Published in final edited form as:

Am J Phys Anthropol. 2014 December ; 155(4): 621–634. doi:10.1002/ajpa.22618.

Neutral Nuclear Variation in Baboons (genus *Papio*) Provides Insights into their Evolutionary and Demographic Histories

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Abstract

Baboons (genus *Papio*) are distributed over most of sub-Saharan Africa and in the southern portion of the Arabian Peninsula. Six distinct morphotypes, with clearly defined geographic distributions, are recognized (the olive, chacma, yellow, Guinea, Kinda and hamadryas baboons). The evolutionary relationships among baboon forms have long been a controversial issue. Phylogenetic analyses based on mitochondrial DNA sequences revealed that the modern baboon morphotypes are mitochondrially paraphyletic or polyphyletic. The discordance between mitochondrial lineages and morphology is indicative of extensive introgressive hybridization between ancestral baboon populations. To gain insights into the evolutionary relationships among morphotypes and their demographic history, we performed an analysis of nuclear variation in baboons. We sequenced 13 non-coding, putatively neutral, nuclear regions and scored the presence/absence of 18 polymorphic transposable elements in a sample of 45 baboons belonging to five of the six recognized baboon forms. We found that the chacma baboon is the sister-taxon to all other baboons and the yellow baboon is the sister-taxon to an unresolved northern clade containing the olive, Guinea and hamadryas baboons. We estimated that the diversification of baboons occurred entirely in the Pleistocene, the earliest split dating ~1.5 million years ago, and that baboons have experienced relatively large and constant population sizes for most of their evolutionary history (~30,000 to 95,000 individuals).

Keywords

neutral variation; retrotransposon; species tree

The genus *Papio* (the baboons) is one of the most widespread and ecologically successful primate genera. Baboons are found across sub-Saharan Africa, only avoiding the tropical humid forests of Central Africa, and in the southern portion of the Arabian Peninsula. Historically, six distinct forms of baboons have been recognized based on morphology

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(Frost et al. 2003; Jolly 1993): the chacma baboon (*P. ursinus*) found in the Southern part of the African continent, the yellow baboon (*P. cynocephalus*) from Eastern Africa, the olive baboon (*P. anubis*) which distribution extends from western Kenya and south Ethiopia to Guinea and Southern Mali, the Guinea baboon (*P. papio*) which is limited to Senegal and western Guinea, the hamadryas baboon (*P. hamadryas*) which inhabits semi-desert habitats in Ethiopia, Eritrea and the Arabian peninsula and the Kinda baboon (*P. kindae*) from Zambia. Depending on the authors, these forms have been considered either sub-species of *Papio hamadryas* or separate species, but there is currently no consensus on the taxonomic status of the different baboon morphotypes (Frost et al. 2003; Jolly 1993). Although these six forms are morphologically and geographically distinct, they do hybridize in nature showing little reproductive isolation (Alberts and Altmann 2001; Bergman et al. 2008; Jolly 1993; Jolly et al. 2011; Tung et al. 2008). Mitochondrial analyses suggest that baboons diversified during the last 2 million years and that their differentiation could have been driven by glacial and inter-glacial cycles during the late Pliocene and Pleistocene (Newman et al. 2004; Zinner et al. 2009). Because the geography and time scale of the diversification of baboons mirrors the diversification of the genus *Homo*, it has been proposed that baboons constitute a useful model to understand the evolution of the human lineage over the last 2 million years (Jolly 2001). In addition, the past and current hybridization between baboon morphotypes could help elucidate the genetic exchanges that have occurred between ancestral human populations and Neandertals (Green et al. 2010; Prufer et al. 2014; Sankararaman et al. 2014; Sankararaman et al. 2012) or Denisovans (Reich et al. 2010). Finally, the transition from savanna-dwelling baboons to the multi-level social structure of the hamadryas baboon constitute a useful model to understand the evolution of hominin social behavior (Swedell and Plummer 2012).

The evolutionary relationships between the different baboon forms have long been a subject of controversy. Based on morphological similarity it has been proposed that the olive and chacma baboons are sister taxa (Ellerman et al. 1953; Kingdon 1997). Other authors have suggested that Guinea and hamadryas baboons are sister-taxa due to their phenotypic and behavioral similarity and that the yellow baboon branches with the chacma and olive baboons (Hill 1967). Based on socio-ecological arguments, it was proposed that the hamadryas baboon is sister to all other baboons (Buettner-Janusch 1966; Thorington and Groves 1970) whereas biochemical analyses suggested that it was the Guinea baboon that was the sister to all other forms (Williams-Blangero et al. 1990). More recently, a north/south model was proposed (Jolly 1993) with the yellow and chacma baboons as sister taxa and a northern monophyletic group composed of the olive, hamadryas and Guinea baboons.

In the past decade, several groups have attempted to resolve the evolutionary relationships among baboons using mitochondrial DNA sequences (Newman et al. 2004; Sithaldeen et al. 2009; Wildman et al. 2004; Zinner et al. 2009; Zinner et al. 2013). All these studies support the existence of two clades (figure 1): a southern clade consisting of the chacma baboon, Kinda baboon and yellow baboons from Zambia, Malawi and southern Tanzania and a northern clade consisting of the hamadryas baboon, Guinea baboon, olive baboon and yellow baboons from Kenya and northern Tanzania. Depending on the study, the split between the northern and southern mitochondrial lineages occurred between 1.79 and 2.09

million years (my) ago. Within the northern clade, there is a clear break dated around 1.34 – 1.89 my between western baboons (Guinea baboon and olive baboons from Nigeria, Cameroon and Ivory Coast) and eastern baboons (hamadryas, olive baboons from Kenya, Eritrea and Ethiopia, and yellow baboons from Kenya and Tanzania). In the southern clade (which might be paraphyletic based on complete mitochondrial genome analyses; (Zinner et al. 2013)), there is a distinct south/north split around 1.80 my between south chacma (South Africa and coastal Namibia) and a group composed of Kinda, northern chacma (Zimbabwe, south Zambia, Mozambique and eastern Namibia) and southern yellow baboons.

The different clades and sub-clades recovered by analysis of the mitochondrial genome have clearly defined geographic distributions, possibly reflecting ancient fragmentation and speciation events in the late Pliocene and Pleistocene (Zinner et al. 2011; Zinner et al. 2009). However, the discordance between mitochondrial lineages and the distribution of morphotypes suggests that introgressive hybridization has occurred frequently (Keller et al. 2010; Newman et al. 2004; Wildman et al. 2004; Zinner et al. 2011; Zinner et al. 2009). For instance, southern and northern yellow baboons carry two highly divergent mitochondrial lineages while western and eastern olive baboons carry mitochondrion that diverged approximately 1.4 to 1.9 my (Zinner et al. 2011; Zinner et al. 2009). In contrast, northern yellow, eastern olive and hamadryas baboons share a 0.6 my old mitochondrial lineage, although they have maintained their morphological distinctiveness (Zinner et al. 2011; Zinner et al. 2009). This pattern is best explained by extensive and asymmetric gene flow. The proposed model, called “nuclear swamping”, posits that hybridization followed by repeated asymmetric backcrossing between hybrid females and males of one of the parental morphotypes will result in individuals with the mitochondrion of one form and the nuclear genome of another form. For instance, when olive baboons expanded their distribution into Ethiopian hamadryas territory (Wildman et al. 2004), hybrid females mated preferentially with olive males while the hybrid males had a lower reproductive success (Phillips-Conroy and Jolly 2004; Wildman et al. 2004). Subsequent and numerous generations of backcrossing resulted in baboons that are morphologically olive-like, but carry a hamadryas mitochondrion.

