Baboon biogeography, divergence and evolution: morphological and paleoecological perspectives.

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Abstract

Papio originated in the early Pleistocene and diverged into multiple species, six of which are extant. Among parapatric *Papio* species there are obvious phenotypic differences that arose during the radiation of the genus. We use data from modern baboon ecology and morphology as well as fossils and paleoecology to examine baboon biogeography, divergence and evolution, focusing on skull form and body mass. To provide context, techniques of historical biogeography, combining data from modern distributions in statistical models alongside qualitative assessments of the fossil record were used to estimate ancestral ranges in papionins. The ancestral range of *Papio* was estimated to be in South Tropical Africa rather than in the far south of the continent, followed by multiple movements south and west. Progress north and east may have been slowed because of high-density blocking of niches by other monkeys. Geometric morphometric data were used in partial least squares analysis with dietary, environmental and other variables to investigate skull differentiation. Environment was significantly correlated with skull form, but diet emerged as more significant. Exploitation of subterranean foods was found to be an important influence on skull morphology. Bayesian modelling of cercopithecid body mass data allowed reconstruction of ancestral body mass, and showed a pattern of accelerating body mass evolution in a number of lineages. This appears to be related to exploitation of terrestrial niches in the Pliocene, with terrestriality also implicated in the large geographic distributions of many fossil and modern papionins, including *Papio*. Given the greater heterogeneity of body masses in males, size differentiation within *Papio* seems most likely to be linked to sexual selection rather than environmental factors, although further work is required to examine the relative importance of plasticity versus local adaptation in shaping baboon phenotypic variation.

1.0 Introduction

The evolutionary history of *Papio* is complex, with the scant fossil record (reviewed in Gilbert et al., 2018) failing to reflect the patterns of divergence, reticulation and introgression revealed by molecular analyses, which have also highlighted the presence of 'ghost' lineages (Rogers et al., 2019). Given the remarkable insights from molecular studies, and the paucity of fossils, it is tempting to downplay the importance of morphological insights when considering the evolutionary history of *Papio*. But, alongside molecular work, detailed studies of morphological variation in extant *Papio* (Frost et al., 2003; Dunn et al., 2013) have been extremely valuable in revealing the complexities of baboon evolution and filling some paleontological gaps. External form is a fundamental way in which organisms recognise each other, and as the phenotype is the product of gene-environment interaction, questions about evolutionary processes as well as patterns can be addressed by examining morphology. Similarly, understanding the paleoecological record and reconstructing ancestral ranges provides vital context when considering the evolutionary history of a group.

In this article we examine baboon biogeography, divergence and evolution from morphological and paleoecological perspectives, drawing on data from modern baboon socioecology and biology as well as the fossil record to complement Gilbert et al.'s (2018) comprehensive account of *Papio* paleontology. We first use techniques of historical biogeography, combining data from modern distributions in statistical models alongside qualitative assessments of the fossil record, to estimate ancestral ranges in papionins, including *Papio*. This provides a background for considering species movement and subsequent morphological divergence. As illustrated in Fischer et al. (2019) and summarised in Jolly (1993), there are obvious phenotypic differences among *Papio* species, in body mass as well as soft and hard tissue morphology. Here, we focus on skull form and body mass, two cardinal elements of morphological study, to provide different perspectives on baboon divergence. We use multivariate morphometric and evolutionary modelling frameworks to consider ancestral states, trait polarities and the mechanisms by which differentiation may have occurred in the genus *Papio*.

Study of the skull provides detailed taxonomic and socioecological information, and understanding its form is essential in appreciating diversity, especially in evolutionary contexts. Thus, geometric morphometric data are used to expand previous work on the baboon skull (Frost et al., 2003; Dunn et al., 2013) to infer how differentiation is linked to modern baboon environments, geography, phylogeny and diet, and what this might tell us about *Papio* adaptation and evolution. Body mass is one very obvious phenotypic feature that has diverged during the *Papio* radiation, yet surprisingly little recent research has been undertaken on its paleobiological context and the evolutionary processes underlying its differentiation, hence our focus on it in this contribution. It is a fundamental biological characteristic of an organism, related to diet, habitat, activity and life history (Damuth and MacFadden, 1990; Delson et al., 2000). Reconstructing ancestral body mass in *Papio* and investigating subsequent divergence is thus vital to understanding its evolutionary history, especially when placed in a broader papionin context. It provides a vehicle for considering evolutionary processes, such as whether change has been stochastic or adaptive and, if adaptive, whether via natural or sexual selection. Study of body mass also gives the opportunity to think about proximate / ultimate explanations, including the role of plasticity versus local adaptation. Throughout this contribution, we integrate new findings based largely on analysis of extant monkeys with a review of existing knowledge of baboon adaptations and the fossil and paleoecological records. Some of our discussion is deliberately speculative, with the aim to stimulate further detailed work into *Papio* evolutionary history and morphological divergence.

1.1 Background

Molecular data indicate that *Papio* forms a clade with *Theropithecus, Lophocebus* and *Rungwecebus* (hereinafter referred to as P/T/L/R) that probably originated and radiated quickly ~5 Ma (Liedigk et al., 2014). Relationships within the clade are far from clear cut (Liedigk et al., 2014). On balance, *Theropithecus* is most likely to be sister to a *Lophocebus* / *Papio* clade (Harris, 2000; Guevara and Steiper, 2014), although *Theropithecus* and *Lophocebus* may have continued to hybridise after the initial split (Guevara and Steiper, 2014), and there is also mounting evidence for introgression, potentially over a long period, between *Theropithecus* and *Papio* (Walker et al., 2019). Introgression between *Rungwecebus* and *Papio* is certain (Burrell et al., 2009; Zinner et al., 2009b, 2018; Roberts et al., 2010), with *Papio* mtDNA introgression in the Mount Rungwe *Rungwecebus* population and vice versa in the Udzungwa Mountains (Zinner et al., 2018). Cladistic analysis (using a molecular backbone, and resulting in a majority rule consensus tree) of fossil papionin morphology suggests a clade comprising modern and fossil P/T/L/R, with extinct *Gorgopithecus* as sister to P/L/R and extinct *Dinopithecus* sister to *Theropithecus* (Gilbert et al., 2018). Based on the fossil first appearance datum (FAD) (Harris et al., 2003; Frost et al., 2020), the *Theropithecus* lineage diverged before 4.2 Ma. *Papio* and *Lophocebus* diverged from each other at some point after this, prior to the *Papio* FAD in southern Africa (Gilbert et al., 2018) and the secure *Lophocebus* FAD at ~2 Ma (Jablonski and Leakey, 2008). However, given the probable rapidity of the *Theropithecus* / *Papio* / *Lophocebus* divergence (Harris, 2000; Liedigk et al., 2014), the *Papio* and *Lophocebus* FADs are likely to underestimate the origination date of the separate lineages, possibly substantially. Indeed, fossils that can be tentatively assigned to *Lophocebus* have been dated to ~3.5 Ma (Harrison and Harris, 1996). Molecular data indicate that *Papio* and *Rungwecebus* diverged around 3 Ma (Zinner et al., 2018).

Each of the six recognised *Papio* species[1] (*Papio hamadryas*, *Papio anubis*, *Papio papio*, *Papio cynocephalus*, *Papio kindae* and *Papio ursinus*) is phenotypically distinctive, notwithstanding the complexities of evolutionary history revealed by molecular analyses (Jolly, 1993; Gilbert et al., 2018; Rogers et al., 2019). In some *Papio* species, structured morphological variation in soft and hard tissue (reviewed in Martinez et al., 2019) indicates the presence of subspecies. Within the six extant species of *Papio* there are five different adult dorsal coat colors, mapping to species, although *P. cynocephalus* and *P. kindae* share a similar yellowish-brown coat (Jolly, 1993). Comparison with an outgroup of close papionin relatives *Theropithecus*, *Lophocebus* and *Rungwecebus* (Table 1) gives little clue to ancestral state for coat color on dorsum, belly or cheeks. Hand and foot hair color take a number of states that seem unrelated to phylogeny. There is no clear polarity to tail shape in *Papio*, but comparison with *Theropithecus* and *Rungwecebus* suggests tentatively that the arched shape is primitive (and if so, the bent shape seen in *P. anubis* and *P. ursinus* / *P*. *cynocephalus* probably evolved convergently); the upright tail that curves over the back is almost certainly derived in *Lophocebus* and relates to above-branch arboreal locomotion. It is clear, however, that a purple-black face is plesiomorphic, diverging only in *P. hamadryas*, which has a pink-red face. This, like its light coat color, may be linked to high ultraviolet light exposure in its open habitat (Bradley and Mundy, 2008), and could indicate that its pigmentation has been under strong selection pressure.

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[1] Following Rogers et al. (2019), we adopt the phylogenetic species concept here and recognise six species of modern *Papio*. These can also be reasonably described as ‘allotaxa’ (Jolly, 2001). For consistency, we also recognise phenotypically-distinct fossil *Papio* taxa as full species, noting that some descriptions prefer to describe some of these taxa as subspecies of *Papio hamadryas (*Williams et al., 2012; also see Gilbert et al., 2018 for a comprehensive review).

Given that this distinctive coloration is most pronounced in adult males and is less well developed in females and juveniles, sexual selection could have contributed to the divergence of pigmentation in *P. hamadryas*. Another aspect of coloration, natal coat, for which the plesiomorphic state is black, is polymorphic in *P. kindae* infants, which show white, grey and patchy coats as well as black ones (Petersdorf et al., 2019). This may be the result of stochastic evolutionary processes (e.g. founder effect), although conspicuous natal coats may also have adaptive functions (reviewed in Bradley and Mundy, 2008).

Fossil species of *Papio* can only be diagnosed morphologically, primarily craniodentally, using metric and non-metric traits (Gilbert et al., 2018). Cranial and dental size varies among fossil species (Williams et al., 2012; Gilbert et al., 2018). In modern baboons, cranial size varies clinally, with smaller individuals in eastern and western Africa, and larger individuals in central and southern Africa (Frost et al., 2003; Dunn et al., 2013). As might be expected, allometry has some influence over interspecific differences in cranial shape (Dunn et al., 2013). Nonetheless, discriminant function analyses (DFA) show the six species to be distinct in size-controlled shape as well as cranial form (size and shape), with relatively few misclassifications that, when they occur, generally fall into the geographically adjacent species (Dunn et al., 2013). The Guinea and hamadryas baboons, for example, although fairly similar in size, are distinct in cranial shape, which indicates they have undergone considerable independent morphological evolution (Dunn et al., 2013). This pattern emphasises that morphological divergence in *Papio* has not simply gone along a line of least evolutionary resistance based on body mass (sensu Marroig and Cheverud, 2007) but that other processes have contributed towards phenotypic differentiation of baboon species, which we examine below through our analysis of skull morphology.

Alongside interspecific phenotypic differences, pelage and morphology reflect a deeper phylogenetic split between northern and southern *Papio* lineages identified in molecular analyses (Zinner et al., 2009, 2013; Rogers et al., 2019). As noted by Jolly (1993), there are clear differences in pelage between the clades, with northern species (*P. papio*, *P. hamadryas*, *P. anubis*) having an obvious, wavy mane and cheek tufts in contrast to the straighter mane hair and absent cheek tufts in the southern species (*P. cynocephalus*, *P. ursinus*, *P. kindae*). Comparison with *Theropithecus*, *Lophocebus* and *Rungwecebus* (Table 1) suggests that moderate or strong mane relief is an ancestral feature, with loss in the southern baboon clade and the black mangabey (although both *Lophocebus* species groups display an apparently apomorphic crest of hair on the crown, a trait also seen in *Rungwecebus*). The two geographic clades of *Papio* are also recovered in analysis of cranial morphology, with variation in size-controlled cranial shape structured along a north-south axis (Frost et al., 2003; Dunn et al., 2013). There seems to be little convergence in shape between the largest-bodied members of each clade, *P. anubis* and *P. ursinus*, which in DFA are rarely misclassified as one another (Dunn et al., 2013). This fits with findings based on captive baboons that variation in craniofacial morphology cannot simply be explained by differences in body mass and thus other selective pressures have been in play (Joganic et al., 2017). Interestingly, in DFA, whereas *P. ursinus* is only misclassified into the southern clade species, *P. cynocephalus* is misclassified into *P. anubis* as well as *P. ursinus* (Dunn et al., 2013), which reflects the porous nature of the boundary not only between species but also geographic clades that is evident in hybrid zones. *Papio kindae* is not misclassified when form is analysed, but when size-controlled shape is included, it is misclassified at a high rate as *P. ursinus* but never other species (Dunn et al., 2013), despite molecular evidence that the Kinda baboon arose recently (~100 ka) via admixture from the northern and southern clades (Rogers et al., 2019), even though the Kinda mitochondrial lineage is very old (Zinner et al., 2009a, 2013). The high rates of misclassification into *P. ursinus* may reflect the recent divergence of *P. kindae*, and the ongoing hybridisation between the two species, and further work is required to explore this, as well as any morphological affinities with the northern as well as the southern clade.

The northern and southern *Papio* clades diverged ~1.4 Ma (Rogers et al., 2019). This estimate is based on analysis of whole genome data, which gives a picture of divergence and cladogenesis of populations, often thought of as speciation. Estimates based on mtDNA give an earlier date of ~2.2 Ma (Roos et al., 2019). Mitochondrial analysis yields a phylogeny of mitochondrial haplotypes rather than actual populations. Mitochondrial divergences are often older than the true population divergence because of a phenomenon known as incomplete lineage sorting, whereby ancestral polymorphisms are retained across often rapidly radiating species, with alternate haplotypes only later reaching fixation in different clades (Tang et al., 2012). After the north-south split there were speciation events, mostly in the middle Pleistocene, giving rise to the species that survive today (Rogers et al., 2019). Presumably other speciation events, in both the early and middle Pleistocene, gave rise to the fossil species, *P. angusticeps* and *Papio (hamadryas) botswanae* (Freedman, 1957; Williams et al., 2012; Gilbert et al., 2018), that are now assigned relatively securely to the modern baboon lineage. The fossil species *Papio robinsoni* may also be a modern baboon, although it does exhibit some primitive features (Gilbert et al., 2018). A fourth fossil species, the early Pleistocene *Papio izodi*, is also recognised but has uncertain taxonomic status, and may be better placed outside *Papio* given its morphological differences from other definitive members of the genus (Gilbert et al., 2018).

The distinct morphologies (and indeed behaviors and social organisations) found in the six modern *Papio* species imply past physical barriers to gene flow. One scenario is that the different *Papio* species diverged allopatrically, followed by secondary contact and gene flow. Recent ecological niche modelling, pointing to periods when habitat shifts may have caused periods of separation and reconnection of baboon populations (Chala et al., 2019), supports this, as does the distribution pattern of baboon haplogroups, which indicates that some populations were isolated for a time and underwent independent evolution (Zinner et al., 2015). However, other evolutionary niche modelling suggests that once it split from other members of the P/T/L/R clade, *Papio* underwent parapatric speciation (Fuchs et al., 2018). Its widespread occupation of a range associated with environmental gradients (Winder, 2014; Fuchs et al. 2018) coupled with contiguous distributions of species that split at different times and are interspersed by hybrid zones (Zinner et al., 2009) is consistent with general theoretical formulations of parapatry (see review in Garcia-Ramos et al., 2000). Put another way, movement from one region to another favored adaptation to the new environment, with subsequent divergence and a hybrid zone emerging where the ranges of the two demes, or local populations, abutted. Parapatric speciation differs from allopatric (vicariant) speciation in that there is no assumption of physical, usually geographic, barriers between populations, although reproductive isolation does occur between the majority of individuals in each parapatric taxon. Further investigation of modes of speciation in *Papio*, combining multiple lines of evidence and using more detailed paleoenvironmental data, would be valuable.

There is compelling paleontological and molecular evidence that *Papio* originated in southern hemisphere Africa prior to dispersing throughout much of sub-Saharan Africa and into Arabia. The deepest mitochondrial divergences are in the southern taxa (Zinner et al., 2015). In particular, deep mtDNA splits have been noted between *P. ursinus* and other species (Newman et al., 2004; Wildman et al., 2004; Zinner et al., 2013), and one study has identified deep splits in *P. ursinus* itself

(Sithaldeen et al., 2009), although this may be confounded by swamping. Zinner et al. (2015) also found a deep split between the Mahale baboons (likely to be Kinda), which carry one of the oldest baboon mitochondrial lineages, and other groups of *P. kindae*. The earliest fossils come from South Africa (Gilbert et al., 2018). The paleontological FAD for modern baboons is 2.4–2.0 Ma, based on the likely date of *P. angusticeps* from Malapa, or even slightly earlier (~2.5 Ma) if the presence of *P. robinsoni* at Sterkfontein Member 4 is ascertained (Gilbert et al., 2015, 2018). As reviewed by Gilbert et al. (2018), the fossil FAD is congruent with molecular estimates (~2.5 – 1.8 Ma) for the origin of modern *Papio* (Newman et al., 2004; Wildman et al., 2004; Zinner et al., 2009, 2013; Dolotovskaya et al. 2017). Since species are unlikely to have originated precisely where their fossils are first recorded, and the karstic South African cave sites (along with those in the Rift) dominate the extremely geographically-clustered Pleistocene mammal record, it is likely that the record in South Africa represents movement from an origination region further north, to the east or even west.

Papio is the only member of the P/T/L/R clade with a presence in South Africa today, but in the early Pleistocene it formed part of a southern African assemblage of large-bodied and predominantly terrestrial monkeys that included the papionins *Parapapio*, *Procercocebus*, *Dinopithecus, Gorgopithecus* and *Theropithecus* as well as the colobine *Cercopithecoides* (Elton, 2007; Gilbert et al., 2016a). With the exception of *Procercocebus* (more closely related to *Mandrillus / Cercocebus* than to P/T/L/R) and *Dinopithecus*, these genera are also present in eastern Africa. The earliest *Theropithecus* fossils are found ~4.2 Ma at Kanapoi, in eastern Africa (Harris et al., 2003; Frost et al., 2020), and it is not until much later (~3/2.5 Ma) that they are found in southern Africa (Hughes et al., 2008; Herries et al., 2013). The *Theropithecus oswaldi* lineage, likely to be sister to the extant *T. gelada* (Pugh and Gilbert, 2018), was established by ~3.9 Ma, dominating the faunal assemblage at Woranso-Mille in eastern Africa even though other monkeys are also represented (Frost et al., 2014). Sister to P/L/R, *Gorgopithecus* is also found in eastern Africa (Gilbert et al., 2016b), and *Lophocebus* fossils are found only in eastern Africa. Notwithstanding its abundance and wide geographic distribution today, *Papio* did not dominate the Pleistocene monkey fossil record and indeed is very poorly represented in the Plio-Pleistocene of eastern Africa (Gilbert et al., 2018). Definitive *Papio* material, usually attributed to one of the modern species, only appears in eastern Africa in middle and late Pleistocene deposits (Gilbert et al., 2018), which is consistent with the evolutionary history of the genus based on current molecular evidence (Rogers et al., 2019). This poor or even non-existent record in the early Pleistocene of eastern Africa could be a taphonomic artefact, but this is unlikely given the extensive large-bodied and taxonomically disparate monkey record at many Rift Valley sites. Why *Papio* apparently failed to colonize the eastern African Rift sites in the early Pleistocene is an important and fascinating question, and could be related to competitive exclusion, other ecological barriers, or geographic barriers.

1.2 Hypotheses

Our study, with its morphological and paleoecological perspectives on baboon biogeography, divergence and evolution, incorporates three complementary elements: historical biogeography, skull differentiation among species, and macroevolutionary trends in body mass. Although the *Papio* fossil record is concentrated in South Africa, modern P/T/L/R are all found in eastern Africa, which has much greater extant monkey diversity than southern Africa (Elton, 2007). We thus hypothesize a scenario whereby the ancestor of the P/T/L/R clade arose in tropical Africa, with the origin of *Papio* also occurring in the tropical zone, albeit at its southern end, with subsequent movement further south, where it is captured in the fossil record.

