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Evolutionary history of the genus *Capra* (Mammalia, Artiodactyla): Discordance between mitochondrial DNA and Y-chromosome phylogenies

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Abstract

The systematics of the genus *Capra* remain controversial in spite of studies conducted using morphology, mtDNA, and allozymes. Here, we assess the evolutionary history of *Capra* (i) using phylogenetic analysis of two nuclear genes located on the Y-chromosome and (ii) previously published and new cytochrome *b* sequences. For the Y-chromosome phylogeny, we sequenced segments from the amelogenin (AMELY) and zinc finger (ZFY) genes from all of the eight wild taxa and from domestic goats (*Capra hircus*). Phylogenetic analysis of the Y-chromosome data revealed two well-defined clades. The domestic goat (*C. hircus*), the bezoar (*Capra aegagrus*), and the markhor (*C. falconeri*) belong to one clade (ML bootstrap value [BP]: 98%), suggesting that domestic goats originated from one or both of these wild species. The second clade (ML BP: 92%) is comprised of all the other wild species. Horn morphology is generally concordant with the Y-chromosome phylogeny. The mtDNA data also revealed two well-defined clades. However, the species in each clade are different from those inferred from the Y-chromosome data. To explain the discordance between Y-chromosome and mtDNA phylogenies, several hypotheses are considered. We suggest that a plausible scenario involves mtDNA introgression between ancestral taxa before the relatively recent colonization of Western Europe, the Caucasus Mountains, and East Africa by *Capra* populations.

Keywords: Caprinae; *Capra*; Y-chromosome evolution; Introgression; Goat domestication

1. Introduction

The genus *Capra*, which contains domestic goats and their wild relatives (bezoars, turs, markhors, and ibex) displays a uniquely old-world distribution. Fossil data suggest that the *Capra* first appeared in Central Asia (Pilgrim, 1947) and that a species radiation occurred in the Plio-Pleistocene (Hartl et al., 1990; Pilgrim, 1947). Very few paleontological data are available for species of this genus because their preferred mountainous habitats are not favorable for fossil preservation (Simpson, 1945, pp. 172). Consequently, the evolutionary history of *Capra* species is poorly understood. This is compounded by the fact that the radiation of *Capra* taxa apparently occurred rapidly (Hartl et al., 1990; Manceau et al., 1999b), making it difficult to assess the number of species and their phylogenetic relationships.

The number and status of *Capra* species and subspecies is still under debate, with estimates ranging from 6 to 9 species (Schaller, 1977, pp. 21; Shackleton, 1997, pp. 12–13).

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Moreover, hybridization between different taxa in captivity can produce fertile offspring (Couturier, 1962, pp. 517–532; Mason, 1984, pp. 85–99). In the wild, hybridization between wild taxa and the domestic goat has been documented (Zalikhanov, 1967). However, there is no reliable observational evidence of natural hybridization between wild taxa in the genus *Capra*.

Wild *Capra* are highly sexually dimorphic and include five major adult male horn morphotypes as shown in Fig. 1: (1) the ibex, (2) the Spanish ibex [also called the Spanish goat, Valdez, 1985, pp. 11], (3) the eastern tur, (4) the markhor and (5) the bezoar. Taxonomic classification within the genus *Capra* is mainly based on the horn morphology of adult males and on the shape of the cross-section of the horn sheaths and cores (Veinberg, 1993). Adult males of *Capra ibex* have scimitar-shaped horns, oval-shaped (or subtriangular) cross-sectionally with well-defined frontal surfaces broken by prominent transverse ridges. Horn cores are more distinctly isosceles triangular with narrower frontal surface. This general morphotype is shared by *C. [i.] ibex*, *C. [i.] nubiana*, *C. [i.] sibirica* (Schaller, 1977; Shackleton, 1997). With certain reservations, *C. [i.] caucasica* may be added to this morphotype. It differs in displaying a subtriangular equilateral horn cross-section without a well-defined frontal surface and with less prominent transverse knobs (Veinberg, 1993). The Spanish ibex (*Capra pyrenaica*) presents a totally different morphotype (Fig. 1b), with horns curved like a lyre, and triangular in cross-section without flat clashing surface and transverse knobs. Fully developed horns of eastern tur males (*C. cylindricornis*) have a subtriangular cross-section and form approximately 3/4 curl of an open spiral. The markhor (*C. falconeri*) has somewhat laterally compressed and spiraling horns while the bezoar (*C. aegagrus*) has scimitar-shaped horns that are also laterally compressed or, more precisely, teardrop-shaped in cross-section (Veinberg, 1993).

Facial features and pelage colors have also been used as taxonomic characters. Such classification based on morphological characters is controversial, and is not supported by allozyme studies (Hartl et al., 1990, 1992) or mtDNA (Manceau et al., 1999b). The taxonomy used here (Table 1) is that recognized by the IUCN (Shackleton, 1997, pp. 12–13).

The wild species are found in restricted mountain areas in Europe, Africa, and Asia (Fig. 2) while the domestic goat is cosmopolitan. The ibex morphotype is the only wild *Capra* morphotype found on all three of these continents (Fig. 2, see also Table 1 for more information on geographic distribution). Limited allozyme studies (Hartl et al., 1990, 1992; Randi et al., 1991; Stüwe et al., 1992) and DNA investigations (Hassanin et al., 1998; Manceau et al., 1999a,b) of *Capra* have been conducted. All these studies, except that of Manceau et al. (1999b), failed to include all *Capra* taxa, and/or used small taxonomic sample sizes. Furthermore, some of these studies included animals from zoos, in spite of the fact that all *Capra* species can interbreed in captivity. Therefore, the systematics of the genus *Capra* remain unclear.

