New Holocene *Capra pyrenaica* (Mammalia, Artiodactyla, Bovidae) skulls from the southern Pyrenees

Nouveaux crânes holocènes de *Capra pyrenaica* (Mammalia, Artiodactyla, Bovidae) des Pyrénées méridionales

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Abstract

Three *Capra pyrenaica pyrenaica* skulls from the Holocene found in different karstic sinkholes in the mid-western Pyrenees are described. Two of the locations were at the highest elevations known for *Capra* fossils in the Pyrenees, which provides insights into the timing of the Holocene deglaciation. The skulls of the males were particularly large relative to those of other *Capra* from the Upper Pleistocene found in south-western Europe. An increase in the availability of food, rather than a direct influence of global warming, during the Holocene (Bergmann's Rule) was likely responsible for the large size of the skulls. Comparisons between the horn sections of the Pyrenean skulls and those of neighbouring taxa show a morphological similarity between the former and *C. i. ibex*.

Keywords: Pyrenean wild goat, *Capra* evolution, south-western Europe, Caprinae, sexual dimorphism

Résumé

Trois crânes de *Capra pyrenaica pyrenaica* de l'Holocène trouvés dans différents avens karstiques dans les Pyrénées centre-occidentales sont décrits. Deux des sites se situent à la plus haute altitude connue pour des restes fossiles de *Capra* dans les Pyrénées, ce qui est intéressant pour documenter la chronologie de la déglaciation holocène. Les crânes des mâles sont extrêmement grands par rapport aux autres restes de *Capra* du Pléistocène supérieur trouvés au sud-ouest de l'Europe. Un accroissement de la disponibilité des ressources alimentaires pendant l'Holocène, plutôt qu'une influence directe du réchauffement climatique (règle de Bergmann), fut probablement la cause de la grande taille des crânes. L'étude comparative de la

section des cornes des crânes pyrénéens (*C. p. pyrenaica*) et de celles d'autres taxons voisins montre une similitude morphologique entre ces premiers et *C. i. ibex*.

Mots clés : bouquetin des Pyrénées, évolution *Capra*, Europe sud-occidentale, Caprinae, dimorphisme sexuel

Introduction

The Pyrenean wild goat (*Capra pyrenaica pyrenaica*) is a recently extinct subspecies of the Iberian wild goat (*C. pyrenaica*) that was characteristic of the Pyrenees, the type species of which was defined by Schinz in 1838 (Cabrera, 1911). The last individual died in Jan 2000, when many of the biological and phylogenetic attributes of this subspecies had yet to be studied (García-González & Herrero, 1999). Although the taxonomy of extant *C. pyrenaica* at the subspecies level is controversial (Acevedo & Cassinello, 2009), three other subspecies, all of which are endemic to the Iberian Peninsula, are usually accepted: the extinct *C. p. lusitanica* from north-western Iberia, *C. p. victoriae*, which is found in the mountains of central Spain, and *C. p. hispanica* from the south and western sierras of Spain. Taxonomic names follow Shackleton (1997).

Some (Crégut-Bonnoure, 1992; Rivals, 2002) have suggested that *C. pyrenaica* evolved during the second half of the Upper Pleistocene from an ancestor that is related to *C. caucasica*. That ancestral species would have migrated from the Middle East to Western Europe at the beginning of the last glacial period (120-80 ky). Eventually, it reached southern France and the Pyrenees, where it evolved into *C. pyrenaica* during the Würm III/IV transition (18 ky). That ancestor, named *C. caucasica praepyrenaica* Crégut-Bonnoure, 2002, differed from and did not have contact with the ibex of the Alps (*C. i. ibex*), which evolved there after a previous migration about 300 ky earlier (Crégut-Bonnoure, 2009). Contrary to that hypothesis, however, the molecular data of extant individuals indicated that *C. pyrenaica* and *C. ibex* share a monophyletic origin (Manceau et al., 1999a).

