

## THE LATE PLEISTOCENE APENNINE CHAMOIS FROM GROTTA MORA CAVORSO (SIMBRUINI MOUNTAINS, CENTRAL ITALY)

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**Abstract.** This paper describes a sub-entire, partially articulated skeleton of chamois found together with other vertebrate remains in a silty lens with limestone clasts between the 104 and 105 SSUU of Grotta Mora Cavorso (Latium, Italy). This silty lens is chronologically correlatable to a temperate oscillation of MIS 3. The skull and post-cranial remains from Grotta Mora Cavorso were compared with the fossil remains of chamois from numerous Late Pleistocene and older Holocene sites of Italy and of Pyrenees and Iberian Peninsula. Additional comparisons were made with large samples of extant chamois, *Rupicapra pyrenaica ornata*, *R. pyrenaica pyrenaica* and *R. rupicapra rupicapra*. Morphological and morphometric features of the skull and the horn-core, as well as other characters of the metacarpus suggest to refer the fossil remains from Grotta Mora Cavorso to Apennine chamois, *R. pyrenaica ornata*. This is the earliest ascertained record in Central-Southern Italy of the *ornata*-like chamois, a subspecies so far known with certainty only in the Holocene, or possibly in the Lateglacial.

### Introduction

The Late Pleistocene bone remains of chamois from Grotta Mora Cavorso (Jenne, Latium, Italy), more specifically a sub-entire, partially articulated skeleton, are described in this paper.

Remains of *Rupicapra* de Blainville, 1816 occur in Western Europe since the Middle Pleistocene and are relatively common in the Late Pleistocene of Italy (Masini & Lovari 1988; Crégut-Bonnoure 2007; Masseti & Salari 2012a, 2012b).

Current distribution of this genus includes several portions of the middle to high-altitude mountain ranges

of Southern Europe and Near East (from 35° to 50° N) (Aulagnier et al. 2008; Herrero et al. 2008), but in the Late Pleistocene its spread was much wider, including low-altitude regions and also coastal areas (Masini 1985; Masini & Lovari 1988; Masseti & Salari 2012b).

The genus is currently divided into two species (Masini & Lovari 1988; Grubb 2005): the Alpine chamois, *Rupicapra rupicapra* (Linnaeus, 1758), divided into seven regional subspecies, spread from Anatolia and the Caucasus to the Alps; that of the Pyrenees, *Rupicapra pyrenaica* Bonaparte, 1845, widespread in the Iberian Peninsula, with its subspecies from the Pyrenees and the Cantabrian Mountains, which has survived up to present in Italy only within the Abruzzi National Park in the form of the subspecies *R. pyrenaica ornata* Neumann, 1899 (see Aulagnier et al. 2008; Herrero et al. 2008). Recently, the Apennine chamois, *R. pyrenaica ornata*, has been successfully reintroduced in other National Parks in Central Italy (Mari & Lovari 2009).

The earliest fossil records of chamois in Western Europe, referred to *Rupicapra* cf. *pyrenaica*, come from layer «F» of the Caune de l'Arago (Tautavel, Pyrénées-Orientales, France), dated about 440,000 years BP and correlated with the Marine Isotope Stage 12 (MIS 12) (Crégut 1979; Moigne et al. 2006; Crégut-Bonnoure 2007). The same taxon was also recorded from the site of Orgnac 3 (Ardèche, France) in layers dated between 339,000 and 298,000 years BP (MIS 9) (Rivals 2004). The finds then become slightly more numerous in the final stages of Middle Pleistocene (MIS 6) and among

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Fig. 1 - Grotta Mora Cavorso: A) location of the site; B) partial longitudinal section (up) and complete plan (down) of the cave.

these we can mention other French fossil remains: from the Grotte du Cap de la Bielle (Nestier, Hautes-Pyrénées), referred to *Rupicapra* cf. *pyrenaica*; from the Grotte des Cèdres (Le Plan d'Aups, Var) and the Grotte du Lazaret (Nice, Alpes-Maritimes), attributed to *R. rupicapra*; from the Grotte de la Niche (Montmaurin, Haute-Garonne), attributed to *R. pyrenaica* and from Romain-la-Roche (Romain, Doubs), referred to *Rupicapra* cf. *rupicapra* (see Clot & Marsan 1986; Masini & Lovari 1988; Defleur et al. 1989; Tavano et al. 1990; Crégut-Bonnoure 1992, 2007; Valensi 2009; Vercoutère & Guérin 2010).

Fossil remains attributed to *Rupicapra* in Italy are relatively numerous during the Late Pleistocene, especially from sites referred to the Last Glacial (Würm *Auctorum*), but the taxon probably reached the peninsula during the final stages of the Middle Pleistocene (MIS 6) (Masini 1985; Petronio et al. 2007, 2011; Palombo et al. 2011). The assumed distribution of *Rupicapra* in Italy in the Late Pleistocene and the older Holocene, based on the current distribution of chamois populations and the well-preserved remains of only 5-7 sites, seems to be as follows. Alpine chamois was widespread in the Alpine arch, between the Eastern Alps

and the Maritime Alps, as well as in the Northern Apennines (Masini 1985; Masini & Lovari 1988), or possibly slightly farther south, at least up to Pisano Mount, Tuscany, Tyrrhenian side (Masetti & Salari 2012b). The Apennine chamois was confined to a portion of peninsula between northern Calabria and the Sibillini Mountains (southern Umbria-Marche Apennines) (Masini 1985; Masini & Lovari 1988), or probably slightly farther north, up to the central Umbria-Marche Apennines, Adriatic side (Masetti & Salari 2012b).

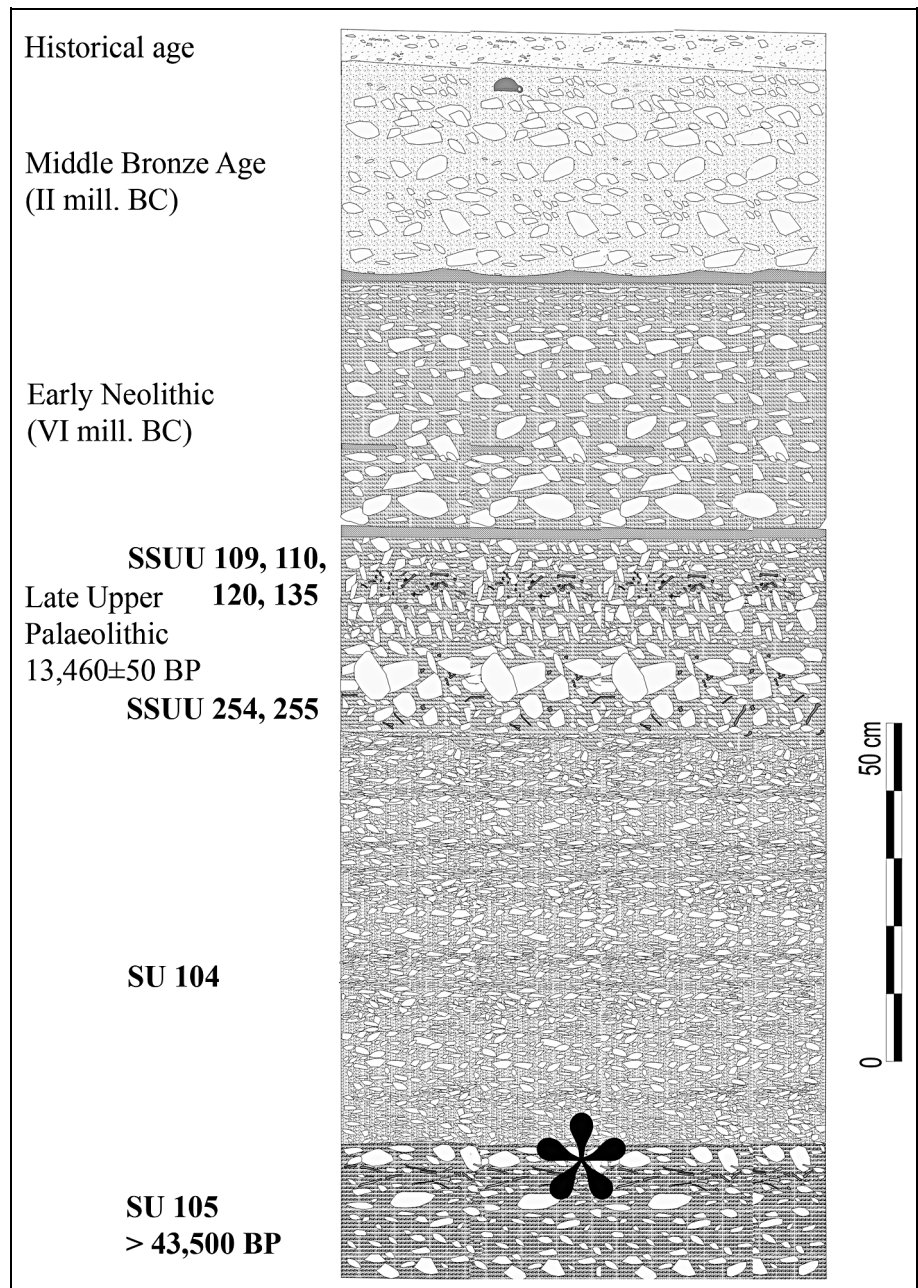
Masini (1985, with references) quoted 32 Italian sites with fossil and sub-fossil remains of chamois and Masetti & Salari (2012b, with references) 43 localities of Central-Southern Italy with the chamois finds referred to the Late Pleistocene and the older Holocene according to the literature after 1988. Apart from these above, in Italy we can add some pre-alpine north-eastern and Ligurian sites (e.g., Tagliacozzo & Cassoli 1990, 1992; Cassoli & Tagliacozzo 1991, 1994a, 1994b; Fiore & Tagliacozzo 2005, with references; Wierer & Boscato 2006; Valensi 2009, with references; Gurioli et al. 2010a, 2010b; Bertolini et al. 2012) and the insular finds of Elba island (Masetti *in litteris*). Indeed, except for a few cases,

such as Grotta di Equi, Monte Sumbra and Ripa Grande (Masini 1985) and Riparo di Fumane (Cassoli & Tagliacozzo 1991; Romandini et al. 2014), the remains of chamois are relatively poor and/or highly fragmented. Frequently they are in such a state of preservation that the lack of diagnostic osteological materials does not allow definite attributions to one or the other species. Chamois is also well represented from Grotta delle Balze with bone remains of almost four young and two adult individuals but, unfortunately, the horn-cores with frontal bones mentioned in Masini & Lovari (1988) and published by Loreti & Salerno (1989) were not newfound. Therefore, the sub-entire skeleton from Grotta Mora Cavorso is really an exceptional and interesting case study.

### Stratigraphic notes of Grotta Mora Cavorso

Grotta Mora Cavorso opens to 715 m a.s.l. near Jenne (Latium, Central Italy) and it leans out on the right slope of the upper Aniene River valley inside the Simbruini Mountains Regional Natural Park (Fig. 1A). This karst cavity hold a succession of rooms and ducts (Fig. 1B) and is carved in the “Calcilutiti e Calcareniti del Conaciano-Campaniano” formation (C9-11/38, Upper Cretaceous) (Damiani et al. 1998; Rolfo et al. 2009). Following the fortuitous discovery of human bones inside the cave, archaeological investigations started in 2006 by “Tor Vergata” University of Rome, in agreement with the “Soprintendenza per i Beni Archeologici” of Latium and with the collaboration of

Fig. 2 - Grotta Mora Cavorso: stratigraphy of the room 1. \*approximate position of the silty lens with the partially articulated skeleton of chamois.



“Shaka Zulu” speleological group. The inner rooms held the remains of at least 21 individuals, the largest Neolithic human community of Latium and one of the richest of Europe (Rolfo et al. 2009, 2010, 2012b, 2012c; Salari et al. 2012). In the room 1, just below the disturbed surface and some Holocene layers (Neolithic, Bronze Age and historical age, see Rolfo et al. 2010, 2012a, 2013; Silvestri et al. in press), the Late Pleistocene sequence was found (Fig. 2).

The Stratigraphic Units (SSUU) 109, 110, 120, 135, 254 and 255 are characterized by a compact reddish-brown silty ground with limestone clasts with sharp edges that vary in diameter from few millimeters to one centimeter, where many fossil remains of vertebrate were found together with a moderate number of lithic artefacts referable to late Upper Palaeolithic (final Epigravettian). Frontal scraper on a retouched blade of jaspered flint, fragments of backed blade lets, a fragment of backed point and a multiple burin are the findings. In this Epigravettian layer, about 30 cm thick, the most abundant taxon is *Marmota marmota* (94 specimens, about half of the determined remains and one third of the individuals) followed by *Cervus elaphus*, *Capra ibex*, *Rupicapra* sp. and *Lepus* sp., present with a significant number of fragments, *Sus scrofa*, *Capreolus capreolus* and *Vulpes vulpes* with few finds, and *Mustela nivalis* with only a single fragment of mandible (digs 2008-2009; see Salari et al. 2011). A radiometric dating performed on a marmot mandible has provided the age of 13,460±50 years BP (CNRS Lyon - 4568, calibrated 14,175 - 13,910 BC 1σ). This agrees with the attribution of the lithic artefacts to the cultural horizon of the final Epigravettian, and of the mammal assemblage to the Lateglacial (see Salari et al. 2011). The finds of mammals above are accompanied by several birds bones, few amphibious bones and several micromammal remains, par-

ticularly *Microtus (Microtus) arvalis* and *Arvicola amphibius* with rare *Talpa caeca*, *T. romana*, *Rhinolophus ferrumequinum*, *Myotis bechsteinii*, *M. emarginatus*, *Miniopterus schreibersii*, *Microtus (Terricola) savii* and *Apodemus sylvaticus/flavicollis* (excavation 2008; see Salari 2014).

Below the aforementioned contexts is the 104 SU, investigated between 2008 and 2012. This layer consists of incoherent soil, mainly characterized by centimetric limestone clasts. In this SU, about 60 cm thick, no human artefacts, but very abundant microvertebrate remains together with several bone fragments of macro-mammal have been found. Preliminary analysis shows that the dominant taxon is *M. (M.) arvalis* (almost 480 mandibles, about 40% of determined remains and more than 70% of individuals among the mammals) followed by several remains of *A. amphibius* and birds, *Lepus* sp. and *Martes martes*, scarce *M. marmota*, *A. sylvaticus/flavicollis* and *C. ibex*, and rare Reptilia, *T. caeca*, *T. romana*, *Sorex samniticus*, *Myodes glareolus*, *Mustela putorius*, *Rupicapra* sp. and *Bos primigenius*. For stratigraphic position and for the composition of mammal assemblage, dominated by *M. (M.) arvalis* accompanied by “cold” mammals, such as marmot and ibex, this layer was correlated with the Last Glacial Maximum (LGM) (Orlacchio 2012; Ricci 2012).

