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Evidence of three maternal lineages in near eastern sheep supporting multiple domestication events

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The variability of mtDNA was analysed in local sheep breeds reared throughout Turkey, for which a fragment of the *D-loop* region and the complete cytochrome *b* were sequenced. Phylogenetic analyses performed independently for the *D-loop* and the *Cyt b* gene revealed three clearly separated clusters indicating three major maternal lineages, two of which had been previously described as types B and A. The new type, C, was present in all the breeds analysed and showed considerable mtDNA variability. Divergence time was obtained on the basis of *Cyt b* gene and was estimated to be around 160 000–170 000 years ago for lineages B and A, whereas the divergence of lineage C proved to have occurred earlier (between 450 000 and 750 000 years ago). These times greatly predate domestication and suggest that the origin of modern sheep breeds was more complex than previously thought and that at least three independent sheep domestication events occurred. Our results, together with archaeological information and the current wild sheep populations in the Near East region support the high importance of this area in the sheep domestication process. Finally, the evidence of a third maternal lineage has important implications regarding the history of modern sheep.

Keywords: sheep; mitochondrial DNA; maternal lineages; domestication

1. INTRODUCTION

The Neolithic period was an era of major changes in human life. Sheep and goat domestication played an important role in the phenomenon of neolithization occurring in the late prehistory of the Near and Middle East, during the climatic optimum (between 9000 and 5000 BC), giving rise to a sedentary way of life. Perrot (2000) states that the spread of the Neolithic process found its strength in the fusion of two complementary food production strategies developed independently, cereal growing and small livestock rearing, centred respectively on the Levant and the Taurus–Zagros zone, which merged during the second half of the eighth millennium BC. Numerous Neolithic settlements have been discovered in the Near East, some spanning three millennia (from 9000 BC onwards), where data on faunal remains support their general consideration as among the oldest animal domestication centres and as the primary centre of sheep and goat origin.

A very useful approach to investigate the history of modern domestic animals is based on mitochondrial DNA analysis, which has allowed for the identification in modern breeds of different maternal lineages supposed to derive from distinct original wild populations domesticated independently. In this regard, the situation described so far for goat and sheep differs somewhat. Multiple goat domestication events are supported from genetic investigations revealing three distinct maternal lineages (Luikart *et al.* 2001). For two of these, an origin in the Near East was claimed whereas it was proposed that the third derived from the Indus Basin. In sheep, Hiendleder *et al.* (1998*a*, 2002), in a survey of breeds from different parts of the world, concluded that all current domestic breeds originated from only two maternal lineages. The so-called European lineage or mtDNA type B, predominant in European sheep, proved closely phylogenetically related to the European mouflon (*Ovis musimon*). For lineage A, or the Asian type, no relationship has been identified with any of the current wild sheep species investigated.

However, the number of individuals and breeds sampled so far from the Near East area has been very limited and a more extensive analysis of domestic sheep reared in this region seems necessary. Sheep from this part of the world, where domestication is known to have occurred, are expected to have high genetic variability. Moreover, most of these local breeds have not undergone modern selection strategies, so they have probably preserved a genetic background which may provide invaluable information about the origin of domestic sheep.

Within the Near East and because of its strategic situation at the intersection of Asia and Europe, Anatolia has been a cradle for civilizations since prehistoric times. Data from the numerous neolithic human settlements found throughout this region strongly point to it as a major domestication centre for livestock species, mainly goats and sheep, but also cattle and pigs (Gupta 2004). Archaeological data suggest two different areas with independent sheep domestication events in Turkey: the

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upper Euphrates valley in eastern Turkey, where the most important reference is the Nevali Cori settlement, considered the oldest domestication site in the Near East (Peters *et al.* 1999) and Central Anatolia (particularly, the Catal höyük and Asikli höyük sites; Vigne *et al.* 1999).

We present here an investigation into mitochondrial DNA variability in domestic sheep reared throughout Turkey. We have studied two mtDNA regions supplying complementary information, which have been extensively used in livestock (Bruford *et al.* 2003): the D-loop region and the cytochrome *b* gene. Our purpose is to obtain genetic information which might contribute to a better understanding of the history of modern sheep.

