

EXTINCTION AND PALEOECOLOGY OF THE LATE PLEISTOCENE CAVE BEAR FROM NORTHEASTERN ITALY: RADIOCARBON AND STABLE ISOTOPE EVIDENCE

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ABSTRACT: We present here the chronometric, isotopic and taphonomic evidence of cave bear from three Palaeolithic sites in north-eastern Italy: Paina, Trene and Buso doppio del Broion (Berici Hills - Vicenza). Two direct radiocarbon dates yielded an age around 24 ka BP, which make these remains the latest known representatives of the species in Europe and confirmed that demise of cave bear falls during the LGM. The carbon and nitrogen isotopic values of bone collagen do not show any marked ecological change since 33 ka BP, suggesting an essential vegetarian diet. Several bear bones preserved traces of human modification such as cut marks, which enables a reconstruction of the main steps of butchering process.

KEYWORDS: Cave bear, extinction, palaeoecology, cave bear hunting, northeast Italy

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, $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ 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 1 and 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

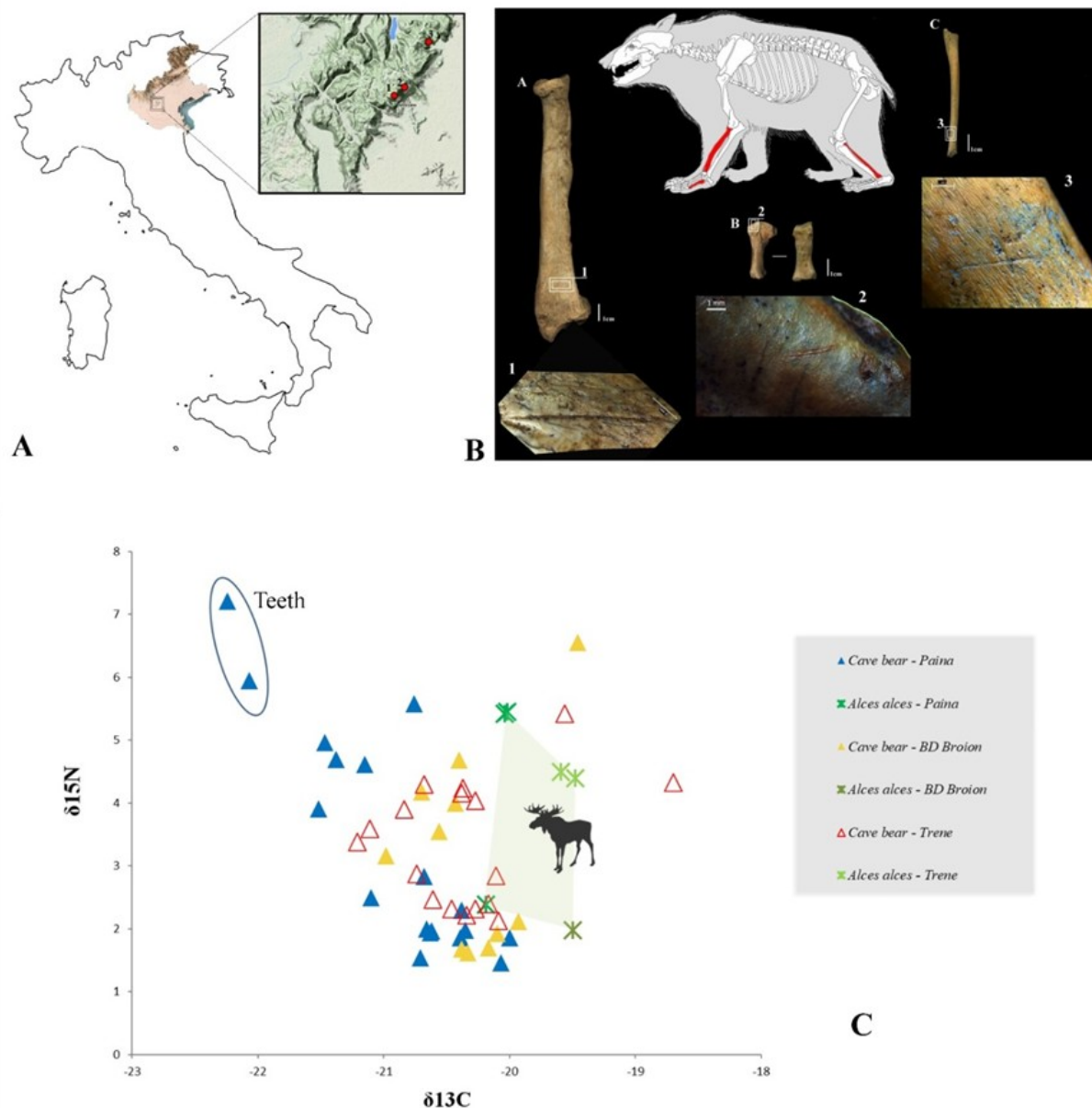


Fig. 1 - (A) Position of the palaeolithic caves in the Berici Hills considered in this work; (B) localization and details of anthropic traces; (C) $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values of cave bear and moose.

bones were selected. In addition, 6 moose *Alces alces* bones from the same sites and units were sampled. The $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ 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). Colla-

gen 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 $\delta^{13}\text{C}$ were calibrated to VPDB and values of $\delta^{15}\text{N}$ were calibrated to AIR. Measurement error was ± 0.1 ‰ for $\delta^{13}\text{C}$, and ± 0.2 ‰ for $\delta^{15}\text{N}$.

