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URSUS SPELAEUS FROM GROTTA SOPRA FONTANA MARELLA, CAMPO DEI FIORI MASSIF (VARESE, ITALY): MORPHOMETRY AND PALEOECOLOGY.

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Riassunto. In questo lavoro vengono presentati i risultati dello studio paleontologico dei reperti fossili di *Ursus spelaeus* rinvenuti nella Grotta Sopra Fontana Marella (Monte Campo dei Fiori, Varese, Italia). Il materiale paleontologico esaminato proviene da tre distinti livelli stratigrafici attribuiti al Pleistocene Superiore, in base alle datazioni radiometriche e al metodo della racemizzazione degli amminoacidi. La presenza di tre differenti fasi di frequentazione della grotta ha consentito di condurre un'analisi biometrica comparativa tra resti di orsi vissuti nella medesima area geografica, ma in diversi intervalli di tempo. Gli orsi rinvenuti nel livello fossilifero più vecchio (FM4) si distinguono per la morfologia della mandibola e per la taglia corporea più piccola. Si discute l'ipotesi che questa variazione di taglia tra gli orsi del livello FM4 e quelli dei due livelli superiori FM1 e FM2 abbia un significato paleoclimatico, segno del passaggio da una fase più calda a una fase più fredda, coincidente con l'ultimo massimo glaciale. Gli studi morfometrici dei reperti ossei e dentari hanno permesso di ricavare il numero minimo degli individui, le classi d'età e la ripartizione dei sessi per ciascuna associazione fossile individuata.

Abstract. The paleontological study on cave bear remains from the Grotta Sopra Fontana Marella (Campo dei Fiori massif, Varese, Italy) is presented here. The cave bear material was collected in three different levels of the cave stratigraphical sequence which are assigned to Late Pleistocene by radiometric ages and aminoacid racemization analysis. This deposit gives us the rare opportunity to compare cave bear remains that lived in the same geographical areas but at different time intervals. Cave bears from the oldest level (FM4) had a peculiar mandible morphology and a smaller body size than cave bears from the uppermost levels (FM1 and FM2). We propose that this change in body size is related to a paleoclimatic trend from FM4 towards a colder phase (FM1 and FM2), the latter corresponding to the last maximum expansion of glaciers in the Italian Alps. Morphometric analysis of bones and teeth allowed to determine minimum number of individuals, class ages and sex ratio for each cave bear fossil assemblage.

Introduction.

Caves with *Ursus spelaeus* remains are widespread all over the carbonatic regions of the Alps. Most of them have been excavated during the first half of the 20th century, or even before, without paying attention to the stratigraphical position of fossil remains. In this way finds of different ages had been studied as coeval, therefore today it is not possible to use this undated material for new investigation. Only the caves recently discovered allowed a modern approach. This requires above all to focus not only on the paleontological material but also on the paleoenvironmental context revealed by the deposit, integrating results from different research fields (sedimentology, geomorphology, palinology, paleontology, etc.). Mammalian fossil assemblages provide ecological features of the environment in the past. The comparison of different sites, all investigated with a multidisciplinary approach, give us indications in order to better define changes in the alpine environment during Pleistocene. Till nowadays few deposits have been investigated with this modern aim. The Broion cave (Colli Berici, Veneto), excavated in 1950s, was one of the first caves of northern Italy where paleontological excavations included consideration of the stratigraphy and all other characteristics of the deposit (Leonardi 1951; Pasa 1953; Sala 1980; Zanalda 1994c).

In this work we present the detailed study of *Ursus spelaeus* remains found in the Grotta Sopra Fontana Marella (cadastral number: 2236 LO VA). The identification in this deposit sequence of different fossil assemblages allowed to compare bears from different levels, that means bears that lived in the same region but at different time intervals. We will try, in this paper, to explain the reasons of variations observed in the cave bear remains along the stratigraphical sequence.

The Grotta Sopra Fontana Marella cave is located in north-western Lombardy (Northern Italy). It opens on the north-eastern slope of the calcareous-dolomitic massif of Monte Campo dei Fiori, at 1040 m a.s.l., so above the MEG (Maximum Extension of the Glaciers)

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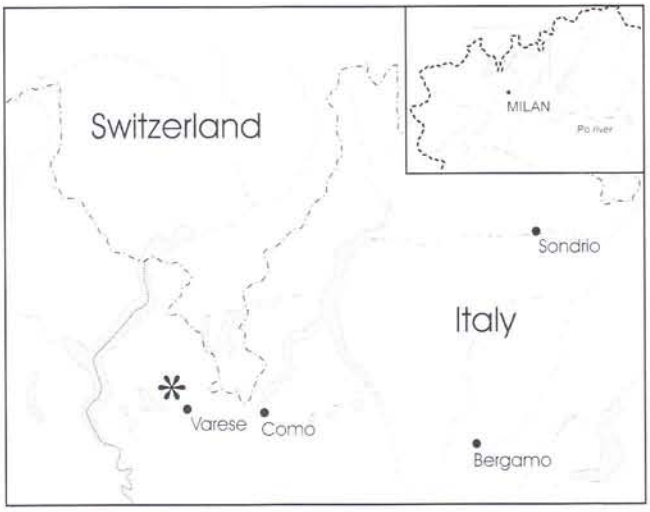

Fig. 1 - The geographical position of the Grotta Sopra Fontana Marella cave (*).

which is 910 m a.s.l. locally (Bini et al. 1997). The massif is located in the Lombardian Pre-Alps at the Po Plain border with maximum elevation of 1226 m (Fig. 1). This cave has been known since 1920s. The first paleontological excavations were carried out by Chiesa in 1926 (Airaghi 1927). Later, Brunella in 1932 and Sommaruga in 1941 carried out further investigations of the cave. These yielded mammal remains as well as prehistoric artefacts (Sommaruga 1942). Each of these studies focused on the external part of the cave. Only in the autumn of 1989, when the obstructing rockfall was removed, a cavity extension containing the undamaged fossiliferous deposit was discovered (Tintori et al. 1993; Zanalda & Perego 1994). The discovery of this new deposit provides the opportunity to carry out excavations with systematic methods allowing to collect complete information. We examined the exact stratigraphical position of each remain, and each stratigraphical level underwent a palynological (Ravazzi & Perego 1997), sedimentological and paleontological analysis.

Stratigraphical sequence.

The deposit fills a vertical fissure with intense karstic phenomena. The thickness of the investigated sequence is about 2 m (Fig. 2). It includes 12 stratigraphical levels (Bini et al. 1997). In this paper we discuss the large mammal that come from three of the four upper levels.

Follow a brief sedimentological description of the four Upper Pleistocene levels bottom to top:

FM4: a thin layer, composed of rare clasts and cave bear bones in a dark clay matrix. Fossil remains are dark and brittle. This layer is supposed to be in primary deposition, as there are not depositional evidences of mass transport and frail bones are only a bit fractured.

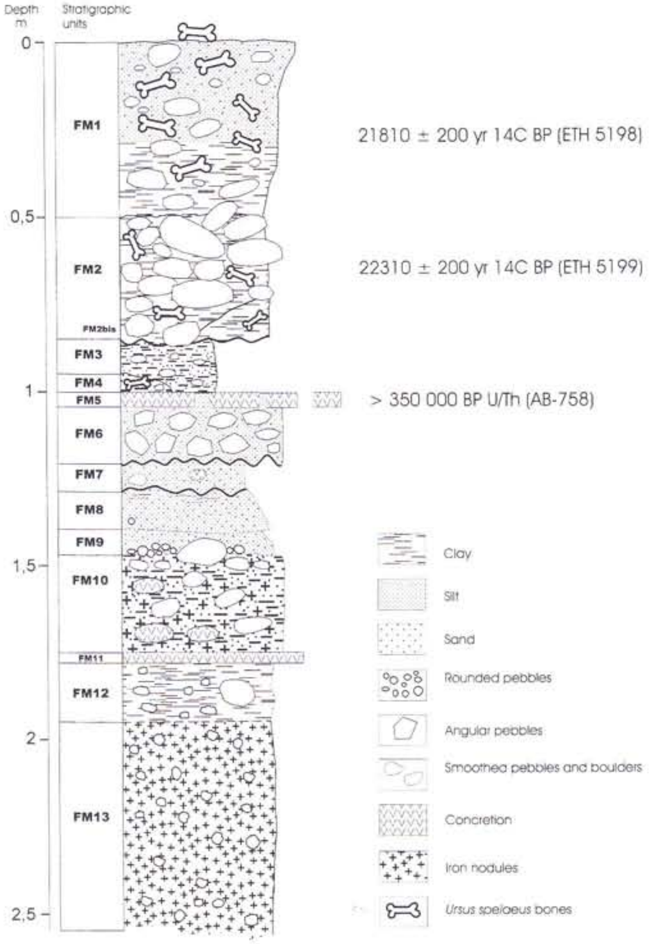

Fig. 2 - The stratigraphical sequence of the Grotta Sopra Fontana Marella cave.

FM3: no cave bear bones have been found in this level; only remains belonging to micromammals have been recovered. Among them, voles are dominant with *Microtus agrestis* (Linnaeus, 1761) and *M. arvalis* (Pallas 1779); *Sorex* Linnaeus, 1758 and *Lepus* Linnaeus, 1758 are also represented.

FM2: fossil remains are well preserved and the bones are often complete. Sediment is very dark to indicate a great amount of organic matter content. According to radiocarbon dating the time interval spanning from FM1 to FM2 is rather short, it takes no more than 600 years cal BP.

A grey-greenish wedge-shaped sediment level lays down between FM2 and FM3. This level is called FM2bis because it is lighter in colour than FM2 and replaces it in the most external portion of the cave.

FM1: a thin and dark layer separates this unit from the lower one (FM2). FM1 is composed by angular clasts in a clay matrix, it has a regular thickness across the investigated section. Fossil remains recovered from this level are very abundant and have a light colouring. This level has an inverse gradation due to local movements and not to mass transport of all sediment. In fact a mass transport could not have preserved the complete bones of large size and the six dorsal vertebrae in anatomical connection recovered inside a little lateral niche of the cave. Due to the bears continuous walking along the frequentation surface of the cave, bones of dead bears were pushed into these lateral shelters where they have been preserved complete or only slightly damaged.

Chronology.

The lowermost levels, from FM12 to FM6, have been dated to Middle Pleistocene on the basis of occurence of micromammals *Dinaromys bogdanovi* Martino, 1922 and *Pliomys episcopalis* (Mehely, 1914) (Zanalda 1994a). They are lying below a speleothem (FM5) older than 350,000 years by U/Th method, sample AB758 (Uggeri et al. 1991; Bini et al. 1997). The four upper levels, above the dated speleothem, have been attributed to Late Pleistocene according to ^{14}C dating on cave bear bones from levels FM2 and FM1, which gave an age of 22,310 ± 200 BP (sample UZ-2513/ETH-5199) for FM2 and 21,810 ± 200 BP (sample UZ-2512/ETH-5198) for FM1 (Bini et al. 1997; Zanalda et al. 1997). These ages are respectively calibrated 26,266 cal BP and 25,688 cal BP according to Bard et al. (1998). The radiocarbon dating of FM4 stratigraphical unit on the bones gave an age of 4,040 ± 65 BP (sample UZ-2817/ETH-8948). This age disagrees with stratigraphical evidences and with the extinction dating of *Ursus spelaeus*. The aminoacid racemization analysis, by Zanalda (unpublished data), confirmed the proposed chronology of stratigraphical sequence. Hence the radiocarbon date has to be considered wrong, FM4 must be older than 26,000 years cal BP .

Material and methods.

Vertebrate remains recovered from the Fontana Marella deposit consist of bones and teeth from large and small mammal taxa.

The macrofauna was only found in four of the five Upper Pleistocene levels (FM1, FM2, FM2bis, and FM4). It consists of more than 2,700 determinable remains and numerous fragments (Tab. 1).

Bones and teeth of small mammals were recovered by systematic screening of representative samples from all depositional units (levels FM1-FM12). These studies are not discussed in this paper (Tintori et al. 1995; Zanalda 1994b; Zanalda et al. 1997).

The macrofauna mainly consists of *Ursus spelaeus*; only a few remains of *Rupicapra rupicapra* Linnaeus, 1758 (two fragmentary metacarpal bones and one phalanx), *Marmota marmota* (Linnaues, 1758) (one emimandible) and *Ursus* cf. *arctos* (one mandible and two isolated canines) have been found in the uppermost level (FM1).

Cave bear remains are generally well preserved, despite some variations depending on the level: fossil bones from the two upper levels (FM1 and FM2) are better preserved than those from FM4. In this last level, the water, restrained by the lying below waterproof level, has altered and weakened the bone tissue.