Geographic expansion was accompanied by morphological differentiation, at least some of which may have been adaptive and linked to ecology. Previous work shows a strong spatial component to *Papio* skull variation (Frost et al., 2003; Dunn et al., 2013), but a much weaker link between morphology and climate, and considerable unexplained variance (Dunn et al., 2013). Informed by this, we expect that diet accounts for some unexplained skull variance among species. Particularly, we hypothesise that the proportion of underground storage organs (USOs) consumed will be linked to variations in skull morphology, as USOs are generally stiffer than fruits and leaves (Dominy et al., 2008). The exact nature of the morphological variation is difficult to predict given the complexities of feeding behavior, food mechanical properties and their relationships with cranial form (Berthaume, 2016). However, given the higher stiffness of USOs compared to fruit, greater bite force may be required to deform and fracture USOs. In the papionin *Macaca mulatta*, occlusal force is proportional to jaw length (Dechow and Carlson, 1990) so we propose that baboons consuming a greater proportion of subterranean resources will have a longer and more robust skull.

Body masses diverged during the *Papio* expansion and radiation, and the pattern of this is well documented (e.g. Fischer et al., 2019; Rogers et al., 2019). The evolutionary processes that contributed to this differentiation are less well understood. Given the patchy coverage of *Papio* in the fossil record combined with the high and probably skewed representation of large, terrestrial fossil monkeys, we use data from a large sample of extant cercopithecids to investigate body mass evolution in papionins. Using phylogenetically-informed evolutionary modelling techniques, we first reconstruct the body masses of the papionin and *Papio* most recent common ancestors (MRCA). Drawing on Jolly (2007), we hypothesise that the papionin MRCA was ‘medium’-sized, similar to mangabeys or macaques (although Jolly [2007] was referring specifically to the afro-papionins rather than the clade as a whole). Based on cranial analysis that indicates dissimilarity of shape in *P. ursinus* and *P. anubis* despite their large sizes (Dunn et al., 2013), a second hypothesis is that large body mass was attained independently in the northern and southern *Papio* lineages, with the *Papio* MRCA being somewhat smaller than the chacma and olive baboons. Although the fossil record of Old World monkeys is dominated by large species, relatively few modern taxa attain similarly large body masses. We thus predict that taxa in clades characterised by large-bodied forms evolved large body mass after their lineages were established, and explore the possible evolutionary processes underlying such differentiation.

2.0 Methods

2.1 Historical biogeography

Occurrence data for modern African papionins were collated from the IUCN Red List (IUCN, 2019). Occurrences were coded according to regions based on the scheme described in Brummitt (2001), which divides Africa into Northern, West Tropical, West-Central Tropical, Northeast Tropical, East Tropical, South Tropical, and Southern regions (Table 2). Originally developed to help standardize plant distribution recording, the regions are phytogeographically (and hence biogeographically) meaningful, with some large politically-defined entities, such as South Africa, divided between regions according to floristic boundaries. However, Brummitt’s (2001) scheme is pragmatic in that political units (such as countries or provinces), which often form the basis of cataloguing efforts, are listed for each region (Table 2). The aim of this work is to reconstruct ancestral ranges based on modern occurrence data rather than ecological association. As the modelling approach chosen limits the number of geographic units included in analysis, the large-scale regions described by Brummitt (2001) were used in preference to vegetation zones (such as those described by White [1983]), which tend to be at a finer scale and can be discontinuous.

An ultrametric consensus tree for African papionins was downloaded from Time Trees of Life (TTOL; Kumar et al., 2017) and converted from Newick to Nexus format in TreeGraph 2.0 (Stöver and Müller, 2010). The RASP (Reconstruct Ancestral State in Phylogenies) program (Yu et al., 2015) running the BioGeoBEARS model testing R package (Matzke, 2013) was used to identify the best model for inferring biogeographic histories of African papionin lineages. As the papionin with the widest modern distribution, *P. anubis*, is found in four regions, the maximum area occupancy in the models was also set to four, with non-contiguous area combinations excluded. As many modern species have wide distributions and fossil papionins (e.g. *Theropithecus*, *Gorgopithecus*, *Soromandrillus*) have been found at very geographically distant sites (Gilbert, 2013; Gilbert et al., 2016b), no further constraints were placed on range or movement ability. Model selection via Akaike information criterion corrected for sample size (AICc; Table 3) indicated that the DEC (Dispersal-Extinction-Cladogenesis) model of geographic range evolution (Ree and Smith, 2008) was the best fit. This model uses a phylogenetic tree to identify transitions between ranges in evolutionary time then uses likelihood methods to estimate ancestral ranges at nodes, which represent cladogenesis events (Ree and Smith, 2008).

2.2 Dietary, environmental and other contributions to morphological divergence

Geometric morphometric data on provenanced baboon skulls were collected and masculinized to maximise sample size as described in Dunn et al. (2013). Detailed dietary data for sites across the *Papio* range were collated from the literature and assigned to several standard and frequently used categories: fruits, subterranean foods, leaves, flowers, animal matter and other (Dunbar and Dunbar, 1974; Norton et al., 1987; Barton, 1989). Baboon skull specimens were linked to the dietary information from one of the sites if they were taken from within 100km of that site and were within the same vegetation zone as defined by White (1983). Dietary data have not been collected evenly across the baboon range and as morphological samples from museums are also patchily distributed and may not fall within the defined radius and vegetation zone of a dietary site, dietary and morphological data from only 10 sites and 45 specimens (Table 4) could be used in analysis. This skull sample is small compared to previous studies on the same material (Dunn et al., 2013) but sufficient to make some broad conclusions about the relative influences of different variables, including diet, on morphology. To our knowledge, no other studies have considered the links between *Papio* diet and skull morphology at such a fine geographical scale.

The data were multivariate, so to help tease out the relationships between skull morphology and its external influences, partial least squares (PLS; Rohlf and Corti, 2000) was conducted using MorphoJ (Klingenberg, 2011) to obtain correlation (RV) coefficients between blocks of variables. Blocks with variables of different units were standardised using NTSys (Rohlf, 2008) to have a mean of 0 and a variance of 1. Plots of the partial least squares axes were used to visualise the relationships underlying these values and to test for outliers. Shape contains a size related component, the pattern of which varies between species. Consequently, analysis with size-controlled shape (see Dunn et al., 2013 for details) may reveal different relationships, so it was also included in the dietary PLS. The independent variables included in the analysis were diet (the proportion by time spent feeding of fruit, leaves, subterranean items, flower, animal and other in the diet), phylogeny (principal coordinates expressing the major axes of phylogenetic variation taken from a phylogenetic distance matrix derived from mtDNA [Zinner et al., 2009]), geography (the terms of the expanded polynomial [$y\ x^2\ xy\ y^2\ x^3\ x^2y\ y^3$] of longitude (x) and latitude (y) found to be significant in trend surface analysis reported in Dunn et al. [2013]), and environment. Data in the environment variable comprised mean temperature taken from the Willmott and Matsuura database (Willmott et al., 1998; Willmott and Matsuura, 2001; Willmott et al., 2001), seasonality index (based on the Willmott and Matsuura data and calculated as the difference between minimum and maximum rainfall divided by mean annual rainfall), mean and standard deviation of normalised difference vegetation index [NDVI] downloaded from the Africa Data Dissemination Service (ADDS, 2005), and altitude (extracted from the Earth Resource and Information Centre [USGS EROS, 2009]).

2.3 Ancestral body mass and evolutionary trends in Papio *size*

Body masses for 111 male and 110 female Asian and African extant cercopithecids (Supplementary Online Material [SOM] Table S1) were collated from the literature (Oates et al., 1994; Smith and Jungers, 1997; Delson et al., 2000; Rowe and Myers, 2017; Rogers et al., 2019) using the taxonomic scheme presented in the Red List (IUCN, 2019). Guenons and colobines were included as outgroups to facilitate the modelling of papionin body mass evolution. Taxa (including *Rungwecebus*) for which no reasonable body mass estimates were available were excluded from analysis; the male and female samples were identical other than the exclusion of *Macaca munzala* from the female sample. There is considerable intra- as well as interspecific variation in primate body masses (Smith and Jungers, 1997; Delson et al., 2000), but the comparative method used here does not enable such variation to be taken into account. There are inevitably compromises in choice of body mass values, so in preference we used data from Smith and Jungers (1997), who undertook a comprehensive assessment of intraspecific variation when compiling mean measured values for species. For *Papio*, the focus of our study, we used updated consensus data reported in Rogers et al. (2019) for all species but *P. anubis*, for which the Smith and Jungers (1997) data provided better coverage of geographic variation. Fossil taxa were not included in the evolutionary modelling because of the patchy nature of the mainly African Old World monkey fossil record, whereby terrestrial (and hence probably larger) species are over-sampled compared to arboreal species.

A consensus ultrametric tree comprising the same 111 or 110 cercopithecid taxa was downloaded from TTOL (Kumar et al., 2017) and converted from Newick to Nexus format in TreeGraph 2.0 (Stöver and Müller, 2010). Phylogenetically-informed body masses for the MRCA of the *Papio /* papionin clades were estimated from extant cercopithecid data using BayesTraits V3 (Meade and Pagel, 2017). The continuous: random walk (model A) Monte Carlo Markov chain (MCMC) procedure in BayesTraits with a burn in of 10,000 interations, a chain of 10^5 iterations, a sample period of 1000 and a uniform (U) prior (minimum 0, maximum 50) on all rate parameters was used as the basis for the male analysis, with identical parameters other than a prior of U (0, 30) for the female. Adequacy of priors, chain mixing and effective sample size (which was 890) were inspected using the Tracer program (Rambaut et al., 2018). The *Papio* and papionin clades and MRCA nodes were defined with the ‘AddTag’ and ‘AddMRCA Node-’ commands.

To investigate whether the rate of body mass evolution in the *Papio* clade differed relative to other Old World monkey clades, a variable rates (independent contrast) model using reversible jump (RJ) MCMC was employed in BayesTraits for both males and females using the full Old World monkey datasets. Such is the complexity of RJ models that burn in rates and iterations need to be greater than standard models (Meade and Pagel, 2017), so burn in was set to 10^6 iterations with a chain of 10^7 iterations and a sample period of 10000 after convergence. Uniform priors (σ 0 to 100) were used, and models were run several times to ensure stability. Log marginal likelihoods were estimated using a stepping stone sampler (Meade and Pagel, 2017) using 100 stones for 10000 iterations. Null (Brownian motion) models without variable rates were run with the same parameters, so that log Bayes factors (Meade and Pagel, 2017) could be calculated (2[log marginal likelihood variable rates model – log marginal likelihood null model]).

Body mass estimates for fossil taxa were used to provide context for the results of the extant analysis. These estimates were drawn from Delson et al. (2000), with body masses recalculated for fossil *Papio* based on the revised taxonomy of Gilbert et al. (2018). To enable comparability between taxa and using the regression equation with the consistently highest R^2 for all the data available, body masses for securely taxonomically assigned fossil *Papio* specimens were estimated using upper second molar (M^2) lengths (taken from Williams et al. [2012] for *P. [h.] botswanae* and Gilbert et al. [2018] for the other species) plus the relevant equations (male, female or 'all' for individuals of unknown sex) from Delson et al. (2000). Although calculating body mass rather than using fossil dimensions as size proxies adds error, comparisons using such body masses were exclusively qualitative, and values given in kg are more easily appreciated than linear dimensions of specific traits.

3.0 Results and discussion

3.1 Historical biogeography

Using modern distributions only, estimated ancestral ranges (Fig. 1 [including probabilities]) for the MRCA of the African papionins always included West Central Tropical Africa, with other tropical regions, especially West Tropical, Northeast Tropical and East Tropical, commonly included. This reflects the high degree of modern monkey diversity in these regions and is also congruent with a previous historical biogeographic study using different methods suggesting that the African tropics were a very likely source region for papionins (Böhm and Mayhew, 2005). Conforming to our hypothesis, the most probable ancestral range of the P/T/L/R clade was estimated to be West Tropical, West Central Tropical, Northeast Tropical and East Tropical Africa, but in a reasonably high proportion of estimates, South Tropical Africa was included in place of either West Tropical or West Central Tropical Africa. In a small number of estimates, Northeast Tropical Africa alone was recovered as the most probable ancestral range. This alongside the inclusion of East Tropical Africa in the rest of the estimates is consistent with the earliest fossil record known for this clade, the occurrence of *Theropithecus* at Kanapoi (East Tropical Africa) ~4.2 Ma and its abundance at Woranso-Mille (Northeast Tropical Africa) shortly after 4 Ma.

The range for the *Papio* MRCA was estimated to be West, Northeast, East and South Tropical Africa, corresponding to much of the modern range and being consistent with our hypothesis, but incongruent with the fossil record, which exists only in the Southern region until well into the Pleistocene (Gilbert et al., 2018). The southern *Papio* clade ancestral range was estimated to be South Tropical (rather than Southern) Africa, with the northern clade range estimate being West Tropical, Northeast Tropical and East Tropical Africa. The ancestral range of *Mandrillus* and *Cercocebus* was estimated to be West Central Tropical Africa, with a smaller probability of the range also including West and East Tropical Africa. This lends support to the hypothesis that the *Mandrillus-Cercocebus* clade has a westerly rather than easterly origin (Devreese and Gilbert, 2015). Nonetheless, the known fossils of this clade, including *Soromandrillus* and *Procercocebus*, are found in Southern, South Tropical, East and Northeast Tropical Africa (Jablonski, 1994; Gilbert 2013). When papionin fossils were included in the DEC analysis (not shown) as MRCAs at relevant nodes, the ancestral ranges were estimated as the fossil location regions only. This is problematic because it is unlikely that the known fossils are directly ancestral to their closest living relatives and hence do not reflect the distribution of the MRCA accurately. Taphonomic factors, whereby most fossils are found clustered in the karst cave sites of South Africa and the Rift (with a notable exception being the record of *Soromandrillus*, found at the Humpata Plateau in Angola [Jablonski, 1994; Gilbert, 2013]), also skew reconstructions of past distributions, as does the fact that not every ancestral node could be assigned a fossil. Future work could use statistical historical biogeography techniques with the full known phylogeny of papionins, including fossils, to estimate ancestral ranges, alongside other dispersal and species movement models to extend and refine previous research on Old World monkey Pleistocene biogeography (Foley, 1999; Strait and Wood, 1999; Gilbert et al., 2016b).

What, if anything, does the historical biogeography model using extant species interpreted alongside molecular data and qualitative assessments of the fossil record, tell us about ancestral ranges and movement routes of papionins, including *Papio*? It is immediately clear that although past distributions are different from present distributions (e.g., *Soromandrillus*, an extinct member of the *Mandrillus* clade, being found in Southern Tropical and Northeast Tropical Africa in the Pleistocene compared to the West Central Tropical and West Tropical distribution of the clade today), some fossil papionins, like several modern papionins, occupied large ranges. Large geographic ranges may have been facilitated by terrestriality. It is very likely that the earliest papionins originated in tropical Africa, which during the middle Pliocene had an evergreen forest belt in the West Central region in much the same position as today, although its north-south extent was smaller and gave way to deciduous forest and woodland to the west and south (Salzmann et al., 2008). The Sahara desert was smaller than it is currently, fringed with shrubland, which also occurred in Arabia (Salzmann et al., 2008). Grassland and woodland occurred in eastern and southern Africa (Salzmann et al., 2008). The conditions were thus ideal for the evolution of terrestrial and semi-terrestrial monkeys, ecologically dependent on trees but increasingly exploiting more open and less densely forested, non-evergreen habitats. Even though environments would be spatially and temporally variable, forest and grassland movement corridors would have existed alongside habitats easily penetrable by terrestrial and semi-terrestrial papionins, promoting movement around Africa, and out into Eurasia (Hughes et al., 2008).

Estimates of the range of the *Papio* MRCA include South Tropical Africa. The boundary between the northern and southern *Papio* mitochondrial clades occurs in central Tanzania, along the Ugalla-Malagarasi and Ruaha-Rufiji Rivers, which are biogeographic boundaries for other primate taxa (Zinner et al., 2015). Jolly (in press) provides an extensive review of *Papio* distributions and hypotheses relating to movement, and notes that an area between southern Tanzania and the Orange River in South Africa contains modern baboons with mitochondrial haplotypes closest to the ancestral stock from the south. Analyses of mtDNA give the northern part of southern Africa as a likely point of origin for *P. ursinus*, with the oldest lineages possibly found in north Namibia (Sithaldeen et al., 2009). These multiple proxies indicate a South Tropical African origin of *Papio*, which then dispersed rapidly southwards, where it is represented in the fossil record of South Africa. Gilbert et al. (2018) argue that *P. robinsoni* has morphological affinity with *P. anubis/P. hamadryas* and *P. angusticeps* looks most like *P. cynocephalus*/*P. kindae*. This is unlikely to be a purely allometric effect (Gilbert et al., 2018) and one interpretation is that if *P. robinsoni* is more primitive, and not a member of modern *Papio*, the similarities with the northern forms are because of retention of ancestral characters or homoplasy. However, it also opens the intriguing scenario that *P. robinsoni* is a member of the lineage that became the northern clade and *P. angusticeps* belongs to the southern clade. Such a scenario is biogeographically possible, and the fossil FADs are just within the range of divergence estimates of the northern and southern clades, as reviewed above. If *P. robinsoni* is indeed found at South African sites only after 2 Ma (see Gilbert et al. [2018] and below for a review), one possibility is that from the hypothesised source region in South Tropical Africa, there were several waves of movement. The first may have been a *P. angusticeps*-like animal dispersing far to the south, where it left its trace in the fossil record of South Africa, with an early *P. ursinus*-like form pushing towards northeastern Namibia before dispersing east around the Kalahari and into northern South Africa (sensu Sithaldeen et al., 2009). After the north-south split, another wave of movement far to the south, this time of northern clade *P. robinsoni*-like animals, could have occurred. A second *P. ursinus* clade that originated slightly later than the first clade, possibly as a result of allopatric divergence because of barriers created by arid regions, dispersed to the Cape, then expanded northwards into Namibia (Sithaldeen et al., 2009). This could have displaced or replaced early Pleistocene *Papio* in South Africa, possibly because of its ability to exploit seasonal environments and subterranean resources very effectively (see below).

Based on the fossil record and the molecular data derived from *P. ursinus* (Sithaldeen et al., 2009), the northwards movement of *Papio*, at least up the east side of Africa, was much slower than its progress south and west. As discussed by Jolly (in press), this may have been because of a physical barrier, unsuitable habitat, or competition. The paleoenvironmental and paleogeographic records from the early Pleistocene are insufficiently resolved to identify specific physical and environmental barriers, but given the faunal (including monkey) interchange between eastern and southern African sites at that time (Foley 1999; Strait and Wood, 1999; Gilbert et al., 2016b), it is very unlikely that there were physical barriers to *Papio* movement that prevented it from reaching eastern Africa. Extreme aridity and dense forest probably limit dispersal in baboons (slowing progression if not halting it entirely) but since the fundamental niche of baboons is wide, it is likely that major changes in biome or vegetation that act as a barrier to dispersal pose less of a challenge to *Papio* than to other animals. Although considerable further work is required to reconstruct habitat and corridors at sufficiently fine spatial and temporal scales, it certainly seems implausible that *Papio* could not move between east and southern Africa when other large-bodied cercopithecids could. For this reason, it seems likely that that the ‘baboon’ niche was occupied fully by other primates in eastern Africa during the early Pleistocene, which prevented early baboon movement northwards along the Rift.

The taxonomic structure of African monkey communities was very different in the Pleistocene compared to today, especially because of the presence of large-bodied, semi-terrestrial colobines (which are particularly well-represented at Koobi Fora [Jablonski and Leakey, 2008]), but also because of the widespread and abundant *T. oswaldi*. Based on their presence and tenure in eastern Africa these taxa could potentially have halted *Papio* colonization in the early Pleistocene, just as the macaque radiation in northern Africa and Eurasia may have prevented *Papio* from expanding out of sub-Saharan Africa and Arabia. Due to the eurytopic nature of both baboons and macaques, the lack of *Papio* in Eurasia could have been because of classic competitive exclusion. In eastern Africa, however, adaptive competitive exclusion was less likely as *Theropithecus*, *Papio* and *Cercopithecoides* are found in close geographic proximity (and potentially sympatry) in southern Africa (Elton, 2007, 2012). Information on large colobine paleobiology is quite sparse, but microwear data from southern African *Cercopithecoides williamsi* suggest leaf and grass eating (El-Zataari et al., 2005). This indicates that *C. williamsi* was less catholic in its diet than *Papio*, although as microwear samples only a very short time window, such a conclusion is necessarily tentative. *Theropithecus* is likely to have been much more stenotopic than *Papio*, having dental and postcranial adaptations to graminivory (Jolly, 1972) and becoming increasingly dependent on grazing in C_4 ecosystems as the Pleistocene progressed (Cerling et al., 2013). *Papio* is more generalist, and depends mainly on C_3 resources, with more limited use of C_4 plants (Codron et al., 2006; Cerling et al., 2013). Competition for food and habitat between the colobines, *Theropithecus* and *Papio* was thus probably limited. Instead, the process that prevented *Papio* becoming established at the eastern African Rift sites was more likely to have been neutral high-density blocking, whereby dispersers arriving in a region cannot maintain populations because previous colonizers have occupied it densely (Waters et al., 2013).

