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# Ancient and modern DNA reveal dynamics of domestication and cross-continental dispersal of the dromedary

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Dromedaries have been fundamental to the development of human societies in arid landscapes and for long-distance trade across hostile hot terrains for 3,000 y. Today they continue to be an important livestock resource in marginal agro-ecological zones. However, the history of dromedary domestication and the influence of ancient trading networks on their genetic structure have remained elusive. We combined ancient DNA sequences of wild and early-domesticated dromedary samples from arid regions with nuclear microsatellite and mitochondrial genotype information from 1,083 extant animals collected across the species' range. We observe little phylogeographic signal in the modern population, indicative of extensive gene flow and virtually affecting all regions except East Africa, where dromedary populations have remained relatively isolated. In agreement with archaeological findings, we identify wild dromedaries from the southeast Arabian Peninsula among the founders of the domestic dromedary gene pool. Approximate Bayesian computations further support the "restocking from the wild" hypothesis, with an initial domestication followed by introgression from individuals from wild, now-extinct populations. Compared with other livestock, which show a long history of gene flow with their wild ancestors, we find a high initial diversity relative to the native distribution of the wild ancestor on the Arabian Peninsula and to the brief coexistence of early-domesticated and wild individuals. This study also demonstrates the potential to retrieve ancient DNA sequences from osseous remains excavated in hot and dry desert environments.

anthropogenic admixture | *Camelus dromedarius* | demographic history | paleogenetics | wild dromedary

The dromedary (*Camelus dromedarius*) is one of the largest domestic ungulates and one of the most recent additions to livestock. Known as the "ship of the desert" (1), it enabled the transportation of people and valuable goods (e.g., salt, incense, spices) over long distances connecting Arabia, the Near East, and North Africa. This multipurpose animal has outperformed all other domestic mammals, including the donkey, in arid environments and continues to provide basic commodities to millions of people

inhabiting marginal agro-ecological zones. In the current context of advancing desertification and global climate change, there is renewed interest in the biology and production traits of the species (2), with the first annotated genome drafts having been recently released (3, 4).

## Significance

The dromedary is one of the largest domesticates, sustainably used in arid and hostile environments. It provides food and transport to millions of people in marginal agricultural areas. We show how important long-distance and back-and-forth movements in ancient caravan routes shaped the species' genetic diversity. Using a global sample set and ancient mitochondrial DNA analyses, we describe the population structure in modern dromedaries and their wild extinct ancestors. Phylogenetic analyses of ancient and modern dromedaries suggest a history of restocking from wild animals from the southeast coast of the Arabian Peninsula. Dromedaries now extend the list of species for which classic models of domestication from a single center and from wild conspecific individuals in isolation are rejected.

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Data deposition: The sequences reported in this paper have been deposited in the Genbank database (accession nos. JX946206–JX946273, KF719283–KF719290, and KT334316–KT334323).

See Commentary on page 6588.

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In contrast to other livestock species, the evolutionary history and domestication of Old World camelids (Camelini) have remained largely unexplored because of the scarcity of camel bone assemblages from well-dated archaeological contexts (5). Following the Pleistocene, the wild dromedary retreated to ecologically favored areas (i.e., mangrove habitats) on the Arabian Peninsula (6), a rather small geographic region compared with the native distributions of the wild ancestors of other domesticates (*SI Appendix*). The domestication of the dromedary likely happened in the late second millennium BCE as deduced from: (i) diachronic osteometric analysis illustrating a significant decrease in bone size in remains dating to the very end of the second or beginning of the first millennium BCE (ca. 1,100–800 BCE) (7–12); (ii) changes in the cultural context, i.e., increased representation of dromedary bones in settlement refuse vs. large concentrations in sites without architecture, e.g., site of Al-Sufouh, United Arab Emirates (UAE); and (iii) figurines and representations of indubitably domesticated dromedaries (13). Based on the available zooarchaeological records, it is assumed that the wild one-humped camel did not survive the start of the CE (8, 9, 12, 14), in contrast to the wild ancestors of most other livestock species (15, 16). Small numbers of domesticated dromedaries likely arrived in Mesopotamia by the second quarter of the first millennium BCE, but there, as well as in northeast Africa, larger herds appeared only during Late Antiquity and/or early medieval times (fourth to seventh centuries CE) (1, 11, 17). If its use as “camelry” in warfare was minor compared with the horse (1), the dromedary was readily adopted as beast of burden and continued fulfilling this role well into the 20th century CE in caravans sometimes encompassing thousands of animals (18, 19).

