

An Ancient Baboon Genome Demonstrates Long-Term Population Continuity in Southern Africa

Iain Mathieson^{1,*†}, Federico Abascal^{2,†}, Lasse Vinner³, Pontus Skoglund⁴, Cristina Pomilla^{2,12}, Peter Mitchell^{5,6}, Charles Arthur⁵, Deepti Gurdasani⁷, Eske Willerslev^{2,3,8,9}, Manj S. Sandhu¹⁰, and Genevieve Dewar^{6,11}

¹Department of Genetics, Perelman School of Medicine, University of Pennsylvania

²Wellcome Sanger Institute, Hinxton, United Kingdom

³Centre for GeoGenetics, University of Copenhagen, Denmark

⁴Francis Crick Institute, London, United Kingdom

⁵School of Archaeology, University of Oxford, United Kingdom

⁶School of Geography, Archaeology and Environmental Studies, University of the Witwatersrand, Braamfontein, South Africa

⁷William Harvey Research Institute, Queen Mary's University of London, United Kingdom

⁸Department of Zoology, University of Cambridge, United Kingdom

⁹The Danish Institute for Advanced Study, University of Southern Denmark, Odense, Denmark

¹⁰Department of Medicine, University of Cambridge, United Kingdom

¹¹Department of Anthropology, University of Toronto Scarborough, Toronto, Ontario, Canada

¹²Present address: Omnigen Biodata Ltd., Cambridge, United Kingdom

*Corresponding author: E-mail: mathi@pennmedicine.upenn.edu.

†These authors contributed equally to this work.

Accepted: January 22, 2020

Data deposition: Sequence read data for the ancient baboon have been deposited at the European Nucleotide Archive under the accession ERP119178.

Abstract

Baboons are one of the most abundant large nonhuman primates and are widely studied in biomedical, behavioral, and anthropological research. Despite this, our knowledge of their evolutionary and demographic history remains incomplete. Here, we report a 0.9-fold coverage genome sequence from a 5800-year-old baboon from the site of Ha Makotoko in Lesotho. The ancient baboon is closely related to present-day *Papio ursinus* individuals from southern Africa—indicating a high degree of continuity in the southern African baboon population. This level of population continuity is rare in recent human populations but may provide a good model for the evolution of *Homo* and other large primates over similar timespans in structured populations throughout Africa.

Key words: ancient DNA, baboons, demography.

Introduction

Baboons (genus *Papio*) are Old World Monkeys, widely distributed throughout Africa and the Arabian Peninsula. The six extant species of baboon occupy largely independent geographic ranges (Jolly 1993; Zinner et al. 2013) but readily hybridize in contact regions (Nagel 1973; Samuels and Altmann 1986; Jolly 1993; Jolly et al. 2011). The oldest splits among them date to 1.5–2 Ma, between Northern (*Papio hamadryas*,

Papio anubis, and *Papio papio*) and Southern (*Papio ursinus* and *Papio cynocephalus*) clades (Zinner, Groeneveld, et al. 2009; Zinner et al. 2013; Rogers et al. 2019). The southernmost species (*P. ursinus*) has two deeply diverged subspecies (*ursinus* and *griseipes*), whose history and distribution may have been shaped by historical changes in range driven by aridification cycles (Sithaldeen et al. 2009; Sithaldeen et al. 2015). Thus, the boundary between the *P. ursinus* subspecies,

© The Author(s) 2020. Published by Oxford University Press on behalf of the Society for Molecular Biology and Evolution.

This is an Open Access article distributed under the terms of the Creative Commons Attribution License (<http://creativecommons.org/licenses/by/4.0/>), which permits unrestricted reuse, distribution, and reproduction in any medium, provided the original work is properly cited.

as well as between *P. ursinus* and other species, may have shifted over time. Here, we test this by analyzing the genome of a 5800-year-old baboon from close to the present-day *ursinus/griseipes* contact zone. As well as illuminating this phylogeographic question, our results show more broadly the usefulness of ancient DNA for understanding the history, evolution and paleoenvironmental context of African primates.