After cleaning the bones accordingly to their different degrees of preservation, we consolidated them with a solution of "Paraloid B72" (Rohm and Haas-U.S.A) and acetone.

A biometric study on macro remains was carried out. Each bone and tooth was measured following the methodology developed by Von der Driesch (1976) and Torres (1988). The good preservation of the bones allowed the introduction of new measurements. For instance we measured the transversal diameter of the diaphysis, the most commonly preserved skeletal part of long bones.

We provided a summary table for each skeletal element, including, at each stratigraphical level, the following parameters: the number of measured remains (n), the minimum value (min), the maximum value (max), the mean (X) and the standard deviation (s.d.) (Tabs. 2-15).

Only the most meaningful tables are included here in an appendix, the complete set of data is available on web site (www.gp.terra.unimi.it/107N3.html) or at the correspondent author address.

We compared our results with data reported by Torres (1988) and Capasso Barbato et al. (1990; 1993) on cave and brown bears remains from Spain and Italy. Torres' data on *Ursus spelaeus*, *U. deningeri* Von Reichenau, *U. etruscus* G. Cuvier, and *U. arctos* Linnaeus from the Iberian peninsula were of particular interest.

The cave bears Minimal Number of Individuals (M.N.I.) has been calculated for each level on the most frequent skeletal part using a procedure calling "matching" (Krantz 1968; Bokonyi 1970; Klein & Cruz-Uribe 1984). As M.N.I. we consider the number of pairs of the most frequent bone, plus the unpaired lefts, plus the unpaired rights. We prefer not to sort lefts from rights because usually for the large mammals it's possible to determine whether two bones are from the same individual using either criteria of size or valuing the growth stage of bones. Anyway summing up lefts and rights one introduces a less significant error than the risk of loosing individuals by sorting rights and lefts.

Analysis of the remains.

The list of the cave bear remains (Tab. 1) shows that FM1 is the richest fossil assemblage, and that FM4 is richer than FM2. However, vertebrae, metapodials, carpal, and tarsal bones are present in almost the same amount in all these three assemblages.

Since data from FM2bis are scanty, we decided not to include them in the comparative biometric study, anyway they are listed in the tables to give a complete view. Some relevance has the finding of two almost complete female skulls in this level.

Mandible

Sixty mandibles, well preserved and belonging to different age classes, were found. Their distribution into each fossiliferous unit is as follows:

FM4: 8 adults, 4 youngs and 2 cubs
FM2bis: 2 cubs
FM2: 8 adults, 5 youngs and 4 cubs
FM1: 8 adults, 9 youngs and 10 cubs

Mandibles with both permanent and deciduous teeth not completely replaced yet (at least a permanent tooth is still included in bone), are identified as cubs. This age class extends from the first hibernation (that of birth) to the second one. Youngs have already secondary dentition well set, and teeth are not worn apart from canines and first molars which could present small worn faces. The mandible has not yet reached its definitive morphology: the horizontal ramus is low, and the fossa

Fig. 3 - Cave bear: buccal side of two emimandibles from level FM1.

masseterica is shallow and smooth. The age class of adults consists of adult and old individuals, whose mandibles have already concluded their growth, have reached a definitive morphology, and whose teeth are more or less worn. In some case teeth are so worn that the pulp cavity is visible.

On the basis of the size and morphology of the teeth, the shorter diastema, and the presence of the first and third premolars we identified a little subadult mandible found in FM1 as belonging to *Ursus* cf. *arctos*.

By analysing data shown in the table 2 and comparing them to those known in the literature, we see that mandibles of cave bears from Grotta Sopra Fontana Marella have some peculiar morphological features. The morphometric comparison between remains from the three main fossiliferous units and data from literature have pointed out the general large size of mandibles found.

Our results regarding the mandible lengths are closes to the maximum values of the *Ursus spelaeus* reported by Torres (1988). The values of the mandible total length (measure 1, Tab. 2) observed in FM1 and FM2 are higher than those in FM4. This result can not be ascribed to differences in age classes among levels as in FM4 we could only measure the mandibles of adult individuals, while in the uppermost levels we also gauged the samples for young and subadult bears. Surprisingly, the measures 11, 12, and 13 (concerning the height of

Fig. 4 - Cave bear: buccal side of two emimandibles from level FM4.

the horizontal ramus) in FM4 are higher than in FM1 and FM2 as shown in the table.

Furthermore, the *U. spelaeus* of Campo dei Fiori shows unusual morphological features. First, the diastema length (measure 10) and the molariform length (measure 8) are respectively shorter and longer in the two upper levels as compared to both FM4 and Torres' findings. Second, the heights of the horizontal and vertical rami differ from the normal values as measures 11, 12, and 13 of the horizontal ramus in FM1 and FM2 are lower than the minimum ones in Torres, while measure of the vertical ramus (measure 18) in the same upper levels reaches values above the maximum indicated by Torres. Thus, bears from the Campo dei Fiori deposit are characterized by higher mandibles with a low horizontal ramus. To show this particular feature, we computed an index of the ratio between the measures 12 and 18 (measure 32). This shows that the horizontal ramus of mandibles in FM4 is slightly higher than in the other levels.

Summarizing, the mandibles from FM4 resulted smaller but with a proportionally higher horizontal ramus, a lower vertical ramus and a longer diastema (Fig. 3 and 4).

Skull

Among the numerous skull fragments found in Grotta Sopra Fontana Marella, only 16 crania are in such

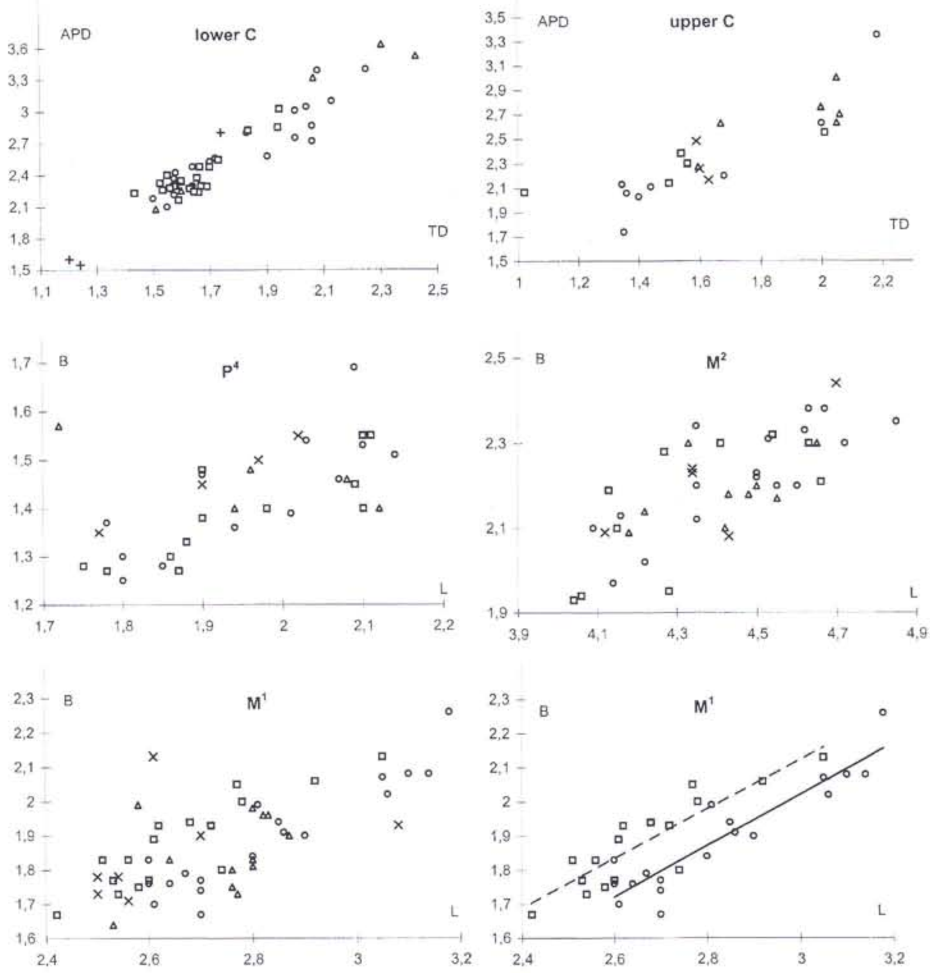

Fig. 5 - The dispersal diagrams of transversal (TD) and antero-posterior (APD) diameters of lower and upper canines (C); the dispersal diagrams of length (L) and breadth (B) of fourth upper premolars (P^4), first upper molars (M^1), second upper molars (M^2), and first upper molars from FM1 and FM4 with the regression line for each distribution (full line for FM1 and dotted line for FM4).

Symbols legend: ○ FM1; ● FM1; △ FM2; ▲ FM2; □ adults from FM4; x FM2 bis; + *Ursus cf. arctos.*

well preserved condition to allow the identification by age classes and sex. The two best preserved skulls (FM1 and FM2) belong to old male individuals. The other 14 crania are recorded as follows:

_ 3 skulls in FM4: 2 cubs and 1 female sub adult;

_ 2 skulls in FM2bis: 2 old females;

_ 4 skulls in FM2: 1 young, 2 sub adults and 1 adult female;

_ 5 skulls in FM1: 2 cubs, 1 young, 1 old male, and 1 adult female.

All the other skull remains are individual skull bones and fragments. Cranial morphology and the degree of wear in upper teeth have been used to distinguish age groups. The skull of cubs is nearly spherical (globose), and its neurocranium prevails on splancnocranium; the latter is seldom preserved. The sagittal crest is not formed yet; the two frontal crests extend on the parietal bones till the parieto-occipital suture. These two crests run parallel to each other and to the sagittal plane.

We grouped as young and subadult individuals all the samples with a cranial morphology apparently well defined but with cranial sutures still open and with a slightly developed sagittal crest. The different knitting degree of parieto-temporal and spheno-occipital sutures enabled us to distinguish youngs from subadults. Moreover teeth of subadults presented a slight wear, while teeth of youngs did not show any wear.

The age group of adults includes samples with all cranial sutures knitted, only the sutures between nasals and upper jaws may still be open, as they are usually the last ones to be knitted. The sagittal crest of adults is longer and higher than that one of youngs and subadults. Their canines and incisors have a perceptible wear, while lingual cusps of cheek teeth are affected by a pronounced wear.

When cranial sutures are no more evident and teeth are completely worn we list as old individuals.

We mainly sexed skulls samples on the base of size measurements. This practice is more reliable for adult and old individuals because size of young and subadults is not definitive. However, we sexed subadult skulls too in case when the size was diagnostic: females were determined as their skull is slender and smaller.

The paucity of the measured skulls, their preservation state, and the age difference do not allow a comparison among skulls from different levels. At best, one sample for each level was available for measurements. All these skulls belong to individuals with a definitive morphology and with typical characters of *Ursus*

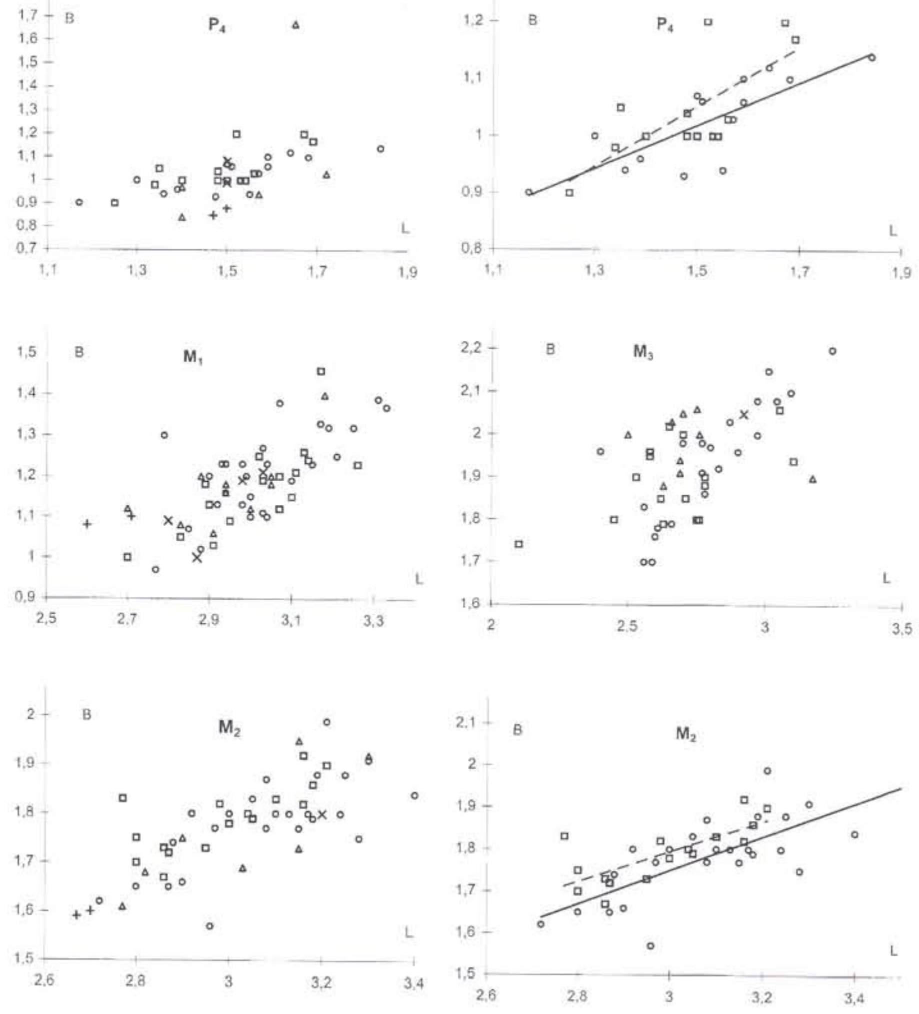

Fig. 6 - The dispersal diagrams of length (L) and breadth (B) of fourth lower premolars (P_4), fourth lower premolars from FM1 and FM4 with the regression line for each distribution (full line for FM1 and dotted line for FM4), first lower molars (M_1), third lower molars (M_3), second lower molars (M_2), and second lower molars from FM1 and FM4 with the regression line for each distribution (full line for FM1 and dotted line for FM4).