105 SU below follows; this is the deepest level excavated so far, measuring about 20 cm at time (summer 2013). It is characterized by a silty dark reddish soil with rare centimetric limestone clasts and a large amount of fossil remains of vertebrate, but without human artefacts. Preliminary analysis shows that the most abundant taxon is *Lepus* sp. (51 specimens, about 20% of determined remains and 15% of individuals among the mammals) followed by *C. ibex* and birds, and then by *A. amphibius*, *C. elaphus*, *Canis lupus* and *Glis glis*

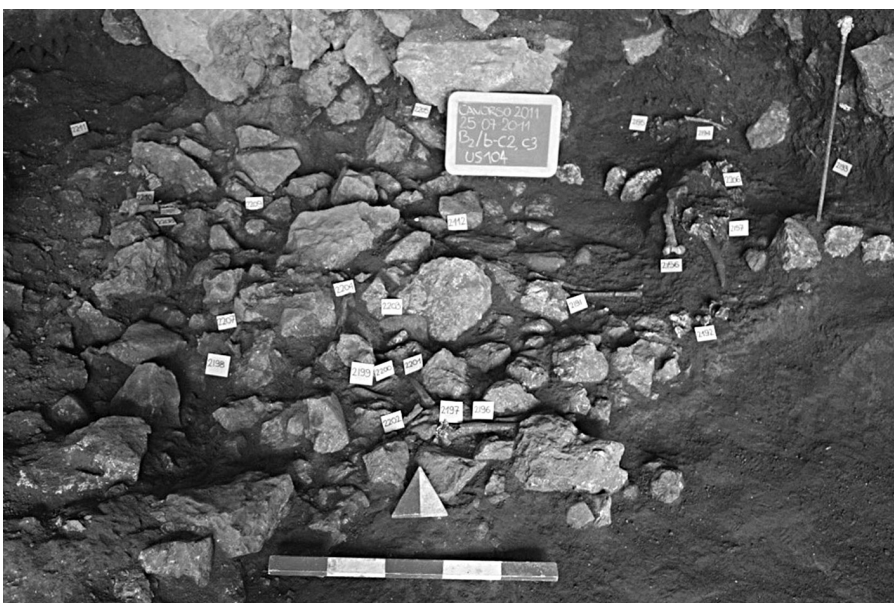


Fig. 3 - Grotta Mora Cavorso, room 1: the silty lens with limestone clasts of medium and great size and the partially articulated bone remains of chamois.

with some finds, scarce *M. (M.) arvalis*, *M. marmota*, *Rupicapra* sp., and rare *A. sylvaticus/flavicollis*, *Sorex* sp. and *T. romana*. A radiometric dating performed on a skull fragment of wolf from this layer has provided an age higher of 43,500 years BP (Beta Analytic Inc., Miami - 365375).

Between SSUU104 and 105, there was a silty lens with limestone clasts of medium and great size (Fig. 3). Here, in a surface of about two sqm, more than 90 skeletal elements of chamois were found, including skull, part of the sternum, about twenty ribs and as many vertebrae, and the limb bones.

In this silty lens with limestone clasts and the sub-entire skeleton of chamois, scattered bone remains of two red deer and at least three hare, a sub-entire partially articulated skeleton of marmot, few remains of Birds and *A. amphibius*, and a mandible of *G. glis* have been also found. For the occurrence of *C. elaphus* and *G. glis*, this assemblage is ecologically closer to the mammal assemblage of 105 SU than to 104 SU. Considering that this silty lens with limestone clasts is placed between the LGM (20±2 ka cal BP, see Antonioli & Vai 2004) and at least 43,500 years BP, these bone remains can be correlated to a temperate oscillation of MIS 3.

### Taxonomy of *Rupicapra* species

The systematic of the genus *Rupicapra* is debated, particularly the taxonomic position of the Apennine chamois.

At the beginning of the last century, essentially on the basis of coat color pattern, Trouessart (1910) recognized two species of chamois, *R. ornata*, located only in the Abruzzi mountains, and *R. rupicapra*, spread in other mountain ranges of Southern Europe, from the Pyrenees and Cantabrian Mountains to the Alps, Carpathians, Greece and Caucasus. On the basis of external and cranial morphology, Miller (1912) and Camerano (1916a, 1916b) divided the genus into the following species: the Apennine chamois, *R. ornata*, the Pyrenean chamois, *R. pyrenaica*, the Alpine chamois, *R. rupicapra*, divided into various subspecies, and the small size Cantabrian chamois was considered a fourth species, *Rupicapra parva* Cabrera, 1910, by Miller (1912), and a subspecies or variety of *R. pyrenaica* by Camerano (1916c). Instead, Lydekker (1913), then Couturier (1938) followed by Dolan (1963) and Blahout (1972), regrouped the chamois into a single species, *R. rupicapra*, divided into seven, then nine or, possibly, ten regional subspecies, including *R. rupicapra ornata*. Even some paleontologists recognized only one species, *R. rupicapra* (see Prat 1966; Kurtén 1968).

In the 1980s, several comparisons of a morphological, biometrical, eco-ethological, biochemical, and paleontological nature (Lovari & Scala 1980; Scala & Lovari 1984; Masini 1985; Nascetti et al. 1985; Masini & Lovari 1988), enabled the recognition of two distinct species of chamois in the primary distribution from the Western Palearctic: *R. rupicapra*, divided into various subspecies, and *R. pyrenaica*, divided into three subspecies, including *R. pyrenaica ornata*. Furthermore, Lovari & Scala (1980) and Masini & Lovari (1988) in particular, repropounded in modern form a hypothesis that had already been advanced by Camerano (1916a). According to such theory, the populations of South-western chamois (Pyrenean and Apennine chamois), who were living since the time of Riss glaciation in Western Europe, were separated by a new immigration wave of North-eastern chamois (Alpine chamois) during the Würm glaciation. As we saw in the "Introduction", in the MIS 12 and MIS 9 of Western Europe there were chamois remains referred to *Rupicapra* cf. *pyrenaica*, but in the MIS 6 there were already two species, *R. rupicapra* and *R. pyrenaica*.

After 1988, the classification above has been widely accepted by zoologists (e.g., Grubb 1993, 2005; Amori et al. 1999; Pedrotti & Lovari 1999a, 1999b; Aulagnier et al. 2008; Herrero et al. 2008; Corlatti et al. 2011). Instead, most paleontologists and archaeozoologists have kept on attributing the osteological materials of chamois from Central-Southern Italy to *R. rupicapra* or to *Rupicapra* sp., and those from Pyrenees and Iberian Peninsula to *R. rupicapra pyrenaica* or *R. rupicapra* (see Masseti & Salari 2012a, 2012b, with references and discussion therein).

Also several studies of molecular biology have confirmed the distinction between *R. rupicapra* and *R. pyrenaica* and the close genetic affinity between the chamois of Abruzzi and those of the Pyrenees and Iberian Peninsula (see Hammer et al. 1995; Mucci et al. 1998). Conversely, Rodríguez et al. (2009, 2010) claim that postglacial recolonization was accompanied by hybridization between the *pyrenaica* and *rupicapra* clades, and conclude that only one *Rupicapra* species exists divided into 3 lineages, Western (*pyrenaica* and *parva*), Central (*ornata* and *cartusiana*) and Eastern (the other *rupicapra* subspecies). Instead, Pérez et al. (2002, 2013) and Crestanello et al. (2009) hypothesized that the Apennine chamois could be considered a third species.

Recently, on the basis of biometrical, ethological and biomolecular considerations, Groves & Grubb (2011) and Groves et al. (2011) proposed the rank of full species for almost all the regional subspecies of the genus, including *ornata*, and also Gippoliti (2013) suggests this rank for the Apennine chamois. In this paper we adhere to the current classification of the cha-

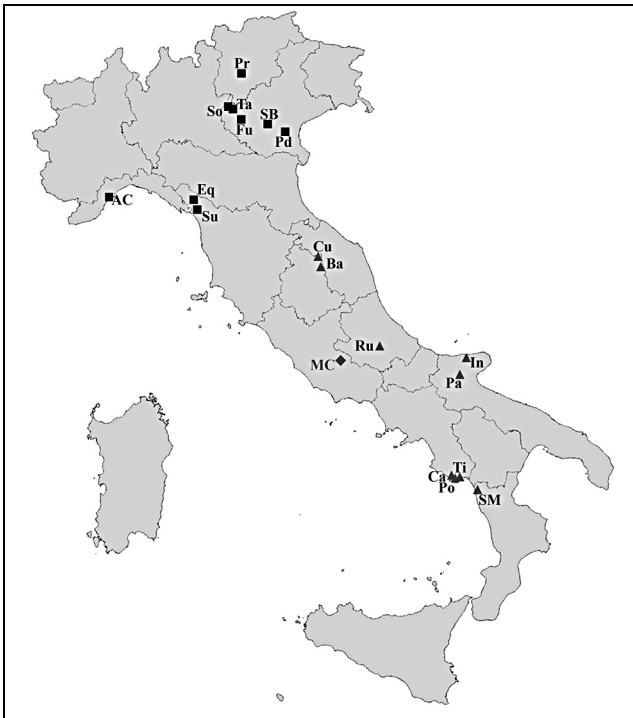


Fig. 4 - Map of the main Late Pleistocene and older Holocene Italian sites for comparisons. Pr: Pradestel; So: Riparo Soman; Ta: Riparo Tagliente; Fu: Riparo di Fumane; SB: Grotta San Bernardino; Pd: Padova; AC: Caverna delle Arene Candide; Eq: Grotta di Equi; Su: Monte Sumbra; Cu: Monte Cucco; Ba: Grotta delle Balze; Ru: Grotta Rutina; In: Ingarano; Pa: Grotta Paglicci; Ca: Grotta della Cala; Po: Riparo del Poggio; Ti: Grotta Tina; SM: Santuario della Madonna. Square: Alpine arc and Northern Apennine; triangle: Central-Southern Italy; rhombus, MC: Grotta Mora Cavorso.

mois populations in two species, *R. rupicapra* and *R. pyrenaica*.

The Alpine chamois, *R. rupicapra rupicapra*, has perpendicular horns, the bony bases of which are not very expanded and are separated by a relatively large area of the frontal bones; the throat patch is little wide and does not reach the chest and the winter coat pattern has three small spots. The Apennine chamois, *R. pyrenaica ornata*, instead, has slightly back-tilted horns, whose bony bases are expanded and leave little space between them; the throat patch is wide and reaches the chest and the winter coat pattern has five large and one small spots. The Pyrenean chamois, *R. pyrenaica pyrenaica* and *R. pyrenaica parva*, lastly, has slightly anteriorly-inclined horns, and the bony bases of the horns are expanded and leave little space between them; the throat patch is wide, but a little less than in Apennine chamois, and the winter coat pattern has five large and one small spots (Camerano 1914a, 1914b, 1916a, 1916b; Couturier 1938; Toschi 1965; Lovari & Bruno 2003; Tosi & Pedrotti 2003; García-González & Herrero 2007).

The osteological distinction between Alpine, Pyrenean and Apennine chamois is possible for intact

skulls, or at least for portion of skull with the horn-cores. Besides the insertion and inclination of the above mentioned horn-cores, certain additional diagnostic characters have been identified, such as the thickness and the regularity or complexity of various sutures or the obliteration of the ethmoidal vacuity (between the lachrymal, nasal, frontal and maxillary bones) that is fully closed in Pyrenean and Apennine chamois and variously open in Alpine chamois and in the other *R. rupicapra* subspecies (Camerano 1914b, 1916a, 1916b; Couturier 1938; Toschi 1965; Prat 1966; Altuna 1972; Lovari & Scala 1980; Masini 1985; Masini & Lovari 1988). In the vertebrate fossil deposits, however, intact skulls are very rare, but cranial fragments are more frequently found, and in these cases the morphometric diagnostic criteria relate to the distance (at the base and apex) between the horn-cores (Altuna 1972; Lovari & Scala 1980; Masini 1985), while the length and the diameters of each horn-core and their ratios are not very significant (Altuna 1972), but useful for distinguishing between Apennine and Pyrenean chamois (Couturier 1938; Scala & Lovari 1984; Masini 1985). Moreover, the ratio between the antero-posterior diameter and the distance at the base of the horn-cores is a good method for distinguishing between Alpine, Apennine and Pyrenean chamois (Masini 1985). Certain distinctive morphometric features between Alpine and Pyrenean chamois have been identified for some post-cranial bones, such as the metacarpus (Crégut-Bonnoure 1992).

## Materials and methods

### Fossil material from Grotta Mora Cavorso

The sub-entire skeleton of chamois:

2157: part of splanchnocranium; 2157a: orbital bones; 2157b: horn-core with part of frontal bones; 2157c: portion of right maxillary with  $M^1$ - $M^3$ ; 2157d: portion of left maxillary with  $M^1$ - $M^3$ ; 2203: left mandible; 2218: right fragmented mandible with  $P_3$ - $M_1$ ; 2250a:  $M_2$ ; 2250:  $M_3$ ; without number:  $I_2$ ; 2289: atlas; 2731: axis; 2192, 2192a, 2198a, 2205, 2206, 2218d, 2236, 2251c, 2253, 2257, 2259, 2278, 2283, 2286, 2288, 2289a and 2731b: 17 vertebrae and many vertebra fragments; 2210 and 2237: three fragments of sternum; 2209, 2210a, 2212, 2217, 2218e, 2261a, 2280, 2287, 2290, 2299 and 2320: 27 fragments of ribs; 2285: portion of right scapula; 2204: left fragmented humerus; 2208: right fragmented humerus; 2260-2261: fragmented left radius; 2291a: distal part of right radius; 2291: proximal part of right ulna; 2298b: right lunate; 2249: left metacarpus; 2232: proximal part of right metacarpus; 2258: distal part of right metacarpus; 2207, 2260, 2284, 2291: anterior first phalanges; without number: some fragments of pelvis; 2156: fragmented left femur; 2197: fragmented left tibia; 2199: distal part of right tibia; 2255: right calcaneus; 2265: left calcaneus; 2218a: left talus; 2264: right talus; 2256: right central tarsal bone; 2201: proximal part of right metatarsus; 2296: proximal part of left metatarsus; 2202 and 2251: posterior first phalanges; 2198, 2202a, 2202b, 2218b, 2251a and 2258a: second phalanges; 2218c, 2240, 2251b and 2258b: third phalanges.