In contrast to *Papio*, *Theropithecus* is extremely well sampled in the Plio-Pleistocene of eastern Africa, where it is found in the record from ~4 to 0.5 Ma, and is sometimes incredibly abundant (Frost et al., 2014). Its age as a lineage makes it a good candidate for a 'founder' terrestrial cercopithecid in the Pliocene, and its abundance and high density at sites such as Woronso-Mille suggest that as a founder, it 'took all' (sensu Waters et al., 2013). Large-bodied colobines are also speciose in the eastern African Pleistocene, being present at Koobi Fora from ~1.9 – 1.4 Ma, in the KBS and Okote Members (Jablonski and Leakey, 2008), alongside up to four species of hominin. It is possible that the patterns observed are taphonomic, whereby sites in eastern Africa, for example, sample habitats, such as those near water, possibly preferred by *Theropithecus*. More work must be done to explore this. But, if high-density blocking was at play, the extinction of large-bodied colobines in the late early Pleistocene and *T. oswaldi* in the middle Pleistocene freed up space for *Papio.* This is consistent with the fossil record of eastern Africa, which shows that *Papio* specimens with affinity to extant species were present by the middle Pleistocene (Gilbert et al., 2018). What caused the extinction of large-bodied colobines and *Theropithecus* is the subject of ongoing debate (see, for example, Cerling et al., 2013) but, building on previous work (e.g. Shipman et al., 1981), it would be worth examining further whether another member of the primate community, *Homo*, had a disruptive effect on monkey communities in the African Pleistocene. *Papio* colonization of eastern Africa came at a time when *Homo erectus* was a fully-fledged member of the carnivore guild (Plummer, 2004), and there is evidence that *Theropithecus* was one of its prey species (see review in Meloro and Elton, 2012). This could have caused direct extirpation in parts of eastern Africa, which then released the demographic block that previously prevented *Papio* (which today lives almost commensally with humans in many parts of Africa) from moving into the region (sensu Fraser et al., 2015).

3.2 Dietary, environmental and other contributions to morphological divergence

Movement across sub-Saharan Africa and into Arabia exposed *Papio* to varying environments, with the most widespread species experiencing considerable heterogeneity within their ranges (Winder, 2014), which extends to diet. As anticipated, there is a significant correlation in the partial least squares (PLS) analysis (Table 5) between baboon skull shape and diet (RV = 0.3303, $p < 0.0001$). The first and only significant PLS axis reveals morphological extremes of an elongated, ventrally flexed morphology versus an unelongated slightly dorsally flexed morphology (SOM Fig. S1). The former, as predicted, corresponds to a diet high in subterranean foods while the latter is high in fruit. Removal of the chacma baboon does not eliminate the significance of the relationship between shape and diet. Loadings of PLS 1 reveal that the elongated, now no longer ventrally flexed, morphology corresponds to a high subterranean diet, as was the pattern before, while the unelongated morphology corresponds to a frugivorous diet (SOM Fig. S2). This reveals the ventral flexion to be chacma-specific. Removal of the chacma baboon reduced the RV coefficient from 0.337 to 0.270, demonstrating the chacma baboon is an important component of this relationship, but that the trend exists without this taxon. Compared to full shape, size-controlled shape has reduced covariance with diet in the PLS analysis but the correlation is still significant (RV = 0.2162, p = 0.0020), as it is in the sample with chacma removed (RV = 0.1948, p = 0.0154). The morphological extremes show a klinorhynch form at the subterranean food eating extreme and an airorhynch form at the fruit eating extreme (SOM Fig. S3). Removal of the chacma removes the ventral flexion of the rostrum, and the subterranean food eating form appears more robust, with the frugivorous form appearing gracile, as predicted (SOM Fig. S4).

The significant covariation between baboon diet and morphology can be summarised as a divergence between long-faced robust specimens with a diet high in subterranean foods or USOs, and short faced animals associated with a diet containing a higher proportion of fruit. Of course this finding is based on a small sample, with data from observational studies of diet extrapolated to specimens from different locations and times. This may be problematic in that the baboons may be from a different population or from a time when they were behaving quite differently. For instance, dietary shifts have been noted over time at Amboseli (Alberts et al. 2005). It would be beneficial to repeat the analysis if more dietary data that can be linked to skull specimens become available (especially from *P. kindae* and including a greater spread of *P. ursinus* groups, as the Giant's Castle population may be at the limits of ecological tolerance [sensu Barrett and Henzi, 1997]). However, from the perspective of broad evolutionary adaptations, and even based on the limited data presented, it seems unlikely that a strong trend would be detected if there were not genuine broad scale differences in morphology that were influenced by diet.

Such broad-scale differences, driven by the relative importance of subterranean foods in the baboon diet, are evident intraspecifically as well as at genus level. This is shown by the olive baboon, which occupies a wide but middle-centred spread across the diet-shape axis and has a highly varied diet, eating subterranean foods, especially in dry environments (Whiten et al., 1991), but also a higher proportion of fruit in the forests of the moist savannah (Rowell, 1966) and in West Africa (Kunz and Linsenmair, 2008). It is interesting therefore that analysis after removal of the chacma baboon, a long-faced species that eats a considerable amount of subterranean foods, still shows a link between long-faced skulls and subterranean food eating. Thus, the olive baboon tends towards the same dietary-shape covariation as found in the chacma baboon, rather than being discretely different. *Papio ursinus* and *P. anubis* are both large-bodied so the association between morphology and subterranean food might be the consequence of size / allometry. However, size-controlled shape demonstrated an only slightly reduced correlation coefficient, and clear morphological distinctions were present. When the chacma was included, this related to a ventrally flexed rostrum. When it was excluded, specimens, mainly *P. anubis*, showed a robust morphology with a deep mandibular corpus and rostrum corresponding to subterranean food eating versus a more gracile form, corresponding to fruit eating. *Papio papio* exemplified this, but the trend was also seen in other species. It is very likely that there is a biomechanical basis to the relationship between longer faces and USO consumption, possibly related to a requirement for greater bite force when masticating subterranean resources. Given that there is considerable variation in the mechanical properties of USOs, which are stiffer than fruits and leaves but not necessary tougher than mature leaves (Dominy et al., 2008), further work to explain the morphological patterns identified here would be beneficial. However, this will require much more detailed data on dietary components within broad categories such as USOs, and a larger skull sample.

Diet was not the only contributor to *Papio* skull variation in the PLS analysis (Table 5). Baboon skull shape was significantly correlated with variation in latitude and longitude (RV = 0.3093, $p < 0.0001$). The first PLS axis (SOM Fig. S5), statistically significant, reveals a relationship between geography and shape, largely made up of the variation between the chacma baboon and the other species. The shorter rostrum and larger neurocranium corresponds to the northern species while the longer rostrum the southerly. The PLS between shape and phylogeny is significant (RV = 0.2024, p = 0.0057) overall and for all but the last PLS axis. The correlation between environment and shape is significant (RV = 0.2122, p = 0.0104). The first two partial least squares axis account for the majority of the covariation and are both significant. The environmental axis runs between high altitude and high mean temperature and seasonality. The high altitude corresponds to an elongated klinorhynch shape and the high temperature a shorter muzzled airorhynch one (SOM Fig. S6).

Attributing causality to correlations in morphological studies tends to be problematic, and the variables used here are not truly independent (explored in more detail in Dunn et al. [2013]). Nonetheless, models based on fundamental principles can be proposed to explore the factors that contribute to morphological differentiation. Figure 2 is a schematic (sensu Plavcan and van Schaik, 1997) to illustrate how external variables may interact and influence baboon skull morphology. As in previous studies using different methods (Frost et al, 2003; Dunn et al., 2013), and unsurprisingly given the spatial structure of baboon taxa, there is a significant relationship between geography (longitude and latitude) and shape. The PLS with geography, like diet, has an RV >3. Phylogeny and environment have lower RVs, but are both significantly correlated with skull shape. Partial least squares analysis of phylogeny and size-controlled shape (full results not shown) yields an identical and significant RV to the analysis with shape, indicating a phylogenetic component to *Papio* skull differentiation that is not related merely to size. The results also indicate an environmental influence on baboon skull shape but the correlation between environment and shape is less strong than that between environment and diet. Environment and diet are highly correlated in partial least squares (RV = 0.6327, $p < 0.0001$, full results not shown), so environment may exert influence on skull shape indirectly via structural properties of diet as well as directly. Diet emerges as the variable with the highest correlation with baboon skull shape. The correlation between diet and environment as well as the dietary/morphological variation within *P. anubis* suggests that the response of skull morphology to diet is localised rather than phylogenetically set at the species level. Whether this is due to relative lack of canalisation in baboon skull form or local directional adaptation needs further study.

Of particular interest is the role subterranean foods play in skull divergence among and within baboon species, both between *P. ursinus* and other taxa and among populations of *P. anubis*. Gilbert et al. (2018) note that *P. ursinus* is derived in its cranial morphology, even when compared to fossil specimens from southern Africa. Isotope data from Pleistocene papionins in southern Africa indicate that they were consuming some C_4 foods but are silent on whether these were grasses, sedges or underground storage organs. The extensive pitting on *P. ursinus* teeth revealed by microwear analysis and caused by consumption of hard USOs and grit is not seen in a similar sample of Pleistocene southern African papionins (El-Zataari et al., 2005), so it is reasonable to assume that either they were not eating or ingesting these items in high quantities, or that they did so only occasionally. This alongside the analysis presented here suggests that consumption of USOs is heavily implicated in *P. ursinus* divergence from congeners in southern Africa and elsewhere. Codron et al. (2005) also observed that the amount of C_4 vegetation in the modern *P. ursinus* diet is less than in southern African fossil papionins. This could help to account for differences in morphology noted by Gilbert et al. (2018) between it and fossil *Papio* species. It certainly supports the notion that the different *Papio* lineages and species, even those found in the same region, may have pursued different adaptive strategies, helping to explain the polymorphism of the genus.

3.3 Ancestral body mass and evolutionary trends in Papio *size*

Investigating the processes leading to phenotypic variation first requires an understanding of the pattern of such variation and ancestral state. The body masses of the male papionin and *Papio* MRCAs were estimated as 10.9 ± 2.2 kg and 21.6 ± 1.1 kg respectively. Estimates for females were 6.7 ± 1.1 kg for the papionin and 12.4 ± 0.6 kg for the *Papio* MRCAs. These results are consistent with our first hypothesis, inspired by Jolly (2007), that the papionin ancestor was a 'medium'-sized primate, and also our second, that the big body masses observed in *P. anubis* and *P. ursinus* evolved convergently. When the process of body mass evolution was investigated via the variable rates model, to evaluate whether body mass evolved at a different rate in different clades, the log marginal likelihood in the male analysis was -295.99, compared to -318.22 under the null model. This gives a log Bayes factor of 44.5. A log Bayes factor >10 is usually interpreted as strongly against the null model, so there is good evidence to favor the variable rates model for males. This is supported by the likelihood distributions shown in SOM Figure S9, and the number of branches (25/221 in six independent lineages; Table 6) that were rescaled over 95% of the time in the analysis. For the female dataset, the log marginal likelihood under the variable rates model was -238.97, compared to the null model value of -244.40, resulting in a log Bayes factor of 10.83. Although this is still strong support for the variable rates model (SOM Fig. S10), no branches were rescaled over 95% of the time, and the signal for variable rates of evolution in females seems less strong overall.

The signal in males and females (Figs. 3 and 4) could differ for a number of reasons. First, it has been noted that within Old World monkeys, female size and body mass appear less sensitive to extrinsic environmental factors than they are in males, possibly because female growth is truncated proximately by the energetic demands of pregnancy and lactation whereas males are more likely to reach their individual genetic potential for growth (Barrett and Henzi, 1997; Cardini and Elton, 2008; Cardini and Elton, 2017). A mostly complementary ultimate explanation is that if females are the 'ecological sex' because of such energetic constraints (Wrangham, 1980; Gaulin and Sailer, 1985), it might be beneficial to limit female growth in resource poor or seasonal environments, especially those where scramble competition is the norm, in a trade-off between survival and reproduction (Gordon et al., 2013). This would lead to increased female homogeneity because, in environments with finite resources that are not easily monopolised, female body size should hit a ceiling and hence variance would be reduced. This is discussed further below.

Another explanation is that pressures of sexual selection on morphology are more pronounced in male than female monkeys (Cardini and Elton, 2017); indeed, a recent study of papionin facial evolution indicated that, compared to females, males probably underwent further morphological evolution (Joganic et al., 2017). Although patterns between sexes have been most extensively studied within species (see Cardini and Elton, 2017, for a review), it is possible that the intraspecific trends translate to interspecific patterns, specifically leading to more homogeneity within female cercopithecid body masses and greater heterogeneity in males (Figs. 3 and 4). This is emphasised by the non-phylogenetically corrected standard deviation of the grand mean of body masses used in this analysis (equivalent to the standard error, as it is effectively the standard deviation of the sample means), which for the whole male cercopithecid sample is 5.27 and in females is 2.94. In *Papio*, these are 4.18 and 1.88 for males and females respectively. In males, there is a ~12 kg range between the mean body masses of the smallest *Papio* species and the largest, compared to ~5 kg in females. A similar pattern has been noted in other work on baboons (Barrett and Henzi, 1997), and the implications of increased male heterogeneity for understanding body size differentiation in *Papio* are also discussed further below. A wider issue (and one that may also affect the male results) is the accuracy of body mass data used, given intraspecific variation. Although error due to choice of body mass values will be reduced with a sufficiently large sample, if a taxon is poorly sampled there is the possibility that outliers may skew the results. The possibility of poor sampling is greater for females, as they are less well represented in reference collections and databases than males.

Focusing on papionin males, the modal scalar values in Table 6 indicate a higher rate of body mass evolution in *Papio*, *Theropithecus* and *Mandrillus* compared to the *Lophocebus* and *Cercocebus* mangabeys, which had modal scalars ~1. The [*Macaca arctoides, Macaca assamensis, Macaca munzala, Macaca radiata, Macaca thibetana*] clade, commensurate with the *sinica* species group (sensu Li et al., 2009) also shows evidence of accelerated evolution, with the branch scalar for the full *sinica* group, including *M. sinica*, having a modal value of 4.53 (with 92% of the iterations rescaled). *Macaca tonkeana* also had accelerated male body mass evolution. It is a member of the *silenus* group (sensu Ziegler et al., 2007), and several other members of that group also showed accelerated evolution at a similar scale between 85% and 93% of the time. The scaling results for *Papio*, *Mandrillus*, *Theropithecus* are further supported by modal delta values >1, which indicate longer paths and hence accelerated evolution that has occurred after the lineages were established (values <1, conversely, indicate an early burst of evolution commensurate with adaptive radiation [Venditti et al., 2011; Baker and Venditti, 2019]). The macaque delta values present a more complex picture, with the [*Macaca arctoides, Macaca assamensis, Macaca munzala, Macaca radiata, Macaca thibetana*] clade having a delta value well below 1, but with the individual taxa having values above 1, suggesting that there was an initial evolutionary burst as the taxa in the clade evolved and radiated, followed by accelerating evolution once the individual species were established. Additional work, beyond the scope of the current study, is required to explore this further. Nonetheless, it appears that accelerating evolution across extant papionins is related to increasing rather than decreasing body masses, and occurred in the Pliocene and Pleistocene.

The afro-papionin scalar and delta values conform to the picture given by the ancestral trait analysis, whereby the papionin MRCA was considerably smaller than *Papio*, *Theropithecus* and *Mandrillus*. Given that *Papio* and *Lophocebus* are probably more closely related to each other than they are to *Theropithecus*, we posit on the basis of analyses of extant data that *Papio* and *Theropithecus* evolved larger body size convergently, with *Mandrillus* also evolving large body mass independently. This runs contrary to Kingdon's (1997) argument that the afro-papionin ancestor was large-bodied. However, there must also be consideration of the fossil record. The relatively large body masses of the Pliocene and early Pleistocene *Parapapio* (facially conservative and generally at the lower end of the extant *Papio* body range [Delson et al., 2000]) reinforces the fact that large body mass was a feature shared by several papionin lineages and established in the Pliocene. Several large-bodied monkey taxa were contemporaneous and possibly sympatric with early Pleistocene *Papio* fossils in southern Africa. Appearing in the South African fossil record after 2 Ma at geographically very close sites, *Gorgopithecus major* and *Dinopithecus ingens* were particularly large, having estimated male body masses well in excess of 30 or even 50 kg (Delson et al., 2000). At Swartkrans, *T. oswaldi* also appears to have been very large, reaching, like *Dinopithecus*, male masses possibly in excess of 50 kg based on dental estimates, with even the smallest male specimen estimated at 35kg (Delson et al., 2000). *Cercopithecoides williamsi*, from Swartkrans and Kromdraai, has an estimated male body mass ~25 kg (Delson et al., 2000). Although *C. williamsi* is a member of the same clade as extant African colobines (Frost et al., 2015), it is very big compared to the modern species. Together with *Papio*, these fossil taxa represent a brief southern African radiation of large bodied, terrestrial monkeys that has no modern analogue (Elton, 2007), even if time averaging has inflated the number of species apparently present in the South African karst cave sites at a given moment.

Future studies merging extant and fossil data must be undertaken to explore ancestral body mass polarity, as inclusion of fossils record may give a different picture to that indicated by the extant analyses reported here. The very large *G. major* is a basal member of the P/L/R clade (Gilbert et al., 2018), so although the extant analysis indicates little body mass evolution in *Lophocebus* once it had diverged from *Papio*, and hence convergent evolution of large body size in *Gorgopithecus* and *Papio*, it is conceivable that large body size is ancestral. Under this scenario, the lineages that led to *Lophocebus* and *Rungwecebus* (not included in the extant analysis because of paucity of data) evolved smaller body mass. The very large *D. ingens* is basal to the *Theropithecus* clade (Gilbert et al., 2018), so the common ancestor of *Dinopithecus* / *Theropithecus* may have been quite large, also providing some support to the notion that smaller body mass may be derived. This notwithstanding, the temporal trend of increasing size in *Theropithecus* (Leakey, 1993; Delson et al., 2000; Frost et al., 2017) suggests that the evolution of very large body mass (>40-50 kg) in *D. ingens* and *T. oswaldi* most probably occurred in parallel. A primary reason for considering fossils only qualitatively in the current work, excluding them from the formal evolutionary models, was the likelihood of taphonomic bias, whereby large, terrestrial species are more likely to be represented than smaller, arboreal ones. A major challenge when designing a future study incorporating fossils is thus to account for this. In the meantime, we weight our conclusions towards the results of the extant modelling, and assume that large body mass evolved convergently from a smaller ancestor in various fossil and modern papionin lineages. This argument is supported by the macaque models presented here that indicate evolution of large body mass from a smaller ancestor in some lineages (including members of the *sinica* group that increased in mass after an initial burst of radiation), rather than size decreases from a larger ancestor in a bigger number of clades.

Concentrating on *Papio*, qualitative comparisons show a fairly congruent picture between the results of the evolutionary modelling reported above and evidence from its fossil record. Reasonably in line with previous dentally-based estimates (Delson et al., 2000), recalculated body masses using the revised taxonomic assignments provided in Gilbert et al. (2018) for *P. izodi* (not a secure member of the genus *Papio* [Gilbert et al., 2018]), *P. angusticeps* (likely to be close to the base of the modern *Papio* radiation [Gilbert et al., 2018]) and *P. robinsoni* (possibly not a member of the modern baboon clade [Gilbert et al., 2018]) are given in Table 7, alongside the estimate for *P. (h.) botswanae*. The *P. (h.) botswanae* body mass estimate is consistent with comparison of overall craniodental dimensions that suggest similarity in size to *P. papio* and *P. hamadryas* (Williams et al., 2012; Gilbert et al., 2018). Although published estimates based on cranial dimensions are somewhat lower (Delson et al., 2000), the dentally-based published and recalculated body mass estimates for male *P. izodi* and *P. angusticeps* are quite similar to the phylogenetically-informed estimate for the MRCA of the *Papio* clade (~22 kg). The female estimates are more divergent.

