

***Ursus spelaeus* from the Buco dell'Orso Cave (Laglio, Lombardy, North Italy): an evolutionary hypothesis**

G. Santi[#] & M. Rossi^{*}

[#]corresponding author
Dipartimento di Scienze della Terra
Via Ferrata 1 I-27100
Pavia, Italy
gsanti@unipv.it

^{*}Museo Civico di Storia Naturale
Lungadige Porta Vittoria 4 I-37127
Verona, Italy

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Abstract

Ursus spelaeus from the Buco dell'Orso Cave (Lombardy, North Italy) has some peculiar metrical characteristics that make it more close to *Ursus deningeri* rather than to the typical *spelaeus*. In particular, it is the smaller size that makes the difference. In this study, the 'regressive evolution' is proposed; a hypothesis linked to possible climatic cooling and presented here on the basis either of new data or in comparison with observed analogies on fossils from Italian and foreign caves.

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1. Introduction and generalities

Caves of the Alpine and pre-alpine area of northern Italy often represent very rich deposits of bear fossils. The object of this study are fossils of the cave bear (*Ursus spelaeus* Rosenmüller, 1794) found in the Buco dell'Orso Cave (Laglio, Lombardy, north Italy) (figure 1). The faunistic association of this cave was studied by Cornalia (1850, 1858–71), Airaghi (1922, 1927), Rossi Ronchetti (1958), Santi (2000) and Arduini *et al.* (2002).

