

First morphometric data from the metapodial bones of *Ursus* from Cerè Cave (Venetia Region, North Italy)

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Summary

Numerous metapodial remains of bears from the Cerè Cave (Verona Province, Venetia Region, North Italy), are morphologically and morphometrically analysed here. Three species of *Ursus* are represented (*U. deningeri* Von Reichenau, 1904; *U. spelaeus* Rosenmüller-Heinroth, 1794 and *U. arctos* Linnaeus, 1758), but in different proportions, with the deningerian and speloid being more numerous than the arctoid forms. Two populations of *U. spelaeus* of different sizes are shown and this could reflect their different (geological) ages. In particular, the significant presence of deningerian fossils in the Cerè Cave, when compared to data from other caves in the Lombardy and Piedmont regions, could indicate a strong presence of these species solely for the Venetia region with very limited numbers in surrounding areas until we reach Central Italy. Lastly, the fossil findings in the Cerè Cave derive from more than one level of the Pleistocene and the presence of *U. deningeri* justifies the extension of the lower boundary to the Early Pleistocene.

Samenvatting

Een groot aantal overblijfselen van middenhands- en middenvoetsbeenderen van beren uit de Cerè grot (provincie Verona, regio Venetië, Noord-Italië) worden hier morfologisch en morfometrisch geanalyseerd. Drie soorten van *Ursus* zijn vertegenwoordigd (*U. deningeri* Von Reichenau, 1904; *U. spelaeus* Rosenmüller-Heinroth, 1794 en *U. arctos* Linnaeus, 1758), maar in verschillende verhoudingen, waarbij de twee eerste soorten meer talrijk zijn dan de laatste. Twee populaties van *U. spelaeus* van verschillende grootte worden aangetoond, hetgeen op een verschillende geologische ouderdom kan wijzen. *Ursus deningeri* komt in de Cere-grot veelvuldig voor, in vergelijking met andere grotten in de Lombardije en Piedmont. Dit wijst op een sterke aanwezigheid van deze soort in de regio Venetië; dit in tegenstelling met het gebied tot aan Midden-Italië, waar *U. deningeri* een veel zeldzamere verschijning was. Tenslotte, de fossiele vondsten in de Cerè grot zijn afkomstig van meer dan één niveau van het Pleistoceen en de aanwezigheid van *U. deningeri* rechtvaardigt de uitbreiding van de ondergrens tot het Vroeg Pleistoceen.

Introduction

Bear fossils from a number of caves in North Italy are a rich source of information to explain the behavioural and the evolutionary paths of this vertebrate. Caves in the Venetia Region, compared to those found in the nearby Lombardy and Piedmont regions, have particular value because they contain remains both of probable archaic and recent forms of *Ursus*. The Cerè Cave (Verona Province) (fig. 1) is the most significant from this point of view. Altogether these caves contain a great quantity of mammal fossils which "...sembrano rappresentare in realtà più momenti del Pleistocene" (Bon *et al.*, 1991: 189).

This work will confirm that different species of bears lived inside the Cerè Cave and indicate a possible evolutionary step through morphometric and morphological analyses of metapodial bones. The morphodynamic analyses of the teeth following the Rabeder's (1999) method is in progress, but the former data at least in this preliminary phase of the work, seem to present

a statistically significant low morphodynamic index.

Previous works

Studies on *U. spelaeus* fossils are the richest most numerous but they frequently concern the cranial and mandibular remains. We refer to the studies by Santi and Rossi (2001a) and Rossi and Santi (2001) for a more extensive review. We here list the main works that have emphasised on *Ursus* limb and metapodial bones.

Dubois and Stehlin (1933), Koby and Fritz (1950) analysed in particular metatarsial and phalange remains. Subsequently, Koby (1950), after studying different fossils, was able to re-assemble an anterior, almost complete paw (with only one missing uncinate) and compared it with that from the modern brown bear.

Many studies concerning the bones of the locomotor apparatus of these bears, focus on sexual dimorphism (i.e. Kurtén, 1955). In this regard

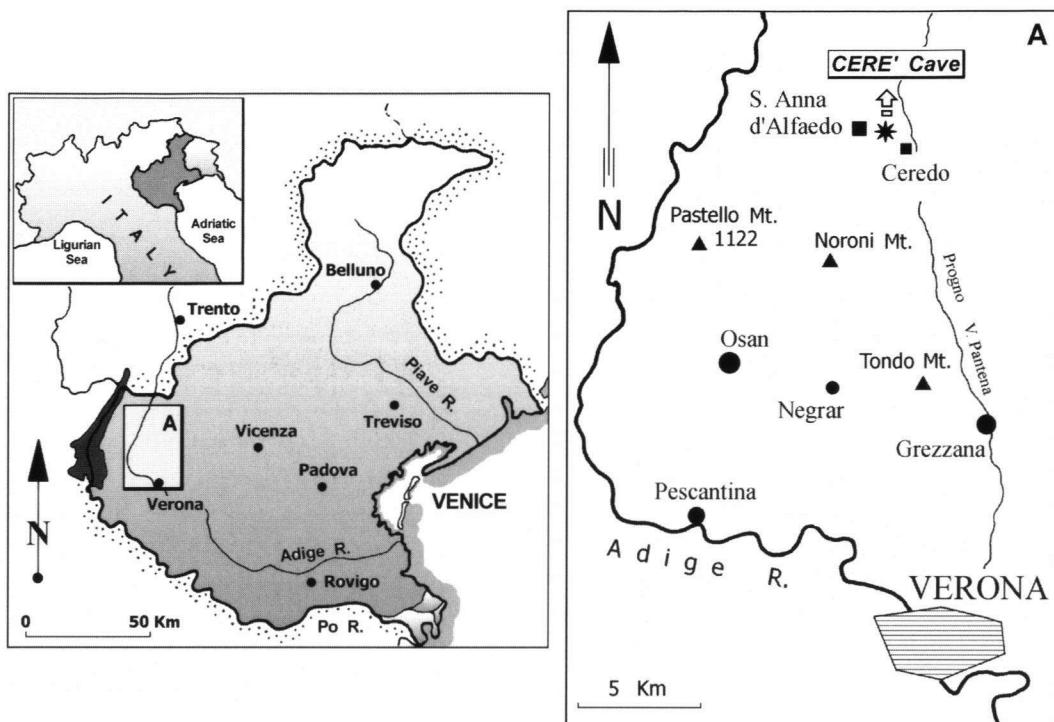


Fig 1 Geographic position of the Cerè Cave (Venetia Region, Northern Italy)

Geografische positie van de Cerè grot (regio Venetië, noord Italië)

Cuggiani's (1981) analysis of the long bones from Equi Cave (Tuscany Region) is worth noting. Recently, other interesting hypotheses concerning the sexual dimorphism were advanced by: Kunst (1992) through bivariate analysis using greatest distal metapodal length and width as variables; Grandal D'Anglade (1993, 2001), who indicated that this dimorphism does not equally affect the various bones of the skeleton and who noted a different degree of sexual dimorphism in separate populations; Rustichelli (1993) and, more in particular Reisinger & Hohenegger (1998), who proposed a sexual dimorphism hypothesis based on biometrical characters of the limb bones.

