

Distribution of Mitochondrial Clades and Morphotypes of Baboons *Papio* spp. (Primates: Cercopithecidae) in Eastern Africa

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Source: Journal of East African Natural History, 104(1-2) : 143-168

Published By: Nature Kenya/East African Natural History Society

URL: <https://doi.org/10.2982/028.104.0111>

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**DISTRIBUTION OF MITOCHONDRIAL CLADES AND
MORPHOTYPES OF BABOONS *PAPIO* SPP. (PRIMATES:
CERCOPITHECIDAE) IN EASTERN AFRICA**

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ABSTRACT

Recent genetic studies, using maternally inherited mitochondrial DNA, indicate a complex evolutionary history for baboons *Papio* spp. in general, and for eastern African baboons in particular. To further address this topic and to improve our understanding of phylogeographic patterns of baboons in eastern Africa, mitochondrial cytochrome *b* sequence data were analysed from 148 baboon samples from 103 locations in eastern Africa. The resultant phylogenetic reconstructions suggest an initial split of baboons into four main clades: southern chacma baboons, baboons from Mahale Mountains in Tanzania, main southern, and main northern. We confirm that the boundary between southern and northern clades lies along the Ugalla-Malagarasi River and Ruaha-Rufiji River of central Tanzania. We detected new mitochondrial haplogroups, most notably the Mahale Mountains clade, and refined haplogroup distributions. The evolutionary divergence of baboons in eastern Africa was most likely triggered and maintained by numerous episodes of population division and reconnection, probably related mainly to climate change. To better understand these processes, nuclear DNA information is required, especially to assess gene flow among populations.

Keywords: phylogeography, cytochrome *b*, Ruaha-Rufiji River, Ugalla-Malagarasi River

INTRODUCTION

Baboons (genus *Papio* Erxleben, 1777) are widely distributed over most of sub-Saharan Africa, occupying the greatest diversity of habitats of any genus of non-human primates. Baboons are found in all terrestrial habitats from moist forest to the edge of deserts, and from sea level to >3300 m (Swedell, 2011; Butynski *et al.*, 2013; Jolly, 2013). In the savannas and woodlands of eastern Africa, from northeast Sudan southward to Malawi and Zambia, baboons are, second to humans, the most abundant catarrhine species. Several taxa of *Papio* have been described for eastern Africa (Elliot, 1913; Napier & Napier, 1967; Hill, 1970). Their validity and taxonomic ranks are, however, still disputed (Jolly, 1993, 2013; Sarmiento, 1998; Groves, 2001; Grubb *et al.*, 2003; Butynski *et al.*, 2013). The main eastern African forms are olive baboon *Papio anubis* (Lesson, 1827) and yellow baboon *Papio cynocephalus* (Linnaeus, 1766) (figure 1; appendix 1).

Across the distribution of baboons in Africa, morphological clines (Frost *et al.*, 2003; De Jong & Butynski, 2009) and evidence of interspecific hybridization in contact zones (*P. kindae* x *P. ursinus griseipes*, e.g. Jolly *et al.*, 2011; *P. anubis* x *P. cynocephalus*, e.g. Charpentier *et al.*, 2012; *P. hamadryas* x *P. anubis*, e.g. Bergey, 2015) complicate this problem. Taxa are identified primarily by the colour, length, and texture of the pelage (including their mane), body size, body shape, and skull morphology (Hill, 1970; Kingdon, 1971, 2015; Jolly, 1993; Rowe, 1996; Alberts & Altmann, 2001; Groves, 2001; De Jong & Butynski, 2009, 2012; Butynski *et al.*, 2013) (see appendix 1 and visit <http://wildsolutions.nl/photomaps/Papio/> to view a large selection of photographs of *Papio* spp. with localities depicted on an interactive digital map). In eastern African baboon populations, comparisons of cranial and dental morphologies indicate that the morphotypes are distinct, but that intermediate forms do exist (Hayes *et al.*, 1990; Frost *et al.*, 2003; Jolly, 2003). Molecular studies, mainly applying mitochondrial (mt) markers, have not

solved this “taxonomic tangle” (Groves, 2001). Phylogenetic reconstructions, based on parts or even complete mt-genomes, reveal several mt-haplogroups or clades. These, however, are only marginally concordant with the morphological variation or taxa (Newman *et al.*, 2004; Zinner *et al.*, 2009a, 2011, 2013).

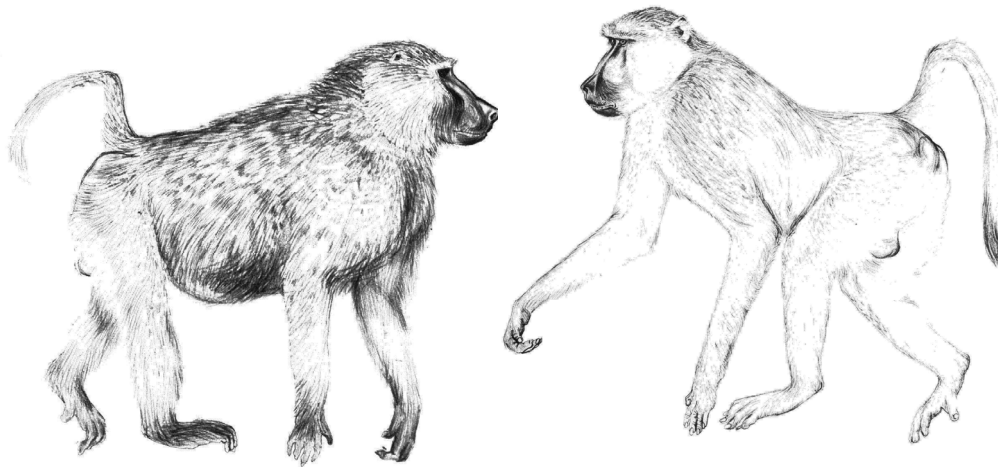


Figure 1. Adult male eastern Africa baboons; olive baboon *Papio anubis* (left) and yellow baboon *Papio cynocephalus*. Drawings by Jonathan Kingdon (Kingdon, 1971).

The deepest split in the phylogenetic tree of *Papio* divides the genus into two main mtDNA clades, a northern clade and a southern clade (Burrell, 2008; Zinner *et al.*, 2009a, 2013). The northern clade includes Guinea baboon *P. papio* (Desmarest, 1820) from West Africa, hamadryas baboon *P. hamadryas* (Linnaeus, 1758) from the Horn of Africa and southwest Arabia, *P. anubis* from central and northeast Africa, and *P. cynocephalus* from Somalia and southeast Kenya, as well as east and central Tanzania. The southern clade includes *P. cynocephalus* from south Tanzania to north Mozambique, as well as Kinda baboon *P. kindae* (Lönnberg, 1919) from Zambia, and chacma baboon *P. ursinus* (Kerr, 1792) from southern Africa. The two main mtDNA clades come into contact within the distribution of *P. cynocephalus* in central Tanzania, along a line following the Ruaha-Rufiji River from the coast inland westward to the eastern shore of Lake Tanganyika at the mouth of the Malagarasi River (5.25°S, 29.81°E; Zinner *et al.*, 2009a). No morphological differences have been reported among *P. cynocephalus* within this contact area. Hill (1970) reports only *P. cynocephalus cynocephalus* for Tanzania (figure 2). Others report *P. anubis* in northwest Tanzania (Groves, 2001; Anandam *et al.*, 2013; Butynski *et al.*, 2013) and *P. kindae* in central west Tanzania (Butynski & De Jong, 2009; De Jong & Butynski, 2012). Based on present knowledge, the Ibean baboon *P. cynocephalus ibeanus* Thomas, 1893 of Somalia and Kenya, and the Nyasa baboon *P. cynocephalus strepitus* Elliot, 1907 from Malawi (Hill, 1970), are distributed at least 500 km north and south, respectively, from where the two main mtDNA clades meet in central Tanzania.