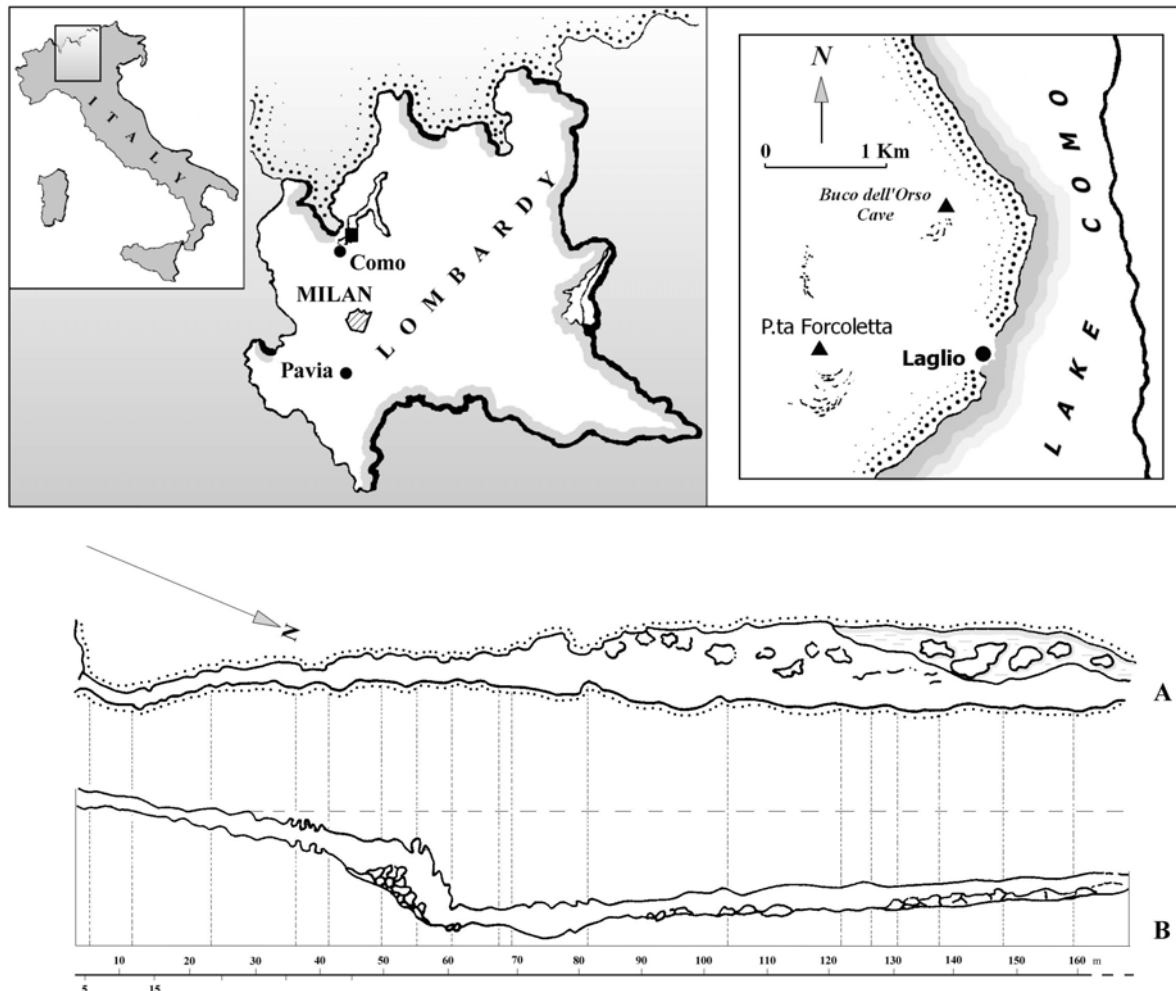


Figure 1. Geographic position, longitudinal (A) and transversal (B) sections of the Buco dell'Orso Cave (after Cornalia, 1858–1871).

Morphological data (Santi & Rossi, 2001a; Rossi & Santi, 2001; Santi *et al.*, 2003) allow us to identify most of the material as *Ursus spelaeus* while recognising that some isolated teeth are identified as those of the brown bear (*Ursus arctos* Linnaeus, 1758) by Santi & Rossi (2001a). The co-existence of the two species is documented several times, but the number of specimens of the cave bear is always fewer relative to the brown bear (Kurtén, 1976; Stiner, 1998). The recent discovery of remains of *Myotis* (*Selysius*) *bechsteini* (Leisler, 1818) (Santi, 2000) and *Panthera leo spelaea* (Goldfuss, 1810) (Arduini *et al.*, 2002) added greatly to the fauna association of the Buco dell'Orso Cave.

The cave (land propriety register nr. 2207 LoCo), opens out on Mt. Generoso at 648 m above sea level, on the western side of Lake Como. The cave is a typical karst phenomenon (dolina–sink), set in the grey calcareous micritic limestones of the Lower Middle Lias Period. The Buco dell'Orso Cave is a large cavity about 300 m long and with a maximum height of 15 m. Initially it runs in an east/northeast–west/southwest direction but then changes direction into west/northwest–east/southeast. It finally terminates following a narrow passage in an underground lake.

Briefly, starting at the base, the following layers have been identified in the cave: a) Stalagmitic layer covering one of shale, b) Yellow shale with a few calcareous fragments and iron oxides, c) Brown shale, d) Very

pure shale, e) Stalagmitic crust evenly widened, f) Sand and calcareous fragments. The bone remains originate from the yellow shale layer.

A deepening of the studies on the bear remains from the Buco dell'Orso cave will be done using mtDNA analysis, together with the overall radiometric age of the fossiliferous layer. At present, a first evaluation using mtDNA is in progress.

2. Material and methods

The fossils found in the cave include about 350 metapodials, 100 long bones, and some 50 cranial and mandibular parts. The fossils are stored in three institutes: the Dipartimento di Scienze della Terra of Pavia University, the Museo Civico di Storia Naturale of Milano (Lombardy) and the museum linked to the "A. Volta" Classic High School in Como (Lombardy). The various portions of the skeleton are well-represented and the good preservation of the cranial bones together with only very few traces of gnawing and/or predation traces, clearly indicates that little disturbance of the remains occurred over time. Furthermore, the large quantity of long bones might indicate a rapid fossilisation, as explained by Fosse *et al.* (1997), for at least part of the material. A series of measurements, using codified parameters (Hue, 1907; Von den Driesch, 1976; Torres Pérez Hidalgo, 1988) are taken.

3. Brief morphometric analysis

Before discussing the morphometric analysis, a brief summary is presented indicating the main anatomical differences of the different species of bears (*Ursus deningeri* Von Reichenau, 1906–*Ursus spelaeus* group and *Ursus arctos*). For a detailed analysis of features, reader is referred to Torres Pérez Hidalgo (1988).

