

Seasonal insights into the dietary ecology of Eastern European cave bears: a story of evolution, specialisation, competition, and ecological collapse

MASTER THESIS





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Seasonal insights into the dietary ecology of Eastern European
cave bears: a story of evolution, specialisation, competition,
and ecological collapse

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*“Clearly, the bears are on a very different evolutionary tack, and again we have the cave bear as the culmination, **the most bearish of bears**” (Kurtén, 1976, p. 19)*



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Abstract

Cave bears (*Ursus spelaeus* sensu lato) represent a remarkable example of Late Pleistocene megafauna, whose ecology and extinction dynamics remain a subject of intense debate. This study investigates the short-term dietary ecology of Eastern European cave bear populations using dental microwear analysis (DMA) on specimens from Romanian Carpathians, Moldavian Highlands, Western Balkans and Western Rhodopes, Central Balkans and the Eurasian reaches of the continent; namely the Greater Caucasus and the Northern Urals. By analysing and quantifying microwear features, this research captures the final days-to-weeks dietary behaviour prior to death, offering a high-resolution perspective complementary to isotopic and morphological analyses. Complementing the prevailing view of cave bears as highly specialised herbivores adapted to the Mammoth Steppe biome, based on morphological evolution and stable isotope values, our results suggest a behavioural ecology more comparable to that of extant northern hemisphere ursids, characterised by landscape-based dietary opportunism. This inferred dietary flexibility is further supported by partial niche overlap with contemporaneous southern refugia dwellers *U. arctos* populations. The results challenge the long-standing paradigm of entirely separate ecological niches for these co-extinct species (*U. spelaeus* and *U. arctos*), instead suggesting a more complex relationship involving regional niche overlap and possible local-scale partitioning, with implications for interspecific competition. Additionally, the case of the *U. kudarensis* lineage from the Caucasus, which appears to shift diet in response not only to climate but also to the presence of other ursids and humans, underscores the role of ecological pressures in shaping cave bears evolutionary trajectories. Taken together, these findings call for a reassessment of cave bear extinction dynamics. Climate change alone is unlikely to explain their disappearance. Rather, ecological specialisation, particularly during resource-scarce seasons and to refugia areas, combined with pre-hibernation competition for food and denning space with *U. arctos* and humans, likely contributed to a gradual, multifactorial extinction process.

Keywords: *Ursus spelaeus* sensu lato, *Ursus arctos*, dental microwear analysis, Eastern Europe, Pleistocene, seasonal flexibility

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INTRODUCTION

1. Introduction

This master's thesis employs dental microwear analysis to characterize the short-term dietary patterns of cave bear (*Ursus spelaeus* sensu lato) species across different regions in Eastern Europe during the Late Pleistocene, with particular emphasis on Marine Isotopic Stage 3 (MIS 3). The study also incorporates fossil specimens of contemporaneous brown bear species, as well as post-Last Glacial Maximum (LGM) brown bears, to infer potential dietary differences and ecological niche interactions between cave and brown bears. Additionally, a Middle to Late Pleistocene cave bear lineage (*Ursus kudarensis* clade) from the Greater Caucasus is included to provide an exceptional case of study that allows to examine the evolutionary trajectory of a cave bear clade in terms of short-term dietary adaptations over time. Finally, a population of MIS 7 (Middle Pleistocene) *Ursus savini rossicus* from Mishin Cave (Western Balkans) is included to further assess the ecological plasticity of cave bears, as this form has been inferred to represent the most specialized member of the clade (Baryshnikov, 2007).

This master thesis is product of a two-month research stay that was undertaken at the "Emil Racoviță" Institute of Speleology (Romanian Academy of Sciences, Bucharest), under the supervision of Dr. Marius Robu. This stay provided access to key collections and allowed for the direct study and sampling of the fossil materials analysed in this thesis.

1.1 Too specialized to survive? The rapidly changing Late Pleistocene and the decline of cave bears

The Late Pleistocene was marked by significant climatic changes, particularly during the Last Glacial Period, the Weichselian glaciation, in Europe (Dansgaard et al., 1993; Bond et al., 1999; Rasmussen et al., 2014). The Dansgaard-Oeschger (D-O) climatic fluctuations, especially during MIS 3 (60–27 ka B.P.), resulted in persistent ecological instability, causing rapid and frequent shifts between drastically different vegetation, within brief time intervals (Wohlfarth et al., 2008; Huntley et al., 2013; Sánchez Goñi, 2022). The environmental instability at the end of the Pleistocene was a primary factor in the extinction or displacement of a significant portion of the European megafauna that dominated European landscapes since the Middle Pleistocene, including the iconic large herbivores, as well as members of the carnivore clade (Stuart and Lister, 2012). Carnivores, despite their further adaptability to various biomes, do not depend directly on a specific habitat like herbivores (Hunter and Turner, 1997). However, they also experienced a significant population decline and displacement (Varela et al., 2010; Stuart and Lister, 2011), and in some cases extinction (Pacher and Stuart, 2009). This phenomenon has been proposed as being greatly influenced by the displacement and extinction

of populations of large herbivores, which formerly constituted their primary food source (Brugal and Coitor, 2010; Varela et al., 2010; Stuart and Lister, 2011). The carnivores that prevailed and occupied the ecological niche of those extinct species were smaller-sized carnivores and omnivores with broad dietary habits, such as brown bears (*Ursus arctos*) (Sommer and Benecke, 2005; Bocherens et al., 2011), which during the end of the Pleistocene decreased in size as a response to the climatic and environmental instability (Marciszak et al., 2015). An ecologically singular member of the Carnivora order that was among the first to go extinct was the cave bear (*U. spelaeus*), at about 28 ka B.P. in western Europe (Pacher and Stuart, 2009; Bocherens et al., 2014a; Baca et al., 2016). There are various hypotheses regarding the causes of extinction. One identified factor contributing to the extinction is a long genetic decline leading to populations shrinking (Stiller et al., 2010). Furthermore, particular hibernation behaviours linked to a dependency on caves, unlike the closely related lineage of brown bears (*U. arctos*), led them to indirectly compete for these spaces with humans and to be especially susceptible to hunting (Fortes et al., 2016). This last theory, which attributes part of the reasons for the extinction to humans, is supported by evidence of cut marks found on cave bear remains throughout Europe during the MIS 3 period (e.g., Armand et al., 2004; Münzel and Conard, 2004; Terlato et al., 2019; Blasco et al., 2020; Toniato et al., 2024). A well-supported hypothesis attributes the extinction of cave bears to the declining availability of plant-based resources during the Late Pleistocene (Pacher and Stuart, 2009; Bocherens et al., 2019). Cave bears represent a remarkable example of evolutionary dietary specialization, having shifted from an omnivore ancestry to a predominantly herbivorous lifestyle (Kurtén, 1976; Bocherens, 1994). Their ecological role became increasingly analogous to that of the large herbivores of the “Mammoth Steppe”, which originated during the Middle Pleistocene and with which they likely competed for similar plant resources (Guthrie, 2001; Croitor and Brugal, 2010; Bocherens, 2015). Despite this ecological convergence and apparent dietary specialization towards herbivory, cave bears were taxonomically diverse and geographically widespread, with multiple forms recognized across Europe based on both morphological traits and genetic evidence (Baryshnikov and Puzachenko, 2011, 2020).

1.2 Multiple evolutionary paths, yet a shared fate: diversity in taxonomy and biogeographical distribution of cave bears

Among the megafauna that inhabited Europe during the Middle to Late Pleistocene, the cave bear (subgenus *Spelearctos* GEOFFROY SAINT HILAIRE, 1833 of the genus *Ursus* LINNAEUS, 1758) is a distinctive representative, with its remains among the most frequently

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recorded in cave fossil assemblages across the European continent, probably due to dying during hibernation (Kurtén, 1976; Rabeder, 1999, Rabeder et al., 2000; Grandal-d'Anglade et al., 2019). The Pliocene-Early Pleistocene *U. etruscus* CUVIER, 1823 gave pass to the Middle Pleistocene *U. deningeri* VON REICHENAU, 1904 from which highly diverse multiplicity of forms evolved into distinct species (Dabney et al., 2013; Baryshnikov and Puzachenko, 2020). The two derived forms were *U. spelaeus* ROSENMÜLLER, 1794 and the *U. kanivetz* VERESHCHAGIN, 1973 (= *ingressus* RABEDER, 2004) (Rabeder et al., 2004b; Baca et al., 2016). These two species, from which some authors had pointed out to be subspecies (Baryshnikov and Puzachenko, 2011), diverged from each other between 173 and 414 ka B.P. (Knapp et al., 2009), conforming a different distribution, although confined to Europe from which they did not extend beyond the Ural Mountains. *U. spelaeus* inhabited the western part of Europe, where two alpine adapted dwarfed forms of cave bears were identified as subspecies of it, the *U. s. eremus* RABEDER, 2004 and *U. s. ladinicus* RABEDER, 2004 (Rabeder et al., 2004a; Rabeder et al., 2008). On the other hand, *U. kanivetz*—originally described as *Ursus kanivetz* by Vereshchagin (1973) but commonly recognized as *U. ingressus* (Rabeder, 2004)—inhabited regions of central and eastern Europe as well as the Urals (Baca et al., 2014; Baryshnikov and Puzachenko, 2020). Currently, *U. ingressus/kanivetz*, has two defined subspecies; *U. k. kanivetz* that inhabited the Urals region, and *U. k. ingressus* in south-eastern Europe, where the species originated (Baryshnikov and Puzachenko, 2011, 2020; Baca et al., 2012).

Finally, regarding the European large cave bears, it existed another species known as *U. kudarensis* BARYSHNIKOV, 1985, which diverged from *U. deningeri* prior to the separations of *U. spelaeus* and *U. ingressus* (Knapp et al., 2009; Stiller et al., 2014). Their early differentiation in comparison to the other cave bears, occurred around *ca.* 800 ka B.P., during the end-Early Pleistocene. This premature separation has been further confirmed by both nuclear and mitochondrial DNA analysis (Barlow et al., 2021). Furthermore, this Middle to Late Pleistocene cave bear populations inhabited the Southern Greater Caucasus, where several skulls and mandibles were found in the Kudaro-1 and Kudaro-3 caves, and subsequently classified as *U. kudarensis* by Baryshnikov (1985). Initially, Baryshnikov distinguished two chronological/stratigraphic subspecies based on the tooth morphotypes, that succeeded each other over time: the end-Middle Pleistocene *U. k. praekudarensis* and the Late Pleistocene *U. k. kudarensis* (Baryshnikov, 1998). However, DNA analysis revealed that they were distinct species rather than subspecies, albeit from the same lineage (Barlow et al., 2021). Paleogenetic

data further indicate that *U. praekudarensis* and *U. kudarensis* diverged around 500 ka B.P., this is long before bone accumulations began in the Kudaro cave deposits, supporting the view that these forms should be regarded as two independent species that occupied the Kudaro caves at different times (Barlow et al., 2021).

Apart from the large cave bears, there existed the small cave bears, which were stated as a united evolutionary lineage, forming a monophyletic group categorized under a common Early Pleistocene species known as *Ursus savini* ANDREWS, 1922 (Baryshnikov, 2007; Baryshnikov and Puzachenko, 2017). Hence, their evolution from *U. savini* early-Middle Pleistocene form would have happened in parallel to the one of large cave bears which were in turn derived from its “cousin” *U. deningeri* (García, 2003; Grandal-d’Anglade and López-González, 2004; Baryshnikov and Puzachenko, 2017). This taxonomic group comprised distinct (sub)species; *U. s. savini*, *U. s. rossicus* BORISSIAK, 1930, *U. s. uralensis* VERESHCHAGIN, 1973, *U. s. nordostensis* BARYSHNIKOV, 2011. This small cave bears (*U. savini* spp.), with the most widely distributed being *U. s. rossicus*, were recorded from the Ukrainian steppes passing through the Altai Mountains until Siberia (Vereshchagin and Baryshnikov, 2000; Spassov et al., 2017). Therefore, exhibiting the most extensive distribution eastwards and northwards among Late Pleistocene cave bears.

The presence of multiple forms, distributed across a diverse range of biotopes, suggests that their ecology—and more specifically, their diet—likely varied among them.

1.3 Palaeodiet

Studying the diet of the cave bear (*U. spelaeus* sensu lato) is crucial for understanding its ecological niche and geographical distribution during the Pleistocene, as it does not closely resemble any extant bear species. Furthermore, the feeding ecology of mammals plays a fundamental role in their evolutionary processes (e.g., Wu, 2022), shaping selective pressures that have likely influenced not only survival and extinction but also the taxonomic diversification within *U. spelaeus* sensu lato. As a result, numerous studies have aimed to reconstruct its palaeodiet to better define its dietary niche, which remains a subject of ongoing scientific debate. Methodologically, these diet-inferring studies can be categorized into long-term or short-term (Davis and Pineda-Muñoz, 2016).

1.3.1 Long-term diet

Long-term dietary-inferring methods assess the dietary adaptations of a lineage at an evolutionary scale, primarily through the analysis of morpho-functional traits related to food

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acquisition and processing of a species (e.g., teeth or mandible morphology). These studies can infer general evolutionary trends that have been shaped over millions (or several hundreds of thousands) of years in response to an average diet (e.g., Anderson et al., 2011).

1.3.1.1 Morphology

The bear lineage underwent a progressive enlargement of the lower second molar (m2) (Jiangzuo and Flynn, 2020), interpreted as an evolutionary shift from carnivory (in the Early Miocene *Ballusia elmensis*) to balanced omnivory during the Middle to Late Miocene (e.g., *Aurorarcos tirawa*, *Ursavus tedfordi*, among others), and ultimately, in Early Pleistocene species such as *U. etruscus* and *U. deningeri*, to a plant-dominated omnivory, and finally, in the Middle-Late Pleistocene, towards “pure” herbivory in *U. spelaeus* (Figure 1).

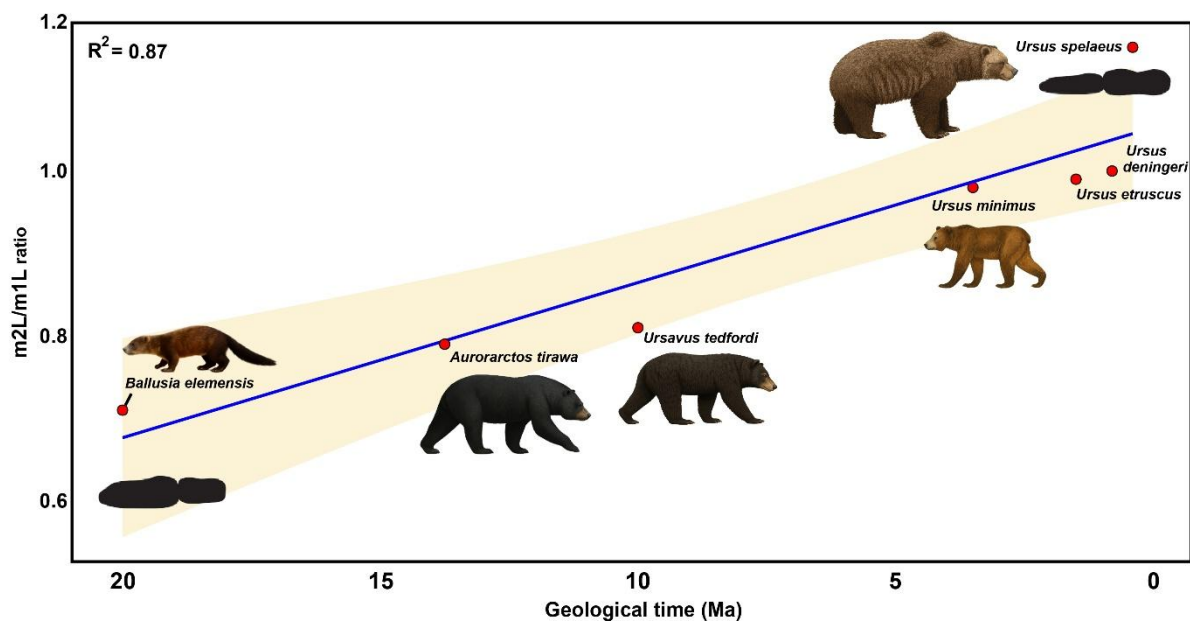


Figure 1. The plot displays the ratio between the second and first lower molar lengths (m2L/m1L) in representative ursid taxa spanning from the early Miocene to the Late Pleistocene, plotted against their geological age (in millions of years ago, Ma). A significant positive trend ($R^2 = 0.87$) highlights a progressive evolutionary enlargement of m2 relative to m1. This morphological trajectory is interpreted as reflecting a dietary shift from early carnivory to increased omnivory and eventual herbivory in later taxa such as *U. spelaeus*. Ratio data for most taxa are derived from Jiangzuo and Flynn (2020), while the ratio for *Ursus minimus* was calculated based on measurements provided in Baryshnikov and Lavrov (2013). Silhouettes and life reconstructions are included for illustrative purposes.

Middle to Late Pleistocene herbivorous cave bears

The diet of the cave bear has been inferred as having predominantly relied on plants, as indicated by wear gradients and dental morphology (Terzea, 1966; Kurtén, 1976; Jurcsák et al., 1981), as well as by three-dimensional analysis of tooth-root morphology (Pérez-Ramos et al., 2019). The evolutionary shift toward herbivory in cave bears began with the earliest members of their lineage (*U. deningeri*) and became more pronounced in its descendants (*U. spelaeus*

sensu lato), as evidenced by significant cranial, dental, and mandibular adaptations (Mazza and Rustioni, 1994; van Heter and Figueirido, 2019). A key adaptation is the "molarization" of the fourth premolar (P4/p4), characterized by crown enlargement, cusp proliferation, and the development of a rounded protoconid apex, distinguishing it from the tall, single-coned premolar of *U. arctos* (Baryshnikov, 1998; Jiangzuo et al., 2019). These changes extended the masticatory function of molars to premolars, facilitating increased consumption of phytolith-rich plant material, such as grasses (Butler, 2009; Selig and Silcox, 2022). This trait, commonly observed in herbivorous mammals, is exemplified by the giant panda for the Ursidae family (*Ailuropoda melanoleuca*) (Wang et al., 2017; Jiangzuo et al., 2019). Additionally, cave bear molars underwent progressive enlargement and broadening (especially the lower second molar), accompanied by accessory cusps and crests, further enhancing their ability to process fibrous plant matter (Kurtén, 1976; Charters et al., 2022). Moreover, analyses of cranial and mandibular morphology corroborate the existence of a trend toward herbivory in the cave bear lineage, revealing similarities in chewing mechanisms between Middle and Late Pleistocene forms (*U. deningeri* and *U. spelaeus*), both of which exhibit adaptations for plant-based diets (van Heteren et al., 2019; van Heteren and Figueirido, 2019).

1.3.2 Short-term diet

The short-term diet-inferring methods assess the dietary preferences of an individual during its lifetime (Figure 2), specifically used in palaeontology research are stable isotopes studies and dental wear analyses. Regarding *stable isotopes analyses*, those can be performed on either:

A) **Bone collagen**, providing a time resolution that reflects dietary intake over several years prior to death (Ambrose, 1993; Naito et al., 2016a). Stable isotopes in bone collagen are incorporated gradually and reflect the averaged dietary input over extended periods—typically years to decades—making them unsuitable for detecting seasonal variation or dietary changes occurring within the final months or year of life of the studied individual (Ambrose, 1993; Cox and Sealy, 1997). In most bones, collagen isotopes record dietary signals at a resolution not much finer than the overall lifespan of the individual, typically ranging from several years to decades (Ambrose, 1993; Hedges et al., 2007). Turnover rates vary by skeletal element, with cancellous bones such as ribs reflecting diet over *ca.* 2–5 years, mandibles over *ca.* 5–10 years, and dense cortical bones like the femur over *ca.* 10–30 years (Ambrose, 1993). In paleontological studies, since collagen preservation is often best in dense cortical bones (such as mandibles and long bones), bone isotopic analyses typically reflect lifespan-level dietary averages (Bocherens et al., 1991; Davis and Pineda-Muñoz, 2016).

1. Introduction

B) **Tooth enamel** organic portion (bioapatite), which can be analysed either in bulk or through sequential sampling, can capture dietary signals during tooth development, offering high-resolution insights, including seasonal changes when using sequential sampling (e.g., Díez-Canseco et al., 2022; Ramírez-Pedraza et al., 2024), into diet during early life stages, depending on the species-specific timing of tooth formation (Hoppe et al., 2004; Ventresca-Miller et al., 2018).

Finally, *dental microwear analysis* reflects diet over the final days to weeks of life of an individual (Grine, 1986; Teaford and Oyen, 1986).

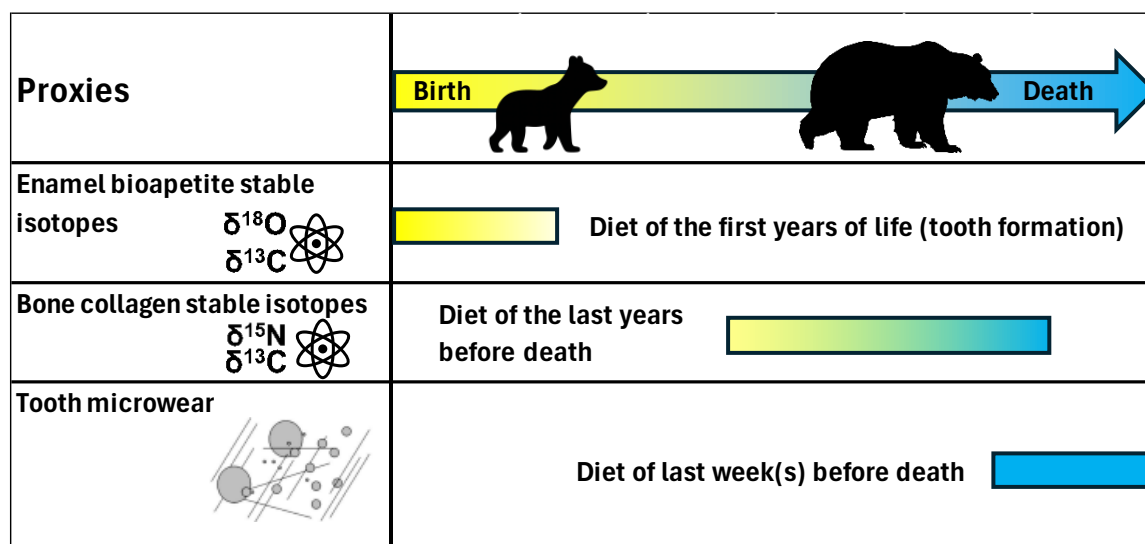


Figure 2. Schematic representation of dietary time resolution associated with different “short-term” palaeodietary proxies. Enamel bioapatite stable isotopes ($\delta^{13}\text{C}$, $\delta^{18}\text{O}$) reflect dietary intake during early life stages, corresponding to the period of tooth formation. Bone collagen stable isotopes ($\delta^{13}\text{C}$, $\delta^{15}\text{N}$) integrate dietary signals over the last several years before death, depending on bone turnover rates. In contrast, dental microwear captures the most precise dietary signal, typically reflecting the diet during the final days to weeks of life.

1.3.2.1 Stable isotopes

The transition towards herbivory in cave bears is further supported by multiple isotope analyses of both carbon ($\delta^{13}\text{C}$) and nitrogen ($\delta^{15}\text{N}$) on bone collagen (Bocherens et al., 1994, 1997, 2006, 2011, 2014; Nelson et al., 1998; Vila-Taboada et al., 1999; Mosquera et al., 2001; Münzel et al., 2011; Krajcarz et al., 2016; Naito et al., 2016b; Bocherens, 2019; Ramírez-Pedraza et al., 2019).

Conversely, some other studies on Romanian Carpathian cave bears have pointed towards a flexible omnivore diet suggested by a wide range of $\delta^{15}\text{N}$ values (Richards et al., 2008; Robu et al., 2013, 2018b), which is supported by morphological and dental wear analysis (Figueirido et al., 2009; Peigné et al., 2009). However, a following study conducted on Romanian cave bears analysing nitrogen isotopes in specific amino acids has presented evidence for a

predominantly herbivorous diet for these populations (Naito et al., 2020). The study revealed that the elevated nitrogen values previously recorded in some Romanian cave bears could be attributed to the consumption of specific plant species characterized by high bulk $\delta^{15}\text{N}$ values (Naito et al., 2020). In addition, Grandal-d'Anglade et al. (2019) suggested that the high nitrogen values observed in Romanian cave bears could potentially be attributed to urea reuse processes during hibernation. Nevertheless, the wide range of results obtained using lifespan average dietary proxies (isotopes and isotopes on specific amino acids) might suggest lifelong dietary flexibility of this species depending on multiple factors such as the geographical and ecological context, as well as the degree of competition for available resources, but under a plant dominated diet (Robu et al., 2013; Krajcarz et al., 2016; Naito et al., 2020; Meleg et al., 2024).

Isotopic signatures of directly dated cave bear individuals from multiple regions, compiled from various published studies (Bocherens et al., 2006, 2014a, 2015; Pérez-Rama et al., 2011; Robu et al., 2018b), provide evidence of an east-west gradient in $\delta^{15}\text{N}$ values and, to a lesser extent, of $\delta^{13}\text{C}$ values across MIS 3 (Figures 3 and 4). For more detailed information about the data used for these plots see Appendix, section A.2 – Table A2.

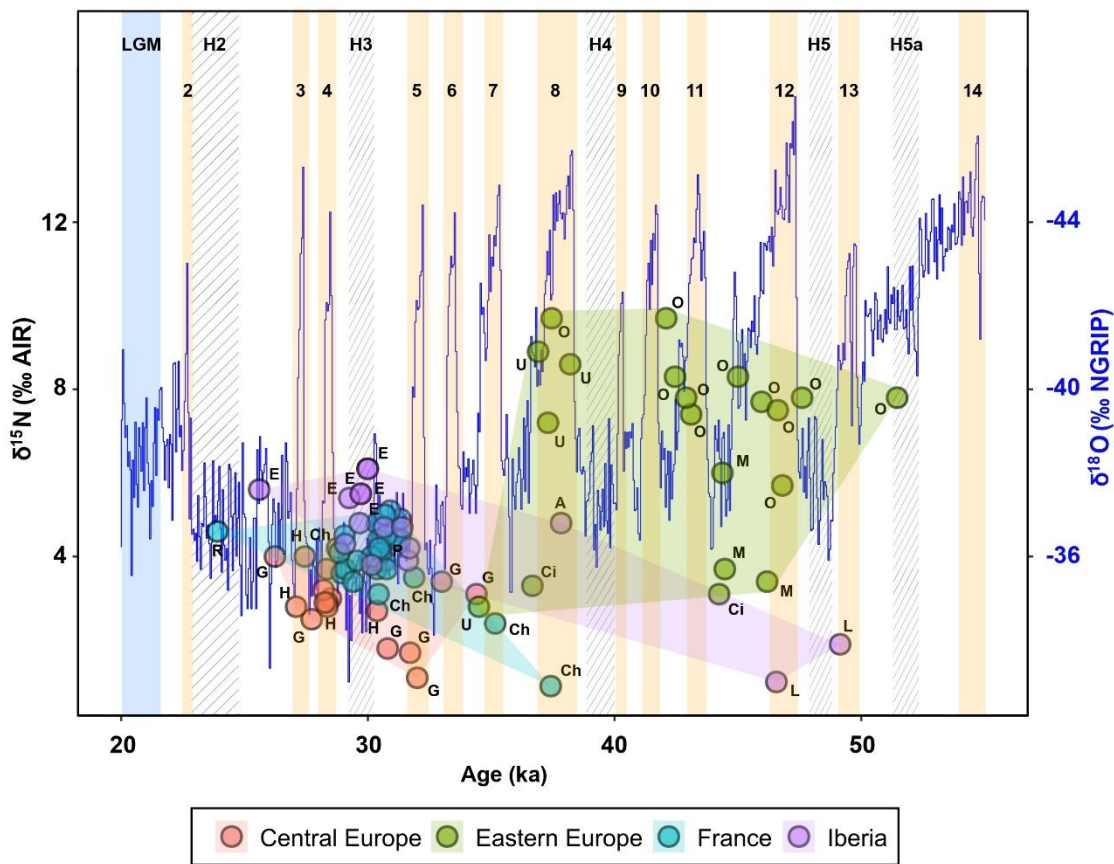


Figure 3. Comparison of $\delta^{15}\text{N}$ values of radiocarbon calibrated cave bear individuals from Central European ($n = 17$) sites: Geissenklösterle (G), Hohle Fels (H), Eastern European sites ($n = 20$): Cioclovina (Ci), Muierilor (M), Oase (O), Urşilor (U), French sites ($n = 28$): Chauvet (Ch), Rochedane (R), Iberian sites ($n = 15$): A Ceza 1 (A), Eirós (E), Liñares (L), Pala de Reboral (P) across time, with convex hulls highlighting regional groupings. The overlaid $\delta^{18}\text{O}$ curve (NGRIP) (Andersen et al., 2004) reflects climatic conditions, providing context for isotopic variation among regions. The Dansgaard-Oeschger (DO) cycles and Heinrich Events (H) have been included for enhanced climatic characterization.

Regarding nitrogen ($\delta^{15}\text{N}$) values, there is a higher variability displayed by Eastern European, i.e., Romanian Carpathian populations (from the main sites of Cioclovina, Muierilor, Oase and Urşilor) compared to Central European, French, and Iberian populations in western Europe. This information is coupled by the fact that most of the radiocarbon calibrated populations from the Romanian Carpathians, display slightly older radiocarbon dates. Furthermore, when plotted with the $\delta^{18}\text{O}$ curve (NGRIP), the individuals that display high nitrogen values seem to fall within interstadial periods. However, there are exceptions, and the existence of a chronological range subject to error for radiocarbon dates should also be taken into account. Nevertheless, a discernible trend is observable, in which $\delta^{15}\text{N}$ values tend to decrease as the Last Glacial Maximum (LGM) approaches, while higher $\delta^{15}\text{N}$ values are predominantly associated with warmer interstadial periods, as stated before.

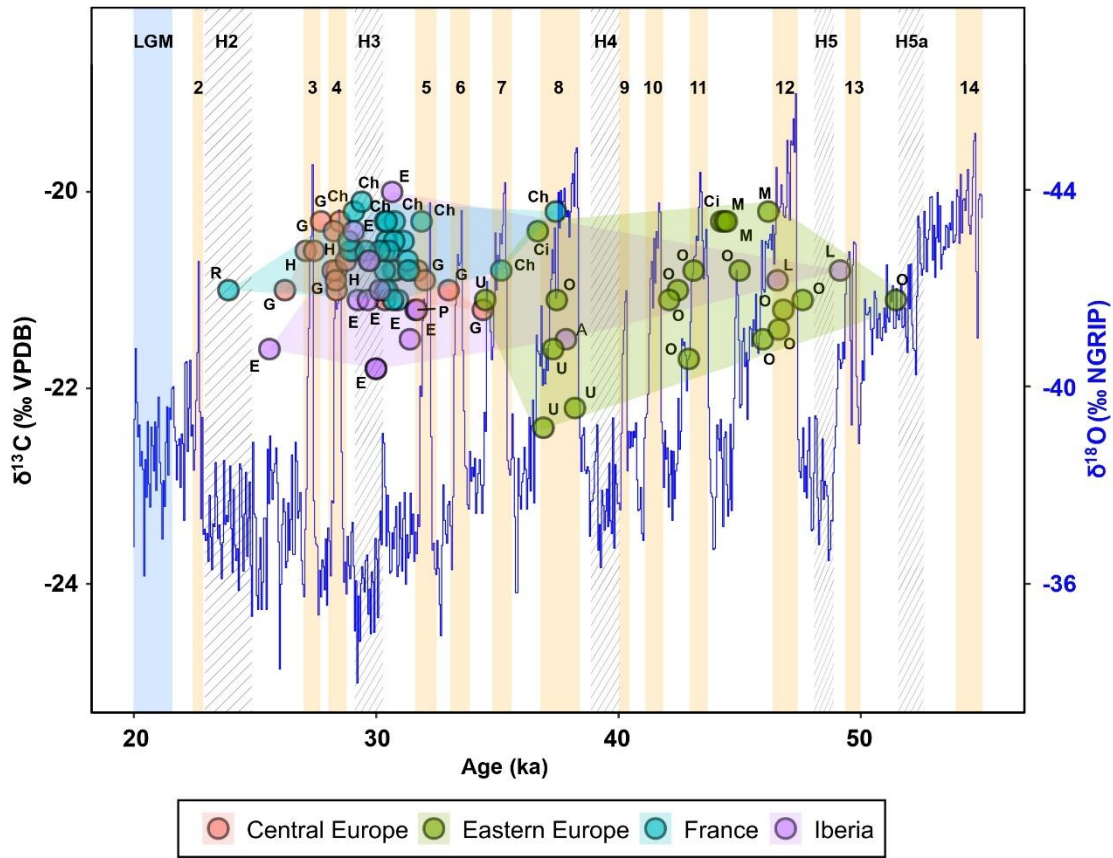


Figure 4. Comparison of $\delta^{13}\text{C}$ values of radiocarbon calibrated cave bear individuals from Central European ($n = 17$) sites: Geissenklösterle (G), Hohle Fels (H), Eastern European sites ($n = 20$): Cioclovina (Ci), Muierilor (M), Oase (O), Urşilor (U), French sites ($n = 28$): Chauvet (Ch), Rochedane (R), Iberian sites ($n = 15$): A Ceza 1 (A), Eirós (E), Liñares (L), Pala de Reboral (P) across time, with convex hulls highlighting regional groupings. The overlaid $\delta^{18}\text{O}$ curve (NGRIP) (Andersen et al., 2004) reflects climatic conditions, providing context for isotopic variation among regions. The Dansgaard-Oeschger (DO) cycles and Heinrich Events (H) have been included for enhanced climatic characterization.

When carbon ($\delta^{13}\text{C}$) values are plotted, populations from France and Central Europe exhibit significant overlap, while Iberian populations generally show lower $\delta^{13}\text{C}$ values, though still within an overlapping range. Eastern European populations from the Romanian Carpathians, also overlap with the other regions but display, on average, lower $\delta^{13}\text{C}$ values, with some of the lowest recorded values. This pattern reflects differences in vegetation cover across regions. French and Central European sites are located in steppe environments and associated with cold stadial periods, in which climatic continentality and open steppe environments predominated (Helmens, 2014). In contrast with Iberian populations, which inhabited more temperate, vegetation-rich refugia at lower latitudes (Sommer and Zachos, 2009; Desprat et al., 2015). Meanwhile, Romanian Carpathians cave bear populations, situated in the Carpathian refugia, exhibit lower $\delta^{13}\text{C}$ values, which have been suggested to result from a greater diversity of plant resources consumed (Robu et al., 2013, 2018; Meleg et al., 2024).

1.3.2.2 Dental microwear

A well-established method to infer short-term dietary patterns is microwear analysis. Microwear analyses identify microscopic features left by abrasive particles on the enamel of the occlusal surface during chewing with the goal of inferring the dietary ecology of the animal (Solounias and Semprebon, 2002; Semprebon et al., 2004). The constant formation of new features erases the previous ones, which means there is a record of the diet on a much shorter time scale than morphological, macroscopic dental wear and isotopic or amino acids analyses (Solounias and Semprebon 2002). Thus, one can detect seasonal or occasional dietary regimes that would not be seen through other methods (Grine, 1986). Dental microwear studies had been carried out on cave bears in the past years (e.g., Ramírez-Pedraza et al., 2019, 2020, 2022). These have revealed a high variability in dietary habits among cave bear populations from different locations in Europe during the Late Pleistocene. For example, the short-term microwear signal exhibited a varied and less specialized diet, before death, for individuals with low nitrogen values (i.e., long-term herbivorous diet) (Ramírez-Pedraza et al., 2019). For a more detailed review on cave bear microwear studies see Methodological framework section 3.5.

OBJECTIVES AND STRUCTURE

2. Objectives and structure

The absence of a macro-regional dental microwear analysis on cave bear populations, combined with the exceptional abundance of well-preserved dental remains in Eastern European cave sites—many of which remain unanalysed—highlights the need for a comprehensive investigation. This need is further reinforced by the presence of cave bear populations in this region exhibiting abnormally high and variable $\delta^{15}\text{N}$ values, suggesting potential ecological diversity. These factors collectively underscore the importance of conducting a large-scale short-term dietary assessment of cave bear populations across Eastern Europe, spanning a broad geographic range characterized by highly diverse landscapes and biotopes. Such diversity provides a unique opportunity to investigate potential ecological adaptations and regional dietary variation within the species.

To enable this research, a **two-month research stay** was undertaken at the "**Emil Racoviță**" **Institute of Speleology** (Romanian Academy of Sciences, Bucharest), under the supervision of **Dr. Marius Robu**. This stay provided access to key collections and allowed for the direct study and sampling of the fossil materials analysed in this thesis. High-resolution dental moulds were prepared on-site and subsequently transported to the facilities of **IPHES-CERCA** (Tarragona, Spain), where the microwear analyses were carried out, under the supervision of **Dr. Florent Rivals** and **Dr. Iván Ramírez-Pedraza**.

This master's thesis integrates data previously published in form of **three scientific peer-reviewed articles** in the **Q1-indexed scientific journal** of *Palaeogeography*, *Palaeoclimatology*, *Palaeoecology* (see at Appendix section A.1), providing a robust foundation for the analyses presented herein, alongside new unpublished results.

2.1 Thesis objectives

2.1.1 Main objective

The first objective of this thesis is to evaluate the hypothesis that the diet of cave bears (*U. spelaeus* sensu lato) exhibited greater short-term (seasonal) variability than is detectable through derived morphological adaptations and isotopic analyses. This hypothesis is grounded in the observation that cave bears occupied a broad range of biogeographic regions and exhibited considerable morphological diversity—suggesting adaptation to distinct local environments and, potentially, divergent dietary strategies. To test this, we apply dental microwear analysis, a method particularly suited to capturing short-term dietary signals, with

the aim of reconstructing the dietary habits of Eastern European cave bear populations at finer ecological scales.

2.1.2 Secondary objectives

The secondary objectives of this research are three, plus two sub-objectives.

- 1) **Intra-regional dietary patterns:** First, to evaluate the degree of dietary difference or similarity among cave bear and brown bear populations within the same biogeographic regions of Eastern Europe (Romanian Carpathians, Moldavian Plateau, Western Balkans-Western Rhodope Mountains, Central Balkans, Greater Caucasus and Northern Urals). This will allow an assessment of the degree of ecological flexibility or specialization in cave bears in relation to regional-specific landscapes and environmental conditions. Contributing to a better understanding of whether the dietary ecology of the cave bear was regionally specific, or broadly uniform at the species level across its range.

- 2) **Temporal trends:** Second, to investigate potential evolutionary trends in short-term dietary patterns, including:

A) Cave bear evolution: Investigate the cave bear evolution by analysing the seasonal diets of three chronologically distinct, yet phylogenetically related, populations of the Greater Caucasus representing a single cave bear lineage. This diachronic approach aims to evaluate whether dietary adaptations on cave bears emerged over time in response to local environmental fluctuations or broader ecological pressures.

B) Temporal niche dynamics between *U. spelaeus* and *U. arctos*: Investigate temporal changes in niche relationships between cave bears and brown bears, with a focus on brown bear dietary patterns before and after the Last Glacial Maximum (LGM). This objective aims to assess the hypothesis of niche inheritance—wherein *U. arctos* may have partially occupied the ecological space left vacant following the extinction of *U. spelaeus* in Europe.

- 3) **Inter-regional and inter-chronological dietary comparison:** Third, to evaluate dietary similarities or differences between cave bear populations from distinct biogeographic regions across Eastern Europe and from different time periods. This

2. Objectives and structure

broader comparison aims to assess whether contrasting landscapes, environmental contexts, and competition pressures influenced foraging strategies, and to what extent regional and local ecological pressures may have driven divergent dietary adaptations within the cave bear lineage.

2.2 Thesis structure

This master's thesis is structured into eight main chapters, followed by the references and appendix sections. These chapters aim to provide a theoretical framework, followed by a description of the methodologies and results obtained. At the end a thorough interpretation based on previously published works is presented, culminating in the final conclusions. Finally, the last chapter is dedicated to outlining future research directions, addressing the needs identified through this study. The language chosen for this work is English, the current international language of research.

Chapter 1: This chapter introduces the theoretical paradigms and the state of the art related to this work, specifically addressing the history, evolution, and ecology of *U. spelaeus*, with a focus on diet as interpreted through both short- and long-term dietary inference proxies.

Chapter 2: Explains the objectives to answer through the present research and explain how the study is organized.

Chapter 3: Encompasses the theoretical foundations and history underlying the methodology used, from which the author develops the research approach and conducts the necessary analyses to achieve the stated objectives.

Chapter 4: It provides the necessary geographical and historical context for each site studied. The sites are grouped and explained by study region, based on geographical coherence rather than political boundaries.

Chapter 5: It covers all technical aspects related to the procedures involved in the selection and preparation of the material, as well as the specific considerations for the application and analysis through the various techniques used. Finally, it also explains the statistical analyses performed and the software tools employed.

Chapter 6: The results are presented in this chapter, following the structure defined by the objectives of this study. First, results are shown for each site within regions (intra-regional results). Second, the results pertaining to the second objective, evolution of dietary niches, are

discussed, beginning with the *U. kudarensis* lineage, followed by an analysis of the interactions between brown bears and cave bears through time. Finally, inter-regional and inter-chronological comparisons are presented, addressing the third objective.

Chapter 7: This chapter presents the general discussion of the study, structured in alignment with the objectives previously outlined. The first section provides a detailed interpretation of the empirical dental microwear patterns. The second section expands the scope to a broader discussion, integrating current paradigms of cave bear dietary ecology and evaluating the broader implications of the results for understanding the species' ecological adaptations, evolutionary trajectory, and extinction dynamics.

Chapter 8: Final conclusions drawn from the comparison between the results of this research and the current scientific paradigms. Methodological insights derived from the study are also discussed.

Chapter 9: This chapter presents the future research initiatives that have been initiated following the completion of this study, aiming to address the needs identified through its findings.

References: It contains the alphabetically ordered bibliography of the articles cited in the present master's thesis.

Appendix: The appendix provides supplementary information and materials (e.g., articles published, tables and figures) and additional explanations developed throughout this work.

METHODOLOGICAL FRAMEWORK

3. Methodological framework

Dental microwear analysis (DMA) is a methodological approach developed within the field of palaeontology (from the Greek *palaios*, meaning “ancient,” and *ontos*, meaning “being”). More specifically, it falls under the domain of paleoecology, the branch of palaeontology concerned with understanding the interactions between extinct organisms and their environments. Paleoecology is generally divided into two subfields: palaeosynecology, which examines the structure and dynamics of ancient populations, communities, and ecosystems; and palaeoautoecology, which focuses on the ecological traits of individual species or populations; such as diet, habitat, or niche. Dental microwear analysis belongs to this latter branch, as it aims to reconstruct short-term dietary patterns by studying microscopic wear features on teeth.

This chapter outlines the methodological foundations of the present study, with a particular focus on the development and application of DMA as a tool for dietary reconstruction. It begins by introducing the principles of DMA and then traces the historical evolution of the technique. Special attention is given to the low-magnification stereomicroscopy method employed in this study. Lastly, the chapter reviews the application of DMA to carnivorans, more specifically bears as subjects of this work. This chapter aims to contextualize this work at the forefront of decades of dental microwear research, and more specifically on DMA on bears.

3.1 Dental microwear analysis (DMA)

Dental microwear analyses consist in the identification of microscopic features imprinted by abrasive particles on the enamel of the surface of teeth during chewing with the objective to infer the dietary traits of the studied animal (Ungar and Teaford, 1996; Solounias and Semprebon, 2002). During chewing, the constant formation of new features erases the previous ones, leaving a dietary record of a shorter time scale in comparison to morphological, macroscopic dental wear and isotopic analyses of bone collagen (Grine, 1986; Teaford and Oyen, 1986; Bocherens et al., 1991). Microwear analyses, with a specific focus on the occlusal surface, have been conducted following various protocols and employing a range of microscopes, such as the scanning electron microscope (Rensberger, 1978; Walker et al., 1978; Van Valkenburgh et al., 1990), the optical microscope (e.g., stereomicroscope) (Solounias and Semprebon, 2002; Semprebon et al., 2004) and the confocal microscope applying a scale-sensitive fractal analysis or textures analysis (Ungar et al., 2003; Scott et al., 2005). In the past two decades, low-magnification microwear analysis using stereomicroscopy has gained prominence in archaeological sciences over other techniques due to its low-cost and proven reliability in inferring animal diets (Solounias and Semprebon, 2002; Semprebon et al., 2004).

This is the method employed in this work for the inference of dietary ecology of *U. spelaeus* (sensu lato).

3.2 History of the method

The earliest microwear studies, using the optical microscope and conducted from the early 20th century through the 1950s, focused on two main areas: the general relationship between tooth morphology and microwear features on an evolutionary scale (Simpson, 1933), and the connection between jaw movement and microwear patterns (Butler, 1952; Mills, 1955). However, Dahlberg and Kinzey (1962) were the first to propose a direct link between microwear features on enamel and the dietary habits of an individual or population, after conducting a study on human dental remains using an optical microscope (Dahlberg and Kinzey, 1962).

By the late 1970s, the scanning electron microscope (SEM) revolutionized microwear analysis by allowing for higher magnifications, which enabled the observation of smaller microwear features with improved resolution (Ryan, 1980; Ungar et al., 2008). The first study focused on comparing the differences between the diets of Paleo-Indians and contemporary Americans (Shkurkin et al., 1975). Studies were also conducted on the microwear of *Homo erectus* from Tautavel (Puech, 1977). This technological advancement facilitated the development of the first microwear analysis methodologies, enabling researchers to identify and quantify microwear features, ultimately leading to the earliest proposals for distinguishing dietary regimes and to establishing direct links between specific microfeatures and specific food items (Grine, 1977, Rensberger, 1978; Walker et al., 1978; Ryan, 1979a, 1979b; Gordon, 1982). These studies led to important definitions regarding the capacities of microwear analysis. Walker et al. 1978, determined that; 1) microwear patterns change according to diet, being capable of distinguishing between browsing and grazing animals, and 2) microwear patterns change according to the season of death of individuals, i.e., in response to climatic fluctuations. Thus, the microwear pattern was produced in very short-term event, reflecting the last dietary regime and, therefore, the environment in which the specimen lived just before dying. These conclusions highlighted the potential of microwear analysis for palaeodietary and paleoenvironmental studies.

In the 1980s, experimental studies investigated the precise formation timing of microwear features, demonstrating that their turn-over is continuous throughout an animal's life, leaving a record of the diet on a very brief time scale, corresponding to the last weeks or even days before

3. Methodological framework

the animal's death (Grine, 1986; Teaford and Oyen, 1986; Solounias, 1988). The 90s saw a dominance of SEM in microwear studies, which more accurately quantify microwear using a variety of approaches and variables (Solounias et al., 1988; Maas, 1991; Solounias and Hayek, 1993; Solounias and Moelleken, 1992a, 1992b; Ungar, 1995). By the early 2000s, it became evident that the lack of observer consistency in recognizing and measuring microwear features on SEM images constrained interpretations (Grine et al., 2002). Additionally, the high costs in terms of time and budget (e.g., Maas, 1991; Ungar, 1995), limited the widespread of dental microwear analysis and the study of large samples (Solounias and Semprebon, 2002).

3.3 Low-magnification optical microscopy using a stereomicroscope

In this context, Solounias and Semprebon (2002) and Semprebon et al. (2004) suggested the return to optical microscopy through use of a stereomicroscope at low magnification. The effectiveness of this method was coupled with its low cost and flexibility, allowing for the analysis of large samples (several individuals) in a very short time (Solounias and Semprebon, 2002). Moreover, the margin of error between observers during the quantification of microwear features was proven to be very low, enabling the reliable and reproducible identification of dietary trends in the studied specimens and populations (Semprebon et al., 2004). The authors demonstrated the method's ability to distinguish between browsing and grazing in herbivores and plant-based omnivores better than any other before (Solounias and Semprebon, 2002). Furthermore, they were able to distinguish between graminivores, folivores, frugivores, as well as those consuming seeds and hard objects, such as roots (Godfrey et al., 2004; Semprebon et al., 2004). The ability to successfully discern between dietary regimes, coupled with its efficiency in terms of time and cost compared to previous methods, extended its use until it became the most used dental microwear approach for reconstructing diets in both modern ecological studies and in paleontological and archaeological research (Green and Croft, 2018).

The low-magnification method has allowed to detected dietary plasticity and diversity in Pleistocene mammalian herbivores, either according to season such as for equids (Uzunidis, 2021) and pronghorns (Semprebon and Rivals, 2007), to latitude for reindeer (*Rangifer tarandus*) (Rivals and Semprebon, 2017), geography for *Bison* (Rivals et al., 2007) or to both geographic and phylogenetic factors for Quaternary proboscideans (*Mammuthus*, *Palaeoloxodon*, and *Mammut*) (Rivals et al., 2012).

Aiming to avoid interobserver error that human subjectiveness burdened in the action of quantification of microwear features (Ungar et al., 2008; Scott et al., 2008; DeSantis et al.,

2013), three-dimensional microwear texture analysis, employing confocal scanning microscopy was developed in parallel (Ungar et al., 2003; Scott et al., 2005). The quantification of features was replaced by surface quantification using software that measured the selected surface three-dimensionally through mathematical geometric parameters, assigning a specific value to each parameter (Ungar et al., 2003).

3.4 Dental microwear on Carnivora

Dental microwear analysis in carnivorans (Mammalia: order Carnivora) has been thoroughly studied (Van Valkenburgh et al., 1990; Dewar, 2004; Goillot et al., 2009; Schubert et al., 2010; Bastl et al., 2012; DeSantis et al., 2012; Donohue et al., 2013; Pappa, 2016; Xafis et al., 2017; Tanis et al., 2018; Pappa et al., 2019). However, because their diet is not strongly connected to their environment as that of mammalian herbivores (Hunter and Turner, 1997), those have received less attention regarding dietary plasticity or to infer paleoenvironments. The research focused on palaeodietary inferences and ecological behaviour, such as distinguishing between durophagous and non-durophagous diets and differentiating between hunting or scavenging behaviours. Moreover, microwear analyses mainly focused on carnassial teeth (i.e., upper fourth premolar / lower first molars), and more specifically focusing on faceted surfaces or facets (Xafis et al., 2017).

The first dental microwear analysis on Carnivora is attributed to Van Valkenburgh et al. (1990). Employing the SEM at x250 magnifications, the work aimed to determine the dietary strategy (infer the presence or absence of durophagy, i.e., scavenging behaviour) of extinct sabretooth cat *Smilodon fatalis* comparing its microwear patterns to those of eight extant large carnivorans; spotted hyaena (*Crocuta crocuta*), striped hyaena (*Hyaena hyaena*), wolverine (*Gulo gulo*), grey wolf (*Canis lupus*), African wild dog (*Lycaon pictus*), African lion (*Panthera leo*), leopard (*Panthera pardus*), and cheetah (*Acinonyx jubatus*) (Van Valkenburgh et al., 1990). Anyonge (1996) employed the SEM aiming to determine killing strategy of *S. fatalis* through the comparison of the canines microwear of different extant carnivorans.

Dewar (2004) employed a stereomicroscope following the technique described by Solounias and Semperebon (2002) to examine the paracone of the upper first molar (M1). The author compared extinct carnivorous mammals from Palaeocene Epoch (e.g., miacids, condylarths, creodonts) with extant species from six genera (*Ursus*, *Canis*, *Lycaon*, *Otocyon*, *Urocyon*, and *Ailuropoda*). Dewar concluded that, in Carnivora, pits are the primary features distinguishing meat consumption, rather than scratches (Dewar, 2004). Goillot et al. (2009) used a

3. Methodological framework

stereomicroscope, incorporating an image-automated variant (from Merceron et al. 2004, 2005) of the method developed by Solounias and Semperebon (2002), to observe and quantify microfeatures on the slicing and grinding facets of the upper and lower first molars (M1/m1) in extant carnivorans, including species from the families Ursidae (*Ursus maritimus*, *A. melanoleuca*, *Melursus ursinus*, *Tremarctos ornatus*), Ailuridae (*Ailurus fulgens*), Hyaenidae (*H. hyaena*, *C. crocuta*), Mustelidae (*Lutra lutra*, *Enhydra lutris*, *Meles meles*), Eupleridae (*Eupleres goudotii*, *Fossa fossana*), Herpestidae (*Galerella sanguinea*, *Mungos mungo*), Felidae (*Leptailurus serval*), Procyonidae (*Potos flavus*), and Canidae (*Vulpes vulpes*). This study aimed to infer the palaeodiet of the Miocene caniform *Amphicyon major*. They concluded that the stereomicroscope is an effective tool for quantitatively distinguishing between different diets in carnivorous and omnivorous members of Carnivora (Goillot et al., 2009). Their results demonstrated that the number of total scratches, total pits, coarse scratches, large pits, fine scratches, and small pits on the slicing facet are sufficiently distinct to differentiate dietary habits on carnivorans. For the grinding facet, the presence of curve scratches and oval pits (= puncture pits) on grinding facet was found to be linked to specific omnivore and carnivore diets in the Carnivora clade (Goillot et al., 2009).

Applying low-magnification microwear analysis developed by Solounias and Semperebon (2002), Bastl et al. (2012) created a comprehensive microwear reference dataset of extant carnivorans with different diets that included species from the families Hyaenidae (*Parahyaena brunnea*, *H. hyaena*, *C. crocuta*), Felidae (*A. jubatus*, *P. leo*), Canidae (*V. vulpes*), Viverridae (*Genetta genetta*), and Nandiniidae (*Nandinia binotata*). This study examined the carnassial teeth (P4/m1) of extant carnivorans to infer the diet of the extinct *Hyaenodon*. This genus, which lived during the Eocene to Miocene epochs, had its carnassial function performed by the lower second molar (m2), for which microwear was observed. The analysis revealed that the number and size of pits, rather than scratches (as is the case for herbivores), were effective discriminants for identifying carnivorous taxa, thereby confirming Dewar's (2004) conclusions. Hence, the pits made it possible to distinguish between soft diets, such as those of exclusive flesh eaters like the cheetah (*A. jubatus*), bone-crushing diets as seen in the spotted hyena (*C. crocuta*), and intermediate dietary adaptations like those of the lion (*P. leo*) (Bastl et al., 2012). Moreover, specific microwear patterns, particularly puncture pits and large pitted surfaces, were directly associated with a frugivorous diet in omnivorous carnivorans (Bastl et al., 2012). These variables effectively differentiated species based on the amount of fruit consumed.

Xafis et al. (2017) also applied low-magnification microwear analysis to eight Carnivora guild species with differentiated diets, including *A. jubatus*, *C. crocuta*, *G. genetta*, *H. hyaena*, *L. lutra*, *N. binotata*, *P. brunnea*, and *V. vulpes*. The study aimed to compare the microwear patterns of premolars and non-carnassial teeth with those of the second permanent molars and carnassial teeth. The results revealed an almost identical statistical microwear signal between non-carnassial and carnassial teeth in these carnivorous species. Additionally, dietary distinctions, such as preferences for meat/bone, frugivorous, or mixed diets, indicated by variations in pit size frequency among carnivorous taxa, as observed in previous studies using the carnassial teeth (P4/m1) (Dewar, 2004; Goillot et al., 2009; Bastl et al., 2012), could also be differentiated on non-carnassial tooth positions (Xafis et al., 2017).

Dental microwear analysis using confocal microscopy and texture analysis, as developed by Ungar et al. (2003), has also been applied to study diet in Carnivora. Stynder et al. (2012) analysed the upper first molars (M1) of Mio-Pliocene hyaenids and compared their textures with those of extant feliforms (*C. crocuta*, *A. jubatus*, *P. leo*). They concluded that the fossil hyaenids exhibited smoother microwear textures than extant hyenas and, conversely, displayed patterns similar to those of the extant African lion (*P. leo*). Thus, they suggested low bone consumption by Mio-Pliocene hyaenid species (Stynder et al., 2012). The same methodology was used to infer the diet of the extinct sabre-toothed cat (*S. fatalis*) and American lion (*P. leo atrox*) (DeSantis et al., 2012). The results indicated that while *S. fatalis* did not avoid bones, as suggested by its microwear patterns being similar to those of the extant African lion (*P. leo*), *P. leo atrox* did avoid bones, displaying a texture pattern more akin to that of the extant cheetah (*A. jubatus*) (DeSantis et al., 2012).

3.5 Dental microwear on bears (Ursidae family)

Although dental microwear studies on carnivores have occasionally included bear species in their reference datasets (e.g., *U. arctos* and *A. melanoleuca* in Dewar, 2004; *U. maritimus*, *A. melanoleuca* and *M. ursinus* in Goillot et al. 2009), studies specifically focused on developing a reference collection to infer the diet of extinct ursids have only recently been undertaken (Pinto-Llona, 2006; Peigné et al., 2009; Donohue et al., 2013; Münzel et al., 2014; Pappa, 2016; Pappa et al., 2019), and their application to fossil populations remains limited (e.g., Jones and DeSantis, 2016; Medin et al., 2017, 2019; Ramírez-Pedraza et al., 2019, 2020, 2022)

The first dental wear study to observe microwear features, albeit in a qualitative and not standardized manner, was conducted by Pinto-Llona and Andrews (2001) using an optical

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microscope at unspecified low magnifications. They examined the microfeatures on the occlusal surfaces of the extinct *U. spelaeus* and *U. arctos*, as well as the extant *U. arctos*, all from northern Iberia, to assess degree of abrasiveness of their respective diets. The authors concluded that cave bears from northern Iberia had a more carnivorous diet, displaying low grit content in their foods, when compared to both extinct and extant brown bears, which in turn would have had a highly abrasive diet (Pinto-Llona and Andrews, 2001). A few years later the authors better standardized the method of analysis, thus observing two facets of the lower first molar (m1) using SEM at x200 magnifications: the distal facet of the protoconid and the lingual facet of the hypoconid (Pinto-Llona, 2006). According to this study, *U. spelaeus* exhibited a high proportion of pits relative to scratches on both facets, whereas *U. arctos* showed a higher concentration of scratches on both surfaces. This was interpreted, as in their previous study, as indicative of meat consumption for *U. spelaeus* and of grass consumption for *U. arctos*. Finally, Pinto-Llona (2013) re-examined both species with an expanded sample size and reached the same conclusions regarding the relative proportions of pits and scratches. They further hypothesised that the large number of pits observed in cave bears could be attributed to bone consumption.

Peigné et al. (2009) conducted the first detailed microwear study on cave bear (*U. spelaeus*) palaeodiet using the low-magnification method developed by Merceron et al. (2004) and Merceron (2005) and compared their findings to the extant carnivoran dataset from Goillot et al. (2009), which was developed employing the same methodology. They investigated the short-term pre-dormancy diet of cave bears from Goyet Cave in Belgium by analysing the labial facet of the m1 paraconid. The study concluded that cave bears were not strictly herbivorous, as previously suggested by stable isotopic studies (e.g., Bocherens et al., 1994, 1997), but instead had a generalist omnivorous diet that included a wide range of items, such as hard objects (e.g., bone), vertebrates and invertebrates (meat and insects) and plant foods like herbs and fruits (Peigné et al., 2009). However, the reference dataset used had significant limitations, as noted by Bocherens (2009) in a response to the article. First, the study included a broad range of carnivorans with distant phylogenetic relationships to the analysed *U. spelaeus* population, making comparisons inappropriate due to distinct tooth morphology and dietary behaviours (Bocherens, 2009). Moreover, the only Ursidae members included were the polar bear (*U. maritimus*) and the giant panda (*A. melanoleuca*), both of which have evolved in highly specialized diets —hypercarnivore for *U. maritimus* and specialized bamboo diet for *A. melanoleuca*— adapting to niches and environments that are not representative of Pleistocene

ecosystems or neither to the behaviour of temperate bear species (Bocherens, 2009). Therefore, to ensure reliability, it was necessary to compare *U. spelaeus* with closely related bear species living in temperate environments, such as *U. arctos*, *U. thibetanus*, or *U. americanus* (Bocherens, 2009).

Donohue et al. (2013) used confocal microscopy and texture analysis, as developed by Ungar et al. (2003), on a collection of extant bear species (*U. americanus*, *U. maritimus*, *A. melanoleuca*, *Helarctos malayanus*, and *T. ornatus*) to infer the diet of the extinct short-faced bear (*Arctodus simus*) from North America. They concluded that the lower second molar (m2) mesial facet (hypoconulid) was the most reliable tooth position for differentiating dietary regimes from sampled extant specimens. The m2 texture comparison demonstrated that extant carnivorous and omnivorous bears (*U. maritimus* and *U. americanus*) exhibit higher and more variable complexity of surfaces (i.e., pitted surface) when compared to species with a plant-based diet (*A. melanoleuca*, *T. ornatus*, *H. malayanus*) (Donohue et al., 2013). *A. melanoleuca*, with an obligate herbivorous diet clearly distinguished from meat eaters such as *U. maritimus* and *U. americanus*, on bases of the “anisotropy” variable which is linked to more scratched rather than pitted surfaces (Donohue et al., 2013). The analysed fossil *A. simus* exhibited anisotropy and complexity values similar to those of *T. ornatus*, indicating the consumption of hard objects, which suggested bone consumption and possible scavenging behaviour (Donohue et al., 2013). Moreover, applying the methodology and reference developed by Donohue et al., (2013), Jones and DeSantis (2012) analysed *U. spelaeus* specimens from two different museums (the American Museum of Natural History, New York, and the Field Museum of Natural History, Chicago), of unknown or unpublished origin, and analysed them as a unique population. They concluded that cave bears, as a species, exhibited a highly variable omnivorous diet (Jones and DeSantis, 2016). This microwear analysis using confocal microscopy presented several limitations. First, the origin of the samples analysed was unknown, making it unclear whether they were collected from wild populations or captive individuals. Second, the omission of *U. arctos*, the bear species with the broadest distribution and most variable diet today, is a significant limitation, as highlighted by Münzel et al. (2014). Third, in the study by Jones and DeSantis (2016), the lack of information on the origin of *U. spelaeus* specimens and the treatment of cave bears with different chronological and geographical backgrounds as a single population is problematic. Given that bears are opportunistic feeders whose diets are heavily influenced by their environment and the resources

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available (Bojarska and Selva, 2012), these factors are critical for accurate dietary interpretations.

Münzel et al. (2014) combined low-magnification stereomicroscope method developed by Solounias and Semperebon (2002) with stable isotopes analysis ($\delta^{13}\text{C}$, $\delta^{15}\text{N}$ and $\delta^{18}\text{O}$) to infer the ecology of phylogenetically different cave bear populations. They included (1) two *U. spelaeus* populations from the southwestern Germany sites of Hohle Fels and Geißenklösterle, (2) *U. ingressus* holotype population (Rabeder et al., 2004a) from Gamssulzen in Austria, (3) *U. s. eremus* holotype population (Rabeder et al., 2004b) from Ramesch (Münzel et al., 2014). The cave bear populations were compared with a newly developed microwear dataset of extant bears, including *U. arctos*, *U. americanus*, *U. maritimus*, *U. thibetanus*, and *A. melanoleuca*. The analysis quantified microwear features in two distinct regions near the protoconid on the grinding surface of the lower first molar (m1): (1) faceted (worn) surfaces and (2) un-faceted (unworn) surfaces. The results obtained questioned the assertion by Pinto-Llona et al. (2013) that the prevalence of pits observed in cave bears from northern Iberia was indicating a more carnivorous diet. Instead, it suggested that a higher number of pits combined with fewer scratches is indicative of a more herbivorous diet, a pattern seen in the most herbivorous bears, exemplified by *A. melanoleuca* which displayed the highest numbers (Münzel et al., 2014).

The reference collection was latter used to infer the palaeodiet of Late Pleistocene cave bears with successful results (Ramírez-Pedraza, 2017). The analysis suggested that *U. spelaeus* from Toll Cave (NE Iberia, Spain) had an omnivorous pre-dormancy diet. However, the author acknowledged the limitations of the reference collection owing to a small sample size which constrained the interpretation of the results (Ramírez-Pedraza, 2017).

In a multidisciplinary study on Early Pleistocene carnivores from Orce (Guadix-Baza, Spain), Medin et al. (2017) applied the low-magnification microwear method to Late Villafranchian (ca. 1.2 Ma) *U. etruscus*. They analysed both the grinding and slicing facets (P4/p4, M1/m1, M2/m2) using the protocol from Münzel et al. (2014) and included *U. arctos* ($n = 17$) from its dataset and *U. maritimus* ($n = 11$) from Dewar (2004) for comparison. However, the authors employed a feature-density-based quantification differing slightly from Münzel et al. (2014). The results demonstrated that densities of pits, gouges, and scratches effectively discriminate the dietary habits of both extant and extinct carnivores and omnivores. Statistical analyses among all carnivores, including *U. etruscus*, indicated a varied omnivorous diet in *U. etruscus*, closely mirroring that of extant *U. arctos*. In a follow-up study, Medin et al. (2019)

examined *U. etruscus* from Dmanisi (1.8 Ma) using the same methodology and reached the same conclusion: *U. etruscus* exhibited a highly variable omnivorous diet.

Up until this point, the analysis of microwear in ursids faced limitations due to constraints related to the reference collection. While the reference dataset established by Münzel et al., 2014 proved to be useful, it lacked sufficient sample size and included individuals whose wild-caught status and locations were not well-documented, factors that significantly influence dietary regimes. Consequently, there was a clear need for a new reference collection comprising wild ursids from known locations, with well-documented diets.

Spyridoula Pappa's PhD thesis focused on developing a microwear reference collection of extant bears to reconstruct the diet of Pleistocene fossil bear populations from UK and Greece, including *U. spelaeus*, *U. ingressus* as well as *U. arctos* (Pappa, 2016). This new collection was established using a stereomicroscope at low magnification (x35), following the methodology of Solounias and Semprebon (2002), and was later published (Pappa et al., 2019). The reference collection comprised 110 wild-caught adult specimens of all eight extant bear species (*U. arctos*, *U. maritimus*, *U. americanus*, *U. thibetanus*, *H. malayanus*, *Tremarctos ornatus*, *M. ursinus* and *A. melanoleuca*). For *U. arctos*, specimens were sourced from various geographical regions, including Greece, central and northern Europe, Kamchatka (Russia), and North America (USA, including Alaska, and Canada). Microwear analysis on all extant species specimens was conducted on the non-faceted occlusal surface of the lower first molar (m1), as established by Münzel et al. (2014), examining both the slicing and grinding areas. The study concluded that the grinding area (talonid) provided the best differentiation between dietary regimes (Pappa et al., 2019).

The previously described methodology was applied in the present study, and since its publication, it has contributed to various articles on the ecology of Pleistocene cave bear populations (Pappa, 2016; Pappa et al., 2019; Ramírez-Pedraza et al., 2019, 2020, 2022). The first application of this method to fossil specimens demonstrated significant dietary variability between Pleistocene bear species (*U. deningeri*, *U. spelaeus*, and *U. arctos*), as well as intraspecific (between populations of the same species) and intrapopulation variability, according to geographical region and chronology (Pappa, 2016). Following the publication of the method and to prove reliability on a fossil population, the authors analysed brown bears (*U. arctos*) from the late Middle Pleistocene site of Grays Thurrock (UK). They concluded that the

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MIS 9 *U. arctos* had an omnivorous, plant-based diet as an adaptation to warm climate conditions (Pappa et al., 2019).

Furthermore, Ramírez-Pedraza et al. (2019) compared the collection from Pappa et al. (2019) to the *U. spelaeus* population from Toll Cave, which had previously been compared with the collection from Münzel et al. (2014). This new comparison provided stronger support for seasonal omnivorous behaviour in this population (Ramírez-Pedraza et al., 2019). Ramírez-Pedraza et al. (2020) conducted a regional microwear analysis of cave bear and brown bear populations from northeastern Iberia (Arbreda Cave, Ermitons Cave, Teixonerres Cave, Toll Cave, Mollet Cave, and Llenes Cave), concluding that the southern-European MIS 3 *U. spelaeus* populations exhibited omnivorous seasonal diets with significant variability between them. In a subsequent study, Ramírez-Pedraza et al. (2022) analysed three different cave bear species (*U. ingressus*, *U. kenivetz* and *U. rossicus*) from the Ural Mountains that coexisted during MIS 3. The authors identified distinct dietary regimes for the three different cave bear species analysed, although all within a plant-based abrasive diets typical of the Mammoth Steppe biome, and demonstrated niche partitioning between the two cave bear species, *U. kenivetz* and *U. rossicus*, that coexisted in the same area (Ramírez-Pedraza et al., 2022). This study only selected the *U. arctos* from various regions and *U. americanus* from North America from the collection of Pappa et al. (2019), as they are the closest extant relatives to the cave bear lineage, which can be reflected in similar behaviours such as hibernation. Moreover, their distribution in the northern hemisphere, within environments analogous to those of the Pleistocene, suggested comparable dietary patterns (Ramírez-Pedraza et al., 2022). The authors excluded other bear species from comparisons with fossil cave bears for two primary reasons. First, these species were phylogenetically or evolutionarily too distant, exhibiting behaviours and diets markedly different from those of cave bears (e.g., *A. melanoleuca*, with an obligate bamboo diet, or *U. maritimus*, inhabiting the polar regions and subsisting exclusively on seals and fish). Second, some species inhabited regions with climates and environments incomparable to those of Pleistocene Europe (e.g., tropical forest from south-east Asia for *H. malayanus* or the Andean rainforests of South America for *T. ornatus*).

The methodology applied in the present work builds upon insights gained over years of research in microwear analysis on bears, with a particular focus on cave bear short-term diet investigations. This study represents the first comprehensive macro-scale analysis of cave bear populations with a substantial sample size using this method, aiming to elucidate the degree of dietary diversity within the cave bear lineage.

GEOGRAPHICAL CONTEXT

4. Geographical context

This study includes populations from the eastern regions of the European continent; from the Romanian Carpathians, Moldavian Plateau, Western Balkans and Western Rhodopes, and Central Balkans, as well as from the Eurasian reaches of the continent; namely the Greater Caucasus and the Northern Urals (Figure 5).

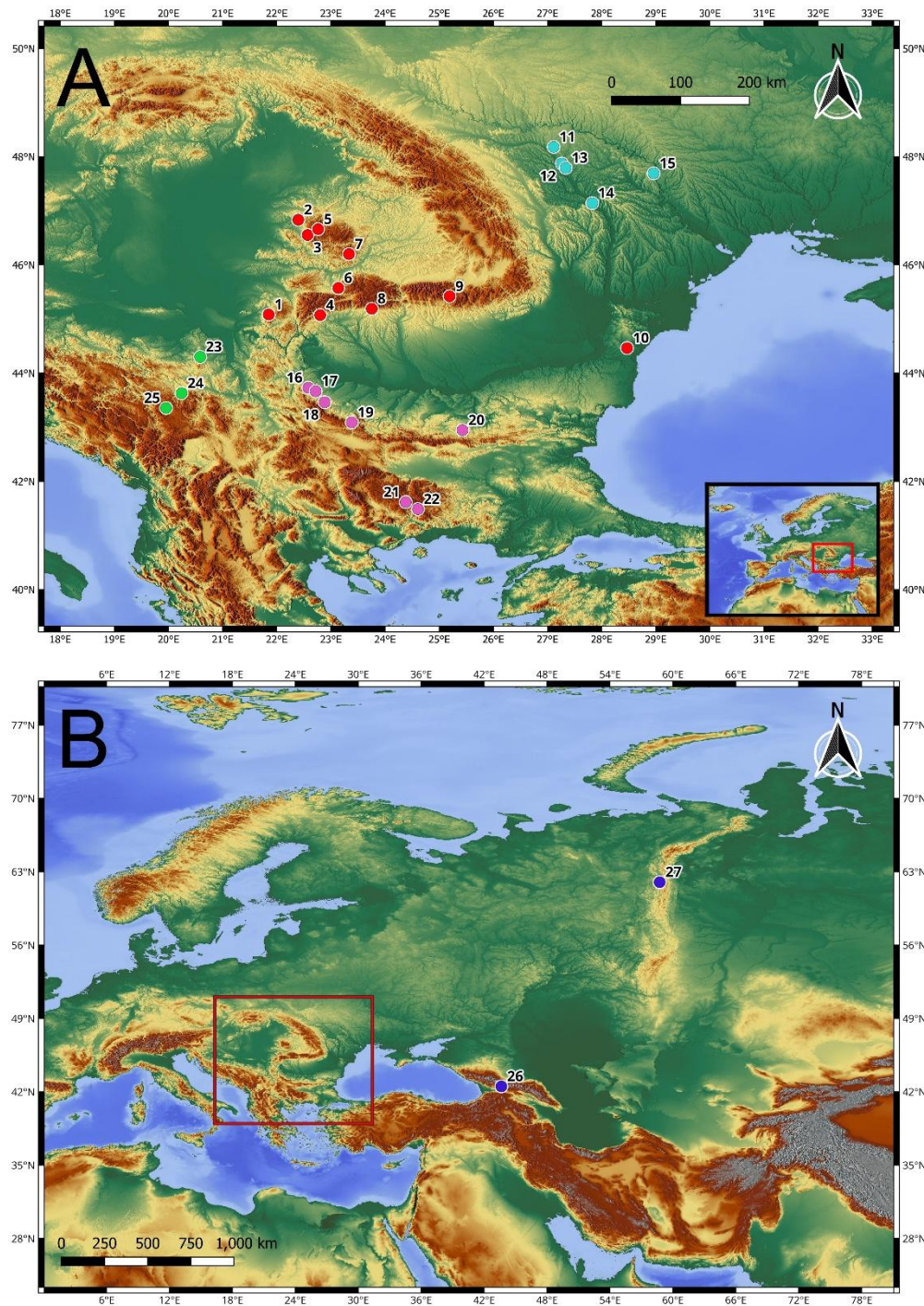


Figure 5. Mapa of the location of the sampled populations of cave bears (*U. spelaeus* sensu lato) and brown bears (*U. arctos*) for this study. **A) Eastern Europe (1 to 25): Romanian Carpathians (1-10):** 1. Oase. 2. Avenul Măţului. 3. Urşilor. 4. ACCG.

5. Onceasa. 6. Cioclovina Uscată. 7. Bisericuța. 8. Muierilor. 9. Colțul Surpat. 10. La Adam. **Moldavian Plateau** (11-15): 11. Trinca 12. Duruitoarea Veche. 13. Butești. 14. Buzdujeni. 15. Saharna. **Western Balkans and Western Rhodopes** (16-22): 16. Magura. 17. Bashovichki Pech. 18. Mishin Kamik. 19. Lakatnik. 20. Bacho Kiro. 21. Triagalna. 22. Borikovska. **Central Balkans** (23-25): 23. Risovača. 24. Hadži Prodanova. 25. Ušačka. **B) Eurasia** (26 and 27): **Greater Caucasus** 26. Kudaro 1 and 3. **Northern Urals** 27. Medvezhiya.

4.1 Romanian Carpathians

The populations from the Romanian Carpathians region, sites 1 to 9, are distributed across the Apuseni Mountains (2,3,5 and 7) and the Southern Carpathians, or also named Transylvanian Alps (1,4,6,8 and 9), while number 10 is in the Black Sea coast (Figure 6).

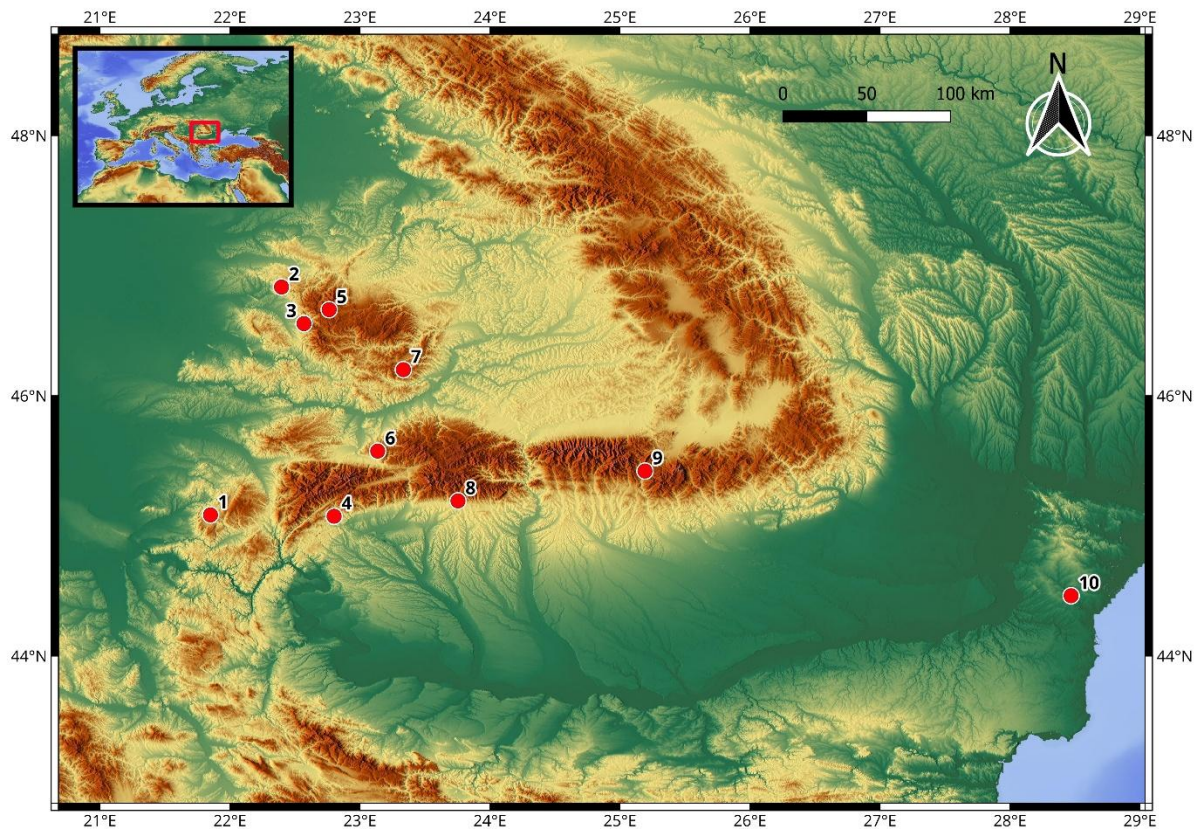


Figure 6. Location of the sampled populations of cave bears (*U. spelaeus*) and brown bears (*U. arctos*) from the Romanian Carpathians: 1. Oase. 2. Avenul Mățului. 3. Urșilor. 4. ACCG. 5. Onceasa. 6. Cioclovina Uscată. 7. Bisericuța. 8. Muierilor. 9. Colțul Surpat. 10. La Adam.

1. Oase

Oase Cave (=Peștera cu Oase) is located in the central part of Anina in Caraș-Severin (Banatuli Mountains), at *ca.* 600 meters a. s. l. in the Western Carpathians (southwestern Romania), with the following coordinates 45° 05' 00" N, 21° 51' 00" E (Constantin et al., 2013). The discovery of the cave can be attributed to a speleologist group regarded as “Pro Acva Grup of Timișoara” that in 2001 starts the exploration and documentation of the Peștera Ponor-Plopa karstic system (Milota et al., 2013). The cave represents the upper levels of Ponor-Plopa Cave system (Figure 7 and 8), which comprehends more than 2,000 meters of karstic galleries, formed through the drainage of the Ponor stream (Constantin et al., 2013).

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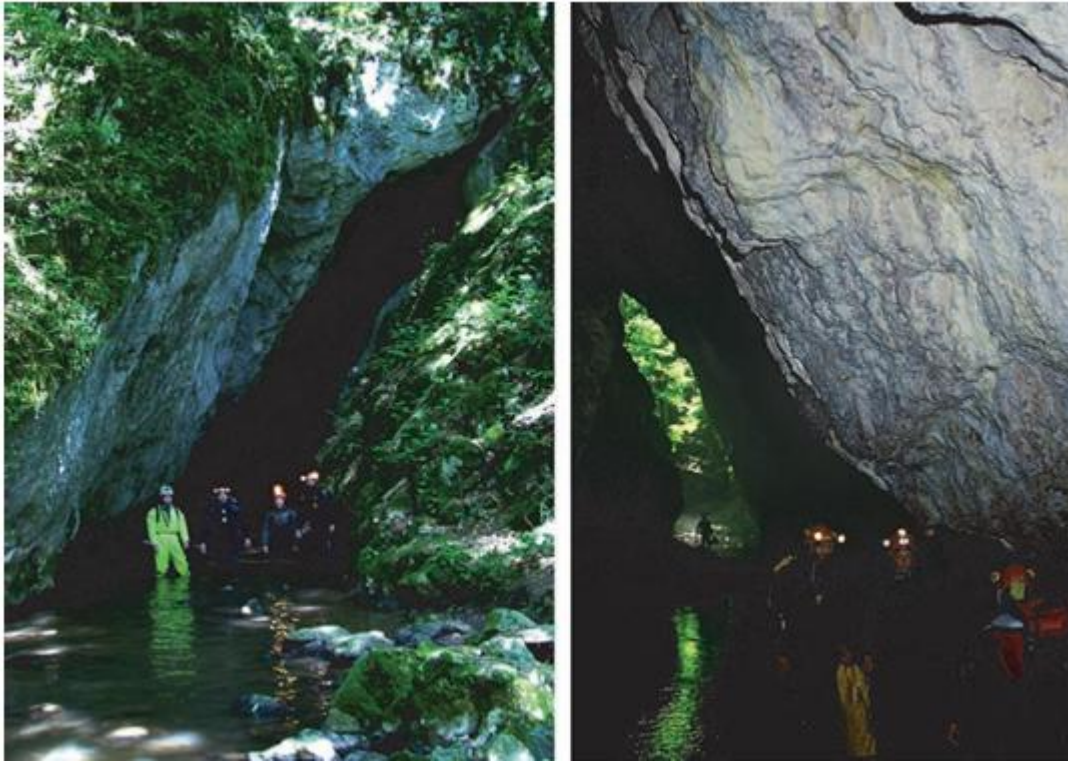


Figure 7. View of the entrance to Peștera Plopa-Ponor, located along the Miniș River, showing the external perspective on the left photo and the internal perspective on the right one (extracted from Trinkaus et al., 2013).

Oase Cave has two karstic levels, a hydrologically inactive upper karstic level and an active lower one (Figure 8). The upper level was sealed since the Late Pleistocene and was found during the exploration of the cave by entering through the southern river by the speleologists Milota, Bîlgăr and Sarcină in February 2002 (Milota et al., 2013). This group cleared the clay and cave bear bones blocking a narrow passage, later named Poarta (Gate), which allowed them to access a series of galleries that had remained sealed, protected, and untouched since the end of the Pleistocene. Navigating the newly discovered passages, later named Galeria Culcușurilor (Gallery of the Nests) and Panta Strămoșilor (Slope of the Ancestors), while carefully avoiding the widespread remains of Pleistocene cave bears (*U. spelaeus*), they reached a large chamber. Resting on the undisturbed surface of calcite, the explorers discovered an almost entirely intact human mandible (to be designated as Oase 1) in what would later be named Sala Mandibulei (Room of the Mandible) (Trinkaus and Rougier, 2013). Additionally, during the mapping of the karstic galleries, Milota uncovered a complete human facial skeleton (to be designated Oase 2) while measuring the passage width of Panta Strămoșilor. Further human remains, all belonging to the same individual (Oase 2), including fragments of an almost complete cranium, were also documented in the area of Panta Strămoșilor during subsequent years of excavation (Rougier and Trinkaus, 2013). Since then, Sala Mandibulei and Panta Strămoșilor sections of

Oase Cave are renowned for containing the remains of the earliest anatomically modern humans in Europe (Trinkaus and Rougier, 2013; Trinkaus et al., 2013).

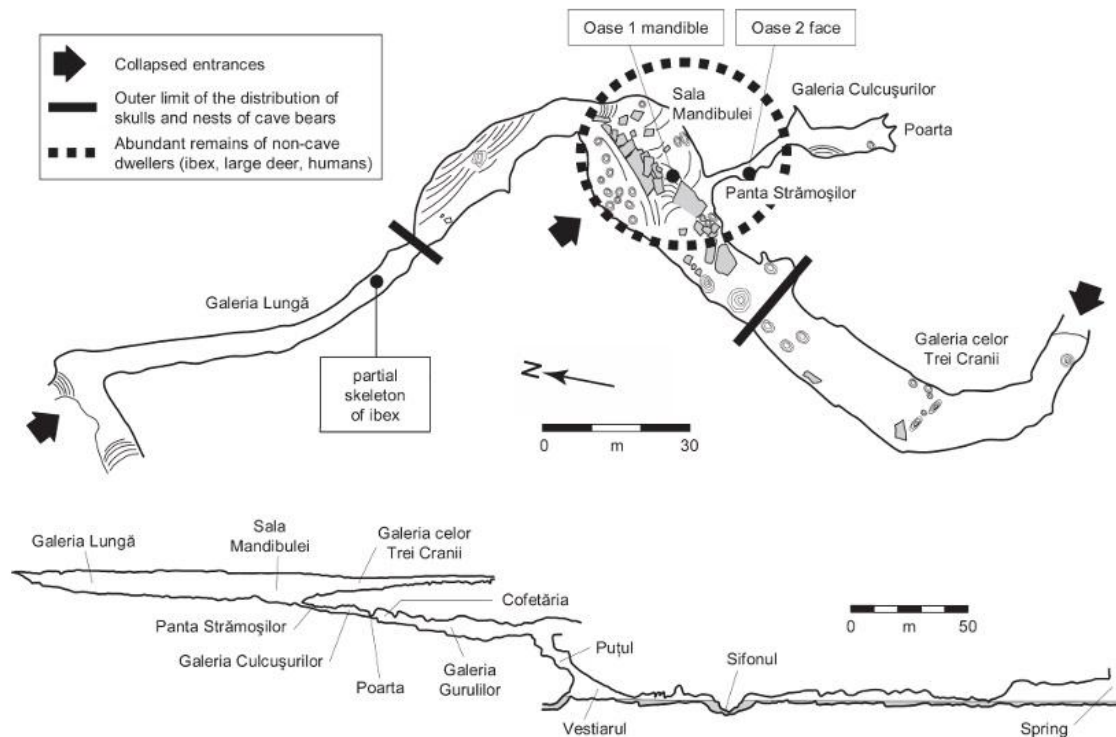


Figure 8. Planimetry of Oase Cave (from Zilhão, et al., 2013)

In 2004, a team led by João Zilhão and Ricardo Rodrigo began an initial documentation campaign of the cave's surface (Zilhão et al., 2013a). They concluded that the galleries had been frequently used by cave bears, as evidenced by numerous hibernation nests, especially in Sala Mandibulei, Panta Strămoșilor, and Galeria Culcușurilor. This conclusion was further supported by the large number of *U. spelaeus* bones found on the gallery surface, particularly in Panta Strămoșilor. The surface bones appeared to be in secondary position, and there were also signs of recent incursions by small carnivores and mesocarnivores, which disturbed the record by creating burrows and leaving bones on the surface. The team decided that the first site to excavate in order to understand the cave's complex dynamics would be Panta Strămoșilor. A grid was established, and from 2004 to 2005, they began an extensive excavation of the bone bed in Panta Strămoșilor, covering an area of approximately 10 m² and with a maximum depth of 80 cm (Zilhão et al., 2007; Zilhão et al., 2013a).

The first excavation defined three stratigraphic levels for Panta Stramoșilor gallery (Figure 9), from the top to the bottom (Zilhão et al., 2013b):

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- Surface Level: The superficial unit comprises a collection of visible fossil remains, either loose or exposed on the deposit's surface. Some of these finds are coated with a thin layer of clayey silts, less than 1 cm thick, which accumulated between the deposit surface and the cave wall in some border grids.
- Level 1: The first core layer, which ranges in thickness from 5 to 30 cm, comprises a densely packed and entangled layer of bones, primarily from cave bears. These are associated with unweathered rock, including fractured speleothems and limestone blocks fallen from the nearby cave walls. The gaps in between were filled with a fine, gritty cave earth matrix. In some areas flowstone patches covered the deposit, with notable areas of subsurface carbonate hardening due to dripping.

The bones in Surface Level and Level 1, were white in colour and exhibited poor preservation, as evidenced by severe leaching, fresh breaks and a surface covered by bone debris. The extensive breakage and poor preservation of the bones suggests prolonged exposure to surface weathering, namely cave humidity and karstic flows. Additionally, the low percentage of smoothed, abraded or polished elements suggests that the final stage of the Panta Stramoșilor accumulation occurred under much drier conditions, with only low-energy water flow (Pacher and Quilès, 2013b).

- Level 2: The unit is characterised by a matrix comprising sandy to coarse-grained sediments, including pebbles, rounded limestone cobbles, and rolled speleothems. The deposit contains a high concentration of cave bear bones, representing up to a quarter of the total volume. These bones are small in size, including teeth, phalanges, and unfused long bones from prenatal and juvenile individuals. However, larger material was discovered at the base of the level, including a complete skull of cave bear. Various subunits, characterised by differing matrix textures (exemplified by homogeneous clay layers and coarse sand and gravel bars), were identified across the *ca.* 65 cm thick excavated package. This diversity in the size of the sediment grain of the deposit suggests a long-term, fluctuating-energy accumulation process.



Figure 9. Panta Stramoșilor stratigraphy and excavation levels overview (from Zilhão et al., 2013b); a) Stratigraphic profile of the 37 number row of the excavation grid. b) The O35–36 section with its materials infills as seen against profiles along the middle of the 36 row (in the foreground) and the middle of the 37 number row (in the background) of the excavation grid. c) Surface view of units O34–35 of the grid. d) Overview of the Level 1 bone accumulation in O34. e) N33 square with the surface of Level 2 exposed f) Detailed view of Level 2 package on the N32 to N33 section profile.

The bones of Level 2 appeared very well preserved both morphologically and chemically, with orange to brown coloration (Zilhão et al., 2013b). These presented only slight to no polished surfaces, preserving all the anatomical details, and the tissue remained solid with no leaching. Their excellent state of preservation was further confirmed by their high collagen content (Higham and Wild, 2013). The exceptional preservation of the bones indicates those were

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rapidly buried due to the occurrence of a series of high to very high energy torrential events, that, in turn, explain the presence of distinct sedimentological subunits within the deposit. Furthermore, a higher degree abraded, smoothed, and polished bones in comparison to Surface Level and Level 1, further supports high energy water flows for Level 2 (Pacher and Quilès, 2013b).

The excavation of Panta Stramoșilor uncovered large bone beds with almost all cave bears (*U. spelaeus*) (MNI = 3,267 identified remains; MNI = 130) (Pacher and Quilès, 2013a, 2013b). followed by a variety of remains of *C. lupus*, more specifically in Level 1 and 2 from Panta Stramoșilor gallery. Furthermore, a single red fox (*V. vulpes*) and cave hyena (*C. c. spelaea*) remains were discovered in the surface of Galeria Lungă. The spatial and taphonomic study of the gallery indicates that most of cave bear remains derive principally from higher galleries of the Peștera cu Oase and were transported by water into the Panta Strămoșilor (Pacher and Quilès, 2013b; Zilhão, et al., 2013b). Furthermore, the gnawing of cave bear bones represents the second most common modification, which has been identified to be produced mainly by wolves (Pacher and Quilès, 2013b). The analysed cave bear teeth of this work were recovered during the excavations performed in Sala Mandibulei and Panta Stramoșilor, levels 1 and 2 and dated to *ca.* 50–41.5 ka. cal B.P. (Higham and Wild, 2013). Given the short evolutionary timespan, the cave bear sample can be treated as a single population, allowing for comprehensive palaeodietary inferences to be drawn from the entire group.

The age-at-death of the *U. spelaeus* specimens, attributed following the protocol established by (Stiner, 1998, 1994) and using the lower first molars (m1) and fourth premolars (p4), concluded that the cave bear assemblage is juvenile dominated (Pacher and Quilès, 2013a). Juvenile individuals constitute 73.8% of the sample, followed by adults at 18.5%, while senile bears represent only 7.7% of the population. The distinct U-shaped mortality pattern indicates a natural, nonviolent cause of death, likely occurring during hibernation.

Sex determination, based on both upper and lower canines, whether isolated or attached, revealed a predominantly male-dominated assemblage, though relatively balanced (Pacher and Quilès, 2013a). The study resulted in 27 females to 36 males (42.9% vs 57.1%), yielding a male-to-female ratio of 0.8 (Pacher and Quilès, 2013a).

Hence, Oase Cave provides a well-preserved and representative population of cave bears, with a balanced distribution of sex and age, reflecting the natural demographic structure of a living population that perished during hibernation.

2. Avenul Mățului

Avenul Mățului (with the following coordinates: 46° 50' 07" N, 22° 23' 46" E) is a *ca.* 100-meters-long vertical and horizontal cave from the Cuților Gorges, in the western part of the Apuseni Mountain group (Pădurea Craiului Mountains) at 400 meters a. s. l.. In 2018, Dr. Marius Robu (ERIS) collected samples from a female brown bear skeleton, found at the base of a *ca.* 20-meter drop, inside the cave. The remains were dated to the Holocene, 891 ± 24 years cal B.P. (Ersmark et al., 2019).

3. Urșilor

Urșilor Cave (=Peștera Urșilor) is located in the western slope of the Apuseni Mountains, in the Western Carpathians (northwestern Romania). The entry to the endokarst is located on the left side of the Crăiasa Valley, at 492 meters a. s. l. with the following coordinates 46° 55' 37" N, 22° 56' 92" E (Constantin et al., 2014). The cave was discovered in 1975 through an artificial opening of a near-by marble quarry (Vălenaș, 1979). However, owing the finding of rich assemblage of Late Pleistocene fossil remains and the abundance of speleothems, the cave was promptly protected and studied (e.g., Jürsák et al., 1981; Rusu and Racoviță, 1981). The cave was opened to tourism in 1980, stating today as one of the most visited caves in Romania (Constantin et al., 2014).

The cave consists of 1,500 meters of horizontal and sub-horizontal passages (Figure 10). Two artificial entrances align with former natural entrances, now sealed by sediment and flowstone deposits. The cave has two distinct levels separated by 17-meter-high slope. The hydrologically inactive upper level comprises five primary passages totalling approximately 1,000 meters of horizontal galleries. This is the Bones Passage (access passage), Candlesticks Passage, Twisted Passage, Passage of the Pits, and Emil Racoviță Passage, as well as a large chamber regarded as the Intersection Chamber (Constantin et al., 2014).

At the end of the “Emil Racoviță” Passage, an ascending narrower section known as “The Gate” opens into a breakdown cone, culminating in an 18-meter drop, the Shaft, that descends right into a small chamber, the Excavation Chamber (*ca.* 20 meters wide, 6 to 10 meters in length and 20 meters high just below the Shaft). The Chamber locates <500 meters deep into the karstic system and marks the beginning of the large horizontal passages (10 × 15 meters) of the Scientific Reserve, that extend over 500 meters in length in the lowest levels of Urșilor Cave (Constantin et al., 2014).

4. Geographical context

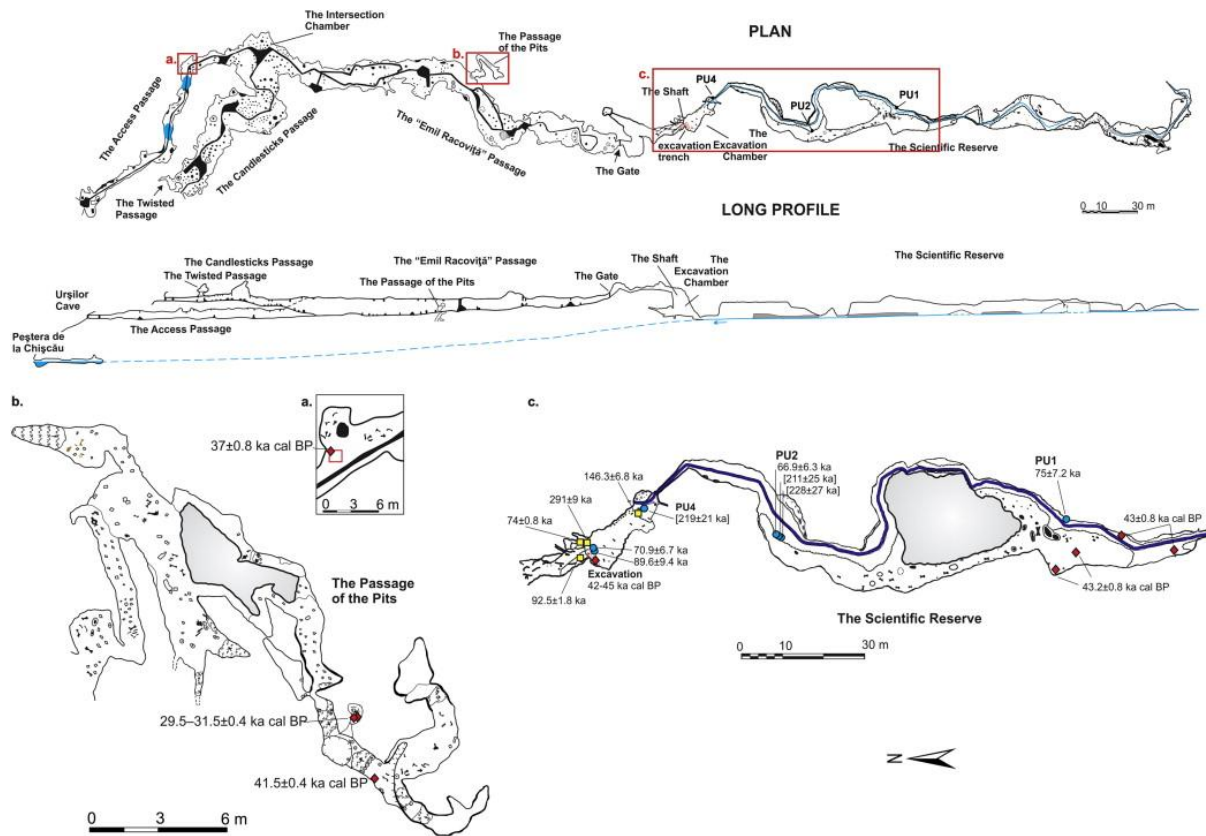


Figure 10. Planimetry of Urșilor Cave (from Constantin et al., 2014).

The first excavations campaigns at Urșilor Cave were conducted in the late 1970s and early 1980s by Terzea and Jurcsak through test pits done near the entrance in the Bones Passage (Jurcsák et al., 1981; Terzea, 1978). Although Urșilor Cave was the subject of numerous studies across various fields, including palaeontology (Terzea, 1978, 1989; Jurcsak et al., 1981; Diedrich et al., 2008, 2009; Robu et al., 2009a, 2009b), geomorphology, tectonics, hydrology (Vălenaș, 1979), sedimentology (Hadrnagy, 1977), and paleoclimate reconstructions (Onac et al., 2002), the inner-most passages, beyond the Excavation Chamber, remained unexcavated until 2010. Since the year 2010 a paleontological excavation extending 10 m², and 2.3 meters deep has been conducted at the Excavation Chamber, by members of Emil Racoviță Speleological Institute from the Romanian Academy of Science (Robu, 2016a). The Excavation Chamber was chosen for study as being situated between two karstic levels at the bottom of a pit fall, and therefore fossil accumulations related to fall and entrapment were expected. Additionally, seasonal floodings with a low-energy hydraulic gradient facilitated sediment deposition, effectively sealing and preserving the fossil assemblage more thoroughly than in other areas of the karst system (Robu et al., 2011, 2016).

Regarding the stratigraphy of the Excavation Chamber (Figure 11), eight different sediment layers (labelled L1 to L8) were defined (Robu, 2015b). While L1, L3, and L5 were abundant in cave bear remains, the other layers were sterile of such findings. The cave bear bone beds are homogeneous, spanning the entire perimeter of the excavation area. The sterile layers, however, were notably thicker in squares A1 to D1 and gradually thinned towards square D4, where they rested on a flowstone terrace. The stratigraphy revealed a channel facies with a low hydraulic gradient corresponding to the main flow direction of the subterranean stream (A1-D1), and a cave terrace facies towards the margins (D1-D4), comprising interbedded cave sediments and flowstone above L5.

The paleontological excavation of sediment deposits in the Excavation Chamber within the Scientific Reserve protected gallery of Urşilor Cave uncovered a large bone bed, almost monospecific and primarily consisting of cave bear (*U. spelaeus*) remains (NISP = 11,511; MNI = 150) (Robu et al., 2016). The only exogenous taxa found were cave lion (*P. spelaea*) bones (MNI = 4; Robu et al., 2018a), one hyena canine (*Crocuta c. spelaea*), and a fox long bone (*Vulpes* sp.) (Robu, 2015b). The cave bear dominated assemblage spans from 47 ka cal B.P. to 27.1 ka cal B.P., based on direct radiocarbon dates on bear mandibles (Constantin et al., 2014; Robu, 2016a; Duñó-Iglesias et al., 2024a).

4. Geographical context

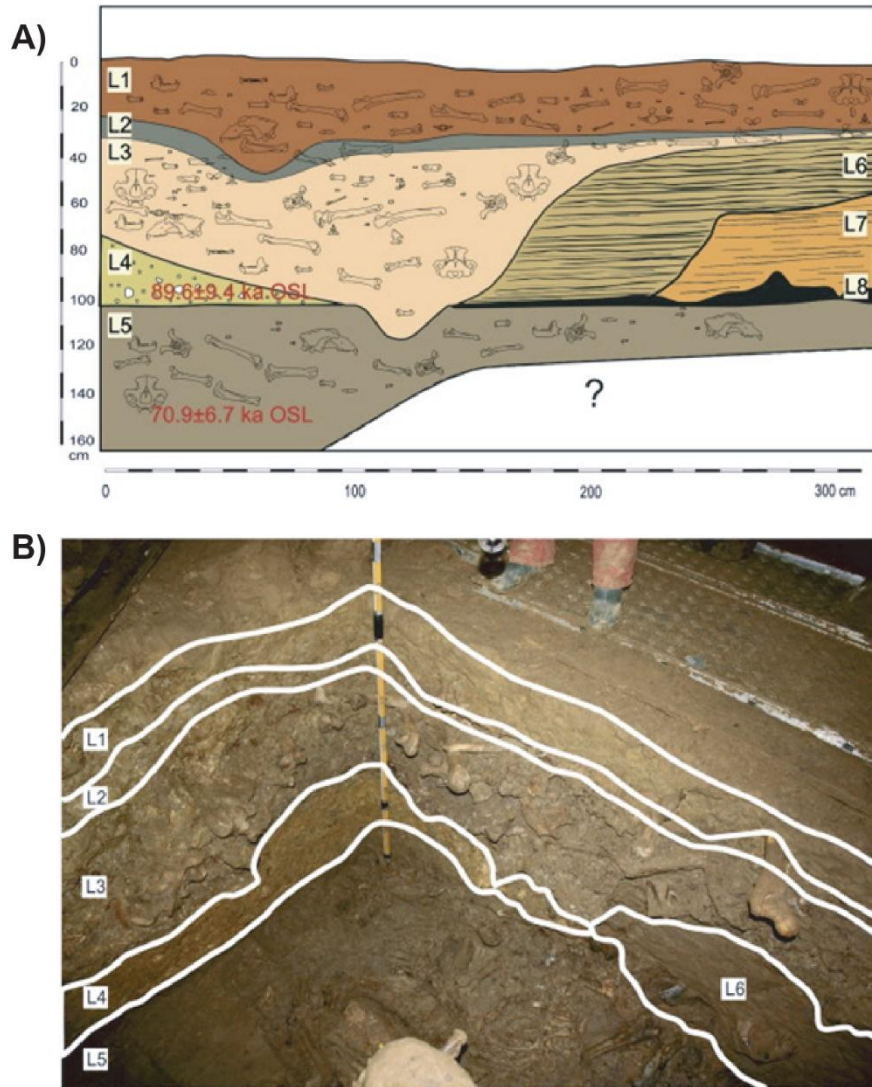


Figure 11. A) Stratigraphic profile of the excavation trench in Urşilor Cave Excavation Chamber along the D1–D4 transect (with 8 layers identified L1–L7) and B) Photography illustrating the main stratigraphic layers identified (extracted and modified from Constantin et al., 2014).

The spatial distribution study of the bones and teeth within the surface of the Excavation Chamber showed a random pattern rather than a preferential orientation of the elements (Robu et al., 2016). Moreover, the presence of several fully-articulated (two skeletons belonging to *U. spelaeus* and *P. spelaea* (Figure 12) respectively) and semi-articulated fossil skeletons and skeletal remains (hind and fore limbs, mandibles, skulls, etc.), supported the idea that the accumulation formed due to pitfall or natural entrapment, discarding the possibility of fluvial transport previously suggested (Robu et al., 2011, 2016).



Figure 12. Fully articulated cave lion (*P. spelaea*) skeleton from Excavation Chamber Level 5 (photo by Dr. M. Robu).

The age-at-death profiles of the cave bear population established using the cheek teeth wear stages developed by (Stiner, 1994, 1998) and applied to both isolated teeth and mandibles, resemble those of a catastrophic mortality event, reflecting the structure of a living population (Robu, 2015a). The juveniles are the dominant age class (57.69–83.33%), followed by the adult individuals (16.66–38.63%), and the senile individuals are seldom represented (0–3.84%) (Robu, 2016b). This can be explained as the Excavation Chamber is located just beneath an 18-meter drop, which suggests that the specimens accumulated by falling and getting trapped within the lower level of the cave in the Scientific Reserve gallery, for which is it not possible to escape (Robu et al., 2011; Constantin et al., 2014). Multiple claw scratches attributed to cave bears were recorded on the clay walls of the lowest gallery in the Scientific Reserve (Robu et al., 2018a). These marks further support the hypothesis that the Scientific Reserve worked as a natural trap for individuals entering the cave to hibernate.

The sex ratio, using the lower and upper canines' measurements reveal an overwhelming predominance of females over males (84.35%:15.64%), providing a ratio of 5.4:1, one of the highest among all European cave bear assemblages (Robu, 2015a). Most of bear remains being females could be explained by the Urșilor inner-most galleries were used as a maternity den by female cave bears, this could be explained by space constraints or partition between males and

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females, for which females might have had to distance themselves into the more inner areas of the caves. This is supported by hibernation nests size. A total of 140 hibernation beds were identified within the cave (Robu et al., 2018a). Comparison with other fossil cave bear nests preserved from other caves (i.e., Oase and Șălitrari), revealed that the hibernation beds in Urșilor Cave were larger (Robu et al., 2018a). This size difference is attributed to the sex ratio, as females, which dominated in Urșilor Cave, likely hibernated with their cubs, thereby increasing the nest dimensions. This is supported by footprints in clay surface portrait a female and a juvenile individual thoroughly searching for a suitable place to hibernate (Robu et al., 2018a).

Hence, the fossil accumulation in the Excavation Chamber provides a reliable representation of the cave bear population that inhabited the Western Carpathians during the MIS 3 period, particularly of females that died during hibernation.

4. Peștera-Aven din Cracul de la Cioaca Goală

Peștera-Aven din Cracul de la Cioaca Goală a (henceforth: ACCG or Cloșani area) is a *ca.* 50 meters-long vertical-horizontal cave, with a *ca.* 20-meter drop from its entrance, situated in the Cloșani area of the Mehedinți Mountains, in the southwestern Carpathians at *ca.* 430 meters a. s. l. (with the following coordinates: *ca.* 45° 03' 50" N, 22° 41' 49" E). In 2011, Dr. Marius Robu (Emil Racoviță” Institute of Speleology; ERIS) collected, from the undisturbed surface of the cave, the bones of three medieval brown bear individuals (one sub-adult female, a juvenile and a sub-adult male; Ersmark et al., 2019) which were found close to the shaft’s bottom, identified and partially collected. The dating of the remains indicates they belong to the late-Holocene period, specifically the medieval age, with a radiocarbon date of $1,109 \pm 26$ years cal B.P. (Duñó-Iglesias et al., 2024a).

5. Onceasa

Onceasa Cave (=The Shepherdess's Cave, henceforth: Onceasa) is located in the Apuseni Mountains, northwestern Romania at *ca.* 1,300 meters a. s. l. (with the following coordinates: 46° 39' 41" N, 22° 45' 46" E). It is one of the richest MIS 3 cave bear bone deposits in the Romanian Carpathians and it consist of *ca.* 350 meters of large passages. The analysed MIS 3 cave bear bone material was sampled from the ERIS’s palaeontological collection and was extracted from the cave during the 1960s (Terzea, 1966).

6. Cioclovina Uscată

Cioclovina Uscată Cave (=Dry Cioclovina Cave, henceforth: Cioclovina) is located in the northwestern part of the Southern Carpathians (Șureanu Mountains) with the following coordinates 45° 34' 27" N, 23° 08' 10" E (Soficaru et al., 2007; Onac et al., 2011). The cave is a 2,002-meter-long fossil karst gallery forming the upper section of the 7.8-kilometer Ponorici-Cioclovina system. During the Pleistocene it was used as a hibernation site for cave bears (*U. spelaeus*). The site, which yielded a human cranium among the oldest in Europe, dated to 32,500 years cal B.P., as well as Upper Palaeolithic lithic artifacts has been the subject of sporadic geological and vertebrate paleontological studies (Soficaru et al., 2007; Onac et al., 2011). The cave primarily contains remains of *U. spelaeus*, with occasional finds of *U. arctos*, *C. lupus*, *P. spelaea*, and *C. ibex* (Rădulescu and Samson, 1959; Păunescu, 1980). The faunal assemblage suggests the site was mainly a hibernation location for cave bears, with occasional use by brown bears and wolves (Soficaru et al., 2007). Results of AMS radiocarbon dating indicate that *U. spelaeus* dwelled the cave from 44.2 to 31.4 ka cal B.P. (Soficaru et al., 2007; Robu et al., 2019).

7. Bisericuța

Bisericuța Cave (=Small Church Cave) is located in the Trascaului Mountains, western Romania at ca. 1200 meters a. s. l. (with the following coordinates: ca. 46° 12' 00" N, 23° 20' 00" E). It consists of ca. 100 meters of hydrologically inactive passages. The sampling area is situated at the bottom of a small shaft in the Excavation Chamber (3 meters deep). The deposit comprises an important MIS 3 cave bear bone assemblage at the lower level of the cave, dated to ca. 50–31 ka cal B.P. (Duñó-Iglesias et al., 2024a).

8. Muierilor

Muierilor Cave (=Woman's Cave) is located in the southeastern Parâng Mountains, in the Southern Carpathians, on the right side of the Galbenul Gorge, and at ca. 645 meters a. s. l. with the following coordinates 45° 11'29" N, 23° 45' 14" E (Mirea et al., 2021). The karstic system is more than 8,000 meters long, and is constituted of five levels (0-4, with only the lowest level 0 being hydrologically active) summing a total of 80 meters of elevation range (Figure 13) (Mirea et al., 2021). Its main galleries include the Touristic Passage (Level 2), accessible to the public, and the Scientific Reserve (Level 1), which encompasses the Hades, Galeria Urșilor (=Bears' Passage), and Electricians passages.

4. Geographical context

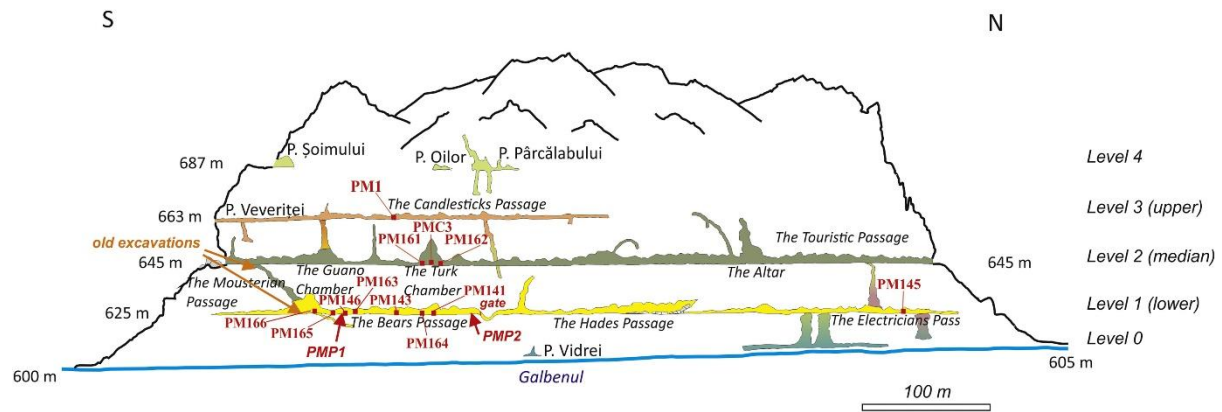


Figure 13. Simplified section of the Muierilor Cave system, displaying all five levels (Level 0 to Level 4) across the limestone formation (extracted from; Mirea et al., 2021).

Excavations of the Late Pleistocene bone deposits began in the early 20th century (Nicolăescu-Plopșor, 1938) and continued in the 1950s (Bombiță, 1954; Nicolăescu-Plopșor et al., 1957) in the cave's lower level (Figure 14), specifically in the Urșilor and Musterian passages (where early human remains were discovered) (Doboș et al., 2010). The Bears' Passage, *ca.* 800 meters long, has been excavated since 2012 by member of the “Emil Racoviță” Institute of Speleology (Figure 15). The fossil material uncovered in the excavation (designed as trench “PMP1”) originates from a secondary thanatocoenosis, reworked from the upper sections of the cave (Mirea et al., 2021). This reworking of bones and sediments from the cave's upper levels likely occurred during four deglaciation pulses, between approximately 22.5 and 14.7 ka cal B.P. (Mirea et al., 2021).



Figure 14. First excavations of Muierilor Cave in 1952. The individual with the beard in the right of both photos is the director Constantin S. Nicolăescu-Plopșor (extracted from Doboș et al., 2010).

