General palaeontology, systematics and evolution (Vertebrate palaeontology)

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

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

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A B S T R A C T

Three *Capra pyrenaica pyrenaica* skulls from the Holocene found in different karstic sink-holes in the mid-western Pyrénées are described. Two of the locations were at the highest elevations known for *Capra* fossils in the Pyrénées, which provides insights into the tim-ing of the Holocene deglaciation. The skulls of the males were particularly large relative to those of other *Capra* from the Upper Pleistocene found in southwestern Europe. An increase in the availability of food, rather than a direct influence of global warming, dur-ing 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*.

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R É S U M É

Trois crânes de *Capra pyrenaica pyrenaica* de l'Holocène trouvés dans différents avens kars-tiques des 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 intéres-sant 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 ali-mentaires 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*.

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1. 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 Pyrénées, the type species of which was defined by Schinz in

1838 (Cabrera, 1911). The last individual died in January 2000, when many of the biological and phylogenetic attributes of this subspecies had yet to be studied (García-González and Herrero, 1999). Although the taxonomy of extant *C. pyrenaica* at the subspecies level is controversial (Acevedo and Cassinello, 2009), three other subspecies, all of which are endemic to the Iberian Peninsula, are usually accepted: the extinct *C. p. lusitanica* from northwestern 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 Shacketlon (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 Pyrénées, 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 Pyrénées (Clot and Duranthon, 1990; Crégut-Bonnoure, 2005; Magniez, 2009; Rivals and Testu, 2006); however, few remains have been found in the southern Pyrénées (Blasco, 1995). This article describes three Holocene skulls (two adult males, one adult female) found in the southern Pyrénées, 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 Pyrénées during the Holocene and their possible influence on sexual dimorphism, based on a theory of caprine evolution (the "dispersal hypothesis" of Geist, 1987a,b). In addition, some of their morphological characteristics are interpreted within the context of current hypotheses on *C. pyrenaica* systematics.

2. 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 Pyrénées, 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, Navarra), 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 Pyrénées (Clot and 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 ^{14}C 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 and 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 Radiocarbone, 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.