Results

We extracted and sequenced DNA from a baboon proximal phalanx excavated at the archaeological site of Ha Makotoko, western Lesotho, and directly dated to ~5,800 calBP (fig. 1A and B, supplementary table 1 and methods, Supplementary Material online). We generated, sequenced and aligned 13 libraries (supplementary table 2, Supplementary Material online) to the Panu_2.0 (*P. anubis*) nuclear genome, and to the *P. ursinus* mitochondrial genome. For these libraries, we estimated an average endogenous DNA content of 8.5% and obtained a total mean mapped autosomal coverage of 0.93× and mitochondrial coverage of 36.6×. The Panu_2.0 reference genome does not contain a Y chromosome, but comparison of coverage on the X chromosome (0.47) to the autosomes (mean 0.93, range 0.84–1.04) indicates that the phalanx belonged to a male. Fragment lengths (supplementary fig. 1, Supplementary Material online) and damage patterns are consistent with authentic ancient DNA (Dabney et al. 2013) with C>T transitions at 5' ends affecting ~15% of bases in the last position (supplementary fig. 2, Supplementary Material online). Low mitochondrial (1.3%) and X chromosome (0.47%) consensus mismatch at nonreference, nondamage sites indicates that contamination (from other baboons) is low. We restricted our analysis to reads with evidence of cytosine deamination, characteristic of authentic ancient DNA (Skoglund et al. 2014), and find results consistent with the unrestricted data (supplementary table 3, Supplementary Material online).

We compared the ancient baboon with mitochondrial data from 66 present-day baboons (Zinner, Groeneveld, et al. 2009), including Guinea (*P. papio*), olive (*P. anubis*), hamadryas (*P. hamadryas*), Kinda (*P. kindae*), yellow (*P. cynocephalus*), and chacma (*P. ursinus*) baboons. We included geladas (*Theropithecus gelada*) as an outgroup. These publicly available data include the complete coding sequence (CDS) of *CYTB*, part of the CDS of *NADH5* and the complete tRNA-His, tRNA-Ser, and tRNA-Leu sequences. The resulting tree (fig. 1C) shows that the ancient baboon has haplogroup U13/U14 and clusters with southern *P. ursinus* (i.e., Cape chacma, *P. ursinus ursinus*). Ha Makotoko is at the eastern end of the range of this subspecies, which extends to the south and west of the Kalahari Desert (Sithaldeen et al. 2015). The most closely related specimens come from the Giant's Castle Game Reserve and the Goegap Nature Reserve (fig. 1A). We also compared

the complete ancient mitochondrial genome (36× coverage) with complete mitochondrial genomes from 10 present-day baboons (Zinner et al. 2013), and to the 16 present-day baboons from the baboon genome project diversity panel (Rogers et al. 2019), confirming that it is closely related to present-day southern *P. ursinus* (supplementary fig. 3, Supplementary Material online).

Next, we analyzed the autosomal genome together with 14 present-day baboons sequenced as part of the baboon genome project diversity panel (Rogers et al. 2019). Heterozygosity at sites polymorphic in *P. cynocephalus* is similar in the ancient baboon (8.5%) to present-day *P. ursinus* (8.7%), suggesting a relatively constant level of genetic diversity. In principal component analysis (PCA), the ancient baboon falls closest to the two *P. ursinus* individuals (fig. 2A). D statistics (Patterson et al. 2012) suggest that the ancient baboon might carry some ancestry related to Northern clade subspecies such as *P. anubis*. In particular, $D(T. gelada, P. anubis, P. ursinus, Ancient)$ has a Z score of 12.1 suggesting that the ancient baboon shares significant drift with *P. anubis* to the exclusion of *P. ursinus*. However, this is also consistent with differential attraction to the reference genome (generated from a *P. anubis* individual)—a common source of bias in ancient DNA studies (Cahill et al. 2018; Gunther and Nettelblad 2019; Sheng et al. 2019). This interpretation is supported by the D statistic $D(T. gelada, Ancient, P. anubis, papAnu2)$ that has a Z score of 18.6 indicating that the ancient baboon shares more drift with the reference than other *P. anubis* individuals.