3.1. Main anatomical differences

In lateral view, in *Ursus deningeri* and *Ursus spelaeus* the posterior border of the vertical branch of the mandible appears as a rectilinear line, about regular and dipped to the back and downwards. This feature also produces the increase of the area for the masseter housing that supports the decrease of the lever arm linked to the undertaking of the vertical branch over the horizontal one. Inside *Ursus etruscus* and *Ursus arctos*, having a supposed more carnivorous diet, the posterior border is featured by a regularly concave line (Torres Pérez Hidalgo, 1988). From *U. etruscus* to *U. arctos* and overall to *U. spelaeus*, a profound uplift of the condyle is shown (Kurtén, 1976; Ficcarelli, 1979; Mazza & Rustioni, 1994). Consequently, in *U. deningeri* and in *U. spelaeus* the articulation point of the mandible with the skull is clearly over the extension of the hypothetical line drawn on the base of the teeth line rather than above it rather than to find it over the extension of the hypothetical line drawn on the base of the teeth line. The condyle in *U. etruscus* and in *U. arctos* are of large size in transversal view but shorter in vertical view; they have a cylindrical morphology in the more internal third, and conical in the remaining part. In *U. deningeri* an important variation is shown: a strong increase of the height of the condyle because it is cylindrical in the more internal middle. In *U. spelaeus* this phenomenon is even more marked; the conical portion of the condyle is strongly reduced (Torres Pérez Hidalgo, 1988; Mazza & Rustioni, 1994).

An uplift of the forehead compared to the upper border of the snout with consequent breakage of the profile to the height of the eyes and formation of a profound hollow that divides the facial portion from the cerebral one is observed in *Ursus spelaeus* and in *Ursus deningeri* (Kurtén, 1976; Torres Pérez Hidalgo, 1988; Mazza & Rustioni, 1994). This feature is not observable among the more ancient forms of *U. deningeri*, but only in the final ones of the species (Torres Pérez Hidalgo, 1988). Furthermore, compared to the *U. arctos*, a strong decrease of the convexity of the neurocranium is noted.

The morphological differences in the long bones are overall concentrated in the proximal epiphyses, with their main torsion in the forms belonging to the cave bears group in comparison to the brown bear. In the metacarpi and metatarsi some differences referring to the articular surface of the proximal epiphyses are observable.

3.2. Analysis

In general, the morphometric data show inferior sizes relative to the typical *Ursus spelaeus*, of which one of the main characteristics is its large size (*i.e.* Kurtén, 1976; Torres Pérez Hidalgo, 1988; Mazza & Rustioni, 1994) (figures 2, 3, 4) for which the following reasons can be suggested:

- The degree of wear of the teeth and the suture fusion of the skull, the data (figures 2A–B) point to a sub-adult age of the specimens. More in particular in figure 2A division of the two species is clear; the