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Figure 15. Palaeontological excavation campaign (2016) from the PMP1 area, Urşilor Passage (Scientific Reserve). The "Emil Racoviță" Institute of Speleology team (Photography courtesy of Dr. Marius Robu).

The faunal assemblage is exceptionally diverse (in comparison to the others MIS 3 cave bear dominated karstic assemblages of the region), including large and small mammals such as *U. spelaeus* (MNI = 82), *P. spelaea* (MNI = 4), *C. c. spelaea* (MNI = 3), *C. lupus* (MNI = 25), *Vulpes* sp. (MNI = 3), *Cervus elaphus* (MNI = 6), and several rodent species (Robu et al., 2024). Bone density in the upper section is notably high (200 bones per 0.1 m³), with over 12,000 bones and fragments recovered from PMP1 to date (Robu et al., 2024). The fossil fauna from the excavation and surrounding areas dates from *ca.* 50 to around 22.5 ka cal B.P. (Mirea et al., 2021). However, the MIS 3 cave bear material, extracted from Galeria Urşilor (Bears' Passage; Figure 16), was directly dated between *ca.* 51–29 ka cal B.P. (Doboş et al., 2010; Robu, 2015b; Mirea et al., 2021; Duñó-Iglesias et al., 2024a).

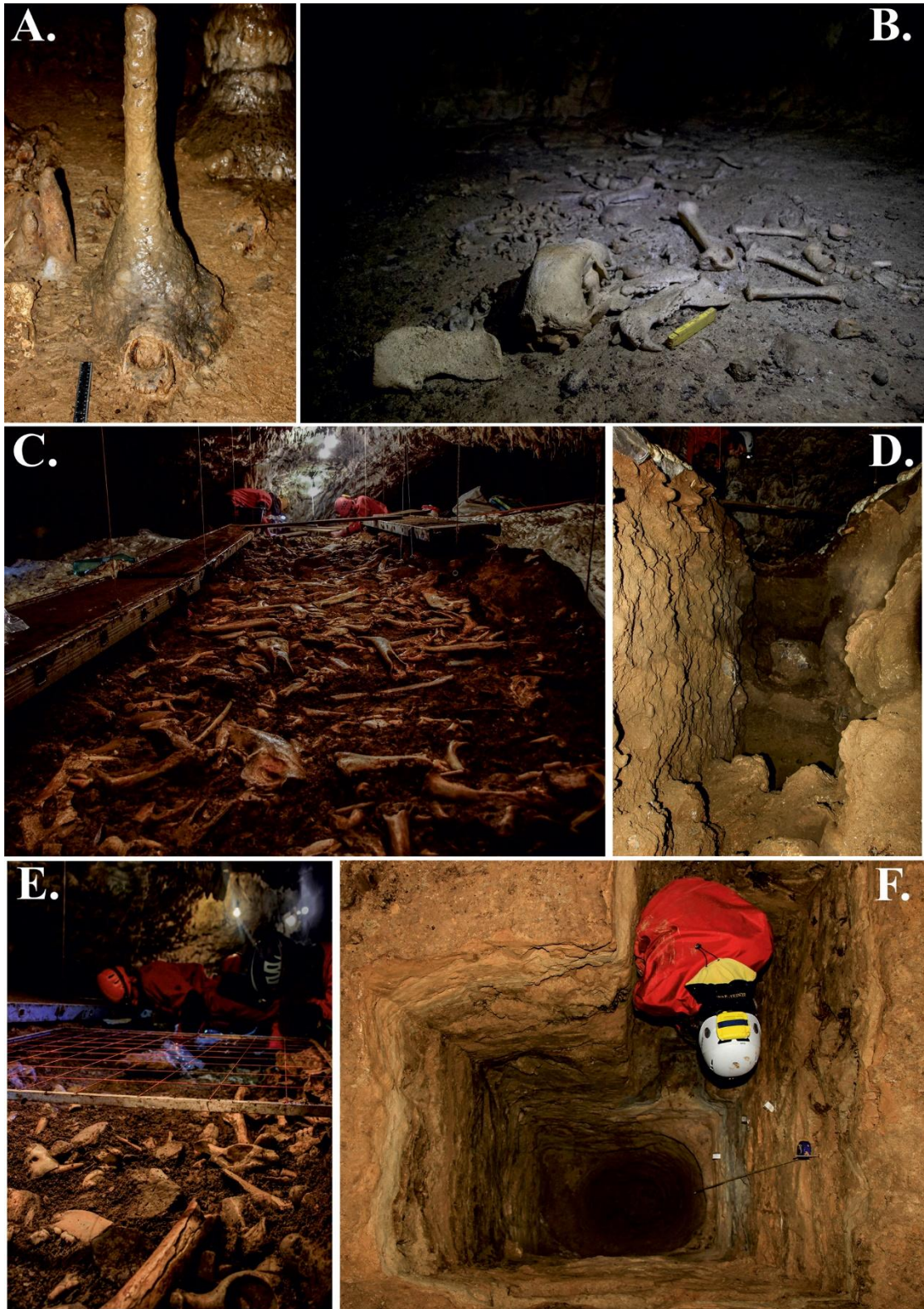


Figure 16. A. Skull of a bear trapped within a stalagmite in the Bears Passage (source of our material). B. Fully articulated skeleton of *U. spelaeus* recovered from the Hades Passage (ca. 33 ka cal B.P.). C. Level 2 of the excavation in the Bears' Passage. D. Excavation trench at the PMP1 test pit (ca. 2 meters deep). E. Overview of the surface level at the beginning of the excavation (PMP1). F. The PMP2 test pit (4.80 meters deep). Photo courtesy of Dr. Marius Robu.

9. Colțu Surpat

Peștera Colțul Surpat (=Peștera Colțul Surpat) is located in the Dâmbovița Valley, approximately 2 km from the village of Podul Dâmboviței, within the region of Argeș, Romania (with the following coordinates: 45° 25' 14" N, 25° 11' 32" E). The cave's entrance lies at an altitude of 850 meters a. s. l., accessible via a trail with steps and railings that begins 300 meters after entering the Cheile de Sus section of the Dâmbovița Gorges (Duñó-Iglesias et al., 2024a). The cave was formed as a result of limestone erosion by a tributary of the Dâmbovița River.

The cave was discovered in 1951, and initially the cave was covered by speleothems, many of which were removed due to its popularity as a tourist destination. In 1956, paleontological excavations were conducted, and in 1973, Traian Constantinescu produced the first cave map (Constantinescu, 1973) (Figure 17).

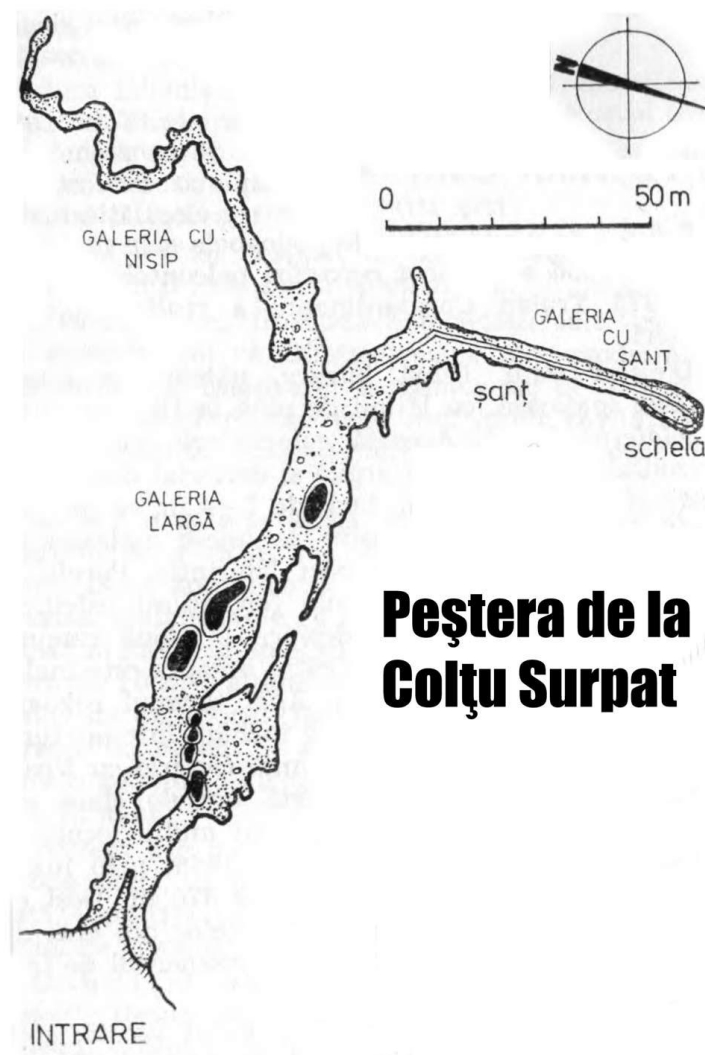


Figure 17. Map of Colțul Surpat by T. Constantinescu (1973).

The cave extends for 370 meters in length and features a spacious, sub-horizontal layout. Its main gallery, known as the “Galeria Largă,” spans widths of up to 10 meters, with a ceiling height ranging from 2 to 4 meters supported by seven massive columns (Bleahu et al., 1976). The floor is covered with fine clay, sand, and gravel, while the walls and ceiling exhibit sparse calcite formations (Bleahu et al., 1976). At 130 meters from the entrance, the gallery splits into two branches. The right branch, “Galeria cu Șanț,” initially reaches heights of 6–8 meters but narrows into a cul-de-sac after 100 meters. The left branch, “Galeria cu Nisip,” follows a sinuous path with clear evidence of water flow (Bleahu et al., 1976). In certain sections, the gallery requires crawling through sandy passages. There is no published information about this cave. And therefore, no available context for the cave bears studied in this work.

10. La Adam

La Adam Cave is situated in the Dorobanțului Plateau, in the southeastern part of Romania, close to the Black Sea (44° 27' 44" N, 28° 28' 15"E). It is one of the richest Late Pleistocene sites from this region, in terms of species' diversity and has a total length of *ca.* 100 meters. The MIS 3 cave bears, stored in the ERIS's collection and analysed here, were excavated during the 1960s (Dumitrescu et al., 1966).

4.2 Moldavian Plateau

The populations from the Moldavian Plateau region (sites 11 to 15) are located within the Prut River Basin, along its eastern drainage area, including sites 11, 12, 13 and 14, while the site 15 is located within the Dniester River Basin, at its western drainage area (Figure 18).

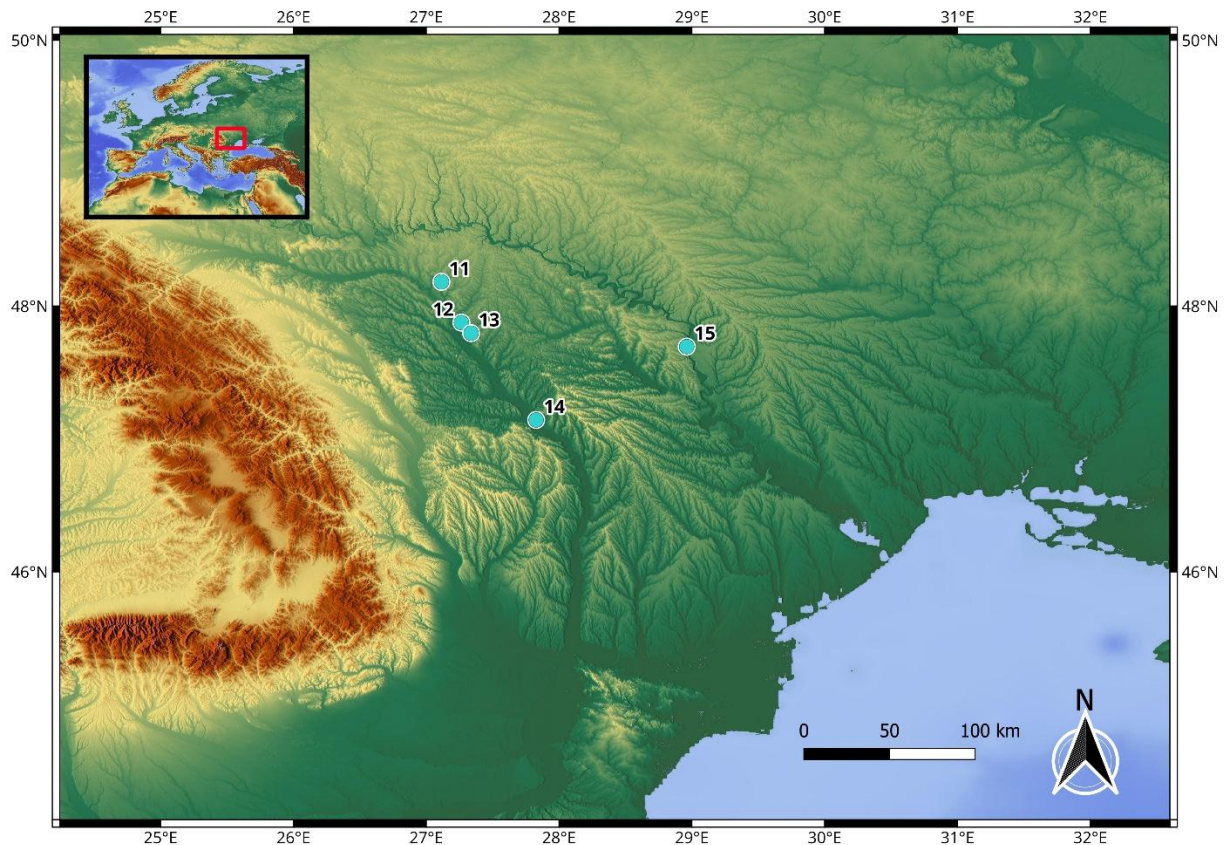


Figure 18. Location of the sampled populations of cave bears (*U. spelaeus*) and brown bears (*U. arctos*) from Moldavian Plateau: 11. Trinca 12. Duruitoarea Veche. 13. Butești. 14. Buzdujeni. 15. Saharna.

11. Trinca

Trinca Cave is located in the Edineț District, Moldavian Plateau, on the right side of the Draghiște River gorge, near the village of Trinca. It lies at an elevation of approximately 250 meters a. s. l., with the following coordinates: 48° 10' 55" N, 27° 06' 50" E. The cave is part of a karstic landscape with multiple rock shelters and caves. The material was recovered from surface during the 20's of the XX century, no more information about the stratigraphical context is available. The fauna corresponds to MIS 3, and the sampled individuals correspond to *U. spelaeus* species based on morphological parameters (Dr. M. Robu personal communication).

12. Duruitoarea Veche

Duruitoarea Veche Cave is located in the northwestern part of the Republic of Moldova, in the Costești Village, Râșcani District (with the following coordinates: 47° 52' N, 27° 15' E). The

cave is situated within Lower Sarmatian limestone formations on Duruitoarea Hill, with its entrance facing west-southwest at an elevation of 143 metres a. s. l., approximately 100 metres above the Prut River. Extending 49 metres along a north-south axis along the rocky ridge, the cave comprises three chambers (Robu et al., in prep.). The northern chamber measures 12 metres in length, 3–4 metres in width, and 4–7 metres in height. The central chamber spans 9 metres in length, 6–7 metres in width, and 3–6 metres in height. The southern chamber is 13–18 metres long, 7–10 metres wide, and narrows towards its terminus, where the ceiling height reduces to 1 meter. The cave floor is predominantly flat and covered with loose sediment.

The first paleontological and archaeological investigations at the site were conducted during 1958 to 1960, during the year 1965, and during 1973 campaigns (Chetraru, 1965, 1973b). Those excavations yielding a rich archaeological and palaeontological material that enhanced the understanding of the Late Palaeolithic in southwestern Eastern Europe. Chetraru (1964) classified the assemblages from the lower cave layers, which featured abundant Late Pleistocene faunal remains but relatively few lithic artefacts, as representative of the "Alpine Mousterian" or Pre-Mousterian traditions (Anisyutkin et al., 2017). In recent years, new excavations have been conducted, and the stratigraphy has been clearly defined into distinct units (Robu et al., in prep.; Figure 19).

4. Geographical context

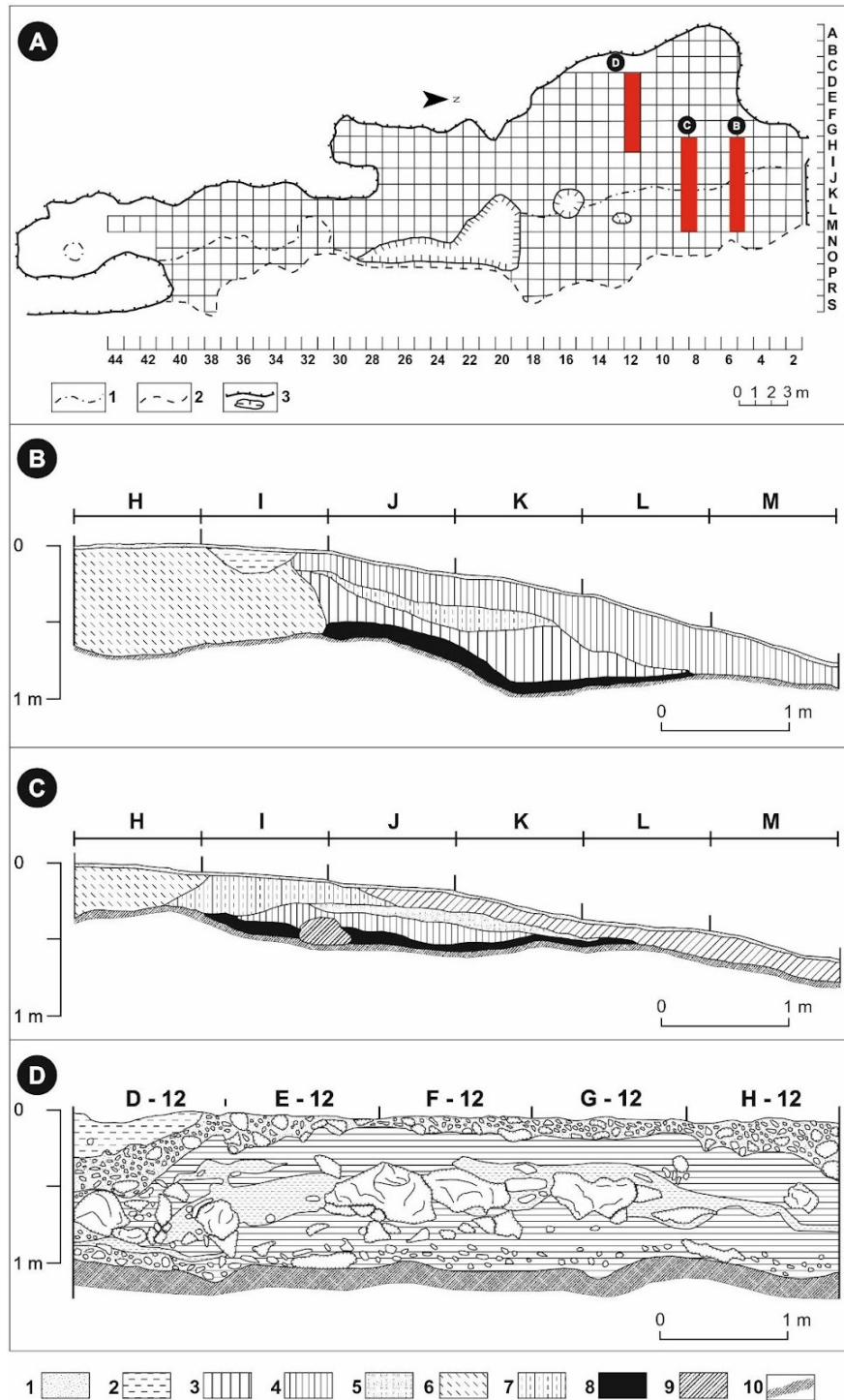


Figure 19. Plan and sections of Duruitoarea Veche site (Robu et al., in prep.). A: cave map (plan); 1 – limit of the cave ceiling; 2 – limit of the cave entrance; 3 – collapsed limestone blocks; B and C: longitudinal sections of the cave deposit; D: transversal section of the cave deposit; 1 – surface layer; 2 – remains of fireplace; 3 – clay; 4 – loam; 5 – accumulation of bones; 6 – remains of whitewash and crushed stone; 7 – gravel; 8 – hearth; 9 – collapsed blocks; 10 – bedrock.

The bone assemblage, stored at the Institute of Zoology of the Moldovan State University, comprises *ca.* 20,000 remains (Anisyutkin et al., 2017). The faunal remains represent a diverse range of large mammals. Layers VI and V do not contain stone artefacts, but displayed Late Pleistocene species such as horse (*Equus*), cave bear (*U. spelaeus*), cave lion (*Panthera l.*

spelea), and hyena (*C. c. spelea*). Layer IV displayed a faunistically more diverse assemblage, including horse (*Equus* sp.), bison (*Bison* sp.), red deer (*C. elaphus*), giant deer (*Megaloceros giganteus*), reindeer (*R. tarandus*), cave bear (*U. spelaeus*), hyena (*C. c. spelea*), and cave lion (*P. l. spelea*). Layer III expands the diversity further, adding wolves (*C. lupus*), foxes (*V. vulpes*), arctic foxes (*V. lagopus*), brown bears (*U. arctos*), hares (*Lepus* sp.), steppe pikas (*Ochotona pusilla*), hamsters (*Cricetinae*), and water voles (*Arvicola amphibius*) (Chettraru, 1970; David, 1980). Overlap exists across the lower layers, though cave bear remains are notably scarce in Layer II. Reindeer appear consistently in all layers, peaking in abundance in the tundra-associated Late Palaeolithic Layer II. Rodent species are primarily restricted to the topmost Layer I (Anisyutkin et al., 2017). Biostratigraphy and pollen analysis indicate that Layers VI and IV were accumulated during cold periods. Layer VI is characterized by cool forest-steppe environments and open landscapes, while Layer IV accumulated during the predominance of forested areas, reflecting a more humid although still cold climate. Layer III, attributed to an interstadial phase, exhibits elevated concentrations of pollen from thermophilus woody plants. The overlying sediments, dated to the Late Pleistocene, include artefacts associated with the Upper Palaeolithic (Anisyutkin et al., 2017).

The Late Pleistocene faunal assemblage is dominated by hyenas, ranging from 15 (counting lower first molar m1) to 21 (counting the upper right canine C1) MNI, although the number might be even higher (Robu et al., in prep.). Cave bears are the second most numerous species of Duruitoarea Veche, at between 12 (counting the upper left canine C1) and 18 (counting the lower left canines) (Robu et al., in prep.). Among carnivores, other identified are *C. lupus* (MNI = 3), *P. spelaea* (MNI = 1), *C. alpinus* (MNI = 1), *U. arctos* (MNI = 1), and *Gulo gulo* (MNI = 1). Regarding herbivores, there is a dominance of *E. ferus* (MNI = 11) followed by *B. priscus* (MNI = 7). As well as *M. giganteus* (MNI = 4), *C. elaphus* (MNI = 2), *R. tarandus* (MNI = 1), *C. antiquitatis* (MNI = 1) and *M. primigenius* (MNI = 1) (Robu et al., in prep.).

Regarding the cave bears, those present fourth molars (p4/P4) morphotypes indicate bears affinities with *U. ingressus* lineage, together with an evolved morphology which cluster the population with most recent cave bears, close to the cave bear extinction around the LGM (Robu et al., in prep.). Nine cave bear mandibles were directly dated by radiocarbon, indicating that the use of the cave by ursids happened, at least, from 42.6 ka cal B.P. until 31 ka cal B.P., therefore supporting the late placement of this populations within the cave bear lineage (Robu et al., in prep.).

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The palaeodemography of the cave bear population indicates a predominance of juveniles (57.1%), followed by adults in their prime (38.1%) and finally senile individuals (4.8%). The mortality profile, based on age categories, reveals elevated mortality rates among young individuals and increased survival rates with advancing age. This pattern aligns with a mortality profile characteristic of hibernation-related mortality (Robu et al., in prep.).

13. Butești

Butești is situated in the Moldavian Plateau territory, at 47° 47' 46" N, 27° 20' 13" E, and at an elevation of 97 meters a. s. l.. The site is part of a karstic system, with geological formations consistent with other caves and rock shelters in the region. It is located near the village of Butești, within the "Butești Gorges" State Protected Natural Area. This represents a coral reef through which the Camenca River has carved a gorge. The cave bear specimens analysed originate from stratigraphic lack stratigraphic context but were directly dated via radiocarbon analysis of mandibles, yielding late MIS 3 ages ranging from 41 to 35 ka cal B.P. (Duñó-Iglesias et al., 2025).

14. Buzdujeni

Buzdujeni (=Buzdujeni I) is a cave located on the right slope of the Racovăț river valley, at the northeast of the village of Buzdujeni in Moldavian Plateau 's Edineț district at 50 meters a. s. l., with the coordinates *ca.* 47° 08' 33" N, 27° 49' 40" E. Positioned just below the watershed plateau, the cave opens to the east and lies 66 meters above the Racovăț river and around 100 meters above the Prut river at their confluence. Formed within Sarmatian reef limestones, the cave has a maximum width of 10 meters, a length of 11 meters, and covers approximately 60 square meters, with a central ceiling height of 5 meters (Vishnyatsky et al., 2020).

The site was first discovered in 1970 by I. A. Borziac and extensively excavated in the mid-70s by N. A. Chetraru, yielding thousands of Middle Palaeolithic artifacts and faunal remains (Borziac, 1973; Chetraru, 1973a). In 1993 excavations were restarted by Ph. Allsworth-Jones, which focused its research on stratigraphy study (Allsworth-Jones et al., 2018). In 2017, Leonid Vishnyatsky from the Institute for the History of Material Culture of the Russian Academy of Sciences, started new excavations and excavated a test pit, as well as reviewed all lithic industry recovered by previous excavations (Vishnyatsky et al., 2020; Vishnyatsky and Burlacu, 2021).

The stratigraphic sequence at Buzdujeni consists of a 2-meter-thick Pleistocene loamy deposit divided into nine layers (1–9) (Figure 20), with Layer 1 being a thin and discontinuous Holocene layer (Allsworth-Jones et al., 2018; Vishnyatsky et al., 2020).

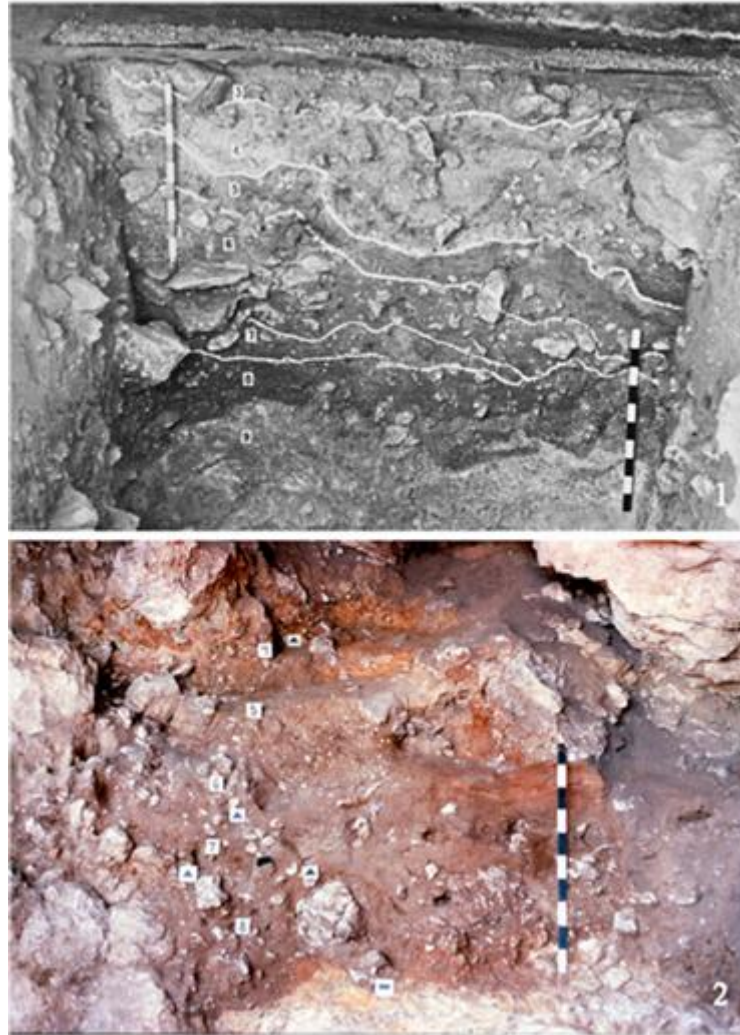


Figure 20. Stratigraphic section of Buzdujeni established by Chetaru in 1993; 1) South to north section. 2) Squares 3-7 west section. Both are equivalent and share the same stratigraphical layers (extracted from: Allsworth-Jones et al. 2018).

These sediments overlay archaeologically sterile Layer 9, that transitions into limestone bedrock (Croitor and Burlacu, 2020). The faunal assemblage is dominated by big and medium-sized mammals (David et al., 2006). From those, the identifiable specimens are dominated by *U. spelaeus* remains (69%), followed by *E. ferus* (10-12%), *C. c. spelaea* (14%-8%) and *B. priscus* (8-7%) (Croitor and Burlacu, 2020; Vishnyatsky et al., 2020). Other large mammals, including *Saiga tatarica*, *Equus hemionus hydruntinus*, *C. elaphus*, *V. vulpes*, *M. giganteus*, *R. tarandus*, *M. primigenius*, and *C. antiquitatis* are represented by only a limited number of remains (Croitor and Burlacu, 2020). The MIS 3 faunal composition indicates an open steppe

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environment at the moment of accumulation (Croitor and Burlacu, 2020). The dominance of *U. spelaeus* bones suggests alternate human and bear occupation of the site (Vishnyatsky et al., 2020). Furthermore, taphonomic analysis of the bone deposits indicates that *C. c. spelaea* was the primary accumulation agent when humans were not occupying the cave (Croitor and Burlacu, 2020).

The initial radiocarbon dating was conducted in 1993 and provided dates of $35,400 \pm 1,400$ years cal B.P. (OxA-4897) for layer 6 and $35,300 \pm 1,500$ years cal B.P. (OxA-4896) for Layer 8 (Hedges et al., 1996). However, more recent radiocarbon analyses performed in 2017 on faunal remains yielded a date of $43,100 \pm 1070$ years cal B.P. (IGAN_{AMS}6788/UGAMS-39739) for Layer 6 and a result of $44,110 \pm 320$ years cal B.P. (IGAN_{AMS}6789/UGAMS-43667) for Layer 2, probably reflecting a more reliable data due to advancements in extraction methods, summed to the fact that there are Middle Palaeolithic artifacts contained within the sequence, for which the former dates seem too recent (Vishnyatsky et al., 2020). The cave bear specimens analysed originate from stratigraphic layers II to V and were directly dated via radiocarbon analysis of mandibles, yielding late MIS 3 ages ranging from 43 to 40 ka cal B.P. (Duñó-Iglesias et al., 2025).

15. Saharna

Saharna, located within north-east Moldavian Plateau highlands, is positioned at 47° 41' 40" N, 28° 57' 40" E, at 95 meters a. s. l.. The cave is located within the Saharna River gorge, near its confluence with the Dniester River, and is part of a karstic system. The fossil record from this site was recovered without a clear stratigraphic context, though it is tentatively attributed to the MIS 3 period based on comparative analysis. Recent direct radiocarbon dates on cave bear mandibles place the accumulation in late MIS 3, between 43 and 40 ka cal B.P. (Duñó-Iglesias et al., 2025). Hence, confirming a late-MIS 3 accumulation for the cave bears.

4.3 Western Balkans and Western Rhodopes Mountains

The populations from the Western Balkans region (sites 16, 17, 18, 19, and 20) are located on the northern slopes of the Western Balkan Mountains, while sites 21 and 22 are situated in the western part of the Rhodope Mountains (in present Bulgaria), near the northern border of the country of Greece (Figure 21).

These two regions were examined as a whole due to their geographical proximity and landscape similarities. Both are characterized by moderately elevated terrain and comparable altitudinal gradients, which likely supported similar ecological conditions during the Pleistocene. The grouping also reflects the continuity in biogeographic and climatic parameters across this central Balkan corridor, which would have influenced resource availability and bear foraging strategies in similar ways during the Pleistocene. Finally, these sites were not grouped with the Southern Carpathian cave bear populations, as the Romanian Carpathians functioned as a distinct glacial refugium with unique environmental and ecological characteristics throughout the Late Pleistocene (e.g., Sommer and Benecke, 2005), and this regional singularity is reflected in the palaeoecological signatures of cave bears from the area (e.g., Richards et al., 2008; Meleg et al., 2024).

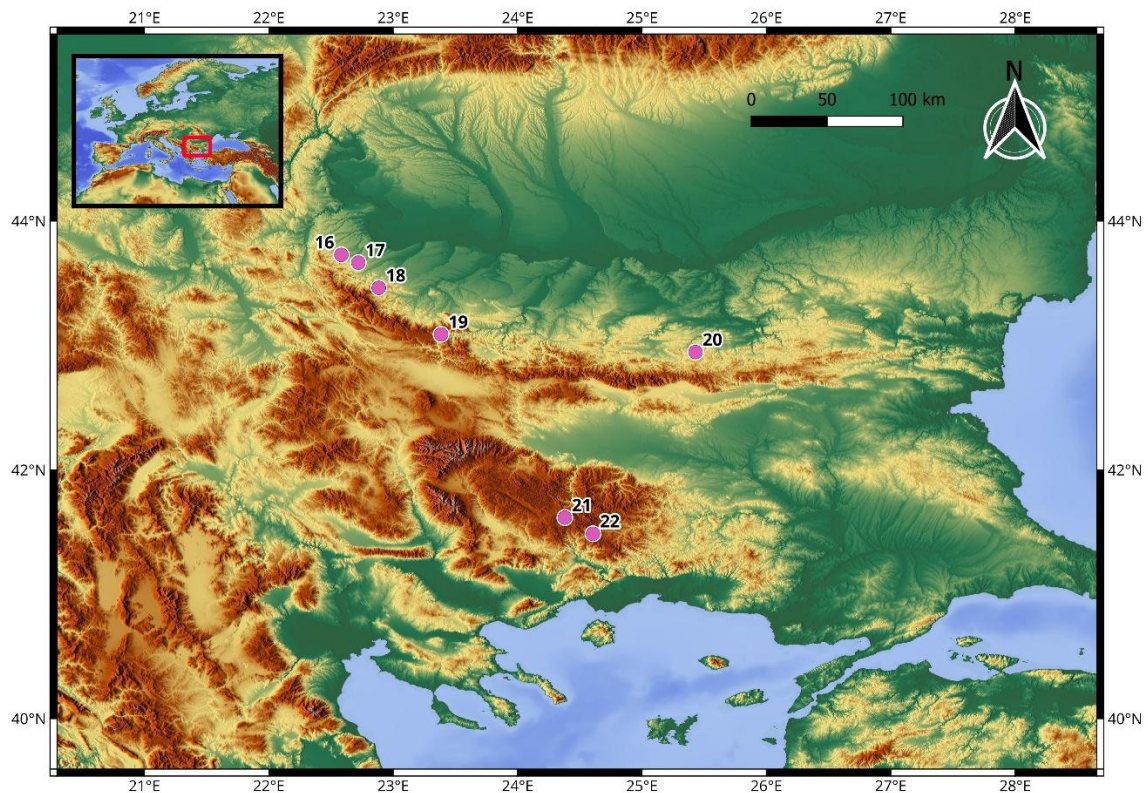


Figure 21. Location of the sampled populations of cave bears (*U. spelaeus* and *U. savini rossicus*) from Western Balkans and Western Rhodopes Mountains: 16. Magura. 17. Bashovichki Pech. 18. Mishin Kamik. 19. Lakatnik. 20. Bacho Kiro. 21. Triagalna. 22. Borikovska.

16. Magura

Magura Cave is a limestone karst located in western Stara Planina (Balkan Mountains), a range extending from northwestern to central Bulgaria, with the Thracian Plain situated to the southeast, bordered at its western margin by the Rhodope Mountains. The cave is located at an altitude of 375 meters a. s. l. and within the following coordinates: 43° 43' 41" N, 22° 34' 57" E. The cave extends over 2,500 meters in total length and comprises ten spacious halls along with numerous smaller side galleries and branching passages (Ivanova et al., 2016). The initial archaeological investigations of the cave were conducted in 1961 within the entrance hall, known as the "Triumphant Hall," approximately at 20 meters from the main entrance (Dzhambazov and Katincharov, 1961). This big hall measures 120 meters in length, 58 meters in width, and reaches a ceiling height of 28 metres. The construction of a winery in one of the side galleries discovered several cave bear bones (*U. spelaeus* / *U. ingressus*) as well as Bronze Age human remains (Ivanova et al., 2016).

Between 2011 and 2012, excavations were conducted in Trenches I and III, situated in the "Triumphant Hall" approximately 25 meters from the cave entrance (Ivanova et al., 2012, 2013). The 2011 and 2012 excavations in Magura Cave recovered over 1,400 animal remains; The fossil bone remains of large mammals from Trenches I and III correspond to Late Pleistocene faunas, including *Lepus* sp., *C. lupus*, *Cuon* sp., *V. vulpes*, *U. spelaeus* (sensu lato), *U. arctos*, *C. c. spelaea* (with several coprolites a part from bones), *P. spelaea*, *Equus germanicus*, *Equus hydruntinus*, *Rhinocerotidae* sp., *C. elaphus*, *M. giganteus*, *B. primigenius*, *B. priscus*, *R. rupicapra*, and *Aves* indet., with 80% of the identified specimens (NISP = 563) belonging to the Ursidae. The cave bear remains date from more than >50 ka B.P. (out of radiocarbon range) to ca. 35 ka B.P. (Ivanova et al., 2016).

Sex determination on 35 canine specimens revealed an almost equal distribution of males and females. Age analysis, based on tooth eruption and wear, encompassed all developmental stages, from cubs to senile individuals, indicating a mortality pattern consistent with hibernation-related deaths, likely due to starvation (Ivanova et al., 2016). Additional palaeontological analysis of metapodial morphology and tooth morphotypes showed significant variability in the bears from Magura (Ivanova et al. 2016). The diversity in tooth morphotypes observed suggested the presence of both *U. spelaeus* and *U. ingressus* at the site. Preliminary mitochondrial DNA analysis identified a specimen with distinct *U. spelaeus* traits

that carried *U. ingressus* mtDNA (Ivanova et al. 2016). Nonetheless, all the bears studied in this work were classified as *U. spelaeus* based on morphological and genetic analyses.

17. Bashovishki Pech

Bashovishki Pech is situated between the villages of Oreshets and Granitovo, at an elevation of 302 metres a. s. l. and with the following coordinates 43° 39' 57" N, 22° 43' 09" E. The cave constitutes a karstic gallery approximately 3,300 metres in length. Notably, it is located in close proximity to Kozarnika Cave, with a distance of approximately 2 km between the two sites. The cave bear remains analysed in this study were recovered from the surface of the cave, with no clear stratigraphic context or associated sedimentary deposits. However, their accumulation is most likely attributed to MIS 3 stage (Dr. M. Robu personal communication).

18. Mishin Kamik

Mishin Kamik Cave (=Mishin Cave) is situated in the northern foothills of the Stara Planina (Western Balkans) mountain range, in the western region of Bulgaria. The cave, located at 43° 27' 45" N 22° 53' 01" E, lies at an altitude of 463 meters a. s. l., approximately 30 meters above the Prevalaska River, a tributary of the Ogosta River that ultimately drains into the Danube. It is found within the Chiprovtsi municipality, between the villages of Gorna Luka and Prevala. Extending horizontally for most of its 695 meters in length, the cave's structure exhibits minimal variation, with only a few galleries showing slight undulations. The cave entrance connects to a narrow gallery (approximately 20 meters in length), where Trenches 3 and 4 are located. From 2013 to 2017, the Bulgarian Academy of Sciences' National Institute of Archaeology conducted excavations in the cave, opening a total of four trenches (Gurova and Ivanova, 2021). The trenches that yielded well-preserved stratigraphy and mammalian remains are Trench 1 and Trench 4. The bear remains studied in this work come from Trench 1 (Figure 22).

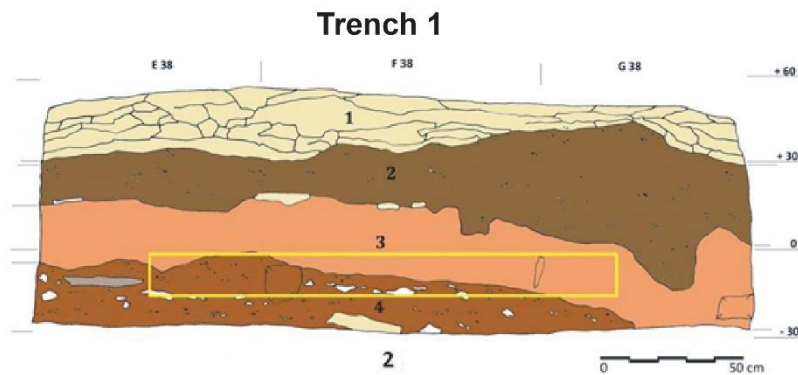


Figure 22. Stratigraphic sequence of Trench 1 (extracted and modified from Gurova and Ivanova (2021)).

Trench 1 (Middle Pleistocene)

A cave bear skull structure was found within the trench stratigraphy, with possible anthropogenic origin, although debated (Gurova et al., 2021). Animal bones are distributed throughout the sequence, with the highest frequency observed in Layer 4 (the same layer that contains the bear skull structure).

The stratigraphic layers, described based on the northwestern profile, are as follows:

- Layer 1; A calcite crust (flowstone) measuring 22 to 28 cm in thickness, intact and undisturbed, covering the entire Pleistocene sequence.
- Layer 2; Brown to dark-brown greasy clay with minimal sand content and sub-angular limestone clasts.

- Layer 3; Light brown, fine-grained, compact, and homogeneous clay, greasy and sticky when wet, containing very few small limestone clasts. Fragments of calcite flowstone are noted at the interface between layers 2 and 3.
- Layer 4; Similar to Layer 3 but with darker hues and a higher concentration of small limestone clasts. A prominent manganese-rich deposit separates layers 3 and 4. The bear skull structure, projected onto this profile, is situated in the upper portion of Layer 4.

The taxonomic assemblage is dominated by *Ursus savini rossicus* (Spassov et al., 2017), which include the five cave bear skulls recovered from the bear skull structure, plus additional two skulls of the same small cave bear species recovered in Layer 4 (Gurova and Ivanova, 2021). The terrestrial faunal remains also include specimens attributed to cf. *P. (l.) spelea*, cf. *Cyrnaonix antiqua*, *Cuon* sp., *C. lupus*, *V. vulpes*, *Mammuthus* sp., Rhinocerotidae sp., *Equus* sp., *Megaloceros* sp., *C. elaphus*, and Bovidae sp.. Molluscan taxa include *Cattania balcanica* and *Fruticicola fruticum*, while evidence of coprolites attributed to porcupines (*Hystrix*) were also documented (Gurova and Ivanova, 2021). A relatively small and late form of *Panthera (leo) fossilis* has been identified within the assemblage (Marciszak et al., 2014; Sotnikova and Foronova, 2014), suggesting a late-Middle Pleistocene age for the bear sample. This interpretation aligns with preliminary Uranium-Thorium dating results from a stalagmite within the cave obtaining a range of 143.1–85.6 ka B.P. (Spassov et al., 2017). However, a subsequent study that dated several calcite depositions (U-series) and re-evaluated the accumulation history revised the age estimate, suggesting that the bear skull accumulation dates to approximately 250–220 ka B.P. (MIS 7), indicating an older chronology than previously thought. Furthermore, associated faunal and palynological data (Gurova et al., 2017) suggest a mosaic environment composed of forested and open landscapes when the bears dwelled the cave in Layer 4. It is during this period that the accumulation of the *U. s. rossicus* individuals analysed in this study occurred.

19. Lakatnik

Lakatnik Cave (=Temnata Dupka, in English “Dark Hole”) is located in northern Bulgaria, near Sofia, within the Iskâr Gorge, and is part of the region's Middle Triassic limestone formations. The entrance to Lakatnik Cave is located 27 meters above the Iskar River (at 480 meters a. s. l. and with the following coordinates 43° 05' 21" N, 23° 23' 05" E), on the left bank, northwest of Lakatnik municipality, within a vertical cliff (Figure 23; named “Lakatnik Rocks”) on the southeastern slope of Koznitsa Mountain in the Western Stara Planina.

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Figure 23. Overview of the entrance to Lakatnik Cave (Photo by Konstantin Stoichkov and Aleksandal Lazarov, Bulgarian Federation of Spelology: <https://esf2019.speleo-bg.org/>).

The cave system is regarded as the Dark Hole (Temnata Dupka), a karstic gallery extending more than 8,000 meters-long and throughout 4 different levels. The cave was discovered at the beginning of the XX century, and first excavated by R. Popov between 1925-26 (Popov, 1986). In the 1980s, a Polish-Bulgarian-French archaeological team conducted excavations at the site, uncovering Pleistocene faunal remains, including *C. lupus*, *M. primigenius*, *B. primigenius*, *R. tarandus* and *U. spelaeus* (Popov, 1986).

The stratigraphy of the site, according to the small mammals biochronology spans from Early Pleistocene until the Holocene. However, several dating methods indicated a Late Pleistocene chronology spanning at between 120 to 13 ka B.P. for the main trench (Ginter et al., 2000; Popov, 1986, 2000). The cave also contains record of Middle to Upper Palaeolithic repeated human occupations (Ginter et al., 2000). Limited information is available about the cave excavations; however, several dating on faunal remains position the Late Pleistocene deposit from Trench I at between 40 to 31 ka B.P. (Ginter et al., 2000). The new dating, with a more precise ultrafiltration method, of *P. spelaea* dates the deposit at $31,200 \pm 330$ years B.P. (OxA-11422), reported by Stuart and Lister (2011), suggesting that Late Pleistocene mammalian

assemblage from Lakatnik date from Marine Isotope Stage 3 (MIS 3) (Stuart and Lister, 2011). The analysed cave bear specimens originate from the MIS 3 deposit of Trench I.

20. Bacho Kiro

Bacho Kiro Cave (5 km west of Dryanovo, Bulgaria) is located on the northern slope of the Balkan mountain range (Stara Planina), at roughly 70 km from Danube River at 335 meters a. s. l. and with the following coordinates 42° 56' 48" N, 25° 25' 49" E (Sinert-Mathiot et al., 2023; Tsanova et al., 2024). The cave is found within the Dryanovo River canyon, and its deposits are formed at the mouth of a large karstic system over 3,000 meters long. Excavations in the cave began in the 1930s under the direction of R. Popov and D. Garrod (Garrod et al., 1939). In the 1970s, a Bulgarian-Polish team, led by B. Ginter and J. K. Kozłowski, resumed the work (Kozłowski and Ginter, 1982). In 2015 the National Archaeological Institute and the Bulgarian Academy of Science (Sofia, Bulgaria), together with the Max Planck Institute for Evolutionary Anthropology (Leipzig, Germany) resumed the excavations (Tsanova et al., 2024). The archaeological sequence extends 5 meters in depth, encompassing Middle Palaeolithic and Upper Palaeolithic deposits, separated by a clear technological transition (Kozłowski and Ginter, 1982; Tsanova et al., 2024). The archaeological material recovered from layers I and J was identified as Initial Upper Palaeolithic, representing one of the first occurrences of *H. sapiens* in Europe (Hublin et al., 2020), with layer J dated to 45,990 years cal B.P. containing numerous bone tools and ornaments, and layer I, dated to 45,040-43,280 years cal B.P., showing evidence of increased human activity (Fewlass et al., 2020; Pederzani et al., 2021; Martisius et al., 2022). Layer K contains Middle Palaeolithic artifacts and has been dated to between 61 ka B.P. and 51,000 years cal B.P. (Fewlass et al., 2020; Tsanova et al., 2024).

The faunal assemblage of Bacho Kiro is extremely diverse, including several large to medium size herbivores, namely, *E. ferus*, *E. hydruntinus*, *M. giganteus*, *C. ibex* and *R. rupicapra*, alongside megafaunal species represented by limited remains, such as *M. primigenius* (Layer K) and *Stephanorhinus hemitoechus* (layers I and J) (Smith et al., 2021). Carnivora species include *U. spelaeus*, *U. arctos*, *P. (l.) spelaea*, *P. pardus*, *C. c. spelaea*, *C. lupus*, and *V. vulpes*. The dominant taxa is *Bos/Bison* among herbivores (Layer I: 19.8%; Layer J: 6.7%; Layer K: 19.5%), cave bear (*U. spelaeus*; I: 16.6%; J: 45.4%; K: 20.1%), and red deer (*C. elaphus*; I: 11.9%; J: 1.7%; K: 3.2%), while other carnivores (I: 4.6%; J: 8.8%; K: 7.1%) and herbivores (I: 18.2%; J: 9.6%; K: 27.3%) are represented in smaller numbers (Smith et al., 2021; Sinert-Mathiot et al., 2023).

21. Triagalna

Triagalna Cave, also known as Devil's Throat, is located at an elevation of *ca.* 1,200 metres a.s.l., with coordinates 41° 36' 55" N, 24° 22' 46" E. The cave is a well-known speleological site and is currently open to tourism (Figure 24). The cave bear remains analysed in this study were found on the surface, lacking any clear stratigraphic context or associated sedimentary deposits. However, their accumulation is most likely attributed to the MIS 3 stage (M. Robu personal communication).



Figure 24. Inner section of Devil's Throat Cave, now part of the tourist route.

22. Borikovska

Borkiovaska Cave (=Boritza Cave; in English, "Red Hole") is located at the eastern foothills of the Rhodope Mountains, at the Arda River valley, near the village of Borikovo (Smolân), at the Southern-most Bulgarian territory (roughly 2 km from the boarder with Greece), at 1,250 meters a. s. l. with the following coordinates: 41° 29' 08" N, 24° 36' 21" E. The main gallery of the cave measures 4–10 meters in width and 1.5–8 meters in height. At around 270 meters from the entrance, the floor is covered by a thick clay deposit containing abundant fossil remains of large mammals, predominantly cave bear (*U. spelaeus*). Several deep trench excavations, reaching depths of up to 2 meters were performed during the 80's. At the innermost section of the cave, significant speleothems deposits are present. The rest of the cave

is poor in speleothems formations but rich in paleontological materials (Petrov and Stoev, 2007).

Excavations were started in 1963 by D. Raichev, G. Raichev, and T. Cholakov, and further continued by D. Rajčev in 1981 (Boev, 2021). These excavations uncovered a large mammal assemblage from the Late Pleistocene including *U. arctos*, *U. spelaeus*, *Lynx lynx*, *C. c. spelaea*, among others (Petrov and Stoev, 2007; Boev, 2021). The cave is the largest known site for fossil remains of the cave bear (*U. spelaeus*) in the Rhodopes Mountains region (Petrov and Stoev, 2007). The remains of cave bear are from MIS 3 (Dr. M. Robu personal communication).

4.4 Central Balkans

The Central Balkans populations (sites 23–25) are in a transitional zone between the Dinaric Alps and the Pannonian Basin (Figure 25). Site 23 is located in the Šumadija region, on the eastern slopes of Rudnik Mountain (Morava River Basin). Site 24 is in the Morava River Basin, between the Šumadija Highlands and the Kopaonik Mountains. Site 25 lies on the Drina River Basin, near Tara Mountains (Dinaric Alps).

This region was not grouped with the Western Balkans and Western Rhodopes for the comparative analysis due to its markedly different environmental context. In particular, it lies considerably closer to the Adriatic Sea, suggesting a more temperate climatic influence and differing ecological dynamics. Moreover, the transitional nature of the landscape—between mountainous and basin environments—further distinguishes its ecological conditions from the predominantly continental and highland landscapes of the Western Balkans and Western Rhodopes, configuring a single region in our study.

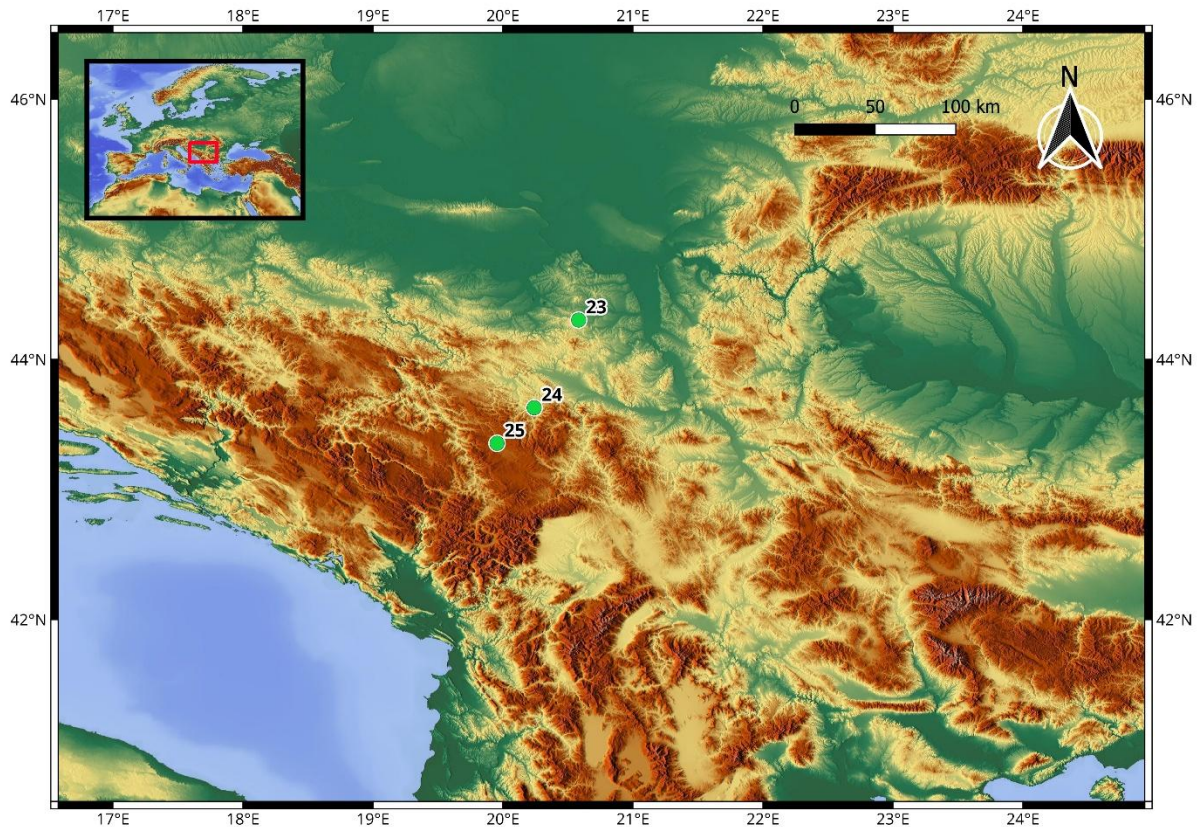


Figure 25. Location of the sampled populations of cave bears (*U. spelaeus*) from Central Balkans (23–25): 23. Risovača. 24. Hadži Prodanova. 25. Ušačka.

23. Risovača

Risovača Cave is located in central Serbia (Morava River Basin) Šumadija region (with the following coordinates: 44° 18' 07" N, 20° 34' 56" E) at the Aranđelovac municipality, in the northeastern part of Risovača Hill at 273 meters a. s. l. and at *ca.* 17 meters above the Kubrušnica River (Antić and Tomic, 2020). It represents the largest known cave in this region. The cave extends 149.5 meters in length and features a primary passage measuring 100 meters, along with several smaller side galleries totalling 49.5 meters. The entrance is situated within a 20-meter-high limestone section and measures 5.5 meters in height and 2.8 meters in width (Rakić, 1980). Archaeological and paleontological excavations on Risovača Cave began in 1953, led by Professor Branko Gavella from the Archaeological Institute of the Serbian Academy of Science and Art and the Faculty of Philosophy in Belgrade, continuing intermittently until 1976.

Late Pleistocene sediments containing Middle Palaeolithic remains discovered within the cave, including lithic tools and processed faunal remains, evidenced the presence of *H. neanderthalensis* at the cave. The Late Pleistocene faunal assemblages comprehended remains of *Mammuthus* sp., *P. l. spelaea*, *E. ferus*, *C. elaphus*, *Dicerorhinus* sp., *Bison* sp., etc. (Dimitrijević, 1997). However, the most numerous species (representing 2/3 of the faunal assemblage) is *U. spelaeus* (Rakovec, 1965; Forsten and Dimitrijevic, 1995). The dating of the faunal deposits of this cave is placed around 36,400 years cal B.P., this is within the Marine Isotopic Stage 3 (MIS 3) (Forsten and Dimitrijevic, 1995).

24. Hadži Prodanova

Hadži Prodanova Cave (=Hadži Prodan) is located near the village of Lisa (Ivanjica municipality, Serbia) with the following coordinates *ca.* 43° 37' 41" N, 20° 14' 25" E, and at 630 meters a. s. l. and at 40 meters from the valleys floor (Lješević, 2002). Excavations began in 2003 following the unveiling the original position of the Church of St. Archangel Michael (Bulić, 2006). The entrance of the cave is very narrow and high (1.75 for 7 meters), it continues with a 40-meters corridor, with the total system length expanding *ca.* 345 meters (Lješević, 2002). Excavations were undertaken in the beginning of this corridor, as well as in the outside front of the entrance, in a total of 16 m² surface (Mihailović and Mihailović, 2006). Five archaeological horizons were excavated within 2.5 meters thick package (Mihailović and Mihailović, 2006; Bogićević et al., 2017).

Layer 1, consisting of a Holocene-formed surface deposit, is composed of grey sediment and is associated with modern and Early Iron Age artifacts as well as some reworked bones of

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Pleistocene mammals. Layer 2 consists of brown-yellowish clay with fine stone inclusions, containing Late Upper Palaeolithic materials; specifically, Epigravettian artifacts. Layer 3 composed of light brown clay with coarse stone inclusions and larger stone blocks, is archaeologically sterile. Layer 4 comprising light brown clay sedimentation, with fine stone inclusions and variable concentrations of fine gravel, contained Middle Palaeolithic artifacts. Layer 5 consisted of dark brown sediment, with coarse stone inclusions and larger fragments, and yielded Middle Palaeolithic materials as well. This layer can be divided into four distinct horizons: a, b, c, and d, and reaches up to 4.4 meters in depth, whose bedrock has not been yet arrived (at the time of the publication) (Mihailović, 2014).

The cave bear (*U. spelaeus*) is the most dominant species in the faunal assemblage, particularly in the upper levels, with a slightly reduced presence in Layers 5b and 5c (Mihailović and Mihailović, 2006; Bogićević et al., 2017). The cave bear predominance is followed by *C. ibex* and *C. lupus*. Other mammal species are *U. arctos*, *R. rupicapra* (especially common in Layers 4 and 5), *C. elaphus*, *L. lynx* and *C. c. spelaea* (Mihailović and Mihailović, 2006; Bogićević et al., 2017). Apart from large mammals several rodents and bird remain have been found (Bogićević et al., 2017). The composition of rodent populations, comprising 13 different taxa, suggests a mosaic environment with a predominant forest cover. The rodent accumulation further suggested that Late Pleistocene layers formed during a humid and relatively warm period within MIS 3 (Bogićević et al., 2017). The cave bear specimens analysed originate from the upper archaeological levels containing Middle Palaeolithic artefacts, which are biochronologically attributed to late MIS 3 based on the associated rodents and large faunas composition (Bogićević et al., 2017).

25. Ušačka

Ušačka Cave is located at 1,600 meters a. s. l. near the village of Gornje Lopize (Serbia), near the settlement of Usak, for which it receives the name (with the following coordinates: 43° 21' 16.2" N, 19° 57' 15.2" E). The cave entrance is nowadays at the river level and its entrance is flooded (Figure 26), so the only way to enter is by boat. The Usacki Potok stream, a tributary of the Uvac River, traverses the limestone plateau of the canyon, forming a wide karstic network (Petrović, 1976). This system, referred to as the Usacki Cave System, comprises three distinct sections; Ušačka Pećina (Ušačka Cave), Ledena Pećina (Ice Cave), and Bezdana Jama (Bottomless Pit), and is characterised by its complexity and considerable length of

approximately 6,185 metres, with the Ušačka Cave accounting for *ca.* 2,000 metres (Petrović, 1976). The faunal deposits are mainly composed of cave bear remains, which correspond to the Late Pleistocene (MIS 3) (Dr. M. Robu personal communication).



Figure 26. Ušačka Cave entrance.

4.5 Greater Caucasus

26. Kudaro 1 and Kudaro 3 caves

Kudaro 1 cave and Kudaro 3 cave are situated in the Rioni River basin on the southern slope of the Central Caucasus (with the following coordinates: 42° 31' N, 43° 38' E; Figure 27).

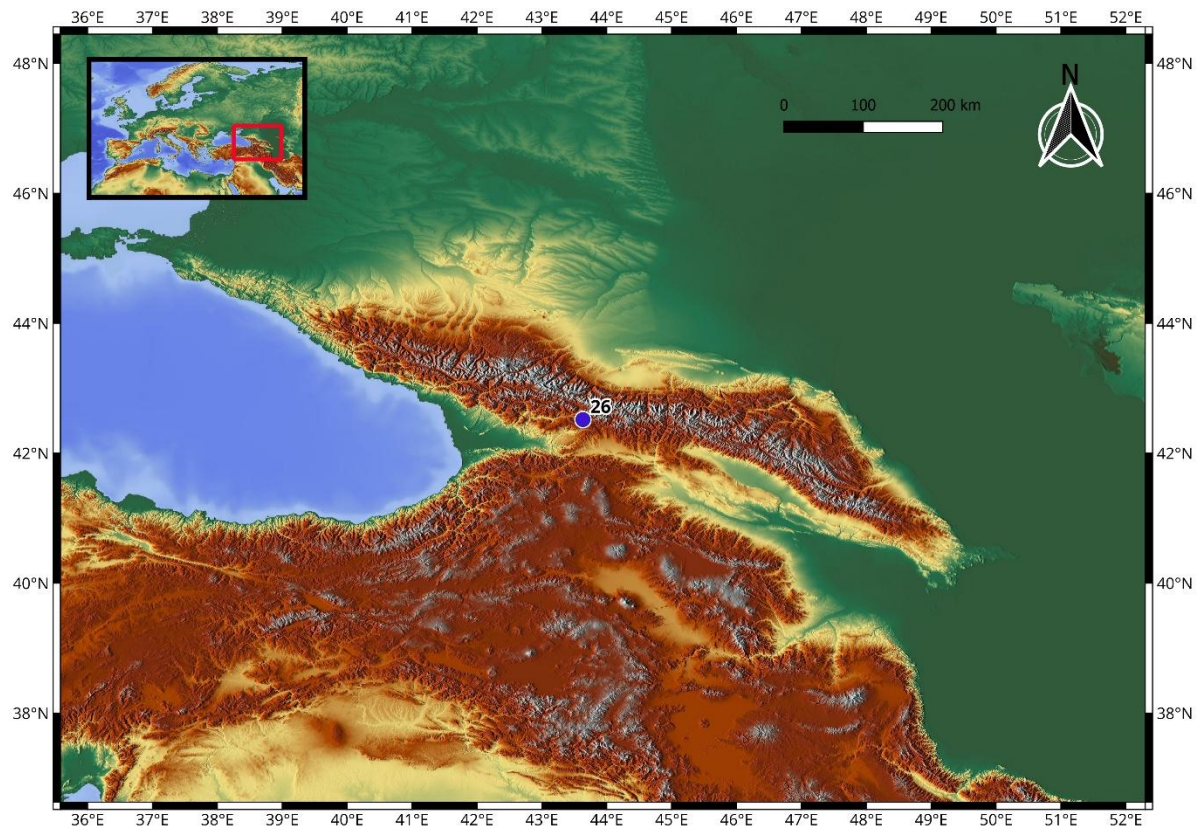


Figure 27. Location of the Kudaro Caves: 26. Kudaro 1 and 3 (Greater Caucasus).

Both caves have a gallery-type structure and are located at an altitude of 1,600 meters a. s. l., with one lying directly beneath the other in the valley of the Dzhodzhori River near the village of Kvaisa in South Ossetia (Baryshnikov, 2011, 2020a).

The Palaeolithic sites at the Kudaro caves were excavated under the direction of Prof. V.P. Lioubine. The palaeontological collections analysed in this study are hosted and stored at the Zoological Institute of Russian Academy of Sciences in Saint Petersburg, Russia (ZIN).

The sampled individuals were obtained from the caves at Kudaro 1 and 3.

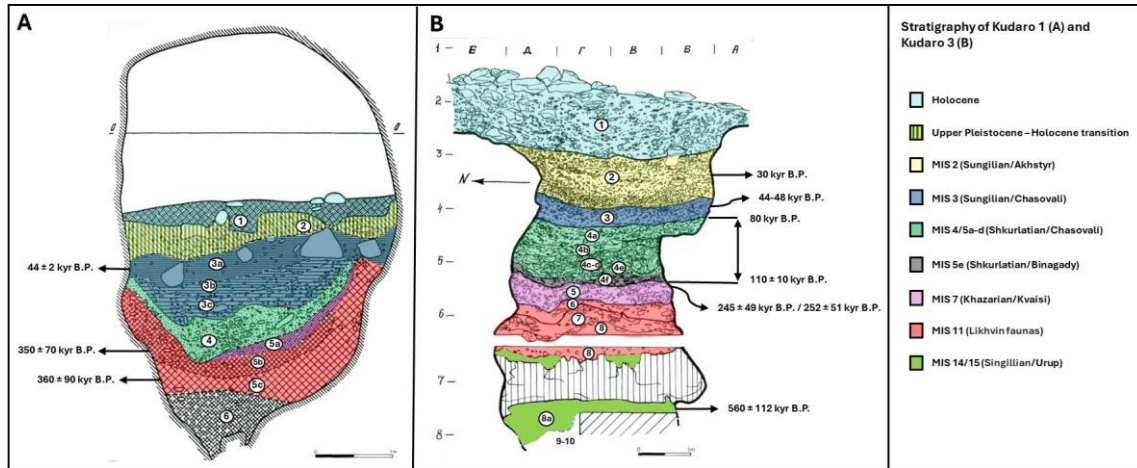


Figure 28. Stratigraphic sequence of Kudaro 1 (A) and Kudaro 3 (B) caves, extracted and modified from Lioubine and Bosinski (1995). Chronology has been established based on thermoluminescence/uranium-thorium dating and biostratigraphy correlations (mammal age/faunal units) and further supported by pollen analysis (Čerdynece et al. 1959; Lioubine and Bosinski, 1995; Lioubine, 1998, 2002; Baryshnikov, 1998, 2002).

For Kudaro 1 six distinct stratigraphic levels were discerned within the eastern gallery (Lioubine and Bosinski 1995; Figure 28A). The uppermost layer 1, composed of black loam with sporadic angular stones and limestone blocks, displayed Eneolithic period artifacts as well as from earlier periods. Layer 2, consisting of yellow-grey loam with sharp-edged stones and large blocks, contained artifacts from the end-Palaeolithic and Mesolithic periods. Layers 3 and 4, which are composed of greyish loam sediment, displayed Middle Palaeolithic lithic tools. Layer 3a was dated by radiocarbon to 44 ± 2 ka B.P. (Gr-6079) (Lioubine, 1998). Layer 5, characterized by a yellowish fuscous loam matrix and Acheulean artifacts, is subdivided into 5a, 5b (dated to 350 ± 70 ka B.P. (RTL-373)), and 5c (Lioubine and Bosinski 1995; Baryshnikov, 2011). The deepest horizon is layer 6, which was found to be sterile. The contact zone between Acheulean and Mousterian layers presents stratigraphic interruptions, likely caused by sediment erosion or periods of non-deposition during colder climatic phases (Lioubine and Bosinski 1995; Baryshnikov, 1999).

From Kudaro 1, molars were sampled from layer 5c ($n = 20$ specimens; Figure 29A) dated to 360 ± 90 ka B.P. (RTL-379), from which Acheulean artefacts have been recovered (Lioubine, 1998). The layer, composed by 1 meter of yellow-brownish loam, remains unaffected by any taphonomic processes, thus it is classified as undisturbed (Lioubine and Bosinski 1995; Figure 28A). This layer contains very diverse fauna, including several species of carnivores, herbivores, and other mammals. These are classified within Likhvin faunas of Eastern Europe or with the Fontana Ranuccio fauna (MIS 11) from the late Galerian of Italy (Alekseeva et al., 1977; Azzaroli, 1983; Zastrozhnov et al., 2018). Among the carnivores, there are several felids, including leopard (*P. pardus*) and extinct jaguar (*Panthera gombaszoegensis*). The canids are

4. Geographical context

represented by red fox (*V. vulpes*), dhole (*Cuon alpinus*), Middle Pleistocene wolf (*Canis mosbachensis*), and Caucasian coyote (*Canis kudarensis*). The bear species present include Asian black bear (*Ursus thibetanus mediterraneus*) and *U. praekudarensis*. There are also different mustelids: European badger (*M. meles*), beech marten (*Martes foina*), marbled polecat (*Vormela peregusna*), and least weasel (*Mustela nivalis*), as well as two porcupines, the large porcupine (*Hystrix* cf. *refossa*) and the small porcupine (*H. brachyura vinogradovi*). Herbivores are well-represented with several cervids: red deer (*C. elaphus*) and roe deer (*Capreolus capreolus*), along with extinct giant deer (*Megaloceros* sp.) and moose (*Alces alces*). Additionally, there are remains of bison (*Bison* sp.). Bovids are also found, including gazelle (*Gazella* sp.), West Caucasian tur (*Capra caucasica*), argali (*Ovis ammon antiqua*) and extinct tahr (*Hemitragus bonali*). At the very bottom of layer 5c giant muskox (*Praeovibos priscus*) was found. Particularly interesting is the discovery of a macaque (*Macaca* sp.), the only one from the Pleistocene of the Caucasus (Baryshnikov, 1999, 2002, 2020a). The presence of the Middle Pleistocene wolf, whose disappearance and transition to the current wolf (*C. lupus*) is now known to have occurred no later than 400 ka B.P. (Iurino et al., 2022), along with the presence of thermophilous-adapted fauna (*Macaca* sp. and large and small porcupines) and the warm climatic conditions indicated by pollen analysis, situates layer 5c within the MIS 11 Interstadial (Baryshnikov, 2002; Lioubine, 2002; Nitychoruk et al., 2006).

The remaining specimens were recovered from two different layers of Kudaro 3. For Kudaro 3 section (O, - K, - M.), ten levels were identified (Lioubine and Bosinski 1995; Figure 28B). Layer 1 consists of loam and debris accumulated during the Holocene. Layer 2, dated at around 30 ka B.P. (Baryshnikov, 2002), is composed of grey to brownish loam with slope debris and large limestone blocks. Layer 3 and 4 contained Middle Palaeolithic artifacts. Layer 3 cave bear bones yielded three AMS radiocarbon dates of >41 ka cal B.P. (OxA-19611), 47 ka cal B.P. (OxA-19612) and 47 ka cal B.P. (OxA-19613), respectively.

Furthermore, layers 5, 6, 7 and 8a (which basal layer was dated by thermoluminescence at 560 ± 112 ka B.P.) contained Acheulean lithic tools (Lioubine and Bosinski 1995). Layer 9, formed by compact clay, and layer 10, formed by yellow sandy loam, were found to be sterile. A study of the sediment dynamics found that Kudaro 3 was exposed to erosion dynamics which might explain the significant time-gap in the deposition between the Acheulian and Mousterian layers showed by RTL dates (Lioubine and Bosinski 1995; Baryshnikov, 2011).

The two layers from which the studied materials were recovered are:

1) The Acheulean layer 5 ($n = 19$ specimens; Figure 29C), which is composed by compact yellowish loam with rounded debris, has been dated by thermoluminescence to between 245 ± 49 ka B.P. (RTL-534) and 252 ± 51 ka B.P. (RTL-511) in the uppermost part (Lioubine and Bosinski 1995; Lioubine, 1998; Figure 28B). This layer is characterised by the presence of small porcupine (*H. brachyura vinogradovi*), gray wolf (*C. lupus*), *V. vulpes*, *U. thibetanus*, *U. praekudarensis/kudarensis*, *M. meles*, cave lion (*P. spelaea*), *P. pardus*, *C. capreolus*, *C. elaphus*, and *Bison* sp. Based on the fauna appearance, layer 5 in Kudaro 3 cave could be correlated with the MIS 7 thermochron as stated by Baryshnikov (2002). However, as the dating was performed on the uppermost part of the package, indicating a minimum age, and considering the wide range of error, this layer could be related to older interglacial periods (Baryshnikov, 1999). Nevertheless, the presence of clearly defined Khazarian faunas (equivalent to Aurelian faunas in Western Europe) distances it from older periods and situates it in a much earlier chronology than layer 5c from Kudaro 1, which contained late Galerian faunas (Baryshnikov, 2002). More specifically, *Canis mosbachensis*, which appears in layer 5c, is succeeded in layer 5 (from Kudaro 3) by the later species, *C. lupus* (Baryshnikov, 2002; Iurino et al., 2022). Furthermore, the structure of the upper incisors of the cave bears from layer 5 in Kudaro 3 cave is similar to *U. kudarensis* (Baryshnikov et al., 2019). Therefore, we can assume that the *U. praekudarensis/kudarensis* sample is represented by an early *U. kudarensis* population. The greater morphological similarity to *U. kudarensis* compared to *U. praekudarensis* strengthens the idea that the *U. praekudarensis/kudarensis* accumulation occurred during MIS 7, rather than during older interglacials.

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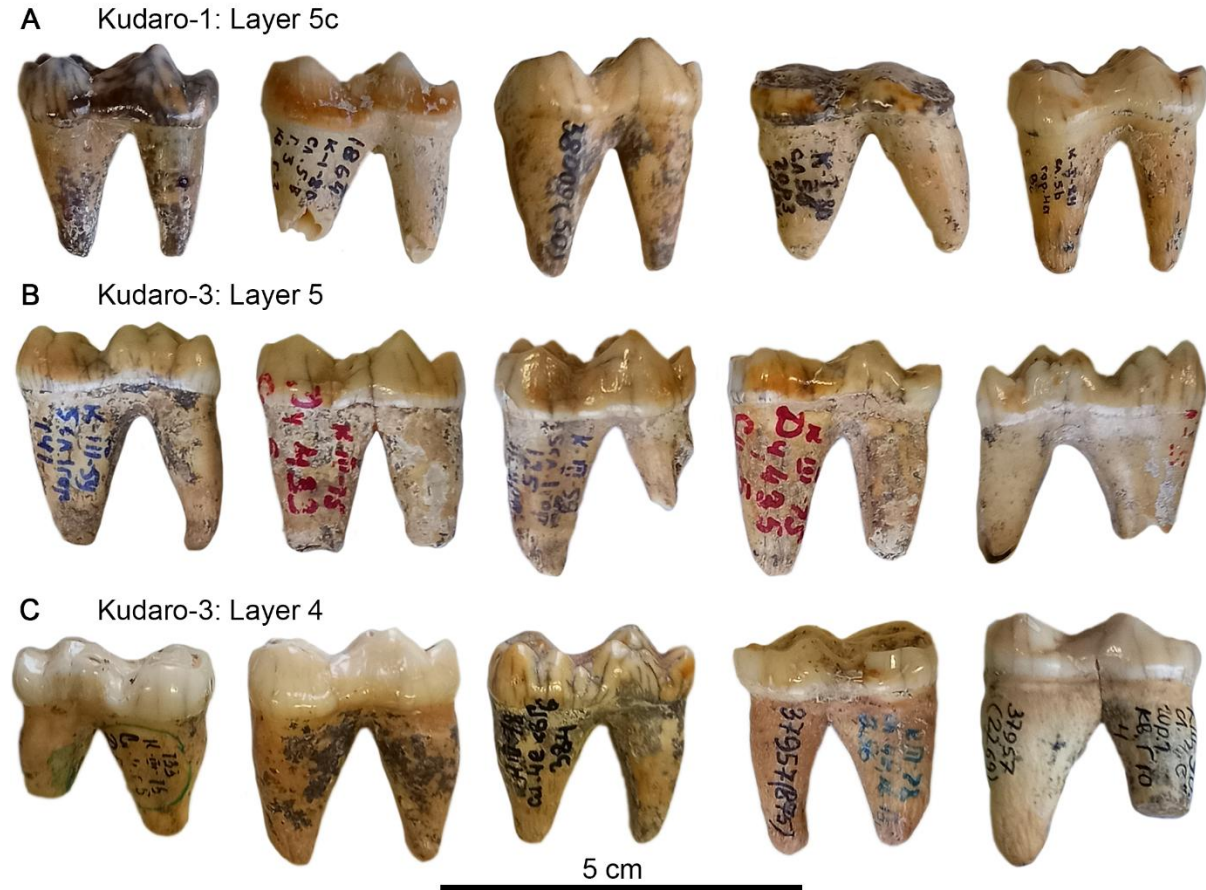


Figure 29. Studied material. The first lower molar (m1) in cave bears from the Kudaro caves (side view). A: *U. praekudarensis*; B: *U. praekudarensis/kudarensis*; C: *U. kudarensis*.

2) The Mousterian layer 4 ($n = 21$ specimens; Figure 29C), composed by dark greyish loam with limestone fragments and debris, has been directly dated by two uranium-thorium dates on bone material, falling between 110 ± 10 ka B.P. and 80 ka B.P. (Ĉerdynceev et al. 1959; Lioubine and Bosinski, 1995; Figure 28B). Hence, it is a transition period between the end of last interstadial 5e (Eemian), for basal layer 4f, and in between MIS substage 5a and beginning of MIS 4, for layers 4d to 4a. This layer is characterised by the presence of *U. thibetanus*, *U. kudarensis*, *C. capreolus*, *C. elaphus*, *Bison* sp., and *C. caucasica*. However, *U. thibetanus* appear only in the basal level 4f. Moreover, temperate and forest-related species such as red deer and roe deer predominate in the basal levels and are reduced through the sequence in favour of a greater predominance of the colder-adapted West Caucasian tur (Baryshnikov, 1999, 2002). A transition from a closed to a more open landscape is also observed in the pollen analysis of the layer (Lioubine, 2002).

4.6 Northern Urals

27. Medvezhiya

Medvezhiya cave (with the following coordinates 62° 00' N, 58° 44' E; Figure 27) is located in the Troisko-Pechora district of the Komi Republic, Russia at *ca.* 300 meters a. s. l.. The cave is situated on the right bank of the Pechora River, 40 meters above water level. The entrance of the cave is shaped like a large arch, with a width of 12 meters and a height of 3 meters. The cave contains Upper Palaeolithic stone artifacts (Guslitser and Pavlov, 1988), and 1,156 cave bear bones from 34 individuals were collected within its stratigraphy (Kuzmina, 1971). The new species, *Ursus kanivetz* VERESTCHAGIN, 1973, was described in this cave (lectotype: skull, ZIN O.30354).

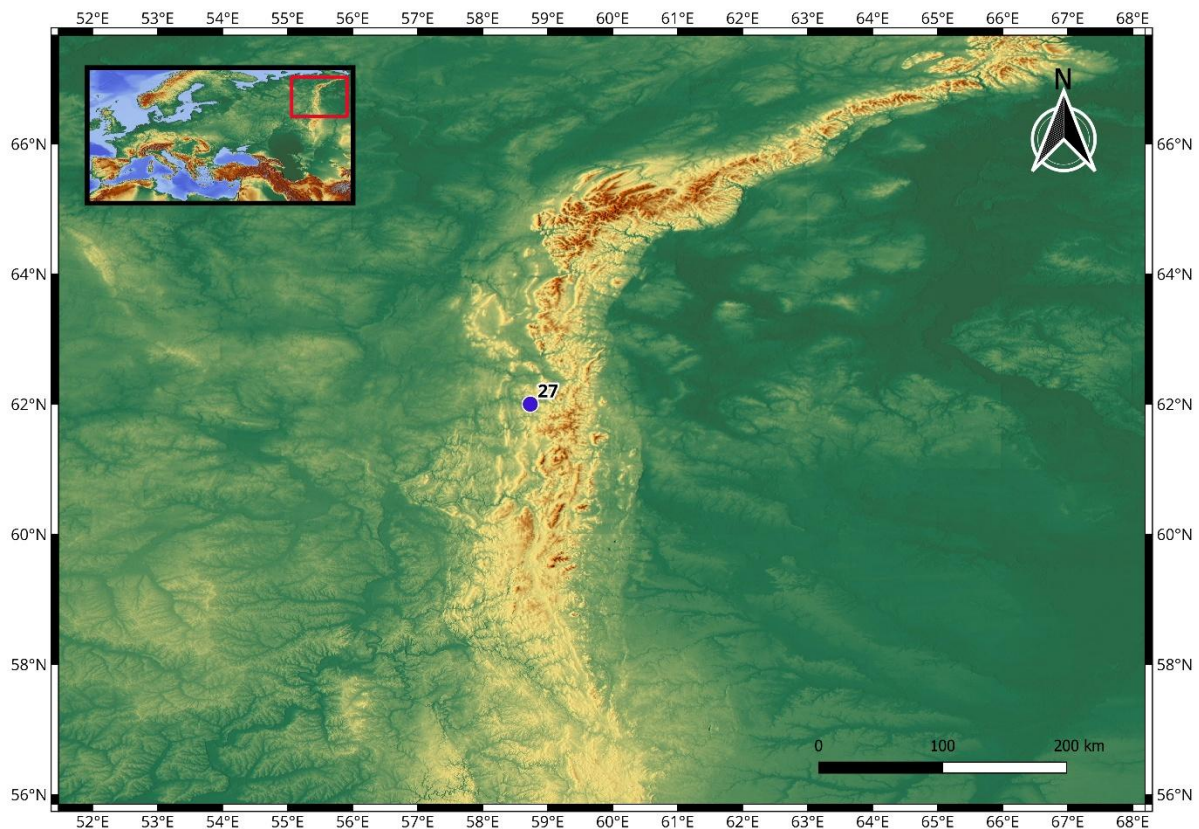


Figure 30. Location of site Medvezhiya cave (site 27, Northern Urals region).

Stratigraphic layers could not be identified during the cave excavations. Radiocarbon (AMS) dating of cave bear remains yielded dates of $45,150 \pm 600$ years cal B.P. (OxA-19568) from a skull fragment (ZIN O.34991-6) and $42,000 \pm 450$ years cal B.P. (OxA-19608) from a mandible (ZIN 34991-19; (Stiller et al., 2014)). These dates correspond to the Late Pleistocene, specifically to the first half of the MIS 3.

MATERIALS AND METHODS

5. Materials and methods

5.1 Materials

A total of 584 lower first molars (m1; $n = 584$) of different ursid species have been selected for this work, from a wide range of individuals, including juveniles, prime adults, and old adults of both sexes (Table 1), hence, ensuring a comprehensive and reliable assessment of the population's variability. The m1 specimens comprise teeth preserved within mandibles (Figure 32) as well as isolated teeth (Figure 31). The studied Pleistocene Ursidae fossil collection taxonomically comprehends seven different species: *U. spelaeus* ($n = 486$), *U. s. rossicus* ($n = 9$), *U. praekudarensis* ($n = 20$), *U. praekudarensis/kudarensis* ($n = 19$), *U. kudarensis* ($n = 21$), *U. kenivetz* ($n = 17$) and *U. arctos* ($n = 12$). The specimens come from 30 different populations, from 28 different palaeontological/archaeological sites distributed across 6 different regions; Romanian Carpathians ($n = 246$), Moldavian Plateau ($n = 95$), Western Balkans and Western Rhodopes Mountains ($n = 112$), Central Balkans ($n = 54$), Greater Caucasus ($n = 60$), and Northern Urals ($n = 17$) (Table 1; Figure 31 and 32).

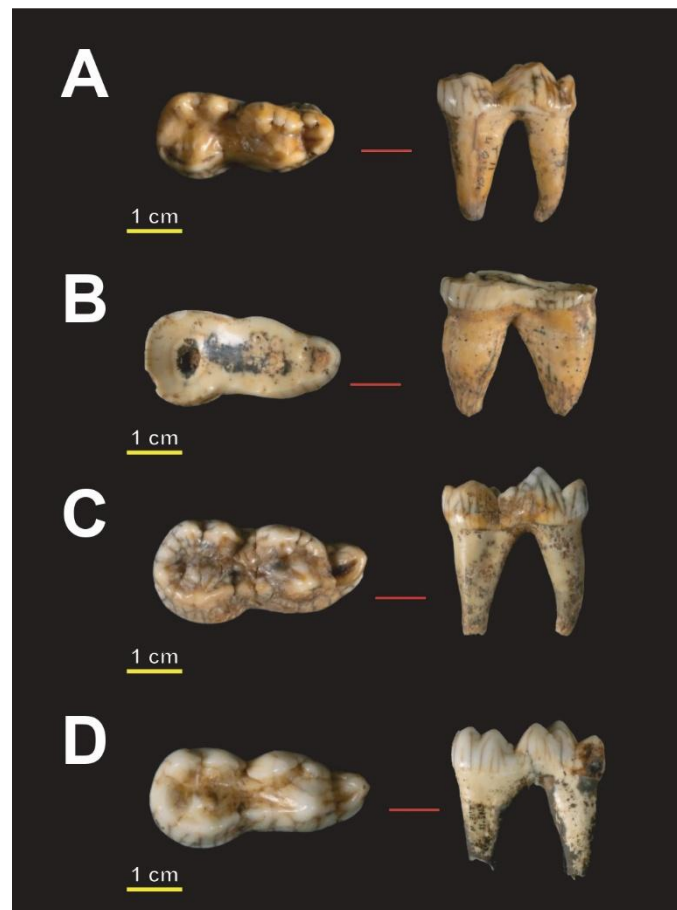


Figure 31. Isolated *U. spelaeus* lower first molars (m1) from MIS 3 cave sites, presented in occlusal (left) and buccal (right) views. Specimens exhibit morphological variation reflecting differences in wear patterns, preservation, and phylogeny. (A) Well-preserved adult molar with moderate wear; (B) Molar displaying heavy wear from a senile individual; (C and D) Molars

displaying almost no wear, likely from very young individuals. The photographs were taken by María Guillén / IPHES-CERCA using a Nikon D850 camera.



Figure 32. *U. spelaeus* mandibles from MIS 3 cave sites in buccal (left) and occlusal (right) views, displaying morphological variation across different age and sex categories: (A) Adult male. (B) Adult female. (C) Senile male. The photographs were taken by María Guillén / IPHES-CERCA using a Nikon D850 camera.

The materials for this work are hosted and stored in various institutions, including the Emil Racoviță Institute of Speleology (Bucharest, Romania), the Zoological Institute of the State University of the Republic of Moldova (Chișinău, Republic of Moldova), the National Museum of Natural History (Sofia, Bulgaria), the University of Belgrade (Serbia), and the Zoological Institute of the Russian Academy of Sciences (Saint Petersburg, Russia).

Region	Cave	Species	<i>n</i> = m1	incl.	excl.
Romanian Carpathians			246	161	85
	Urşilor	<i>U. spelaeus</i>	70	54	16
	Cioclovina	<i>U. spelaeus</i>	45	35	10
	Muierilor	<i>U. spelaeus</i>	75	32	43
	Oase	<i>U. spelaeus</i>	34	26	8
	Bisericuța	<i>U. spelaeus</i>	5	5	0
		<i>U. arctos</i>	1	1	0
	Onceasa	<i>U. spelaeus</i>	6	3	3
	La Adam	<i>U. spelaeus</i>	2	2	0
	ACCG (Cloșani area)	<i>U. arctos</i>	5	2	3
	Avenul Mâțului	<i>U. arctos</i>	1	1	0
	Colțu Surpat	<i>U. spelaeus</i>	2	0	2
Moldavian Plateau			95	57	38
	Trinca	<i>U. spelaeus</i>	16	16	0
		<i>U. arctos</i>	5	5	0
	Saharna	<i>U. spelaeus</i>	20	17	3
	Buzdujeni	<i>U. spelaeus</i>	18	11	7
	Duruitoarea Veche	<i>U. spelaeus</i>	11	6	5
	Butești	<i>U. spelaeus</i>	25	2	23
Western Balkans and Western Rhodopes Mountains			112	74	38
	Borikovska	<i>U. spelaeus</i>	76	48	28
	Magura	<i>U. spelaeus</i>	12	8	4
	Mishin	<i>U. s. rossicus</i>	9	5	4
	Bacho Kiro	<i>U. spelaeus</i>	6	5	1
	Lakatnik	<i>U. spelaeus</i>	5	4	1
	Bashovishki Pech	<i>U. spelaeus</i>	2	2	0
	Triagalna	<i>U. spelaeus</i>	2	2	0
Central Balkans			54	32	22
	Ušačka	<i>U. spelaeus</i>	18	11	7
	Hadži Prodanova	<i>U. spelaeus</i>	14	11	3
	Risovača	<i>U. spelaeus</i>	22	10	12
Greater Caucasus			60	41	19
	Kudaro 1 (layer 5c)	<i>U. praekudarensis</i>	20	15	5
	Kudaro 3 (Layer 5)	<i>U. praekudarensis/kudarensis</i>	19	14	5
	Kudaro 3 (Layer 4)	<i>U. kudarensis</i>	21	12	9
Northern Urals					
	Medvezhiya	<i>U. kenivetz</i>	17	10	7
TOTAL			584	375	209

Table 1. List of Pleistocene bear assemblages sampled for this work by region, cave site, identified species and the total number of lower first molars sampled (m1), the number of successfully analysed specimens and therefore included (incl.), and the number of specimens excluded due to ontogenetic or taphonomic reasons (excl.).

This study encompasses a diverse geographical range, spanning from the southernmost site, Borikovska Cave (41° 29' 08" N, 24° 36' 21" E), to the northernmost site, Medvezhiya Cave (62° 00' N, 58° 44' E). It also extends from the westernmost site, Risovača Cave (44° 18' 0" N, 20° 33' 59" E), to the easternmost site, Kudaro 1 and Kudaro 3 caves (42° 31' N, 43° 38' E). These sites encompass a wide range of geographical settings, from valleys and plains to high mountain ranges, resulting in a wide diverse array of biotopes. When examined collectively, the cave bear populations from these locations provide a robust framework for evaluating the species' adaptability to varied ecological conditions.

The chronological range of these bear populations extends from the Middle Pleistocene (MIS 11) to the Late Pleistocene (MIS 3). Of the 29 populations analysed, 24 date to the Late Pleistocene, and 3 to the Middle Pleistocene, (1) Kudaro 1 (*U. praekudarensis*) (2) Kudaro 3; (*U. praekudarensis* / *kudarensis*) (3) Mishin (*U. savini rossicus*), and two sites, whose *U. arctos* were used as reference, to the Holocene (ACCG; Cloșani area and Avenul Mățului). This broad chronological framework, combined with the extensive geographical range, facilitates the examination of cave bear dietary patterns under diverse climatic conditions and ecological settings, thereby offering a comprehensive perspective on their adaptive strategies and ecology through time.

5.2 Methods

5.2.1 Dental microwear analysis

For the microwear analysis, the preparation of the sample followed the protocol developed by Solounias and Semprebon (2002) and Semprebon et al. (2004).

First, the occlusal surface of the teeth was cleaned using cotton swabs soaked in acetone and then applying 96% ethanol aiming to remove traces of sediment, adhesive residues, or dust (Solounias and Semprebon, 2002; Ungar et al., 2003; Figure 33A). High-precision moulds of the surface were made using first, polyvinylsiloxane silicone (Heraeus Provil® novo, Light CD2, regular set; Figure 33B-D) and after it solidified (around 5 minutes later), a second layer using silicone putty was added, coating the first one, to form the wall of the mould (Heraeus Provil novo, Putty; Figure E-H). Finally, transparent high-resolution casts were produced using epoxy resin (CTS EPO150 resin + K151 hardener).

5. Materials and methods

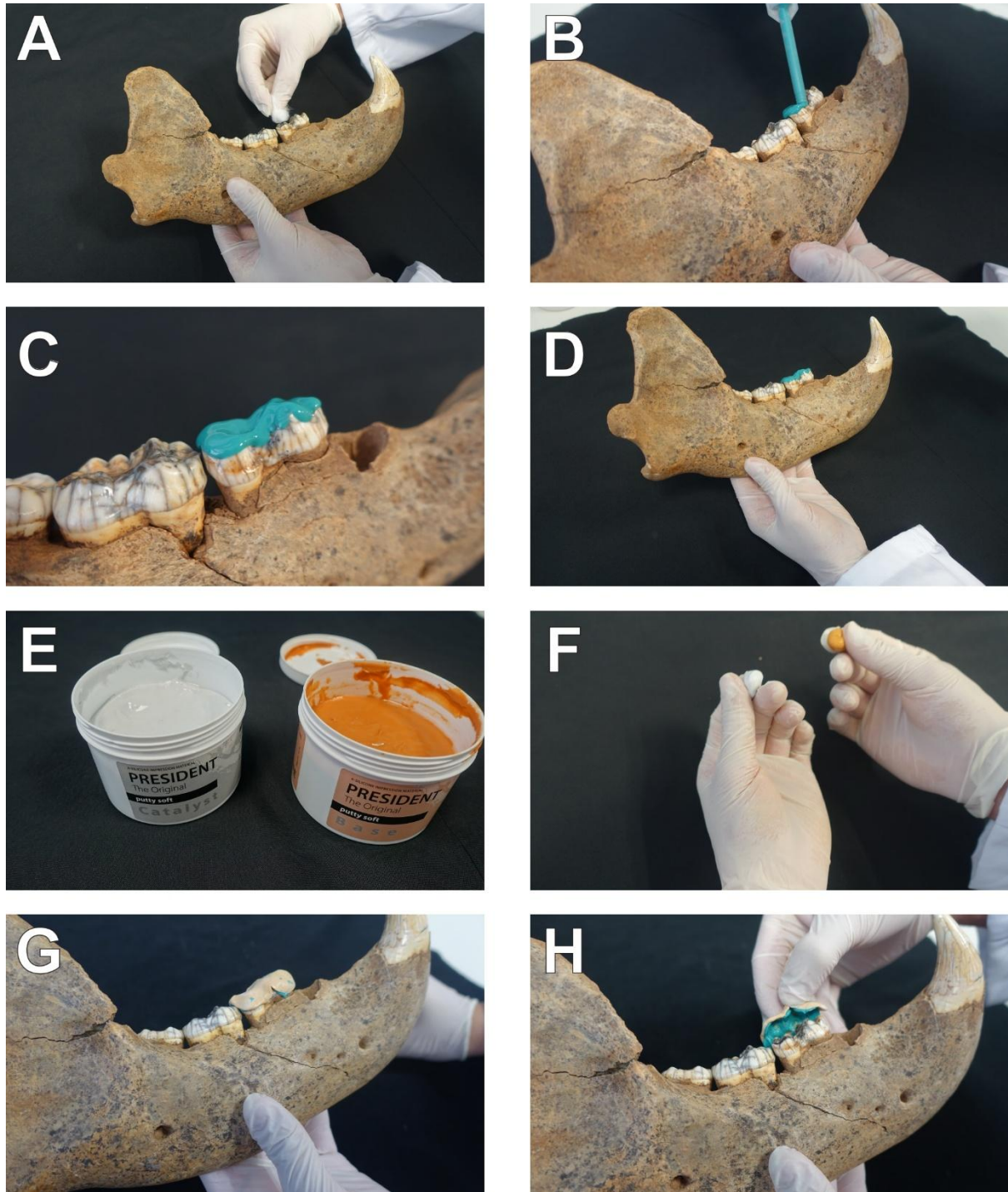


Figure 33. Sequence illustrating the procedure for producing dental moulds (negative impressions). A: Cleaning of the occlusal surface using cotton swabs. B-D: Application of high-resolution vinylpolysiloxane silicone (Heraeus Provil® novo Light CD2, regular set) onto the occlusal surface of the molar. E-F: Preparation by mixing of silicone putty (catalyst and base). G-H: Occlusal surface fully covered by both silicone layers, followed by the extraction of the mould (negative impression), preserving the morphology of the molar. Photographs taken with a Sony Alpha a6000 digital camera.

After 24 hours, and once the epoxy resin was solidified (Figure 34), the transparent casts were observed using a standard light stereomicroscope (Zeiss Stemi 2000C; Figure 36) at $\times 35$ magnification to identify and quantify the microfeatures using an optical reticule of 0.16 mm^2 (Solounias and Semprebon, 2002; Semprebon et al., 2004).



Figure 34. Final outcome of the tooth cast replication process. High-resolution resin cast (left) accurately preserving the dental morphology and detailed structures captured by the mould (right). Photograph taken with a Sony Alpha a6000 digital camera.

The non-faceted area of the grinding enamel surfaces of the m1 (Figure 35) was chosen for the analysis as it provides the most reliable representation of the dietary patterns of ursid specimens when compared to other areas of the occlusal surface of the tooth (Ungar and Teaford, 1996; Münzel et al., 2014; Pappa, 2016; Pappa et al., 2019; Ramírez-Pedraza et al., 2019, 2020, 2022). The deepest “valleys” in between the cusps were chosen, as being pointed, they were more protected from taphonomic alteration by sediment from post-depositional processes (i.e., trampling and sediment transport) in bunodont teeth (Uzunidis et al., 2021; Micó et al., 2024).

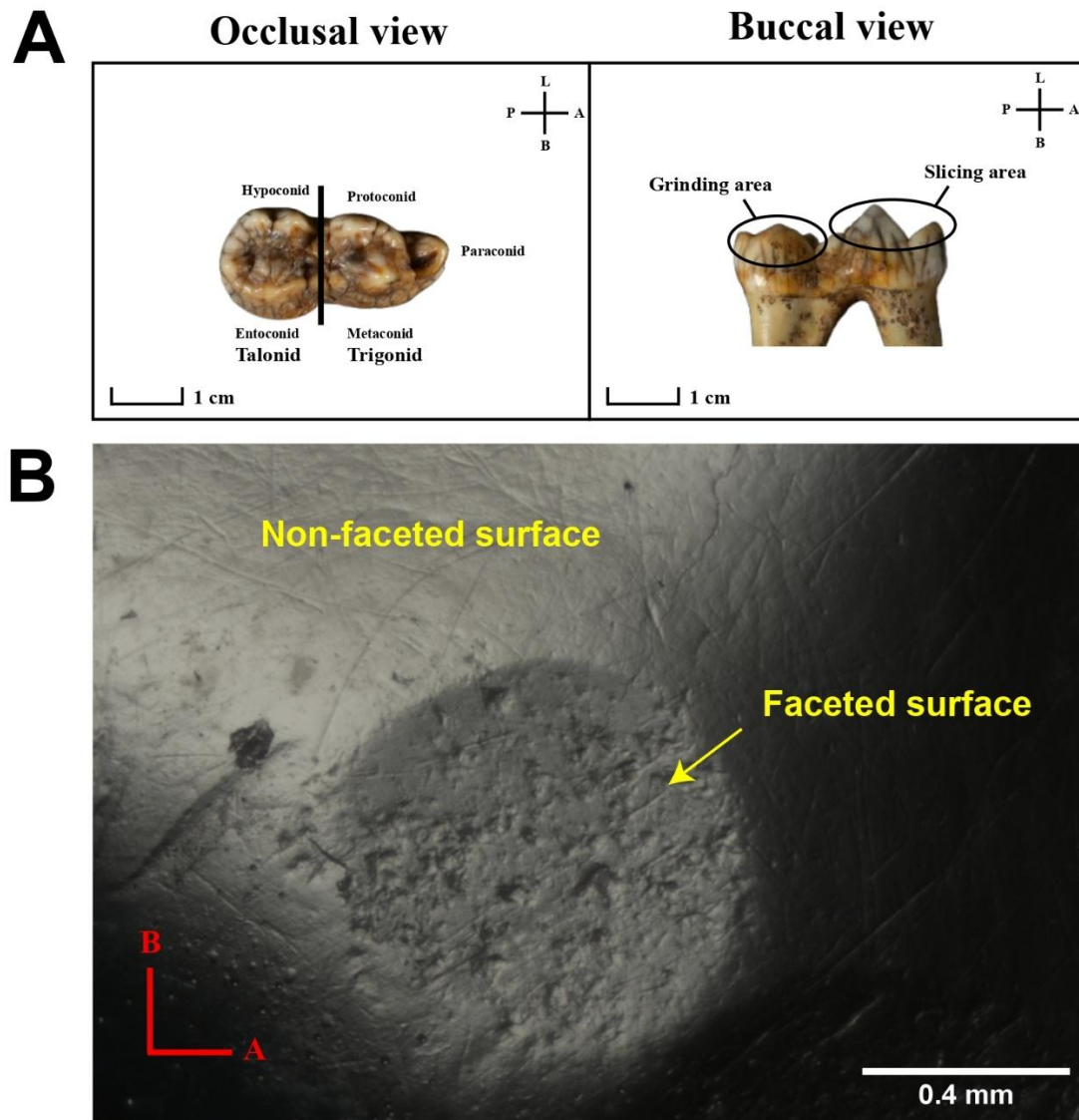


Figure 35. A) Occlusal and buccal views of the lower first molar (m1) of *U. spelaeus* showing anatomical landmarks relevant for ensuring methodological clarity and the reproducibility of this work. The occlusal view highlights the trigonid (metaconid, protoconid) and talonid (entoconid, hypoconid) areas. The buccal view indicates the grinding area (posterior) and slicing area (anterior) of the tooth. B) Microphotograph of the enamel surface of the grinding area of the talonid, highlighting the differentiation between non-faceted and faceted surfaces. The non-faceted area was chosen for analysis as it provides the most reliable representation of dietary patterns in *U. spelaeus* specimens. Abbreviations: A = anterior, P = posterior, B = buccal, L = lingual.

Once the cast is positioned on the microscope slide, it is illuminated using a transmitted light source (Figure 36). The angle of the light reaching the cast is adjustable, allowing for the observation of various microwear marks. This adjustability is crucial, as many marks differ in depth, causing them to reflect or absorb light differently, creating contrasts of light and shadow that aid in their identification (Solounias and Semprebon, 2002).

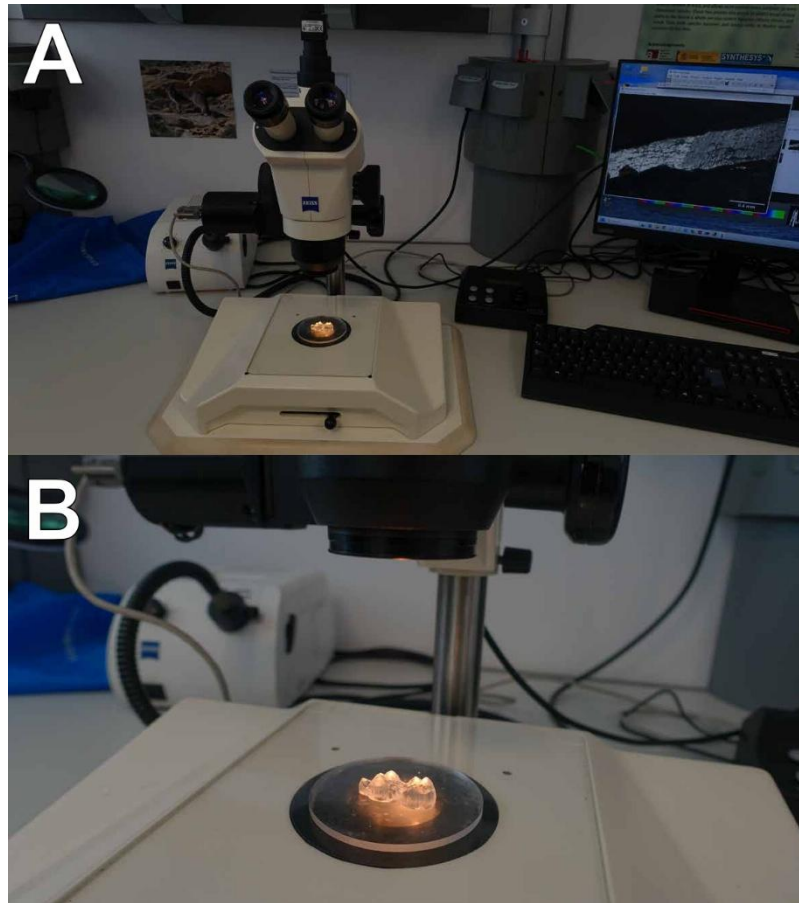


Figure 36. (A) Zeiss Stemi 2000C stereomicroscope. (B) Positive replica placed on the same microscope under transmitted light. Photographs taken with a Sony Alpha a6000 digital camera.

The features examined in this study include 1) the number of fine and coarse scratches (Figure 37) – elongated and narrow features, which can be classified as either fine (characterised by narrow and shallow marks) or coarse (characterised by wider and deeper marks); and 2) the number of small and large pits (Figure 37): circular or semicircular shapes of similar length and width. They can be classified as either small pits, which are characterised by being shallow and appearing as shiny, bright, white dots, or large pits, which are wider and deeper, and reflect less light. The scratch width score (SWS) was assessed by assigning a score of 0 to enamel surfaces with predominantly fine scratches, a score of 1 to surfaces with a mixture of coarse and fine scratches, and a score of 2 to surfaces with predominantly coarse scratches. We also quantified the number of puncture pits (very deep and symmetrical crater-like morphology with regular edges), the number of gouges (crater-like but with irregular edges), and the presence of more than four hypercoarse scratches (very deep and wider than fine and coarse scratches, resulting in very low reflectivity and appearing as dark features, they have a distinctive “trench-like” shape with symmetrical edges) (Solounias and Semprebon, 2002).

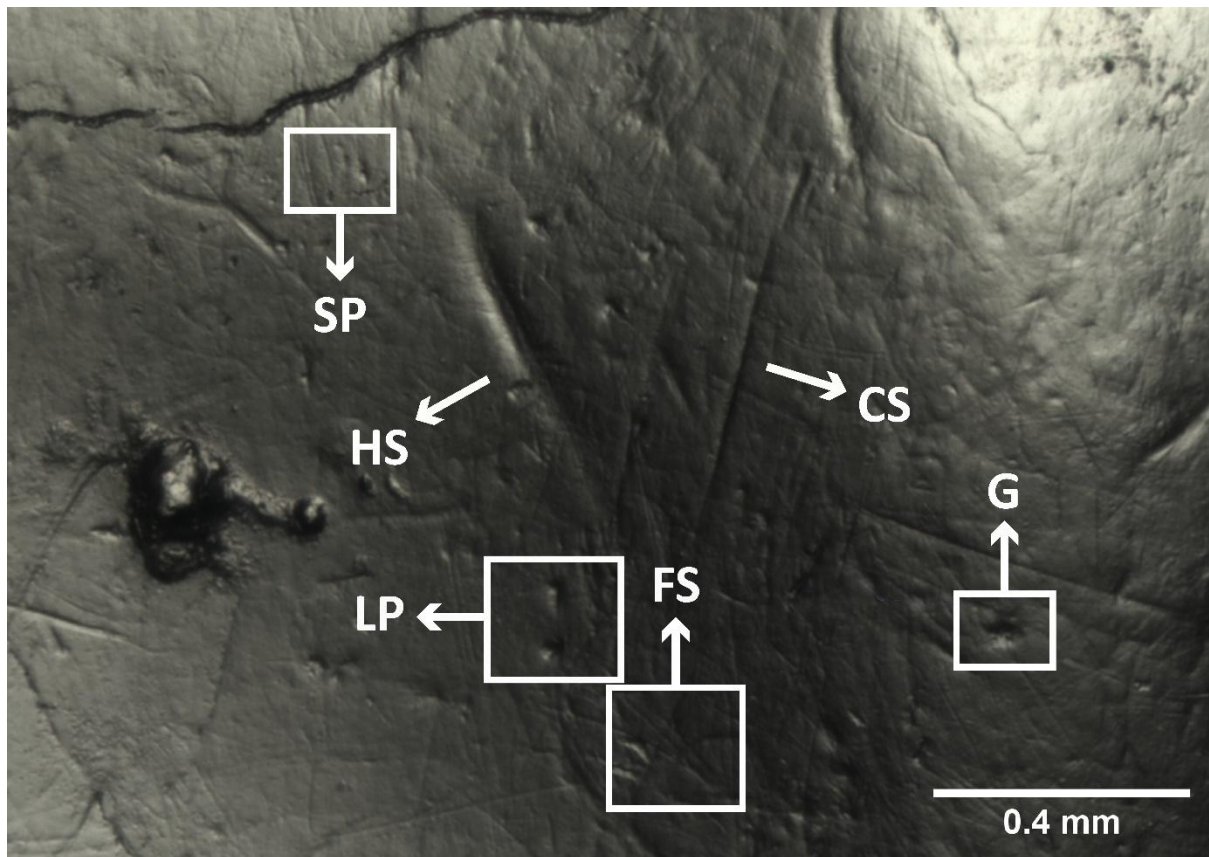


Figure 37. Photomicrograph of the tooth enamel surface ($\times 35$ magnification) of an individual of *U. praekudarensis* (ZIN 38010–89) from Kudaro 1 cave, layer 5c. Features: fine scratches (FS), coarse scratches (CS), hypercoarse scratch (HS), small pit (SP), large pit (LP), and gouges (G).

To avoid the possibility of inter-observer error, as pointed out for this technique when different observers analyse a population (DeSantis et al., 2013), a single observer (PDI) performed the analysis on all specimens.

Photomicrographs were captured using an Invenio 5SII digital camera in extended focus mode and the Helicon Focus software to combine the images acquired at different focal planes to create a single image with an increased depth of field. The scale bars were incorporated using ImageJ software.

5.2.2 Confocal profilometry for enhanced image resolution

A confocal profilometer was used to scan the same surfaces previously analysed and quantified with a stereomicroscope ($\times 35$) to obtain higher-resolution images and produce more detailed photographs of the microwear features. While the stereomicroscope was sufficient for quantification and analysis (Solounias and Semprebon, 2002), the confocal profilometer was employed solely to capture higher-quality images of specific microfeatures and enamel surfaces for clearer visual representation in this work. Therefore, the confocal profilometer was used exclusively to obtain better-resolution images, without implying additional analysis.

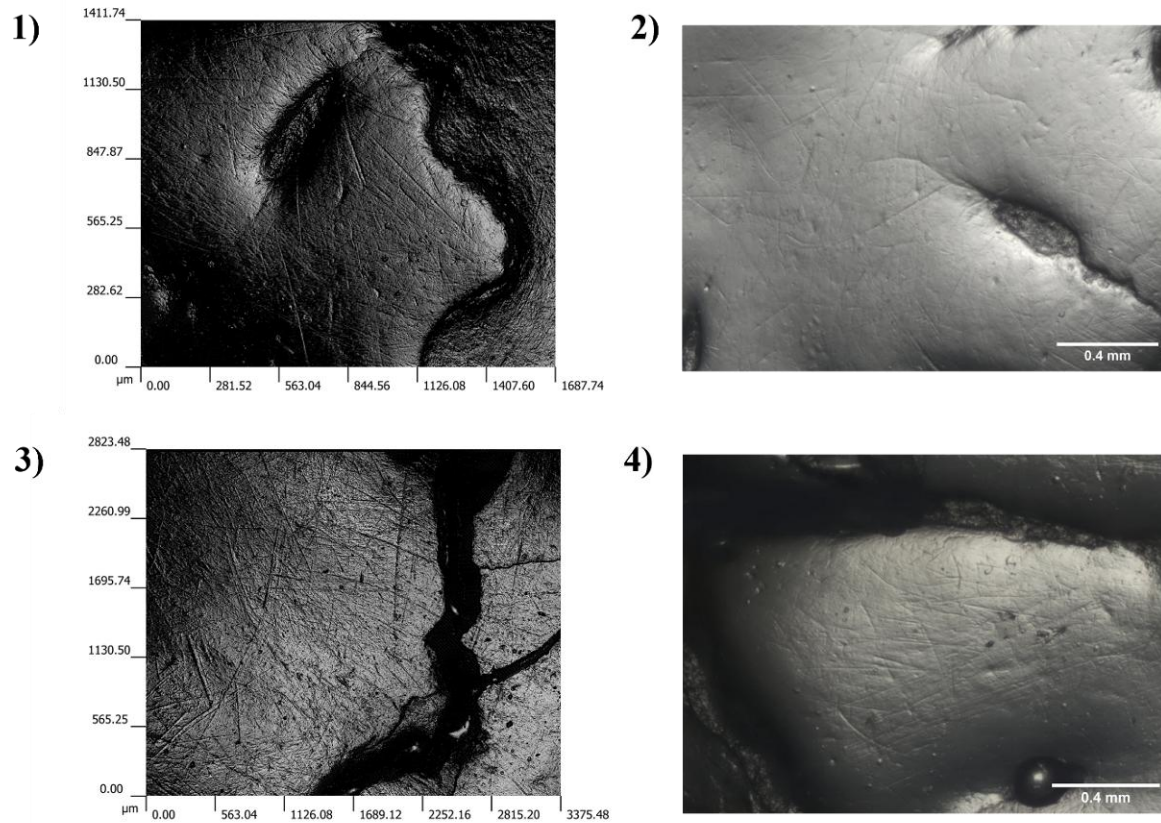


Figure 38. Three-dimensional scans and photomicrographs of identical occlusal surface regions in a fossil *U. arctos* lower first molar (m1). Images (1) and (2) depict the same occlusal region; similarly, images (3) and (4) depict a different occlusal region, with each pair corresponding to the same area respectively. Images (1) and (3) are taken through 3D scans using a confocal profilometer (Sensofar® S Neox, x20 lens (1411.74 x 1687.74 μm) image 1 and x10 lens (2823.48 x 3375.48 μm) image 3), while images (2) and (4) are photomicrographs taken with a stereomicroscope (Zeiss Stemi 2000C, x35 magnifications, scale bar: 0.4 mm.). Note that the confocal profilometer reveals considerably more microwear features, and in greater detail and resolution, compared to the stereomicroscope. However, the stereomicroscope is enough to quantify the microwear features in the surface for this microwear method, as proven by Solounias and Semperebon (2002).

