# The goat domestication process inferred from large-scale mitochondrial DNA analysis of wild and domestic individuals

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**The emergence of farming during the Neolithic transition, including the domestication of livestock, was a critical point in the evolution of human kind. The goat (*Capra hircus*) was one of the first domesticated ungulates. In this study, we compared the genetic diversity of domestic goats to that of the modern representatives of their wild ancestor, the bezoar, by analyzing 473 samples collected over the whole distribution range of the latter species. This partly confirms and significantly clarifies the goat domestication scenario already proposed by archaeological evidence. All of the mitochondrial DNA haplogroups found in current domestic goats have also been found in the bezoar. The geographic distribution of these haplogroups in the wild ancestor allowed the localization of the main domestication centers. We found no haplotype that could have been domesticated in the eastern half of the Iranian Plateau, nor further to the east. A signature of population expansion in bezoars of the C haplogroup suggests an early domestication center on the Central Iranian Plateau (Yazd and Kerman Provinces) and in the Southern Zagros (Fars Province), possibly corresponding to the management of wild flocks. However, the contribution of this center to the current domestic goat population is rather low (1.4%). We also found a second domestication center covering a large area in Eastern Anatolia, and possibly in Northern and Central Zagros. This last domestication center is the likely origin of almost all domestic goats today. This finding is consistent with archaeological data identifying Eastern Anatolia as an important domestication center.**

livestock origins | Neolithic expansion | phylogeography | Middle East

Together with sheep, cattle, and pigs, goats were one of the first domesticated ungulates (1–4). The archaeological evidence traces goat domestication as far back as *ca.* 10,500 calibrated Before Present (cal. B.P.) in the high Euphrates valleys, in Southeastern Anatolia (1–3) and 9900 to 9500 cal. B.P. in the Zagros mountains (4–7). The hypothesis of goat domestication originating in the Southern Levant (8) seems to be now excluded, and the earliest aceramic Neolithic goats in the Lower Indus valley appear to have been imported from a nearby western area (9). It is now widely recognized that the goat's wild ancestor is the bezoar, *Capra aegagrus* (10).

Recent analysis of 2,430 domestic goat individuals revealed a total of six different monophyletic mitochondrial DNA (mtDNA) haplogroups A, B, C, D, F, and G, with the A haplogroup representing >90% of individuals (11). The three goat (*C. hircus*) mtDNA haplogroups (A, B, and C) found by Luikart *et al.* (12) have been interpreted to indicate three distinct domestication events. Assuming a single haplotype domesticated per haplogroup and a coalescence time of 10,000 years for the most common A haplogroup, it was hypothesized that the domestication of B and C haplogroups occurred approximately 2,130 and 6,110 years ago, respectively (12). However, the finding of the C haplogroup dating to 7,500 years ago in Southern France (13), far from putative domestication centers, threw the sequential domestications hypothesis (12) into question.

In this context, our main objective was to better understand the domestication process through an extensive analysis of the mtDNA polymorphism, both in the modern domestic goat and in the present-day descendants of its wild ancestor, postulating that the latter are representative of the early Holocene populations. More specifically, using extensive and well-controlled sampling in the field, we aimed to localize the putative domestication centers by finding the present-day wild populations bearing the closest genotypes when compared to the domestic populations. Thus, we analyzed the mtDNA control region of 473 modern bezoars from 43 localities covering most of the distribution range, and compared it with the polymorphism of the homologous region in domestic goats.

## Results

The genetic diversity of present bezoars was estimated from a sampling that covered the whole distribution range of the species. More than 600 bezoar samples (feces, tissues from dead carcasses, bones) were collected in the field. Out of these samples, a total of 469 mtDNA control-region sequences (hypervariable segment 1) were produced (accession numbers EF989163–EF989596, EF989609, EF989612, EF989613, EF989615–EF989645). Additional sequences corresponding to individuals of known origin were retrieved from GenBank (accession numbers: AJ317866, AJ317867, AB110590, AB110591). Precise information on all samples is supplied in the supporting information (SI) Table S1. The

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Data deposition: The sequences reported in this paper have been deposited in the GenBank database (accession nos. EF989163–EF989596, EF989609, EF989612, EF989613, and EF989615–EF989645).

