	Definition
Os trigonum type (OTT)	Whether the os trigonum is separate or attached.
Medial talar facets (MTF)	Whether there are medial facets on the upper medial surface of the talar neck which do not follow the line of curvature (present/absent).
Lateral facet extension (LFE)	Whether the lateral trochlear facet extends onto the neck of the talus.
Articular facet number (AFN)	Whether the articular facets on the talar head are single, double or conjoined.
Squatting facets (SF)	Whether there are squatting facets laterally, medially, both or continuously.
Curvature of posterior facet (CPF)*	Whether the posterior calcaneal facet is concave, convex, flat or sellar.
Curvature of anterior facet (CAF)*	Whether the anterior calcaneal facet is concave, convex, flat or sellar.
Curvature of medial facet (CMeF)*	Whether the medial calcaneal facet is concave, convex, flat or sellar.

*Scored on a scale from 1-5, where 1 is extremely concave and 5 extremely convex, or as 6 for sellar.

Several of these non-metric traits are of particular relevance to the *use* of the ankle and foot joints, as they occur in populations which perform certain activities (e.g. squatting). They have also been found to vary distinctively between populations, but to date have not proven useful in discrimination, as groups differ only in the prevalence of a trait (Harris, 2009).

Measurements of the Calcaneus

The calcaneus lies directly inferior to the talus, and is another bone typically used in studies of differences between species in the structures of the foot. For the calcaneus, the following metric measurements (see Table 7) are adapted from Kidd and Oxnard (2002) and Kidd et al. (1996). Non-metric measurements (Table 8) are derived from Finnegan (1978) and Aiello and Dean (1990).

Table 7: metric measurements of the calcaneus, after Kidd and Oxnard (2002) and Kidd et al. (1996).

Measurement	Definition
Maximum length (ML)	The linear measurement from the most posterior point on the calcaneal tuber to the most anterior point on the superior edge of the articular surface for the cuboid.
Sustentaculum breadth (STB)	The measurement from the most medial point on the sustentaculum tali to the most lateral point on the posterior talar articular facet, taken at right angles to the above.
Calcaneal body (CB)	The linear dimension between the most anterior part of the posterior talar facet and the most posterior point of the tuberosity.
Overall articular dimension (OAD)	The maximum projected distance between the most posterior part of the posterior talar facet and the most anterior margin of the anterior facet.
Tuber breadth (TB)	Dimension from the most medial to the most lateral surfaces of the calcaneal tuber, taken immediately posteriorly to the talar articulations and perpendicular to above.
Tuberosity breadth (TBB)	The maximum distance between the medial and lateral margins of the tuberosity, taken from posterior aspect parallel to SCBP.
Posterior talar articular surface length (PTAL)	The maximum measurement from the antero-lateral to postero-medial margins along the long axis of the facet.
Posterior talar articular surface breadth (PTAB)	Maximum dimension measured from margin to margin, perpendicular to the above.
Dorsoplantar cuboid facet dimension (DPCF)	The projected measurement from the most dorsal to the most plantar margins of the cuboid facet, measured from posterior. Not taken in SCBP.
Mediolateral cuboid facet dimension (MLCF)	Maximum measurement at right angles to the dorsoplantar measurement, from the medial to the lateral margins, measured parallel to the SCBP.
Sustentaculum tali projection (STP)	The breadth of the anterior talar facet at the maximum breadth of the sustentaculum, parallel to no. 4.

Table 8: non-metric measurements taken on the calcaneus, adapted from Finnegan (1978) and Aiello and Dean (1990).

Variable	Definition
Anterior facet shape (AFS)	Single/ovoid (1), hourglass (2) or two discrete facets (3).
Peroneal tubercule (PT)	Presence or absence, antero-lateral surface.
Lateral tubercule (LT)	Presence or absence, postero-lateral surface.
Calcaneonavicular articulation (CNA)	Presence or absence.
Curvature of anterior talar facet (CATF)*	Whether concave, convex or flat.
Curvature of medial talar facet (CMTF)*	Whether concave, convex or flat.
Curvature of posterior talar facet (CPTF)*	Whether concave, convex or flat.
Curvature of calcaneocuboid facet (CCF)	Whether medially concave and anterolaterally prominent or less pronounced.

*Scored on a scale from 1-5, where 1 is extremely concave and 5 extremely convex, or as 6 for sellar.

Measurements of the Cuboid

The cuboid is a component of the lateral column of the foot, acting as a bridge between the calcaneus posteriorly and the fourth and fifth metatarsals anteriorly. Measurements for the cuboid (see Table 9 and Table 10) were obtained after Kidd et al. (1996), Kidd and Oxnard (2002) and (Aiello and Dean, 1990).

Table 9: metric measurements taken on the cuboid, adapted from Kidd et al. (1996) and Kidd and Oxnard (2002).

Measurement	Definition
Long metatarsal facet dimension (LMFD)	The maximum dimension of the long axis of the metatarsal facet.
Short metatarsal facet dimension (SMFD)	The maximum dimension with of the short axis of the metatarsal facet, perpendicular to the above.
Long calcaneal facet dimension (LCF)	The maximum dimension of the long axis of the calcaneal facet.
Short calcaneal facet dimension (SCF)	The maximum dimension of the short axis of the calcaneal facet, perpendicular to the above.
Medial dorsal length (MDL)	The distance from the most dorsomedial point on the posterior facet (where the line projected from the dorsal aspect of the medial facet meets the corner) and the most dorsomedial aspect of the anterior facet.
Medial plantar length (MPL)	The distance from the most posterior point on the plantar side of the posterior facet to the most anterior aspect of the anterior facet.
Lateral length (LL)	The distance from the metatarsal facet to the calcaneal facet, measured on the lateral side and from the most lateral points of those facets.
Overall breadth (OB)	Measured from the medial side of the bone perpendicularly to the lateral side of the bone, with the bone placed stably on the dorsal surface.
Overall depth (OD)	From the most plantar to the most dorsal points of the bone while resting on dorsal surface.
Medial facet length (MFL_A)	Maximum dimension along the long axis of the medial facet
Medial facet breadth (MFB)	Maximum dimension along the short axis of the medial facet.

Table 10: non-metric measurements taken on the cuboid, adapted from Aiello and Dean (1990).

Variable	Definition
Curvature of calcaneal facet (CCF_A)	Whether medially projecting and laterally concave, or less pronounced.
Curvature of metatarsal five facet (CMF)*	Whether concave, convex, sellar or flat.
Plantar ridge robusticity (PRR)	Well-marked or flat.
Peroneal groove width (GW)	Narrow or broad.

*Scored on a scale from 1-5, where 1 is markedly concave and 5 markedly convex, or as 6 for sellar.

Measurements of the Navicular

The navicular also acts to bridge between the two larger tarsals and the digits, but does not directly articulate with the metatarsals. Instead, it articulates posteriorly with the talar head and acts as a platform upon which the three cuneiforms rest. Metric measurements (Table 11) were adapted from Kidd et al. (1996) and Kidd and Oxnard (2002), while non-metrics (Table 12) were adapted from Aiello and Dean (1990).

Table 11: metric measurements taken on the navicular, after Kidd et al. (1996) and Kidd and Oxnard (2002).

Measurement	Definition
Long talar facet dimension (LTFD)	The maximum dimension of the talar facet, in the long axis.
Short talar facet dimension (STFD)	The maximum span of the short dimension of the talar facet, at right angles to measurement one.
Long cuneiform facet dimension (LCFD)	The maximum dimension of the long axis of the cuneiform facet.
Maximum short cuneiform facet dimension (MaSCFD)	The maximum span of the short axis of the cuneiform fact, measured perpendicular to measurement 3.
Minimum short cuneiform facet dimension (MiSCFD)	The minimum span of the short axis of the cuneiform facet, perpendicular to measurement 3.
Maximum navicular breadth (MNB)	The maximum dimension of the navicular, along the long axis and from the widest points.
Maximum navicular height (MNH)	The maximum measurement along the short axis of the navicular, at right angles to the above.
Maximum navicular depth (MND)	The maximum distance between the talar facet posteriorly and the cuneiform facet anteriorly, perpendicular to measurements 6 and 7. Measured with one arm of the callipers flat against both edges of the talar facet.
Tuberosity projection (TP)	The maximum projection of the navicular tuberosity medially, measured diagonally from the projecting edge of the talar facet to the maximum point.

Table 12: non-metric measurements taken on the navicular, after Aiello and Dean (1990).

Variable	Definition
Cuboid facet (CF)	Presence or absence
Curvature of medial cuneiform facet (CMeF_A)*	Concave, convex, flat or sellar.
Curvature of intermediate cuneiform facet (CIF)*	Concave, convex, flat or sellar.
Curvature of lateral cuneiform facet (CLF)*	Concave, convex, flat or sellar.

*Scored on a scale from 1-5, where 1 is markedly concave and 5 markedly convex, or as 6 for sellar.

Measurements of the Medial Cuneiform

The medial cuneiform articulates posteriorly with the navicular and anteriorly with the first metatarsal, forming a key joint relevant to the evolution of bipedal locomotion in humans. Metric measurements for the medial cuneiform (see Table 13) were modified from those given in Kidd and Oxnard (2005), while the non-metrics (Table 14) include only curvature measurements, which are not adapted from any other study.

Table 13: metric measurements taken on the medial cuneiform, adapted from Kidd and Oxnard (2005).

Measurement	Definition
Anterior facet height (AFH)	The maximum height of the anterior facet for the metatarsal.
Anterior facet breadth (AFB_A)	The maximum breadth of the anterior articular facet, taken at right angles to the above.
Posterior facet height (PFH)	The maximum height of the posterior facet.
Posterior facet breadth (PFB_A)	The maximum breadth of the posterior articular facet, taken at right angles to the above.
Plantar breadth (PB)	The maximum span of the plantar surface, measured at right angles to the bone's long axis at the widest point.
Maximum depth (MD)	The maximum depth of the bone measured parallel to the plane of the anterior facet.
Maximum dorsal length (MDL_A)	The maximum length of the dorsal surface, from the anterior articular facet edge to the posterior articular facet edge.
Maximum plantar length (MPL_A)	The maximum length of the plantar surface, from the anterior articular facet edge to the posterior articular facet edge.
Lateral articular facet length (LFL_A)	Maximum distance along the facet, parallel to the dorsal surface of the bone.
Lateral articular facet depth (LFD)	Maximum depth at right angles to the above.

Table 14: non-metric measurements taken on the medial cuneiform.

Variable	Definition
Curvature of the metatarsal facet (CMTF)*	Concave, convex, flat or sellar.
Curvature of the lateral facet (CLF_A)*	Concave, convex, flat or sellar.
Curvature of the navicular facet (CNF)*	Concave, convex, flat or sellar.

*Scored on a scale from 1-5, where 1 is markedly concave and 5 markedly convex, or as 6 for sellar.

Measurements of Metatarsals I, III and V

The metric (Table 15) and non-metric (Table 16) features of metarsals I, III and V were also scored. These measurements were developed independently of the Oxnard group's work as these earlier studies did not include the metatarsals, and are designed to capture similar characters (articular facets, overall dimensions and the like).

Table 15: metric measurements taken on the metatarsals. Codes in brackets refer to metatarsal one; metatarsal three; and metatarsal five respectively.

Measurement	Definition
Maximum length (ML_A; ML_B; ML_C)	The maximum length of the bone, at right angles to the long axis.
Maximum midshaft depth (MMD; MMD_A; MMD_B)	Measured at half the metatarsal's total length, across the maximum span of the bone.
Minimum midshaft depth (MD_A; MD_B; MD_C)	Measured at half the metatarsal's total length, across the short diameter at right angles to the above.
Proximal articular facet depth (PAFL; PAFL_A; PAFL_B)	The maximum depth of the proximal articular facet.
Proximal articular facet breadth (PAFB; PAFB_A; PAFB_C)	The breadth of the proximal articular facet, measured at right angles to the above.
Distal facet depth (DFD; DFD_A; DFD_B)	The maximum depth of the distal facet, measured from the most inferior point of the plantar articular margin to the most superior point on the dorsal articular margin.
Distal facet breadth (DFB; DFB_A; DFB_B)	The maximum breadth of the metatarsal head, measured at right angles to the above.
Medial facet depth (NA; MFD_B; MFD_C)	The maximum depth of the medial facet(s), measured at right angles to the long axis of the bone.
Medial facet length (NA; MFL_B; MFL_C)	The maximum length of the medial facet(s), measured parallel to the long axis of the bone.
Lateral facet depth (NA; LFD_B; NA)	The maximum depth of the lateral facet, measured at right angles to the long axis of the bone.
Lateral facet length (NA; LFL_B; NA)	The maximum length of the medial facet, parallel to the long axis of the bone.

Table 16: non-metric measurements taken on the metatarsals. Codes in brackets refer to metatarsal one; metatarsal three; and metatarsal five respectively.

Variable	Definition
Orientation of the distal facet (ODF; ODF_A; ODF_B)	The angle of the articulation with the tarsal bones, measured by placing the bone with the articular facet flat on a surface and measuring the angle between a line drawn up the centre of the shaft and the vertical. Scored as low, medium or high.
Curvature of the medial facet (NA; CMeF_C; CMeF_D)*	Concave, convex, flat or sellar.
Curvature of the lateral facet (NA; CLF_B; NA)*	Concave, convex, flat or sellar.
Curvature of the proximal facet (CPF_B; CPF_C; CPF_D)*	Concave, convex, flat or sellar.

*Scored on a scale from 1-5, where 1 is markedly concave and 5 markedly convex, or as 6 (sellar).

Throughout the data collection, measurements were taken to the nearest 0.1mm using Mitutoyo digital callipers and recorded on pre-designed datasheets. The data were entered into Excel and cross-checked against the original records before analysis in SPSS. Lisowski et al. (1974) suggested that there were no significant differences between left and right, but only worked on the talus, so initially twenty specimens of various species from the University of Sheffield were completely sampled and a Student's T-test used to explore left-right differences. No statistically significant differences were found, so just one side – the more complete – was included subsequently.

Data Correction Prior to Analyses

Most palaeoanthropological papers that use morphometrics apply certain corrections (taking natural logs, square root transformations or similar) to their data before analyses are undertaken (Kidd et al., 1996, Kidd and Oxnard, 2002, Kidd and Oxnard, 2005). For this analysis, where the aim is broadly to relate landscape and anatomical variables, we are working with a system like that shown in Figure 2 and there are two alternative models we can use to conceptualise the relationships: one which is additive, which assumes that each metric variable is effectively the sum of components linked to different factors like genes and the environment, and one which is multiplicative and assumes that the variable is the product of the same components. Different adjustments are necessary in each case. Using an additive model, for instance, size-correction may be achieved by subtracting the mean from each specimen's measurement value (i.e. taking simple residuals) while a multiplicative model requires a ratio technique that takes logs and divides by a mean, for instance, a Mosimann geometric mean technique as advocated by Jungers et al. (1995).

For this thesis, a multiplicative model seems appropriate. Although few morphometric studies mention their model of anatomy explicitly, the preponderance and effective performance of logarithmic adjustments in traditional morphometric studies of the foot (Lisowski et al., 1974, Kidd et al., 1996, Kidd and Oxnard, 2002, Kidd and Oxnard, 2005) – and the better performance of ratio methods in explicit tests of alternative techniques for accommodating scale (Albrecht et al., 1993, Jungers et al., 1995) – do suggest that this is more accurate. In addition, while there are instances in anatomical studies in which a multiplicative model is inappropriate (Voordouw, 2001), scholars generally presume that a change in a factor influencing growth – nutrition, for instance – is going to lead an individual to attain a proportionally different size than they would under 'normal' conditions. So, for example, we assume that inadequate nutrition might result in an individual reaching only 90% or 80% of their expected height, not that they will be shorter by some measurable value like 10cm or 15cm irrespective of the heights of their parents and other factors. This is implicitly a multiplicative model. The decision to adopt such a model in this thesis therefore suggested that log-transformation (using natural logs) and a ratio technique for reducing the impact of isometric size variation (where relevant) were the most appropriate transforms, and these were conducted prior to statistical analyses. This means that the results obtained will not inform about the absolute isometric sizes of bones or differences between groups, but instead will focus primarily on the more interesting and potentially informative differences in shape and allometry.

Anatomical Display Conventions

Although there are relatively few different types of primate used here, and the question of symbology is therefore less pressing than for the biogeographic data, a consistent pattern was nonetheless followed for the three human groups in which the Jebel Moyan specimens were coded blue, the Blackgate specimens green and the Barbican specimens red.

ANALYTICAL SOFTWARE

A suite of software packages were used in concert throughout this thesis, including a range of GIS packages and several statistical and phylogenetic tools. These included:

- Global Mapper 12, used to mosaic GIS tiles together, to switch data into accessible file types for importation into other programs, and to generate 3D imagery;
- ArcGIS 10.0, used to display data and generate maps showing their relationships by manipulating symbols, display parameters and so on, and (where relevant) for numerical analysis of patterns;
- Adobe CS5.5 (Illustrator, Photoshop and InDesign), used to add legends, titles and orientating marks to maps exported from ArcGIS, and for further manipulation of imagery (e.g. the substitution of topographic data for ‘depth’ values in CMYK files to create composite maps);
- MAPublisher 8.6, a georeferencing add-in for Adobe Illustrator which was used to maintain the geographic elements of maps manipulated in that software and to plot points against a basemap for exportation as a map layer;
- Quantum GIS ‘Wroclaw’, a free GIS package used primarily to extract single layers (e.g. single species distributions) from large datasets like the IUCN terrestrial mammals databank, and as an alternative to ArcGIS for similar tasks where a simple, quick program was more efficient than a more sophisticated one;
- Google Earth, used to display .kmz files, as an interface to download SRTM tiles using the SRTM 4.1 plugin, and to explore files using fly-by;
- SPSS (the statistical package for the social sciences), used to manipulate and analyse metric and non-metric anatomical data, and;
- PAST (the palaeontological statistics program), used for analyses beyond those possible in SPSS, including multivariate techniques for sparse anatomical data;

The Microsoft Office programs – particularly Excel and Access – were used to transfer data from ArcGIS, which outputs text or database files, into other packages like SPSS.

SPECIFIC METHODS FOR THIS THESIS

Within the broad approaches described in outline above, specific techniques were chosen on a case by case basis within each set of analyses. These often draw on statistical techniques like generating descriptive statistics, tests of difference and multivariate data reduction techniques like principal components analysis (PCA) and discriminant functions analysis (DFA). Explanations of these techniques and justifications for their use are presented in the relevant chapters.

Chapter Three: Extant African Landscapes

INTRODUCTION

Chapter One identified King and Bailey's TLM (King and Bailey, 2006, Bailey and King, 2011, Bailey et al., 2011) as contributing to a debate traditionally dominated by vegetation- and climate-based hypotheses of human evolution. The authors identify the association between hominin sites and tectonic landscapes as a key piece of evidence in support of their model. However, while they deal with challenges from those who attribute this pattern to taphonomy – for instance noting that "statistical analysis indicates that preservation factors alone cannot account for the distribution of different categories of sites in Ethiopia and South Africa" (Reynolds et al., 2011, 296) – they examine the relative distributions of vegetative, climatic and physical landscape factors only in passing. It is possible therefore that the association of sites and tectonic activity actually results from a correlation between the latter and a particular habitat – like savannah or woodland – which is the actual attractor for hominins. More plausibly, it might be that several different landscape factors are relevant and interact to determine the settings of hominin sites. Far from occupying tectonic landscapes because of the presence of attractive mosaic habitats, for example, it might be that the hominins are actually occupying only fragments of a particular vegetative or climatic context that just happen to be more accessible (less isolated or more interconnected) on such terrain. Untangling the relationships between different components of the broader landscape system is therefore a priority for this thesis' exploration of the TLM.

This type of study becomes even more important with the recognition of scale-dependence in environmental and ecological patterns. Many disciplines cope with this phenomenon by partitioning work at different scales (Chapter One), and consequently do not particularly emphasise understanding interactions across or between scales, despite recognising their probable importance. In palaeoanthropology, restrictions imposed by the preservational biases and patchy distributions of sources of direct palaeoenvironmental evidence, and by the assumptions and uncertainties of indirect models or reconstructions force a focus on either the small (site or locality) or the large (regional or continental) scales. For primatologists and other ecologists, however, a conceptualisation of environments as multi-scalar, dynamic and hierarchical (with troop ecology, for instance, related in a complex but important way to the ecology and anatomy of the species and the evolutionary history of the genus or family) is central. For exploring a theory like the TLM, which crosses scales (identifying a continental pattern in site distributions and proposing an explanation in terms of interacting processes – like habitat choice and the production of tectonically active landscapes – which occur at different scales to one another and to the original observations, understanding the nature and prominence of scale dependence is therefore also important.

In this chapter, therefore, the focus is on the spatial structure of extant African landscapes, with an emphasis on the ways patterns differ for different variables and at different scales. It emphasises three regions of palaeoanthropological relevance: east and south Africa, where there are extensive hominin fossil records, and west Africa, where – one or two finds notwithstanding (Brunet et al., 1995, 2002) – there is not. All three regions are home to dense human populations (see also Chapter Five) and at least one baboon taxon (Chapter Four). It begins at the largest scale with a very brief discussion of the Earth system itself, before proceeding to mapping exercises focused at the continental, regional and ultimately local scales. All maps are derived from the datasets described in Chapter Two.

An Overarching Context: the Earth System

Environmental scientists conceptualise Earth as a single system (see Figure 5) of interlinked atmospheric, cryospheric, hydrospheric, geospheric and biospheric components.

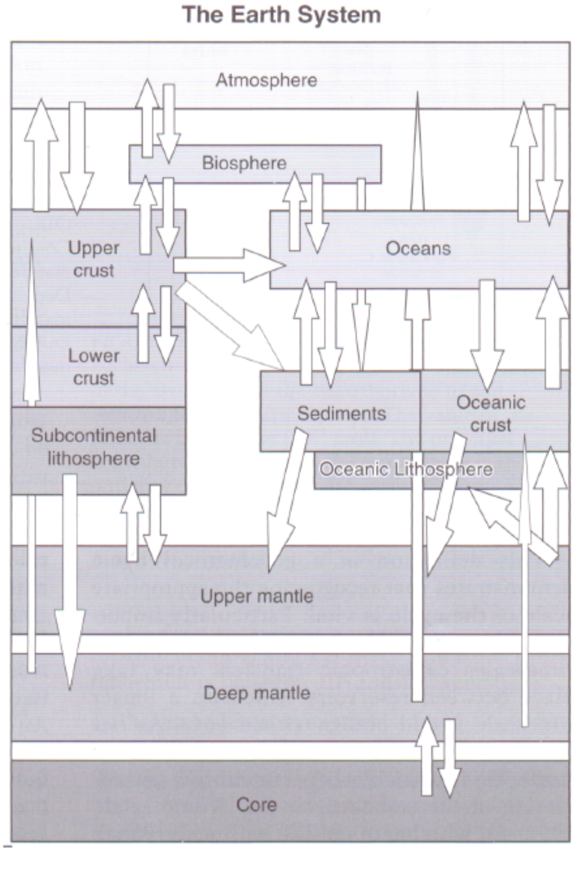


Figure 5: a simple diagram of the Earth system; from Rollinson (2007, figure 1.1).

Conceptual models of this system range from simple diagrams showing interactions between components (which, as in this diagram by Rollinson, 2007, may subdivide some or all of the 'spheres' for clarity) to very complex ones designed to serve directly as a base for mathematical modelling (see for example Schellnhuber, 1999). They may be developed as conceptual wholes, or through the efforts of scientists in different disciplines developing separate, detailed models of their own components and then adapting them to link to one another (e.g. Weaver et al., 2001). They all, however, emphasise the fact that no single environmental component or variable exists in isolation, although the links between them may vary in strength, direction and visibility in different datasets.

As an example (Figure 5), lithospheric landscape formation processes are embedded in constant interactions with the climate system, which may erode or weather land surfaces or (at different explanatory scales) itself be influenced and 'controlled' by patterns of orogeny and land/sea distributions. In the short term, it is obvious that the physical landscape controls river flow, for instance, but at the longer deep-time perspective equally clear that rivers (and winds) shape physical landscapes. Both these views are manifestly true, despite coming into focus at different scales, and they reflect the complexity, logical incoherence and scale-dependence of the Earth system more generally. The environmental patterns we see are probably the emergent results of interacting processes at different scales and within different components of the Earth system; studying any single variable in isolation is thus likely to omit some 'correct' results even while it simplifies analyses, as several spatiotemporal scales are of relevance to almost all environmental research problems (Axel and Maurer, 2011). These concepts (of spatial patterning, scale-dependence and complexity) form the basis for this chapter's analysis of African environments, as they do for most ecological or environmental work of this type, and will be returned to later. As a result, the emphasis will be on the patterns visible in particular maps and not on the precise identities of different soil types, geological units, blocks of vegetation or altitudinal peaks.

AFRICAN LANDSCAPES: THE LARGE SCALE

Many studies of primate and hominin biogeography focus at the large multiregional or continental scale (e.g. Bromage and Schrenk, 1995, Folinsbee and Brooks, 2007, Cote, 2004, Heads, 2010, van der Made, 2011). Patterns at this scale tend to be both relatively simple and easily reduced to direct causes like the action of solar energy driving climate or that of internal geodynamics driving tectonism, as evidenced below.

Climatic Variables: Rainfall, Temperature and Seasonality

The direct influence of the global Earth system on continental environments is most visible in the distribution of climatic variables, directly linked to the global circulation and driven by external forcing (Barry and Chorley, 2003). The four variables analysed here (annual mean temperature and rainfall, and measures of temperature and rainfall seasonality, Hill and Dunbar, 2002) are all basically latitudinally banded in their distribution (e.g Figure 6). These bands split Africa into three regions, the Sahara (hot and dry, with highly seasonal temperatures but uniform rainfall); the immediate sub-Saharan strip (cooler and wetter, with low temperature seasonality and high rainfall seasonality); and southern Africa (intermediate in temperature and to a lesser extent rainfall, with marked temperature seasonality and a little seasonality in rainfall. These zones are modified by some east-west anomalies linked to topography, with the peaks and troughs of the East African Rift Valley (EARV) producing one set and southern coastal processes another in the southernmost zone (Figure 6).

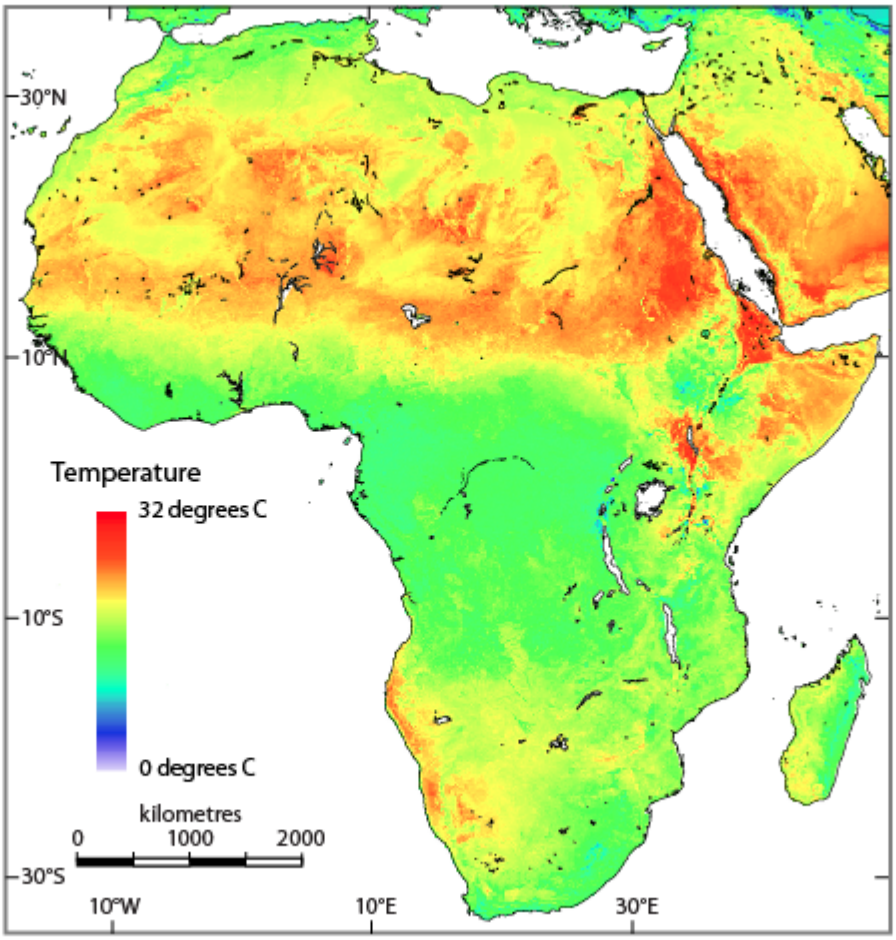


Figure 6: the distribution of mean annual temperature values across Africa, showing the latitudinal banding and topographic/coastal anomalies characteristic of climate.

Physical Landscape Variables: Topography, Roughness, Geology and Soils

The physical landscape variables, in contrast, are linked to the distinctive geophysical and geochemical processes of the planet's interior (Rollinson, 2007) which do not show regular patterning (see Figure 7). There is a general correlation between altitude and roughness at the continental scale (but see also below for discussion at smaller scales), and both are linked to geology and soil variables which are also patchily distributed (see for example Figure 8), especially in the south and east (for soils) and the Sahara zone (for surface geology). Geology and soils, however, also show some influence from climate, reflecting the complex links between geology, soil, climate, vegetation and physical landscape (UNRCS, No date).

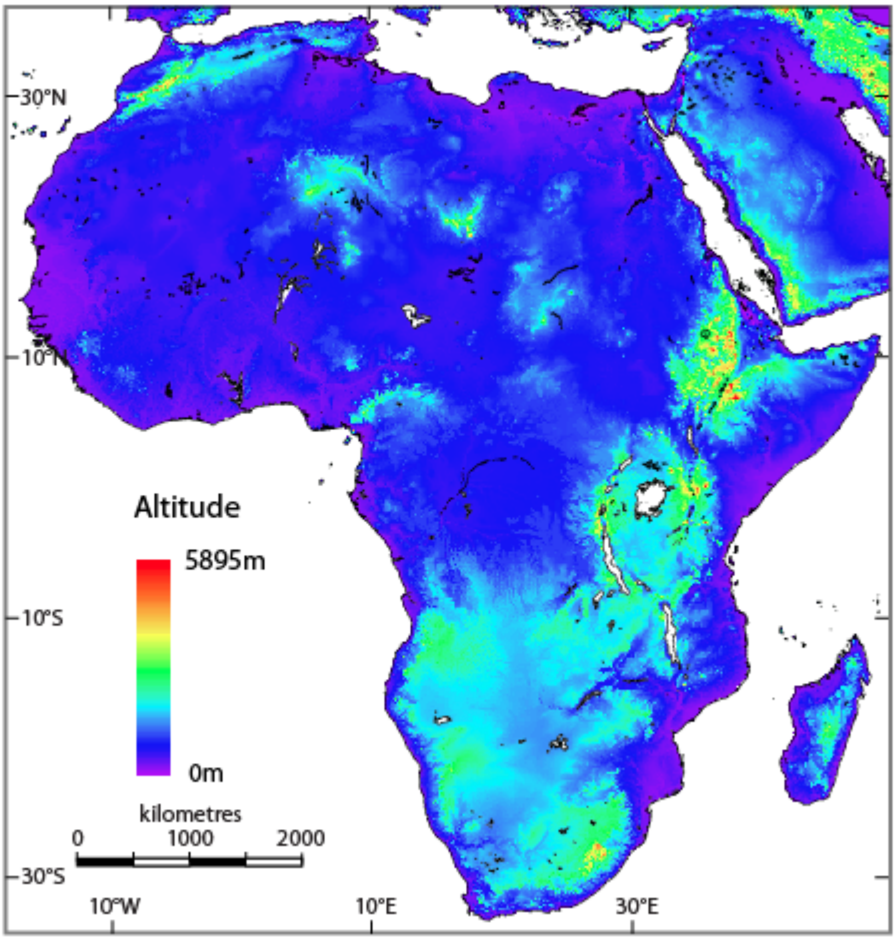


Figure 7: a topography map of Africa, showing the patchy distribution of high and low altitude areas (compare with the map of mean annual temperature above).

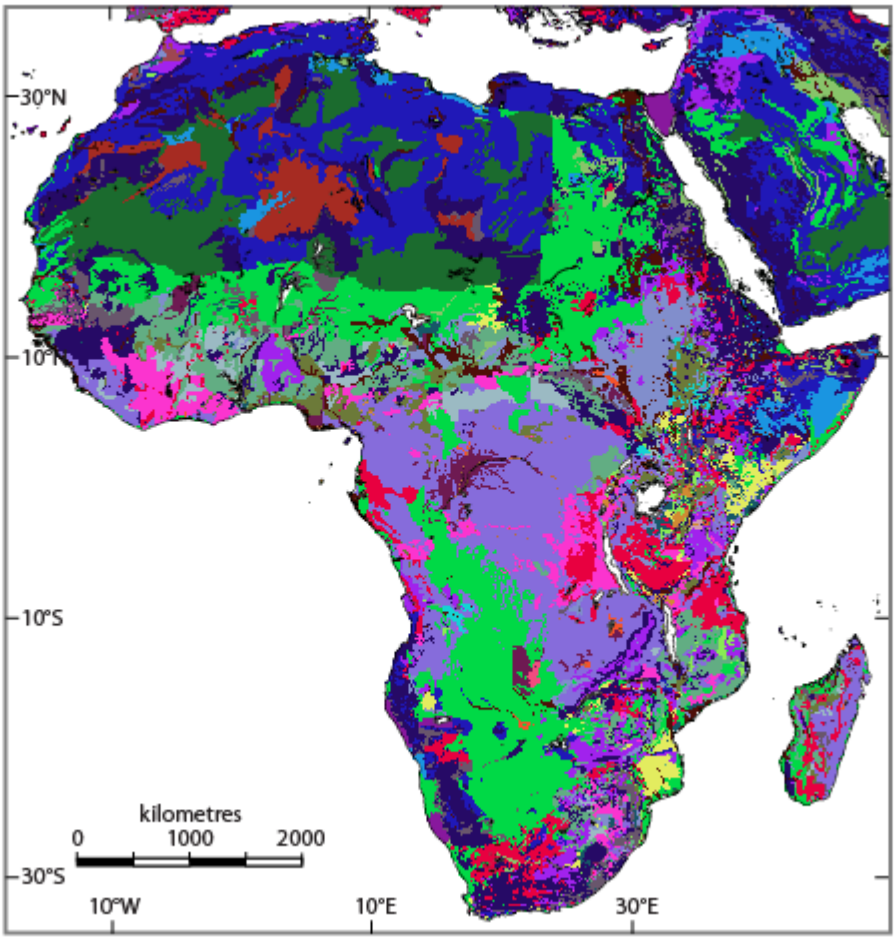


Figure 8: a map showing the distribution of different soil types across Africa, showing the influence of both topography (particularly in the patchy patterns in east and south, compare Figure 7) and climate (particularly in the green and blue banding in the west, compare Figure 6). Different colours indicate different soil types; no detailed legend is provided because it is their distribution rather than their identity which is relevant to this discussion.

Biotic Variables: Vegetation, Ecoregions and Species Richness

Vegetation is a particularly important part of many palaeoanthropological and ecological analyses of species distributions. The vegetation map of Africa (White, 1983, Kindt et al., 2011), Figure 9, shows a distribution of major vegetation types which is a combination of the latitudinal banding patterns seen in climate and the patchy distributions of the physical landscape variables, as we would expect given the close interactions of all these factors in the Earth system (Foley et al., 1998, UNRCS, No date, Retallack, 2007). Both south and east are generally patchy, while the west and north are more predictably banded in vegetation, as the major departures from the latitudinal pattern occur over the areas of high altitude and roughness.

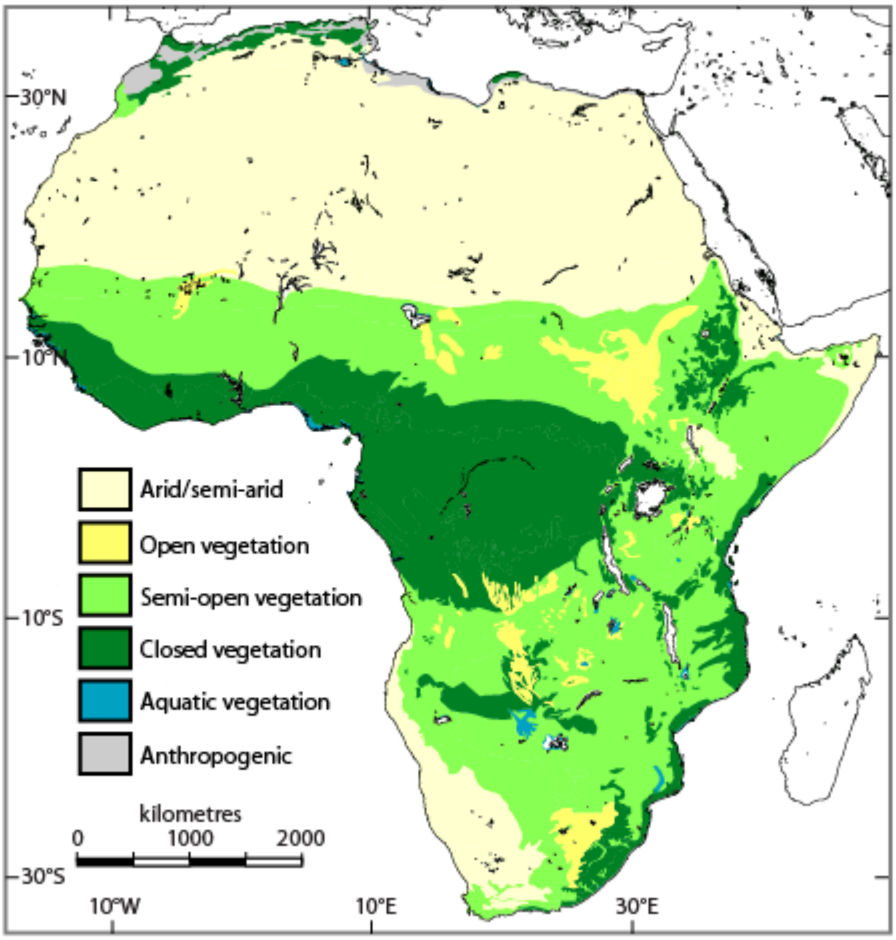


Figure 9: map of major vegetation types in Africa, showing the impact of interactions with both latitudinally banded climatic factors and patchy physical landscape ones.

The species richness map (Figure 10, from Ceballos and Erlich (2006)) also shows a combination of banding – especially in the Sahara and immediate sub-Saharan area – and patchy patterns, with both east and west particularly species rich. It is difficult to map this distribution onto the influence of particular climatic or physical landscape variables, although the anomalies probably reflect certain combinations of landscape variables particularly suited for mammalian survival and diversification. Finally, combining maps of overall species richness and broad habitat types, the WWF have produced an ecoregions map (Figure 11). The distribution of ecoregions in Africa, as this image shows, is very patchy with the exception of a few latitudinal bands in the Sahara, presumably reflecting the influence of climatic, biotic *and* physical landscape factors in this classification of overall habitats.

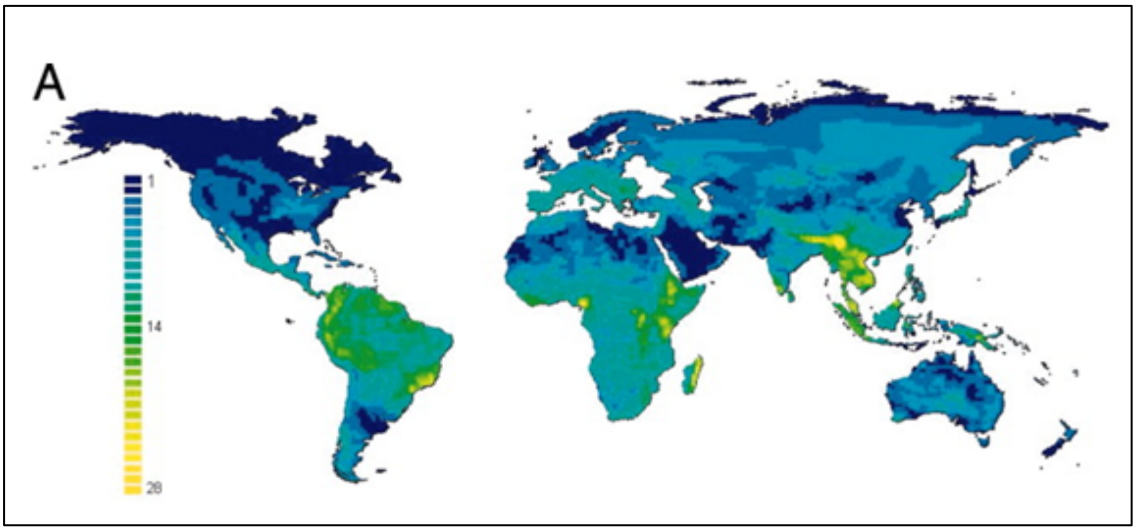


Figure 10: global mammalian species richness map showing another combination of latitudinal banding and patchy distribution. Taken from Ceballos and Erlich (2006, figure 1A),

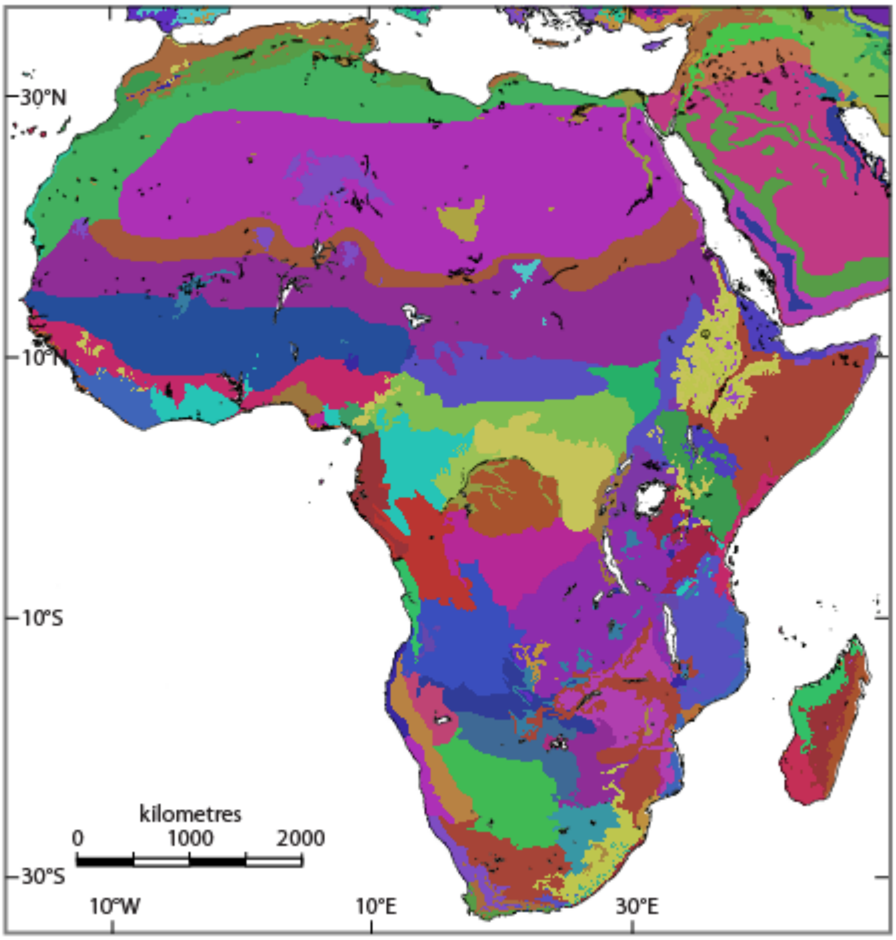


Figure 11: the WWF ecoregions map (Olson et al., 2001), showing the patchy distribution that is the outcome of combining data on vegetation and biota (each influenced by climate and the physical landscape) to produce a broad habitat map. Different types are not labelled because they are locally variable and individual identifications are not useful at this analytical scale.

Summarising Large-Scale Environmental Pattern in Africa

This quick exploration of continental environments has shown that two major patterns dominate: latitudinal banding in the climate variables, and irregular or patchy distributions in the physical landscape variables. There is also a group of intermediate variables – like vegetation and, to a lesser extent, soils – which are banded in certain areas and patchy in others, and seem to be influenced by both the global circulation and the geophysical factors underlying topography and geology. This enables us to build a modified 'environmental system' diagram for Africa based on the broader Earth system and the maps above which classifies these patterns according to position within the system (Figure 12):

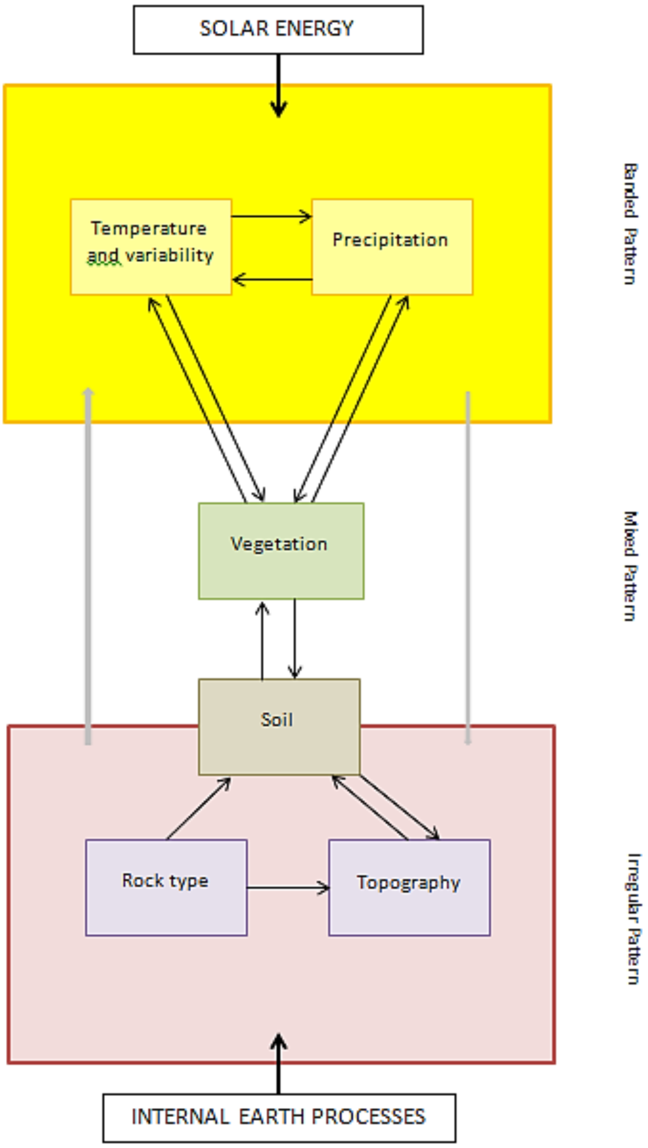


Figure 12: a simplified model of the environmental system controlling continental patterns in Africa. Species richness and ecoregions have been omitted for clarity, but would (as the discussion above suggests) fall into the intermediate zone with their precise placement depending upon the data used.

This fits well with what is known about the basic functioning of the Earth system generally. Patterns in the climate system are driven by incoming solar radiation, which is distributed through the atmosphere via air currents, set up by the uneven distribution of insolation that results from variation in the altitude and distance of particular parts of the Earth's surface from the sun (Barry and Chorley, 2003). Energy is transferred through the atmosphere by radiation, conduction and convection and sets up a three-cell system in each hemisphere (Figure 13) which is driven by differences in the temperature, and hence density, of air at the poles and equator (Barry and Chorley, 2003). The third, central cell is driven indirectly by the other two. This leads to a broadly latitudinal distribution of energy at the Earth's surface which is then modified through local interactions with the land surface and with atmospheric clouds, which have complex influences on both weather (at the local scale) and climate at the larger scale (Lutgens and Tarbuck, 2001).

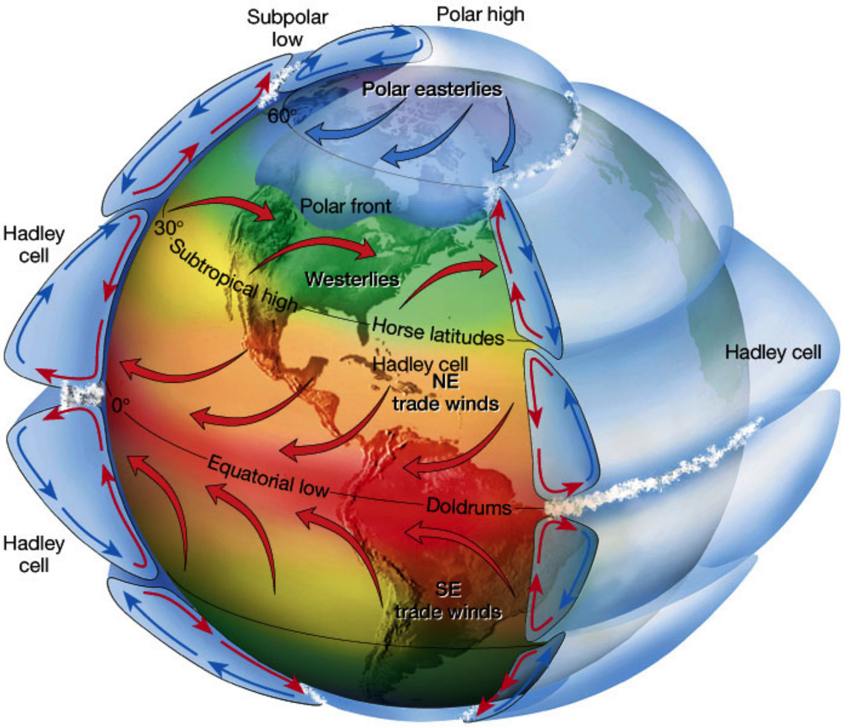


Figure 13: a generalised model of the global atmospheric circulation, showing the origin of the broadly latitudinal distributions of temperature, rainfall and seasonality values observed in the mapping exercises above; from Lutgens and Tarbuck (2001, figure 7.5).

This general circulation then participates in complex, co-dynamic interactions with other elements of the Earth system. The type and density of vegetation plays a part in determining the surface albedo of a region (a measure of the proportion of incoming radiation that is absorbed and reflected), and influences moisture exchange, atmospheric circulation and local weather (Foley et al., 1998), as do other features of the land surface like rocky outcrops and sandy areas. There are also complex feedback loops between atmosphere and ocean which influence the direction and strength of circulation currents in both media and other elements of climate (Barry and Chorley, 2003). The distributions of physical landscape features, in contrast, are controlled by internal Earth processes rather than external forces (Rollinson, 2007). The circulation and convection currents of the interior of the planet influence the location, style and persistence of volcanism and tectonic activity (Partridge, 2010), as does the structure of Earth's crust and surface. These features also interact in complex ways with both climate and biosphere, as illustrated through the maps above. It is important to remember that these maps are therefore static representations (snapshots) of what is, in reality, a complex multi-layered Earth system which is not necessarily in a stable equilibrium at the time of analysis. Processes like desertification which set off rapid feedback loops that rearrange whole environments are indicative of system flips from one equilibrium to another. Modern humans, with their propensity for large-scale environmental modification, are potentially capable of causing such flips as well as responding to them, leading to further interactions between behaviour and environment and indicating even greater complexity in the landscape systems associated with human evolution.

The discovery of differing broad patterns in climate, physical landscape and vegetation or soils at the large scale is particularly significant for this thesis. It seems reasonable to assume that the basic structure of the global circulation has not changed much over the last 6Ma despite periodic and idiosyncratic changes to overall energy balances (Behrensmeyer, 2006), while the tectonic structure of the Rift Valley, while undoubtedly subject to development and change, has persisted as the dominant feature of African physical landscapes for many millions of years (Tiercelin and Lezzar, 2004). This means that the same broad patterns – latitudinal banding, patchiness and intermediate patterning – are likely to have dominated African landscapes throughout that time, with spatio-temporal changes in conditions mostly affecting the extent of patches and/or bands and the specific conditions within them. It would therefore seem plausible at least to begin to work on distinguishing the effects of different landscape preferences on the distributions of organisms. For the hominins, for example, the presence of sites across pretty much the full latitudinal range of Africa (Figure 14) argues against a simple climatic preference as a determinant of their distribution, even when the effects of taphonomy – which preferentially destroys remains or moves them over (comparatively) short distances, and cannot 'create' spurious data points from nothing (Cote, 2004) – are taken into account.

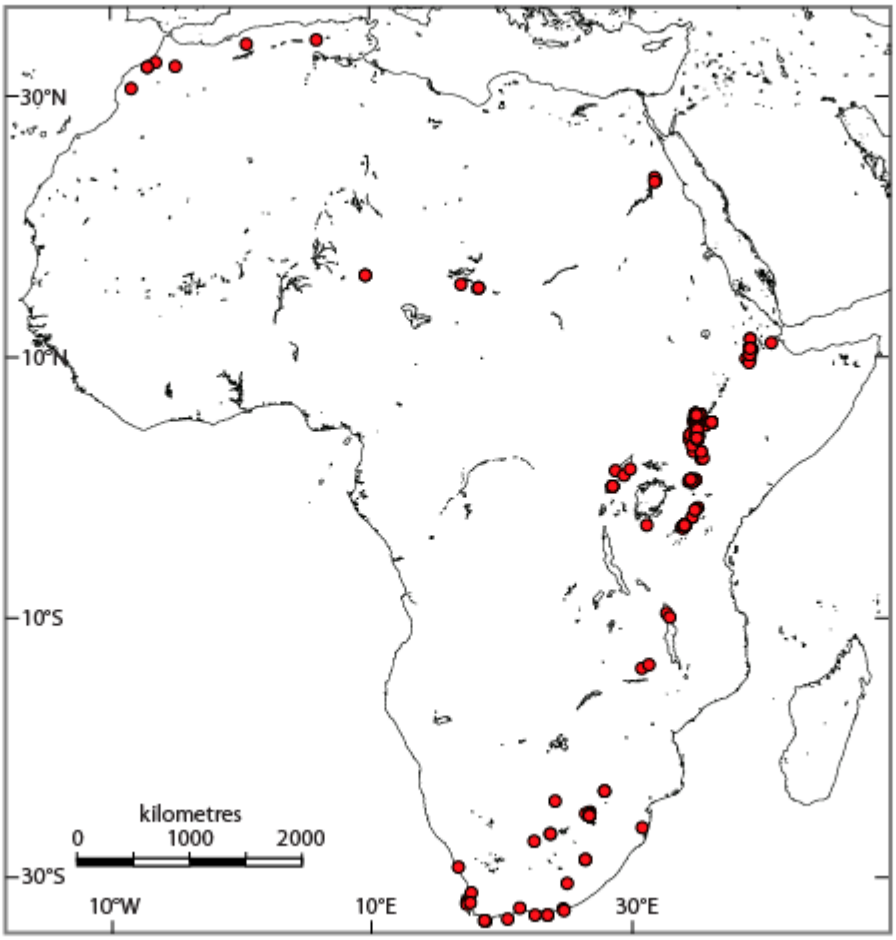


Figure 14: the distribution of known fossil sites in Africa (including sites with fossils of early hominins, australopiths and members of the genus *Homo*), showing that these sites span the full range of latitudes despite any taphonomic influences.

While these results of course do not imply that it is possible to accurately reconstruct past landscapes by extrapolation from current conditions – the uncertainties on all sorts of important parameters and on the precise interactions between different variables make this virtually impossible – they do suggest that further investigation of extant landscapes might shed light on certain aspects of them. The presence of regional differences in the balance between variables, visible on the continental maps particularly in the spatial patterning of intermediate variables like vegetation (Figure 9) which seem to be dominated by the effects of climate in some areas and physical landscapes in others, is next to be explored.

AFRICAN LANDSCAPES: THE REGIONAL SCALE

The continental maps above suggested some key differences between east, south and west Africa – the study regions chosen for this study – in terms of the distribution of major environmental variables, particularly vegetation and other intermediate variables. Here, these regional patterns are explored in more detail. For each area (east, west and south) a 15 by 15 degree tile was chosen for analysis on the basis of palaeoanthropological relevance.

Environmental Patterning in East Africa

The part of east Africa chosen for analysis centres roughly on Lake Victoria, and ranges from 25-40ºE and 10ºS to 5ºN (see Figure 15 below). The region contains a number of fossil hominin sites of species from *Ardipithecus* through to *Homo*, and is home to dense modern human populations (see Chapter Five) and two baboon allotaxa, *P. anubis* and *P. cynocephalus*. Figure 15 shows the regional topography.

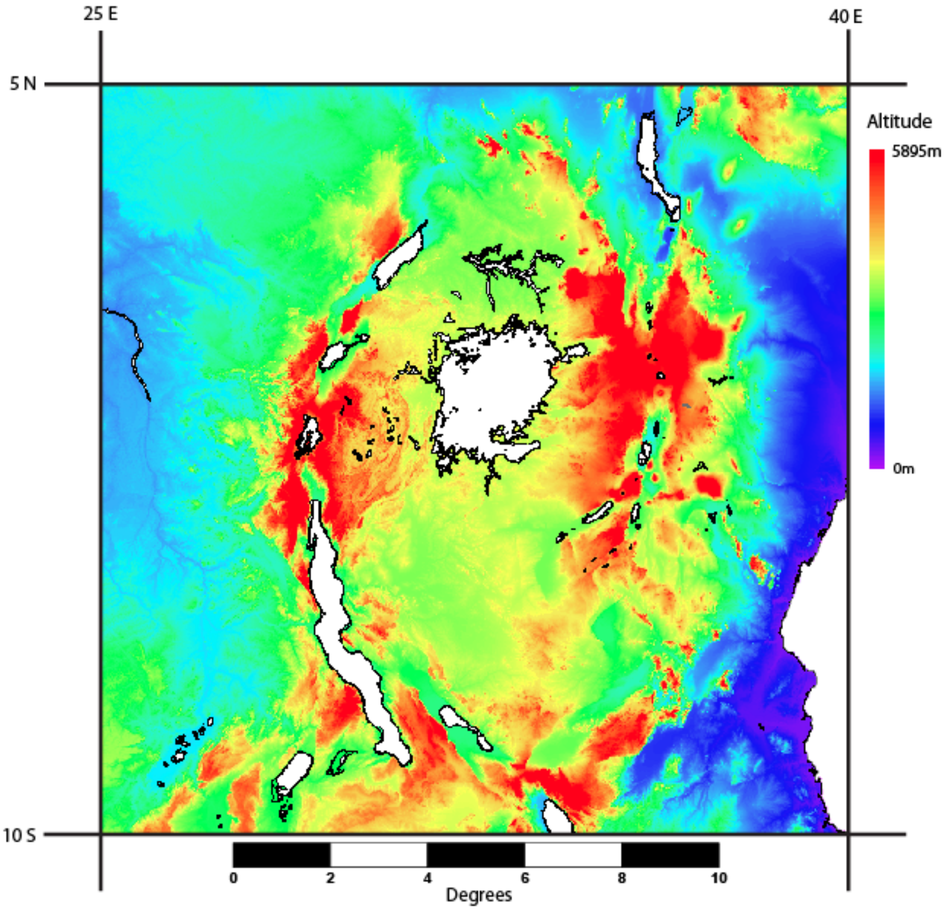


Figure 15: map of east African topography, the pattern of which forms the basis for the regional environmental structure (compare figures below).

This topography is dominated by the two curved linear ridges of the eastern and western sides of the Rift which link the area's altitudinal peaks and enclose an area of moderately high altitude (yellow on Figure 15) within which the Rift Valley lakes are embedded. The outer edges of each ridge drop rapidly down to the coast in the east and the plain to the west. The corresponding roughness map (Figure 16) is very similar, although zones of high roughness extend beyond the zones of high altitude. The relationship between altitude and roughness is more complex in this region than at the continental scale, with areas of high altitude and lower roughness visible east of Lake Victoria and areas of moderate-high roughness in low-moderate altitude regions of the coastal strip.

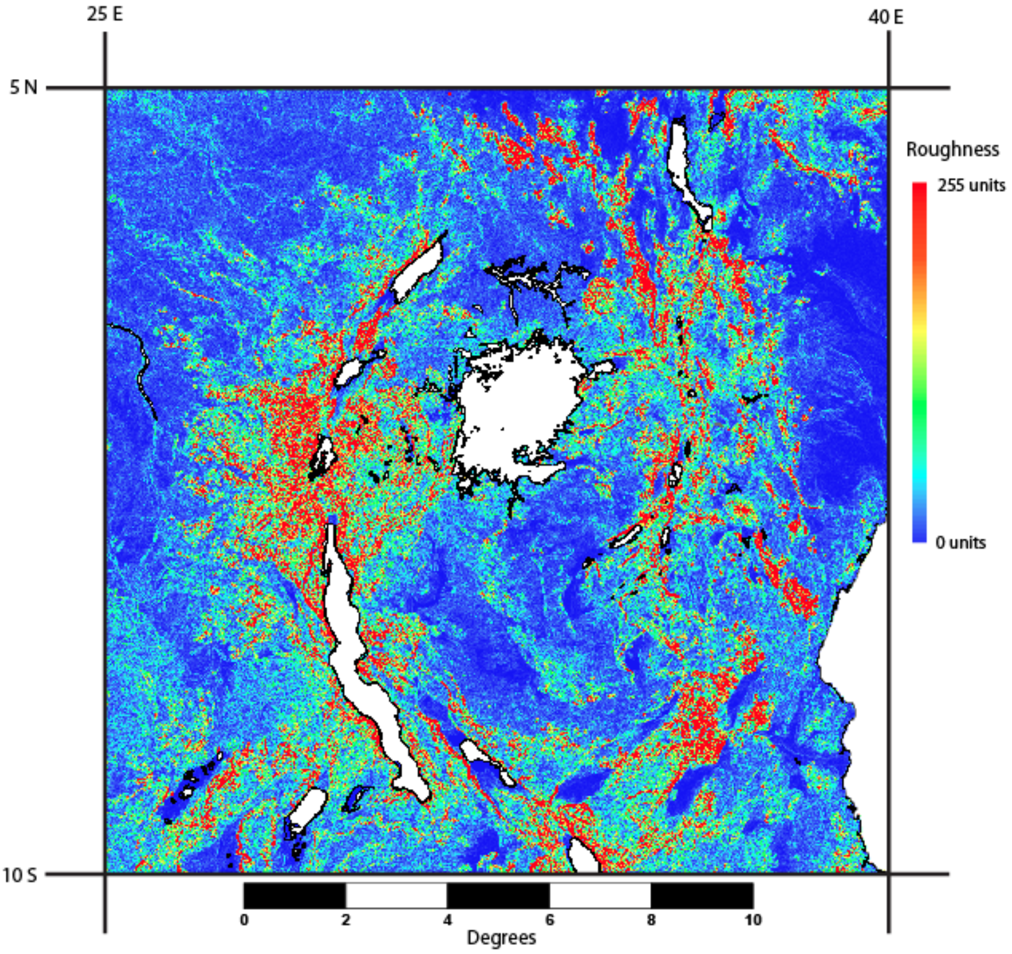


Figure 16: topographic roughness map of the same area as in Figure 15. Lake Victoria is the central (rounded) white shape.

The surface geology also follows a similar pattern, with the area consisting broadly of Precambrian rocks with small areas of more recent rock, mostly from the Quaternary, visible along the Rift Valley ridges and in blocks across the surrounding areas. Soils (Figure 17), in contrast, show a more patchy distribution with a very fine mosaic visible to the northeast of the eastern rift ridge and a coarser grained pattern elsewhere. There is some banding in the west of this study region, but it runs longitudinally rather than latitudinally and presumably occurs in response to rifting rather than climatic variables.

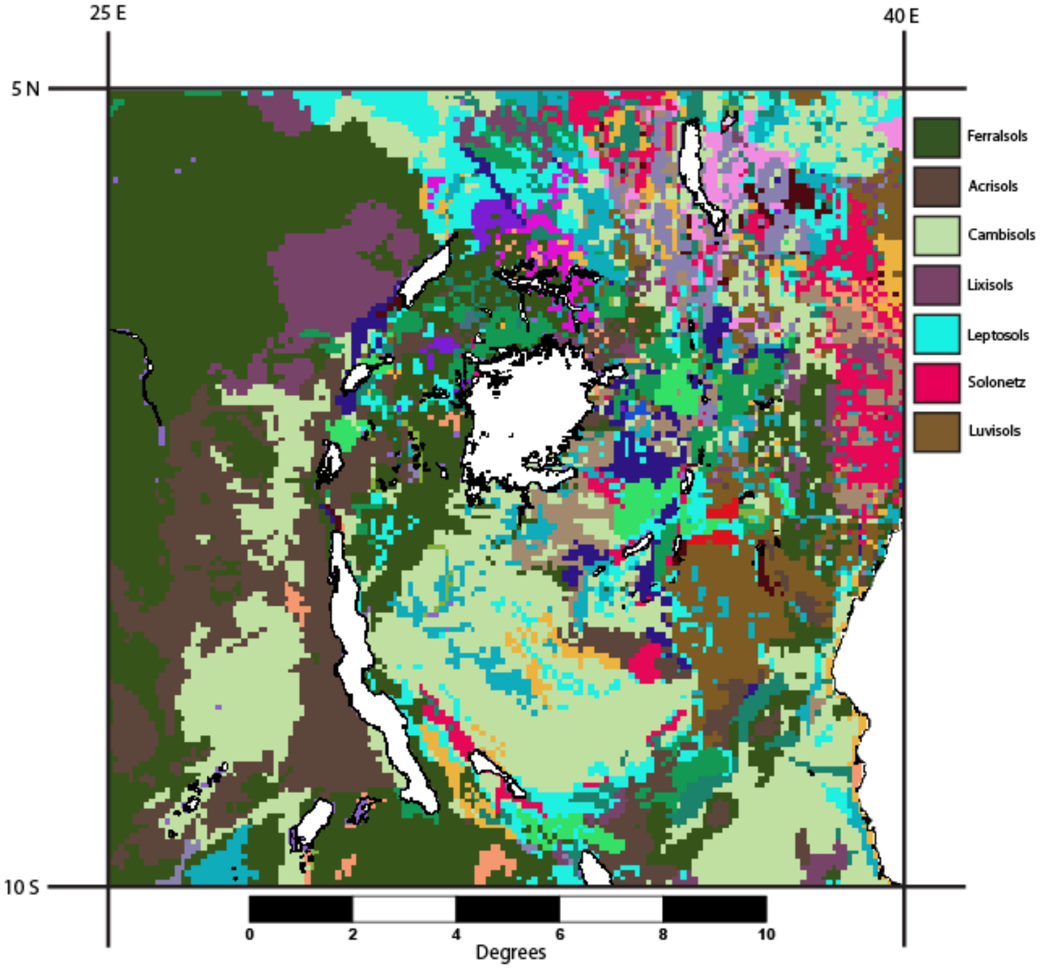


Figure 17: a soils map of east Africa, showing a patchy distribution of soil types across the whole region and especially in the northeast. Only major soil types are labelled, as it is the pattern – not the identity of individual zones – which is important.

For the climate variables, there is no latitudinal banding in east Africa (see for example Figure 18) despite the broad prevalence of this patterning at the continental scale. Instead, for temperature, rainfall and temperature seasonality we see spiral patterns where patches of high and low mean values run around the edges of the rift valley, break through at low altitude spots, and alternate with one another along the ridges. The only exception appears in a map of rainfall seasonality, which shows a single latitudinal band of higher rainfall seasonality across at about the equator. This does veer slightly northward at the northern edge of Lake Victoria, however (Figure 19), and is not uniform so may represent a weak spiral pattern. This is the only latitudinal banding pattern visible in any of the east African maps.

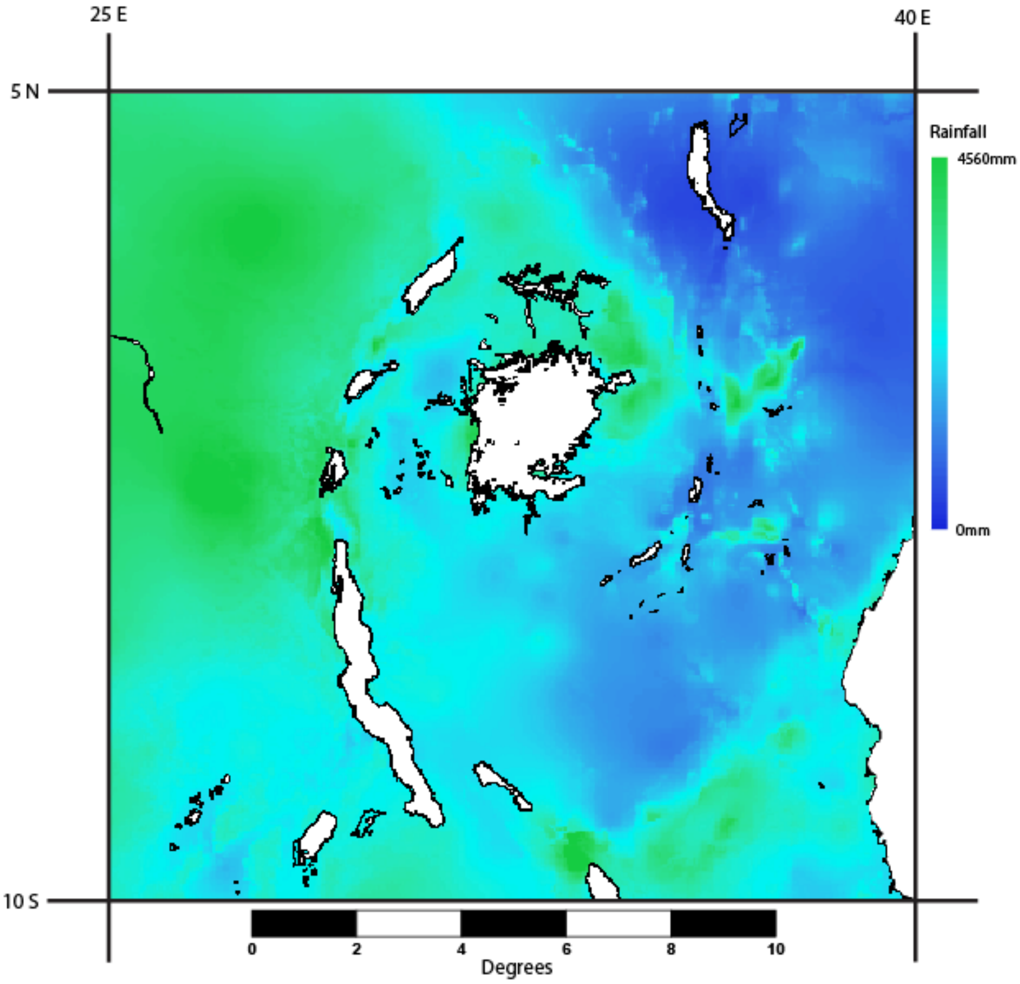


Figure 18: annual mean precipitation map for east Africa, showing the lack of latitudinal banding in this region.

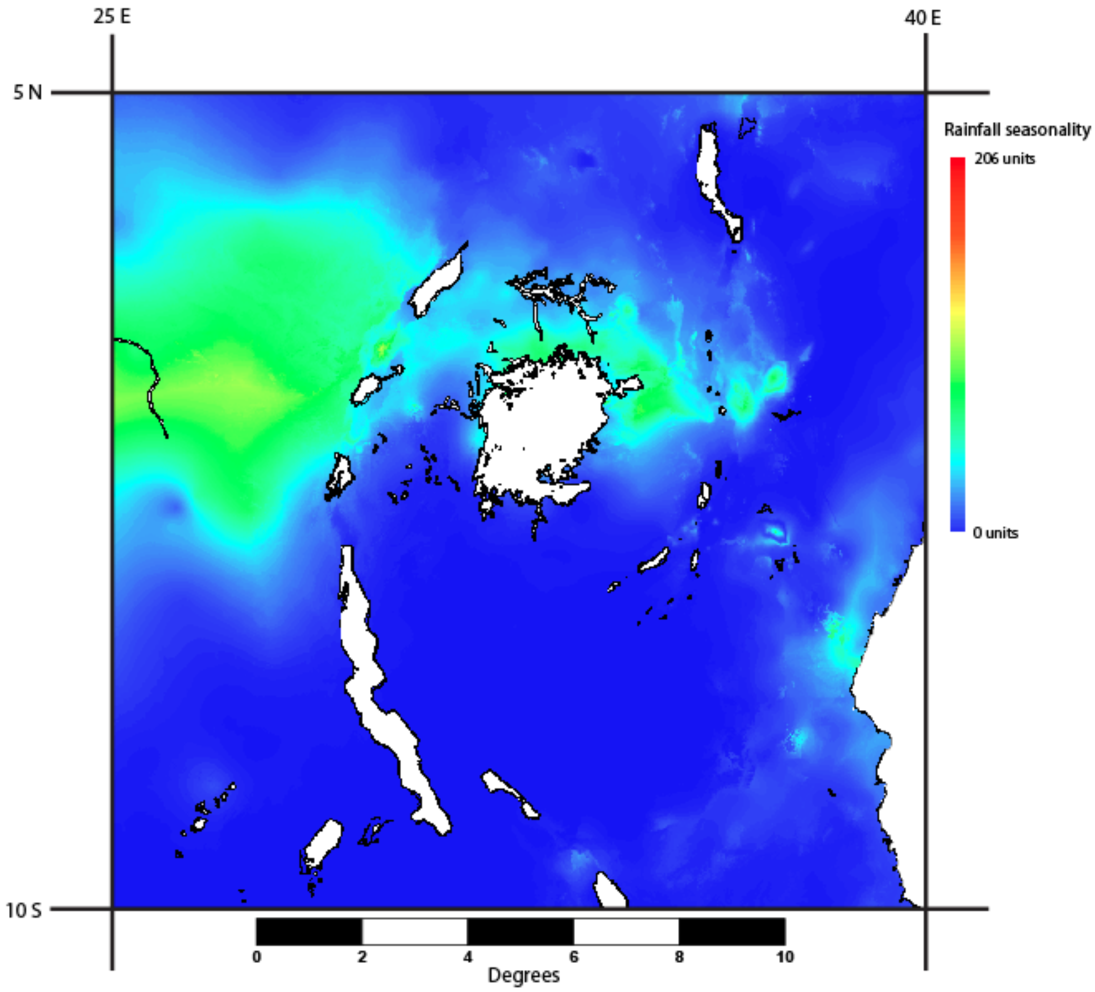


Figure 19: a map of rainfall seasonality (in units of variance) showing what may be a weak latitudinal banding pattern near the equator.

Vegetation (Figure 20) shows a spiral of closed habitats (forests and forest mosaics) to the west and north of the rift valley, with scattered patches of open grassland and semi-open contexts (bushlands, thickets and sparser woodlands) covering much of the east and south. There are also coastal bands of aquatic and closed vegetation. The east African region's topographic anomalies seem to completely eradicate the influence of latitudinal banding from the continental and global climate system on regional vegetation.

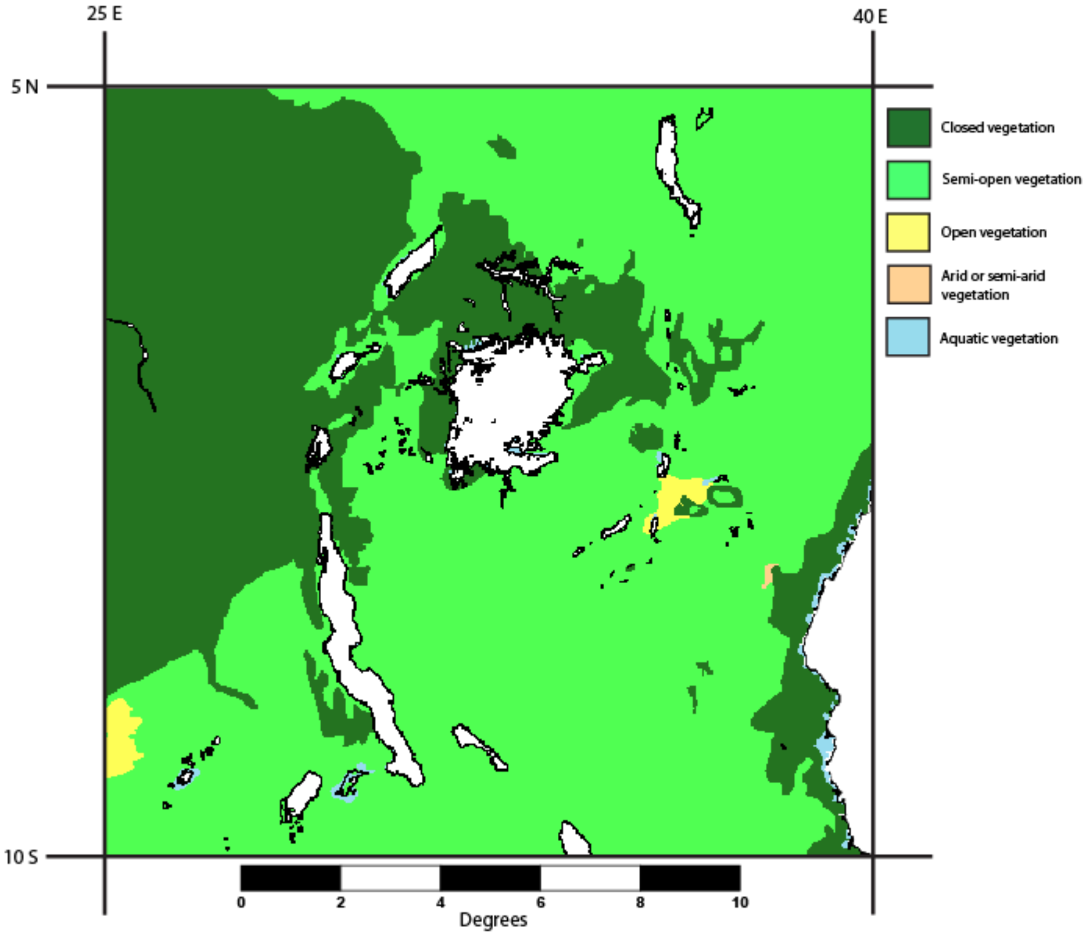


Figure 20: east African vegetation map, showing the spiral patterns in the distribution of different vegetation types.

Looking at ecoregions in more detail (Figure 21), the spirals subdivide into patches. The forest along the western ridge is Albertine rift montane forest, while the altitudinal peaks on the east show small areas of east African montane moorland embedded in east African montane forest. The wider areas of closed and semi-open habitats surrounding these areas, and filling the gaps between Lake Victoria and the rift ridges have subdivided into closely related groups of habitats, typically labelled Congolian to the west and with a variety of names to the east. The coastal forest mosaics and mangroves along the coast remain visible, but the open habitat patches do not appear in the same configuration as in Figure 20.