Three-dimensional scans of the same analysed area were obtained using a Sensofar® S Neox microscope powered by the SensoSCAN® 6.2 software at IPHES (Tarragona, Spain). The molars were positioned under the microscope in different orientations, aiming to achieve flatness and optimal illumination in the analysed area, due to the different morphologies of the talonid grinding surface in cave bears (Grandal-d'Anglade and López-González, 2005; Baryshnikov and Puzachenko, 2020). Scans of the surface were generated with magnifications of 10 $\times$ (in an area of 1680 μm $\times$ 1400 μm integrated into four fields of view) and 20 $\times$ (in an area of 840.42 $\times$ 702.42 μm integrated into four fields of view), one or the other chosen depending on the size of the features to be observed.

5.2.3 Comparison with extant bears

The dental microwear quantifications obtained for the analysed cave bear fossil populations were compared with the reference dataset of extant bear species established by Pappa et al. (2019) to reconstruct their short-term palaeodiet. The reference collection allowed the direct

5. Materials and methods

comparison of extinct ursids with their closely related living counterparts, such as *U. arctos* from different regions including Kamchatka ($n = 23$), Greece ($n = 4$), Central Europe ($n = 10$), Northern Europe ($n = 9$), and North America ($n = 8$), as well as *U. americanus* from North America ($n = 9$). Both species show a wide range of dietary preferences, which include the consumption of vertebrates and invertebrates as well as hard mast and soft mast diets (Table 2).

Species	Geographic origin	Dietary group	Description
<i>U. arctos</i>	Greece	Soft mast (P)	Green vegetation and soft fruits
<i>U. arctos</i>	Central Europe	Hard mast (P) , soft mast and vertebrates	Nuts, fleshy fruits, fish and vertebrates
<i>U. arctos</i>	North America	Vertebrates (P) , soft mast, hard mast	Vertebrates, fish, nuts and fleshy fruits
<i>U. arctos</i>	Kamchatka	Vertebrates (P) , soft mast	Vertebrates, fish, nuts and fleshy fruits
<i>U. arctos</i>	Northern Europe	Soft mast (P) , vertebrates, invertebrates	Fleshy fruits, invertebrates, and vertebrates (more carnivorous tendencies compared to southern bears)
<i>U. americanus</i>	North America	Soft mast (P) , vertebrates	Mostly fibrous and abrasive food such as leaves, also soft fruits and occasionally fish
<i>U. thibetanus</i>	Japan and Tibet	Hard mast (P) , soft mast invertebrates and occasional vertebrates	Highly variable mostly herbivorous diet with seeded fruits, insects and flesh consumption
<i>U. maritimus</i>	North Pole	Vertebrates (Only)	Mainly seals, with occasional fish
<i>A. melanoleuca</i>	China	Abrasive foliage (Only)	Obligate bamboo diet

Table 2. Dietary classifications and consumed food items for each extant bear population included in this study. Abbreviations: (P): Preferred, (Only): Indicates a food item that is consumed exclusively, signifying an obligate dietary specialization (modified from Pappa, 2016).

The reason *U. arctos* and *U. americanus* were chosen for the comparison in this study, while other bears from the Pappa et al. (2019) dataset were excluded, is because 1) *U. arctos* and *U. americanus* are the closest extant relatives to the cave bear lineage phylogenetically (Loreille et al., 2001; Knapp et al., 2009), as evidenced by similar behaviours, such as hibernation. 2) The extant populations of *U. arctos* and *U. americanus* from the reference collection inhabited temperate and cold regions from the north hemisphere, with climates and environments analogous to those of the Pleistocene. Therefore, these two populations provide the most reliable and comparable dietary patterns for inferring the cave bear diet, as evidenced by previous microwear studies (Ramírez-Pedraza et al., 2022). Additionally, for all the analysed fossil populations, with some displaying microwear features indicative of bone consumption or highly abrasive herbivorous diets, the hypercarnivorous *U. maritimus* and the hyper-herbivorous *A. melanoleuca* were included in every comparison, serving as extremes to infer the degree of carnivory and herbivory (Table 2).

Finally, for specific fossil populations that coexisted with Asian black bear (*U. thibetanus*) (belonging to the *U. kudarensis* lineage from Kudaro 1 and Kudaro 3 caves), an extant population of this species from the Pappa et al. (2019) collection was included in the comparison to explore potential ecological interactions between the diet of *U. thibetanus* and that of the studied fossil populations (Table 2).

5.2.4 Assessing the relationship of microwear with climatic and geographic variables, and time

In order to investigate potential environmental drivers underlying microwear variation among cave bear populations, the potential for meaningful patterns between climatic, geographic and time variables, and microwear variables was examined. The central objective was to assess whether ecological conditions could help explain observed differences in microwear, possibly reflecting dietary or behavioural adaptations. Furthermore, this analysis aimed to determine whether any statistically significant patterns in microwear features could be identified over time, thereby indicating a potential trend in the evolution of seasonal diets.

To approach this, the *pastclim* package in RStudio was employed (Leonardi et al., 2023), and the Barreto et al. (2023) paleoclimatic dataset was used, which offers high-resolution reconstructions of key bioclimatic variables for the Late Quaternary (from 800 ka B.P. onwards). The variables extracted included Mean Annual Temperature (bio01), Temperature Seasonality (bio04), Maximum Temperature of the Warmest Month (bio05), Minimum

5. Materials and methods

Temperature of the Coldest Month (bio06), Temperature Annual Range (bio07), and Annual Precipitation (bio12). These were matched to each site and time point associated with individual specimens using geographic coordinates (latitude and longitude) and radiocarbon dates (based either on direct radiocarbon dating of the specimen or on chronological attribution from the associated stratigraphic context; this being through direct dating methods or relative dating). In addition to climatic data, geographic variables were independently computed—specifically, altitude (present-day meters above sea level), latitude, and longitude—to complement the environmental context. This multi-scalar dataset allowed for an integrated analysis of how environment might structure microwear patterns of cave bears.

Finally, temporal data (i.e., ka B.P.), both from directly dated and calibrated individuals ($n = 11$) and from stratigraphic level mean dates of the populations ($n = 355$), bringing the total sample to $n = 366$, were assigned to each individual and used to explore potential correlations with microwear variables, aiming to detect trends in seasonal dietary patterns over time.

5.3 Statistical methods and software employed

In terms of statistical analysis, basic boxplots and bivariate plots were employed to describe distributions and visualize variability within the data. Additionally, to explore the relationship between fossil individuals and those in the reference dataset, correspondence analysis (CA) was applied, as this method is well-suited to the discrete, quantitative nature of microwear data (i.e., feature counts).

To examine the potential associations between microwear variables and environmental factors, both climatic, geographic, and temporal, a Pearson correlation matrix was first computed to assess overall linear relationships among variables. Based on these results, a series of regression analyses—primarily linear models—were subsequently performed on selected variable pairs that exhibited a Pearson's correlation coefficient (r) greater than ± 0.30 . These models aimed to explore potential trends between microwear features (e.g., hypercoarse scratches, fine-to-coarse scratch ratio) and environmental and time predictors such as annual precipitation, longitude, elevation, temperature parameters and ka B.P.. When appropriate, regression models were accompanied by standard diagnostic tests to evaluate the validity of model assumptions, particularly in cases where model reliability remained uncertain even after visual inspection of the bivariate plots. These included: the Shapiro-Wilk test for assessing normality of residuals, the Breusch-Pagan test for homoscedasticity, and the Durbin-Watson test to detect autocorrelation.

Maps were generated using ArcGIS version 10.6.1 (Esri, 2018), while graphs, statistical tests, and analyses were performed using RStudio version 4.1.2 (RStudio Team, 2021).

RESULTS

6. Results

6.1 Romanian Carpathians

A total of 161 lower first molars (m1), out of 246 examined, were deemed suitable for analysis. These included specimens of *U. spelaeus* from Urşilor ($n = 54$), Cioclovina ($n = 35$), Muierilor ($n = 32$), Oase ($n = 26$), Bisericuța ($n = 5$), Onceasa ($n = 3$), and La Adam ($n = 2$). Additionally, from the identified *U. arctos* specimens were found suitable: one from Bisericuța ($n = 1$), two from Peștera-Aven din Cracul de la Cioaca Goală, also known as ACCG or Cloșani area ($n = 2$), and one from Avenul Mățului ($n = 1$).

Therefore, 85 lower first molars (m1) had to be excluded from the analysis, those included the youngest individuals lacking wear facets (Rivals et al., 2007) and those with damaged occlusal surfaces due to taphonomic processes (King et al., 1999; El-Zaatari, 2010; Uzunidis et al., 2021; Micó et al., 2024). These excluded samples belonged to *U. spelaeus* from Urşilor ($n = 16$), Cioclovina ($n = 10$), Muierilor ($n = 43$), Oase ($n = 8$), Onceasa ($n = 3$) and Colțu Surpat ($n = 2$). Additionally, three *U. arctos* specimens from ACCG ($n = 3$) had to be excluded.

Location	Species	<i>N</i>	NFS	NCS	NTS	SWS	NLP	NSP	NPP	NTP	NG
Extinct											
Urşilor	<i>U. spelaeus</i>	54	10.58	8.84	19.55	1.04	2.31	20.04	1.27	23.59	0.94
Cioclovina	<i>U. spelaeus</i>	35	15.29	5.33	20.88	0.37	1.67	27.17	2.34	31.30	1.03
Muierilor	<i>U. spelaeus</i>	32	16.75	3.81	21.24	0.22	1.64	30.34	3.14	35.17	1.34
Oase	<i>U. spelaeus</i>	26	13.00	10.05	23.05	1.04	3.60	19.35	2.87	25.81	1.12
Bisericuța	<i>U. spelaeus</i>	5	14.27	9.10	23.37	0.80	2.80	19.03	2.50	24.33	0.60
	<i>U. arctos</i>	1	6.00	21.00	27.00	2.00	27.00	9.00	2.00	38.00	1.00
Onceasa	<i>U. spelaeus</i>	3	15.17	10.00	25.17	1.00	5.00	17.33	1.00	23.17	0.00
La Adam	<i>U. spelaeus</i>	2	16.00	4.00	20.00	0.50	2.00	25.00	2.00	29.00	0.00
ACCG	<i>U. arctos</i>	2	10.50	14.75	25.25	1.50	5.50	14.25	1.50	21.25	1.00
Avenul Mățului	<i>U. arctos</i>	1	4.00	20.00	24.00	2.00	10.00	20.00	3.00	33.00	0.00
Extant											
North America	<i>U. americanus</i>	9	13.56	2.56	16.12	0.00	5.44	19.00	3.00	27.44	0.00
Greece	<i>U. arctos</i>	4	13.00	7.00	20.00	0.5	9.25	8.50	2.25	20.00	2.00

Central Europe	<i>U. arctos</i>	10	17.50	3.40	20.90	0.00	5.40	22.50	8.30	36.20	2.10
North America	<i>U. arctos</i>	8	18.25	3.00	21.25	0.00	6.75	18.38	3.25	28.38	0.25
Kamchatka	<i>U. arctos</i>	23	16.22	3.83	20.05	0.10	6.96	19.78	4.78	31.52	0.35
Northern Europe	<i>U. arctos</i>	9	15.78	3.78	19.56	0.00	6.44	23.33	2.67	32.44	0.22
Eastern Asia	<i>A. melanoleuca</i>	4	19.25	0.00	19.25	0.00	8.50	46.25	0.00	54.75	0.00
Polar circle	<i>U. maritimus</i>	13	11.00	3.21	14.23	2.79	4.50	16.21	0.07	20.15	0.00

Table 3. Comparison of the dental microwear results of the fossil populations of cave bear (*U. spelaeus*) and brown bear (*U. arctos*) from the Romanian Carpathians with the reference dataset of extant bear species of *U. arctos*, *U. americanus*, *A. melanoleuca* and *U. maritimus* established by Pappa et al. (2019). Abbreviations: *N* = number of specimens, NFS = number of fine scratches, NCS = number of coarse scratches, NTS = number of total scratches, SWS = scratch width score, NLP = number of large pits, NSP = number of small pits, NPP = number of puncture pits, NTP = number of total pits, NG = number of gouges.

6.1.1 *U. spelaeus* from the Romanian Carpathians

Microwear analysis of *U. spelaeus* from the Romanian Carpathians reveals notable differences between cave sites (Table 3). Among caves with significant sample sizes ($n \geq 5$; Urşilor, Cioclovina, Muierilor, Oase, and Bisericuța), the total number of scratches (NTS) shows variability across populations. The lowest NTS value is recorded at Urşilor (NTS = 19.55), the population with the largest sample size ($n = 54$), while the highest NTS value is found at Bisericuța (NTS = 23.37, $n = 5$). Among populations with smaller sample sizes ($n < 5$), Onceasa ($n = 3$) exhibits the highest NTS value (NTS = 25.17), while La Adam ($n = 2$) presents a lower value (NTS = 20.00).

Fine scratches (NFS) predominate over coarse scratches (NCS) in all *U. spelaeus* populations, with variability in the scratch width score (SWS). Populations such as Cioclovina (SWS = 0.37) and Muierilor (SWS = 0.22) display a predominance of fine scratches, resulting in SWS values close to 0. In contrast, populations such as Urşilor (SWS = 1.04), Oase (SWS = 1.04), and Onceasa (SWS = 1.00) exhibit a more balanced distribution of fine and coarse scratches, with higher SWS values.

The total number of pits (NTP) also shows variability among caves, with Muierilor (NTP = 35.17) presenting the highest value, while Urşilor (NTP = 23.59) exhibits the lowest among populations with significant sample sizes. Small pits (NSP) consistently outnumber large pits (NLP) across all populations. For instance, NSP ranges from 19.03 at Bisericuța to 30.34 at Muierilor, while NLP values are relatively high, ranging from 1.64 at Muierilor to 3.60 at Oase.

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Among smaller sample populations, Onceasa ($n = 3$) exhibits the highest NLP (5.00), while La Adam ($n = 2$) presents a comparable NLP of 2.00.

Regarding puncture pits (NPP), Muierilor (NPP = 3.14) shows the highest value, followed by Oase (NPP = 2.87) and Cioclovina (NPP = 2.34). All populations exhibit a significant presence of puncture pits (Figure 39), with average counts consistently at or above a minimum of one. Finally, gouges (NG) are observed in all populations with significant sample sizes ($n \geq 5$), with Muierilor (NG = 1.34) recording the highest value and Bisericuța (NG = 0.60) the lowest.

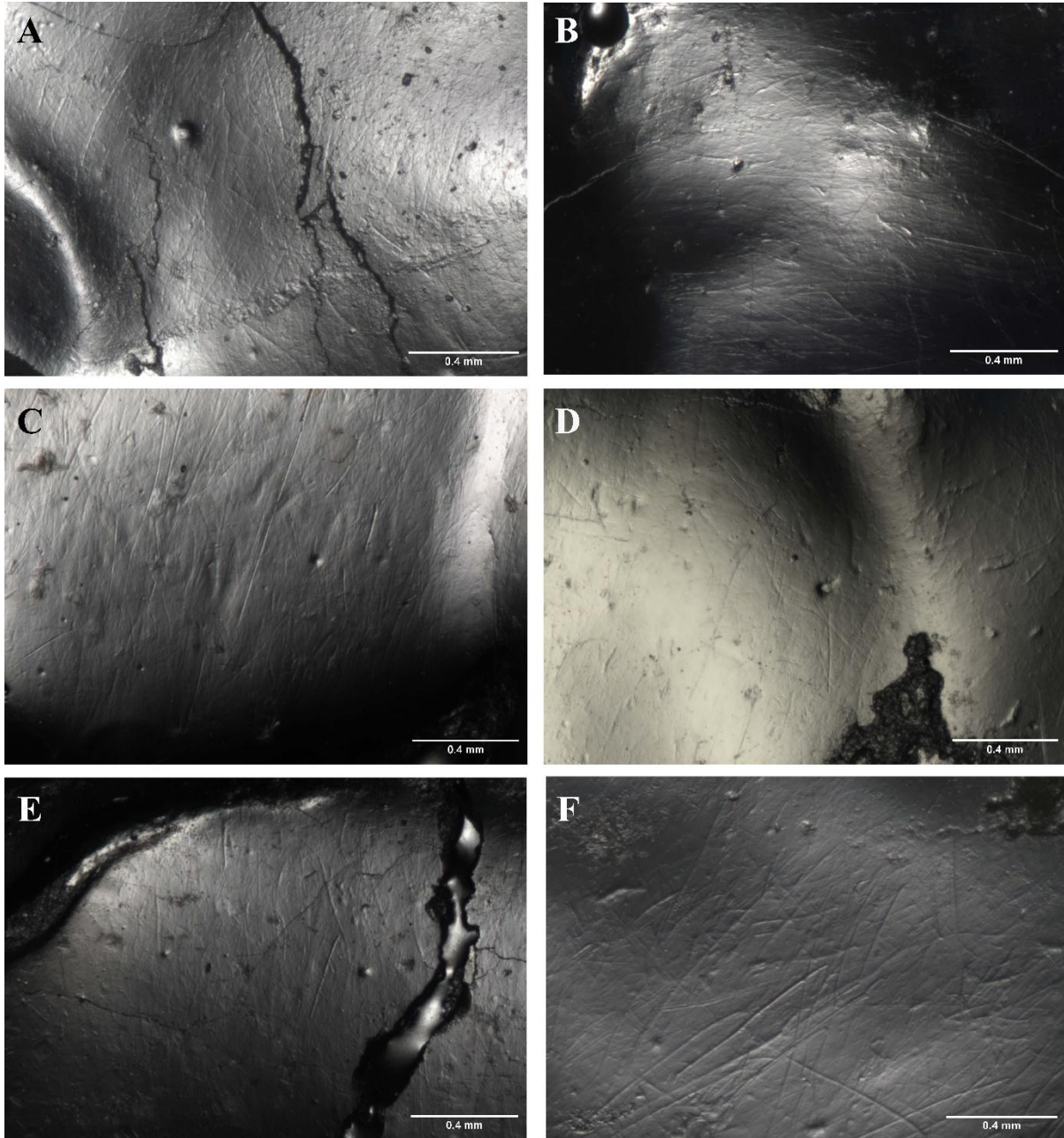


Figure 39. Photomicrographs (at $\times 35$ magnification) of the grinding non-faceted enamel surface of selected fossil individuals of *U. spelaeus* from the Romanian Carpathians. A: Urşilor (#PU/F); B: Urşilor (#PU/E2-III-1164); C: Oase (#O35.138); D: Bisericuța (#PB/C1-IX); E: Bisericuța: #PB/A1-I-II-1); F: Onceasa (#POc/016). Puncture pits are observable in high numbers across all individuals.

6.1.1.1 Comparison with extant bears

When compared with extant bear populations, the most numerous *U. spelaeus* populations, such as Urşilor (NTS = 19.55), Cioclovina (NTS = 20.88), and Muierilor (NTS = 21.24), as well as smaller populations such as La Adam (NTS = 20.00), exhibit a similar total number of scratches to *U. arctos* populations from Northern Europe (NTS = 19.56), Greece (NTS = 20.00), Kamchatka (NTS = 20.05), Central Europe (NTS = 20.90), and North America (NTS = 21.25). In contrast, *U. spelaeus* populations from Oase, Bisericuța, and Onceasa display

slightly higher numbers of scratches compared to extant bear populations (Table 3). Regarding the distribution of scratches, extant bear populations of *U. arctos* and *U. americanus* also exhibit a predominance of fine scratches over coarse scratches, similar to what is observed in *U. spelaeus* populations. However, populations with a higher number of coarse scratches (Urşilor, Oase, Onceasa, and Bisericuța), present similarities with the *U. arctos* population from Greece (NFS = 13.00; NCS = 7.00; SWS = 0.5), which also demonstrates a relatively high number of coarse scratches.

Concerning the total number of pits (NTP), Muierilor, with the highest number of total pits (NTP = 35.17), shows a count comparable to that observed in *U. arctos* from Central Europe (NTP = 36.20), while the sites with NTP around 30, i.e., Cioclovina and La Adam, display averages closer to those of *U. arctos* from Kamchatka (NTP = 31.52), Northern Europe (NTP = 32.44), and North America (NTP = 28.38). For puncture pits (NPP), the fossil populations with more puncture pits (Muierilor, Oase, Bisericuța and Cioclovina) display similarities with *U. americanus* (NPP = 3.00) and *U. arctos* from North America (NPP = 3.25) as well as *U. arctos* from Northern Europe (NPP = 2.67) and in lesser extent from Greece (NPP = 2.25). The populations of Urşilor and Onceasa display slightly lower averages numbers of puncture pits to those from extant omnivorous bear species. Regarding gouges (NG), the most numerous fossil populations (Urşilor, Cioclovina, Muierilor and Oase, with NG around or slightly higher than 1) are comparable, albeit with slightly lower values, to *U. arctos* populations from Central Europe (NG = 2.10) and Greece (NG = 2.00).

6.1.2 *U. arctos* from the Romanian Carpathians

For the fossil specimens of brown bear *U. arctos*, although the number of individuals per site is small (Bisericuța: $n = 1$, ACCG: $n = 2$, Avenul Măţului: $n = 1$), making them statistically insignificant, there is a notable consistency in the total number of scratches (NTS) observed, ranging from 24 (Avenul Măţului) to 27 (Bisericuța) (Table 3). However, when considering the total number of pits (NTP), there is a higher range of variability, spanning from 21 (ACCG) to 38 (Bisericuța). The Holocene *U. arctos* individuals from Avenul Măţului (NTP = 33.00) and the Pleistocene individual from Bisericuța (NTP = 38.00) exhibit a notably high total number of pits (NTP) compared with *U. spelaeus* populations from the same region. Among cave bears, this NTP score is only comparable to that observed in the *U. spelaeus* population from Muierilor (NTP = 35.17). The Pleistocene *U. arctos* from Bisericuța clearly exhibits a higher count of coarse scratches (NCS), as evidenced by an SWS of 2.00 for the individual from

Bisericuța (Figure 41). This is also true for the Holocene individual from Avenul Mățului (SWS = 2), while a slightly lower SWS of 1.50 is scored by the medieval individuals from the Cloșani area (or ACCG) (Table 3; Figure 40A). These results suggest a greater proportion of coarse scratches in these fossil *U. arctos* individuals compared to the contemporaneous *U. spelaeus* populations (Figure 40A). In terms of pit distribution, the Bisericuța specimen shows a higher count of large pits (NLP = 27.00) compared to small pits (NSP = 9.00), which opposes the general trend observed in *U. spelaeus* with a predominance of small pits (Figure 40B). Conversely, the Holocene brown bears from the ACCG (Cloșani area) exhibit a distribution pattern similar to *U. spelaeus*, with a higher count of small pits (NSP = 14.25) compared to large pits (NLP = 5.50). Similarly, the Holocene individual from Avenul Mățului exhibits a higher prevalence of small pits (NSP = 20.00) compared to large pits (NLP = 10.00), a pattern comparable to that observed in extinct *U. spelaeus*. However, the number of small pits (NSP) for Holocene brown bears is smaller (ACCG) or overlapping (Avenul Mățului) when compared to fossil *U. spelaeus* (Figure 40B). For the Holocene brown bears the NSP score closely resembles those of Oase, Bisericuța, Urșilor, and Onceasa, although they display a slightly higher number of large pits (NLP) (Figure 40B). The number of puncture pits (NPP) shows a consistent distribution, ranging from 2.00 (Bisericuța) to 3.00 (for Holocene Avenul Mățului individual), and with a 1.50 for the medieval Cloșani area individuals. In terms of gouges, both Cloșani area (ACCG) and Bisericuța exhibit an average count of 1, while the individual from Avenul Mățului does not show any gouges. The puncture pits and gouges observed in the fossil *U. arctos* specimens are consistent with those observed in *U. spelaeus* populations.

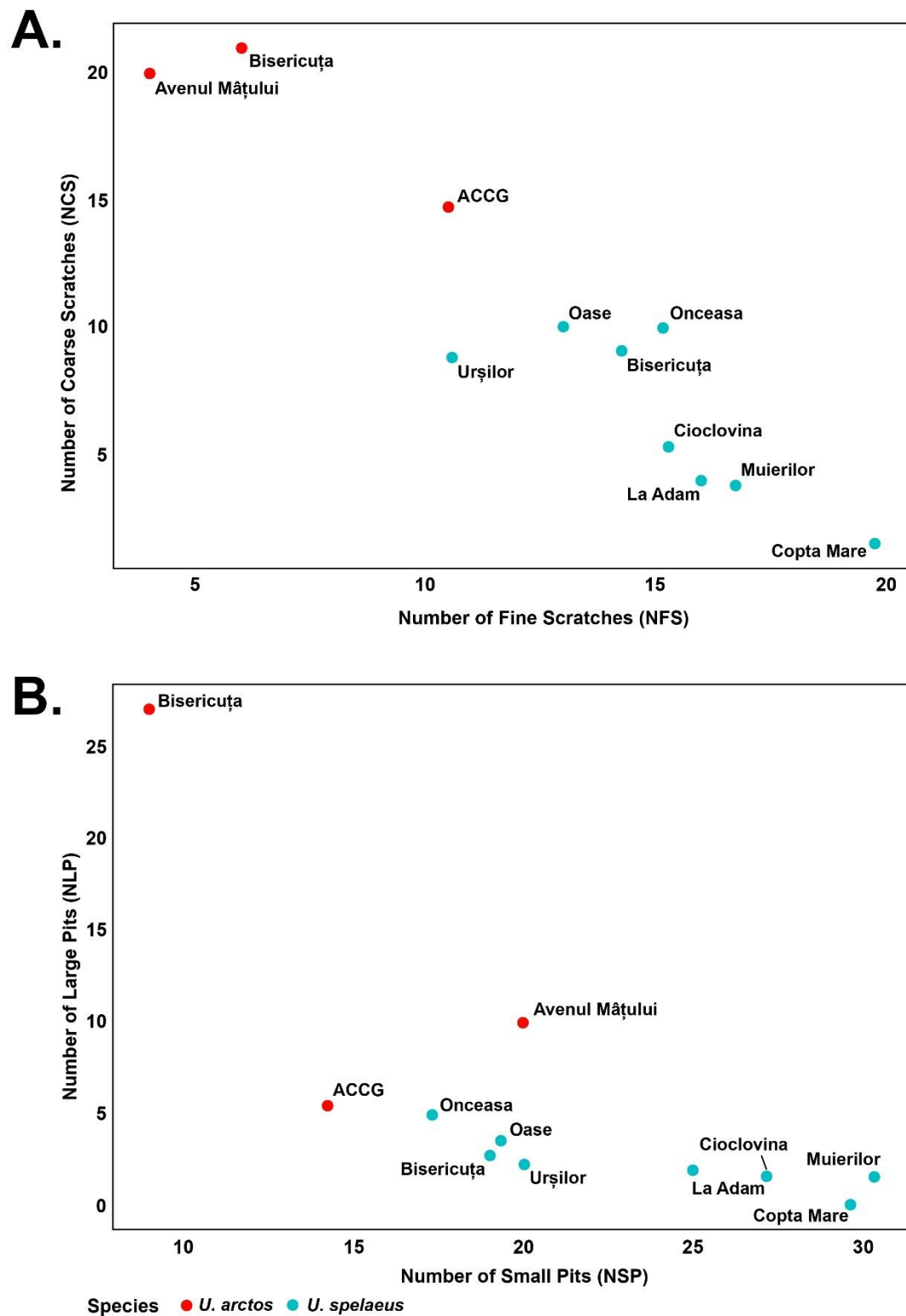


Figure 40. Bivariate plot of the mean number of fine and coarse scratches (A) and small and large pits (B) for the fossil bear populations of *U. arctos* (red) and *U. spelaeus* (blue) from the Romanian Carpathians.

6.1.2.1 Comparison with extant bears

Compared to extant bear populations, the fossil *U. arctos* exhibits a higher total number of scratches, with a greater prevalence of coarse scratches relative to fine scratches (Table 3). This pattern contrasts with that observed in extant bear populations, where fine scratches predominate (Table 3). Regarding pits, the Holocene individual from Avenul Mățului has a total number of pits (NTP = 33.00) comparable to *U. arctos* populations from Northern Europe, Kamchatka, and Central Europe (Table 3). However, the Holocene specimen displays a significantly higher proportion of large pits (NLP = 10.00) compared to any extant species, with only *U. arctos* from Greece approaching this value (NLP = 9.25). Conversely, the number of small pits (NSP = 20.00) aligns with those of *U. arctos* from Kamchatka and *U. americanus*. Furthermore, the two medieval individuals from ACCG are characterized not by a high number of large pits (NLP = 5.50) but rather by a dominance of small pits (NSP = 14.25), similar to what is observed in modern *U. arctos* populations and fossil *U. spelaeus* (Table 3). Finally, the Pleistocene *U. arctos* from Bisericuța exhibits a high number of large pits (NLP = 27.00), surpassing any other ursid (Table 3), extant or extinct, included in this study. In contrast, it shows a notably low number of small pits (NSP = 9.00).

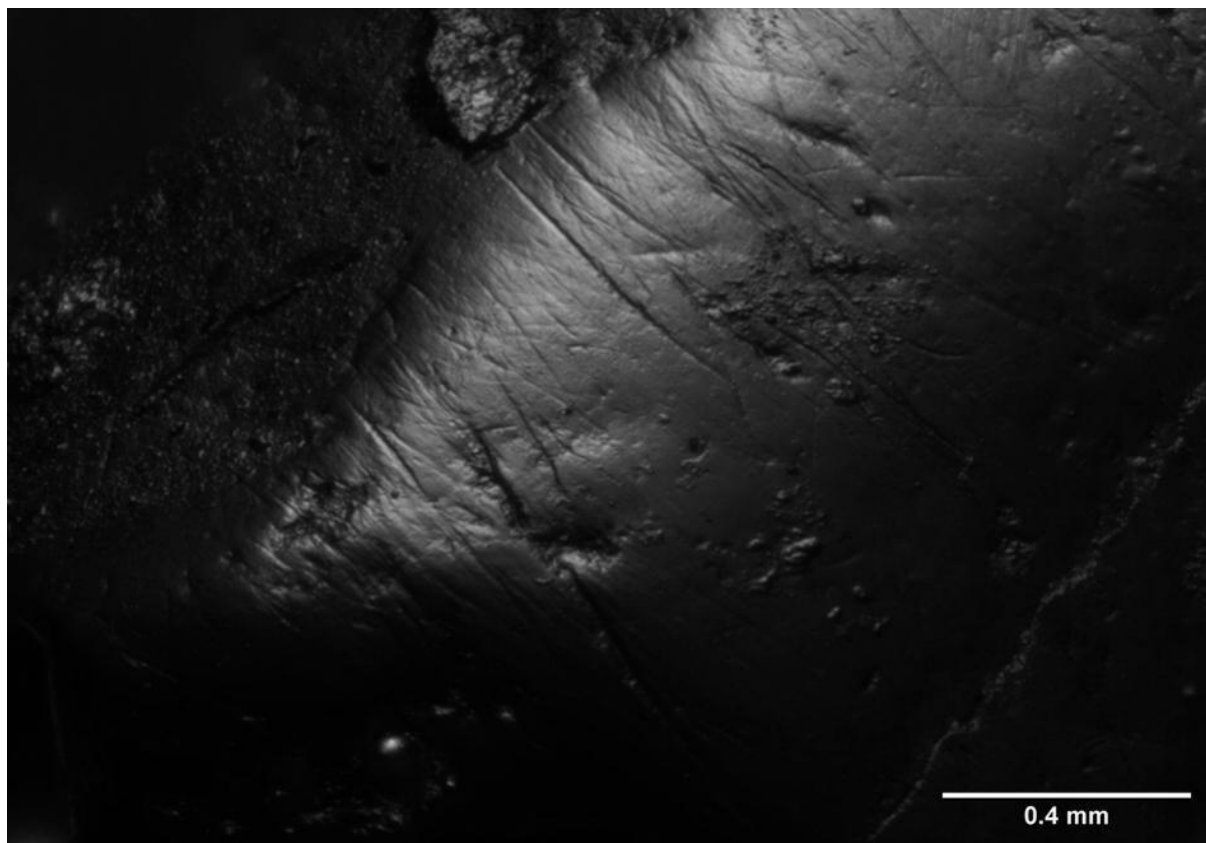


Figure 41. MIS 3 *U. arctos* from Bisericuța displaying coarse scratches, large pits and gouges (#PB/B1-X-XI).

6.1.3 Dietary inference

6.1.3.1 Bivariate analysis of the total number of scratches and pits

The bivariate plot of the total number of pits (which includes the count of small and large pits as well as puncture pits) and the number of total scratches (accounting for the sum of fine and coarse scratches) shows that the three fossil populations' distribution closely relates them to dietary regimes of extant bear species (Figure 42). The extant bear populations distribute themselves according to their main dietary preferences (omnivorous with a preference for soft mast, hard mast or vertebrates, and a pure herbivorous diet). The omnivorous bears, including *U. arctos* and *U. americanus*, are distributed across three different regions of the plot which can be related to their main dietary preferences (Figure 42). First, the soft mast specialised *U. arctos* from Greece is positioned on the left side of the plot, with a low number of pits and a high number of scratches. Second, *U. arctos* from northern latitudes with a higher proportion of vertebrates in their diet (from Northern Europe, North America, and Kamchatka) fall within the middle range of the plot. Third, *U. arctos* from Central Europe, with a hard mast diet, falls within the right side of the plot, accounting for a high number of pits. Nevertheless, its range also overlaps with the vertebrate-dominated diet populations (Figure 42), due to its significant proportion of vertebrates in its diet. *U. maritimus* has a specialised marine mammal diet in an arctic landscape; therefore, with a lack of vegetation resources and a very soft diet that does not include rough plant items, it falls on the left side of the plot, with a number of total pits comparable to that of soft mast-dominated *U. arctos* from Greece. However, because *U. maritimus* inhabits a landscape lacking in vegetation, it presents a comparatively lower number of scratches, features that are directly related to a phytophagous diet (Solounias and Semperebon 2002), and falls within the lower part of the plot (Figure 42).

U. americanus from Alaska, which inhabits a semi-arctic landscape and occasionally consumes vertebrates, particularly fish, falls between the vertebrate-dominated northern latitude populations and the soft mast-dominated population from Greece (Figure 42). Due to a low number of scratches, it falls not far from *U. maritimus*. Finally, *A. melanoleuca*, having an extremely hard and abrasive diet, based on bamboo, which is very rich in phytoliths, appears isolated in the rightmost of the plot due to the very high number of total pits (NTP = 54.75).

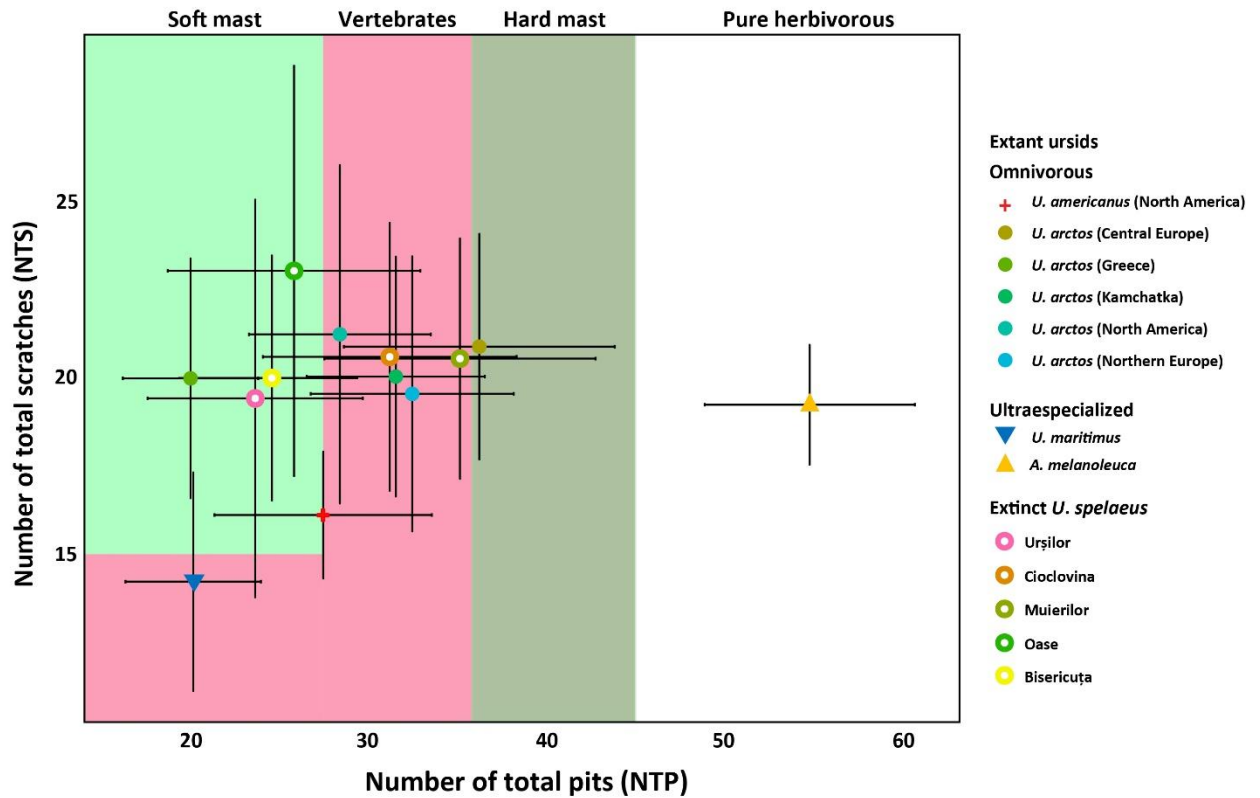


Figure 42. Bivariate plot of the number of total pits (NTP) and the number of total scratches (NTS) comparing the extant bear populations and the fossil populations. Highlighted are four distinct eco-regions (soft mast, hard mast, vertebrates, and pure herbivorous) based on the predominant diet of extant bear populations as established by Pappa et al. (2019).

The fossil populations occupy distinct eco-regions within the plot (Figure 42). Urşilor, Bisericuța, and Oase are primarily distributed within the soft mast-dominated region, situated near the omnivorous *U. arctos* population from Greece. However, their error bars extend into regions associated with omnivorous bears exhibiting vertebrate-dominated diets, overlapping with populations from northern latitudes, such as *U. arctos* from North America. Notably, Oase displays the most extensive extension into the vertebrate-dominated region, overlapping with *U. arctos* populations from Kamchatka and Northern Europe. The Cioclovina population falls within the vertebrate-dominated region but its error bars extend into both the soft mast- and hard mast-dominated regions, exhibiting the most extensive variability among populations. This wide range mirrors the dietary breadth displayed by *U. arctos* from Kamchatka and Northern Europe, which are characterised by highly variable omnivorous diets. Finally, the Muierilor population is located within the vertebrate-dominated eco-region, overlapping with northern omnivorous bears, while its error bars extend significantly into the hard mast-dominated region, overlapping with *U. arctos* from Central Europe.

6.1.3.2 Correspondence analysis

In order to investigate the relationships, distribution and variability of the studied populations between them and with the extant ursids reference dataset a correspondence analysis (CA) was conducted (Figure 43; detailed explanation in Materials and Methods section 5.3). The analysis included seven microwear variables, namely small pits, large pits, fine scratches, coarse scratches, SWS, gouges and puncture pits. The first dimension (Dim. 1) explains 42.3% of the variance, and the second dimension (Dim. 2) accounts for 24.9%, collectively capturing 67.15% of the total variance (Figure 43; Appendix section A.3.1, Table A3). Thus, these two dimensions were selected for analysis and visualization (Figure 43).

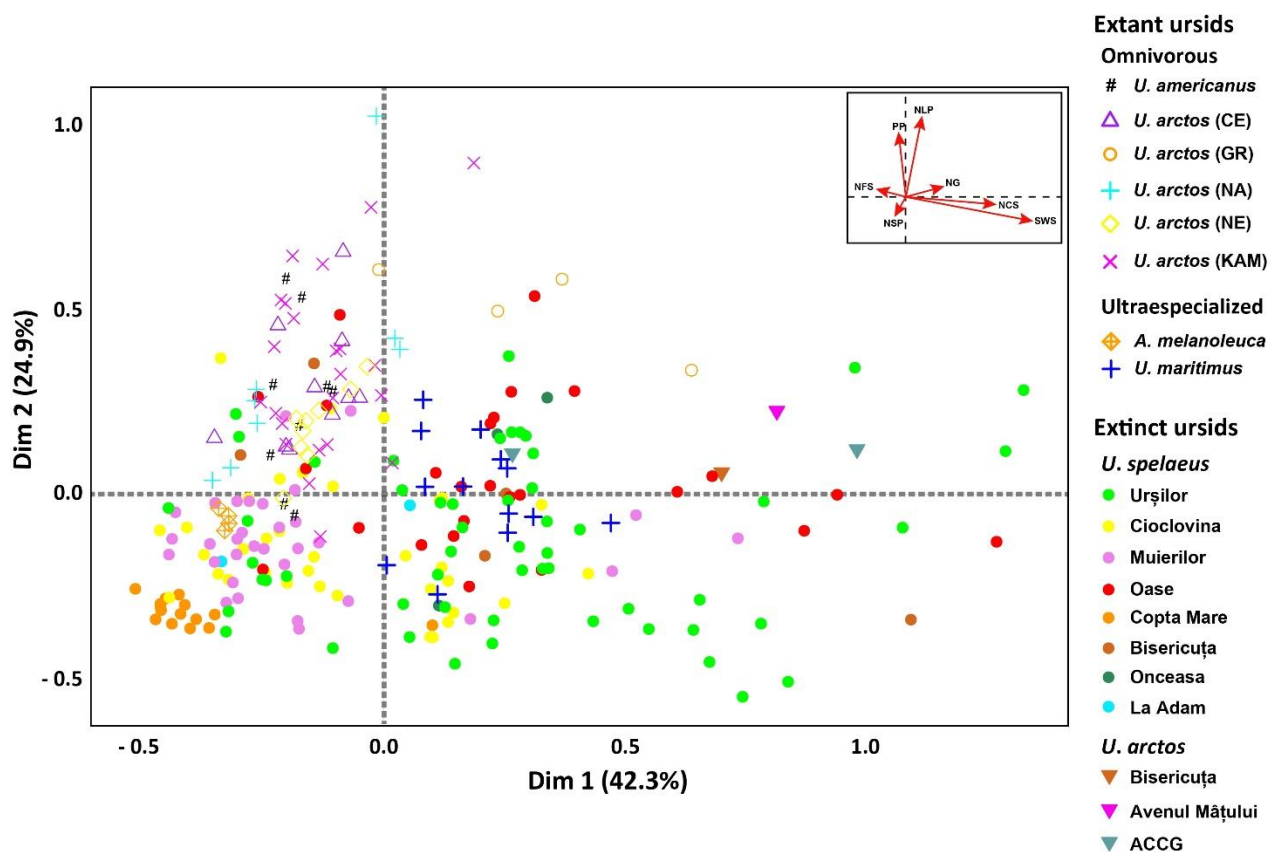


Figure 43. Correspondence analysis (CA) based on seven microwear variables: number of fine scratches (NFS), coarse scratches (NCS), small pits (NSP), large pits (NLP), gouges (NG), puncture pits (NPP), and the scratch width score (SWS). The analysis compares fossil populations of *U. spelaeus* and *U. arctos* from the Romanian Carpathians with a reference dataset of extant ursids established by Pappa et al. (2019). The direction and contribution of the variables in the CA plot are depicted in the top-right inset of the figure. Abbreviations: CE = Central Europe; GR = Greece; NA = North America; NE = Northern Europe; KAM = Kamchatka.

A) Extant bears dispersion

The CA reveals that the extant omnivorous bear populations, including *U. arctos* and *U. americanus*, exhibit a similar distribution pattern (Figure 43). However, hard mast-dominated populations, primarily represented by *U. arctos* from Central Europe, tend to be distributed in

the upper-right part of the omnivorous bears cluster due to their higher presence of puncture pits, gouges, and large pits (in respect to the other reference populations). Omnivorous populations from northern latitudes with a high component of vertebrates and soft mast items in their diet, such as *U. arctos* from Northern Europe and *U. americanus* from Alaska, are placed in the middle to lower part of the extant bears' clustering due to their predominance of small pits and fine scratches (Figure 43). Furthermore, bears with highly variable omnivorous diets, including hard and soft mast as well as vertebrates and invertebrates, are distributed vertically along the omnivore bears' grouping (i.e., *U. arctos* from Kamchatka and *U. arctos* from North America).

The *U. arctos* population from Greece stands out as a significant outlier (Figure 43), due to its Mediterranean latitude specialised soft mast diet, which positions it alone in the upper part of the plot. This unique placement is due to its distinct characteristics. Having the lower number of small pits and the highest number of large pits makes it fall within a higher position in comparison to the other omnivorous ursids. Moreover, its high number of coarse scratches in comparison to the other omnivorous bear species positions it in the central-right part of the plot.

Finally, it can be observed that the highly specialised bear species, the hypercarnivore *U. maritimus* and the highly abrasive diet of *A. melanoleuca*, also occupy distinct positions in the plot (Figure 43). *U. maritimus* is distinguished by its high SWS, while *A. melanoleuca* is characterised by the highest number of small pits and fine scratches above all extant bear populations.

B) Fossil bears dispersion

The extinct ursid populations exhibit distinct distributions within the CA plot. *U. spelaeus* from the Romanian Carpathians displays a wide range of distribution, in comparison to any other species represented in the analysis (Figure 43). This can be attributed to the species capacity to have a flexible dietary niche. However, the majority of *U. spelaeus* individuals are positioned below the Dim. 1 axis due to their overall lower frequency of large pits and puncture pits, combined with a prevalence of small pits compared to extant bear populations and with fossil *U. arctos* (Figure 43). The different *U. spelaeus* populations show variability in their placement on the plot, reflecting differences based on their cave of origin. Within each cave population, some groups cluster tightly, indicating more uniform diets, while others are more dispersed, suggesting greater dietary diversity.

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The *U. spelaeus* populations from Urşilor and Oase exhibit a broad spatial distribution along both the x-axis (Dim. 1) and y-axis (Dim. 2), with some degree of overlap (Figure 43). However, the Urşilor population predominantly occupies the lower half of the x-axis, with the majority of individuals (39: 72.22%) positioned below the 0.0 x-axis. In contrast, the Oase population shows a slightly different pattern, with the majority of its specimens (53.84%) distributed above the 0.0 x-axis. Furthermore, the Cioclovina and Muierilor populations are slightly more clustered, with Cioclovina primarily occupying the centre and Muierilor positioned on the left side of the plot, except for a few outlier specimens. Finally, the *U. spelaeus* specimens from Onceasa and La Adam occupy distinct ecological regions on the plot, with the specimens from La Adam positioned further to the left and the specimens from Onceasa extending more towards the right (Figure 43). However, due to their lack of statistical significance ($n < 5$), their positions should be interpreted as approximations, falling within the broader range of variation observed in other populations.

The fossil *U. arctos* populations, specifically the two individuals from Bisericuța and Avenul Mâțului, are positioned further to the right along the x-axis (Figure 43). This placement indicates a higher number of coarse scratches relative to fine scratches, and consequently, a higher SWS. Regarding the y-axis, these individuals position themselves above it, due to their relatively high number of large pits in comparison to most *U. spelaeus* individuals. However, there is an important degree of overlap between MIS 3 *U. arctos* and *U. spelaeus* from the Romanian Carpathians.

C) Comparison with the extant bears

Urşilor and Oase

When compared to extant bear populations, the majority of *U. spelaeus* specimens from the Urşilor and Oase populations cluster on the right side of the x-axis, separating from the extant omnivorous bear populations (*U. arctos* and *U. americanus*) while some of them display an overlap with *U. maritimus* (Figure 43). This positioning can be attributed to their higher number of coarse scratches and, consequently, a higher SWS compared to the omnivorous reference bears, aligning more closely with the microwear pattern observed in the hypercarnivorous *U. maritimus*. However, a significant portion of the individuals from the Urşilor (11: 20.37%) and Oase (4: 15.38%) populations overlap with extant omnivorous bear species. Specifically, these cave bear individuals fall within the range of *U. americanus* and *U. arctos* populations from Kamchatka, North America, and the northern regions of Europe, as well as with the central European population (Figure 43). Therefore, it is important to highlight the shared omnivorous

nature of these extant species, which include a wide range of items in their diets (soft and hard mast plants, as well as vertebrates), that are exhibiting some degree of overlap with the fossil samples.

Muierilor

The Muierilor population has the majority of its individuals (26: 81.25%) positioned in the negative region of both the x-axis and y-axis, clustering just below the extant omnivorous ursids, and thus, distancing from them (Figure 43). Within this cluster, some individuals overlap with *A. melanoleuca* (with a highly abrasive graminivorous diet based on bamboo), and others are positioned close to *U. americanus* and *U. arctos* from North America, which are characterized by predominantly soft-mast-dominated omnivorous diets (Figure 43).

Additionally, two individuals (6.25%) are positioned higher on the plot, overlapping towards a more central position in the extant omnivorous bear cluster, due to higher number of puncture pits and large pits (Figure 43). This positioning overlaps with omnivorous species with highly flexible diets composed of hard and soft mast items; while their highest similarities are found with *U. arctos* populations from Central and Northern Europe, which exhibit a significant consumption of vertebrates (Rigg and Gorman, 2005; Bojarska and Selva, 2012). Hence, the Muierilor population exhibits an omnivorous (i.e., including vertebrates) diet predominantly composed of soft-mast abrasive items, with some individuals showing dietary diversification toward hard-mast items.

Cioclovina

Almost half of the Cioclovina population (15: 42.85%) occupies the negative region of both the x-axis (Dim. 1) and y-axis (Dim. 2) in the CA plot, clustering in the lower-most part of the extant omnivorous bear populations, falling close to *A. melanoleuca* and soft mast-dominated omnivorous *U. arctos* populations (Figure 43). This positioning suggests a diet heavily focused on soft mast and abrasive items, similar to the feeding habits of extant omnivorous bears from northern latitudes, such as *U. americanus* from North America (Alaska) and *U. arctos* from Northern Europe. However, a significant proportion (12: 34.28%) of specimens extend toward the right side of the y-axis while remaining in the negative region of the x-axis, overlapping partially with *U. maritimus* (Figure 43). This placement indicates a higher frequency of coarse scratches and, consequently, a higher SWS. Meanwhile, a smaller subset of individuals (6: 17.14%) extends upwards on the plot (Figure 43), reflecting a higher number of large pits and puncture pits, aligning with more diverse omnivorous bears exhibiting highly flexible diets,

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such as those of *U. arctos* from Kamchatka and North America, which consume both hard and soft mast items along with vertebrates.

Summarizing, the *U. spelaeus* population from Cioclovina likely had a diverse omnivorous diet that included both soft and hard mast as well as occasional vertebrate consumption; however, the majority of the population's positioning in the lower region of the plot (Figure 43) suggests a primary reliance on a soft mast, within an omnivorous diet.

Bisericuța

The five *U. spelaeus* specimens from Bisericuța are distributed in the upper part of the plot, overlapping with the range of omnivorous bear species (Figure 43). Specifically, they align with omnivorous populations from northern latitudes, such as *U. americanus* from Alaska and *U. arctos* from Kamchatka and Northern Europe, which are characterized by diets rich in soft mast and a significant vertebrate component. Additionally, some individuals extend toward the right side of the plot (Figure 43), displaying a higher number of coarse scratches. This positioning suggests similarities to *U. maritimus*, indicating potential consumption of harder or rougher items. Overall, the dietary profile of the cave Bisericuța population suggests a predominantly omnivorous diet with a notable emphasis on vertebrate consumption.

Onceasa

Two of the three individuals of *U. spelaeus* from Onceasa are positioned in the right region of the plot, overlapping with those from Urșilor and Oase, while one individual aligns closely with members of the Cioclovina population in the lower right section (Figure 43). In comparison to extant bears, the individuals from Onceasa distance themselves from omnivorous populations while they overlap with the hypercarnivorous *U. maritimus*. However, this is due to a high SWS, which can be attributed to consumption of harder or more abrasive items (i.e., not necessarily a carnivorous diet).

La Adam

The two individuals of *U. spelaeus* from La Adam are distributed in distinct regions of the plot, with one positioned near *A. melanoleuca* and the other near *U. maritimus* (Figure 43). While the small sample size limits the ability to accurately determine the ecological characteristics of this population, it does highlight variability within the two specimens.

U. arctos

The *U. arctos* individuals from Bisericuța ($n = 1$; dating to the Pleistocene), and Avenul Mățului ($n = 1$; dating to the Holocene) plot on the right side, overlapping with certain Oase and Urșilor cave bear individuals (Figure 43). Among extant reference bears, this directional placement is exclusively associated with the hypercarnivorous *U. maritimus*, whose diet is characterized by a high proportion of vertebrates. Thus, we infer that the *U. arctos* individuals analysed here similarly consumed a diet rich in vertebrates or hard objects, as driven by their high SWS. Nevertheless, two individuals from ACCG ($n = 2$) which date of medieval times, present a more diverse distribution, with one falling closer to the left side of the plot, while the other falls not far from the Pleistocene *U. arctos* from Bisericuța and the Holocene *U. arctos* from Avenul Mățului, within the right side of the plot (Figure 43). Nevertheless, all *U. arctos* analysed tend to differentiate from Pleistocene cave bears and extant reference bears. Furthermore, due to their statistically null ($n = 1$) in case of Bisericuța and Avenul Mățului and statistically insignificant ($n = 2$) due to low number of ACCG, their ecological niche cannot be inferred properly as lacking more individuals.

6.2 Moldavian Plateau

A total of 57 lower first molars (m1), out of 95 examined, were deemed suitable for analysis. These included specimens of *U. spelaeus* from Trinca ($n = 16$), Saharna ($n = 17$), Buzdujeni ($n = 11$), Duruitoarea Veche ($n = 6$), Butești ($n = 2$). Additionally, five *U. arctos* specimens from Trinca ($n = 5$) were found to be positive.

Therefore, 38 lower first molars (m1) had to be excluded from the analysis, those included the youngest individuals lacking wear facets (Rivals et al., 2007) and those with damaged occlusal surfaces due to taphonomic processes (King et al., 1999; El-Zaatari, 2010; Uzunidis et al., 2021; Micó et al., 2024). These excluded samples belonged to *U. spelaeus* from Saharna ($n = 3$), Buzdujeni ($n = 7$), Duruitoarea Veche ($n = 5$), and Butești ($n = 23$).

Location	Species	N	NFS	NCS	NTS	SWS	NLP	NSP	NPP	NTP	NG
Trinca	<i>U. spelaeus</i>	16	19.91	0.63	20.53	0.00	0.50	11.05	0.44	11.99	0.09
	<i>U. arctos</i>	5	16.70	3.60	20.20	0.40	2.00	18.80	0.40	21.20	1.70
Saharna	<i>U. spelaeus</i>	17	16.41	2.09	18.42	0.06	0.50	33.40	3.26	36.61	0.29
Buzdujeni	<i>U. spelaeus</i>	11	17.41	3.82	27.45	0.36	0.68	24.59	2.59	27.45	0.14
Duruitoarea Veche	<i>U. spelaeus</i>	6	19.00	3.00	22.00	0.29	2.42	30.21	0.64	33.28	0.57
Butești	<i>U. spelaeus</i>	2	19.25	5.00	24.25	0.50	0.50	36.50	0.25	37.25	0.00
Extant											
North America	<i>U. americanus</i>	9	13.56	2.56	16.12	0.00	5.44	19.00	3.00	27.44	0.00
Greece	<i>U. arctos</i>	4	13.00	7.00	20.00	0.5	9.25	8.50	2.25	20.00	2.00
Central Europe	<i>U. arctos</i>	10	17.50	3.40	20.90	0.00	5.40	22.50	8.30	36.20	2.10
North America	<i>U. arctos</i>	8	18.25	3.00	21.25	0.00	6.75	18.38	3.25	28.38	0.25
Kamchatka	<i>U. arctos</i>	23	16.22	3.83	20.05	0.10	6.96	19.78	4.78	31.52	0.35
Northern Europe	<i>U. arctos</i>	9	15.78	3.78	19.56	0.00	6.44	23.33	2.67	32.44	0.22
Eastern Asia	<i>A. melanoleuca</i>	4	19.25	0.00	19.25	0.00	8.50	46.25	0.00	54.75	0.00
Polar circle	<i>U. maritimus</i>	13	11.00	3.21	14.23	2.79	4.50	16.21	0.07	20.15	0.00

Table 4. Comparison of the dental microwear results of the fossil populations of cave bear (*U. spelaeus*) and brown bear (*U. arctos*) from Moldavian Plateau with the reference dataset of extant bear species of *U. arctos*, *U. americanus*, *A. melanoleuca* and *U. maritimus* established by Pappa et al. (2019). Abbreviations: N = number of specimens, NFS = number of fine scratches, NCS = number of coarse scratches, NTS = number of total scratches, SWS = scratch width score, NLP = number of large pits, NSP = number of small pits, NPP = number of puncture pits, NTP = number of total pits, NG = number of gouges.

6.2.1 *U. spelaeus* from Moldavia

Microwear analysis of *U. spelaeus* from Moldavian Plateau reveals notable differences between cave sites (Table 4; Figure 44). In terms of the total number of scratches (NTS), *U. spelaeus* from Saharna exhibited the lowest value (NTS = 18.42), closely followed by populations from Trinca (NTS = 20.53) and Duruitoarea Veche (NTS = 22.00). In contrast, the Buzdujeni population displayed a significantly higher value (NTS = 27.00), with the Butești population showing a slightly lower NTS, though the small sample size ($n = 2$) renders this result statistically insignificant. Regarding the nature of the scratches, all populations exhibited a clear predominance of fine scratches over coarse ones. Consequently, the SWS is very low, approaching 0.

The total number of pits (NTP) shows significant differences between the populations from Moldavian Plateau (Table 4). While *U. spelaeus* from Trinca exhibits the lowest value (NTP = 11.99), *U. spelaeus* from Saharna (NTP = 36.61) and Butești (NTP = 37.25, although $n = 2$) display much higher and comparable scores. Populations from Buzdujeni (NTP = 27.45) and Duruitoarea Veche (NTP = 33.28) follow with slightly lower values, though still considerably high compared to Trinca. In all *U. spelaeus* populations, small pits consistently outnumber large pits (Table 4). Most populations exhibit very low numbers of large pits (NLP), including Trinca (NLP = 0.50), Saharna (NLP = 0.50), Buzdujeni (NLP = 0.68), and Butești (NLP = 0.50), while Duruitoarea Veche shows a slightly higher value (NLP = 2.42).

Concerning puncture pits (NPP), Saharna (NPP = 3.26; Figure 44B) and Buzdujeni (NPP = 2.59) recorded significantly high values, while Trinca (NPP = 0.44; Figure 44A), Duruitoarea Veche (NPP = 0.64), and Butești (NPP = 0.25) also showed presence, but with much lower numbers (Table 4). Regarding gouges, all populations exhibit values ranging from low gouge counts, such as Duruitoarea Veche (NG = 0.57) and Saharna (NG = 0.28), to negligible levels: Trinca (NG = 0.09), Buzdujeni (NG = 0.14; Figure 44C). While no gouges were observed in Butești (NG = 0.00).

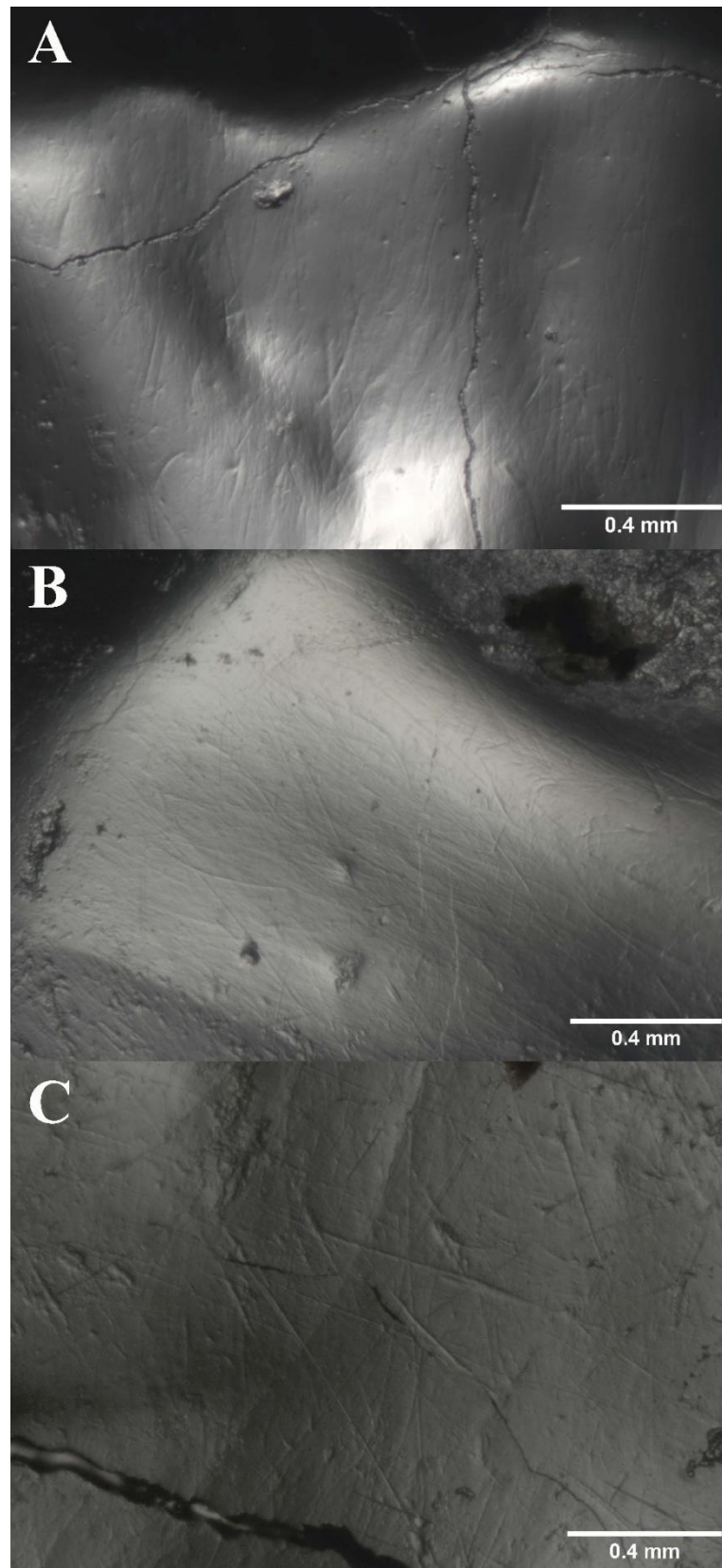


Figure 44. Photomicrographs (at $\times 35$ magnification) of the grinding non-faceted enamel surface of selected fossil specimens of *U. spelaeus* from Moldavian Plateau. A: Trinca (#Tr-I-80-41) individual displaying puncture pits and a pattern dominated by fine over coarse scratches; B: Saharna (#SH/3-31/55) individual exhibiting puncture pits and predominantly fine scratches; C: Buzdujeni (#ERIS-25) individual displaying high counts of coarse scratches as well as presence of gouges.

6.2.1.1 Comparison with extant bears

The comparison with extant ursids reveals that the total number of scratches (NTS) for *U. spelaeus* from Saharna is similar to that of *U. americanus* (Table 4). The NTS for *U. spelaeus* from Trinca is comparable to *U. arctos* populations from Central Europe, Kamchatka, and Greece, while *U. spelaeus* from Duruitoarea Veche aligns with *U. arctos* from North America. In contrast, the populations from Buzdujeni and Butești exhibit much higher NTS values than any extant bear populations in the reference dataset (Table 4).

Regarding scratch distribution, extant bear species show a dominance of fine scratches over coarse ones, with SWS values close to zero, similar to fossil populations of *U. spelaeus* from Trinca and Saharna (Table 4). However, the populations from Buzdujeni, Duruitoarea Veche, and Butești exhibit SWS values comparable to *U. arctos* from Greece.

In terms of the total number of pits (NTP), *U. spelaeus* from Trinca exhibits the lowest values compared to the extant populations (Table 4). Saharna, with higher NTP values (NTP = 36.61), is comparable to *U. arctos* from Central Europe, as is *U. spelaeus* from Butești (NTP = 37.25). The population from Buzdujeni (NTP = 27.45) matches the NTP of *U. americanus* (NTP = 27.44) and is also close to *U. arctos* from North America (NTP = 28.38). Finally, *U. spelaeus* from Duruitoarea Veche (NTP = 33.28) resembles *U. arctos* from Northern Europe (NTP = 32.44). Regarding pit distribution, all *U. spelaeus* populations display the same predominance of small pits over large pits observed in extant bears, though with generally lower counts of large pits (Table 4).

The puncture pits (NPP) in *U. spelaeus* populations vary widely (Table 4), with Saharna (NPP = 3.26) and Buzdujeni (NPP = 2.59) presenting values comparable to extant *U. americanus* (NPP = 3.00) and *U. arctos* populations from North America (NPP = 3.25). In contrast, the remaining *U. spelaeus* populations exhibit lower NPP values, such as Trinca (NPP = 0.44) and Duruitoarea Veche (NPP = 0.64), which are closer to the low values observed in *U. maritimus* (NPP = 0.07). Regarding gouges (NG), most *U. spelaeus* populations show negligible values (NG ≤ 0.29), aligning with *U. americanus* (NG = 0.00) and *U. maritimus* (NG = 0.00). However, Duruitoarea Veche (NG = 0.57) exhibits slightly elevated values, approaching those of *U. arctos* from Northern Europe (NG = 0.22) and Kamchatka (NG = 0.35) (Table 4).

6.2.2 *U. arctos* from Trinca

The *U. arctos* population from Trinca has a limited sample size ($n = 5$), though it is deemed significant (≤ 5). The *U. arctos* population exhibits a similar total number of scratches to the

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co-existing *U. spelaeus* population from the same site (Table 4). Moreover, while *U. spelaeus* also shows a predominance of fine scratches over coarse ones (Figure 45A), the SWS is higher for *U. arctos* (SWS: *U. spelaeus* = 0.00 vs *U. arctos* = 0.40). Although the number of coarse scratches of *U. arctos* (NCS = 3.60) is higher than *U. spelaeus* from Trinca, is not greater than that of other *U. spelaeus* populations from Moldavian Plateau, being surpassed by those from Buzdujeni (NCS = 3.82), with a very similar score, and Butești (NCS = 5.00, although $n = 2$) (Figure 45A). Regarding the total number of pits (NTP), *U. arctos* displays a significantly higher value compared to *U. spelaeus* from Trinca (NTP: *U. spelaeus* = 11.99 vs. *U. arctos* = 21.20). This difference is primarily due to a higher count of small pits (NSP: *U. spelaeus* = 11.05 vs. *U. arctos* = 18.80), along with a slightly higher presence of large pits (NLP: *U. spelaeus* = 0.50 vs. *U. arctos* = 2.00) (Figure 45B). Furthermore, the NLP of *U. arctos* (NLP = 2.00) is higher than that of other *U. spelaeus* populations (Figure 45B), except for *U. spelaeus* from Duruitoarea Veche, which exhibits slightly higher values (NLP = 2.42). Regarding puncture pits (Table 4), both species from the same site present the same scores (NPP: *U. spelaeus* = 0.44 vs *U. arctos* = 0.40). Finally, the *U. arctos* population from Trinca presents significant presence of gouges (NG = 1.70), while *U. spelaeus* from same site presents insignificant counts (NG = 0.09).

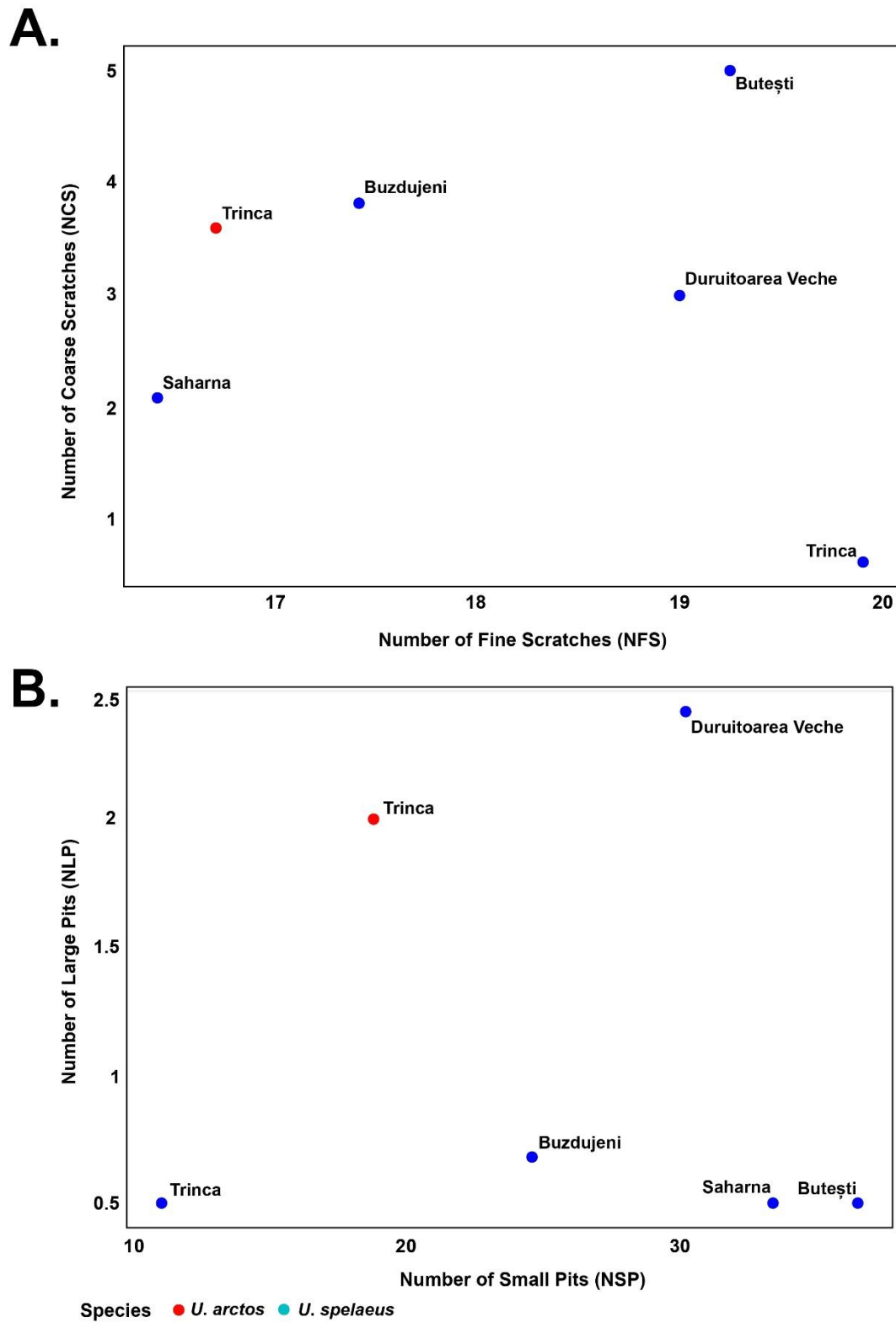


Figure 45. Bivariate plot of the mean number of fine and coarse scratches (A) and small and large pits (B) for the fossil bear populations of *U. arctos* (red) and *U. spelaeus* (blue) from Moldavian Plateau.

6.2.2.1 Comparison with extant bears

The comparison with extant ursids (Table 4), reveals that the total number of scratches (NTS) for the *U. arctos* population from Trinca (NTS = 20.20) is similar to *U. arctos* populations from Central Europe (NTS = 20.90) and Kamchatka (NTS = 20.05) and closely aligns with *U. arctos* from Greece (NTS = 20.00). Additionally, it falls within the range of *U. arctos* populations from North America (NTS = 21.25). Regarding scratch distribution, the *U. arctos* population from Trinca exhibits a predominance of fine scratches over coarse ones, with an SWS of 0.40. This value is notably higher than those observed in most extant bear species (Table 4), which generally display SWS values near zero, but it closely resembles the higher SWS values of *U. arctos* from Greece (SWS = 0.50). In terms of the total number of pits (NTP), the *U. arctos* population from Trinca (NTP = 21.20) exhibits higher values than *U. spelaeus* populations from the same site (NTP = 11.99) and is comparable to *U. arctos* from Greece (NTP = 20.00). However, it remains lower than *U. arctos* populations from Kamchatka (NTP = 31.52), Central Europe (NTP = 36.20), and Northern Europe (NTP = 32.44), as well as extant *U. americanus* (NTP = 27.44) and *U. arctos* from North America (NTP = 28.38).

Regarding pit distribution, *U. arctos* from Trinca demonstrates a predominance of small pits over large pits (Table 4), similar to patterns observed in extant bear species, with relatively low NLP values (NLP = 2.00). For puncture pits (NPP), the Trinca population (NPP = 0.40) exhibits values lower than most extant *U. arctos* populations, such as those from Kamchatka (NPP = 4.78) and Northern Europe (NPP = 2.67), but it aligns more closely with *U. arctos* from Greece (NPP = 2.25). The gouge count (NG = 1.70) for *U. arctos* from Trinca is notably higher than that of most extant bear species, which generally exhibit negligible values ($NG \leq 0.25$), but aligns more closely with *U. arctos* populations from Central Europe (NG = 2.10) and Greece (NG = 2.00).

6.2.3 Dietary inference

6.2.3.1 Bivariate analysis of the total number of scratches and pits

As previously discussed, (see section 6.1.3.1), the bivariate plot of total pits (NTP) and total scratches (NTS) reflects the dietary regimes of extant bear species, with populations distributed according to their dietary preferences: omnivorous diets with a focus on soft mast, hard mast, or vertebrates, as well as pure herbivory. This prior framework provides a reference for interpreting the positions of the fossil populations analysed here, allowing comparisons of their ecological and dietary traits to those of extant bears.

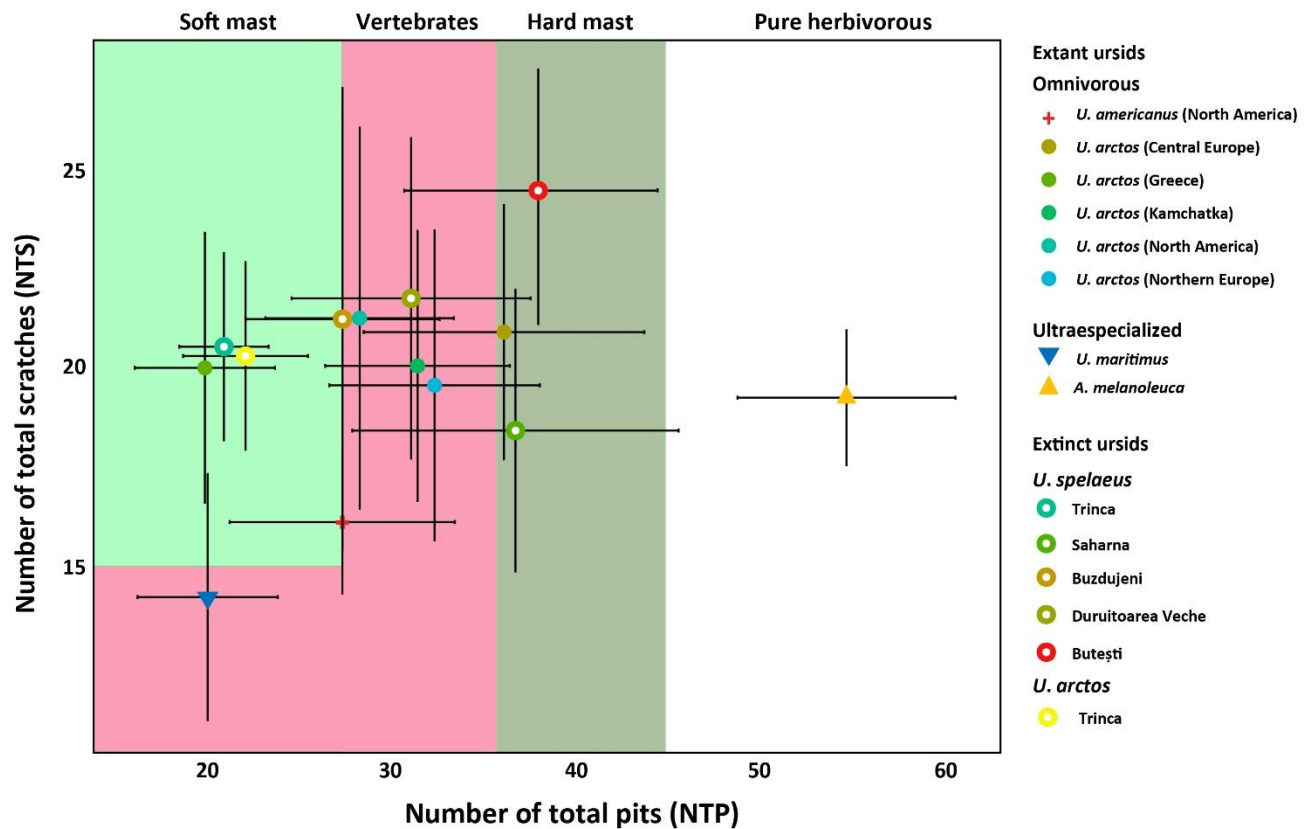


Figure 46. Bivariate plot of the number of total pits (NTP) and the number of total scratches (NTS) comparing the extant bear populations and the fossil populations from Moldavian Plateau. Highlighted are four distinct eco-regions (soft mast, hard mast, vertebrates, and pure herbivorous) based on the predominant diet of extant bear populations as established by Pappa et al. (2019).

The fossil populations from Moldavian Plateau are distributed across distinct ecological regions within the plot (Figure 46). *U. spelaeus* and *U. arctos* from Trinca are positioned within the soft mast-dominated region, closely aligning with the omnivorous *U. arctos* population from Greece. Furthermore, *U. spelaeus* from Buzdujeni falls near the border between the soft mast- and vertebrate-dominated regions, situated very close to *U. arctos* from Kamchatka, which has a high vertebrate intake within an omnivorous diet primarily based on soft mast. The Buzdujeni population also overlaps in its error bars with *U. americanus* from North America, which is positioned lower due to its lower scratch count (Figure 46), reflecting an omnivorous diet consisting of soft mast and vertebrates, particularly fish.

Additionally, *U. spelaeus* from Duruitoarea Vechi is positioned within the vertebrate-dominated region, overlapping with extant *U. arctos* populations from Northern Europe and Kamchatka, and extending its error bars slightly into both the soft mast- and hard mast-dominated regions (Figure 46). The Duruitoarea Vechi population also shows some overlap

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with *U. arctos* from Central Europe, a population known for its omnivorous and variable diet, which often includes significant vertebrate intake.

Finally, *U. spelaeus* from Saharna and Butești are positioned within the hard mast-dominated region, overlapping with *U. arctos* from Central Europe and extending its error bars into the vertebrate-dominated region, aligning with omnivorous bears from the Northern Hemisphere that exhibit high vertebrate intake (Figure 46). While the Saharna population is positioned lower on the plot compared to other bears in this region, aligning more closely with the *U. americanus* population, the Butești population is positioned higher due to its elevated scratch counts (Figure 46). However, given the small sample size of the Butești population ($n = 2$), its position on the plot should be interpreted with caution. Nevertheless, the high density of pits suggests a hard mast-dominated omnivorous diet (Figure 46).

6.2.3.2 Correspondence analysis

In order to investigate the relationships, distribution, and variability of the studied populations between them and the extant ursid reference dataset, a correspondence analysis (CA) was conducted (Figure 47; detailed explanation in Materials and Methods, section 5.3). The analysis included seven microwear variables, namely small pits, large pits, fine scratches, coarse scratches, SWS, gouges, and puncture pits. The first dimension (Dim. 1) explains 36.4% of the variance, and the second dimension (Dim. 2) accounts for 26.0%, collectively capturing 62.4% of the total variance (Figure 47; Appendix section A.3.1, Table A4). Thus, these two dimensions were selected for analysis and visualization.

As previously detailed (see section 6.1.3.2A), the correspondence analysis (CA) highlights the dietary adaptations of extant bear populations, with omnivorous species distributed according to their primary dietary components, such as soft mast, hard mast, or vertebrates. These patterns provide a comparative framework for positioning fossil populations within the CA plot, allowing insights into their dietary and ecological similarities with extant species.

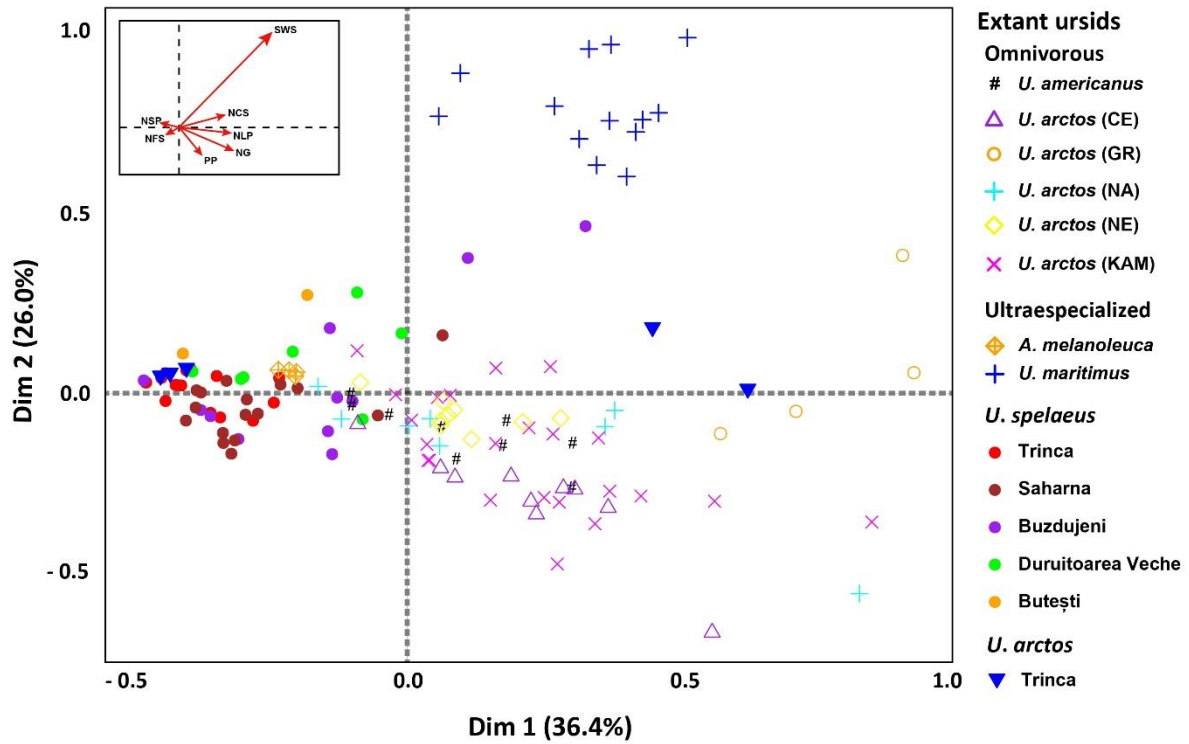


Figure 47. Correspondence analysis (CA) based on seven microwear variables: number of fine scratches (NFS), coarse scratches (NCS), small pits (NSP), large pits (NLP), gouges (NG), puncture pits (NPP), and the scratch width score (SWS). The analysis compares fossil populations of *U. spelaeus* and *U. arctos* from Moldavian Plateau with a reference dataset of extant ursids established by Papp et al. (2019). The direction and contribution of the variables in the CA plot are depicted in the top-right inset of the figure. Abbreviations: CE = Central Europe; GR = Greece; NA = North America; NE = Northern Europe; KAM = Kamchatka.

A) *U. spelaeus*

The fossil populations of *U. spelaeus* exhibit a clustered (and concentrated) distribution within the CA plot, with most *U. spelaeus* individuals positioning in the lower-left quadrant of the plot, below the Dim. 1 axis and to the left of the Dim. 2 axis (Figure 47). This distribution is indicative of a microwear pattern dominated by small pits (NSP) and fine scratches (NFS), with lower presence of large pits (NLP), gouges (NG) and coarse scratches (NCS), distinguishing them from extant omnivorous bears and overlapping them close to *A. melanoleuca* with a graminivorous diet based on abrasive foliage. The *U. spelaeus* population from Trinca clusters tightly in this lower-left quadrant of the plot, close to *A. melanoleuca* (Figure 47), indicating relatively uniform dietary habits primarily focused on soft mast consumption. In contrast, the populations from Saharna, Duruitoarea Veche, and particularly Buzdujeni exhibit a broader distribution, extending towards the right side of the plot, overlapping with the dietary range of omnivorous bear species (Figure 47). Few individuals from Saharna (4: 2.4%) overlap with *U. americanus* and *U. arctos* from North America, Kamchatka, and Central Europe, which are

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characterized by highly variable omnivorous diets with a significant vertebrate intake alongside soft mast consumption. Similarly, several individuals from Duruitoarea Veche (3: 50%) fall within the dietary range of *U. arctos* from Kamchatka and Central Europe (Figure 47). This rightward extension in the plot is associated with a higher proportion of coarse scratches relative to fine scratches, reflecting a higher SWS and suggesting a diet incorporating harder items. This trend reaches its peak in some individuals from Buzdujeni (6: 54.6%), which closely approach the position of northern latitude omnivorous bears as well as *U. maritimus*, indicating a potential shift toward a more vertebrate-based dietary signal (Figure 47). This distribution further supports the presence of dietary variability within the *U. spelaeus* populations from Moldavian Plateau.

B) *U. arctos*

The fossil *U. arctos* population from Trinca exhibits a broad distribution on the CA plot (Figure 47). While three individuals cluster near *A. melanoleuca*, alongside other *U. spelaeus* specimens, two individuals deviate significantly towards the lower-right region of the plot, overlapping with the dietary range of omnivorous bear species. This divergence is driven by a higher number of large pits (NLP) and an increased proportion of coarse scratches relative to fine scratches, resulting in a higher SWS. However, rather than fully aligning with highly omnivorous and vertebrate-consuming *U. arctos* populations, these individuals position themselves closer to *U. arctos* from Greece (Figure 47), a population primarily associated with an omnivorous diet dominated by soft mast.

6.3 Western Balkans and Western Rhodopes Mountains

A total of 74 lower first molars (m1), out of 112 examined, were deemed suitable for analysis. These included specimens of *U. spelaeus* from Borikovska ($n = 48$), Magura ($n = 8$), Mishin ($n = 5$), Bacho Kiro ($n = 5$), Lakatnik ($n = 4$), Bashovishki Pech ($n = 2$) and Triagalna ($n = 2$).

Therefore, 38 lower first molars (m1) had to be excluded from the analysis, those included the youngest individuals lacking wear facets (Rivals et al., 2007) and those with damaged occlusal surfaces due to taphonomic processes (King et al., 1999; El-Zaatari, 2010; Uzunidis et al., 2021; Micó et al., 2024). These excluded samples belonged to *U. spelaeus* from Borikovska ($n = 28$), Magura ($n = 4$), Mishin ($n = 4$), Bacho Kiro ($n = 1$) and Lakatnik ($n = 1$).

Location	Species	<i>N</i>	NFS	NCS	NTS	SWS	NLP	NSP	NPP	NTP	NG
Extinct											
Borikovska	<i>U. spelaeus</i>	48	11.53	2.55	14.07	0.19	2.34	30.63	0.64	33.61	1.48
Magura	<i>U. spelaeus</i>	8	11.94	4.38	15.06	0.38	1.44	25.40	1.31	28.15	1.29
Mishin	<i>U. s. rossicus</i>	5	14.50	5.80	20.40	0.60	1.40	27.37	1.00	29.77	0.30
Bacho Kiro	<i>U. spelaeus</i>	5	10.00	3.60	14.10	0.20	2.00	31.67	1.70	35.37	0.90
Lakatnik	<i>U. spelaeus</i>	4	11.88	0.38	12.50	0.00	0.25	20.63	0.13	21.00	0.50
Bashovishki Pech	<i>U. spelaeus</i>	2	13.00	3.75	16.42	0.00	4.50	22.00	7.75	34.25	2.00
Triagalna	<i>U. spelaeus</i>	2	11.00	0.50	11.50	0.00	3.25	34.50	2.00	39.75	1.25
Extant											
North America	<i>U. americanus</i>	9	13.56	2.56	16.12	0.00	5.44	19.00	3.00	27.44	0.00
Greece	<i>U. arctos</i>	4	13.00	7.00	20.00	0.5	9.25	8.50	2.25	20.00	2.00
Central Europe	<i>U. arctos</i>	10	17.50	3.40	20.90	0.00	5.40	22.50	8.30	36.20	2.10
North America	<i>U. arctos</i>	8	18.25	3.00	21.25	0.00	6.75	18.38	3.25	28.38	0.25
Kamchatka	<i>U. arctos</i>	23	16.22	3.83	20.05	0.10	6.96	19.78	4.78	31.52	0.35
Northern Europe	<i>U. arctos</i>	9	15.78	3.78	19.56	0.00	6.44	23.33	2.67	32.44	0.22
Eastern Asia	<i>A. melanoleuca</i>	4	19.25	0.00	19.25	0.00	8.50	46.25	0.00	54.75	0.00
Polar circle	<i>U. maritimus</i>	13	11.00	3.21	14.23	2.79	4.50	16.21	0.07	20.15	0.00

Table 5. Comparison of the dental microwear results of the fossil populations of cave bear (*U. spelaeus*) from Western Balkans and Western Rhodopes Mountains with the reference dataset of extant bear species of *U. arctos*, *U. americanus*, *A. melanoleuca* and *U. maritimus* established by Pappa et al. (2019). Abbreviations: *N* = number of specimens, NFS = number of fine scratches,

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NCS = number of coarse scratches, NTS = number of total scratches, SWS = scratch width score, NLP = number of large pits, NSP = number of small pits, NPP = number of puncture pits, NTP = number of total pits, NG = number of gouges.

6.3.1 *U. spelaeus* and *U. (savini) rossicus* from Western Balkans and Rhodopes

The microwear analysis of the cave bear populations from Western Balkans and Western Rhodopes Mountains reveals that the total number of scratches (NTS) varies significantly among the different cave populations (Table 5). The lowest NTS values were recorded for Triagalna (NTS = 11.50) and Lakatnik (NTS = 12.50), while Mishin (NTS = 20.40) displayed the highest value. Borikovska (NTS = 14.07), Magura (NTS = 15.06), Bacho Kiro (NTS = 14.10), and Bashovishki Pech (NTS = 16.42) exhibited intermediate values. The scratch width score (SWS) remains low across all populations, with most values below 0.5, confirming the dominance of fine scratches over coarse ones (Table 5). Mishin (SWS = 0.60) displayed the highest score (Figure 48C), while Lakatnik and Triagalna had the lowest (SWS = 0.00).

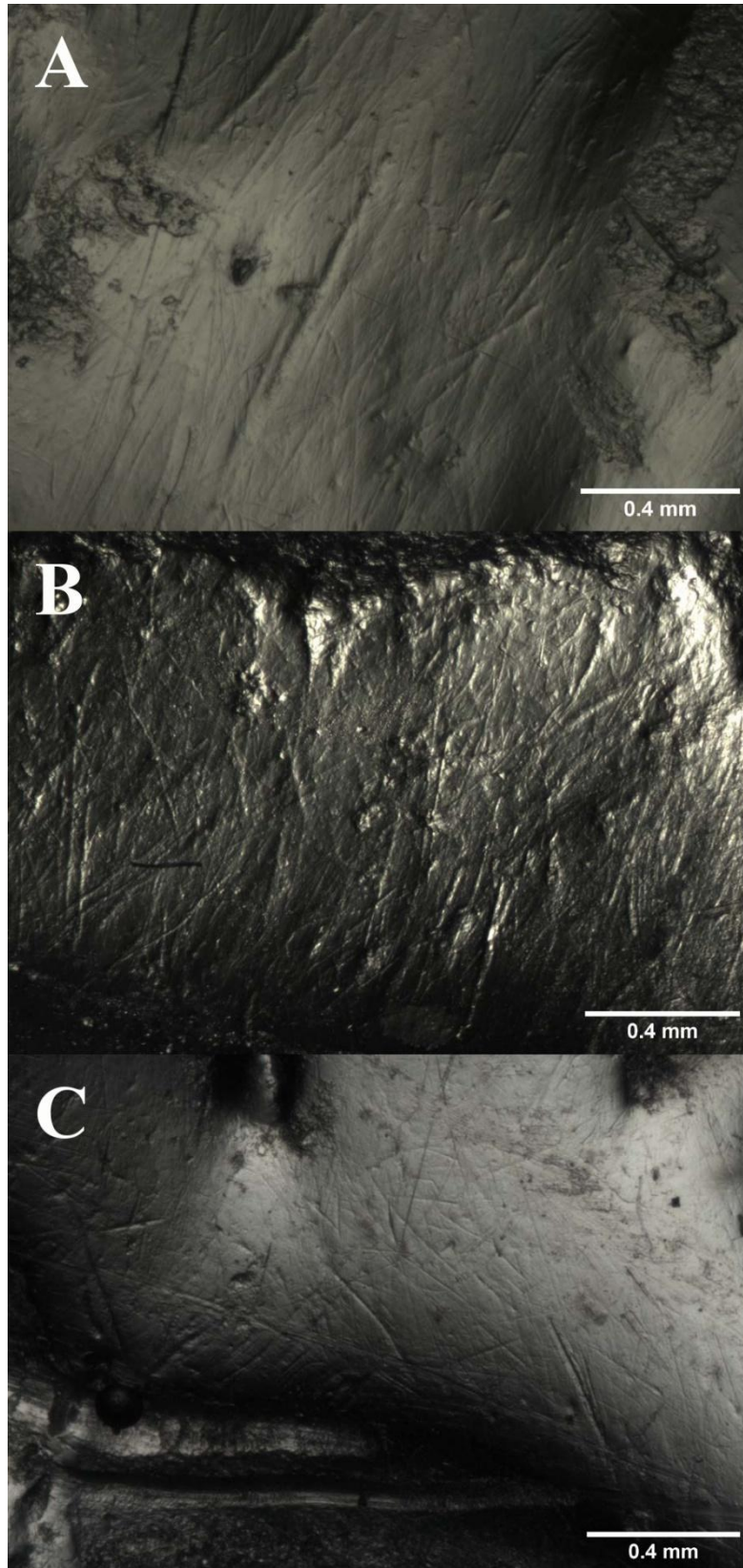


Figure 48. Photomicrographs (at $\times 35$ magnification) of the grinding non-faceted enamel surface of selected fossil specimens of cave bear from Western Balkans and Western Rhodopes Mountains. A: Borikovska (*U. spelaeus*; #116C) individual displaying hypercoarse and coarse scratches, along with small and large pits; B: Magura (*U. spelaeus*; #MII/53) individual exhibiting gouges, large pits and a clear predominance of coarse over fine scratches; C: Mishin (*U. s. rossicus*; #MK1/2137) individual exhibiting both coarse and fine scratches, along with large and small pits, and gouges.

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The total number of pits (NTP) also varies considerably (Table 5), with Triagalna (NTP = 39.75) and Borikovska (NTP = 33.61) exhibiting the highest values. In contrast, Lakatnik (NTP = 21.00) recorded the lowest NTP. Small pits (NSP) consistently outnumber large pits (NLP) in all populations. Bashovishki Pech (NLP = 4.50) exhibited the highest number of large pits, while Lakatnik (NLP = 0.25) and Mishin (NLP = 1.40) had the lowest. A significant variation is observed in puncture pits (NPP), with Bashovishki Pech (NPP = 7.75) recording very high values, followed by much lower values of Triagalna (NPP = 2.00). Magura population also displayed low yet significant presence of puncture pits (NPP = 1.31; Figure 48B). In contrast, Lakatnik (NPP = 0.13) and Borikovska (NPP = 0.64) showed the lowest NPP values. Regarding gouges (NG), Bashovishki Pech (NG = 2.00) and Borikovska (NG = 1.48) displayed the highest values, while Mishin (NG = 0.30) exhibited lower gouge counts. Moreover, the population of Magura exhibited consistent presence of gouges (NG = 1.29; Figure 48B).

Finally, it is important to note that the Borikovska cave bear specimens exhibited a notable presence of hypercoarse scratches (Figure 48A), with a mean value of 0.5, observed in 30% of the individuals ($n = 48$).

6.3.1.1 Comparison with extant bears

In comparison to extant ursids, the populations from Western Balkans and Western Rhodopes Mountains exhibit lower total scratch counts (NTS) compared to omnivorous ursid specimens (Table 5). The only exception is Mishin (NTS = 20.40) the highest NTS, which falls within the range of *U. arctos* from Kamchatka (NTS = 20.05), Greece (NTS = 20.00) or Central Europe (NTS = 20.90). The Bashoviski Pech population displays a similar NTS value as *U. americanus* (NTS = 16.12). The remaining populations display progressively lower NTS values, with the lowest recorded for Triagalna (NTS = 11.50), followed by Lakatnik (NTS = 12.50), Borikovska (NTS = 14.07), Bacho Kiro (NTS = 14.10), and Magura (NTS = 15.06). These values are similar to those of *U. maritimus* (NTS = 14.23).

The distribution of fine (NFS) and coarse (NCS) scratches among fossil populations closely resembles that of extant ursids, with fine scratches consistently outnumbering coarse scratches (Table 5). However, *U. spelaeus* from Western Balkans and Western Rhodopes Mountains generally exhibits higher NCS values than most extant ursids, with the exception of *U. arctos* from Greece (NCS = 7.00). The highest NCS values were recorded for Mishin (NCS = 5.80) and Magura (NCS = 4.38), whereas Bashovishki Pech (NCS = 3.75) displayed values similar to those of *U. arctos* from Northern Europe (NCS = 3.78) and Kamchatka (NCS = 3.83).

Regarding fine scratches (NFS), fossil populations generally exhibit lower values than extant bears (Table 5). The highest values were observed in Mishin's *U. s. rossicus* (NFS = 14.50), somehow resembling those of *U. americanus* (NFS = 13.56) and *U. arctos* from Northern Europe (NFS = 15.78). Bashovishki Pech (NFS = 13.00) displayed values similar to *U. arctos* from Greece (NFS = 13.00) and *U. americanus*. The remaining populations exhibited comparable NFS values: Magura (NFS = 11.94), Lakatnik (NFS = 11.88), Borikovska (NFS = 11.53), and Triagalna (NFS = 11.00), with Bacho Kiro (NFS = 10.00) recording the lowest score. These values align closely with *U. maritimus* (NFS = 11.00).

Regarding the total number of pits (NTP), the fossil populations exhibit overall high values compared to extant bears (Table 5), with only Lakatnik scoring lower values (NTP = 21.00). Conversely, Triagalna (NTP = 39.75), Bacho Kiro (NTP = 35.37), Bashovishki Pech (NTP = 34.25) and Borikovska (NTP = 33.61) exhibit the highest values, comparable to *U. arctos* from Central Europe (NTP = 36.20), Northern Europe (NTP = 32.44) and Kamchatka (NTP = 31.52). Moreover, Mishin (NTP = 29.77) and Magura (NTP = 28.15) populations exhibit slightly lower values similar score to that of *U. arctos* from North America (NTP = 28.38) and *U. americanus* (NTP = 27.44). Regarding pit distribution, both extinct and extant bears exhibit a predominance of small pits over large pits (Table 5). However, extant bears generally show higher large pit counts (except for *U. maritimus*, NLP = 4.50, which matches the highest large pit count among fossil bears, recorded in Bashovishki Pech). In contrast, extinct bears tend to have higher small pit counts, with the exception of *A. melanoleuca* (NSP = 46.25).

Regarding puncture pits for the *U. spelaeus* populations, Bashovishki Pech (NPP = 7.75) exhibits the highest value, closely resembling *U. arctos* from Central Europe (NPP = 8.30). Other fossil populations, such as Triagalna (NPP = 2.00) and Bacho Kiro (NPP = 1.70), present values within the range of *U. arctos* from Greece (NPP = 2.25). The lowest values are recorded for Lakatnik (NPP = 0.13) and Borikovska (NPP = 0.64), which align more closely with the numbers scored by *U. maritimus* (NPP = 0.07) and *A. melanoleuca* (NPP = 0.00), with none to negligible presence of puncture pits.

Concerning gouges, the *U. spelaeus* populations exhibit a broader range of values (Table 5). The highest count is observed in Bashovishki Pech (NG = 2.00), resembling the value of *U. arctos* from Greece. Other fossil populations exhibit lower gouge values, such as Borikovska (NG = 1.48), Magura (NG = 1.29), and Triagalna (NG = 1.25), although still scoring a significant presence. In contrast, some populations, such as Mishin (NG = 0.30), Bacho Kiro

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(NG = 0.90), and Lakatnik (NG = 0.50), show values more comparable to *U. arctos* from Kamchatka (NG = 0.35). Overall, extinct cave bear populations number of gouges overlap with that of extant omnivorous *U. arctos* populations (Table 5).

6.3.2 Dietary inference

6.3.2.1 Bivariate analysis of the total number of scratches and pits

The cave bear populations from Western Balkans and Western Rhodopes Mountains display intra-population variability among them (Figure 49), although they predominantly cluster within the vertebrate-dominated region of the bivariate plot, with the exception of Triagalna, which falls within the hard-mast-dominated region. However, given the small sample size ($n = 2$), caution is required when interpreting this placement.

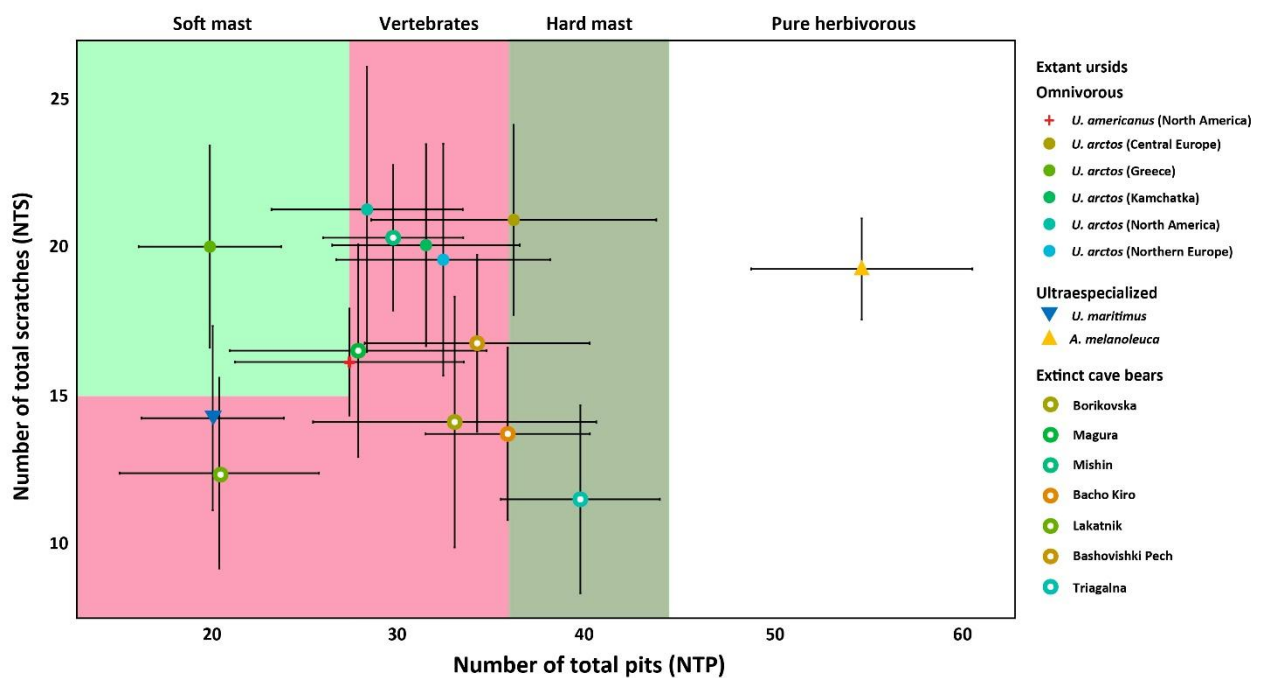


Figure 49. Bivariate plot of the number of total pits (NTP) and the number of total scratches (NTS) comparing the extant bear populations and the fossil populations from Western Balkans and Western Rhodopes Mountains. Highlighted are four distinct eco-regions (soft mast, hard mast, vertebrates, and pure herbivorous) based on the predominant diet of extant bear populations as established by Pappa et al. (2019).

Notably, Triagalna error bars extend partially into the vertebrate-dominated region, indicating potential dietary overlap. The Lakatnik population exhibits a close alignment with *U. maritimus*, with its y-axis (NTS) error bars extending partially into the soft-mast-dominated region, suggesting some degree of dietary plasticity (Figure 49). Meanwhile, the Magura and Mishin populations both cluster within the vertebrate-dominated region, with Magura extending into the soft-mast-dominated region. Interestingly, Magura individuals overlap almost entirely with *U. americanus*, whereas Mishin specimens align more closely with *U.*

arctos populations from North America, Kamchatka, and Northern Europe, both populations highlighting a broader dietary range, although within the vertebrate dominated eco-regions (Figure 49).

The Borikovska population also falls within the vertebrate-dominated region, but it exhibits high variability along the x-axis (NTP), extending towards the hard-mast-dominated ecoregion. Notably, its y-axis (NTS) overlaps with *U. maritimus*, indicating a microwear signature similar to that of the hypercarnivorous bear.

Additionally, the Bacho Kiro population positions itself along the border between vertebrate- and hard-mast-dominated dietary regimes (Figure 49). In terms of x-axis placement (NTP), this population aligns closely with *U. arctos* from Central Europe, suggesting similarities in dietary composition, possibly incorporating significant amounts of hard mast alongside meat. Finally, the Bashovishki Pech population falls within the vertebrate eco-region, with its error bars extending towards the hard-mast region.

6.3.2.2 Correspondence analysis

In order to investigate the relationships, distribution, and variability of the studied populations between them and the extant ursid reference dataset, a correspondence analysis (CA) was conducted (see more in Materials and Methods, section 5.3). The analysis included seven microwear variables, namely small pits, large pits, fine scratches, coarse scratches, SWS, gouges, and puncture pits. The first dimension (Dim. 1) explains 37.5% of the variance, and the second dimension (Dim. 2) accounts for 27.5%, collectively capturing 65% of the total variance (Figure 50; Appendix section A.3.1, Table A5). Thus, these two dimensions were selected for analysis and visualization.

As previously detailed (see section 6.1.3.2A), the correspondence analysis (CA) highlights the dietary adaptations of extant bear populations, with omnivorous species distributed according to their primary dietary components, such as soft mast, hard mast, or vertebrates. These patterns provide a comparative framework for positioning fossil populations within the CA plot, allowing insights into their dietary and ecological similarities with extant species.

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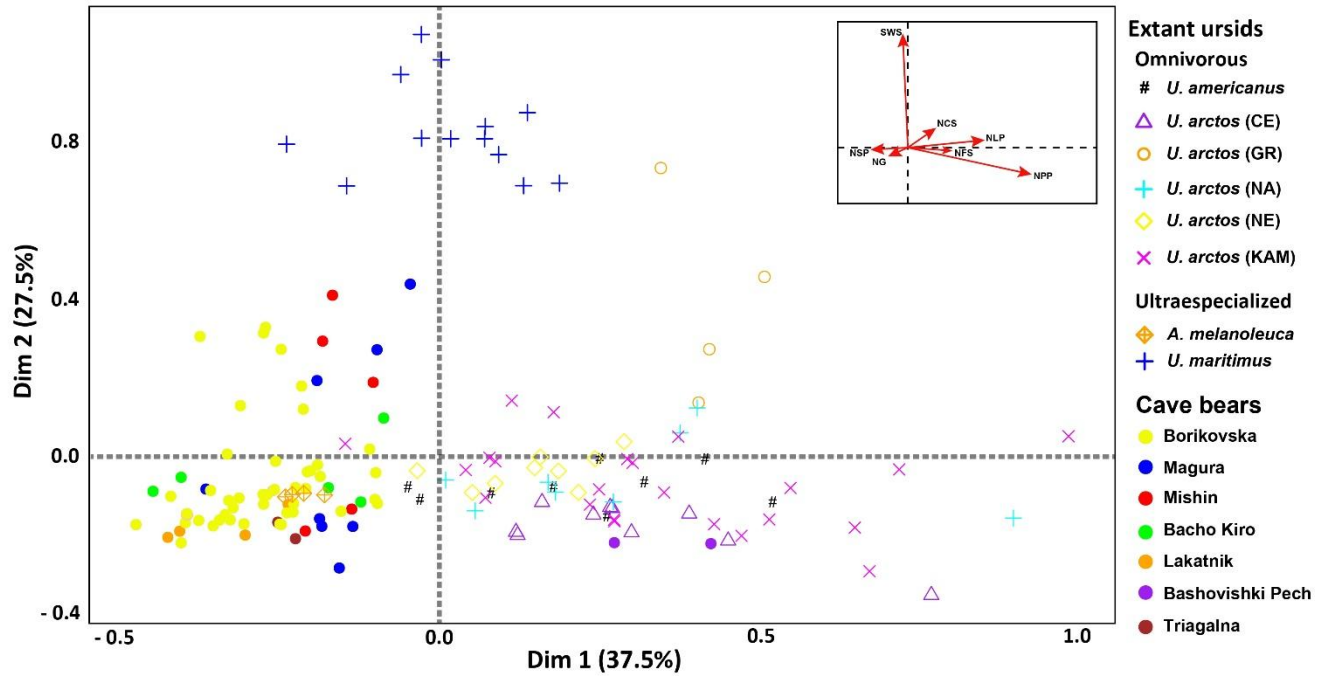


Figure 50. Correspondence analysis (CA) based on seven microwear variables: number of fine scratches (NFS), coarse scratches (NCS), small pits (NSP), large pits (NLP), gouges (NG), puncture pits (NPP), and the scratch width score (SWS). The analysis compares fossil populations of cave bear from Western Balkans and Western Rhodopes Mountains with a reference dataset of extant ursids established by Pappa et al. (2019). The direction and contribution of the variables in the CA plot are depicted in the top-right inset of the figure. Abbreviations: CE = Central Europe; GR = Greece; NA = North America; NE = Northern Europe; KAM = Kamchatka.

The fossil cave bear populations from Western Balkans and Western Rhodopes Mountains are clustered in the lower-left region of the plot, occupying the negative space along both the x- and y-axes (Figure 50). This placement differentiates them from extant omnivorous bears and makes them fall close to *A. melanoleuca* and *U. arctos* from Northern Europe and *U. americanus*. The distinction is driven by a high number of small pits and gouges, combined with a lower frequency of large pits, fine and coarse scratches and puncture pits compared to extant *U. arctos* and *U. americanus* (Figure 50).

Nevertheless, some individuals from Magura and Mishin, as well as the individuals from Triagalna, which cluster in the lower-left region of the plot, exhibit partial overlap along the y-axis (explaining 27.5% of the variance) with *U. arctos* from Central Europe and Kamchatka (Figure 50). This suggests that, despite their overall differentiation from extant omnivorous bears, these fossil populations retain some degree of similarity in microwear patterns. More specifically with a low SWS that favours fine to coarse scratches.

Furthermore, some individuals from Borikovska (8: 16.66%), Magura (3: 37.5%), Mishin (3: 60%), and Bacho Kiro (1: 20%) extend upwards, influenced by a higher SWS, with some approaching the ecoregion occupied by the hypercarnivorous *U. maritimus* (Figure 50).

Additionally, the two individuals from Bashovishki Pech fall within the extant omnivorous bear cluster, overlapping with *U. arctos* from Central Europe and Kamchatka. This is primarily driven by their exceptionally high puncture pit counts (NPP = 7.75).

6.4 Central Balkans

A total of 32 lower first molars (m1), out of 54 examined, were deemed suitable for analysis. These included specimens of *U. spelaeus* from Ušačka ($n = 11$), Hadži Prodanova ($n = 11$) and Risovača ($n = 10$).

Therefore, 22 lower first molars (m1) had to be excluded from the analysis, those included the youngest individuals lacking wear facets (Rivals et al., 2007) and those with damaged occlusal surfaces due to taphonomic processes (King et al., 1999; El-Zaatari, 2010; Uzunidis et al., 2021; Micó et al., 2024). These excluded samples belonged to *U. spelaeus* from Ušačka ($n = 7$), Hadži Prodanova ($n = 3$) and Risovača ($n = 12$).

