UNIVERSITAT ROVIRA I VIRGILI

FATE OF THE CAVE BEAR IN NORTHEASTERN ITALY: ANTHROPIC IMPACT, EXTINTION CHRONOLOGY, STABLE ISOTOPE AND GENETIC EVIDENCE

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UNIVERSITAT
ROVIRA i VIRGILI

International
Doctorate in
Quaternary and
Prehistory
IDQP

Università
degli Studi
di Ferrara

EBERHARD KARLS
UNIVERSITÄT
TÜBINGEN

Fate of cave bear in northeastern Italy:

anthropic impact, extinction chronology,

stable isotope and genetic evidence

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Gabriele Terlato

Doctoral Thesis
2015-2018

Gabriele Terlato - Fate of cave bear in northeastern Italy: anthropic impact, extinction chronology, stable isotope and genetic evidence - Doctoral Thesis

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I STATE that the present study, entitled "**Fate of cave bear in northeastern Italy: anthropic impact, extinction chronology, stable isotope and genetic evidence**", presented by **GABRIELE TERLATO** for the award of the degree of Doctor, has been carried out under my supervision at the Department d'Història I Història de l'Art of Universitat Rovira I Virgili and at Department of Humanistic Studies of University of Ferrara.

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Doctoral Thesis Supervisor/s

Jordi Rosell Ardèvol   Marco Peresani   Hervé Bocherens

Fate of cave bear in northeastern Italy:

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Department d'Història I Història de l'Art of Universitat Rovira I Virgili and

Department of Humanistic Studies of University of Ferrara.

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2015-2018

To Adele

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ABSTRACT

Cave bears were one of the most impressive animals of the Late Pleistocene in Europe and are well known from many caves. Despite the enormous quantities fossils unearthed, some aspects of their history/habits, such as interaction with humans, ecology and extinction chronology, are still little known from the Mediterranean area in the Southern Alps. This research aims at revisiting the debate about the extinction and paleoecology of cave bear, *Ursus spelaeus* (sensu lato), through archaeozoological, taphonomic and chemical analysis of the bones of this species, from Middle and Upper Palaeolithic sites of northeastern Italy. Key sites for this purpose are Rio Secco, Fumane, Buso doppio del Broion, Paina and Trene caves. Cave bear remains are very often found in these caves and, in several cases are the most frequent fossils found in the assemblages. The remains of cave bear analyzed came from layers dated 49 – 42 ky cal. BP (Rio Secco and Fumane) and 33 – 23 ky cal. BP (Buso doppio del Broion, Trene and Paina), most of them associated with evidence of human presence.

Archaeozoological and taphonomic analysis were performed to better understand the role of human impact on cave bear populations during a wide span of time. Further techniques, such as a stable isotope, radiometric and ancient DNA analysis were applied to cave bear bones, selected from Buso doppio del Broion, Paina and Trene caves, in order to acquire a detailed picture of the ecology, diet, population dynamics and extinction chronology of cave bears. Only thanks this cross-disciplinary perspective was it possible to significantly improve our understanding of the difficult issue of extinction of this "iconic" animal.

Paper I introduces the interaction between Neanderthal and bears (*Ursus spelaeus* and *Ursus arctos*) from Rio Secco and Fumane caves and is also an important contribution to Neanderthal behavioural complexity. Using archeozoological and taphonomic analysis of unpublished bear bone remains we show the systematic and consolidated exploitations of bears by different hunting groups of Neanderthals. This evidence suggests that bears had a strategic role in the nomadic economy of Middle Palaeolithic humans.

Paper II - III introduces the new chronometric, isotopic and taphonomic evidence of cave bear fossil remains preserved at three Paleolithic cave bear sites in Northeastern Italy: Buso doppio del Broion Cave, Paine Cave and Trene Cave. Following the chonometric results, we present the latest known representatives of cave bears in Europe as the bones have an age of 24,200-23,500 ky cal.

BP. The additional merit is the evidence for ecological stability of one of the last cave bear populations, and the evidence for human impact.

Paper IV introduces the complete cave bear mitochondrial genomes from different countries of Europe. We present the first mitochondrial genome of *Ursus spelaeus ladinicus* as well as the youngest cave bear DNA sequences, dates 23-24 ky cal. BP (Trene and Paina caves – Berici Hills). The advantage of the methods used in this paper is the reconstruction of the population dynamics and phylogeography during the Late Pleistocene. Our study can support a potential human impact in the general disappearance of European cave bear.

RESUM

L'ós de les cavernes és un dels animals més emblemàtics del Pleistocè superior final a Europa i és una espècie molt ben coneguda per la quantitat de restes localitzades a múltiples coves. Malgrat això, alguns aspectes de la seva història evolutiva, com per exemple la interacció amb els humans, l'ecologia i la cronologia de la seva extinció són encara desconeguts a l'àrea mediterrània del Sud dels Alps. Aquesta recerca té com objectiu revisar el debat sobre l'extinció i la paleoecologia dels óssos de les cavernes, *Ursus spelaeus* (*sensu lato*), a partir de les anàlisis arqueozoològiques, tafonòmiques i químiques de les restes trobades en alguns jaciments del Paleolític mig i superior del Nord-est d'Itàlia: Rio Secco, Fumane, Buso doppio del Broion, Paina i Trenes Caves. Les restes d'ós de les cavernes són freqüentment recuperats a les coves i, en molts casos, representen els animals més abundants dels conjunts faunístics. Les restes analitzades provenen dels nivells datats entre 49-42 ky cal. BP (Rio Secco i Fumane) i 33-23 ky cal. BP (Buso doppio del Broion, Trene i Paina), i moltes d'elles estan associades a evidències de presència humana.

Les anàlisis arqueozoològiques i tafonòmiques han estat dirigides a entendre el rol de l'impacte humà sobre les poblacions d'ós de les cavernes durant el citat rang temporal. Altres tècniques, com per exemple els isòtops estables, l'anàlisi ADN antic i datacions radiomètriques han estat aplicades als ossos d'aquests animals dels jaciments de Buso doppio del Broion, Trene i Paina Caves, per tal d'adquirir una visió detallada de la seva ecologia, dieta, dinàmica de població i cronologia de la seva extinció. Solament una perspectiva holística com la utilitzada en aquesta tesi doctoral pot aportar llum a aquest difícil tema sobre l'extinció d'un animal tan icònic com l'ós de les cavernes.

Els articles realitzats durant el període de formació permeten assenyalar que la desaparició d'aquests animals al Nord-est d'Itàlia es va produir entre els 24-23 ky cal. BP. Aquest estudi permet suportar la idea d'un potencial impacte humà com un dels condicionants més significatius de la desaparició d'aquest animal no solament en aquesta àrea geogràfica, sinó a tota Europa.

Resumen

El oso de las cavernas es uno de los animales más emblemáticos del Pleistoceno superior final de Europa y es muy bien conocido como especie por la cantidad de restos localizados en múltiples cuevas. A pesar de esto, algunos aspectos relacionados con su historia evolutiva, como por ejemplo la interacción con los humanos, su ecología o la cronología de su extinción, son aún desconocidos en el área mediterránea del Sur de los Alpes. Esta investigación tiene como objetivo revisar el debate sobre la extinción y la paleoecología de los osos de las cavernas, *Ursus spelaeus* (*sensu lato*), a partir de los análisis arqueozoológicos, tafonómicos y químicos de los restos recuperados en algunos yacimientos del Paleolítico medio y superior del Nordeste de Italia: Rio Secco, Fumane, Buso doppio del Broion, Paina y Trenes Caves. Los restos de osos de las cavernas son frecuentemente recuperados en las cuevas y, en muchos casos, ellos representan a los animales más abundantes en los conjuntos faunísticos. Los restos analizados provienen de los niveles datados entre 49-42 ky cal. BP (Rio Secco i Fumane) i 33-23 ky cal. BP (Buso doppio del Broion, Trene i Paina), y muchos de ellos están asociados a evidencias de presencia humana.

Los análisis arqueozoológicos y tafonómicos han estado dirigidos a entender el rol del impacto humano sobre las poblaciones de oso de las cavernas durante el citado rango temporal. Otras técnicas, como por ejemplo los isótopos estables, el análisis de ADN antiguo y las dataciones radiométricas han sido aplicadas a los huesos de estos animales en los yacimientos de Buso doppio del Broion, Trene i Paina Caves, para adquirir una visión detallada de su ecología, dieta, dinámica de poblaciones y cronología de su extinción. Solamente una perspectiva holística como la utilizada en esta tesis doctoral puede aportar luz a este difícil tema sobre la extinción de un animal tan icónico como el oso de las cavernas.

Los artículos realizados durante el periodo de formación permitan señalar que la desaparición de estos animales se produjo en el Nordeste de Italia entre los 24-23 ky cal. BP. Este estudio permite soportar la idea de un potencial impacto humano como uno de los condicionantes más significativos de la desaparición de este animal no solo en esta área geográfica, sino en toda Europa.

LIST OF PUBLICATIONS

Publications submitted or in preparation to fulfil the requirements for a cumulative dissertation. Percentage of the own contribution to the articles or manuscripts are listed in parentheses (original idea/data collection/data analysis/writing and publication).

Paper I (40/80/70/50)

Romandini M., **Terlato G.,** Nannini N., Tagliacozzo A., Benazzi S., Peresani M. (2018). Bears and humans, a Neanderthal tale. Reconstructing uncommon behaviors from zooarchaeological evidence in southern Europe. *Journal of Archaeological Science* 90, 71-91. doi: org/10.1016/j.jas.2017.12.004.

Paper II (50/100/50/70)

Terlato G., Bocherens H., Romandini M., Nannini N., Hobson K.A., Peresani M. (2018). Chronological and Isotopic data support a revision for timing of cave bear extinction in Mediterranean Europe. *Historical Biology*. doi:10.1080/08912963.2018.1448395.

Paper III (50/100/50/80)

Terlato G., Bocherens H., Romandini M., Nannini N., Hobson K.A., Peresani M. (2018). Extinction and paleoecology of the late Pleistocene cave bear from northeastern Italy: radiocarbon and stable isotope evidence. *Alpine and Mediterranean Quaternary* Vol. 31, 99-103. Extended Abstract.

Paper IV (0/20/20/10)

Gretzinger J., Molak M., Reiter E., Pfrengle S., Urban C., Neukamm J., Sabol M., Blant M., Conard N.J., Cupillard C., Dimitrijevic V., Drucker G.D., Kowalzcyk R., Krajcarz M.T., Krajcarz M., Münzel S., Pavi S., Peresani M., Romandini M., Rufí Casals I., Soler Subils J., **Terlato G.,** Krause J., Bocherens H., Schuenemann J.V. Large-scale mitogenomic analysis of the phylogeography of the Late Pleistocene cave bear. Manuscript close to submission to Scientific Reports - Nature.

1. INTRODUCTION

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1.1 Background

For more than two centuries, the cave bear has an important place in palaeontological and archaeological studies, thanks to their highly abundant remains recovered in European Late Pleistocene caves. The rich fossil assemblages represent natural deaths (during winter or hibernation) or anthropic accumulation. During the Middle Ages, cave bear bones were believed to be the remains of dragons or other mythological beasts and, were collected as remedies for diseases (Pacher and Stuart, 2009). For this reason, there are some "dragon caves" across Europe, famous especially in Switzerland (e. g. Drachenloch Cave), Austria (e. g. Drachenhohle Cave) or Slovakia (e.g. Dračia jaskyňa Cave). At the end of the 18th century, a young physician, J. Rosenmüller, first described in 1794 the bones from Zoolithenhohle in Bavaria Germany as representing a new extinct species of bear (*Ursus spelaeus*). Nevertheless, this accomplishment was not entirely unexpected; rather it resulted from a series of works taken by Rosenmüller's scientific predecessors. The almost mythical value of this species and their abundance even in Paleolithic sites has raised the interest of prehistoric researchers who, at the beginning of 20th century, proposed theories and behavioural models in relation to prehistoric man. The "Bear cult" theory was born. This was largely due to the works of Bächler (1920-21, 1923, 1940) who postulated the existence of a culture unique to the Alps, "Alpine Mousterian". This culture was associated with a specialized hunting of cave bears that was practiced in the summer at highland sites where, in addition to bear remains, bone tools and lithic industries were identified at the time, often described as Quina Mousterian type. Based on his works on cave bear caves and ethnographic comparison, he interpreted burnt, broken bear bones, and skulls on or under rock slabs or in niches, as peculiar and likely "symbolic" dispositions. These theories or hypotheses saw undeniable comparisons in archaeological evidence from Germany, Austria, Hungary, Slovenia, and Croatia (Pacher, 2003). However, his analysis and theory did not stand up to scrutiny and was rejected by some authors such as Koby (1941, 1943) and Kurtén (1976). Those authors affirmed that the accumulation of cave bear remains was the result of natural bear death during hibernation and that the presence of skulls in niches and of broken, polished bear bones were not the result of human intervention. Decades later, the theory of the "Bear Cult" was totally abandoned following further scientific investigations challenging the origin and anthropic modifications of bear remains (Fosse et al., 2002; Auguste, 2003; Germonpré and Hämäläinen, 2007; Münzel and Conard, 2004a-b; Wojtal et al., 2015; Paper I).

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1.2 Human – Bear interaction

During the last 20 years, the study of faunal assemblages has been refined by microscopic and taphonomic investigative techniques, accompanied by reviews of the materials excavated in the early to middle part of the last century. The taphonomic history of bear bones is therefore the most significant aspect in investigating the interaction between ursids and Palaeolithic human groups. The story of human - bear interactions is both important and enigmatic, their evolutionary histories following biogeographic contact must have affected one another to some extent (Stiner, 1999). The ecological and ethological links led bears and humans to live in the same habitats and shelters, cohabiting in a good part of Europe all through the Pleistocene (Turner, 1992, 1994; Hemmer, 2000; Brugal and Fosse, 2004). Many examples link the anthropic exploitation of this animal in multiple periods and cultural contexts, thanks to the discovery of cut-marks made by lithic tools, percussion marks and projectile impact marks on the surfaces of ursid bones from recently excavated sites or from review of ancient excavation materials. The evidence for exploitation of bears (*Ursus spelaeus* sensu lato and *Ursus arctos*) in Europe was found and documented in several sites from the Middle Palaeolithic to the Epigravettian (Paper I, II; Duches et al., 2018). Different Mousterian sites suggest exploitation or carcass manipulation at the bears' natural place of death (Paper I; Tab.1).

Tab.1: Middle Palaeolithic sites in Europe with evidence of bear exploitation

*Site*s	*References*
Goyet and Scladina caves (Belgium)	Germonpré and Sablin, 2001; Abrams et al.,2014
Regourdou (France)	Cavanhié, 2009-2010
Geißenklösterle, Hohle Fels and Balve Cave (Germany)	Kitagawa et al., 2012; Münzel, 1997; Münzel and Conard, 2004b; Münzel et al., 2011; Kindler, 2012
Salzofen Cave (Austria)	Ehrenberg, 1958-59, cited by Armand et al., 2004
Nietoperzowa (Poland)	Wojtal, 2007; Wojtal et al., 2015
Divje Babe (Slovenia)	Turk, 1997, 2014
Pešturina Cave (Serbia)	Majkić et al., 2017
Crvena Stijena (Montenegro)	Morin and Soulier, 2017
Caverna delle Fate, Madonna dell'Arma, Badalucco, Le Manie and Sant'Agostino (Italy)	Valensi and Psathi, 2004; Quilès, 2003, 2004

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However, only in some sites the finding of consistent bear bone accumulations, associated with a high rate of anthropic marks, supports the hypothesis of active and directed hunting: Rio Secco Cave in Italy; Biache-Saint-Vaast in France; Taubach in Germany and Krapina in Croatia (Paper I). Regarding the Upper Palaeolithic, there is scarce information from Aurignacian contexts. Signs of human activity on bear remains were noted: in Abri Castanet in France (Armand, 2006); in Geißenklösterle and Hohle Fels in Germany (Münzel, 1997; Münzel et al., 2011); in Deszczowa Cave in Poland (Wojtal, 2007). The notable exception is Potočka zijalka in Slovenia, where several osseous projectile points mostly made from ursids were found (Hofreiter and Pacher, 2004; Jéquier, 2016). The archaeozoological record show that the ursids (in particular *Ursus spelaeus*) constitute the overwhelming majority of the faunal material, but its accumulation was in most cases natural, as suggested by the very large amount of cave bear bones and the presence of gnawing marks on the bones, according to Pacher (2001) and Pacher and Marinelli (2004). Traces of human interaction with bears are well documented in Gravettian sites of Central Europe: Hohle Fels (Germany); Deszczowa Cave (Poland); Pavlov I southeast (Czech Republic) (Wojtal et al., 2015). In Hohle Fels, butchering marks are present on all skeletal elements and document all steps of the dismemberment of cave bear carcass. Here exceptional evidence of cave bear hunting was documented by a projectile impact mark recorded on the *processus transversus* of a thoracic vertebra dated to 27,830±150-140 uncal BP. It is a failed shot, but the success of the hunt is demonstrated by cut marks on the spinal process (Münzel et al., 2001; Münzel and Conard, 2004a; Wojtal et al., 2015). Recently, a rib of *Ursus arctos* with projectile impact mark was found at the Late Epigravettian site of Cornafessa (Italy). The injury consists of a drag with several flint fragments embedded (Duches et al., 2018). Besides these traces of butchering, other bear bones and teeth show clear evidence of human manipulation as bone tools or ornaments, e.g. at Kraków Spadzista pendants made from bear incisors, and at Pavlov I an awl made from a bear fibula (Wojtal et al., 2015). Human interaction with cave bear is also documented in Rochedane (France), where a metatarsal with cut marks was found, dated to 28,730-28,500 cal BP (Bocherens et al., 2014a). Conspicuous bear bone assemblages come from Gravettian and Epigravettian sites located in Berici Hills in northeastern Italy, which testify both bear hibernation and human occupations. Taphonomic analysis revealed in fact several anthropic traces on cave bear remains stratigraphically associated with shouldered and backed points (Romandini and Nannini, 2012; Papers II, III).

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In this very long-time span of human-bear interaction, the question of whether hunting by Neanderthals or Modern Humans played a role on the demise and final extinction of cave bear is discussed (Münzel et al., 2011; Bocherens et al., 2014a; Paper II). Sites across Italy have produced examples of alternating human/bear encounters by the presence of lithic artifacts in association with abundant cave bone remains, supposedly the result of natural deaths (Bartolomei, 1982; Boschian, 2003; Argenti and Mazza, 2006; Bona et al., 2007). Detailed taphonomic analyses are still lacking and there is no evidence for human-bear interactions. In contrast several sites in northeastern Italy document a long-term influence and continuity of bears hunting (Paper I, II). However, it appears unclear why hunting would have affected cave bears more than brown bears. Differences in behaviour between the two species may have played a role, as dietary flexibility high for brown bears and low fro cave bears. Different hibernation strategies could have made a difference? According to the relative amounts of cave bear and brown bear remain in European caves, cave bears were more dependent on caves for hibernation (Kurtén, 1976; Rabeder et al., 2000). Furthermore, the high dependence of cave bears on their birth caves, which is best described as homing behaviour – characterized by the strong association between mitochondrial haplotype and cave – would have made them comparatively predictable prey (Fortes et al., 2016; Grandal D'Anglade et al., 2018). Both Neaderthals and Modern Humans would have been strong competitor for caves or shelters and have forced cave bears into less suitable sites for hibernation (Grayson and Delpech, 2003). As suggested by Grayson and Delpech (2003), competition might have arisen not only from increases in human group sizes but also from increased human residence times.

1.3 Extinction chronology and paleoecology of cave bears

Many large mammal species went extinct at the end of the Pleistocene epoch in Europe. Who or what caused the extinctions of Quaternary megafauna remains one of the most contested topics in the historical sciences. The discussed explanations include climate and environmental change, human impact or a combination of both (e.g. Lorenzen et al., 2011; Sandom et al., 2014, Stuart, 2015). In any case, a better understanding why some groups succumbed while others survived could provide insights into how modern-day species might - or might not - survive climatic and environmental changes, and into the resilience of natural ecosystems to increasing anthropogenic impact. Cave bear (*Ursus spelaeus* sensu lato) is an iconic component of the Pleistocene

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megafauna and was taken as a model to understand the causes of the extinction species. Thanks to the very good general molecular preservation of cave bear bones in karst contexts, numerous studies dealing with stable isotopes of collagen and ancient DNA have yielded invaluable information about the paleoecology of this extinct species.

To better understand the paleoecology and the reasons of cave bears extinction, it is of fundamental importance to know well what they ate. For this reason, to investigate its paleodiet different approaches were used, such as functional morphology, dental microwear, and isotope geochemistry. The dietary range of the extinct cave bear has been of interest since it was assessed by Kurtén (1976), from the dental morphology and powerful cranial musculature, to be primarily vegetarian. In the last three decades, this interpretation has been supported by a series of stable isotope (δ^{13}C and δ^{15}N) analyses on cave bear bones. This method is based on predictable changes in the isotopic composition of carbon and nitrogen in animal tissues in relationship to their position in the trophic system (Deniro and Epistein, 1981; Bocherens and Drucker, 2003; Krajcarz et al., 2018; Bocherens, 2018) and is the most powerful tool to address questions about diet and palaeobiology of extinct species. Cave bear was the first Pleistocene extinct mammals for which carbon (δ^{13}C) and nitrogen (δ^{15}N) stable isotopes were used to investigate its paleodiet (Bocherens et al., 1990; 1991; 1994). In the last 30 years, more than 300 cave bear bones from all over Europe have given isotopic carbon and nitrogen compositions that suggest an essentially vegetarian diet (Bocherens et al., 1997; 2006; 2011; 2014a-b-c; Bocherens, 2015; 2018; Vila-Taboada et al., 1999; Fernandez-Mosquera, 2001; Grandal-d'Anglade et al., 2011; Münzel et al., 2011; Horaceck et al., 2012; Pacher et al., 2012; Krajcarz et al., 2016; Naito et al., 2016; Paper II; Paper III). In contrast, samples from two caves in Romania yielded nitrogen isotopic values higher than those of other cave bears from Europe and in a similar range of the carnivores, leading some authors to conclude that these bears could have had an omnivorous diet including animal food resources (Richards et al., 2008; Trinkaus and Richards, 2013; Robu et al., 2013; 2018). Moreover, several ecomorphological approaches based on geometric morphometrics of craniomandibular skeleton as well tooth microwear studies suggested that cave bear was not adapted to a pure herbivorous diet (Figueirido et al., 2009; Peigné et al., 2009; Jones and DeSantis, 2016). These studies raising doubts on the herbivory hypothesis for cave bears, even if some other tooth microwear and morphometric analyses on cave bear skulls and mandibles confirmed an herbivorous diet (van Heteren et al., 2014; 2016; Münzel et al., 2014). So far, the stable isotopic values of cave bears from Europe, dating from 100,000 and 20,000 years ago, do not exhibit variation in their feeding

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behaviour, suggesting that they have a fully herbivorous diet (Krajcarz et al., 2016; Bocherens et al., 2014a; Bocherens, 2018, Paper II-III).

The cave bear evolved from Middle Pleistocene *Ursus deningeri* (Rabeder et al., 2000) as indicated by morphological and molecular studies and established a vast distribution extending eastwards from Northwest Spain across central Europe and the Urals to Arctic North-Eastern Siberia and Altai Mountains (Rabeder et al., 2004b; Knapp et al., 2009; Sher et al., 2011; Baca et al., 2014), and from Belgium and Harz region of Germany in the north as far south as Italy and Greece (Kostopoulos, 2006; Pacher and Stuart, 2009; Martini et al., 2014; Rossi et al., 2018; Paper I; Paper II). Due to their high intra-specific morphological variability, several groups have been distinguished on the basis of morphological and metrical studies on teeth and metapodials, in combination with aDNA analysis. Paleogenetic research revealed three main haplogroups of cave bear in Europe, *Ursus spelaeus*, *U. ingressus* and *U. kudarensis* (e.g Hofreiter et al., 2002; Rabeder et al., 2004b; Baca et al., 2014; 2016; Stiller et al., 2014).

Additional, two small cave bear forms that had preserved some primitive traits were distinguished as subspecies of *U. spelaeus*: *U. spelaeus eremus* and *U. spelaeus ladinicus*. Their distribution was confined to the high alpine caves in Austria and Italy (Rabeder and Hofreiter, 2004; Rabeder et al., 2004a). By the end of the Pleistocene, all these cave bear forms were extinct. Direct radiocarbon dating indicates that the cave bears became extinct prior to the Late Glacial Maximum (LGM) and disappeared from the fossil record quite simultaneously in different part of Europe about 26-30 ky cal. BP (e.g. Hofreiter et al., 2004; Grandal-d'Anglade et al., 2006; Münzel et al., 2011; Bocherens et al., 2014a; Martini et al., 2014; Sabol et al., 2014; Baca et al., 2016; Rossi et al., 2018). However, new radiocarbon dating, younger than 26 ky cal. BP, documents the survival of fragmented populations during the LGM, conceding with maximum extent of the ice sheets (Baca et al., 2016; Paper II, Paper III). Paleogenetic analyses showed that the demise of cave bears started ca. 50,000 years BP, thus about 25,000 years before their final extinction (Stiller et al., 2010), coinciding with the replacement of Neanderthals by modern humans in Europe. The decline of cave bear was slow and continuous may be correlated with changing environmental condition and human pressure. However, no cave bear has awoken from the final "hibernation", but recently as demonstrated by Barlow et al., 2018 about 0.9 to 2.4 percent of living DNA traces back to the extinct cave bear. This indicates that extinction does not always vanquish a species' genes.

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This thesis focuses on the extinction of the cave bears from Italy acquiring new archaeozoological and taphonomic information, isotopic, radiometric and paleogenetic data. Below I first give a short introduction of origins and discussed evidence of cave bear extinction in the light of human interaction, chronology, and paleobiology. This section is followed by a brief presentation of the materials and methods used in this thesis. The objectives and results of this study, published in, or in preparation for journal papers, are presented in the final section.

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2. OBJECTIVES

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Objectives

The objectives of this thesis are as follows:

(1) The acquisition of new archaeozoological and taphonomic data about the interaction between humans and bears during Middle and Upper Palaeolithic in northeastern Italy. This information helps to clarify whether Palaeolithic hunters played a role in the extinction process by continuous tracking and hunting of bears.

(2) The acquirement of a detailed picture of the ecology and diet of this great Pleistocene plantigrade using isotopic analyses on bone collagen. Isotopic data of cave bear from Italy are still missing and could reveal new information or confirm the existent hypotheses on diet. In some archaeological levels in sites of the Berici Hills, fish remains have been found in association with bear remains. It thus is important to understand if there has been a variation in the diet in contexts of territorial continuity and contemporary human occupation.

(3) The comparison of data obtained using different methods, with that coming from radiometric and paleogenetic analyses to possibly unveil a new European scenario on the extinction of one of the most common mammals in the Pleistocene record.

3. MATERIAL AND METHODS

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3.1 Brief presentation of cave sites

1. Rio Secco Cave
2. Fumane Cave
3. Buso doppio del Broion
4. Paina Cave
5. Trene Cave
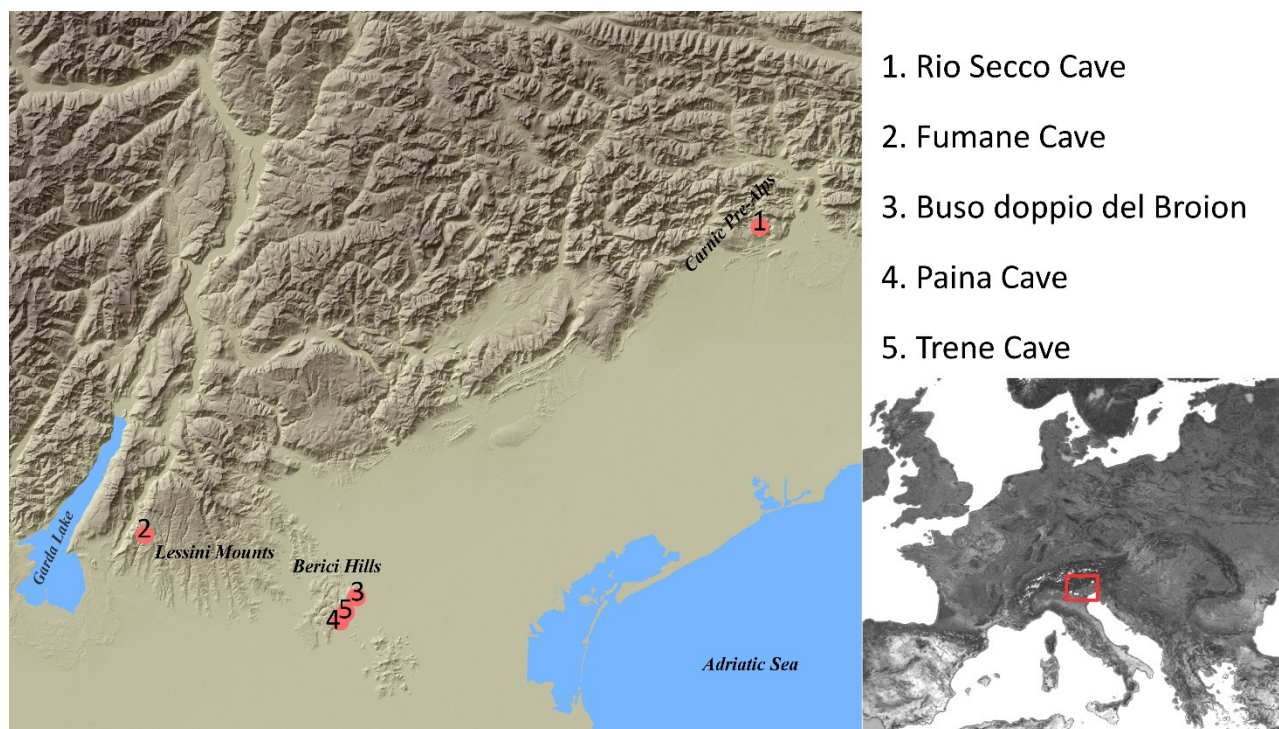
Fig. 1*: Geographical location of the studied cave sites

- Rio Secco Cave

Rio Secco cave is located in a stream gorge at 580m asl on the Pradis Plateau in the eastern part of the Carnic Pre-Alps. The site is a flat and wide south-facing shelter, with a gallery completely filled with sediments. Discovered in 2002 and systematically investigated since 2010, the cavity contains a sedimentary succession made of stones and loams that records human occupations during the Middle Palaeolithic and Upper Palaeolithic (Peresani et al., 2014; Talamo et al., 2014). The focus of this thesis is the Middle Palaeolithic layers (5top, 7, 5, and 8) with radiocarbon dates ranging from 47.9–45.8 ky cal BP (US 5top) to more than 49 ky BP (lower level of US 7) (Talamo et al., 2014). The Mousterian assemblages are characterized by the use of Levallois and Discoid technologies. The faunal assemblage shows the predominance of carnivores (*Ursus arctos*, *Ursus spelaeus*, mustelids, and canids) over ungulates. Amongst the latter, the most abundant species are the cervids (*Megaloceros giganteus*, *Cervus elaphus*, *Alces alces*), followed by caprids (chamois and ibex), wild boar, *Sus scrofa*, and bovids (*Bos/Bison*). Human interest in ungulates is evidenced by cut-marks on red deer bones. In addition, several remains of *Ursus spelaeus* and *Ursus* sp. show traces of butchering, skinning, and the deliberate fracturing of long bones (Peresani et al. 2014;

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Paper I). Bird remains are rare, but appear well-preserved, notable is a terminal pedal phalanx of a cfr. golden eagle from layer 7 that shows cut-marks on the proximal articular facet (Romandini et al., 2014).