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 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 $\delta^{13}\text{C}$ 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 $\delta^{15}\text{N}$ 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 $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values measured for *Alces alces* ranged from -20.2‰ to -19.5‰ and from 2.0‰ to 5.4‰ (Fig.1). The ranges of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ 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 $\delta^{15}\text{N}$ and low $\delta^{13}\text{C}$ values (Terlato et al., 2018) and one tibia from Buso doppio del Broion with high $\delta^{15}\text{N}$ and high $\delta^{13}\text{C}$ 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 $\delta^{15}\text{N}$ values, in the range of herbivores (here *Alces alces*) and lower $\delta^{13}\text{C}$ 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 $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ 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 $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values, that may be related to hibernation or nursing signals (Terlato et al., 2018). Only one specimen from Buso doppio del Broion has high $\delta^{15}\text{N}$ and high $\delta^{13}\text{C}$ values which reveals a more omnivore diet of a cave bear, if it will be confirmed by DNA retrieving. The high $\delta^{13}\text{C}$ values of *Alces alces*, suggest a relatively open environment, but with clearings available (Drucker et al., 2010; Terlato et al., 2018). A final thought 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

Cave site	Layer	Element	CM	Isotope sample	Sample nr	Age (^{14}C ka BP)	2 σ calibration (cal ka BP) IntCal13	1 σ 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	

Tab. 1 - Radiocarbon dates of cave bear from Paina Cave, Trene Cave and Buso doppio del Broion calibrated.

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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REFERENCES

