



Unraveling the genetic history of the European wild goats

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ABSTRACT

The population history of the Iberian wild goat and the Alpine ibex has been closely related to that of humans since the Palaeolithic. Current molecular and paleontological studies differ substantially on the phylogenetic origin of the European wild goats, possibly due the loss of genetic variation through time.

We investigated the phylogenetic relationship between the Alpine ibex (*Capra ibex*) and the Iberian wild goat (*Capra pyrenaica*) including different Iberian wild goat subspecies by applying ancient DNA techniques combined with Next Generation Sequencing technologies. We analysed the cytochrome b gene of the mitochondrial genome in 33 ancient and modern European wild goats from Spain and France together with publicly available genetic information of modern wild goats. This work uncovers for the first time ancient genetic information of the Iberian wild goat and the Alpine ibex, spanning a time range of approximately 40,000 years to the present. Our results suggest genetic continuity between ancient and modern populations and indicate a monophyletic origin of the Alpine ibex and the Iberian wild goat when compared to other *Capra* species. The monophyly of both species is in agreement with other molecular studies based only on modern populations, therefore supporting one-wave migration of wild goats into Western Europe followed by possible allopatric speciation. We observe three major clades of wild goats in Western Europe: *Capra ibex*, *Capra pyrenaica pyrenaica* and the group containing the subspecies *Capra pyrenaica hispanica* and *Capra pyrenaica victoriae*. This genetic structure recognizes the distinctiveness of the bucardo (*C. p. pyrenaica*) from the rest of Iberian wild goats and thus supports the idea that this group is an Evolutionary Significant Unit. The divergence time estimated here indicates an almost contemporaneous split between the three clades around 50,000–90,000 years BP.

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1. Introduction

The genus *Capra* comprises several forms of wild goats living in mountain habitats, as well as a domestic species of cosmopolitan distribution, *Capra hircus*. However, the number and status of these

Capra species and subspecies is still under debate (Couturier, 1962; Schaller, 1977; Shackleton, 1997). This is likely the result of traditional taxonomic studies using mainly morphological characters, particularly the horn shape and the fur colour distribution of adult males. It has been argued that these features do not provide enough information to define species or subspecies because these can be related to environmental factors, are highly variable within the populations and can undergo convergent evolution (Schaller, 1977). In addition, some authors have reported hybridization between different species producing fertile offspring (Couturier, 1962). The two forms of the genus *Capra* that inhabit Western Europe are the Alpine ibex and the Iberian wild goat (the latter also called Spanish ibex or Spanish wild goat). Morphological characters such as horn shape and fur colour distribution of males have also been used to describe these species. Different authors have described the Alpine ibex either as a single species, *Capra ibex* (Groves and Grubb, 2011; Wilson et al., 2005), or as a subspecies, *Capra ibex ibex*, comprising with other goats with scimitar-shaped horns (Shackleton, 1997). Likewise, four different subspecies for the Iberian wild goat, *Capra pyrenaica*, have been described (Cabrera, 1911), however these are not recognized by other authors (Groves and Grubb, 2011; Manceau et al., 1999a; Nowak, 1991; Schaller, 1977). In this study, we use the taxonomy accepted by the IUCN: nine species for the genus *Capra*, four subspecies for *C. pyrenaica* (Herrero and Pérez, 2008): *C. p. pyrenaica* (also known as Pyrenean wild goat, Pyrenean ibex or bucardo), *C. p. victoriae*, *C. p. hispanica* and *C. p. lusitanica* and the Alpine ibex wild goat considered as a single species: *C. ibex* (Aulagnier et al., 2008) and not as a subspecies (Fig. 1).

Although neither of the species are considered threatened at present (Herrero and Pérez, 2008; Aulagnier et al., 2008), there is concern regarding genetic diversity after centuries of population decline. At the beginning of the 19th century, only about fifty Alpine ibex survived in the Gran Paradiso massif (Italy) and current ibex populations are the result of both translocation and natural colonization from this core (Grodinsky and Stuwe, 1987). From the four described subspecies of *C. pyrenaica*, only two remain extant: *C. p. victoriae* and *C. p. hispanica*. *C. p. lusitanica* died out at the end of the 19th century (França, 1917) and *C. p. pyrenaica* went extinct in

2000 (Pérez et al., 2002). The main factors affecting the populations have been the excessive hunting, habitat fragmentation, competition with exotic ungulates and domestic livestock as well as several diseases as sarcoptic mange (Acedo and Cassinello, 2009; Pérez et al., 2002).