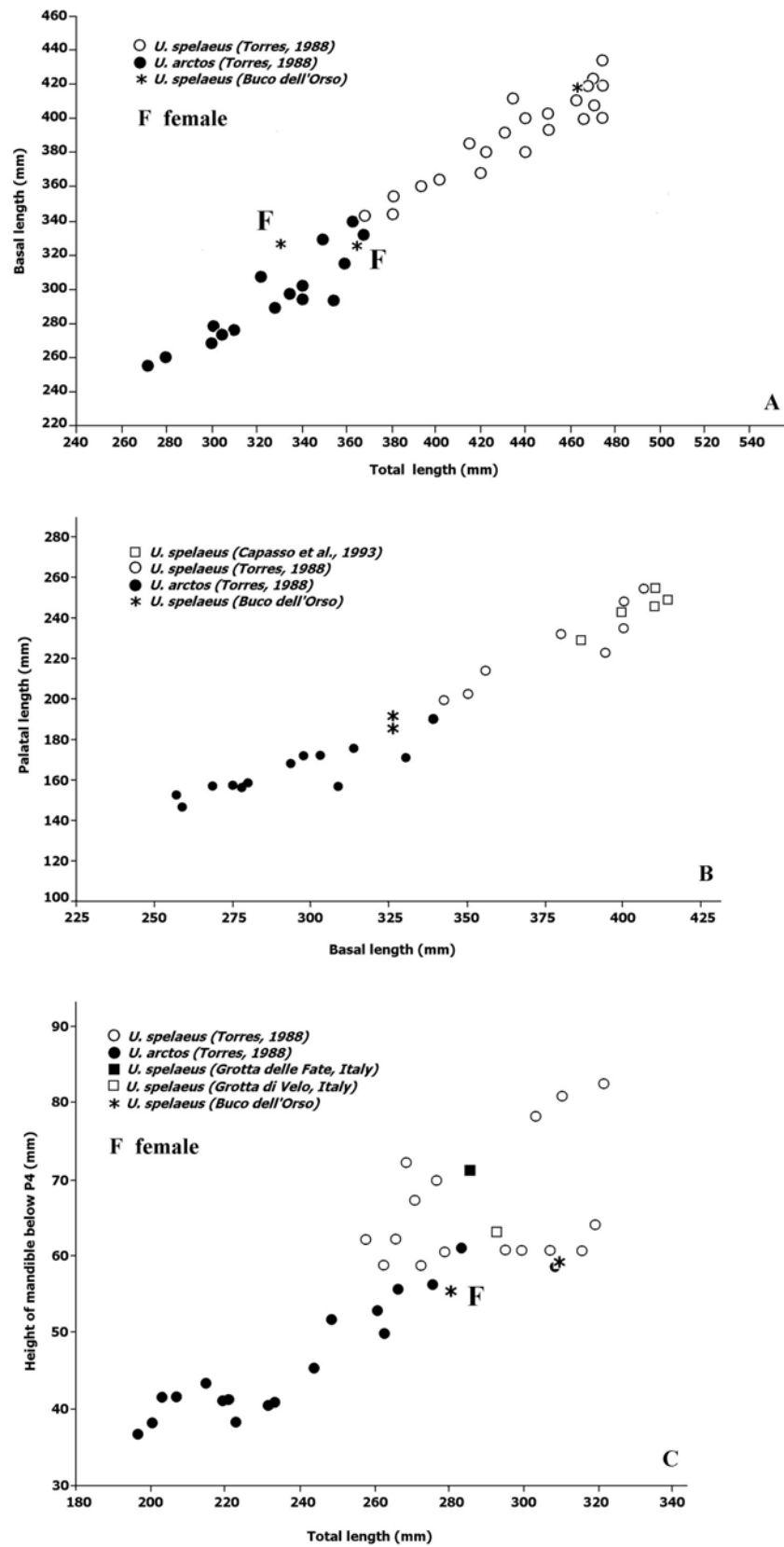


Figure 2. Bivariate plots of cranium (A–B) and mandibular (C) measurements of the bears (Santi & Rossi, 2001a). Measurements taken as in Von den Driesch (1976).