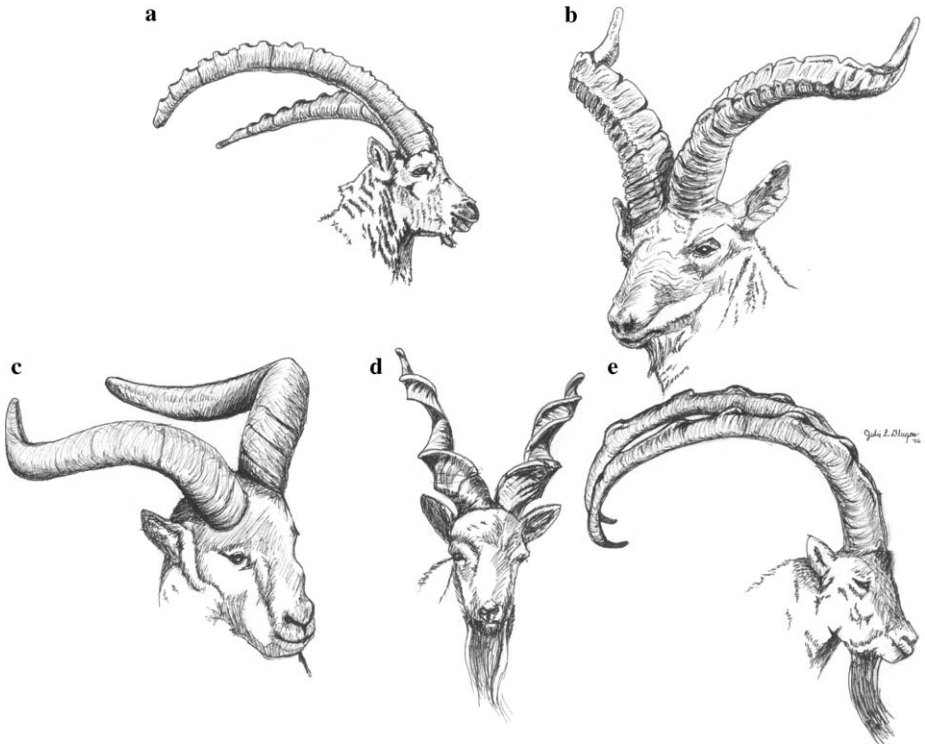

Fig. 1. Horn morphology of the five major morphotypes: (a) the generalized ibex-type (*C. [i.] ibex*, *C. [i.] nubiana*, *C. [i.] sibirica*, and *C. [i.] caucasica*), (b) the Spanish goat (*C. pyrenaica*), (c) the eastern tur (*C. cylindricornis*), (d) the markhor (*C. falconeri*), and (e) the bezoar-type (*C. aegagrus*). Artwork by Julie Dlugos.

Table 1
Taxonomy and geographic distribution of the genus *Capra* (except the cosmopolitan domestic goat *C. hircus*) according to Shackleton (1997, pp. 12–13)

Species	Subspecies	Common name	Geographic range
Capra aegagrus Erxleben, 1777	*C. a. aegagrus*	Bezoar (or wild goat)	Afghanistan, Armenia, Azerbaijan (Nakhichevan), Lebanon (extinct), Russia (East Caucasus), Turkey, Georgia, Iran
	C. a. blythi		Pakistan, Iran, Iraq, Turkmenistan
	C. a. chialtanensis	Chiltan's Wild Goat	Pakistan
	C. a. cretica		Greece
Capra falconeri Wagner, 1839	*C. f. falconeri*	Markhor	India, Pakistan
	C. f. heptneri		Afghanistan, Tajikistan, Turkmenistan, Uzbekistan
	C. f. megaceros		Afghanistan, Pakistan
Capra [ibex][a] ibex Linnaeus, 1758		Alpine ibex	Austria, France, Germany, Italy, Switzerland
Capra [ibex] nubiana F. Cuvier, 1825		Nubian ibex	Egypt, Ethiopia, Israel, Jordan, Lebanon (extinct), Oman Saudi Arabia, Sudan, Syria (extinct), Yemen
Capra pyrenaica Schinz, 1838	*C. p. hispanica*	Spanish ibex	Spain
	C. p. lusitanica		Extinct
	C. p. pyrenaica		Extinct
	C. p. victoriae		Spain
Capra [ibex] sibirica Pallas, 1776		Asiatic or Siberian ibex	Afghanistan, China, India, Kazakhstan, Tajikistan Kyrgyzstan, Mongolia, Pakistan, Russia (Altai, Sayan, and Tuva)
Capra [ibex] walie Rüppell, 1835		Walia ibex	Ethiopia
Capra [ibex] caucasica Güldenstaedt and Pallas, 1783		Kuban or West Caucasian tur	Georgia, Russia (West Caucasus)
Capra cylindricornis Blyth, 1841		Daghestan or East Caucasian Tur	Azerbaijan, Georgia, Russia (East and Central Caucasus)

This study included all eight wild taxa and the domestic goat.
[a] *The IUCN uses brackets, e.g., Capra [ibex] nubiana when the species versus subspecies level of taxonomy is controversial.*