- Fumane Cave

Fumane Cave is located on the southern slope of the Veneto Prealps in northern Italy, at 350 m a.s.l., and has provided a dated sequence spanning from MIS 5 to 2 (López-García et al., 2015; Martini et al., 2001; Obradović et al., 2015; Peresani et al., 2008;). At Fumane, the Late Middle-Early Upper Palaeolithic deposits consist of numerous thin to very thin parallel levels and lenses that are grouped into stratigraphic units labeled from bottom to top A13 to A1. Mousterian industries are found in A12-A11, A10, A9, A6-A5, Uluzzian in A4 and A3, and Aurignacian in A2 and A1 (Broglio et al., 2006; Peresani, 2012; Peresani et al., 2011a-b; 2016). The Mousterian levels, which were investigated over areas varying from 6 to 75 m^2 in size, are characterized by lithic and faunal remains that are densely scattered on the living floors, as is the case in units A11, A10, A9 and A6. Flints in A12-A11, A10V, A10, and A6-A5 were exploited mostly through Levallois technology (Peresani, 2012; Peresani et al., 2013). The focus of this thesis is the stratigraphic complex A5-A6, dated to 44.8–42.2 ky cal B.P. (Higham et al., 2009). Faunal remains and lithic artifacts are referable to site occupations shifting from intense and persistent (A6) to more ephemeral (A5-A5+A6). Of these levels, A6 in particular, has provided evidence of a well-structured use of the living spaces, covering the whole entrance area (Peresani et al., 2011a). Over 40 combustion structures and dumps of combustion debris are associated with zones used for *Levallois* manufacture, tool shaping and curation, ungulate butchery, and the treatment of hides and furs. The faunal assemblage includes a rich association of ungulates, carnivores, and birds from diverse environments and climates. The most abundant faunal remains are red deer, roe deer, ibex and chamois whereas, bison, and giant deer are less frequent. Moose, horse, and wild boar are rare. All ungulate species, with the exception of horse and wild boar, bear traces of human exploitation. Cave bear, brown bear, fox and wolf, are the most numerous carnivores. The current state of research shows the complex A5-A6 to be unique within the entire stratigraphic sequence due to evidence for attention to the treatment of carnivore carcasses (Romandini et al., 2018, Paper I). Except for wolves, carnivore remains show butchery marks from skinning and defleshing. This data, together with the scarcity of carnivore gnawing on bones and an elevated number of anthropically modified bones, supports the anthropic nature of the bone accumulation

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in these units (Peresani et al., 2011a). In addition to the butchery marks on ungulate and carnivore bones, we also report on the discovery of human modifications to some anatomical elements of large raptors and Passeriformes (Peresani et al., 2011b).

- *Buso doppio del Broion Cave*

The Buso doppio del Broion Cave is a karst cavity of Berici Hills (northeastern Italy), opening at 150 m a.s.l. on their eastern slope. The cave contains Upper Pleistocene deposits and the archaeological excavation is ongoing, carried out by University of Ferrara. It is formed by a system of galleries that reaches a horizontal depth of more than 17m. The stratigraphic sequence provides evidence of short-term human occupations at around the end of MIS 3 and the onset of the LGM. The finding of several lithic implements (among which a few shouldered points) mostly in the upper reworked sediment, suggests early Epigravettian frequentation, whereas the presence of gravettes and microgravettes in the medium-basal portion of Layer 1 is indicative of Gravettian (Romandini et al., 2015). The lower portion of the stratigraphic sequence (Layers 4-7) yielded other lithic implements (micro-bladelets, possibly Aurignacian), the study of which is still underway (Romandini and Nannini, 2012; Romandini et al., 2015). The focus is the zooarchaeological content of layers 1 and 2. The faunal remains of these layers record the predominance of carnivores (*Ursus spelaeus*, *Vulpes vulpes*, *Felis silvestris*, *Canis lupus*) over ungulates (*Alces alces*, *Cervus elaphus*, *Rupicapra rupicapra*). The sediments also contained fish remains, which mostly consist in cyprinid and salmonid vertebrae, and birds (Romandini et al., 2015; Carrera et al., 2018). Human modifications such as cut-marks are present on ungulate and cave bear bones. The amount and the state of preservation of cave bear remains suggest that this mammal used the cave as a shelter for several hibernation cycles, comparably to other caves in Berici Hills.

- *Paina Cave*

Paina cave is located in the Berici Hills in northeastern Italy, about 350 m a.s.l., on the edge of a steep slope connecting the plateau to the alluvial plain. Field investigations revealed a stratigraphic series of about 1.50 m in thickness, which includes 12 layers containing Middle (Units 12–10) and Upper Palaeolithic (Units 9–5) artefacts. The focus is the zooarchaeological content of layers 5 and 6, radiocarbon dated from 20,120 ± 220 to 19,430 ± 150 14C yr BP (layer 6) and to 19,861 ± 70 14C yr BP (layer 5) based on cave bear bones (Parere et al. 2006; Gurioli et al. 2006). The lithic artifacts have been referred to the Early Epigravettian with shouldered points

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(Bartolomei et al., 1988). The faunal remains of these Units record the predominance of carnivorans (cave bear, fox and mustelids) over ungulates. Amongst the latter, the most abundant species are the cervids (*Cervus elaphus* and *Alces alces*), followed by caprids and wild boar (Paper II).

- Trene Cave (Covolo forticato di Trene)

Trene cave is located in the Berici Hills in northeastern Italy, at about 360 m a.s.l. The cavity was the subject of systematic excavations made by the University of Ferrara in 1956, which yielded a 1.14 m thick deposit, subdivided into three macro-units: A, B and C. The focus of this paper is the macro-unit B with radiocarbon dates on ungulate bones ranging from 17,640 ± 140 14C yr BP to 18.630 ± 150 14C yr BP. The lithic industry ascribes the anthropic frequentation to the early Epigravettian (Leonardi, 1959). The faunal assemblage shows a clear dominance of cave bear over other taxa, followed by ungulates (*Alces alces*, *Cervus elaphus* and *Sus scrofa*), fishes and birds (Romandini and Nannini, 2012; Paper II-III).

3.2 Material

The bones assemblage examined for the studies in this thesis are stored at University of Ferrara and have been discovered mostly in the last decade of excavations using dry and wet sieving. Zooarchaeological and taphonomic analysis were performed on bones assemblage from Rio Secco Cave (layers 5top, 7, 5, and 8), Fumane Cave (layers A5-A6) and Buso doppio del Broion (layers 1-2) (Tab.2). Afterwards, we focused on more than 600 bear bones for taphonomic analysis. At Paina and Trene caves, taxonomic, skeletal identification and preliminary taphonomic analysis of bone assemblages have been conducted and published by Gurioli et al. (2006), Parere et al. (2006), Nannini and Romandini (2015). Taphonomic analysis was performed on cave bear bones from Unit 5 and 6 – Paina Cave and macro-unit B – Trene.

For stable isotope analysis, 46 cave bear bones (different anatomical elements of several individuals), from Buso doppio del Broion, Paina and Trene, were selected and sampled, especially those with a good state of conservation. In addition, 6 moose *Alces alces* bones from the same sites and units were sampled (Tab.3). Part of collagen of 11 cave bear bones, prepared for stable isotope analysis, was sent to the Laboratory of Ion Beam Physics, ETH, Zurich (Switzerland) for AMS radiocarbon dating (Tab. 3). Between 150 and 500 mg of powder of 15 cave bear bones (Tab.2) were sent to Paleogenetic groups of Prof. Verena J. Schuenemann, University of Tübingen (Germany) and University of Zurich (Switzerland).

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Tab 2: Mammal Nisp and Nisp % from the sites and levels considered in this thesis. RS – Rio Secco; FC – Fumane cave; BdB – Buso doppio del Broion; PC – Paina cave; TC – Trene cave

Taxa	RS – levels 5 top - 8		FC – levels A5 - A6		BdB – levels 1 - 2		PC – levels 5 - 6		TC – macrounit B	
	NISP	NISP %	NISP	NISP %	NISP	NISP %	NISP	NISP %	NISP	NISP %
Lepus timidus					1	0.4				
Lepus europeaus					2	0.9	1	0.2		
Lepus sp.	1	0.1	1		6	2.7	2	0.4	2	0.2
Marmota marmota	300	31.3	1		17	7.6	5	1.1	5	0.6
Castor fiber					2	0.9				
Erinaceus europaeus	1	0.1								
Rodentia									3	0.3
Total Lagomorpha and Rodentia	302	31.5	2	0.1	28	12.5	8	1.8	10	1.1
Canis lupus	3	0.3	11	0.3	4	1.8			1	0.1
Vulpes vulpes	4	0.4	46	1.4	13	5.8	22	5	4	0.5
Vulpes/Alopex			3	0.1						
Ursus arctos	**7**	**0.7**	**14**	**0.4**						
Ursus spelaeus	**305**	**31.8**	**2**	**0.1**	**82**	**36.6**	**302**	**69.1**	**604**	**69.1**
Ursus sp.	**130**	**13.5**	**34**	**1.1**	**24**	**10.7**	**4**	**0.9**	**70**	**8**
Martes martes	3	0.3			5	2.2	6	1.4		
Martes sp.	1	0.1					1	0.2		
Meles meles	2	0.2			8	3.6			2	0.2
Mustela erminia	4	0.4			1	0.4				
Mustela nivalis			1							
Mustelidae	2	0.2								
Felis silvetris					9	4	3	0.7		
Carnivora indet.	52	5.4	16	0.5	13	5.8	2	0.4	28	3.2
Total Carnivora	513	53.5	127	4	159	70.9	340	77.8	709	81.1
Sus scrofa	3	0.3	2	0.1			2	0.4	3	0.3
Megaloceros giganteus	19	2	38	1.2			1	0.2		
Alces alces	7	0.7	5	0.1	5	2.2	19	4.4	58	6.6
Cervus elaphus	13	1.3	1392	44.7	5	2.2	30	6.8	18	2.1
Capreolus capreolus	1	0.1	230	7.4	1	0.4				
Cervidae indet.	25	2.6	167	5.3	7	3.1	19	4.4	42	4.8
Bison priscus	3	0.3	2	0.1	1	0.4				
Bos/Bison	18	1.8	23	0.7	2	0.9				
Capra ibex	7	0.7	84	2.7	1	0.4	4	0.9	1	0.1
Rupicapra rupicapra	3	0.3	87	2.8	3	1.3			3	0.3
Caprinae indet.	1	0.1	19	0.6					2	0.2
Ungulata indet.	43	4.5	932	30	12	5.3	10	2.3	28	3.2
Total Ungulata	143	14.9	2981	95.8	37	16.5	89	20.4	155	17.7
Total NISP	**958**	*100*	**3110**	*100*	**224**	*100*	**437**	*100*	**874**	*100*
Total indeterminate	3867		168161		1245		285		2548	
Pisces					447		3		26	
Total	**4825**		**171271**		**1916**		**725**		**3448**	

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Tab 3. Cave bear bones selected for Stable isotope analysis, mtDNA and radiocarbon dating. CM – cut-marks

Isotope sample	Inventory nr	Cave Site	Level	Animal	Element	Age	CM	mtDNA Sample nr	AMS lab sample nr
CBV1	314	PAINA	6	Cave bear	Humerus	Young			
CBV2	374	PAINA	6	Cave bear	II Metacarpal	Adult		**TU841**	**ETH-82963**
CBV3	749	PAINA	6	Cave bear	I Metacarpal	Adult		**TU842**	
CBV4	60	PAINA	5	Cave bear	II Phalanx				
CBV5	26	PAINA	5cp	Cave bear	Humerus	Young			
CBV6	156	PAINA	5	Cave bear	I Phalanx				**ETH-79366**
CBV7	542	PAINA	6	Cave bear	Metapodial	Young			
CBV8	386	PAINA	6	Cave bear	IV Metatarsal	Adult		**TU843**	**ETH-82964**
CBV9	66	PAINA	5	Cave bear	Tarsal-astragalus			**TU844**	**ETH-82965**
CBV10	368	PAINA	6	Cave bear	Rib				
CBV11	547	PAINA	6	Cave bear	Mandible with M1	Young			
CBV12	52	PAINA	5	Cave bear	p^4				
CBV13	750	PAINA	6	Cave bear	I_3				
CBV14	561	PAINA	6	Cave bear	p^4	> 16 months			
CBV15	560	PAINA	6	Cave bear	M^1				
CBV16	1327	PAINA	7	Cave bear	I Phalanx				
CBV17	1150	PAINA	7b	Cave bear	Fibula				
CBV18	1072	PAINA	7c	Cave bear	Rib			**TU846**	**ETH-82966**
CBV19	875	PAINA	7a	Cave bear	Metapodial			**TU847**	
CBV20	584	PAINA	6	*Alces alces*	Tibia				
CBV21	107	PAINA	5	*Alces alces*	Tibia				
CBV22	572	PAINA	6	*Alces alces*	Metatarsal				
CBV23	BDB366	BD BROION	1 base	Cave bear	Rib		x	**TU848**	**ETH-79367**
CBV24	BDB785	BD BROION	1 tg IV	Cave bear	Radius	Young	x		
CBV25	BDB830	BD BROION	1 base/2	Cave bear	Tibia	Adult	x		
CBV26	BDB564	BD BROION	1/2	Cave bear	Rib			**TU851**	
CBV27	BDB311	BD BROION	1 base	Cave bear	V Metacarpal	Adult			
CBV28	BDB3000	BD BROION	1 tg I	Cave bear	I Phalanx				
CBV29	BDB3001	BD BROION	1 tg IV	Cave bear	IV Metacarpal	Adult			
CBV30	BDB3002	BD BROION	1 tg IV cp	Cave bear	I^3	Senile			

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CBV31	BDB3003	BD BROION	1 tg II	Cave bear	I Metatarsal				
CBV32	BDB3004	BD BROION	1 tg IV	Cave bear	I Metatarsal				
CBV33	BDB3005	BD BROION	1 tg IV	Cave bear	IV Metacarpal			**TU852**	**ETH-82967**
CBV35	BDB742	BD BROION	1 tg IV	*Alces alces*	Mandible with d3	Young			
CBV37	TR288	TRENE	B1 VIII	Cave bear	Humerus	Young	x		**ETH-79368**
CBV38	TR931	TRENE	B3 VIII	Cave bear	Fibula		x		
CBV39	TR437	TRENE	B2 VII	Cave bear	III Metacarpal	Young	x	**TU853**	**ETH-82968**
CBV40	TR692	TRENE	B2 VII	Cave bear	Mandible with M1	Adult II	x	**TU854**	**ETH-82969**
CBV41	TR37	TRENE	B	Cave bear	Radius	Adult	x		
CBV42	TR39	TRENE	B	Cave bear	III Metatarsal	Adult		**TU855**	**ETH-82970**
CBV43	TR1166	TRENE	B	Cave bear	III Metatarsal	Adult			
CBV44	TR108	TRENE	B IV	Cave bear	Canine tooth	Adult			
CBV45	TR 241	TRENE	B1	Cave bear	V Metatarsal	Adult			
CBV47	TR387	TRENE	B2	Cave bear	I Phalanx	Adult		**TU857**	
CBV49	TR466	TRENE	B2 VII	Cave bear	II Phalanx				
CBV50	TR484	TRENE	B2 VII	Cave bear	Rib				
CBV52	TR439	TRENE	B2 VII	Cave bear	I Metacarpal	Adult			
CBV53	TR440	TRENE	B2 VII	Cave bear	I Metacarpal	Adult			
CBV54	TR934	TRENE	B3 VIII	Cave bear	Rib				
CBV56	TR695	TRENE	B3	Cave bear	IV Metacarpal	Adult			
CBV57	TR389	TRENE	B2	*Alces alces*	Pelvis	Young			
CBV59	TR80	TRENE	B	*Alces alces*	I Phalanx	Adult	x		

3.3 Methods

Taxonomic and skeletal identifications of the faunal remains are based on the complete alpine fauna reference collection from the Department of Humanities at the University of Ferrara, featuring Pleistocene and modern fauna with reliable chronological attribution. Regarding the analysis of age groups, many studies have documented how the approximate age at death of cave bears may be inferred from the stages of dental development or occlusal wear (Torres, 1976, 1984, 1988; Stiner, 1998; Torres et al., 2007). The "tooth eruption wear stages" (Stiner, 1998; Fosse and Cregut-Bonnoure, 2014) and epiphyseal fusion (Weinstock, 2009) were the methods taken into consideration for the allocation of individuals' age. The quantitative analysis was

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conducted with standard procedures, such as the Number of Identified Specimens (NISP), Minimum Number of Individuals (MNI) and Minimum Number of Elements (MNE) as well as bone weight. Value of NISP, MNI and MNE were calculated following (Binford, 1981; Klein and Cruz-Bökönyi, 1970; Stiner, 1994;).

Taphonomy

The bone surfaces were analyzed both macroscopically and microscopically using a small magnifying lens (10-20x) with incident white light and a Leica S6D Greenough stereomicroscope with 0.75-70X magnification range for capturing images. In order to identify the nature of surface alterations and to distinguish human from animal traces, trampling abrasion, and modern mechanical modifications produced by excavation tools, reference was made to well-established taphonomic literature. Combustion degree has been distinguished between moderate (200-500 °C, black/brown) and elevated with calcination (>700 °C, grey/white) (Stiner et al., 1995; Costamagno et al., 2005). Cut-marks were identified using criteria described by e.g. Potts and Shipman (1981); Shipman (1981); Shipman and Rose (1984); Fernández-Jalvo and Andrews (2016). Attention was paid to differentiating between trampling and butchery marks (Domínguez-Rodrigo et al., 2009). Regarding the traces left by carnivores, these were identified as deep punctures in the cortical bone surface, concentrated on the articular ends of the bones, as well as pits and scores with U-shaped striations on bone surfaces. These results were compared with data from Fisher (1995), Selvaggio and Wilder (2001), Domínguez-Rodrigo and Piqueras (2003), Diedrich (2012), Fourvel et al. (2014) and Camaros et al. (2017). Potential burnt bones were determined by combustion grade level following the criteria described by Stiner et al. (1995). According to the analytical protocol, natural post-depositional degradations have been searched for only on bones longer than 3 cm or on bone relevant at the taxonomical level.

Collagen extraction and C and N stable isotopes

For stable isotope analysis, cave bear bones from Buso doppio del Broion, Paina and Trene were selected. In addition, some *Alces alces* bones from the same sites and units were sampled, as ecological comparison. For each specimen, a small fragment was carefully sawn with a Dremmel© rotating tool equipped with a circular diamond-coated blade, ultrasonicated in acetone and water, rinsed with distilled water, dried and crushed to a powder of 0.7 mm grain size. Then an aliquot of around 5 mg was used to measure the nitrogen content (%N) of the whole bone, in order to

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screen out samples with excessive collagen loss (Bocherens et al., 2005). For instance, fresh bones contain 4% nitrogen while ancient bones with less than 0.4% nitrogen usually fail to yield good collagen (Bocherens et al. 2005). The measurements were performed using a Vario EL elemental analyser using Acetanilid from Merck as internal standard at the Department of Geosciences of the University of Tubingen. The mean standard error was better than of 0.1% for %C and %N. The collagen was purified according to well-established protocol (Bocherens et al., 1997). This preparation was performed at the Biogeology unit of the Geoscience Department at the University of Tübingen (Germany). Carbon and nitrogen elemental and stable isotope measurements were performed at the LSIS-AFAR stable isotope facility of the University of Western University, Canada. Collagen samples (0.5 mg) were weighed into tin capsules and combusted in a Costech Elemental Analyzer coupled to a Thermo Delta Plus XL isotope ratio mass spectrometer operated in continuous flow mode, with helium carrier gas. Two standards, USGS-40 and USGS-41 were included for every ten samples and two internal laboratory standards, powdered keratin (MP Biomedicals Inc., Cat No. 90211, Lot No.9966H) and IAEA-CH-6 were included to monitor instrument drift and provide a check on accuracy over the course of each analytical session. Values of $\delta^{13}C$ were calibrated to VPDB and values of $\delta^{15}N$ were calibrated to AIR. Measurement error was ±0.1 ‰ for $\delta^{13}C$, and ±0.2 ‰ for $\delta^{15}N$. Part of collagen of some cave bear bones prepared for stable isotope analysis, was sent to the Laboratory of Ion Beam Physics, ETH, Zurich (Switzerland). The dates were calibrated to the years BP (i.e. 1950) in Oxcal v4.2.4 (Bronk Ramsey et al., 2013) using intCal13 atmospheric curve (Reimer et al., 2013).

4. RESULTS

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Paper I

This thesis consists of four papers:

- PAPER I

Bears and humans, a Neanderthal tale. Reconstructing uncommon behaviors from zooarchaeological evidence in southern Europe.

In this paper we focused on bear bone remains from Rio Secco Cave and Fumane Cave in northeast Italy. The caves are geographically distant but chronologically related and provide several distinct Neanderthal frequentations that attest systematic and consolidated exploitations of bears, during 49-42 ky cal. BP. Zooarchaeological and taphonomic analyses demonstrate clear evidence for interactions between Neanderthals and cave and brown bears, which were targeted for the acquisition of fur, meat, bones, and possibly other materials that were considered plantigrade resources. Our analyses partially enable to distinguish between hunting and the exploitation of animals that died of natural causes. However, the data clearly demonstrate that the first manipulation of the bear carcass by humans was targeted at fur recovery, a task accomplishable only on animals that died very shortly before being skinned and was probably planned to occur during denning time. This is also indicated by the activities aimed at the extraction of meat and marrow, the consumption of which is not strictly fixed in a timeframe, as it depends on taste preferences and food tolerances unknown today.

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1. Introduction

From the Middle to the Upper Pleistocene, humans and bears coexisted and cohabitated in a good part of Europe. This is demonstrated by numerous findings of plantigrade remains in as- sociation with artifacts, interpreted over the course of the 20th century to demonstrate both the hunting of these carnivores and the accumulation of their bones following natural deaths in con- texts that also indicate anthropic frequentations (Fedele, 1968; Jéquier, 1975; Hille and Rabeder, 1986; Tillet, 1997; Le Tensorer, 1998; Tillet and Bernard-Guelle, 1998; Fosse et al., 2002; Auguste, 2003; Bona et al., 2007; Torres et al., 2007; Cvetković and Dimitrijević, 2014; Bocherens et al., 2014; Fourvel et al., 2014). However, the taphonomic history of these faunal assemblages within caves is very complex and has only been refined in the last 20 years by microscopic and taphonomic investigative techniques, accompanied by reviews of the materials excavated in the early to middle of the last century that have shown that between these large carnivores and Neanderthals, a consolidated and probably "symbiotic" interactive relationship was established (Koby, 1951; Kurtén, 1976; Fosse et al., 2002; Stiner, 1998; Auguste, 2003). The ecological and etological characteristics shared by humans and ursids (*Ursus arctos* and *Ursus spelaeus*) were not, in fact, insignificant. Besides adopting prey acquisition and related alimentary regime strategies, they shared habitat types and shelters, which were utilized for hibernation and protection, especially of the youngest (Turner, 1992, 1994; Arribas and Palmqvist, 1999; Hemmer, 2000; Brugal and Fosse, 2004), whose distribution and density is equally a regulating factor within species assemblages that can live in territorial or family communities. Human and bear interactions are particularly observed in Europe throughout the Upper Pleistocene, with abundant ursid populations and numerous Mousterian frequentations attested by archaeological finds in caves and shelters (Petram et al., 2004; Bona et al., 2007; Diedrich, 2012; Viranta and Grandal d'Anglade, 2012). In terms of contributing factors to the overall interaction, climatic conditions had greater impact in respect to the more temperate regions, which were differentiated by environments, types of vegetation, geological substrates, and by populations and the structure of ursid commu- nities (Turner, 1995). Lastly, the quality of the fossil record and the level of archaeozoological and taphonomic research must also be considered.

The sizes of *Ursus arctos* and *Ursus spelaeus*, averaging 260 and 600 kg, respectively, are markedly different, but their eto-ecological behaviours are very similar. With a longer life span among the carnivores (20-30 years), these ursids were adapted to temperate- cold climes, preferring semi-forested vegetation, and could live in groups or individually, moving through a territory estimated to between 100 and 1,000km2 for females and males, respectively, (Caloi et al., 1997; Couturier, 1954; Jakubiek, 1993; Brugal et al., 2001; Brugal and Fosse, 2004; Torres et al., 2007). The di- mensions of the ursid groups, their structural stability, and the size of their populations are in most cases strongly influenced by the presence of water, which determines the choice of a suitable place of refuge, the abundance of herbivorous prey, and even, for mothers and young, the orientation of slopes (S, S-E), fundamental to the micro-climatic conditions in the critical phases of hibernation. If one talks of taphonomy and archaeozoology in relation to the ursids, it is impossible not to take into consideration the theory of the "Bear Cult," which was widely diffused in the first half of the 20th century by Emil Bächler (Bächler, 1920-1921, 1923, 1940), who hypothesized the existence of a culture unique to the Alps, associated to the Riss-Würm Interglacial: the "Palaeolithic" or "Alpine Mousterian." This "culture" was associated with a specialized hunting of young cave bears that was practiced in the summer at highland sites where, in addition to bear remains, bone tools and lithic industries were identified at the time, often described as Quina Mousterian type. The true "Bear Cult," "Cave Cult," and/or "Cult of Hunting and Sacrifice" (Bächler, 1920-1921) is manifested through the presumed deposition or replacement of cave bear long bones and crania. These theories or hypotheses saw undeniable comparisons in archaeological evidence from Germany, Austria, Hungary, Slovenia, and Croatia (Pacher, 2003). Decades later, the theory of the "Bear Cult" was totally abandoned by challenging the origin and anthropic modification of bear remains (Koby, 1943, Kurtén, 1976; Fosse et al., 2002; Stiner, 1998; Auguste, 2003).

However, aside from the discussed practice of burying human remains in association with brown bear bones as funerary goods at Le Régourdou in France (Cavanhié, 2009-2010), many examples linking Neanderthals and bears are now known thanks to the dis- covery of lithic tool cut-marks on the surfaces of ursid bones from

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recently excavated sites or from review of ancient excavation ma- terials. At Taubach, the systematic destruction of 80% of the brown bear canines (Kurtén, 1976), based on the current state of knowledge, cannot be explained by the vague term "symbolic," as in the majority of cases it is "utilitarian." The main difficulty, then, lies in evaluating the degree active hunt against scavenging. The hypotheses of carcass manipulation at the bears' natural place of death seems plausible for the Mousterian: evidence for such behavior has been observed in Belgium at Goyet and Scladina caves (Germonpré and Sablin, 2001; Germonpré and Hämäläinen, 2007; Abrams et al., 2014), in France at Regourdou (Cavanhié, 2009-2010; Bonifay et al., 2007), in Germany at Geißenklößterle, Hohle Fels and Balve Cave (Kitagawa et al., 2012; Münzel, 1997; Münzel and Conard, 2004b; Münzel et al., 2011; Kindler, 2012), in Austria at Salzofen Cave (Ehrenberg, 1958-59, cited by Armand et al., 2004), in Poland at Nietoperzowa (Wojtal, 2007; Wojtal et al., 2015), in Slovenia at Divje Babe (Turk, 1997, 2014), in Serbia at Pešturina Cave (Majkić et al., 2017), in Montenegro at Crvena Stijena (E. Morin personal communication) and in Italy at Caverna delle Fate, Madonna dell'Arma, Ciota Ciara, Badalucco, Le Manie, and Sant'Agostino (Stiner, 1994; Valensi and Psathi, 2004; Quilès, 2003, 2004; Buccheri et al., 2016) (Fig. 1, Table 1). In light of these findings, it is thus possible to distinguish two principal European regions of Neanderthal ursid exploitation from OIS6 to OIS-3: one in north-central Europe (Germany, France, and Belgium), and one in the central-eastern Mediterranean (northern Italy and the Balkans) (Fig. 1, Table 1).

Within a framework that addresses rather fragmented and patchy taphonomic evidence, this work seeks to reinforce this view through the presentation of two cave contexts, Rio Secco Cave (Grotta de Rio Secco) and Fumane Cave (Grotta di Fumane) in the Italian Alps (Supplementary Information), which are geographically distant but chronologically related, and that provide several distinct Neanderthal frequentations that attest to the systematic and consolidated exploitations of bears (*Ursus arctos* and *Ursus spelaeus*) (See Fig. 2).

2. The use of cavities by bears

"Bear sites" are characterized by a percentage of bear remains within caves or shelters equal to 80-99% of the total recovered bones (Quilès, 2004), "charriage a sec" (Koby, 1941, 1943; Andrews and Turner, 1992) on the bone surface, traces of frequentation (including claw marks and polishing of the cave walls), and/or the presence of "bear earth," rich in phosphate nodules derived from the decomposition of their carcasses (equaling 10-17 kg of phosphate per individual). Bear caves can be divided into "bear hibernation den" and "cave/shelter den." These attributions are secondary to the function of the cave and the identity of its occu- pants: bear (male adults or females with cubs and young), carnivore, or man (Quilès, 2004). Other parameters include the representative indexes of bone destruction and the proportions of axial skeletons. In the "bear hibernation den," the appendicular skeleton will be strongly represented, in some cases with intact skeletons recovered in anatomical connection. The "cave/shelter den", however, is characterized by a major percentage of bone destruction and dispersal due to continuous trampling over a lesser occupational duration.