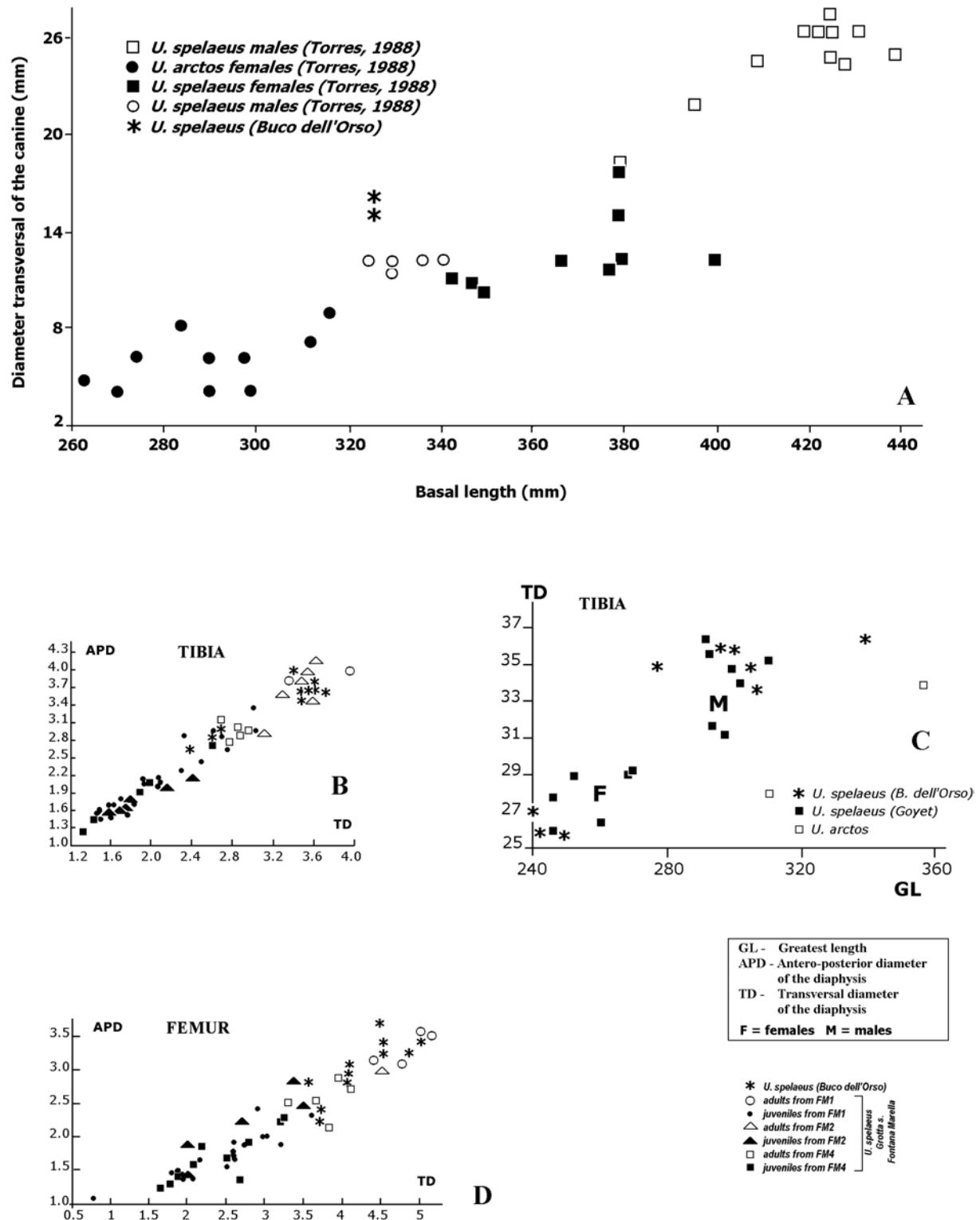


Figure 3. Bivariate plots of the transverse diameter of the canine and basal skull length (A). Bivariate plots related to tibia (B). Bivariate plots related to tibia (C) in bear from Buco dell'Orso and Goyet (Belgium) in order to better clarify the male and female separation and bivariate plots related to femur (D) of the Buco dell'Orso fossils and those from Grotta Sopra Fontana Marella. Measurements taken as in Von den Driesch (1976).

total length of *Ursus spelaeus*'s skull is proportionately bigger. Overlapping only occurs in the skulls of male *Ursus arctos* and female *U. spelaeus*. Using a parameter not subjected to further growth, such as the 'Canine Transversal Diameter' (figure 3A), one can suppose that in the adult stage these specimens could reach the dimensions of a small sized male. It is probable that the large size measured by Capasso Barbato *et al.* (1993) should be linked to bears at the uppermost part of bear evolution (Santi & Rossi, 2001b). Furthermore, observing figure 2B the correlation (0.94) is very good for *U. spelaeus* but also reasonably good for *U. arctos* (0.70), then the palatal length in relation to the basal length in *U. spelaeus* is higher than in *U. arctos*. The consequence is that the snout of *U. arctos* is squatter than that of *U. spelaeus*.

- Even data relative to the mandibles (figures 2C–3A) suggest dimensions in general inferior to typical *Ursus spelaeus*. Figure 2C shows a scatter diagram of the relation between the total length and height of the mandible below P₄ of the material from Buco dell'Orso Cave (surely with speloid morphology Delle Fate Cave, Liguria Region) and Covoli di Velo (Venetia Region). The Buco dell'Orso Cave material is smaller in size.

