Exploring morphological generality in the Old World monkey postcranium using an ecomorphological framework

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Abstract

Nearly all primates are ecologically dependent on trees but they are nonetheless found in an enormous range of habitats, from highly xeric environments to dense rainforest. Most primates have a relatively 'generalised' skeleton, enabling locomotor flexibility and facilitating other crucial functions, such as manual foraging and grooming. In this paper we explore associations between habitat, locomotion and morphology in the forelimbs of cercopithecids (Old World monkeys), contextualising their skeletal ecomorphological patterns with those of other mammals, and complementing functional morphological analyses with phylogenetic comparative techniques. We investigate the ecomorphological signals present in the generalised primate postcranium, and how an ancestral arboreal 'bauplan' might be modified to incorporate terrestriality or exploit distinct arboreal substrates. Analysis of ecomorphological variation in guenons indicates that terrestrial *Chlorocebus* species retain core elements of a general guenon form, with modifications for terrestriality that vary by species. Adaptation to different modes of arboreality has also occurred in *Cercopithecus*. The considerable morphological similarity in the guenons sampled emphasises the importance of generality in the primate postcranium – much forelimb variation appears to have emerged stochastically, with a smaller number of traits having a strong functional signal. Analysis of a broader sample of cercopithecids and comparison with felids, suids and bovids indicates that although the cercopithecid humerus has functional morphological signals that enable specimens to be assigned with a reasonable degree of certainty to habitat groups, there is considerable overlap in the specimens assigned to each habitat group. This probably reflects ecological dependence on trees, even in predominantly terrestrial species, as well as the multiple functions of the forelimb and, in some cases, wide geographic distributions that promote intraspecific variation. The use of phylogenetic correction reduced the discriminatory power of the models, indicating that, like allometry, phylogeny contains important ecomorphological information, and should not necessarily be factored out of analyses.

Key words

Cercopithecid, suid, felid, bovid, habitat, arboreality, discriminant function analysis, phylogenetic comparative methods.

1. Introduction

Examining the relationships between skeletal form and function is a cornerstone of ecomorphological enquiry, which seeks to understand the relationships between morphology and ecology. Although there are non-functional influences on form, such as genetic drift and phylogeny, there are also many, often interacting, functional demands, including locomotion and posture, diet, thermoregulation and social behaviour. One of the earliest studies of 'ecological morphology' – now more often referred to as ecomorphology – examined the ecological underpinnings of a variety of form-function relationships in *Anolis* lizards, correlating substrate use, location and perch height with body mass and shape, and considering differences in locomotion, foraging and display behaviour (Williams 1972). In the forty years since then, numerous studies have demonstrated the links between form, function, and ecology in a wide range of animals, including primates. Although there is huge potential to examine ecomorphological correlates of social behaviour in primates, many existing studies focus on form-function relationships in a dietary context, or the direct associations between habitat, locomotion, and morphology. In this paper, we explore the latter, examining ecomorphological variation in the forelimbs of cercopithecids (Old World monkeys), contextualising their skeletal patterns with those of felids (cats), suids (pigs) and bovids (antelopes), and complementing our functional morphological analyses with phylogenetic comparative techniques.

Nearly all primates are dependent ecologically on trees but they are nonetheless found in an enormous range of habitats, from highly xeric environments to dense rainforest. Even in very closely related species, clear morphological differences related to habitat preference, locomotor behaviour and ecology may be evident. In what are now regarded as classic papers on Old World monkey ecomorphology, Fleagle (1977) and Rodman (1979) explored postcranial divergence in sympatric species of *Presbytis* and *Macaca* respectively. Their elegant analyses demonstrated that within the same broad environment, differences in locomotor behaviour (linked to differences in the part of the canopy exploited in *Presbytis* and to terrestrial versus arboreal travel during foraging in *Macaca*) resulted in divergent limb proportions, muscle lever arms and joint mobility, which could be correlated with skeletal traits. Understanding the correlations between ecology and function that are reflected in the skeleton allows ecomorphological approaches to be used in palaeobiology to reconstruct the behaviours and habitats of extinct organisms. Underpinning this is an assumption of uniformitarianism – that there is a consistent and predictable relationship between the morphology of a structure and the task to which it is adapted. When compared across different species or families, this may be indicated through the presence of convergent, homoplastic features linked to the morphology of the quadrupedal mammalian skeleton. Femoral head morphology is a classic example of such an 'ecomorphological' feature, with more oblong (and hence stable) femoral heads found in open-country bovids (even when not shared by a common ancestor) and more spherical heads (allowing a greater range of motion at the hip joint) being seen in forest-living bovids (Kappelman 1988). A similar but albeit less pronounced pattern is evident in primates, with predominantly arboreal species having more spherical femoral heads than do predominantly terrestrial ones (Elton 2000).

The femoral head example is deceptively straightforward. For other skeletal traits, distinctions between animals occupying different habitats may not be as clear cut or easy to interpret (Elton 2000), and there are a number of factors that potentially confound direct ecomorphological inference. When considering form-function relationships in an ecological context, it is frequently assumed that morphology is an accurate reflection of current behaviours and ecology, but in fact the environment may have recently changed and the traits examined might not yet have evolved to be optimal in that new environment. This highlights another assumption – that traits are 'optimised' by natural selection to a given environment. In fact, compromises between different functional pressures may result in a feature being just adequate for a particular task. Defining the environment or ecology of a species is also complex. Many Old World monkey species have large geographic ranges (Elton and Dunn 2015) and are relatively eurytopic. In some cases, closely related species – or even conspecifics – inhabit almost the full primate habitat spectrum. A case in point is the modern olive baboon (*Papio anubis*), populations of which are found in environments as diverse as dense bush and forest in Uganda (Rowell 1966) and desert scrub in Kenya (de Jong and Butynski 2013). This example also illustrates that although a species may have a large fundamental niche, populations or individuals are more likely to have a realised niche that contains only some elements of it. When thinking about ecomorphology in eurytopic species, we need to determine whether we are interested in correlations between species and fundamental niche or populations / individuals and realised niche. This in turn may require consideration of phylogeny at species level and developmental plasticity at population levels (Elton and Dunn 2015). In reality, with the skeletal samples available for study and patchy observational records, even for the very well-studied Old World monkeys, it is difficult to make such a clear choice. It thus might be difficult to assess with confidence whether a eurytopic species has a 'catch all' morphology to cope with the demands of its entire geographic range, or whether populations occupy distinct adaptive peaks for a given trait, allowing them to more effectively exploit their realised niche (Elton and Dunn 2015).

Most primates have a relatively generalised skeleton, retaining a clavicle and pentadactyl extremities (Le Gros Clark 1959). The generalised skeleton enables great locomotor flexibility, particularly important for exploiting varied arboreal or terrestrial / arboreal environments, as well as being crucial for other aspects of primate life, such as manual foraging and grooming. Even primate taxa that are viewed as being quite ecologically stenotopic can exhibit considerable ecological flexibility. The genus *Theropithecus* provides a good example of this. The one extant species, *Theropithecus gelada*, inhabits a restricted geographic range in the highlands of Ethiopia and Eritrea, and feeds almost exclusively on grasses, including their rhizomes and seeds. It spends a large proportion of its day sitting to forage (Iwamoto and Dunbar 1983) and has evolved some distinctive postcranial features to facilitate this, including a highly opposable thumb and forefinger to pluck grass and seeds, short phalanges to dig for rhizomes (Jablonski 1986), and distolateral splay of the femur to assist in bottom-shuffling around its feeding patch (Krentz 1993). These features are evident in most of its extinct congeners, indicating that members of the lineage were, to a greater or lesser extent, specialist grass foragers (Jablonski 1986; Krentz 1993). However, the skeleton of *Theropithecus* is not so highly specialised that the predominantly terrestrial genus is precluded from 'arboreal' activity: modern gelada climb cliffs to find sleeping places, and ecomorphological analysis of the skeleton of fossil *Theropithecus oswaldi* indicates that its terrestriality was akin to that seen in modern *Papio* baboons, with the ability to use arboreal substrates as necessary (Elton 2002). Its postcranial form also did not prevent *T. oswaldi* from dispersing widely in the Plio-Pleistocene, occupying parts of Spain and India as well as southern, eastern and northern Africa (Hughes et al. 2008). Morphological generality of the type seen in primates (and some other mammals, such as many carnivorans) is thus interesting from an ecomorphological perspective. If animals with a relatively generalised skeleton have considerable adaptive flexibility, how is that skeleton ‘fine-tuned’ to a given environment, how do we interpret and understand ecomorphological signals in generalised skeletons, how ‘strong’ are ecomorphological correlates likely to be, and how might these factors influence reconstructions of locomotor behaviours and habitat preferences in extinct animals?

By examining ecomorphological variation in cercopithecids, we aim to address the questions above by assessing how adaptation to different habitats might shape the forelimb in the generalised primate skeleton. Arboreality is an ancestral condition in the primate order (Cartmill 1972; Gebo 2004), so consideration of how an arboreal ‘bauplan’ might be modified to incorporate terrestriality or to exploit distinct arboreal substrates is integral to our research. To accomplish this, we use the guenons as a case study, comparing the ecomorphology of the terrestrial *Chlorocebus* clade with that of the arboreal *Cercopithecus* clade. Guenon crania are often viewed as being fairly homogeneous compared to their soft tissue facial features (Cardini and Elton 2008), so we examine the degree of hard-tissue heterogeneity within our forelimb sample. *Chlorocebus* and *Cercopithecus* are phylogenetic as well as ecological groupings, and we incorporate phylogenetic information alongside functional morphological analyses to help unravel the evolutionary differentiation of guenon species and their postcranial traits. For a second case study, we use multivariate techniques with and without phylogenetic correction to explore the ‘strength’ of the relationship between habitat and functional morphological signals in a wider sample of cercopithecid humeri. Alongside a general ecological dependence on trees, many cercopithecids have large geographic ranges with attendant variation in exploited habitats and are behaviourally flexible, even if their locomotor mode is dominated by terrestriality. Their forelimbs are used for manual foraging and grooming as well as locomotion. By comparing their humeral ecomorphological patterns with those of felids (that also have generalised skeletons, use their forelimbs during prey capture and, in some species, are either arboreal or incorporate climbing into an otherwise terrestrial repertoire [Meachen-Samuels and Van Valkenburgh 2008]), suids and bovids (both of which have more specialised skeletons, do not engage in manual foraging, and tend to exploit forested environments using terrestrial locomotion), we can investigate whether the less-derived humeri found in primates and felids discriminate habitat groups less well than the humeri of bovids and suids. This has implications for reconstructing the palaeobiologies and ecologies of extinct animals. We also evaluate the role that phylogeny plays in understanding ecomorphological patterns through the inclusion of phylogenetic information in some of our models.

2. Arboreality, terrestriality and generality in the guenons

2.1 Background

In our first case study, the ‘terrestrial’ guenons provide a good example of how environmental differences influence the skeleton, but also show how morphology in closely related primates can be relatively homogeneous, even if different habitats are occupied. Molecular data have indicated that the three groups of terrestrial guenons – patas (*Chlorocebus patas*), vervets (used here in the inclusive sense to encompass all taxa in the *Chlorocebus aethiops* superspecies) and monkeys of the L’Hoest’s group (*Chlorocebus lhoesti, Chlorocebus preussi* and *Chlorocebus solatus*) – are a monophyletic group and hence had a single transition to terrestriality (Tosi et al. 2004). In recognition of this, they are now all included in the genus *Chlorocebus*. All three groups move and feed on the ground for a reasonable proportion of their time (Supporting Information (SI) Table S1), although the amount of time spent in terrestrial activity is highly variable and in some groups can be less than the time spent in the trees (McGraw 2002). The patas monkey has a large home range and is particularly associated with acacia woodland (Chism and Rowell 1988). It is one of the most terrestrial extant primates, and has been described as cursorial (Isbell et al. 1998). The vervet is very versatile, but commonly exploits habitats that are ecotonal between forests and open environments (‘ecotones’ are areas of transition between one habitat type and another, such as between forest and savanna), and is also found in much more open regions (Fedigan and Fedigan 1988) such as the southern African Karoo. Although they can spend a great deal of time in the trees, especially while resting, terrestrial locomotion is more common than arboreal (Rose 1979). Members of the L’Hoest’s group inhabit montane forest and, although relatively poorly studied, appear to travel on the ground for long distances and feed terrestrially (Kingdon 1971, Kaplin 2002, McGraw 2002). It is assumed parsimoniously (Tosi et al. 2004) that the common ancestor of the terrestrial guenons (genus *Chlorocebus*) and the members of its arboreal sister clade (genus *Cercopithecus*) shared an arboreal common ancestor. Thus, the terrestrial guenon clade can be viewed as a natural experiment in primate ecomorphology, demonstrating how taxa in closely-related groups with an arboreal ancestor adapt to moving and feeding terrestrially in distinct environments. The various ways in which efficient terrestriality can emerge in primates from a form phylogenetically predisposed to arboreality is especially interesting as arboreality is the probable primitive strategy for the Order (Cartmill 1972; Gebo 2004).

2.2 Sample and data collection methods

Morphological data, in the form of traditional linear measurements, were collected by one of us (AUJ) using Sylvac digital calipers and a computer interface on the shoulder and elbow joint complexes (see below), following Ciochon (1994) and augmented by measurements described in Ashton *et al.* (1965), Larson (1995) and Gebo and Sargis (1994). Measurements were size adjusted using the Mosimann method (in which each measurement is divided by the geometric mean of all the measurements for the individual in question: Mosimann and James 1979). The sample comprised seven guenon species including representatives of the three terrestrial guenon groups (Table 1). Postcranial skeletons for primates are relatively scarce, and some taxa, particularly *Ch. patas,* were poorly sampled in our study. We chose to retain species with small samples in analyses because of their importance for understanding the adaptive spectrum within the *Chlorocebus* and *Cercopithecus* clades. Sample sizes were broadly comparable to those reported in previous locomotor studies of guenons (Gebo and Sargis 1994; Sargis et al. 2008). Analyses were performed on pooled sexes, as sample sizes were small; size correction reduces the effects of sexual size dimorphism, and Gebo and Chapman (1993) found negligible differences in locomotion, support-use and postural behaviour between male and female guenons. Measurements (listed in Tables 2 and 3; full descriptions are available in Jansson [2006] or on request from the authors) taken on the scapula, humerus, radius and ulna were grouped according to the ‘morphological complex’, shoulder or elbow, to which they belonged. These measurements did not simply include joint surface measurements but also attachment sites for the major muscles that acted over the given joint. Thus, for example, supraglenoid tubercle length, from the scapula, was included in the elbow complex as it represents the origin of the m. biceps brachii long head, an elbow flexor. We focus on the forelimb as previous studies have indicated that it is more likely than the hindlimb – which provides power and drive – to show functional differences between taxa (Krentz 1993; Elton 2001). Measurement error was assessed by comparing measurements to a control sample comprising ten of the most complete specimens – one individual each from *C. pogonias*, *C. lhoesti*, and *C. patas*, and two individuals each from *C. mitis*, *C. ascanius*, and *C. aethiops*. These individuals were measured twice, and the accuracy of the measurements assessed using the procedure outlined by White (1991). The mean error for each measurement was then calculated, as were the mean and standard deviation of the measurement error of all the measurements. Measurements which had a measurement error above one standard deviation from this mean (> 5.04%) were omitted from analyses.

2.3 Analytical methods, results and discussion

2.3.1 Ecomorphological differences between *Chlorocebus* and *Cercopithecus*

One-way ANOVAs (analyses of variance) were conducted in SPSS 20 on the size-adjusted measurements, grouped by species and divided into functional complexes; ANOVA is robust to departures from normality although the vast majority of dimensions included were normally distributed according to Shapiro Wilk tests. For the elbow ANOVA, *Ch. patas* was excluded as it was represented by a single individual. Stepwise linear discriminant function analysis (LDA; F to enter = 3.84; prior probabilities set according to group size; covariance matrices homogeneous according to the Box's M test) was performed to determine how well the specimens discriminated into two groups, arboreal (*Cercopithecus*) and terrestrial (*Chlorocebus*), for both of the functional complexes. Tables 2 and 3 give ANOVA results. Although over half of the variables included in ANOVA had significance levels <0.05, Bonferroni post hoc tests (full numeric results not shown but divergent pairs are indicated in Tables 2 and 3) indicated nonetheless that differences were not simply driven by dichotomies between the terrestrial and arboreal guenon groups. This is illustrated for the most highly significant (<0.0001) variables in Figures 1 and 2. The results of the LDA, including the variables selected, are given in SI Tables S2 and S3. For the shoulder and elbow LDAs, 88.9% and 90.0%, respectively, of cross-validated grouped cases were classified correctly, with most misclassifications being *Chlorocebus* assigned to the *Cercopithecus* group.

As might be expected from the LDA results, *Chlorocebus* and *Cercopithecus* formed distinct groups for some variables, such as coracoid process maximum width, scapula morphological length (length of the scapula along the scapula spine) and supraspinatus fossa length (Figure 1), as well as humerus mediolateral articular surface width (Figure 2). The mediolateral articular surface width of the distal humerus, part of the elbow joint complex, is smaller in *Chlorocebus* compared to *Cercopithecus* and is consistent with previous observations in Old World monkeys that smaller joint surface sizes promote greater stability in anteroposterior 'cursorial' limb movement (Elton 2001). In the shoulder joint complex, the smaller coracoid process maximum width in *Chlorocebus* may reflect the finding that the relative mass and physiological cross sectional area (PCSA) of m. coracobrachialis, which originates on the coracoid process, were less in vervets compared to the arboreal red-tailed monkeys (*Cercopithecus ascanius*) (Anapol and Gray 2003). This, and by extension the differences between *Cercopithecus* and *Chlorocebus* coracoid process widths more generally, may be because a powerful m. coracobrachialis in arboreal guenons helps to move the forelimb medially towards branches as well as being an accessory stabiliser during descent (Anapol and Gray 2003), although as discussed below, there are numerous complexities in inferring muscle action from single skeletal traits.