Alongside the patterns evident in the modern species, the fossil data suggest that increased body mass compared to the papionin MRCA was a primitive aspect of the *Papio* clade and fundamental to the origins of the lineage. Examining intrageneric patterns of body mass in *Papio* helps to provide a more detailed picture of baboon evolution. *Papio papio, P. hamadryas* and *P. cynocephalus* are close to the ancestral *Papio* mean body mass of ~22 kg for males and ~12 kg for females (based on the extant analysis above), as are *P. angusticeps* and *P. (h.) botswanae*. Once the *Papio* lineage was established, size decreased in *P. kindae* and increased in *P. ursinus* and *P. anubis*. Lack of misclassification of cranial form and size-controlled shape in *P. anubis* and *P. ursinus* indicates parallel evolution in these two species (Dunn et al., 2013), which, as hypothesized, appears also to extend to size. This is reinforced by body mass patterns in the other extant members of the northern and southern lineages, as well as two of the fossil forms, *P. angusticeps* and *P. (h.) botswanae*, which are smaller than the olive and chacma baboons. It is thus parsimonious to assume independent increases in body mass in *P. anubis* and *P. ursinus* after *Papio* originated. The early Pleistocene fossil species *P. robinsoni*, likely to be close chronologically to the FAD of the clade, also has body mass substantially larger than the ancestral mean calculated from extant data. Interpreting the significance of this requires consideration of its equivocal taxonomic position as a true member of the modern baboon clade alongside when it appears in the fossil record (Gilbert et al., 2018).

Based on current evidence, it seems unlikely that the large size of *P. robinsoni* represents the ancestral state of the 'true' *Papio* clade. Most, if not all *P. robinsoni* material is currently younger than 2 Ma, postdating the FAD of *P. angusticeps*, an unequivocal member of modern *Papio*. *Papio robinsoni* is found with certainty at Drimolen Main Quarry and Swartkrans Member 1, as well as Skurweberg, and Bolt's Farm Pit 23 (Gilbert et al., 2018). Drimolen and Swartkrans Member 1 are both younger than 2 Ma (Herries and Adams, 2013; Gilbert et al., 2016b). Cooke (1991) estimated Pit 23 of Bolt's Farm to be dated at 2 Ma; Pit 23 is likely to be the source of the Femur Dump material, which has been dated faunally to 2 – 1.5 Ma (Gommery et al., 2008). *Papio robinsoni* is also probably found at Swartkrans Member 2 and Kromdraai B, both dated to <1.8 Ma (Herries and Adams, 2013), as well as potentially Bolt's Farm Pit 10 (Gilbert et al., 2018), of unknown date. The *P. robinsoni* fossils from Skurweberg (alternatively known as Skurveberg, Schurveberg, and Schurweberg) are also of unknown date. Skurweberg is a collection of fossils made by Robert Broom from limestone caves in the eponymous mountain region (Adams et al., 2010). Material from the Pliocene Hoogland site, which has yielded *Theropithecus* but not *Papio*, is very likely to be included in the Skurweberg collection (Adams et al., 2010) but it is not clear that a Pliocene date can be similarly assigned to the Skurweberg *P. robinsoni*. Some of the specimens identified originally as *P. robinsoni* (now *Papio* sp. indet.) from Sterkfontein Member 4, which pre-dates 2 Ma, may actually come from Member 5 (Gilbert et al., 2018). The mean upper and lower dental dimensions of *Papio* sp. indet. from Member 4 and putative Member 4 are slightly higher than those of *P. angusticeps,* but dimensions of the lower dentition fall within the overall range of *P. angusticeps* (Gilbert et al., 2018 [their Tables 1 and 2]). Some of the upper dental dimensions of *Papio* sp. indet. exceed the *P. angusticeps* range, but the largest individuals are not securely from Member 4 (Gilbert et al., 2018 [their SOM Table S3]). On balance, this suggests that the size of *Papio* specimens at Sterkfontein Member 4 did not exceed that of *P. angusticeps*, even if a species somewhat larger than *P. izodi* (identified with certainty at Sterkfontein Member 4) occurred there.

There is overlap in the dental dimensions of fossil *Papio* material from southern Africa (Gilbert et al., 2018). Although the male body mass estimates for *P. angusticeps* calculated here do not exceed ~31 kg (unlike the ~37 kg maximum estimate for male *P. robinsoni*) its upper size range overlaps with the lower end of the *P. ursinus* range, as well as the *P. izodi* and *P. robinsoni* ranges. This is consistent with patterns of variation across modern baboon species. Some *P. robinsoni* individuals fall outside the range of extant and other fossil baboon variation (Gilbert et al., 2018). Examining body mass estimates for securely-sexed specimens of known species from localities with reasonable date estimates (i.e. excluding material that is not definitely from Sterkfontein Member 4 alongside material from Pit 6 (Baboon Cave) of Bolt's Farm, which has not been dated [Monson et al., 2015]), indicates a temporal dimension to the data (SOM Table S2). Fossil material that predates or is around 2 Ma is smaller than material that post-dates 2 Ma. The smaller size of *P. izodi* (found only before 2 Ma) contributes modestly to this trend. There is no strong evidence for tooth size (and by inference, body mass) change in earlier versus later *P. angusticeps*: material from the earlier Haasgat assemblage has estimated means of 21.5 ± 4.6 kg (males, *n* = 4) and 14.6 ± 3.0 kg (females, *n* = 2) compared to the pooled means of later sites (Cooper's A and Kromdraai A; males, *n* = 5, 23.2 ± 4.6 kg; females, *n* = 4, 15.7 ± 2.4 kg). The trend of increasing size over time is driven mainly by the large size of *P. robinsoni* fossils (extending the body mass range beyond that seen in other extinct and extant *Papio*) from sites that are dated to after 2 Ma (Swartkrans, Drimolen and Bolt's Farm Pit 23).

Examination of the fossil record provides good evidence that baboon body masses vary temporally. In extant baboons they also vary spatially, both inter and intra-specifically (Dunbar, 1990; Barrett and Henzi, 1997) but given the paucity of the *Papio* fossil record this is difficult to assess for ancient taxa. Variation among modern populations is seen, for example, in the geographically widespread *P. ursinus*, the largest extant species (Barrett and Henzi, 1997). The relatively small size of Drakensberg *P. ursinus*, which also has long interbirth intervals, appears to be related to its existence in an environment that has high wind chill, low minimum temperature, and high rainfall (Barrett and Henzi, 1997). Indeed, extremes of rainfall have been linked to body mass variation more generally in baboons (Popp, 1983; Dunbar, 1990). It is also possible that predictability of food resources from year to year may influence body mass (Jolly, 2012). Life history variation may be the mechanism that mediates morphological differentiation, and links the environment with form. Adult morphology is the endpoint of growth, the amount of which is determined by a trade-off between growth/maintenance and reproduction (Hennemann, 1983). This in turn is related to mortality risk, with high levels favoring earlier reproductive maturity (Charnov, 1993). The rate of growth is determined by resource availability (Janson and van Schaik, 1993), comprising how much food the environment supports and how much an individual has access to depending on intragroup competition (Barton et al., 1996; Bettridge et al., 2010). Between adult morphology and environmental variation, therefore, lies a range of ecological and life history parameters. The timing of life history events in *Papio* (Lee, 1996; Leigh and Bernstein, 2006; Swedell and Leigh, 2006), ecological factors such as predation risk (Hill and Weingrill, 2007), and social information such as group size (Barton, 1989; Barton et al., 1996; Henzi and Barrett, 2005) exert an effect on the adaptive investment of food resources into growth and thus adult form. Fruits tend to be rich in energy, and easy to process, with baboons that eat more fruit spending less of their time foraging (Hill and Dunbar, 2002). Subterranean foods in contrast are often fibrous, poor quality, and chiefly eaten in the absence of other foods (Norton et al., 1987, Rhine et al., 1989). Large-bodied, fruit eating *P. anubis* individuals in eastern Africa have a faster growth rate than conspecifics in grassland environments (Rowell, 1964, 1966). This is consistent with the prediction that if resources are more plentiful, faster growth is expected (Janson and van Schaik, 1993). Conversely, the reduced and seasonal resources in parts of southern Africa (Anderson, 1982), where consumption of USOs is quite common, may prevent fast growth and early maturation (sensu Janson and van Schaik, 1993). The male chacma baboon takes longer (up to an additional year) to reach maturity than some yellow baboons (Beehner et al., 2009), again consistent with predictions based on life history theory. It must be remembered, however, that other factors, such as mating strategy, could also influence development, as indicated by earlier maturation in *P. hamadryas* males when compared to *P. anubis* (Jolly and Phillips-Conroy, 2003). This notwithstanding, the apparently contrasting life history strategies in *P. anubis* and *P. ursinus* fit with the hypothesis that they independently evolved larger body masses. In future work it would be worth exploring in more detail whether the large sizes attained by *P. anubis* and *P. ursinus* are truly because of faster growth versus longer growth.

The proposed mechanism for modern baboon body mass differentiation via environment and life history is probably a bit too tidy. Although an adaptive response via life history and genetically-determined patterns of growth may occur, body mass and to some extent structural size are labile features likely to respond rapidly to proximate environmental conditions. Thus, factors that influence body size variation are complex and relationships are unlikely to be identical across populations and species. Teasing out the adaptive signal versus the plastic response is likely to be challenging (Cardini et al., 2013). Among a number of African monkeys, including *P. anubis*, skull centroid size is bigger in central African specimens, which may be explained, as above, by higher rainfall and greater productivity (Cardini et al., 2013). Nonetheless, it must be emphasised that environmental variables on their own explain relatively little morphological variance (including size) in *Papio* skulls, with the spatial signal being stronger and the residual (unexplained) variance large (Dunn et al., 2013). At least some differentiation, as described above, is likely to be environmental, with further indirect environmental influences via diet, but the modest RV values in the PLS alongside the large proportion of unexplained variance noted by Dunn et al. (2013) fits with Jolly's (2012) argument that a range of evolutionary factors (rather than simply proximate environmental differences) need to be considered more fully when explaining morphological diversity within *Papio*.

What, then, might be plausible explanations for body mass and structural size differentiation within *Papio* and indeed African papionins more generally? Pattern, as described above, is more straightforward to infer than process, but may help to narrow down causal factors. It is possible that body mass increase across papionin clades is an outcome of stochastically variable rates of evolution (sensu Raup and Gould, 1974). The log Bayes Factors indicate that the variable rates model holds more explanatory weight than the null Brownian motion model, which indicates that the pattern is not stochastic. This is reinforced by the fact that in all the papionin clades with good statistical support for accelerating evolution, body mass is increasing, suggesting an adaptive rather than stochastic process. At a very fined-grained level, however, it could be that stochastic effects, such as genetic drift and genetic bottlenecking, have caused size reduction in *P. kindae*, pushing it away from the other baboon species on the adaptive landscape. Further detailed analyses are required to test this. This notwithstanding, for the papionins as a whole, including most of the genus *Papio*, directional selection for increased body mass is assumed here. Body mass increase could be related to exploitation of more terrestrial niches, pressure from predators, shift in dietary niche, buffering against seasonality and less predictable resource availability, or a combination of these factors. Sexual selection, specifically selection for large male body mass, could also have contributed to body mass increases across lineages.

It is likely that with the increasing availability of open environments in the Plio-Pleistocene, body masses increased convergently in a number of papionin and colobine lineages, including the now-extinct *Parapapio* and *Cercopithecoides*, in adaptation to expansion into more terrestrial niches. It has been hypothesised that the ancestor of *Mandrillus* evolved during a dry period in the Pliocene when forest cover was reduced (Dixson, 2015), presumably then recolonizing dense forest areas. This is consistent with the fossil record of *Soromandrillus*, a member of the same clade (Gilbert, 2013), which is found at sites reconstructed as woodland and bushland (Reed, 1997). An alternative explanation is that the *Mandrillus-Soromandrillus* ancestor evolved in dense forest, increasing its body mass to reduce competition with other species, with *Soromandrillus* then moving into more open areas. Other lineages expanded into terrestrial niches in woodland and bushland and largely kept to such habitats, although some taxa (*P. hamadryas, T. gelada* and middle Pleistocene *T.*

oswaldi) evolved to exploit much more open grassland / desert habitats, and others (some *P. anubis* populations [Rowell, 1966; Ross et al., 2011], and potentially *Parapapio broomi* [Elton, 2001]) denser forest. Among the large papionin species there seems to be no consistent relationship between body mass and habitat preference, given that *Mandrillus sphinx*, the largest modern monkey, exists in tropical forest and *T. oswaldi*, the largest monkey ever to have existed, inhabited grassland, emphatically so towards the end of its tenure (Cerling et al., 2013). Thus, although convergent exploitation of terrestrial niches is likely to have been the initial driver of independent body mass increase among African papionin lineages, including *Mandrillus*, *Theropithecus* and *Papio*, different evolutionary processes and selection pressures beyond this would been at play to determine patterns of body mass differentiation between and within genera, as well as between males and females.

Spatially, there is very little evidence of latitudinal trends in extant African monkeys (Cardini et al., 2013), and based on the presence of monkeys in the eastern African fossil record that are as large or even larger than *P. robinsoni* and other southern African cercopithecids (Delson et al., 2000) there seems to be no relationship between higher latitude and big body mass in Pleistocene monkeys. There is certainly a temporal dimension to the evolution of very large size in papionins, though, as the biggest body masses occur after 2 Ma (Leakey, 1993; Delson et al., 2000; Frost et al., 2017). ‘Very large’ is a relative term here – compared to the gigantism in other Pleistocene and Holocene mammal lineages, mass increase in even the biggest monkeys is only two to three times that seen in their closest relatives, whereas in other mammals it can be much bigger. The capybara, for example, is 60 times larger than its closest living relative (Herrera-Álvarez et al., 2018). The increase in body masses in the southern African papionin fauna goes hand-in-hand with faunal turnover, whereby *Gorgopithecus* and *Dinopithecus* join *Papio* and *Theropithecus*, and *Parapapio* largely disappears (Elton, 2007). It is interesting to note that there are links between body size and diversification, as well as extinction risk, in primates (Matthews et al., 2011). Thus, size may be implicated in the radical taxonomic turnover in monkeys during the Pleistocene, and future studies could usefully explore this.

In another primate lineage, the hominins, *Australopithecus africanus* disappears from the record after ~2 Ma (Herries et al., 2013) and *Paranthropus robustus* appears (Herries and Adams, 2013). Although pulses of turnover are not the norm in the Plio-Pleistocene cercopithecid record (Elton, 2007; Frost, 2007), the extinction / speciation that occurs at this time appears to occur in concert, in monkeys and hominins. An origination pulse between 2 and 1.7 Ma has also been noted in eastern African bovids, and although (as in southern Africa) the pattern could be a taphonomic artefact, the intensification of the Walker circulation is a plausible climatic driver (Bibi and Kiessling, 2015). This could equally have influenced the evolution of southern African primates. Environments at the Cradle of Humankind (northwest of Johannesburg in South Africa, including Sterkfontein, Swartkrans, Malapa and other adjacent sites) became more open and arid after 2 Ma (reviewed in Elton [2007] and Ecker et al. [2018]), so larger body size may have been advantageous in buffering against big seasonal differences in resource availability. However, recent stable isotope data from Wonderwerk Cave (several hundred km to the southwest of the Cradle region) that show a much wetter environment at a similar time highlight that responses to global circulation effects can be local or regionalized (Ecker et al., 2018). In addition, flowstone formation and dating at the Cradle sites indicate that the record is skewed towards drier periods and their communities (Pickering et al., 2019). These data raise questions about how selection pressures are identified and what inferences about causal relationships can be made when considering the highly patchy fossil record of the

African Plio-Pleistocene. One question is whether it is accurate to assume that the sites from which the majority of fossils are recovered actually represent the environments (and hence the environmental pressures) experienced by the species more generally. Another is whether, in a geographically widespread species, the traits identified at a particular site or in a particular region are an example of reaction norm (i.e. plasticity / a proximate response) or local adaptation (an ultimate response). More research on widespread fossil species with a good fossil record, such as *T. oswaldi*, may help to shed further light on these issues.

Per the Jarman-Bell model (see Gaulin, 1979, for applicability to primates), could adaptation to lower quality, bulk diets associated with a shift from more closed environments explain the very large body masses that are seen in South African papionins after 2 Ma? This may have been especially marked if competition with *Paranthropus* and early *Homo*, eclectic feeders that probably could procure (and no doubt favoured) relatively high-quality diets, forced papionins out of the frugivorous niches. Stable isotope data show considerable exploitation of C_4 resources among post-2 Ma monkeys in southern Africa, consistent with a shift to a more arid, open environment (Codron et al., 2005). Nonetheless, the data give a fairly 'generalist' signal for most specimens including *Theropithecus* (Codron et al., 2005), something that is also seen in molar microwear (El-Zataari et al., 2005). Microwear data indicate that *P. robinsoni* from Swartkrans fed electically on leaves/grasses and fruits (El-Zataari et al., 2005), which is in line with the isotope data that indicate that several individuals consumed between 20% and 40% C_4 resources (Codron et al., 2005), potentially the folivorous portion of the diet. Even *D. ingens*, which from microwear data seems to be a fruit eater (El-Zataari et al., 2005), has an isotope signature consistent with consumption of up to 30% C_4 foods (Codron et al., 2005). *Gorgopithecus major* has dental microwear similar to modern leaf eaters such as *Colobus guereza* (El Zataari et al., 2005). The dual dietary proxies of microwear and stable carbon isotopes point to a degree of bulk in the diets of papionins from South Africa, but even *Theropithecus* does not appear to be the bulk grass feeder it became later in the Pleistocene of eastern Africa (Cerling et al., 2013). The dietary data provide no equivocal support for the argument that extensive exploitation of low-quality bulk resources caused body mass increase in South African papionins after 2 Ma. Nonetheless, it is possible that modern *P. ursinus* differentiation occurred because of its greater reliance on USOs in an unpredictable environment, as discussed above.

Could predation risk have contributed to the evolution of large body masses in terrestrial fossil papionins, including *P. angusticeps* and *P. robinsoni*? Fossil primates in open and closed habitats, including in South Africa, have been subject to predation (see review in Meloro and Elton, 2012) and the carnivore guild in the region was large, including the leopard (O'Regan and Reynolds, 2009), a key predator of modern baboons. Carnivore action has been presented as a major accumulator of primate material at cave sites, most famously studied at Swartkrans (Brain, 1993), although caves are also likely to be natural death traps occupied by both primates and carnivorans such as hyena (Val et al., 2014). It has been suggested that terrestriality makes primates vulnerable to predation, but there is no hard evidence in modern species that this is the case (Isbell, 1994). Nonetheless, it may be that the increased risk of predation has caused the evolution of anti-predator strategies in terrestrial primates, reducing predation rates today (Isbell, 1994). There is taphonomic evidence that papionins were among the prey species of carnivores at South African cave sites, so predation risk may have been a selective pressure in the Pleistocene. Some of the fossil carnivorans in southern African deposits were extremely large, reaching body masses in excess of 200 kg (O'Regan and Reynolds, 2009). The largest, *Dinofelis*, may have preyed on browsing and grazing monkeys, although it was more likely to have been a predator of large bovids (Lee-Thorp et al., 2000, 2007).

Circumstantially, therefore, a predator-prey 'arms race' may have existed, whereby size increase in one group led to size increase in another. However, for modern Old World monkeys living together in a shared ecological community there is no good evidence that increased body size confers protection: recent work suggests that small-bodied vervets are no more likely to fall prey to leopards than are sympatric large-bodied baboons (Isbell et al., 2018). This is in addition to stable isotope data suggesting that the medium-sized carnivorans *Megantereon whitei* and *Panthera pardus* (~30 – 65 kg [O'Regan and Reynolds, 2009]) were probably the key predators of monkeys at Swartkrans (Lee-Thorp et al., 2000), and by inference other sites close by. Thus, although body sizes in some (but not all) southern African carnivorans were higher that they are today, support for concerted evolution of papionin body size is equivocal, especially as the ecological communities in the Pleistocene were so different from those currently observed.