3. Description of the fossil material

Skulls were measured using a Vernier caliper (0.02 mm Nonius). Most of the measurements follow Driesch (1976), except HN, HNFM, HNP and HVE (Table 1). 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
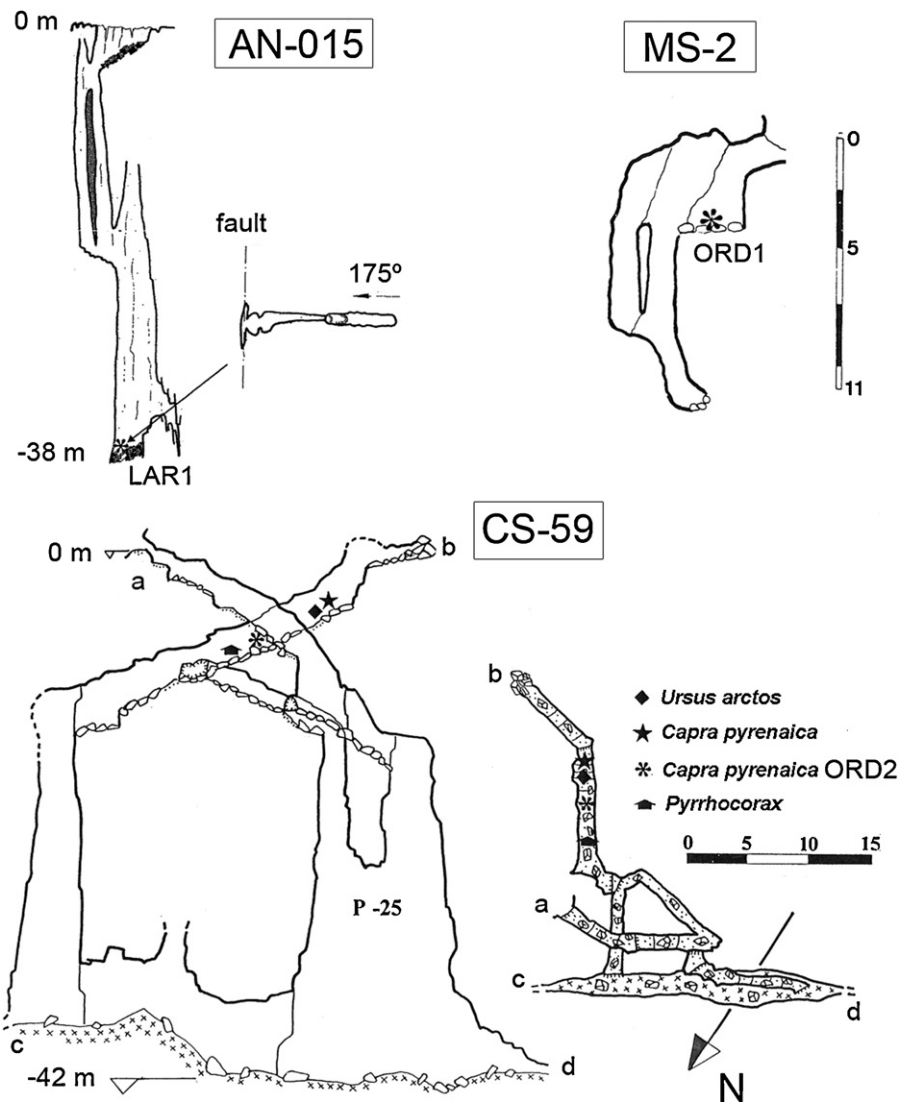
Fig. 1. Plans and sections of sinkholes where skulls of *Capra pyrenaica* were found (asterisks). Adapted from drawings of Estella/Lizarra Speleological Group (GEE/LET) and Pedraforca Speleological Group (GEP).
Fig. 1. Plans et élévations coupes des avens où les crânes de *Capra pyrenaica* (astérisques) ont été trouvés. Adapté à partir des dessins de Estella/Lizarra Speleological Group (GEE/LET) et Pedraforca Speleological Group (GEP).

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., 2012).

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 sutures, including the pre- and basi-sphenoids, are obliterated, which suggests that the ORD1 animal was older than the LAR1 animal.

The skulls of the two males are remarkably large (Fig. 3) and their dimensions greatly exceed those of most

Table 1
Measurements of the *Capra pyrenaica* skulls in millimetres. In brackets: approximate values. Number in brackets following definition: codes used in Driesch (1976).

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).

Measurement (mm)	LAR1	ORD1	ORD2
Maximum nasal length (15)	69.6		
Nasion–Bregma length (10)	141.5		
Parietal length in the sagittal plane	22.4	(23)	(37.8)
Bregma–Akrokranion length (9)	46.4	(59.4)	65.3
Nasion–Akrokranion 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°	

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).

of the fossil and extant *Capra* in southwestern Europe (Crégut-Bonnoure, 2009). In the Pyrénées and southern France, only the skulls found in Tournal (Magniez, 2009) and Malarnaud (Griggo, 1991) have dimensions similar to those described here. The *C. ibex* fossils from Monaco-Grimaldi (Chaix and Desse, 1983) have slightly higher antero-posterior diameters (DAP) at the horn base, but the transversal diameters (DLM) are similar, and extant *C. i. ibex* are significantly smaller in horn thickness. Only a few fossils (*C. dalii*; Bukhsianidze and Vekua, 2006) or extant *C. caucasica* have horns (Couturier, 1962) or skull dimensions (Crégut-Bonnoure, 2009) that are larger than those of the LAR1 and ORD1 skulls (Fig. 3). On the contrary, in the LAR1 and ORD1 skulls, the parietal sagittal length and the size of the foramen magnum are remarkably small compared to other southwestern European *Capra* (Table 1).