Location	Species	<i>N</i>	NFS	NCS	NTS	SWS	NLP	NSP	NPP	NTP	NG
Extinct											
Ušačka	<i>U. spelaeus</i>	11	10.41	5.14	15.48	0.64	1.09	20.14	0.05	21.27	0.27
Hadži Prodanova	<i>U. spelaeus</i>	11	13.86	2.27	16.29	0.00	1.23	22.02	0.14	23.38	0.59
Risovača	<i>U. spelaeus</i>	10	17.35	0.90	18.15	0.00	0.65	28.00	0.30	28.95	0.40
Extant											
North America	<i>U. americanus</i>	9	13.56	2.56	16.12	0.00	5.44	19.00	3.00	27.44	0.00
Greece	<i>U. arctos</i>	4	13.00	7.00	20.00	0.5	9.25	8.50	2.25	20.00	2.00
Central Europe	<i>U. arctos</i>	10	17.50	3.40	20.90	0.00	5.40	22.50	8.30	36.20	2.10
North America	<i>U. arctos</i>	8	18.25	3.00	21.25	0.00	6.75	18.38	3.25	28.38	0.25
Kamchatka	<i>U. arctos</i>	23	16.22	3.83	20.05	0.10	6.96	19.78	4.78	31.52	0.35
Northern Europe	<i>U. arctos</i>	9	15.78	3.78	19.56	0.00	6.44	23.33	2.67	32.44	0.22
Eastern Asia	<i>A. melanoleuca</i>	4	19.25	0.00	19.25	0.00	8.50	46.25	0.00	54.75	0.00
Polar circle	<i>U. maritimus</i>	13	11.00	3.21	14.23	2.79	4.50	16.21	0.07	20.15	0.00

Table 6. Comparison of the dental microwear results of the fossil populations of cave bear (*U. spelaeus*) from Central Balkans with the reference dataset of extant bear species of *U. arctos*, *U. americanus*, *A. melanoleuca* and *U. maritimus* established by Pappa et al. (2019). Abbreviations: *N* = number of specimens, NFS = number of fine scratches, NCS = number of coarse scratches, NTS = number of total scratches, SWS = scratch width score, NLP = number of large pits, NSP = number of small pits, NPP = number of puncture pits, NTP = number of total pits, NG = number of gouges.

6.4.1 *U. spelaeus* from Central Balkans

The microwear analysis of *U. spelaeus* populations from Central Balkans reveals that the total number of scratches (NTS) varies among different cave populations (Table 6). The lowest NTS values were recorded for Ušačka (NTS = 15.48) and Hadži Prodanova (NTS = 16.29), with similar averages, while Risovača (NTS = 18.15) displayed the highest value. The scratch width score (SWS) remains low across all populations, with most values below 0.5, confirming the dominance of fine scratches over coarse ones (Table 6; Figure 51B). Ušačka exhibited the

highest SWS (0.64), while both Hadži Prodanova and Risovača had the lowest values (SWS = 0.00).

The total number of pits (NTP) also varies considerably, with Risovača (NTP = 28.95) exhibiting the highest value, followed by Hadži Prodanova (NTP = 23.38). In contrast, Ušačka (NTP = 21.27) recorded the lowest NTP. Small pits (NSP) consistently outnumber large pits (NLP) in all populations. Risovača (NSP = 28.00) exhibited the highest number of small pits, while Ušačka (NSP = 20.14) displayed the lowest. Large pits (NLP) remain relatively low across all populations (Table 6), with Hadži Prodanova (NLP = 1.23) showing the highest count and Risovača (NLP = 0.65) the lowest.

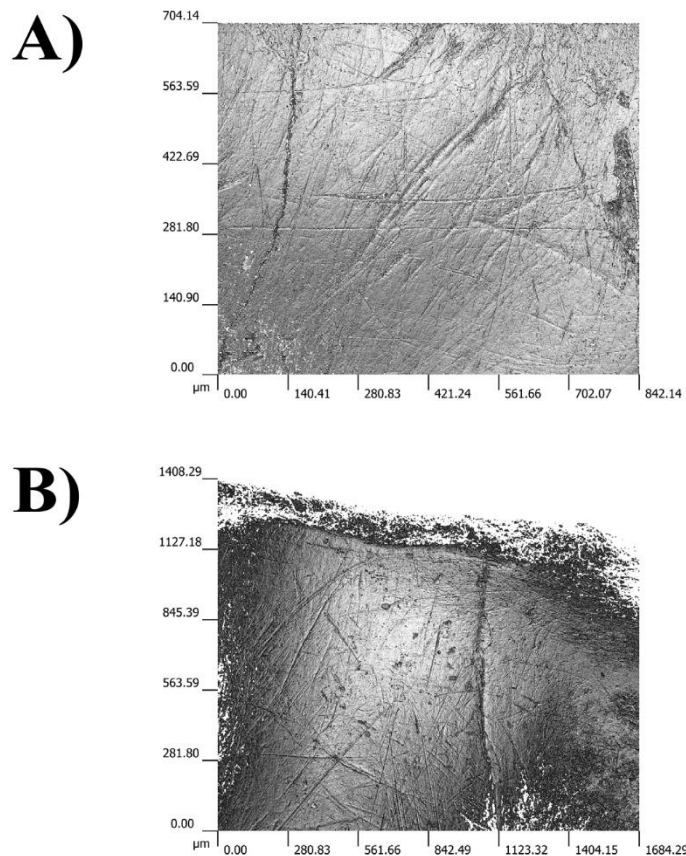


Figure 51. Three-dimensional scans of the occlusal surface of the talonid of the lower first molar (m1) of different cave bear specimens from the Central Balkans performed by a Sensofar® S Neox microscope. A) Surface topography (employing a $\times 20$ lens) of a *U. spelaeus* from Risovača (#RIS92/284), displaying fine and coarse scratches and one hypercoarse scratch. B) Surface topography (employing a $\times 10$ lens) of a *U. spelaeus* from Hadži Prodanova (#HPP04/172/5), exhibiting fine and coarse scratches.

A significant variation is observed in puncture pits (NPP), with Risovača (NPP = 0.30) recording the highest value, followed by Hadži Prodanova (NPP = 0.14). In contrast, Ušačka (NPP = 0.05) showed the lowest NPP values. Regarding gouges (NG), Hadži Prodanova (NG

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= 0.59) displayed the highest values, followed by Risovača (NG = 0.40). Ušačka (NG = 0.27) exhibited the lowest gouge counts.

Finally, regarding hypercoarse scratches, those were only displayed by Risovača population specimens (Figure 51A), although in low numbers ($n = 3$: 30%), as well as for Ušačka ($n = 1$: 9%).

6.4.1.1 Comparison with extant bears

In comparison to extant ursids, the *U. spelaeus* populations from Central Balkans exhibit lower total scratch counts (NTS) than most omnivorous *Ursus* species (Table 6). The highest NTS value among the Central Balkans populations was recorded for Risovača (NTS = 18.15), which is lower than *U. arctos* from Kamchatka (NTS = 20.05), Greece (NTS = 20.00), or Central Europe (NTS = 20.90), but still falls within the range of omnivorous extant bears. The Hadži Prodanova population (NTS = 16.29) closely aligns with *U. americanus* (NTS = 16.12), while Ušačka (NTS = 15.48) exhibits the lowest value among Central Balkans cave bears, aligning closely with *U. maritimus* (NTS = 14.23) and falling below most extant *U. arctos* populations.

The distribution of fine (NFS) and coarse (NCS) scratches among the fossil populations closely resembles that of extant ursids, with fine scratches consistently outnumbering coarse ones (Table 6). However, *U. spelaeus* from Central Balkans generally displays higher NCS values than most extant bears, with Ušačka (NCS = 5.14) exhibiting values comparable to *U. arctos* from Kamchatka (NCS = 3.83) and Northern Europe (NCS = 3.78), though lower than *U. arctos* from Greece (NCS = 7.00). *U. maritimus* (NCS = 3.21) falls below Ušačka but is higher than Hadži Prodanova (NCS = 2.27), with a similar score, and Risovača (NCS = 0.90), with the latter showing values comparable to *A. melanoleuca* (NCS = 0.00). Fine scratches (NFS) are relatively low in Ušačka (NFS = 10.41), closely aligning with *U. maritimus* (NFS = 11.00), while Hadži Prodanova (NFS = 13.86) and Risovača (NFS = 17.35) display higher values, approaching those observed in *U. arctos* from Central Europe (NFS = 17.50) and North America (NFS = 18.25).

Regarding the total number of pits (NTP), Central Balkans fossil populations exhibit moderate to high values when compared to extant bears (Table 6). The highest NTP value is recorded for Risovača (NTP = 28.95), which is comparable to *U. arctos* from North America (NTP = 28.38). Hadži Prodanova (NTP = 23.38) falls within the range of *U. arctos* from Greece (NTP = 20.00) and slightly below *U. americanus* (NTP = 27.44). Ušačka, with the lowest NTP (NTP = 21.27), aligns more closely with *U. maritimus* (NTP = 20.15) and *U. arctos* from Greece.

As seen in both fossil and extant bears, small pits (NSP) consistently outnumber large pits (NLP) (Table 6). However, extant bears show higher large pit counts than extinct *U. spelaeus* populations from Central Balkans. Large pits values are low across all Central Balkans populations, with the highest recorded for Hadži Prodanova (NLP = 1.23), which is significantly lower than *U. arctos* from Greece (NLP = 9.25) or Central Europe (NLP = 5.40). Conversely, small pits (NSP) dominate across the fossil Central Balkans populations, with Risovača (NSP = 28.00) showing values comparable to *U. arctos* from Northern Europe (NSP = 23.33) and Central Europe (NSP = 22.50).

Puncture pits (NPP) show minimal variation among Central Balkans cave bears. Risovača (NPP = 0.30) exhibits the highest value but is still considerably lower than *U. arctos* from Greece (NPP = 2.25) with the lowest values among the omnivorous bears. Hadži Prodanova (NPP = 0.14) and Ušačka (NPP = 0.05) show the lowest values, aligning more closely with *A. melanoleuca* (NPP = 0.00) and *U. maritimus* (NPP = 0.07). Regarding gouges (NG), Central Balkans *U. spelaeus* populations exhibit lower values than most extant *U. arctos* populations (Table 6). Hadži Prodanova (NG = 0.59) and Risovača (NG = 0.40) show values closer to *U. arctos* from Kamchatka (NG = 0.35) or North America (NG = 0.25). Ušačka (NG = 0.27) exhibits the lowest NG counts among the Central Balkans cave bears, aligning with *U. arctos* from Northern Europe (NG = 0.22).

6.4.2 Dietary inference

6.4.2.1 Bivariate analysis of the total number of scratches and pits

The *U. spelaeus* populations from Central Balkans exhibit a degree of intra-population variability (Figure 52); however, their distribution on the bivariate plot remains clustered near the boundary between vertebrate-dominated and soft-mast-dominated dietary regions.

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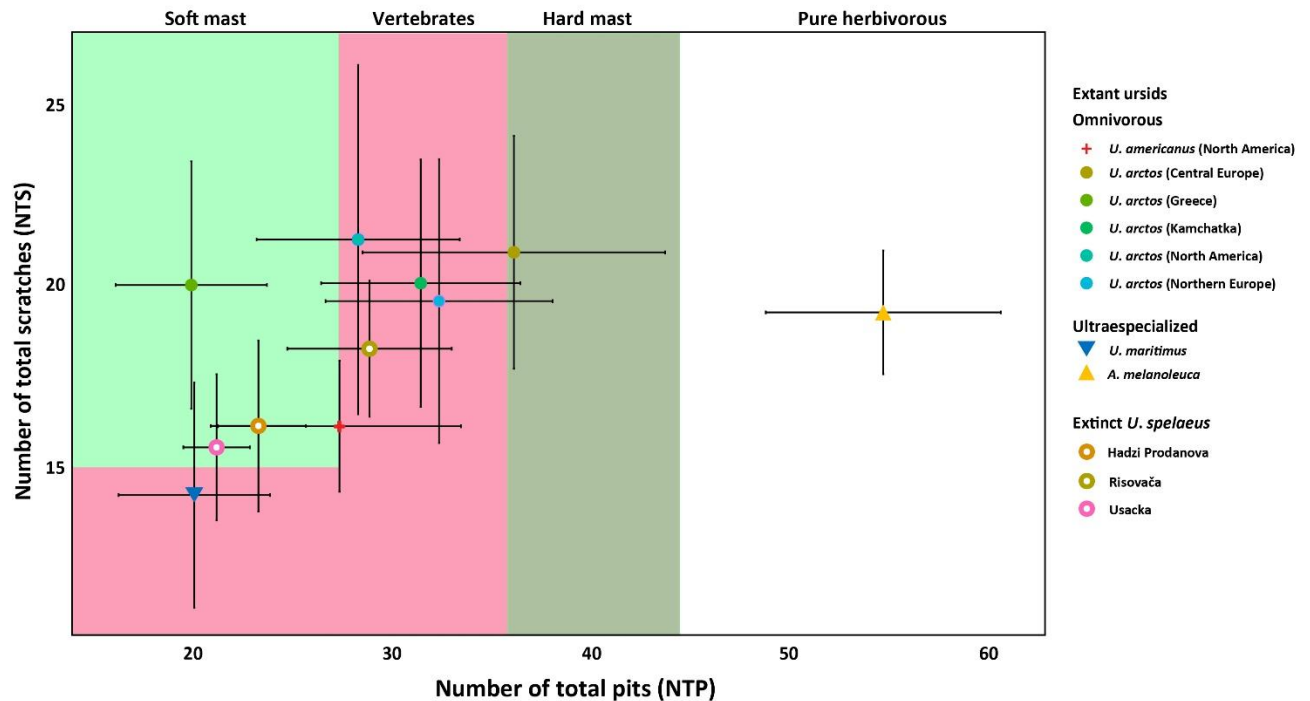


Figure 52. Bivariate plot of the number of total pits (NTP) and the number of total scratches (NTS) comparing the extant bear populations and the fossil populations from Central Balkans. Highlighted are four distinct eco-regions (soft mast, hard mast, vertebrates, and pure herbivorous) based on the predominant diet of extant bear populations as established by Pappa et al. (2019).

The *U. spelaeus* populations from Hadži Prodanova and Ušacka are positioned in the lower-most section of the soft-mast-dominated region, with total pit values (x-axis) overlapping those of *U. arctos* from Greece and *U. maritimus* (Figure 52). Additionally, the error bars for Hadži Prodanova extend into the range of *U. americanus* within the soft-mast-dominated region. Despite this, their relatively low total scratch counts (y-axis) bring them closer to *U. maritimus*, while their error bars extend toward the vertebrate-dominated region. In contrast, the Risovača population falls within the vertebrate-dominated region, positioned higher on the y-axis, overlapping with *U. arctos* from Northern Europe, Kamchatka, and North America, as well as with *U. americanus* (Figure 52).

6.4.2.2 Correspondence analysis

In order to investigate the relationships, distribution, and variability of the studied populations between them and the extant ursid reference dataset, a correspondence analysis (CA) was conducted (see more in Materials and Methods, section 5.3). The analysis included seven microwear variables, namely small pits, large pits, fine scratches, coarse scratches, SWS, gouges, and puncture pits. The first dimension (Dim. 1) explains 36.5% of the variance, and the second dimension (Dim. 2) accounts for 28.8%, collectively capturing 65.3% of the total

variance (Figure 53; Appendix section A.3.1, Table A6) Thus, these two dimensions were selected for analysis and visualization.

As previously detailed (see section 6.1.3.2A), the correspondence analysis (CA) highlights the dietary adaptations of extant bear populations, with omnivorous species distributed according to their primary dietary components, such as soft mast, hard mast, or vertebrates. These patterns provide a comparative framework for positioning fossil populations within the CA plot, allowing insights into their dietary and ecological similarities with extant species.

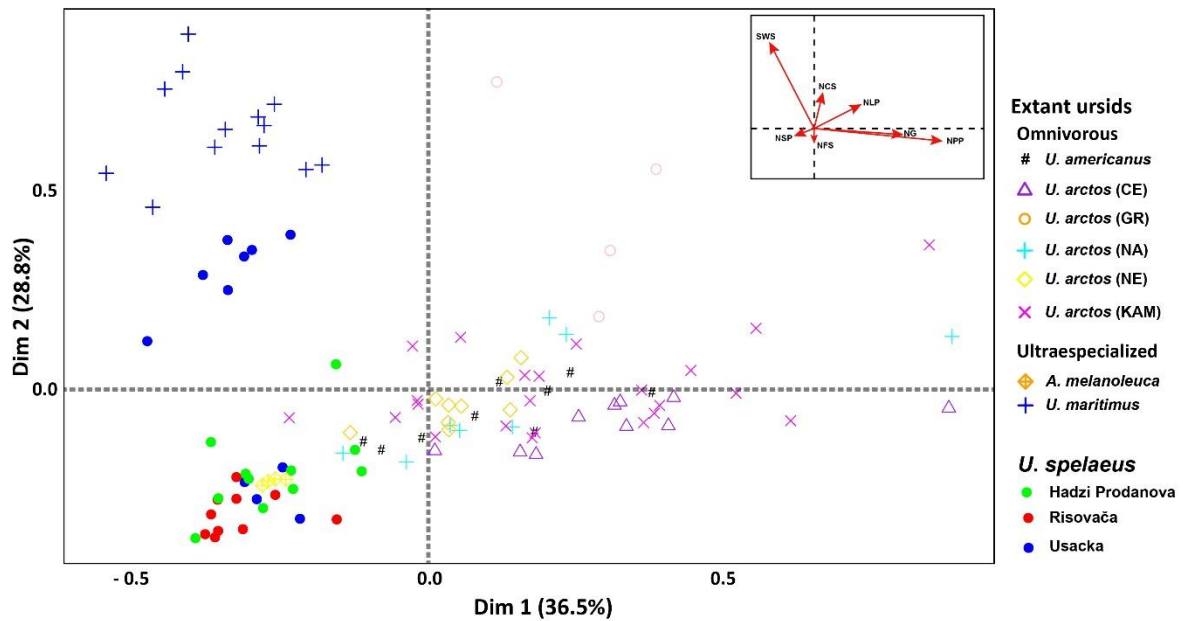


Figure 53. Correspondence analysis (CA) based on seven microwear variables: number of fine scratches (NFS), coarse scratches (NCS), small pits (NSP), large pits (NLP), gouges (NG), puncture pits (NPP), and the scratch width score (SWS). The analysis compares fossil populations of *U. spelaeus* from Central Balkans with a reference dataset of extant ursids established by Pappa et al. (2019). The direction and contribution of the variables in the CA plot are depicted in the top-right inset of the figure. Abbreviations: CE = Central Europe; GR = Greece; NA = North America; NE = Northern Europe; KAM = Kamchatka.

The fossil *U. spelaeus* populations from Central Balkans exhibit a clustered distribution in the lower-left region of the plot, occupying negative values along both the x- and y-axes (Figure 53). This placement differentiates them from extant omnivorous bears, positioning them closer to *A. melanoleuca*, *U. arctos* from Northern Europe, and *U. americanus*. However, some individuals from Hadži Prodanova ($n = 3$; 27.27%) extend towards the cluster of omnivorous bears from the northern-most hemisphere such as *U. arctos* from North America and Northern Europe, as well as *U. americanus* (Figure 53). Hence, Hadzi Prodanova exhibits a degree of intra-population variability, which is associated with the presence of gouges and puncture pits, which are more characteristic of extant omnivorous bears. Furthermore, most of the Ušacka population ($n = 7$; 63.63%) deviates from this main cluster, positioning itself closer to *U.*

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maritimus. This differentiation is primarily driven by a higher scratch width score (SWS), indicating higher counts of coarse to fine scratches in comparison to other Central Balkans *U. spelaeus* populations (Figure 53).

6.5 Northern Urals (Medvezhiya)

A total of 10 lower first molars (m1), out of 17 examined, were deemed suitable for analysis. Therefore, 7 lower first molars (m1) had to be excluded from the analysis, those included the youngest individuals lacking wear facets (Rivals et al., 2007) and those with damaged occlusal surfaces due to taphonomic processes (King et al., 1999; El-Zaatari, 2010; Uzunidis et al., 2021; Micó et al., 2024).

Species – (Location)	<i>N</i>	NFS	NCS	NTS	SWS	NLP	NSP	NPP	NTP	NG
Extinct										
<i>U. kanivetz</i> (Medvezhiya)	10	13.75	3.55	17.53	0.10	3.5	25.75	0.60	29.85	1.85
Extant										
<i>U. americanus</i> (North America)	9	13.56	2.56	16.12	0.00	5.44	19.00	3.00	27.44	0.00
<i>U. arctos</i> (Greece)	4	13.00	7.00	20.00	0.5	9.25	8.50	2.25	20.00	2.00
<i>U. arctos</i> (Central Europe)	10	17.50	3.40	20.90	0.00	5.40	22.50	8.30	36.20	2.10
<i>U. arctos</i> (North America)	8	18.25	3.00	21.25	0.00	6.75	18.38	3.25	28.38	0.25
<i>U. arctos</i> (Kamchatka)	23	16.22	3.83	20.05	0.10	6.96	19.78	4.78	31.52	0.35
<i>U. arctos</i> (Northern Europe)	9	15.78	3.78	19.56	0.00	6.44	23.33	2.67	32.44	0.22
<i>A. melanoleuca</i>	4	19.25	0.00	19.25	0.00	8.50	46.25	0.00	54.75	0.00
<i>U. maritimus</i>	13	11.00	3.21	14.23	2.79	4.50	16.21	0.07	20.15	0.00
<i>U. thibetanus</i>	6	13.56	2.56	16.12	0.00	5.44	19.00	3.00	27.44	0.00

Table 7. Comparison of the dental microwear results of the fossil population of cave bears (*U. kanivetz*) from Northern Urals (Medvezhiya cave), with the reference dataset of extant bear species of *U. arctos*, *U. americanus*, *A. melanoleuca* and *U. maritimus* established by Pappa et al. (2019). Abbreviations: *N* = number of specimens, NFS = number of fine scratches, NCS = number of coarse scratches, NTS = number of total scratches, SWS = scratch width score, NLP = number of large pits, NSP = number of small pits, NPP = number of puncture pits, NTP = number of total pits, NG = number of gouges.

6.5.1 *U. kanivetz* from the Urals

The microwear analysis of *U. kanivetz* from Medvezhiya reveals variation in the total number of scratches (NTS), comparable to some extant ursid populations (Table 7). The average NTS for the Northern Urals population is 17.53, positioning it between *U. americanus* (NTS = 16.12) and *U. arctos* from Northern Europe (NTS = 19.56), but below *U. arctos* from Kamchatka (NTS = 20.05) and Central Europe (NTS = 20.90).

The scratch width score (SWS) remains low (0.10), indicating the predominance of fine scratches over coarse ones, a pattern observed in most extant ursids (Table 7). This value aligns with *U. arctos* from Kamchatka (SWS = 0.10) but is higher than *U. americanus* (SWS = 0.00) and *U. arctos* from Central Europe (SWS = 0.00). However, it is significantly lower than *U. maritimus* (SWS = 2.79), which exhibits the highest SWS among the compared ursids.

The total number of pits (NTP) in *U. kanivetz* (NTP = 29.85) is relatively high, surpassing that of *U. americanus* (NTP = 27.44) and *U. arctos* from North America (NTP = 28.38), and falling

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within the range of *U. arctos* from Kamchatka (NTP = 31.52). Small pits (NSP) consistently outnumber large pits (NLP) in all extant populations, as well as in *U. kanivetz* (Table 7). The NSP in *U. kanivetz* (NSP = 25.75) is among the highest values observed (Table 7), exceeding that of *U. arctos* from North America (NSP = 18.38) and Northern Europe (NSP = 23.33). The number of large pits (NLP = 3.50) is lower than those recorded for *U. arctos* from Greece (NLP = 9.25) and *A. melanoleuca* (NLP = 8.50) but higher than in *U. arctos* from Kamchatka (NLP = 6.96) and North America (NLP = 6.75).

A significant variation is observed in the number of puncture pits (NPP; Table 7), with *U. kanivetz* exhibiting a value of 0.60. This is higher than *U. maritimus* (NPP = 0.07) but lower than *U. americanus* (NPP = 3.00) and *U. arctos* from Central Europe (NPP = 8.30). Regarding gouges (NG), *U. kanivetz* displays a relatively high value (NG = 1.85), falling below *U. arctos* from Greece (NG = 2.00) and Central Europe (NG = 2.10), but significantly higher than *U. americanus* (NG = 0.00) and *U. maritimus* (NG = 0.00), which do not display any (Table 7).

6.5.1.1 Comparison with extant bears

When compared to extant ursids, *U. kanivetz* from Medvezhiya exhibits intermediate microwear values, suggesting an omnivorous dietary pattern with regional variability. The NTS value (17.53) is higher than in *U. americanus* (16.12) but lower than in *U. arctos* from Kamchatka (20.05) and Central Europe (20.90).

The distribution of fine (NFS) and coarse (NCS) scratches among *U. kanivetz* aligns closely with omnivorous extant ursids. Fine scratches (NFS = 13.75) fall within the range of *U. arctos* from Greece (NFS = 13.00) and *U. americanus* (NFS = 13.56), while coarse scratches (NCS = 3.55) are similar to *U. arctos* from Central Europe (NCS = 3.40) and Northern Europe (NCS = 3.78). These values suggest an omnivorous diet with a moderate level of dietary toughness, similar to generalist *U. arctos* populations.

Regarding the total number of pits (NTP), *U. kanivetz* (NTP = 29.85) exhibits a relatively high value, comparable to *U. arctos* from Kamchatka (NTP = 31.52) and North America (NTP = 28.38). This pattern suggests that *U. kanivetz* had a diet incorporating a substantial proportion of harder food items, such as nuts or seeds. Small pits (NSP = 25.75) are notably high, aligning with values seen in *U. arctos* from Central Europe (NSP = 22.50) and Northern Europe (NSP = 23.33), reinforcing the interpretation of a diet with moderate levels of hard-object processing.

In terms of large pits (NLP), *U. kanivetz* (NLP = 3.50) exhibits values higher than those of *U. arctos* from Kamchatka (NLP = 6.96) and North America (NLP = 6.75), but lower than *U.*

arctos from Greece (NLP = 9.25). This suggests less frequent hard-object feeding compared to the most omnivorous *U. arctos* populations but still higher than more specialized taxa like *U. maritimus*.

The puncture pit counts are relatively low in *U. kanivetz* (NPP = 0.60) but still higher than in *U. maritimus* (NPP = 0.07), suggesting occasional consumption of tougher or more resistant food items. Finally, gouges (NG = 1.85) are higher than in most *U. arctos* populations (Figure 54), except for Central Europe (NG = 2.10), indicating some level of hard-mast items inclusion in its diet.

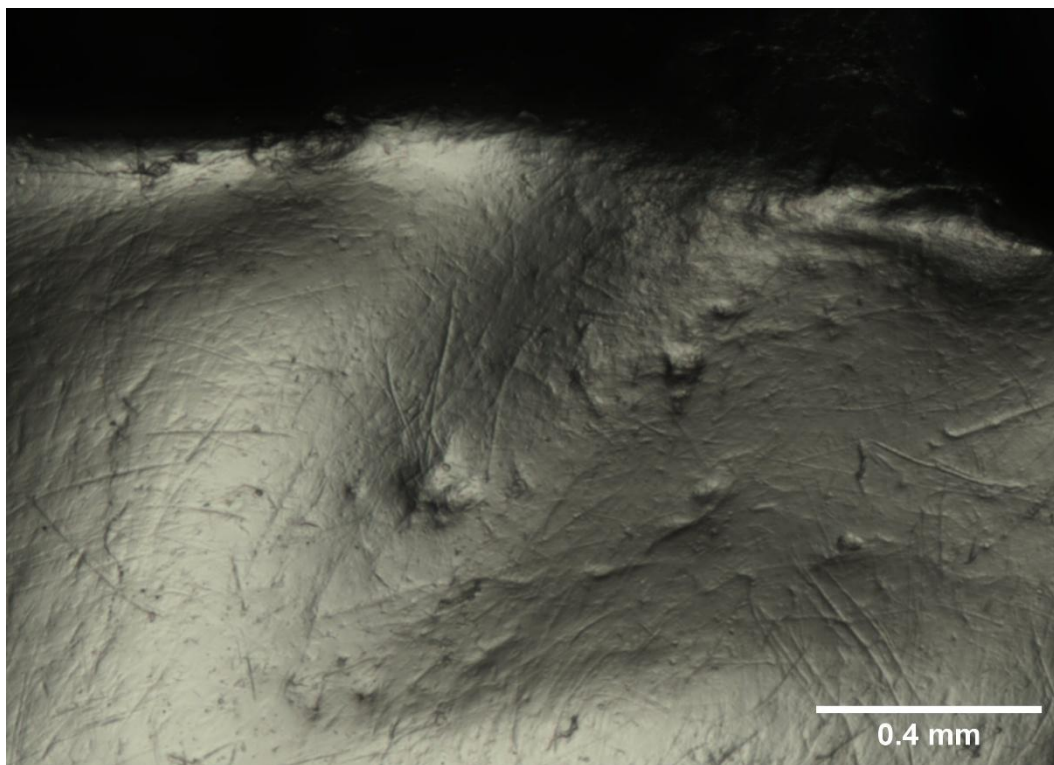


Figure 54. Photomicrographs (at $\times 35$ magnification) of the grinding non-faceted enamel surface of a fossil specimens of *U. kanivetz* (ZIN 34756-138) from Medvezhiya Cave. The specimen displays multiple gouges, as well as fine and coarse scratches.

6.5.2 Dietary inference

6.5.2.1 Bivariate analysis of the total number of scratches and pits

The population from Medvezhiya falls within the vertebrate-dominated dietary region, positioned very close to *U. americanus* from North America, with which it overlaps, as well as *U. arctos* from Northern Europe (Figure 55).

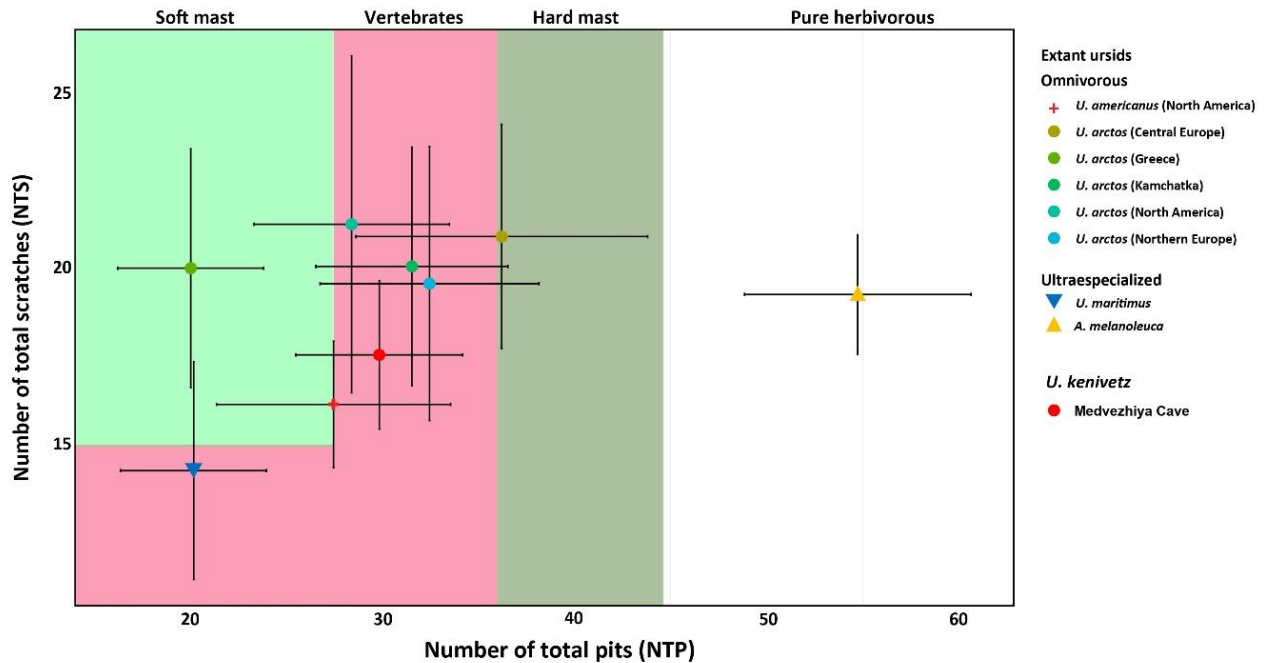


Figure 55. Bivariate plot of the number of total pits (NTP) and the number of total scratches (NTS) comparing the extant bear populations and the fossil *U. kanivetz* population from Medvezhiya (Northern Urals). Highlighted are four distinct eco-regions (soft mast, hard mast, vertebrates, and pure herbivorous) based on the predominant diet of extant bear populations as established by Pappa et al. (2019).

However, *U. kanivetz* error bars extend towards the soft-mast-dominated dietary region. The two extant populations for which it displays the higher similarity have in common the consumption of significant amounts of vertebrates (fish for *U. americanus* and terrestrial mammals from *U. arctos* from Northern Europe, such as ungulates), as well as a plant-dominated diet based on soft mast, such as foliage, grasses and fleshy fruits.

6.5.2.2 Correspondence analysis

In order to investigate the relationships, distribution, and variability of the studied populations between them and the extant ursid reference dataset, a correspondence analysis (CA) was conducted (see more in Materials and Methods, section 5.3). The analysis included seven microwear variables, namely small pits, large pits, fine scratches, coarse scratches, SWS, gouges, and puncture pits. The first dimension (Dim. 1) explains 37.8% of the variance, and the second dimension (Dim. 2) accounts for 26.7%, collectively capturing 64.5% of the total

variance (Figure 56; Appendix section A.3.1, Table A7) Thus, these two dimensions were selected for analysis and visualization.

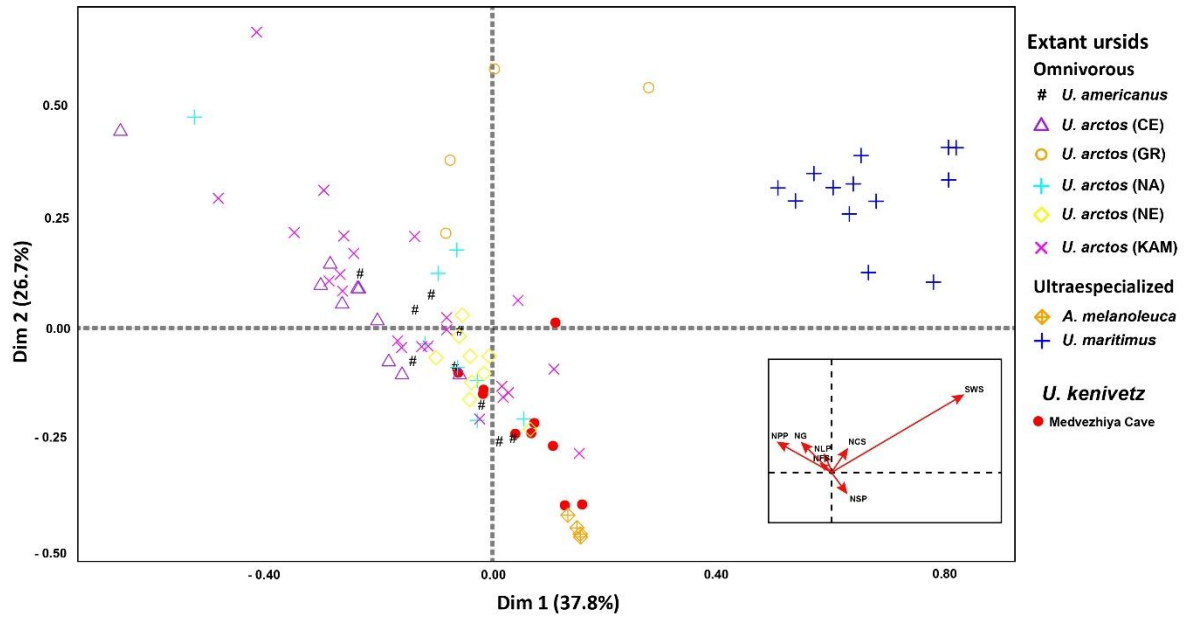


Figure 56. Correspondence analysis (CA) based on seven microwear variables: number of fine scratches (NFS), coarse scratches (NCS), small pits (NSP), large pits (NLP), gouges (NG), puncture pits (NPP), and the scratch width score (SWS). The analysis compares the fossil population of *U. kanivetz* from Medvezhiya (Northern Urals) with a reference dataset of extant ursids established by Pappa et al. (2019). The direction and contribution of the variables in the CA plot are depicted in the top-right inset of the figure. Abbreviations: CE = Central Europe; GR = Greece; NA = North America; NE = Northern Europe; KAM = Kamchatka.

The diet of the *U. kanivetz* overlaps with that of *U. arctos* from Northern Europe, with an omnivorous diet with a predominance of soft mast consumption, comprehending, fibrous plants and fleshy fruits, but also with the consumption of both vertebrates and invertebrates (Figure 56). Furthermore, it also displays high similarities with *U. americanus* from North America (Alaska), with also a soft mast dominated omnivorous diet based on fibrous food (leaves and flowers) as well as soft fruits and occasionally fish and vertebrates. Finally, *U. kanivetz* also displays similarities with *U. arctos* from Kamchatka, with also a predominance of soft mast in its diet, and the consumption of vertebrates.

Therefore, the diet of *U. kanivetz* would be a plant-dominated soft mast diet, with the consumption of fibrous plants and fleshy fruits, while the occasional consumption of vertebrates cannot be ruled out due to overlap with omnivorous northern hemisphere species (Figure 56). However, the absence of hypercoarse scratches and a microwear signal far from that of the polar bear, makes it unlikely a short-term diet based on vertebrates. Furthermore, some individuals in the CA fall close to *A. melanoleuca*, with a highly rough and fibrous specialized diet on bamboo. This further supports the soft-mast consumption of highly fibrous

items for *U. kanivetz* from Medvezhiya. However, the presence of gouges and puncture pits, opens the possibility of seasonal hard-object consume for some individuals.

6.6 Inter-regional and inter-chronological comparison

To comprehensively evaluate inter-regional and inter-chronological dietary variability in cave bears, a combined analysis was conducted across all studied sites. This approach integrates key microwear variables to investigate dietary patterns and ecological adaptations in *U. spelaeus* sensu lato from the Middle to Late Pleistocene.

Hence, cave bear populations from the Romanian Carpathians, Moldavian Plateau, Western Balkans and Western Rhodopes Mountains, Central Balkans, and Eurasian reaches of the continent (namely, Greater Caucasus and Northern Urals), were compared to assess the extent of microwear variability across distinct biogeographic regions. This analysis aims to determine whether differences in landscape, environmental context, and competitive pressures shaped divergent foraging strategies within the cave bear lineage.

6.6.1 Number of total scratches (NTS) and number of total pits (NTP)

Regarding the number of total scratches (NTS) and the number of total pits (NTP), the studied populations present intra- and inter- population variability (Figure 57).

The number of total scratches (NTS) exhibits substantial variability across regions. The Romanian Carpathians display the highest values (Figure 57), as well as the highest overall average (Figure 58), followed closely by Moldavian Plateau, which shows a similar distribution and a slightly lower average (Figure 57 and 58). In contrast, Western Balkans and Western Rhodopes Mountains, Central Balkans, and Eurasia (including the Greater Caucasus and Northern Urals) exhibit overall lower NTS values with reduced inter-population variability (Figure 57). The distribution of the number of total pits (NTP) presents a wide intra-regional distribution, which is similar across Romanian Carpathians, Moldavian Plateau, Western Balkans and Western Rhodopes Mountains, and Eurasia, although Moldavian Plateau exhibits the greatest variability (Figure 57 and 58). A great intra-region variability is observed among the Greater Caucasus cave bear populations. However, it is important to note the distinct chronological attributions of the Caucasian bears—*U. praekudarensis* from MIS 11, *U. praekudarensis/kudarensis* from MIS 8/7, and *U. kudarensis* from MIS 5/4—which may contribute to differences in microwear variability due to changing climatic conditions and ecological contexts. In contrast, the other MIS 3 populations included in the analysis (excluding

U. s. rossicus which dates to MIS 7) are more temporally consistent, representing a relatively similar period. Central Balkans, in contrast to the other regions, presents a more uniform and narrower distribution with a narrower range of NTP values, which fall within the lower end of the observed spectrum compared to the other regions in the plot (Figure 57). However, slight differences between Central Balkans populations can be observed.

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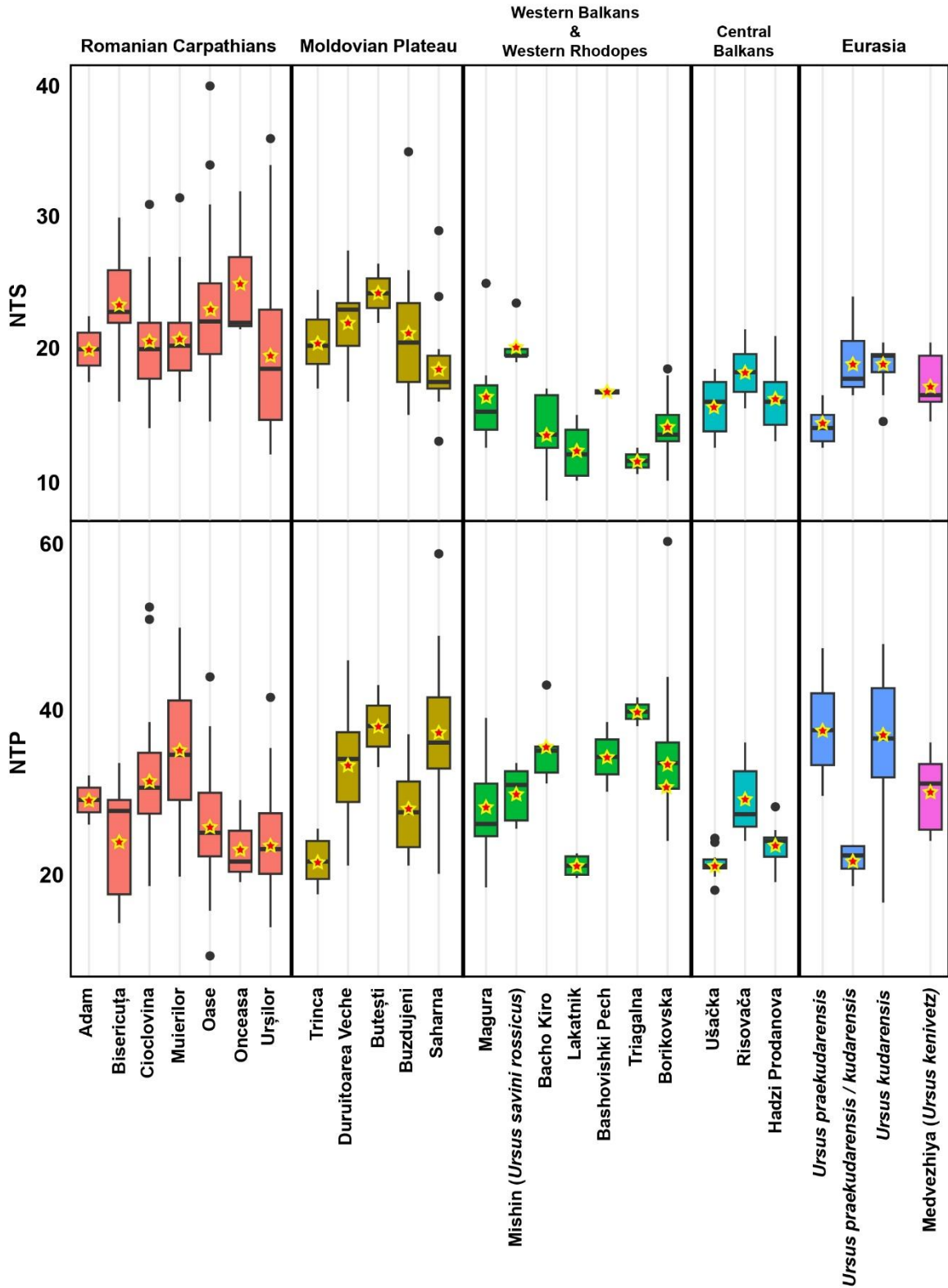


Figure 57. Boxplot illustrating the distribution of the number of total scratches (NTS) and the number of total pits (NTP) recorded for the cave bear populations analysed in this study, categorized by region. The regions include the Romanian Carpathians, Moldavian Plateau, Western Balkans and Western Rhodopes Mountains, Central Balkans, and Eurasia; specifically, the Greater Caucasus (*U. kudarensis* lineage) and the Northern Urals (including Medvezhiya). Palaeontological sites names are displayed below each respective region. Red and yellow stars indicate the mean values.

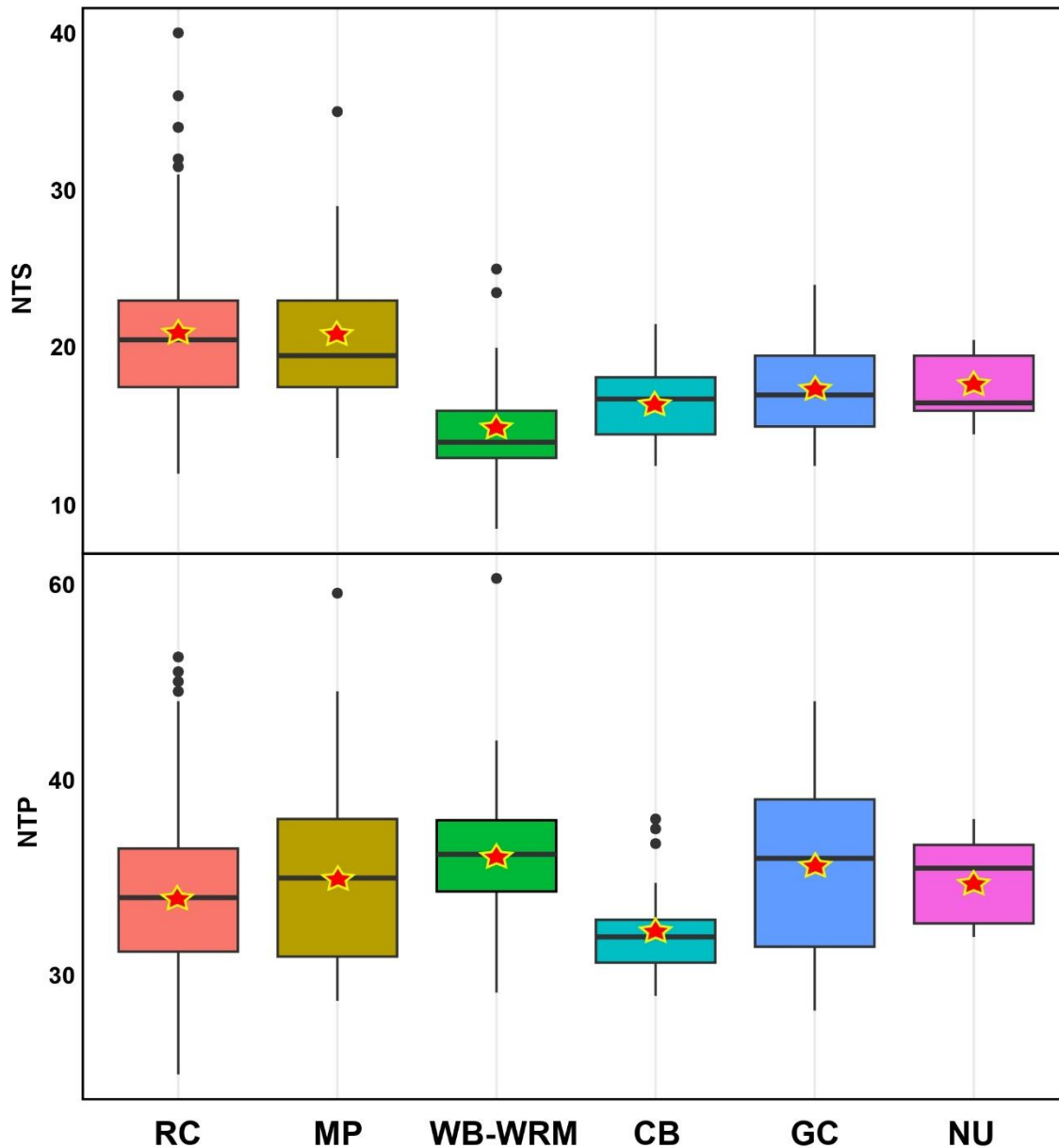


Figure 58. Boxplot displaying the distribution of the number of total scratches (NTS) and the number of total pits (NTP) for cave bear populations across regions: Romanian Carpathians (RC), Moldavian Plateau (MP), Western Balkans and Western Rhodopes Mountains (WB-WRM), Central Balkans (CB), the Greater Caucasus (GC), and the Northern Urals (NU). Red and yellow stars indicate the mean values.

6.6.2 Number of fine (NFS) and coarse (NCS) scratches

Regarding the number of fine scratches (NFS) and the number of coarse scratches (NCS), the studied populations present intra- and inter- population variability (Figure 59 and 60).

Concerning the number of coarse scratches (NCS), the highest values are observed in the Romanian Carpathian populations, which also exhibit the greatest variability both among and within populations (Figure 59 and 60). Only the *U. praekudarensis* (MIS 11) population from the Greater Caucasus presents a higher average, though with a clustered distribution that does

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not extend upwards. Additionally, *U. praekudarensis/kudarensis* (MIS 8/7) also displays a high NCS distribution. Nevertheless, Moldavian Plateau, Western Balkans and Western Rhodopes Mountains, Central Balkans, and the Northern Urals regions, as well as the Late Pleistocene (MIS 5/4) *U. kudarensis* exhibit lower values, with much narrower intra- and inter-population variability. When grouped by region, the highest averages are scored for Romanian Carpathians, and followed by the Caucasian populations (Figure 59).

Regarding the number of fine scratches (NFS), the highest distribution and averages are observed in the Moldavian Plateau populations (as overall regional average), while the widest inter-regional variability is displayed by the Romanian Carpathians (Figure 59 and 60). Notably, the Buzdujeni population exhibits the greatest intra-population variability, comparable to the populations from Romanian Carpathians, which also show extensive inter-population variation. Central Balkans presents high intra-regional variability but relatively low intra-population variability. The Western Balkans and Western Rhodopes Mountains region displays overall lower values compared to Romanian Carpathians and Moldavian Plateau, while the Northern Urals (Medvezhiya) falls within the range observed for Western Balkans and Western Rhodopes Mountains. The Caucasian cave bear lineage exhibits considerable variability (Figure 59), with *U. praekudarensis/kudarensis* showing the highest NFS values, comparable to those of Moldavian Plateau, whereas *U. praekudarensis* and *U. kudarensis* presents low NFS values, the lowest in the entire sample.

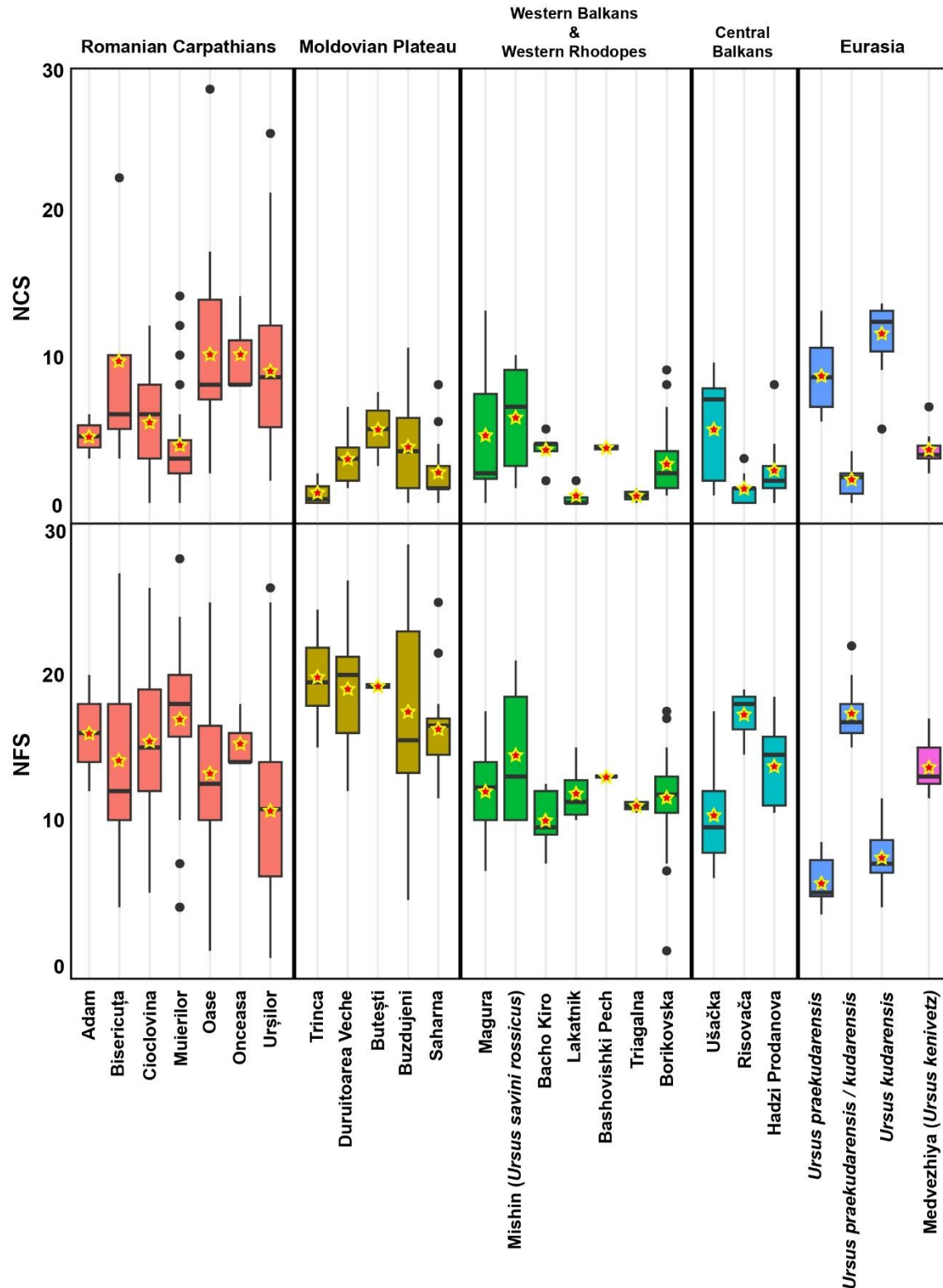


Figure 59. Boxplot illustrating the distribution of the number of coarse scratches (NCS) and the number of fine scratches (NFS) recorded for the cave bear populations analysed in this study, categorized by region. The regions include the Romanian Carpathians, Moldavian Plateau, Western Balkans and Western Rhodopes Mountains, Central Balkans, and Eurasia; specifically, the Greater Caucasus (*U. kudarensis* lineage) and the Northern Urals (including Medvezhiya). Palaeontological sites names are displayed below each respective region. Red and yellow stars indicate the mean values.

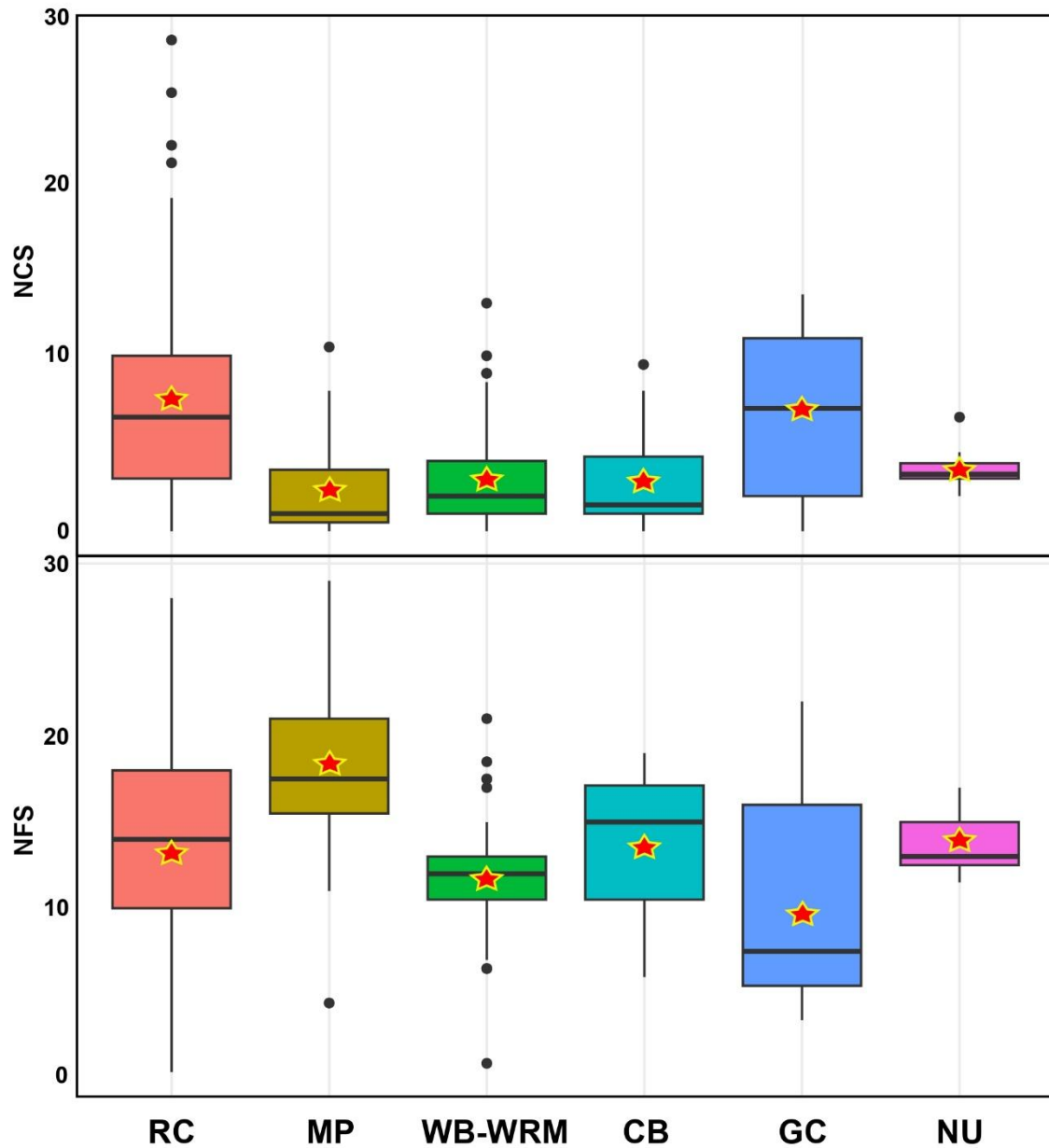


Figure 60. Boxplot displaying the distribution of the number of coarse scratches (NCS) and the number of fine scratches (NFS) for cave bear populations across regions: Romanian Carpathians (RC), Moldavian Plateau (MP), Western Balkans and Western Rhodopes Mountains (WB-WRM), Central Balkans (CB), the Greater Caucasus (GC), and the Northern Urals (NU). Red and yellow stars indicate the mean values.

6.6.3 Numbers of small (NSP) and large (NLP) pits

Regarding the number of small pits (NSP) and large pits (NLP), both intra-regional and inter-regional variability is high, with substantial differences observed within populations as well as among regions (Figure 61 and 62). Concerning the number of large pits (NLP), the highest distribution is presented by Romanian Carpathians (Figure 61), although the overall regional highest average is presented by Medvezhyia (Northern Urals) (Figure 62). Western Balkans and Western Rhodopes Mountains also presents a high NLP distribution (Figure 61), with an average similar to that of Romanian Carpathians region (Figure 62). Moldavian Plateau,

Central Balkans and the Caucasian cave bears (*U. kudarensis* clade) present overall lower NLP distribution, although Duruitoarea Veche is an exception, with a high distribution and a high average (Figure 61).

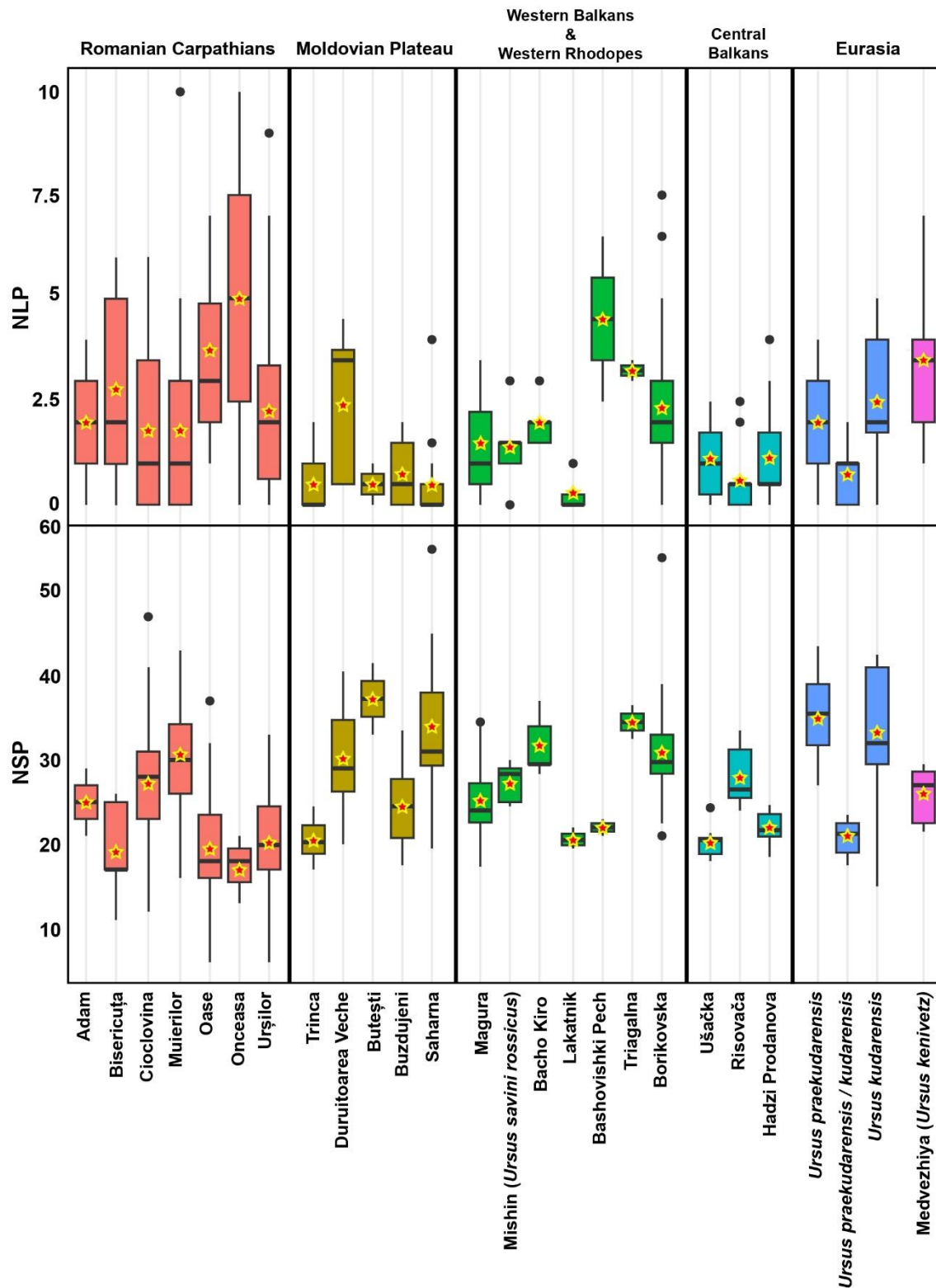


Figure 61. Boxplot illustrating the distribution of the number of large pits (NLP) and the number of small pits (NSP) recorded for the cave bear populations analysed in this study, categorized by region. The regions include the Romanian Carpathians,

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Moldavian Plateau, Western Balkans and Western Rhodopes Mountains, Central Balkans, and Eurasia; specifically, the Greater Caucasus (*U. kudarensis* lineage) and the Northern Urals (including Medvezhiya). Palaeontological sites names are displayed below each respective region. Red and yellow stars indicate the mean values.

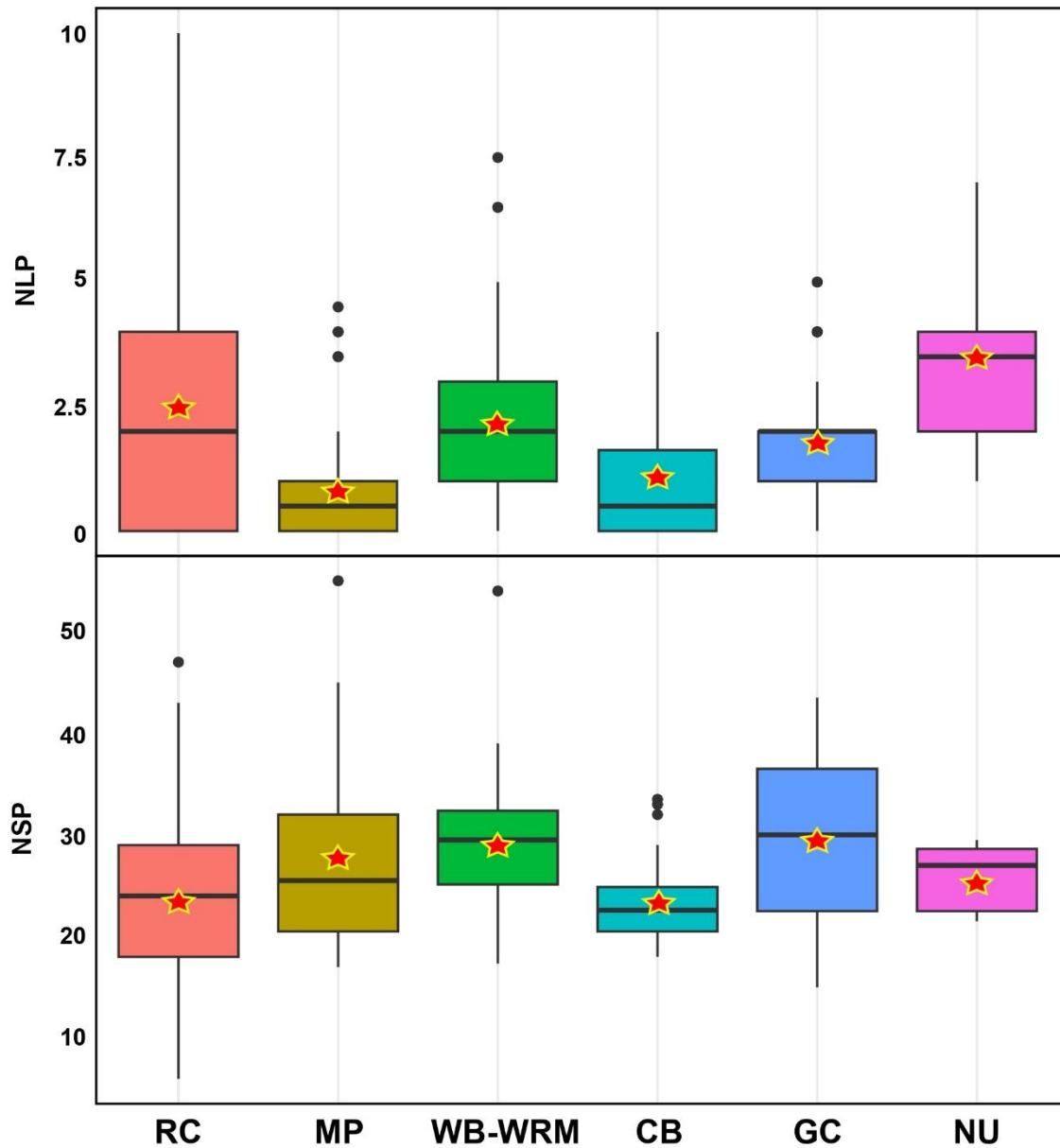


Figure 62. Boxplot displaying the distribution of the number of large pits (NLP) and the number of small pits (NSP) for cave bear populations across regions: Romanian Carpathians (RC), Moldavian Plateau (MP), Western Balkans and Western Rhodopes Mountains (WB-WRM), Central Balkans (CB), the Greater Caucasus (GC), and the Northern Urals (NU). Red and yellow stars indicate the mean values.

Regarding the number of small pits (NSP), the distributions are similar among the regions of Romanian Carpathians, Moldavian Plateau, and Western Balkans and Western Rhodopes Mountains (Figure 61). Although Moldavian Plateau contains individual sites with the highest NSP averages, when analysed at the regional scale, Western Balkans and Western Rhodopes Mountains populations exhibits the highest overall averages, followed by Moldavian Plateau and Romanian Carpathians, respectively. Conversely, the Central Balkans sites display slightly

lower NSP values, resulting in a lower regional average. Similarly, the Medvezhiya Cave population shows a comparatively low NSP distribution, falling below the ranges of Western Balkans and Western Rhodopes Mountains, Moldavian Plateau, and Romanian Carpathians, and overlapping with values from Central Balkans (Figure 61). Finally, the Caucasian cave bears exhibit significant variability, with *U. praekudarensis* presenting the highest NSP averages, closely followed by *U. kudarensis*. In contrast, *U. praekudarensis/kudarensis* displays markedly lower NSP values, overlapping the ranges observed in the Central Balkans populations from Ušačka and Hadži Prodanova (Figure 61).

6.6.4 Gouges (NG) and puncture pits (NPP)

Regarding gouges (NG), considerable variability exists both within and between regions. At the population level (Figure 63), the widest variability is observed among the Romanian Carpathian populations; however, the highest averages are recorded first by *U. kudarensis*, followed by Bashovishki Pech and Medvezhiya populations. When grouped by region (Figure 64), the highest average is observed in Medvezhiya, followed by Western Balkans and Western Rhodopes Mountains and Romanian Carpathians, which exhibit similar averages. In contrast, populations from Moldavian Plateau and Central Balkans show distinctly low distributions and averages for NG.

Regarding puncture pits (NPP), considerable variability exists both within and among regions (Figure 63 and 64). The Romanian Carpathian populations exhibit consistent high distributions and averages, and when analysed at a regional scale (Figure 64), the Romanian Carpathians show both the highest overall average and the widest distribution. Conversely, the Moldavian Plateau, Western Balkans and Western Rhodopes Mountains, Central Balkans, and Eurasian populations display lower NPP distributions. However, some notable exceptions exist: the Moldavian Plateau populations of Buzdujeni and Saharna exhibit high distributions comparable to those from Romanian Carpathians (Figure 63). Additionally, the Western Balkans and Western Rhodopes Mountains population of Bashovishki Pech presents an exceptionally high distribution, the highest among all studied populations.

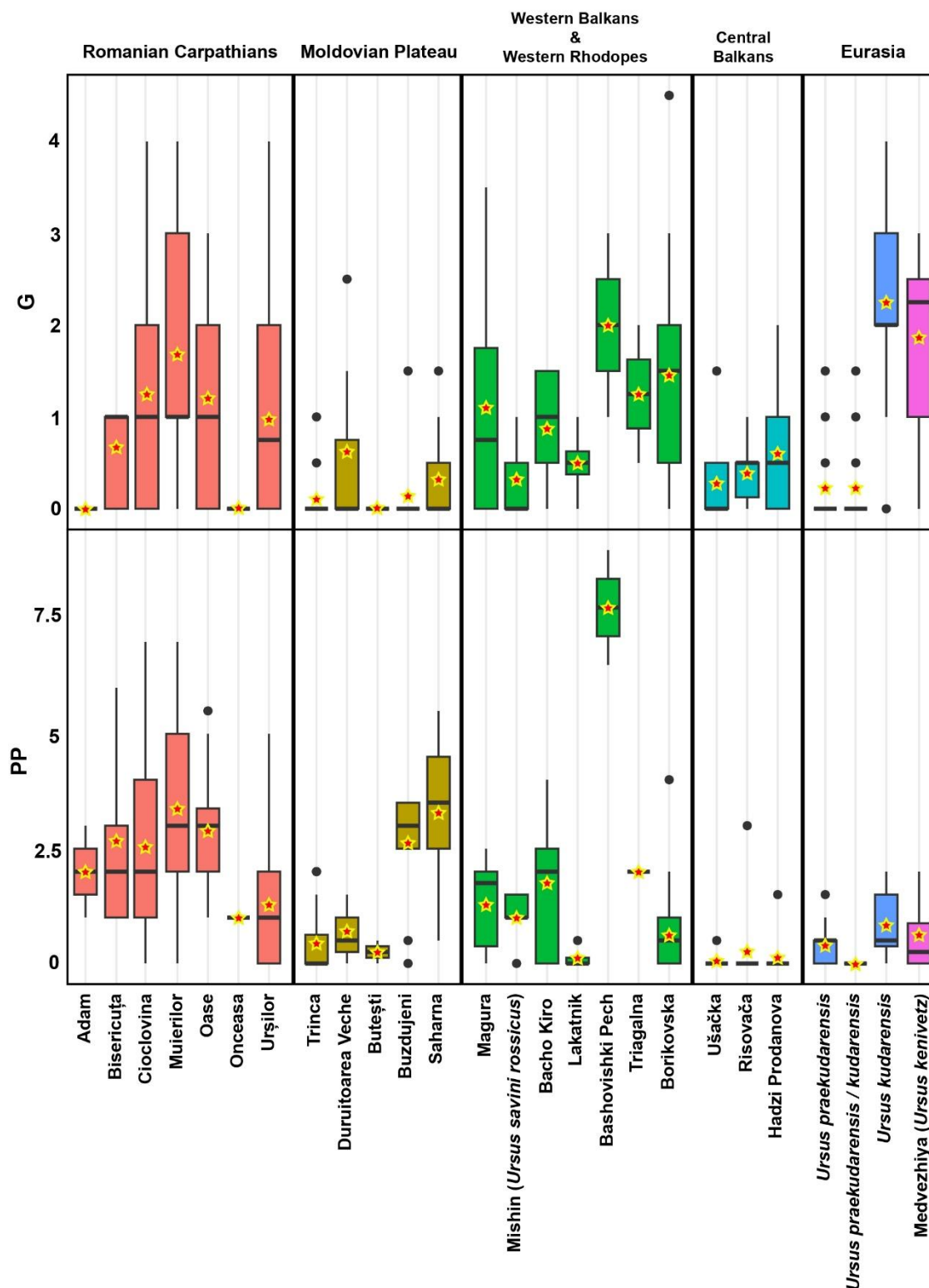


Figure 63. Boxplot illustrating the distribution of the number of gouges (NG) and the number of puncture pits (NPP) recorded for the cave bear populations analysed in this study, categorized by region. The regions include the Romanian Carpathians, Moldavian Plateau, Western Balkans and Western Rhodopes Mountains, Central Balkans, and Eurasia; specifically, the Greater Caucasus (*U. kudarensis* lineage) and the Northern Urals (including Medvezhiya). Palaeontological sites names are displayed below each respective region. Red and yellow stars indicate the mean values.

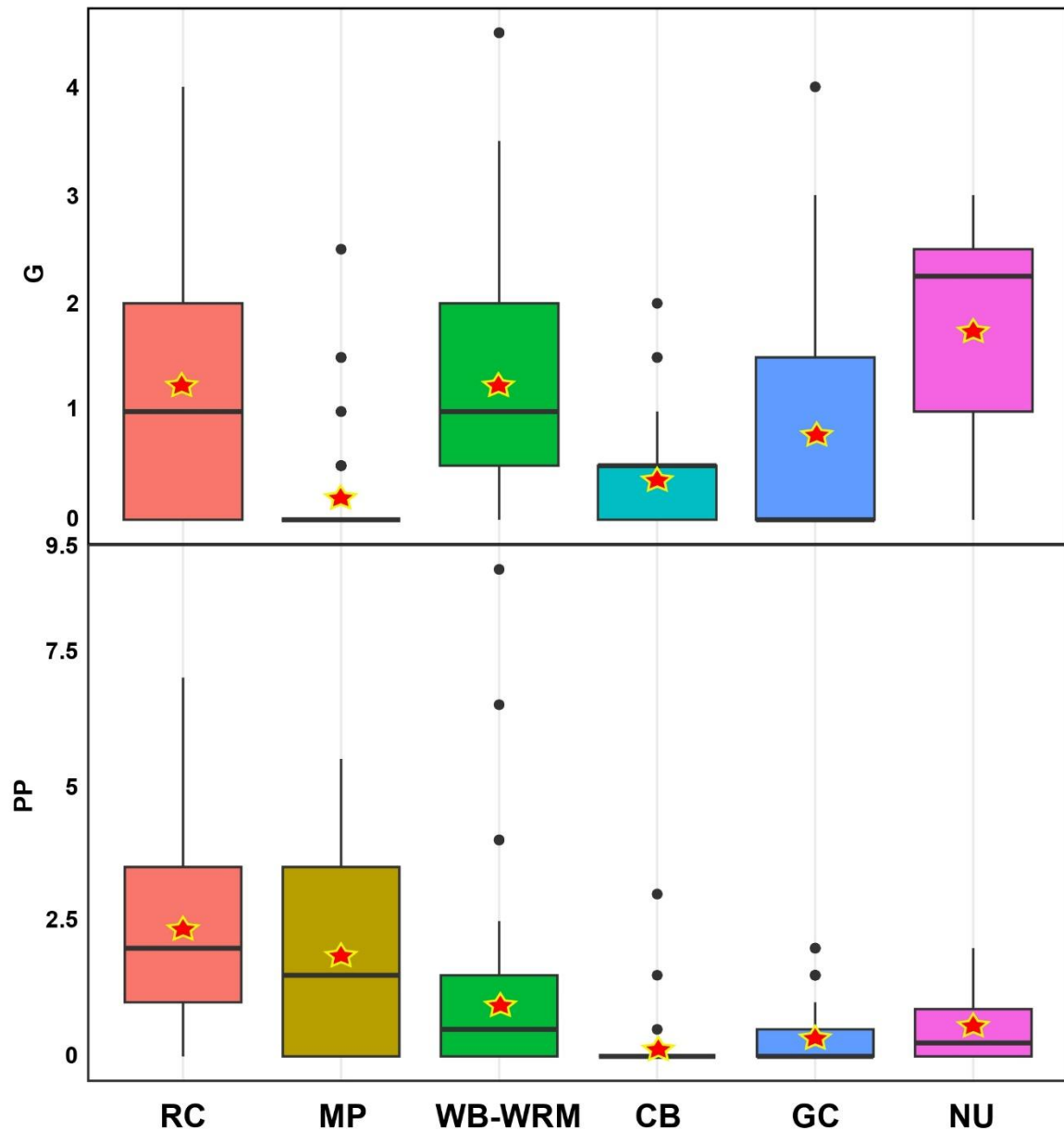


Figure 64. Boxplot displaying the distribution of the number of gouges (NG) and the number of puncture pits (NPP) for cave bear populations across regions: Romanian Carpathians (RC), Moldavian Plateau (MP), Western Balkans and Western Rhodopes Mountains (WB-WRM), Central Balkans (CB), the Greater Caucasus (GC), and the Northern Urals (NU). Red and yellow stars indicate the mean values.

6.6.5 Correspondence analysis

In order to investigate the relationships, distribution, and variability among the studied cave bear populations, a correspondence analysis (CA) by regions was conducted (Figure 65). The analysis included seven microwear variables, namely small pits, large pits, fine scratches, coarse scratches, SWS, gouges and puncture pits. The first dimension (Dim. 1) explains 50% of the variance, and the second dimension (Dim. 2) accounts for 17.7%, collectively capturing 67.7% of the total variance (Figure 65; Appendix section A.3.1, Table A8). Hence, these two dimensions were selected for analysis and visualization. Additionally, the same CA plot, but

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displaying only the 95% confidence ellipses, was generated to enhance visualization of regional-scale patterns.

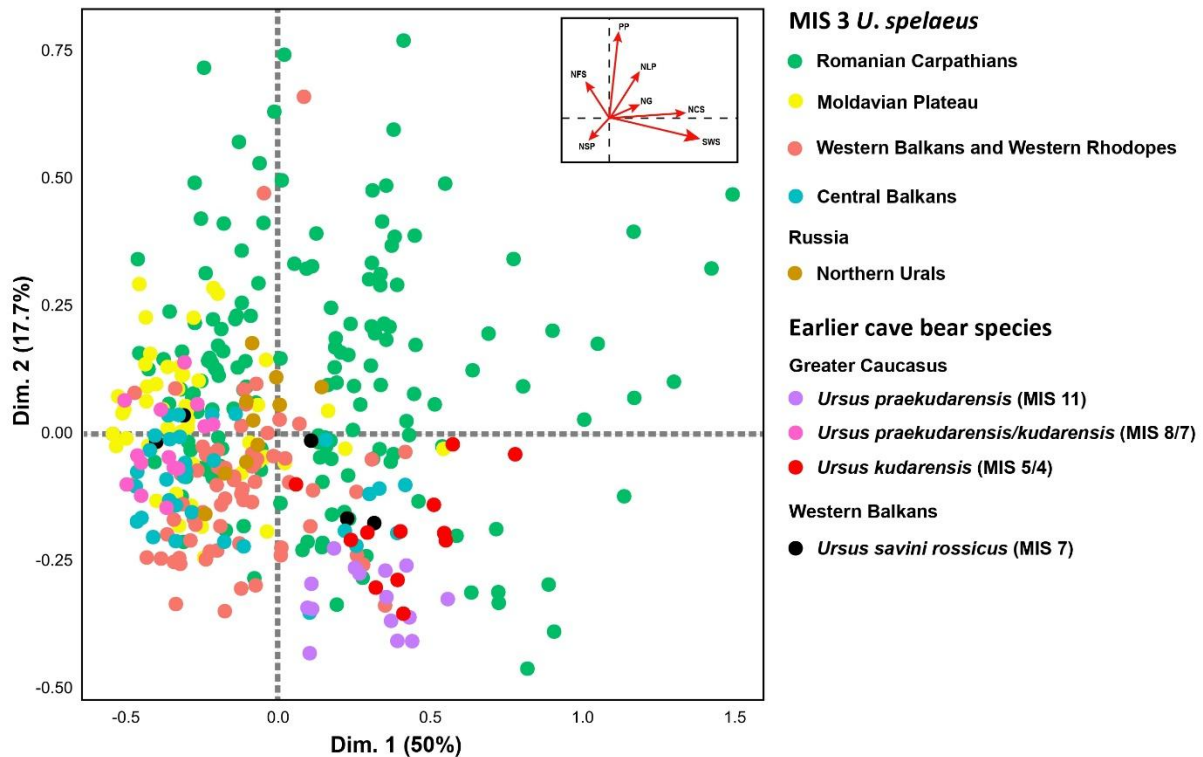


Figure 65. Correspondence analysis (CA) based on seven microwear variables: number of fine scratches (NFS), coarse scratches (NCS), small pits (NSP), large pits (NLP), gouges (NG), puncture pits (NPP), and the scratch width score (SWS). The analysis compares cave bear (*U. spelaeus* sensu lato) populations from different regions: Romanian Carpathians, Moldavian Plateau, Western Balkans and Western Rhodopes Mountains, Central Balkans and Eurasia (Northern Urals and the Greater Caucasus). The Greater Caucasus populations (*U. praekudarensis*, *U. kudarensis*, and *U. praekudarensis/kudarensis*) and *U. savini rossicus* from Western Balkans have been analysed separately due to their distinct chronological attributions.

The regions exhibit considerable overlap, although a certain degree of clustering by region is also evident (Figure 65). Among the populations analysed, the Romanian Carpathians display the broadest distribution, indicating the highest variability. This pattern is clearly visible in the 95% confidence ellipses (Figure 66), where all regional ellipses are nested within the Romanian Carpathians ellipse, with only small portions of the Central Balkans and *U. praekudarensis* ecological spaces extending slightly beyond its boundary. Furthermore, considerable overlap exists among the regions of Moldavian Plateau, Central Balkans, and Western Balkans and Western Rhodopes Mountains (Figure 66). Notably, the *U. praekudarensis/kudarensis* population falls entirely within the ecological space of Moldavian Plateau. This central area of the plot is characterized by a high number of small pits (NSP) and fine scratches (NFS), coupled with a relatively low number of coarse scratches (NCS), resulting in a low scratch width score (SWS). Additionally, puncture pits (NPP), gouges (NG), and large pits (NLP) exhibit moderate

to low frequencies in this area, indicative of diets dominated by soft mast items. In contrast, the Central Balkans and Western Balkans and Western Rhodopes Mountains populations partially extend toward the right side of the plot, overlapping with *U. kudarensis* and *U. praekudarensis*, both of which are distinctly positioned on the right side, separate from other regions (Figure 66). This right-side region is characterized by a higher prevalence of coarse scratches (NCS), thus resulting in elevated SWS values.

Consequently, two distinct microwear patterns emerge: one characterized predominantly by fine scratches, abundant small pits, and relatively low occurrences of puncture pits, gouges, and large pits (indicative of softer dietary items), and another distinguished by a higher proportion of coarse scratches and elevated SWS values, associated with the consumption of harder, potentially more carnivorous dietary items (Figure 66). Additionally, a third distinct area, occupied exclusively by Romanian Carpathian individuals, appears in the upper-right portion of the plot, characterized by elevated numbers of puncture pits and large pits (Figure 66). This microwear signature likely corresponds to a diet enriched with hard mast resources, such as seeds and tough-coated fruits, a pattern characteristic of some Romanian Carpathian populations. Finally, *U. savini rossicus* exhibits a very high degree of variability, primarily along the NCS/SWS and NFS axes; however, it also falls very close to the NG and NLP variables.

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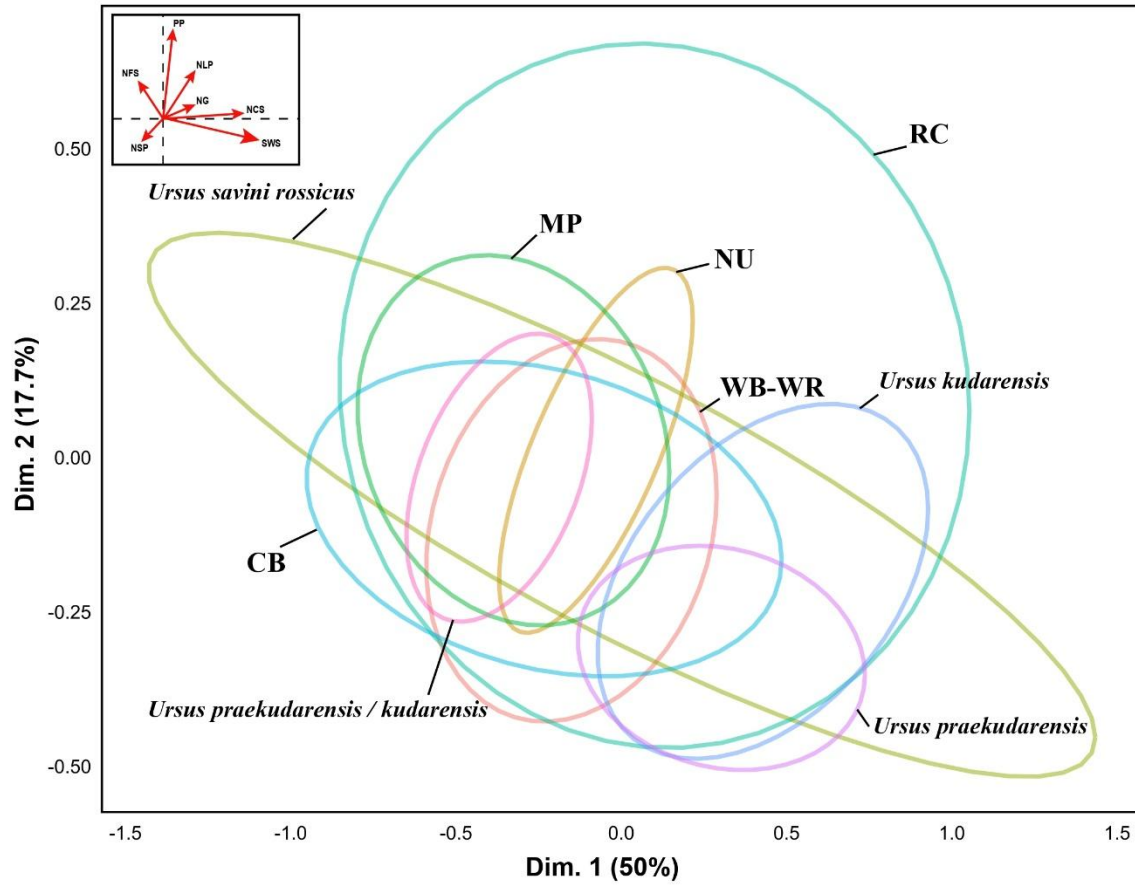


Figure 66. Correspondence analysis (CA) displaying 95% confidence ellipses based on seven microwear variables: number of fine scratches (NFS), coarse scratches (NCS), small pits (NSP), large pits (NLP), gouges (NG), puncture pits (NPP), and the scratch width score (SWS). The ellipses illustrate the spatial distribution and variability of cave bear (*U. spelaeus sensu lato*) populations among the studied regions: Romanian Carpathians (RC), Moldavian Plateau (MP), Western Balkans and Western Rhodopes Mountains (WB-WR), Central Balkans (CB), Northern Urals (NU) and Greater Caucasus. The Greater Caucasus populations (*U. praekudarensis*, *U. praekudarensis/kudarensis* and *U. kudarensis*) and *U. savini rossicus* (from Western Balkans) have been plotted separately to reflect their distinct chronological attributions.

6.6.6 Exploring correlations among microwear, climate, and geography on cave bears

To explore potential relationships between microwear variables (e.g., fine and coarse scratches), bioclimatic parameters (e.g., mean annual temperature, annual precipitation), and geographic factors (elevation, latitude, and longitude), a Pearson correlation matrix was generated (Figure 67). The corresponding r-values for each pairwise comparison are provided in detail in Appendix section A.3.3.

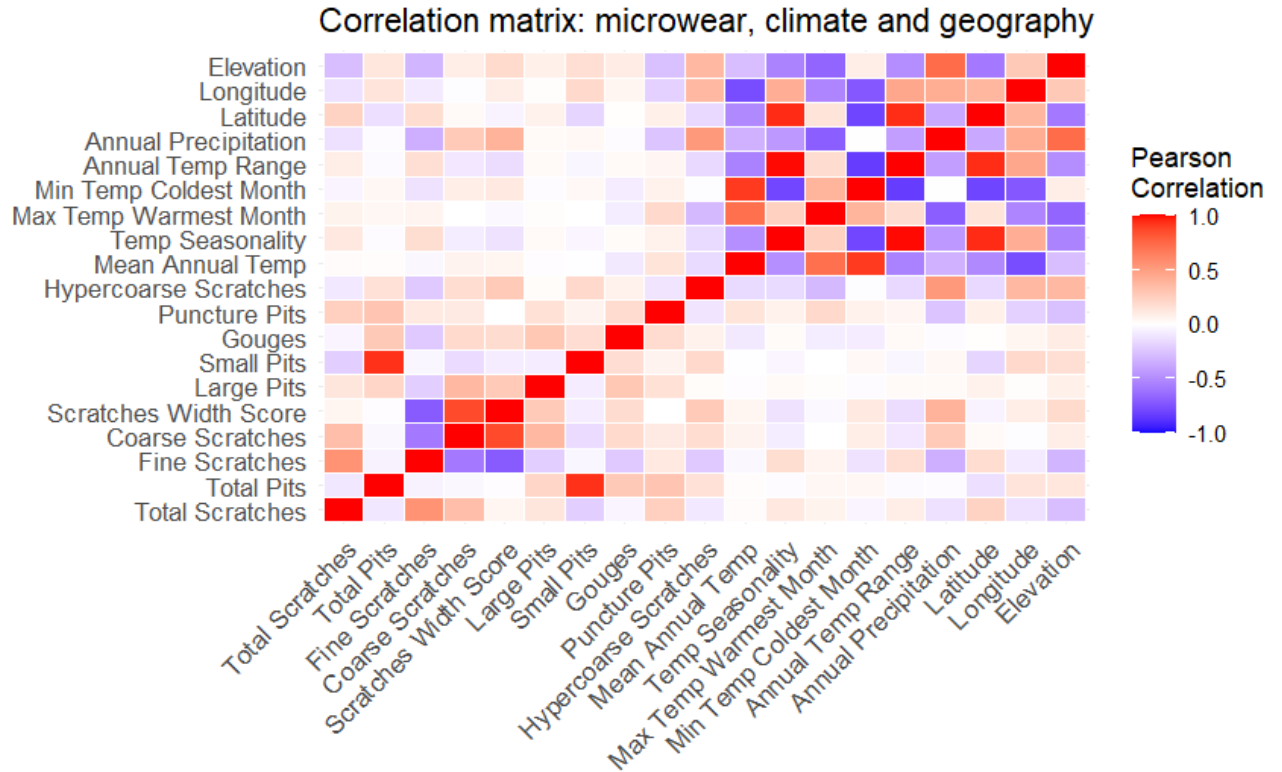


Figure 67. Pearson correlation matrix illustrating the relationships between microwear variables (e.g., fine and coarse scratches), bioclimatic parameters (e.g., annual temperature and annual precipitation), and geographic factors (elevation, latitude, longitude). Colour intensity reflects the strength and direction of the correlation, ranging from strong negative (blue) to strong positive (red). While strong correlations are observed among climatic and geographic variables (as expected), no strong associations are evident between microwear features and environmental factors.

To explore potential relationships between microwear features and environmental variables, a set of linear regression analyses was conducted focusing on variable pairs with a Pearson correlation coefficient (r) greater than ± 0.3 . Among the most notable associations were: hypercoarse scratches with annual precipitation ($r \approx +0.52$), longitude ($+0.37$), elevation ($+0.36$), and maximum temperature of the warmest month (-0.30); and the fine-to-coarse scratch ratio (a proxy for scratch width score, SWS) with annual precipitation ($r \approx -0.25$). In terms of model performance, the highest R^2 was observed between hypercoarse scratches (NHC) and annual precipitation ($R^2 = 0.27$), followed by longitude ($R^2 = 0.14$), elevation (R^2

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= 0.13), and maximum temperature of the warmest month ($R^2 = 0.09$). The model for fine-to-coarse ratio vs. annual precipitation explained approximately 6.5% of the variance ($R^2 = 0.065$).

While all of these models reached conventional thresholds of statistical significance (p -values < 0.001), their validity is undermined by systematic violations of key linear regression assumptions (Table 8). Specifically, the Shapiro-Wilk test consistently indicated non-normal residuals across all models (e.g., $W = 0.76$, $p < 2.2 \times 10^{-16}$), which challenges the assumption of normally distributed errors. Additionally, the Breusch-Pagan tests for homoscedasticity revealed significant heteroscedasticity, indicating that the variance of residuals is not constant across fitted values (e.g., $BP = 112.4$, $p < 2.2 \times 10^{-16}$ for the NHC vs precipitation model). Finally, the Durbin-Watson tests uncovered autocorrelation in residuals, suggesting dependence between observations and further compromising model reliability. Together, these diagnostic results suggest that the linear models, although statistically significant, do not meet the assumptions required.

Microwear variable	Biogeographic variable	Pearson's r (>0.3)	Normality of residuals (Shapiro-Wilk)	Homoscedasticity of residuals (Breusch-Pagan)	Independence of residuals (Durbin-Watson)
Hypercoarse scratches	annual precipitation	0.52	0.7182, $p = 2.2e-16$	112.40, $p < 2.2e-16$	1.65, $p = 0.004$
Hypercoarse scratches	longitude	0.36	0.5316, $p < 2.2e-16$	67.61, $p < 2.2e-16$	1.37, $p = 0$
Hypercoarse scratches	elevation	0.36	0.6116, $p < 2.2e-16$	56.71, $p < 2.2e-16$	1.39, $p = 0$
Hypercoarse scratches	warmest maximum temp	-0.30	0.5119, $p < 2.2e-16$	39.59, $p < 2.2e-16$	1.35, $p = 0$
Fine to coarse ratio (SWS)	annual precipitation	-0.25	0.76, $p < 2.2e-16$	3.99, $p = 0.0457$	1.65, $p = 0.004$

Table 8. Summary of Pearson's correlation coefficients (r) between microwear variables and biogeographic factors, along with diagnostic test results for regression model assumptions. The Shapiro-Wilk test assesses normality of residuals, the Breusch-Pagan test evaluates homoscedasticity, and the Durbin-Watson test detects autocorrelation. Statistically significant p -values indicate violations of model assumptions.

Consequently, the analyses did not reveal any statistically reliable associations between microwear features and the geographic or climatic context of the cave bear populations.

6.6.7 Correlation between microwear and time

No significant correlations were found between microwear variables and time, whether considering the relative stratigraphic position of levels or directly calibrated dates of the bears. Further details can be found in Appendix section A.3.4.

6.7 Evolution of seasonal dietary niches

The following two sections present the results concerning seasonal dietary evolution in short-term feeding patterns across two ursid clades. The first case focuses on the *U. kudarensis*

lineage from the Greater Caucasus (Kudaro 1 and Kudaro 3 caves), evaluating dietary changes across three populations spanning the Middle to Late Pleistocene. The second case examines temporal niche relationships between cave bears (*U. spelaeus*) and brown bears (*U. arctos*), with particular emphasis on shifts in *U. arctos* dietary patterns before and after the Last Glacial Maximum (LGM).

6.7.1 Insights into short-term dietary evolution from the Middle to Late Pleistocene of *U. kudarensis*

6.7.1.1 The Greater Caucasus (Kudaro 1 and 3)

A total of 41 lower first molars of *U. praekudarensis* ($n = 15$), *U. praekudarensis/kudarensis* ($n = 14$), and *U. kudarensis* ($n = 12$) were suitable for the analysis. Hence, 19 specimens had to be excluded from the analysis, including the youngest individuals lacking wear facets (Rivals et al., 2007) and those with occlusal surface damage attributable to taphonomic processes (King et al., 1999; El-Zaatari, 2010; Uzunidis et al., 2021; Micó et al., 2024).

The microwear results from *U. preakudarensis*, *U. praekudarensis/kudarensis*, and *U. kudarensis* displayed differences between them (Table 9). Regarding the number of total scratches (NTS), *U. preakudarensis* displayed the lowest number (NTS = 14.07), while *U. praekudarensis/kudarensis* (NTS = 18.89) and *U. kudarensis* (NTS = 18.63) displayed similar averages. Furthermore, there was a prevalence of coarse scratches, which translates into a high scratch width score (SWS) for both *U. praekudarensis* (NFS = 5.67; NCS = 8.57; SWS = 1.53) and *U. kudarensis* (NFS = 7.46; NCS = 11.25; SWS = 1.75). Conversely, *U. praekudarensis/kudarensis* exhibited a prevalence of fine scratches (NFS = 17.36; NCS = 1.50) with a SWS of 0.

The presence of hypercoarse scratches was observed in all three samples (Figure 68). Among *U. kudarensis* individuals, 83% displayed hypercoarse scratches, followed by 47% of *U. praekudarensis* specimens. In much lower proportions, 14% of the *U. praekudarensis/kudarensis* specimens displayed such hypercoarse scratches.

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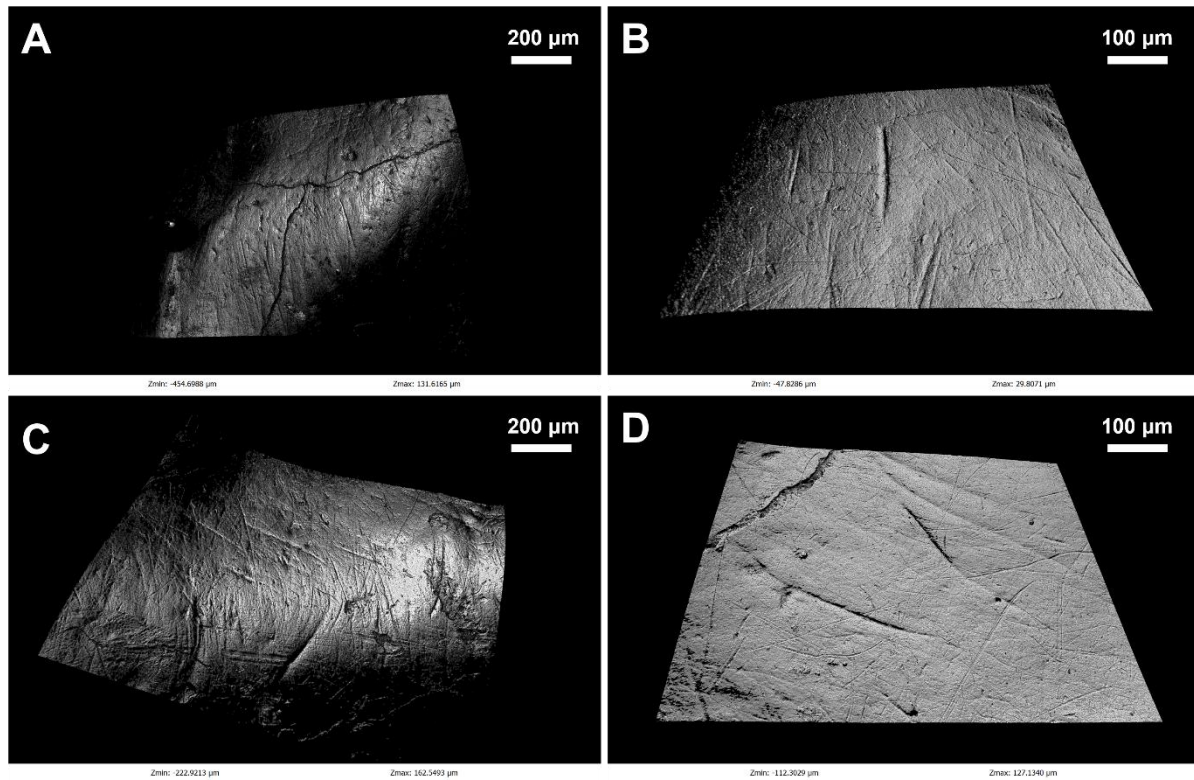


Figure 68. Three-dimensional scans of the occlusal surface of the talonid of the lower first molar (m1) of different cave bear specimens from the Kudaro caves performed by a Sensofar® S Neox microscope. A: Surface topography (employing a $\times 10$ lens) of the occlusal surface of *U. praekudarensis/kudarensis* (ZIN 3758-1127) from Kudaro 3 layer 3, displaying both fine and coarse scratches, although with a predominance of fine scratches. Some gouges can also be observed. B: Surface topography (employing a $\times 20$ lens) of *U. praekudarensis* (ZIN 37957-1417) from Kudaro 1, layer 5c, displaying hypercoarse scratches in addition to coarse and fine scratches. C: Surface topography (employing a $\times 10$ lens) of *U. kudarensis* (ZIN 37954-37) from Kudaro 3 layer 4, showing a majority of coarse scratches compared to fine scratches. Additionally, two hypercoarse scratches, as well as multiple gouges, puncture pits, and large pits, can be observed. D: Surface topography (employing a $\times 20$ lens) of *U. praekudarensis* (ZIN 37998-83) from Kudaro 1, layer 5c, which displays two hypercoarse scratches.

Concerning the total number of pits (NTP), the highest averages are exhibited by *U. praekudarensis* (NTP = 37.10) and *U. kudarensis* (NTP = 35.88), which closely resemble each other. In contrast, the lowest counts are exhibited by *U. praekudarensis/kudarensis* (NTP = 21.71), with notably lower counts than the other two populations. In all three populations, small pits (NSP) prevail in comparison to large pits (NLP): *U. praekudarensis* with NSP = 35.10; NLP = 2.00, *U. praekudarensis/kudarensis* with NSP = 20.93; NLP = 0.79, *U. kudarensis* with NSP = 33.38; NLP = 2.50. *U. kudarensis* exhibits the highest number of large pits (NLP = 2.50), closely followed by *U. praekudarensis* (NLP = 2.00), while *U. praekudarensis/kudarensis* displays the lowest number (NLP = 0.79). The three samples exhibited gouges, with the highest numbers observed in *U. kudarensis* (NG = 2.38), followed by *U. praekudarensis* (NG = 0.20) and *U. praekudarensis/kudarensis* (NG = 0.21). The highest number of puncture pits (NPP) were observed in *U. kudarensis*, with an average of 0.83 puncture pits per counting area. This was followed by *U. praekudarensis*, with an average of 0.40 puncture pits per counting area. In contrast, *U. praekudarensis/kudarensis* displayed no puncture pits.

Species – (Location)	<i>N</i>	NFS	NCS	NTS	SWS	NLP	NSP	NPP	NTP	NG	NHC%
Extinct											
<i>U. praekudarensis</i>	15	5.67	8.57	14.07	1.53	2.00	35.10	0.40	37.10	0.20	47%
<i>U. praekudarensis/kudarensis</i>	14	17.36	1.50	18.89	0.00	0.79	20.93	0.00	21.71	0.21	14%
<i>U. kudarensis</i>	12	7.46	11.25	18.63	1.75	2.50	33.38	0.83	35.88	2.38	83%
Extant											
<i>U. americanus</i> (North America)	9	13.56	2.56	16.12	0.00	5.44	19.00	3.00	27.44	0.00	0%
<i>U. arctos</i> (Greece)	4	13.00	7.00	20.00	0.5	9.25	8.50	2.25	20.00	2.00	0%
<i>U. arctos</i> (Central Europe)	10	17.50	3.40	20.90	0.00	5.4	22.50	8.30	36.20	2.10	0%
<i>U. arctos</i> (North America)	8	18.25	3.00	21.25	0.00	6.75	18.38	3.25	28.38	0.25	0%
<i>U. arctos</i> (Kamchatka)	23	16.22	3.83	20.05	0.10	6.96	19.78	4.78	31.52	0.35	0%
<i>U. arctos</i> (Northern Europe)	9	15.78	3.78	19.56	0.00	6.44	23.33	2.67	32.44	0.22	0%
<i>A. melanoleuca</i>	4	19.25	0.00	19.25	0.00	8.50	46.25	0.00	54.75	0.00	0%
<i>U. maritimus</i>	13	11.00	3.21	14.23	2.79	4.50	16.21	0.07	20.15	0.00	100%
<i>U. thibetanus</i>	6	14.33	3.33	15.33	0.00	4.50	15.33	0.00	20.33	17.67	0%

Table 9. Comparison of the dental microwear results of the cave bear populations from the Kudaro caves, *U. praekudarensis* (Kudaro 1; layer 5c), *U. praekudarensis/kudarensis* (Kudaro 3; layer 5), and *U. kudarensis* (Kudaro 3; layer 4), with the reference dataset of extant bear species of *U. arctos*, *U. americanus*, *A. melanoleuca*, *U. maritimus* and *U. thibetanus* established by Pappa et al. (2019). Abbreviations: *N* = number of specimens, NFS = number of fine scratches, NCS = number of coarse scratches, NTS = number of total scratches, SWS = scratch width score, NLP = number of large pits, NSP = number of small pits, NPP = number of puncture pits, NTP = number of total pits, NG = number of gouges, NHC% = presence of hypercoarse scratches.

6.7.1.2 Comparison with extant bears

When compared to the extant bear populations (Table 9), *U. praekudarensis* presents the lowest number of total scratches (NTS = 14.07), closely followed by the *U. maritimus* with 14.23 scratches. *U. praekudarensis/kudarensis* (NTS = 18.89) and *U. kudarensis* (NTS = 18.63), also display a low number of total scratches compared to extant bears. Only *U. maritimus* (NTS = 14.23) and *U. americanus* (NTS = 16.12) present lower counts. The average of both fossil populations is comparable to that of *A. melanoleuca* (NTS = 19.25) and *U. arctos* from Northern Europe (NTS = 19.56). The scratch distribution for *U. praekudarensis* and *U. kudarensis* favours coarse scratches, which differs from that observed in extant bear populations. Furthermore, the SWS of both populations is the highest in comparison to extant bears, only surpassed by *U. maritimus* (SWS = 2.79). Conversely, the *U.*

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praekudarensis/kudarensis population exhibits a higher proportion of fine scratches in comparison to coarse scratches, with a SWS value of 0.

Regarding the total number of pits, *U. praekudarensis* (NTP = 37.10) and *U. kudarensis* (NTP = 35.88) exhibited high numbers that are comparable to that of *U. arctos* from Central Europe (NTP = 36.10). Conversely, *U. praekudarensis/kudarensis* exhibited a low number of pits, similar to that observed in *U. arctos* from Greece and *U. maritimus*. Furthermore, *U. praekudarensis* and *U. kudarensis* displayed a very high number of small pits, only surpassed by *A. melanoleuca*, while the number of large pits were observed to be lower than the extant specimens. *U. kudarensis* exhibited a number of gouges comparable to that of *U. arctos* from Central Europe, although slightly higher. In contrast, *U. praekudarensis* and *U. praekudarensis/kudarensis* displayed a number of gouges similar to that of *U. arctos* from Northern Europe and North America. With regard to puncture pits (NPP), the *U. praekudarensis* and *U. kudarensis* fossil populations displayed a relatively low number compared to extant species.

Finally, concerning the presence of hypercoarse scratches, these were observed in all fossil populations although with different percentages: *U. kudarensis*, HC = 83%; *U. praekudarensis*, HC = 47%; and *U. praekudarensis/kudarensis*, HC = 14%. These particular features are exclusively exhibited by the extant *U. maritimus*, which has a carnivorous diet of marine mammals, presenting them in all individuals of its sample (HC = 100%).

6.7.1.3 Dietary inference

6.7.1.4 Bivariate analysis of the total number of scratches and pits

The bivariate plot of the number of total pits (which includes the count of small and large pits as well as puncture pits) and the number of total scratches (accounting for the sum of fine and coarse scratches) shows that the three fossil populations' distribution closely relates them to dietary regimes of extant bear species (Figure 69). The extant bear populations distribute themselves according to their main dietary preferences (omnivorous with a preference for soft mast, hard mast or vertebrates, and a pure herbivorous diet). The omnivorous bears, including *U. arctos* and *U. americanus*, are distributed across three different regions of the plot which can be related to their main dietary preferences. First, the soft mast-specialized *U. arctos* from Greece is positioned on the left side of the plot, with a low number of pits and a high number of scratches. Close to it, though with a slightly lower number of scratches, is *U. thibetanus*, which also has a predominantly plant-based diet. Second, *U. arctos* from northern latitudes

with a higher proportion of vertebrates in their diet (from Northern Europe, North America, and Kamchatka) fall within the middle range of the plot. Third, *U. arctos* from Central Europe, with a hard mast diet, falls within the right side of the plot, accounting for a high number of total pits. Nevertheless, its range also overlaps with the vertebrate-dominated diet populations, due to its significant proportion of vertebrates in its diet. *U. maritimus* has a specialised marine mammal diet in an arctic landscape; therefore, with a lack of vegetation resources and a very soft diet that does not include rough plant items, it falls on the left side of the plot, with a number of total pits comparable to that of soft mast-dominated *U. arctos* from Greece. However, because *U. maritimus* inhabits a landscape lacking in vegetation, it presents a comparatively lower number of scratches, features that are directly related to a phytophagous diet (Solounias and Semprebon 2002), and falls within the lower part of the plot.

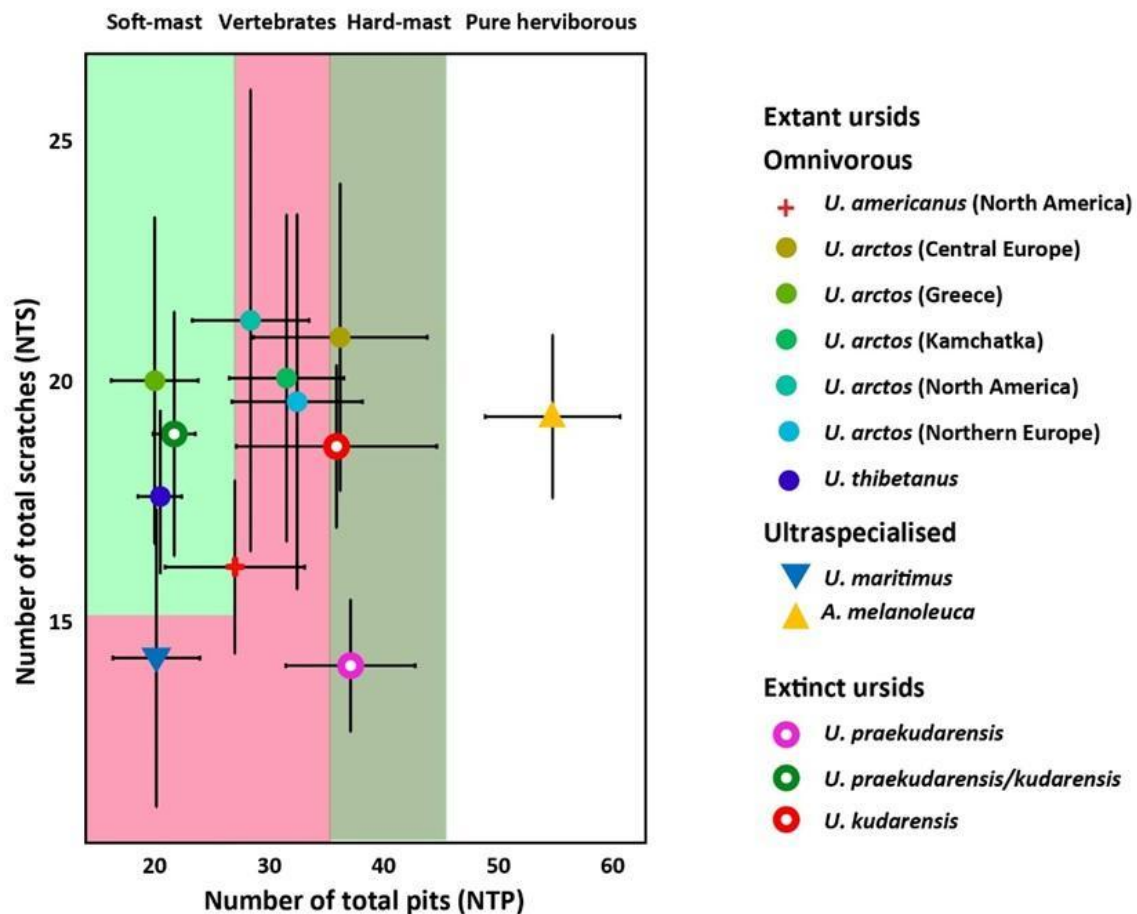


Figure 69. Bivariate plot of the average number of total pits (NTP) and the number of total scratches (NTS) comparing the extant bear populations and the fossil populations. Error bars representing the standard deviation within the populations were added. Highlighted are four distinct eco-regions (soft mast, hard mast, vertebrates, and pure herbivorous) based on the predominant diet of extant bear populations as established by Pappa et al. (2019).