The ratio of cave bear remains to other animals in bear sites and the ratio of cave bear to brown bear remains appears to be 10:1, if not higher (Quilès, 2004). Both the cave bear and modern bears appear to be long-lived animals with a low reproductive success that rarely confers to their respective populations a high density. This is due to factors of an ecological order, such as trophic capacity, living space, infant mortality rate, and, in modern populations, human disturbances, either direct or indirect. According to studies carried out in North America, females grizzly give birth on average every two to three years, and individuals of both sexes, at a ratio of 1:1, are considered fertile at around the age of four to five years (Craighead et al., 1974). Females are fertile until the age of 18 and the number of cubs born is usually one or two, rarely three or four. The mating period for European brown bears is around the months of May and July, while the American grizzly mates between June and August. The gestation period varies from seven to eight months. At birth, which takes place between January and March in various species (during the wintering), the cubs weigh 250-400g, about 1/500 of the female's weight. The bear spends the cold season sheltered in refuges (dens) in semi-hibernation, a torpor produced by a more or less prolonged state of sleep induced by low temperature and the length of photoperiod. This state of immobility is achieved gradually in the den two to three weeks after entrance: during this transitional period,

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and even when slumber is reached, the bear is able to temporarily resume activity. During hibernation, which lasts for 4-5 months, the animal's metabolism is very slow: the state of fasting is complete (excrement and urine in dens or in the vicinity thereof have not been found in the current bear populations). According to observations made of grizzlies in a state of induced hibernation (Watts and Jonkel, 1988), a bear weighing 200 kg consumes a quantity of fat of about 50 kg during or almost six months of inactivity period, an average rate of about 400g/day. The resumption of normal metabolic activity occurs gradually; immediately after the exit from the den, the movements are limited to patrolling the wintering area. The female usually leaves her den only when the cubs are able to walk. Mortality in modern bears tends to be cyclical, and occurs especially in the period at the end of hibernation. Hunger is the most common cause of death of individuals during hibernation, especially cubs and young individuals, while adults rarely perish for this reason, anticipating awakening if their energies are exhausted and the search for food sources becomes imperative. If these aims are not achieved, death occurs in the territory around the wintering site. Juveniles or young adults may also be particularly vulnerable at the moment of or prior to awakening from hibernation and at the gradual resumption of activities when the mother leaves to explore the hibernation range.
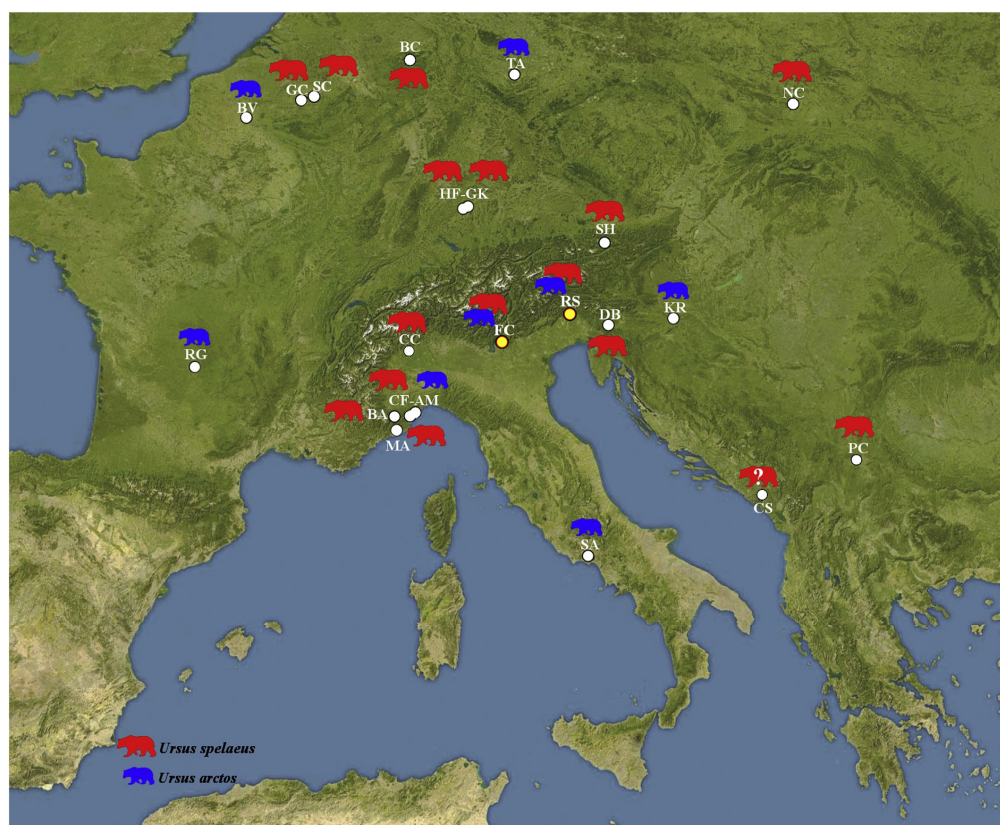

Fig. 1. Middle Palaeolithic European sites with evidence of bear exploitation cited in this study. BV (Biache-Saint-Vaast), KR (Krapina), DB (Divje Babe), SC (Scladina Cave), BC (Balve Cave), TA (Taubach), CF (Caverna delle Fate), AM (Arma delle Manie), MA (Madonna dell'Arma), CS (Crvena Stijena); RG (Regourdou), CC (Ciota Ciara Cave), SA (Sant'Agostino), BA (Badalucco), SH (Salzofenhöhle), RS (Rio Secco Cave), FC (Fumane Cave), PC (Pešturina Cave), GK (Geißenklößsterle), HF (Hohle Fels), GC (Goyet), NC (Nietoperzowa Cave).

3. This study: materials and methods

The bear bones examined in this study have been discovered at Rio Secco Cave and Fumane Cave, mostly in the last decade of excavations (see SI). Taxonomic and skeletal identifications are based on the complete alpine fauna reference collection from the Department of Humanities at the University of Ferrara, featuring

Pleistocene and modern fauna with reliable chronological attribution. Regarding the analysis of age groups, many studies have documented how the approximate age at death of cave bears may be inferred from the stages of dental development or occlusal wear (Kurtén, 1958; Dittrich, 1960; Torres, 1976, 1984, 1988; Stiner, 1998; Torres et al., 2007). The "tooth eruption wear stages" Stiner, 1998; Fosse and Cregut-Bonnoure, 2014) and epiphyseal fusion (Weinstock, 2009) were the methods taken into consideration for the allocation of individuals' age.

Table 1:

Middle Palaeolithic sites in Europe with evidence of bear exploitation; dates with (*REF)* references and *REF* of *MP* Middle Palaeolithic/Mousterian + *CM* cut-marked bear bones. B07-Blackwell et al. (2007); N97-Nelson and Ku (1997); B07-Bonifay et al. (2007); S94-Stiner (1994); P03-Pacher (2003); P14-Peresani et al. (2014); T14-Talamo et al. (2014); H09-Higham et al. (2009); A14-Alex and Boaretto (2014) ; C11-Conard (2011); A92-95-03-Auguste (1992-1995-2003); T14-97 Turk (2014-1997); M07-Miracle (2007); A14-Abramas et al. (2014); K12-Kindler (2012); G11-Gaudzinski-Windheuser and Roebroeks (2011); B99-Bratlund (1999); V04-Valenci and Psathi (2004); C09-10-Cavanhié (2009-2010); B16-Buccheri et al. (2016) ; E58/59- Ehrenberg (1958/1959); Q03-05-Quilès (2003-2005); A04-Armand et al. (2004); P14-Peresani et al. (2014); R13-14-Romandini et al. (2013-2014); P11-Peresani et al. (2011a); M17-Majkić et al. (2017); M11-Münzel et al. (2011); M04b-M04a-Münzel and Conard (2004a-b); M97-Münzel (1997); K12-Kitagawa et al. (2012); W15-Wojtal et al. (2015); G01-Germonpré and Sablin (2001); G07-Germonpré and Hämäläinen (2007); W07-Wojtal (2007).

Sites Layer	Date – (REF) Kyr Cal BP or MIS	REF (MP/Mousterian + CM on Bears)
Biache-Saint-Vaast (BV) IIa-IIα-II base	250–200	A92-A95-A03
Krapina (KR) 5–6	130–100	M07
Divje Babe (DB) A, A/B, B, C, D-1, D-2, E-1, E-2	115-30 (B07-N97)	T14-T97
Scladina Cave (SC) Unit 5	MIS 5d-5b	A14
Balve Cave (BC)		K12
Taubach (TA)	MIS 5	G11-B99
Caverna delle Fate (CF)	OIS 5 to 3	V04
Arma delle Manie (AM)	OIS 5 to 3	V04
Madonna dell'Arma (MA)	OIS 5	V04
Crvena Stijana (CS)	MIS 3	E. Morin (personal communication)
Regourdou (RG)	90-60 (B07)	C09-10
Ciota Ciara Cave (CC)	MIS 5	B16
Sant'Agostino (SA) S1	~55-43 (S94)	S94
Badalucco (BA)	~50	Q03-Q04
Salzofenhöhle (SH)	>49 (P03)	E58/59
Rio Secco Cave (RS) 5top+7 and 5 + 8	49-42 (P14-T14)	P14-R13-R14-this article
Fumane Cave (FC) A5-A5+A6 and A6	44-42 (H09)	P11-this article
Pešturina Cave (PC) 4	44-43 (A14)	M17
Geißenklösterle (GK) IV-VIII	43 (C11)	M11-M04b-M97-K12
Hohle Fels (HF)	40-33 (C11)	M11-M04a-W15
Goyet (GC) B4	40–41	G01-G07
Nietoperzowa cave (NC)		W07-W15

The bone surfaces were analyzed both macroscopically and microscopically using a small magnifying lens (10-20x) with incident white light and a Leica S6D Greenough stereo microscope with 0.75-70X magnification range for capturing images. Further qualitative data were collected via SEM observations at the MUSE (Science Museum of Trento) using a ZEISS EVO XVP microscope, at high vacuum on gold-coated prepared resin replica (Araldite LY554 with HY956 hardener to 20% weight). In order to identify the nature of surface alterations and to distinguish human from animal traces, trampling abrasion, and modern mechanical modifications produced by excavation tools, reference was

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made to well-established taphonomic literature. Combustion degree has been distinguished between moderate (200-500°C, black/brown) and elevated with calcination (>700 °C, grey/white) (Stiner et al., 1995; Costamagno et al., 2005). Cut-marks have been classified as incisions, like skinning marks, defleshing marks, and scrapes (Binford, 1981; Potts and Shipman, 1981; Shipman, 1981; Shipman and Rose, 1984). The documented incisions appear linear, with great variability in length, width and depth, V-shaped section, and internal microstriation at the base of the groove. Attention was paid to differentiating between trampling and butchery marks (Domìnguez-Rodrigo et al., 2009). Recording the localization of trampling striae on the bone yields indirect information on the extent of animal occupation at the site (Koby, 1941-1943). Intentional bone breakage to access marrow was documented by diagnostic elements like percussion marks/notches and impact flakes, and positive flakes of the percussion marks (Blumenschine and Selvaggio, 1988; Villa and Mahieu, 1991; Capaldo and Blumenschine, 1994; Pickering and Egeland, 2006).

Regarding the traces left by carnivores, these were identified as deep punctures in the cortical bone surface, concentrated on the articular ends of the bones, as well as pits and scores with U-shaped striations on bone surfaces. These results were compared with data from Fisher (1995), Selvaggio and Wilder (2001), Domìnguez-Rodrigo and Piqueras (2003), Diedrich (2012), Fourvel et al. (2014) and Camarós et al. (2017), The analysis of modifications left by carnivore gnawing also included traces left by human teeth, which were documented and compared with the data from Landt (2007), Fernández-Jalvo and Andrews (2011), and Saladie et al. (2013). Potential burnt bones were determined by combustion grade level following the criteria described by Stiner et al. (1995). Evidence of anthropic peeling by flexion (Pickering et al., 2013) on some elements at Rio Secco Cave is clearly differentiated from peeling associated with carnivore mastication events (Arilla et al., 2014).
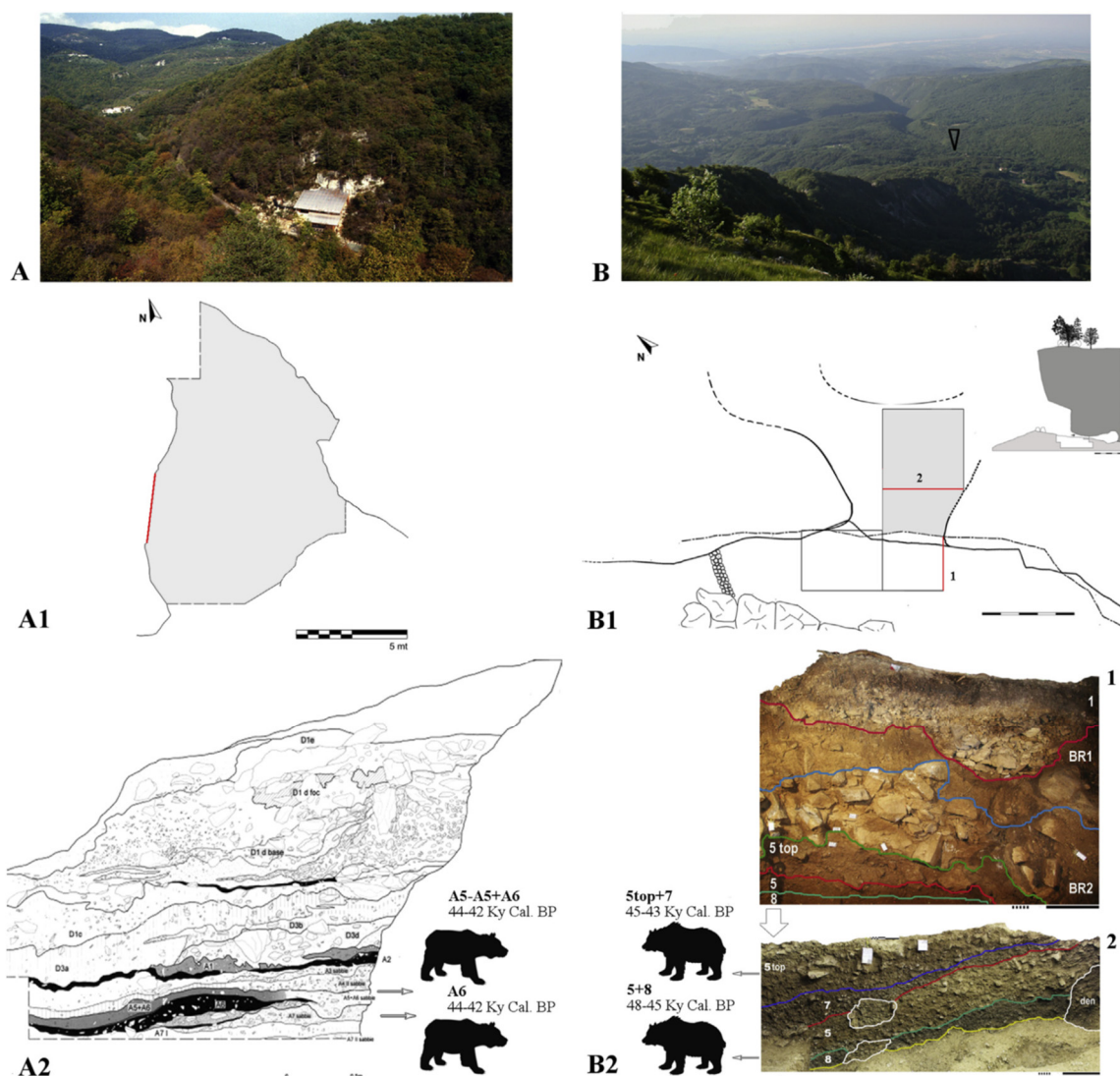

A5-A5+A6
44-42 Ky Cal. BP

A6
44-42 Ky Cal. BP

5top+7
45-43 Ky Cal. BP

5+8
48-45 Ky Cal. BP

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Fig. 2. Panoramic views, schematic plan, and location of stratigraphic profiles (in red) of Fumane Cave (A-A1-A2) and Rio Secco Cave (B-B1-B2), with Mousterian layers indicated.

According to the analytical protocol, natural post-depositional degradations have been searched for only on bones longer than 3 cm or on bone relevant at the taxonomical level. Smoothed bone edges and root grooves have been ascribed to biological as well as several physical processes.

In order to evaluate species abundance, number of remains (NR) (Grayson, 1984), minimum number of elements (MNE) (Binford, 1981; Klein and Cruz-Uribe, 1984; Stiner, 1994), and the minimum number of individuals (MNI) (Bökönyi, 1970) were used. The age range estimates (Tab. 5) included five age groups: I (Infant, 0-1 years); Y (Young, 1>4 years); Y-AD (Young-Adult, 4>8 years); A (Adult, 8>20 years); S (Senile, 20>30 years). The fragmentation index (MNE/NISP) and the coefficient of the survival of the anatomical elements were calculated by dividing the minimum number of elements (MNE) for the number of elements expected (MNE/NEE). NEE was factored as if the carcasses had been transported whole to the site. To achieve broad indirect indicators of human-bear interactions, although combined with the above-described taphonomic type of evidence, carnivore-herbivore ratios (Enloe, 2012) have also been calculated for each archaeological layer investigated.

4. Results

The Rio Secco Cave archaeological investigations have so far been conducted on about $18m^2$ of the Mousterian occupation levels (5top+7 and 5+8) and the analyses of the faunal remains are still ongoing (see SI). In both levels, the differences in the conservation of fossorial animal remains (*Marmota marmota*) are easily visible, macroscopically evident by their fresher aspects in respect to the remains ascribable to the Middle Paleolithic levels. Taphonomic agents such as roots, manganese oxidesroots, and concretions are present in less than 9% of the marmot bones (n. 300).

In the total faunal assemblage, bone surfaces are well preserved: 32% of bone remains bear root etching, while on other fragments micro-fissures result from weathering phenomena. Rodent gnaw marks are almost absent (n=43), while carnivore marks, in the form of scoring, pits, or gastric juice erosion, were detected only on 86 specimens. In 5top+7, while the bone assemblage is fragmentary (total no. 524 83.2% <3cm; 16.8% >3cm), the high percentage (NISP 376, higher than 70%) of the number of determined individuals (Tab. 2) is certainly influenced by the quantity of carnivore remains (NISP 249), equal to 66.2%, and the instance of ursids (NISP 220), equal to 58.2%, which are more easily determinable thanks to the dimension, structure, and greater resistance to mechanical strength of the bones. In layers 5+8, such determinations cannot be made: from a total of 4,301 analyzed remains, 13.5% (NISP 582) of remains were determined at the level of species, genus, or family; of these, 257 (44.1%) were marmots intruding into the Mousterian sequence, while 222 ursids (38%) reveal high fragmentation (11.9% < 3cm; 88.1% >3cm). Excluding the marmots, the most represented animal is *Ursus spelaeus,* at 39.3% of the remains in 5top+7 and 27% of 5+8, followed by small elements of *Ursus arctos,* at 1.6% and 0.2%, respectively. In both layers, from a total of 130 remains (*Ursus* sp.), nearly equally subdivided between the two stratigraphic assemblages, it was not possible to precisely attribute taxonomy to either *U. arctos* or *U. spelaeus* (Tab. 2).

At Fumane Cave, excavations have covered around $65m^2$ of the A5-A6 stratigraphic assemblage (see SI). The high fragmentation of bone remains (4.6% <3cm; 96.4% >3cm) limited the number of determined remains NISP= 836, equal to 1.4% of the 60,494 total (Tab. 2). This is also the case in A6, where of the 110,777 analyzed remains, 2,274 (2%) were determinable at a specific level. The ursid remains totaled 19 (2.2%) in A5-A5+A6 and 31 (1.4%) in A6 (Tab. 2). For the most part, in both levels it was not possible to certainly identify taxonomic attribution to *U. arctos* and/or *U. spelaeus* (Total no. *U.* sp.= 34). Overall, despite the small number of determined remains, it is clear that the brown bear (n=4 in A5-A5+A6; n=10 in A6) is better represented in respect to the cave bear (n=2), of which a rib and a proximal portion of the ulna were isolated exclusively in A5-A5+A6.

4.1 Taphonomy

4.1.1 Rio Secco Cave

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In levels 5top+7 and 5+8, the bear remains reporting evident traces of butchery marks are abundant (Tab. 3), numbering 47 (21.4%) and 34 (15.3%), respectively. These are observed as isolated or as series of cuts, testifying to short and medium-length gestures; however, only in 5top+7 scraping is observed (Fig. 3A and Fig. 4A_1).

Table 2
Mammal *NISP* and *NISP*% for the late Mousterian layers at Rio Secco Cave (RS) and Fumane Cave (FC). The countings are based on bones and teeth

Taxa	RS – levels 5 top+7		RS – levels 5 + 8		FC - levels A5-A5+A6		FC – level A6	
	NISP	NISP %	NISP	NISP%	NISP	NISP %	NISP	NISP%
Lepus sp.			1	0.2	1	0.1		
Marmota marmota	43	11.4	257	44.1			1	0.1
Erinaceus europaeus			1	0.2				
Total Lagomorpha and Rodentia	**43**	**11.4**	**259**	**44.5**	**1**	**0.1**	**1**	**0.1**
Canis lupus			3	0.5	4	0.5	7	0.3
Vulpes vulpes	1	0.3	3	0.5	26	3.1	20	0.8
Vulpes/Alopex					3	0.4		
Ursus arctos	6	1.6	1	0.2	4	0.5	10	0.5
Ursus spelaeus	148	39.3	157	27	2	0.2		
Ursus sp.	66	17.5	64	11	13	1.5	21	0.9
Martes martes			3	0.5				
Martes sp.	1	0.3						
Meles meles			2	0.3				
Mustela erminia			4	0.7				
Mustela nivalis							1	0.1
Mustelidae			2	0.3				
Carnivora indet.	27	7.8	25	4.3	2	0.2	14	0.6
Total Carnivora	**249**	**66.2**	**262**	**45.3**	**54**	**6.4**	**73**	**3.2**
Sus scrofa	1	0.3	2	0.3			2	0.1
Megaloceros giganteus	14	3.7	5	0.9	10	1.2	28	1.2
Alces alces	5	1.3	2	0.3	1	0.1	4	0.2
Cervus elaphus	6	1.6	7	1.2	297	35.5	1095	48
Capreolus capreolus			1	0.2	48	5.7	182	8
Cervidae indet.	19	5.1	6	1	39	4.6	128	5.6
Bison priscus	2	0.5	1	0.2			2	0.1
Bos/Bison	8	2.1	10	1.7	10	1.2	13	0.6
Capra ibex	2	0.5	5	0.9	30	3.6	54	2.4
Rupicapra rupicapra			3	0.5	32	3.9	55	2.4
Caprinae indet.	1	0.3			12	1.4	7	0.3
Ungulata indet.	26	6.9	17	2.9	302	36.2	630	27.8
Total Ungulata	**84**	**22.3**	**59**	**10.2**	**781**	**93.4**	**2200**	**96.7**
Total NISP	**376**	**100**	**582**	**100**	**836**	**100**	**2274**	**100**
Indeterminate								
Mammals small size	1		20		10		7	
Mammals medium-small size	1		17		7		8	
Mammals medium size	5		1		223		325	
Mammals large-medium size	8		620		318		715	
Mammals large size	79		93		839		1716	
Fragm. Indet.	54		2968		58261		105732	
Total indeterminate	**148**	**28.2**	**3719**	**86.5**	**59658**	**98.6**	**108503**	**98**
Total	**524**		**4301**		**60494**		**110777**	

Percussion marks (PM) on long bones for the extraction of marrow are around 10.6% and 11.8% of the total remains with traces (Tab. 3), respectively per frequentation phase, and in some cases are accompanied by cut-marks (CM) from lithic tools. In general, in comparing the two frequentation levels at Rio Secco, a certain equilibrium in the processing of bear carcasses is observed (Fig. 3A and B). The most intense traces are around the ribs and the anterior and posterior limbs (Tab. 3, Fig. 3A and B), which refer (in order of frequency), to skinning, defleshing and the removal of muscle mass, disarticulation, and the percussion and combustion/burning of bones (burned remains 11.3% and 5.8%) (Tab. 3, Fig. 3A and B).

Some phalanges (Nr. 2, Fig. 4I) show short, persistent cut-marks, transversal to the major axis of the element, testifying to the first phases of fur recovery. The anterior and posterior limb elements from the two investigated levels show that these were targeted anatomical parts for muscle removals (Tab. 3, Fig. 4, and Fig. 6), while radii and ulna, in the proximal portions, bear major evidence of anthropic activity linked to the removal of bicep and tricep muscles and the severing of flexors and tendons from the main articulations of the forearm (Fig. 4A-E and Fig. 6D-F). Femurs, tibiae, and a fibula (Tab. 3) show actions respective to the removal of the vastus intermedius muscle, the grand adductor of the thigh, and the flexor or extensor of the digits (Fig. 4G-H and Fig. 6G-I). For both levels the anterior and posterior limbs show the highest percentage of BM and an intentional extraction of marrow, with the radius and

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humerus with between 50 and 67% and the femur and tibia between 39 and 46% (Tab. 3, Fig. 4F and Fig. 6G). It should, however, be clarified that in some cases, for certain anatomical elements where the bone is less protected from the muscular tissue, cut-marks may also refer to the recovery of skin or to disarticulation (Fig. 4C and I, Fig. 6H). In more than one case it is clear that the age of the butchered individuals is Young (n=5) or even Infant (n=1, about 8-12 months).

Tab.3

Number of anatomical elements of Ursidae with anthropogenic modifications and carnivore marks; *CM* cut-marks, *PM* percussion marks, *CM+PM* cut-marks + percussion marks, *Pe* peeling, *BM* butchery marks, *%BM*, *R* retoucher, *TM* tooth marks, *B* burned, *GM* gnaw marks.

	Ursidae (Ursus arctos, U. spelaeus, U.sp.) RS - levels 5 top + 7										Ursidae (Ursus arctos, U. spelaeus, U.sp.) RS – levels 5+8										Ursidae (Ursus arctos, U. spelaeus, U.sp.) FC - levels A5-A5+A6							Ursidae (Ursus arctos, U. spelaeus, U.sp.) FC - level A6								
	NISP	CM	PM	CM+PM	Pe	TOT. BM	%BM	R	B	GM	NISP	CM	PM	CM+PM	Pe	TOT. BM	%BM	R	B	GM	NISP	CM	TOT. BM	%BM	TM	B	GM	NISP	CM	PM	TOT. BM	%BM	R	TM	B	GM
Cranium	18									3	14							1			3							3								
Hemimandible	13										21	1			1	1	4.7	1			1							3								
Tooth indet.	2										14										1	1						3								
Hyoid	2										6																									
Total cranial	**35**									**3**	**55**	**1**			**1**	**1**	**1.8**	**3**	**1**		**4**							**9**								
Atlas-axis	3										2																									
Vertebra	12								1		21	3				3	14.2											1								
Rib	54	10		6		16	29.6	1	9	9	39	6				6	15.3	3	1		3							1								
Clavicle	1									1																										
Baculum	2										1																									
Total axial	**72**	**10**		**6**		**16**	**22.2**	**1**	**11**	**10**	**63**	**9**				**9**	**14.2**	**3**	**1**	**3**	**3**							**2**								
Scapula	3										3	1				1	33.3																			
Humerus	3		1	1		2	66.6				2			1		1	50																			
Radius	15	6	1	2		9	60	4	1		3	1		1		2	67	1	1	1	1	1			1	1		1	1						1	
Ulna	4	3				3	75		1		6	1				1	16.6	1	1		1	1			1			1	1					1		
Carpals	7										6										1													1		
Metacarpal	12									3	4																									
Total frontal limb	**44**	**9**	**2**	**3**		**14**	**31.8**	**5**	**4**		**24**	**3**		**2**		**5**	**17.3**	**1**	**1**		**3**	**2**	**2**	**66.6**	**1**	**2**	**1**	**2**	**1**	**1**	**2**	**100**	**1**		**1**	
Coxal																																				
Femur	24	5	2	4		11	45.8	3	4		28	5	4	2		11	39.2	2	4									2	1	1	2					
Patella											1																									
Tibia	8	2	1			3	37.5				10	2		2		4	40	3										1	1		1			1		
Fibula	4										4	1				1	25				1				1	1	1									
Calcaneum	2																																			
Astragalus	1				1																															
Tarsals	3																				2	1			1			1	1					1		
Metatarsal	1										5									3	1	1						1	1					1		
Total hind limb	**43**	**7**	**3**	**4**		**14**	**32.5**	**3**	**5**		**49**	**8**	**4**	**4**		**16**	**32.6**	**5**	**7**		**3**	**2**	**2**	**66.6**				**5**	**4**	**1**	**5**	**100**	**1**			
Metapodial											2																	2								2
First phalanx	8	2				2	25		2		11										1	1			1	1		1	1						1	1
Second phalanx	8										6											1				2		3	1						1	
Third phalanx	6									1	6										1							4								
Sesamoid											2										4	1			1	1		3	1					1		2
Total distal. limb	**22**	**2**				**2**	**9.1**	**2**	**1**		**27**							**1**		**3**	**6**	**2**	**2**	**33.3**	**1**	**2**		**13**	**3**		**3**	**23**	**1**		**4**	**2**
Indet.	4	1	1			2	50	1			4			2		2	50		2		2															
Tot.	**220**	**29**	**5**	**7**	**6**	**47**	**21.4**	**1**	**25**	**20**	**222**	**23**	**4**	**6**	**1**	**34**	**15.3**	**3**	**13**	**15**	**19**	**6**	**6**	**30**	**2**	**4**	**1**	**31**	**8**	**2**	**10**	**32.2**	**2**	**1**	**4**	**2**
MNI	**12**										**16**										**5**							**6**								

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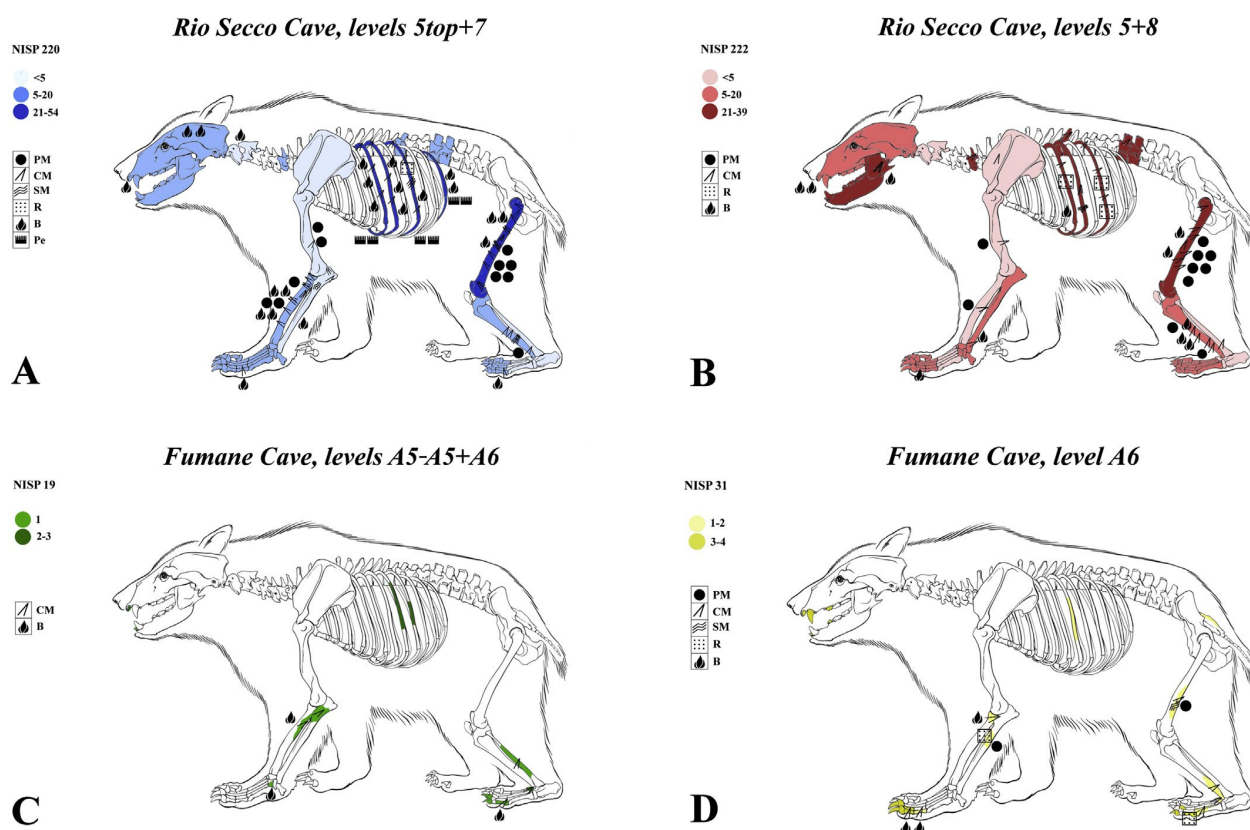Gabriele Terlato

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Fig. 3. Distribution of butchery marks on the *Ursidae* skeletal elements (*Ursus spelaeus, Ursus arctos*, and *Ursus* sp.) from Rio Secco Cave (A-B) and Fumane Cave (C-D)

The quality of the different types of anthropogenic traces recognized on the rib elements (Fig. 5, 6, and 10) enables many actions performed by Neanderthals on ursid carcasses to be detailed (Tab. 3). Both archaeological levels show a high number of cut-marks on the dorsal and ventral surfaces of many ribs, which in most cases are presented as short, persistently deep, and transverse to the major axis. In those cases where cut marks are positioned in lateral pattern (skull-caudal), the consequent detachment of the serratus muscles, latissimus dorsi, external oblique muscle of abdomen, thoracic serratus ventralis, serratus anterior, or intercostal muscles can be hypothesized, but it cannot be excluded that some traces may have been impressed during the phases of skin detachment from this anatomical region (Fig. 5, 6B-C and Fig. 10A). Less frequently, the presence of cut-marks on the medial (or ventral) surface, also in proximity to the epiphyses, can describe attempts to sever the levatores costarum muscle or to overcome the resistance of articulation with the spinal column (Fig. 5C). The desire to obtain diaphyseal portions of the rib cage is clear and documented for now only in 5top+7 (Fig. 5C-D) by evident traces of peeling (Tab. 3, n. Pe = 6), which were produced by flexing the element in a fresh state in a direction opposite to the articulation of the bone (Pickering et al., 2013). Confirming the particular interest for ribs, four diaphyses from the two levels of Mousterian frequentation furthermore show their use as retouchers (Fig. 10 and Tab. 6), while in other cases localized combustion is present, some of which is posterior to peeling and/or are associated with cut-marks (Fig. 5C). The search for muscle groups (e.g. transversospinalis) is demonstrated by medium to long cut-marks on the dorsal face of the vertebral arch, at the base of the spinous processes of some vertebrae (Fig. 6F). From the cranial region, a portion of masseteric fossa and portions of the condyloid process of a right hemimandible from an adult *Ursus spelaeus* individual show clear cut-marks, which are oblique to the longitudinal axis of the element and present on the interosseous space that divides the angular process from the neck of the condyle (Fig. 6A_1+1a). The intention might be to remove the masseter muscle and possibly to disarticulate the jaw from its seat, as shown by extensive peeling (Tab. 3 and Fig. 6A), which is visible in the medial view and is also accompanied by clear combustion.