We again refer to research carried out by Torres (1988) and by Kunst (1996) which involved the biometrical analysis of femurs from Pleistocene bears in Europe. These authors discovered that this bone structure originally sought to provide static stability. Weinstock (1999) described the locomotor apparatus bones of bears from the material gathered in the Grosse Grotte (Blau-beuren, SW Germany). He compared their morpho-dimensional characteristics with fossils from other German caves (most of the remains

had dimensions correlating with juveniles), noting sexual differentiation. Using a mathematical model, Viranta (1994) highlighted some correlations between limb proportions and mass of cave bears and compared them to those from modern bears. The shafts were wider in cave bears' limbs and hence, their body mass was greater.

In the morpho-dimensional analysis of the remains from Arcy-sur-Cure (Yonne, France) Baryshnicov and David (2000) confronted the problem of classifying fossils of small dimensions with certainty. Argant (1991) and Bonifay (1975) described the different osteological remains of *Ursus* from Bourgogne and from Corrèze (France).

Di Canzio & Petronio (2001) studied the carpal, metacarpals, tarsal and metatarsal remains, most likely from a female, coming from Cola Cave (Aquila, Abruzzo Region, Central Italy). Lastly, Rossi and Santi (2001) preliminarily proposed a biometrical analysis of the long bones of the *Ursus* from the Buco dell'Orso Cave (Laglio, Como Province, Lombardy, Italy). Gerhard (2001) undertook a most detailed study on *Ursus* metapodial bones from Austrian caves

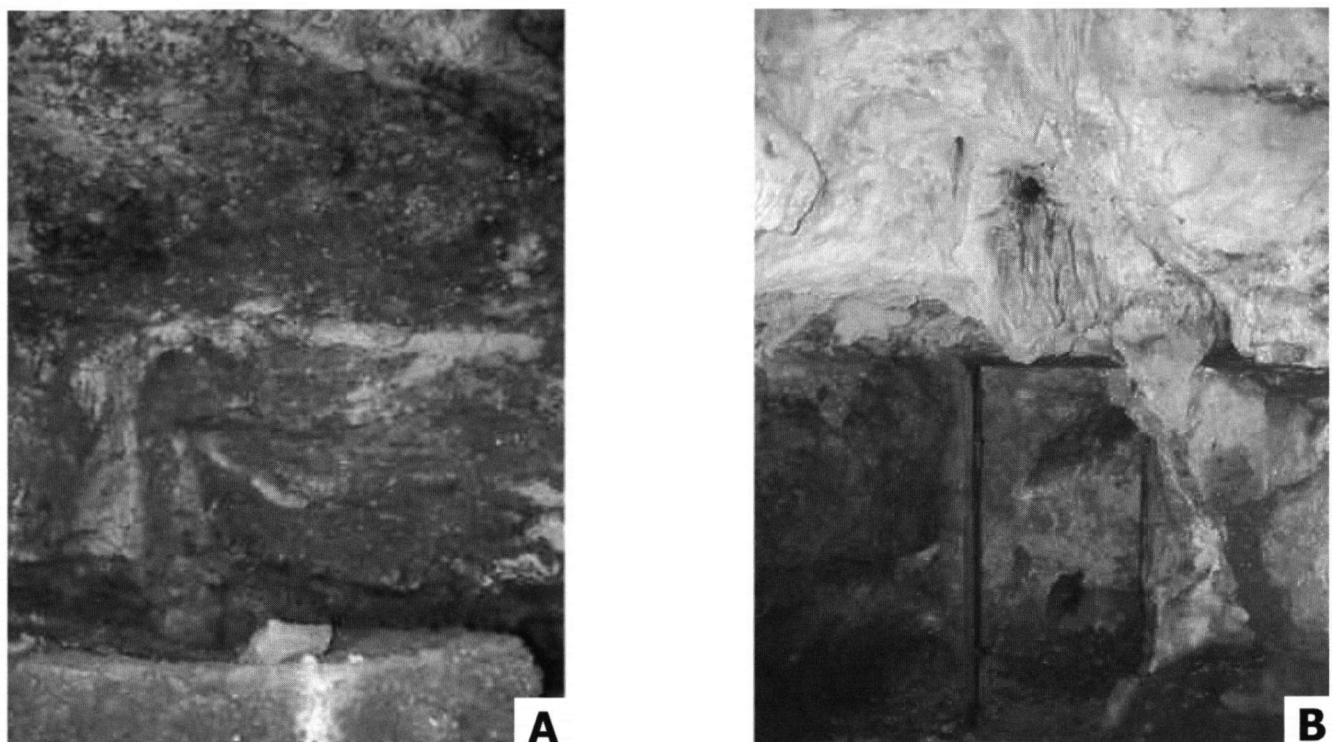


Fig 2 A – Lateral wall of the Cerè cave showing bone breccias. **B** – Entry of the Cerè Cave seen from within
A - Zijwand van de Cerè grot met bottenbreccie. B - ingang van de Cerè grot gezien van binnenuit

advancing an evolutionary hypothesis. Later, Germonpré and Sablin (2001) studied fossils from Goyet (Belgium). Santi *et al.* (2003) analysed metapodial remains from the Buco dell'Orso Cave. Jambrešić and Paunović (2002) performed detailed osteometrical, biomechanical and locomotion analyses on the *Ursus* limb remains from Croatian caves. Withalm (2001) undertook a thorough study of the metapodial evolution of the cave bears group, while Athen *et al.* (2004), with biostatistical methods, analysed the different features among the cave bear species, especially *Ursus spelaeus* and *Ursus deningeri*. Lastly, Perego *et al.* (2001) extensively studied a great number of *U. spelaeus* bones from Campo dei Fiori Massif (Varese, Lombardy Region, Italy) highlighting new and interesting biometrical correlations between *Ursus* limbs of different geological ages. More recently, the evolution of the metapodial bones together with the morphodynamic indices of the teeth and the fossil mtDNA analyses, has allowed to support the hypothesis of the presence of new taxa within the cave bear group of the Alps (Rabeder & Nagel 2001; Rabeder *et al.*, 2004). They are: *Ursus ingressus* n. sp., which occurred in the eastern parts of the Alpine region and in the Dinarids of Slovenia and Croatia and the subspecies *Ursus spelaeus*

ladinicus n. ssp. and *Ursus spelaeus eremus* n. ssp. in the Totes Gebirge (Rabeder *et al.* 2004).