Symbols legend: ○ FM1; △ FM2; ❑ FM4; x FM2 bis; + *Ursus cf. arctos*.

spelaeus. The different size of skulls, as shown in table 3, is due to sexual dimorphism. We measured male skulls in both FM1 and FM2, while female ones in both FM2bis and FM4.

These measurements are in line with Torres (1988) and Capasso Barbato et al. (1993) for *Ursus spelaeus*.

- Teeth

133 deciduous and 766 permanent teeth have been found, taking into consideration both isolated and still placed teeth; morphometric and morphological study was conducted only on permanent teeth.

We determined the upper and lower canines according to the following considerations: lower canines are less sturdy, and their crown strongly turned upward to become almost vertical. Crown and root alignment slightly bends in a "S" shape so that the crown is turned outward. Completely worn canines and crowns without root are not distinguishable in upper and lower ones, preventing their measurement.

Morphometric analysis pointed out that FM4 canines are significantly smaller than those from the two uppermost levels. This feature is also detected by visual observation of the teeth and by distribution drawn in the dispersal diagram of transversal and antero-posterior diameters of lower canines (Fig. 5). The three canines assigned to *Ursus arctos* are also drawn in this diagram: two of them belong to female individuals and one to a male. The spatial distribution of these teeth agrees with *Ursus arctos*.

Fig. 5 shows the sexual dimorphism that characterised cave bears (Koby 1949a, 1949b; Kurtén 1955; Rustichelli 1993). In fact two clear groups distinguishing males and females appear in all the three main fossil assemblages. Male data are much more dispersed, which means a greater variability in size. Besides, Fig. 5 shows an almost 1:1 sex ratio in levels FM1 and FM2, while female individuals are predominant in FM4 (5,6:1). Males from FM4 are among the smaller males, while females of the three assemblages are homogeneously distributed. The same considerations can be inferred for the upper canines (Fig. 5) but here the data are very poor. One canine from FM4 is characterised by a very narrow transversal diameter.

As regards molars we totally found 78 M_1, 75 M_2, 65 M_3, 80 M^1, and 79 M^2, mostly from FM1. Morphology and measurements values match the characteristics of *Ursus spelaeus* (Torres 1988; Capasso Barbato et al. 1990).

Only the morphology of M^2 is somewhat variable:

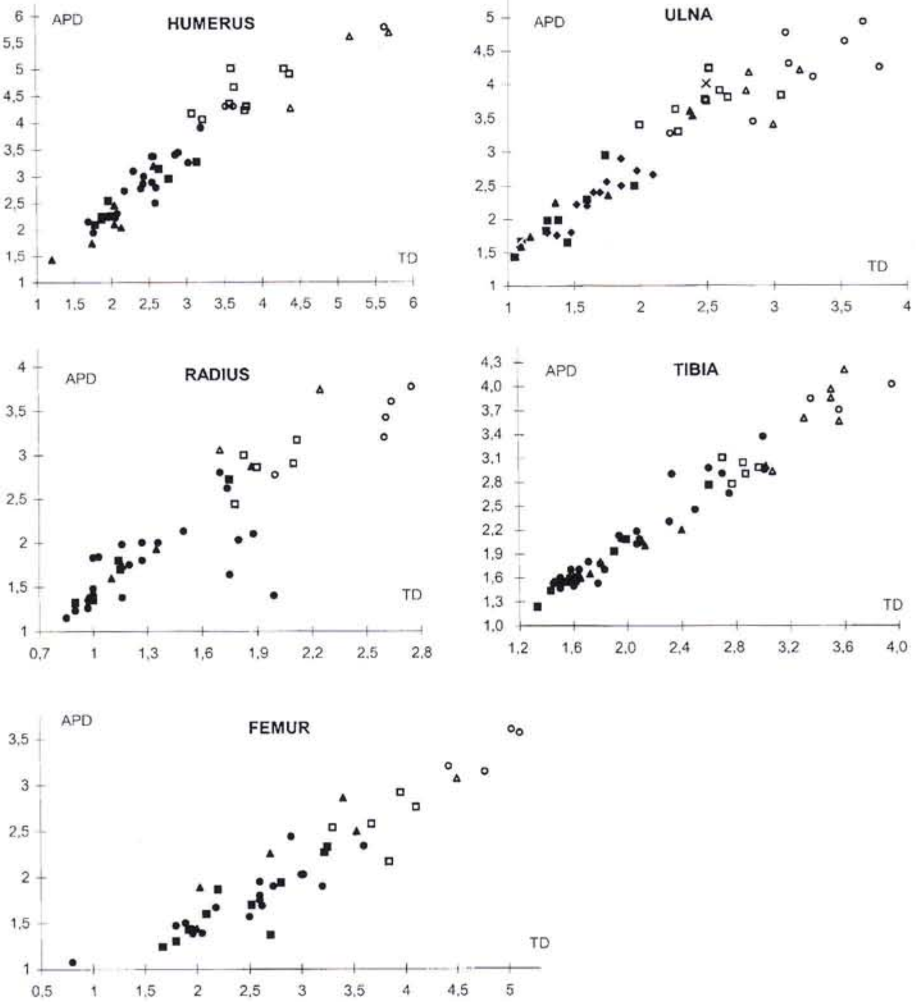

Fig. 7 - The dispersal diagrams of transversal (TD) and antero-posterior (APD) diameters of diaphysis of humerus, ulna, radius, tibia, and femur.

Symbols legend: ○ adults from FM1; ● juveniles from FM1; △ adults from FM2; ▲ juveniles from FM2; □ adults from FM4; ■ juveniles from FM4; ⊓ FM2 bis; + *Ursus cf. arctos*.

some teeth are nearly straight, others are more or less bent. Still, the degree of crown torsion is not constant and in some teeth it is even absent. Another morphological feature is the number of accessory cusps composing the posterior masticatory surface of M^2. These cusps can be small and numerous or, otherwise, large and few. Generally the measurements are comprised in Torres' data ranges, near to their minimum values. Only a disagreement appears in the measure of the distance between protocone and hypocone (measure 7) which is smaller in Torres' measures. The hypocone is formed by two cusps, so it is possible that the remarked disagreement is due to a different method to measure the distance between protocone and hypocone. We always considered the hypocone second cusp, which is well defined and readily distinguishable. Unfortunately Torres does not explain in detail how to take this measurement.

According to Crusafont & Truyols (1957) the carnivore cheek dentition can be subdivided in three areas with different functional meanings: crushing, cutting, and shearing. Crusafont & Truyols compare the lengths of these three areas among several carnivore families, pointing out great differences related to their ecological specialization and dietary adaptations. We performed the same comparison among our three assemblages. No significant differences have been highlighted in the length of cheek dentition, while the breadth seems to vary significantly. In order to compare the cheekteeth dimensions we have elaborated length-breadth dispersal diagrams for every tooth (Fig. 5 and 6). We have elaborated further diagrams for P_4, M_2 and M^1 limiting the comparison to FM1 and FM4 levels and adding the regression line (Fig. 5 and 6). These diagrams show that with the same length the breadth is larger in FM4 than in the uppermost level. Instead those of P^4 and M^2 do not show this diversity and the morphological variability of the third lower molars is so high that a meaningful comparison between teeth from each level is not significant.

Postcranial skeleton

Most postcranial skeletal elements are from FM1 as we can observe in the tables for biometrical analysis (Tabs. 11-15). We found several metapodia and a large number of long bones on which we counted the minimum number of individuals for each level. Since only three entire fibulas have been found we could not include them in the analysis.

Among long bones, the largest number of data concerns the diaphysis, commonly in fragmentary bones. Diaphysis is the section of long bones less affected by damage and fracturing caused by post-mortem transport. In addition, in samples of young individuals, the diaphysis is separated by the two extremities of the bone and fossilized separately. Thus, data based on diaphysis measurements include a great amount of young individuals, higher than in any other measurements of skeleton elements. This feature can be observed in their measures intervals which extend towards low values more than in other cases. The biometric comparison could be affected by this kind of bias.

In the limb bones dispersal diagrams (Fig. 7) we reported the transversal and antero-posterior diameters of the diaphysis because they are the most numerous data. We could not use the length because there are only a few complete limb bones. The majority of long bones has not the epiphyses joined, and we attribute these to young individuals still in growth. Only long bones with at least one epiphysis joined to the diaphysis and with an adult size have been considered as adult individuals. These diagrams show a linear distribution which corresponds to the different phases of bones development. The youngs are grouped according to age classes distinguished because the growth stage corresponding to summer periods is missing in our record. As regards to the adults the few remains do not enable to determine a correct sex ratio. Nevertheless in the diagrams of humerus, femur and radius adults are set in two groups probably due to sexual dimorphism. This observation is supported from other studies which show sexual dimorphism and in particular in the humerus and femur. A study on the Cave of Equi (Tuscany) cave bears' long bones indicates a sexual dimorphism based on the correlation between length and width of the single bones (Cuggiani 1981). This dimorphism emerges also from the multivariate analysis of the limbs bones of Conturines Cave, Gamssulzen Cave, Herdengel Cave (Reisinger & Hohenegger 1998) and from the study of the Basura Cave remains (Giacobini & D'Errico 1985). These results are obtained from a large and statistically significant sample and also when different measures were used.

In Fig. 7, the line separating the two sexed groups is different in FM1, FM2, and FM4. Actually, males from FM4 are placed near the separation between males and females of the two uppermost assemblages, or even among females. Females from the lowermost level can be placed near youngs from FM1 and FM2. These differences also suggest that bears from FM1 and FM2 are bigger than those from FM4.

In the diagram concerning the tibia (Fig. 7) the sexual dimorphism is not shown, but the tibiae of adult bears from FM4 are placed with those individuals from FM1 and FM2 who did not reach their final stage of growth. In the diagram concerning the femur (Fig. 7) a partial overlap is shown between subadults of FM1 and FM2 and adults of FM4. These bones also indicate the smaller dimensions of the FM4 bears.

Discussion.

The morphometric analysis of fossil remains has revealed some interesting morphological aspects requiring discussion.

Morphological features of FM4 mandibles have pointed out a strengthened structure, in spite of their general small size. The strengthening occurs in order to support the concentrated mechanical stress due to chopping great amount of food (Torres 1988). It is strictly related to a more vegetarian diet which requires a continuos nourishment. According to Torres, mandibles modifications due to changes in diet are evident not only in the vertical development of mandible, that is the height of the horizontal ramus, but also in the transversal one at the correspondence of the chopping area of cheek dentition (Crusafont & Truyols 1957). On the base of Torres' arguments we can compare mandibles from the three fossil assemblages studied from Fontana Marella. The main differences lyes in the horizontal ramus height, whereas transversal strengthening related to the width of teeth masticatory surface is not highlighted. Although the observed differences are slight, we consider them meaningful as they occurred in all the mandibles. Furthermore, we are comparing individuals of the same species, hence differences are less pronounced than among different species as shown by Torres (1988).

The narrower masticatory surface, showed in the teeth diagrams (Fig. 5 and 6), for P_4, M_2, and M^1 from the uppermost two assemblages, also argues for a change in diet from FM4 to FM2 and FM1 bears. Mandible morphology features and wider masticatory surface in FM4 cave bears suggest a strictly vegetarian nourishment, as is typical for *Ursus spelaeus*, while cave bears from FM1 and FM2 seem to be more omnivorous, that is their diet may have included a greater amount of meat and fish.