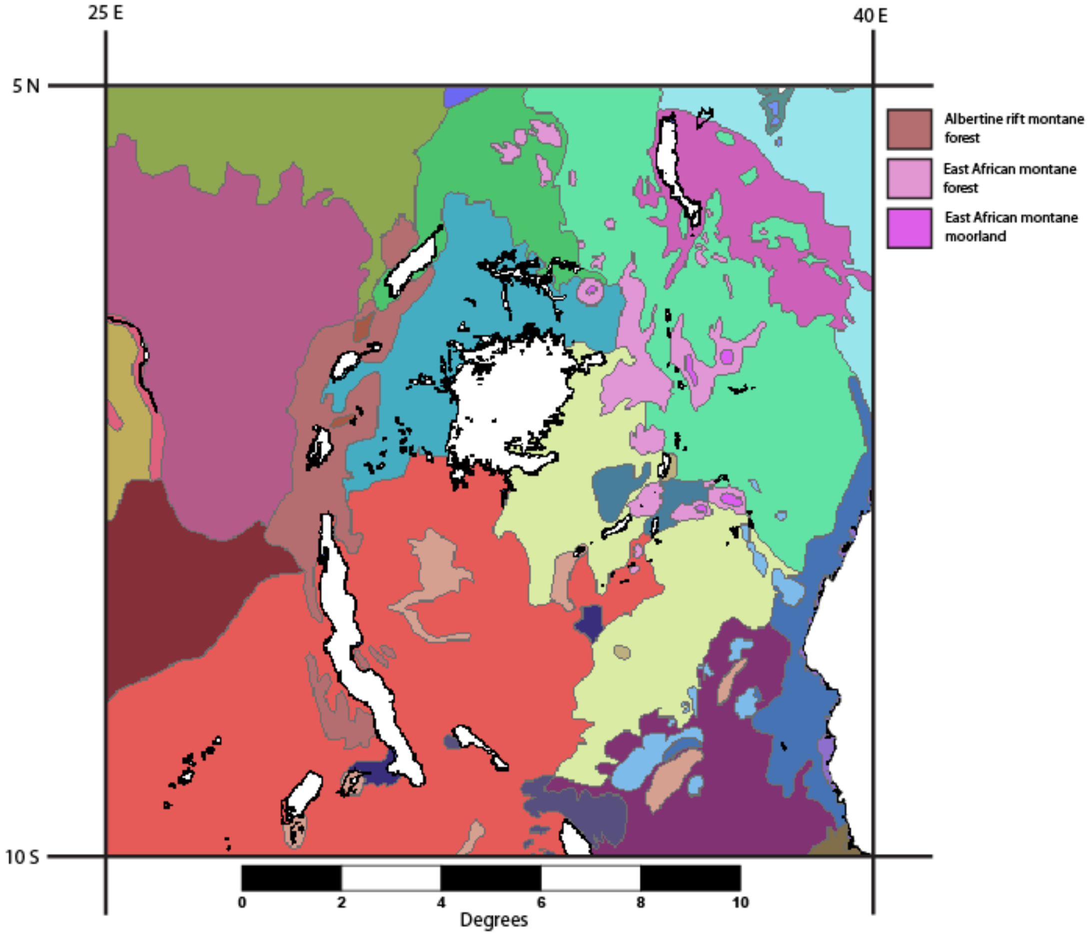


Figure 21: WWF ecoregion map of east Africa showing the patchy, but partially topographically influenced, distribution of habitats/ecosystems in this area. Only those ecoregions which are discussed are labelled, as it is the pattern – not the identity of individual patches – which is important.

Overall, east Africa thus does not show neatly scaled-down versions of the continental patterns in environments summarised in Figure 12. Instead we see a landscape shaped almost exclusively by physical landscape patterns linked to the rift valley tectonics. This results in more correlation between vegetation, climate and topography than we see at the continental level, with interesting implications; while at the continental/global scale the outcomes of climatic, vegetational and topographic theories of hominin evolutionary environments are plausibly distinguishable, within the east African region this is much less likely as all patterns are relatively similar and patchy rather than latitudinally banded.

Environmental Patterning in South Africa

For the south African regional analysis, the 15 by 15 degree block chosen spans the Cradle of Humankind and ranges from 20-35ºS and 20-35ºE. The cradle itself comprises a small area containing 30+ fossil sites of australopiths – including members of *Paranthropus* – and *Homo* specimens. Later sites are also found further south, and the area is currently home to chacma baboons (*Papio ursinus*) and dense human populations on the coast. It is tectonically active, albeit at a somewhat smaller scale than the rift valley (King and Bailey, 2006), and there are several recently discovered faults and tectonic features in the area which lend additional support to the TLM (Bailey and King, 2011). The regional topography is shown in Figure 22. It is simple, with a single altitudinal peak of 3473m (compared to 5895m in east Africa) located near Lesotho, and a coastal plain of varying width to the south and east. Much of the southern coastal strip, although low-lying, is rough (Figure 23), as is the high altitude zone, while the northwest and northeast coastal plains are flat.

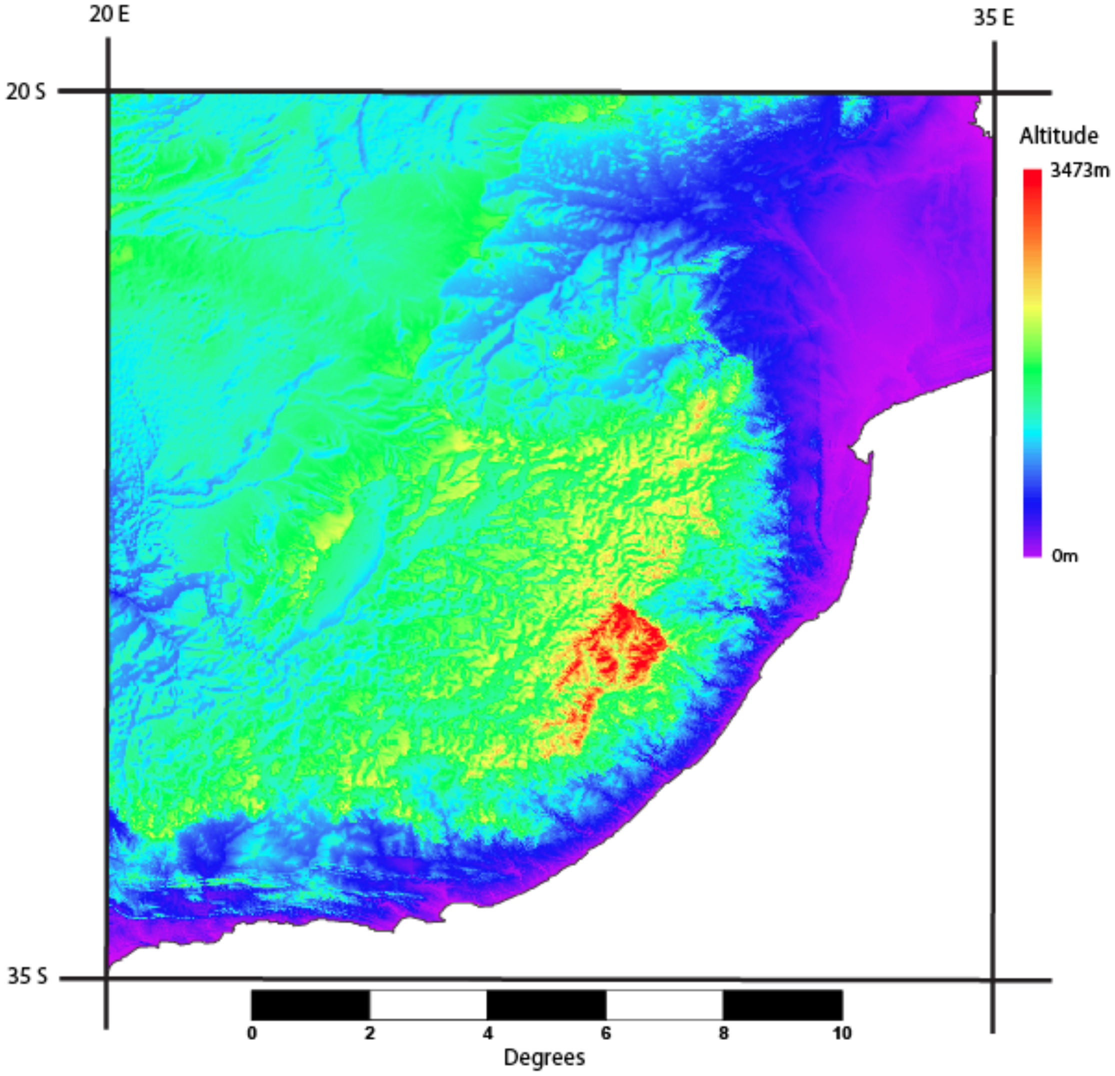


Figure 22: a topography map of the south African region.

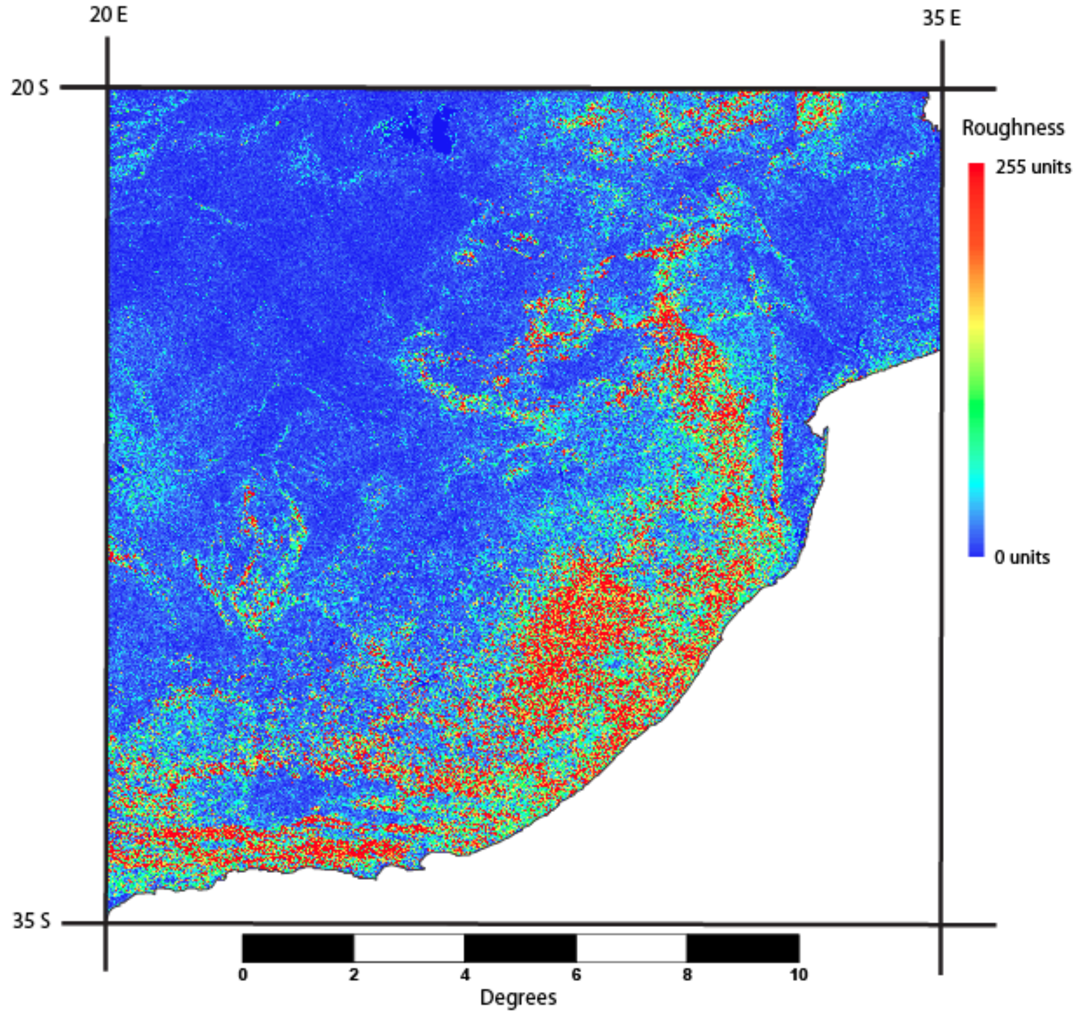


Figure 23: a roughness map of the south African region, showing the multiple peaks on the coast and in and to the north of Lesotho.

Geologically, the Lesotho area stands out as a single region of Mesozoic igneous rock surrounded by concentric rings of Triassic and Permian geologies (Figure 24). The relatively rough area bordering this and reaching up into southern Zambia is older (Precambrian), while the flat coastal plains and interior are more recent (Pleistocene and Cenozoic respectively).

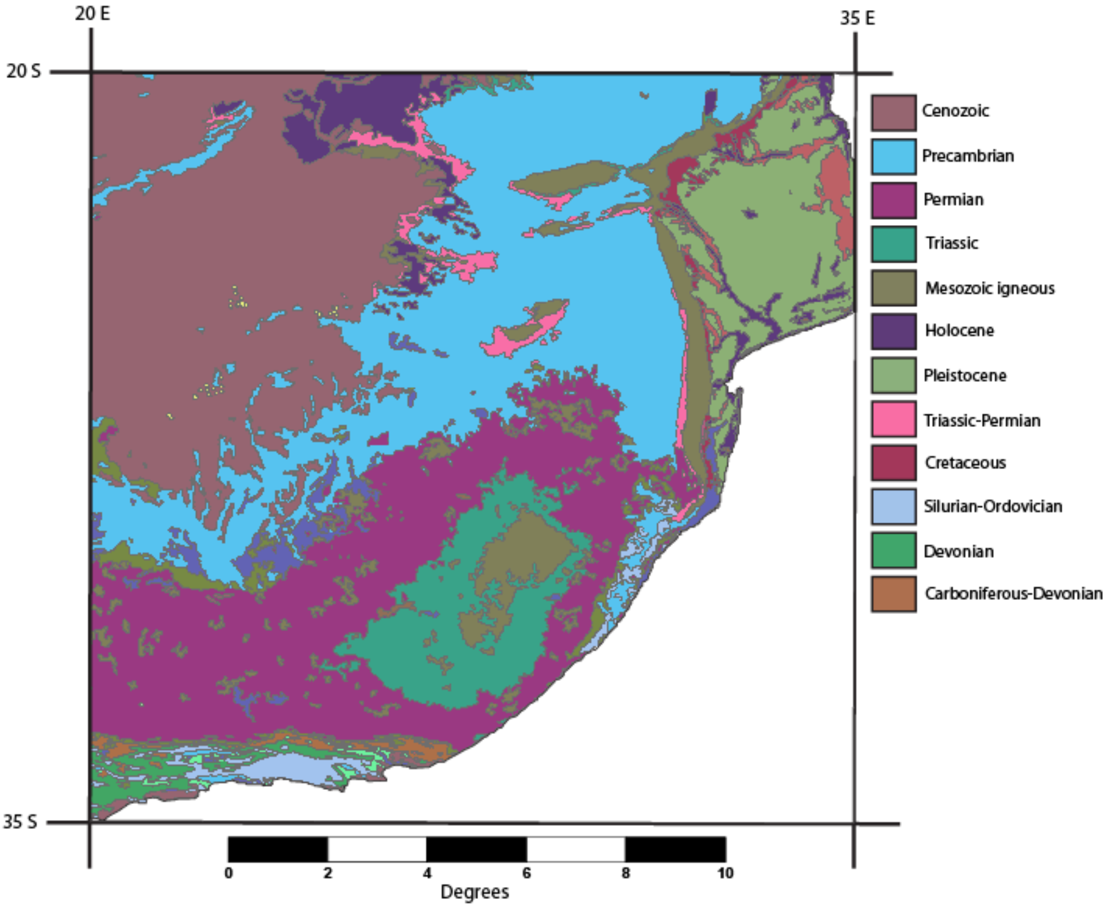


Figure 24: geological map of south Africa showing the structure of the physical landscape. Lesotho is located just south of the centre of the tile.

The soil map, however, is less clear with only the Cenozoic interior and Pleistocene coastal plain represented in zones of particular soils, specifically arenosols and solonetz soils respectively. The remainder is covered with a patchwork that shows no clear patterning.

In southern Africa the broad distinction in pattern between physical landscape and climate visible at the continental scale does seem to hold truer than for the eastern region described above. In the south, climate shows at least partial latitudinal banding (Figure 25). The modifications to this pattern here are both topographic and coastal, with the latitudinal bands deflected northward where they meet the east coast. This type of coastal modification of weather and climate is well known at a range of scales (Barry and Chorley, 2003).

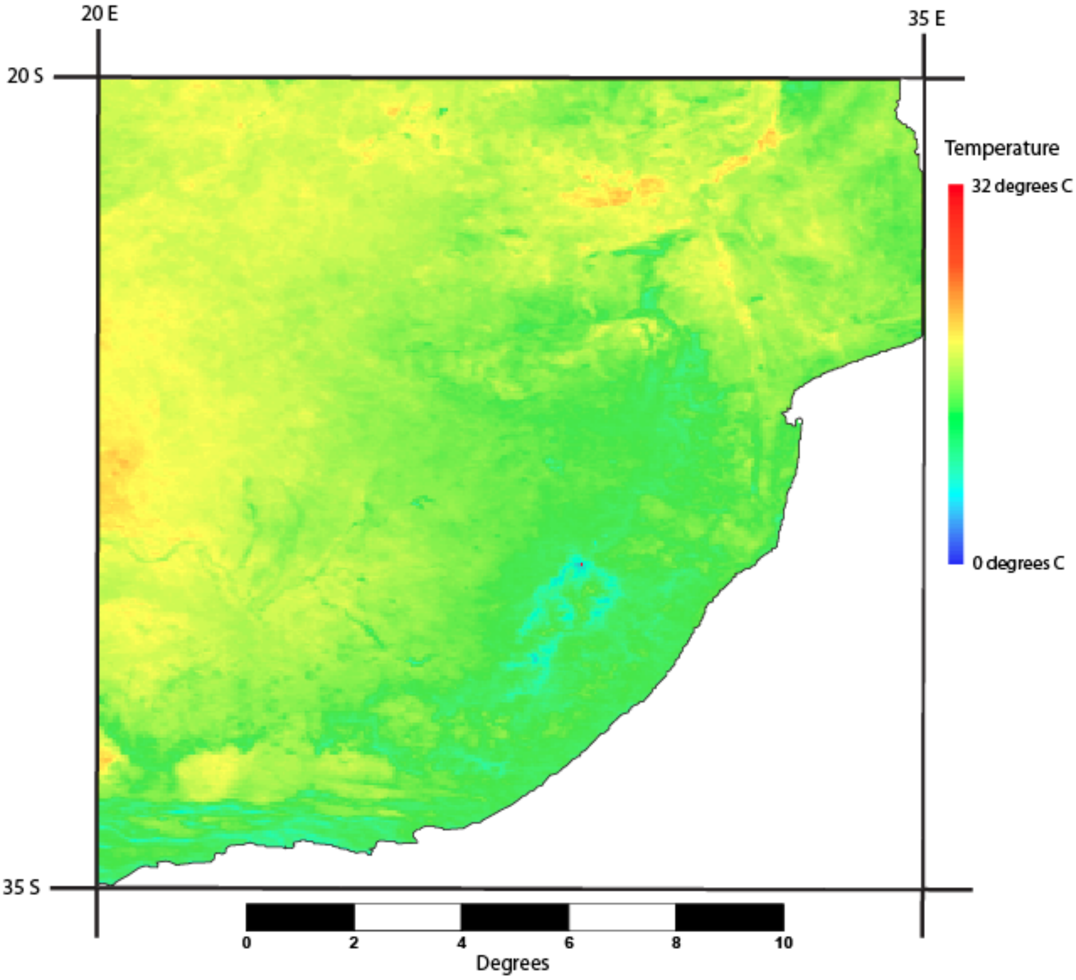


Figure 25: distribution of different mean annual temperatures in southern Africa, showing a modified latitudinal banding pattern presumably produced by the coastal weather effect.

Both seasonality maps show similar patterns, with the band of relatively low annual mean temperature around the coast replicated in coastal bands of relatively high seasonality compared to inland zones. While latitudinal banding is apparent in south Africa, however, it is somewhat modified by topography – the altitude peak in Lesotho clearly modifies the temperature (Figure 25) and precipitation maps (Figure 26), for example, as does the linear topographic feature where the northeast coastal plain meets rougher, higher altitude inland zones (compare Figure 24).

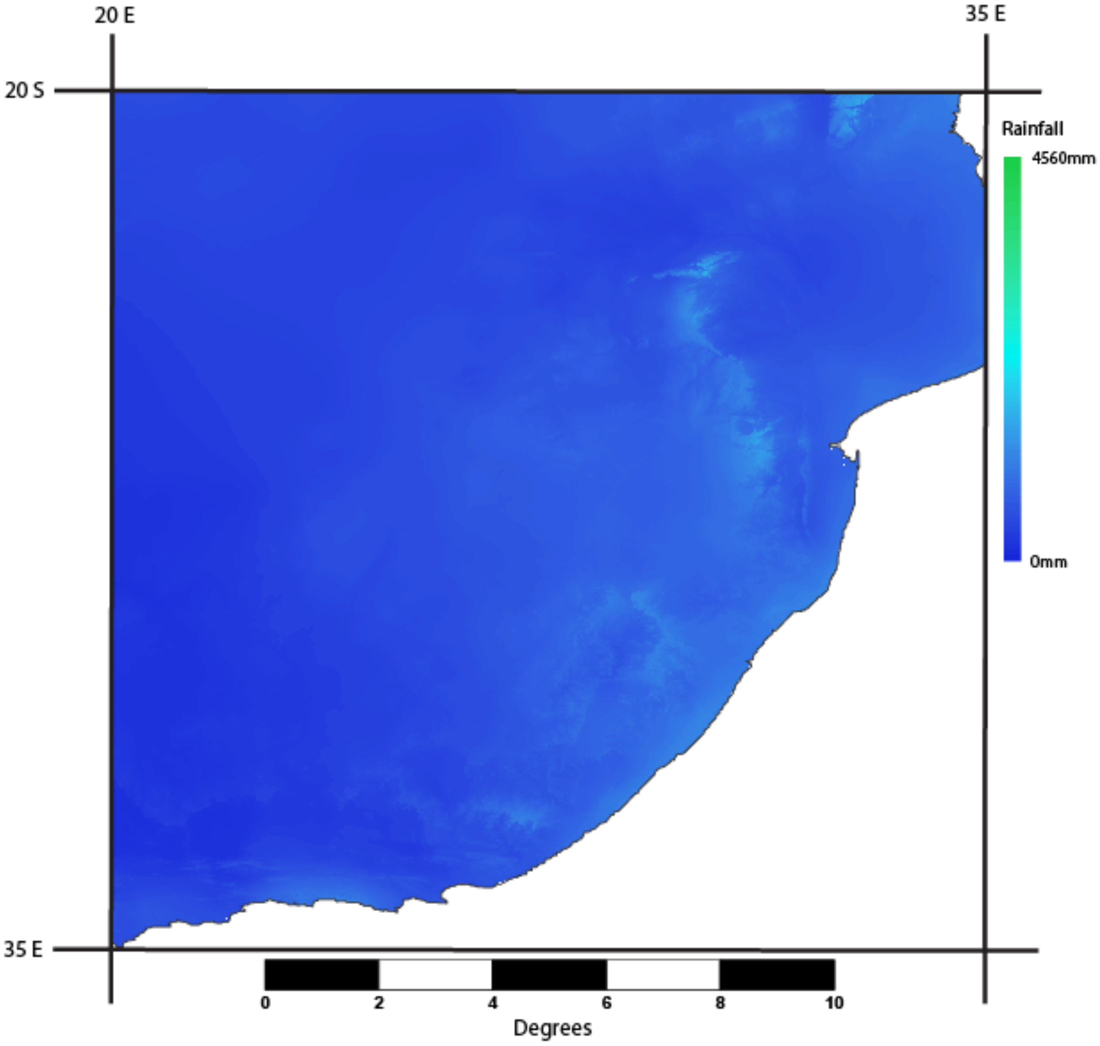


Figure 26: map of annual mean precipitation values for southern Africa, showing the slightly increased values associated with topographic peaks (Lesotho) and boundaries (along the edge of the coastal plain).

Both physical landscape and climate seem to have impacted vegetation and ecoregion patterns. The vegetation map (Figure 27) shows a stripe of closed forested vegetation along the southeast and east coasts which extends up the coastal slope of the Lesotho peak. The other side is covered in grasslands, with no apparent regard to either climate or geology/soil distributions, while elsewhere there are several areas of aquatic vegetation and a large zone of arid/semi-arid vegetation in the south west of the study area. This is likely the result of complex interactions between physical landscape and climate factors, as the lack of direct correspondence between vegetation and other variables suggests the former is an emergent property of these interactions.

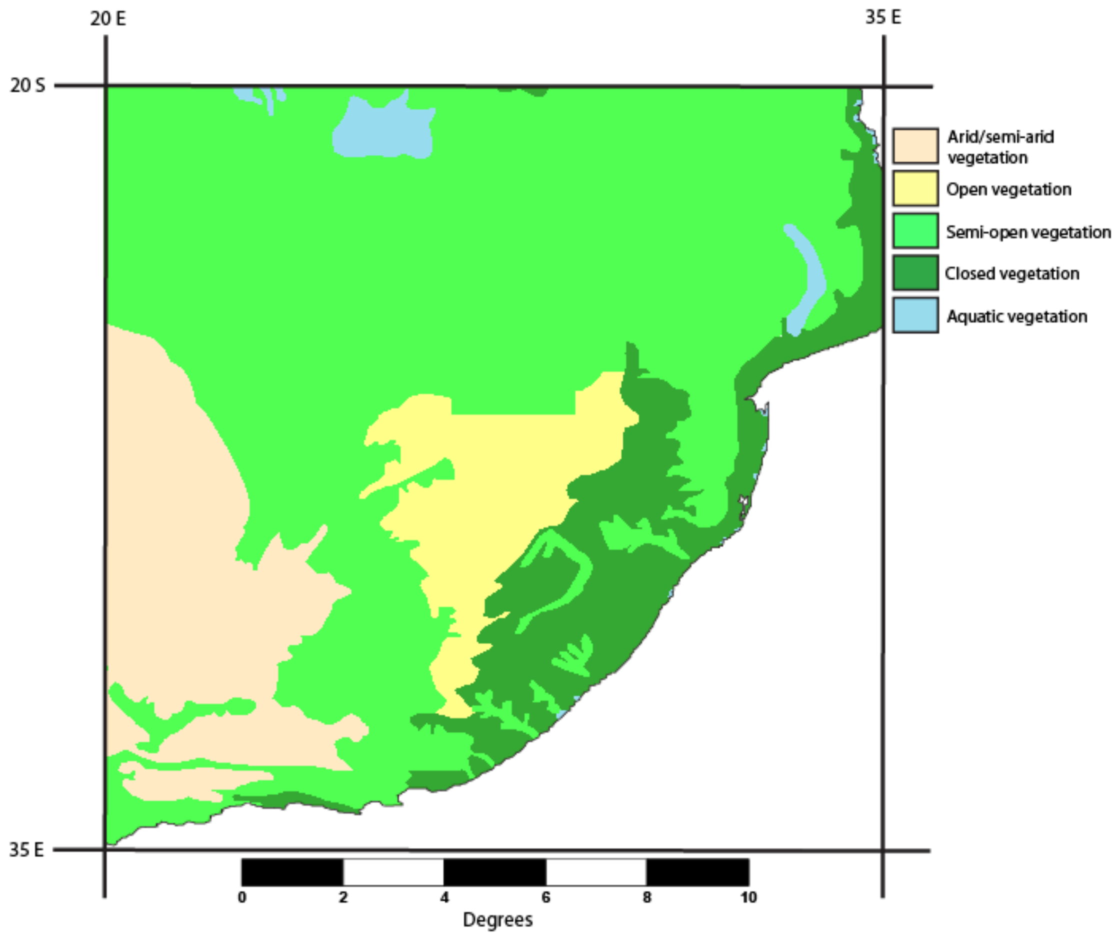


Figure 27: vegetation map of southern Africa.

The ecoregion distribution is similar but not identical, with the aquatic vegetation, coastal forests and Lesotho grasslands mapping directly onto specific ecoregion units while the remaining semi-open and arid/semi-arid regions are further subdivided into latitudinal units in the west and longitudinal zones to the northeast. The precise identity of these ecoregions is not particularly important, but the fact that their boundaries do not coincide with the edges of major vegetation zones identified above is interesting, although a quick exploration of the literature suggests it may represent nothing more than different definitions of boundaries in different datasets (Olson et al., 2001).

Overall, in south Africa the regional environmental structures reflect those seen at the continental scale rather better than those in east Africa (above). There is some latitudinal banding in climate which was absent in east Africa, and vegetation/ecoregion distributions are influenced by both this banding and the topographic features, although the zone boundaries do not map neatly onto either influencing component. If past environments followed similar patterns, then the distributions of fossil sites produced by specific climatic, topographic and vegetational preferences might be relatively (though not wholly) distinguishable in this region, depending upon the influence of taphonomy.

Environmental Patterning in West Africa

The final regional case study chosen is a complementary region to the hominin-rich areas of east and south Africa described above. It is located between 5-20ºE and 15-0º N, at approximately the same latitude as the east Africa region, and spans the Nigeria-Cameroon border, an area which is very primate rich (Sommer and Ross, 2011) and home to both *P. anubis* and dense human populations. It does not contain any hominin sites, although two species – *Sahelanthropus tchadensis* and *Australopithecus bahrelghazali* – have recently been discovered to the northeast in Chad. The absence of hominins may be taphonomic or ecological. The regional topography and roughness are shown in Figure 28 and Figure 29.

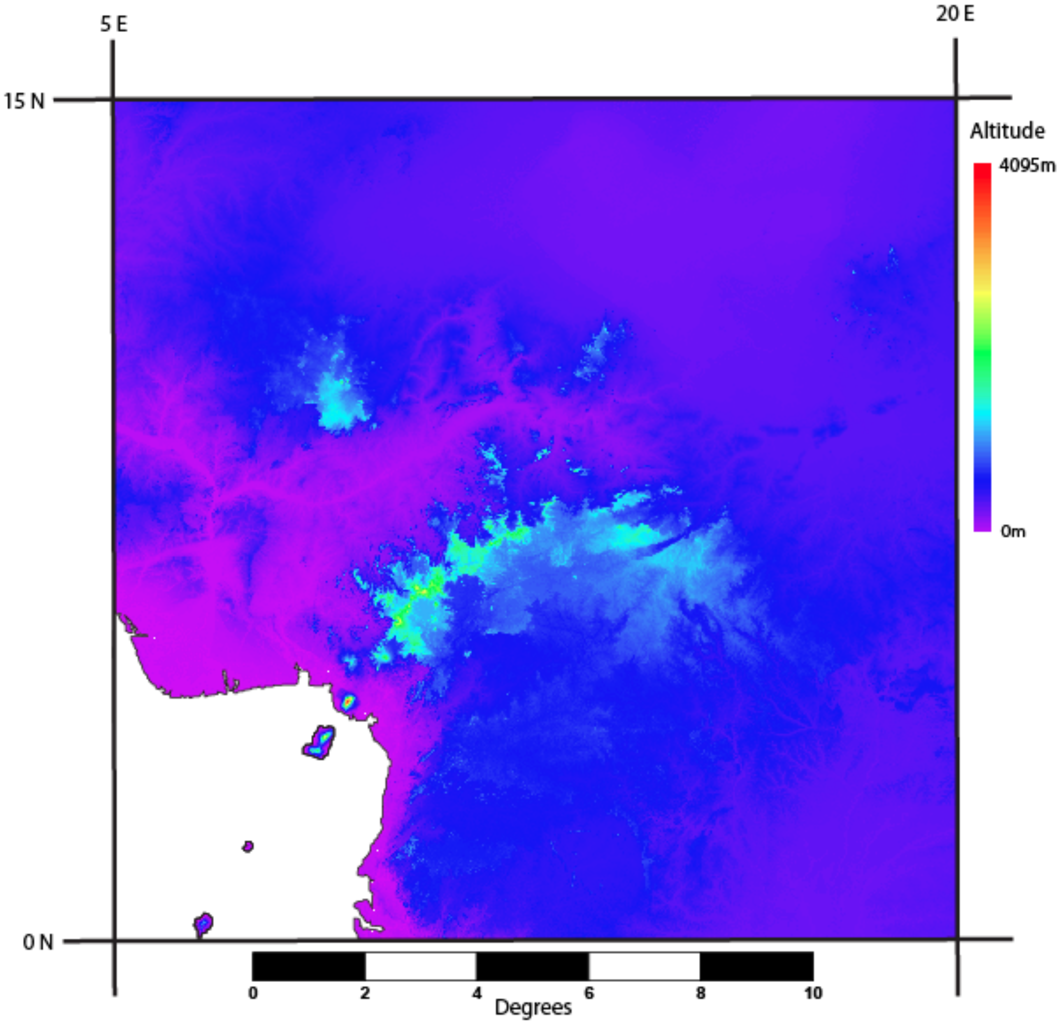


Figure 28: topography map of the west African region.

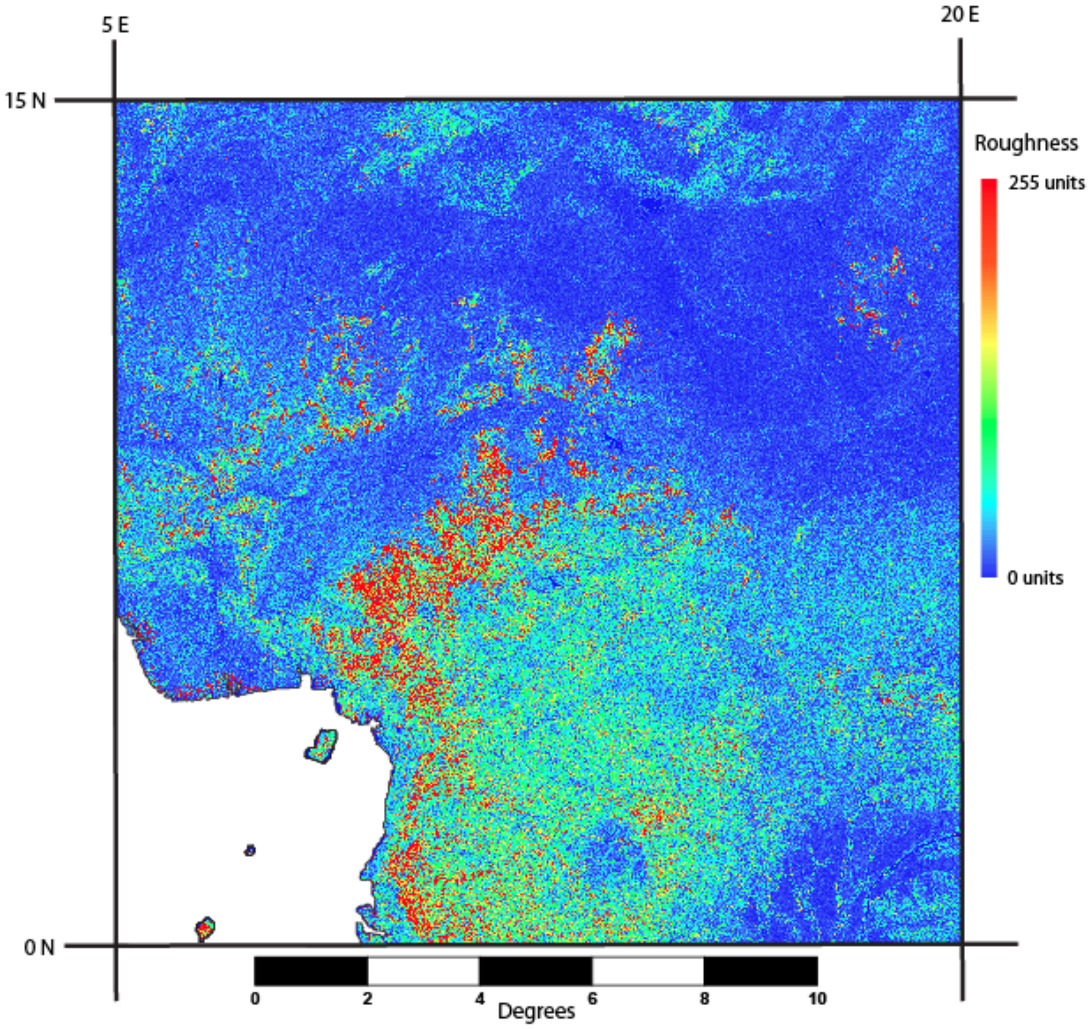


Figure 29: roughness map of the west African region.

As these figures show, the west African region is generally lower in both altitude and roughness than either east or south. The ridge along the Nigeria-Cameroon border is the key exception, providing both the areas altitudinal peaks (of around 4000m) and the zone of highest roughness, although this extends significantly beyond the limit of the high-altitude area south into Cameroon and north into Nigeria. The regional geology also follows the ridge. The dominant rock type, particularly in the rough part of Cameroon and through to the northwest corner of the study area, is Precambrian, while the altitudinal peaks are underlain by small patches of Tertiary igneous rock presumably representing ancient tectonic activity. The same rock forms the islands to the southwest of the coastal strip. There is no one to one correspondence between soils and the underlying rock, but the boundaries of the geological units can often be picked out in the soil maps.

Climatically, as we might expect given the relatively flat and homogeneous physical landscape, the west African region shows much clearer latitudinal banding patterns than was seen in either the east or the south (see Figure 30). The figure shows temperature seasonality, but that for annual mean temperature is almost identical and that for precipitation seasonality

(Figure 31) is similar but with a different placement of bands and a small coastal influence in the west. The only exception is to this occurs on the map of mean annual rainfall, which is uniformly high across the region.

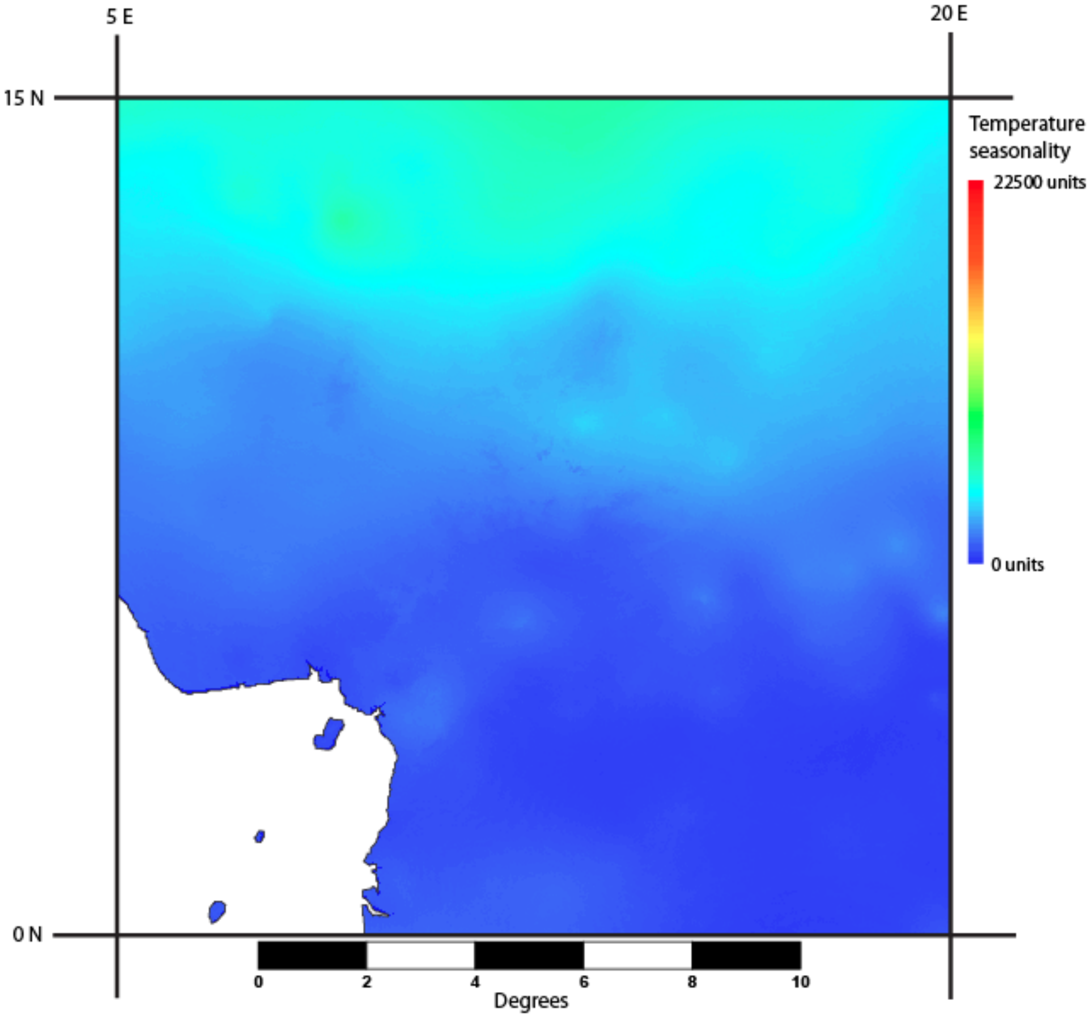


Figure 30: map showing the distribution of temperature seasonality values and the marked latitudinal banding characteristic of the region.

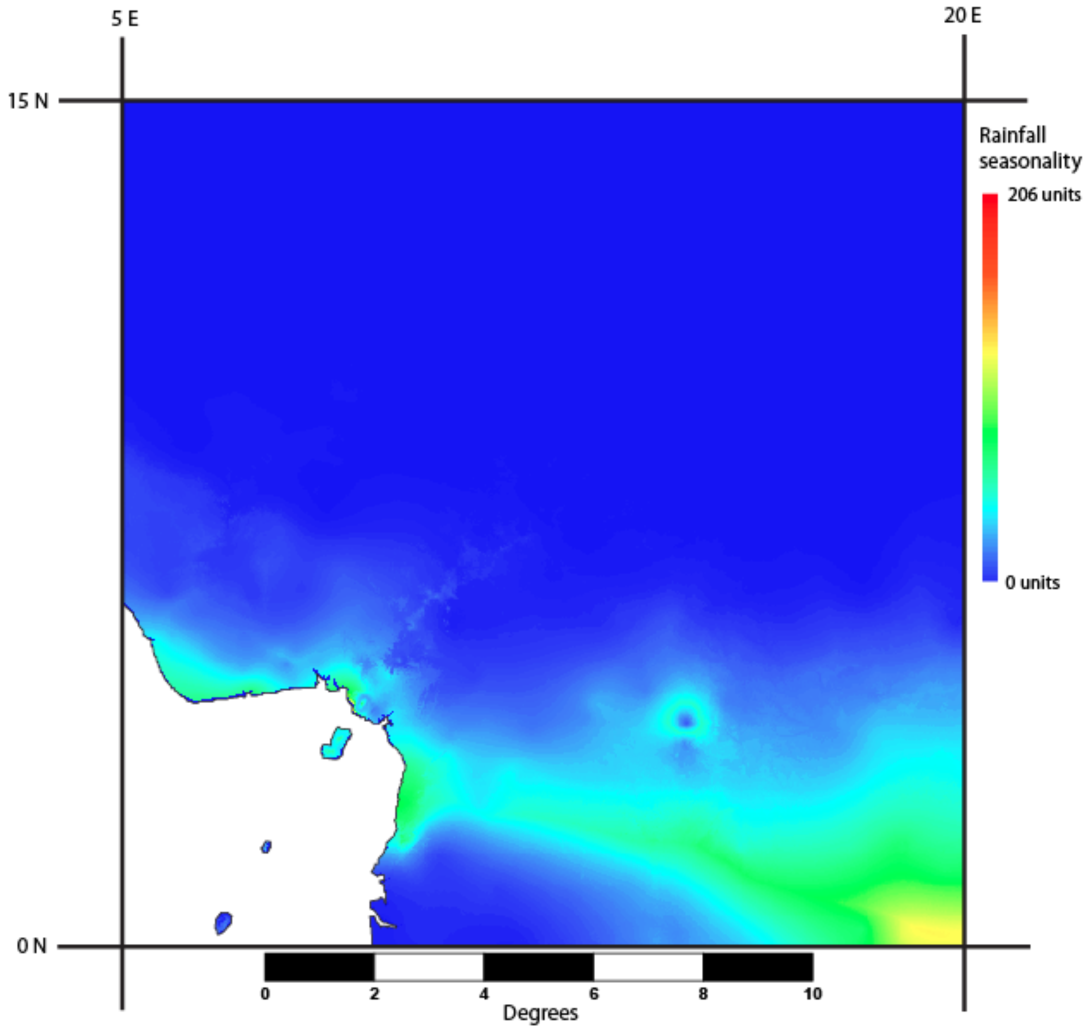


Figure 31: map of rainfall seasonality values showing a banding pattern with some coastal modification.

This climatic latitudinal banding is also clearly visible as the dominant influence on vegetation (Figure 32), with – from north to south – bands of arid/semi-arid vegetation, semi-open habitats and closed (forested) habitats, and a couple of patches of aquatic vegetation associated with a lake in the north of the study region and the coastal strip.

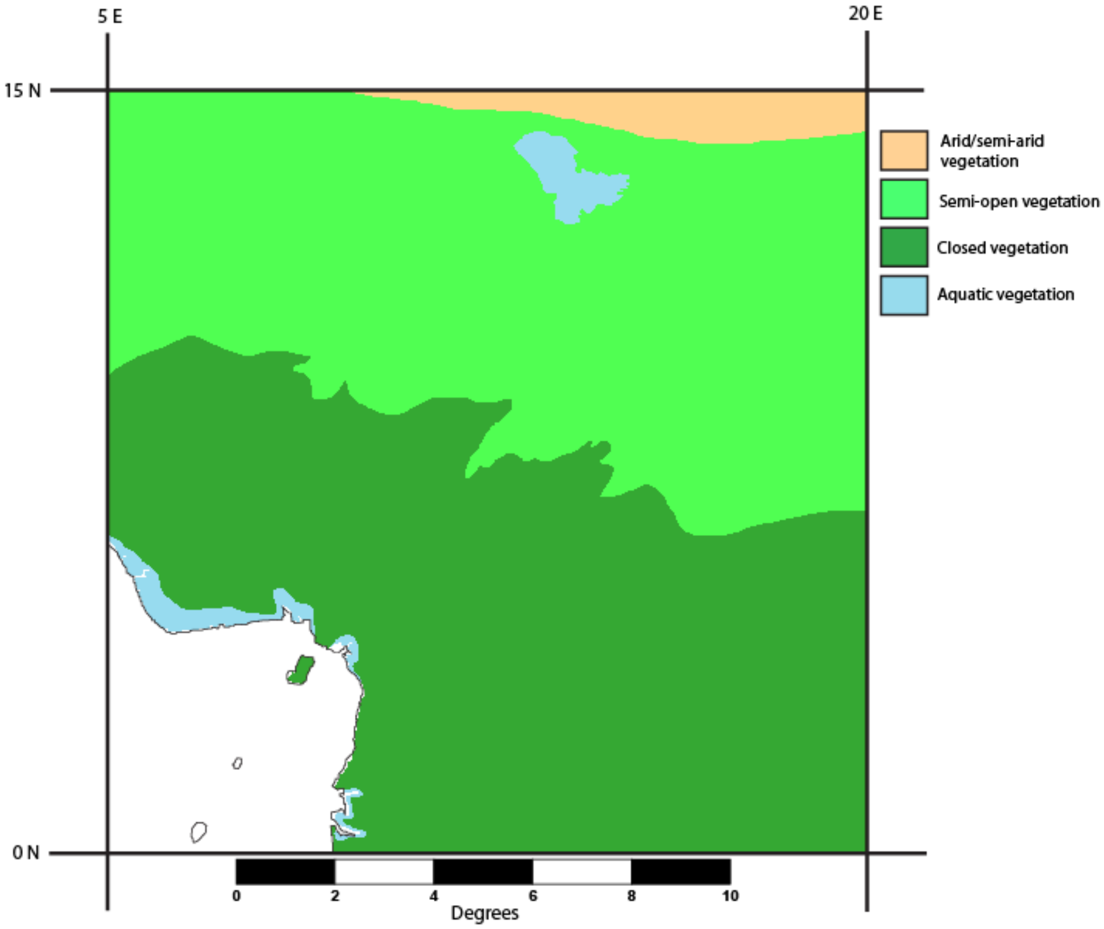


Figure 32: vegetation map of west Africa, showing the near-total dominance of climatic (latitudinally banded) patterns. The smaller islands in the south were not included in this map and are therefore blank.

The corresponding ecoregion map (Figure 33) looks very similar, but more detailed, with an additional latitudinal band in each of the major stripes seen in Figure 32 and a separation of east and west along the line of the topographic peaks in Nigeria/Cameroon. Pairs on either side of this ridge are similar – the most northerly, coloured dark green and pink, are called 'West sudanian savannah' and 'East sudanian savannah', and are presumably delineated on the grounds of different animal diversity or endemic taxa; the same is true of the peach/pale green pair to the south called 'Guinea forest-savannah mosaic' and 'Northern Congolian forest-savannah mosaic' respectively. This map also highlights the Tertiary igneous peaks as a separate ecoregion, suggesting a slight influence from physical landscape on biota despite the apparent dominance of climatic patterning.

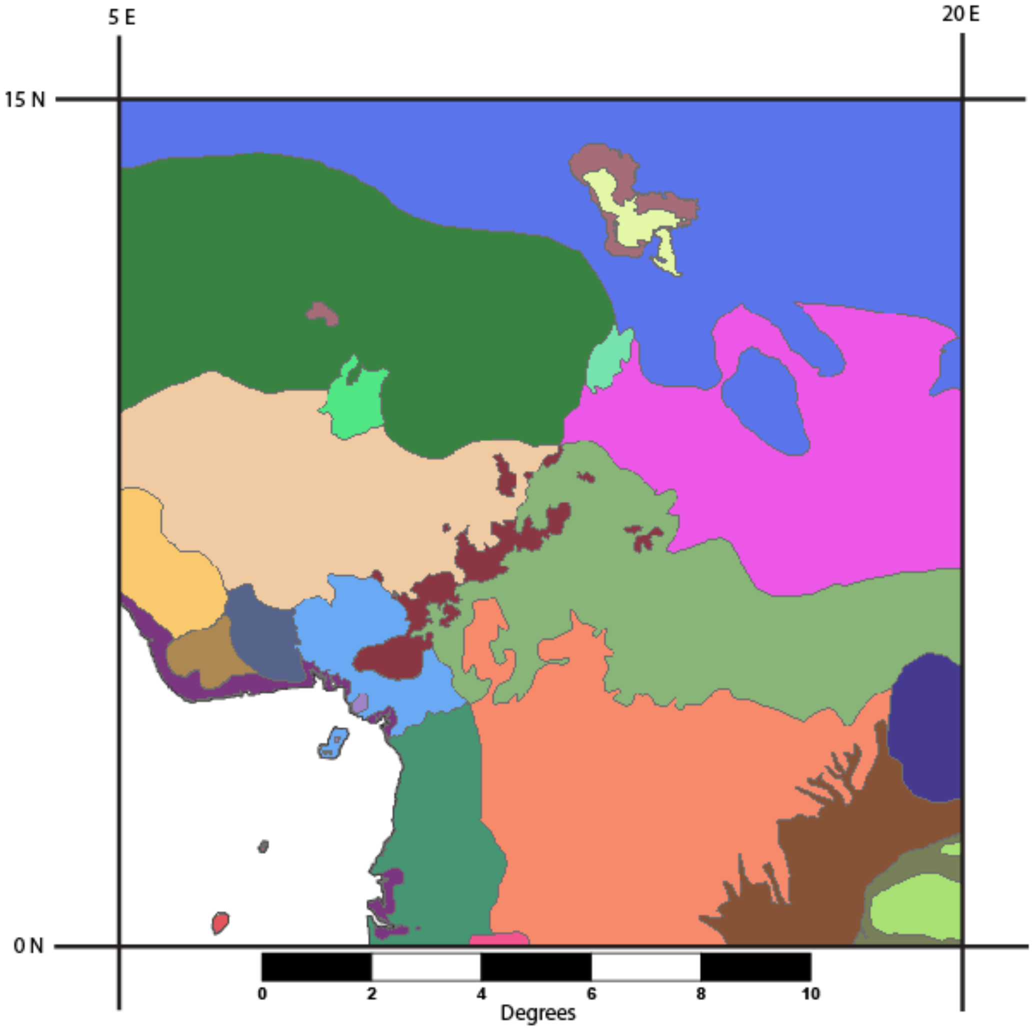
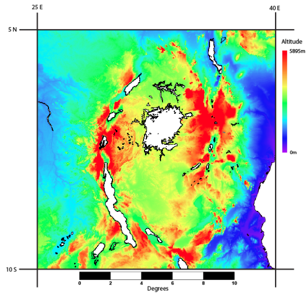
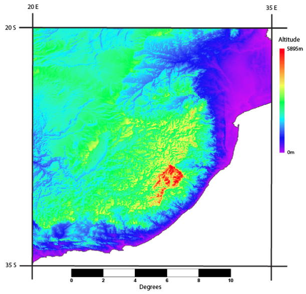
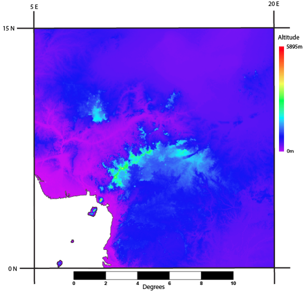
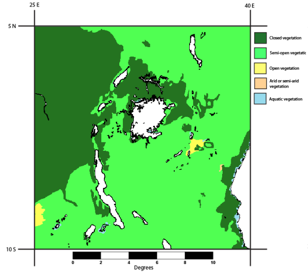
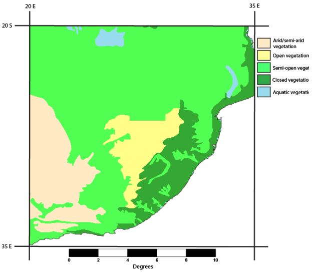
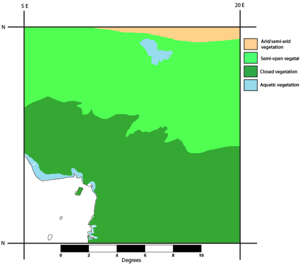
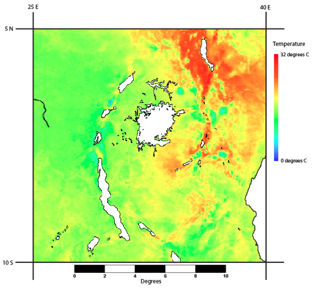
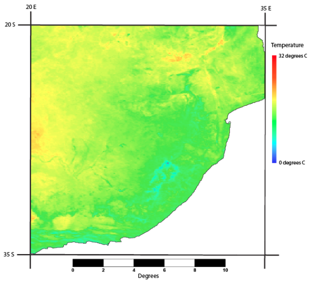
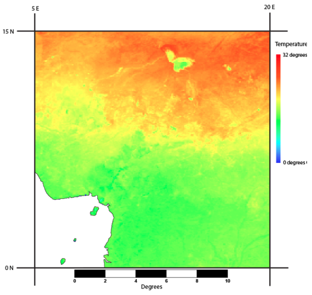
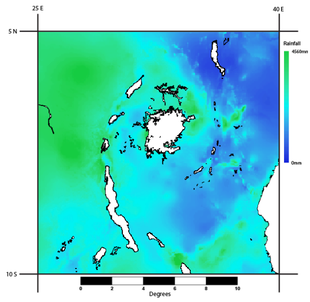
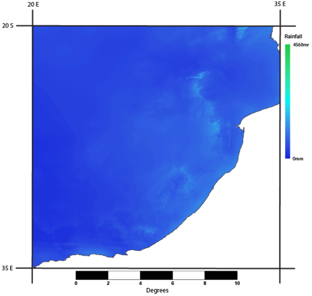
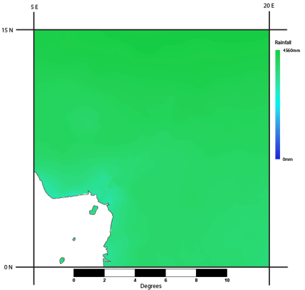


Figure 33: the ecoregions of west Africa, showing another latitudinal banding pattern separated along a northeast-southwest line. Specific ecoregions are not identified as their precise identity is unimportant for understanding pattern, but some are discussed in the text.

In the west of Africa, then, landscape patterns are shaped by climate. In the east, they are shaped by the physical landscape – lithology and topography. Finally, in the south, landscapes are intermediate, with evidence of influence from both sets of factors. Table 17 gives a pictorial summary of the key variables and patterns.

Table 17: a pictorial summary of the environments of east, south and west Africa showing the differences between the three regions.

	East Africa	**South Africa**	**West Africa**
Topography			
Vegetation			
Temperature			
Rainfall			

The snapshot images in this table demonstrate side-by-side the swirly pattern that results from the east African regions' high level of tectonic activity, the mixed patterns that appear in intermediate south Africa, where climate and physical landscape factors are closely interwoven, and the latitudinal banding patterns that dominate west Africa.

Each region thus presents unique challenges for attempts to distinguish climatic, vegetational and physical landscape based preferences among living taxa, and (if we again assume that broad *patterns* in environments remain similar even where specific values change) potentially for the hominins as well; in the west it would be easier to distinguish patterns linked to the physical landscape than to separate climatic or vegetational influences on species distributions, while in the east the near complete physical landscape dominance makes it potentially difficult to distinguish *any* pair of potential causal variables (depending on specific details of species preference) and in the south it is generally simpler to begin distinguishing the three groups as they all display different broad patterns. This regional analysis has thus added additional detail to the picture of landscape structures developed in the continental equivalents above, has confirmed the presence of scale-dependence and has identified regional (geographic) differences in the steady-state of the Earth system.

AFRICAN LANDSCAPES: LOCAL CASE STUDIES

The final stage in this analysis of extant African landscapes focuses on the small (local) scale and explores one case study from each study region. These were selected to (a) reflect – as much as possible – the 'natural' state of the region and (b) represent areas that are relatively well-known ecologically and environmentally. Specifically, three national parks were chosen, namely Gashaka Gumti National Park in Nigeria, De Hoop Nature Reserve in South Africa and Amboseli National Park in Kenya. The key aim remains to establish how patterns at different scales are interlinked. These three parks are also important to the study of papionins (baboons), and thus form the basis for small-scale studies in Chapter Four.

East Africa: Amboseli National Park

Amboseli National Park is 392km^2 in area and is located in south-central Kenya, just north of the border with Tanzania. The local topography is shown in Figure 34. Despite the high altitudes of the east African region as a whole, this small area is relatively low-lying, with a single peak just south of the Amboseli park, and is characteristically rough (Figure 35), with the exception of the coastal plain which is both the lowest altitude and the flattest area. The park itself, however, lies in an area of low roughness surrounded by these characteristic east African rough landscapes.

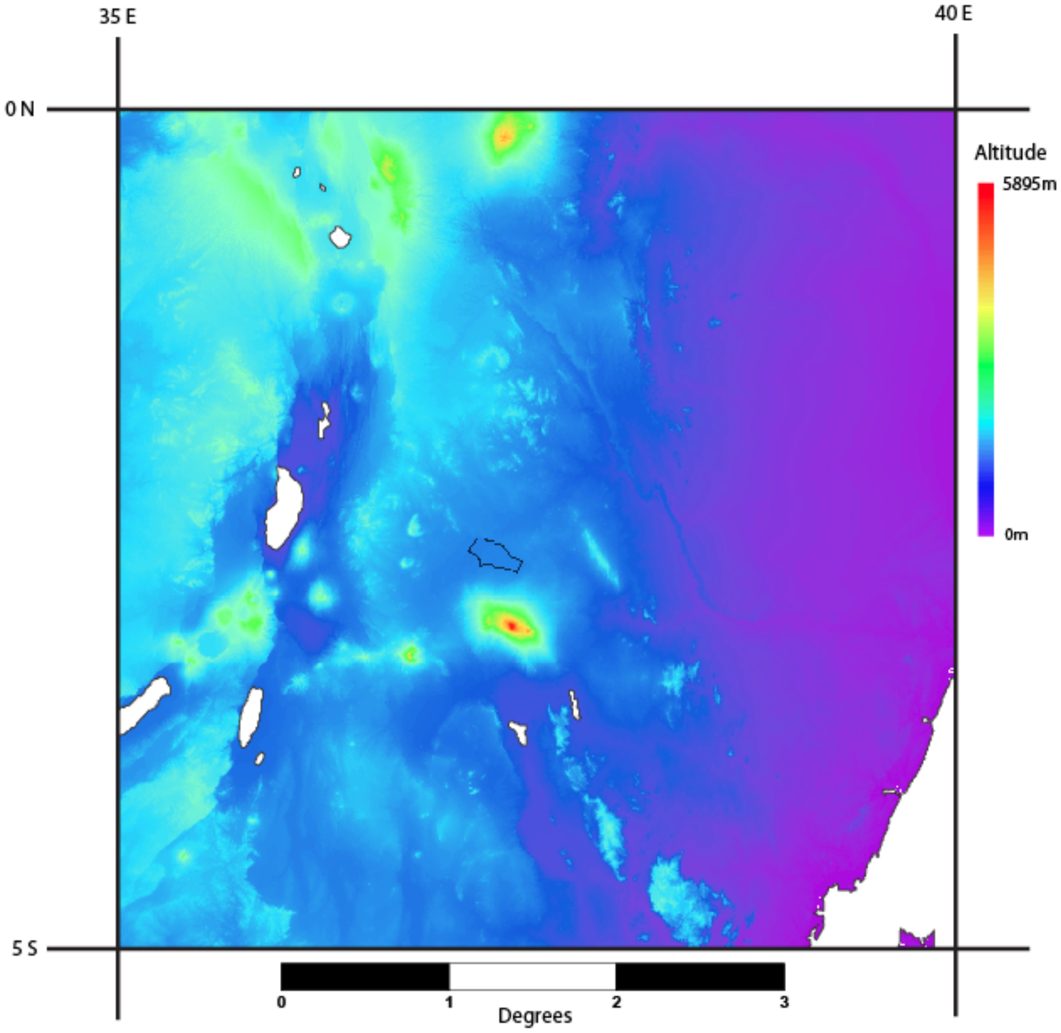


Figure 34: the detailed topography of the region surrounding Amboseli National Park, showing the uniformity of the area and the peaks to the south. The park is indicated by the black outline.

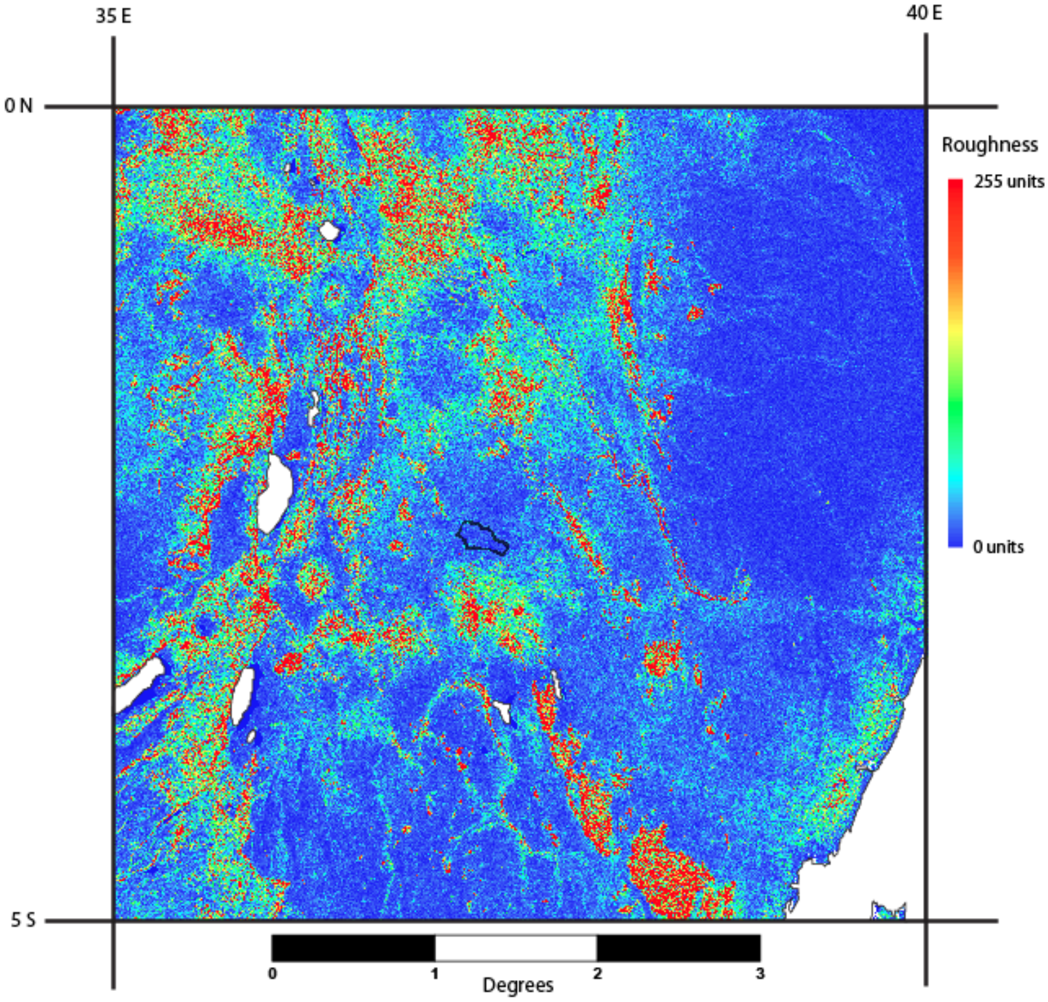


Figure 35: a roughness map of the area around Amboseli. The park is indicated by the black outline.

This suggests that the correlation between high altitude and high roughness observed at the continental and (to a somewhat lesser extent) regional scales is yet weaker for the local area of Amboseli, with the full range of roughness values seemingly found no matter what area is studied or whether this is high or low altitude overall.

The underlying geology is uniform within Amboseli but very variable outside, as the mosaic pattern at the regional scale suggested (see above). The park is located on Mesozoic igneous rock, and borders a block of Quaternary igneous material to the south. The soil matrix is more complex, but generally patchy across the whole area considered, within and outside the park.

Climatically, the large scale maps above placed the Amboseli area in a region of fairly high average temperatures (about 33ºC), moderate day ranges of about 15ºC and moderate rainfall levels (about 600-700mm/year), although the picture is somewhat different in small-scale work; Stelzner (1988), for example, working within the park itself notes that monthly maximum temperatures averaged 29.0ºC, monthly minima 12.8ºC, and rainfall just 36.1 ±

38.2mm/month, although the discrepancy is likely in part due to a lack of direct comparability between data (Stelzner's were recorded only in 1979, the large-scale averages used here over the period 1950-2000). This suggests that for Amboseli the local landscape's physical and climatic state is not easily extrapolated from large scale study: local climate and topography at Amboseli are not representative of the wider region and are better studied at the small scale.

In terms of vegetation, the large scale ecoregions and vegetation maps both suggest the park is uniformly covered by semi-open vegetation, specifically an ecoregion called the Northern acacia-commiphora bushland and thicket zone. Just to the south, the topographic peaks are covered at their points with east African montane moorland and around their slopes with east African montane forest, in concentric rings (see Figure 36).

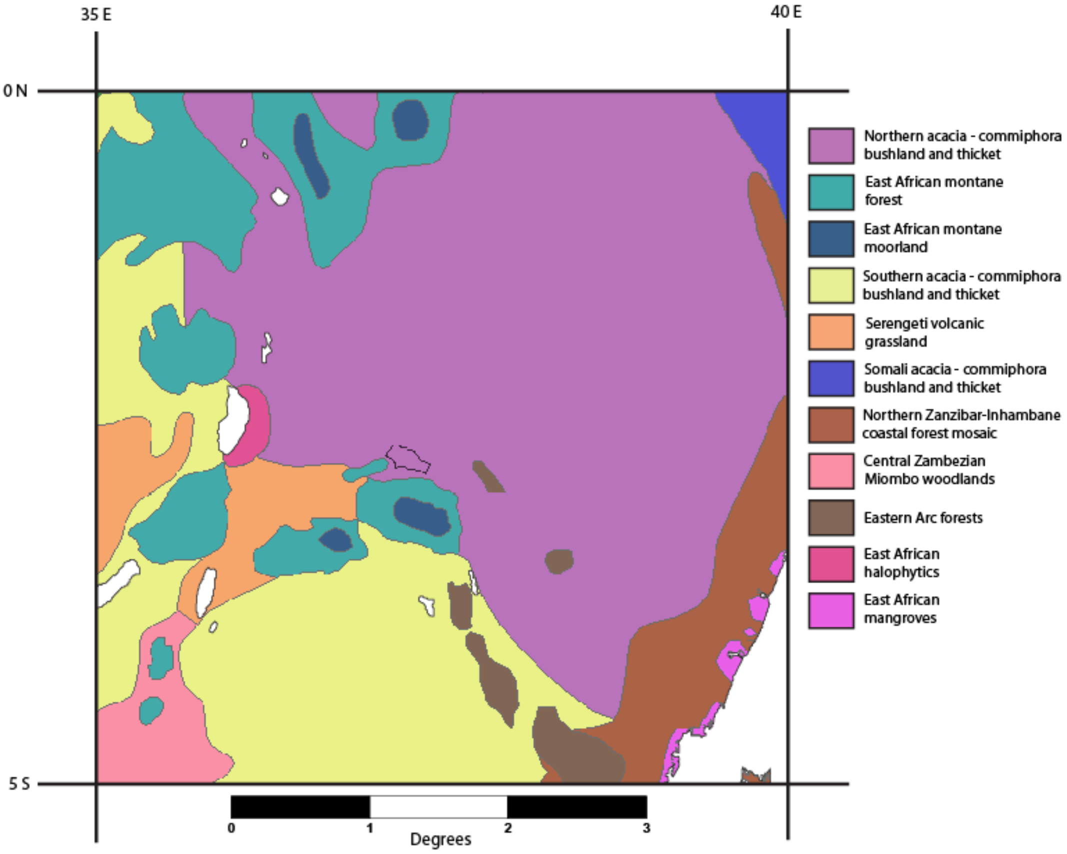


Figure 36: an ecoregion map of Amboseli (outlined) and the surrounding region. The park is indicated by the black outline.

The discrepancy between local and regional climate estimates raises doubts about large-scale vegetation maps, as we have already observed a link between climate and vegetation at the largest scales, but local LANDSAT images confirm the validity of large scale patterns. The local satellite imagery cannot distinguish vegetation types (except through quantitative analyses of chlorophyll layers), but the broad patterns, especially in the concentric bands around the area's altitudinal peaks, are similar. There are small variations, presumably due to anthropogenic modification or other change too recent to be incorporated into the larger maps.

In particular, green vegetation is seen only in certain parts of the park, presumably because of human clearing activities as discussed in Altmann et al. (1985). Interestingly, this is also a region known to have undergone rapid recent climatic change, which might explain both the discrepancy between local and regional climate estimates and this pattern in vegetation (Alberts and Altmann, 2001).

Overall, this local analysis suggests that simply scaling data from one scale to fit another analysis is not always consistent. Both the specific patterning of variables and the relationships between them appear different when analysed at the local scale than when continental or regional analyses are conducted; for instance, here in east Africa, both local and regional analyses identified a weaker topography-roughness relationship than seemed visible at the large scale and in other regional analyses. This case study also highlights the possible role of local data as a check on potentially outdated regional maps, as the former are typically published much more regularly than new GIS-compatible maps but may only provide spatially unresolved parameters or conditions at specific points.

South Africa: De Hoop Nature Reserve

De Hoop Nature Reserve occupies about 340km^2 near the South African coast, and is environmentally distinct from both Amboseli and Gashaka Gumti, principally in climate. De Hoop is home to chacma baboons, *Papio ursinus*, and protects part of the world's smallest and most threatened plant kingdom, the Cape Floral Kingdom. The local topography is shown in Figure 37.

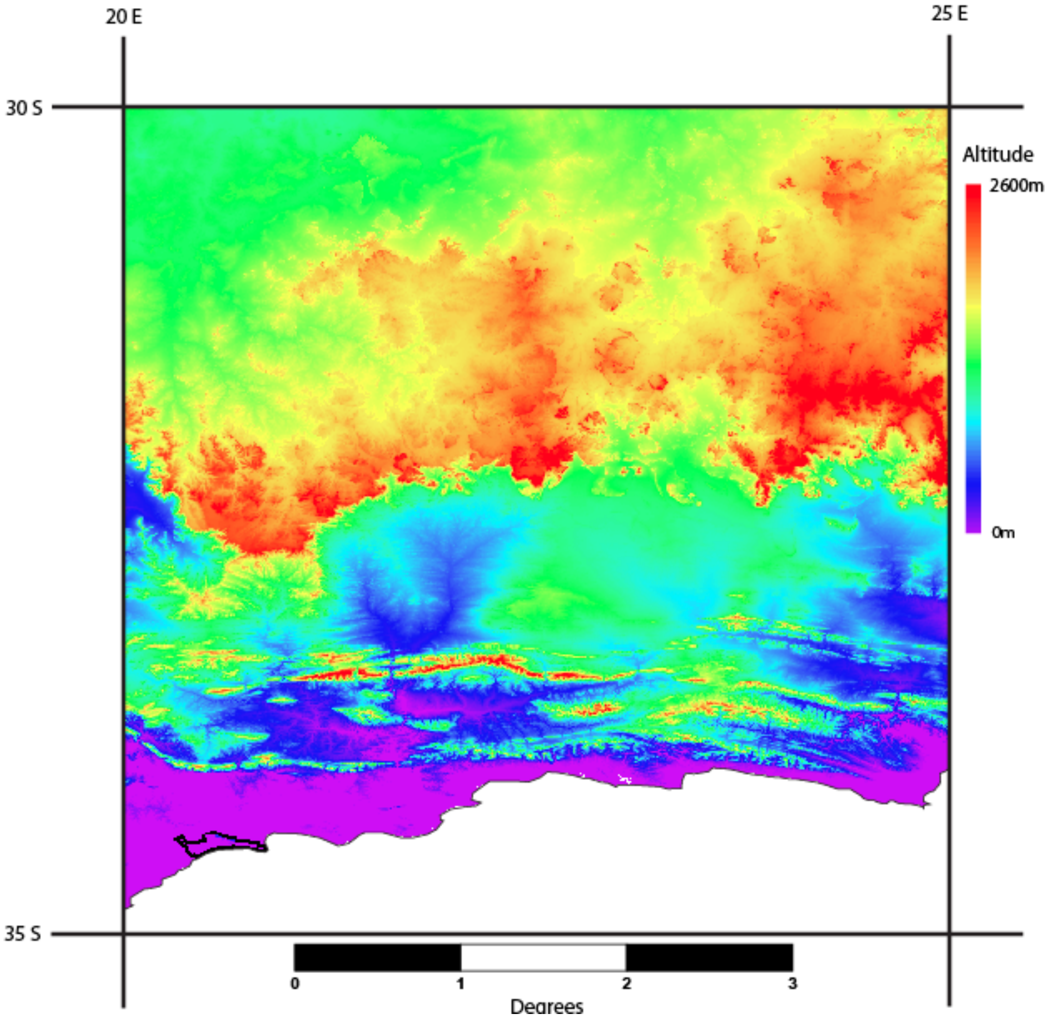


Figure 37: the topography of the region surrounding De Hoop in South Africa. The park is indicated by the black outline.

As this figure shows, although there are high altitude areas north of De Hoop, in the Karoo range, the maximum altitude of these is significantly lower than in the eastern and western study areas, at just under 2600m. De Hoop is located on the low-lying coastal plain, and ranges in altitude from 0-611m (Hill et al., 2003). This is not, however, a particularly flat area (Figure 38), with the local roughness values spanning the full range from 0-255 units. Within the park the range is slightly smaller, but still considerable.

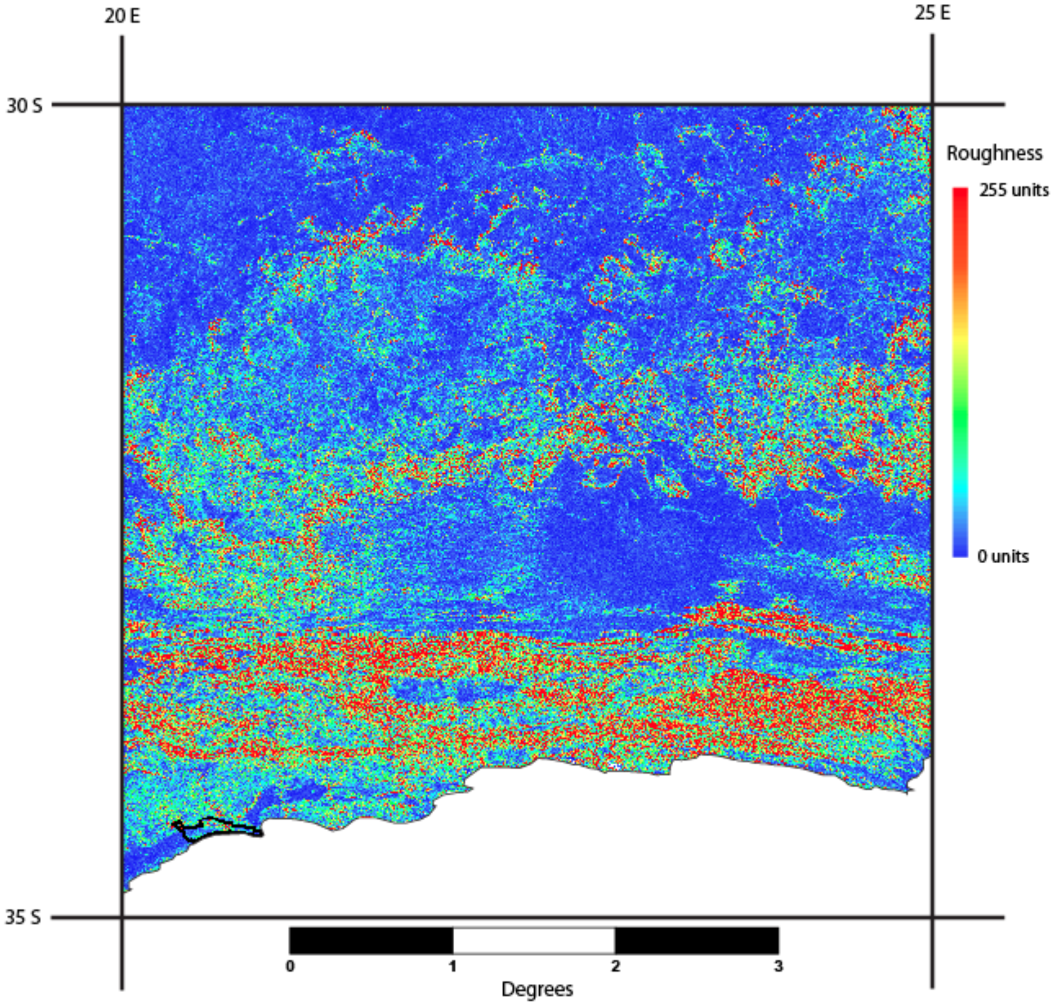


Figure 38: a roughness map of the De Hoop area. The park is indicated by the black outline.

These two maps show that at this scale, the link between altitude and roughness is at best tenuous in south Africa, just as it was in east Africa near Amboseli. The zone of highest roughness in this south African study area is towards the south, in an area of moderate altitude, while the high altitude Karoo mountains are rough only around the edges.

Turning to climate, the De Hoop area is characterised as ‘Mediterranean’, with a mean annual temperature in the park of 17ºC and mean annual rainfall of 428mm (Hill et al., 2003). Both temperature and rainfall are seasonally variable, as is day length (van Doorn et al., 2010). Climate at De Hoop is thus significantly different from both Amboseli and Gashaka Gumti, which are located much further north. Large-scale maps of the area, however, seem to be at too low a resolution to identify local patterning, and it is thus impossible to say whether local climatic patterns replicate regional ones.

In terms of vegetation, the Cape Peninsula and De Hoop fall within the coastal (or lowland) fynbos zone (Figure 39), and the general distribution of different vegetation types is latitudinally banded, at least near the coast. This banding, however, seems more likely to be linked to physical landscape patterning (as are the non-banded areas of succulent Karoo and Drakensberg montane grasslands/woodlands/forests to the north, which border high-altitude areas) than to climate, as significant climatic variation is not visible at this scale, as discussed above.

