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The latest *Ursus spelaeus* in Italy, a new contribution to the extinction chronology of the cave bear

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ABSTRACT

The skeleton of a young prime adult cave bear, *Ursus spelaeus*, was found in Chiostraccio Cave (Siena, Tuscany, central Italy), only slightly buried under rock falls. The specimen was dated yielding a conventional age of 24,030 ± 100 ^{14}C yr BP (29,200–28,550 cal yr BP), which makes it the latest known representative of the species in Italy. The skeleton was accompanied by the remains of wolf (*Canis lupus*), wild boar (*Sus scrofa*), aurochs (*Bos primigenius*), red deer (*Cervus elaphus*), roe deer (*Capreolus capreolus*), bat (*Vespertinus murinus*), and crow (*Corvus monedula*). The site seems confirming that the latest Italian *U. spelaeus* populations shared the risk of intrusion. The association of the cave bear with other animals suggests that the assemblage is an attritional palimpsest of remains of different species not originally associated in life. Cave bears were probably more vegetarian than brown bears and possibly became extinct when plant productivity dropped at the onset of MIS 2. Central and southern Italy may have offered isolated and sheltered refugia for cave bears.

Introduction

The disappearance of the cave bear (*Ursus spelaeus*) is one of the many major megafaunal extinctions that occurred within the late Pleistocene (Pleistocene megafauna includes species weighing more than 40 kg: Stuart, 1999). Stuart and Lister (2007) supposed that cave bears had adapted to a diet essentially made of high-quality herbaceous vegetation and became extinct when climatic cooling affected vegetational productivity around the onset of Marine Oxygen Isotope Stage (MIS) 2. Stuart and Lister (2007) and Pacher and Stuart (2009) found that cave bears probably disappeared from the Alps and adjacent areas about 24,000 ^{14}C yr BP (ca. 27,800 cal yr BP), approximately at the end of Greenland Stadial 3 (Lowe et al., 2008), which corresponds to the transition from the MIS 3, a period between 48 and 27 ka to MIS 2 (Dansgaard et al., 1993; Johnsen et al., 2001; Bocherens et al., in press). Stuart and Lister (2007) theorized that cave bears may have survived significantly later elsewhere, especially in southern Europe. To test these hypotheses, we need to detect when cave bears became extinct from its different areas of distribution, and particularly from southern districts.

To discover why cave bears disappeared we need to assess the degree of correlation between the time of its extinction and the occurrence of specific environmental circumstances. Attempts to date the extinction of cave bears are based on a direct-dating approach (e.g. Stuart et al., 2004; Stuart and Lister, 2007; Pacher and Stuart, 2009). A chronology for cave bear extinction is gradually being built up by putting together radiocarbon-dated cave bear remains (Münzel et al., 2011; Bocherens et al., in press). This paper is a contribution to the creation to this data bank, providing information on one of the latest known radiocarbon-dated cave bears from an area south of the Alps.

To our knowledge, cave bear remains from only two Italian caves, Conturines Cave (Corvara, Bozen, northeastern Italy), and Generosa Cave (Canton Ticino, northeastern Italy) have been dated radiometrically (Table 1). Both caves are located at high elevation in areas that were glaciated at the beginning of MIS 2. The absence of bear remains from younger stratigraphic levels is easily explained because with these areas invaded by glaciers environmental conditions had become unsuitable for bears. More problematic is explaining why cave bear is absent from south of the Alps, and especially from caves situated in the western side of the Italian Peninsula, where caves, but also human settlements, yielded remains of large herbivores for most of MIS 3 and 2 (Boscato, 2005). The Chiostraccio Cave is located in an area that was not involved in the glacial processes. It yielded the youngest known Italian representative of *U. spelaeus*. It can therefore bring significant insights on the latest cave bear of central and southern Italy.

The Chiostraccio Cave, geological setting and history of the discoveries

The Chiostraccio Cave (T/SI 364 in the Tuscan register of caves, geographic coordinates 43.372740 N, 11.185370 E) is located in the Montagnola Senese (Figs. 1A, B), a N–S ridge west of Siena (Tuscany,

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Table 1
Radiocarbon dates of fossil bones from Chiostraccio Cave (Siena, central Italy) and from other Italian localities.

	Sample number	Bone	Measured radiocarbon age (^{14}C yr BP, 1σ)	δ^{13}C (‰)	Conventional age (^{14}C yr BP, 1σ)	2σ calibration (cal yr BP) IntCal09	1 calibration (cal yr BP) IntCal09
Cave bear of the Chiostraccio Cave	Beta-340969	*Ursus spelaeus* phalanx[a]	23,930 ± 100	−18.9	24,030 ± 100	29,200–28,550	28,950–28,610
	Beta-285012	Long bone fragment[a]	22,670 ± 130	−19.4	22,760 ± 100	27,890–26,980	27,800–27,600
Cave bear of the Conturines Cave[b]			? 44,260 ± 900– > 39,000 cal yr BP				
Cave bear of the Generosa Cave[c]			51,200 ± 4,000– 38,200 ± 1,400 (cal?)				