2. MATERIAL AND METHODS

Genomic DNA was obtained from 79 unrelated individuals of both sexes, representing five Turkish domestic sheep breeds: Akkaraman (AKA, $n=16$), Hemshin (HEM, $n=16$), Karayaka (KAR, $n=17$), Morkaraman (MOR, $n=15$) and Tuj (TUJ, $n=15$). These samples were used for amplifying a fragment of the mtDNA D-loop region and the complete cytochrome *b* gene. Primers were designed from the published ovine sequence *Ovis aries* [AF010406] (Hiendleder *et al.* 1998*b*). For the D-loop the primers were tRNA-proline (5′-CAGTGCCTTGCTTTGGTTAAGC-3′) and tRNA-phenylalanine (5′-CACCATCAACCCCAAAGCTGAAG-3′). This allowed us to obtain a sequence between sites 15 945 and 16 616. For amplifying the complete *Cyt b* gene the primers were: forward CYTB_F (5′-CCCCACAAAA-CCTATCACAAA-3′) and reverse CYTB_R (5′-AGGGA-GGTTGGTTGTTCTCC-3′). Sequences at D-loop were determined using two additional internal primers: BDG (5′-CATCTGCTTCTTTCTTCAGGGCCATC-3′) and HC3 (5′-TGGACTCAGCTATGGCCGTC-3′). The internal primers for *Cyt b* were: CYTB_IN_F (5′-ACCTC-CTTTCAGCAATTCCA-3′) and CYTB_IN_R (5′-CCT-GTTTCGTGGAGGAAGAG-3′). Both strands of DNA were sequenced and each sequence trace was carefully checked to make sure that each base was unequivocally designated.

A sample of European mouflon (*O. musimon*) was also analysed both for the D-loop fragment and *Cyt b* gene. Other sequences, obtained from Genbank, were *O. aries*, two D-loop sequences of Merinolandschaf breed, corresponding to the mtDNA types B and A, as defined by Hiendleder *et al.* (1998*a*) referenced as [AF039577] and [AF039578], respectively; *O. musimon*, [AF039579] (Hiendleder *et al.* 1998*a*) for D-loop and [D84203] for *Cyt b*; *Ovis ammon ammon*, [AF242347] for D-loop and [AF242349] for *Cyt b* (Hiendleder *et al.* 2002); *Ovis vignei arkal* [AY091489] and *Ovis vignei bochariensis* [AY091489] (Hiendleder *et al.* 2002) for D-loop; and *Ovis vignei* [AF034729] (Hassanin *et al.* 1998) for *Cyt b*.

Alignment of sequences (excluding the 75 nt tandem-repeat element in the D-loop region) was achieved using the *DNA alignment software* (Fluxus technology, http://www.fluxus-engineering.com/). Indices of sequence variation and haplotype structure were calculated using the DnaSP 4.00 program (Rozas *et al.* 2003). A pairwise distance matrix between mtDNA haplotypes was independently calculated for D-loop and *Cyt b*, using the nucleotide *p*-distance (Nei & Kumar 2000). A neighbour-joining (NJ) tree was constructed on the basis of these distances. Bootstrap analyses (1000 replications) were used to assess the confidence of each node. Phylogenetic analyses were performed using the Mega 2.1 software (Kumar *et al.* 2000). The values of sequence divergence between clades (K) were calculated for the synonymous and non-synonymous nucleotide substitutions in the *Cyt b* gene. Time-since-divergence (T) estimates were obtained from the molecular clock equation $T=K/2r$ (Li 1997), where r is the rate of nucleotide substitution estimated for different mtDNA regions by Pesole *et al.* (1999).

3. RESULTS

Analysis of the 663 bp D-loop sequence and the complete *Cyt b* gene revealed 71 and 36 distinct haplotypes, respectively. Sixty-nine polymorphic sites were detected in the D-loop sequence, corresponding to one indel and 68 SNPs. Within the *Cyt b* gene 45 polymorphic sites were found, all SNPs.

NJ trees obtained independently from D-loop and *Cyt b* haplotypes (figure 1) revealed that Turkish sheep appeared in three clearly separated clusters, the distribution of sequences in these clusters being totally coincident in the two trees. Phylogenetic analysis was also performed combining D-loop and *Cyt b* haplotypes and the resulting dendrogram is available (Electronic Appendix A). Trees (not shown) with a similar shape were also obtained by maximum likelihood (Philip 3.55 by Felsenstein 1995), maximum parsimony (Paup* 4.0 by Swofford 2003) and Bayesian methods (Mrbayes 3.0 by Huelsenbeck & Ronquist 2001). Inclusion of reference samples allowed for the identification of clusters B and A as defined by Hiendleder *et al.* (1998*a*), the new cluster being designated type C. These results indicate that three distinct maternal lineages are involved in the origin of domestic sheep. The new maternal lineage, or type C, did not show a close relationship to either of the wild sheep in the dendrogram: urial (*O. vignei*) and argali (*Ovis ammon*). Type C sequences were frequent (21.5%) and they appeared in all the breeds, reaching a high frequency in Akkaraman (0.38) and Karayaka sheep (0.35) (table 1). Type B clearly predominated in Hemshin and Tuj sheep, while type A was the most frequent in the Morkaraman population. Number of haplotypes and polymorphic sites as well as nucleotide diversity indicated a high variability within cluster C. Actually, nucleotide diversity proved greater for cluster C than for types B and A.