In the present study, we address the questions of domestication and demographic history of the dromedary across its geographic range, combining information from ancient DNA Sanger and next-generation sequencing data of wild and early-domestic dromedary osseous remains with modern nuclear (microsatellites) and mitochondrial genetic diversity. Our results show that the domestication process and the current diversity of the species were shaped by early introgression from the wild as well as by human-mediated factors.

## Results and Discussion

**Little Population Structure in Modern Dromedaries, a Consequence of Cross-Continental Back-and-Forth Movements.** By examining modern genetic diversity and its global distribution, it is possible to gain insight into the domestication process, because, in the absence of recurrent introgression, populations close to the putative domestication centers are assumed to retain higher levels of ancestral polymorphism (20). Such distribution of genetic diversity has been suggested to explain the frequently observed negative correlation between genetic diversity and the geographic distance from the place of origin in numerous livestock species (20–25). In the case of the dromedary, before the introduction of the domestic form, there had been no representatives of *Camelus* on the African continent since the Late Pleistocene, and the Holocene native distribution of wild dromedaries seems to have been restricted to the Arabian Peninsula (6, 7). Modern dromedary populations from the Arabian Peninsula therefore were expected to display the highest level of genetic diversity and variation. To test this expectation, we combined two comprehensive datasets encompassing 759 mitochondrial (867 bp; end of cytochrome B, tRNAs threonine and proline, beginning of control region; MT-CR) and 970 multiloci (17 autosomal microsatellites) genotypes, covering five defined geographical regions (26): Eastern Africa (EAF,  $n = 170$ ), Western and Northern Africa (WNAF,  $n = 233$ ), North Arabian Peninsula (NAP,  $n = 349$ ), South Arabian Peninsula (SAP,  $n = 181$ ), and Southern Asia including Australia (SAS,  $n = 150$ ) (Dataset S1).

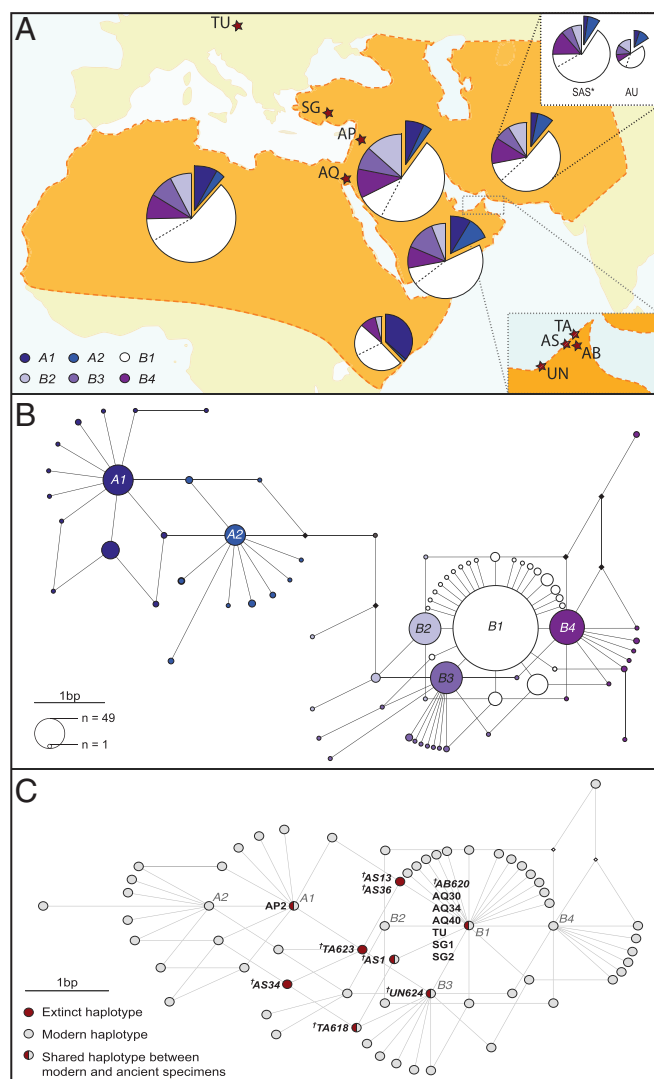
**Shared genetic diversity and population structure in modern dromedaries.** In contrast to the hypothesis that the greatest ancestral variation is retained close to the area of domestication (20), we observed similar amounts of heterozygosity ( $H_E$ : 0.58–0.63) and allelic richness ( $A_r$ : 4.88–6.47) among the different populations (Bonferroni corrected Wilcoxon rank-sum test;  $P > 0.05$ ) (*SI Appendix*, Table