[a] Material dated: collagen, extracted with alkali.
[b] Hofreiter et al. (2004); Pacher (2003); Pacher and Stuart (2009).
[c] Hofreiter et al. (2004); Bianchi-Demicheli and Oppizzi (2001); Pacher and Stuart (2009).

Italy). The Montagnola Senese is mainly constituted by metamorphic and non-metamorphic karst terrain. The area is affected by widespread hypogean and epigean phenomena, which have recently been investigated by a number of authors (Pascucci and Bianciardi, 2001; Pascucci, 2004; Martini, 2011; Iacoviello and Martini, 2012, 2013).

The Chiostraccio Cave is entirely developed in the "Calcare Cavernoso" Formation (Fig. 1B), a Triassic dolomitic limestone brecciated by complex destabilization/dissolution processes during the Neogene (Gandin et al., 2000; Lugli, 2001). The single-chambered Chiostraccio Cave is one of the largest caves in the Montagnola Senese area (Figs. 2A–B). Today a vertical 18-m-deep shaft leads into the cave (Fig. 2A) while in the past the cave could be accessed through another entrance at the bottom of a nearby doline (Fig. 2B). A steep (ca. 45°) debris cone was accumulated directly under the vertical shaft entrance. It consists of loose, fresh angular rock debris and blocks, wood debris, and recent to sub-recent mammal bones. In the distal part of the cone at the base of the shaft, the debris covers an older larger debris fan with a convex upward profile (Fig. 2A) caused by the presence of very large blocks (locally up to many m^3 in size). The scars of these rock falls are still recognizable on the overhanging ceiling. The blocks of this older debris fan are usually corroded and have a whitish or blackish patina. The whitish patina is associated with processes of dissolution of

