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***Ursus deningeri-spelaesus* group from Cerè Cave (Veneto, North Italy) in the new evolutionary frame of the cave bear. Part one: skulls and mandibles**

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(With 17 figures and 1 table)

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Abstract

Recently, during the first evolutive phases of the *Ursus deningeri-spelaesus* group new forms have been identified, that shared the same environment for a long time till the extinction of Upper Pleistocene. A more detailed morphological and morphometrical analysis of the remains from Cerè Cave (Veneto, Northern Italy) showed: 1) some intermediary features between those typical of Upper Pleistocene forms and those typical of Lower Pleistocene *Ursus savini* from Bacton in the *Ursus deningeri* remains; 2) some archaic features in the *Ursus spelaesus* remains. It is possible that, after a first fast evolutionary phase, these forms remained at least partially isolated. The second evolutionary phase was characterized by the preservation of some archaic features, as occurred in the Caucasian population. Differently, it may be possible that in this population the *Ursus deningeri-Ursus spelaesus* transition occurred later than in other Europeans countries.

Keywords: *Ursus deningeri-Ursus spelaesus* group, evolution, Pleistocene, Cerè Cave, Northern Italy

Introduction

Recent studies (PACHER 2004a, b; RABEDER et al. 2004, 2006, 2010; KNAPP et al. 2009) showed a more complicated evolutionary frame of the *Ursus deningeri-Ursus spelaesus* group, particularly for the initial phases. In fact, a growing number of authors (ANDREWS & TURNER 1992; MAZZA & RUSTIONI 1994; VILA TABOADA & GRANDAL D'ANGLADE 2001; ROSSI & SANTI 2001; GRANDAL D'ANGLADE & LÓPEZ-GONZÁLEZ 2004; GARCÍA et al. 2006) think that it

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would be opportune to include in *Ursus spelaeus* ROSENMÜLLER, 1794 also those species representing the more primitive stages, as *Ursus savini* (ANDREWS, 1922) and *Ursus deningeri* VON REICHENAU, 1906, but some others maintain that at least five different evolutive lines were present (RABEDER et al. 2004, 2006; KNAPP et al. 2009; RABEDER et al. 2010), bringing to five the total count of species (*Ursus spelaeus* ROSENMÜLLER, 1794, *U. ingressus* RABEDER et al., 2004, *U. ladinicus* RABEDER et al., 2004, *U. eremus* RABEDER et al., 2004 and *U. kudarensis*).

The presence inside Cerè Cave (Veneto, Northern Italy) of the species *U. deningeri* and *U. spelaeus* – the first only supposed in some previous works (ROSSI & SANTI 2001a, 2001b) and successively confirmed by new studies (ROSSI & SANTI 2005; SANTI & ROSSI 2006) – give us an interesting opportunity for trying to place these forms within this new evolutive frame. Some morphometrical and morphodynamical features suggest that, after a first fast evolutionary phase, these forms remained at least partially isolated. The second evolutionary phase was characterized by the preservation of some archaic features, as occurred in the Caucasian population. Differently, it may be possible that in this population the *Ursus deningeri*-*Ursus spelaeus* transition occurred later than in other Europeans countries. The small number of remains do not allow us to consider decisive the formulated theory. Moreover, the specific data and some morphological and morphometrical features, particularly those about the dentition, give us some sure data useful to consider this theory an excellent starting point for future and deeper studies about the Cerè Cave and its deposit.

Due to the paucity of morphometric data, the specimens belonging to *U. deningeri* have been classified above all on the base of the morphological features.

Study area

Cerè Cave (Fig. 1), also known as “Tana dell’Orso” or “La Tanasela”, is located about 750 m above sea level and opens on the right hydrographical side of Vajo dell’Anguilla, inside of the Rosso Ammonitico Limestones. The cave had been excavated for the first time in the Fifties and its stratigraphy is not known in detail. Only recently, some explorative tests were performed, which provided this first summary stratigraphy from bottom to top (ZORZIN et al. 2003):

- 1 – concretionated ferrous-manganesiferous clay (to the karst bed rock contact)
- 2 – concretion, locally very thick
- 3 – calcareous-siliceous fine sand with gravels and not much clay that fills the bottom depression and the karst fissures of the same. Locally, yellow or reddish clays are also present in a thin level below concretion 4
- 4 – concretion containing detrital siliceous and patinated materials
- 5 – plastic clay containing pebbles up to 1 cm in size
- 6 – horizon with concretions

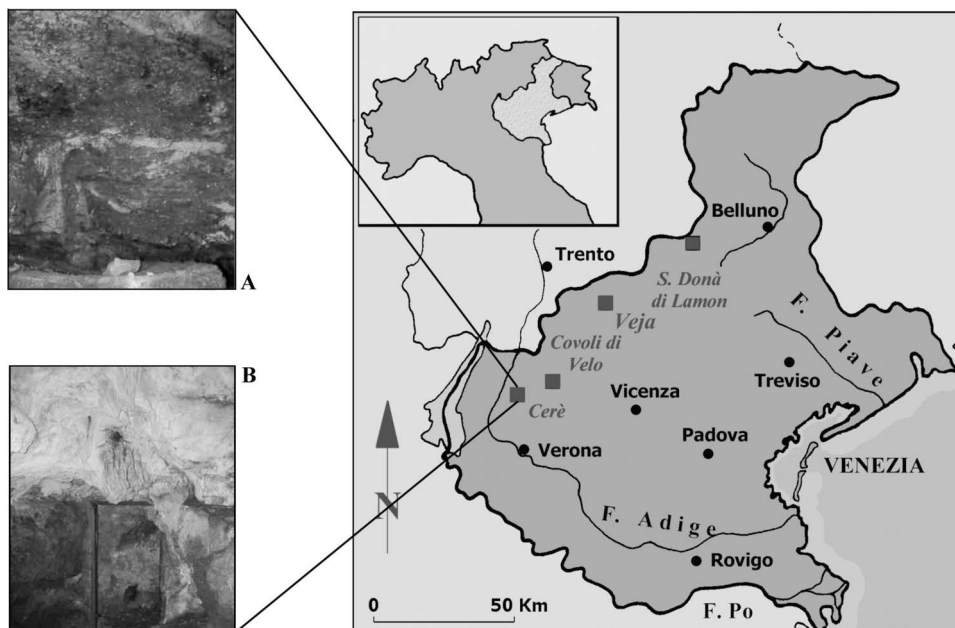


Fig. 1. Position of the main caves within the Veneto region (North Italy). Cerè Cave, Covoli di Velo, Veja and San Donà di Lamon. A-B: Details of the Cerè Cave.