S1). This finding precluded any conclusion about the existence of an ancestral population or a geographic center of dispersion (for comparisons with other camelids, see *SI Appendix*). Shared diversity also was revealed by the analysis of molecular variance with 95.7% (nuclear) and 95.3% (mtDNA) of the variation distributed within populations. Hence, we investigated genetic population structure in modern dromedaries disregarding their geographic origins. Mitochondrial median-joining network (MJN) analysis (27) split the 76 haplotypes into two haplogroups,  $H_A$  and  $H_B$ , containing six major haplotypes ( $H_A$ : A1 and A2;  $H_B$ : B1–4) (Fig. 1B). This partition was supported by Bayesian phylogenetic analysis [posterior probability (PP) = 0.98] (*SI Appendix*, Fig. S1). No phylogeographic pattern was detectable, because the six major haplotypes were observed across the global range of the species (Fig. 1A). In contrast, with the nuclear structure analysis we retrieved an optimal number of two ancestral populations (*SI Appendix*, Fig. S2A), clearly separating EAF dromedaries from all other populations (Fig. 2). This separation also is reflected in the 3D factorial correspondence analysis (*SI Appendix*, Fig. S3) and in the limited population differentiation (nuclear  $F_{ST} = 0.013$ –0.070) (*SI Appendix*, Table S2), a plausible consequence of the intense back-and-forth movements that characterized the use of dromedaries in cross-continental trading.

**Genetic distinctiveness of East African dromedaries.** Modern EAF dromedaries exhibit the lowest nuclear ( $H_E = 0.58$ ,  $A_r = 4.48$ ) but the highest mtDNA ( $H_d = 0.79$ ,  $\theta_\pi = 3.62$ ) diversity of all populations (*SI Appendix*, Table S1). These elevated values could, in principle, be explained by a large proportion of ancestral diversity in the mtDNA or by a cryptic population structure not accounted for in the analysis (28). Although 85% of the investigated haplotypes belonged to  $H_B$ , dromedaries in Eastern Africa exhibited a more balanced ratio between  $H_A$  (38%) and  $H_B$  (62%) (Fig. 1A). These results may be interpreted as the consequence of a random founder effect followed by successive gene flow with a restricted number of sires. Globalization of genetic diversity might not have affected the EAF as much as other populations, likely because of its isolation from the northern part of the continent by eco-geographical obstacles (e.g., the Ethiopian Plateau and the swamps of the Sudd), physiological constraints (humidity, food plants, lack of salt, disease) and, perhaps most importantly, cultural barriers (*SI Appendix*, Fig. S4).

**Subtle population structure within the SAP.** To investigate subtle population structure that might have been masked by the high distinctiveness of EAF, we excluded the latter from structure analysis and observed nine independent clusters (Fig. 2 and *SI Appendix*, Fig. S2B). Despite substantial admixture, two dromedary populations (Awari and Awadi; Dataset S1) from an isolated mountainous region in southwestern Saudi Arabia segregated. Dromedaries from Oman and UAE separated from the cluster containing Southern Asian individuals, whereas WNAF and NAP populations shared common ancestry and genetic diversity. Within the latter only the Hadana breed (Dataset S1) appeared to have a contrasting genetic makeup (Fig. 2).

**Introduction of Arabian dromedaries into Africa.** The absence of genetic structure between WNAF and NAP ( $\phi_{ST} = 0.006$ ;  $P < 0.001$ ;  $F_{ST} = -0.002$ ;  $P > 0.05$ ) points to an extensive exchange of dromedaries introduced into northeastern Africa from the Arabian Peninsula via the Sinai (*SI Appendix*, Fig. S4), possibly starting in the early first millennium BCE and intensifying in the Ptolemaic period (1, 17). From here, dromedaries spread across northern Africa, but their adoption into local economies may have been slow, considering that the first unequivocal evidence for their presence in northwestern Africa comes from archaeological layers dating to the fourth to the seventh century CE (Late Antiquity/Early Middle Ages) (*SI Appendix*). Although WNAF–NAP showed close cross-continental affinities with Southern Arabian and Asian dromedaries, the two African populations were genetically the most distant (EAF/WNAF–NAP  $\phi_{ST} = 0.164$ ;  $F_{ST} = 0.040$ ;  $P < 0.001$ ), in contrast with their geographical proximity. The lowest pairwise genetic distances for Eastern African dromedaries were actually measured with the SAP populations (*SI Appendix*, Table S2), suggesting a few possible routes for domestic dromedaries to be introduced to Eastern Africa. These involve the