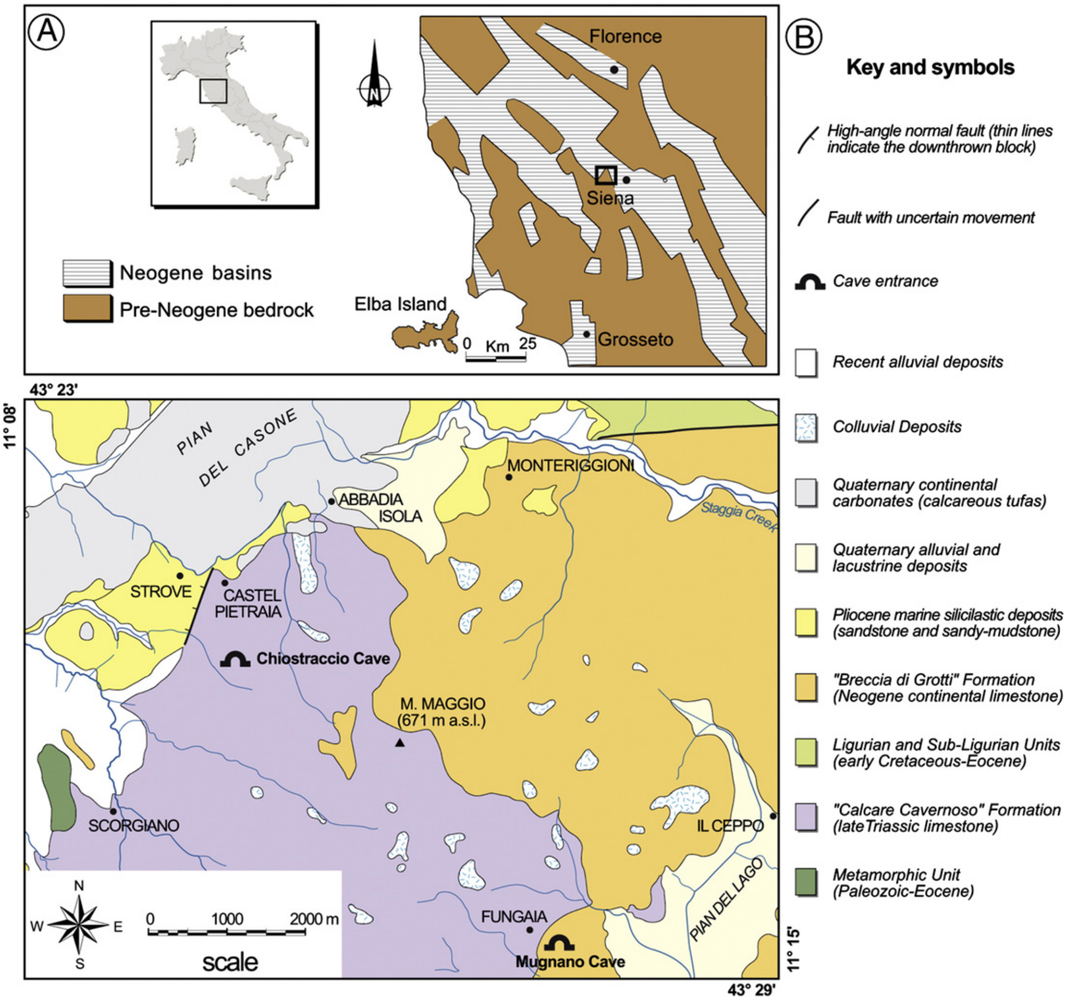

Figure 1. (A) Geographic location and tectonic sketch of the Inner Northern Apennines. (B) Simplified geological map of the Montagnola Senese area with the location of the Chiostraccio Cave.

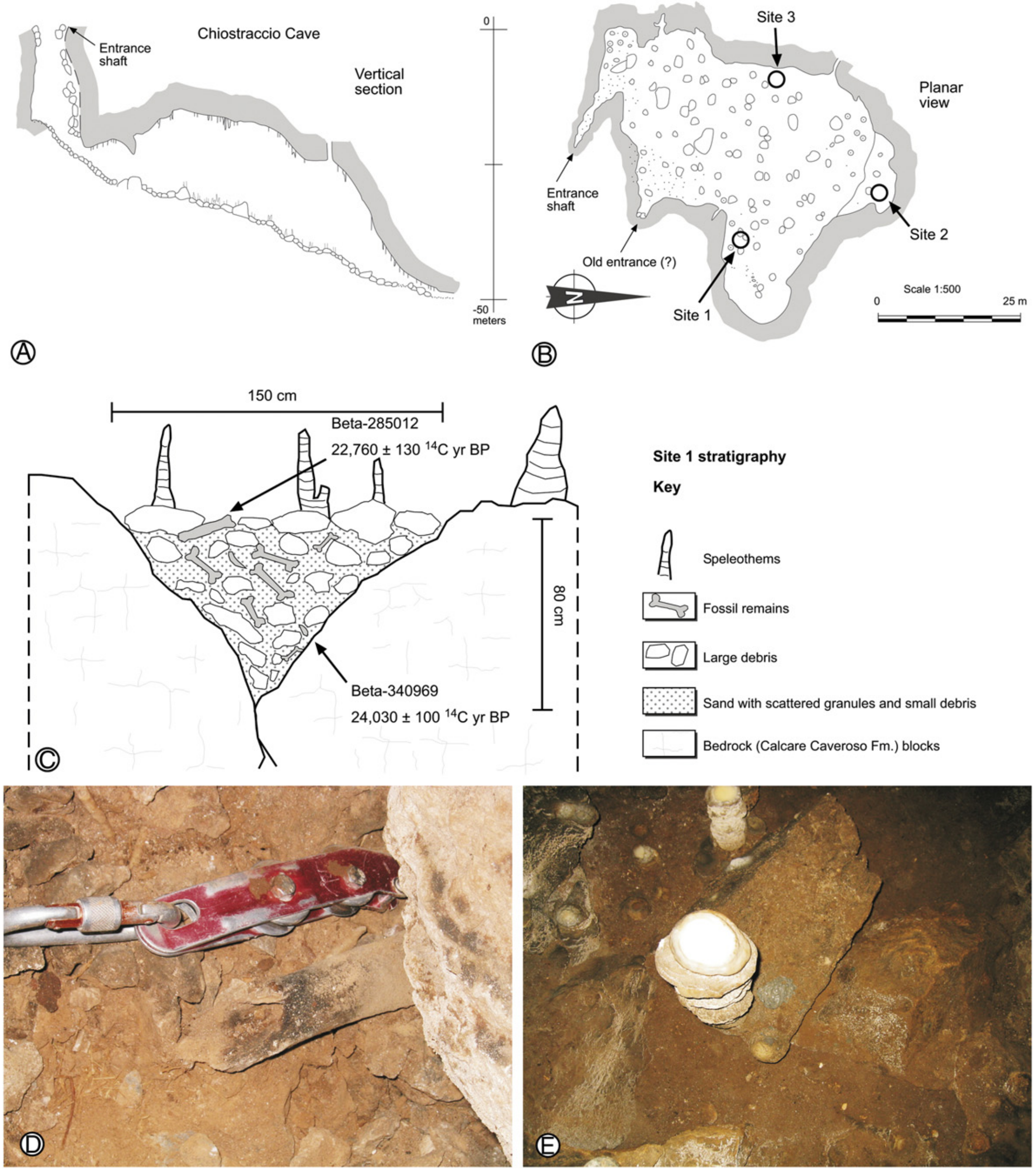

Figure 2. (A) Vertical and (B) planar view of the Chiostraccio Cave. (C) Stratigraphic sketch of Site 1. (D) Distal end of the diaphysis of right femur of *Ursus spelaeus* (same shown in Fig. 3C) partially buried by a rock block. The specimen is stained black with manganese oxides. (E) Speleothem covering a rock block, which in turn lies over the *U. spelaeus* bones. The two pictures were collected in 2004 before the excavations.