The observed differences in the postcranial skeleton suggest an increase in body size from FM4 to FM2 and FM1. Body size of a mammal is affected by a number of ecological factors, including climate, food availability, population density, the colonisation of new habitats and interspecific competition (Weinstock 1997).

The best-known principle for size change in mammals is Bergmann's rule (1847). It argued that body size is related to thermoregulatory advantages: heat loss in larger body is less due to the lower surface to volume ratio (Boyce 1978). So larger races would be distributed in cooler regions.

Kurtén (1965) pointed out that changes in size have been observed in a number of mammals during Pleistocene cold-warm oscillations, among them brown bear. According to Kurtén, Bergmann's rule is one of the possible explanations for these variations in size, even if the applicability of this principle does not avoid problems and requires other factors being equal.

The Grotta Sopra Fontana Marella deposit enabled to compare fossil cave bears living in the same home-ranges during different time intervals. Differences in the environment are concerned above all with climatic conditions and vegetation. We could exclude any effect of home-range altitude, as it has been supposed for dwarfing races (Kurtén 1955, 1965). Criticisms to Bergmann's rule have been moved by several authors (Scholander 1955; 1956; Geist 1987; Boyce 1978) arguing that larger body requires more food and in a cool environment this could be a disadvantage. Boyce (1978) said over again that "the length of time that an individual can survive without food is positively correlated with body weight (Morrison 1960)". According to this last observation a larger size for cave bears could mean enhanced survival during winter hibernation lasting much longer in a colder period.

Therefore, climatic change over time provides a more likely explanation in the case of the Grotta Sopra Fontana Marella.

Conclusion.

This deposit is important in Northern Italy for the good preservation of cave bear fossil remains, the performed excavations systematic approach and the results of interdisciplinary studies.

In the level FM4 we have unearthed 782 finds of *Ursus spelaeus*, corresponding to 23 individuals (M.N.I.); instead in the levels FM2 and FM1 we collected respectively 590 and 1330 cave bear remains, amounting to 76 M.N.I.

The Grotta Sopra Fontana Marella cave was used by bears for winter refuge, and inhabited in different ages: three fossiliferous units with *Ursus spelaeus* remains have been distinguished. Two of them (FM1 and FM2) have been dated about 22,000 years BP (26,000 cal BP), the third one (FM4), though not dated directly, is clearly older as suggested by its stratigraphical position and the amino acid racemization performed on fossil remains from all the three fossiliferous units. The FM1 and FM2 ages are important because near to the extinction of *Ursus spelaeus* and to the last maximum expansion of glaciers in the Italian Alps.

In spite of the reduced inhabitation surface of the cave, it was used by adults of both sexes during all these three time intervals. Sexual dimorphism and sex distribution studies indeed indicate the presence of bears of both sexes, although in different percentages. So the Grotta Sopra Fontana Marella cave was not occupied preferentially by females with their cubs, as the small caves were used to be (Kurtén 1958, 1972).

The observed size differences in skeletal elements from the three fossil levels testify actual differences in body size of cave bears belonging to the three populations. Bears from FM4 are distinctly smaller. As discussed, a great amount of females (85%) seems to be present in FM4, but the lower male percentage is not the only reason for the body size differences mentioned above. In fact in all three assemblages we have cubs, youngs and adults of both sexes, and above all the females from FM4 are smaller than the females from FM1 and FM2 too. This is clearly shown by the long bones graphs.

As supported by the Bergmann's rule (1847), this body size increase could represent an adaptive response to a climatic change occurring between these time intervals (Kurtén 1965, 1976): the smaller bears from FM4 lived in a warmer climate than the bears of the uppermost two levels.

Radiocarbon dating on fossil bones collected in these levels gave an age of nearly 22,000 years ^{14}C BP: this is a cold period as it corresponds to the approaching last maximum advance of glaciers about 18-20,000 years ^{14}C BP (Orombelli 1997). The Grotta Sopra Fontana Marella cave was used as a shelter from winter also in this period as it was located above the elevation limit reached by glaciers during the last maximum expansion (Uggeri et al. 1991; Bini et al. 1997).

The lower level may correspond to a warmer period as also suggested by the associated small mammals. Hence, glirids are dominant and murids suggest great wood extension along the slopes, while voles, typical for alpine grasslands, indicate that this habitat was present on top of the massif. Instead, in the upper levels (FM1 and FM2) cold (*Chionomys nivalis* (Martins, 1842)) and open (*Microtus agrestis* and *Microtus arvalis*) environmental micromammals, in addition to some *Marmota marmota* remains, have been found. They can be related to an environment devoid of trees and the most part of the mountain was covered by herb vegetation above tree limit.

The finding of a great amount of bones with punctures (Binford 1981), due to cave bears' behaviour (Tintori & Zanalda 1992), should also be related to a harsh paleoenvironment. During the last maximum expansion of glaciers, wintertime and thus hibernation span were likely prolonged. Mortality was higher than usually and at the end of their hibernation, exhausted bears could feed on dying or dead individuals. This hypothesis is supported also by the morphological and biometric differences on mandibles and molar teeth: FM2 and FM1 mandibles are less suitable for a prolonged chewing as they are not enough sturdy and at the same time cheek dentitions have narrow masticato-

TAB. 1

	FM1	FM2	FM2bis	FM4	Total
Skull	124	46	10	54	234
Mandible	50	23	2	22	97
$I_1 - I_2 - I_3$	24	7	0	12	43
$I^1 - I^2 - I^3$	49	21	6	28	104
C	80	20	4	35	139
P_4	23	8	2	12	45
P^4	23	14	5	16	58
M_1	41	13	4	20	78
M_2	41	12	1	21	75
M_3	31	12	2	20	65
M^1	30	21	12	17	80
M^2	37	16	8	18	79
Atlas	11	2	0	9	22
Axis	7	4	0	4	15
Other cervical vertebrae	12	11	1	17	41
Thoracic vertebrae	50	17	1	19	87
Lumbar vertebrae	11	13	0	13	37
Caudal vertebrae	6	4	0	7	17
Sacral vertebrae	16	4	0	5	25
Undeterminated vertebrae	9	2	0	30	41
Sternum	4	5	1	3	13
Ribs	59	35	11	63	168
Scapula	24	15	1	16	56
Humerus	43	11	4	26	84
Radius	39	10	1	20	70
Ulna	39	13	2	24	78
Scaphoid (radial carpal)	7	6	1	7	21
Pyramidal (ulnar carpal)	8	3	1	7	19
Pisiform (accessory carpal)	8	2	1	8	19
Uncinate (fourth carpal)	8	4	0	8	20
Magnum (third carpal)	3	3	0	2	8
Trapezoid (second carpal)	3	5	0	3	11
Trapezium (first carpal)	2	2	2	5	11
First metacarpal	5	2	1	3	11
Second metacarpal	4	5	2	6	17
Third metacarpal	10	4	0	14	28
Fourth metacarpal	9	3	0	10	22
Fifth metacarpal	8	4	2	10	24
Baculum	7	5	4	6	22
Pelvis	30	13	2	33	78
Femur	51	10	3	25	89
Patella	5	7	0	2	14
Tibia	42	15	1	22	80
Perone	9	5	2	4	20
Astragalus	11	7	0	8	26
Calcaneum	17	4	0	12	33
Navicular	6	6	0	7	19
First cuneiform (first tarsal)	6	0	0	1	7
Second cuneiform(second tarsal)	0	0	1	3	4
Third cuneiform (third tarsal)	4	2	0	3	9
Cuboid (fourth tarsal)	4	7	1	6	18
First metatarsal	4	7	0	8	19
Second metatarsal	7	5	1	8	21
Third metatarsal	8	8	1	6	23
Fourth metatarsal	10	3	0	11	24
Fifth metatarsal	17	3	2	10	32
First phalanx	68	46	1	58	173
Second phalanx	30	20	3	26	79
Third phalanx	40	17	4	28	89
Os sesamoide	26	18	0	23	67

TAB. 4

	FM1					FM2					FM2bis					FM4				
	n	min	max	X	s.d.	n	min	max	X	s.d.	n	min	max	X	s.d.	n	min	max	X	s.d.
1	18	1,17	1,84	1,51	0,15	8	1,40	1,80	1,63	0,15	2	1,50	1,50	1,50	0,00	16	1,25	1,69	1,48	0,11
2	16	0,90	1,14	1,03	0,07	5	0,84	1,67	1,09	0,30	2	0,99	1,08	1,04	0,05	13	0,90	1,20	1,04	0,09
3	13	0,82	1,10	1,00	0,07	3	0,92	1,03	0,98	0,05	2	1,00	1,00	1,00	0,00	12	0,83	1,12	1,00	0,08
4	15	0,48	0,80	0,62	0,07	4	0,44	0,58	0,51	0,05	2	0,65	0,69	0,67	0,02	12	0,47	0,72	0,61	0,08
5	15	60,64	76,92	67,98	4,58	5	59,87	101,21	70,05	16,00	2	66,00	72,00	69,00	3,00	13	64,93	78,94	70,40	4,28
6	13	52,90	79,48	65,89	6,72	3	57,55	65,71	61,89	3,35	2	66,66	66,66	66,66	0,00	12	58,58	76,29	67,06	4,61
7	14	35,29	52,30	41,96	5,34	4	28,48	37,86	32,87	3,43	2	43,33	46,00	44,67	1,34	12	32,33	48,64	41,79	4,96

TAB. 5

	FM1					FM2					FM2bis					FM4				
	n	min	max	X	s.d.	n	min	max	X	s.d.	n	min	max	X	s.d.	n	min	max	X	s.d.
1	13	1,78	2,14	1,95	0,13	10	1,38	2,12	1,88	0,21	4	1,77	2,02	1,92	0,09	15	1,75	2,11	1,93	0,11
2	15	1,25	1,70	1,45	0,14	5	1,40	1,57	1,46	0,06	6	1,23	1,55	1,39	0,12	13	1,27	1,55	1,40	0,10
3	13	1,01	1,38	1,19	0,10	2	1,19	1,25	1,22	0,03	3	1,00	1,12	1,06	0,05	11	1,07	1,26	1,17	0,06
4	14	0,86	1,08	0,96	0,07	5	0,80	1,02	0,94	0,07	6	0,82	1,03	0,92	0,07	11	0,85	1,06	0,95	0,07
5	15	0,69	0,91	0,81	0,06	2	0,79	0,92	0,86	0,07						10	0,62	0,91	0,79	0,09
6	13	0,58	0,80	0,73	0,05	2	0,69	0,75	0,72	0,03	4	0,66	0,76	0,70	0,04	11	0,61	0,80	0,71	0,06
7	13	69,15	80,86	72,66	3,71	5	66,04	91,28	75,04	8,68	4	76,14	76,73	76,36	0,22	12	66,67	77,89	71,46	2,86
8	12	56,74	66,11	60,62	3,06	2	58,96	60,71	59,84	0,88	1	58,94	58,94	58,94		10	55,71	65,14	60,19	3,07
9	12	43,96	53,93	48,86	2,61	5	45,19	50,51	47,76	1,81	4	47,36	52,28	49,57	1.76	10	42,85	53,03	48,65	2,74
10	13	36,71	46,06	41,51	2,67	2	37,26	46,94	42,10	4.84						10	33,15	45,78	40,98	3,53

Tab. 1. List of cave bear skeletric elements and number of remains recovered from each level.

Tab. 2. Mandible (all the measures are taken on the lingual side): 1) Length from the condyle process (median point on the aboral border of the condyle process) to Infradentale; 2) Length from the angular process to Infradentale; 3) Length from the indentation between the condyle process and the angular process to Infradentale; 4) Length from the condyle process to the aboral border of the canine alveolus; 5) Length from the indentation between the condyle process and the angular process to the aboral border of the canine alveolus; 6) Length from the angular process to the aboral border of the canine alveolus; 7) Length from the aboral border of the M$_3$ alveolus to the aboral border of the canine alveolus; 8) Length of the cheektooth row, P$_4$-M$_3$, measured along the alveoli; 9) Length of the molar row, measured along the alveoli; 10) Length of the diastema (from the aboral border of the canine alveolus to the oral border of the P$_4$ alveolus); 11) Height of the mandible at the median point of P$_4$; 12) Height of the mandible at the median point of M$_1$ (in the middle of the tooth); 13) Height of the mandible at median point of M$_3$ (in the middle of the tooth); 14) Thickness of the mandible between P$_4$ and M$_1$; 15) Thickness of the mandible between M$_2$ and M$_3$; 16) Transverse diameter of the condyle process; 17) Vertical diameter of the condyle process; 18) Height of the vertical ramus (total height of the mandible); 19) 10/1 %; 20) 11/1 %; 21) 12/1 %; 22) 11/12 %; 23) 15/1 %; 24) 7/1 %; 25) 9/1 % ; 26) 16/17 %; 27) Total length of P4; 28) Total length of M$_1$; 29) Total length of M$_2$; 30) Total length of M$_3$; 31) Transverse diameter of the canine; 32) 12/18 %.