In addition to the sub-entire skeleton described below, the following remains of chamois at Mora Cavorso have been found:

– Epigravettian layer: 53: left M<sub>1</sub>; 1002 right P<sub>4</sub>; without number: a portion of left mandible with P<sub>2</sub>P<sub>3</sub>; right I<sub>2</sub> and M<sub>2</sub>; left I<sub>1</sub>, I<sub>2</sub>, I<sub>3</sub> and P<sub>4</sub>; right upper deciduous cheek-tooth; a fragment of lower molar; proximal part of right ulna; distal fragment of second phalanx; these fossil remains have been referred to a fully grown and a young individual (see Salari et al. 2011);

– SU 104: without number: right P<sub>3</sub>; 2315: left talus; 41: posterior first phalanx;

– SU 105: 2656-2739: fragmented right mandible with M<sub>1</sub> and M<sub>2</sub>; 2782: articular condyle of metapodial bone.

All the Late Pleistocene remains of chamois from Grotta Mora Cavorso are located in the Laboratory of Prehistory of the University of Rome “Tor Vergata”.

#### Comparison samples

Morphological and morphometric features of chamois from Grotta Mora Cavorso have been compared with Late Pleistocene and Holocene chamois remains from several sites of Italy, Pyrenees and Iberian Peninsula (Tab. 1 and Fig. 4).

Craniometric data of fossil chamois P6311, skull from Riparo di Fumane, and P140, right horn-core with frontal bone from the palaeovenetian settlement of Padova, were taken by the authors. Both specimens are stored in the National Museum of Prehistory and Ethnography “Luigi Pigorini” of Rome. The measurements of horn-cores from Grotta Rutina (Saccà 2006), Grotta di Equi (Masini 1985; Clot & Marsan 1986), Monte Sumbra (Masini 1985), Aitzbitarte and Ur-tiaga (Altuna 1972) and various Würmian sites from French Pyrenees (Clot & Marsan 1986) are taken from literature. These data are exposed in Tab. 2.

Craniometric data of the extant Alpine, Pyrenean and Apennine chamois were taken by Camerano (1914b, 1916a), Couturier (1938) and Masini (1985); the young individuals and the specimens from Dauphiné and Bosnia-Herzegovina were not considered. These data were integrated with the measurements, taken by authors, of 21 skulls of Apennine chamois from Abruzzi National Park (specimens 11, 14, 20, 21, 26, 29, 29, 43, 58, 218, 220, 221, 547, 1096, 1156, 1203, 1205, 1208, 1215, 1216 and 1217) housed at the Scientific Service of “Ente Autonomo Parco Nazionale d’Abruzzo, Lazio e Molise” of Pescasseroli. These data are exposed in Tab. 3.

The sizes of the mandible and the postcranial bones of the chamois from Mora Cavorso have been also compared with the chamois remains from several sites of Italy, Pyrenees and Iberian Peninsula. For these comparisons, the osteometric measurements have been in part taken from literature and in part directly by the authors (see Tab. 1), in particular the samples from Grotta delle Balze, housed at the Gualdo Tadino Speleological Group’s office, from Ingarano, housed in the Earth Science Department of “Sapienza” University of Rome, and from Riparo di Fumane, Riparo Soman and Grotta Santuario della Madonna, stored in the National Museum of Prehistory and Ethnography “Luigi Pigorini” of Rome (see Tab. 4 and Appendix 2).

In addition, we measured a mandible (specimen P134/2) and the postcranial bones of two Alpine chamois from Gran Paradiso National Park (specimens P506 and without number), stored in the National Museum of Prehistory and Ethnography “Luigi Pigorini” of Rome, and 13 postcranial skeletons of Apennine chamois from Abruzzi National Park (specimens 21, 26, 27, 33, 35, 47, 58, 191, 201, 238, 239, 1100 and without number) housed at the Scientific Service of “Ente Autonomo Parco Nazionale d’Abruzzo, Lazio e Molise” of Pescasseroli (see Appendix 3).

#### Methods

The recent and fossil material was measured according to the methodology of Driesch (1976) and, only for the metacarpus, also according to Crégut-Bonnoure (1992) (see Fig. 5). Measurements are expressed in mm. These data are reported in tables and diagrams.

We have also calculated the ratios humerus/metacarpus and radius/metacarpus following Capasso Barbato et al. (1985). The measures of limb bones of *R. pyrenaica parva* from Arceredillo et al. (2011) were used only for these ratios and not for comparisons on the anatomical elements, being known the small size of this Cantabrian Mountains subspecies.

The age of death of the specimen from Grotta Mora Cavorso was estimated through comparison with mandibles of chamois of known age, considering the age of eruptions, change, and attrition of the teeth, according to the tables and the observations reported in Arceredillo & Díez (2009).

### The chamois from Grotta Mora Cavorso

#### Taphonomic observations

In summer 2011, at the time of the archaeological excavation of the silty lens with limestone clasts of medium and great size between SSUU 104 and 105, the skull, the right mandible, the pelvis and several long bones were fragmented; left scapula, left ulna, right femur, some phalanges and most of the small bones of carpus and tarsus are missing. Some vertebrae, right humerus, ulna, radius and lunate were articulated, as well as both metacarpal bones and phalanges, right tibia, talus, calcaneus and central tarsal bone. The other bones were scattered: left humerus and radius were very close, as well as left tibia and metatarsus, but the left femur was found next to the skull and the mandibles near the right metacarpus. Evidently, the carcass was partially dismembered by natural agents (anthropogenic input can be excluded) before being buried by mud and clasts, presumably from overlying sinkholes. These two sinkholes have controlled the sediments deposition in room 1 at least until to the Bronze Age (Rolfo et al. 2013).

After cleaning and washing, the fossil bones appear whitish or Havana-tortoiseshell and are very fragile. Preliminary and macroscopic analysis on the bone surfaces did not reveal any traces of human activity nor signs of carnivores. Several breakages presumably caused by the weight of the sediments and the continuous trampling in confined spaces or when digging were then reassembled in the laboratory.

#### Descriptions and comparisons

*Skull and mandible.* The skull is fragmented and two inferior portions of maxillaries with the molars were recovered together with a part of splanchnocranium with nasal and pre-maxillary bones and part of the maxillary and lachrymal bones, the right orbital bones and the right horn-core with part of the right and left frontal bones (Pl. 1, fig. 1). The portion of splanchnocranium shows a fully closed ethmoidal vacuity, as in the Pyrenean and Apennine chamois. The horn-core shows ellipsoidal section at the base and a slightly medio-lateral compression that evolve to a



Site	Geographic area	Age	References
Gruta do Caldeirão	Centro, Portugal	Late Pleistocene	Davis 2002
Gruta das Salemas	Lisboa, Portugal	Late Pleistocene	Cardoso & Antunes 1989
Cueva del Nacimiento	Andalucia, Spain	Late Pleistocene	Afárez Delgado et al. 1981
Cueva Millan	Castilla y Leon, Spain	Late Pleistocene	Alvarez et al. 1992; Pérez Lepido & Cerdeño 1992
Rascaño	Cantabria, Spain	Late Pleistocene	Altuna 1981
La Riera	Cantabria, Spain	Late Pleistocene	Altuna 1986
Zatoya	Navarra, Spain	Late Pleistocene	Altuna & Mariezkurrena 2001
Cueva de Abauntz	Navarra, Spain	Late Pleistocene	Altuna et al. 2002
Cueva de Santimamiñe	Vizcaya, Spain	Late Pleistocene	Castaños 1984
Aitzbitarte	Guipúzcoa, Spain	Late Pleistocene	Altuna 1972
Ermittia	Guipúzcoa, Spain	Late Pleistocene	Altuna 1972
Lezetxiki	Guipúzcoa, Spain	Late Pleistocene	Altuna 1972
Marizulo	Guipúzcoa, Spain	Late Pleistocene	Altuna 1972
Urtiaga	Guipúzcoa, Spain	Late Pleistocene	Altuna 1972
Cueva de Ekain	Guipúzcoa, Spain	Late Pleistocene	Altuna & Mariezkurrena 1984
Urtao II	Guipúzcoa, Spain	Late Pleistocene	Mariezkurrena 1989
Cueva de Erralla	País Vasco, Spain	Late Pleistocene	Altuna & Mariezkurrena 1985
Labeko Koba	País Vasco, Spain	Late Pleistocene	Altuna & Mariezkurrena 2000
Grotte du Cantet	Hautes-Pyrénées, France	Late Pleistocene	Clot 1984
Grotte de Labastide	Hautes-Pyrénées, France	Late Pleistocene	Clot 1988
various Würmian sites	Pyrénées, France	Late Pleistocene	Clot & Marsan 1986
Grotte de Castel 2	Aude, France	Late Pleistocene	Pernaud et al. 2005
Riparo Soman	Trentino Südtirol, Italy	Late Pleistocene, early Holocene	Tagliacozzo & Cassoli 1992 and this work
Pradstel	Trentino Südtirol, Italy	early Holocene	Boscato & Sala 1980
Grotta Maggiore San Bernardino	Veneto, Italy	Late Pleistocene	Cassoli & Tagliacozzo 1994b
Riparo di Fumane	Veneto, Italy	Late Pleistocene	Cassoli & Tagliacozzo 1991 and this work
Riparo Tagliente	Veneto, Italy	Late Pleistocene	Capuzzi & Sala 1980
Padova	Veneto, Italy	Holocene	Tagliacozzo & Cassoli 1990 and this work
Arene Candide	Liguria, Italy	Late Pleistocene	Cassoli & Tagliacozzo 1994a
Grotta di Equi	Tuscany, Italy	Late Pleistocene	Masini 1985; Clot & Marsan 1986
Monte Sumbra	Tuscany, Italy	Holocene	Masini 1985
Monte Cucco	Umbria, Italy	Late Pleistocene	Capasso Barbato et al. 1985
Grotta delle Balze	Umbria, Italy	early Holocene	Loreti & Salerno 1989 and this work
Grotta Rutina	Abruzzi, Italy	Late Pleistocene	Saccà 2006
Grotta della Cala	Campania, Italy	Late Pleistocene	Benini et al. 1997; Boscato et al. 1997
Grotta del Poggio	Campania, Italy	Late Pleistocene	Sala 1979
Grotta Tina	Campania, Italy	Late Pleistocene	Martini et al. 1974
Grotta Paglicci	Apulia, Italy	Late Pleistocene	Boscato 1994
Ingarano	Apulia, Italy	Late Pleistocene	Petronio et al. 1996 and this work
Grotta Santuario della Madonna	Calabria, Italy	Late Pleistocene, early Holocene	Fiore et al. 2004 and this work

Tab. 1 - List of comparative sites, their age and geographic area.



Horn-core	MC	Ru	Eq	Eq	Eq	Eq	Su	Su	Su	Su	Pd	Fu	Fu	IP	IP	IP	IP	FP	FP	FP	FP
			n.	max	min	mea	n.	max	min	mea				n.	max	min	mea	n.	max	min	mea
<b>L.</b>	128.0		20	104.0	57.0	78.6					86.5	120.0	79.9	4	90.0	77.0	83.3	17	112.0	67.0	92.7
<b>APD</b>	24.4	19.6	31	23.6	15.0	19.2	3	26.0	22.8	24.5	25.1	27.7	19.8	10	23.5	16.5	18.6	29	23.5	14.0	18.7
<b>TD</b>	22.7		28	20.2	12.1	16.6	3	22.2	20.0	20.7	22.9	26.0	18.0	9	16.5	14.3	16.3	28	23.0	12.4	17.5
<b>BC</b>	84.0										78.5	95.0	65.0	6	72.0	50.0	58.2	27	78.0	45.0	60.9
<b>MD</b>	10.4	12.6	13	19.0	12.0	14.9	3	19.0	14.5	16.8	15.6	10.2		2			11.0				

Tab. 2 - Horn-core measurements (mm) of fossil chamois from some Late Pleistocene and older Holocene sites of Central-Southern Italy, Alpine arc and Northern Apennine, Pyrenees and Iberian Peninsula. MC: Grotta Mora Cavorso; Ru: Grotta Rutina (Saccà 2006); Eq: Grotta di Equi (Masini 1985; Clot & Marsan 1986); Su: Monte Sumbra (Masini 1985); Pd: Padova (P140 - this work); Fu: Riparo di Fumane (P6311 - this work); IP: Iberian Peninsula (Altuna 1972); FP: French Pyrenees (Clot & Marsan 1986). Measurement abbreviations: L.: length; APD: antero-posterior diameter; TD: transverse diameter; BC: basal circumference; MD: minimum distance at the base of the horn-cores; n.: number of specimens; max: maximum; min: minimum; mea: mean.

Horn-core	n.	max	min	mea	s.d.	n.	max	min	mea	s.d.	n.	max	min	mea	s.d.
<b><i>R. r. rupicapra</i></b>	1)	1)	1)	1)	1)						3)	3)	3)	3)	3)
<b>L.</b>	142	124.0	62.0	87.4	13.33										
<b>APD</b>	142	27.0	13.0	20.7	3.32						135	27.0	15.0	20.9	3.43
<b>TD</b>	142	26.0	12.0	18.4	3.41						139	26.0	12.0	18.4	3.56
<b>MD</b>	142	21.0	9.0	16.0	2.58						132	24.0	9.0	16.2	2.59
<b><i>R. p. pyrenaica</i></b>	1)	1)	1)	1)	1)	2)	2)	2)	2)	2)	3)	3)	3)	3)	3)
<b>L.</b>	4	100.0	60.0	87.0	18.29	14	101.0	55.0	82.9	12.51					
<b>APD</b>	4	22.0	15.0	18.5	2.89	14	21.0	12.5	17.0	2.07	18	22.0	12.5	17.4	2.29
<b>TD</b>	4	19.5	14.5	16.9	2.06	14	19.5	10.5	15.1	2.13	18	19.5	10.5	15.5	2.21
<b>MD</b>	4	10.0	8.0	9.0	0.82	14	17.0	10.5	13.4	1.53	18	15.0	8.0	12.3	2.36
<b><i>R. p. ornata</i></b>	1)	1)	1)	1)	1)	4)	4)	4)	4)	4)	3)	3)	3)	3)	3)
<b>L.</b>	5	141.0	70.0	120.2	29.58	14	124.0	96.0	107.6	8.37					
<b>APD</b>	5	29.0	19.0	25.4	4.62	19	28.0	20.2	23.9	2.67	32	29.0	19.8	24.8	3.32
<b>TD</b>	5	24.5	17.5	21.4	3.17	19	24.4	17.8	20.7	2.23	32	26.0	17.7	21.2	3.18
<b>MD</b>	5	14.0	10.0	11.9	1.60	19	16.0	10.6	13.4	1.79	21	15.8	9.5	12.7	1.93

Tab. 3 - Horn-core measurements (mm) of current populations of *R. rupicapra rupicapra*, *R. pyrenaica pyrenaica* and *R. pyrenaica ornata*. Data from: 1) Camerano (1914b, 1916a); 2) Couturier (1938); 3) Masini (1985); 4) this work. Measurement abbreviations: L.: length; APD: antero-posterior diameter; TD: transverse diameter; MD: minimum distance at the base of the horn-cores; n.: number of specimens; max: maximum; min: minimum; mea: mean; s.d.: standard deviation.

sub-triangular section with caudal base at the apex; the medio-lateral compression is less significant than in the current Apennine chamois. The horn-core from Mora Cavorso is the longest among the fossil specimens, even than the great specimen from Fumane (Tab. 2), and it is longer than the living Alpine and Pyrenean chamois, with dimensions slightly greater than the mean of the living Apennine chamois (Tab. 3). The diameters are close to the maximum values of Monte Sumbra and the French Pyrenees, slightly smaller than the specimens from Padova and Fumane and larger than the other fossil specimens (Tab. 2). The two dimensions are greater than in the modern Pyrenean chamois, smaller than the maximum values of the current Alpine and Apennine chamois, but close to the mean values of the latter (Tab. 3).

