Species, populations and groups in hominin evolution

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ABSTRACT

In this chapter we explore the possibility of subspecific divergence in Plio-Pleistocene hominins. The fossil record is patchy and hence it is notoriously difficult to assess adequately whether structured variation, required to assign subspecies, is present. We therefore use a referential models to investigate the likelihood of tropical hominin subspecies in the context of knowledge about modern African catarrhines, emphasising the relationship between subspecies occurrence and species range. Hominin species ranges are reconstructed on the basis of known fossil localities and with GIS tools designed to model distributions of living organisms. Palaeontological and palaeobiological evidence is then used within these models to make predictions about subspecies occurrence. We argue that two Plio-Pleistocene hominins, *Australopithecus afarensis* and *Paranthropus boisei*, may have included subspecies. Finally, we discuss how the behaviours of individuals and groups could provide the raw material for subspecific differentiation in hominins, using Wright's adaptive landscape as a framework.

KEYWORDS

Geographic range, subspecies, Plio-Pleistocene, *Paranthropus*, *Australopithecus*, catarrhine, Africa, modelling.

INTRODUCTION

Hominins underwent an extensive adaptive radiation in the late Miocene, Pliocene and Pleistocene. Over twenty species have been identified in the human fossil record (Wood and Lonergan 2008), some of which were contemporaneous and possibly sympatric. Although extremely well-studied, most hominins are not particularly abundant in the fossil record, and some are known from only a small number of sites. Thus, much attention has been paid to the diagnosis of and differences between species and fewer studies have examined variation and populations below species level. Similarly, the pressures that may cause speciation to occur, such as global climatic fluctuation (DeMenocal 2004), have been much better studied than the factors that may have caused intraspecific divergence and hence the formation and dynamics of populations or subspecies and sub-populations or groups. The paucity of the fossil record and the patchy distribution of individuals geographically and over time present numerous challenges when considering hominin populations and sub-populations. Thus, we use a referential modelling approach in this chapter, taking data from modern African primates to investigate the likelihood of hominin subspecies in the Pliocene and Pleistocene and some of the environmental and behavioural conditions under which population and sub-population differentiation may be most likely.

African primates, particularly chimpanzees and baboons, are often used as models for hominins (Elton 2006). Baboons and some other Old World monkeys are in many ways likely to be ecologically similar to hominins, being predominantly terrestrial yet exploiting a wide range of habitats, behaviourally flexible and able to respond to changing and changeable environments, and feeding eclectically off a wide range of resources, including C4 (tropical grass) derived foodstuffs (Elton 2006; Ulijaszek et al. 2012). Chimpanzees, on the other hand, are probably more cognitively similar to hominins, more similar in body plan and likely to share important aspects of social structure, such as male kin bonding (Foley and Lee 1989; Elton 2006). Thus, we use both African monkeys and apes in this chapter to provide context for hominin subspecies and groups. Along with examining modern primate geographic ranges and relationships, if any, with patterns of intraspecific variation, we consider the processes that contribute to creating this variation. This includes using Sewall Wright's concept of the 'fitness landscape' (Wright 1932) to explore how shifts in plastic features such as body weight may contribute to differentiation. Even small behavioural and biological differences can alter an organism's ecological niche, and abiotic and biotic environmental factors also influence niches and the settlement patterns and dispersals of populations and subpopulations in their own right. Thus, we also touch on these to help shed light on what shapes the composition and structure of distinctive hominin subpopulations.

SUBSPECIFIC DIVERSITY: A BRIEF REVIEW

Botany and zoology have very different conventions when considering variation within species, with botanists often recognizing varieties and forms as well as subspecies and species (Mallet 2007); only zoological conventions and examples are considered hereinafter. In zoology, a population is commonly defined as a set of organisms in which any pair of members can breed together. Implicit in this is that populations comprise individuals of the same species, living within the same geographic area. In this paper, the concept of the 'population' is closely aligned to that of a subspecies, albeit with the caveat that it is unlikely that every possible breeding pair actually has the opportunity to breed. Subspecific designations can be an important means of describing diagnosable features of non-reproductively isolated populations, an approach favoured by Mayr and Wright, the originators of the biological species concept (Isaac et al. 2004). Dividing species into subspecies assumes structured variation. Variation is a fundamental of biology, and species obviously do not comprise a set of homogenous individuals. Even if the genotype is identical, variation is expressed in the phenotype through the influence of external agents - climate, nutrition, illness and so on. Variation can be stochastic – as might commonly arise through developmental insults to an individual - but for it to be seen as meaningful for demarcation of subspecies it must be structured, with members sharing recognizable characteristics. Variation within species is often spatially structured (Thorpe 1987; Winker 2010). This was recognized taxonomically over a century ago by Sundevall who was first to use trinomial terms for geographic varieties (Winker 2010). Polytypy – ordered subdivision within a taxonomic unit – including subspecific differentiation is extensive across the animal world (Thorpe 1987). This may be clinal variation related to a changing environmental variable, such as the size of deer in the Americas related to temperature (Millien et al. 2006). Other variation is categorical, for example where distinct lineages 'remeet' at a hybrid zone, such as the hooded and carrion crow (Saino 1998). Indeed, true panmixia (the potential for random mating across the whole of the geographic range of a species) is rare and thus homogeneity is almost nonexistent, except in species that breed in only one locality (Thorpe 1987).

Just as the concept of 'a species' is open to debate, defining a subspecies is not straightforward (Winker 2010). Quantitative criteria such as the '75% rule' have been proposed (Amadon 1945), which states that for a group to be considered a subspecies it must be 75% different in some trait or traits from other putative subspecies. However, this is not widely employed – often subspecies are defined on the basis of some arbitrary level of diagnosable phenotypic differentiation, especially when it is geographically based (Winker 2010). While objectivity can be difficult, being able to categorize at subspecies level is highly useful, allowing intraspecific variation to be quantified and helping to detect reduction in gene flow between populations. The highly polytypic baboons (*Papio hamadryas* subspecies), for example, have extensive, spatially structured biological and behavioural variation across their geographic range, including hybrid zones between populations (Jolly 1993). So extensive is the variation in *Papio hamadryas* that many researchers view the six commonly recognized subspecies as separate species (see Jolly 1993 for a review, and see also Figure 1). Within these major divisions, subforms are also recognized, such as the division of chacma baboons into the grey footed and southern / Cape forms (Grubb et al. 2003). Among primates as a whole, structured variation and hence subspecific designation is very common (e.g. Grubb et al. 2003; Brandon Jones et al. 1994), although variants may be viewed as species to promote conservation (Mace 2004).

Figure 1 around here

Subspecific differentiation occurs in ways similar to specific differentiation, with geographic and hence reproductive isolation being highly influential. Within a wide geographic distribution, there may be insular populations (cut off by sea or areas of unsuitable habitat) where divergence is pronounced and a subspecific designation is warranted. There are excellent examples of this in primates, including the morphologically distinctive Bale monkey (*Chlorocebus aethiops djamjamensis*, part of the vervet group), which is found within a relatively small area of Ethiopia, isolated from other vervet subspecies, and, unusually for *C. aethiops*, is dependent on highland bamboo forest (Elton et al. 2010). Even if clinal variation is present, the systematic, population-based differences between forms at geographical extremes of the whole species range (in which populations are contiguous) may be sufficient to make subspecific designations. This is again evident in vervet monkeys, where populations in western, eastern and southern Africa are morphologically distinct even when size differences are taken into account and hence seem to be 'good' subspecies (Elton et al. 2010). This notwithstanding, there are some classic zoological examples (especially in birds) of geographically unstructured variation (and hence few subspecies) even in species with very large geographic distributions. The European robin (*Erithacus rubecula*) is a case in point. Although some insular forms (for example on the Canary Islands and Great Britain) are recognised as distinct subspecies, most forms across mainland Europe, from Spain to Siberia, are not given subspecific designation (Dietzen et al. 2003).

There are a number of possible explanations for the relative lack of subspecific diversity in European robins. It has been suggested (Phillimore and Owens 2006) that the modest phylogenetic divergence, which results in fewer good subspecies, in Palearctic (and Nearctic) birds may be because the taxa in these areas are evolutionarily 'young' due to the effects of post-glacial re-colonization and so may not have had time to diverge. In general, taxonomic diversity tends to be higher in the tropics than in temperate regions, which may be linked to the fact that tropical environments are more ancient than temperate ones (and hence have had the opportunity to 'build' diversity), or even because greater biotic interaction (as a result of existing species diversity) may promote taxonomic diversification (see Mittelbach et al. 2007 for an extensive review of this topic). Even in African catarrhines, species diversity appears to be greater at the equator than in the subtropics (Eeley and Foley 1999). Patterns of subspecific diversity are also likely to be shaped by the movement patterns and hence opportunities for gene flow within a species. In British birds, for example, increased dispersal distance is related to lower subspecific diversity (Belliure et al. 2000). A significant proportion of mainland European robins are migratory (Dietzen et al. 2003). Thus, chances of gene flow across the whole geographic range, creating spatially unstructured patterns of variation, are higher than in species that do not habitually migrate, working against the formation of subspecies.