Alignment of variable positions in D-loop and *Cyt b* sequences are shown in figures 2 and 3. Sequences are presented grouped by cluster, revealing a complete coincidence of patterns evidenced for types B and A with those found by Hiendleder *et al.* (2002). Cluster C sequences show, both for D-loop and *Cyt b*, a markedly different pattern to those previously described. Of particular interest was the situation at *Cyt b* gene, a much more constrained sequence than D-loop, showing several positions exhibiting differences with regard to other clusters. A representative sample of sequences is available in GenBank accession no. DQ097407–DQ097468.

Divergence time between clusters, based on the *Cyt b* gene, was independently estimated for synonymous and non-synonymous positions, known to vary greatly in nucleotide substitution rate (table 1). Cluster C revealed an earlier divergence from the others, estimated at around

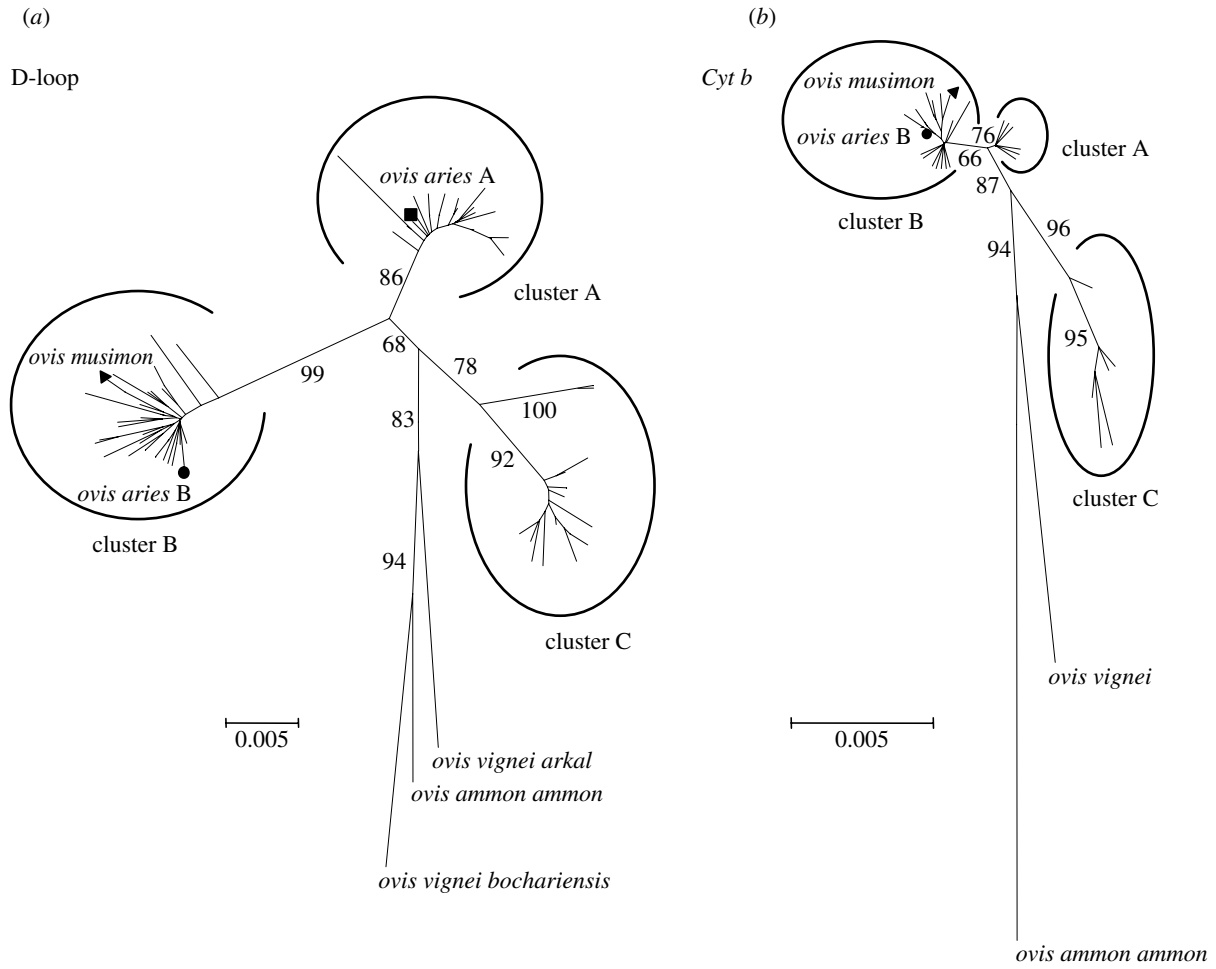


Figure 1. Neighbour-joining trees of (*a*) D-loop and (*b*) *Cyt b* mtDNA types. Bootstrap supporting values are shown on the nodes.