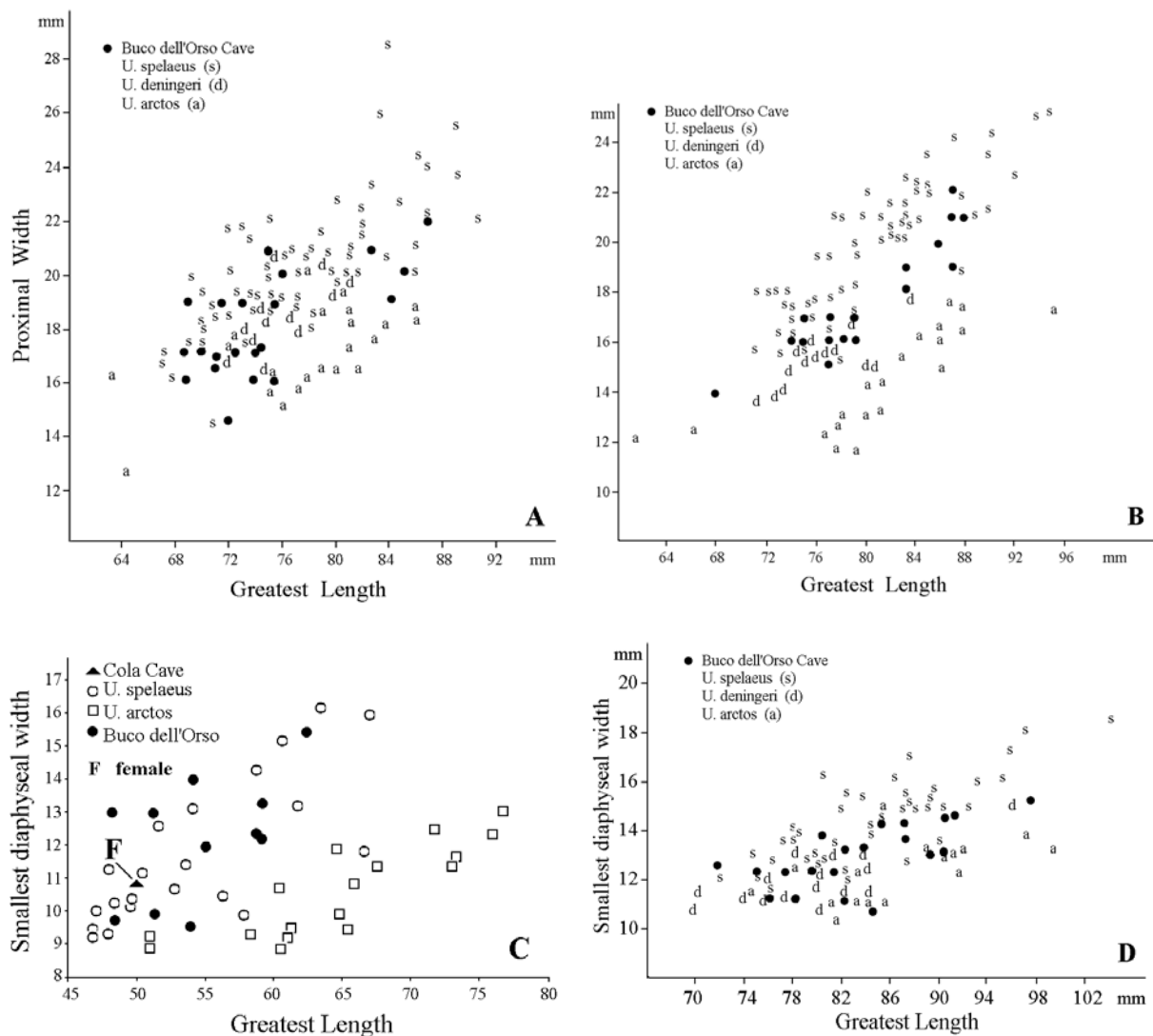


Figure 4. Bivariate plot related to the proximal width and the greatest length in III metacarpus from Spanish and Buco dell'Orso caves (A). Bivariate plot related to the proximal width and the greatest length in V metacarpus from Spanish and Buco dell'Orso caves (B). Bivariate plot related to the smallest diaphyseal width and the greatest length in I metatarsus from Spanish, Buco dell'Orso and Cola caves (C). Bivariate plot related to the smallest diaphyseal width and the greatest length in V metatarsus from Spanish and Buco dell'Orso caves (D) (after Santi *et al.*, 2003). Parameters from Von den Driesch (1976).