So what might be expected for Plio-Pleistocene hominins, found in tropical and subtropical Africa? Inhabiting the tropics, the probability of taxonomic diversity – at the subspecific as well as the specific level – is relatively high. Prior to two million years, there is no good palaeontological reason to assume that hominin movement patterns would differ greatly to those seen in modern sub-Saharan African primates, as hominin fossils from this period are not found outside Africa. Extrapolating from modern humans and primates, there is indeed no compelling reason to believe that any hominin practiced the type of migration seen commonly in birds, even though the dispersal ability of *Homo* is very well documented, albeit with movement probably occurring over many generations (Anton et al. 2002). On these bases, therefore, tropical mammals, especially primates, seem much more appropriate models when considering subspecific diversity than do temperate birds.

Widespread modern primates show considerable spatially-structured variation (Cardini et al. 2010). Given that genetic diversity is also spatially structured in humans (Lawson-Handley et al. 2007), with observable phenotypic differences in different regions, it can be assumed broadly that variation in hominins would also follow the patterns seen in modern human and non-human primates, at least some of the time. However, assuming that some subspecific diversity was present in hominin species is a long way from actually being able to identify such diversity securely or even predict the extent to which that diversity occurred.

Subspecies have been recognised in the hominin fossil record: several authorities demarcate Neanderthals and modern humans only at the subspecific level (see review in Harvati et al. 2004), for instance. As might be expected, determining hominin subspecies is fraught with difficulty. Given the nature of the terrestrial fossil record, with a paucity of specimens patchily distributed in time and space, it is inevitable that palaeoanthropologists view hominins primarily as either species or individuals rather than subspecies and groups. Necessarily, hominin species are described on the basis of very few, often fragmentary, specimens, and their palaeobiology is reconstructed from the characteristics of a small number of individuals and extrapolated to the species. Quantifying intraspecific variation and demonstrating that it is structured rather than stochastic can be challenging even if working with large samples of extant organisms that can be mapped and observed behaviourally as well as studied morphologically and genetically (*sensu* Cardini et al. 2007). In hominins (and indeed, most other extinct terrestrial animals), there are insufficient fossils to robustly quantify intraspecific variation, even in species that appear abundant and are relatively well represented in the fossil record. For example, fossils of *Paranthropus boisei*, a Plio-Pleistocene hominin from East Africa, are numerous but in a study of its dental microwear, only seven out of a possible 53 specimens preserved the features necessary for analysis (Ungar et al. 2008). Theoretically, however, given patterns of variation in modern primates, subspecies may have occurred in hominins with a relatively wide geographic distribution. It is possible, for example, that *Australopithecus bahrelghazali*, dated to around 3 –

3.5 Ma and found only in Chad in central Africa, is a regional variant of the more-or-less contemporaneous *Australopithecus afarensis*, found in East Africa (Wood and Lonergan 2008).

Examining populations within hominin species is made even more challenging by the fact that their fossils are not evenly distributed in space or time, with the majority of specimens coming from a small number of highly productive fossiliferous regions such as the East African Rift Valley or the Cradle of Humankind in South Africa. Given that subspecific variation is often spatially structured (Thorpe 1987; Winker 2010), the lack of knowledge about actual geographic ranges (or even lack of hypothesized ranges) makes it difficult to construct a framework for exploring population-level variation in hominins. So why bother about populations and subpopulations in hominins at all? Darwin (1874) noted that species could arise as the result of subspecific diversity and differentiation. One compelling reason for considering hominin populations is thus the potential for them to provide the 'raw material' for speciation. It is a logical extension to assume that populations would be further subdivided, again based on analogy with modern primates, into smaller breeding groups with a distinct home range. This links to another reason why it is useful to think about populations and also sub populations: behavioural and ecological differences. Even on such a small scale, these are evident between groups, and may help reduce competition and subtly partition niches. Considering populations and subpopulations therefore helps to understand palaeobiology and adaptation.

HOMININ SUBSPECIES: USING MODERN PRIMATES AS MODELS

The first aim of this chapter is to model the possible subspecific diversity within African Plio-Pleistocene hominins. We reconstruct the possible geographic ranges of three African Plio-

Pleistocene hominin species (*A. afarensis, A. africanus* and *P. boisei*) using simple GIS distribution models, and also calculate the extent of their ranges (plus that of *P. robustus*) based solely on recorded fossil localities. The links between geographic range and subspecific diversity are explored in modern primates and used alongside the hypothesized species ranges in a simple referential model to assess the likelihood of subspecific diversity in each hominin species. In passing, we also consider potential subspecific differentiation in Pleistocene *Homo neanderthalensis*, although it is not the focus of this chapter.

Methods

Modern primate species ranges were calculated in ArcGIS 9.1 from distribution polygons based on observational data, downloaded from the IUCN Red List (IUCN 2011). The IUCN Red List favours a 'splitting' taxonomy whereby many taxa recognized by most authorities as subspecies are inflated to species, so we manually reassigned species to subspecies where appropriate, based on Grubb et al. (2003), one of the most widely used and accepted taxonomic authorities, and which represents a consensus view. Informed by our research (Dunn et al. in press), Jolly (1993) was used as the authority for subspecific differentiation in the *Papio* baboons (*Papio hamadryas* subspecies). These subspecies were then grouped together as species and the area of each species distribution calculated from polygons using the ArcGIS *geometry* tools. Spearman's rank correlation in SPSS 19.0 was used to explore the relationship between geographic species range and number of subspecies. Linear regression, also in SPSS 19.0, was used to examine the predictive value of the relationship between log10 species range and number of subspecies. To account for lack of independence of data due to phylogeny, independent contrasts (Felsenstein 1985), using a consensus ultrametric tree downloaded from 10K Trees (Arnold et al. 2010), were also calculated for these data and used in regression via the R (R Core Team 2013) package ‘caper’ (Orme et al. 2012). As body mass is a fundamental ecological variable that is both available in hominins and often correlated with animal life history variables that in turn may influence speciation rates (Cardillo et al. 2003), the relationships between species range, subspecies number and log10 male and female body masses were also explored using Spearman’s rank correlation, linear regression and independent contrasts. It has been suggested widely that forest fragmentation promotes speciation (see, for example, Cardini and Elton 2009), so a Mann Whitney U in SPSS 19.0 was used to test whether there was a significant difference in subspecies number between arboreal and terrestrial taxa.

Species ranges for the hominins were first reconstructed on the basis of recorded fossil finds (Table 1). For *A. afarensis, A. africanus* and *P. boisei*, that have a spread of localities, simple polygons based on the findspots at the geographic extremes of the range were constructed in QGIS Application (QGIS Development Team 2013) using the World Equidistant Cylindrical (Sphere) projection. Given the small numbers of localities for each species, this meant practically that most findspots were used to define the edges of the polygon, and all the localities for each species, regardless of their date, were included. For *A. afarensis* a second polygon was drawn, incorporating the one findspot, Bahr-el-Ghazal in central Africa, of *A. bahrelghazali*. The area of each polygon was calculated using the geometry ‘area’ function in QGIS. No polygon based on finds was constructed for *P. robustus*, as it is found from only five localities (listed in Table 1) situated in a highly restricted geographic area. Instead, its geographic species range was calculated from the published area (<47,000 hectares) for the Cradle of Humankind (Berger

2005). For *H. neanderthalensis*, the range was calculated on the basis of a polygon adapted from the distributed given in Krause et al. (2007).