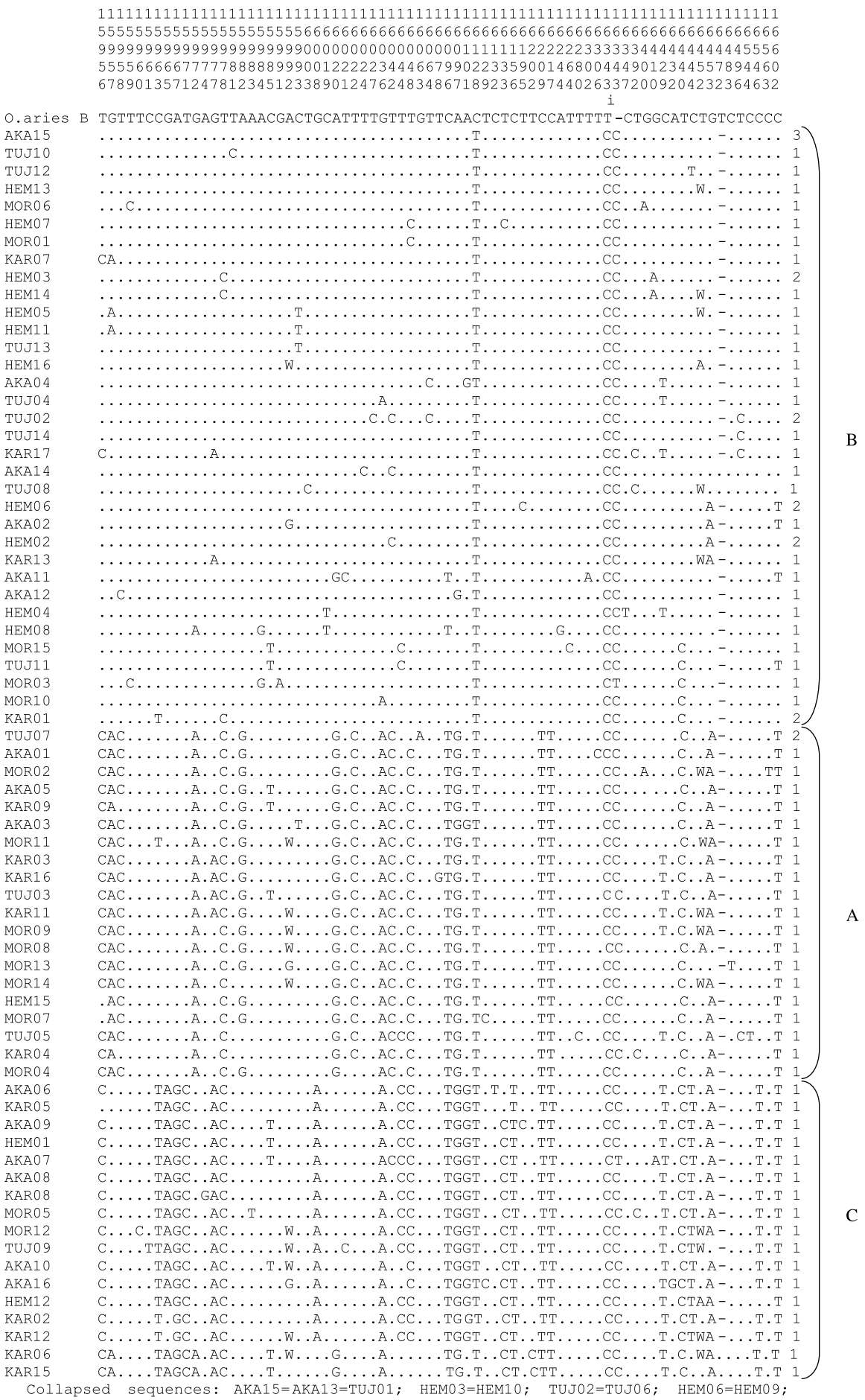
Table 1. Parameters of mtDNA variability within clusters.
(Average distance (K, %) and time of divergence (T, $\times 10^3$) between clusters.)