Numerous remains of *C. pyrenaica* from the Upper Pleistocene and Holocene have been found in southern France and in the northern Pyrenees (Clot & Duranthon, 1990; Crégut-Bonnoure, 2005; Magniez, 2009; Rivals & Testu, 2006); however, few remains have been found in the southern Pyrenees (Blasco, 1995). This article describes three Holocene skulls (two adult males, one adult female) found in the southern Pyrenees, which are remarkable because of the high elevation at which two of the findings were made and the exceptional size of the male skulls. I discuss their significance within the context of the ecological conditions in the Pyrenees during the Holocene and their possible influence on sexual dimorphism, based on a theory of caprine evolution (the "dispersal hypothesis" of Geist, 1987 a, b). In addition, some of

their morphological characteristics are interpreted within the context of current hypotheses on *C. pyrenaica* systematics.

The fossil sites

The three incomplete skulls of adult *Capra* (male LAR1, male ORD1, and female ORD2) were found during several speleological explorations by the Estella/Lizarra Speleological Group (GEE/LET), Navarre, Spain, and the Pedraforca Speleological Group (GEP), Barcelona, Spain, in the karstic regions of Larra (Navarre) and Millaris (Ordesa, Huesca, Spain) in the Western and Middle Pyrenees, respectively. Both are notable karst areas, where caves and sinkholes are common. The LAR1, ORD1, and ORD2 skulls were found in sinkholes near the Spanish-French border, and their reference numbers and locations are AN-015 (Larra, Navarre), 0° 46' 57" W - 42° 56' 52" N, 1718 m a.s.l.; MS-2 (Millaris, Huesca), 0° 2' 47" W - 42° 40' 50" N, 2390 m a.s.l.; and CS-59 (Millaris, Huesca), 0° 2' 44" W - 42° 40' 55" N, 2500 m a.s.l., respectively. The latter two sites are at the highest elevation known for the fossil remains of *Capra* in the Pyrenees (Clot & Duranthon, 1990).

The holes in which the skulls were found were structurally similar (Fig. 1). Typically, the entrances to the holes had an inclination of between 30° and 45°, which led to vertical gaps that varied in depth. Frequently, the hole was interrupted by short horizontal or inclined shelves, where mineral and animal debris accumulated, including the *Capra* skulls (Fig. 1). Along with other highly decomposed animal remains, which were not removed, the LAR1 skull was found partially buried between the blocks of an alluvial fan at the bottom of the hole. In addition to the ORD1 skull, a scapula and two ribs from another *Capra* were removed from the site. In addition to the ORD2 skull, 24 of the animal's postcranial bones were collected, some of which were used in ¹⁴C dating. Those remains were found amongst the remains of other *Capra* sp., *Pyrrhocorax* sp., and *Ursus arctos* (Fig. 1). All of the fossil materials are stored in the zoological collections of the Pyrenean Institute of Ecology (CSIC, Spain).

In karstic areas, sinkholes often act as natural traps that lead to the death of some animals because, once they fall into the hole, they cannot escape (Clot & Evin, 1986), which was the likely origin of the fossils described here, and is relevant because, unlike the remains found in caves that were inhabited by humans and where the remains of hunted animals accumulated (Castaños, 1993; Pailhaugue, 1995), the remains found in the sinkholes can be assumed to have been random samples from the population to which they belonged.

The LAR1 and ORD1 skulls were radiocarbon dated using the AMS Method at the ORAU Laboratory, Oxford University (ref. OxA-6012 and OxA-6013, respectively). The ORD2 individual, which provided more material, was aged using liquid scintillation at the Centre de Datation par le Radiocarbène, University of Lyon (ref. UBAR-448). The

radiocarbon data were calibrated using the IntCal09 calibration curves of Bronk Ramsey (2009). The estimated ages of the LAR1, ORD1, and ORD2 skulls were 2136-1774, 3635-3366, and 5221-4842 cal years BC, respectively, which give approximate antiquities of 3900 (LAR1), 5500 (ORD1), and 7000 (ORD2) years BP.

Description of the fossil material

Skulls were measured using a Vernier caliper (0.02 mm Nonius). Most of the measurements follow Driesch (1976), except the following (Table 1): HN, from the highest (most distal) point of the frontals in the median plane to the distal point of the occipital condyles; HNFM, from the highest point of the frontals in the median plane to the opisthion; HNP, height from the basi-occipital to the top of the parietal; and HVE, from the highest point of the frontals in the median plane to the interesphenoideal suture (measured using a curved calliper). Left and right measurements were averaged, and each average was based on three measurements.