1.1. Arrival of wild goat into Western Europe

The history of the genus *Capra* is poorly understood. These animals appear to have evolved almost exclusively in mountainous areas and the fossil record is scarce and inadequately preserved (Schaller, 1977; Simpson, 1945). The origin of the Genus *Capra* is set in the Plio-Pleistocene according to paleontological evidence (Couturier, 1962; Crégut-Bonnoure, 2002; Fedosenko and Blank, 2001; Hartl et al., 1990; Pilgrim, 1947; Schaller, 1977), mitochondrial DNA studies (Manceau et al., 1999b) and mitochondrial and nuclear analyses (Ropiquet and Hassanin, 2006).

There are two main hypotheses to explain the expansion of *Capra pyrenaica* and *Capra ibex* into Europe: a) the two-wave migration hypothesis and b) the single wave migration hypothesis (see Fig. 2).

A) The two-wave migration hypothesis is mainly supported by morphological studies based on the fossil record (Crégut-Bonnoure, 1992, 2002, 2006, 2009) (Fig. 2A). This hypothesis implies that *Capra ibex* arrived into the Alps from Asia sometime between 250,000–127,000 years ago (MIS 7–6), as indicated by the presence of the species in the French Lazaret cave and the Italian Prince cave. At this time, an Asian bovid species related to the wild goats, the tahr (genus *Hemitragus*), occupied all Western Europe. Around 80,000 years ago (MIS 5a), a different form of ibex, more closely related to the West Caucasian tur (*Capra caucasica*), would have arrived in France, avoiding the Southern and Western fringes of the Alps, which were occupied by *C. ibex* (Crégut-Bonnoure, 2002). It settled on the Eastern slope of the Massif Central and later reached the Eastern part of the Pyrenees. Populations of the *C. caucasica* group remained in the Eastern part of the French Pyrenees until 40,000 years ago (MIS 3) (Magniez, 2009). This hypothesis suggests an anagenetic evolutionary lineage of *C. caucasica* into *C. pyrenaica*

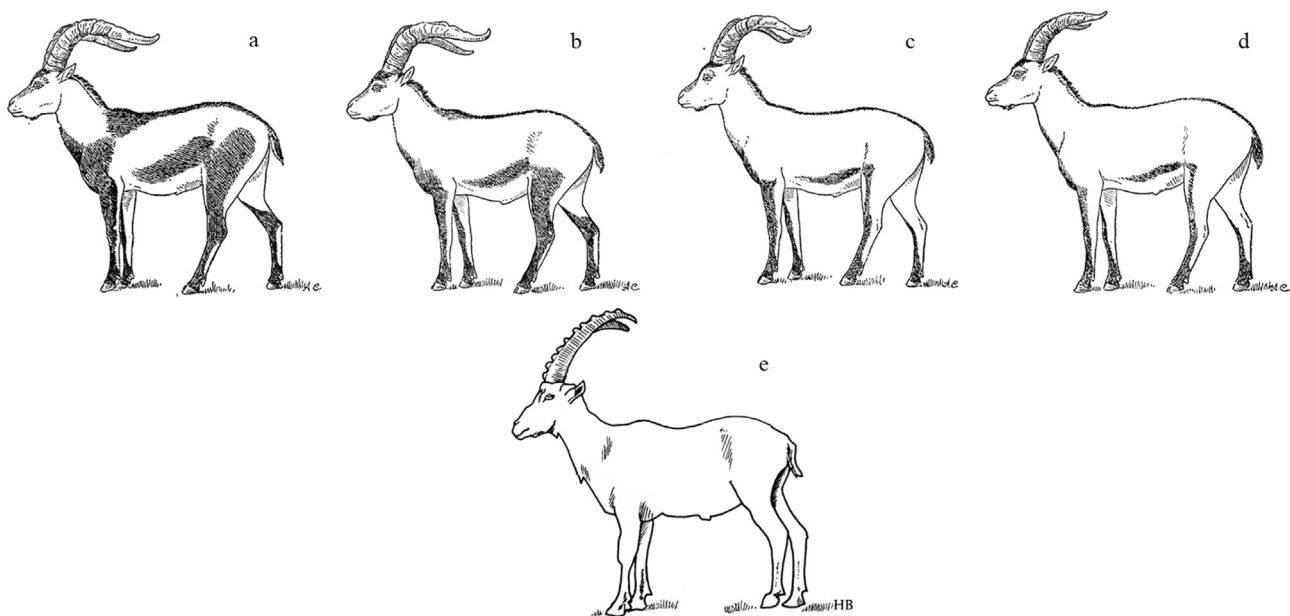


Fig. 1. Subspecies of Iberian wild goat according to Cabrera (1914) a) *C. p. pyrenaica*, b) *C. p. victoriae*, c) *C. p. hispanica* and d) *C. p. lusitanica* (Artwork by Cabrera); and Alpine ibex e) *Capra ibex* (Artwork by HBS).

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