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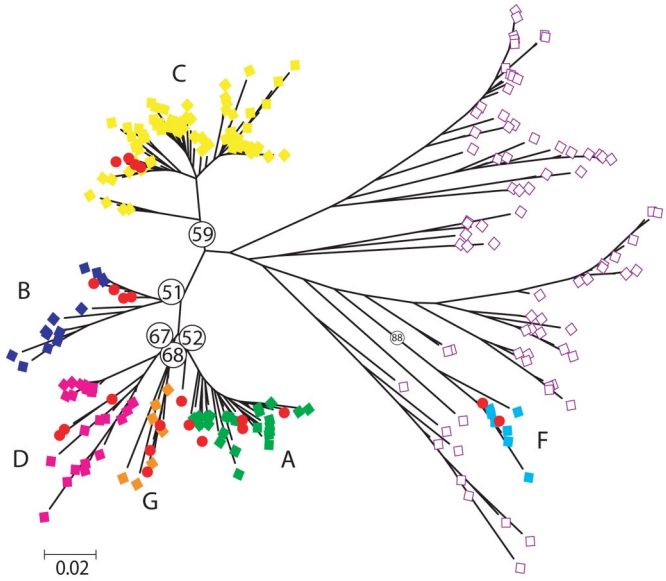


**Fig. 1.** Phylogenetic relationships of the 243 haplotypes from the 473 bezoars studied. This tree was obtained with the NJ method. To identify shared mtDNA haplogroups, 22 haplotypes chosen to represent the overall diversity of modern domestic goats (11) have also been included in the analysis (*red*). The scale represents the genetic distance. The different colors correspond to the haplotypes from the different mtDNA haplogroups found in domestic goat (A, *green*; B, *dark blue*; C, *yellow*; D, *purple*; F, *light blue*; G, *orange*). The other bezoar haplotypes are represented in white.

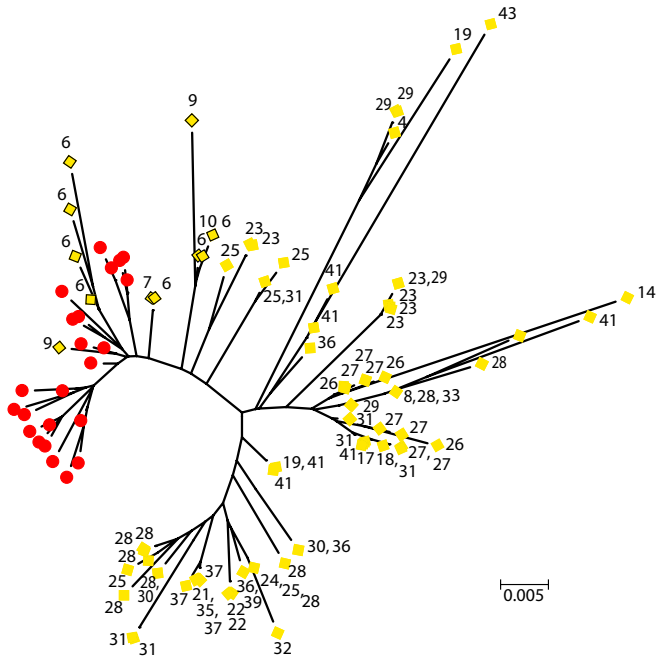


**Fig. 2.** Phylogenetic tree (NJ) of the C haplogroup in both goats (*red*) and bezoar (*yellow with black border* from Eastern Turkey, *yellow* from other locations). The numbers represent the populations as in Fig. 3*B* and Table S1. The close relationships between bezoars from Eastern Turkey and goats suggest that the domestication of the C haplogroup occurred in this area.

473 bezoar sequences corresponded to 221 unique haplotypes (haplotype diversity: 0.9884). According to insertion/deletion events, the analyzed sequences range from 481 to 558 bp and showed a high polymorphism, with 256 sites with substitutions over the 558 bp of the alignment (225 sites with transitions, 84 sites with transversions).

The tree topologies obtained with neighbor-joining (NJ), Bayesian (MB), and maximum likelihood (ML) phylogenetic methods for the 243 haplotypes (221 haplotypes from bezoar, 22 reference haplotypes from goat) were very similar, and only the NJ result is presented in Fig. 1. Among the 221 haplotypes found in the 473 studied bezoars, 142 were within all of the haplogroups previously identified in domestic goats (11). Within the largest haplogroup (i.e., the C haplogroup), goats' haplotypes were grouped together, and were closer to bezoars from Eastern Turkey than to those from Iran (Fig. 2). The total genetic variation estimated with analysis of molecular variance (AMOVA) (14) was distributed within populations (42.66%) and among populations within a geographic region (42.35%). Only 14.99% of the diversity was distributed among regions, which reflects the low phylogeographic structure in bezoars (Table 1). The geographic distribution of the different bezoar haplogroups clearly illustrates this low phylogeographic structure (Fig. 3).