The minimum distance at the base of the horn-cores was calculated, as for the Mousterian specimen

from Grotta Rutina (Saccà 2006), for that of Iron age from Padova and, presumably, for the specimens from Grotta di Equi (see Masini 1985; Masini & Lovari 1988), doubling the distance between the base of the right horn-core and the midpoint of the inter-frontal suture. The ratio between the antero-posterior diameter and the minimum distance at the base of the horn-cores shows that the specimen from Mora Cavorso is clearly placed in the range of the living Apennine chamois (Fig. 6).

Upper molars are without interlobar lingual column; on the occlusal surface they have a small circle of enamel between the two main fossettes. M<sup>1</sup> and M<sup>2</sup> are bilobed and of similar shape, but M<sup>1</sup> is slightly smaller, and it has the first lobe more lingually projecting. M<sup>3</sup> is bilobed and it has a distal vestibular stylus relatively developed and distally convex. The length of the upper molar row is slightly lower than that of the other Italian fossil remains; it is close to the mean of the Late Pleis-

Maxilla	MC	Ti	Ti	Cu	SM	SM	Ru	Fu	Fu	Fu	So	AC	PIP	PIP	PIP	PIP	GP NP	ANP	ANP	ANP	ANP
																		n.	max	min	mea
22	38.0				41.6			42.0			40.4	39.1	5	43.0	38.0	40.5		17	39.2	35.4	36.7
<b>Mandible</b>																					
1	158.0																144.0	5	152.0	142.0	147.2
2	168.0																153.0	5	158.0	146.5	153.1
3	49.0																37.3	5	41.0	39.0	40.4
4	107.8																104.2	5	109.5	101.5	105.1
5	113.0																98.4	5	104.4	100.0	101.7
6	128.0																123.0	5	128.2	121.5	124.2
7	58.0			66.7			64.0		65.9	65.2		62.1	5	70.0	57.0	63.3	58.1	5	62.0	58.5	60.5
8	38.8	36.6	39.0	43.9			42.0	43.2	43.3	41.0		42.5	18	48.0	39.0	42.5	38.9	5	42.0	34.5	39.2
9	19.0			22.8	21.8	19.2	22.0		21.9	25.0		18.2	18	24.0	17.1	20.1	18.9	5	25.0	19.5	21.7
10a	17.8						19.0	20.3	19.4	20.5			10	19.0	17.0	17.8	17.3	4	17.8	16.0	16.9
10b	7.0						7.0	8.2	7.8	8.7			4	8.0	6.3	7.2	6.8	4	7.1	6.0	6.6
11	43.0																39.9	5	41.2	35.0	37.6
12	63.5																61.5	5	55.2	49.2	53.6
13	58.6																58.2	5	53.6	49.8	51.8
14																	83.0	5	85.2	80.0	82.0
15a	28.8			33.8			30.4	33.1	33.9	35.0			1			32.0	28.3	5	30.2	21.2	26.4
15b	22.5			20.0		20.4	21.3	25.8	23.4			23.3	4	28.6	20.0	23.2	19.7	5	20.9	18.3	19.1
15c	17.8			15.4	18.7	18.9	15.8		19.4								18.4	5	19.4	16.6	17.7

Tab. 4 - Measurements (mm) of upper molars and mandible of living chamois and of remains from some Late Pleistocene and early Holocene sites of Central-Southern Italy, Alpine arc, Pyrenees and Iberian Peninsula. MC: Grotta Mora Cavorso; Ti: Grotta Tina (Martini et al. 1974); Cu: Monte Cucco (Capasso Barbato et al. 1985); SM: Santuario della Madonna (P136/2 and P136/4 - this work); Ru: Grotta Rutina (Saccà 2006); Fu: Riparo di Fumane (Cassoli & Tagliacozzo 1991); So: Riparo Soman (RS860 - this work); AC: Caverna delle Arene Candide (Cassoli & Tagliacozzo 1994a); PIP: Pyrenees and Iberian Peninsula; GPNP: *R. rupicapra rupicapra* from Gran Paradiso National Park (P134/2); ANP: *R. pyrenaica ornata* from Abruzzi National Park (nn. 26, 29, 1205, 1215 and without number); n.: number of specimens; max: maximum; min: minimum; mea: mean.

Measurement abbreviations: Maxilla, 22: length of the molar row; Mandible, 1: length gonion caudale - infradentale; 2: length aboral border of condyle process - infradentale; 3: length gonion caudale - aboral border of alveolus of M<sub>3</sub>; 4: length aboral border of alveolus of M<sub>3</sub> - infradentale; 5: length gonion caudale - oral border of alveolus of P<sub>2</sub>; 6: length gonion caudale - the most aboral indentation of mental foramen; 7: length of the cheektooth row; 8: length of the molar row; 9: length of the premolar row; 10a: length of M<sub>3</sub>; 10b: breadth of M<sub>3</sub>; 11: length of the diastema; 12: height gonion ventrale - highest point of condyle process; 13: height gonion ventrale - deepest point of mandibular notch; 14: height gonion ventrale - coronion; 15a: height behind M<sub>3</sub>; 15b: height in front of M<sub>1</sub>; 15c: height in front of P<sub>2</sub>.

tocene chamois from Pyrenees and Iberian Peninsula and to the higher values of the current Apennine chamois (Tab. 4).

The left mandible is almost intact (Pl. 1, fig. 2), missing only the coronoid apophysis, the incisors, ca-

nine and premolars. The right one is very fragmented: a fragment with P<sub>3</sub>, P<sub>4</sub> and M<sub>1</sub>, and isolated M<sub>2</sub> and M<sub>3</sub> were found. Lower teeth are overall rounded and slightly hypsodont, the molars are without interlobar vestibular column. P<sub>3</sub> has a mesio-lingual not bilobed

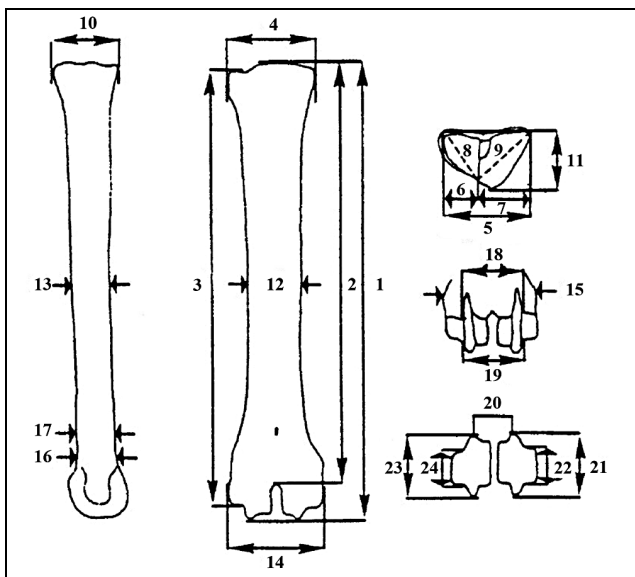


Fig. 5 - Measurements of metacarpus (from Crégut-Bonnoure 1992, redrawn).

PLATE 1

*Rupicapra pyrenaica ornata* from Grotta Mora Cavorso (Latium, central Italy), Late Pleistocene. 1) 2157b horn-core: a- lateral view, b- frontal view; 2) 2203 mandible in labial view; 3) 2289 atlas in dorsal view; 4) 2731 axis in lateral view; 5) 2285 distal scapula in lateral view; 6) 2204 humerus in cranial view; 7) 2208 humerus in caudal view; 8) 2191 proximal ulna in lateral view; 9) 2260-2261 radius in dorsal view; 10) 2249 metacarpus: a- dorsal view, b- palmar view; 11) 2156 femur in cranial view; 12) 2197 tibia in cranial view; 13) 2199 distal tibia in caudal view; 14) 2218a talus in dorsal view; 15) 2264 talus in plantar view; 16) 2255 calcaneus in medial view; 17) 2256 central tarsal bone in proximal view; 18) 2201 proximal metatarsus in dorsal view; 19) 2196 proximal metatarsus in plantar view; 20) 2207 anterior first phalanx in lateral view; 21) 2251 posterior first phalanx in lateral view; 22) 2218b second phalanx in lateral view; 23) 2218c third phalanx in lateral view.

Scale bar: 5 cm.



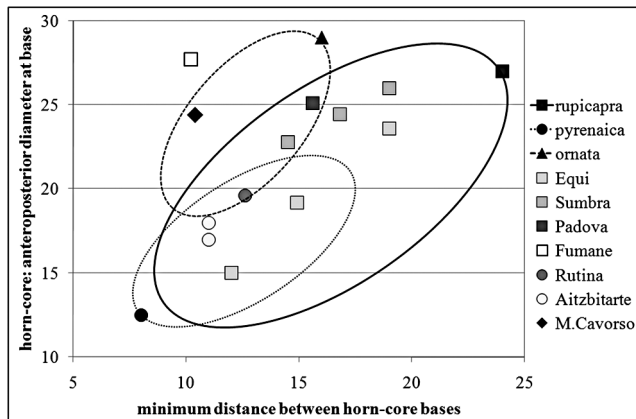


Fig. 6 - Scattergram of antero-posterior diameter versus minimum distance at the base of horn-cores (mm) of the specimen from Grotta Mora Cavorso compared with some Late Pleistocene and the living chamois. Square: attributed to *R. rupicapra*; circle: attributed to *R. r. pyrenaica* or *Rupicapra* cf. *pyrenaica*. The measurements of the Holocene *R. pyrenaica ornata* from Ripa Grande and Grotta delle Balze were not published (see Masini 1985; Masini & Lovari 1988; Loreti & Salerno 1989).

relief, a shallow distal-vestibular groove and the side edges diverging upwards.  $P_4$  with mesial lobe slightly smaller than the posterior lobe, and that is composed of two denticles separated by a fossette.  $M_1$  and  $M_2$  are bilobed and of similar shape, but  $M_1$  is slightly smaller, and it has the posterior lobe most prominent lingually and the lateral edges are sharply diverging upwards, while in  $M_2$  they are sub-parallel.  $M_3$  is trilobed, with the third lobe of reduced thickness and distally convex. Overall, the mandible is similar in shape, but larger than those of current chamois (Tab. 4; see also Camerano 1914b, 1916a). The rounded posterior profile of the mandible, with the caudal gonion slightly protruding backwards, is common in the Apennine chamois, but not so frequent among the Alpine chamois (see Camerano 1914b, 1916a). However, the length (alveolar) of the lower cheek-teeth row is close to the specimen from Gran Paradiso National Park, to the minimum values of the current Apennine chamois and the Late Pleistocene chamois from Pyrenees and Iberian Peninsula, but less than the other fossil remains. The  $M_1$ - $M_3$  length is close to the specimen from Gran Paradiso National Park, to the mean of the current Apennine chamois, to the minimum values of the Late Pleistocene chamois from Pyrenees and Iberian Peninsula and to the size of the specimen from Grotta Tina, but lower than the other fossil remains examined (Tab. 4).

*Post-cranial bones.* The post-cranial bones have all the epiphyses fused and they have the typical features of Caprinae and in particular of the genus *Rupicapra*, being much more slender, both in the epiphyses that in the middle of the diaphysis, than to those of *Capra ibex* and *C. hircus*, but less slender than *Ovis aries*.

Atlas and axis have the same proportions as the current chamois (Pl. 1, figs 3 and 4); the atlas, however, is larger and the axis is close to the greater dimensions of Alpine and Apennine chamois; furthermore, the atlas is also larger than those from Balze, Santuario della Madonna and Santimamiñe, but smaller than that from Fumane.

The articular portion of the scapula (Pl. 1, fig. 5) deep a glenoid cavity, relatively narrow and elongated in the antero-posterior direction, the rear edge is protruding and the coracoid apophysis is thick and protruding downward and forward. The dimensions are close to the minimum values of the current Alpine and Apennine chamois and of all the fossils used in the comparisons.

The humerus (Pl. 1, figs 6 and 7) is slender; in the distal end, the olecranon fossa has ogival shape, the ridges that border this are located more or less at the same level; the trochlea with inner lip prominent and fossette relatively deep. The humerus of chamois from Mora Cavorso is slightly compressed in the medio-lateral direction and less compressed in the antero-posterior direction that the current Apennine chamois. The proportions between the length and the distal epiphysis approach rather to those of *R. rupicapra* specimens from Gran Paradiso National Park (Fig. 7). The maximum length is less than the specimen from Fumane, but it has the same size as the living Alpine chamois, while it is bigger than both the living Apennine chamois that the specimen from Balze (the latter being close to the minimum values of the modern Apennine chamois). The size of the distal epiphysis are in the range of fossil specimens from Central-Southern Italy, they are smaller than the specimen from Fumane, close to those of modern Alpine chamois and the minimum values of Apennine chamois, and slightly below the average of the Late Pleistocene chamois from Pyrenees and Iberian Peninsula.