The ORD2 skull includes the braincase, the upper portion of the orbits, the lower half of the left horn core and the base of the right (Fig. 2). Interfrontal and fronto-parietal sutures are visible. The suture between the pre- and basi-sphenoids, which does not close (Couturier, 1962) in females, is open. The dimensions were identical to those of extant Pyrenean goats (*C. p. pyrenaica*), which are significantly greater than those of the other Iberian subspecies (Fig. 4 and García-González et al., 2012). The ORD2 and extant Pyrenean goats have horns that are slightly thicker than those of Magdalenian *C. pyrenaica* (13 ky) from La Vache (Pailhaugue, 1995) and Eralla (Altuna et al., 1985), but thinner than those of the Upper Pleistocene female from Castel 2 (Pernaud et al., 2004). In addition, horn width

(DLM) is greater than it is in extant *C. i. ibex*, but the antero-posterior diameter (DAP) is similar, which made the horns of *C. i. ibex* more medio-laterally compressed. Fossil *C. ibex* skulls have larger horns and higher compression indices (DAP/DLM) than do *C. p. pyrenaica*, but their 95% C.I. overlap (Figs. 3 and 4). The ORD2 female and females of extant *C. p. pyrenaica* have horns that are significantly thicker than those of extant *C. caucasica*. The compression indices of the horn core bases of female *Capra* skulls follows a pattern that is similar to that of the males, i.e., an increasing gradient from South Iberia to the Alps (see also García-González, 2011), but the values of females are higher (within the same taxon, the horns of females are more compressed).

4. Discussion

4.1. Location of the fossil sites

Unlike in the northern Pyrénées, southwestern France, and the Cantabrian Mountains, in the southern Pyrénées, 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 Pyrénées, and those from Cova 120, Olopte, Els Ermitons, and Cau del Duc de Torroella in the eastern Pyrénées (Yravedra, 2004-2005). All of those sites are below 1200 m of altitude. In southern France and the northern Pyrénées, *Capra* remains from the Upper Pleistocene and Holocene have been found between 350–925 m and between 1190–2240 m, respectively (Clot, 1984). The
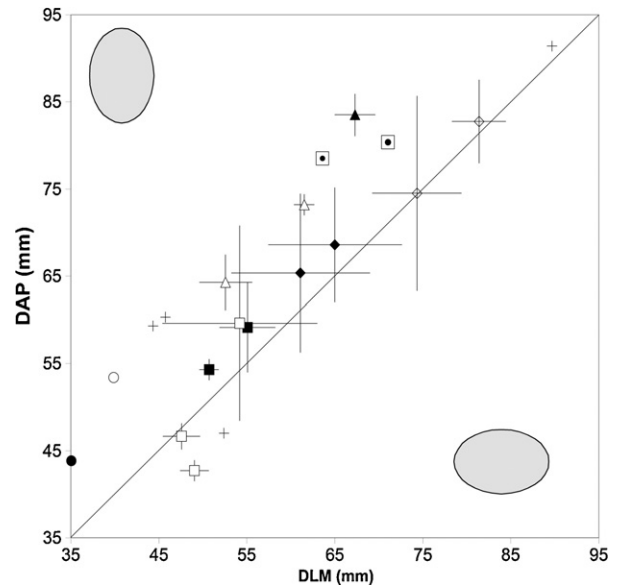
Fig. 2. LAR1 (above), ORD1 (middle) and ORD2 (bottom) *Capra pyrenaica* skulls in frontal and lateral view. Scale bar = 5 cm.
Fig. 2. Crânes de *Capra pyrenaica* LAR1 (au-dessus), ORD1 (centre) et ORD2 (en bas) en vues frontale et latérale. Échelle = 5 cm.