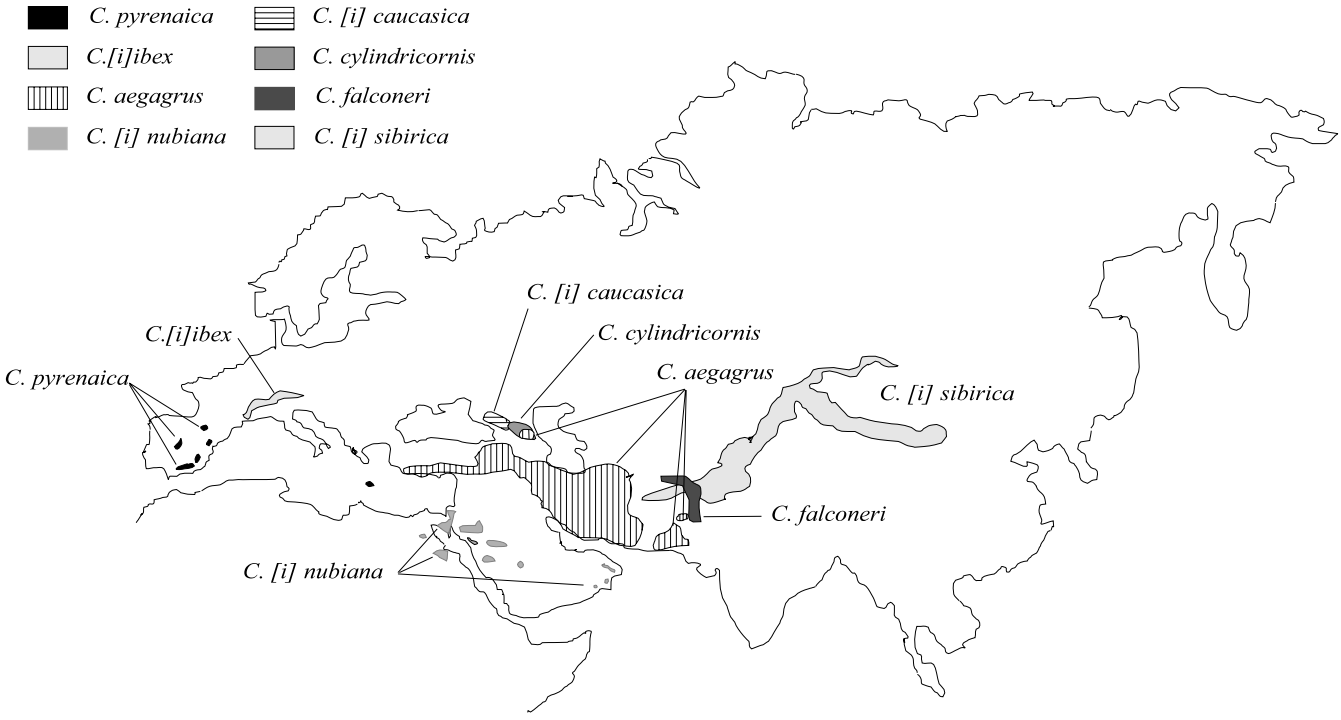

Fig. 2. Approximate geographic distributions of wild *Capra*: the Spanish goat (*C. pyrenaica*), the eastern tur (*C. cylindricornis*), the markhor (*C. falconeri*), the generalized ibex-type (*C. [i.] ibex*, *C. [i.] nubiana*, *C. [i.] sibirica*, and *C. [i.] caucasica*) and the bezoar-type (*C. aegagrus*). Distribution areas are synthesized from Shackleton (1997).

Mitochondrial (mt) DNA has characteristics making it ideal for phylogenetic studies. It is haploid, with no recombination and uniquely maternal inheritance. Likewise, the Y-chromosome is a useful molecule for phylogenetic studies. This sex chromosome is paternally inherited and, with the exception of the pseudoautosomal region, it does not undergo homologous recombination at meiosis. Y-chromosome and mitochondrial DNA give independent and complementary information. Studies comparing these two classes of sequence data are especially useful for resolving the phylogeny of closely related species. Studies have shown that maternal and paternal markers can give either concordant and/or discordant phylogeographic patterns (Boissinot and Boursot, 1997), and can reveal sex-biased gene flow (Gibbons, 1997; Seielstad et al., 1998).

Here, we present analyses of two polymorphic Y-chromosome genes (amelogenin—AMELY and zinc finger—ZFY) and one mitochondrial gene (cytochrome *b*). Phylogenetic analysis of Y-chromosome genes revealed two main lineages within *Capra* and suggested that *C. aegagrus* is the most likely progenitor of domestic goats. We also qualitatively investigated whether male horn morphology is concordant with phylogeny, and found some similarities between horn morphology and the Y-chromosome phylogeny. Comparisons between our mtDNA and Y-chromosome data, along with archaeological information and horn morphology, provide a possible scenario explaining the evolution of this genus.

2. Materials and methods

2.1. Y-chromosome data

2.1.1. Samples and DNA extraction

Because of possible hybridization in captivity, no animals from zoos were considered in this study. Samples from 144 male *Capra* were collected in Europe, Asia, and Africa thanks to multiple collaborations (Table 2). Sampled tissues included muscle and skin from hunter kills, winter kills, and ear punches of captured animals, as well as bones, blood, and fresh hair. The following samples represented all taxa of the genus *Capra* according to Shackleton (1997, pp. 12–13, number of individuals in parentheses): *C. aegagrus* (23), *C. hircus* (78), *C. [ibex] ibex* (2), *C. [i.] sibirica* (16), *C. [i.] nubiana* (8), *C. pyrenaica* (7), *C. cylindricornis* (5), *C. falconeri* (2), and *C. [i.] caucasica* (3). One sample from the genus *Hemitragus* was used as an outgroup. Total DNA was extracted from fresh-plucked hair, blood, skin biopsies, or bones using the chelex method (Walsh et al., 1991), QIAamp Blood kit (Qiagen), QIAamp Tissue kit (Qiagen) or the method described in Taberlet and Fumagalli (1996), respectively.

2.1.2. PCR amplification and sequencing

Our Y-chromosome dataset included partial sequences of AMELY and ZFY. Both of these Y-chromosome genes have counterparts on the X-chromosome. Amelogenin is a protein which contributes to tooth enamel (Lau et al., 1989). The zinc finger protein is thought to influence testis development (Page et al., 1987). Primers for the 5th exon region of the amelogenin gene were designed by comparing the X- and Y-linked chromosome sequences of *Bos taurus* (Accession Nos.: M63499 and M63500 [Gibson et al., 1991]). The primers are CAPY1F: 5′-CCCAGCAGACTCCCCAGAATC-3′ and CAPY1R: 5′-CCAGAGGGAGGTCAGGAAGCA-3′. PCR was performed with 45 cycles (95 °C 30 s, 60 °C 40 s, and 72 °C 40 s). Two PCR products (320 and 400 bp) were obtained for males. The *Bos* sequences show that the AMELY protein is about 60 bp shorter than the AMELX protein. The 320 bp Y-chromosome-linked band was therefore purified using a QIAquick Gel Extraction kit (Qiagen).

One thousand bp of the last intron of ZFY were amplified using primers specifically designed for the Y-chromosome copy of the zinc finger gene: ZF2F: 5′-AAG ACC TGA TTC CAG GCA GTA-3′, and ZFY: 5′-CTT CTT ATT GGT AGT GTA GTA ATC-3′ (Lawson and Hewitt, 2002). The PCR was conducted using 45 amplification cycles (95 °C 30 s, 64 °C 40 s, and 72 °C 120 s).

All sequences were obtained for both DNA strands using the above primers and an ABI PRISM Dye Terminator Cycle Sequencing Ready Reaction Kit (Perkin-Elmer) in a 20 μl volume containing 40–50 ng of purified DNA, and 3.2 pmol of primer, according to the manufacturer's specifications. Sequencing reactions underwent 25 cycles of 30 s at 96 °C, 30 s at 58 °C, and 4 min at 72 °C on either a PE 2400, PE 9600 or PE 9700 thermocycler (Perkin-Elmer). Following this step, excess dye terminators were removed by spin-column purification. The sequencing reaction products were visualized on an ABI 377 PRISM™ DNA sequencer (Perkin-Elmer) in a 5% Long Ranger™ gel (FMC).