Table 1 around here

Fossil (and for later hominins, archaeological) finds are the only secure evidence that a species was present in an area. However, it is possible to employ species distribution models, developed for modern biodiversity assessment and based on known occurrence in conjunction with environmental data, such as temperature, precipitation, vegetation and elevation, for the area of interest (in this case Africa) to explore potential ranges of extinct organisms (Maguire and Stigall 2009). Distributions were thus modelled for *A. afarensis* (excluding *A. bahrelghazali*), *A. africanus* and *P. boisei* (but not *P. robustus*) using the BIOCLIM/DOMAIN 'Predict' tool in DIVA-GIS (Hijmans et al. 2012). Considerable amounts of data on Plio-Pleistocene palaeoclimates and environments are available, based on many different lines of evidence (Elton 2008). Nonetheless, past climates and environments were highly variable spatially as well as temporally (Trauth et al. 2009) and there are significant challenges extrapolating from global to regional to local scales of evidence (Elton 2008). We therefore chose to keep the environmental data used in the distribution modelling as simple as possible, to offset error caused by over-interpretation / extrapolation. Hence, we used only elevation and biome (vegetation) information in the *A. afarensis* and *A. africanus* models. Africa has experienced significant topographic changes since the Plio-Pleistocene, including the uplift of the East African Rift (Trauth et al. 2007; Sohl et al. 2009). Thus, the PRISM3 Pliocene topographic dataset (Sohl et al. 2009) was used to approximate elevation across Africa. The biome dataset for Africa, based on palaeobotanical and palaeoclimatic reconstructions, was also taken from PRISM3/BAS (Salzmann et al. 2008). Although the *A. afarensis* sites span one million years (4 – 3 Ma; Table 1) and *A. africanus* sites have been dated to between 2.85 Ma and 2.0 Ma, the paucity of data meant that all fossil localities for each species (as listed in Table 1) were included for each species model. Hence, the PRISM3 dataset, developed to represent the period between 3.3 and 3.0 Ma, was used without further amendment for both species, as our exercise is at best an approximation.

The earliest *P. boisei* fossils are dated to 2.6 Ma (Table 1), around the time of the onset of glaciation in the Northern Hemisphere (Trauth et al. 2007) which marks the shift from Pliocene to Pleistocene climatic patterns. *P. boisei*, present in East Africa for over a million years (Table 1), therefore experienced profound changes in global climate over its tenure (Wood et al. 1992; Elton 2008). By 1.5 Ma, the topography of the East African Rift stabilized into more or less the formation seen today (Trauth et al. 2007). To reflect the shift in climate and topography from Pliocene to Pleistocene patterns during the time of *P. boisei*, two distribution models were constructed for this species, again pooling all localities regardless of date because of paucity of sites. The first used the PRISM3 datasets as described above to model possible African distribution. To account for the stabilizing of the East African Rift, the second model used modern elevation data drawn from the WORLDCLIM (Hijmans et al. 2005) altitude dataset (resolution 2.5 by 2.5 arc minutes, which is approximately 25 km^2 in area at the Equator). To account for climatic shifts between the Pliocene and Pleistocene, modern annual average precipitation and temperature data (which have a close functional relationship with biome) for Africa were also taken from WORLDCLIM (BIO12 and BIO1, 2.5 by 2.5 arc minutes) for use in the second *P. boisei* model. These values are obviously not identical to those that would have prevailed in the past: in the early Pleistocene, African climate was wetter than today and extremely spatially and temporally variable because of changes in solar intensity due to the orbital precession of the Earth (Trauth et al. 2009). Some precipitation estimates for hominin localities do exist (e.g. Hernandez-Fernandez and Vrba 2006), but they have their own limitations and could compound error, especially as the climate data required for distribution models necessarily must extend beyond the occurrence sites themselves. Temperature estimates based on larger-scale continental or global data (that could be extended to the wider area of interest) would necessitate all points being altered by the same amount (for example, raising or lowering the whole dataset by 1°C), which would negate any effect in a single model. It was thus assumed that because of the temporal averaging of localities and the likelihood of localized climatic variability, not only in time but also over small areas, internal model consistency should take precedence over absolute palaeoclimatic accuracy, if such a phenomenon is even possible, and the modern data were used without adjustment.

DIVA-GIS distribution models report probability of occurrence on a sliding scale from ‘excellent’ to ‘not suitable’ (Hijmans et al. 2012). To calculate the areas of potential species ranges, polygons were constructed in QGIS quantifying the continuous distribution of ‘excellent’ and ‘very good’ probabilities for each species, radiating from the fossil findspots. Some areas were deemed to have ‘excellent’ probability of occupation but were separated from the continuous distribution and were thus not included in the polygons. Again, the World Equidistant Cylindrical (Sphere) projection was used and the area of each polygon calculated using the geometry ‘area’ function in QGIS.

Results and discussion

The modern primate data in Table 2 show that there is a positive trend in geographic range versus subspecific diversity: pooling arboreal and terrestrial species, those with larger ranges tend to have greater numbers of subspecies (Spearman's rho, one-tailed significance test: $N = 47$, $r = 0.48$, $p < 0.001$). Extremely similar trends (results not shown) occur when arboreal and terrestrial samples are analyzed separately. In the pooled sample, the predictive value of the relationship between subspecies number and log10 range is fairly small but significant (Table 3). When independent contrasts for subspecies number and log10range are used in linear regression, the adjusted r^2 increases (Table 3). There was no significant correlation between male body mass (Spearman's rho, two-tailed, $N=46$) and species range ($r = 0.09$) or number of subspecies ($r = 0.10$). A similar result was found for analysis of female body mass ($N = 45$) and species range ($r = 0.05$) or number of subspecies ($r = 0.11$). Results of the linear regression and independent contrasts linear regression for log10 species range / subspecies number and log10 body masses were also non-significant (Tables 3 and 4). There was no significant difference between numbers of arboreal and terrestrial subspecies (Mann Whitney U, $P > 0.05$; arboreal $N = 31$, $\bar{x} = 2 \pm 3$, terrestrial $N = 16$, $\bar{x}$ 2 ± 2).

Tables 2 – 4 around here

Although there were significant relationships with and without phylogeny between geographic range and subspecific diversity, there were many deviations from the overall trend. The terrestrial *Chlorocebus preussi* has one of the smallest geographic ranges of sub-Saharan African catarrhines but two subspecies, one of which is found on Bioko Island (Oates 2008). *Mandrillus leucophaeus*, also terrestrial, also has two subspecies in a relatively small range; again, one subspecies is found on Bioko Island (Oates and Butynski 2008). Insularity can accelerate morphological evolution (Nowak et al. 2008), which is a likely cause of the diversity evident in *C. preussi* and *M. leucophaeus*, as well as contributing to divergence in the arboreal *Piliocolobus pennantii*, which has a small range and four subspecies, one of which is found on Bioko (Oates et al. 2008). *Gorilla beringei*, another terrestrial catarrhine with a relatively small species range, is currently divided into two subspecies, the highland and lowland forms (Robbins and Williamson 2008). This geographic difference, combined with the small population size of the highland form, is likely to have promoted subspecific diversity and is a reminder that the exploitation of different types of terrain can promote reproductive isolation and hence diversification (Winder et al. 2013). *Theropithecus gelada*, found only in the Ethiopian and Eritrean highlands, has two subspecies, *T. g. obscurus* (distributed east of the Rift Valley) and *T. g. gelada* (west of the Rift) (Groves 2001). The Rift may be a natural geographic boundary, inducing vicariance.

Towards the upper end of geographic range size, *Cercopithecus mitis* has the highest number of subspecies (eighteen). *C. mitis* is an arboreal primate, found in diverse habitats (Lawes 1990), which may have encouraged divergence. The *C. mitis* range is also discontinuous, which probably reflects climate change and forest history since its evolution (Lawes 1990) around 2.2 Ma (Tosi et al. 2005). This forest fragmentation was probably a key factor in monkey subspecific and specific differentiation in the Pleistocene, creating refugial islands and restricting gene flow (Cardini and Elton 2009). Although neither arboreal nor terrestrial primates showed greater subspecific diversity across the sample as a whole, fragmentation may help to explain why some arboreal primates in Africa (such as *P.pennentii*, *Colobus guereza*, *C. angolensis*, *Cercopithecus pogonius* and the central assemblage of *Piliocolobus*, as well as *C. mitis*), have relatively large numbers of subspecies (Cardini et al. 2010). However, not all arboreal primates have high levels of subspecific diversity. In contrast to its sister taxa *Piliocolobus* (the red colobus monkeys), *Procolobus verus* (the olive colobus) has been described as monotypic (Nowak et al. 2008) and has no diagnosed subspecies (Grubb et al. 2003). Even more strikingly, *Cercopithecus neglectus* has a very large range but no diagnosed subspecies (Grubb et al. 2003). This lack of subspecific differentiation may be because their range is continuous across central Africa (Aghokeng et al. 2010). However, the observation that they host geographically distinct strains of simian lentivirus (Aghokeng et al. 2010) indicates the potential for population divergence. Detailed geometric morphometric analyses of *C. neglectus* skulls across their range, shown in studies of other African primates to quantify very small but evolutionarily meaningful variation (Cardini and Elton 2009), may help to identify incipient or realized subspecific divergence.