LAR1 was the most complete skull and retains all of the frontal bone including the horn cores (tips broken), the parietal, occipital, and sphenoid bones, two complete orbits with zygomatic arches, nasal bones, and the remains of nasal turbinate in the sinuses (Fig. 2). In the LAR1 skull, the fronto-nasal, middle-frontal, and fronto-parietal sutures are fully merged and not visible. Only a portion of the parieto-occipital suture, the zygomatic bone to the temporal suture (zygomatic arch) and the suture between the pre- and basi-sphenoid are visible. The shape of the horn cores fit the Pyrenean type (Couturier, 1962). The bases of the horns are close and, in its central part, they diverge outward (Fig. 2). Horn cores form a divergence angle of 46° in the frontal view. Perpendicular sections of the horn core bases are elliptical and the main axis of the ellipsis opens fronto-laterally at a 27° angle to the median plane in the dorsal view. The nasal bones are abnormally short and have a rectangular shape with parallel sides (except at the tip), which is characteristic of the *C. p. pyrenaica* subspecies (Cabrera, 1911). The eye orbits are flattened, which is characteristic of *C. pyrenaica*, but unlike Alpine ibexes, which have orbits that are rounded or laterally compressed (Fandos et al., 1993; García-González et al., in prep.).

The ORD1 skull included the braincase, almost the entire right horn core, and the base of the left horn core (Fig. 2). The dimensions of the skull are slightly smaller than those of LAR1 (Table 1), but the horn core is longer and thicker. The right horn core diverges outwards and, distally, they twist slightly inward, indicating a second postero-distal curvature, which is typical of *C. pyrenaica*. Right horn core twists clockwise, indicating the heteronym character of the horns. The divergence angle between horn cores is 45° in the frontal view. Perpendicular section of the horn core base is elliptical and slightly less compressed than that of LAR1. The main axis opens fronto-laterally at a 16° angle to the median plane in the dorsal view. All of the

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4 sutures, including the pre- and basi-sphenoids, are obliterated, which suggests that
5 the ORD1 animal was older than the LAR1 animal.
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7 The skulls of the two males are remarkably large (Fig. 3) and their dimensions
8 greatly exceed those of most of the fossil and extant *Capra* in south-western Europe
9 (Crégut-Bonnoure, 2009). In the Pyrenees and southern France, only the skulls found
10 in Tournal (Magniez, 2009) and Malarnaud (Griggo, 1991) have dimensions similar to
11 those described here. The *C. ibex* fossils from Monaco-Grimaldi (Chaix & Desse, 1983)
12 have slightly higher antero-posterior diameters (DAP) at the horn base, but the
13 transversal diameters (DLM) are similar, and extant *C. i. ibex* are significantly smaller
14 in horn thickness. Only a few fossils (*C. dalii*; Bukhsianidze & Vekua, 2006) or extant
15 *C. caucasica* have horns (Couturier, 1962) or skull dimensions (Crégut-Bonnoure,
16 2009) that are larger than those of the LAR1 and ORD1 skulls (Fig. 3). On the
17 contrary, in the LAR1 and ORD1 skulls, the parietal sagittal length and the size of the
18 foramen magnum are remarkably small compared to other south-western European
19 *Capra* (Table 1).
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21 The ORD2 skull includes the braincase, the upper portion of the orbits, the
22 lower half of the left horn core and the base of the right (Fig. 2). Interfrontal and
23 fronto-parietal sutures are visible. The suture between the pre- and basi-sphenoids,
24 which does not close (Couturier, 1962) in females, is open. The dimensions were
25 identical to those of extant Pyrenean goats (*C. p. pyrenaica*), which are significantly
26 greater than those of the other Iberian subspecies (Fig. 4 and García-González et al.,
27 in prep.). The ORD2 and extant Pyrenean goats have horns that are slightly thicker
28 than those of Magdalenian *C. pyrenaica* (13 ky) from La Vache (Pailhaugue, 1995) and
29 Eralla (Altuna et al., 1985), but thinner than those of the Upper Pleistocene female
30 from Castel 2 (Pernaud et al., 2004). In addition, horn width (DLM) is greater than it is
31 in extant *C. i. ibex*, but the antero-posterior diameter (DAP) is similar, which made the
32 horns of *C. i. ibex* more medio-laterally compressed. Fossil *C. ibex* skulls have larger
33 horns and higher compression indices (DAP/DLM) than do *C. p. pyrenaica*, but their
34 95% C.I. overlap (Fig. 3 and 4). The ORD2 female and females of extant *C. p.*
35 *pyrenaica* have horns that are significantly thicker than those of extant *C. caucasica*.
36 The compression indices of the horn core bases of female *Capra* skulls follows a
37 pattern that is similar to that of the males, i.e., an increasing gradient from South
38 Iberia to the Alps (see also García-González, 2011), but the values of females are
39 higher (within the same taxon, the horns of females are more compressed).
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54 **Discussion**