**Fig. 1.** Representation of the mitochondrial haplotypes retrieved from 759 modern dromedaries and 15 archaeological specimens. (A) Geographical distribution of the modern haplogroups across the species range (delimited by orange dashed line). Pie charts are proportional to sample sizes of the five distinctive regions (Dataset S1). Haplogroups were defined according to Bayesian analysis of population structure (BAPS) clustering (*SI Appendix*). The proportion of singletons diverging from B1 by one or two mutations (seventh cluster) is depicted by the dotted line within B1 (white). The chart in the upper right corner represents haplogroups retrieved from Southern Asian (SAS\*;  $n = 87$ ) and Australian (AU;  $n = 38$ ) dromedaries. Stars depict locations of the archaeological sites: SG, Sagalassos, Turkey (Early Byzantine, 450–700 CE); TU, Tulln, Austria (second Ottoman–Habsburg war, ca. 1683 CE); AP, Apamea, Syria (Early Byzantine, 400–600 CE); AQ, Aqaba, Jordan (Mamluk and Ottoman periods, 1260–1870 CE). The inset in the lower right corner shows sites in the UAE: AB, Al-Buhais (5000–4000 BCE); AS, Al-Sufouh (ca. 2400–1400 BCE); TA, Tell Abraq (Late Bronze–Iron Age, 1260–500 BCE); UN, Umm-an-Nar (Early Bronze Age, 3000–2000 BCE). (B) MJN displaying 76 haplotypes grouped into two maternal lineages,  $H_A$  (A1 and A2) and  $H_B$  (B1–4). Haplotypes diverging from A1 and A2 and from B1–4 are colored according to BAPS clustering (*SI Appendix*). Circles are proportional to the sample size. Small diamonds represent median vectors corresponding to missing haplotypes or homoplasies. (C) Parsimonious representation of the occurrence and sharing of mitochondrial haplotypes (531 bp) between modern (light gray) and ancient (dark red) samples. Wild dromedary samples are marked with a dagger (†). Taxonomic determinations of ancient specimens are detailed in *SI Appendix*. Umm-an-Nar's sample (UN624) was represented assuming the most frequent nucleotide (nt15486: G). In the case of the alternative allele (nt15486: A), UN624 shared its haplotype with the specimen from Tell Abraq (TA623) (*SI Appendix*). For both networks, consensus network of all shortest trees is shown; branch lengths are proportional to number of mutations.

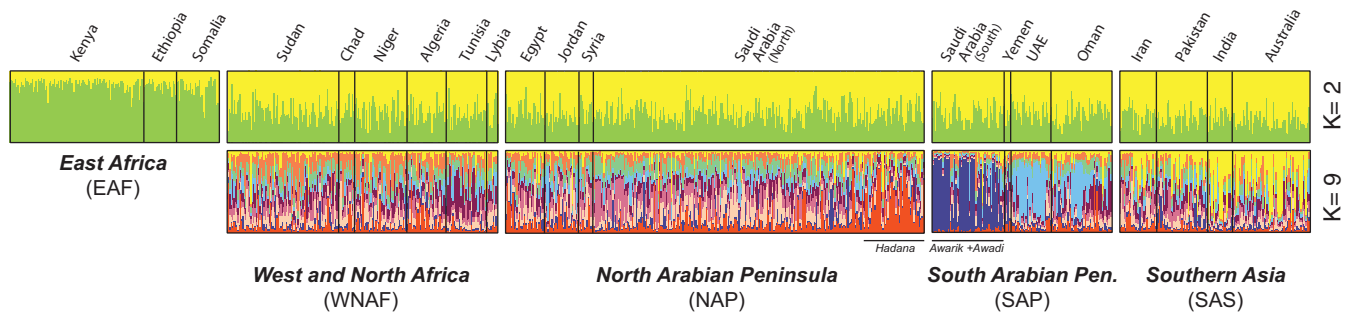
transfer from the Arabian Peninsula by boat either directly across the Gulf of Aden or further north across the Red Sea to Egypt and then traveling south along the western coast of the Red Sea to northwestern Sudan, Eritrea, and Ethiopia (*SI Appendix*, Fig. S4). A seaborne introduction appears likely, because there is increasing evidence that the southern Arabian Peninsula played an important role in domestication [e.g., African wild ass (29)] and in the transfer of crops and livestock [e.g., zebu cattle, fat-tailed sheep (30, 31)] between South Asia and the African continent. Additional evidence for a separate introduction might come from socio-ethological observations; today's Eastern African dromedaries are used largely for milk production rather than for riding and transportation, and this use could be rooted in practices associated with the early stage of dromedary husbandry in the southern Arabian Peninsula (1, 7).