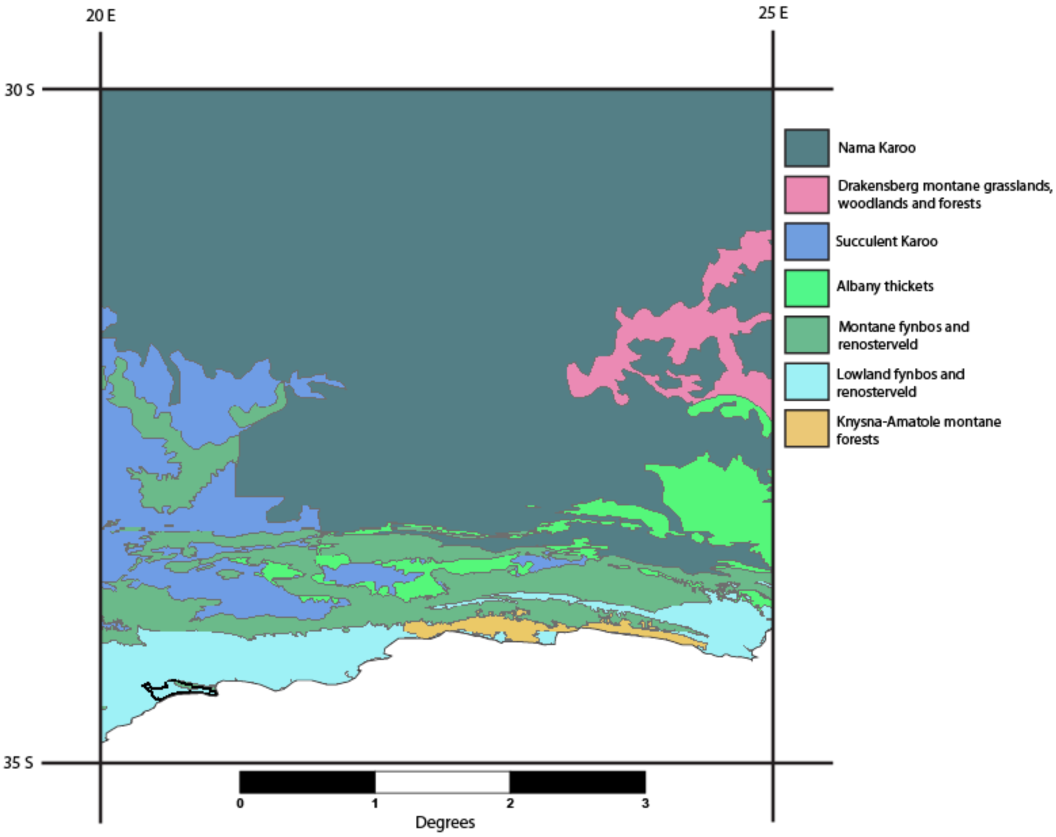


Figure 39: an ecoregions map of the region around De Hoop. The park is indicated by the black outline.

The cape fynbos and renosterveld zone is described by the WWF as being one of the richest floras in the world, with more diversity than any comparably sized area in Africa and 9000 plant species, roughly 69% of which are endemic (Cowling, 2011). It is underlain by fine, relatively infertile soils and, although it boasts a number of endemic reptiles, amphibians and freshwater fish, both bird and mammal biodiversity are relatively low (Cowling, 2011).

Overall, then, the relationships between the physical landscape, climate and vegetation for the De Hoop region are once again different from their regional equivalents. The relationship between altitude and topography, which seemed to hold well at continental and, to a slightly lesser extent, the south African regional scale, is here particularly weak. At the regional scale, in addition, climate was latitudinally banded and the physical landscape was not, while at the local level climate is relatively uniform and the physical landscape – particularly altitude – is latitudinally banded along the coast. This suggests that distinguishing the effects of physical landscape, vegetational and climatic patterns in south African species' distributions is again harder at the local than at the regional scale.

West Africa: Gashaka Gumti National Park

The final case study area, Gashaka Gumti National Park, spans 6731km^2 of northeast Nigeria, and is the amalgamation of three game sanctuaries from 1972 created to protect the region's abundant wildlife (Barnwell, 2011). As well as other species, it houses olive baboons (*Papio anubis*), putty-nosed guenons; mona, tantalus and patas monkeys; black-and-white colobus; grey-cheeked mangabeys and chimpanzees (Sommer and Ross, 2011) and is thus an area of particular scientific interest for primatologists and other biologists.

The protected area is topographically diverse, as it spans part of the ridge along the Nigeria/Cameroon border identified above (see also Figure 40), and there is significant variation in roughness (Figure 41). The northern part of the park is thus fairly flat and low altitude, and the south is rougher and higher in altitude. The correlation between altitude and roughness noted above, which seemed fairly robust at the continental scale and reasonably so within individual regions, is once again less consistent at this local scale, however, with the area of high roughness considerably larger than the high altitude zone and small areas of both smooth highland (e.g. just south of the park boundary) and rough lowland (along the northern park boundary at about 11-12ºE).

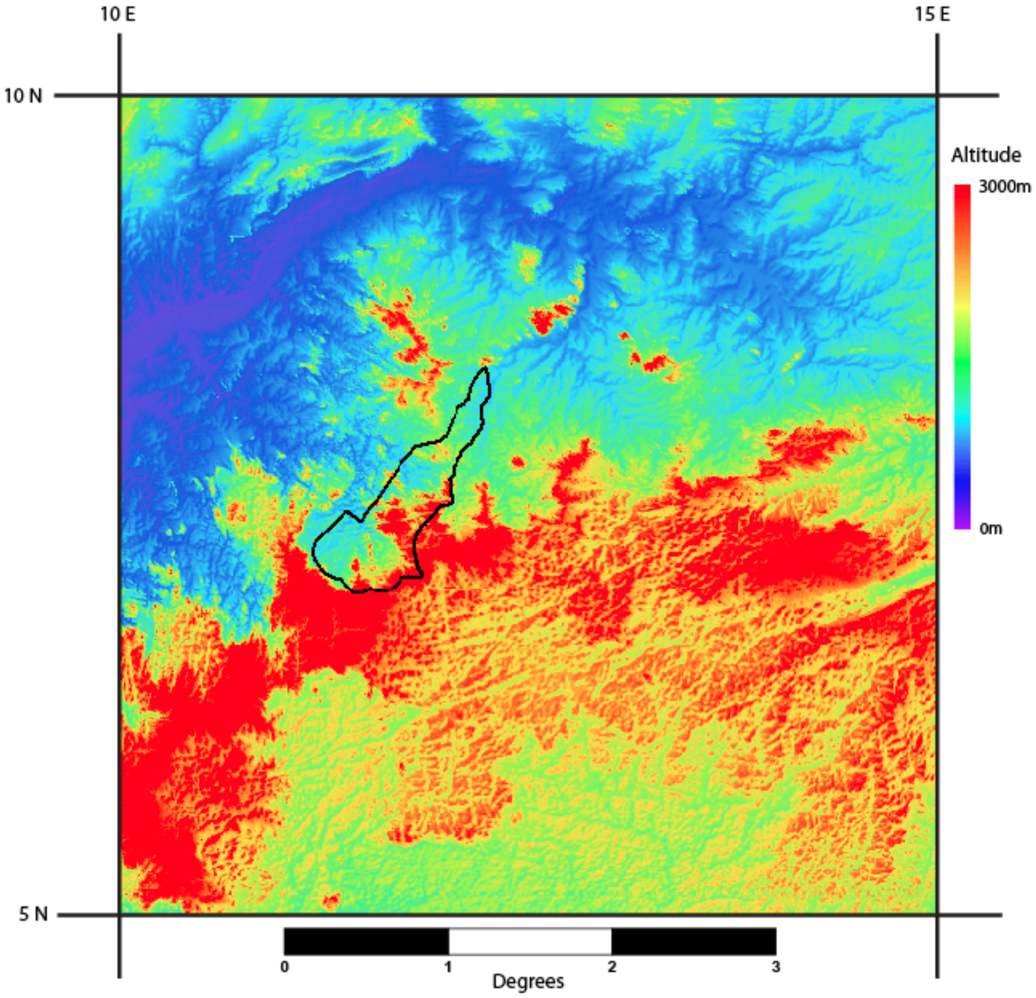


Figure 40: the detailed topography of the region surrounding Gashaka Gumti National Park, showing the diversity of altitudes within the park. The park is indicated by the black outline.

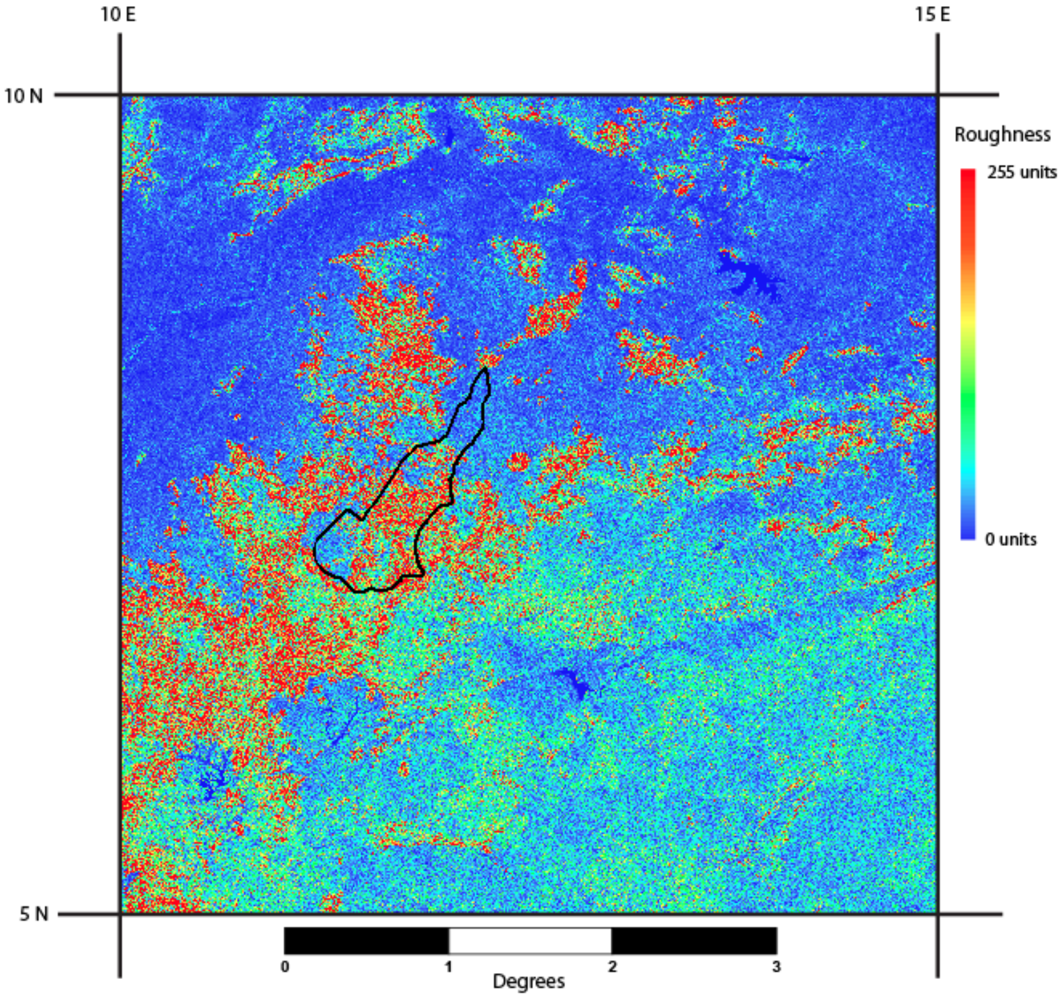


Figure 41: a roughness map of the area around Gashaka Gumti. Compare Figure 40 to see the imperfect relationship between topography and roughness. The park is indicated by the black outline.

In terms of climate, both the broad datasets (cut down from the continental maps used in the preceding sections) and more detailed evidence from weather stations in Gashaka and Kwano (Sommer and Ross, 2011) suggest that Gashaka Gumti is in an area of high rainfall with warm, somewhat seasonal, temperatures – at Gashaka and Kwano respectively, 2000-2008 saw mean annual precipitation levels of 1897mm and 1973mm, average monthly minimum temperatures of 21ºC and 20.9ºC and average monthly maxima of 32.5ºC and 31.9ºC respectively (Sommer and Ross, 2011).

The vegetation map of Africa suggests that Gashaka Gumti lies within an area of 'forest transition and mosaic' vegetation, with little internal variation. The ecoregion map (Figure 42) in contrast shows the park spanning two zones – the Guinean forest-savannah mosaic, found along the northern edge, and the Cameroonian highlands forest zone, which occupies the higher altitude zone in the south and east of the park and around its southern border. The distribution of these vegetation types seems to map almost perfectly onto the topography (Figure 40), with none of the fuzzy edges seen in the roughness figure, although other ecoregion boundaries (for instance between west and east Sudanian savannah and latitudinally between these zones and those immediately to the south) do not map onto topographic patterns so clearly. At the local scale, however, the distribution of vegetation types seems to be controlled largely by the physical landscape, while at the regional scale the same pattern seemed climatic and banded. This presumably relates to the precise nature of the diverse landscape captured in the small-scale sample area compared to the region as a whole.

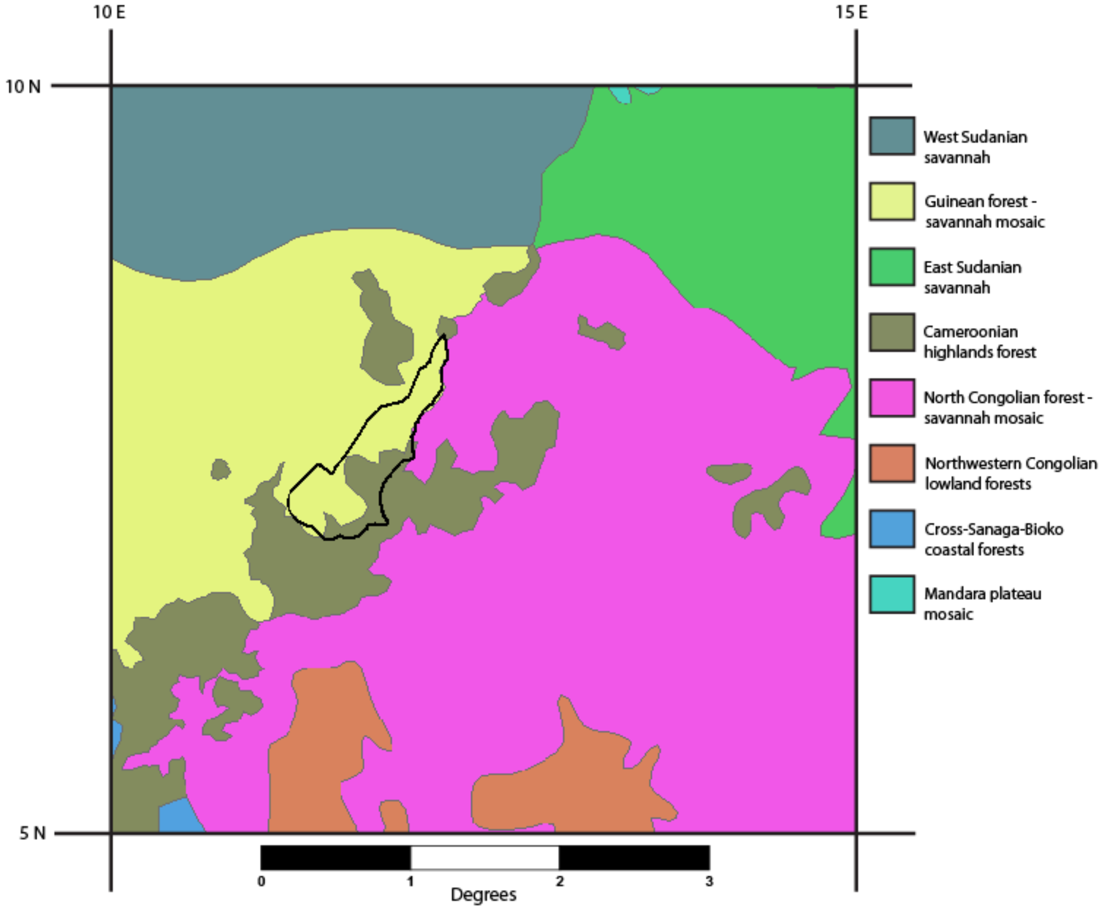


Figure 42: a close up of the WWF ecoregion map showing the two zones within Gashaka Gumti National Park. The park is indicated by the black outline.

At the local scale in west Africa, patterns do appear different to those visible at the larger regional scale, just as these regional patterns differed from the overall continental ones. The west African regional landscape is more influenced by climate than is typical of Africa as a whole, but this shift in balance between landscape and climate is reversed at the local scale, where topography – not climate – dominates the distribution of ecoregions more visibly. This may be due to our focusing in on a specific (and potentially not representative) part of the regional case study, but could also result from different scales bringing different processes and hence different overall balances of environmental factors into focus.

DISCUSSION

This chapter's explorations of extant African landscapes thus make several points of relevance to this thesis' aim of evaluating the TLM. The development of the African landscape system model (Figure 12), suggests that at large scales at least there are definable relationships between the patterns shown by different variables. The climatic variables (controlled by solar energy inputs) are latitudinally banded; the physical landscape variables (controlled by internal Earth processes) are patchily or randomly distributed with a basic division between the low altitude/smooth north-west and the high altitude/rough south-east; and the intermediate variables, whose expression is influenced by both other groups, show intermediate patterns. This suggests a balance in the landscape system as a whole between solar and geophysical forcing which, although shifting in response to changes in energy budgets, local landscape configurations and modifications to the feedback loops between variables, is characteristic of the wider Earth system. Reconstructions of palaeoclimates are also typically banded (Hetherington and Reid, 2010, Haywood et al., 2000, Alverson, 2007), and maps reconstructing vegetation are usually banded with some influence from landmass configuration and topography (Holmes, 2007a), suggesting that this sort of balance between climate and topography, with vegetation intermediate, is maintained even when specific conditions change. Were these patterns apparent only in the palaeoclimatic/palaeovegetational reconstructions we might suggest that they resulted from simplifications in the models and assumptions used to generate maps of palaeoconditions, but their visibility in *both* sets of data suggests they are more likely to be real and to represent a similarity in the structure of the landscape system in different periods.

Moving to the regional scale, however, the patterns change. East African landscapes are shaped by topography and lithology and the balance between landscape components has shifted in favour of the geophysical factors (as reflected in the lack of banding patterns in both vegetation/soils *and* climate). The west African landscape, in contrast, is shaped by climate, with banding dominating the intermediate variables, while south Africa is more intermediate. This is suggestive of a shifting, more dynamic environmental balance at the regional scale (perhaps closer to Huxley's characterisation of disequilibrium dynamics in evolutionary contexts, see Chapter One), as regional environmental changes will tend to occur over smaller timescales than continental ones. The East African rift, for instance, formed over the period from 23Ma to present (Logatchev et al., 1972), while the continental structure itself, apart from this component, originated in the Jurassic-Cretaceous (Van Hinsbergen et al., 2011); a similar pattern is found in climate, for instance in the greater duration and slower progress of glacial/interglacial cycles which influence continents and the briefer span of regional changes linked to factors like changes in circulation (Barry and Chorley, 2003). The complex relationship between regional and continental patterns, then, suggests that (a) interpreting alternative hypotheses of hominin landscape use and site distribution is likely to be more complex than simply mapping sites against (palaeo)environments at a single scale, as both taphonomy and regional variations in equilibrium states complicate broader pictures, and (b) if the presence of hominins in (lithologically/topographically influenced) eastern Africa and (intermediate) southern Africa, and their near absence from (climatically shaped) western African landscapes can be substantiated, this pattern itself might inform us about hominin habitat preferences and the validity of the TLM.

At the local scale of the three national parks, patterns are even more complex. In all three localities, the influence of the physical landscape on previously ‘intermediate’ factors like vegetation becomes more apparent, but this is especially true for the De Hoop region and its surrounds in South Africa and the Gashaka Gumti National Park in Nigeria/Cameroon. This leads to yet another set of balances between different components of the landscape system which are distinct both from their regional equivalents and one another. In addition, links between landscape variables – like the high altitude=high roughness relationship observed at continental and, to a lesser extent, regional scales, and in prior work (King and Bailey, 2006, Bailey and King, 2011) – are much weaker at the local scale. This has obvious implications for testing environmental hypotheses of primate (and hominin) evolution in that it might allow easier discrimination at small scales between certain factors that at larger ones are too closely linked to be effectively teased apart, though the fact that patterns are not uniform suggests that extrapolating general rules from such scale-dependent studies would be difficult.

CONCLUSIONS

This chapter has shown that there are indeed characteristic patterns in the spatial structures of different landscape variables in Africa and that these patterns, and the relationships between them, are not only scale-dependent within particular regions but differ between regions too. In general, the continental patterns are the simplest to identify and interpret and complexity increases as the scale of study decreases. In all three study locales, the influence of the physical landscape on intermediate variables like vegetation and soil distributions increases at the smallest scales, but at the regional scale there are clear geographic differences. Eastern African landscape structures are dominated by the topography of the Rift Valley, while western Africa is climatically dominated and south Africa intermediate and akin to the overall continental pattern. This suggests that our abilities to discriminate organismal distributions dependent on different specific landscape preferences (and hence to begin to test the TLM and other hypotheses of hominin evolutionary environments using distribution data) depend upon the combination of the scale, theory and geographic area studied, as well as on taphonomy, but that some such work may be plausible with judicious selection of study areas and sites. In brief, this chapter has shown that:

1. The spatial patterns displayed by different elements of the African landscape system are basically predictable at the continental scale from a basic knowledge of the global energy budget and Earth system structure;
2. As the scale of study decreases, both the spatial patterns shown by individual landscape variables and the relationships between them become more complex. Geographic effects are dominant at the regional scale, while at the local scale topographic influences on vegetation and habitats generally increase. This suggests that the landscape system as a whole is complex, and that patterns at a given scale are *emergent*, influenced by interactions with a range of scale- and location-dependent patterns and processes;
3. The structure of the physical landscape is variable and, though interacting with both vegetation and climate, can vary independently of these components. This suggests that the physical landscape probably has at least indirect impacts on primate ecology and evolution (via influences on other factors, especially at the regional and local scales) and may also have its own, direct effects (to be explored below);
4. While continental analyses like those of King and Bailey (2006) suggest that we could expect to distinguish distributions of organisms – and potentially fossils – based on different landscape preferences, the evidence for complexity in this system (particularly at the regional to local scales where many ecological processes occur), suggests that this is best undertaken (a) from a perspective which explicitly takes account of complexity and spatial structure and (b) following explicit consideration of the choice of scale and study locale. It may be better, given the added complication of taphonomic bias and uncertainties over the structures of palaeolandscapes, to develop alternative approaches – like the comparative method or palaeoenvironmental studies of site contexts, rather than of distributions – which can provide supporting evidence, before attempting further direct tests of hominin site distributions.

The analyses conducted in this chapter therefore provide basic data on landscape structures which will be used in the development of the comparative approach to hominin landscapes and the TLM. Chapter Four, which focuses on the *Papio* baboons, will build on this data and take account of scale and locality dependence by considering a range of case studies of different *Papio* allotaxa in different contexts.

Chapter Four: *Papio* Baboon Landscape Use and Anatomy

INTRODUCTION

Chapter Three has demonstrated the existence of complex, scale-dependent patterns in modern African landscapes and has suggested that the physical landscape might be as important as climate or vegetation to African primate ecology. The influences of different landscape structures (in the broad sense) on primates probably vary significantly. Some landscape patterns – like patchiness in the distribution of fruit trees, for example – can be accommodated simply through a change in behaviour. Others, perhaps like a faulting event or a longer term change in local climate, might require an ecological or adaptive (evolved) change and might be linked into longer-term evolutionary trends more directly. The next step in this thesis' analysis of the role of landscapes in primate evolutionary ecology (and, ultimately of the TLM as a model for hominin evolution) is therefore to explore the links between these landscapes and their occupants. This analysis will focus initially on the baboons, as well-known terrestrial primates occupying the same landscapes as modern humans and with potential ecological similarities to the hominins (Jolly, 2001), and will continue to consider Chapter One's three key concepts of *landscape* (defined broadly), *complexity* (already identified in landscape structures and scale- and location-dependence, and presumably extended when intelligent agents are introduced) and *agency*, so far unexplored. Baboons are not as cognitively complex as modern *Homo sapiens*, but the role of behavioural flexibility in determining their interactions with the landscapes they occupy will be the subject of several of the case studies chosen.

Our knowledge of the baboons is relatively detailed. Researchers have explored baboon ecology (e.g. Hill and Dunbar, 2002, Kamilar, 2006), phylogenetic history (Disotell, 1992, 1994, Bohm and Mayhew, 2005) and interactions with humans (Higham et al., 2009, Warren et al., 2011) in great depth, and have even worked on the spatial ecology and palaeobiogeography of the genus (Bettridge and Dunbar, In Press, Hoffman and O'Riain, 2011), although current understanding of this topic is still limited. This chapter therefore begins by summarising briefly what is already known about *Papio* baboon evolution and ecology, before moving on to characterise the gross morphologies of the landscapes occupied by different allotaxa at the relatively large scale, to see whether there are any systematic differences in the spatial structures of their ranges. All data are once again as described in Chapter Two. These analyses are then supplemented and extended through a series of small-scale case studies of well-known baboon troops from the three National Parks – Amboseli, Gashaka Gumti and De Hoop – considered in Chapter Three. Each case study represents a different attempt to simplify the complex primate-landscape system and lay it open to empirical analysis via a focus on a relatively small area or short time-span and, although it cannot prove causality because of the potential effects of logical incoherence on these systems, provides useful insights into the relationships between baboon socioecology and landscape at these three sites. Finally, an explicit attempt is made to explore the links between landscape and anatomy via a detailed study of a sample of baboons from known localities across the *P. anubis* x *P. cynocephalus* hybrid zone in southern Kenya, using skeletons collected by Maples (1967).

THE BABOONS: BACKGROUND INFORMATION

Comparative studies of living primates are often used to inform interpretations of extinct hominin ecology, anatomy and behaviour (Sussman and Hart, 2007), and the baboons have been one mainstay of such analyses because of their possible ecological similarities to early hominins (Jolly, 1970, 2001). Both hominins and baboons are large-bodied, highly social primates showing complex evolutionary, ecological and behavioural patterns (Henzi and Barrett, 2003), and they may have experienced similar evolutionary histories (Arnold, 2009). However, baboons have also been studied extensively in their own right. Some research is motivated by the need to understand these primates' interactions with humans (Warren, 2008, Warren et al., 2011) or their potential for biomedicine – baboons are the most widely used models for humans in medical studies, especially genetic analyses of susceptibility to disease (Vandeberg et al., 2009) – but much is also based on a genuine interest in what is probably the most widespread, and most often encountered, nonhuman primate. This means there is already a considerable literature on baboon evolution and ecology on which this thesis can build.

Baboon Phylogenetics and Evolutionary History

The taxa called 'baboons' comprise two genera, *Papio* and *Theropithecus* (or savannah and gelada baboons respectively). These groups differ in their genetic and evolutionary histories, ecologies and biogeographies. *Theropithecus gelada* is the only species in its genus and occupies a restricted range (see Figure 43). The several members of the genus *Papio*, in contrast, occupy most of sub-Saharan Africa and comprise five or more closely related taxa, often referred to as 'allotaxa' (Newman et al., 2004). These may be classified as separate species or subspecies depending upon the species concept used (see below) and display a wide range of genetic, ecological and behavioural patterns as well as differences in external and – to a lesser extent – internal anatomy.

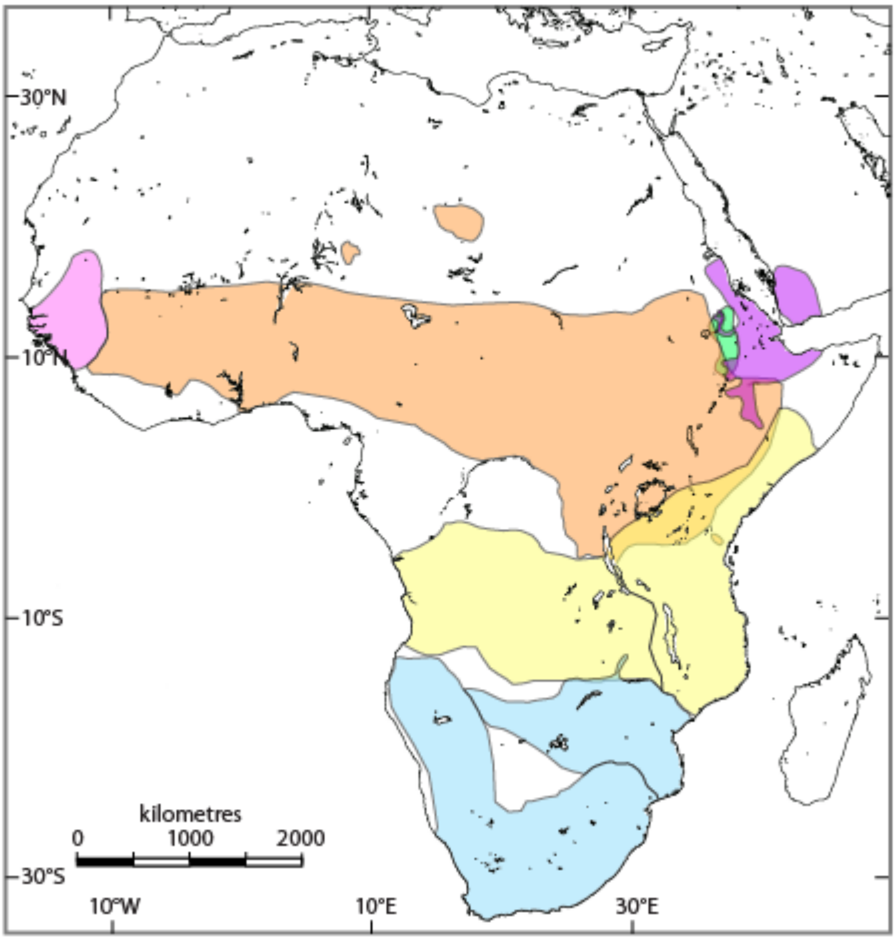


Figure 43: map showing the distribution of members of *Papio* and *Theropithecus* (the baboons). Distributions are based on data from the IUCN red list database. Key: *P. anubis* = orange, *P. cynocephalus* = yellow, *P. papio* = pink, *P. hamadryas* = purple, *P. ursinus* = blue and *Theropithecus gelada* = green.

It is these five savannah baboon taxa which will be the subject of this thesis' analyses of baboon ecology and anatomy, as they provide a useful group of closely-related, wide-ranging primate taxa. They are members, together with *Theropithecus*, of the tribe Papionini.

Papionin Evolutionary Relationships

The papionin group comprises seven extant genera: *Papio* and *Theropithecus* (the baboons), *Lophocebus* and *Cercocebus* (the mangabeys), *Macaca* (the macaques), *Mandrillus* (combining drills and mandrills) and *Rungwecebus*, a recently discovered taxon called the kipunji (Gilbert, 2008, Davenport et al., 2006). Before the advent of genetics, these were traditionally grouped into four clades comprising the macaques, the mangabeys, the savannah baboons and mandrills, and the gelada (*Theropithecus*), with both the second and third groups sometimes considered single genera (Gilbert, 2011). There was general agreement that the macaques formed a sister clade to the African papionins, but relationships between these latter groups were less clear: *Theropithecus* was sometimes classified as the sister group to a combined mangabey-baboon clade, and sometimes as more closely related to the baboons and mandrills (Gilbert et al., 2009). The placement of *Lophocebus*, in those instances when it was recognised as distinct from *Cercocebus*, also varied (Disotell, 1994).

Molecular techniques, in contrast, produce a different picture, linking *Theropithecus* and *Papio* (without the mandrills) in the modern baboon clade, and splitting the mangabeys, placing *Lophocebus* in or near the baboon group and *Cercocebus* with *Mandrillus* in a sister clade (Disotell, 1992, Disotell et al., 1992, Disotell, 1994). This was initially taken as evidence for disparity between molecular and morphological classifications of the group – and hence by some as evidence for genetic analyses' superiority over those based on skeletal anatomy – but more recent work, particularly by Gilbert and colleagues, has found that morphological studies produce similar classifications when appropriate characters are selected for analysis (Gilbert and Rossie, 2007, Gilbert, 2007, Gilbert et al., 2009, Gilbert, 2008). A consensus phylogeny based on both genetic and anatomical analyses, primarily of the cranium and mandible, is shown in Figure 44 below.

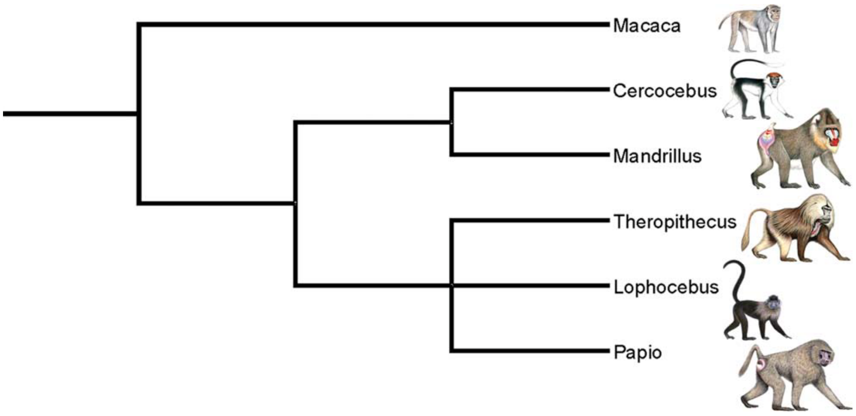


Figure 44: a summary phylogeny of the Papionini, based on both molecular and recent morphological research, from Gilbert (2011, figure 2).

The recent discovery of the kipunji raises the only major outstanding question regarding the broad pattern of papionin phylogeny. This species, described in 2005 (Jones et al., 2005), was originally placed in the genus *Lophocebus* on the basis of a single specimen and photographs of others. Following genetic analysis, however, it was re-classified as a separate genus *Rungwecebus* placed close to *Papio* although the specimens lacked the external features required to fit it within that genus (Davenport et al., 2006). Even more recent study has suggested that the kipunji may actually be a baboon, as it is more closely related to nearby populations of *Papio* than distant ones, and questions of the nearness of its relationship and the role of hybridisation between the two taxa in the context of broader taxon patterns (see also below) have been raised (Burrell et al., 2009, Zinner et al., 2009a). The relative contributions of hybridisation and sister-clade relationships to the genetic similarities of the two groups remain uncertain.

Relationships Within Papio

Theropithecus, as noted above, comprises a single geographically restricted species. The genus *Papio*, in contrast, is wide-ranging and shows no clear internal phylogeny. There are five widely recognised subtaxa: the hamadryas ('sacred') baboon, *P. hamadryas*; the Guinea (or red) baboon, *Papio papio*; the chacma baboon, *P. ursinus*; the olive (or Anubis) baboon, *P. Anubis*; and the yellow baboon, *P. cynocephalus* (Newman et al., 2004), as well as many proposed minor taxa like the Kinda baboon and the grey-footed baboon which are not as widely accepted. These allotaxa may be given specific status – as above – or lumped in various ways as some authors recognise just one species or even superspecies, called *P. hamadryas*, while others recognise two, *P. hamadryas* sensu stricto and *P. cynocephalus*, or more. Jolly (1993) argued that the lack of both major anatomical differences between forms and their ecological similarity (also assessed by Kamilar, 2006) justified a single species designation, but the debate typically focuses on genetic separation – or its lack – as the baboon allotaxa typically retain their distinct features but hybridise readily in the wild and in captivity (Phillips-Conroy and Jolly, 1981, Bergman and Beehner, 2004, Zinner et al., 2008). Members of *Papio* can in fact also hybridise with more distant relatives, although this typically only occurs in colonies or zoos and may produce infertile offspring. Intergeneric hybrids are known with *Theropithecus* (Markarjan et al., 1974, Dunbar and Dunbar, 1974, Jolly et al., 1997) and even *Macaca* (Markarjan et al., 1974), despite lineage separation times of ~5 and 10 million years respectively (Jolly, 2001).

Given this hybridisation (which in the wild occurs between most groups that share borders, irrespective of subspecies), it is hard to accurately assess the relationships between the baboon allotaxa. A mitochondrial study aiming to elucidate intrageneric relationships generated a phylogeny based on samples from all five major allotaxa (

Figure 45), however, and found that this model performed better at explaining the observed differences than various other models (Newman et al., 2004). The alternatives these authors tested included both geographical and socioecological lumping models, and all performed significantly less well than the phylogeny presented below (Newman et al., 2004). While this is only a mitochondrial phylogeny (and thus probably does not fully capture introgression from recent hybridisation), in studies like this thesis' work on distributions, the precise phylogeny is not as important as the ecology and geography of the allotaxa concerned.

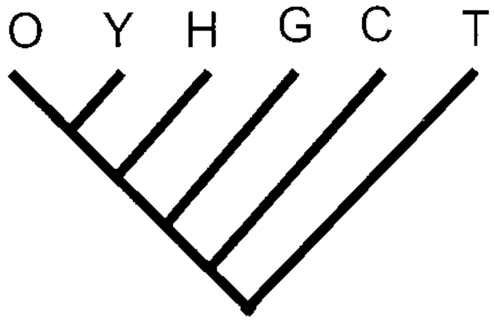


Figure 45: a mitochondrial phylogeny of the five major *Papio* allotaxa, taken from Newman et al. (2004, table 4). O = olive, Y = yellow, G = Guinea, H = hamadryas and C = chacma baboons; T = *Theropithecus gelada*, the outgroup.

There are also several fossil baboons, with those identified as closely related to the *Papio* and *Theropithecus* group including the species *Papio izodi*, the members of the genus *Parapapio* (*Pa. ado*, *Pa. broomi*, *Pa. jonesi*, *Pa. lothagamensis*, *Pa. whitei* and *Pa. antiquus*), several members of *Theropithecus* (*T. darti*, *T. brumpti*, *T. oswaldi*, *T. baringensis* and *T. quadratirostris*) and *Pliopapio alemui* (Jablonski, 2002, Jablonski and Frost, 2010) as well as the genera *Gorgopithecus* and *Dinopithecus* (Bettridge and Dunbar, In Press). These however are generally not well enough known ecologically or – in many cases – anatomically to be included in the work presented here.

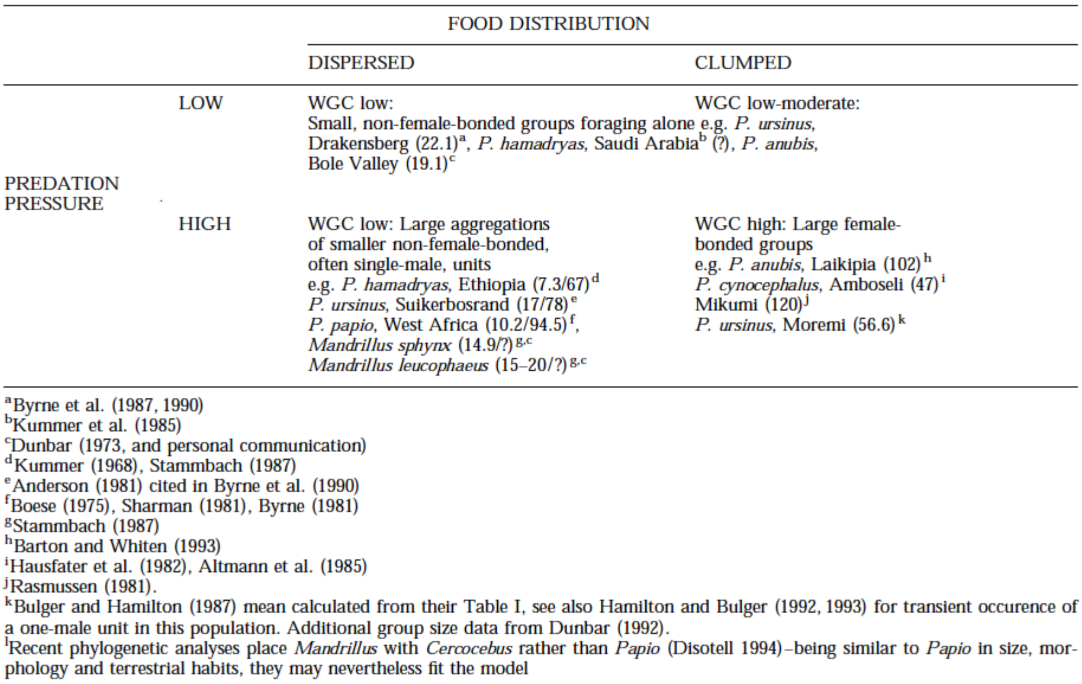
Baboon Ecology and Behaviour: A Brief Survey

There is notable variation across the major *Papio* allotaxa in many ecological variables, including diet, environmental preferences, activity budget and social organisation, although the overall level of difference between them does not necessarily support their specific status (Kamilar, 2006, though see also Henzi and Barrett, 2003). Some of this variation seems to follow geographic clines (for instance the association between group size and altitude in chacma baboons found by Whiten et al., 1987, and the links with weather shown by Bronikowski and Altmann, 1996). Baboon ecology and behaviour thus varies both within and between allotaxa, to differing degrees, a pattern which has led researchers to focus primarily on populations as the unit of study (see for instance the studies cited by Baldwin and Teleki, 1972, and Kamilar, 2006), although some have suggested that the social group might be a better unit for understanding socioecological patterns (Bronikowski and Altmann, 1996). In this chapter, the choice to analyse patterns at both the species/genus level (the continental or regional scale) *and* the population/group level (the local scale), in order to capture landscape use patterns at a range of scales, means that an exhaustive exploration of the ecological literature and the pros and cons of different units of study is not needed at this time. Instead, this section provides a very broad overview of baboon ecology and social behaviour and more detailed parameters are considered in the relevant case study analyses below.

The *Papio* allotaxa (here referred to using common names or species designations, for simplicity), in contrast to the gelada, range across most of sub-Saharan Africa. They occupy a wide range of habitats, with differing population densities and ranges depending upon the type of environment and local ecology (Whiten et al., 1987). It is thus rather harder to identify a specific 'savannah baboon niche' than it is to characterise those of some primate species; indeed, there is as much variation in diet among populations of a single *Papio* species as between members of different species despite the formers' almost identical basic biology (Dunbar 1988, as referenced in Barton et al., 1996). In a survey of 27 wild savannah baboon populations, Kamilar (2006), for example, found wide variation across all four of his key datasets on environment, diet, activity budget and social organisation despite being unable to include hamadryas baboons, thought to be the most distinctive ecologically (Newman et al., 2004). The variables this author studied were able to discriminate baboon allotaxa, although only the analysis of environmental differences was statistically significant, primarily in the separation of chacma baboons – living at high altitudes – from members of the other lower altitude groups (Kamilar, 2006). The most overlap between populations/allotaxa was found for the analysis of social organisation variables (Kamilar, 2006), suggesting the different savannah baboon groups represent broadly the same *animals* (in terms of their basic biology and socioecology) operating in different ecological settings and consequently adapting their diet, activity budget and – potentially – landscape use.

Instead of summarising all the permutations of *Papio* baboon socioecology, then, this section will focus on describing the *range* of patterns observed. In terms of environment, the chacma baboons (*Papio ursinus*) occupy the widest range of habitats including the high-altitude regions of the Drakensberg mountains (Henzi and Barrett, 2003), while the hamadryas baboon tends to occupy semi-arid areas of low food availability (Barton et al., 1996) and other species occupy the full range of 'savannah' environments (Lang, 2006a, Lang, 2006b). Barton et al. (1996) proposed an ecological model of the baboons in terms of two key ecological variables – food distribution and predation pressure – which, between them, influenced intragroup competition and social organisation (see below):

Table 18: an ecological model of the influences on baboon social structure. WGC = within group competition; table taken from Barton et al. (1996, table 3).



		FOOD DISTRIBUTION	
		DISPERSED	CLUMPED
PREDATION PRESSURE	LOW	WGC low: Small, non-female-bonded groups foraging alone e.g. *P. ursinus*, Drakensberg (22.1)[a], *P. hamadryas*, Saudi Arabia[b] (?), *P. anubis*, Bole Valley (19.1)[c]	WGC low-moderate:
	HIGH	WGC low: Large aggregations of smaller non-female-bonded, often single-male, units e.g. *P. hamadryas*, Ethiopia (7.3/67)[d] *P. ursinus*, Suikerbosrand (17/78)[e] *P. papio*, West Africa (10.2/94.5)[f], *Mandrillus sphynx* (14.9/?)[g,c] *Mandrillus leucophaeus* (15–20/?)[g,c]	WGC high: Large female-bonded groups e.g. *P. anubis*, Laikipia (102)[h] *P. cynocephalus*, Amboseli (47)[i] Mikumi (120)[j] *P. ursinus*, Moremi (56.6)[k]

[a] Byrne et al. (1987, 1990)
[b] Kummer et al. (1985)
[c] Dunbar (1973, and personal communication)
[d] Kummer (1968), Stammbach (1987)
[e] Anderson (1981) cited in Byrne et al. (1990)
[f] Boese (1975), Sharman (1981), Byrne (1981)
[g] Stammbach (1987)
[h] Barton and Whiten (1993)
[i] Hausfater et al. (1982), Altmann et al. (1985)
[j] Rasmussen (1981).
[k] Bulger and Hamilton (1987) mean calculated from their Table I, see also Hamilton and Bulger (1992, 1993) for transient occurence of a one-male unit in this population. Additional group size data from Dunbar (1992).
[l] Recent phylogenetic analyses place *Mandrillus* with *Cercocebus* rather than *Papio* (Disotell 1994)–being similar to *Papio* in size, morphology and terrestrial habits, they may nevertheless fit the model

As Table 18 suggests, where there is no intra- or intergroup (predator) competition, baboons generally live in small, single-male units; where predation occurs but there is no intragroup competition, these units come together to form larger – but only loosely coherent – bands; and where there is *both* predation and intragroup competition, these large bands are re-organised into socially coherent, female bonded troops (Barton et al., 1996).

In this way, therefore, although it is hard to characterise a savannah baboon 'niche' – groups vary in their diet, habitat choice, social organisation, activity budget, life history and other variables – it is possible to demonstrate certain large-scale patterns. All baboon allotaxa are ecologically flexible and social; they all possess the ability to exploit their environment to their advantage (for instance by using trees, or more preferably, cliffs, as sleeping sites - see Lang, 2006a, 2006b) and they all possess a relatively generalised anatomy which permits them to eat omnivorously and behave opportunistically (Barrett and Henzi, 2008). Cranial anatomy supports the idea of clinal variation in anatomy linked to geographic patterns (Frost et al., 2003), suggesting that the basic adaptations of the baboon are generalistic and the differences between taxa represent relatively small-scale adaptations to local conditions, while the presence of hybrid zones where allotaxa meet (Jolly et al., 1997) and the fact that wild hybrids generally can succeed socially and behaviourally among at least one of the parent populations (Phillips-Conroy and Jolly, 1981, Phillips-Conroy and Jolly, 1986) suggest that flexibility – rather than adaptation to a specific range of conditions – is the vital characteristic of the *Papio* genus. This would imply that there are no differences in the possibility space available for each baboon allotaxon (all allotaxa can cope with any of a large range of landscapes), but there are differences in the subregions of that possibility space which each allotaxon has access to. This would imply that we expect the baboon-landscape system to be very resilient in the face of change, which might explain the success of these primates where others have experienced local extinction.

THE GROSS MORPHOLOGY OF *PAPIO* BABOON LANDSCAPES

The original intention of this project was for the analyses of primate distributions in each chapter to proceed through the scales from large (continental/genus) to small (local/troop). Initial analyses of the continental scale distribution of the *Papio* genus, however, served simply to confirm that these creatures are ecological generalists, capable of living across almost the full range of habitats avaible in Africa, and did not provide any additional detail on landscape use. Instead of taking this analysis further, then, this section will focus initially on mapping the ranges of individual allotaxa – known to be ecologically different but in ways which have not been investigated systematically in this way – before moving on to study well known small-scale case studies from the three major regions of Africa (south, east and west respectively) emphasised in this thesis as a whole. It is important to note that baboons are not distributed evenly across the territories described. However, a lack of systematic data on population density means that analyses can only consider presence/absence at the broad scale, and it is only possible *a priori* to say that a given allotaxon ranges through a particular area, not where it is most densely concentrated. A later section will consider what is known about baboon population densities, which is largely based on values at specific points.

Individual Papio Allotaxa at the Regional Scale

Plotting the distribution of *Papio* baboons at the continental level showed that these taxa avoided the deepest/wettest areas of rainforest, the driest parts of the semi-arid and arid Sahara, and a couple of zones in South/Central Africa (in the region of Botswana and southern Angola/Zambia) where standing water is sparse and predator density relatively high, but could be found everywhere else. The individual allotaxa, however, do not overlap throughout their ranges – there are only a few major overlaps, all in East Africa (see below) – but rather seem to replace each other across the continent, suggesting that perhaps they differ either in their tolerance of different conditions or in their preferences for them. Alternatively, it might be that partial isolation is causing differentiation. Given that hybrid *Papio* baboons – particularly *P. hamadryas* x *P. anubis* and *P. anubis* x *P. cynocephalus* specimens – are well known to occur in the wild (Detwiler et al., 2005), and reticulate evolution, including the production of intergeneric hybrids is seemingly common among the cercopithecines (Arnold and Meyer, 2006, Arnold, 2009), however, this seems less likely. The sections below will explore the range of each taxon in turn, followed by a brief examination of the nature of these zones of overlap. In each case, rather than present every map discussed (especially as many of these replicate patterns already seen in Chapter Three), only a few examples, of those variables which most epitomise the patterns described, are included.

Papio papio (the Guinea baboon)

Papio papio has the smallest range of any of the savannah baboon allotaxa, being restricted to a small area in western Africa covering a small part of northern Sierra Leone, the whole of Guinea-Bissau and The Gambia, and parts of Guinea, Senegal, Mali and Mauritania. This species is also the most differentiated within *Papio*, according to genetic work done over the last two decades, although whether it is that the ecological distinctiveness of the taxon has led to genetic differentiation or the other way around is unclear. One possibility is that a small founder population – perhaps of *P. anubis* – experienced prolonged allopatry in this area, only later coming back into contact with neighbouring populations. The environments occupied by *Papio papio* are summarised in Table 19 below.

Table 19: basic data on the environmental conditions in the *P. papio* range in north-west Africa.

Continuous Variable	**Minimum**	**Maximum**	**Mean**	**Median**
Altitude (m)	0	1328	172.8	82
Roughness (in arbitrary units from 1-255)	0	255	51.51	33
Annual temperature (degrees C)	20.0	30.5	27.6	27.8
Annual rainfall (mm)	117.2	3804.7	1054.7	835.9
Temperature seasonality (units from 0-22500)*	807.0	4663.6	2384.7	2209.4
Precipitation seasonality (units from 0-300)*	0.6	6.4	0.6	0.6
Discontinuous variable	**Description**			
Vegetation	Covers a closed-semi open gradient along the north-south axis, with some semi-arid vegetation in the very north and mangroves along the coast			
Geology	Generally Tertiary to the west and Precambrian (with inclusions) to the east, with a major anomaly in west Guinea			
Soil types	Very complex and non-patterned, except for an area of leptosols above the rocky anomaly in west Guinea			
Standing water (rivers)	Generally uniformly distributed, with some reduction in density in the north and drainage patterns linked to topography			

*The units for temperature seasonality represent the standard deviation of annual temperature x 100; those for rainfall seasonality represent the coefficient of variation on annual rainfall.

Table 19 shows that in addition to having a relatively small range (at least in comparison to other *Papio* allotaxa like *P. anubis* or *P. cynocephalus*, see Figure 43), the Guinea baboon also differs from these other taxa (see tables below) in having a relatively well-defined environmental range. In particular, looking at the data above, it becomes apparent that *P. papio* occupies relatively low altitude, smooth terrain with a climatic regime characterised by high temperatures and moderate rainfall and with low temperature and low rainfall seasonality, as one might expect given the relatively low latitude setting. Generally speaking, the mean and median values for these continuous variables are similar, with the key exceptions of altitude (for which the mean value of 172.8m is more than twice the median 82m) and roughness, which displays the same pattern. Both these anomalies result from the inclusion of a single area of higher altitude and roughness than the remainder of the range, located in west Guinea (see Figure 46). The climatic variables, in contrast, display more graduated variation along the north-south axis of the taxon's range (see Figure 47), with no major anomalies visible on the maps.

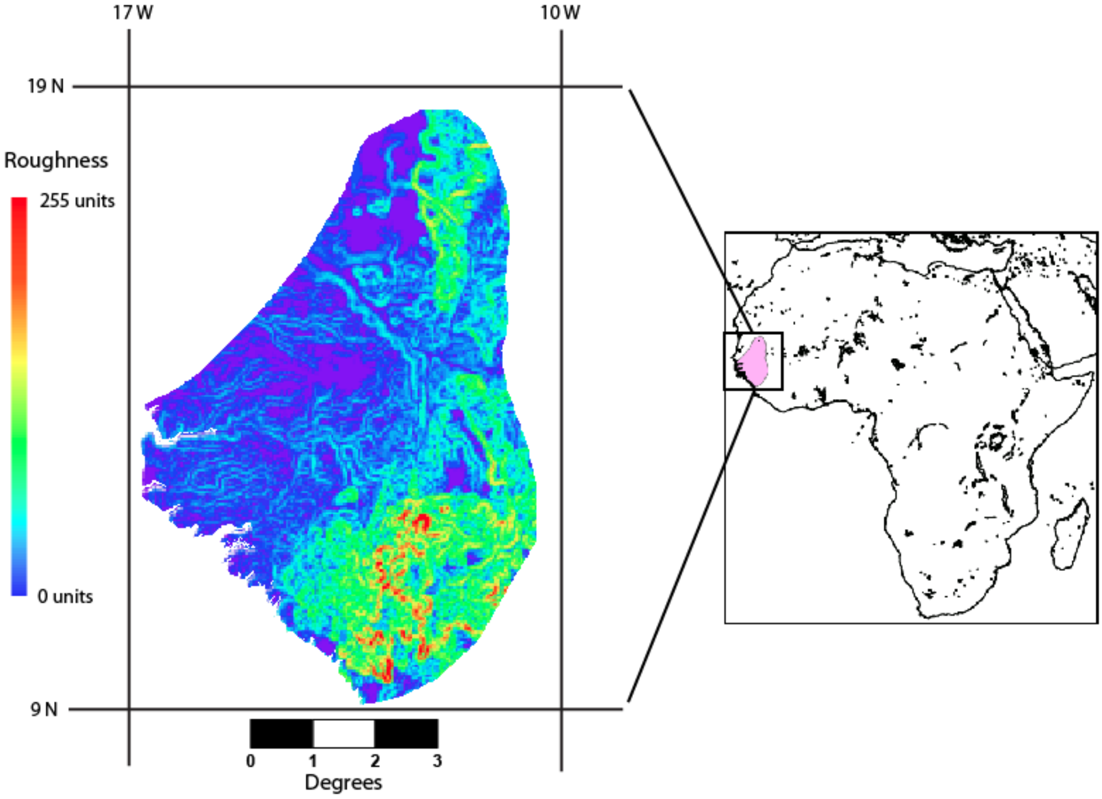


Figure 46: map showing the distribution of topographic roughness in the *P. papio* range in western Africa, with the 'anomalous' zone of hard rock/high altitude/high roughness visible in the lower right hand corner.

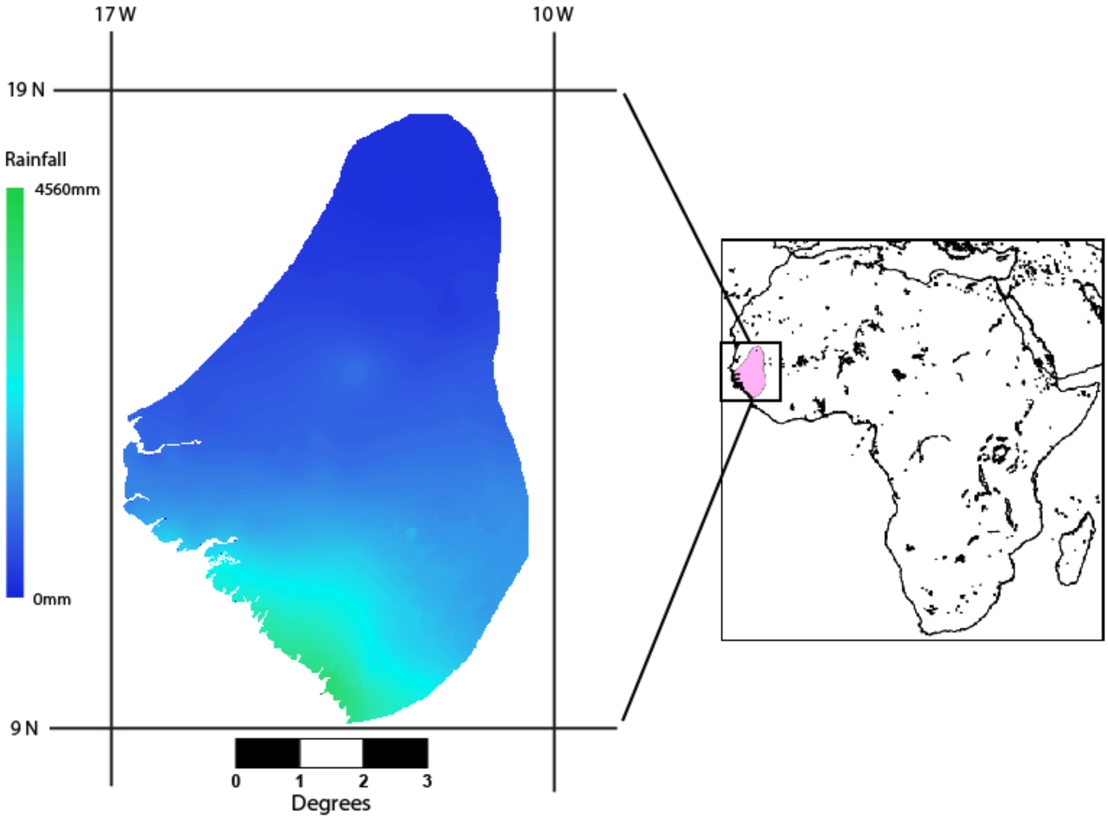


Figure 47: map showing the range of annual precipitation values across the *P. papio* range, and the generally more latitudinally banded pattern shown by the climatic variables as compared to the physical landscape ones (see above).

The regional geology is complex (Figure 48), but broadly speaking shows the same anomaly as the topographic/roughness maps (suggesting that this is due to a different underlying rock type) in west Guinea, with the remainder of the range divided between Tertiary rocks in the west and Precambrian rocks with later inclusions in the east. Soil types show even less patterning, again with the exception of this anomaly which forms a large block of leptosol, defined as a very shallow soil over hard rock or highly calcareous material (FAO/IIASA/ISS-CAS/JRC, 2009). Surface water, perhaps because of the area's moderate and non-seasonal rainfall levels, is relatively uniformly distributed with a small decrease in river density towards the northern semi-desert area. River drainage shows a radial pattern around the hard rock peak discussed above.

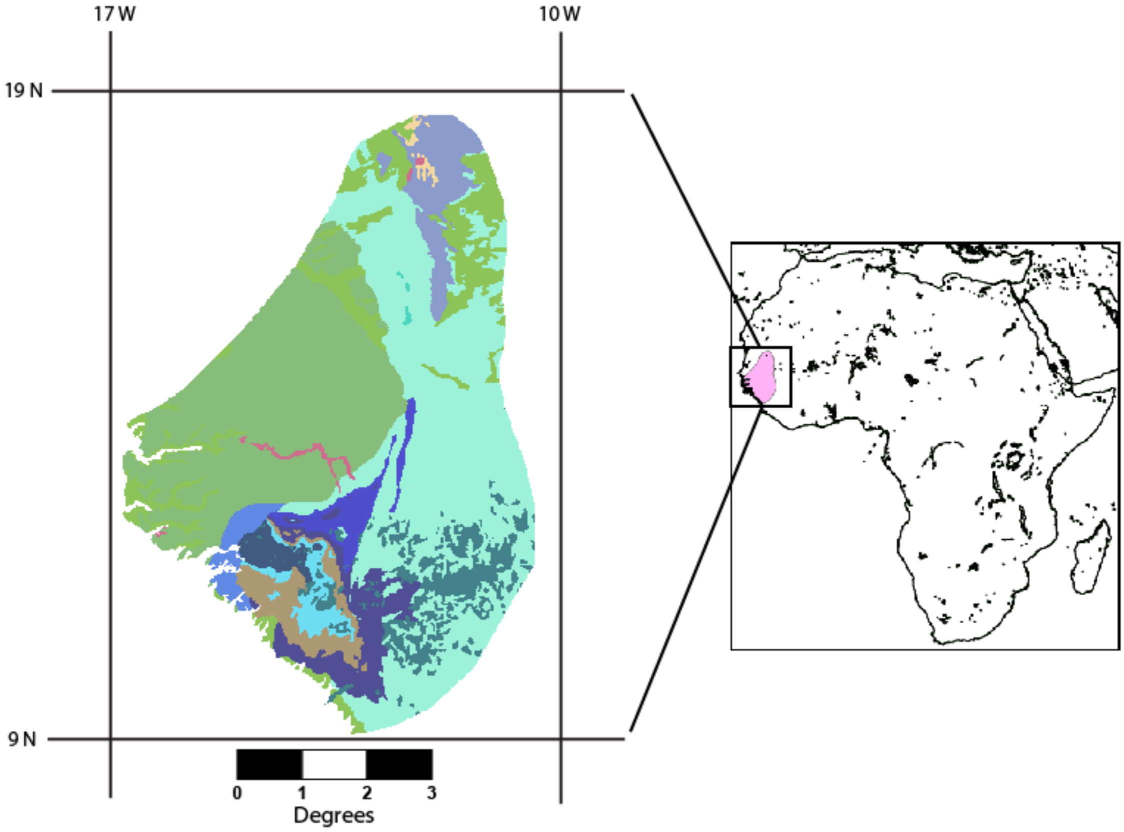


Figure 48: map showing the surface geology of the *P. papio* range, with the physical landscape anomaly discussed above again visible to the bottom right as an area of complex geology. A full key is not given as it is the relative pattern that is relevant, but as a whole, outside this complex region the area is either Precambrian (pale green) or Tertiary (darker green).

Finally, the vegetation map for the region – which, on the basis of Chapter Three's analyses of regional landscapes we would expect to show some influence from both climate and the physical landscape, and (given that *P. papio* occupies the west) potentially to be more affected by climate – shows the pattern in Figure 49. There is clear latitudinal banding, with closed vegetation to the south, semi-open vegetation in the centre of the range and arid/semi-arid vegetation to the north, with some small zones of aquatic vegetation around the coastline. This aquatic zone does not follow the latitudinal banding pattern completely, instead being clustered around certain bays and inlets on the coastline.

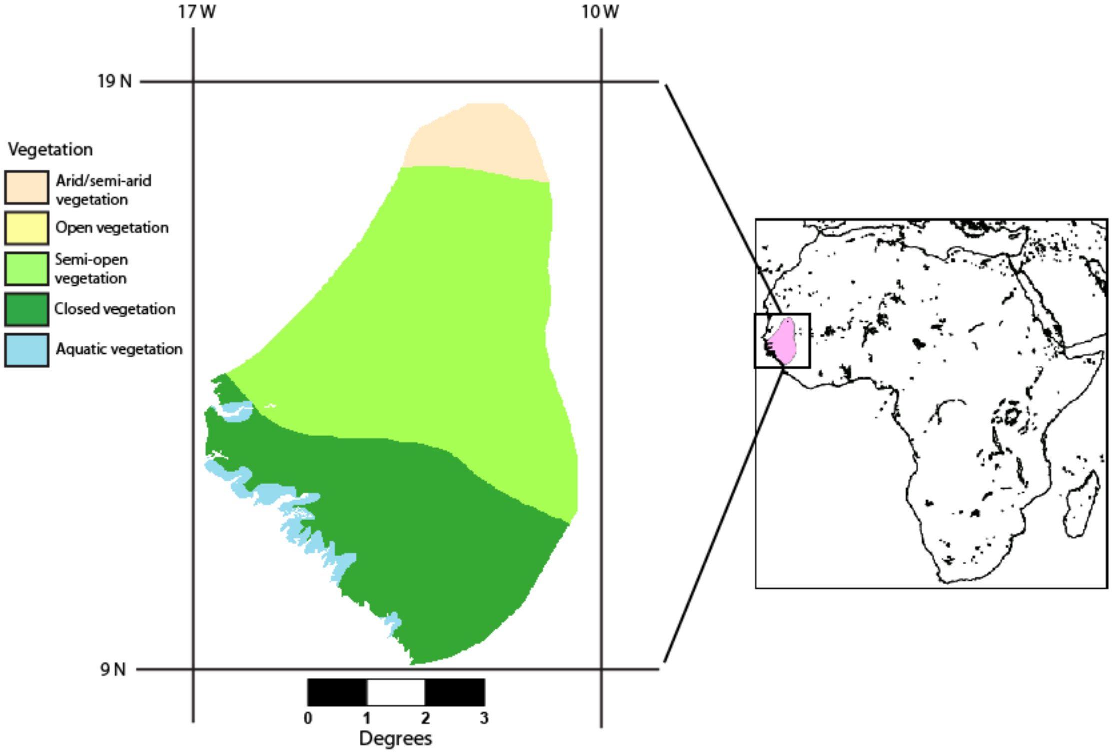


Figure 49: map of vegetation in the *P. papio* territory, showing the latitudinal banding pattern characteristic of the western regions of Africa.

Papio anubis (the olive baboon)

Papio anubis has the largest range of all the savannah baboon allotaxa, stretching across almost the full breadth of Africa just south of the Sahara. As noted above, although the eastern side of this range overlaps with those of both *P. hamadryas* and *P. cynocephalus*, the west borders, but does not overlap with, that of *P. papio*. The environmental conditions characteristic of this range are described in Table 20, below.

Table 20: basic data on the environmental conditions in the *P. anubis* range in north-west Africa.

Continuous Variable	**Minimum**	**Maximum**	**Mean**	**Median**
Altitude (m)	17	4310	655.7	483
Roughness (in arbitrary units from 1-255)	0	200	63.0	64
Annual temperature (degrees C)	-5.1	30.8	25.5	26.4
Annual rainfall (mm)	7.8	3070.3	976.6	960.9
Temperature seasonality (units from 0-22500)*	105.8	6405.2	1595.9	1420.6
Precipitation seasonality (units from 0-300)*	0.6	113.1	8.9	0.6

Discontinuous variable	**Description**
Vegetation	Spans the full range from closed to open habitats, with the main part of the range ending at the edge of the desert but two 'outposts' in semi-arid northwest Niger and northern Chad. Some aquatic contexts, though these are small in area.
Geology	Highly complex and ranges across almost all geological ages
Soil types	Equally highly complex; largely randomly distributed and wide-ranging, with a few areas of (weak) latitudinal banding
Standing water (rivers)	Consistently relatively common though less so in the north-east of the range; the 'outposts' are both located near rivers.

*The units for temperature seasonality represent the standard deviation of annual temperature x 100; those for rainfall seasonality represent the coefficient of variation on annual rainfall.

This table shows that as we would expect for a more widely-ranging taxon, the *P. anubis* distribution spans a much wider range of environmental conditions that the nearby *P. papio* one, with almost all variables more spatially heterogeneous for the former than the latter. The key exception, interestingly, is roughness, for where the *P. papio* range spans the full 255 unit range for this variable, the *P. anubis* range spans only the bottom 200 units of it. Interestingly though, despite having an overall roughness range that is both smaller than their neighbour's and does not reach into the very highest values, the *average* roughness for *P. anubis* is higher, at a mean of 63 and median of 64 compared to 51.51 and 33 respectively for *P. papio*. The anubis baboon range, other than being more variable than the Guinea baboon equivalent, is generally comparable in climate with similarly high average temperatures, moderate rainfall and low seasonality in both temperature and rainfall (it shows an average temperature seasonality of about 1500 units as opposed to 2500 for the Guinea baboon, but these are both low scores compared to the maximum value of 22500). In terms of the physical landscape things are rather different, however, with *P. anubis*' range higher in both average roughness and altitude than *P. papio*'s and showing a larger range from lowest to highest point (see Figure 50). The peaks of altitude and roughness generally coincide, in parts of Nigeria/Cameroon and the East African Rift Valley (EARV), with the areas that are responsible for the range's major climatic anomalies (particularly in temperature – though not the associated seasonality measure – and rainfall amount and seasonality). In addition, the two 'outposts' of *P. anubis* in the Sahara are both areas of relatively high altitude and roughness, although whether it is this or the associated standing water which makes them attractive to the baboons would require further field research. The topography of the *P. anubis* range is shown in Figure 50.

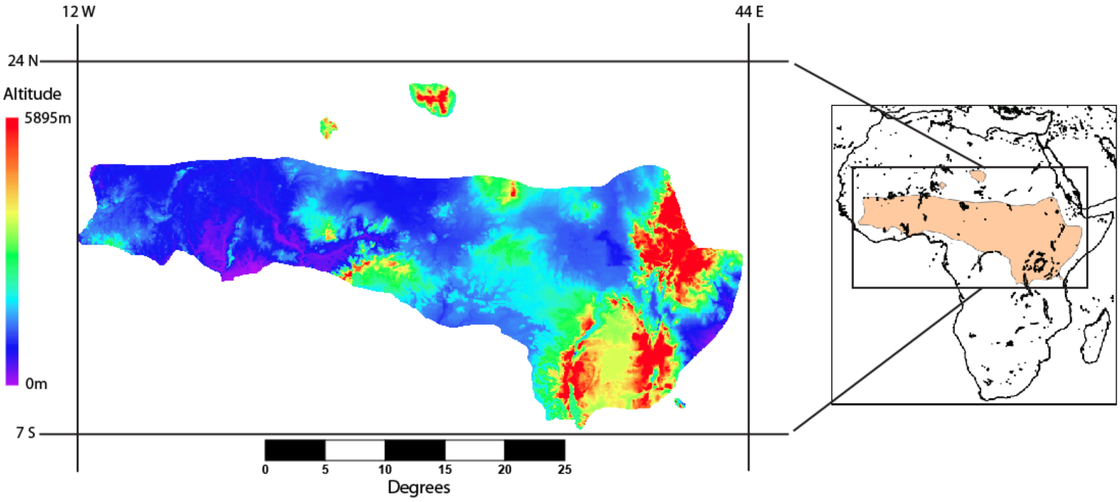


Figure 50: map showing the topography within the *P. anubis* range across sub-Saharan Africa including parts of the EARV in the east which represent the highest altitudes and roughnesses on the continent.

It is difficult to say much convincingly about the geology and soil conditions characteristic of the *P. anubis* range, as this species occupies areas spanning essentially the full range of these variables and there is not much clear spatial patterning in either variable. At the larger scale of this range, some latitudinal banding does become apparent in the distribution of soils (see Figure 51), but this is still only a weak signal among largely random patterns. In terms of standing water, the local drainage patterns are linked to topography and the overall density of drainage systems decreases towards the north but is otherwise fairly consistent across the *P. anubis* distribution.

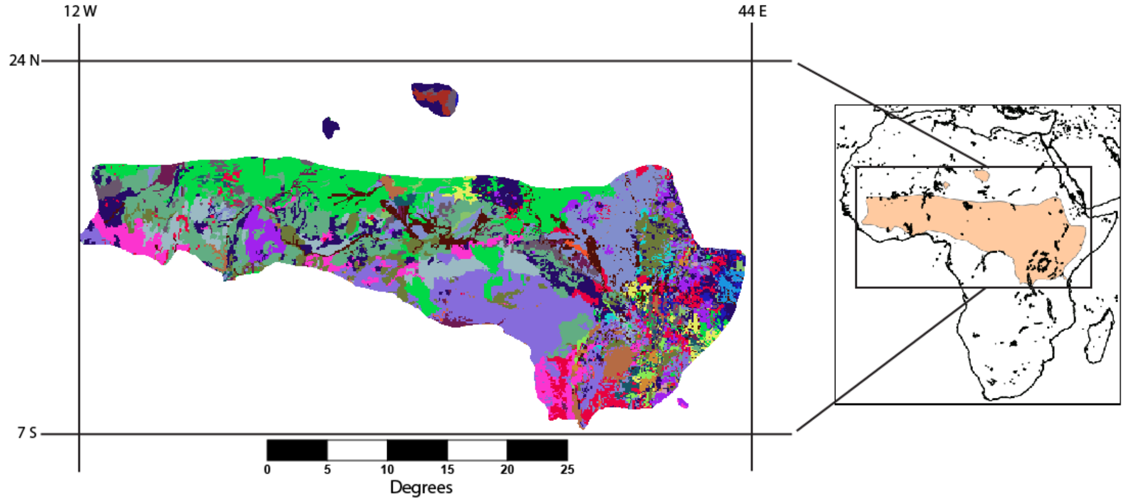


Figure 51: map showing the distribution of soils across the range of *P. anubis* showing a pattern with a small amount of latitudinal banding (for instance in the distribution of the green bands along the Saharan frontier) but predominantly illustrating the complexity and random spatial distribution associated with geological variables at the regional and continental scale. Again, a key is not provided because it is the pattern of soil distribution not the precise nature of each soil that is of relevance to understanding landscape.

Overall, the dominant spatial patterning in the landscapes of *P. anubis* range is unclear. In some areas (particularly in the west) and some variables (particularly the climatic, see Figure 52) there is a bit of latitudinal banding; in the east, however, these patterns disappear and all variables are heavily influenced by topography and lithology. This is in keeping with the findings of Chapter Three and suggests that this allotaxon ranges throughout landscapes shaped by climate and those shaped by the physical landscape. The patterning in intermediate variables like vegetation and soils is influenced by both (see Figure 51) and generally complex.

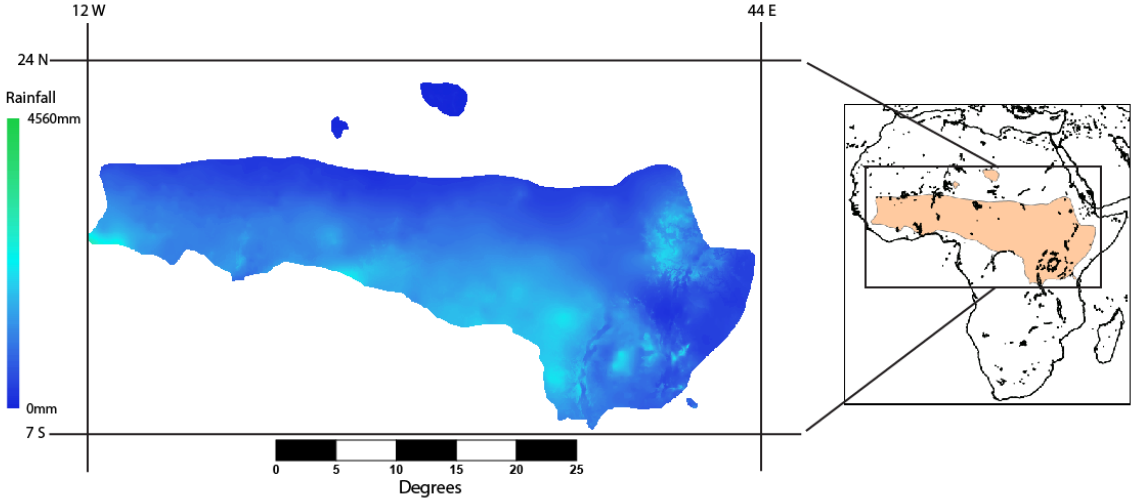


Figure 52: map showing the distribution of annual mean rainfall levels across the *P. anubis* range, and recording the differing influences of climate (to the west) and the physical landscape (to the east).

Papio cynocephalus (the yellow baboon)

The range of *P. cynocephalus* spans much of central Africa in a band across the northern parts of Angola, Zimbabwe and Mozambique, the entirety of Malawi, and the southern regions of the Democratic Republic of the Congo, most of Tanzania, and parts of Kenya and Somalia/Ethiopia where the eastern side of the range stretches northwards. This area covers a reasonable range of environments, as summarised in

Table 21 below. There are no obvious differences between the ranges of the two sub-groups of this species, *P. cynocephalus cynocephalus* and *P. cynocephalus kindae*, so the allotaxon is treated as one unit in this text.

Table 21: basic data on the environmental conditions in the *P. cynocephalus* range in north-west Africa.

Continuous Variable	**Minimum**	**Maximum**	**Mean**	**Median**
Altitude (m)	0	2500	835.8	901
Roughness (in arbitrary units from 1-255)	0	255	65	66
Annual temperature (degrees C)	11.2	30.5	23.1	22.8
Annual rainfall (mm)	242.2	2570.3	1117.1	1117.1
Temperature seasonality (units from 0-22500)*	193.5	3436.5	1508.2	1420.6
Precipitation seasonality (units from 0-300)*	0.6	67.4	2.9	0.6
Discontinuous variable	**Description**			
Vegetation	Spans the full range of vegetation types excepting arid/semi-arid habitats, although the distribution of these is less clinal and more patchy across the range			
Geology	Complex, but less so than for *P. anubis*; generally seems to occupy an area of old (Precambrian) rock with numerous later inclusions and modifications and particularly a large western Cenozoic formation			
Soil types	In the west, longitudinal bands of ferralsol and arenosol corresponding to the sides and peak of the Cenozoic rock formations there; in the east, complex and patchy			
Standing water (rivers)	Generally uniformly distributed and common			

*The units for temperature seasonality represent the standard deviation of annual temperature x 100; those for rainfall seasonality represent the coefficient of variation on annual rainfall.

Overall, then, the range of *P. cynocephalus*, being more southerly than those of *P. anubis* and *P. papio*, is broadly similar in climatic terms but has slightly lower average temperatures and higher average rainfall. Seasonality values are much the same as for these other taxa, however, and the overall ranges of climate conditions are of the same order as, though typically slightly narrower than, *P. anubis*, perhaps reflecting the fact that although *P.*

cynocephalus lives south of this latter taxon, the size of the latitudinal band over which it is spread is similar. Interestingly, the lowest minimum temperatures encountered by any baboon taxon are those for *P. anubis*, despite the much more southerly range of *P. ursinus*, suggesting that it is topography, rather than the broad pattern of climate across the African continent, which is responsible for the wide range of conditions encountered by the group.

In terms of the physical landscape, *P. cynocephalus* falls approximately in the middle of the range occupied by the savannah baboons for both average altitude (901m) and average roughness, which is the same as for *P. anubis*. Interestingly, the range of altitudes encountered by this species is smaller than for the olive baboon despite the latter occupying a range with a much lower average (mean/median) altitude; the area used by *P. cynocephalus* is more uniformly of moderate altitude and roughness, with only the very northeast of the range (see Figure 53) showing a low altitude and even then generally a moderate roughness.