- 7 – plastic red clay with rare fossils remains and siliceous detrital fragments
- 8 – red clay with abundant flint and slightly altered gravel
- 9 – dark earth rich in bones remains prevalently belonging to *Canis lupus* with concretions and rare flint fragments
- 10 – dark earth rich in bone remains 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

The faunal association is very rich and in addition to *Ursus* includes: *Amphibia* indet., *Reptilia* indet., *Aves* indet., *Sorex* sp., *Talpa* sp., *Marmota marmota* LINNAEUS, 1758, *Evotomys* [recte *Clethrionomys*] sp., *Dolomys* [recte *Dinaromys*] *bogdanovi* MARTINO, 1922, *Arvicola* sp., *Allophaiomys* sp., *Microtus agrestis* LINNAEUS, 1761, *Microtus arvalis* PALLAS, 1778, *Microtus nivalis* (MARTINS, 1842), *Microtus* sp., *Apodemus sylvaticus* LINNAEUS, 1758, *Glis glis* LINNAEUS, 1766, *Canis lupus* LINNAEUS, 1758, *Canis lupus* aff. *mosbachensis* SOERGEL, 1925, *Canis* sp., *Vulpes vulpes* (LINNAEUS, 1758), *Vulpes vulpes crucigera* BECHSTEIN, 1789, *Vulpes* sp., *Mustela putorius* LINNAEUS, 1758,

Gulo gulo LINNAEUS, 1758, *Martes martes* (LINNAEUS, 1758), *Martes* sp., *Panthera leo spelea* (GOLDFUSS, 1810), *Panthera* cf. *pardus* LINNAEUS, 1758, *Panthera* sp., *Sus priscus* GOLDFUSS and DE SERRES, *Sus scrofa* LINNAEUS, 1758, *Sus* sp., *Cervus elaphus* LINNAEUS, 1758, *Cervus* sp., *Bos* sp., *Rupicapra rupicapra* LINNAEUS, 1758, *Capra ibex* LINNAEUS, 1758, *Capra* sp. (BON et al. 1991 cum bibl.). The contemporaneous presence of *Allophaiomys* typically of the Early Pleistocene and other more recent forms indicates a mixture of forms with different ages from different levels. Consequently, the *Allophaiomys* presence and the lack of a precise stratigraphy don't allow us to make sure that the material dates back only to the Upper Pleistocene. It could go back to the Middle or even Lower Pleistocene. Surely in the future, a detailed study level by level must be undertaken to evaluate the faunistic change.

The significance of Cerè Cave is primarily due to the presence of the species *U. deningeri*, the remains of which initially were assigned to the species *U. spelaeus minor* GAUDRY & BOULE, 1892 and secondly to the presence of the two other species of ursids, *U. spelaeus* and *U. arctos* LINNAEUS, 1758.

Materials and methods

The cranial and mandibular remains (17 specimens) are stored in the Museo Civico di Storia Naturale di Verona (Veneto Region) and are catalogued with the abbreviation "V" (Vertebrates) followed by a progressive number. They are very incomplete, especially in the masseter fossa and condyles, missing in all specimens except in specimen V4886. In several specimens the incisive portion of the horizontal branch is lacking or damaged. Among the cranial remains, the specimens V160 and V162 are almost complete while specimen V161 is very deformed at the orbits. In Table 1 the bear remains from Cerè Cave are reported, while in Table 2 the measurements of the skulls, mandibles and teeth with the morphodynamic index of the P4/4 of the *Ursus* remains, are shown.

Since the possibility to ascribe these remains to the new species suggested by RABEDER et al. (2004, 2006) was already excluded in a recent work (STOPPINI et al. 2007), the comparison is restricted to remains of *U. deningeri* and *U. spelaeus* from other European deposits. The lack of a detailed stratigraphical analysis suggested the exclusive use of the remains with morphological and morphometrical characteristics useful for a safe specific determination. For this reason, we have selected only the mandibular and cranial specimens sufficiently complete in the bone or with some teeth, with particular attention to P4/4 and M₁.

Results

Specific morphological features of the skull and mandible

The most important structural changes of the cave bear skull and mandible are due to the adaptation to an omnivorous diet, predominantly vegetarian (TORRES PÉREZ-HIDALGO 1988b), and the subsequent development of the grinding area between the protoconid of M1 and the posterior edge of M3 (CRUSAFONT & TRUYOLS 1957). In the cave bears the grinding function is fundamental, so it is very developed, determining several changes both in the mandible, especially at the ascending branch, and in the skull. The main morphological features used for the specific determination of the fossils are here reported.

Skull – the structural changes in the skull are connected with the increase of: 1) the height and verticalization of the mandibular ascending branch; 2) the verticalization of the fibers of the temporal muscle. These factors cause:

1) the raising of the forehead in comparison with the superior edge of the snout, the consequent breaking of the outline at the eye level and the appearance of a deep depression separating the facial and cerebral portions (KURTÉN 1972, 1976; TORRES PÉREZ-HIDALGO 1988a; CAPASSO BARBATO et al. 1993; MAZZA & RUSTIONI 1994; GARCIA et al. 2006);

2) a strong decrease of the neurocranial convexity in comparison to the *Ursus arctos* (MAZZA & RUSTIONI 1994; GARCIA et al. 2006). This feature is likely linked to the readjustment of the temporal muscle described by KURTÉN (1976);

3) a considerable development of the sagittal crest along the length. This feature is not shown by any author in the bibliography known to us, but it agrees with the readjustment of the temporal muscle.

Mandible – the most important features are:

1) the horizontal branch shows a great strengthening both transversally, under the grinding area, and vertically, along the whole branch, that becomes higher from M₁ to M₃. Probably this feature is also influenced by the exemplar's sex and age. Studying the fossils from Bourgogne (France), ARGANT (1991) observed that both the female and male juvenile exemplars showed a slender mandible ("type A" *sensu* Argant, characterized by a slender and long horizontal branch). During growth, the females retain this morphology, whereas the males assume a more massive morphology ("type B" *sensu* Argant, characterized by a stout and shorter horizontal branch);

2) the anterior profile of the ascending branch can be divided in two areas: i) a shorter, subvertical and almost straight inferior area; ii) a longer and slightly convex area running up to the coronoid process (TORRES PÉREZ-HIDALGO 1988b; MAZZA & RUSTIONI 1994). On the contrary, the whole anterior area of the ascending branch of *U. etruscus* and *U. arctos* shows in lateral view a regularly convex profile. However, it is necessary to consider that this morphological feature is also influenced by the morphology of the coronoid crest. This last depends on the development of the temporal muscle, which is influenced

by the individual and sexual variations and by the ontogenetic development (BALLESIO et al. 2003);

3) in lateral view, the posterior edge of the ascending branch looks like a fairly uniform straight line, sloping downwards and backwards. This feature also produces the increased accommodation area for the masseter muscle, counterbalancing the shortening of the lever arm caused by the buttressing of the ascending branch on that horizontal. The posterior edge of the other species, adapted to a more carnivore diet, shows a regularly concave profile (TORRES PÉREZ-HIDALGO 1988b);

4) from *U. etruscus* to *U. spelaeus* the mandible is characterized by a more and more pronounced raising of the condyle (FICCARELLI 1979; MAZZA & RUSTIONI 1994). Consequently, the mandible articulation joint with the skull lies well above the hypothetical line drawn extending the dental line. Therefore, the action of the dental battery works like a nut-cracker. This kind of mandibular action is observable in all the omnivorous and especially vegetarian animals, [e.g. antelope, buffalo, horse and others (KURTÉN 1976)]. In the brown bear in most cases the highest point of the condyle lies on the hypothetical line drawn extending the occlusal dental surface. When it lies in the raised position, this morphological feature is less emphasized than in the cave bear (BALLESIO 1983). This phenomenon also causes a global bending of the horizontal branch and a more pronounced buttressing of the ascendant branch on the horizontal one (TORRES PÉREZ-HIDALGO 1988b);

5) in *U. etruscus* and *U. arctos* the condyles are very large transversally but not vertically. Moreover, they are cylindrical in their inner third and conical in the remaining portion. In *U. deningeri* the height of the condyles increases significantly and are cylindrical in their inner half. This phenomenon is more pronounced in *U. spelaeus*, in which condyles are characterized by a very reduced conical portion (TORRES PÉREZ-HIDALGO 1988b; MAZZA & RUSTIONI 1994). The combination of these features probably permit a greater lateral movements of the mandibles, as demonstrated by the development of the surfaces for the pterigoid muscle insertion. In fact, these surfaces and particularly that for the insertion of the lateral pterigoid muscle are much more developed in *U. spelaeus* than in the others species. The development of these surfaces demonstrates that these muscles are very developed (FRIANT 1959).