		clusters					
		A	B	C			
sequences		21	41	17			
nucleotide diversity (π)	D-loop	0.006 79	0.007 01	0.008 81	synonymous positions		
	Cyt b	0.000 59	0.001 20	0.002 26	A–B	A–C	B–C
haplotypes	D-loop	20	34	17	$K=0.933$	$K=3.29$	$K=4.059$
	Cyt b	8	20	8	$T=170$	$T=600$	$T=741$
polymorphic sites	D-loop	26	44	29	non-synonymous positions		
	Cyt b	7	19	15	A–B	A–C	B–C
clusters frequency	Akaraman	0.19	0.43	0.38	$K=0.057$	$K=0.163$	$K=0.197$
	Hemshin	0.06	0.81	0.13	$T=158$	$T=453$	$T=547$
	Karayaka	0.30	0.35	0.35			
	Morkaraman	0.53	0.34	0.13			
	Tuj	0.27	0.66	0.07			

550 000 to 750 000 years from type B and 450 000 to 600 000 years from type A, whereas results between types B and A indicate they diverged more recently, between 160 000 and 170 000 years ago.

4. DISCUSSION

The origin of current domestic livestock has been extensively investigated, with bi- or multiphyletic origins proposed. Independent domestication from two different subspecies of *Bos primigenius* leading to *Bos taurus* and *Bos indicus* cattle is widely accepted (Bradley *et al.* 1996). A pattern much more complex of multiple domestication events has been proposed for horses (Jansen *et al.* 2002) and, very recently, for pigs (Larson *et al.* 2005). Luikart *et al.* (2001) found evidence for three main maternal lineages in goats, diverging between two and three hundred thousand years ago. They concluded that goats were domesticated from local wild animals at least three times, proposing a first domestication site in southern



Collapsed sequences: AKA15=AKA13=TUJ01; HEM03=HEM10; TUJ02=TUJ06; HEM06=HEM09; HEM02=KAR14; KAR01=KAR10; TUJ07=TUJ15.

Figure 2. Alignment of variable positions in D-loop sequences. Nucleotide numbering is based on *Ovis aries* [AF010406] (Hiendleder *et al.* 1998*b*).

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                  1111111111111111111111111111111111111111111111111
                  4444444444444444444444444444444445555555555555555
                  2223334444444455566688888889999990000111111222
                  1682680167889925535923566790223782369444788235
                  8313562679692941443273436133078192437468567663

O.aries B         TTATTCAGCTCGAAGTTAGTTCTACTCTCACAGACTGTGCATTTCA
AKA15             ..................................................  20
TUJ13             ..........A.......................................   1
TUJ04             ..................................................G..   1
TUJ06             .C................................................   1
KAR13             ...C..............................................   1
KAR07             .........C........................................   1
HEM13             ..................CC..................C....        1
HEM11             ............S.....................................   1
HEM04             ..................................................C...   1
HEM02             ...................................A..............   1
HEM03             ...................................A......C...   1
HEM05             ........................C.........A..............   1
HEM06             ........................C.........................   3
KAR14             ........................C........T...............   1
TUJ01             ........................C................G..   1
AKA13             ....................................C.............   1
TUJ11             ....................T......T.....................   1
AKA02             ......T...........................................   1
TUJ12             ..................................................G   1
TUJ08             ...................................A......G..   1
TUJ07             ........T.........A.............................  14
KAR09             ........T.........A.....T.......................   1
KAR04             ........T.........A..........G..................   1
MOR04             ........T....G....A.............................   1
MOR02             ........T.........A.....................G.....   1
MOR09             ..G.....T.........A.............................   1
MOR11             ........T.........A.............A..............   1
MOR13             ........T.........A....T........................   1
AKA06             ....C...T......CCGA...C...T....G....A..T......   6
HEM01             ....C...T......CCGA...C...T....G....A.AT......   1
KAR02             ....C...T......CCGA...C...T....G.G..A..T......   1
AKA07             ....C...T.T.G..CCGA...C...T....G....A..T......   1
AKA10             ....C...T.T....CCGA...C...T....G....A..T......   4
HEM12             C...CT..T.T...SCCGA...C...T....G....A..T.C....   1
MOR12             ....C...T.T....CCGA...CG..TC..TG....A..T......   1
KAR06             ....C...T......C.GA...C........G....A.......T.   2
 Collapsed sequences: AKA15/04/11/12/14=MOR01/03/06/10/15/
 =TUJ10/14/=KAR01/10/17=HEM07/08/10/14/16; HEM06/09=TUJ02;
 TUJ07/03/05/15=AKA01/03/05=HEM15=KAR03/11/16=MOR07/08/14;
 AKA06/08/09=KAR05/08/12; AKA10/16=MOR05=TUJ09; KAR06=KAR15
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B

A

C

Figure 3. Alignment of variable positions in *Cyt b* sequences. Nucleotide numbering is based on *Ovis aries* [AF010406] (Hiendleder *et al.* 1998*b*).