- Similar considerations can be carried out with regard to the post-cranial skeleton (figures 3B–D, 4). A small overlap between the two bear species (*Ursus spelaeus* and *Ursus arctos*) is visible, especially in the absolute length. The plumpness index of the anterior and posterior metapodia, which are more slender than the typical forms (Santi *et al.*, 2003), confirms this observation. More in particular figure 4A (III metacarpus) shows that many points fall in the lower area of the dispersion cloud of the *U. spelaeus* fossils and confirming that in general the Buco dell'Orso bears were small sized. Of particular interest is the comparison of some femora and tibia remains from the Sopra Fontana Marella Cave (Varese Province, Lombardy, north Italy) (Perego *et al.*, 2001). These authors noted a variation in size from the most ancient levels to the more recent ones. Several remains from the Buco dell'Orso Cave (figures 3B–D) show sizes that correspond to the small sized adult remains from Sopra Fontana Marella Cave's FM4 level (which is the oldest in the succession of levels of this cave). The four levels richest in bear remains from the Grotta Sopra Fontana Marella are studied by Perego *et al.* (2001, figure 2). They are indicated from the oldest (FM4, older than 26000 years) to the youngest FM1 (22310 ±200 years).
- The morphometric analysis of the mandibles (figures 2C, 3A), the metapodia and the long bones indicate the presence, among the remains found, of female specimens (Santi & Rossi, 2001; Santi *et al.*, 2003). The comparison with recently discovered tibia remains from Goyet, Chamber B (Belgium) (Germonpré & Sablin, 2001) (figure 3C) confirms this. In fact, this diagram better clarifies the male and female separation as the diagram of the figure 4B (V metacarpus); in this last the fossils from Buco dell'Orso fall in a lower position in the dispersion cloud. This concept is also carried observing figure 4C (I metatarsus) whose the Cola Cave specimen is surely a female (Di Canzio & Petronio, 2001).

4. Discussion

The smaller size observed in a good part of the *Ursus spelaeus* remains from the Buco dell'Orso Cave can be explained by the action of several factors.

- Climatic. The presence, close to the small size remains, of specimens of dimensions almost those of the typical *Ursus spelaeus*, suggests the possibility that the cave represents different periods of the Pleistocene, to which the different sizes could be associated. Perego *et al.* (2001) studying the remains from the Sopra Fontana Marella Cave, link the FM4 level, which contains the smallest samples, to a warmer climatic event compared to that associated with the upper layers. Variations in size depends according to Bergmann's rule (1847). It argues that the body size is related to thermoregulatory advantages: heat loss in larger size is due to the lower surface to volume ratio. So larger forms would be distributed in cooler regions. Criticism to Bergmann's rule was published by several authors (Scholander, 1955, 1956; Geist, 1987; Boyce, 1978) arguing that larger bodies require more food and in a cool environment this can be a disadvantage. Boyce (1978) suggests: "the length of time that an individual can survive without food is positively correlated with the body weight (Morrison, 1960)". According to this note and to Perego *et al.* (2001: 460): "...a larger size for cave bears could mean enhanced survival during winter hibernation lasting much longer in a colder period." Rabeder & Nagel (2001) link the size reduction to the 'regressive evolution' phenomenon in order to explain the bear sizes of the Ramesch–Knochenhöhle Cave (Austria), which has an estimated age of at least 35000 years. These authors link the smaller sizes to a climate cooling event, which caused inferior growth of the skeleton. Gerhard (2001) comes to the same conclusions, studying the metapodia from Italian and Austrian caves.
- Evolutionary. Some authors link the reduced dimensions of *Ursus spelaeus* in some deposits to evolution (*i.e.* Perego *et al.*, 2001). Confirmation comes from Rabeder & Nagel (2001), because they explain the reduced size of the cranial remains from Buco dell'Orso Cave by assigning it to a different, smaller, species, namely *Ursus deningeri* species (*pers. comm.*). Withalm (*pers. comm.*), comparing data relative to metapodia from Buco dell'Orso Cave with material collected in Austrian caves, locates the bear of this deposit much closer to the remains from Repolust Cave (Stiria, Austria) (*U. deningeri* of small dimensions) and to the bear from Conturines Cave (Tyrol, north Italy) (which seems closely related to *U. deningeri*). Bear remains with morphological and morphometrical characteristics very similar to those observed in the fossils from Laglio are discovered in the Cerè Cave (Ceredo village, Verona, Venetia Region, north Italy) (Rossi & Santi, 2001). The morphological and morphometric analysis and a preliminary morpho–dynamic teeth examination show how these bears, even if belonging to the *U. spelaeus* group, are close to the transition forms between *U. deningeri* and *U. spelaeus* (Rossi & Santi, 2001; Santi & Rossi, 2001b). At present the distinction between *U. deningeri* and *U. spelaeus* is still debated (most recently by Ballesio *et al.*, 2003, and references therein).
- Sexual dimorphism. The material from Buco dell'Orso Cave can be divided in two sizes categories. The first category is characterised by values below the typical values of the species: the cranial and