The two other features of the scapula that clearly distinguished *Chlorocebus* from *Cercopithecus* are less easy to interpret. Scapula morphological length is greater in *Chlorocebus* than in *Cercopithecus.* Terrestrial primates generally have longer scapulae than arboreal ones (Preuschoft et al. 2010), cursorial mammals have a trend towards long, vertically-orientated scapulae (Zihlman and Underwood 2013), and a long, narrow scapula has been specifically noted to be a terrestrial adaptation in vervets, albeit without an extensive consideration of function (Manaster 1979). Indeed, linking function to scapula morphology is notoriously difficult (Ashton et al. 1965; Schmidt and Krause 2011). Scapular length is understood to be linked to maximum range of shoulder motion, although the exact relationships are difficult to untangle, especially as quadrupedal primates in general have long and narrow scapulae, regardless of locomotor mode, which may be related to phylogenetic inertia (Schmidt and Krause 2011). The vervet scapula has been shown to have a relatively low degree of cranial rotation (Whitehead and Larson 1994), and based on analogy with non-primate cursorial mammals, this is also assumed for *Chlorocebus patas* (Schmidt and Krause 2011). As might be expected in a terrestrial mammal, vervet scapula movement occurs in the parasagittal plane (Schmidt and Krause 2011). Our data indicate that scapular length is ecomorphologically informative in guenons, possibly related to range of movement in terrestrial versus arboreal forms. However, motion in the shoulder joint and related structures is also determined by other factors, such as clavicle length (Schmidt and Krause 2011), and the relations between these inter-related structures need to be taken into consideration when seeking morpho-functional correlates. This has an obvious disadvantage when the ultimate aim of a study is to identify functionally informative metrics that can be applied to fossils, for which associated elements of the skeleton are rarely found, and when recovered are often incomplete.

The complexities of inferring function solely from skeletal remains are also exemplified when interpreting another variable that discriminated between *Cercopithecus* and *Chlorocebus*, supraspinatus fossa length. Musculus supraspinatus, one of the rotator cuff muscles, stabilises the shoulder joint alongside m. infraspinatus (Larson and Stern 1989; Anapol and Gray 2003). Fossa size is often used as a proxy of muscle size, so a longer supraspinatus fossa, as seen in *Chlorocebus*, may be indicative of a larger m. supraspinatus. However, a large m. supraspinatus has been interpreted as a trait in arboreal primates necessary to facilitate arm-raising in the face of reduced mechanical advantage caused by a greater tubercle that projects less in order to allow greater mobility at the glenohumeral joint (Larson and Stern 1989). In vervets, m. supraspinatus is not active during the swing phase of walking but is used during support phase (Larson and Stern 1989). Musculus supraspinatus might work with m. infraspinatus to stabilise the shoulder when walking on the ground as well as providing joint stability during arm-raising when fast movement from the ground to the trees is required (as might occur with a predator threat for example) (Anapol and Gray 2003). Thus, a large m. supraspinatus (or, more accurately in our case, a large m. supraspinatus proxy) does not necessarily equate simply to arboreality but may instead reflect glenohumeral joint stability under a range of situations. Our data indicate that supraspinatus fossa length groups terrestrial guenons to the exclusion of arboreal ones; a logical ecomorphological conclusion from this is that patas and L’Hoest’s monkeys may also benefit from a stable shoulder joint used under fast velocity to move from the ground to the trees. Nonetheless, it must also be considered that muscle size in a functionally informative sense may include both muscle mass and PCSA (a measure of the number of muscle fibres in parallel), which may not give convergent perspectives. This is because muscles of similar masses might have different fibre architectures, PCSAs and hence force production capabilities (Myatt et al. 2011; Larson 2015). Conversely, muscles of different masses might have quite similar PCSAs (Thorpe et al. 1999; Larson 2015). As such, fossa size alone is unlikely to simply reflect muscle size. In any case, muscle size does not necessarily provide full information about muscle action and thus function: fibre and fascicle lengths, which dictate speed of shortening and range of motion (Wickiewicz et al. 1983; Thorpe et al. 1999), should also be considered, for example. Unfortunately, data on fibre architecture are not available for the rotator cuff muscles in *Ch. patas* (see review in Larson 2015) or *Ch. lhoesti*, but in a comparison with *C. ascanius*, the m. supraspinatus of *Ch. aethiops* appears better adapted for velocity, even though the size-adjusted masses of m. supraspinatus were not significantly different in the two species (Anapol and Gray 2003). In our study the highly significant difference ($p < 0.0001$) in supraspinatus fossa length in the Bonferroni test between *C. ascanius* and *Ch. aethiops* may indicate differences in muscle action and architecture, and by extension it may be these factors, rather than muscle mass per se, that have influenced supraspinatus fossa size in *Cercopithecus* versus *Chlorocebus*. Alternatively, overall morphology of the scapula (determined in part by the required actions of other muscles) may influence how the rotator cuff muscles attach, and hence have an impact on required muscle architecture given the functional demands of the animal (Larson 2015). Overall morphology may also constrain the morphology of constituent features. In our sample there is a highly significant correlation ($p < 0.0001$, $r = 0.817$) between scapular morphological length and supraspinatus fossa length, and thus one feature – probably relative scapula length – may be driving the other and reducing its functional meaning.

For some variables (humeral head maximum proximal projection, acromion length, delto-pectoral crest length in the shoulder complex, and anteroposterior and mediolateral radial head diameters, trochlear-radial notch combined width and bicipital tuberosity width in the elbow complex), visual inspection of plots (Figures 1 and 3) indicated that *Ch. patas* diverged from the other guenons in the sample, including its congeners. There was some statistical support for this from the Bonferroni tests, with significant differences at the alpha < 0.05 level between *Ch. patas* and *C. ascanius* plus *C. mitis* for proximal head projection, all species for acromion length, and all species except *Ch. lhoesti* for delto-pectoral crest length. Given the small sample sizes (for the elbow, data were available from only a single individual), no detailed functional interpretations will be offered here. However, based on the marked divergence in means, these differences are unlikely to be merely an artefact of sampling and reflect real interspecific differences, possibly related to function (although as *Ch. patas* has a substantially greater body mass than other guenons, this may also be influential, even with size correction). The patas monkey makes extensive use of terrestrial substrates, has a large home range and can run fast (Isbell et al. 1998; Zihlman and Underwood 2013). It has long hind and forelimbs, long tarsal bones and employs hindfoot digitigrady (Gebo and Sargis 1994; Isbell 1998; Zihlman and Underwood 2013). These are all features reminiscent of cursoriality, leading *Ch. patas* to be described as such (Isbell et al. 1998). In contrast, the congeneric vervet is described as terrestrial or even semi-terrestrial (Fedigan and Fedigan 1988; Gebo and Sargis 1994; Anapol and Gray 2003; Sargis et al. 2008), with no suggestion of specialised cursoriality. For one measurement, humeral head maximum proximal projection, which describes the humeral head projection in relation to the tubercles, *Ch. patas* is at the end of an albeit highly variable continuum of declining humeral head projection. This is entirely consistent with morphology in other terrestrial Old World monkeys (Jolly 1967; Larson and Stern 1989; Elton 2001), in which a less projecting head (or more projecting tubercles) is an adaptation for terrestriality, probably due to reduction of mobility around the shoulder (see Larson and Stern 1989 for a full review). For the other divergent variables, *Ch. patas* seems to be much more of an outlier, which may be indicative of its greater commitment to terrestriality in an open environment – ‘cursoriality’ – compared to the other representatives of *Chlorocebus*.

Strictly defined, cursoriality is a locomotor mode employing extensive long distance running, although the term is used in a highly variable fashion. Many ungulates are cursorial, and show derived postcranial features, such as loss of the clavicle (allowing an increase in stride length), loss of digits, an almost completely fused tibia and fibula, and a fused radioulnar (with consequent decrease in the ability to pronate and supinate the forelimb), that facilitate long distance running. Although *Ch. patas* has some adaptations, including longer limbs and short clavicles, that allow efficient long-distance travel (Manaster 1979; Zihlman and Underwood 2013), it is immediately obvious that it is not morphologically committed to cursoriality in the way that, for example, many ungulates are. In common with the vast majority of other primates, the patas monkey has a ‘generalised’ skeletal form (sensu Le Gros Clark 1959), retaining a clavicle and having a separate tibia and fibula, and radius and ulna. These features facilitate mobility, important for arboreality but also other tasks central to primate life such as manual foraging and grooming. Indeed, mobility, behavioural and ecological flexibility, and efficient manual foraging are probably why the *Ch. patas* musculo-skeletal system (or those of other habitually terrestrial primates living in open environments) has not converged more on the more derived cursorial form (Zihlman and Underwood 2013).

2.3.2 Function and ‘fine-tuning’

The degree of morphological overlap between the different guenons in our sample is very striking, and emphasises the importance of generality in the primate postcranium. Not all variables emerged as significant in the ANOVA, and the stepwise LDA of the shoulder and elbow selected five and seven variables respectively. Distributions that overlap between taxa indicate a morphological continuum between many of the guenons in our sample, with significant differences in species means representing modifications to an overall guenon ‘bauplan’ rather than absolute morphological commitment to a given locomotor mode, even in *Ch. patas.* Whether very similar traits are highly developmentally canalised in guenons, or maintain their similarities due to strong stabilising selection across taxa requires further investigation, which is unfortunately beyond the scope of work reported here. For the significant ANOVAs, Bonferroni tests indicate that significant results are often driven by one or two particularly divergent species, which varied trait by trait, rather than by more consistent and extensive separation of group means across the sample. From the simplest ecomorphological perspective, observational studies indicate that ‘terrestrial’ guenons do not confine themselves to the ground, and some ‘arboreal’ guenons (such as *Cercopithecus neglectus*; Gautier-Hion 1988) spend a reasonable portion of their time out of the trees. With a more fine-grained view, arboreality and terrestriality are not homogeneous entities, and there are multiple ways in which a primate can exploit the ground, the trees, or in many cases both. In the variables that emerged as significant in the ANOVA, there was no straightforward distinction between the arboreal and terrestrial clades, but instead significance was influenced inconsistently by different taxa in the analysis. One ecomorphological implication of this is that, from a common ancestor adapted to arboreality, there has been differentiation within both *Cercopithecus* and *Chlorocebus*, probably driven at least in part from relatively fined-grained locomotor adaptation. This has been noted in previous studies of guenons (Manaster 1979; Gebo and Sargis 1994; Sargis et al. 2008).

Using an example from our study, *C. ascanius* diverges (Figure 3, Table 3) from the other guenons in bicipital tuberosity width (the insertion site for the long head of m. biceps brachii), similar to *Ch. patas* but in the opposite direction. With caveats over uncritically correlating the skeletal trait with muscular characteristics, this pattern may be related to the importance of speed versus power: although relative m. biceps brachii caput longus masses do not differ significantly between *C. ascanius* and *Ch. aethiops*, relative PCSA does (with vervets being greater), as does the ratio indicating velocity (for which *C. ascanius* has the greater value) (Anapol and Gray 2003). *Cercopithecus ascanius* is highly arboreal, spending 90% of its time in the canopy and prefers slender, oblique and vertical supports in the middle canopy (Gebo and Sargis 1994). Approximately 43% of its locomotor repertoire consists of climbing and 15% leaping, higher proportions of these modes than are found in many other arboreal guenons (McGraw, 2002). Conversely it spends less time, only 39%, locomoting quadrupedally, which is low compared to many other species (McGraw, 2002), and has been argued to be highly acrobatic (McGraw 2000). This acrobatic nature in combination with its preference for slender supports (twigs) rather than branches may require greater m. biceps brachii velocity, influencing morphological divergence. Conversely, as a terrestrial animal *Ch. patas* may benefit from power rather than speed. Another example of divergence within the arboreal clade, this time from the shoulder complex, is the relatively short scapular morphological and supraspinatus fossa lengths in *Cercopithecus pogonias* (Figure 1, Table 2). This species spends less than 2% of its time on the ground (McGraw, 2002), mainly exploiting the middle and upper canopy (Gautier-Hion, 1988). As discussed above, interpreting supraspinatus fossa length is far from straightforward but this pattern could suggest that m. supraspinatus may not be as important in shoulder stabilisation in *C. pogonias* as in other sampled guenons. However, it is just as possible that the functionally informative morphological divergence is in the relatively very short scapular morphological length, a feature consistent with the committed arboreality of *C. pogonias*. *Cercopithecus pogonias* also diverges from the arboreal guenon group in having a wider distal surface of the humeral capitulum, which is consistent with its high commitment to arboreality. The narrower distal capitular widths in the other species of *Cercopithecus* may reflect retention of the ancestral form, or a functional need to maintain greater elbow stability than *C. pogonias*.

In identifying morphological overlap and generality in the shoulder and elbow complexes, we are not arguing that guenons – or indeed any other primates – show no ecomorphological adaptation to habitat or locomotor mode. Instead, we are emphasising that different preferred habitats, which may themselves be subtle, such as relative canopy position or whether the substrate routinely includes terminal branches, fine-tune musculo-skeletal traits, leading to the uneven, heterogeneous patterns we observe within and between clades. The *Cercopithecus* and *Chlorocebus* clades evolved from a common, probably arboreal, ancestor but that does not mean that members of *Chlorocebus* adopted a single terrestrial mode (see discussion in Sargis et al. 2008) nor that species of *Cercopithecus* retained the ancestral morphotype with no further modification, whether ecomorphological or not. Morphological features commonly show compromises for different functional demands, as well as exhibiting variation in response to non-functional pressures. Locomotion and posture (as adaptation to habitat use) are only two influences in a list that also includes diet, ontogeny and developmental plasticity, social behaviour and sexual dimorphism, geography, environment, and evolutionary history. It is highly likely, for instance, that some of the intraspecific variation observed, which for some traits is considerable (e.g. maximum radial neck length in vervets, Figure 2), is due to developmental plasticity, whereby individuals engage in slightly different activities during ontogeny with the skeleton and musculature responding accordingly.

2.3.3 Intraspecific variation

Six of the seven species in our analysis have geographic ranges well in excess of 1,500,000 km^2 (*Ch. lhoesti*, with a range < 200,000 km^2 is the exception; Elton and Dunn 2015), so it is also likely that for those taxa, some intraspecific variation maps onto geographic and climatic variation. The effects of geographic and climatic variation on guenon, especially vervet, cranial form has been explored in some detail (Cardini et al. 2007; Cardini et al. 2010; Elton et al. 2010). Geographic variation in guenon postcrania has received relatively little attention, primarily because of the paucity of specimens available that sample a representative proportion of the total range. The sample sizes in this study are too small, and the specimens too patchily distributed, to undertake an ecogeographic analysis, but as guenon subspecies map onto distinct geographic areas, we undertook a preliminary analysis using subspecies for the two best sampled species (*Ch. aethiops* and *C. mitis*) to assess whether there were any intraspecific differences in humeral traits. This does not give direct information about factors influencing intraspecific humeral differences, and does not show whether geography and climate has an effect on humeral morphology (because, for example, genetic drift may contribute to divergence of traits in distinct breeding populations). Nevertheless, it is a small first step in thinking about how humeral morphology in guenons varies across geographic ranges. Due to sample size considerations, not all vervet subspecies could be included in these analyses. For the shoulder complex, Mann-Whitney U indicated statistically significant differences between *Ch. aethiops pygerythrus* (n = 13) and *Ch. aethiops cynosuros* (n = 6) in supraspinatus fossa length (u = 8.000, p = 0.005) and scapula morphological length (u = 3.000, p = 0.001). For the elbow complex (*Ch. a. pygerythrus* n = 6; *Ch. a. cynosuros* n = 3), there were significant differences at an alpha level < 0.05 between the two subspecies in coronoid process projection (u = 1.000), anteroposterior radial head diameter (u = 1.000) and bicipital tuberosity width (u = 1.000). Three *C. mitis* subspecies were included in independent samples Kruskal-Wallis tests: *C. mitis stuhlmanni* (n = 15 for shoulder, n = 9 for elbow, *C. mitis albogularis* (n = 6 for shoulder, n = 3 for elbow), *C. mitis kolbi* (n = 6 for shoulder, n = 5 for elbow). For the *C. mitis* shoulder and elbow complexes, six and 10 variables respectively (SI Table S4) emerged as significant. These results suggest that, just as in guenon cranial morphology, there may be structured intraspecific difference in the postcranium, and if samples permit, further analysis taking into consideration possible explanatory variables such as climate may be fruitful.

2.3.4 Phylogeny

Inter- and intraspecific differences notwithstanding, those elements of the guenon shoulder and elbow that retain a similar blueprint highlight that there are many basic similarities in core guenon activity, such as quadrupedalism (regardless of how it is fine-tuned), manual foraging, and grooming. It is important to recognise such core similarities in ecomorphological studies. How morphological similarity reflects phylogenetic relatedness should also be considered: organisms that are more closely related may be expected to be more similar in form due to shared heritage than those that are more distantly related. We examined the role of phylogeny in contributing to guenon postcranial similarity and difference with two widely used phylogenetic comparative methods, Moran’s I (first developed to examine spatial autocorrelation but applicable in assessing the presence of phylogenetic non-independence) and Blomberg’s K (Blomberg et al. 2003; Münkemüller et al. 2012). A statistically significant positive deviation from zero in the Moran’s I test indicates phylogenetic autocorrelation (Münkemüller et al. 2012). When Blomberg's K is significantly different to zero (i.e. when $p < 0.05$), phylogenetic signal is present (Blomberg et al. 2003). When it is equal to (or very close to) 1, it indicates that change has occurred as would be expected under Brownian motion – essentially the neutral scenario, assuming constant rates of evolution over time, and one in which close relatives look more similar whereas more distant relatives accumulate differences under a random walk model (Blomberg et al. 2003). When K is below 1, there is less resemblance between closely related species than would be expected under Brownian motion (although significant results may nonetheless be obtained if K is below 1, as the phylogenetic signal may still be more than expected by chance), indicating either the effects of measurement error (on the trait or the phylogeny) or that a particular trait has adapted in some but not all members of a clade (Blomberg et al. 2003). When K is above 1, there is more resemblance between closely-related species than would be expected under the null Brownian motion model (Blomberg et al. 2003). A consensus ultrametric tree representing all the guenon species in this study was downloaded from 10K Trees (Arnold et al. 2010). Analyses were performed in R (R Core Team 2014) on species means for the variables listed in Tables 2 and 3, using the function phylosig in the picante package to estimate Blomberg's K (Kembel et al. 2010), and the function abouheif.moran in the adephylo package to calculate Moran's I (Jombert and Dray 2008).