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U. americanus from Alaska, which inhabits a semi-arctic landscape and occasionally consumes vertebrates, particularly fish, falls between the vertebrate-dominated northern latitude populations and the soft mast-dominated population from Greece. Due to a low number of scratches, it falls not far from *U. maritimus*. Finally, *A. melanoleuca*, having an extremely hard and abrasive diet, based on bamboo, which is very rich in phytoliths, appears isolated in the rightmost of the plot due to the very high number of total pits (NTP = 54.75).

Regarding the fossil samples, *U. praekudarensis* and *U. kudarensis*, due to their high total number of pits, fall within the hard mast-dominated diet area, comparable to that of *U. arctos* from Central Europe. The variability ranges of *U. kudarensis* also overlap with those of omnivorous bear species of northern latitudes, including both hard and soft mast, although with a higher proportion of vertebrates in their diet. As for *U. praekudarensis*, while also partially falling within the range of omnivorous bears that include vertebrates, due to its low number of total scratches, it plots at the same height on the graph as *U. maritimus*, albeit with a much higher proportion of total pits. Finally, concerning *U. praekudarensis/kudarensis*, it is situated within the soft mast-dominated region, close to *U. arctos* from Greece, due to its low number of total pits. However, the extant *U. arctos* population from Greece presents a slightly higher total number of scratches.

6.7.1.5 Correspondence analysis

To illustrate the distribution and variability of the studied populations, a correspondence analysis (CA) was conducted. The analysis incorporated seven microwear variables, namely small pits, large pits, fine scratches, coarse scratches, SWS, gouges, and puncture pits. The microwear signal of the fossil samples was compared with a reference dataset. The results for the first two dimensions (i.e., Dim 1 and Dim 2), which exhibited 44.6% and 22.4% of variance respectively, capturing the 67% of the total variance (Figure 70; Appendix section A.3.1, Table A9), were utilised and plotted.

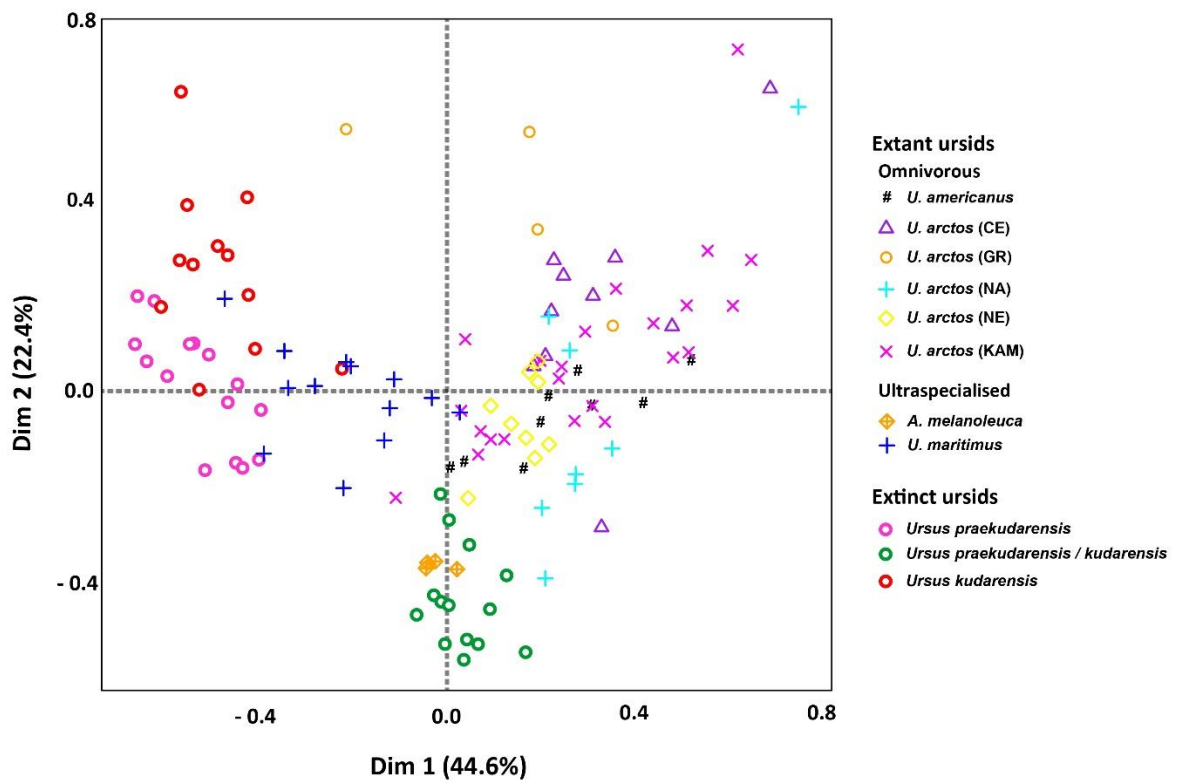


Figure 70. Correspondence analysis using seven microwear variables, namely the number of fine and coarse scratches, small and large pits, gouges, puncture pits, and the scratch width score. Comparison of the fossil populations of the Kudaro Caves, including the Middle Pleistocene *U. praekudarensis* (layer 5c from Kudaro 1) and *U. praekudarensis/kudarensis* populations (layer 5 from Kudaro 3), as well as the Late Pleistocene *U. kudarensis* (layer 4 from Kudaro 3), with the extant bear populations. Abbreviations: CE = Central Europe; GR = Greece; NA = North America; NE = North Europe; KAM = Kamchatka.

The CA reveals that the extant omnivorous bear populations, including *U. arctos* and *U. americanus*, exhibit a similar distribution pattern (Figure 70). However, hard mast-dominated populations, primarily represented by *U. arctos* from Central Europe, tend to be distributed in the upper-right part of the plot due to their higher presence of puncture pits, gouges, and large pits. Omnivorous populations from northern latitudes with a high component of vertebrates and soft mast items in their diet, such as *U. arctos* from Northern Europe and *U. americanus* from Alaska, are situated around and under the Dim 1 axis, hence in the middle to lower part of the clustering due to their predominance of small pits and fine scratches. Furthermore, bears with highly variable omnivorous diets, including hard and soft mast as well as vertebrates and invertebrates, are distributed vertically along the omnivore bears' grouping (i.e., *U. arctos* from Kamchatka and *U. arctos* from North America).

The *U. arctos* population from Greece stands out as a significant outlier, due to its Mediterranean latitude specialised soft mast diet, which positions it alone in the upper part of the plot. This unique placement is due to its distinct characteristics. Having the lower number

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of small pits and the highest number of large pits makes it fall within a higher position in comparison to the other omnivorous ursids. Moreover, its high number of coarse scratches in comparison to the other omnivorous bear species positions it in the central part of the plot.

Finally, it can be observed that the highly specialised bear species, the hypercarnivore *U. maritimus* and the highly abrasive diet of *A. melanoleuca*, also occupy distinct positions in the plot. *U. maritimus* is distinguished by its high SWS, while *A. melanoleuca* is characterised by the highest number of small pits and fine scratches above all extant bear populations.

Regarding the cave bears from the Kudaro caves, namely *U. praekudarensis* (Kudaro 1; layer 5c), *U. praekudarensis/kudarensis* (Kudaro 3; layer 5), and *U. kudarensis* (Kudaro 1; layer 4), those fall within three distinct regions of the CA plot (Figure 70).

U. praekudarensis/kudarensis falls within the lower central part of the plot. This is due to the high number of fine scratches in comparison to coarse scratches, and the absence of puncture pits, and the almost absence of large pits and gouges. Hence, *U. praekudarensis/kudarensis* overlaps with *A. melanoleuca* with a highly abrasive, herbivorous diet. Furthermore, *U. praekudarensis/kudarensis* overlaps partially with omnivorous bears inhabiting northern latitudes, like *U. arctos* from Northern Europe and North America as well as *U. americanus* from Alaska, which predominantly consume soft mast items in their diets as well as vertebrates. Finally, *U. praekudarensis/kudarensis* falls close to *U. maritimus*, which is specialised in consuming marine fauna.

Conversely, *U. praekudarensis* and *U. kudarensis* individuals are positioned on the left side of the plot, distancing themselves from the extant omnivorous bear populations on the left side of the Dim 2 axis. This can be attributed to their higher count of coarse scratches compared to a lower number of fine scratches, resulting in a high SWS. Consequently, they exhibit partial overlap with *U. maritimus*, which also displays a high SWS. Nevertheless, the two species fall within two different regions of the CA plot, while partially overlapping.

On the one hand, regarding the Dim 1 axis, *U. kudarensis* falls within the upper half of the extant omnivorous bear cluster, which includes omnivorous species that predominantly consume hard mast items, driven by a higher amount of gouges and puncture pits, i.e., *U. arctos* from Central Europe, which also has a high consumption of vertebrates (Rigg and Gorman, 2005; Bojarska and Selva, 2012). Hence, *U. kudarensis* displays an uppermost distribution among fossil populations, which can be attributed to the highest counts for gouges across both fossil and extant bears, as well as displaying the highest counts for puncture pits and large pits

compared to the other cave bear species. Therefore, it is suggested that *U. kudarensis* individuals would have had an omnivorous diet with an overall predominance for hard mast items in their diets.

On the other hand, *U. praekudarensis* falls within a lower range in comparison to *U. kudarensis*, extending beyond the Dim 1 axis. This closely associates it with omnivorous bear populations with highly variable omnivorous diets including both hard and soft mast items as well as vertebrates and invertebrates (i.e., *U. arctos* from Kamchatka, Northern Europe and North America, as well as *U. americanus*). Consequently, *U. praekudarensis* exhibits an omnivorous diet characterised by high flexibility, very similar to the range exhibited by *U. arctos* from Kamchatka (Bergman, 1936; Kistchinski, 1972; Vereschagin, 1976; Krechmar, 1995) and *U. arctos* from Northern Europe (Elgmork and Kaasa, 1992; Persson et al., 2001; Bojarska and Selva, 2012), as well as *U. arctos* from North America (Mattson, 1998; Hilderbrand et al., 1999; Mowat and Heard, 2011) and *U. americanus* (Hatler, 1967; Raine and Kansas, 1990). Consequently, *U. praekudarensis* would have exhibited a high degree of variability in the nature of the items consumed, ranging from hard mast to soft mast as well as vertebrates and invertebrates. However, most of its individuals fall within the upper part of the Dim 1 axis, while partially overlapping with *U. kudarensis*, indicating an overall predominant preference for consumption of hard mast items.

6.7.1.6 Ecological niche interactions: comparison with *U. thibetanus*

To identify potential ecological-niche interactions between the studied fossil populations (*U. praekudarensis*, *U. praekudarensis/kudarensis* and *U. kudarensis*) and *U. thibetanus*, a correspondence analysis (CA) was performed (Figure 71). The same seven microwear variables utilized in the section 4.3.1 CA were employed. The microwear signal of the fossil samples was compared with population of extant *U. thibetanus* ($n = 6$) from Asia temperate latitudes (Japan and Tibet) (Pappa et al., 2019). The results for the first two dimensions (i.e., Dim 1 and Dim 2), which exhibited 65.9% and 15.7% of variance respectively, hence capturing the 81.6% of the total variance, were utilised and plotted (Figure 71; Appendix section A.3.1, Table A10).

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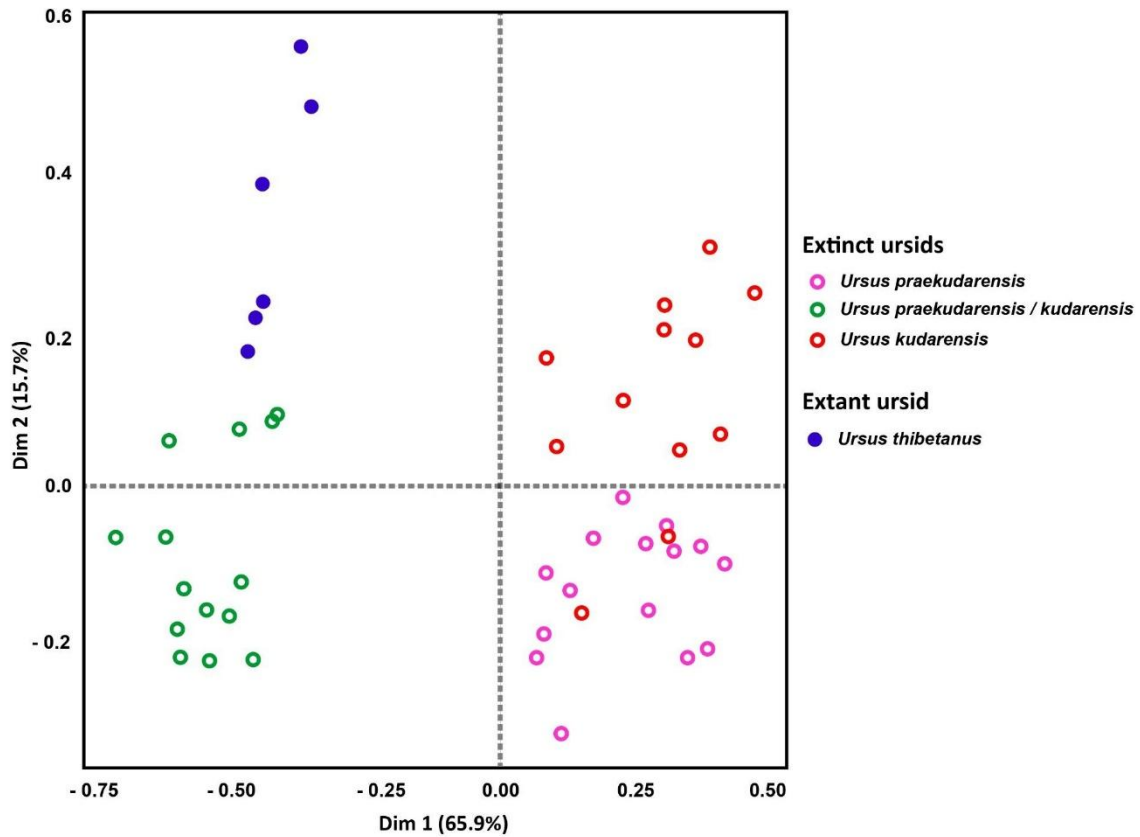


Figure 71. Correspondence analysis employing seven microwear variables, namely the number of fine and coarse scratches, small and large pits, gouges, puncture pits, and the scratch width score. Comparison of the fossil populations of the Kudaro Caves, including the Middle Pleistocene *U. praekudarensis* (layer 5c from Kudaro 1) and *U. praekudarensis/kudarensis* (layer 5 from Kudaro 3) populations, as well as the Late Pleistocene *U. kudarensis* (layer 4 from Kudaro 3) with extant *U. thibetanus* sample from Pappa et al. 2019.

The CA plot reveals previously observed differences among the three studied populations, with *U. praekudarensis* and *U. kudarensis* displaying partial overlap and *U. praekudarensis/kudarensis* separating from them (Figure 71). When plotted alongside the extant *U. thibetanus*, it is evident that although *U. thibetanus* distances itself from the three fossil populations, the degree of differentiation varies. On one hand, while *U. praekudarensis* and *U. kudarensis* significantly distance themselves from *U. thibetanus* along the most significant dimension (Dim 1), which explains 65.9% of the variance, *U. praekudarensis/kudarensis* overlaps with *U. thibetanus*, falling within the same area on the x-axis (Figure 71). The similarity between *U. praekudarensis/kudarensis* and *U. thibetanus* is driven by a high number of fine scratches and a low number of coarse scratches, resulting in an SWS of 0 for both populations. In contrast, *U. praekudarensis* and *U. kudarensis* display a significantly lower number of fine scratches and a higher number of coarse scratches, with higher SWS values. Furthermore, they exhibit the presence of puncture pits, which are absent in both *U. praekudarensis/kudarensis* and *U. thibetanus* (Table 9).

The microwear pattern observed in *U. praekudarensis/kudarensis* and in *U. thibetanus* reveals similar dietary characteristics within the predominantly herbivorous diet ecological niche (Furusaka et al., 2017; Panthi et al., 2019; Basnett et al., 2021).

6.7.2 Brown bears short-term dietary evolution: from cave bear coexistence to post-extinction contexts

To assess dietary differences and ecological interactions between cave bears (*U. spelaeus*) and brown bears (*U. arctos*) during the MIS 3, as well as the dietary evolution of *U. arctos* from the Pleistocene to the Holocene, microwear patterns were analysed across all studied populations. These populations included *U. spelaeus* ($n = 321$) and *U. arctos* from MIS 3 ($n = 6$), excluding earlier MIS populations (*U. praekudarensis* from MIS 11, *U. savini rossicus* from MIS 7, *U. praekudarensis/kudarensis* from MIS 7/8, and *U. kudarensis* from MIS 5/4), as well as Holocene *U. arctos* from Romanian Carpathians ($n = 3$). Although the sample size for *U. arctos* is limited, it remains sufficient for detecting general dietary trends and differences through time.

6.7.2.1 Bivariate analyses

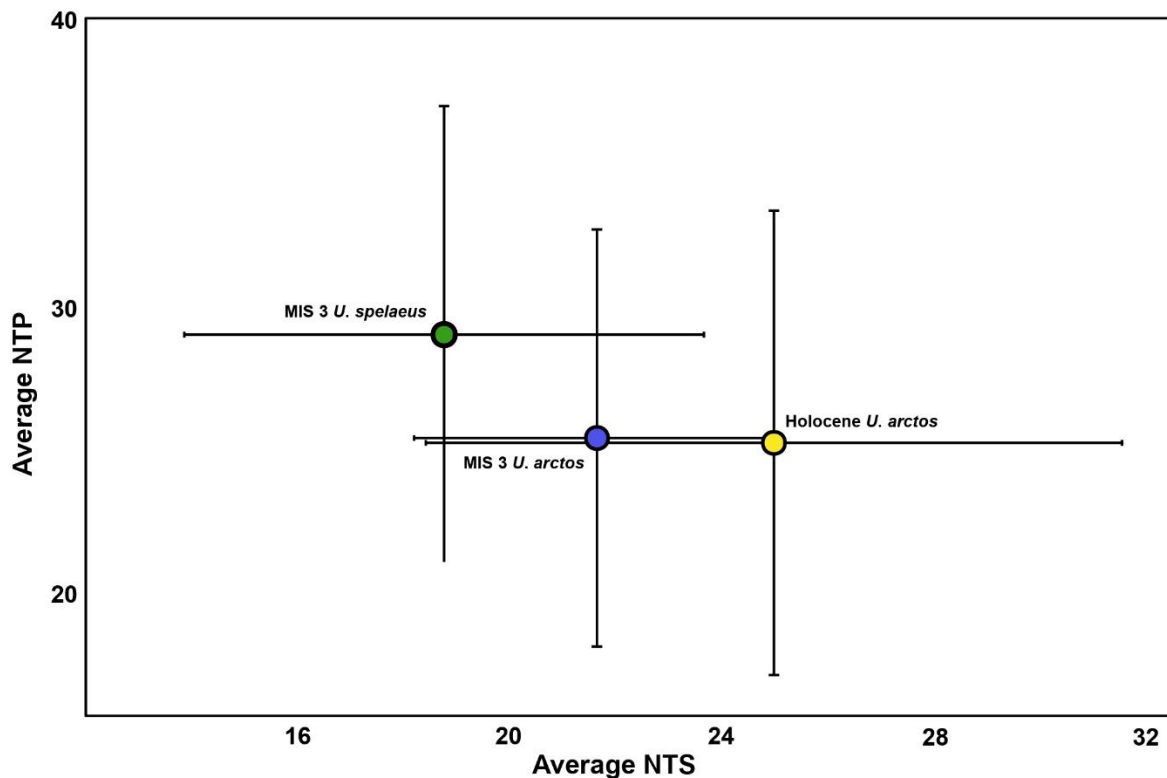


Figure 72. Bivariate plot displaying the relationship between the average number of total scratches (NTS) (x-axis) and total pits (NTP) (y-axis) across different bear populations: MIS 3 *U. spelaeus* (in green; $n = 321$), MIS 3 *U. arctos* (in blue; $n = 6$), and Holocene *U. arctos* from the Romanian Carpathians (in yellow; $n = 3$). Error bars represent the standard deviation for each population.

Regarding the number of total scratches (NTS) and the number of total pits (NTP), the three macro-populations present some degree of difference that can be interpreted as occupying different ecological niches (Figure 72); however, their error bars overlap to some extent. The Holocene *U. arctos* population displays the highest mean number of total scratches (NTS), as

well as the widest and highest NTS distribution. *U. arctos* from MIS 3 overlaps with the lower half of the Holocene *U. arctos* NTS distribution and with the upper half of the MIS 3 *U. spelaeus* NTS distribution, representing a middle position (Figure 72). *U. spelaeus* from MIS 3 exhibits the lowest NTS mean, although its error bars overlap at their upper end with MIS 3 *U. arctos*.

Regarding NTP, *U. arctos* from the Holocene overlaps with MIS 3 *U. arctos*, with an identical average and distribution (Figure 72). Conversely, MIS 3 *U. spelaeus* presents a slightly higher mean number of total pits (NTP) compared to the other two *U. arctos* groups, although with some overlap.

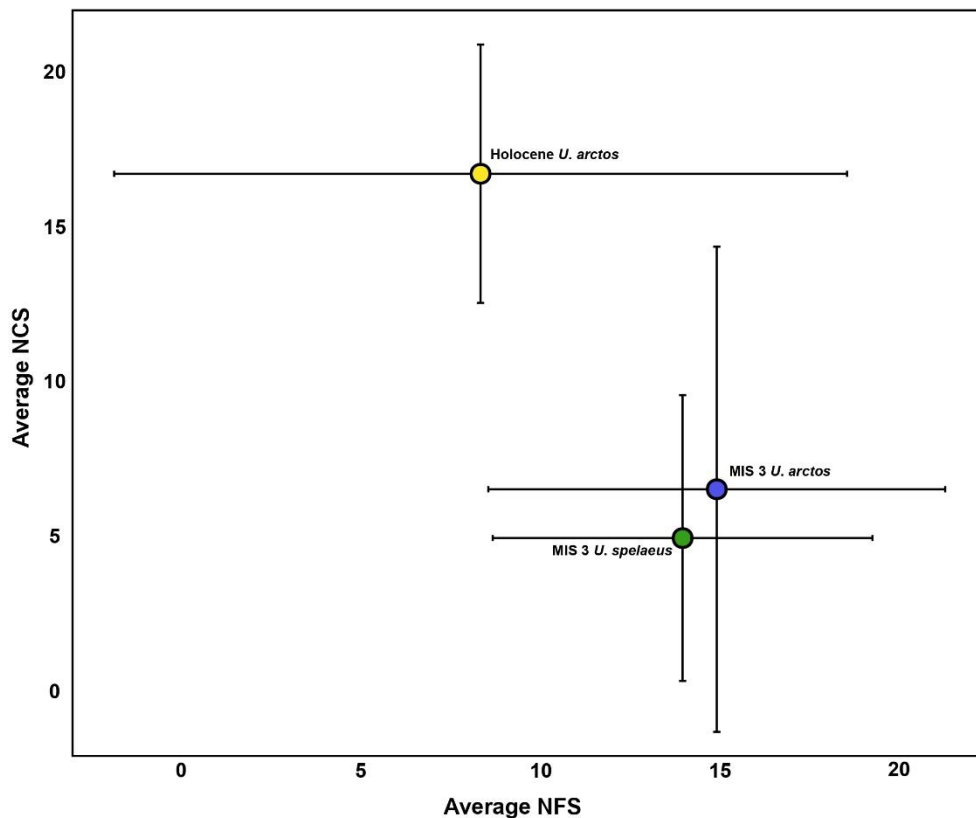


Figure 73. Bivariate plot displaying the relationship between the average number of fine scratches (NFS) (x-axis) and coarse scratches (NCS) (y-axis) across different bear populations: MIS 3 *U. spelaeus* (in green; $n = 321$), MIS 3 *U. arctos* (in blue; $n = 6$), and Holocene *U. arctos* from the Romanian Carpathians (in yellow; $n = 3$). Error bars represent the standard deviation for each population.

Concerning the number of fine scratches (NFS) and coarse scratches (NCS), a clear differentiation is observed (Figure 73). MIS 3 *U. spelaeus* and MIS 3 *U. arctos* exhibit overlapping patterns, both showing high averages of fine scratches and relatively low numbers of coarse scratches. However, MIS 3 *U. arctos* displays a slightly wider and higher NCS

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distribution compared to *U. spelaeus*. In contrast, Holocene *U. arctos* stands out by exhibiting notably higher numbers of coarse scratches.

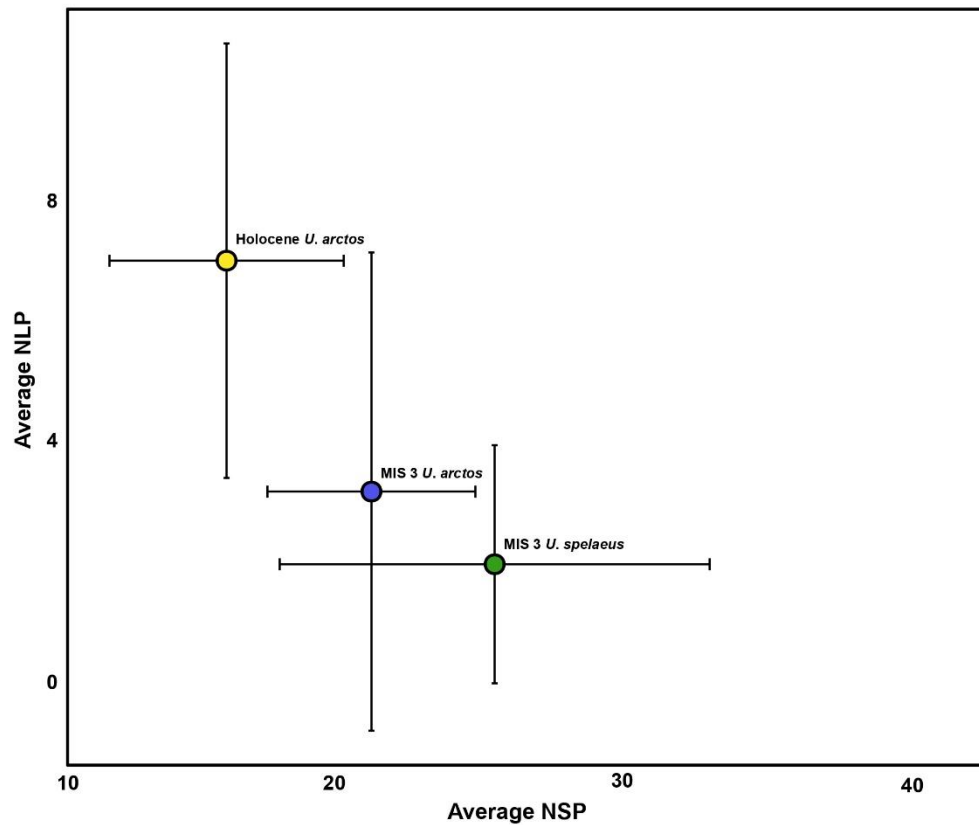


Figure 74. Bivariate plot displaying the relationship between the average number of small pits (NSP) (x-axis) and large pits (NLP) (y-axis) across different bear populations: MIS 3 *U. spelaeus* (in green; $n = 321$), MIS 3 *U. arctos* (in blue; $n = 6$), and Holocene *U. arctos* from the Romanian Carpathians (in yellow; $n = 3$). Error bars represent the standard deviation for each population.

Regarding the number of small pits (NSP) and large pits (NLP), the three groups are differentiated in mean number, although with some overlap in error bars (Figure 74). Holocene *U. arctos* exhibits the highest average number of NLP and a slightly lower NSP compared to the MIS 3 populations. Conversely, MIS 3 *U. spelaeus* and *U. arctos* show higher NSP values paired with lower NLP counts, with overlapping error bars. Specifically, MIS 3 *U. spelaeus* presents significantly lower NLP averages compared to MIS 3 *U. arctos*, though its error bars extend upwards, partially overlapping with the lower-most range of Holocene *U. arctos*. Finally, *U. spelaeus* has notably higher NSP counts than MIS 3 *U. arctos*, with broader error bars extending towards higher values, whereas MIS 3 *U. arctos* demonstrates a narrower variability range (Figure 74).

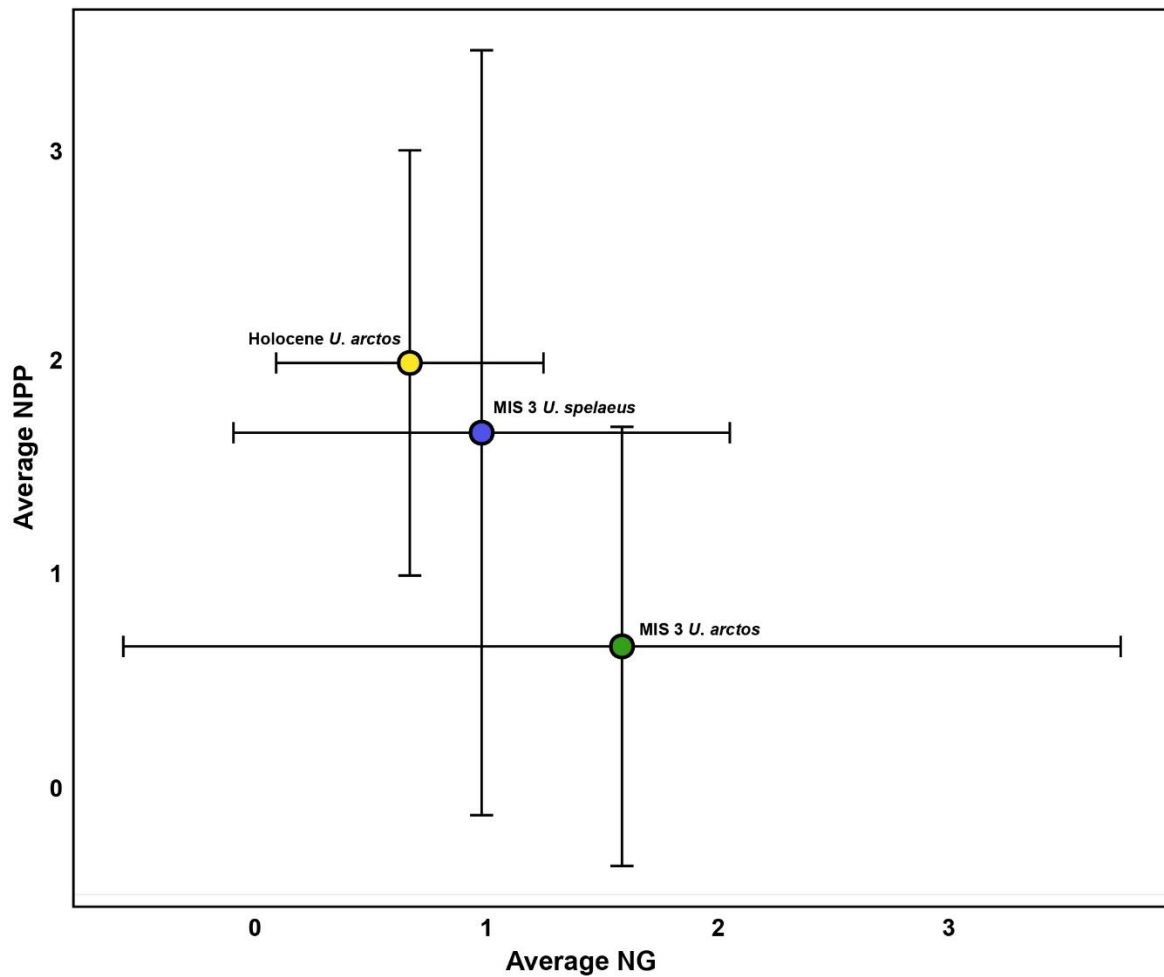


Figure 75. Bivariate plot displaying the relationship between the average number of gouges (NG) (x-axis) and puncture pits (NPP) (y-axis) across different bear populations: MIS 3 *U. spelaeus* (in green; $n = 321$), MIS 3 *U. arctos* (in blue; $n = 6$), and Holocene *U. arctos* from the Romanian Carpathians (in yellow; $n = 3$). Error bars represent the standard deviation for each population.

Regarding the number of gouges (NG) and puncture pits (NPP), the three groups present notable differences (Figure 75). While the Holocene *U. arctos* exhibits the highest average number of NPP, it maintains a relatively low NG count. Conversely, MIS 3 *U. spelaeus* displays intermediate average values for both variables; however, its error bars overlap with both Holocene *U. arctos* and MIS 3 *U. arctos* for NPP (showing a higher distribution but a lower mean than Holocene *U. arctos*) and for NG (with a distribution similar to that of Holocene *U. arctos*) (Figure 75). Finally, MIS 3 *U. arctos* presents the lowest NPP average but the highest NG average and distribution, with wide error bars extending across the range of both *U. spelaeus* and Holocene *U. arctos*.

6.7.2.2 Correspondence analysis

In order to investigate the relationships, between *U. spelaeus* niche and *U. arctos* from MIS 3 and Holocene *U. arctos*, two correspondence analyses (CA) were conducted. The analysis included seven microwear variables, namely small pits, large pits, fine scratches, coarse scratches, SWS, gouges, and puncture pits.

In the first CA, based on population averages, the first dimension (Dim. 1) explained 93.9% of the total variance, while the second dimension (Dim. 2) accounted for 6.1%, together capturing 100% of the dataset's variability. These two dimensions were therefore selected for interpretation and visualization (Figure 76; Appendix section A.3.1, Table A11). In the second analysis, performed at the individual level, Dim. 1 accounted for 47.78% of the variance and Dim. 2 for 21.56%, again capturing 69.34% of the total variance. These two dimensions were likewise retained for graphical representation and interpretation (Figure 77; Appendix section A.3.1, Table A12).

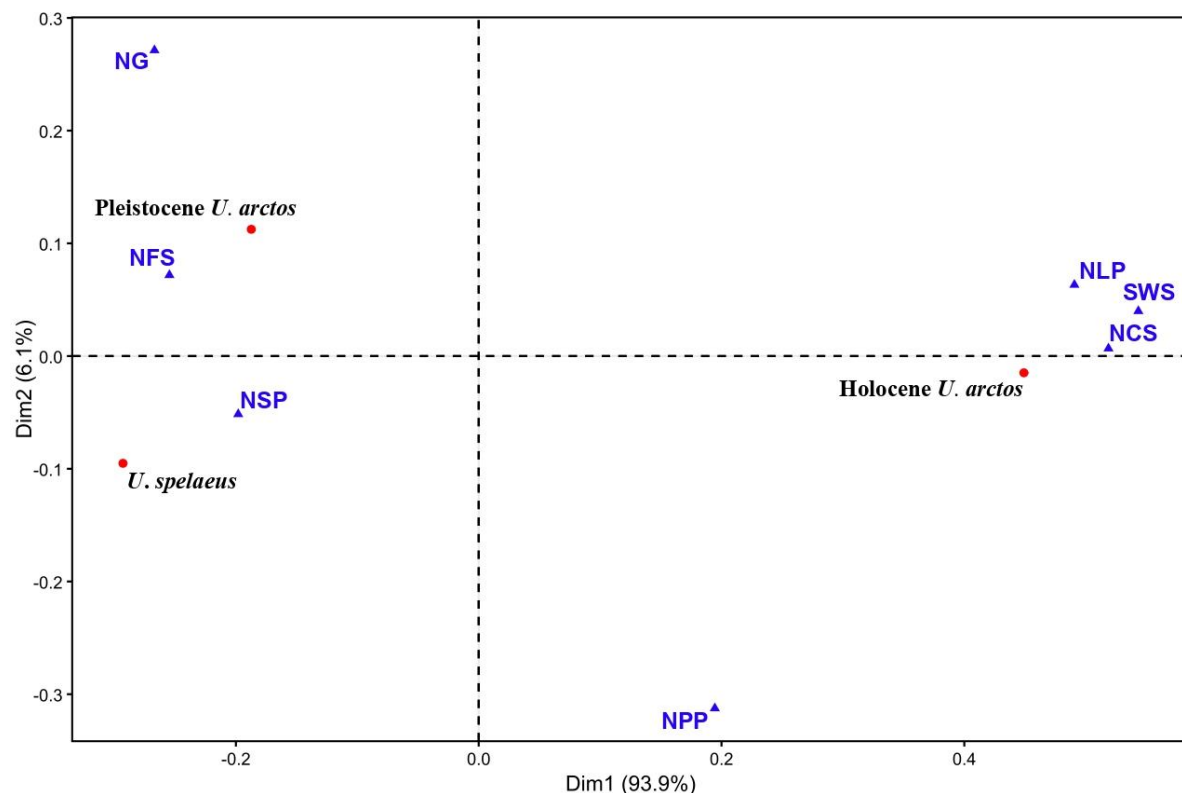


Figure 76. Correspondence analysis of populations means for seven microwear variables: number of fine scratches (NFS), coarse scratches (NCS), small pits (NSP), large pits (NLP), gouges (NG), puncture pits (NPP), and the scratch width score (SWS). The analysis compares the Late Pleistocene (MIS 3) populations of *U. spelaeus* sensu stricto ($n = 321$) and *U. arctos* ($n = 6$), with the post-LGM (Holocene) *U. arctos* ($n = 3$) from Central Europe (Romanian Carpathians).

When examining the correspondence analysis based on population averages, a clear pattern emerges (Figure 76). Holocene *U. arctos* plots in proximity to large pits (NLP), coarse

scratches (NCS), and scratch width score (SWS), suggesting an association with harder or more resistant food items. In contrast, Pleistocene *U. arctos* and *U. spelaeus* cluster together, closer to fine scratches (NFS), small pits (NSP), and gouges (NG), which may reflect a softer or more mixed diet. This spatial proximity indicates a notable overlap in dietary niche between these two coexisting Late Pleistocene ursid species, particularly during MIS 3 (Figure 76).

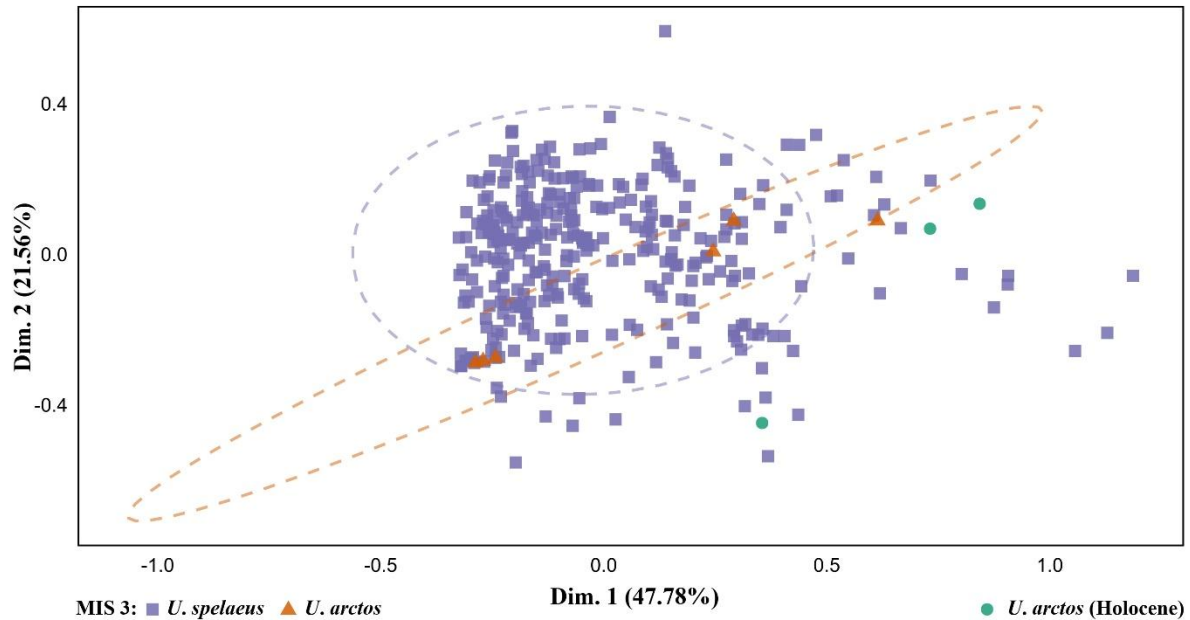


Figure 77. Correspondence analysis at the individual level of *U. spelaeus* and *U. arctos* for seven microwear variables: number of fine scratches (NFS), coarse scratches (NCS), small pits (NSP), large pits (NLP), gouges (NG), puncture pits (NPP), and the scratch width score (SWS). Confidence ellipses (95%) illustrate species-level variation.

This observation, of niche overlap of *U. spelaeus* and *U. arctos* during MIS 3, is further supported by the correspondence analysis including all individuals (Figure 77), where 5 out of 6 *U. arctos* specimens from MIS 3 (83.3%) fall within the 95% confidence ellipse of the *U. spelaeus* cluster (Figure 77). Only one pre-LGM *U. arctos* individual (16.6%) plots closer to the post-LGM *U. arctos*, though it still overlaps with the *U. spelaeus* distribution. In contrast, Holocene *U. arctos* individuals occupy the margins of the overall distribution, lying outside the 95% confidence ellipses of both *U. spelaeus* and Pleistocene *U. arctos*, thereby indicating a distinct dietary niche (Figure 77).

DISCUSSION

7. Discussion

7.0 Intra-regional dietary variability in cave bears

The following first sections (7.1 to 7.5) discuss the first objective, the dietary regimes of cave bear populations by region, aiming to explore the underlying causes and ecological factors shaping the observed local dietary patterns. The regional grouping follows that established in the preceding sections, ensuring coherence in the geographical grouping of the populations.

7.1 Romanian Carpathians

The microwear results obtained for *U. spelaeus* from the Carpathians provide compelling evidence of intra- and inter-population dietary flexibility during the pre-dormancy phase, although not related to age or sex. Their diet did not exhibit specialization, being neither fully herbivorous nor carnivorous, but rather omnivorous. While some populations exhibited a preference for soft mast (e.g., Muierilor, Cioclovina), others favoured harder food items (e.g., Urşilor, Oase) or vertebrates (e.g., Bisericuța, Onceasa). However, all populations demonstrated intra-population dietary flexibility, with individuals exhibiting varying degrees of resource utilization across a broad dietary spectrum. This dietary pattern persisted throughout the MIS 3 period, spanning from over 46 to 27.1 cal ka B.P. at least, despite the climatic fluctuations (Constantin et al., 2007). We analysed individuals from both distant and recent time periods leading up to their extinction around 27.8 cal ka B.P. (Pacher and Stuart, 2009; Terlato et al., 2019); however, no dietary changes or differences were observed among them. This supports the hypothesis that dietary diversity in cave bears from the Romanian Carpathians was not determined by geographic or climatic factors, as recently stated by Meleg et al. (2024) for long-term diet (based on stable isotope values). Similarly, no such influence was observed for seasonal diets.

7.1.1 Average life (stable isotopes) vs seasonal (dental microwear) dietary patterns

Distinctly, the isotopic results of nitrogen ($\delta^{15}\text{N}$) for the analysed individuals exhibit substantial variability ($\delta^{15}\text{N}$ values range from 3.3 to 11.5‰) (Richards et al., 2008; Robu et al., 2013, 2018). This may suggest that over the year, there was indeed a differentiated diet. However, during this pre-dormancy specific period of the year, Carpathian cave bear populations from Urşilor, Oase, Muierilor and Bisericuța had a similar dietary pattern, characterized by a highly flexible omnivorous intake. Therefore, no correlations between stable isotopes and dental microwear at the individual or population-level were identified due to the different time resolutions of each method (see more at section A.3.2). Bone collagen stable isotopes provide

the average annual dietary signal while dental microwear indicate a short term and seasonal dietary signal (Davis and Pineda-Muñoz, 2016). The substantial significance of this common dietary regime (i.e., high intrapopulation flexibility) is underscored by the notable geographic separation between the studied populations. These populations, situated within the Carpathian region, were at a significant distance from one another (mean *ca.* 100 km) and at different altitudes (mean *ca.* 452 meters a.s.l.), but still had highly variable diet during predormancy period.

7.1.2 Omnivory during the predormancy period

The microwear patterns of the cave bear specimens differ from those of extant *U. arctos* and *U. americanus*. This differentiation may be attributed to the consumption of particular items, potentially consisting of plant matter, such as roots (Mattson, 1998; Athen, 2006; Ramírez-Pedraza et al., 2022), as opposed to other bear species (Krajcarz et al., 2016; Bocherens, 2019; Naito et al., 2020). However, the correspondence analysis (CA) reveals some intra-population variability, with some individuals falling within the range of extant species that share a highly variable (including both hard and soft mast) omnivorous diet, mainly *U. americanus* (Hatler, 1967; Raine and Kansas, 1990), *U. arctos* from Kamchatka (Bergman, 1936; Kistchinski, 1972; Vereschagin, 1976; Krechmar, 1995) and *U. arctos* from Northern Europe (Elgmork and Kaasa, 1992; Persson et al., 2001; Bojarska and Selva, 2012), as well as *U. arctos* from North America (Mattson, 1998; Hilderbrand et al., 1999; Mowat and Heard, 2011) and Central Europe (Rigg and Gorman, 2005; Bojarska and Selva, 2012), respectively. In contrast, cave bears significantly differentiate from the diet-specialized *U. arctos* from Greece (i.e., soft-mast consumer) (Vlachos et al., 2000; Paralikidis et al., 2010).

7.1.3 Cave bear seeded and hard-shelled fruit consumption

The observed omnivorous trends for the cave bear, distinct from the specialized diet of the Greek *U. arctos*, may be inferred from the consumption of a diverse array of dietary food types during this pre-dormancy period, a trend observed in modern bear species. Ursids actively forage for food sources rich in lipids or carbohydrates during the pre-hibernation/dormancy hyperphagic period, which typically takes place in late summer and autumn (e.g., Coogan et al., 2014; Soofi et al., 2017). This behaviour is driven by their physiological need to accumulate energy reserves before entering hibernation, and in the case of females, to support the energy demands associated with reproduction and the production of milk for lactation (Farley and Robbins, 1995; López-Alfaro et al., 2013). Therefore, in extant bears, it translates into diet diversification, particularly through the substantial consumption of core carbohydrate items

(Bojarska and Selva, 2012; Coogan et al., 2018). Consequently, bears ranging from northern cold regions to mild Mediterranean zones (Graber and White, 1983; Cicnjak et al., 1987; Clevenger et al., 1992; Vlachos et al., 2000; Persson et al., 2001) heavily rely on the ingestion of small wild fruits like berries or nuts which serve as a principal means of accumulating energy reserves (Welch et al., 1997; Stenseth et al., 2016; Soofi et al., 2017; Ogurtsov, 2018; García-Rodríguez et al., 2021). On the other hand, in regions with harsh winters, particularly those characterized by heavy snowfall, bears may rely more heavily on a meat-based diet (Wiegand et al., 2008; Bojarska and Selva, 2012), although one does not necessarily exclude the other (e.g., Dahle et al., 1998, 2013; Persson et al., 2001). Regarding this particular behaviour, the presence of puncture pits and gouges was consistently observed in all fossil populations, a microwear feature characteristic of hard-object consumers (Solunias and Semprebon 2002; Godfrey et al., 2004; Semprebon et al., 2004; Williams and Geissler, 2014). Specifically, carnivore clade omnivores from temperate woodland environments (e.g., *V. vulpes*, *Genetta genetta* or *Nandinia binotata*) present puncture pits, due to the consume of fruit coverings and seed coats (Xafis et al., 2017). This evidence suggests, for the first time, the consumption of seeded and hard-shelled fruits, for *U. spelaeus*. It is important to stress that the presence of puncture pits (i.e., hard-object consumption) was not observed, until this point, in other cave bears analysed using low-magnification microwear techniques (Ramírez-Pedraza et al., 2019, 2020, 2022). This applies to cave bears residing in both steppe-like habitats in northern latitudes (Ramírez-Pedraza et al., 2022), and forested landscapes in southern latitudes (Ramírez-Pedraza et al., 2019, 2020).

During the Last Glacial Period, the Carpathian Mountain range has been recognized as a large forest refugium (Jankovská and Pokorný, 2008; Tzedakis et al., 2013; Juříčková et al., 2014). This region exhibited a diverse range of canopy forest landscapes, with certain valleys with more humid and enclosed environments maintaining temperate plant specimens (Jankovská et al., 2002; Juříčková et al., 2014). Dominant tree species during this time included larch (*Larix*), Swiss stone pine (*Pinus cembra*), Scots pine (*Pinus sylvestris*), and spruce (*Picea*), forming a relatively dense forest canopy (Jankovská et al., 2002). In more favourable locations within the Carpathian region, isolated patches of temperate broadleaf trees, such as hazel (*Corylus avellana*), black alder/grey alder (*Alnus glutinosa/A. incana*), linden (*Tilia*), elm (*Ulmus*), oak (*Quercus*), beech (*Fagus*), hornbeam (*Carpinus*), fir (*Abies*), and maple (*Acer*) managed to persist even during the most severe glacial periods, including the Last Glacial Maximum (LGM) (Magri et al., 2006; Jankovská and Pokorný, 2008). The consumption of fruits produced

by these plant specimens, such as beechnuts, hazelnuts, acorns, and linden nutlets, is compatible with the microwear pattern found on cave bear individuals (Godfrey et al., 2004; Xafis et al., 2017), potentially suggesting the inclusion of these specific items in the diet of cave bears inhabiting the Carpathian region during MIS 3.

Our results are particularly intriguing as they suggest that the dietary patterns of Carpathian cave bears may exhibit similarities to those of extant brown bears inhabiting the same region. This is noteworthy considering that modern brown bears in the Carpathians predominantly consume seeded fruits as their primary food source during the hyperphagia period in autumn (Slobodyan, 1976; Štofik et al., 2013; García-Rodríguez et al., 2021). During autumn bears collect the remaining raspberries (*Rubus idaeus*) and whortleberries (*Vaccinium myrtillus*) from summer; they also eat mature blackberries (*Rubus fruticosus*), mountain-ash fruits (*Sorbus aucuparia*), fruits from wild apple (*Malus* spp.) and pear trees (*Pyrus* spp.), blackthorn (*Prunus spinosa*), and dog rose (*Rosa canina*), as well as beechnuts (*Fagus* spp.) and acorns (*Quercus* spp.) (Slobodyan, 1976; Kalabér et al., 1994).

The singular presence of hard items in the Carpathian cave bear diet during the Late Pleistocene, in contrast to other European regions, in conjunction with the observed similarities between the dietary patterns of cave bears and extant brown bears in the same region, yields valuable insights into the enduring presence of specific tree species and their associated food resources within the Carpathian ecosystem over time. Moreover, a new unpublished date released in Duñó-Iglesias et al. 2024a for an individual from Urşilor, calibrated to 27,056 years cal B.P. (median age), which closely aligns with the species' extinction and stands as one of the earliest recorded dates for Eastern Europe, may suggest the prolonged existence of cave bears (*U. spelaeus*) in the Carpathians, owing to favourable ecological conditions and the availability of reliable herbivorous food resources. Consequently, the Carpathians may have functioned as a refuge for cave bears, sustaining a consistent availability of food sources for ursids, even during periods of severe glaciation.

7.1.4 Dietary comparison between fossil *U. spelaeus* and *U. arctos*

Finally, the microwear results refute that the fossil populations from the Carpathians had a carnivorous diet, which is supported by the barely-present hypercoarse scratches, which are only displayed by hyper-carnivores and bone-consumers such as polar bears (*U. maritimus*) (Pappa et al., 2019) and hyenas (*Crocuta* spp.) (Rivals et al., 2022). Nevertheless, the presence of certain fossil individuals overlapping with omnivorous ursids, known to consume both

vertebrates and invertebrates, could suggest at least sporadic meat consumption among the cave bear individuals examined in this study. This could be explained as that towards the end of autumn, when winter approaches, resource availability diminishes, and diet becomes restricted; some individuals who have not been able to accumulate sufficient lipid reserves for the winter begin to consume meat to further supplement their reserves, as recorded in extant *U. arctos* from the Carpathians (Slobodyan, 1976; Frackowiak, 1997). However, Carpathian cave bears did not have such a carnivorous diet during the pre-dormancy period, unlike some cave bear populations from the northern regions of the Iberian Peninsula (Pinto-Llona, 2013; Ramírez-Pedraza et al., 2020).

Additionally, *U. spelaeus* exhibited narrower scratches (lower SWS) compared to the contemporaneous (pre-LGM) *U. arctos* specimen from Bisericuța (Romanian Carpathians) (Figure 40A). The brown bears, both Pleistocene ($n = 1$) and Holocene ($n = 3$), despite the limited sample size, showed a clear trend of a higher number of coarse scratches relative to fine scratches (Figure 40A). Furthermore, cave bears exhibit a higher frequency of small pits relative to large pits, whereas brown bears show a greater prevalence of large pits compared to small pits (Figure 40B). This distinction in scratch width and pit size between Carpathian cave bears and brown bears may suggest divergent seasonal niches, with brown bears displaying a propensity toward a more specialized carnivorous diet (in the case of Pleistocene *U. arctos* from Bisericuța) or a hard-object diet (in the case of Holocene brown bears, as observed by Slobodyan, 1976). Pleistocene brown bears appear to have exhibited more carnivorous dietary behaviour compared to contemporary brown bears (Bocherens et al., 2011; Münzel et al., 2011), while Holocene bears from the Carpathians might share more dietary similarities with cave bears from the same region during MIS 3, as inferred from pit size comparisons; however, a clear separation remains (Figure 40B). Furthermore, the three Holocene *U. arctos* individuals from the Carpathians, dated to medieval times, displayed a diverse scratch width pattern: the ACCG individuals were similar to Pleistocene *U. spelaeus*, while the Avenul Mățului specimen showed a comparable score to Pleistocene *U. arctos*.

Overall, these findings could support the hypothesis of a more omnivorous diet for *U. arctos* in the post-Last Glacial Maximum (LGM); however, the concept of niche inheritance between *U. spelaeus* and *U. arctos* remains questionable, as differences in microwear patterns persist between species and similarities between MIS 3 *U. arctos* and Holocene *U. arctos* are also noticed (for example in number of coarse scratches). This hypothesis is further explored at species-wide scale in section 7.6.2.

Nevertheless, given the absence of statistical significance from the three Holocene *U. arctos* individuals from the Carpathians, further microwear studies with larger sample sizes are needed to compare their diet with that of Late Pleistocene *U. spelaeus* populations from the same region. This will help to better establish potential dietary similarities and niche inheritance patterns between Pleistocene cave bears and pre-LGM *U. arctos* in the Carpathians.

7.2 Moldavian Plateau

The microwear analysis of *U. spelaeus* populations from Moldavian Plateau reveals notable dietary variability, indicating both specialized and more generalized feeding strategies. The Trinca population exhibits a highly specialized soft mast-dominated diet, characterized by small pits and fine scratches, with minimal evidence of large pits or coarse scratches. Its microwear pattern closely resembles that of the omnivorous *U. arctos* population from Greece (based on the numbers of pits and scratches) and *A. melanoleuca* in the correspondence analysis (CA), both associated with abrasive diets. Conversely, the Buzdujeni population demonstrates a more variable omnivorous diet, primarily incorporating soft mast and vertebrates. The Duruitoarea Veche population also follows a diverse dietary pattern, including vertebrates as well as both soft and hard mast. Similarly, the Saharna population exhibits an omnivorous diet with a mix of hard and soft mast, along with vertebrate consumption. The Butești population, though based on a small sample size ($n = 2$), presents a high density of pits, suggesting a diet dominated by hard mast. Overall, these *U. spelaeus* populations exhibit distinct dietary strategies, with Trinca displaying a more specialized reliance on soft mast, while others, particularly those from Buzdujeni, Duruitoarea Veche, Saharna, and possibly Butești, demonstrate greater dietary flexibility, incorporating a wider range of plant and vertebrate resources.

7.2.1 Palaeoenvironment of Moldavian Plateau during the late MIS 3: a mix of tundra-steppe and forest refugia

The dietary flexibility observed in these populations aligns with the environmental diversity of the Moldavian Plateau region during MIS 3, which supported a mosaic of landscapes ranging from tundra-steppe to forested environments (Gerasimenko, 2006). This period, preceding the Last Glacial Maximum (LGM), was characterized by significant climatic fluctuations that shaped the regional faunal composition (e.g., David and Lungu, 1972; Markova, 2007; Puzachenko and Markova, 2019). The region generally featured a mix of steppe habitats supporting *Mammuthus* faunas; including *M. primigenius*, *Coelodonta antiquitatis*, *R. tarandus*, *M. giganteus* and *Ovis moschatus*; alongside open-landscape taxa such as *Bison* sp.

and *Equus* sp. Additionally, more temperate and forest-adapted species, including *C. capreolus*, *S. scrofa*, and the ecologically flexible *C. elaphus*, indicate the persistence of wooded refugia (e.g., Croitor, 2008; Demay et al., 2019, 2024). The Moldavian Plateau region's proximity to the Carpathians has been linked to the existence of glacial refugia, which may have provided habitat stability for certain taxa during the climatic oscillations of MIS 3 (Sommer and Benecke, 2005; Sommer and Nadachowski, 2006; Sommer and Zachos, 2009; Stewart et al., 2010). This can be linked to the high counts of puncture pits in Saharna (NPP = 3.26), Buzdujeni (NPP = 2.59) and Duruitoarea Veche (NPP = 0.64), which are linked to the consumption of hard objects such as nuts and hard-shelled fruits in carnivores inhabiting temperate forested environments (Xafis et al., 2017). Saharna and Butești both correspond to the late and terminal phases of MIS 3, representing some of the last known cave bear populations in the region. At Saharna, newly published radiocarbon dates from mandibles place the accumulation between 43 and 40 ka cal B.P. (Duñó-Iglesias et al., 2025), and the high number of puncture pits (NPP) suggests the presence of forest refugia in the Moldavian Plateau during this time. Similarly, the Butești site, dated between 41 and 35 ka cal B.P. (Duñó-Iglesias et al., 2025), also likely reflects occupation of refugial habitats, as indicated by microwear patterns consistent with hard-mast consumption, despite the limited sample size ($n = 2$).

The faunal assemblage from Buzdujeni, dominated by *Equus* sp. and *Bison* sp., suggests an open tundra-steppe environment at the time of accumulation (Croitor and Burlacu, 2020), which is supported by the climatically-cold moment of accumulation, between 40 and 43 ka cal B.P.. However, the presence of *C. elaphus* (albeit in low numbers), might indicate patches of forested habitat (Croitor and Burlacu, 2020). Although *C. elaphus* is not exclusively forest-dependent and exhibits ecological flexibility, its occurrence during cold phases of MIS 3 typically correlates with forest refugia (Sommer, 2020). Moreover, Duruitoarea Veche also shows a relatively high NPP score, although lower than that of Saharna and Buzdujeni. Regarding the Duruitoarea Veche *U. spelaeus* population, the microwear pattern likely reflects environmental conditions shaped by alternating colder and temperate phases, supporting a mosaic landscape that included both open and forested temperate environments, as well as tundra-steppe biomes during the coldest phases of the upper stratigraphic levels, as inferred from its faunal composition (Robu et al., in prep.).

Hence, the microwear analysis from Moldavian Plateau populations displays flexibility that can be linked to alternance of cold and temperate cycles during MIS 3, as well as reinforces the notion of the existence of some vegetation and tree refugia in Moldavian Plateau before the

faunal turnover that happened around *ca.* 20 ka B.P., during the LGM. These refugia likely provided suitable habitats for bear species such as *U. spelaeus* and *U. arctos*, which may have survived in isolated forested patches. From these refugia, brown bear populations are thought to have expanded post-LGM, facilitating the recolonization of northern Europe (Sommer and Benecke, 2005).

7.2.2 Dietary comparison between *U. spelaeus* and *U. arctos* from Trinca (Moldavian Plateau)

The *U. spelaeus* individuals from Trinca represent the only cave bears among Moldavian Plateau populations exhibiting a clearly specialized soft-mast diet. This dietary specialization was likely driven by their coexistence with *U. arctos* at the same locality and the resulting necessity for niche differentiation within an eco-region marked by progressively limited vegetation resources and the total disappearance of temperate forest cover as the Last Glacial Maximum approached (Willis and Van Andel, 2004). Such ecological partitioning is evident from microwear patterns, particularly in variations of scratch width. *U. arctos* from Trinca exhibits a high frequency of coarse scratches (NCS = 3.60), whereas *U. spelaeus* shows very few coarse scratches (NCS = 0.63) and a clear predominance of fine scratches, further reinforcing its reliance on softer dietary resources compared to *U. arctos* (Figure 45A). Additionally, the significant number of gouges observed in *U. arctos* from the Moldavian Plateau suggests the consumption of hard objects, potentially including hard-shelled fruits or bone (Godfrey et al., 2004; Goillot et al., 2009). Niche partitioning between MIS 3 *U. spelaeus* and *U. arctos* has previously been inferred from microwear analyses in the Carpathians (Duñó-Iglesias et al., 2024a), and this may also apply to the site of Trinca.

In contrast, the other Moldavian Plateau *U. spelaeus* populations from MIS 3 exhibit scratch-width patterns comparable to those of contemporary MIS 3 *U. arctos*, indicating a more omnivorous or flexible dietary strategy. Such variability in microwear features underscores distinct ecological adaptations among cave bear populations within the region, likely influenced by local environmental conditions, resource availability, and niche partitioning.

7.3 Western Balkans and Western Rhodopes Mountains

The sites of Bashovichki Pech, Lakatnik, Borikovska, and Triagalna lack a well-defined stratigraphic context. The cave bear population from Bashovichki Pech exhibits a vertebrate-to-hard mast dietary regime, overlapping in the CA with *U. arctos* from Central Europe and Kamchatka, which are characterized by flexible omnivorous diets and hard-mast consumption. The presence of hard objects in the diet of Bashovichki Pech specimens is further supported by

the high number of puncture pits ($NPP = 7.75$), the highest among all fossil populations analysed in this study. Similarly, Triagalna also displays a hard-mast-dominated diet, as indicated by a relatively high number of puncture pits ($NPP = 2$) and gouges ($NG = 1.25$). However, in the CA plot, it falls near *A. melanoleuca* due to the high number of small pits, suggesting a predominantly herbivorous diet.

Borikovska, in contrast, exhibited a predominantly vertebrate-based diet, overlapping with *U. maritimus* along the y-axis of the bivariate plot. However, it showed a higher number of pits, a trait correlated with substantial plant intake in bear microwear studies (Münzel et al., 2014), likely reflecting its occupation of habitats richer in vegetation compared to the sparse Arctic environments. The CA results further distinguish Borikovska from omnivorous bears, with some individuals clustering near *A. melanoleuca* while others align more closely with *U. maritimus*. Notably, hypercoarse scratches were present in 30% of the individuals ($n = 14$). While such microwear features are not commonly observed in herbivorous dominant diets, previous studies have documented their occurrence in omnivorous carnivores inhabiting temperate regions, where they have been linked to bone contact during feeding (Goillot et al., 2009; Semperebon et al., 2011). These distinctive microwear patterns, commonly linked to piscivorous and carnivorous feeding behaviours (Goillot et al., 2009), are also evident in the Borikovska population, reinforcing the notion of dietary flexibility and potential consumption of animal resources.

7.3.1 Refugia mosaic environments in mountain ranges from Western Balkans and Western Rhodopes Mountains during the MIS 3

Among the sites that paleoenvironmental data is available Magura provide evidence of a mosaic environment. In particular, stable isotope analyses on herbivore taxa from Magura, as well as pollen extracted from hyena coprolites (Ivanova et al., 2016; Frémondeau et al., 2020), indicate the presence of steppe vegetation interspersed with patches of taiga and more humid aquatic environments. Isotopic analysis of cave bear remains further reveals long-term dietary flexibility, with some individuals exhibiting omnivorous tendencies (Frémondeau et al., 2020). While the co-occurrence of *U. arctos* alongside cave bears in some layers suggests niche partitioning based on the same stable isotope values (Frémondeau et al., 2020). Notably, the isotopic results match with microwear results, the Magura cave bear population exhibits a preference for soft mast foods, although certain individuals show a seasonal dietary shift towards vertebrate consumption. The diversification towards animal resources might have

responded to the necessity to fulfil the energetic requirements of hibernation (Farley and Robbins, 1995; López-Alfaro et al., 2013; Coogan et al., 2014).

Bacho Kiro also reflects a mosaic environment, characterized by steppe-adapted cold-fauna species alongside woodland taxa. Individuals from this site display a high number of pits, positioning them within the vertebrate-soft mast dietary ecoregion in the bivariate analysis (Figure 49). However, in the correspondence analysis, their dietary pattern overlaps with *A. melanoleuca* (with also a high number of pits), indicating a predominantly herbivorous diet, likely with significant hard-object consumption (Figure 50). This interpretation is supported by the strong association between a high number of pits and herbivorous feeding behaviour, as seen in *A. melanoleuca* (Münzel et al., 2014; Pappa et al., 2019). The presence of puncture pits (NPP = 1.70) and gouges (NG = 0.90) further reinforces the interpretation of hard-mast consumption in woodlands (i.e., providing hard-shelled seeds and nuts) within a mosaic landscape, though the relatively low scores suggest a diet not heavily reliant on this type of foods. This diversification may be related to the pursuit of substantial consumption of core carbohydrate-rich resources prior to hibernation characteristics of ursids (Bojarska and Selva, 2012; Coogan et al., 2018) and previously observed in MIS 3 cave bear populations from the Carpathians (Duñó-Iglesias et al., 2024a).

The Balkan Mountains are recognized, through genetic, and pollen and mammal fossil analyses, as a refuge from which temperate species expanded throughout Eastern Europe after the Last Glacial Maximum (e.g., Hewitt, 2000; Tzedakis et al., 2002; Sommer and Zachos, 2009; Sadori et al., 2016; Lang et al., 2023). Recent palynological analyses of sediments and coprolites, combined with vegetation reconstructions from Pešturina in the Central Balkans of Serbia (integrated with other paleoenvironmental data of the area such as northern Balkan slopes and south-west of Southern Carpathians), have suggested a mosaic landscape characterized by dense patches of temperate woodland with high botanical diversity (Carrión et al., 2024; Ochando et al., 2024). Specifically, these studies reported a diverse assemblage of woody taxa persisting continuously throughout the Late Pleistocene, particularly during the final phases of MIS 3 (Ochando et al., 2024). This assemblage includes *Pinus*, *Juniperus*, deciduous *Quercus*, *Acer*, *Alnus*, *Betula*, *Carpinus betulus*, *Corylus*, *Tilia*, *Ulmus*, *Buxus*, *Genisteae*, and *Cistus*, confirming that the Central Balkans served as a refugial area for mesothermophilic vegetation during MIS 3, with a mosaic landscape encompassing open habitats in high altitude with densely forested patches in the valleys (Carrión et al., 2024). The

microwear results support the presence of mosaic environments in the Western Balkans and Western Rhodopes Mountains territory during MIS 3, particularly in the northern slopes of the Balkan Mountains ranges and the southern Rhodope Mountains.

Finally, the Borikovska population, dwelling high altitude environments (*ca.* 1,250 meters a. s. l.) might have had to rely to other resources, specifically to a higher component of vertebrates and soft mast vegetation, moved by scarcity of plant resources in the alpine areas (Ochando et al., 2024). This dietary adaptation might reflect limited plant-based resource availability resulting from increased snowfall at higher altitudes, as documented for extant *U. arctos* populations (Bojarska and Selva, 2012).

The diversity of dietary signals among cave bear populations suggests that these regions encompassed a diverse biome, where steppe habitats coexisted with patches of boreal taiga and temperate tree refugia. Such ecological heterogeneity likely provided varied resources before hibernation, allowing for dietary flexibility among cave bears. The presence of individuals exhibiting different microwear patterns demonstrates their capacity to adapt to distinct biomes, as well as different feeding strategies before hibernation. This evidence reinforces the idea that cave bears in this region were not confined to a single ecological setting but instead thrived in dynamic, heterogeneous landscapes, adapting their diets accordingly.

7.3.2 *U. savini rossicus* diet during MIS 7

U. s. rossicus from Mishin, despite the small sample size ($n = 3$), exhibits a diet that includes both soft mast and vertebrates. In the bivariate plot, it overlaps with omnivorous bear populations from northern latitudes, while in the CA plot, some individuals (40%) align closely with *A. melanoleuca*, whereas others (60%) cluster near *U. maritimus* due to a high proportion of coarse scratches (SWS = 0.60). This suggests a highly abrasive diet, with certain individuals incorporating hard objects into their food intake. Previous studies on *U. rossicus* have also reported a high number of coarse scratches, linking this microwear pattern to Mammoth Steppe biome (Ramírez-Pedraza et al., 2022). The substantial presence of coarse scratches (SWS = 0.60) in *U. s. rossicus* could reflect the increased aridity during MIS 7 and the subsequent expansion of open grassland habitats, as supported by pollen records from Balkan lacustrine sediments (Ioannina, NW Greece) (Roucoux et al., 2008). This suggests that some individuals inhabited more open landscapes, leading to the formation of coarse scratches, while others may have preferred wooded environments with mostly fine scratches. The similarity to *U. maritimus* in the CA plot is unlikely to reflect hypercarnivorous behaviour, as no hypercoarse scratches

were observed. However, given the overlap with northern latitude species, the inclusion of vertebrates in the diet cannot be ruled out. Additionally, evidence of a mosaic environment in the immediate locality (Gurova et al., 2017) likely contributed to the dietary variability observed within this population.

7.4 Central Balkans

The microwear analysis of *U. spelaeus* populations from Central Balkans reveals some-degree of dietary homogeneity (soft-mast dominated) within the region, although with some singularities, across the three studied populations from Hadži Prodanova, Risovača, and Ušačka.

7.4.1 Omnivorous soft mast diets with evidence of diversification

Hadži Prodanova individuals exhibit a general tendency towards a soft-mast-dominated diet in both the bivariate plot and correspondence analysis (CA). However, in the CA, three individuals ($n = 3$: 27.27%) overlap with omnivorous bear populations from northern latitudes, suggesting dietary flexibility. Similarly, in the bivariate plot, while the average of the population falls within the soft-mast region, its error bars extend slightly into the vertebrate-dominated area, indicating the possibility of occasional vertebrate consumption. Therefore, while the primary diet of this population appears to have been based on soft mast and abrasive food items, some individuals might have diversified towards omnivorous diet with hard-object consumption. The Hadži Prodanova faunal assemblage suggest that Late Pleistocene layers formed during a humid and relatively warm period within MIS 3, with a dense forest cover (Bogićević et al., 2017). The presence of *U. arctos* suggests niche partitioning (Bogićević et al., 2017). As evidenced by isotopic (Bocherens et al., 2011) and microwear analyses (Duñó-Iglesias et al., 2024a), *U. spelaeus* and *U. arctos* partitioned their niches, when occupying the same landscapes. *U. spelaeus* consumed a predominantly plant-based diet, whereas *U. arctos* exhibited a more carnivorous dietary pattern (but see section 7.6). This aligns well with the present findings, although microwear analysis of *U. arctos* is necessary to confirm this hypothesis, and such data are currently lacking. However, although *U. spelaeus* from Hadži Prodanova had a predominantly diet based on soft-mast (i.e., grasses), it diversified towards hard-object consumption (e.g., hard-shelled fruit and nuts) as recorded by gouges and puncture pits presence in some individuals, probably due to physiological requirements and fat storage before hibernation as observed in Carpathian MIS 3 cave bears (Duñó-Iglesias et al., 2024a).

The cave bear population from Risovača predominantly exhibits a vertebrate-dominated dietary signal in the bivariate plot, overlapping with *U. arctos* from Northern Europe, which is characterized by an omnivorous diet based on soft-mast vegetation with occasional vertebrate inclusion. Notably, the error bars of the Risovača population extend towards the soft-mast-dominated region. In the correspondence analysis (CA) plot, the Risovača population clusters near the eco-region occupied by *A. melanoleuca*, which is associated with highly abrasive diets primarily based on grasses. This positioning is not contradictory to the patterns observed on the bivariate plot (Figure 52), as northern latitude bears also exhibit a soft-mast-dominated diet, albeit with occasional vertebrate consumption. Moreover, the occasional (although scarce) presence of hypercoarse scratches within the Risovača population ($n = 3$; 30%) further supports a casual inclusion of vertebrate material in their diet. While predominantly linked to carnivorous and durophagous diets (Pappa et al., 2019; Rivals et al., 2022), hypercoarse scratches have also been documented in omnivorous carnivores inhabiting temperate regions, where they are attributed to bone contact during feeding (Goillot et al., 2009; Semperebon et al., 2011). Hence, the microwear signal can be defined as omnivorous, although within a soft-mast-dominated diet. The herbivore faunal assemblage of Risovača presents a dominance of open-landscape species (i.e., *Equus* and *Bison*) (Forsten and Dimitrijevic, 1995), this landscape matches with a diet based on abrasive diet for cave bear populations, while some individuals might have diversified towards vertebrate consumption, in order to diversify the resources to survive hibernation as observed in extant bears from northern latitudes (e.g., Bojarska and Selva, 2012).

The Ušačka cave bear population exhibits dietary patterns ranging from soft-mast consumption to predominantly vertebrate-based diets, as indicated by both the bivariate and correspondence analysis (CA) plots. A subset of individuals clusters closely with *A. melanoleuca*, suggesting an abrasive herbivorous diet, whereas the majority ($n = 7$; 63.63%) align more closely with *U. maritimus* due to coarser scratches. While their similarity to *U. maritimus* may indicate the consumption of harder dietary items within a different ecological context compared to individuals resembling *A. melanoleuca*, it could also reflect the high-altitude habitat (1,600 meters a. s. l.) occupied by the Ušačka individuals. Such elevated environments likely provided harsher conditions and more abrasive, open-habitat food resources. This interpretation is supported by the virtual absence of hypercoarse scratches, indicating limited vertebrate consumption prior to death. Overall, microwear data suggest an abrasive, predominantly herbivorous diet.

The dietary variability observed in the Hadži Prodanova, Risovača, and Ušačka cave bear populations can be directly linked to the ecological heterogeneity of the Central Balkans during MIS 3, a mosaic highly heterogeneous landscape characterized by dense patches of temperate woodland interspersed with more open steppe habitats (e.g., Argant and Dimitrijević, 2007; Jovanović et al., 2022; Carrión et al., 2024). The open landscapes provided abundant soft mast resources (e.g., sprouts, grasses, flowers and tubs, leaves), with occasional hard-mast consumption in the temperate woodland patches (with the consumption of hard-shelled fruits and nuts), evidenced by gouges and puncture pits in the Hadži Prodanova population, likely as a strategy to supplement their predominantly herbivorous diet during scarcity or hibernation preparation. This dietary flexibility may have been a critical adaptive strategy to ensure sufficient energy reserves during the harsher months (Duñó-Iglesias et al., 2024a). In contrast, the Ušačka population, residing at higher altitudes where conditions were likely colder and more exposed, displayed microwear patterns indicative of a diet dominated by abrasive plant materials. This aligns with the expectation that open habitats at higher elevations would have offered fewer hard-mast resources, compelling cave bears to rely more heavily on fibrous, grassy vegetation, or possibly low-quality browse.

Overall, the varied diets of cave bear populations across these Central Balkans sites highlight the intricate interplay between regional paleoecology, local resource availability, and species-specific foraging strategies. Such adaptability likely contributed to their resilience during MIS 3, although it may not have been sufficient to withstand the increasingly harsh conditions and habitat fragmentation that followed during the LGM.

7.5 Northern Urals

The diet of *U. kanivetz* from the Northern Urals (Medvezhiya Cave) was predominantly plant-based, focusing on fibrous plants and fleshy fruits, with limited evidence of vertebrate consumption. Its microwear pattern, resembling that of *A. melanoleuca*, supports a soft mast diet rich in fibrous items, with no indication of a vertebrate-dominated diet. However, some degree of diversification through hard mast items was observed, as evidenced by a high number of gouges and the presence of puncture pits.

During the Late Pleistocene, cave bears coexisted with brown bears, but their ecological relationships are still unclear. The differences between their ecological niches remain debatable. However, brown bears are generally considered to be ecologically flexible, while cave bears are more specialized (Drucker, 2022). Several very large ursid bones were

discovered in the Medvezhiya Cave, which presumably belong to *U. arctos*. In the northern part of its distribution range, the modern-day brown bear consumes more animal food compared to those in southern regions (Bojarska and Selva, 2012). In northeastern Siberia, remains of exceptionally large brown bears dating to the Late Pleistocene have been discovered, with stable isotopic evidence suggesting a predominantly predatory diet that may have facilitated their survival in the harsh Arctic environment (Rey-Iglesia et al., 2019; Kryazheva et al., 2022).

During the Late Pleistocene, the climate of the Northern Urals was noticeably colder than today. This was reflected in the vegetation of the region; instead of the taiga that currently grows there, the Medvezhiya Cave area had a more open landscape (Marchenko-Vagapova, 2012; Kryazheva et al., 2022). Palynological data of the Middle Valdai in the Northern Urals indicate the existence of shrubby tundra dominated by Poaceae and Chenopodioideae, with birch being the most common woody plant (Marchenko-Vagapova, 2012). Conifers, on the other hand, occupy only a minor position. The Pechora Urals fauna of small mammals was dominated by tundra forms (~75%; mainly *Lemmus sibiricus*), but the presence of forest species (~10%; *Craseomys rufocanus*, *Microtus agrestis*) indicates the existence of woodlands and gallery forests (Kryazheva et al., 2022). The presence of woody plants and scattered forest patches aligns with the occurrence of gouges and puncture pits, as well as the overlap with northern extant *U. arctos* populations that consume a diverse diet including both soft and hard mast resources, such as fleshy fruits, seeds, and nuts (Persson et al., 2001; Ogurtsov, 2018).

Stable isotope analysis suggests that cave bears in Europe and *U. kanivetz* in the Middle Urals were predominantly vegetarians (Bocherens, 2019; Kosintsev et al., 2024). This type of diet causes an intensification of abrasion of the molars. The strong abrasion of the masticatory surface of lower first molars analysed m1 is in good agreement with these data. Of the 18 studied specimens, 3 belong to the slightly worn group, whose roots are not yet closed (immatures), 6 specimens belong to the moderately worn group (adults), and 9 specimens (half of the sample) belong to the strongly worn group (adults and olds). Abrasion of the masticatory surface can indicate not only the age of the animal but also the fact that the animal consumed solid food (Stiner, 1994, 1998). It is possible that, given the scarcity of food resources, animals could eat not only soft mast, grasses, eggs, invertebrates, and small vertebrates, but also pine nuts, bark, and young tree shoots, as well as dig up underground rhizomes.

Some details of cave bear anatomy may indicate that these animals must have been less efficient chasers and predators than brown bears. For instance, cave bears have narrower posterior choanae than brown bears, which may limit their respiration and consequently their ability to endurance running. Also, cave bears metacarpal and metatarsal bones of the limbs were shorter than those of brown bears, which probably limited their running ability as well (Baryshnikov, 2007). This could, overall, have limited their predatory behaviour specially in open landscapes.

The distribution of *U. kanivetz* in the Urals supports its herbivorous nature. This species is found on the western, European slope of the Ural Range and absent on its eastern, Asian slope. In the eastern slope Urals only the small cave bear *U. s. rossicus*, which is probably a steppe dweller, occurs (Gimranov and Kosintsev, 2020). The climate conditions on the eastern slope were more severe, and the plant resources there were insufficient to meet the needs of large cave bears such as *U. kanivetz*.

Cave bears in the Medvezhiya cave area had access to all resources they needed to survive. Thus, one of the specimens from Medvezhiya Cave (ZIN O.34756-10) was estimated to have reached the maximum individual age recorded for cave bears (Prilepskaya et al., 2022). This may indicate that even in the far north, the cave bears were able to find enough food to sustain themselves. This is in accordance with the capacity for resources diversification observed through microwear analysis.

The *U. kanivetz* individuals from Medvezhiya Cave were likely constrained by limited vegetation resources and competition with *U. arctos* in the same region, relying primarily on a highly abrasive herbivorous diet. This interpretation is strongly supported by microwear molar wear patterns, indicating significant consumption of fibrous plants and other abrasive resources. However, dietary diversification towards hard mast vegetation likely occurred either as a preparatory strategy for hibernation (Duñó-Iglesias et al., 2024a), or as an opportunistic response to resource scarcity (Ramírez-Pedraza et al., 2022; Duñó-Iglesias et al., 2024b).

7.6 Tracing niche evolution in cave and brown bears: from the Middle to Late Pleistocene *U. kudarensis* lineage to pre- and post-LGM *U. arctos*

The first part of this section (7.6.1) focuses on a cave bear lineage, that of *U. kudarensis*, which evolved in the high Greater Caucasus ranges from the Middle to Late Pleistocene. Investigating the dietary evolution of this single lineage provides a rare opportunity to infer broader evolutionary dynamics within the *U. spelaeus* sensu lato clade. In particular, it can provide

insights into how cave bears may have responded to long-term ecological pressures, such as climate change, competition, niche partitioning, and potential anthropogenic impacts shaping their dietary adaptations.

The second part (7.6.2) examines the evolution of short-term diets in European brown bears (*U. arctos*) across two key periods. First, during the Late Pleistocene MIS 3 period, when they coexisted with *U. spelaeus*, sharing the same landscapes. Second, in the post-LGM period, when *U. arctos* occupied these environments alone. This comparison provides an opportunity to assess potential shifts in dietary strategies of *U. arctos* in response to the extinction of *U. spelaeus*, and the subsequent availability of new niches, together with the environmental transformations associated with the onset of the Holocene.

7.6.1 Climate and competition as drivers of dietary evolution during the Middle to Late Pleistocene in the High Caucasus

The dental microwear of *U. praekudarensis*, *U. praekudarensis/kudarensis*, and *U. kudarensis* indicates an omnivorous diet for all three populations.

However, there are differences in the preferred food items between the three cave bear species studied. The Middle Pleistocene *U. praekudarensis* displays an omnivorous diet with its individuals exhibiting a highly variable diet, encompassing soft and hard mast items, while still predominantly favouring a hard mast diet, while *U. praekudarensis/kudarensis* presents a different microwear pattern with an omnivorous diet dominated by soft mast highly abrasive items. Finally, the Late Pleistocene *U. kudarensis* is characterised by an omnivorous diet strongly dominated by hard mast consumption. This can be related to climatic changes experienced in the southern Greater Caucasus during the Pleistocene, as well as the mortality profile and season of accumulation of the three cave bear populations (Lisiecki and Raymo, 2005; Baryshnikov, 2020b). Furthermore, the presence of varying rates of hypercoarse scratches indicates the strong possibility of vertebrate intake and carnivorous behaviour, although in different proportions among the three species.

7.6.1.1 Palaeoenvironmental data from Kudaro Cave during the Middle and Late Pleistocene

The Middle Pleistocene *U. praekudarensis* lived in very warm and stable climatic conditions during MIS 11 (Likhvian Interglacial) (Lioubine, 1998), as assessed by thermophilous mammalian fauna such as *Macaca* sp. and large and small porcupines found in the same stratigraphic horizon (Loutre and Berger, 2003; Nitychoruk et al., 2006; Baryshnikov, 2011).

Moreover, the palynological analysis of the oldest Acheulean layer 5c supported these very warm temperature conditions, which oscillate from dry to very wet conditions during MIS 11 (Figure 78; Lioubine, 2002). In the dry stage, which occupies most of layer 5c where *U. praekudarensis* remains were recovered, there was a mosaic landscape composed of mixed forests of xerophilous species, those formed by broad-leaved trees and warm Pinidae family conifers, as well as more open areas of shrubs and grasses (Lioubine, 2002), a landscape dominated by warm forest-steppe landscapes with savanna-like areas (Lioubine, 2002). Although there is a poor record of pollen and spores in the second half of the stratigraphic package due to conservation constraints (Lioubine, 2002), the remains of arboreal-adapted *U. thibetanus* suggests the existence of dense and tall forest vegetation not far from the cave during the formation of layer 5c (Baryshnikov, 2010). The presence of wooded areas is further supported by the fact that during the subsequent wetter phases, at the beginning of layer 5b, the caves were surrounded by a thick forest, composed of broad-leaved trees, similar to the vegetation found in lowland modern Colchian forests (Lioubine, 2002). The *U. praekudarensis* remains from layer 5c are composed mostly of females and young individuals that died due to natural causes during hibernation (Baryshnikov, 2020b). They would have inhabited a very diverse landscape, encompassing densely forested areas of deciduous trees and more open landscapes, including conifers, woodlands and meadows. These diverse biotopes would have provided a wide variety of plants, comprising soft foodstuffs such as leaves in the forest understorey, and forbs and grasses in more open areas, as well as hard objects such as hard-shelled fruits like chestnuts, beechnuts, acorns, or pinecones from forested areas. Therefore, the prevalence of hard mast items in the diet of *U. praekudarensis* before dormancy could be attributed to the search for high-calorie resources to survive hibernation (Duñó-Iglesias et al., 2024a). However, the diversification of their diet, in search of alternative means to accumulate reserves, may be associated with challenges in accessing abundant enough resources solely from forested items. In extant bears the hyperphagia period is characterised by a narrowing of their dietary niche to single patches of landscape (e.g., Soofi et al., 2017; Ogurtsov, 2018). Usually, only those bears who are not storing enough reserves diversify their diet to include other foods (Wiegand et al., 2008).

7. Discussion

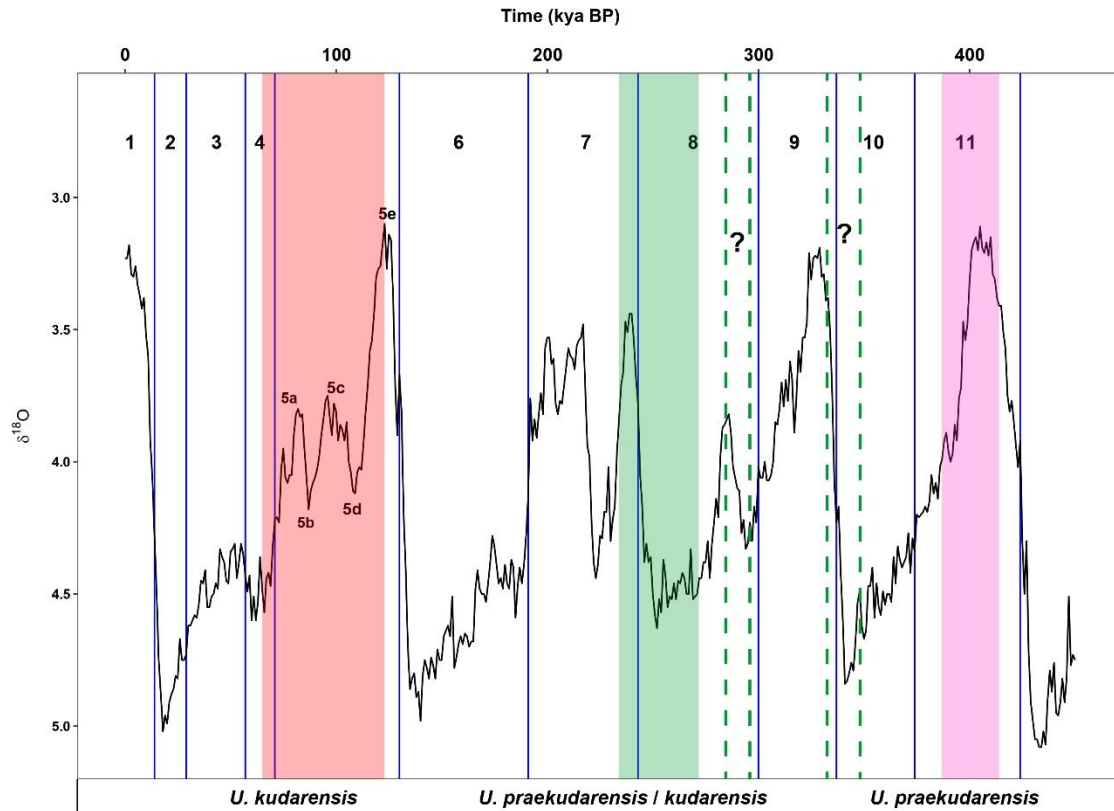


Figure 78. Chronological time-range of the Kudaro cave bear populations in relation to the isotopic oxygen ($\delta^{18}\text{O}$) curve by Lisiecki and Raymo (2005) and Ruan et al. (2016). *U. praekudarensis* accumulated during a warm interstadial (MIS 11). *U. praekudarensis/kudarensis* accumulated during a cold to temperate interstadial, most likely at the end of MIS 8 / MIS 7 transition, although older periods such as the mid-MIS 8 warm event the transition from the MIS 10 stadial to the MIS 9 interstadial might also be considered. Finally, *U. kudarensis* remains accumulated during a temperate interstadial transitioning to a cold stadial (MIS 5 / MIS 4).

The palynological studies of layer 5 (Kudaro 3) have recorded the presence of an open landscape with alpine herbaceous vegetation transitioning to an open spruce forest, because of a colder to a more temperate period at the end of the layer (Baryshnikov, 1998; Liubine, 2002). The end of layer 5 from Kudaro 3, has been correlated with layer 5a from Kudaro 1 based on pollen analysis (Liubine and Bosinski 1995; Baryshnikov, 1998; Liubine, 2002). Therefore, pollen analysis suggests that *U. praekudarensis/kudarensis* population inhabited the region from end-MIS 8 and the beginning of MIS 7 (Figure 78; Baryshnikov, 1998; Lisiecki and Raymo, 2005). During this period, the palaeoclimatic records, spanning from Western Europe to Siberia, revealed a prevalence of open vegetation dominated by grassland communities, due to the prevailing cold and arid climatic conditions, which resulted in the retreat of temperate woodlands (Prokopenko et al., 2001; Desprat et al., 2007; Roucoux et al., 2008). Similarly, the palaeoecological records of the Southern Caucasus using small mammals, amphibians, and gastropods indicate a highly arid environment with a meadow steppe and alpine grasslands

around 1000 meters a.s.l. (Blain, 2016; Sevilla, 2016; Richter et al., 2020; Rey-Rodríguez et al., 2022). This arid period is evidenced by an unprecedented peak in herbaceous vegetation and a significant decline in woodlands, as recorded in the pollen analysis of layer 5 (Lioubine, 2002).

The assemblage of *U. praekudarensis/kudarensis* bones accumulated throughout the year, probably brought to the cave by predators or dying there due to disease (Baryshnikov, 1999). Arid and open habitat conditions in high altitudes could explain the soft mast and highly abrasive diet of *U. praekudarensis/kudarensis*, characterised by a high number of fine scratches, as having relied most of the year on its preferred forage of short steppe grasses mostly composed of Gramineae plants rich in phytoliths. Therefore, it resembles the diet of the ultra-phytophagous giant panda, with an obligate bamboo diet (Goillot et al., 2009; Wei et al., 2015). A very abrasive diet based on grasses has also been observed in *U. kanivetz* populations from the Urals inhabiting a mammoth steppe biome (Ramírez-Pedraza et al., 2022). Furthermore, isotopic analysis on Late Pleistocene cave bears have also suggested the prevalence of a vegetarian diet throughout the year as an adaptation to the Mammoth Steppe biome (Bocherens, 2015, 2019).

Finally, the studied *U. kudarensis* individuals inhabited the cave from 110 ± 10 ka B.P., during the MIS 5 substage 5e (Eemian) until the beginning of MIS 4 (around 80 ka B.P.) (Ĉerdyncey et al. 1959; Baryshnikov, 2002). This corresponds with the transition from a relatively warm and humid interstadial (Odderade), characterised by the development of temperate deciduous forests in the region, to an overall drier and cooler phase (Figure 78; Dansgaard et al., 1993; Sanchez Goñi et al., 2013; Helmens, 2014; Pickarski et al., 2015). This last stage is defined by the expansion of open vegetation that became predominant in the south of the Caucasus mountains around 70 ka B.P. (Pickarski et al., 2015). This climatic transition was determined by the pollen record of layer 4 (Kudaro 3) (Lioubine, 1985). During the initial phase of stratigraphic unit formation, wooded areas were the dominant feature, with deciduous trees reaching the cave in a more closed landscape, while in the second half of the layer, open landscapes began to expand up the mountain, with a forest belt descending to the bottom of the valley (Lioubine, 1985). The assemblage of *U. kudarensis* bones suggests death by natural causes by mainly old adult male individuals that could not endure the harsh climate during hibernation (Baryshnikov, 1999; Baryshnikov, 2020b). These cave bears must have inhabited a temperate woodland and would have had access to hard-shelled fruits such as beechnuts, hazelnuts and acorns before dormancy. This is supported by a microwear pattern similar to that

of *U. arctos* from Central Europe, with an omnivorous diet based on hard food from temperate forests (Rigg and Gorman, 2005; Bojarska and Selva, 2012). This similarity is confirmed by high amounts of puncture pits and gouges, which are defining features of hard-object consumers (Solounias and Semprebon, 2002; Godfrey et al., 2004; Semprebon et al., 2004; Williams and Geissler, 2014). In particular, puncture pits are presented by carnivore clade omnivores consuming fruit coverings and seed coats in temperate deciduous woodland environments (Xafis et al., 2017). A similar microwear pattern, with a high presence of puncture pits and gouges, has been previously observed in the pre-dormancy diet of Romanian Carpathian omnivorous *U. spelaeus*, which inhabited a broad-leaf glacial refugia throughout MIS 3 (Duñó-Iglesias et al., 2024a).

For the last two populations, another hypothesis for their food evolution can be proposed. *U. praekudarensis/kudarensis* or early *U. kudarensis* might have evolved in other conditions and then settled in the area of the Kudaro caves, retaining their mainly herbivorous feeding habits. Late *U. kudarensis* might have already adapted to life in the mountains of the Greater Caucasus and acquired feeding habits reminiscent of those of *U. praekudarensis*.

7.6.1.2 Vertebrate consumption for cave bear populations at Kudaro

Hypercoarse scratches, which are unique to hyper-carnivores and bone consumers like polar bears (Pappa et al., 2019) and hyenas (*Crocuta* spp.; Rivals et al., 2022), were observed in all three fossil populations. These microwear features were previously observed in low numbers in MIS 3 cave bears from the Urals; six specimens of *U. kanivetz* from Secrets Cave, two of *U. ingressus* from Shiriaevo 1 Cave, and one of *U. rossicus* from Kizel Cave (24%, 28.5%, and 5.5% of the studied specimens, respectively; Ramírez-Pedraza et al., 2022). The authors of this study attributed the observed microwear features to an extreme environment, given that among the extant populations used as reference only the arctic dwelling polar bear exhibited them, and that hypercoarse scratches had so far not been observed in other extant or fossil bears in southern latitudes (Pappa et al., 2019; Ramírez-Pedraza et al., 2019, 2020, 2022). However, in other microwear studies, such features were observed in omnivorous carnivores inhabiting temperate latitudes and related to the contact of the enamel surface with bones (Goillot et al., 2009; Semprebon et al., 2011). Furthermore, a high number of hypercoarse scratches on the grinding area of the m1 was associated with species exhibiting a piscivorous diet, exemplified by the European river otter (*L. lutra*), malacophagy observed in the sea otter (*E. lutris*), and a carnivorous diet represented by the Malagasy civet (*F. fossana*) and serval (*L. serval*) (Guillot et al., 2009). Additionally, species with a carnivorous diet exhibit predominantly coarse

scratches compared to fine ones (Xafis et al., 2017). These piscivorous/carnivorous microwear patterns are exhibited by *U. kudarensis* and *U. praekudarensis*, which have a high number of hypercoarse scratches with 83% ($n = 10$) and 47% ($n = 7$), respectively, together with high numbers of coarse scratches in comparison to low counts of fine scratches. On the other hand, *U. praekudarensis/kudarensis* present a prevalence of fine scratches over coarse ones and only 14 % ($n = 2$) of specimens exhibited hypercoarse scratches.

Previous isotopic studies of carbon ($\delta^{13}\text{C}$), nitrogen ($\delta^{15}\text{N}$), and sulphur ($\delta^{34}\text{S}$) in Kudaro yielded no evidence of a lifespan fish or meat-based diet for the Late Pleistocene *U. kudarensis* (Bocherens et al., 2014b). However, this study primarily analysed individuals from MIS 3 layer 3 ($n = 6$), dated between 42 and 48 ka B.P. (Baryshnikov, 2011), and layer 2 ($n = 2$) of Kudaro 3, which yielded dates around 30 ka B.P. (Baryshnikov, 2002). These are from much younger layers than the individuals analysed in this work, with only one individual of *U. kudarensis* coming from layer 4, the same layer sampled for *U. kudarensis* in the present study (Bocherens et al., 2014b). Therefore, due to the relatively small sample size, predominantly derived from younger layers, and the different temporal resolutions of stable isotopes and microwear methods, we state that the intake of animal protein cannot be ignored for *U. praekudarensis*, *U. praekudarensis/kudarensis*, and *U. kudarensis* populations coming from older layers, although within a plant-dominated diet. It is important to remark that, while the two populations that died during hibernation show significant amounts of vertebrate intake before dying (*U. praekudarensis* and *U. kudarensis*), *U. praekudarensis/kudarensis* teeth, which accumulated all year around, display fewer individuals with traces of animal protein consumption. Hence, the differences in the degree of vertebrate intake between the three populations could be related to the season of death, as microwear infers the diet of the last weeks before dying. Since *U. praekudarensis* and *U. kudarensis* died before entering dormancy, their dental microwear would be displaying hyperphagia. On the other hand, *U. praekudarensis/kudarensis* remains were mainly accumulated throughout the year by predators; consequently, its microwear signal would portray different seasons of death, and therefore the hypercoarse mean of the population would reflect a dietary signal representative of the mean annual diet (i.e., with a seasonal intake of vertebrates within an overall plant-based diet).

U. praekudarensis separated from *U. deningeri* around 800 ka B.P. (Stiller et al., 2014; Barlow et al., 2021). This is the earliest divergence among the cave bear lineage (Knapp et al., 2009). *U. praekudarensis* remains are only found in Kudaro caves, hence, it is a species that evolved in the high-altitude environments of the Caucasus in isolation from European cave bears

(Baryshnikov, 1998; Baryshnikov, 2007). Consequently, we can hypothesize that carnivorous behaviour during certain seasons might have been a retained characteristic of this early cave bear, while more advanced species specialised towards herbivory as reflected in the evolution of cheek teeth morphology (Baryshnikov and Puzachenko, 2020).

During the formation of Kudaro 1 layer 5c, the cave was used as a maternity den during winter hibernation, as suggested by the accumulation of females and first-year cubs that probably did not reach the requirements in energy reserves to endure it, although their death would not be due to harsh winters as in this layer winters were short and mild (Levkovskaya 1980; Baryshnikov, 2020b). Therefore, different explanations based on ecological niche competition with other species could explain this dietary behaviour in which *U. praekudarensis* would have had a carnivorous diet as fall-back food during certain seasons of the year. The presence of three plant-dominated omnivorous species might have shaped the ecology of the *U. praekudarensis* bear. Moreover, the hunting activities of two felids and human populations, which inhabited the cave more or less regularly, would have also contributed to the forming of *U. praekudarensis*' dietary niche before dormancy.

7.6.1.3 Intra-specific niche competition by *U. thibetanus*

First, the presence of *U. thibetanus* (subspecies *mediterraneus*, Forsyth Major, 1873) in the same layer (Baryshnikov, 2010), is a factor that should be considered to understand the reasons that could have driven *U. praekudarensis* to its dietary niche. The Asian black bear is a species with a highly variable omnivorous diet, almost completely based on plant resources, that varies seasonally from hard to soft mast, as well as invertebrates and with occasional intake of vertebrates (Hwang et al., 2001; Huygens et al., 2009; Furusaka et al., 2017; Panthi et al., 2019; Basnett et al., 2021). Furthermore, as stated before, the Asian black bear from layer 5c has been found to have had an arboreal lifestyle (Baryshnikov, 2010). The plant-based dietary niche of *U. thibetanus* might have overlapped to some degree with that of *U. praekudarensis* populations, with a highly variable diet, with a predominance of hard mast items, but also with soft mast consumption. The existence in the same landscape of two plant-dominant bear species, which are within a similar dietary niche, would have certainly created high competition for resources during the most energy demanding season of the year, i.e., during the period before dormancy.

Ecologically similar species can coexist by selecting different habitats or resources within a shared landscape (Schoener, 1974). Moreover, morphology and behaviour might influence

resource and habitat partitioning (Rosenzweig, 1991; Wisheu, 1998). For example, in North America, brown bears mainly obtain their food in open habitats, whereas American black bears prefer densely forested areas for foraging (Aune, 1994; Apps et al., 2006; Belant et al., 2006). This might be the case of *U. thibetanus*, well-adapted to dwelling high in the trees, favoured by its lighter weight and curved claws which allowed it to easily climb and reach places with high fruit concentration. This would be their preferred location in which they would have dwelled the most, as bears inhabit landscape areas with high food availability, and those which allow them to minimize their fitness requirements, especially during the hyperphagia period (Clark et al., 1994; Ruiz-Villar et al., 2019). Furthermore, minimizing their exposure to the risk of predation by other animals represents the second factor considered by a species when selecting a preferred area (Brown, 1988). Hence, the presence of two large felids in layer 5c, *P. gombaszoegensis* and *P. pardus*, as well as human populations, would have further shaped the forested and tree niche for *U. thibetanus* (Lioubine, 1998; Baryshnikov, 2011). In direct competition would be the two bear species inhabiting similar niches, at least during seasons low in resources, as smaller carnivores tend to distance themselves from larger ones (Creel et al., 2001). For example, in the tropical forest mosaics of Southeast Asia, sun bears (*H. malayanus*) systematically avoid eating in places where *U. thibetanus* recently exploited to avoid confrontation (Steinmetz et al., 2011). When food sources are concentrated in certain areas of the landscape, like in colder environments, competition by interference happens more frequently, for example, large brown bears from North America are reported to exclude the American black bear from places where salmon aggregate (Belant et al., 2006). Hence, as in the case of American bears, *U. thibetanus* from the Kudaro caves, with its smaller size and better adaptations to forest exploitation, could have been pushed by *U. praekudarensis* to forested areas, at least during times of the year with more diminished resources. In addition, another way in which niche displacement occurs is through exploitation competition, which tends to favour those morphologically better adapted to exploit a particular resource, e.g., Asian black bears avoid locations already harvested by sun bears because of the lower fruit density (Welch et al., 1997; Steinmetz et al., 2011). This scenario could apply to *U. praekudarensis*, which might have avoided the forested patches more effectively exploited by *U. thibetanus* due to the low availability of fruit, particularly during energetically demanding periods of the year, such as times of hyperphagia when energy reserves are stored in preparation for hibernation, and high food availability is needed (Coogan et al., 2014, 2018).

The hypothesis of niche partitioning with sympatric *U. thibetanus* during certain seasons is supported by the comparison of *U. praekudarensis* with extant *U. thibetanus* (Figure 69 and 71). The microwear analysis suggests a different dietary ecology for *U. praekudarensis* compared to the plant-based diet of *U. thibetanus*. Taking into account that the accumulation happened due to deaths during dormancy (Baryshnikov, 2020b), we can reinforce the idea that *U. praekudarensis* had a more carnivorous diet during hyperphagia, the reason which was niche partitioning with plant-based diet of *U. thibetanus*.

7.6.1.4 Competition for soft mast and underground vegetation

The presence of two porcupine species (*H. cf. refossa* and *H. brachyura*) in the same layer as *U. praekudarensis* suggests direct competition for herbivore resources. Porcupines have an opportunistic diet, considered strictly herbivorous, which changes according to food availability, shaped by seasonal variations, habitat diversity, and other factors, resulting in high ecological flexibility (Bruno and Riccardi, 1995; Chaudhary et al., 2015; Khan et al., 2022). Their diet is mainly based on bulbs, tubers, and roots, excavated with their limbs adapted for digging, but also includes soft and hard mast items such as forbs, grasses, leaves, and fleshy fruits as well as woody plants and hard-shelled and seeded fruit such as bark, twigs, and wild berries, corns, and seeds (Hafeez et al., 2011; Akram et al., 2017). However, their diet may include insects (Mori et al., 2020), and some species have been recorded to exhibit highly infrequent scavenger behaviour (Coppola et al., 2020). Furthermore, porcupines are known for gnawing bones as a source of calcium and phosphorus, which is consistent with the abundance of gnawing marks observed on bear bones from layer 5c (Duthie and Skinner, 1986; Baryshnikov, 2010; Baryshnikov, 2020a, b). Furthermore, the presence of *Macaca* sp. has also been recorded in layer 5c (Baryshnikov, 2002, 2020a). Macaques are generalist primates that have flexible foraging strategies that allow them to adapt to different environments, more specifically to northern latitudes and to higher altitudes (Cui et al., 2018, 2019; Zhang et al., 2023). Macaques living at high altitudes have been found to prefer herbaceous plants and leaves during the warm season (spring to summer) (Cui et al., 2019), but also fruit and seeds, although in lower proportions (Zhang et al., 2023). However, during autumn and winter, they mainly feed on plant roots, which is their dominant food during the cold season, followed by bark and fallen leaves as fallback foods (Cui et al., 2019; Zhang et al., 2023). Plant roots, as their principal fallback food, represent a key item for their survival in high-altitude severe winters (Zhang et al., 2023).

Therefore, both porcupines and macaques tend to adopt a generalist diet dominated by plant-based foods, which includes both soft and hard mast items. This diet overlaps with *U. praekudarensis*' dietary niche in layer 5c, consequently intensifying competition with omnivorous guild, mirroring the situation observed with *U. thibetanus*. Moreover, the preference for roots and tubers by porcupines year-round, and the utilization of plant roots and bark as fallback food by macaques living at high altitudes during the cold season indicate a niche overlap with the predominantly vegetarian diet of the European cave bear lineage (*Ursus spelaeus* - *deningeri*). Morphological studies on European cave bears have suggested the inclusion of underground storage organs of plants, such as roots and tubers, in their diets (Kurtén, 1976; Mattson, 1998; Athen, 2006). This assumption is indirectly supported by the very high frequency of canine breakage in cave bears, which exceeds that of aggressive hypercarnivores such as the extant polar bear and the extinct American lion (Valkenburgh, 2009; Prilepskaya et al., 2022), as well as microwear analysis (Ramírez-Pedraza et al., 2022; Duñó-Iglesias et al., 2024a). Hence, during the hyperphagia period, *U. praekudarensis* might have faced limited access to underground resources, which could have been more efficiently exploited by porcupines and macaques, similar to how *U. thibetanus* better exploited hard mast items from treetops of forested areas. During the period of hyperphagia, *U. praekudarensis* would probably need to broaden its diet by exploiting food areas that could offer abundant resources while also being energetically rich enough to survive the winter dormancy.

7.6.1.5 Female bear salmon exploitation and carcass scavenging during the hyperphagia period

Taphonomy of the *U. praekudarensis* accumulation of Kudaro 1 layer 5c, resembling a catastrophic mortality profile, indicates that their death occurred due to natural causes during the hibernation period (Baryshnikov, 2020a, b). This is further supported by sex and age ratios, as females and young individuals are predominant in layer 5c. This has been explained by how in warm periods males do not need to hibernate, only females and their cubs do (Baryshnikov, 2020b). If so, males may have died in Kudaro 1 during the warm season, as shown for *U. kudarensis* during MIS 3 (Prilepskaya et al., 2022). Cave bear females probably died due to not being able to fulfil the energetic requirements associated with reproduction and lactation (Farley and Robbins, 1995; López-Alfaro et al., 2013), while the young individuals could have died (in addition to nourishment deficiencies) due to a high predatory environment in which they were attacked in the den by large felids, such as jaguars and leopards (Baryshnikov, 2020b). Salmon (*Salmo* spp.) represents one of the most nutritionally rich resources available

for bears to accumulate protein and fat reserves before entering dormancy (Hilderbrand et al., 1999). The spawning season, which coincides with hyperphagia in bears, results in salmon concentrating in certain shallow rivers or streams, which makes them easier to hunt by bears (Gende et al., 2001; Belant et al., 2006). Therefore, given the presence of a river at the bottom of the valley, just 260 meters below the Kudaro Caves at present, and in the past much less, where humans had exploited fish resources during the latter Late Pleistocene layers (Baryshnikov, 1999; Bocherens et al., 2014b), we suggest the possibility of *U. praekudarensis* females exploiting this source during the hyperphagia period before dormancy. Bears display notably greater consumption rates when catching salmon compared to foraging for berries or herbaceous vegetation, leading to larger body sizes and higher reproductive rates in females, as the reproductive success of female bears is directly linked to sufficient body fat before entering dormancy (Samson and Pettorelli, 1995; Gende and Quinn, 2004). Salmon intake could have been driven by the need to accumulate energy reserves in a season with high competition for resources within the omnivorous guild, in which other species capitalised on plant resources. However, the analysed bears were unsuccessful in their attempt to achieve their energy requirements through salmon as they died in the den. This phenomenon may be attributed to the fact that access to salmon is constrained by socially dominant larger bears (potentially males), which significantly reduces the salmon intake of subordinates, and therefore their reproductive and survival success through confrontation in the salmon-rich streams (Gende and Quinn, 2004).

Furthermore, there is significant human occupation during the formation of layer 5c, due to the recurrent presence of Acheulean artefacts (Lioubine, 1998). However, there is no evidence of cut marks on *U. praekudarensis* bones, indicating the alternation between humans and bears in the cave. The age and sex profile of leopard remains suggest that *P. pardus* used the cave as a temporary shelter as well as to hide carcasses from its prey from other predators (Baryshnikov, 2020a, b). While fossil jaguar remains are limited to layer 5c, leopards appear in all levels, which suggest that this would have held the same top predator niche (Baryshnikov, 2011). Moreover, two canid species (*Canis kudarensis* and *C. mosbachensis*) were also recorded in layer 5c (Baryshnikov, 2002). The Middle Pleistocene *C. mosbachensis* had a predominantly carnivorous diet, although with the capacity to diversify into an omnivorous diet (Flower and Schreve, 2014). In landscapes with high competition for animal resources, *C. mosbachensis* scavenged ungulate carcasses already hunted by large felid predators (Courtenay et al., 2023), while coyotes were also social hunters with a meat-based diet (Hayward et al., 2023). Hence,

the presence of three top large predators, humans, jaguars, and leopards, together with two different canid species with predatory behaviour suggests that hunting competition was very high. So, carcasses would have been regularly found in the cave and its surroundings benefiting scavengers (Elbroch et al., 2017). The intense competition for dietary resources among the carnivore guild may explain the absence of specialised scavengers like hyenas (except for the vultures) while boosting the available carcasses for multiple facultative scavengers (Levi and Wilmers, 2012; Pereira et al., 2014; Sivy et al., 2018). Moreover, the absence of hyenas could have allowed the cave bear *U. praekudarensis* to occupy the scavenger niche seasonally, during the hyperphagia period, in a way to further supplement its diet. Being the largest specimen with facultative scavenger behaviour (Rabal-Garcé et al., 2012), *U. praekudarensis* could have potentially outcompeted smaller mesocarnivores like canids and the smaller Asian black bear in carcass scavenging (Allen et al., 2015; Inagaki et al., 2023). The partitioning of scavenger niches seasonally by different species while coexisting could be possible as observed in other ecosystems (Selva et al., 2005).

U. praekudarensis/kudarensis individuals displayed a much more plant-based diet in the weeks before their death, while still overlapping with northern omnivore populations in the CA and some of its individuals presented hypercoarse scratches. Therefore, this suggests a lower protein intake for *U. praekudarensis/kudarensis* in comparison to *U. praekudarensis*. However, it is important to note that *U. praekudarensis/kudarensis* populations probably accumulated throughout the year after being hunted by *P. pardus* or having died due to disease (Baryshnikov, 1999). Their mortality throughout the year could explain the low percentage of hypercoarse scratches, as only the individuals displaying those would have died during hibernation and therefore showed evidence of a hyperphagia diet. Hence, we cannot discard a carnivorous diet during specific moments of the year by *U. praekudarensis/kudarensis* populations, as the climate was more rigorous and access to plant foods would have been harder during certain seasons (Bojarska and Selva, 2012). Moreover, its year-round very abrasive diet could be also explained by a cold and arid environment, and the presence of grasslands through this period.

The accumulation of *U. kudarensis* bones suggests death by natural causes during hibernation, in which mostly old male cave bears occupied the cave and died due to not being able to endure harsh winter conditions (Baryshnikov, 2020b). Hence, as in *U. praekudarensis*, the microwear would portray their diet before entering dormancy. Their hard mast-dominated pattern would be related to the hyperphagia period as observed in Romanian Carpathian cave bears (Duñó-Iglesias et al., 2024a). Moreover, a diet almost completely based on hard mast could be easier

as competitors such as *Macaca* and *U. thibetanus* were no longer present in the landscape, and only porcupines remained, but in declining numbers and only during the initial MIS 5 warmer phases and finally disappearing during subsequent substages of layer 4 characterised by colder conditions (Baryshnikov, 1999). Their carnivorous microwear pattern, which is the highest among the three populations, could be explained by colder climatic conditions. Recent studies on isolated extant brown bear populations have suggested a transition towards more carnivorous behaviour in alpine cold high-altitude environments (García-Vázquez et al., 2023). This shift is likely influenced by the limitations on plant-based resources due to increased snowfall at higher altitudes (Bojarska and Selva, 2012). This adaptation could also apply to *U. kudarensis* populations, especially considering the increasingly harsher winters they had to endure during the end of MIS 5 and the beginning of MIS 4. Finally, we can consider that, as large old bears, they would have had the ability to consume higher quantities of salmon (and their better-quality parts) as well as carrion, as seen in extant bears (Creel et al., 2001; Gende et al., 2001). Furthermore, human populations are recorded to have an increasing role in the accumulation of ungulate bones in the cave throughout layer 4 (Baryshnikov, 1999, 2020b). Hence, numerous carcasses would have been found in the cave too, much more than in older layers. This is recorded, for example, with red deer (Baryshnikov, 1999). In summary, we cannot discount fish consumption and scavenging of abandoned carcasses by *U. kudarensis* bears during hyperphagia as alternative food, as plants were increasingly restricted during colder phases in high-altitude environments of the Caucasus. This high-altitude adaptation would have resembled the diet of the Middle Pleistocene *U. praekudarensis*.

