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NEW EVIDENCE FROM THE BEARS OF THE VENETO REGION (NORTHERN ITALY) IN THE EVOLUTIONARY PICTURE OF THE ITALIAN CAVE BEARS

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Abstract: New morphological and morphometric data concerning the mandibular and dental (P_4 and M_1) remains of *Ursus* gr. *deningeri-spelaeus* from Grotta del Cerè and Covoli di Velo (Veneto region, Northern Italy) have allowed further consideration of the phyletic step reached by the cave bears in this part of Italy. Based on the new data, the *U.* gr. *deningeri-spelaeus* remains from Grotta del Cerè should be at least Middle Pleistocene in age, while those from Covoli di Velo are ascribed to the Upper Pleistocene. A question occurs concerning the possible distinction of the two species *U. deningeri* and *U. spelaeus*. In this first analysis the few observed morphological differences indicate the hypothesis of a unique species of *Ursus* (*spelaeus*) but divided into 'old' and 'modern' rather than two distinct species (*deningeri* and *spelaeus*).

Key words: *Ursus* gr. *deningeri-spelaeus*, mandibles, dentition, phylogenetic degree, Pleistocene, Northern Italy.

INTRODUCTION

Ursus spelaeus Rosenmüller, 1794 left a great amount of fossil evidence within the caves of northern Italy. Those mainly studied to date are, in the Lombardy region, the Caverna Generosa, Grotta Sopra Fontana Marella (Varese Province) (Perego *et al.,* 2001; Bona, 2004), and Grotta del Buco dell'Orso (Laglio, Como) (Rossi & Santi, 2001a,b; Santi & Rossi, 2001; Santi *et al.,* 2003) and in the Veneto region, the Grotta del Cerè and the Covoli di Velo (Verona Province) (Zorzin & Bona, 2002; Zorzin *et al.,* 2003; 2004; 2005; Galli *et al.,* 2005) (fig. 1). Less well known are the caves in the Piedmont (Grotta delle Streghe-Sambughetto Valstrona-Mt. Fenera, Vercelli Province) (Santi *et al.,* 2005) and in the Liguria (Grotta delle Fate) (Quiles, 2004). Until now the Grotta delle Ossa (Zandobbio, Bergamo Province, Lombardy) and the Grotta del Bandito (Cuneo Province, Piedmont) have been even less studied (Bonin *et al.,* 2005; Zunino & Pavia, 2005). Notwithstanding that further work is required, on the basis of the abundant analysed remains it is possible to drawn a coherent phyletic picture of the "Italian cave bears" pertaining to the *deningeri-spelaeus* group.

URSUS DENINGERI VON REICHENAU, 1906 AND *URSUS SPELAEUS* ROSENMÜLLER, 1794 IN THE VENETO

In northern Italy *Ursus deningeri* Von Reichenau, 1906 did not colonise wide areas, as its remains show. In fact, based on the current data, only rare fossils (particularly of the skull and mandibles) pertain to this species. They were only discovered within the Grotta del Cerè (Verona), a place in which more abundant fossils of *U. spelaeus* and less frequently *U. arctos* LINNAEUS, 1758, have been gathered. This cave holds many bone remains, forming a very rich association: Amphibia indet., Reptilia indet., Aves indet., *Sorex* sp., *Talpa* sp., *Marmota marmota*, *Evotomys* [recte *Clethrionomys*] sp., *Dolomys* [recte *Dinaromys*] *bogdanovi*, *Arvicola* sp., *Allophaiomis* sp., *Microtus agrestis*, *Microtus arvalis*, *Microtus nivalis*, *Microtus* sp., *Apodemus sylvaticus*, *Glis glis*, *Canis lupus*, *Canis lupus* aff. *mosbachensis*, *Canis* sp., *Vulpes vulpes*, *Vulpes vulpes crucigera*, *Vulpes* sp., *Ursus arctos*, *Ursus spelaeus*, *Ursus spelaeus minor*, *Ursus* sp., *Mustela putorius*, *Gulo gulo*, *Martes martes*, *Martes* sp., *Panthera leo spelea*, *Panthera* cf. *pardus*, *Panthera* sp., *Sus priscus*,