Geographic-stratigraphical setting

Cerè Cave, also known as "Tana dell'orso" or "La Tanasela", is positioned about 750m above sea level. It is 12m deep and opens 150 m east of Ceredo village (S. Anna d'Alfaedo) inside the Rosso Ammonitico Limestones. Its opening is circular with small dimensions, and in the proximity of an evident slope breach that characterises the right side of the Vajo dei Falconi. This entry leads to a wide door with a sub-quadrangular floor about 6,5m x 5m and is over 6m in height. Walls are often covered by older and deteriorated concretions. On the southern side of the hollow, a chimney 1m in diameter is present that was originally connected to the exterior. The Cerè Cave is considered a karst hole filled to its apex by bone-breccias (fig. 2). It was partially dug further during a second karst cycle forming a smaller cave. Today it opens across a short tunnel which had originally evolved from a pyroclastic cone (Pasa, 1954). From bottom to top the stratigraphic succession consists of:

- 1. Concretionated ferrous-manganesiferous clay (to the karst bed rock contact)
- 2. Concretion, still very thick locally
- 3. Calcareous-siliceous fine sand with gravels and not much clay that fills the bottom depressions and the karst fissures of the same. Locally, yellow or reddish clays are also present in a thin level below concretion 4
- 4. Concretion rich in siliceous and patinated detrital material
- 5. Plastic clay containing pebbles up to 1 cm in size
- 6. Horizon with concretions
- 7. Plastic red clay with rare fossil remains and with siliceous detrital fragments
- 8. Red clay with abundant flint and slightly altered gravel
- 9. Dark earth rich in bone remains prevalently belonging to *Canis lupus* with concretions and rare flint fragments
- 10. Dark earth rich in bone remains prevalently belonging to *Ursus*, with calcareous fragments
- 11. Bone-breccias very cemented, with prevailing *Ursus*, *Canis lupus* and *Marmota* remains
- 12. Breccias with little earthy sediment composed of strongly cemented big blocks
- 13. Red earth cemented with breccias
- 14. Calcareous breccias with flint
- 15. Breccias with pebbles and rare red earth

Results

Morphological analysis has shown that the fossils measured using Torres' (1988) parameters and presently stored in Museo Civico di Storia Naturale di Verona, belong to a different species of bear than *U. spelaeus* Rosenmüller-Heinroth, 1794, *U. deningeri* Von Reichenau, 1904 and *U. arctos* Linnaeus, 1758). The main morphometrical results are given below.

I° metacarpus - The ratio between the antero-posterior diameter of the proximal epiphysis

and the transversal width of the proximal epiphysis is shown in figure 3. The points position of the Cerè fossils shown refer to: a) *U. spelaeus*, whose remains fit its wide dispersion cloud very well and are morphometrically close to the large sized remains from Buco dell'Orso Cave and the Spanish caves, b) two populations of *spelaeus* whose different sizes admit comparison to arctoid proportions and probably indicating different climatic or evolutionary phases, if sexual dimorphism within the same population cannot be eliminated *a priori*, c) possible *U. arctos* fossils that could be considered an arctoid form given the wide distribution shown by this species.

II° metacarpus - The ratio between the absolute length and the transversal breadth of the distal epiphysis is shown in figure 4. The diagram is subdivided into two clear parts: one related to the *deningeri-spelaeus* and the other to the *arctos* group. The Cerè fossils either refer to *deningeri* or *spelaeus* and correspond very closely to their wide dispersion cloud. Altogether, the fossils studied show less massive epiphyses, unlike those taken from comparison populations.

III° metacarpus - The ratio between the absolute length and the transversal diameter of the diaphysis is given in figure 5. As already shown for the II° metacarpus, the gap between the typical field of the *deningeri-spelaeus* and the *arctos* groups, is clear. Moreover, another gap also exists inside the dispersion points cloud of the *deningeri-spelaeus* remains (that could simply be attributable to lack of data). In the right upper sector, at least some of the fossils morphologically referred to *U. cf. deningeri* are dimensionally similar to those from the Buco dell'Orso Cave. Globally, the Cerè bear sizes are similar to those from Buco dell'Orso and Spanish caves.

IV° metacarpus-V° metacarpus -Figure 6 shows for the IV° metacarpus the ratio between the absolute length and the antero-posterior diameter of the diaphysis", while figure 7 presents the ratio between the absolute length and the antero-posterior breadth of the proximal epiphysis of the V° metacarpus. In regard to the former, the only two fossils considered correspond very well to the respective existence fields of the *deningeri-spelaeus* and *arctos* groups. In this case too, the proportions of the specimen belonging to the *spelaeus* group are indicative of their slender forms.

Referring to the V° metacarpus specimens, similar comments can be made.

I° metatarsus - The diagram in figure 8 makes very interesting reading, showing the ratio between the absolute length and the transversal breadth of the diaphysis. The diagram is clearly subdivided into three fields related to the *U. spelaeus*, the Cerè Cave fossils and *U. arctos*. By estimating the regression lines of *U. arctos* and the Cerè population, we observed good correlation (0,62 and 0,70 respectively). Line slope comparison showed that the diaphyses's widths were even greater among the Cerè remains compared to the arctoid elements. Given that the *spelaeus* forms from Buco dell'Orso Cave (already of smaller size) are clearly separated from the "deningerian" ones in Cerè, we have reason to believe that the latter effectively belong to a different species. Moreover, the intermediate position they occupy between the *arctos* and *spelaeus* confirms this hypothesis.

II° metatarsus - Figure 9 shows how the ratio between the absolute length and the transversal breadth of the diaphysis was drawn using the fundamental traits following the observations applied to the I° metatarsus. In fact, points

related to possible and certain Cerè "deningerian" forms follow an intermediate trend between the *spelaeus* and arctoid elements whilst approaching the former with smaller dimensions. Therefore, the same conclusions advanced for the I° metatarsus can also be applied to them. An interesting fact is that the point referred to a possible *U. arctos* specimen falls between the reference elements of the main sizes. According to Capasso Barbato's *et al.* (1990) a size increase should be manifest within the more recent *arctos*, following a dimensional trend similar to the one which *U. spelaeus* underwent during its evolution.