2.2. Mitochondrial data

The phylogeny of *Capra* has recently been assessed using 500 bp of mtDNA sequence data obtained from wild populations (Manceau, 1997; Manceau et al., 1999b). These mtDNA sequences offered relatively low bootstrap values (BP) to the connection of *Capra [i.] sibirica* to a node basal to the remainder of the genus (60% for MP and 71% for NJ) (Manceau, 1997, p. 63).

To better understand the relationship of *C. [i.] sibirica* to other *Capra* species, we analyzed 22 longer sequences of the cytochrome *b* gene (983–1140 bp). Eleven sequences were obtained from GenBank (Table 3) and we generated 12 new sequences (1096–1140 bp one haplotype was shared between individuals) of the cytochrome *b* gene from wild samples (Table 4). Sequencing of the cytochrome *b* gene was performed as described in Manceau et al. (1999b) using primers L14841 and H15915 of Irwin et al. (1991). All samples from *C. cylindricornis*, *C. [i.] nubiana*, and *C. [i.] sibirica* for which we obtained new cytochrome *b* sequences were also included in the Y-chromosome analysis. One sample from the genus *Hemitragus* was used as an outgroup.

Table 2
Number of Y-chromosome samples analyzed and haplotypes found in each of 28 countries

Species	Geographic Origin	Samples[a]	Haplotypes[b]	GenBank accession:	
				AMELY	ZFY
C. aegagrus	Greece	3/3/3	C2	AY082488	AY082496
	Russia (East and Central Caucasus)	14/14/8	C1	AY082491	AY082500
	Turkey	6/6/3	C1(1)		
			C4(2)	AY082487	AY082495
C. hircus	Cyprus	1/1/0	—		
	Spain	2/2/1	C1		
	France	2/2/2	C2		
	Greece	1/1/1	C2		
	Iceland	1/1/0	—		
	Portugal	5/5/2	C1		
	Great Britain	2/2/1	C2		
	Romania	1/1/1	C3	AY082492	AY082496
	Slovenia	1/1/1	C2		
	Switzerland	8/7/8	C2		
	Bhutan	2/1/2	C1		
	Russia(East and Central Caucasus)	2/2/0	—		
	Malaysia	1/1/1	C2		
	Mongolia	15/14/10	C2		
	Pakistan	3/3/2	C2		
	Vietnam	2/2/0	—		
	Turkey	15/15/14	C1(12)C2(2)		
	Iraq	4/4/4	C1(2)C2(2)		
	Botswana	2/2/2	C2		
	South Africa	5/5/4	C1(2)C2(2)		
	Nigeria	1/1/1	C1		
	Zimbabwe	2/1/2	C2		
C. cylindricornis	Russia (East and Central Caucasus)	5/5/5	Cc1(3)	AY082490	AY082497
			Cc2(2)	AY082489	AY082497
C. falconeri	Turkmenistan	2/2/2	Cf1(1)	AY082491	AY082499
			Cf2(1)	AY082491	AY082498
C. [i.] caucasica	Russia (West Caucasus)	3/3/1	Cc1		
C. [ibex] ibex	France	2/2/2	Ci1	AY082490	AY082501
C.[i.] nubiana	Saudi Arabia	4/4/3	Cin1(2)	AY082490	AY082502
			Cin3(1)	AY082490	AY082504
	Israel	4/4/1	Cin2	AY082490	AY082503
C.[i.] sibirica	China	1/1/0	—		
	Kazakhstan	1/1/0	—		
	Mongolia	9/9/6	Cis1(1)	AY082490	AY082507
			Cis2(3)	AY082490	AY082508
			Cis3(2)	AY082490	AY082509
	Tadjikistan	5/5/3	Cis4(3)	AY082490	AY082506
C. pyrenaica	Spain	3/3/1	Ci2	AY082490	AY082505
C. p. victoria	Spain	4/4/4	Ci1		

GenBank accession numbers are only indicated for the first occurrence of a given haplotype in the table.
[a] Number of samples: tested/successfully sequenced for AMELY/successfully sequenced for ZFY.
[b] Haplotypes indicated in the tree (Fig. 3b). (n) number of each haplotype found when several haplotypes were found in the same geographic location.
"—" indicates samples not successfully sequenced for both AMELY and ZFY.

2.3. Sequence analysis

Phylogenetic analyses of the Y-chromosome sequences included maximum parsimony (MP), neighbor-joining (NJ), and maximum likelihood (ML) methods using PAUP* version 4.0b4-10 (Swofford, 1998), and Bayesian methods using MrBayes V 3.0b4 (Huelsenbeck and Ronquist, 2001). For the MP and NJ search, trees were constructed with each locus separately and with both loci together. Since the same trees were obtained in all cases using these methods, data from both loci were analyzed together in the ML and Bayesian searches. The robustness of nodes in the MP analysis were inferred using 2000 bootstrap replicates. We used Modeltest (Posada and Crandall, 1998) to select a ML model that was appropriate for the data. This model (HKY+ Γ) was used to perform a heuristic search in the following manner. Model parameters were estimated on a neighbor-joining tree and fixed. A heuristic search was conducted (10 random-addition-sequence replicates, TBR branch swapping) and model parameters were re-estimated. The values were fixed again, and this iterative process was continued until ML heuristic searches found the same tree two times in a row. Maximum likelihood bootstrapping was also per-

Table 3
References of previously available cytochrome *b* sequences used in this study

Species	GenBank Accession Number	Citation
C. [i.] caucasica	AF034738 (1140 bp)	Hassanin et al. (1998)
C. cylindricornis	AF034737 (1143 bp)	Hassanin et al. (1998)
C. falconeri	AB044309 (1140 bp)	Mannen et al. (2001)
	AB034736 (1140 bp)	Hassanin et al. (1998)
C. hircus	AB044308 (1140 bp)	Mannen et al. (2001)
C. [i.] ibex	AJ010055 (987 bp)	Manceau et al. (1999a)
	AF034735 (1140 bp)	Hassanin et al. (1998)
C. [i.] nubiana	AF034740 (1140 bp)	Hassanin et al. (1998)
C. pyrenaica	AJ010048 (983 bp)	Manceau et al. (1999a)
	AJ010056 (983 bp)	Manceau et al. (1999a)
Hemitragus	AF034733 (1143 bp)	Hassanin et al. (1998)

formed using 200 pseudoreplicates and the same heuristic search parameters as above.