Teeth – the most important evolutive changes are:

1) from *U. etruscus* to the cave bear (*U. deningeri*-*spelaeus* group), the number of premolars is reduced in accordance with a rather uniform pattern: before P2, then P1 and finally P3 (RABEDER 1992). However, there are some exceptions to this pattern: in fact, in *U. deningeri* the dental formula shows a great variability especially in the premolar number and this reduction may be minimal (only one premolar), intermediate (two premolars) or maximum (all first three premolars reduced) (TORRES PÉREZ-HIDALGO 1988e; ZANALDA 1994; RABEDER et al 2010). Several examples are reported in literature: Von Reichenau (in TORRES PÉREZ-HIDALGO 1988e) mentions some mandibles from Mosbach and Mauer (Germany) with P₃ and some skulls from the same deposit with P¹ and P³. ZAPFE (1946)

describes a skull from Hundsheim (Germany) with alveoli of P^1 and P^3 and KURTÉN (1977), studying the material from Petralona (Greece), reports three mandibles lacking the first three premolars and one mandible with the alveolus of P_3 . Finally, TORRES PÉREZ-HIDALGO (1988e) describes some mandibles with P_3 (Lezetxiki, Spain), with P_1 and P_2 (Cueva Mayor, Spain) and mandibles lacking the first three premolars (Cueva de Santa Isabel, Spain). Generally, in *U. spelaeus* the reduction is extreme, but also in this species some exemplars with P_3 are reported (TORRES PÉREZ-HIDALGO 1988e). The comprehensive evolutive trend is characterized by a progressive complication of the masticatory surface, due to the development of new cusps and crests. This phenomenon particularly involves the premolars (premolars “molarization”) (RABEDER 1992). The dentition is a clear evidence of a very fast evolution of the cave bear (TORRES PÉREZ-HIDALGO 1988e; RABEDER 1992): it permits the creation of some morphodynamical schemes (RABEDER 1989, 1992, 1999). These schemes are very useful to determine the evolutive degree of the fossils and their age approximate.

Systematic Palaeontology

Skulls – *Ursus deningeri* VON REICHENAU, 1906

V160 – Skull of a young individual, as demonstrated by the low wear of the teeth, corresponding with the juvenile stage described by STINER (1998). The cranial morphology is not fully developed but the typical step of the forehead, so characteristic of the cave bear group, is clearly visible (Fig. 2).

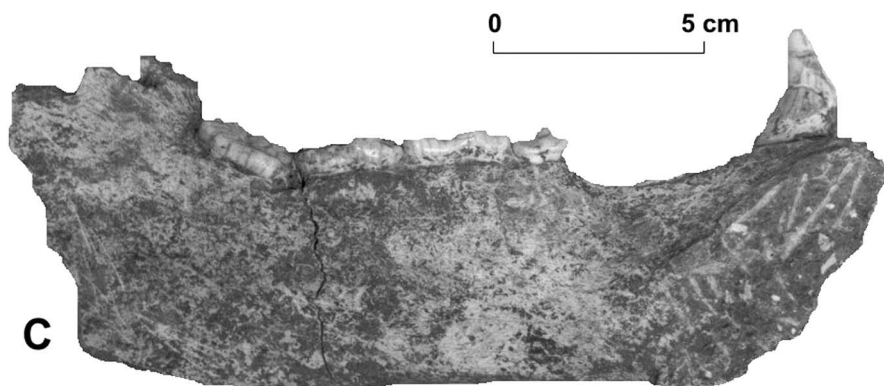
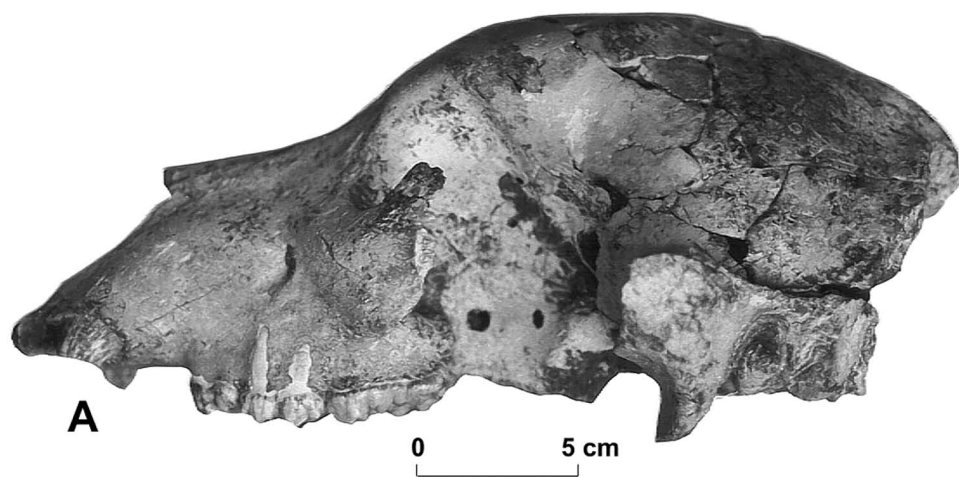
V161 – The deformation caused by the post mortem processes makes the identification of the glabella difficult. Nevertheless, both the morphology of the cranial fragments at the orbits and the nasal one suggest similar features also for this fossil: particularly, the nasal bone shows a clear concavity at the posterior portion, which is a typical feature of the cave bear (TORRES PÉREZ-HIDALGO 1988a). On the contrary, the brown bear shows a straight nasal bone (MAZZA & RUSTIONI 1994). The neurocranial convexity is very low. The alveoli of P^1 and P^3 are present.

V162 – Skull of an adult individual characterized by the step at the frontal bones, a very low neurocranial convexity and a very developed sagittal crest.

Mandibles – *Ursus deningeri* VON REICHENAU, 1906

V4670 – The horizontal branch is stout and grows from M_1 to M_3 . The morphology of its inferior edge suggests a significant buttressing of the ascending branch.

V4673 – The horizontal branch is stout and grows from M_1 to M_3 . The diastema shows a concave edge. The internal pterygoid muscle insertion does not show any apophysis but is not very wide. The ascending branch shows a slightly concave posterior edge and a deep anteroposterior profile of the masseteric fossa. The morphology of the inferior



edge of the horizontal branch and the position of the condyle suggests some buttressing of the ascending branch.

V4886 – This specimen shows a slender morphology, particularly at the horizontal branch and the diastema, that is long and characterized by a very concave profile. The horizontal branch grows from M_1 to M_3 . The internal pterygoid muscle insertion shows a small apophysis in the ventral portion of the mandible. According to TORRES PÉREZ-HIDALGO (1988b), this feature is typical of *U. arctos* but is also present in some remains from Veja and Covoli di Velo (Verona, Veneto region), that certainly belong to *U. spelaesus* and in the specimens belonging to *U. ingressus* (RABEDER et al. 2010: Fig. 16): therefore, this feature is unsuitable as diagnostic character at species level, at least for the Veronese sites. The ascending branch shows a straight posterior edge. The masseteric fossa is deep and shows a very concave anteroposterior profile. The angular process and the condyle are in a raised position. The latter lies well above the line containing the masticatory surface, is stout and has parallel inferior and superior edges and a conical portion, which is not much developed.