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 *Capra ibex* from Chaix et Desse (1983) below and Couturier (1962) above. **Filled triangle**: Riss-Würm *C. ibex* from Chaix and 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* (Pyrénées). **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-Pyrénées (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 and 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:** *Capra ibex* actuels; en bas d'après Chaix et Desse (1983), au-dessus d'après Couturier (1962). **Triangle noir:** *C. ibex* du Riss-Würm d'après Chaix et Desse (1983). **Carrés blancs:** *C. pyrenaica* (données personelles), 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 droit 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 et 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 jemlahicus* actuels et fossiles d'après Rivals (2002).
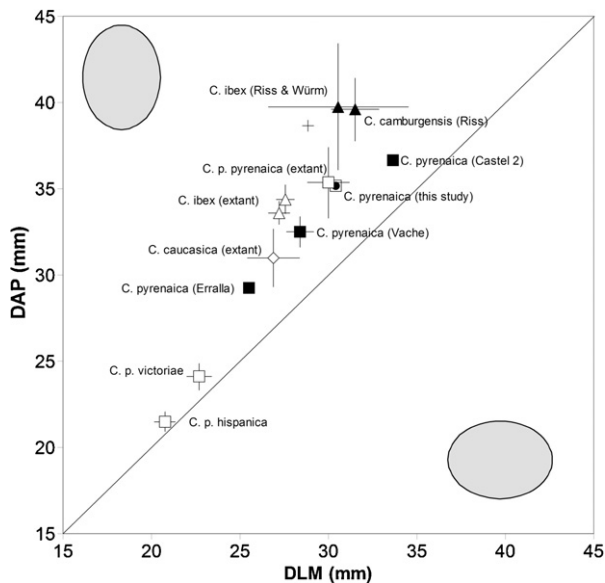
elevations (2390 and 2500 m) at which the fossils from Millaris (ORD1, ORD2) were found were remarkably higher and are the highest known elevations for *Capra* in the Pyrénées.

In the first half of the Holocene (specifically, at 7 ky), deglaciation would have already occurred at 2500 m in Millaris (Ordesa, central Pyrénées), where traces of the last Pyrenean glaciers remain (Martí-Bono and 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 Pyrénées (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,

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 *Capra 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* (Pyrénées), *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 (Pernaud 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 :** *Capra ibex* actuels ; en bas d'après Chaix et Desse (1983), au-dessus d'après Couturier (1962). **Triangles noirs :** *C. ibex* du Riss-Würm (Chaix et 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 (Pernaud 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).

vertically (Michallet, 1994). In addition, the disappearance of reindeers and horses in the Pyrénées during the Holocene (Altuna, 1992) might have reduced the competition for food and, thereby, increased the amount of food available to goats.

4.2. 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-Bonnoure, 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., 2012). 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 hypotheses 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 and Reitz, 1993). The reduction in body size in some southwestern 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 and 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 Pyrénées 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 Pyrénées (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 and 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 and García-González, 2006), provide ungulates with fat reserves for winter, and contribute to high reproductive potential. Summer feeding is crucial for the survival and reproductive success of mountain ungulates (Albon and Langvatn, 1992; Pettorelli et al., 2007). The optimization of resource use might have fostered the development of large body size in males during the Holocene in the Pyrénées.

The selection pressures for males to be large are very strong, but not in females, which invest more energy into offspring survival (Geist, 1987b). Rather than investing in the pursuit of reproductive opportunities, females invest in the search for food or parental care, which are not enhanced by an increase in the size of adult females, which might explain why the dimensions of the ORD2 skull are nearly identical to those of present-day female Pyrenean goats (Fig. 4).

4.3. Phylogeographical considerations

Based on skulls found in the Pyrénées that resembled those of Caucasian goats (Pales, 1976-1977), and after a thorough study of the dentition of Pyrenean and Alpine *Capra*, Crégut-Bonnoure (1992) proposed that *C. pyrenaica* originated from a migration of an ancestor related to *C. caucasica* at the beginning of Würm, which surrounded the northern Alps, descended along the French Central Massif, and settled in the Pyrénées at the beginning of Magdalenian period (18 ky). *C. pyrenaica* descended directly from that ancestor related to *C. caucasica* and would not have encountered *C. ibex*, which had become established in the Alps earlier (Crégut-Bonnoure, 2005). Presumably, the other Iberian subspecies would have differentiated from those Pyrenean goats.