Hypothesised geographic species range areas for the hominins are given in Table 5, with polygons of the distribution models shown in Figures 2 and 3. Although African Plio-Pleistocene hominins are the focus of this chapter, we briefly consider subspeciation in Neaderthals, as an example of a temperate latitude hominin. The Eurasian robin, as discussed above, is not an ideal comparator for any primate (least of all one belonging to the genus *Homo*), but it does provide a classic example of a widespread temperate species with very few subspecies. This prompts the question about whether subspecies should be expected in Neanderthals. Ancient DNA supports the division of Neanderthals into three distinct geographic groups - in Western Europe, Western

Asia and in the south of their range, between which there was nonetheless some gene flow (Fabre et al. 2009). It is not clear whether these genetic differences map onto subspecies, especially as most morphological work on Neanderthals stresses their similarities rather than differences (Hawks 2012). The estimated Neanderthal geographic range lies towards the upper end of species range sizes for African catarrhines. Eeley and Foley (1999) noted a strong skew towards smaller ranges in African catarrhines, replicated in our data, and also observed that species ranges were smaller nearer the Equator. Given the temperate, Eurasian distribution of Neanderthals, therefore, a more appropriate comparator might be the most geographically widespread macaque, *Macaca mulatta*, found in tropical, subtropical and temperate Asia at more northerly latitudes than any sub-Saharan African primate. *M. mulatta* has a species distribution (extracted from IUCN data as described above) of 6,647,129km^2, somewhat less than that estimated for Neanderthals. Like Neanderthals, distinct molecular clades (in west and east) have been reported (Brandon Jones et al. 2004). However, a highly comprehensive and detailed analysis of *M. mulatta* morphology suggests that the species is monotypic, with no ‘good’ subspecies (Fooden 2000), even though multiple subspecies have been identified in the past (Brandon Jones et al. 2004). Subspecies can be defined on the basis of molecular evidence but the available data for *M. mulatta* do not appear to identify clades consistently (Brandon Jones et al. 2004). Hence, for the time being, influential authorities do not attribute any subspecies to *M. mulatta* (Brandon Jones et al. 2004), providing important context for interpreting Neanderthal intraspecific diversity. In particular, inferences about hominin subspecies made on the basis of molecular data alone should be treated with caution, and further research on subspecific divergence in temperate mammals would be useful in constructing a framework in which to investigate intraspecific variation in temperate hominins.

Table 5, Figures 2 and 3 around here

Reference to modern African primates indicates that subspecific diversity is possible in the tropics even in species with very small distributions, influenced by modern and past environmental factors and evolutionary history. Nonetheless, at 470 km^2 the tiny *P. robustus* range in southern Africa seems more consistent with a home range rather than the total geographic range of a species. Only one of the geographic ranges calculated for the modern African catarrhines (Table 2), that of *Piliocolobus rufomitratus*, is smaller, as is the range of the poorly known and relatively newly discovered *Rungwecebus kipunjii* (insufficiently studied to include in the analysis here), currently estimate at 20.6km^2 (Davenport and Jones 2008). The range of the insular Zanzibar red colobus (*P. kirkii*) is over twice the size of the apparent *P. robustus* range and the highly endangered *P. gordonorum* has a range nearly eight times larger. Given that the *P. robustus* geographic range is at the very bottom of the distribution of modern African catarrhine primates, it is very possible that its actual distribution was much larger than the fossil record suggests. This is supported by the observation that *P. robustus* was likely to have been a highly flexible feeder (Lee-Thorp et al. 2003), a generalist rather than a specialist, which would imply a much larger geographic distribution than is evident from the fossil record. Unfortunately, the clumping of *P. robustus* fossil localities makes it impossible to employ GIS prediction models.

The question of whether *P. robustus* would have diverged into subspecies is also vexed. There has been much debate (reviewed in Cofran and Thackeray 2010) over whether its fossil record is too variable to be contained in a single species, with some assigning the Swartkrans specimens to *Australopithecus crassidens*. The variability present in the *P. robustus* fossil record may be attributed to change over time, with different forms representing chronospecies or chronosubspecies, but given the imprecise dating of cave sites this is very difficult to test. It is difficult to see that subspecific diversity could be maintained contemporaneously if the geographic range of *P. robustus* was as small as the fossil locality distribution suggests, as subspecies would be living sympatrically. Sympatric subspecies are found in plants and invertebrates, and may co-exist because of reproductive isolation (caused, for example, by different flowering or breeding seasons; Arista et al. 1997, Binks et al. 2012) or differential resource / habitat exploitation (Forbes et al. 2009). Sympatric subspeciation is highly uncommon in mammals. It is possible – but by no means probable – that significant morphological divergence, possibly resulting in the formation of a second subspecies, could have occurred in sympatric groups of *P. robustus* because of differential resource exploitation and hence morphological character displacement. However, dietary variation is reasonably well-documented in *P. robustus* (Lee-Thorp et al. 2003) and although seasonal variations within individuals are evident (Sponheiner et al. 2006), there is nothing to suggest systematic differences between different groups that may cause divergence. This notwithstanding, even with such a small range, *P. robustus* would have been divided into subpopulations (such as mating groups) which may have adopted localized behaviours and traditions (see below).

The other southern African hominin considered here, *Australopithecus africanus*, has a geographic range based on fossil localities that also falls around the bottom of the African catarrhine distribution. When interpreting the likelihood of subspecific diversity in hominins, there is the added complexity that the localities are drawn from the whole known tenure in the fossil record and may be widely separated in time, with the consequent possibility that the range may have shifted over the lifetime of the species. Thus, even a range based on known localities may be artificially large for the species at a particular point in time. Predicated on the notion that the distribution of fossil sites accurately reflects the range of the species, which is obviously far from certain, subspecific diversity would be unlikely in *A. africanus*, even though it has significant cranial (Ahern 1998) and postcranial (Harmon 2009) variation. All the modern catarrhines with similar ranges either have no subspecies or subspecies due to insularity (specifically, on Bioko). Although *P. pennantii* has a range only slightly larger than the estimated range based on localities for *A. africanus*, its subspeciosity is probably the product not only of 'the Bioko effect' but also because of intense fragmentation of its forest habitat (Cardini and Elton 2009). *A. africanus*, found in central southern Africa and inhabiting woodland and grassland as well as forested areas (Elton 2008), was unlikely to have experienced vicariant subspeciation due to isolation on an oceanic or forest island. It must be considered, however, that because of the uneven nature of the terrestrial fossil record and consequent sampling bias the known range captures only a fraction of the actual range. Hence, a second hypothesized range, based on GIS distribution modeling, predicts a much larger geographic spread for *A. africanus*, towards the upper end for modern catarrhines. Given that there was a statistically significant positive relationship between geographic range size and subspecific diversity, structured variation (translating to subspecies) would be much more likely in *A. africanus* with this range. *Pan troglodytes*, which has a slightly larger geographic distribution has four subspecies, for example. Nonetheless, another appropriate comparator for *A. africanus*, the terrestrial guenon *C. patas*, has a very large range but no valid subspecies recognized by Grubb et al. (2003). Other authorities (e.g. Kingdon 1997) do recognize subspecies, for example subdividing eastern and western forms, but further research is required before subspecific differentiation can be securely identified (Grubb et al. 2003). This indicates that although diversity can be present in a widespread primate, it does not automatically or easily equate to the structured variation necessary to allocate groups to subspecies. Thus, it cannot be assumed automatically that given a large range *A. africanus* would subspeciate, although the general trend within modern catarrhines points to increased probability of subspecific differentiation as geographic range size gets larger.

The estimated ranges based on fossil localities for *A. afarensis sensu stricto* (i.e. without *A. bahrelghazali*) and *P. boisei* could incorporate subspecific diversity, even though they both fall in the lower half of the modern catarrhine distribution. *T. gelada* and *G. berengei* provide examples of terrestrial primates with smaller ranges that each have two subspecies, although *C. patas*, *Mandrillus sphinx* and *Cercocebus torquatus*, other terrestrial primates with larger ranges have no recognized subspecies. In Plio-Pleistocene East African hominins, the presence of the Rift and geologically active environments may have facilitated structured population differentiation due to the presence of natural barriers to gene flow. It has been argued that *P. boisei* is polytypic (Suwa et al. 1997), but interestingly its intraspecific variation does not appear particularly high compared to that seen in modern humans, apes and colobus monkeys (Wood & Lieberman, 2001) and aspects of its morphology show stasis over time (Wood et al. 1994) and by implication from locality to locality. This relative homogeneity is mirrored in diet, at least on the basis of stable isotope analysis (Cerling et al. 2011). According to studies of dental microwear, the diet of *A. afarensis* was also not very variable, either over time or across different environments (Grine et al. 2006). However, *A. afarensis* does show significant cranial variation over time and also between the two sites where it is best sampled, Hadar and Laetoli (Lockwood et al. 2000). These morphological differences could be evidence for structured differentiation at the subspecific level, either temporally (chronosubspecies), or spatially, or both. Indeed, the variation within *A. afarensis* is substantial, even though care must be taken when determining whether the variation is caused by sexual dimorphism, geography or time (Kimbel and Delezene 2009). Adding the locality of Bahr-el-Ghazal to the *A. afarensis* range estimation not unexpectedly increased it considerably, bringing it to the higher end of the modern catarrhine range, similar to *P. troglodytes* but not yet approaching the very large distributions of *C. aethiops* and *P. hamadryas*. *A. bahrelghazali* is known only from a small amount of mandibular material with associated dentition (Brunet et al. 1995) and relatively little has been published on it. The material that is known appears to fit within *A. afarensis* (Kimbel and Delezene 2009) and these simple comparisons of geographic range indicate the feasibility of treating *A. bahrelghazali* as a subspecies of *A. afarensis*.