The extensive discordance between mitochondrial lineages and morphology indicates that the evolution of baboons has been extremely complex and that mitochondrial analyses are of limited use to resolve the evolutionary relationships among baboons as well as the origin of the modern morphotypes. To decipher the evolutionary relationships among baboons we decided to perform an analysis using neutral nuclear polymorphisms. We analyzed 12 non-coding autosomal segments, one X-linked region and 18 polymorphic transposable element insertions in a sample of 45 baboons representing 5 of the 6 recognized morphotypes.

MATERIALS AND METHODS

Samples

DNA samples were obtained from the Southwest National Primate Research Center (SNPRC) in San Antonio, Texas, for the olive baboon (*P. anubis*), hamadryas baboon (*P. hamadryas*), yellow baboon (*P. cynocephalus*), and Guinea baboon (*P. papio*) (table 1). As the exact geographic origin was not available for most of the individuals provided by

SNPRC, we sequenced the “Brown” region of the mitochondrial DNA to determine the region of origin of our samples (figure 1). It has been shown that mitochondrial sequences can be used to determine the origin of baboons because mitochondrial clades have a well-defined geographic distribution (Zinner et al. 2011; Zinner et al. 2009). We used the primers and methods described in Zinner et al. (2009) and we phylogenetically compared our sequences to previously published datasets. We determined that our samples of hamadryas baboons group with all *P. hamadryas* previously sequenced, in the “North-East olive – hamadryas” clade defined by Zinner et al. (2009) and that our Guinea baboons branch with all other Guinea baboons sequenced so far. The olive and yellow baboons branch in the composite “east olive – north yellow” clade which is found in Kenya and western Tanzania. In this region of Africa, mitochondrial sequences do not allow unambiguous identification of the morphotypes because of past hybridization between olive and yellow baboons. Yet, this analysis suggests that the olive and yellow baboons used in our study come from eastern Africa (Kenya or Tanzania). The origins of our samples as identified by mitochondrial DNA sequencing is consistent with the determination of Newman et al. (2004) who also used baboons from the SNPRC. Tissue samples of chacma baboons (*P. ursinus*) from the Cape region of South Africa were obtained from Dr. Larissa Swedell. As expected, the mitochondrial genome of these individuals belong to the “South chacma” clade (Zinner et al. 2009).

Molecular analyses

We amplified by PCR and sequenced 12 autosomal, non-coding regions of the baboon genome, for a total of ~6,300bp. These 12 fragments overlap with regions that have previously been sequenced in human (Chen and Li 2001; Yu et al. 2002), chimpanzee (Yu et al. 2003) and gorilla (Yu et al. 2004) thus allowing for comparisons among species. To ensure that these segments have been evolving neutrally, they were specifically chosen to avoid coding regions or close linkage to coding regions (Chen and Li 2001; Yu et al. 2002). We also sequenced three non-overlapping segments (~1,200bp) of the X chromosome located in the non-coding Xq13.3 region and previously analyzed in humans (Kaessmann et al. 1999). Due to their genomic proximity, these three segments were concatenated in a single fragment. All loci were amplified by PCR and the amplicons were directly sequenced in both directions by the high throughput genomics unit at the University of Washington, Seattle. The chromosomal location and the primers used for PCR amplification are provided on table 2. The sequences have been deposited in Genbank under accession numbers KJ683066-KJ683722.

We also used polymorphic transposable element insertions as genetic markers. Primate genomes are dominated by two categories of transposable elements, *LINE-1* (or *LI*) and *Alu*, which have been shown to be important sources of polymorphisms for population genetics (Batzler et al. 1994; Boissinot et al. 2000; Witherspoon et al. 2006) and phylogenetic analyses (Ray et al. 2005; Shedlock and Okada 2000; Xing et al. 2005). *LI* is a retrotransposon (i.e. a transposable element that use an RNA intermediate during replication) that lacks long terminal repeats and encodes the biochemical machinery necessary for its own replication and is thus called autonomous. Meanwhile, *Alu* transposition is mediated by *LI* and is non-autonomous. In general, *LI* evolves as a single

lineage in mammals so that a single group of closely related elements, referred to as a family, is active at a time. In this model of *LI* evolution, a family emerges and becomes replicatively dominant until it becomes extinct and is replaced by a more recently evolved family (Khan et al. 2006). Thus only the most recently evolved *LI* family is active in a modern genome and is the main source of novel polymorphic insertions (Boissinot et al. 2000). We used this unusual mode of *LI* evolution to guide our characterization of polymorphic *LI* insertions in baboons. The first step was to identify the *LI* family that is currently active in baboons. To this end we collected a large number of *LI* insertions from the macaque and baboon draft genomes (versions RheMac3 and papAnu2 available at <http://genome.ucsc.edu>). These insertions were aligned using CLUSTAL-W (Larkin et al. 2007) in BioEdit (Hall 1999) and a neighbor joining phylogeny of the elements was constructed using MEGA5.0 (Tamura et al. 2011) (figure 2). The most recent elements form species-specific clusters with small branch lengths, indicative of their young age. After identifying putatively baboon-specific *LI* elements, we aimed to verify that these elements had been inserted into the baboon genome after the separation between baboon and macaque. We performed a BLAT search (Kent 2002) of the macaque draft genome using the flanking sequences of the baboon *LI* and, as expected, the corresponding locations in the macaque genome did not contain *LI* insertions (as the elements inserted after the split between the two species). We then examined our alignments by eye to identify characters in the *LI* sequences that would be diagnostic of the active family in baboons. We found a mutation at the 3' end of the *LI* sequence that is absent from all *LI* in the macaque genome and is thus baboon-specific (figure 2). We then performed a BLAST (Altschul et al. 1990) search of the baboon draft genome using a 20-mer motif containing the diagnostic mutation. We selected 20 short insertions for further analyses, because short insertions are easier to screen in populations by PCR and are more likely to be selectively neutral (Boissinot et al. 2006). Although *Alu* elements can also be classified in families, their short length (~300bp) makes the identification of species-specific families difficult. To rapidly identify polymorphic *Alu* insertions we performed a BLAT search of the baboon draft genome using an *Alu* element that has been shown to be polymorphic in baboons (Szmulewicz et al. 1999) and selected 15 *Alu* loci for experimental validation. For both *Alu* and *LI* insertions, we designed primers in the flanking sequences and we determined the presence/absence status of each insertion in our baboon sample (table 3).