55 *Location of the fossil sites*

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Unlike in the northern Pyrenees, south-western France, and the Cantabrian Mountains, in the southern Pyrenees, few paleontological deposits of *Capra* sp. remains have been described. Among the most well known are those from Chaves Cave (Castaños, 1993) and Gabasa Cave (Blasco, 1995) in the Middle Pyrenees, and those from Cova 120, Olopte, Els Ermitons, and Cau del Duc de Torroella in the Eastern Pyrenees (Yravedra, 2004-5). All of those sites are below 1200 m of altitude. In southern France and the northern Pyrenees, *Capra* remains from the Upper Pleistocene and Holocene have been found between 350-925 m and between 1190-2240 m, respectively (Clot, 1984). The elevations (2390 and 2500 m) at which the fossils from Millaris (ORD1, ORD2) were found were remarkably higher and are the highest known elevations for *Capra* in the Pyrenees.

In the first half of the Holocene (specifically, at 7 ky), deglaciation would have already occurred at 2500 m in Millaris (Ordesa, Central Pyrenees), where traces of the last Pyrenean glaciers remain (Martí Bono & García Ruiz, 1993). Thus, it can be assumed that, at that elevation, alpine pastures would have already developed above the forest limit, which might have reached 2400 m (González-Sampériz et al. 2005). In addition, a rudimentary pastoral activity might have been present (Miras et al. 2007), which would have increased the amount of alpine grasslands because of the clearing of the alpine forest. During the Holocene, the elevation range of *C. pyrenaica* expanded in the Pyrenees (Clot and Duranthon, 1990). It is very likely that those Holocene goats undertook seasonal vertical migrations to take advantage of the resources in alpine pastures in summer and those in the valley bottoms in winter, just as wild and domestic ungulates do, today (García-González et al. 1990). In alpine environments, seasonal migrations of *C. ibex* can cover more than 1000 m, vertically (Michallet, 1994). In addition, the disappearance of reindeers and horses in the Pyrenees during the Holocene (Altuna, 1992), might have reduced the competition for food and, thereby, increased the amount of food available to goats.

Exceptional size of the male skulls

The horns of the Pyrenean male skulls (LAR1, ORD1) are considerably larger than those of most of the southern European *Capra* (Fig. 3). They were larger than the horns of the other Magdalenian (18-10 ky), Holocene, and present-day *C. pyrenaica*, and were within the upper limit of the sizes of those of pre-Magdalenian *Capra* (*C. caucasica praepyrenaica* per Crégut-Bonnou, 2005)(Fig. 3). In addition, other skull dimensions are larger than those of present-day *C. pyrenaica* subspecies or *C. ibex* (Fandos et al., 1993; García-González et al. in prep.). Usually, body size and horn size are positively correlated (Kitchener, 1985); hence, we can assume that those specimens had large body sizes. The diachronic and fortuitous nature of the male LAR1 and ORD1 findings suggests that the large size of the males is not a bias induced by

human hunting of the animals, and that they are random samples of their populations. It seems unlikely they would represent outliers in their populations. Therefore, although one or two specimens cannot provide statistical reliability, it is reasonable to postulate that the Pyrenean Holocene males would have had larger horns and body size than they do today.