We carried out a Bayesian analysis using the model identified above (HKY+ Γ), 1 million generations, and uniform priors. A Metropolis coupled Markov chain Monte Carlo method was employed with four chains, three heated, and one cold. Trees from a burnin period of 5000 generations were discarded before clade probabilities were estimated.

Bayesian and ML analyses of the cytochrome *b* data were conducted in the same manner as those for the Y-chromosome data outlined above, with some slight exceptions. First, we selected the HKY+I+ Γ model with Modeltest (Posada and Crandall, 1998). Second, the appropriate burnin period for the Bayesian analysis was determined to be 10,000 generations.

To test the discrepancy between the mitochondrial and Y-chromosome topologies, a Shimodaira–Hasegawa test (Shimodaira and Hasegawa, 1999) was performed using the GTR+I+Γ model (1000 bootstrap replicates) on 70 most-parsimonious trees from the Y-chromosome analysis and the MP mtDNA topology.

3. Results

Of our 144 samples used for the Y-chromosome analysis, 98 successfully yielded PCR products and sequences for the two Y-chromosome genes (140 sequences for AMELY and 101 for ZFY). Fewer sequences were obtained for ZFY because the sequence is longer and thus more difficult to amplify from poor quality DNA such as that obtained from old museum skins or bones.

We sequenced 265–279 nucleotides from the fifth exon of AMELY and 919–929 nucleotides from the last intron of ZFY in *Capra* and *Hemitragus*, and found 17 unique haplotypes within *Capra* for the combination of these loci. Within *Capra* AMELY sequences, six sites were variable and three were parsimony informative. There were 17 variable sites for ZFY and 10 were parsimony informative. The percentages of A, T, C, and G were 22.2, 15.3, 47.8, and 14.7% for AMELY, and 31.7, 35.8, 14.8, and 17.8% for ZFY in the genus *Capra*. Base frequencies did not significantly vary between taxa ($p = 1.0$). The last intron of ZFY exhibited a frequency bias against G and C. Pecon-Slattery and O'Brien (1998) also found such a frequency bias for 34 Felidae species.

All phylogenetic methods converged on the same topology using the Y-chromosome data. Under MP and NJ methods, this same topology was obtained with the AMELY sequence alone, ZFY alone, and with both sequences together. As expected, the best resolution was achieved when using both sequences (Fig. 3b). The MP analysis produced a single most-parsimonious tree (length 34) with a consistency index of 1.0. The same topology, with similar bootstrap values, was found with NJ and ML methods. Bayesian analysis also recovered the same topology, but posterior probabilities were generally higher than bootstrap values (Fig. 3b).

Y-chromosome data supported two major clades with high MP (98 and 93%, data not shown) and ML BP (98 and 92%, Fig. 3b). The first clade (Clade A, Fig. 3b) contained two wild species (*C. aegagrus* and *C. falconeri*) and the domestic goat (*C. hircus*). Within this first clade, the two *C. falconeri* haplotypes grouped separately from the 14 *C. aegagrus* and the 56 domestic goats. The second major clade (Clade B, Fig. 3b) included *C. ibex, C. cylindricornis* and *C. pyrenaica*. Within clade B, *C. [i.] sibirica* and *C. [i.] nubiana* were found to be monophyletic (ML BP 62 and 60%), but *C. cylindricornis* was not (Fig. 3b).

Table 4
Geographic origin and code for *Capra* samples used to obtain new sequences of the cytochrome *b* gene (sequence length in bp in parentheses)

Species	Origin	Code in Fig. 3a	GenBank accession:
C. aegagrus	Asia, Russia (East and Central Caucasus)	CaDak40 (1140 bp)	DQ514541
		CaDmr416 (1140 bp)	DQ514542
C. cylindricornis	Asia, Russia (East and Central Caucasus)	CcylDNO443 (1140 bp)	DQ514543
		CcylDNO440 (1140 bp)	DQ514549
C. hircus	Africa, South Africa	ChGr642 (1140 bp)	DQ514544
	Europeb, Slovenia	ChSo1 (1140 bp)	DQ514547
	Europe, Switzerland	ChTo2992 (1140 bp)	DQ514548
	Asia, Malaysia	ChMy50 (1140 bp)	DQ514545
		ChMy57 (1140 bp)	DQ514546
C.[i.] nubiana	Middle/Near East, Israel	CnubNiSB (1096 bp)	DQ514552
C.[i.] sibirica	Asia, Mongolia	CisIB10 (1140 bp)	DQ514550
		CisIB2 (1140 bp)	DQ514551

All samples of wild *Capra* came from natural populations.