Mandibles – *Ursus cf. deningeri* VON REICHENAU, 1906

V4761 – This remain is characterized by a very slender horizontal branch. This, however, is due to the juvenile age of the individual as demonstrated by the very low wear of the masticatory surface, it is a very juvenile exemplar. The alveoli of P_1 and P_2 are present.

Mandibles – *Ursus spelaesus* ROSENMÜLLER, 1794

V4671 – Fragment of a fairly stout horizontal branch, characterized by a long and slightly concave diastema.

V4672 – Fragment of horizontal branch very deformed by the fossilization. Its determination is based on the morphology of P_4 .

V4674 – Mandibular fragment characterized by a stout morphology. The profile of the inferior edge suggests a considerable buttressing of the ascending branch on the horizontal one and the consequent raising of the condyle and the angular process. The specimen lacks P_4 and its alveolus and does not show any trace of new bony growth. This should indicate a tooth agenesis. GRANDAL D'ANGLADE (1993) reports a similar case from Cova Eiros.

V4675a – Mandibular fragment characterized by a fairly slender morphology. The horizontal branch grows from M_1 to M_3 .

V4675b – Condyle characterized by a considerable development of the conical portion.

◀ Fig. 2. *Ursus deningeri* VON REICHENAU, 1906. Cerè Cave. **A:** Specimen V 160 (skull), lateral view; **B:** Specimen V 162 (skull), lateral view; **C:** Specimen V 4673 (mandible), internal view. All specimens are stored into Museo Civico di Storia Naturale in Verona.

V4676 – Fragment of a horizontal branch determined by analysing the first molar, well preserved and little worn.

Mandibles – *Ursus cf. spelaeus* ROSENMÜLLER, 1794

V4669b – The mandible shows a slender morphology and its horizontal branch grows from M_1 to M_3 . The angle formed by the two branches suggests a considerable buttressing of the ascending branch on the horizontal one. On the whole, its morphology is more similar to “type A” *sensu* ARGANT (1991) and suggests that this remain belongs to a female exemplar.

Mandibles – *Ursus arctos* LINNAEUS, 1758

V4762 – Fragment of horizontal branch characterized by a slender morphology. The pterigoid muscle insertion shows a small apophysis over-going up to the ventral portion of the mandible. The specific determination is based on the morphology of the last molar, well preserved and little worn.

Mandibles – *Ursus cf. arctos* LINNAEUS, 1758

V4778 – Mandible characterized by a slender morphology. The horizontal branch shows an almost straight inferior edge and its morphology at M_3 suggests a slightly accentuated raising of the condyle and the angular process. The alveoli of P_2 and P_3 are present.

Morphometric analysis

Skulls – The diagram in Fig. 3 shows the ratio between the basal length and the total length. The size of the adult exemplar (V162) is in the typical range of *U. spelaeus* and

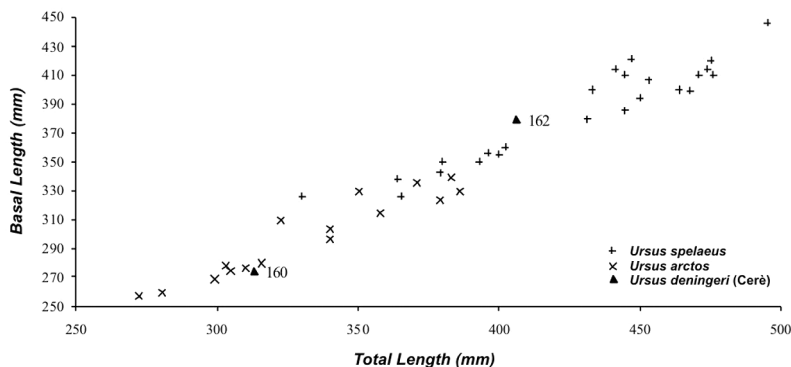


Fig. 3. Relationships between the total length and the basal length in skulls of bears (*U. spelaeus* and *U. arctos*) and specimen from Cerè Cave. Data from TORRES PÉREZ HIDALGO (1988a) and CAPASSO BARBATO et al. (1993).

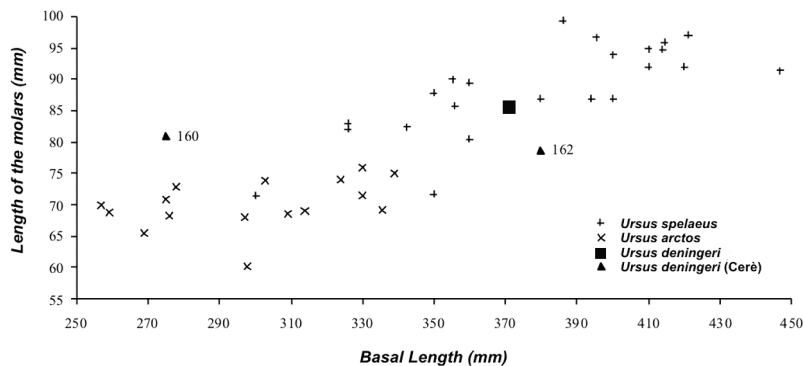


Fig. 4. Relationships between the basal length and the length of the molars in bear's skulls (*deningeri-spelaesus* group and *U. arctos*) and *U. deningeri* from the Cerè Cave. Data from TORRES PÉREZ HIDALGO (1988e), CAPASSO BARBATO et al. (1993) and BALLELIO et al. (2003).

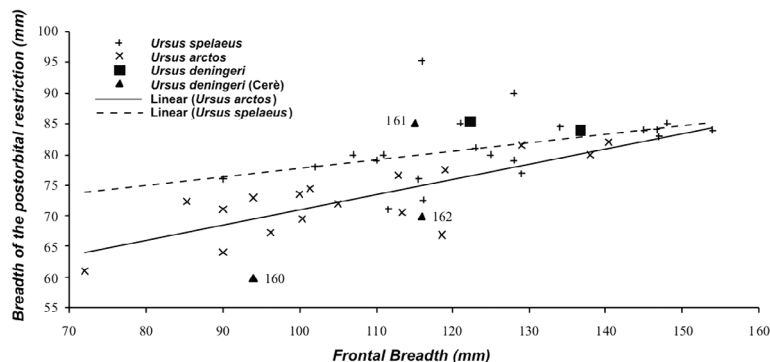


Fig. 5. Relationships between the frontal breadth and the breadth of the postorbital restriction in bear's skulls (*deningeri-spelaesus* group and *U. arctos*) and *U. deningeri* from the Cerè Cave. Data from TORRES PÉREZ HIDALGO (1988a), CAPASSO BARBATO et al. (1993) and BALLELIO et al. (2003).

confirms the morphological data. The size of juvenile exemplar (V160) is only due to its age: in fact, though lack of the data prevented us from comparing the studied remains with exemplars belonging to *U. deningeri*, we can assume, however that this size is also typical of the species on the basis of some others morphometric parameters (see the graphs of the teeth measurements).

The diagram in Fig. 4 shows the ratio between the basal length and the molariform length. The size of the studied remains corresponds to that typical of the speloid forms: in fact, in both cases the molariform length falls within the limits of the cave bear range, albeit in its lower range.