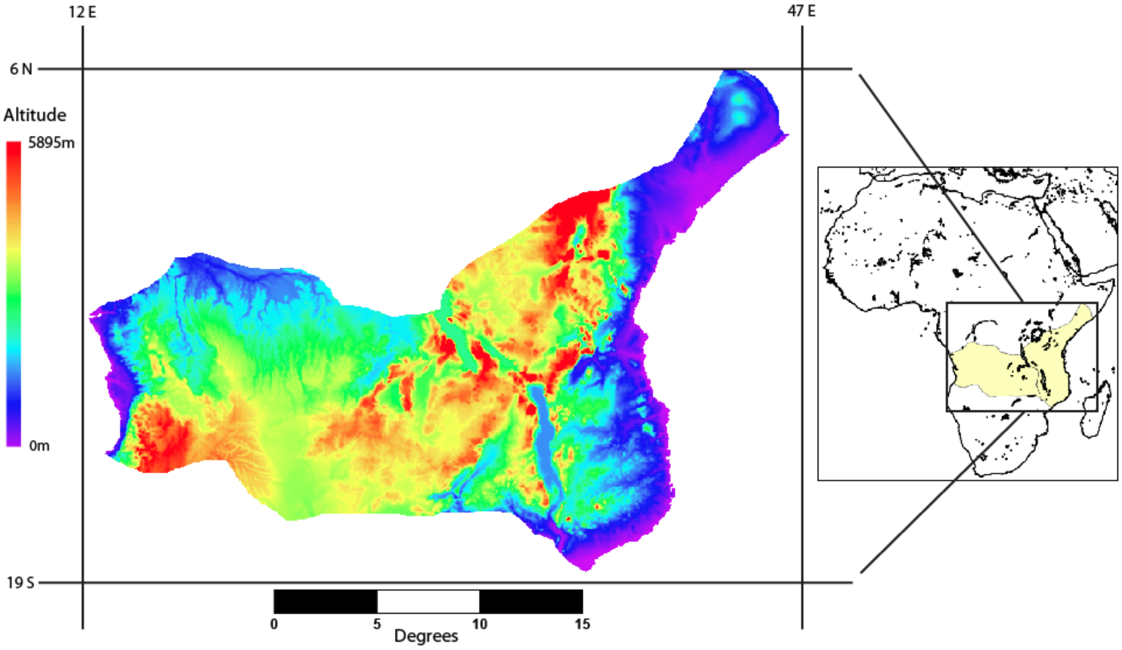


Figure 53: map showing the topography across the *P. cynocephalus* range, including the low altitude area to the northeast.

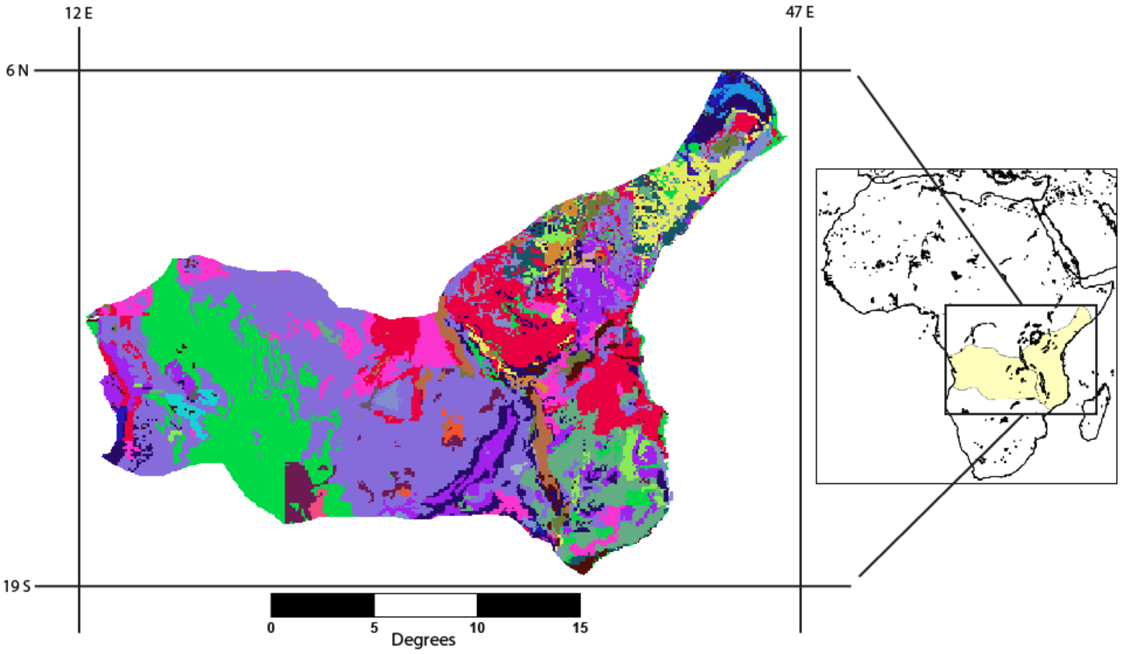


Figure 54: map showing the distribution of different soil types across the range of *P. cynocephalus*, showing the longitudinal patterning in the west and the more complex, random soils in the east. Precise details of soil type are not relevant, so a key to the pattern is not given here.

In terms of the discontinuous environmental variables, standing water is relatively evenly distributed across the yellow baboon range with little north-south or east-west variation, while geology and soils show some patterning towards the west (see Figure 54) where Cenozoic rock formations have been introduced into older terrain and have produced bands of ferralsol and arenosol over different areas. The eastern side, however, perhaps because of the upheaval associated with the rift, shows no clear patterning. In terms of vegetation, *P. cynocephalus* ranges across open, semi-open, closed and aquatic habitats, while avoiding arid or semi-arid areas and the deepest forests. The distribution of these different types of vegetation is less clinal in this area, however (see Figure 55). Like *P. anubis*, then, this allotaxon lives in a complex set of landscapes although overall there is less evidence of clinal (latitudinally banded) patterning in this range than in the former taxon's.

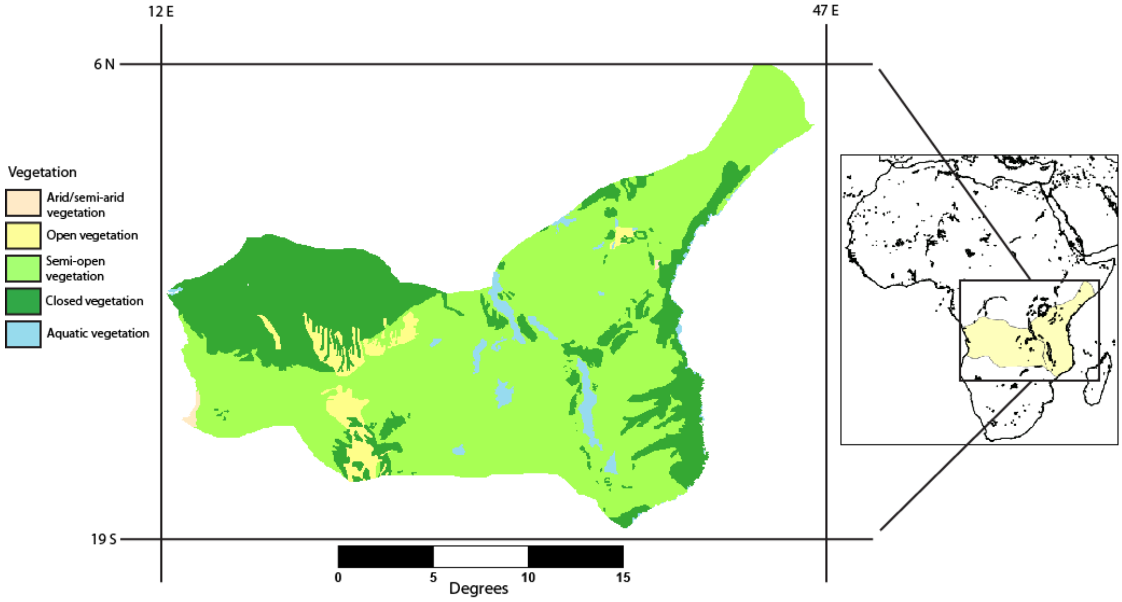


Figure 55: map showing the distribution of different vegetation types in the *P. cynocephalus* range.

Papio hamdryas (the sacred baboon)

P. hamadryas, like *P. papio*, has a relatively restricted range in the low latitudes, although this taxon occupies the east where the latter is found in the west. The *P. hamadryas* range is mostly contained within Ethiopia, Djibouti and Eritrea, but also extends into northwestern Somalia and a tiny area of northeastern Sudan. There is also a population of hamadryas baboons on the Arabian Peninsula, across the Red Sea from their conspecifics. The range of these Arabian baboons is shown on figures where available, for comparative purposes, but is not included in the statistics and discussion below because data for these specimens is sparser and less relevant to this thesis' focus on African primates. The environmental conditions across the African *P. hamadryas* range are summarised in Table 22.

Table 22: basic data on the environmental conditions in the *P. hamadryas* range in north-west Africa.

Continuous Variable	**Minimum**	**Maximum**	**Mean**	**Median**
Altitude (m)	0	4002	1026.5	972
Roughness (in arbitrary units from 1-255)	0	255	100.2	81
Annual temperature (degrees C)	4	32.0	24.0	24.5
Annual rainfall (mm)	7.8	1273.4	351.6	273.4
Temperature seasonality (units from 0-22500)*	631.7	4488.3	2560.0	2647.6
Precipitation seasonality (units from 0-300)*	0.6	36.9	4.1	2.9

Discontinuous variable	**Description**
Vegetation	A large area of arid/semi-arid habitat along the coast, with semi-open vegetation and closed patches inland
Geology	Very complex and patchy, especially near the coast
Soil types	Randomly distributed pockets of various soils within a leptosol matrix
Standing water (rivers)	Common in the south and west highlands, sparse on the coastal lowland; drainage follows topographic patterns

*The units for temperature seasonality represent the standard deviation of annual temperature x 100; those for rainfall seasonality represent the coefficient of variation on annual rainfall.

The relatively small range of *P. hamadyras*, unlike that of *P. papio* (discussed above) spans a relatively wide range for many environmental variables despite its small overall size. In particular, this allotaxon has only the second largest range of altitudes of the five *Papio* baboon taxa (see Figure 56), and spans the full range of roughness values, a temperature range twice as wide as that of *P. papio*, and broader ranges of seasonality for both temperature and rainfall. Average precipitation itself varies less within *P. hamadryas*' range than that of *P. papio*, although it remains typical of the genus as a whole.

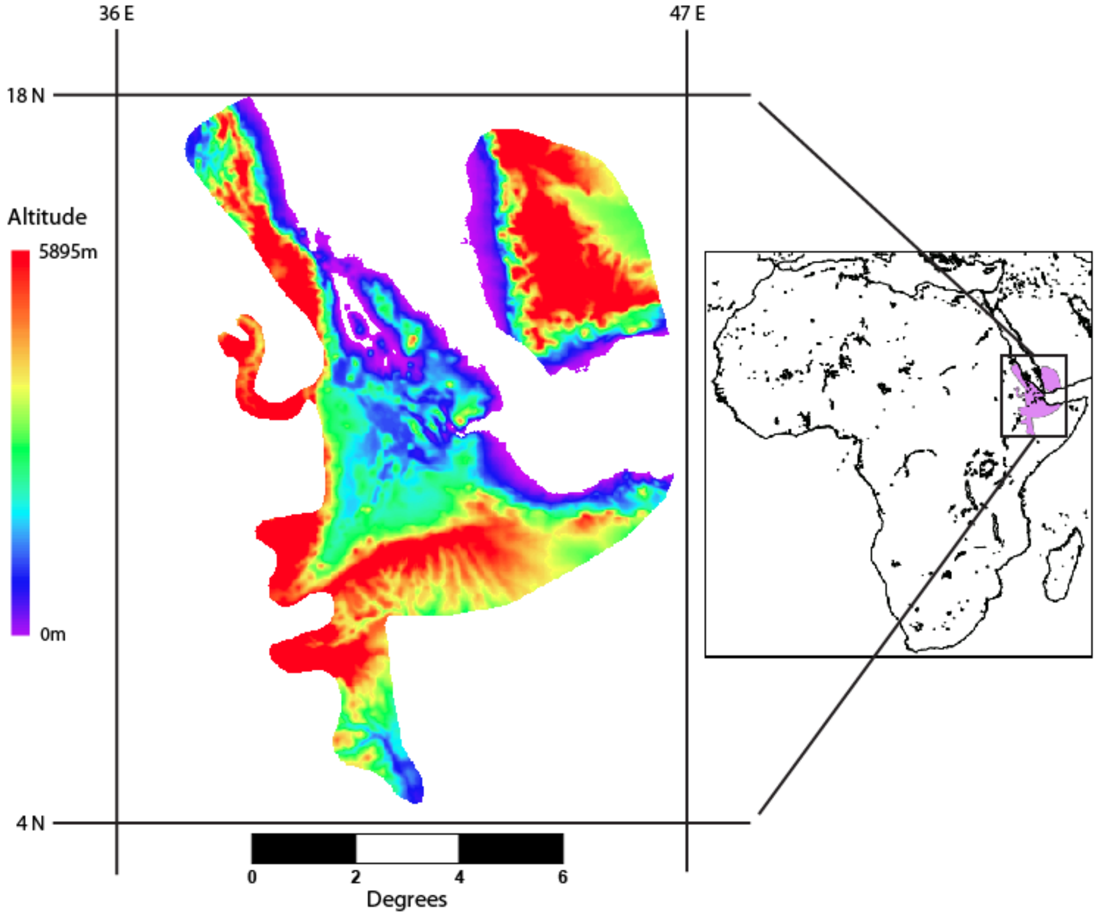


Figure 56: map showing the topography of the *P. hamadryas* range, with the dicotomy between lowlying coastal areas and highlands.

In terms of the spatial patterning of environmental variables, moreover, it is notable that in this area there is little clinal patterning even in the climatic variables (see Figure 58). Instead, the regional topography seems to present a dichotomous separation of the lowlying north-east coastal plain and highlands in the south and west (Figure 56) which is reflected in vegetation as a dichotomy between arid/semi-arid and other vegetation types (Figure 57) and, to a lesser extent, in climate. In terms of topographic roughness, however, this is one area where the different altitude zones do not correspond to different roughness zones: roughness in the *P. hamadryas* range is, on average, higher than in the range of any other allotaxon (see tables above) and although not uniformly distributed is high both on the coast and inland.

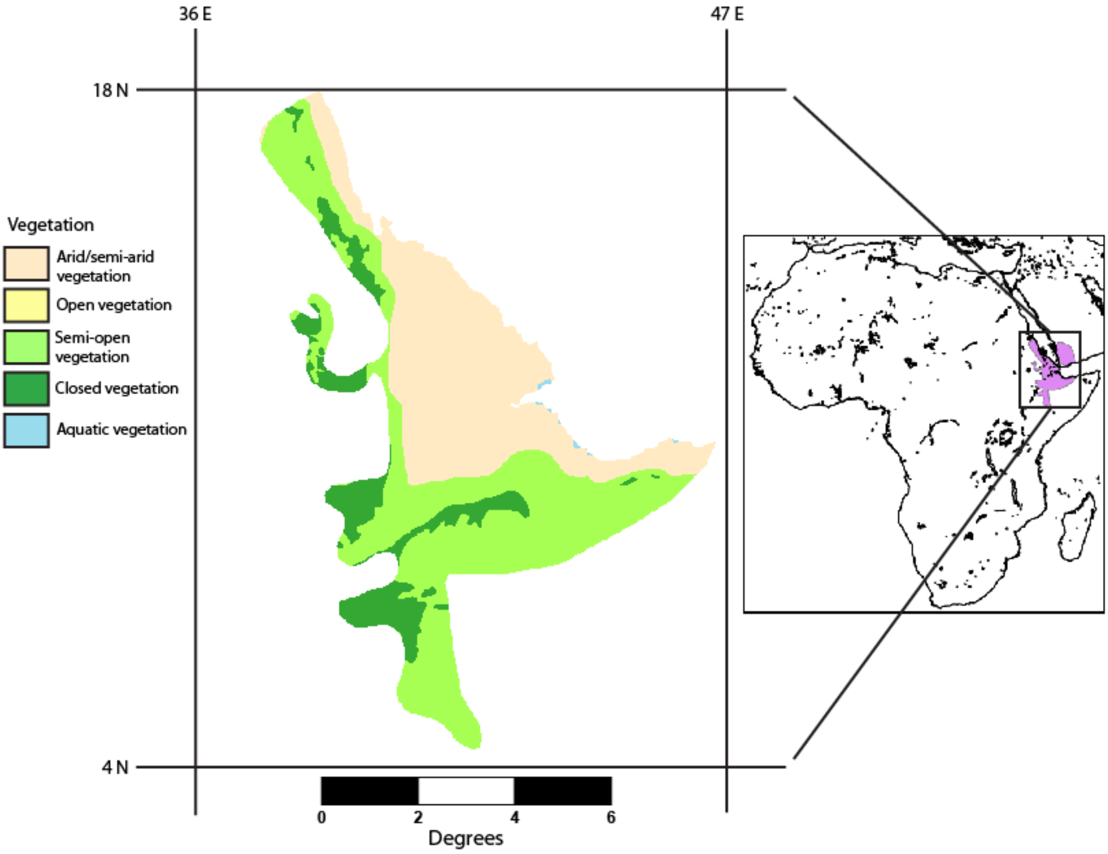


Figure 57: map showing the distribution of vegetation types associated with the differing topographies in the *P. hamadryas* range.

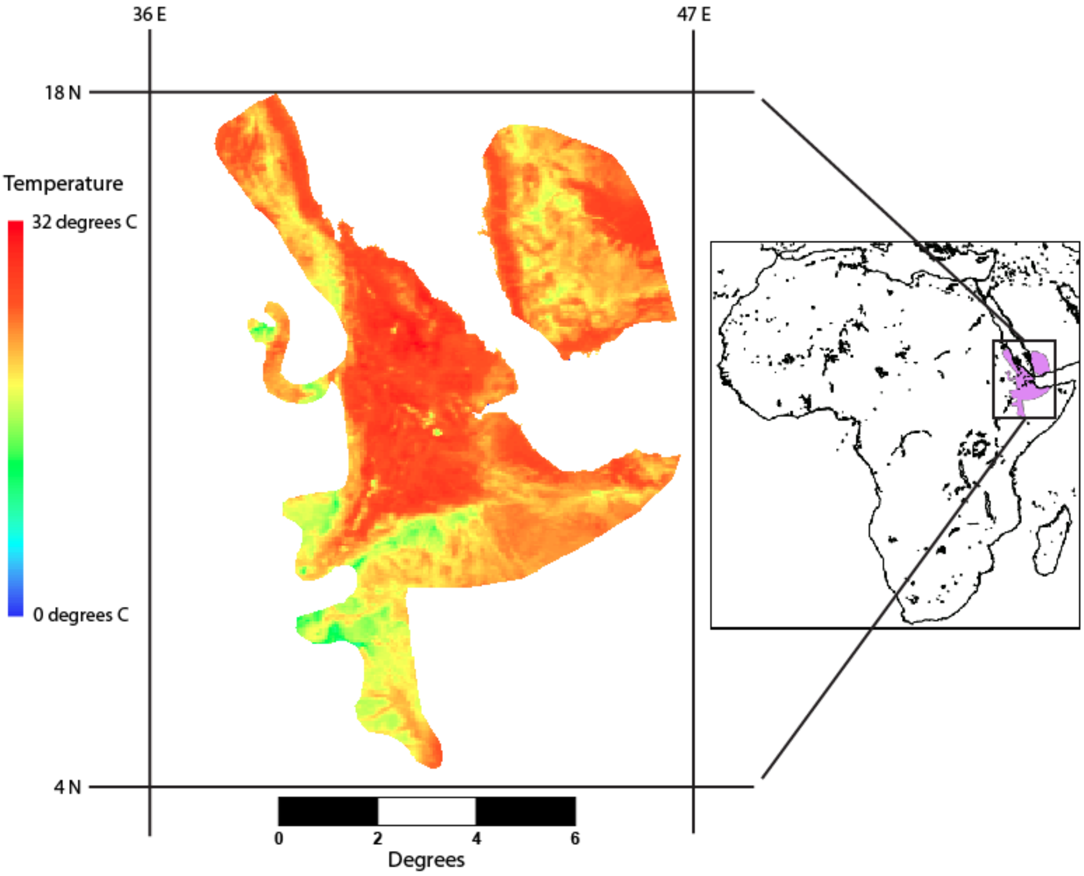


Figure 58: map showing the distribution of mean annual temperature across the *P. hamadryas* range in east Africa. Note the difference between the relatively warmer coastal plain areas (predominantly red) and the cooler highlands (yellow and orange).

The surface geology of the *P. hamadryas* range is complex, as we would expect from an area in the EARV, but the overlying soils are a little more uniform, comprising a mosaic of small patches of various soil types in a leptosol matrix. These are the same very shallow soils as were found overlying the high altitude/rough areas of the *P. papio* range, and are associated with hard rock substrates, presumably (at least in this case) linked to the rift. Surface water is relatively common across the highland areas, with drainage following the topography, but rarer on the plains as the semi-arid vegetation there would suggest.

<u>*Papio ursinus*</u> *(the chacma baboon)*

The most southerly of the *Papio* allotaxa, the range of *P. ursinus* covers South Africa, Lesotho and Swaziland, most of Namibia, parts of southern Angola and Zambia, northern Botswana, Zimbabwe and parts of western Mozambique. There is a notable gap in the centre of this range, across the majority of Botswana, where no baboon species occur, while at the northern boundary with *P. cynocephalus* the range abuts that of the latter species in the east but not in the west. Table 23 summarises the environments encountered by *P. ursinus*.

Table 23: basic data on the environmental conditions in the *P. ursinus* range in north-west Africa.

Continuous Variable	Minimum	Maximum	Mean	Median
Altitude (m)	0	3215	983.6	1052
Roughness (in arbitrary units from 1-255)	0	255	64.9	66
Annual temperature (degrees C)	4	26.7	19.5	19.7
Annual rainfall (mm)	23.4	2539.1	507.8	539.1
Temperature seasonality (units from 0-22500)*	1157.6	6679.5	3699.4	3524.1
Precipitation seasonality (units from 0-300)*	0.6	76.8	5.3	1.8
Discontinuous variable	**Description**			
Vegetation	Patchy, with a sizeable area of arid/semi-arid vegetation in the west and representation of all other types			
Geology	A Precambrian base, with three main anomalies: a large Cenozoic mass centred on Botswana; sizeable Tertiary and Pleistocene coastal deposits, and a block of Triassic/Permian and Mesozoic igneous rocks in South Africa			
Soil types	Largely random, though reflecting the underlying geology a bit with extensive arenosol deposits over the Cenozoic block and some clear areas of solonetz across the coastal plains			
Standing water (rivers)	Relatively common and randomly distributed across the range			

*The units for temperature seasonality represent the standard deviation of annual temperature x 100; those for rainfall seasonality represent the coefficient of variation on annual rainfall.

The *P. ursinus* range, as Table 23 suggests, is overall the highest in altitude of any *Papio* allotaxon and shows relatively high overall roughness, with a good range in both. It has the lowest average temperature, moderate rainfall, and the most seasonal climate of all allotaxa (as would be expected given that it is the most southerly of the five *Papio* ranges), and climate also displays a relatively large spatial variation across the range. As a result, every major class of vegetation is represented (including a swath of arid/semi-arid vegetation in Namibia, see Figure 59), but there is no evidence of the latitudinal banding pattern seen further north.

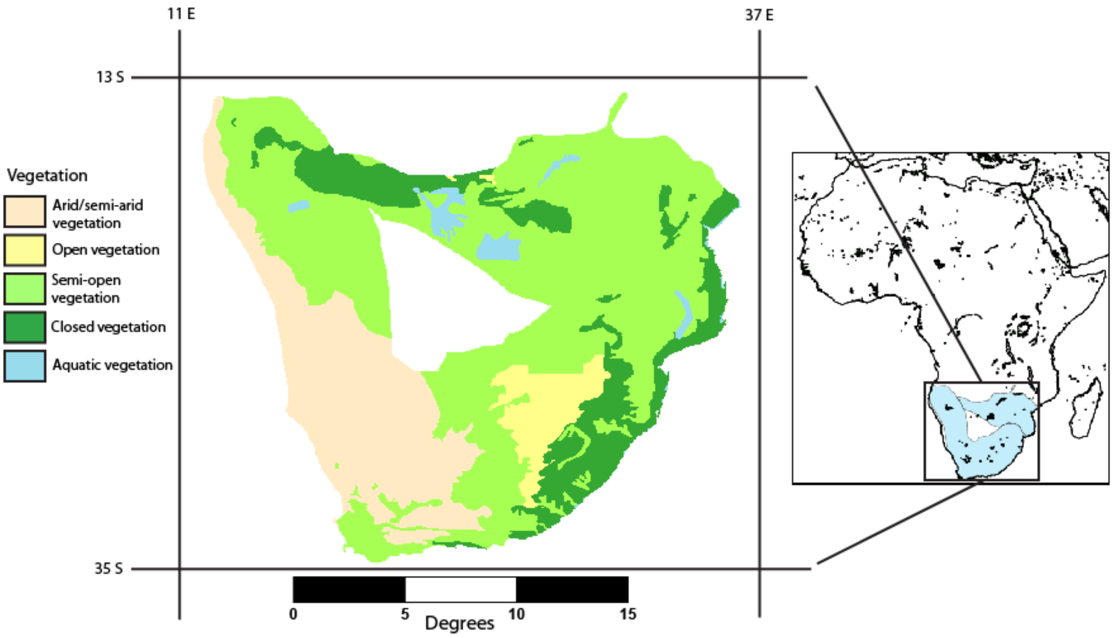


Figure 59: map showing the distribution of vegtation types in the *P. ursinus* range.

Considering spatial patterning in these environments, the topographic map again identifies several well-defined regions with distinctive patterns which are reflected to a greater or lesser extent in various other variables. The highest altitudes are found in two parts of the *P. ursinus* range: in a broad area of eastern South Africa, and in a north-south band through Namibia in the west. In addition, along the east coast of southern Mozambique, there is a low altitude anomaly – a very broad, low lying coastal strip (see Figure 60).

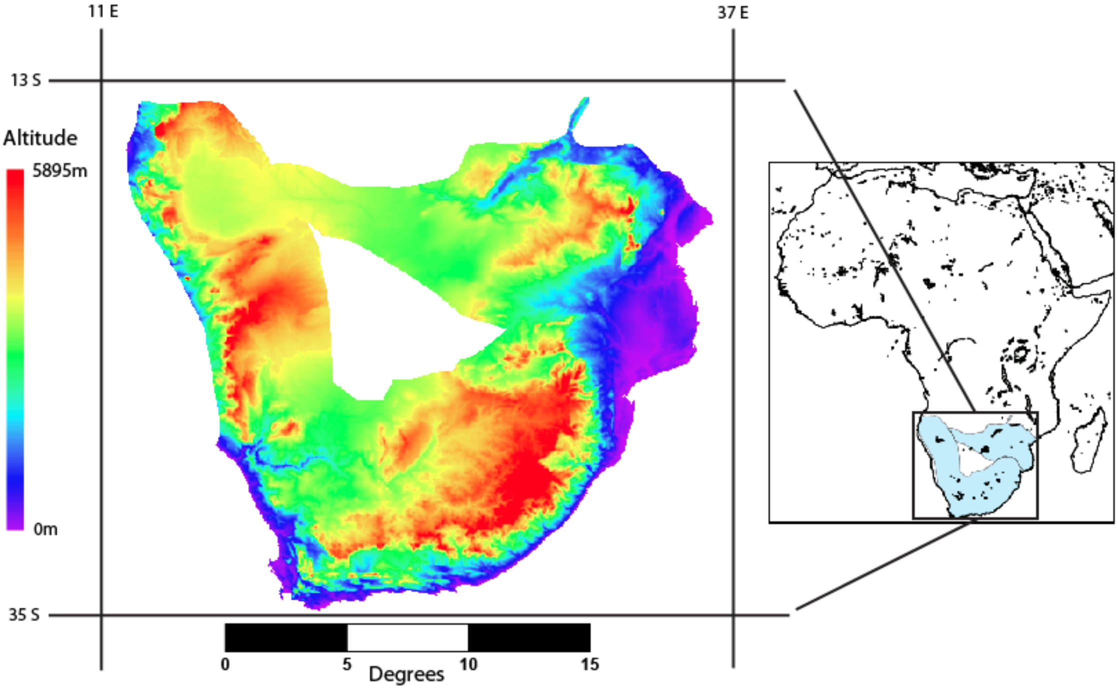


Figure 60: map showing the topography of the P. ursinus range in southern Africa.

As in the case of the *P. hamadryas* range, however, although these areas do stand out as distinctive in certain ways (for instance, in the geological map where the South African high-altitude area is clearly visible as nested blocks of Permian, Triassic and Mesozoic igneous rocks, see Figure 61), they are not so in all ways. In roughness, for instance, the pattern does not reflect these three areas – although the coastal strip is notably smooth, it is no more so than inland areas of more moderate altitude (Figure 62) – and for the climatic variables there is some patchiness but no clear spatial patterning linked to topography. The distribution of surface water resources is generally random across the area.

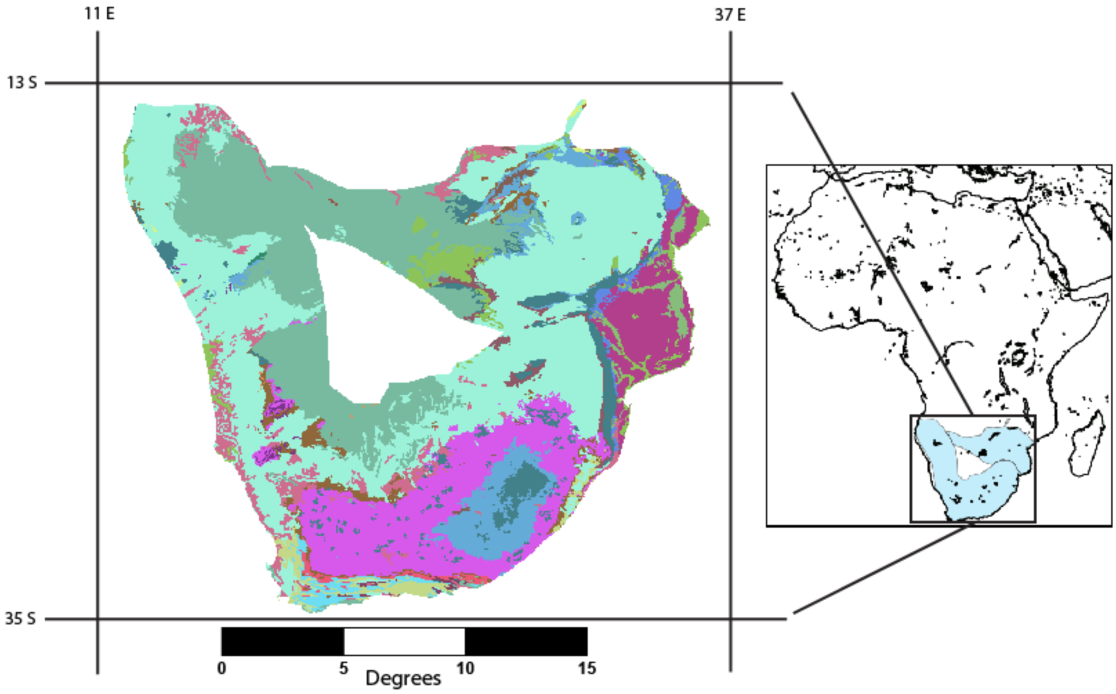


Figure 61: map showing the distribution of different surface rocks in the P. ursinus range, particularly the large nested blocks of Permian (pink), Triassic (mid-blue) and Mesozoic igneous (dark blue-green) rocks associated with the topographic anomaly in South Africa and Lesotho.

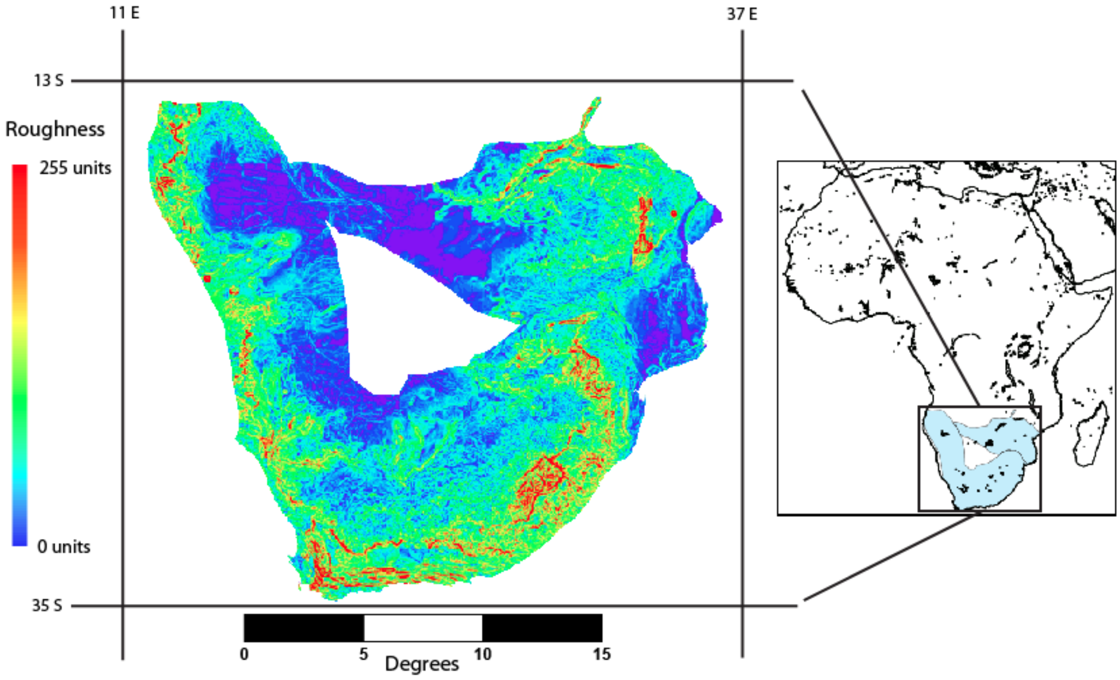


Figure 62: map showing the distribution of topographic roughness in the P. ursinus range. Note the differences between this figure and the topographic map above.

Differences in the Ranges of Papio *Allotaxa: A Summary*

To summarise the information on *Papio* baboon ranges provided above, then, we can say that the five major allotaxa each encounter somewhat different conditions across the landscapes they occupy, with differences not restricted to climate and vegetation – both of which have already been noted as important (e.g. Dunbar, 1996, Hill and Dunbar, 2002) – but also encompassing surface geology, soils, topography and topographic roughness. In addition, as identified in the brief analysis of extant African environments presented in Chapter Three, these variables may or may not reflect one another, with topographic anomalies in some areas, like the hard rock intrusion in the southeast of the *P. papio* range, apparently influencing not just topography, geology and roughness but dominant soil types and climatic patterns, while those in other areas, for instance in the *P. ursinus* range, have much less immediate impact on other variables. This fits with the differing balances between climate and physical landscape factors identified for these different geographic regions.

Speaking generally, and looking at the average conditions in each allotaxon's range, it becomes apparent that there are certain distinctive features for each taxon, including:

- That *P. papio* occupies one of the smallest ranges, with relatively uniform conditions broken by one geological/topographic anomaly with wide-reaching impacts on other variables. This range has the highest average temperature and the lowest average altitude and roughness values of the *Papio* baboons;

- *P. anubis*, in contrast, occupies a very large and diverse range, with generally the widest range of conditions of any allotaxon. This range is notably spatially variable in all landscape components but temporally (at least seasonally) relatively uniform. In particular, it spans the full range from the apparently climatically dominated landscapes of the west to the topographically dominated ones of the east;
- For *P. cynocephalus*, conditions are only slightly less variable than for *P. anubis*, although the climate reflects the shift southwards. The range is the wettest of all the allotaxa, and again only minimally seasonal;
- The range of *P. hamadryas* is the smallest in area, and notable for spanning the roughest and driest landscapes occupied by the savannah baboons. It is markedly seasonal, especially with regards to precipitation, and seems to span a marked contrast between the north-east coastal lowland and the south-west highlands in most, but not all, variables;
- Finally, *P. ursinus* occupies the most southerly range, as reflected in its climate, which is the coldest and most seasonal in temperature. It is also the range with the highest altitude, although roughness is moderate, and topographic features seem to have somewhat less impact on climatic and vegetational conditions than in other ranges;

As the above brief summary shows, each of the *Papio* allotaxa is notable in some respects for the range of conditions occupied, but while these 'average' differences have long been recognised in, for instance, the use of the name 'mountain baboons' for *P. ursinus* (Whiten et al., 1987, Henzi et al., 1997) and papers on the impacts of different conditions on baboon socioecology (Barton et al., 1992, Hill and Dunbar, 2002), the inclusion of a spatial element in this type of analysis certainly adds detail and flags the appearance of variable spatial associations between landscape components and of identifiable sub-parts of a single range. Explaining the observable differences between the allotaxa is much harder, however. It may be that the different baboon allotaxa are in some ways evolutionarily or ecologically adapted to slightly different average conditions, or that local populations are fitted directly for differences in their ranges without much overall influence across an allotaxon. Identifying whether the observable differences between allotaxa are adaptive, and whether the environmental patterns pre- or post-date differentiation, remains difficult, although it is notable that the taxa with the most restricted ranges have been proposed – although not always supported – as the most distinctive genetically and behaviourally (Newman et al., 2004). In addition, establishing how much of the spatial variation in landscapes and co-variation between baboon distributions and environments is due to spatial autocorrelation remains complicated.

This implies that analyses which aim to link anatomical differences between baboon allotaxa directly with average differences in the landscapes they occupy are likely to oversimplify matters to a point where meaningful information is difficult to obtain. The variation in landscapes within a range – particularly for the more widespread taxa *P. anubis*, *P. cynocephalus* and *P. ursinus* – dwarfs the differences between ranges, the same pattern Kamilar (2006) found for baboon socioecology. Unless this landscape variation is strongly systematically patterned (such that only a very small number of the possible combinations of landscape variables are actually realised), which the maps presented in Chapter Three and the analyses above suggest is only rarely the case, mapping anatomy onto landscape is likely to be extremely complex. The best way forward, therefore, is presumably to focus on baboons of known ecology and location, and this is the strategy adopted in this thesis (below). Before this can happen, however, there are a couple of loose ends to be tied up – specifically, the questions of the nature of areas of overlap between ranges, and of the relationship between landscape and socioecology (which is likely to influence anatomy at the small scale).

Areas of Overlap: Marginal or Core?

Within the broad distribution pattern explored above there is variation in the degree of overlap among allotaxa. Members of *Papio papio*, for example, share a range boundary – but do not noticeably overlap – with *P. anubis* along a frontier crossing Mali, Guinea and Sierra Leone, while the Southern *P. ursinus* show only marginal overlap with neighbouring *P. cynocephalus* populations in Zambia, Zimbabwe and Mozambique (see Figure 43). The three remaining major allotaxa, in contrast, share much larger parts of their ranges.

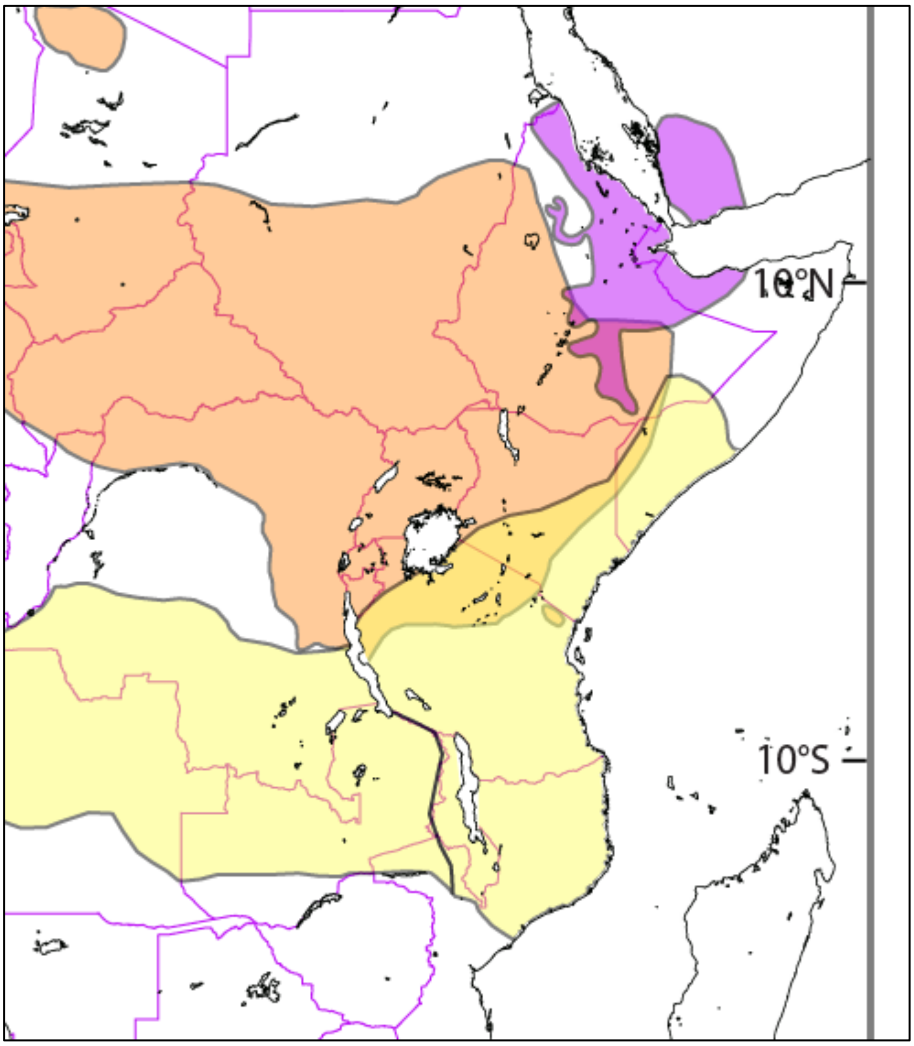


Figure 63: a subsection of the map of *Papio* baboon distributions in Figure 43 showing the zones of overlap in the horn of Africa region. Colouring is the same as for the earlier figure (*P. anubis* = orange, *P. cynocephalus* = yellow and *P. hamadryas* = purple), and political boundaries have been added for reference.

The largest areas of overlap occur where *P. cynocephalus* and *P. anubis* meet in a region spanning parts of Ethiopia, Somalia, Kenya and Tanzania and includes one group of *P. anubis* in North East Tanzania which is entirely surrounded by *P. cynocephalus.* However while the actual area of overlap between *P. anubis* and *P. hamadryas* may be smaller, the latter taxon's smaller overall range may make it particularly influential as a source of new genes and behaviours. Interestingly, even at this broad scale of analysis, it is notable that the major regions of overlap between allotaxa occur in East Africa, roughly along the line of the Rift Valley (see Figure 63 and Figure 43). This is the same pattern as was found for hominin sites by King and Bailey (2006) – although exactly what causes it remains unclear in both cases.

There are many possible reasons for this pattern of overlap and mutual exclusivity, but of these myriad options there are four which can be clearly expressed and contrasted:

1. As a null hypothesis, the pattern might be random and have no clear explanation.

2. The overlapping allotaxa may be those which are more socially or genetically compatible, such that the pattern has little to do with environment.
3. The East African Rift Valley (EARV) might be a particularly attractive area for baboons – or have a very high carrying capacity.
4. Finally, the EARV might be a marginal part of the savannah baboon range such that there are several allotaxa which have peripheral populations in the area but density remains low (these would potentially be demographic sink populations, or at least relatively small and sparse).

Information from the literature on baboon population density, troop size, genetics and social structure can be used to test these alternatives.

Baboon Population Densities

Wrangham et al. (1993) lists the population densities of three *Papio* allotaxa as *P. cynocephalus* – 9.7 individuals/km^2; *P. ursinus* – 2.4 to 4 individuals/km^2 (based on different authors' estimates, giving a mean of 3.2 individuals/km^2) and *P. hamadryas* – 3 individuals/km^2. These values go with average troop sizes of 80, 46.1 and 68 individuals respectively (Wrangham et al., 1993), and suggest that *P. cynocephalus* generally lives at higher densities and in larger groups than the other taxa, while *P. hamadryas* and *P. ursinus* live at about the same density but in differently sized groups. This, however, tells us nothing about *P. anubis* or *P. papio* and is not conclusive as *P. cynocephalus* has an extremely large range and this figure might easily hide significant regional variations.

Looking at geographically-located populations, in contrast, provides patchier but potentially more accurate data. Figure 64 summarises data from the literature on baboon population densities at various localities.

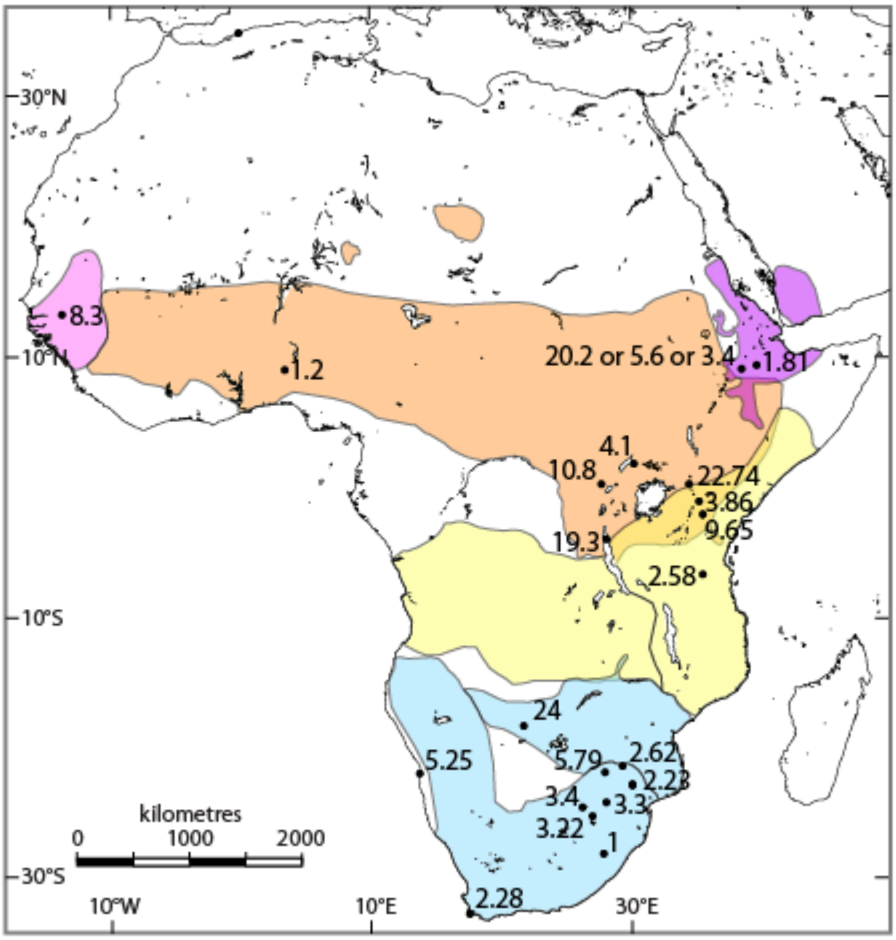


Figure 64: baboon population densities (in individuals per square kilometre) for a range of troops reported in the literature. Data from Anderson (1981 and references therein), supplemented with a point for Ivory Coast *P. anubis* (Kunz and Linsenmair, 2008) and one for *P. papio* in Senegal (Byrne, 1981). Locations of sites are approximate and obtained by entering place names into Google Earth.

As this figure demonstrates, density estimates do not show a clear geographical or taxonomic pattern. For *P. anubis* it is true that the lowest density population lives in the west and the highest density ones live in or very close to the zones of overlap with *P. hamadryas* (at Awash) and *P. cynocephalus* (at Gilgil and Gombe), but there are substantial gaps in the data. This is particularly true for the west of the *P. anubis* and *P. cynocephalus* ranges, which are virtually unknown. In addition, as demonstrated for the Awash baboons, it is hard to get an accurate or repeatable estimate of population density at a single site. At Awash, three different groups of baboons have very different population densities – 20.2 and 5.6 individuals/km^2 for two *P. anubis* populations and 3.4 for a nearby population of *P. hamadryas* (see Anderson, 1981 and references therein) – and estimates at the same site, for example at Amboseli, show that various factors including anthropogenic and natural environmental change and can cause significant discrepancies in estimates at different times (Altmann et al., 1985). Certainly the variation in density that seems clear across different landscapes in the same area – and in a single landscape at different times – suggests that no simple resolution to the question of the nature of the areas of overlap is available from demography.

Genetic Evidence for Interaction in the Rift Valley

Papio baboon taxonomy is uncertain, so the question of whether there is a closer relationship between the three allotaxa that overlap in east Africa than between other combinations remains uncertain. Recent mitochondrial DNA studies have suggested that these three taxa form an ancient trichotomy, with *P. anubis* and *P. cynocephalus* mixed together as the closest relatives of *P. hamadryas* (Newman et al., 2004, Wildman et al., 2004). Earlier studies, however, suggested alternatives, for instance that *P. hamadryas* was the most distinctive (and hence oldest and first branching) allotaxon, potentially meriting a specific designation where other allotaxa could be lumped as one species (Buettner-Janusch, 1966), or that the five major allotaxa could be better grouped in other ways (see discussion in Newman et al., 2004), though genetic studies have weakened support for these options. This has mainly been because the five allotaxa discussed have rarely fallen into separate groups, as illustrated by the work of Zinner et al. (2009b) which sampled baboons from across Africa and found geographic rather than traditional taxonomic groupings.

One possible reason for this taxonomic uncertainty is hybridisation, discussed briefly above in a mainly intergeneric context. Within the genus *Papio*, hybridisation is rife and the two best known natural hybrid zones are in exactly those areas identified in Figure 63, the *P. anubis* x *P. cynocephalus* hybrid zone near Amboseli in Kenya and the *P. anubis* x *P. hamadryas* hybrid zone in Ethiopia (Zinner et al., 2011). In the Awash (Ethiopia), hybrid individuals may make up as much as 25-30% of the baboon population and, while this proportion is unknown at Amboseli, it has clearly had a significant impact on the local baboons' behaviour and ecology (Zinner et al., 2011). Little is known of other natural baboon hybrids. This, however, is inconclusive on its own: it may be that no studies have been done of other possible hybridising regions, or that (for some other reason) overlap between other pairs of *Papio* allotaxa is too small to produce hybrids. Gray (1972, as cited in Wilson et al., 1974), for instance, notes that virtually all combinations of *Papio* allotaxa that have been tested are capable of producing fertile hybrids and there is extensive evidence of intergeneric interbreeding among the papionins as a whole. Information from genetics, therefore, is possibly indicative of closer genetic relationships and more natural hybridisation among these three allotaxa than others, but there are many other possible explanations for this and the evidence does not rule out the EARV being an attractive area with a high carrying capacity. More direct evidence is needed.

Zones of Overlap: The State of Play

We cannot yet rule out any of the possibilities listed above for the explanation of the zones of overlap, although we can say that interbreeding between *P. anubis* and *P. hamadryas* occurs despite a significant difference in social and mating systems (Phillips-Conroy and Jolly, 1986). This, coupled with evidence that patterns in DNA similarity rely more on geography than on traditional taxonomy, suggests that all baboon allotaxa ought to be interfertile and that option two is perhaps less likely to be correct. Interestingly, this suggests another alternative. It may be that the rift landscapes, by virtue of their complexity and mosaic nature (as described in Chapter Three and King and Bailey, 2006, Bailey and King, 2011), offer opportunities for a wider range of social, ecological and behavioural strategies to be adopted within local populations. A wider range of niches available to baboons, and a wider range of foraging and behavioural strategies within a given area, might then lead to more interaction between members of different groups and ultimately to hybridisation. This would mean rift landscapes are different to those outside, though perhaps not that they were generally more or less attractive, and would fit with both the patchwork of density data and the geographic clustering of genotypes.

Baboon Landscapes and Socioecology at the Local Scale

To relate large-scale patterns of baboon biogeography to the small scale of landscape use by populations and troops three case studies of *Papio* populations were chosen. These populations live in national parks in three different parts of Africa – Nigeria, Kenya and South Africa – and represent particularly well-studied groups whose socioecology, behaviour and population dynamics have been reported in the primatological literature. In each case, socioecological and environmental data were synthesised with information from the maps presented in Chapter Three to explore the links between these variables.

Papio anubis at Gashaka Gumti, Nigeria/Cameroon

At Gashaka Gumti there are two particularly well known baboon troops, called the Gamgam and Kwano troops respectively. These troops show different socioecological patterns which may be linked to their occupation of rather different local landscapes within the park (see Table 24).

Table 24: table summarising the socioecology of two troops from the Gashaka Gumti National Park. Information comes from Ross et al. (2011), Warren et al. (2008, 2011), Koutsioni and Sommer (2011) and Sommer and Ross (2011).

Feature	**Gamgam troop**	**Kwano troop**
Troop size	19.3 (range 14-23)	28.4 (range 26-35)
Diet	Crops and wild foods eaten by all members	Exclusive use of wild foods
Range location	Just outside the park boundary (see Figure 65)	Slightly southeast of Gamgam troop (see Figure 65)
Dominant vegetation	Open, largely grassland	Higher proportion lowland and gallery forest
Altitude	320m	583m
Climate	Slightly warmer and drier (mean maximum/minimum temperatures of 32.5ºC and 21ºC, 1897mm rainfall/year)	Slightly cooler and wetter (mean maximum/minimum temperatures of 31.9ºC and 20.9º; 1973mm rainfall/year)
Activity budget	More time resting and socialising; less forage and travel time	More time travelling and foraging, less on socialising and resting
Ranging behaviour	Day journey length = 3.1km, home range 1.5km^2	Day journey length = 2.4km, home range 1.5km^2
Life history	Short inter-birth intervals, reducing cycling duration, low infant mortality	Long inter-birth intervals, extended cycling, higher infant mortality

As this table shows, the Gamgam and Kwano troops occupy ranges of a similar size (which is useful for comparisons) but which are found on rather different landscapes. Kwano troop lives at higher altitude and in a region with a higher proportion of lowland and gallery forest than Gamgam troop (who live in open vegetation). The climate of the Gamgam range is warmer and drier than that of the Kwano range, but not by a significant amount; the differences just about register on high resolution global maps of climate, but are pixelated at this resolution. There is also a difference in the dominant vegetation type, which for the Gamgam troop is open and for the Kwano troop more semi-open or closed.

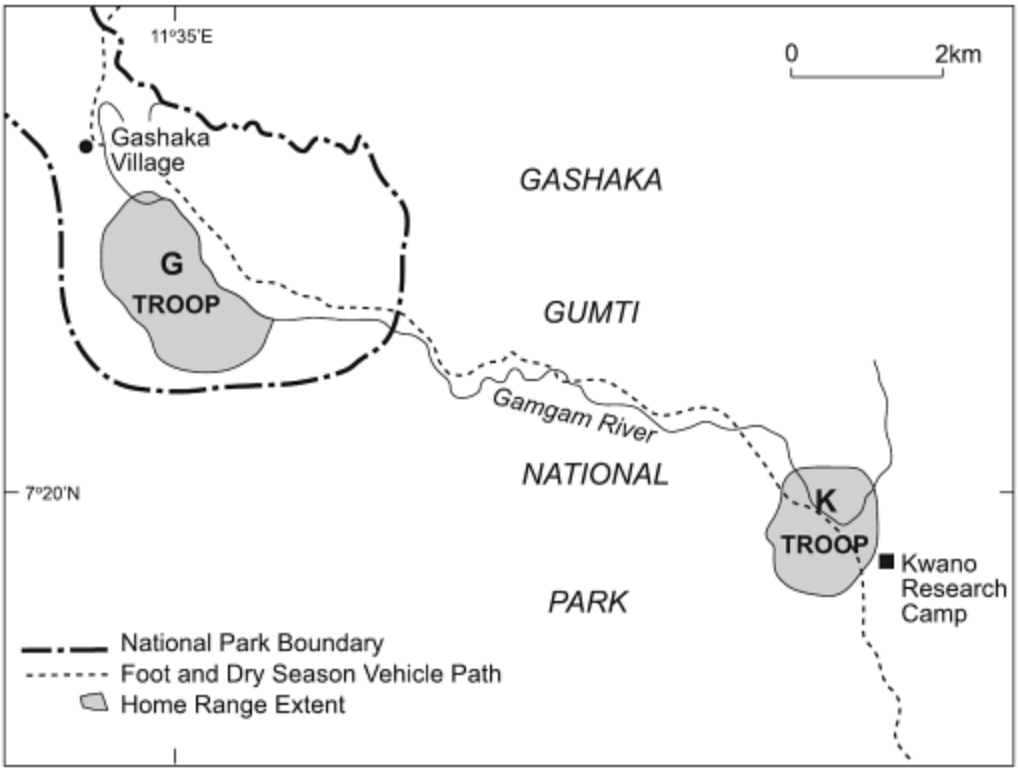


Figure 65: map showing the locations of the Gamgam and Kwano troop ranges near the boundary of Gashaka Gumti National Park; from Warren et al. (2011, figure 8.2).

In fact, these two troops sit across an ecoregion boundary, with the Gamgam troop range located in the Guinean forest-savannah mosaic and the Kwano range in the Cameroonian Highlands forest part of the national park (see Figure 42 in Chapter Three).

Whether the manifest differences in socioecology and behaviour between the two troops result from these landscape differences, however, remains unclear. The differences in climate in particular are fairly small – perhaps too small for Hill and Dunbar's (2002) temperature effect to have a significant influence in this case. Vegetation and physical landscape differences are more marked, with the two troops living in different ecoregions and at different altitudes in a park where there is a reasonably robust relationship between altitude and roughness (see Chapter Three), but are complicated by the fact that the Gamgam troop participates in crop-raiding, which also influences their behaviour and ecology. Warren and colleagues (Warren, 2008, Warren et al., 2011) note that raided foods are eaten by all members of the Gamgam troop, from weaned infants to old adults, and suggest that this has a significant effect on life history. In particular, females of the Gamgam troop produce more offspring over a ten year period than their Kwano counterparts and succeed in rearing a much higher proportion. Gamgam females produce an average of 7.6 offspring in ten years, of which 7.1 survive to one year old; the corresponding figures for Kwano troop are 6.1 and 3.2 (Warren et al., 2011).

Warren et al. (2011) also note, however, that crop-raiding and anthropogenic influence seems to be smaller for other aspects of ecology like troop size, activity budget and ranging behaviour. It is plausible (though impossible to prove) that the *natural* landscape differences between the two sites – which these authors considered less important when interpreting difference – are responsible for these contrasts. In particular, it seems quite sensible that a troop occupying higher altitude, and hence rougher, terrain might move less distance in an average day as measured horizontally, both because this environment (forested and with mosaic habitats) may be richer and because a horizontal measure ignores movement up or down slopes. The (relatively small) differences in troop activity budgets might reflect this pattern, or be linked to crop-raiding in more complex ways, for instance via the differing three-dimensional structures of landscapes with concentrated human habitation as opposed to dispersed fruit trees and natural resources. The difference in mean troop size could be linked to a higher carrying capacity for forest as opposed to grassland, or to the effects of human guarding of crops against crop-raiders, or even to historical factors and the time-lag effect as populations reproduce. The relationship between landscape (natural and cultural/anthropogenic) and baboon socioecology at Gashaka is thus clearly complex, with biological processes, abiotic conditions, human influence and other factors all interacting in nonlinear, time- and space-dependent ways.

Papio ursinus at De Hoop, South Africa

The baboons at De Hoop in South Africa offer a contrast to those of Gashaka as they are found in a region characterised by rather different landscapes (see Chapter Three). Specifically, the De Hoop baboons live at much lower altitudes than those of Gashaka, near sea level as opposed to up to 3000m above sea level, and live on the coast in a region dominated by fynbos vegetation and with a highly seasonal climate. The key questions for this study, therefore, are whether these baboons display significant socioecological differences from those further north and whether any visible differences are related to landscape differences. Table 25 summarises baboon socioecology at De Hoop where, again, extensive data are available for two troops (compare Table 24).

Table 25: table summarising the socioecology of two troops from De Hoop Nature Reserve. Information is taken from Hill (1999).

Feature	Small Troop	Vlei Troop
Troop size	17-21	40-44
Diet	Fruits, seeds, leaves and other foods, with high-quality fruit and seeds making up the dominant proportion	Fruits, seeds, leaves and other foods, with herbaceous foods and leaves dominant
Range composition and vegetation	Significantly more access to cliff refuges, and 43% burnt fynbos, 31.8% fynbos, 13.2% vlei, 11% acacia woodland and 0.1% grassland.	Less secure, 27.6% burnt fynbos, 25.7% fynbos, 18.7% vlei, 15.8% acacia woodland, 11% grassland and 0.1% burnt acacia woodland.
Altitude	Low, but more variable (higher average slope values)	Low, coastal
Climate	Mediterranean (ranges overlap so no significant differences between troops)	Mediterranean (ranges overlap so no significant differences between troops)
Activity budget	58% feeding, 15% moving, 14.3% grooming and 12.8% resting	36.3% feeding, 35.7% moving, 12.1% grooming and 15.9% resting
Ranging behaviour*	Spends time close to sleeping sites and forages more in lower quality habitat than Vlei troop	Ranges further from sleeping sites/refugia and spends more time, on average, in high quality habitat

*Hill (1999) cites a single figure of 5.2km as a day journey length for the De Hoop baboons, after Whiten et al. (1987) but does not give separate values for the Vlei and Small troops.

At De Hoop too, then, despite the significant overall differences in habitat compared to Gashaka, there are some indications of a relationship between landscape and baboon socioecology. For these troops, however, the causal links may have reversed: instead of the landscape influencing the strategies chosen by baboons (and the data collected by observers), it seems that at De Hoop the socioecology and structure of baboon troops influences the landscapes chosen. In particular, Hill (1999) suggests that troop size in De Hoop influences the strategies available for ranging, with the larger Vlei troop forced (by relatively shorter and more seasonal day lengths) into spending more time in high quality habitats where a lot of food is available despite the fact that these areas are often further from cliff and cave refuges and therefore experience higher predator risks. The Small troop, in contrast, does not experience the same demographic and nutritional pressure because it occupies its range at a lower density and can therefore choose lower quality but safer habitats.

This pattern clearly suggests a feedback between socioecology and landscape; the same was probably the case at Gashaka where activity budgets, ranging, diet and troop size were also linked in a complex fashion. Dietary differences between troops are thus explained both as a product of landscape differences and as the result of socioecological constraints on ranging, which themselves are influenced by landscape characteristics like seasonality, temperature and day length. The physical landscape effect at De Hoop, however, is less clear. 'Small' troop occupies a range with higher slopes than Vlei troop (although in the absence of actual range maps, it is hard to confirm the overall pattern of physical landscape differences), which may influence ranging behaviour but also may be the result of a preference for caves and cliffs to act as refuges from predation. The interactions between biosphere, abiotic environment and organism are thus complex at both De Hoop *and* Gashaka, with the former displaying more definite feedback loops between variables and the latter a more complex suite of interactions that also encompass anthropogenic factors.

Papio cynocephalus at Amboseli

The baboons at Amboseli national park were first studied in the early 1960s by several primatologists, who mainly focused on the so-called 'main group' of *P. cynocephalus* (Altmann and Altmann, 1970). The significance of this region for characteristing baboon landscapes therefore lies not in the potential for comparison of contemporary troops from different landscapes but rather in the fact that the Amboseli baboons have been studied intensively since 1960, a period which spans both significant landscape changes (particularly in climate) and significant changes to the socioecology of the main group itself, as described in Table 26 below.

Table 26: summary of differences in landscape and baboon socioecology at Amboseli from the 1960s to the 1980s. Information comes from Altmann and Altmann (1970), Post (1981, 1982), Altmann et al. (1985), Altmann and Muruthi (1988) and Altmann et al. (2002). NB these data are all from the 'main group' of baboons, though different sets of troops within that sample have been used by different authors. No outliers (extreme values) have been reported here to ensure unusual troops do not bias the results.

Feature	State in the 1960s	State in the 1980s
Number of baboons in park	2500	150
Population density	73 baboons/km^2	2.2 baboons/km^2
Median troop size	43	28
Vegetation	Mixed, with some closed (wooded) and semi-open areas and some grasslands.	More open, fewer trees, more savannah; more xeromorphic and halophytic vegetation present.
Temperature	Relatively low	Higher (mean daily maximum temperature increased by 0.275ºC per year from 1976 onwards till 2002)
Rainfall	Drought in 1960-61, followed by heavy rainfall in subsequent years	Highly variable, though with no clear trend present from 1976-2002
Baboon diet	Grasses and acacia tree products, with other plants, insects and animal foods also used	Grasses and acacia tree products, with other plants, insects and animal foods also used. Some troops also eat human refuse.
Activity budget	In 1974 (the earliest data available), about 50% of time was spent feeding, 25% travelling, 20% resting and the remainder socialising. Patterns are seasonally variable.	Variable. Animals with access to human refuse spend some 22% of their time feeding and 50% resting; wild-feeding groups 62.5% foraging and 10% resting. All spent approximately 20% on travel, and the remainder on social activity. This is seasonally variable.
Ranging behaviour	The main group range is 24.1km^2, and an average day-journey is about 5.5km.	On an annual basis, wild groups range over 40km^2 and move considerable distances between groves and sleeping site; the refuse eating group occupies 4km^2 and travels much less widely.

Within the park, the sequence of landscape changes included a significant drought in 1960-61, followed by heavy rainfall that raised the water table and caused salt inundation of much of the park (Altmann et al., 1985). This triggered a significant change in the vegetation of the area, with a decline in tree cover and an increase in the presence of salt-tolerant plants and marshand swamp species (Altmann et al., 1985) which was presumably the major landscape change driving much of the corresponding change in baboon density, behaviour and ecology as the troops in this area rely on grasses and acacia trees (now much reduced in number) for food (Altmann and Altmann, 1970, Post, 1982). The general effect has probably been to break up the attractive landscapes into smaller, more isolated fragments – where once there were woodlands, there are now stands of trees embedded in a matrix of open savannah habitat which, especially in the dry season, is less productive. These changes have been documented by Western (2007) and can be seen in Figure 66 and Figure 67.

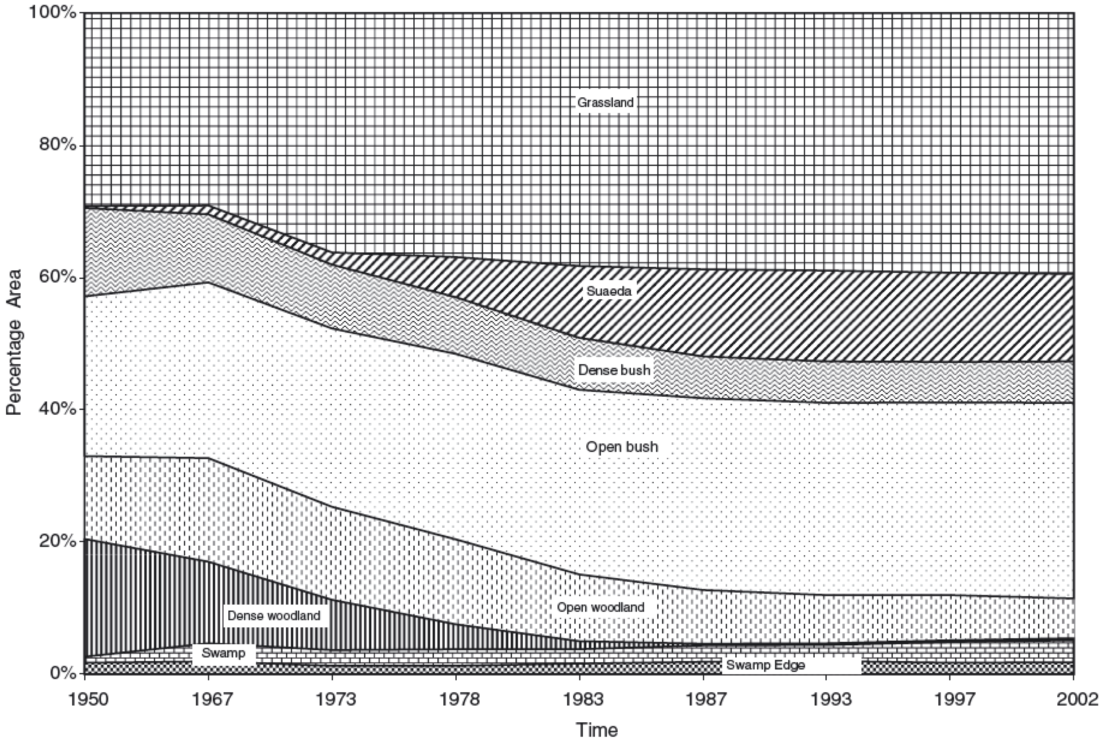


Figure 66: chart showing the changes in vegetation types present in Amboseli National Park between 1950 and 2002; from Western (2007, figure 1). From top to bottom, the vegetation types described are grassland, suaeda, dense bush, open bush, open woodland, dense woodland, swamp and swamp edge. Suaeda is a form of scrubland dominated by *Suaeda monoica* and *Salvadora persica*.

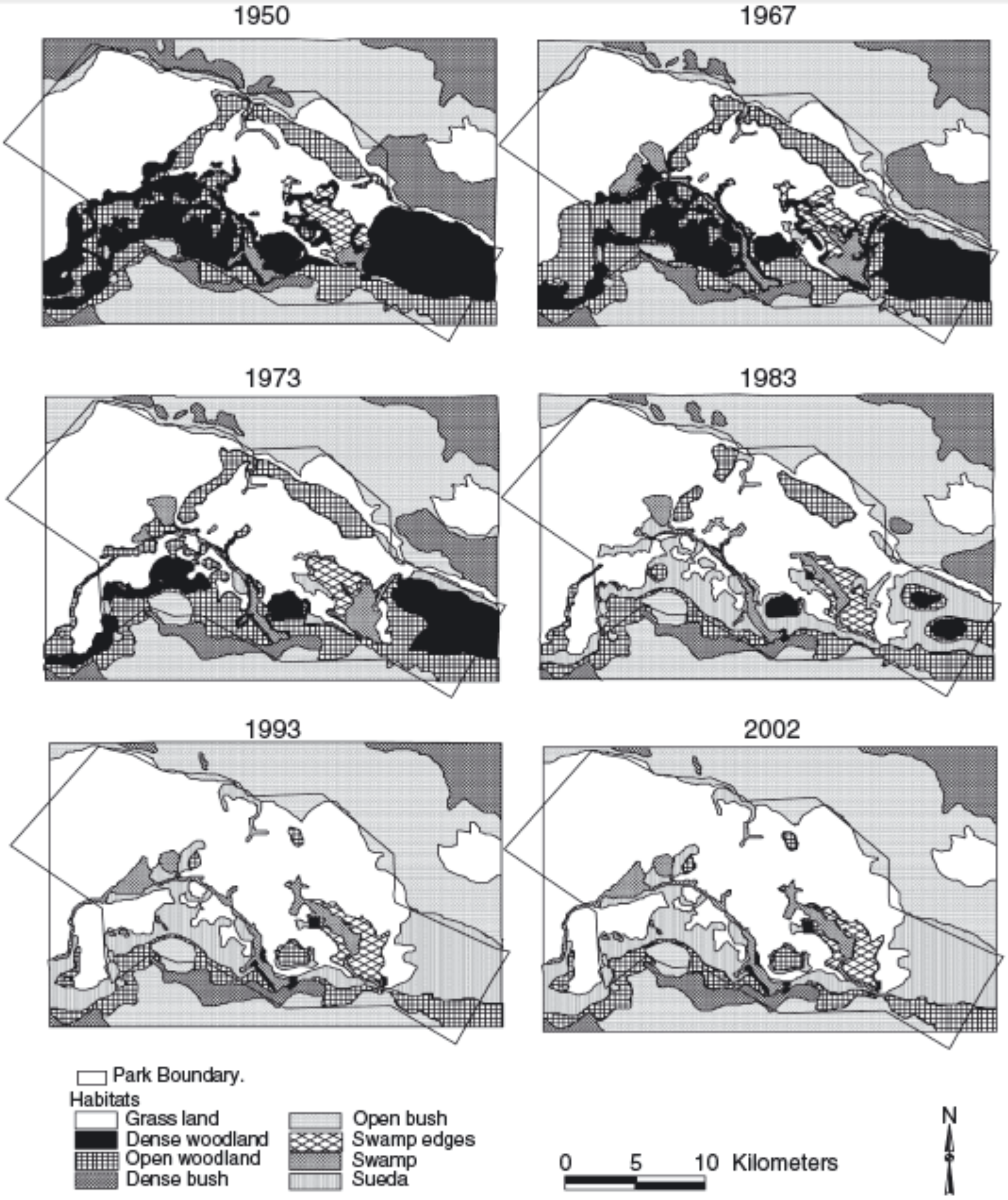


Figure 67: successive maps of Amboseli (outlined on the figures) showing the changing distribution of different vegetation types through time; from Western (2007, figure 3). Most notable are changes in the distribution of dense woodland (coloured black) and grassland (white), as described above.

Overall, activity budgets for the Amboseli baboons seem to have changed little except for those troops which are now able to access human garbage (which, by its nature, is calorie rich and highly localised). Day ranges have not changed much over the study period, though annual ranges seem to have increased from about 24km^2 to about 40km^2, perhaps reflecting the more broken up landscape and the need for more movement between patches. Demographically, it is notable that the main change to these baboons has been in the lowering of infant and juvenile survival rates (Altmann et al., 1977, Altmann et al., 1985, Samuels and Altmann, 1991), perhaps relating to these individuals higher vulnerability to seasonal and spatial fluctuations in the presence of food plants.

This case study highlights that even where topographic change is minimal (as in this 20 year period), other changes to landscape composition can play an important role in shaping baboon ecology and behaviour. It does not, however, suggest a simple relationship between landscape and socioecology any more than the case studies at Gashaka or De Hoop did; instead, the effects of climatic and vegetational change in the Amboseli basin interact in a complex way with demographic variables, socioecology and seasonality, as well as with anthropogenic influences on certain troops, to push baboons towards a new steady state in which certain variables (like the activity budget) have changed relatively little, while others (like population density, population and troop sizes and possibly home range size/foraging patterns) have changed rather more. Even for less cognitively complex primates like *Papio* baboons, in spatially and temporally variable landscapes, it seems, behaviour (and presumably also choice, or agency) play a role in determining the relationships between organism and landscape.

LINKING ECOLOGY AND ANATOMY: THE KENYAN BABOONS

The small-scale analyses of baboon landscape use and ecology (above) suggest that the relationship between these factors is not simple even at the smallest scales, and that variation is present even between troops a few kilometres from one another (the Gashaka troops are separated by a gap of about 10km, while those at De Hoop overlap by between 25% and 35% of their range; the Amboseli case study, of course, considered variation through time rather than in space). This suggests that attempts to make conceptually clear links between landscape and foot anatomy may be frustrated by this complexity and are best based not on allotaxon differences and average landscape preferences but on specimens of known origin and identity. Such samples are rare, but one does exist from Maples' (1967) work on the *P. anubis* x *P. cynocephalus* hybrid zone in Kenya. This sample originally contained some 45 individuals, but some – including two individuals from Tanzania, a couple of females, and a few incomplete skeletons) were discarded to leave a total of 38 male baboons including 6 *P. anubis* x *P. cynocephalus* hybrids, 17 *P. cynocephalus* and 15 *P. anubis* skeletons. These came from 15 capture sites in southern Kenya (see Figure 68 for details). These capture sites were chosen by Maples to maximise coverage of the local baboon troops and obtain a balanced sample of *P. anubis*, *P. cynocephalus* and potential hybrid specimens. This means that although they do not represent a 'random' sample of baboon living sites, they do capture individuals from across the local range and a variety of different local troops. During the landscape study, a further four specimens (UF24755 and UF24787-89) were identified which were not associated with specific co-ordinates. These were subsequently also excluded from analysis, leaving the sample described in Table 27.

Table 27: a list of the *Papio* baboon specimens used in this study, by taxonomic assignment (*P. anubis*, *P. cynocephalus* or potential hybrid). This table can be used to identify specimens referenced in the text below.

	Papio anubis	***Papio cynocephalus***	**Hybrid sample**
Specimen numbers	UF24750-54, UF24756-63, UF24765-66 and UF24776	UF24768, UF24775, UF24777-86 and UF24792	UF24769-24774

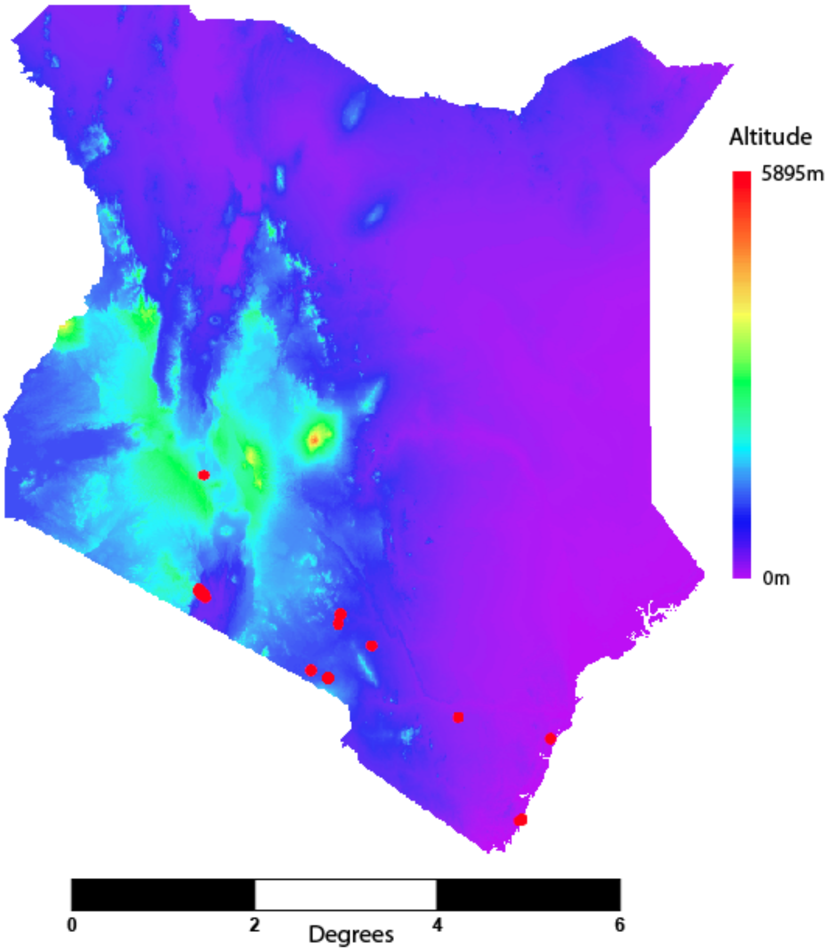


Figure 68: map of Kenyan topography showing where Maples (1967) baboon samples were obtained. Red dots indicate trapping locations, while the map itself displays the national topography. These points are assigned letters from top left to bottom right, and in several cases multiple trapping localities overlap on the map (see Table 28 below).

As this figure shows, Maples' samples came from sites that span almost the full range of topography found in Kenya. The inland localities are of intermediate altitude, while those on the coast are almost at sea level. In terms of local ecology, the majority of specimens come from the Northern acacia/commiphora bushland and thicket zone (Table 28 and Figure 69), though there are some which are from mangrove swamps and coastal forests. In terms of roughness, the sites range from relatively smooth to moderately rough (Table 28).

Table 28: conditions at the points identified in Figure 68. Where several points occur near to one another on that figure, they can be assumed to be the same unless otherwise noted. The significance of the blue shading is explained in the text below.