Data analyses

Following sequencing of the nuclear loci, chromatograms were imported into Geneious Pro version 5.6.5 created by Biomatters (available at <http://www.geneious.com>). For each sample, the forward and reverse reads were assembled into contigs. Putative heterozygote sites were assessed based on quality score. The contigs were then aligned to each other using the MUSCLE alignment implemented in Geneious (Edgar 2004). When necessary, the alignments were further edited by eye. The gametic phase of each nuclear haplotype was resolved computationally using the program PHASE 2.1 implemented in the DnaSP program, with a 90% cut off (Librado and Rozas 2009; Stephens et al. 2001). We constructed haplotype networks for each locus using the median joining method (Bandelt et al. 1999) with the program Network 4.6 (available at <http://www.fluxus-engineering.com>). We computed standard measurements of sequence diversity for each locus using DnaSP

version 5 (Librado and Rozas 2009) including the number of haplotypes (h), the number of segregating sites (S), nucleotide diversity (π), and Waterson's estimator of diversity (θ). Genetic differentiation between taxa was assessed for each locus using F_{st} and D_{xy} , calculated using DnaSP version 5. The nuclear sequences were tested for neutrality by calculating Tajima's D (Tajima 1989) in DnaSP, as well as with the Hudson-Kreitman-Aguade test (HKA test; Hudson et al. 1987). The HKA test is based on the assumption that, under neutrality, polymorphism and divergence should be the same across the genome and compares the ratio of polymorphism to divergence between a locus of interest and genomic regions that are known to be neutral. If the difference between the two ratios is significant using a goodness-of-fit test, we can reject the hypothesis of neutrality. We tested all loci for each morphotype using the multi-locus HKA implemented in J. Hey's HKA software (<http://genfaculty.rutgers.edu/hey/software#HKA>).

To delimit populations, the phased nuclear haplotypes and transposable element insertion polymorphisms were analyzed using the Bayesian clustering program STRUCTURE 2.3.3. (Pritchard et al. 2000). STRUCTURE estimates the likelihood of a user-set number of K clusters and provides estimates of the proportion of each individual's genome derived from each of the K clusters. The admixture model with independent allele frequency was used. STRUCTURE analyses were run with 100,000 steps for burn-in followed by 500,000 generations for K values ranging from 1 to 8. Each simulation was completed five times and results files were compressed and submitted to Structure Harvester (Earl and Vonholdt 2011) which selects the most likely K value based on the delta- K criterion described by Evanno (Evanno et al. 2005).

We reconstructed the evolutionary relationships among baboons using several approaches. First, we used the overall genetic distance between currently-recognized forms to infer their evolutionary affinities. To this end, we computed the average pairwise genetic distance between baboon forms with the Jukes and Cantor correction in MEGA 5.0 (Tamura et al. 2011) and we used the resulting matrix to build a neighbor joining tree. Second, the differences in allelic frequencies among forms was estimated by calculating pair wise F_{ST} for the entire dataset (sequences and insertion polymorphisms) in Arlequin v3.5 (Excoffier and Lischer 2010). The resulting F_{ST} matrix was used to build a neighbor joining tree in MEGA 5.0 (Tamura et al. 2011). Finally, we built a baboon species tree using *BEAST (Heled and Drummond 2010) with the autosomal sequences. This program uses multiple loci and multiple individuals per taxon to infer a species tree that takes into account stochastic differences in the coalescent histories of the sampled gene genealogies. The DNA substitution model used was TN93 (Tamura and Nei 1993). We used the rhesus macaque (*Macaca mulatta*) as an outgroup to root the species tree. The analysis was performed with a Yule prior, which assumes a constant birth rate of lineages. The *BEAST analysis was run for 500,000,000 generations, sampling every 50,000 generations for a total of 10,000 trees. To assess convergence, we monitored the effective sample size (ESS) values and consistency of parameter estimates using Tracer v1.5 (Rambaut et al. 2013). From the 10,000 sampled genealogies we obtained the maximum-clade credibility tree using TreeAnnotator in BEAST v1.8 (Drummond et al. 2012), discarding the first 1,000 trees as burn-in.

In order to estimate key demographic parameters in the history of baboons, including population sizes (θ), population divergence times (τ), and migration rates (m), we used the MCMC sampling algorithm implemented in the General Phylogenetic Coalescent Sampler (G-PHoCS) (Gronau et al. 2011). G-PHoCS accepts multiple unlinked neutral loci and can integrate over all possible phases of diploid genotype data, thus removing the need for computational or experimental haplotype inference. For this analysis, we used the 12 autosomal loci. To account for the phylogenetic uncertainty in the grouping of the olive, hamadryas and Guinea baboons (see results), we performed the analysis using two alternative topologies (((olive, hamadryas) Guinea) yellow) chacma) and (((olive, Guinea) hamadryas) yellow) chacma). We set the priors for the alpha and beta parameters of the gamma distribution as $\sim G(2, 2000)$. We ran five replicate analyses with random seeds for 400,000 generations and sampled every 50 generations, confirming the convergence across separate runs with Tracer v1.5 (Rambaut et al. 2013). G-PHoCS parameters are given as relative values and thus absolute values are obtained through a calibration step as outlined in Gronau et al. (2011) and demonstrated in (Freedman et al. 2014). We assumed a generation time of 8 years (Charpentier et al. 2012). Using human as outgroup and assuming a divergence time between human and baboon at ~ 30 Ma (Chatterjee et al. 2009; Finstermeier et al. 2013; Perelman et al. 2011; Pozzi et al. 2014; Steiper and Young 2006; Wilkinson et al. 2011), a mutation rate of $7.6 \cdot 10^{-10}$ substitutions / site / year was estimated for the autosomal nuclear loci. This mutation rate is substantially lower than the average estimated for Old World primates (Liu et al. 2003) but is consistent with the lower mutation rate previously reported in the baboon lineage (Elango et al. 2009).

RESULTS

We identified 86 single nucleotide polymorphisms (SNPs) and 4 insertion/deletion polymorphisms in ~ 7.5 Kb sequenced in 45 baboons. A STRUCTURE analysis determined that the most likely number of populations in our sample is 5, based on the delta-K criterion (figure 3). The five clusters identified by STRUCTURE correspond perfectly to the morphotype identification provided by the SNPRC and confirmed by analysis of the mitochondrial DNA (figure 1).