- Adams B. (2002) - New radiocarbon dates from Szeleta and Istállóskó Caves, Hungary. *Praehistoria*, 3, 53-55.
- Baca M., Popović D., Stefaniak K., Marciszak A., Urbanowski M., Nadachowski A., Mackiewicz P. (2016) - Retreat and extinction of the Late Pleistocene cave bear (*Ursus spelaeus sensu lato*). *The Science of Nature*, 103 (92).
- Barnosky A.D., Koch P.L., Feranec R.S., Wing S.L., Shabel A.B. (2004) - Assessing the causes of late Pleistocene extinctions on the continents. *Science*, 306, 70-75.
- Blant M., Bocherens H., Bochud M., Braillard L., Constantdache M., Jutzet J.M. (2010) - Le gisement à faune würmienne du Bärenloch: Préalpes fribourgeoises, Suisse. *Bulletin de la Société Fribourgeoise des Sciences Naturelles*, 99, 149-170.
- Bocherens H., Billiou D., Patou-Mathis M., Bonjean D., Otte M., Mariotti A. (1997) - Paleobiological implications of the isotopic signatures (^{13}C , ^{15}N) of fossil mammal collagen in Scladina Cave (Sclayn, Belgium). *Quaternary Research*, 48, 370-380.
- Bocherens H., Drucker D.G., Billiou D., Geneste J.M., van der Plicht J. (2006) - Bears and humans in Chauvet Cave (Vallon-Pont-d'Arc, Ardèche, France): insights from stable isotopes and radiocarbon dating of bone collagen. *Journal of Human Evolution*, 50, 370-376.
- Bocherens H., Stiller M., Hobson K.A., Pacher M., Rabeder G., Burns J.A., Tütken T., Hofreiter M. (2011) - Niche partitioning between two sympatric genetically distinct cave bears (*Ursus spelaeus* and *Ursus ingressus*) and brown bear (*Ursus arctos*) from Austria: isotopic evidence from fossil bones. *Quaternary International*, 245, 238-248.
- Bocherens H., Bridault A., Drucker D.G., Hofreiter M., Münzel S.C., Stiller M., van der Plicht J. (2014) - The last of its kind? Radiocarbon, ancient DNA and stable isotope evidence from a late cave bear (*Ursus spelaeus* ROSENMÜLLER, 1794) from Rochedane (France). *Quaternary International*, 339-340, 179-188.
- Drucker D.G., Hobson K.A., Ouellet J.P., Courtois R. (2010) - Influence of forage preferences and habitat use on ^{13}C and ^{15}N abundance in wild caribou (*Rangifer tarandus caribou*) and moose (*Alces alces*) from Canada. *Isotopes in Environmental and Health Studies*, 46, 107-121.
- Grandal-d'Anglade A., Pérez-Rama M., Fernández-Mosquera D. (2011) - Diet, physiology and environment of the cave bear: a biogeochemical study. In: Toskan B. (ed.), *Fragments of Ice Age environments. Proceedings in Honour of Ivan Turk's Jubilee 21. Ljubljana, Slovenia: Opera Instituti Archaeologici*, 111-125.
- van Heteren A.H., MacLarnon A., Rae T.C., Soligo C. (2009) - Cave bears and their closest living relatives: a 3D geometric morphometrical approach to the functional morphology of the cave bear *Ursus spelaeus*. *Slovenský Kras Acta Carsologica Slovaca*, 47, 33-46.
- Hofreiter M., Serre D., Roland N., Rabeder G., Nagel D., Conard N., Münzel S., Pääbo S. (2004) - Lack of phylogeography in European mammals before the last glaciation. *PNAS*, 10, 12963-12968.
- Horacek M., Frischauf C., Pacher M., Rabeder G. (2012) - Stable isotopic analyses of cave bear bones from the Conturines cave (2800 m, South Tyrol, Italy). *Braunschweiger Naturkundliche Schriften*, 11, 47-52.
- Krajcarz M., Pacher M., Krajcarz M.T., Laughlan L., Rabeder G., Sabol M., Wojtal P., Bocherens H. (2016) - Isotopic variability of cave bears ($\delta^{15}\text{N}$, $\delta^{13}\text{C}$) across Europe during MIS 3. *Quaternary Science Reviews*, 131, 51-72.
- Kurtén B. (1976) - The cave bear story: life and death of a vanished animal. New York (NY): Columbia University Press, pp. 163.
- Lorenzen E.D., Nogués-Bravo D., Orlando L., Weinstock J., Binladen J., Marske K.A., Ugan A., Borregaard M.K., Gilbert M.T.P., Nielsen R., et al. (2011) - Species-specific responses of Late Quaternary megafauna to climate and humans. *Nature*, 479, 359-364.
- Martini I., Coltorti M., Mazza P.P., Rustioni M., Sandrelli F. (2014) - The latest *Ursus spelaeus* in Italy, a new contribution to the extinction chronology of the cave bear. *Quaternary Research*, 81, 117-124.
- Monegato G., Scardia G., Hajdas I., Rizzini F., Picin A. (2017) - The Alpine LGM in the boreal ice-sheets game. *Nature Scientific Reports*, 7, 2078.
- Münzel S.C., Stiller M., Hofreiter M., Mitnik A., Conard N.J., Bocherens H. (2011) - Pleistocene bears in the Swabian Jura (Germany): genetic replacement, ecological displacement, extinctions and survival. *Quaternary International*, 245, 1-13.
- Münzel S.C., Rivals F., Pacher M., Döppes D., Rabeder G., Conard N.J., Bocherens H. (2014) - Behavioural ecology of Late Pleistocene bears (*Ursus spelaeus*, *Ursus ingressus*): insight from stable isotopes (C, N, O) and tooth microwear. *Quaternary International*, 339-340, 148-163.