Site	Specimens *	Ecoregion and vegetation[1]	Roughness / altitude	Geology and soil	Temperature and rainfall
1	UF24776	Northern acacia-commiphora bushland and thicket	169 units, 1905m	Quaternary igneous rocks, andosols/ phaeozems	17.2ºC, 732mm
2	UF24763 and UF24765	“ ”	120 units, 864m	Quaternary igneous rocks, planosols	23.9ºC, 516mm
3	UF 24751-4 and UF24757	“ ”	120 units, 770m	Quaternary igneous rocks, planosols	24.0ºC, 514mm, 6 units
4	UF24759 and UF24766	“ ”	120 units, 737m	Holocene rocks, planosols	24.5ºC, 504mm
5	UF24750	“ ”	120 units, 669m	Holocene rocks, planosols	24.9ºC, 492mm, 5 units
6	UF24760-2	“ ”	185 units, 676m	Holocene rocks, planosols/ nitisols	24.8ºC, 493mm
7	UF24758	“ ”	167 units, 661m	Holocene rocks, nitisols	24.9ºC, 484mm
8	UF2469-71	“ ”	23 units, 1149m	Holocene rocks, arenosols/ ferralsols	21.8ºC, 753mm
9	UF24772-4	“ ”	82 units, 1027m	Quaternary igneous rocks, nitisols	22.3ºC, 650mm
10	UF24756	“ ”	9 units, 1132m	Holocene rocks, solonchaks	21.3ºC, 706mm
11	UF24775 and UF24777-83	“ ”	82 units, 1211m	Quaternary igneous rocks, cambisols	20.8ºC, 809mm
12	UF24786	“ ”	23 units, 923m	Quaternary igneous rocks, ferralsols/ leptosols	22.9ºC, 631mm
13	UF24792	“ ”	82 units, 370m	Precambrian rocks, vertisols	25.4ºC, 711mm
14	UF24785	East African mangroves	30 units, 31m	Pleistocene rocks, ferralsols	25.9ºC, 1014mm
15	UF24784	Northern Zanzibar-Inhambane coastal forest mosaic	46 units, 20m	Pleistocene rocks, ferralsols	26.5ºC, 1280mm

*The labels Maples gave to these specimens' locations are as follows: 1 – Miti Mingi; 2 – Endosapia River; 3 – Ngurumani Escarpment/Fig Tree Camp; 4 – Fig Tree Camp; 5 – Ewaso Ngiro Site 5; 6 – Ewaso Ngiro Site 2; 7 – Ewaso Ngiro Site 3; 8 – Ithumba; 9 – Simba Springs; 10 – Ol Tukai; 11 – Namelok; 12 – Kibwezi; 13 – Kitui Bridge; 14 – Roka; 15 – Diani Beach (shot near). [1]Ecoregion data are checked against the vegetation map of Africa.

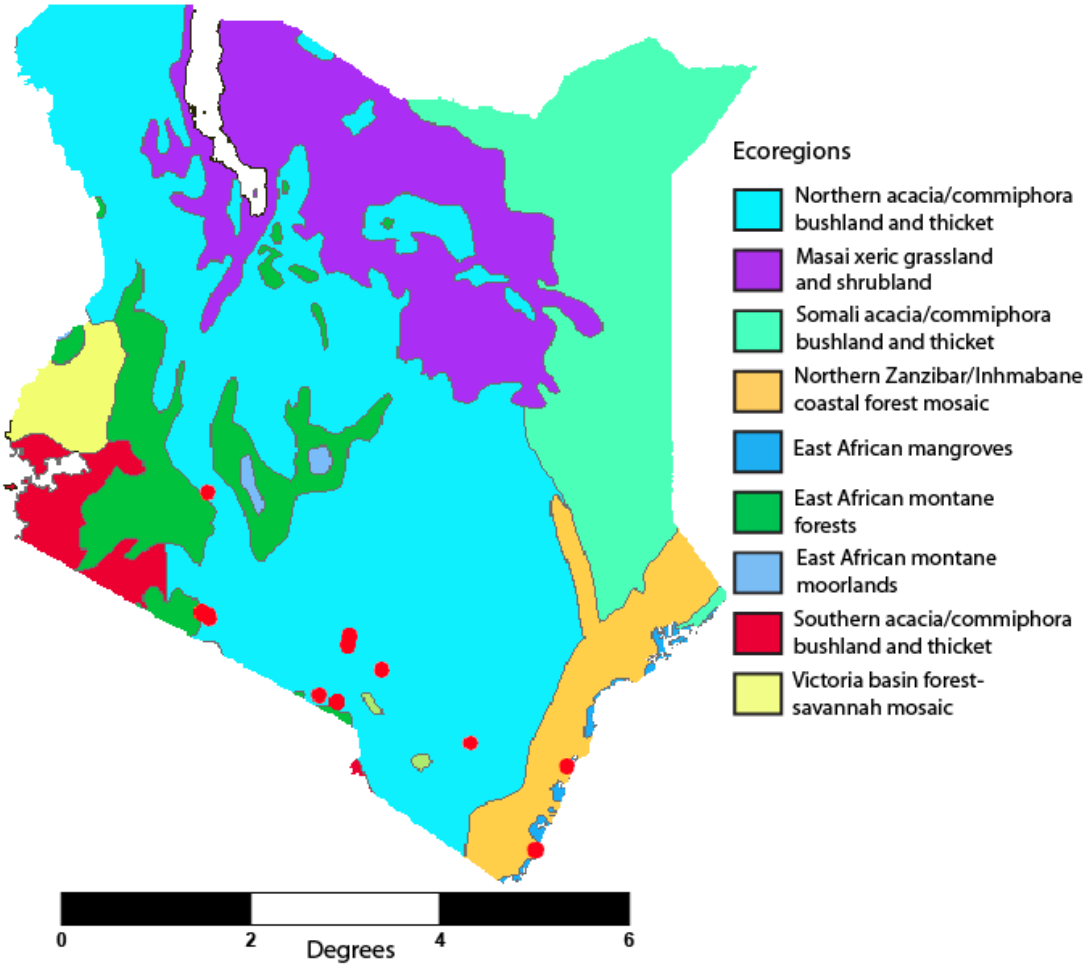


Figure 69: map of the ecoregions of Kenya, showing the locations where Maples' (1967) baboons were trapped (isolated red dots; there were no sites in the southern acacia/commiphora region which is also red).

Climatically, all 15 sites lie in the same broad zone but there are local differences, with the major anomaly (see Figure 70 for one example) centred on the topographic high visible in Figure 68. This is a region of relatively lower average temperatures and higher and more seasonal average annual rainfall. Temperature seasonality is uniformly low across the country. For further analyses, both temperature and rainfall seasonality values were ignored as the former is uniform throughout the sites and the latter, although a little more variable, spans such a small range that observed differences are too small to measure reliably or invoke as explanations of differences in anatomy.

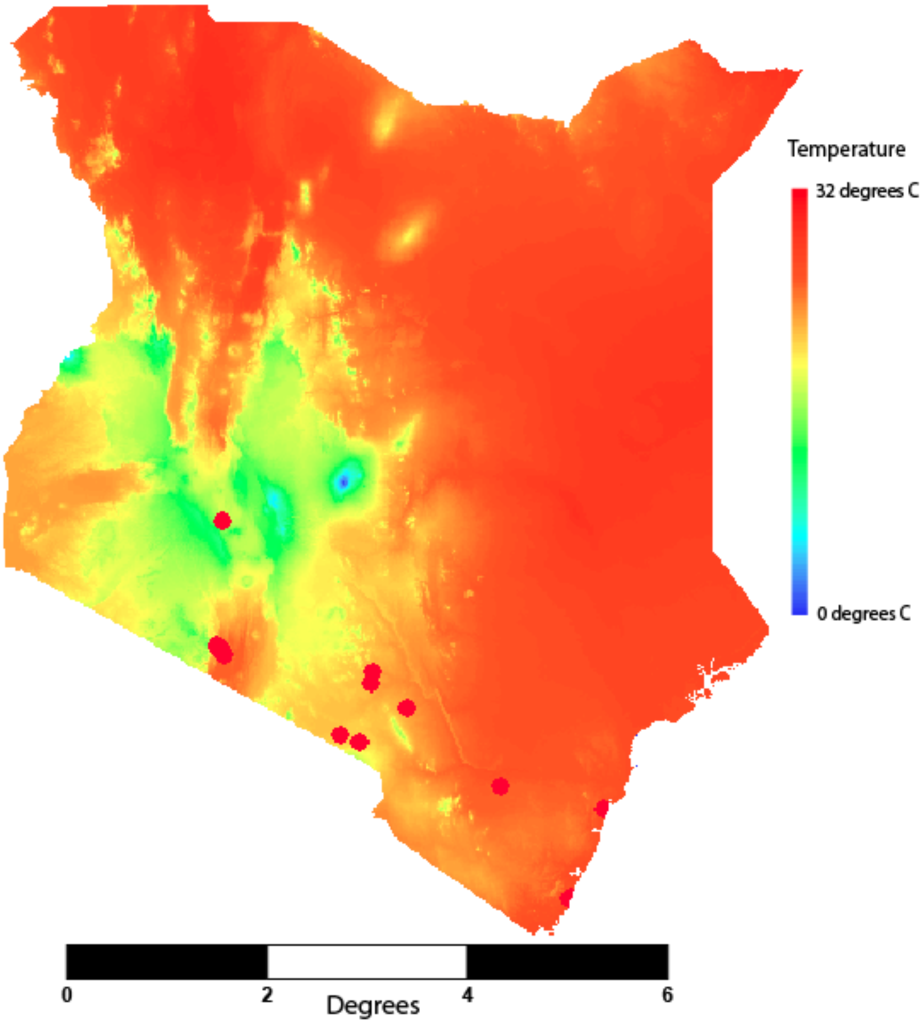


Figure 70: map of annual mean temperatures across Kenya showing the lower temperatures associated with the topographic peak to the south west.

This overview suggests that although Maples' sample is drawn from a relatively small area of southern Kenya, it represents a reasonable range of local conditions from the coast (which is warmer, wetter and more forested in addition to being lower altitude) to inland (which is higher altitude, cooler, drier and has more open vegetation).

Dealing with Landscape: Analytical Strategies

The remaining analyses of the Kenyan baboon sample aimed to explore the relationships between landscape variables (as summarised above) and anatomy. Maples (1967) conducted only basic, uni- or bivariate analyses of the anatomy of his sample, and assumed that most of the differences between specimens were linked to age, size, status or nutrition rather than locomotor ecology. This chapter's attempt to consider landscapes, however, requires a more subtle multivariate approach which can deal with variation in shape as well. For this analysis, data were log transformed and subjected to Mosimann geometric mean adjustments (as described in Chapter Two) prior to analysis, to remove major isometric size differences that probably are not functionally relevant.

Data Handling and Site Classification

The landscape data for the 15 capture sites studied were obtained from regional or global maps of particular environmental variables, but for the purposes of this study values at those sites (extracted using ArcGIS' 'sample' protocol from the regional and continental maps described in Chapter Two) are used in isolation. This strategy is selected because the anatomical data, despite representing more baboons than there are points, cannot be mapped discontinuously onto the environment. Instead, each specimen is known only from the location it was trapped at. The analyses presented here therefore focus on the landscapes at these points, treating them as sample points within the home ranges of these individuals. Any attempt to estimate actual home range areas based on these points, or to assume that the conditions at sample points are representative of the whole range the specimen used, would further complexify the system by introducing unquantifiable sample bias into the analysis. There were seven landscape variables of potential use: ecoregion, geology and soil type distributions (all nominal variables) and altitude, roughness, temperature and precipitation (all continuous). All were multimodal when plotted (see for instance Figure 71) except for the ecoregions information, which was unimodal as almost all the sampled baboons came from one habitat.

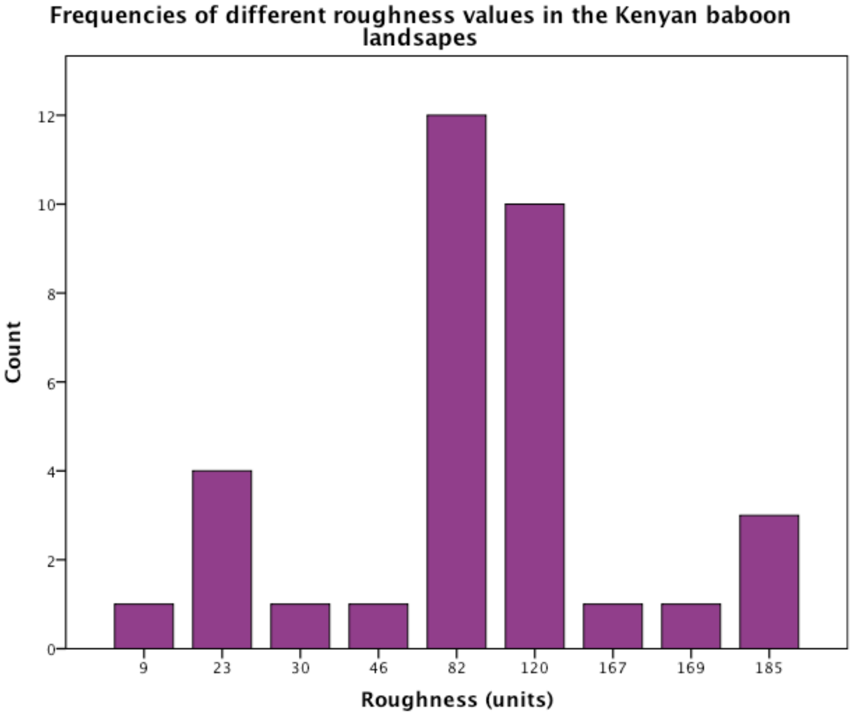


Figure 71: histogram showing the distribution of different roughness values at the sites of origin of the Kenyan baboons.

This meant it was possible to convert the four continuous variables into ordinal categorical equivalents (thus making them directly comparable to the three discontinuous ones) without losing much information. Bin boundaries were chosen to reflect the range of values present at the 15 capture locations and the positions of the modal peaks, so that each peak in a multimodal distribution ended up in a separate category. The roughness data were reclassified into three bins (0-75 units, 76-150 units and 150+ units respectively); altitude fell into four bins (0-500m, 501-1000m, 1001-1500m and 1501-2000m); temperature values were grouped into five bins (each of 2 degrees Centigrade and starting from 17ºC), and rainfall fell into three bins (400-700mm, 701-1000mm and 1001-1300mm).

Once the landscape data had been converted in this way, the first analyses were conducted to establish whether there was a robust taxonomy of capture locations that might be used to simplify later analyses. Hierarchical cluster analysis was therefore used to construct dendrograms of the relationships between sites based on their landscape configurations. Several analyses, using different clustering methods and similarity measures, were run in SPSS and PAST to check for the robusticity of the groupings produced. Perhaps the most appropriate measure of distance for this categorical data is the Bray-Curtis index, commonly used in ecological analysis of assemblages. This index is useful primarily because it – unlike other indices – focuses only on shared traits. So, in this case, two capture sites within ecoregion one would be grouped together, but two which share the fact that they are *not* in ecoregion one would not – the shared absence of the trait does not count. This is ideal for this work, where the emphasis is on similarities in landscapes themselves. Figure 72 shows the dendrogram produced using Bray-Curtis measures and a paired group algorithm.

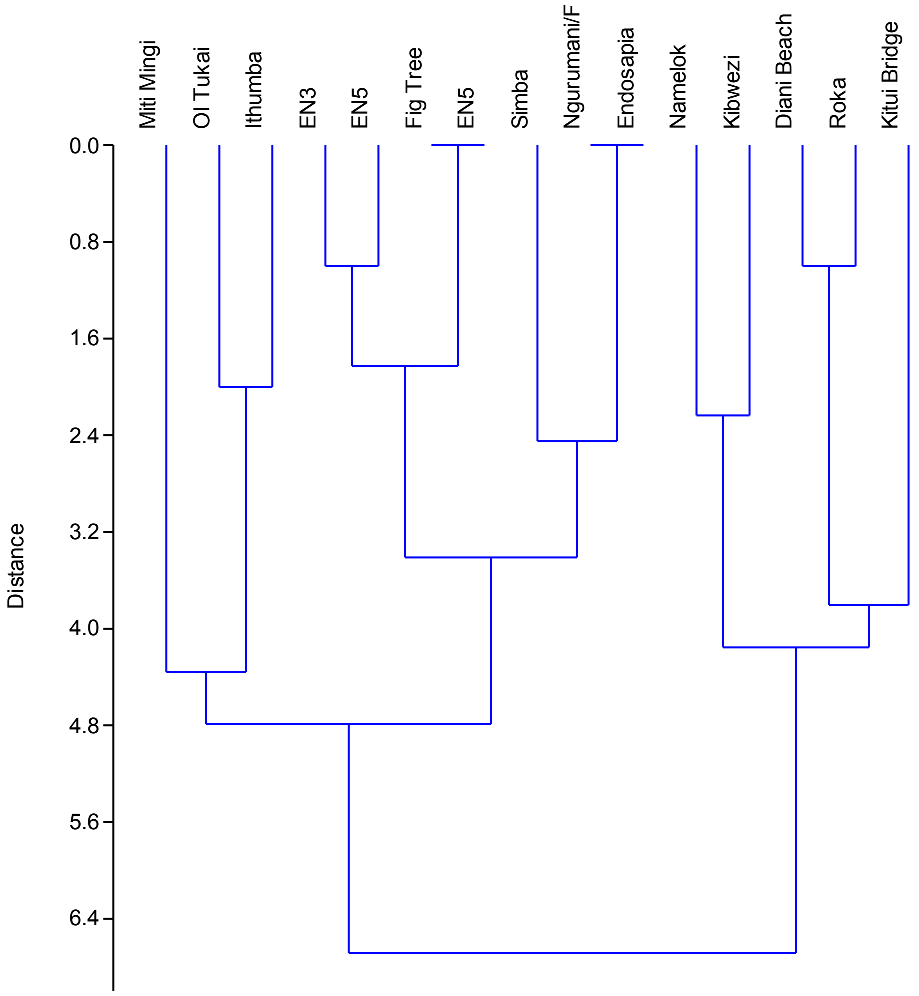


Figure 72: dendrogram showing the relationships between the landscapes of different capture locations. Constructed using Bray-Curtis indices and an average linkage algorithm. Several site names have been abbreviated. EN2, EN3 and EN5 are Ewaso Ngiro sites 2, 3 and 5 respectively; Fig Tree is short for Fig Tree Camp; Simba = Simba Springs and Ngurumani/F = Ngurumani/Fig Tree Camp.

This classification shows two major groups of sites, group one which includes Miti Mingi, Ol Tukai, Ithumba, three Ewaso Ngiro localities, Fig Tree Camp, Endosapia, Simba Springs and Ngurumani/Fig Tree Camp; and group two of Namelok, Kibwezi, Diani Beach, Roka and Kitui Bridge. These groups are very robust, with only minor (internal) shifts occurring when different clustering algorithms and distance measures are used instead. Substituting a Euclidean distance measure for the Bray-Curtis one used above, for example, produces a dendrogram with exactly the same pattern of linkages.

The existence of robust groupings in this dendrogram suggests that we can simplify the landscape data in Table 28 yet further to characterise the two major 'types' of landscape in this sample. Adding shading to Table 28 (blue = group one, clear = group two), which is organised such that numbering of sites proceeds from northwest to southeast, suggests a geographic separation at right-angles to this axis. The two groups differ appreciably in their mean and median landscape values, as shown in Table 29.

Table 29: characteristics of the capture sites in the two major groups. Group one falls to the left of Figure 72 and group two to the right.

Variable	Group One	Group Two
Altitude	Mean 959m above sea level, range 661-1905m	Mean 511m above sea level, range 20-1211m
Roughness	Mean 111.5 units, range 9-185 units	Mean 52.6 units, range 23-82 units
Ecoregions	All 10 sites located in Northern acacia/commiphora bushland and thicket	Variable. Three sites in the northern acacia bushland; one in East African mangroves and one in the Northern Zanzibar/Inhambane coastal forest mosaic
Annual mean temperature	Mean 23.0ºC, range 17.2-24.9ºC	Mean 24.3ºC, range 20.8-26.5ºC
Annual mean rainfall	Mean 533mm/year, range 484-753mm/year	Mean 889mm/year, range 631-1280mm/year
Geology	Six sites on Holocene bedrock, four on Quaternary igneous rocks	Two sites on Quaternary igneous, two on Pleistocene rocks and one on Precambrian rocks.
Soil type	Four sites on planosols, one on planosols/nitisols, two on nitisols, one on arenosols/ferralsols, one on phaeozems and one on solonchaks	Two sites on ferralsols, one on ferralsols/leptosols, one on cambisols and one on vertisols.

This suggests that there are broad differences between these sites in pretty much all variables. Sites in group one are generally located on landscapes that are higher in altitude and rougher; have slightly lower annual mean temperatures, and receive less rainfall than those in group two. These differences vary in magnitude, from very small (a difference of just 1.3ºC in annual mean temperature) to significantly larger (for example, a difference of over 50 units of roughness, 300mm of annual rainfall and 400m altitude). In terms of ecoregions, all 10 sites in group one are located in a single ecoregion, while those of group two span three. Geologically, again, group one (although larger) is less variable, with all sites on either Quaternary igneous or Holocene bedrocks while group two spans Quaternary igneous, Pleistocene and Precambrian rocks, and for soils, both groups are variable but with little overlap in the soil types represented. These categorical differences are arguably less significant (particularly in the case of geology, as Holocene, Quaternary and Pleistocene types are overlapping categories), but are still visible in the dataset.

Relationships Between Landscape and Anatomy

The existence of a reasonably robust classification of capture locality landscapes means we can reduce landscape variation to a simple composite descriptor and classify specimens into two groups from different broad landscapes. This distinction has a taxonomic correlation. When the specimens from each group are themselves compared, there is a clear allotaxon separation: group one landscapes are the source of all specimens of *P. anubis*, together with all six *P. anubis* x *P. cynocephalus* hybrids and one specimen of *P. cynocephalus* from Ol Tukai, while group two is entirely composed of *P. cynocephalus*. However, the existence of consistent taxonomic differences between groups does not vitiate the aim of this chapter, which is to explore possible landscape patterns. The two taxa seem to be fully interfertile, producing a range of hybrid forms. It remains possible – indeed, likely – that primate landscapes are patterned by a range of factors that include geomorphology, foot anatomy and socioecological organisation, among others. Moreover, the hybrid specimens from Ithumba and Simba Springs are nested within the wider group one clade in terms of their landscape preference, suggesting that in this area, different baboon allotaxa occupy different landscapes but there is no definable 'hybrid zone' landscape; instead, the hybrids range across several subtypes within group one, with some closest to the Ol Tukai *P. cynocephalus* and specimens of *P. anubis* from Miti Mingi while others are closely linked to individuals from Ngurumani and the Endosapia River landscapes (see Figure 72). This implies that differences between the two groups of specimens may be functional (and linked to landscape), but may also be influenced by the different genetic histories of *P. cynocephalus* and *P. anubis* or other historical factors.

This section, then, will use discriminant functions analysis (DFA) to explore morphology. The aim is to explore how well the different foot bones discriminate specimens from the five main groups of sites analysed, which will then allow any observed differences to be related back to the landscapes characteristic of those sites. Table 30 summarises the results.

Table 30: the results of bone-by-bone and combined discriminant function analyses aimed at discriminating baboons from different landscapes. Definitions of variables can be found in Chapter Two.

Analysis	**Success rate**	**Structure and function of DF1**
Talus*	70.6%	Group one scores positively, group two negatively. Linked to PFL (posterior facet length, r = 0.781) and MeFL (medial facet length, r = -0.542).
Calcaneus	76.5%	Group one scores positively, group two negatively. Linked to PTAB (posterior talar articular surface breadth, r = 1).
Cuboid	94.1%	Group one scores negatively, group two positively. Linked to MPL (maximum plantar length, r = 0.707) and LL (lateral length, r = 0.535), with a weaker link to the (non-contributing) SMFD (short metatarsal facet dimension, r = -0.433).
Navicular	76.5%	Group one scores positively, group two negatively. Linked to MNH (maximum navicular height, r = 0.779) and MND (maximum navicular depth, r = -0.627).
Medial cuneiform	88.2%	Group one scores negatively, group two positively. Linked to MDL_A (maximum dorsal length, r = 1), and to several non-contributing variables, including MD (maximum depth, r = 0.569), PFH (posterior facet height, r = -0.511), AFH (anterior facet height, r = 0.481) and MPL_A (maximum plantar length, r = 0.454).
First metatarsal	85.3%	Group one scores negatively, group two positively. Linked to ML_A (maximum length, r = 0.527) and DFB (distal facet breadth, r = -0.522).
Third metatarsal	85.3%	Group one scores positively, group two negatively. Linked to MMD_A (maximum midshaft dimension, r = -0.547), MFL_B (medial facet length, r = 0.533) and the non-contributing PAFB_A (proximal articular facet breadth, r = -0.434).
Fifth metatarsal	88.2%	Group one scores positively, group two negatively. Linked to DFB_B (distal facet breadth, r = 1).
Combined (all bones)	100%	Group one scores positively, group two negatively. The function is built using the following variables: talar ATB (anterior trochlear breadth), calcaneal STB (sustentaculum breadth), cuboid SCFD (short calcaneal facet dimension), navciular MaSCFD (maximum short cuneiform facet dimension), medial cuneiform PB (plantar breadth), MD (maximum depth) and MDL_A (maximum dorsal length), third metatarsal MMD_A (maximum midshaft dimension) and fifth metatarsal PAFL_B (proximal articular facet breadth) and DFB_B (distal facet breadth), all with small correlation values (under ±0.4).

*two pairs of talar variables, ATB/AFL (anterior calcaneal facet breadth and length) and MeFL2/MeFB (medial calcaneal facet length and breadth) were omitted as they were sparse and interdependent.

This analysis shows that individual bones can indeed discriminate between baboons from the two major groups of landscapes with a success rate significantly higher than would be expected by chance (50%). It is unsurprising, then, that the whole dataset describing the foot can also be used to make this discrimination, because each bone is a subset of the whole foot. Perhaps a more interesting question concerns the nature of this discriminatory pattern. The foot is an integrated structure in which changes in muscle development and the articular surfaces that have a direct impact on one bone may also have indirect, knock-on consequences for neighbouring bones (Oxnard, 2008). We need to know whether these patterns are simply crude indicators of residual size or whether there are functional differences between groups and, if so, whether these changes can be related to the landscapes in which the baboons were captured.

Interpreting Landscape/Anatomy Links

Although there were no consistent patterns in the relationships between landscape and socioecology considered above, patterns in landscape and anatomy do seem clearer, at least for the small Kenyan sample considered here. The final stage in this analysis, therefore, is to explore the functional significance of the observed differences, with reference to the literature on baboon and wider primate anatomy and the known differences in landscape between the two samples studied.

Group Identities: Cause and Effect

Throughout the discriminant function analysis, the skeletons were distinguished purely on the basis of their locality. However, we have already observed a clear taxonomic split with one group containing all the specimens of *P. anubis*, the six hybrid baboons and one *P. cynocephalus* from Ol Tukai, while the other comprises only *P. cynocephalus*. In a classical, simple study of landscape preferences this taxonomic pattern would be treated as a cause – it would be assumed that the specimens fall into two groups because the allotaxa show different landscape preferences.

The Darwin-Huxley model of evolutionary theory (see Chapter One), in contrast, suggests that the existence of identifiable populations is not necessarily the cause of spatial pattern, as this results from complex baboon-landscape interactions that include physical, behavioural and possibly ‘cultural’ factors (in the sense of culture as a set of socially learned norms and behaviours). Agency and complexity may affect organism-landscape relationships, and – as in any complex evolutionary system – patterns may not be logically coherent at all, even if they are empirically visible. All we can say on the basis of this evidence is that the DFA allows us to distinguish the two groups on the basis of foot morphology alone and even on the morphology of a single foot bone. This discriminant function seems to work as well for hybrids as for non-hybrids. With this in mind, this section summarises the observed differences between the two groups and explores their potential significance.

The Talus

In the talar analysis, group one (*P. anubis*/hybrids) were distinguished on the basis of their longer posterior articular facets and shorter medial articular facets than group two (*P. cynocephalus*). The differences, however, are absolutely and relatively small (see Table 31).

Table 31: summary statistics for the talar differences between baboon groups.

Variable	Group one mean and range	Group two mean and range	Overall mean
Medial facet length (MeFL)	0.38, range 0.17-0.51	0.43, range 0.37-0.51	0.40
Posterior facet length (PFL)	0.26, range 0.18-0.32	0.22, range 0.13-0.31	0.24
Ratio (MeFL/PFL)	1.47, range 0.76-2.61	2.12, range 1.29-3.08	1.76

As this table suggests, the difference between groups in MeFL seems to be robust, as it is reflected in both a difference in the groups' means and their overall ranges, while the difference in PFL, although similar in overall size, is less useful as a discriminator. The general shape of the talar trochlea is functionally relevant in that it affects the degree and direction of movement at the ankle joint (Kidd et al., 1996). Both the ratio of anterior to posterior trochlear breadth and that of medial and lateral facet length are thought to be relevant in determining the orientation of the ankle joint axes and the degree of movement possible. In humans, a relatively long medial facet is associated with a highly mobile ankle joint that permits a high degree of plantarflexion and dorsiflexion (Elftman and Manter, 1935, Wood-Jones, 1944), and a moderate amount of variation is found among different populations. The difference in the two *Papio* groups observed here, then, could be functional – as some differences between aboriginal Australians and Europeans, for example, are thought to be – or an artefact of genetic history and differentiation of the two groups. If it is functional, it implies that the *P. anubis* and hybrid specimens are able to plantarflex and dorsiflex the ankle more effectively than *P. cynocephalus*. This might (speculatively) be related to the fact that the former occupy landscapes which are higher altitude and higher in roughness, where increased ankle joint mobility would facilitate moving across variably inclined surfaces, while *P. cynocephalus*, on the flatter coastal plain, has less need of mobility at this joint.

The Calcaneus

In the calcaneal analysis, the group one baboons were distinguished from group two in having a wider posterior talar articular facet. The mean values and ranges for this variable are: group one mean 0.06, range -0.06 to 0.18; group two mean -0.02, range -0.08 to 0.06. This thus appears to be a robust difference (present in the ranges as well as in the mean values), and furthermore is not linked to overall bone size as the average geometric mean is in fact larger for group two than for group one.

The relative sizes of the subtalar facets are functionally relevant in that they determine the range of movement at the subtalar joint (Kidd et al., 1996), which is involved in a set of complex movements the most obvious of which is inversion/eversion of the foot (Elftman and Manter, 1935). In the baboon sample studied here, of course, no use is made of the long axis of the posterior facet in discriminating groups suggesting that the difference in this variable is sufficiently small for it not to contribute to telling specimens from the different groups apart. The calcanei of *P. anubis* and hybrid baboons, then, might be slightly better at inversion/eversion due to their broader posterior talocalcaneal facet than those of *P. cynocephalus*, but the difference is probably small and there is considerable overlap between the two groups. This means that once again, while it is possible to come up with a landscape related scenario which might explain the difference – that *P. anubis* and the hybrids occupy rougher physical landscapes – it is equally plausible that the pattern is linked to other, more complex combinations of social, behavioural, ecological and environmental variables or to inheritance, and no firm conclusion can be drawn.

The Cuboid

The cuboid was the bone best able to separate the two groups of baboons, distinguishing them on the basis that group one (*P. anubis* and hybrids) had a shorter maximum plantar length and lateral length, and a slightly wider short metatarsal facet dimension than did group two (*P. cynocephalus*). Table 32gives details.

Table 32: summary statistics for the cuboid differences between baboon groups.

Variable	Group one mean and range	Group two mean and range	Overall mean
Maximum plantar length (MPL)	0.25, range 0.18 to 0.33	0.30, range 0.24 to 0.36	0.27
Lateral length (LL)	-0.18, range -0.36 to -0.01	-0.07, range -0.17 to 0.03	-0.14
Short metatarsal facet dimension (SMFD)	-0.1, range -0.2 to -0.03	-0.12, range -0.16 to -0.07	-0.10

As this table suggests, the differences are small and there is some overlap between specimens, with MPL being the variable for which the difference is most apparent and SMFD that for which it is least clear that the difference between groups is significant, as the range of group two is entirely encompassed within that of group one for this variable. This is as we would expect based on the differing levels of correlation with the discriminant function given in Table 30.

Kidd et al. (1996) suggest that the relative breadth of the metatarsal facet might be informative about the robusticity of the metatarsal bases, while the proportions of various measures of the calcaneal body shape are informative about the stability of the calcaneocuboid joint. This would suggest that the *P. anubis* and hybrid baboon group has somewhat more robust metatarsal bases than the *P. cynocephalus* group, with a blockier cuboid indicating lower stability in the calcaneocuboid joint as the plantar protrusion that blocks excessive rotation is relatively smaller and the bone smaller in comparison to the joint surfaces at either end. Given that the calcaneocuboid joint is primarily involved in midfoot flexion and extension, but is also key to several other movements, this might imply more mobility in *P. anubis* which, once again, can be explained in the same way as for the other two bones but may still represent differences that are due to inheritance, behaviour or development rather than evolutionary adaptation to a particular landscape.

The Navicular

For the navicular, group one was distinguished by a relatively large navicular height and small navicular depth. The mean and range data for maximum navicular height (MNH) are: group one mean 0.16, range 0.06 to 0.27; group two mean 0.09, range -0.01 to 0.2; and for maximum navicular depth (MND) group one mean -0.14, range -0.22 to -0.03; group two mean -0.09, range -0.18 to 0.02. Once again, although the differences are thus present both in the mean values for each group and their ranges, there is considerable overlap between the two groups.

Navicular height is presumably significant because of the effect it will have on the area available for articulation with the talus posteriorly and the cuneiforms anteriorly, while depth is not necessarily functionally relevant but may influence the stability of these joints (if the depth of the bone is related to the depth of the facets which, unfortunately, this project did not collect data on) or may have no functional relevance save for its impact on the relative proportions of the tarsals, which are difficult to interpret. It is impossible to interpret these differences in terms of landscape without collecting further data.

The Medial Cuneiform

Group one is characterised by a medial cuneiform which is relatively short both dorsally and plantarly, and which is shallow (low maximum depth) and has short anterior and posterior facets compared to group two. It is worth noting that this analysis includes relatively more variables than were used or linked to the discriminant function in other cases and that this may be linked to the overall size difference between the two groups in which specimens of *P. cynocephalus* (group two) have higher geometric means than *P. anubis* and hybrid baboons from group one. While this difference may have some functional significance, it is likely to result from size via a complex suite of interacting landscape, genetic and behavioural factors and cannot be simply interpreted.

The Metatarsals

Finally, for the metatarsals the observed differences seem linked to robusticity. For metatarsal one, group one is characterised by a shorter bone with a broader distal facet; the third metatarsal of group one is less robust (has a smaller maximum midshaft dimension), and has a longer medial facet and narrower proximal facet than in group two; and for the fifth metatarsal, the two groups of baboons are separated by the fact that group one has a broader distal facet than group two. Table 33 shows the mean values and ranges for these variables.

Table 33: summary statistics for the metatarsal differences between baboon groups.

Bone	**Variable**	**Group one mean and range**	**Group two mean and range**	**Overall mean**
Metatarsal One	Maximum length (ML_A)	1.24, range 1.13-1.31	1.29, range 1.24-1.35	1.26
	Distal facet breadth (DFB)	-0.18, range -0.31 to -0.08	-0.23, range -0.31 to -0.16	-0.2
Metatarsal Three	Maximum midshaft depth (MMD_A)	-0.56, range -0.67 to -0.47	-0.52, range -0.61 to -0.46	-0.55
	Medial facet length (MFL_A)	0.02, range -0.1 to 0.1	0.04, range -0.04 to 0.07	0.03
	Proximal facet breadth (PAFB_A)	-0.98, range -1.26 to -0.78	-1.01, range -1.17 to -0.93	-1.01
Metatarsal Five	Distal facet breadth (DFB_B)	-0.28, range -0.34 to -0.21	-0.32, range -0.37 to -0.27	-0.29

As this table shows, all of these differences are reasonably robust despite the two groups ranges overlapping. They may have significance in the function of the metatarsals. In particular, group one seems to have generally smaller metatarsal dimensions (presumably again reflecting their slightly smaller overall bone size), but has a notably broader distal facet on both the first and fifth metatarsals, perhaps reflecting greater strength in the first and fifth metatarsophalangeal joints. This might also be linked either to landscape or to other features (particularly, in this case, grasping activities which might influence toe anatomy), or to behavioural patterns.

DISCUSSION: COMPLEXITY IN THE PRIMATE-LANDSCAPE SYSTEM

This chapter has demonstrated the presence, in the baboon-landscape system, of complex patterning (which may resist simple causal explanations) and causal links between organism and landscape which work only on specific space-time scales. This is suggestive of a system which is both complex and potentially inaccessible to logic. Despite this complexity, however, the analyses presented here have shown that firstly, it *is* possible to characterise and begin to interpret the relationships between baboons and their landscapes, even if these interpretations are scale- and location dependent, and secondly that it does seem likely that moden *Papio* baboons are influenced not just by the vegetation types and climates which characterise their ranges but by the unique spatiotemporal configurations of local landscapes. The interactions between baboons and their landscapes may manifest themselves in several ways: via modifications to group socioecology and/or behaviour (mediated, at least to a certain extent, by cognition and agency); in changes to baboon biogeography or relationships with parts of the 'natural' landscape; or in developmental or evolutionary changes to anatomy.

The analyses presented here took a hierarchical approach, like that used in Chapter Three, because the existence of perspective-dependent patterns in landscape suggested that a series of case studies moving from the general to the specific might be informative. At the largest scales covered emphasis was placed on characterising the ranges of specific allotaxa. This analysis found that these ranges' landscapes are consistently variable and, while there are some differences in the average conditions in each allotaxon's range, there is considerable variation within taxa too. The allotaxon ranges overlap considerably on almost every variable considered. This suggests that just as baboon ecology is more variable within than between allotaxa (Kamilar, 2006), the variability within a single allotaxon's range (particularly of widespread taxa like *P. anubis* and *P. cynocephalus*) dwarfs the differences between them. *P. anubis*, for example, ranges from the west of Africa, where (as Chapter Three showed) climate and (to a lesser extent) vegetation are generally latitudinally banded and the physical landscape shows a different configuration, through to east Africa where the physical landscape structures of the Rift Valley dominate and landscapes are locally variable and patchily patterned. Western *P. anubis* may thus have more in common in their relationships with landscape with neighbouring *P. papio* troops than their eastern conspecifics, and eastern ones more in common with *P. hamadryas* or some (north-eastern) groups of *P. cynocephalus*, for example.

The presence of zones of overlap between some pairs of neighbouring allotaxa but not others has proven difficult to explainin part because of confounding among social, ecological and landscape variables which make it hard to distinguish the predictions of genetic and landscape-based explanations from one another. Studies of baboon densities across Africa cannot resolve the problem, as while there are some particularly high density populations living in these zones of overlap there are also some sparse ones, and some densely occupied zones elsewhere. This suggests that grand explanatory models which link baboon ecology, behaviour, anatomy and environment are unlikely to be able to effectively capture the full range of variation in these creatures and their landscapes, and that smaller scale studies are required to establish whether it is simple confounding or complexity that is the cause of these problems.

Small-scale studies of baboon landscape use focused therefore on Amboseli, where a troop had been followed through temporal changes in environment and landscape, and on De Hoop and Gashaka where multiple troops were known from different local landscapes. The results suggest that complexity is inescapable when dealing with baboon ecology, and cast doubt on earlier studies' hypothetico-deductive approaches to primate ecology (which typically assume simplexity and logical coherence) and broad models for relating activity budgets or other aspects of primate socioecology to environmental conditions. At De Hoop there is evidence for feedback between landscape, social and behavioural parameters, and anthropogenic influence, while at Gashaka relationships between landscape and behaviour are clearly complex but harder to unpick. Even at Amboseli, where the problem – forging links between temporal changes in landscape and troop ecology – seemed much simpler, complexity was apparent in the responses of baboons to spatial and temporal changes in landscape, in the effect of a time-lag following drought and successive changes in local climate and vegetation, and in the influence of anthropogenic factors on the baboons' recovery. Although these studies represent just a small sample of baboon troops, purposely selected to represent a wide range of landscapes and taxa, they do suggest that complexity rather than simplexity and a lack of 'general' rules relating ecology to environment are typical of the baboons. Every troop – not just population – studied showed a different relationship with landscape and there was no sign of the broader allotaxon differences found earlier. These analyses also suggested that behavioural patterns were closely tied to the biological aspects of the baboon-landscape relationship, and that agency therefore might be important even in 'normal' nonhuman primates.

Given this complexity, it was decided to focus on a sample of baboons of known origin for the final stage of this chapter where anatomy and landscape were linked. The patterns characterised by this research seemed simple enough. When landscapes were classified, the two broad groups identified corresponded nearly exactly to the allotaxon divisions within the study sample. This suggests a simplex explanation of allotaxon-specific landscape preferences which would make sense if one was to take the allotaxon boundaries as fixed and immutable; but does not work if one takes account of the deep-time perspective of co-evolutionary ecology or the small space-time scales of socially learned behaviours, choice and chance. This is reflected in the fact that larger-scale analyses failed to find consistent associations between allotaxa and landscape types and in the smaller studies of landscape use at Amboseli, Gashaka and De Hoop.

For the Kenyan baboons, statistical analysis showed the existence of consistent patterns in foot morphology that could be used to discriminate groups from different landscapes, but whether one interprets this genetically – as a consistent difference between stable allotaxa – or ecologically as the products of patterns emerging through chance or agency, is unclear. This, combined with uncertainty in the literature over the precise functional relevance of individual features and the relatively small observed differences between baboons from different landscapes, suggests that anatomy and landscape form yet another complex system. There may be some relationship in this case between the physical landscape and adaptations for mobility or stability in the larger tarsals, but it is impossible to unpick the precise nature of these effects from the system as a whole, in which baboon foot anatomy is undoubtedly influenced both by genetic and epigenetic processes and by a suite of factors which, the preceding analyses suggest, may interact in complex ways.

CONCLUSIONS

Overall, this chapter has contributed to the overarching aim of the thesis (to evaluate King and Bailey's TLM) in several ways. Specifically, these analyses suggest that:

1. Complexity, in the sense described in Chapter One (logical incoherence and ill-boundedness), is a ubiquitous feature of the primate-landscape system, but carefully designed investigations of case studies at varying scales do produce interesting insights into the relationships between primate ecology, anatomy and behaviour and the landscape around them;
2. These insights may, however, be perspective-dependent and it is often hard to identify causes and effects or to generalise from specific cases to the bigger picture of baboon socioecology. No clear, repeatable, *a priori* predictable patterns are seen even where local troop ecology and landscape are well known, and patterns of landscape use vary significantly both within and between baboon allotaxa;
3. Behaviour (and by implication, culture and agency) is important in mediating the interactions between baboons and their landscapes. Different troops, even in adjacent or overlapping ranges, can strike different balances between ecological, behavioural and evolutionary strategies to deal with the landscape, and may show different relationships with their environments, as at De Hoop and Gashaka;
4. Landscape and anatomy do seem to be linked. For the Kenyan baboon sample studied here, samples from different landscapes can be distinguished on the basis of potentially functional differences in foot bone shape, for example, but distinguishing the effects of genetic history from those of landscape is impossible as the groups defined on the basis of landscape type coincide with the division between *P. cynocephalus* and *P. anubis* (with hybrids);
5. A Darwin-Huxley or Extended Synthesis perspective on evolutionary history, which can recognise this kind of complexity and interaction between factors, may be more useful for future research than an adaptationist one which presumes simplexity, especially if we accept that complex scale-dependent relationships between organism

and landscape (as found throughout these analyses) probably have knock-on effects for the types and complexities of the ongoing evolutionary processes and resulting biogeographical and ecological patterns;

In most of the case studies explored here (with the exception of Amboseli, where observed landscape changes were almost exclusively climatic), the physical landscape seemed as closely linked with baboon socioecology and anatomy as vegetation and climate.

The findings of this chapter thus confirm the validity of the three-pronged conceptual structure proposed in Chapter One by identifying the presence of complexity in primate-landscape systems (building on the discovery of complex landscape structures in Chapter Three), finding a clear role for agency and behaviour in mediating baboon interactions with their landscapes, and demonstrating that both the spatial structure of environments generally and the shape of the physical landscape specificially seem important to *Papio* baboon socioecology and anatomy. There is no evidence for a clear physical landscape preference among either the genus *Papio* as a whole or any individual allotaxa within it, but the discovery of differing ecological, anatomical and behavioural strategies among individuals from different landscapes does suggest that the underlying principle of the TLM – that physical landscape structures can be important – is valid at least for the baboons and deserves further investigation for other taxa. In particular, it remains to be seen whether modern humans (which Chapter One suggested might differ from other primates in their use of primarily or purely cultural strategies to deal with environmental changes or variations) display similar relationships with landscapes.

Chapter Five: Human Relationships with Landscape

INTRODUCTION

So far, this thesis has developed a baseline understanding of the structures of extant African landscapes at different scales and in different regions and gone on to populate these landscapes with *Papio* baboons, to explore the relationships between primates and their landscapes. This latter study found that socioecology and behavioural strategies were important parts of the baboon-landscape systems studied, and suggested that agency – and possibly culture – were therefore likely to be important to all primate-landscape interactions and particularly those of the cognitively complex hominins. This chapter therefore focuses on modern *Homo sapiens* for whom it is 'obvious' that social interaction, politics and culture have played a major role in determining key ecological traits. This taxon can thus be used as an extreme example of a primate (with the most sophisticated cultural and cognitive strategies for dealing with the landscape and environmental change) to test the suggestion that humans – and perhaps some or all of the hominins – were 'independent' of natural selection and biological evolution. The geographic focus, once again, is on Africa, as the discovery of perspective-dependent patterning in landscapes (Chapter Three) and primate interactions with landscape (Chapter Four) suggest that not only would moving this emphasis elsewhere require that initial mapping studies and analyses of landscape structures be repeated, the results would not be comparable (or necessarily commensurable) with those obtained above. The same maps and sources of evidence are therefore used (see Chapter Two). The question raised in this chapter is to what extent modern human anatomies and distributions show evidence of influence from the natural and sociocultural components of landscape respectively.

That social systems have impacted the distribution of people in modern-day Africa is hard to dispute. The Colonial period, for example, may have exerted a major influence on human geography and demography that is only partially concerned with landscape and 'typical' behavioural patterns (Green, 2012). However, Africa contains a number of regions where indigenous state formation led to major urban developments that continue to influence demographic patterns today. Adepoju (1995, 89) identified three major phases of human migration in Africa: a pre-Colonial phase where migration "aimed at restoring ecological balance" and was probably linked to a search for more attractive social and physical landscapes; a Colonial phase of (en)forced economic and labour migrations, and a post-Colonial phase with very varied mobility patterns arising from a complex nexus of historical and recent processes. Today, mobility is increasing and mobility patterns are diversifying across Africa (van Dijk et al., 2001). In the sections which follow, therefore, instead of summarising distributions relative only to physical factors and interpreting behavioural data from socioecological sources in the literature, maps of social patterning, urban development and so on are also included.

The extent to which social and cultural patterns have influenced foot anatomy, however, is harder to pinpoint. It is relatively well known that the use of footwear and locomotion on modern, often smoothed, substrates (itself socially mediated) can cause deformity and other developmental changes to the shapes of tarsals and metatarsals (Zipfel and Berger, 2007, D'Aout et al., 2009), and some authors have suggested that it is possible to identify the use of shoes in antiquity through studies of the comparative biomechanics of the feet of Palaeolithic people (Trinkaus, 2005, Trinkaus and Shang, 2008). However, we also know that modern human anatomy retains a number of supposedly ‘relic’ traits, associated not with modern functionality but with the adaptations of our ancestors (Aiello and Dean, 1990). The first foot that looked rather like a modern human’s appeared some 2Ma, although this is debated as different interpretations of specific fossils abound (Klenerman and Wood, 2006). The focus of the second suite of analyses in this chapter, therefore, will be to establish whether there are functionally relevant differences in the bones of the foot among populations of modern humans from different landscapes. To mitigate confounding by shared genetic history (found to be a problem in Chapter Four), samples from Neolithic Africa are contrasted with those from the very different landscapes and cultural systems of medieval Britain.

THE GROSS MORPHOLOGY OF MODERN HUMAN LANDSCAPES

Figure 73 shows the population density distribution of people in Africa in the year 2000. There are five areas with above-average population density: the Nile valley; the northwest coast of Morocco, Algeria and Tunisia; the Ethiopian highlands; the Lake Victoria area; and in Nigeria/western Africa, with smaller dense zones also occurring in South Africa, along the west coast, and in the southern rift valley. The Sahara and parts of southeast and central Africa, in contrast, are home to only small, sparse populations, presumably because the combination of social and physical conditions make these areas less attractive.

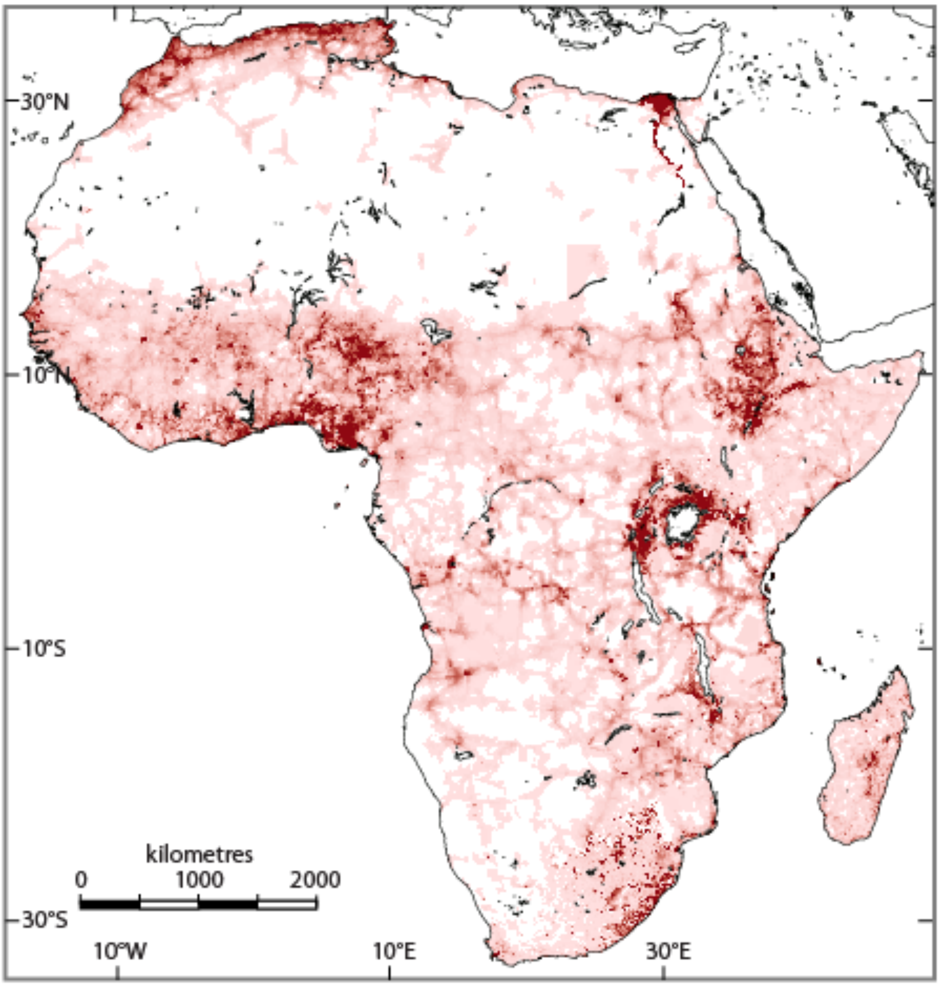


Figure 73: human population density map for modern Africa (from the 2000 census).

The reasons for the abandonment of the Sahara are relatively clearly linked to aridity (see Chapter Three for maps of continental rainfall and seasonality), but the influence of water elsewhere is less clear. Several densely occupied regions – the Nile Valley, around Lake Victoria, and the west African zone – are characterised by the presence of substantial water resources either in freshwater bodies or high rainfall levels, but the northern coast and Ethiopian highlands are less water rich, while the sparsely occupied parts of the southwest are also intermediate. The character of these presumably 'attractive' landscapes is therefore explored below in more detail.

Physical Landscapes, Soils and Geology

There are significant differences in topography across the five densely occupied regions (Figure 74). The Ethiopian highlands and Lake Victoria regions sample some of the highest altitudes in the continent, while the Nile and Nigeria are low lying. Mean altitudes are 1201m (Lake Victoria), 1657m (Ethiopia), 165m (Nile Valley), 716m (the north coast) and 347m (Nigeria), and the altitudinal ranges follow a similar pattern, with altitudes of zero occurring in all five areas and differences in maximum altitude ranging from 5895 in the Lake Victoria area (at Mount Kibo in Tanzania) to just 765m in the Nile Valley.

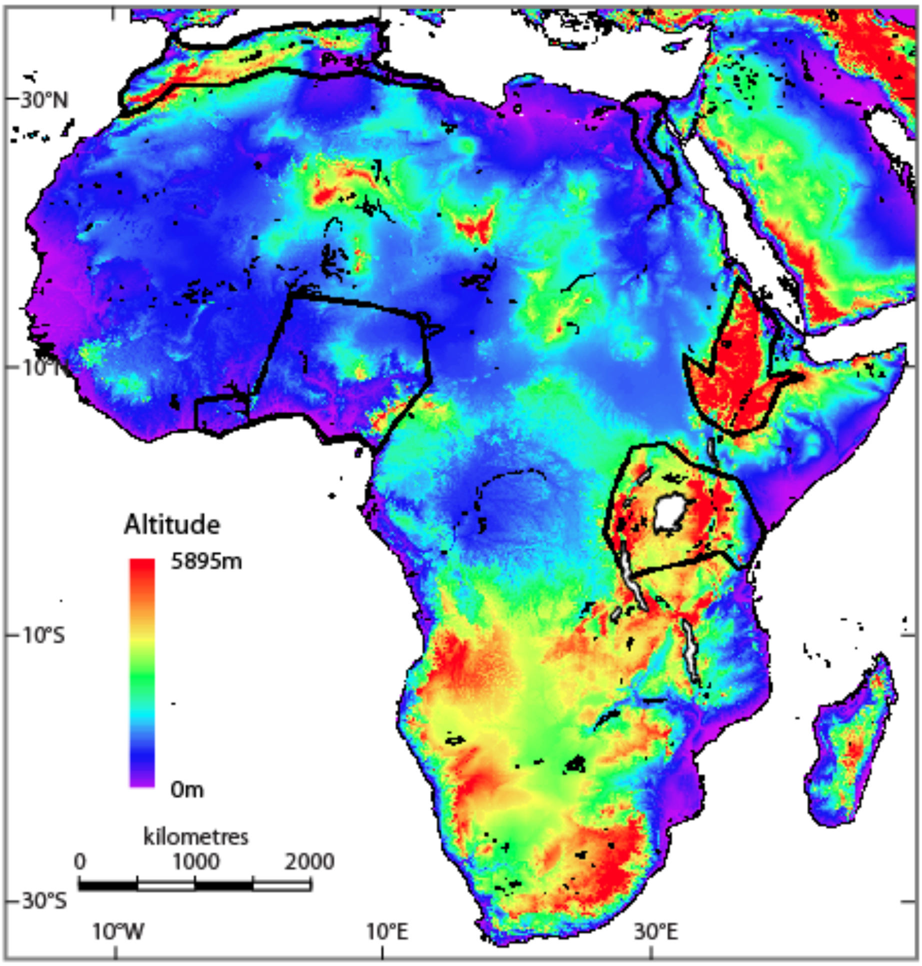


Figure 74: a map showing the substantial variation in topography between the five densely populated regions (outlined in black).

Roughness, in contrast, shows little regional variation. All five densely populated zones span the range from 0-200 units (of a maximum of 255), except for the north coast which ranges from 0-204 units. This omission of the highest roughnesses in these areas is probably because the defined regions do not cross coastlines where the sharp boundary between defined land surfaces and undefined 'no data' values in the ocean produces a narrow zone with the highest slopes, and therefore roughnesses, of the continent. While four of these five zones are generally fairly rough throughout, however (Figure 75), the Nile Valley is generally smooth with just one or two small roughness peaks. This difference is hard to interpret more thoroughly as the precise boundaries used for each region determine the precise values included and, although these seem robust to small changes, mobility since 2000 might cause shifts which, were they known, would re-define regions.

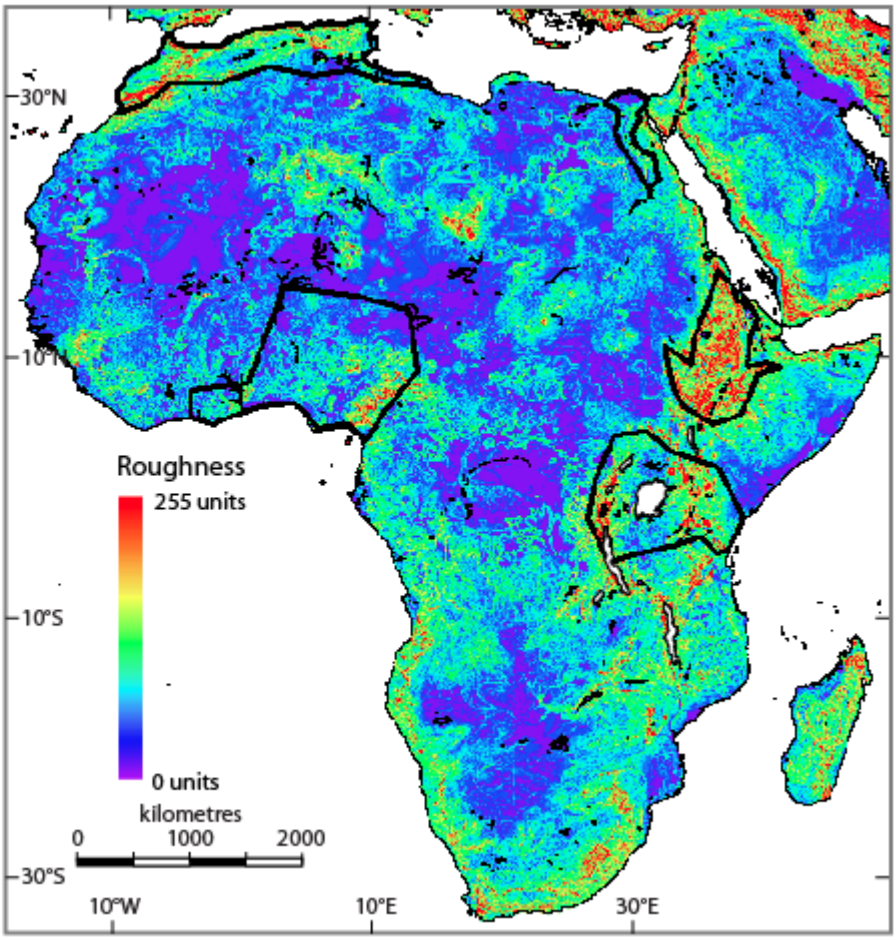


Figure 75: roughness map with the five densely populated regions outlined in black.

Regional median roughness values (Lake Victoria: 74 units, Ethiopia: 122 units, the Nile Valley: 64 units, the coast: 73 units and Nigeria: 66 units) do modify the picture somewhat, suggesting that the Nile Valley is not as unusual as might be assumed on the basis of minima and maxima and cautioning against overinterpretation of extreme values. Overall the Ethiopian highland region seems to fit well with King and Bailey's (2006) observations of a preference for high roughness among modern humans, but conditions in the other four densely populated areas do not.

Neither surface geology nor soils show any really clear differences between densely and sparsely occupied regions. In very general terms, the Lake Victoria and Nigerian regions are both based on Precambrian rocks (with significant intrusions of other ages), while the Nile Valley substrate is Tertiary and Quaternary, the Ethiopian highlands are Tertiary igneous rock, and the north coast region has no dominant rock type, being instead simply a patchwork of types. The soils, in contrast, are broadly uniform calcisols along the north coast, calcisols and fluvisols in Egypt, and patchier and less easily described in the other regions. Overall, the physical landscapes of the densely populated areas of Africa are thus best characterised as 'variable', and do not show any clear patterning that might relate to preferences.

Climate and Seasonality

In climate too we can see appreciable differences between the five densely populated regions (Table 34).

Table 34: average values and ranges for climatic conditions in the five populous regions.

Variable	Lake Victoria	Ethiopian Highlands	Nile Valley	North Coast	Nigeria
Mean annual temperature (ºC)	5.3-51.6, mean 28.1	11.9-50.1, mean 31.0	23-44.3, mean 33.0	13-36.6, mean 28.7	17.8-42.1, mean 30.5
Annual rainfall (mm/year)	238-2606, mean 1060	114-2213, mean 1018	0-182, mean 21	55-1411, mean 340	153-3586, mean 1104
Temperature seasonality (arbitrary units)	69-1882, mean 832	52-436, mean 1312	4484-6752, mean 5678	2443-8231, mean 6539	656-4032, mean 1926
Rainfall seasonality (arbitrary units)	0-112.6, mean 19.9	0-55, mean 10.8	0 across range	0-28.9, mean 3.7	0-66.9, mean 4.9

Annual average temperatures are only slightly variable (around 30ºC in all five areas), but mean rainfall and seasonality vary more significantly. Rainfall is low in the Nile Valley and along the north coast while temperature seasonality is high in these two regions and low elsewhere. Rainfall is most seasonal in the Lake Victoria region and displays little or no seasonal variation in the Nile Valley, on the north Coast and in Nigeria.

Other than recognising that this table describes a variable set of climates, however, it is hard to interpret this data without understanding continental variation (as discussed in Chapter Three). In this case, we know that within Africa, the four climatic variables have ranges of 0.8-51.6ºC for temperature, 0-4560mm/year for rainfall, 0-10276 for temperature seasonality (a measure of the variance of temperature with arbitrary units) and 0-167.9 for rainfall seasonality (another set of arbitrary units based on a measure of variability). We see, then, that Lake Victoria, the Ethiopian Highlands and the Nigeria region are relatively hot, dry and non-seasonal from a continental perspective, while the Nile Valley and north coast regions are similar in temperature but differ in being even drier and substantially seasonal at least in temperature. This pattern does not help identify a 'preferred' external environment for modern human occupation and suggests that human climatic tolerance – like that for physical landscape variation – is also broad.

Vegetation and Ecoregions

Means and ranges for vegetation data, which is categorical, cannot be computed easily for metric comparison of regions. It is clear, however, that the areas of dense occupation vary in vegetative terms as much as they do in climate and physical landscape (Figure 76). The Nile Valley area is completely covered by arid/semi-arid vegetation; the north coastal strip is arid/semi-arid with patches of closed and semi-open vegetation; the Lake Victoria area ranges from open to closed vegetation and includes patches of aquatic plants; and the Ethiopian highlands and west African regions span closed and semi-open habitats, with minor patches of arid/semi-arid and aquatic respectively.

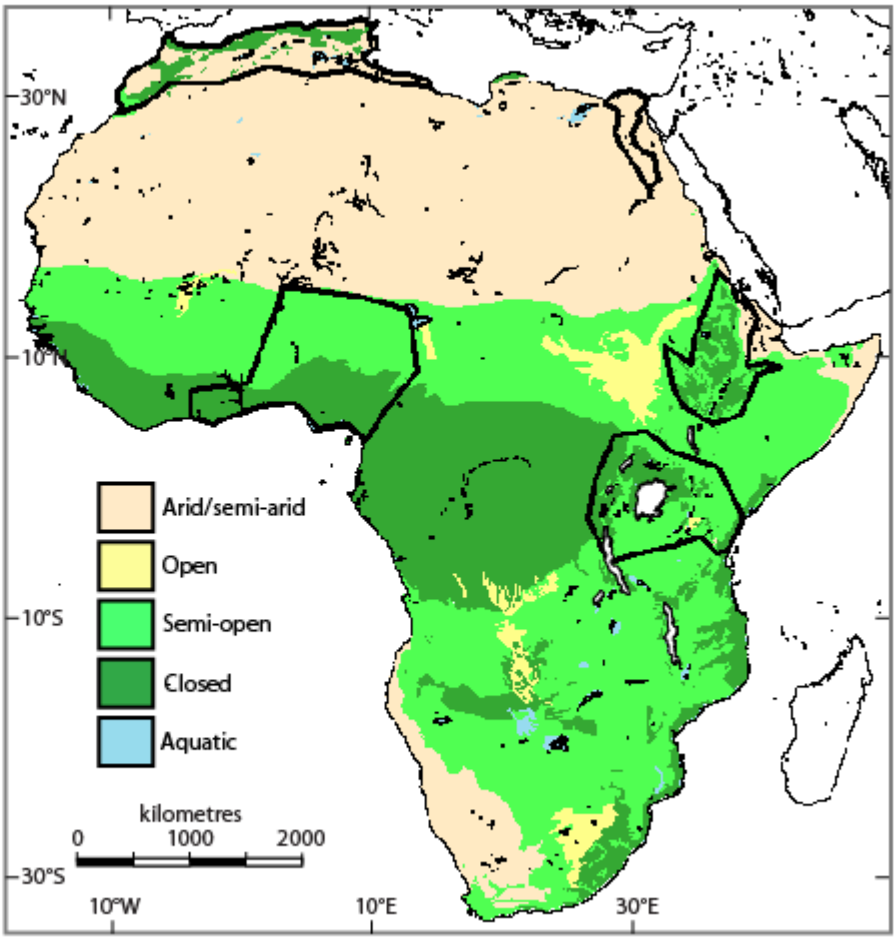


Figure 76: a vegetation map showing the heterogeneity in both vegetation type and distribution across the densely occupied regions (outlined in black).

The spatial patterning of vegetation across these regions also varies, with Nigeria and the northern coast being latitudinally banded while the Nile Valley is homogenous throughout and the east African areas are patchily covered with different types of vegetation – as we would expect from Chapter Three's description of large-scale environments. The same patterns, but with regionally different labels for specific habitats, are seen on the WWF ecoregions map (see Figure 77) with the major exception that this map recognises a distinct stripe of 'Nile Delta flooded savannah' running up the middle of the arid/semi-arid Nile Valley, the rest of which is labelled as showing affinities to the Sahara desert.

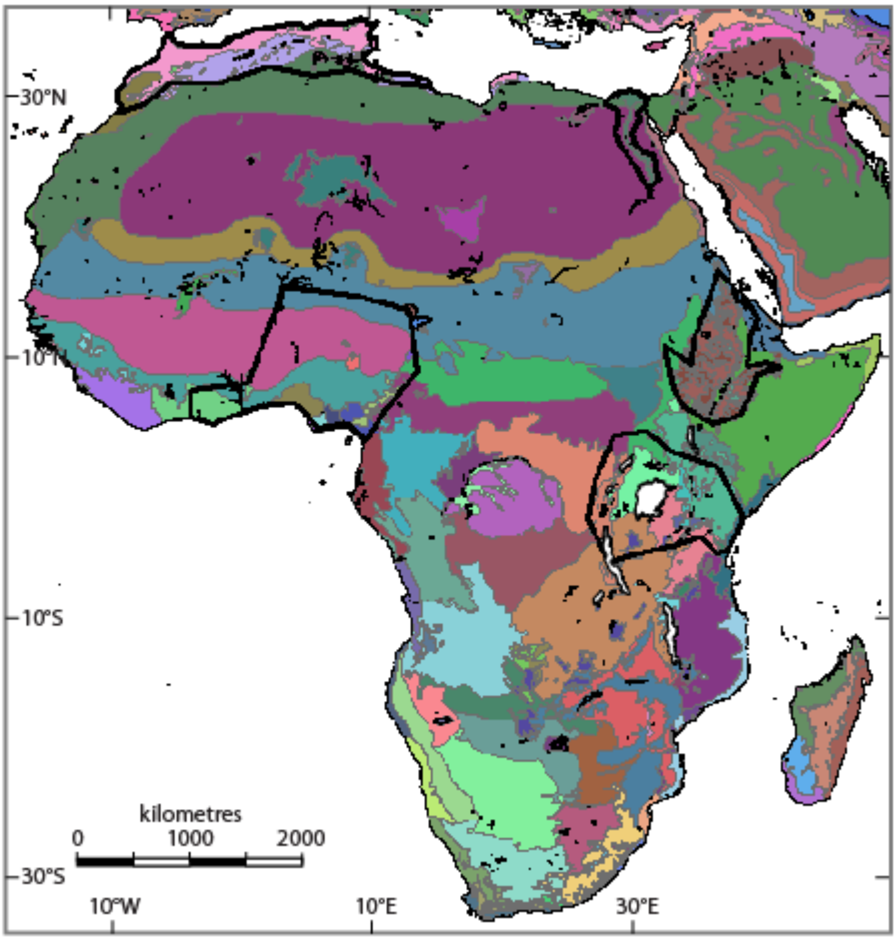


Figure 77: ecoregions map showing the diversity in types (different colours) of more specific ecoregions identified by the WWF and the broad similarity in their distribution to the broader pattern shown above. The five densely occupied regions are outlined in black.

Social Landscapes

There seems to be no single ‘attractive’ physical environment which can explain human population distributions across Africa. Instead, each region is different. Climatically, the five regions studied split into a northern and a southern group. The Nile Valley and Nigeria show physical landscapes which are low altitude and smoother, while the Ethiopian highlands, Lake Victoria and North Coast regions are rough and high altitude. The vegetation is different in each case. This is probably because modern humans are culturally and ecologically flexible and can occupy whole range of conditions, making choices of where to live based not on the natural landscape but a combination of natural, social and cultural factors, but it also might be because the current distribution of people in Africa does not reflect active choice, but rather is determined by other factors, like the presence of (imperially initiated) urban resources or forced limits to mobility in the recent past or present. In fact, of course, human-landscape interactions are rarely purely ‘social’ (or cultural) or purely determined by the external environment. Instead, they lie on a spectrum from a dominant – though presumably not exclusive – sociocultural influence to a similar dominant environmental component. In this section, some evidence of the social influence(s) on these five areas are therefore explored, although this cannot be considered certain as it involves simplifying the complexity of a dataset which is not only socially, culturally and politically variable but also a historical palimpsest of many major periods. In addition, unpicking cause and effect in these datasets can be difficult. For instance, it's hard to tell whether densely populated areas attract people because of their urban centres, or whether the urban centres grow because the (natural or cultural) environment is attractive to begin with. It is clear that the presence of a past city at a given site is a good predictor of the presence of a city there today, as has been empirically demonstrated for Europe using the SIMPOP models (Pumain et al., 2009). Simulation studies of urban networks using these models are not able to fully reconstruct the current distributions of European populations (for instance, they consistently underestimate the populations of the largest urban centres), but they do suggest that certain elements of population distributions are at least somewhat predictable despite their complexity (Pumain et al., 2009). Today, there are a whole range of these models, incorporating various social, economic and political processes and employing different algorithms and assumptions. These span a spectrum from the biogeographical to the mathematical (like SIMPOP) and function at various scales. Each one typically works to highlight one or a few elements – or a single scale – in a complex hierarchy of interactions influencing urban centres. It is very likely that in Africa too, population density maps show traces of past population distributions and urban centres.

Even crude demographic and geo-political data can provide useful information on this problem. For instance, the current political boundaries (Figure 78) of Africa reflect a combination of post-Colonial political change and the carving up of the African landscape during the Colonial period. Green (2012) notes that the largest states in Africa today were generally both resource and trade poor in the pre-Colonial period, and low in population density. The five regions of dense occupation today often overlap political boundaries – except for the Nile Valley region, entirely contained within Egypt – and while some are found in areas with many small states (e.g. Lake Victoria and the western African region) others, like the north coastal strip and the Ethiopian highland area are part of or overlap relatively large ones.

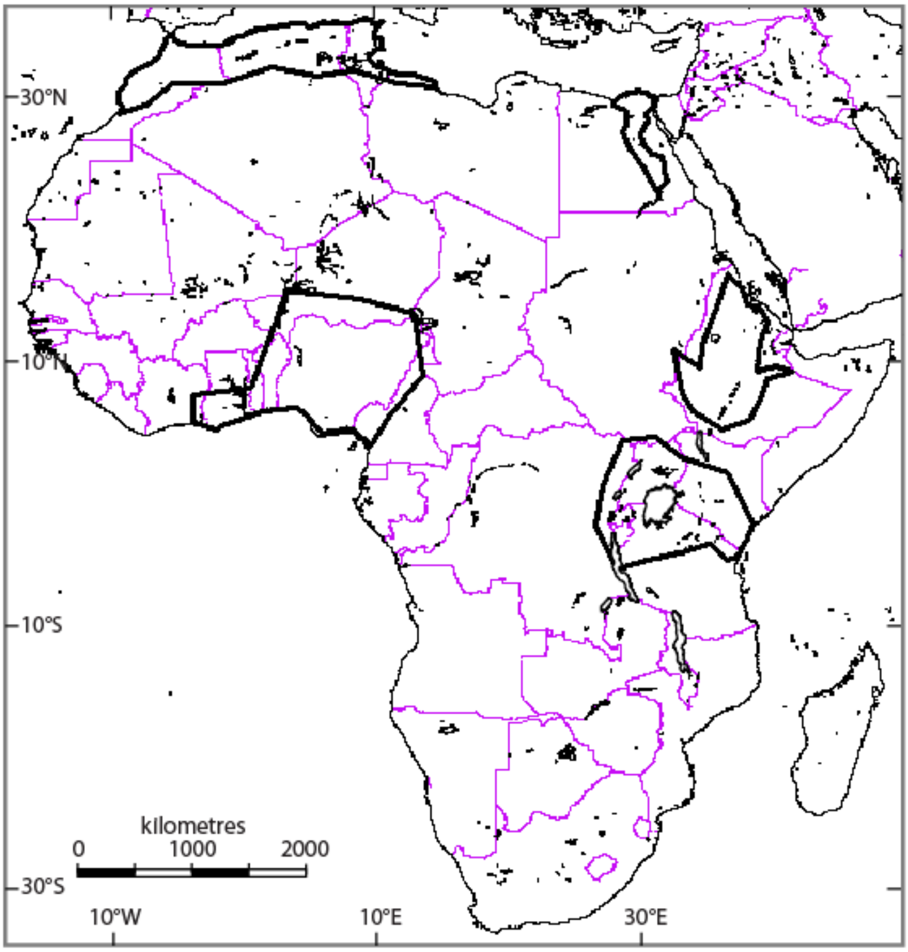


Figure 78: a map of the political boundaries of Africa, showing that several of these regions do cross the political boundaries of even relatively large (and by implication resource-poor) countries.

This might be an indication, therefore, that some of these regions have grown either during, or after, the Colonial period. Looking at maps of population density and the distribution of major urban areas immediately after the last states became independent (1950-1960), we see a very similar pattern to today, though with smaller total populations and cities. Figure 79 below shows the distribution of major urban areas in Africa in 1950, for instance, and these are concentrated in – though not restricted to – the current densely occupied areas.

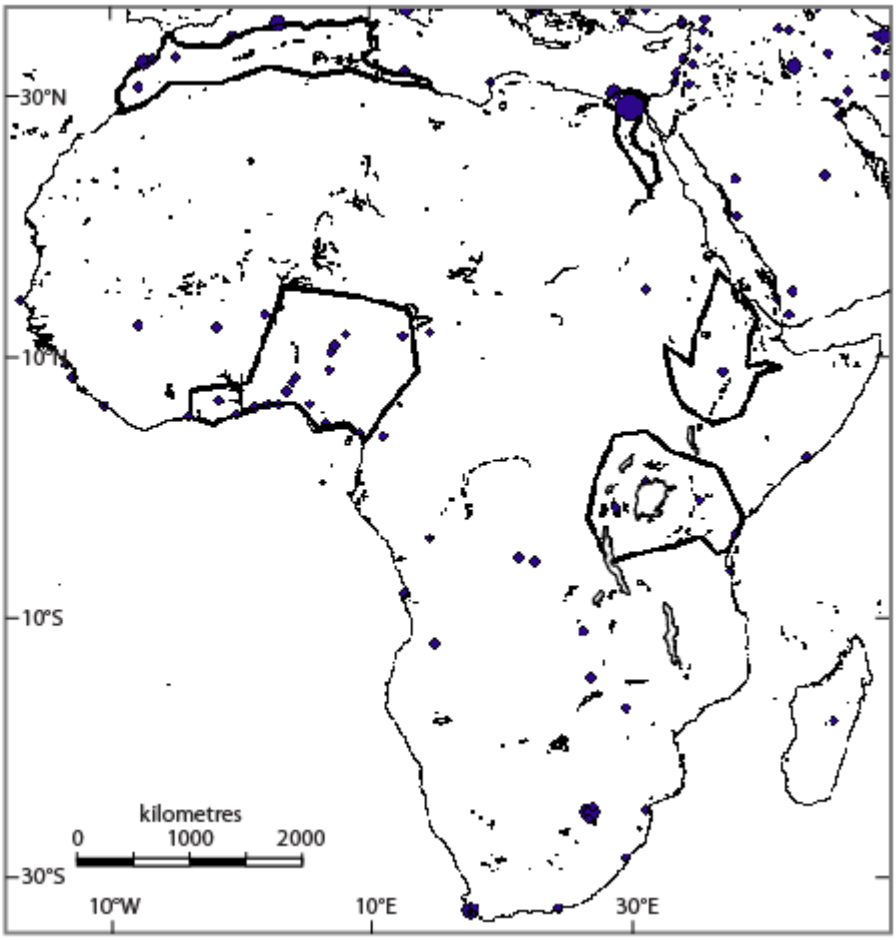


Figure 79: a map showing the major population centres of Africa in 1950, with the size of the dark blue circles showing relative population size.

Comparing the 1950 distribution with that of 2010 (Figure 80) shows some broad similarity but clear evidence also of regional differences and mobility over the 60 year gap. Three of the four biggest population centres in Africa in 2010, for instance, including those in the Democratic Republic of the Congo (Kinshasa), in Nigeria (Lagos) and in the Sudan (Khartoum), have become dominant since the 1950s, with only the Nile delta urban block (Cairo) having been as significant originally. The urban areas along the north Africa coast, in contrast, remain roughly of the same relative size (although their populations are larger absolutely now than they were in 1950), while others have grown relatively larger but have not shifted in their overall dominance of the urban landscape.

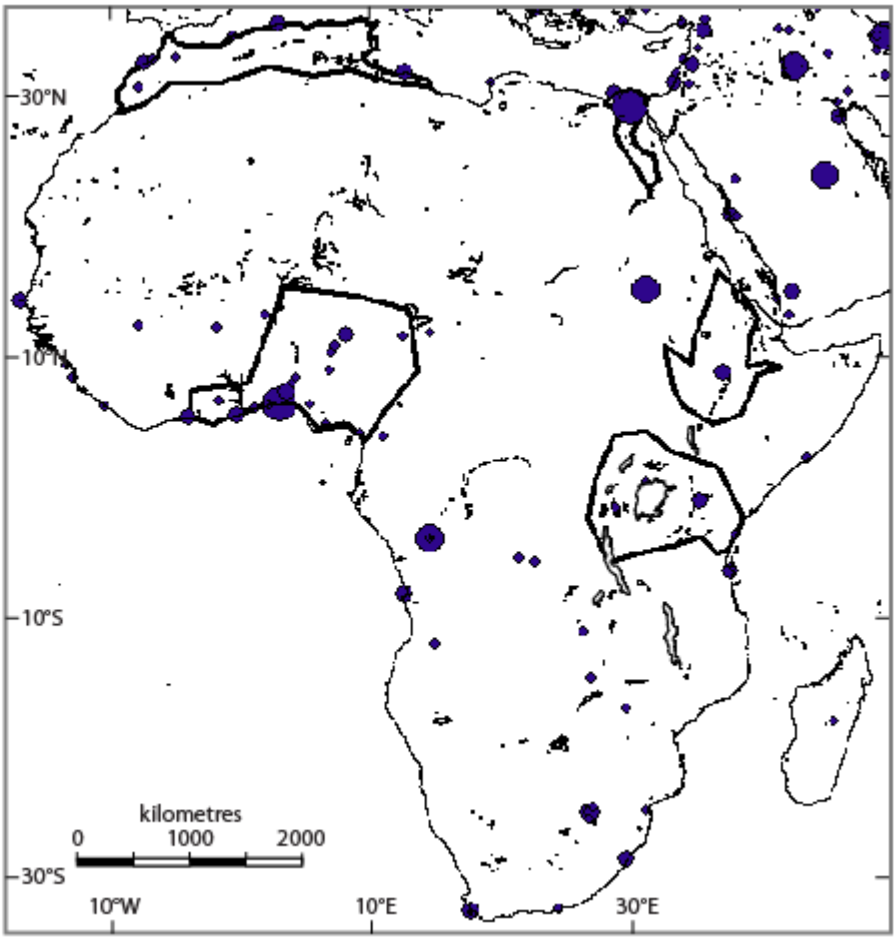


Figure 80: a map of major urban centres in the year 2010, with dark blue circles representing city sizes for comparison with the above.