the block surface possibly caused by the CO_2 content of the air. The blackish patina is likely due to bat guano, locally present in small mounds. Stalagmites (rarely higher than 3 m) and flowstones are scattered across the rest of the chamber, between the guano mounds and the debris and blocks. A large speleothem column seals also a secondary debris cone, made of breakdown debris and blocks, just under the past entrance of the cave. The evenness of the slope of the talus is disturbed in three places by boulders that collapsed along the lines of weakness. The vault of the cave is crossed by two major fractures roughly oriented N30E that drove the most intense dissolution and rock-fall processes.

The first mammal remains were found in 1965 (site 2 in this work, Fig. 2B) by speleologists of the Associazione Speleologica Senese (A.S.S.). The cave yielded a relatively low number of fossils, but bones possibly collected during early explorations of the cave might have been lost. The cave bear remains were all retrieved from site 1 by one of the writers (IM) in 2004. They were initially found at the surface of the most superficial part of the talus (Figs. 2C–D), which was locally covered by speleothems (Fig. 2E). A detailed, about 1-m-deep excavation showed that the bones were contained in a 2.5 × 1.5 m depression enclosed between two large blocks. No layering was observed. The specimens were mixed with, and sometimes even trapped by, large blocks and debris, but with little matrix. The bone assemblage recovered from the excavation of site 1 included the carcass of *U. spelaeus* accompanied by bones of wolf (*Canis lupus*), wild boar (*Sus scrofa*), aurochs (*Bos primigenius*), red deer (*Cervus elaphus*), roe deer (*Capreolus capreolus*), bat (*Vespertinus murinus*), and crow (*Corvus monedula*).

Bones of other animals were found at the surface or slightly buried under debris in distinct areas of the cave. A nearly complete skeleton of brown bear (*Ursus arctos*) was discovered in Site 2. Site 3 yielded remains of a wild boar (*S. scrofa*). Late Pleistocene human bones were also found lying on the cave floor.

Attempts to establish how the cave bear entered the cave, whether by accident via the vertical shaft, or through the now-sealed entrance, were fruitless. If the animal fell accidentally into the cave it must have survived some time, because its bones were found in the innermost part of the cave, far from any entrance. The bones of cave bear are mixed with those of other animals possibly because of an attritional accumulation of carcasses through time, or of carcass parts carried in by predators/scavengers.

Radiometric dating of a few animal and human bones suggests that the top of the debris talus deposited during and soon after the Last Glacial Maximum (LGM; 26.5 to 19.0 cal ka BP: Clark et al., 2009). This indicates that the rockfalls were likely triggered by cryoclastic processes induced by the general decrease of the mean annual temperature. Alternatively, the boulders may have collapsed during a catastrophic event such as an earthquake. A stalagmite capping the debris talus was dated to around 7 ka (Fornaca Rinaldi and Radmilli, 1968).

Material and methods

The cave yielded a total of 120 bones, 69 of which belong to an individual skeleton of *U. spelaeus* (Fig. 3). The fossils are now preserved at the Department of Physical, Earth and Environmental Sciences of the University of Siena (Italy). The analysis focused on the remains of the cave bear. To assess the ontogenetic age of the bears we used both the age-scoring technique proposed by Stiner (1998), and the timing of postcranial appendicular epiphyseal fusion indicated by Weinstock (2009). Stiner's (1998) age-scoring technique is an eruption and wear scheme based on cheek teeth. The scheme includes nine successive stages of crown growth and wear. The wear stages, however, do not correspond to true ontogenetic ages, because wear rates might differ in populations from distinct habitats. Stiner (1998) advised clustering the eruption–wear stages into three age categories, juveniles (stages I–III), prime adults (stages IV–VII), and old adults (stages VIII–IX).

Figure 3. Selected remains of *Ursus spelaeus* from Chiostraccio Cave. (A) Left upper canine, lingual view. (B) Left humerus, cranial view. (C) Right femur, cranial view (same shown in Fig. 2C). (D) Right first metacarpal, dorsal view. (E) Left fourth metatarsal, dorsal view. (F) Left third metatarsal, dorsal view. (G) Left fourth metatarsal, dorsal view. (H) First phalanx, dorsal view: this specimen was used to obtain the radiometric dating reported in the paper. Scale bars — 5 cm.