Not only did we find a strong signature of population expansion in domestic goats, but also in close-to-domestic bezoars (bezoars bearing mtDNA haplotypes close to those found in domestic goats). On the other hand, bezoars not-close-to-domestics exhibited a very weak historical population expansion (Table 2). The results of a Bayesian skyline plot (15) confirmed these results and provided further details on the demographic history (Fig. 4). Both domestic goats from Iran and bezoars of the C haplogroup exhibited a strong population expansion, more or less at the same time. Such a population expansion was not found in bezoars not-close-to-domestics, and bezoars of the A, B, D, F, and G haplogroups (except for A haplotypes from Iran, see *SI Discussion*).

## Discussion

None of the haplogroups of wild bezoar appear to have undergone a significant reduction in population size since the Early Holocene (see Fig. 4). This suggests that bezoar populations were not modified so much by humans that present-day genetic structures would not reflect those of the Early Holocene. Thus, it makes sense to base historical assumptions on the genetic patterns observed today, even while hoping that they will someday be strengthened by studies of ancient DNA.

**Table 1. Partition of the genetic variance among geographic regions and populations by analysis of molecular variance for bezoars (*Capra aegagrus*)**

| Source of variation | df | Sum of squares | Variance components | % of variation |
|---|---|---|---|---|
| Among Regions | 7 | 4170.112 | 6.08135 | 14.99** |
| Among populations within regions | 35 | 6828.453 | 17.18020 | 42.35** |
| Within populations | 430 | 7443.019 | 17.30935 | 42.66* |
| Total | 472 | 18441.584 | 40.5709 | |

All percentages of variations are significantly different from 0 (*,: $P < 0.001$; **,: $P < 0.00001$). d.f.,: degree of freedom.