What about sex-based explanations? The female *P. robinsoni* and *P. angusticeps* estimates given in Table 7 are very similar in mean and standard deviation; two much bigger specimens attributed to female *P.* cf *robinsoni* are very clear outliers (SOM Table S2). Very similar means and ranges to these are reported for *P. ursinus* across populations (Barrett and Henzi, 1997). In African non-theropith fossil papionins, estimated female means in all species except *D. ingens* are under ~20 kg, with reasonably tight ranges (Delson et al., 2000). *Dinopithecus* and most Pleistocene *Theropithecus* females weigh less than 30 kg, again with smaller ranges than in males, although *T. oswaldi* specimens from late early / middle Pleistocene Hopefield and Olorgesailie have means closer to 40 kg (Delson et al., 2000). Thus, in most papionin females, including *Papio*, size in extant and extinct forms plateaus around 20 kg. Only in the very large Pleistocene species *D. ingens* and *T. oswaldi* does female size exceed this, and even then (small sample size notwithstanding) ranges are smaller than in males. Patterns in the fossil record as well as modern samples are thus consistent with the notion that *Papio* females reach a body mass ceiling, due either to proximate truncation of growth with first reproduction or ultimate life history trade offs. It would be interesting to examine whether the much larger female body masses in *D. ingens* and *T. oswaldi* are the result of faster or longer growth, which may shed some light on life history. The large size attained by these females may also provide support for explanations that implicate lower quality diet and / or predation pressure in pushing up overall body mass in *D. ingens* and *T. oswaldi*.

Gaulin and Sailer (1985) suggest that diet (specifically dietary quality) sets an optimal body mass, and that males in polygynous or promiscuous mating systems will be less likely to conform to this due to the advantages that larger size confers in male-male competition. For Old World monkeys, this requires detailed testing using more up-to date data plus comparative phylogenetic methods, but qualitatively the hypothesis makes sense in explaining *Papio* patterns. Aggression varies across the baboon range (Kalbitzer et al., 2016), with considerable male-male competition in the larger *P. ursinus* being consistent with its larger size. *Papio anubis*, the other large species, also has high levels of male-male competition (reviewed in Kalbitzer et al., 2016). *Papio hamadryas* and particularly *P. papio* have high levels of male tolerance (Fischer et al., 2017; Kalbitzer et al., 2016), which is qualitatively correlated with their slightly smaller size, although *P. cynocephalus* has higher competition (Kalbitzer et al., 2016). Males of the smallest species, *P. kindae,* which are smaller than expected compared to females, may rely more on sperm than contest competition (see comprehensive account in Petersdorf et al. [2019]). Thus, sexual selection could help to explain the substantial disparity in male baboon body masses among extant species, even if other factors such as resource availability also serve to differentiate interspecific body masses. Further work is required before the precise role of sexual selection in determining male size in baboons can be confirmed and extended to the large extinct papionin species from South Africa.

In summary, the *Papio* ancestor probably evolved a relatively large body mass (~22 kg in males, and roughly half that in females) as part of the shift to a more terrestrial niche, something that also occurred in other extinct and extant Old World monkey lineages. Although diet, in particular the exploitation of subterranean resources, very likely contributed to morphological differentiation in extant baboon skulls, and increased reliance on unpredictable resources may have contributed to size increase in *P. ursinus*, there is no clear evidence that reduced dietary quality and greater bulk was a major driver in increased *Papio* or papionin body masses in the early part of the Pleistocene radiation. There is also no evidence that larger body masses in the Pleistocene papionins of southern Africa were a response to competition with hominins or protection from predation. Evidence for spatial and environmental influences on body mass evolution and other aspects of morphological differentiation in extinct and extant taxa are similarly equivocal. It is very possible, however, that sexual selection, related to larger increases in male body mass in species with more aggressive male-male competition, contributed to the marked differences between males of different *Papio* species, whereas female body mass, constrained by the trade off between survival and reproduction, plateaued (hence leading to more interspecific homogeneity in extinct and extant female body masses). Within modern *Papio*, differences in growth and life histories, alongside marked differences in skull shape and the polarity of traits in the fossil record, point to independent increases in body mass in *P. anubis* and *P. ursinus*. It is likely that *P. robinsoni* also independently attained its large size. Once the extant species were established, further population-based shifts occurred, some of which are likely to be plastic responses to proximate environments. In a similar fashion to the skull analysis, the body mass findings indicate that to shed light on the processes and mechanisms that influenced fine-scale differentiation, further work exploring reaction norms versus local adaptation in baboon populations is needed.

4.0 Summary and conclusion

Lengthy as this contribution and review is, we feel that researchers are only beginning to scratch the surface of the work that must be done to understand baboon evolution. Under the scenario we propose here, *Papio* was one of several African papionin lineages to evolve large body size as a means to exploit the increasing availability of open habitats in the Pliocene. The shift to terrestriality, albeit maintaining an ecological dependence on trees, also facilitated efficient species movement and consequently large geographic ranges. *Papio* originated in the southern hemisphere, but probably in the tropical part rather than the more southerly region (now South Africa) where it is best represented in the fossil record. It may have been blocked from expansion north and east by the early colonizer *Theropithecus*, as well as by the presence of terrestrial and semi-terrestrial colobines, and it is possible that there were several waves of movement south and west in the early Pleistocene, before making progress into other parts of Africa during the middle Pleistocene. *Papio* exploits a large variety of habitats and experiences many differences in localised climate and environment across its full geographic range, but divergence in skull form seems more closely linked to dietary adaptation, particularly consumption of USOs. The correlations between geography and shape are nearly as strong, suggesting that population dynamics (dispersal, gene flow) as well as localized responses (which may be proximate or ultimate) both contribute to differences in baboon skull morphology. Environmental factors may contribute to intraspecific patterns of body mass differentiation, and may also explain disparity between some extinct papionin species, but comparison of male and female patterns suggests that sexual selection has been a strong contributor to interspecific divergence in *Papio* body mass. This article thus sheds light on some processes of differentiation in baboon morphology and highlights a number of important areas for future study. In particular, now that there is a good understanding of morphological pattern among baboons, more needs to be done to explore evolutionary process, including the relative contributions of plasticity, adaption and stochastic factors. This will require ever-deeper combination of molecular, paleontological and modern morphological data within sophisticated evolutionary modelling frameworks.

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References

Adams, J. W., Herries, A. I., Hemingway, J., Kegley, A.D.T., Kgasi, L., Hopley, P. J., Reade, H., Potze, S., Thackeray, F. 2010. Initial fossil discoveries from Hoogland, a new Pliocene primate-bearing karstic system in Gauteng Province, South Africa. Journal of Human Evolution 59: 685 – 691.

ADDS (2005) NDVI Long Term Mean. Available at http://earlywarning.usgs.gov/fews/.

Alberts, S. C., Altmann, J., Hollister-Smith, J. A., Mututua, R. S., Sayialel, S. N., Muruthi, P. M., Warutere, J. K. 2005. Seasonality and long term environmental change in a savanna environment. In: Brockman, D. K. & van Schaik, C. P. (Eds.) Seasonality in Primates: Studies of Living and Extinct Human and Non-Human Primates. Cambridge: Cambridge University Press.

Anderson, C. M. 1982. Baboons below the Tropic of Capricorn. Journal of Human Evolution 11: 205-217.

Baker, J., Venditti, C. 2019. Rapid change in mammalian eye shape is explained by activity pattern. Current Biology 29: 1082-1088. doi: https://doi.org/10.1016/j.cub.2019.02.017.

Barrett, L., Henzi, S. P. 1997. An inter-population comparison of body weight in chacma baboons. South African Journal of Science 93: 436-438.

Barton, R. A. 1989. Foraging strategies, diet and competition in olive baboons. PhD dissertation, University of St Andrews.

Barton, R. A., Byrne, R. W., Whiten, A. 1996. Ecology, feeding competition and social structure in baboons. Behavioral Ecology and Sociobiology 38: 321-329.

Beehner, J. C., Gesquiere, L., Seyfarth, R. M., Cheney, D. L., Alberts, S. C., Altmann, J. 2009. Testosterone related to age and life-history stages in male baboons and geladas. Hormones and Behavior 56: 472-480.

Bergman, T.J., Beehner, J.C. 2013. *Theropithecus gelada*. In Kingdon, J., Happold, D., Butynski, T. (Eds) The Mammals of Africa Volume II. Primates. London: Bloomsbury Press, pp. 240-244.

Berthaume, M.A. 2016. Food mechanical properties and dietary ecology. Yearbook of Physical Anthropology S61: 79-104.

Bettridge, C., Lehmann, J., Dunbar, R. I. M. 2010. Trade-offs between time, predation risk and life history, and their implications for biogeography: A systems modelling approach with a primate case study. Ecological Modelling 221: 777-790.

Bibi, F., Kiessling, W. 2015. Continuous evolutionary change in Plio-Pleistocene mammals of eastern Africa. Proceedings of the National Academy of Sciences of the United States of America 112: 10623-8. DOI: 10.1073/pnas.1504538112.

Böhm, M., Mayhew, P.J. 2005. Historical biogeography and the evolution of the latitudinal gradient of species richness in the Papionini (Primata : Cercopithecidae). Biological Journal of the Linnean Society 85: 235-246.

Bradley, B.J, Mundy, N.I. 2008. The primate palette: the evolution of primate coloration. Evolutionary Anthropology 17: 97-111.

Brain, C.K. 1993. Swartkrans: A Cave's Chronicle of Early Man. Pretoria: Transvaal Museum Monograph.

Brummitt, R.K. 2001. World Geographical Scheme for Recording Plant Distributions. Plant Taxonomic database Standards No. 2. Edition 2. Pittsburgh: International Working Group on Taxonomic Databases for Plant Sciences, Carnegie Mellon University.

Burnett, C. D. 1983. Geographic and climatic correlates of morphological variation in *Eptesicus fuscus.* Journal of Mammalogy 64: 437-444.

Burrell A.S., Jolly C.J., Tosi A.J., Disotell T.R. 2009. Mitochondrial evidence for the hybrid origin of the kipunji, *Rungwecebus kipunji* (Primates: Papionini). Molecular Phylogenetics and Evolution 51: 340-348.

Byrne, R. W., Whiten, A., Henzi, S. P., McCulloch, F. M. 1993. Nutritional constraints on mountain baboons (*Papio ursinus*): implications for baboon socioecology. Behavioral Ecology and Sociobiology 33: 233-246.

Cardini, A., Elton, S. 2008. Variation in guenon skulls I: species divergence, ecological and genetic differences. Journal of Human Evolution 54: 615-637.

Cardini, A., Elton, S. 2017. Is there a 'Wainer's rule'? Testing which sex varies most as an example analysis using GueSDat, the free Guenon Skull Database. Hystrix 28: 147–156. doi:10.4404/hystrix-28.2-12139.

Cardini, A., Jansson, A-U., Elton, S., 2007. Ecomorphology of vervet monkeys: a geometric morphometric approach to the study of clinal variation. Journal of Biogeography 34: 1663-1678.

Cardini, A., Dunn, J., O'Higgins, P., Elton, S. 2013. Clines in Africa: does size vary in the same way among widespread Sub-Saharan monkeys? Journal of Biogeography 40: 370–381. DOI:10.1111/j.1365-2699.2012.02783.x.

Caumul, R., Polly, P. D. 2005. Phylogenetic and environmental components of morphological variation: skull, mandible, and molar shape in marmots (Marmota, Rodentia). Evolution 59: 2460-2472.

Cerling T.E., Chritz K.L., Jablonski N.G., Leakey M.G., Manthi F.K. 2013. Diet of *Theropithecus* from 4 to 1 Ma in Kenya. Proceedings of the National Academy of Sciences of the United States of America 110: 10507-12. DOI: 10.1073/pnas.1222571110.

Chala, D., Roos, C., Svenning, J., Zinner, D. 2019. Species-specific effects of climate change on the distribution of suitable baboon habitats – Ecological niche modelling of current and Last Glacial Maximum conditions. Journal of Human Evolution 132: 215-226.

Charnov, E. L. 1993. Life History Invariants: Some Explorations of Symmetry in Evolutionary Ecology. New York, Oxford University Press.

Codron, D., Luyt, J., Lee-Thorp, J.A., Sponheimer, M., De Ruiter, D., Codron, J. 2005. Utilization of savanna-based resources by Plio-Pleistocene baboons. South African Journal of Science 101: 245-248.

Codron, D., Lee-Thorp, J.A., Sponheimer, M., de Ruiter, D., Codron, J. 2006. Inter- and intrahabitat dietary variability of chacma baboons (*Papio ursinus*) in South African savannas based on fecal delta13C, delta15N, and %N. American Journal of Physical Anthropology 129: 204-14. DOI: 10.1002/ajpa.20253.

Cooke, H.B.S., 1991. *Dinofelis barlowi* (Mammalia, Carnivora, Felidae) cranial material from Bolt’s Farm, collected by the University of California African Expedition. Paleontologia Africana 28: 9–21.

Damuth, J., MacFadden, B.J. 1990. Body Size in Mammalian Paleobiology: Estimation and Biological Implications. Cambridge: Cambridge University Press.

Dechow, P. C., Carlson, D. S. 1990. Occlusal force and craniofacial biomechanics during growth in rhesus monkeys. American Journal of Physical Anthropology 83: 219-237.

Delson, E., Terranova, C.J., Jungers, W.L., Sargis, E.J., Jablonski, N.G., Dechow, P.C. 2000. Body mass in Cercopithecidae (Primates, Mammalia): estimation and scaling in extinct and extant taxa. Anthropological Papers of the American Museum of Natural History 83: 1-159.

Devreese, L., Gilbert, C.G. 2015. Phylogenetic relationships within the *Cercocebus-Mandrillus* clade as indicated by craniodental morphology: implications for evolutionary biogeography. American Journal of Physical Anthropology 158: 227-241.

Dixson, A.F. 2015. The Mandrill: A Case of Extreme Sexual Selection. Cambridge: Cambridge University Press.

Dolotovskaya, S., Torroba, J.B., Haus, T., Noll, A., Hofreiter, M., Zinner, D., Roos, C. 2017. Comparing mitogenomic timetrees for two African savannah primate genera (*Chlorocebus* and *Papio*). Zoological Journal of the Linnean Society 181: 471–483. DOI: 10.1093/zoolinnean/zlx001.

Dominy, N., Vogel, E., Yeakel, J., Constantino, P., Lucas, P. 2008. Mechanical properties of plant underground storage organs and implications for dietary models of early hominins. Evolutionary Biology 35: 159-175.

Dunbar, R. I. M. 1990. Environmental determinants of intraspecific variation in body weight in baboons (*Papio* spp.). Journal of Zoology 220: 157-169.

Dunbar, R. I. M., Dunbar, E. P. 1974. Ecological relations and niche separation between sympatric terrestrial primates in Ethiopia. Folia Primatologica 21: 36-60.

Dunn J., Cardini, A., Elton, S. 2013. Biogeographic variation in the baboon: dissecting the cline. Journal of Anatomy 223: 337–352. DOI: 10.1111/joa.12085.

Ecker, M., Brink, J.S., Rossouw, L., Chazan, M., Horwitz, L.K., Lee-Thorp, J.A. 2018. The paleoecological context of the Oldowan-Achuelean in southern Africa. Nature Ecology and Evolution 2: 1080-1086.

Ehardt, C.L., Butynski, T. 2006. The recently described highland mangabey, *Lophocebus kipunji* (Cercopithecoidea, Cercopithecinae): current knowledge and conservation assessment. Primate Conservation 21: 81-87.

El Zaatari, S., Grine, F.E., Teaford, M.F., Smith, H.F. 2005. Molar microwear and dietary reconstructions for fossil Cercopithecoidea from the Plio-Pleistocene deposits of South Africa. Journal of Human Evolution 49: 180-205.

Elton, S. 2001. Locomotor and habitat classification of cercopithecoid postcranial material from Sterkfontein Member 4, Bolt's Farm and Swartkrans Members 1 and 2, South Africa. Paleontologia Africana 37: 115-126.

Elton, S. 2007. Environmental correlates of the cercopithecoid radiations. Folia Primatologica 78: 344-364.

Elton, S. 2012. Impacts of environmental change and community ecology on the composition and diversity of the southern African monkey fauna from the Plio-Pleistocene to the present. In Reynolds, S.C., Gallagher, A. (Eds.) African Genesis. Perspectives on Hominin Evolution. Cambridge: Cambridge University Press, pp. 471-486.

Fischer, J., Kopp, G. H., Pesco, F. D., Goffe, A., Hammerschmidt, K., Kalbitzer, U., Klapproth, M., Maciej, P., Ndao, I., Patzelt, A., Zinner, D. 2017. Charting the neglected West: the social system of Guinea baboons. American Journal of Physical Anthropology 162 (Yearbook of Physical Anthropology S63): 15 – 31.

Foley, R. A. 1999. Evolutionary Geography of Pliocene African Hominids. In Bromage, T. G., Schrenk, F. (Eds.) African Biogeography, Climate Change, and Human Evolution. New York: Oxford University Press, pp. 328-348.

Fraser, C.I., Banks, S.C., Waters, J.W. 2015. Priority effects can lead to underestimation of dispersal and invasion potential. Biological Invasions 17: 1-8.

Freedman, L. 1957. The fossil Cercopithecoidea of South Africa. Annals of the Transvaal Museum 23: 122-262.

Frost, S. R., Marcus, L. F., Bookstein, F. L., Reddy, D. P., Delson, E. 2003. Cranial allometry, phylogeography, and systematics of large-bodied papionins (Primates: Cercopithecinae) inferred from geometric morphometric analysis of landmark data. The Anatomical Record Part A 275A: 1048-1072.

Frost, S.R. 2007. African Pliocene and Pleistocene cercopithecid evolution and global climatic change. In: Bobe, R., Alemseged, Z., Behrensmeyer, A.K. (Eds.) Hominin environments in the East African Pliocene: An Assessment of the Faunal Evidence. Dordrecht: Springer, pp. 51-76.

Frost, S.R., Jablonski, N.G., Haile-Selassie, Y. 2014. Early Pliocene Cercopithecidae from Woranso-Mille (Central Afar, Ethiopia) and the origins of the *Theropithecus oswaldi* lineage. Journal of Human Evolution 76: 39-53.

Frost, S.R., Gilbert, C.C., Pugh, K.D., Guthrie, E., Delson, E. 2015. The hand of *Cercopithecoides williamsi* (Mammalia, Primates): earliest fossil evidence for pollical reduction among colobine monkeys and its implications for their evolution. PLoS ONE 10: e0125030. doi:10.1371/journal.pone.0125030.

Frost, S.R., Saanane, C., Starkovich, B.M., Schwartz, H., Schrenk, F., Harvati, K. 2017. New cranium of the large cercopithecid primate *Theropithecus oswaldi leakeyi* (Hopwood, 1934) from the paleoanthropological site of Makuyuni, Tanzania. Journal of Human Evolution 109: 46-56.

Frost, S.R., Ward, C.V., Manthi, F.K., Plavcan, J.M. 2020. Cercopithecid fossils from Kanapoi, West Turkana, Kenya (2007- 2015). Journal of Human Evolution 140: 102642.

Fuchs, A.J., Gilbert, C.C., Kamilar, J.M. 2018. Ecological niche modeling of the genus *Papio*. American Journal of Physical Anthropology 166: 812-823.

Garcia-Ramos, G., Sanchez-Garduno, F., Maini, P.K. 2000. Dispersal can sharpen parapatric boundaries on a spatially varying environment. Ecology 83: 749-760.

Gaulin, S. J. 1979. A Jarman/Bell model of primate feeding niches. Human Ecology 7: 1-20.

Gaulin, S.J.C., Sailer, L.D. 1985. Are females the ecological sex? American Anthropologist 87: 111-119.

Gilbert, C.C. 2013. Cladistic analysis of extant and fossil African papionins using craniodental data. Journal of Human Evolution 64: 399-433.

Gilbert, C.C., Steininger, C.M., Kibii, J.M., Berger, L.R. 2015. *Papio* cranium from the hominin-bearing site of Malapa: implications for the evolution of modern baboon cranial morphology and South African Plio-Pleistocene biochronology. PLoS ONE 10(8), e0133361. doi:10.1371/journal.pone.0133361

Gilbert, C.C., Takahashi, M.Q., Delson, E. 2016a. Cercopithecoid humeri from Taung support the distinction of major papionin clades in the South African fossil record. Journal of Human Evolution 90: 88-104.