**Representation of the global genetic diversity in Australian dromedaries.** An interesting observation concerns the genetic makeup of the Australian population. Although animals were imported from a single geographic area (northwest of the Indian subcontinent) between the 1860s and 1920s (2, 32), domestic and feral Australian dromedaries possess all mtDNA haplogroups observed in the global population (Fig. 1A) and nuclear diversity similar to that of the global population (Fig. 2 and *SI Appendix*, Table S3). This diversity mirrors the extensive admixture in the dromedary population of the Old World through historical cross-continental exchanges that was already attained by the middle of the 19th century.

### Domestication of Dromedaries and Restocking from the Wild in the Southeast Coast of the Arabian Peninsula.

**Ancient mitochondrial haplotypes in early-domestic and wild (extinct) dromedaries.** In absence of phylogeographic signals supporting the hypothesis of ancestral populations, we investigated the historic genetic repartition before the intensive gene flow induced by large-scale back-and-forth movements. Because poor DNA preservation in arid regions poses significant technical challenges (33), there are only a few findings from hot areas, where ancient DNA (aDNA) contributed significantly to the understanding of prehistoric events (34–37). In this study, we retrieved aDNA from up to 7,000-y-old wild dromedary specimens originating from archaeological contexts in the Arabian desert (*SI Appendix*, Table S4). We successfully amplified 531-bp mtDNA using 10 overlapping primer pairs (*SI Appendix*, Table S5) from eight wild dromedary bones from the sites Al-Sufouh (AS), Tell Abraq (TA), Umm-an-Nar (UN), and Al-Buhais (AB) in the UAE and from seven early-domesticated dromedary specimens excavated in Apamea (AP; Syria), Aqaba (AQ; Jordan), Sagalassos (SG; Turkey), and Tulln (TU; Austria) (Fig. 1A). No novel mitochondrial haplotypes were retrieved in the early-domesticated individuals, because six of them (AQ30, AQ34, AQ40, SG1, SG2, and TU) exhibited MT-CR sequences identical to those of the modern dromedaries belonging to the frequent haplotype B1 (Fig. 1C). Only the Syrian specimen was characteristic of the rare haplotype A1 (AP2) (Fig. 1C). This finding implies that both haplogroups ( $H_A$  and  $H_B$ ) were already present in the Levantine herds of the fourth to seventh century CE. Different estimates of the time to the most recent common ancestor (TMRCA) of  $H_A$  and  $H_B$  [ $>5,700$  y ago (ya)] (*SI Appendix*, Table S6) predate the assumed period of domestication during the end of the second or beginning of the first millennium BCE (7, 8, 12, 14), suggesting that at least two, but more likely a minimum of six wild maternal lineages were captured during the process of domestication. The eight ancient wild dromedary samples from four different locations in the UAE presented at least six different mitochondrial haplotypes (Fig. 1C) with a diversity of  $\theta_\pi = 1.643$  and  $H_d = 0.929$  (*SI Appendix*, Table S1). At least three of these remains (AS1, AB620, and TA618) shared their respective haplotypes with modern dromedaries belonging to haplogroup  $H_B$ . The last three retrieved haplotypes were unique to wild camels (AS13 with AS36, AS34, TA623) and occupied an intermediate position between the modern haplogroups  $H_A$  and  $H_B$  (Fig. 1C; see *SI Appendix* for UN624).

**Wild dromedaries from the southeast coast of the Arabian Peninsula contribute to the domestic gene pool.** The sharing of MT-CR sequences characteristic of  $H_B$  haplotypes between wild and modern



**Fig. 2.** Individual assignment (structure) plots of 970 (global dataset) and 810 dromedaries (excluding EAF) for a theoretical number of ancestral genetic populations ( $K$ ) set at 2 and 9, respectively. Optimal clustering solution determined with DeltaK is reported in *SI Appendix*, Fig. S2. Sample sizes of the distinctive regions and countries are presented in *SI Appendix*, Table S1 and Dataset S1.