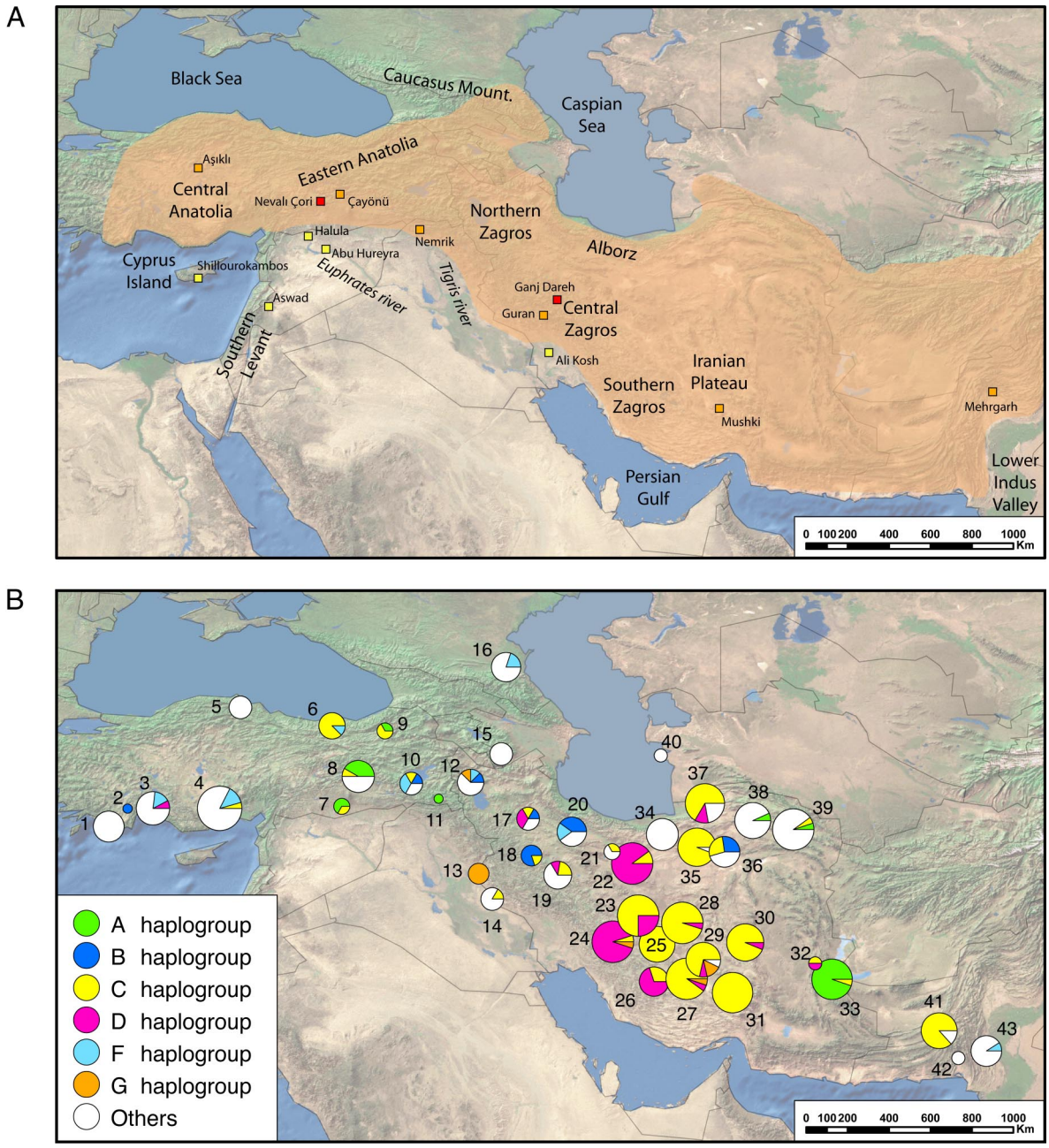


**Fig. 3.** Study area and geographic distribution of the mtDNA haplogroups in the bezoar. (*A*) Natural distribution of the bezoar according to Uerpmann (38). This distribution may not have changed since the beginning of goat management/domestication, and stops at the eastern limit of the map. The archaeological sites that give evidence of local pre-Neolithic goat domestication are represented in red. The sites that suggest either local goat domestication or early prepottery Neolithic transfer of domesticated goat are represented in orange. Finally, the sites that provide evidence of transfer of domestic goats out of the original geographic range of the bezoar before the middle of the 10th millennium cal. B.P. are represented in yellow (see Table S1). The northern Zagros comprises the Iranian Provinces of Azerbaijan Gharbi, Zanjan and Kurdistan; the Central Zagros comprises Kermanshah, Lorestan, Khuzestan, and Isfahan Provinces. The Southern Zagros mainly comprises the Fars Province. (*B*) Geographic distribution of the mtDNA haplogroups in the bezoar. The size of the circles is proportional to the number of individuals analyzed. The different bezoar haplogroups are color-coded as in Fig. 1. Different localities are identified by numbers, as in Table S1.

The phylogeographic structure of the bezoar is weak (see Table 1 and Fig. 3*B*) compared to other wild ungulates (see e.g., ref. 16), and the same mtDNA haplotypes can be found in very distant localities (e.g., 1,635 km for haplotype 54 found in localities 8 and 28; 3,022 km for haplotype 134 found in localities 6 and 43, and so forth). Such mixing of haplotypes is very unusual in natural populations (except for animals with high dispersal abilities such as birds; e.g., refs. 17, 18). The most likely explanation for this mixing in bezoars is that humans translocated many animals in the past, probably during the early domestication phase before morphological modifications, or even that some early domestic animals have feralized (returned to the wild). Such a transfer and subsequent feralization are archaeologically attested in Cyprus (19, 20). This mixing is particularly obvious in the C haplogroup that now occupies almost all of the bezoar distribution area (see Fig. 3*B*).