7.6.1.6 Final remarks

The Caucasian cave bears are a singular case of evolution in high-altitude isolation. The dental microwear analysis of the Kudaro cave bear populations reveals a complex and varied dietary adaptation influenced by climatic changes and ecological pressures throughout the Middle and Late Pleistocene. These findings highlight the complexity of Pleistocene ecosystems and the adaptive responses of early cave bears to climatic and environmental changes over time. Moreover, the resilience of the Kudaro bears underscores the capacity of cave bears to endure climatic shifts, although they were vulnerable to the presence of other omnivorous guild competitors, which could have been the driving force in shaping their dietary niche throughout the Pleistocene. Hence, it is important to consider the possibility of large omnivores (humans and other bear species) shaping the cave bear diet over time (Medin et al., 2019). Nevertheless, this suggests that their disappearance would have not only been through direct hunting

(Verheijen et al., 2023; Toniato et al., 2024), but also through ecological exclusion during harsher climatic conditions.

7.6.2 Seasonal niche overlap between *U. arctos* and *U. spelaeus* during MIS 3

First, based on our results, there was an overlap in seasonal dietary niches between Late Pleistocene *U. arctos* populations from Eastern Europe and *U. spelaeus* during MIS 3 (Figure 76 and 77; For a more detailed description of the bivariate plots and correspondence analyses, see Appendix section A.4.1) Although the isotopic signatures of pre-Last Glacial Maximum (LGM) brown bears have been interpreted as indicative of a predominantly carnivorous diet (Münzel et al., 2011; Bocherens, 2015; Bocherens et al., 2015; Ersmark et al., 2019), elevated isotopic values may reflect adaptations to colder, more open environments. This was the case for steppe-adapted giant brown bear *U. arctos* “*priscus*”, with a diet based on scavenging in northern latitudes of European continent during MIS 3 and MIS 2, and with daily meat intakes up to 50 kg in order to maintain its body-size (Mattson et al., 1991; Schwartz et al., 2014; Marciszak et al., 2019b). In contrast, smaller-sized brown bears inhabiting temperate refugia may have maintained a more omnivorous diet, with a substantial intake of plant matter (Sommer and Benecke, 2005).

This interpretation is supported by $\delta^{15}\text{N}$ values consistent with an intermediate trophic level compatible with omnivory in MIS 3 *U. arctos* from Duruitoarea Veche, Buzdujeni, and Butești, which notably overlap with the $\delta^{15}\text{N}$ values recorded for *U. spelaeus* from the same sites—all included in our study (Robu et al., in prep.). This is further reinforced by the observed overlap in seasonal dietary patterns at the species level between MIS 3 *U. arctos* and *U. spelaeus* in Eastern Europe glacial refugias.

Moreover, while some differences in the mean quantity of coarse scratches are observed in the microwear analyses, suggesting locally distinct dietary preferences between coexisting Late Pleistocene *U. arctos* and *U. spelaeus* populations in the Romanian Carpathians, the individual population distribution pattern indicates a stronger degree of dietary overlap than distinction, as observed in the CA (Figure 43). This overlap is evident at both regional and local scales—for instance, in the Romanian Carpathians, MIS 3 *U. arctos* overlaps with some extreme-range *U. spelaeus* individuals from Oase, Urșilor, and Muierilor (CA; Figure 43), and in the Moldavian Plateau, where the correspondence analysis shows proximity between *U. spelaeus* and *U. arctos* from Trinca (Figure 47). Additionally, in the Moldavian Plateau region, the

bivariate plot of coarse and fine scratches further supports seasonal dietary overlap with *U. spelaeus* from the same area (Figure 46; as also indicated by overlapping $\delta^{15}\text{N}$ values reflecting lifespan dietary signals in the same individuals analysed in this study; Robu et al., in prep.). However, local niche partitioning between *U. spelaeus* and *U. arctos* at Trinca is suggested by differences in the average quantities of coarse and fine scratches (Figures 45).

Therefore, these microwear patterns support the hypothesis that *U. arctos* populations from temperate Eastern European refugia competed with *U. spelaeus*, at least seasonally during the pre-dormancy period; a critical time for accumulating energy reserves for hibernation. This seasonal competition may have disproportionately affected *U. spelaeus*, a larger species more reliant on plant-based resources, especially under conditions of declining availability of high-quality vegetation and increasingly open landscapes (Pacher and Stuart, 2009).

7.6.2.1 Holocene *U. arctos* divergent dietary trajectory

The comparison between the microwear patterns of MIS 3 *U. spelaeus* and *U. arctos*, and those of Holocene *U. arctos* from the Romanian Carpathians, reveals a clear divergence of the latter from both MIS 3 ursids (see detailed discussion in Appendix section A.4.1). Notably, the hypothesis of niche inheritance—where post-LGM *U. arctos* would have occupied the ecological niche left vacant by *U. spelaeus* following its extinction (Münzel et al., 2011; Bocherens, 2015; Mackiewicz et al., 2017; Duñó-Iglesias et al., 2024a)—is not supported by our data. While MIS 3 *U. arctos* from the temperate refugia of Eastern Europe overlapped seasonally with *U. spelaeus*, suggesting potential competition, Holocene *U. arctos* appears to have shifted toward a distinct dietary strategy, occupying a niche that does not overlap with that of the extinct cave bear.

This suggests that, rather than inheriting the niche of *U. spelaeus*, Holocene *U. arctos* adapted to a transformed postglacial landscape and its associated resource base (Sommer and Benecke, 2005). Its diet was likely more strongly plant-based, reflecting the highly forested temperate forest conditions of the Romanian Carpathians, with a diet heavily herbivorous, depending highly in hard-shelled and seeded fruit as observed for extant brown bear of the region (Slobodyan, 1976; Kalabér et al., 1994; Bojarska and Selva, 2012). This new niche, characterized by a more herbivorous dietary strategy adapted to temperate forest environments—and potentially extrapolatable to other regions of Eastern, Central, and broader Europe—would be consistent with the overall reduction in body size observed in Holocene *U. arctos* populations from the region (Marciszak et al., 2015). Consequently, any discussion of

niche continuity must account for the broader ecological transformations that accompanied the onset of the Holocene, which likely shaped new dietary trajectories for surviving ursid populations.

7.7 Inter-regional and inter-chronological dietary comparison

The following section addresses the third objective of this study: to assess inter-regional and inter-chronological dietary variability within *U. spelaeus* populations across Eastern Europe. By comparing cave bear populations from distinct biogeographic regions and different chronological contexts, this section explores whether variations in landscape structure, environmental conditions, and competition pressures influenced seasonal foraging strategies. The aim is to determine the extent to which regional and local ecological factors may have driven divergent dietary adaptations within the cave bear lineage.

7.7.1 Local dietary flexibility in cave bears: lack of species-level trends and no correlation with chronological, geographic or climatic variables

The combined analysis of all studied populations revealed substantial variability in cave bear microwear patterns, with dietary flexibility becoming increasingly pronounced at finer spatial scales, from inter-regional to local and individual levels (see detailed discussion in Appendix section A.4.2).

Hence, the study did not identify consistent dietary trends at the species level, though slight regional patterns were observed—albeit with substantial overlap. More pronounced trends emerged at the local population level, along with notable variability at the individual level. Moreover, the chronological range attributed to each population, as well as the calibrated dates of single individuals, did not appear to be driving differences in seasonal dietary patterns (see in detail in Appendix section A.3.4).

The exploratory analysis of potential correlations between microwear features and biogeographic or climatic variables revealed no statistically reliable associations. Almost all Pearson correlations were very low (<0.3). While moderate correlations were observed between hypercoarse scratches and several climatic variables, i.e., annual precipitation ($r = +0.52$) and maximum temperature of the warmest month ($r = -0.30$), as well as geographic variables, including longitude ($r = +0.37$) and elevation ($r = +0.36$), none of the corresponding regression models met the core assumptions required for valid linear modelling. This is largely due to the very limited number of populations exhibiting hypercoarse scratches, specifically *U. praekudarensis* (MIS 8/7) and *U. kudarensis* (MIS 5/4) from the Caucasus; which not only

share identical geographic conditions (i.e., originating from the same cave, Kudaro-1, but different stratigraphic levels) and similar climatic settings (despite a temporal gap between them), but also differ markedly from the other 25 populations in the dataset in both geography (being located much further east) and climate (a high mountain climate, as being in Southern slope of Greater Caucasus at an elevation of 1,600 meters a.s.l.). This lack of variability severely limits the reliability and interpretability of the regression models.

The same outcome was observed when correlating microwear features with time (based on stratigraphic level of population mean dates). The only variable with a Pearson's r value exceeding 0.3 was NHC (number of hypercoarse scratches); however, the apparent trend was primarily driven by a few outlier populations (Greater Caucasus *U. praekudarensis* and *U. kudarensis*) with extreme values, rather than reflecting a consistent temporal pattern across the dataset. For a more detailed explanation see Appendix, section A.3.4.

7.7.2 Flexible opportunism or inherited foraging—or both?

However, the lack of association between microwear patterns and climatic or geographic factors may also be explained by ecological behaviour of cave bears. The lack of clear patterns could potentially be reflecting the inherently opportunistic and flexible feeding behaviour of ursids, which Pleistocene cave bears are included, which would have adapted their diet in response to highly variable seasonal resource availability, inter- and intra-specific competition pressures, etc. This pattern is also observed in extant brown bear populations from different regions, which exhibit local adaptations to resource availability and seasonally adjust their diets in response to the specific ecological conditions of their landscapes (e.g., Frackowiak, 1997; Persson et al., 2001; Rigg and Gorman, 2005; Paralikidis et al., 2010; Bojarska and Selva, 2012; Stenset et al., 2016; Ogurtsov, 2018).

However, an alternative explanation may lie in the inheritance of foraging behaviours through social learning in cave bears. A recent study by Meleg et al. (2024), which correlated isotopic signals from bone collagen with geographic location, sex, and genetic data (DNA) at the individual level, revealed that cave bears adapted their feeding strategies primarily through individual experience rather than being constrained by genetic or environmental factors. The authors concluded that time period, geographic context, sex, and population affinity were not the main drivers of dietary variation in Carpathian cave bears (Meleg et al., 2024). Instead, social learning—where younger individuals adopt foraging behaviours from older group

members—may account for the intrapopulation dietary variability observed in Romanian Carpathian populations.

Further support for this hypothesis comes from a recent preliminary study by Duñó-Iglesias et al. (2024c), which explored whether short-term, seasonal pre-dormancy dietary differences among MIS 3 cave bear populations in the Romanian Carpathians could be linked to sex or age. While no significant dietary differences were found between sexes, individuals in more advanced wear stages exhibited a higher frequency of puncture pits. This pattern suggests that age-related dietary variation, rather than sex-based differences, played a more significant role in shaping short-term feeding behaviour. The observed microwear trends by age lend further support to the social learning hypothesis proposed by Meleg et al. (2024), implying that younger bears likely acquired foraging strategies from older individuals (Duñó-Iglesias et al., 2024c).

Hence, given that dietary variation cannot be accounted for by climatic, geographic, or chronological factors, it may instead reflect locally inherited foraging behaviours within specific groups, shaping their adaptability to particular local biomes. This interpretation aligns with evidence of extreme fidelity to birth site in cave bears, known as “homing behaviour” (Fortes et al., 2016). A mitochondrial DNA study suggests that specific lineages of cave bears may have repeatedly hibernated in the same caves (Fortes et al., 2016), thereby remaining within the same local area. Such site fidelity could have favoured the development of distinct foraging strategies through social learning over time, potentially explaining the observed dietary variability among populations at a seasonal scale.

This potential for dietary differentiation at the local scale may help explain the high morphological variability observed within the same clade—even within *U. spelaeus* sensu stricto—and even from geographically proximate cave sites (Baryshnikov, 1998; Torres et al., 2002; Baryshnikov and Puzachenko, 2011; Goubel et al., 2012; Millán-Arnau, 2023), as diet is a key evolutionary driver that may have shaped both cranial and postcranial morphology in response to specific biomes over relatively short geological timescales. This theory is further supported by evidence of rapid evolutionary change in dental morphology within a single local population at Scladina Cave (Belgium), where statistically significant thickening of the lower second molar (M2) occurred within less than 100,000 years—a remarkably short timescale in evolutionary terms (Charters et al., 2019).

7.7.3 Constraints in data acquisition

However, the absence of correlations between microwear patterns and climatic, geographic, or chronological variables may reflect limitations inherent to the dataset, including uncertainties in dating resolution and temporal mismatches between short-term dietary signals and broader-scale climatic reconstructions.

The climatic data used are based on the *Paleoclim* package (see more detailed description in Materials and Methods section 5.2.4), which links climate variables to specific coordinates and time periods; that is, the same geographic location will yield different climatic values depending on the selected time slice (in years B.P.), as expected. The main issue lies in the absence of direct radiocarbon dating for most of the studied remains, with the exception of a small subset of calibrated specimens ($n = 11$). As a result, broad chronological assignments must be made based on the stratigraphic level from which the specimens were recovered. Moreover, in several cases, no absolute dating is available at all, and only relative dating through biochronology has been used, often assigning the specimens to MIS 3, a period characterized by high climatic variability. Consequently, the climatic conditions attributed to a given individual, which were averaged from its attributed time-span, may not accurately reflect those experienced during its lifetime.

Additionally, dental microwear captures only a short-term dietary signal, typically representing the last days or weeks before death. Importantly, as inferred by Prilepskaya et al. (2022) through the study of dental cementum layers, cave bears did not use caves exclusively during the autumn for hibernation but may have entered them year-round. Therefore, aside from certain sites where mortality profiles suggest a specific seasonal (hibernation-related) accumulation, many other sites without such contextual data may reflect individuals that died during different seasons. As a result, the observed microwear patterns could correspond to varying seasonal diets, formed under different climatic conditions, given that not all seasons are climatically equivalent.

7.8 Too locally specialized to survive?

This study first aimed to assess dietary differences among cave bear populations across Eastern Europe. The results reveal pronounced variation in foraging strategies, both inter- and intra-region. These differences likely reflect seasonal dietary shifts and provide direct evidence for omnivory at a seasonal scale in *U. spelaeus* sensu lato. The presence of such seasonal dietary flexibility suggests that cave bears may have adopted diverse foraging strategies prior to

hibernation, particularly during this season given their widespread accumulation in karstic systems, typically linked to hibernation deaths (Kurtén, 1976; Grande d'Anglade et al., 2019)—though not exclusively, as bears might have entered caves at different seasons (Prilepskaya et al., 2022). This dietary plasticity challenges the long-standing hypothesis that cave bears declined due to the disappearance of the Mammoth Steppe ecosystem, as was the case for much of the herbivorous European megafauna (e.g., *Mammuthus*, *Celodonta*, *Megaloceros*). Moreover, their disappearance happens around ca. 27 ka B.P. (Pacher and Stuart, 2012), although its populations start diminishing much earlier (e.g., Stiller et al., 2010; Robu et al., 2024). Long before Mammoth Steppe herbivorous megafauna disappeared after the LGM (Stuart and Lister, 2012).

The capacity for dietary flexibility may have enabled cave bears to specialize in the specific biomes they inhabited, thereby promoting morphological diversification (see section 7.7.2). Building on these observations, a more nuanced extinction scenario for *U. spelaeus* is proposed—one that emphasises ecological specialization not at the species level, but at regional or even population scales. While cave bears were clearly capable of exploiting a broad spectrum of dietary resources, such localised adaptations may have restricted their wider ecological plasticity, rendering populations increasingly vulnerable to environmental and competitive pressures. This adaptive behaviour likely gave rise to highly specialised forms, each shaped by their immediate environments during the latter half of MIS 3—for example, the high-altitude *U. kudarensis* in the Caucasus Mountains (Baryshnikov, 1998); the diminutive alpine *U. s. eremus* and *U. s. ladinicus* in the Austrian Alps (Rabeder et al., 2004b, 2008); and multiple interspecific forms within the western European *U. spelaeus*, as evidenced by distinct dental morphotypes, while similar diversification is observed among eastern European populations, including *U. (k.) ingressus* and subspecific forms such as *U. k. uralensis* (Rabader, 2004; Baryshnikov and Puzachenko, 2011). The steppe-adapted *U. s. rossicus*, in turn, occupied the open landscapes of the eastern European plains and western Siberia (Baryshnikov and Foronova, 2001; Spassov et al., 2017). Within each form, distinct local foraging adaptations arose across Eurasia, resulting in increasingly specialised and genetically isolated populations—consistent with the long-term genetic decline documented prior to extinction (Stiller et al., 2010). This would be supported by a high incidence of skeletal pathologies (Marciszak et al., 2024), potentially reflecting elevated levels of endogamy resulting in a genetic bottleneck (Stiller et al., 2010). Their foraging adaptations to the immediate local environment may have limited their ability to disperse over long distances and reduced

opportunities for gene flow between populations. This restricted mobility, coupled with an increasingly fragmented landscape, declining resource availability, and rising interspecific competition with *U. arctos*; as evidenced by overlapping stable isotope signatures (Richards et al., 2008; Robu et al., 2013, 2018; Robu et al., in prep.) as well as dental microwear patterns, indicating niche overlap—would have further constrained their ecological resilience. In addition, competition for cave space with *H. sapiens*, as suggested by widespread cut marks on cave bear bones across Europe (e.g., Terlato et al., 2019; Blasco et al., 2020; Toniato et al., 2024), likely exacerbated the pressures contributing to their decline (Fortes et al., 2016).

Ultimately, a confluence of habitat degradation, intensified competition with more generalist species such as *U. arctos* (which exhibits overlapping lifespan and seasonal dietary signatures; see section 7.6.2), and anthropogenic disturbance—particularly of hibernation cycles and cave occupancy—may have collectively driven the extinction of *U. spelaeus*.

CONCLUSIONS

8. Conclusions

This Master's thesis presents conclusions of relevance to palaeontological field research, specifically concerning cave bear ecology and the evolutionary history of the species. The present work represents a pioneering investigation into the seasonal dietary patterns of cave bears, a topic that has remained largely underexplored. Unlike previous macro-regional studies that focused on cave bear diets through evolutionary-scale proxies, such as morphological adaptations or lifespan average diets inferred from isotopic analyses, this work examines short-term, seasonal dietary variability across a broad geographical expanse of Eastern Europe. Hence, the results provide meaningful contributions to the general understanding of cave bear ecology and the evolutionary history of this taxon across several key scientific debates. The key findings of this study have been organised into four thematic areas: cave bear ecology, cave bear dietary evolution, *U. arctos* seasonal niche evolution, extinction dynamics of cave bears and methodological insights derived from this work.

8.1 Cave bear ecology

This work highlights first, the seasonal flexibility of cave bear ecology. Hence, rather than a species-wide, uniform herbivorous dietary regime dependent on the Mammoth Steppe biome and consistent across their Eurasian range, as previously suggested by the study of isotopic values (e.g., Bocherens et al., 1994, 1997, 2014a, 2015; Naito et al., 2020) and morphological studies (e.g., Kurtén, 1976; van Heteren et al., 2016; van Heteren and Figueirido, 2019), the cave bears displayed capacity for at least seasonal ecological flexibility, more comparable to that observed on extant omnivorous bears from northern hemisphere such as brown bears. This plasticity in the diet, though adapted to Pleistocene ecological landscapes, can be interpreted as indicative of omnivory. Such variation in microwear signals may reflect the capacity to exploit a broad spectrum of both plant and animal resources. The capacity for occasional meat inclusion is further supported by microwear patterns that overlap with those of extant bear species, particularly *U. arctos* and, in certain populations, with the hypercarnivorous *U. maritimus*, reinforcing the inference of a broader, more diverse foraging ecology in *U. spelaeus* than previously assumed. Further support for this interpretation comes from evidence that cave bears were facultative scavengers (Rabal-Garcés et al., 2021).

Furthermore, this plasticity appears to have been highly responsive to local ecological and competitive pressures, suggesting an adaptable foraging strategy. The perpetuation of these seasonal diets through stratigraphy, regionally to some extent (e.g., high plasticity in the Romanian Carpathians or soft mast dominance in Central Balkans populations), but more

consistently at the local population level, suggests that cave bear ecology may have involved a degree of behavioural inheritance, with foraging strategies transmitted from older to younger individuals over time, as suggested by Meleg et al., 2024 for Romanian Carpathians cave bears. However, the present work infers such behavioural inheritance not only in the Romanian Carpathians, but also across other Eastern European cave bear populations, suggesting it may represent a species-wide ecological trait.

The foraging behaviour of cave bears, particularly during the hyperphagic period preceding hibernation, a critical time for survival, was likely closely tied to the surrounding landscape. As a result, their diets became increasingly dependent on the specific environmental conditions and resources available within each biome, reinforcing a strong ecological link between foraging strategies and the immediate landscape. This is supported by the highly divergent microwear patterns observed among populations, which contrast with uniform expectations at the species level.

Their foraging strategies thus adapted to specific biomes and the resources those environments provided, becoming increasingly localised during the Late Pleistocene, as suggested by their long-term homing behaviour (Fortes et al., 2016). A period marked by growing climatic instability and a progressively more homogeneous landscape likely pushed MIS 3 cave bears into restriction within refugial areas. This is supported by very late dates associated with the studied cave bear populations, for which 27 ka B.P. represents the latest known extinction date in Eastern Europe.

8.2 Cave bear dietary evolution

This work has inferred through the study of *U. kudarensis* lineage of the Greater Caucasus that cave bears might have evolved their dietary niche not only adapting to the Pleistocene climate but more driven by competition with other agents of the landscape. This study proposes the possibility that large omnivores (humans and other bear species) shaped the cave bear diet over time (Duñó-Iglesias et al., 2024b). This remark has two major implications, the first regarding the evolution towards a plant-based diet, the second for their extinction dynamics (as discussed in detail in section 8.4).

The morphological evolution of the cave bear appears to have started to shift towards increased herbivory around 1-0.9 Ma B.P., however a plant-based diet is not inferred through lifespan proxies (i.e., stable isotopes) until the end-Middle Pleistocene. While the Late Villarfranchian *U. etruscus* from Orce (ca. 1.2 Ma) had an omnivorous opportunistic diet including both plants

8. Conclusions

and fish, as inferred by dental microwear and stable isotopes, similar to extant *U. arctos* (Medin et al., 2017). The derived *U. deningeri* (which diverged *ca.* 1-0.9 Ma; Madurell-Malapeira et al., 2010) already exhibits morphological adaptations for a plant-based diet (van Heteren et al., 2019). Nonetheless, isotopic studies from Yarimburgaz Cave (Turkey, *ca.* 600 ka B.P.) still suggest lifespan omnivorous diet similar to that of co-existing *U. arctos* (Stiner et al., 1998), while lifespan herbivory is inferred from stable isotopes in later forms from Sima de los Huesos (*ca.* 350 ka B.P.) (García, 2009).

The inference of a plant-based diet, based on both evolutionary-scale and lifespan average dietary proxies, aligns with two key chronological moments, respectively:

- 1) The onset of global climatic cooling during the early Weichselian Glaciation (e.g., Rasmussen et al., 2014), which coincides with morphological adaptations toward herbivory at the evolutionary scale (*ca.* 1 – 0.9 Ma); namely, the emergence of the first cave bear species, *U. deningeri*.
- 2) The appearance of a fully hunter-gatherer subsistence strategy and the intensification of human impact on the environment, marked by the introduction of Acheulian technology *ca.* 650 ka B.P. in Europe (e.g., Moncel and Schreve, 2020). This precedes the isotopically inferred plant-based, lifespan average diet of cave bears.

Both our results and other dietary proxies, when considered in light of their respective resolutions (evolutionary, lifespan and seasonal), suggest that climatic cooling alone was not the sole driver pushing this taxon towards herbivory, but that other agents, such as other bear species (*U. arctos* and *U. thibetanus*), and more significantly, human presence, also played a significant role. Hence, while climate and landscape changes might have started this dietary transition, it is probable that humans and more efficient and smaller omnivores (i.e., *U. arctos*) further displaced cave bears from the omnivorous dietary niche. Nonetheless, cave bears retained seasonal capacity for omnivory, particularly during the pre-hibernation hyperphagic period, to accumulate energy reserves for surviving hibernation and enabling reproduction (Duñó-Iglesias et al., 2024a, b; Duñó-Iglesias et al., 2025), although their diet remained primarily plant-based throughout the year. This capacity for flexibility may have been a plesiomorphic trait that enhanced survival during ecologically harsh seasons, therefore cave bears might have maintained it until its extinction.

8.3 Brown bear seasonal niche evolution

The results of this study challenge the long-standing paradigm of entirely separate ecological niches for the co-extinct species *U. spelaeus* and *U. arctos*. Instead, they suggest a more complex relationship, involving regional niche overlap and possible local-scale partitioning, with important implications for interspecific competition. Microwear data presented in this work reveals overlapping dietary patterns between the two species in Eastern European glacial refugia, although at the local scale, niche partitioning appears to have occurred, likely as a strategy to reduce direct competition.

Another important insight from this study is that, although *U. arctos* and *U. spelaeus* exhibited seasonal dietary overlap during MIS 3 in Eastern European refugia, our results do not support the hypothesis that post-LGM brown bears inherited the ecological niche of the extinct cave bear (e.g., Münzel et al., 2011; Bocherens, 2015; Mackiewicz et al., 2017; Duñó-Iglesias et al., 2024a). Instead, Holocene *U. arctos* populations appear to have diverged ecologically from their MIS 3 counterparts, occupying a distinct niche adapted to the transformed, forested landscapes of the postglacial period. This suggests that *U. arctos* was not a direct ecological successor to *U. spelaeus* but rather became a more efficient flexible generalist capable of adapting to major biome shifts, further underscoring its long-term ecological success relative to its extinct counterpart.

8.4 Extinction dynamics of cave bears

Finally, this work infers that the cave bear extinction cannot be explained the climate instability as extinction cause alone. The same agents that may have driven the dietary evolution of this species could also have played a role in its decline and eventual extinction.

The climatic cooling and homogenization of the landscape, and therefore, the disappearance of the biomes to which each local clade had adapted was compounded by the pressure of other agents, namely the arrival of anatomically modern humans (*H. sapiens* ca. 50 ka B.P.).

While *H. sapiens* might have displaced them from their ancestral lineage-specific dens and areas, potentially disrupting their essential pre-dormancy hyperphagia; a period focused on acquiring large amounts of energy to survive hibernation and, crucially, to enable female reproduction. The increasing presence of human groups in the landscape could have disrupted cave bear hibernation, with major cave bear accumulations likely resulting not from direct hunting, but rather from ecological displacement and disturbance.

8. Conclusions

Regarding *U. arctos*, this study demonstrates seasonal dietary niche overlap with *U. spelaeus*. Although both species shared the same landscapes for millennia, diminishing resources and rapidly changing environments intensified competition. *U. arctos*, having a lower caloric requirement due to its smaller body size, may have required fewer resources to survive.

Moreover, the wide genetic flow and the presence of brown bear populations across northern and mid-latitude Europe (Marciszak et al., 2019a), even during the LGM (Ersmark et al., 2019), suggest a greater dispersal capacity compared to *U. spelaeus* (Marciszak et al., 2019b). This is further supported by mitochondrial DNA studies indicating continuous gene flow and a lack of long-term population isolation across the continent for *U. arctos* (Dröppes and Pacher, 2014; Edwards et al., 2014; Çilingir et al., 2016; Ersmark et al., 2019). This continuous gene flow might explain why no speciation is documented in brown bears, in contrast to the cave bear lineage, where recurrent isolation favoured regional diversification and speciation (e.g., Puzachenko and Baryshnikov, 2011, 2017).

As a result, *U. arctos* was not strictly dependent on specific landscapes or cave systems, which likely provided an advantage for its long-term survival and genetic viability. Unlike *U. spelaeus*, it faced fewer constraints on movement between populations and was able to colonise new areas more rapidly, maintaining healthy gene flow. In contrast, the cave bear experienced a long-term genetic decline traceable over more than 50 ka (Stiller et al., 2010). All this multiplicity of factors led to its eventual extinction.

8.5 Methodological insights

The present study highlights the potential of low-magnification dental microwear analysis to reconstruct the diets of Pleistocene ursids without requiring integration with stable isotope data, as the two proxies reflect different temporal scales, lifespan averages versus short-term, seasonal dietary signals. While the integration of dental microwear and stable isotope analyses can be informative in omnivorous species, the seasonal resolution of microwear signals requires further investigation and refinement to fully realise its interpretive potential.

This study underscores the need to develop a new reference framework that accounts for:

- 1) Seasonal variation in bear diets, as these animals are known to adjust their foraging strategies throughout the year. Such a framework could help identify seasonal dietary patterns across different populations. It would also be of interest to explore whether microwear analysis can be used to infer seasonality in the accumulation of the studied

populations, as has been successfully done in strictly herbivorous taxa that, like ursids, undergo seasonal dietary shifts (Rivals et al., 2015).

- 2) Precise knowledge of the biome the studied bear inhabited the weeks before dying would be essential for improving palaeoecological reconstructions through ursids microwear patterns.

Finally, it is important to highlight that other microscopy techniques with greater quantitative power should be applied, ideally in combination with machine learning approaches, to detect dietary patterns in omnivorous ursid species with greater precision. The following chapter, "Future research", addresses the methodological challenges raised in this study and outlines the development of a new reference collection of extant bears, supported by the implementation of novel analytical techniques and the integration of multiple microscopes.

FUTURE RESEARCH

9. Future research

The need for a new dental microwear referential for bears has been highlighted by the present study, particularly for improving the resolution of dietary inferences in omnivorous species. Consequently, a new microwear reference collection comprising *U. arctos* specimens from various regions across Eurasia has been proposed, combining different microscopes and methodologies.

9.1 Species selection

The selection of *U. arctos* as the sole species in this collection is primarily based on its close phylogenetic relationship with the *Spelearctos* subgenus, specifically the *U. spelaeus* clade, with which it shares a common ancestor (García et al., 2003; Knapp et al., 2009; Barlow et al., 2021).

9.2 Sampling area

The area selected comprehends the northern latitudes of the Eurasian continent (Figure 79). The selected specimens span a broad geographical range across Eurasia—from the Carpathians and Caucasus in the west, through the Urals and Central Asia, to Eastern Siberia, the Russian Far East, the Hokkaido and Kuril Islands and even Alaska—thus encompassing a diverse array of biomes including temperate forests, alpine zones, steppe, taiga, and costal environments. The map (Figure 79) shows all *U. arctos* populations sampled for the dental microwear reference collection. These specimens were hunted during the XIX and XX centuries, with both the date and location of death recorded. This information allows for precise determination of the biome each individual occupied prior to death (e.g., steppe, taiga, alpine...), as well as the season in which they died. These data can be cross-referenced with regional ecological studies documenting the dietary habits of local *U. arctos* populations in each region, thereby enabling a more accurate correlation between specific biotopes, seasonal diets, and the observed dental microwear patterns.

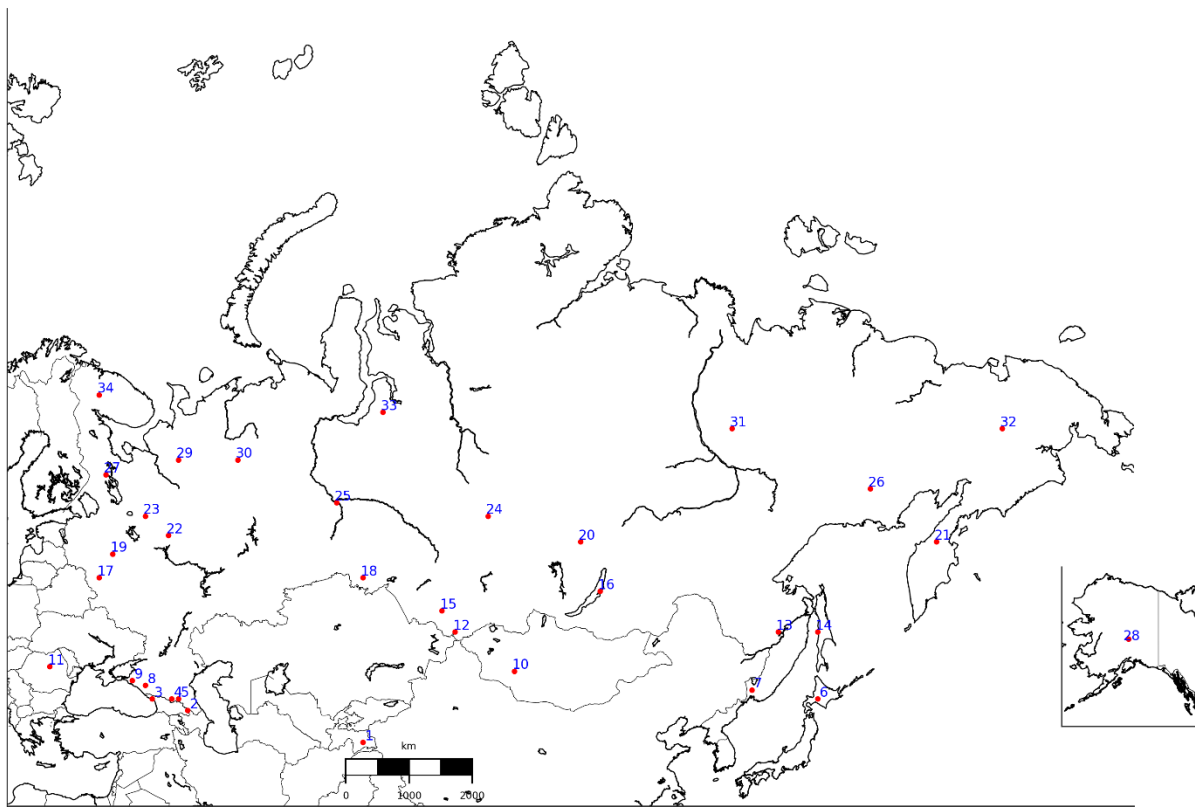


Figure 79. Geographic distribution of *U. arctos* populations included in the dental microwear reference collection, with precise location and date of death recorded for each specimen. Numbered points indicate regional sampling sites across Eurasia and Alaska, encompassing diverse biomes (e.g., steppe, taiga, alpine, coastal) and enabling detailed ecological and seasonal dietary patterns information to be attributed to each individual.

Given that *U. arctos* exhibits marked seasonal variation in diet (e.g., Bojarska and Selva, 2012), this approach significantly enhances the resolution of dietary reconstructions based on microwear analysis.

9.3 Microscopes and methodologies employed

The aim of building this referential is to explore dental microwear using multiple methods, leveraging the strengths of each to scientifically refine dietary determinations. Hence, the aim is to integrate low-magnification microscopy with confocal profilometry and texture analysis. This combined methodological approach has previously been applied to primate reference collections and was successfully used to infer diet in a fossil macaque (*M. cf. sylvanus*) dated to the Plio-Pleistocene transition (~2.4 Ma) in North Africa (Ramírez-Pedraza et al., 2023). This approach has also been applied in dental microwear analysis of Caprinae to distinguish management practices in the Neolithic fossil record based on microwear patterns (Ibáñez et al., 2020). Hence, the following microscopes will be employed, (1) the stereomicroscopy under

9. Future research

transmitted light at low magnification ($\times 35$), following the methodology of Solounias and Semprebon (2002), (2) the Sensofar® S Neox microscope (Figure 80) operated with SensoSCAN® 6.2 software and located at IPHES-CERCA (Tarragona, Spain), coupled with Scale-Sensitive Fractal Analysis conducted using *Mountains*® software—officially distributed as SensoMap® version 10.3, the customized edition developed for the Sensofar® microscope (Ungar et al., 2003; Scott et al., 2006).

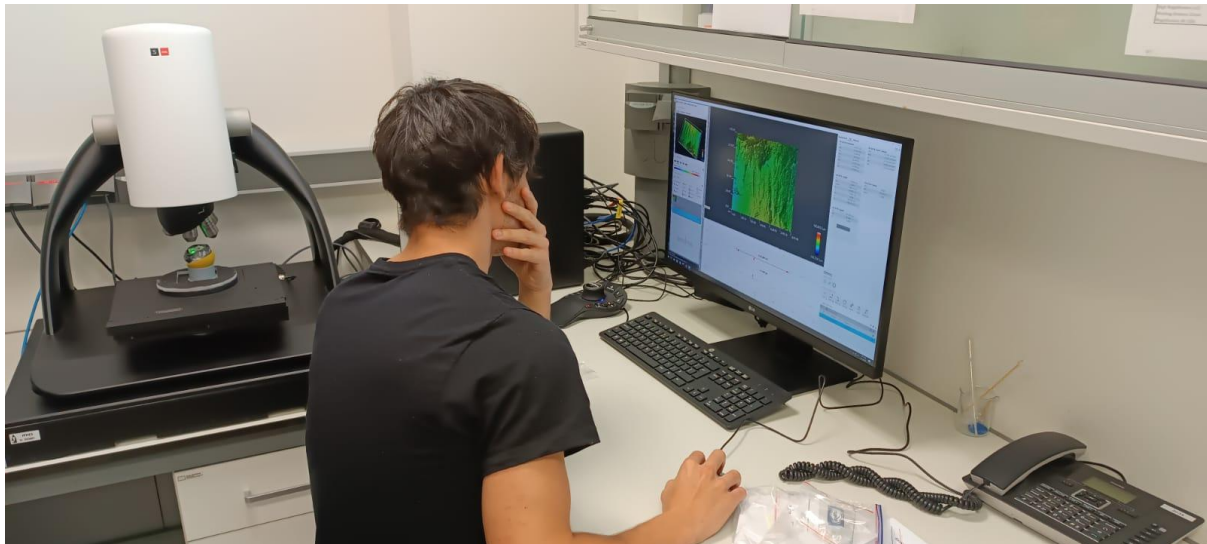


Figure 80. Use of the Sensofar® S Neox microscope in IPHES-CERCA (Tarragona, Spain), to examine a M1 of referential collection brown bear.

9.3.1 Stereomicroscopy at low magnification; new quantification considerations

The method employed will follow the protocols established by Solounias and Semprebon (2002) and Semprebon et al. (2004). However, the quantification of microwear features in omnivorous mammals, such as bears, requires reconsideration. To this end, the counts of pits and scratches—along with their various morphological classifications—will be examined in greater detail to determine which features are most informative for dietary classification.

As suggested by the present study, the number of coarse scratches (NCS), fine scratches (NFS), and the total number of pits (NTP) appear to be the most diagnostic variables for distinguishing among dietary regimes in bears. Additionally, the frequency of puncture pits (NPP) warrants further investigation, as it may serve as a strong indicator of hard-mast consumption. To enhance interpretability and integrate these variables effectively, multivariate statistical methods such as correspondence analysis (CA) or discriminant function analysis (DFA) could be applied. These techniques allow for the simultaneous evaluation of multiple variables and may help identify patterns that discriminate among dietary strategies in extant *U. arctos* populations.

9.3.2 Confocal microscopy texture analysis with SSFA: technical considerations

9.3.2.1 Lens

The lens employed will be of x100 as it is the required magnification and more recommended for applying texture analysis (Scott et al., 2006), although other magnifications have been successfully employed (e.g., Ibañez et al., 2020; Martínez et al., 2022; Ramírez-Pedraza et al., 2023).

9.3.2.2 Surface analysis

The scanned area was acquired using a $\times 100$ objective lens, applying a 2-row $\times$ 2-column stitching pattern, with each individual scan covering $140.35 \times 165.95 \mu\text{m}$. This produced a combined surface of $280.70 \times 331.90 \mu\text{m}$. From this stitched area, a centered $200 \times 200 \mu\text{m}$ region was extracted for analysis, with its position randomly determined but applied consistently across samples to ensure standardized comparisons.

9.3.2.3 Workflow

Adhering to a clear workflow and providing justification for each step is essential, as studies employing texture analysis often lack detailed explanations for their methodological choices. Therefore, our workflow will be based on previous studies (e.g., Scott et al., 2006; Calandra et al., 2022). In particular, works focusing on omnivorous mammals with bunodont tooth morphology, such as members of the Suidae family (e.g., Souron et al., 2015; Louail et al., 2021), are of special interest. Although our workflow is currently under testing and has not yet been fully finalized, our primary objective is to apply the minimal possible modifications to the analysed surfaces, in order to preserve their original texture characteristics.

9.4 Preliminary results

Figures 81 and 82 illustrate the bivariate distribution of *U. arctos* first upper molar (M1) grinding facet microwear data using the texture parameters Smfc (Scale of maximum complexity) and epLsar (Length-scale anisotropy).

In Figure 81, some clustering by region is evident, particularly among individuals from Kamchatka and Northern Caucasus, as well as the single specimen from Tibet, which displays notably high complexity values.

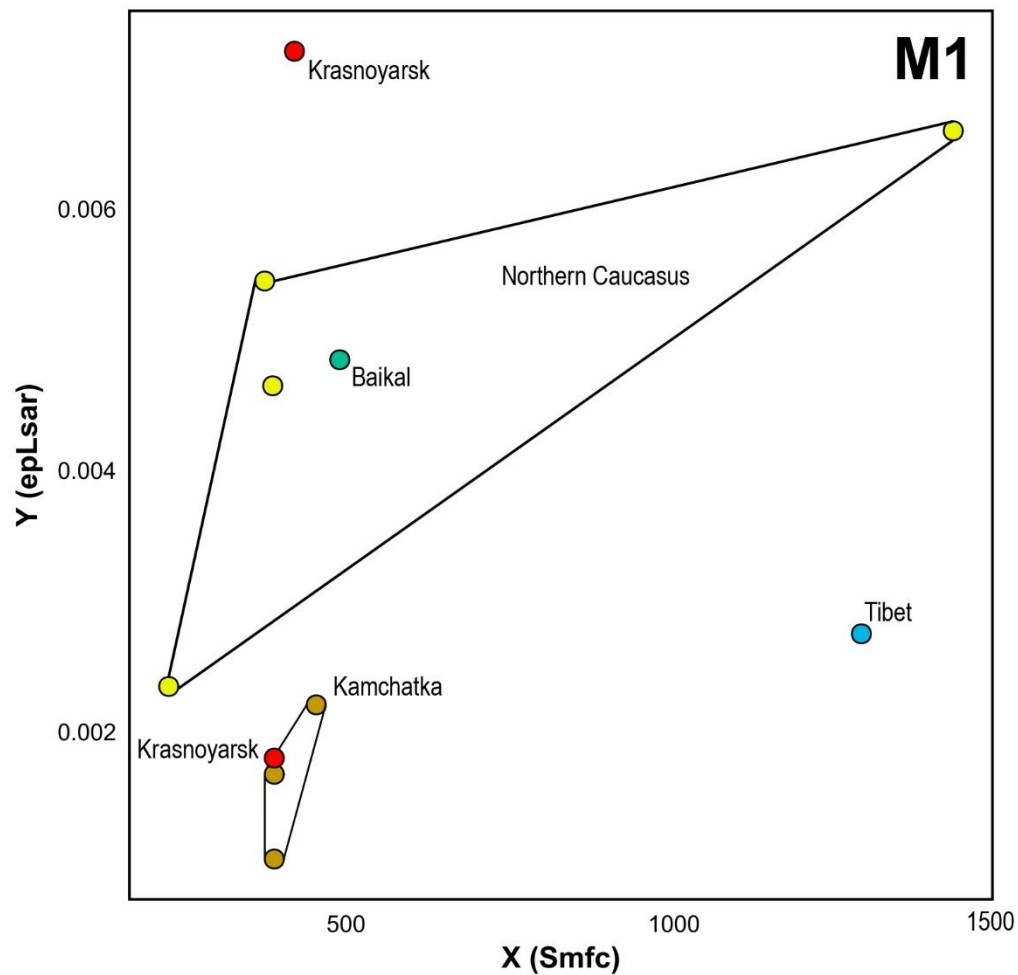


Figure 81. Bivariate plot of *U. arctos* first upper molar (M1) microwear data, showing the relationship between the texture parameters Smfc (X-axis) and epLsar (Y-axis) across different geographic regions.

In Figure 82, the inclusion of seasonal color grouping suggests potential variation across seasons, although no strong pattern is apparent. Individuals hunted in autumn appear to show a wider range of values for both variables, possibly indicating a broadening of dietary behavior during the pre-dormancy period.

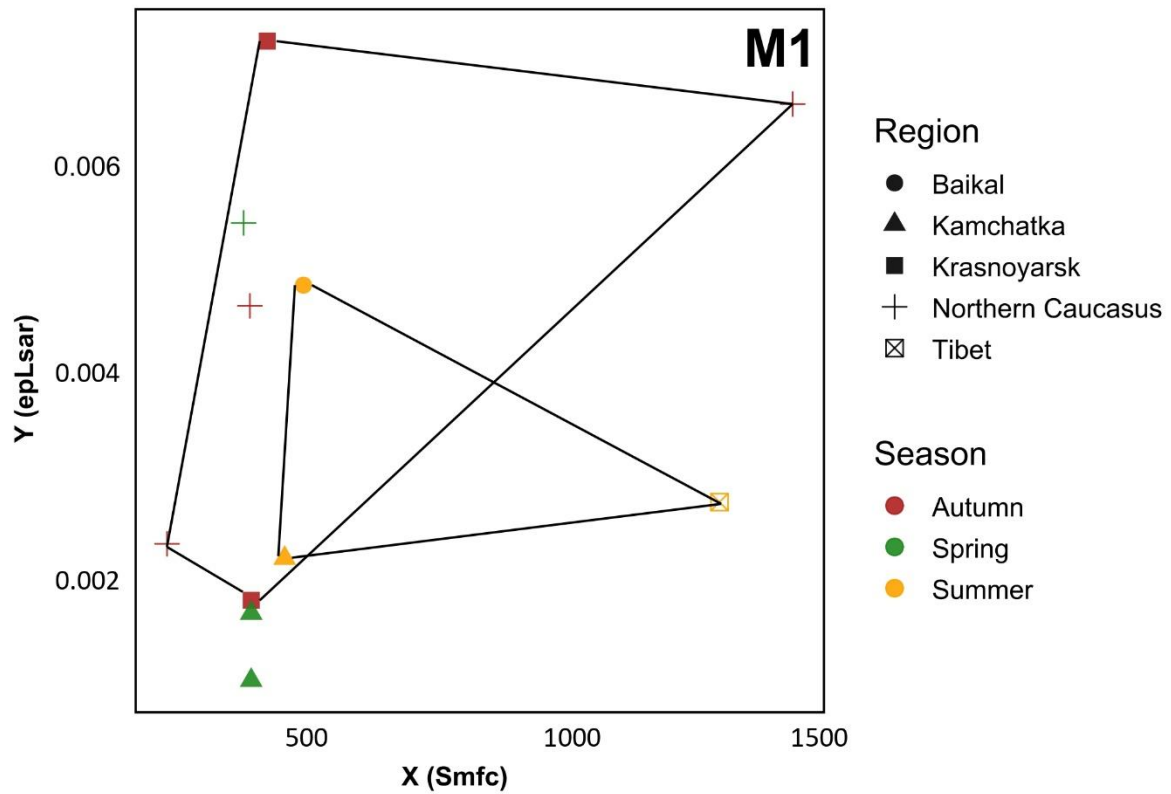


Figure 82. Bivariate plot of *U. arctos* first upper molar (M1) microwear data, displaying the relationship between Smfc (X-axis) and epLsar (Y-axis). Points are distinguished by shape according to region and by color according to the inferred season of death (spring, summer, autumn) based on the collection month.

Overall different patterns in the texture parameters may reflect differences in foraging behaviour seasonally, or due to different ecological scenarios but conclusions remain preliminary.

REFERENCES

10. References

- Akram, F., Ilyas, O., Haleem, A., 2017. Food and feeding habits of Indian crested porcupine in Pench tiger reserve, Madhya Pradesh, India. *Amb. Sci.* 4(1).
<https://doi.org/10.21276/ambi.2017.04.1.ra02>
- Alekseeva, L.I., 1977. Theriofauna of early anthropogene of Eastern Europe. *Trudy Geologicheskogo Instituta SSSR* 30, 214
- Allen, M.L., Elbroch, L.M., Wilmers, C.C., Wittmer, H.U., 2015. The comparative effects of large carnivores on the acquisition of carrion by scavengers. *Am. Nat.* 185(6), 822–833.
<https://doi.org/10.1086/681004>
- Allsworth-Jones, P., Borziac, I.A., Chetaru, N.A., French, C., Mihailescu, C.D., Medyanik, S.I., 2018. The middle palaeolithic site of Buzdujeni in Moldova: establishing the archaeological and environmental record. *J. Paleolit. Archaeol.* 1(2), 139–177. <https://doi.org/10.1007/s41982-018-0009-7>
- Ambrose, S.H., 1993. Isotopic analysis of paleodiets: methodological and interpretive considerations. In: Sandford, M.K. (Ed.), *Investigations of ancient human tissue*. Gordon and Breach Science, Langhorne, Publishers, pp. 59–130.
- Andersen, K.K., Azuma, N., Barnola, J.-M., Bigler, M., Biscaye, P., Caillon, N., Chappellaz, J., Clausen, H.B., Dahl-Jensen, D., Fischer, H., Flückiger, J., Fritzsche, D., Fujii, Y., Goto-Azuma, K., Grønvald, K., Gundestrup, N.S., Hansson, M., Huber, C., Hvidberg, C.S., Johnsen, S.J., Jonsell, U., Jouzel, J., Kipfstuhl, S., Landais, A., Leuenberg, M., Lorrain, R., Masson-Delmotte, V., Miller, H., Motoyama, H., Narita, H., Poop, T., Rasmussen, S.O., Raynaud, D., Rothlisberger, R., Ruth, U., Samyn, D., Schwander, J., Shoji, H., Siggard-Andersen, M.-L., Steffensen, J.-P., Stocker, T., Sveinbjörnsdóttir A.E., Svensson, A., Takata, J.-L., Thorsteinsson, Th., Watanabe, O., Wilhelms, F., White, J.W.C.; Northern Greenland Ice Core Project members, 2004. High-resolution record of northern hemisphere climate extending into the last interglacial period. *Nature* 431(7005), 147–151. <https://doi.org/10.1038/nature02805>
- Anderson, P.S.L., Friedman, M., Brazeau, M.D., Rayfield, E.J., 2011. Initial radiation of jaws demonstrated stability despite faunal and environmental change. *Nature* 476, 206–209.
<https://doi.org/10.1038/nature10207>
- Anisutkin, N.K., Chetaru, N.A., Covalenko, S.I., 2017. Multilayered Paleolithic Site in the Grotto of Starye Durutory and the Place of Its Stone Industries in the Early and Middle Paleolithic of Europe. *St. Petersburg: Nestor-History*.
- Antić, A., Tomic, N., 2020. Assessing the Speleotourism Potential together with Archaeological and Palaeontological Heritage in Risovača Cave (Central Serbia). 10, 1–11.
- Anyonge, W., 1996. Locomotor behaviour in Plio-Pleistocene sabre-tooth cats: a biomechanical analysis. *J. Zool.* 238(3), 395–413. <https://doi.org/10.1111/j.1469-7998.1996.tb05402.x>
- Apps, C., McLellan, B., Woods, J., 2006. Landscape partitioning and spatial inferences of competition between black and grizzly bears. *Ecography* 29, 561–572. <https://doi.org/10.1111/j.0906-7590.2006.04564.x>
- Argant, J., Dimitrijevic, V., 2007. Pollen analyses of Pleistocene hyaena coprolites from Montenegro and Serbia. *Geoloski Anali Balkanskoga Poluostrva* 68, 73–80.
<https://doi.org/10.2298/GABP0701073A>

- Armand, D., Plassard, F., Prat, F., 2004. L'ours de Font-de-Gaume III et le problème de l'exploitation de l'ours des cavernes. In: Actes du 9^e symposium international sur l'ours des cavernes (Entremont-le-Vieux, septembre 2003) (pp. 103–110). Lyon: Muséum, Département du Rhône, Cahiers scientifiques, Hors-série n°2.
- Athen, K., 2006. Biostatistical investigation of long bones and metapodial bones of *Ursus spelaeus* and *Ursus deningeri*. Sci. Annals. Geol. School. AUTH. special 98, 159–162.
- Aune, K.E., 1994. Comparative ecology of black and grizzly bears on the Rocky Mountain Front, Montana. Bears: Their Biology and Management 9, 365–374. <https://doi.org/10.2307/3872723>
- Azzaroli, A., 1983. Quaternary mammals and the “end-Villafranchian” dispersal event — A turning point in the history of Eurasia. Palaeogeogr. Palaeoclimatol. Palaeoecol. 44(1–2), 117–139. [https://doi.org/10.1016/0031-0182\(83\)90008-1](https://doi.org/10.1016/0031-0182(83)90008-1)
- 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). Sci. Nat. 103(11), 92. <https://doi.org/10.1007/s00114-016-1414-8>
- Baca, M., Stankovic, A., Stefaniak, K., Marciszak, A., Hofreiter, M., Nadachowski, A., Wegleński, P., Mackiewicz, P., 2012. Genetic analysis of cave bear specimens from Niedźwiedzia cave, sudetes, Poland. Palaeontol. Electron. 15(2). <https://doi.org/10.26879/301>
- Barlow, A., Pajmians, J.L.A., Alberti, F., Gasparyan, B., Bar-Oz, G., Pinhasi, R., Foronova, I., Puzachenko, A., Pacher, M., Dalén, L., Baryshnikov, G.F., Hofreiter, M., 2021. Middle Pleistocene genome calibrates a revised evolutionary history of extinct cave bears. Curr. Biol. 31(8), 1771–1779. <https://doi.org/10.1016/j.cub.2021.01.073>
- Barreto, E., Holden, P.B., Edwards, N.R., Rangel, T.F., 2023. PALEO-PGEM-Series: A spatial time series of the global climate over the last 5 million years. Glob. Ecol. Biogeogr. 32(7), 1034–1045. <https://doi.org/10.1111/geb.13683>
- Baryshnikov, G.F., 1998. Cave bears from the Paleolithic of the Greater Caucasus, in: Saunders, J.J., Styles, B.W., Baryshnikov, G.F. (Eds.), Quaternary paleozoology in the Northern hemisphere, Illinois State Museum Scientific Papers 27, pp. 69–118.
- Baryshnikov, G.F., 1999. Bone assemblage from Acheulean and Mousterian levels in the Kudaro caves in the Caucasus mountains. *Römisch-Germanisches Zentralmuseum Monographien* 42, 237–253.
- Baryshnikov, G.F., 2002. Local biochronology of the Middle and Late Pleistocene mammals from Caucasus. Russ. J. Theriol. 1(1), 61–67.
- Baryshnikov, G.F., 2007. Fauna of Russia and neighbouring countries. Mammals. Ursidae. Nauka, Saint Petersburg, pp. 541 [in Russian]
- Baryshnikov, G.F., 2010. Middle Pleistocene *Ursus thibetanus* (Mammalia, Carnivora) from Kudaro caves in the Caucasus. Tr. Zool. Inst. RAS. 314(1), 67–79. <https://doi.org/10.31610/trudyzin/2010.314.1.67>
- Baryshnikov, G.F., 2011. Pleistocene Felidae (Mammalia, Carnivora) from the Kudaro Paleolithic cave sites in the Caucasus. Tr. Zool. Inst. RAS. 315, 197–226. <https://doi.org/10.31610/trudyzin/2011.315.3.197>
- Baryshnikov, G.F., 2020a. Large mammals of Kudaro Pleistocene fauna from Caucasus. Tr. Zool. Inst. RAS. (9)1–399 [in Russian].

10. References

- Baryshnikov, G.F., 2020b. Kudaro cave bear: evolution, taphonomy, extinction. Transactions of the institute for the history of material culture RAS. 22, 158–175. <https://doi.org/10.31600/2310-6557-2020-22-158-175>
- Baryshnikov, G.F., Gimranov, D.O., Kosintsev P.A. 2019. Variability of the upper incisors in the cave bears (Carnivora, Ursidae) from the Caucasus and Urals. C.R. Palevol 18(2), 209–222. <https://doi.org/10.1016/j.crpv.2018.08.001>
- Baryshnikov, G., Lavrov, A. 2013. Pliocene bear *Ursus minimus* Devuize de Chabriol et Bouillet, 1827 (Carnivora, Ursidae) in Russia and Kazakhstan. Russ. J. Theriol. 12, 107–118. <https://doi.org/10.15298/rusjtheriol.12.2.07>
- Baryshnikov, G.F., Puzachenko, A.Y. 2011. Craniometrical variability in the cave bears (Carnivora, Ursidae): Multivariate comparative analysis. Quat. Int. 245(2), 350–368. <https://doi.org/https://doi.org/10.1016/j.quaint.2011.02.035>
- Baryshnikov, G.F., Puzachenko, A.Y., 2017. Morphometric analysis of metacarpal and metatarsal bones of cave bears (Carnivora, Ursidae). Foss. Imp. 73(1–2), 7–47. <https://doi.org/10.2478/if-2017-0001>
- Baryshnikov, G.F., Puzachenko, A.Y., 2020. Morphometry of lower cheek teeth of cave bears (Carnivora, Ursidae) and general remarks on the dentition variability. Boreas 49(3), 562–593. <https://doi.org/10.1111/bor.12447>
- Basnett, R., Kumar, A., Vishwakarma, A., Boro, B., 2021. Seasonal diets of Asiatic black bear (*Ursus thibetanus*) in the Khangchendzonga National Park, Eastern Himalaya India. J. Nat. Hist. 55, 163–175. <https://doi.org/10.1080/00222933.2021.1899324>
- Bastl, K., Semprebon, G., Nagel, D., 2012. Low-magnification microwear in Carnivora and dietary diversity in Hyaenodon (Mammalia: Hyaenodontidae) with additional information on its enamel microstructure. Palaeogeogr. Palaeoclimatol. Palaeoecol. 348–349, 13–20. <https://doi.org/10.1016/j.palaeo.2012.05.026>
- Belant, J.L., Kielland, K., Follmann, E.H., Adams, L.G., 2006. Interspecific resource partitioning in sympatric ursids. Ecol. Appl. 16(6), 2333–2343. [https://doi.org/10.1890/1051-0761\(2006\)016\[2333:irpisu\]2.0.co;2](https://doi.org/10.1890/1051-0761(2006)016[2333:irpisu]2.0.co;2)
- Bergman, S., 1936. Observations on the Kamchatkan Bear. J. Mammal. 17(2), 115–120. <https://doi.org/10.2307/1374183>
- Blain, H.A., 2016. Amphibians and Squamate Reptiles from Azokh 1, in: Fernández-Jalvo, Y., King, T., Yepiskoposyan, L., Andrews, P. (Eds.), Azokh Cave and the Transcaucasian Corridor, Vertebr. Paleobiol. Pa. Ser. Springer pp. 191–210.
- Blasco, R., Arilla, M., Domínguez-Rodrigo, M., Andrés, M., Ramírez-Pedraza, I., Rufà, A., Rivals, F., Rosell, J., 2020. Who peeled the bones? An actualistic and taphonomic study of axial elements from the Toll Cave Level 4, Barcelona, Spain. Quat. Sci. Rev. 250, 106661. <https://doi.org/https://doi.org/10.1016/j.quascirev.2020.106661>
- Bleahu, M., 1976. Report on the exploration of Colțu Surpat Cave. Lucrările Institutului de Speologie “Emil Racoviță,” [In Romanian]
- Bocherens, H. 2009. Dental microwear of cave bears: The missing temperate/boreal vegetarian “carnivore.” P.N.A.S. 106(48). <https://doi.org/10.1073/pnas.0910368106>
- Bocherens, H., 2015. Isotopic tracking of large carnivore palaeoecology in the mammoth steppe. Quat. Sci. Rev. 117, 42–71. <https://doi.org/10.1016/j.quascirev.2015.03.018>

- Bocherens, H., 2019. Isotopic insights on cave bear palaeodiet. *Hist. Biol.* 31(4), 410–421.
<https://doi.org/10.1080/08912963.2018.1465419>
- Bocherens, H., Baryshnikov, G.F., Van Neer, W., 2014b. Were bears or lions involved in salmon accumulation in the Middle Palaeolithic of the Caucasus? An isotopic investigation in Kudaro 3 cave. *Quat. Int.* 339–340: 112–118.
- 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). *Quat. Res.* 48(3), 370–380.
<https://doi.org/https://doi.org/10.1006/qres.1997.1927>
- Bocherens, H., Bridault, A., Drucker, D.G., Hofreiter, M., Münzel, S.C., Stiller, M., van der Plicht, J., 2014a. The last of its kind? Radiocarbon, ancient DNA and stable isotope evidence from a late cave bear (*Ursus spelaeus* ROSENMÜLLER, 1794) from Rochedane (France). *Quat. Int.* 339–340, 179–188. <https://doi.org/10.1016/j.quaint.2013.05.021>
- Bocherens, H., Drucker, D., Billiou, D., Geneste, J.-M., 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. *J. Hum. Evol.* 50, 370–376.
<https://doi.org/10.1016/j.jhevol.2005.12.002>
- Bocherens, H., Drucker, D.G., Germonpré, M., Láznicková-Galetová, M., Naito, Y.I., Wissing, C., Brůžek, J., Oliva, M., 2015. Reconstruction of the Gravettian food-web at Předmostí I using multi-isotopic tracking (^{13}C , ^{15}N , ^{34}S) of bone collagen. *Quat. Int.* 359–360, 211–228.
<https://doi.org/10.1016/j.quaint.2014.09.044>
- Bocherens, H., Fizet, M., Mariotti, A., 1994. Diet, physiology and ecology of fossil mammals as inferred from stable carbon and nitrogen isotope biogeochemistry: implications for Pleistocene bears. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 107(3), 213–225.
[https://doi.org/https://doi.org/10.1016/0031-0182\(94\)90095-7](https://doi.org/https://doi.org/10.1016/0031-0182(94)90095-7)
- Bocherens, H., Fizet, M., Mariotti, A., Lange-Badre, B., Vandermeersch, B., Borel, J.P., Bellon, G., 1991. Isotopic biogeochemistry (^{13}C , ^{15}N) of fossil vertebrate collagen: application to the study of a past food web including Neandertal man. *J. Hum. Evol.* 20(6), 481–492.
[https://doi.org/10.1016/0047-2484\(91\)90021-M](https://doi.org/10.1016/0047-2484(91)90021-M)
- Bocherens, H., Stiller, M., Hobson, K., Pacher, M., Rabeder, G., Burns, J., 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. *Quat. Int.* 245, 238–248. <https://doi.org/10.1016/j.quaint.2010.12.020>
- Boev, Z., 2021. Past distribution of *Ursus arctos* in Bulgaria: fossil and subfossil records (Carnivora: Ursidae). *Lynx New Series*, 51(1), 5–18. <https://doi.org/10.37520/lynx.2020.001>
- Bogićević, K., Nenadić, D., Milošević, S., Mihailović, D., Vlastić, S., Tosovic, R., 2017. A Late Pleistocene rodent fauna (Mammalia: Rodentia) from Hadži Prodanova Cave near Ivanjica (western Serbia). *Riv. Ital. Paleontol. Stratigr.* 123: 23–38.
- Bojarska, K., Selva, N., 2012. Spatial patterns in brown bear *Ursus arctos* diet: The role of geographical and environmental factors. *Mammal Rev.* 42, 120–143.
<https://doi.org/10.1111/j.1365-2907.2011.00192.x>
- Bombiță, G., 1954. Mamiferele din glaciarul peșterilor de la Baia de Fier. Rezultatele paleontologice ale săpăturilor din anul 1951. *Buletin Științific, Secțiunea de Științe*. [In Romanian]

10. References

- Bond, G.C., Showers, W., Elliot, M., Evans, M., Lotti, R., Hajdas, I., Bonani, G., Johnson, S., 1999. The North Atlantic's 1-2 kyr climate rhythm: relation to Heinrich events, Dansgaard/Oeschger cycles and the Little Ice Age. *Geophys. Monogr.* 112, 35–58.
- Borziac, I.A., 1973. Reconnaissance for stone age sites in Moldavia. In G.F. Chebotarenko (Ed.), *Archaeological Investigations in Moldova in 1970 -1971*. Kishinev pp. 27–34.
- Brown, J.S., 1988. Patch use as an indicator of habitat preference, predation risk, and competition. *Behav. Ecol. Sociobiol.* 22(1), 37–47. <http://www.jstor.org/stable/4600116>
- Bruno, E., Riccardi, C., 1995. The diet of the Crested porcupine *Hystrix cristata* L., 1758 in a Mediterranean rural area. *Z. Saugetierkunde* 60, 226–236. <https://api.semanticscholar.org/CorpusID:130088299>
- Bulić, D., 2006. Archaeological research of Hadži-Prodan's cave in Ivanjica. *Archaeological Reports of the Serbian Archaeological Society* 1, 55–57.
- Butler, P.M., 1952. The milk-molars of Perissodactyla, with remarks on molar occlusion. *Proc. Zool. Soc. Lond.* 121, 777–817. <https://doi.org/10.1111/j.1096-3642.1952.tb00784.x>
- Butler, P.M., 2009. Molarization of premolars in Perissodactyla. *Proc. Zool. Soc. Lond.* 121, 819–843. <https://doi.org/10.1111/j.1096-3642.1952.tb00785.x>
- Calandra, I., 2022. A workflow for quality control in surface texture analysis applied to teeth and tools. *J. Archaeol. Sci. Rep.* 46, 103692. <https://doi.org/10.1016/j.jasrep.2022.103692>
- Carrión, J., Amorós, G., Ochando, J., Magri, D., Marín-Arroyo, A.B., Sánchez-Giner, M. V., Amorós, A., Munuera, M., Di Rita, F., Michelangeli, F., Roksandic, M., Mihailović, D., 2024. Welcome to the forest theatre: Unveiling a Balkan refugium through paleoart. *Quat. Sci. Rev.* 338, 108829. <https://doi.org/https://doi.org/10.1016/j.quascirev.2024.108829>
- Čerdynceev, V.V., Strašnikov, N.S., Poljakova, L.M., Borisenko, T.I., Enikeev, R.S., Neučesov, S.N., 1959. Determination of the absolute age of paleolithic sites Kudaro and Kostenki. *Optics and Nuclear Processes (Kazakh University Publishing, Alma Ata)*, 59–63. [translated in English]
- Charters, D., Abrams, G., De Groote, I., Di Modica, K., Bonjean, D., Meloro, C., 2019. Temporal variation in cave bear (*Ursus spelaeus*) dentition: The stratigraphic sequence of Scladina Cave, Belgium. *Quat. Sci. Rev.* 205, 76–85. <https://doi.org/10.1016/j.quascirev.2018.12.012>
- Charters, D., Brown, R.P., Abrams, G., Bonjean, D., De Groote, I., Meloro, C., 2022. Morphological evolution of the cave bear (*Ursus spelaeus*) mandibular molars: coordinated size and shape changes through the Scladina Cave chronostratigraphy. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 587, 110787. <https://doi.org/https://doi.org/10.1016/j.palaeo.2021.110787>
- Chaudhary, R., Khan, J., Zehra, N., 2015. Abundance and dietary composition of indian crested porcupine in western part of Gir National Park and Sanctuary, Gujarat, India. *Int. J. Ecol. Environ. Sci.* 41, 377–392.
- Chetraru, N.A., 1965. Issledovaniya paleoliticheskikh grotov Severo-Zapada Moldavii. *Okhrana Prirody Moldavii*, 3. [In Moldavian]
- Chetraru, N.A., 1970. Paleoliticheskaya stoyanka v grote Buteshty. *Okhrana Prirody Moldavii*, 8, 113–132. [In Moldavian]
- Chetraru, N.A., 1973a. New Mousterian site in the grotto of Buzdujeni I. In: G.F. Chebotarenko (Ed.), *Archaeological investigations in Moldova in 1970-1971*. Kishinev, pp. 10–15.

- Chettraru, N.A., 1973b. Pamyatniki Epokh Paleolita i Mezolita. Știința. Chișinău: Știința.
- Cicnjak, L., Roth, H., Ruff, R., Huber, D., 1987. Food habits of brown bears in Plitvice Lakes National Park, Yugoslavia. Int. Conf. Bear. Res. Manage. 7, 221–226. <https://doi.org/10.2307/3872628>
- Çilingir, F.G., Akın Pekşen, Ç., Ambarlı, H., Beerli, P., Bilgin, C.C., 2016. Exceptional maternal lineage diversity in brown bears (*Ursus arctos*) from Turkey. Zool. J. Linn. Soc. 176, 463–477. <https://doi.org/10.1111/zoj.12322>
- Clark, J.D., Clapp, D.L., Smith, K.G., Ederington, B., 1994. Black bear habitat use in relation to food availability in the Interior Highlands of Arkansas. Ursus 9(1), 309–318. <https://pubs.usgs.gov/publication/70170455>
- Clevenger, A., Purroy, F.J., Pelton, M.R., 1992. Food habits of brown bears (*Ursus arctos*) in the Cantabrian Mountains, Spain. J. Mammal. 73, 415–421. <https://doi.org/10.2307/1382077>
- Constantin, S., Bojar, A.V., Lauritzen, S.E., Lundberg, J., 2007. Holocene and Late Pleistocene climate in the sub-Mediterranean continental environment: A speleothem record from Poleva Cave (Southern Carpathians, Romania). Palaeogeog. Palaeoclimatol. Palaeoecol. 243(3–4), 322–338. <https://doi.org/10.1016/j.palaeo.2006.08.001>
- Constantin, S., Munteanu, C. M., Milota, S., Sarcina, L., Gherase, M., Zilhão, J., 2013. The Ponor-Plopa Cave system: description, sediments, and genesis. In: Trinkaus E., Constantin S., Zilhão J. (Eds.), Life and death at Pesteră cu Oase. A setting for modern human emergence in Europe, Oxford University Press pp. 41–55.
- Constantin, S., Robu, M., Munteanu, C.-M., Petculescu, A., Vlaicu, M., Mirea, I., Keneszi, M., Drăgușin, V., Hoffmann, D., Anechitei, V., Timar-Gabor, A., Roban, R.-D., Panaiotu, C.G., 2014. Reconstructing the evolution of cave systems as a key to understanding the taphonomy of fossil accumulations: The case of Urșilor Cave (Western Carpathians, Romania). Quat. Int. 339–340, 25–40. <https://doi.org/10.1016/j.quaint.2013.10.012>
- Coogan, S.C.P., Raubenheimer, D., Stenhouse, G.B., Coops, N.C., Nielsen, S.E., 2018. Functional macronutritional generalism in a large omnivore, the brown bear. Ecol. Evol. 8(4), 2365–2376. <https://doi.org/10.1002/ece3.3867>
- Coogan, S.C.P., Raubenheimer, D., Stenhouse, G.B., Nielsen, S.E., 2014. Macronutrient optimization and seasonal diet mixing in a large omnivore, the grizzly bear: A geometric analysis. PLOS ONE. 9(5), e97968. <https://doi.org/10.1371/journal.pone.0097968>
- Coppola, F., Guerrieri, D., Simoncini, A., Varuzza, P., Vecchio, G., Felicioli, A., 2020. Evidence of scavenging behaviour in crested porcupine. Sci. Rep. 10(1), 12297. <https://doi.org/10.1038/s41598-020-69252-z>
- Courtenay, L.A., Yravedra, J., Herranz-Rodrigo, D., Rodríguez-Alba, J.J., Serrano-Ramos, A., Estaca-Gómez, V., González-Aguilera, D., Solano, J.A., Jiménez-Arenas, J.M., 2023. Deciphering carnivorous competition for animal resources at the 1.46 Ma early Pleistocene site of Barranco León (Orce, Granada, Spain). Quat. Sci. Rev. 300, 107912. <https://doi.org/10.1016/j.quascirev.2022.107912>
- Cox, G., Sealy, J., 1997. Investigating identity and life histories: isotopic analysis and historical documentation of slave skeletons found on the Cape Town foreshore, South Africa. Int. J. Hist. Archaeol. 1, 207–224. <https://doi.org/10.1023/A:1027349115465>

10. References

- Creel S., Spong G., Creel N., 2001. Interspecific competition and the population biology of extinction-prone carnivores, in: Gittleman J.L., Funk S.M., Macdonald D., Wayne R.K., (Eds.), *Carnivore conservation*. Cambridge: Cambridge University Press, pp. 35–6.
- Croitor, R., 2008. Giant deer *Megaloceros giganteus* (Cervidae Mammalia) from Late Pleistocene of Moldova. *Oltenia Journal for Studies in Natural Sciences* 24, 262–266.
- Croitor, R., Brugal, J.P., 2010. Ecological and evolutionary dynamics of the carnivore community in Europe during the last 3 million years. *Quat. Int.* 212(2), 98–108.
<https://doi.org/10.1016/j.quaint.2009.06.001>
- Croitor, R., Burlacu, V., 2020. The Middle Paleolithic site of Buzdujeni 1 (Northern Moldova): evidence on periodic occupation by cave hyena. *Rev Arheologică* 16(1), 136–144.
<https://hal.science/hal-03126336>
- Cui, Z., Shao, Q., Grueter, C.C., Wang, Z., Lu, J., Raubenheimer, D., 2019. Dietary diversity of an ecological and macronutritional generalist primate in a harsh high-latitude habitat, the Taihangshan macaque (*Macaca mulatta tcheliensis*). *Am. J. Primatol.* 81(4), e22965.
<https://doi.org/10.1002/ajp.22965>
- Cui, Z., Wang, Z.L., Shao, Q., Raubenheimer, D., Lu, J.Q., 2018. Macronutrient signature of dietary generalism in an ecologically diverse primate in the wild. *Behav. Ecol.* 29(4), 804–813.
<https://doi.org/10.1093/beheco/ary003>
- Dabney, J., Knapp, M., Glocke, I., Gansauge, M.T., Weihmann, A., Nickel, B., Valdiosera, C., García, N., Pääbo, S., Arsuaga, J.L. Meyer, M., 2013. Complete mitochondrial genome sequence of a Middle Pleistocene cave bear reconstructed from ultrashort DNA fragments. *P.N.A.S.* 110(39), 15758–15763. <https://doi.org/10.1073/pnas.1314445110>
- Dahlberg, A.A., Kinzey, W., 1962. Etude microscopique de l'abrasion et l'attrition sur la surface des dents. *Int. J. Sci. Stomatol.* 5, 242–251.
- Dahle, B., Sørensen, O., Wedul, E., Swenson, J., Sandegren, F., 1998. The diet of brown bears *Ursus arctos* in central Scandinavia: Effect of access to free-ranging domestic sheep *Ovis aries*. *Wildlife Biol.* 4, 147–158. <https://doi.org/10.2981/wlb.1998.017>
- Dahle, B., Wallin, K., Cederlund, G., Persson, I.L., Selvaag, L., Swenson, J., 2013. Predation on adult moose *Alces alces* by European brown bears *Ursus arctos*. *Wildlife Biol.* 19, 165–169.
<https://doi.org/10.2981/10-113>
- Dale Guthrie, R., 2001. Origin and causes of the mammoth steppe: a story of cloud cover, woolly mammal tooth pits, buckles, and inside-out Beringia. *Quat. Sci. Rev.* 20(1–3), 549–574.
[https://doi.org/10.1016/S0277-3791\(00\)00099-8](https://doi.org/10.1016/S0277-3791(00)00099-8)
- Dansgaard, W., Johnsen, S., Clausen, H., Dahl-Jensen, D., Gundestrup, N., Hammer, et al., 1993. Evidence of general instability of past climate from a 250-kyr ice-core record. *Nature* 364, 218–220. <https://doi.org/10.1038/364218a0>
- David, A.I., 1980. Teriofauna Pleistotsena Moldavii. Chişinău: Ştiinţa pp. 185. [in Russian]
- David, A.L., Lungu, A.N., 1972. Mammal remains from Karagash quarry. In: *Neogene and Pleistocene Vertebrates of Moldavia*. Shtiintsa Press pp. 19–24.
- David, A.L., Pascaru, V., Rusu, V., Găleanu, L., 2006. Caracteristica reminiscentelor scheletice şi componenţei sistematice a mamiferelor de la staţiunea paleolitică pluristratificată Buzdujeni I. *Rev. Arheologică*. 2, 387–392.

- Davis, M., Pineda Munoz, S., 2016. The temporal scale of diet and dietary proxies. *Ecol. Evol.* 6(6), 1883–1897. <https://doi.org/10.1002/ece3.2054>
- Demay, L., Croitor, R., Covalenco, S., Obadă, T., Pascari, V., 2024. Zooarchaeological analysis of the Raşcov 7 Upper Palaeolithic site (Republic of Moldova). *L'Anthropologie* 128(4), 103299. <https://doi.org/10.1016/j.anthro.2024.103299>
- Demay, L., Obadă, T., Péan, S., Prepeliță, A., 2019. Utilization of mammoth resources and occupation of the Dniester-Prut basin territory: The Upper Palaeolithic site of Valea Morilor (Republic of Moldova). *Quat. Sci. Rev.* 222, 105898. <https://doi.org/10.1016/j.quascirev.2019.105898>
- DeSantis, L.R.G., Schubert, B.W., Scott, J.R., Ungar, P.S., 2012. Implications of diet for the extinction of saber-toothed cats and American lions. *PLoS ONE* 7(12), e52453. <https://doi.org/10.1371/journal.pone.0052453>
- DeSantis, L.R.G., Scott, J.R., Schubert, B.W., Donohue, S.L., McCray, B.M., Van Stolk, C.A., Winburn, A.A., Greshko, M.A., O'Hara, M.C., 2013. Direct comparisons of 2D and 3D dental microwear proxies in extant herbivorous and carnivorous mammals. *PLoS ONE* 8(8), e71428. <https://doi.org/10.1371/journal.pone.0071428>
- Desprat, S., Fernández, P., Coulon, T., Ezzat, L., Pessarossi-Langlois, J., Gil, L., Morales-Molino, C., Sanchez Goñi, M., 2015. *Pinus nigra* (European black pine) as the dominant species of the last glacial pinewoods in south-western to central Iberia: A morphological study of modern and fossil pollen. *J. Biogeogr.* 42, 1998–2009. <https://doi.org/10.1111/jbi.12566>
- Desprat, S., Sanchez Goñi, M., Jean Louis, T., Duprat, J., Malaizé, B., Peypouquet, J.P., 2007. Climatic variability of Marine Isotope Stage 7: direct land–sea–ice correlation from a multiproxy analysis of a north-western Iberian margin deep-sea core. *Quat. Sci. Rev.* 1010–1026. <https://doi.org/10.1016/j.quascirev.2006.01.001>
- Dewar, E., 2004. Microwear of carnivorous mammals described by low-magnification dental stereomicroscopy. *J. Vertebr. Paleontol.* 24(3), 52A.
- Diedrich, C., Moldovan, O., Constantin, S., 2008. Cave bear tracks, scratchmarks, hair traces and hibernation nests in the Urşilor Cave (Transilvania, Romania) – preliminary report from a famous European cave bear den. *Stalaktit*, 58(2), 48–52.
- Diedrich, C., Robu, M., Drăguşin, V., Constantin, S., Moldovan, O., 2009. New Upper Pleistocene steppe lion skeleton finds in the Urşilor Cave bear den, Romania. *Proceedings of the 15th International Cave Bear Symposium*, 10.
- Díez-Canseco, C., Aguilera, M., Tornero, C., 2022. Intra-tooth isotopic analysis ($\delta^{13}\text{C}$ and $\delta^{15}\text{N}$) of dentine collagen in high-crowned teeth: A new experimental study with modern sheep specimens. *Int. J. Osteoarchaeol.* 32(5), 962–975. <https://doi.org/10.1002/oa.3138>
- Dimitrijević, V., 1997. Upper Pleistocene mammals from the cave deposits of Serbia. *Geološki anali Balkanskog poluostrva*. Faculty of Mining and Geology.
- Doboş, A., Soficaru, A., Popescu, A., Trinkaus, E., 2009. Radiocarbon dating and faunal stable isotopes for the Galeria Principală, Peştera Muierii, Baia de Fier, Gorj County, Romania. *Materiale Şi Cercetări Arheologice (Serie Nouă)*, 5(1), 15–20. <https://doi.org/10.3406/mcarh.2009.1066>
- Doboş, A., Soficaru, A., Trinkaus, E., 2010. The prehistory and palaeontology of the Peştera Muierii, Romania. ERAUL 124. Liège. University of Liège.

10. References

- Donohue, S.L., DeSantis, L.R.G., Schubert, B.W., Ungar, P.S., 2013. Was the giant short-faced bear a hyper-scavenger? A new approach to the dietary study of ursids using dental microwear textures. *PLoS ONE* 8(10), e77531. <https://doi.org/10.1371/journal.pone.0077531>
- Drucker, D.G., 2022. The isotopic ecology of the mammoth steppe. *Ann. Rev. Earth Planet. Sci.* 50(1), 395–418. <https://doi.org/10.1146/annurev-earth-100821-081832>
- Dumitrescu, M., Samson, M., Terzea, E., Radulescu, C., Ghica, M., 1966. Pestera “La Adam” - Statiune pleistocena. *Lucrările Institutului Speologic “E. Racovita,”* 6(9–88).
- Duñó-Iglesias, P., Rivals, F., Lloveras, L., Nadal, J., 2023. Seasonality and mobility of Epipaleolithic groups in the north-east of the Iberian Peninsula: tooth wear analysis of ungulates from Balma del Gai. *Archaeol. Anthropol. Sci.* 15, 89. <https://doi.org/10.1007/s12520-023-01788-3>
- Duñó-Iglesias, P., Ramírez-Pedraza, I., Rivals, F., Mirea, I.C., Faur, L.M., Constantin, S., Robu, M., 2024a. Palaeodiet during the pre-dormancy period of MIS 3 Romanian cave bears as inferred from dental microwear analysis. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 636, 111988. <https://doi.org/https://doi.org/10.1016/j.palaeo.2023.111988>
- Duñó-Iglesias, P., Ramírez-Pedraza, I., Rivals, F., Mirea, I.C., Faur, L.M., Vlaicu, M., Obadă, T., Croitor, R., Pascari, V., Delinschi, E., Hristova, L., Spassov, N., Gospodinov, M., Dimitrijević, V., Alaburić, S., Bogićević, K., Stefanović, I., Robu, M., 2025. Dental microwear of cave bear (*Ursus spelaeus*) reveals locally adapted foraging strategies in South-Eastern Europe during late MIS 3. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 677, 113200. <https://doi.org/10.1016/j.palaeo.2025.113200>
- Duñó-Iglesias, P., Ramírez-Pedraza, I., Rivals, F., Prilepskaya, N.E., Belyaev, R.I., Baryshnikov, G.F., 2024b. Dental microwear analysis of Kudaro cave bears: Insights into dietary evolution from the Middle to Late Pleistocene. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 653, 112417. <https://doi.org/10.1016/j.palaeo.2024.112417>
- Duñó-Iglesias, P., Robu, M., Rivals, F., 2024c. Correlations between age, sex, and short-term diet in MIS 3 cave bear populations from Romanian Carpathians and the northern Moldavian uplands during predormancy. *Karst Science Days Symposium Proceedings*, 2024, 39–42. <https://doi.org/10.70655/KSD.2024.11>
- Duthie, A.G., Skinner, J.D., 1986. Osteophagia in the Cape porcupine *Hystrix africaeaustralis*. *S. Afr. J. Zool.* 21 (4), 316–318. <https://doi.org/10.1080/02541858.1986.11448005>
- Döppes, D., Pacher, M., 2014. 10,000 years of *Ursus arctos* in the Alps – A success story? Analyses of the Late Glacial and Early Holocene brown bear remains from Alpine caves in Austria. *Quat. Int.* 339–340, 266–274. <https://doi.org/10.1016/j.quaint.2013.11.039>
- Dzhambazov, N., Katincharov, R., 1961. Archaeological finds from Magura cave. *Archaeology* 3(3), 56–64.
- Elbroch, L.M., O'Malley, C., Peziol, M., Quigley, H., 2017. Vertebrate diversity benefiting from carrion provided by pumas and other subordinate, apex felids. *Biol. Conserv.* 215, 123–131. <https://doi.org/10.1016/j.biocon.2017.08.026>
- Elgmork, K., Kaasa, J., 1992. Food habits and foraging of the brown bear *Ursus arctos* in Central South Norway. *Ecography.* 15(1), 101–110. <http://www.jstor.org/stable/3682968>
- El-Zaatari, S., 2010. Occlusal microwear texture analysis and the diets of historical/prehistoric hunter-gatherers. *Int. J. Osteoarchaeol.* 20, 67–87. <https://doi.org/10.1002/oa.1027>

- Edwards, C.J., Ho, S.Y.W., Barnett, R., Coxon, P., Bradley, D.G., Lord, T.C., O'Connor, T., 2014. Continuity of brown bear maternal lineages in northern England through the Last-glacial period. *Quat. Sci. Rev.* 96, 131–139. <https://doi.org/10.1016/j.quascirev.2013.10.015>
- Ersmark, E., Baryshnikov, G., Higham, T., Argant, A., Castaños, P., Döppes, D., Gasparik, M., Germonpré, M., Lidén, K., Lipecki, G., Marciszak, A., Miller, R., Moreno-García, M., Pacher, M., Robu, M., Rodriguez-Varela, R., Rojo Guerra, M., Sabol, M., Spassov, N., Storå, J., Valdiosera, C., Villaluenga, A., Stewart, J.R., Dalén, L., 2019. Genetic turnovers and northern survival during the last glacial maximum in European brown bears. *Ecol. Evol.* 9(10), 5891–5905. <https://doi.org/10.1002/ece3.5172>
- Esri., 2018. ArcGIS Desktop: Release 10.6.1.
- Farley, S.D., Robbins, C.T., 1995. Lactation, hibernation, and mass dynamics of American black bears and grizzly bears. *Can. J. Zool.* 73(12), 2216–2222. <https://doi.org/10.1139/z95-262>
- Fewlass, H., Talamo, S., Wacker, L., Kromer, B., Tuna, T., Fagault, Y., Bard, E., McPherron, S.P., Aldeias, V., Maria, R., Martisius, N.L., Paskulin, L., Rezek, Z., Sinet-Mathiot, V., Sirakova, S., Smith, G.M., Spasov, R., Welker, F., Sirakov, N., Tsanova, T., Hublin, J.J., 2020. A ¹⁴C chronology for the Middle to Upper Palaeolithic transition at Bacho Kiro Cave, Bulgaria. *Nat. Ecol. Evol.* 4(6), 794–801. <https://doi.org/10.1038/s41559-020-1136-3>
- Fernández-Mosquera, D., Vila-Taboada, M., Grandal-d'Anglade, A., 2001. Stable isotopes data ($\delta^{13}\text{C}$, $\delta^{15}\text{N}$) from cave bear (*Ursus spelaeus*): A new approach to its paleoenvironment and dormancy. *Proc. R. Soc. London. Ser. B Biol. Sci.* 268, 1159–1164. <https://doi.org/10.1098/rspb.2001.1639>
- Figueirido, B., Palmqvist, P., Pérez-Claros, J., 2009. Ecomorphological correlates of craniodental variation in bears and paleobiological implications for extinct taxa: An approach based on geometric morphometrics. *J. Zool.* 277, 70–80. <https://doi.org/10.1111/j.1469-7998.2008.00511.x>
- Flower, L.O.H., Schreve, D.C., 2014. An investigation of palaeodietary variability in European Pleistocene canids. *Quat. Sci. Rev.* 96, 188–203. <https://doi.org/10.1016/j.quascirev.2014.04.015>
- Forsten, A., Dimitrijevic, V., 1995. The Paleolithic horses (genus *Equus*) from Risovaca, Arandjelovac, Serbia. *Neues Jahrbuch Für Geologie Und Paläontologie - Abhandlungen*, 196(3), 395–409. <https://doi.org/10.1127/njgpa/196/1995/395>
- Fortes, G., Grandal-d'Anglade, A., Kolbe, B., Fernandes, D., Meleg, I., García-Vázquez, A., Pinto-Llona, A., Constantin, S., Torres, T., Ortiz, J., Frischauf, C., Rabeder, G., Hofreiter, M., Barlow, A., 2016. Ancient DNA reveals differences in behaviour and sociality between brown bears and extinct cave bears. *Mol. Ecol.* 25(19), 4907–4918. <https://doi.org/10.1111/056119>
- Frackowiak, W., 1997. Diet and food habits of the brown bear (*Ursus arctos* L.) in Polish Eastern Carpathians. *J. Wildl. Res.* 2, 154–160.
- Frémonteau, D., Ottoni, C., Ivanova, S., Marinova, E., Spassov, N., Hristova, L., Konyovska, R., Van Neer, W., Lupianez, N., Gurova, M., 2020. New mtDNA and isotopic evidence on Late Pleistocene cave bears in the Balkans: The case-study of Magura Cave, NW Bulgaria. *Acta Zoologica Bulgarica* 72 (3), 461–478.
- Furusaka, S., Kozakai, C., Nemoto, Y., Umemura, Y., Naganuma, T., Yamazaki, K., Koike, S., 2017. The selection by the Asiatic black bear (*Ursus thibetanus*) of spring plant food items according to their nutritional values. *ZooKeys* 672, 121–133. <https://doi.org/10.3897/zookeys.672.10078>

10. References

- García, N., 2003. Osos y otros carnívoros de la Sierra de Atapuerca. Fundación Oso de Asturias, Proaza, Asturias. <https://api.semanticscholar.org/CorpusID:126421318>
- García, N., Feranec, R.S., Arsuaga, J.L., Bermúdez de Castro, J.M., Carbonell, E., 2009. Isotopic analysis of the ecology of herbivores and carnivores from the Middle Pleistocene deposits of the Sierra De Atapuerca, northern Spain. *J. Archaeol. Sci.* 36, 1142–1151. <https://doi.org/10.1016/j.jas.2008.12.018>
- García-Rodríguez, A., Albrecht, J., Szczutkowska, S., Valido, A., Farwig, N., Selva, N., 2021. The role of the brown bear *Ursus arctos* as a legitimate megafaunal seed disperser. *Sci. Rep.* 11(1), 1282. <https://doi.org/10.1038/s41598-020-80440-9>
- García-Vázquez, A., Crampton, D.A., Lamb, A.L., Wolff, G.A., Kiriakoulakis, K., Guidarelli, G., Loy, A., Ciucci, P., Groff, C., Pinto-Llona, A.C., Grandal-d'Anglade, A., Meloro, C., 2023. Isotopic signature in isolated south-western populations of European brown bear (*Ursus arctos*). *Mamm. Res.* 68(1), 63–76. <https://doi.org/10.1007/s13364-022-00654-2>
- Garrod, D.A.E., Howe, B., Gaul, J.H., 1939. Excavation in the cave of Bacho Kiro, North-East Bulgaria. *BASPR* 15, 46–70.
- Gende, S.M., Quinn, T.P., Willson, M.F., 2001. Consumption choice by bears feeding on salmon. *Oecologia* 127(3), 372–382. <http://www.jstor.org/stable/4222942>
- Gende, S.M., Quinn, T.P., 2004. The relative importance of prey density and social dominance in determining energy intake by bears feeding on Pacific salmon. *Can. J. Zool.* 82(1), 75–85. <https://doi.org/10.1139/z03-226>
- Gerasimenko, N., 2006. Upper Pleistocene loess–palaeosol and vegetational successions in the Middle Dnieper Area, Ukraine. *Quat. Int.* 149, 55–66. <https://doi.org/10.1016/j.quaint.2005.11.018>
- Giannakos, P., 1997. Frugivory and seed dispersal by carnivores in the Rhodopi mountains of northern Greece. PhD Thesis. Durham University, Department of Biological Sciences.
- Gimranov, D., Kosintsev, P., 2020. Quaternary large mammals from the Imanay Cave. *Quat. Int.* 546, 125–134. <https://doi.org/10.1016/j.quaint.2020.01.014>
- Ginter, B., Kozłowski, J.K., Guadelli, J.L., Laville, H., 2000. Temnata Cave. Excavations in Karlukovo karst area, Bulgaria. 2.1. Jagellonian University, Cracow. <https://shs.hal.science/halshs-00133843>
- Godfrey, L.R., Semprebon, G.M., Jungers, W.L., Sutherland, M.R., Simons, E.L., Solounias, N., 2004. Dental use wear in extinct lemurs: evidence of diet and niche differentiation. *J. Hum. Evol.* 47(3), 145–169. <https://doi.org/https://doi.org/10.1016/j.jhevol.2004.06.003>
- Goillot, C., Blondel, C., Peigné, S., 2009. Relationships between dental microwear and diet in Carnivora (Mammalia) — Implications for the reconstruction of the diet of extinct taxa. *Palaeogeog. Palaeoclimatol. Palaeoecol.* 271(1–2), 13–23. <https://doi.org/10.1016/j.palaeo.2008.09.004>
- Gordon, K.D., 1982. A study of microwear on chimpanzee molars: Implications for dental microwear analysis. *Am. J. Phys. Anthropol.* 59(2), 195–215. <https://doi.org/10.1002/ajpa.1330590208>
- Goubel, H., Auguste, P., Crônier, C., Germonpré, M., 2012. Intra-specific morphological variability in the cave bear *Ursus spelaeus* (Mammalia, Carnivora, Ursidae) from the Trou du Sureau (Montaigle caves, Belgium) using an outline analysis. *Geodiversitas* 34(4), 961–975. <https://doi.org/10.5252/g2012n4a13>

- Graber, D.M., White, M., 1983. Black bear food habits in Yosemite National Park. *Bears: Their Biology and Management*. 5, 1–10. <https://doi.org/10.2307/3872514>
- Grandal-d'Anglade, A., López-González, F., 2004. A study of the evolution of the Pleistocene cave bear by a morphometric analysis of the lower carnassial. *Oryctos* 5, 83–94.
- Grandal-d'Anglade, A., López-González, F., 2005. On factors that influence the morphology of the cave bear dentition and a study of the geographical variation in the lower carnassial. *Mitteilungen Der Kommission Für Quartärforschung* 14, 41–52.
- Grandal-d'Anglade, A., Pérez-Rama, M., García-Vázquez, A., González-Fortes, G.M., 2019. The cave bear's hibernation: reconstructing the physiology and behaviour of an extinct animal. *Hist. Biol.* 31(4), 429–441. <https://doi.org/10.1080/08912963.2018.1468441>
- Green, J.L., Croft, D.A., 2018. Using dental mesowear and microwear for dietary inference: A review of current techniques and applications. *Vertebr. Paleobiol. Paleoanthropol.* 53–73. https://doi.org/10.1007/978-3-319-94265-0_5
- Grine, F.E., 1977. Analysis of early hominid deciduous molar wear by scanning electron microscopy: a preliminary report. *J. Electron Microsc. Soc. S. Afr.* 7, 157–158.
- Grine, F.E., 1986. Dental evidence for dietary differences in *Australopithecus* and *Paranthropus*: a quantitative analysis of permanent molar microwear. *J. Hum. Evol.* 15(8), 783–822. [https://doi.org/10.1016/S0047-2484\(86\)80010-0](https://doi.org/10.1016/S0047-2484(86)80010-0)
- Grine, F.E., Ungar, P.S., Teaford, M.F., 2002. Error rates in dental microwear quantification using scanning electron microscopy. *Scanning* 24(3), 144–153. <https://doi.org/10.1002/sca.4950240307>
- Gurova, M., Ivanova, S., 2021. Mishin Kamik Cave: an unusual Pleistocene site in Northwestern Bulgaria. *Materiale Și Cercetări Arheologice (Serie Nouă)* 1(1), 85–104. <https://doi.org/10.3406/mcarh.2021.2204>
- Gurova, M., Ivanova, S., Spassov, N., Hristova, L., Popov, V., Marinova, E., Böhme, M., 2017. Excavations at Mishin Kamik Cave: 2016 season. In: *Archaeological discoveries and excavations in 2016*. NAIM-BAS. Sofia.
- Gurova, M., Verheyden, S., Marinova, E., Ivanova, S., Cheng, H., Edwards, R., Goovaerts, T., Burlet, C., 2021. Speleothem-based chronology and environmental context of deposits from the Mishin Kamik Cave, NW Bulgaria – A contribution to the archaeological study of the Late Pleistocene human occupation in the Balkans. *J. Quat. Sci.* 36, 1221–1233. <https://doi.org/10.1002/jqs.3364>
- Guslitser, B.I., Pavlov, P.Y., 1988. Upper Paleolithic site Medvezhiya cave. *The Stone and Metal Age Sites of the Northern Urals* 11, 5–18.
- Hadnagy, A., 1977. Studiu micromineralogic și rolul mineralelor grele în corelarea sedimentelor de peșteră. *Nymphaea*, 5, 107–128. [In Romanian]
- Hafeez, S., Khan, G., Ashfaq, M., Khan, Z., 2011. Food habits of the Indian crested porcupine (*Hystrix Indica*) in Faisalabad, Pakistan. *Pak. J. Agric. Sci.* 48, 205–210.
- Hatler, D.F., 1967. Some aspects in the ecology of the black bear (*Ursus americanus*) in interior Alaska. Master of Science, University of Alaska. <http://hdl.handle.net/11122/5224>
- Hayward, M.W., Mitchell, C.D., Kamler, J.F., Rippon, P., Heit, D.R., Nams, V., Montgomery, R.A., 2023. Diet selection in the Coyote *Canis latrans*. *J. Mammal.* 104(6), 1338–1352. <https://doi.org/10.1093/jmammal/gyad094>

10. References

- Hedges, R.E.M., Clement, J.G., Thomas, C.D.L., O'Connell, T.C., 2007. Collagen turnover in the adult femoral mid-shaft: Modelled from anthropogenic radiocarbon tracer measurements. *Am. J. Phys. Anthropol.* 133, 808–816. <https://doi.org/10.1002/ajpa.20605>
- Helmens, K.F., 2014. The Last Interglacial–Glacial cycle (MIS 5–2) re-examined based on long proxy records from central and northern Europe. *Quat. Sci. Rev.* 86, 115–143. <https://api.semanticscholar.org/CorpusID:54791099>
- Hewitt, G., 2000. The genetic legacy of the Quaternary ice ages. *Nature* 405(6789), 907–913. <https://doi.org/10.1038/35016000>
- Higham, T., Wild, E.M., 2013. Radiocarbon dating of the Pestera cu Oase faunal remains. In: E. Trinkaus, S. Constantin, J. Zilhão (Eds.), *Life and death at Pestera cu Oase. A setting for modern human emergence in Europe*. Oxford University Press pp. 77–85
- Hilderbrand, G., Schwartz, C., Robbins, C.T., Jacoby, M.E., Hanley, T.A., Arthur, S., Servheen, C., 1999. The importance of meat, particularly salmon, to body size, population productivity, and conservation of North American brown bears. *Can. J. Zool.* 77, 132–138. <https://doi.org/10.1139/cjz-77-1-132>
- Hoppe, K.A., Stover, S.M., Pascoe, J.R., Amundson, R., 2004. Tooth enamel biomineralization in extant horses: implications for isotopic microsampling. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 206(3–4), 355–365. <https://doi.org/10.1016/j.palaeo.2004.01.012>
- Hublin, J.J., Sirakov, N., Aldeias, V., Bailey, S., Bard, E., Delvigne, V., Endarova, E., Fagault, Y., Fewlass, H., Hajdinjak, M., Kromer, B., Krumov, I., Marreiros, J., Martisius, N.L., Paskulin, L., Sinet-Mathiot, V., Meyer, M., Pääbo, S., Popov, V., Rezek, Z., Sirakova, S., Skinner, M.M., Smith G.M., Spasov, R., Talamo, S., Tuna T., Wacker, L., Welker, F., Wilcke, A., Nikolay, Z., McPherron, Sp., Tsanova, T., 2020. Initial Upper Palaeolithic *Homo sapiens* from Bacho Kiro Cave, Bulgaria. *Nature* 581(7808), 299–302. <https://doi.org/10.1038/s41586-020-2259-z>
- Hunter, L., Turner, A., 1997. The big cats and their fossil relatives: An illustrated guide to their evolution and natural history. *Biosci.* 47. <https://doi.org/10.2307/1313168>
- Huntley, B., Allen, J.R.M., Collingham, Y.C., Hickler, T., Lister, A.M., Singarayer, J., Stuart, A. J., Sykes, M.T., Valdes, P.J., 2013. Millennial climatic fluctuations are key to the structure of Last Glacial ecosystems. *PLoS ONE.* 8(4), e61963. <https://doi.org/10.1371/journal.pone.0061963>
- Huygens, O., Manen, F., Martorello, D., Hayashi, H., Ishida, J., 2009. Relationships between Asiatic black bear kills and depredation costs in Nagano Prefecture, Japan. *Ursus* 15, 197–202. [https://doi.org/10.2192/1537-6176\(2004\)015<0197:RBABBK>2.0.CO;2](https://doi.org/10.2192/1537-6176(2004)015<0197:RBABBK>2.0.CO;2)
- Hwang, M.H., Garshelis, D., Wang, Y., 2001. Diets of Asiatic black bears in Taiwan, with methodological and geographical comparisons. *Ursus* 13, 111–125.
- Ibáñez, J.J., Jiménez-Manchón, S., Blaise, É., Nieto-Espinet, A., and Valenzuela-Lamas, S., 2020. Discriminating management strategies in modern and archaeological domestic caprines using low-magnification and confocal dental microwear analyses. *Quat. Int.* 557, 23–38. <https://doi.org/10.1016/j.quaint.2020.03.006>
- Inagaki, A., Allen, M.L., Tochigi, K., Maruyama, T., Koike, S., 2023. Evidence for interspecific modulation of carcass consumption among facultative scavengers in Asian temperate forest. *Food Webs* 37, e00324. <https://doi.org/10.1016/j.fooweb.2023.e00324>

- Iurino, D.A., Mecozzi, B., Iannucci, A., Moscarella, A., Strani, F., Bona, F., Gaeta, M., Sardella, R., 2022. A Middle Pleistocene wolf from central Italy provides insights on the first occurrence of *Canis lupus* in Europe. *Sci. Rep.* 12(1), 2882. <https://doi.org/10.1038/s41598-022-06812-5>
- Ivanova, S., Gurova, M., Spassov, N., 2012. Investigations of the Pleistocene sediments in Magura Cave. In: *Archaeological discoveries and excavations in 2011*. NAIM-BAS. Sofia.
- Ivanova, S., Gurova, M., Spassov, N., Hristova, L., Gyaurova, B., Makedonska, J., Anastassova, E., Marinov, E., Miller, C., Hodgkins, J., Strait, D., 2013. Archaeological investigations in Magura Cave. In: *Archaeological discoveries and excavations in 2012* NAIM-BAS. Sofia.
- Ivanova, S., Gurova, M., Spassov, N., Hristova, L., Tzankov, N., Popov, V., Marinova, E., Makedonska, J., Smith, V., Ottoni, C., Lewis, M., 2016. Magura Cave, Bulgaria: A multidisciplinary study of Late Pleistocene human palaeoenvironment in the Balkans. *Quat. Int.* 415, 86–108. <https://doi.org/10.1016/j.quaint.2015.11.082>
- Jankovská, V., Chromý, P., Nižnianská, M., 2002. Šafárka - First palaeobotanical data of the character of Last Glacial vegetation and landscape in the West Carpathians (Slovakia). *Acta Palaeobot.* 42, 39–50.
- Jankovská, V., Pokorný, P., 2008. Forest vegetation of the last full-glacial period in the Western Carpathians (Slovakia and Czech Republic). *Preslia -Praha-*. 80, 307–324.
- Jiangzuo, Q., Flynn, J.J., 2020. The earliest ursine bear demonstrates the origin of plant-dominated omnivory in Carnivora. *IScience* 23(6). <https://doi.org/10.1016/j.isci.2020.101235>
- Jiangzuo, Q., Liu, J., Chen, J., 2019. Morphological homology, evolution and proposed nomenclature for bear dentition. *Acta Palaeontol. Pol.* 64. <https://doi.org/10.4202/app.00629.2019>
- Jones, D., DeSantis, L., 2016. Dietary ecology of the extinct cave bear (*Ursus spelaeus*): evidence of omnivory as inferred from dental microwear textures. *Acta Palaeontol. Pol.* 61. <https://doi.org/10.4202/app.00253.2016>
- Jovanović, M., Bogićević, K., Nenadić, D., Agustí, J., Sánchez-Bandera, C., López-García, J.M., Blain, H.A., 2022. New paleoecological perspectives on Late Pleistocene Neanderthals in Western Balkans: the rodent assemblages from Smolučka cave (Serbia). *Archaeol. Anthropol. Sci.* 14(9), 169. <https://doi.org/10.1007/s12520-022-01624-0>
- Jurcsák, T., Plopiș, R., Ignat, D., Șerban, M., Popa, E., 1981. Date privind fauna fosilă a Pașterii Urșilor (M. Bihor). *Nymphaea*. 8–9, 161–257.
- Juříčková, L., Horáčková, J., Ložek, V., 2014. Direct evidence of central European forest refugia during the last glacial period based on mollusc fossils. *Quat. Res.* 82(1), 222–228. [https://doi.org/DOI: 10.1016/j.yqres.2014.01.015](https://doi.org/DOI:10.1016/j.yqres.2014.01.015)
- Kalabér, L., Negrutiu, A., Micu, I., Dogaru, A., Mihai, B., 1994. Distribution and ecology of brown bear in Romania. *Int. Conf. Bear. Res. Manage.* 9, 173–178.
- Khan, M.B., Irshad, N., Ahmed, B., Khan, M.R., Minhas, R.A., Ali, U., Mahmood, M., Muhammad, A., Sheikh, A.A., Ashraf, N., 2022. Food habits of indian crested porcupine (*Hystrix indica*) (Kerr 1792), in district Bagh, Azad Jammu and Kashmir. *Braz. J. Biol.* 82. <https://doi.org/10.1590/1519-6984.243063>
- King, T., Andrews, P., Boz, B., 1999. Effect of taphonomic processes on dental microwear. *Am. J. Phys. Anthropol.* 108 (3), 359–373. [https://doi.org/10.1002/\(SICI\)1096-8644\(199903\)108:33.O.CO;2-9](https://doi.org/10.1002/(SICI)1096-8644(199903)108:33.O.CO;2-9)

10. References

- Kistchinski, A.A., 1972. Life history of the brown bear (*Ursus arctos* L.) in North-East Siberia. Bears: Their Biology and Management 2, 67–73. <https://doi.org/10.2307/3872570>
- Knapp, M., Rohland, N., Weinstock, J., Baryshnikov, G.F., Sher, A., Nagel, D., Rabeder, G., Pinhasi, R., Schmidt, H., Hofreiter, M., 2009. First DNA sequences from Asian cave bear fossils reveal deep divergences and complex phylogeographic patterns. Mol. Ecol. 18, 1225–1238. <https://doi.org/10.1111/j.1365-294X.2009.04088.x>
- Kosintsev, P.A., Konovalova, K.Y., Simonova, G.V., 2024. Diet of the small cave bear *Ursus* (Spelaearctos) *rossicus* Borissak, 1930 (Mammalia, Carnivora, Ursidae) as revealed by ¹³C and ¹⁵N isotope analyses in bone collagen. Dokl. Biol. Sci. 513. <https://doi.org/10.1134/S0012496623700825>
- Kozłowski, J. K., Ginter, B., 1982. Excavation in the Bacho Kiro Cave (Bulgaria). Państwowe Wydawnictwo Naukowe. KIP Articles 1893.
- 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. Quat. Sci. Rev. 131, 51–72. <https://doi.org/10.1016/j.quascirev.2015.10.028>
- Krechmar, M.A., 1995. Geographical aspects of the feeding of the brown bear (*Ursus arctos* L.) in the extreme northeast of Siberia. Russ. J. Ecol. 26(6), 436–443. <https://eurekamag.com/research/002/852/002852483.php>
- Kryazheva, I.V., Ponomarev, D.V., Van, K., Van, D., 1970. New data on the Holocene history of the rodent fauna in the Pre-Uralian Subarctic (the Chernyshev Ridge, northeastern part of European Russia). Russ. J. Theriol. 21(1), 82–93. <https://doi.org/10.15298/rusjtheriol.21.1.10>
- Kurtén, B., 1976. The cave bear story; Life and death of a vanished animal. Columbia University Press.
- Kuzmina, I.E., 1971. Forming of theriofauna of the North Urals during the Late Anthropogenic. Tr. Zool. Inst. 69, 44–122.
- Lang, G., Ammann, B., van der Knaap, P., del Molino, C., Schwörer, C., Tinner, W., 2023. Regional vegetation history. In: W. Tinner (Ed.), Vegetation History and Archaeobotany of Europe. Springer. <https://doi.org/TBD>
- Leonardi, M., Hallett, E. Y., Beyer, R., Krapp, M., Manica, A., 2023. pastclim 1.2: an R package to easily access and use paleoclimatic reconstructions. Ecography 2023(3). <https://doi.org/10.1111/ecog.06481>
- Levi, T., Wilmsers, C.C., 2012. Wolves–coyotes–foxes: a cascade among carnivores. Ecology 93(4), 921–929. <https://doi.org/10.1890/11-0165.1>
- Levkovskaya G.M., 1980. Palynological characterization of deposits in caves Kudaro I and Kudaro III, in: Ivanova I.K., Chernyakhovsky A.G. (Eds.), Kudaro Cave Paleolithic sites in South Ossetia. Moscow, Nauka, pp. 128–151.
- Lioubine, V.P., Bosinski, G., 1995. The earliest occupation of the Caucasus region, in: Roebroeks, W., van Kolfschoten, T. (Eds.), The Earliest Occupation of Europe. University of Leiden, Leiden, pp. 207–253.
- Lioubine V.P., Tcherniachovski A.G., Barychnikov G.F., Levkovskaia G.M., Selivanova N.B., 1985. La grotte de Koudaro 1 (Résultats de recherches pluridisciplinaires). L'Anthropologie (Paris), 89, 159–180. [In French]

- Lioubine, V.P., 1989. Paleolithic of the Caucasus, in: Boriskovsky P.I. (Eds.), Paleolithic of the Caucasus and North Asia. Leningrad, Nauka, pp. 7-142. [In Russian].
- Lioubine, V.P., 1998. The Acheulian epoch on the Caucasus. Publishing house of IHMC RAS, Saint Petersburg. 192 pp. [In Russian].
- Lioubine, V.P., 2002. La grotte de Kudaro 1, in: L'Acheuléen du Caucase, Liège, ERAUL 93, 41-59. [In French]
- Lisiecki, L.E., Raymo, M.E., 2005. A Pliocene-Pleistocene stack of 57 globally distributed benthic ^{18}O records. *Paleoceanography* 20 PA1003 <https://doi.org/10.1029/2004PA001071>
- Lješević, M., 2002. Hadži Prodanova pećina. *Zbornik Radova Odbora Za Kras i Speleologiju*, 7, 71–92. [In Serbian]
- López-Alfaro, C., Robbins, C., Zedrosser, A., Nielsen, S., 2013. Energetics of hibernation and reproductive trade-offs in brown bears. *Ecol. Model.* 270, 1–10. <https://doi.org/10.1016/j.ecolmodel.2013.09.002>
- Loreille, O., Orlando, L., Patou-Mathis, M., Philippe, M., Taberlet, P., Hänni, C., 2001. Ancient DNA analysis reveals divergence of the cave bear, *Ursus spelaeus*, and brown bear, *Ursus arctos*, lineages. *C. Biol.* 11(3), 200–203. [https://doi.org/10.1016/S0960-9822\(01\)00046-X](https://doi.org/10.1016/S0960-9822(01)00046-X)
- Louail, M., Ferchaud, S., Souron, A., Walker, A.E.C., Merceron, G., 2021. Dental microwear textures differ in pigs with overall similar diets but fed with different seeds. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 572, 110415. <https://doi.org/10.1016/j.palaeo.2021.110415>
- Loutre, M.F., Berger, A., 2003. Marine Isotope Stage 11 as an analogue for the present interglacial. *Global Planet. Change* 36, 209–217. [https://doi.org/10.1016/S0921-8181\(02\)00186-8](https://doi.org/10.1016/S0921-8181(02)00186-8)
- Maas, M.C., 1991. Enamel structure and microwear: An experimental study of the response of enamel to shearing force. *Am. J. Phys. Anthropol.* 85(1), 31–49. <https://doi.org/10.1002/ajpa.1330850106>
- Mackiewicz, P., Baca, M., Popović, D., Socha, P., Stefaniak, K., Marciszak, A., Nadachowski, A., 2017. Estimating the extinction time of two cave bears, *Ursus spelaeus* and *U. ingressus*. *Acta Zool. Crac.* 60(2), 1–14. https://doi.org/10.3409/azc.60_2.01
- Madurell-Malapeira, J., Minwer-Barakat, R., Alba, D.M., Garcés, M., Gómez, M., Aurell-Garrido, J., Ros-Montoya, S., Moyà-Solà, S., Berástegui, X., 2010. The Vallparadís section (Terrassa, Iberian Peninsula) and the latest Villafranchian faunas of Europe. *Quat. Sci. Rev.* 29, 3972–3982. <https://doi.org/10.1016/j.quascirev.2010.09.020>
- Magri, D., Vendramin, G.G., Comps, B., Dupanloup, I., Geburek, T., Gömöry, D., Latałowa, M., Litt, T., Paule, L., Roure, J.M., Tantau, I., van der Knaap, W.O., Petit, R.J., de Beaulieu, J.-L., 2006. A new scenario for the Quaternary history of European beech populations: palaeobotanical evidence and genetic consequences. *New Phytol.* 171(1), 199–221. <https://doi.org/10.1111/j.1469-8137.2006.01740.x>
- Marchenko-Vagapova, T.I., 2012. Palynological characteristics of the Middle Valday megainterstadial (Late Pleistocene) in the Northeastern European Russia. *Litosfera*, 1, 38–53.
- Marciszak, A., Kotowski, A., Przybylski, B., Badura, J., Wiśniewski, A., Stefaniak, K., 2019a. Large mammals from historical collections of open-air sites of Silesia (southern Poland) with special reference to carnivores and rhinoceros. *Hist. Biol.* 31, 696–730. <https://doi.org/10.1080/08912963.2017.1388377>