As for the modes of limb exploitation, these are typified by the cut-marks presented on a right, semi-complete cave bear scapula. The element was clearly disarticulated from the trunk, isolated or in connection with the stylopod. Short and persistent as well as long and isolated cut-marks are clearly visible both in the dorsal and the ventral view. In the

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medial view, transversal-oblique cuts present on the supraspinous fossa are of short and medium length and clearly distinguish and document the detachment of the homonymous muscle (Fig. 7A_1-3). In medial pattern (ventral), short, single, or groups of cut-marks with varying orientation are concentrated on the subscapular fossa (Fig. 7B_4-5), while some, shorter and more persistent, can be noted on the neck at the base of the articular epiphyses. All of these gestures in these patterns are attributable to the detachment of the extended subscapular muscle. It is important to note that in correspondence to the bitemark area, part of the supraspinous fossa is involved also with external combustion (Fig 7B_6). In general, at Rio Secco there are many bear remains that present traces of combustion, extensive or localized, isolated or in association with cut-marks, peeling, and/or percussion marks (See SI; Tab. 3, Fig. 4-7). It is noted that the near totality of the anatomic elements on which traces of anthropic origin are recognized are almost always associated with combustion (Tab. 3).

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Fig. 4 Rio Secco Cave levels 5top + 7, localization and details of the cut marks: A) right ulna of *U. spelaeus* with traces on the proximal end (1-close-up of triae); B) right radius of *U. spelaeus* with traces on the proximal end (2); C) right ulna of *U. arctos* with traces on proximal epiphysis (3e4); D) right radius of infant (8-12 months) *U.* sp. with traces on proximal end (5); E) right radius of *U. spelaeus* with traces on diaphysis (6) and burning (red arrow); F) left femur of *U. spelaeus* with percussion marks (white arrow); G) right tibia of *U. spelaeus* with traces on diaphysis (7); H) left tibia of *U. spelaeus* with traces on diaphysis (8); I) first phalanx of *U. spelaeus* with traces (9) and localization and detail of burned portion (red arrow - 10).

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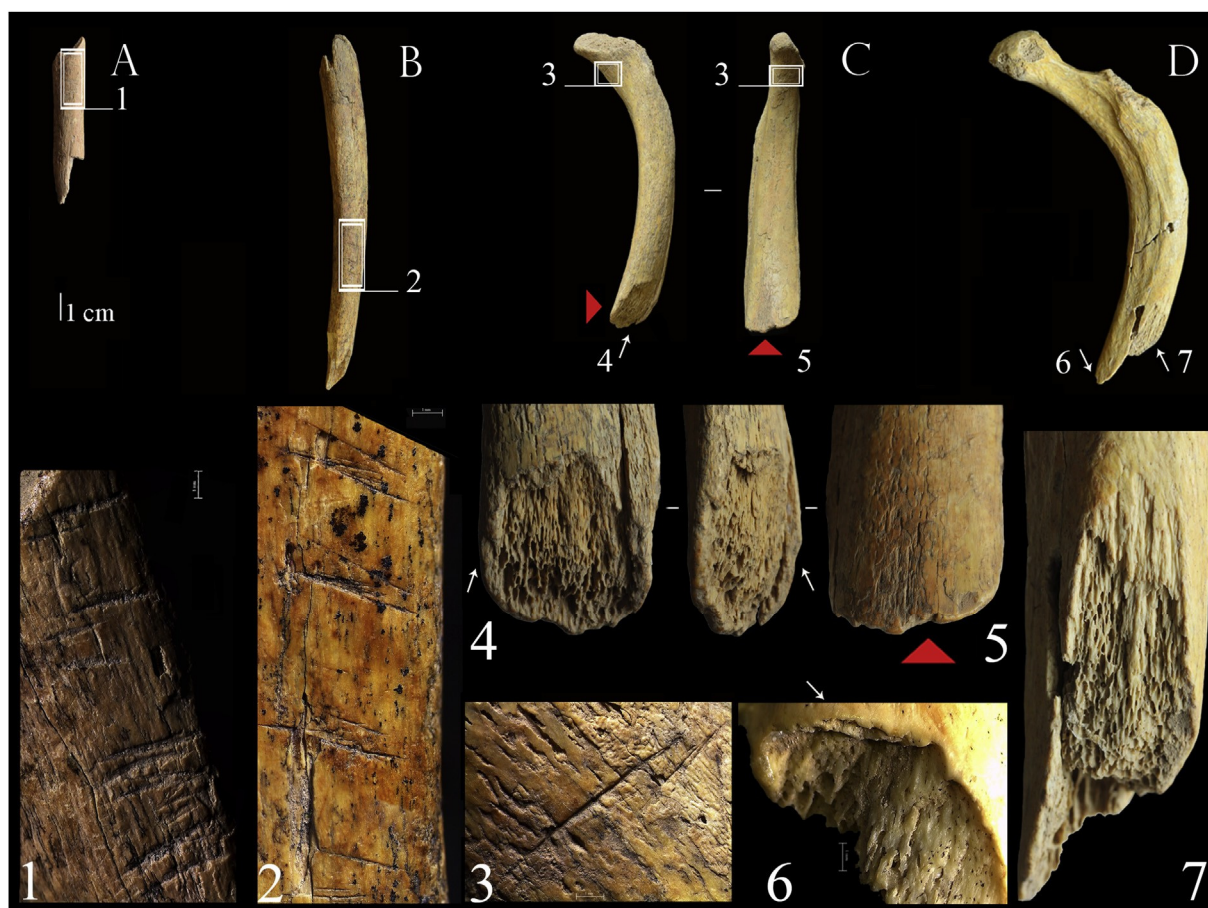
Fig. 5 Rio Secco Cave levels 5topþ7, localization and details of bear ribs (*U*. sp. A-B; *U. spelaeus* C-D) with cut-marks (1-2-3), peeling (4-6-7), and burned portion (5 and red arrow), oriented according to figures A-B-C-D. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

4.1.2. Fumane Cave

In levels A5-A5+A6 and A6, ursid report evident traces of butchery (Tab. 3), numbering 6 (30%) and 10 (32.2%). The cuts appear isolated or in series, are of short or medium length, and only present as scrapes (Fig. 8C_4) or percussion marks (n=2) in A6, resulting from intentional fracturing aimed at the consumption/removal of marrow (Fig. 8D). While recalling the small presence of axial skeleton remains, these findings nonetheless emphasize how the traces related to the treatment of the carcass, which in both cases are exclusively concentrated on elements of the limbs and their extremities (Tab. 3, Fig. 3C-D). Some phalanges, sesamoids, and a metatarsal (Fig. 8H_8 and G_7; Fig. 9D_11 and C_9; Fig. 10F_8) show short cut-marks, which are sometimes deep and persistent and transversal and oblique to the major axis of the element, attesting to some of the early phases of fur recovery. The defleshing and detachment of muscle mass is evident: two radii from different individuals, two femurs, a tibia, and a fibula from adult specimens, and an ulna of *Ursus spelaeus*, indicate actions that must have been intended first to detach the muscles and then to deflesh the remnants (Fig. 8A_1+1a and C_4, B_2+3; Fig. 9A_1+5, B_6+7). For certain anatomical elements, the cut-marks can persist where the soft tissues around the bone are thinner (proximal and distal parts of the ulna and radii), and therefore these refer also to some of the phases of hide recovery. As an example, the cut-marks present on a lateral diaphysis of a left fibula can be attributed to both the detachment of the lateral extensor muscles of the digits and/or the peroneus brevis at some stages of fur removal (Fig. 8B_2+3). Percussion marks are visible on a diaphyseal portion of a femur and an ulnar medial diaphysis (Fig. 8D and Fig. 10E_7). In both levels, disarticulation is documented by two tarsals (Fig. 8E_5+5a and F_6) a left cuboid from an Infant individual (around 3<6 months) and a right Adult cuneiform, respectively. Their medial plantar and lateral localizations could thus, in this case, also have been produced during phases of hide removal.

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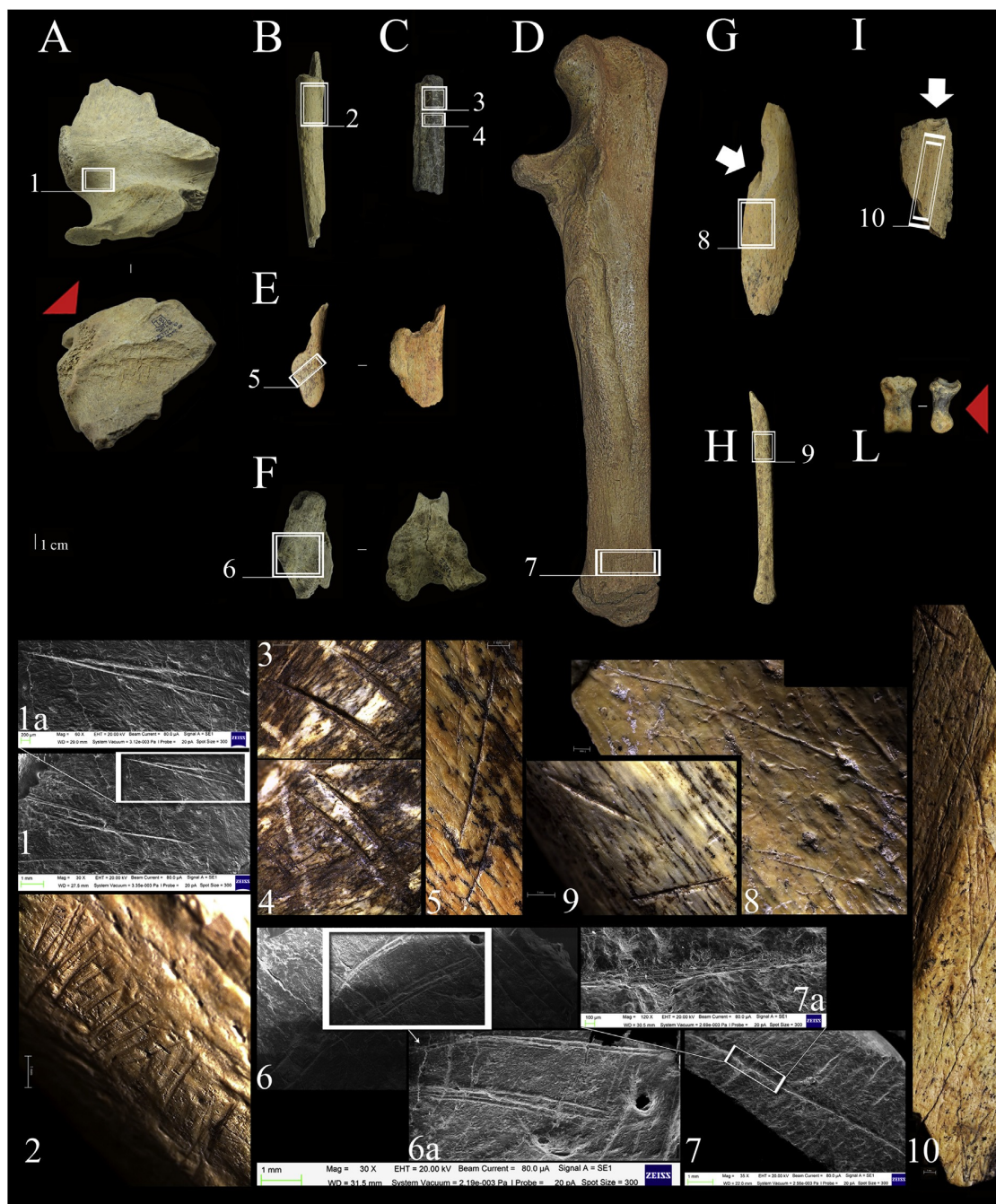
Fig. 6. Rio Secco Cave levels 5 + 8, localization and details of cut-marks: A) right hemimandible of *U. spelaeus* with traces on condylar portion acquired by SEM (1-1a) and burning (red arrow); B) rib of *U.* sp. with traces (2); C) rib of *U.* sp. with different traces (3e4); D) left ulna of *U. spelaeus* with traces on distal end acquired by SEM (7-7a); E) right radius of *U.* sp. with traces on diaphysis (5); F) thoracic vertebra of *U.* sp. with traces acquired by SEM (6-6a); G) left femur of *U.* sp. with traces on diaphysis (8) and percussion marks (white arrow) and percussion cone in connection; H) left fibula of generic young *U.* sp. with traces on diaphysis (9); I) left tibia of *U. spelaeus* with traces on distal diaphysis (10); L) second phalanx of *U. spelaeus* with traces of burning (red arrow).

Of great importance are the large carnivore remains that are accompanied by combustion. At Fumane, four remains from A5-A5+A6 (13%) and four from A6 (21%) show traces of thermal alteration. In four cases, a proximal epiphysis of a radius, a sesamoid, and two first phalanges were associated with cut-marks and localized combustion (Fig. 9A_4 and C_10, D_11 ; Fig. 10F). A single sesamoid without cut-marks was fully calcined (Fig. 9E_12). In general, these are

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primarily associated with small elements from appendicular extremities or particular portions of the limbs (radius), where the bone can be unprotected or insufficiently covered by important muscle mass. In at least two cases, there is an exceptional association of cut-marks, combustion, and human tooth marks. In fact, bitemarks compatible with human teeth (Saladiè et al., 2013) are recognized on a proximal epiphysis of a partially-combusted first phalanx, recovered within a combustion structure (USA5, SIII) (removal of part of one of the two proximal insertion tubercles), a lateral-distal diaphyseal flake from a tibia, and along the fractured edge of a proximal portion of a radius (Fig. 9 A_2+2a, 3+3a and B_7, C_8) in proximity to a marginal combustion. In general, all tooth marks are shallow and the pits are crescent-shaped. In the case of the radius, some cut-marks (Fig. 9A) are interpose (Fig. 9A_2I) or close (III-IV) to the tooth marks, which appear regular, equidistant (dental arch), and, towards the fracture margin, assume the characteristics of punctures with incomplete fractures, perimeter-contour, and flaking on the edges.
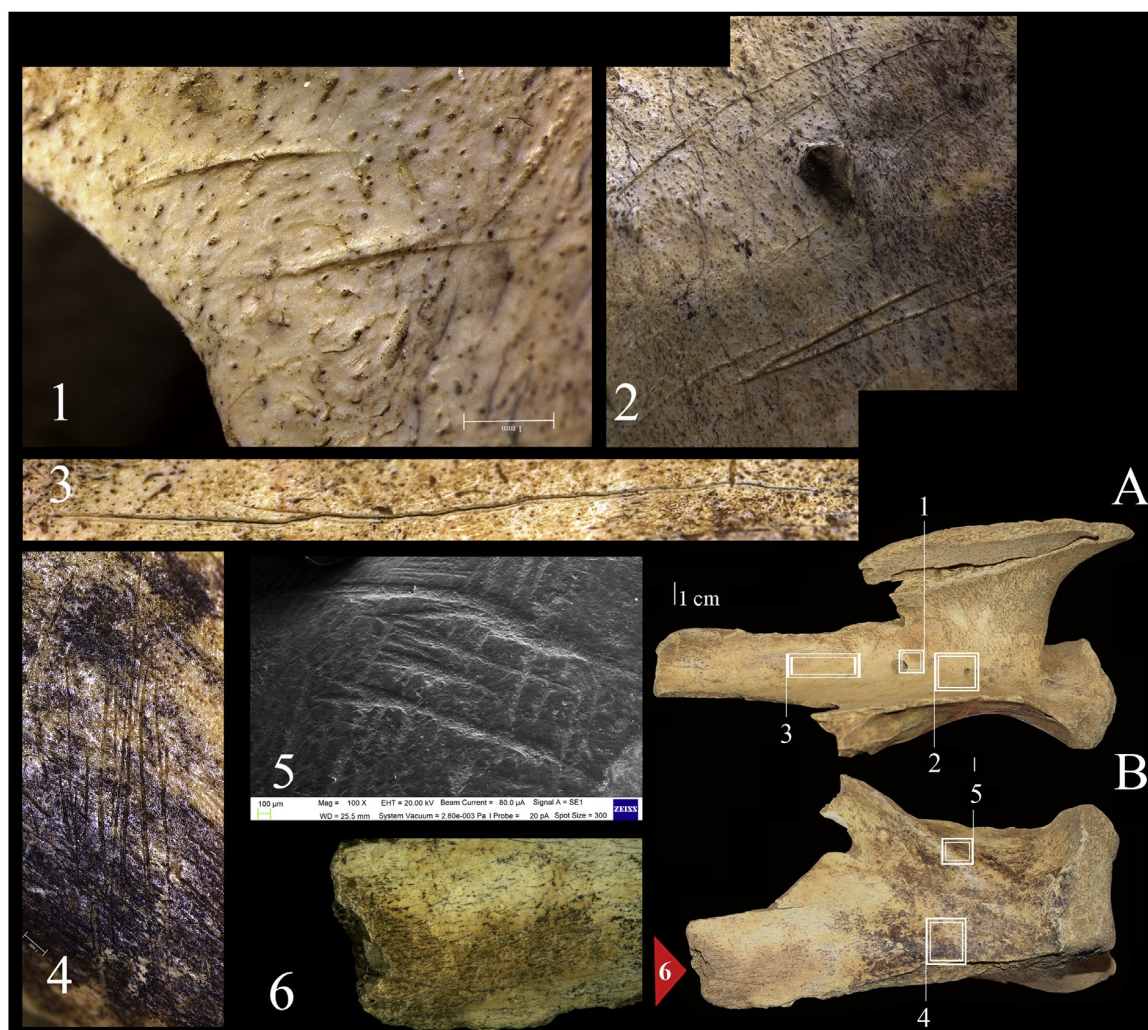
Fig. 7. Rio Secco cave (level 8), right scapula of *U. spelaeus* No. RIL. 226, different views: (A) lateral view; (B) medial view. The numbers 1-5 indicate the localization and close-ups of the traces oriented according to figures A and B. The red arrow indicate localization of burned portion and picture detail (6).

4.2 Skeletal part representation

The high number of remains of *Ursus spelaeus, Ursus arctos* and indeterminate bears, classified as *Ursus* sp. has permitted more detailed analyses to be proposed for the composition of the bear carcasses at Rio Secco Cave, but not Fumane Cave. Although a larger area was investigated at Fumane than Rio Secco, it did not return a number of remains sufficiently representative for calculations of % of Skeletal Survival Rate and Fragmentation Index (Tab. 4). Nevertheless, the distribution of the determined ursid remains across the two different levels of Fumane and the

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relative MNE (Tab. 4 and Fig. 3) shows that the cranial and limb regions are best represented. The trunk region is only represented by four ribs and a portion of vertebra.

At Rio Secco Cave, the remains, subdivided by anatomic element in craniocaudal order, show that the entire carcass is represented, with the exclusion of the coxal; the stilopodium (humerus/femur) and zeugopodium (radius-ulna/tibia-fibula) are well-represented in both stratigraphic units, in contrast with the low number of findings from the extremities of the limbs, like phalanges and sesamoids. The cranial remains (maxilla, hemimandible, and teeth) are certainly very well represented, by virtue of their resistance to mechanical and chemical stress (Tab. 4).
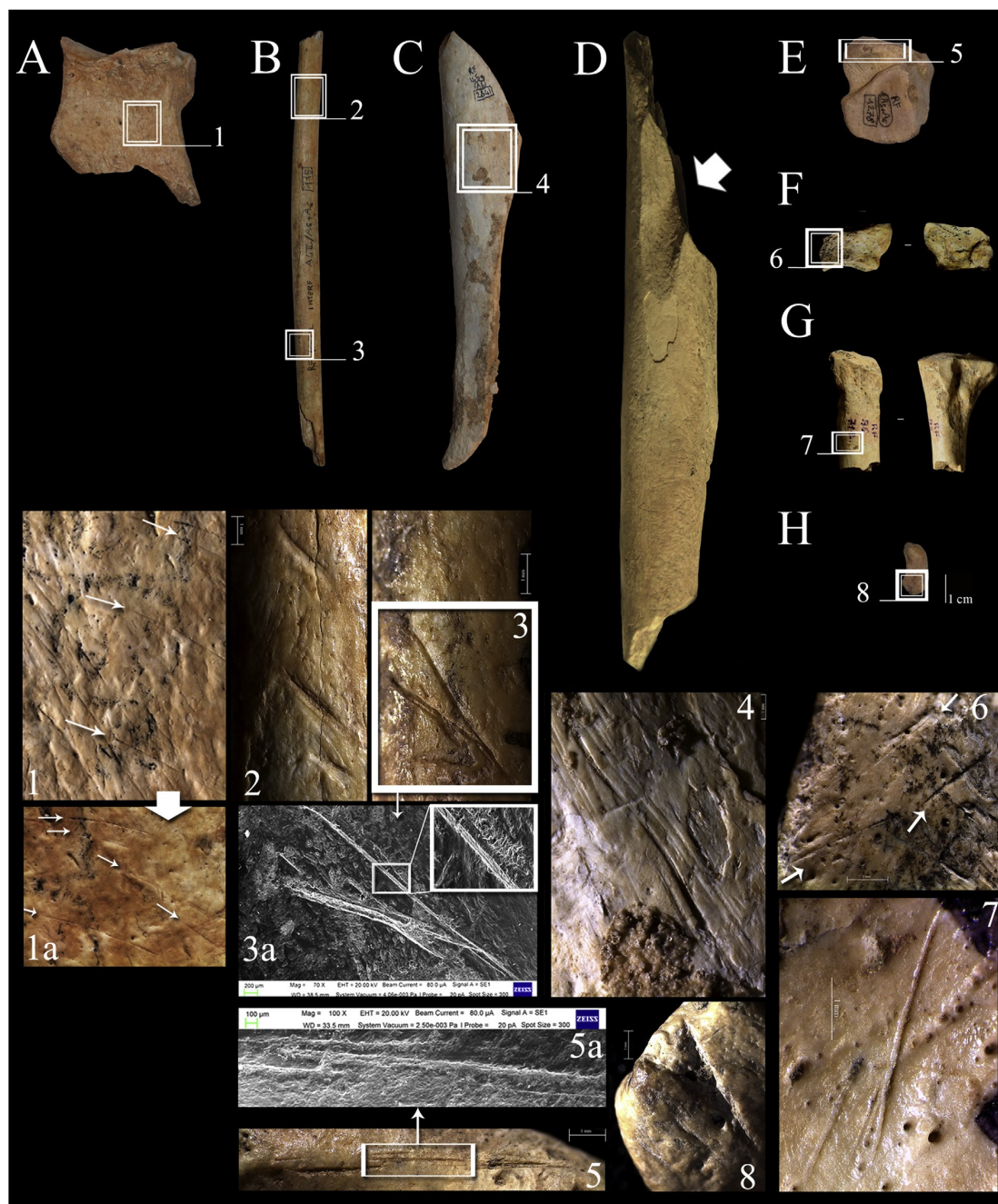
Fig. 8. Fumane Cave (A5-A6), localization and details of anthropic traces: A) right radius of *U*. sp. with traces on proximal end (1-1a); B) left fibula of *U. arctos* with traces on diaphysis (2e3 and 3a acquired by SEM); C) left femur of *U. arctos* with scrapers on diaphysis (4); D) right femur of *U. arctos* with percussion marks (white arrow); E) left cuboid of infant (3 < 6 months) *U*. sp, with traces (5 and 5a acquired by SEM); F) right cuneiform of *U. arctos* with traces (6); G) third right metapodial of *U. arctos* with traces (7); H) sesamoid of *U*. sp with traces (8).

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The MNE shows that the axial skeleton, with both vertebrae and ribs, is numerically the most abundant portion of the body. The survival coefficient (Skeletal Survival Rate), however, reveals a contrast with these results, showing that certain elements are clearly selectively underrepresented. Vertebrae and ribs, less resistant and thinner, have low values (<8.9%) as compared with cranial remains (37.5-50.0%), mandibles (37.5-40.6%), and long bones like femurs (34.3-50%), radii (9.3-41.6%), and tibias (21.8-25%).
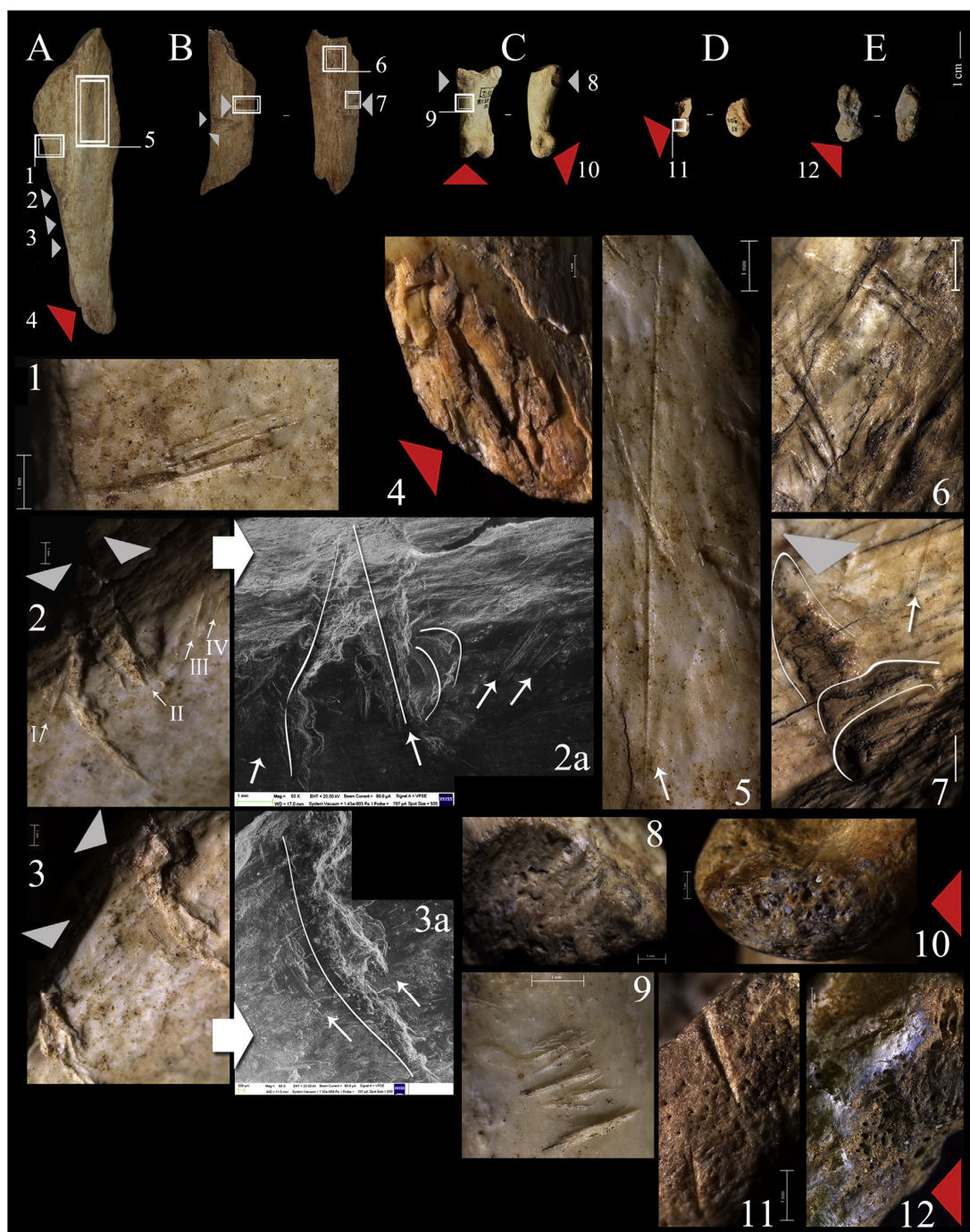
Fig. 9. Fumane Cave (A5-A6), localization and details of anthropic traces: A) right radius of *U*. sp. with traces on diaphysis (1e2_III-IV and 5), tooth marks (grey arrows e 2 and 3), details of tooth marks acquired by SEM (2a-3a), localization and detail of burned portion (red arrow e 4); B) tibia of *U*. sp. with traces on diaphysis (6) and tooth marks (grey arrows e 7); C) first phalanx of *U. arctos* with traces (9), tooth marks (grey arrows e 8), localization and detail of burned portion (red arrows e 10); D) sesamoid of *U*. sp. with cut marks and detail of burned (11); E) sesamoid of *U*. sp. localization and details of calcination (red arrow -12).