This shows that mobility has indeed been important in the post-Colonial period. It is, however, difficult to identify the reasons for these population shifts. All four of these cities are economically increasingly significant, with a positive feedback loop set up whereby the larger the cities grow, the more attractive they are to immigrants (another manifestation of the accretion phenomena known from urban simulations, see above). In addition, however, it is clear comparing Figure 73 and Figure 80, that the five regions with the densest populations are also home to significant non-urban populations, presumably including people living in both the surrounding shanty towns and the rural areas. Van der Leeuw et al. (2009) have proposed that complex societies are best considered as webs of interlinked social and physical networks, held together by information flows and (sometimes) modified by innovation and cultural or economic changes. This more complex model would allow both for the historical constraints of accretion and the appearance and rise to dominance of new centres of economic or social power, and would encompass rural and suburban populations within the same complex system as urban centres.

While there are no pre-Colonial population density maps, a certain amount is known about the locations of major civilisations and urban centres (see Figure 81), although this is certainly incomplete and potentially inaccurate in places. It does, however, suggest that there were major pre-Colonial civilisations in all the same areas as are densely occupied today – including Egypt, along the north coast (although these extended a long way further than the densely populated zone today), Ethiopia, the Lake Victoria area and Nigeria. There are also several major civilisations in the western Sahara, presumably during periods that were more climatically tolerable. This suggests that accretion of urban and densely populated areas around existing – sometimes ancient – towns and cities is apparent in Africa, and that endemic states or towns have been persistent and significant landscape features despite the political, economic and cultural upheaval of the Colonial and post-Colonial periods.

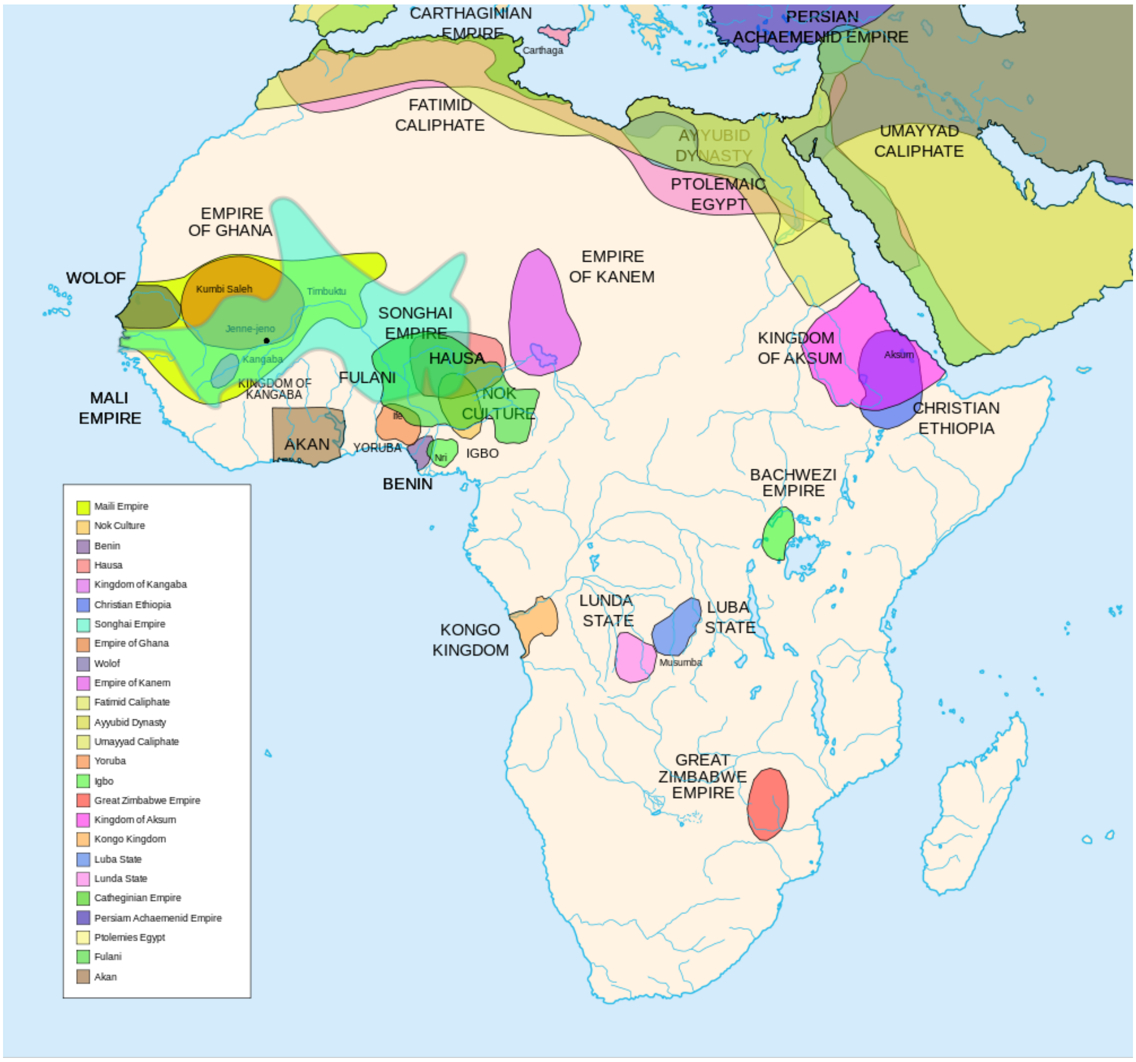


Figure 81: a map showing the major pre-Colonial civilisations of Africa, compiled from various literature sources by Jeff Israel for the History Atlas of Africa (available online at http://en.wikipedia.org/wiki/File:African-civilizations-map-pre-colonial.svg).

It seems, from this evidence, that all five of these densely populated areas have been reasonably attractive to humans, producing major civilisations with towns and cities, a level of organisation equivalent to the state and high relative population densities – since the pre-Colonial period, and have been occupied ever since. This suggests that a combination of social and physical factors have produced adaptive (or attractive) peaks in each of these five areas that have lasted a long time. Without looking at individual city or state histories (which would undoubtedly illuminate specific cases but would require a much more detailed study than is possible here to enable the extraction of general principles of interest), we can therefore say that all the most densely populated areas of Africa are influenced by both social and physical factors. They differ in both their physical environments – physical landscapes, climates and biospheres – and their social histories, and it seems that the natural landscape exerts relatively little constraint on human settlement (barring the obvious problems with occupying very arid regions), but may work with social and political factors to produce consistently attractive landscapes. Environmental determinism (even in a relatively weak form) clearly does not work as an explanation for human population distributions, any more than it did for the less culturally complex *Papio* baboons, and where the latter seemed to show preferences for particular natural landscapes modified by socioecological and behavioural concerns, humans show no apparent preference or restriction but rather distributions that result from complex interactions between factors. It has even been demonstrated for certain cases (e.g. at Epirus, Greece) that people's visual perception of their landscapes differs depending upon social, historical and spatial factors and the action of cultural filters (Green and King, 2001).

This analysis of human landscapes in Africa, then, suggests that one part of the answer to this chapter's key question about the role of landscapes in determining human ecology is that the 'natural' landscape seems to serve as a backdrop, but not to constrain, human dispersal. Instead, it is the cultural elements of landscape which seem to determine where people live, at least where urban settlements are concerned, and any physical landscape effect like that King and Bailey have proposed (King and Bailey, 2006, Bailey and King, 2011) is probably a modification or addition to this cultural pattern. It remains possible, however, that landscape does not determine *where* humans live but might still impact *how* they live, for instance by effecting physical or behavioural differences between populations. This possibility is the subject of the second half of this chapter, which focuses on the more concrete subject of physical adaptations (anatomies).

HUMAN LANDSCAPES AND ANATOMY

The discussion above suggests that we cannot fully partition the effects of sociocultural and physical components of human landscapes any more than it was possible to separate behaviour, culture and landscape ecology in baboons. These factors interact at various levels and in complex ways to produce the observable distribution of people and activities in Africa and, presumably, elsewhere. This suggests that the holistic approach to landscape advocated in Chapter One is especially useful when dealing with modern humans and that it may be necessary to define cultural factors, like the use of shoes or anthropogenic modifications of the land surface, as parts of the landscape of equal importance to the natural components of land surface, vegetation and climate. An alternative would be to view human landscapes as comprising a 'natural' layer viewed and interacted with through a cultural filter.

This makes it seem as though any analysis of human landscapes and anatomy must logically be even more difficult and subject to more problems of complexity and confounding than the Kenyan baboon analysis already presented (Chapter Four), but in fact also offers a means of simplifying analyses. Specifically, if we incorporate both sociocultural and natural components of the environment into a single 'landscape', this suggests that human populations – who typically share much of their culture – have a certain coherence that baboon allotaxa, for instance, may lack. This means that for a preliminary analysis at least, treating the three major study samples of this thesis' dataset as hailing from separate landscapes may allow for some amelioration of the confounding between genetic history and landscape differences seen in Chapter Four. The Jebel Moyan sample, then, hails from both a separate genetic pool *and* a separate landscape (with a natural landscape rather like that of the Nile Valley region in south Sudan and cultural attributes which did not extend to paving or the use of restrictive footwear), while the two British Medieval samples share more of their genetic history and landscape – with both anthropogenic urban surfaces and footwear more common – and provide a means of assessing the role of small genetic distances and variation between groups from similar (though surely internally variable and non-identical) landscapes. Given that there is no logical reason here for assuming males and females of any specific group occupied different landscapes – too little is known of cultural and social roles – sexual dimorphism is not considered.

Non-Metric ('Character' Based) Variation

The discussion of method in Chapter Two noted that certain non-metric characters are known to differ between species and genera of extant primates, and between sub-specific (population) groups in modern humans. The first question this chapter deals with, therefore, is that of the relative frequency of characteristic non-metric traits in the study samples.

Non-Metric Differences Between Populations

Table 35 below summarises the frequencies of different non-metric in each of the three populations/groups – Jebel Moyan, Blackgate and Barbican – studied. Those variables for which there were no differences between groups were omitted, or where differences were extremely small and seemed likely to be down to a low frequency of unusual patterns are omitted from the table, bringing the original total of 39 non-metric variables in the dataset down to 18.

Table 35: summary of the differences in the frequencies of non-metric traits across the four human groups sampled. A cell with a single value indicates uniformity, 'slightly variable' a case where only a few specimens differ from the majority, and 'variable' one where the spread across categories is more even. Particularly variable *traits* (as opposed to populations) are highlighted.

Trait	**Jebel Moya**	**Blackgate**	**Barbican**
Talar LFE (lateral facet extension)	Slightly variable: 88% absent	Slightly variable: 98% absent	Absent
Talar AFN (articular facet number) – scores give percentages of single, single/conjoined, conjoined, conjoined/double and double facets respectively	42%, 22%, 32%, 2%, 2%	34%, 9.5%, 32%, 9.5%, 15%	28.6%, 6%, 36.8%, 0%, 28.6%
Talar CAF (curvature of the anterior facet)	Variable: 54% markedly convex	Variable: 47% markedly convex	Variable: 54% flat
Talar CMeF (curvature of the medial calcaneal facet)	Variable: 72% flat	Slightly variable: 91% flat	Slightly variable: 95% flat
Calcaneal AFS (articular facet shape) – as for the talar equivalent	57.2%, 10.2%, 12.2%, 6.2%, 14.2%	6%, 2%, 40%, 4%, 48%	8%, 0%, 48%, 0%, 44%
Calcaneal PT (peroneal tubercule)	Slightly variable: 81% present	Slightly variable: 89% present	Slightly variable: 93% present
Calcaneal LT (lateral tubercule)	Present	Present	Slightly variable: 98% present
Calcaneal CATF (curvature of anterior talar facet)	Slightly variable: 79% markedly concave	Variable: 54.1% flat	Variable: 51% markedly concave
Calcaneal CMTF (curvature of medial talar facet)	Variable: 73% flat	Variable: 72% flat	Slightly variable: 96% flat
Cuboid CMF (curvature of metatarsal facet)	Variable: 63% flat	Flat	Flat
Navicular CF (cuboid facet)	Variable: 74% absent	Variable: 51% absent	Variable: 48% absent
Navicular CMeF_A (curvature of medial cuneiform facet)	Slightly variable: 81% slightly convex	Slightly variable: 95% slightly convex	Slightly convex
Navicular CIF (curvature of intermediate cuneiform facet)	2x2, 27x3, 1x4, 1x5	5x2, 38x3	All 3
Navicular CLF (curvature of lateral cuneiform facet)	20x2, 11x3	20x2, 23x3	22x2, 22x3
Medial cuneiform CLF_A (curvature of lateral facet)	8x2, 17x3, 2x4	16x2, 24x3, 2x4	4x2, 44x3
Medial cuneiform CMeF_B (curvature of medial facet)	Slightly concave	Variable: 57% slightly concave, 43% markedly concave	Slightly concave
3rd metatarsal CLF_B (curvature of lateral facet)	Slightly variable: 83% flat	Slightly variable: 94% flat	Flat
5th metatarsal CMeF_D (curvature of medial facet)	Variable: 63% flat, 37% slightly concave	Slightly variable: 98% flat	Flat

The variables omitted include 11 for which there was complete uniformity across all populations (these predominantly represented features like the orientation of the distal facets of the metatarsals which were chosen to capture variation between species/genera) and 10 others for which there seemed only to be differences of one or two specimens. It is assumed that for these variables – OTT (talar os trigonum type), MTF (the presence of medial facets on the talar neck), CPF (the curvature of the posterior facet on the talus), CNA (the presence on the calcaneus of a facet for the navicular), CPTF (the curvature of the posterior talar facet on the calcaneus), PRR (cuboid plantar ridge robusticity), GW (cuboid peroneal groove width), CPF_B (the curvature of the first metatarsal proximal facet), ODF_A (the orientation of the third metatarsal distal facet) and CPF_D (the curvature of the fifth metatarsal proximal facet) – the small variations were due to a low prevalence of the 'unusual' trait and random differences in sample composition. This may also be the case for a couple of the characters which remain in Table 35, particularly where it is the smallest sample which is distinctive. For the variable LT, for instance, the smallest, variable 'other African' sample differs from the larger ones from other populations, but this may simply reflect a chance bias in the former.

Overall, then, we can see several non-metric variables which seem to show clear differences between the populations studied. There is apparently significant variation in the distribution of talocalcaneal facet shapes across the four samples, for instance, and some other features, primarily related to articular facet curvature, differ in specific populations. Overall, the relatively small sample sizes – around 50 specimens of each bone for each sample, and often fewer for the Jebel Moyan group, see Chapter Two – mean these differences are difficult to interpret by eye. Those traits accounted 'variable' in Table 35 were therefore subjected to Chi-squared tests of difference. Statistically significant relationships between study sample and non-metric trait expression (with p values under 0.01) were found for several variables, specifically talar AFN (p=0.001), calcaneal AFS (p=0.000), medial cuneiform CMeF_B (p=0.000) and fifth metatarsal CMeF_D (p=0.000); see Table 35 for definitions of abbreviations. This suggests that for these four variables at least there are significant differences between populations, with these being most marked between the Jebel Moyans and the two British samples (see Table 35). Interpreting these functionally is challenging as many of these traits are presumed to relate to random variation and genetic history. The variation in AFN and AFS, however, might relate to the mobility of the subtalar joint. The Jebel Moyan group has a far higher proportion of single or conjoined anteromedial facets on both talus and calcaneus, and thus might be expected to have more mobility at this joint – especially in an anteroposterior direction – than the two British samples which more commonly have two separate facets.

Metric Variation in the Human Foot

Metric variation in the bones of the human foot is most easily explored using multivariate data reduction techniques like principal components analysis (PCA) and discriminant functions analysis (DFA), and these methods are the mainstay of this work. PCA acts to summarise variation within a group or groups and is used here to look at overall variation in each bone, while DFAs are then used to identify the features which best discriminate the populations, so that these features' functionality and potential to inform us on landscape differences can be assessed. In all cases corrected (logged and with a Mosimann correction for isometric size) data are used, as described in Chapter Two. Logs are taken because (once again) a multiplicative model for the action of individual factors on morphology seems most likely, while isometric size correction is undertaken because intra-sample differences in size probably relate to nutrition and social status as well as landscape differences (Worthman, 1993) and these effects cannot be distinguished.

The Talus

A simple PCA on the talar dataset (which comprised thirteen variables, as the dimensions of the anterior and medial calcaneal facets were too sparse for inclusion – they would have reduced the number of available specimens for analysis to zero) identified two major principal components (PCs) that explained 73.2% and 9.3% total variation respectively. The first of these was strongly correlated (with coefficients over ±0.8) with all the original variables save posterior trochlear breadth (PTB, r=0.207). This would seem to be a residual size factor, picking out the fact that most variation in the talus, even after isometric size has been removed, is related (presumably allometrically) to the overall size of the bone. PC2, in contrast, was strongly correlated (r=0.946) only with PTB, suggesting that residual variation in this factor is the next most important component in the dataset. When scores on these factors were plotted graphically they did not act to separate populations (see Figure 82), and seemed to summarise overlapping variation within groups.

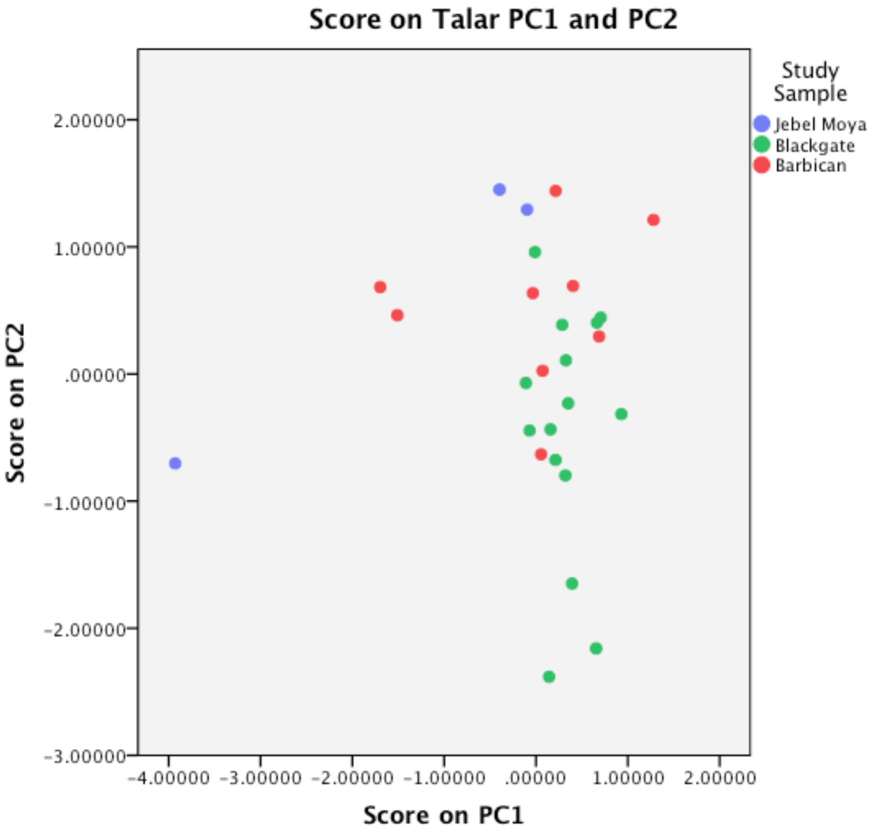


Figure 82: scatterplot of the scores on talar principal components one and two, showing the lack of separation between study samples on these axes.

As this figure shows, although there is some partial separation of groups on PC2 – with almost all the specimens that scored negatively from Blackgate, for instance – there is considerable overlap among all three groups. There is a clear outlier on PC1 in the form of a single particularly small specimen (in the far left), although this – like the partial separation noted above – might be the result of small sample sizes, particularly for Jebel Moya which is represented by just three specimens. There are differences in the average scores for each sample on each component (see Figure 83 and Figure 84), though still considerable overlap in the ranges spanned by each group.

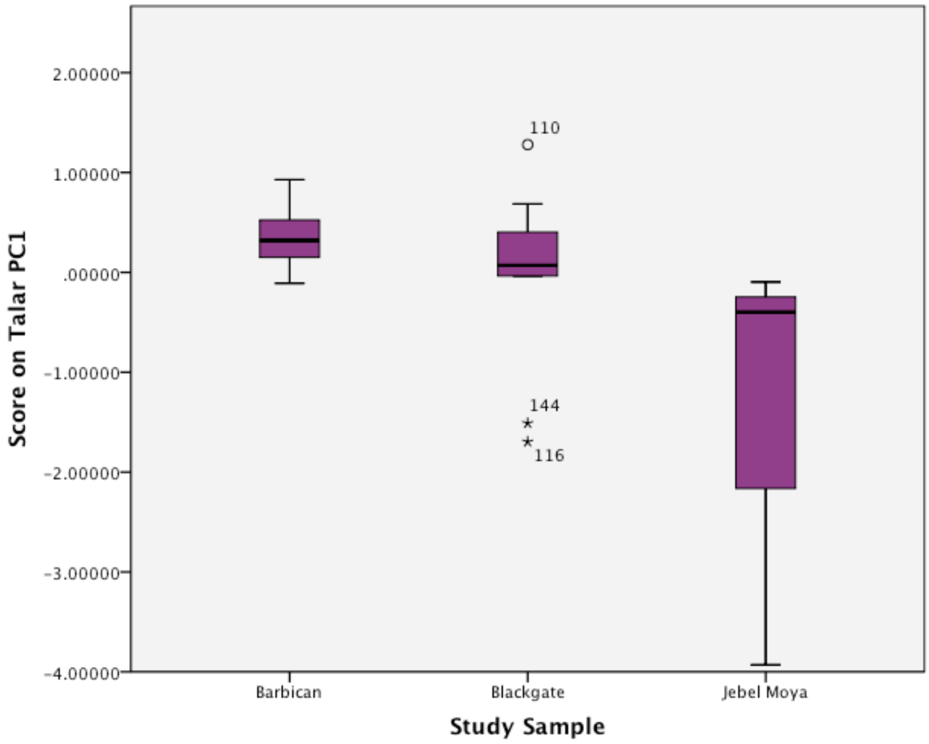


Figure 83: boxplot showing the scores for each study sample on the first talar principal component.

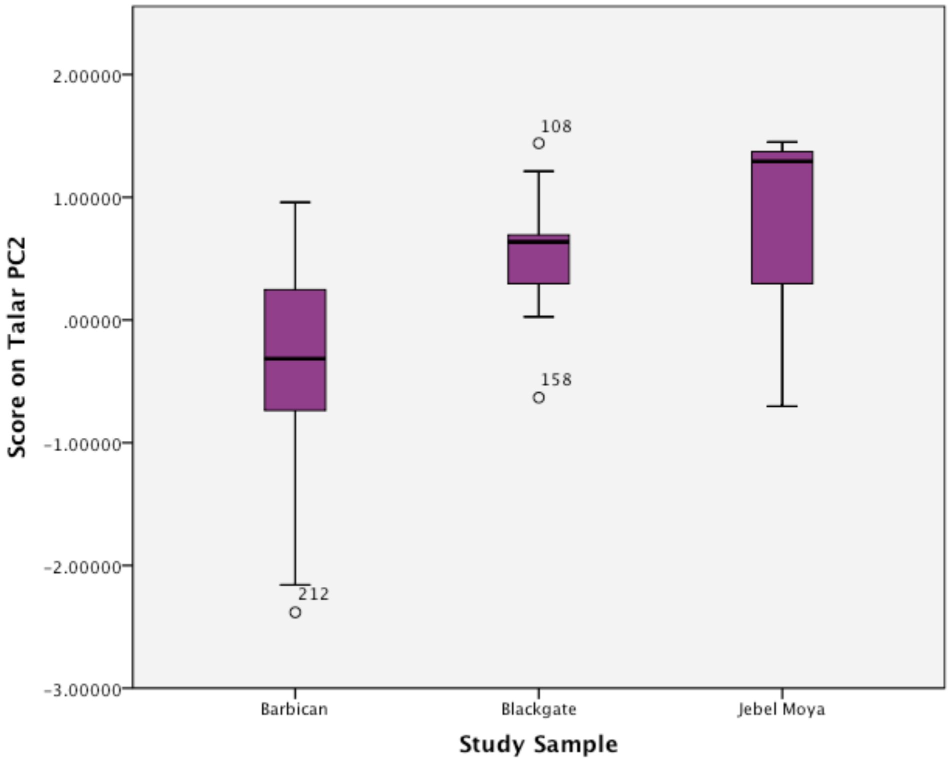


Figure 84: boxplot showing the scores for each study sample on the second talar principal component.

The overlap is greater for PC2 than for PC1, though there are clear differences in *average* score for each sample for both variables. A Kruskal-Wallis test (chosen because scores were not normally distributed within samples) suggested that the differences were significant at the p<0.05 level for both PC1 (p=0.039) and PC2 (p=0.024). For PC1 there were significant differences between the Jebel Moya and Barbican samples, and for PC2 between the Blackgate and Barbican samples.

A stepwise DFA of the same data, however, was able to correctly classify 77.9% of the cases included using two discriminant functions (DFs) based on the variables MLH (the maximum lateral height of the talar trochlea), PTB, PFL (posterior calcaneal facet length) and MB (maximum talar breadth). The resulting separation of the groups concerned can be seen in Figure 85.

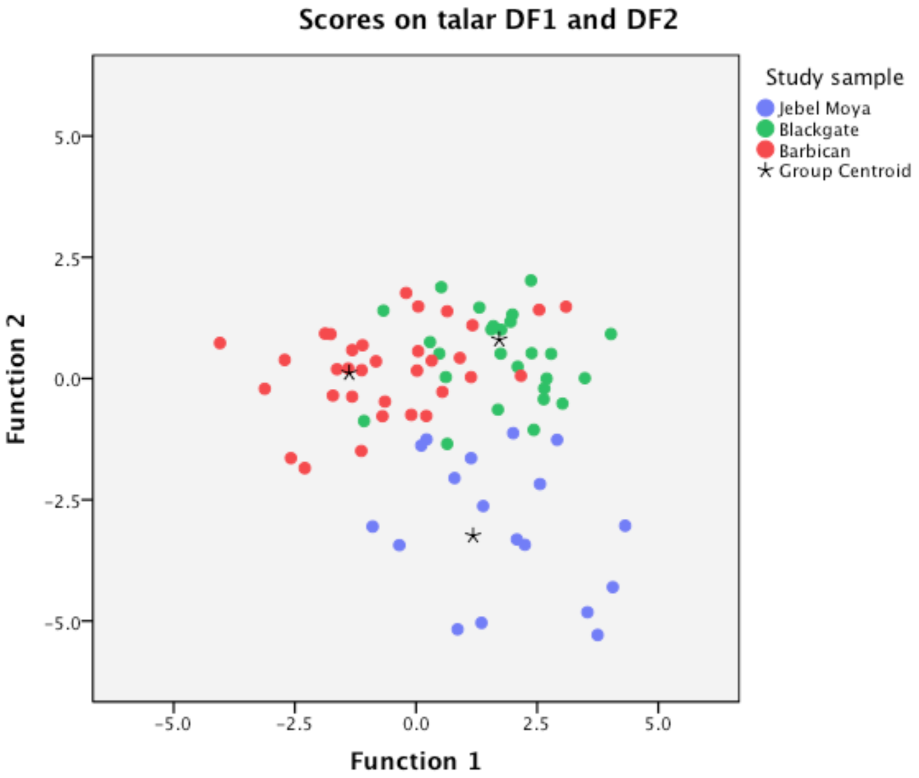


Figure 85: scatterplot of the scores on talar discriminant functions one and two, showing the separation between samples achieved by this analysis.

DF2, which discriminates Jebel Moyan specimens from the British samples, is strongly correlated with MLH (r = 0.778), which is also one of the main variables contributing to separation with a coefficient of 1.255. It is also dependent on PFL (coefficient -1.113) and PTB (coefficient 0.583), but not much linked to MB. DF1, in contrast, is not strongly correlated with any original variables and uses all four predictor variables with coefficients of -1.101 for MLH, 1.469 for PTB, 1.845 for MB and -1.972 for PFL. It acts to partially separate Barbican and Blackgate samples, on the basis of very small overall differences (hence the lack of correlations with the original variables). It is worth noting that all this analysis uses functions based on just 28 cases, of which 3 were from Jebel Moya, 10 from Blackgate and 15 from the Barbican, which means all interpretations are weaker than would be ideal. Interestingly, sample-specific correct classification rates were 77.8% for Jebel Moya, 88.5% for Blackgate and 69.7% for the Barbican sample, though the major overlap was between the two British samples with 10/17 misclassified specimens being Barbican individuals placed in Blackgate.

Interpreting these differences between populations in terms of their function is thus challenging. Differences on DF1, in particular, seem so small that a functional rationale – let alone one that characterises their landscape context – is implausible. The difference between Jebel Moyan and British samples in MLH and possibly also PFL, however, may be functionally relevant in that it relates to trochlear shape (specifically, wedging and orientation) which is known to be important in determining the direction and degree of movement at the ankle joint (Kidd et al., 1996). Unfortunately, given the complexity of this joint and its interactions with others (Elftman and Manter, 1935, Wood-Jones, 1944), specifying the effect of a relatively deeper lateral trochlea precisely is impossible, though it may relate to the stability of the fibular connection with the talus. The effect of a wider posterior facet might be to increase mobility in the subtalar joint (Elftman and Manter, 1935) and/or to subtly change the position of the foot in stance with regards to inversion/eversion which takes place at this joint. However, the subtalar facets are known to be variable both within and between human populations, as indicated in the analyses of non-metric facet configurations and in the literature (Finnegan, 1978, Aiello and Dean, 1990) and it is not clear whether this variation has any impact on function – it certainly seems that all variants survive throughout modern human history, suggesting that any functional implications are probably minor.

The Calcaneus

The calcaneal PCA identified only one major principal component, which explained 72.9% of overall variation. It was strongly correlated (with correlation coefficients over 0.7) with all the original variables, suggesting that it represents a residual size component. This PC is based on an extremely small complete dataset, however, (just 24 individuals, with 17 coming from the Barbican and just 5 and 2 from Blackgate and Jebel Moya respectively).

A stepwise DFA correctly classified just 55% of calcaneal specimens, using a single DF based on the variable PTAL (the length of the posterior talar articular facet). This DF is moderately or strongly correlated with all other variables and seems to be linked to overall size. It segregates Jebel Moyan specimens – with a centroid score of -3.75 – from the two British samples, with the Barbican sample centroid at 0.460 and the Blackgate one at -0.063. Misclassified specimens span all possible combinations, suggesting that the actual differences between groups are small and all three samples overlap in posterior facet length. This difference is thus not functionally interpretable.

The Cuboid

The cuboid PCA, in contrast, identified two major PCs which explained 56.9% and 10.6% of total variation respectively. As in the talar case, PC1 looks to be a residual size factor despite the Mosimann correction of the data, with strong correlations (r values over 0.7) with all original variables save short calcaneal facet dimension (SCF, r=0.682), lateral length (LL, r=0.605) and medial facet length (MFL_A, r=0.391). PC2 is linked to variation in LL (r=0.612) and MFL_A (r=.660). This suggests that there are two major factors in cuboid variation in these human samples: overall residual size – perhaps allometric size – and patterning in lateral length and medial facet length, which may be linked as one component. These components do not separate out different samples (Figure 86), and althought there are small differences in the mean value for each study sample (Figure 87 and Figure 88), these are not statistically significant according to the Kruskal-Wallis test.

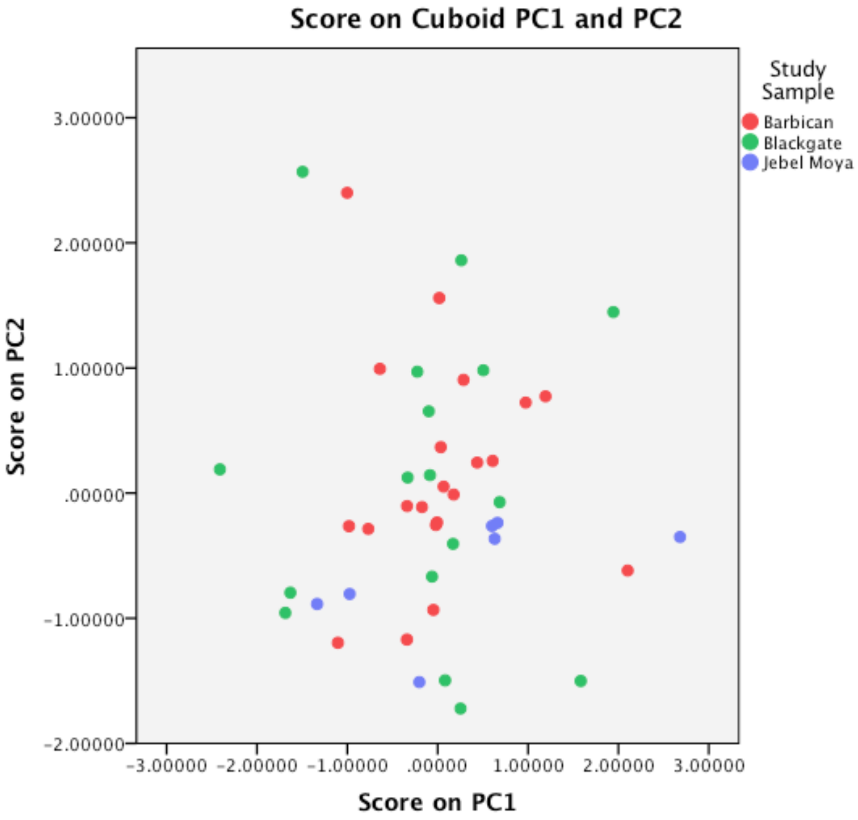


Figure 86: scatterplot of the scores on cuboid principal components one and two, showing the lack of separation between study samples on these axes.

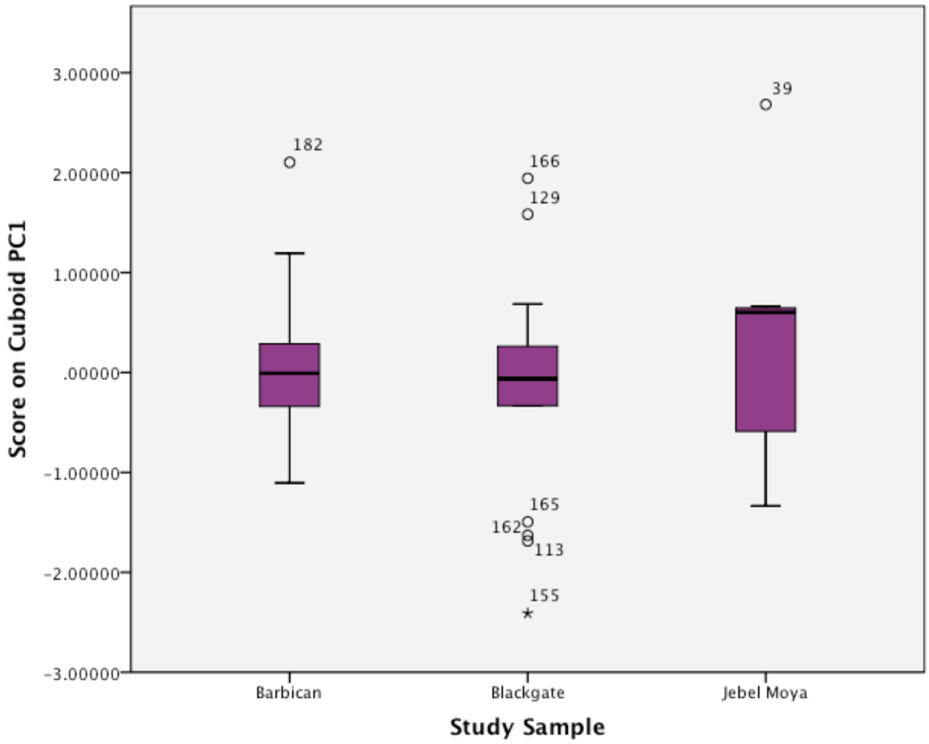


Figure 87: boxplot showing the scores for each study sample on the first cuboid principal component.

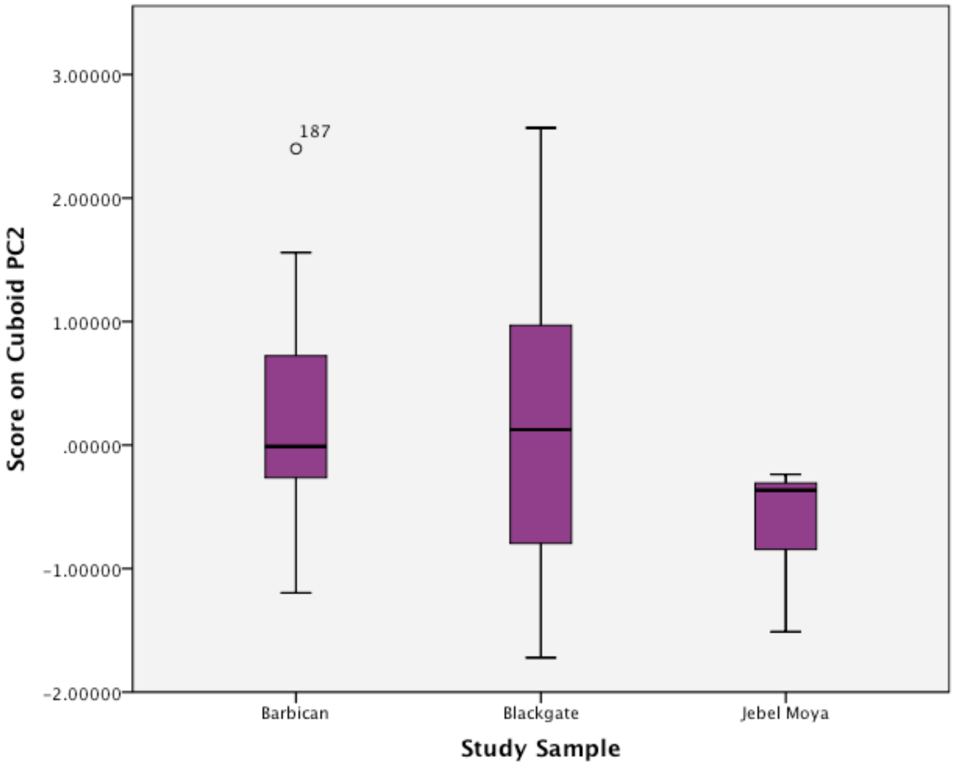


Figure 88: boxplot showing the scores for each study sample on the second cuboid principal component.

A stepwise DFA on the cuboid analysis correctly classified just 49.5% of cases, using two DFs based on the variables SMFD (the short metatarsal facet dimension) and MDL (maximum dorsal length). The resulting separation of the three samples can be seen in Figure 89.

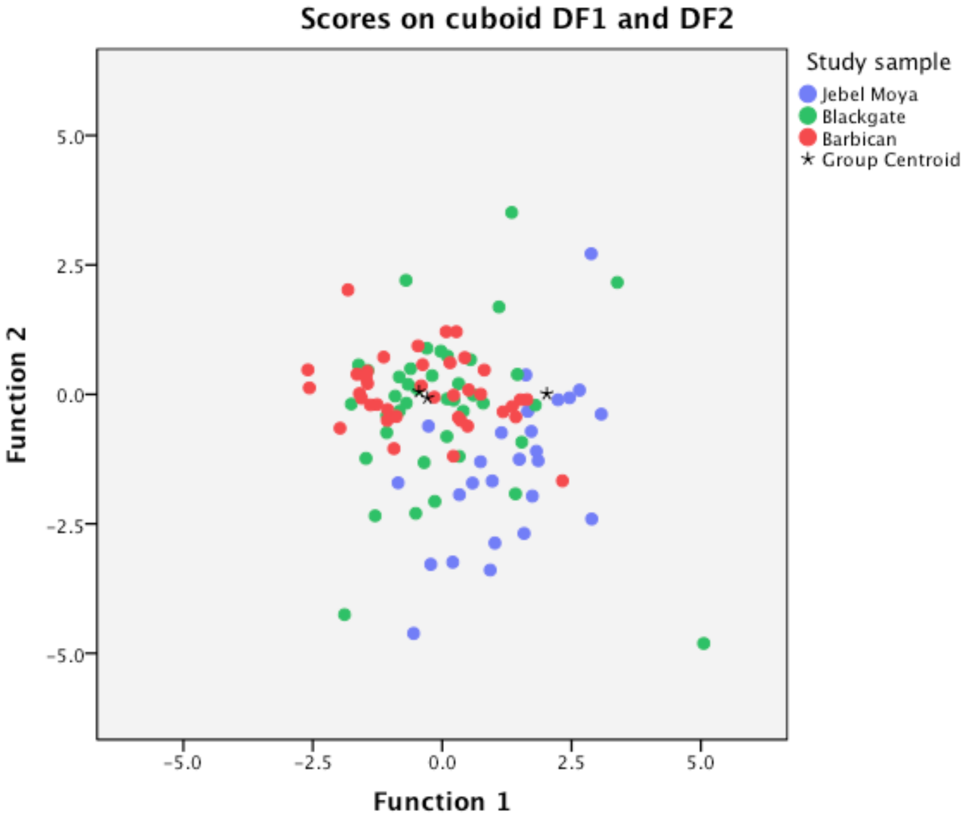


Figure 89: scatterplot of the scores on cuboid discriminant functions one and two, showing the separation between samples achieved by this analysis.

DF1, which acts to separate the Jebel Moyan sample from the two British groups, is linked to SMFD (r = 0.626), and is calculated based on both SMFD (coefficient = 1.288) and MDL (coefficient = -1.022). DF2 is correlated with all original variables with r values over 0.5 except in the case of medial facet length (MFL_A, r = 0.361). Thus this seems to be a residual size factor, and acts to very slightly separate Blackgate and Barbican samples, the former of which scores slightly negatively and the latter slightly positively. The overall difference, however, is tiny, and this is reflected in the classification values by sample: over 60% of Jebel Moyan specimens were correctly classified, compared to around 30% of Blackgate specimens and some 50% of Barbican specimens. DF1 is also a composite of SMFD (coefficient = 0.248) and MDL (coefficient = 0.821).

Interpreting these differences – which essentially reflect the fact that Jebel Moyan specimens have a slightly wider metatarsal facet of the cuboid than do British ones – is complex. The size of this metatarsal facet reflects the robusticity of the fourth and fifth metatarsals and may be functionally relevant, in that it affects the stability of the latitudinal arch of the foot and the range of movement possible at the midtarsal joint (Proctor, 2010). Comparative studies of the nonhuman apes suggest that human metatarsal bases are characteristically narrower, reflecting a closer packing of this joint and higher stability/reduced mobility at these joints (Proctor, 2010), while interpopulation studies of *Homo sapiens* suggest that habitually shod specimens – at least those wearing restrictive footwear – show more gracile metatarsals than barefoot walkers (Trinkaus, 2005, Trinkaus and Shang, 2008). This difference, then, would seem to be linked to the higher incidence of restrictive footwear and anthropogenically modified land surfaces in the landscapes of the British humans than those of the Jebel Moyans, although again this might be epigenetic (developmental) or evolutionary and there may be a random or historical component as well as the functional change. It is impossible to say using these data whether the differences in relative size of the cuboid might be linked with these differences in joint stability and metatarsal robusticity.

The Navicular

The navicular PCA identified two major PCs that explained 60.6% and 12.5% of total variation respectively. Once again, PC1 seems to be a residual size factor, with correlations over 0.7 with all original variables save MND (maximum navicular depth, r = 0.611) and TP (tuberosity projection, r = 0.577). PC2 is linked to variation in precisely these two variables, with a correlation of 0.601 with MND and one of 0.685 with TP. Other variables are only weakly correlated with this component. This suggests that there is a residual size component that dominates variation in the navicular among these three samples, with additional patterning relating to independent variation in the maximum depth of the navicular and the projection of the tuberosity from the body of the bone. The two PCs do not act to separate the samples studied (see Figure 90).

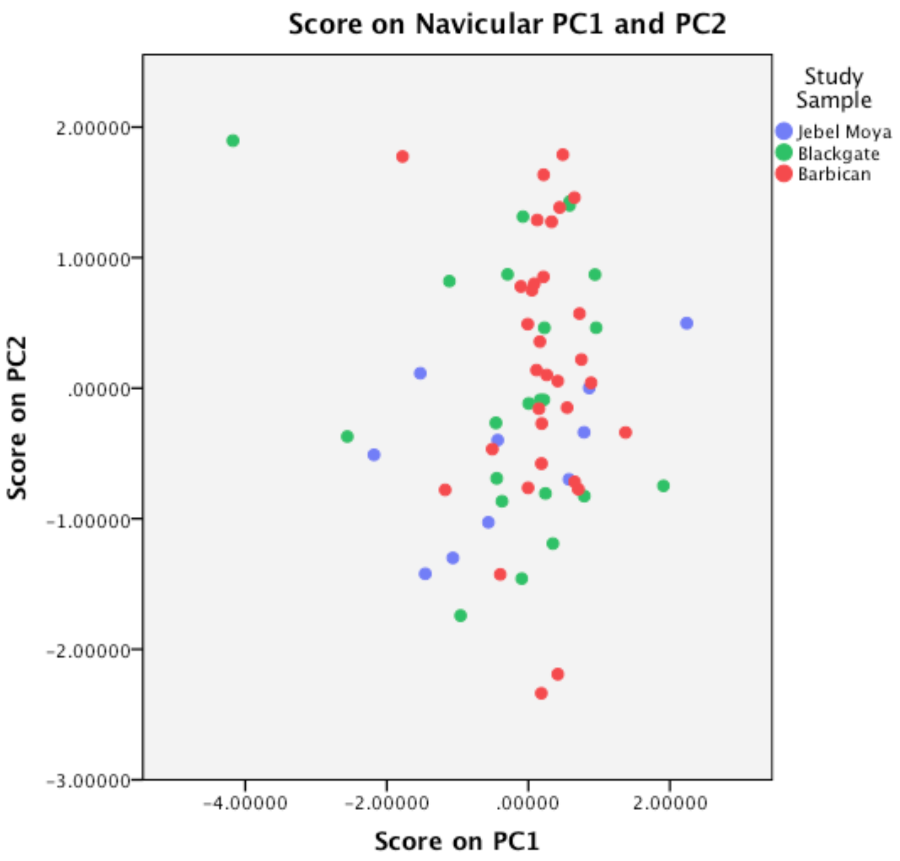


Figure 90: scatterplot of the scores on navicular principal components one and two, showing the lack of separation between study samples on these axes.

The differences between groups again may be due to differing valid sample sizes – as in previous analyses, the Jebel Moya group is represented by relatively few specimens – but there are differences in mean values (Figure 91 and Figure 92). These differences are not statistically significant.

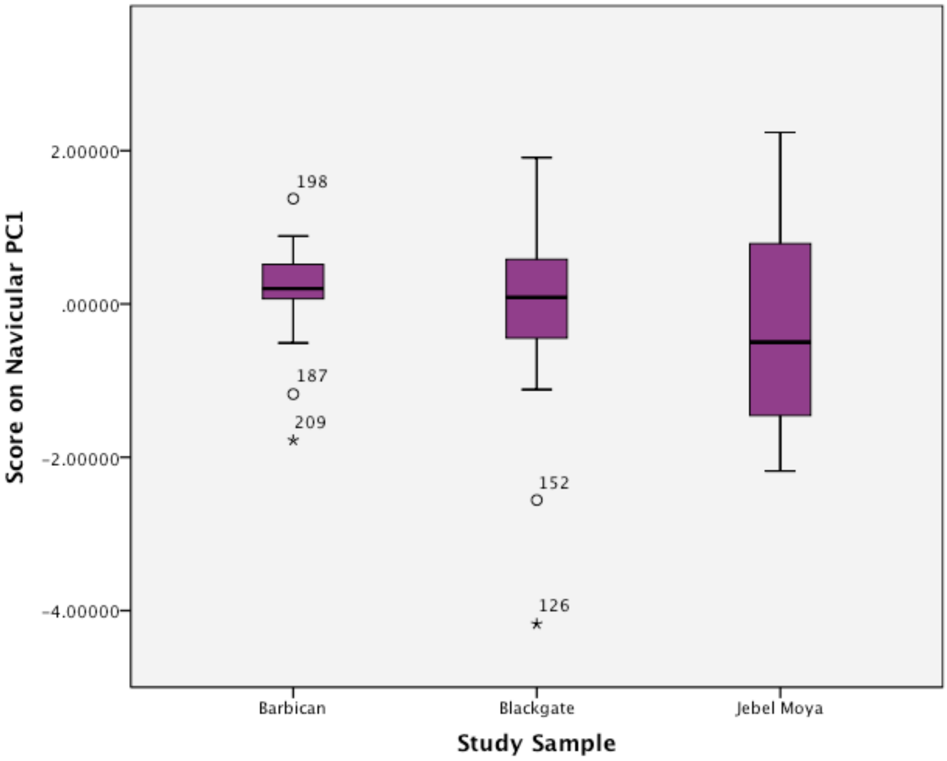


Figure 91: boxplot showing the scores for each study sample on the first navicular principal component.

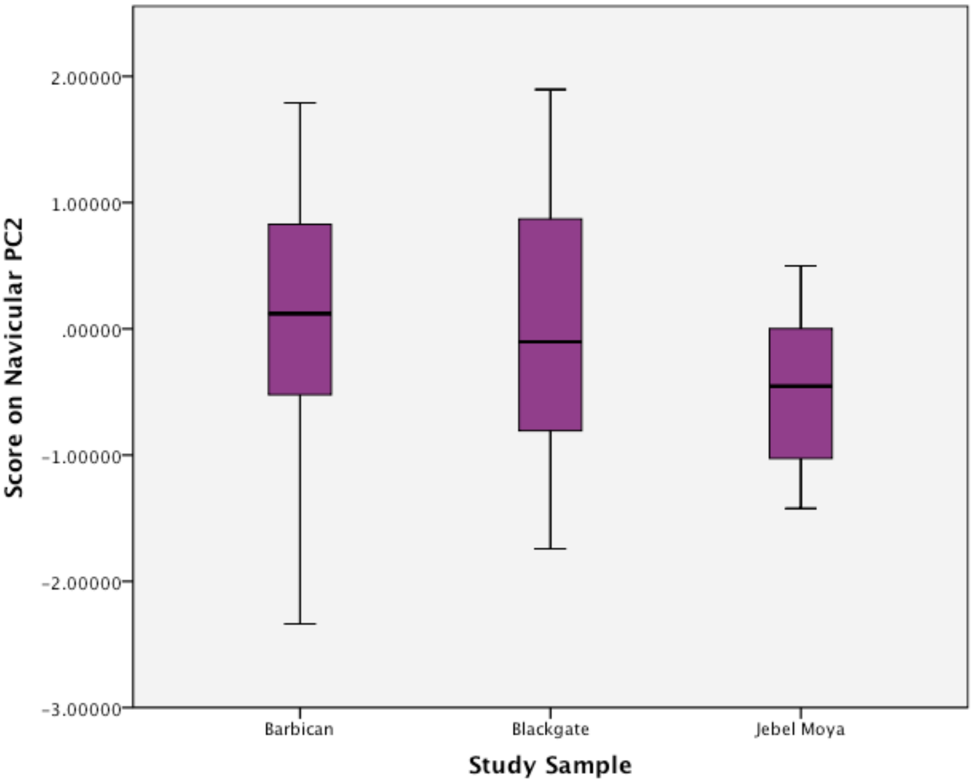


Figure 92: boxplot showing the scores for each study sample on the second navicular principal component.

A stepwise discriminant function of the navicular dataset correctly classified 62.7% of specimens, with the success rate again highest for the Jebel Moyan sample (80% correctly identified in contrast to 50% of Blackgate specimens and just 43% of Barbican specimens). The separation used two DFs based on four variables: MND, MaSCFD (the maximum short cuneiform facet dimension), STFD (the short talar facet dimension) and MNH (maximum navicular height). The resulting separation of samples is shown in Figure 93.

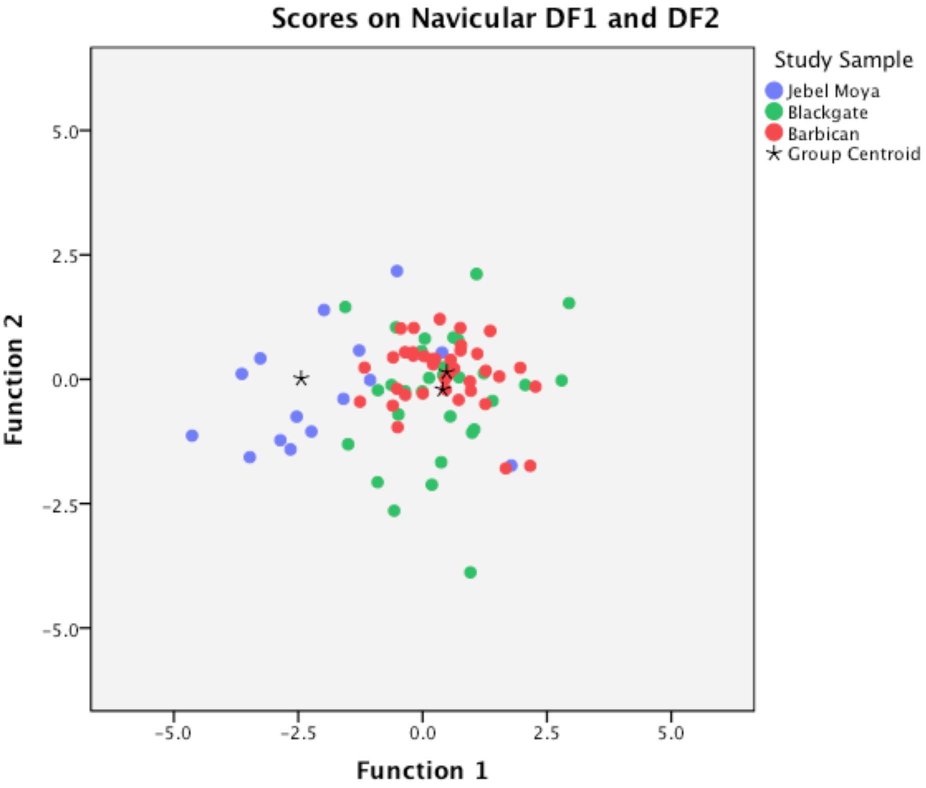


Figure 93: scatterplot of the scores on navicular discriminant functions one and two, showing the separation between samples achieved by this analysis.

DF1 acts to separate the Jebel Moyan group from the British samples and is linked to MND (r = 0.515). The score on DF1 is based on all four of the included variables however, with coefficients of 1.639 (STFD), -0.924 (MaSCFD), -1.092 (MNH) and 0.801 (MND). This suggests that Jebel Moyan specimens have shallower naviculae than the British specimens, as well as slightly shallower talar facets, higher navicular heights and higher maximum short cuneiform dimensions. DF2, in contrast, is correlated with all the original variables with r values over 0.5 and once again seems to be a residual size component that partially separates the two British groups (though with minimal success).

For the navicular, then, it is possible that there is an *overall* shape difference between the British and Jebel Moyan samples that relates to the latter having a bone which is deep and short while the former displays the opposite pattern (low MND, high MNH). Interpreting this as anything other than the product of a complex interplay between bones which has modified the overall shape and size of different components is difficult, especially in light of the fact that it is also linked to variation in facet sizes. The facet variations may be linked to mobility at the talonavicular and naviculocuneiform joints, but a crucial piece of information on the latter component is missing: specifically, where in the cuneiform facet the point of maximum short dimension size is located, without which it is impossible to identify which cuneiform(s) might be affected. In short, and given the still relatively low overall classification success rates, it is probable that this pattern is a complex – potentially emergent – upshot of a combination of factors and its implications for foot function cannot be reliably determined.

The Medial Cuneiform

The medial cuneiform PCA identified three major principal components explaining 48.8%, 13.4% and 10.2% of total variation respectively. PC1 is a residual size factor, with correlations over 0.5 with all original variables save LFL_A (lateral facet length, r = 0.454) and LFD (lateral facet depth, r = 0.377). PC2 shows a strong correlation with just one variable, LFL_A (r = 0.684) and PC3 with LFD (r = 0.590) only. The differences between groups on PC1 are small and not statistically significant according to a Kruskal-Wallis test, but those on PC2 and PC3 are significant and partially separate out the different study samples (see Figure 94).

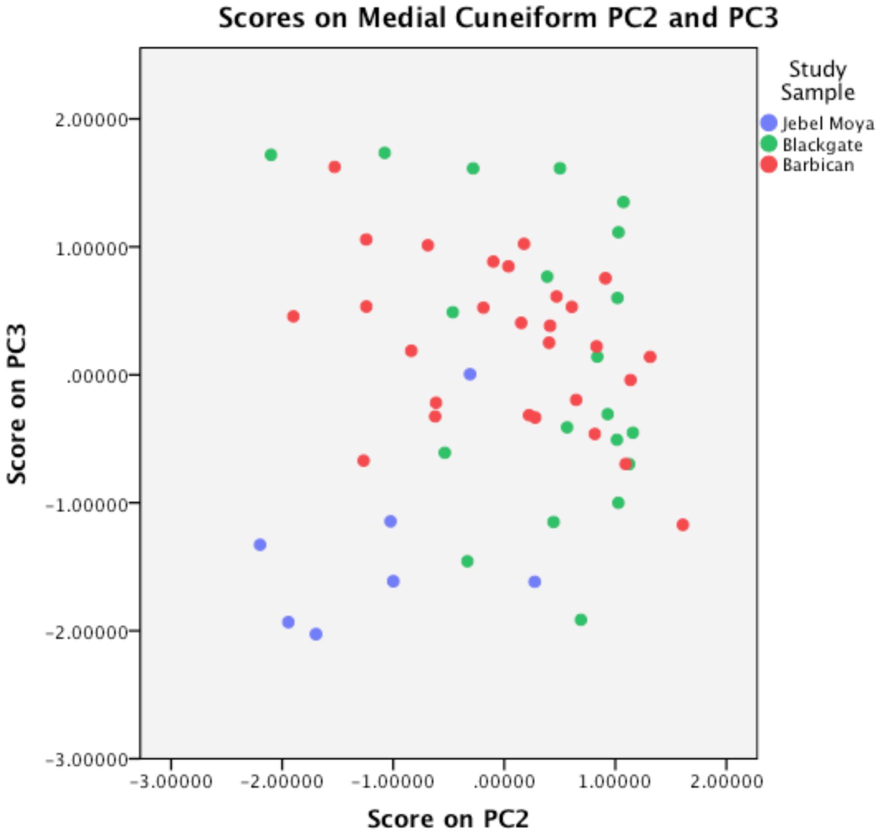


Figure 94: scatterplot of the scores on medial cuneiform principal components two and three, showing the partial separation between study samples on these axes.

There are statistically significant differences on PC2 between the Jebel Moya sample and both British groups (though not between Blackgate and Barbican samples, see Figure 95). The same is true for PC3 (see Figure 96).

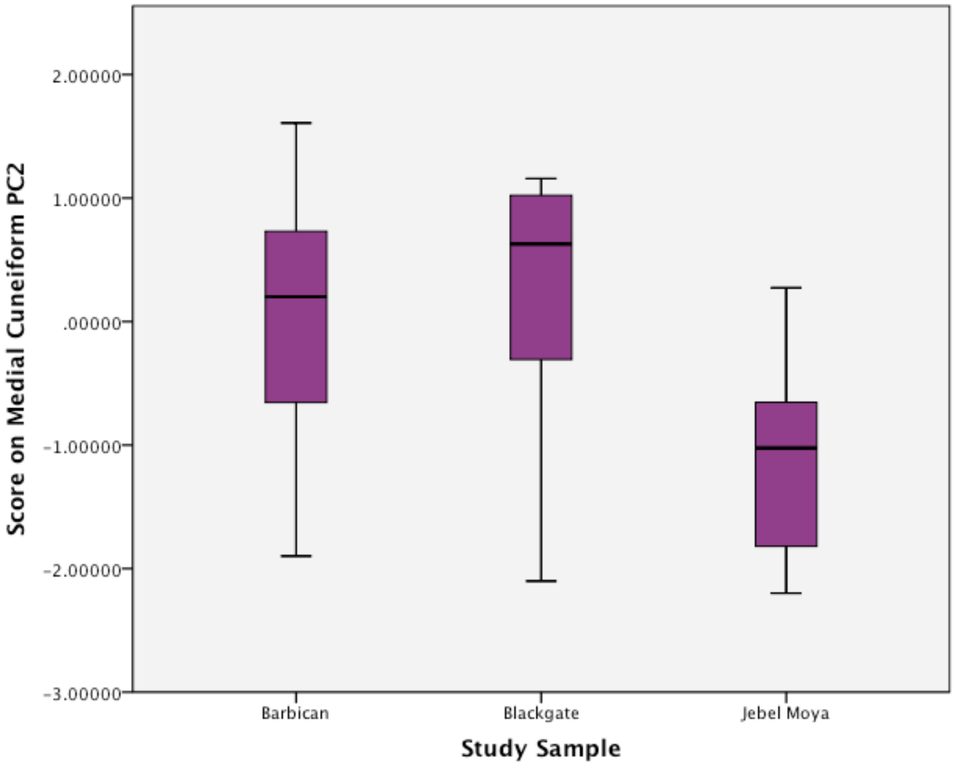


Figure 95: boxplot showing the scores for each study sample on the second medial cuneiform principal component.

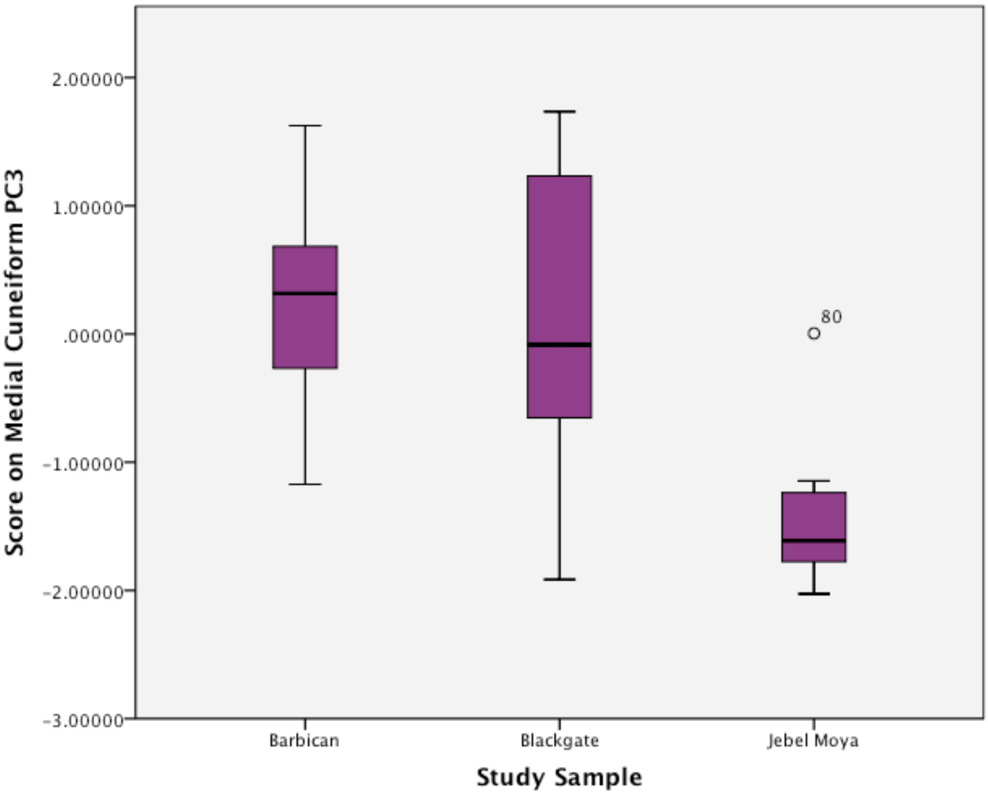


Figure 96: boxplot showing the scores for each study sample on the third medial cuneiform principal component.

A stepwise DFA on the medial cuneiform data correctly classifies 59.4% of the total sample using two DFs based on the variables LFD and PFH (posterior (navicular) facet height). DF1 acts to separate Jebel Moyan specimens from the British samples, though it also contributes something to separating Blackgate and Barbican specimens (see Figure 97), and the Jebel Moyan sample is again most often correctly identified, with 81.8% correct classifications compared to 55.6% of Blackgate specimens and 54.8% of Barbican specimens. DF1 is linked to LFD (r = 0.721) only and calculated on the basis of LFD (coefficient = 0.998) and PFH (coefficient = -0.746).

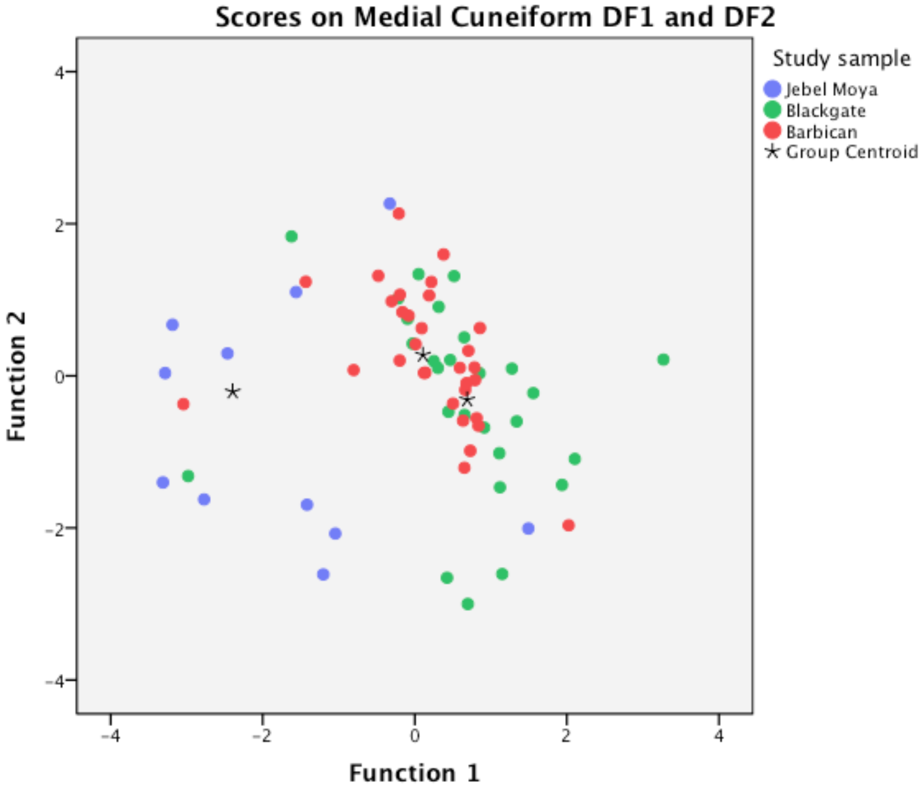


Figure 97: scatterplot of the scores on medial cuneiform discriminant functions one and two, showing the separation between samples achieved by this analysis.

This suggests that Jebel Moyan samples are characterised by the possession of a relatively shallow lateral facet and a somewhat taller posterior facet compared to other groups, although there is considerable overlap. DF2, in contrast, seems to be a residual – though weak – size factor, with correlations over 0.4 with all original variables save LFL_A (0.055), MPL_A (maximum plantar length, r = 0.352) and AFB_A (anterior (metatarsal) facet breadth, r = 0.351). The difference between groups is small, though not as tiny as for the navicular and cuboid, and may or may not have functional implications – if they are present, they are likely to result from complex interactions between factors, particularly given the lack of comparability in the variables which go into generating scores on DF2 – PFH and LFL_A – and those which are correlated with the function.

In terms of function, DF1 is the only factor likely to be interpretable and suggests that Jebel Moyan individuals have a taller posterior facet and shallower lateral facet than do those in the British samples. This is difficult to interpret. The posterior facet, of course, is involved in articulation with the navicular and this might indicate a more robust medial cuneiform (perhaps linked through knock-on effects to a more robust first metatarsal, although this remains to be seen) or greater movement at this joint for the African sample. The lateral facet articulates with the intermediate cuneiform, and is very variable. The difference may therefore be historical or random/genetic – or it may be linked to the stability of the foot arch that passes through these bones, with the unsupported foot of the (unshod) Jebel Moyans more stable than that of the shod, supported British samples, though this interpretation is speculative.

The First Metatarsal

The first metatarsal PCA identified just on major PC which explained 72.5% of total variation. It was apparently a residual size component, with correlations over 0.7 with all original variables and does not effectively separate out the major groups, instead capturing intrasample variation in overall size/robusticity.

The stepwise DFA of the same data, in contrast, correctly identified some 61.8% of specimens, including 88.2% Jebel Moyan, 43.3% Blackgate and 53.3% Barbican specimens. Once again, of the two DFs the first separated Jebel Moyans from British individuals while the second produced a very minor separation of the Blackgate and Barbican samples (Figure 98).

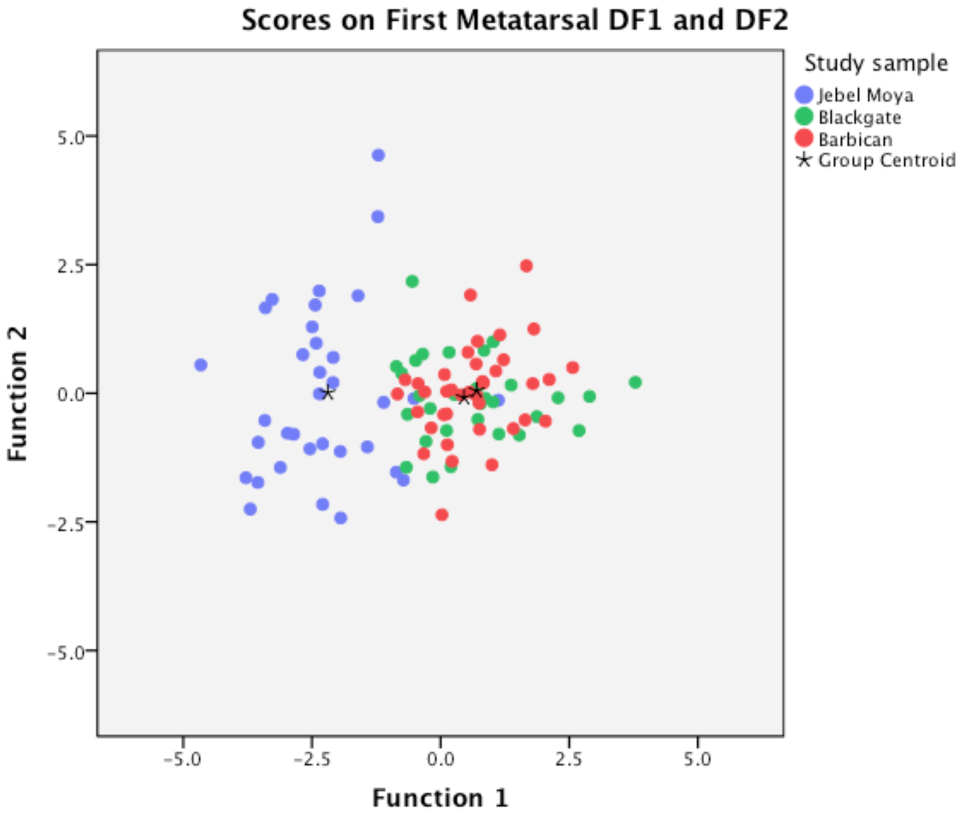


Figure 98: scatterplot of the scores on first metatarsal discriminant functions one and two, showing the separation between samples achieved by this analysis.

DF1 is linked most strongly to DFD (distal facet depth, though with a correlation of just 0.418) and is based on the variables DFD (coefficient 0.957), ML_A (maximum bone length, coefficient -1.773) and DFB (distal facet breadth, coefficient 1.031). This suggests that the Jebel Moyans, which score negatively on DF1, have relatively longer first metatarsals with smaller distal facets than do the British samples. DF2 is based on the same three variables (with coefficients of 0.109 with ML_A, -1.105 with DFD and 1.573 with DFB) but is correlated with all variables except ML_A (r = 0.251) and PAFB (r = 0.396) with coefficients over 0.4. This would seem to represent a robusticity measure, although further interpretation is impossible because the overall differences between samples on this variable are so small. It may be linked to PC1, which also seemed to represent 'size' or robusticity.

The functional relevance of a longer and distally less robust first metatarsal presumably relates to leverage (which would be higher in the Jebel Moyan foot) and the structure of the longitudinal arch which runs through this digit (Trinkaus, 2005, Trinkaus and Shang, 2008). The metatarsophalangeal joint would be smaller, perhaps indicating more stability at this joint in the Jebel Moyans. This could once again be related to the functional differences between locomotion in supportive footwear on man-made or modified surfaces and unshod on natural (presumably more variable) landscapes.

The Third Metatarsal

The third metatarsal PCA identified two major PCs that explained 65.5% and 11.1% of total variation respectively. PC1 was a residual size component, with correlations of over 0.7 with all original variables except LFL_B (lateral facet length, r = 0.391), while PC2 is linked only to LFL_B (r = 0.702) and MFD_B (medial facet depth, r = 0.518). Other than the fact that the highest robusticity scores were all from the Jebel Moyan sample (though all three samples overlapped significantly around the middle and bottom of the range), there was no separation by sample on these axes. There is, however, evidence of complex patterning as in many other bones (see Figure 99).

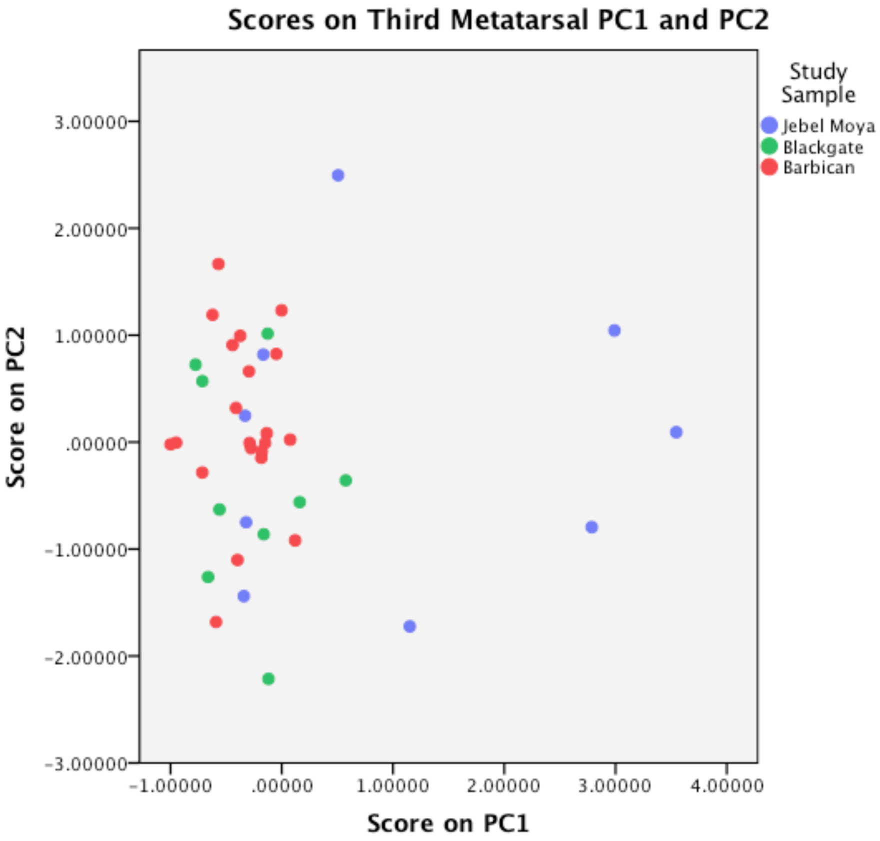


Figure 99: scatterplot of the scores on third metatarsal principal components one and two, showing the partial separation between study samples on these axes.

Complex patterning is particularly apparent in the distribution of scores on PC1 for the Jebel Moya sample, which is significant – especially compared with the range for Blackgate and the Barbican (Figure 100). Scores on PC2 overlap more (Figure 101).

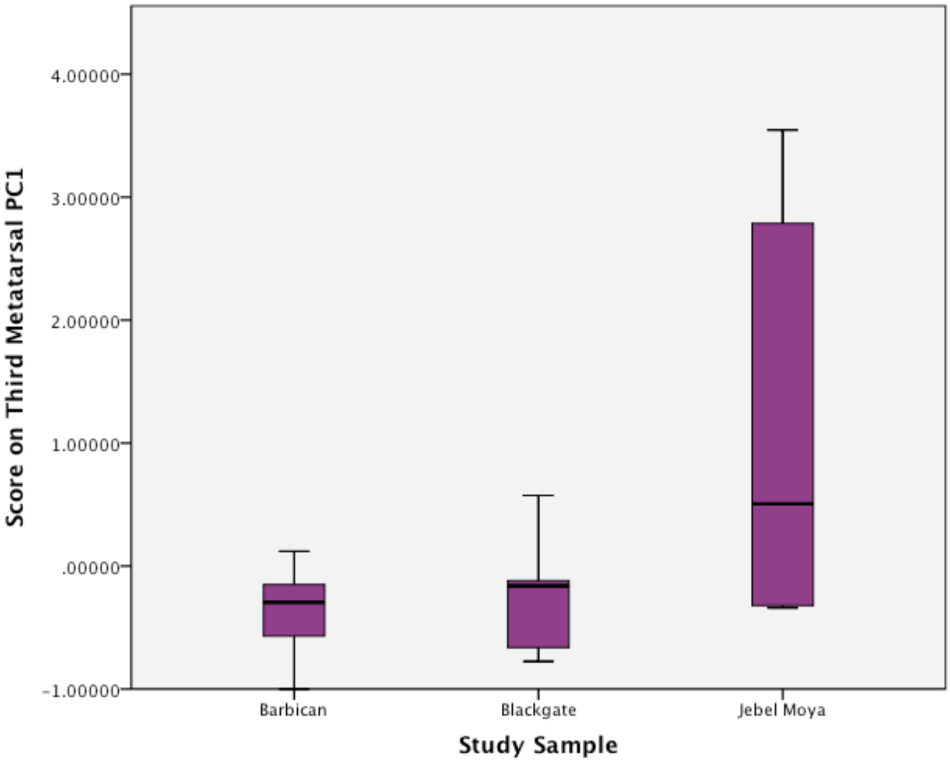


Figure 100: boxplot showing the scores for each study sample on the first principal component of the third metatarsal analysis.