Morphology and size of the proximal ulna (Pl. 1, fig. 8) fall within the variability of the current chamois and of the fossil specimens used in the comparison; however, the width of the coronoid process is relatively narrow. Radius has relatively slender morphology (Pl. 1, fig. 9); the proximal end has the inside articular edge slightly protruding and the posterior articular profile with the characteristic narrow, angular and shallow incisure; in the distal end, the internal condyle for articulation with the scaphoid is non-edged ridges and the internal condyle for articulation with the lunate is shallow. The dimensions are larger than those of the extant Apennine chamois and slightly lower than those of the specimens from Gran Paradiso National Park. The proportions between the length and the proximal and distal epiphyses, however, are the same of the extant Alpine and Apennine chamois and the early Holocene sample from Balze (smaller than the minimum values of living

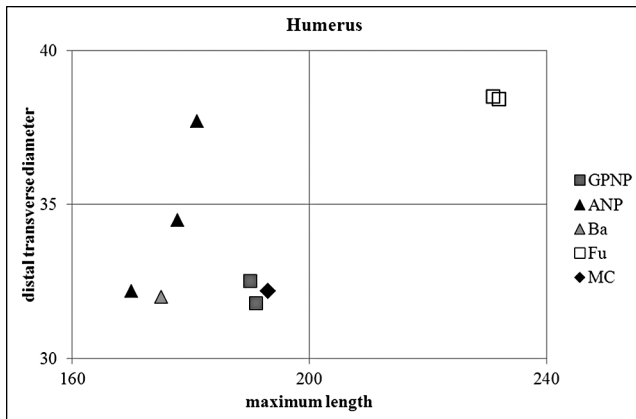


Fig. 7 - Scattergram of distal transverse diameter versus maximum length of humerus (mm) of the specimen from Grotta Mora Cavorso compared with some Late Pleistocene, early Holocene and living chamois. MC: Grotta Mora Cavorso; Ba: Grotta delle Balze; Fu: Riparo di Fumane. GPNP: living *R. rupicapra* from Gran Paradiso National Park; ANP: maximum, minimum and mean of living *R. pyrenaica ornata* from Abruzzi National Park.

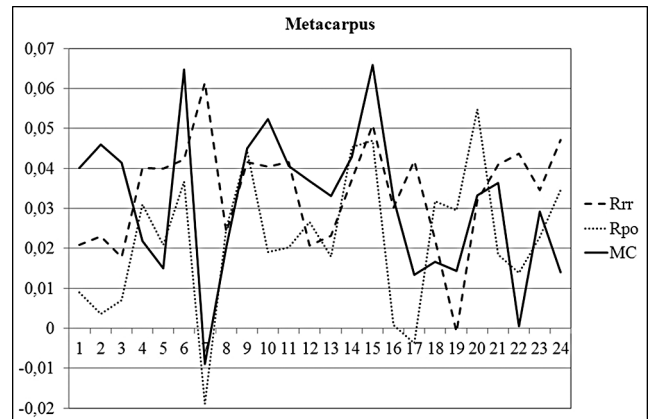


Fig. 9 - Ratio diagram of decimal logarithmic differences between measurements of the metacarpus of chamois from Grotta Mora Cavorso (MC), the mean of 6 *R. pyrenaica ornata* individuals (Rpo) and the mean of 8 *R. rupicapra rupicapra* individuals (Rrr) compared with the mean of 8 *R. pyrenaica pyrenaica* individuals (0). Measurement system, symbolology (see Fig. 5) and data of *R. rupicapra rupicapra* and *R. pyrenaica pyrenaica* from Crégut-Bonnoure (1992).

Apennine chamois). While the Late Pleistocene chamois from Pyrenees and Iberian Peninsula show a higher sturdiness in the middle of the diaphysis and in Fig. 8 follow a different alignment, with little variation in length, but big differences in the width of the distal end.

The metacarpus (Pl. 1, fig. 10) is very slender; the proximal epiphysis has relatively prominent dorsomedial tuberosity and the fossettes between the articular facets which also extends below the articular surface. Its length is greater than the current Apennine chamois and of the specimens from Gran Paradiso National Park, but smaller than that of the Late Pleistocene chamois

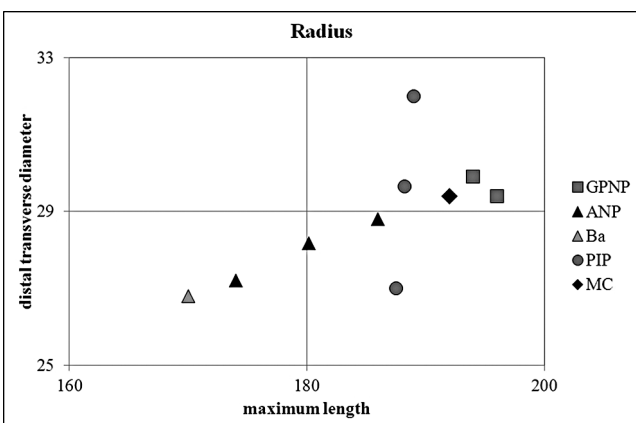


Fig. 8 - Scattergram of distal transverse diameter versus maximum length of radius (mm) of the specimen from Grotta Mora Cavorso compared with some Late Pleistocene, early Holocene and living chamois. MC: Grotta Mora Cavorso; Ba: Grotta delle Balze; PIP: maximum, minimum and mean of Late Pleistocene *R. pyrenaica* from Pyrenees and Iberian Peninsula. GPNP: living *R. rupicapra* from Gran Paradiso National Park; ANP: maximum, minimum and mean of living *R. pyrenaica ornata* from Abruzzi National Park.

from the Pyrenees and Iberian Peninsula. The proximal epiphysis is less compressed in the antero-posterior direction than in the current chamois: the proximal transverse diameter (Bp) measure 24.0 mm on average, the proximal antero-posterior diameter (Dp) measure 18.6 mm on average, so that the ratio between the transverse diameter and antero-posterior diameter is 1.29, that of the specimens from Gran Paradiso National Park is 1.31 and 1.34, and that of the sample from Abruzzi National Park is between 1.39 and 1.46, with a mean of 1.42 (see the values in Appendix 3).

Regarding the metacarpus, Crégut-Bonnoure (1992) has shown that in *R. rupicapra* and *R. pyrenaica* of France the proportions of the metacarpal bones relative to the length (measurements 1, 2, 3) and their size in the middle of the diaphysis (measurements 12, 13) are more or less the same. In Alpine chamois, in the proximal end, the surface for carpal bones is wider (measurements 5 to 9 and 11), especially the surface for the *os magnum*, and in the distal end (measurements 14 to 24) the tubercles of the distal diaphysis are more developed than the trochlea. Conversely, in the Pyrenean chamois the tubercles are less developed laterally (Crégut-Bonnoure 1992). The measurements of Alpine chamois from Gran Paradiso National Park are close to the mean values provided by Crégut-Bonnoure (1992) for *R. rupicapra* of France (Tab. 5). The Apennine chamois generally show intermediate values between those of the Alpine and Pyrenean chamois (Tab. 5 and Fig. 9). However, we may notice a greater robustness in the middle of the diaphysis (measurements 12, 13) and, in the proximal end (measurements 5 to 9 and 11), a strong reduction of the articular surface for the *os magnum*; in the distal end (measurements 14 to 24) the tubercles of the

	GNP	GNP	R.r.r.	R.r.r.	R.r.r.	R.p.p.	R.p.p.	R.p.p.	R.p.o.	R.p.o.	R.p.o.	SM	Ba	MC	MC
measure			max	min	mea	max	min	mea	max	min	mea				
1	149.0	146.0	164.8	130.1	146.4	145.2	129.2	139.5	145.0	135.5	142.4				153.0
2	137.6	134.7	151.0	118.0	135.2	134.1	117.6	128.2	131.0	122.5	129.2				142.5
3	143.6	140.6	157.7	128.1	141.1	140.6	123.9	135.4	139.5	131.4	137.6				149.0
4	24.5	24.1	29.0	22.9	24.9	24.4	21.6	22.7	25.5	23.0	24.4			24.1	23.9
5	24.0	23.5	28.0	22.4	24.3	24.5	20.8	22.1	23.8	22.5	23.2			23.1	22.9
6	10.1	9.8	11.8	9.1	10.2	10.1	8.4	9.2	10.3	9.4	10.0			10.8	10.7
7	16.1	15.7	18.6	14.7	16.2	15.1	12.8	14.1	14.4	12.6	13.5			13.9	13.8
8	14.4	14.8	17.2	13.4	14.5	14.5	12.8	13.7	15.2	13.5	14.6			14.5	14.4
9	19.1	19.7	22.8	17.8	19.3	18.5	16.0	17.5	20.0	18.4	19.4			19.4	19.4
10	18.3	18.4	20.3	16.6	18.0	17.1	15.6	16.4	17.7	16.5	17.1			18.8	18.5
11	16.7	16.9	19.4	15.1	16.5	15.8	13.7	15.0	16.7	15.2	15.7			16.6	16.5
12	15.3	14.6	19.5	12.9	15.5	15.6	13.9	14.8	16.0	15.2	15.7		15.7		16.1
13	11.8	11.0	14.1	10.1	11.7	12.2	10.2	11.1	11.8	11.2	11.6		11.0		12.0
14	29.0	27.9	32.8	24.9	28.7	27.4	25.2	26.4	30.5	28.0	29.3	29.4	27.7	29.2	29.1
15	28.6	27.0	32.5	24.3	27.8	27.0	24.6	25.8	28.6	26.8	27.6	27.7	27.7	29.1	28.8
16	13.8	13.1	15.1	11.3	13.4	13.5	12.0	12.5	13.8	8.0	12.6	12.6	12.8	13.7	13.5
17	11.6	11.6	14.3	9.9	12.0	11.9	9.3	10.9	11.8	8.0	10.8	11.2	11.0	11.3	11.2
18	15.1	16.5	19.0	15.0	17.0	16.9	15.4	16.2	18.4	16.0	17.4	16.4	17.2	16.8	16.8
19	17.0	16.1	18.6	14.5	16.6	16.5	14.5	16.6	18.8	17.0	17.8	17.8	16.6	17.3	17.2
20	13.0	14.0	16.3	12.1	14.4	14.2	12.5	13.3	15.8	14.0	15.1	14.6	14.2	14.2	14.4
21	16.8	17.8	19.8	15.7	17.5	16.7	15.1	15.9	17.0	15.8	16.6	16.7	15.9	17.3	17.3
22	10.8	11.6	13.2	9.8	11.4	10.9	9.6	10.3	10.9	10.2	10.6	10.8	10.4	10.2	10.3
23	17.4	17.4	19.6	15.7	17.1	16.4	15.0	15.8	17.2	16.0	16.7	17.4	16.1	17.2	16.9
24	10.5	11.1	12.3	9.4	10.9	10.5	9.2	9.8	11.1	10.2	10.6	10.7	10.2	10.1	10.1
specimen	P506/93	WN										P136/12	WN	2232-2258	2249

Tab. 5 - Measurements (mm) of metacarpus in recent Alpine, Apennine and Pyrenean chamois and fossil remains from some Late Pleistocene and early Holocene sites of Central-Southern Italy. Rrr: maximum, minimum and mean of specimens of 8 *R. rupicapra rupicapra* (data from Crégut-Bonnoure 1992); Rpp: maximum, minimum and mean of specimens of 8 *R. pyrenaica pyrenaica* (data from Crégut-Bonnoure 1992); Rpo: maximum, minimum and mean of specimens of 6 *R. pyrenaica ornata* from Abruzzi National Park; MC: Grotta Mora Cavorso; Ba: Grotta delle Balze; SM: Santuario della Madonna; GPNP: Alpine chamois from Gran Paradiso National Park.

Measurement system and symbology (see Fig. 5) from Crégut-Bonnoure (1992).

distal diaphysis are more developed than the trochlea (more than in Alpine chamois, measurements 14, 15) and also it is less compressed in the antero-posterior direction (as Pyrenean chamois, measurements 16, 17) and with the articular condyles slightly less raised but more spaced (measurements 18, 19 and 20). The metacarpus from Mora Cavorso is longer (measurements 1, 2, 3) and more robust in the middle of the diaphysis (measurements 12, 13) than the average values of current populations of chamois. The other portions of the curve of this metacarpus follow the curve of the Apennine chamois, but there is a generally minor compression in the antero-posterior direction (measurements 10, 11, 13, 16, 17) and, in the distal end, a greater reduction of the external condyle can be noticed (measurements 23, 24) (Tab. 5 and Fig. 9).

Regarding the femur (Pl. 1, fig. 11), the neck is shortly elongated in the proximal epiphysis; in the distal end the lips of the trochlea are almost similar and the intercondylar fossa is relatively wide. The dimensions are close to those of the specimens from Gran Paradiso National Park and of the maximum values of the chamois from Abruzzi National Park, but smaller than the Pleistocene specimen from Fumane (Fig. 10).

The tibia appears slender (Pl. 1, figs 12 and 13), with distal epiphysis showing the facets for the articulation with malleolar bone prominent and separated by a deep fissure; the anterior fibular facet is small. In the middle of the diaphysis and in the distal end the dimensions are close to those of the specimens from Gran Paradiso National Park, to the fossil remains from Poggio and Monte Cucco, and to the average of living

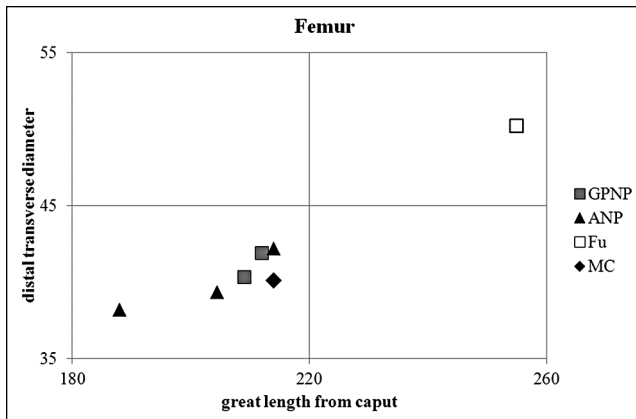


Fig. 10 - Scattergram of distal transverse diameter versus great length from caput of femur (mm) of the specimen from Grotta Mora Cavorso compared with some Late Pleistocene and living chamois. MC: Grotta Mora Cavorso; Fu: Riparo di Fumane. GPNP: living *R. rupicapra* from Gran Paradiso National Park; ANP: maximum, minimum and mean of living *R. pyrenaica ornata* from Abruzzi National Park.