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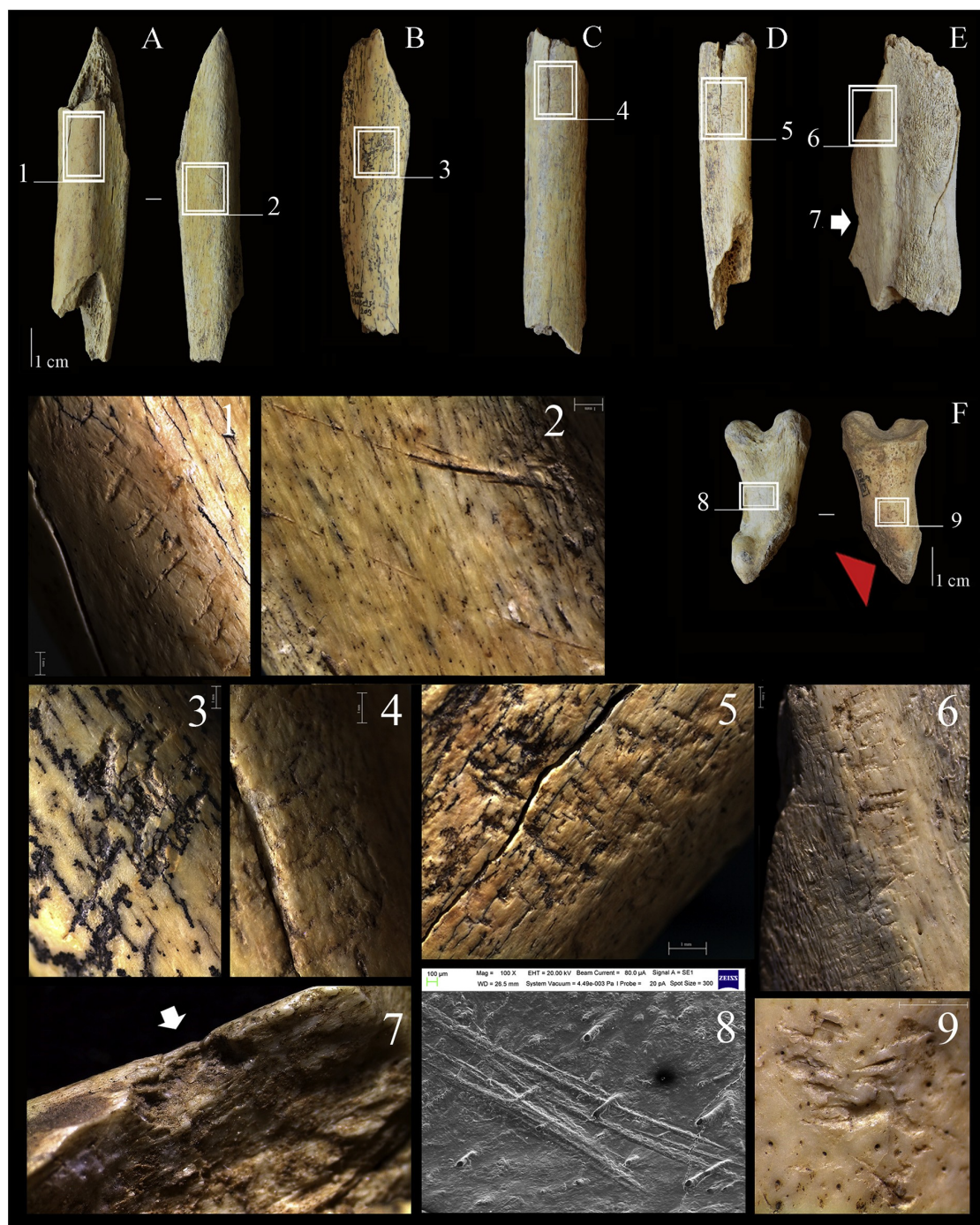
Fig. 10. Bear bone retouchers from Rio Secco (A-D) and Fumane Cave (E and F): A) rib of *U. spelaeus* with linear marks produced during knapping on ventral surface (1) and cut- marks on dorsal surface (2); B) rib of *U. spelaeus* with pits produced during knapping (3); C-D) ribs of *U.* sp. with linear marks (4 and 5); E) left ulna of young/adult *U. arctos* with linear marks (6) and impact point on medial surface (7); F) first phalanx of *U. arctos* with cut-marks on plantar diaphysis (8 acquired by SEM) and pits produced during knapping on dorsal surface (9). The red arrow indicates the localization of burned portion; the white arrow indicates percussion marks.

4.3 Estimation age and minimum number of individuals

The estimation of minimum number of individuals and age at death was difficult to ascertain due the fragmentation of the remains that mostly involved the long bones, ribs, cranium, or some teeth, which were frequently burnt and cracked into several fragments, and thus it was not always possible to advance comparisons between the different

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elements (Tab. 5 and Tab. 1 SI). In order not to distort the proportions of age groups present in the various units and in both cultural frequentations, estimations were also calculated for the remains generally determined as *U.* sp., considering only age or the sizes of animal not present in the two categories of determined taxa certain (*U. arctos* and *U. spelaeus*).

Table 4

Anatomical elements of Ursidae (*Ursus arctos*, *Ursus spelaeus,* and *Ursus* sp.); *NISP*, *MNE*, *NEE*, % skeletal survival rate, and breakage index.

	Ursidae (*Ursus arctos, U. spelaeus, U. sp.*) RS - levels 5 top + 7					Ursidae (*Ursus arctos, U. spelaeus, U. sp.*) RS - levels 5 + 8					Ursidae (*Ursus arctos, U. spelaeus, U. sp.*) FC - levels A5-A5+A6			Ursidae (*Ursus arctos, U. spelaeus, U. sp.*) FC - level A6		
	NISP	MNE	NEE	Skeletal surv. Rate(%)	Fragm. Index MNE/NISp	NISP	MNE	NEE	Skeletal surv. Rate(%)	Fragm. Index MNE/NISp	NISP	MNE	NEE	NISP	MNE	NEE
Cranium	18	6	12	50	0.3	14	6	16	37.5	0.4	3	3	5	3	3	6
Hemimandible	13	9	24	37.5	0.7	21	13	32	40.6	0.6	1	1	10	3	3	12
Tooth indet.	2					14								3		
Hyoid	2	2	12	16.6	1	6	6	16	37.5	1						
Total cranial	**35**	**17**	**48**	**35.4**	**0.5**	**55**	**25**	**64**	**39**	**0.4**	**4**	**4**	**15**	**9**	**6**	**18**
Atlas-axis	3	3	24	12.5	1	2	2	32	6.2	1						
Vertebra	12	12	384	3.1	1	21	21	512	4.1	1				1	1	192
Rib	54	28	312	8.9	0.5	39	18	416	4.3	0.4	3	3	130	1	1	780
Clavicle	1	1	24	4.1	1											
Baculum	2	2	12	16.6	1	1	1	16	6.2	1						
Total axial	**72**	**46**	**756**	**6**	**0.6**	**63**	**42**	**976**	**4.2**	**0.6**	**3**	**3**	**130**	**2**	**2**	**972**
Scapula	3	3	24	4.1	1	3	2	32	6.2	0.6						
Humerus	3	3	24	12.5	1	2	1	32	3.1	0.5						
Radius	15	10	24	41.6	0.6	3	3	32	9.3	1	1	1	10	1	1	12
Ulna	4	4	24	16.6	1	6	6	32	15.6	1	1	1	10	1	1	12
Carpals	7	7	168	4.1	1	6	6	224	2.6	1	1	1	70			
Metacarpal	12	12	120	10	1	4	4	160	2.5	1						
Total frontal limb	**44**	**39**	**384**	**9.6**	**0.8**	**24**	**22**	**512**	**4.1**	**0.9**	**3**	**3**	**90**	**2**	**2**	**24**
Femur	24	12	24	50	0.5	28	11	32	34.3	0.4				2	2	12
Patella						1	1	32	3.1	1						
Tibia	8	6	24	25	0.7	10	7	32	21.8	0.7				1	1	12
Fibula	4	4	24	16.6	1	4	3	32	9.3	0.7	1	1	10			
Calcaneum	2	2	24	8.3	1											
Astragalus	1	1	24	4.1	1											
Tarsals	3	3	120	2.5	1	1	1	160	0.6	1	2	2	20	1	1	60
Metatarsal	1	1	120	0.8	1	5	5	160	3.1	1				1	1	60
Total hind limb	**43**	**29**	**360**	**8**	**0.6**	**49**	**28**	**448**	**6.2**	**0.5**	**3**	**3**	**30**	**5**	**5**	**144**
Metapodial						2	2							2	2	
First phalanx	8	8	240	3.3	1	11	11	320	3.4	1	1	1	100	1	1	120
Second phalanx	8	8	192	4.2	1	6	6	256	2.3	1				3	3	96
Third phalanx	6	6	240	2.5	1	6	6	320	1.8	1	1	1	100	4	4	120
Sesamoid						2	2	640			4	4	200	3	3	240
Total distal limb	**22**	**22**	**672**	**3.3**	**1**	**27**	**27**	**1536**	**3**	**1**	**6**	**6**	**400**	**13**	**13**	**576**
Indet.	4					4										
Tot.	**220**	**153**	**2220**	**6.9**	**0.7**	**222**	**144**	**3536**	**4,1**	**0.6**	**19**	**19**	**665**	**31**	**28**	**1734**
MNI	**12**					**16**					**5**			**6**		

Table 5

NISP and MNI divided by age of *Ursus arctos*, *Ursus spelaeus,* and *Ursus* sp. in the late Mousterian layers at Rio Secco Cave (RS) and Fumane Cave (FC)

Taxa	RS - levels 5 top + 7						RS - levels 5 + 8							FC - levels A5-A5+A6					FC — level A6					
	NISP	I	Y	A	S	Total MNI	NISP	I	Y	Y-A	A	S	Total MNI	NISP	I	Y	A	Total MNI	NISP	I	Y	Y-A	A	Total MNI
Ursus arctos	6			1		1	1				1		1	4			1	1	10			1	2	3
Ursus spelaeus	148	2	2	4	3	11	157	1	2	1	8	3	15	2			1	1	–					
Ursus sp.	66	1		1		(2)	64	1		1	1		(3)	13	1	2	1	3 (1)	21	2	1		1	3 (1)
TOT.	**220**	**2**	**2**	**5**	**3**	**12**	**222**	**1**	**2**	**1**	**9**	**3**	**16**	**19**	**1**	**2**	**2**	**5**	**31**	**2**	**1**	**1**	**2**	**6**

At Rio Secco Cave, the data indicate the presence in both levels of individuals of all ages, with a prevalence somewhat of adults and sub-adults (Tab. 5). In 5top+7 specifically, the MNI estimates at least 12 ursids (11 *U. spelaeus*; 1 *U. arctos*): *U. Spelaeus*- 2 Infants (around 1-12 months); 2 Young (2-3 years); 4 Adults of diverse ages, amongst which were two males (MNE=2 *baculum*); 3 Seniles (>20 years); *U. arctos*- 1 Generic Adult. Of the identified

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characteristics, no individual amongst the determined *Ursus* sp. remains (1 Infant and 1 Adult) increases the estimation in these levels. To date, in 5+8 an MNI of 16 ursids has been estimated (15 *U. spelaeus*; 1 *U. arctos*): *U. Spelaeus*- 1 Infant (4 months); 2 Young (12-20 months); 1 Young-Adult; 8 Adults of various ages and sizes amongst which is a probable female specimen and a male (MNE=1 *baculum*); 3 Seniles (>20 years) were predominately identified by teeth and/or portions of mandibles with teeth in place; *U. Arctos*- 1 Generic Adult. Also in this level, of those individuals associated with the remains determined as *U.* sp. (1 Infant- 4 months; 1 Young-Adult, 1 Adult), none increase the MNI estimate.

At Fumane Cave, a combination of Infants, Young, and Adult individuals is noted amongst the levels, while Senile individuals are absent. In A5-A5+A6, an MNI of 5 ursids was estimated (1 *U. spelaeus,* 1 *U. arctos,* and 3 *U.* sp.): *U. spelaeus*- 1 Adult; *U. arctos*- 1 Adult; *U.* sp.- 1 Infant; 2 Young were not present amongst the age classes of the determined remains, which were taken into account for the MNI estimation; 1 Adult (>16 years) was not considered in the calculation. In A6, the MNI estimation included six ursids (3 *U. arctos* and 3 *U.* sp.): *U. arctos*- 1 Young-Adult, 2 Adults (two femurs of different sizes); 3 *U.* sp.- 2 Infants; 1 Young was not present in the age classes of determined remains and 1 Adult (>16 years) was not considered in the calculation for the opposite reason.

Taking into consideration the partiality of the distribution area under investigation, it seems relevant to point out that: 1) despite the presence amongst the sites of infant and neonatal individuals, excavations have not revealed the presence of bear hibernation dens; 2) the presence/absence of older individuals could be a useful indicator of the typology of the differentiated use of the two cavities on the part of the two ursid species; in the case of Fumane Cave, this may indicate the result of "selection" by hunters.

4.4 Bear bone retouchers

To date, five brown bear bone retouchers (Auguste, 2003; Valensi and Psathi, 2004) and seven cave bear bone retouchers, made from bone flakes from a femur, tibia and humerus (Abrams et al., 2014), can be accounted for in the Middle Palaeolithic of Europe. An additional six retouchers recovered in the two sites of this study can be added to this assemblage. At Rio Secco Cave, four retouchers (Tab. 6) were manufactured from rib diaphyses (2 *Ursus* sp. and 2 *Ursus spelaeus*), and present fractures attributable to the fresh state of the bone and are very homogenous in their dimensions and weight (Tab. 6 and Fig. 10A – D; L between 7 and 8.3cm; W between 1.4 e 1.7cm; and weight between 10.3 and 12.6gm). In general, the impressions are of linear type, rarely punctiform. On only one find (Fig. 10A_2), two cut-marks on the dorsal face (flaying or defleshing) were noted in association with the area utilized for retouching, which was localized ventrally (Fig. 10A_1), as in all the other cases (Fig. 10B, C and D). Only one retoucher present specific traces of combustion (Fig. 10F). At Fumane Cave, two retouchers are present, made from a first phalanx and an ulna from two brown bears of different ages (Tab. 6); both were recovered from A6 (Jéquier et al., 2012). The retoucher RIL 5805 was made from a left ulnar diaphysis medial from a Young/Adult individual, which is suggested by the muscular insertion surfaces that were still being formed. Fractures, cracks, and an impact notch (Fig. 10E_7), present medially, show the bone was fresh at the time of intentional fracturing. The linear-type impressions are present next to a long, fractured edge, positioned laterally to the element (Fig. 10E_6). The second brown bear retoucher (D853) is a phalanx from a Generic Adult individual, and presents a short, precise, and persistent series of striae on the plantar surface (Fig. 10F_8), attributable to one of the early stages of the hide removal from the extremities of the limbs. The distal epiphyses moreover show combustion- absent from one of the two condyles (Fig. 10F). The linear-type and punctiform impressions are localized on the dorsal proximal diaphyseal surfaces (Fig. 10F_9) and are characterized by their precision and the reduced number of impacts (around ten).

In general, at Fumane and Rio Secco some of the surfaces of ungulate bones retouchers have been scraped before being used, probably to remove meat and tendon residues or the periosteum (Jéquier et al., 2012; Peresani et al., 2014). This pattern is not observable on the ursid diaphyses retouchers from either site, which were utilized little following or during the butchery phase. At Fumane, punctiform and linear impressions, striations, and pits usually characterize functional areas on retouchers (Jéquier et al., 2012). Three different functional zones can be identified on some retouchers made from ungulate diaphyses; however, the totality of the ursid retouchers from both sites shows a single functional zone.

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Taxa	RS - levels 5 top + 7				RS - levels 5 + 8				FC - levels A5-A5+A6				FC — level A6			
	NISP	MNI by age		Total MNI	NISP	MNI by age			Total MNI	NISP	MNI by age		Total MNI	NISP	MNI by age		Total MNI
		I Y A S				I Y Y-A A S					I Y A				I Y Y-A A		
Ursus arctos	6	1		**1**	1	1			**1**	4	1		**1**	10	1		2 **3**
Ursus spelaeus	148	2 2 4 3		**11**	157	1 2 1	8 3		**15**	2	1		**1**	–			
Ursus sp.	66	*1* *1*		**(2)**	64	*1* *1*	*1*		**(3)**	13	*1* *2* *1*		**3 (1)**	21	*2* *1*		*1* **3 (1)**
TOT.	**220**	**2 2 5 3**		**12**	**222**	**1 2 1**	**9 3**		**16**	**19**	**1 2 2**		**5**	**31**	**2 1 1**		**2 6**

Table 6
Identification number, site, layer, anatomical portion, taphonomy, and measurement of the bear bones retouchers; *FfrB* fresh bone fracture, *CM* cut-marks, *PM* percussion marks, *B* burned, *L* length, *Wi* width, *T* thickness, *We* weight

5. Discussion

The data presented above demonstrate clear evidence for interactions between Neanderthals and cave and brown bears, which were targeted for the acquisition of fur, meat, bones, and possibly other materials that were considered plantigrade resources. However, as also demonstrated by the carnivore to herbivore ratios at both the sites, respectively 1:0.27 (Rio Secco) and 1:23 (Fumane), much of the variability between these caves can be contextualized in terms of the ways and the rhythms of bear exploitation. The survival coefficient describes a fragmentation rate that is not very high when compared with other Palaeolithic contexts where values are never less than 0.4. The smaller and more compact bones with values that tend toward an index of 1 could in reality be overestimated due to the low number of finds (carpals, tarsals, metapodials, and phalanges). The low representation of phalanges could be ascribed to their removal with animal fur (Fumane Cave), but also a differentiation of findings in the investigated area (Rio Secco Cave).

Like numerous caves across Europe, Rio Secco was almost exclusively used for bear hibernation, while Fumane shows evidence for intense and repeated Neanderthal settlement. Evidence from Rio Secco suggests targeted cave visits and the exploitation of bears by humans, which is comparable to three Mousterian sites in Europe that have been interpreted as evidence of active and directed hunting: Biache-Saint-Vaast in France (Auguste, 1992, 1995, 2003), Taubach in Germany (Bratlund, 1999; Gaudzinski et al., 2011), and Krapina in Croatia (Miracle, 2007). The bear bone accumulations are consistent: 7,013 bones at Biache (NISP with cut-marks 2,496; *U. arctos* and *U. deningeri*), 1,537 at Taubach (NISP with cut-marks 292; *U. arctos*), and 527 at Krapina (NISP with cut-marks 23; *U. spelaeus, U. arctos,* and *U.* sp.). These interpretations are based on the dominance of adults over young and senile individuals- a structure inverted with respect to that of a living population (adults in the minority, young and senior individuals the majority)- and traces of cuts of an anthropic origin, indicating diverse slaughtering activities (total extraction of hide or fur, disarticulation, and defleshing). At Biache, Auguste (1995) observes that young bear cubs are absent, while adults and sub-adults dominate and «*a male/female ratio slightly biased in favor of the former indicates the predation of isolated individuals; this reflects the solitary behavior of ursids and rejects the killing of hibernated animals*». He puts forward the hypothesis that the bear hunt occurred in the autumn, as it is the meat, fatty in this season, which was mostly used. The numerous cut-marks present on 10% of the ursid remains were mostly on the cranial and thoracic skeletal elements, and an analysis of age cohorts (Auguste, 2003) demonstrates that Biache is a kill site. The hypothesis is that Neanderthals took advantage of wetland areas and surrounding waterways to render vulnerable animals otherwise highly dangerous on dry ground (bear, aurochs, and rhinoceros) (Auguste, 1995). At Taubach, brown bears were exploited following their deaths (Bratlund, 1999): cut-marks are visible on a huge number of remains including maxillary and mandibular bones, vertebrae, long bones, pelvis, calcaneus, metapodial bones, and phalanges. At Krapina, the cut-marks are concentrated on the mandible and metapodials and may be related to the skinning of bear carcasses. At Caverna delle Fate, striae on a hyoid bone could attest to the extraction of the tongue by the Mousterians (Quilès, 2003), an operation that demands rapid execution following the plantigrade's death.

Rio Secco Cave is an isolated example in the Late Middle Palaeolithic contexts of northeast Italy although farther east in the Trieste karst there are many karstic cavities with an abundant presence of cave bear remains that are

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associated with some ungulate and carnivore remains and lithic artifacts, including Grotta Pocala (Bartolomei, 1982), Caverna degli Orsi (Boschian, 1992, 2001, 2003; Boschian and Ota, 2002) and Riparo di Visogliano (Abbazzi et al., 2000; Cattani et al., 1991). However, detailed taphonomic analyses are still lacking and there is no evidence for human-bear interactions. In-depth documentation of cut-marked bone surfaces should be required from Ciota Ciara Cave in order to confirm or refute if this context was also used for the exploitation of cave bears (Buccheri et al., 2016), as it is comparable to other sites across Italy where examples of alternating Neanderthal-large carnivore frequentations are often attested by handfuls of lithic artifacts in association with abundant bone remains, supposedly the result of natural deaths. This evidence can be characterized by the extreme conditions in which they are found, as in the case of Caverna Generosa, located at around 1,500m asl in the central Italian pre-Alps (Bona et al. 2007), and Grotta Lattaia, on Cetona Mountain in southern Tuscany (Argenti and Mazza, 2006), the southern limit of the population range of the cave bear. At Grotta Lattaia, 107 *Ursus spelaeus* bones were found in association with Levallois tools dated to 48±4ky 14C BP.

In contrast, Fumane Cave (Fig. 2 and SI) is set in a region where variable evidence of human frequentation has been produced, even if ephemeral in some cases, from Riparo Tagliente (Thun-Hohenstein and Peretto, 2005) in the Lessini Mountains and from Grotta Maggiore di San Bernardino (Peresani, 1996), Grotta Paina (Gurioli et al., 2006), Grotta Col della Stria (Romandini, 2012), Grotta de Nadale (Jéquier et al., 2015), and Grotta del Broion (Peresani and Porraz, 2004) in the Berici Hills. Due to its geographic setting, Fumane holds a strategic position, which may have facilitated human penetration into the mountain region. Each of these sites is located in different contexts, and their faunal assemblages indicate that the hunted ungulates- mostly red deer and roe deer with lesser incidence of chamois and ibex and limited exploitation of *Bos*/*Bison*, giant deer, elk and wild boar (Fiore et al., 2004; Thun-Hohenstein and Peretto, 2005) fit the ecological conditions around each site, showing shifts correlated with the most relevant climatic oscillations (Lopez-García et al., 2015).

In the atrial area of Fumane Cave, the extensive excavations of two Mousterian levels have yielded the ursid remains that have been analyzed here. These seem more to fit the treatment of carcasses within a human settlement equipped with hearths rather than bear hibernation. The total absence of atlas, axis, elements of the hyoid apparatus, scapula, and coxal remains, which could indirectly indicate a primary treatment of the carcass in a place other than the cave itself and the transport of limbs and crania, richest in meat. It cannot be excluded that the repeated Neanderthal frequentation of the cave contributed to the dispersion of the plantigrade elements toward the atrial area of the cavity. In contrast, at Rio Secco Cave, the bear carcasses, always recovered intact, are the result of capture and slaying late in their winter hibernation or approaching its beginning, as is demonstrated by the traces of anthropic modifications observed on Infant, Young and Adult individuals.

The presence of cubs at both sites further suggests that killing was also aimed at mothers (Rio Secco), although there is additionally evidence of some males frequenting the cavity (*os penis* present at Rio Secco in both levels). Ethnographic comparisons suggest coherence in the interpretation of the archaeological data and attest to butchery and skinning nearly always occurring at the entrance to the den (cave/shelter), with particular care and attention paid to the fur removal (Binford, 2002).

According to the zooarchaeological bear assemblages from Rio Secco and Fumane, our data partially enable the procurement mode to be determined. This can be envisaged especially in the case of a hibernation site like Rio Secco, where the taphonomic background makes it almost impossible to distinguish between hunting and the exploitation of animals that died of natural causes. However, our data clearly demonstrate that the first manipulation of the bear carcass by humans was targeted at fur recovery, a task accomplishable only on animals that died very shortly before being skinned, and was probably planned to occur during denning time. This is also indicated by the activities aimed at the extraction of meat and marrow, the consumption of which is not strictly fixed in a timeframe, as it depends on taste preferences and food tolerances unknown today (Stiner et al., 1996). Given our certitude that the period of procurement has been established to be early spring at Fumane and early spring and/or preceding hibernation at Rio Secco, we suggest, following Stiner's ethnographic observations of Native American Indians (1994) and Pacher's (2000) and Münzel and Conard's (2004a, b) analyses of ethnographic data on bear hunting since the 17th century, that the Neanderthal predation model was based on the opportunistic predation of bears during the first stages of hibernation and during winter, the favored season for hunting this plantigrade. It remains, however, problematic to imagine the possibilities and existing hunting techniques on the part of Neanderthal hunters in northern Italy, even

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knowing that the lithic assemblages are extremely lacking in stone points and that the prey species are among the largest represented of the carnivore order.

6. Conclusion

In general, the relation of Pleistocene trophic resources to vegetation zones rendered prey animals available only in accordance with seasonal rhythms, creating large geographic biozones and higher ranges of mobility (Kelly, 1995). The cycles and climate events furthermore diversely influenced the community structure depending on the regions considered. Interactions between Neanderthals and bears are inevitable in ecosystems in which two such similar species cohabitate, as they find or happen upon the remains of a carcass, near or around a cave/shelter (Blumenshine, 1986; Dominguez Rodrigo, 2000). This is evident at Rio Secco cave, where several indicators suggest that Neanderthals purposefully targeted this resource by moving across land devoid of lithics, at the edge of the alpine ridge and in an area peripheral to the alluvian plain to the south and the frequented regions to the west.

This is in contrast to Fumane cave, which was situated in a context proximal to widely available, productive lithic resources; as game, bears were secondary to ungulates. In this scenario, bears were a strategic or occasional resource for Neanderthals during their nomadic movements between the plain and the Alps.

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- PAPER II

Chronological and Isotopic data support a revision for timing of cave bear extinction in Mediterranean Europe.

In this article, we analysed cave bear bones from Paina Cave and Trene Cave (Berici Hills). We performed a Taphonomic analysis on cave bear bones from Units 5 and 6 – Paina Cave and macro-unit B – Trene. Different anatomical elements of several individuals cave bear (n. 12) and 4 moose bones, were selected and sampled for stable isotope analysis. In addition, collagen of two bones was used for radiocarbon dating. Collagen extraction for C and N stable isotopes was performed at the Department of Geosciences of the University of Tubingen (Germany). Whit this study we contributed to better understanding about the extinction of cave bear and their paleoecology. The radiocarbon dates obtained here suggest that these cave bears have survived until 24,000 cal yr BP, during the LGM (Last Glacial Maximum) and are the latest known representative of the species in Europe. Human modifications such as cut marks are present on several skeletal elements, which enables a reconstruction of the main steps of hide recovery and the butchering process. Stable isotopic analyses confirmed that these cave bears did not eat meat and are similar to other cave bear populations; with low $\delta^{15}N$ values in the range of herbivores and lower $\delta^{13}C$ values as ungulates. The broad range of plant types available and the favourable location of Berici Hills may have played an important role in the range expansion of cave bears and their interaction with the Palaeolithic hunters settled in the same area.

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Introduction

The extinction of large mammals that occurred between around 40,000 and 10,000 years ago in Europe is one of the most controversial and relevant issues of the Late Quaternary. The ultimate causes that led to this extinction, with humans and climate change being the main potential agents discussed, are not yet well understood, and both are assumed to have played an important role (Barnosky et al. 2004; Koch and Barnosky 2006; Lorenzen et al. 2011; Stuart 2015). A typical representative of the megafauna is the cave bear *Ursus spelaeus* (sensu lato), that has possibly yielded the largest amount of fossil material in Late Pleistocene caves in Europe, most of which associated with human deposits (Kurtén 1958; Peigné et al. 2009).

Apart from the changing climate and environment (Pacher and Stuart 2009; Stuart and Lister 2007), several other factors may have contributed to the decline of cave bears, including anthropogenic interference (Münzel et al. 2011; Wojtal et al. 2015; Fortes et al. 2016) such as competition for caves or shelter (Grayson and Delpech 2003), as well as possibly predation from large carnivores such as cave lions and cave hyenas (Bocherens et al. 2011; Diedrich 2012, 2014, Bocherens 2015) and reduction in genetic variance (Stiller et al. 2010).

Radiocarbon dating indicates that the last cave bears became extinct simultaneously in different parts of Europe about 25-28 thousand yr BP, close to the onset of the Last Glacial Maximum during MIS 2 (Morel and Schifferdecker 1997; Adams 2002; Hofreiter et al. 2004a, 2004b; Grandal-d'Anglade et al. 2006; Wojtal 2007; Nadachowski et al. 2009; Blant et al. 2010; Münzel et al. 2011; Bocherens et al. 2014a; Martini et al. 2014; Sabol et al. 2014; Baca et al. 2016). Previously published radiocarbon dates on cave bears from caves in northeastern Italy were younger (Gurioli et al. 2006; Parere et al. 2006), but since many such dates had to be revised with the improvement of radiocarbon dating techniques during the last decade (Münzel et al. 2011), we decided to redate some material to check if these dates are correct.

Cave bear bones are often associated with stone tools or with other evidence of human presence, suggesting possible interactions between the two species. The taphonomic history of cave bear bones is very complex and has only been refined in the last 20 years by microscopic and taphonomic research techniques, accompanied by reviews of the materials excavated in the early to middle of the last century (Stiner et al. 1998). During the first decades of the 20th century the concepts in the interpretation of the archaeological findings were based on excavations in the caves of the Alps where numerous cave bears remains were found sometimes in association with lithic industries. With these evidences some scientists considered the theory that cave bears were hunted and celebrated in cult (Bächler 1921). The "Bear Cult" is manifested through the presumed deposition of cave bear long bones and crania. These theories or hypotheses saw undeniable comparisons in archaeological evidence from Germany, Austria, Hungary, Slovenia, and Croatia (Pacher 2003). Decades later, the theory of the "Bear Cult" was totally abandoned by challenging the origin and anthropic modification of bear remains (Koby 1943, 1951, 1953; Kurten 1976; Stiner 1998; Fosse et al. 2002; Auguste 2003).

Cave bears exhibit high morphological variability, which was and still is discussed by many researchers regarding phylogenetic, geographic and intra-population variability (Kurten 1976; Rabeder et al. 2000; Grandal-d'Anglade and López-González 2004; Hofreiter et al. 2004a, 2004b; Rabeder and Hofreiter 2004; Rabeder et al. 2008; Baryshnikov and Puzachenko 2011; Münzel et al. 2014) and has raised questions about this species' genetic diversity (Hofreiter et al. 2002; Orlando et al. 2002). Palaeogenetic research revealed three main haplogroups of cave bear in Europe including numerous haplotypes (Stiller et al. 2014; Baca et al. 2016), but without any apparent behavioral and ecological differences amongst these lineages as inferred from their stable isotopic signatures (Bocherens 2015). Cave bear was the first Pleistocene extinct species for which carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) stable isotopes were used to investigate its palaeodiet (Bocherens et al. 1990, 1991, 1994). This method has been applied to cave bears from many European cave sites, ranging from Spain to Romania, suggesting an essentially vegetarian diet (Bocherens et al. 1997; Vila Taboada et al. 1999; Bocherens et al. 2006, 2011; Grandal-d'Anglade et al. 2011; Münzel et al. 2011; Horacek et al. 2012; Pacher et al. 2012; Bocherens et al. 2014a, 2014b; Bocherens 2015; Krajcarz et al. 2016; Naito et al. 2016). These results are also confirmed by several studies based on tooth microwear, ecomorphology and taphonomy (van Heteren et al. 2009; Münzel et al. 2014; van Heteren et al. 2016). In contrast, $\delta^{13}C$ and $\delta^{15}N$ analyses on cave bears from two Romanian sites (Richards et al. 2008; Robu et al. 2013; Trinkaus and Richards 2013) as well some morphometric (Figueirido et al. 2009) tooth microwear and taphonomical studies (Peigné et al. 2009; Rabal-Garcés et

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al. 2012; Jones and DeSantis 2016) suggested that some cave bears included a substantial amount of meat in their diet.