To further investigate the effect of reference bias, we constructed admixture graphs using TreeMix (Pickrell and Pritchard 2012) and qpGraph (Patterson et al. 2012) (fig. 2B and C, supplementary fig. 4 and methods, Supplementary Material online). TreeMix finds evidence of “gene flow”—in reality the effect of reference bias—between the Ancient lineage and the reference genome (fig. 2B). Similarly, qpGraph shows that the observed D statistics can be explained with small amounts of gene flow from the reference into other samples (fig. 2C). The qpGraph model suggests that, relative to the ancient baboon, present-day *P. ursinus* may carry a small amount (2%) of ancestry related to *P. cynocephalus*. However, we do not detect this signal using ADMIXTURE (Alexander et al. 2009) (supplementary fig. 5, Supplementary Material online) or f_3 statistics (Patterson et al. 2012) ($f_3(P. ursinus; Ancient; P. cynocephalus)$; $Z = 15.9$) so it may be an artefact of the graph fitting or reflect structure within the *P. ursinus* population rather than admixture.

The Y chromosomal *TSPY* locus can distinguish between subspecies (Tosi et al. 2003; Jolly et al. 2011). We aligned reads to the *T. gelada* *TSPY* sequence (Tosi et al. 2003) and compared with seven reported sequences (Tosi et al. 2003; Zinner, Arnold, et al. 2009; Jolly et al. 2011) (supplementary table 4, Supplementary Material online). High coverage at this locus (because of multiple *TSPY* copies) confirms the male sex