Surprisingly, bezoars bearing haplotype close-to-domestic goats have had a significantly higher population growth rate, compared to other bezoars (see Table 2). This evidence of a

**Table 2. Estimation of population growth rates (most probable estimates and credible intervals) for domestic goat and for two categories of bezoar (wilds close-to-domestics; wilds not-close-to-domestics) using Lamarc v2.2 (34)**

| | Growth rate | 95% Credible intervals |
|---|---|---|
| No gene flow with domestics | | |
| Domestics | 260.73 | 252.77–268.47 |
| Wilds close-to-domestics | 68.72 | 60.87–85.22 |
| Wilds not-close-to-domestics | 26.84 | 19.62–35.64 |
| Gene flow with domestics | | |
| Domestics | 155.56 | 123.29–164.09 |
| Wilds close-to-domestics | 60.15 | 53.14–76.09 |
| Wilds not-close-to-domestics | 36.55 | 25.01–45.84 |

The demographic model always assumes migration between wild populations. Results presented in the upper half of the table assume no migration between wilds and domestics. Results presented in the bottom half assume migration between wilds and domestics. Four independent runs gave similar results (one run presented). The growth rate given is equal to $g/m$, where $g$ is the parameter governing the exponential growth model used by Lamarc and $m$ is the mutation rate.

population growth suggests a phase of demographic control and protection of some populations of bezoars in the wild, before the isolation of the true early domestic herds by humans [i.e., Horwitz's incipient domestication (21)]. This scenario is consistent with archaeological predictions (22), and maybe also with the presence of a male- and young-biased culling pattern without size decrease, as at Ganj Dareh in the Central Zagros, although sometimes interpreted as true domestication (6). Such biased culling patterns reflect a demographic control that would have occurred before the practice of captivity, which is considered to lead to size decreases (23). This early phase of management (19) has been suggested by some archeologists to have lasted several centuries or even millennia (2, 24).