Tables 4 and 5 give the Blomberg's K estimations and Moran's I results. The two types of analysis were largely congruent: for the shoulder variables, four out of the five significant K values were also (and the only) significant variables in Moran's I (Table 4); for the elbow complex variables, six out of the seven significant K values were also significant in Moran's I, which recovered only two additional variables that were significant for Moran's I but not Blomberg's K (Table 5). A caveat when interpreting these analyses is that although Blomberg's K performs better than Pagel's lambda with smaller sample sizes (hence not including Pagel's lambda values), our sample (with seven species) conforms to the minimum advised sample size but is far from the recommended sample of over 20 (Blomberg et al. 2003; Kamilar and Cooper 2013). Similar sample size considerations apply to Moran's I. This may mean that the p values in our study are less robust; however the K statistic itself should give a reasonably good approximation of phylogenetic signal (sensu Blomberg et al. 2003). This assumption is supported by the fact that the results of the two approaches were largely congruent (and our discussion of significant traits will be confined mainly to these congruent significant variables). In addition to the sample size caveat, use of species mean values inevitably smooths out intraspecific variation, which may be highly biological and ecologically meaningful. Blomberg's K has been used to help incorporate intraspecific variation into phylogenetic analyses (see, for example, Ives et al. 2007; Revell and Reynolds 2012), but as the approach has not been very widely used (Revell and Reynolds 2012) and the majority of mammalian ecomorphic studies (Scott and Barr 2014; Barr 2014, 2015) use species means without sample variation in phylogenetic analyses, for comparability we adopt the more traditional method.

The vast majority of variables are non-significant for Blomberg's K and Moran's I, and there are similar numbers of variables with K above and below 1, although no value is closer to 0 than 1. Confidence intervals for K are likely to be large, so interpretations are necessarily cautious, but it is possible that for some traits, such as distal capitular width (with one of the lowest K values), the within-clade variation is being driven by ecomorphological shifts in only some of the members (in that case, *C. pogonias*). Bearing limitations in mind, some other intriguing patterns emerge. Humeral head maximum proximal projection is significant for both Moran's I (> 0) and Blomberg's K (> 1). This variable is also highly significant in ANOVA and included in the LDA. Other shoulder variables falling into this category are coracoid process width and supraspinatus fossa length, as well as the elbow variable mediolateral articular surface width (distal humerus). These are functionally informative traits (discussed above) that also have a strong phylogenetic signal. This was not unexpected, as the *Chlorocebus* clade (phylogenetic similarity) shares terrestrial preferences (function), whereas the *Cercopithecus* clade is arboreal. There has been increasing debate in the literature over how phylogeny should be assessed and incorporated into classic ecomorphological analyses (Louys et al. 2013; Barr 2014, 2015; Scott and Barr 2014; Plummer et al. 2015), including whether traits with a strong phylogenetic signal pose a 'risk' when interpreting ecomorphological signal. However, function and phylogeny often travel hand in hand (Louys et al. 2013; Plummer et al. 2015), as is seen in alcelaphin bovids, for example, as well as the guenons. The advantage of examining phylogenetic signal alongside ecomorphological signal is that it enables more in-depth consideration of the evolutionary processes that gave rise to ecomorphic adaptations, including evolutionary conservatism, niche filling scenarios, and the effects of stabilising selection.

Two variables, lesser tuberosity maximum width and olecranon fossa depth, with significant Moran's I and K values do not emerge as significant in ANOVA but are selected in the stepwise LDA. The between clade variation indicated by the K value thus maps onto the LDA, for which a priori groups were *Chlorocebus* and *Cercopithecus*. Trochlear notch posterior width is significant in Blomberg's K, Moran's I, and ANOVA (with a difference in the Bonferroni tests between *Ch. aethiops* and *C. pogonias*). Again the pattern appears to be logical – divergence between clades. However, not all the patterns are as straightforward to interpret. Mediolateral humeral head diameter, trochlear gutter width, middle trochlear notch width and anteroposterior radial neck width have significant values of K (>1) and I (>0) but are not significant in ANOVA nor selected in LDA. Visual inspection of plots (not shown) indicates large standard deviations around means (and hence considerable intraspecific variation) for all four variables, probably accounting for the ANOVA and LDA results. However, for trochlear gutter width, *Ch. lhoesti* and *Ch. patas* have very similar means and were outliers compared to the other species; re-running the elbow complex ANOVA with *Ch. patas* included yields a significant result (F = 2.439; p = 0.036). Although they are not as obviously divergent in mediolateral humeral head diameter, *Ch. patas* and *Ch. lhoesti* also have very similar means for that variable. Both of these variables are proxies of joint surface size (at the elbow and shoulder respectively), and the *Ch. patas* and *Ch. lhoesti* means are lower than those of the other species, which is consistent with the more stable (or less mobile) joint expected in terrestrial animals. It seems highly probable that the close association of *Ch. patas* and *Ch. lhoesti* for these variables plus the fact that they are sister taxa in our consensus tree is influencing the K and I values. Again, this might demonstrate the interplay between function and phylogeny, with divergence from *Ch. aethiops* being marked by a different use of terrestrial habitats. Indeed, although Sargis et al. (2008) noted numerous postcranial differences between the two taxa, they also argued that for many features they were more similar to each other than either was to *Ch. aethiops.*

Coming back to our 'natural experiment', exploring how a closely-related group with an arboreal ancestor adapts to moving and feeding terrestrially in distinct environments, it appears that terrestrial guenons retain core elements of the ancestral arboreal guenon 'bauplan', even when, as is the case in *Ch. patas*, the commitment to terrestrial locomotion is great. The large number of non-significant variables for K and the clustering around 1 is consistent with our arguments for generality in the guenon postcranium, with much forelimb variation emerging stochastically and only a small number of traits appearing to have stronger functional and/or phylogenetic signals. Nonetheless, the different environmental influences on *Chlorocebus* species are apparent: rather than a single terrestrial guenon form having to fit into numerous habitats, there have been relatively modest but functionally important adaptations in each taxon. In the case of *Ch. aethiops*, noted in previous studies to be more generalist and semi-terrestrial (Manaster 1979; Gebo and Sargis 1994; Sargis et al. 2008), it is probable that its less committed terrestrial form facilitates its broad fundamental niche and, across its range, its various realised niches. Given the phylogenetic and functional relationships, it seems parsimonious to argue, as did Sargis et al. (2008) using slightly different reasoning, that *Ch. aethiops* is most similar to the ancestral terrestrial guenon. However, our analyses identified several variables in which *C. aethiops* was divergent, and character polarity is not yet clear: it is possible that some of the less terrestrial characteristics in *Ch. aethiops* represent reversals as it evolved to exploit a broader niche. The ecotone model (Smith et al. 1997) may provide a plausible partial explanation for differentiation in vervets and the other terrestrial guenons. Research on morphological divergence and gene flow in the little greenbul (*Eurillas virens*), a West African forest passerine bird, has shown that although there are high levels of gene flow between forest and transition zone populations, their morphological differences indicate selection for different forms (Smith et al. 1997). This is probably because the more variable ecotone environment promotes divergent selection and hence morphological change (Smith et al. 1997). Thus, evolutionarily significant morphological change can occur even without the strict reproductive isolation invoked in allopatric speciation / forest refuge models (Smith et al. 1997), underlining the potential importance of ecomorphological adaptation. The modern vervet is often described as a forest fringe inhabitant (Fedigan and Fedigan 1988), so the ancestral vervet may have diverged from other terrestrial guenons in such a setting through the selective pressures of the less stable ecotone between forest and savanna, leading to its observed morphology. Although this scenario is highly speculative, members of the *Ch. lhoesti* group, the terrestrial forest guenons, descending from the trees to exploit a novel niche may thus bear more resemblance to the first terrestrial guenons, with the highly open habitat-adapted *Ch. patas* becoming highly morphologically and behaviourally divergent through commitment to terrestriality in savannas.

3. Skeletal ‘generality’ and implications for ecomorphic analysis

3.1 Background

The retention of morphological features that facilitate ecological and behavioural flexibility is a hallmark of the primate order as a whole, both now and in the past (Le Gros Clark 1959). Primates retain a clavicle and the vast majority of extant and extinct species have separate radii and ulnae (allowing pronation and supination of the forelimb), and separate leg bones (even though, within mammals, it is the presence of a mobile fibula that is less common [Marchi 2015]). Indeed, there are few examples of major skeletal modifications within the primates. In cercopithecids, the focus of our study, the one such example is the massive reduction in the thumbs of African colobines, usually assumed to be an adaptation to arboreal suspension, as pollical reduction has also evolved convergently in the suspensory Neotropical primate genera *Ateles* and *Brachyteles* (Frost et al. 2015). However, the pattern we observed in guenons, in which a generalised skeleton was overlain by relatively modest but functionally and evolutionarily vital adaptations, is probably not unusual in other primate groups. Figure 4, a principal component analysis of size-adjusted humerus variables (see Elton 2001 and section 3.2 below), undertaken in PAST (Hammer et al. 2001), helps to visualise general ecomorphological patterns within a sample of Old World monkeys grouped by habitat preference (Table 6). The overlap between the groups is striking. Despite this overlap and the rarity of major skeletal modifications, previous studies and our discussion above have shown that there are definite functional morphological and ecomorphological adaptations across the primates based on fairly subtle alterations to a common taxonomic 'bauplan' (e.g. Fleagle 1977; Rodman 1979; Elton 2001; Ankel-Simons 2007; Michilsens et al. 2009).

For our second case study, we explore the strength of the relationship between habitat and functional morphological signals in cercopithecids in the context of other mammalian groups, specifically felids (e.g. Meloro et al. 2013), suids (Bishop 1994; Bishop et al. 1999), and bovids (e.g. Kovarovic and Andrews 2007; Plummer et al. 2008). Although numerous and diverse skeletal elements have been used in previous ecomorphological studies, we focus here on the humerus. Humeral morphology discriminates individuals from different habitat categories well in Old World monkeys (Elton 2001), and is functionally informative in other groups such as the felids (Meloro et al. 2012). This good discrimination is especially interesting considering that primates groom, forage and mechanically prepare food manually, so their forelimbs are regularly used for purposes other than locomotion. Functional traits related to foraging have been identified in the cercopithecid humerus, for example in the enlarged humeral head of the extinct, grass-plucking *Theropithecus oswaldi* (Ruff 2002), the expanded medial epicondyle (to which digital and other hand muscles are attached) of *Theropithecus* brumpti (Jablonski et al. 2002), and in the elbow flexion of the powerful manual forest floor foragers *Mandrillus* and *Cercocebus* (Fleagle and McGraw 2002). Felids, although they do not engage in the relatively fine manipulation evident in primate grooming and feeding, use their forelimbs in foraging to a degree, for example to catch or subdue prey. In contrast, the forelimbs of bovids and suids are used much more exclusively for locomotion (although even amongst these taxa forelimbs may also be used for other activities, such as kneeling to forage in some suids, and browsing or defensive strikes in some bovids). We predict that habitat signal will be stronger in the samples of non-manual foragers, as their humeri are less likely to show the compromises that are likely in a generalist forelimb engaged in a number of tasks with different functional demands.

3.2 Methods

Linear measurements on humeri were collected by the authors (cercopithecids: SE; felids: CM; suids: LCB; bovids: LCB and TP) using digital calipers attached to a computer interface. The samples are detailed in Table 6 for the cercopithecids and SI Tables S5 – S7 for the other taxa. The full measurement protocols, including assessment of measurement error, for cercopithecids, felids and suids are reported in previous publications (cercopithecids: Elton 2001; felids: Meloro et al. 2012; suids: Bishop 1994, Bishop et al. 1999). The full bovid humeral dataset is currently unpublished, but follows similar measurement protocols to the other samples in the present study, with acceptable levels of measurement error (data not shown). The linear measurements were size adjusted using the Mosimann method as described in section 2.2 above, and as each dataset had a range of species with big differences in body masses, normalised using the natural log [following Barr in press] prior to discriminant analysis. Datasets were inspected for outliers, which were removed prior to analysis. Each species or subspecies was assigned to a habitat category based on its modal wild preference. Further details are available in previous publications (Bishop 1994, Bishop et al. 1999; Elton 2001;

Meloro et al. 2013; Plummer et al. 2015) but in brief, each dataset used three or four similar categories: open (animals living and moving in savanna grassland and environments with little tree cover), mixed / intermediate (animals either using environments with greater canopy cover, or exploiting forest edges, or using open and closed environments across their range or within a given region), and forest (exploiting closed environments with considerable canopy cover, either on the ground or, in the case of felids and cercopithecids, in the trees). For the bovid sample (following Kappelman et al. 1997) the intermediate category was divided into 'light cover' and 'heavy cover'. For the cercopithecid sample, the forest category was divided into 'forest terrestrial' (including the forest floor dwellers *Mandrillus* and *Cercocebus*) and 'forest arboreal' (predominantly tree-living monkeys).

Stepwise LDAs (p to enter < 0.05 for cercopithecids, suids and felids, F to enter 3.84 for bovids [different entry criteria were used to optimise models]; prior probabilities calculated from group size), including leave-one-out cross-validation scores, were calculated in SPSS 20.0. The selected variables are detailed in Table 7 for the cercopithecids and SI Tables S8 – S10; prior to LDA, family-specific correlations were performed and individual variables excluded if they were highly correlated with others in the datasets. Linear discriminant analysis requires homogeneity of covariance matrices. Box's M was used to explore this. The suid covariance matrices were homogeneous (p = 0.118). Box's M for felids returned a p value of 0.002 (as Box's M is highly sensitive, the usual significance level for rejecting the null hypothesis of homogeneity is 0.001). The null hypothesis of homogeneity was rejected for bovids (p < 0.0001) and cercopithecids (p < 0.0001). The LDA for bovids, cercopithecids and, being conservative, felids was thus repeated using separate-groups covariance matrices rather than the standard within-groups covariance matrices, which yielded negligible differences in resubstitution rates. Linear discriminant analysis results using within-groups matrices are thus reported as that enables inclusion of the leave-one-out cross-validation that is commonly reported in ecomorphological studies (sensu Kovarovic et al. 2011); the LDA results are also useful for comparisons with other studies. In the light of the heterogeneous covariance matrices in bovids, cercopithecids and, conservatively, felids, quadratic discriminant function analysis (QDA) was performed for those groups in JMP 12.1.0. The resulting resubstitution results from QDA were then validated through the use of a 25% hold-out sample (i.e. the analyses for each taxon, using the original model variables, were re-run using only a randomly-selected 75% of the sample). For cercopithecids, analyses using further holdouts (using 50%, 25%, 10% of the sample) were also performed; specimens were also randomised into one of four categories and a separate LDA (given that covariance matrices were homogeneous) using the same variables as in the 'true' discriminant analysis was undertaken. A stepwise discriminant analysis using the same starting dataset as for the habitat-based analysis but with 'genus' as the grouping variable was also undertaken for cercopithecids.

We used two approaches to examine the effects of phylogeny on the cercopithecid humeral data. First, a phylogenetic functional discriminant analysis (pFDA), based on the method devised and described in detail by Motani and Schmitz (2011), was performed in R (R Core Team 2014). In brief, this method helps to account for phylogenetic non-independence in the categorical variable that groups classes. For our analysis, this was habitat – as discussed above and below, clades may show phylogenetic 'bias' towards a certain environment. We chose this method in preference to examining variables using phylogenetic least squares (PGLS), an increasingly commonly used technique in functional and ecomorphological studies (e.g. Walmsley et al. 2012; Scott and Barr 2013; Barr 2014, in press), partly because we wanted to explore alternative analytical methods, but also because PGLS performed on single variables does not allow consideration of phylogenetic signal in the residuals of the multivariate models that are often fundamental to ecomorphological methods. Initial analyses (full results not shown) using the standard method of including just the species means yielded an optimal Pagel's lambda of zero (equating to zero phylogenetic signal in our multivariate dataset) and a 100% classification success across all groups. Given that consideration of variation is a fundamental part of understanding ecomorphology, we extended the analysis to include all specimens per species (and hence habitat group) by treating them as individual Operational Taxonomic Units (OTUs) and adding them as polytomies at the tips of the tree. To do this, we first downloaded an ultrametric consensus tree from 10K Trees (Arnold et al. 2010) incorporating all our study species, then used TreeGraph (Stöver and Müller 2010) to add the individual specimens, relabelling them with a numeric suffix (e.g. *Chlorocebus_aethiops*1) that matched the row identifier in the datafile. We then built pFDA models using the full suite of cercopithecid humerus variables (listed in Table 8), as well as just the variables selected in the stepwise non-phylogenetic discriminant analysis (listed in Table 7). Reclassification rates and overall model structure were very similar for the two analyses, so for brevity and consistency we report in Table 9 the results from the analysis using the smaller number of variables. We also report the results of a second pFDA of those variables, undertaken on a sample restricted to the cercopithecines (i.e. excluding *Colobus*). In addition to the pFDA, we examined the phylogenetic signal of the variables themselves, using Blomberg's K and Moran's I on species means as described in section 2.3.4 above.

3.3 Results and discussion

3.3.1 Comparison of the four major taxonomic groups

Numeric results of the discriminant analyses are given in Tables 7 (cercopithecids; see also Figure 5), S8 (felids; Figure 6), S9 (suids; Figure 7) and S10 (bovids; Figure 8). Bovids were classified most successfully, followed by felids and suids. The cercopithecids had the highest numbers of misclassifications overall. There were some common trends between taxa. Open and forest samples separated on discriminant function (DF) 1 in all four taxonomic groups. This is not unexpected as the greatest ecomorphological distinction is likely to be between the open and closed (forest) habitat categories, but its consistent pattern across taxa underlines the strength of ecomorphological signals in the mammalian postcranium at the extremes of the adaptive spectrum. The intermediate / mixed groups were less straightforwardly distributed, but again some common trends were evident. In bovids and felids, the light/heavy cover and mixed groups, respectively, lay between the open and forest samples on DF1. In the bovids, the light and heavy cover groups were distinguished on DF2, and felid and suid mixed / intermediate categories occupied some distinct space on DF2. The cercopithecid open mixed category also grouped on DF2, but occupied very little distinct canonical space (overlapping considerably with the three other groups), with the forest terrestrial group also showing large overlap, albeit with slightly more distinction on DF2. Overlap occurred to a much smaller degree in the felid, suid and bovid samples.