Three bone samples, i.e., a calcaneum and a first phalanx of *U. spelaeus*, and an undetermined long bone fragment, were sent to the Beta Analytic Inc. Laboratory (Miami, Florida, USA) for radiometric dating. The first phalanx and the undetermined long-bone fragment were sent to the laboratory without any pre-treatment and/or manipulation. As for the calcaneum, only the inner, cancellous part of the bone was sent to the laboratory, because the specimen had been treated externally during preliminary observations. The material was first tested for friability. Very soft bone material is an indication of the potential absence of the collagen fraction. After that it was washed in de-ionized water, the surface scraped free of the outer most layers and then gently crushed. Dilute, cold HCl acid was repeatedly applied and replenished until the mineral fraction (bone apatite) was eliminated. The collagen was subsequently dissected and inspected for rootlets and other readily visible organic debris, most of which was removed when replenishing the acid solutions. The collagen was extracted using alkali solutions (i.e., the bones were pre-treated with sodium hydroxide to eliminate secondary organic acids). After drying through vacuum desiccation, the $^{13}C/^{12}C$ ratio was measured as the final proxy prior to the dating. Each sample was subjected to Accelerator Mass Spectrometry (AMS) analysis. The C/N ratio was not calculated because this value does not reflect the net collagen obtained from the material, but only the gross collagen present in the bone before pre-treatment.

We report the conventional and the calibrated radiocarbon dates (Table 1). For the conversion from conventional or non-conventional to calibrated ages reference was made to Oeschger et al. (1975), Stuiver et al. (1998), and Heaton et al. (2009), especially to the IntCal09 radiocarbon calibration curves (Reimer et al., 2009).

Results

Death trap or hibernation den?

Based on the dental wear stage, as well as on the degree of fusion of the limb bones, the cave bear is a young prime adult which died at 5–6 yr of age. Some bones show evidence of post-mortem damage caused by falling rocks. The parts of the bones that were originally exposed appeared patinated in contrast to the fresher, unpatinated buried sections. The few patinated fractures on elements that were broken in past times are of sawtoothed, splintered and oblique irregular type. The fracture surfaces appear jagged. The bones were therefore broken in a dry state (Villa and Mahieu, 1991), likely by rocks that collapsed from the cavern's ceiling on the already skeletonized cave bear carcass. There is scant evidence of carnivore ravaging. The only sign of interaction with other species is represented by two tooth marks on an unfused caput humeri, and by two more on a distal femoral condyle. The evidence is patently insufficient to prove that the specimen is a hibernating bear killed by predators. This also rules out that the cave bear carcass was transported into the cave by active predators or scavengers. The cave bear, but also the accompanying species are represented only by single individuals. Like the bear, none of the carcasses of the other species show signs of carnivore ravaging. The accumulated evidence thus suggests two scenarios, 1) the cave became a death trap for the bear, as well as for the associated animals, or 2) the bear died from non-violent causes, most likely during hibernation.

The first option seems a weaker, but not impossible, alternative. In fact, young prime-adult bears are at risk of entrapment in natural-trap caves and are highly susceptible to death in such settings (Wolverton, 2006). A natural trap is assumed to catch animals of a range of ontogenetic ages. The epiphyses of the long bones of all the species represented in the assemblage, not only those of the bear, are often incompletely fused. The Chiostraccio Cave is therefore strongly skewed towards prime adults. Moreover, the absence of green-wood (i.e., fresh-state) fractures on the bones, which are expected in animals that fall into caverns through vertical shafts, suggests that the cave was rather easily reached and used for shelter. We cannot exclude, though, that accidental falls might have been cushioned by the loose talus cone under the cave's vertical shaft entrance. In this case, the animals would have died of hunger and thirst.

The second hypothesis, which assumes that the bear carcass belongs to a debilitated individual that died in the cave from non-violent causes, likely during hibernation, seems quite more convincing. In this hypothesis also the carcasses of the other, non-hibernating species, would be of weakened or injured animals that sought refuge in the cave and died there.

Stiner (1998) reported that hibernation-related deaths normally peak in post-weaning, dental-wear stage III juveniles, as well as in very old, wear stage IX individuals. Stage III juveniles often die from starvation. Peaks in wear stages V and VI, by contrast, are usually rare, because these stages are a phase of high survivorship in bear's lifetime. Hence, predator-independent deaths of prime adult individuals during seasonal denning with no involvement of humans likely indicate that the animals were underweight and debilitated. Weakened bears that go into hibernation are doomed to certain death. Presuming this implies that the bone accumulation was at a time of very harsh, demanding and highly competitive environmental circumstances.