Gilbert, C.C., Frost, S.R., Delson, E. 2016b. Reassessment of the Olduvai Bed I cercopithecoids: a new biochronological and biogeographical link to the South African fossil record. Journal of Human Evolution 92: 50-59.

Gilbert, C.C., Frost, S.R., Pugh, K.D., Anderson, M., Delson, E. 2018. Evolution of the modern baboon (*Papio hamadryas*): a reassessment of the African Plio-Pleistocene record. Journal of Human Evolution 122: 38-69.

Gommery, D., Senegas, F., Thackeray, J.F., Potze, S., Kgasi, L., Claude, J., Lacruz, R. 2008. Plio-Pleistocene fossils from Femur Dump, Bolt's Farm, Cradle of Humankind World Heritage Site. Annals of the Transvaal Museum 45: 67-76.

Gordon, A.D., Johnson, S.E., Louis, E.E. 2013. Females are the ecological sex: sex-specific body mass ecogeogeography in wild sifaka populations (*Propithecus* spp.). American Journal of Physical Anthropology 151: 77-87.

Guevara, E.E., Steiper, M.E. 2014. Molecular phylogenetic analysis of the Papionina using concatenation and species tree methods. Journal of Human Evolution 66: 18-28.

Harding, R. S. O. 1976. Ranging patterns of a troop of baboons (*Papio anubis*) in Kenya. Folia Primatologica 25: 143-185.

Harris, E.E. 2000. Molecular systematics of the Old World monkey tribe Papionini: analysis of the "total" available genetic sequences. Journal of Human Evolution. 38: 235-256.

Harris, J.M., Leakey, M.G., Cerling, T.E., 2003. Early Pliocene tetrapod remains from Kanapoi, Lake Turkana Basin, Kenya. Contributions in Science, Natural History Museum of Los Angeles County 468: 39-112.

Harrison, T., Harris, E.E. 1996. Undescribed fossil cercopithecids from the Plio-Pleistocene of Kanam East in Western Kenya. Journal of Human Evolution 30, 539-561.

Hennemann, W. W. 1983. Relationship among body mass, metabolic rate and the intrinsic rate of natural increase in mammals. Oecologia 56: 104-108.

Henzi, S. P, Barrett, L. 2005. The historical socioecology of savanna baboons (*Papio hamadryas*). Journal of the Zoological Society London, 265, 215-226.

Herrera-Álvarez, S., Karlsson., E., Ryder, O.A., Lindblad-Toh, K., Crawford, A. 2018. How to make a rodent giant: genomic basis and tradeoffs of gigantism in the capybara, the world's largest rodent. BioRxiv doi: http://dx.doi.org/10.1101/424606.

Herries, A.I., Adams, J.W. 2013. Clarifying the context, dating and age range of the Gondolin hominins and *Paranthropus* in South Africa. Journal of Human Evolution 65: 676 – 681.

Herries A.I.R., Pickering, R., Adams, J.W., Curnoe, D., Warr, G., Latham, A.G., Shaw, J., 2013. A multi-disciplinary perspective on the age of *Australopithecus* in southern Africa. In: Reed K., Fleagle J., Leakey R. (Eds) The Paleobiology of *Australopithecus*. Dordrecht: Springer, pp. 21-40.

Hill, R. A., Dunbar, R. I. M. 2002. Climatic determinants of diet and foraging behaviour in baboons. Evolutionary Ecology 16: 579-593.

Hill, R. A., Weingrill, T. 2007. Predation risk and habitat use in chacma baboons (*Papio hamadryas ursinus*). In Gursky, S.L., Nekaris, K. A. I. (Eds.) Primate Anti- Predator Strategies. Boston: Springer US, pp. 339-354.

Hughes, J.K., Elton, S., O'Regan, H.J. 2008. *Theropithecus* and 'out of Africa' dispersal in the Plio-Pleistocene. Journal of Human Evolution 54: 43-77.

Isbell, L.A. 1994. Predation on primates: ecological patterns and evolutionary consequences. Evolutionary Anthropology. 3: 61-71.

Isbell, L.A., Bidner, L.R., Van Cleave, E.K., Matsumoto-Oda, A., Crofoot, M.C. 2018. GPS-identified vulnerabilities of savannah-woodland primates to leopard predation and their implications for early hominins. Journal of Human Evolution 118: 1-13.

IUCN 2019. The IUCN Red List of Threatened Species. Version 2019-1. http://www.iucnredlist.org. Downloaded on 01 June 2019.

Jablonski, N.G. 1994. New fossil cercopithecid remains from the Humpata Plateau, southern Angola. American Journal of Physical Anthropology 94: 435-464.

Jablonski, N.G., Leakey, M.G. 2008. Koobi Fora Research Project: Volume 6 The Fossil Monkeys. San Francisco: California Academy of Sciences.

Janson, C. H., Van Schaik, C. P. 1993. Ecological risk aversion in juvenile primates: slow and steady wins the race. In Pereira, M. E., Fairbanks, L. A. (Eds.) Juvenile Primates: Life history, Development, and Behavior. New York: Oxford University Press, pp. 57-74.

Joganic, J.L., Willmore, K.E., Richtsmeier, J.T., Weiss, K.M., Mahaney, M.C., Rogers, J., Cheverud, J.M. 2017. Additive genetic variation in the craniofacial skeleton of baboons (genus *Papio*) and its relationship to body and cranial size. American Journal of Physical Anthropology 165: 269-285.

Jolly, C.J. 1972. The classification and natural history of *Theropithecus* (*Simopithecus*) (Andrews, 1916) baboons of the African Plio-Pleistocene. Bulletin of the British Museum of Natural History - Geology 22:1–123.

Jolly, C. 1993. Species, subspecies and baboon systematics. In: Kimbel, W., Martin, L. (Eds) Species, Species Concepts and Primate Evolution. New York: Wiley, pp.67-107.

Jolly, C.J. 2001. A proper study for mankind: Analogies from the papionin monkeys and their implications for human evolution. American Journal of Physical Anthropology 116: 177-204.

Jolly, C.J., 2007. Baboons, mandrills, and mangabeys: Afro-papionin socioecology in a phylogenetic perspective. In Campbell, C.J., Fuentes, A., MacKinnon, K.C., Bearder, S.K. (Eds.) Primates in Perspective, pp 240-251. New York: Oxford University Press.

Jolly, C. J. 2012. Rainfall is not a genus-wide predictor of mean body mass in baboon populations. Journal of Zoology 286: 185-193.

Jolly, C.J. in press. Philopatry at the frontier: a demographically-driven scenario for the evolution of multi-level societies in baboons (*Papio*). Journal of Human Evolution, in press.

Jolly, C.J., Phillips-Conroy, J.E., 2003. Testicular size, mating system and maturation schedules in wild anubis and hamadryas baboons. International Journal of Primatology 24: 125-142.

Kalbitzer, U., Roos, C., Kopp, G.H., Butynski, T., Knauf, S., Zinner, D., Fischer, J. 2016. Insights into the genetic foundation of aggression in *Papio* and the evolution of two length-polymorphisms in the promoter regions of serotonin-related genes (5-HTTLPR and MAOALPR) in Papionini. BMC Evolutionary Biology 16: 121. DOI: 10.1186/s12862-016-0693-1.

Kingdon, J. 1997. The Kingdon Field Guide to African Mammals. San Diego: Academic Press.

Kingdon, J., Happold, D., Butynski, T. 2013. Mammals of Africa Volume II. Primates. London: Bloomsbury.

Klingenberg, C. P. 2011. MorphoJ: an integrated software package for geometric morphometrics. Molecular Ecology Resources 11: 353-357.

Kumar, S., Stecher, G., Suleski, M., Hedges, S.B. 2017. TimeTree: a resource for timelines, timetrees, and divergence times. Molecular Biology and Evolution 34: 1812–1819. doi:10.1093/molbev/msx116.

Kummer, H. 1968. Social Organization of Hamadryas Baboons. Chicago: Aldine.

Kunz, B. K., Linsenmair, K. E. 2008. The disregarded west: diet and behavioural ecology of olive baboons in the Ivory Coast. Folia Primatologica 79: 31-51.

Leakey, M.G. 1993. Evolution of *Theropithecus* in the Turkana Basin. In: Jablonski, N.G. *Theropithecus*: The Rise and Fall of a Primate Genus pp. 85-124. Cambridge: Cambridge University Press.

Lee, P. C. 1996. The meaning of weaning: growth, lactation, and life history. Evolutionary Anthropology 5: 87-96.

Lee-Thorp, J., Thackeray, J.F., van der Merwe, N. 2000. The hunters and the hunted revisited. Journal of Human Evolution 39: 565-576.

Lee-Thorp, J.A., Sponheimer, M., Luyt, J. 2007. Tracking changing environments using stable carbon isotopes in fossil tooth enamel: an example from the South African hominin sites. Journal of Human Evolution 53: 595-601.

Leigh, S. R., Bernstein, R. M. 2006. Ontogeny, life history, and maternal investment in baboons. In Swedell, L., Leigh, S.R. (Eds) Reproduction and Fitness in Baboons: Behavioral, Ecological, and Life History Perspectives. Boston: Springer, pp. 225-255.

Li, J., Han, K., Xing, J., Kim, H.S., Rogers, J., Ryder, O.A., Disotell, T., Yue, B., Batzer, M.A. 2009. Phylogeny of the macaques (Cercopithecidae: *Macaca*) based on Alu elements. Gene 448: 242-249. doi: 10.1016/j.gene.2009.05.013.

Liedigk, R., Roos, C., Brameier, M., Zinner, D. 2014. Mitogenomics of the Old World monkey tribe Papionini. BMC Evolutionary Biology 14: 176.

Marroig, G., Cheverud, J.M. 2007. Size as a line of least evolutionary resistance: diet and adaptive morphological radiation in New World monkeys. Evolution 59: 1128-1142.

Martinez, F.I., Capelli, C., Ferreira da Silva, M.J., Aldeias, V., Alemseged, Z., Archer, W., Bamford, M., Biro, D., Bobe, R., Braun, D.R., Habermann, J.M., Lüdecke, T., Madiquida, H., Mathe, J., Negash, E., Paulo, L.M., Pinto, M., Stalmans, M., Carvalho, S. 2019. A missing piece of the *Papio* puzzle: Gorongosa baboon phenostructure and intrageneric relationships. Journal of Human Evolution 130: 1-20.

Matthews, L.J., Arnold, C., Machanda, Z., Nunn, C.L. 2011. Primate extinction risk and historical patterns of speciation and extinction in relation to body mass. Proceedings of the Royal Society B: Biological Sciences. 278: 1256-1263. DOI:10.1098/rspb.2010.1489.

Matzke, N. J. 2013. Probabilistic historical biogeography: new models for founder-event speciation, imperfect detection, and fossils allow improved accuracy and model-testing. Frontiers of Biogeography 5: 242-248.

Meade, A., Pagel, M. 2017. BayesTraits. http://www.evolution.rdg.ac.uk/BayesTraitsV3.0.1.html.

Meloro, C., Elton S. 2012. The evolutionary history and palaeo-ecology of primate predation: *Macaca sylvanus* from Plio-Pleistocene Europe as a case study. Folia Primatologica 83: 216-235.

Monson, T., Brasil, M.F., Hlusko, L.J. 2015. Materials collected by the southern branch of the UC Africa Expedition with a report on previously unpublished Plio-Pleistocene fossil localities. PaleoBios 32: 1-17.

Newman, T. K., Jolly, C. J., Rogers, J. 2004. Mitochondrial phylogeny and systematics of baboons (*Papio*). American Journal of Physical Anthropology 124, 17-27.

Norton, G. W., Rhine, R. J., Wynn, G. W., Wynn, R. D. 1987. Baboon diet: a five-year study of stability and variability in the plant feeding and habitat of the yellow baboons (*Papio cynocephalus*) of Mikumi National Park, Tanzania. Folia Primatologica 48: 78-120.

Oates, J. F., Davies, A.G., Delson, E. 1994. The diversity of living colobines. In David, A.G., Oates, J.F. (Eds) Colobine Monkeys: Their Ecology, Behaviour and Evolution. Cambridge: Cambridge University Press, pp. 45–73.

O'Regan, H.J., Reynolds, S.C. 2009. An ecological reassessment of the southern African carnivore guild: a case study from Member 4, Sterkfontein, South Africa. Journal of Human Evolution 57: 212-222.

Petersdorf, M., Weyher, A.H., Kamilar, J., Dubuc, C., Higham, J. 2019. Sexual selection in the Kinda baboon. Journal of Human Evolution 135: 102635.

Pickering, R., Herries, A.I.R., Woodhead, J.D., Hellstrom, J.C., Green, H.E., Paul, B., Ritzman, T., Strait, D.S., Schoville, B.J., Hancox, P.J. 2019. U–Pb-dated flowstones restrict South African early hominin record to dry climate phases. Nature 65: 226-229. https://doi.org/10.1038/s41586-018-0711-0.

Plavcan, J. M., van Schaik, C. P. 1997. Intrasexual competition and body weight dimorphism in anthropoid primates. American Journal of Physical Anthropology 103: 37-68.

Plummer, T. W. 2004. Flaked stones and old bones: biological and cultural evolution at the dawn of technology. Yearbook of Physical Anthropology 47: 118-164.

Popp, J.L. 1978. Male baboons and evolutionary principles. Ph.D. Thesis, University of Harvard.

Popp, J.L. 1983. Ecological determinism in the life histories of baboons. Primates 24: 198-210.

Post, D.G. 1978. Feeding and ranging behaviour of the yellow baboon (*Papio cynocephalus*). Ph.D. Thesis, Yale University.

Pugh, K.D., Gilbert, C.C. 2018. Phylogenetic relationships of living and fossil African papionins: combined evidence from morphology and molecules. Journal of Human Evolution 123: 35-51.

Rambaut, A., Drummond, A.J., Xie, D., Baele, G., Suchard, M.A. 2018. Posterior summarisation in Bayesian phylogenetics using Tracer 1.7. Systematic Biology 67: 901-904. doi:10.1093/sysbio/syy032.

Raup, D.M., Gould, S.J. 1974. Stochastic simulation and evolution of morphology – towards a nomothetic paleontology. Systematic Zoology 23: 305-322.

Ree, R.H., Smith, S.A. 2008. Maximum likelihood inference of geographic range evolution by dispersal, local extinction and cladogenesis. Systematic Biology 57: 4-14.

Reed, K. 1997. Early hominid evolution and ecological change through the African Plio-Pleistocene. Journal of Human Evolution 32: 289-322.

Rhine, R. J., Norton, G. W., Wynn, G. W., Wynn, R. D. 1989. Plant feeding of yellow baboons (*Papio cynocephalus*) in Mikumi National Park Tanzania and the relationships between seasonal feeding and immature survival. International Journal of Primatology 10, 319-342.

Roberts, T.E., Davenport, T.R.B., Hildebrandt, K.B.P., Jones, T., Stanley, W.T., Sargis, E.J., Olson, L.E. 2010. The biogeography of introgression in the critically endangered African monkey *Rungwecebus kipunji*. Biology Letters 6: https://doi.org/10.1098/rsbl.2009.0741.

Rogers, J., Raveendran, M., Harris, R.A., Mailund, T., Leppälä, K., Athanasiadis, G., Schierup, M., Cheng, J., Munch, K., Walker, J.A., Kongel, M.K., Jordan, V.E., Steely, C.J., Beckstrom, T.O., Bergey, C., Burrell, A., Schrempf, D., Noll, A., Kothe, M., Kopp, G.H., Liu, Y., Murali, S., Billis, K., Martin, F.J., Muffato, M., Cox, L., Else, J., Disotell, T., Muzny, D.E., Phillips-Conroy, J., Aken, B., Eichler, E.E., Marques-Bonet, T., Kosiol, C., Batzer, M., Hahn, M.W., Tung, J., Zinner, D., Roos, C., Jolly, C.J., Gibbs, R.A., Worley, K.C. 2019. The comparative genomics and complex population history of *Papio* baboons. Science Advances 5: eaau6947. DOI: 10.1126/sciadv.aau6947.

Rohlf, F. J. 2008. NTSYSpc. 2.20 version. Setauket, NY: Exeter Software.

Rohlf, F., Corti, M. 2000. Use of two-block partial least squares to study covariation in shape. Systematic Biology 49: 740-753.

Roos, C., Kothe, M., Alba, D.M., Delson, E., Zinner, D. 2019. The radiation of macaques out of Africa: evidence from mitogenome divergence times and the fossil record. Journal of Human Evolution 133: 114-132. DOI: 10.1016/j.jhevol.2019.05.017.

Ross, C., Warren, Y., Maclarnon, A.M., Higham, J.P. 2011. How different are Gashaka's baboons? Forest and open country populations compared. In Sommer, V., Ross, C. (Eds.) Primates of Gashaka. Socioecology and Conservation in Nigeria's Biodiversity Hotspot. New York: Springer, pp. 333–361.

Rowe, N., Myers, M. 2017. All the world's primates. In Fuentes, A. (Ed.) The International Encyclopedia of Primatology. Oxford: Wiley-Blackwell. https://doi.org/10.1002/9781119179313.wbprim0086.

Rowell, T. 1964. The habit of baboons in Uganda. Proceedings of the East African Academy 2: 121-127.

Rowell, T. E. 1966. Forest living baboons in Uganda. Journal of the Zoological Society London 149: 344-364.

Salzmann, U., Haywood, A.M., Lunt, D.J., Valdes, P.J., Hill, D.J. 2008. A new global biome reconstruction and data-model comparison for the middle Pliocene. Global Ecology and Biogeography 17: 432-447.

Sithaldeen, R., Bishop. J.M., Ackermann, R.R. 2009. Mitochondrial DNA analysis reveals Plio-Pleistocene diversification within the chacma baboon. Molecular Phylogenetics and Evolution 53: 1042-1048.

Sharman, M. 1981. Feeding, ranging and social organisation of the Guinea baboon. PhD dissertation, University of St Andrews.

Shipman, P., Bosler, W., Davis, K.L. 1981. Butchering of giant geladas at an Acheulian site. Current Anthropology 22: 257-264.

Smith, R.J., Jungers, W.L. 1997. Body mass in comparative primatology. Journal of Human Evolution 32: 523-559.

Stöver B. C., Müller K. F. 2010. TreeGraph 2: combining and visualizing evidence from different phylogenetic analyses. BMC Bioinformatics 11: 7. DOI: 10.1186/1471-2105-11-7.

Strait, D.S., Wood, B.A. 1999. Early hominid biogeography. Proceedings of the National Academy of Sciences of the United States of America 96: 9196-9200.

Swedell, L., Leigh, S. R. 2006. Reproduction and Fitness in Baboons: Behavioral, Ecological and Life History Perspectives. New York: Springer.

Tang, Q-Y., Liu, S-Q., Yu, D., Liu, H-Z., Danley, P.D. (2012). Mitochondrial capture and incomplete lineage sorting in the diversification of balitorine loaches (Cypriniformes, Balitoridae) revealed by mitochondrial and nuclear genes. Zoologica Scripta 41: 233-247.

USGS (EROS) (2009) Digital Elevation Model. Sioux Falls, South Dakota: USGS (EROS).

Val, A., Taru, P., Steininger, C. 2014. New taphonomic analysis of large-bodied primate assemblage from Cooper's D, Bloubank Valley, South Africa. The South African Archaeological Bulletin 69: 49-58.

Venditti, C., Meade, A., Pagel, M. 2011. Multiple routes to mammalian diversity. Nature 479: 393-396. doi: https://doi.org/10.1038/nature10516.

Walker, J.A., Jordan, V.E., Storer, J.M., Steely, C.J., Gonzalez-Quiroga, P., Beckstrom, T.O., Rewerts, L.C., St. Romain, C.P., Rockwell, C.E., Rogers, J., Jolly, C.J., Konkel1, M.K., The Baboon Genome Analysis Consortium, Batzer, M.A. (2019). Alu insertion polymorphisms shared by *Papio* baboons and *Theropithecus gelada* reveal an intertwined common ancestry. Mobile DNA: 10: 46 https://doi.org/10.1186/s13100-019-0187-y

Waters, J.M., Fraser, C.I., Hewitt, G.M. 2013. Founder takes all: density-dependent processes structure biodiversity. Trends in Ecology and Evolution 28: 78-85.

White, F. 1983. The Vegetation of Africa. UNESCO, Paris.

Whiten, A., Byrne, R.W., Barton, R.A., Waterman, P.G., Henzi, S.P. 1991. Dietary and foraging strategies of baboons. Philosophical Transactions: Biological Sciences 334: 187-197.