Tab. 3. Skull: 1) Total antero-posterior length: Akrokranion - Prosthion; 2) Condylobasal length: aboral border of the occipital condyles - Prosthion; 3) Basal length: Basion - Prosthion; 4) Length sopraorbital apophysis - occipital: Ectorbitale - Akrokranion; 5) Median palatal length: Prosthion - Straphylion; 6) Upper neurocranium length: Akrokranion - Frontal midpoint; 7) Viscerocranium length: Nasion-Prosthion; 8) Facial length: Frontal midpoint - Prosthion; 9) Greatest length of the nasals: Nasion - Rhinion; 10) Length: oral border of the orbits (Median) - Prosthion; 11) Length of cheektooth row: oral border of canine alveolus - aboral border of M^2 alveolus; 12) Length: aboral border of canine alveolus - aboral border of M^2 alveolus; 13) Length: oral border of P^4 alveolus - aboral border of M^2 alveolus; measured on the buccal side; 14) Length of molar row: oral border of M^1 alveolus - aboral border of M^2 alveolus; measured on the buccal side; 15) Greatest mastoid breadth (greatest breadth of the occipital triangle): Otion - Otion; 16) Greatest breadth of the occipital condyles; 17) Greatest breadth of the bases of the paraoccipital processes; 18) Greatest breadth of the foramen magnum; 19) Height of the foramen magnum; 20) Greatest neurocranium breadth: Euryon - Euryon; 21) Zygomatic breadth: Zygion - Zygion; 22) Least breadth at the postorbital constriction; 23) Frontale breadth at the sopraorbital apophysis: Ectorbitale - Ectorbitale; 24) Least breadth between the orbits, orbital constriction at the lower inner corner.; 25) Greatest palatal breadth: measured across the outer borders of the M^2 alveoli; 26) Least palatal breadth: measured behind the canines; 27) Palatal breadth: measured across the outer borders of the canines alveoli; 28) Greatest inner height of the orbit; 29) Skull height: measured from the basioccipital to the highest elevation of the sagittal crest; 30) Skull height without the sagittal crest; 31) Height of the occipital triangle: Akrokranion - Basion.

Tab. 4. Fourth Lower Premolar: 1) Greatest length; 2) Greatest breadth; 3) Height of protoconid; 4) Height of paraconid (highest cusp); 5) 2/1%; 6) 3/1%; 7) 4/1%.

Tab. 5. Fourth Upper Premolar: 1) Greatest length; 2) Greatest breadth; 3) Height of paracone; 4) Height of metacone; 5) Height of deuterocone; 6) Distance between paracone and metacone; 7) 2/1%; 8) 3/1%; 9) 4/1%; 10) 5/1%.

TAB. 2

	FM1					FM2					FM2bis					FM4				
	n	min	max	X	s.d.	n	min	max	X	s.d.	n	min	max	X	s.d.	n	min	max	X	s.d.
1	1	33,60				4	29,00	35,50	33,13	2,46	0					5	27,45	31,00	29,25	1,39
2	0					0					0					2	27,55	27,57	27,56	0,01
3	1	23,55				2	26,00	26,70	26,35	0,35	0					4	24,06	26,80	25,88	1,12
4	1	26,85				1	25,40	25,40	25,40	0,00	0					2	25,40	25,50	25,45	0,05
5	3	20,80	26,00	23,67	2,16	3	23,05	23,55	23,30	0,20	0					4	21,00	24,45	23,30	1,35
6	1	25,92				0					0					3	24,57	26,65	25,31	0,95
7	3	14,46	15,30	14,76	0,38	5	14,72	18,00	16,34	1,42	0					6	13,55	15,98	15,10	0,74
8	4	9,98	11,78	10,65	0,72	7	9,95	11,65	10,55	0,61	0					7	9,30	10,00	9,81	0,23
9	4	6,01	9,97	8,18	1,41	7	8,30	9,80	8,84	0,50	0					5	8,19	8,40	8,31	0,08
10	9	2,60	5,64	4,05	1,16	4	2,90	5,30	4,35	0,92	1	2,44				5	3,85	5,93	5,17	0,70
11	12	2,90	6,77	5,13	1,12	6	4,50	7,76	6,24	1,08	1	4,69				7	5,30	6,36	5.91	0,44
12	14	2,83	7,12	4,88	1,26	7	4,30	7,39	5,89	1,10	2	3,22	4,33	3,78	0,55	7	5,52	6,50	6,07	0,30
13	5	4,74	7,78	5,86	1,09	6	4,12	7,50	6,29	1,24	1	3,80				6	5,12	6,78	6,25	0,56
14	17	1,34	2,66	1,90	0,36	8	1,60	2,60	2,09	0,39	1	1,67				7	1,80	2,12	1,92	0,09
15	13	2,14	3,40	2,52	0,33	10	2,36	3,79	2,76	0,46	1	2,40				8	2,25	2,86	2,49	0,18
16	1	6,80				2	7,10	8,04	7,57	0,47	0					0				
17	5	2,35	3,01	2,79	0,25	4	2,53	3,05	2,82	0,19	0					7	2,39	2,81	2,65	0,16
18	2	15,85	17,20	16,53	0,68	3	17,50	18,12	17,87	0,27	0					2	14,70	15,50	15,10	0,40
19	1	16,78				4	14,62	21,86	17,97	2,98	0					3	18,56	19,28	18,93	0,29
20	1	20,15				4	19,85	20,82	20,42	0,42	0					4	19,30	21,19	20,41	0,69
21	1	21,19				4	19,85	20,81	20,41	0,39	0					4	20,16	21,92	21,15	0,67
22	12	90,22	107,44	99,21	4,29	5	97,19	105,01	100,46	3,08	1	108,31				7	89,52	102,60	97,33	4,75
23	1	10,12				4	8,34	11,15	9,44	1,06	0					5	8,19	9,30	8,64	0,39
24	0					4	47,65	52,94	50,44	1,88	0					4	49,45	53,71	52,11	1,66
25	0					4	25,55	29,03	27,57	1,44	0					3	26,63	29,42	27,65	1,26
26	0					2	20,88	22,65	21,77	0,88	0					0				
27	7	1,17	1,69	1,46	0,15	7	1,40	1,80	1,66	0,13	0					8	1,25	3,07	1,60	0,56
28	7	2,60	3,21	2,94	0,21	3	2,91	3,05	2,99	0,06	0					6	2,67	2,93	2,80	0,10
29	10	2,67	3,54	3,01	0,27	3	2,93	3,30	3,13	0,15	1	3,20				6	2,62	2,95	2,82	0,11
30	5	1,78	2,65	2,44	0,33	4	2,66	3,17	2,82	0,21	1	2,95				5	1,64	3,10	2,52	0,48
31	5	1,55	2,27	1,93	0,25	4	2,06	2,48	2,32	0,16	0					8	1,55	1,70	1,64	0,05
32	2	39,43	40,05	39,74	0,31	3	37,50	40,28	39,03	1,15						2	40,00	42,58	41,29	1,29

TAB. 3

	FM1					FM2					FM2bis					FM4				
	n	min	max	X	s.d.	n	min	max	X	s.d.	n	min	max	X	s.d.	n	min	max	X	s.d.
1	1	44,70				1	47,00				2	39,70	43,20	41,45	1,75	1	37,19	37,19	37,19	
2	1	43,50				0					1	40,20				1	36,40			
3	1	40,00				1	41,00				0					1	34,40			
4	5	12,60	28,00	18,99	6,50	6	17,70	26,10	21,25	2,96	2	20,90	23,20	22,05	1,15	3	12,27	19,47	15,16	3,11
5	0					1	24,15				0					1	19,69			
6	0					0					0					2	11,83	16,74	14,29	2,45
7	1	22,40				0					2	18,50	19,90	19,20	0,70	1	17,10			
8	1	23,40				0					2	20,30	22,70	21,50	1,20	1	22,20			
9	0					0					0					1	12,78			
10	1	16,00				0					0					1	14,29			
11	1	17,30				0					1	15,82				1	14,14			
12	0					1	14,07				0					1	11,40			
13	4	8,05	10,15	8,84	0,85	4	8,78	9,74	9,23	0,44	1	8,40				2	8,12	8,63	8,38	0,25
14	5	6,54	8,05	7,28	0,62	2	7,64	7,94	7,79	0,15	2	6,70	6,76	6,73	0,03	2	6,07	7,11	6,59	0,52
15	0					0					1	19,00				3	10,20	16,00	12,65	2,45
16	0					3	7,50	8,52	8,14	0,46	0					1	7,28	7,28	7,28	0,00
17	2	12,20	13,80	13,00	0,80	3	12,90	21,80	17,90	3,72	0					1	8,76			
18	1	4,07				3	3,65	3,90	3,75	0,11	0					1	3,10			
19	1	3,27				0					0					1	1,90			
20	6	9,30	12,04	10,46	0,84	5	10,00	11,90	11,05	0,76	2	10,62	10,94	10,78	0,16	3	9,78	10,48	10,10	0,29
21	1	29,10				0					0					0				
22	1	8,30				1	8,40				2	7,10	7,35	7,23	0,13	3	6,57	7,95	7,27	0,56
23	4	7,10	9,60	8,30	1,20	3	9,84	14,00	11,29	1,92	2	10,09	11,42	10,76	0,67	3	6,73	9,90	8,33	1,29
24	5	6,35	10,04	7,43	1,33	4	6,95	10,36	8,25	1,28	2	8,62	9,43	9,03	0,41	2	6,20	8,13	7,17	0,97
25	1	11,13				0					2	10,31	10,75	10,53	0,22	1	9,16			
26	1	8,10				1	8,70				0					1	6,30			
27	0					0					0					0				
28	1	5,90				0					0					1	5,65			
29	1	15,20				0					0					2	8,67	10,71	9,69	1,02
30	1	10,80				0					0					2	7,93	9,48	8,71	0,78
31	1	11,97				0					0					2	7,67	9,73	8,70	1,03

TAB. 6

	FM1					FM2					FM2 bis					FM4				
	n	min	max	X	s.d.	n	min	max	X	s.d.	n	min	max	X	s.d.	n	min	max	X	s.d.
1	30	2,77	3,33	3,03	0,14	10	2,70	3,18	2,95	0,13	4	2,80	3,03	2,92	0,09	18	2,67	3,26	2,98	0,16
2	27	1,48	1,97	1,79	0,12	9	1,57	1,94	1,73	0,13	4	1,75	1,87	1,81	0,04	16	1,68	2,01	1,83	0,08
3	31	0,97	1,46	1,22	0,11	10	1,06	1,40	1,17	0,09	4	1,00	1,21	1,12	0,08	16	1,00	1,46	1,17	0,11
4	26	1,02	1,29	1,16	0,08	10	1,05	1,37	1,17	0,09	4	1,12	1,27	1,19	0,06	16	1,10	1,34	1,21	0,08
5	30	1,26	1,66	1,43	0,10	10	1,28	1,53	1,37	0,08	4	1,35	1,52	1,43	0,06	16	1,30	1,60	1,46	0,07
6	31	0,99	1,27	1,09	0,07	10	1,00	1,20	1,09	0,06	4	1,05	1,18	1,11	0,05	16	1,07	1,26	1,16	0,05
7	24	0,80	1,10	0,95	0,08	7	0,68	0,97	0,85	0,11	4	0,83	0,95	0,89	0,05	11	0,93	1,04	0,97	0,03
8	23	0,47	1,44	0,71	0,23	7	0,33	0,72	0,53	0,13	4	0,63	0,78	0,70	0,05	11	0,66	0,74	0,69	0,02
9	23	0,74	1,08	0,88	0,08	7	0,68	0,94	0,80	0,10	4	0,86	0,97	0,91	0,04	11	0,70	1,09	0,95	0,10
10	21	0,80	1,66	1,35	0,16	6	1,22	1,44	1,35	0,07	4	1,36	1,54	1,47	0,07	10	1,28	1,50	1,40	0,07
11	25	0,42	0,69	0,55	0,06	9	0,40	0,59	0,52	0,06	4	0,46	0,58	0,52	0,04	14	0,43	0,57	0,50	0,04
12	22	0,79	1,10	0,98	0,09	5	0,83	1,13	0,97	0,10	4	0,93	1,00	0,97	0,03	10	0,89	1,08	1,00	0,07
13	24	1,12	1,43	1,28	0,09	7	1,14	1,43	1,29	0,09	4	1,21	1,24	1,22	0,01	12	1,08	1,42	1,30	0,09
14	19	0,77	0,91	0,84	0,04	5	0,79	0,89	0,84	0,03	4	0,73	0,86	0,81	0,05	14	0,80	0,97	0,88	0,05
15	19	0,94	1,36	1,15	0,07	5	1,04	1,20	1,13	0,06	4	1,01	1,15	1,08	0,05	9	1,09	1,30	1,17	0,06
16	20	0,70	0,97	0,84	0,06	8	0,73	0,92	0,81	0,06	4	0,80	0,88	0,84	0,03	12	0,75	0,98	0,87	0,07
17	23	0,69	0,93	0,84	0,06	7	0,79	0,93	0,84	0,04	3	0,87	0,90	0,89	0,01	10	0,79	1,00	0,93	0,07
18	21	0,84	1,10	0,96	0,06	4	0,92	1,00	0,95	0,03	4	0,89	0,97	0,95	0,03	11	0,82	1,04	0,99	0,06
19	27	35,50	41,40	36,89	7,42	10	37,73	45,66	39,90	2,29	4	39,72	41,91	40,81	0,96	15	37,13	42,67	40,23	1,50
20	26	43,60	54,60	46,62	2,02	10	42,66	49,83	46,47	1,93	4	46,97	51,07	48,81	1,84	16	46,25	51,90	48,37	1,31
21	26	112,06	137,25	121,78	5,63	10	93,43	127,60	116,94	9,55	4	112,90	127,67	119,67	5,28	16	111,94	130,43	120,36	4,91
22	27	52,00	65,10	59,13	3,04	9	54,40	63,57	58,72	2,68	4	59,73	63,41	62,10	1,41	16	56,68	64,60	60,71	2,21
23	23	59,15	76,86	67,50	5,67	7	50,74	69,78	61,44	6,60	4	55,55	67,85	60,33	4,61	11	58,75	71,42	65,39	3,46
24	22	60,62	90,90	76,86	6,76	7	60,17	78,33	69,45	5,85	4	74,19	77,19	76,13	1,16	11	67,66	85,82	78,53	4,98