This paper is a further contribution to understanding the extinction of the cave bear by adding radiocarbon dating, isotopic data and taphonomy of the latest *Ursus spelaeus* (*sensu lato*) remains from a Mediterranean area in the Southern Alps. Mediterranean Europe was a refugia for many plant and animal species (Stuart and Lister 2007; Svenning et al. 2008; Martini et al. 2014) during long-lasting major glaciation periods but also recorded marked changes in faunal assemblages in coincidence with dramatic climatic drivers. Concerning cave bears, data are still scanty about their population dynamics, ecology and particularly their extinction.

Cave sites

Paina and Trene caves are located in the Berici Hills in northeastern Italy (Figure 1). On the eastern slope of the hills there are several shelters and caves in the Eocene and Oligocene limestone cliffs. These cavities contain, in a several of cases, evidence of human presence during the Middle and Upper Palaeolithic. Cave bear remains are very often found in these caves and they are the most frequent fossils found in the assemblage (Sala 1990; Cassoli and
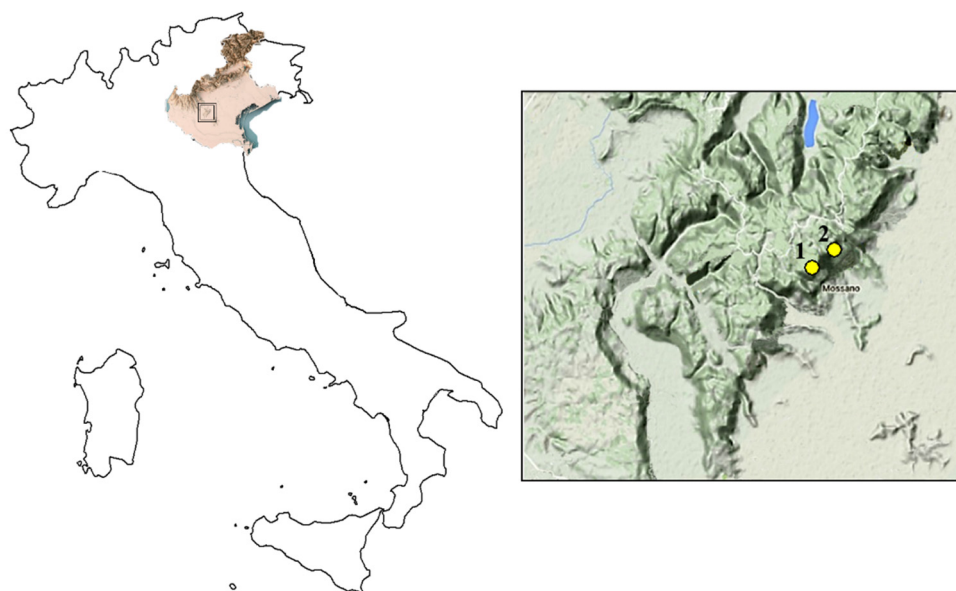
Tagliacozzo 1994; Gurioli et al. 2006; Broglio et al. 2009; Romandini and Nannini 2012; Nannini and Romandini 2015).

Figure 1. Geographical location of cave sites in the Berici Hills: 1 Paina Cave, 2 Trene Cave

Paina Cave - is located about 350 m a.s.l., on the edge of a steep slope connecting the plateau to the alluvial plain. Field investigations revealed a stratigraphic series of about 1.50 m thickness, which includes 12 layers containing Middle (Units 12-10) and Upper Palaeolithic (Units 9-5) artefacts. The focus is the zooarchaeological content Units 5 and 6, radiocarbon dated from 20,120±220 to 19,430±150 uncal y. BP (Unit 6) and to 19,861±70 uncal y. BP (Unit 5) based on cave bear bones (Parere et al. 2006, Gurioli et al. 2006). The lithic artifacts have been referred to Early Epigravettian with "cran" points.

The faunal remains of these Units record the predominance of carnivorans (cave bear, fox and mustelids) over ungulates. Amongst the latter, the most abundant species are the cervids (*Cervus elaphus* and *Alces alces*), followed by caprids and wild boar. Fish and birds remains are also present (Bartolomei et al. 1987-1988; Parere et al. 2006, Gurioli et al. 2006) (Table 1). Evidences of carcass exploitation by humans are rare and consist of few butchering marks.

Trene Cave is located on the eastern slope of the Berici Hills, at about 360 m a.s.l. The cavity was subject of systematic excavations made by the University of Ferrara in 1956, which yielded a 1.14 m thick deposit, subdivided

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into three macro-units: A, B and C. The focus of this paper is the macro-unit B with radiocarbon dates on ungulate bones ranging from 17,640±140 uncal y. BP to 18.630±150 uncal y. BP (Broglio and Improta 1995). The lithic industry ascribes the anthropic frequentation to the early Epigravettian.

The faunal assemblage shows a clear dominance of cave bear over other taxa, followed by ungulates (*Alces alces*, *Cervus elaphus* and *Sus scrofa*), fishes and birds (Table 1). Human interest in ungulates is documented by cut-marks on moose bones. In addition, several remains of cave bear show traces of butchering and skinning (Romandini and Nannini 2012; Nannini and Romandini 2015). During human occupation, the caves were in a predominantly forested environment under cold-temperate climate conditions with wetland areas on the underlying plain, as shown by the presence of moose, deer, wild boar and fish vertebrae (Gurioli et al. 2006).

Material and Methods

Taxonomic, skeletal identifications and preliminary taphonomic analysis of bones assemblage have been conducted and published by Gurioli et al. (2006); Parere et al. (2006); Nannini and Romandini (2015). Taphonomic analysis was performed on cave bear bones from Units 5 and 6 – Paina Cave and macro-unit B – Trene. For the initial stable isotope study different anatomical elements of several individuals cave bear were selected and sampled, especially those with a good state of conservation.

Table 1. Mammal NISP and NISP% from Paina Cave (Units 5-6) and Trene Cave (macrounit B)

Taxa	Paina Cave (Units 5 and 6)		Trene Cave (macrounit B)	
	NISP	NISP %	NISP	NISP %
Lepus sp.	2	0.4	2	0.2
Lepus cfr. europeaus	1	0.2		
Marmota marmota	5	1.1	5	0.6
Rodentia			3	0.3
Total Lagomorpha and Rodentia	8	1.8	10	1.1
Canis lupus			1	0.1
Vulpes vulpes	22	5	4	0.5
Ursus spelaeus	302	69.1	604	69.1
Ursus sp.	4	0.9	70	8
Martes martes	6	1.4		
Martes sp.	1	0.2		
Meles meles			2	0.2
Felis silvetris	3	0.7		
Carnivora indet.	2	0.4	28	3.2
Total Carnivora	340	77.8	709	81.1
Sus scrofa	2	0.4	3	0.3
Megaloceros giganteus	1	0.2		
Alces alces	19	4.4	58	6.6
Cervus elaphus	30	6.8	18	2.1
Capreolus capreolus	4	0.9		
Cervidae indet.	19	4.4	42	4.8
Capra ibex	4	0.9	1	0.1
Rupicapra rupicapra			3	0.3
Caprinae indet.			2	0.2
Ungulata indet.	10	2.3	28	3.2
Total Ungulata	89	20.4	155	17.7
Total NISP	437	100	874	100
Total Indeterminate	285		2548	
Pisces	3		26	
Aves	6		19	
Total NR	731		3467	

Taphonomy

For taphonomic material was considered only cave bear bones with a firm specific attribution and determination, and greater than 2 cm. in length. Bone surfaces were analyzed both macroscopically and microscopically using a small magnifying lens (10-20x) with incident white light and a Leica S6D Greenough stereo microscope with 0.75-70X

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magnification range for capturing images. In order to identify the nature of surface alterations and to distinguish human from animal traces, trampling abrasion, and modern mechanical modifications produced by excavation tools, reference was made to well-established taphonomic literature. Combustion degree has been distinguished between moderate (200-500°C, black/brown) and elevated temperature with calcination (>700 °C, grey/white) (Stiner et al. 1995; Costamagno et al. 2002). Cut-marks have been classified as incisions, like skinning marks, defleshing marks, and scrapes (Binford 1981; Potts and Shipman 1981; Shipman 1981; Shipman and Rose 1984). The documented incisions appear linear, with great variability in length, width and depth, V-shaped section, and internal microstriation at the base of the groove. Intentional bone breakage to access marrow was documented by diagnostic elements like percussion marks/notches and impact flakes, and positive flakes of the percussion marks (Blumenschine and Selvaggio 1988; Villa and Mahieu 1991; Capaldo and Blumenschine 1994; Pickering and Egeland 2006).

Collagen extraction and C and N stable isotopes

For stable isotope analysis, 12 cave bear bones (six for each site) were selected. In addition, 4 moose *Alces alces* bones from the same sites and units were sampled (Table 2), as ecological comparison to evaluate whether dietary proteins derived mainly from plants or from higher trophic level protein sources were consumed by cave bears. For each specimen, a small fragment was carefully sawn with a Dremmel© rotating tool equipped with a circular diamond-coated blade, ultrasonicated in acetone and water, rinsed with distilled water, dried and crushed to a powder of 0.7 mm grain size. Then an aliquot of around 5mg was used to measure the nitrogen content (%N) of the whole bone, in order to screen out samples with excessive collagen loss (Bocherens et al. 2005). For instance, fresh bones contain 4% nitrogen while ancient bones with less than 0.4% nitrogen usually fail to yield good collagen (Bocherens et al. 2005). The measurements were performed using a Vario EL elemental analyser using Acetanilid from Merck as internal standard at the Department of Geosciences of the University of Tübingen. The mean standard error was better than of 0.1% for %C and %N.

The collagen was purified according to well establish protocol (Bocherens et al. 1997). This preparation was performed at the Biogeology unit of the Geoscience Department at the University of Tübingen (Germany).

Carbon and nitrogen elemental and stable isotope measurements were performed at the LSIS-AFAR stable isotope facility of the University of Western University, Canada. Collagen samples (0.5mg) were weighed into tin capsules and combusted in a Costech Elemental Analyzer coupled to a Thermo Delta Plus XL isotope ratio mass spectrometer operated in continuous flow mode, with helium carrier gas. Two standards, USGS-40 and USGS-41 were included for every ten samples and two internal laboratory standards, powdered keratin (MP Biomedicals Inc., Cat No. 90211, Lot No.9966H) and IAEA-CH-6 were included to monitor instrument drift and provide a check on accuracy over the course of each analytical session. Values of δ^{13}C were calibrated to VPDB and values of δ^{15}N were calibrated to AIR. Measurement error was ± 0.1 ‰ for δ^{13}C, and ± 0.2 ‰ for δ^{15}N.

Part of collagen of a first phalanx (Paina Cave) and a humerus with butchering marks (Trene Cave) prepared for stable isotope analysis, was sent to the Laboratory of Ion Beam Physics, ETH, Zurich (Switzerland). We report the conventional and calibrated radiocarbon dates (Table 3). The dates were calibrated to the years BP (i.e. 1950) in Oxcal v4.2.4 (Bronk Ramsey et al. 2013) using intCal13 atmospheric curve (Reimer et al. 2013).

Table2. Stable isotope results of δ^{13}C and δ^{15}N for cave bear and Alces alces from Paina Cave and Trene Cave, included in Figure 3.

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Isotope sample	Cave site	Inventory numbers	Layer	Animal	Element	Age	CM	Coll. Yield	%C	%N	C/N	δ¹³C	δ¹⁵N
CBV1	PAINA	314	6	*Cave bear*	Humerus	Young		153.3	42.4	15.1	3.3	−21.5	3.9
CBV2	PAINA	374	6	*Cave bear*	Metacarpal II – right			104.5	39.1	13.9	3.3	−20.4	2.3
CBV4	PAINA	60	5	*Cave bear*	Phalanx II			165.2	42.9	15.2	3.3	−20.4	1.9
CBV6	PAINA	156	5	*Cave bear*	Phalanx I			43.3	39.1	13.8	3.3	−20.0	1.9
CBV11	PAINA	547	6	*Cave bear*	Mandible with M1 – right	Young		131.1	40.6	14.5	3.3	−22.2	7.2
CBV14	PAINA	561	6	*Cave bear*	Tooth p⁴ – left	Young >16 months		112.6	40.7	14.5	3.3	−22.1	6.0
CBV20	PAINA	584	6	*Alces alces*	Tibia – left			81	40.6	14.2	3.3	−20.0	5.4
CBV22	PAINA	572	6	*Alces alces*	Metatarsal – right			97.2	39.5	13.8	3.3	−20.2	2.4
CBV37	TRENE	TR288	B1 VIII	*Cave bear*	Humerus – right	Young	x	38.9	33.9	11.7	3.4	−21.2	3.4
CBV40	TRENE	TR692	B2 VII	*Cave bear*	Mandible – right	Adult II	x	39.5	37.1	12.9	3.4	−20.7	2.9
CBV41	TRENE	TR37	B	*Cave bear*	Radius – left	Adult	x	nd	33.4	11.5	3.4	−20.2	2.4
CBV43	TRENE	TR1166	B	*Cave bear*	Metatarsal III – left	Adult		18.3	36.0	12.5	3.4	−20.1	2.1
CBV47	TRENE	TR387	B2	*Cave bear*	Phalanx I	Adult		99.7	22.2	7.6	3.4	−19.6	5.4
CBV52	TRENE	TR439	B2 VII	*Cave bear*	Metacarpal I – right	Adult		63.1	36.2	12.1	3.5	−20.4	4.2
CBV57	TRENE	TR389	B2	*Alces alces*	Pelvis – left	Young		nd	27.0	9.3	3.4	−19.5	4.4
CBV59	TRENE	TR80	B	*Alces alces*	Phalanx I		x	81.4	40.4	13.6	3.5	−19.6	4.5

Note: CM: Cut marks.

Table3. New radiocarbon dates of cave bear from Paina Cave and Trene Cave, calibrated with Reimer et al., 2013.

Inventory number	Cave site	Layer	Element	CM	Isotope sample	Sample nr	Age (¹⁴C yr BP)	2σ calibration (cal yr BP) IntCal13	1σ calibration (cal yr BP) IntCal13
156	Paina	5	Phalanx I		CBV6	ETH-79366	19,686 ± 54	23,948–23,489	23,830–23,600
TR288	Trene	B1	Humerus	X	CBV37	ETH-79368	19,948 ± 55	24,220–23,795	24,108–23,900

Results

Anthropogenic impact

Taphonomic analysis on cave bear bones from Trene Cave suggest close interactions between humans and bears. Human modifications such as cut marks are present on several skeletal elements, which enables a reconstruction of the main steps of hide recovery and the butchering process (Figure 2). Cut marks caused by skinning are present on three mandibles of different individuals (e.g. Figure 2 (a-1)). On one mandible belonging to a young-adult individual, the cut marks are present on the angle between the lingual and the buccal sides and on a portion of the masseteric fossa. A right calcaneus and a third metacarpal show short cut marks (Figure 2 (d-4-5)), which are sometimes deep and persistent, attesting the early phases of hide recovery or disarticulation. Evidence of defleshing and detachment of muscle mass is evident on a right humerus, on a right fibula and on a left radius (Figure 2 (b-2), (c-3)) for which skinning is not excluded. A percussion mark is visible only on a portion of mandible completely burned suggesting a fracturing action in order to extract the marrow and use the same remain as fuel.

At Paina Cave, evidence for bear exploitation by humans are rare and consist of few butchering marks, intentionally fractured diaphysis and burned bones. This cave may have been rarely inhabited by human groups, while it was repeatedly occupied and for a long time by cave bears, during hibernation and cub nursing.

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Figure 2. Trene Cave, localization and details of anthropic traces: (a) right mandible with cut mark on buccal side (1); (b) left radius with traces on diaphysis (2); (c) right fibula with traces on diaphysis (3); (d) third metacarpal with short cut marks on proximal portion (4) and diaphysis (5).

Stable isotopes and radiocarbon dating

At Paina and Trene caves the C:N ratios, %N and %C demonstrated the very good quality of collagen preservation (Table 2). The δ^{13}C values on cave bear ranged from –22.2‰ to –20‰ (Paina Cave) and from –21.2‰ to –19.6‰ (Trene Cave). The δ^{15}N on cave bear ranged from 1.9‰ to 7.2‰ (Paina Cave) and from 2.1‰ to 5.4‰ (Trene Cave). The δ^{13}C and δ^{15}N values measured for *Alces alces* ranged respectively from –20.2‰ to –19.5‰ and from 2.4‰ to 5.4‰ (Table 2 and Figure 3).

The ranges of δ^{13}C and δ^{15}N values overlap considerably for adult bones of cave bears and moose. There are a few exceptions to this pattern: one tooth (CBV14) and one mandible (CBV11) of young individuals from Paina Cave with high δ^{15}N and low δ^{13}C values (Table 2 and Figure 3).

Two direct radiocarbon dates on well-preserved collagen were similar. The conventional age of the phalanx from Paina Cave is determined as 19686±54 [14]Cyr BP (23,948 to 23,489 cal yr BP. Sample ETH-79366: Table 3). These new data confirm a previous result obtained on the astragalus of cave bear from the same Unit (US 5). The specimen had a conventional age of 19681±70 [14]Cyr BP (23,960 to 23,464 cal yr BP. Sample LTL1829A. Parere et al. 2006). The radiocarbon age of a humerus from Trene Cave is measured as 19948±55 [14]Cyr BP (24,220 to 23,795 cal yr BP. Sample ETH-79368: Table 3). These new data were not correlated with a previous one obtained on ungulate bone from the same fossil assemblage (Unit B1), which was given a conventional age of 17640±140 [14]Cyr BP (21,761 to 20,930 cal yr BP. sample UtC-2691, Broglio and Improta 1995).

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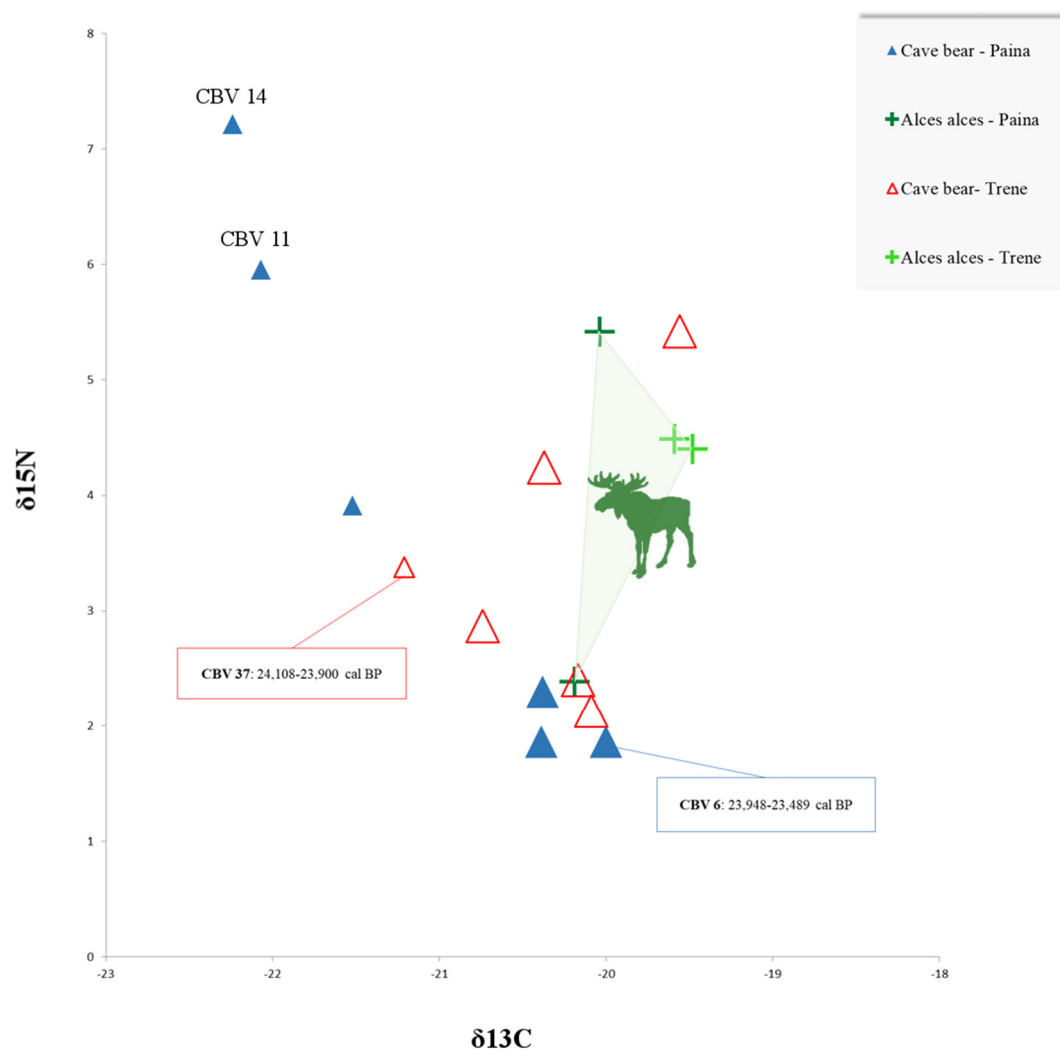
Figure 3. δ¹³C and δ¹⁵N values of cave bear and moose from Paina and Trene caves. The smaller symbol represents young individuals.

Discussion

The radiocarbon dates obtained here are based on well-preserved collagen and therefore can be considered as reflecting the real age of the dated bones. These dates on cave bear from Paina and Trene caves, around 24,200-23,500 cal yr BP, are more recent than others measured in Europe, about 2,000/3,000 years younger than the latest ages recorded in Poland (around 25,200 cal yr BP - Stajnia Cave: Baca et al. 2016), Italy (around 27-25,000 cal yr BP - Grotta Sopra Fontana Marella and Chiostraccio Cave: Perego et al. 2001; Martini et al. 2014), Hungary (around 26,300 cal yr BP – Szeleta Cave: Adams 2002) and Spain (around 26,800 cal yr BP – Rebolal Cave: Grandal-d'Anglade et al. 2006) (Table 4 and Figure 4). The young dates from Vindija should be taken with caution since dates on hominid bones from this cave have been revised dramatically to earlier values due to problematic collagen preservation (Higham et al. 2006; Devièse et al. 2017). With these dates there is no doubt that the disappearance of cave bear from Italy occurred during the LGM (Last Glacial Maximum), more or less coinciding with the maximal expansion of south Alpine glaciers (Monegato et al. 2017). As the glacial expansions fragmented the ranges of many animal and plant species throughout Europe, the southern part of the Prealps might have preserved isolated and sheltered refugia for cave bears. Especially the Berici Hills represented a kind of refuge area for the plantigrade, with availability of trophic resources and shelter suitable to overcome harsh winter periods during LGM relative to other zones in the Lessini Mountains or at higher altitude as in the Alps (Spötl et al 2017). The orientation of the caves (S, S-E), located generally

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on steep slopes, provided a protected niche fundamental to the microclimatic conditions in the critical phases of hibernation and weaning.

Considering that the cave bears from Paina and Trene are the most recent ones known from Europe, it was interesting to obtain δ^{13}C and δ^{15}N values to establish if these late surviving individuals exhibited any variation in their feeding behaviour compared to earlier ones. Isotopic data of these cave bears are similar to other cave bear populations, with low δ^{15}N values, in the range of herbivores (here *Alces alces*) and lower δ^{13}C values as ungulates, here again *Alces alces*. This situation is typical for cave bears, not an indication of carnivore diet, rather a hibernation and nursing signal (Bocherens 2015). The high δ^{13}C values of *Alces alces*, suggest a relatively open environment, but with clearings available (Drucker et al. 2010; Bocherens et al. 2015).

The δ^{13}C and δ^{15}N values are similar to those of older cave bears from Germany, Austria, Switzerland and France (Bocherens et al. 2011; Münzel et al. 2011; Pacher et al. 2012; Bocherens et al. 2014a), suggesting that the diet of cave bears remained unchanged until the disappearance of this species. Only two specimens of young individuals showed different δ^{13}C and δ^{15}N values, that may be related to hibernation or nursing. Hibernation has a significant impact on bear physiology. During hibernation bears use fat stores and they do not defecate or urinate (Nelson et al. 1975), so the tissues formed may record more negative values of δ^{13}C and more positive δ^{15}N values (Hilderbrand et al. 1996; Bocherens et al. 1997). Nursing causes an additional effect on C and N isotopic composition similar to a higher trophic level, since milk consumed by young mammal during suckling will place them one trophic level higher than adults of the same species (Fogel et al. 1989; Bocherens 2000; Jenkins et al. 2001; Dalerum et al. 2007).

A final observation deduced from the taphonomical study on cave bear bones from Paina and Trene caves suggests that humans were exploiting the cave bears for meat and hides and therefore may have had an impact in the demise of this species. The data presented above demonstrate clear evidence for interactions between Epigravettian hunters and cave bears, which were used for the acquisition of hides, meat and possibly other resources. At that time, the bear was more susceptible to human hunting (Kurten 1958; Grayson and Delpech 2003; Stiller et al. 2010; Münzel et al. 2011) and attacks by predators (Diedrich 2014) for meat acquisition as well as competition for the cave and denning space. This could be an important factor in its extinction, since the cave bear was dependent on caves for hibernation.

During the last twenty years evidence of interaction between human and bear in Europe was well documented in many sites from the Middle to Upper Paleolithic (Auguste 2003; Valensi and Psathi, 2004; Münzel and Conard 2004; Germonpré and Hämäläinen 2007; Bocherens et al. 2011; Turk 2014; Wojtal et al. 2015; Majkić et al. 2017). Sites across Italy have produced examples of alternating human/bear encounters by the presence of lithic artifacts in association with abundant cave bone remains, supposedly the result of natural deaths (Bartolomei 1982; Boschian 2003; Argenti and Mazza 2006; Bona et al. 2007). Detailed taphonomic analyses are still lacking and there is no evidence for human-bear interactions. In contrast several sites in northeastern Italy clearly show hunting and exploitation of bears by Neanderthals or modern humans (Romandini and Nannini 2012; Peresani et al. 2014; Nannini and Romandini 2015; Romandini et al. 2018). This could possibly reveal a continuity in the hunting and subsistence strategies between hunter-gatherers group during a wide span of time, a situation that was probably not favourable to the survival of the species.

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Table 4. Direct radiocarbon dates of MIS2 cave bear sites in Europe considered in Figure 4.

Cave/Site	Country	Element	Species (method)	Unc. Date Years BP	Calibrated Age (cal BP)*	References
Stajnia Cave	Poland	3rd Phalanx	*U. ingressus* (mtDNA)	20,930 ± 140	24,807–25,648	Baca et al. 2016;
Stajnia Cave	Poland	3rd Phalanx	*U. ingressus* (mtDNA)	21,900 ± 90	25,905–26,360	Baca et al. 2016;
Vindija Cave	Croatia	?	*U. ingressus* (mtDNA)	22,020 ± 100	25,985–26,516	Hofreiter, Serre, et al. 2004
Geißenklösterle	Germany	Maxilla	*U. ingressus* (mtDNA)	24,210 ± 100	27,940–28,560	Münzel et al. 2008, 2011
Vindija Cave	Croatia	?	*U. ingressus* (mtDNA)	23,780 ± 120	27,624–28,103	Hofreiter, Rabeder, et al. 2004; Hofreiter, Serre, et al. 2004
Paina Cave	Italy	Astragalus	*U. spelaeus* (morpho.)	19,681 ± 70	23,960–23,464	Parere et al. 2006;
Grotta Sopra Fontana Marella	Italy	?	*U. spelaeus* (morpho.)	21,810 ± 200	25,712–26,516	Perego et al. 2001;
Szeleta Cave	Hungary	Bone	*U. spelaeus* (morpho.)	22,107 ± 130	26,006–26,681	Adams 2002;
Grotta Sopra Fontana Marella	Italy	?	*U. spelaeus* (morpho.)	22,310 ± 200	26,102–27,122	Perego et al. 2001;
Chiostraccio Cave	Italy	Long bone	*U. spelaeus* (morpho.)	22,670 ± 130	26,595–27,340	Martini et al. 2014;
Rebolal Cave	Spain	Jaw adult	*U. spelaeus* (morpho.)	22,915 ± 445	26,202–27,886	Grandal-d'Anglade et al. 2006;
Rochedane	France	Metatapodial	*U.spelaeus* (mtDNA)	23.900 ± 110	27,701–28,231	Bocherens, Bridault, et al. 2014
Cova Eiros	Spain	Humerus	*U. spelaeus* (morpho.)	24,090 ± 440	27,475–29,070	Grandal-D'Anglade and Vidal Romani 1997; Stiller et al. 2010;
Bame aux Pirotas	Switzerland	Metapodial	*U. spelaeus or ingressus* (morpho.)	24,170 ± 230	27,783–28,679	Morel and Schifferdecker 1997;
Bärenloch	Switzerland	?	*U. spelaeus* (morpho.)	24,175 ± 365	27,634–28,956	Blant et al. 2010;.
Komarowa Cave	Poland	Skull	*U. spelaeus* (morpho.)	24,550 ± 220	28,050–29,075	Nadachowski et al. 2009 Wojtal 2007; Wojtal et al. 2015;
Deszczowa Cave	Poland	Mandible fr	*U. spelaeus* (morpho.)	24,580 ± 200	29,069–28,129	Nadachowski et al. 2009; Wojtal et al. 2015;
Izabela Textorisová Cave	Slovakia	Metacarpal IV	*U. spelaeus* (morpho.)	24,640 ± 170	29,076–28,280	Sabol et al. 2014

*calibrated with Oxcal v4.2.4, using intCal13 atmospheric curve.

Figure 4. Localization and radiocarbon dating of young cave bears remains in Europe, including Paina and Trene caves**.**

Conclusion

The new radiocarbon dates in Trene and Paina are an important contribution to the extinction chronology of cave bear and make it the latest known representative of the species in Europe.

This study demonstrates that the cave bear specimens with young radiocarbon dates are not outliers in terms of isotopic composition, suggesting that they lived in similar conditions as earlier ones (as in France and Swabian Jura) and had similar diets. Several bear remains reveal well preserved traces of human modification such as cut marks, which enable a reconstruction of the main steps of the butchering process and hide recovery. We can hypothesize that the combination of climatic deterioration and increasing human pressure could be responsible to the extinction of cave bear in northern Italy, and the final extinction of the species since this population seems to have been the last to survive. Further research combining specific (amino acid) isotope analyses and palaeogenetic investigations, together with a robust chronology of the skeletal remains, will allow a better understanding of population dynamics

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and will support the view of multiple coinciding factors including environmental change, intra- and inter-specific competition, and anthropogenic interference jointly leading to the final extinction of cave bears.