Typically, two hypothesis are advanced to explain temporal changes in body size within the same or closely related taxa: a metabolic adaptation to changes in air temperature (Bergmann's Rule) (usually, the largest forms of a species occurred during the coldest climates in the past (Kurtén, 1968; Smith et al. 1995)), or a change in the environment lead to changes in the abundance of food resources, which results in changes in body size (Geist 1987a; Purdue & Reitz, 1993). The reduction in body size in some south-western European ungulates during the Pleistocene-Holocene transition might appear to support the first hypothesis. For example, in northern Spain, the size of *Cervus elaphus* has decreased since the final Würm (Altuna, 1992), and fossil Alpine ibex are larger than their present-day counterparts (Chaix & Desse, 1994). If that hypothesis is true, Pyrenean goats from the Upper Pleistocene should have been larger than those that lived during the Holocene, which is contrary to the results shown in the present work.

The apparently large size of male goats in the Pyrenees during the Holocene suggests that they might have been "Ice Age giants" (*sensu* Geist, 1987a), the hypothetical products of the process in which glaciations led to periods of great environmental alterations and species found new habitats and more food resources. According to Geist's hypothesis, periods of resource abundance are dominated by the dispersive morphs, i.e., individuals that have large body sizes and males that carry large "display organs" (e.g., large horns) that serve to deter competitors, reduce fighting, and give females a visual cue to a male's ability to obtain material resources and the quality of his sperm (Malo et al. 2005). On average, the males that had the largest horns had the greatest reproductive success. In addition, in mountains, migratory populations that can exploit a wide elevational range will have larger body sizes than will individuals in populations that can exploit a narrow range (Geist, 1987b).

With the retreat of the ice during the Holocene, large areas with new food resources became available to the herbivores in the Pyrenees (González-Sampériz et al., 2005). An expanded vertical range allowed a more complete and continuous use of those resources by following new plant growth with elevational displacements throughout the growing season (phenological wave; Morgantini & Hudson, 1989). The Holocene skulls that were found at the highest elevations indicate that deglaciation had occurred and herbivores likely were taking advantage of alpine grassland resources at that time. Alpine grasslands have high nutritional value (Körner, 1989; Marinas & García-González, 2006), provide ungulates with fat reserves for winter, and contribute

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4 to high reproductive potential. Summer feeding is crucial for the survival and
5 reproductive success of mountain ungulates (Albon & Langvatn, 1992; Pettorelli et al.,
6 2007). The optimization of resource use might have fostered the development of large
7 body size in males during the Holocene in the Pyrenees.
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10 The selection pressures for males to be large are very strong, but not in
11 females, which invest more energy into offspring survival (Geist, 1987b). Rather than
12 investing in the pursuit of reproductive opportunities, females invest in the search for
13 food or parental care, which are not enhanced by an increase in the size of adult
14 females, which might explain why the dimensions of the ORD2 skull are nearly
15 identical to those of present-day female Pyrenean goats (Fig. 4).
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20 *Phylogeographical considerations*