In the cercopithecid sample, six of the 12 variables selected in the stepwise DFA were from the distal humerus, and of those four were dimensions related to the trochlea. The trochlea emerged as a key discriminating structure in all the mammalian groups, being represented in three out of the five suid variables, four of the 13 bovid variables, and one of the felid variables, even though distal humerus (elbow) variables seem less informative than proximal humerus variables in felids (Meloro et al. 2013). A complex structure integral to elbow function, trochlea morphology determines the relative ability to flex and extend the elbow, as well as stabilise the joint. Underlining the predictive importance of elbow function in our ecomorphological analyses, bicipital groove morphology (providing information about the elbow flexor biceps brachii) also emerged as informative in the cercopithecid, bovid and felid analyses. Four other variables selected in the cercopithecid stepwise DFA were from the proximal humerus, including deltopectoral crest length, greater tubercle maximum width, and maximum diameters of the mediolateral and anteroposterior articular surfaces of the humeral head. As mentioned above, deltopectoral crest length was also divergent in guenons, with *Ch. patas* having higher values than the other species. This is consistent with the data (not shown) in the bigger cercopithecid sample (that does not include *Ch. patas*) in which deltopectoral crest length is greatest in open terrestrial and least in forest arboreal monkeys. Although Krentz (1993), using a different scaling method, found no locomotor-related differences in deltopectoral crest length in cercopithecids, deltopectoral crest length is likely to indicate the mechanical advantage of the deltoid and pectoral musculature, with mechanical advantage and torque increasing as the attachment site moves away from the joint (as would occur with a longer deltopectoral crest), but at the cost of a decreased range of motion (Bonnan 2007). This is consistent with the pattern seen in our data, whereby more terrestrial animals would require more powerful fore-aft shoulder movement and arboreal animals a greater range of motion. Greater tubercle morphology was one of the discriminating variables in the bovid and cercopithecid analyses. As discussed for the guenons above, the relative size and projection of the greater tubercle influences m. supraspinatus function and also glenohumeral joint stability. Maximum mediolateral humeral head diameter, an indicator of head shape and hence relative stability (just as in the femoral head [Kappelman 1998], more cylindrical humeral heads promote stability) was selected in felids as well as cercopithecids. In the felid analysis, mediolateral humeral head diameter was joined by humeral head projection, a variable that also distinguished arboreal and terrestrial guenons.

Our comparison of the four mammalian families reveals several interesting patterns. Some humeral structures, in particular the trochlea, may consistently provide ecomorphological information across different taxonomic groups. However, proximal variables related to shoulder function were selected less than elbow variables in the suid and bovid samples. This may indicate that there is greater ecomorphological information in the artiodactyl elbow than shoulder. In other words, the shoulder joint may be more ecomorphologically informative in some taxa than others. In our case, bolstered by the analysis of guenons above, it seems that the shoulder diverges more between habitat / locomotor groups in the ‘generalist’ cercopithecids and felids. This may be related to the greater demands placed on the shoulder joint by arboreal activity in the canopy as opposed to negotiating closed environments on the ground. It may also be associated with a greater degree of flexibility required for manual grooming, foraging or grappling prey. Our results provide only equivocal support for the prediction that non-manual foragers will have a stronger habitat signal, i.e. will have lower misclassification rates in the discriminant analyses. Bovids had the best classification success, with groups that were more clearly separated on the discriminant functions. Suids, on the other hand, performed less well, with fewer discriminating variables emerging in the LDA, although this may have been a consequence of the much lower sample size, with interpretation made more complex by the fact that QDA (which yielded higher classification success overall) was not appropriate for their sample. Felids performed slightly better than suids, and both had lower misclassification rates than observed in cercopithecids. What did emerge from our analyses was that cercopithecids, as well as having lower overall classification rates, had much more overlap and less separation between groups than the other taxa. This is likely to be because of the differences in 'ecological commitment' between the groups – whereas open country bovids are totally committed to terrestriality, all cercopithecids retain a strong arboreal / generalist blueprint, with many that live terrestrially in either open habitats (such as baboons) or forests (such as mandrills) still dependent on trees, ascending them, for example, to sleep, gain protection from predators, or to forage. Another contributing factor is probably individual developmental plasticity or even subspecific adaptation in cercopithecid species with large geographic ranges and fundamental niches. Populations, as seen in olive baboons, may have distinct realised niches that could lead to morphological divergence within a species and thus increase variation. The variation we observed within *C. mitis* hints at this, but we lack a large enough sample to explore this more fully. However, it is theoretically possible, based on the premise of convergence due to function, that forest-living baboons, for example, may be morphologically closer to some arboreal monkeys than they are to their desert-living conspecifics.

3.3.2 Generality and phylogeny in the cercopithecid postcranium

The classification rates for cercopithecids, although less than for the other taxa, were well above chance, and also exceeded the 'random habitat' classification rate (used as a baseline of accuracy, sensu DeGusta and Vrba 2003) of 35.2% (20.7% crossvalidated). No single taxon drove the misclassification in the cercopithecid QDA. The single open terrestrial specimen misclassified was a *Theropithecus gelada* assigned to open mixed. One *Ch. aethiops* and two *Macaca mulatta* were incorrectly assigned to forest arboreal. The three misclassified *Papio anubis* were assigned to each of the three other habitat categories, one *Papio cyncocephalus* was misclassified as open terrestrial, and one *Papio ursinus* forest terrestrial. Three *Cercopithecus neglectus* and four *Lophocebus albigena* were assigned incorrectly to open mixed, with another three *L. albigena* misclassified as forest terrestrial; *L. albigena* had the highest number of misclassifications but visual inspection of plots and assessment for possible outliers did not highlight any anomalies other than some large standard deviations around some (but not all) variables. Two of the three *Macaca cyclopis* were incorrectly assigned to open terrestrial and open mixed. Of the open terrestrial species, one *Cercocebus torquatus* individual was misclassified as open mixed and two *Mandrillus leucophaeus* were wrongly assigned to forest arboreal. The lack of a misclassification pattern indicates that the analysis was not biased by a small number of groups consistently assigned inaccurately, and again suggests that within the sample there is a basic 'cercopithecid' form modified by habitat preference as well as influenced by other aspects of primate life and developmental plasticity. There is also no evidence that specimens were being misclassified along phylogenetic lines.

The ecomorphological groupings in the cercopithecid sample used in this case study do not map as neatly onto phylogeny as the arboreal and terrestrial guenons do. Nonetheless, within the cercopithecids as a whole, there are obvious associations between ecology and phylogeny in the *Cercocebus* / *Mandrillus* clade, terrestrial forest dwellers that forage manually on the forest floor, as well as in the exclusively arboreal extant African colobine clade. To help understand the taxonomic and hence phylogenetic structure of the cercopithecid humerus data, visual inspection of a canonical plot of the logged and size-adjusted variables by genus (Figure 9) indicated that all *Macaca* specimens grouped very closely together on DF1, separate to the other (sub-Saharan African) taxa, which (including *Colobus guereza*) also grouped together. Discriminant function 2 separated cercopithecines and colobines, and the classification rates were highly accurate (>90%), with the small number of misclassified specimens generally being assigned to a closely related genus, although a handful were misclassified along ecological lines. The very distinctive canonical space occupied by *Macaca* on DF1 (which accounts for ~46% of the variance) is intriguing, especially as it has been argued that *Mandrillus, Cercocebus* and *Macaca* share primitive papionin traits, with the *Papio / Theropithecus / Lophocebus* clade being more derived (Fleagle and McGraw 2002). The pattern we observe is unlikely simply to reflect phylogenetic 'depth' as colobines (including the ancestors of *Colobus*) diverged from cercopithecines between 14.4 and 17.9 Ma (millions of years ago), guenons split from papionins 10.3 – 12.9 Ma, and *Macaca* from the other papionins 8.6 – 10.9 Ma (Raaum et al. 2005). It is possible that although overall structure of mammalian ecological communities is convergent in Africa and Asia (Louys et al. 2011), the ways in which the members of those communities exploit their environments may be different, with consequences for morphology. Alternatively, it may reflect ecomorphological drift and convergence: Asian and African tropical environments are different, and it is thus possible that macaques, isolated from other cercopithecines, became distinct due to this geographic and ecological distance, whereas inhabiting the same types of forests led to humeral convergence between the less-closely related African colobines, guenons and papionins.

Phylogenetic comparative methods provide an alternative way to examine the phylogenetic structure of our data. For the whole cercopithecid sample, successful classification rates were considerably lower (54%) in the pFDA (Table 9) than in the QDA (or indeed the LDA, including the cross-validation). Visual inspection of the plot (Figure 10) of phylogenetic discriminant function (pDF) 1 versus pDF2 indicated that *Colobus* occupied some distinct space within the forest arboreal grouping. Analyses were therefore re-run for the sample minus *Colobus*, resulting in 10% of specimens being misclassified in QDA, 26% in the LDA and 36% in the cross-validated LDA (full results not shown, but overall model success was very similar to those using the full sample), compared to a misclassification rate of 38% in the pFDA (Figure 11, Table 9). Thus, adding phylogenetic information to our models did not improve their classification accuracy, in contrast to the findings of at least one previous study, of form-function relationships in vision (Motani and Schmitz 2011). Indeed, the lower classification successes and inspection of groupings on the discriminant function plots suggested a loss of ecomorphological structure in the data when phylogeny was built formally into our model. This implies that ecological information essential to ecomorphological studies is contained within phylogenetic non-independence. However, our cercopithecid sample – originally chosen to form the 'training set' for a discriminant analysis designed to ecomorphologically classify Plio-Pleistocene monkey fossils from African palaeoanthropological sites (Elton 2001, 2002) – was selected to represent the taxonomic structure of those extinct African monkey assemblages (dominated by large papionins and terrestrial colobines), and is not balanced across all cercopithecid tribes. It would be interesting to explore whether increasing the sample of Asian colobines would alter the patterns that emerge from ecomorphological and phylo-ecomorphological analyses of the cercopithecid postcranium, something that might also help to shed further light on the differences between macaques and sub-Saharan African monkeys.

The phylogenetic signal in the multivariate analysis (indicated by an optimal Pagel's lambda of 0.23 for the pFDA of the whole sample) was relatively modest. The values of K recovered for individual variables ranged from 0.311 – 2.061 (Table 8). Twelve out of 24 variables had significant K values, indicating that phylogenetic signal (under a Brownian motion model) was more than might be expected by chance for those traits. Moran's I (Table 8) returned statistically significant values above 1 (indicating phylogenetic autocorrelation) for ten variables, of which seven were also significant for K. Although the sample size for this set of analyses was greater than for the guenons discussed above, similar caveats about interpreting results for small samples apply. Three variables (bicipital groove depth, biepicondylar width and medial epicondyle/trochlear projection) significant for both I and K were included in the non-phylogenetic discriminant analysis. Bicipital groove depth and biepicondylar width were close to one, indicating evolution that conformed to expectations under Brownian motion. Medial epicondyle / trochlear projection, however, had a particularly high K value, suggesting greater resemblance between closely-related species than under Brownian motion, which we interpret as functional morphological adaptation maintained by stabilising selection in some clades. Visual inspection of plots (not shown) show lower values in forest arboreal monkeys (very low in *Colobus*) and higher values in open habitat / terrestrial monkeys; interestingly in the context of our discussion of guenons, *Chlorocebus* and *Cercopithecus* group together. Another variable significant for K (trochlear gutter width) had a value well above 1 (as was also observed in the separate guenon analysis). This may reinforce our argument that the trochlea is an adaptively significant structure, with its functional morphology maintained by stabilising selection, and future work would benefit from considering non-Brownian motion models to explore selection on this region. Not chosen in our DFA, humeral head maximum projection also had a significant K value well above 1, which aligns with the guenon analysis. However, by no means did all the variables selected for discriminant analysis have statistically significant K values – six of the 12 did not. Ecomorphological analysis of the type we perform here is underpinned by the assumption of morphological convergence and divergence relative to phylogeny (Kappelman et al. 1997; DeGusta and Vrba 2003; Plummer et al., 2008; Louys et al. 2103). We have seen this in the case studies we present, with comparisons between tribes and even families identifying similar, convergent solutions to the same ecological problems. Equally implicit within this assumption is that closely-related species evolve divergent solutions to different ecological problems, and the selected variables with non-significant K values below 1 may reflect the effects of such ecomorphological divergence within cercopithecid clades.

Our analyses suggest that the relationships between phylogeny, ecology, and morphology are complex. They also suggest that ecologically important information is contained in phylogeny, and that accounting for phylogenetic non-independence is not necessarily an essential part of ecomorphological enquiry. Phylogenetic non-independence may be 'risky' if it is a source of noise, but our results indicate that it provides meaningful, structured and predictable information within an ecomorphological framework. As with all studies, it is necessary to think about the purpose of an ecomorphological analysis, for example whether it is performed to understand evolution and adaptation, or to build models that give us information about how the skeleton reflects function and thus habitat preferences, even if it retains phylogenetic information. Thus, how a particular study approaches the question of phylogenetic non-independence will be dependent on its a priori hypotheses. The discussions over how to consider phylogenetic effects in ecomorphology resemble previous discussions over whether to remove or incorporate size information, with most researchers now agreeing that as the allometric component of size retains important functional and biological signals, size should not be removed but rather controlled by correcting for the isometric component. We concur with previous authors (Scott and Barr 2013; Barr 2014, 2015) who have suggested that although researchers should be mindful of its contribution, it is not necessary to factor phylogeny out completely or even partially. We also note that a number of different methods, such as the divergence-convergence (DIVCON) analysis proposed by Louys et al. (2013), exist to assess the influence of phylogeny without screening each individual variable or performing a formal comparative analysis. We thus advocate the development of further methods and approaches within multivariate frameworks that also incorporate intraspecific variation and treat ecology, allometry, and phylogeny (also employing non-Brownian motion assumptions) as potentially complementary lines of ecomorphological evidence.

4. Conclusion

Our two case studies provide convergent perspectives on the ecomorphology of the cercopithecid forelimb, helping to understand how a 'generalist' forelimb might be fine-tuned to use different locomotor strategies and exploit different habitats. Although there were some very clear adaptations to terrestriality and different types of arboreality, the guenon ANOVAs and the discriminant analysis of the cercopithecid humerus by habitat category indicate significant morphological overlap in the cercopithecid shoulder and elbow between taxa or ecological groupings. This is likely to be related to a common ecological dependence on trees in the vast majority of species, even if they are predominantly terrestrial, as well as the need to use the forelimb for non-locomotor activities – no monkey shows the clear morphological commitment to terrestriality evident in bovids for example. The large geographic ranges of some cercopithecid species are likely to promote variation that may lead to overlap between groups. The number of variables that showed no significant difference between cercopithecid groups (either *Chlorocebus* and *Cercopithecus*, or habitat categories) indicates that not all traits are under strong selective pressure due to locomotion, and this is reinforced by the results of the Blomberg K analyses that suggest that some evolutionary divergence between taxa has been stochastic. Nonetheless, differentiation related to habitat exploitation and locomotor strategy has occurred, with ecomorphologically informative regions including the humeral head, bicipital groove, deltopectoral crest and the trochlea. Some of these regions also had strong phylogenetic signals, and although 'function' and 'phylogeny' are frequently positioned diametrically in the morphological literature, our study indicates that they are highly complementary when considering ecomorphological patterns.

Our results underline the complexity of interpreting ecomorphological signals in relation to habitat preference and locomotion, which in turn is driven by the complexities of animal movement and substrate use. Most terrestrial cercopithecids are not confined to the ground, and many arboreal monkeys will leave the trees from time to time. Arboreal environments themselves are complex and heterogeneous, and cercopithecids use a multitude of locomotor behaviours depending on which parts of the canopy they exploit and how they do so, which may be reflected in their morphologies. This immense, yet often morphologically subtle, range of behaviours poses a challenge when reconstructing the habitat preferences and locomotor behaviours of extinct monkeys. It is heuristically useful to think in terms of 'terrestrial' or 'arboreal' in palaeobiological research, but a monkey faced with a predator or a tasty foodstuff is unlikely to be so prescriptive. The challenge of pinpointing a clear locomotor signal and habitat preference from the cercopithecid skeleton is exemplified by research into the behaviour of the extinct *Theropithecus brumpti*. Variously reconstructed as an arboreal quadruped (Krentz 1993), predominantly forest-living and partly arboreal similar to modern *Mandrillus* (Ciochon 1993), having a preference for closed environments but not wholly dependent on them (Elton 2000), a generally terrestrial inhabitant of riverine forest (Jablonski et al. 2002), a terrestrial quadruped similar to modern *Papio* (Gilbert et al. 2011), and a terrestrial quadruped with adaptations related to locomotion and foraging on the forest floor (Guthrie 2011), it seems logical to assume that *T. brumpti* exploited forested environments, foraging on the forest floor and travelling terrestrially most of the time, with a skeleton 'optimised' for this behaviour, but (in common with most other cercopithecids) being sufficiently ecologically, behaviourally and morphologically flexible to ascend into the canopy as required.

Having a broad ecomorphological perspective is useful in gaining a general picture of cercopithecid habitats at palaeontological sites, especially when specimens are fragmentary or not assigned to taxon (Elton 2001). However, distilling behavioural and ecological complexity into a discrete habitat category will obviously lead to imprecision and helps to illustrate why cercopithecids had generally higher misclassification rates than the other mammalian taxa in our study. We thus concur with Jablonski et al. (2002), who point out that the key to understanding the ecomorphological subtleties of individual species (considering locomotion alongside other behaviours) lies in detailed study of more complete skeletons when available. This notwithstanding, applying the principles of ecomorphology has proven extremely fruitful in efforts to reconstruct past environments, especially at palaeoanthropogical sites, with some groups (bovids) being used more frequently than others. Our results indicated that although all the taxa we studied had functional morphological adaptations that correlated with their habitat preferences and locomotor behaviours, there was a stronger and more consistent relationship between morphology and habitat preference in bovids than in other taxa, including monkeys, which, like bovids, are relatively abundant in the fossil record. This reinforces the utility of bovids, with their less generalist skeletal forms, in ecomorphically-based palaeoecological reconstruction. However, because sympatric taxa exploit the same general environment in varying ways, and because understanding the ecomorphology of multiple members of a community will yield different perspectives on palaeoecology, there is considerable scope to extend ecomorphological research beyond mammalian families to extinct communities, even if some members have relatively generalist skeletal forms.

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Table 1: Sample composition for the guenon shoulder and elbow analyses

	Shoulder analysis			**Elbow analysis**[a]		
Species	**Male *n***	**Female *n***	**Total *n***	**Male *n***	**Female *n***	**Total *n***
Cercopithecus mitis	13	16	29	7	12	19
Cercopithecus ascanius	6	4	10	4	3	7
Cercopithecus neglectus	3	4	7	4	3	7
Cercopithecus pogonias	11	5	16	12	5	17
Chlorocebus patas[a]	1	1	2	1	0	1
Chlorocebus lhoesti	2	2	4	2	2	4
Chlorocebus aethiops	10	12	22	5	6	11
Total	46	44	90	35	31	66

[a] *Ch. patas* excluded from elbow ANOVA but included in elbow DFA.