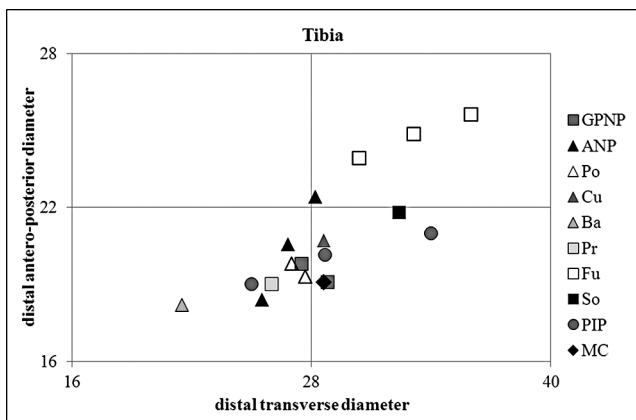


Fig. 11 - Scattergram of antero-posterior diameter versus transverse diameter of tibia distal epiphysis (mm) of the specimen from Grotta Mora Cavorso compared with some Late Pleistocene, early Holocene and living chamois. MC: Grotta Mora Cavorso; Po: Grotta del Poggio; Cu: Monte Cucco; Ba: Grotta delle Balze; Pr: Pradestel; Fu: Riparo di Fumane; So: Riparo Soman; PIP: maximum, minimum and mean of Late Pleistocene *R. pyrenaica* from Pyrenees and Iberian Peninsula. GPNP: living *R. rupicapra* from Gran Paradiso National Park; ANP: maximum, minimum and mean of living *R. pyrenaica ornata* from Abruzzi National Park.

Apennine chamois and Late Pleistocene chamois from Pyrenees and Iberian Peninsula, but smaller than Soman and Fumane and larger than Pradestel and Balze (see Fig. 11).

The talus (Pl. 1, figs 14 and 15) is wide and relatively low, with the lips of the trochlea proximal divaricated and with the side edges diverging upwards; the posterior-distal fossette is shallow. The dimensions fall within the variability of the fossils used in the comparison, being slightly greater than the current Apennine

and Alpine chamois. In the calcaneus (Pl. 1, fig. 16), in dorsal view, the articulation with malleolar bone is elongated and narrow, with the condyle distally limited by a transverse depression net and, below this, followed by a convex portion. The dimensions are slightly greater than the current Apennine chamois and fossils from Monte Cucco, close to those of the existing Alpine chamois, from Ingarano, Santuario della Madonna and Pradestel and to the lower values of the Late Pleistocene chamois from Pyrenees and Iberian Peninsula, but much smaller than the specimen from Fumane. Central tarsal bone with typical morphology of Caprinae (Pl. 1, fig. 17) and sizes that fall within the variability of the current chamois and the fossil specimens for comparison.

The proximal portion of metatarsus (Pl. 1, figs 18 and 19) shows the front of the main articular facets crossed by a transverse depression relatively pronounced and the small facet for articulation with the central tarsal bone little protruding. The transverse diameter (Bp) are smaller than those of the specimen from Fumane, and are close to those of other Italian fossil remains, to the existing Alpine and Apennine chamois and to the minimum values of the Late Pleistocene chamois from Pyrenees and Iberian Peninsula. The proximal transverse diameter (Bp) measure 22.75 mm on average, the proximal antero-posterior diameter (Dp) measure 20.8 mm on average, so that the ratio between the transverse diameter and antero-posterior diameter is 1.09 and falls within the variability of Italian recent and fossil chamois: Gran Paradiso National Park 1.07 and 1.09, Abruzzi National Park between 1.03 e 1.18 with a mean of 1.11, Balze 1.02 and 1.03, Fumane 1.05 and 1.07, Monte Cucco 1.13 (see the values in Appendices 2 and 3).

The proximal phalanges (Pl. 1, figs 20 and 21) are relatively elongated and slender, slightly compressed in the medial-lateral direction; the anterior ones are compact and straight, the posteriors slightly curved upwards and with relatively narrow distal epiphysis. The dimensions, both of the anteriors and the posteriors, are larger than those of current Apennine chamois and of most Italian comparative sites, close to the maximum values of the Late Pleistocene chamois from Pyrenees and Iberian Peninsula, but smaller than the specimen from Fumane. In addition, the size of the anterior phalanges are close to the specimens from Gran Paradiso National Park which have, however, the posterior phalanges of smaller size (Tab. 6 and Appendices).

The second phalanges (Pl. 1, fig. 22) are relatively slender and slightly compressed in the medial-lateral direction. The dimensions are close to specimens from Gran Paradiso National Park, to the fossil remains of the Santuario della Madonna and the maximum values of the Late Pleistocene chamois from Pyrenees and



	Po	Po	Po	Po	Cu	Ca	Ca	Ca	Ca	Ca	Ca	Fu	Fu	Fu	Fu	Fu	SB	SB	SB	PIP	PIP	PIP	PIP
Ph. I																				n.	max	min	mea
GL	50.6	50.0			46.0					46.7	46.0	59.8	58.2	57.7	54.2	55.6	54.5	54.9	52.7	54	50.8	36.5	45.5
Bp	13.5	14.8			14.9	13.3	12.2	12.1	12.4		14.6	16.9	17.3	16.8	16.5	15.1	16.7	15.3	16.4	52	15.7	11.3	13.7
SD	9.7	10.0								10.3		12.7	12.2	11.5	12.0	11.1	12.2	10.9	12.3	49	11.5	8.4	9.7
Bd	13.0	13.0			12.6	13.5	14.0			14.3	11.6	15.9	15.7	15.9	14.6	13.6	16.0	14.5	15.1	46	14.2	10.5	12.7
Ph. II																							
GL	28.0	29.0	34.5	30.3		28.0						40.1	37.9	34.6	35.7	37.1	31.5	33.9		42	33.1	20.5	29.6
Bp	12.5	12.5	14.0	13.4		12.7	12.8	14.0	13.9			16.2	16.0	15.9	16.1	14.7	25.5	14.6		40	15.5	9.4	13.0
SD	8.6	7.6	9.0			7.6						10.4	10.3	9.7	10.2	9.6	9.6	9.2		13	9.5	6.6	8.2
Bd	9.5	9.5		10.8		9.0	10.1	11.0				12.1	12.6	11.6	11.7	11.5	11.1	10.5		16	11.2	7.6	10.1
Ph. III																							
DLS										38.3		34.7								12	38.6	26.5	33.2
Ld										32.3		28.8								7	31.5	22.0	26.2
MBS												7.8								3	11.3	8.3	9.5

Tab. 6 - Measurements (mm) of first, second and third phalanges of some Late Pleistocene sites of central-southern Italy, Alpine arc and Pyrenees and Iberian Peninsula, taken by literature. Po: Grotta del Poggio (Sala 1979); Cu: Monte Cucco (Capasso Barbato et al. 1985); Ca: Grotta della Cala (Benini et al. 1997; Boscato et al. 1997); Fu: Riparo di Fumane (Cassoli & Tagliacozzo 1991); SB: Grotta Maggiore San Bernardino (Cassoli & Tagliacozzo 1994b); PIP: Pyrenees and Iberian Peninsula (see "Materials and methods"); Ph. I: first phalanx; Ph. II: second phalanx; Ph. III: third phalanx; n.: number of specimens; max: maximum; min: minimum; mea: mean. For the measurements of phalanges from Grotta Mora Cavorso and other Late Pleistocene, early Holocene and living chamois taken by authors, see the Appendices.

Measurement abbreviations: GL: greatest length; Bp: breadth of proximal end; SD: smallest breadth of the diaphysis; Bd: breadth of distal end; DLS: diagonal length of the sole; Ld: length of dorsal surface; MBS: breadth in the middle of the sole.

Iberian Peninsula, they are smaller than the largest specimen from Fumane, but generally larger than the other Italian sites and the existing chamois from Abruzzi National Park (Tab. 6 and Appendices).

The third phalanges (Pl. 1, fig. 23) are relatively high and compressed in medial-lateral direction, and show the front part of the lower face of ogival shape. The length is significantly larger than all the existing and fossil specimens used in the comparison, but the midpoint breadth of the sole is similar to the Italian chamois and slimmer than the Late Pleistocene chamois of Pyrenees and Iberian Peninsula (Tab. 6 and Appendices).

### Sex and age of the specimen

**Sex.** In the chamois both sexes have hook-shaped horns, those of the males being longer and thicker and showing more closed apical hook (Camerano 1914a; Couturier 1938; Lovari & Bruno 2003; Tosi & Pedrotti 2003; García-González & Herrero 2007). Table 7 shows the variability of the length and the transverse diameter at the base of horn-core between males and females of extant Alpine, Apennine and Pyrenean chamois. The data of Apennine chamois are inferred by using both the values reported in Camerano (1916a) and the values of our sample of *R. pyrenaica ornata* from Abruzzi National Park (except for young individuals and those of "undetermined sex"). According to the large size of its horn-core (length: 128.0; transverse diameter at the base: 22.7; see Tab. 2) the specimen from Grotta Mora Cavorso is very likely to be a male.

**Age.** The Alpine and Pyrenean chamois have the complete permanent dentition at about 5 years (Cam-

Horn-core	males			females		
	max	min	mea	max	min	mea
<i>R. r. rupicapra</i>						
L.	124.0	62.0	94.8	102.0	62.0	77.8
TD	26.0	16.0	20.7	25.0	12.0	15.5
<i>R. p. pyrenaica</i>						
L.	101.0	95.0	98.0	93.0	55.0	77.6
TD	19.5	15.5	17.3	17.0	10.5	17.3
<i>R. p. ornata</i>						
L.	141.0	105.0	122.6	117.0	96.0	107.3
TD	24.5	17.8	22.4	20.3	18.3	18.9

Tab. 7 - Horn-core measurements (mm) of modern males and females of *R. rupicapra rupicapra* (data from Camerano 1914b), *R. pyrenaica pyrenaica* (data from Couturier 1938) and *R. pyrenaica ornata* (data from Camerano 1916a and this work); max: maximum; min: minimum; mea: mean; L.: length; TD: transverse diameter.

erano 1914b; Couturier 1938; Tosi & Pedrotti 2003; Arceredillo & Diez 2009), at 9 years the lower cheek-teeth shown a little wear and at 15 years a great state of wear except M<sub>1</sub> (Couturier 1938; Arceredillo & Diez 2009). The mandible of our chamois has medium-worn molars, and the height of the unworn crown of M<sub>2</sub> is 16.7 mm; the lower molars show intermediate wear stage between the mandibles G (9 years) and H (15 years) illustrated by Arceredillo & Diez (2009, fig. 3), and slightly greater than the wear stage of lower cheek-teeth of Apennine chamois from Abruzzi National Park of 12 years (specimen 47). The wear stage of upper molars are similar to that of the specimens 11 and 14, respectively of 12 and 14 years. Thus, the

dental wear indicates an age probably slightly greater than 12 years; also the maximum height of the horizontal branch at the second lobe of  $M_3$ , rather than posteriorly, indicates an advanced age.

### Remarks

Morphological and morphometric features of skull and horn-core of chamois from Grotta Mora Cavorso are typical of the extant Apennine chamois, in particular the fully closed ethmoidal vacuity and the ratio between the antero-posterior diameter and the minimum distance at the base of the horn-cores.

Regarding the post-cranial skeleton, the bones of this specimen (as well as most other Late Pleistocene specimens) are generally greater than the post-cranial bones of early Holocene and living chamois, but it was already noticed that from the Late Pleistocene to the Holocene the body size of some species, such as *Capra ibex* (Bartolomei & Sala 1972), *Equus ferus* (Eisenmann 1991; Conti et al. 2010, and references therein), *Vulpes vulpes* (Petronio et al. 2006) and *Bos primigenius* (Pandolfi et al. 2011, with references) diminished, particularly in the dimensions of the limbs.

The limb bones of the specimen from Mora Cavorso are mostly similar to the corresponding skeletal elements of the extant Apennine chamois, except for the humerus and the distal tibia, that morphometrically are closer to those of Alpine chamois. The eldest difference from the fossil and modern chamois is the length of the phalanges, particularly of the third phalanx. In the current chamois, the third phalanges are relatively small, short and thin, and so favor the motion, jumping and running on the rocks. The structure of the hooves gives it greater ability to move on the mountain ground: the outside edge is hard and sharp allowing the support even on small rocky outcrops, the front pointing down slightly favoring walking on ice, the sole of the foot is elastic, strong and slightly concave, increasing adherence to the steep rocky slopes; moreover, the presence of an interdigital skin fold, increasing the bearing surface, facilitates walking on soft and snowy soils (Couturier 1938; Lovari & Bruno 2003; Tosi & Pedrotti 2003). In the specimen of Mora Cavorso, the relatively long posterior first phalanges and the long and thin third phalanges may be an adaptation to motion on soft soils (grasslands and forests of the more or less snowy valley floor) being the rocky areas of high altitude of the Central Apennines covered with snow and ice during the Last Glacial. In particular, each pair of longer third phalanges, although thin, allow increasing the bearing surface. In the genus *Equus*, for example, it has already been observed that the hemionas, the asses and the Burchell's zebras, which live on hard grounds,

have smaller and narrower third phalanges than the kiang and the Przewalski's horses which run most of the year on relatively soft ground, sandy or snowy (Eisenmann 1984; Conti et al. 2010). In the presence of the same, or similar, environmental conditions (walk and run for part of the year on relatively soft or snowy ground), it seems that the Late Pleistocene Pyrenean chamois had a different adaptive response, in order to increase the supporting surface: they have the third phalanx relatively short and a greater amplitude of the sole. Instead, the Late Pleistocene chamois of Santuario della Madonna and Grotta della Cala, localities near the sea in Southern Italy, had the third phalanges of the same size of the modern chamois, as similar conditions at high altitudes in the mountains could be found in rocky coastal areas.

Regarding the proportions of limb bones, Capasso Barbato et al. (1985, tab. 1) have shown that in the extant *R. rupicapra* (*sensu* before 1988) the ratios humerus/metacarpus and radius/metacarpus are on average equal to 1.28 and to 1.29, while for example in *C. ibex* these ratios are an average respectively of 1.54 and 1.22, revealing that the latter species has the metacarpus significantly shorter than the humerus and slightly shorter than the radius. These ratios in chamois from Mora Cavorso are respectively 1.261 and 1.255. We have ascertained that the values given by Capasso Barbato et al. (1985) are intermediate between the mean values of our samples of the extant Alpine and Apennine chamois. Table 8 shows the ratios humerus/metacarpus and radius/metacarpus for the specimen from Mora Cavorso and the samples for comparison. The values of lengths of these skeletal elements of Mora Cavorso chamois are in Appendix 1, those of the Alpine chamois from Gran Paradiso National Park and Apennine chamois from Abruzzi National Park are in Appendix 3. In the males of extant *R. pyrenaica parva* the length of humerus ranges from 163.5 to 175.9 mm, with a mean of 168.8 mm, the length of radius from 165.0 to 185.9 mm, with a mean of 174.2 mm, and the length of metacarpus from 136.8 to 152.3 mm, with a mean of 143.0 mm (Arceredillo et al. 2011), while in the Late Pleistocene specimens from Pyrenees and Iberian Peninsula the length of radius ranges from 187.5 to 189.0 mm, with a mean of 188.3 mm, the length of metacarpus from 157.3 to 162.5 mm, with a mean of 159.7 mm (see Altuna 1972, 1985; Mariezkurrena 1989; Davis 2002).