10. References

- Marciszak, A., Mackiewicz, P., Borówka, R.K., Capalbo, C., Chibowski, P., Gąsiorowski, M., Hercman, H., Cedro, B., Kropczyk, A., Gornig, W., Moska, P., Nowakowski, D., Ratajczak-Skrzatek, U., Sobczyk, A., Sykut, M.T., Zarzecka-Szubińska, K., Kovalchuk, O., Barkaszi, Z., Stefaniak, K., Mazza, P.P.A., 2024. Fate and preservation of the Late Pleistocene cave bears from Niedźwiedzia Cave in Poland, through taphonomy, pathology, and geochemistry. *Sci. Rep.* 14, 9775. <https://doi.org/10.1038/s41598-024-60222-3>
- Marciszak, A., Schouwenburg, C., Darga, R., 2014. Decreasing size process in the cave (Pleistocene) lion *Panthera spelaea* (Goldfuss, 1810) evolution – A review. *Quat. Int.* 339–340, 245–257. <https://doi.org/10.1016/j.quaint.2013.10.008>
- Marciszak, A., Schouwenburg, C., Lipecki, G., Talamo, S., Shpansky, A., Malikov, D., Gornig, W., 2019b. Steppe brown bear *Ursus arctos* “priscus” from the Late Pleistocene of Europe. *Quat. Int.* 534, 158–170. <https://doi.org/10.1016/j.quaint.2019.02.042>
- Marciszak, A., Stefaniak, K., Mackiewicz, P., Ridush, B., 2015. *Ursus arctos* L., 1758 from Bukovynka Cave (W Ukraine) in an overview on the fossil brown bears size variability based on cranial material. *Quat. Int.* 357, 136–148. <https://doi.org/10.1016/j.quaint.2014.09.052>
- Markova, A.K., 2007. Pleistocene mammal faunas of Eastern Europe. *Quat. Int.* 160(1), 100–111. <https://doi.org/10.1016/J.QUAINT.2006.09.011>
- Martínez, L. M., Estebarez-Sánchez, F., Romero, A., Ibáñez, J. J., Hidalgo-Trujillo, L., Avià, Y., et al., 2022. Effectiveness of buccal dental-microwear texture in African Cercopithecoidea dietary discrimination. *Am. J. Biol. Anthropol.* 179, 678–686. <https://doi.org/10.1002/ajpa.24635>
- Martisius, N.L., Spasov, R., Smith, G.M., Endarova, E., Sinet-Mathiot, V., Welker, F., Aldeias, V., Horta, P., Marreiros, J., Rezek, Z., McPherron, S.P., Sirakov, N., Sirakova, S., Tsanova, T., Hublin, J.J., 2022. Initial Upper Paleolithic bone technology and personal ornaments at Bacho Kiro Cave (Bulgaria). *J. Hum. Evol.* 167, 103198. <https://doi.org/10.1016/j.jhevol.2022.103198>
- Mattson, D.J., 1998. Diet and morphology of extant and recently extinct northern bears. *Ursus* 10, 479–496. <http://www.jstor.org/stable/3873160>
- Mattson, D.J., Blanchard, B.M., Knight, R.R., 1991. Food habits of Yellowstone grizzly bears, 1977–1987. *Can. J. Zool.* 69, 1619–1629. <https://pubs.usgs.gov/publication/70125376>
- Mazza, P., Rustioni, M., 1994. On the phylogeny of Eurasian Bears. *Palaeontogr. Abt. A.* 230(1–3), 1–38. <https://doi.org/10.1127/pala/230/1994/1>
- Medin, T., Martínez-Navarro, B., Madurell-Malapeira, J., Figueirido, B., Kopalani, G., Rivals, F., Kiladze, G., Palmqvist, P., Lordkipanidze, D., 2019. The bears from Dmanisi and the first dispersal of early *Homo* out of Africa. *Sci. Rep.* 9(1), 17752. <https://doi.org/10.1038/s41598-019-54138-6>
- Medin, T., Martínez-Navarro, B., Rivals, F., Madurell-Malapeira, J., Ros-Montoya, S., Espigares, M. P., Figueirido, B., Rook, L., Palmqvist, P., 2017. Late Villafranchian *Ursus etruscus* and other large carnivores from the Orce sites (Guadix-Baza basin, Andalusia, southern Spain): Taxonomy, biochronology, paleobiology, and ecogeographical context. *Quat. Int.* 431, 20–41. <https://doi.org/10.1016/j.quaint.2015.10.053>
- Meleg, I., Alberti, F., Drucker, D., Năpăruș-Aljančić, M., Feurdean, A., Robu, M., Vlaicu, M., Naito, Y., Boroneant, A., Marin, C., Nitu, E., Hofreiter, M., Bocherens, H., Barlow, A., 2024. Ancient biomolecules suggest learned foraging strategy in extinct cave bears. [Pre-print] *BioRxiv* <https://doi.org/10.1101/2024.09.23.614392>

- Merceron, G., 2005. A new method of dental microwear analysis: Application to extant primates and *Ouranopithecus macedoniensis* (Late Miocene of Greece). *PALAIOS*, 20(6), 551–561. <https://doi.org/10.2110/palo.2004.p04-17>
- Merceron, G., Blondel, C., Brunet, M., Sen, S., Solounias, N., Viriot, L., Heintz, E., 2004. The Late Miocene paleoenvironment of Afghanistan as inferred from dental microwear in artiodactyls. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 207(1), 143–163. <https://doi.org/10.1016/j.palaeo.2004.02.008>
- Micó, C., Blasco, R., Muñoz Del Pozo, A., Jiménez-García, B., Rosell, J., Rivals, F., 2024. Differentiating taphonomic features from trampling and dietary microwear, an experimental approach. *Hist. Biol.* 36(4), 760–782. <https://doi.org/10.1080/08912963.2023.2184690>
- Mihailović, D., 2014. Paleolit na centralnom Balkanu - kulturne promene i populaciona kretanja. Serbian Archaeological Society.
- Mihailović, D., Mihailović, B., 2006. The Palaeolithic site Hadži Prodan's Cave by Ivanjica. *Arheološki Pregled Srpskog Arheološkog Društva* 1, 13–16.
- Millán-Arnau, F., 2023. L'ós de les caveres (*Ursus spelaeus*) a Catalunya. PhD thesis.
- Mills, J.R.E., 1955. Ideal dental occlusion in primates. *Dent. Pract.* 6, 47–61.
- Milota, Ș., Gherase, M., Sarcină, L., Rodrigo, R., Moldovan, O., Trinkaus, E., Constantin, S., Zilhão, J., 2013. Exploration and documentation of the Peștera cu Oase. In: E. Trinkaus, S. Constantin, & J. Zilhão (Eds.), *Life and death at Peștera cu Oase. A setting for modern human emergence in Europe*. University, Oxford Press. pp. 5–15.
- Mirea, I.C., Robu, M., Petculescu, A., Kenesz, M., Faur, L., Arghir, R., Tecsa, V., Timar-Gabor, A., Roban, R.-D., Panaiotu, C.G., Sharifi, A., Pourmand, A., Codrea, V.A., Constantin, S., 2021. Last deglaciation flooding events in the Southern Carpathians as revealed by the study of cave deposits from Muierilor Cave, Romania. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 562, 110084.
- Moncel, M., Schreve, D., 2016. The Acheulean in Europe: Origins, evolution and dispersal. *Quat. Int.* 411, 1–8. <https://doi.org/10.1016/j.quaint.2016.08.039>
- Mori, E., Di Gregorio, M., Mazza, G., Ficetola, G.F., 2020. Seasonal consumption of insects by the crested porcupine in Central Italy. *Mammalia* 85. <https://doi.org/10.1515/mammalia-2020-0131>
- Mowat, G., Heard, D., 2011. Major components of grizzly bear diet across North America. *Can. J. Zool.* 84, 473–489. <https://doi.org/10.1139/z06-016>
- 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. *Quat. Int.* 339–340, 148–163. <https://doi.org/10.1016/j.quaint.2013.10.020>
- Münzel, S.C., Conard, N., 2004. Cave bear hunting in the Hohle Fels, a cave site in the Ach Valley, Swabian Jura. *Rev. Paléobiologie*. 23, 877–885.
- Münzel, S.C., Stiller, M., Hofreiter, M., Mittnik, A., Conard, N.J., Bocherens, H., 2011. Pleistocene bears in the Swabian Jura (Germany): Genetic replacement, ecological displacement, extinctions and survival. *Quat. Int.* 245(2), 225–237. <https://doi.org/10.1016/j.quaint.2011.03.060>
- Naito, Y.I., Germonpré, M., Chikaraishi, Y., Ohkouchi, N., Drucker, D., Hobson, K., Edwards, M., Wissing, C., Bocherens, H., 2016b. Evidence for herbivorous cave bears (*Ursus spelaeus*) in

10. References

- Goyet Cave, Belgium: implications for palaeodietary reconstruction of fossil bears using amino acid $\delta^{15}\text{N}$ approaches. *J. Quat. Sci.* 31, 598–606. <https://doi.org/10.1002/jqs.2883>
- Naito, Y.I., Chikaraishi, Y., Drucker, D.G., Ohkouchi, N., Semal, P., Wißing, C., Bocherens, H., 2016a. Ecological niche of Neanderthals from Spy Cave revealed by nitrogen isotopes of individual amino acids in collagen. *H. Hum. Evol.* 93, 82–90. <https://doi.org/https://doi.org/10.1016/j.jhevol.2016.01.009>
- Naito, Y., Meleg, I.N., Robu, M., Vlaicu, M., Drucker, D.G., Wißing, C., Hofreiter, M., Barlow, A., Bocherens, H., 2020. Heavy reliance on plants for Romanian cave bears evidenced by amino acid nitrogen isotope analysis. *Sci. Rep.* 10, 6612. <https://doi.org/10.1038/s41598-020-62990-0>
- Nelson, D.E., Angerbjörn, A., Lidén, K., Turk, I., 1998. Stable isotopes and the metabolism of the European cave bear. *Oecologia* 116(1), 177–181. <https://doi.org/10.1007/s004420050577>
- Nicolăescu-Plopşor, C.S., 1938. Le paléolithique en Roumanie. *Dacia*, 5–6.
- Nicolăescu-Plopşor, C.S., Comşa, E., Nicolăescu-Plopşor, D.C., Bolomey, A., 1957. Şantierul arheologic Baia de Fier (reg. Craiova, r. Novaci) / Chantier archéologique de Baia de Fier. *Materiale Şi Cercetări Arheologice* 3(1), 13–27. <https://doi.org/10.3406/mcarh.1957.1086>
- Nitychoruk, J., Bińka, K., Ruppert, H., Schneider, J., 2006. Holsteinian Interglacial=Marine Isotope Stage 11? *Quat. Sci. Rev.* 25, 2678–2681. <https://doi.org/10.1016/j.quascirev.2006.07.004>
- Ochando, J., Carrión, J.S., Magri, D., Marín-Arroyo, A.B., Di Rita, F., Munuera, M., Michelangeli, F., Amorós, G., Milošević, S., Bogićević, K., Dimitrijević, V., Nenadić, D., Roksandic, M., Mihailović, D., 2024. Balkan Neanderthals: The Late Pleistocene palaeoecological sequence of Peşturina Cave (Niš, Serbia). *Quat. Sci. Rev.* 330, 108600. <https://doi.org/10.1016/j.quascirev.2024.108600>
- Ogurtsov, S., 2018. The diet of the brown bear (*Ursus arctos*) in the Central Forest Nature Reserve (West-European Russia), based on scat analysis data. *Biol. Bull.* 45, 1039–1054. <https://doi.org/10.1134/S1062359018090145>
- Onac, B., Effenberger, H., Collins, N., Kearns, J., Breban, R., 2011. Revisiting three minerals from Cioclovina Cave (Romania). *Int. J. Speleol.* 40(2), 99–108. <https://doi.org/10.5038/1827-806X.40.2.2>
- Pacher, M., Quilès, J., 2013a. Cave bear paleontology and paleobiology at Peştera cu Oase: Fossil population structure and size variability. In: E. Trinkaus, S. Constantin, J. Zhilao (Eds.), *Life and death at Peştera cu Oase. A setting for modern human emergence in Europe*. Oxford University Press pp. 127–146.
- Pacher, M., Quilès, J., 2013b. Taphonomic analysis of the cave bear remains from Peştera cu Oase. In: E. Trinkaus, S. Constantin, J. Zhilao (Eds.), *Life and death at Peştera cu Oase. A setting for modern human emergence in Europe*. Oxford University Press pp. 147–158.
- Pacher, M., Stuart, A.J., 2009. Extinction chronology and palaeobiology of the cave bear (*Ursus spelaeus*). *Boreas* 38(2), 189–206. <https://doi.org/10.1111/j.1502-3885.2008.00071.x>
- Panthi, S., Aryal, A., Coogan, S.C.P., 2019. Diet and macronutrient niche of Asiatic black bear (*Ursus thibetanus*) in two regions of Nepal during summer and autumn. *Ecol. Evol.* 9(7), 3717–3727. <https://doi.org/10.1002/ece3.4926>

- Pappa, S., 2016. Palaeoecology and palaeodiet: reconstructing adaptations in the Middle and Late Pleistocene Ursidae through dental microwear and geochemistry. PhD thesis. Royal Holloway University of London.
- Pappa, S., Schreve, D.C., Rivals, F., 2019. The bear necessities: A new dental microwear database for the interpretation of palaeodiet in fossil Ursidae. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 514, 168–188. <https://doi.org/https://doi.org/10.1016/j.palaeo.2018.10.015>
- Paralikiidis, N.P., Papageorgiou, N.K., Kontsiotis, V.J., Tsiompanoudis, A.C., 2010. The dietary habits of the brown bear (*Ursus arctos*) in western Greece. *Mammal. Biol.* 75(1), 29–35. <https://doi.org/10.1016/j.mambio.2009.03.010>
- Păunescu, A., 1980. Evoluția istorică pe teritoriul României din paleolitic până la începutul neoliticului. *Studii Și Cercetări de Istorie Veche Și Arheologie*, 31, 519–545. [In Romanian]
- Pederzani, S., Britton, K., Aldeias, V., Bourgon, N., Fewlass, H., Lauer, T., McPherron, S.P., Rezek, Z., Sirakov, N., Smith, G.M., Spasov, R., Tran, N.H., Tzanova, T., Hublin, J.J., 2021. Subarctic climate for the earliest *Homo sapiens* in Europe. *Sci. Adv.* 7(39). <https://doi.org/10.1126/sciadv.abi4642>
- Peigné, S., Goillot, C., Germonpré, M., Blondel, C., Bignon, O., Merceron, G., 2009. Predormancy omnivory in European cave bears evidenced by a dental microwear analysis of *Ursus spelaeus* from Goyet, Belgium. *Proc. Natl. Acad. Sci.* 106(36), 15390–15393. <https://doi.org/10.1073/pnas.0907373106>
- Pereira, L., Owen-Smith, N., Moleón, M., 2014. Facultative predation and scavenging by mammalian carnivores: Seasonal, regional and intra-guild comparisons. *Mammal Rev.* 44, 44–55. <https://doi.org/10.1111/mam.12005>
- Pérez-Rama, M., Mosquera, D., Grandal-d'Anglade, A., 2011. Effects of hibernation on the stable isotope signatures of adult and neonate cave bears. *Quaternaire (Special Issue)* 79–88.
- Pérez-Ramos, A., Kupczik, K., Van Heteren, A.H., Rabeder, G., Grandal-D'Anglade, A., Pastor, F.J., Serrano, F.J., Figueirido, B., 2019. A three-dimensional analysis of tooth-root morphology in living bears and implications for feeding behaviour in the extinct cave bear. *Hist. Biol.* 31(4), 461–473. <https://doi.org/10.1080/08912963.2018.1525366>
- Persson, I., Wikan, S., Swenson, J., Myrsetrud, I., 2001. The diet of the brown bear *Ursus arctos* in the Pasvik Valley northeastern Norway. *Wildl. Biol.* 7, 27–37. <https://doi.org/10.2981/wlb.2001.006>
- Petrov, B., Stoev, P., 2007. The underground world of the mountain Rhodopes. UNDP. [Bulgarian]
- Petrović, J., 1976. Jame i pećine SR Srbije. Vojnoizdavački zavod. Belgrade pp. 512. [In Serbian]
- Pickarski, N., Kwiecien, O., Langgut, D., Litt, T., 2015. Abrupt climate and vegetation variability of eastern Anatolia during the last glacial. *Clim. Past* 11(11), 1491–1505. <https://doi.org/10.5194/cp-11-1491-2015>
- Pinto-Llona, A., 2006. Comparative dental microwear analysis of cave bears *Ursus spelaeus* ROSENMÜLLER, 1794 and brown bears *Ursus arctos* LINNAEUS, 1758.
- Pinto-Llona, A., Andrews, P., 2001. Dental wear and grit ingestion in extant and extinct bears from N. Spain. *Cad. Lab. Xeol. Laxe* 26, 465–477.
- Pinto-Llona, A.C., 2013. Macrowear and occlusal microwear on teeth of cave bears *Ursus spelaeus* and brown bears *Ursus arctos*: Inferences concerning diet. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 370, 41–50. <https://doi.org/https://doi.org/10.1016/j.palaeo.2012.11.017>

10. References

- Popov, V., 1986. Early Pleistocene Rodentia (Mammalia) from the “Temnata Dupka” Cave near Karlukovo (North Bulgaria). *Acta Zool. Bulg.* 30, 2–14.
- Popov V., 2000. The small mammals (Mammalia: Insectivora, Chiroptera, Lagomorpha, Rodentia) from Cave 16 and the paleoenvironmental changes during the Late Pleistocene. In: Ginter, B., Kozowski, J.K., Laville, K., (Eds.), *Temnata Cave. Excavations in Karlukovo Karst Area, Bulgaria*. Jagellonian University Press. Krakow pp. 159–240.
- Prilepskaya, N.E., Bachura, O.P. Baryshnikov, G.F., 2022. Season-of-death and age-at-death of the easternmost European cave bears: Cementum and dentine increment analysis provides new insight into the cave bear ecology. *Boreas* 51, 810–823. <https://doi.org/10.1111/bor.12590>.
- Prokopenko, A.A., Karabanov, E.B., Williams, D.F., Kuzmin, M.I., Shackleton, N.J., Crowhurst, S.J., Peck, J.A., Gvozdkov, A.N., King, J.W., 2001. Biogenic silica record of the Lake Baikal response to climatic forcing during the Brunhes. *Quat. Res.* 55(2), 123–132. <https://doi.org/10.1006/qres.2000.2212>
- Puech, P.F., 1977. Nutrition of *Homo erectus* of Tautavel, the oldest human skull and face in Europe. *Inf. Dent.* 59(28), 13–18.
- Puzachenko, A.Y., Markova, A.K., 2019. Evolution of mammal species composition and species richness during the Late Pleistocene - Holocene transition in Europe: A general view at the regional scale. *Quat. Int.* 530–531, 88–106. <https://doi.org/10.1016/j.quaint.2018.12.025>
- Rabal-Garcés, R., Cuenca-Bescós, G., Canudo, J.I. de Torres, T., 2012. Was the European cave bear an occasional scavenger? *Lethaia* 45, 96–108.
- Rabeder, G., 1999. Die Evolution des Höhlenbärengabisses. *Österreichische Akademie der Wissenschaften* (11).
- Rabeder, G., Debeljak, I., Hofreiter, M., Withalm, G., 2008. Morphological responses of cave bears (*Ursus spelaeus* group) to high-alpine habitats. *Die Höhle* v.59(59-72), 59.
- Rabeder, G., Hofreiter, M., 2004. Der neue Stammbaum der alpinen Höhlenbären. *Die Höhle*, v.55(58-77), 55.
- Rabeder, G., Hofreiter, M., Withalm, G., 2004a. The systematic position of the cave bear from Potočka zijalka (Slovenia). *Mitt. Komm. Quartärforsch. Österr. Akad. Wiss.* 13.
- Rabeder, G., Hofreiter, M., Withalm, G., Nagel, D., 2004b. New taxa of alpine cave bears (Ursidae, Carnivora). *Publ. Mus. Confluences* 2(1), 49–67.
- Rabeder, G., Nagel, D., Pacher, M., 2000. *Der Höhlenbär: Species 4*. Verlag Thorbecke. Stuttgart, pp. 256.
- Rădulescu, C., Samson, P., 1959. Contribution à la connaissance de la dentition lactéale d'*Ursus spelaeus*. *Eiszeit Alter Und Gegenwart*, 10(205), 16.
- Raine, R.M., Kansas, J.L., 1990. Black bear seasonal food habits and distribution by elevation in Banff National Park, Alberta. *Bears: Their Biology and Management* 8, 297–304. <https://doi.org/10.2307/3872932>
- Rakić, R., 1980. Risovača - the largest cave in Šumadija. *Collection of Papers - Institute of Archaeology*, 29, 55–62.
- Rakovec, I., 1965. Pleistocene mammalian fauna from Risovača near Arandelovac (Serbia). *Razprave*, 8, pp. 223–317.

- Ramírez-Pedraza, I., 2017. Investigating dietary habits through tooth microwear and stable isotope analyses ($\delta^{13}\text{C}$ and $\delta^{15}\text{N}$) in bone collagen of cave bear (*Ursus spelaeus*) in southern latitudes of Europe during the Late Pleistocene: the case of Toll Cave (MIS3; Spain). Master thesis. Universitat Rovira i Virgili.
- Ramírez-Pedraza, I., Baryshnikov, G.F., Prilepskaya, N.E., Belyaev, R.I., Pappa, S., Rivals, F., 2022. Paleodiet and niche partitioning among the easternmost European cave bears based on tooth wear analysis. *Hist. Biol.* 34(6), 1063–1071. <https://doi.org/10.1080/08912963.2021.1960324>
- Ramírez-Pedraza, I., Martínez, L.M., Aouraghe, H., Rivals, F., Tornero, C., Haddoumi, H., Estebarez-Sánchez, F., Rodríguez-Hidalgo, A., van der Made, J., Oujaa, A., Ibáñez, J.J., Mhamdi, H., Souhir, M., Aissa, A.M., Chacón, M.G., Sala-Ramos, R., 2023. Multiproxy approach to reconstruct fossil primate feeding behavior: Case study for macaque from the Plio-Pleistocene site Guefaït-4.2 (eastern Morocco). *Front. Ecol. Evol.* 11. <https://doi.org/10.3389/fevo.2023.1011208>
- Ramírez-Pedraza, I., Pappa, S., Blasco, R., Arilla, M., Rosell, J., Millán, F., Maroto, J., Soler, J., Soler, N., Rivals, F., 2020. Dietary habits of the cave bear from the Late Pleistocene in the northeast of the Iberian Peninsula. *Quat. Int.* 557, 63–69. <https://doi.org/https://doi.org/10.1016/j.quaint.2019.09.043>
- Ramírez-Pedraza, I., Tornero, C., Aouraghe, H., Rivals, F., Patalano, R., Haddoumi, H., Expósito, I., Rodríguez-Hidalgo, A., Mischke, S., van der Made, J., Piñero, P., Blain, H.A., Roberts, P., Jha, D.K., Agustí, J., Sánchez-Bandera, C., Lemjidi, A., Benito-Calvo, A., Moreno-Ribas, E., Oujaa, A., Mhamdi, H., Souhir, M., Aissa, A., Gema-Chacón, M., Sala-Ramos, R., 2024. Arid, mosaic environments during the Plio-Pleistocene transition and early hominin dispersals in northern Africa. *Nat. Commun.* 15(1), 8393. <https://doi.org/10.1038/s41467-024-52672-0>
- Ramírez-Pedraza, I., Tornero, C., Pappa, S., Talamo, S., Salazar-García, D.C., Blasco, R., Rosell, J., Rivals, F., 2019. Microwear and isotopic analyses on cave bear remains from Toll Cave reveal both short-term and long-term dietary habits. *Sci. Rep.* 9(1). <https://doi.org/10.1038/s41598-019-42152-7>
- Rasmussen, S.O., Bigler, M., Blockley, S.P., Blunier, T., Burchardt, S.L., Clausen, H.B., Cvijanovic, I., Dahl-Jensen, D., Johnsen, S.J., Fischer, H., Gkinis, V., Guillevic, M., Hoek, W.Z., Lowe, J.J., Pedro, J.B., Popp, T., Seierstad, I.K., Steffensen, J.P., Svensson, A.M., Vellelonga, P., Vinther, B.M., Walker, M.J.C., Wheatley, J.J., Winstrup, M., 2014. A stratigraphic framework for abrupt climatic changes during the Last Glacial period based on three synchronized Greenland ice-core records: Refining and extending the INTIMATE event stratigraphy. *Quat. Sci. Rev.* 106, 14–28. <https://doi.org/10.1016/j.quascirev.2014.09.007>
- Rensberger, J., 1978. Scanning electron microscopy of wear and occlusal events in some small herbivores. In: P. Butler and K. Joysey (Eds.), *Development, function and evolution of teeth*. pp. 415–348.
- Rey-Iglesia, A., García-Vázquez, A., Treadaway, E.C., van der Plicht, J., Baryshnikov, G.F., Szpak, P., Bocherens, H., Boeskorov, G.G., Lorenzen, E.D., 2019. Evolutionary history and palaeoecology of brown bear in North-East Siberia re-examined using ancient DNA and stable isotopes from skeletal remains. *Sci. Rep.* 9(1), 4462. <https://doi.org/10.1038/s41598-019-40168-7>
- Rey-Rodríguez, I., López-García, J.M., Stoetzel, E., Denys, C., Arnaud, J., Parfitt, S., Fernández-Jalvo, Y., King, T., 2022. Palaeoecological reconstructions of the Middle to Late Pleistocene

10. References

- occupations in the Southern Caucasus using rodent assemblages. *Archaeol. Anthropol. Sci.* 14(5), 96. <https://doi.org/10.1007/s12520-022-01555-w>
- Richards, M.P., Pacher, M., Stiller, M., Quilès, 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. *Proc. Natl. Acad. Sci.* 105(2), 600–604. <https://doi.org/10.1073/pnas.0711063105>
- Richter, C., Wolf, D., Walther, F., Meng, S., Sahakyan, L., Hovakimyan, H., Wolpert, T., Fuchs, M., Faust, D., 2020. New insights into Southern Caucasian glacial–interglacial climate conditions inferred from Quaternary gastropod fauna. *J. Quat. Sci.* 35(5), 634–649. <https://doi.org/10.1002/jqs.3204>
- Rigg, R., Gorman, M., 2005. Diet of brown bears (*Ursus arctos*): new results from the Tatras region and a comparison of research methods. *Výskum a Ochrana Cicavcov Na Slovensku* 7, 61–79.
- Rivals, F., Baryshnikov, G.F., Prilepskaya, N.E., Belyaev, R.I., 2022. Diet and ecological niches of the Late Pleistocene hyenas *Crocota spelaea* and *C. ultima ussurica* based on a study of tooth microwear. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 601, 111125. <https://doi.org/10.1016/J.PALAEO.2022.111125>
- Rivals, F., Prignano, L., Semprebon, G.M., Lozano, S., 2015. A tool for determining duration of mortality events in archaeological assemblages using extant ungulate microwear. *Sci. Rep.* 5, 1–12. <https://doi.org/10.1038/srep17330>
- Rivals, F., Semprebon, G., 2017. Latitude matters: an examination of behavioural plasticity in dietary traits amongst extant and Pleistocene *Rangifer tarandus*. *Boreas* 46, 254–263. <https://doi.org/10.1111/bor.12205>
- Rivals, F., Semprebon, G., Lister, A., 2012. An examination of dietary diversity patterns in Pleistocene proboscideans (*Mammuthus*, *Palaeoloxodon*, and *Mammot*) from Europe and North America as revealed by dental microwear. *Quat. Int.* 255, 188–195. <https://doi.org/https://doi.org/10.1016/j.quaint.2011.05.036>
- Rivals, F., Solounias, N., Mithlacher, M.C., 2007. Evidence for geographic variation in the diets of Late Pleistocene and early Holocene Bison in North America, and differences from the diets of recent *Bison*. *Quat. Res.* 68(3), 338–346. <https://doi.org/DOI: 10.1016/j.yqres.2007.07.012>
- Robu, M., 2009. Upper Pleistocene *Panthera leo spelaea* (Goldfuss, 1810) from Urșilor Cave, Romania. *Proceedings of the Seventh Romanian Symposium on Palaeontology* 92–97.
- Robu, M., 2015a. Fossil population structure and mortality analysis of the cave bears from Urșilor Cave, north-western Romania. *Acta Palaeontol. Pol.* <https://doi.org/10.4202/app.00201.2015>
- Robu, M., 2015b. The palaeontology of the cave bear bone assemblage from Urșilor Cave of Chișcău – Osteometry, Palaeoichnology, Taphonomy, and Stable Isotopes. PhD thesis.
- Robu, M., 2016a. Age re-assessment of the cave bear assemblage from Urșilor Cave, north-western Romania. *Int. J. Speleol.* 45(2), 123–133. <https://doi.org/10.5038/1827-806X.45.2.1947>
- Robu, M., 2016b. The assessment of the internal architecture of an MIS 3 cave bear bone assemblage. Case study: Urșilor Cave, Western Carpathians, Romania. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 444, 115–123. <https://doi.org/10.1016/j.palaeo.2015.12.012>
- 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*). *Can. J. Zool.* 91(4), 227–234. <https://doi.org/10.1139/cjz-2012-0222>

- Robu, M., Marom, N., Mirea, I.C., Faur, L.M., Petculescu, A., Kenesz, M., Shafir, R., Égüez, N., Constantin, S., 2024. Intraguild interactions among carnivorans of the last glacial: The case of wolves and bears from Muierilor Cave, Romania. *Quat. Sci. Rev.* 334, 108720. <https://doi.org/10.1016/j.quascirev.2024.108720>
- Robu, M., Mirea, I.C., Petculescu, A., Constantin, S., 2018a. Palaeoichnology of an MIS 3 cave bear settlement – Urşilor Cave (Western Carpathians, Romania). *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 493, 126–135. <https://doi.org/10.1016/j.palaeo.2018.01.009>
- Robu, M., Petculescu, A., Mirea, I., Kenesz, M., Vlaicu, M., Munteanu, C., Nae, A., Valerică, T., 2016. Size of the cave bear population and skeletal distribution from Urşilor Cave, Romania. *Trav. Inst. Speol. "E. Racovitza"* 55, 63–80.
- Robu, M., Venedict, B., Drăguşin, V., Cotiugă, V., 2009. Preliminary report on the laser scanning of the cave bear ichnofabrics from Urşilor Cave, Bihor Mountains, Romania. *Proceedings of the Seventh Romanian Symposium on Palaeontology* 13–14.
- Robu, M., Wynn, J., Puşcaş, C.M., Meleg, I.N., Martin, J.E., Constantin, S., 2019. Palaeoecology and palaeoclimatic context of Romanian Carpathian MIS 3 cave bears using stable isotopes ($\delta^{13}\text{C}$ and $\delta^{18}\text{O}$). *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 534, 109288. <https://doi.org/10.1016/j.palaeo.2019.109288>
- Robu, M., Wynn, J.G., Mirea, I.C., Petculescu, A., Kenesz, M., Puşcaş, C.M., Vlaicu, M., Trinkaus, E., Constantin, S., 2018b. The diverse dietary profiles of MIS 3 cave bears from the Romanian Carpathians: insights from stable isotope ($\delta^{13}\text{C}$ and $\delta^{15}\text{N}$) analysis. *Palaeontology* 61(2), 209–219. <https://doi.org/10.1111/pala.12338>
- Robu, M., Petculescu, A., Panaiotu, Döppes, Vlaicu, M., Drăguşin, V., Kenesz, M., 2011. New insights on the cave bear population from the Urşilor cave, Romania. *Quaternaire (Special Issue)* 107.
- Robu, M., Rivals, F., Vlaicu, M., Duñó-Iglesias, P., Ramírez-Pedraza, Croior, R., Ionuţ-Cornel, M., Marom, N., Egüez, N., Demay, L., Obadă, T., Burlacu, V., Meloro, C., Martin, J.E., (in preparation). The paleoecology of the large mammals from Duruitoarea Veche Cave (Moldova).
- Rosenzweig, M.L., 1991. Habitat selection and population interactions: the search for mechanism. *Am. Nat.* 137, S5–S28. <http://www.jstor.org/stable/2462286>
- Roucoux, K.H., Tzedakis, P.C., Frogley, M.R., Lawson, I.T., Preece, R.C., 2008. Vegetation history of the marine isotope stage 7 interglacial complex at Ioannina, NW Greece. *Quat. Sci. Rev.* 27(13–14), 1378–1395. <https://doi.org/10.1016/j.quascirev.2008.04.002>
- Rougier, H., Trinkaus, E., 2013. The human cranium from the Peştera cu Oase, Oase 2. In: Trinkaus E., Constantin S., Zilhão J. (Eds.), *Life and death at Peştera cu Oase. A setting for modern human emergence in Europe*, Oxford University Press pp. 257–320.
- RStudio Team., 2021. RStudio: Integrated Development Environment for R. <http://www.rstudio.com/>
- Ruan, J., Kherbouche, F., Genty, D., Blamart, D., Cheng, H., Dewilde, F., Hachi, S., Edwards, R.L., Régnier, E., Michelot, J.L., 2016. Evidence of a prolonged drought ca. 4200 yr BP correlated with prehistoric settlement abandonment from the Gueldaman GLD1 Cave, Northern Algeria. *Clim. Past* 12(1), 1–14. <https://doi.org/10.5194/cp-12-1-2016>
- Ruiz-Villar, H., Morales-González, A., Bombieri, G., Zarzo-Arias, A., Penteriani, V., 2019. Characterization of a brown bear aggregation during the hyperphagia period in the Cantabrian Mountains, NW Spain. *Ursus* 29(2), 93. <https://doi.org/10.2192/URSU-D-29-1.1>

10. References

- Rusu, T., Racoviță, G., 1981. Peștera Urșilor de la Chișcău. Ocrotirea Naturii Și Mediului Înconjurător 25(1), 57–71. [In Romanian]
- Ryan, A.S., 1979a. A preliminary scanning electron microscope examination of wear striation direction on primate teeth. *J. Dent. Res.* 58(1), 525–530. <https://doi.org/10.1177/00220345790580011401>
- Ryan, A.S., 1979b. Wear striation direction on primate teeth: A scanning electron microscope examination. *Am. J. Phys. Anthropol.* 50(2), 155–167. <https://doi.org/10.1002/ajpa.1330500204>
- Ryan, A.S., 1980. Anterior dental microwear in hominid evolution: comparisons with human and nonhuman primates. University of Michigan. [PhD thesis]
- Sadori, L., Koutsodendris, A., Panagiotopoulos, K., Masi, A., Bertini, A., Combourieu-Nebout, N., Francke, A., Kouli, K., Joannin, S., Mercuri, A.M., Peyron, O., Torri, P., Wagner, B., Zanchetta, G., Sinopoli, G., Donders, T.H., 2016. Pollen-based paleoenvironmental and paleoclimatic change at Lake Ohrid (south-eastern Europe) during the past 500 ka. *Biogeosciences* 13(5), 1423–1437. <https://doi.org/10.5194/bg-13-1423-2016>
- Samson, C., Pettorelli, J., 1995. Reproductive biology of female black bears in relation to body mass in early winter. *J. Mammal.* 76, 68–77. <https://doi.org/10.2307/1382315>
- Sanchez Goñi, M., Bard, E., Landais, A., Rossignol, L., d'Errico, F., 2013. Air-sea temperature decoupling in western Europe during the last interglacial-glacial transition. *Nat. Geosci.* 6, 837–841. <https://doi.org/10.1038/ngeo1924>
- Sánchez Goñi, M.F., 2022. Chapter 2 - The climatic and environmental context of the Late Pleistocene, in: Romagnoli, F., Rivals, F., Benazzi, S.B.T.-U.N., (Eds.), Academic Press, pp. 17–38. <https://doi.org/10.1016/B978-0-12-821428-2.00017-2>
- Schoener, T.W., 1974. Resource partitioning in ecological communities. *Science* 185(4145), 27–39. <https://doi.org/10.1126/science.185.4145.27>
- Schubert, B.W., Ungar, P.S., DeSantis, L.R.G., 2010. Carnassial microwear and dietary behaviour in large carnivores. *J. Zool.* 280(3), 257–263. <https://doi.org/10.1111/j.1469-7998.2009.00656.x>
- Schwartz, C.C., Fortin, J.K., Teisberg, J.E., Haroldson, M.A., Servheen, C., Robbins, C.T., Van Manen, F.T., 2014. Body and diet composition of sympatric black and grizzly bears in the Greater Yellowstone Ecosystem. *J. Wildl. Manag.* 78(1), 68–78. <https://doi.org/10.1002/jwmg.633>
- Scott, R., Schubert, B., Grine, F., Teaford, M., 2008. Low Magnification Microwear: Questions of Precision and Repeatability. *J. Vertebr. Paleontol.* 28, 139A.
- Scott, R.S., Ungar, P.S., Bergstrom, T.S., Brown, C.A., Childs, B.E., Teaford, M.F., Walker, A., 2006. Dental microwear texture analysis: technical considerations. *J. Hum. Evol.* 51, 339–349. <https://doi.org/10.1016/j.jhevol.2006.04.006>
- Scott, R., Ungar, P.S., Bergstrom, T.S., Brown, C.A., Grine, F.E., Teaford, M.F., Walker, A., 2005. Dental microwear texture analysis shows within-species diet variability in fossil hominins. *Nature* 436(7051), 693–695. <https://doi.org/10.1038/nature03822>
- Selig, K., Silcox, M., 2022. Measuring molarization: Change through time in premolar function in an extinct stem primate lineage. *J. Mamm. Evol.* 29. <https://doi.org/10.1007/s10914-022-09623-7>

- Selva, N., Jędrzejewska, B., Jędrzejewski, W., Wajrak, A., 2005. Factors affecting carcass use by a guild of scavengers in European temperate woodland. *Can. J. Zool.* 83(12), 1590–1601. <https://doi.org/10.1139/z05-158>
- Semprebon, G.M., Godfrey, L.R., Solounias, N., Sutherland, M.R., Jungers, W.L., 2004. Can low-magnification stereomicroscopy reveal diet? *J. Hum. Evol.* 47 (3), 115–144. <https://doi.org/10.1016/j.jhevol.2004.06.004>.
- Semprebon, G.M., Rivals, F., 2007. Was grass more prevalent in the pronghorn past? An assessment of the dietary adaptations of Miocene to Recent Antilocapridae (Mammalia: Artiodactyla). *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 253(3), 332–347. <https://doi.org/https://doi.org/10.1016/j.palaeo.2007.06.006>
- Semprebon, G.M., Sise, P.J., Coombs, M.C., 2011. Potential bark and fruit browsing as revealed by stereomicroscopy analysis of the peculiar clawed herbivores known as Chalicotheres (Perissodactyla, Chalicotherioidea). *J. Mammal. Evol.* 18(1), 33–55. <https://doi.org/10.1007/s10914-010-9149-3>
- Sevilla, P., 2016. Bats from Azokh Caves. In: Fernández-Jalvo, Y., King, T., Yepiskoposyan, L., Andrews, P. (Eds.), *Azokh Cave and the Transcaucasian Corridor*, *Vertebr. Paleobiol. Pa. Ser.* Springer, pp. 177–189. https://doi.org/10.1007/978-3-319-24924-7_8
- Sher, A., Kuzmina, S., 2013. Late Pleistocene of Northern Asia. *Encyclopedia of Quaternary Science: Second Edition*, 255–273. <https://doi.org/10.1016/B978-0-444-53643-3.00270-3>
- Shkurkin, G.V., Almquist, A.J., Pfliehofer, A.A., Stoddard, E.L., 1975. Scanning electron microscopy of dentition: Methodology and ultrastructural morphology of tooth wear. *J. Dent. Res.* 54, 402–406.
- Simpson, G.G., 1933. Paleobiology of Jurassic mammals. *Palaeobiologica* 127–158.
- Sinet-Mathiot, V., Rendu, W., Steele, T. E., Spasov, R., Madelaine, S., Renou, S., Soulier, M.C., Martisius, N.L., Aldeias, V., Endarova, E., Goldberg, P., McPherron, S.J.P., Rezek, Z., Sandgathe, D., Sirakov, N., Sirakova, S., Soressi, M., Tsanova, T., Turq, A., Turq, Alain., Hublin, J.J., Welker, F., Smith, G.M., 2023. Identifying the unidentified fauna enhances insights into hominin subsistence strategies during the Middle to Upper Palaeolithic transition. *Archaeol. Anthropol. Sci.* 15(9), 139. <https://doi.org/10.1007/s12520-023-01830-4>
- Sivy, K.J., Pozzanghera, C.B., Colson, K.E., Mumma, M.A., Prugh, L.R., 2018. Apex predators and the facilitation of resource partitioning among mesopredators. *Oikos* 127(4), 607–621. <https://doi.org/10.1111/oik.04647>
- Slobodyan, A.A., 1976. The European brown bear in the Carpathians. *Bears: Their Biology and Management*. 3, 313–319. <https://doi.org/10.2307/3872781>
- Smith, G.M., Spasov, R., Martisius, N.L., Sinet-Mathiot, V., Aldeias, V., Rezek, Z., Ruebens, K., Pederzani, S., McPherron, S.P., Sirakova, S., Sirakov, N., Tsanova, T., Hublin, J.J., 2021. Subsistence behavior during the Initial Upper Paleolithic in Europe: Site use, dietary practice, and carnivore exploitation at Bacho Kiro Cave (Bulgaria). *J. Hum. Evol.* 161, 103074. <https://doi.org/10.1016/j.jhevol.2021.103074>
- Soficaru, A., Doboş, A., Trinkaus, E., 2006. Early modern humans from the Peștera Muierii, Baia de Fier, Romania. *P.N.A.S.* 103(46), 17196–17201. <https://doi.org/10.1073/pnas.0608443103>
- Soficaru, A., Petrea, C., Doboş, A., Trinkaus, E., 2007. The human cranium from the Peștera Cioclovina Uscată, Romania. *Curr. Anthropol.* 48(4), 611–619. <https://doi.org/10.1086/519915>

10. References

- Solounias, N., 1988. Prevalence of ossicones in Giraffidae (Artiodactyla, Mammalia). *J. Mammal.* 69(4), 845–848. <https://doi.org/10.2307/1381645>
- Solounias, N., Hayek, L.A.C., 1993. New methods of tooth microwear analysis and application to dietary determination of two extinct antelopes. *J. of Zool.* 229, 421–445.
- Solounias, N., Moelleken, S.M.C., 1992. Dietary adaptation of two goat ancestors and evolutionary considerations. *Geobios* 6, 797–809.
- Solounias, N., Semprebon, G., 2002. Advances in the reconstruction of ungulate ecomorphology with application to early fossil equids. *Am. Mus. Novit.* 3366, 1–49. [https://doi.org/10.1206/0003-0082\(2002\)366<0001:AITROU>2.0.CO;2](https://doi.org/10.1206/0003-0082(2002)366<0001:AITROU>2.0.CO;2)
- Solounias, N., Teaford, M., Walker, A., 1988. Interpreting the diet of extinct ruminants: the case of a non-browsing giraffid. *Paleobiology* 14(3), 287–300. <https://doi.org/10.1017/S009483730001201X>
- Sommer, R.S., Benecke, N., 2005. The recolonization of Europe by brown bears *Ursus arctos* Linnaeus, 1758 after the Last Glacial Maximum. *Mammal Rev.* 35, 156–164. <https://doi.org/10.1111/j.1365-2907.2005.00063.x>
- Sommer, R.S., Nadachowski, A., 2006. Glacial refugia of mammals in Europe: Evidence from fossil records. *Mammal Rev.* 36(4), 251–265. <https://doi.org/10.1111/j.1365-2907.2006.00093.x>
- Sommer, R.S., 2020. Late Pleistocene and Holocene history of mammals in Europe. In: *Handbook of the Mammals of Europe*. Springer International Publishing. pp. 1–16. https://doi.org/10.1007/978-3-319-65038-8_3-1
- Sommer, R.S., Zachos, F.E., 2009. Fossil evidence and phylogeography of temperate species: ‘glacial refugia’ and post-glacial recolonization. *J. Biogeogr.* 36(11), 2013–2020. <https://doi.org/10.1111/j.1365-2699.2009.02187.x>
- Soofi, M., Qashqaei, A., Aryal, A., Coogan, S., 2017. Autumn food habits of brown bear *Ursus arctos* in the Golestan National Park: a pilot study in Iran. *Mammalia* 82. <https://doi.org/10.1515/mammalia-2016-0051>
- Sotnikova, M.V., Foronova, I.V., 2014. First Asian record of *Panthera (leo) fossilis* (Mammalia, Carnivora, Felidae) in the Early Pleistocene of Western Siberia, Russia. *Integr. Zool.* 9(4), 517–530. <https://doi.org/10.1111/1749-4877.12082>
- Souron, A., Merceron, G., Blondel, C., Brunetière, N., Colyn, M., Hofman-Kamińska, E., Boisserie, J.R., 2015. Three-dimensional dental microwear texture analysis and diet in extant Suidae (Mammalia: Cetartiodactyla). *Mammalia* 79. <https://doi.org/10.1515/mammalia-2014-0023>
- Spassov, N., Hristova, L., Ivanova, S., Georgiev, I., 2017. First record of the “small cave bear” in Bulgaria and the taxonomic status of bears of the *Ursus savini* Andrews – *Ursus rossicus* Borissiak group. *Foss. Imp.* 73(3–4), 275–291. <https://doi.org/10.2478/if-2017-0015>
- Steinmetz, R., Garshelis, D.L., Chutipong, W., Seuaturien, N., 2011. The shared preference niche of sympatric Asiatic black bears and sun bears in a tropical forest mosaic. *PLoS ONE* 6(1), e14509. <https://doi.org/10.1371/journal.pone.0014509>
- Stenseth, N.E., Lutnæs, P., Bjarnadóttir, V., Dahle, B., Fossum, K., Jørgensen, P., Johansen, T., Neumann, W., Opseth, O., Rønning, O., Steyaert, S., Zedrosser, A., Brunberg, S., Swenson, J., 2016. Seasonal and annual variation in the diet of brown bears (*Ursus arctos*) in the boreal forest of southcentral Sweden. *Wildl. Biol.* 22, 107–116. <https://doi.org/10.2981/wlb.00194>

- Stewart, J.R., Lister, A.M., Barnes, I., Dalén, L., 2010. Refugia revisited: individualistic responses of species in space and time. *Proc. R. Soc. B-Biol. Sci.* 277(1682), 661–671. <https://doi.org/10.1098/rspb.2009.1272>
- Stiller, M., Baryshnikov, G., Bocherens, H., Grandal D'Anglade, A., Hilpert, B., Münzel, S.C., Pinhasi, R., Rabeder, G., Rosendahl, W., Trinkaus, E., Hofreiter, M., Knapp, M., 2010. Withering away-25,000 years of genetic decline preceded cave bear extinction. *Mol. Biol. Evol.* 27(5), 975–978. <https://doi.org/10.1093/molbev/msq083>
- Stiller, M., Molak, M., Prost, S., Rabeder, G., Baryshnikov, G., Rosendahl, W., Münzel, S., Bocherens, H., Grandal-d'Anglade, A., Hilpert, B., Germonpré, M., Stasyk, O., Pinhasi, R., Tintori, A., Rohland, N., Mohandesan, E., Ho, S.Y.W., Hofreiter, M., Knapp, M., 2014. Mitochondrial DNA diversity and evolution of the Pleistocene cave bear complex. *Quat. Int.* 339–340, 224–231. <https://doi.org/10.1016/j.quaint.2013.09.023>
- Stiner, M.C., 1990. The use of mortality patterns in archaeological studies of hominid predatory adaptations. *J. Anthropol. Archaeol.* 9, 305–351. [https://doi.org/10.1016/0278-4165\(90\)90010-B](https://doi.org/10.1016/0278-4165(90)90010-B)
- Stiner, M.C., 1994. Honor among thieves: a zooarchaeological study of Neandertal ecology. Princeton University Press.
- Stiner, M.C., 1998. Mortality analysis of Pleistocene bears and its paleoanthropological relevance. *J. Hum. Evol.* 34(3), 303–326. <https://doi.org/10.1006/jhev.1997.0198>
- Stiner, M.C., Achyuthan, H., Arsebük, G., Howell, F., Josephson, S., Juell, K., Pigati, J., Quade, J., 1998. Reconstructing cave bear paleoecology from skeletons: A cross-disciplinary study of middle Pleistocene bears from Yarimburgaz Cave, Turkey. *Paleobiology* 24, 74–98. <https://doi.org/10.1017/S0094837300019989>
- Štofík, J., Merganič, J., Merganičová, K., Saniga, M., 2013. Seasonal changes in food composition of the brown bear (*Ursus arctos*) from the edge of its occurrence - Eastern Carpathians (Slovakia). *Folia Zool.* 62(3), 222–231. <https://doi.org/10.25225/fozo.v62.i3.a8.2013>
- Stuart, A., Lister, A., 2011. Extinction chronology of the cave lion *Panthera spelaea*. *Quat. Sci. Rev.* 30, 2329–2340. <https://doi.org/10.1016/j.quascirev.2010.04.023>
- Stuart, A., Lister, A., 2012. Extinction chronology of the woolly rhinoceros *Coelodonta antiquitatis* in the context of late Quaternary megafaunal extinctions in northern Eurasia. *Quat. Sci. Rev.* 51, 1–17.
- Stynder, D.D., Ungar, P.S., Scott, J.R., Schubert, B.W., 2012. A dental microwear texture analysis of the Mio-Pliocene Hyaenids from Langebaanweg, South Africa. *Acta Palaeontol. Pol.* 57(3), 485–496. <https://doi.org/10.4202/app.2011.0053>
- Tanis, B.P., DeSantis, L.R.G., Terry, R.C., 2018. Dental microwear textures across cheek teeth in canids: Implications for dietary studies of extant and extinct canids. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 508, 129–138. <https://doi.org/10.1016/j.palaeo.2018.07.028>
- Teaford, M.F., Oyen, O.J., 1986. Dental microwear in vervets raised on different diets. *Am. J. Phys. Anthropol.* 69(2), 270.
- Terlato, G., Bocherens, H., Romandini, M., Nannini, N., Hobson, K.A., Peresani, M., 2019. Chronological and Isotopic data support a revision for the timing of cave bear extinction in Mediterranean Europe. *Hist. Biol.* 31(4), 474–484. <https://doi.org/10.1080/08912963.2018.1448395>

10. References

- Terzea, E., 1966. Particularități morfologice ale ursului de peșteră și răspândirea sa pe teritoriul României. *Lucrările Institutului de Spelologie "Emil Racoviță,"* 5, 195–233. [In Romanian]
- Terzea, E., 1978. Dépôts de remplissage et mammifères quaternaires de "Peștera Urșilor" de Chișcău, département de Bihor (note préliminaire). *Lucrările Institutului de Spelologie "Emil Racoviță,"* 7, 139–144. [In Romanian]
- Terzea, E., 1989. Les Arvicolidés (Rodentia, Mammalia) du Pléistocène Moyen de Chișcău-1 (Départ. de Bihor, Roumanie). *Lucrările Institutului de Spelologie "Emil Racoviță,"* 28, 57–72. [In Romanian]
- Toniato, G., Russo, G., Verheijen, I., Serangeli, J., Conard, N., Leder, D., Terberger, T., Starkovich, B., Münzel, S., 2024. A diachronic study of human-bear interactions: An overview of ursid exploitation during the Paleolithic of Germany. <https://doi.org/10.1016/j.quascirev.2024.108601>
- Torres, T., García-Martínez, M.J., Morena, M.A., Chacón, E., Llamas, J., Cobo, R., Ortiz, J., 2002. Iberian "*Ursus spelaeus*" cheek-teeth size distribution through time. *ROS.-HEIN. Cadernos Do Laboratorio Xeológico de Laxe* 27, 117–129.
- Trinkaus, E., Constantin, S., Zilhão, J., 2013. *Life and Death at Pesteră cu Oase. A Setting for Modern Human Emergence in Europe.* Oxford University Press.
- Trinkaus, E., Richards, M., 2013. Stable isotopes and dietary patterns of the faunal species from the Pesteră cu Oase. In: E. Trinkaus, S. Constantin, J. Zilhão (Eds.), *Life and death at Pesteră cu Oase. A setting for modern human emergence in Europe.* Oxford University Press pp. 211–226.
- Trinkaus, E., Rougier, H., 2013. The human mandible from the Pesteră cu Oase, Oase 1. In: E. Trinkaus, S. Constantin, J. Zilhão (Eds.), *Life and death at Pesteră cu Oase. A setting for modern human emergence in Europe.* Oxford University Press pp 234–256.
- Tsanova, T., Delvigne, V., Sirakova, S., Anastasova, E., Horta, P., Krumov, I., Marreiros, J., Nacheva, E., Rezek, Z., Hublin, J.J., Sirakov, N., 2024. Curated character of the Initial Upper Palaeolithic lithic artefact assemblages in Bacho Kiro Cave (Bulgaria). *PLoS ONE* 19(9), e0307435. <https://doi.org/10.1371/journal.pone.0307435>
- Tzedakis, P.C., Emerson, B., Hewitt, G.M., 2013. Cryptic or mystic? Glacial tree refugia in northern Europe. *Trends Ecol. Evol.* 28, 696–704. <https://doi.org/10.1016/j.tree.2013.09.001>
- Tzedakis, P.C., Lawson, I.T., Frogley, M.R., Hewitt, G.M., Preece, R.C., 2002. Buffered tree population changes in a Quaternary Refugium: Evolutionary implications. *Science* 297(5589), 2044–2047. <https://doi.org/10.1126/science.1073083>
- Ungar, P.S., 1995. A semiautomated image analysis procedure for the quantification of dental microwear II. *Scanning* 17, 57–59.
- Ungar, P.S., Brown, C.A., Bergstrom, T.S., Walkers, A., 2003. Quantification of dental microwear by tandem scanning confocal microscopy and scale-sensitive fractal analyses. *Scanning* 25(4), 185–193. <https://doi.org/10.1002/sca.4950250405>
- Ungar, P.S., Teaford, M.F., 1996. Preliminary examination of non-occlusal dental microwear in anthropoids: implications for the study of fossil primates. *Am. J. Phys. Anthropol.* 100(1), 101–113. [https://doi.org/10.1002/\(SICI\)1096-8644\(199605\)100:1<101::AID-AJPA10>3.0.CO;2-4](https://doi.org/10.1002/(SICI)1096-8644(199605)100:1<101::AID-AJPA10>3.0.CO;2-4)

- Ungar, P.S., Scott, R., Scott, J.R., Teaford, M.F., 2008. Dental microwear analysis: Historical perspectives and new approaches. In: *Technique and Application in Dental Anthropology*. pp. 389–425. <https://doi.org/10.1017/CBO9780511542442.017>
- Uzunidis, A., 2021. Middle Pleistocene variations in the diet of *Equus* in the South of France and its morphometric adaptations to local environments. *Quaternary* 4(3). <https://doi.org/10.3390/quat4030023>
- Uzunidis, A., Pineda, A., Jiménez-Manchón, S., Xafis, A., Ollivier, V., Rivals, F., 2021. The impact of sediment abrasion on tooth microwear analysis: an experimental study. *Archaeol. Anthropol. Sci.* 13(8), 134. <https://doi.org/10.1007/s12520-021-01382-5>
- Vălenaș, L., 1979. Studiu complex al zonei Valea Crăiasa-Valea Vărtoape, cu referire specială la Peștera Urșilor (Munții Bihor). *Nymphaea* 7, 139–175. [In Romanian]
- van Heteren, A.H., MacLarnon, A., Soligo, C., Rae, T.C., 2016. Functional morphology of the cave bear (*Ursus spelaeus*) mandible: a 3D geometric morphometric analysis. *Org. Divers. Evol.* 16, 299–314. <https://doi.org/10.1007/s13127-015-0238-2>
- van Heteren, A.H., Arlegi, M., Santos, E., Arsuaga, J.L., Gómez-Olivencia, A., 2019. Cranial and mandibular morphology of Middle Pleistocene cave bears (*Ursus deningeri*): implications for diet and evolution. *Hist. Biol.* 31(4), 485–499. <https://doi.org/10.1080/08912963.2018.1487965>
- van Heteren, A.H., Figueirido, B., 2019. Diet reconstruction in cave bears from craniodental morphology: past evidences, new results and future directions. *Hist. Biol.* 31(4), 500–509. <https://doi.org/10.1080/08912963.2018.1547901>
- van Valkenburgh, B., 2009. Costs of carnivory: tooth fracture in Pleistocene and Recent carnivorans. *Biol. J. Linn. Soc.* 96, 68–81.
- van Valkenburgh, B., Teaford, M., Walkers, A., 1990. Molar microwear and diet in large carnivores: inferences concerning diet in the sabretooth cat, *Smilodon fatalis*. *J. Zool.* 222, 319–340. <https://doi.org/10.1111/j.1469-7998.1990.tb05680.x>
- Varela, S., Lobo, J.M., Rodríguez, J., Batra, P., 2010. Were the Late Pleistocene climatic changes responsible for the disappearance of the European spotted hyena populations? Hindcasting a species geographic distribution across time. *Quat. Sci. Rev.* 29(17), 2027–2035. <https://doi.org/https://doi.org/10.1016/j.quascirev.2010.04.017>
- Ventresca-Miller, A., Fernandes, R., Janzen, A., Nayak, A., Swift, J., Zech, J., Boivin, N., Roberts, P., 2018. Sampling and pretreatment of tooth enamel carbonate for stable carbon and oxygen isotope analysis. *J. Vis. Exp.* 138. <https://doi.org/10.3791/58002>
- Vereschagin, N.K., 1976. The brown bear in Eurasia, particularly the Soviet Union. *Bears: Their Biology and Management* 3, 327–335. <https://doi.org/10.2307/3872784>
- Vereshchagin, N.K., Baryshnikov, G., 2000. Small cave bear *Ursus (Spelearctos) rossicus uralensis* from the Kizel Cave in the Ural (Russia). *Geol. Zb.* 15(53–66).
- Verheijen, I., Starkovich, B.M., Serangeli, J., van Kolfshoten, T., Conard, N.J., 2023. Early evidence for bear exploitation during MIS 9 from the site of Schöningen 12 (Germany). *J. Hum. Evol.* 177, 103294. <https://doi.org/10.1016/j.jhevol.2022.103294>
- Vila-Taboada, M., Fernández-Mosquera, D., González, F., Grandal-d'Anglade, A., Vidal-Romani, J.R., 1999. Paleoeological implications inferred from stable isotopic signatures ($\delta^{13}\text{C}$, $\delta^{15}\text{N}$) in

10. References

- bone collagen of *Ursus spelaeus*. ROS.-HEIN. Cadernos Do Laboratorio Xeolóxico de Laxe 24, 73-87.
- Vishnyatsky, L., Burlacu, V., 2021. New research on the Middle Paleolithic of the Middle Prut Basin, Moldova. *Materiale Şi Cercetări Arheologice (Serie Nouă)* 1(1), 105–124.
<https://doi.org/10.3406/mcarh.2021.2205>
- Vishnyatsky, L., Burlacu, V., Voskresenskaya, E., Nekhoroshev, P.E., 2020. New research at the Middle Palaeolithic cave site of Buzdujeni. *Stratum Plus* 1, 187–200.
- Vlachos, C., Bakaloudis, D., Dimitriou, K., Chouvardas, D., 2000. Seasonal food habits of the European brown bear (*Ursus arctos*) in the Pindos Mountains, Western Greece. *Folia Zool.* 49(1), 19–25.
- Walker, A., Hoeck, H.N., Perez, L., 1978. Microwear of mammalian teeth as an indicator of diet. *Science* 201(4359), 908–910. <https://doi.org/10.1126/science.684415>
- Wang, H., Zhong, H., Hou, R., Ayala, J., Liu, G., Yuan, S., Yan, Z., Zhang, W., Liu, Y., Cai, K., Cai, Z., Huang, H., Zhang, Z., Wu, D., 2017. A diet diverse in bamboo parts is important for giant panda (*Ailuropoda melanoleuca*) metabolism and health. *Scientific Reports* 7.
<https://doi.org/10.1038/s41598-017-03216-8>
- Wei, F., Hu, Y., Yan, L., Nie, Y., Wu, Q., Zhang, Z., 2015. Giant pandas are not an evolutionary cul-de-sac: evidence from multidisciplinary research. *Mol. Biol. Evol.* 32(1), 4–12.
<https://doi.org/10.1093/molbev/msu278>
- Welch, C.A., Keay, J., Kendall, K.C., Robbins, C.T., 1997. Constraints on frugivory by bears. *Ecology* 78(4), 1105–1119. <https://doi.org/10.2307/2265862>
- Wiegand, T., Naves, J., Garbulsky, M.F., Fernández, N., 2008. Animal habitat quality and ecosystem functioning: exploring seasonal patterns using NDVI. *Ecol. Monogr.* 78(1), 87–103.
<http://www.jstor.org/stable/27646120>
- Williams, F.L., Geissler, E., 2014. Reconstructing the diet and paleoecology of plio-pleistocene *Cercopithecoides williamsi* from Sterkfontein, South Africa. *PALAIOS* 29(9), 483–494.
<https://doi.org/10.2110/palo.2014.046>
- Willis, K., Vanandel, T., 2004. Trees or no trees? The environments of central and eastern Europe during the Last Glaciation. *Quat. Sci. Rev.* 23(23–24), 2369–2387.
<https://doi.org/10.1016/j.quascirev.2004.06.002>
- Wisheu, I.C., 1998. How organisms partition habitats: different types of community organization can produce identical patterns. *Oikos* 83(2), 246. <https://doi.org/10.2307/3546836>
- Wohlfarth, B., Veres, D., Ampel, L., Lacourse, T., Blaauw, M., Preusser, F., Andrieu-Ponel, V., Kéravis, D., Lallier-Vergès, E., Björck, S., Davies, S. M., de Beaulieu, J.L., Risberg, J., Hormes, A., Kasper, H. U., Possnert, G., Reille, M., Thouveny, N., Zander, A., 2008. Rapid ecosystem response to abrupt climate changes during the last glacial period in western Europe, 40–16 ka. *Geology* 36(5), 407–410. <https://doi.org/10.1130/G24600A.1>
- Wu, Y., 2022. Diet evolution of carnivorous and herbivorous mammals in Laurasiatheria. *BMC Ecol. Evol.* 22(1), 82. <https://doi.org/10.1186/s12862-022-02033-6>
- Xafis, A., Nagel, D., Bastl, K., 2017. Which tooth to sample? A methodological study of the utility of premolar/non-carnassial teeth in the microwear analysis of mammals. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 487, 229–240. <https://doi.org/10.1016/j.palaeo.2017.09.003>

- Zastrozhnov, A., Danukalova, G., Shick, S., van Kolfschoten, T., 2018. State of stratigraphic knowledge of Quaternary deposits in European Russia: Unresolved issues and challenges for further research. *Quat. Int.* 478, 4–26.
<https://doi.org/https://doi.org/10.1016/j.quaint.2017.03.037>
- Zhang, K., Karim, F., Jin, Z., Xiao, H., Yao, Y., Ni, Q., Li, B., Pu-Cuo, W., Huang, Z., Xu, H., 2023. Diet and feeding behavior of a group of high-altitude rhesus macaques: high adaptation to food shortages and seasonal fluctuations. *Curr. Zool.* 69(3), 304–314.
<https://doi.org/10.1093/cz/zoac047>
- Zilhão, J., Milota, Ș., Rodrigo, R., Constantin, S., Trinkaus, E., 2013a. Problems, approaches, and fieldwork: 2004–2005. In: E. Trinkaus, S. Constantin, J. Zilhão (Eds.), *Life and death at Pesteră cu Oase. A setting for modern human emergence in Europe*. Oxford University Press pp. 16–30.
- Zilhão, J., Rodrigo, R., Hélène, R., Milota, Ș., 2013b. The distribution of findings and features. In: E. Trinkaus, S. Constantin, J. Zilhão (Eds.), *Life and death at Pesteră cu Oase. A setting for modern human emergence in Europe*. Oxford University Press. pp. 100–123.
- Zilhão, J., Trinkaus, E., Constantin, S., Gherase, M., Danciu, A., Rougier, H., Rodrigo, R., 2007. The Peștera cu Oase People, Europe's Earliest Modern Humans. In: *Rethinking the Human Revolution*. pp. 249–262.

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APPENDIX

Appendix

A.1 Appendix 1: articles published

The first section of the Appendix presents three peer-reviewed articles published as part of this Master's Thesis. All three articles were published in *Palaeogeography, Palaeoclimatology, Palaeoecology*, a Q1-ranked scientific journal. The first article, titled "*Palaeodiet during the pre-dormancy period of MIS 3 Romanian cave bears as inferred from dental microwear analysis*", Explores the short-term diet of various cave bear populations from the Romanian Carpathians, incorporating only a subset of the Romanian Carpathians samples analysed in the present thesis, as some data presented here was published in the third article. The second article, titled "*Dental microwear analysis of Kudaro cave bears: Insights into dietary evolution from the Middle to Late Pleistocene*", examines the short-term diet of the *U. kudarensis* lineage from the Middle to Late Pleistocene through dental microwear analysis. This article represents the published version the study of *U. kudarensis* cave bear lineage, from the present thesis. Finally, the third article, titled "*Dental microwear of cave bear (*Ursus spelaeus*) reveals locally adapted foraging strategies in South-Eastern Europe during late MIS 3*", investigates the short-term dietary ecology of 316 individuals from 20 palaeontological sites across the Romanian Carpathians, Moldavian Plateau, Western and Central Balkans, and the Western Rhodopes, and represents the core dataset of populations presented in this thesis. These publications have contributed to the understanding of cave bear ecology, and are integrated into the scientific community knowledge, receiving numerous citations and further reinforcing the scientific significance of this thesis.

**A.1.1 Article 1 titled “*Palaeodiet during the pre-dormancy period of MIS 3 Romanian cave bears as inferred from dental microwear analysis*”
Palaeogeography, Palaeoclimatology, Palaeoecology (2024)**



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Palaeodiet during the pre-dormancy period of MIS 3 Romanian cave bears as inferred from dental microwear analysis

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ABSTRACT

Cave bears (*Ursus spelaeus*) have been recognized as being predominantly herbivorous. However, Romanian Carpathian cave bears have displayed a flexible diet based on a wide range of $\delta^{15}\text{N}$ values. In this work, we analyse 97 lower first molars of *Ursus spelaeus* and contemporaneous *Ursus arctos* from different sites in this region, using dental microwear analysis to reconstruct their pre-dormancy diets during MIS 3. Newly obtained radiocarbon dates of the individuals are also reported. The short-term diet of all populations studied is identified as omnivorous, with a preference for the consumption of hard objects. For the first time, the widespread presence of puncture pits on *U. spelaeus* populations has been observed, which could be linked to the intake of seeded and hard-shelled fruits from temperate broadleaf trees. Hence, the dietary patterns of Carpathian cave bears exhibit similarities to those of present-day brown bears inhabiting the same region and suggests that the Carpathians served as an ecological refuge for cave bear specimens. This is reinforced by an early 27.1 cal kyr B.P. date from an individual from Urșilor Cave, which sheds light on the potential dietary continuity of Romanian Carpathian cave bear populations even during the final phases leading up to their extinction.

1. Introduction

The Late Pleistocene was marked by significant climatic changes, particularly during the Last Glacial Period, the Weichselian glaciation, in Europe (Bond et al., 1999; Dansgaard et al., 1993; Rasmussen et al., 2014). The Dansgaard-Oeschger (D–O) climatic fluctuations, especially during MIS 3 (60–27 kyr B.P.), resulted in persistent ecological instability, causing rapid and frequent shifts between drastically different vegetation, within brief time intervals (Wohlfarth et al., 2008; Huntley et al., 2013; Sánchez Goñi, 2022). The environmental instability at the end of the Pleistocene was a primary factor in the extinction or

displacement of a significant portion of the European megafauna that dominated European landscapes since the Middle Pleistocene, including the iconic large herbivores, as well as members of the carnivore clade (Stuart and Lister, 2012). Carnivores, despite their further adaptability to various biomes, do not depend directly on a specific habitat like herbivores (Hunter and Turner, 1997). They also experienced a significant population decline and displacement (Varela et al., 2010; Stuart and Lister, 2011), and in some cases extinction (Pacher and Stuart, 2009). This phenomenon has been proposed as being greatly influenced by the displacement and extinction of populations of large herbivores, which formerly constituted their primary food source (Croitor and

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Brugal, 2010; Stuart and Lister, 2011; Varela et al., 2010). The carnivores that prevailed and occupied the ecological niche of those extinct species were smaller-sized carnivores and omnivores with broad dietary habits (Sommer and Benecke, 2005; Croitor and Brugal, 2010) such as brown bears (*Ursus arctos*), which during the end of the Pleistocene decreased in size as a response to the climatic and environmental instability (Marciszak et al., 2015). An ecologically singular member of the carnivore order that was among the first to go extinct was the cave bear (*Ursus spelaeus*), at about 28 kyr B.P. in western Europe (Pacher and Stuart, 2009; Bocherens et al., 2014; Baca et al., 2016). There are various hypotheses regarding the causes of extinction. One identified factor contributing to the extinction is a long genetic decline leading to populations shrinking (Stiller et al., 2010). Furthermore, particular hibernation behaviours linked to a dependency on caves, unlike the closely related lineage of brown bears (*U. arctos*), led them to indirectly compete for these spaces with humans and to be especially susceptible to hunting (Fortes et al., 2016). This last theory, which attributes part of the reasons for the extinction to humans, is supported by evidence of cut marks found on cave bear remains throughout Europe during the MIS 3 period (Armand et al., 2004; Münzel and Conard, 2004; Terlato et al., 2019; Blasco et al., 2020). Finally, a well-established theory suggests that their extinction can be attributed to the declining availability of plant-based resources (Pacher and Stuart, 2009; Bocherens, 2019). The cave bear is an exceptional example of an evolutionary adaptation, transitioning from a carnivore-scavenger dominated niche to establishing an ecological similarity with the niche occupied by the large-sized herbivores of the Middle Pleistocene (Croitor and Brugal, 2010).

Studying the diet of this species is crucial to understand its ecological and geographical distribution during the Pleistocene, as it currently does not seem to resemble any of the extant bear species alive today. The diet of the cave bear has been inferred as having predominantly relied on plants, as indicated by wear gradients and dental morphology (Terzea, 1966; Kurten, 1976; Juresák et al., 1981) and further supported by multiple isotope analyses of both carbon ($\delta^{13}\text{C}$) and nitrogen ($\delta^{15}\text{N}$) on bone collagen (Bocherens et al., 1994, 1997, 2006, 2011, 2014; Nelson et al., 1998; Vila-Taboada et al., 1999; Fernández-Mosquera et al., 2001; Münzel et al., 2011; Krajcarz et al., 2016; Naito et al., 2016; Bocherens, 2019; Ramírez-Pedraza et al., 2019) and three-dimensional analysis of tooth-root morphology (Pérez-Ramos et al., 2019).

Nevertheless, some other studies of Romanian Carpathian cave bears have pointed towards a flexible omnivore diet suggested by a wide range of $\delta^{15}\text{N}$ values (Richards et al., 2008; Robu et al., 2013, 2018), which is supported by morphological and dental wear analysis (Figueirido et al., 2009; Peigné et al., 2009). However, a recent study conducted on Romanian cave bears analysing nitrogen isotopic amino acids has presented evidence for a predominantly herbivorous diet for these populations (Naito et al., 2020). The study revealed that the elevated nitrogen values previously recorded in some Romanian cave bears could be attributed to the consumption of specific plant species characterized by high bulk $\delta^{15}\text{N}$ values (Naito et al., 2020). In addition, Grandal-d'Anglade et al. (2019) suggested that the high nitrogen values observed in Romanian cave bears could potentially be attributed to urea reuse processes during hibernation. Nevertheless, the wide range of results obtained using long-term inferences of dietary proxies (isotopes and amino acids) might suggest lifelong dietary flexibility of this species depending on multiple factors such as the geographical and ecological context, as well as the degree of competition for available resources, but under a plant dominated diet (Robu et al., 2013; Krajcarz et al., 2016; Naito et al., 2020).

A well-established method to infer short-term dietary patterns is microwear analysis. Low magnification microwear analyses identify microscopic features left by abrasive particles on the enamel of the occlusal surface during chewing with the goal of inferring the dietary ecology of the animal (Solounias and Semperebon, 2002; Semperebon et al., 2004). The constant formation of new features erases the previous ones, which means there is a record of the diet on a much shorter time

scale than morphological, macroscopic dental wear and isotopic or amino acids analyses (Solounias and Semperebon, 2002). Thus, one can detect seasonal or occasional dietary regimes that would not be seen through other methods (Grüne, 1986). Dental microwear studies had been carried out on cave bears in the past years (Ramírez-Pedraza et al., 2019, 2020, 2022). These have revealed a high variability in dietary habits among cave bear populations from different locations in Europe during the Late Pleistocene. The short-term microwear signal exhibited a varied and less specialized diet, before death, for individuals with low nitrogen values (i.e. long-term herbivorous diet) (Ramírez-Pedraza et al., 2019). Furthermore, when comparing different populations of cave bears from distinct yet closely located geographical areas in north-eastern Iberia, they exhibit significant dietary variability. This variation ranges from carnivorous to more omnivorous signals, as documented by Ramírez-Pedraza et al. (2020) and could be attributed to different ecological adaptations to distinct paleoenvironmental contexts from different periods of the highly climatically variable MIS 3. Furthermore, cave bears from northeastern Europe displayed a general herbivorous diet but also exhibited occasional consumption of other things, demonstrating a remarkable capacity for dietary flexibility linked to a locally specific adaptability due to niche partitioning (Ramírez-Pedraza et al., 2022).

In this work our purpose is to analyse several populations from the Romanian Carpathians using dental microwear analysis (DMA) to infer the diet of the last weeks before the death of the individuals. It is interesting to study this region during a period close to the extinction of the cave bear, in a context where the Carpathians experienced significant climatic instability (Constantin et al., 2007), although they also served as a refuge for fauna and flora, hosting diverse ecosystems beyond the steppe (Sommer and Nadachowski, 2006; Magyari et al., 2014). Therefore, the Carpathian Mountains recorded a wider range of dietary patterns than other more environmentally homogeneous regions. Furthermore, we present the largest sample of cave bear individuals from southeastern Europe analysed using this method, in relation to already published stable isotopes ($\delta^{15}\text{N}$ and $\delta^{13}\text{C}$) (Richards et al., 2008; Robu et al., 2013, 2018) and new chronological dates. This allows us to correlate them with the climatic conditions they experienced and to examine their lifelong diet as well as their diet during specific periods, particularly before hibernation. Additionally, our work includes samples from different regions of the Carpathian Mountains: Urşilor Cave (northwest), Oase (southwest), Bisericuța (central-northwest), Muierilor Cave (central-southwest), Onceasa (northwest), Avenul Măpului (northwest), La Adam (southeast) and the Cloșani area (southwest) which can indicate different paleoenvironmental contexts and specific adaptations. To these we added contemporary *U. arctos* individuals with which we compare patterns and observe different dietary responses and adaptations to varying geographic and paleoclimatic contexts.

2. Materials and methods

2.1. Sample selection

The materials analysed in this study are housed at the ‘Emil Racoviță’ Institute of Speleology (ERIS), Romanian Academy. A total of 97 lower first molars ($n = 97$) were carefully selected, belonging to a diverse range of individuals, including juveniles, adults in their prime, and older adults of both sexes. The inventory of specimens – sampled and analysed along with its microwear raw data and their corresponding previously recorded stable isotopes ($\delta^{13}\text{C}$ and $\delta^{15}\text{N}$) (Robu et al., 2013, 2018) – is available in the Supplementary Materials (ST1).

2.2. Sampled sites and context

We sampled MIS 3 cave bears and modern brown bears from some of the most relevant sites from the Romanian Carpathians (Fig. 1), where

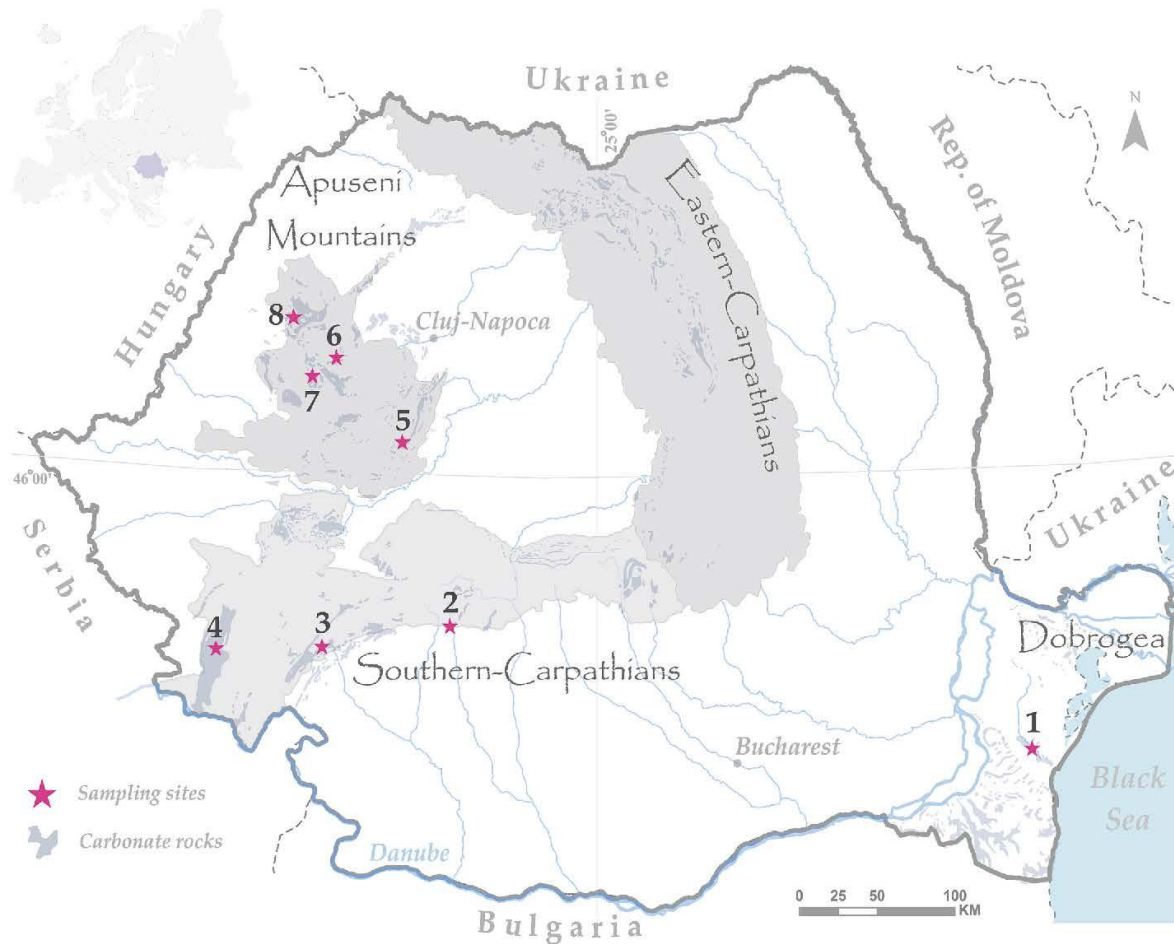


Fig. 1. Location of the sampled MIS 3 cave bear sites in the Romanian Carpathians. 1 – La Adam; 2 – Muierilor; 3 – P-Aven nr. din Cracul de la Gioaca Goală (ACCG; Cloşani); 4 – Oase; 5 – Giclovina; 6 – Onceasa; 7 – Urşilor; 8 – Avenul Măţului.

systematic palaeontological excavations have been carried out during the last two decades, primarily by our team (e.g. Constantin et al., 2014; Mirea et al., 2021).

Urşilor Cave (henceforth: Urşilor) is situated in the Apuseni Mountains, northwestern Romania ($46^{\circ}55'37''\text{N}$, $22^{\circ}56'92''\text{E}$; Fig. 1). Urşilor is one of the most emblematic show caves in the region, given the impressive MIS 3 cave bear bone assemblage (Robu, 2016a). The cave has a total length of ca. 1500 m, roughly divided into two levels (a hydrologically inactive upper one and a hydrologically active lower one; Constantin et al., 2014). The sampled area was the Excavation Chamber, from the lower level of the cave (the scientific reserve), where a ca. 10 m² paleontological excavation has been in progress since 2010. The thanatocoenosis is cave bear dominated and spans the time from ca. 47 to 39.5 cal kyr B.P. (Constantin et al., 2014; Robu, 2016b).

Peştera cu Oase (henceforth: Oase) is located in the Banatului Mountains, southwestern Romania ($45^{\circ}05'\text{N}$, $21^{\circ}51'\text{E}$ – coordinates imprecise for conservation concerns; Fig. 1). Oase is a typical through-cave, with a total length of ca. 2000 m (Constantin et al., 2013; Fig. 1), famous for harbouring one of the earliest anatomically modern humans in Europe (Trinkaus et al., 2013). The cave has roughly two karstic levels, a hydrologically inactive upper karstic level and an active lower one. The analysed cave bear samples were excavated from the

upper level of the cave (Sala Mandibulei and Panta Strămoşilor) and were dated to ca. 50–41.5 cal kyr B.P. (Higham and Wild, 2013).

Muierilor Cave (henceforth: Muierilor) is situated in the Căpăţanii Mountains, in the southern part of the Southern Carpathians ($45^{\circ}11'29''\text{N}$, $23^{\circ}45'14''\text{E}$; Fig. 1). It is a ca. 8000 m long complex cave system along five levels, the lowest one being hydrologically active. The cave is also known for the discovery of early modern human remains (Doboş et al., 2010). The MIS 3 cave bear material was extracted from Galeria Urşilor (Bears' Passage), from a 9 m² palaeontological excavation and was dated between ca. 51–29 cal kyr B.P. (Doboş et al., 2010; Robu, 2015; Mirea et al., 2021).

Onceasa Cave (henceforth: Onceasa) is located in the Apuseni Mountains, northwestern Romania ($46^{\circ}39'41''\text{N}$, $22^{\circ}45'46''\text{E}$). It is one of the richest MIS 3 cave bear bone deposits in the Romanian Carpathians and it consists of ca. 350 m of large passages. The analysed MIS 3 cave bear bone material was sampled from the ERIS's palaeontological collection and was extracted from the cave during the 1960s (Terzea, 1966).

Biseriçuţa Cave (henceforth: Biseriçuţa) is located in the Trascăului Mountains, western Romania ($46^{\circ}12'\text{N}$, $23^{\circ}20'\text{E}$ – coordinates imprecise for conservation concerns). It consists of ca. 100 m of hydrologically inactive passages. The sampling area is situated at the

bottom of a small shaft in the excavation chamber (3 m²). The deposit comprises an important MIS 3 cave bear bone assemblage at the lower level of the cave, dated to ca. 50–31 cal kyr B.P. (unpubl. data).

La Adam Cave (henceforth: Adam) is situated in the Dorobanțului Plateau, in the southeastern part of Romania, close to the Black Sea (44° 27' 44" N, 28° 28' 15" E). It is one of the richest Late Pleistocene sites from this region, in terms of species' diversity and has a total length of ca. 100 m. The MIS 3 cave bears, stored in the ERIS's collection and analysed here, were excavated during the 1960s (Dumitrescu et al., 1966).

Peștera-Avenul din Cracul de la Cioaca Goală (henceforth: ACCG; 45° 03' 50" N, 22° 41' 49" E) is a ca. 50 m-long vertical-horizontal cave, with a ca. 20 m drop from its entrance, situated in the Cloșani area of the Mehedinți Mountains, in the southwestern Carpathians. In 2011, our team collected, from the undisturbed surface of the cave, the bones of three medieval brown bear individuals (one sub-adult female, a juvenile and a sub-adult male; Erismark et al., 2019) were found close to the shaft's bottom, identified and partially collected.

Avenul Măpului (46° 50' 07" N, 22° 23' 46" E) is a ca. 100 m-long vertical and horizontal cave from the Cușilor Gorges, in the western part of the Apuseni Mountain group (Pădurea Craiului Mountains). In 2018, our team collected samples from a female brown bear skeleton, found at the base of a ca. 20 m drop, inside the cave.

2.3. Tooth microwear

The samples were prepared following the protocol developed by Solounias and Semperebon (2002) and Semperebon et al. (2004). The occlusal surface of the teeth was cleaned using acetone, then 96% ethanol. A high-precision mould of the surface was made using polyvinylsiloxane silicone (Heraeus Provil novo, Light CD2, regular set) and a second layer using silicone putty (Heraeus Provil novo, Putty). Finally, transparent high-resolution casts were produced using epoxy resin (CTS EPO150 resin+K151 hardener). The casts were observed using a standard light stereomicroscope (Zeiss Stemi 2000C) at $\times 35$ magnification to identify and quantify the microfeatures using an optical reticule of 0.16 mm² (Solounias and Semperebon, 2002; Semperebon et al., 2004). We examined the non-faceted and grinding enamel surfaces of the molars because they provide the most reliable reflection of the dietary patterns of ursid specimens, in comparison to other areas of the tooth surface (Ungar and Teaford, 1996; Münzel et al., 2014; Pappa, 2016; Pappa et al., 2019; Ramírez-Pedraza et al., 2019, 2020, 2022).

The features analysed in this work include (1) the number of fine and coarse scratches – elongated and narrow features, that can be classified as either fine (characterized by narrow and shallow marks) or coarse (distinguished by wider and deeper marks); and (2) the number of small and large pits: circular or semi-circular shapes with similar length and width. They can be classified as either small, which are characterized by being shallow and appearing as shiny, bright, white dots, or large, which are wider and deeper, reflecting less light. The scratch width score (SWS) was assessed by giving a score of 0 to enamel surfaces with predominantly fine scratches, a score of 1 to surfaces with a mixture of coarse and fine scratches, and a score of 2 to surfaces with predominantly coarse scratches. We also quantified the number of puncture pits (very deep and symmetrical crater-like morphology with regular margins) and number of gouges (crater-shaped but with irregular margins).

To reconstruct the paleodiet of the fossil populations, the obtained results were compared to the reference dataset of extant bear species established by Pappa et al. (2019). The reference collection allowed us to compare extinct ursids with their closely related living counterparts, *U. arctos*, from various regions (Kamchatka, Greece, Central Europe, Northern Europe, and North America) and *U. americanus* from North America. Both species exhibit a variety of food preferences, including consumption of vertebrates, invertebrates, hard mast, and soft mast. To prevent any inter-observer error, a sole observer (PDI) conducted the analysis on all specimens.

The graphs were generated using the software Past 4.02 (Hammer

et al., 2001) and RStudio (version 4.1.2) (RStudio Team, 2021). Photomicrographs were captured using an Invenio 5SII digital camera in extended focus mode and the Helicon Focus software to combine the images acquired at different focal planes to create a single image with an increased depth of field. The scale bars were incorporated using ImageJ software.

2.4. Radiocarbon dating

For radiocarbon dating, we sampled cave bear ($n = 18$) and brown bear ($n = 1$) mandible bones from: Urșilor ($n = 10$), Oase ($n = 3$), Muierilor ($n = 4$) and Biserița ($n = 2$). The AMS ¹⁴C dating was performed at the Poznań Radiocarbon Laboratory (Poland). Analytical procedures were described by Longin (1971) and modified by Piotrowska and Goslar (2002). The bone treatment followed the method described by Brock et al. (2010), including the collagen extraction, purification (using Elkay 8 μ m filters) and ultrafiltration (Vivaspin 15 MWCO 30 kD filters). All radiocarbon data used here was calibrated using the OxCal v4.4.2 software (Bronk Ramsey, 2009; Bronk Ramsey, 2020) against the INTCAL13 radiocarbon calibration curve (Reimer et al., 2020). Moreover, available results from radiometric dating of the studied MIS 1 brown bears, previously published (Erismark et al., 2019; $n = 1$), were added to our new data.

3. Results

3.1. Tooth microwear

A number of the 71 lower first molars (out of 97) were suitable for microwear analyses: 28 from Urșilor, 26 from Oase, 6 from Biserița, 3 from Muierilor, 3 from Onceasa, 2 from Adam, 2 from the Cloșani area and 1 from Avenul Măpului. A total of 26 individuals were excluded from the analysis, comprising the youngest individuals without wear facets (sensu Rivals et al., 2007), as well as those with occlusal surface damage resulting from taphonomic processes (sensu King et al., 1999; El-Zaatari, 2010; Uzunidis et al., 2021; Micó et al., n.d.); from Cioclovina ($n = 2$) from the Cloșani area ($n = 3$), from Colțu Surpat ($n = 2$), from Magura ($n = 2$), Onceasa ($n = 3$), Oase ($n = 8$), and Urșilor ($n = 6$).

The tooth microwear results obtained for *U. spelaeus* from Urșilor ($n = 28$), Oase ($n = 26$) and Biserița ($n = 5$) present a very similar average for both the number total of scratches and pits (NTS and NTP) (Table 1). There is an analogue distribution of the numbers of fine (NFS) and coarse (NCS) scratches which slightly favours fine scratches, therefore reflected in a SWS close to 1 for all three populations. They also present similar average values of number of total pits (NTP), with a clear predominance of small pits. The number of small pits (NSP) ranges from 17.65 to 19.35 per counting area, while the number of large pits (NLP) ranges from 2.60 to 3.60 on average. All three populations exhibited puncture pits (NPP) (Fig. 2) which appeared equally distributed without significant variations within populations and between populations ($F = 0.9889$, $p = 0.3784$, mean square value = 2.04) and with a similar mean value ranging from 2.23 to 2.87 per counting area. Finally, regarding gouges, these are also present, with an average of around 1, varying from 0.60 to 1.12 per counting area.

The individuals from Muierilor ($n = 3$), despite constituting a small sample, exhibit a total score of scratches and pits that aligns with the trend observed in the more representative sites, albeit slightly lower (which can be attributed to the smaller number of individuals). As a result of the insufficient number of reliable samples, Muierilor was excluded from the further statistical multivariate analysis. The average number of total scratches (NTS) is 17 and the average number of total pits (NTP) is 21.72 per counting area. In addition, the three individuals from Muierilor display a higher average number of coarse scratches (NCS) compared to the sites of Urșilor, Oase, and Biserița. This is reflected by a higher SWS with an average of 1.67. When it comes to the distribution of pits, there is a clear predominance of small pits (NSP =

Table 1

Comparison of the dental microwear results of the fossil populations of *U. spelaeus* and *U. arctos* from the Romanian Carpathians with the reference dataset of extant bear species of *U. arctos* from different locations and *U. americanus* established by Pappa et al. (2019). Abbreviations: *n* number of specimens, NFS number of fine scratches, NCS number of coarse scratches, NTS number of total scratches, SWS scratch width score, NLP number of large pits, NSP number of small pits, NPP number of puncture pits, NTP number of total pits, NG number of gouges.

Species - Location	<i>n</i>	NFS	NCS	NTS	SWS	NLP	NSP	NPP	NTP	NG
Extinct										
<i>U. spelaeus</i> (Urşilor)	28	12.66	10.27	22.93	1.04	3.39	17.65	2.23	23.28	0.86
<i>U. spelaeus</i> (Oase)	26	13.00	10.05	23.05	1.04	3.60	19.35	2.87	25.81	1.12
<i>U. spelaeus</i> (Bisericuța)	5	14.27	9.10	23.37	0.80	2.80	19.03	2.50	24.33	0.60
<i>U. spelaeus</i> (Muierilor)	3	7.00	10.00	17.00	1.67	0.67	19.39	1.67	21.72	1.67
<i>U. spelaeus</i> (Onceasa)	3	15.17	10.00	25.17	1.00	5.00	17.33	1.00	23.17	0.00
<i>U. spelaeus</i> (Adam)	2	16.00	4.00	20.00	0.50	2.00	25.00	2.00	29.00	0.00
<i>U. arctos</i> (ACCG)	2	10.50	14.75	25.25	1.50	5.50	14.25	1.50	21.25	1.00
<i>U. arctos</i> (Bisericuța)	1	6.00	21.00	27.00	2.00	27.00	9.00	2.00	38.00	1.00
<i>U. arctos</i> (Avenul Măjului)	1	4.00	20.00	24.00	2.00	10.00	20.00	3.00	33.00	0.00
Extant										
<i>U. americanus</i> (North America)	9	13.56	2.56	16.12	0.00	5.44	19.00	3.00	22.00	0.00
<i>U. arctos</i> (Greece)	4	13.00	7.00	20.00	0.5	9.25	8.50	2.25	20.00	2.00
<i>U. arctos</i> (Central Europe)	10	17.50	3.4	20.90	0.00	5.4	22.50	8.30	36.20	2.10
<i>U. arctos</i> (North America)	8	18.25	3.00	21.25	0.00	6.75	18.38	3.25	28.38	0.25
<i>U. arctos</i> (Kamchatka)	23	16.22	3.83	20.05	0.1	6.96	19.78	4.78	31.52	0.35
<i>U. arctos</i> (North Europe)	9	15.78	3.78	19.56	0.00	6.44	23.33	2.67	32.44	0.22

19.39) over large pits (NLP = 0.67). Additionally, the number of PP is 1.67, slightly exceeding the count in other sites. Finally, the number of gouges (NG) is higher in comparison to all other sites, scoring at 1.67.

The Onceasa site has a limited sample size, consisting of only 3 individuals. Consequently, the obtained values lack statistical significance and hold limited statistical value. As a result, it was excluded from the further statistical multivariate analysis. The average number of total pits (NTP = 23.17) is nearly identical to Urşilor's average (NTP = 23.28). The pits exhibit a similar distribution pattern as observed in the other sites, with a clear preponderance for small pits. On the other hand, the average number of total scratches (NTS = 25.17) is slightly higher in comparison to the other fossil populations. However, the scratch distribution follows the same pattern observed for Urşilor, Oase, and Bisericuța, with an SWS of 1. The individuals from Onceasa exhibited a presence of puncture pits (NPP = 1), but no gouges (NG = 0). It is important to note that the sample size for the Onceasa site is relatively small, which should be taken into consideration when interpreting these results.

The Adam site also exhibits a limited sample size, comprising only 2 individuals. Consequently, the obtained values lack statistical significance and have limited statistical value. As a result, they were excluded from the further statistical multivariate analysis. The average number of total pits (NTP = 29) for the two specimens from Adam is higher than that exhibited by the other fossil populations. However, the average number of total scratches (NTS = 20) falls within the range observed in the other cave bears. Furthermore, the distribution of pits and scratches follows the same trend observed in Urşilor, Oase, Bisericuța, and Onceasa, with a predominance of small pits and fine scratches, respectively. Notably, the average number of puncture pits (NPP) for Adam is 2. However, the two individuals from this site did not exhibit gouges (NG = 0).

3.2. AMS ¹⁴C dating

11 samples (*n* = 11) out of 19 which had ¹⁴C AMS dating, with a yield higher or equal to 1%, were considered suitable for our analyses (according to Van Klinken, 1999; Brock et al., 2010; Table 2). Eight (*n* = 8) bear samples provided reliable data for both radiocarbon and microwear data. The majority of the radiocarbon ages belong to the MIS 3 cave bears (ca. 46–27 cal kyr B.P.; median ages), whereas one sample is a MIS 3 brown bear (ca. 41.6 cal kyr B.P.; median age) (Fig. 3). To these, a medieval brown bear (Cl/009 from ACCG site; 1 cal kyr B.P.; median age; Erismark et al., 2019) was added to our analyses as a reference. The highest number of cave bears with reliable data from both sets are

derived from Urşilor (*n* = 5) and belong to the ca. 46–27 cal kyr B.P. time interval. Except for the ages of ca. 35 cal kyr B.P. and ca. 27 cal kyr B.P., the rest of the MIS 3 bear samples range from ca. 45.5 to 41.7 cal kyr B.P.

3.3. MIS 3 cave bears from the Romanian Carpathians

When compared with the extant ursid populations, the *U. spelaeus* specimens from the most numerous sites (Urşilor, Oase, Bisericuța) display a slightly higher number of scratches. Regarding pits, the fossil specimens from the most significant populations aforementioned display a similar number of small pits (NSP) when compared to extant ursids (*U. americanus* and *U. arctos*) from North America. Moreover, they also display a smaller number of large pits (NLP) compared to extant populations. Regarding gouges, the populations of Urşilor, Oase, and Bisericuța exhibit higher values compared to other extant bear populations, excepting the brown bears from Central Europe and Greece, which display even higher counts. Finally, the most numerous fossil populations (Urşilor, Oase, and Bisericuța) display a number of puncture pits similar to that found in *U. americanus* and *U. arctos* from North America and Northern Europe, respectively.

A hierarchical clustering analysis was conducted using the paired group method with Euclidean distance (Fig. 4A). The analysis incorporated seven microwear variables, namely small pits, large pits, fine scratches, coarse scratches, SWS, gouges and puncture pits. We compared the microwear signal of the most numerous fossil populations with that from extant populations of *U. arctos* from different regions and *U. americanus*.

The cave bear populations of Urşilor, Oase, and Bisericuța show a high degree of similarity, indicating a close relationship without significant intergroup distinctions (Table 3). On the other hand, extant bear populations of *U. arctos* from Kamchatka and North America are grouped together, which both include a hard and soft mast diet but with a predominance of vertebrates (Fig. 4A). Grouped on a closely related level is *U. americanus* which has a predominant soft mast diet but is classified as omnivorous, including a variety of food types in its diet. The *U. arctos* population from Greece is notably distinct from the other groups, as it exhibits a specialized dietary preference for exclusively soft food. Furthermore, the fossil populations exhibit the greatest resemblance to the extant populations of *U. americanus* (Table 3). However, there are also nearly equal similarities with the extant populations of *U. arctos* from Kamchatka, North America, and the northern regions of Europe. All the most-related extant species share an omnivorous nature, encompassing a wide range of dietary components including soft and hard mast, as well as vertebrates and invertebrates. However, it is

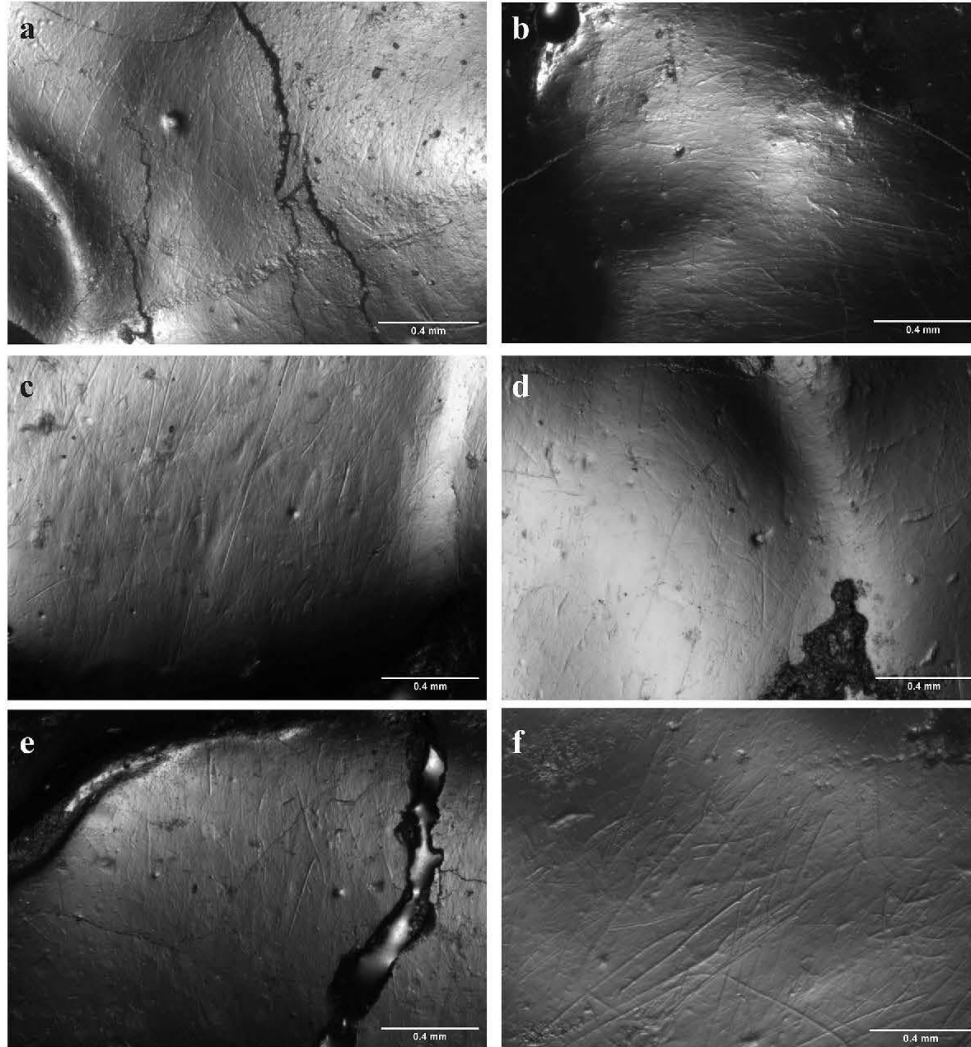


Fig. 2. Photomicrographs (at $\times 35$ magnification) of the grinding non-faceted enamel surface of selected fossil individuals of *U. spelaeus* from the Carpathians. (a): Urşilor (#PU/F); (b): Urşilor (#PU/E2-III-1164); (c): Oase (# O35.138); (d): Bisericuța (#PB/C1-IX); (e) Bisericuța: #PB/A1-I-II-1; (f): Onceasa (#POC/016).

noteworthy that the species with an extreme dietary preference, specifically *U. arctos* from Greece, which is clearly specialized in consuming soft mast, displays the highest level of differentiation.

To display the distribution and variability of the samples, a correspondence analysis (CA) was conducted using the same variables and individuals as in the hierarchical clustering analysis (Fig. 4B). The results for the first two dimensions (i.e. Dim. 1 and Dim. 2), owing to their higher percentage of variance, were utilized, and plotted (Table 4 and Fig. 4B). The correspondence analysis plot illustrates a similar and overlapping distribution pattern among the extant bears, *U. arctos* from various regions, and *U. americanus*. Significantly, these extant species are predominantly clustered on the left side of the Dim 1 axis, showing both intra-population and inter-population variability. However, the extant *U. arctos* population from Greece stands out as a distinctive outlier, occupying a solitary position in the upper section of the CA plot. This distinct placement can be attributed to its unique characteristics, higher average number of large pits compared to small pits and the highest number of coarse scratches, setting them apart from the other

extant bear species.

The extinct *U. spelaeus* populations from the Carpathians (Urşilor, Oase, Bisericuța) are predominantly clustered together and overlap on the right side of the first-dimensional axis in the CA plot. This distinct positioning, separate from the extant bear species, aligns with the grouping of the three sites observed in the hierarchical clustering results (Fig. 4A) and in the similarity and distance indices (Table 3).

In relation to the second dimension, the fossil populations show a tendency to cluster in the lower section or around the 0.0 axis of the second dimension. This clustering pattern can be attributed to their relatively higher number of small pits, ranging from 17.65 to 19.35, although it is lower compared to other populations such as *U. arctos* from Central Europe or North America. This feature distinguishes them from the *U. arctos* population in Greece, which, in contrast, displays a low number of small pits. The dissociation between the fossil populations and *U. arctos* from Greece is consistent with the highest divergence observed in the similarity and distance indices (Table 3).

Finally, the plot reveals that some cave bear individuals fall within

Table 2

The microwear samples which were AMS ^{14}C dated (mandible bone). The radiocarbon dates were calibrated using the IntCal13 calibration dataset (Reimer et al., 2013). * Source. 1 – This study; 2 – Ersmark et al., 2019; 3 – Mirea et al., 2021. Notes: All depths are in cm below surface. Collagen yields are given in percent of extracted collagen with respect to the initial weight of the sample. PU: Urşilor; PM: Muierilor; PB: Bisericuța; CL: P.-Aven nr. 2 from Cracul de la Cioaca Goeală (ACCG; Cloșani); N32, N35, O36: Oase. PB/C1-IV-V is associated with PB/A1-V (both hemimandibles belong to the same specimen).

#ERIS	#PRL	#Microwear	Specimen	Depth (cm)	Coll. Yield (%)	% Cb	% Nb	^{14}C age (uncalibrated)	Cal yr B.P. age (median)	Age range cal yr B.P. (2 σ)	*
Urşilor Cave											
PU/YI	Poz-161,933	–	<i>U. spelaeus</i>	–10	1.3	3.9	0.6	36,900 $\pm$ 800	41,653	42,529–40,572	1
PU/B-I-14	Poz-161,894	58	<i>U. spelaeus</i>	–10	6.1	9.9	3.1	37,300 $\pm$ 800	41,883	42,730–40,912	1
PU/G-I-13a	Poz-161,928	83	<i>U. spelaeus</i>	–10	1.4	3.1	0.5	43,000 $\pm$ 2000	46,363	52,322–42,845	1
PU/B-II-a1	Poz-161,895	–	<i>U. spelaeus</i>	–20	1.5	3.1	0.6	38,200 $\pm$ 900	42,385	43,478–41,312	1
PU/EI-III-125	Poz-162,373	42	<i>U. spelaeus</i>	–30	1.7	3.3	0.6	41,000 $\pm$ 2000	44,696	50,623–42,016	1
PU/EI-III-808	Poz-162,375	43	<i>U. spelaeus</i>	–30	1.8	5.1	1	42,000 $\pm$ 2000	45,474	51,485–42,427	1
PU/DI-VIII-116	Poz-53,620	35	<i>U. spelaeus</i>	–80	1	1.6	0.6	22,690 $\pm$ 130	27,056	27,281–26,860	1
Muierilor Cave - Bears' Passage											
PM/S6-I-II-1	Poz-161,930	–	<i>U. spelaeus</i>	–15	1.4	4.4	1.1	39,500 $\pm$ 1100	43,223	44,852–42,071	1
PM/U6-II-III-C	Poz-161,929	–	<i>U. spelaeus</i>	–25	2.3	6.3	1.4	38,500 $\pm$ 1000	42,575	44,205–41,476	1
Bisericuța											
PB/C1-IV-V/01	Poz-109,333	93	<i>U. spelaeus</i>	–50	2.1	9.1	3.6	31,300 $\pm$ 500	35,229	36,095–34,513	1
PB/B1-X-XI	Poz-161,818	1	<i>U. arctos</i>	–100	6.7	8.3	2.8	37,000 $\pm$ 1200	41,668	43,269–39,717	1
Cloșani											
CL/009		91	<i>U. arctos</i>	–10				1109 $\pm$ 26	1007	1065–956	2
Discarded ages											
PU/F-I-12b	Poz-0	32	<i>U. spelaeus</i>	–10		1.9	0.1	>0 BP			1
PU/D1-V-146	Poz-161,927	82	<i>U. spelaeus</i>	–50	0.3	4.8	0.8	34,700 $\pm$ 600	39,895	41,203–38,393	1
PU/C1-VIII-110	Poz-53,619	–	<i>U. spelaeus</i>	–80		4.6	2.1	30,780 $\pm$ 290	35,129	35,821–34,545	1
PM/O6-0-89	Poz-77,727	60	<i>U. spelaeus</i>	0	0.4	3.8	1.0	27,980 $\pm$ 210	31,941	32,886–31,455	3
PM/U6-I-14	Poz-0	–	<i>U. spelaeus</i>	–10		3.5	0.5	>0 BP			1
PM/V6-II-III-B	Poz-0	–	<i>U. spelaeus</i>	–25		2.5	0.2	>0 BP			1
N32.27	Poz-161,934	17	<i>U. spelaeus</i>		0.7	3.7	0.6	35,500 $\pm$ 700	40,616	41,846–39,428	1
N35.143	Poz-161,935	–	<i>U. spelaeus</i>		0.7	5.9	0.6	39,000 $\pm$ 1000	42,863	44,444–41,934	1
O36.113	Poz-161,936	–	<i>U. spelaeus</i>		0.7	3.2	0.5	37,300 $\pm$ 800	41,883	42,730–40,912	1

the range of *U. americanus* and *U. arctos* from Kamchatka, North America, and the northern regions of Europe, with a small overlap observed with the central European population. The compatibility towards these extant populations aligns with the associations observed in the similarity and distance indices (Table 3). Therefore, it is important to highlight the shared omnivorous nature of these extant species that exhibit some degree of overlap with the fossil samples.

3.4. Fossil *U. arctos* from the Romanian Carpathians

For the fossil specimens of brown bear *U. arctos*, although the number of individuals per site is small (Bisericuța: $n = 1$, ACCG: $n = 2$, Avenul Măpului: $n = 1$), making them statistically insignificant, there is a notable consistency in the total number of scratches (NTS) observed, ranging from 24 to 27 (Table 1). However, when considering the total number of pits (NTP), there is a higher range of variability, spanning from 21 to 38. The Pleistocene individuals from Avenul Măpului and Bisericuța exhibit a higher total number of pits compared to *U. spelaeus* from the most numerous sites (Urşilor, Oase and Bisericuța), but their counts are similar to those from Adam, which also has a small sample size. The distribution of scratches clearly exhibits a higher count of

coarse scratches (NCS), as evidenced by an SWS of 2 for the individuals from Bisericuța and Avenul Măpului, and an SWS of 1.50 for the medieval individuals from the Cloșani area (Table 1; Fig. 5). These results suggest a greater proportion of coarse scratches in these fossil *U. arctos* individuals compared to the contemporaneous *U. spelaeus* populations (Fig. 6). In terms of pit distribution, the Bisericuța population shows a higher count of large pits (NLP = 27) compared to small pits (NSP = 9), which opposes the general trend observed in *U. spelaeus* with a predominance of small pits. Conversely, the Holocene brown bears from the Cloșani area exhibit a distribution pattern similar to *U. spelaeus*, with a higher count of small pits (NSP = 14.25) compared to large pits (NLP = 5.50). Likewise, the Avenul Măpului individual demonstrates a prevalence of small pits (NSP = 20) over large pits (NLP = 10). The number of puncture pits (NPP) displays a consistent distribution, ranging from 2.00 (Bisericuța) to 3.00 (Avenul Măpului), and with a 1.50 for the medieval Cloșani area individuals. In terms of gouges, both the Cloșani area and Bisericuța populations exhibit an average count of 1, while the individual from Avenul Măpului does not show any gouges. The puncture pits and gouges observed in the fossil *U. arctos* specimens are consistent with those observed in *U. spelaeus* populations.

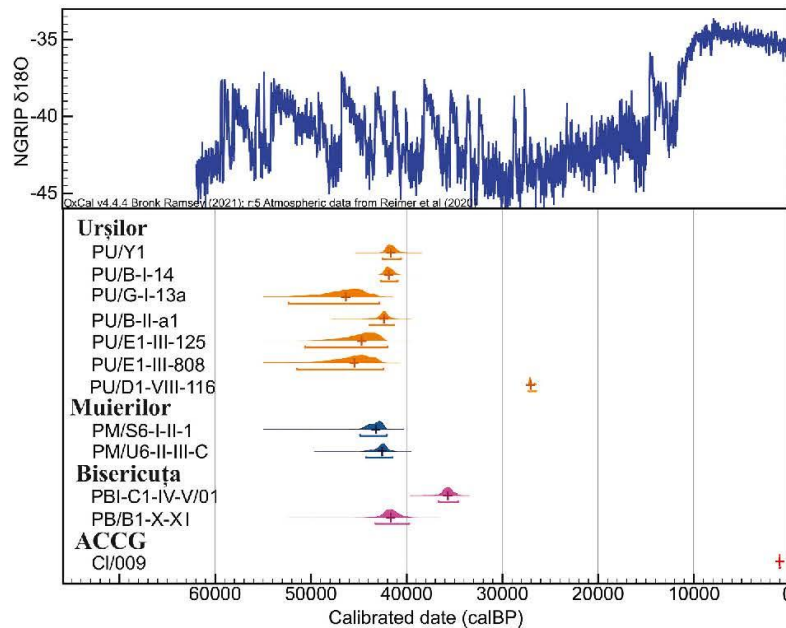


Fig. 3. Calibration of the reliable AMS ^{14}C data of the analysed bears.

4. Discussion

The microwear results obtained for *U. spelaeus* specimens from the Carpathians provide compelling evidence of dietary homogeneity during the pre-dormancy phase within and among the examined populations, regardless of age and sex. Their diet did not exhibit specialization, being neither fully herbivorous nor carnivorous, but rather omnivorous, with a preference for the consumption of hard objects. This dietary pattern persisted throughout the MIS 3 period, spanning from over 46 to 27.1 cal kyr B.P. at least, despite the climatic fluctuations (Constantin et al., 2007). We analysed individuals from both distant and recent time periods leading up to their extinction around 27.8 cal kyr B.P. (Pacher and Stuart, 2009; Terlato et al., 2019); however, no dietary changes or differences were observed among them.

4.1. Long-term (stable isotopes) vs short-term (dental microwear) dietary patterns

Distinctly, the isotopic results of nitrogen ($\delta^{15}\text{N}$) for the analysed individuals exhibit substantial variability ($\delta^{15}\text{N}$ values range from 3.3 to 11.5‰) (Richards et al., 2008; Robu et al., 2013, 2018). This may suggest that over the year, there was indeed a differentiated diet. However, during this pre-dormancy specific period of the year, Carpathian cave bear populations from Urşilor, Oase, and Bisericuța had a similar dietary pattern, characterized by a highly flexible omnivorous intake. Therefore, no correlations between stable isotopes and dental microwear at the individual or population-level were identified due to the different time resolutions of each method. Bone collagen stable isotopes provide the average annual dietary signal while dental microwear indicate a short term and seasonal dietary signal. The substantial significance of this common dietary regime is underscored by the notable geographic separation between the Urşilor, Oase, and Bisericuța populations. These populations, situated within the Carpathian region, were at a significant distance from one another. Specifically, there was 180 km between Urşilor and Oase, the same distance between Bisericuța and Oase, and 70 km separating Bisericuța from Urşilor.