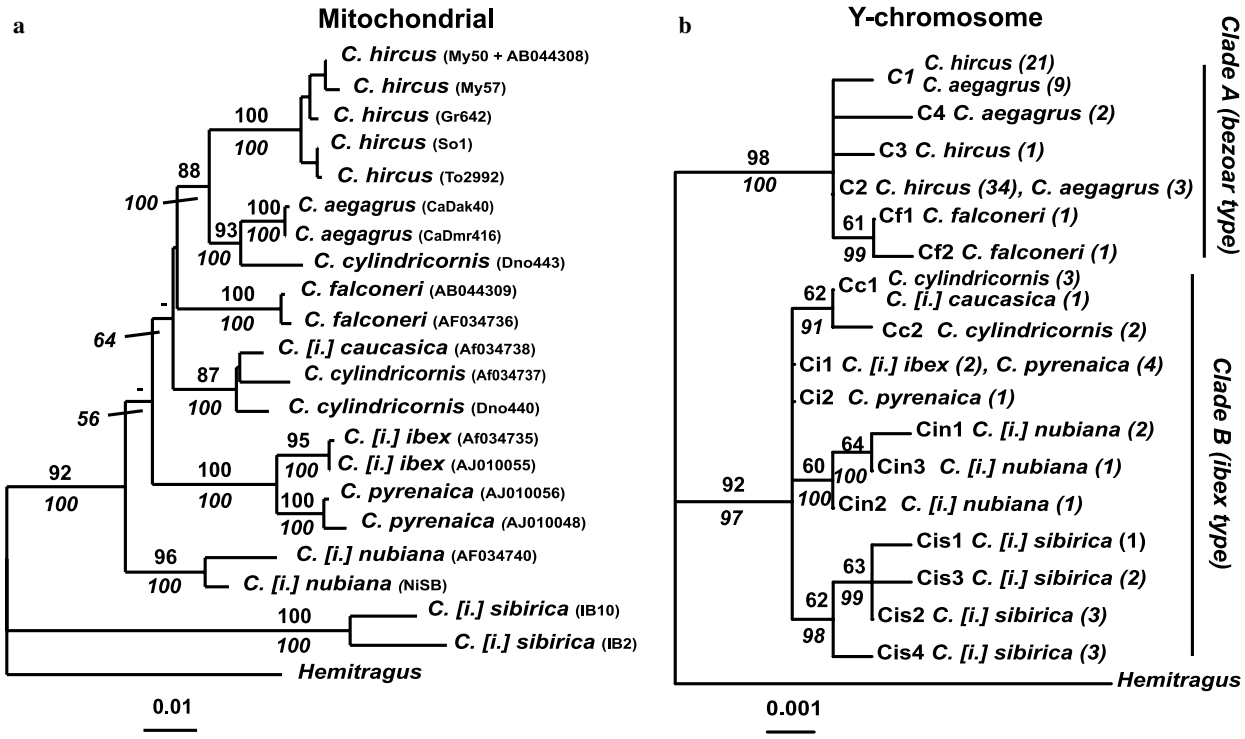

Fig. 3. (a) Phylogenetic tree constructed with cytochrome *b* sequences using Maximum Likelihood (ML) and Bayesian analyses. Numbers above the line are ML bootstrap values (BP) based on 200 pseudoreplicates. Numbers below the line are Bayesian posterior probabilities based on one million step Markov chain Monte Carlo simulations. See Tables 3 and 4 for details on location codes and GenBank accession numbers which follow species names in parentheses. (b) Phylogenetic tree constructed with AMELY and ZFY sequences using ML and Bayesian analyses. The same topology was obtained using maximum parsimony, and neighbor-joining methods. The (n) indicates the number of samples sequenced for both AMELY and ZFY. Numbers above the line are ML BP based on 200 pseudoreplicates. Numbers below the line are Bayesian posterior probabilities based on one million step Markov chain Monte Carlo simulations.

The mean corrected pairwise distance for AMELY was 0.003 ± 0.002 for clade A, 0.001 ± 0.001 for clade B and 0.0130 ± 0.006 between clade A and clade B. The mean pairwise distance for ZFY was 0.002 ± 0.001 for clade A, 0.003 ± 0.001 for clade B, and 0.007 ± 0.002 between clade A and clade B.

Both ML and Bayesian analyses of the new cytochrome *b* dataset arrived at the same topology, which was extremely similar to that published by Manceau et al. (1999b). However, this new analysis, using much longer sequences, found significantly more support for the monophyly of all *Capra* taxa excluding *C. ibex sibirica* than that of Manceau et al. (1999b) (ML BP value 92% and Bayesian Posterior = 1.0 vs. MP BP 60% and NJ BP 71%). Hassanin et al. (1998) also found that *C. [i.] sibirica* appeared divergent and basal to all other *Capra* in their weighted MP analysis of complete cytochrome *b* sequences (1140 bp). Their study represented each taxon by a single individual and did not include *C. pyrenaica*. Using mtDNA data, we also found that *C. cylindricornis* is paraphyletic. An individual from Daghestan (Dno443) is in a strongly supported clade with *C. aegagrus* from Daghestan.

The discrepancy between the mitochondrial and Y-chromosome topologies was highly significant ($p = 0.002$) according to the Shimodaira–Hasegawa test.

4. Discussion

A comparison between the mitochondrial and Y-chromosome *Capra* phylogenies gives some clues about the evolutionary histories of wild and domestic goats. Particularly, our results give insights into the monophyly of the alpine and Spanish ibex, as well as the origin of the domestic and wild goat species.

4.1. Monophyly of the alpine and spanish ibex

In the Y-chromosome sequence analysis, four individuals from *C. pyrenaica* (the Spanish ibex), including widely distributed populations, have exactly the same Y-chromosome haplotype as *C. [i.] ibex* (from the Alps). This supports the monophyly of the two European species. Previous results from allozyme data (Hartl et al., 1992) and mitochondrial data (Manceau et al., 1999b) favored only one wave of *Capra* immigration into Europe. Our results (both Y-chromosome and mitochondrial phylogenies) are concordant with this scenario of immigration followed by a geographic separation and speciation giving rise to *C. pyrenaica* and *C. [i.] ibex*. Fossil records show that colonization of the Iberian Peninsula likely occurred between the Riss-Würm glaciations (Engländer, 1986). Only two *C. [i.] ibex* individuals were included here but this species

experienced a severe bottleneck of <100 individuals in a single population in the 1800 s (Gauthier et al., 1991) and has severely reduced microsatellite DNA variation (Maudet et al., 2002). Therefore, few Y-chromosome lineages are expected in *C. [i.] ibex*. The "one wave" immigration model is consistent with our hypothetical scenario of evolution of the genus *Capra* (see below).

4.2. Origin of domestic goats

Most of the individuals sampled from *C. aegagrus* (the bezoar) share Y-chromosome haplotypes with domestic goats (*C. hircus*). Thus, *C. aegagrus* seems to be the most probable paternal ancestor of the domestic goat. This is consistent with paleontological evidence (Porter, 1996, p. 3), and previous mtDNA data (Luikart et al., 2001; Takada et al., 1997) suggesting that the maternal ancestor of the domestic goat is *C. aegagrus*. Both samples from *C. falconeri* included here had Y-chromosome haplotypes distinct from those of *C. aegagrus* and *C. hircus* (Clade A, Fig. 3b). Further studies of both mtDNA and Y-chromosome DNA with more samples of *C. falconeri* should be performed to examine whether the markhor was a progenitor to some domestic goat breeds as has been suggested (Hassanin et al., 1998; Schaller, 1977, pp. 27–28, and references therein).