Although the *Papio* mtDNA phylogeny has been recently intensively studied, only a few samples from eastern Africa have been analysed. In particular, central Tanzania, where the southern and northern clades meet, has not been sampled in detail. To fill this geographic

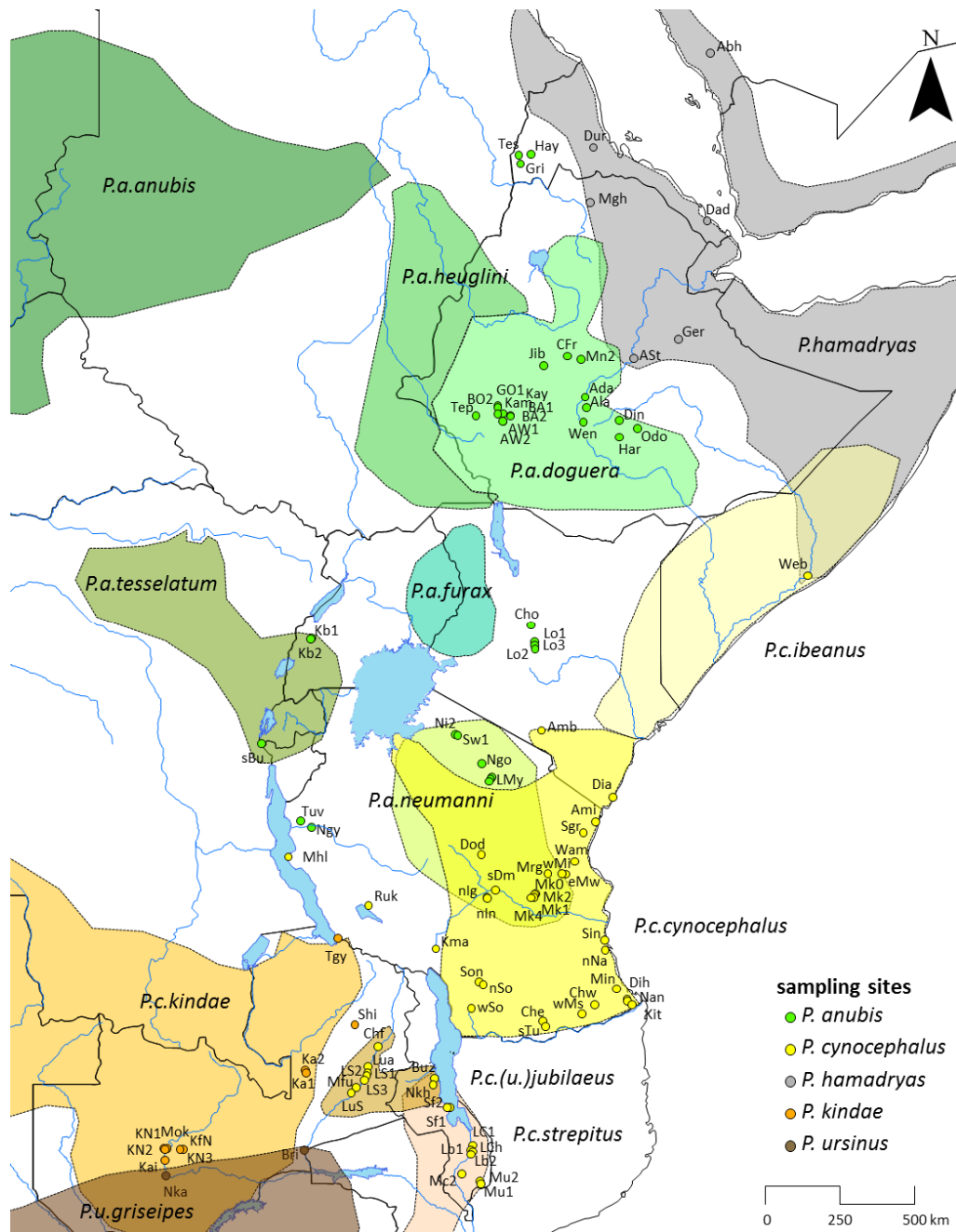


Figure 2. Distribution of *Papio* taxa in eastern Africa according to Hill (1970), and locations of sampling sites for this study. A photograph of an adult male baboon from each of 21 widely-spaced sites on this map is presented in appendix 1. More photographs of baboons in the wild from many sites across Africa can be viewed at: <http://wildsolutions.nl/photomaps/Papio/>

sampling gap, this study focused on *P. cynocephalus* in Tanzania, Malawi and Zambia, but also includes samples from *P. anubis* and *P. hamadryas* in Eritrea, Ethiopia, Kenya, Uganda, Democratic Republic of Congo (DRC), and northwest Tanzania. The aim of this study is to clarify the geographic distribution of *Papio* mtDNA clades in eastern Africa, and to relate and combine these clades with previous maps of *Papio* distributions (e.g. Hill, 1970) and photographs of *Papio* from the region (e.g. appendix 1).

MATERIAL AND METHODS

Sample Collection

We obtained 147 non-invasively collected baboon faecal samples from sites in eastern Africa (figure 2, appendix 2). To these we added one *P. hamadryas* tissue sample from southwest Saudi Arabia and one museum tissue sample from Somalia [see Zinner *et al.* (2008) and Kopp *et al.* (2014) for detailed information on these samples]. The samples originate from 104 locations (103 in eastern Africa and one from southwest Saudi Arabia). Of the 149 samples, 45 were used in previous studies, including the samples from Saudi Arabia and Somalia (Zinner *et al.*, 2008, 2009a; Kopp *et al.*, 2014). For those 45 samples we retrieved respective mtDNA sequence information from GenBank. We also included mtDNA sequence information for two southern chacma *P. ursinus ursinus*, two grey-footed chacma baboons *P. ursinus griseipes* Pocock, 1911, two *P. papio*, and, as outgroup, gelada *Theropithecus gelada* (Rüppell, 1835), from GenBank (accession numbers in appendix 2).

Faecal samples were collected and stored following the two-step protocol of Roeder *et al.* (2004) and Nsubuga *et al.* (2004). Samples were stored at ambient temperature for up to 6 months in the field and at -20°C upon arrival in the laboratory. For each sample, consecutive number, date, location, and GPS coordinates were recorded. Sample collection complied with the laws of the respective countries of origin and Germany, and with the guidelines of the International Primatological Society.

Laboratory Work

We extracted DNA from 104 faecal samples using the QIAamp DNA Stool Mini Kit (Qiagen, Hilden, Germany) and First DNA All Tissue Kit (Gen-Ial, Troisdorf, Germany) according to the manufacturers' protocols. DNA was eluted in 20 µl water (HPLC grade) and stored at -20°C until further processing. To avoid contamination, all working steps (*i.e.* DNA extraction, PCR set-up, PCR amplification, gel electrophoresis, gel extraction and sequencing) were performed in separate laboratories. All PCR reactions were performed with negative (HPLC-grade water) controls.

We amplified and sequenced the complete mitochondrial cytochrome *b* gene (cyt *b*, 1140 bp). This allowed us to include published data in the statistical analyses. In addition, this marker can be reliably amplified from low quality samples, such as faecal material and tissue samples from museum specimens. We used established protocols (Zinner *et al.*, 2009a) and amplified cyt *b* via two over-lapping fragments to ensure that sequences were obtained even if DNA was degraded. Zinner *et al.* (2009a) showed that the primers and PCR conditions applied here solely amplify mtDNA and not nuclear mitochondrial pseudogenes (numts). PCR reactions with a total volume of 30 µl included 1 U BiothermTaq 5000 DNA polymerase (Genecraft, Cologne, Germany), 1x reaction buffer, 0.16 mM dNTPs, and 0.33 µM of each primer. PCR conditions for amplification comprised a pre-denaturation step at 94°C for 2 min, followed by

40 cycles at 94°C for 1 min, 60°C for 1 min, 72°C for 1 min, and a final extension step at 72°C for 5 min. Results of the PCR amplifications were checked on 1% agarose gels. PCR products were cleaned with the Qiagen PCR Purification Kit and subsequently sequenced on an ABI 3130xL sequencer using the BigDye Terminator Cycle Sequencing Kit (Applied Biosystems, Foster City, USA) and both amplification primers.

Phylogenetic Reconstruction

Sequences were checked, edited, and aligned manually using BIOEDIT 7.5.0.2 (Hall, 1999). The final alignment comprised 156 sequences of which 149 derived from eastern African and Saudi Arabian baboons, two sequences each from *P. papio*, *P. u. ursinus*, and *P. u. griseipes*, and as outgroup, one sequence from *T. gelada*. All sequences were deposited in GenBank (details of samples and accession numbers are given in Table S1).

Phylogenetic trees were reconstructed with maximum-likelihood (ML) and Bayesian methods using RAxML 8 (Stamatakis, 2014) as implemented in raxmlGUI 1.5b.1 (Silvestro & Michalak, 2012) and MrBayes 3.2.6 (Ronquist *et al.*, 2012), respectively. ML calculations were run with the GTR-CAT-I model and 1,000 rapid bootstrapping replications. For Bayesian tree reconstructions, we conducted four Markov Chain Monte Carlo (MCMC) runs with a default temperature of 0.2 and the HKY+I+G model as selected as best-fit model in jModeltest 2.1.7 (Darriba *et al.*, 2012) under the Bayesian information criterion (BIC) and the Decision Theory Performance-based Selection (DT). All repetitions were run for 1 million generations with tree and parameter sampling setting in every 100 generations. The first 25% of samples were discarded as burn-in. The adequacy of the burn-in and convergence of all parameters was assessed via the uncorrected Potential Scale Reduction Factor (PSRF) (Gelman & Rubin, 1992) as calculated by MrBayes and by visual inspection of the trace of the parameters across generations using TRACER 1.6 (Rambaut *et al.*, 2014). To check whether posterior clade probabilities were also converging, AWTY (Nylander *et al.*, 2008) was applied. Posterior probabilities for each split and a phylogram with mean branch lengths were calculated from the posterior density of trees. Trees were visualized and edited in FigTree 1.4.2. Additionally, a haplotype network was built in POPART 1.7 (Leigh & Bryant, 2015) using the median-joining network algorithm (Bandelt *et al.*, 1999).