A more detailed analysis of this population growth in bezoar close-to-domestics showed that this signal is predominantly a result of the individuals of the C haplogroup. According to the Bayesian skyline plots (see Fig. 4), this population expansion occurred at about the same time as that of domestics from Iran, probably ≈10,000 years ago (4, 6–7). Other close-to-domestic wild haplotypes do not show such a strong population expansion (see Fig. 4). Given the strong predominance of the C haplogroup in Southern Zagros (Fars Province) and in the Central Iranian Plateau (Yazd and Kerman Provinces), and to its significant population expansion at the time of domestication, one can hypothesize that these regions were at the origin of the C haplogroup, and that an incipient domestication phase began there. This phase of control in the wild would also have occurred in the Central Zagros, and could have been characterized by culls of younger males and older females, which is, however, interpreted as true domestication in ref. 6.

Today, 90% of the domestic goat mtDNA haplotypes belong to the A haplogroup, a proportion that cannot have changed dramatically in the expanding goat population since domestication. It is

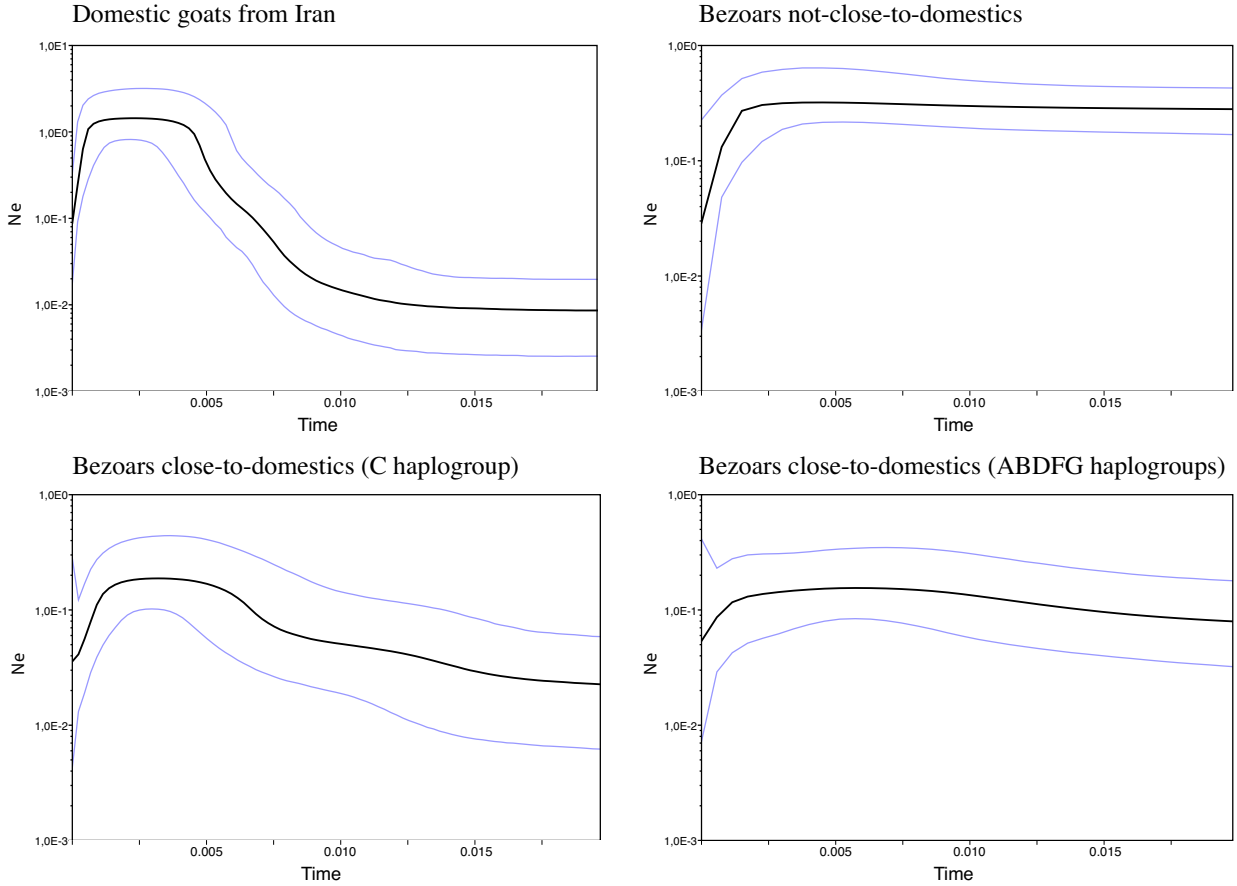


**Fig. 4.** Comparison of the Bayesian skyline plots (15) for domestic goats from Iran and for three different categories of bezoars. The thick solid lines correspond to the median estimate of the effective population size (*Ne*) according to time. The blue lines show the 95% highest posterior densities limits. *Ne* is presented on a logarithmic scale. Time is plotted linearly, the scale corresponding to the number of mutations per nucleotide site. Both domestic goats from Iran and bezoars close-to-domestics of the C haplogroup show a strong population expansion, probably at the domestication time ≈10,000 years ago.

highly unlikely that the frequency of goats from the A haplogroup at the time of domestication was <87% (see *SI Methods* and Fig. S1). The A haplogroup is missing in bezoars from the Zagros and from the Iranian Plateau, and its presence in the easternmost locality analyzed in Iran (locality 33 in Fig. 3*B*: Sistan) most probably results from introgression from or feralization of domestic goats (see *SI Discussion*). The most likely origin of the A haplogroup in goats therefore lies in Eastern Anatolia, where it is common in wild populations. This is fully consistent with recent archaeological evidence of goat domestication there *ca.* 10,500 cal. B.P. (e.g., Nevalı Çori, 3, 5) (see Fig. 2*A*). The bezoar C haplogroup has a widespread geographic distribution, but the closest haplotypes to the domestics are found in Eastern Anatolia (see Figs. 2 and 3*B*), suggesting that the domestic goat C haplogroup also originates from this region. Bezoars of the C haplogroup in Eastern Anatolia might have been translocated from the Southern Zagros or the Central Iranian Plateau during the early domestication phases, as suggested by the presence of the same C haplotype in localities 8 and 28 (see Fig. 3*B*). The other haplotypes B, D, F, and G are also found in domestics, but with a low contribution (7.69%; ref. 11). These haplotypes might have integrated the domestic goat gene pool either during the early spread of domestics in the Northern and Central Zagros, or by small-scale domestications in this area. It is possible that these different events occurred at different times, over a long period between the earliest known ungulate domestications, *ca.* 10,500 cal. B.P., and the latest neolithisation steps in the Near and Middle East during the eighth and seventh millennia cal. B.P. On the other hand, our results confirm that goats were not domesticated in the area of the Indus Valley (9) and suggest that the early Neolithic domestic goats in this area came from >1,000 km to the west: that is, much further than previously suspected. The C haplotypes from this region (locality 41, Pakistani Balochistan) are not closely related to the domestic haplotypes that should originate from Eastern Anatolia. Moreover, the unique bezoar of the F haplogroup that was found in the Lower Indus Valley (locality 43) is geographically isolated from all other bezoars of this haplogroup, and shared its haplotype with domestics. Thus, this probably results from an introgression or a feralization.