Capra hircus has two common and one rare Y-chromosome haplotypes. There is no geographic structure in the distribution of the two common haplotypes (C1 and C2, Table 2); both types are found throughout the old world ($p = 0.81$, AMOVA analysis performed using Arlequin, Schneider et al., 2000). The rare type (C3) was found in only one individual from Romania. Interestingly, three divergent haplotypes within domestic goats were also identified in a mtDNA study (Luikart et al., 2001). This could be explained by several hypotheses. It is possible that one domestication event incorporated three different lineages, or that three independent domestications occurred. The divergent mtDNA types within domestic goats and recent archeological data suggest that multiple domestications are probable (Luikart et al., 2001). To resolve the question of domestication, additional studies including ancient DNA should be conducted.

4.3. Discordance between mtDNA and Y-chromosome phylogenies

Both mitochondrial and Y-chromosome phylogenetic analyses strongly support the division of *Capra* species into two main groups. These groups, however, do not have the same species composition (Fig. 3). With mtDNA, one clade (ML BP 92%, Bayesian posterior probability 1.0) was composed of *C. hircus*, *C. aegagrus*, *C. falconeri*, *C. pyrenaica*, *C. [i.] ibex*, *C. [i.] nubiana*, *C. cylindricornis*, and *C. [i.] caucasica*. The second clade (ML BP 100%, Bayesian posterior probability 1.0) contained only one species: *C. [i.] sibirica*. For the Y-chromosome data, the two groups consisted of (i) *C. aegagrus*, *C. falconeri*, and *C. hircus* and (ii) all other species. According to the Y-chromosome data, Clade A (Fig. 3b) could have been derived from an ancestral "bezoar-type" taxon, and Clade B from a hypothetical "ibex-type" taxon. The existence of an "ibex-type" is consistent with morphology as most ibexes have similar horns and horn cores, except for *C. pyrenaica* (Schaller, 1977, pp. 26–27)—a recent form appearing in Europe <150,000 years ago (Engländer, 1986). *Capra pyrenaica* is very similar to *C. [i.] ibex* at both mtDNA (this study and Manceau et al., 1999b) and Y-chromosome loci (this study).

4.4. Explanations for mtDNA and Y-chromosome discordance

Several hypotheses may explain the discordance between mtDNA and Y-chromosome phylogenies. Processes that could result in different topologies are: (i) amplification of nuclear mtDNA copies, (ii) selection, (iii) lineage sorting of ancestral polymorphisms, or (iv) horizontal transfer of genes (i.e., introgression).

The discordant topologies for mtDNA and Y-chromosome phylogenies may be simply explained by laboratory PCR artifact (e.g., amplification of nuclear copies of mitochondrial-like DNA sequences). Such copies are frequent in the nuclear genomes of many organisms (Bensasson et al., 2001). But Manceau et al. (1999b) used two sets of primers to amplify cytochrome *b* and control region genes. The phylogeny of these two mitochondrial genes is consistent. Moreover, the authors have used many bone samples, for which nuclear amplification is less probable than mitochondrial amplification because of DNA quantity and quality. Finally, Hassanin et al. (1998) found a topology similar to that of Manceau et al. (1999b).

Selection may act on mitochondrial and/or Y-chromosome genes (Gerber et al., 2001; Jobling et al., 1998). Some studies have shown that Y-chromosome diversity may reflect the effects of demographic events or selective pressures such as selective sweeps, positive selection of Y-chromosome markers, or sexual selection (Boissinot and Boursot, 1997; Clark, 1987). Sexual selection is a mechanism that could promote rapid divergence of genetic systems. Moreover, since Y-chromosome genes are involved in male reproductive functions, some of them could be subject to sexual selection. It was recently shown that numerous genes related to sperm production and dimorphic traits (such as body size and tooth development) are localized on the Y-chromosome (Roldan and Gomendio, 1999). In *Capra*, horn size and shape are sexually dimorphic: males present massive horns and females have smaller horns. Horns of males may be adapted for fighting during mating and for defense against predators.

Although regulation of horn morphology is unclear, it appears that sex-linked genes often affect secondary sexual characteristics (Reinhold, 1998). Accordingly, horn morphology may be a Y-chromosome linked trait that is affected by sexual selection. If linkage exists between genes affected by sexual selection and our Y-chromosome mark-

ers (which is possible because of limited recombination of Y-linked genes), our Y-chromosome markers may be sexually selected. However, tests using Tajima's D showed no deviation from neutrality for Y-chromosome sequences within *Capra* sp. ($p > 0.10$, test performed using DnaSP 3.53, Rozas and Rozas, 1999). But this result may be an effect of low levels of polymorphism or of population history. Ibex horn morphotypes (including *C. [i.] sibirica*, *C. [i.] nubiana*, *C.[i.] ibex*, *C. pyrenaica*, *C. [i.] caucasica*, and *C. cylindricornis*) appear monophyletic with Y-chromosome data and paraphyletic with mtDNA (with the *C. pyrenaica* horn type autapomorphic in each case). Thus, the Y-chromosome phylogeny seems concordant with horn morphology. We may hypothesize that Y-chromosome haplotypes from the B clade (ibex-type) may be linked to the ibex morphotype and Y-chromosome haplotypes from the A clade (bezoar-type) to bezoar morphology. More studies comparing horn morphology and DNA sequences are necessary. This would require larger samples of same sex and same age individuals than previously studied.

The ancestral sorting hypothesis would imply that many divergent mtDNA and Y-chromosome lineages existed in the ancestral population gene pool. Subsequently, different lineages were randomly sorted into different daughter populations or taxa. For example, three different daughter populations would have acquired the following lineage combinations: (i) ibex-type Y-chromosome and mtDNA, (ii) bezoar-type Y-chromosome and mtDNA, and (iii) ibex-type Y-chromosome and bezoar-type mtDNA. This could also explain the discordance between the maternal and paternal tree topologies. However, it seems unlikely that two such highly divergent mtDNA and Y-chromosome lineages could evolve in a single population. It seems more likely that two isolated ancestral populations existed (see scenario below).