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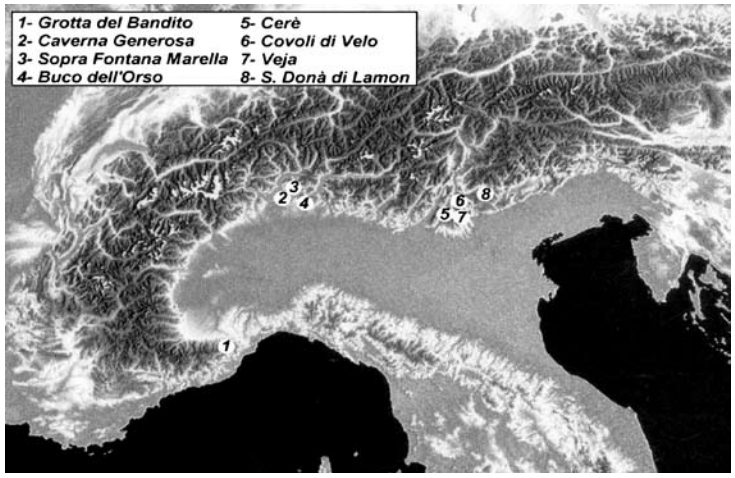

Figure 1. Distribution of the main caves in northern Italy containing remains of *Ursus* gr. *deningeri-spelaeus*.

Sus scrofa, *Sus* sp., *Cervus elaphus*, *Cervus* sp., *Bos* sp., *Rupicapra rupicapra*, *Capra ibex* and *Capra* sp. (Bon *et al.,* 1991). The presence of the three species of bear mirrored a long inhabitation of the cave by this vertebrate: considering the other species allied to the bear remains, particularly the micromammals, it is likely that the older fossils are at least 400.000-500.000 years old. Globally the Cerè's fauna might be referred to the uppermost Galerian?-Aurelian. Fossils from Covoli di Velo are certainly more recent, pertaining to the Late Pleistocene.

A distribution of the fossil bears in northern Italy can be listed: Piedmont: (1) Grotta delle Streghe: *Ursus spelaeus*; (2) Mt. Fenera: *Ursus spelaeus*; (3) Grotta del Bandito: *Ursus spelaeus*. Lombardy: (1) Grotta Sopra Fontana Marella: *Ursus spelaeus*, *Ursus arctos*; (2) Grotta Generosa: *Ursus spelaeus*, *Ursus arctos*; (3) Grotta Buco dell'Orso: *Ursus spelaeus*, *Ursus arctos*; (4) Grotta delle Ossa: *Ursus spelaeus*, *Ursus arctos*. Veneto: (1) Cerè: *Ursus deningeri*, *U. spelaeus*, *U. arctos*; (2) Covoli di Velo: *Ursus spelaeus*; (3) Veja: *Ursus spelaeus*; (4) S. Donà di Lamon: *Ursus spelaeus*. Considering the rarity of *Ursus deningeri* not only in northern Italy, but also in the whole Italian peninsula (other fossils are found in Central Italy), its presence within the Grotta del Cerè has great importance. There are possible signs of this species even in the Grotta delle Ossa in neighbouring Zandobbio village (Bergamo Province, north of Milan, Lombardy), but we need to wait for the conclusions of the research in order to confirm the eventual presence of this species. If future research confirms the uniqueness of the discovery in the Grotta del Cerè, it might become even more significant. In fact, on the basis of these data, this area could represent at least a regional expansion nucleus.

The possibility that the species *Ursus deningeri* Von Reichenau, 1906 and *Ursus spelaeus* Rosenmüller, 1794 should not really be two different taxa, but of the same taxon, has been advanced by several authors previously, and is still an unsolved problem. In recent years more detailed studies have been conducted, examining morphological and morphometric features for a distinct separation of the two species. Referring to the bears from Veneto, the first step involved the mandibles from Grotta del Cerè; a range of fundamental taxonomic elements were noted, above all concerning the vertical branch and the dentition. The main features are: (1) high condyle and angular process; (2) large masseteric fossae with right posterior border; (3) great diminution of the conic portion of the condyle; (4) complication of the masticatory surfaces.