III° metatarsus - The gap between the dispersion fields among the different species of *Ursus* is evident when observing the diagram in figure 10. Here the ratio between the absolute length and the maximum transversal breadth of the diaphysis is shown. Cerè arctoid remains can be classified among the referring specimens of smaller size. On the basis of what we have advanced for the arctoid specimens of the II° metatarsus, we should have a chronologically older population in this case. Thus, if the Capasso Barbato *et al.* (1990) hypothesis is

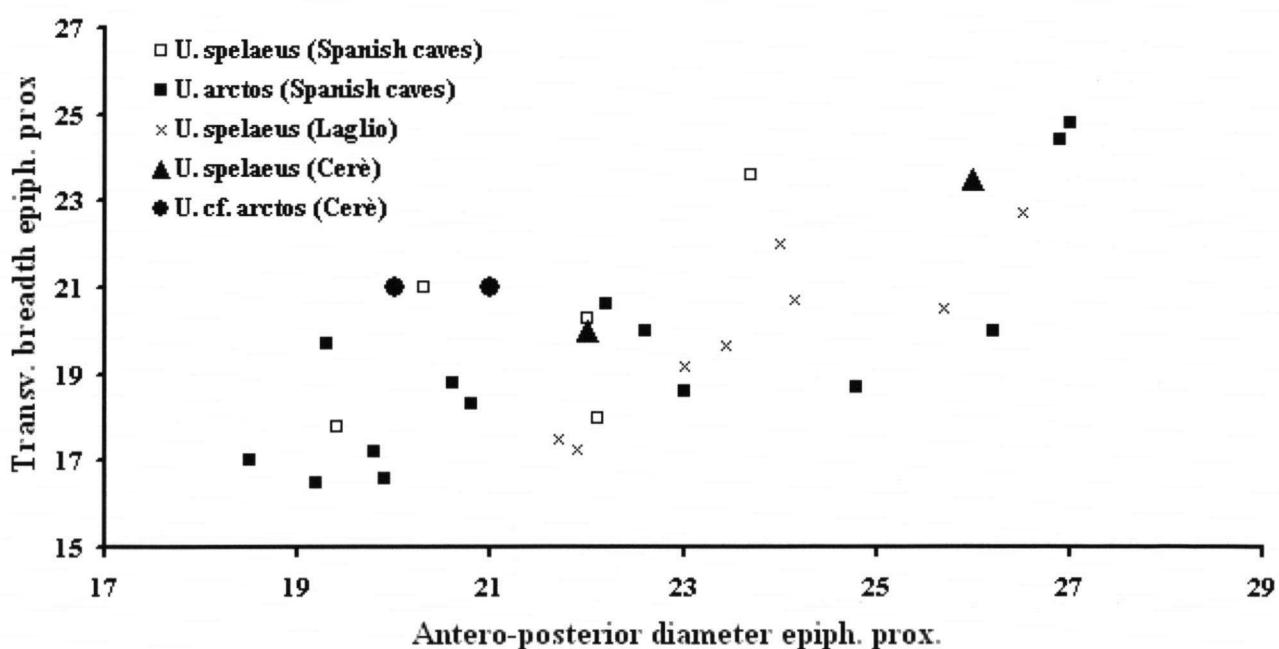


Fig 3 Ratio between the antero-posterior diameter of the proximal epiphysis and the transversal breadth of the proximal epiphysis for the first metacarpus in bears from Cerè Cave and from other caves

Verhouding tussen de antero-posterior diameter van de bovenste groeischijf en de overlangse breedte van de bovenste groeischijf voor het eerste middenhandsbeen in beren van de Cerè grot en van andere grotten

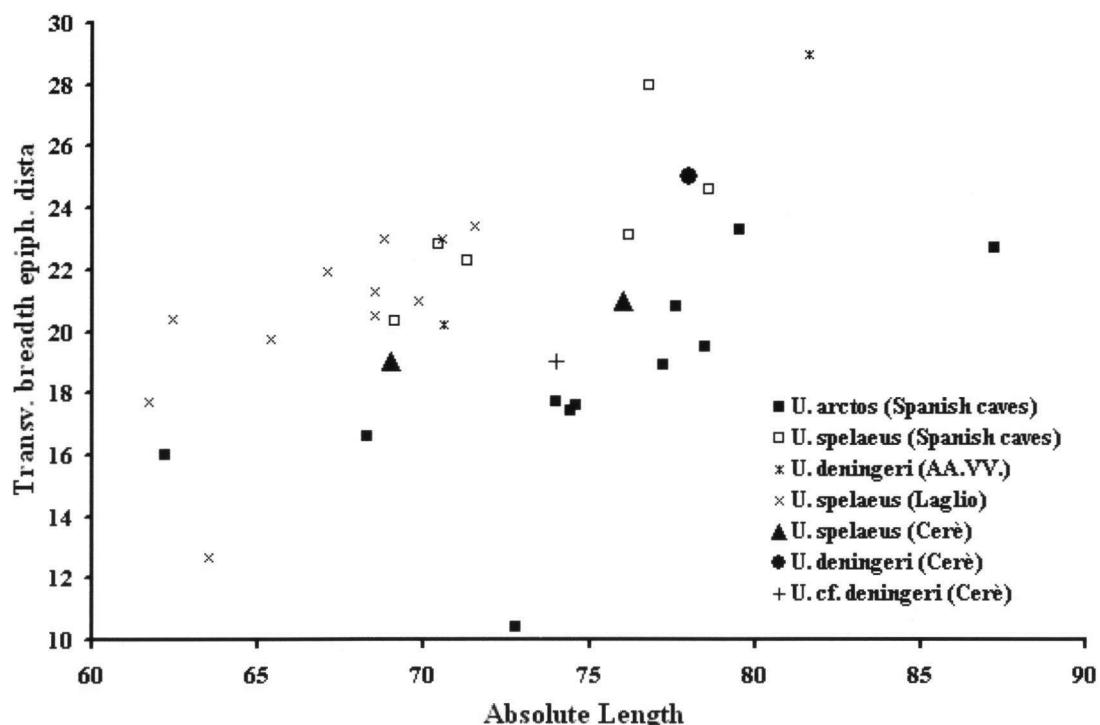


Fig 4 Ratio between the absolute length and the transversal breadth of the distal epiphysis for the II^o metacarpus in bears from Cerè Cave and from other caves

Verhouding tussen de absolute lengte en de overlangse breedte van de onderste groeischijf voor het tweede middenhandsbeen in beren van de Cerè grot en van andere grotten