Wildman, D. E., Bergman, T. J., Al-Aghbari, A., Sterner, K. N., Newman, T. K., Phillips-Conroy, J. E., Jolly, C. J., Disotell, T. R. 2004. Mitochondrial evidence for the origin of hamadryas baboons. Molecular Phylogenetics and Evolution 32: 287-296.

Williams, B.A., Ross, C.F., Frost, S.R., Waddle, D., Gabadirwe, M., Brook, G. 2012. Fossil *Papio* cranium from !Ncumtsa (Koanaka) Hills, western Ngamiland, Botswana. American Journal of Physical Anthropology 149:1-17. DOI: 10.1002/ajpa.22093.

Willmott, C. J., Matsuura, K. 2001. Willmott and Feddema's Moisture Index Archive: Gridded Monthly Climatologies. University of Delaware, Newark. Retrieved from https://climatedataguide.ucar.edu/climate-data/global-land-precipitation-and-temperature-willmott-matsuura-university-delaware.

Willmott, C. J., Matsuura, K., Legates, D. R. 1998. Global Air Temperature and Precipitation: Regridded Monthly and Annual Climatologies. University of Delaware, Newark. Retrieved from https://climatedataguide.ucar.edu/climate-data/global-land-precipitation-and-temperature-willmott-matsuura-university-delaware.

Willmott, C. J., Matsuura, K., Legates, D. R. 2001. Global Air Temperature: Regridded Monthly and Annual Climatologies. University of Delaware, Newark. Retrieved from https://climatedataguide.ucar.edu/climate-data/global-land-precipitation-and-temperature-willmott-matsuura-university-delaware.

Wilson, D.E., Mittermeier, R. 2009. Handbook of the Mammals of the World. Barcelona: Lynx Edicions, Conservation International.

Winder, I.C. 2014. The biogeography of the *Papio* baboons. Folia Primatologica 85: 292-318. https://doi.org/10.1159/000362545.

Wrangham, R. W. 1980. An ecological model of female-bonded primate groups. Behaviour 75: 262-300.

Yu, Y., Harris, A.J., Blair, C., He, X.J. 2015. RASP (Reconstruct Ancestral State in Phylogenies): a tool for historical biogeography. Molecular Phylogenetics and Evolution 87:46-49.

Ziegler, T., Abegg, C., Meijaard, E., Perwitasari-Farajallah, D., Walter, L., Hodges, J.K., Roos, C. 2007. Molecular phylogeny and evolutionary history of Southeast Asian macaques forming the *M. silenus* group. Molecular Phylogenetics and Evolution 42: 807-816.

Zinner, D., Groeneveld, L., Keller, C., Roos, C. 2009a. Mitochondrial phylogeography of baboons (*Papio* spp.) – Indication for introgressive hybridization? BMC Evolutionary Biology 9: 83.

Zinner, D., Arnold, M.L., Roos, C. 2009b. Is the new primate genus *Rungwecebus* a baboon? PLoS One 4: e4859.

Zinner, D., Wertheimer, J., Liedigk, R., Groeneveld, L.F., Roos, C. 2013. Baboon phylogeny as inferred from complete mitochondrial genomes. American Journal of Physical Anthropology 150: 133-140.

Zinner, D., Keller, C., Nyahongo, J.W., Butynski, T.M., de Jong, Y.A., Pozzi, L., Knauf, S., Liedigk, R., Roos, C. 2015. Distribution of mitochondrial clades and morphotypes of baboons *Papio* spp. (Primates: Cercopithecidea) in eastern Africa. Journal of East African Natural History 104: 143-168.

Zinner, D., Chuma, I.S., Knauf, S., Roos, C. 2018. Inverted intergeneric introgression between critically endangered kipunjis and yellow baboons in two disjunct populations. Biology Letters 14. DOI: 10.1098/rsbl.2017.0729.

Figure captions

Figure 1: Results of the DEC historical biogeography analysis. Letters indicate biogeographic regions as detailed in Table 2. The most likely ancestral range estimates (sometimes several regions lumped) are indicated in the middle of the circles. Most likely state probabilities: basal papionin node, B = 0.13, ABCD = 0.11; *Mandrillus* / *Cercocebus* common ancestor B = 0.47; *Cercocebus* B = 0.44; *Mandrillus* B = 0.71; *P/T/L/R* common ancestor ABCD = 0.41, ACDE = 0.26; *Papio* ACDE = 0.68; *Papio* northern clade = ACD; *Papio* southern clade E = 1. Black* indicates pooled probabilities of estimates that each account for <5%.

Figure 2: Schematic showing how variables may interact and influence baboon skull morphology. Phylogeny, geography, environment and diet are all likely to contribute to variation among modern *Papio* skull shapes. The phylogenetic component acts directly on skull shape and reflects genetic distinctiveness as well as reduced gene flow between different clades. Phylogeny is spatially structured, but geography also acts directly on skull shape, reflecting the clinal and parapatric nature of modern baboons. Diet, partly through the different mechanical properties and nutritional value of foods, acts directly on skull shape (including the size component). Environment and diet are correlated, so environment may act indirectly through diet to influence skull shape. Environment, possibly through habitat productivity or seasonality, also contributes to skull shape. Of the four independent variables listed here, diet and geography have the highest correlations with shape, suggesting that population dynamics (dispersal, gene flow) and localized responses (which may be proximate or ultimate) are both at work to influence baboon skull morphology.

Figure 3: Phylogenetic structure of body mass differentiation in male Old World monkeys (trait value in kg).

Figure 4: Phylogenetic structure of body mass differentiation in female Old World monkeys (trait value in kg).

Table 1: Soft tissue features in *Papio*, *Theropithecus*, *Lophocebus* and Rungwecebus.[a]

Species	**Dorsal colour**	**Ventral hair colour**	**Cheek hair colour**	**Hand/foot hair colour**	**Tail shape**	**Facial colour**	**Natal coat colour**	**Main hair relief**	**Crest of hair on crown**
Papio papio	Reddish brown	Like dorsum	Like dorsum	Like arms	Arched	Purple-black	Black	Moderate	Absent
Papio hamadryas	Grey-brown	Like dorsum or darker	Lighter than dorsum	Like arms	Arched	Pink-red	Black	Strong	Absent
Papio anubis	Olive-brown	Like dorsum	Like dorsum	Black or like arms	Bent	Purple-black	Black	Moderate	Absent
Papio cynocephalus	Yellowish brown	Lighter than dorsum	Lighter than dorsum	Like arms	Bent	Purple-black	Black	Absent	Absent
Papio kindae	Yellowish brown	Lighter than dorsum	Lighter than dorsum	Like arms	Arched	Purple-black	White, grey, patchy	Absent	Absent
Papio ursinus	Dark brown	Lighter than dorsum	Like dorsum	Black	Bent	Purple-black	Black	Absent	Absent
Theropithecus gelada	Pale brown to near black with gold, red, grey tones	Lighter than dorsum	Lighter than dorsum	Black	Arched	Purple-black	Black	Strong	Absent
Lophocebus albigena	Blackish	Like dorsum	Lighter than dorsum	Like arms	Held up and curved over back	Purple-black	Black	Moderate (cape)	Present
Lophocebus aterrimus	Blackish	Like dorsum	Lighter than dorsum	Like arms	Held up and curved over back	Purple-black	Black	Absent	Present
Rungwecebus kipunji	Brown	Lighter than dorsum	Like dorsum	Black	Arched	Purple-black	Black	Moderate	Present

[a] Data sources: *Papio* from Jolly (1993); *Theropithecus* from Bergman and Beehner (2013), Wilson and Mittermeier (2009); *Lophocebus* from Kingdon et al. (2013), Wilson and Mittermeier (2009); *Rungwecebus* from Ehardt and Butynski (2006). Note that some features are most pronounced in adult males.

Table 2: Regions (after Brummitt, 2001) and papionin species used in historical biogeography analysis.

Region	**Countries / areas included**	**Code**
West Tropical Africa	Benin, Burkina, Gambia, Ghana, Guinea-Bissau, Guinea, Ivory Coast, Liberia, Mali, Mauritania, Nigeria, Niger, Senegal, Sierra Leone, Togo	A
West-Central Tropical Africa	Burundi, Cabinda, Central African Republic, Cameroon, Congo, Equatorial Guinea, Gabon, Rwanda, DRC	B
Northeast Tropical Africa	Chad, Djibouti, Eritrea, Ethiopia, Somalia, Sudan	C
East Tropical Africa	Kenya, Tanzania, Uganda	D
South Tropical Africa	Angola, Malawi, Mozambique, Zambia, Zimbabwe	E
Southern Africa	Botswana, Cape Provinces (South Africa), Caprivi Strip, Lesotho, Namibia, KwaZulu-Natal, Free State, Northern Provinces (South Africa), eSwatini	F
Arabian Peninsula	Gulf States, Kuwait, Oman, Saudi Arabia, Yemen	G
Species	**Regions inhabited**	
Cercocebus agilis	B	
Cercocebus atys	A	
Cercocebus galeritus	D	
Cercocebus torquatus	AB	
Lophocebus albigena	BD	
Lophocebus aterrimus	BE	
Mandrillus leucophaeus	AB	
Mandrillus sphinx	B	
Papio anubis	ABCD	
Papio cynocephalus	CDE	
Papio kindae	BDE	
Papio hamadryas	CG	
Papio papio	A	
Papio ursinus	EF	
Rungwecebus kipunji	D	
Theropithecus gelada	C	

Table 3: Biogeographic model testing in BioGeoBEARS.

Model	**Log likelihood**	**Number of parameters**	**Dispersal rate per million years (*d*)**	**Extinction rate per million years along branches (*e*)**	**Founder event speciation weighted per speciation event (*j*)**	**AICc[a]**	**Relative likelihood for each model (AICc_wt)**
DEC	-55.67	2	0.0054	1.00E-12	0	116.3	1
DEC+J	-60.15	3	0.0031	1.00E-12	0.058	128.3	0.0024
DIVALIKE	-63.09	2	0.0047	0.0023	0	131.1	0.0006
DIVALIKE+J	-62.07	3	0.0037	0.0009	0.054	132.1	0.0004
BAYAREALIKE	-63.31	2	0.0046	0.024	0	131.5	0.0005
BAYAREALIKE+J	-62.42	3	0.0031	0.016	0.029	132.8	0.0003

[a] Aikaike information criterion corrected for sample size.

Table 4: Sites and baboon skull specimens used in partial least squares analysis.

Site	**Source**	**Species**	**Specimens**[a]	**Specimen longitude (decimal degrees)**	**Specimen latitude (decimal degrees)**
Mount Assirik	Sharman (1981)	*P. papio*	USNM381435	13.3	-12.9
			USNM381434	13.3	-12.9
			USNM381430	13.3	-12.9
			USNM381437	13.3	-12.9
			USNM381433	13.3	-12.9
			L82.214	13.3	-12.9
Erer-Gota	Kummer (1968)	*P. hamadryas*	B74844	9.6	41.9
			B16705	9.6	41.9
			B17256	9.6	41.9
			Zu6933	9.6	41.9
			Zu6936	9.6	41.9
Comoe	Kunz and Linsenmair (2008)	*P. anubis*	B74866	9.3	0.8
			Te73.009M049	9.4	1.5
			L71.2352	9.7	-1.8
			L71.2352	9.4	0.6
Gombe	Oliver (personal communication)[a]	*P. anubis*	B75015	-5.2	30.3
			Te12575	-4.0	29.6
Masai Mara	Popp (1978) [a]	*P. anubis*	USNM216605	-2.1	34.6
			MCZ21160	-1.8	34.5
			MCZ21161	-1.8	34.5
			FMNH73028	-2.3	34.8
			MCZ27557	-1.3	35.6
Chololo	Barton (1989)	*P. anubis*	USNM162899	-1.0	36.3
			FMNH135067	-1.2	36.4
			FMNH135055	-1.2	36.4
			FMNH135069	-1.2	36.4
Gilgil	Harding (1976)	*P. anubis*	NY80207	-0.2	37.3
			MCZ17343	-0.4	37.0
			L62.25	-0.2	36.8
			L36.12.28.1	-0.2	37.0
			L36.12.28.2	-0.2	37.0
Amboseli	Post (1978) [a]	*P. cynocephalus*	USNM384239	-2.6	38.1
			B74877	-2.4	37.9
			B74930	-2.4	37.9
			B74943	-2.4	37.9
			B74994	-3.4	37.3
Mikumi	Norton et al. (1987)	*P. cynocephalus*	MCZ23082	-6.8	37.0
			B11541	-7.3	37.0
			L27.2.9.1	-6.8	37.0
			L24.1.1.6	-6.8	37.0
			L24.1.1.4	-6.8	37.0
Giant's Castle	Byrne et al. (1993)	*P. ursinus*	FMNH101803	-31.8	22.8
			B74898	-32.3	24.5
			L6.5.12.2	-32.3	24.5
			L3.6.4.1	-31.0	23.8

[a] Cited in Hill and Dunbar (2002)

[b] Museum codes: USNM = Smithsonian National Museum of Natural History; L = Natural History Museum, London; B = Museum fuer Naturkunde, Berlin; Te = Royal Museum of Central Africa, Tervuren; Zu = University of Zurich; MCZ = Museum of Comparative Zoology; FMNH = Field Museum of Natural History; NY = American Museum of Natural History.

Table 5: Singular values and pairwise correlations of partial least squares (PLS) scores.[a]

	Singular value	% Total covariance	Correlation	p
Diet and shape blocks (whole PLS RV = 0.3303, $p < 0.0001$)				
PLS1	0.43138	83.531	0.72533	<0.0001
PLS2	0.17236	13.336	0.72168	0.0844
PLS3	0.06313	1.789	0.62518	0.3256
PLS4	0.04982	1.114	0.62162	0.1198
PLS5	0.0226	0.229	0.7868	0.2405
PLS6	0.00065	0	0.6557	0.0114
Diet and shape blocks, *P. ursinus* excluded (whole PLS RV = 0.2656, $p = 0.008$)				
PLS1	0.33597326	77.48	0.71289	0.0016
PLS2	0.16440227	18.552	0.72083	0.1014
PLS3	0.05497679	2.075	0.62505	0.672
PLS4	0.04720539	1.53	0.66949	0.0244
PLS5	0.0230183	0.364	0.70617	0.1106
PLS6	0.00037771	0	0.59439	0.0339
Diet and size-controlled shape blocks (whole PLS RV = 0.2162, p = 0.0020)				
PLS1	0.28172	76.822	0.70749	0.0039
PLS2	0.13714	18.205	0.59102	0.1112
PLS3	0.05666	3.108	0.51538	0.1371
PLS4	0.03896	1.469	0.38817	0.1343
PLS5	0.02023	0.396	0.62423	0.0605
PLS6	0.00041	0	0.54258	0.1593
Diet and size-controlled shape blocks, *P. ursinus* excluded (whole PLS RV = 0.1948, $p = 0.0154$)				
PLS1	0.23285	70.184	0.72735	0.0321
PLS2	0.13848	24.822	0.60946	0.0701
PLS3	0.04288	2.38	0.39873	0.6724
PLS4	0.04079	2.153	0.54563	0.0068
PLS5	0.01888	0.461	0.60279	0.0670
PLS6	0.00029	0	0.49949	0.0459
Longitude/latitude and shape blocks (whole PLS RV = 0.3093, $p < 0.0001$)				
PLS1	0.02833	61.704	0.69801	0.0004
PLS2	0.02031	31.692	0.81844	0.0001
PLS3	0.00878	5.929	0.77502	0.0135
PLS4	0.00278	0.593	0.77171	0.0004
PLS5	0.00091	0.063	0.77571	0.0973
PLS6	0.0005	0.019	0.65857	0.0351
PLS7	9.9E-05	0.001	0.63283	0.9322
Phylogenetic principal coordinates and shape blocks (whole PLS RV = 0.2024, $p < 0.0057$)				
PLS1	0.0490597	69.393	0.81776	0.0354
PLS2	0.0271755	21.292	0.74668	<0.0001
PLS3	0.0141334	5.759	0.76687	0.0011
PLS4	0.0101493	2.97	0.75355	0.0044
PLS5	0.0041962	0.508	0.80969	0.0022
PLS6	0.0016428	0.078	0.74682	0.4698
Environment and shape blocks (whole PLS RV = 0.2122, $p = 0.0104$)				

PLS1	0.02172891	63.703	0.59554	0.0368
PLS2	0.01244105	20.883	0.81198	0.0281
PLS3	0.00736664	7.322	0.82353	0.0598
PLS4	0.00613107	5.072	0.65294	0.0028
PLS5	0.00381496	1.964	0.62655	0.1774
PLS6	0.00279903	1.057	0.67237	0.173

[a] Analyses ordered as mentioned in the text.

Table 6: Scaling and delta values for male cercopithecid branches that returned a scale value above 1 in 95% or more body mass analytical iterations.

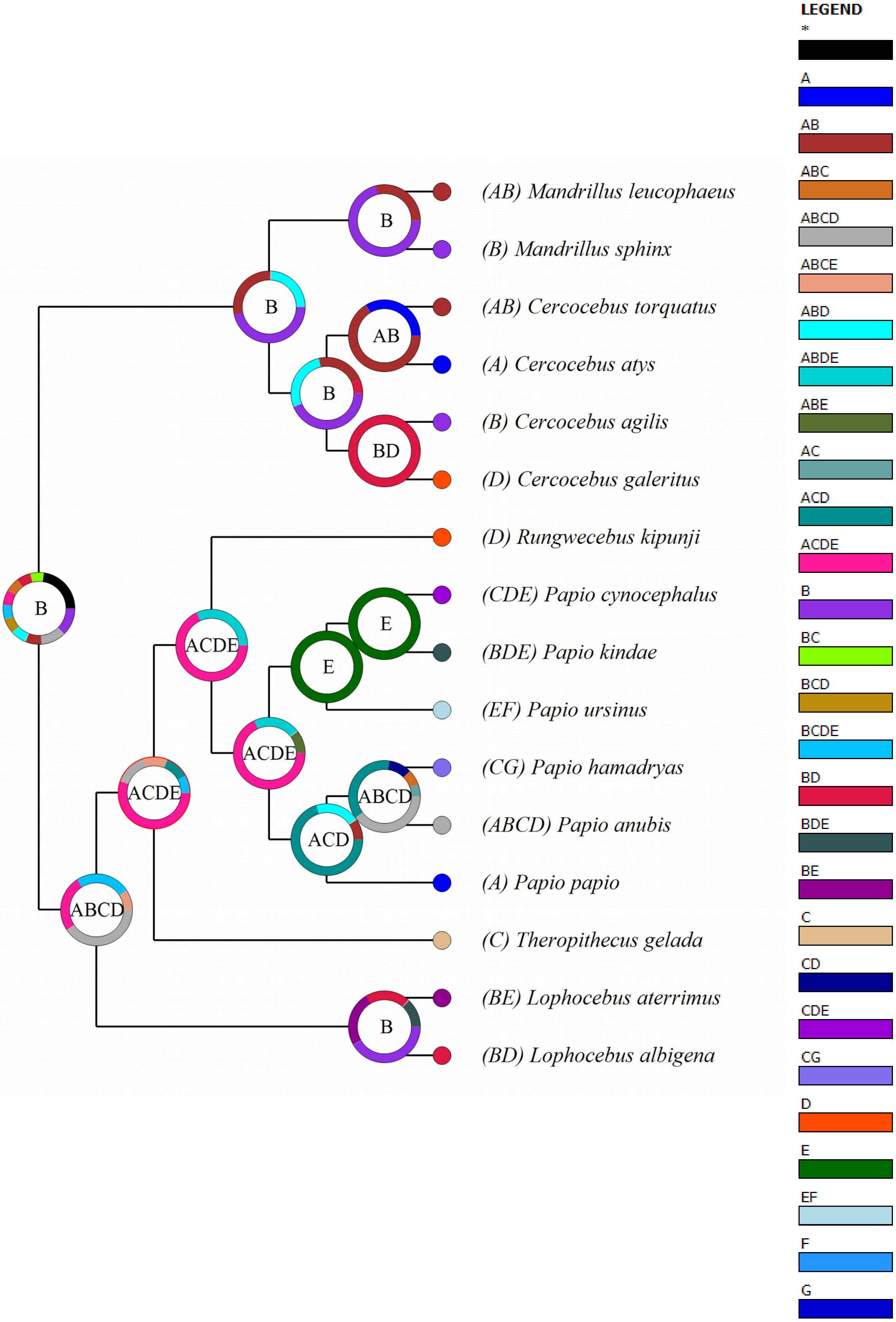
Branch description	**Descendant taxa**	**Modal scalar**[a]	**Modal delta**
Mandrillus	*M. leucophaeus, M. sphinx*	5.79	16.98
Mandrillus	*M. leucophaeus*	5.24	11.37
Mandrillus	*M. sphinx*	21.66	40.40
Papio / Theropithecus	*P. anubis, P. cynocephalus, P. hamadryas, P. kindae, P. papio, P. ursinus, T. gelada*	6.00	10.22
Papio	*P. anubis, P. cynocephalus, P. hamadryas, P. kindae, P. papio, P. ursinus*	6.22	12.11
Papio	*P. cynocephalus, P. kindae*	6.27	2.03
Papio	*P. cynocephalus*	5.97	9.42
Papio	*P. kindae*	6.19	9.52
Papio	*P. ursinus*	6.28	10.67
Papio	*P. anubis, P. hamadryas*	5.82	2.93
Papio	*P. hamadryas*	5.66	7.21
Papio	*P. anubis*	5.61	7.76
Papio	*P. papio*	5.81	10.43
Theropithecus	*T. gelada*	5.66	22.38
Macaca	*Macaca arctoides, Macaca assamensis, Macaca munzala, Macaca radiata, Macaca thibetana*	4.37	0.07
Macaca	*Macaca arctoides, Macaca assamensis, Macaca thibetana*	9.51	0.98
Macaca	*Macaca assamensis, Macaca thibetana*	4.84	6.88
Macaca	*Macaca thibetana*	5.60	5.77
Macaca	*Macaca assamensis*	4.97	5.71
Macaca	*Macaca arctoides*	4.59	12.50
Macaca	*Macaca munzala, Macaca radiata*	5.53	10.01
Macaca	*Macaca munzala*	4.69	6.17
Macaca	*Macaca radiata*	4.86	5.91
Macaca	*Macaca tonkeana*	4.19	10.81