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23 Based on skulls found in the Pyrenees that resembled those of Caucasian goats
24 (Pales, 1976-77), and after a thorough study of the dentition of Pyrenean and Alpine
25 *Capra*, Crégut-Bonnoure (1992) proposed that *C. pyrenaica* originated from a
26 migration of an ancestor related to *C. caucasica* at the beginning of Würm, which
27 surrounded the Northern Alps, descended along the French Central Massif, and settled
28 in the Pyrenees at the beginning of Magdalenian period (18 ky). *C. pyrenaica*
29 descended directly from that ancestor related to *C. caucasica* and would not have
30 encountered *C. ibex*, which had become established in the Alps earlier (Crégut-
31 Bonnoure, 2005). Presumably, the other Iberian subspecies would have differentiated
32 from those Pyrenean goats.
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37 Other paleontological studies suggest that three species (*C. caucasica*, *C.*
38 *pyrenaica* and *C. ibex*) might have coexisted in the Pyrenees during the Upper
39 Pleistocene (Clot and Duranthon, 1990; Pales, 1976-77), or that *C. pyrenaica* and *C.*
40 *ibex* had differentiated, separately, before the Würm, sharing a common ancestor *C.*
41 *camburgensis* (Chaix & Desse, 1994; Couturier, 1962).
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44 The hypothesis of Crégut-Bonnoure (1992, 2005) appears to be untenable in
45 view of the molecular data and recent paleontological findings. The morphological
46 characters on which the hypothesis relies are highly variable (García-González, 2011;
47 Magniez, 2009). In addition, numerous *Capra* remains that are older than the final
48 Würm (> 35 ky) have been found in Iberia (García-González, 2011), including two new
49 species of *Capra* from the Lower Pleistocene found in southern Spain (Arribas &
50 Garrido, 2008; Made et al., 2008; Moyà-Solà, 1987). Finally, phylogenetic studies
51 based on molecular data have indicated that *C. ibex* and *C. pyrenaica* have a
52 monophyletic origin and, therefore, are closely related (Kazanskaya et al., 2007;
53 Manceau et al., 1999a; Pidancier et al., 2006). According to Manceau et al. (1999a),
54 the two species form a single clade that excludes species such as *C. caucasica* and, it
55 supports the hypothesis of "a single wave of migration" by the *Capra* genus into
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4 Western Europe, which is in contrast to the proposition of Crégut-Bonnoure. The
5 hypothesis of a common ancestor related to *C. camburgensis* seems the most
6 plausible. The recent discovery of a 300 ky *Capra* from south-eastern Iberia that has
7 been assigned to *C. cf. camburgensis* might provide support for this hypothesis
8 (Sarrión, 2010).
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11 Beyond the hypothesis of Crégut-Bonnoure, other scenarios are possible for the
12 evolution of the south-western European *Capra* species. Geist (1987b) suggested that
13 *C. pyrenaica* occupied the Iberian Peninsula during the Riss or earlier, which predates
14 the existence of ibexes in the Alps. The Iberian Peninsula has been a glacial refuge for
15 other old taxa of Pleistocene ungulates; e.g., *Rupicapra* sp. (Rodríguez et al., 2010),
16 *Capreolus capreolus* (Randi et al., 2004), and *Cervus elaphus* (Sommer et al., 2008).
17 Taberlet et al. (1998) suggested that the Pyrenees was a "suture" area where
18 hybridization occurred among taxa in the Iberian refugia and others from central
19 Europe.
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22 It appears that *Capra* was present in the Iberian Peninsula throughout the
23 Pleistocene (García-González, 2011). The relationship between the ancient Iberian
24 *Capra* from the Lower and Middle Pleistocene and the common ancestor of *C. pyrenaica*
25 and *C. ibex* suggested by the molecular data is unknown. Some morphological traits
26 revealed in the present study (Fig. 3 and 4) place Upper Pleistocene, Holocene, and
27 extant *C. p. pyrenaica* close to *C. i. ibex* or at an intermediate position between *C. i.*
28 *ibex* and central-southern Iberian *Capra*, which is compatible with the molecular data,
29 which indicates an equivalent genetic distance of *C. p. pyrenaica* to *C. i. ibex* and to
30 central-southern Iberian goats (*C. p. victoriae* and *C. p. hispanica*) (Manceau et al.
31 1999b). An intermediate position of Pyrenean goats might be explained by two non-
32 exclusive hypotheses: Pyrenean goats (*C. p. pyrenaica*) have maintained some of the
33 genetic traits that are typical of the common ancestor of the two species (*C. pyrenaica*
34 and *C. ibex*) or a process of hybridization might have occurred more recently (Upper
35 Pleistocene). During the last glaciation, the Iberian goats and ibexes from Middle
36 Europe might have encountered each other in the Pyrenees or surrounding areas.
37 Holocene Pyrenean goats might have incorporated some morphological characters that
38 had been transmitted from Alpine ibex, such as compressed horn core bases (Fig. 3)
39 and large size, which is not incompatible with the Food Abundance Hypothesis of Geist,
40 (1987a,b).
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43 The origin of *C. pyrenaica* and its differentiation into the present subspecies
44 remains unclear. New paleontological records and more molecular studies of fossils and
45 recent materials probably will be needed to clarify the phylogeny of south-western
46 European *Capra* and their diversification.
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48 **Acknowledgements**

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Table 1. Measurements of the *Capra pyrenaica* skulls in millimetres. In brackets: approximate values. Number in brackets following definition: codes used in Driesch (1976). For acronyms HN, HNFM, HNP and HVE see Description section.

Tableau 1. Mensurations des crânes de *Capra pyrenaica* en millimètres. Entre parenthèses : valeurs approximatives. Les chiffres entre parenthèses après la définition correspondent aux codes utilisés dans Driesch (1976). Pour les acronymes HN, HNFM, HNP et HVE consulter la section Description.