RESULTS

Among the 149 eastern African and Arabian baboon sequences, we detected 69 unique cyt *b* haplotypes. Phylogenetic analyses were conducted with these unique sequences, plus the additional six non-eastern African sequences and the outgroup sequence. The final alignment comprised 76 sequences. Phylogenetic trees derived from Bayesian inference and the ML algorithm yielded identical tree topologies and mostly well-supported terminal clades (ML bootstrap values: >75%, Bayesian posterior probabilities: >0.95) (figure 3). The analysis suggests that baboons initially divided into four clades [southern chacma, Mahale Mts (central west Tanzania), main southern, main northern], although the branching pattern among them remains largely unknown. The main southern clade contains Kinda, northern chacma, and southern yellow baboons, while the main northern clade comprises Guinea, hamadryas, eastern olive, and northern yellow baboons.

For eastern Africa, our reconstruction shows nine well-supported mt-clades or haplogroups. These indicate paraphyletic or polyphyletic relationships within at least the two main East African

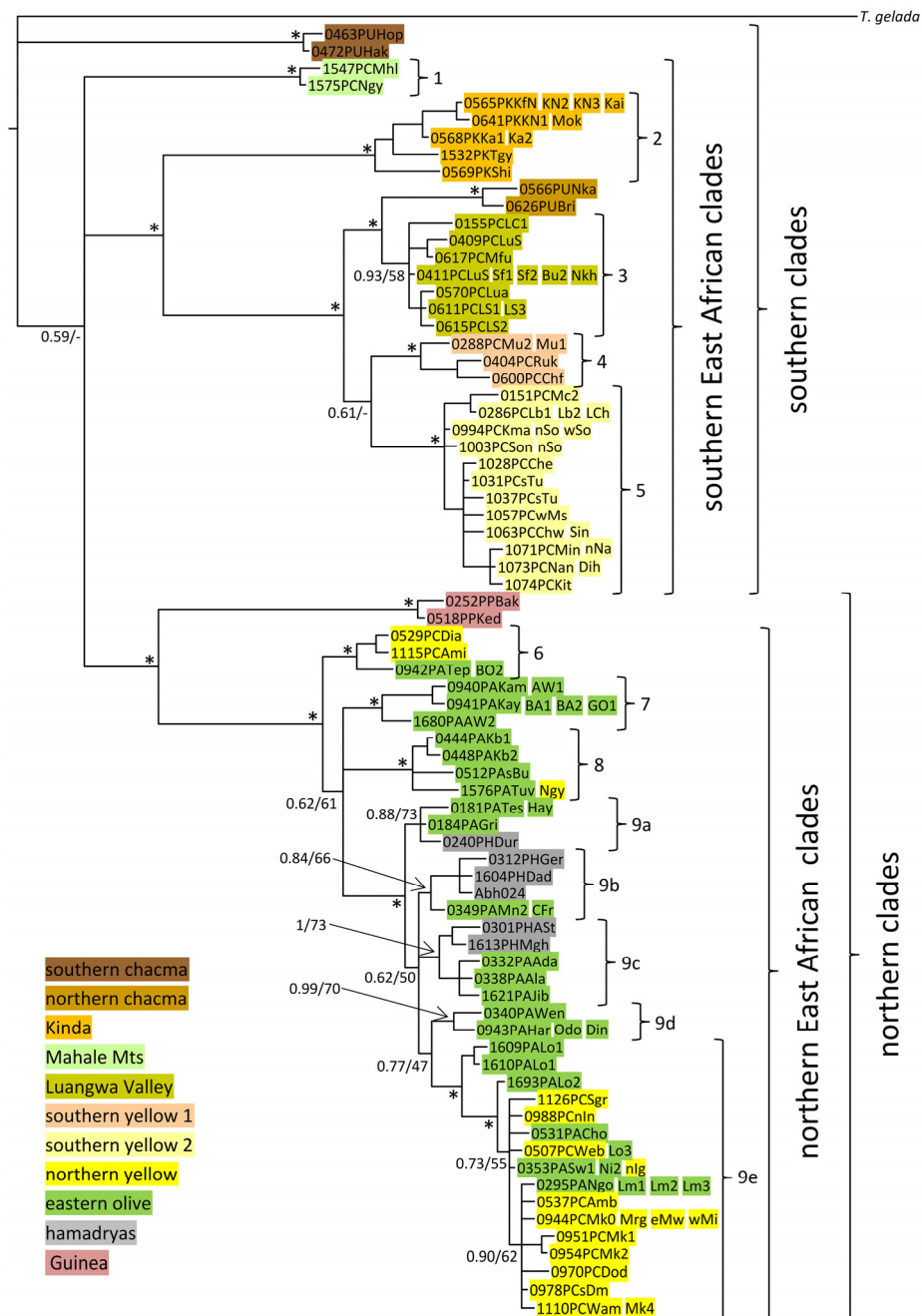


Figure 3. Bayesian phylogram of *Papio* cyt b haplotypes (Bayesian tree reconstruction for identification of clades) (* Bayesian posterior probabilities > 0.95, ML bootstrap support values > 75%). Tip labels refer to the species (as identified by phenotypic characters; PA = *P. anubis*; PC = *P. cynocephalus*; PH = *P. hamadryas*; PK = *P. kindae*; PP = *P. papio*; PU = *P. ursinus*) together with the sampling location. Several haplotypes were found at more than one site. This is indicated by the listing of more than one site abbreviation at some branch tips.

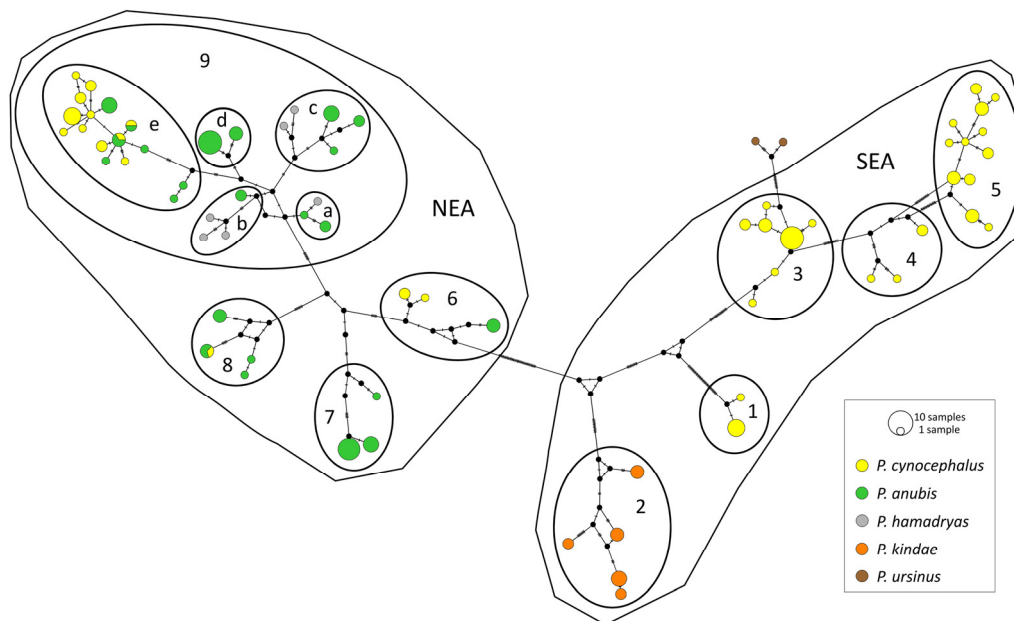


Figure 4. Median-joining mt-haplotype network of eastern African baboons (1–9 = haplogroups or clades of East African baboon as in figure 3; SEA = main southern East African clade; NEA = main northern East African clade). *Papio ursinus* are northern chacma baboons from Zambia. These appear to be *P. u. griseipes*.

baboon taxa (*P. cynocephalus* and *P. anubis*). The nine mt-clades (figures 3 & 4) are: (1) Mahale Mts baboons; (2) Kinda baboons; (3) Luangwa Valley (Zambia) and west Malawi baboons (with northern chacma baboons as a sister clade); (4) southern yellow baboons 1 from southwest Tanzania, north Zambia, and south Malawi; (5) southern yellow baboons 2 from southeast Tanzania and south Malawi east of the Shire River; (6) yellow baboons from northeast Tanzania and olive baboons from central Ethiopia; (7) olive baboons from central Ethiopia; (8) olive baboons from Uganda, east DRC and west Tanzania, and one yellow baboon from the Ugalla region; and (9) hamadryas baboons from Saudi Arabia, Eritrea, and Ethiopia, and eastern and northern clades of olive baboons and yellow baboons from Eritrea, Ethiopia, Somalia, Kenya, and north Tanzania. Clades 2–5 represent the main southern East African clade, while clades 6–9 represent the main northern East African clade. Within clade 9, distinctions can be made among possible clades 9a to 9e. Hamadryas baboons cluster with olive baboons from Eritrea (9a) and Ethiopia (9b and 9c). Olive baboons from east of the Ethiopian Rift Valley form another clade (9d). Northern yellow baboons from Somalia, Kenya and north Tanzania cluster with olive baboons from Kenya and north Tanzania (9e).