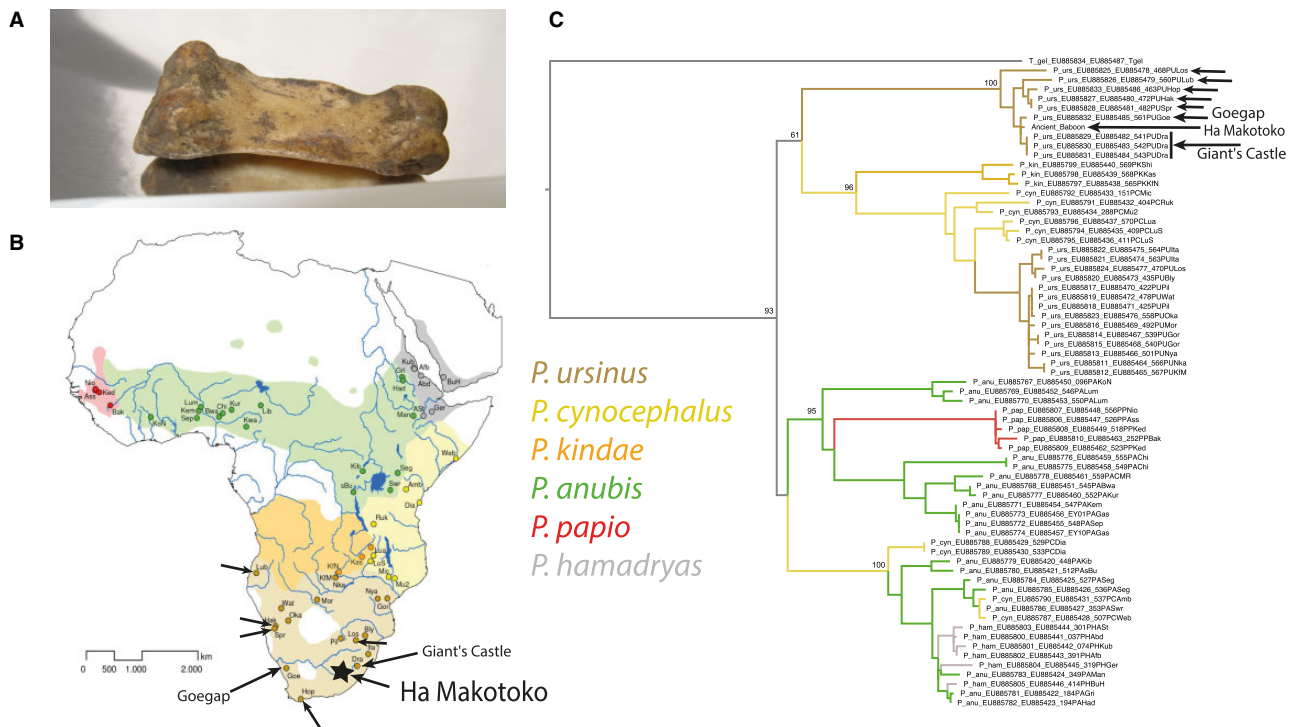


FIG. 1.—Mitochondrial genome analysis. (A) Image of the ancient baboon phalanx. (B) Location of ancient baboon and geographic distribution of baboon species. Map: modified from Zinner, Groeneveld, et al. (2009) (CC BY). (C) Phylogenetic tree of the ancient baboon and present-day baboons using partial mitochondrial sequences from Zinner, Groeneveld, et al. (2009). The locations of the two most closely related mitochondrial genomes (U13/14) are indicated with labeled arrows in B and C, and those in the other southern *ursinus* haplogroups U10,11,12 and 15 are indicated with unlabeled arrows.

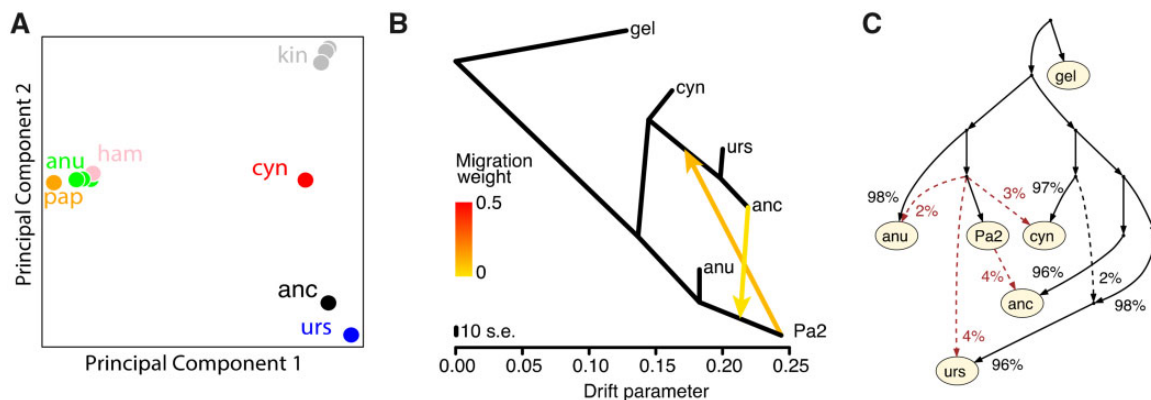


FIG. 2.—Autosomal genome analysis. (A) First two principal components of genome-wide data. (B) TreeMix (Pickrell and Pritchard 2012) analysis of southern clade baboons with one northern clade representative (*Papio anubis*) and the papAnu2 (Pa2) reference genome with two migration edges (worst outlier 3.9 S.E.). (C) An admixture graph that is consistent with the data (worst *D*-statistic *Z* score 0.4) of southern clade baboons with one northern clade representative (*P. anubis*) and the papAnu 2 reference genome. Other graphs may be equally consistent. Apparent gene flow (dashed red lines) between the Pa2 lineage and other samples likely reflects the effect of reference mapping bias. *Abbreviations*: anc, ancient baboon; anu, *P. anubis*; cyn, *Papio cynocephalus*; gel, *Theropithecus gelada*; ham, *Papio hamadryas*; kin, *Papio kindae*; pap, *Papio papio*; Pa2, papAnu2 reference genome.

determination. The ancient baboon haplotype appears consistent with that reported for *P. ursinus griseipes* in the *ursinus/kindae* hybrid zone in Zambia (Jolly et al. 2011). At least one other *P. ursinus ursinus* individual from Southern Africa (Zinner, Arnold, et al. 2009) has a different haplotype (supplementary table 4, Supplementary Material online), raising

the possibility of discordant mitochondrial and Y chromosome phylogenies, consistent with female philopatry and male dispersal in *P. ursinus* (Kopp et al. 2014).