Genetic variation and differentiation based on nuclear sequences

The amount of genetic variation differs considerably among baboons (table 4). The total number of SNPs in the yellow baboon (45 SNPs; ~ 6 SNPs/Kb) is more than 5 times larger than in the Guinea and chacma baboons (8 and 7 SNPs, respectively, corresponding to ~ 1 SNP/Kb), the olive and hamadryas baboons showing intermediate number of SNPs (~ 4 SNPs/Kb). Similarly the average number of haplotypes per locus is 3 times higher in the yellow baboon (~ 4.2 haplotype/locus) than in the Guinea and chacma baboons (~ 1.5 haplotype/locus) and .5 times higher than in the hamadryas and olive baboons (~ 2.8 haplotype/locus). The average nucleotide diversity π is also much higher in the yellow baboon (0.185; based on the 12 autosomal loci) than in the Guinea (0.023) and chacma baboons (0.042), the olive and hamadryas baboons exhibiting intermediate values (0.140 and 0.131, respectively). Clearly, all measures of variation indicate that the yellow baboon is the most genetically diverse and that the Guinea and chacma baboons are the least diverse.

Multi-locus HKA analyses computed for each morphotype failed to identify a single locus deviating from neutral expectations. Values of Tajima's D calculated for each locus are all consistent with neutrality, with a single exception (locus T2568 in the chacma baboon). At this locus, two haplotypes differing by three mutations are found at near equal frequency in the chacma, which could be interpreted as evidence for balancing selection. However, other tests of neutrality (such as Fu and Li's F and D; data not shown) suggest that variation at this locus is consistent with neutrality. In addition, we verified using a BLAT search of the baboon and human genome (at <http://genome.ucsc.edu>) that the T2568 locus is not closely linked to a gene under balancing selection. In fact, the nearest gene (*PTPRT*) is located ~200Kb from T2568, which is too far to affect variation at T2568 by linkage. It is very likely that this locus can be considered neutral and that the significant deviation from neutrality detected by Tajima's D results from the stochasticity of the coalescent process. Thus, we are reasonably confident that the collection of loci we analyzed can be considered neutral and should reflect accurately the demographic history of the baboon forms.

Haplotype networks (figure 4) reveal that most of the haplotypes are shared between at least two morphotypes. At four loci (T1506, T2560, T1469 and T2064), some haplotypes are shared among all five taxa. There are however differences in the amount of haplotype sharing. For instance, the yellow and olive baboons share 30 haplotypes while the chacma and Guinea baboons have only 4 haplotypes in common. There are only five cases where one of the forms does not share any haplotype with any other forms. Three of these cases concern the chacma baboon (at loci T2609, T2085 and T2986) and two cases concern the Guinea baboon (T2609 and Xchr). This is consistent with the fact that only 7 polymorphisms (6 SNPs and 1 indel) out of 90 are fixed in one of the morphotypes. Despite extensive allele sharing the amount of genetic differentiation can be quite high due to important differences in allele frequency. Levels of genetic differentiation measured by F_{st} are highly variable among loci (data not shown), ranging from 0 (no differentiation) to 1 (no allele in common). The level of differentiation among baboons calculated across all autosomal loci is quite high, ranging from 0.277 to 0.889 (table 5). The highest F_{st} values are found between the chacma baboon and all the other morphotypes suggesting this taxon might be the most divergent. On average, higher F_{st} values are found at the X-linked locus, which is expected considering the smaller effective population size of the X relative to autosomes. Genetic differentiations measured by D_{xy} are also highly variable across loci, ranging from 0 to 1.09%. D_{xy} among forms calculated across all autosomal loci ranges from 0.126 to 0.331% (table 5). Again, the highest values were between the chacma baboons and the other forms.

Genetic variation based on transposable element insertions

Out of the 20 *LI* insertions tested by PCR, 12 were polymorphic in baboons (table 3). This indicates that *LI* is actively amplifying in the baboon genome and constitutes a significant source of polymorphisms in this genus. This validates the approach we used to identify an active, baboon-specific *LI* family. Not surprisingly, we found that the *Alu* element, which relies on *LI* activity for its own mobility, is also active in baboons as 6 of the 15 insertions tested were polymorphic. The frequency of *LI* and *Alu* insertions is highly variable among taxa, ranging from 0 (the element is absent from the population) to 1.0 (the element is fixed

in one of the populations) (table 3). Out of 18 loci, only two were detected as polymorphic in the chacma baboon, the other 16 being absent from this form. In general, the highest insertion frequencies were observed in the olive baboon, which is not surprising as the elements were identified in the published genome, which is of olive ancestry. The level of genetic differentiation estimated by F_{st} was also highly variable among loci, ranging from 0 to 1.0 (data not shown). The level of differentiation among morphotypes and across all loci is high, ranging from 0.371 to 0.840 (table 6), and very close to values calculated with the sequence data (table 5). The highest F_{st} values were found between the chacma baboon and the olive, hamadryas and Guinea baboons. On average, the F_{st} values between the olive baboons and the other baboons were ~25 to 50% higher than for sequence data, which could be due to a bias in our collection as all insertions come from the published genome, which is of olive origin.

Phylogenetic relationships among baboons

The neighbor joining trees based on average divergence and on F_{st} have identical topology (figure 5) and suggest that the chacma baboon is the sister taxon to all other baboons and that the yellow baboon is the sister taxon to the olive, hamadryas and Guinea baboons. On those trees the Guinea and olive baboons appear more closely related to each other than to the hamadryas baboon. The species tree analysis (figure 6) produced a robust topology (with posterior support ranging from 46 to 100%), extremely similar to the trees on figure 5. The only difference is that the olive baboon is closer to the hamadryas baboon than to the Guinea baboon, although this node has the lowest posterior support (46%).

Demography and divergence time of baboons

The estimates of modern and ancestral effective population sizes (θ), population divergence times (τ) and migration rates (m) obtained with G-PHoCS, are shown in table 7. The two analyses were performed with alternative topologies, one with the olive and Guinea baboons as sister-taxa and one with the hamadryas and olive baboons as sister-taxa, and produced similar results. The root of the tree, which correspond to the split between the chacma baboon and the other morphotypes was estimated to be 1.3 - 1.5 my (~0.5 – 2.5 my 95% HPD). The second split, between the yellow baboon and the olive-Guinea-hamadryas clade, is dated around 0.9 - 1.2 my (~0.4 – 1.6 my). The split between the olive, Guinea and hamadryas has occurred in the last 0.5 my and could be as recent as 0.19 my. The θ estimates for ancestral effective population size (N_e) indicate that, for most of their history, baboons have experienced relatively large effective population sizes, between 37,000 and 73,000 individuals. The modern effective population size of the olive baboon is in the same range as ancestral populations (~40,000 individuals) while the hamadryas baboon has a slightly smaller effective population size (~31,000). Consistent with a high level of variation, the yellow baboon has the largest estimated effective population size, which could be as high as 94,000. In contrast, the Guinea and chacma baboons have apparently experienced a drastic reduction in effective population size relative to ancestral populations, with estimates of ~11,000 and ~7,000 respectively. The amount of gene flow among morphotypes is highly variable and seems the highest between the olive and the yellow baboons. Patterns of gene flow between morphotypes suggest that migration is asymmetric

and occurs predominantly from the olive baboon to adjacent forms (Guinea, hamadryas and yellow baboons).