The GIS model for *A. afarensis* (Figure 2), which used only *A. afarensis s.s.*, predicts an even wider species range than is seen based on localities, approaching that of the extremely widespread *P. hamadryas* and *C. aethiops*. Unlike in these modern taxa, however the *A. afarensis* predicted range does not extend into West Africa. Associated with woodland and bushland habitats, it is uncertain whether *A. afarensis* exploited tropical forest, even though earlier hominins probably did (Elton 2008). Thus, rainforest regions may have been a barrier to dispersal across Africa and pockets of rainforest may have acted to isolate populations and hence promoted diversity. In the context of large, mainly terrestrial and eurytopic primate ranges – descriptors that can each be applied to *A. afarensis* and indeed most Plio-Pleistocene hominins –

all the species ranges predicted here using GIS-based modelling seem appropriate, especially given that many modern primate distributions have been negatively affected by anthropogenic factors. Again, *C. patas* serves to provide a cautionary note when extrapolating from size of range to the probability of structured diversity, but it stands out as an exception compared to other primates with substantial ranges that all contain subspecies. Thus, given the models and comparison with modern primate, the spatial patterning of its sites (including Bahr-el-Ghazal), and the considerable variation within the species, subspecific diversity in *A. afarensis* seems highly likely.

Incorporating *A. bahrelghazali* into *A. afarensis* substantially widens an east-west distribution in Africa that was already larger than that seen in other Plio-Pleistocene hominins, including *P. boisei* (Table 1). Although its specimens are found as far apart as Malawi and Ethiopia (a distance of over 1600 km), *P. boisei* localities occupy a very restricted longitudinal range (37 – 33°E). However, its GIS models (Figure 3), using both Pliocene and modern data, predict an extensive westward distribution. Much spatially structured variation in widespread modern African primates is longitudinal rather than latitudinal (vervets: Cardini et al. 2007; red colobus: Cardini and Elton 2009; blue monkeys: Cardini et al. 2010). In baboons, significant west-east variation also exists, and the north-south variation that is observed occurs over a large area that covers most of sub-Saharan Africa (Dunn et al. in press), considerably more than that occupied by *P. boisei*. Morphological differentiation in widespread African primates is driven in part by allometry caused by environmentally-induced body size divergence (Cardini et al. 2010). Although *P. boisei* occupied heterogeneous environments, with habitat shifts in time as well as space (Elton 2008), the known north-south fossil distribution, at least on present evidence, shows little spatial patterning. Environmental gradients significant enough to promote subspecific divergence might only be experienced on greater longitudinal or latitudinal scales. If east-west distributions in African Plio-Pleistocene hominins, including *P. boisei*, were as wide as predicted here they may well have promoted structured geographic variation, but as fossils are sampled only from a more restricted area, this may be difficult to detect with current samples.

To sum up this section, using modern African catarrhines as referents in combination with species range estimates for Plio-Pleistocene hominins indicates that subspecific diversity was probable in the East African species *A. afarensis* and *P. boisei* and possible for the southern African *A. africanus*, with fossil data for *P. robustus* too clumped to make any inference. Better resolution palaeoenvironmental data would help to improve our understanding of potential hominin occupation areas and hence geographic ranges. Distributions are also influenced by abiotic and biotic environmental factors, including biome, food availability, competitors and geographic barriers such as mountain ranges and large rivers, which may also ‘feed’ genetic and morphological divergence. Although it may be possible to include some of these features in a model, even apparently ‘fixed’ features such as mountain ranges and rivers can appear, disappear or move over the course of three million years. A classic example is the River Nile, a major geographic entity in Africa which did not follow its present course until the late Pleistocene (Goudie 2005). Accurate geomorphological and ecological data for the past would also improve predictions about species range and the features that may promote subspecific divergence. Hence, one challenge is now to improve upon and test the predictions made in this chapter. Quantifying subspecific diversity would also benefit from the development of more sophisticated analytical techniques to allow variance due to temporal, spatial and other influences on morphology to be partitioned meaningfully within the relatively small Plio-Pleistocene hominin sample available.

THE ROLE OF HOMININ SUB-POPULATIONS AND GROUPS IN THE ADAPTIVE LANDSCAPE

In the final part of this chapter, we consider briefly the role of hominin subpopulations and groups in providing the ‘raw material’ for structured intraspecific divergence, which may in turn lead to full speciation. Wright (1932) envisaged a species occupying a position on a topographically varied evolutionary landscape. In his conceptual model, elevated locations equate to adaptive states and depressed areas maladaptive ones. Natural selection is the driving force that pushes a species up the hill in the model, or adapts it to its surroundings in reality. Different species inhabit different adaptive landscapes and these vary with environment. The varied topography of the landscape results in discrete rather than continuous variation, producing the discrete species observed in nature, each notionally hovering over some adaptive peak. The evolutionary importance of subspecific variation can be viewed within this context. Wright (1932) recognised that species were not homogenous and thus considered a species to be a cloud rather than a point on an adaptive landscape. This has profound implications. A species spread widely over an adaptive landscape is likely to constitute subspecies occupying different but adjacent peaks. As such the species is less likely to go extinct when certain local conditions change either by stochastic effects such as drought, famine or disease or more long term environmental change. Additionally a wide distribution over this theoretical landscape increases the catchment area for the adaptive peaks essential to evolutionary survival if the environment should change.

The cohesiveness of a species is maintained by reproduction (Wright, 1932). A reduction in gene flux facilitates the actions of differential selection and genetic drift, enabling divergence. Using Wright's model, a breakdown in reproduction leads to constriction in the species 'cloud' on the adaptive landscape. Each resulting discrete entity may occupy a separate adaptive peak, which over time may lead to further constriction and eventual splitting of the groups. For this reason some authors have considered subspecific differentiation as representing incipient speciation. However, low levels of gene flow can impede speciation, which requires divergent selection on several traits (Rice and Hostert, 1993). As such the notion that subspecies are incipient species can be challenged. Jolly (1993) argued that subspecies may be stable and longstanding features of a species rather than on the verge of budding off. While evolutionary trajectories may begin to diverge, secondary contact between recently separated taxa ('reticulation') may result in hybrids that are adaptively suited to the environment and change the adaptive trajectory of a lineage (Hey et al., 2003). Nevertheless, the forces that sculpt subspecies, whatever their destiny, are the same as the forces that sculpt species, and heterogeneity within a species thus presents an important insight into natural selection (Winker, 2010).

Several hominin species survived in the fossil record for a million years or more, around five times as long as our own species, *Homo sapiens sensu stricto*, has existed. These species, including *A. afarensis* and *P. boisei*, experienced profound climatic change which required responses, which may have been ecological, behavioural, genetic, morphological and possibly even cultural, and may have led to biological adaptation. Although not truly formalized in Linnaean taxonomy, species may have subspecies or populations which in turn may have subordinate groups or subpopulations (Figure 4). In a species that has a reasonably large range, responses to environmental change may differ from population to population and group to group, partly because environments tend to differ over large areas. In the previous section, we argued that *P. boisei* and *A. afarensis* were both likely to have had extensive geographic ranges. Based on modern African primates, we also put forward the hypothesis that they would have been divided into subspecies. But how might those subspecies have formed, and how might individuals – on which natural selection generally acts - have been grouped and behaved within those subspecies?