The nine mt-clades are also visible within the haplotype network (figure 4), and the subdivision within clade 9 becomes even more obvious than in the tree reconstruction. Among the northern East African clades, olive baboon haplotypes appear in every clade—usually in combination with yellow baboon or hamadryas baboon haplotypes. Interestingly, hamadryas and yellow baboons do not share the same clade or subclade.

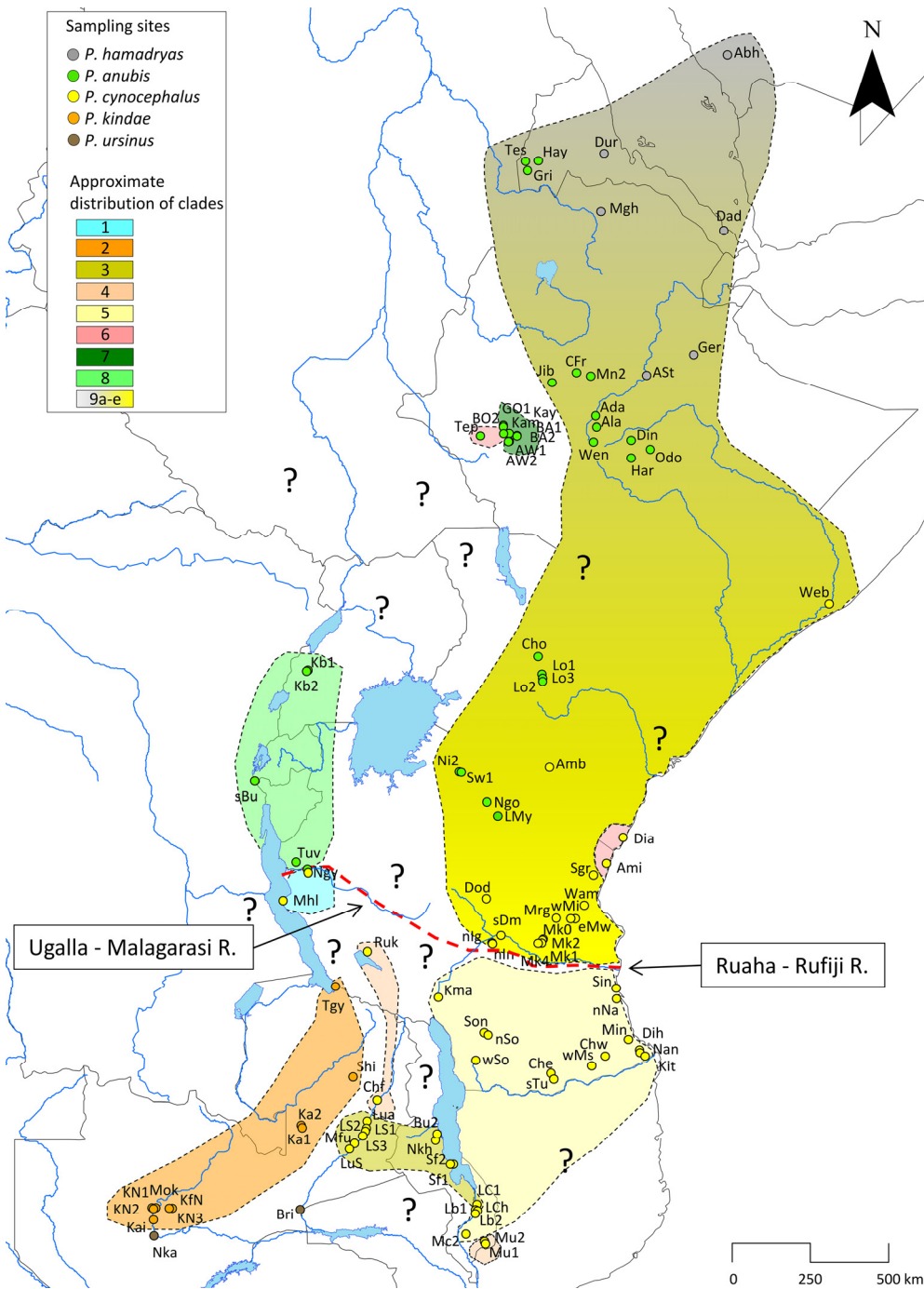


Figure 5. Approximate distribution of the nine *Papio* mt-haplogroups or clades within eastern Africa and sampling sites. Broken red line depicts the approximate position of the boundary between the distributions of northern East African and southern East African mt-clades. “?” indicates an important geographic sampling gap (see Discussion).

Identical mt-haplotypes were mainly found in samples collected at the same locality (same social group or neighbouring groups), but identical sequences were found at different sites and in different taxa. Median distance between sites with identical sequences was 63 km (quartiles 39–121; $n=49$ sites with distance >10 km). Largest distances among sites (figures 2 & 5) with identical haplotypes were between Webi Shebelli River, south Somalia (Web, yellow baboon) and Lolldaiga Hills Ranch, central Kenya (Lo3, olive baboon; *ca.* 950 km), and between Serengeti National Park, north Tanzania (Ni2, olive baboon) and Dodoma-Iringa, central Tanzania (nIg, yellow baboon; *ca.* 550 km).

DISCUSSION

The general topology of our phylogenetic tree for *Papio* in eastern Africa is similar to those found in earlier studies (Zinner *et al.*, 2009a, 2011, 2013; Liedigk *et al.*, 2014).

There are unresolved relationships between the two main East African clades, and with the southern chacma and Mahale Mts clades (figures 3 & 4). The major split separates southern and northern clades. This is the first study to reveal the Mahale Mts clade (as no samples from Mahale Mts were included in previous studies).

We confirm the previously assumed boundary between the distributions of southern and northern clades in Tanzania (figure 5; Zinner *et al.*, 2011). This boundary runs from the lower Rufiji River in the east across central Tanzania to the mouth of the Malagarasi River at Lake Tanganyika in the west. These two large rivers are biogeographic barriers, or at least boundaries, for a number of genera, species, and subspecies of terrestrial mammals (Kingdon, 1971–1982, 2015; Kingdon *et al.*, 2013; Butynski & De Jong, *in press*). As concerns primates:

- The Ugalla-Malagarasi River appears to be a barrier between *P. anubis* (north) and *P. cynocephalus* (south) (Kano, 1971).
- The Ruaha-Rufiji River represents the south limit for colobus monkeys (subfamily Colobinae) in coastal eastern Africa (Rodgers, 1981; Butynski *et al.*, 2013; Butynski & De Jong, *in press*).
- The Ruaha-Rufiji River seems to be the south limit in coastal Tanzania for the Zanzibar dwarf galago *Galagoides zanzibaricus* (Matschie, 1893) (Butynski *et al.*, 2006, 2013; De Jong, 2012; Butynski & De Jong, *in press*).
- The Ruaha-Rufiji River appears to be the north limit for the Mozambique dwarf galago *Galagoides granti* (Thomas & Wroughton, 1907) (Butynski *et al.*, 2006, 2013; De Jong, 2012; Butynski & De Jong, *in press*).