DISCUSSION

The present analysis of neutral nuclear variation in baboons showed that (1) the amount of genetic variation differs considerably among baboon forms; (2) baboons have experienced relatively large and constant effective population sizes for most of their evolutionary history, with the exception of the chacma and Guinea baboons which both have reduced population size; (3) the chacma baboon is the sister-taxon to all other baboons and the yellow baboon is the sister-taxon to an unresolved clade containing the olive, Guinea and hamadryas baboons; (4) the diversification of baboons occurred entirely in the Pleistocene. This analysis constitutes a significant contribution to our understanding of baboon evolution, yet it is important to remain cautious in interpreting these results because of the nature of the samples used here. First, our sample is not representative of the entire diversity of baboons as several populations have not been sampled, such as Kinda baboons and northern chacma, southern yellow or western olive populations. Clearly, a larger sample, based on wild individuals, will be necessary to obtain a more complete picture of baboon genetic diversity and evolution. Second, most of our samples are from captive origin, which can potentially lead to an underestimate of genetic variation and, consequently, of effective population size. This is however unlikely to be the case, as the mitochondrial diversity recovered in our samples is similar to the one reported in other studies based on wild samples. Our sample of Guinea baboon contains 3 mitochondrial haplotypes representative of the diversity found in nature (Zinner et al. 2009), and our sample of hamadryas includes representatives of three main mitochondrial lineages reported before in this taxon (Wildman et al. 2004; Zinner et al. 2009). Similarly, the mitochondrial diversity of our yellow and olive baboons is representative of the diversity of the East African “east olive / north yellow” clade identified by (Zinner et al. 2009). In addition, the effective population sizes we estimated are relatively large, both for modern forms (yellow, hamadryas and olive baboons) and for ancestral populations. If anything, a larger sample would inflate these estimates but would not drastically affect our conclusions. The situation of the chacma baboon is more problematic as natural populations of chacma harbor a remarkable diversity of mitochondrial lineages, which dates back 1.22 my (Sithaldeen et al. 2009). Our sample, limited to two populations in the Cape region of South Africa and nearly monomorphic for mitochondrial sequences, is clearly not representative of the diversity of chacma baboons. Additional samples from other parts of the chacma range will be necessary to infer the effective population size and demographic history of the chacma baboon.

Three of the modern morphotypes (the hamadryas, olive and yellow baboons) exhibit relatively large effective population size, ranging from 31,000 in hamadryas to 80,000-95,000 in yellow baboon. Not surprisingly, the Guinea baboon, which has the smallest geographic range of all baboons studied here, has a significantly smaller effective population size than other baboons (between 10,000 and 12,000). Our estimates of past demographic parameters suggest that, for most of their history, baboons have experienced similarly large effective population sizes, from ~37,000 to ~73,000 individuals. Thus, it does not seem that the fragmentation of savannah habitats, caused by Pleistocene climatic

fluctuations, had a significant impact on baboon effective population sizes. The demographic history of the yellow baboon had previously been investigated using a microsatellite dataset in a sample of ~100 individuals from a contiguous area in East Africa (Storz et al. 2002). Using a Bayesian hierarchical model Storz et al. (2002) determined that the yellow baboon had experienced a pronounced and progressive population decline over the past 1,000 to 250,000 years. They estimated that the yellow baboon population contracted by about 8-fold from an ancestral population size ranging from 5,000-60,000 to a current size between 200 and 10,000 individual. The ancestral population size for yellow baboon calculated by Storz et al. (2002) is consistent with our estimate. However, our data did not provide evidence for a recent contraction in population size of the yellow baboon. This is likely due to the nature of the molecular markers we used. The low level of sequence variation at nuclear loci combined with the relatively small number of individuals and loci studied here is not expected to recapitulate demography (particularly recent demographic changes) with the same resolution as a dataset based on hyper-variable microsatellite loci.

All the analyses we performed indicate that the chacma baboon is the sister taxon to all other forms and that the yellow baboon is sister to an unresolved clade containing the olive, hamadryas and Guinea baboons. This topology is consistent with the north/south model of Jolly (Jolly 1993) with the difference that yellow baboon is sister to the northern clade (olive, Guinea and hamadryas) and not to chacma. It is however possible that ancient gene flow between olive and yellow baboons in the northern part of the range could have distorted the phylogenetic reconstruction. Thus, the evolutionary position of the yellow baboon will need to be confirmed with additional samples, particularly from the southern part of the range. The topology retrieved using nuclear data is largely consistent with the scenario proposed by Zinner et al. (Zinner et al. 2011; Zinner et al. 2009) based on mitochondrial data to explain the differentiation of baboon morphotypes. Briefly, these authors propose that baboons migrated from their South-African center of origin following a north-east route and became isolated. This first event of migration corresponds to the deepest split in our tree, between chacma baboons and the ancestor of all other forms. Baboons migrated further north through a savannah corridor in eastern Africa and then west, across the entire continent. Eventually, the northern populations became isolated from eastern populations, possibly because of an eastward extension of tropical forests during a humid inter-glacial period. This vicariant event accounts for the second oldest split, between the yellow baboon and the olive-hamadryas-Guinea clade. This northern clade could have evolved into the three modern morphotypes, but the diversity of mitochondrial lineages in West Africa suggests that additional populations existed at some point and were absorbed into the olive baboon gene pool (Zinner et al. 2009).

Our analysis suggests that baboon evolution occurred entirely during the Pleistocene, with the root of the baboon tree dating ~1.5 my (0.5 – 2.5 my 95% HPD) and the divergence of morphotypes belonging to the Northern clade being less than 0.5 my old (0.1 – 0.9 my 95% HPD). Climatic instability in sub-Saharan Africa during the Pleistocene was characterized by a succession of cold and dry phases alternating with hot and humid phases (deMenocal 2004; Hamilton and Taylor 1991; Hewitt 2000; Turner 1999). The closing of savannah corridors during humid periods provides a possible mechanism for the evolution of baboon morphotypes by vicariance, while the opening of these corridors during dry periods would

have facilitated baboon's expansion and hybridization between ancestral populations. Our estimates of baboon divergence times are substantially younger than those obtained by authors who relied solely on mitochondrial data (Newman et al. 2004; Sithaldeen et al. 2009; Wildman et al. 2004; Zinner et al. 2009; Zinner et al. 2013). There is however no real contradictions between these different estimates as divergences between mitochondrial lineages are expected to pre-date population divergences.