Table 2: ANOVA results for the guenon shoulder complex

Variable	Bone	F	p^a	Significantly different pairs in post hoc Bonferroni test
Anteroposterior humeral head diameter	Humerus	1.601	0.157	–
Mediolateral humeral head diameter	Humerus	1.253	0.288	–
Humeral head maximum proximal projection	**Humerus**	**5.601**	**0.000**	***Ch. aethiops – C. ascanius*** ***Ch. aethiops – C. mitis*** ***Ch. patas – C. ascanius*** ***Ch. patas – C. mitis***
Greater tubercle maximum width	Humerus	1.213	0.308	–
Lesser tubercle maximum width	Humerus	0.570	0.753	–
Delto-pectoral crest length	**Humerus**	**6.737**	**0.000**	***Ch. patas – Ch. aethiops*** ***Ch. patas – C. ascanius*** ***Ch. patas – C. mitis*** ***Ch. patas – C. neglectus*** ***Ch. patas – C. pogonius***
Glenoid fossa width	Scapula	2.045	0.069	–
Glenoid fossa length	**Scapula**	**3.091**	**0.009**	***C. pogonias – Ch. aethiops*** ***C. pogonias – C. mitis***
Coracoid process length	**Scapula**	**3.971**	**0.002**	***C. pogonias – C. mitis***
Coracoid process width	**Scapula**	**6.347**	**0.000**	***Ch. patas – C. neglectus*** ***C. pogonias – Ch. aethiops*** ***C. pogonias – C. ascanius*** ***C. pogonias – C. mitis*** ***C. pogonius – Ch. patas***
Acromion process length	**Scapula**	**8.696**	**0.000**	***Ch. patas – Ch. aethiops*** ***Ch. patas – Ch. lhoesti*** ***Ch. patas – C. ascanius*** ***Ch. patas – C. mitis*** ***Ch. patas – C. pogonias*** ***C. pogonias – C. mitis***
Acromion process width	Scapula	1.788	0.111	–
Supraspinatus fossa depth	Scapula	1.491	0.191	–
Supraspinatus fossa length	**Scapula**	**20.572**	**0.000**	***Ch. aethiops – C. ascanius*** ***Ch. aethiops – C. mitis*** ***Ch. aethiops – C. neglectus*** ***Ch. aethiops – C. pogonias*** ***Ch. patas – C. ascanius*** ***Ch. patas – C. mitis*** ***Ch. patas – C. pogonias*** ***Ch. lhoesti – C. pogonias*** ***C. pogonias – C. mitis*** ***C. pogonias – C. neglectus***
Supraspinatus fossa width	Scapula	1.862	0.097	–
Infraglenoid/coracoid process distance	**Scapula**	**3.684**	**0.003**	***Ch. aethiops – C. mitis***
Infraglenoid/acromion distance	**Scapula**	**3.098**	**0.009**	***C. pogonias – C. neglectus***
Medial extreme of acromial facet to inferior angle	Scapula	1.898	0.091	–
Scapula morphological length	**Scapula**	**13.243**	**0.000**	***Ch. aethiops – C. ascanius*** ***Ch. aethiops – C. mitis***

				Ch. aethiops – C. pogonias ***Ch. patas – C. ascanius*** ***Ch. patas – C. pogonias*** ***Ch. lhoesti – C. pogonias*** ***C. pogonias – C. mitis*** ***C. pogonias – C. neglectus***

[a]Statistically significant results highlighted in bold text

Table 3: ANOVA results for the guenon elbow complex

Variable	Bone	F	p[a]	Significantly different pairs in post hoc Bonferroni test
Bicipital groove width	**Humerus**	**2.447**	**0.044**	***Ch. lhoesti – C. mitis***
Bicipital groove depth	**Humerus**	**3.953**	**0.004**	***Ch. aethiops – C. ascanius*** ***Ch. aethiops – C. pogonias***
Mediolateral articular surface width	**Humerus**	**6.551**	**0.000**	***Ch. aethiops – C. ascanius*** ***Ch. aethiops – C. mitis*** ***Ch. aethiops – C. pogonias***
Posterior trochlear articular surface width	**Humerus**	**4.934**	**0.001**	***C. ascanius – Ch. aethiops*** ***C. ascanius – Ch. lhoesti*** ***C. ascanius – C. neglectus*** ***C. ascanius – C. pogonias***
A-P lateral trochlear diameter	Humerus	0.998	0.427	–
Distal trochlear width	**Humerus**	**4.314**	**0.002**	***Ch. aethiops – C. mitis***
Distal capitular width	**Humerus**	**5.449**	**0.000**	***C. pogonias – Ch. aethiops*** ***C. pogonias – C. mitis*** ***C. pogonias – C. neglectus***
Maximum capitular height	**Humerus**	**3.059**	**0.016**	***C. ascanius – C. neglectus*** ***C. ascanias – C. pogonias***
Medial epicondyle/Trochlear projection	Humerus	2.088	0.080	–
Trochlear gutter width	Humerus	2.311	0.055	*Ch. lhoesti – C. mitis*
Olecranon fossa depth	Humerus	1.535	0.193	–
Olecranon fossa width	Humerus	1.147	0.346	–
Supraglenoid tubercle length	**Scapula**	**3.801**	**0.005**	***Ch. aethiops – C. pogonias***
Coronoid process projection	**Ulna**	**2.808**	**0.024**	**–**
Coronoid-olecranon height	**Ulna**	**2.795**	**0.025**	**–**
Trochlear notch-olecranon length	Ulna	2.334	0.053	–
Trochlear notch-olecranon width	Ulna	0.535	0.749	–
Trochlear notch medial height	Ulna	1.311	0.272	–
Trochlear notch midline height	Ulna	0.668	0.649	–
Trochlear notch posterior width	**Ulna**	**2.421**	**0.046**	***Ch. aethiops – C.pogonias***
Trochlear notch depth	Ulna	0.746	0.592	–
Proximal trochlear notch width	Ulna	1.148	0.345	–
Middle trochlear notch width	Ulna	1.093	0.374	–
Distal trochlear notch width	Ulna	2.295	0.057	*Ch. lhoesti – C. neglectus*
Trochlear-radial notch combined width	**Ulna**	**4.860**	**0.001**	***C. pogonias – C. mitis*** ***C. pogonias – C. neglectus***
Radial notch width	Ulna	1.673	0.155	–
Radial notch height	**Ulna**	**3.592**	**0.007**	***Ch. aethiops – C. pogonias***
Radial notch posterior width	Ulna	1.838	0.119	–
Anteroposterior radial head diameter	**Radius**	**2.955**	**0.019**	***C. pogonias – C. mitis***
Mediolateral radial head diameter	**Radius**	**5.096**	**0.001**	***C. neglectus – Ch. aethiops*** ***C. neglectus – C. mitis*** ***C. neglectus – C. pogonias***
Radial head maximum articular surface width	**Radius**	**2.928**	**0.020**	**–**
Maximum neck length	**Radius**	**6.767**	**0.000**	***Ch. lhoesti – C. ascanius*** ***Ch. lhoesti – C. pogonias*** ***C. pogonias – Ch. aethiops***

				C. pogonius – C. mitis
Mediolateral neck width	Radius	2.299	0.056	–
Anteroposterior neck width	Radius	0.991	0.431	–
Bicipital tuberosity width	**Radius**	**4.778**	**0.001**	***C. ascanius – Ch. aethiops*** ***C. ascanius – C. mitis*** ***C. ascanius – C. neglectus***

[a] Statistically significant ANOVA results highlighted in bold text

Table 4: Blomberg's K and Moran's I values for the guenon shoulder complex variables[a]

Variable (mean)	**Blomberg's K**		**Moran's I**	
	K	**p**	**I**	**p**
Anteroposterior humeral head diameter	0.931	0.423	-0.269	0.636
Mediolateral humeral head diameter	**1.329**	**0.007**	**0.463**	**0.008**
Head maximum proximal projection	**1.313**	**0.005**	**0.395**	**0.002**
Greater tubercle maximum width	0.751	0.931	-0.495	0.905
Lesser tubercle maximum width	**1.117**	**0.043**	0.138	0.078
Delto-pectoral crest length	1.065	0.106	0.010	0.176
Glenoid fossa width	0.885	0.645	-0.520	0.924
Glenoid fossa length	1.007	0.220	0.060	0.093
Coracoid process length	0.807	0.831	-0.336	0.771
Coracoid process width	**1.289**	**0.005**	**0.345**	**0.004**
Acromion process length	1.017	0.235	-0.151	0.382
Acromion process width	0.931	0.492	-0.356	0.749
Supraspinatus fossa depth	0.754	0.933	-0.529	0.945
Supraspinatus fossa length	**1.264**	**0.043**	**0.326**	**0.046**
Supraspinatus fossa width	1.158	0.076	0.273	0.070
Infraglenoid/coracoid process distance	0.843	0.671	-0.433	0.756
Infraglenoid/acromion distance	0.870	0.632	-0.106	0.307
Medial extreme of acromial facet to the inferior angle	0.894	0.639	-0.499	0.893
Scapula morphological length	1.208	0.086	0.277	0.066

[a] values in bold are statistically significant.

Table 5: Blomberg's K and Moran's I values for the guenon elbow complex variables[a]

Variable (mean)	**Blomberg's K**		**Moran's I**	
	K	**p**	**I**	**p**
Bicipital groove width	1.129	0.095	0.134	0.147
Bicipital groove depth	1.048	0.215	-0.178	0.471
Mediolateral articular surface width	**1.490**	**0.020**	**0.534**	**0.028**
Posterior trochlear articular surface width	1.078	0.127	**0.238**	**0.017**
Anteroposterior lateral trochlear diameter	0.893	0.659	-0.530	0.905
Distal trochlear width	0.903	0.543	-0.320	0.614
Distal capitular width	0.808	0.859	-0.389	0.835
Maximum capitular height	0.973	0.357	0.022	0.263
Medial epicondyle/Trochlear projection	0.883	0.620	-0.395	0.816
Trochlear gutter width	**1.310**	**0.014**	**0.409**	**0.026**
Olecranon fossa depth	**1.342**	**0.007**	**0.441**	**0.006**
Olecranon fossa width	0.786	0.892	-0.453	0.902
Supraglenoid tubercle length	0.919	0.496	-0.215	0.485
Coronoid process projection	0.865	0.725	-0.371	0.795
Coronoid-olecranon height	0.982	0.269	0.014	0.266
Trochlear notch-olecranon length	1.060	0.102	0.016	0.142
Trochlear notch-olecranon width	1.041	0.174	-0.105	0.181
Trochlear notch medial height	0.902	0.606	-0.490	0.996
Trochlear notch midline height	1.006	0.300	-0.203	0.662
Trochlear notch posterior width	**1.304**	**0.016**	**0.356**	**0.011**
Trochlear notch depth	0.849	0.634	-0.449	0.885
Proximal trochlear notch width	0.830	0.770	-0.323	0.725
Middle trochlear notch width	**1.146**	**0.032**	**0.174**	**0.038**
Distal trochlear notch width	0.890	0.648	-0.524	0.966
Trochlear-radial notch combined width	0.887	0.649	-0.228	0.571
Radial notch width	**1.141**	**0.030**	0.068	0.058
Radial notch height	1.012	0.199	-0.171	0.463
Radial notch posterior width	0.944	0.431	-0.365	0.865
Anteroposterior radial head diameter	1.043	0.184	-0.088	0.307
Mediolateral radial head diameter	0.986	0.335	-0.184	0.652
Head maximum articular surface width	1.122	0.055	**0.114**	**0.019**
Maximum neck length	0.991	0.223	0.038	0.197
Mediolateral neck width	0.845	0.693	-0.260	0.543
Anteroposterior neck width	**1.104**	**0.041**	**0.059**	**0.032**
Bicipital tuberosity width	0.938	0.461	-0.196	0.556

[a] values in bold are statistically significant.

Table 6: Sample for the cercopithecid analysis

Species	**Habitat category**	**Male *n***	**Female *n***	**Total *n***
Cercopithecus neglectus	Forest arboreal	13	3	16
Colobus guereza	Forest arboreal	17	13	30
Lophocebus albigena	Forest arboreal	10	6	16
Macaca cyclopis	Forest arboreal	-	4	4
Cercocebus galeritus	Forest terrestrial	2	1	3
Cercocebus torquatus	Forest terrestrial	4	6	10
Macaca nemestrina	Forest terrestrial	2	1	3
Mandrillus leucophaeus	Forest terrestrial	4	1	5
Mandrillus sphinx	Forest terrestrial	4	3	7
Chlorocebus aethiops	Open mixed	8	8	16
Macaca mulatta	Open mixed	4	6	10
Papio anubis	Open mixed	8	8	16
Papio cynocephalus	Open mixed	8	8	16
Papio ursinus	Open mixed	10	4	14
Papio hamadryas	Open terrestrial	9	2	11
Theropithecus geleda	Open terrestrial	3	13	16
Total		106	87	193

Table 7: Results of the discriminant function analysis for the cercopithecid humerus

i. Standardised canonical discriminant function

Variable[a]	Function 1[b]	Function 2[c]	Function 3[d]
Trochlear gutter width, maximum mediolateral dimension	0.056	0.568	-0.106
Biepicondylar width: maximum width across the distal humerus between the epicondyles	-0.683	-0.343	0.216
Medial epicondyle / trochlear projection: measure of the maximum size and projection of the medial trochlear ridge	0.370	-0.219	0.206
Deltopectoral crest maximum length	0.265	0.232	0.350
Olecranon fossa depth	-0.292	0.094	0.370
Mediolateral width of shaft at its midpoint	-0.282	-0.401	-0.334
Maximum width of the greater tubercle	0.064	0.432	0.838
Maximum diameter of the humeral head in the anteroposterior dimension	0.519	0.406	-0.422
Maximum distal projection of the medial side of the trochlea	0.296	-0.142	0.244
Distal trochlea width, greatest width across distal articular surface	0.376	0.280	-0.193
Bicipital groove depth	0.174	0.275	-0.653
Maximum diameter of the humeral head in the mediolateral dimension	-0.173	-0.236	-0.405
Percentage of variance	70.7%	22.1%	7.3%

[a] Arranged in order of stepwise entry to model

[b] Wilk's lambda = 0.223, F = 9.393 ($p < 0.0001$)

[c] Wilk's lambda = 0.575, F = 5.179 ($p < 0.0001$)

[d] Wilk's lambda = 0.860, 2.926 ($p = 0.002$)

ii. Classification matrix

	Group	Predicted group membership				Total
		Open terrestrial	Open mixed	Forest terrestrial	Forest arboreal	
LDA standard classification	Open terrestrial	21 (78%)	6 (22%)	0	0	27
	Open mixed	2 (3%)	57 (79%)	5 (7%)	8 (11%)	72
	Forest terrestrial	1 (4%)	4 (14%)	18 (64%)	5 (18%)	28
	Forest arboreal	0	9 (14%)	6 (9%)	51 (77%)	66
LDA cross-validated ('leave-one-out') classificaton	Open terrestrial	17 (63%)	9 (33%)	1 (4%)	0	27
	Open mixed	5 (6%)	53 (74%)	5 (7%)	9 (13%)	72
	Forest terrestrial	1 (4%)	6 (21%)	15 (54%)	6 (21%)	28
	Forest arboreal	0	10 (15%)	6 (9%)	50 (76%)	66
QDA standard	Open	26 (96%)	1 (4%)	0	0	27

classification[c]	terrestrial					
	Open mixed	2 (3%)	64 (88%)	2 (3%)	4 (6%)	72
	Forest terrestrial	0	1 (4%)	25(89%)	2 (7%)	28
	Forest arboreal	0	8 (12%)	4 (6%)	54 (82%)	66
QDA validation sample[d]	Open terrestrial	20 (100%)	0	0	0	20
	Open mixed	0	55 (97%)	2 (3%)	0	57
	Forest terrestrial	0	1 (5%)	19 (90%)	1 (5%)	21
	Forest arboreal	0	4 (9%)	2 (4%)	40 (87%)	46
QDA 50% holdout sample[e]	Open terrestrial	17 (100%)	0	0	0	17
	Open mixed	0	33 (94%)	0	2 (6%)	35
	Forest terrestrial	0	0	13 (1005)	0	13
	Forest arboreal	0	2 (6%)	0	29 (94%)	31
QDA 75% holdout sample[f]	Open terrestrial	8 (100%)	0	0	0	8
	Open mixed	0	19 (100%)	0	0	19
	Forest terrestrial	0	0	4 (100%)	0	4
	Forest arboreal	0	0	0	17 (100%)	17
QDA 90% holdout sample[g]	Open terrestrial	2 (50%)	2 (50%)	0	0	4
	Open mixed	6 (75%)	2 (25%)	0	0	8
	Forest terrestrial	2 (67%)	0	1 (33%)	0	3
	Forest arboreal	3 (75%)	0	0	1 (25%)	4

[a] 76.2% of original grouped cases correctly classified.

[b] 69.9% of cross-validated grouped cases correctly classified.

[c] 87.6% of original grouped cases correctly classified.