mandibular bones, the metapodia and a part of the long bones belong to this group. The other long bones belong to the second category, which is characterised by values close to the typical values of the species. The presence of remains of cubs and young bears have been noted among the fossils from this cave (Santi & Rossi, 2001a); consequently, the dimensional dualism could be explained more easily through the sex separation, a phenomenon already observed by different authors (Kurtén, 1976; Tintori & Zanalda, 1992). Recently, a discussion about the sex-ratio among the cave bears populations has been published by Schweizer (2004). It seems classic enough to observe the differences among the male and female elements within the cave bears populations discovered in caves, and is not linked to a difference in the birth number as in the past (Kurtén, 1955). In Kurtén's opinion the lack of balance in sexes should have some ecological origin; the males and females choose different caves for the winter. The females should prefer the caves of small size, the ones with bigger dimensions preferred by the males animals. The caves of intermediate size would have been inhabited by both sexes together (Kurtén, 1976). Kurtén's theory on sexes and cave-size preferences has recently been criticised by Weinstock (2000).

5. Conclusions

Rossi Ronchetti (1958), on the basis of the fauna list compiled by Cornalia (1850, 1858–1871) and Airaghi (1927), links the fossil deposit of the Buco dell'Orso Cave to the Würmian age, but the attribution to such a chronological interval is proposed on the basis of the presence in the cave of *Ursus spelaeus*. The recent discoveries of *Myotis (Selysius) bechsteini* (see Santi, 2000) and of *Panthera leo spelaea* as presented by Arduini *et al.* (2002) seem to confirm the chronological data.

It seems improbable that the fossils studied belong to forms close to the *Ursus deningeri*–*Ursus spelaeus* transition. As Withalm (pers. comm.) notes, on the basis of the comparison between the metapodia of bears from Buco dell'Orso Cave and from other Austrian and Italian caves, that the morphometric likeness to archaic forms can simply be linked to the poor number of bones analysed and the same can be concluded for the other parts of the skeleton. It is more likely, then, that the size reduction evidenced in most of the fossils should be ascribed to a climate-cooling event, similar to what Rabeder & Nagel (2001) suggest for the *U. spelaeus* population of the Ramesch–Knochenhöhle Cave. Moreover, Hofreiter *et al.* (2002: 1244) on the DNA analysis effected on chronologically different *U. spelaeus* specimens advance: "... that geographically separated populations of the high-Alpine cave bear form were polyphyletic with respect to their mtDNA. This suggests that small size may have been an ancestral trait in cave bears and that large size evolved at least twice independently". Finally, one cannot exclude that beside this phenomenon, called 'regressive evolution' in the present work, that the two size categories is the consequence of sex separation during winter hibernation.

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