Figure 4 around here

Primates, like humans, are social and live in groups that form subsets of populations, below the subspecific level. These are not defined on the basis of structured morphological or genetic variation but are instead identified usually through observation of association, competition, cooperation and breeding patterns. As is the case in humans, these groups often contain related individuals: chimpanzees are male-kin bonded for example, whereas most Old World monkeys are female-kin bonded. We can reasonably assume that extinct hominins also lived in groups, but these are considered only rarely. Hominins were probably male-kin bonded, a parsiminous assumption based on the mating systems of African apes and most humans (Foley and Lee 1989). Recently, independent palaeobiological data have been collected that support this for at least one Plio-Pleistocene hominin species. Strontium isotope analysis of the teeth of *P. robustus* indicates that larger individuals, inferred to be male, came from a much smaller geographic area than their smaller, probably female, conspecifics (Copeland et al. 2011). This suggests male philopatry and female dispersal, as is seen in chimpanzees (Copeland et al. 2011). Further, it is possible that some hominins lived in multi-female groups monopolised by a single male, suggested by evidence for extended male growth (continuing into adulthood) in the skulls of *P. robustus* (Lockwood et al. 2007). Although this gorilla-like pattern is somewhat at odds with the isotope data and it is highly likely that the social system of *P. robustus* does not have a direct analogue in the modern world (Copeland et al. 2011), these lines of evidence shed important light on the structure of hominin groups and possible population genetics in at least one species.

Individual movement between subgroups is important for gene flow, which in turn maintains both genetic heterozygosity in a given mating group and a level of genetic homozygosity over a given area. Dispersing only relatively small distances to breed, as occurs in catarrhines, can help to structure subspecific variation, especially if natural barriers prevent extensive gene flow between distinct populations. Depending on circumstances, however, localized individual transfer out of a group may not happen routinely or even at all. Female chimpanzees may take up to two years to move fully into a new group, dividing their time between that and the group in which they were born (Goodall 1986). In some chimpanzee subpopulations, such as Gombe, female transfer rates are lower than in nearby groups such as Mahale, possibly because of isolation, and behavioural measures are taken to avoid inbreeding (Goodall 1986). This indicates how groups within a subspecies may become isolated and yet avoid the deleterious consequences of inbreeding. It further suggests how different groups have the opportunity to exploit their own adaptive peak and diversify even over very small spatial scales. A good example of this diversification – albeit cultural – is the different discrete traditions, maintained for generations, observed in nearby chimpanzee groups. For example, in Tanzania, Gombe chimpanzees used levers and pound objects whereas those at Mahale do not (Whiten et al. 1999). Further, based on research in captive chimpanzees, it appears that small groups living in close proximity can adopt and maintain their own distinct cultural norms in a short period of time (Whiten et al. 2005).

Behavioural and biological traits, including some chimpanzee traditions, can emerge stochastically but may then go onto produce evolutionarily-meaningful differentiation. However, differentiation can also be more ordered, as occurs under selection. The environment – broadly defined – often provides the impetus for this selection, and acts as an important interacting factor when considering group composition, ecology and behaviour. Although group sizes vary from species to species and place to place, there is often an ecologically optimal group size and groups can split permanently, to facilitate feeding or reproduction, if they exceed that (Dunbar 1988). This could give realistic opportunities to exploit varying adaptive landscapes. Such ‘budding’ also promotes wider-scale dispersal, which has occurred many times during primate and hominin evolution and may, like environmental change in a given place, fuel evolutionary novelty as groups or populations come across novel competitors, predators, habitats and foodstuffs and exploit the potential for reaction norm - phenotypic variation in a species along an environmental gradient – to diversify.

When considering subspecific differentiation in hominins, it is possible that small differences in the local environment, reinforced by competition for food and differential reproductive success, may lead to morphological shifts that are initially plastic but later genetic. Research into the widespread African vervet monkey has suggested that differentiation of body size (a labile feature that profoundly influences ecology and behaviour) could be the first step in population divergence and a way of moving from one adaptive peak to another (Elton et al. 2010). Indeed, size is so plastic that it has been shown to differ considerably in Kenyan vervets even over a few kilometres in response to environmental changes, specifically the presence of human food discards (Turner et al. 1997). Such a response requires morphological plasticity – the ability to gain weight, which if it occurs in juveniles can lead to structural skeletal change caused by increased growth – but also behavioural plasticity. Dietary flexibility, whereby conspecifics are able to exploit (and indeed may choose to exploit) different foods, is a good example of behavioural plasticity (Ulijaszek et al. 2012), which is probably the result of interaction between learned and pre-programmed (i.e. genetically determined) behaviours (Mery and Burns 2010).

This vervet scenario – of dietary and body mass shifts that allow the potential for movement between peaks in an adaptive landscape - might seem difficult to tie up with what is known from the hominin fossil record. For example, *P. boisei* shows no evidence of body size increase over time (Wood et al. 1994), and dietary reconstructions for both *A. afarensis* (Grine et al. 2006) and *P. boisei* (Cerling et al. 2011) suggest that these species had little temporal or spatial change in diets. However, a single line of evidence, such as dental microwear or stable isotope analysis, only provides one facet of a complex entity such as diet (Ulijaszek et al. 2012). Given the variability in feeding behaviour in many modern non-human primates and humans, in which food preferences may differ by population, by group, by season, by individual, by age (Ulijaszek et al. 2012), and the palaeobiological evidence for individual dietary variability in certain hominin species (e.g. Sponheiner et al. 2006), it is reasonable to assume that all hominins had some degree of behavioural plasticity that extended to diet and enabled a response to novel environments or circumstances. Just as vervet exploitation of cultivated foods emerged opportunistically and may be missed in a snapshot observation of their feeding behaviour, small alterations to behaviour or feeding preferences in individual hominin groups might not be identified palaeontologically but nonetheless could provide the raw material for future significant change.

Plastic behavioural responses to challenges in slightly different environments may cause two sister groups (or, on a larger scale, populations) to diverge. Initially, this behavioural plasticity may influence morphology plastically, such as exploitation of slightly different foodstuffs leading to different bone deformation during ontogeny of the masticatory system (Ulijaszek et al. 2012). Plasticity could then play a facilitating role in evolutionary change if individuals exhibiting those morphological shifts had a competitive and hence reproductive advantage and the trait was reinforced by selection (Ulijaszek et al. 2012). Essentially, behavioural plasticity at the individual level may be one of the elements needed for groups and hence higher organizational units to move between adaptive peaks. Despite apparent dietary homogeneity, there is evidence for morphological change over time in *A. afarensis*, with more recent individuals having a larger mandibular corpus (Lockwood et al. 2000), a plastic or even selected trait shift that could be related to dietary diversification within at least some of the population or species. In *P. boisei*, more recent specimens exhibit a larger P4 crown area (Wood et al. 1994). Since tooth morphology is genetically determined and not remodelled in the way that bone is, this could indicate either genetic adaptation – presumably to diet – or genetic drift, both of which are evolutionary forces. Although relatively modest morphological changes such as these seem a long way from the appearance of a new species, the process of intraspecific divergence, which may lead ultimately to speciation, is dependent on them.

CONCLUSION

In this chapter, we have attempted to explore the potential for subspecific differentiation in African hominins and identify some of its possible drivers. Our approach is no substitute for study of fossil and genetic material but instead has generated some predictions about intraspecific diversity that may be empirically testable. Gaining a deeper understanding of pattern and process in human evolution will require better knowledge about intraspecific diversity in hominins. This needs not only sophisticated morphological and molecular tools but also a better integration of palaeoanthropological discoveries into a wider theoretical evolutionary biology framework.

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Table 1: geographic coordinates for Plio-Pleistocene hominin localities

Hominin locality	Region	Species[a]	Longitude (decimal degrees)	Latitude (decimal degrees)	Date (millions of years ago)
Taung	Southern Africa	*A. africanus*	25	-28	2.6 – 2.8
Makapansgat	Southern African	*A. africanus*	29	-24	2.85 – 2.58
Sterkfontein	Southern Africa	*A. africanus*	28	-26	2.6 – 2.0
Swartkrans	Southern Africa	*P. robustus*	28	-26	1.8 – 1.0
Kromdraai	Southern Africa	*P. robustus*	28	-26	2.0 – 1.5
Coopers	Southern Africa	*P. robustus*	28	-26	1.9 – 1.4
Drimolen	Southern Africa	*P. robustus*	28	-26	2.0 – 1.5
Gondolin	Southern Africa	*P. robustus*	28	-26	1.9 – 1.5
Malapa	Southern Africa	*A. sediba*	28	-26	1.99
Bahr-el-Ghazal	Central Africa	*A. bahrelghazali*	19	16	3.6
Hadar	East Africa	*A. afarensis*	41	11	3.4 – 3.0
Dikika	East Africa	*A. afarensis*	41	11	3.4
Laetoli	East Africa	*A. afarensis*	31	-4	3.85 – 3.63
Omo Shungura	East Africa	*A. afarensis*	36	5	3.4

Maka	East Africa	*A. afarensis*	42	11	3.4
Fejej	East Africa	*A. afarensis*	36	5	4.0 – 4.18
Belohdelie	East Africa	*A. afarensis*	42	11	3.4
Koobi Fora	East Africa	*A. afarensis*	36	4	3.3
Lothagam	East Africa	*A. afarensis*	36	3	3.9 – 3.0
Konso	East Africa	*P. boisei*	37	5	1.43
Omo Shungura	East Africa	*P. boisei*	36	5	2.6 – 2.2
Koobi For a	East Africa	*P. boisei*	36	4	1.9 – 1.52
Chesowanja	East Africa	*P. boisei*	36	1	1.4
Peninj	East Africa	*P. boisei*	36	-2	1.4
Nachukui	East Africa	*P. boisei*	35	3	2.6 – 1.78
Olduvai	East Africa	*P. boisei*	35	-3	1.8 – 1.7
Chiwondo	East Africa	*P. boisei*	33	-9	2.3

[a]target species for this analysis: other hominin species may also have been recovered from the same locality. Longitude and latitude from Holmes et al. (2005); dates from Wood (2011).