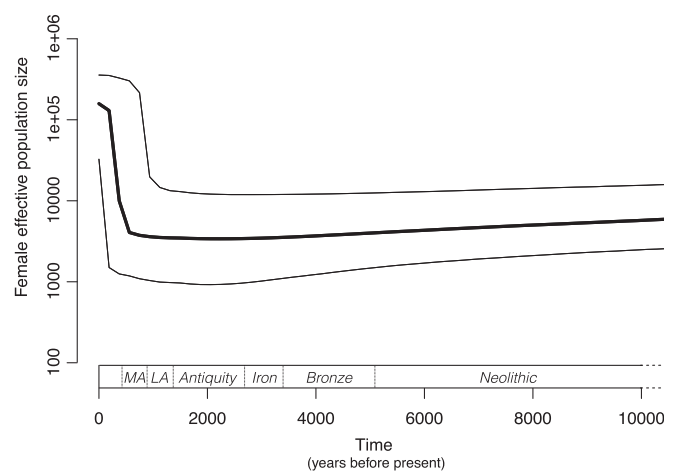
dromedaries from the same geographical region (today's UAE) illustrates the contribution of ancient relatives of these wild dromedary populations to the modern domestic gene pool. Although the wild specimens in our sample set come from a limited geographical distribution, large prehistoric faunal assemblages from sites dating from 5000–500 BCE in other parts of the Arabian Peninsula, such as coastal Yemen (38), have not yielded wild dromedary remains so far, indicating that at the time people started domesticating dromedaries, the native distribution of the wild ancestor of the one-humped camel already may have been limited to the Arabian southeast coast. This finding, together with the low frequency of  $H_A$  in modern dromedaries, suggests that the  $A$ -haplotypes were already present in lower frequency in the ancestral wild dromedary population, or, alternatively, were restricted to regions where there has been less intense archaeological research and/or poor faunal preservation.

### Dynamics of Dromedary Domestication.

**Population expansion in the context of domestication.** In the context of domestication, molecular signals of sudden expansion are often interpreted as population growth or diffusion of domesticates across a wider geographic range (39). From the mtDNA, we obtained negative values of Tajima's  $D$  ( $-1.735$ ;  $P = 0.021$ ) and Fu's  $F_S$  ( $-87.48$ ;  $P < 10^{-5}$ ), which, in the absence of selection, indicate past demographic expansion. In the MJN analysis, we distinguished two haplogroups harboring six haplotypes at high frequencies, from which singletons radiate differing by one or two mutations (Fig. 1B). We could not reject the hypothesis that the pairwise differences between sequences of  $A1$  and  $A2$  and  $B1-4$  and their respective “derived” haplotypes were distributed according to a Poisson distribution, which indicates sudden expansion (40) and provides support for multiple contributions of ancestral female lineages to the current gene pool of modern dromedaries (*SI Appendix*). The Bayesian Skyline Plot (BSP) obtained from modern and early-domesticated maternal sequences (448 bp) shows a rise of the domestic  $N_e$ , around 600 ya [95% highest posterior density (HPD): 300–1,000 ya] (Fig. 3). This finding coincides with the Arab expansion in general and with the rise of the Ottoman Empire, the conquest of Constantinople (1453 CE), and of Southern Asia, including the Red Sea coasts, in the following century (41). Once Medina and Mecca had become part of the Empire (in the early 16th century CE), dromedaries were widely used for long-distance trade along the ancient Incense Route and for pilgrim transport (42) (*SI Appendix*, Fig. S4). There is tentative evidence that trade between southwest and southeast Arabia began as early as the first centuries of the first millennium BCE. This exchange was almost certainly camel-borne (13).

**Approximate Bayesian computation inferences of domestication scenarios.** Four scenarios can potentially explain the patterns of genetic diversity recorded in modern dromedaries: at the time of domestication, the initial gene pool was captured from: (i) one unique and diverse wild dromedary population; (ii) a primary