[d] 93.1% of validation sample (n = 144) correctly classified

[e] 95.9% of holdout sample (n = 96) correctly classified

[f] 100% of holdout sample (n = 48) correctly classified

[g] 31.6% of holdout sample (n = 19) correctly classified

Table 8: Blomberg’s K and Moran’s I values for the cercopithecid humerus variables[a]

Variable (mean)	**Blomberg’s K**		**Moran’s I**	
	K	**p**	**I**	**p**
Maximum diameter of the humeral head in the anteroposterior dimension	*0.522*	*0.160*	*0.057*	*0.224*
Maximum diameter of the humeral head in the mediolateral dimension	*0.620*	*0.071*	*0.185*	*0.065*
Humeral head maximum proximal projection	**1.507**	**0.001**	**0.647**	**0.001**
Anterior extension of the humeral head articular surface	0.594	0.078	-0.035	0.413
Bicipital grove width	0.455	0.223	**0.206**	**0.048**
Bicipital groove depth	***0.845***	***0.003***	***0.341***	***0.009***
Maximum width of the greater tubercle	***0.943***	***0.009***	*0.072*	*0.210*
Maximum width of the lesser tubercle	0.576	0.114	**0.317**	**0.023**
Biepicondylar width: maximum width across the distal humerus between the epicondyles	***0.942***	***0.004***	***0.324***	***0.022***
Maximum mediolateral width of the articular surface across the anterior distal humerus	0.608	0.108	0.146	0.074
Maximum distal projection of the medial side of the trochlea	***1.163***	***0.008***	*0.087*	*0.170*
Distal trochlea width, greatest width across distal articular surface	*0.360*	*0.489*	*0.142*	*0.109*
Greatest width of the capitulum across the distal articular surface	**0.713**	**0.034**	0.194	0.070
Maximum anteroposterior diameter of the lateral aspect of the trochlea	**0.669**	**0.023**	0.178	0.091
Maximum height of the capitulum in the dorsoventral (proximodistal) plane	**0.776**	**0.021**	**0.262**	**0.038**
Medial epicondyle / trochlear projection: measure of the maximum size and projection of the medial trochlear ridge	***2.061***	***0.001***	***0.284***	***0.024***
Olecranon fossa depth	*0.311*	*0.631*	*-0.162*	*0.696*
Projection of the lateral margin of the olecranon fossa	**1.553**	**0.006**	**0.580**	**0.003**
Olecranon fossa width	0.603	0.084	0.190	0.076
Greatest mediolateral width of the posterior trochlea articular surface	**1.615**	**0.001**	**0.296**	**0.012**
Trochlear gutter width, maximum mediolateral dimension	***1.796***	***0.001***	*0.180*	*0.058*
Mediolateral width of shaft at its midpoint	*0.599*	*0.067*	***0.428***	***0.004***
Deltopectoral crest maximum length	*0.623*	*0.080*	*0.047*	*0.241*
Humerus maximum length	0.498	0.175	0.079	0.190

[a] variables in bold are statistically significant; variables in italics were included in the discriminant analyses.

Table 9: Results of the phylogenetic functional discriminant analyses (pFDA), with [a] and without[b] *Colobus*

	Group	Predicted group membership				Total
		Open terrestrial	Open mixed	Forest terrestrial	Forest arboreal	
pFDA classification (including *Colobus*)[c]	Open terrestrial	16 (59%)	3 (11%)	1 (4%)	7 (26%)	27
	Open mixed	3 (4%)	21 (29%)	0	48 (67%)	72
	Forest terrestrial	0	6 (22%)	2 (7%)	20 (71%)	28
	Forest arboreal	0	1 (2%)	0	65 (98%)	66
pFDA classification (excluding *Colobus*)[d]	Open terrestrial	15 (56%)	7 (26%)	3 (11%)	2 (7%)	27
	Open mixed	2 (3%)	59 (82%)	0	11 (15%)	72
	Forest terrestrial	3 (11%)	18 (64%)	3 (11%)	4 (14%)	28
	Forest arboreal	0	11 (31%)	1 (3%)	24 (66%)	36

[a] Optimal Pagel's lambda = 0.23
[b] Optimal Pagel's lambda = 0.27
[c] 54% of original grouped specimens correctly classified
[d] 62% of original grouped specimens correctly classified

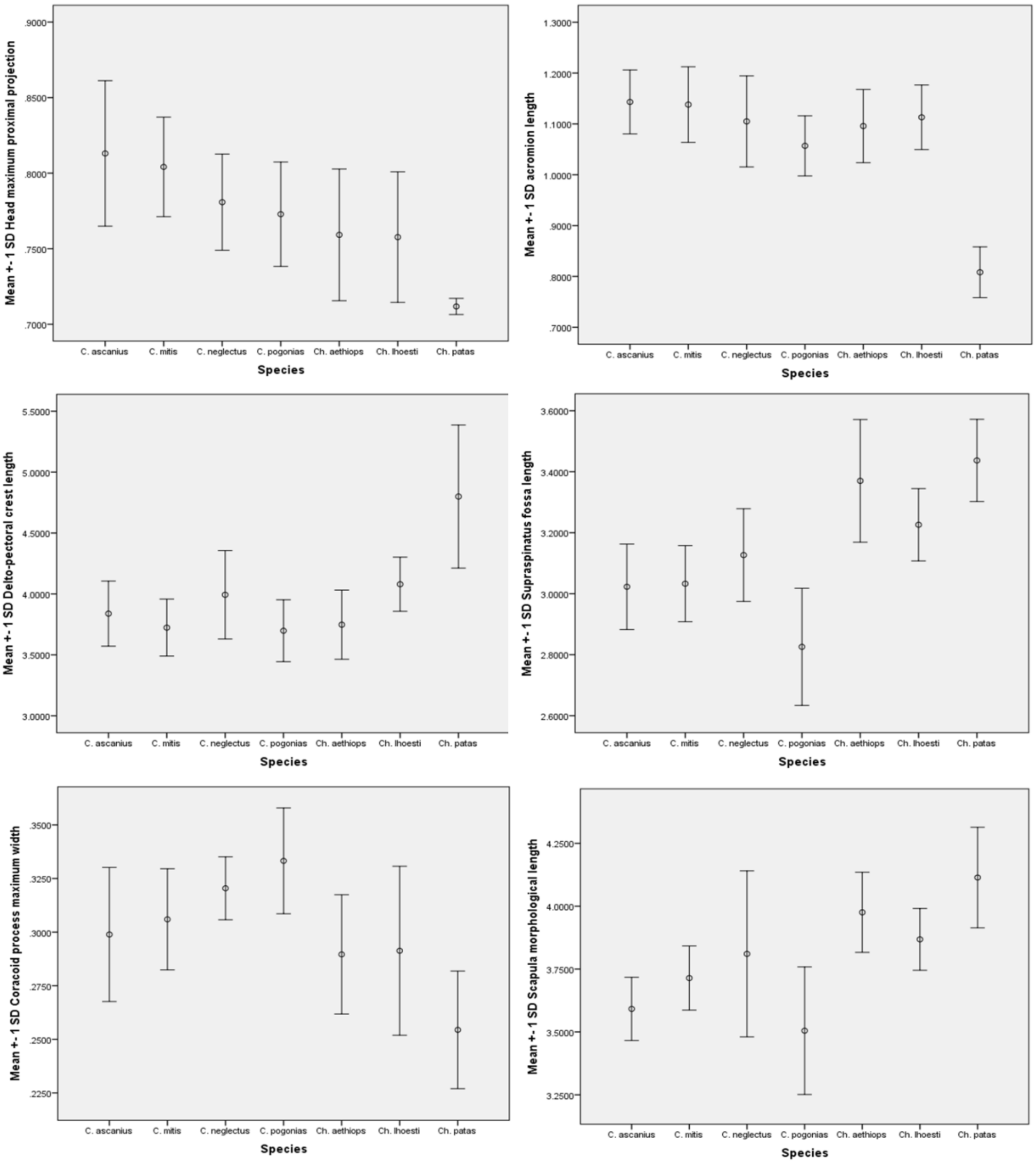

Figure 1: Means and standard deviations for the guenon shoulder complex variables that were highly significant ($p<0.0001$) in ANOVA.

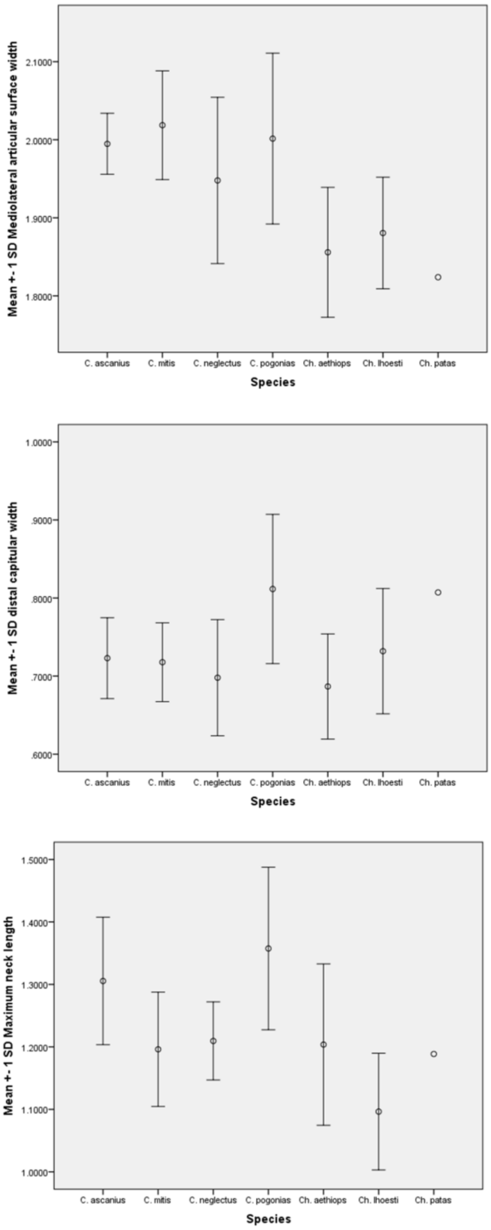

Figure 2: Means and standard deviations for the guenon elbow complex variables that were highly significant ($p<0.0001$) in ANOVA.

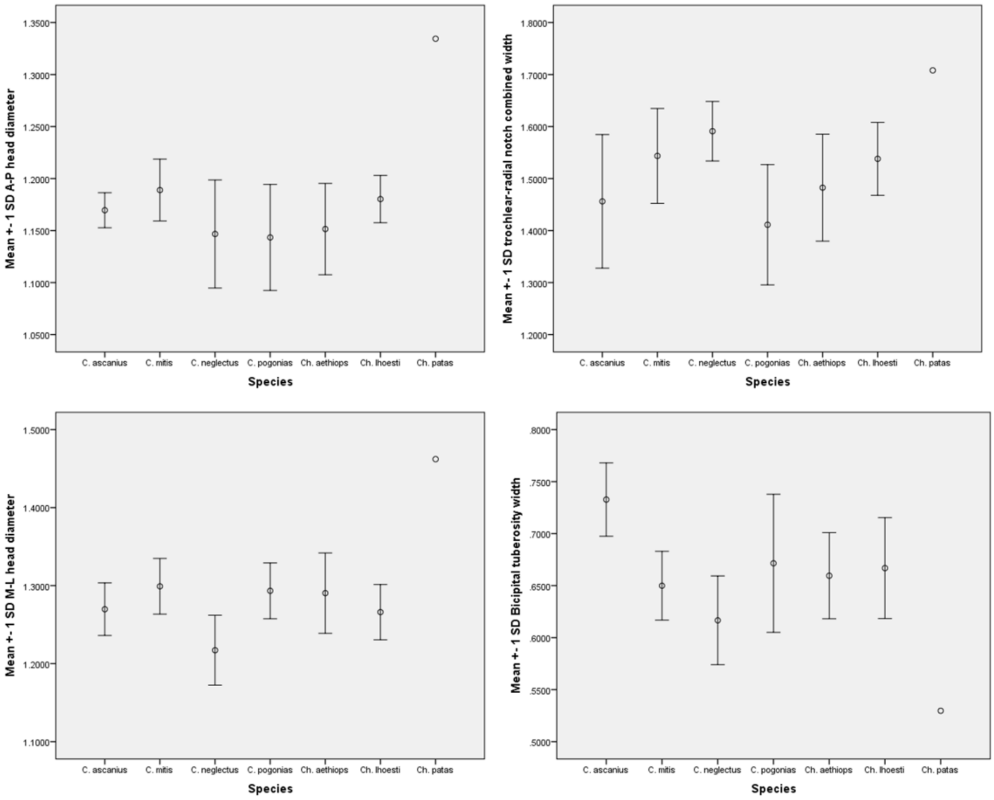

Figure 3: Elbow variables for which *Chlorocebus patas* appeared outlying (for *Ch. patas* shoulder variables see Figure 1).

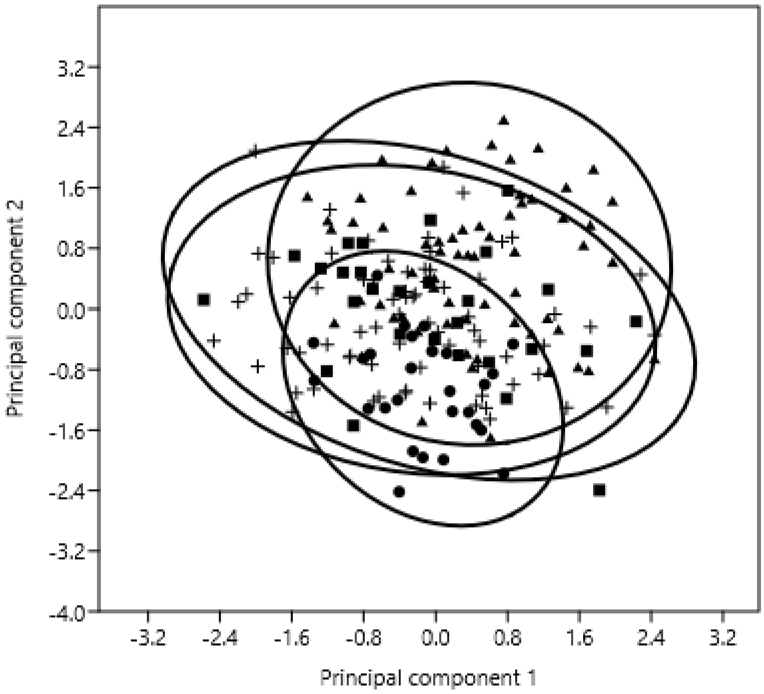

Figure 4: Principal component plot of the four cercopithecid habitat groups with 95% confidence ellipses. Filled circles represent open terrestrial monkeys, crosses open mixed monkeys, filled squares forest terrestrial monkeys and filled triangles forest arboreal.

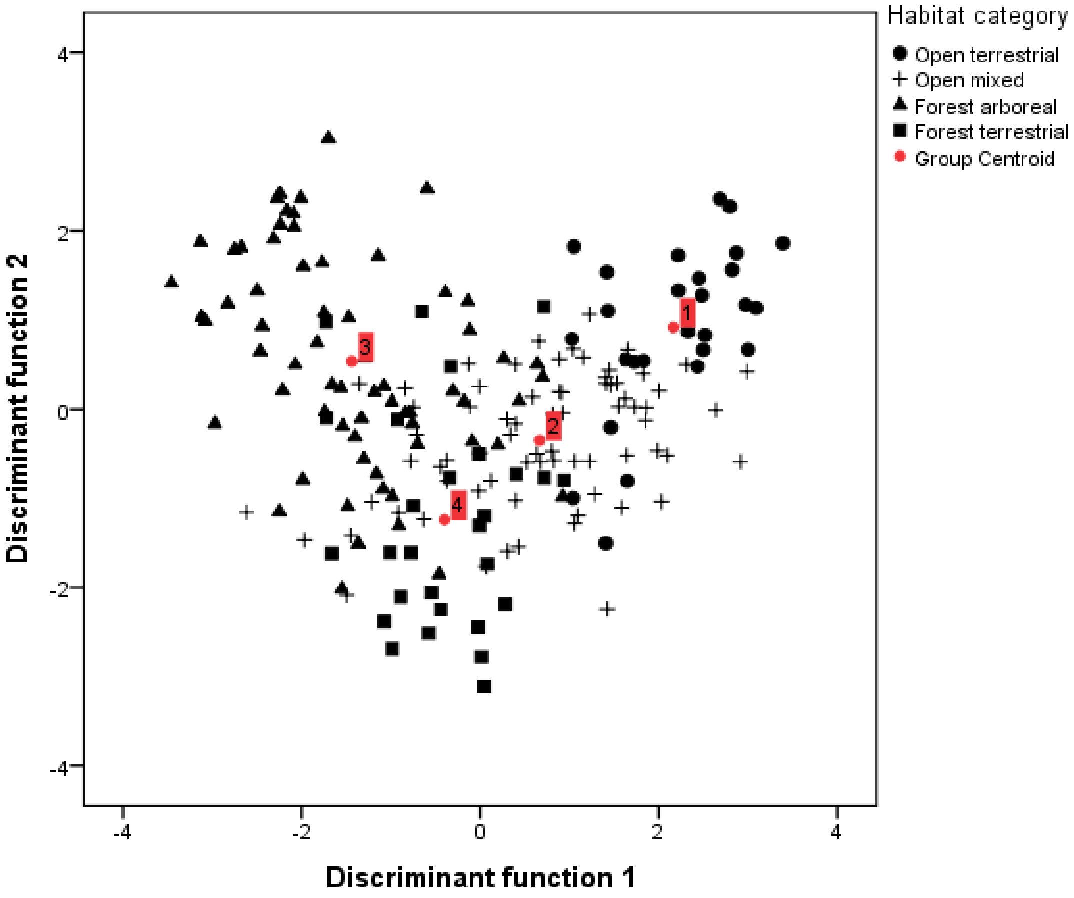

Figure 5: Discriminant plot (non phylogenetic) for the cercopithecoid sample by ecomorphological category. Discriminant function 1 separates forest arboreal and open terrestrial, with DF2 separating (modestly) forest terrestrial from forest arboreal and open terrestrial. Open mixed samples are not separated clearly on either axis but form a group in the centre of Function 2.