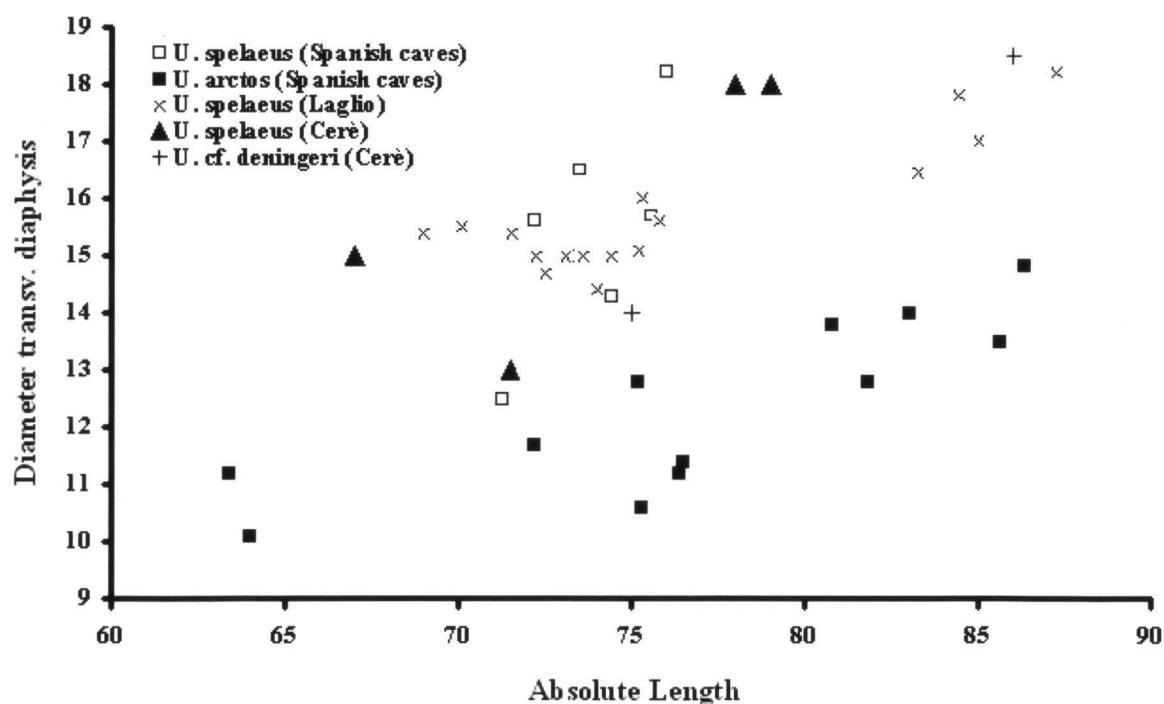


Fig 5 Ratio between the absolute length and the transversal diameter of the diaphysis for the III^o metacarpus in bears from Cerè Cave and from other caves

Verhouding tussen de absolute lengte en de overlangse diameter van de schacht voor het derde middenhandsbeen in beren van de Cerè grot en van andere grotten

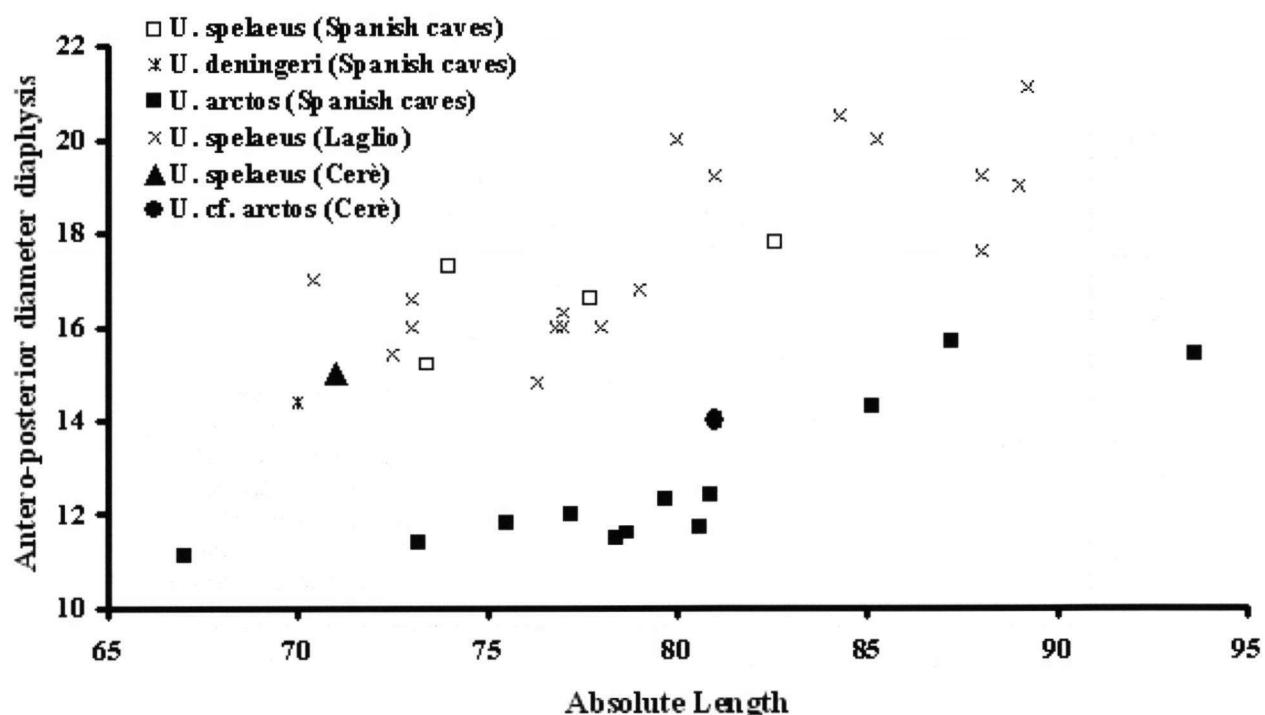


Fig 6 Ratio between the absolute length and the antero-posterior diameter of the diaphysis for the IV^o metacarpus in bears from Cerè Cave and from other caves

Verhouding tussen de absolute lengte en de antero-posterior diameter van de schacht voor het vierde middenhandsbeen in beren van de Cerè grot en van andere grotten