small population of domesticates, with subsequent introgression of wild lineages into the early-domesticated gene pool; (iii) two independent source populations, each represented by one of the two observed ancestral lineages; or (iv) two source populations at successive time periods. Using approximate Bayesian computation (ABC) algorithms (43) on a combined mitochondrial and microsatellite dataset ( $n = 642$ ), we simulated these four different scenarios (*SI Appendix*, Fig. S6). We obtained realistic PPs for up to 11 historic and demographic parameters (*SI Appendix*, Fig. S7), with the exception of the first scenario, for which the  $N_e$  of “Pop 2” was larger than  $10^8$  individuals and could not be reduced to a biologically meaningful value, and the time of divergence between populations was around 50 ya (generation time of 5 y). Thus, the remaining scenarios were compared to assess the one that best fit the data. The highest PP and Bayes Factor (BF) (*SI Appendix*, Tables S7 and S8) were obtained for the second scenario involving one domestication mode with introgression from a wild unsampled source population. In all pairwise comparisons the second scenario had a higher probability, with the BF ranging from  $\sim 63$  to  $\sim 10^{23}$ . The remaining comparisons had substantially smaller BF values, mostly lower than 1 (*SI Appendix*, Table S8). This endorsement of the second scenario mirrors recent studies in pigs and other livestock in which a model incorporating continuous gene flow between a wild and a domestic species was better supported than traditional



**Fig. 3.** BSP derived from the alignment of 759 modern with seven early-domesticated dromedary MT-CR sequences. The thick solid line depicts the median estimate of  $N_e$ , with black thin lines delimiting the 95% HPD. We used the archaeological dating of the wild and early-domesticated dromedary samples (*SI Appendix*, Table S4) to estimate the substitution rate  $\mu = 1.232 \times 10^{-6}$  substitution-site $^{-1}$ yr $^{-1}$  (95% HPD:  $4.435 \times 10^{-7}$ ,  $2.213 \times 10^{-6}$ ). LA, Late Antiquity; MA, Middle Ages.



hypotheses assuming reproductive isolation (15, 16). Because wild and early-domesticated dromedaries coexisted in the Arabian Peninsula for only a short time [probably less than 2,000 y (8)], the period of potential gene flow was rather short compared those for cattle (16), pigs (15), or horses (25, 44, 45). This short period for potential gene flow, together with the possible existence of genomic islands of domestication, as recently proposed in pigs (15), likely explains the maintenance of the domestic phenotype in dromedaries. However, in the absence of complete genomes from wild dromedaries, this question requires further investigation.

Regarding the later introgression of an unsampled wild gene pool, the poor knowledge of the Holocene distribution of wild one-humped camels on the Arabian Peninsula is a limiting factor. Concentrations of bones indicative of larger camel herds have been found only in Neolithic to Bronze Age contexts on the eastern coast of the Arabian Peninsula (8, 14, 46, 47). The presence of pre-Iron Age camel remains in the Southern Levant has been controversial, because these specimens were considered to be intrusive to the archaeological context or unreliably  $^{14}\text{C}$ -dated (9, 48).

**Population bottlenecks predating domestication.** Using coalescent simulations based on microsatellite diversity (MSVAR 1.3) in modern dromedaries, we captured several signals of severe bottlenecks ( $N_e$  reductions up to 65-fold) predating domestication (~8,600 ya in EAF; ~5,100 ya in the other populations) (*SI Appendix*, Fig. S8 and Table S9). The genetic distinctiveness of the EAF population, which could be a consequence of a random founder effect, might explain the precocity of its  $N_e$  decline. The drastic population reduction observed across all populations possibly relates to abrupt worldwide climate events, which triggered a general cooling and drying of the northern hemisphere, causing region-wide crop failures and the collapse of several civilizations (49–55). By the time cultural control over the wild dromedary was initiated, its native population and distribution may already have become diminished (*SI Appendix*, Fig. S5) and increasingly disjointed before the global extinction of the wild populations less than two millennia after the appearance of the domestic form (8, 14).

Given the environmental context in which the wild dromedary would have evolved, it can be assumed that its native distribution and population size were generally quite restricted compared with the ancestral ranges of other livestock species before domestication. As suggested by the environmental context of the archaeological findings, the wild ancestors of *C. dromedarius* spent part of their lives foraging in coastal habitats including mangroves (6). Salt is crucial to the health of camels (47, 56), and feeding in coastal habitats might have offered possibilities to enhance salt intake because of sea spray and the presence of halophyte vegetation. Because in prehistoric times mangroves may have occurred on the coastal southern Arabian Peninsula, the possibility that this region also sustained a wild dromedary population cannot be excluded. However, elevated sea levels and the lack of (zoo)archaeological investigations in the southern Arabian Peninsula may explain why genetic screening of the ancestral diversity remains incomplete.