The diagram in Fig. 5 shows the ratio between the frontal breadth and the postorbital restriction breadth. On the whole, the brown bears are characterized by a more pronounced postorbital restriction than the speloid forms. The dispersion point cloud of the remains

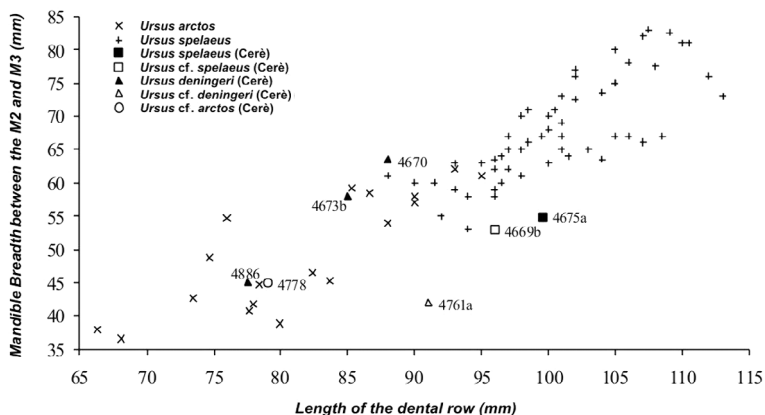


Fig. 6. Relationships between the length of the dental row and the mandible breadth in the different species of bear and the Cerè's specimens. For details see text. Data from TORRES PÉREZ HIDALGO (1988b) and CAPASSO BARBATO et al. (1993).

from Cerè Cave corresponds to that of *U. spelaeus*, with the exception of the specimen V160, which belongs to a juvenile exemplar.

Mandible – The diagram in Fig. 6 shows the ratio between the teeth row length and the mandible breadth between M_2 and M_3 . All the specimens belonging to the cave bear show small to medium sizes: particularly those belonging to *U. deningeri* (V4673b and V4670) are characterized by sizes corresponding to those typical of *U. spelaeus*, with the only exception of the specimen V4886, which shows a size comparable to that of a medium-sized brown bear. As for the remains V4669b and V4675a, it is possible that its size is also conditioned by the sex: in fact, their slender morphology is a typical feature of female specimens (ARGANT 1991).

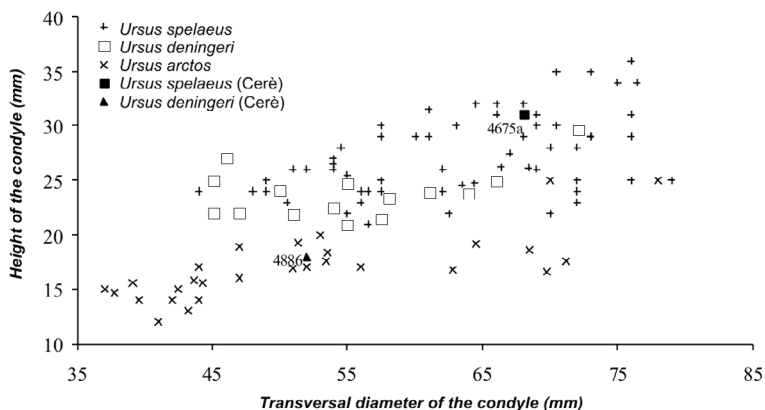


Fig. 7. Relationships between the transversal diameter of the condyle and the height of the condyle in the different species of bear and the Cerè's specimens. Data from TORRES PÉREZ HIDALGO (1988b), CAPASSO BARBATO et al. (1993) and BALLESTO et al. (2003).

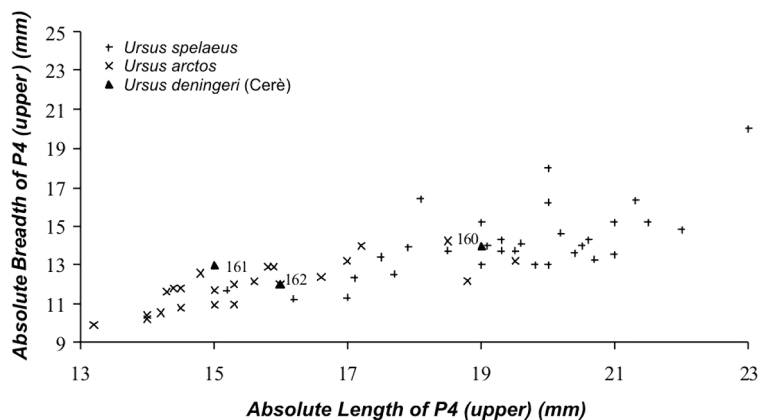


Fig. 8. Relationships between the absolute length and the absolute breadth in the P⁴ in *U. spelaeus*, *U. arctos* and the specimens (*U. deningeri*) from the Cerè Cave. Data from TORRES PÉREZ HIDALGO (1988e) and CAPASSO BARBATO et al. (1993).

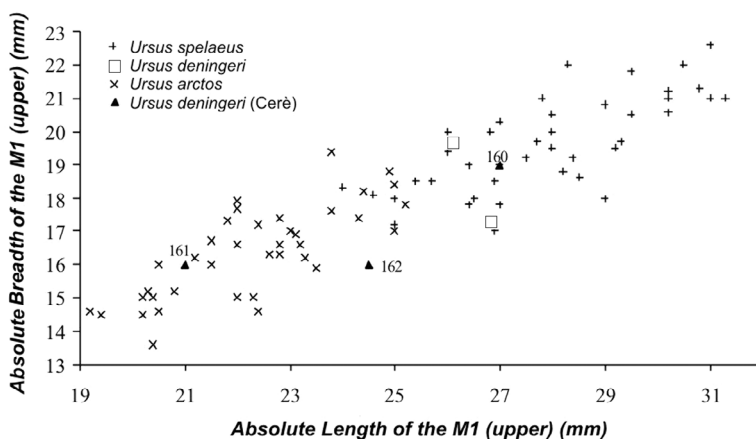


Fig. 9. Relationships between the absolute length and the absolute breadth in the M¹ in different species of bears and the specimens (*U. deningeri*) from the Cerè Cave. Data from TORRES PÉREZ HIDALGO (1988e), CAPASSO BARBATO et al. (1993) and BALLELIO et al. (2003).

Anyway, the morphometric data referring to the remains V4670 and V4673b show the typical pattern of the speloid forms towards the horizontal branch strengthening. Finally, the horizontal branch size of V4761 is linked to its juvenile age.

The diagram in Fig. 7 shows the ratio between the transversal and vertical diameters of the condyle. The remains of *U. deningeri* show a smaller size than that typical of this species; therefore the morphometric data does not confirm the morphology. This may depend on a paucity of the data and/or a sexual factor (female exemplar) and an evolutive factor (primitive exemplar).

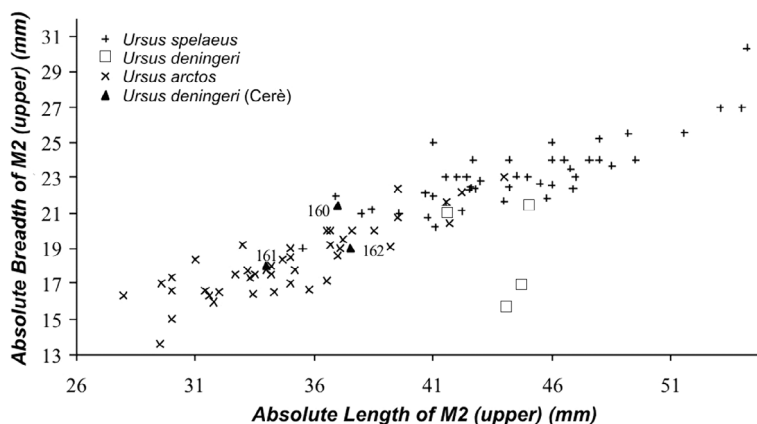


Fig. 10. Relationships between the absolute length and the absolute breadth in the M^2 in different species of bears and the specimens (*U. deningeri*) from the Cerè Cave. Data from TORRES PÉREZ HIDALGO (1988e), CAPASSO BARBATO et al. (1993) and BALLESEO et al. (2003).