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Measurements and morphometric description of both dated bones

- **Humerus (TR288)** – Trene cave: it belongs to a young individual and for this reason it is inappropriate for taking conventional measurements. The taxonomic identification is based on the complete *Ursus spelaeus* and *Ursus arctos* osteological collection stored at the University of Ferrara. Difference with *U. arctos* is shown in figure 1 which compares humerus TR288 with the humerus of a young individual of *U. arctos*.
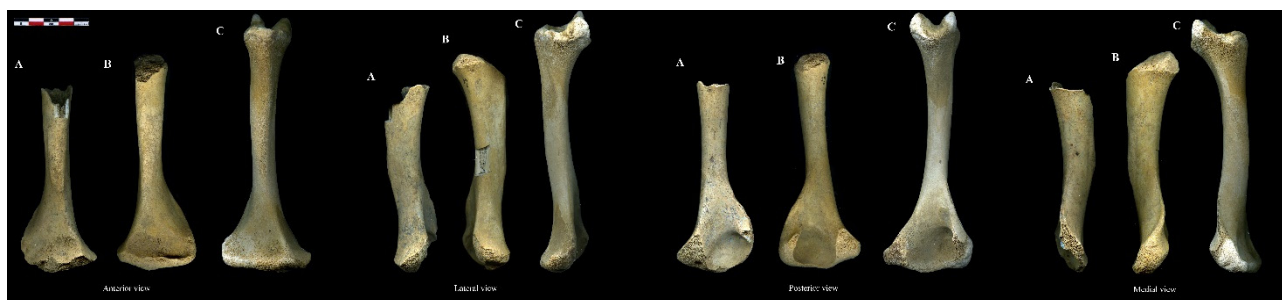
Figure 1: (A) TR288 – right humerus of young cave bear (sample dated); (B) left humerus of young cave bear (osteological collection University of Ferrara); (C) right humerus of young *Ursus arctos* from Slovenia (osteological collection University of Ferrara).

The cave bear humerus is slightly larger, sturdy and more columnar than in *U. arctos* which is slimmer and more arcuate. The cave bear humerus diaphysis has stout shape and a much bigger transversal diameter than in *U. arctos*. In anterior view, the medial transverse diameter height reveals a well-marked swelling. The posterior view shows that the lateral segments that define the shaft are one slightly concave and the other convex. The oleocranic fossa is slightly larger and shallower than in *U. arctos.*

- **Phalanx I (156)** – Paina cave: conventional measurements are GL: 43.1 mm; Bp: 24.5mm; Bd: 17.3mm and SD: 16.2 mm (Figure 2).
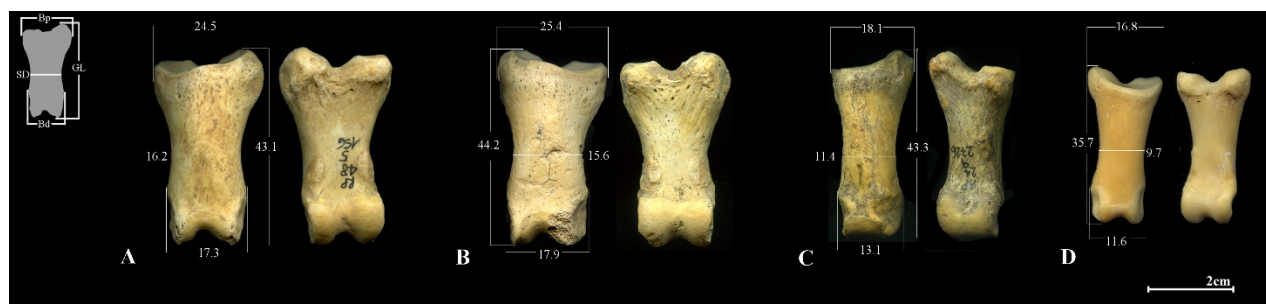
Figure 2: Phalanx I of cave bear (A) Paina cave – In. number 156 (sample dated); (B) Osteological collection University of Ferrara.

Phalanx I of *U. arctos* from Paina cave US 9 (C) and *U. arctos* from Slovenia, osteological collection University of Ferrara (D). In comparison to *U. arctos,* the phalanx I of cave bear shows pronounced differences: it is wider, slightly convex in the dorsal face, with broader proximal and distal extremities. If we consider the absolute bone length, the proximal epiphysis is proportionally wider in cave bear. Morphometrical data show that transversal diameter of the proximal and distal epiphysis and transversal diameter of the diaphysis are larger in cave bear.

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Paper III

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Extinction and paleoecology of the late Pleistocene cave bear from northeastern Italy: radiocarbon and stable isotope evidence.

In this brief article we focused on cave bear bones from Paina, Trene and Buso doppio del Broion (Berici Hills). As the Paper I, here we applied some techniques that allowed us to fit these specimens into a chronological and ecological context and yielded further information to understand the extinction process of cave bear in this area of southern Alps. Taphonomic analyses on cave bear bones from Buso doppio del Broion suggest close interaction between bears and humans as already identified to Trene Cave. We identified some cut-marks on cave bear bones, which refer to skinning and defleshing. Our isotopic analyses showed that in all three sites the C:N ratios, %N and %C demonstrated the very good quality of collagen preservation. The δ^{13}C and δ^{15}N values did not show any obvious ecological change since 33,000 cal yr BP (new radiocarbon data on rib from Buso doppio del Broion).

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1. INTRODUCTION

The Late Quaternary witnessed extinction of large mammals in Europe. The course and the timing of these events differ from region to region and the causes of these extinctions are the subject of an on-going debate (Barnosky et al., 2004; Lorenzen et al., 2011; Sandom et al., 2014 Stuart, 2015). In any case, a better understanding of the mechanisms that led to extinction of several large mammal species in a context of climate instability and changing human impact on the ecosystems will have implications for anticipating possible future extinctions. The cave bear (*Ursus spelaeus* sensu lato) is an interesting species to focus upon because has possibly yielded the largest amount of fossil remains in Late Pleistocene caves in Europe, with a large part associated with human deposits. Cave bear bones are often associated with stone tools or with other evidence of human presence, possible interactions between the two species. Radiocarbon dating suggests that they went extinct simultaneously in different parts of Europe about 25-28 ka BP, close to the onset of the Last Glacial Maximum (LGM) during MIS 2 (Adams, 2002; Hofreiter et al., 2004; Wojtal, 2007; Blant et al., 2010; Münzel et al., 2011; Bocherens et al., 2014; Martini et al., 2014; Sabol et al., 2014; Baca et al., 2016). Understanding feeding habits of cave bear is essential as it might give insight into those factors contributing to their extinction: whether they were strictly herbivores or more flexible omnivores could have resulted in different scenarios, whereby the relative influence of climate change, human pressure could have played different roles (Pacher & Stuart, 2009; Bocherens et al., 2014a). In this context, herbivorous feeding habits inferred from tooth, skull and jaw morphology (Kurté, 1976; Münzel et al., 2014; van Heteren et al., 2016) as well as the stable isotopic composition of cave bear collagen from a large majority of European sites, ranging from Spain to Romania, indicate an essentially vegetarian diet (Bocherens et al., 1997; 2006; 2011; 2014; Vila Taboada et al., 1999; Grandal-d'Anglade et al., 2011; Münzel et al., 2011; Horacek et al., 2012; Pacher et al., 2012; Krajcarz et al., 2016; Naito et al., 2016). In contrast, $\delta^{13}C$ and $\delta^{15}N$ analyses on cave bears from two Romanian sites (Richards et al., 2008; Robu et al., 2013) suggested that some cave bears included a substantial amount of meat in their diet. In this present work, we report the results of such investigation carried out on cave bear bones from three sites: Paina Cave, Trene Cave and Buso doppio del Broion (Berici Hills – Vicenza), part of them recently published (Terlato et al., 2018). We applied to these bones some techniques that allow us to fit these specimens into a chronological and ecological context and yield further information that help to understand the extinction process of cave bear in this area of the Southern Alps.

2. MATERIAL AND METHODS

Paina Cave (Units 5 and 6), Trene Cave (macro-unit B) and Buso doppio del Broion (Units 1and 2) are located in Berici Hills in northeastern Italy. Taxonomic, skeletal identifications and preliminary taphonomic analysis of bones assemblage have been conducted and published by Nannini and Romandini (2015) and Terlato et al. (2018). For stable isotope analysis, 49 cave bear bones were selected. In addition, 6 moose *Alces alces* bones from the same sites and units were sampled. The $\delta^{13}C$ and $\delta^{15}N$ values as well as C:N atomic ratio of bone collagen for 12 bear samples and 4 moose samples from Paina and Trene caves have already been published in a previous study (Terlato et al., 2018). The collagen extraction was performed following Bocherens et al. (1997) at Biogeology unit of the Geoscience Department at the University of Tübingen (Germany). C and N elemental and stable isotope measurements were performed at the LSIS-AFAR stable isotope facility of the University of Western University (Canada). Collagen samples (0.5mg) were weighed into tin capsules and combusted in a Costech Elemental Analyzer coupled to a Thermo Delta Plus XL isotope ratio mass spectrometer operated in continuous flow mode, with helium carrier gas. Two standards, USGS-40 and USGS-41 were included for every ten samples and two internal laboratory standards were included to monitor instrument drift and provide a check on accuracy over the course of each analytical session. Values of $\delta^{13}C$ were calibrated to VPDB and values of $\delta^{15}N$ were calibrated to AIR. Measurement error was ± 0.1 ‰ for $\delta^{13}C$, and ± 0.2 ‰ for $\delta^{15}N$.

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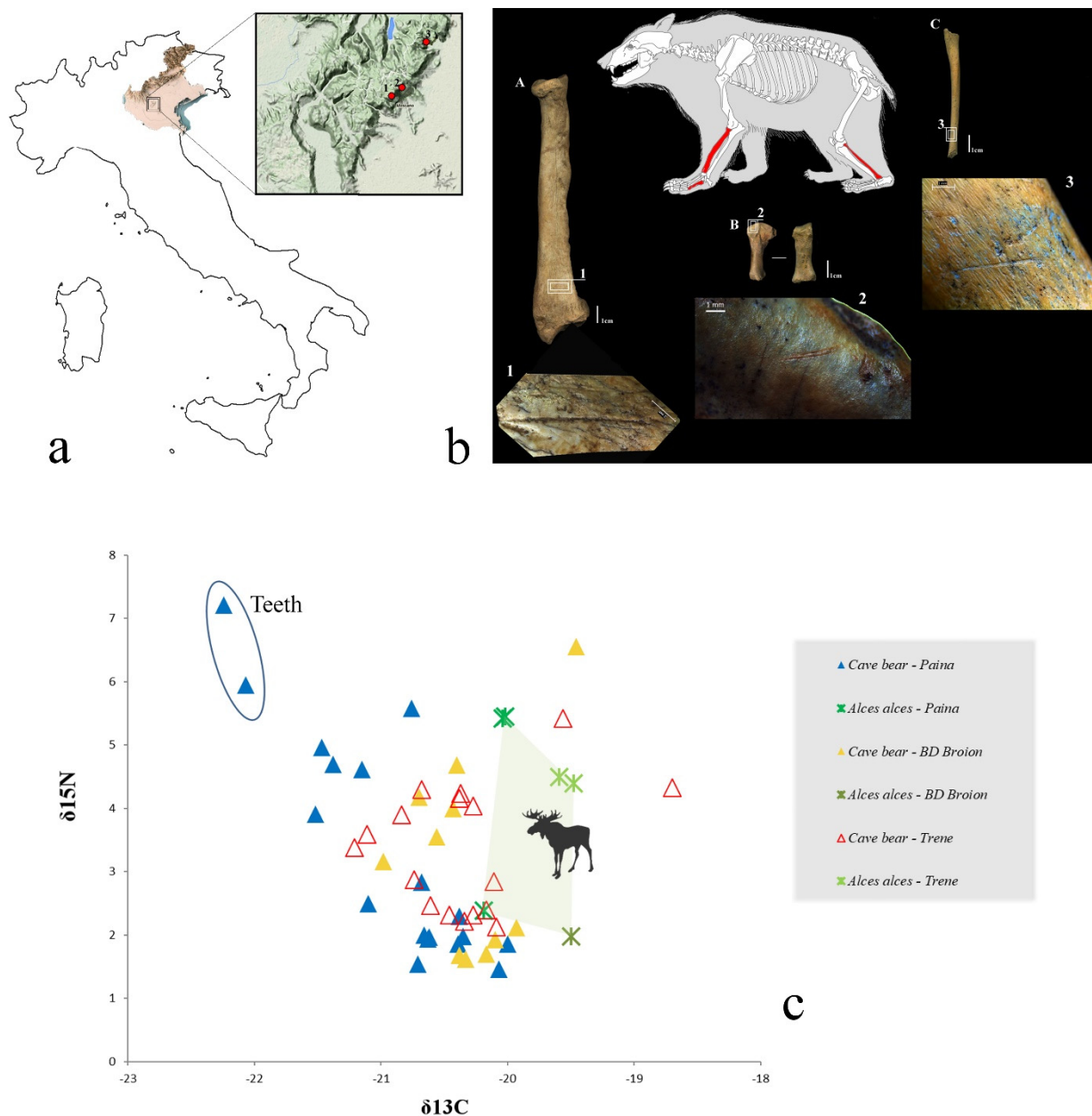Gabriele Terlato

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Figure 1: (a) Position of the Palaeolithic caves in the Berici Hills considered in this work; (b) localization and details of anthropic traces. A - left radius with traces on diaphysis (1), B - third metacarpal with short cut marks on proximal portion (2), C - right fibula with traces on diaphysis (3); (c) δ^{13}C and δ^{15}N values of cave bear and moose.

3. RESULTS

Taphonomic analysis on cave bear bones from Trene Cave and Buso doppio del Broion has revealed human modification traces like cut marks on several skeletal elements, which enables a reconstruction of the main steps of hide recovery and the butchering process (Fig. 1). At Trene Cave cut marks caused by skinning are present on three mandibles of different individuals. A right calcaneus and a third metacarpal show short cut marks, which are sometimes deep and persistent, attesting the early phases of hide recovery or disarticulation. Evidence of defleshing and detachment of muscle mass is evident on a right humerus, on a right fibula and on a left radius for which skinning is not excluded. A percussion mark is visible only on a portion of mandible completely burned suggesting a fracturing action in order to extract the marrow and use the same remain as fuel (Terlato et al., 2018). At Buso doppio del Broion

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traces are around one rib, which refer to defleshing. The cut marks on the metatarsal certainly indicate skinning of the bear. At Paina Cave, evidence for bear exploitation by humans are rare. This cave may have been rarely inhabited by human groups, while it was repeatedly occupied and for a long time by cave bears, during hibernation and cub nursing (Terlato et al., 2018). In all three sites the C:N ratios, %N and %C demonstrated the very good quality of collagen preservation. The δ^{13}C values on cave bear ranged from −22.2‰ to −20‰ (Paina Cave), from −21.2‰ to −19.6‰ (Trene Cave) and from −21.0‰ to −19.9‰ (Buso doppio del Broion). The δ^{15}N on cave bear ranged from 1.5‰ to 7.2‰ (Paina Cave), from 2.1‰ to 5.4‰ (Trene Cave) and from 1.6‰ to 6.6‰. The δ^{13}C and δ^{15}N values measured for *Alces alces* ranged from −20.2‰ to −19.5‰ and from 2.0‰ to 5.4‰ (Fig.1). The ranges of δ^{13}C and δ^{15}N values overlap considerably for adult bones of cave bears and moose. There are a few exceptions to this pattern: one tooth and one mandible of young individuals from Paina Cave with high δ^{15}N and low δ^{13}C values (Terlato et al., 2018) and one tibia from Buso doppio del Broion with high δ^{15}N and high δ^{13}C values. Three direct radiocarbon dates on well-preserved collagen were carried out and two of them yielded dates tightly clustered (Tab.1). The conventional age of the phalanx from Paina Cave is determined as 19,686±54 ^{14}C BP (23,948 to 23,489 cal BP. Sample ETH-79366: Terlato et al., 2018). The radiocarbon age of a humerus from Trene Cave is measured as 19,948±55 ^{14}C BP (24,220 to 23,795 cal BP. Sample ETH-79368: Terlato et al., 2018). At Buso doppio del Broion the rib gave a conventional age as 29,001±123 ^{14}C BP (33,597 to 32,844 cal BP. Sample ETH-79367).

4. DISCUSSION AND CONCLUSION

These dates on cave bear from Paina and Trene caves, around 24,200-23,500 cal BP, are more recent than others measured in Europe and make it the latest known representative of the species. With these dates there is no doubt that the disappearance of cave bear from Italy occurred during the LGM (Terlato et al., 2018), more or less coinciding with the expansion of south Alpine glaciers (Monegato et al., 2017). As the glacial expansions fragmented the ranges of many animal and plant species throughout Europe, the southern part of the Prealps might have preserved isolated and sheltered refugia for cave bears. Especially the Berici Hills represented a kind of refuge area for the plantigrade, with availability of trophic resources and shelters suitable to overcome harsh winter periods, relative to other zones in the Lessini Mountains or at higher altitude as in the Alps (Spötl et al., 2017). Isotopic data of these cave bears are similar to other cave bear populations, with low δ^{15}N values, in the range of herbivores (here *Alces alces*) and lower δ^{13}C values as ungulates, here again *Alces alces*. This indicates that cave bears from Berici Hills did not differ in their dietary habits from the pattern of the species in western and central Europe, an essential vegetarian diet (Bocherens et al., 2011; 2014; Münzel et al., 2011; Pacher et al., 2012). However, the δ^{13}C and δ^{15}N values do not show any obvious ecological change since 33,000 cal BP (radiocarbon data of rib from Buso doppio del Broion) despite climatic fluctuations, suggesting a strong niche conservatism for this species, leading to a possible lack of ecological flexibility in the LGM. There are a few exceptions to this pattern. Two specimens of young individuals from Paina Cave showed different δ^{13}C and δ^{15}N values, that may be related to hibernation or nursing signals (Terlato et al., 2018). Only one specimen from Buso doppio del Broion has high δ^{15}N and high δ^{13}C values which reveals a more omnivore diet of a cave bear, if it will be confirmed by DNA retrieving. The high δ^{13}C values of *Alces alces*, suggest a relatively open environment, but with clearings available (Drucker et al., 2010; Terlato et al., 2018). A final though on cave bear bones from Trene Cave and Buso doppio del Broion concerns human exploitation for meat and hides may have had an impact on the demise of this species. This could possibly reveal continuity in the hunting and subsistence strategies between hunter-gatherers group during a wide span of time, a situation that was probably not favourable to the survival of the species. We can speculate that the combination of climatic deterioration and increasing human pressure could be responsible to the extinction of cave bear in northern Italy, and the final extinction of the species since this population seems to have been the last to survive. This scenario is unfortunately very similar to the situation of numerous mammal species nowadays.

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Cave site	Layer	Element	CM	Isotope sample	Sample nr	Age (^{14}C ka BP)	2σ calibration (cal ka BP) IntCal13	1σ calibration (cal ka BP) IntCal13	Reference
Paina	5	I phalanx		CBV6	ETH-79366	19,686±54	23,948-23,489	23,830-23,600	Terlato et al., 2018
Trene	B1	humerus	X	CBV37	ETH-79368	19,948±55	24,108-23,900	24,220-23,795	Terlato et al., 2018
Buso doppio del Broion	1	Rib	X	CBV23	ETH-79367	29,001±123	33,597-32,844	33,440-33,036	

Table 1: radiocarbon dates of cave bear from Paina Cave, Trene Cave and Buso doppio del Broion calibrated

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Paper IV

- PAPER IV

Large-scale mitogenomic analysis of the phylogeography of the Late Pleistocene cave bear.

In this paper have been analysed 59 new complete mitochondrial DNA sequences from 14 sites in Western, Central and Eastern Europe. The bone specimens morphologically identified as cave bears were selected from Bärenloch (Switzerland), Perspektywiczna cave (Poland), Casamène and Prélétang (France), l'Arbreda (Spain), Hohle Fels (Germany), Broion, Paina and Trene (Italy) as well as Vrelsa, Kovačevića, Vasiljska, Smolućka, and Mirilovska cave (Serbia), covering temporally spaced sites from the Iberian Peninsula to the Balkans in a time range from >49 to 23 cal. ka before present. The phylogenetic analyses detected five major European lineages; consistent with the major haplogroups taxonomically designated as *Ursus ingressus* and *Ursus spelaeus* (including *U. s. eremus*, *U. s. ladinicus* and *U. s. spelaeus*). However, we presented the youngest cave bear DNA sequences thus far, which dates to 19,656 ^{14}C years before present (23,907-23,461 cal. yr. BP). The late cave bears came from Italy (Berici Hills) and belong to haplogroup of *Ursus ingress*. Our results demonstrated that using complete mitochondrial genomes covering spatially widespread sites, help to clarify the phylogeography, population dynamics and, the general extinction and local extirpation of the European cave bear.

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Abstract.

The cave bear (*Ursus spelaeus*) is one of the iconic Late Pleistocene megafauna species that faced extinction at the edge the last ice age. Although it is represented by the largest fossil records in Europe and has been subject to several interdisciplinary studies including palaeogenetic research, its fate remains highly controversial. Here, we used a combination of hybridisation capture and next generation sequencing to reconstruct 59 complete cave bear mitochondrial genomes from 14 sites in Western, Central and Eastern Europe. In a Bayesian phylogenetics analysis we compared them to 64 published cave bear sequences to reconstruct the population dynamics and phylogeography during the Late Pleistocene. We found five major mitochondrial DNA lineages resulting in a noticeably more complex biogeography of the European lineages during the last 50,000 years than previously assumed. Furthermore, our calculated effective female population sizes suggest a drastic cave bear population decline starting around 40,000 years ago at the onset of the Aurignacian, coinciding with the arrival of anatomically modern humans in Europe. Thus, our study supports a potential significant human role in the general extinction and local extirpation of the European cave bear and illuminates the fate of this iconic megafauna species.

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Introduction. Today in the Holocene epoch, the northern hemisphere is zoologically impoverished in large terrestrial species[1,2]. Astonishingly, this is a relatively recent phenomenon. During the Late Pleistocene, until around 50,000 years ago, the continents were still populated with a spectacular fauna consisting of some of the largest mammals that ever roamed the earth[2]. More than 150 genera of megafauna such as mammoths, woolly rhinoceros, and sabre-toothed cats inhabited the steppes of Eurasia and North America[1,2]. However, by 10,000 years ago, these ecosystems had lost between around 36% and 72% of their large-bodied mammalian genera respectively[3], and at least 97 genera in total[1]. This extinction wave affecting the largest members of the herbivorous guild had cascading consequences on terrestrial ecosystems with consequences still to be seen in modern ecosystems[4–6]. Understandably, the potential causes of these incisive extinctions have remained subject to highly controversial debates. The discussed explanations include prevalently anthropogenic contribution, climate and environmental changes or a combination of both[2,3]. However, with a growing body of data, the patterns and processes of these extinctions appear more complex. For example, whereas the proportion of dwindling megafauna species was greatest on continents that underwent the most dramatic climatic and environmental changes, the extinction events in North America and Australia rather coincided with the first arrival of anatomically modern humans[3]. The circumstances are apparently in contradiction with cross-taxa response to global climatic or anthropogenic factors, indicating a species-specific response to one or both factors. Furthermore, it was previously argued that the population development of different taxa is contingent on the geographic scale and the methodological approaches used[3]. For instance, while the woolly mammoth and cave lion experienced sudden losses of genetic diversity and subsequent stability long before their final extinction, it was shown that genetic diversity in bison and musk ox declined gradually though the course of Late Quaternary[3]. The latter pattern of *withering away* was also assumed for the iconic Pleistocene cave bear *Ursus spelaeus* sensu lato[7]. Considered as the Late Quaternary mammal that gave rise to the largest fossil record in Europe[8], the cave bear is a predestined model to study the causes of the extinction of a species, especially in the context of population dynamics, climate instability, and changing human impact. Descending from the Middle Pleistocene *Ursus deningeri*[9] as indicated by morphological and molecular studies[10], the Late Pleistocene cave bear established a vast distribution extending eastwards from Northwest Spain across Central Europe and the Urals to Arctic North-Eastern Siberia and the Altai Mountains[11,12]. Due to their high intra-specific morphological variability observed across the Eurasian cave sites, at least six morphotypes have been described mostly on the basis of morphological and metrical studies of teeth[13] and metapodials[14,15]. However, despite its substantial diversity and distribution, the cave bear became extinct at the beginning of the Last Glacial Maximum (LGM)[16–18]. The timing of its final extinction as well as the cause of the extinction, with climate change in the context of its herbivorous diet[19–22] or human hunting impact commonly regarded as potential factors[8], remain subject of controversial debates. Whereas comprehensive radiocarbon dating indicates that the extinction took place at the onset of the LGM around 28-26 ka years before present[16,17,18], a small number of fossils younger than 26,000 calibrated years BP[17,18] documents the survival of fragmented populations during the maximum extent of the ice sheets[24]. In fact, Stiller and colleagues[7] demonstrated based on population size reconstruction that 25,000 years of genetic decline preceded not only the cave bear extinction, but also the onset of the LGM. Since this circumstance eliminates a correlation between cave bear population decline and substantial climate change, human impact, either due to direct hunting[25] or resource competition[26–28] emerges as the major extinction cause, albeit, archaeological evidence remains sparse for now[25,29,30]. In this context, molecular analysis of ancient DNA (aDNA) from cave bear fossils has provided substantial insights into cave bear evolution and extinction, since it allows us to identify even subtle demographic developments invisible in the palaeontological record[31]. However, previous ancient DNA studies were based on relatively small sample sizes[32] or focused on geographically limited areas[33]. The majority of these studies was restricted to the mitochondrial D-loop sequence[34], a 285 base pair short fragment comprising only ~1.7% of the whole bear mitogenome. As demonstrated by previous studies[35,36], inferred genealogical reconstructions based on the D-loop region tend to contradict inferences based on the entire mitogenome. Thus, the current knowledge regarding cave bear population dynamics and phylogeography during the Late Pleistocene is substantially constrained. To overcome these limitations, here we analysed 59 new complete mitochondrial DNA sequences, representing populations from a Europe-wide transect. Moreover, we present the first mitochondrial genome of *Ursus spelaeus ladinicus* as well as the youngest cave bear DNA sequences thus far, which dates to 19,656 ^{14}C years before present (23,907-23,461 cal. yr. BP) and can help to illuminate the fate of the European cave bear.

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Results.

Sample Collection and processing. For ancient mtDNA extraction, 81 bone specimens morphologically identified as cave bears were selected from Bärenloch (Switzerland), Perspektywiczna cave (Poland), Casamène and Prélétang (France), l'Arbreda (Spain), Hohle Fels (Germany), Broion, Paina and Trene (Italy) as well as Vrelsa, Kovačevića, Vasiljska, Smolućka, and Mirilovska cave (Serbia), covering temporally spaced sites from the Iberian Peninsula to the Balkans in a time range from >49 to 23 cal. ka before present (Fig 1, Table 1). A short description of each site can be found in Supplementary Data S1. We then used double-stranded Illumina sequencing libraries in combination with in-solution bait-capture and high-throughput sequencing to generate mitochondrial sequences for 59 of the 81 specimens. For 19 samples it was not possible to recover sufficient amounts of aDNA to reliably infer the taxonomic position, while three individuals were subsequently identified as *Ursus arctos* during the phylogenetic analysis. The obtained mitochondrial genomes feature a coverage between 4.5 and 752.46-fold with 72%–100% of the mitochondrial genome covered (Table 1). All mitochondrial genomes had C to T damage patterns indicative of authentic aDNA. The number of samples for each site producing mitochondrial genomes is as follows: Bärenloch (n=7), Perspektywiczna Cave (n=7); Casamène (n=8), Prélétang (n=5), l'Arbreda (n=2), Hohle Fels (n=1), Broion (n=3), Paina (n=6), Trene (n=4), Vrelsa cave (n=7), Kovačevića cave (n=6), Vasiljska cave (n=1), Smolućka cave (n=1), and Mirilovska cave (n=1). Subsequently, we compared these sequences with 64 previously published complete mitochondrial genomes, resulting in an alignment of in total 123 specimens. On this final alignment, we performed Bayesian phylogenetic analysis as well as calculation of the effective female population size through time.

Phylogenetic analysis. Our Bayesian phylogenetic analyses detected five major European lineages, sharing a most recent common ancestor (MRCA) ~451 ka BP (~314-623 ka BP 95% CI) (Fig. 2). These lineages are consistent with the major haplogroups taxonomically designated as *Ursus ingressus* and *Ursus spelaeus* (including *U. s. eremus*, *U. s. ladinicus* and *U. s. spelaeus*). Whereas *U. s. eremus* appears to be distinct from both *U. s. spelaeus* and *U. s. ladinicus*, samples from Prélétang, Casamène, and Grotte d'Ours assigned to *U. s. ladinicus* form a paraphyly excluding *U. s. spelaeus*. Furthermore, we detected a noticeable subdivision of the *U. ingressus* clade that does not correspond to any previous classification based on morphological features. For the purpose of describing these novel groups, since there is no association with certain morphotypes or taxonomic designations, we divided the three lineages by their approximate distribution into a Western, Central and South-Eastern European group. These three groups shared a most recent common ancestor (MRCA) ~211 ka BP (~154-273 ka BP 95% CI), preceding the initial divergence of the *U. spelaeus* complex by roughly 73 ka (138 ka BP; 115-167 ka BP 95% CI). The most basal of these groups contains only five samples from two Western European sites, namely Casamène in France and Zoolithen cave in Germany, whereas the Central European and South-Eastern European group are well represented, comprising 33 samples from thirteen sites assigned to the Central European group and 23 samples from eight sites assigned to the South-Eastern European group.

Population size analysis. We calculated the changes in the effective female population sizes (N_e) of European cave bears during the Late Pleistocene and visualized them in Bayesian skyline plots (BSP)[32] (Fig.3). In general, our population size reconstruction resembles previously published calculations, featuring a stable population size through the last 150 to 50 ka. This is intriguing, since this period of time encompasses two cold periods (MIS 6 and MIS 4), as well as two warmer periods (MIS 5 and the onset of MIS 3). However, our extended plot illustrates that the known initial reduction in population size starting about 50 ka BP is followed by a more drastic decline beginning 15 ka later and persisting until the ultimate extinction of the cave bear in Europe approximately 19 ^{14}C ka BP (23 cal. ka BP) (Fig. 3).

Discussion

Phylogeography and population dynamics. Until now, the population dynamics of the European cave bear was mainly described by the westward migration of *U. ingressus* from South-Eastern Europe to the eastern Alps starting 60 ka BP[37]. Subsequently, *U. ingressus* cohabited since 50 ka BP with the Alpine forms of the *U. spelaeus* complex, *U. s. ladinicus* and *U. s. eremus*, ultimately replacing these older haplotypes[34] except in remote and/or high-altitude sites such as Bärenloch. Towards the onset of the LGM, the *U. ingressus* haplotypes retracted from their eastern habitats

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and advanced westwards, replacing the *U. s. spelaeus* haplotypes in the Ach valley at the eastern extension of the *U. s. spelaeus* distribution between 36 and 32 ka BP[8,34,38].