We investigated the metrics of the phalanx (supplementary fig. 6, Supplementary Material online). The maximum length and medio-lateral midshaft breadth, at 26.3 and 7.1 mm,

respectively are within the range of variation of an identified male *P. ursinus* (UCT/87/09) ($n = 7$, mean = 28.3 and 6.3 mm, SD = 5.1 and 0.8 mm) and a larger sample of $n = 16$ males represented by one third phalanx per individual (mean = 28.5 and 7.2 mm, SD = 2.4 and 0.7 mm) (Vernon 2013). However, the medio-lateral breadth at the base (the proximal joint) is 12.5 mm larger and outside the range of variation of both comparative samples (mean = 10.5 and 10.5 mm, SD = 0.9 and 0.8 mm). This suggests that it was more robust than a modern animal. Because the genetic data show that it is not a hybrid, this could reflect the effect of altitude (Bergman 1847; Sayers 2014). Carbon and nitrogen isotope values ($\delta^{13}\text{C} = -16.99 \pm 0.19\text{‰}$ and $\delta^{15}\text{N} = 4.46 \pm 0.18\text{‰}$ and a C:N ratio of 3.3) reflect a predominantly C_3 diet, typical of *P. ursinus*, although the low value may reflect a diet more heavily focused on browse or fleshy fruits. The nitrogen values reflect low trophic level species and a largely vegetarian diet.

Discussion

Our data demonstrate that *P. ursinus ursinus* persisted in the foothills of the Maloti-Drakensberg Mountains throughout the past 6,000 years. This is despite the fact that paleoenvironmental proxies predict drier conditions across the summer rainfall zone which may, for example, have limited human occupation across all of southeastern Southern Africa from 6.0 to 3.5 ka (Stewart and Mitchell 2018). It remains to be seen how far back in time this continuity extends, but more ancient genomes would address that question. Additional nuclear genomes from ancient and present-day baboons will allow us to estimate the extent and timing of gene flow between the *ursinus* and *griseipes* subspecies.

These data demonstrate that it is possible to extract and sequence high quality ancient genomes from southern Africa. This 0.9× genome is ~3,500 years older than the oldest human shotgun genome from the region (Schlebusch et al. 2017) and demonstrates that it should be possible to obtain much older human genomes, but also genomes from the different baboon species and other nonhuman primates. In particular, the temporal resolution provided by ancient DNA allows precise comparisons with paleoclimate data, allowing tests of specific hypotheses about the relationship between climatic variation and phylogeography. Although the vast majority of effort in ancient DNA is geared toward humans or domesticated species, this study underscores the utility of ancient DNA for understanding the history and evolution of nonhuman species under natural conditions.

Materials and Methods

Data Processing and Quality Control

All ancient DNA work was performed in the aDNA clean lab facility of GeoGenetics, Copenhagen. From bone material

obtained from the center of the phalanx, we extracted DNA (Allentoft et al. 2015) for 13 libraries, 9 of which were treated with the Uracil-Specific Excision Reagent (USER). aDNA libraries were prepared according to Meyer and Kircher (2010), using the modification described by Allentoft et al. (2015). The libraries were 75-bp paired-end sequenced on the Illumina platform HiSeq-2000 v4. Sequence reads were processed with AdapterRemoval v2.1.7 (Schubert et al. 2016) to: Remove adaptor remnants and low-quality ends ("Ns" and bases with quality < 20); merge read pairs when mate-pairs overlap at least 11 bp; and discard reads shorter than 30 bp. Parameters were "--collapse --minalignmentlength 11 --minlength 30 --trimqualities --minquality 20 --trimns --qualitybase 33 --qualitymax 42 --mm 3."

We aligned reads to the *P. anubis* (papAnu2) reference sequence (Rogers et al. 2019) using the *aln* algorithm of *bwa* v0.7.12 (Li and Durbin 2009), disabling seeding (-l 10000). We removed duplicates from each library BAM file using Picard tools v1.127 (<http://broadinstitute.github.io/picard>) and merged libraries using Samtools v1.2 (Li et al. 2009). Finally, we ran *GATK's* *RealignerTargetCreator* and *IndelRealigner* v3.4.0 (McKenna et al. 2010) to identify potential indels and realign reads around them. The ancient baboon's mitochondria clustered with *P. ursinus*, so to produce a more accurate whole-mitochondrial sequence, we replaced the reference *P. anubis* mitochondrial sequence with the complete mitochondrial sequence of *P. ursinus* from Zinner et al. (2013) (GenBank accession JX946205.2). We removed unplaced contigs and scaffolds.