Our phylogenetic reconstruction and the haplotype network reveal nine reasonably well-supported mt-haplogroups or clades within eastern African baboons. Tree topology and statistical support values suggest five clades for southern East African baboons: Mahale Mts, Kinda, Luangwa Valley, and two southern yellow clades. Luangwa Valley baboons form the sister group of northern chacmas, whereas southern chacmas are either basal among baboons or represent the first split in the southern baboon clade (Zinner *et al.*, 2009a, 2013). For the main northern East African clade, the situation looks different. Here we found only three well-supported haplogroups, but a diverse clade consisting of hamadryas, eastern olive, and northern yellow baboons stretching from Eritrea and southwest Saudi Arabia south to the Ruaha-Rufiji River in central Tanzania (clade 9). Within the distribution of clade 9, identical

haplotypes occur at sites that are almost 1,000 km apart and in different baboon species (*e.g.* yellow and olive baboons [this study], and olive and hamadryas baboons [Hapke *et al.*, 2001]). In general, the distribution pattern of baboon haplotypes appears to be in a geographic cline—irrespective of their taxonomic relationships.

Mapping the approximate distributions of the mt-haplogroups reveals some disjunct distributions. Among southern East African baboons, clade 4 was found in southeast Tanzania and northeast Zambia, but also east of the Shire River in south Malawi. Between these two distributions, there are haplotypes belonging to clade 3 (Luangwa Valley baboons). Among northern East African baboons, haplotypes of clade 6 occur in yellow baboons at the south Kenyan and north Tanzanian coast, and in olive baboons in west Ethiopia. A possible explanation for such disjunct distributions is that they are relicts of a former wider distribution; the respective haplotypes are now extinct, having been replaced by haplotypes of other clades or haplogroups in parts of the former distribution. Alternatively, the disjunct pattern is a result of incomplete geographic sampling. Increasing the number of samples from areas in between the two distributions might resolve this question.

As in previous studies, the mt-clades only partly match with recognized baboon taxa, most obvious in the case of southern and northern yellow baboons. Their mt-genomes diverged around 2 million years ago (Zinner *et al.*, 2013), though no taxonomic differentiation was reported among yellow baboons from northeast and southeast Tanzania; both are regarded as *P. c. cynocephalus*. Several of the clades, however, occur in areas where Hill (1970) identified different morphotypes or subspecies of baboons, *e.g.* Luangwa Valley baboon *P. c. (u.) jubilaeus* Schwarz, 1928 and central olive baboon *P. a. tessellatum* Elliot, 1909 (figure 2, appendix 1). Whether *P. c. strepitus* Elliot, 1907 is at least partly equivalent with our clade 4 needs further investigation. MtDNA information is often used to delimit species within taxonomic groups (*e.g.* barcoding; Blaxter, 2004; Galimberti *et al.*, 2015; Raupach *et al.*, 2016). This study, however, indicates that (at least) the two main East African baboon taxa are paraphyletic or polyphyletic groups. As such, mtDNA information alone cannot delimit species within *Papio* in East Africa.

The geographic pattern of mt-haplogroup distributions suggests a complicated biogeographic history for baboons. Like other savanna-living mammals (Lorenzen *et al.*, 2012), baboons were impacted by multiple cycles of expansion and retreat of savanna biomes during Pleistocene glacial and inter-glacial periods, and other climatic changes (Maslin *et al.*, 2015; Trauth *et al.*, 2015). Recurrent fragmentation and reconnection of populations, extinctions, and distribution shifts of demes likely led to multiple phases of isolation, hybridization, and introgression among populations (Zinner *et al.*, 2009a, 2011).

The geographic distribution pattern of mt-haplogroups can provide insights into the biogeographic history of taxa (Avise, 2000, 2004). We found better supported clades, and geographically more confined clades, among southern East African baboons than among northern East African baboons. This suggests that southern East African baboons were affected more by ecological change, leading to longer periods of isolation (thereby hampering movement among demes and/or dispersal into new areas), than northern East African baboons. Northern East African baboons, on-the-other-hand, seem to have experienced more introgression due to more frequent reconnection of populations. Here the possible introgression of olive baboons into hamadryas and yellow baboons might be of particular interest (see Zinner *et al.*, 2011 for a more detailed scenario). There is some evidence that ancient introgression occurred even beyond the species level, as found in kipunji *Rungwecebus kipunji* (Ehardt, Butynski, Jones & Davenport, 2005) (Jones *et al.*, 2005).

Individuals from the Mt Rungwe population carry mitochondrial DNA-sequences that are highly similar to those in south Tanzanian yellow baboons (Zinner *et al.*, 2009b), whereas the Udzungwa Mts population seems not to be affected by baboon introgression (Roberts *et al.*, 2010).

It also might be that at least part of the difference between southern East African and northern East African populations is the result of incomplete geographic sampling. It is, therefore, important to collect more samples in under-sampled areas: (1) central and west Kenya, eastern and central Uganda, south South Sudan into Ethiopia; (2) Somalia, north coast of Kenya; (3) west Uganda, east DRC; (4) southwest Tanzania; (5) north Mozambique, east of Lake Malawi, and (6) Mahale Mts, Ugalla, east DRC west of Lake Tanganyika. The latter is of particular interest since the Mahale Mts baboons share morphological traits with Kinda baboons. Here are two scenarios for this similarity: (1) Kinda baboons once occurred east of Lake Tanganyika as far north as Mahale Mts; (2) during times of extreme lake level lowstands a land bridge connected the east and west shores of Lake Tanganyika (Scholz & Rosendahl, 1988; Lezzar *et al.*, 1996; Cohen *et al.*, 1997; Nevado *et al.*, 2013) that enabled Kinda baboons from the west side to come into contact with yellow baboons from the east side—and the possibility of gene flow.

CONCLUSIONS

This study provides further insights into the evolutionary history of eastern African baboons and confirms the Ugalla-Malagarasi River and Ruaha-Rufiji River as the boundary between the main southern East African and main northern East African baboon clades. Subclades are obvious in both of these main clades. Interestingly, the distribution of the subclades seems to be more geographically structured in southern East African baboons, while a more clinal pattern is evident in northern East African baboons. A possible explanation is that southern East African baboons were historically affected more by population division due to changing ecological conditions, while northern East African baboons were affected more by frequent reconnection and gene flow among populations.

Although we obtained new information and insights on the phylogeographic pattern of baboons in eastern Africa, there are several topics that remain to be addressed. For instance, the disjunct distribution of several subclades could be a relict of a former wide distribution, but the possibility that the distribution pattern of subclades is due to incomplete geographic sampling cannot be ruled out. Likewise, it remains unknown (1) how Mahale Mts baboons are related to Kinda baboons on the west shore of Lake Tanganyika; (2) which yellow baboon haplotypes occur around Lake Malawi, particularly in Mozambique, and (3) how baboons in central and west central Ethiopia are related to baboons in Uganda and DRC. To address these topics, additional sampling is required. Further, since gene flow and hybridization among baboon populations most likely occurred repeatedly, nuclear DNA information, ideally nuclear genome data, are required to better reconstruct the evolutionary history and phylogeography of *Papio*. In combination with baboon genomics, spatial and ecological modelling of historic and current distributions of *Papio* taxa and clades will provide insights into habitat preferences (niches) and adaptations.

ACKNOWLEDGMENTS

We thank the national administrations of countries in which samples were collected. We are particular grateful to the University of Dodoma, TAWIRI, and COSTECH in Tanzania (Research Permit issued 24th September 2008, 2008-272-NA-2008-64), and ZAWA in Zambia (Research Permit issued 13th July 2007, Export Certificate 212007007240). We are grateful to the many colleagues and field assistants who helped collect the samples, to Lorna Depew and two anonymous reviewers for their comments on the manuscript, and to Hakan Pohlstrand, Chris Roche, Katerina Guschanski, Ian Salisbury, Dean Gaffigan, Celesta von Chamier, Daniel Cara, Colleen Begg, Anna Weyher, Jim Auburn, and Mike Haworth for the use of their photographs in appendix 1. Jonathan Kingdon kindly allowed the reproduction of his drawings of *Papio anubis* and *Papio cynocephalus* in figure 1. This paper is dedicated to Jonathan Kingdon on the event of his 80th birthday and in gratitude for all that he has accomplished on behalf of the conservation of East Africa's mammals.