TAB. 7

	FM1					FM2					FM 2bis	FM4				
	n	min	max	X	s.d.	n	min	max	X	s.d.	n=1	n	min	max	X	s.d.
1	30	2,72	3,54	3,08	0,19	8	2,77	3,30	3,01	0,17	3,20	18	2,77	3,21	2,98	0,14
2	27	1,65	2,17	1,85	0,13	6	1,70	1,88	1,76	0,06	1,94	16	1,70	1,96	1,81	0,08
3	26	1,00	1,75	1,23	0,15	6	1,02	1,47	1,19	0,16	1,28	16	1,00	1,32	1,18	0,10
4	27	1,22	1,79	1,57	0,13	7	1,18	1,91	1,51	0,21	1,63	16	1,44	1,75	1,60	0,09
5	26	1,13	1,67	1,43	0,14	6	1,20	1,44	1,32	0,09	1,40	16	1,08	1,58	1,35	0,14
6	26	1,57	1,99	1,78	0,10	7	1,61	1,95	1,76	0,12	1,80	16	1,67	1,92	1,79	0,07
7	24	1,70	2,04	1,84	0,11	7	1,68	1,92	1,80	0,08	1,80	16	1,65	1,93	1,78	0,09
8	27	1,36	1,70	1,55	0,07	7	1,42	1,65	1,52	0,07	1,50	16	1,44	1,70	1,57	0,07
9	19	1,12	1,53	1,31	0,09	6	1,10	1,34	1,26	0,08	1,24	15	1,10	1,49	1,27	0,09
10	18	0,65	1,28	1,08	0,13	7	1,03	1,23	1,11	0,07	1,10	14	1,00	1,27	1,12	0,07
11	19	0,90	1,28	1,09	0,10	5	1,00	1,10	1,05	0,04	1,05	10	1,00	1,30	1,12	0,09
12	19	0,76	1,06	0,93	0,07	7	0,86	1,00	0,92	0,06	0,95	15	0,86	1,09	0,98	0,06
13	20	0,70	0,94	0,82	0,06	5	0,70	0,84	0,79	0,05	0,92	14	0,74	1,00	0,88	0,08
14	17	0,96	1,25	1,08	0,10	6	0,90	1,18	1,04	0,09	1,12	11	0,94	1,17	1,06	0,07
15	24	53,04	61,99	57,94	2,36	7	54,90	61,90	58,40	2,29	56,25	16	57,59	66,06	60,24	2,00
16	23	93,58	109,75	103,77	4,29	7	97,20	107,10	100,72	3,67	100,00	16	95,00	107,51	98,84	3,93
17	22	53,05	64,38	59,70	2,87	7	56,50	61,70	59,63	1,82	56,25	16	56,01	64,81	59,82	2,69
18	24	43,60	57,14	50,47	3,23	7	46,66	52,48	50,55	1,90	46,87	16	49,34	56,67	52,60	1,89
19	25	35,64	53,53	46,50	3,81	6	41,21	46,53	44,20	1,74	43,75	16	36,24	49,68	45,20	3,68
20	25	35,06	44,28	39,57	2,66	6	33,66	44,54	39,57	3,36	40,00	16	35,52	43,05	39,39	2,20
21	16	63,63	81,17	71,66	5,38	6	65,47	74,86	70,40	3,45	68,88	15	65,59	80,10	71,43	3,62
22	18	39,39	72,12	61,07	6,47	7	60,00	67,05	63,15	2,35	61,11	14	58,24	69,39	62,58	2,98
23	19	30,82	38,57	35,19	1,86	5	33,01	36,30	34,92	1,55	32,81	10	33,88	41,13	36,55	2,24

TAB. 8

	FM1					FM2					FM 2bis	FM4				
	n	min	max	X	s.d.	n	min	max	X	s.d.	n=1	n	min	max	X	s.d.
1	25	2,40	3,24	2,77	0,20	10	2,50	3,17	2,72	0,16	2,92	18	2,10	3,10	2,68	0,21
2	21	1,70	2,20	1,94	0,14	9	1,88	2,06	1,97	0,06	2,05	17	1,74	2,06	1,89	0,09
3	21	1,60	2,08	1,87	0,13	9	1,88	2,06	1,96	0,07	2,01	18	1,74	2,05	1,88	0,08
4	22	1,18	2,15	1,81	0,20	8	1,70	2,00	1,81	0,08	2,00	16	1,60	2,00	1,77	0,12
5	21	100,00	123,75	103,68	5,32	9	100,00	103,01	100,63	1,01	101,99	17	100,00	102,56	100,59	0,80
6	21	65,63	81,66	69,46	3,35	9	59,93	80,00	72,68	5,26	70,20	17	62,58	82,86	70,86	5,08
7	21	57,76	80,83	67,12	4,15	9	59,30	80,00	72,24	5,37	68,83	18	62,58	82,86	70,39	4,78

TAB. 9

	FM1					FM2					FM2bis					FM4				
	n	min	max	X	s.d.	n	min	max	X	s.d.	n	min	max	X	s.d.	n	min	max	X	s.d.
1	19	2,60	3,18	2,83	0,19	13	2,53	3,00	2,77	0,12	8	2,50	3,08	2,67	0,20	16	2,42	3,05	2,66	0,16
2	19	1,23	1,50	1,35	0,09	12	1,21	1,42	1,30	0,07	7	1,22	1,34	1,28	0,04	16	1,16	1,43	1,29	0,08
3	18	1,30	1,69	1,49	0,12	14	1,30	1,74	1,48	0,12	7	1,30	1,72	1,42	0,14	16	1,24	1,60	1,38	0,08
4	17	0,86	1,20	1,04	0,08	12	0,84	1,16	1,02	0,07	7	1,00	1,05	1,03	0,01	16	0,90	1,18	1,02	0,08
5	18	0,90	1,16	0,99	0,07	13	0,80	1,20	0,96	0,10	6	0,87	1,04	0,96	0,06	16	0,75	1,10	0,93	0,10
6	18	1,67	2,26	1,90	0,16	13	1,64	2,10	1,87	0,12	8	1,71	2,13	1,88	0,15	16	1,67	2,13	1,88	0,13
7	16	1,73	2,06	1,86	0,10	13	1,65	2,18	1,88	0,11	8	1,75	2,06	1,90	0,10	16	1,64	2,10	1,86	0,12
8	18	1,60	2,11	1,79	0,15	13	1,60	2,01	1,80	0,10	8	1,68	1,97	1,79	0,10	16	1,64	1,99	1,78	0,10
9	13	0,72	1,19	0,95	0,14	11	0,83	1,35	1,05	0,15	1	1,15	1,15	1,15	0,00	14	0,76	1,07	0,96	0,10
10	14	1,00	1,18	1,08	0,05	8	0,92	1,18	1,08	0,07	5	0,86	1,19	1,00	0,12	13	0,94	1,20	1,09	0,07
11	15	0,93	1,13	1,00	0,05	10	0,90	1,07	0,99	0,05	5	0,90	1,13	0,96	0,09	12	0,88	1,10	1,00	0,05
12	13	1,24	1,57	1,35	0,10	11	0,80	1,57	1,31	0,19	1	1,50	1,50	1,50	0,00	12	1,18	1,53	1,36	0,11
13	18	61,85	71,06	66,88	2,22	12	62,45	77,13	67,33	3,90	7	62,66	81,60	70,27	5,35	16	65,69	74,01	70,55	2,28
14	16	96,48	105,38	99,87	2,42	13	95,45	104,00	100,72	2,54	8	93,42	106,73	100,99	4,57	16	93,90	104,00	98,88	2,75
15	16	64,14	69,23	66,49	1,43	12	64,98	75,97	67,58	2,95	7	66,88	76,24	71,51	3,05	16	65,57	74,04	69,74	2,36
16	14	36,30	40,74	38,51	1,28	8	36,36	41,84	39,41	1,67	5	34,40	42,00	37,58	2,61	13	38,75	42,51	40,67	1,22
17	15	32,48	37,12	35,73	1,32	10	33,92	38,76	35,85	1,29	5	34,44	37,60	36,11	1,04	12	35,40	39,52	37,25	1,46
18	17	101,51	123,35	110,63	5,08	12	98,59	127,64	111,18	6,98	6	103,17	132,30	111,87	9,64	16	97,01	114,40	106,70	4,76
19	16	31,69	41,15	36,65	2,79	11	30,32	40,69	36,70	2,58	6	34,09	41,20	38,84	2,36	16	31,47	41,89	37,93	2,78

TAB. 10

	FM1					FM2					FM2bis					FM4				
	n	min	max	X	s.d.	n	min	max	X	s.d.	n	min	max	X	s.d.	n	min	max	X	s.d.
1	20	3,70	5,13	4,45	0,30	11	4,18	4,65	4,45	0,15	7	4,12	4,70	4,43	0,17	14	4,04	4,66	4,33	0,20
2	20	1,03	1,54	1,35	0,14	9	1,09	1,54	1,24	0,16	8	1,19	1,50	1,30	0,09	12	1,26	1,55	1,43	0,11
3	19	0,74	1,35	1,07	0,18	9	0,85	1,03	0,95	0,05	8	0,95	1,22	1,09	0,10	11	0,93	1,20	1,07	0,08
4	21	1,87	2,54	2,24	0,17	9	2,04	2,39	2,21	0,13	7	2,12	2,37	2,21	0,09	12	2,02	2,31	2,20	0,09
5	20	1,97	2,38	2,22	0,12	9	2,09	2,30	2,18	0,07	6	2,06	2,44	2,19	0,13	10	1,93	2,32	2,15	0,15
6	17	1,03	1,47	1,22	0,11	9	1,17	1,48	1,27	0,11	2	1,15	1,24	1,20	0,05	12	1,12	1,44	1,26	0,09
7	15	1,43	2,39	2,13	0,28	9	2,08	2,32	2,22	0,08	2	1,25	2,46	1,86	0,61	11	2,03	2,34	2,18	0,12
8	16	44,83	54,11	50,08	2,62	9	46,15	54,73	49,99	2,80	6	47,85	52,66	49,82	1,85	10	49,24	54,18	51,14	1,79
9	18	57,55	112,50	81,12	12,44	9	62,00	94,49	77,99	10,47	8	74,82	96,80	84,35	8,12	11	66,66	85,82	74,36	6,38