We assessed the authenticity of the ancient DNA by confirming damage patterns characteristic of ancient samples, that is, DNA fragmentation and increased C>T transitions at the 5' ends of DNA molecules. We used *bamdamage* (v20140602) from the *bamdds* package (Malaspinas et al. 2014). The distribution of read lengths shows a peak around 40 bp. C>T transitions show high rates at 5' ends, affecting 15% of cytosines (supplementary fig. 1, Supplementary Material online), consistent with the presence of authentic ancient DNA. For some analyses, we restricted to reads with evidence of damage using *pmdtools* (Skoglund et al. 2014) with the option `-threshold = 3`.

We tested for contamination by counting the proportion of reads that mapped to the mitochondria and did not match the majority call at sites where the majority call was nonreference. Across all sites we found that 3.6% of reads did not match, and at sites where a mismatch could not be the result of deamination, 1.3% of reads did not match. Because it is possible that potential contaminants share nonreference variants with the ancient individual, this is not a direct estimate of contamination, but nevertheless supports the authenticity of the data. We repeated the same analysis for the X chromosome, finding that 0.63% of all sites and 0.47% of nondeamination sites did not match.

Mitochondrial Analysis

To call the mitochondrial genome of our ancient baboon we skipped the removal of nonuniquely aligned reads, as NUMTs in the nuclear genome result in missed coverage in the mitochondrial genome. We required each site to be covered by 10 or more reads with base qualities > 30 and that at least 80% consensus. For the partial mitochondrial genomes of Zinner, Groeneveld, et al. (2009) we aligned the data using Mafft v7.305b (Kato and Standley 2013) and built a tree using *Phyml* v3.0 (Guindon et al. 2010) with a TN93+G+I+F model. For the complete mitochondrial genomes from Zinner et al. (2013) and Rogers et al. (2019), we aligned the whole-mitochondrial sequences with MUSCLE (Edgar 2004; Madeira et al. 2019), and estimated the maximum clade credibility tree using Beast2 (Bouckaert et al. 2019) with a GTR model.

Autosomal Analysis

We generated pseudohaploid calls by picking a random base from all reads covering each site in the genome. We obtained baboon genome project diversity panel SNP calls from Rogers et al. (2019), merged with the pseudohaploid ancient calls, and restricted to transversions that were polymorphic in present-day baboons for all analysis. We ran TreeMix v1.13 (Pickrell and Pritchard 2012) with the “-root” option to use *T. gelada* as an outgroup, and the option “-noss” to turn off sample size correction. We ran qpGraph v6065 (Patterson et al. 2012), starting with the tree inferred by TreeMix and manually adding admixture edges until the absolute value of the worst *D* statistic *Z* score was <3.

We estimated conditional nucleotide diversity (CND) by restricting to sites that were polymorphic in a single *P. cynocephalus* individual, and counted how many were heterozygous in present-day *P. ursinus*. For the ancient baboon, we counted total n_i and alternative k_i allele counts at each SNP i , restricted to the N SNPs where $n_i > 1$ and then estimated $CND = (2/N) \sum_{i=1}^N \left\{ [n_i^2 - k_i^2 - (n_i - k_i)^2] / [n_i(n_i - 1)] \right\}$. We averaged the results obtained from ascertaining sites in each of the two *P. cynocephalus* individuals, which were very similar.

To analyze *TSPY* we aligned reads from the ancient baboon that had not aligned to the reference to the *T. gelada TSPY* sequence; GenBank: AF284278.2 (Tosi et al. 2003). We also obtained the *P. hamadryas* sequence from the same reference, and four other partial sequences (Zinner, Arnold, et al. 2009) which we aligned to the *T. gelada* sequence to identify differences.

Supplementary Material

Supplementary data are available at *Genome Biology and Evolution* online.