Morphologically the main differences occurred in the vertical branch: in *U. deningeri* there is less elevation of the condyle and angular process compared with *U. spelaeus*. Morphometrically *U. deningeri* (compared with *U. spelaeus*) presents: (1) less sturdiness of the horizontal branch, either vertically or horizontally; (2) less height of the condyle; (3) less breadth of P_4. On the basis of current data, a distinction between the two species is not clear, and the transition between *U. deningeri* and *U. spelaeus* is gradual and almost insignificant. This may confirm the hypothesis that, at least for the *deningeri-spelaeus* group in Italy as well as in other European areas, we cannot speak of two clearly different species (Grandal d'Anglade & López González, 2004), but rather of an intraspecifical variability. In future, new studies on the material will give us further knowledge in order to confirm this belief.

Morphology: Referring to the bears from Grotta del Cerè and Covoli di Velo (the most significant caves for this study) it is possible to summarize as follows. Fossils from Cerè show features globally approximating to those typical of the cave bears group (in the widest view)

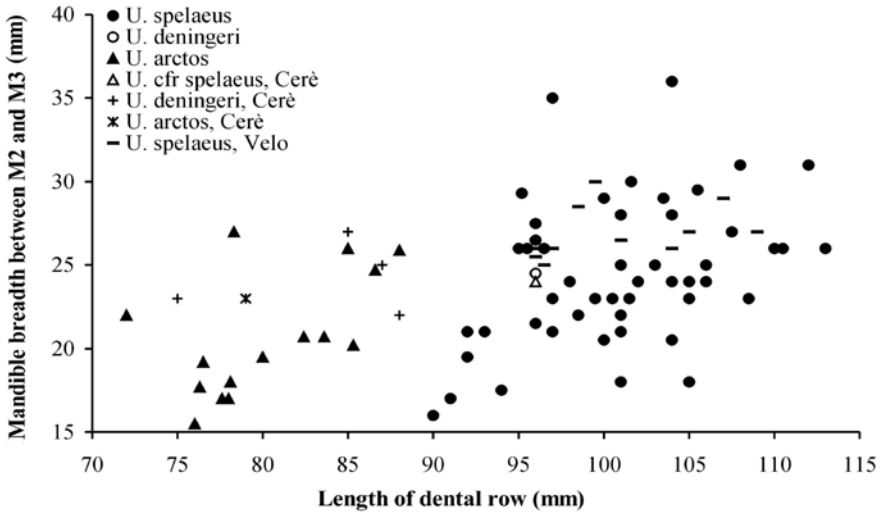

Figure 2. "Length of the dental row" and "Breadth of the mandible between M_2 and M_3" relationships in cave bears from Veneto and other caves.

comprising the two species *U. deningeri* and *U. spelaeus* (Kurtén, 1976; Ficcarelli, 1979; Ballesio, 1983; Torres Perez-Hidalgo, 1988; Argant, 1991; Mazza & Rustioni, 1994; Ballesio *et al.,* 2004). The vertical branch is characterized by rising of the condyle and angular process with consequent undertaking on the horizontal branch of the same. Except the smallest remain where the P_1 alveolus is still observable and the diastema shows a great concavity, the horizontal branch maintains the almost sturdy proportions. In all cases condyles show strong development of the cylindrical portion compared with the conic one.

Spelean bear remains from Covoli di Velo can be divided into two main groups: a group related to the female and juvenile elements, with the horizontal branch of the mandible being longer and less sturdy, and a second ascribed to the adult males with a more sturdy morphology and a shorter horizontal branch. The vertical branch always is more or less greatly leaning against the horizontal branch, with consequent rising of the condyle and of the angular process. Condyles are sturdy and more developed in the cylindrical portion than in the conic one.

Morphometry: Referring to the bears from Cerè and Covoli di Velo, utilising the more meaningful parameters indicated by Torres Perez-Hidalgo (1988) and their more important relationships, it is possible to introduce some considerations.