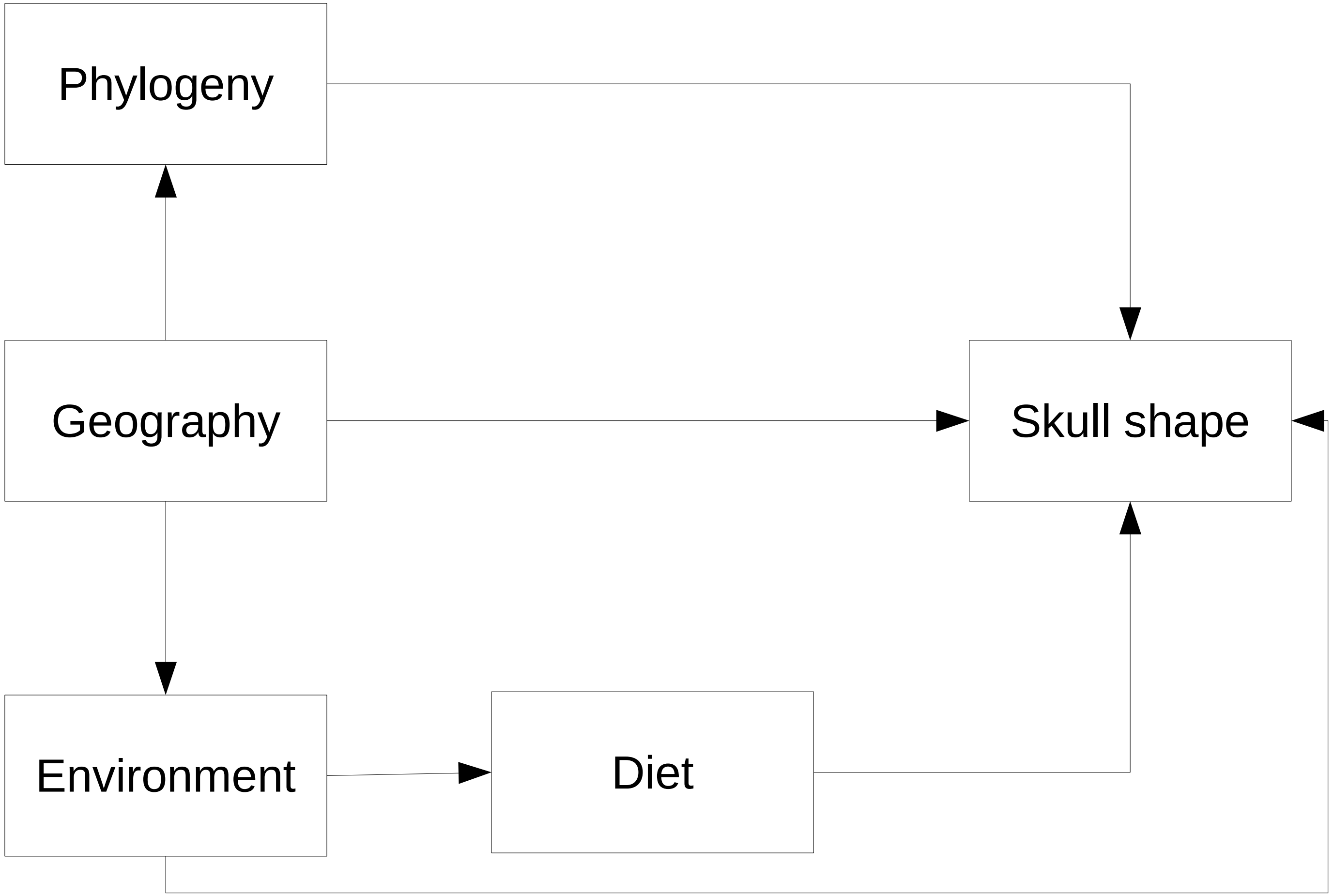
[a] Papionin branches for which the value was greater than 1 for 95% or more of the iterations. Within the rest of the cercopithecids, only *Nasalis larvatus* had a modal scalar value (12.46) that met the inclusion criteria. Female data are not shown as no branch met the inclusion criteria.

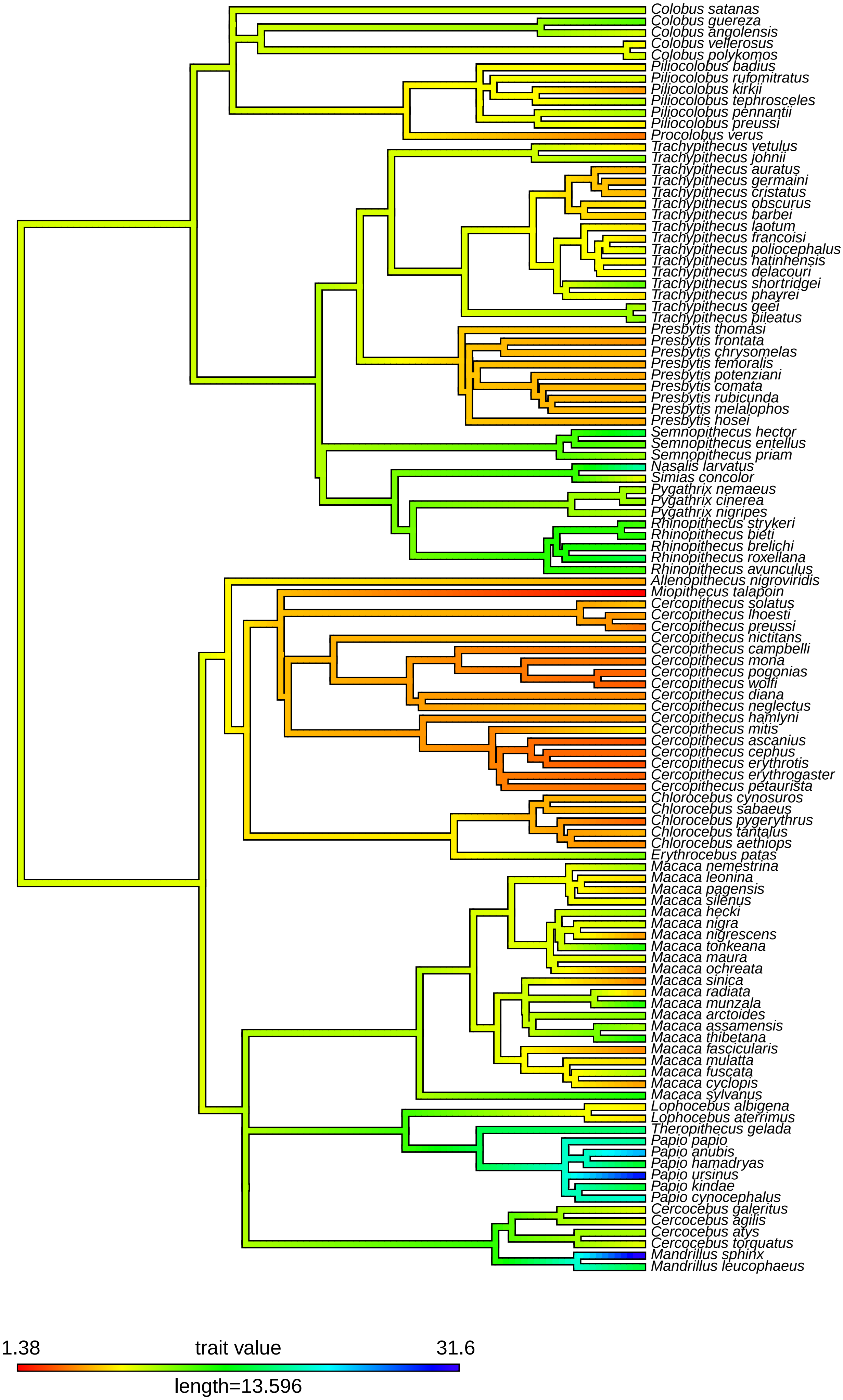
Table 7: Body mass estimates for southern African *Papio* species[a].

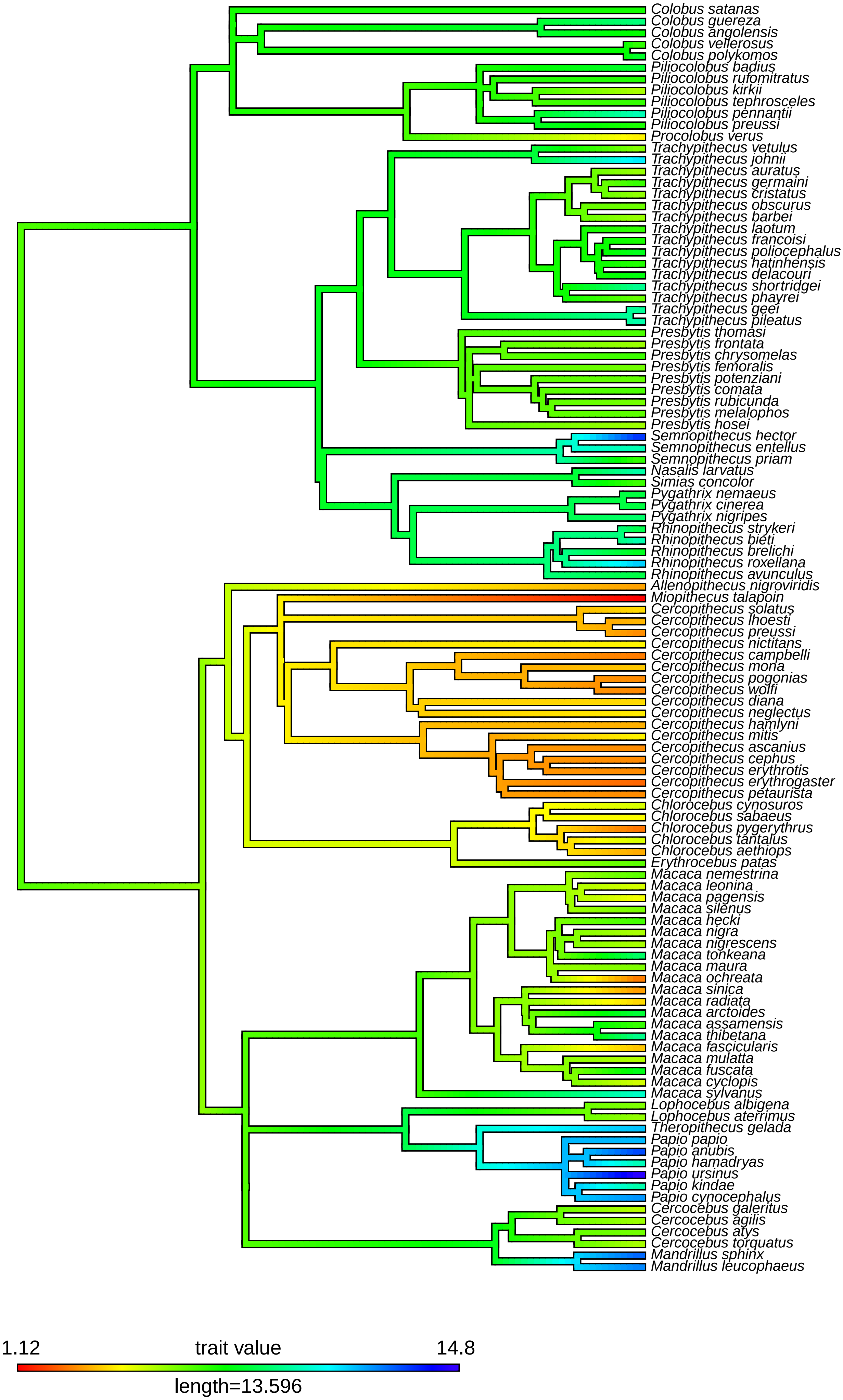
Species	Male *n* / Female *n*	Estimated male body mass (kg ± standard deviation)	Estimated female body mass (kg ± standard deviation)
Papio izodi	3/9	20.9 ± 3.7	13.5 ± 1.4
Papio angusticeps	11 / 7	23.4 ± 4.5	15.2 ± 2.2
Papio robinsoni	14/5	28.0 ± 4.8	15.2 ± 1.7
Papio (h.) botswanae	1 / 0	21.6	-

[a] Only securely sexed individuals included. Details of *P. izodi*, *P. angusticeps, P. robinsoni* specimens given in SOM Table S2. The *P. (h.) botswanae* specimen (male) is BNMM FC346.


(AB) Mandrillus leucophaeus
(B) Mandrillus sphinx
(AB) Cercocebus torquatus
(A) Cercocebus atys
(B) Cercocebus agilis
(D) Cercocebus galeritus
(D) Rungwecebus kipunji
(CDE) Papio cynocephalus
(BDE) Papio kindae
(EF) Papio ursinus
(CG) Papio hamadryas
(ABCD) Papio anubis
(A) Papio papio
(C) Theropithecus gelada
(BE) Lophocebus aterrimus
(BD) Lophocebus albigena
B
B
B
AB
B
BD
ACDE
ACDE
ACDE
E
E
ABCD
ACD
ABCD
B
LEGEND
*
A
AB
ABC
ABCD
ABCE
ABD
ABDE
ABE
AC
ACD
ACDE
B
BC
BCD
BCDE
BD
BDE
BE
C
CD
CDE
CG
D
E
EF
F
G


Phylogeny
Geography
Skull shape
Environment
Diet


Colobus satanas
Colobus guereza
Colobus angolensis
Colobus vellerosus
Colobus polykomos
Piliocolobus badius
Piliocolobus rufomitratus
Piliocolobus kirkii
Piliocolobus tephrosceles
Piliocolobus pennantii
Piliocolobus preussi
Procolobus verus
Trachypithecus vetulus
Trachypithecus johnii
Trachypithecus auratus
Trachypithecus germaini
Trachypithecus cristatus
Trachypithecus obscurus
Trachypithecus barbei
Trachypithecus laotum
Trachypithecus francoisi
Trachypithecus poliocephalus
Trachypithecus hatinhensis
Trachypithecus delacouri
Trachypithecus shortridgei
Trachypithecus phayrei
Trachypithecus geei
Trachypithecus pileatus
Presbytis thomasi
Presbytis frontata
Presbytis chrysomelas
Presbytis femoralis
Presbytis potenziani
Presbytis comata
Presbytis rubicunda
Presbytis melalophos
Presbytis hosei
Semnopithecus hector
Semnopithecus entellus
Semnopithecus priam
Nasalis larvatus
Simias concolor
Pygathrix nemaeus
Pygathrix cinerea
Pygathrix nigripes
Rhinopithecus strykeri
Rhinopithecus bieti
Rhinopithecus brelichi
Rhinopithecus roxellana
Rhinopithecus avunculus
Allenopithecus nigroviridis
Miopithecus talapoin
Cercopithecus solatus
Cercopithecus lhoesti
Cercopithecus preussi
Cercopithecus nictitans
Cercopithecus campbelli
Cercopithecus mona
Cercopithecus pogonias
Cercopithecus wolfi
Cercopithecus diana
Cercopithecus neglectus
Cercopithecus hamlyni
Cercopithecus mitis
Cercopithecus ascanius
Cercopithecus cephus
Cercopithecus erythrotis
Cercopithecus erythrogaster
Cercopithecus petaurista
Chlorocebus cynosuros
Chlorocebus sabaeus
Chlorocebus pygerythrus
Chlorocebus tantalus
Chlorocebus aethiops
Erythrocebus patas
Macaca nemestrina
Macaca leonina
Macaca pagensis
Macaca silenus
Macaca hecki
Macaca nigra
Macaca nigrescens
Macaca tonkeana
Macaca maura
Macaca ochreata
Macaca sinica
Macaca radiata
Macaca munzala
Macaca arctoides
Macaca assamensis
Macaca thibetana
Macaca fascicularis
Macaca mulatta
Macaca fuscata
Macaca cyclopis
Macaca sylvanus
Lophocebus albigena
Lophocebus aterrimus
Theropithecus gelada
Papio papio
Papio anubis
Papio hamadryas
Papio ursinus
Papio kindae
Papio cynocephalus
Cercocebus galeritus
Cercocebus agilis
Cercocebus atys
Cercocebus torquatus
Mandrillus sphinx
Mandrillus leucophaeus
1.38
trait value
31.6
length=13.596


Colobus satanas
Colobus guereza
Colobus angolensis
Colobus vellerosus
Colobus polykomos
Piliocolobus badius
Piliocolobus rufomitratus
Piliocolobus kirkii
Piliocolobus tephrosceles
Piliocolobus pennantii
Piliocolobus preussi
Procolobus verus
Trachypithecus vetulus
Trachypithecus johnii
Trachypithecus auratus
Trachypithecus germaini
Trachypithecus cristatus
Trachypithecus obscurus
Trachypithecus barbei
Trachypithecus laotum
Trachypithecus francoisi
Trachypithecus poliocephalus
Trachypithecus hatinhensis
Trachypithecus delacouri
Trachypithecus shortridgei
Trachypithecus phayrei
Trachypithecus geei
Trachypithecus pileatus
Presbytis thomasi
Presbytis frontata
Presbytis chrysomelas
Presbytis femoralis
Presbytis potenziani
Presbytis comata
Presbytis rubicunda
Presbytis melalophos
Presbytis hosei
Semnopithecus hector
Semnopithecus entellus
Semnopithecus priam
Nasalis larvatus
Simias concolor
Pygathrix nemaeus
Pygathrix cinerea
Pygathrix nigripes
Rhinopithecus strykeri
Rhinopithecus bieti
Rhinopithecus brelichi
Rhinopithecus roxellana
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Cercopithecus solatus
Cercopithecus lhoesti
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Cercopithecus neglectus
Cercopithecus hamlyni
Cercopithecus mitis
Cercopithecus ascanius
Cercopithecus cephus
Cercopithecus erythrotis
Cercopithecus erythrogaster
Cercopithecus petaurista
Chlorocebus cynosuros
Chlorocebus sabaeus
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Macaca maura
Macaca ochreata
Macaca sinica
Macaca radiata
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Macaca assamensis
Macaca thibetana
Macaca fascicularis
Macaca mulatta
Macaca fuscata
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Papio ursinus
Papio kindae
Papio cynocephalus
Cercocebus galeritus
Cercocebus agilis
Cercocebus atys
Cercocebus torquatus
Mandrillus sphinx
Mandrillus leucophaeus
1.12
trait value
14.8
length=13.596