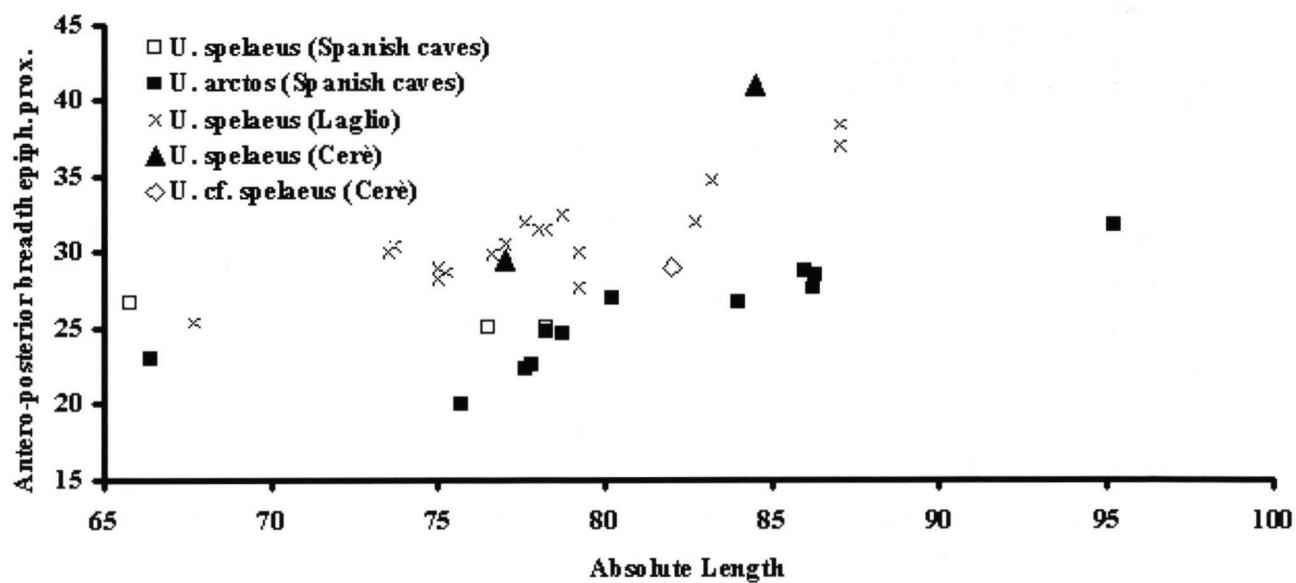


Fig 7 Ratio between the absolute length and the antero-posterior breadth of the proximal epiphysis for the V^o metacarpus in bears from Cerè Cave and from other caves

Verhouding tussen de absolute lengte en de antero-posterior breedte van de bovenste groeischijf voor het vijfde middenhandsbeen in beren van de Cerè grot en van andere grotten

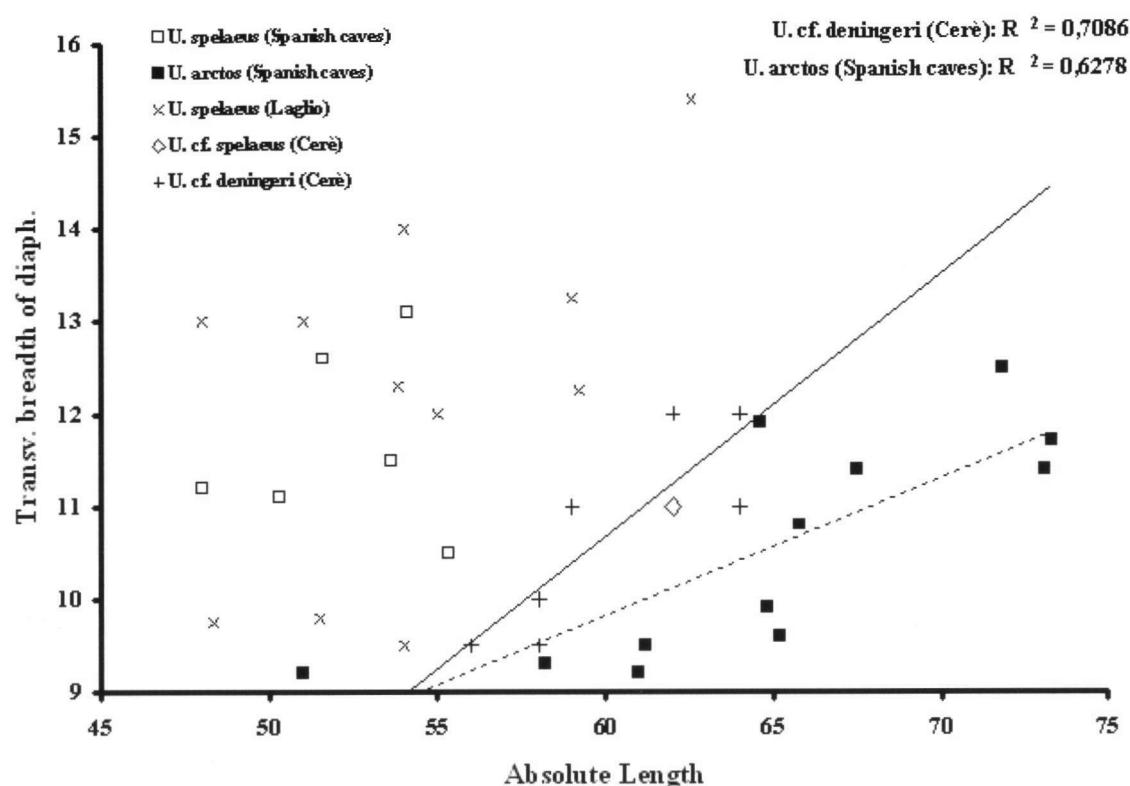


Fig 8 Ratio between the absolute length and the transversal breadth of the diaphysis for the I° metatarsus in bears from Cerè Cave and from other caves

Verhouding tussen de absolute lengte en de overlangse breedte van de schacht voor het eerste middenvoetsbeen in beren van de Cerè grot en van andere grotten