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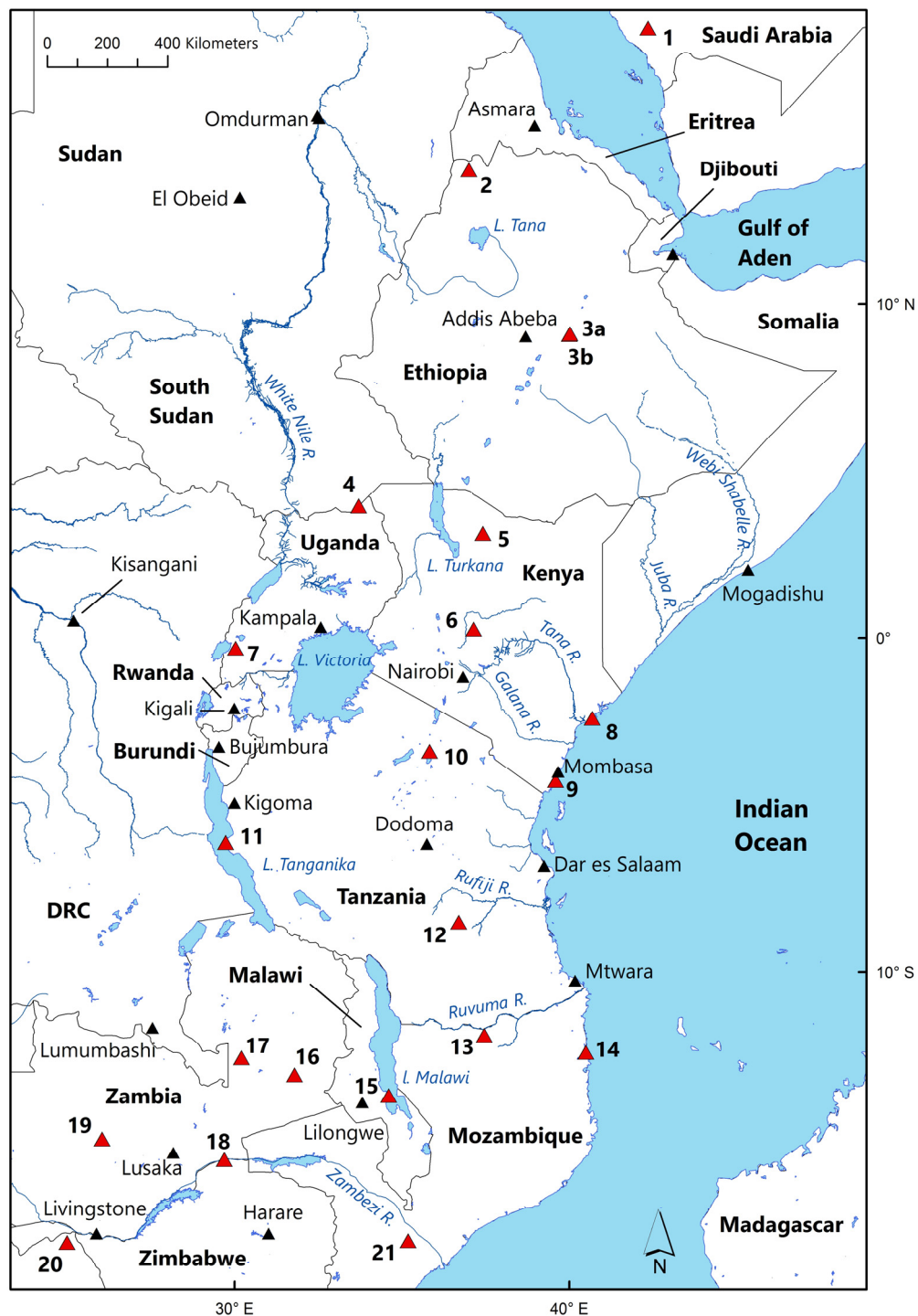
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Appendix 1a. Supporting information for 22 photographs of adult male baboons from 21 sites in eastern Africa. The baboons in these 22 photographs represent five *Papio* species and 11 *Papio* subspecies. The taxonomy followed here is that of Hill (1970), except for the Kinda baboon, which is here recognized as species *P. kindae*. Numbers in the first column correspond to the numbers on the map (appendix 1b) and with the photographs (appendix 1c). More than 650 photographs of baboons in the wild from many sites across Africa can be viewed at: <http://wildsolutions.nl/photomaps/Papio/>

Number	Locality	Taxon	mt-clade	Photographer(s)
1	Raidah Forest, Saudi Arabia	<i>Papio hamadryas</i> (Linnaeus, 1758)	9a or 9b	Tom Butynski & Yvonne de Jong
2	Kafta Sheraro National Park, Ethiopia	<i>Papio anubis heuglini</i> Matschie, 1898	9a	Hakan Pohlstrand
3a	Awash National Park, Ethiopia	<i>Papio anubis doguera</i> (Pucheran & Schimper, 1856)	9c	Hakan Pohlstrand
3b	Awash National Park, Ethiopia	<i>Papio hamadryas</i> (Linnaeus, 1758)	9c	Chris Roche
4	Kidepo Valley National Park, Uganda	<i>Papio anubis furax</i> Elliot, 1907	?	Yvonne de Jong & Tom Butynski
5	Kalacha, Kenya	<i>Papio anubis furax</i> Elliot, 1907	?	Yvonne de Jong & Tom Butynski
6	Lolldaiga Hills Ranch, Kenya	<i>Papio anubis neumanni</i> Matschie, 1897	9e	Yvonne de Jong & Tom Butynski
7	Kigezi Game Reserve, Uganda	<i>Papio anubis tessellatum</i> Elliot, 1909	8	Katerina Guschanski
8	Mpeketoni, Kenya	<i>Papio cynocephalus ibeanus</i> Thomas, 1893	?	Yvonne de Jong & Tom Butynski
9	Diani, Kenya	<i>Papio cynocephalus</i> <i>cynocephalus</i> (Linnaeus, 1766)	6	Yvonne de Jong & Tom Butynski
10	Lake Manyara National Park, Tanzania	<i>Papio anubis neumanni</i> Matschie, 1897	9e	Tom Butynski & Yvonne de Jong
11	Mahale Mountains National Park, Tanzania	<i>Papio c.f. kindae</i> Lönnerberg, 1919	1	Yvonne de Jong & Tom Butynski
12	Mahenge, Tanzania	<i>Papio cynocephalus</i> <i>cynocephalus</i> (Linnaeus, 1766)	5	Yvonne de Jong & Tom Butynski
13	Niassa National Reserve, Mozambique	<i>Papio cynocephalus</i> ssp.?	?	Colleen Begg
14	Quirimbas National Park, Mozambique	<i>Papio cynocephalus</i> ssp.?	?	Daniel Cara
15	Senga Hills Forest Reserve, Malawi	<i>Papio cynocephalus</i> (u.) <i>jubilaeus</i> Schwarz, 1928	3	Jim Auburn
16	Mfuwe, South Luangwa National Park, Zambia	<i>Papio cynocephalus</i> (u.) <i>jubilaeus</i> Schwarz, 1928	3	Ian Salisbury
17	Kasanka National Park, Zambia	<i>Papio kindae</i> Lönnerberg, 1919	2	Anna Weyher
18	Lower Zambezi, Zambia	<i>Papio ursinus griseipes</i> Pocock, 1911	northern chacma*	Dean Gaffigan
19	Lufupa River, Kafue National Park, Zambia	<i>Papio kindae</i> Lönnerberg, 1919	2	Jim Auburn
20	Chobe National Park, Botswana	<i>Papio ursinus chobiensis</i> Roberts, 1932	northern chacma*	Mike Haworth
21	Catapu, Mozambique	<i>Papio cynocephalus strepitus</i> Elliot, 1907	?	Celesta von Chamier

* The northern chacma clade is not regarded as an eastern African baboon clade and, therefore, was not given a number.

Appendix 1b. Map of eastern Africa with localities where the photographs (1–21) presented in appendix 1c were taken. See appendix 1a for locality and taxon names.



Appendix 1c. Photographs of adult male baboons in eastern Africa. See appendix 1a for locality, taxon, and name of the photographer. A map depicting the locations at which these photographs were taken is presented in appendix 1b. More photographs of baboons in the wild from many sites across Africa can be viewed at: <http://wildsolutions.nl/photomaps/Papio/>



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3a



3b



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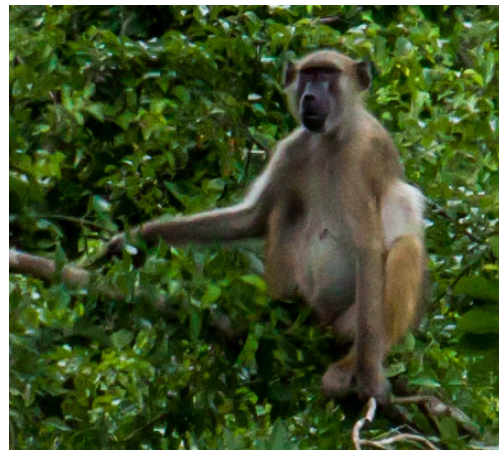
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Appendix 2. List of *Papio* spp. samples. The following information is given: taxon (based on morphotype and location), sample ID, country and site of origin (coordinates in decimal degrees), haplotype ID, and GenBank accession number. Abbreviations for taxa are given at the end of this table.