Our results challenge this assumption, considering that we were able to identify a deeply divergent branch clustering within the *U. ingressus* clade from Casamène, France. These specimens not only extend the *U. ingressus* distribution westwards across the Rhine river, but they also predate the presence of *U. ingressus* in Western Europe by nearly 15 ka[38]. Furthermore, the obtained mitochondrial genomes are only closely related to one other specimen from Zoolithen cave, Germany. Besides Herdengel, Austria, and the Ach valley caves in Southern Germany, Zoolithen cave represents a third site where both major haplogroups were genetically observed. However, Zoolithen cave is the only of these three cases where the *U. s. spelaeus* remains are consistently younger than the *U. ingressus* fossil previously molecularly dated to 37.7[34] or 49[33] ka BP. In Casamène, *U. ingressus* and *U. s. ladinicus* haplotypes coexisted at least ~4.5 ka between 39.5 and 43.9 ka ^{14}C BP, whereby *U. ingressus* inhabited the cave from 47.4 ka to 30.5 ^{14}C BP. Since a basal *U. ingressus* lineage continuously populated parts of the French Jura already for 15,000 years before the Ach valley haplogroup replacement, it appears unlikely that the expansion of *U. ingressus* occurred as a single, gradual westward migration. Instead, our results suggest that the original distribution of *U. ingressus* spanned much larger parts of Central Europe than previously assumed and that some relict populations persisted after the eastwards shift of their habitat.

Our analyses revealed new evidence for a second, eastward migration of *U. ingressus*. Noticeably, 16 out of 17 Serbian samples branch within the South-Eastern *U. ingressus* subclade. However, one specimen from Kovačevića clusters with samples that originate from the Ural Mountain region (Bolshoi Glukhoi, Medvezhiya and Serpievskaya caves) within in the Middle European *U. ingressus* subclade. This result may reflect, as previously suggested by Baca and colleagues[39], eastward migrations or gene flow between Central Europe and the Ural Mountains populations. So far, this hypothesis was only supported by the comparatively old samples from Niedźwiedzia cave, Poland, dating between 41.5 and 87 ka BP[39,40]. In comparison, no published date of *U. ingressus* remains from the Ural Mountain region is older than 47.6 ka BP so far. The Polish specimens share mitochondrial control region haplotypes closely related to the Ural Mountains ones, potentially indicating long-distance genetic exchange[40]. Forming an outgroup to all three Russian sequences, our sample from Vrelsa cave suggests that this migration or gene flow did not only comprise the East European Plain north of the Carpathian but also the southern Balkan Peninsula and that the distribution of this Central European haplogroup at the time of its highest diversity[34] extended further eastward at least until the early Middle Weichselian (Fig. 4), potentially representing a morphotype previously designated as *Ursus kanivetz kanivetz* by Baryshnikov and colleagues[41]. In contrast, specimens from Serbia belonging to the South-Eastern group all together yield radiocarbon dates ranging between 48.1 and 28.8 ^{14}C ka BP. The persisting presence of only the Southern-Eastern lineage and the lack of the Central European one may be associated with a subsequent replacement of the latter population at the Southern Balkan Peninsula. However, more mitochondrial genomes from South-Eastern Europe are needed to confirm this hypothesis.

Similarly, we investigated the phylogeography of the *U. spelaeus* complex. To infer the topology within the *U. spelaeus* clade, we generated sequences of *U. s. eremus* from Bärenloch as well as the first mitogenome of *U. s. ladinicus* from Casamène and Prélétang. Notably, it was not possible to phylogenetically classify the cave bears from Bärenloch using the mitochondrial control region-based approach. Whereas these reconstructions place the Bärenloch specimens within the *U. s. ladinicus* branch (Figure S1), the tree featuring complete mitochondrial genomes yields another topology. These findings confirm that phylogenetic relationships within branches of the mitochondrial control region tree should be interpreted with caution as discussed previously[36]. This observation could be explained by the impact of recurrent mutation that appears most acute in closely related control region haplotypes exhibiting a low level of evolutionary divergence[36]. Using complete mitochondrial genomes, *U. s. eremus* forms a distinct outgroup to all the other *U. spelaeus* sequences. Regarding *U. s. ladinicus*, our analysis demonstrated that this group previously described as monophyletic[37] forms a paraphyletic clade branching of basally to the *U. s. spelaeus* clade, and comprising haplotypes from Casamène, Prélétang, and the Grotte d'Ours. Thus, the morphotype described as *U. s. ladinicus* does not represent a genetically distinct unit (based on the mtDNA), but rather a transitional form between the MRCA shared with *U. s. eremus* and the typical *U. s. spelaeus*. However, without knowledge of the nuclear genome, it is not

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possible to exclude gene flow as a potential reason for shared haplotypes. In general, the basal position of these specimens as well as of *U. s. spelaeus* samples from Zoolithen cave, Germany, within the *U. spelaeus* haplogroup may indicate an eastern French or north-western alpine origin of the *ladinicus/spelaeus* (sensu stricto) haplogroup complex.

Extinction. As demonstrated by Stiller and colleagues[7], the start of the cave bear population decline preceded its final extinction by approximately 25 ka. A slow and continuous decline may be correlated with changing environmental conditions. Yet, climate and associated vegetation change as main factors appear improbable, albeit their strictly herbivorous feeding preferences remained unchanged during the Late Pleistocene[8,18,42], since cave bears were well adapted to continental climate as indicated by their appearance beyond the Arctic Circle. This is also congruent with our estimations of the cave bear population size development through the last 150 to 50 ka, exhibiting a relatively stable population size even during the two cold periods MIS 6 and MIS 4. Therefore, it appears unlikely that these previous climatic fluctuations did substantially affect the cave bear population in Europe. Furthermore, as emphasized by Stiller and colleagues[7], the cooling climate of the beginning LGM did not start before 30 ka BP, nearly 20 ka after the beginning of the cave bear population decline, suggesting instead a major impact of human activities related to the expansion of modern humans in Europe that took place at the same time[43–45]. As documented in the present study, the cave bear demise did not proceed slowly. Although the initial decline in population size started shortly before 50 ka BP during the end of the Mousterian associated with Neanderthals, the more drastic downturn of the European cave bear took place at around 35 to 40 ka BP at the onset of the Aurignacian and the arrival of anatomically modern humans in Europe[46]. As demonstrated by Fortes and colleagues[33], cave bears supposedly exhibited a homing behaviour indicated by the strong association between mitochondrial haplotype and cave. Such high dependence of cave bears on their birth caves may have created severe competition with Neanderthals but especially with anatomically modern humans. This was due not only to growing human density and group sizes but also increased human residence times[7,28,29] as well as making the cave bears more at risk for direct hunting by both hominins[25,29,47]. The negative human effect on cave bear populations would have been increased at the onset of the LGM by the cooling climate and subsequently lower vegetation productivity, fragmenting the population into various subpopulations inhabiting small refugial habitats[8] with suitable, stable microclimates as suggested by Baca and colleagues[17]. For many late Pleistocene megafauna species, such changes in habitat range and population size are intrinsically linked over evolutionary time[3]. Until the end of the maximum extent of the Scandinavian Ice sheet, only a few populations survived across Central and Eastern Europe[16,17]. Consequently, the *U. ingressus* specimens from Stajnia cave and the Venetian Pre-Alps (Paina and Trene) dating to 25,648–24,807 and 26,360–25,905 cal. yr. BP[17] respectively between 23,907–23,461 and 24,234–23,839 cal. yr. BP[18] represent the isolated and genetically impoverished relict of the much larger and more diverse cave bear population in Europe.

Thus, our study highlights the potential role of human activity in the general extinction and local extirpation of the European cave bear. Furthermore, we have shown that our current knowledge of cave bear phylogeography is biased by the employed methodology and the small and/or sparse number of sampled specimens. Using complete mitochondrial genomes covering spatially widespread sites can mitigate these problems, allowing such studies to gain deeper insight into the population dynamics of Late Pleistocene megafauna species such as the cave bear. Even if these insights are restricted to the maternal lineage and limited by the available number and length of DNA sequences, the conclusions already provide a more detailed understanding of cave bear population dynamics than previously reported before. In the future, new high quality AMS radiocarbon dates of more extensive geographic coverage and in particular nuclear DNA data, combined with high-resolution palaeoecological data for each population and individual studied, will shed light on the evolution and extinction of cave bears.

Material and methods

Sample collection. We selected 81 assumed cave bear specimens to be included in this study, featuring geographic regions that have been underrepresented in previous genetic work. We then generated 59 complete mitochondrial genome sequences using the approach described below. In addition, we obtained direct Accelerator Mass Spectrometry (AMS) radiocarbon dates on bone collagen for 37 (XX) samples for which no ^{14}C age was available so far.

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DNA extraction. To minimize environmental contamination, bone samples were exposed to UV-light at least 30 minutes from all sides. Afterwards, 30–54.9 mg bone powder was removed from the inside of a long bone of each specimen using a dentistry drill. Afterwards, ancient DNA was extracted according to the method described by Dabney and colleagues[10]. DNA extracts were converted into double-indexed Illumina libraries using the approaches described elsewhere[48,49]. All extractions and pre-amplification steps of the library preparation were performed in a designated ancient DNA clean room facility. Indexed libraries were amplified in 100 µl reactions with AccuPrime Pfx and Herculase II Fusion followed by purification. Target enrichment of mitochondrial DNA was performed by in-solution capture of the pooled libraries using baits generated from modern polar bear (*Ursus maritimus*) mitochondrial DNA as described by Furtwängler and colleagues[50]. Finally, the enriched libraries were multiplex sequenced on an Illumina HiSeq 4000 using 75+8+8 cycles at the Max Planck Institute for Science of Human History, Jena, Germany.

Sequence Processing. De-indexing was performed by sorting all sequences corresponding to their p7 and p5 index combinations. Next, read processing, including adaptor trimming, quality filtering and duplicate removal, was performed using the software EAGER. Mapping of single-end reads to a reference cave bear mitochondrial genome (NC_011112.1) using CircularMapper and generating 3-fold consensus sequences was also conducted using EAGER[51].

Data from other studies. We included in our study complete mitochondrial genome sequences of 66 European and Asian cave bears previously published.

Alignment and model selection. Multiple Sequence Alignment was conducted in MAFFT 7.310[44]. Model selection was performed using ModelFinder by Kalyaanamoorthy and colleagues, integrated in IQ-Tree 1.5.5[45].

Inferring phylogenetic relationships. Phylogenies were constructed from a total of 16,360 positions using MEGA 7.1.014[46] and IQ-Tree 1.5.5 including ultrafast bootstrap (UFBoot). Maximum-likelihood topologies were generated for all positions for which coverage was at least three-fold in each of the reconstructed sequences. Alignment columns with gaps or missing data were included. Bootstrap support values were obtained over 1000 replicate data sets, using the American black bear (*Ursus americanus*, JX196366.1) as an outgroup. The phylogenetic trees were edited in FigTree version 1.4.3 (http://tree.bio.ed.ac.uk/software/figtree).

Comparison of D-Loop and Mitogenome Tree Topology Differences. To identify D-Loop coordinates within our reconstructed mitochondrial sequences, these were aligned to D-Loop sequences of *Ursus spelaeus* previously published by Stiller and colleagues[28] using MEGA 7.1.0 and sequences outside of the aligned regions were discarded. Calculated maximum-likelihood topologies were then compared using the tanglegram function integrated in Dendroscope 3.5.9 by Huson and Scornavacca (http://dendroscope.org)47.

Bayesian phylogenetic inference and demographic reconstruction. Dated Bayesian phylogeny and demographic reconstructions were obtained using BEAST 1.8.4 (Drummond et al. 2012). The alignment, including 59 new mitogenomes and 64 previously published mitogenomes (five previously published mitogenomes were excluded from the Bayesian analysis as they fell outside the phylogenetic variation of the studied samples), 16,360 nt long, was partitioned using PartitionFinder 2.1.1 (Lanfear et al. 2016) using six input data blocks (noncoding, tRNA, rRNA, and codon position 1, 2 and 3 of the protein coding genes), greedy search scheme and BIC model selection. The selected five partitions (tRNA and rRNA were combined into one partition by PartitionFinder) were included in BEAST analysis. We used tipdating to calibrate the relaxed molecular clock (uncorrelated, lognormal, separate clock for each partition). For radiocarbon and stratigraphy-based dated samples we used midpoint ages as point tipdates. For samples, for which age estimates have been previously estimated using molecular dating and published, we used their ages as distributions rather than points in the analysis with normal priors (the estimated molecular age as the mean and 10% of the molecular age estimate standard deviation). Undated samples were assigned uniform age priors between 20,000 and 120,000 years old. Bayesian skyline population model was used. Markov Chain was run under for 200 million steps with sampling every 20,000th step. Mixing and convergence was inspected using Tracer 1.7.1 (Rambaut et al. 2018)

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To test the influence of age uncertainty introduced with the undated samples on the timescale estimates we additionally rerun the analysis with the same settings but including only the ^{14}C dated samples (direct and stratigraphy-related datings). The *U. ingressus*/*U. spelaeus* split was dated to 322 ka (201 – 476 ka 95% HPD). Although somewhat younger than the age estimated using the full dataset, which is most likely influenced by the removing half of the sequences, it supports an old split time estimate. Therefore, our full dataset estimate is not a product of age uncertainty introduced to the analysis by the undated or molecularly dated samples.

ID	Site	Mean Cov.	3X Cov. in %	Classification	^{14}C	Cal. ^{14}C
TU1	Bärenloch	142.4	98.98	eremus	28,415±605 r	32,310–33,579
TU2	Bärenloch	275.6	99.3	eremus	NA	
TU3	Bärenloch	245.7	99.27	eremus	>40,000 r	
TU5	Bärenloch	19.7	92.21	eremus	26,745±490 r	30,880-31,858
TU6	Bärenloch	32.4	95.59	eremus	NA	
TU7	Bärenloch	130.2	98.61	eremus	NA	
TU8	Bärenloch	260.3	99.08	eremus	NA	
TU76	Casamène	19.2	97.59	ladinicus	NA	
TU77	Casamène	79.8	100	ingressus WE	47406 r	
TU78	Casamène	10.8	89.23	ladinicus	NA	
JK3204	Casamène	100.2	99.33	ladinicus	39456 r	
JK3206	Casamène	38.1	99.35	Ladinicus	43890 r	
JK3212	Casamène	51.2	99.82	ingressus WE	38153 r	
JK3215	Casamène	49.5	99.26	ingressus WE	30518 r	
JK3216	Casamène	80.7	99.86	ingressus WE	41366 r	
JK1726	Hohle Fels	16.9	97.19	spelaeus	NA	
TU151	Vrelsa Cave	97.9	99.36	ingressus SE	40470 r	

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TU152	Kovačevića	75.4	97.79	ingressus SE	48116 r
TU153	Vrelsa	16.9	90.49	ingressus ME	40595 r
TU154	Vrelsa	22.4	92.6	ingressus SE	45918 r
TU155	Kovačevića	125.2	98.44	ingressus SE	45673 r
TU156	Vrelsa	16.2	94.37	ingressus SE	42687 r
TU157	Vrelsa	363.5	99.68	ingressus SE	38330 r
TU158	Kovačevića	5.1	72.19	ingressus SE	NA
TU163	Vrelsa	44.7	97.76	ingressus SE	44748 r
TU166	Kovačevića	80.2	97.65	ingressus SE	46429 r
TU167	Vrelsa Cave	9.1	87.84	ingressus SE	43641 r
TU168	Kovačevića	79.1	98.58	ingressus SE	46376 r
TU169	Kovačevića	7.3	83.21	ingressus SE	40848 r
TU170	Kovačevića	278.9	98.85	ingressus SE	45449 r
TU172	Vasiljska	10.2	89.19	ingressus SE	43027 r
TU173	Smolućka	6.7	72.59	ingressus SE	30649 r
TU174	Mirilovska	32.7	98.68	ingressus SE	28807 r
TU511	l'Arbreda	5	84.99	spelaeus	NA
TU512	l'Arbreda	7.5	98.02	spelaeus	NA
TU779	Prélétang	240.7	99.58	ladinicus	>49788 r
TU781	Prélétang	59	99.33	spelaeus	42400 r
TU782	Prélétang	133.7	99.45	spelaeus	40423 r

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TU783	Prélétang	184.8	99.46	spelaeus	38742 r	
TU784	Prélétang	324.5	99.59	ladinicus	>40000	
TU841	Paina	4.5	73.2	ingressus ME	20015 r	24,275-23,880
TU842	Paina	17	97.34	ingressus ME	NA	
TU843	Paina	25.8	98.77	ingressus ME	19914 r	24.167-23.764
TU844	Paina	6.5	87.18	ingressus ME	19975 r	24,234-23,839
TU847	Paina	17.7	98.22	ingressus ME	NA	
TU848	Broion	121.5	99.67	ingressus ME	29001 r	33,597-32,844
TU851	Broion	9.2	93.68	ingressus ME	NA	
TU852	Broion	6.2	84.06	ingressus ME	25978 r	30.630-29,855
TU853	Trene	4.9	75.44	ingressus ME	25290 r	29,599-29,079
TU854	Trene	27	98.64	ingressus ME	24755 r	28,977-28,566
TU855	Trene	27.7	98.81	ingressus ME	19656 r	23,907-23,461
TU857	Trene	73	99.14	ingressus ME	NA	
TU860	Perspektywiczna	39.2	99.44	ingressus ME	NA	
TU861	Perspektywiczna	752.5	99.74	ingressus SE	40200±1200 r	42,976-45,018
TU863	Perspektywiczna	319.5	99.73	ingressus SE	41600±1400 r	43,797-46,672
TU865	Perspektywiczna	219.2	99.72	ingressus ME	NA	
TU866	Perspektywiczna	114.4	99.64	ingressus SE	NA	
TU867	Perspektywiczna	551.7	99.74	ingressus SE	NA	

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| **TU868** | Perspektywiczna | 101.4 | 99.64 | ingressus ME | NA |

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Paper IV

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Author Contributions

V.S. and H.B. conceived and designed the research. M.S., H.B., J.K., M.P., M.R., N.J.C., and G.T. provided samples and palaeontological context. J.G., E.R., S.P., and C.U. performed sampling, DNA extraction and library preparation of sequencing libraries. J.G., J.N., and M.M. performed aDNA bioinformatic and population genetic analysis. J.G., M.M., H.B., and V.J.S. wrote the manuscript with input from all authors. All authors reviewed the manuscript.

5. CONCLUSIONS

Conclusions

Cave bears have a long history of contact with humans, mainly because of our shared preference for habitat types and shelters. These characteristics led humans and bears to live together in many parts of Europe for thousands of years. During the last 20 years, more evidence of human exploitation - either Neanderthals and modern humans - of cave bears were documented in almost all regions. Although the genetic decline of cave bear started shortly before 50 ka BP during the end of the Mousterian, the more drastic downturn of the European cave bear took place at around 35 to 40 ka BP in coincidence with the spread of anatomically modern humans in Europe (Higham et al., 2014). It seems likely that Palaeolithic hunters played a role in the extirpation of cave bears.

Thus, the vast majority of cave bears certainly died by natural causes, but careful taphonomical inspections in the course of this study have provided evidence of hunting by butchering marks.

In northeastern Italy the exploitation of cave bear starts with Neanderthals, during 49-42 cal. ka BP. This was determined at Rio Secco cave and Fumane cave, which can be considered rare cases of remain accumulations generated by the human predation of bears (mostly cave bear) of varied age classes during or near the end of hibernation. All this evidence suggests that Neanderthals were exploiting bears as a resource at both sites; however, the sites were slightly different in terms of the ways and the rhythms of bear exploitation. At Rio Secco cave, Neanderthals targeted this resource by moving across lands devoid of lithics, in contrast to Fumane cave, which was situated in a context proximal to widely available, productive resources of knappable chert; as a game, bears were secondary to ungulates.

Human modification such as cut-marks on several skeletal elements of cave bear from Trene cave and Buso doppio del Brion, reveals a continuity in the hunting and subsistence strategies during a wide span of time. A situation that was probably not favorable to the survival of the species.

The radiocarbon dates obtained on cave bear from Berici Hills ranging from 33 cal. ka BP (Buso doppio del Broion) to 23 cal. ka BP (Trene and Paina), represent the most recent ones known from Europe. With these dates there is no doubt that the disappearance of cave bear from Italy occurred during the LGM (Last Glacial Maximum). The late cave bears from these sites belonged to the haplogroup of *Ursus ingressus* and represent the isolated and genetically impoverished relict of the much larger and more diverse cave bear population in Europe. As the cooling climate of LGM fragmented the ranges of many animals and plants as suggested throughout Europe, the southern part of the Prealps have preserved small refugial habitats with suitable, stable

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microclimates and sheltered refugia for cave bears. The area of Berici Hills was gifted with two major characteristics of Pleistocene refugia, availability of trophic resources and shelters suitable to overcome harsh winter. The orientation of the caves (S, S-E), located generally on steep slopes, provided a protected niche fundamental to the microclimatic conditions in the critical phases of hibernation and weaning.

However, this study demonstrates that cave bears from northeastern Italy are not outliers in terms of isotopic composition, suggesting that they had similar diets as earlier ones, an essentially vegetarian diet. The δ^{13}C and δ^{15}N values do not show any obvious ecological change since 33 cal. ka BP despite climatic fluctuations, suggesting a strong niche conservatism for this species, leading to a possible lack of ecological flexibility in the LGM.

The cave bears probably became extinct because of a combination of factors: climatic deterioration and increasing human pressure. In fact, it is not to exclude that deliberate hunting by humans might have caused the extirpation of the last residual cave bear populations, which were already severely stressed by the intense climate changes of the time.

Thus, this dissertation is the "another brick in the wall" of our knowledge on the cave bear extinction.

6. FUTURE WORK

- The cave bear bones analyzed show important modification by humans through the time, but in a discussion of increasing human impact on cave bear population further archaeozoological and taphonomic investigation are required.

- To reinforce the behavioural ecology of late cave bears, further research combining specific isotope analyses (amino acid), tooth microwear and, morphometric studies should be developed.

- To shed light on the evolution and population dynamics of the cave bear, combined nuclear DNA data with palaeoecological data should be useful.

  o Increase samples of cave bear from different archaeological contexts with human presence from Middle Palaeolithic to Upper Palaeolithic.
  o Collect isotopic and palaeogenetic data of cave bears from southern Europe or from contexts of central region of Italy.

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SCIENTIFIC DISSEMINETION

A small part of this project was dedicated to dissemination and promotion of research results to make known to wider public the scientific activities. For this reason, I took care of the realization of the temporary exhibition entitled "Bears and Humans: a Prehistory of Berici Hills" at Natural History and Archaeological Museum of Vicenza. The exhibition is part of a project supported by Museums of Vicenza, University of Ferrara and Bologna. Below the poster of exhibition.

L'INCONTRO. Sabato alle 17 al Museo naturalistico a S.Corona il prof.Mezzalira sull'iconografia

L'ERA GLACIALE
E L'ULTIMO ORSO

Nicola Nannini
Gabriele Terlato*

Per un archeozoologo che si occupa di Paleolitico, l'opportunità di studiare resti animali conservati per migliaia e migliaia di anni nelle grotte e nei ripari dei Colli Berici significa poter ricostruire una serie di "fotografie" di ambienti e di habitat popolati da animali oggi scomparsi in queste zone e le strategie di sussistenza attuate dai gruppi di cacciatori neandertaliani e sapiens per la loro sopravvivenza.

Da singole ossa, anche di pochi centimetri, è possibile determinare la specie, il sesso dell'animale, mentre attraverso analisi al microscopio di sezioni sottili dei denti si può conoscere l'età di morte e la stagione di abbattimento.

Un insieme di ossa analizzate permette dunque di ricostruire quadri delle popolazioni animali e degli ecosistemi in determinati momenti storici anche a distanza di migliaia di anni e, nel nostro caso, ci permette di delineare l'aspetto dei Colli Berici nella preistoria. Attraverso la collezione dei vari reperti ossei, l'archeozoologo riesce a determinare se l'animale sia stato trasportato nell'insediamento intero oppure se sia stato introdotto a "pezzi" dopo essere stato macellato e sporzionato sul luogo di abbattimento.

Di fondamentale importanza è verificare se e quale preda sia stata utilizzata interamente ed esclusivamente a fini alimentari oppure se da essa siano stati ricavati pellame, corna, palco, denti e porzioni ossee particolari per la produzione di strumenti. A questi quesiti risponde la tafonomia, una disciplina utile alla ricostruzione delle tecniche e delle modalità di macellazione utilizzate, che analizza lo stato di frammentazione delle ossa e delle tracce involontariamente lasciate sulle loro superfici da attrezzi in pietra scheggiata.

Enormi cervidi come il megacero (una specie di cervo gigante con palchi palmati larghi anche più di 3 metri oggi estinto) e alci (oggi presenti in regioni fredde dell'Asia, Europa e America) potevano pascolare sfruttando le zone umide ai piedi dei Colli, da dove con tutta probabilità provenivano i numerosi resti di pesce, ossa di castoro e resti di uccelli di ambiente acquatico ritrovati nei siti archeologici. Insieme ai "giganti" megacero e alce, di oltre 500 kg, erano molto diffusi i cugini più piccoli come cervo e capriolo sempre presenti nel record archeologico a partire dal Paleolitico medio.

Altre ossa di "pesi massimi" come il bisonte e l'uro (l'antenato dell'odierno bue), pascolatori nella pianura sottostante, sono state identificate grazie alla possibilità di confrontare i reperti archeologici con le collezioni osteologiche presenti nei laboratori universitari dove lavorano insieme archeozoologi e paleontologi. Gli ambienti rocciosi e dirupati, caratteristici di certi versanti dei Colli Berici offrivano invece rifugio e habitat ideali a camosci e stambecchi, nonché a una grande quantità di uccelli come rondoni, gracchi, corvi e aquile reali.

In questi ambienti molto diversificati trovava posto anche una grande ricchezza di animali carnivori come gatti selvatici, mustelidi, volpi, lupi e leoni delle caverne, oggi estinti, ben raffigurati a grotta Chauvet nell'Ardèche in Francia e a Riparo Tagliente a Grezzana (Verona) in Valpantena.

Tuttavia la specie animale che più trovava nei Colli Berici preistorici un habitat per sé congeniale era l'orso delle caverne o Ursus spelaeus, oggi estinto.

Grazie a recenti studi paleogenetici, è emerso che le popolazioni di orso delle caverne hanno subìto un grave calo numerico circa 50.000 anni fa, quando l'uomo anatomicamente moderno (Homo sapiens) cominciava a sostituire i Neandertal in Europa. In numerose regioni europee a nord delle Alpi l'estinzione definitiva di questo animale è avvenuta molto prima dell'ultima grande glaciazione (28-20.000 anni fa).

Ma quando e perché è avvenuta esattamente l'estinzione dell'orso delle caverne?

Le risposte più sorprendenti provengono da recentissi-

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mi studi delle ossa di orso provenienti dalle grotte di Paina (Comune di Mossano) e di Trene (Comune di Nanto). A questa ricerca hanno collaborato ricercatori dell'Università di Ferrara, Tubingen (Germania) e Western University (Canada).

Le ossa analizzate con il metodo del radiocarbonio hanno restituito una datazione di 23.500 anni fa, in piena Era Glaciale: ciò vuol dire che gli ultimi esemplari europei di orso delle caverne hanno trovato l'ultima area rifugio proprio in Italia, nelle grotte del territorio vicentino.

La mancanza di adattabilità ai nuovi assetti ambientali glaciali e le pressioni della caccia da parte degli uomini potrebbero aver aumentato lo stress sugli orsi delle caverne – così da non permettere la loro sopravvivenza a un clima più rigido e con minori risorse alimentari disponibili. Dunque, la combinazione di fattori climatici e antropogenici ha portato alla loro estinzione.

Università di Ferrara

Sui Berici forse le ultime tracce dei plantigradi rifugiatisi nelle caverne durante la glaciazione. Così gli archeozoologi analizzano le ossa

Continuano gli incontri legati alla mostra "Orsi e uomini. Una preistoria dei Colli Berici" allestita al Museo Naturalistico Archeologico di Vicenza, contrà S.Corona, aperta fino a giugno 2019. Dopo il racconto in ottobre delle ultime ricerche preistoriche nei Colli Berici, sabato 17 novembre alle 17 si tiene una nuova conversazione dal titolo "Immagini dell'orso dai graffiti rupestri ai trattati zoologici", ingresso libero. Interverrà Francesco Mezzalira, docente di scienze al liceo Brocchi di Bassano e socio dell'Associazione nazionale di insegnanti di Scienze naturali. Qui sotto pubblichiamo un contributo di due studiosi dell'università di Ferrara su come gli archeozoologi leggono i resti degli animali preistorici.

Una delle ossa esaminate

Cranio di orso delle caverne ritrovato a Grotta del Buso Doppio del Broion

LIST OF PUBLICATIONS OUT OF THIS RESEARCH

1. **Terlato G.,** Livraghi A., Romandini M., Peresani M. (Resubmitted after review). Large bovids on Neanderthal menu: exploitation of *Bison priscus* and *Bos primigenius* in northern Italy. *Journal of Archaeological Science*: *Reports*.

2. Maini E., **Terlato G.** (2018). Analisi Archeozoologica e Tafonomica preliminare di un campione faunistico dal sito di Ponticelli di Malalbergo, in: Gabusi R., Miari M., Trocchi T., (a cura di), Ponticelli di Malalbergo. Un abitato del II millennio a.C. e le successive trasformazioni del territorio. Collana Documenti ed evidenze di Archeologia 11, ISBN 978-88-7849-134-2.

3. Romandini M., Thun Hohenstein U., Fiore I., Tagliacozzo A., Perez A., Lubrano V., **Terlato G.,** Peresani M. (2018). Late Neandertals and the exploitation of small mammals in Northern Italy: fortuity, necessity or hunting variability? *Quaternarie* 29, 61-67.

4. Gonzato F., Peresani M., Montanaro C., Imhoff I., **Terlato G.** (2017). Telling by images: The first cinema of history ("focus" on the Palaeolithic). *Annali dell'Università degli Studi di Ferrara Museologia Scientifica e Naturalistica* 13, 37-39. doi:10.15160/1824-2707/1518.

5. Peresani M., Duches R., Romandini M., Aleo A., Bussola B., Camilloni N., Delpiano D., Forte M., Gennai J., Gubbiotti A., Lopez García J.M., Nannini N., **Terlato G.** (2017). Neandertal e Sapiens, contatti ravvicinati nella Grotta di Fumane. *Archeologia Viva*, n. 184, luglio-agosto 2017, pp. 46-59.

6. **Terlato G**., Romandini M., Peresani M. (2016). Bovines, food resource and prey during Middle and Upper Palaeolithic in North-East Italy. The case studies of Fumane Cave and San Bernardino cave. *The Horse and the Bull in Prehistory and History,* Cordero Editore, Genova, pp. 33-48.

7. Romandini M., de Missier F., Cescutti G., Aviani C., dal Bello V., **Terlato G.,** Scaramucci S., Léone A., Zunnui E., Carrera L., Peresani M. (2015). Experience of Archaeological didactics and Museal Interaction on the Paleolithic of the Pradis Plateau (Italy, Pn). Annali on-line della Didattica e della Formazione docente – *Musei e Didattica*, v.10, pp. 64-72. ISSN 2038-1034.

8. Peresani M., Romandini M., **Terlato G.** (2014). I primi occupanti delle Prealpi Carniche, l'Archeologia del Paleolitico svela le tracce degli ultimi Neandertal nelle Grotte di Pradis. *Atti e Memorie della Commissione Grotte "E. Boegan"* vol. 45, pp. 39-46.

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