Upper teeth – All three diagrams (Figs 8, 9, 10) provide very similar indications: the teeth sizes correspond to the lower range of the typical field of *U. spelaeus* group, or, in the case of V161, to that typical of the *U. arctos*.

Lower teeth – The diagram in Fig. 11 shows the ratio between the length and the breadth of P_4 . The remains from Cerè Cave lie in the overlap of the morphometric range of *U. spelaeus*, *U. deningeri* and *U. arctos*. The more important morphometric data are: 1) the size of all the remains belonging to *U. deningeri* are in the typical range of this

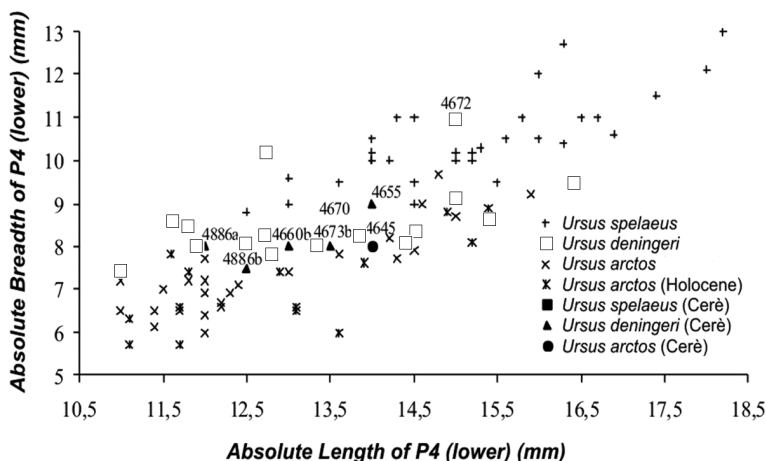


Fig. 11. Relationships between the absolute length and the absolute breadth in the P_4 in different species of bears, in *U. arctos* (Holocene) and the specimens from the Cerè Cave. Data from TORRES PÉREZ HIDALGO (1988f), CAPASSO BARBATO et al. (1993) and BALLESEO et al. (2003).

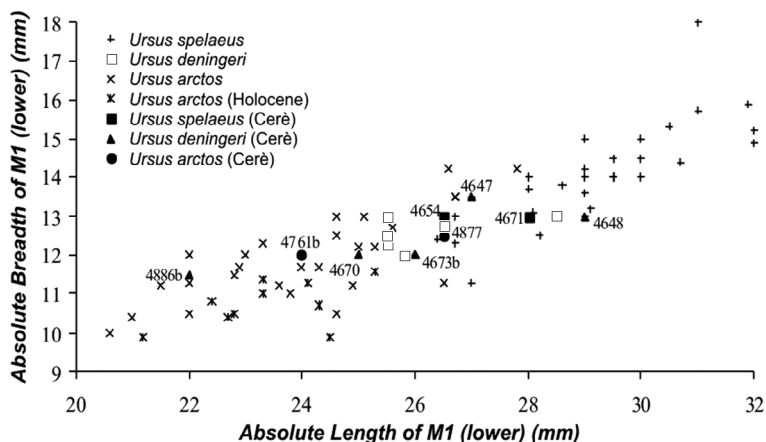


Fig. 12. Relationships between the absolute length and the absolute height in the M_1 in different species of bears, in *U. arctos* (Holocene) and the specimens from the Cerè Cave. Data from TORRES PÉREZ HIDALGO (1988f), CAPASSO BARBATO et al. (1993) and BALLESEO et al. (2003).

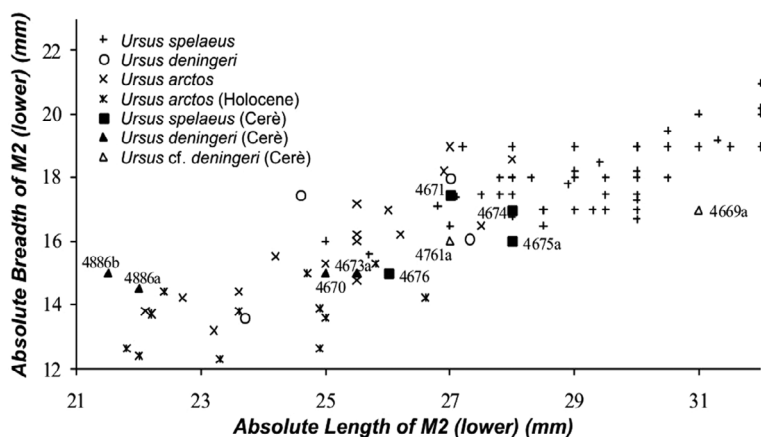


Fig. 13. Relationships between the absolute length and the absolute breadth in the M_2 in different species of bears, in *U. arctos* (Holocene) and the specimens from the Cerè Cave. Data from TORRES PÉREZ HIDALGO (1988f), CAPASSO BARBATO et al. (1993) and BALLESEO et al. (2003).

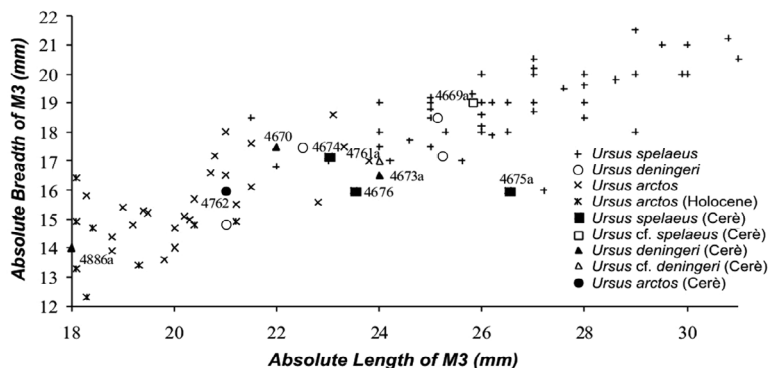


Fig. 14. Relationships between the absolute length and the absolute breadth in the M_3 in different species of bears, in *U. arctos* (Holocene) and the specimens from the Cerè Cave. Data from TORRES PÉREZ HIDALGO (1988f), CAPASSO BARBATO et al. (1993) and BALLESEO et al. (2003).

species; 2) these remains show intermediate sizes between the species *U. spelaeus* and the species *U. arctos*. Therefore, the pattern of the molarization of this tooth, already mentioned by RABEDER (1992), is confirmed.

The diagrams in Figs 12, 13, 14 show the ratio between the length and the breadth of the molars. They show that: 1) the *U. deningeri* remains from Cerè Cave have sizes at the limit or lower to that typical of this species; 2) those belonging to *U. spelaeus* are small-medium sized.