Taxon	ID	Country	Site Code	Site	Longitude	Latitude	Haplo	Acc. Num.
Tg	149*							EU885487
Pu	463	RSA	Hop	DeHoop Nature Reserve	20.40658	-34.45621		EU885486
Pu	472	NAM	Hak	Hakos Gästefarm	16.36463	-23.23708		EU885480
Pp	252	GUI	Bak	Bakaria, Haute Niger	-10.31542	10.54267		EU885463
Pp	518	SEN	Ked	Kedougou	-12.12472	12.57556		EU885449
Pg	566	ZAM	Nka	Kafue Middle, New Kalala	26.01077	-15.77360		EU885464
Pg	626	ZAM	Bri	Lower Zambezi (Bridge Camp)	30.21516	-15.00530		GQ148683
Pc	961	TZA	Mrg	north of Morogoro	37.58342	-6.62653	1	KU871141
Pc	963	TZA	Mrg	north of Morogoro	37.58342	-6.62653	1	KU871142
Pc	1106	TZA	eMw	east of Mwindu	38.13203	-6.63574	1	KU871165
Pc	1109	TZA	wMi	west of Mwindu	38.06753	-6.63987	1	KU871166
Pc	944	TZA	Mk0	Mikumi Nat. Park	37.20976	-7.23480	1	KU871137
Pc	970	TZA	Dod	30 km west of Dodoma	35.57563	-6.05992	2	KU871143
Pc	978	TZA	sDm	Dodoma->Iringa	35.98829	-7.13016	3	KU871144
Pc	1110	TZA	Wam	Wami River	38.38786	-6.24847	4	KU871167
Pc	1112	TZA	Wam	Wami River	38.38786	-6.24847	4	KU871168
Pc	951	TZA	Mk1	Mikumi Nat. Park	37.18905	-7.26596	5	KU871138
Pc	960	TZA	Mk4	Mikumi Nat. Park	37.16463	-7.34651	6	KU871140
Pc	954	TZA	Mk2	Mikumi Nat. Park	37.06127	-7.35522	6	KU871139
Pc	537	KEN	Amb	Amboseli	37.39000	-2.29000	7	EU885431
Pa	295	TZA	Ngo	Ngorongoro	35.59039	-3.28206	8	KU871123
Pa	1696	TZA	Lmy	Lake Manyara National Park	35.78283	-3.49483	8	KU871218
Pa	1697	TZA	Lmy	Lake Manyara National Park	35.78283	-3.49483	8	KU871219
Pa	1698	TZA	Lmy	Lake Manyara National Park	35.78283	-3.49483	8	KU871220
Pa	351	TZA	Ni2	Serengeti National Park 2	34.79356	-2.42233	9	KU871126
Pa	353	TZA	Sw1	Serengeti National Park 1	34.85236	-2.43100	9	EU885427
Pc	983	TZA	nlg	Dodoma->Iringa	35.73175	-7.33854	9	KU871145
Pc	507	SOM	Web	Webi Shebelli	45.43333	2.42083	10	EU885428
Pa	1699	KEN	Lo3	Lolldaiga Hills Ranch	37.12340	0.26432	10	KU871221
Pc	988	TZA	nIn	Dodoma->Iringa	35.74325	-7.37304	11	KU871146
Pc	990	TZA	nIn	Dodoma->Iringa	35.74325	-7.37304	11	KU871147
Pa	531	KEN	Cho	Chololo Ranch	37.06000	0.91000	12	KU871131
Pc	1126	TZA	Sgr	Segera	38.65102	-5.38707	13	KU871170
Pa	1609	KEN	Lo1	Lolldaiga Hills Ranch north	37.09806	0.33667	14	KU871183
Pa	1610	KEN	Lo1	Lolldaiga Hills Ranch north	37.09806	0.33667	15	KU871184
Pa	1693	KEN	Lo2	Lolldaiga Hills Ranch cental	37.13736	0.21279	16	KU871217
Pa	340	ETH	Wen	Wendo Genet	38.64965	7.07127	17	KM267363
Pa	341	ETH	Wen	Wendo Genet	38.64965	7.07127	17	KU871124
Pa	343	ETH	Wen	Wendo Genet	38.64965	7.07127	17	KU871125
Pa	1624	ETH	Din	Dinsho, Bale Mts. Nat. Park	39.73464	7.12239	18	KU871189
Pa	1625	ETH	Din	Dinsho, Bale Mts. Nat. Park	39.73464	7.12239	18	KU871190
Pa	1626	ETH	Din	Dinsho, Bale Mts. Nat. Park	39.73464	7.12239	18	KU871191
Pa	1627	ETH	Din	Dinsho, Bale Mts. Nat. Park	39.73464	7.12239	18	KU871192
Pa	1628	ETH	Din	Dinsho, Bale Mts. Nat. Park	39.73464	7.12239	18	KU871193
Pa	1629	ETH	Din	Dinsho, Bale Mts. Nat. Park	39.73464	7.12239	18	KU871194
Pa	1630	ETH	Din	Dinsho, Bale Mts. Nat. Park	39.73464	7.12239	18	KU871195
Pa	1623	ETH	Odo	Odobulu Forest	40.28572	6.86631	18	KU871188
Pa	943	ETH	Har	Harennia 2	39.73718	6.61577	18	KU871136
Ph	1604	ERI	Dad	Dada (Bolo) Assab Area	42.40194	13.15556	19	KM267378
Ph	Abh24	ARA	Abh	Abha	42.50523	18.21639	20	KM267380
Ph	312	ETH	Ger	Gerba Luku/ Erer Gota	41.53400	9.58740	21	KM267351
Pa	509	ETH	CFr	Chilimo Forest	38.16333	9.07167	22	KU871128
Pa	349	ETH	Mn2	Managasha Nat. Park	38.57125	8.96838	22	EU885424
Pa	200	ERI	Hay	Haykota, R. Gash	37.06600	15.15695	23	KM267341
Pa	181	ERI	Tes	Tesseney, R. Gash	36.70142	15.14510	23	KM267339