Because of their great vulnerability during winter retreats, hibernating bears are cautious. They are very alert to the presence of predators, including other bears (cannibalism is not infrequent), or humans, and attentive to keeping secret their hibernation lairs, to reduce the risk of intrusion. The non-exclusive presence of cave bear, but rather its association with other animals, and especially with another active predator (the wolf), suggests that the cave was probably occupied by bears after fairly long intervals between successive occupations. The Chiostraccio Cave assemblage could thus be an attritional accumulation of carcasses over a certain lapse of time. This is suggested by the presence of red deer (*C. elaphus*) and roe deer (*C. capreolus*). These species are typical woodland dwellers. Their presence indicates milder environmental conditions than that at the onset of MIS 2. A few rock falls actually seem to have occurred after the emplacement of the bones of *U. spelaeus*.

Chronology of the cave bear

The Chiostraccio Cave assemblage has little biochronological relevance. It comprises only long-lasting mammalian species of minor stratigraphic value. Most of them appeared in western Europe already during the 0.9–065 Ma time span (i.e., *S. scrofa*, *C. capreolus*, *C. elaphus*, *B. primigenius*, *C. lupus*). Dating the first appearance of the typical *U. spelaeus* is problematic because of its gradual emergence from *Ursus deningeri*. It is generally accepted that the first true *U. spelaeus* bears start appearing during the late middle Pleistocene (e.g., Rabeder, 1983; Malez, 1986; Tsoukala, 1991; Rabeder et al., 2000; Forsten and Dimitrijević, 2004; Kahlke et al., 2011). The Chiostraccio Cave fauna can therefore be generically referred to the middle-late Pleistocene.

Of the two remains of *U. spelaeus* sent for radiocarbon dating, the first phalanx contained sufficient collagen. In contrast, the collagen contained in the cancellous part of the calcaneum was expectedly insufficient for AMS dating. The phalanx is short and stout and its dimensions (greatest length: 38.8; breadth of the proximal epiphysis: 20.7; depth of the proximal epiphysis: 19; diaphysis breadth: 13; diaphysis depth: 15.7; breadth of the distal epiphysis: 15; breadth of the distal epiphysis: 12.9; all measures in mm) fall in the range of the first phalanges of cave bears. The conventional age of the phalanx was determined as 24,030 ± 100 ^{14}C yr BP (29,200 to 28,550 cal yr BP. Sample Beta-340969: Table 1). This dating makes the Chiostraccio Cave *U. spelaeus* Italy's latest known representative of the species and refers it to the mid part of Greenland Stadial 3 (Lowe et al., 2008). The dated phalanx was found in the deepest part of the deposit, 1 m below the surface, very close to the margin of the depression that contained the rest of the skeleton.

The interest in the cave bear of the Chiostraccio Cave was actually stirred by a previous radiocarbon-dating obtained on the long-bone fragment of uncertain classification from the same fossil assemblage. The specimen had given a conventional age of 22,760 ± 130 ^{14}C yr BP (27,890–26,980 cal yr BP. Sample Beta-285012: Table 1). The bone fragment was retrieved from the superficial part of the fill. It was only partly exposed from the debris. Because the splint of bone is impossible to identify anatomically and taxonomically, it is also impossible to establish whether or not it belongs to the bear carcass that yielded the dated phalanx. If it does, the different age of the two specimens could be explained invoking a slight contamination of one of them, possibly the unidentified bone fragment which lied more superficially and had probably been exposed to contaminants such as guano. An actual chronological difference of the various taxa in the deposit would support the assumption that the Chiostraccio Cave fossil assemblage is an attritional, time-averaged bone accumulation.

Italy, a southern refugium for cave bears

The Pleistocene Epoch was climatically unstable. Its rapid and extensive fluctuations considerably influenced the diversity and distribution of plants and animals. The Italian peninsula, together with the rest of southern Europe, underwent dramatic landscape changes at different latitudes and altitudes. The highest Apennine peaks were episodically glaciated, and cirque and valley glaciers developed as low as ca. 800–1000 m asl (above modern sea level) (Jaurand, 1999). Nivation was especially intense on north-facing slopes, which were also struck by cold easterly winds (Coltorti and Dramis, 1988, 1995). Vast nival niches were modeled also at 700–800 m asl in elevation. Frost shattering generated scree and stratified slope-waste deposits down to the very bottom of the valleys, causing severe river aggradation. Scree deposits that formed at sea level are found in many districts, including Sardinia (Andreucci et al., 2010; Coltorti et al., 2010).

During these cold periods sets of valley glaciers characterized by amphitheater-front moraines developed along the northern side of the Po plain (Monegato et al., 2011; Ravazzi et al., 2012). The Adriatic Sea dropped and the northern coastline withdrew southwards, so that the Po River entered the sea south of Ancona (Trincardi et al., 1996; Trincardi and Correggiari, 2000).