Several authors have proposed that baboons constitute a useful model for the study of human evolution (Elton 2006; Jolly 2001; Jolly 2009; Swedell and Plummer 2012). Our results suggest that, indeed, baboons and humans have much in common evolutionarily. First, the Pleistocene time frame of baboon evolution coincides remarkably well with the diversification of the genus *Homo* (reviewed in Carrion et al. 2011). Second, hybridization between divergent populations has significantly affected the evolution of both humans and baboons. Recent genomic analyses have revealed that human populations hybridized with Neanderthals and Denisovans following the "out-of-Africa" migration and that the genetic signature of these past hybridizations has been retained in the genetic make up of European and Asian populations (Green et al. 2010; Meyer et al. 2012; Prufer et al. 2014; Reich et al. 2010; Sankararaman et al. 2014; Sankararaman et al. 2012). Ancient hybridizations have had a significant adaptive impact as genes involved in pathogen defense (Mendez et al. 2012; Mendez et al. 2013) and adaptation to high elevation (Huerta-Sanchez et al. 2014) were transferred to the human gene pool by hybridization. It is thus important to understand the evolutionary processes facilitating, or preventing, hybridization between genetically differentiated primate taxa. Baboons constitute an excellent comparative model to address this question as the divergence between baboon morphotypes, which also have a complex history of hybridization, closely matches the divergence between modern humans, Neanderthals and Denisovans. Genome-wide analyses indicate that Neanderthals and Denisovans diverged from the modern human lineage 550,000 to 765,000 my ago (Meyer et al. 2012; Prufer et al. 2014), a time that coincides roughly with the diversification of the yellow, hamadryas, olive and Guinea baboons (which ranges from 1.0 to 0.2 my). The main differences between humans and baboons reside in their effective population sizes. The majority of studies in humans concur in suggesting that the effective population size of modern humans is ~10,000 (Gronau et al. 2011; Yu et al. 2001) while our study indicates that baboons have a 3 to 9 time larger effective population size. However, the reduction in effective population size observed in modern human populations is recent (~100 to 120,000 years) and it is very likely that older human populations had a larger effective population size (Li and Durbin 2011), similar to the one experienced by baboons and ancestral hominoids (Burgess and Yang 2008). In conclusion, our analysis validates the use of baboons as a useful model for human evolution, particularly at a time when the role of hybridization in human evolution has come under intense scrutiny.

Acknowledgments

We thank Larissa Swedell and Esme Beamish for providing the tissue samples of chacma baboon. We also thank the Associate Editor of the American Journal of Physical Anthropology and two anonymous reviewers for their comments on an earlier version of the manuscript. This research was supported by the National Science Foundation Undergraduate Research mentoring program at Queens College (award 0731613 to S.B.)

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Figure 1.

Phylogeny of mitochondrial sequences. We used a representative subset of the sequences used by Zinner et al. (2009) and we named the clades following the nomenclature proposed by these authors. The samples used in the present study are indicated with colored circles. The tree was built using the maximum likelihood method implemented in MEGA 5.0 (Tamura et al. 2011) using the HKY+G model of substitution. The tree was rooted using sequences from *Theropithecus gelada*. Numbers at the nodes indicate the robustness of each node assessed using 1,000 bootstrap replicates. Only bootstrap values >80% are shown.

Figure 2.

A- Structure of a full-length L1 element which contains a 5' untranslated region (5' UTR) that acts as internal promoter, two open-reading frames (ORF1 and ORF2), a 3'UTR and a poly-A tail at the 3' end. B- Neighbor-joining phylogeny of baboon and macaque L1 elements and partial alignment of the 3' extremity of L1, showing the site diagnostic of the baboon-specific L1 family (indicated by the black arrow).

Figure 3. Visualization of the Bayesian clustering analysis from the program STRUCTURE (Pritchard et al. 2000), with the most likely number of genetic clusters $K = 5$.

Figure 4.

Haplotype networks constructed with the median-joining method implemented in Network 4.6.

Figure 5. Neighbor-joining trees built using the average sequence divergence between forms (A) and the level of differentiation estimated by F_{st} (B).

Figure 6.

Species tree depicting the branching order of baboon forms. Shown is the maximum clade credibility from a *BEAST analysis using 12 autosomal loci. The numbers at the nodes correspond to the Bayesian posterior probability values.

Table 1

Samples used in this study.

Species	ID	Source ^a	Mitochondrial lineage ^b
<i>Papio anubis</i>	12835	SNPRC	East olive - North yellow
<i>Papio anubis</i>	1×1032	SNPRC	East olive - North yellow
<i>Papio anubis</i>	1×2176	SNPRC	East olive - North yellow
<i>Papio anubis</i>	1×2684	SNPRC	East olive - North yellow
<i>Papio anubis</i>	1×2509	SNPRC	East olive - North yellow
<i>Papio anubis</i>	1×1956	SNPRC	East olive - North yellow
<i>Papio anubis</i>	1×2498	SNPRC	East olive - North yellow
<i>Papio anubis</i>	1×2644	SNPRC	East olive - North yellow
<i>Papio cynocephalus</i>	1×1734	SNPRC	East olive - North yellow
<i>Papio cynocephalus</i>	1×2117	SNPRC	East olive - North yellow
<i>Papio cynocephalus</i>	9089	SNPRC	East olive - North yellow
<i>Papio cynocephalus</i>	1×0102	SNPRC	East olive - North yellow
<i>Papio cynocephalus</i>	1×2049	SNPRC	East olive - North yellow
<i>Papio cynocephalus</i>	1×2304	SNPRC	East olive - North yellow
<i>Papio cynocephalus</i>	1×3321	SNPRC	East olive - North yellow
<i>Papio cynocephalus</i>	1×1487	SNPRC	East olive - North yellow
<i>Papio cynocephalus</i>	1×2892	SNPRC	East olive - North yellow
<i>Papio cynocephalus</i>	1×3548	SNPRC	East olive - North yellow
<i>Papio hamadryas</i>	11440	SNPRC	Hamadryas - North-east olive
<i>Papio hamadryas</i>	11445	SNPRC	Hamadryas - North-east olive
<i>Papio hamadryas</i>	2×0209	SNPRC	Hamadryas - North-east olive
<i>Papio hamadryas</i>	13997	SNPRC	Hamadryas - North-east olive
<i>Papio hamadryas</i>	2×0331	SNPRC	Hamadryas - North-east olive
<i>Papio hamadryas</i>	12726	SNPRC	Hamadryas - North-east olive
<i>Papio hamadryas</i>	11442	SNPRC	Hamadryas - North-east olive
<i>Papio hamadryas</i>	17817	SNPRC	Hamadryas - North-east olive
<i>Papio hamadryas</i>	2×0121	SNPRC	Hamadryas - North-east olive
<i>Papio hamadryas</i>	9969	SNPRC	Hamadryas - North-east olive
<i>Papio papio</i>	7357	SNPRC	Guinea
<i>Papio papio</i>	12633	SNPRC	Guinea
<i>Papio papio</i>	12639	SNPRC	Guinea
<i>Papio papio</i>	5×0049	SNPRC	Guinea
<i>Papio papio</i>	5×0037	SNPRC	Guinea
<i>Papio papio</i>	5×0032	SNPRC	Guinea
<i>Papio papio</i>	9020	SNPRC	Guinea
<i>Papio ursinus</i>	C1	Wild	South chacma
<i>Papio ursinus</i>	C2	Wild	South chacma
<i>Papio ursinus</i>	C3	Wild	South chacma
<i>Papio ursinus</i>	C4	Wild	South chacma

Species	ID	Source ^a	Mitochondrial lineage ^b
<i>Papio ursinus</i>	C5	Wild	South chacma
<i>Papio ursinus</i>	C6	Wild	South chacma
<i>Papio ursinus</i>	C7	Wild	South chacma
<i>Papio ursinus</i>	C8	Wild	South chacma
<i>Papio ursinus</i>	C9	Wild	South chacma
<i>Papio ursinus</i>	C10	Wild	South chacma

^aSNPRC = Southwest National Primate Research Center

^bMitochondrial lineages as in Zinner et al. (2009)

Table 2

Genomic location and PCR primers for the nuclear fragment sequenced. The position of the fragments is based on the second draft of the baboon genome (papAnu2).