Measurement (mm)	LAR1	ORD1	ORD2
Maximum nasal length (15)	69.6		
Nasion - Bregma length (10)	141.5		
Parietal length in the sagital plane	22.4	(23)	(37.8)
Bregma - Akrokranium length (9)	46.4	(59.4)	65.3
Nasion - Akrokranium length (8)	177.1		
Maximum inner height of the orbit (25)	46.4		
Maximum inner length of the orbit (24)	48.6		
Maximum inter-orbital width (34)	169.2		(126.3)
Minimum inter-orbital width (35)	128.9		
Maximum mastoid width (26)	127.2	(109.4)	(81.2)
Zygomatic width	165.1		
Maximum neurocranium breadth	99.2	(96.4)	81.2
Neurocranium length a (HN)	161.3	145.9	127.5
Neurocranium length b (HNFM)	141.0	126.0	113.1
Braincase height (HNP)	93.0	90.2	77.5
Neurocranium height (HVE)	144.5	114.8	75
Height of foramen magnum (30)	20.8	19.9	21.0
Maximum breadth of foramen magnum (29)	21.5		23.2
Circumference of horn core base (40)	229	236.3	105
Minimum distance between horn core base	25.5	21.1	42.6
Maximum breadth between lateral borders of horn core base (32)	143.9		(104.4)
Antero-posterior diameter of horn core base (41)	78.5	80.3	35.2
Latero-medial diameter of horn core base (42)	63.6	71.1	30.5
Anterior length of horn core (string) (43)	(350)	(448)	

Horn divergence angle	46°	45°
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Fig. 1. Plans and sections of sinkholes where skulls of *Capra pyrenaica* were found (asterisks). Adapted from drawings of GEE/LET and GEP.

Fig. 1. Plans et coupes des avens où les crânes de *Capra pyrenaica* (astérisques) ont été trouvés. Adapté à partir des dessins de GEE/LET et GEP.

Fig. 2. LAR1 (above), ORD1 (middle) and ORD2 (bottom) *Capra pyrenaica* skulls in frontal and lateral view. Scale bar = 5 cm.

Fig. 2. Crânes des *Capra pyrenaica* LAR1 (au-dessus), ORD1 (centre) et ORD2 (en bas) en vue frontale et latérale. Échelle = 5 cm.

Fig. 3. Bivariate plot of longitudinal (DAP) and transverse diameter (DLM) of basal horn core section of some European extant and fossil *Capra* males. Mean values and 95% confidence limits (thin lines). **Open triangles**: extant *C. ibex* from Chaix et Desse (1983) below and Couturier (1962) above. **Filled triangle**: Riss-Würm *C. ibex* from Chaix & Desse (1983). **Open squares**: extant *C. pyrenaica* (own data), from bottom to top: *C. p. hispanica* (Cazorla Sierra), *C. p. victoriae* (Gredos Sierra), *C. p. pyrenaica* (Pyrenees). **Filled squares**: Magdalenian *C. pyrenaica* from Pailhaugue (1995) below, and Pyrenean Holocene *C. pyrenaica* from Clot (1988) and own data (above). **Open squares with dot**: LAR1 below-left, ORD1 above-right (this study). **Open diamonds**: extant *C. caucasica-cylindricornis* from Couturier (1962) above, and Rivals (2002) below. **Filled diamonds**: above, Middle Würm *C. pyrenaica* from Spanish Pre-Pyrenees (Gabasa cave) own data; below, mean of South-French Lower-Middle Würm skulls of *C. caucasica praepyrenaica* (*sensu* Crégut-Bonnoure, 2005), data from Griggo (1991), Rivals (2002) and Magniez (2009). **Crosses**: old *Capra* (>1 My), above: *C. dalii* (Georgia), below: *C. baetica* (South Spain) from Arribas & Garrido (2008), middle-left: *C. alba* (South Spain) from Moyà-Solà (1987) and Made et al. (2008). **Open and filled circles**: extant and fossil *Hemitragus jemlahicus* from Rivals (2002).