Turkey, a second one in the Near Eastern Zagros region and a third, more recent event, in the Indus Basin.

The situation found so far in sheep varies somewhat from that described for goats. Hiendleder *et al.* (2002) propose that all current domestic breeds are derived from two different subspecies, each leading to one of the two maternal lineages (B and A). Unlike other species, populations of the wild sheep that may have been the ancestors of modern breeds still exist. Initially, certain authors such as Zeuner (1963) had considered the urial (*O. vignei*) as strongly contributing to Middle East and European sheep after its domestication in the Aralo-Caspian basin. According to this view, certain contributions from the argali (*O. ammon*) were also of importance. Another line of domesticated sheep was thought to derive from mouflon populations. Later, based on cytogenetic analyses, Nadler *et al.* (1973) suggested ancestral mouflon populations ($n=54$) as a more probable origin of domestic sheep ($n=54$), rather than argali ($n=56$) or urial stocks ($n=58$). This postulate was supported by Hiendleder *et al.* (1998*a*), who found no evidence for contributions from urial or argali to mtDNA maternal lineages B and A. Also, Wu *et al.* (2003) sampled most of the currently recognized subspecies of argali and obtained a clear separation from *O. aries* sequences. On the other hand, the contribution of mouflon stock to domestic sheep seems widely accepted. Actually, the European mouflon (*O. musimon*) has revealed a close phylogenetic relationship with mtDNA lineage B, and is now considered a descendant of feral sheep. Hiendleder *et al.* (2002) proposed the mouflon populations found in Turkey and western Iran (*Ovis orientalis anatolica* and *Ovis orientalis gmelini*) as ancestors of lineage B, suggesting that lineage A may have derived from eastern mouflon populations (*Ovis orientalis*).

Our results for mtDNA in Turkish domestic sheep provide evidence for three clearly differentiated maternal lineages and allow us to conclude that mtDNA variability

in domestic sheep is greater than previously thought. As was reported for types B and A, the third maternal lineage (type C) did not show a close relationship with argali or urial sequences. The urial is represented here by two distinct types (*Ovis vignei arkal* and *Ovis vignei bochariensis*), with different positions with regard to argali in the study by Hiendleder *et al.* (2002), our results, including mtDNA type C, revealing a similar clustering pattern. Examination of both trees (figure 1) reveals that the differentiation of cluster C from B and A was much greater in the tree obtained from codifying *Cyt b* gene than in the one derived from the regulatory D-loop sequence, which makes this differentiation particularly relevant. Mitochondrial variability in Turkish sheep was very high. The three lineages B, A and C were found in all the breeds analysed, with different types predominating in each population. It is to be noted that the new lineage C reached a high frequency in Akkaraman and Karayaka breeds, while another interesting fact is the high variability found in cluster C. Interestingly, within cluster C, two very strongly supported and quite differentiated branches were apparent from both the D-loop and *Cyt b* sequences (figure 1). The nature of this finding is not clear and it could be clarified by the analysis of local breeds from other areas of the Near East where the mtDNA type C is also very probably present.

Theoretically, the presence of various maternal lineages may be interpreted as originating from distinct wild populations or from a single large population containing highly divergent lineages. However, Luikart *et al.* (2001), who analysed the situation in goats, concluded that the latter hypothesis may be ruled out since it would imply an extremely large ancestral population, which is not in accordance with domestication datings. Archaeological information widely supporting domestication events from small populations also strengthens the former postulate (Gupta 2004). By its part, introgression is generally ruled out as the cause of clearly differentiated maternal lineages in livestock, since introgression via females seems quite improbable.

On the basis of all this, the multiple sheep maternal lineages revealed in our study suggest that the process of sheep domestication was more complex than previously thought. Estimated divergence time, long before domestication dating (around 8000 BC), suggests that at least three independent domestication events were involved in the origin of modern domestic sheep.

Time since divergence of types B and A estimated from the *Cyt b* gene (around 150 000 to 170 000 years ago) agrees with the values obtained from *Cyt b* for goat lineages by Luikart *et al.* (2001; around 200 000 years ago) as well as those obtained for cattle (Bradley *et al.* 1996). Lineage C proved to have diverged earlier (between 450 000 and 700 000 years ago). Much earlier divergence times had been estimated for types B and A (1 500 000 years ago) by Hiendleder *et al.* (2002), which was probably an overestimation, since it was based on the hypervariable mtDNA control region. In this regard, the codifying *Cyt b* gene is considered more accurate for calibrating a molecular clock among mtDNA lineages in livestock, because its pattern of evolution is well understood and presumably relatively constant among most mammals (Irwin *et al.* 1991).