Taxon	ID	Country	Site Code	Site	Longitude	Latitude	Haplo	Acc. Num.
Ph	240	ERI	Dur	Durfo, SC1	38.96458	15.37370	24	KM267348
Pa	184	ERI	Gri	Griset, R.	36.76018	14.88322	25	EU885422
Ph	301	ETH	ASt	Awash Station	40.17775	8.99268	26	EU885444
Ph	1613	ETH	Mgh	3,3 km NW of Menghi, Tigray	38.86666	13.70865	27	KU871185
Pa	1621	ETH	Jib	Jibat Forest	37.46302	8.77871	28	KU871186
Pa	1622	ETH	Jib	Jibat Forest	37.46302	8.77871	28	KU871187
Pa	338	ETH	Ala	Alambada	38.74768	7.50463	29	KM267362
Pa	332	ETH	Ada	Adami Tulu	38.71493	7.82558	30	KM267358
Pa	334	ETH	Ada	Adami Tulu	38.71493	7.82558	30	KM267359
Pa	335	ETH	Ada	Adami Tulu	38.71493	7.82558	30	KM267360
Pa	336	ETH	Ada	Adami Tulu	38.71493	7.82558	30	KM267361
Pa	1576	TZA	Tuv	Tubila	30.09739	-5.01438	31	KU871181
Pa	1578	TZA	Tuv	Tubila	30.09739	-5.01438	31	KU871182
Pc	1574	TZA	Ngy	Nguye	30.42222	-5.22556	31	KU871179
Pa	444	UGA	Kb1	Kibale Forest 1	30.43333	0.51667	32	KU871127
Pa	448	UGA	Kb2	Kibale Forest 2	30.40000	0.48333	33	EU885420
Pa	512	DCR	sBu	south Bukavu	28.91092	-2.68258	34	EU885421
Pa	513	DCR	sBu	south Bukavu	28.91092	-2.68258	34	KU871129
Pa	516	DCR	sBu	south Bukavu	28.91092	-2.68258	34	KU871130
Pc	529	KEN	Dia	opp. TwoFishes Hotel, Diani Beach	39.55000	-4.32000	35	EU885429
Pc	533	KEN	Dia	opp. TwoFishes Hotel, Diani Beach	39.55000	-4.32000	35	EU885430
Pc	1115	TZA	Ami	Amboni River	39.02847	-5.05471	36	KU871169
Pa	1688	ETH	BO2	Boginda Forest	36.06189	7.50829	37	KU871214
Pa	1692	ETH	BO2	Boginda Forest	36.06189	7.50829	37	KU871216
Pa	942	ETH	Tep	Tepi	35.40529	7.25132	37	KU871135
Pa	1680	ETH	AW2	Bonga, Sheaka Forest, Awurada Valley 2	36.20730	7.08558	38	KU871207
Pa	940	ETH	Kam	Kama1	36.07014	7.31731	39	KU871133
Pa	1675	ETH	AW1	Bonga, Sheaka Forest, Awurada Valley 1	36.22529	7.09305	39	KU871204
Pa	1677	ETH	AW1	Bonga, Sheaka Forest, Awurada Valley 1	36.22529	7.09305	39	KU871205
Pa	1679	ETH	AW1	Bonga, Sheaka Forest, Awurada Valley 1	36.22529	7.09305	39	KU871206
Pa	1689	ETH	GO1	Saja Forest, Gojeb wetland	36.06092	7.55529	40	KU871215
Pa	941	ETH	Kay	Kayakela3	36.22385	7.32184	40	KU871134
Pa	1681	ETH	BA1	Bonga, Bamboo Forest1	36.45549	7.26829	40	KU871208
Pa	1682	ETH	BA2	Bonga, Bamboo Forest2	36.45636	7.24365	40	KU871209
Pa	1683	ETH	BA2	Bonga, Bamboo Forest2	36.45636	7.24365	40	KU871210
Pa	1684	ETH	BA2	Bonga, Bamboo Forest2	36.45636	7.24365	40	KU871211
Pa	1685	ETH	BA2	Bonga, Bamboo Forest2	36.45636	7.24365	40	KU871212
Pa	1686	ETH	BA2	Bonga, Bamboo Forest2	36.45636	7.24365	40	KU871213
Pc	1547	TZA	Mhl	Kasiha, Mahale Mts Nat. Park	29.72477	-6.11688	41	KU871174
Pc	1548	TZA	Mhl	Kasiha, Mahale Mts Nat. Park	29.72477	-6.11688	41	KU871175
Pc	1549	TZA	Mhl	Kasiha, Mahale Mts Nat. Park	29.72477	-6.11688	41	KU871176
Pc	1550	TZA	Mhl	Kasiha, Mahale Mts Nat. Park	29.72477	-6.11688	41	KU871177
Pc	1551	TZA	Mhl	Kasiha, Mahale Mts Nat. Park	29.72477	-6.11688	41	KU871178
Pc	1575	TZA	Ngy	Nguye	30.42222	-5.22556	42	KU871180
Pk	641	ZAM	KN1	North Kafue (Tar road)	25.95237	-14.95338	43	GQ148708
Pk	645	ZAM	Mok	North Kafue (Mokambi Lodge)	25.99480	-14.98034	43	GQ148707
Pk	642	ZAM	KN2	North Kafue (Tar road)	26.06321	-14.95601	44	GQ148709
Pk	565	ZAM	KfN	North Kafue	26.53577	-14.96779	44	EU885438
Pk	649	ZAM	KN3	North Kafue (Tar road)	26.44522	-14.97154	44	GQ148710
Pk	658	ZAM	Kai	between Kaingu & New Kalala	25.99285	-15.30998	44	GQ148711
Pk	581	ZAM	Ka2	Kasanka Nat Park 2	30.24556	-12.57860	45	GQ148705
Pk	582	ZAM	Ka2	Kasanka Nat Park 2	30.24556	-12.57860	45	GQ148706
Pk	568	ZAM	Ka1	Kasanka Nat Park 1	30.25202	-12.59059	45	EU885439
Pk	1532	ZAM	Tgy	Kalambo Falls, south Lake Tanganyika	31.23650	-8.59283	46	KU871171

Taxon	ID	Country	Site Code	Site	Longitude	Latitude	Haplo	Acc. Num.
Pk	1533	ZAM	Tgy	Kalambo Falls, south L. Tanganyika	31.23650	-8.59283	46	KU871172
Pk	1536	ZAM	Tgy	Kalambo Falls, south L. Tanganyika	31.23650	-8.59283	46	KU871173
Pk	569	ZAM	Shi	Shiwa N'gandu	31.73892	-11.19677	47	EU885440
Pk	593	ZAM	Shi	Shiwa N'gandu	31.73892	-11.19677	47	GQ148704
Pc	1031	TZA	sTu	Amani (south of Tunduru)	37.51363	-11.26054	48	KU871154
Pc	1037	TZA	sTu	Amani (south of Tunduru)	37.51363	-11.26054	49	KU871155
Pc	1057	TZA	wMs	west of Masasi	38.60093	-10.86915	50	KU871156
Pc	1096	TZA	Sin	east of Sinza	39.30755	-8.63751	51	KU871164
Pc	1063	TZA	Chw	Chiwata	38.98838	-10.59470	51	KU871157
Pc	1028	TZA	Che	Chem-Chem (south of Tunduru)	37.43273	-11.08541	52	KU871153
Pc	1092	TZA	nNa	15 km north of Nangurukuru	39.31910	-8.95165	53	KU871163
Pc	1071	TZA	Min	Mingoyo	39.65751	-10.10855	53	KU871158
Pc	1074	TZA	Kit	north of Kitaya	40.13528	-10.59522	54	KU871160
Pc	1080	TZA	Dih	Dihimbo	39.97846	-10.41007	55	KU871162
Pc	1077	TZA	Dih	Dihimbo	39.97846	-10.41007	55	KU871161
Pc	1073	TZA	Nan	Nanguruwe	39.99297	-10.49506	55	KU871159
Pc	292	MLW	LCh	Liwonde Nat. Park	35.26033	-15.01481	56	KU871122
Pc	286	MLW	Lb1	Liwonde Nat. Park	35.25392	-15.03905	56	KU871120
Pc	282	MLW	Lb2	Liwonde Nat. Park	35.25343	-15.04134	56	KU871119
Pc	151	MLW	Mc2	Michiru Mountains Cons. Area 2	34.98668	-15.72307	57	EU885433
Pc	994	TZA	Kma	Kamani	34.19086	-8.90926	58	KU871148
Pc	1007	TZA	nSo	north of Songea	35.62780	-9.98347	58	KU871150
Pc	1010	TZA	wSo	west of Songea	35.26643	-10.71346	58	KU871152
Pc	1003	TZA	Son	100 km north of Songea	35.50796	-9.90943	59	KU871149
Pc	1009	TZA	nSo	north of Songea	35.62780	-9.98347	59	KU871151
Pc	288	MLW	Mu2	Mulanje Mt. 2	35.51849	-15.93561	60	EU885434
Pc	287	MLW	Mu1	Mulanje Mt. 1	35.52112	-15.94492	60	KU871121
Pc	404	TZA	Ruk	Tanzania, NO Ufer Lake Rukwa	32.15517	-7.58297	61	EU885432
Pc	600	ZAM	Chf	Chifunde (North Luangwa)	32.43357	-11.86058	62	GQ148698
Pc	409	ZAM	LuS	South Luangwa Nat. Park	31.63793	-13.26840	63	EU885435
Pc	617	ZAM	Mfu	Mfuwe (Flatdogs)	31.77836	-13.10128	64	GQ148703
Pc	615	ZAM	LS2	between Luambe & Mfuwe	32.09203	-12.75000	65	GQ148700
Pc	611	ZAM	LS1	between Luambe & Mfuwe	32.12490	-12.66336	66	GQ148701
Pc	612	ZAM	LS1	between Luambe & Mfuwe	32.12490	-12.66336	66	KU871132
Pc	616	ZAM	LS3	between Luambe & Mfuwe	32.01766	-12.88562	66	GQ148702
Pc	570	ZAM	Lua	Luambe Nat. Park	32.14550	-12.45780	67	EU885437
Pc	604	ZAM	Lua	Luambe Nat. Park	32.14550	-12.45780	67	GQ148699
Pc	155	MLW	LC1	JB, Liwonde Nat. Park	35.30171	-14.85281	68	KU871118
Pc	1639	MLW	Bu2	Bua River, SE Nkhotakota GR	34.15217	-12.83150	69	KU871200
Pc	1640	MLW	Bu2	Bua River, SE Nkhotakota GR	34.15217	-12.83150	69	KU871201
Pc	1649	MLW	Nkh	Western Nkhotakota	34.10867	-13.00967	69	KU871202
Pc	1651	MLW	Nkh	Western Nkhotakota	34.10867	-13.00967	69	KU871203
Pc	411	ZAM	LuS	South Luangwa Nat. Park	31.63793	-13.26840	69	EU885436
Pc	1637	MLW	Sf2	Senga Hills Forest Reserve	34.61853	-13.70677	69	KU871199
Pc	1631	MLW	Sf1	Senga Hills Forest Reserve	34.62217	-13.70967	69	KU871196
Pc	1632	MLW	Sf1	Senga Hills Forest Reserve	34.62217	-13.70967	69	KU871197
Pc	1636	MLW	Sf1	Senga Hills Forest Reserve	34.62217	-13.70967	69	KU871198