(1) Firstly, considering the relationship between the mandibular parameters (breadth of the mandible between M_2 and M_3 and length of the dental row) (fig. 2), in a general viewpoint the sizes of *U. deningeri* are approximately the same as those of a great brown bear, except for one mandible having a smaller size. The nearly complete lack of data concerning *U. deningeri* from other caves does not allow for much comparison; therefore in the former analysis the Deninger bears from Cerè overlap the dimensional range of the Spanish populations. For all mandibles the size of the horizontal branch compared with the length of the dental row seems to show the mandibular branch reinforcement typical of the speloid evolutionary line. This trend is confirmed by data of the mandible from Covoli di Velo, featuring strong development in a transversal line of the horizontal branch. The increase in size reached by *U. deningeri* at the *U. spelaeus* transition (Torres Perez-Hidalgo, 1988) allows us to consider the Cerè's deningerians as almost primitive forms, particularly the specimen having a smaller size characterised by an almost frail horizontal branch.

(2) The morphometric analysis of the condyles (fig. 3) confirms all previous data. In particular, main heights in the *spelaeus* bears are shown, while in *U. deningeri* the sizes and dimensions are intermediate between the two species. The fossil from Grotta del Cerè has the smallest size, smaller than typical of the species (Torres Perez-Hidalgo, 1988). This might be a consequence of two factors: lack of comparative data, or a particularly small individual for this species. However, the designation as *U. deningeri* for this fossil is defined by the morphology of the condyle. Fossils from Covoli di Velo, even if characterised by squashed condyles, are within the dimensional

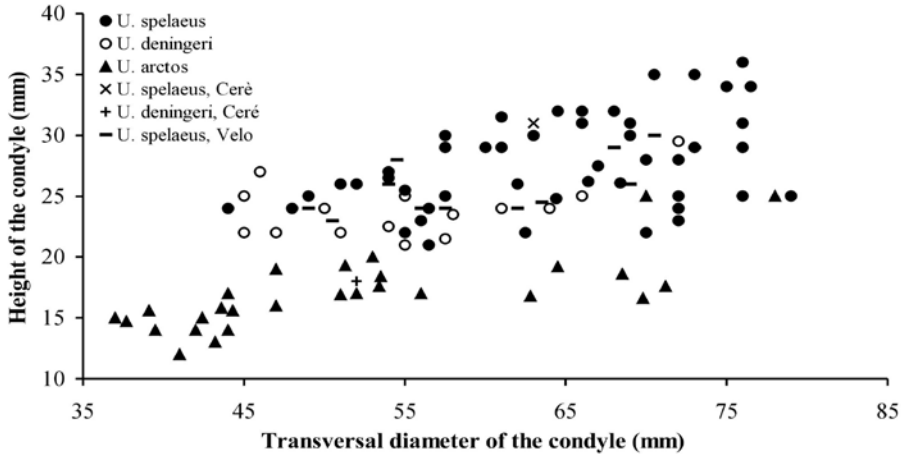

Figure 3. "Transversal diameter of the condyle" and "Height of the condyle" relationship in cave bears from Veneto and other caves.

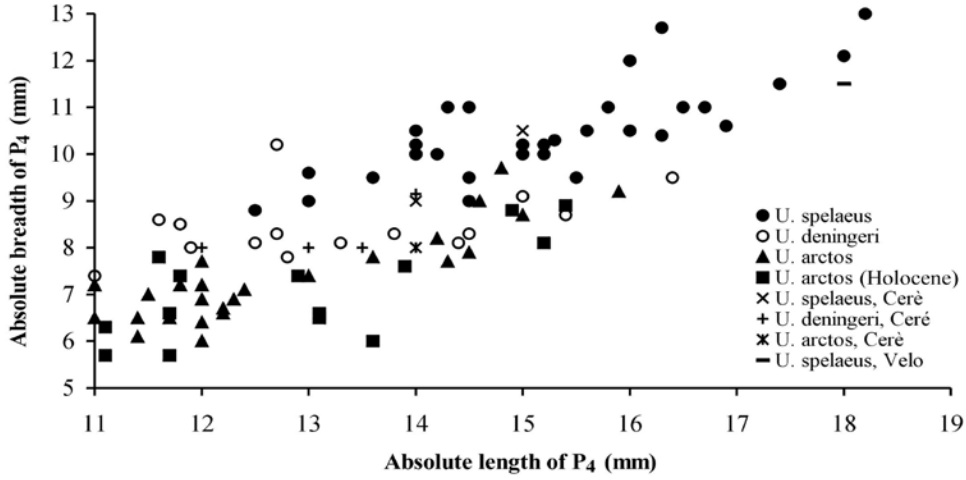

Figure 4. "Absolute length of P_4" and "Absolute breadth of P_4" relationship in cave bears from Veneto and other caves.

range typical of the cave bears.