It is possible, with all of the mtDNA data on goats and bezoars, to infer a domestication scenario. The domestication process in goats probably occurred in two different areas, starting independently in both the Southern Zagros/Central Iranian Plateau, and in Eastern Anatolia. Archaeozoological data showing morphological changes associated with the domestication process support the latter center (1–3, 5). They also indicate early and independent bezoar domestication without morphological modification in Ganj Dareh, which is located in the Central Zagros (4, 6). The discrepancy between the genetic and archaeological data may be because of the lack of Neolithic sites in the Southern Zagros older than those found in the Central Zagros (Ganj Dareh). Genetic data therefore suggest unknown early Neolithic bezoar management in the Southern Zagros (Fars Province) earlier than 9900 to 9700 BP. In the Central Iranian Plateau (Yazd and Kerman Provinces), the absence of archaeological data on the early Neolithic should direct future research for testing and dating the genetic indications of local goat domestication. These future studies should consider that the early domestication steps might not have induced any detectable morphological change. The Bayesian skyline plots for domestic goats from Iran and for bezoars of the C haplogroup showed a significant population expansion at nearly the same time. We cannot confirm, based on these data, the archaeological statement that domestication in the Near East center might have begun a few centuries earlier than the Zagros center (3, 6). The very low percentage of individuals of the C haplogroup in modern domestic goats (1.44%) (11) suggests that the domestication center in Southern Zagros/Central Iranian Plateau did not significantly contribute to the goat gene pool. That population probably collapsed when domestic goats from the Anatolian center spread in this region, much as did the population of Near Eastern domestic pigs during Neolithic times in Europe (25). Nevertheless, the Southern Zagros and Central Iranian Plateau might have played a key role in this first phase, being the source of several translocated populations over almost the whole geographic distribution of the bezoar. According to the over-representation of the A haplotype in modern domestic goats, Eastern Anatolia was undoubtedly the center that most contributed to the modern-goat gene pool. It would be interesting to compare the picture offered by the maternally inherited mtDNA with the polymorphism obtained from autosomal markers or from Y-chromosome sequences.

## Materials and Methods

**Sampling.** More than 600 bezoars were sampled from 42 geographic localities representing the whole distribution area, mostly using a noninvasive approach (26). Fresh feces were collected in the field, after observation of the bezoar from a distance to ensure the species origin of the sample. For each individual, two samples were collected and preserved using two methods (silica gel and ethanol 96%). Some samples also consisted of skin and muscle obtained from hunters' kills and carcasses. No samples from zoos were considered in this study because of the risk of hybridization in captivity. To supplement the samples collected in the field, we retrieved four sequences of *C. aegagrus* from GenBank. For comparison with domestic goats, the data set was completed with 22 reference sequences of the mtDNA control region of different haplogroups of *C. hircus* (11). All *C. aegagrus* samples used for the mtDNA analysis are listed in Table S1.

**DNA Extraction.** The whole genomic DNA was extracted from fecal samples after 20 min in washing buffer (Tris·HCl 0.1 M, EDTA 0.1 M, NaCl 0.1 M, N-lauroyl sarcosine 1%, pH 7.5–8.0), using DNAeasy extraction blood kit (Qiagen) following the manufacture's protocol for animal blood, except for the incubation with protease (2 h at 56 °C with 55 $\mu$l of protease). For tissue samples, DNA was extracted using the tissue extraction kit QIAamp Animal Tissue kit (Qiagen) following the manufacture's instructions.

**Mitochondrial DNA Amplification.** A 598-bp fragment was amplified using the primer pair CAP-F (5′-CGTGTATGCAAGTACATTAC-3′) - CAP-R (5′-CTGATTAGTCATTAGTCCATC-3′) or an 893-bp fragment with the primer pair CAP-pro (5′-AGCCTCACTATCAGCACC-3′) - CAP-R. PCR amplifications were conducted in a 25-$\mu$l volume with 2-mM $MgCl_2$, 200 $\mu$M of each dNTP, 1 $\mu$M of each primer, and 1 unit of AmpliTaq Gold Polymerase (Applied Biosystems). After a 10-min period at 95 °C for polymerase activation, 35 cycles for tissue samples and 40 cycles for feces samples were run with the following steps: 95 °C for 30 sec, 55 °C for 30 sec, and 72 °C for 1 min.

**DNA Sequencing.** PCR products were purified using the Qiaquick PCR purification kit (Qiagen). Purified DNA (35 ng) from this PCR product was used for sequencing with the primers used for the amplification (either CAP-F/CAP-R or CAP-pro/CAP-R). Sequence reactions were performed for both DNA strands by using the ABI PRISM Dye Terminator Cycle Sequencing Reaction Kit (Applied Biosystems) in a 20-$\mu$l volume with 2 $\mu$M of each primer. Twenty-five cycles were run with the following steps: 96 °C for 30 sec, 55 °C for 30 sec, and 60 °C for 4 min. Excess dye terminators were removed by spin-column purification and the products were electrophorezed on an ABI 3700 PRISM DNA sequencer (Applied Biosystems) using the POP 7 polymer.

Sequences were edited for correction with the SeqScape v2.5 software (Applied Biosystems), aligned with Mega v3.1 (27), and adjusted by eye when relevant. For the 469 sequences obtained, we kept only the region used in ref. 12 for further analysis, because this informative region is available for most of the GenBank records. This region is 481-bp long on the *C. hircus* reference sequence [mtDNA complete sequence of *C. hircus* (28), Accession number AF533441].