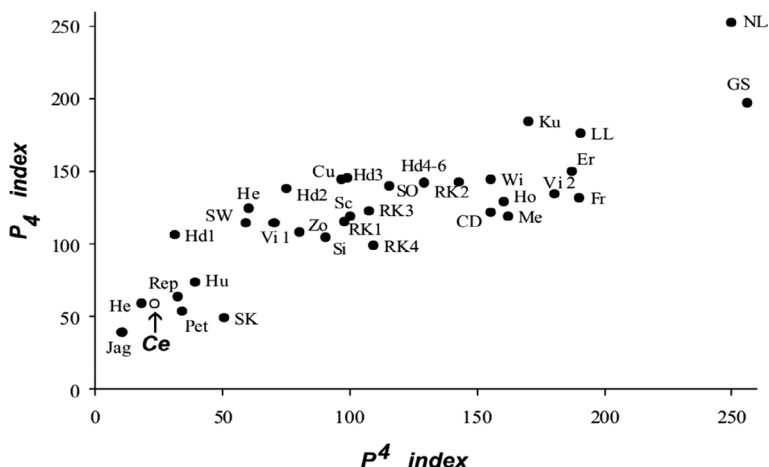


Fig. 15. Position of the Cerè Cave (white point labelled "Ce") utilising the P4/4 index of specimens from several European caves. Data from RABEDER (1999).

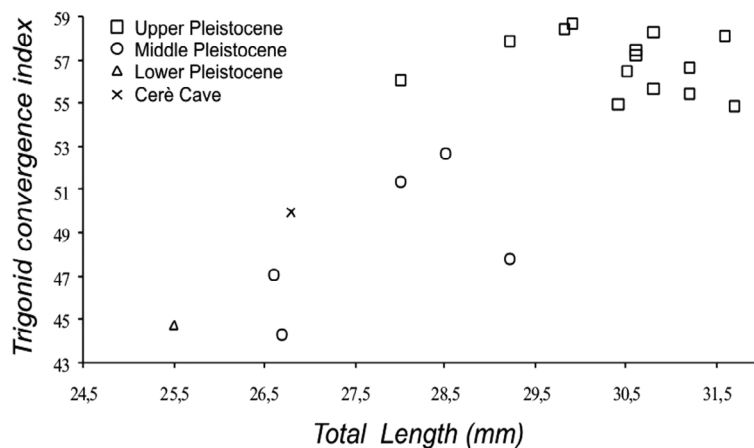


Fig. 16. Total length and the trigonid convergence index relationship in M_1 of bear from caves of different chronology and Cerè's specimens. Data from GRANDAL D'ANGLADE & LÓPEZ-GONZÁLEZ (2004).

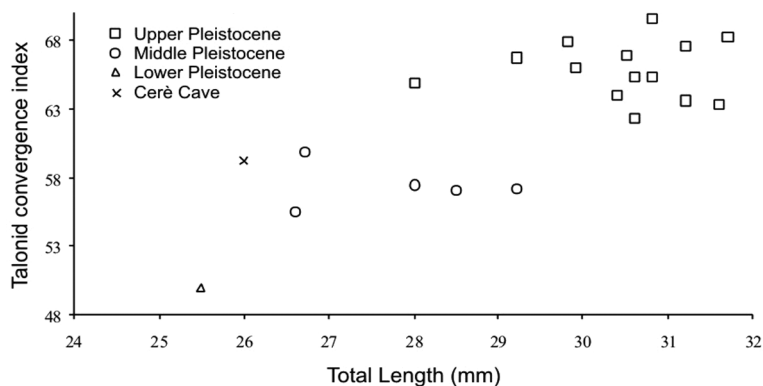


Fig. 17. Total length and the talonid convergence index relationship in M_1 of bear from caves of different chronology and Cerè's specimens. Data from GRANDAL D'ANGLADE & LÓPEZ-GONZÁLEZ (2004).

Coll. No	Species	Bone type	Left	Right
160	<i>Ursus deningeri</i>	Skull		
161	<i>Ursus deningeri</i>	Skull		
162	<i>Ursus deningeri</i>	Skull		
4669b	<i>Ursus cf. spelaeus</i>	Mandible		x
4670	<i>Ursus deningeri</i>	Mandible	x	
4671	<i>Ursus spelaeus</i>	Mandible	x	
4672	<i>Ursus spelaeus</i>	Mandible	x	
4673a	<i>Ursus deningeri</i>	Mandible	x	
4673b	<i>Ursus deningeri</i>	Mandible		x
4674	<i>Ursus spelaeus</i>	Mandible	x	
4675a	<i>Ursus spelaeus</i>	Mandible		x
4675b	<i>Ursus spelaeus</i>	Condyle		
4676	<i>Ursus spelaeus</i>	Mandible		x
4761	<i>Ursus cf. deningeri</i>	Mandible	x	
4762	<i>Ursus arctos</i>	Mandible		x
4778	<i>Ursus cf. arctos</i>	Mandible		x
4886a	<i>Ursus deningeri</i>	Mandible	x	
4886b	<i>Ursus deningeri</i>	Mandible		x
160	<i>Ursus deningeri</i>	upper teeth	x	
160	<i>Ursus deningeri</i>	upper teeth		x
161	<i>Ursus deningeri</i>	upper teeth	x	
161	<i>Ursus deningeri</i>	upper teeth		x
162	<i>Ursus deningeri</i>	upper teeth	x	
162	<i>Ursus deningeri</i>	upper teeth		x
4645	<i>Ursus arctos</i>	P ₄		
4655	<i>Ursus deningeri</i>	P ₄		
4660b	<i>Ursus deningeri</i>	P ₄		
4670	<i>Ursus deningeri</i>	P ₄	x	
4672	<i>Ursus spelaeus</i>	P ₄	x	
4673b	<i>Ursus deningeri</i>	P ₄		x
4886a	<i>Ursus deningeri</i>	P ₄	x	
4886b	<i>Ursus deningeri</i>	P ₄		x
4647	<i>Ursus deningeri</i>	M ₁		
4648	<i>Ursus deningeri</i>	M ₁		
4654	<i>Ursus spelaeus</i>	M ₁		
4670	<i>Ursus deningeri</i>	M ₁	x	
4671	<i>Ursus spelaeus</i>	M ₁	x	
4673b	<i>Ursus deningeri</i>	M ₁		x
4676	<i>Ursus spelaeus</i>	M ₁		x
4877	<i>Ursus arctos</i>	M ₁		
4886a	<i>Ursus deningeri</i>	M ₁	x	
4886b	<i>Ursus deningeri</i>	M ₁		x
4669a	<i>Ursus cf. deningeri</i>	M ₂		
4670	<i>Ursus deningeri</i>	M ₂	x	
4671	<i>Ursus spelaeus</i>	M ₂	x	
4673a	<i>Ursus deningeri</i>	M ₂	x	
4673b	<i>Ursus deningeri</i>	M ₂		x
4674	<i>Ursus spelaeus</i>	M ₂	x	
4675a	<i>Ursus spelaeus</i>	M ₂		x
4676	<i>Ursus spelaeus</i>	M ₂		x
4761	<i>Ursus cf. deningeri</i>	M ₂	x	
4886a	<i>Ursus deningeri</i>	M ₂	x	
4886b	<i>Ursus deningeri</i>	M ₂		x
4669a	<i>Ursus cf. spelaeus</i>	M ₃		
4670	<i>Ursus deningeri</i>	M ₃	x	
4673a	<i>Ursus deningeri</i>	M ₃	x	
4673b	<i>Ursus deningeri</i>	M ₃		x
4674	<i>Ursus spelaeus</i>	M ₃	x	
4675a	<i>Ursus spelaeus</i>	M ₃		x
4676	<i>Ursus spelaeus</i>	M ₃		x
4761a	<i>Ursus cf. deningeri</i>	M ₃	x	
4762	<i>Ursus arctos</i>	M ₃		x
4886a	<i>Ursus deningeri</i>	M ₃	x	
4886b	<i>Ursus deningeri</i>	M ₃		x

◀ Table 1 – The *Ursus* remains from the Cerè Cave (Verona, Veneto region, North Italy) housed at the Museo Storia Naturale Verona.