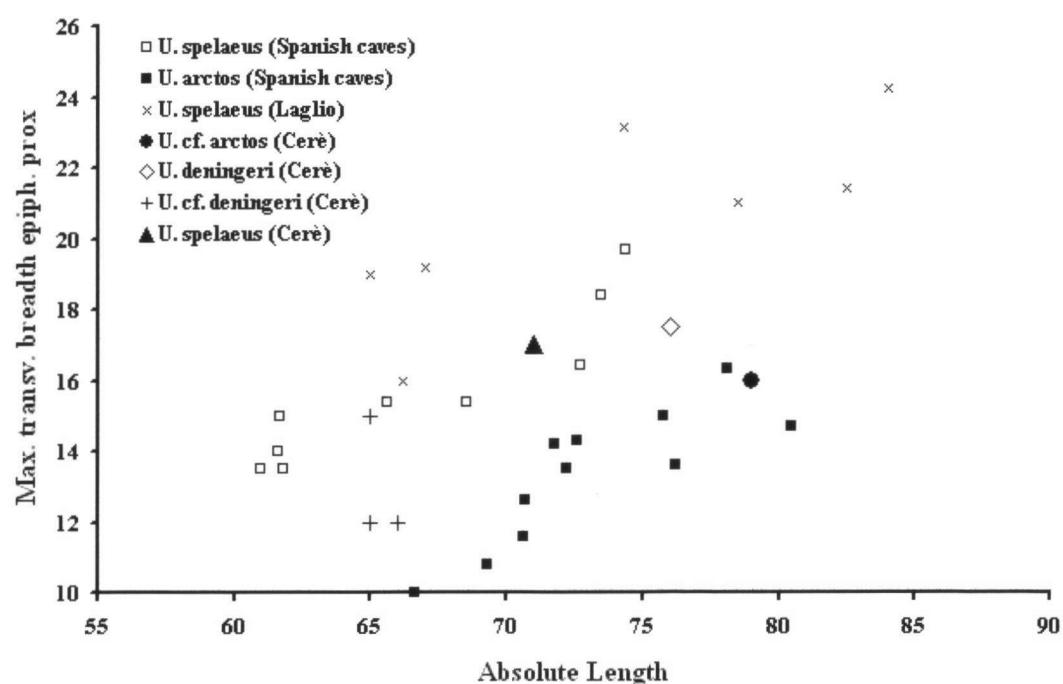


Fig 9 Ratio between the absolute length and the transversal breadth of the diaphysis for the II° metatarsus in bears from Cerè Cave and from other caves

Verhouding tussen de absolute lengte en de overlangse breedte van de schacht voor het tweede middenvoetsbeen in beren van de Cerè grot en van andere grotten

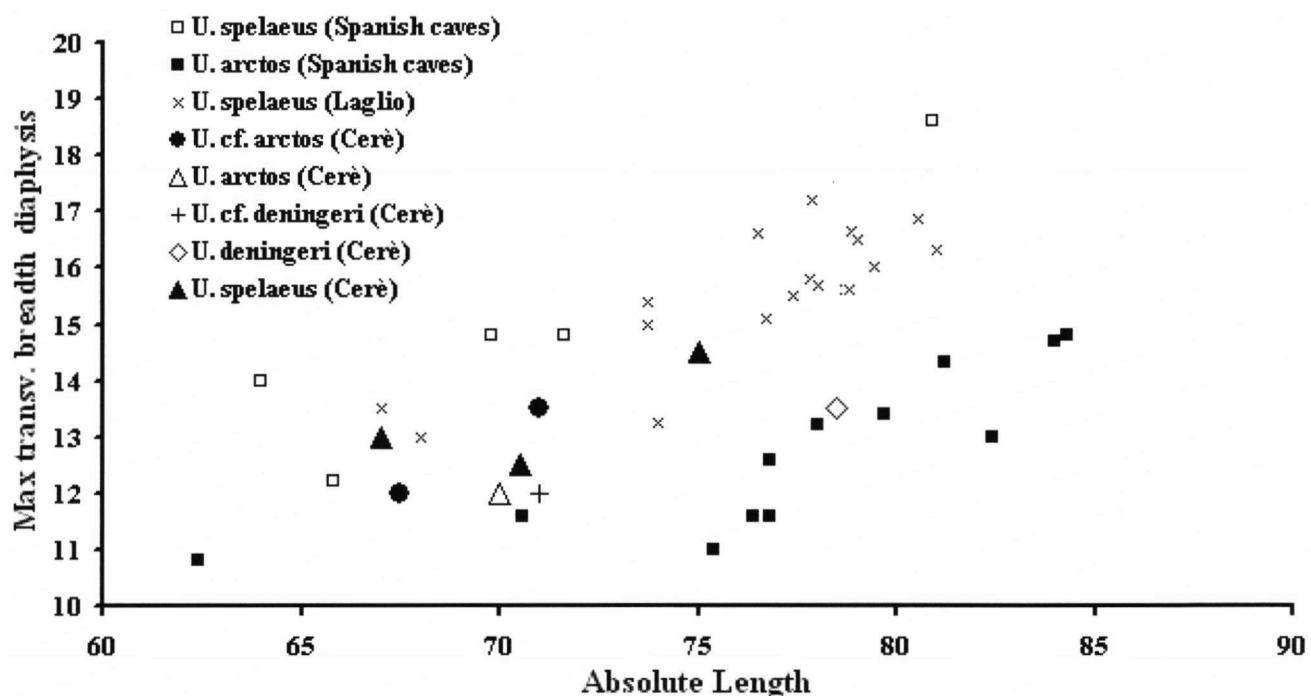


Fig 10 Ratio between the absolute length and the maximum transversal breadth of the diaphysis for the III^o metatarsus in bears from Cerè Cave and from other caves

Verhouding tussen de absolute lengte en de maximale overlangse breedte van de schacht voor het derde middenhandsbeen in beren van de Cerè grot en van andere grotten