Acknowledgments

We thank Anders Bergström, Jeffrey Rogers, and Dietmar Zinner for helpful comments on an earlier version of the manuscript. Archaeological excavations at Ha Makotoko were undertaken at the invitation of the Metolong Authority and with the permission of the Department of Culture of the Kingdom of Lesotho and Chief Makotoko and the people of Aupolasi. The export of the phalanx from Lesotho for identification and analysis was made possible by an excavation and export permit issued to PM by Lesotho’s Department of Culture. I.M. was supported by a Research Fellowship from the Alfred P. Sloan foundation (FG-2018-10647) and a New Investigator Research Grant from the Charles E. Kaufman Foundation (KA2018-98559) and the National Institutes of Health (R35GM133708). P.S. was supported by the European Research Council (No. 852558), a Wellcome Trust Investigator award (217223/Z/19/Z) and by Francis Crick Institute core funding (FC001595) from Cancer Research UK, the UK Medical Research Council, and the Wellcome Trust. E.W. and L.V. were supported by the Danish National Research Foundation (DNRF94) and the Lundbeck Foundation. E.W. was additionally supported by the Novo Nordic Foundation, the Carlsberg Foundation, and the Wellcome Trust. Funding for fieldwork at Ha Makotoko was provided by the World Bank, the British Academy, and the University of Oxford (the Boise and James Fell Funds). Sequencing was funded by the Wellcome Trust (Grant No. WT098051) and used the core facilities of the Wellcome Sanger Institute. The content is solely the responsibility of the authors and does not necessarily represent the official views of the National Institutes of Health or other funders.

Literature Cited

- Alexander DH, Novembre J, Lange K. 2009. Fast model-based estimation of ancestry in unrelated individuals. *Genome Res.* 19(9):1655–1664.
- Allentoft ME, et al. 2015. Population genomics of Bronze Age Eurasia. *Nature* 522(7555):167–172.
- Bergman C. 1847. Über die Verhältnisse der Wärmeökonomie der Thiere zu ihrer Grösse. *Göttinger Studien.* 3:595–708.
- Bouckaert R, et al. 2019. BEAST 2.5: an advanced software platform for Bayesian evolutionary analysis. *PLoS Comput Biol.* 15(4): e1006650.
- Cahill JA, et al. 2018. Genomic evidence of widespread admixture from polar bears into brown bears during the last ice age. *Mol Biol Evol.* 35(5):1120–1129.
- Dabney J, Meyer M, Paabo S. 2013. Ancient DNA damage. *Cold Spring Harb Perspect Biol.* 5:a012567.
- Edgar RC. 2004. MUSCLE: multiple sequence alignment with high accuracy and high throughput. *Nucleic Acids Res.* 32(5):1792–1797.
- Guindon S, et al. 2010. New algorithms and methods to estimate maximum-likelihood phylogenies: assessing the performance of PhyML 3.0. *Syst Biol.* 59(3):307–321.
- Gunther T, Nettelblad C. 2019. The presence and impact of reference bias on population genomic studies of prehistoric human populations. *PLoS Genet.* 15:e1008302.