(3) To conclude, concerning the dimensional parameters of P_4 (fig. 4) with the same absolute length, the breadth values are higher in *U. spelaeus* than *U. arctos*, while in *U. deningeri*, intermediate values occurred. Also in this case the data confirm those of the morphology: in fact, the crown boundary that more usually is shown within the three species is ellipsoidal acute in the arctoid forms, ellipsoidal large in the deningerians, and sub-circular in the speleoid specimens too. Some of the fossils from Grotta del Cerè overlap with the variability of *U. deningeri*, also showing low values even for this species, and in two cases corresponding to the *U. spelaeus* dimensions, indicating a medium-small size.

MORPHODYNAMIC ANALYSIS OF P_4 AND M_1

The morphodynamic analysis of P_4 and M_1 *sensu* Rabeder (1999) and Grandal d'Anglade & López González (2004) is the key for establishing the step reached by the cave bear in its phyletic path. This approach was applied on teeth coming either from the various Italian caves (i.e. Bona, 2004; Quiles, 2004; Zunino & Pavia, 2005; Stoppini *et al.*, 2005 an so on) or others (Grandal d'Anglade & López González, 2004).

Bears from Cerè pertaining to *U. deningeri* show P_4 with a very simple morphology characterised by a few developed paraconids and with two accessory tubercles (lingual and postero-lingual). They show some analogies either with fossils from Petralona of the Middle Pleis-