Table 2: calculated geographic ranges and number of subspecies for modern African catarrhine primate species.

Species	Geographic range (km^2)	Number of subspecies	Primary habitat classification	Male body mass (kg)	Female body mass (kg)
Piliocolobus rufomitratus	165	0	Arboreal	9.67	7.21
Piliocolobus kirkii	1,300	0	Arboreal	5.8	5.46
Piliocolobus gordonorum	4,806	0	Arboreal	No data	No data
Chlorocebus solatus	9,933	0	Terrestrial	6.89	3.92
Chlorocebus preussi	14,172	2	Terrestrial	4.5	4.5
Piliocolobus pennantii	19,937	4	Arboreal	9.0	5.8
Cercopithecus sclateri†	29,645	0	Arboreal	4.0	2.5
Mandrillus leucophaeus	36,210	2	Terrestrial	17.5	12.5
Cercopithecus erythrotis	45,808	2	Arboreal	3.6	2.9
Gorilla beringei	53,399	2	Terrestrial	162.5	97.5
Cercopithecus erythrogaster	60,369	2	Arboreal	4.1	2.4
Theropithecus gelada	86,234	2	Terrestrial	19.0	11.7
Chlorocebus lhoesti	176,931	0	Terrestrial	5.97	3.45
Cercopithecus hamlyni	195,235	2	Arboreal	5.49	3.36
Cercocebus torquatus	235,465	0	Terrestrial	9.47	5.5
Mandrillus sphinx	266,234	0	Terrestrial	31.6	12.9
Colobus satanus	269,108	2	Arboreal	10.4	7.42

Colobus polykomos	281,386	0	Arboreal	9.9	8.3
Cercopithecus Diana	285,617	2	Arboreal	5.2	3.9
Miopithecus talapoin	320,577	0	Arboreal	2.5	2.0
Procolobus verus	330,697	0	Arboreal	4.7	4.2
Pan paniscus	341,643	0	Terrestrial	45.0	33.2
Cercocebus atys	360,297	2	Terrestrial	11.0	6.2
Piliocolobus badius	360,568	3	Arboreal	8.36	8.21
Colobus vellerosus	392,658	0	Arboreal	8.5	6.9
Miopithecus ogouensis[b]	398,813	0	Arboreal	1.38	1.12
Allenopithecus nigroviridis	414,829	0	Arboreal	6.13	3.18
Cercopithecus petaurista	437,286	2	Arboreal	4.4	2.9
Cercopithecus mona	508,489	0	Arboreal	5.1	No data
Cercopithecus campbelli	508,774	2	Arboreal	4.5	2.7
Gorilla gorilla	570,056	2	Terrestrial	170.4	71.5
Lophocebus aterrimus	590,644	2	Arboreal	7.84	5.76
Cercopithecus cephus	638,393	3	Arboreal	4.29	2.88
Cercocebus galeritus	1,052,221	4	Terrestrial	9.61	5.26
Piliocolobus (un-named species from central assemblage)	1,093,445	8	Arboreal	9.72[c]	7.13[c]
Cercopithecus nictitans	1,097,211	2	Arboreal	6.67	4.26
Lophocebus albigena	1,197,865	0	Arboreal	8.25	6.02
Cercopithecus pogonias	1,728,454	7	Arboreal	4.26	2.90

Cercopithecus neglectus	1,877,687	0	Arboreal	7.35	4.13
Colobus angolensis	1,888,514	7	Arboreal	9.68	7.57
Cercopithecus mitis	1,925,484	18	Arboreal	7.70[d]	4.36[d]
Pan troglodytes	2,045,671	4	Terrestrial	49.57[e]	40.37[e]
Cercopithecus ascanius	2,149,685	5	Arboreal	3.7	2.92
Colobus guereza	2,507,400	8	Arboreal	11.70[f]	8.55[f]
Chlorocebus patas	5,920,182	0	Terrestrial	12.4	6.5
Chlorocebus aethiops	11,931,093	6	Terrestrial	4.89[g]	3.54[g]
Papio hamadryas	13,818,390	6	Terrestrial	21.86[h]	11.91[h]

[b] Sequences unavailable in GenBank and hence species removed from independent contrasts analysis. All body mass data taken from Smith and Jungers (1997) except for *Piliocolous pennantii* from Groves (2007) based on the Bioko Island form. [c] Mean of *P. sp. parmentieri*, *P. sp. langi*, *P. sp. oustaleti*. [d] Mean of *C. mitis*, *C. m. stuhlmanni*, *C. m. erythrarchus*. [e] Mean of *P. t. troglodytes*, *P. t. verus*, *P. t. schweinfurthii*. [f] Mean of *C. g. matschiei* and *C. g. guereza*. [g] Mean of *C. aethiops* populations from Kenya and Botswana. [h] Mean of all subspecies except *P. h. kindae* for females and all except *P. h. kindae* and *P. h. papio* for males. For records marked as 'no data', no precise body mass data for indigenous African populations were available.

Table 3: Results of linear regressions of number of subspecies (dependent variable, y) on species range and body mass.

Model	Predictor variable (x)	N	Adjusted r^2	F	P
Linear regression	Log10 range	47	0.155	9.466	<0.001
Linear regression	Log10 male body mass	46	-0.021	0.063	Ns
Linear regression	Log10 female body mass	45	-0.023	0.028	Ns
IC linear regression	Log10 range	45	0.272	17.46	<0.0001
IC linear regression	Log10 male body mass	44	0.009	1.371	Ns
IC linear regression	Log10 female body mass	43	0.011	1.467	Ns

IC = independent contrasts. Ns = non significant ($p > 0.05$).

Table 4: Results of linear regressions of log10 species range (dependent variable, y) on body mass.

Model	Predictor variable (x)	N	Adjusted r^2	F	P
Linear regression	Log10 male body mass	46	-0.020	0.055	Ns
Linear regression	Log10 female body mass	45	-0.023	0.005	Ns
IC linear regression	Log10 male body mass	44	-0.004	0.850	Ns
IC linear regression	Log10 female body mass	43	-0.022	0.082	Ns

IC = independent contrasts. Ns = non significant ($p > 0.05$).

Table 5: areas of hypothesised ranges for fossil hominin species

Hominin species	Distance between two furthest fossil sites (km)	Area of hypothesised species range (km^2)	First and last appearance dates (Ma)
A. afarensis	1847	A: 270,558 B: 8,677,224 C: 2,542,155	3.9 – 2.9
A. africanus	668	A: 15,737 B: 1,614,269	2 – 3 Ma
P. boisei	1618	A: 181,155 B: 3,859,234 D: 7,869,705	2.4 – 1.2 Ma
P. robustus	~25	E: 470	2 – 1 Ma
H. neanderthalensis	N/A	F: 8,013,426	0.2 – 0.028 Ma

The number of kilometers between the two most distant points was calculated on the basis of longitude and latitude coordinates (Table 1) using the US government National Hurricane Center longitude / latitude distance calculator (http://www.nhc.noaa.gov/gccalc.shtml). For hypothesized species ranges: A = polygon area based on sites; B = polygon area based on DIVA-GIS model using PRISM3 data; C = polygon based on sites including *A. bahrelghazali*; D = polygon area based on DIVA-GIS model using WORLDCLIM data; E = based on published hectare value (Berger 2005); F = polygon area constructed from the distribution given in Krause et al. (2007).

FIGURE LEGENDS

Figure 1: the many faces of *Papio hamadryas.* Left: *P. h. ursinus* from southern Africa (http://commons.wikimedia.org/wiki/File:Papio_ursinus_2.jpg). Right: *P. h. hamadryas* from East Africa (http://commons.wikimedia.org/wiki/File:Papio_hamadryas_(aka).jpg).