Other paleontological studies suggest that three species (*C. caucasica*, *C. pyrenaica* and *C. ibex*) might have coexisted in the Pyrénées during the Upper Pleistocene (Clot and Duranthon, 1990; Pales, 1976-1977), or that *C. pyrenaica* and *C. ibex* had differentiated, separately, before the Würm, sharing a common ancestor *C. camburgensis* (Chaix and Desse, 1994; Couturier, 1962).

The hypothesis of Crégut-Bonnoure (1992, 2005) appears to be untenable in view of the molecular data and recent paleontological findings. The morphological characters on which the hypothesis relies are highly variable (García-González, 2011; Magniez, 2009). In addition, numerous *Capra* remains that are older than the final Würm (> 35 ky) have been found in Iberia (García-González, 2011), including two new species of *Capra* from the Lower Pleistocene found in southern Spain (Arribas and Garrido, 2008; Made et al., 2008; Moyà-Solà, 1987). Finally, phylogenetic studies based on molecular data have indicated that *C. ibex* and *C. pyrenaica* have a monophyletic origin and, therefore, are closely related (Kazanskaya et al., 2007; Manceau et al., 1999a; Pidancier et al., 2006). According to Manceau et al. (1999a), the two species form a single clade that excludes species such as *C. caucasica* and, it supports the hypothesis of "a single wave of migration" by the *Capra* genus into western Europe, which is in contrast to the proposition of Crégut-Bonnoure. The hypothesis of a common ancestor related to *C. camburgensis* seems the most plausible to these authors. The recent discovery of a 300 ky *Capra* from southeastern Iberia that has been assigned to *C.* cf. *camburgensis* might provide support for this hypothesis (Sarrión, 2010).

Beyond the hypothesis of Crégut-Bonnoure, other scenarios are possible for the evolution of the southwestern European *Capra* species. Geist (1987b) suggested that *C. pyrenaica* occupied the Iberian Peninsula during the Riss or earlier, which predates the existence of ibexes in the Alps. The Iberian Peninsula has been a glacial refuge for other old taxa of Pleistocene ungulates; e.g., *Rupicapra* sp. (Rodríguez et al., 2010), *Capreolus capreolus* (Randi et al., 2004), and *Cervus elaphus* (Sommer et al., 2008). Taberlet et al. (1998) suggested that the Pyrénées were a "suture" area where hybridization occurred among taxa in the Iberian refugia and others from central Europe.

It appears that *Capra* was present in the Iberian Peninsula throughout the Pleistocene (García-González, 2011). The relationship between the ancient Iberian *Capra* from the Lower and Middle Pleistocene and the common ancestor of *C. pyrenaica* and *C. ibex* suggested by the molecular data is unknown. Some morphological traits revealed in the present study (Figs. 3 and 4) place Upper Pleistocene, Holocene, and extant *C. p. pyrenaica* close to *C. i. ibex* or at an intermediate position between *C. i. ibex* and central-southern Iberian *Capra*, which is compatible with the molecular data, which indicates an equivalent genetic distance of *C. p. pyrenaica* to *C. i. ibex* and to central-southern Iberian goats (*C. p. victoriae* and *C. p. hispanica*) (Manceau et al., 1999b). An intermediate position of Pyrenean goats might be explained by two non-exclusive hypotheses: Pyrenean goats (*C. p. pyrenaica*) have maintained some of the genetic traits that are typical of the common ancestor of the two species (*C. pyrenaica* and *C. ibex*) or a process of hybridization might have occurred more recently (Upper Pleistocene). During the last glaciation, the Iberian goats and ibexes from Middle Europe might have encountered each other in the Pyrénées or surrounding areas. Holocene Pyrenean goats might have incorporated some morphological characters that had been transmitted from Alpine ibex, such as compressed horn core bases (Fig. 3) and large size, which is not incompatible with the Food Abundance Hypothesis of Geist (1987a,b).

The origin of *C. pyrenaica* and its differentiation into the present subspecies remains unclear. New paleontological records and more molecular studies of fossils and recent materials probably will be needed to clarify the phylogeny of southwestern European *Capra* and their diversification.

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