Although the specimens of modern Alpine chamois and the Late Pleistocene chamois from Pyrenees and Iberian Peninsula are not numerous, it just seems that the proportions of the front limb of the Mora Cavorso specimen are the same, or very similar, as the extant Apennine chamois. It can be also seen that the ratio radius/metacarpus for the modern *R. pyrenai-*

	MC	PIP	PIP	PIP	GPNP	GPNP	GPNP	ANP	ANP	ANP	<i>parva</i>	<i>parva</i>	<i>parva</i>
		max	min	mea	max	min	mea	max	min	mea	max	min	mea
Humerus / Metacarpus	1.261				1.308	1.275	1.292	1.271	1.228	1.251	0.991	0.946	0.969
Radius / Metacarpus	1.255	1.192	1.163	1.179	1.342	1.302	1.322	1.292	1.214	1.268	1.195	1.155	1.180

Tab. 8 - Ratios, according to Capasso Barbato et al. (1985), between the great lengths of front limb bones of the specimen from Grotta Mora Cavorso compared with living chamois and Late Pleistocene chamois from Pyrenees and Iberian Peninsula. MC: Grotta Mora Cavorso; PIP: Pyrenees and Iberian Peninsula; GPNP: *R. rupicapra rupicapra* from Gran Paradiso National Park; ANP: *R. pyrenaica ornata* from Abruzzi National Park; *parva*: *R. pyrenaica parva* from the Cantabrian range; max: maximum; min: minimum; mea: mean.

*ca parva* is very similar, or the same, to that of the Late Pleistocene chamois from Pyrenees and Iberian Peninsula.

### Conclusions

The systematics of the genus *Rupicapra* is based on some features of the skull and of the horn-cores (see "Taxonomy of *Rupicapra* species"). In this paper, also among the limb bones some morphometric differences between the modern Alpine, Pyrenean and Apennine chamois were noted.

The skull and horn-core features of chamois from Grotta Mora Cavorso are typical of the living Apennine chamois. Also the morphometry of the epiphyses of the metacarpus are similar to those of extant Apennine chamois, although the morphological differences also in this bone between Apennine, Alpine and Pyrenean chamois are not very noticeable. Additionally, the proportions of the front limb have values closer to those of the extant Apennine chamois than to the Alpine and Pyrenean chamois. For all these reasons the sub-entire, partially articulated skeleton from Grotta Mora Cavorso, an over 12-years chamois, for the large size of its horn-core probably a male, can be ascribed to *Rupicapra pyrenaica ornata*.

The specimen from Mora Cavorso is to be correlated to a temperate oscillation of MIS 3, thus it is the first ascertained occurrence of *ornata*-like chamois, so far known with certainty only in the Holocene (Ripa Grande and Balze, see Masini 1985; Masini & Lovari 1988; Loreti & Salerno 1989) and possibly in the Late-glacial (the two horn-cores, one juvenile, without frontal bones from Romito di Papisidero, Southern Apennines, northern Calabria, see Masini 1985; Masini & Lovari 1988). Most likely also the others chamois remains from SU 105, SU 104 and Epigravettian layer of Grotta Mora Cavorso, preliminary and cautiously re-

ferred to *Rupicapra* sp., can be attributed to *R. pyrenaica ornata*.

Comparisons with samples of extant Alpine, Apennine and Pyrenean chamois and with fossil remains from many Late Pleistocene and older Holocene sites of Italy and Pyrenees and Iberian Peninsula have shown that the bones of the specimen from Mora Cavorso (as well as most other Late Pleistocene specimens) are usually greater than those of Holocene and living chamois. However, we can point out some peculiarities.

The third phalanges and the posterior first phalanges are relatively more elongated than to the extant chamois and fossil samples for comparison. This particular feature may be an adaptation to walk and run most of the year on relatively soft and snowy soils. Furthermore, humerus and distal tibia are morphometrically closer to those of the modern Alpine chamois than to of the Apennine chamois. Maybe this difference could be due to normal intraspecific variability, but cannot be excluded that the humerus, slightly compressed in the antero-posterior direction and less in the medio-lateral direction, and the distal epiphysis of the tibia, rather squat, are recent adaptations of modern Apennine chamois. In such case, we can remember that even the smaller body size of Cantabrian chamois and the perpendicular insertion of horn-cores of the Alpine chamois are some features that would have been acquired only during the Holocene (Altuna 1972; Masini 1985).

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Specimen	n.	Measurements (mm) according von den Driesch (1976)							
		GL	GB	Bfcr	Bfcd	GLF	H		
Atlas	2289	50.7		43.2	41.5	42.3	31.5		
		LCDe	LAPa	Bfcr	BPacd	BPtr	SBV	Bfcd	H
Axis	2731	55.4	49.5	39.4	27.4		24.2	22.0	45.5
		HS	DHA	Ld	SLC	GLP	LG	BG	
Scapula	2285					29.1	26.3	21.1	
		GL	GLC	Bp	Dp	SD	Bd	Dd	BT
Humerus	2204	193.0	178.0		46.0	13.2	31.4	29.3	30.0
Humerus	2208	193.0	178.0	40.0	45.6	13.6	32.2	29.3	30.3
Femur	2156		214.0	47.0	21.2	16.1	40.1	48.9	
		GL	LO	DPA	SDO	BPC			
Ulna	2191		37.3	28.4	23.6	14.3			
		GL	Bp	Dp	SD	Bd	Dd		
Radius	2261	192.0	32.5	18.2	17.9	29.4	20.4		
Radius	2191a				17.8	29.4	20.2		
Tibia	2197				15.1	28.6	19.1		
Tibia	2199					28.6	19.3		
Metacarpus	2249	153.0	23.9	18.5	16.1	29.1	17.3		
Metacarpus	2232		24.1	18.7					
Metacarpus	2258					29.2	17.3		
Metatarsus	2196		22.7	20.8	14.9				
Metatarsus	2201		22.8	20.8	15.0				
		GLI	GLm	DI	Dm	Bd			
Talus	2264	31.4	30.5	17.7	18.2	20.5			
Talus	2218a	31.1	30.2	17.8	18.2	20.5			
Talus *	2315	27.5	26.8	14.9	15.7	18.4			
		GL	GB						
Calcaneus	2255	65.1	22.2						
Calcaneus	2265	66.6	22.3						
Centrotarsale	2256		24.4						
		GL	Bp	SD	Bd				
Phalanx Ia	2207	47.6	14.3	9.0	13.4				
Phalanx Ia	2260	47.3	13.3	10.5	13.1				
Phalanx Ia	2284	47.1	13.4	10.5	13.1				
Phalanx Ia	2291	46.3	13.6	11.2	13.3				
Phalanx Ip	2202	52.4	13.8	10.0	12.9				
Phalanx Ip	2251	52.3	13.7	9.9	13.4				
Phalanx Ip *	41	46.4	11.6	8.2	11.4				
Phalanx II	2198	30.6	12.6	9.0	10.9				
Phalanx II	2202 a	32.7	13.3	9.0	9.9				
Phalanx II	2202 b	32.6	13.6	8.8	10.1				
Phalanx II	2218b	31.1	13.2	9.1	10.8				
Phalanx II	2251a	32.6	13.6	8.7	10.1				
Phalanx II	2258a	30.5	13.3	8.7	10.8				
		DLS	Ld	MBS					
Phalanx III	2218c	40.6	31.2	8.3					
Phalanx III	2258b	41.7	31.3	8.5					
Phalanx III	2240	42.2		7.9					
Phalanx III	2251b			8.2					

## Appendix 1

Measurements (mm) of post-cranial remains of Apennine chamois from Grotta Mora Cavorso.

Measurement abbreviations: Atlas: GL: greatest length; GB: greatest breadth over the wings; Bfcr: breadth of cranial articular surface; Bfcd: breadth of caudal articular surface; GLF: greatest length from the facies articularis cranialis to the caudalis; H: height; Axis: LCDe: length in the region of the body including the dens; LAPa: greatest length of the arc; Bfcr: breadth of cranial articular surface; BPacd: breadth across the processus articulares caudales; BPtr: breadth across the transverse processus; SBV: smallest breadth; Bfcd: breadth of caudal articular surface; H: height; Scapula: H: height along the spine; DHA: diagonal height; Ld: dorsal length; SLC: smallest length of collum scapulae; GLP: greatest length of glenoid process; LG: length of glenoid cavity; BG: breadth of glenoid cavity; Humerus and Femur: GL: greatest length; GLC: greatest length from caput; Bp: breadth of proximal end; Dp: depth of the proximal end (in the femur only caput); SD: smallest breadth of the diaphysis; Bd: breadth of distal end; Dd: depth of the distal end; BT: breadth of the troclea (only humerus); Ulna: GL: greatest length; LO: length of the olecranon; DPA: depth across the processus anconaeus; SDO: smallest depth of olecranon; BPC: breadth across the coronoid process; Radius, Tibia, Metacarpus, Metatarsus: GL: greatest length; Bp: breadth of proximal end; Dp: depth of the proximal end; SD: smallest breadth of the diaphysis; Bd: breadth of distal end; Dd: depth of the distal end; Talus: GLI: greatest length of lateral half; GLm: greatest length of medial half; DI: depth of lateral half; Dm: depth of medial half; Bd: breadth of distal end; Calcaneus and central tarsal bone: GL: greatest length (only calcaneus); GB: greatest breadth; First and Second Phalanx (a: anterior; p: posterior): GL: greatest length; Bp: breadth of proximal end; SD: smallest breadth of the diaphysis; Bd: breadth of distal end; Third Phalanx: DLS: diagonal length of the sole; Ld: length of dorsal surface; MBS: breadth in the middle of the sole. \* from 104 SU, this specimens are not of the sub-entire skeleton.

## Appendix 2

Measurements (mm) taken directly by the authors on post-cranial bones of the chamois remains of Late Pleistocene and early Holocene from Grotta delle Balze (Ba), housed at the Gualdo Tadino Speleological Group, Ingarano (In), housed in the Earth Science Department of "Sapienza" University of Rome, Riparo di Fumane (Fu), Riparo Soman (So) and Santuario della Madonna (SM), stored in the National Museum of Prehistory and Ethnography "Luigi Pigorini" of Rome (for abbreviations of measurements see caption of Appendix 1).

site	Specimen	n.	Measurements (mm) according von den Driesch (1976)								
			GL	GB	Bfcr	Bfcd	GLF	H			
Ba	Atlas	wn				40.0	42.0	29.5			
SM	Atlas	P136/5	47.4	60.7	39.6	37.4	43.2	34.0			
			LCDe	LAPa	Bfcr	BPacd	BPtr	SBV	Bfcd	H	
SM	Axis	P136/6			37.2						
			HS	DHA	Ld	SLC	GLP	LG	BG		
SM	Scapula	P136/7				22.7	34.9	28.3	23.1		
			GL	GLC	Bp	Dp	SD	Bd	Dd	BT	
Ba	Humerus	wn	175.0	165.0		45.0	15.2				
Ba	Humerus	wn					15.5	32.0	23.6	30.5	
Ba	Humerus	wn					15.4	31.8	24.2	29.0	
In	Humerus	FG45						28.1	25.7	26.4	
SM	Humerus	P136/8						33.3	29.0	31.0	
SM	Humerus	P136/9						32.8	27.4	30.6	
			GL	LO	DPA	SDO	BPC				
Ba	Ulna	wn			25.0	21.5	14.8				
SM	Ulna	P136/10		43.6	28.2	24.2	18.0				
			GL	Bp	Dp	SD	Bd	Dd			
Ba	Radius	wn	170.0	28.8	18.0	17.0	28.6	21.0			
Ba	Tibia	wn				15.7	21.5	18.2			
So	Tibia	A51-20					32.4	21.8			
Ba	Metacarpus	wn				15.7	27.7	16.4			
SM	Metacarpus	P136/12					29.4	17.5			
Ba	Metatarsus	wn	153.0	24.2	23.6	15.8	28.3	18.9			
Ba	Metatarsus	wn	155.0	21.2	21.0	14.3	26.5	17.4			
SM	Metatarsus	P136/15					29.7	19.8			
			GLI	GLm	DI	Dm	Bd				
Ba	Talus	wn	30.8	30.0	17.7	18.3	20.0				
SM	Talus	P136/18	33.0	31.5	17.9	19.8	20.7				
So	Talus	RS360	34.3	33.0	19.2	21.1	22.0				
			GL	GB							
Ba	Calcaneus	wn		20.1							
In	Calcaneus	FG43	63.5	22.5							
SM	Calcaneus	P136/16	70.5	24.0							
SM	Calcaneus	P136/17	63.2	22.4							
Ba	Centrotarsale	wn		22.5							
SM	Centrotarsale	P136/19		26.4							
SM	Centrotarsale	P136/20		25.2							
			GL	Bp	SD	Bd					
Ba	Phalanx I	wn	40.7	12.6	10.7	12.2					
Ba	Phalanx I	wn	45.1	12.7	10.5	12.3					
Ba	Phalanx I	wn	45.1	12.6	10.1	12.2					
SM	Phalanx I	P136/22		13.6	8.9						
SM	Phalanx I	P136/23		13.1							
SM	Phalanx I	P136/25				14.2					
Ba	Phalanx II	wn	28.3	12.0	8.8	10.8					
SM	Phalanx II	P136/27	31.3	12.7	8.3	10.2					
SM	Phalanx II	P136/28	31.6	14.2	8.9	10.6					
			DLS	Ld	MBS						
Fu	Phalanx III	P6316	34.7	28.8	7.8						
SM	Phalanx III	P136/29	33.4	28.7	7.4						
SM	Phalanx III	P136/30	33.8	27.9	7.3						