Fig. 3. Graphique bivarié du diamètre longitudinal (DAP) et transversal (DLM) de la section basale des chevilles osseuses de *Capra* mâles européens actuels et fossiles. Valeurs moyennes et limites de confiance à 95% (lignes minces). **Triangles blancs** : *C. ibex* actuels; en bas d'après Chaix & Desse (1983), au-dessus d'après Couturier (1962). **Triangle noir** : *C. ibex* du Riss-Würm d'après Chaix & Desse (1983). **Carrés blancs** : *C. pyrenaica* actuels (données personnelles), de bas en haut: *C. p. hispanica*

(Cazorla Sierra), *C. p. victoriae* (Sierra de Gredos), *C. p. pyrenaica* (Pyrénées). **Carrés noirs** : en bas *C. pyrenaica* du Magdalénien d'après Pailhaugue (1995), en haut *C. pyrenaica* de l'Holocène (d'après Clot 1988 et données personnelles). **Carrés blancs avec point** : en bas à gauche LAR1, en haut à droite ORD1 (cette étude). **Losanges blancs** : *C. caucasica-cylindricornis* actuels d'après Couturier (1962) en haut et Rivals (2002) en bas. **Losanges pleins** : au-dessus, *C. pyrenaica* du Würm moyen des Pré-Pyrénées espagnoles (grotte de Gabasa, données personnelles); en bas, moyenne des crânes du sud de la France du Würm moyen-récent (*C. caucasica praepyrenaica* selon Crégut-Bonnoure, 2005), données de Griggo (1991), Rivals (2002) et Magniez (2009). **Croix** : anciennes *Capra* (>1 Ma), en haut *C. dalii* (Géorgie), en bas *C. baetica* (sud de l'Espagne) d'après Arribas & Garrido (2008), au milieu à gauche *C. alba* (sud de l'Espagne) d'après Moya-Solà (1987) et Made et al. (2008). **Cercles blancs et noirs** : *Hemitragus jemtahicus* actuels et fossiles d'après Rivals (2002).

Fig. 4. Bivariate plot of longitudinal (DAP) and transverse diameter (DLM) of basal horn section of some European living and fossil *Capra* females. Mean values and 95% confidence limits (thin lines). **Open triangles**: extant Alpine *C. ibex* from Chaix et Desse (1983) below, and Couturier (1962) above. **Filled triangles**: Riss-Würm *C. ibex* from Chaix et Desse (1983) and *C. camburgensis* from Made et al. (2008). **Open squares**: extant *C. pyrenaica* (own data), from top to bottom: *C. p. pyrenaica* (Pyrenees), *C. p. victoriae* (Gredos Sierra), *C. p. hispanica* (Cazorla Sierra). **Filled squares**: Magdalenian *C. pyrenaica* from Eralla (Altuna et al., 1985) below, from La Vache (Pailhaugue, 1995) middle, and Castel 2 (Pernaude et al., 2004) above. **Open square with dot**: Holocene *C. pyrenaica* (ORD2 this study). **Open diamond**: extant *C. caucasica-cylindricornis* from Couturier (1962). **Cross**: *C. alba* from Quibás (South Spain) (Made et al. 2008).

Fig. 4. Graphique bivarié du diamètre longitudinal (DAP) et transversal (DLM) de la section basale des chevilles osseuses de *Capra* femelles européennes actuelles et fossiles. Valeurs moyennes et limites de confiance à 95% (lignes minces). **Triangles blancs** : *C. ibex* actuels; en bas d'après Chaix & Desse (1983), au-dessus d'après Couturier (1962). **Triangles noirs** : *C. ibex* du Riss-Würm (Chaix & Desse, 1983) et *C. camburgensis* (Made et al. 2008). **Carrés blancs** : *C. pyrenaica* actuels (données personnelles), de haut en bas : *C. p. pyrenaica* (Pyrénées), *C. p. victoriae* (Sierra de Gredos), *C. p. hispanica* (Cazorla Sierra). **Carrés noirs** : *C. pyrenaica* du Magdalénien d'Eralla (Altuna et al., 1985) en bas, de La Vache (Pailhaugue, 1995) au milieu, et de Castel 2 (Pernaude et al., 2004) en haut. **Carrés blancs avec point** : *C. pyrenaica* de l'Holocène (ORD2 cette étude). **Losange blanc** : *C. caucasica-cylindricornis* actuels d'après Couturier (1962). **Croix** : *C. alba* de Quibás (sud de l'Espagne) d'après Made et al. (2008).

Figure

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