Table 2 – Measurements of the skulls, mandibles, teeth and morphodynamic index of *Ursus* from Cerè Cave. Parameters from TORRES PÉREZ HIDALGO (1988a).

SKULL			
Parameters	160	161	162
1	313		406
2	275*		380
3			
4	146	139	182.5
5	78	92	95
6	164.5		230
7	81.5		
8		155	
9		70.5	72
10		40	30.5
11		202	
12	60	85	70
13	94	115	116
14	67.5		104
15	49.5		54
16	58		76.5
17	105	105.5	127
18	81	70	78.8
19	64	54	62.5
20		13.5	16

Table 2. (continued)

MANDIBLE													
Parameters	4669b	4670	4671	4673a	4673b	4674	4675a	4675b	4676	4761a	4762	4778	4886a 4886b
1													247 245
2	39	41.5	65		47					37		34.5	46 45.5
3	53	63.5	68		58		55			42		45*	45 46
4	57	66	71	56	61	70*	57		51	41	46		47 47.5
5	60	67	70*	56.5	58.5	78*	58		55	47	48.5	46.5	51.5 51
6	20	22	22.5	21	22	23			15	16		17	16.5 17
7	24	22	26	25	27	28.5			23.5	21	21.5	23	21 23
8	131.5	129			129					125.5			124 121
9	96	88		87	85		99.5			91		79	77.5 75
10	79	73		72	71.5	79	82			77		62	62 62.5
11													11
12								68*					51 52
13								31					18 18
14		17	20		15.5					14.5			12
15				147									123

P ₄	Morphotype	Factor	Product	P ⁴	Morphotype	Factor	Product
A/B1	1	0.25	0.25	A	8	0	0
B1	5	0.5	2.5	A/B	3	0.5	1.5
C1/C2	1	1.5	1.5	B	1	1	1
TOTAL	7		4.25	TOTAL	12		2.5

TEETH (UPPER)

Parameters	160 (l)	160 (r)	161 (l)	161 (r)	162 (l)	162 (r)
Length P4	13	19	15	15	16	15
Breadth P4	14	14	12.5	13	12	13
Length M1	27	28	21	21	24.5	26
Breadth M1	19	18.5	16	16.5	16	18
Length M2	37	38	33.5	34	37.5	37.5
Breadth M2	21.5	21	18	18	19.5	19

TEETH (LOWER)

Parameters	4645	4655	4660b	4670	4672	4673b	4886a	4886b			
Length P4	14	14	13	13.5	15	13.5	12	12.5			
Breadth P4	8	9	8	8	11	8	8	7.5			
Parameters	4647	4648	4654	4670	4671	4673b	4676	4781b	4877	4886a	4886b
Length M1	27	29	26.5	25	28	26	25	24	26.5	22	22
Length M1	13.5	13	13	12	13	12		12	12.5	11	11.5
Parameters	4669a	4670	4671	4673a	4673b	4674	4675a	4676	4761a	4886a	4886b
Length M2	31	25.5	27	25	25	28	28	26	27	22	21.5
Breadth M2	17	15	17.5	15	16	17	16	15	16	14.5	15
Parameters	4669a	4670	4673a	4673b	4674	4675a	4676	4761a	4762	4886a	4886b
Length M3	26	22	24	24	23	26.5	23.5	24	21	18	18.5
Breadth M3	19	17.5	16	16	17	16	16	17	16	14	14

P⁴ index = 20.8 P₄ index = 60.7 P⁴/₄ index = 35.5 * partial l = left r = right

Morphodynamic analysis

P4/4 – The P4/4 index (*sensu* RABEDER 1999) (Fig. 15) corresponds to that of the oldest sites and particularly to those characterized by the presence of the species *U. deningeri*, as Petralona (Greece) and Repolust (Austria). Thus, it confirms the morphological and morphometric data.

M₁ – The convergence indices (GRANDAL D'ANGLADE & LÓPEZ-GONZÁLEZ, 2004) (Figs 16, 17) also confirm the morphometric analysis: in fact, the remains from Cerè Cave show values of the two considered convergence indices which correspond to those of sites from the Middle Pleistocene of Europe. This chronological indication is consistent with the presence of *U. deningeri* at this site.

Discussion and conclusions

Despite the scarcity of the stratigraphic data and the low number of examined specimens, the Cerè Cave material still provided some very interesting indications. The *U. deningeri* remains are characterized by: 1) medium-small sizes, corresponding to the lower limit of the dimensional range of this species; 2) P4/4 indices and M₁ convergence indices corresponding to those of the European populations from Middle Pleistocene; 3) M² sizes intermediate between those typical of the European populations from Upper-Middle Pleistocene sites and those typical of the population from Bacton Lower Pleistocene site (*U. savini*) (BARYSHNIKOV 2006); 4) archaic features of M₁, in two cases as long or longer than M₂ (BARYSHNIKOV 2006). The species *U. savini* has been recently reviewed by RABEDER et al. (2010), who consider it a synonym of *U. deningeri*. This form is considered by the authors very primitive and is placed at the base of the phyletic tree of the cave bear (RABEDER et al. 2010: Fig. 48).

The *U. spelaeus* remains are characterized by medium-small sizes and morphodynamic features of the premolars typical of the archaic forms.

The presence of the species *U. arctos* in Cerè Cave and the coexistence of archaic and more advanced features in the *U. spelaeus* remains can be explained in two ways:

- 1) The remains are not representative of all the stratigraphic levels and it is possible that also some speloid remains with more advanced features are present in the site;
- 2) The remains are representative of all the stratigraphic levels and so it is possible that also *U. spelaeus* from Upper Pleistocene preserves some archaic features, as in the Caucasian populations (BARYSHNIKOV 1998).

If the second hypothesis is correct, then two causes can be proposed:

- 1) The *Ursus deningeri*-*Ursus spelaeus* transition occurred later than in other European countries. Recently, GRANDAL D'ANGLADE & LÓPEZ-GONZÁLEZ (2004) confirmed that the

transition between these species really occurred independently in the different European sectors.

2) After a first fast evolutionary phase, the population remained at least partially isolated and the second evolutionary phase was characterized by the preservation of some archaic features.

Finally, our data confirm the doubts advanced by several authors (EHRENBERG 1928; ERDBRINK 1953; KURTÉN 1976; ANDREWS & TURNER 1992; MAZZA & RUSTIONI 1994; VILA TABOADA & GRANDAL D'ANGLADE 2001; GRANDAL D'ANGLADE & LÓPEZ-GONZÁLEZ 2004; GARCIA et al. 2006) about the validity of a specific separation of the species *U. spelaeus* and *U. deningeri*.

These preliminary data are only indicative and exclusively a theoretical base for future investigations: therefore, the opening of a systematic excavation in Cerè Cave is desirable. These excavations are essential to supplement new data about the bear population with those on the associated fauna and, above all, their stratigraphy.

It would be interesting to further compare, the Cerè Cave data with the ones from other Italian and foreign sites to identify some possible common evolutive patterns. Particularly, it would be useful to compare the new data with those from European areas which show a geographic element similar to Italy. For example, the presence of mountain chains that could have represented a barrier, causing at least a partial isolation of the bear populations, may have determined such similar evolutive patterns in Italy and Spain.

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