Figure 2: Fossil occurrences and hypothesized geographic ranges for *Australopithecus* species. *A. bahrelghazali* site represented by white triangle, *A. afarensis* by white squares, *A. africanus* by white circles. The hypothesized range for *A. afarensis* is shown in dark grey shading and hypothesized range of *A. africanus* shown in black stipple.

Figure 3: Fossil occurrences and hypothesized geographic range for *Paranthropus boisei*. *P. boisei* sites represented by white pentagons, *P. robustus* by white star. Hypothesized ranges for *P. boisei* based on WORLDCLIM and PRISM3 data shown in dark grey shading and black hatching respectively.

Figure 4: schematic of species subdivisions.

Figure 1

Figure 2

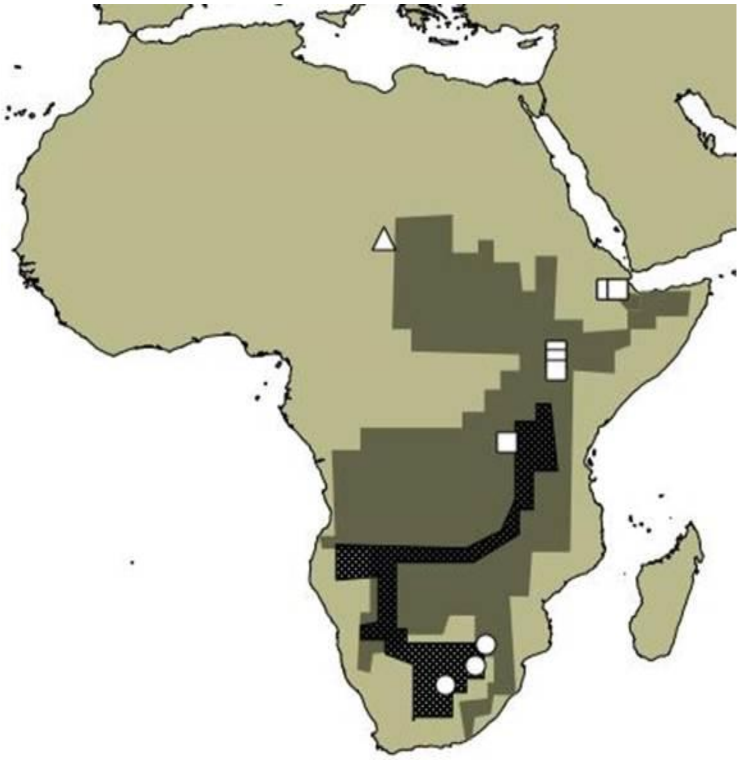


Figure 3

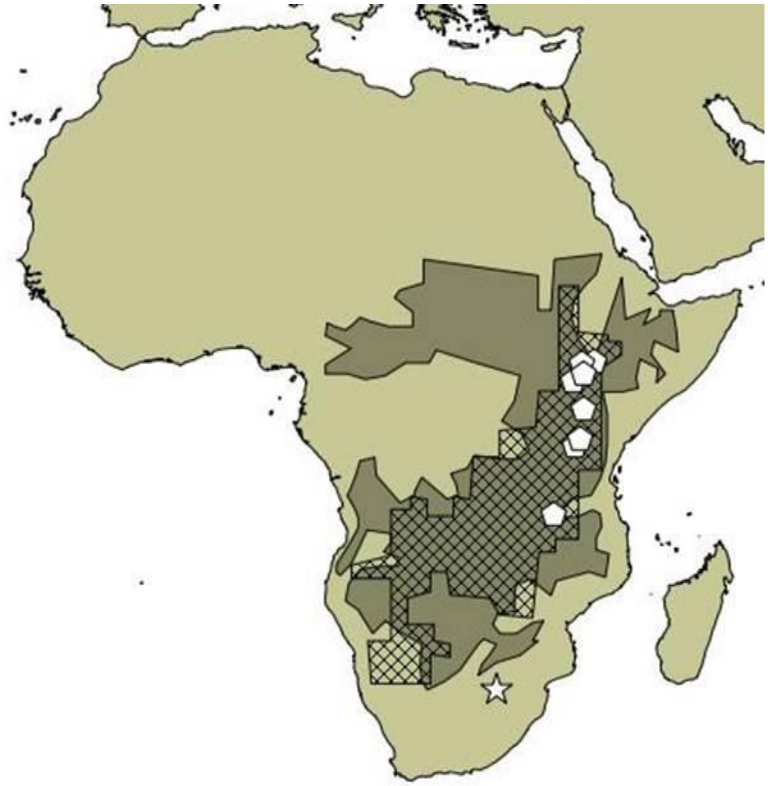
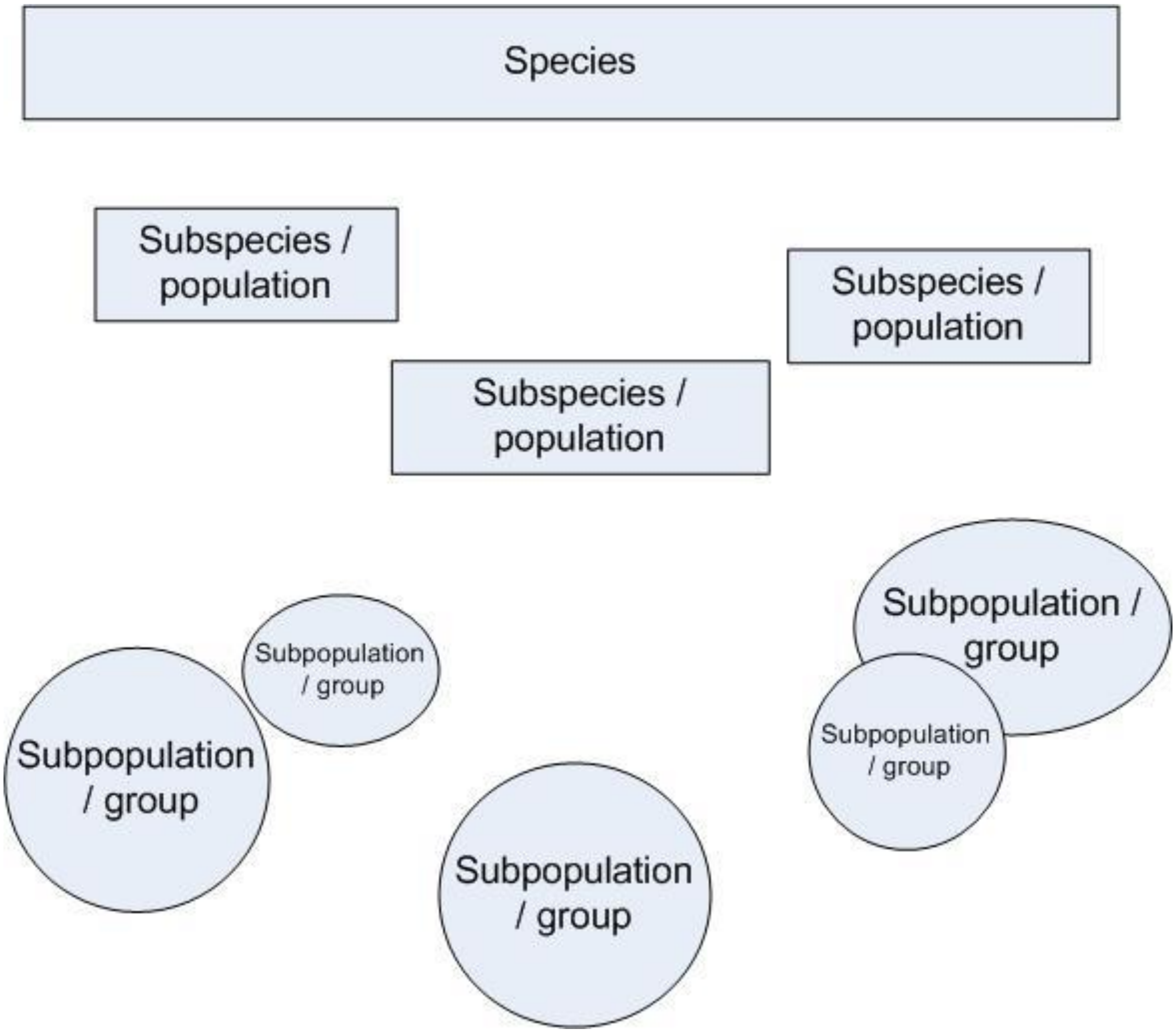


Figure 4


Species
Subspecies / population
Subspecies / population
Subspecies / population
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