- Naito Y., Germonpré M., Chikaraishi Y., Ohkouchi N., Drucker D.G., Hobson K.A., Edwards M.A., Wißing C., Bocherens H. (2016) - Evidence for herbivorous cave bears (*Ursus spelaeus*) in Goyet Cave, Belgium: implications for palaeodietary reconstruction of fossil bears using amino acid $\delta^{15}\text{N}$ approaches. *Journal of Quaternary Science*, 31, 598-606.
- Nannini N., Romandini M. (2015) - Gravettian and Epigravettian hunters in the Berici Hills (Vicenza): two cases of cave bear (*Ursus spelaeus*) exploitation. In: Thun Hohenstein U., Cangemi M., Fiore I., De Grossi Manzorin J., (eds). *Atti del 7° Convegno Nazionale di Archeozoologia*. Ferrara: Annali Università di Ferrara 11, 29-38.
- Pacher M., Stuart A.J. (2009) - Extinction chronology and palaeobiology of the cave bear (*Ursus spelaeus*). *Boreas*, 38, 189-206.
- Richards M.P., Pacher M., Stiller M., Quilés J., Hofreiter M., Constantin S., Zilhão J., Trinkaus E. (2008) - Isotopic evidence for omnivory among European cave bears: late Pleistocene *Ursus spelaeus* from the Peștera cu Oase, Romania. *PNAS*, 105, 600-604.
- Robu M., Fortin J.K., Richards M.P., Schwartz C.C., Wynn J.G., Robbins C.T., Trinkaus E. (2013) - Isotopic evidence for dietary flexibility among European Late Pleistocene cave bears (*Ursus spelaeus*). *Canadian Journal of Zoology*, 91, 227-234.
- Sabol M., Bendík A., Grivalský M.M., Lizák J., Michlík I. (2014) - Latest and highest fossil record of cave bears (*Ursus ex gr. spelaeus*) in Slovakian Western Carpathians. *Quaternary International*, 339-340, 189-196.
- Sandom, C., Faurby, S., Sandel, B., Svenning, J.C. (2014) - Global Late Quaternary megafauna extinctions linked to humans, not climate change. *Proceedings of the Royal Society of London. Biological Sciences*, 281, 20133254.
- Spötl C., Reimer P., Rabeder G., Bronk Ramsey C. (2017) - Radiocarbon Constraints on the Age of the World's Highest-Elevation Cave-Bear Population, Conturines Cave (Dolomites, Northern Italy). *Radiocarbon* 1-9.
- Stuart A.J. (2015) - Late Quaternary megafaunal extinctions on the continents: a short review. *Geological Journal*, 50, 338-363.
- Terlato G., Bocherens H., Romandini M., Nannini N., Hobson K.A., Peresani M. (2018) - Chronological and Isotopic data support a revision for the timing of cave bear extinction in Mediterranean Europe. *Historical Biology*.
Doi: 10.1080/08912963.2018.1448395.
- Vila Taboada M., Fernandez Mosquera D., Lopez Gonzalez F., Grandal-d'Anglade A., Vidal Romani J.R. (1999) - Paleoecological implications inferred from stable isotopic signatures ($\delta^{13}\text{C}$, $\delta^{15}\text{N}$) in bone collagen of *Ursus spelaeus* ROS. - HEIN. *Cadernos Lab Xeoloxico de Laxe*, 24, 73-87.
- Wojtal P. (2007) - Zooarchaeological studies of the Late Pleistocene sites in Poland. *Institute of Systematics and Evolution of Animals, Polish Academy of Sciences*, pp.189.