TAB. 11

	FM1					FM2					FM4				
	n	min	max	X	s.d.	n	min	max	X	s.d.	n	min	max	X	s.d.
1	1	43,00				1	43,50				3	34,00	38,80	36,10	2,00
2	1	9,50				2	7,90	9,50	8,70	0,80	4	7,23	8,90	8,11	0,66
3	1	11,00				1	11,53				2	8,73	9,23	8,98	0,25
4	1	8,30				2	6,44	7,32	6,88	0,44	3	5,76	8,75	6,96	1,29
5	1	8,88				0					2	6,52	7,10	6,81	0,29
6	23	1,69	5,64	2,66	0,80	10	1,20	5,70	3,01	1,47	18	1,78	4,37	2,96	0,86
7	1	13,03				1	12,75				5	9,86	11,51	10,68	0,70
8	1	9,30				1	9,20				6	6,80	8,18	7,51	0,51
9	1	7,77				1	7,70				5	5,93	6,80	6,32	0,33
10	1	8,02				1	7,80				1	5,62			
11	1	25,58				1	26,50				2	25,67	26,00	25,84	0,17
12	1	20,65				0					2	19,17	20,00	19,59	0,41
13	1	30,30				1	29,30				3	29,61	32,42	30,60	1,29
14	21	1,94	5,77	3,16	0,86	9	1,43	5,67	3,17	1,54	18	2,09	5,01	3,54	1,06

TAB. 12

	FM1					FM2					FM2bis					FM4				
	n	min	max	X	s.d.	n	min	max	X	s.d.	n	min	max	X	s.d.	n	min	max	X	s.d.
1	2	37,50	37,90	37,70	0,20	1	31,50				0					2	30,50	31,70	31,10	0,60
2	3	6,48	8,87	7,92	1,03	1	8,57				0					2	6,77	6,90	6,84	0,07
3	1	3,86				2	4,13	5,89	5,01	0,88	0					2	3,17	3,30	3,24	0,06
4	22	1,76	4,92	3,06	0,98	11	1,59	4,20	2,94	0,99	2	1,67	4,00	2,84	1,17	17	1,43	4,23	2,96	0,90
5	3	2,20	5,60	4,27	1,48	3	4,64	6,10	5,15	0,67	0					6	3,15	5,20	4,30	0,87
6	3	5,30	5,76	5,60	0,21	2	4,38	5,10	4,74	0,36	0					7	3,84	5,38	4,63	0,47
7	1	13,33				1	14,90				0					1	15,90	15,90	15,90	0,00
8	2	15,19	15,28	15,24	0,05	1	13,90				0					1	14,60	14,60	14,60	0,00
9	0					0					0					0				
10	21	1,30	3,80	2,32	0,82	11	1,09	3,20	2,10	0,78	2	1,10	2,50	1,80	0,70	17	1,05	3,06	2,01	0,58
11	2	5,30	5,35	5,33	0,03	1	5,25				0					2	4,03	4,42	4,23	0,20

TAB. 13

	FM1					FM2					FM4				
	n	min	max	X	s.d.	n	min	max	X	s.d.	n	min	max	X	s.d.
1	3	31,10	33,50	32,30	0,98	1	31,00				3	26,50	27,40	26,97	0,37
2	4	4,47	5,68	5,26	0,47	4	2,80	7,60	5,16	1,70	4	4,30	4,57	4,41	0,10
3	8	1,92	3,65	2,99	0,66	3	2,33	3,59	3,13	0,57	12	1,96	3,50	2,62	0,44
4	2	4,55	4,80	4,68	0,12	1	4,30				1	3,34			
5	26	1,15	3,77	2,11	0,74	7	1,38	3,74	2,33	0,82	12	1,32	3,17	2,16	0,72
6	3	7,30	7,94	7,65	0,26	1	7,83				7	1,03	6,38	4,99	1,80
7	4	4,05	5,45	4,85	0,51	1	5,20				7	3,90	7,55	4,82	1,36
8	3	16,50	17,60	17,13	0,46	1	17,25				3	16,22	16,67	16,40	0,20
9	3	10,74	11,30	11,10	0,25	1	11,58				3	10,94	11,10	11,02	0,07
10	2	14,32	14,63	14,48	0,15	1	13,87				1	12,40			
11	2	115,20	118,00	116,60	1,40	1	124,41				1	131,40			
12	3	10,60	12,12	11,15	0,69	1	12,06				2	10,43	10,70	10,57	0,14
13	2	23,70	24,75	24,23	0,52	1	25,25				2	21,82	22,80	22,31	0,49
14	2	15,75	16,26	16,01	0,25	1	16,77				2	14,44	15,09	14,77	0,32
15	3	145,68	157,41	149,70	5,46	1	150,57				3	153,77	160,70	157,56	2,87
16	25	0,85	2,75	1,57	0,59	7	0,97	2,25	1,49	0,43	11	0,90	2,12	1,51	0,46

TAB. 14

	FM1					FM2					FM2bis					FM4				
	n	min	max	X	s.d.	n	min	max	X	s.d.	n	min	max	X	s.d.	n	min	max	X	s.d.
1	3	43,70	46,60	45,07	1,19	1	43,80				0					1	38,20			
2	3	11,00	11,47	11,19	0,20	1	10,66				0					1	9,43			
3	4	3,27	8,49	6,95	2,14	1	7,60				0					5	1,85	6,90	4,89	2,05
4	3	12,50	14,05	13,26	0,63	1	13,20				0					1	9,80			
5	3	5,56	6,30	6,01	0,32	1	5,60				0					1	4,40			
6	3	10,22	10,73	10,51	0,22	1	10,24				1	8,17				2	8,40	9,08	8,74	0,34
7	23	0,80	5,11	2,87	1,06	6	2,00	4,50	3,03	0,89	2	1,69	3,55	2,62	0,93	15	1,67	4,10	2,87	0,79
8	2	9,34	10,58	9,96	0,62	1	9,60				0					2	8,15	8,24	8,20	0,04
9	3	26,80	31,29	29,45	1,92	1	30,10				0					1	25,65			
10	3	16,50	19,42	18,15	1,22	1	17,35				0					1	18,06			
11	3	10,11	11,38	10,76	0,52	1	10,27				0					1	10,05			
12	3	22,70	23,89	23,32	0,49	1	23,40				0					1	21,98			
13	2	21,37	23,56	22,47	1,10	1	21,90				0					1	21,33			
14	22	1,07	3,60	2,04	0,71	6	1,44	3,07	2,34	0,55	2	1,22	2,66	1,94	0,72	15	1,24	2,92	2,00	0,54

TAB. 15

	FM1					FM2					FM4				
	n	min	max	X	s.d.	n	min	max	X	s.d.	n	min	max	X	s.d.
1	1	30,20				3	30,10	30,60	30,30	0,22	1	26,10			
2	2	1,15	1,61	1,38	0,23	6	1,17	1,60	1,42	0,16	2	1,20	1,59	1,40	0,20
3	2	8,60	9,36	8,98	0,38	3	8,70	10,70	9,40	0,92	2	6,70	8,35	7,53	0,82
4	31	1,45	3,95	2,16	0,66	12	1,65	3,60	2,77	0,74	14	1,33	2,97	2,12	0,61
5	2	10,53	10,56	10,55	0,02	3	9,10	10,80	10,07	0,71	2	8,80	8,85	8,83	0,03
6	2	8,43	8,81	8,62	0,19	4	6,66	8,88	8,07	0,88	2	6,90	6,95	6,93	0,02
7	2	4,79	4,85	4,82	0,03	6	3,56	4,80	4,26	0,41	2	3,95	3,97	3,96	0,01
8	1	28,47				3	28,90	34,96	30,99	2,81	1	31,99			
9	1	34,80				3	29,74	35,76	33,23	2,55	1	33,90			
10	1	81,67				3	81,48	117,58	94,51	16,36	1	94,35			
11	1	27,90				2	29,06	29,40	29,23	0,17	1	26,62			
12	1	16,00				2	15,06	15,90	15,48	0,42	1	15,13			
13	31	1,47	4,02	2,23	0,74	12	1,60	4,20	2,86	0,93	13	1,24	3,10	2,23	0,68

Tab. 6. First Lower Molar: 1) Greatest length; 2) Length of trigonid, measured on the labial side; 3) Length of talonid, measured on the labial side; 4) Breadth of trigonid; 5) Breadth of talonid; 6) Breadth of central shrinking of tooth; 7) Distance between hypoconid and entoconid; 8) Distance between metaconid (the main cusp) and protoconid; 9) Distance between protoconid and paraconid; 10) Distance between protoconid and hypoconid; 11) Distance between anterior edge of teeth and sulcus divides protoconid and paraconid; 12) Distance between the major cusps of the protoconid and the oral border of the tooth; 13) Distance between the main cusps of the metaconid and the oral border of the tooth; 14) Height of paraconid; 15) Height of protoconid; 16) Height of metaconid; 17) Height of entoconid; 18) Height of hypoconid; 19) 4/1%; 20) 5/1%; 21) 5/4%; 22) 2/1%; 23) 7/5%; 24) 9/4%.

Tab. 7. Second Lower Molar: 1) Greatest length; 2) Length of trigonid, measured on labial side; 3) Length of talonid, measured on labial side; 4) Length of trigonid, measured on lingual side; 5) Lenght of talonid, measured on lingual side; 6) Breadth of trigonid; 7) Breadth of talonid; 8) Breadth of tooth at central shrinking; 9) Distance between hypoconid and entoconid (highest cusp); 10) Distance between metaconid (the major cusp) and protoconid; 11) Height of protoconid; 12) Height of metaconid (highest and central cusp); 13) Height of entoconid (the anterior cusp); 14) Height of hypoconid; 15) 6/1%; 16) 7/6%; 17) 7/1%; 18) 8/1%; 19) 5/1%; 20) 3/1%; 21) 9/7%; 22) 10/6%; 23) 11/1%.

Tab. 8. Third Lower Molar: 1) Greatest length; 2) Greatest breadth; 3) Breadth of anterior lobe; 4) Breadth of posterior lobe; 5) 2/3%; 6) 2/1%; 7) 3/1%.

Tab. 9. First Upper Molar: 1) Greatest length; 2) Length of anterior lobe (measured on labial side); 3) Length of posterior lobe (measured on labial side); 4) Length of paracone; 5) Length of metacone; 6) Breadth of anterior lobe; 7) Breadth of posterior lobe; 8) Breadth of tooth at central shrinking; 9) Distance between paracone and protocone; 10) Height of paracone; 11) Height of metacone; 12) Distance between protocone and hypocone; 13) 6/1%; 14) 7/6%; 15) 7/1%; 16) 10/1%; 17) 11/1%; 18) 3/2%; 19) 4/1%.

Tab. 10. Second Upper Molar: 1) Greatest length; 2) Lenght of paracone; 3) Length of metacone; 4) Breadth of anterior lobe; 5) Breadth of posterior lobe (measured at the first cusp of metacone); 6) Distance between paracone and protocone; 7) Distance between protocone and hypocone; 8) 4/1%; 9) 3/2%.

Tab. 11. Humerus: 1) Greatest length; 2) Greatest antero-posterior diameter of the humerus head (caput); 3) Greatest antero-posterior diameter of the proximal epifysis; 4) Greatest transverse diameter of the humerus head; 5) Greatest transversal diameter of the proximal epifysis; 6) Transversal diameter of the diaphysis; 7) Greatest transversal diameter of the distal epifysis; 8) Transversal diameter of the trochlea; 9) Greatest transversal diameter of the lower articular surface; 10) Length of the greater tuberosity; 11) 3/1 %; 12) 5/1 %; 13) 7/1 %; 14) Antero-posterior diameter of the diaphysis.

Tab. 12. Ulna: 1) Greatest length; 2) Greatest antero-posterior diameter of the olecranon; 3) Transversal diameter of the of the olecranon; 4) Antero-posterior diameter of the diaphysis; 5) Greatest diameter of the semilunare cavity; 6) Antero-posterior diameter of the distal epiphysis; 7) 5/1%; 8) 6/1%; 9) 2/1%; 10) transversal diameter of the diaphysis; 11) Greatest breadth of the proximal articular surface (including articular surface for radius and for humerus).

Tab. 13. Radius: 1) Greatest length; 2) Antero-posterior diameter of the proximal epiphysis; 3) Antero-posterior diameter of the neck of the radius; 4) Transversal diameter of the proximal epiphysis; 5) Antero-posterior diameter of the diaphysis (measured in the median point of the diaphysis); 6) Antero-posterior diameter of the distal epiphysis; 7) Transversal diameter of the distal epiphysis; 8) 2/1%; 9) 3/1%; 10) 4/1%; 11) 2/4%; 12) 5/1%; 13) 6/1%; 14) 7/1%; 15) 6/7%; 16) Transversal diameter of the diaphysis (measured in the median point of the diaphysis).

Tab. 14. Femur: 1) Greatest length; 2) Distance between greater and lesser trochanter; 3) Femur neck length; 4) Transversal diameter of the proximal end; 5) Transversal diameter of the head of femur; 6) Transversal diameter of the distal end; 7) Transversal diameter of the diaphysis (measured at half length); 8) Transversal diameter of the Condyli; 9) 4/1%; 10) 3/1%; 11) 7/1%; 12) 6/1%; 13) 8/1%; 14) Antero-posterior diameter of the diaphysis (measured at half length).