**Phylogenetic Analysis.** The Kimura 2-parameters (K2P) was used as the substitution model used. The heterogeneity in substitution rates among nucleotide sites was modeled by a gamma distribution. The alpha parameter was estimated by a maximum-likelihood method under the K2P model using PAML v 2.0.2 (phylogenetic analysis by maximum likelihood) (29). The estimated value ($\alpha = 0.29$) was similar to that estimated for the same region on a smaller sample of domestic and wild goats (12). These settings were used for further phylogenetic reconstruction and analysis of genetic diversity.

Data were analyzed using NJ methods, MB, and ML, using the 221 bezoar haplotypes, together with 22 domestic goat haplotypes from the different haplogroups used as references (11). MB analyses were performed using MrBayes V3.1.2 (30). The Markov Chain Monte Carlo search was run with $3 \times 10^6$ gener-

ations (repeated three times), sampling the Markov chain every 100 generations, with a burn-in of 10,000 trees (as detected by plotting the log likelihood scores against generation number). The most appropriate likelihood model was determined using the Akaike Information Criterion implement in ModelTest 3.07 (31). ML analyses were first performed with PHYML 2.4.4 (32), using a K2P model of sequence evolution. Using the best tree found by PHYML as a starting tree, heuristic ML searches were executed with PAUP* 4.0 (33), with a tree bisection reconnection (TBR) branch swapping, and all parameter values estimated. Clade stability was estimated by nonparametric bootstrapping in 100 replicates with PHYML. NJ (34) trees were constructed by using MEGA v.3.1 (27). We chose the K2P mutation model (35). The robustness of each branch was determined by a nonparametric bootstrap test with 1,000 replicates and a TBR branch-swapping algorithm. We also analyzed all individuals (bezoars and domestic goats) from the C haplogroup using the same phylogenetic approach.

**Analysis of Molecular Variance.** The ARLEQUIN v 3.0 software (14) was used to estimate the percentage of variance among regions and localities by an AMOVA. The AMOVA was performed on 473 wild individuals from the 43 populations divided into eight geographic regions (Eastern Anatolia, Northern Zagros and Caucasus: 6, 7, 8, 9, 10, 11, 12, 15, 16; Central Anatolia: 1, 2, 3, 4, 5; Albroz and Turkmenistan: 17, 20, 21, 34, 35, 36, 37, 38, 39, 40; Central Zagros: 13, 14, 18, 19; Southern Zagros: 23, 24, 25, 26; Central Iranian Plateau: 22, 27, 28, 29, 30, 31; Eastern Iranian Plateau: 32, 33; Lower Indus Valley: 41, 42, 43) Population numbers refer to Fig. 3*B* and Table S2.

**Estimation of Population Growth Rate.** Growth rates of mitochondrial groups were estimated with Lamarc v2.2 (36) using a Bayesian framework. Three groups were designed for this purpose: (*i*) 1,540 domestic goat haplotypes (11), (*ii*) 142 bezoar haplotypes close-to-domestics, and (*iii*) 79 bezoar haplotypes not-close-to-domestics. The analysis was implemented either allowing migration across groups (with a maximum of 10,000 migration events; default priors used for migration rate estimations) or without migration. The estimation of growth rates was done with a flat prior (upper bound of 1,000 and lower bound of −500), ten initial chains (500 samples, sampling interval of 20 and burn-in period of 1,000) and two final chains (10,000 samples, sampling interval of 20 and burn-in period of 1,000).

**Bayesian Skyline Plot.** Effective population sizes (*Ne*) against time were drawn using BEAST v1.4.6 (15) for (*i*) goats from Iran (222 individuals), (*ii*) bezoars not-close-to domestics (163 individuals), (*iii*) bezoars of the C haplogroup (183 individuals), and (*iv*) bezoars of the A, B, D, F, and G haplogroup (without A haplotypes from Iran, presumably coming from introgressions from domestics; 107 individuals; see *SI Discussion*). The analyses were run for 200 or 300 million iterations [300, 200, 200, and 200 million iterations for analysis (*i*), (*ii*), (*iii*), and (*iv*), respectively], using default parameters and priors (HKY substitution model without site heterogeneity and partition into codon positions; strict molecular clock model; tree prior: coalescent, Bayesian skyline, with 10 groups and constant skyline model; operators: autooptimize; log parameters: every 1,000 iterations). Results of the analyses were visualized using Tracer v1.4 (37). Convergence of the chains to the stationary distribution was systematically confirmed by visual inspection of plotted posterior estimates.

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