Another factor to take into consideration is the location of the sheep analysed, a region considered as a major centre of sheep domestication. Archaeological data from Early Neolithic human settlements distant from one another throughout the Near East support the occurrence of independent domestication events in this area. The first region of importance, with the oldest human settlements in the Near East (Nevali Cori and Çayönü Tepesi), is dated about 8500 BC and located in the upper Euphrates valley in eastern Turkey, near the northern arc of the so-called Fertile Crescent (Peters *et al.* 1999). The Zagros region of modern day Iran and Iraq is also recognized as a primary centre of sheep domestication (Zeder 1999). In central Anatolia, the Asikli Höyük and Çatalhöyük sites have also revealed morphologically domestic caprines (Vigne *et al.* 1999). Finally, the Southern Levant region of southern Syria, western Jordan and Israel has also been suggested as a centre of sheep domestication (Horwitz *et al.* 1999). Actually, the first two regions, the upper Euphrates valley and Zagros were proposed by Luikart *et al.* (2001) as the origin of two out of the three goat lineages, presumably rising from independent domestications.

Finally, we have to point out the current presence in this area of numerous mouflon populations, widely accepted as the presumable ancestors of domestic sheep. The recently revised taxonomy of the mouflon (IUCN/SSC 2000), now renamed *Ovis gmelini*, differentiates several subspecies. The Armenian mouflon (*Ovis gmelini gmelini*) of northwestern Iran and easternmost Turkey is one of the most probable ancestors of domestic sheep. Also, the Turkish mouflon, considered by some authors as a distinct subspecies (*Ovis gmelini anatolica*), and geographically separated from the Armenian mouflon, is of great interest in this regard. It was endemic to central Anatolia in the past, but is now only represented by a single population around Konya. Apart from a geographical separation from the Armenian mouflon, certain morphological characteristics support its consideration as a different subspecies, the most surprising being the absence of horns in females (Kaya *et al.* 2000). Hiendleder *et al.* (2002) had already pointed out Armenian and Turkish mouflon as probable wild ancestors of lineage B, whereas for type A, the populations of the eastern mouflon range were suggested. These are mainly represented by two subspecies restricted to Iran: the Estefahan mouflon (*Ovis gmelini isphahanica*) and the Laristan mouflon (*Ovis gmelini laristanica*). The finding of a third maternal lineage in domestic Turkish sheep suggests three independent domestication events. Our results, together with archaeological information available and the numerous wild sheep populations found in a wide region of the Near East stretching from Turkey to Iran support the high importance of this area in the sheep domestication process. Research including samples of the different mouflon subspecies is necessary for a better understanding of the origin of domestic sheep. Also, investigation of local sheep from other Asian regions proposed as domestication centres would help in clarifying the situation. The identification in our study of a third maternal lineage opens new perspectives in the investigation of the history of modern sheep.

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REFERENCES

Bradley, D. G., MacHugh, D. E., Cunningham, P. & Loftus, R. T. 1996 Mitochondrial diversity and the origins of African and European cattle. *Proc. Natl Acad. Sci. USA* **93**, 5131–5135. (doi:10.1073/pnas.93.10.5131.)

Bruford, M. W., Bradley, D. G. & Luikart, G. 2003 DNA markers reveal the complexity of livestock domestication. *Nat. Rev. Genet.* **4**, 900–910. (doi:10.1038/nrg1203.)

Felsenstein, J. 1995 *PHYLIP (phylogeny inference package)*, version 3.55. Seattle, WA: University of Washington. See http://evolution.genetics.washington.edu/phylip.html.

Gupta, A. K. 2004 Origin of agriculture and domestication of plants and animals linked to early Holocene climate amelioration. *Curr. Sci.* **87**, 54–59.

Hassanin, A., Pasquet, E. & Vigne, J. D. 1998 Molecular systematics of the subfamily Caprinae (Artiodactyla, Bovidae) as determined from cytochrome b sequences. *J. Mamm. Evol.* **5**, 217–236. (doi:10.1023/A:1020560412929.)

Hiendleder, S., Mainz, K., Plante, Y. & Lewalski, H. 1998*a* Analysis of mitochondrial DNA indicates that domestic sheep are derived from two different ancestral maternal sources. No evidence for contributions from urial and argali sheep. *J. Hered.* **89**, 113–120. (doi:10.1093/jhered/89.2.113.)

Hiendleder, S., Lewalski, H., Wassmuth, R. & Janke, A. 1998*b* The complete mitochondrial DNA sequence of the domestic sheep (*Ovis aries*) and comparison with the other major ovine haplotype. *J. Mol. Evol.* **47**, 441–448.

Hiendleder, S., Kaupe, B., Wassmuth, R. & Janke, A. 2002 Molecular analysis of wild and domestic sheep questions current nomenclature and provides evidence for domestication from two different subspecies. *Proc. R. Soc. B* **269**, 893–904. (doi:10.1098/rspb.2002.1975.)