Tab. 15. Tibia: 1) Total length; 2) Distance between the tubercles of spina; 3) Antero-posterior diameter of the proximal extremity (including external tuberosity of tibia cresta); 4) Transversal diameter of the diaphysis (measured at half lenght); 5) Greatest transversal diameter of the proximal extremity; 6) Greatest transversal diameter of the distal extremity; 7) Antero-posterior diameter of the distal extremity; 8) 3/1%; 9) 5/1%; 10) 3/5%; 11) 6/1%; 12) 7/1%; 13) Antero-posterior diameter of the diaphysis (measured at half lenght).

ry surface that can be related to a general change in diet, less strictly vegetarian during a colder period. The shortage of vegetables due to rigorous climate led the cave bears from the uppermost levels to feed much more meat. In such a short feeding season, meat food assured the right nutritive requirement to survive during the long winter.

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REFERENCES

Airaghi C. (1927) - Elenco dei mammiferi fossili delle grotte lombarde - *Atti Soc. It. Sci. Nat.*, 66: 141-154, Pavia.

Bard E., Arnold N., Hamelin B., Tisnerat-Laborde N. & Cabioch G. (1998) - Radiocarbon Calibration by Means of Mass Spectometric 230Th/234U and 14C Ages of Corals: An Updated Database Including Samples from Barbados, Mururoa and Tahiti. *Radiocarbon* 40, 3: 1085-1092, New Haven.

Bergmann C. (1847) - Ueber die Verhaeltnisse der Waermeoekonomie der Thiere zu ihrer Groesse. *Goettinger Studien* 3, Pt. 1: 595-708, Goettinger.

Bini A., Uggeri A. & Quinif Y. (1997) - Datazioni U/Th effettuate in grotte delle Alpi (1986-1987). Considerazioni sull'evoluzione del carsismo e del paleoclima. *Geologia Insubrica* 2, 1: 31-58, Lugano.

Binford L.R. (1981) - Bones, ancient man and modern myths. 313 pp, *Academic Press Inc* New York..

Bokonyi S. (1970) - A new method for the determination of the number of individuals in animal bone material. *Am. Journ. Arch.* 74: 291-292, New York.

Boyce M.S. (1978) - Climatic variability and body size variation in Muskrats (Ondatra bzibethicus) of North America. *Oecologia* 36: 1-19 Berlin.

Capasso Barbato, L., M. R. Minieri, C. Petronio & A. Vigna Taglianti (1990) - Strutture dentarie di Ursus arctos e di Ursus spelaeus della grotta di Monte Cucco (Sigillo, Perugia, Italia). *Boll. Soc. Paleont. It.* 29 (3): 321-333, Modena.

Capasso Barbato L., Cerilli E. & Petronio C. (1993) - Differenze morfologiche e morfometriche nei crani di *Ursus spelaeus e Ursus arctos. Il Quaternario* 6 (1): 67-76, Verona.

Cuggiani M.C. (1981) - Studio biometrico sulle ossa lunghe della popolazione di *Ursus spelaeus* della Grotta di Equi (Toscana). *Boll. Serv. Geol. It.* 102: 173-198, Roma.

Crusafont Pairo' M. & Truyols Santonja J. (1957) - Estudios masterométricos en la evolucion de los Fisipedos. *Boletin Inst. Geol. y Min. Espana* 68: 85-224, Madrid.

Geist V. (1987) - Bergman's rule is invalid. *Can. Journ. Zool.* 65: 1035-1038, Ottawa.

Giacobini G. & D'errico F. (1985) - La fauna. In AA. VV. - La grotta preistorica della Basura. *Ist. Int. Studi Liguri* 4: 345-352, Bordighera.

Klein R.G. and Cruz-Uribe K. (1984) - The analysis of animal bones from archeological sites. *The University of Chicago Press*: 266 pp. Chicago.

Koby F.E. (1949a) - Le dimorphisme sexuel des canines d'Ursus spelaeus. C.R. Soc. Paleont. Suisse, *Ecl. Geol. Helv.* 42 (2): 490, Basel.

Koby F.E. (1949b) - Le dimorphisme sexuel des canines d'*Ursus arctos* et *d'Ursus spelaeus. Rev. Suisse Zool.* 56 (36): 675-687, Geneve.

Kurtén B. (1955) - Sex dimorphisme and size trends in the cave bear, *Ursus spelaeus* Rosenmüller and Heinroth. *Acta Zool. Fenn.* 90: 4-48, Helsinki.

Kurtén B. (1958) - Life and death of the Pleistocene cave bears. A study in paleoecology. *Acta Zool. Fenn.* 95: 4-59, Helsinki.

Kurtén B. (1965) - The Carnivora of the Palestine caves. *Acta Zool. Fenn.* 107: 1-74, Helsinki.

Kurtén B. (1972) - L'orso delle caverne. *Le Scienze* 46: 62-69, Milano.

Kurtén B. (1976) - The cave bear story. *Columbia University Press*, New York PP.

Krantz G.S. (1968) - A new method of counting mammal bones. *Am. Journ. Arch.*.72: 285-288, New York.

Leonardi P. (1951) - La Grotta del Broion nei Colli Berici (Vicenza). Nuova stazione preistorica con industria paleolitica gravettiana. *Riv. Sc. Preist.*, 6 (3-4): 141-150, Firenze.

Morrison P. (1960) - Some interrelations between weight and hibernation function. Proc. First International Symp. Mat. Mammalian Hibernation, *Bull. Mus. Comp. Zool.* 124: 75-91.

Orombelli G., 1997 - Recenti progressi nella valutazione del paleoclima: le variazioni climatiche negli ultimi 150.000 anni. in: *"Ist. Lomb. Sci. Lett.", Ciclo di lezioni 1995/1996 'La Terra nel Sistema Solare'*: 73-97.Milano.

Pasa A. (1953) - Primi risultati dell'indagine paleontologica sui materiali scavati nelle grotte di S. Cassiano (Colli Berici, Vicenza).*Ann. Univ. Ferrara*, sez. 9, 1 (6): 169-183, Ferrara.

Ravazzi C., Perego R. (1997) - Late Weichselian cave bear environment in Lombardian Pre-Alps as reconstructed by means of new pollen records from cave deposits. *Extended abstract, Proceedings del 1° Simposio Internazionale sull'Archeologia e la Paleontologia di grotta*, 12° Congresso Internazionale di Speleologia, 10-17 agosto 1997, La Chaux-de-Fonds (Neuchatel, Svizzera).

Reisinger C. & Hohenegger J. (1998) - Sexual dimorphism in limb bones of Late Pleistocene cave bear (*Ursus spelaeus, Carnivora, Mammalia*) from three caves in Eastern Alps (Austria and Italy). *Boll. Soc. Pal. It.* 37 (1): 99-116, Modena.

Rustichelli S. (1993) - Importanza delle collezioni museali per la conoscenza dei mammiferi pleistocenici. Studio morfometrico di una popolazione di *Ursus spelaeus. Museol. Sci.* 10 (3-4): 269-281, Milano.

Sala B. (1980) - Interpretazione crono-bio-stratigrafica dei depositi pleistocenici della Grotta del Broion (Vicenza). *Geogr. Fis. Dinam. Quat.*: 66-71,.

Scholander P.F: (1955) - Evolution of climatic adaptation in homeotherms. Evolution 9: 15-26, Lawrence KA.

Scholander P.F: (1956) - Climatic rules. *Evolution* 10: 39-40, Lawrence KA.

Sommaruga C. (1942) - Sulla presenza di manufatti preistorici nella grotta di Fontana Marella -2236 Lo (Varese). *Atti Soc. It. Sci. Nat.* 81: 28-41, Milano.

Tintori A., Bini A., Zanalda E., Felber M., Bianchi-Demicheli F. & Studer G. (1993) - Nota preliminare relativa ai primi scavi sistematici in grotte delle Prealpi Lombarde (Italia) e Ticinesi (Svizzera). *Abstract Symp.* ARGE ALP: L'orso delle caverne nelle Alpi, Coira (Svizzera), 18-19 Novembre 1993. Coira.

Tintori A., Perego R. & Zanalda E. (1995) - Paleoenvironmental analysis of Middle and Late Pleistocene mammalian faunas from caves in central southern Alps. *Poster IGCP-378 Circumalpine Quaternary Correlations*. INQUA International Congress, august 1995, Berlin.

Tintori A. & Zanalda E. (1992) - *Ursus spelaeus* dal Massiccio di Campo dei Fiori (VA): tracce di predazione. *Boll. Soc. Tic. Sci. Nat.* 80 (1): 97-103, Lugano.

Torres P.H. (1988) - Osos (Mammalia, Carnivora, Ursidae) del Pleistocene ibericos (*U. deningeri* Von Reichenau, *U. spelaeus* Rosenmuller-Heinroth, *U. arctos* Linneo). I Filogenia; Distribucion estratigrafica y geografica. Estudio anatomico y metrico del Craneo. *Boletin Geologico y minero*, 909: 3-46 Madrid.

Torres P.H. (1988) - Osos (Mammalia, Carnivora, Ursidae) del Pleistocene ibericos (*U. deningeri* Von Reichenau, *U. spelaeus* Rosenmuller-Heinroth, *U. arctos* Linneo). - II Estudio anatomico y metrico de la mandibula, hioides atlas y axis. *Boletin Geologico y minero*, 909: 220-249 Madrid.

Torres P.H. (1988) - Osos (Mammalia, Carnivora, Ursidae) del Pleistocene ibericos (*U. deningeri* Von Reichenau, *U. spelaeus* Rosenmuller-Heinroth, *U. arctos* Linneo). III Estudio anatomico y metrico del miembro toracico, carpo y metacarpo. *Boletin Geologico y minero*, 909: 356-412 Madrid.

Torres P.H. (1988) - Osos (Mammalia, Carnivora, Ursidae) del Pleistocene ibericos (*U. deningeri* Von Reichenau, *U. spelaeus* Rosenmuller-Heinroth, *U. arctos* Linneo). IV Estudio anatomico y metrico del miembro pelviano, tarso metatarsa y dedos. *Boletin Geologico y minero*, 909: 516-577 Madrid.

Torres P.H. (1988) - Osos (Mammalia, Carnivora, Ursidae) del Pleistocene ibericos (*U. deningeri* Von Reichenau, *U. spelaeus* Rosenmuller-Heinroth, *U. arctos* Linneo). V Dencicion decidual, formula dentaria y denticion superior. *Boletin Geologico y minero*, 909: 660-714 Madrid.

Torres P.H. (1988) - Osos (Mammalia, Carnivora, Ursidae) del Pleistocene ibericos (*U. deningeri* Von Reichenau, *U. spelaeus* Rosenmuller-Heinroth, *U. arctos* Linneo). VI Dencicion inferior. *Boletin Geologico y minero*, 909: 886-940 Madrid.

Uggeri A., Bini A. & Quinif Y. (1991). Contribution of isotope geochemistry to the study of climatic and environmental evolution of Monte Campo dei Fiori massif (Lombardy, Italy). *Speleochronos* 3: 17-28, Mons, Belgique.

Von der Driesch A. (1976) - A guide to the measurement of animal bones from archaelogical sites. *Peabody Mus. Bull.*, 1: 136 pp., Harvard.

Weinstock J. (1997) - The relationship between body size and environment: the case of Late Pleistocene reindeer (*Rangifer tarandus*). *Archaeofauna* 6: 123-135, Madrid.

Zanalda E. (1994b) - Middle-Late Pleistocene fauna from western Lombardy cave. *Neogene and Quaternary mammals of the Palaearctic*. May 1994: 17-21, Krakow, Poland.

Zanalda E. (1994a) - *Dinaromys bogdanovy* (Mammalia: Rodentia) from the Middle Pleistocene of western Lombardy (Italy). *Riv. It. Paleont. Strat.* 100: 143-148, Milano.

Zanalda E. (1994c). Variazioni nelle Associazioni a micromammiferi indicatrici dei cambiamenti climatico-ambientali dell'ultimo glaciale. Unpublished PhD Thesis, Università Studi Milano.

Zanalda E. & R. Perego (1994) - Studio dei mammiferi di un deposito fossilifero di Campo dei Fiori ed interpretazioni paleoambientali. *Riunione autunnale del Gruppo nazionale Geografia Fisica e Geomorfologia*. CNR, 3-7 ottobre 1994: 202-205, Varese.

Zanalda E., Tintori A. & Perego R. (1997) - Middle and Late Pleistocene Mammals from Insubrian Pre-Alps. *Geologia Insubrica*, 2 (2): 137-141.