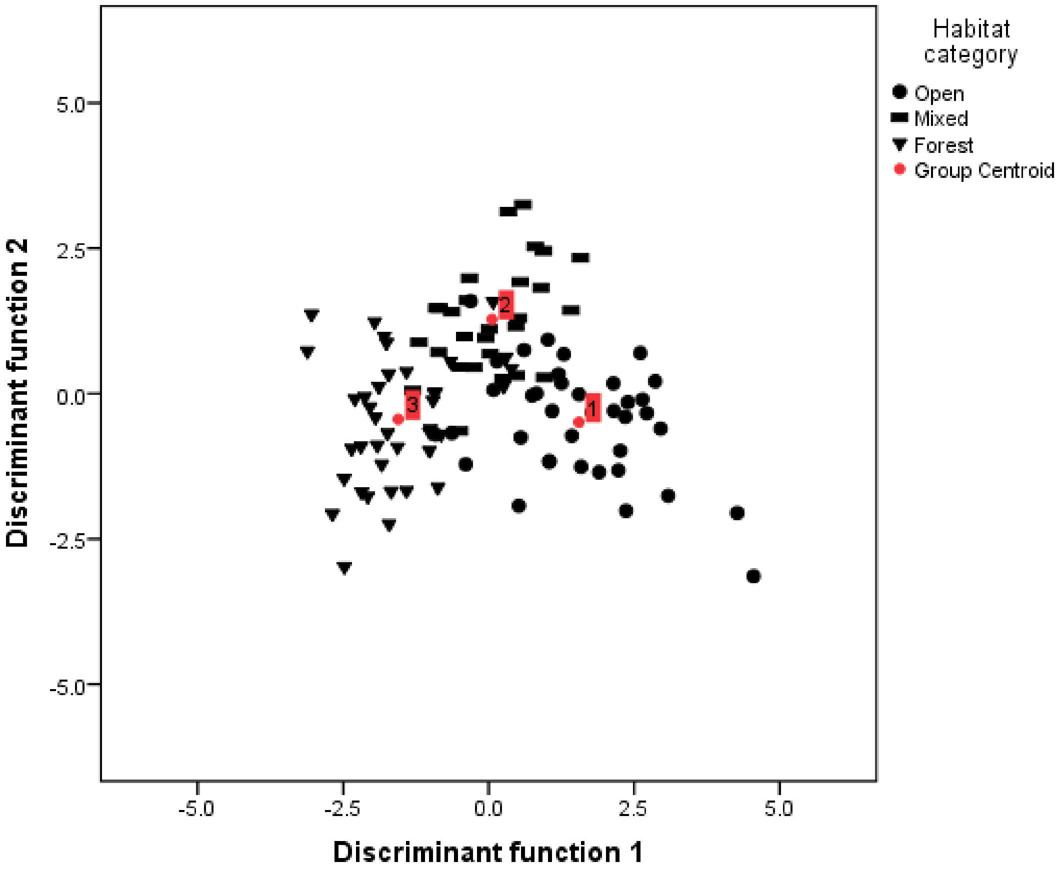

Figure 6: Discriminant plot for the felid sample by ecomorphological category. Open and forest categories are separated on DF1, with mixed lying intermediate and slighted separated on DF2.

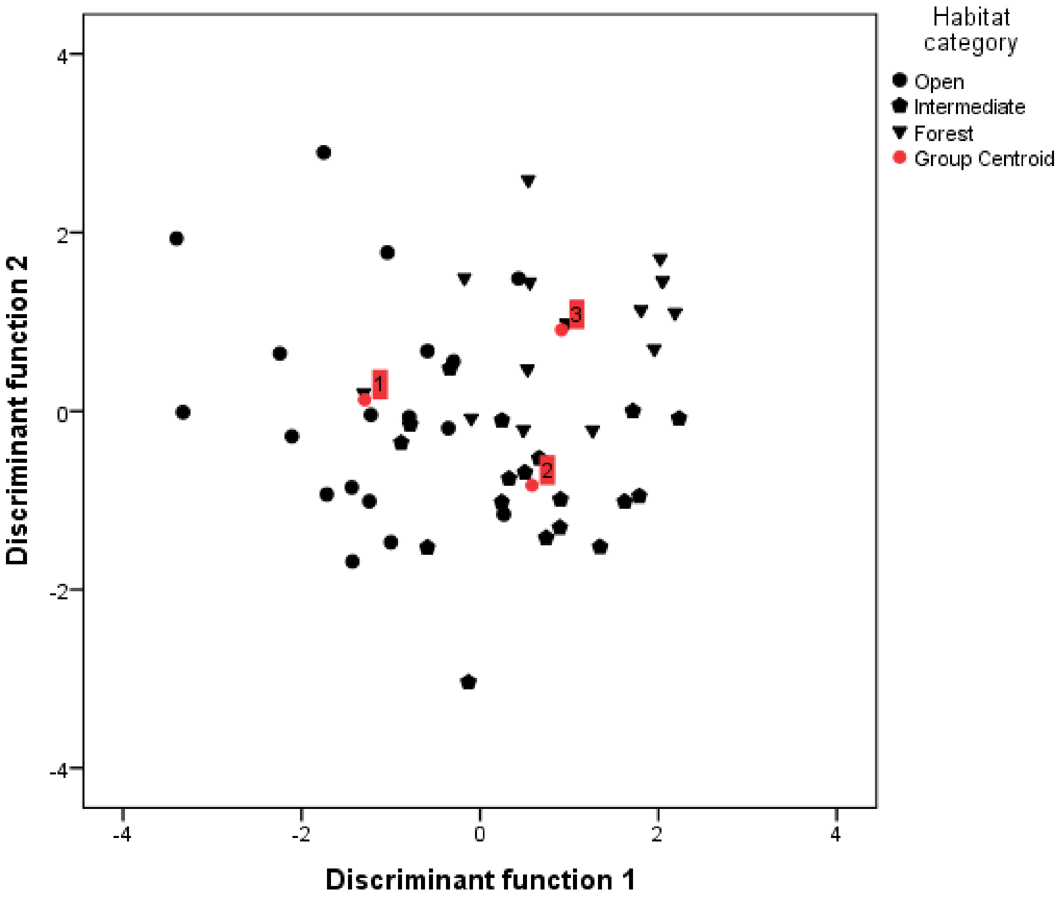

Figure 7: Discriminant plot for the suid sample by ecomorphological category. Possibly due to relatively small sample size, the groups appear less 'cohesive' than in the other taxonomic groups, with open and forest separated on DF1, with intermediate grouping more with forest on DF1, the two being separated more on DF2.

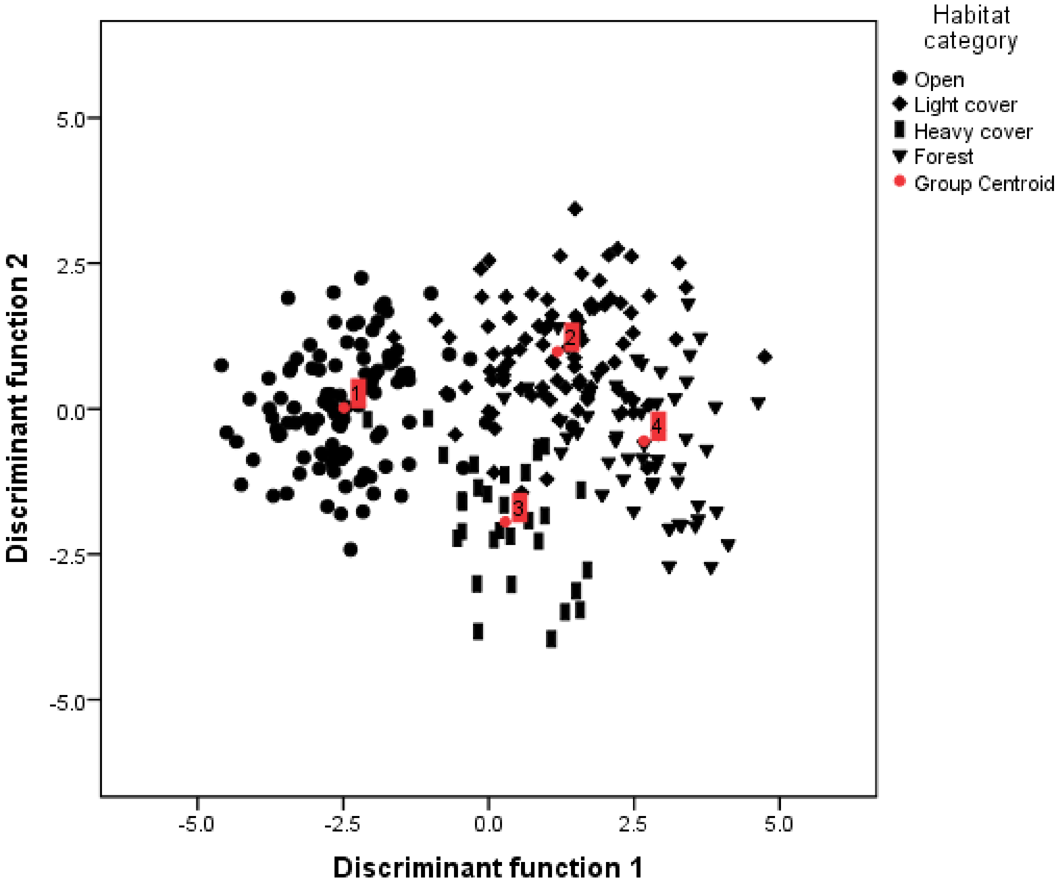

Figure 8: Discriminant plot for the bovid sample by ecomorphological category. Forest and open samples are separated on DF1, with light and heavy cover lying between and separated from each other on DF2.

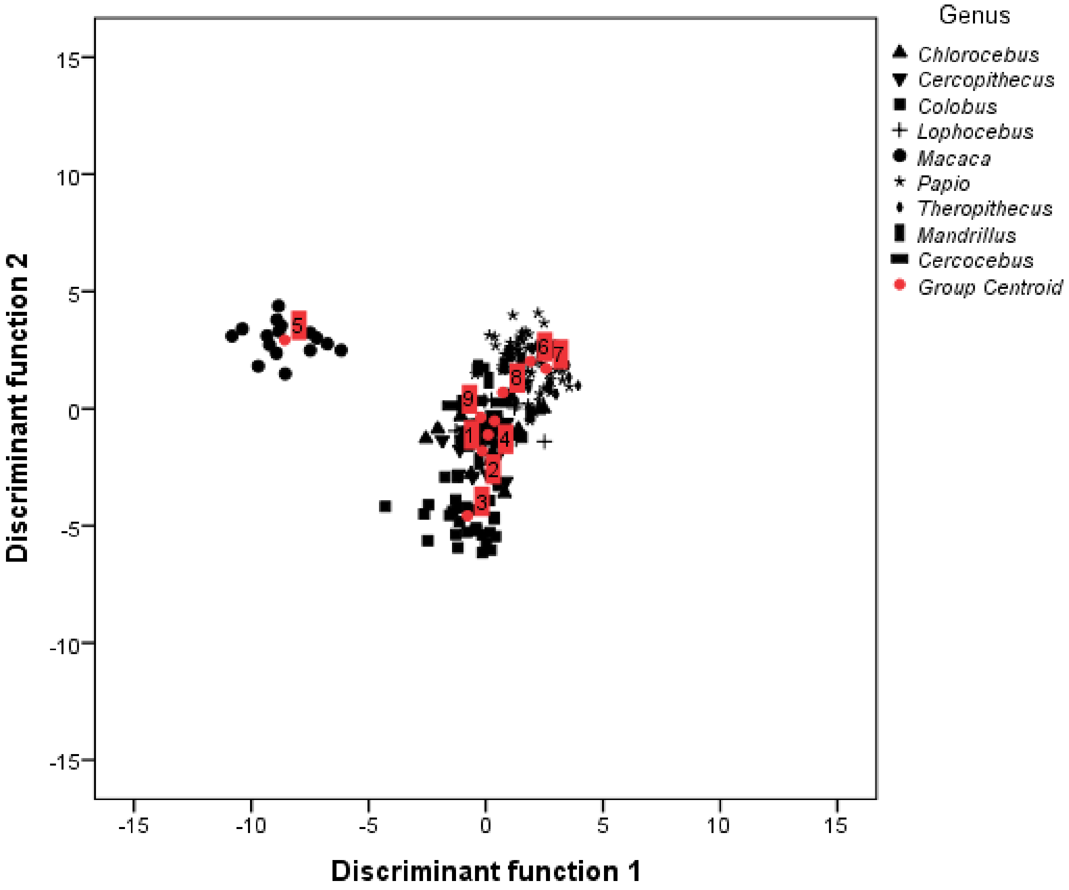

Figure 9: Discriminant plot for the cercopithecid sample by genus. Asian and African cercopithecids are separated on DF1 (45.7% of variance), and colobines and cercopithecines on DF2 (34% of variance).

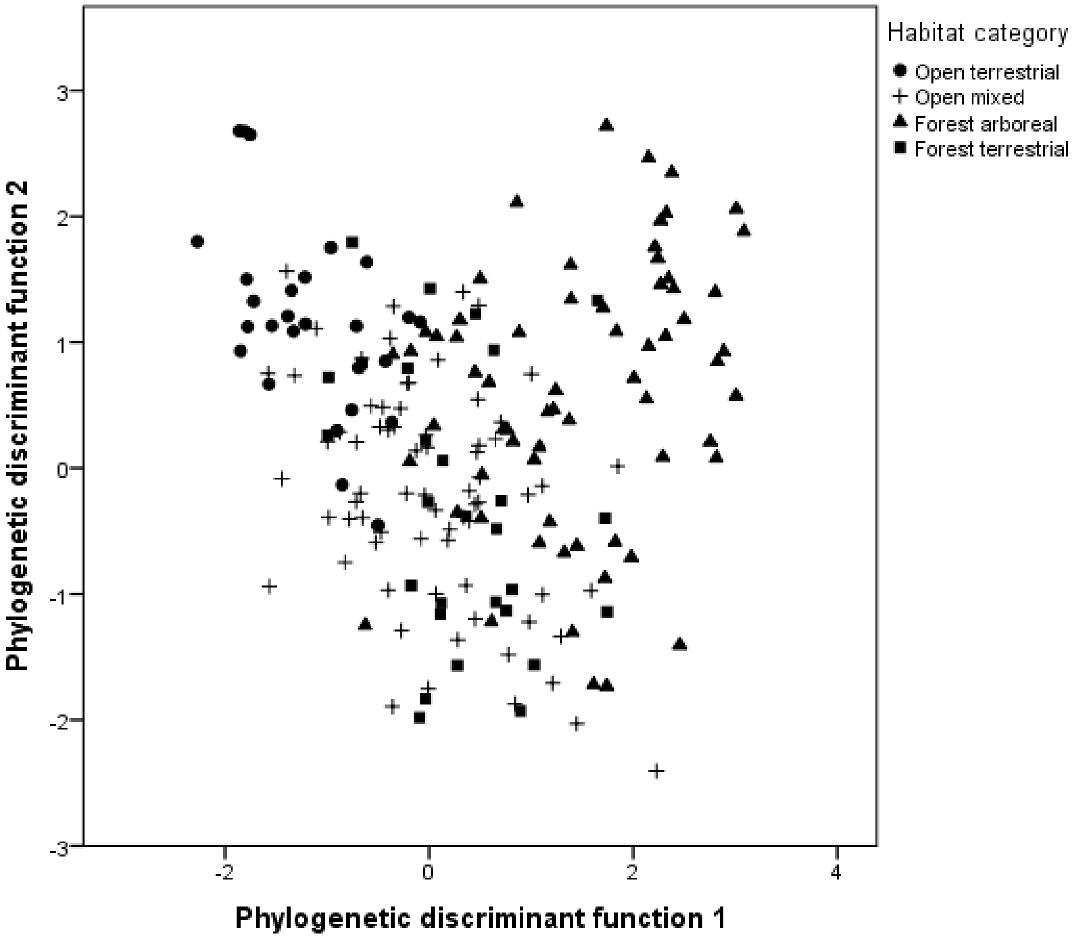

Figure 10: Discriminant plot for the pFDA (including *Colobus*). Note that for Figures 10 and 11, phylogenetic covariance as well as morphology influences the position of specimens. The percentage of between-group variance explained by Function 1 was 68.7%, with Function 2 explaining 28.2% and Function 3 explaining 3.1%. Open terrestrial and forest arboreal were separated on Function 1, with open terrestrial also being separated modestly on Function 2. Open mixed and forest terrestrial were dispersed widely across Function 2.

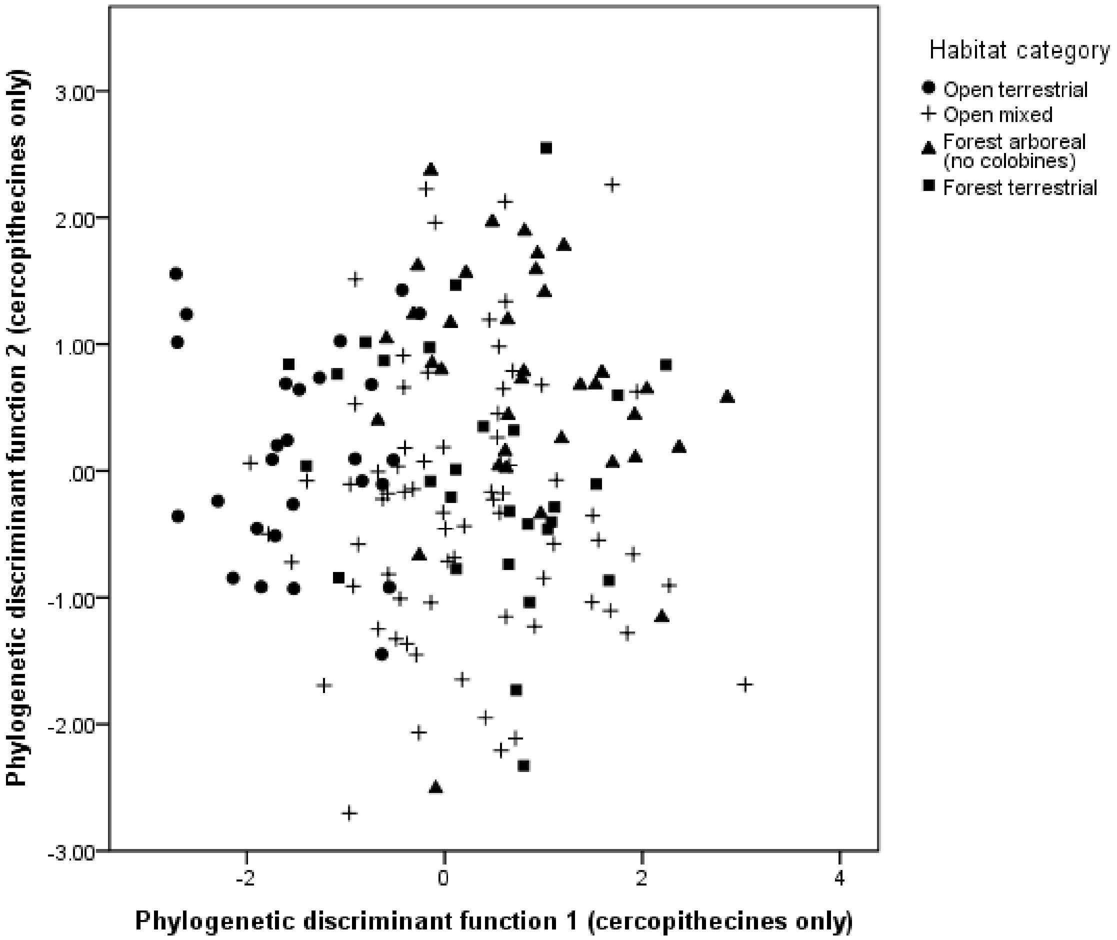

Figure 11: Discriminant plot for the pFDA (excluding *Colobus*). The percentage of between-group variance explained by Function 1 was 77.0%, with Function 2 explaining 18.9% and Function 3 explaining 4.1%. Open mixed occupied the central portion of Function 1, being widely dispersed on Function 2, and open terrestrial and forest arboreal were distinguished on Function 1.