site	Specimen	n.	Measurements (mm) according von den Driesch (1976)							
			GL	GB	Bfcr	Bfcd	GLF	H		
ANP	Atlas	27	47.3	57.6	40.5	40.0	41.2	29.4		
ANP	Atlas	35	42.3	52.5	37.2	36.7	38.4	26.7		
ANP	Atlas	201	46.2	57.0	40.2	40.2	43.0	29.0		
ANP	Atlas	238	47.5	59.2	41.4	40.0	41.5	30.5		
ANP	Atlas	wn	45.2	52.6	39.0	39.4	45.5	30.5		
GPNP	Atlas	wn	45.7	56.8	41.4	38.3	39.6	31.1		
			LCDe	LAPa	Bfcr	BPacd	BPtr	SBV	Bfcd	H
ANP	Axis	27	55.1	50.4	37.2	28.2	37.3	22.6	18.1	45.5
ANP	Axis *	35	49.8	47.4	35.2	27.0	34.2	25.0	16.7	37.5
ANP	Axis	58	54.2	46.2	38.6	30.0	38.5	28.2	18.8	41.3
ANP	Axis	201	54.2	49.5	38.0	29.0	37.0	21.8	18.5	45.0
ANP	Axis	238	56.5	50.8	37.8	28.5	38.0	22.2	18.8	41.5
ANP	Axis	239	52.7	46.1	34.9	23.8	34.2	20.8	16.4	42.2
ANP	Axis *	wn	54.0		37.5	25.0	35.5	22.5	17.5	41.5
GPNP	Axis	wn	52.4		36.1	24.6	31.8	18.5	19.7	42.3
			HS	DHA	Ld	SLC	GLP	LG	BG	
ANP	Scapula	26	154.0	165.0	92.5	21.1	30.3	27.7	22.7	
ANP	Scapula	35	139.0	150.0	85.0	18.8	30.2	24.4	20.0	
ANP	Scapula	47	158.0	170.0	96.0	22.0	30.5	27.0	22.7	
ANP	Scapula	201	151.0	164.0	93.5	19.0	31.5	25.0	21.0	
ANP	Scapula	238	158.0	170.0	97.5	21.5	31.4	26.1	22.5	
ANP	Scapula	239	147.0	158.0	84.5	18.8	30.7	26.8	20.6	
ANP	Scapula	wn	144.0	156.0	85.0	19.0	30.5	24.2	21.6	
GPNP	Scapula	P506/73	157.0	171.0	98.0	20.5	32.5	26.6	22.3	
GPNP	Scapula	wn	147.0	163.0	93.0	20.2	28.1	25.5	20.9	
			GL	GLC	Bp	Dp	SD	Bd	Dd	BT
ANP	Humerus	26	180.5	165.0	38.4	49.8	14.8	34.4	26.7	29.7
ANP	Humerus *	35	169.0	153.0	35.0	41.6	13.3	31.2	25.4	28.0
ANP	Humerus	47	178.0	163.0	38.7	44.0	14.4	34.6	27.0	31.3
ANP	Humerus	191	178.0	164.0		43.6	14.8	37.7	25.6	29.7
ANP	Humerus	201	179.0		36.5	43.5	14.8	32.2	25.5	29.5
ANP	Humerus	238	181.0	176.0	38.2	43.5	16.0	34.5	27.8	31.2
ANP	Humerus	239	170.0	157.0	37.2	43.1	14.4	33.3	25.1	28.2
ANP	Humerus *	wn	171.0	157.0	36.8	43.2	13.8	32.2	25.5	30.5
GPNP	Humerus	P506/75	190.0	176.0	40.0	46.5	13.5	32.5	29.5	30.5
GPNP	Humerus	wn	191.0	173.0	38.8	46.2	13.8	31.8	26.8	29.7
ANP	Femur	21		210.0		20.5	17.5	42.2	49.4	
ANP	Femur	26		206.0		20.5	15.9	38.2	47.8	
ANP	Femur *	35		199.0	42.0	19.0	16.0	38.8	43.2	
ANP	Femur	58	211.5	210.0	45.7	21.7	17.1	38.8	47.6	
ANP	Femur	201	205.0	200.0	44.4	20.2	18.2	39.1	47.8	
ANP	Femur	238	220.0	214.0	47.2	21.1	16.8	40.4	49.9	
ANP	Femur	239	196.0	188.0	43.6	20.0	16.5	38.2	46.8	
ANP	Femur	1100		203.0	44.0	20.4	16.8	38.3	47.8	
ANP	Femur *	wn	205.0	200.0	45.2	20.3	17.5	39.6	45.0	
GPNP	Femur	P506/120	216.0	212.0	49.4	21.7	16.5	41.9	49.7	
GPNP	Femur	wn	215.0	209.0	45.0	20.2	16.8	40.3	47.2	
			GL	LO	DPA	SDO	BPC			
ANP	Ulna	26	228.0	36.1	22.2	24.2	15.6			
ANP	Ulna *	35		34.6	22.3	20.0	15.0			
ANP	Ulna	47		36.7	24.8	22.2	15.3			
ANP	Ulna	191	224.0	34.8	22.3	24.6	16.8			
ANP	Ulna	201	224.0	32.1	21.5	24.7	15.6			
ANP	Ulna	238	221.0	32.0	23.4	26.4	15.5			
ANP	Ulna	239	210.0	34.5	21.1	23.9	14.8			
ANP	Ulna *	wn	220.0	37.5	20.8	22.8	14.3			

### Appendix 3

Measurements (mm) taken directly by the authors on post-cranial bones of Apennine chamois from Abruzzi National Park (ANP) housed in the Scientific Service of “Ente Autonomo Parco Nazionale d’Abruzzo, Lazio e Molise” of Pescasseroli (L’Aquila) and of Alpine chamois from Gran Paradiso National Park (GPNP) stored in the National Museum of Prehistory and Ethnography “Luigi Pigorini” of Rome (for abbreviations of measurements see caption of Appendix 1). \*specimens with the proximal and/or distal epiphysis not completely fused and, therefore, excluded by statistical analyses.

site	Specimen	n.	Measurements (mm) according von den Driesch (1976)						
GPNP	Ulna	P506/79		36.6	25.6	24.5	17.8		
			<b>GL</b>	<b>Bp</b>	<b>Dp</b>	<b>SD</b>	<b>Bd</b>	<b>Dd</b>	
ANP	Radius	26	178.0	29.4	17.4	17.3	28.8	20.4	
ANP	Radius *	35	160.0	27.5	15.2	15.2	25.2	20.4	
ANP	Radius	47	176.0	33.6	16.5	17.5	28.4	19.7	
ANP	Radius	191	183.0	29.2	17.4	17.4	27.6	19.8	
ANP	Radius	201	184.0	28.8	16.2	17.5	28.6	19.4	
ANP	Radius	238	186.0	31.2	17.1	17.4	28.4	20.2	
ANP	Radius	239	174.0	28.5	16.1	16.5	27.2	18.9	
ANP	Radius *	wn	182.0	28.8	17.5	17.8	27.5	21.6	
GPNP	Radius	P506/77	194.0	30.5	17.0	17.8	29.9	22.4	
GPNP	Radius	wn	196.0	29.2	15.9	16.5	29.4	19.5	
ANP	Tibia	21	272.0	43.3	44.2	14.7	26.7	21.2	
ANP	Tibia	26	266.0	43.1	42.2	16.0	27.2	20.2	
ANP	Tibia	33	253.0	41.4	40.2	19.2	26.5	20.6	
ANP	Tibia *	35	252.0	39.8	39.0	15.6	24.2	20.0	
ANP	Tibia	58	272.0	42.2	43.6	16.0	28.2	20.8	
ANP	Tibia	201	265.0	43.4	42.6	15.5	26.6	20.4	
ANP	Tibia	238	268.0	43.6	44.4	15.6	27.0	22.4	
ANP	Tibia	239	254.0	42.5	41.1	15.2	25.5	18.4	
ANP	Tibia *	wn	265.0	43.2	42.3	16.0	26.5	20.8	
GPNP	Tibia	P506/124	273.0	47.2	41.0	15.5	28.8	19.1	
GPNP	Tibia	wn	273.0	43.0	42.0	15.8	27.5	19.8	
ANP	Metacarpus	26	142.0	24.5	17.3	15.8	29.2	17.0	
ANP	Metacarpus	26	143.0	24.5	17.1	15.7	29.4	16.8	
ANP	Metacarpus *	35	139.0	22.8	16.2	15.3	29.0	15.8	
ANP	Metacarpus *	35	139.0	23.4	16.2	15.0	28.3	15.4	
ANP	Metacarpus	47	145.0	24.8	17.7	15.0	30.0	16.6	
ANP	Metacarpus	191	143.0	24.7	16.9	16.0	29.4	16.9	
ANP	Metacarpus	191	143.0	24.5	16.8	16.0	29.2	16.9	
ANP	Metacarpus	201	143.0	24.0	17.0	16.0	28.8	16.8	
ANP	Metacarpus	201	143.0	24.2	17.2	16.0	28.8	16.8	
ANP	Metacarpus	238	144.0	25.5	17.7	15.8	30.5	17.2	
ANP	Metacarpus	239	135.5	23.0	16.5	15.2	28.0	16.0	
ANP	Metacarpus *	wn	142.0	24.2	17.0	16.8	28.2	16.5	
GPNP	Metacarpus	P506/93	149.0	24.5	18.3	15.3	29.0	17.8	
GPNP	Metacarpus	wn	146.0	24.1	18.4	14.6	27.9	17.8	
ANP	Metatarsus	21	165.0	24.2	22.2	14.3	29.2	19.3	
ANP	Metatarsus	26	162.0	22.8	19.3	13.8	28.5	17.8	
ANP	Metatarsus *	35	157.5	21.8	18.8	14.2	21.7	17.3	
ANP	Metatarsus	58	163.0	22.4	20.2	14.6	29.3	18.9	
ANP	Metatarsus	201	163.0	22.7	21.1	14.4	27.9	15.4	
ANP	Metatarsus	238	161.0	23.0	20.0	14.2	28.8	19.2	
ANP	Metatarsus	239	153.0	21.1	20.5	13.5	26.5	16.9	
ANP	Metatarsus *	wn	160.0	22.8	19.5	14.5	27.2	18.6	
GPNP	Metatarsus	P506/138	171.0	22.1	20.6	13.8	28.9	18.5	
GPNP	Metatarsus	wn	179.0	22.0	20.1	13.4	26.6	17.8	
			<b>GLI</b>	<b>GLm</b>	<b>DI</b>	<b>Dm</b>	<b>Bd</b>		
ANP	Talus	21	29.2	29.0	16.2	18.0	20.6		
ANP	Talus	26	28.5	28.2	16.3	17.6	19.9		
ANP	Talus	35	27.7	27.4	15.8	16.2	19.4		
ANP	Talus	58	28.5	28.1	17.4	18.3	21.2		
ANP	Talus	201	28.1	27.6	17.5	18.1	20.5		
ANP	Talus	238	30.1	29.2	17.3	18.6	20.0		
ANP	Talus	239	27.5	27.3	15.8	17.0	19.2		
ANP	Talus	wn	28.2	28.0	16.5	17.0	19.5		
GPNP	Talus	P506/132	31.2	30.3	17.5	18.5	19.8		
GPNP	Talus	wn	29.8	29.2	17.4	17.8	19.2		
			<b>GL</b>	<b>GB</b>					
ANP	Calcaneus	21	63.0	23.5					

site	Specimen	n.	Measurements (mm) according von den Driesch (1976)						
ANP	Calcaneus	26	60.6	22.0					
ANP	Calcaneus	35	58.2	19.6					
ANP	Calcaneus	58	61.5	21.2					
ANP	Calcaneus	201	61.5	20.2					
ANP	Calcaneus	238	62.6	22.2					
ANP	Calcaneus	239	59.4	21.5					
ANP	Calcaneus *	wn	59.0	20.7					
GPNP	Calcaneus	P506/133	65.6	21.5					
ANP	Centrotarsale	21		26.4					
ANP	Centrotarsale	35		24.1					
ANP	Centrotarsale	58		25.4					
ANP	Centrotarsale	201		24.5					
ANP	Centrotarsale	238		25.4					
ANP	Centrotarsale	wn		24.8					
GPNP	Centrotarsale	P506/134		25.2					
GPNP	Centrotarsale	wn		23.5					
			<b>GL</b>	<b>Bp</b>	<b>SD</b>	<b>Bd</b>			
ANP	Phalanx Ia	26	42.5	12.8	11.1	13.2			
ANP	Phalanx Ia	26	42.7	13.4	10.7	13.2			
ANP	Phalanx Ia	35	41.2	13.4	9.9	12.4			
ANP	Phalanx Ia	201	43.1	12.9	11.1	12.8			
ANP	Phalanx Ia	238	45.0	14.6	11.2	13.5			
ANP	Phalanx Ia	239	42.0	12.5	10.2	12.0			
ANP	Phalanx Ia	wn	41.8	13.5	10.5	12.1			
GPNP	Phalanx Ia	P506/101	45.8	13.3	10.0	12.7			
GPNP	Phalanx Ia	wn	41.5	13.4	9.9	11.8			
ANP	Phalanx Ip	21	47.0	13.5	10.0	12.0			
ANP	Phalanx Ip	26	47.0	12.8	10.8	12.5			
ANP	Phalanx Ip	35	42.7	12.4	9.3	11.7			
ANP	Phalanx Ip	58	47.0	13.0	10.2	12.7			
ANP	Phalanx Ip	201	46.5	12.5	10.7	12.4			
ANP	Phalanx Ip	238	46.2	13.4	10.5	12.0			
ANP	Phalanx Ip	239	45.5	12.5	9.5	12.0			
ANP	Phalanx Ip	wn	44.2	13.1	9.2	11.6			
GPNP	Phalanx Ip	P506/146	49.1	13.4	9.3	12.2			
GPNP	Phalanx Ip	wn	46.0	13.4	9.1	11.7			
ANP	Phalanx II	21	31.8	13.0	8.6	10.0			
ANP	Phalanx II	26	28.8	13.5	9.4	10.3			
ANP	Phalanx II	26	28.8	13.1	9.3	10.5			
ANP	Phalanx II	201	29.1	13.2	8.8	10.2			
ANP	Phalanx II	238	29.8	13.7	9.4	10.5			
ANP	Phalanx II	239	29.5	11.8	8.5	9.5			
ANP	Phalanx II	wn	28.6	12.5	8.6	9.5			
GPNP	Phalanx II	P506/103	30.7	12.0	8.8	10.1			
GPNP	Phalanx II	P506/147	31.2	12.4	8.0	10.0			
			<b>DLS</b>	<b>Ld</b>	<b>MBS</b>				
ANP	Phalanx III	26	34.1	25.3	8.2				
ANP	Phalanx III	26	33.5	24.3	7.9				
ANP	Phalanx III	26	32.8	25.8	7.2				
ANP	Phalanx III	26	32.7	25.3	7.2				
ANP	Phalanx III	201	35.2	26.5	7.4				
ANP	Phalanx III	238	33.3	25.3	7.6				
ANP	Phalanx III	239	34.0	25.0	7.5				
ANP	Phalanx III	wn	32.2	24.2	6.9				
GPNP	Phalanx III	P506/148	36.5	30.6	7.2				