- Jolly CJ. 1993. Species, subspecies and baboon systematics. In: Kimbel W, Martin L, editors. *Species, species concepts and primate evolution*. New York: Wiley. p. 67–107.
- Jolly CJ, Burrell AS, Phillips-Conroy JE, Bergey C, Rogers J. 2011. Kinda baboons (*Papio kindae*) and grayfoot chacma baboons (*P. ursinus griseipes*) hybridize in the Kafue river valley, Zambia. *Am J Primatol*. 73(3):291–303.
- Katoh K, Standley DM. 2013. MAFFT multiple sequence alignment software version 7: improvements in performance and usability. *Mol Biol Evol*. 30(4):772–780.
- Kopp GH, et al. 2014. The influence of social systems on patterns of mitochondrial DNA variation in baboons. *Int J Primatol*. 35(1):210–225.
- Li H, Durbin R. 2009. Fast and accurate short read alignment with Burrows–Wheeler transform. *Bioinformatics* 25(14):1754–1760.
- Li H, et al. 2009. The sequence alignment/map format and SAMtools. *Bioinformatics* 25(16):2078–2079.
- Madeira F, et al. 2019. The EMBL-EBI search and sequence analysis tools APIs in 2019. *Nucleic Acids Res*. 47(W1):W636–W641.
- Malaspina AS, et al. 2014. bammds: a tool for assessing the ancestry of low-depth whole-genome data using multidimensional scaling (MDS). *Bioinformatics* 30(20):2962–2964.
- McKenna A, et al. 2010. The Genome Analysis Toolkit: a MapReduce framework for analyzing next-generation DNA sequencing data. *Genome Res*. 20(9):1297–1303.
- Meyer M, Kircher M. 2010. Illumina sequencing library preparation for highly multiplexed target capture and sequencing. *Cold Spring Harb Protoc*. 2010(6):pdb.prot5448.
- Nagel U. 1973. A comparison of anubis baboons, hamadryas baboons and their hybrids at a species border in Ethiopia. *Folia Primatol*. 19(2–3):104–165.
- Patterson N, et al. 2012. Ancient admixture in human history. *Genetics* 192(3):1065–1093.
- Pickrell JK, Pritchard JK. 2012. Inference of population splits and mixtures from genome-wide allele frequency data. *PLoS Genet*. 8(11):e1002967.
- Rogers J, et al. 2019. The comparative genomics and complex population history of *Papio* baboons. *Sci Adv*. 5(1):eaau6947.
- Samuels A, Altmann J. 1986. Immigration of a *Papio anubis* male into a group of *Papio cynocephalus* baboons and evidence for an anubis-cynocephalus hybrid zone in Amboseli. *Int J Primatol*. 7(2):131–138.
- Sayers K. 2014. High altitude primates, extreme primates, and anthropological primatology: or, there is more to human evolution than tool use, culture, or African apes. In: Grow N, editors. *High altitude primates. Developments in primatology: progress and prospects*. New York: Springer.
- Schlebusch CM, et al. 2017. Southern African ancient genomes estimate modern human divergence to 350,000–260,000 years ago. *Science* 358(6363):652–655.
- Schubert M, Lindgreen S, Orlando L. 2016. AdapterRemoval v2: rapid adapter trimming, identification, and read merging. *BMC Res Notes*. 9:88.
- Sheng GL, et al. 2019. Paleogenome reveals genetic contribution of extinct giant panda to extant populations. *Curr Biol*. 29(10):1695–1700.e1696.
- Sithaldeen R, Ackermann RR, Bishop JM. 2015. Pleistocene aridification cycles shaped the contemporary genetic architecture of Southern African baboons. *PLoS One* 10(5):e0123207.
- Sithaldeen R, Bishop JM, Ackermann RR. 2009. Mitochondrial DNA analysis reveals Plio-Pleistocene diversification within the chacma baboon. *Mol Phylogenet Evol*. 53(3):1042–1048.
- Skoglund P, et al. 2014. Separating endogenous ancient DNA from modern day contamination in a Siberian Neandertal. *Proc Natl Acad Sci USA*. 111(6):2229–2234.
- Stewart BA, Mitchell PJ. 2018. Late Quaternary palaeoclimates and human–environment dynamics of the Maloti-Drakensberg region, southern Africa. *Quat Sci Rev*. 196:1–20.
- Tosi AJ, Disotell TR, Morales JC, Melnick DJ. 2003. Cercopithecine Y-chromosome data provide a test of competing morphological evolutionary hypotheses. *Mol Phylogenet Evol*. 27(3):510–521.
- Vernon DS. 2013. A morphometric analysis of the phalanges and a fragmentary first metatarsal from the Drimolen hominin site [MPhil. thesis]. South Africa: University of Johannesburg.
- Zinner D, Arnold ML, Roos C. 2009. Is the new primate genus *Rungwecebus* a baboon? *PLoS One* 4(3):e4859.
- Zinner D, Groeneveld LF, Keller C, Roos C. 2009. Mitochondrial phylogeography of baboons (*Papio* spp.): indication for introgressive hybridization? *BMC Evol Biol*. 9(1):83.
- Zinner D, Wertheimer J, Liedigk R, Groeneveld LF, Roos C. 2013. Baboon phylogeny as inferred from complete mitochondrial genomes. *Am J Phys Anthropol*. 150(1):133–140.

Associate editor: Naruya Saitou