During the climatic amelioration that occurred during MIS 3, fluvial sedimentation dwindled and rivers attained anastomosing patterns even at low elevation in the Marche region (Adriatic side of central Italy) (Coltorti and Dramis, 1995). The stable part of the plain experienced the growth of steppe and prairie vegetation. Thin A1 soil horizons show that this kind of vegetation colonized also the higher parts of the slopes (Chiesa et al., 1990; Giraudi and Frezzotti, 1997). However, during MIS 3, trees, mostly pine and birch, grew along the river banks. *Pinus* trees at 200 m asl along the Esino river valley had growth rings deformed by nival overburden (Coltorti and Dramis, 1995). A modern equivalent of what occurred at least in central Italy, can be found in the present-day tundra. Around 27 ka steppe–prairie soils disappeared from the colluvial wedges at the feet of the slopes. From this time on, no trunks are found buried in alluvia and the rivers attained braided patterns with very flat channels and bars with very rapid aggradation. Although evidence of severe periglacial features (ice wedges, patterned ground, convolutions) has not been not found in the fluvial deposits of this period along the alluvial plain of the entire Adriatic margin, the widespread occurrence of stratified slope deposits suggests a mean temperature slightly above 0 °C. Today this scenario characterizes the transition to the polar desert. These conditions extended to southern Italy where *Capra ibex*, *Rupicapra rupicapra* and *Equus* sp. were among the most commonly hunted mammals near present-day sea level (Bon and Boscato, 1996). The pollen records from crater-lake sequences, including the Lagaccione succession in the Bolsena volcanic area, ca. 120 km SW of the Chiostraccio Cave, indicate the occurrence of scattered patches of *Pinus*-dominated woodlands during the MIS 3 mid-glacial interstadials. During the following LGM, this vegetation alternated with steppes dominated by *Artemisia*, Gramineae, and Chenopodiaceae (Follieri et al., 1998).

This evidence suggests that the MIS 3 time period, when the last cave bears were lingering throughout Europe, was characterized by habitat fragmentation with patchy woodland remnants. The species' Last Occurrence, during MIS 2, occurred when the climatic conditions climaxed, and the landscapes turned completely open, cold and dry. In the Late Glacial period, dominated by tundra, remnants of Pleistocene wooden vegetation co-existed apparently until 9 ka (Huntley, 1988, 1990, 1992; Starkel, 1991; Grove and Rackham, 2001). These patches of Pleistocene vegetation offered refugia for other Pleistocene fauna (Bennett et al., 1991; Taberlet and Bouvet, 1994; Hewitt, 1996; Stewart and Lister, 2001; Reumer, 2007). Cave bears, however, were already extinct by then. This scenario suggests that the Mediterranean flora and mammalian fauna probably found residual areas, especially in karst districts, where suitable microclimatic conditions persisted and water was almost always supplied by deeper aquifers. Moreover, the high degree of porosity that protected surface rocks against frost shattering somehow preserved slope stability. In fact, all around the Montagnola Senese, mostly modeled on massive limestones, the scree deposits have a limited thickness (Coltorti et al., 2012b). The fact that scree deposits are thicker in micritic and marly limestones has also been observed in other areas of the Apennines (Coltorti and Dramis, 1987). Therefore limited slope deposition and presence of water resources co-occurred in the Montagnola Senese area.

According to the proposers of the refugium hypothesis (e.g., Bennett et al., 1991; Taberlet and Bouvet, 1994; Hewitt, 1996, 2000; Taberlet et al., 1998), at the onset of glacial conditions temperate plant and animal species survived in restricted refugia which due to local conditions were less affected by the general cooling. Areas with similar conditions in the Italian peninsula, as well as in other areas of southern Europe, would have been one of the main European refugia (Bennett et al., 1991; Taberlet and Bouvet, 1994; Hewitt, 1996). The high number of cave bears found in the Conturines and Generosa caves shows that *U. spelaeus* survived well until MIS 3, even at high elevation and under the extreme climatic conditions that prevailed at the margins of glaciated terrains. During MIS 3, glacial advances forced *U. spelaeus* south of the Alps. As the glacial expansions fragmented the ranges of many animal and plant species throughout Europe, the karst terrains of central and southern Italy might have contained isolated and sheltered refugia for cave bears.

Brown bears survived in mainland southern Europe, and were fairly uniformly distributed throughout Eurasia and not restricted only to Mediterranean peninsulas during the glacial maxima. In contrast, cave bears seem to have had a more discontinuous distribution (Musil, 1980; Hofreiter et al., 2002; Valdiosera et al., 2007). The fragmented distribution possibly created bottleneck populations causing reduced genetic variation (Hewitt, 1996; Taberlet et al., 1998; Hewitt, 1999; Randi, 2003; Rowe et al., 2004). Nonetheless, although bottlenecks have been detected in brown bear populations, they have not been found in the latest cave bear populations (e.g., Ramakrishnan and Hadly, 2009). In fact, Hofreiter et al. (2002) observed that the mtDNA diversity in cave bears was similar to the diversity observed in current brown bear mtDNA gene pools. However, molecular studies on Italian cave bears dating to around 24 ka still need to be carried out.