Locus name	Chromosome	Position	F primer	R primer
T2609	1	72989414-72989882	TGCCTTAACCTTCTGTGACA	ATGGAACTCAAGAGCAAGTA
T1412	9	105666326-105666993	GCAACAAGAAATTGTTGACTC	ACTACGAGTACACAAACCAAT
T866	18	53567576-53568160	AGGGACATTCCAAAAGAAATTC	CAGAA TCAAAATGCTTTCTGC
T2568	10	22342227-22342780	TTGAAAAGACACTTGGCACAA	TGCATCTCATGATGGTCTAT
T1506	18	48326152-48326650	CACTGGTCAGGCCTATGTGA	GAA TGGCTTCAAGCTGGATT
T2560	10	24150617-24151174	CCAAATACAAGCCTATTGACG	GCCAA TTCTGCAAAATGGTCT
T2085	10	55559014-55559461	GGGTAAAACACAGGGCTTGG	TCTGTGGTTTGGCTCATGGTC
T1469	2	93116496-93117023	GCTTCCTTGATGGGGAGCTA	ACACCAATTC TGGTGGGAGAG
T812	16	24552186-24552684	CACATTACCCACTGCCCTCT	TGAGCACCTCAGCAGACAAG
T2191	18	57445871-57446232	CAAAATACTTCATGGGACCACA	TTCCATTGCTTTTGGAGCAC
T2064	10	48402646-48403152	TGGCTACTTGGAAATGCCCTT	GCCTGAGCCCAAAATCAAGAG
T2986	16	62022617-62023214	TCAAATTAAAATCATGGAAGCAA	TTGAAGGACCATAATTGCAAAA
Xchr	X	69350978-69351395	AAGTTCAGCCTTACTGGATAGCA	ACTGCA TTGGCCAGAGAAT
Xchr	X	69354297-69354677	CCAA TGCAGATTTCATGCCGTA	GTCTGTGGGCTTGTCAATCCT
Xchr	X	69355798-69356224	GCACAA CGCTGAGCTAGTTG	TCACATCTCAACTCCCATTTT

Table 3

Genomic location, PCR primers and insertion frequency of polymorphic L1 and Alu insertions. The position of the loci is based on the second draft of the baboon genome at <http://genome.ucsc.edu> (papAnu2). Three elements could not be located in the draft available at the UCSC website. For these elements, we indicate their location on the Genbank entry from where they were identified.

Locus name	Chr	Position	F primer	R primer	Olive	Hamadryas	Guinea	Yellow	Chacma
L1-2	3	138491225-138492832	TAAAGGTCCATGACCAAGT	GGAATGTGCTATCCTAGAAT	0.89	0.06	0.00	0.70	0.00
L1-5	X	135688263-135690257	ATGCAAGGATGTCATTAAAC	TTAATGTTGCTGACAAAGGC	0.97	1.00	1.00	0.10	0.00
L1-8	3	AC099555.4 (77099-79273)	CAACAGCTTCCTGGTAATAT	TGCTGAGGCTGATCAAAAT	0.68	0.83	1.00	0.50	0.00
L1-10	11	35576759-35577757	AGTCCTCGGATGAGAGCTACA	TGAAGCATTATCTGCCACTTTT	0.36	0.00	0.00	0.15	0.00
L1-11	7	18047231-18047723	CTTCCCAAACTGGAAGCAT	CCAGATTGCTTTGGGTTCTC	0.97	0.50	1.00	0.55	0.28
L1-18	6	62190401-62191998	CTCCAGCCTAAGCCACAGAC	TGCAACTGATTCACTCCAC	0.87	0.33	1.00	0.15	0.00
L1-20	14	59736367-59737704	TGGTATTGGTAGTGCTGTCTGG	CCCCTGAGTCCTGTGAAATGT	0.66	0.00	0.14	0.00	0.90
L1-22	18	56378881-56379383	CCCCGGTGTGCTGTATTTA	CGCAGTTGCTGTTGAAAAGA	0.16	0.00	0.00	0.00	0.00
L1-25	3	149048051-149053338	ACGCCAGGCAACATACCTAC	TCAAAGGAGGGCTGAGAAA	0.87	0.28	0.36	0.35	0.00
L1-28	3	148828133-148828584	TTTTCCTGCATGGTCAAAA	TTGGATTGCTGTGGACAAG	0.45	0.72	0.00	0.15	0.00
L1-44	4	130504588-130505459	GTAATGGATGCCACTTCCAG	AAGTGAAAGTGGGGTTTGACA	0.09	0.00	0.07	0.10	0.00
L1-46	3	107011307-107011942	GGAGGAGGCTCTATTCTG	TCGGTGTGTTAGGGTGTGTTGT	0.75	0.00	0.07	0.10	0.00
Alu-4	3	AC091001.3 (107231-108539)	GGCGCAGACCAAGGAGATTTT	AGCTGAGTCAATGTCAGTTT	0.00	0.00	0.00	0.50	0.00
Alu-8	8	17873865-17874025	TCATGTCATTAGGATAAATGCTGG	CTCCTCTCCAAATATAAATAGCTC	0.55	0.39	0.00	0.05	0.00
Alu-10	3	44705840-44706597	CCCTGTGAGCTCATGTTCTT	TCTGAGGGTGCTATGGTTCC	0.71	0.28	0.35	0.50	0.00
Alu-11	3	44576389-44576922	GAGCAAAATGCCAAATTGAGGT	GCAGCATGTATTAAAGAGTTGAGTAGC	0.85	0.00	0.00	0.00	0.00
Alu-12	20	AC119422.47 (18145-18811)	TCACTGAGAAAGGAAGATGCTG	TGATGTCAGTGTGTGGAAAAGG	0.82	1.00	0.86	0.05	0.00
Alu-14	20	16990465-16990981	CCATTGGGTTTTCATCTTTGA	TTCACCAAGTGTCTTTAGGTT	0.03	0.00	0.00	0.00	0.00

Table 4

Summary statistics for nuclear loci.