4.5. Introgression and evolution of the genus Capra

In mammals, horizontal transfer may result from hybridization and introgression. Our own data show a possible case of recent introgressive hybridization in *Capra*. Under the mtDNA analysis, one of the *C. cylindricornis* individuals from Daghestan groups with Daghestan *C. aegagrus* rather than with its conspecifics, as it does under the Y-chromosome analysis (Fig. 3). This affinity between *C. cylindricornis* and *C. aegagrus* is also supported by mtDNA control region sequences obtained independently in our laboratory (unpublished). Several authors have reported hybridization between wild and domestic *Capra* species (Corbet, 1978, pp. 213–217; Couturier, 1962, pp. 517–532; Mason, 1984, pp. 85–99; Porter, 1996, pp. 1–2). The strong possibility of introgressive hybridization in *Capra* suggests a possible evolutionary scenario explaining our results. Near the beginning of the evolutionary history of the genus *Capra*, there could have been two ancestral *Capra* taxa. According to fossil data, the "bezoar-type" was localized near the Fertile Crescent (Mason, 1984, pp. 88–89). We can assume that the "ibex-type" was located in Central Asia (Fig. 4), where the genus is thought to have originated (Pilgrim, 1947). This is further supported by the connection of *C. [i.] sibirica* to the basal *Capra* node in the mitochondrial phylogeny.

The discrepancy between mtDNA and the Y-chromosome data could be explained by hybridization between these two ancestral taxa. When the "ibex-type" began to spread westward (e.g., at the first stage of the colonization of Europe and Africa), it might have hybridized with the "bezoar-type." The offspring of such hybridizations could have captured the mtDNA from the "bezoar-type" taxon and maintained the "ibex-type" Y-chromosome (Fig. 4). Such introgression of mtDNA has already been described

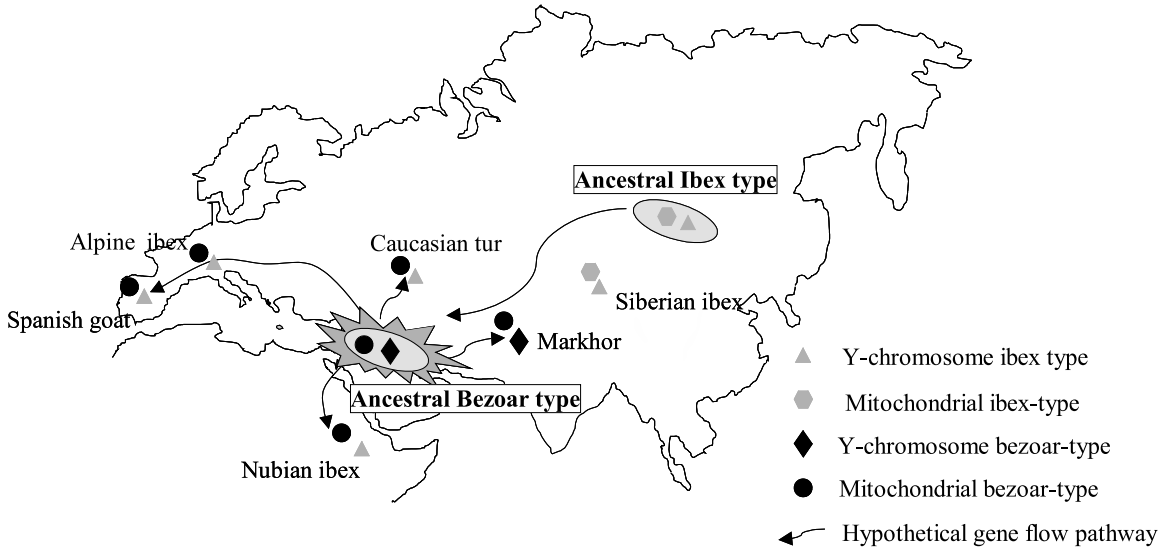

Fig. 4. Hypothetical evolutionary scenario of the genus *Capra*. The encircled symbols represent the possible geographic location of the ancestral ibex-type and bezoar-type. For more details see Section 4.

in canids (Lehman et al., 1991), rodents (Ferris et al., 1983; Ruedi et al., 1997; Tegelström, 1987), lagomorphs (Alves et al., 2003), and ungulates (Carr et al., 1986; Goodman et al., 1999). These "hybrid" offspring may have given rise to *C. pyrenaica* in Spain, *C. [i.] ibex* in the Alps, and *C. [i.] nubiana* in the Nubian Desert (Fig. 4). *Capra cylindricornis* and *C. [i.] caucasica* could also have been derived from such a hybridization. We are not suggesting that hybridization has been an important mechanism of speciation in the genus *Capra*. But it has probably led to the introgression of mtDNA in some *Capra* populations. It could also have contributed to increased variation, facilitating adaptive differentiation or speciation.

Although this scenario is speculative, several lines of evidence are consistent with this model. First, our documentation of recent hybridization in Daghestan between wild *Capra* species lends credibility to the possibility of hybridization in the past. Second, fossil evidence indicates that the most ancient *Capra* lineages occurred in Central Asia and that the colonization of Europe was relatively recent (Cregut-Bonnoure, 1992). Third, Central Asian *Capra* taxa (*C. [i.] sibirica*) are generally larger than western species such as *C. aegagrus* (Schaller, 1977, p. 356). So, if competition between males for reproduction occurred during secondary contact (i.e., in a hybridization zone), males of the Siberian species would be likely to win access to females of the smaller species (e.g., *C. aegagrus*). Consequently, the Y-chromosome of the "ibex-type" would preferentially spread in the descendents. In this scenario, the mtDNA from the females of the smaller bodied *C. aegagrus* could have introgressed (via back crossing) into the larger bodied "ibex-type" taxon. The Y-chromosome and the horn morphology of the descendents would be those of the ibex-type as observed today in the European and African species. Under this hypothesis, the resemblance between the horns of *C. pyrenaica*, *C. falconeri*, and *C. aegagrus* would likely be due to convergent evolution.

The data presented here on mtDNA and Y-chromosome are concordant with this scenario. Hybridization has been recently recognized as playing an important role in the evolution of animals (Allendorf et al., 2001; Hosken and Balloux, 2002; Rieseberg et al., 1999; Shaw, 2002). Within mammals, hybridization and the introgression of mtDNA between species has been reported for many other species. This scenario of the evolutionary history of the genus *Capra*, although hypothetical, provides hypotheses that can be tested in future research. Analysis of other nuclear DNA sequences and a broader geographical sampling scheme will add much to our knowledge of the origin and evolutionary history of *Capra* species.

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