Table S1: Locomotion and substrate use in the *Chlorocebus* and *Cercopithecus* species included in this study.

SPECIES	% total time budget on ground	% feeding time on ground	% time quadrupedal walking and running	% time climbing	% time leaping	% time in upper canopy	% time in middle canopy
C. patas	59.6[a]	91[a]	22.98[b]	1.2[b]	0.3[b]	-	-
C. aethiops	20[c]	10-52[d]	53.9[c]	29.5[c]	9.6[c]	17.3[c]	23.6[c]
C. lhoesti	38[e]	-	-	-	-	-	-
C. mitis	5[g]	-	54[h]	35[h]	11[h]	14[f] / 16.5[f] / 31[h]	77[f] / 48[f] / 61[h]
C. ascanius	0-10[f,g]	-	39[h]	43[h]	15[h]	29[f] / 11.5[f] / 26[h]	56[f] / 56.5[f] / 63[h]
C. pogonias	< 2[i]	-	-	-	-	22[f]	67[f]

SPECIES	% time in lower canopy	% time on small branches	% time on medium branches	% time on large branches	% time on horizontal branches	% time on sloping branches	% time on vertical branches
C. patas	-	-	-	-	-	-	-
C. aethiops	38.7[c]	48.8[c]	40.2[c]	11[c]	56[c]	41.6[c]	2.4[c]
C. lhoesti	usually below 5m[f]	-	-	-	-	-	-
C. mitis	9[f]/ 35.5[f] / 7[h]	24[h]	62[h]	14[h]	59[h]	39[h]	2[h]
C. ascanius	15[f] / 32[h] / 11[h]	37[h]	53[h]	10[h]	52[h]	44[h]	4[h]
C. pogonias	11[f]	-	-	-	-	-	-

a. Nakagawa (1989)
b. Isbell *et al.* (1998). Values reported as percentage of total time budget.
c. Rose (1979). Values reported as percentage of locomotor time budget. Upper canopy > 20m, middle canopy 9-20m, lower canopy 1-9m, ground not included.
d. Kavanagh (1980) reported in Nakagawa (1989).
e. Gartlan and Struhsaker (1972) reported in McGraw (2002)
f. Gautier-Hion (1988). Values reported as percentage of total time budget. *C. mitis* and *C. ascanius*: upper canopy > 20m, middle canopy 10-20m, lower canopy < 10m. *C. pogonias*: upper canopy = emergent trees, middle canopy = canopy, lower canopy = inferior levels. Alternative values separated by dividers.
g. Thomas (1991) reported in McGraw (2002)
h. Gebo and Chapman (1993). Values reported as percentage of locomotor time budget. Upper canopy 16-25+m, middle canopy 6-15m, lower canopy 0-5m. Alternative values separated by dividers.
i. Gautier-Hion and Gautier (1974) reported in McGraw (2002)

Table S2: Results of the discriminant function analysis for the guenon shoulder complex

i. Standardised canonical discriminant function[a]

Variable	Function 1[b]
Supraspinatus fossa length	-0.872
Medial extreme of acromial facet to the inferior angle	0.584
Humeral head maximum proximal projection	0.470
Coracoid process maximum width	0.413
Lesser tubercle maximum width	0.369

[a] Arranged in order of stepwise entry to model

[b] Wilk's lambda = 0.374, F = 28.139 ($p < 0.0001$).

ii. Functions at group centroids

Group	Function1
Chlorocebus (Terrestrial)	-1.904
Cercopithecus (Arboreal)	0.860

iii. Classification matrix

	Group	Predicted Group Membership		Total
		Chlorocebus (Terrestrial)	*Cercopithecus* (Arboreal)	
Standard classification[a]	*Chlorocebus* (Terrestrial)	23 (82.1%)	5 (17.9%)	28 (100%)
	Cercopithecus (Arboreal)	4 (6.5%)	58 (93.5%)	62 (100%)
Cross-validated ('leave one out') classification[b]	*Chlorocebus* (Terrestrial)	22 (78.6%)	6 (21.4%)	28 (100%)
	Cercopithecus (Arboreal)	4 (6.5%)	58 (93.5%)	62 (100%)

[a] 90.0% of original grouped cases correctly classified.

[b] 88.9% of cross-validated grouped cases correctly classified.

Table S3: Results of the linear discriminant function analysis for the guenon elbow complex

i. Standardised canonical discriminant function

Variable[a]	Function 1[b]
Mediolateral articular surface width	-0.987
Radial notch height	0.725
Mediolateral radial head diameter	0.456
Coronoid process projection	0.477
Trochlear notch medial height	0.622
Olecranon fossa depth	0.437
Trochlear notch midline height	-0.444

[a] Arranged in order of stepwise entry to model

[b] Wilk's lambda = 0.336, F = 16.356 ($p < 0.0001$).

ii. Functions at group centroids

Group	Function1
Chlorocebus (Terrestrial)	2.446
Cercopithecus (Arboreal)	-0.783

iii. Classification matrix

	Group	Predicted Group Membership		Total
		Chlorocebus (Terrestrial)	*Cercopithecus* (Arboreal)	
Standard classification[a]	*Chlorocebus* (Terrestrial)	13 (81.3%)	3 (18.7%)	16 (100%)
	Cercopithecus (Arboreal)	2 (4%)	48 (96%)	50 (100%)
Cross-validated ('leave one out') classification[b]	*Chlorocebus* (Terrestrial)	13 (81.3%)	3 (18.7%)	16 (100%)
	Cercopithecus (Arboreal)	3 (6%)	47 (94%)	50 (100%)

[a] 92.4% of original grouped cases correctly classified.

[b] 90.9% of cross-validated grouped cases correctly classified.

Table S4: *Chlorocebus mitis* subspecies Kruskal-Wallis results[a]

Variable	Bone	Complex	Chi-square	p
Anteroposterior humeral head diameter	Humerus	Shoulder	7.940	0.019
Glenoid fossa width	Scapula	Shoulder	6.745	0.034
Coracoid process length	Scapula	Shoulder	7.062	0.029
Acromion process length	Scapula	Shoulder	9.200	0.010
Infraglenoid/acromion distance	Scapula	Shoulder	13.885	0.001
Medial extreme of acromial facet to inferior angle	Scapula	Shoulder	6.139	0.046
Anteroposterior lateral trochlear diameter	Humerus	Elbow	8.953	0.011
Distal capitular width	Humerus	Elbow	8.457	0.015
Trochlear gutter width	Humerus	Elbow	7.129	0.028
Coronoid process projection	Ulna	Elbow	9.560	0.008
Coronoid-olecranon height	Ulna	Elbow	6.086	0.048
Trochlear notch-olecranon length	Ulna	Elbow	8.049	0.018
Trochlear notch posterior width	Ulna	Elbow	9.529	0.009
Trochlear notch depth	Ulna	Elbow	7.683	0.021
Anteroposterior radial head diameter	Radius	Elbow	7.686	0.021
Radial head maximum articular surface width	Radius	Elbow	6.114	0.047

[a] Only statistically significant results shown; all other variables (as listed in Tables 5 and 6) were non-significant.

Table S5: Sample for the felid analysis

Taxon	**Habitat category**	**Male *n***	**Female *n***	**Unknown *n***	**Total *n***
Caracal aurata	Forest	–	1	1	2
Felis marmorata	Forest	–	1	–	1
Felis silvestris grampia	Forest	4	4	–	8
Leopardus guigna	Forest	–	–	1	1
Leopardus pardalis	Forest	1	–	3	4
Leopardus wiedii	Forest	–	–	1	1
Neofelis nebulosa	Forest	1	1	1	3
Panthera onca	Forest	2	1	–	3
Panthera tigris	Forest	–	2	1	3
Panthera uncia	Forest	1	2	1	4
Pardofelis badia	Forest	–	1	–	1
Prionailurus bengalensis	Forest	2	–	1	3
Prionailurus planiceps	Forest	–	1	–	1
Prionailurus viverrinus	Forest	1	–	2	3
Puma jaguarundi	Forest	–	–	1	1
Felis chaus	Mixed	1	–	–	1
Leopardus geoffroy	Mixed	–	1	1	2
Lynx canadensis	Mixed	2	1	1	4
Lynx lynx	Mixed	1	1	1	3
Lynx pardinus	Mixed	–	–	2	2
Panthera pardus	Mixed	–	2	8	10
Panthera pardus fusca	Mixed	–	–	2	2
Pardofelis temmincki	Mixed	–	–	1	1
Prionailurus rubiginosus	Mixed	–	–	1	1
Puma concolor	Mixed	–	1	1	2
Acinonyx jubatus	Open	1	1	3	5
Caracal caracal	Open	–	–	2	2
Felis margarita	Open	1	1	–	2
Felis nigripes	Open	1	1	–	2
Felis silvestris lybica	Open	1	1	1	3
Leptailurus serval	Open	2	2	2	6
Lynx rufus	Open	–	–	1	1
Panthera leo	Open	5	6	4	15
Panthera leo persica	Open	1	1	–	2
Total		28	33	44	105

Table S6: Sample for the suid analysis

Species	**Habitat category**	**Male *n***	**Female *n***	**Unknown *n***	**Total *n***
Babyrousa babyrousa	Forest	2	1	–	3
Hylochoerus meinertzhageni	Forest	2	3	2	7
Tayassu pecari	Forest	–	–	4	4
Potamochoerus porcus	Intermediate	5	4	3	12
Sus scrofa	Intermediate	3	1	2	6
Phacochoerus aethiopicus	Open	7	1	2	10
Tatyassu tajacu	Open	4	–	4	8
Total		23	10	17	50

Table S7: Sample for the bovid analysis

Species	**Habitat category**	***n***
Cephalophus dorsalis	Forest	5
Cephalophus leucogaster	Forest	4
Cephalophus monticola	Forest	5
Cephalophus natalensis	Forest	4
Cephalophus nigrifrons	Forest	4
Cephalophus silvicultor	Forest	7
Cephalophus weynsi	Forest	5
Neotragus moschatus	Forest	4
Tragelaphus scriptus	Forest	18
Kobus ellipsiprymnus	Heavy cover	11
Tragelaphus euryceros	Heavy cover	8
Tragelaphus imberbis	Heavy cover	4
Tragelaphus strepsiceros	Heavy cover	7
Aepyceros melampus	Light cover	12
Kobus kob	Light cover	10
Litocranius walleri	Light cover	3
Madoqua kirkii	Light cover	10
Ourebia ourebia	Light cover	4
Raphicerus campestris	Light cover	8
Raphicerus sharpei	Light cover	1
Redunca arundinum	Light cover	6
Redunca fulvorufula	Light cover	8
Redunca redunca	Light cover	10
Sylvicapra grimmia	Light cover	17
Addax nasomaculatus	Open	4
Alcelaphus buselaphus	Open	15
Antidorcas marsupialis	Open	8
Connochaetes gnou	Open	5
Connochaetes taurinus	Open	6
Damaliscus dorcas	Open	8
Damaliscus lunatus	Open	11
Gazella granti	Open	10
Gazella thomsoni	Open	10
Hippotragus equinus	Open	4
Hippotragus niger	Open	9
Oryx gazelle	Open	12
Oryx leucoryx	Open	4
Total		281

Table S8: Results of the discriminant function analysis for the felid humerus

i. Standardised canonical discriminant functions

Variable[a]	Function 1[b]	Function 2[c]
Maximum mediolateral width of the distal epiphysis	-0.581	1.132
Humeral head height	-0.999	-0.816
Minimum superoinferior dimension of the trochlea	0.603	-0.139
Mediolateral head articular surface	0.587	0.101
Humerus maximum length	0.549	1.452
Mediolateral dimension of subspinosus scar	0.428	-0.292
Bicipital groove depth	-0.236	-0.686
Capitulum maximum length	-0.020	-0.728
Percentage of variance	74.9%	25.1%

[a] Arranged in order of stepwise entry to model

[b] Wilk's lambda = 0.220, F = 13.451 ($p < 0.0001$)

[c] Wilk's lambda = 0.620, F = 8.390 ($p < 0.0001$)

ii. Classification matrix

	Group	Predicted Group Membership			Total
		Open	Mixed	Forest	
LDA standard classification[a]	Open	30 (79%)	5 (13%)	3 (8%)	38
	Mixed	1 (4%)	23 (82%)	4 (14%)	28
	Forest	0	5 (13%)	34 (87%)	39
LDA cross-validated ('leave one out') classification[b]	Open	29 (76%)	6 (16%)	3 (8%)	38
	Mixed	3 (11%)	20 (71%)	5 (18%)	28
	Forest	0	5 (13%)	34 (87%)	39
QDA standard classification[c]	Open	37 (97%)	1 (3%)	0	38
	Mixed	3 (11%)	22 (78%)	3 (11%)	28
	Forest	2 (5%)	1 (3%)	36 (92%)	39
QDA validation sample[d]	Open	30 (97%)	1 (3%)	0	31
	Mixed	1 (5%)	19 (90%)	1 (5%)	21
	Forest	2 (8%)	0	24 (92%)	26

[a] 82.9% of original grouped cases correctly classified.

[b] 79.0% of cross-validated grouped cases correctly classified.

[c] 91.5% of original grouped cases correctly classified

[d] 93.6% of validation sample (n = 78) correctly classified

Table S9: Results of the discriminant function analysis for the suid humerus

i. Standardised canonical discriminant function

Variable[a]	Function 1[b]	Function 2[c]
Maximum humerus length	-0.697	-0.134
Trochlea, superior-inferior distance between crest and lateral border	0.630	0.213
Trochlea, narrowest anteroposterior distance	-1.327	-1.583
Anteroposterior distance on the medial aspect of the distal epiphysis	0.593	-0.715
Trochlea, superior-inferior distance between crest and medial border	1.385	2.483
Percentage of variance	66.2%	33.8%

[a] Arranged in order of stepwise entry to model

b Wilk's lambda = 0.326, F = 6.455 (p < 0.0001)

c Wilk's lambda = 0.658, F = 5.713 (p = 0.001)

ii. Classification matrix

	Group	Predicted Group Membership			Total
		Open	Intermediate	Forest	
LDA standard classification[a]	Open	16 (88%)	1 (6%)	1 (6%)	18
	Intermediate	3 (17%)	14 (77%)	1 (6%)	18
	Forest	1 (8%)	3 (21%)	10 (71%)	14
LDA cross-validated ('leave one out') classification[b]	Open	13 (72%)	3 (17%)	2 (11%)	18
	Intermediate	3 (17%)	13 (72%)	2 (11%)	18
	Forest	1 (7%)	3 (21%)	10 (72%)	14

[a] 80.0% of original grouped cases correctly classified.

[b] 72.0% of cross-validated grouped cases correctly classified.

Table S10: Results of the linear discriminant function analysis for the bovid humerus

i. Standardised canonical discriminant function

Variable[a]	Function 1[b]	Function 2[c]	Function 3[d]
Maximum length	0.819	0.404	-0.031
Superior-inferior distance of the lateral border of the trochlea	-0.347	0.572	0.074
Breadth of greater tubercle	0.380	-0.008	0.799
Anteroposterior dimension of the lateral aspect of the distal epiphysis	0.461	-0.032	0.431
Greater tubercle height	0.395	-0.053	0.250
Mediolateral dimension of shaft at deltoid tuberosity	0.134	-0.246	-0.240
Superoinferior dimension of trochlear at medial border	0.084	0.528	0.360
Maximum closure of the bicipital groove	0.103	0.047	0.623
Maximum breadth of bicipital groove	-0.280	0.282	0.037
Mediolateral dimension of trochlea from central crest to medial border	-0.089	0.296	-0.374
Minimum mediolateral breadth of the humeral trochlea, measured between fossae on the medial and lateral sides	0.001	0.268	0.400
Total mediolateral dimension of the trochlea	0.198	0.221	0.102
Anteroposterior distance on the medial aspect of the distal epiphysis	-0.011	-0.419	0.091
Percentage of variance	76.6%	14.0%	9.3%

[a] Arranged in order of stepwise entry to model

b Wilk's lambda = 0.070, F = 29.276 ($p < 0.0001$)

c Wilk's lambda = 0.369, F = 14.306 ($p < 0.0001$)

d Wilk's lambda = 0.658, F = 12.364 ($p < 0.0001$)

ii. Classification matrix

	Group	Predicted group membership				Total
		Open	Light cover	Heavy cover	Forest	
LDA standard classification	Open	102 (96%)	4 (4%)	0	0	106
	Light cover	2 (2%)	75 (84%)	3 (3%)	9 (10%)	89
	Heavy cover	2 (7%)	0	28 (93%)	0	30
	Forest	0	6 (11%)	0	50 (89%)	56
LDA cross-validated ('leave-one-out') classificaton	Open	101 (95%)	4 (4%)	1 (1%)	0	106
	Light cover	4 (5%)	71 (80%)	3 (3%)	11 (12%)	89
	Heavy cover	3 (10%)	1 (3%)	26 (87%)	0	30
	Forest	1 (2%)	6 (11%)	0	49 (88%)	56
QDA standard classification[c]	Open	99 (93%)	6 (6%)	1 (1%)	0	106
	Light cover	1 (1%)	83 (93%)	0	5 (6%)	89
	Heavy cover	0	0	29 (97%)	1 (3%)	30
	Forest	0	1 (2%)	0	55 (98%)	56
QDA validation sample[d]	Open	81 (94%)	4 (5%)	1 (1%)	0	86
	Light cover	1 (2%)	60 (95%)	0	2 (3%)	63
	Heavy cover	0	1 (5%)	21 (95%)	0	22
	Forest	0	1 (3%)	0	38 (97%)	39

[a] 90.7% of original grouped cases correctly classified.

[b] 87.9% of cross-validated grouped cases correctly classified.

[c] 94.7% of original grouped cases correctly classified

[d] 95.2% of validation sample (n = 210) correctly classified