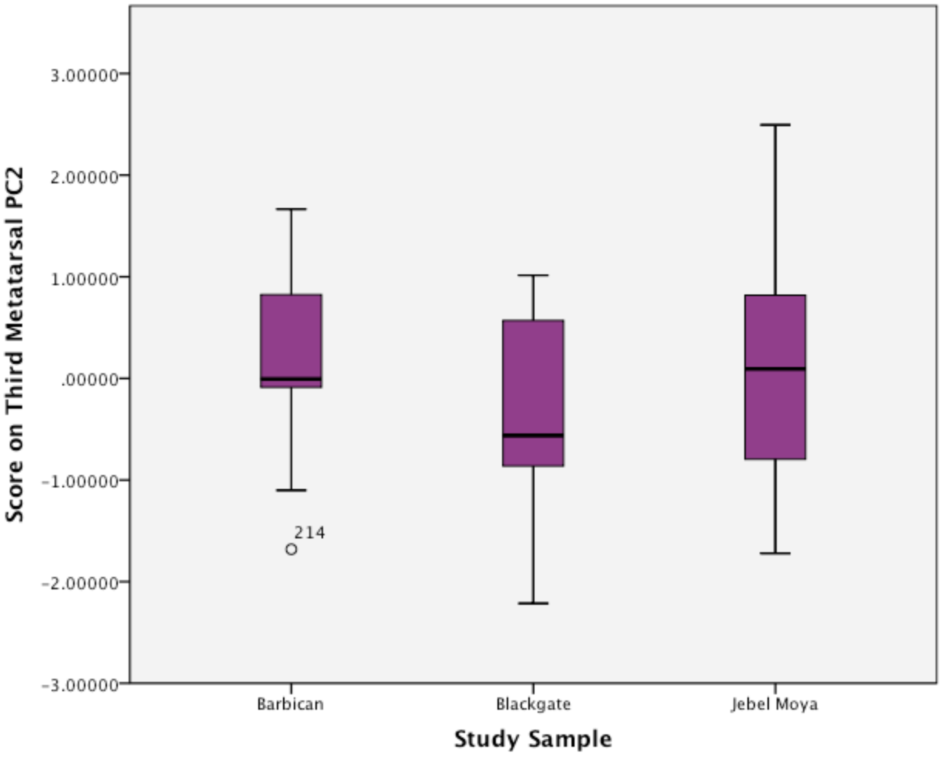


Figure 101: boxplot showing the scores for each study sample on the second principal component of the third metatarsal analysis.

The differences between samples on PC1 are statistically significant – particularly between the Jebel Moya and Barbican samples – while those on PC2 are not significant.

A stepwise DFA on the third metatarsal data correctly classified 69% of specimens, including 90% of individuals from Jebel Moya, 69.2% from Blackgate and 62.9% from the Barbican. The two DFs were based on four variables: ML_B (maximum bone length), DFD_A (distal facet depth), LFD_A (lateral facet depth) and MFL_B (medial facet length). The separation of groups is shown in Figure 102.

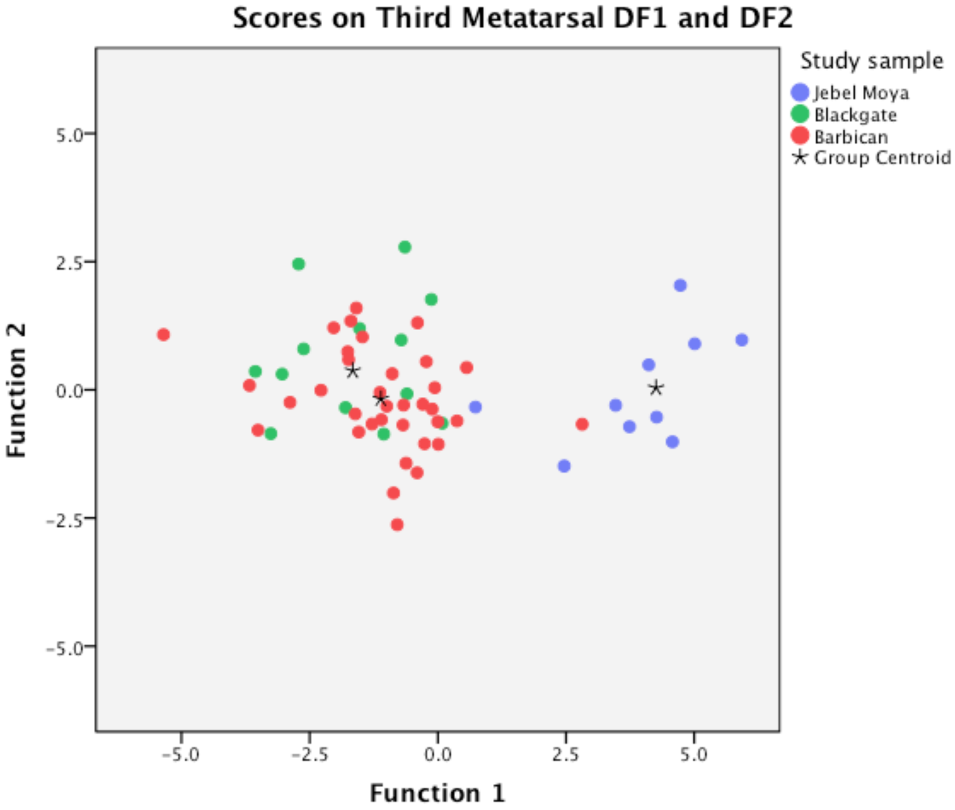


Figure 102: scatterplot of the scores on third metatarsal discriminant functions one and two, showing the separation between samples achieved by this analysis.

DF1 scores are based on all four variables used, with coefficients of 2.418 for ML_B, -1.688 for DFD_A, 0.704 for LFD_A and -0.922 for MFL_B. However, it shows only weak correlations (±0.46 and under) with all original variables, with the strongest links being to PAFL_A (proximal articular facet length, r = 0.458) and ML_B (r = 0.442). This function suggests that Jebel Moyan specimens have longer third metatarsals with shallower distal facets, longer lateral facets and shorter medial facets than do the British samples. It is worth noting, however, that relatively few Jebel Moyan specimens were complete enough for inclusion in this analysis, and this might be important in effecting such a neat separation of this group.

DF2, in contrast, is correlated with DFD_A (r = 0.743) and LFD_A (r = 0.516), two of the variables which contribute to generating the scores, but results in just a small separation of

Blackgate and Barbican specimens. This means that neither of these sets of differences is straightforwardly functionally interpretable: the differences between Jebel Moyan and British specimens may relate once again to leverage and the stability of the unsupported foot (Trinkaus, 2005) at the intermetatarsal and metatarsophalangeal joints, but are clearly complex, while the differences between British samples are objectively tiny and difficult to explain.

The Fifth Metatarsal

The final PCA of the fifth metatarsal dataset produced just one major principal component explaining 65.2% of total variation. This was a residual size factor, with correlations of 0.693 or higher with all original variables. It summarised intra- rather than intergroup variation and did not act to separate out any of the study samples.

The stepwise DFA of these data correctly classified 75.9% of specimens, including 91.4% from Jebel Moya, 41.7% from Blackgate and 71.9% from the Barbican. The two discriminant functions relied on the variables ML_C (maximum bone length), DFB_B (distal facet breadth) and DFD_B (distal facet depth), the same as was observed for the first metatarsal above. DF1 acts to separate the Jebel Moyans from the Blackgate and Barbican samples (see Figure 103) and contributes in a small way to separating the British groups from one another. It is linked most strongly to ML_C ($r = 0.355$), although this is a weak association, and is based on scores on ML_C (coefficient 1.727), DFD_B (coefficient -0.393) and DFB_B (coefficient -1.318).

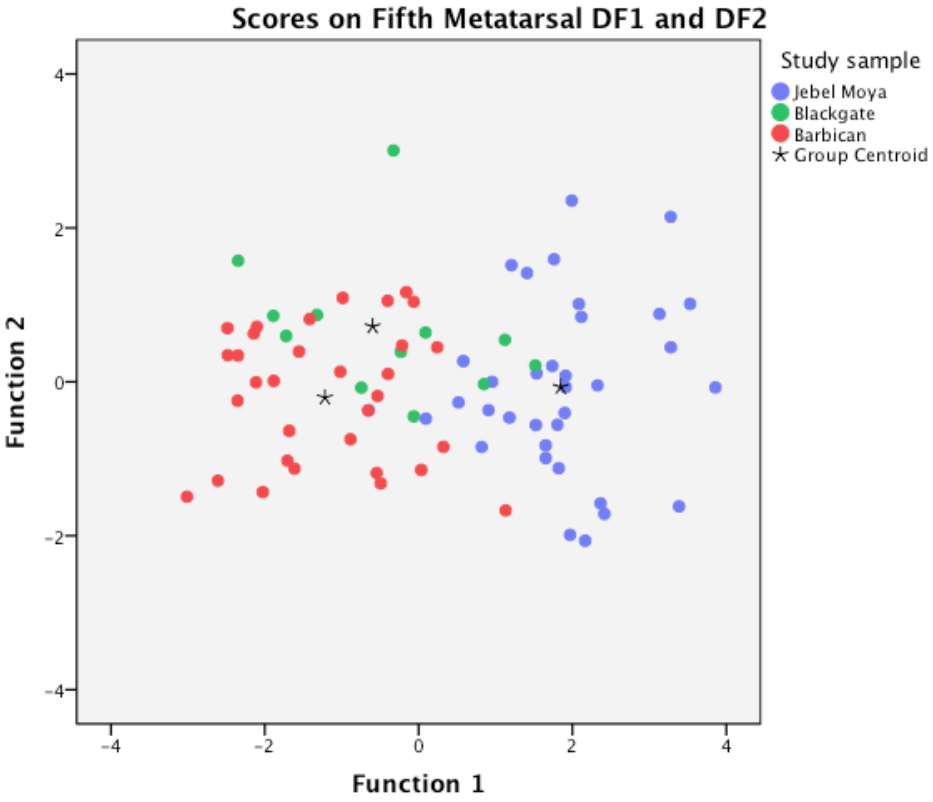


Figure 103: scatterplot of the scores on fifth metatarsal discriminant functions one and two, showing the separation between samples achieved by this analysis.

This is almost exactly the same pattern as was seen for the first metatarsal, where the Jebel Moyan group has a fifth metatarsal that is longer and distally less robust than the British specimens. DF2 is linked most strongly to DFD_B, though only with a correlation coefficient of 0.45, and might suggest that the Blackgate group (which scores positively) has a somewhat higher relative distal facet depth than breadth, while the Barbican group has a ratio of depth to breadth on this facet that is the same as that seen at Jebel Moya. This is difficult to interpret functionally, especially given the small overall size of the differences, but may be genetic or linked to (unknown) differences in the surfaces used.

The functional significance of a longer, less distally robust fifth metatarsal are presumably the same as those for the first metatarsal which showed the same pattern: better leverage in walking, a longer longitudinal arch and greater stability at the metatarsophalangeal joint. This is, once again, probably linked to footwear use (Trinkaus, 2005, Trinkaus and Shang, 2008).

DISCUSSION: HUMAN LANDSCAPES AND ANATOMY

This chapter, on human landscapes and foot bone anatomy, has demonstrated that the human-landscape system, like the baboon-landscape system, is complex. The analyses of gross landscape morphology in areas of high human density in Africa (many of which overlap with areas where many hominin sites are found or where baboons live) suggest that there is no consistent association between landscape and human settlement at this scale. People live in a range of landscapes, for reasons which range from the ecological and (possibly) evolutionary to the cultural and historical. For example, while some areas of high density occupation, in particular around Lake Victoria and the Ethiopian highlands, support King and Bailey's (2006) proposal that the physical landscape – and specifically areas of high roughness, with mosaic landscapes – are especially attractive to modern humans, others (like the Nile Valley) are particularly flat and are clearly attractive for other reasons, like the ready presence of water. This is reminiscent of the finding in Chapter Four that baboon allotaxa do not occupy consistently different landscapes to one another but instead range across a wide variety of conditions, employing different behavioural and historically imposed strategies to deal with local conditions at particular locations.

Small-scale studies of human landscapes, however, were not conducted here – primarily because the evidence from baboons and the greater cultural complexity and agency of modern *Homo sapiens*, combine to suggest that each case study would be unique and could not shed light on the specifics of ecological and co-evolutionary patterning. In particular, it seemed likely that certain cultural factors – for instance in the use of footwear and in anthropogenic modification of land surfaces – would need to be incorporated into definitions of 'landscape' before any meaningful interpretation of the links between landscape and anatomy might be conducted. This is reminiscent of the concepts developed in Chapter One, which recognised the role of cultural landscapes, behaviour and agency, but suggests that it will be harder to distinguish the cultural and natural in these systems than was previously expected. The use of footwear, for instance, obviously co-evolves with the surrounding (or underlying) cultural and natural landscape. This meant that simplification of landscape problems through a reduction in scale was implausible, as it would require extremely detailed information about culture, the landscape in a general sense, and the behaviour of the group concerned. It was impossible to obtain a skeletal sample – let alone two or three samples – for which this level of detail was available.

Instead, a different means of simplifying the human-landscape system was trialled. This involved identifying populations known to come from different landscapes – specifically, from African, predominantly 'natural' landscapes where restrictive footwear was not used and from two more similar British Medieval landscapes where footwear would have been more common but genetic history would not have been identical. Instead of characterising the landscapes more specifically in terms of altitude, roughness, vegetation and climate (as in Chapter Four) therefore, analyses were conducted that attempted to contrast these different study populations and then, via explorations of the functional implications of observed differences, to establish whether differences in landscape, defined broadly, were identifiable and quantifiable. In fact, almost every bone was capable of distinguishing the specimens from Jebel

Moya in the Sudan from those from Britain, and several of the patterns – for example, in the former's having longer, less distally robust and therefore more stable metatarsals than the latter – fitted well with existing knowledge of the differences between shod and unshod groups. There were fewer differences between the Blackgate and Barbican samples, and these were less often functionally relevant. In fact, all three groups could be distinguished to a certain extent on the basis of residual size variation, which may be indicative of allometric size patterns in the foot bones. These allometric residuals could be removed using, for instance, ratio or square root adjustments – presumably on top of the isometric size-adjustment technique applied early in this analysis, to completely adjust for size – but this would add yet another layer of complexity to the dataset and was ultimately rejected as the residual size differences were fairly easily identified and did not overshadow or swamp other (potentially functional) patterns.

The fact that the observed differences *could* be functionally related to landscape in the broad sense, however, does not imply that this must be the case. The patterns observed were clearly complex, and it is – once again – difficult to disentangle the effects of function (locomotion) from those of separate genetic histories, nutrition and similar factors. In several cases, for example, there were ambiguities in the interpretation of discriminant functions, in the impact of sample size on the observed separation of groups, or in the interaction of factors like genetic history, behaviour and evolution/development, many of which could be equifinal.

CONCLUSIONS

Despite the challenges this chapter raised in distinguishing the effects of cultural and natural landscapes (and in pinpointing the precise role of agency in human-landscape interactions), it was possible to draw certain specific conclusions, including that:

1. There is no single 'natural' landscape which is clearly more attractive to humans or to which humans are better suited (this goes against King and Bailey's suggestion that modern humans retain the ancestral preference for active landscapes). Instead, human distributions seem to be linked most clearly to urban accretion processes modified by social and cultural innovations, and the interactions between these different components of the broad natural-cultural landscape are highly complex;
2. Agency and culture thus seem to play a key role in determining how relationships between humans and their landscapes are structured, though evidence that humans are 'exempt' from biological or natural effects is limited. The initial location, and to some extent, later success of urban centres would be influenced by the resources and natural landscapes of the surrounding area, albeit viewed through a cultural 'filter';
3. In anatomy, it is possible to distinguish human populations from different landscapes on the basis of foot morphology alone – and, often, on the basis of single bones – although this is easier for samples which are more distant (biologically and in landscape and

culture) and can be difficult for samples of similar genetic history, like the Blackgate and Barbican samples studied here;

4. Both size and shape seemingly contribute to the separation of human samples, even where strict isometric effects have been partialled out and there are complex relationships between intra- and interpopulation patterns of variation, such that a summary of total variation in a dataset may not actually pick up key differences between groups. This suggests that there is conjoint patterning between foot morphology, genetic distance, landscape and location, but this is highly complex and often uninterpretable;
5. Those differences between samples that are interpretable may be linked to differences in broad landscape, particularly locomotor differences between groups living in highly anthropogenically modified areas and wearing restricted shoes and those not doing so, although the links are complex and interwoven with influences from other factors;
6. Taking the results of this chapter together with those from Chapter Four suggests that overall, a conceptual system which incorporates co-evolution and complexity and recognises the permeability of landscape and population barriers is important for all analyses of primate-landscape interaction, including those of humans, despite the latters' cultural complexity and the partial independence from natural landscape influences on their distribution observed in the study at the start of this chapter.

Obtaining more information on the precise role of landscapes in human evolution, therefore, requires the addition of further information. This could take the form of more detailed studies using culturally and behaviourally known skeletal samples, or it could incorporate other sources of evidence. In Chapter Four, a case study was introduced which contained a time component, which was useful in partially clarifying the relationship between baboon socioecology and landscape at Amboseli because it simplified the structure of possible cause-effect linkages. Although this was not sufficient in itself to resolve the complex baboon-landscape system in this case, our better knowledge of the human evolutionary trajectory – and of the broader morphological (soft-tissue) and comparative context of human evolution – suggests that an explicitly temporally oriented analysis might be informative. This is the subject of the next (and final) analytical chapter, which focuses on the evolutionary trajectory of the human foot at various scales and on actually testing the TLM in light of the findings.

Chapter Six: Time Depth and Human Evolutionary Landscapes

INTRODUCTION

The springboard for this study of primate-landscape systems was King and Bailey's (2006) tectonic landscape model (TLM) of human evolution. This was the first hypothesis about our ancestors' environments to explicitly consider spatial structure and the physical landscape, and the aim of this work as a whole is to test that proposition (see Chapter One). In initial discussions of the TLM's context, however, it was found that relatively little was known about the spatial structure of African landscapes and the ways these interact with living primates, and the decision was taken to explore these questions to generate a baseline understanding of primate interactions with their landscapes before attempting to return to evaluate the claims of the TLM specifically.

Chapter Three's analysis of extant African landscapes suggested that there was indeed spatial structure present in these habitats and that it should be possible to begin to distinguish the effects of different factors on the distribution of living primates. It also demonstrated that landscape patterning was perspective- (scale- and location-) dependent and complex (in the sense of ill-boundedness and logical incoherence raised in Chapter One); a full understanding of evolutionary landscapes cannot afford – as palaeoanthropology has done to date – to ignore a factor like topography. This ultimately suggested that explorations of landscape structures and their relationships with primate ecology/evolution *should* be possible, provided care was taken in research design and appropriate background information was obtained first.

Chapter Four therefore developed this background information, populating the same hierarchy of landscapes with *Papio* baboons and finding that, while this added complexity, it was still possible to identify relationships (if not always directionality in the sense of patterns of cause and effect) that linked baboon behaviour, ecology, anatomy and landscape. The results suggested that the spatial structure of landscapes, and the shape of the physical landscape particularly, were likely to be important to baboon ecology alongside climate and vegetation, and also raised the point that agency and culture might be expected to have a significant impact on hominin landscape use, as they certainly seem to affect other primate species which are not as cognitively sophisticated. In Chapter Five's analysis of modern *Homo sapiens*, however, it was discovered that, while sociocultural factors seem to be the dominant landscape influences on modern human distributions, it is still possible to separate populations from different landscapes on the basis of their anatomy and some 'natural' landscape effects – perhaps viewed through a cultural filter – still seemed probable even for biogeography.

In this final analytical chapter, therefore, we return to evaluate the TLM in light of these findings. So far, this thesis' analyses have been exploratory, but have suggested that specific evaluatory or hypothetico-deductive analyses should be possible, and may even be more informative if the relatively greater success of the Amboseli baboon case study in identifying possible cause-effect relationships than the other two is typical. The TLM gives rise to three corollaries which will be explored here (I hesitate to say 'tested' given that the chapters above have suggested that concrete answers to complex landscape questions are not usually possible). These are specifically that:

1. The earliest hominins were anatomically capable of accessing tectonic landscapes;
2. Exploiting these landscapes offered hominins an advantage over other taxa which were less well suited to them (whether these be prey species or predators);
3. A conceptual framework based on the use of tectonic landscapes can effectively explain the observed trajectory of hominin evolution and modern human anatomical and ecological characteristics;

These hypotheses offer the opportunity for investigations with greater time-depth and in a broader comparative context. Evaluating prediction one requires an evaluation of the anatomy and ecology of the earliest hominins and the panin-hominin last common ancestor (LCA). Moving to assumption two involves fitting these species into a broader context through comparisons with members of the carnivore and ungulate clades (respectively the most likely hominin predators and a key source of protein in later stages of our lineage's evolution). Finally, to explore the validity of the model more generally, this chapter moves to assumption three by constructing a theoretical framework for human evolution in a tectonic context – a theory called the 'complex topography hypothesis' – and employs information on modern human anatomy and ecology as well as palaeontological evidence to see if it works. Before any of this can be done, however, a characterisation of tectonic landscapes is required.

THE CHALLENGES OF TECTONIC LANDSCAPES

King and Bailey (2006) suggested that tectonic landscapes are characterised by *roughness* (that is the presence of broken, uneven terrain which is heterogeneous at various scales) and *mosaic habitats* in which a wide range of conditions (vegetation types, resources, ecosystems etc.) are found within a relatively small area. Each has implications for the species occupying these landscapes.

Rough Terrain

Examples of tectonically active 'rough' landscapes from South Africa (though similar topographies can be found elsewhere) can be seen in Figure 104, Figure 105 and Figure 106.

Figure 104: photograph showing the characteristic rough topography associated with tectonically active landscapes near Magalisberg in South Africa (where there are no hominin fossils due to soil acidity but hominins may have lived), copyright and courtesy Geoffrey King.

Figure 105: a second photograph showing the characteristic rough topography associated with tectonically active landscapes in South Africa, copyright and courtesy Geoffrey King. Note the human figure, for scale.

Figure 106: a third photograph showing the characteristic rough topography associated with tectonically active landscapes in South Africa, copyright and courtesy Geoffrey King. Again, a human figure gives an indication of scale. The roughness continues under the grass in the foreground.

Tectonic roughness, as these figures show, is not just a phenomenon visible on large scale (continental or regional) maps – it also produces features ranging from a few centimetres to metres or kilometres in size which any animals occupying these regions must cope with. Striding or running on such terrain is difficult. Instead, species on tectonic landscapes require a degree of climbing ability and adaptive flexibility to cope with either a specific type (scale) of roughness, which might change or shift as tectonic activity continues, or with a range of landscapes of different 3D structures. The precise structure of a given tectonic landscape depends upon factors like rock type, the age and pattern of tectonic activity, the nature of other environmental components – and particularly erosion rates and properties, as these figures show – and the geomorphological features produced. Some rough landscapes, for instance, comprise stacks and fields of large, blocky boulders and features like scarps and ridges (Figure 104); others have generally flat or undulating surfaces which are broken and uneven at smaller scales (Figure 105); and yet others combine the two with fields of smaller, uneven boulders carpeting larger features like hills, depressions and valleys (Figure 106). They share the fact that the surfaces available to animal locomotion on rough landscapes are highly variable in size, shape, orientation, stability and structural configuration.

The diverse surfaces making up tectonic landscapes make two major demands on the adaptations of their inhabitants. First, species will need to be *flexible*, able to adjust and adapt the positions of different body parts to suit the particular configuration of the surfaces on which they move. This would require flexible joints, particularly (but not exclusively) in the appendicular skeleton, and would probably imply a generalist limb structure with relatively high numbers of bones rather than a specialist structure with elements fused and modified to fit with a particular specialised style of locomotion. In addition, the variation in surface orientation and size on rough landscapes would favour an animal capable of balancing its body mass using various combinations of limbs (e.g. bipedally/tripedally/quadrupedally) and of using locomotor movements in combination. This may involve anatomical adaptations – for flexibility again, as well as strength, rigidity and effective balance – and/or behavioural and ecological strategies for making choices that fit better with the habitats and surfaces encountered.

Habitat Mosaics

King and Bailey (2006) focused primarily on the topographic implications of tectonic landscapes, but later papers by these authors (e.g. Bailey et al., 2011, Reynolds et al., 2011) also emphasised that these areas are home to *mosaic landscapes* "with a diversity of resources in close proximity, including plants and animals from both arid (C_4) and humid (C_3) environments" (Bailey et al., 2011, 275; typo corrected). These mosaics arise because the broken terrain impedes dispersal, gives rise to surface water, modifies local environments and constantly rejuvenates the land surface causing ecological succession and changes in conditions at specific points. Mosaics of this type are thought to be persistent elements of hominin habitats and may have been important in the co-existence of related species throughout the Plio-Pleistocene, as they offer a range of niches in a small area and reduce direct competition between taxa (O'Brien and Peters, 1999). Mosaics are often biodiverse and ecologically complex, although there is a complex relationship between species diversity and abundance and the relative size(s) and interconnections of landscape fragments (Pickett and Cadenasso, 1995, Turner, 2005). Two of the recently discovered early hominins – *Sahelanthropus tchadensis* (Vignaud et al., 2002) and *Orrorin tugenensis* (Pickford, 2006) – are thought to come from mosaic habitats, and similar conditions are apparent at many other sites throughout hominin history (Carrión et al., 2011, Winder, 2012).

Identifying the anatomical implications of mosaic landscapes is difficult, as by definition every mosaic combines different topographies, land forms, climates and ecosystems in different ways. The ecological implications are somewhat more apparent. In a mosaic landscape, a given area (e.g. a home range) will contain more different landscapes and a wider range of resources than a counterpart in a more homogeneous one. Each of these landscapes, however, will occupy a smaller area (for example, compare a subsection of Figure 21 over the Rift Valley system with a similar sized subarea from Figure 33). This means organisms from mosaic areas need to be ecologically flexible – able to exploit resources from various ecosystems or habitats – or able to live at low densities or in small populations that can specialise on a single habitat. Mosaics thus may be home to multiple small troops of a species occupying single ‘patches’ and only occasionally moving between them (for instance to mate), or to larger troops of organisms capable of adapting to variable conditions. Patchiness in habitat and resource distributions has various other implications, especially where taxa respond to patterns at different scales (which can have knock-on effects for community structure and evolution) and is thus part of a complex system (Wiens, 1976, Wiens, 1995, Barton et al., 1996). It is generally supposed, however, that too much patchiness can lead to local or global extinction as carrying capacities shrink and populations become isolated (Dytham, 1995). A more effective strategy, especially where mosaics are persistent features of the landscape rather than new phenomena to be accommodated, is to be a generalist capable of biological (dietary and locomotor) and cultural (cognitive or behavioural) flexibility. Baboons, for example, display different social organisations in differently patchy habitats (Barton et al., 1992, 1996) and are among the most successful African primates largely because of this flexibility.

PREDICTION ONE: EARLY HOMININS

For the tectonic landscape model (TLM) to be viable, it must have been possible for an early hominin to access tectonic landscapes. King and Bailey (2006) place the earliest use of tectonic landscapes very early in our history, suggesting that this might contribute to the evolution of bipedalism and implying that even the earliest hominin (immediately after the panin-hominin last common ancestor or LCA) possessed this capacity. This claim can be evaluated through an exploration of the adaptations of the LCA and succeeding early hominins for locomotion on rough terrain and ecological adaptation to mosaic habitats. It is worth noting that in this thesis the term ‘LCA’ is being used not to denote a hypothetical individual or even troop/population which was ancestral to the hominins and panins, but rather as shorthand for a morphological type, or morphospecies, from which those taxa descended.

The Nature of the LCA: Starting Points for Hominin Evolution

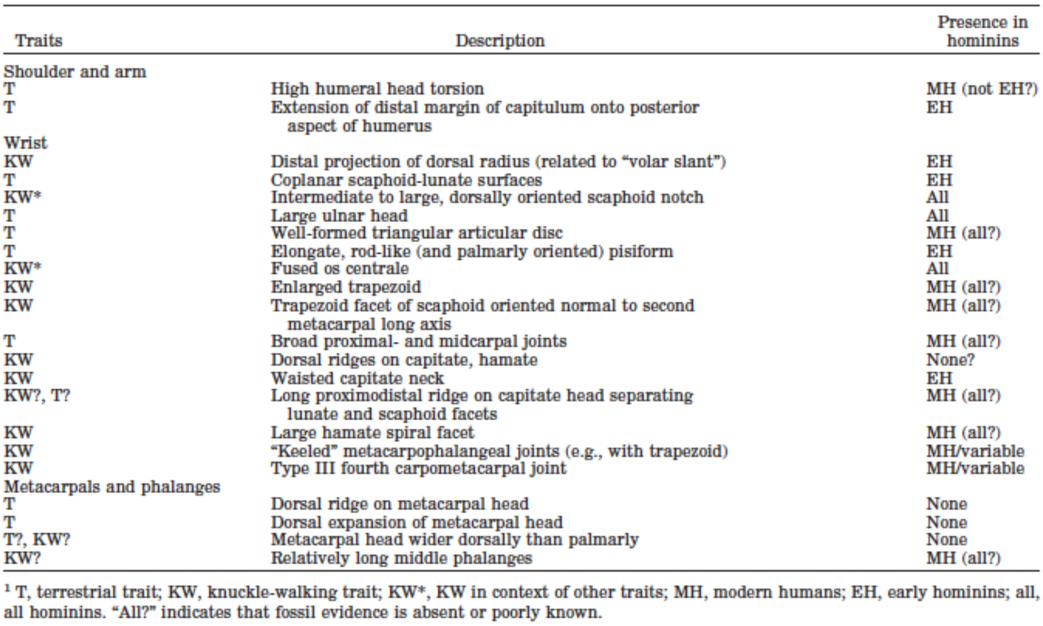
There are many theories about the LCA of hominins and panins, most of them based on comparative analyses of the extant apes (including humans) and current hypotheses of hominin evolutionary environments (as discussed briefly at the start of Chapter One). The most widely acknowledged of these fall into three groups: those that suggest the LCA was a knuckle-walker, (Richmond and Strait, 2000, Richmond et al., 2001); those that suggest a more generalised arboreal or terrestrial quadruped (Gebo, 1996, Sarmiento, 1998); and those who suggest as models various orthograde arboreal primates, whether described as suspensory (Tuttle, 1981), climbing (Prost, 1980) or an arboreal biped (Thorpe et al., 2007). Each suite of hypotheses is supported by observations of primate (and sometimes hominin) anatomy and fits with specific theories of the evolutionary context of human ancestors. While these theories are relevant to assumption three, however, they are less relevant to ascertaining the anatomical and ecological capacities of early hominins and will not be discussed in detail here.

Knuckle-Walking Ancestors

Humans' closest living relatives are the chimpanzees (*Pan troglodytes* and *P. paniscus*), followed by the gorillas (*G. gorilla* and *G. beringei*). The three genera shared a common ancestor some 6.2-8.4 Ma on the basis of genomic evidence (Chen and Li, 2001), and both *Pan* and *Gorilla* species are knuckle-walkers. This suggests that either these lineages have converged, or – more parsimoniously – their common ancestor was also a knuckle-walker. It is interesting that while convergent evolution under the Modern Synthesis is attributed entirely to the action of "repeatable matches of organism to environment" (Travis and Reznick, 2009, 109) – a phenomenon which earlier chapters' analyses suggest would be unlikely and probably apparent only at a single space-time scale in an interlocked hierarchy of causes and effects at multiple scales – under complex co-evolutionary models it may occur under a wider range of conditions. For these theories, there may be 'attractors' in anatomical/ecological space towards which trajectories move through the complex interactions of landscape, behaviour, historical constraint and agency. In a system where cognition and culture are important, moreover, we might expect to see species diverging and converging in many different ways, including via behavioural changes, while under a model of ecological change the colonisation of a new niche must be postulated to explain divergence.

The anatomical evidence in support of the knuckle-walking hypothesis comes mainly from the upper limb. Richmond et al. (2001) provide the summary below (Table 36):

Table 36: Richmond et al.'s (2001, table 3) list of characters supporting a terrestrial and specifically knuckle-walking ancestor for modern African apes, including humans.



Traits	Description	Presence in hominins
Shoulder and arm		
T	High humeral head torsion	MH (not EH?)
T	Extension of distal margin of capitulum onto posterior aspect of humerus	EH
Wrist		
KW	Distal projection of dorsal radius (related to "volar slant")	EH
T	Coplanar scaphoid-lunate surfaces	EH
KW*	Intermediate to large, dorsally oriented scaphoid notch	All
T	Large ulnar head	All
T	Well-formed triangular articular disc	MH (all?)
T	Elongate, rod-like (and palmarly oriented) pisiform	EH
KW*	Fused os centrale	All
KW	Enlarged trapezoid	MH (all?)
KW	Trapezoid facet of scaphoid oriented normal to second metacarpal long axis	MH (all?)
T	Broad proximal- and midcarpal joints	MH (all?)
KW	Dorsal ridges on capitate, hamate	None?
KW	Waisted capitate neck	EH
KW?, T?	Long proximodistal ridge on capitate head separating lunate and scaphoid facets	MH (all?)
KW	Large hamate spiral facet	MH (all?)
KW	"Keeled" metacarpophalangeal joints (e.g., with trapezoid)	MH/variable
KW	Type III fourth carpometacarpal joint	MH/variable
Metacarpals and phalanges		
T	Dorsal ridge on metacarpal head	None
T	Dorsal expansion of metacarpal head	None
T?, KW?	Metacarpal head wider dorsally than palmarly	None
KW?	Relatively long middle phalanges	MH (all?)

[1] T, terrestrial trait; KW, knuckle-walking trait; KW*, KW in context of other traits; MH, modern humans; EH, early hominins; all, all hominins. "All?" indicates that fossil evidence is absent or poorly known.

As this table shows, some of these traits have been identified in hominins as well as modern humans. The hominins also share traits related to heel-strike plantigrady with African apes which suggest a terrestrial ancestor although they cannot be used to distinguish knuckle-walking from other forms of terrestrial locomotion. The transition from knuckle-walking to upright locomotion is assumed to result from selective pressure for carrying and manual dexterity (Richmond et al., 2001), and may have been mediated by a period of tripedalism (Kelly, 2001).

Several challenges to the knuckle-walking hypothesis have been raised. First is the fact that many characteristics of the ulna, radius, humerus and wrist cited in Table 36 are indicators of terrestriality, not of knuckle-walking specifically. In the early hominins studied – which do not include *Orrorin*, *Ardipithecus* and *Sahelanthropus*, and may have been terrestrial for some 2Ma – these may be indicative of current lifestyles rather than the ancestral condition. Some other features are only found in modern humans, which implies that they must be either long-lasting relics that have been missed in fossils or that non-locomotor uses of the human limb maintain them, in which case they may not be indicative of knuckle-walking at all. Furthermore, even if we accept 'knuckle-walking' characters that are shared by humans, hominins and African apes – like the morphology of the distal radius (Richmond and Strait, 2000) –Kivell and colleagues (Kivell and Begun, 2007, Kivell and Schmitt, 2009) have shown that some such features are missing from extant knuckle-walkers, are possessed by species which do not knuckle-walk, and may be indicative of shared arboreal histories rather than terrestriality (see also Corruccini and McHenry, 2001). Some of these knuckle-walking traits are now of uncertain function. There is also evidence for the independent (convergent) evolution of knuckle-walking in *Sivapithecus* (Begun and Kivell, 2011) and evidence for differences among African apes which might suggest independent evolution of similar locomotor styles (Kivell and Schmitt, 2009). This suggests that while some of the anatomical features shared by nonhuman apes and human anatomy may be linked to a shared knuckle-walking ancestor (Richmond et al., 2001, Kelly, 2001), this has not yet been proven.

Quadrupedal or Generalised Primate Ancestors

Other models of the LCA propose quadrupedal ancestors. These theories originally arose when *Pan* and *Gorilla* were considered a clade to the exclusion of hominins and a more generalised primate could be considered ancestral to both groups, but have persisted by being linked to arguments of chimpanzee-gorilla convergence (see above). Gebo (1992, 1996) and Sarmiento (1998) present some of the most recent versions, citing the anatomy of the lower limb as evidence for at least one ancestral phase of quadrupedalism. Sarmiento's model has the ancestor of all African apes (including humans) as a 'cautious climber', which evolved through vertical climbing and semi-terrestrialism into a generalised terrestrial quadruped ranging across a variety of forest, woodland and bushland habitats (see Figure 107). He argues that *Pan* and *Gorilla* moved back into closed forest and specialised as knuckle-walkers, while the hominins specialised into open-country niches (Sarmiento, 1998).

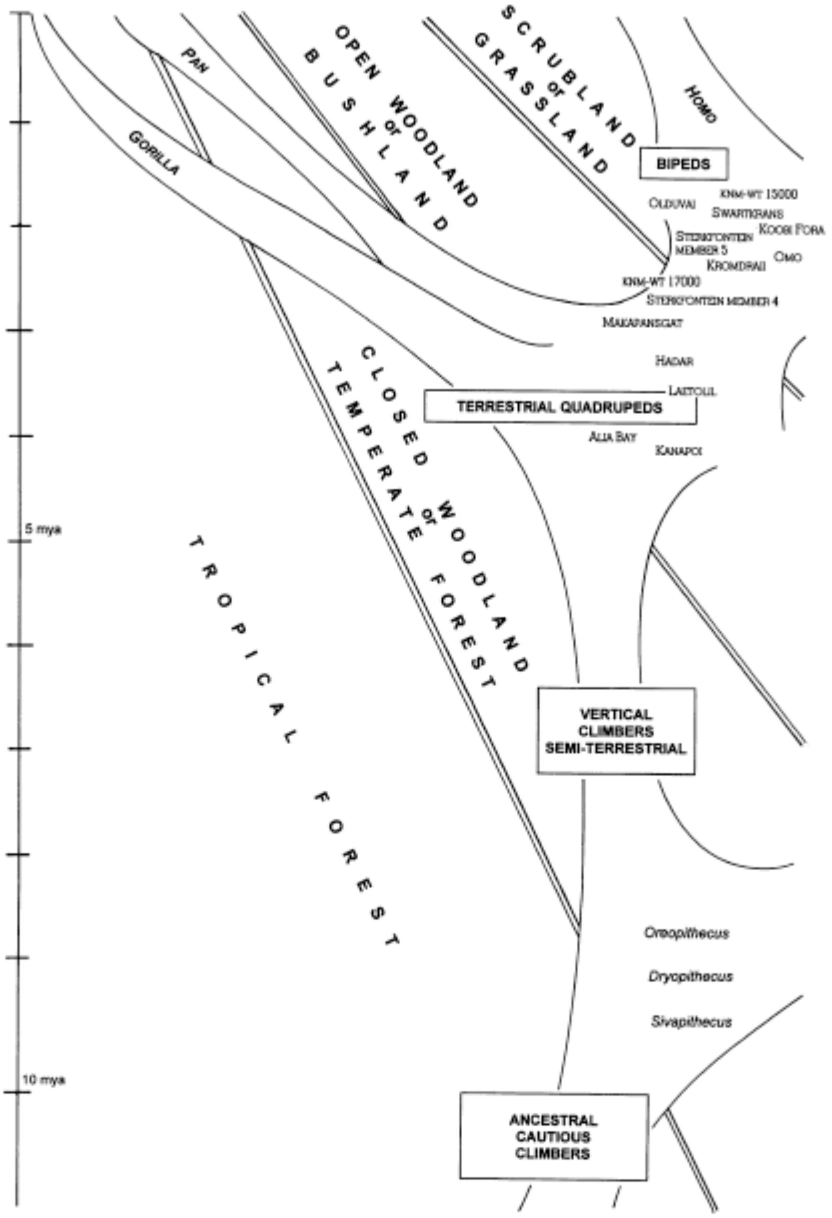


Figure 107: Sarmiento's multi-stage model for the divergence of *Pan* and *Gorilla* from the hominins via an extremely generalist adaptation to vertical climbing/semi-terrestriality and later more concrete terrestrial quadrupedalism; from Sarmiento (1998, figure 1).

This is a more complex model that invokes several evolutionary stages and fits with a range of vegetation and climate-based hypotheses of evolutionary environments (including the savannah hypothesis most obviously). It is based on an exhaustive analysis of primate hard- and soft-tissues, although the significance and occurrence of many of these individual features has been debated. The fact that it is not directly based on palaeoenvironmental evidence, however, is an advantage in that it implies that despite the fact that this model proposes an LCA at 3-4Ma, it may be flexible enough to adjust to currently accepted dates of 5-6Ma.

Gebo's model is similar, citing a trajectory which started with "an arboreal quadrupedal-climbing phase and proceeded through an orthograde, brachiating, forelimb-suspensory phase, which was in turn followed by arboreal and terrestrial quadrupedal phases prior to the advent of hominid bipedality" (Gebo, 1996, 55). It rests on analyses of primate substrate choice and locomotor styles as well as detailed morphological studies of characters shared between humans and a range of other taxa of known behaviour and ecology. Again, the characters listed have often been disputed as either convergent, shared by different locomotor types, or otherwise uninformative about the LCA (for instance, Richmond et al., 2001 suggests that fossil hominin digits are too long and curved to belong to terrestrial quadrupeds and that the shape of the trunk, the anterior placement of the vertebral column and the mobility of the shoulder joint are not quadrupedal features). Hypotheses of arboreal or terrestrial quadrupedal ancestors are also critiqued for their complexity (in comparison with more parsimonious alternatives), for being based on outdated assumptions about phylogeny, and for being mutually inconsistent in their comparisons and the features cited.

Arboreal Bipeds, Hylobatians and Orthograde Climbers

The third major group of hypotheses emphasises the role of orthogrady in hominin history. These hypotheses vary in the precise nature of the proposed LCA. The earliest version invoked a gibbon-like (hylobatian) phase with a relatively small-bodied ancestor adapted for vertical climbing, hindlimb propelled leaping and hand-assisted bipedalism on horizontal branches, justified by analysis of hand and wrist features in hominins that might be linked to manipulation and a 'power grip' for climbing and evidence for the early acquisition of upright gait (Tuttle, 1981). This theory first arose before the close relationship between *Pan* and *Homo* was known, when a single 'split' between the large-bodied apes and humans involving a small-bodied ancestor was considered probable.

Today, 'hylobatian' periods are considered mainly in the context of earlier hominoid divergences (Begun et al., 2012), but other versions of the orthograde hypothesis remain popular. Crompton et al. (2008, 501) note that proposing an arboreal hand-assisted biped as the LCA "requires fewer [locomotor and ecological] transitions, and is also kinematically and kinetically more parsimonious". An arboreal origin of orthogrady – and possibly of bipedalism, via hand-assisted movement on large supports – would again mean the knuckle-walking apes are convergent, but can explain a range of hominin locomotor characters, including the co-existence of features linked to arboreal and terrestrial locomotion, and provides one of only a few explanations for the presumed arboreal-terrestrial transition which does not require survival as a vulnerable terrestrial ape. This type of upright arboreal movement may be prefigured by behaviours observed in chimpanzees (Stanford, 2006), orang-utans (Thorpe et al., 2007, O'Higgins and Elton, 2007) or other arboreal primates. However, arboreal vertical climbing, orthograde supported bipedalism and other forms of upright arboreality *do* differ from terrestrial bipedalism and there are still challenges to these models from researchers who doubt the efficacy of the proposed 'pre-adaptation'. In addition, these hypotheses cannot explain characters shared with the African apes except as residual features from a common ancestor –

even where they do not fit with orthograde climbing – and this model does require that *Pan* and *Gorilla* are convergent.

Fossil Evidence for Early Hominin Characters

Current theories of the LCA characterise it as *either* a knuckle-walker *or* a generalised quadruped *or* an arboreal orthograde climber. One way of attempting to narrow down these options is to evaluate the early hominin fossil record for clues to these species' anatomy and ecology. The earliest hominins include *Sahelanthropus*, *Orrorin* and *Ardipithecus*, succeeded by various australopiths (Figure 108).

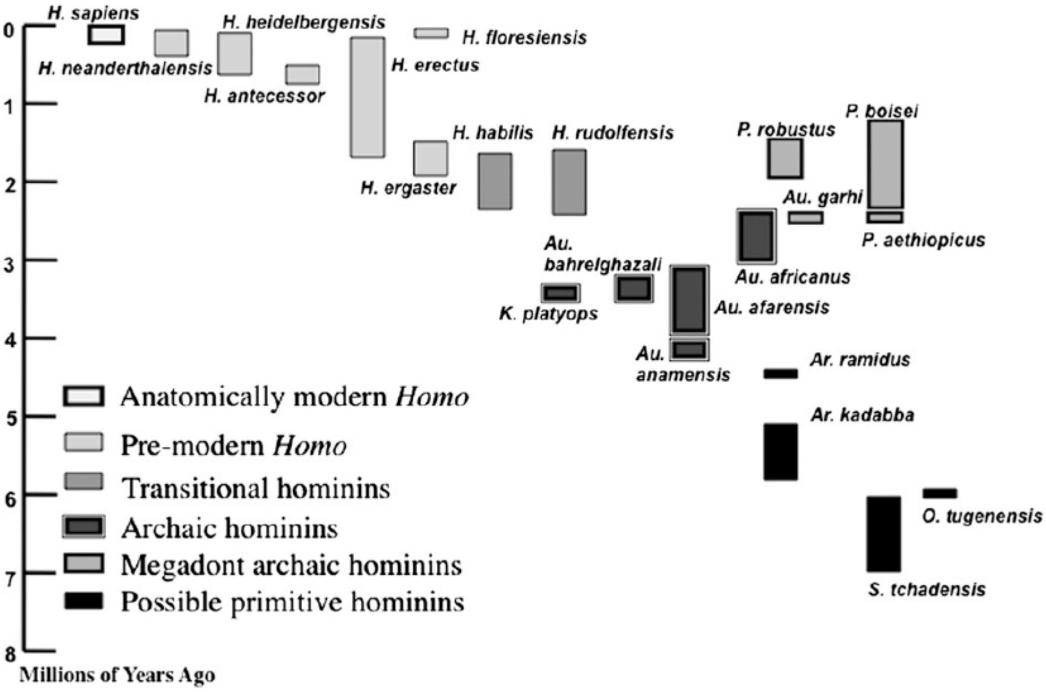


Figure 108: a speciose taxonomy of the hominins, including the earliest taxa (labelled 'possible primitive hominins') and later more certain forms; from Wood (2010, figure 1). A speciose taxonomy is chosen to allow easier location of specimens referred to in the text below.

These early taxa are represented by relatively sparse fossils – save for *Ardipithecus ramidus*, represented by a near-complete skeleton – and are of contested status. As possible hominins (or in any case stem hominines – close relatives of the hominins) they are relevant here as indicators of the locomotor repertoire(s) in use at the time of the panin-hominin divergence.

Sahelanthropus tchadensis is represented only by one cranium and a few dental and mandibular fossils (Brunet et al., 2002, 2005). It thus provides little anatomical information of relevance to this thesis' focus on landscapes. The authors note that there is "not yet sufficient information to infer reliably whether *Sahelanthropus* was a habitual biped" (Brunet et al., 2002, 150). The specimen is a little better known ecologically. The accompanying fauna includes aquatic mammals and fish (including committed piscivores, suggesting a permanent water source like a lake), together with animals from savannah and gallery forest, and the flora and sediments of the site back this up and suggest additional proximity to a desert (Vignaud et al., 2002). If *Sahelanthropus* is accepted as a hominin, then (and this is debated, especially given that the skull shares features with gorillas and is earlier than many dates for the LCA), it would seem to originate in a mosaic habitat but provides no information relevant to the question of rough landscapes.

Orrorin tugenensis from Kenya is represented by 13 fossils, including femora, dental fragments, a humerus and a manual phalanx (Senut et al., 2001). It was recovered from a site that has been characterised as a mosaic, with lacustrine and fluvial sediments containing a fauna indicative of open woodland and denser stands of trees which might have been gallery forests (Pickford and Senut, 2001). Even given the uncertain status of *Orrorin*, this is further evidence for the apes' ability to exploit mosaic habitats at about the time of the chimpanzee-human split. Analyses of the *Orrorin* femoral fragments, furthermore, suggest that this species shares no derived characters with the nonhuman apes but several with australopiths and modern humans (Pickford et al., 2002). These traits are all ones linked with upright bipedal locomotion, and the authors conclude that *Orrorin* was bipedal but not entirely human-like in locomotor patterns, though they note several areas where the specimen is more similar to *Homo sapiens* than the australopiths (Pickford et al., 2002). The bones of the upper limb (humerus and manual phalanx) have features indicative of a degree of arboreal grasping and climbing ability (Senut et al., 2001). This combination of features suggests that *Orrorin*'s morphology cannot resolve the nature of the LCA.

The final genus of putative early hominins is *Ardipithecus*, represented by two species, *Ar. kadabba* (Haile-Selassie, 2001, Haile-Selassie et al., 2004) and *Ar. ramidus* (White et al., 1994). *Ar. kadabba*, however, is represented only by dental remains from a site characterised by relatively wet and wooded environments (WoldeGabriel et al., 2001). This is not informative about the capability of the species in either rough terrain or mosaic habitats, as no estimation of the degree of mosaic patterning in the *Ardipithecus* habitat is given. *Ar. ramidus*, in contrast, is well known and well studied. It is somewhat younger, at about 4.4Ma (White et al., 1994) and was found in sites characterised by habitats ranging from forests to wooded grasslands, but seems – from faunal associations, dental microwear and isotope analyses – to have predominantly occupied the closed areas of these habitats (White et al., 2009a). This, then, is a putative hominin which was probably capable of moving through or around habitat mosaics but does not seem to have occupied them. In anatomy, *Ardipithecus ramidus* is well known. The foot has an abducent hallux but seems more similar in general structure – particularly features linked to rigidity rather than compliance with the substrate – to a generalised quadrupedal primate than to a vertical climber (Lovejoy et al., 2009a). It is proposed as supporting a 'careful climber' as an ancestor, by both Gebo and Sarmiento (Gebo, 1996, Sarmiento, 1998). The hand shows climbing features and manipulative ability without any of the features which limit mobility in the knuckle-walking apes or adapt other species to suspension and vertical climbing (Lovejoy et al., 2009b). Other elements of the lower limb combine adaptations for climbing (typically quadrupedally) with changes that suit *Ardipithecus* to upright terrestrial bipedalism (Lovejoy et al., 2009c), and again show no evidence of adaptations to vertical climbing or knuckle-walking.

Overall, then, the anatomy and ecology of the putative early hominins suggest that (a) these taxa were capable of occupying habitat mosaics and (b) that they do not resolve the question of the anatomy of the LCA. *Ardipithecus ramidus* anatomy is suggestive of a quadrupedal ancestor, but the lack of certainty about this taxon's status (Sarmiento, 2010), and the later persistence of a range of adaptations (Harcourt-Smith and Aiello, 2004, Haile-Selassie et al., 2012) that do not permit further narrowing down of the option-space suggests that any features which fit hominins for using rough terrain are probably general characteristics of the hominoid- and/or primate groups rather than specialist adaptations among the hominoids or hominins. To evaluate hominin access to rough topography therefore requires a broader perspective.

Primate Adaptations and Access to Tectonic Landscapes

The synthesis of the palaeoanthropological literature on early hominin adaptations reduces the question of hominin capabilities on rough terrain to one of *primate* abilities on this substrate. This calls for an exploration of generalised primate characteristics in light of the descriptions of rough terrain and habitat mosaics outlined above.

Primates and Habitat Mosaics

There is some evidence that some hominoid taxa from the period around 5-6Ma occupied mosaic habitats, but given the uncertainty over their taxonomic status, a broadening to include other primates is useful. Table 37 summarises the evidence for primate occupation of habitat mosaics by taxon, including the earlier hominins and other terrestrial apes and monkeys.

Table 37: an idiosyncratic summary of mosaic habitat use by hominins and other primates. Tables of hominin sites in Reynolds et al. (2011) and Winder (2012) are used as a starting point. This summary is incomplete and aims only to establish whether a given taxon *can* use mosaic habitats, not to summarise the prevalence of this use (which is beyond the scope of this thesis).

Taxon	**Evidence for mosaic use**	**References**
Orrorin tugenensis	Yes: found in mosaic environments with lakes, rivers, woodlands and forests	Pickford and Senut (2001)
Sahelanthropus tchadensis	Yes: found in mosaics with deserts, lakes, savannah and gallery forest	Vignaud et al. (2002)
Ardipithecus ramidus	Minimal: occupation restricted to certain zones within mosaics	White et al. (2009a)
Australopithecus anamensis	Yes: Sangatole formation contexts include closed through to semi-open 'grassy' woodlands	White et al. (2006)
Australopithecus afarensis	Yes: at Hadar where bushland, open woodland and edaphic grassland are used	White et al. (1984), Reed (2008)
Australopithecus africanus	Yes: Makapansgat and Sterkfontein show mosaics of woodland, bushland and grassland	Winder (2012) and references therein
Paranthropus boisei and *aethiopicus*	Yes: at Omo and East/West Turkana where various mosaics are found	Winder (2012) and references therein
Paranthropus robustus	Some: at Swartkrans faunas indicate a mix of wetlands, grasslands and some woodland	Reed (1997) and Avery (2001)
Homo habilis and *rudolfensis*	Yes: Olduvai gorge and East Turkana show various mosaics	Winder (2012) and references therein
Homo sapiens	Yes: see maps/summaries in Chapter Five	-
Pan troglodytes	Some: found in forests grading through to savannah woodland	Oates et al. (2008)
Pan paniscus	Some: mosaics of primary and secondary forest are used, together with swamp forest	Fruth et al. (2008)
Gorilla beringei	Some: a mosaic of habitat types is used, but only within the Afromontane zone of the Virunga Volcanoes	Robbins and Williamson (2008)
Gorilla gorilla	Minimal: found in lowland forest and swamp forest, but not in complex mosaics	Walsh et al. (2008)
Papio sp.	Yes: see maps/summaries in Chapter Four	-
Theropithecus gelada	Minimal: occupies mainly grasslands, but with use of cliffs as sleeping sites	Gippoliti and Hunter (2008)

This brief summary, idiosyncratic as it may be, does suggest that the hominins *are* capable of exploiting habitat mosaics (and remained so throughout their evolutionary history, with varying degrees of specialisation on particular diets or niches – e.g. by *Paranthropus boisei* – influencing their abilities to a small extent). Other terrestrial primates, including *Pan* and *Gorilla*, however either use mosaics less often or restrict themselves to mosaics within a single ecological zone (forest for *Pan paniscus* and Afromontane vegetation for *Gorilla beringei*, for example). It is impossible to say why this is (it may be ecological specialisation or it may have to do either with culture/behavioural choice or with anthropogenic habitat modification and competition). Interestingly, of the other African terrestrial primates, the best able to exploit mosaics are the *Papio* baboons, already proposed as good ecological analogues for the hominins. This analysis, then, suggests either that the LCA of panins and hominins was already capable of exploiting mosaics, or that it became capable quite quickly, which implies that any barriers to mosaic use were not significant barriers to evolution at that point.

Primates and Rough Terrain

A detailed analysis of the anatomical flexibility of the primates must take place within a comparative context, as knowing the range of movement at a given joint is unhelpful without some indication of how this compares to other taxa. This is therefore saved for the next section. Table 37, however, has suggested another means of approaching topography in the note that *Theropithecus gelada* is capable of occupying cliffs and other terrains: a geographical approach, focusing on whether primates of different body forms are capable of exploiting tectonically active, rough landscapes, is therefore adopted. This will focus on the body forms proposed as potential ancestors of the LCA, specifically knuckle-walkers, exemplified by *Pan*, as this taxon is similar in size to many early hominins (Robson and Wood, 2008); quadrupeds, represented by the baboons (*Papio* and *Theropithecus*) and the related arboreal quadruped *Lophocebus*; and vertical climbers, here exemplified by the orang-utan *Pongo pygmaeus*. For each of these, therefore, a brief analysis of substrate use and ability to cope with 'complex' surfaces (terrestrial or arboreal) is conducted.

In the text which follows, 'mosaic' landscapes or habitats are those which contain a wide variety of vegetation types, resources, terrains and general conditions within a relatively small area (see above). Often, mosaics are composed of a patchwork of ecoregions, though this need not always be the case: the term denotes overall heterogeneity, and need not imply a mix of internally consistent habitats. Mosaics are often associated with tectonic landscapes, but the relationship is not exclusive, and either landscape can occur without the other. 'Rough' landscapes, in contrast, are those with broken topography (as described above), and are terrestrial. They are a consequence of tectonic activity – though they can also arise elsewhere, for instance on coastlines. Finally, complex arboreal landscapes are those in which there is a diversity of support diameters, structures, orientations and strengths. This is analogous to the definition of a 'rough' terrestrial landscape, but has some key differences, particularly in the fact that arboreal substrates are isolated (they may not abut any other surface), may move when used and are usually rounded. This would thus place similar requirements for adaptive locomotor flexibility as would a terrestrial 'rough' landscape, but with certain modifications, for instance in the need for grasping, presumably prehensile, digits to deal with swinging branches. These arboreal complex landscapes thus might produce some, though not all, of the traits required by a species adapted to rough terrestrial landscapes. They show no particular pattern of co-occurrence with either mosaics or rough terrestrial terrain.

Modern bonobos occupy a restricted area in the central African tropical forests (Oates et al., 2008), while chimpanzees range a little more widely both latitudinally and longitudinally (Fruth et al., 2008). Both taxa are primarily terrestrial, though they remain capable of exploiting arboreal resources. Figure 109 shows the distributions of these species superimposed on a map of landscape roughness.

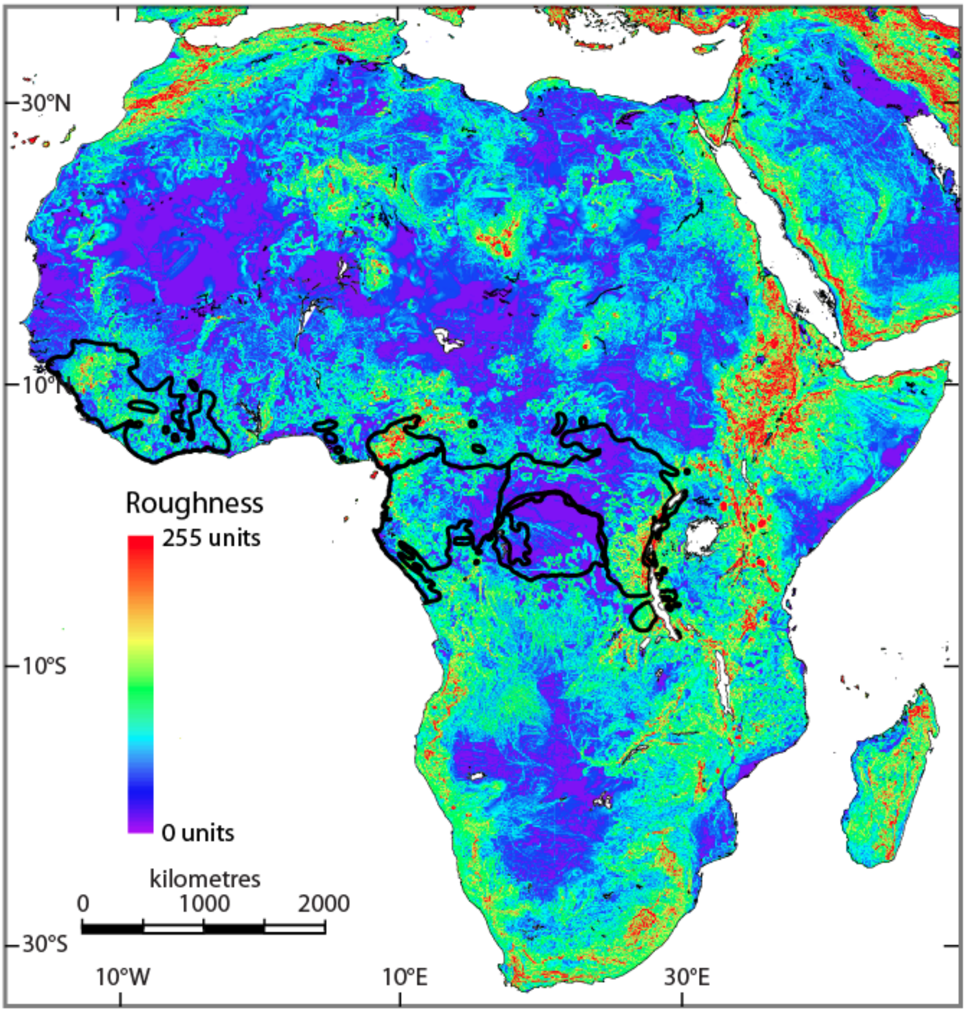


Figure 109: roughness map of Africa showing the extent of the range of *Pan*. The *P. paniscus* range is the oval shape centred on 0ºN and 20ºE, the other polygons are for *P. troglodytes*.

As this map shows, the bonobo range is restricted to a very flat area, but that of *P. troglodytes* extends up the slopes of the Rift Valley in Kenya/Tanzania and right across the Cameroon line in Nigeria/Cameroon. Both these areas are rough and this suggests that a knuckle-walking adaptation *is* sufficient to allow access to such landscapes, at least in some areas. This is confirmed by studies from Gashaka, where the local populations of *Pan troglodytes vellerosus* are known to exploit hillsides and rough areas effectively and to use some inaccessible areas, like forested slopes, as refuges from human hunters (Adanu et al., 2011).

The *Papio* baboons occupy areas with a range of roughness values (see Chapter Four). These include areas across the roughest and highest-altitude area of Africa, the Rift Valley.

Within these areas, as at Amboseli (Chapter Four), the baboons are well able to exploit rough areas. Members of the 'mountain baboon' taxon, and of other *Papio* allotaxa where circumstances permit, are also known to use cliffs and rocky areas as refugia to escape predators (Hill, 1999, Barrett et al., 2004). The closely related but dietarily much more specialised gelada baboon (*Theropithecus gelada*) lives in the high-altitude, high-roughness zone of the Ethiopian highlands and uses cliffs as sleeping sites and for security just like the *Papio* baboons (Dunbar, 1993, Gippoliti and Hunter, 2008). Ecological and anatomical suitability for tectonic landscapes thus do not apparently go together; geladas experience much of the selection which shapes their evolution on the grass plains, where they spend most of their time and are subject to predation and social interaction (Gron, 2008) but retain sufficient anatomical flexibility to exploit cliffs despite there being little evidence for active selection in this case. This suggests that the ability to access rough terrain may be ancestral or ubiquitous among these primates and their relatives.

The close relative of the baboons, *Lophocebus albigena* is arboreal and occupies a range that it shares with common chimpanzees, stretching across central Africa from Cameroon to the western edge of the Rift Valley in Kenya and Tanzania. This range also extends across areas of high roughness, but in an arboreal taxon this is less informative and it is harder to say whether these taxa would be capable of using rough terrain. Being able to navigate complex, three-dimensional arboreal environments with substrates of a range of diameters, surfaces and orientations, however – as *Lophocebus* must to move arboreally – does suggest that rough terrain should pose little problem. This is particularly probable given the findings of Meldrum (1991) that aboreal cercopithecines display kinematic convergences with their terrestrial relatives to the exclusion of other arboreal primates, suggesting that for locomotion at least, who you are is more important than where you live. This coincidentally also further justifies the lumping of 'quadrupedal' theories of the LCA above.

Finally, looking at the orang-utan, the epitome of a vertically climbing or arboreally bipedal great ape (Thorpe et al., 2007) we once again find a species for which terrestrial roughness in their range is unimportant. However, the evidence of locomotor variability in this species – in which one study suggested females use brachiation 11% of the time, quadrupedalism 12%, vertical climbing 18%, tree-swaying for 7% and clambering using varying combinations of limbs, support substrates and support orientations for no less than 51% (Cant, 1987) – suggests that the requisite level of flexibility in locomotor behaviour and in the joints is present. In fact, the orang-utan is by far the largest arboreal primate and remains capable of accessing fine-branch regions and dealing with the challenges posed by tapering, uneven and oddly orientated supports (Thorpe and Crompton, 2006, Thorpe et al., 2007). The complexity of an arboreal habitat may be harder to measure than that of a terrestrial one, but is still considerable. In orang-utans, moreover, locomotor behaviour is primarily related to substrate diameter and type rather than to contextual behaviour, age, sex, size or height in the canopy (Thorpe and Crompton, 2005). This suggests that orang-utans, like chimpanzees, baboons and mangabeys, possess the necessary anatomical capacities to exploit rough terrain, and implies that if the common ancestor of the hominins, which are often found in rough landscapes (King and Bailey, 2006), was like any of these taxa, it would also have had that ability.

PREDICTION TWO: HOMININ ADVANTAGES OVER OTHER TAXA

The analyses above suggest that whatever the earliest hominins looked like, they probably could access tectonic landscapes. King and Bailey's (2006) next proposition is that doing so gave them an advantage either over predators or over potential prey. These advantages are relevant to different stages of our evolution: the earliest hominins, weighing about 30-45kg (McHenry, 1994, Wood and Collard, 1999) and with small brains and little material culture would probably benefit most from the protection afforded by complex topography, while later larger-bodied, larger-brained taxa with more efficient long-distance running and the cultural trappings to defend against predators might gain more benefit from tactical advantages over prey.

The primary predators of the hominins were terrestrial carnivores (Treves et al., 2007) and birds of prey (Berger and Clarke, 1995). Of these taxa, humans and birds are both secondarily bipedal, but evolved from a tetrapodal body plan still seen in hyaenas, canids and felids. An eagle could take an isolated small hominin or juvenile, so small-bodied individuals would need some defence mechanism (fright responses, hiding, alarm calls, co-ordinated defence strategies). All these behaviours are manifest among monkeys and probably predate the ape-monkey divergence. The same tricks work for snakes and some quadrupedal predators. Tectonically active landscapes probably have less vegetation cover than woodland, but would compensate by providing more topographic obstacles (holes, caves and rocks). It is hard to see them as *a priori* safer or less safe for hominins if the threat comes from birds and snakes. The genus *Homo* can use all the same defence strategies as monkeys and small hominins, but their size is such that only isolated juveniles would be vulnerable to birds. Snakes and leopards, which can climb trees or rocky faces, are likely to eat hominins in any context, though large body size probably provides some defence. So the King and Bailey hypothesis probably relates to defence against quadrupedal predators, particularly big cats, hyaenids and potentially canids.

With regards to advantages over prey species, it is worth taking account of potential hominin food sources. While small and/or sedentary animals, or even other 'fallback foods' like tubers probably made up the bulk of the energy-rich food eaten by early members of *Homo* (Sponheimer and Dufour, 2009), larger species – like ungulates – would also have been attractive. These larger, faster species are harder to catch through simple trapping than, for example, rabbits or birds, and would represent the area where tactical exploitation of landscape might make the greatest difference to hunting success rates. The relationships between hominins, carnivores and ungulates are perhaps best approached from a (co)evolutionary and ecological perspective that recognises their common descent, as it is in the modifications of their (broadly) shared body plans that key differences lie.

A Brief History of Locomotor Evolution and the Origin of Mammal Groups

The earliest land-dwelling vertebrates evolved about 370 million years ago from a sarcopterygian fish that probably looked something like the tetrapod-like fishes *Tiktaalik rosae* (Daeschler et al., 2006, Figure 110) or *Panderichthys* (Boisvert et al., 2008). As is usual where palaeontologists hunt for ancestor-descendent relationships (see section above on the panin-hominin LCA, for example) there is disagreement over which of these forms is closer to tetrapods and what they can tell us exactly about the transition from water to land (Ahlberg and Clack, 2006), but the detail of this is not relevant to the brief outline of evolutionary history required to understand mammalian origins and divergences.

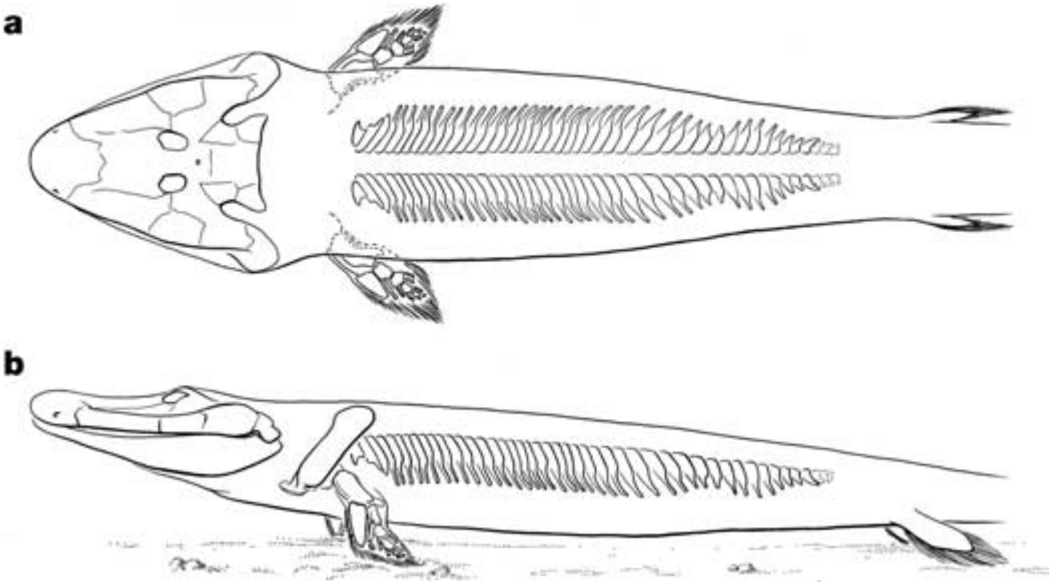


Figure 110: a reconstruction of the Devonian tetrapod-like fish, *Tiktaalik rosae* in superior (a) and lateral (b) views; from Daeschler et al. (2006, figure 6).

The earliest tetrapods were amphibians, followed some 310 million years ago by the appearance of taxa which can be recognised as reptiles – basal members of the amniote radiation to which the mammals belong (Clack, 2012). The early tetrapods had limbs constructed as in Figure 111.

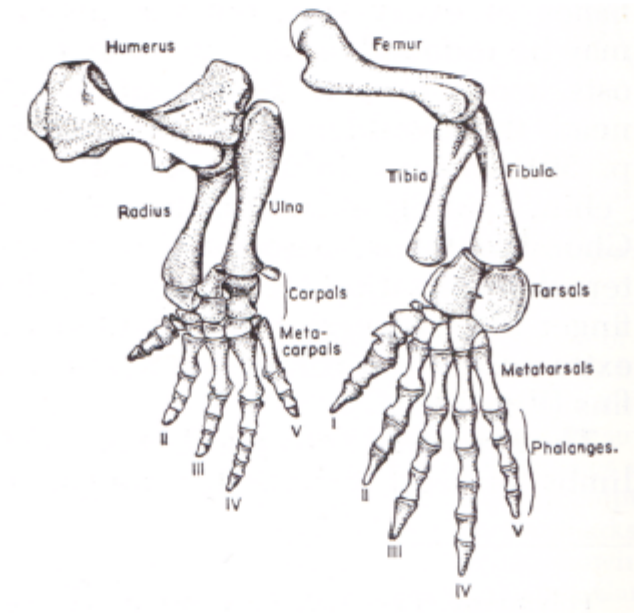


Figure 111: the structure of fore- and hindlimbs in a primitive reptile, *Ophiacodon*, illustrating the general tetrapod limb structure; from Romer (1970, figure 131).

Living tetrapods have then modified this basic structure in various ways, often (though not exclusively) by losing bones, especially from the tarsus and carpus, where the primitive complement in each autopodium is three proximal elements – radiale/intermedium/ulnare in the hand and tibiale/intermedium/fibulare in the foot – four centralia and five distal elements. In each case, the central elements are rapidly reduced to two in primitive reptiles and one in mammals, the fifth distal element is also rapidly lost, and there are additional changes to both hand and foot during subsequent evolutionary history as well (Romer, 1970). In early forms, in particular, there are many more phalanges than in more recent taxa.

The lineage that would ultimately produce the mammals appeared some 305Ma as the ‘mammal-like reptiles’ and the first recognisable mammal appeared 210Ma (Kemp, 2005). As a group, the mammals showed a further reduction of the tarsus and carpus, to a total of seven tarsal and nine carpal bones, with specific shape changes as shown in Figure 112.

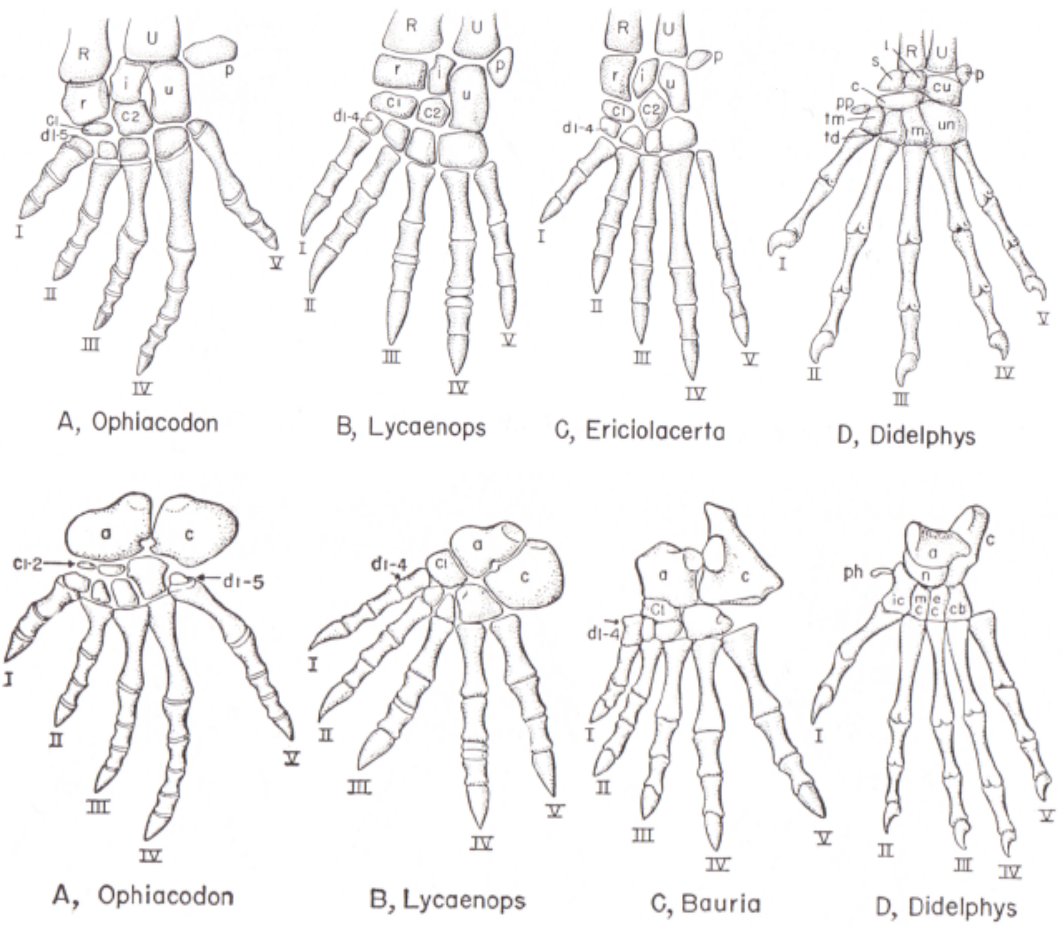


Figure 112: the evolution of the mammalian hand (top) and foot (bottom) through stages representing a primitive reptile (A), a primitive therapsid (B), an advanced therapsid (C) and a primitive mammal (D). Abbreviations for the hand include R: radius, U: ulna, r: radiale, u: ulnare, i: intermedium, C1/C2: centralia 1 and 2; D1-4: distal elements 1-4, and for the mammal l: lunare, s: scaphoid, c: centrale, pp: prepollex, p: pisiform, tm: trapezium, td: trapezoid, m: magnum, cu: cuneiform, un: unciform. Abbreviations for the foot include a: astragalus, c: calcaneum: C1/2: centralia 1 and 2, D1-4: distal elements 1-4, and for the mammal n: navicular, ic: internal cuneiform, mc: medial cuneiform, ec: external cuneiform, cb: cuboid, ph: prehallux. The prepollux and prehallux are unusual in mammals; from Romer (1970, figures 139 and 145.)

As this image shows, by the time of the earliest mammals, the hand and foot had settled into a pattern not so different from that of many modern taxa; this is the generalised mammal form, and includes a digital formula of 2.3.3.3.3 phalanges in digits I-V of each foot. Different orders and groups have then emerged and modified this basic plan in different ways to fit with their preferred locomotor styles.

For much of the early history of the mammals, they remained predominantly small-bodied and relatively taxonomically restricted. The modern placental mammal orders, with the exception of Primates (which diverged some 69-67Ma) and Xenarthra (72-67Ma), emerged in the 20 million year period 65-45Ma following the extinction of the dinosaurs at the Cretaceous-Tertiary boundary (dos Reis et al., 2012). The current phylogeny of the modern orders is shown in Figure 113.

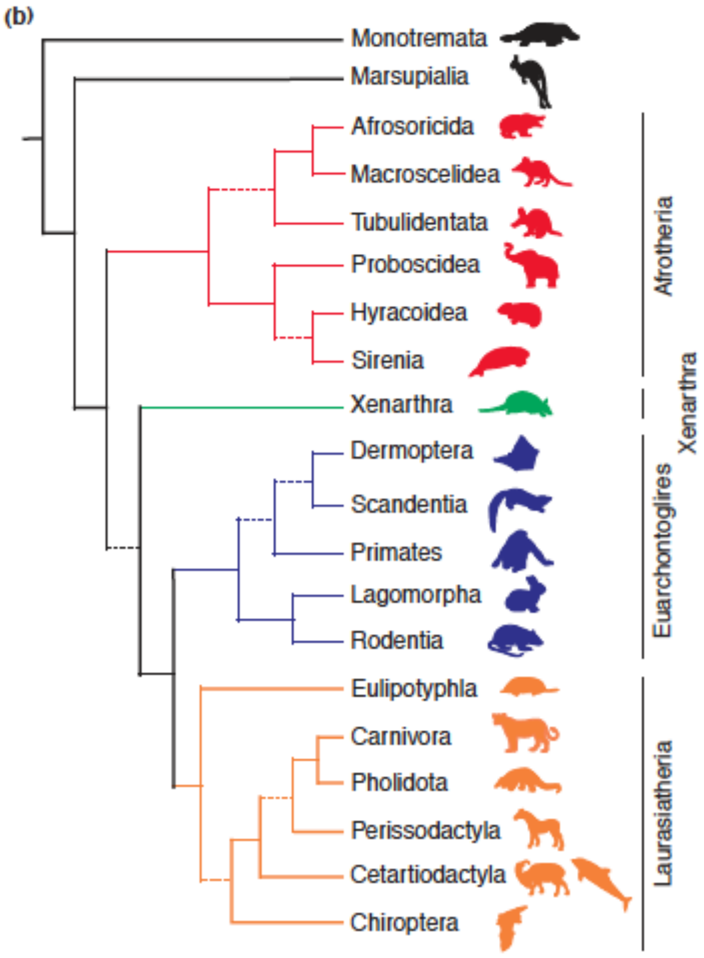


Figure 113: modern molecular phylogeny of the mammals, showing the relationships between modern groups; from Springer et al. (2004, figure 1b).

As this figure shows, the Carnivora, Perissodactyla (odd-toed ungulates) and Cetartiodactyla (even-toed ungulates, including whales) are members of the Laurasiatheria (Springer et al., 2004, Nishihara et al., 2009). Dos Reis et al. (2012) place the 95% confidence intervals for the origins of these groups at 52.0-55.9Ma for Carnivora, 60.7-62.3Ma for Cetartiodactyla and somewhere in the region of 60-40Ma for the Perissodactlya, which is less concretely known, while the primates – as noted above – diverged earlier, at about 67-69Ma. By 40Ma, therefore, all of the orders selected for this thesis were distinct and recognisable. All, as placental mammals, are united in having mammary glands, fur, a single bone in the lower jaw, a relatively large and well-developed brain, endothermy and live birth (Kemp, 2005). The orders are defined as follows:

- The Carnivores share a single unique evolutionary trait, the presence of carnassial (sharp scissorlike) cheek teeth for cutting meat, but otherwise show significant biological variation (Nowak, 2005).