Horwitz, L. K., Tchernov, E., Ducos, P., Becker, C., Von Den Driesch, A., Martin, L. & Garrard, A. 1999 Animal domestication in the Southern Levant. *Paléorient* **25**, 63–80.

Huelsenbeck, J. P. & Ronquist, F. 2001 MRBAYES: Bayesian inference of phylogenetic trees. *Bioinformatics* **17**, 754–755. (doi:10.1093/bioinformatics/17.8.754.)

Irwin, D. M., Kocher, T. D. & Wilson, A. C. 1991 Evolution of the cytochrome b gene of mammals. *J. Mol. Evol.* **32**, 128–144.

IUCN/SSC-Caprine Specialist Group 2000 Workshop on Caprinae taxonomy, Ankara, Turkey, May 8–10. See http://www.callisto.si.usherb.ca:8080/caprinae/taxo.htm.

Jansen, T., Forster, P., Levine, M. A., Oelke, H., Hurles, M., Renfrew, C., Weber, J. & Olek, K. 2002 Mitochondrial DNA and the origins of the domestic horse. *Proc. Natl Acad. Sci. USA.* **99**, 10 905–10 910. (doi:10.1073/pnas.152330099.)

Kaya, M. A., Arihan, O. & Can Bilgin, C. 2000 *General characteristics and taxonomy of the Turkish mouflon (Ovis gmelinii anatolica)* Valenciennes, 1856. International Mouflon Symposium, Sopron, Hungary, October 27–29.

Kumar, S., Tamura, K., Jakobsen, I. B. & Nei, M. 2000 MEGA2: molecular evolutionary genetics analysis software. *Bioinformatics* **17**, 1244–1245. (doi:10.1093/bioinformatics/17.12.1244.)

Larson, G. *et al.* 2005 World-wide phylogeography of wild boar reveals multiple centres of pig domestication. *Science* **307**, 1618–1621. (doi:10.1126/science.1106927.)

Li, W. H. 1997 *Molecular evolution*. Sunderland, MA: Sinauer Associates.

Luikart, G., Gielly, L., Excoffier, L., Vigne, J. D., Bouvet, J. & Taberlet, P. 2001 Multiple maternal origins and weak phylogeographic structure in domestic goats. *Proc. Natl Acad. Sci. USA* **98**, 5927–5932. (doi:10.1073/pnas.091591198.)

Nadler, C. F., Korobitsina, K. V., Hoffmann, R. S. & Vorontsov, N. N. 1973 Cytogenetic differentiation, geographic distribution and domestication of palaearctic sheep (*Ovis*). *Z. Saugetierkd* **38**, 109–125.

Nei, M. & Kumar, S. (eds) 2000 Evolutionary change in DNA sequences. In *Molecular evolution and phylogenetics*, pp. 33–50. New York: Oxford University Press.

Perrot, J. 2000 Réflexions sur l'état des recherches concernant la Préhistoire récente du Proche et du Moyen-Orient. *Paléorient* **26**, 5–28.

Pesole, G., Gissi, C., De Chirico, A. & Saccone, C. 1999 Nucleotide substitution rate of mammalian mitochondrial genomes. *J. Mol. Evol.* **48**, 427–434.

Peters, J., Helmer, D., Von Den Driesch, A. & Saña-Segui, M. 1999 Early animal husbandry in the Northern Levant. *Paléorient* **25**, 27–57.

Rozas, J., Sanchez-del-Barrio, J. C., Messeguer, X. & Rozas, R. 2003 DnaSP, DNA polymorphism analyses by the coalescent and other methods. *Bioinformatics* **19**, 2496–2497. (doi:10.1093/bioinformatics/btg359.)

Swofford, D. L. 2003 *PAUP*. Phylogenetic analysis using parsimony (*and other methods)*, version 4. Sunderland, MA: Sinauer Associates.

Vigne, J. D., Buitenhuis, H. & Davis, S. 1999 Premiers (Les) pas de la domestication animale à l'ouest de l'Euphrate: Chypre et l'Anatolie Centrale. *Paléorient* **25**, 49–62.

Wu, C. H., Zhang, Y. P., Bunch, T. D., Wang, S. & Wang, W. 2003 Mitochondrial control region sequence variation within argali wild sheep (*Ovis ammon*): evolution and conservation relevance. *Mammalia* **67**, 109–118.

Zeder, M. A. 1999 Animal domestication in the Zagros: a review of past and current research. *Paléorient* **25**, 11–26.

Zeuner, F. E. 1963 *A history of domesticated animals*. London: Hutchinson.

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