The fragmentation of the areal distribution of cave bears occurred in conjunction with the altered productivity of the herbaceous vegetation that constituted their primary means of sustenance. Without the evidence of a genetic impoverishment in final cave bear populations, decreasing resource availability during the beginning of MIS 2 seems the most plausible cause of extinction of *U. spelaeus*, as suggested by Stuart and Lister (2007).

Numerous studies on the chronology of cave bear extinction (e.g., Stuart, 1991, 1999; Stuart and Lister, 2007; Pacher and Stuart, 2009; Bocherens et al., in press) indicate that the latest cave bears died out ca. 24 ka. The cave bear of the Chiostraccio Cave is therefore one of the last representatives of the species. It is also one of the southernmost. This specimen can be of great interest for those searching for the causes of cave bear extinction. It can be particularly important for research programs aimed at testing the southern refugium hypothesis, as well as the supposed late Pleistocene reduction of vegetational productivity.

Conclusions

The age of the cave bear carcass from the Chiostraccio Cave locates it in the Greenland Stage 3 (GS3 of Lowe et al., 2008) at the crucial transition from MIS 3 to the following MIS 2 period, which included the LGM. The mammal remains may disclose relevant information on the conditions that characterized this significant climatic change. The relatively young ontogenetic age of this adult specimen is remarkably coincident with those of the other species of the fossil assemblage in Chiostraccio Cave. The bear therefore probably died from declining resource availability. This is perhaps one of the first effects of the climatic changes on the ecosystems of the time. Cave bears were probably more vegetarian than brown bears (Koby, 1939; Erdbrink, 1953; Kurtén, 1976; Mazza et al., 1995; Mattson, 1998; Rabeder et al., 2000; Grandal-d'Anglade and López González, 2005; Pacher and Stuart, 2009). Hence, they might have been more vulnerable than brown bears to climate-driven changes in primary production. This would explain the different evolutionary fate of the two species.

Nonetheless, cave bears endured the rigors of at least two particularly intense glacial events (MIS 6 and MIS 8). There seems to be no significant decline of the cave bear population coincident to any climate or vegetation modification prior to their ultimate demise. During the LGM, starting from around 30 ka (van Andel, 2003), there were significant climate-driven changes in the European and Italian vegetation (Follieri et al., 1998). Cave bears started declining at approximately 50 ka (Stiller et al., 2010), during a period of severe aridity and when mean temperatures were progressively diminishing. The decline continued until the lowest minima of the early LGM. This would be in line with Stuart and Lister's (2007) assumption that alterations in vegetational productivity at the start of the last glacial period caused the extinction of cave bear. Stiller et al. (2010) suggest that cave bears probably became extinct for a complex of factors, including human competition for cave sites. In fact, we cannot exclude that deliberate hunting by humans might have caused the last, residual cave bear populations, which were already severely stressed by the intense climate changes of the time, to disappear (Bocherens et al., in press). Similar cases have been suggested, on a larger scale, for the megafauna of South America (Ficcarelli et al., 1997, 2003; Coltorti et al., 2012a).

The Grotta del Chiostraccio cave bear remains to show no evidence of interactions with humans. They nonetheless contribute to our knowledge of the lifestyle and habits of central Italian cave bear. The evidence seems to confirm the conclusions of earlier studies (e.g., Argenti and Mazza, 2006), which had supposed that the latest Italian *U. spelaeus* populations shared the seasonal denning behavior typical of their central European counterparts (Kurtén, 1958; Andrews and Turner, 1992). Actually, despite the fact that Italy extends into the milder Mediterranean basin, the high peaks of the Apennines were glaciated even in the southernmost regions, and there were only minor climatic differences across the peninsula. Issues that need to be addressed by future research is whether the denning behavior was customary to *U. spelaeus* at these latitudes also under warmer and steadier conditions, or if it was adopted only under altered and more demanding climatic circumstances. Cave bears have long been believed to have been unable to survive in continental climates. Knapp et al. (2009), however, have shown that cave bears were distributed as far north as Siberia and even beyond the Arctic Circle. The Conturines and

Generosa caves, which are still today frequently covered by snow two or three months in winter times, suggest that cave bears could have survived in very extreme environments.

The cave bear of the Chiostraccio Cave is one of the latest southernmost representative of the species. The area in which this bear lived was gifted with two major characteristics of Pleistocene refugia, i.e., availability of water and slope stability. Future research will reveal if these features were shared also by other refugia in Italy, as well as in Mediterranean countries.

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