		Olive	Hamadryas	Yellow	Guinea	Chacma
T2609 (470bp)	S	2	2	4	1	0
	h	3	3	5	2	1
	π	0.076	0.043	0.105	0.03	0
	Θ	0.129	0.121	0.242	0.067	0
	D	-1.038	-1.513	-1.638	-1.155	n/a
T1412 (668bp)	S	2	4	3	0	0
	h	3	5	4	1	1
	π	0.138	0.143	0.106	0	0
	Θ	0.09	0.169	0.127	0	0
	D	1.369	-0.435	-0.443	n/a	n/a
T866 (585bp)	S	3	1	7	0	0
	h	3	2	5	1	1
	π	0.128	0.017	0.148	0	0
	Θ	0.155	0.048	0.337	0	0
	D	-0.494	-1.164	-1.84	n/a	n/a
T2568 (554bp)	S	4	0	4	1	3
	h	4	2	5	2	2
	π	0.266	0	0.2	0.079	0.285
	Θ	0.218	0	0.204	0.057	0.153
	D	0.699	n/a	-0.057	0.87	2.316*
T1506 (499bp)	S	2	3	2	0	0
	h	3	3	4	1	1
	π	0.157	0.169	0.133	0	0
	Θ	0.123	0.175	0.113	0	0
	D	0.71	-0.092	0.414	n/a	n/a
T2560 (559bp)	S	2	1	4	1	0
	h	3	2	5	2	1
	π	0.177	0.034	0.144	0.026	0

	Olive	Hamadryas	Yellow	Guinea	Chacma	
T2085 (448bp)	Θ	0.108	0.05	0.202	0.056	0
	D	1.652	-0.592	-0.827	-1.155	n/a
	S	5	7	4	3	0
	h	4	3	6	3	1
	π	0.275	0.522	0.312	0.096	0
	Θ	0.351	0.44	0.26	0.211	0
T1469 (528bp)	D	-0.752	0.606	0.608	-1.671	n/a
	S	1	1	1	0	1
	h	2	2	2	1	2
	π	0.044	0.051	0.021	0	0.075
	Θ	0.057	0.053	0.055	0	0.053
	D	-0.448	-0.086	-1.165	n/a	0.723
T812 (499bp)	S	1	0	5	0	0
	h	3	1	8	1	1
	π	0.099	0	0.371	0	0
	Θ	0.121	0	0.291	0	0
	D	-0.472	n/a	0.862	n/a	n/a
	S	4	3	5	0	1
T2191 (376bp)	h	3	3	4	1	2
	π	0.206	0.372	0.561	0	0.056
	Θ	0.321	0.225	0.375	0	0.077
	D	-1.117	1.751	1.522	n/a	-0.529
	S	2	1	4	0	2
	h	3	2	3	1	3
T2064 (507bp)	π	0.071	0.02	0.115	0	0.094
	Θ	0.119	0.056	0.228	0	0.115
	D	-1.038	-1.164	-1.435	n/a	-0.438
	S	2	7	0	1	0
	h	2	4	1	2	1
	π	0.042	0.2	0	0.044	0
T2986 (598bp)	Θ	0.101	0.33	0	0.053	0

	Olive	Hamadryas	Yellow	Guinea	Chacma
D	-1.498	-1.29	n/a	-0.341	n/a
Xchr (1215bp)	S	0	3	2	1
	h	1	4	3	2
	π	0	0.051	0.033	0.035
	Θ	0	0.072	0.052	0.032
	D	n/a	-0.819	-0.959	0.334
					n/a

S = number of segregating sites; h = number of haplotypes; π = nucleotide diversity; Θ = Waterston's diversity; D = Tajima's D. Statistically significant deviations from neutrality are indicated with *.

Table 5

Genetic differentiation at autosomal nuclear sequence between baboon species measured by F_{st} (below diagonal) and D_{xy} (above diagonal).

	Olive	Hamadryas	Guinea	Yellow	Chacma
Olive		0.001919	0.001264	0.002051	0.003314
Hamadryas	0.3634		0.001559	0.001912	0.003125
Guinea	0.4047	0.4441		0.001651	0.002904
Yellow	0.3069	0.2772	0.3997		0.002645
Chacma	0.7537	0.7561	0.8893	0.6116	

Table 6

Genetic differentiation between baboon species measured by F_{ST} based on transposable element insertion polymorphisms (below diagonal) and on transposable elements and autosomal sequence data (above diagonal).

	Olive	Hamadryas	Guinea	Yellow	Chacma
Olive					
Hamadryas	0.5021		0.4396	0.3841	0.7642
Guinea	0.4960	0.3707		0.4693	0.7580
Yellow	0.5363	0.4634	0.5244	0.3734	0.8838
Chacma	0.7606	0.7269	0.8401	0.4820	0.5994

Table 7

Bayesian estimation of effective population size (θ), divergence time (τ , in million years) and number of migrants (m) assuming two phylogenetic scenarios. Numbers in parenthesis correspond to the lower and upper 95% highest posterior densities.

Parameter	(((A,G)H)Y)C	(((A,H)G)Y)C
θ_A	40,946 (10,280-76,891)	38,603 (12,747-67,434)
θ_G	11,888 (2,056-25,493)	10,570 (2,467-19,737)
θ_H	31,006 (10,280-53,454)	31,082 (12,336-53,454)
θ_Y	94,034 (46,052-146,792)	81,279 (37,829-128,289)
θ_C	7,130 (822-14,391)	6,703 (1,234-14,391)
$\theta_{AG \text{ or } AH}$	37,667 (2,056-83,882)	64,507 (7,401-129,934)
θ_{AGH}	61,941 (9,046-119,655)	73,150 (18,914-129,112)
θ_{AGHY}	66,250 (8,635-134,046)	61,632 (7,401-127,467)
θ_{AGHYC}	53,964 (4,934-99,918)	47,578 (3,289-93,339)
$\tau_{AG \text{ or } AH}$	0.192 (0.079-0.342)	0.187 (0.092-0.303)
τ_{AGH}	0.440 (0.132-0.855)	0.319 (0.118-0.553)
τ_{AGHY}	0.862 (0.382-1.408)	1.026 (0.408-1.618)
τ_{AGHYC}	1.321 (0.474-2.289)	1.514 (0.566-2.539)
$m_{A \rightarrow G}$	318 (0-1,590)	714 (0-2,451)
$m_{G \rightarrow A}$	36 (0-197)	95 (0-533)
$m_{A \rightarrow H}$	1,161 (0-3,117)	108 (0-741)
$m_{H \rightarrow A}$	125 (0-718)	75 (0-467)
$m_{A \rightarrow Y}$	2,283 (243-4,732)	3,152 (801-5,831)
$m_{Y \rightarrow A}$	1,119 (0-3,617)	557 (0-2,299)
$m_{Y \rightarrow C}$	636 (0-2,120)	735 (0-2,337)
$m_{C \rightarrow Y}$	18 (0-115)	16 (0-104)

A = anubis baboon; G = Guinea baboon; H = hamadryas baboon; Y = yellow baboon; C = chacma baboon.