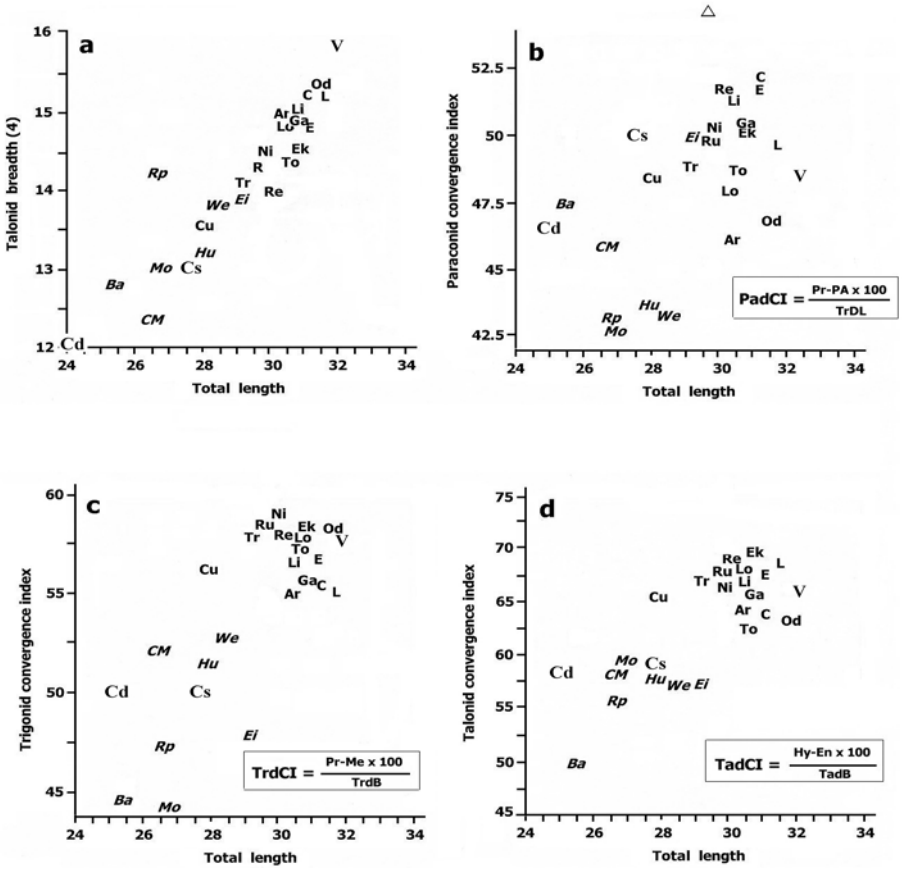

Figure 5. a. Relationship between the "Total length" and "Total breadth", b. Relationship between the "Total length" and the "Paraconid convergence index", c. Relationship between the "Total length" and the "Trigonid convergence index", d. Relationship between the "Total length" and the "Talonid convergence index" in M_1 from Italian and other caves (from Grandal D'Anglade & López-González, 2004, mod.) Symbol legend for M_1 from Italian caves: Cd, Cerè *deningeri*; Cs, Cerè *spelaeus*; V, Covoli di Velo. Other sites: IBERIAN PENINSULA: E, Eirós; C, A Ceza; L, Liñares; Ar, Arrikrutz; Tr, Troskaeta; Ek, Ekain; To, Toll; Re, Reguerillo; CM, Atapuerca (Cueva Mayor). BRITISH ISLES: Ba, Bacton; We, Westbury. CENTRAL EUROPE: Ei, Einhornhöhle (Scharzfeld); Rp, Repolust; Ru, Rubeland; Ga, Gailenreuther (Zoolithenhöhle); Hu, Hundsheim; Ni, Nixloch; Li, Liegloch; Cu, Conturines. EAST: Lo, Loutraki (Greece); Od, Odessa (Ukraine).

tocene (Rabeder & Tsoukala, 1990) or with those ascribed to *U. deningeri* from "Grotte des Fées" (Ballesio *et al.,* 2004). The *U. spelaeus* premolar corresponds to the C1 morphotype *sensu* Rabeder (1999).

P_4 from Covoli di Velo have a more evolute morphology approximating to the C1 morphotype or even more evolute ones, characterised by the appearance of secondary cusps and ridges.

According to Grandal d'Anglade & López González's (2004) interpretation of *spelaeus* bears, two typologies of M_1 exist: one typical of the "primitive" bears and a second concerning the more "modern" ones. In these last the hypothetical trigonid section (protoconid-metaconid) shows a more dipped border, and the surface having these two elements as extremities is wider. Passage from protoconid (where the apex within the modern speleians is more blunted) to metaconid is identified by a less dipped boundary; the metaconid is not directly linked to the protoconid, but it is lightly separated. In the hypoconid side the talonid section (hypoconid-entoconid) shows a much more dipped boundary than in the older populations, and above all, there is a little collar with an inflated appearance. This defines the crown base having a more wavy boundary in the more modern populations. In modern bears the passage from the hypoconid to entoconid, with less blunted apex, is more indented (depending on a prominent hypoconulid).

Globally the morphological features of the tooth correspond to those shown in the evolutionary schema of Grandal d'Anglade & López González (2004, fig.

2). In fact, the *U. deningeri* teeth have the more primitive features, as well as the acute paraconid and fewer of the accessory cusps that, in contrast, appear within the *U. spelaeus* teeth. All remains from Covoli di Velo belong to *U. spelaeus*, and globally show evolutionary features either in the morphology of the cusps or in the complexity of the masticatory surface.

Figs 5 a,b,c,d mirror the relationship between the "*Total Length*" and the "*Talonid Breadth*" of M_1 and those between the "*Total Length*" and the "*Convergence Index*" respectively of the paraconid, trigonid and talonid (*sensu* Grandal d'Anglade & López González, 2004).

1) In the former, the smaller size of the remains pertaining to *U. deningeri* from Cerè is shown, with fewer teeth coming from Bacton, a deposit of Early Pleistocene age (Kurtén, 1969; Bishop, 1982). Those of *U. spelaeus* have a size similar to those of Mosbach and Hundsheim, both ascribed to the Middle Pleistocene (Zapfe, 1946; Kurtén, 1969). Teeth from Covoli di Velo have a large size as well as those of speleians from the caves of the Late Pleistocene.

2) Observing the other diagrams, as already indicated by Grandal d'Anglade & López González (2004), schemas labelled with "C" and "D" are those that best show the evolutionary trend. The remains pertaining to *U. spelaeus* have a lower convergence degree for the paraconid than the bears of the Late Pleistocene caves. Convergence indices of the talonid and trigonid are, instead, very similar for the two species compared with those of the Middle Pleistocene deposits. Probably, the former of these graphs is biased by the morphological variability of this part of the tooth, while referring to the talonid and trigonid, the model is more defined. Hence, based on these data the Cerè cave's speleoid and deningerian forms might be closer together and placed on the transition interval between the two species.