- The perissodactyles are defined as ungulates (mammals in which part of the terminal phalanx is encased in a sturdy hoof) with an odd number of toes (Groves and Grubb, 2011). The weight is typically borne entirely or mostly by the third digit. They comprise the Equidae, Tapiridae and Rhinocerotidae.
- The cetartiodactyls (sometimes called artiodactyls) are ungulates with an even number of toes, typically bearing their weight evenly on the third and fourth digits (Groves and Grubb, 2011). They comprise the remaining ungulates, and include whales, giraffes and antelopes.
- The primates are relatively primitive mammals, defined by more subtle changes to the common body plan (Fleagle, 1998). The precise features chosen vary depending upon the inclusivity of the group considered (for example, whether it includes stem taxa) and the authors' preferences. They often include those identified by Martin (1986), specifically: a well-defined divergent hallux with a flat terminal phalanx, a distally elongated calcaneus, large convergent orbits with restricted interorbital distance and a postorbital bar, a petrosal bulla, a relatively large braincase with a Sylvian sulcus visible on the endocast, a dental formula of maximally 2.1.3.3. in each quadrant, and dental specialisations including a short premaxilla, rounded, low molar cusps with enlarged talonids on the lower molars and upper incisors which are arranged transversely rather than longitudinally. This definition, however, does not work as well for the fossil taxa as for the extant (Wible and Covert, 1987).

The focus of this section is to consider the locomotor adaptations of these taxa, and their implications for joint flexibility, locomotor range/flexibility, gait patterns and compliance and the use of rough topography to compete with, predate or escape from hominins. For the carnivores, the main focus is on the large felids (exemplified by modern lions), as these are the taxa most likely to have competed with or preyed on hominins (Lewis, 1997, Lewis and Werdelin, 2007), while for the ungulates examples are drawn from antelopes – a major group of African and European ungulates that were important in human evolution (Vrba and Schaller, 2000) – where possible and from other related taxa (like deer) otherwise. For the primates the baboon and chimpanzee are used as stock species, as representatives of two of the African groups postulated to be similar to the hominin LCA (see above).

Limb Structures and Locomotor Styles

The structure of the limb plays a role in determining the locomotor range and flexibility of an organism, and is greatly modified from the primitive form in several modern mammalian orders. The skeletons of the lion, the antelope and the baboon are shown in Figure 114, Figure 115 and Figure 116 for comparative purposes. As these figures show, the lion and primate (baboon) limbs remain structurally generalised (with most of the primitive skeletal elements present), while the limbs of the ungulate (antelope) are much more specialised, with extensive reduction of the digits.

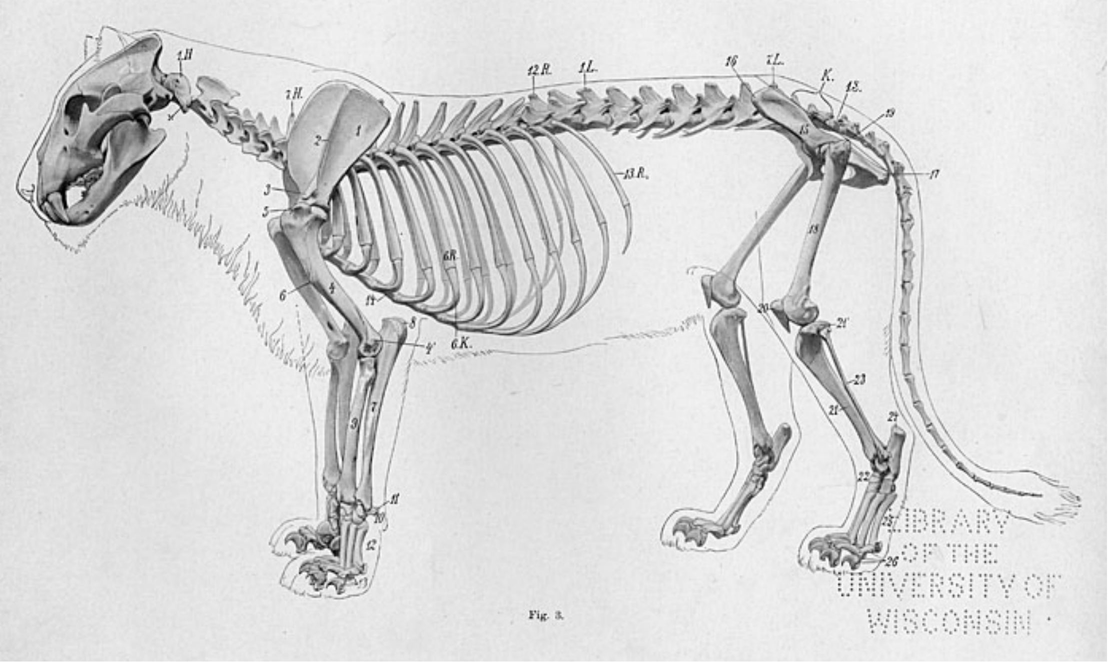


Figure 114: the skeleton of the lion; from the Veterinary Anatomical Illustrations collection online(Ellenberger et al., 1911-1925).

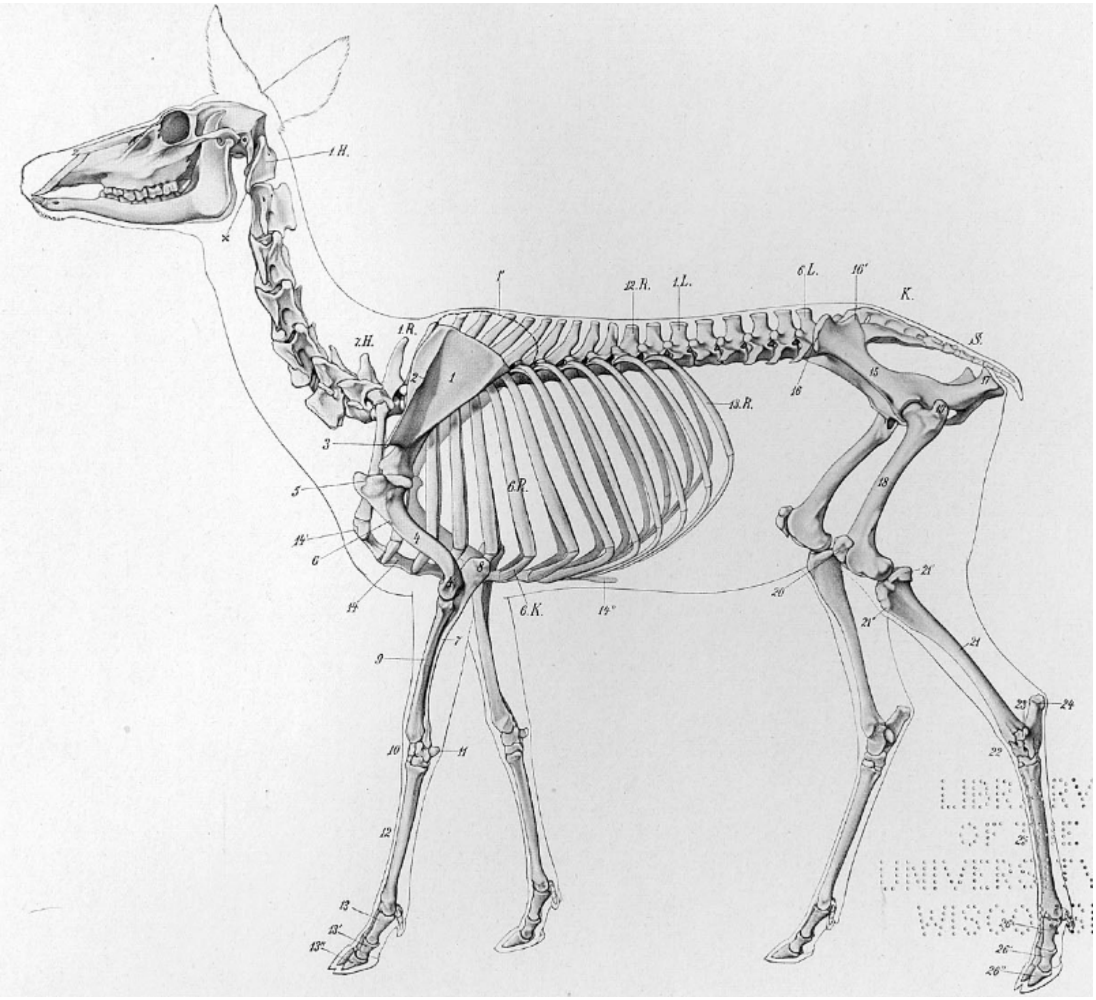


Figure 115: the skeleton of a deer; from the Veterinary Anatomical Illustrations collection online (Ellenberger et al., 1911-1925).

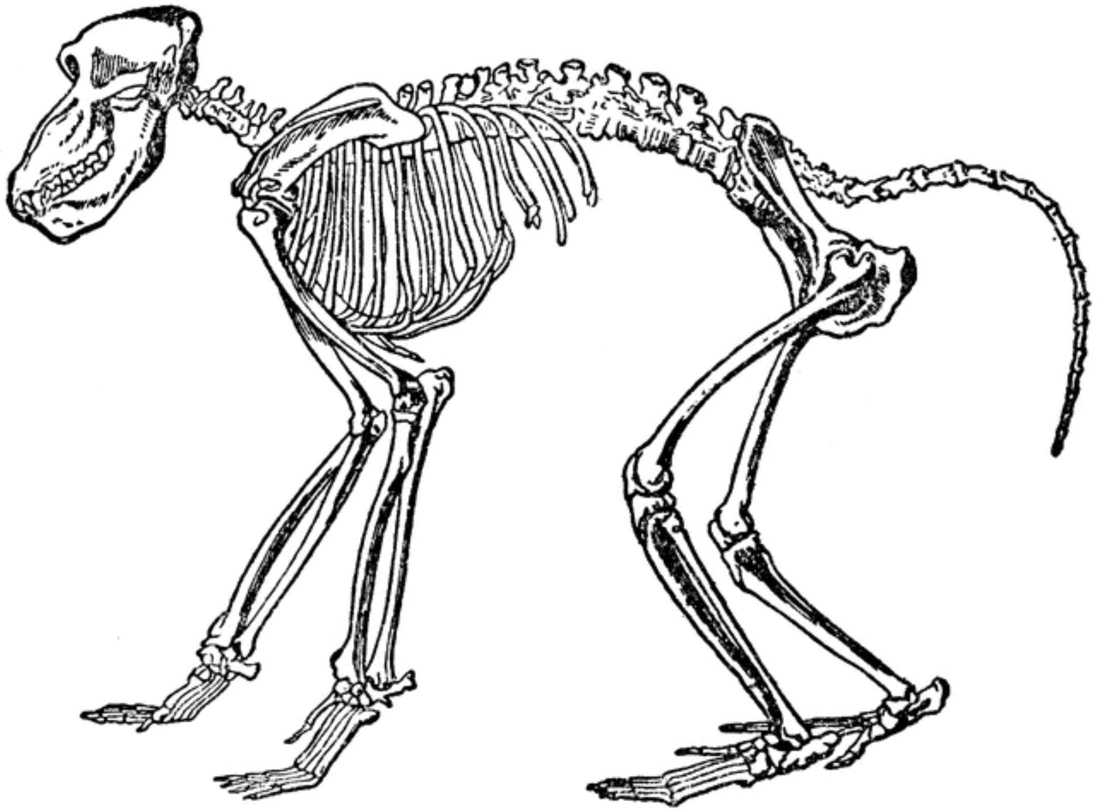


Figure 116: the baboon skeleton (*Papio cynocephalus*); from the Encyclopaedia Britannica 11th edition (Lydekker, 1911).

The lion, shown in Figure 114, is a digitigrade species adapted for speed and power in locomotion, though not stamina (Schaller, 1972). Digitigrady is an adaptation which lengthens the limb and enables the animal to take longer strides and cover the ground faster (Brown and Yalden, 1973). It is common in cursorial mammals, including both carnivores and ungulates. The lion shows a relatively complete complement of bones in the wrist and ankle, but has three wrist bones (scaphoid lunar and centrale) fused into one element and typically lacks the prepollux/prehallux (Davison and Reese, 1917).

Although the ungulates are cursorial and digitigrade like the carnivores, the similarities between them are limited by the formers' specialised limb structure, which includes the presence of a hoof and digital reduction (Groves and Grubb, 2011). In the ungulates, moreover, only the tip of the digits is in contact with the ground and the limb is even further elongated than in the lion, particularly in the distal segments (Brown and Yalden, 1973). This leads to differences in the weight and length ratios of the different limb segments in carnivores and ungulates which leads to these species employing different locomotor styles, with the ungulates notably more specialised for anteroposterior movement and simple flexion/extension (as opposed to more complex movements) at many limb joints, while the carnivores – with more bones making up their limbs – retain more flexibility at the cost of a higher energy expenditure of locomotion (Brown and Yalden, 1973). The exact composition of the ungulate limb varies depending upon the taxonomy of the chosen specimen. As just one example, the nyala

(*Tragelaphus angasi*) has six carpal bones: lunate, magnum, unciform, pisiform, scaphoid and cuneiform, and six tarsals: calcaneum, astragalus, external/middle cuneiform, internal cuneiform, naviculo-cuboid and distal fibula (Klein and Cruz-Uribe, 1984). Among bovids like the antelopes generally, reduction of ulna and fibula is common and there is one fused metapodial bone in each foot, though some species also have residual second and fifth digits.

The primate skeleton is more generalised even than the lion's. The baboon (Figure 116) uses the hindlimbs in a plantigrade (flat-footed) or semi-plantigrade (heel-elevated) position (Gebo, 1992) and the forelimbs in a digitigrade one (Brown and Yalden, 1973), while the hominoids have specialist adaptations in the hand (to arboreality, in the orang-utan, and knuckle-walking in the chimpanzee and gorilla) and use a plantigrade stance for their feet (Gebo, 1992). These species have relatively long proximal limb segments, rather than longer distal elements as in the cursorial mammals, and are not adapted for rapid locomotion but rather for flexible movement on arboreal substrates. Primates also retain almost all of the primitive complement of bones, like the carnivores – the only bones lost in the primates are the prehallux/prepollux (which may be retained in certain specimens) and the centrale, which is fused with the scaphoid (Lewis, 1964). This suggests that the three groups defined here each differ in stance from one another, if not in their basic locomotor patterns (Figure 117).

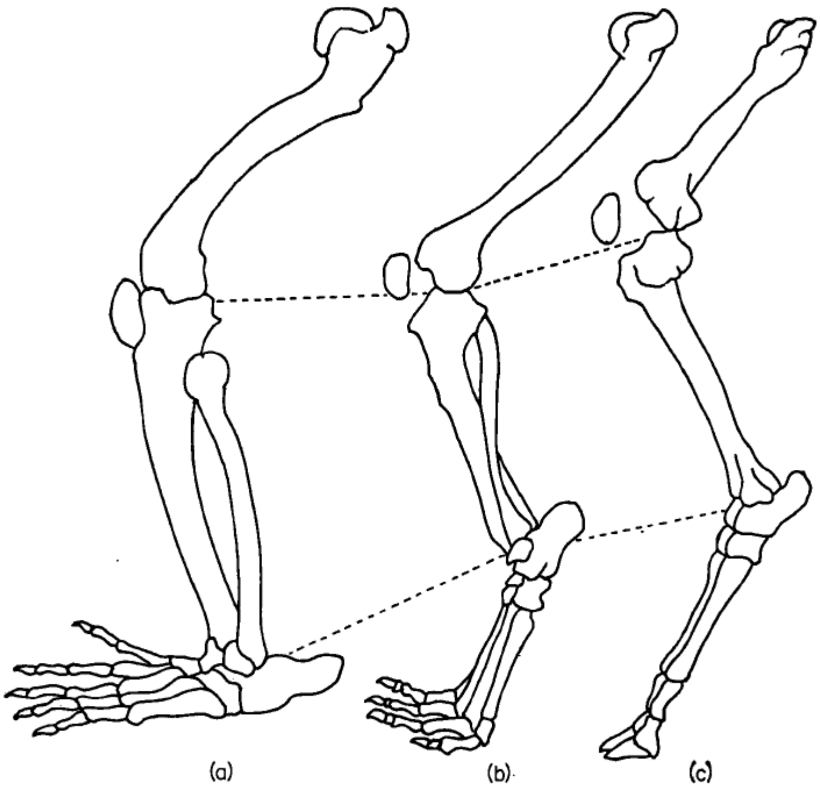


Figure 117: the limbs of a plantigrade, digitigrade and unguligrade mammal (a-c respectively); from Brown and Yalden (1973, figure 4).

Ranges of Movement and Locomotor Possibilities

The range of movement in a given limb is the product of complex interactions between anatomy, historical constraint, ecology, behaviour and various other factors. However, in many cases, the results are linked to broad differences in stance and locomotor style and only slightly modified by the finer-scale differences between taxa. A brief summary of the structural and functional differences between carnivores, ungulates and primates is given in Table 38, with felids (especially lions), antelope and baboon/chimpanzee used as examples where there is significant intragroup variation.

Table 38: a general summary of the anatomical traits of key limb joints and the implications for locomotor patterns and flexibility in the carnivores, ungulates and primates. Compare with skeletal figures above.

Joint(s)	Group	Anatomical Structure	Locomotor Implications
Shoulder (Ljunggren, 1979, Larson et al., 2000).	Carnivore	Shoulder girdle ventrally rotated, so the scapular blade faces laterally. Short clavicle (often reduced/absent), scapula long in glenovertebral and short in craniocaudal dimensions.	Movement restricted largely to the parasagittal plane (flexion/extension). Total forelimb excursion* in gait: 63.1°
	Ungulate	Generally as for carnivores.	Generally as for carnivores. Total forelimb excursion* in gait: 45.5°
	Primate	Shoulder girdle dorsally rotated, so scapula blade faces superiorly. Long clavicle, scapula long craniocaudally and short glenoventrally.	Differentiated movement in a three-dimensional environment (includes flexion/extension, abduction/adduction and rotation). Total forelimb excursion* in gait: 72.1°
Elbow (Parsons, 1899, O'Connor and Rarey, 1979, Larney and Larson, 2004).	Carnivore	Both radius and ulna play a part in weight-bearing, and an orbicular ligament (to restrain the radius and permit extensive pronation/supination) is present.	Significant (~90°) range of pronation-supination. Modest elbow yield (flexion-extension) in locomotion.
	Ungulate	Only the radius bears weight, with the olecranon acting to stabilise the joint. Radius and ulna are strongly bound together by ligaments, and may be ossified (e.g. in the horse). No orbicular ligament.	No pronation/supination is possible. Low elbow yield (flexion/extension) in locomotion.
	Primate	Both radius and ulna are important to weight-bearing, and there is a strong orbicular ligament t. In the baboon, both internal and external lateral ligaments attach to the ulna to check extension.	Significant range of pronation/supination (90-120° in cercopithecoids, and up to ~150-180° in apes). High flexion/extension (elbow yield) in locomotion.

Table 37: continued.

Joint(s)	Group	Anatomical Structure	Locomotor Implications
Wrist (Parsons, 1899, Lewis, 1965, O'Connor, 1975, Richmond, 2006).	Carnivore	The radius articulates with the scapho-lunar and the ulna with the cuneiform and pisiform (to which it is bound by strong ligaments), with a partial or total separation between the two joints by a sheet of fibro-cartilage.	Significant range of pronation/supination and flexion/extension with some abduction/adduction also possible.
	Ungulate	The radius forms the majority or totality of the superior joint surface, and articulates with scaphoid, semilunar and cuneiform. The wrist is almost exclusively a hinge joint.	Only flexion/extension possible.
	Primate	Two types: in cercopithecoids, the ulna, triquetrum and pisiform bones articulate and interlock to check adduction and possibly dorsiflexion. In hominoids, this does not happen but adaptations of the midcarpal joint may act to check extension in knuckle-walking. The radial and ulnar joints may be partially separated in some monkeys. In all taxa, a triangular articular disk intervenes between ulna and carpals.	The range of pronation-supination at the radioulnar joint is higher in hominoids (180º) than cercopithecoids (120º), but that of flexion/extension is a little lower in knuckle-walking apes and cercopithecoids (c.150º) than suspensory taxa (c.220º). The midcarpal joints are flexible, but the range of adduction is smaller in cercopithecoids than hominoids.
Fingers (Brown and Yalden, 1973).	Carnivore	The digits come together at the metacarpophalangeal joints to form the main weight-bearing surface, cushioned by fused interdigital pads. There are also apical pads. The digits are usually held with the metacarpophalangeal joint strongly dorsiflexed and the first interphalangeal joint plantarflexed.	Significant range of flexion/extension and some abduction/adduction possible in the phalangeal portions, the metacarpal joints tend only to flex/extend.
	Ungulate	Digits markedly reduced (to one or two main weight-bearing surfaces) and with clear hooves on the terminal phalanges.	Movement restricted almost entirely to flexion/extension
	Primate	Manual dexterity is high, and joint surfaces are typically rounded and broad. Fingers are prehensile and the pollux opposable.	Significant range of flexion/extension and abduction/adduction (at the metacarpophalangeal joints). The pollux is opposable.

Table 37: continued.

Joint(s)	Group	Anatomical Structure	Locomotor Implications
Hip (Parsons, 1900, Jenkins and Camazine, 1977, Kappelman, 1988, Larson et al., 2001).	Carnivore	The joint capsule is equally strong across its whole surface, and the terrestrial forms have a very strong ligamentum teres. The femoral head is more rounded in ambulatory than cursorial forms. Robust (cursorial) femoral trochanters.	In felids, movements at the hip joint are typically exclusively linked to flexion/extension, but there is the potential for some abduction/adduction of the limb. Total hindlimb excursion* in gait: 51.9°
	Ungulate	Variable configurations exist in groups from different habitats. The ligamentum teres is clear and in some species supplemented by a second, inferior component. Savannah bovids have laterally expanded femoral heads, while forest ones have spherical ones. Robust femoral trochanters, especially the greater trochanter.	Significant flexion/exenstion, coupled with some abduction and axial rotation in the forest forms; these latter movements are limited in savannah types. Total hindlimb excursion* in gait: 39.2°
	Primate	A marked ligamentum teres is present and there are three thickenings in the joint capsule linking pelvis and femur. In the apes, the ilio-femoral band is y-shaped, in monkeys single. The trochanters are less robust.	Very flexible. The primates are unique in the marked degree to which they extend their hip in the stance phase of their gait, and have a wide range of abduction/adduction and rotation too. Total hindlimb excursion* in gait: 63.5°
Knee (Parsons, 1900, Larney and Larson, 2004, Polly, 2007).	Carnivore	Functional varietion in the tibia and fibula is generally less pronounced than in other bones. Carnivores thus have a generalised knee structure with a long, deep patellar groove. In some species, the ligamentum mucosum acts to partition the knee joint anteroposteriorly. The fibula is not reduced.	Moderate knee yield (flexion/extension) in locomotion. Some rotation is possible.
	Ungulate	A generalised mammalian knee structure, with modifications to the ligaments that (in other taxa) attach to the fibula where this bone is absent or reduced. Ligaments may subdivide the joint capsule into two or three separate spaces linking different bones. The patellar groove is long and deep.	Low knee yield (flexion/extension) in locomotion. Some knee rotation is possible.

Table 37: continued.

Joint(s)	Group	Anatomical Structure	Locomotor Implications
Knee cont. (Parsons, 1900, Larney and Larson, 2004, Polly, 2007).	Primate	Another generalised mammalian knee structure in nonhuman taxa. In a few species (like the baboons) the semilunar cartilages are linked posteriorly, to form a single structure, in others this link persists as fibrous tissue. The patellar groove is shallower and shorter.	High knee yield (flexion/extension) in locomotion. Knee rotation is possible to a greater extent, especially in species with broad semilunar cartilages.
Ankle (Parsons, 1900, Lewis, 1983, Klein and Cruz-Uribe, 1984, DeSilva, 2009).	Carnivore	The fibula and tibia are always separate distally, and the external lateral ligament is reduced. There is no fibulocalcaneal articulation. The structure of the lion hindfoot is more generalised than the forefoot.	The separation of fibula and tibia permits some abduction and adduction. Flexion and extension is possible at the ankle and midfoot, and rotation (inversion/eversion) is possible but limited.
	Ungulate	The fibula is often reduced or absent, and may persist only as an additional tarsal. It articulates with the calcaneus where present. The ankle joint is a simple hinge, with a tight fit between tibia and talus and strong, X-shaped external and internal lateral ligaments. The anterior trochlea is bevelled.	Only flexion/extension possible, but this spans an extremely wide range of motion and can take place at high speed to cushion the impact of running.
	Primate	Fibula and tibia both persist and are separate distally. The external lateral ligament is reduced anteriorly. There is no calcaneofibular articulation, but the ankle and subtalar joints communicate. Compared to cercopithecoids, hominoids have a mediolaterally expanded distal tibia and an inverted set to the foot.	A wide range of complex movements are possible at the primate ankle joints, though to varying degrees. Hominoids can dorsiflex the ankle 45.5º in vertical climbing while cercopithecoids only manage 15-20º mostly at the midfoot. Inversion is also greater in the hominoids than cercopithecoids.
Toes (Brown and Yalden, 1973, Polly, 2007).	Carnivore	All five digits are retained, and come together at the metatarsophalangeal joints to create the main weight-bearing surface, covered by a single interdigital pad. Apical pads protect the tips of the digits. The digits are held planterflexed at the interphalangeal joints and dorsiflexed at the metatarsophalangeal joints.	Significant range of flexion/extension and some abduction/adduction possible in the phalangeal portions, the metatarsal joints tend only to flex/extend.

Table 37: continued.

Joint(s)	Group	Anatomical Structure	Locomotor Implications
Toes cont. (Brown and Yalden, 1973, Polly, 2007)	Ungulate	Toes are reduced (to one or two weight-bearing digits), and are adapted to promote motion in the parasagittal plane. The distal phalanx or phalanges are covered with a horny hoof.	Movement generally restricted to flexion/extension.
	Primate	All five digits are retained, and typically possess separate intedigital pads. Toes are elongated and fitted for grasping (prehensile), with rounded joint surfaces.	Significant range of flexion/extension and abduction/adduction (at the metatarsophalangeal joints). The hallux is opposable.

*Total forelimb and hindlimb excursions measured from lateral view, i.e. indicates range of flexion/extension in the parasagittal plane.

This table suggests that the primates are generally the most flexible in limb function, and while these taxa may not always (or uniformly) possess the largest absolute ranges of motion at a given joint, often possess more potential for different *types* of movement, showing no extensive specialisation for movement in the parasagittal plane. The primates have the highest total forelimb and hindlimb excursions during locomotion, and while cercopithcoids and hominoids may differ in the details of their anatomy and potential for movement, as a whole they show flexibility. The cursorial carnivores and ungulates, in contrast, share some specialisations for rapid running (particularly a suite of characters that restrict movement to near the parasagittal plane), but differ in the degree to which these modifications are effected. Ungulate cursorial adaptations are carried much further than those of the carnivores, for whom there seems to be a trade-off with the requirement for grasping prey and (in some taxa) climbing to secrete carcasses. Lewis (1997) identified modern lions as 'generalist' carnivores, while cheetahs show adaptations that are almost exclusively suited to running, and leopards, for instance, are scansorial and retain more climbing ability. Among the Plio-Pleistocene carnivores there would have been an even greater range of locomotor styles and ecologies (Lewis and Werdelin, 2007). Modern ungulates also vary – for instance in having differently shared femoral heads in different contexts (Kappelman, 1988) – but the dominant characters of their limbs are linked to extreme cursorialism and digitigrady. Essentially, then, the major adaptations of these three groups do seem to relate primarily to locomotor style (cursorial versus arboreal) and stance (Figure 117), with intra-group ecological variation accounting for much of the anatomical patterning seen.

The high forelimb and hindlimb excursion angles and flexible joints in primates compared to other species (Larson et al., 2000, Larson et al., 2001) are not purely linked to the former using longer strides. They are also linked to the uniquely 'compliant' gait seen in primates, in which the wide ranges of movement at the limb joints are co-opted to reduce stresses on the body in locomotion and accommodate movements in complex, 3D (presumably originally arboreal) environments (Larson et al., 2001, Larney and Larson, 2004). This gait allows primates to reach relatively high walking speeds using long, low frequency strides with low peak vertical forces and effective shock absorption (Schmitt, 2003). This would suggest that the primates generally possess a suite of features which could easily be exapted (in the sense of Gould and Vrba, 1982) to locomotion on rough terrain and in mosaic landscapes where there is considerable diversity and 3D structure to the substrate. The scansorial carnivores would presumably also be able to make the transition, though perhaps less effectively due to their lack of compliant gait patterns, with the generalist and cursorial carnivores less well suited to these landscapes and the ungulates least capable of exploiting them. This implies that the early hominins would have had *some* advantage over the big cats in tectonic landscapes (with the partial exception of the leopard which, although scansorial, does not have compliant locomotion). Later hominins would have had a significant advantage over the ungulates in the same areas. This implies that both King and Bailey's proposed competitive advantages over other taxa might be valid.

PREDICTION THREE: MODERN HUMAN ANATOMY

The evidence summarised above has suggested that early hominins were both capable of accessing tectonic landscapes and potentially at a competitive advantage if they did so. The final prediction from King and Bailey's papers (King and Bailey, 2006, Bailey and King, 2011, Reynolds et al., 2011) is that a hypothesis of human evolution in tectonic landscapes – here called the 'complex topography hypothesis' in recognition of the precise evolutionary agent invoked – can effectively explain both the evolutionary trajectory of hominins and modern human characteristics.

Existing Hypotheses of the Hominin Niche

As noted in Chapter One and the section on prediction one above, there are many existing hypotheses of hominin evolutionary environments (Potts, 1998a, 2007), of which the complex topography hypothesis (based on the tectonic landscape model) is the first to explicitly invoke agency and spatially structured landscapes. The theories which existed before King and Bailey's (2006) paper all emphasised the role of either climate or vegetation in generating unique ecological niches that might drive hominization (Dart, 1925, Morgan, 1982, Blumenschine et al., 1987, Foley, 1987a, Potts, 1998b, Thorpe et al., 2007). There has recently been a shift towards increasing recognition of the role of woodlands in producing some human characteristics (O'Higgins and Elton, 2007), but many of these theories are derivatives of the original savannah hypothesis (see Figure 118) which itself still underpins many discussions of human origins (Cerling et al., 2011, Feibel, 2011).

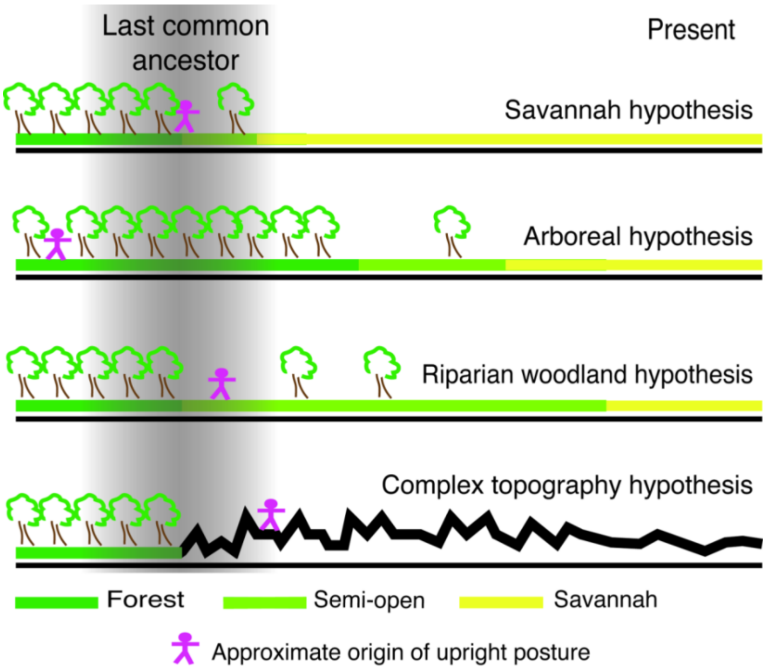


Figure 118: schematic showing the broad similarities in evolutionary patterning and differences in the timings of specific events proposed in different vegetation/climate-based hypotheses of human evolutionary history, and the new approach suggested by the complex topography hypothesis. This cartoon was digitised by Geoffrey King.

The original savannah hypothesis proposed that aridification causes forests to thin, forcing hominins out of the trees onto savannah plains via an intermediate stage in which the remaining trees provided security and shelter (Dart, 1925). It fell out of favour when no savannah niche which could support semi-terrestrial, relatively defenceless apes could be found. Newer 'woodland' hypotheses (Blumenschine et al., 1987, Potts, 2007, Thorpe et al., 2007, and see discussion above), in contrast, propose that upright posture or even bipedalism arose in the ancestral forested environment and served as a 'preadaptation' that facilitated the transition from arboreality to terrestriality as the forests disappeared (O'Higgins and Elton, 2007). These theories thus differ in the relative *timing* of key evolutionary changes (for instance the appearance of upright posture), but retain climatically driven changes in vegetation as the key drivers of hominin evolution. Unfortunately, an upright climbing adaptation evolved in an arboreal context would not produce all the features required for effective, long-distance and rapid terrestrial bipedalism (just as modern orang-utans and other primates with a significant vertical climbing component to their locomotor repertoire are not fitted for this gait). Explaining how our ancestors survived a locomotor transition in a semi-open habitat remains a critical challenge to vegetation and climate based hypotheses, and an area where the complex topography hypothesis might materially contribute to our understanding.

An implicit assumption of most vegetation/climate based hypotheses (henceforth 'traditional' hypotheses) is the equation of terrestrial with flat. While many theories, like that of Thorpe et al. (2007), now recognise the importance of complex three-dimensional environments in forest contexts, very few note the fact that complex topography and vegetation do not co-vary (Figure 119) and that landscapes – rather than being simply characterised as open, semi-open or closed habitats – can consist of any of a variety of combinations of altitude, climate, vegetation, roughness and soil types (see Chapter Three). The ‘great plains’ of the Serengeti and Transvaal are actually rather small, and every vegetation type is found across both complex and smooth topography. This suggests that rather than necessarily *replacing* vegetation and/or climate as a driver of hominin evolution, topography ought to be seen as supplementing and extending the effects of these drivers and, potentially, as offering a ‘missing link’ by explaining transitions and processes which are currently uncertain. With that in mind, we can contrast the complex topography hypothesis – which allows for hominins living in any vegetation type or climate – with purely vegetation-and-climate based models like the traditional hypotheses described above, to explore how well each explains the past.

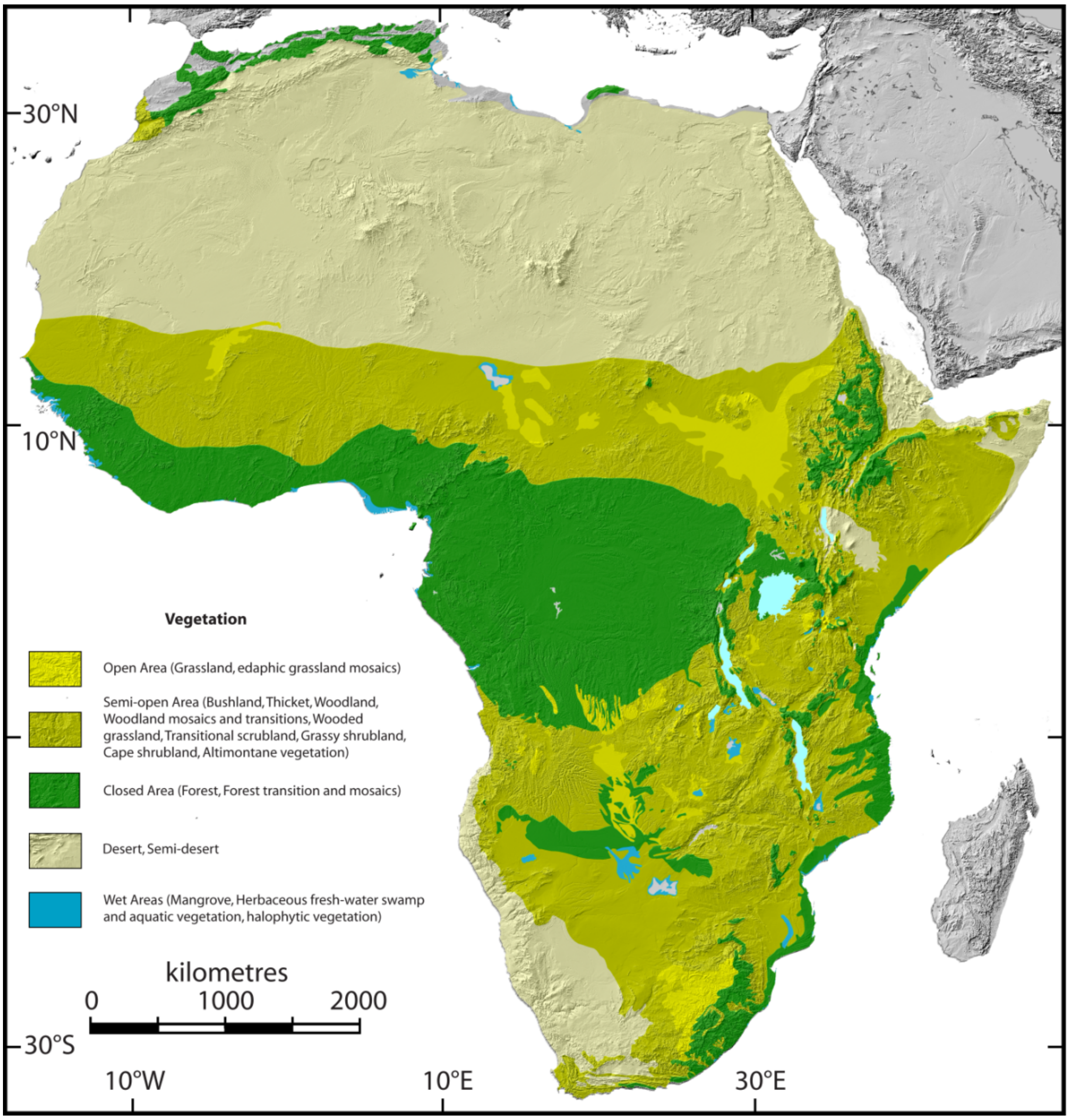


Figure 119: combined vegetation and topography map showing the lack of general co-variance between the two factors. Figure digitised by Geoffrey King.

Alternative Theories: Early Hominin Evolution

To be convincing, any hypothesis of human evolution must explain the emergence of key human adaptations like upright 'striding' bipedalism, endurance running, large brains and bodies, manual dexterity, advanced tool use and changes to the primate pattern of life history, which together form an adaptive suite of interlinked characters. Dexterity and tool use are linked, for example, and may follow naturally from upright gait as arms lose their locomotor function. It is not therefore necessary for a successful hypothesis to advance separate explanations of each adaptation; instead, many focus primarily on explaining bipedality, as this is both the first 'humanlike' character to appear in the fossil record and one which may have permitted or driven many subsequent changes.

If we contrast the predictions for hominin locomotor evolution made by the traditional hypotheses and the complex topography hypothesis (see Figure 120), the first major difference involves the nature of the proposed LCA.

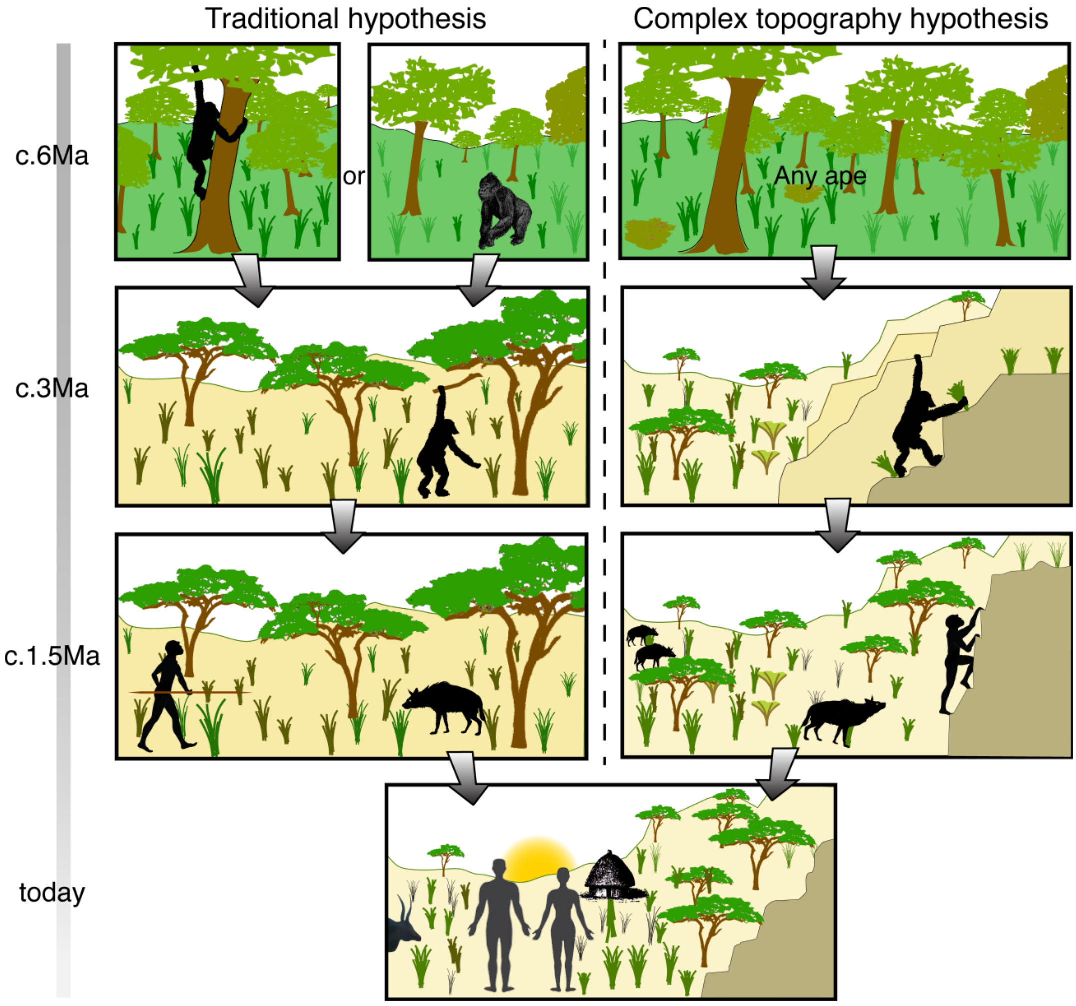


Figure 120: cartoon showing the evolution of hominin locomotion as predicted by the traditional hypotheses (left) and the complex topography hypothesis (right) and illustrating the differences in the two models' explanatory potentials. Both start with the chimpanzee-human LCA, circa 6Ma, and proceed to the modern day at the bottom. Figure digitised by Geoffrey King.

For the traditional hypotheses, the key question remains how hominins shifted from the potential ancestral locomotor mode (which, whatever it was, was not fully equipped for terrestrial bipedalism in a dangerous environment) to upright terrestrial bipedalism. In fact, given that some forms of *Australopithecus* might not have been fully efficient terrestrial bipeds (Harcourt-Smith and Aiello, 2004), this transitional period is not just something we could get through quickly 'with luck'; instead, it remains a formidable obstacle to the occupation of savannah plains, as isolated stands of trees offer little protection. Even a predator that cannot climb trees (like a lion) can simply wait out an ape trapped in a small forest. For the complex topography hypothesis this is not a problem. Whatever body form the LCA had, a transition from climbing in a complex 3D arboreal environment to scrambling across a complex 3D terrestrial landscape is easier to envision than the traditional 3D-2D transition. Complex topography, being associated with habitat mosaics, affords access to resources and protection from predators that cannot scramble, including most large African carnivores. The key exception (as discussed above) would be the leopard, but this species can climb trees as well as rocky faces and would have preyed on hominins under either scenario. Evidence from living primates suggests that the provision of supporting rocky structures might make it easier to acquire bipedal locomotion even for a non preadapted species. Chimpanzees engage in postural or supported bipedalism (tripedalism) more often than in independent walking and can move fluently between quadrupedal, tripedal and bipedal postures (Stanford, 2006).

In fact, as described above, the complex topography hypothesis requires no assumptions about the morphology of the LCA (Figure 120). Any primate would be capable of using rough topography and such a landscape would support any ape- or monkey-like creature in finding a terrestrial niche, as it provides better protection from predators than isolated trees and facilitates locomotor transition and experimentation. This would lead to the development of a generalist, scrambling adaptation which would presumably incorporate a more upright stance, a shortening of the upper limbs and, in the lower limbs, a compromise between adaptations for flexibility and grasping ability and those entailing rigidity and leverage during terrestrial locomotion on uneven surfaces. Under this model, the australopith anatomical mosaics of terrestrial and putatively 'arboreal' traits (Harcourt-Smith and Aiello, 2004) could be identified as adaptations to scrambling as easily as to semi-arboreal locomotion, and a range of different mosaics would be expected as the hominins radiate to fill different ecological niches on complex landscapes. These anatomical complexes would constitute an effective morphology for scrambling, rather than one riddled with relic features or caught uncomfortably between two niches. The shift from one refugium (trees) to another (complex topography) by a group near the LCA might also explain our lineage's divergence from the panins, as such shifts are likely to have been important right up to our own species' evolution (Stewart and Stringer, 2012).

Later Hominins and Modern Human Anatomies

For the earliest stages of hominin evolution, then, the complex topography hypothesis performs better than other hypotheses as an explanatory framework for terrestrialisation. But what of the appearance of obligate (i.e. permanent and necessary) 'striding' bipedalism and endurance running later in our history? This is an area where the implicit 2D 'plains' assumption of older hypotheses comes into its own, and an implicit challenge for a new hypothesis. The two major adaptive changes to the human foot—the aligned hallux (big toe) and the foot arches—seem well fitted to striding and running, as their key function is to make the foot act as a rigid lever during locomotion. This is clearly advantageous on flat terrain, but would also serve an important function on complex topography: it would enable the release of stored energy to lever the body upwards even if only a small part of the foot was in contact with the substrate. This more efficient means of transmitting gait forces and driving locomotion on rough substrates would mean there was less need for scramblers to use their arms to assist locomotion once these features had appeared, thus facilitating further changes to the upper limbs and body proportions and matching the observed adaptive trajectory in the fossil record.

This initial adaptation for efficient scrambling or climbing would open up a broad spectrum of niches, both in complex terrain and elsewhere, that would be unavailable to a more specialised knuckle-walker or arboreal climber. For example, it is easy to see how a hominin with adaptations that include relatively shorter arms, some form of foot arch and some spinal, pelvic and lower limb adaptations for upright posture, could begin to move out of complex terrain to exploit savannah animals. Species tied to particular regions for security (as early hominins probably were to areas of complex topography) are often under strong selective pressures to expand their dietary repertoire, either by eating a wider range of foods or by extending their foraging range. The ability to exploit large savannah animals, perhaps by driving them back onto rough terrain or by making short excursions away from secure areas, would be a major advantage permitting both encephalisation and population growth (Aiello and Wheeler, 1995). This would set off a ratchet effect, whereby the initial adoption of a more savannah-oriented niche by an early hominin would isolate that lineage and lock it into a rapid adaptive change that would drive the elaboration of existing anatomical, cognitive, social and technological capacities to better exploit the new niche. By this account, explanations of human adaptations for running/striding remain the same but are based on earlier scrambling features which allowed hominins to venture onto the plains only when they already possessed traits which aided the pursuit of prey and escape from predators. Complex topography would still be accessible to these lineages, but might cease to be their primary niche as the ratchet continued to act and their morphologies became more specialised.

Expanding this evolutionary trajectory to explain other uniquely human anatomies is fairly simple (Figure 121). Hominins' upper limbs would initially shorten to enable them to pull themselves up when climbing. In fact, this can explain why modern humans' arms are shorter than predicted by energetic considerations of striding bipedalism (Wang and Crompton, 2004). Under traditional hypotheses, this has to be explained through a reliance on regular carrying of fairly heavy weights. Using the hands to grip while climbing also explains grasping adaptations and increasing manual dexterity. The extreme capabilities found in modern humans would be facilitated by decreasing reliance on this form of locomotion as the lever adaptations of the foot developed, with consequent freeing of the pre-adapted hand for dextrous tasks like tool use. The active use of complex topographies for strategic advantage, seen in modern humans (King et al., 1994, Crouch, 2004), can even explain the trends towards larger brains and bodies through the effects of these topographies' enabling relatively defenceless hominins to obtain high quality food (meat), thus initiating a positive feedback which ultimately drove excursions into flat open areas and the development of running adaptations. The relative security offered by topographically complex environments would also facilitate the appearance of the modern human life history, with extended childhood and shorter interbirth intervals. Overall, the complex topography hypothesis explains the key events of hominin evolution better than previous models.

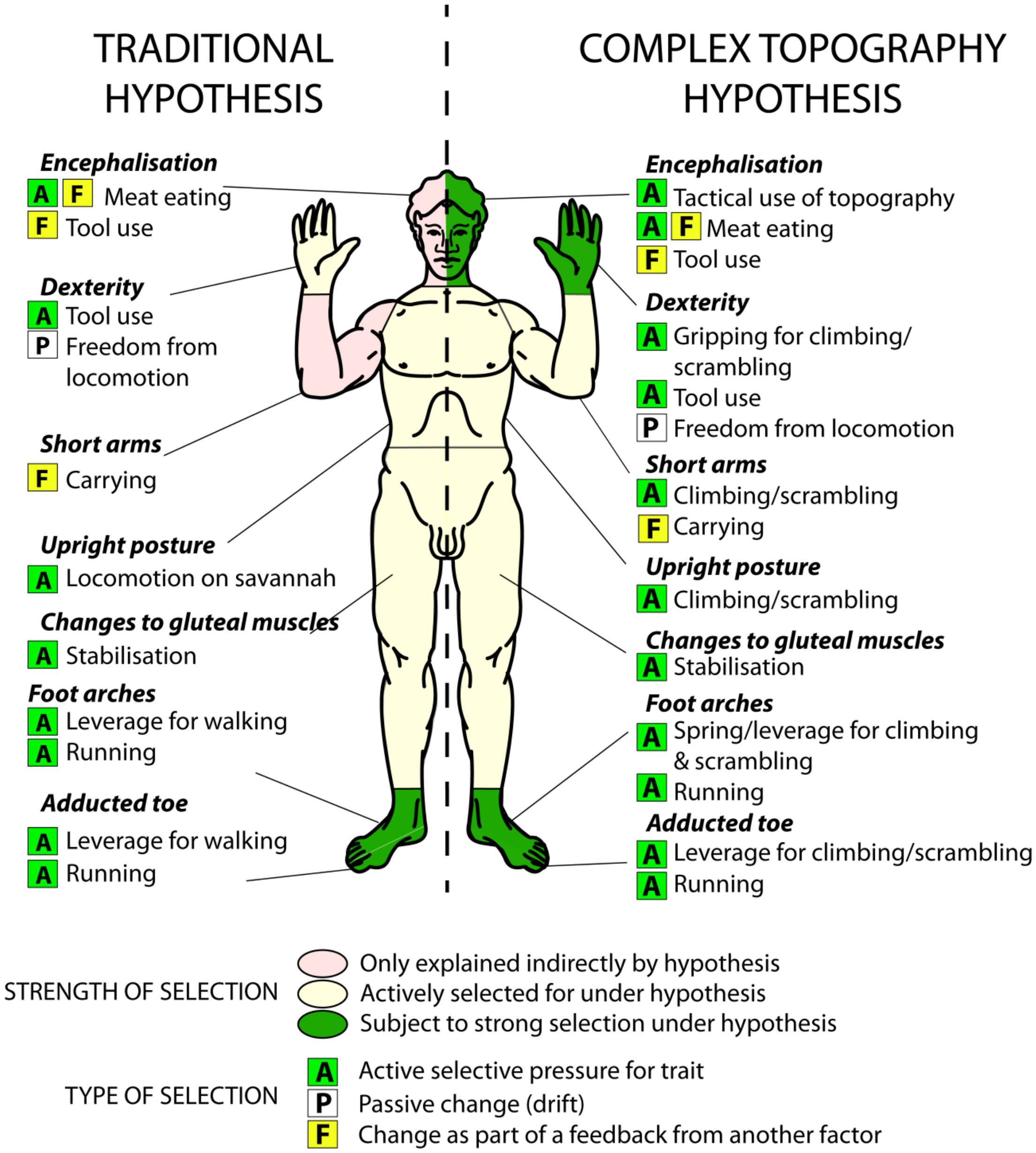


Figure 121: Schematic summarising the ways the traditional hypotheses (left) and complex topography hypothesis (right) explain modern human anatomical features. Explanations are classified – those labelled (A) are based on active selection for the trait, (F) indicates a feedback loop based on selection for another trait, and (P) passive selection or drift. The silhouette is coloured accordingly – red indicates adaptations only indirectly explained by the hypothesis, orange those explicable by a single direct selective pressure, and green those subject to more than one direct selective pressure. Figure digitised by Geoffrey King.

Hominin Ecological Distinctiveness

The final test of any palaeoanthropological hypothesis is its ability to explain why hominins are unique. For hypotheses identifying savannahs as a key component (whether throughout evolution or only in the later stages), a key challenge is the fact that the so-called 'savannah' baboons—Papio spp.—possess none of the adaptations of the hominins. Either these features are not essential adaptations to savannah plains, or adaptation to plains cannot be such a major influence on our history as previously thought. The alternative—that baboons and hominins were in sufficiently close competition as to undergo character displacement (where co-occurring species' adaptations diverge to minimise competition in areas of overlap)—assumes that the two lineages' adaptations are alternative solutions to savannah challenges, and that the adoption of either would serve to aid survival in these environments. The discussion above, however, suggests that the idea that hominin adaptations are fitted to savannah survival is unlikely.

Here again the complex topography hypothesis performs better than the vegetational models. In occupying complex topographies, hominins would have been unique: the only other primates to use rocky slopes are geladas (Theropithecus gelada), which use cliffs as sleeping sites but spend their days on the Ethiopian plains (Gron, 2008). These populations exploit rough topography by night, but their daytime occupation of flat grasslands means that the latter environment exerts the vast majority of the selective pressure, as it is on the plains that they compete with other species. Other than maintaining the ability to climb short distances, geladas would not be expected to be directly adapted to complex topography but rather to plains survival.

If hominins are indeed adapted to using complex topography as their primary habitat rather than as a refuge, we would not expect them to share many adaptations with either savannah baboons or the gelada. According to the complex topography hypothesis, hominins were actively adapting to rough terrain and would have shown a strong preference for it, while Papio baboons living on more open, smoother landscapes would have been driven along a separate evolutionary trajectory. Baboon adaptations – group defences, rapid (rather than endurance) running abilities, sociality, early onset of adulthood (see Table 39) – make them more efficient at plains survival than the australopiths would have been. Once hominins began to access flat areas they would have differed predictably as described above.

Table 39: a summary of the major ecological differences between 'savannah' baboons (Papio spp.) and Homo sapiens, and the abilities of the savannah and complex topography hypotheses to explain them. Also worth noting, although perhaps not adaptively explicable, is the fact that humans climb down cliffs/rock faces by almost exactly reversing the sequence of movements they use to climb up, moving feet first, while other primate species (Theropithecus and Papio) included do not.

	Baboon 	**Human** 	**Explained by:**	
			Traditional hypotheses	**Complex topography**
Locomotion	Quadruped	Biped	No	Yes
Defence strategy	Social	Social *and* technological	Yes	Yes
Brain size	Small	Large	?	Yes
Development	Rapid	Slow	No	Yes
Running	Sprint	Endurance	?	Yes
Dexterity	Low	High	?	Yes

As this table shows, the complex topography hypothesis can explain not only modern human anatomy and the trajectory of hominin evolution (which after all is mostly a story of fossil morphologies) but also human ecological distinctiveness as well as, or better than, existing hypotheses.

CONCLUSIONS: LANDSCAPE AND HUMAN EVOLUTION

The analyses of hominin landscapes and anatomies described above, while primarily qualitative in nature, do suggest that there is merit not only in the general exploration of primate landscapes in an appropriate conceptual context which recognises the importance of complexity and co-evolution but also in the specific proposal that tectonic landscapes are important to human evolution. These analyses suggest that:

1) The earliest hominins, whatever their body form, would have been anatomically and ecologically capable of exploiting tectonically active landscapes as an alternative to forests and semi-arboreal contexts;
2) Occupying complex topographies would have offered a competitive advantage over other taxa, including some carnivores – like lions – and the ungulates;

3) Invoking complex topography as a key component of hominin environments can explain the evolutionary trajectory of hominins and the anatomy and ecology of modern *Homo sapiens* at least as well as existing vegetation or climate based hypotheses;
4) Landscapes were indeed important to hominin (and human) evolution, and the topographies and habitats associated with tectonic activity may have been particularly important as an evolutionary 'missing link' or 'crossroads'. Any ape or monkey could have adapted effectively to complex topography, and this adaptation would then allow transition to almost any other ecological niche via a transition period of brief excursions away from secure areas.
5) Exaptation and co-evolution may have been important evolutionary processes;

This suggests that a transition from arboreality to terrestriality via complex topography can be much more easily explained if landscapes as a whole – rather than 'habitats' or vegetative/climatic zones – are considered in debates over hominin contexts. King and Bailey's TLM, and the complex topography hypothesis which emerges from it, is therefore vindicated in its proposal that landscape structures and physical landscapes specifically ought to be considered as elements of palaeoanthropological contexts. Landscapes have relevance for modern primate ecology and anatomy and (to a lesser extent) for the distributions and anatomies of modern humans, and this chapter's analyses seem to propose that they may have been important in the evolutionary past as well.

Chapter Seven: Moving Forward with Primate Landscapes

INTRODUCTION

This thesis has focused on King and Bailey's (2006) tectonic landscape model, the latest contribution to the ongoing debate over hominin evolutionary environments. Its aim was to evaluate this model's claim that landscape patterning and the physical landscape particularly were important to human evolution (as described in Chapter One). This final discussion returns to this aim to summarise and evaluate the progress which has been made and identify avenues for further exploration of primate (including hominin) landscapes.

A Summary of So Far: Contributions from this Thesis

From the outset, this thesis suggested that dealing with spatial structure in hominin landscapes, and with a model like the TLM which invokes habitat choice among hominins particularly requires that we deal with three major concepts (Chapter One). These were identified as *landscape* (the obvious focus of this work), *agency* (demonstrated to be important via analyses of baboon socioecology and found to be particularly crucial in explaining modern human distributions) and *complexity*, an inherent property of evolutionary systems which deal with ill-bounded categories like species and may be logically incoherent. This led to the proposal, on the basis of the palaeoanthropological and primatological literature and a survey of the impact of these three concepts on the state-of-the-art in the field, that before the TLM could be tested directly it was necessary to develop a basic understanding of primate landscapes more generally, as this would help identify the limitations of further analyses. Four objectives, leading ultimately back to the TLM, were therefore identified (Chapter One) and coupled with a broadly comparative approach to human evolution that might hope to avoid problems of taphonomy and uncertainty, and the progress made in meeting them can be evaluated here.

The first objective was to **map African landscapes and explore the patterns visible at different scales and their implications for the interactions between different components of the landscape system**. This, it was hoped, would help identify any correlations or covariation between factors like climate, vegetation and topography and how far it might be possible to separate their effects on primates. This was done in Chapter Three through a sequence of qualitative mapping analyses, beginning at the continental scale and proceeding down to the local (five by five degree areas, with a particular emphasis on conditions within Amboseli, Gashaka Gumti and De Hoop National Parks). Three regions – east, south and west Africa – were selected as relevant to hominins, modern humans and *Papio* baboons, the case study species used throughout. These analyses identified scale- and location-dependent patterning in extant African landscapes (indicative of a complex landscape system) under which the research designs of workers might impact their findings, but also managed to characterise the broad patterns associated with the Earth system, as manifest in Africa, in a way that suggested that complete and inextricable confounding of the effects of different elements of the landscape system was unlikely. It therefore encouraged further work on primate landscapes despite having identified complex relationships among different components of that system, and produced key information on landscape patterning that formed the basis for all subsequent chapters and will probably play a key part in future work on the topic.

Objective two was to **explore the relationships between primate anatomy, ecology and landscape**, to establish a baseline understanding of the primate-landscape system. This was done via a sequence of analyses of (a) the gross morphology of the landscapes occupied by different *Papio* baboons; (b) the relationships between baboon socioecology and landscape at the small scale; and (c) the links between landscape and the anatomy of the baboon foot (Chapter Four). These explorations showed that introducing biotic agents further complexified the landscape system, but that it remained accessible to empirical analysis provided that the limitations associated with logical incoherence (specifically that it is possible to identify apparent relationships among components of the system but impossible to verify their 'truth' and, often, to identify the direction of cause-effect links) were acknowledged. At the large scale, baboon landscapes vary as much among populations of the same allotaxon as between them, suggesting that further work will need to focus on specific patterns and questions to unpick any 'general' relationships such as overall (allotaxon or genus) habitat preferences.

At smaller scales, different possible cause-effect relationships between baboon socioecology and landscape were found in different localities, and some were observed to shift and flip as different perspectives were used to explore the same problem (the most easily explicable and sensible cause-effect links were found at Amboseli, where temporal depth was incorporated into the analysis). Bailey (2007 and references therein) noted the space-time dependence of archaeological problems and evidence, and what this thesis' analyses have suggested is that this 'time perspectivism' should be supplemented, to include not just time, but space (implicitly present in Bailey's terminology) *and* geography. The perspective we choose – or are forced to choose – in analysing relationships between organism and landscape (natural or cultural) may not only determine the questions we can answer or the phenomena we can observe, but also the spatiotemporal structure of visible relationships between components, including cause-effect links. Chapter Four also demonstrated that agency (as manifest in behaviour and socioecology) was a key component of the baboon-landscape system despite this taxon being less cognitively complex than the hominins, which simultaneously provided support for the TLM's suggestion that habitat choice might be important and raised the question of the extent to which hominins (and particularly humans) might be able to avoid biological adaptation to landscapes in favour of behavioural modification. These analyses were thus successful, even where they didn't completely resolve the relationships between the baboons studied and their landscapes, in that they provided key insights for further exploration and confirmed the relevance of studies of landscape to primate ecology and evolution.

This highlighted the importance of objective three, which was to **evaluate the role of complex cognition and agency in modifying human-landscape interactions** (Chapter Five). The analyses attempted here, which focused first on characterising the landscapes of areas of Africa that are densely occupied and then on exploring the links between human foot anatomy and landscape, were in some ways less successful than those of the preceding chapters. No clear relationship between 'natural' landscapes and human population distributions were found, as sociocultural factors like the urbanisation and migration seemed to dominate the maps produced. This prompted a return to Chapter One's definitions of landscape, and the suggestion that cultural components – like the distribution of urban areas, or even cultural preferences for substrate modification or footwear, among other factors – could best be dealt with through incorporating both natural and cultural landscapes into a single definition. Alternatively, we can view human landscapes as comprising a natural 'layer', viewed through a cultural filter. This new conceptualisation permits some analysis of the impact of landscape on human anatomy and biogeography, but may make it difficult to assess the precise contribution of each suite of factors. While this chapter's finding that human groups from different landscapes can be distinguished anatomically suggests that landscape *does* influence our species, then, it proved impossible to effectively separate out the effects of nature and culture. Viewing these as simply a special case of the interlinked biotic and abiotic components of landscape helps, but reduces our ability to say definitely whether modern humans (and by implication, the later hominins) were in fact influenced by the physical landscapes they occupied. Both Chapter Four and Chapter Five thus stressed the co-evolutionary nature of primate-landscape links and served to confirm that a picture of evolution as occurring within a complex system, perhaps as represented by the Extended Evolutionary Synthesis or Darwin-Huxley synthesis (see Chapter One) might be the most accurate, if entailing certain limitations on our analyses.

The findings of Chapters Three-Five therefore suggested several things. Firstly, they showed that it is likely that landscape pattern (and the physical landscape) were indeed important to primate (co)evolution and ecology. Secondly, they demonstrated that it is possible to begin to explore spatially explicit, complex systems like this one through a range of simplifying strategies (including reduction in the spatial scale of analysis, the incorporation of time-depth, and the generation of specific hypotheses) provided that the fact that results are perspective-dependent manifestations of an irreducibly complex whole is recognised. Finally, they suggested that it would indeed be possible, via judicious selection of comparators and research strategies (preferably incorporating time-depth and explicit, well-defined research questions) to evaluate the TLM in some depth, thus meeting the overall aim of this thesis.

This brings things back to objective four, which was to **generate and test a hypothesis of human evolution, the 'complex topography hypothesis', based on the TLM**. In Chapter

Six, therefore, King and Bailey's TLM was used as a starting point to generate three predictions of the (co-)evolutionary trajectory of the hominins, and these were then explored via qualitative analyses of the appearance and current manifestations of mammal locomotor morphology and an exploration of the 'fit' between the pressures exerted by tectonic landscapes and the pattern of human evolution observed in the fossil record. These analyses found that:

1. The hominins, whatever they evolved from, *would* have been anatomically and ecologically capable of accessing tectonically active (complex) terrestrial landscapes and would have found this easier than moving directly into flat areas;
2. These creatures would have had a competitive advantage over both the ungulates and many (though not all) carnivores, as these latter taxa – with the exception of the scansorial leopard – are not as anatomically suited to such terrain, and;
3. The complex topography hypothesis fits well with the observed trajectory of hominin evolution and can explain uniquely 'human' anatomical and ecological traits at least as well as traditional hypotheses.

Although it is worth noting that even here, cause-effect relationships could not be precisely specified and may change with the scale of observation (for instance, it is intuitively 'obvious' that at the deep-time scale the carnivores and ungulates lost certain limb bones in response to co-evolutionary pressures linked to locomotor requirements, but equally that at a smaller scale, the locomotion of, for example, the lion is at least in part determined by these losses), this chapter's analysis was thus generally successful in determining that landscape has, so far, been unfairly omitted from the palaeoanthropological study of environments.

The Implications of This Thesis

One of the overarching 'themes' of this thesis has been the fact that landscapes, and the evolutionary systems which incorporate them, are inherently complex (co-evolutionary, logically incoherent and ill-bounded). This complexity is something palaeoanthropologists can no longer afford to ignore. There is a tendency, when faced with an irreducibly complex problem of this type, to either suggest that it is interesting but cannot be solved because of imperfections in the data (see Chapter One) or that it can be simplified by selective choices of study samples. A key example here would be in the use of comparisons of 'arboreal' and 'terrestrial' primates in the identification of characteristic anatomies that can then be used to diagnose the adaptations of the hominins. Many studies of this type note ambiguities or complicating factors – like, for instance, the fact that many species are not exclusively arboreal or terrestrial, or that certain anatomical factors are not unique to a single locomotor type, but then proceed to generate a narrative which designates some of these features as relics or convergences and explains observed patterns *as if they are the result of simplex adaptive* *evolution in a historical context*. Such narratives – like the one produced here for the complex topography hypothesis – certainly have their place as sources of predictions, concepts and models and as triggers of further analysis, but cannot in light of this thesis' findings be defended as potentially 'true'; rather, they are perspective-dependent and simplified versions of a complex whole, and, as such, are unlikely to prove mutually exclusive or even opposable. This has a variety of implications for further research on this subject.

Complexity, Landscapes and Research Design

This thesis does not advocate throwing away traditional research design strategies, like the hypothetico-deductive method which contrasts simplified groups of taxa. Rather, it proposes that a more realistic research design – in which a range of studies from different perspectives are integrated, and the simplifications which are made are explicitly registered and justified, would be more promising. We cannot give up on interesting problems just because the data isn't perfect: instead, we need to be upfront about the conceptual and methodological simplifications we have applied, and how these contrast with other situations and projects. An explicit focus on complexity, its sources and products, and on theoretical paradigms which can accommodate these features, is important, especially where new projects and new landscapes are to be tackled.

Conceptualising (Co-)Evolution

One thread which has run throughout this thesis is that of evolutionary theory, to which the analyses above have made several contributions. In Chapter One, the 'neo-Darwinian' (Wallacean) synthesis was contrasted with the Darwin-Huxley model of evolution and its descendent, the 'extended evolutionary synthesis'. This latter model is better able to recognise nonlinear dynamics in evolutionary systems, co-evolutionary processes (especially those involving non-biological agents like natural landscapes or societies, as proposed here) and offers a wide-ranging perspective on evolutionary processes which includes, but is not limited to, 'adaptation'. Its usefulness is demonstrated in later chapters where complexity is apparent in all case studies, and by the general appearance of perspective-dependent, irreducible and highly complex landscape systems.

The evolutionary processes identified in these analyses include not just (complex) co-evolution but also *exaptation*, proposed by Gould and Vrba (1982) as an alternative to the term 'preadaptation'. Preadaptations appear where a suite of adaptations suit an organism for moving into a new niche, but the term carries implications of directed change and can be misinterpreted. Exaptation, in contrast, occurs when any character – previously adaptive or not – is co-opted for a new use (Gould and Vrba, 1982). It implies that the current utility of a feature carries no implication of its original use – which seems fitting in a complex, co-evolutionary scenario and especially where a range of generalist primate adaptations can be co-opted to occupy the same terrain, as proposed here. In fact, in any transition period from one habitat (or niche) to another, exaptation is likely, at least to a certain extent: if the organism concerned completely lacks traits which would enable it to move into the new niche, the transition (however much it re-shapes existing body plans and ecologies) would never be initiated, or would end rapidly in extinction. I therefore propose, on the basis of this thesis' new emphasis on complexity and co-evolution between organisms and landscapes, that exaptation as an evolutionary process is probably more important than has previously been recognised.

It is also interesting that evolutionary processes, like landscape patterns, are perspective dependent. What in Chapter Six is presented as a sort of 'missing link' in human evolutionary theory, the use of complex topography as a step in the evolutionary journey of the hominins, may in fact – at larger spatiotemporal scales – be an example of an entirely different process, specifically refugium shift from trees to rough terrain (Stewart and Stringer, 2012). Following the logic of complex landscapes as a 'crossroads' which can effectively help any ape or monkey to swap from one niche to another, moreover, suggests that this might be a more general pattern in the hominoid (or even primate) fossil record. A sequence of transitions from trees to the ground, via complex topography, could lead to bouts of terrestrialisation and adaptive radiation into niches in both habitats. This matches well with what we see in the fossil record of the hominins, and could (potentially) contribute to our understanding of the Miocene apes, which also seem to undergo rapid adaptive radiations in various contexts and biogeographic expansions and contractions of available landscapes (Folinsbee and Brooks, 2007, Harrison, 2010). This is an area for further study, as the logical and conceptual expansion of this theory – and explorations of its validity – do not fit within this thesis.

In summary, then, this thesis has contributed to evolutionary theorisation both about the hominins specifically (the 'complex topography hypothesis') and more generally. It has highlighted the role of complex co-evolution, not just between taxa but between landscapes and inhabitants, and identified a potentially important role for exaptation. It has also noted that evolutionary processes are scale- and perspective dependent, and that far from identifying a 'unique' factor in hominin history, these studies of landscape may have identified an instance of a more general mechanism for primate evolutionary change.

Dealing with 'Fuzzy' Categories

Another element of this thesis which perhaps has seen less discussion in individual chapters is the importance of categories with fuzzy boundaries in studies of evolution. The definition of complexity given in Chapter One notes that ill-boundedness and logical incoherence are key features of complex systems, and in the case of evolutionary systems, the most obvious ill-bounded categories are species. Throughout this thesis, species have been treated as having 'fuzzy' boundaries (in accordance with Chapter One's note that with strict, well-defined boundaries progress is impeded by logical incoherence and the failure of systems models), but the implications of this choice have not yet been fully spelled out. 'Fuzzy' categories, in evolutionary terms, imply the existence of some specimens which either do not fit neatly within any category or – more likely – lie on the boundaries, often in areas of overlap. This implies interbreeding, known to be extensive in animals and plants and to occur in a range of primate taxa, including the baboons and probably some hominoids/hominins (Arnold and Meyer, 2006, Arnold, 2009). This interbreeding may be historical or extant, and extensive or limited, but must be recognised as a characteristic of systems with ill-bounded categories.

Implied interbreeding, in the past and the present, suggests that evolution among the primates – as conceptualised here – was probably *reticulate*, i.e. involved not simple, clear linear progressions (perhaps including anagenesis, depending upon species definitions) interspersed with cladogenetic events but rather a complex 'web' of exchanges with periodic separations and integrations of populations, lineages and species which interact in different ways. This too has important implications for evolutionary theory and the processes which can be recognised, as it combines with the perspective-dependence observed among primate landscapes to suggest that it is not that we cannot access the 'true' pattern of co-evolutionary history but that this pattern is, in fact, actually plural and complex. This would explain the appearance of broad differences between the landscapes of different baboon allotaxa combined with both (a) very minor differences between overlapping populations of different taxa in the same landscape (e.g. in the Kenyan anatomical study) and (b) major differences in small-scale landscape use patterns among adjacent, presumably interbreeding troops of the same allotaxon; the different perspectives used in these studies are picking up the reticulated web at different resolutions and thus identifying different manifestations of it. This is likely also to be the case for hominins and hominoids more generally, and ought to be considered and incorporated into the research designs and conceptual frameworks used in their study.

A specific issue arising from the incorporation of reticulation into models of human (and other organism) evolution is the question of whether the concept of an 'LCA' (last common ancestor) is actually meaningful. The LCA concept was used in Chapter Six to denote a morphospecies from which the hominins and panins diverged (rather than in the more formal sense of the youngest individual or small group – population or troop – which is actually genetically ancestral to all living chimpanzees and humans). If we recognise reticulation, however, the chance of such an ancestor actually existing decreases dramatically, as it becomes more likely that what actually happened in hominin history was a series of convergences and divergences among populations which were partially separated (perhaps via cultural mechanisms). In a population crash, however, those cultural mechanisms might cease to function and we would expect to see reticulation not only between partially separated lineages but between groups which have become quite distinct and been separate for some time. This would produce a highly complex evolutionary tree (or web), rather than a simplex one (see Figure 122). 'Small-scale' reticulate evolution, with interactions between recently diverging taxa (subspecies or species) would presumably produce a computably complex tree, as in the middle of this figure, but long-term divergence followed by re-integration, and a complex pattern of range expansions and contractions and demographic changes is more likely to produce a model that appears irreducibly complex (like that at the base of Figure 122), where the only true common ancestor of the taxa concerned occurred so much earlier than the morphospecies which gave rise to them, that to speak of an LCA is essentially meaningless. Whichever pattern one chooses to follow through the tree produces a different LCA, a phenomenon already known from genetic research but much less widely discussed in subjects dealing with whole organisms. The reality of the situation, and the implications for our concepts of LCAs throughout evolutionary history thus warrant further research.

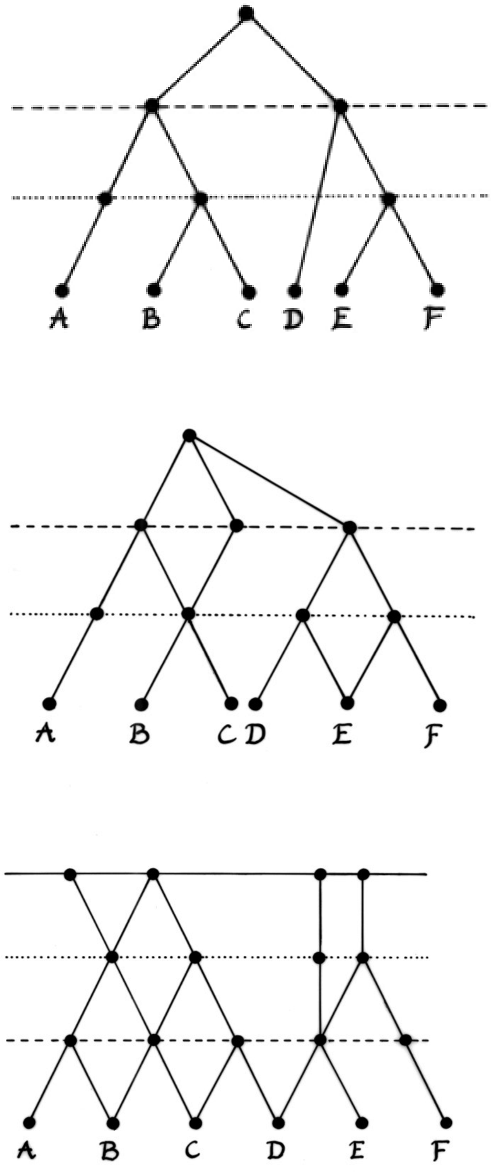


Figure 122: three sample evolutionary trees, one showing a simplex system (top) akin to that predicted by neo-Darwinian theory; one showing a computably complex system (middle) with reticulation among sublineages, and one showing an uncomputably complex system (bottom). Images courtesy of and copyright Nick Winder.

FINAL THOUGHTS AND FUTURE DIRECTIONS

The brief discussion of the findings of this thesis in context has identified several major conclusions, specifically that:

1. Landscape patterning, and the physical landscape particularly, *is* relevant to understanding primate evolution, and would benefit from further research;
2. The ‘complex topography hypothesis’, based on the TLM, is a valid alternative to existing models of hominin evolution;
3. Landscape patterns and evolutionary processes are (space- time- and location-) dependent, and the interactions between factors can shift and flip as the focus moves from one perspective to another;
4. A broad, co-evolutionary theory which can handle complexity, perspective dependence, reticulation and interactions across the nature-culture (or biotic-abiotic) divide is required for research into primate landscapes generally and palaeoanthropology specifically;
5. Such research will almost always require simplifying assumptions, which could take any of a variety of forms but should be explicitly stated, and;
6. Despite this complexity, research into primate-landscape *is* possible and potentially of significance for our broader understanding of evolutionary patterns and processes (among the hominins and other groups), the development of state-of-the-art approaches and methodologies for investigating such topics, and our wider understanding of modern species' anatomy and ecology.

Further work on the subject could usefully include: incorporating time-depth into studies of baboons for comparison with humans; extending the perspective of the hominin studies to consider hominoids and to characterise the broader evolutionary patterns and processes which characterise this group; and working explicitly on a multi-perspective synthesis of the role of landscapes, complexity and reticulation in human evolution. Two specific areas to be followed up include (a) the question of evolutionary processes and scaling effects linked to perspective in the complex topography hypothesis and (b) the role and implications of reticulate evolutionary patterns.

Definitions and Abbreviations

This section collects definitions of some key terms and abbreviations used throughout this thesis, with the exception of the abbreviations of measurements of the foot bones, which are defined in Chapter Two, Tables 5-16 and again where they recur in later analyses.

Agent: an entity capable of making choices in their actions.

Australopiths: hominins of the 'australopith' grade or ecological group, including members of the genera *Australopithecus* and *Paranthropus*.

Complexity: a state of ill-boundedness and logical incoherence (see Chapter One for discussion). Simplexity is its opposite.

EARV: the East African Rift Valley.

Environment: the surroundings in which a subject lives, including both biotic and abiotic (including cultural) components.

GIS: geographical information system.

GMM: geometric morphometrics, a family of techniques for analysis of anatomical co-ordinate data.

Hominid: a member of the family Hominidae or great apes (including *Pan*, *Gorilla*, *Pongo* and the hominins).

Hominin: a member of the tribe Hominini, which comprises all those species more closely related to modern *Homo sapiens* than to *Pan paniscus* and *Pan troglodytes*.

Hominoid: a member of the superfamily Hominoidea or apes (including the gibbons and hominids).

Human: here used only for modern *Homo sapiens*.

Ka: thousands of years ago.

Landscape: at its most basic, a spatially structured **environment**, but see also Chapter One.

Ma: millions of years ago.

MS: modern synthesis (of evolutionary theory).

Physical landscape: the land surface or substrate. Physical landscape variables in this thesis include topography, topographic roughness, geology and soil type.

TLM: the tectonic landscape model, proposed by King and Bailey (2006) and the basis for this thesis' discussion of hominin landscapes.

TMM: traditional morphometrics, a family of techniques for the analysis of measurements of anatomical shape.

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