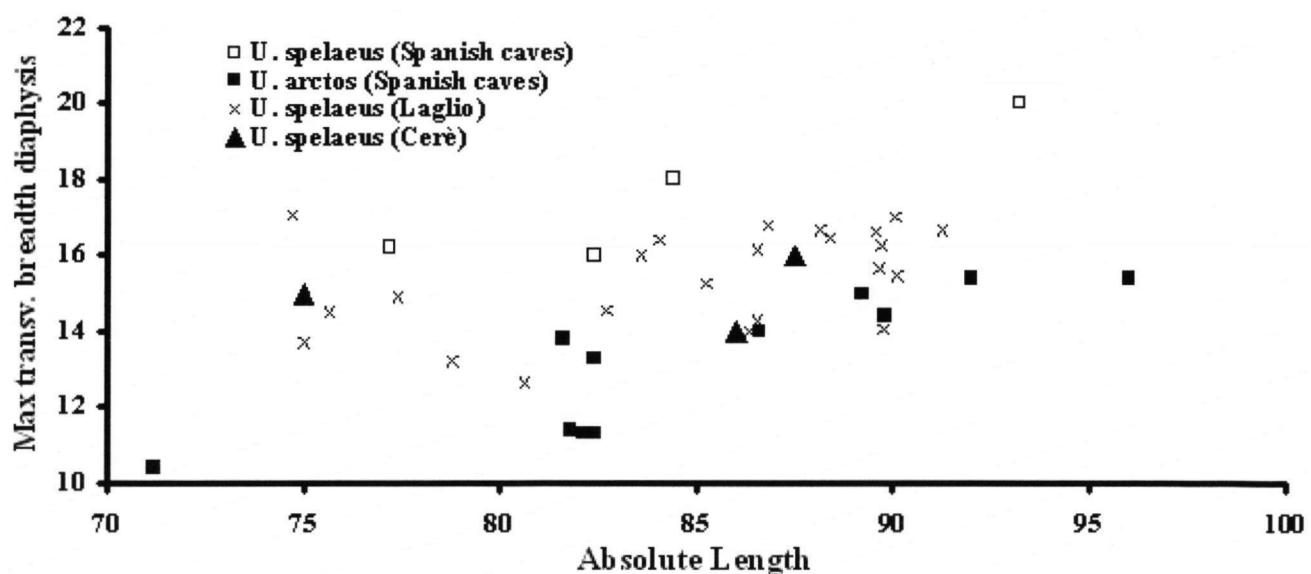
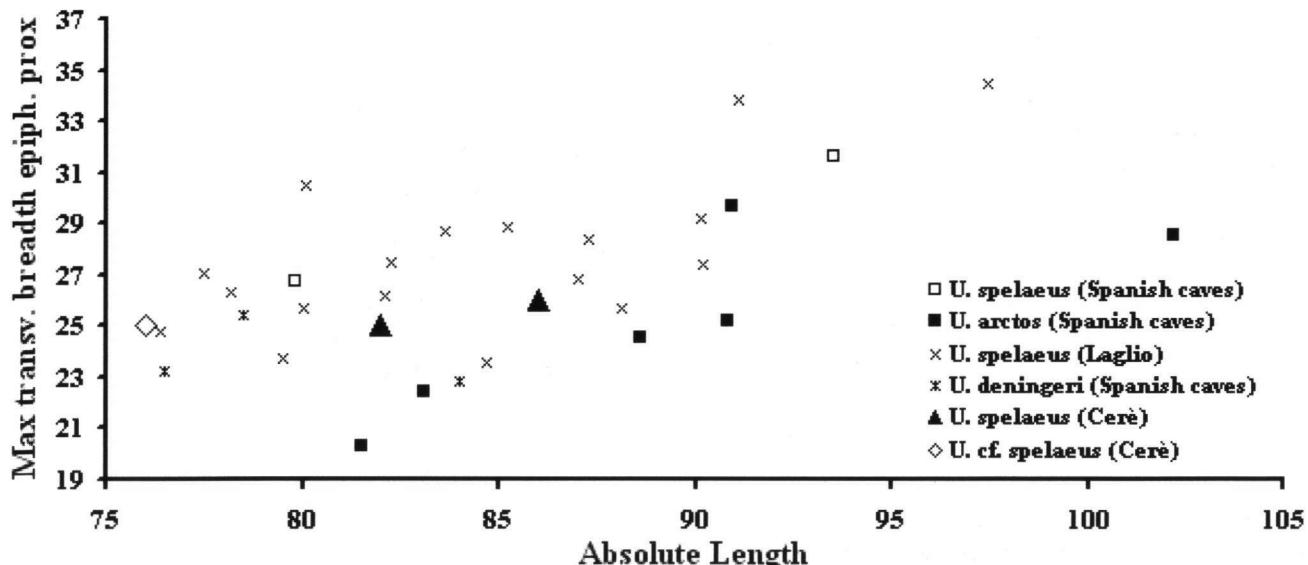


Fig 11 Ratio between the absolute length and the maximum transversal breadth of the diaphysis for the IV^o metatarsus in bears from Cerè Cave and from other caves

Verhouding tussen de absolute lengte en de maximale overlangse breedte van de schacht voor het vierde mid-denvoetsbeen in beren van de Cerè grot en van andere grotten



correct, in addition to the deningerian forms we should also have the chronologically different *spelaeus* populations as well as some *U. arctos* specimens among the Cerè fossils belonging to chronologically different populations.

IV° metatarsus-V° metatarsus - The diagrams in figures 11 and 12 that present the ratios for the IV° metatarsus between the absolute length and the maximum transversal breadth of the diaphysis and between the absolute length and the maximum transversal breadth of the proximal epiphyses of the V° metatarsus respectively are very similar and show that the *spelaeus* specimens from Cerè are similar in size to those from the Buco dell'Orso Cave. Such findings also show that for this anatomical part, part of the globally considered *spelaeus* population had less massive proportions.

Conclusions

Morphological and morphometrical data confirm that certain correlations exist among bears from the Cerè Cave, indicating the presence of three *Ursus* species, *U. deningeri*, *U. spelaeus* and *U. arctos*. The presence of *U. deningeri* had formerly only been hypothesised (Santi

and Rossi, 2001b). *U. spelaeus* is well represented, while *U. arctos* remains are scarcer than the other two.

Overall, the sizes of the speloid group specimens are medium-small, and their proportions also appear to be less massive, unless we failed to find elements with larger dimensions. Considering that *U. deningeri* is certainly present, it is likely, if not probable, that archaic forms of *U. spelaeus* could also be present. This should explain the finding of at least a proportion of the medium-small sized and less sturdy remains. Analyses done by Hofreiter *et al.* (2002) on the DNA of some specimens of *spelaeus* aged between 26500 and 49000 years from different Alpine caves, have led scientists to think that geographically separated populations could be polyphyletic. In addition "...This suggests that small size may have been an ancestral trait in cave bears and that large size evolved at least twice independently." (Hofreiter *et al.*, 2002: 1). The small dimensions of some fossils could be related to cooler climatic phases (Kurtén, 1976; Gerhard, 2001; Rabeder & Nagel, 2001).

The associations among bear remains in the Cerè Cave covers more than one period of the Pleistocene. The presence of *U. deningeri* allows

us to extend their existence to the Lower Pleistocene, the lower boundary of the time phase covered. This species has been little reported in Italy, although it is widespread in countries north of the Alps (France, Austria, etc.). It may be that successive waves of immigration entered Italy, as its successor *U. spelaeus* could not have developed from local Italian populations of *U. deningeri*. Although the normally accepted hypothesis holds that *U. spelaeus* derived from *U. deningeri*, the DNA analyses effected by Orlando *et al.* (2000) and by Loreille *et al.* (2001) instead lead us to the conclusion that this latter species was a "sister" group of the *spelaeus* and not its direct ancestor.

Unlike the cave bear, the *deningeri* forms in Italy only partially occupied the Alpine and Prealpine areas with some isolated pioneers shifting west and probably remaining within the more eastern sectors of the Alps. The complete evolution of Alpine *U. deningeri* occurred in these zones. In fact, the data do not indicate with certainty a common presence of *U. deningeri* in the Lombardy and Piedmont regions. However, it is difficult to justify the hypothesis that further evolution of "Italian" deningerian forms occurred among certain cave bear populations that colonized at least the "Three Venetia" Region. In fact, these may have been the last remnants of a species that preferred to colonize the northern sector of the Alps (but also extending to Spain), with some members moving in isolated groups towards Central Italy (Isernia).

Referring to the associations with other localities where *U. arctos* is missing or its presence very limited (Buco dell'Orso Cave, Sopra Fontana Marella Cave, Delle Streghe Cave, etc.), the numbers found among the Cerè Cave bear populations, whilst not high, are nonetheless meaningful. This could be explained with the coexistence of the last *spelaeus* remnants when the cave bear was finally on the road to extinction having been ousted by the brown bear.

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