3) Concerning the teeth from Covoli di Velo, they have a convergence index corresponding to those typical of the Late Pleistocene deposits.

CONCLUSIONS

Fossils from Grotta del Cerè and Covoli di Velo seem to represent the opposite extremes of the phyletic line of the cave bear. From the former come remains pertaining to the species *U. deningeri* and almost primitive forms of *U. spelaeus*. From the latter come only fossils with morphological and morphometric features typical of the more evolved speleans.

Confirmation of this in particular comes from the morphological and morphometrical features of P_4 and M_1. Comparison with material from other caves seems to confirm this deduction, suggesting for the older fossils from Cerè a chronological data in the Middle Pleistocene, and confirming that already advanced by Zorzin *et al.* (2005) for remains from Covoli di Velo. At the last, even the data concerning the faunal association of these caves seem to agree with this hypothesis.

Inside the Grotta del Cerè, *U. arctos* remains have been also gathered; it surely inhabited this cave successive to the *U. spelaeus* extinction. Paucity of remains pertaining to the more evolved forms of *spelaeus* is probably fortuitous, perhaps linked to the low number of fossils discovered in previous field surveys.

The presence of *U. deningeri* inside the Grotta del Cerè only, may underline the hypothesis that this population was an original stem from where other populations of the caves within the Verona area (i. e. Covoli di Velo and Veja) descended. It will be important to carry out some studies on the mtDNA of these populations, even if the first investigations on Austria's populations seem to indicate substantial isolation among almost closed populations (Hofreiter *et al.,* 2004).

Furthermore, study of the fossils from these caves has indicated some useful morphological and morphometrical features for separating the species *U. deningeri* from *U. spelaeus,* and included these data in the debate about the validity of these two species. Transition between *U. deningeri-U. spelaeus* occurred gradually and independently in the different European areas, and in a general view, cannot be chronologically established for the different sectors of Europe. Therefore it is difficult to show the separation between the two species (Grandal d'Anglade & López González, 2004 and references therein; Rossi & Santi, 2005). Previous authors (Kurtén, 1976; Andrews & Turner, 1992; Mazza & Rustioni, 1994; Vila Taboada & Grandal d'Anglade, 2001) have raised the possibility that the fossils represent not two different taxa, but the first and the last form of the same taxon. This is still an unsolved question. Morphologically the main differences are shown in the vertical branch of the mandible (*U. deningeri* has a lower condyle and angular process than in *U. spelaeus*). Morphometrically in *U. deningeri* the horizontal branch is less sturdy either vertically or horizontally than in *U. spelaeus*, with a lower condyle and narrower P_4 dimensions. This might enhance the hypothesis of a single taxon as suggested by Mazza & Rustioni (1994) and Vila Taboada & Grandal d'Anglade (2001). Fossils from Grotta del Cerè, as well as those of the other populations from Veneto (i.e. S. Donà di Lamon, Veja and Covoli di Velo) and Lom-

bardy (Buco dell'Orso-Laglio, Como Province north of Milan), show morphological and morphometric features that seem to suggest the presence of a unique species. It is possible to distinguish the "old" forms (corresponding to *U. deningeri* and early *U. spelaeus*) and the "modern" ones. Data concerning the metapodial bones from the Busa di Bernardo (Predazzo, Trento Province, Trentino Alto Adige) (data in progress) seem to confirm this. In contrast, recent studies on the mtDNA have caused several authors to exclude the species *U. deningeri* as the ancestor of *U. spelaeus,* rather considering it as a "sister group" of the same (Orlando *et al.,* 2000). Studies yielded by Torres Perez-Hidalgo *et al.* (1991) and Rabeder *et al.* (2004) show a strong differentiation within the speloid phyletic branch, with the appearance of several species and subspecies. Surely the great variability within the cave bear, much clearer within these recently studied populations, and maybe even dependent on the particular geographical situation, is at present still an open question.

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