## Conclusion

The dromedary's fundamental role in the tradition of cross-continental caravan networks gave rise to an intense sharing of genetic variation, blurring genetic signals about ancestral diversity and possible center of domestication. Nevertheless, using a large modern DNA dataset in combination with a number of ancient sequences, we were able to support a scenario with an initial domestication followed by consecutive introgression from wild populations echoing findings from other species (57), such as horses (25, 44, 45), cattle (16), and pigs (15). Interestingly, in dromedaries, this restocking occurred from an unsourced wild "ghost" population, a pattern thus far observed in only few other domestic species (e.g., pigs and dogs). A remarkable feature in the history of dromedary domestication is the substantial genetic diversity of the domestic population, given the temporally and geographically restricted coexistence of early-domestic animals and their wild ancestors, which already were heading to extinction when the domestic form emerged. Modern dromedary populations

largely maintained and consolidated this ancestral diversity, often lost in other livestock, underlining their potential to adapt sustainably to future challenges of desertification and climate change.

## Materials and Methods

**Modern and Ancestral Genetic Diversity.** Hair, blood, and saliva samples were collected commensally during routine veterinary treatments, and all owners agreed to the analysis; no further specific permissions were required from the Ethics Committee of the Vetmeduni Vienna for this study. To infer the genetic diversity, population structure, and differentiation of the modern and ancient dromedary populations, we performed genetic analyses on a total of 1,083 modern dromedaries originating from 21 countries, seven early-domesticated (400–1870 CE) specimens, and eight wild dromedary specimens (5000–1000 BCE) (Fig. 1A). Wild dromedaries were classified based on the archaeological context (*SI Appendix*) and morphological differentiation (12). Detailed information about samples is given in Dataset S1; collection, wet-laboratory, and in silico procedures are given in *SI Appendix*, Table S4.

**Population Genetics and Demographic Analysis.** Genetic diversity estimators, genetic distances on the nuclear and mitochondrial data, and neutrality tests (mtDNA) are detailed in *SI Appendix*. Test of the goodness of fit for the Poisson distribution to the pairwise differences between the haplotypes and minimal mitochondrial diversity in the initial pool of domesticated camels (*SI Appendix*) followed Luikart et al. (58). Historical population demographic dynamics were assessed using the 448-bp MT-CR alignment from modern, early-domesticated, and wild samples. The birth–death skyline plot serial model (59) was implemented in BEAST 2.2.0 (60), accounting for serial samples taken at different time points (*SI Appendix*, Table S4). The resulting substitution rate was used to compute BSPs for domestic and wild dromedaries separately (*SI Appendix*). Coalescent simulations based on microsatellite diversity were implemented in MSVAR 1.3 (61, 62). The model assumes a single stable ancestral population  $N_1$  at some time  $t_1$  ago that experienced a demographic change (bottleneck or expansion) starting at time  $t$  and changed exponentially in size to the current population  $N_0$ . We simulated two different demographic scenarios by choosing (i) larger prior lognormal distribution values for  $N_0$  than for  $N_1$  (expansion) and (ii) vice versa (a bottleneck). In the absence of a species-specific microsatellite mutation rate in camels, we chose an average mammalian microsatellite mutation rate (63) of  $10^{-4}$  (rate variation:  $10^{-3}$ – $10^{-5}$ ) (*SI Appendix*).

**ABC Inferences of Four Alternative Domestication Scenarios.** To test the hypotheses of one independent or multiple domestication scenarios vs. restocking from the wild, we used ABCtoolbox (43) on the combined ( $n = 642$ ) mitochondrial and microsatellite dataset. For each of the four scenarios (*SI Appendix*, Fig. S6) we simulated a large number of datasets (1,000,000) using Fastsimcoal2 (64) under the coalescent model drawing parameter values from prior distribution ranges (*SI Appendix*, Table S10). We tested a maximum of 11 historical parameters and generated 15 summary statistics for each simulation in Arlequin3.5 (65) (*SI Appendix*, Table S11). Summary statistics with highest pairwise correlations (R correlation test with Spearman's rho statistics; *SI Appendix*, Fig. S9) were removed, resulting in 12 summary statistics for further analysis. With the 5,000 simulations closest to the observed dataset, we evaluated model differentiation with the R package abc (66) (*SI Appendix*, Fig. S10) and assessed model fit with the ABC-GLM postsampling adjustment step built into ABCtoolbox (43, 67) to calculate marginal densities and probability of each scenario. Marginal distributions of each scenario were used to calculate PPs and BF for each pairwise comparison between scenarios; the alternative hypothesis can be rejected if the BF between two scenarios is greater than three (43, 68).

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