4.2. Omnivorism during the predormancy period

On the contrary, the microwear patterns of the cave bear specimens differ from those of extant *U. arctos* and *U. americanus*. This differentiation may be attributed to the consumption of particular items, potentially consisting of plant matter, such as roots (Mattson, 1998; Athén, 2006; Ramírez-Pedraza et al., 2022), as opposed to living bear species (Krajcarz et al., 2016; Bocherens, 2019; Naito et al., 2020). However, the correspondence analysis (CA) reveals some intra-population variability, with some individuals falling within the range of extant species that share a highly variable (including both hard and soft mast) omnivorous diet, mainly *U. americanus* (Hailer, 1967; Raine and Kansas, 1990), *U. arctos* from Kamchatka (Bergman, 1936; Kistchinski, 1972; Vereschagin, 1976; Krechmar, 1995) and *U. arctos* from Northern Europe (Elgmork and Kaasa, 1992; Persson et al., 2001; Bojarska and Selva, 2012), as well as *U. arctos* from North America (Mattson, 1998; Hilderbrand et al., 1999; Mowat and Heard, 2011) and Central Europe (Rigg and Gorman, 2005; Bojarska and Selva, 2012), respectively. In contrast, cave bears significantly differentiate from the diet-specialized *U. arctos* from Greece (soft-mast) (Vlachos et al., 2000; Paralikiidis et al., 2010).

4.3. Cave bear seeded and hard-shelled fruit consumption

The observed omnivorous trends, distinct from the specialized diet of the Greek *U. arctos*, may be inferred from the consumption of a diverse array of dietary food types during this pre-dormancy period, a trend observed in modern bear species. Ursids actively forage for food sources rich in lipids or carbohydrates during the pre-hibernation/dormancy hyperphagic period, which typically takes place in late summer and autumn (Coogan et al., 2014). This behaviour is driven by their physiological need to accumulate energy reserves before entering hibernation, and in the case of females, to support the energy demands associated with reproduction and the production of milk for lactation (Farley and Robbins, 1995; López-Alfaro et al., 2013). Therefore, in extant bears, it translates into diet diversification, particularly through

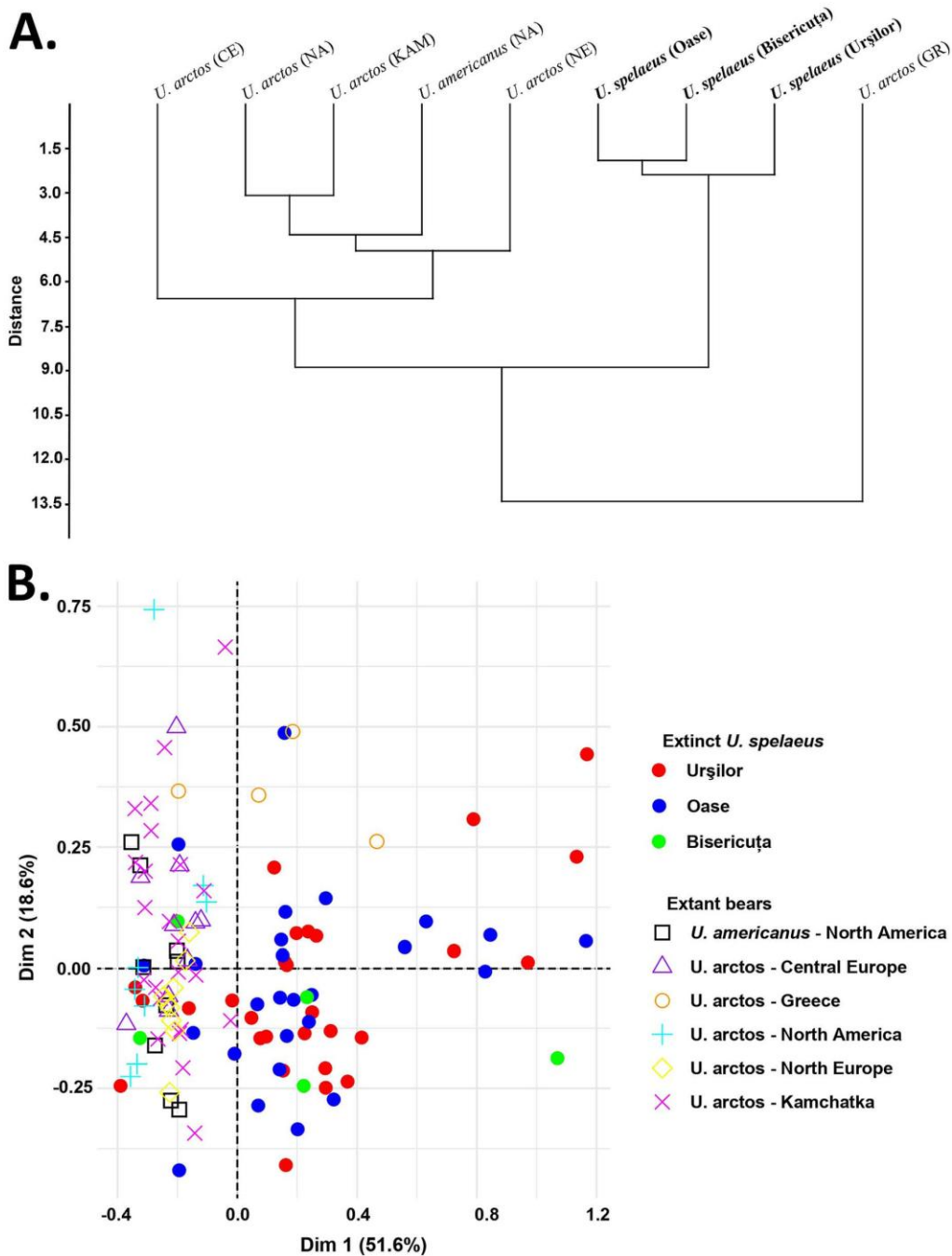


Fig. 4. A) Hierarchical clustering diagram employing seven microwear variables: number of fine and coarse scratches, small and large pits, gouges, puncture pits, and the scratch width score. Comparison of the fossil populations of *U. spelaeus* from Urșilor, Oase and Bisericuța with the extant bears. Abbreviations: CE = Central Europe; NA = North America; KAM = Kamchatka; NE = North Europe; GR = Greece. B) Correspondence analysis (CA) based on seven variables: number of fine and coarse scratches, small and large pits, gouges, puncture pits, and the scratch width score. Comparison of the fossil populations of *U. spelaeus* from Urșilor, Oase and Bisericuța with the extant bears.

Table 3
Euclidean similarity and distance indices based on seven microwear variables (Table 1): number of fine and coarse scratches, small and large pits, gouges, puncture pits, and the scratch width score. Comparison of the fossil populations of *U. spelaeus* from Urşilor, Oase and Bisericuța with the extant bears. Abbreviations: CE Central Europe; NA North America; KAM Kamchatka; NE North Europe; GR Greece.

	<i>U. americanus</i> (NA)	<i>U. arctos</i> (GR)	<i>U. arctos</i> (CE)	<i>U. arctos</i> (NA)	<i>U. arctos</i> (KAM)	<i>U. arctos</i> (NE)	<i>U. spelaeus</i> (Oase)	<i>U. spelaeus</i> (Urşilor)	<i>U. spelaeus</i> (Bisericuța)
<i>U. americanus</i> (NA)	–	12.247143	7.7846002	4.9721726	3.8392708	5.0892043	7.7935871	8.2607506	7.1742595
<i>U. arctos</i> (GR)		–	16.771479	12.348684	12.767635	15.786782	12.719375	11.484446	13.184555
<i>U. arctos</i> (CE)			–	6.9507194	5.2153619	6.2976186	10.383641	11.719215	9.7360156
<i>U. arctos</i> (NA)				–	3.0761177	5.601116	9.4917069	9.958037	8.5030877
<i>U. arctos</i> (KAM)					–	4.1472883	8.0907354	8.9330846	7.4545288
<i>U. arctos</i> (NE)						–	8.436824	9.6932967	7.628237
<i>U. spelaeus</i> (Oase)							–	1.9078784	1.8947295
<i>U. spelaeus</i> (Urşilor)								–	2.8548205
<i>U. spelaeus</i> (Bisericuța)									–

Table 4
Representation of the results for each axis in the correspondence analysis (CA): eigenvalues, percentages of variance, and cumulative percentages.

Axis	Eigenvalue	% total	Cumulative
1	0.120666521	51.564	51.564
2	0.043569598	18.618	70.182
3	0.028035030	11.980	82.162
4	0.021993366	9.398	91.560
5	0.017292613	7.289	98.950
6	0.002456043	1.049	100

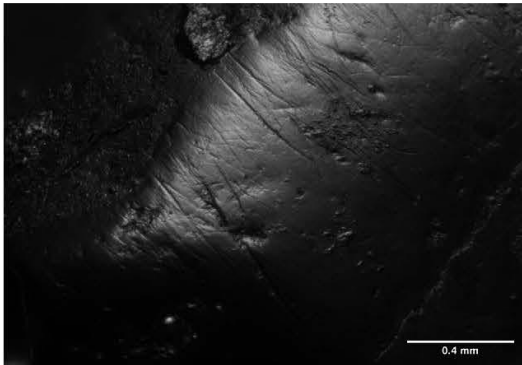


Fig. 5. MIS 3 *U. arctos* from Bisericuța displaying coarse scratches (#PB/B1-X-XI).

the substantial consumption of core carbohydrate items (Bojarska and Selva, 2012; Coogan et al., 2018). Consequently, bears ranging from northern cold regions to mild Mediterranean zones (Graber and White, 1983; Cienjak et al., 1987; Clevenger et al., 1992; Vlachos et al., 2000; Persson et al., 2001) heavily rely on the ingestion of small, wild fruits like berries or nuts which serve as a principal means of accumulating energy reserves (Welch et al., 1997; Stenseth et al., 2016; Soofi et al., 2017; Ogurtsov, 2018; García-Rodríguez et al., 2021). On the other hand, in regions with harsh winters, particularly those characterized by heavy snowfall, bears may rely more heavily on a meat-based diet (Wiegand et al., 2008; Bojarska and Selva, 2012), although one does not necessarily exclude the other (e.g. Dahle et al., 1998; Persson et al., 2001). Regarding this particular behaviour, the presence of puncture pits and gouges was consistently observed in all fossil populations, a microwear feature characteristic of hard-object consumers (Solounias and Semperebon, 2002; Godfrey et al., 2004; Semperebon et al., 2004; Williams and Geissler, 2014). Specifically, carnivore clade omnivores

from temperate woodland environments (e. g. *Vulpes vulpes*, *Genetta genetta* or *Nandinia binotata*) present puncture pits, due to the consume of fruit coverings and seed coats (Xafis et al., 2017). This evidence suggests, for the first time, the consumption of seeded and hard-shelled fruits, for *U. spelaeus*. It is important to stress that the presence of puncture pits (i.e. hard-object consumption) was not observed in other cave bears analysed using low-magnification microwear techniques (Ramírez-Pedraza et al., 2019, 2020, 2022). This applies to cave bears residing in both steppe-like habitats in northern latitudes (Ramírez-Pedraza et al., 2022), and forested landscapes in southern latitudes (Ramírez-Pedraza et al., 2019, 2020).

During the Last Glacial Period, the Carpathian Mountain range has been recognized as a large forest refugium (Jankovská and Pokorný, 2008; Tzedakis et al., 2013; Juričková et al., 2014). This region exhibited a diverse range of canopy forest landscapes, with certain valleys with more humid and enclosed environments maintaining temperate plant specimens (Jankovská et al., 2002; Juričková et al., 2014). Dominant tree species during this time included larch (*Larix*), Swiss stone pine (*Pinus cembra*), Scots pine (*Pinus sylvestris*), and spruce (*Picea*), forming a relatively dense forest canopy (Jankovská et al., 2002). In more favourable locations within the Carpathian region, isolated patches of temperate broadleaf trees, such as hazel (*Corylus avellana*), black alder/grey alder (*Alnus glutinosa/A. incana*), linden (*Tilia*), elm (*Ulmus*), oak (*Quercus*), beech (*Fagus*), hornbeam (*Carpinus*), fir (*Abies*), and maple (*Acer*) managed to persist even during the most severe glacial periods, including the Last Glacial Maximum (LGM) (Magri et al., 2006; Jankovská and Pokorný, 2008). The consumption of fruits produced by these plant specimens, such as beechnuts, hazelnuts, acorns, and linden nutlets, is compatible with the microwear pattern found on cave bear individuals (Godfrey et al., 2004; Xafis et al., 2017), potentially suggesting the inclusion of these specific items in the diet of cave bears inhabiting the Carpathian region during MIS 3.

Our results are particularly intriguing as they suggest that the dietary patterns of Carpathian cave bears may exhibit similarities to those of extant brown bears inhabiting the same region. This is noteworthy considering that modern brown bears in the Carpathians predominantly consume seeded fruits as their primary food source during the hyperphagia period in autumn (Slobodyan, 1976; Štofik et al., 2013; García-Rodríguez et al., 2021). During autumn bears collect the remaining raspberries (*Rubus idaeus*) and whortleberries (*Vaccinium myrtillus*) from summer; they also eat mature blackberries (*Rubus fruticosus*), mountain-ash fruits (*Sorbus aucuparia*), fruits from wild apple (*Malus* spp.) and pear trees (*Pyrus* spp.), blackthorn (*Prunus spinosa*), and dog rose (*Rosa canina*), as well as beechnuts (*Fagus* spp.) and acorns (*Quercus* spp.) (Slobodyan, 1976; Kalabér et al., 1994).

The singular presence of hard items in the Carpathian cave bear diet during the Late Pleistocene, in contrast to other European regions, in conjunction with the observed similarities between the dietary patterns of cave bears and extant brown bears in the same region, yields valuable

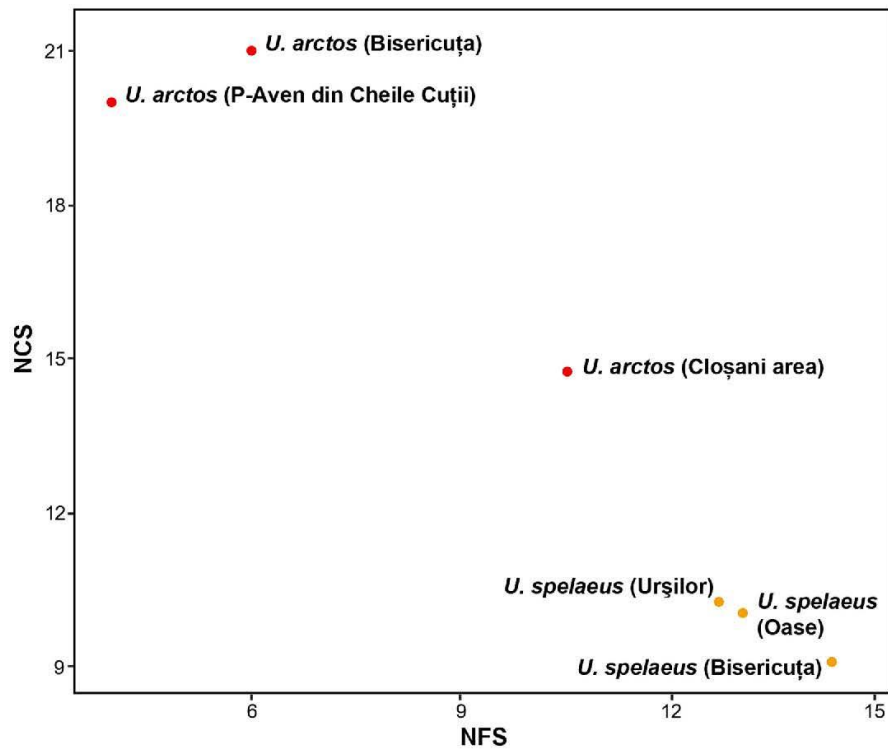


Fig. 6. Bivariate plot of the mean number of fine and coarse scratches for the fossil bear populations of *U. arctos* and *U. spelaeus* from the Romanian Carpathians.

insights into the enduring presence of specific tree species and their associated food resources within the Carpathian ecosystem over time. Moreover, a new unpublished date released in this article for an individual from Urșilor, calibrated to 27,056 cal yr B.P. (median age), which closely aligns with the species' extinction and stands as one of the earliest recorded dates for Eastern Europe, may suggest the prolonged existence of cave bears (*U. spelaeus*) in the Carpathians, owing to favourable ecological conditions and the availability of reliable herbivorous food resources. Consequently, the Carpathians may have functioned as a refuge for cave bears, sustaining a consistent availability of food sources for ursids, even during periods of severe glaciation.

4.4. Dietary comparison between fossil *U. spelaeus* and *U. arctos*

Finally, the microwear results refute that the fossil populations from the Carpathians had a carnivorous diet, which is supported by the barely-present hyper-coarse scratches, which are only displayed by hyper-carnivores and bone-consumers such as polar bears (*U. maritimus*) (Pappa et al., 2019) and hyenas (*Crocota* sp.) (Rivals et al., 2022). Nevertheless, the presence of certain fossil individuals overlapping with omnivorous ursids, known to consume both vertebrates and invertebrates, could suggest at least sporadic meat consumption among the cave bear individuals examined in this study. This could be explained as that towards the end of autumn, when winter approaches, resource availability diminishes, and diet becomes restricted; some individuals who have not been able to accumulate sufficient lipid reserves for the winter begin to consume meat to further supplement their stores, as recorded in extant *U. arctos* from the Carpathians (Slobodyan, 1976; Frackowiak, 1997). However, Carpathian cave bears did not have such a carnivorous diet during the pre-dormancy period, unlike some cave bear populations from the northern regions of the Iberian Peninsula (Pinto-Llona, 2013; Ramirez-Pedraza et al., 2020).

Additionally, *U. spelaeus* exhibited narrower scratches (lower SWS) in comparison to contemporaneous (pre-LGM) *U. arctos* specimens from the Carpathians. The brown bears, despite the limited sample size, displayed a clear trend of a higher number of coarse scratches relative to fine scratches. This distinction in the width of scratches between the Carpathian cave bears and brown bears may suggest divergent dietary niches, with the brown bears displaying a propensity towards a more specialized carnivorous diet. Pleistocene brown bears appear to have displayed a more carnivorous dietary behaviour compared to contemporary brown bears (Bocherens et al., 2011; Münzel et al., 2011), while modern brown bears from the Carpathians might exhibit more dietary similarities to cave bears from the same region during MIS 3. Furthermore, the two Holocene *U. arctos* individuals from the Carpathians (Cloșani area), dated to 1007 cal yr B.P., displayed a scratch width pattern more similar to that of Pleistocene *U. spelaeus*. These findings could support the hypothesis of a more omnivorous dietary change in the post-Last Glacial Maximum (LGM) *U. arctos*, potentially due to occupying the ecological niche of cave bears after their extinction. However, given the absence of statistical significance from two *U. arctos* Holocene individuals from the Carpathians, conducting further microwear studies with a significant sample size to compare its diet with the Late Pleistocene *U. spelaeus* populations of the same region becomes necessary. This will help to firmly establish dietary similarities and potential niche heredity continuities between Pleistocene cave bears and pre-LGM *U. arctos* populations in the Carpathians.

5. Conclusions

Overall, the highly omnivorous diet of cave bears from the Carpathians during the pre-dormancy period represents a dietary profile endemic to this region, which served as a refugium of fauna and flora (Sommer and Nadachowski, 2006; Juričková et al., 2019), and within

which cave bears survived until at least 27.1 cal kyr B.P., close to the time of their extinction. Furthermore, the first observation of microwear features typical of hard-object consumers, i.e. fruit eaters, on cave bears provides more information about the uniqueness of the Carpathians in the context of European cave bears and suggests the possibility of niche heredity with the extant bears of this region. A high variability in their long-term diet is observed using stable isotopes, and the short-term diet of these individuals provides essential insights into the dietary uniqueness of Carpathian bears during the pre-dormancy period, and the high plasticity of their repertoire. This flexibility might explain the consumption of certain high nitrogen bulk items by some individuals while completely discarding the possibility of a meat-based diet for any of the cave bears analysed. These discoveries shed light on the ecological adaptations of cave bears in the Carpathian region during the Late Pleistocene and contribute to a deeper understanding of their dietary habits and responses to the unique environmental conditions of this region.

Ethics approval/declarations

Not applicable.

Consent to participate

Not applicable.

Consent for publication

Not applicable.

Credit authorship contribution statement

Paulo Duñó-Iglesias: Conceptualization, Data curation, Formal analysis, Investigation, Writing – original draft. **Iván Ramírez-Pedraza:** Data curation, Formal analysis, Investigation, Writing – original draft. **Florent Rivals:** Conceptualization, Data curation, Formal analysis, Funding acquisition, Investigation, Supervision, Writing – original draft. **Ionuț-Cornel Mirea:** Conceptualization, Funding acquisition, Writing – review & editing. **Luchiana-Maria Faur:** Conceptualization, Writing – review & editing. **Silviu Constantin:** Funding acquisition, Writing – review & editing. **Marius Robu:** Conceptualization, Data curation, Formal analysis, Funding acquisition, Investigation, Writing – original draft.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have influenced the work reported in this paper.

Data availability

Datasets related to this article can be found at <https://doi.org/10.5281/zenodo.10076736>, an open-source online data repository hosted at Zenodo (Duñó-Iglesias, 2023).

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References

- Armand, D., Plassard, F., Prat, F., 2004. L'ours de Font-de-Gaume III et le problème de l'exploitation de l'ours des cavernes. In: Actes du 9e symposium international sur l'ours des cavernes. Cahiers scientifiques du Muséum d'histoire naturelle de Lyon/Hors-série 2, Entremont-le-Vieux (Savoie, France), pp. 103–110.
- Athen, K., 2006. Biostatistical investigation of long bones and metapodial bones of *Ursus spelaeus* and *Ursus deningeri*. Sci. Annals. Geol. School. AUTH Spec. 98, 159–162.
- 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*). Sci. Nat. 103 (11), 92. <https://doi.org/10.1007/s00114-016-1414-8>.
- Bergman, S., 1936. Observations on the Kamchatka Bear. J. Mammal. 17 (2), 115–120. <https://doi.org/10.2307/1374183>.
- Blasco, R., Arilla, M., Domínguez-Rodrigo, M., Andrés, M., Ramírez-Pedraza, I., Ruñá, A., Rivals, F., Rosell, J., 2020. Who peeled the bones? An actualistic and taphonomic study of axial elements from the Toll Cave Level 4, Barcelona, Spain. Quat. Sci. Rev. 250, 106661 <https://doi.org/10.1016/j.quascirev.2020.106661>.
- Bocherens, H., 2019. Isotopic insights on cave bear palaeodiet. Hist. Biol. 31 (4), 410–421. <https://doi.org/10.1080/08912963.2018.1465419>.
- Bocherens, H., Fizet, M., Mariotti, A., 1994. Diet, physiology and ecology of fossil mammals as inferred from stable carbon and nitrogen isotope biogeochemistry: implications for Pleistocene bears. Palaeogeogr. Palaeoclimatol. Palaeoecol. 107 (3), 213–225. [https://doi.org/10.1016/0031-0182\(94\)90095-7](https://doi.org/10.1016/0031-0182(94)90095-7).
- 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). Quat. Res. 48 (3), 370–380. <https://doi.org/10.1006/qres.1997.1927>.
- Bocherens, H., Drucker, D., Billiou, D., Geneste, J.-M., 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. J. Hum. Evol. 50, 370–376. <https://doi.org/10.1016/j.jhevol.2005.12.002>.
- Bocherens, H., Stiller, M., Hobson, K., Pacher, M., Rabeder, G., Burns, J., 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. Quat. Int. 245, 238–248. <https://doi.org/10.1016/j.quaint.2010.12.020>.
- 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). Quat. Int. 339–340, 179–188. <https://doi.org/10.1016/j.quaint.2013.05.021>.
- Bojarska, K., Selva, N., 2012. Spatial patterns in brown bear *Ursus arctos* diet: the role of geographical and environmental factors. Mammal Rev. 42, 120–143. <https://doi.org/10.1111/j.1365-2907.2011.00192.x>.
- Bond, G.C., Showers, W., Elliot, M., Evans, M., Lotti, R., Hajdas, I., Bonani, G., Johnson, S., 1999. The North Atlantic's 1-2 kyr climate rhythm: relation to Heinrich events, Dansgaard/Oeschger cycles and the Little Ice Age. Geophys. Monogr. Am. Geophys. Union 112, 35–58.
- Bronk Ramsey, C., 2020. OxCal online. <https://c14.arch.ox.ac.uk/oxcal.html>.
- Brock, F., Higham, T., Ramsey, C.B., 2010. Pre-screening techniques for identification of samples suitable for radiocarbon dating of poorly preserved bones. J. Archaeol. Sci. 37 (4), 855–865. <https://doi.org/10.1016/j.jas.2009.11.015>.
- Bronk Ramsey, C., 2009. Bayesian analysis of radiocarbon dates. Radiocarbon. 51 (1), 337–360. <https://doi.org/10.1017/S0033822200033865>.
- Cienjak, L., Roth, H., Ruff, R., Huber, D., 1987. Food habits of brown bears in Plitvice Lakes National Park, Yugoslavia. Int. Conf. Bear. Res. Manag. 7, 221–226. <https://doi.org/10.2307/3872628>.
- Clevenger, A., Purroy, F.J., Pelton, M.R., 1992. Food habits of brown bears (*Ursus arctos*) in the Cantabrian Mountains, Spain. J. Mammal. 73, 415–421. <https://doi.org/10.2307/1382077>.
- Constantin, S., Bojar, A.V., Lauritzen, S.E., Lundberg, J., 2007. Holocene and Late Pleistocene climate in the sub-Mediterranean continental environment: a speleothem record from Pleva Cave (Southern Carpathians, Romania). Palaeogeogr. Palaeoclimatol. Palaeoecol. 243 (3–4), 322–338. <https://doi.org/10.1016/j.palaeo.2006.08.001>.
- Constantin, S., Munteanu, C.M., Milota, S., Sarcina, L., Gherase, M., Zilhão, J., 2013. The Ponor-Plopa Cave system: Description, sediments, and genesis. In: Trinkaus, E., Constantin, S., Zilhão, J. (Eds.), Life and Death at Pesteria Cu Oase. Oxford University Press, A setting for modern human emergence in Europe, pp. 41–55.
- Constantin, S., Robu, M., Munteanu, C.-M., Petculescu, A., Vlaicu, M., Mirea, I., Kenes, M., Drăgușin, V., Hoffmann, D., Anecitei, V., Timar-Gabor, A., Roban, R.-D., Panaioiu, C.G., 2014. Reconstructing the evolution of cave systems as a key to understanding the taphonomy of fossil accumulations: the case of Urșilor Cave (Western Carpathians, Romania). Quat. Int. 339–340, 25–40. <https://doi.org/10.1016/j.quaint.2013.10.012>.

- Coogan, S.C.P., Raubenheimer, D., Stenhouse, G.B., Nielsen, S.E., 2014. Macronutrient optimization and seasonal diet mixing in a large omnivore, the grizzly bear: a geometric analysis. *PLoS One* 9 (5), e97968. <https://doi.org/10.1371/journal.pone.0097968>.
- Coogan, S.C.P., Raubenheimer, D., Stenhouse, G.B., Coops, N.C., Nielsen, S.E., 2018. Functional macronutritional generalism in a large omnivore, the brown bear. *Ecol. Evol.* 8 (4), 2365–2376. <https://doi.org/10.1002/eec3.3867>.
- Croitor, R., Brugal, J.P., 2010. Ecological and evolutionary dynamics of the carnivore community in Europe during the last 3 million years. *Quat. Int.* 212 (2), 98–108. <https://doi.org/10.1016/j.quaint.2009.06.001>.
- Dahle, B., Sørensen, O., Wedul, E., Swenson, J., Sandegren, F., 1998. The diet of brown bears *Ursus arctos* in Central Scandinavia: effect of access to free-ranging domestic sheep *Ovis aries*. *Wildl. Biol.* 4, 147–158. <https://doi.org/10.2981/wlb.1998.017>.
- Dansgaard, W., Johnsen, S., Clausen, H., Dahl-Jensen, D., Gundestrup, N., Hammer, C., Hvidberg, C., Steffensen, J., Sveinbjörnsdóttir, A., Jouzel, J., Bond, G.C., 1993. Evidence of general instability of past climate from a 250-kyr ice-core record. *Nature* 364, 218–220. <https://doi.org/10.1038/364218a0>.
- Dobos, A., Soficaru, A., Trinkaus, E., 2010. The prehistory and paleontology of the Pesteră Muierii, Romania, 124. *Études et Recherches d'Archéologiques de l'Université de Liège*, pp. 1–122.
- Dumitrescu, M., Samson, P., Terzea, E., Radulescu, Costin, Ghica, M., 1966. Pesteră La Adam, stadiune pleistocenă, 1–2. *Lucrările Institutului de Speologie "Emil Racovita"*, pp. 229–284.
- Duñó-Iglesias, P., 2023. Dental microwear raw data for *Ursus spelaeus* from the Romanian Carpathians. Zenodo. <https://doi.org/10.5281/zenodo.10076736>.
- Elgmork, K., Kaasa, J., 1992. Food habits and foraging of the brown bear *Ursus arctos* in Central South Norway. *Ecography* 15 (1), 101–110. <http://www.jstor.org/stable/3682968>.
- El-Zaatari, S., 2010. Occlusal microwear texture analysis and the diets of historical/prehistoric hunter-gatherers. *Int. J. Osteoarchaeol.* 20, 67–87. <https://doi.org/10.1002/oa.1027>.
- Ersmark, E., Baryshnikov, G., Higham, T., Argant, A., Castaños, P., Döppes, D., Gasparik, M., Germonpré, M., Lidén, K., Lipecki, G., Marciszak, A., Miller, R., Moreno-García, M., Pacher, M., Robu, M., Rodríguez-Varela, R., Rojo Guerra, M., Sabol, M., Spassov, N., Stora, J., Valdiosera, C., Villalunga, A., Stewart, J.R., Dalén, L., 2019. Genetic turnovers and northern survival during the last glacial maximum in European brown bears. *Ecol. Evol.* 9 (10), 5891–5905. <https://doi.org/10.1002/eec3.5172>.
- Farley, S.D., Robbins, C.T., 1995. Lactation, hibernation, and mass dynamics of American black bears and grizzly bears. *Can. J. Zool.* 73 (12), 2216–2222. <https://doi.org/10.1139/z95-262>.
- Fernández-Mosquera, D., Vila-Taboada, M., Grandal-d'Anglade, A., 2001. Stable isotopes data ($\delta^{13}\text{C}$, $\delta^{15}\text{N}$) from cave bear (*Ursus spelaeus*): a new approach to its paleoenvironment and dormancy. *Proc. R. Soc. Lond. Ser. B Biol. Sci.* 268, 1159–1164. <https://doi.org/10.1098/rspb.2001.1639>.
- Figuerido, B., Palmqvist, P., Pérez-Claros, J., 2009. Ecomorphological correlates of craniodental variation in bears and paleobiological implications for extinct taxa: an approach based on geometric morphometrics. *J. Zool.* 277, 70–80. <https://doi.org/10.1111/j.1469-7998.2008.00511.x>.
- Fortes, G., Grandal-d'Anglade, A., Kolbe, B., Fernandes, D., Meleg, I., García-Vázquez, A., Pinto-Illona, A., Constantin, S., Torres, T., Ortiz, J., Frischauf, C., Rabeder, G., Hofreiter, M., Barlow, A., 2016. Ancient DNA reveals differences in behaviour and sociality between brown bears and extinct cave bears. *Mol. Ecol.* 25 (19), 4907–4918. <https://doi.org/10.1111/056119>.
- Frackowiak, W., 1997. Diet and food habits of the brown bear (*Ursus arctos* L.) in Polish Eastern Carpathians. *J. Wildl. Res.* 2, 154–160.
- García-Rodríguez, A., Albrecht, J., Szczutkowska, S., Valido, A., Farwig, N., Selva, N., 2021. The role of the brown bear *Ursus arctos* as a legitimate megafaunal seed disperser. *Sci. Rep.* 11 (1), 1282. <https://doi.org/10.1038/s41598-020-80449-9>.
- Godfrey, L.R., Semperebon, G.M., Jungers, W.L., Sutherland, M.R., Simons, E.L., Solounias, N., 2004. Dental use wear in extinct lemurs: evidence of diet and niche differentiation. *J. Hum. Evol.* 47 (3), 145–169. <https://doi.org/10.1016/j.jhevol.2004.06.003>.
- Graber, D.M., White, M., 1983. Black bear food habits in Yosemite National Park. *Bears* 5, 1–10. <https://doi.org/10.2307/3872514>.
- Grandal-d'Anglade, A., Pérez-Rama, M., García-Vázquez, A., González-Fortes, G.M., 2019. The cave bear's hibernation: reconstructing the physiology and behaviour of an extinct animal. *Hist. Biol.* 31 (4), 429–441. <https://doi.org/10.1080/08912963.2018.1468441>.
- Grine, F.E., 1986. Dental evidence for dietary differences in *Australopithecus* and *Paranthropus*: a quantitative analysis of permanent molar microwear. *J. Hum. Evol.* 15 (8), 783–822. [https://doi.org/10.1016/S0047-2484\(86\)80010-0](https://doi.org/10.1016/S0047-2484(86)80010-0).
- Hammer, O., Harper, D., Ryan, P., 2001. PAST: Paleontological statistics software package for education and data analysis. *Palaeontol. Electron.* 4, 1–9.
- Hatter, D.F., 1967. Some Aspects in the Ecology of the Black Bear (*Ursus americanus*) in Interior Alaska. Master of Science. University of Alaska. <http://hdl.handle.net/11122/5224>.
- Higham, T., Wild, E.M., 2013. Radiocarbon dating of the Pesteră cu Oase faunal remains. In: Trinkaus, E., Constantin, S., Zilhão, J. (Eds.), *Life and Death at Pesteră cu Oase. A Setting for Modern Human Emergence in Europe*. Oxford University Press, pp. 77–85.
- Hilderbrand, G., Schwartz, C., Robbins, C.T., Jacoby, M.E., Hanley, T.A., Arthur, S., Servehn, C., 1999. The importance of meat, particularly salmon, to body size, population productivity, and conservation of North American brown bears. *Can. J. Zool.* 77, 132–138. <https://doi.org/10.1139/cjz-77-1-132>.
- Hunter, L., Turner, A., 1997. The big cats and their fossil relatives: an illustrated guide to their evolution and natural history. *Biosci.* 47. <https://doi.org/10.2307/1313168>.
- Huntley, B., Allen, J.R.M., Collingham, Y.C., Hickler, T., Lister, A.M., Singarayer, J., Stuart, A.J., Sykes, M.T., Valdes, P.J., 2013. Millennial climatic fluctuations are key to the structure of Last Glacial ecosystems. *PLoS One* 8 (4), e61963. <https://doi.org/10.1371/journal.pone.0061963>.
- Jankovská, V., Pokorný, P., 2008. Forest vegetation of the last full-glacial period in the Western Carpathians (Slovakia and Czech Republic). *Preslia Praha* 80, 307–324.
- Jankovská, V., Chromý, P., Nižnišská, M., 2002. Šafárka - first palaeobotanical data of the character of Last Glacial vegetation and landscape in the West Carpathians (Slovakia). *Acta Palaeobot.* 42, 39–50.
- Jurcsák, T., Plopiş, R., Ignat, D., Şerban, M., Popa, E., 1981. Date privind fauna fosilă a Pesterii Urşilor (M. Bihor). *Nymphaea* 8–9, 161–257.
- Juríková, L., Horáková, J., Ložek, V., 2014. Direct evidence of central European forest refugia during the last glacial period based on mollusc fossils. *Quat. Res.* 82 (1), 222–228. <https://doi.org/10.1016/j.yqres.2014.01.015>.
- Juríková, L., Horáková, J., Jansová, A., Kovanda, J., Harčár, J., Ložek, V., 2019. A glacial refugium and zoogeographic boundary in the Slovak eastern Carpathians. *Quat. Res.* 91 (1), 383–398. <https://doi.org/10.1017/qua.2018.68>.
- Kalabát, L., Negruţiu, A., Micu, I., Dogaru, A., Mihai, B., 1994. Distribution and ecology of brown bear in Romania. *Int. Conf. Bear. Res. Manag.* 9, 173–178.
- King, T., Andrews, P., Boz, B., 1999. Effect of taphonomic processes on dental microwear. *Am. J. Phys. Anthropol.* 108 (3), 359–373. [https://doi.org/10.1002/\(SICI\)1096-8644\(199903\)108:3<359::AID-AJPA10>3.0.CO;2-9](https://doi.org/10.1002/(SICI)1096-8644(199903)108:3<359::AID-AJPA10>3.0.CO;2-9).
- Kistchinski, A.A., 1972. Life history of the brown bear (*Ursus arctos* L.) in North-East Siberia. *Bears* 2, 67–73. <https://doi.org/10.2307/3872570>.
- 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. *Quat. Sci. Rev.* 131, 51–72. <https://doi.org/10.1016/j.quascirev.2015.10.028>.
- Krechmar, M.A., 1995. Geographical aspects of the feeding of the brown bear (*Ursus arctos* L.) in the extreme northeast of Siberia. *Russ. J. Ecol.* 26 (6), 436–443. <https://eurekamag.com/research/002/852/002852483.php>.
- Kurten, B., 1976. *The Cave Bear Story; Life and Death of a Vanished Animal*. Columbia University Press, 163 pp.
- Longin, R., 1971. New method of collagen extraction for radiocarbon dating. *Nature* 230 (5291), 241–242. <https://doi.org/10.1038/230241a0>.
- López-Alfaro, C., Robbins, C., Zedrosser, A., Nielsen, S., 2013. Energetics of hibernation and reproductive trade-offs in brown bears. *Ecol. Modell.* 270, 1–10. <https://doi.org/10.1016/j.ecolmodel.2013.09.002>.
- Magri, D., Vendramin, G.G., Comps, B., Dupanloup, I., Geburek, T., Gömöry, D., Latawa, M., Litt, T., Paule, L., Roue, J.M., Tantau, I., van der Knaap, W.O., Petit, R.J., de Beaulieu, J.-L., 2006. A new scenario for the Quaternary history of European beech populations: palaeobotanical evidence and genetic consequences. *New Phytol.* 171 (1), 199–221. <https://doi.org/10.1111/j.1469-8137.2006.01740.x>.
- Magyar, E.K., Veres, D., Wennrich, V., Wagner, B., Braun, M., Jakab, G., Karátson, D., Pál, Z., Ferenczy, G., St-Onge, G., Rethemeyer, J., François, J.P., von Reumont, F., Schäbitz, F., 2014. Vegetation and environmental responses to climate forcing during the Last Glacial Maximum and deglaciation in the East Carpathians: attenuated response to maximum cooling and increased biomass burning. *Quat. Sci. Rev.* 106, 278–298. <https://doi.org/10.1016/j.quascirev.2014.09.015>.
- Marciszak, A., Stefaniak, K., Mackiewicz, P., Rduski, B., 2015. *Ursus arctos* L., 1758 from Bukovynka Cave (W Ukraine) in an overview on the fossil brown bears size variability based on cranial material. *Quat. Int.* 357, 136–148. <https://doi.org/10.1016/j.quaint.2014.09.052>.
- Mattson, D.J., 1998. Diet and morphology of extant and recently extinct northern bears. *Ursus* 10, 479–496. <https://www.jstor.org/stable/3873160>.
- Micó, C., Blasco, R., Muñoz Del Pozo, A., Jiménez-García, B., Rosell, J., Rivals, F., in press. Differentiating taphonomic features from trampling and dietary microwear, an experimental approach. *Hist. Biol.* 10.1080/08912963.2023.2184690.
- Mirea, I.-C., Robu, M., Petculescu, A., Kenez, M., Faur, L., Arghir, R., Tecsă, V., Timar-Gabor, A., Roban, R.-D., Panaiotu, C.G., Sharifi, A., Pourmand, A., Codrea, V.A., Constantin, S., 2021. Last deglaciation flooding events in the Southern Carpathians as revealed by the study of cave deposits from Muieril or Cave, Romania. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 562, 110084. <https://doi.org/10.1016/j.palaeo.2020.110084>.
- Mowat, G., Heard, D., 2011. Major components of grizzly bear diet across North America. *Can. J. Zool.* 84, 473–489. <https://doi.org/10.1139/z06-016>.
- Münzel, S.C., Conard, N., 2004. Cave bear hunting in the Hölle Fels, a cave site in the Ach Valley, Swabian Jura. *Rev. Paléobiol.* 23, 877–885.
- Münzel, S.C., Stiller, M., Hofreiter, M., Mittnik, A., Conard, N.J., Bocherens, H., 2011. Pleistocene bears in the Swabian Jura (Germany): genetic replacement, ecological displacement, extinctions and survival. *Quat. Int.* 245 (2), 225–237. <https://doi.org/10.1016/j.quaint.2011.03.060>.
- 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. *Quat. Int.* 339–340, 148–163. <https://doi.org/10.1016/j.quaint.2013.10.020>.
- Naito, Y., Germonpré, M., Chikaraishi, Y., Ohkouchi, N., Drucker, K., Hobson, K., Edwards, M., 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. *J. Quat. Sci.* 31, 598–606. <https://doi.org/10.1002/jqs.2883>.
- Naito, Y., Meleg, I.N., Robu, M., Vlaicu, M., Drucker, D.G., Wissing, C., Hofreiter, M., Barlow, A., Bocherens, H., 2020. Heavy reliance on plants for Romanian cave bears

- evidenced by amino acid nitrogen isotope analysis. *Sci. Rep.* 10, 6612. <https://doi.org/10.1038/s41598-020-62990-0>.
- Nelson, D.E., Angerbjörn, A., Lidén, K., Turk, I., 1998. Stable isotopes and the metabolism of the European cave bear. *Oecologia*. 116 (1), 177–181. <https://doi.org/10.1007/s004420050577>.
- Ogurtsov, S., 2018. The diet of the brown bear (*Ursus arctos*) in the Central Forest Nature Reserve (West-European Russia), based on scat analysis data. *Biol. Bull.* 45, 1039–1054. <https://doi.org/10.1134/S1062359018090145>.
- Pacher, M., Stuart, A.J., 2009. Extinction chronology and palaeobiology of the cave bear (*Ursus spelaeus*). *Boreas*. 38 (2), 189–206. <https://doi.org/10.1111/j.1502-3885.2008.00071.x>.
- Pappa, S., 2016. Palaeoecology and Palaeodiet: Reconstructing Adaptations in the Middle and Late Pleistocene Ursidae through Dental Microwear and Geochemistry. PhD thesis. Royal Holloway University of London.
- Pappa, S., Schreve, D.C., Rivals, F., 2019. The bear necessities: a new dental microwear database for the interpretation of palaeodiet in fossil Ursidae. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 514, 168–188. <https://doi.org/10.1016/j.palaeo.2018.10.015>.
- Paralikiadis, N.P., Papageorgiou, N.K., Kotsiotis, V.J., Tsiompanoudis, A.C., 2010. The dietary habits of the brown bear (*Ursus arctos*) in western Greece. *Mamm. Biol.* 75 (1), 29–35. <https://doi.org/10.1016/j.mambio.2009.03.010>.
- Peigné, S., Goillot, C., Germonpré, M., Blondel, C., Bignon, O., Merceron, G., 2009. Predomancy omnivory in European cave bears evidenced by a dental microwear analysis of *Ursus spelaeus* from Goyet, Belgium. *Proc. Natl. Acad. Sci.* 106 (36), 15390–15393. <https://doi.org/10.1073/pnas.0907373106>.
- Pérez-Ramos, A., Kupezik, K., Van Heteren, A.H., Rabeder, G., Grandal-D'Anglade, A., Pastor, F.J., Serrano, F.J., Figueirido, B., 2019. A three-dimensional analysis of tooth-root morphology in living bears and implications for feeding behaviour in the extinct cave bear. *Hist. Biol.* 31 (4), 461–473. <https://doi.org/10.1080/08912963.2018.1525366>.
- Persson, I., Wikan, S., Swenson, J., Mysterud, I., 2001. The diet of the brown bear *Ursus arctos* in the Pasvik Valley northeastern Norway. *Wildl. Biol.* 7, 27–37. <https://doi.org/10.2981/wlb.2001.006>.
- Pinto-Illona, A.C., 2013. Microwear and occlusal microwear on teeth of cave bears *Ursus spelaeus* and brown bears *Ursus arctos*: Inferences concerning diet. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 370, 41–50. <https://doi.org/10.1016/j.palaeo.2012.11.017>.
- Piotrowska, N., Goslar, T., 2002. Preparation of bone samples in the Gliwice Radiocarbon Laboratory for AMS radiocarbon dating. *Isot. Environ. Health Stud.* 38 (4), 267–275. <https://doi.org/10.1080/10256010208033272>.
- Raine, R.M., Kansas, J.L., 1990. Black bear seasonal food habits and distribution by elevation in Banff National Park, Alberta. *Bears* 8, 297–304. <https://doi.org/10.2307/3872932>.
- Ramírez-Pedraza, I., Tornero, C., Pappa, S., Talamo, S., Salazar-García, D.C., Blasco, R., Rosell, J., Rivals, F., 2019. Microwear and isotopic analyses on cave bear remains from Toll Cave reveal both short-term and long-term dietary habits. *Sci. Rep.* 9 (1), 5716. <https://doi.org/10.1038/s41598-019-42152-7>.
- Ramírez-Pedraza, I., Pappa, S., Blasco, R., Arilla, M., Rosell, J., Millán, F., Maroto, J., Soler, J., Soler, N., Rivals, F., 2020. Dietary habits of the cave bear from the Late Pleistocene in the northeast of the Iberian Peninsula. *Quat. Int.* 557, 63–69. <https://doi.org/10.1016/j.quaint.2019.09.043>.
- Ramírez-Pedraza, I., Baryshnikov, G.F., Prilepskaya, N.E., Belyaev, R.I., Pappa, S., Rivals, F., 2022. Palaeodiet and niche partitioning among the easternmost European cave bears based on tooth wear analysis. *Hist. Biol.* 34 (6), 1063–1071. <https://doi.org/10.1080/08912963.2021.1960324>.
- Rasmussen, S.O., Bigler, M., Blockley, S.P., Blunier, T., Buchardt, S.L., Clausen, H.B., Cuijano, L., Dahl-Jensen, D., Johnsen, S.J., Fischer, H., Gkinis, V., Guillevic, M., Hoek, W.Z., Lowe, J.J., Pedro, J.B., Popp, T., Seierstad, I.K., Steffensen, J.P., Svensson, A.M., Vallelonga, P., Vinther, B.M., Walker, M., Wheatley, J.J., Winstrup, M., 2014. A stratigraphic framework for abrupt climatic changes during the Last Glacial period based on three synchronized Greenland ice-core records: refining and extending the INTIMATE event stratigraphy. *Quat. Sci. Rev.* 106, 14–28. <https://doi.org/10.1016/j.quascirev.2014.09.007>.
- Reimer, P.J., Bard, E., Bayliss, A., Beck, J.W., Blackwell, P.G., Ramsey, C.B., Buck, C.E., Cheng, H., Edwards, R.L., Friedrich, M., Grootes, P.M., Guilderson, T.P., Hafflidason, H., Hajdas, I., Hatté, C., Heaton, T.J., Hoffmann, D.L., Hogg, A.G., Hughen, K.A., Kaiser, K.F., Kromer, B., Manning, S.W., Niu, M., Reimer, R.W., Richards, D.A., Scott, E.M., Southon, J.R., Staff, R.A., Turney, C.S.M., van der Plicht, J., 2013. IntCal13 and Marine13 radiocarbon age calibration curves 0–50,000 years cal BP. *Radiocarbon*. 55 (4), 1869–1887. https://doi.org/10.2458/azu_js_rc.55.16947.
- Reimer, P.J., Austin, W.E.N., Bard, E., Bayliss, A., Blackwell, P.G., Bronk Ramsey, C., Butzin, M., Cheng, H., Edwards, R.L., Friedrich, M., Grootes, P.M., Guilderson, T.P., Hajdas, I., Heaton, T.J., Hogg, A.G., Hughen, K.A., Kromer, B., Manning, S.W., Muscheler, R., Palmer, J.G., Pearson, C., van der Plicht, J., Reimer, R.W., Richards, D.A., Scott, E.M., Southon, J.R., Turney, C.S.M., Wacker, L., Adolphi, F., Büntgen, U., Capano, M., Fahrni, S., Fogtmann-Schulz, A., Friedrich, R., Köhler, P., Kudsk, S., Miyake, F., Olsen, J., Reinig, F., Sakamoto, M., Sookdeo, A., Talamo, S., 2020. The IntCal20 northern hemisphere radiocarbon age calibration curve (0–55 cal kBP). *Radiocarbon*. 62 (4), 725–757. <https://doi.org/10.1017/RDC.2020.41>.
- Richards, M.P., Pacher, M., Stiller, M., Quilès, 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. *Proc. Natl. Acad. Sci.* 105 (2), 600–604. <https://doi.org/10.1073/pnas.0711063105>.
- Rigg, R., Gorman, M., 2005. Diet of brown bears (*Ursus arctos*): new results from the Tatras region and a comparison of research methods. *Výskum a Ochrana Cievcov Na Slovensku* 7, 61–79.
- Rivals, F., Solounias, N., Mithlacher, M.C., 2007. Evidence for geographic variation in the diets of Late Pleistocene and Early Holocene bison in North America, and differences from the diets of recent bison. *Quat. Res.* 68 (3), 338–346. <https://doi.org/10.1016/j.yqres.2007.07.012>.
- Rivals, F., Baryshnikov, G.F., Prilepskaya, N.E., Belyaev, R.I., 2022. Diet and ecological niches of the Late Pleistocene hyenas *Crocuta spelaea* and *C. ultima ussuriica* based on a study of tooth microwear. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 601, 111125. <https://doi.org/10.1016/j.palaeo.2022.111125>.
- Robu, M., 2015. The Palaeontology of the Cave Bear Bone Assemblage from Urșilor Cave of Chișcău – Osteometry, Palaeoichnology, Taphonomy, and Stable Isotopes. PhD thesis. Editura Universităţii, Bucureşti, p. 248. ISBN 978-606-28-0400-8.
- Robu, M., 2016a. Fossil population structure and mortality analysis of the cave bears from Urșilor Cave, North-Western Romania. *Acta Palaeontol. Pol.* 61 (2), 469–476. <https://doi.org/10.4202/app.00201.2015>.
- Robu, M., 2016b. Age re-assessment of the cave bear assemblage from Urșilor Cave, North-Western Romania. *Int. J. Speleol.* 45 (2), 123–133. <https://doi.org/10.5038/1827-806X.45.2.1947>.
- 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*). *Can. J. Zool.* 91 (4), 227–234. <https://doi.org/10.1139/cjz-2012-0222>.
- Robu, M., Wynn, J.G., Mirea, I.C., Petculescu, A., Kenes, M., Pușcas, C.M., Vlaicu, M., Trinkaus, E., Constantin, S., 2018. The diverse dietary profiles of MIS 3 cave bears from the Romanian Carpathians: insights from stable isotope ($\delta^{13}\text{C}$ and $\delta^{15}\text{N}$) analysis. *Palaeontology*. 61 (2), 209–219. <https://doi.org/10.1111/pala.12338>.
- RStudio Team, 2021. RStudio: Integrated Development Environment for R. <http://www.rstudio.com/>.
- Sánchez Goñi, M.F., 2022. The climatic and environmental context of the Late Pleistocene. In: Romagnoli, F., Rivals, F., Benazzi, S. (Eds.), *Updating Neanderthals: Understanding behavioural complexity in the Late Middle Palaeolithic*. Academic Press, pp. 17–38. <https://doi.org/10.1016/B978-0-12-821428-2.00017-2>.
- Sempebre, G.M., Godfrey, L.R., Solounias, N., Sutherland, M.R., Jungers, W.L., 2004. Can low-magnification stereomicroscopy reveal diet? *J. Hum. Evol.* 47 (3), 115–144. <https://doi.org/10.1016/j.jhevol.2004.06.004>.
- Slobodyan, A.A., 1976. The European brown bear in the Carpathians. *Bears* 3, 313–319. <https://doi.org/10.2307/3872781>.
- Solounias, N., Sempebre, G., 2002. Advances in the reconstruction of ungulate ecomorphology with application to early fossil equids. *Am. Mus. Novit.* 3366, 1–49. [https://doi.org/10.1206/0003-0082\(2002\)366<0001:AITROU>2.0.CO;2](https://doi.org/10.1206/0003-0082(2002)366<0001:AITROU>2.0.CO;2).
- Sommer, R., Bencke, N., 2005. The recolonization of Europe by brown bears *Ursus arctos* Linnaeus, 1758 after the Last Glacial Maximum. *Mammal Rev.* 35, 156–164. <https://doi.org/10.1111/j.1365-2907.2005.00063.x>.
- Sommer, R., Nadachowski, A., 2006. Glacial refugia of mammals in Europe: evidence from fossil records. *Mammal Rev.* 36 (4), 251–265. <https://doi.org/10.1111/j.1365-2907.2006.00093.x>.
- Soofi, M., Qashqaei, A., Aryal, A., Coogan, S., 2017. Autumn food habits of brown bear *Ursus arctos* in the Golestan National Park: a pilot study in Iran. *Mammalia*. 82. <https://doi.org/10.1515/mammalia-2016-0051>.
- Stenseth, N.E., Lutra, P., Bjørndal, V., Dahle, B., Fossum, K., Jørgved, P., Johansen, T., Neumann, W., Opseth, O., Rønning, O., Steyaert, S., Zedrosser, A., Brunberg, S., Swenson, J., 2016. Seasonal and annual variation in the diet of brown bears (*Ursus arctos*) in the boreal forest of southern Sweden. *Wildl. Biol.* 22, 107–116. <https://doi.org/10.2981/wlb.00194>.
- Stiller, M., Baryshnikov, G., Bocherens, H., Grandal D'Anglade, A., Hilpert, B., Münzel, S. C., Pinhasi, R., Rabeder, G., Rosendahl, W., Trinkaus, E., Hofreiter, M., Knapp, M., 2010. Withering away-25,000 years of genetic decline preceded cave bear extinction. *Mol. Biol. Evol.* 27 (5), 975–978. <https://doi.org/10.1093/molbev/msq083>.
- Štofik, J., Merganič, J., Merganičová, K., Saniga, M., 2013. Seasonal changes in food composition of the brown bear (*Ursus arctos*) from the edge of its occurrence - Eastern Carpathians (Slovakia). *Folia Zool.* 62 (3), 222–231. <https://doi.org/10.25225/fozo.v62.i3.a8.2013>.
- Stuart, A., Lister, A., 2011. Extinction chronology of the cave lion *Panthera spelaea*. *Quat. Sci. Rev.* 30, 2329–2340. <https://doi.org/10.1016/j.quascirev.2010.04.023>.
- Stuart, A., Lister, A., 2012. Extinction chronology of the woolly rhinoceros *Coelodonta antiquitatis* in the context of late Quaternary megafaunal extinctions in northern Eurasia. *Quat. Sci. Rev.* 51, 1–17.
- Terlato, G., Bocherens, H., Romandini, M., Nannini, N., Hobson, K.A., Peresani, M., 2019. Chronological and isotopic data support a revision for the timing of cave bear extinction in Mediterranean Europe. *Hist. Biol.* 31 (4), 474–484. <https://doi.org/10.1080/08912963.2018.1448395>.
- Terzea, E., 1966. Particularități morfologice ale ursului de peșteră și răspândirea sa pe teritoriul României, 5. Lucrările Institutului de Speologie "Emil Racoviță", pp. 195–233.
- Trinkaus, E., Constantin, S., Zilhão, J., 2013. *Life and Death at the Peștera cu Oase: A Setting for Modern Human Emergence in Europe*. Oxford University Press, p. 431.
- Tzedakis, C., Emerson, B., Hewitt, G.M., 2013. Cryptic or mystic? Glacial tree refugia in northern Europe. *Trends Ecol. Evol.* 28, 696–704. <https://doi.org/10.1016/j.tree.2013.09.001>.
- Ungar, P.S., Teaford, M.F., 1996. Preliminary examination of non-occlusal dental microwear in anthropoids: implications for the study of fossil primates. *Am. J. Phys. Anthropol.* 100 (1), 101–113. [https://doi.org/10.1002/\(SICI\)1096-8644\(199605\)100:1<101::AID-AJPA10>3.0.CO;2-4](https://doi.org/10.1002/(SICI)1096-8644(199605)100:1<101::AID-AJPA10>3.0.CO;2-4).

- Uzunidis, A., Pineda, A., Jiménez-Manchón, S., Xafis, A., Ollivier, V., Rivals, F., 2021. The impact of sediment abrasion on tooth microwear analysis: an experimental study. *Archaeol. Anthropol. Sci.* 13 (8), 134. <https://doi.org/10.1007/s12520-021-01382-5>.
- Van Klinken, G.J., 1999. Bone collagen quality indicators for palaeodietary and radiocarbon measurements. *J. Archaeol. Sci.* 26 (6), 687–695. <https://doi.org/10.1006/jasc.1998.0385>.
- Varela, S., Lobo, J.M., Rodríguez, J., Batra, P., 2010. Were the Late Pleistocene climatic changes responsible for the disappearance of the European spotted hyena populations? Hindcasting a species geographic distribution across time. *Quat. Sci. Rev.* 29 (17), 2027–2035. <https://doi.org/10.1016/j.quascirev.2010.04.017>.
- Vereschagin, N.K., 1976. The brown bear in Eurasia, particularly the Soviet Union. *Bears* 3, 327–335. <https://doi.org/10.2307/3872784>.
- Vila-Taboada, M., Fernández-Mosquera, D., González, F., Grandal-d'Anglade, A., Vidal-Romani, J.R., 1999. Palaeoecological implications inferred from stable isotopic signatures ($\delta^{13}\text{C}$, $\delta^{15}\text{N}$) in bone collagen of *Ursus spelaeus*. *ROS-HEIN. Cuadernos Do Laboratorio Xeolóxico de Laxe* 24, 73–87.
- Vlachos, C., Bakaloudis, D., Dimitriou, K., Chouvardas, D., 2000. Seasonal food habits of the European brown bear (*Ursus arctos*) in the Pindos Mountains, Western Greece. *Folia Zool.* 49 (1), 19–25.
- Welch, C.A., Keay, J., Kendall, K.C., Robbins, C.T., 1997. Constraints on frugivory by bears. *Ecology* 78 (4), 1105–1119. <https://doi.org/10.2307/2265862>.
- Wiegand, T., Naves, J., Garbulsky, M.F., Fernández, N., 2008. Animal habitat quality and ecosystem functioning: exploring seasonal patterns using NDVI. *Ecol. Monogr.* 78 (1), 87–103. <http://www.jstor.org/stable/27646120>.
- Williams, F.L., Geissler, E., 2014. Reconstructing the diet and paleoecology of Mio-Pleistocene *Cercopithecoides williamsi* from Sterkfontein, South Africa. *PALAIOS* 29 (9), 483–494. <https://doi.org/10.2110/palao.2014.046>.
- Wohlfarth, B., Veres, D., Ampel, L., Lacourse, T., Blaauw, M., Preusser, F., Andrieu-Ponel, V., Kéravis, D., Lallier-Vergès, E., Björck, S., Davies, S.M., de Beaulieu, J.-L., Risberg, J., Hormes, A., Kasper, H.U., Possnert, G., Reille, M., Thouveny, N., Zander, A., 2008. Rapid ecosystem response to abrupt climate changes during the last glacial period in western Europe, 40–16 ka. *Geology* 36 (5), 407–410. <https://doi.org/10.1130/G24600A.1>.
- Xafis, A., Nagel, D., Bastl, K., 2017. Which tooth to sample? A methodological study of the utility of premolar/non-carnassial teeth in the microwear analysis of mammals. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 487, 229–240. <https://doi.org/10.1016/j.palaeo.2017.09.003>.

**A.1.2 Article 2 titled “*Dental microwear analysis of Kudaro cave bears: Insights into dietary evolution from the Middle to Late Pleistocene*”
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Dental microwear analysis of Kudaro cave bears: Insights into dietary evolution from the Middle to Late Pleistocene

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ABSTRACT

The dietary changes of early cave bear populations from the Middle to Late Pleistocene are poorly understood. In this study, we analysed 60 m1 through dental microwear analysis of three diachronic Middle (*Ursus praekudarensis* and *U. praekudarensis/kudarensis*) to Late Pleistocene (*U. kudarensis*) populations inhabiting the Kudaro 1 and Kudaro 3 caves in the Southern Caucasus. The diet of all populations was inferred to be omnivorous, although it changed over time, adapting to the climatic and ecological conditions of the period. Bones from *U. praekudarensis/kudarensis* populations accumulated throughout the year; thus, microwear suggests an average annual diet dominated by plant resources. The widespread presence of hypercoarse scratches in *U. kudarensis* and *U. praekudarensis* populations suggests animal protein intake during the hyperphagia. The presence of omnivorous guild competitors and harsh conditions in a high-altitude environment could have driven the Caucasian cave bears to consume animal protein as a fallback diet during their predormancy period. Furthermore, the cave bears' capacity for dietary flexibility through time highlights the ability of cave bears to withstand climatic changes, while competition with other omnivorous species could have driven their dietary niche during their hyperphagia period towards animal protein consumption throughout the Middle to Late Pleistocene.

1. Introduction

The latest studies revealing the feeding patterns of cave bears in different regions of Eurasia were carried out using stable isotope analysis (e.g. Bocherens, 2019; Kosintsev et al., 2023, 2024) and dental microwear analysis (e.g. Peigné and Merceron, 2017; Ramírez-Pedraza et al., 2022; Duñó-Iglesias et al., 2024). These studies predominantly concern Late Pleistocene cave bears: *Ursus spelaeus* (Rosenmüller, 1794) in Western Europe, *U. ingressus* (Rabeder et al., 2004) in Central and Eastern Europe, *U. kanivetz* (Vereschagin, 1976) and *U. rossicus* (Borissiak, 1930, and including *U. uralensis* Vereschagin, 1973) in the Ural Mountains. Researchers have shown that, with some regional deviations, these animals consumed mainly plant foods, including abrasive items, which caused increased wear on the chewing surface of their molars (Bocherens et al., 2014a; Ramírez-Pedraza et al., 2022). Occasionally, cave bears have been shown to be omnivores (Peigné et al.,

2009; Duñó-Iglesias et al., 2024). Taphonomic data suggest that cave bears may have been facultative scavengers (Rabal-Garcés et al., 2012). The diet of cave bears from the Middle Pleistocene (which include several species, including *U. deningeri*, von Reichenau, 1904, in Western Europe; and *U. kudarensis*, Baryshnikov, 1985, and *U. praekudarensis*, Baryshnikov, 1998, in the Southern Caucasus) remains poorly known.

Initially, it was believed that Kudaro cave bears were represented by two stratigraphic subspecies that succeeded each other over time: *U. kudarensis praekudarensis*, which includes fossil remains from the Middle Pleistocene layer 5 in Kudaro 1 cave, and *U. k. kudarensis*, which includes remains from Late Pleistocene layers 3 and 4 in both caves. These taxa may be differentiated by the frequency of the occurrence of cheek tooth morphotypes (Fig. 1). The sample from Middle Pleistocene layer 5 in Kudaro 3 cave had an intermediate position and it was designated as *U. praekudarensis/kudarensis* (Baryshnikov, 1998, 2020a).

Morphological characteristics seem to suggest successive changes in

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the dental system of Kudaro bears. However, analysis of morphometric parameters with the use of univariate and multivariate statistics have revealed a more complex evolutionary variability, which does not show a general trend in the transformation of bear teeth (Baryshnikov and Puzachenko, 2020). New insights into the evolution of Kudaro cave bears have been provided by studying their molecular genetic characteristics, including those obtained from a sample from the lowest stratigraphic level in Kudaro 1 cave (Barlow et al., 2021). Palaeogenomic data have confirmed differences between *U. praekudarensis* and *U. kudarensis* and showed these taxa split about 500 kyr B.P., that is, much earlier than bone material began to accumulate in the cave deposits. Consequently, the taxa can be considered as two independent species that occupied Kudaro caves at different times.

The excavated sediments contain stone artifacts from the late Acheulean industry in layer 5 in Kudaro 1 cave and the Mousterian industry in layers 3 and 4 in both caves (Lioubine, 1989). Cementum increment analysis indicates that Caucasian cave bears visited and died in the caves during MIS 3 year-round (Prilepskaya et al., 2022). Notably, numerous salmon bones were found there, which is unusual for Early and Middle Palaeolithic sites. Their accumulation has been associated with human activity, since the assemblage of fish skeletal elements appears in Neolithic settlements (Tsepkin, 1980). Baryshnikov (1999) suggested another process of accumulation of salmon bones in which hominins, cave bears, and large birds could have participated. To test this hypothesis, stable isotope analysis was carried out on bone samples from the upper layers. It did not detect salmon in the diet of the cave bear, but showed that Kudaro cave bears consumed mainly plant food and might have travelled higher into the mountains to alpine meadows in the summer (Bocherens et al., 2014b).

The aim of this work is to determine the short-term feeding patterns of Caucasian cave bears through the study of their tooth microwear at different stratigraphic levels from the Middle to Late Pleistocene. These three different cave bear populations shared the same habitat, although at different times, and were therefore constrained by different environmental conditions. Therefore, their ecological context could explain their dietary behaviour at the time of death. Our interest is to see whether there are dietary differences between the three populations and, if so, whether these are related to general evolutionary trends or to the specific environments of each moment. To elucidate the short-term diet of these early cave bears, an extensive collection of *U. praekudarensis* and *U. kudarensis* teeth was examined (Fig. 2). This collection was recovered from the archaeological excavations of Palaeolithic sites in the Kudaro 1 and Kudaro 3 caves in South Ossetia.

2. Localities

Kudaro 1 cave and Kudaro 3 cave are situated in the Rioni River

basin on the southern slope of the Central Caucasus (with the following coordinates: 42° 31' N, 43° 38' E; Fig. 3). Both caves have a gallery-type structure and are located at an altitude of 1600 m a.s.l., with one lying directly beneath the other in the valley of the Dzhozdzori River near the village of Kvaisa in South Ossetia (Baryshnikov, 2011, 2020a).

The Palaeolithic sites at the Kudaro caves were excavated under the direction of Prof. V.P. Lioubine. The palaeontological collections analysed in this study are hosted and stored at the Zoological Institute of Russian Academy of Sciences in Saint Petersburg, Russia (ZIN).

The sampled individuals were obtained from the caves at Kudaro 1 and 3.

For Kudaro 1 six distinct stratigraphic levels were discerned within the eastern gallery (Lioubine and Bosinski, 1995; Fig. 4A). The uppermost layer 1, composed of black loam with sporadic angular stones and limestone blocks, displayed Eneolithic period artifacts as well as from later periods. Layer 2, consisting of yellow-grey loam with sharp-edged stones and large blocks, contained artifacts from the end-Palaeolithic and Mesolithic periods. Layers 3 and 4, which are composed of greyish loam sediment, displayed Middle Palaeolithic lithic tools. Layer 3a was dated by radiocarbon to 44 ± 2 kyr B.P. (Gr-6079) (Lioubine, 1998). Layer 5, characterised by a yellowish fuscous loam matrix and Acheulean artifacts, is subdivided into 5a, 5b (dated to 350 ± 70 kyr B.P. (RTL-373)), and 5c (Lioubine and Bosinski, 1995; Baryshnikov, 2011). The deepest horizon is layer 6, which was found to be sterile. The contact zone between Acheulean and Mousterian layers presents stratigraphic interruptions, likely caused by sediment erosion or periods of non-deposition during colder climatic phases (Lioubine and Bosinski, 1995; Baryshnikov, 1999).

From Kudaro 1, molars were sampled from layer 5c ($n = 20$ specimens; Fig. 2A) dated to 360 ± 90 kyr B.P. (RTL-379), from which Acheulean artifacts have been recovered (Lioubine, 1998). The layer, composed by 1 m of yellow-brownish loam, remains unaffected by any taphonomic processes, thus it is classified as undisturbed (Lioubine and Bosinski, 1995; Fig. 4A). This layer contains very diverse fauna, including several species of carnivorans, ungulates, and other mammals. These are classified within Likhvin faunas of Eastern Europe or within the Fontana Ranuccio fauna (MIS 11) from the late Galerian of Italy (Aleksieva, 1977; Azzaroli, 1983; Zastrowzhnov et al., 2018). Among the carnivorans, there are several felids, including leopard (*Panthera pardus*) and extinct jaguar (*Panthera gombaszogensis*). The canids are represented by red fox (*Vulpes vulpes*), Middle Pleistocene wolf (*Canis mosbachensis*), and Caucasian coyote (*Canis kudarensis*). The bear species present include Asian black bear (*Ursus thibetanus mediterraneus*) and *U. praekudarensis*. There are also different mustelids: European badger (*Meles meles*), beech marten (*Martes foina*), marbled polecat (*Vormela peregusna*), and least weasel (*Mustela nivalis*), as well as two porcupines, the large porcupine (*Hystrix cf. refossa*) and the small porcupine

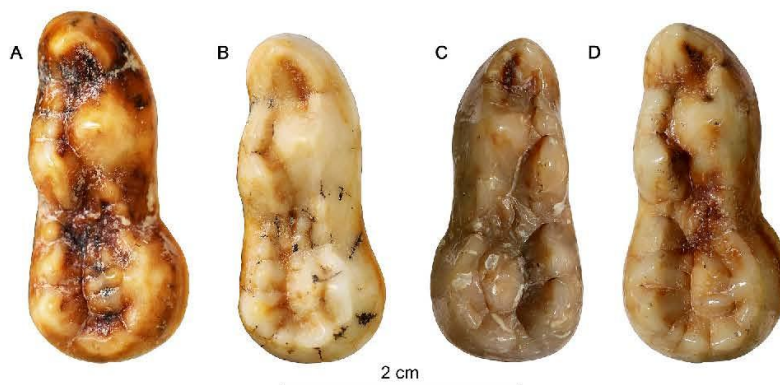


Fig. 1. Variation of the masticatory surface of m1 in cave bears from the Kudaro caves (top view). A–B: *Ursus praekudarensis*; C–D: *U. kudarensis*.

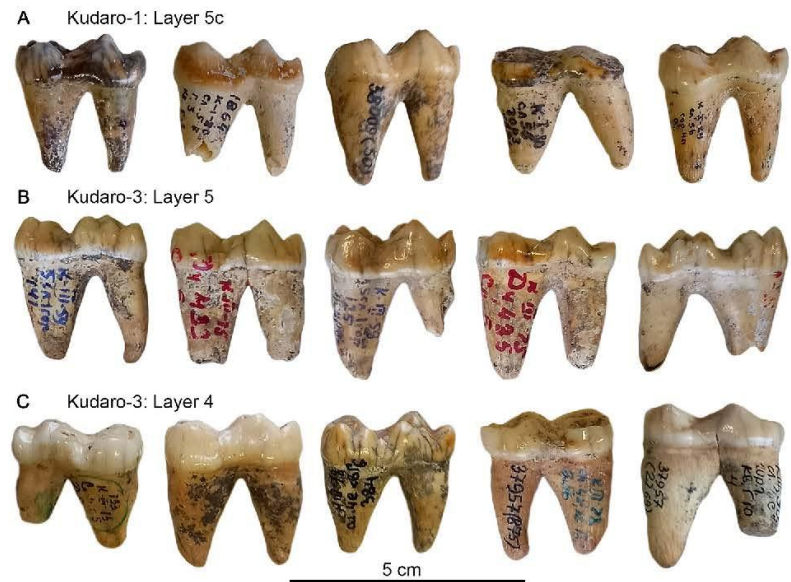


Fig. 2. Studied material. The first lower molar (m1) in cave bears from the Kudaro caves (side view). A: *Ursus praekudarensis*; B: *U. praekudarensis/kudarensis*; C: *U. kudarensis*.

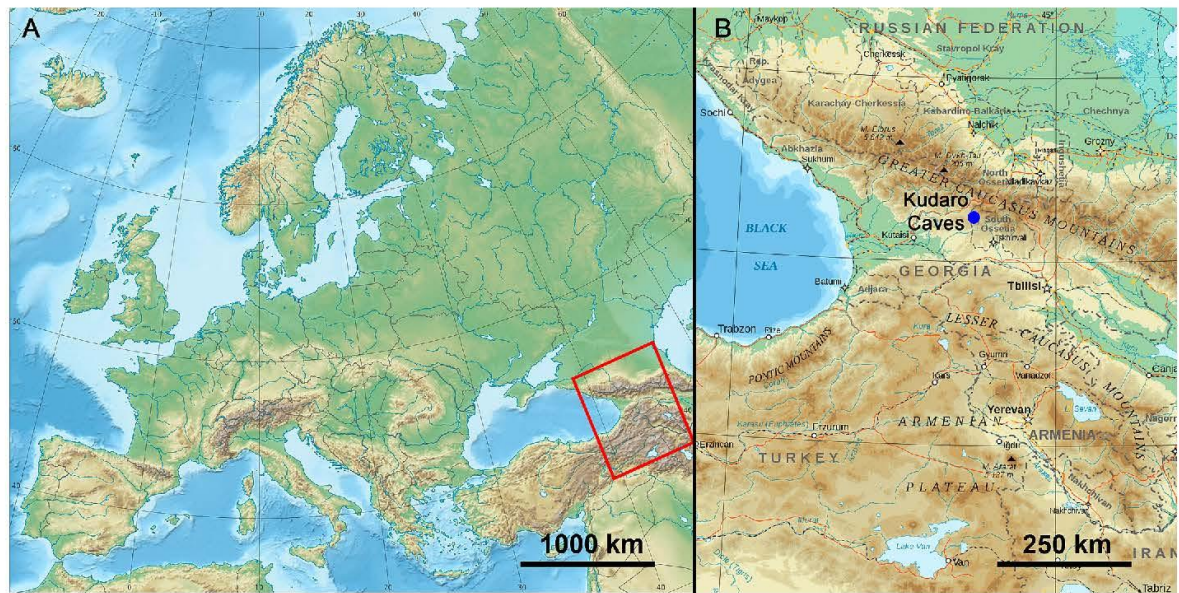


Fig. 3. Location of the Kudaro caves.

(*H. brachyura vinogradovi*). Artiodactyls are well-represented with several cervids: red deer (*Cervus elaphus*) and roe deer (*Capreolus capreolus*), along with extinct giant deer (*Megaloceros* sp.) and moose (*Alces alces*). Additionally, there are remains of bison (*Bison* sp.). Bovids are also found, including gazelle (*Gazella* sp.), West Caucasian tur (*Capra caucasica*), argali (*Ovis ammon antiqua*), and extinct tahr (*Hemitragus bonali*). At the very bottom of layer 5c giant muskox (*Praeovibos priscus*) and rhino (*Stephanorhinus hundsheimensis*) were found. Particularly interesting is the discovery of a macaque (*Macaca* sp.), the only one from

the Pleistocene of the Caucasus (Baryshnikov, 1999, 2002, 2020a). The presence of the Middle Pleistocene wolf, whose disappearance and transition to the grey wolf (*Canis lupus*) is now known to have occurred no later than 400 kyr B.P. (Iurino et al., 2022), along with the presence of thermophilous-adapted fauna (*Macaca* sp. and large and small porcupines) and the warm climatic conditions indicated by pollen analysis, situates layer 5c within the MIS 11 Interstadial (Baryshnikov, 2002; Lioubine, 2002; Nitychoruk et al., 2006).

The remaining specimens were recovered from two different layers

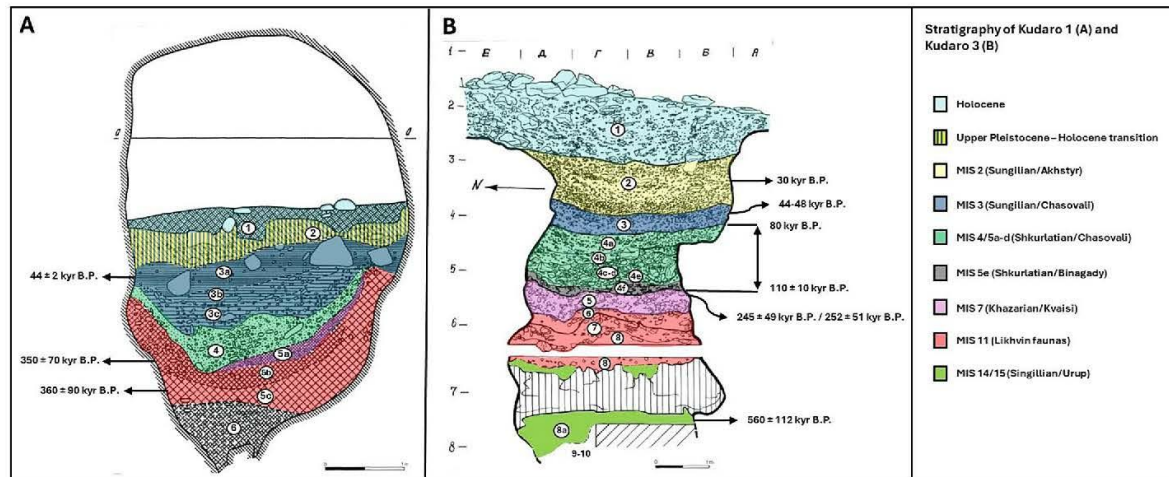


Fig. 4. Stratigraphic sequence of Kudaro 1 (A) and Kudaro 3 (B) caves, extracted and modified from Lioubine and Bosinski (1995). Chronology has been established based on thermoluminescence/uranium-thorium dating and biostratigraphy correlations (mammal age/faunal units) and further supported by pollen analysis (Cerdyncey et al., 1959; Lioubine and Bosinski, 1995; Lioubine, 1998, 2002; Baryshnikov, 1998, 2002).

of Kudaro 3. For Kudaro 3 section (O, – K, – M), ten levels were identified (Lioubine and Bosinski, 1995; Fig. 4B). Layer 1 consists of loam and debris accumulated during the Holocene. Layer 2, dated at around 30 kyr B.P. (Baryshnikov, 2002), is composed of grey to brownish loam with slope debris and large limestone blocks. Layer 3 and 4 contained Middle Palaeolithic artifacts. Layer 3 cave bear bones yielded three AMS radiocarbon dates of >41 kyr B.P. (OxA-19,611), 47 kyr B.P. (OxA-19,612) and 47 kyr B.P. (OxA-19,613), respectively.

Furthermore, Layers 5, 6, 7 and 8a (which basal layer was dated by thermoluminescence at 560 ± 112 kyr B.P.) contained Acheulean lithic tools (Lioubine and Bosinski, 1995). Layer 9, formed by compact clay, and layer 10, formed by yellow sandy loam, were found to be sterile. A study of the sediment dynamics found that Kudaro 3 was exposed to erosion dynamics which might explain the significant time-gap in the deposition between the Acheulean and Mousterian layers showed by RTL dates (Lioubine and Bosinski, 1995; Baryshnikov, 2011).

The two layers from which the studied materials were recovered are:

1) The Acheulean layer 5 ($n = 19$ specimens; Fig. 2B), which is composed by compact yellowish loam with rounded debris, has been dated by thermoluminescence to between 245 ± 49 kyr B.P. (RTL-534) and 252 ± 51 kyr B.P. (RTL-511) in the uppermost part (Lioubine and Bosinski, 1995; Lioubine, 1998; Fig. 4B). This layer is characterised by the presence of small porcupine (*H. brachyura vinogradovi*), *C. lupus*, *V. vulpes*, *U. thibetanus*, *U. praekudarensis/kudarensis*, *M. meles*, cave lion (*Panthera spelaea*), *P. pardus*, *C. capreolus*, *C. elaphus*, and *Bison* sp. Based on the fauna appearance, layer 5 in Kudaro 3 cave could be correlated with the MIS 7 thermochron as stated by Baryshnikov (2002). However, as the dating was performed on the uppermost part of the package, indicating a minimum age, and considering the wide range of error, this layer could be related to older interglacial periods (Baryshnikov, 1999). Nevertheless, the presence of clearly defined Khazarian faunas (equivalent to Aurelian faunas in Western Europe) distances it from older periods and situates it in a much younger chronology than layer 5c from Kudaro 1, which contained late Galerian faunas (Baryshnikov, 2002). More specifically, *Canis mosbachensis*, which appears in layer 5c, is succeeded in layer 5 (from Kudaro 3) by the later species, *Canis lupus* (Baryshnikov, 2002; Iurino et al., 2022). Furthermore, the structure of the upper incisors of the cave bears from layer 5 in Kudaro 3 cave is similar to *U. kudarensis* (Baryshnikov et al., 2019). Therefore, we can assume that the *U. praekudarensis/kudarensis* sample is represented by an early *U. kudarensis* population. The greater morphological similarity to

U. kudarensis compared to *U. praekudarensis* strengthens the idea that the *U. praekudarensis/kudarensis* accumulation occurred during MIS 7, rather than during older interglacials.

2) The Mousterian layer 4 ($n = 21$ specimens; Fig. 2C), composed by dark greyish loam with limestone fragments and debris, has been directly dated by two uranium-thorium dates on bone material, falling between 110 ± 10 kyr B.P. and 80 kyr B.P. (Cerdyncey et al., 1959; Lioubine and Bosinski, 1995; Fig. 4B). Hence, it is a transition period between the end of last interstadial 5e (Eemian), for basal layer 4f, and in between MIS substage 5a and beginning of MIS 4, for layers 4d to 4a. This layer is characterised by the presence of *U. thibetanus*, *U. kudarensis*, *C. capreolus*, *C. elaphus*, *Bison* sp., and *C. caucasica*. However, *U. thibetanus* appear only in the basal level 4f. Moreover, temperate and forest-related species such as red deer and roe deer predominate in the basal levels and are reduced through the sequence in favour of an increasing prevalence of the colder-adapted West Caucasian tur (Baryshnikov, 1999, 2002). A transition from a closed to a more open landscape is also observed in the pollen analysis of the layer (Lioubine, 2002).

3. Materials and Methods

Sixty lower first molars ($m1$; $n = 60$) were selected from a wide range of individuals, including juveniles, adults in their prime, and older adults of both sexes (Fig. 2). The inventory of specimens analysed – together with the raw data generated in this study – is available in Duñó-Iglesias (2024). For this study three populations were selected: *U. praekudarensis* (Kudaro 1 cave, layer 5c), *U. praekudarensis/kudarensis* (Kudaro 3 cave, layer 5), and *U. kudarensis* (Kudaro 3 cave, layer 4).

The occlusal surface of the teeth was cleaned using cotton swabs soaked in acetone and then 96% ethanol to remove traces of sediment, adhesive residues, or dust (Solounias and Semperebon, 2002; Ungar et al., 2003). High-precision moulds of the surface were made using polyvinylsiloxane silicone (Heraeus Provil novo, Light CD2, regular set) and a second layer using silicone putty was added to form the wall of the mould (Heraeus Provil novo, Putty). Finally, transparent high-resolution casts were produced using epoxy resin (CTS EPO150 resin+K151 hardener).

The casts were observed using a standard light stereomicroscope (Zeiss Stemi 2000C) at ×35 magnification to identify and quantify the microfeatures using an optical reticule of 0.16 mm² (Solounias and

Semprebon, 2002; Semprebon et al., 2004).

The non-faceted area of the grinding enamel surfaces of the m1 was chosen for the analysis as it provides the most reliable representation of the dietary patterns of ursid specimens when compared to other areas of the occlusal surface of the tooth (Ungar and Teaford, 1996; Münzel et al., 2014; Pappa, 2016; Pappa et al., 2019; Ramírez-Pedraza et al., 2019, 2020, 2022; Duñó-Iglesias et al., 2024). The deepest “valleys” in between the cusps were chosen, as being pointed, they were more protected from taphonomic alteration by sediment from post-depositional processes (i.e. trampling and sediment transport) in bunodont teeth (Uzunidis et al., 2021; Micó et al., 2024).

The features examined in this study include 1) the number of fine and coarse scratches – elongated and narrow features, which can be classified as either fine (characterised by narrow and shallow marks) or coarse (characterised by wider and deeper marks); and 2) the number of small and large pits: circular or semicircular shapes of similar length and width. They can be classified as either small pits, which are characterised by being shallow and appearing as shiny, bright, white dots, or large pits, which are wider and deeper, and reflect less light. The scratch width score (SWS) was assessed by assigning a score of 0 to enamel surfaces with predominantly fine scratches, a score of 1 to surfaces with a mixture of coarse and fine scratches, and a score of 2 to surfaces with predominantly coarse scratches. We also quantified the number of puncture pits (very deep and symmetrical crater-like morphology with regular edges), the number of gouges (crater-like but with irregular edges), and the presence of more than four hypercoarse scratches (very deep and wider than fine and coarse scratches, resulting in very low reflectivity and appearing as dark features, they have a distinctive “trench-like” shape with symmetrical edges) (Solounias and Semprebon, 2002).

Our findings were compared with the reference dataset of extant bear species established by Pappa et al. (2019) to reconstruct the palaeodiet of the fossil populations. The reference collection allowed us to directly compare extinct ursids with their closely related living counterparts, such as *U. arctos* (Linnaeus, 1758) from different regions including Kamchatka, Greece, Central Europe, Northern Europe, and North America, as well as *U. americanus* (Pallas, 1780) from North America. Both species show a wide range of dietary preferences, which include the consumption of vertebrates and invertebrates as well as a hard mast and soft mast diet. In addition, the hyper-carnivorous *U. maritimus* (Phipps, 1774) and the hyper-herbivorous *Ailuropoda melanoleuca* (David, 1869) were added to the comparison. Furthermore, the reference collection of *U. thibetanus* (Cuvier, 1823) was included in the comparison with the fossil populations, as this species is recorded in the same stratigraphic horizons where the studied *U. praekudarensis* (layer 5c from Kudaro 1) and *U. kudarensis* (layer 4f from Kudaro 3) molars were recovered, although not in the case of *U. praekudarensis/kudarensis* from layer 5 from Kudaro 3. Unfortunately, only one lower first molar (m1) of fossil *U. thibetanus* was recovered from the studied layers (Baryshnikov, 2010). Hence, this comparison aimed to detect possible ecological interactions between *U. thibetanus* diet and the fossil populations. To avoid the possibility of inter-observer error, a single observer (PDI) performed the analysis on all specimens.

Graphs were generated using the RStudio (version 4.1.2) software (R Studio Team, 2021). Three-dimensional scans of the same analysed area were obtained using a Sensofar® S Neox microscope powered by the SensoSCAN® 6.2 software at IPHES-CERCA (Tarragona, Spain). The molars were positioned under the microscope in different orientations, aiming to achieve flatness and optimal illumination in the analysed area, due to the different morphologies of the talonid grinding surface in cave bears (Baryshnikov and Puzachenko, 2020; Grandal-d'Anglade and López-González, 2005). Scans of the surface were generated with magnifications of 10× (in an area of 1.68 × 1.40 mm integrated into four fields of view) and 20× (in an area of 840.42 × 702.42 µm integrated into four fields of view), one or the other chosen depending on the size of the features to be observed.

4. Results

A total of 41 lower first molars of *U. praekudarensis* ($n = 15$), *U. praekudarensis/kudarensis* ($n = 14$), and *U. kudarensis* ($n = 12$) were suitable for the analysis. Hence, 19 specimens had to be excluded from the analysis, including the youngest individuals lacking wear facets (Rivals et al., 2007) and those with occlusal surface damage attributable to taphonomic processes (King et al., 1999; El-Zaatar, 2010; Uzunidis et al., 2021; Micó et al., 2024).

The microwear results from *U. praekudarensis*, *U. praekudarensis/kudarensis*, and *U. kudarensis* displayed differences between them (Table 1). Regarding the number of total scratches (NTS), *U. praekudarensis* displayed the lowest number (NTS = 14.07), while *U. praekudarensis/kudarensis* (NTS = 18.89) and *U. kudarensis* (NTS = 18.63) displayed similar averages. Furthermore, there was a prevalence of coarse scratches, which translates into a high scratch width score (SWS) for both *U. praekudarensis* (NFS = 5.67; NCS = 8.57; SWS = 1.53) and *U. kudarensis* (NFS = 7.46; NCS = 11.25; SWS = 1.75). Conversely, *U. praekudarensis/kudarensis* exhibited a prevalence of fine scratches (NFS = 17.36; NCS = 1.50) with a SWS of 0.

The presence of hypercoarse scratches was observed in all three samples (Fig. 5). Among *U. kudarensis* individuals, 83% displayed hypercoarse scratches, followed by 47% of *U. praekudarensis* specimens. In much lower proportions, 14% of the *U. praekudarensis/kudarensis* specimens displayed such hypercoarse scratches.

Concerning the total number of pits (NTP), the highest averages are exhibited by *U. praekudarensis* (NTP = 37.10) and *U. kudarensis* (NTP = 35.88), which closely resemble each other. In contrast, the lowest counts are exhibited by *U. praekudarensis/kudarensis* (NTP = 21.71), with notably lower counts than the other two populations. In all three populations, small pits (NSP) prevail in comparison to large pits (NLP): *U. praekudarensis* with NSP = 35.10; NLP = 2.00, *U. praekudarensis/kudarensis* with NSP = 20.93; NLP = 0.79, *U. kudarensis* with NSP = 33.38; NLP = 2.50. *U. kudarensis* exhibits the highest number of large pits (NLP = 2.50), closely followed by *U. praekudarensis* (NLP = 2.00), while *U. praekudarensis/kudarensis* displays the lowest number (NLP = 0.79). The three samples exhibited gouges, with the highest numbers observed in *U. kudarensis* (NG = 2.38), followed by *U. praekudarensis* (NG = 0.20) and *U. praekudarensis/kudarensis* (NG = 0.21). The highest number of puncture pits (NPP) were observed in *U. kudarensis*, with an average of 0.83 puncture pits per counting area. This was followed by *U. praekudarensis*, with an average of 0.40 puncture pits per counting area. In contrast, *U. praekudarensis/kudarensis* displayed no puncture pits.

4.1. Comparison with extant ursids

When compared to the extant bear populations (Table 1), *U. praekudarensis* presents the lowest number of total scratches (NTS = 14.07), closely followed by the *U. maritimus* with 14.23 scratches. *U. praekudarensis/kudarensis* (NTS = 18.89) and *U. kudarensis* (NTS = 18.63), also display a low number of total scratches compared to extant bears. Only *U. maritimus* and *U. americanus* (NTS = 16.12) present lower counts. The average of both fossil populations is comparable to that of *A. melanoleuca* (NTS = 19.25) and *U. arctos* from Northern Europe (NTS = 19.56). The scratch distribution for *U. praekudarensis* and *U. kudarensis* favours coarse scratches, which differs from that observed in extant bear populations. Furthermore, the SWS of both populations is the highest in comparison to extant bears, only surpassed by *U. maritimus* (SWS = 2.79). Conversely, the *U. praekudarensis/kudarensis* population exhibits a higher proportion of fine scratches in comparison to coarse scratches, with a SWS value of 0.

Regarding the total number of pits, *U. praekudarensis* (NTP = 37.10) and *U. kudarensis* (NTP = 35.88) exhibited high numbers that are comparable to that of *U. arctos* from Central Europe (NTP = 36.20). Conversely, *U. kudarensis/prækudarensis* exhibited a low number of pits, similar to that observed in *U. arctos* from Greece and *U. maritimus*.

Table 1

Comparison of the dental microwear results of the cave bear populations from the Kudaro caves, *U. praekudarensis* (Kudaro 1; layer 5c), *U. praekudarensis/kudarensis* (Kudaro 3; layer 5), and *U. kudarensis* (Kudaro 3; layer 4), with the reference dataset of extant bear species of *U. arctos*, *U. americanus*, *A. melanoleuca*, *U. maritimus*, and *U. thibetanus* established by Pappa et al. (2019). Abbreviations: *n* number of specimens, NFS number of fine scratches, NCS number of coarse scratches, NTS number of total scratches, SWS scratch width score, NLP number of large pits, NSP number of small pits, NPP number of puncture pits, NTP number of total pits, NG number of gouges, NHC% presence of hypercoarse scratches.

Species – (Location)	<i>N</i>	NFS	NCS	NTS	SWS	NLP	NSP	NPP	NTP	NG	NHC%
Extinct											
<i>U. praekudarensis</i>	15	5.67	8.57	14.07	1.53	2.00	35.10	0.40	37.10	0.20	47%
<i>U. praekudarensis/kudarensis</i>	14	17.36	1.50	18.89	0.00	0.79	20.93	0.00	21.71	0.21	14%
<i>U. kudarensis</i>	12	7.46	11.25	18.63	1.75	2.50	33.38	0.83	35.88	2.38	83%
Extant											
<i>U. americanus</i> (North America)	9	13.56	2.56	16.12	0.00	5.44	19.00	3.00	27.44	0.00	0%
<i>U. arctos</i> (Greece)	4	13.00	7.00	20.00	0.5	9.25	8.50	2.25	20.00	2.00	0%
<i>U. arctos</i> (Central Europe)	10	17.50	3.40	20.90	0.00	5.4	22.50	8.30	36.20	2.10	0%
<i>U. arctos</i> (North America)	8	18.25	3.00	21.25	0.00	6.75	18.38	3.25	28.38	0.25	0%
<i>U. arctos</i> (Kamchatka)	23	16.22	3.83	20.05	0.10	6.96	19.78	4.78	31.52	0.35	0%
<i>U. arctos</i> (Northern Europe)	9	15.78	3.78	19.56	0.00	6.44	23.33	2.67	32.44	0.22	0%
<i>A. melanoleuca</i>	4	19.25	0.00	19.25	0.00	8.50	46.25	0.00	54.75	0.00	0%
<i>U. maritimus</i>	13	11.00	3.21	14.23	2.79	4.50	16.21	0.07	20.15	0.00	100%
<i>U. thibetanus</i>	6	14.33	3.33	15.33	0.00	4.50	15.33	0.00	20.33	17.67	0%

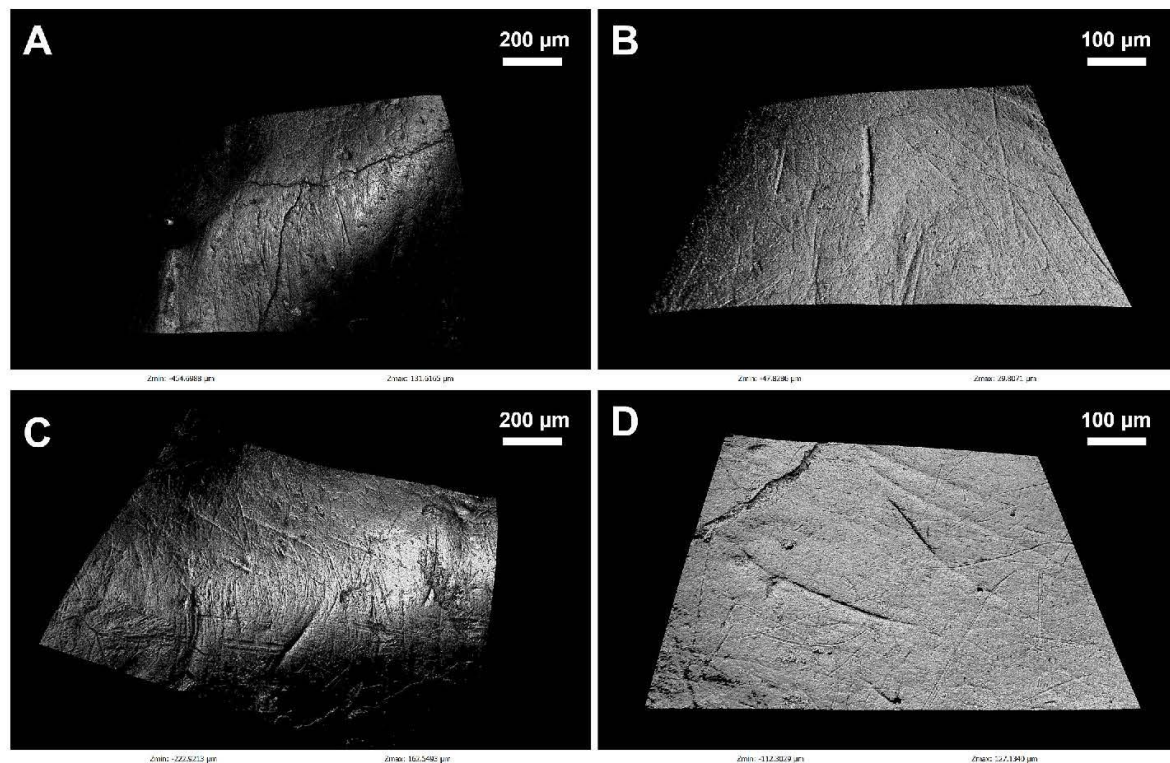


Fig. 5. Three-dimensional scans of the occlusal surface of the talonid of the lower first molar (m1) of different cave bear specimens from the Kudaro caves performed by a Sensofar® S Neox microscope. A: Surface topography (employing a $\times 10$ lens) of the occlusal surface of *U. kudarensis/praekudarensis* (ZIN 3758–1127) from Kudaro 3 layer 3, displaying both fine and coarse scratches, although with a predominance of fine scratches. Some gouges can also be observed. B: Surface topography (employing a $\times 20$ lens) of *U. praekudarensis* (ZIN 37957–1417) from Kudaro 1 layer 5c, displaying hypercoarse scratches in addition to coarse and fine scratches. C: Surface topography (employing a $\times 10$ lens) of *U. kudarensis* (ZIN 37954–37) from Kudaro 3 layer 4, showing a majority of coarse scratches compared to fine scratches. Additionally, two hypercoarse scratches, as well as multiple gouges, puncture pits, and large pits, can be observed. D: Surface topography (employing a $\times 20$ lens) of *U. praekudarensis* (ZIN 37998–83) from Kudaro 1 layer 5c, which displays two hypercoarse scratches.

Furthermore, *U. praekudarensis* and *U. kudarensis* displayed a very high number of small pits, only surpassed by *A. melanoleuca*, while the number of large pits were observed to be lower than that of extant specimens. *U. kudarensis* exhibited a number of gouges comparable to

that of *U. arctos* from Central Europe, although slightly higher. In contrast, *U. praekudarensis* and *U. kudarensis/praekudarensis* displayed a number of gouges similar to that of *U. arctos* from Northern Europe and North America. With regard to puncture pits (NPP), the *U.*

praekudarensis and *U. kudarensis* fossil populations displayed a relatively low number compared to extant species.

Finally, the hypercoarse scratches were observed in all fossil populations although with different percentages: *U. kudarensis*, HC = 83%; *U. praekudarensis*, HC = 47%; and *U. praekudarensis/kudarensis*, HC = 14%. These particular features are exclusively exhibited by the extant *U. maritimus*, which has a carnivorous diet of marine mammals, presenting them in all individuals of its sample (HC = 100%).

4.2. Bivariate analysis of number of total scratches and pits

The bivariate plot of the number of total pits (which includes the count of small and large pits as well as puncture pits) and the number of total scratches (accounting for the sum of fine and coarse scratches) shows that the three fossil populations' distribution closely relates them to dietary regimes of extant bear species (Fig. 6). The extant bear populations distribute themselves according to their main dietary preferences (omnivorous with a preference for soft mast, hard mast or vertebrates, and a pure herbivorous diet). The omnivorous bears, including *U. arctos* and *U. americanus*, are distributed across three different regions of the plot which can be related to their main dietary preferences. First, the soft mast-specialised *U. arctos* from Greece is positioned on the left side of the plot, with a low number of pits and a high number of scratches. Close to it, though with a slightly lower number of scratches, is *U. thibetanus*, which also has a predominantly plant-based diet. Second, *U. arctos* from northern latitudes with a higher proportion of vertebrates in their diet (from Northern Europe, North America, and Kamchatka) fall within the middle range of the plot. Third, *U. arctos* from Central Europe, with a hard mast diet, falls within the right side of the plot, accounting for a high number of total pits. Nevertheless, its range also overlaps with the vertebrate-dominated diet populations, due to its significant proportion of vertebrates in its diet. *U. maritimus* has a specialised marine mammal diet in an arctic landscape; therefore, with a lack of vegetation resources and a very soft diet that does not include rough plant items, it falls on the left side of the plot, with a number of total pits comparable to that of soft mast-dominated *U. arctos* from Greece. However, because *U. maritimus* inhabits a landscape lacking in vegetation, it presents a comparatively lower number of scratches, features that are directly related to a phytophagous diet

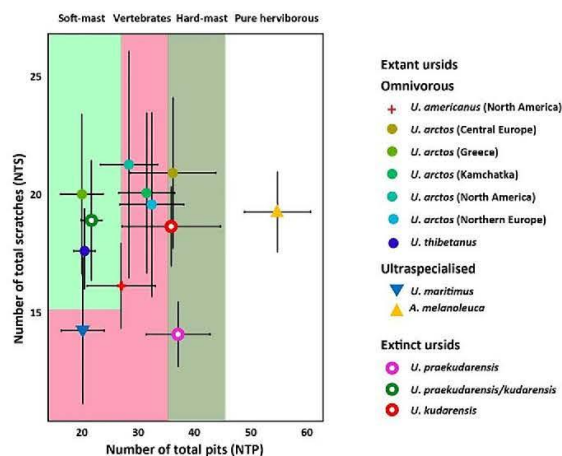


Fig. 6. Bivariate plot of the average number of total pits (NTP) and the number of total scratches (NTS) comparing the extant bear populations and the fossil populations. Error bars representing the standard deviation within the populations were added. Highlighted are four distinct eco-regions (soft mast, hard mast, vertebrates, and pure herbivorous) based on the predominant diet of extant bear populations as established by Pappa et al. (2019).

(Solounias and Sempere, 2002), and falls within the lower part of the plot.

U. americanus from Alaska, which inhabits a semi-arctic landscape and occasionally consumes vertebrates, particularly fish, falls between the vertebrate-dominated northern latitude populations and the soft mast-dominated population from Greece. Due to a low number of scratches, it falls not far from *U. maritimus*. Finally, *A. melanoleuca*, having an extremely hard and abrasive diet, based on bamboo, which is very rich in phytoliths, appears isolated in the rightmost of the plot due to the very high number of total pits (NTP = 54.75).

Regarding the fossil samples, *U. praekudarensis* and *U. kudarensis*, due to their high total number of pits, fall within the hard mast-dominated diet area, comparable to that of *U. arctos* from Central Europe. The variability ranges of *U. kudarensis* also overlap with those of omnivorous bear species of northern latitudes, including both hard and soft mast, although with a higher proportion of vertebrates in their diet. As for *U. praekudarensis*, while also partially falling within the range of omnivorous bears that include vertebrates, due to its low number of total scratches, it plots at the same height on the graph as *U. maritimus*, albeit with a much higher proportion of total pits. Finally, concerning *U. praekudarensis/kudarensis*, it is situated within the soft mast-dominated region, close to *U. arctos* from Greece, due to its low number of total pits. However, the extant *U. arctos* population from Greece presents a slightly higher total number of scratches.

4.3. Correspondence analysis

4.3.1. Dietary inference

To illustrate the distribution and variability of the studied populations, a correspondence analysis (CA) was conducted. The analysis incorporated seven microwear variables, namely small pits, large pits, fine scratches, coarse scratches, SWS, gouges, and puncture pits. The microwear signal of the fossil samples was compared with a reference dataset. The results for the first two dimensions (i.e. Dim 1 and Dim 2), which exhibited 44.6% and 22.4% of variance respectively, were utilised and plotted (Fig. 7).

The CA reveals that the extant omnivorous bear populations, including *U. arctos* and *U. americanus*, exhibit a similar distribution pattern. However, hard mast-dominated populations, primarily represented by *U. arctos* from Central Europe, tend to be distributed in the upper-right part of the plot due to their higher presence of puncture pits, gouges, and large pits. Omnivorous populations from northern latitudes with a high component of vertebrates and soft mast items in their diet, such as *U. arctos* from Northern Europe and *U. americanus* from Alaska, are situated around and under the Dim 1 axis, hence in the middle to lower part of the clustering due to their predominance of small pits and fine scratches. Furthermore, bears with highly variable omnivorous diets, including hard and soft mast as well as vertebrates and invertebrates, are distributed vertically along the omnivore bears' grouping (i.e. *U. arctos* from Kamchatka and *U. arctos* from North America).

The *U. arctos* population from Greece stands out as a significant outlier, due to its Mediterranean latitude specialised soft mast diet, which positions it alone in the upper part of the plot. This unique placement is due to its distinct characteristics. Having the lower number of small pits and the highest number of large pits makes it fall within a higher position in comparison to the other omnivorous ursids. Moreover, its high number of coarse scratches in comparison to the other omnivorous bear species positions it in the central part of the plot.

Finally, it can be observed that the highly specialised bear species, the hypercarnivore *U. maritimus* and the highly abrasive diet of *A. melanoleuca*, also occupy distinct positions in the plot. *U. maritimus* is distinguished by its high SWS, while *A. melanoleuca* is characterised by the highest number of small pits and fine scratches above all extant bear populations.

Regarding the cave bears from the Kudaro caves, namely

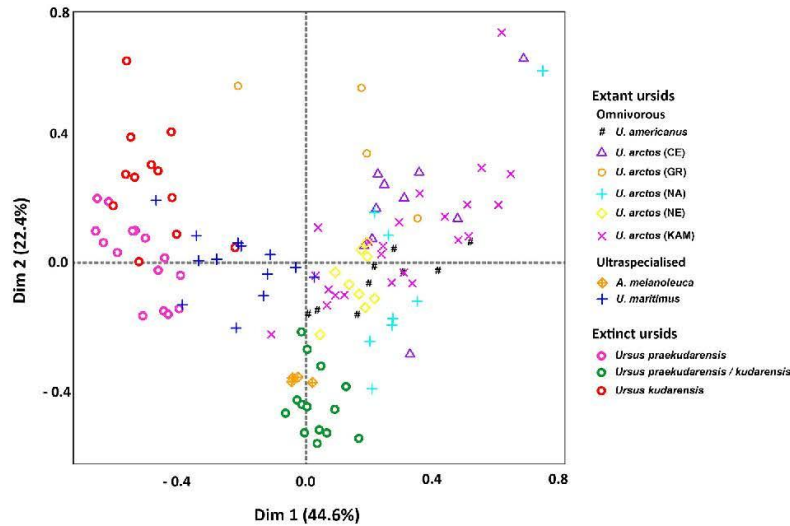


Fig. 7. Correspondence analysis using seven microwear variables, namely the number of fine and coarse scratches, small and large pits, gouges, puncture pits, and the scratch width score. Comparison of the fossil populations of the Kudaro caves, including the Middle Pleistocene *U. praekudarensis* (layer 5c from Kudaro 1) and *U. praekudarensis/kudarensis* populations (layer 5 from Kudaro 3), as well as the Late Pleistocene *U. kudarensis* (layer 4 from Kudaro 3), with the extant bear populations. Abbreviations: CE Central Europe; GR Greece; NA North America; NE North Europe; KAM Kamchatka.

U. praekudarensis (Kudaro 1; layer 5c), *U. praekudarensis/kudarensis* (Kudaro 3; layer 5), and *U. kudarensis* (Kudaro 1; layer 4), those fall within three distinct regions of the CA plot (Fig. 7).

U. kudarensis/prækudarensis falls within the lower central part of the plot. This is due to the high number of fine scratches in comparison to coarse scratches, and the absence of puncture pits, and the almost absence of large pits and gouges. Hence, *U. praekudarensis/kudarensis* overlaps with *A. melanoleuca* with a highly abrasive, herbivorous diet. Furthermore, *U. praekudarensis/kudarensis* overlaps partially with omnivorous bears inhabiting northern latitudes, like *U. arctos* from Northern Europe and North America as well as *U. americanus* from Alaska, which predominantly consume soft mast items in their diets as well as vertebrates. Finally, *U. praekudarensis/kudarensis* falls close to *U. maritimus*, which is specialised in consuming marine fauna.

Conversely, *U. praekudarensis* and *U. kudarensis* individuals are positioned on the left side of the plot, distancing themselves from the extant omnivorous bear populations on the left side of the Dim 2 axis. This can be attributed to their higher count of coarse scratches compared to a lower number of fine scratches, resulting in a high SWS. Consequently, they exhibit partial overlap with *U. maritimus*, which also displays a high SWS. Nevertheless, the two species fall within two different regions of the CA plot, while partially overlapping.

On the one hand, regarding the Dim 1 axis, *U. kudarensis* falls within the upper half of the extant omnivorous bear cluster, which includes omnivorous species that predominantly consume hard mast items, driven by a higher amount of gouges and puncture pits, i.e. *U. arctos* from Central Europe, which also has a high consumption of vertebrates (Rigg and Gorman, 2005; Bojarska and Selva, 2012). Hence, *U. kudarensis* displays an uppermost distribution among fossil populations, which can be attributed to the highest counts for gouges across both fossil and extant bears, as well as displaying the highest counts for puncture pits and large pits compared to the other cave bear species. Therefore, it is suggested that *U. kudarensis* individuals would have had an omnivorous diet with an overall predominance for hard mast items in their diets.

On the other hand, *U. praekudarensis* falls within a lower range in comparison to *U. kudarensis*, extending beyond the Dim 1 axis. This closely associates it with omnivorous bear populations with highly

variable omnivorous diets including both hard and soft mast items as well as vertebrates and invertebrates (i.e. *U. arctos* from Kamchatka, Northern Europe and North America, as well as *U. americanus*). Consequently, *U. praekudarensis* exhibits an omnivorous diet characterised by high flexibility, very similar to the range exhibited by *U. arctos* from Kamchatka (Bergman, 1936; Kistchinski, 1972; Vereschagin, 1976; Krechmar, 1995) and *U. arctos* from Northern Europe (Elgmork and Kaasa, 1992; Persson et al., 2001; Bojarska and Selva, 2012), as well as *U. arctos* from North America (Mattson, 1998; Hilderbrand et al., 1999; Mowat and Heard, 2011) and *U. americanus* (Hutler, 1967; Raine and Kansas, 1990). Therefore, *U. praekudarensis* would have exhibited a high degree of variability in the nature of the items consumed, ranging from hard mast to soft mast as well as vertebrates and invertebrates. However, most of its individuals fall within the upper part of the Dim 1 axis, while partially overlapping with *U. kudarensis*, indicating an overall predominant preference for consumption of hard mast items.

4.3.2. Comparison with *U. thibetanus*

To identify potential ecological-niche interactions between the studied fossil populations (*U. praekudarensis*, *U. praekudarensis/kudarensis*, and *U. kudarensis*) and *U. thibetanus*, a correspondence analysis (CA) was performed. The same seven microwear variables utilised in the section 4.3.1 CA were employed. The microwear signal of the fossil samples was compared with population of extant *U. thibetanus* ($n = 6$) from Asia temperate latitudes (Japan and Tibet) (Pappa et al., 2019). The results for the first two dimensions (i.e. Dim 1 and Dim 2), which exhibited 65.9% and 15.7% of variance respectively, were utilised and plotted (Fig. 8).

The CA plot reveals previously observed differences among the three studied populations, with *U. praekudarensis* and *U. kudarensis* displaying partial overlap and *U. praekudarensis/kudarensis* separating from them (Fig. 8). When plotted alongside the extant *U. thibetanus*, it is evident that although *U. thibetanus* distances itself from the three fossil populations, the degree of differentiation varies. On the one hand, while *U. praekudarensis* and *U. kudarensis* significantly distance themselves from *U. thibetanus* along the most significant dimension (Dim 1), which explains 65.9% of the variance, *U. praekudarensis/kudarensis* overlaps with *U. thibetanus*, falling within the same area on the x-axis (Fig. 8). The

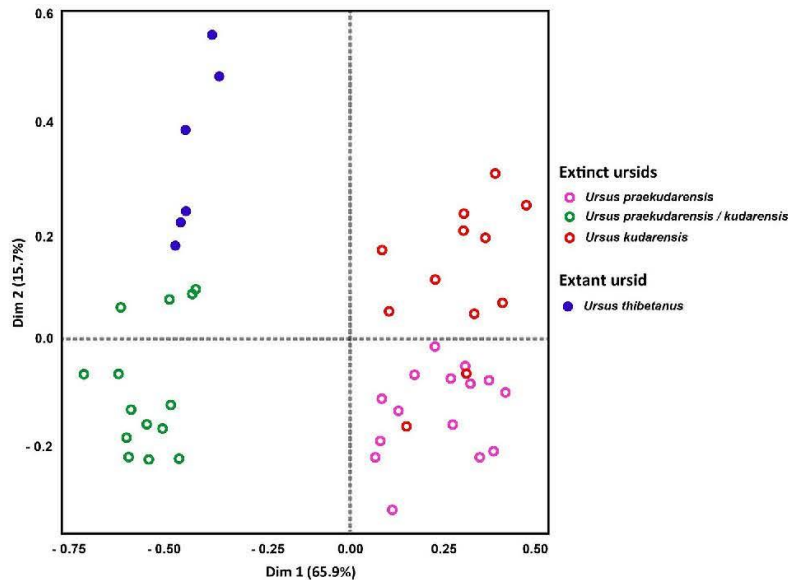


Fig. 8. Correspondence analysis employing the same seven variables as in Fig. 7. Comparison of the fossil populations of the Kudaro caves, including the Middle Pleistocene *U. praekudarensis* (layer 5c from Kudaro 1) and *U. praekudarensis/kudarensis* (layer 5 from Kudaro 3) populations, as well as the Late Pleistocene *U. kudarensis* (layer 4 from Kudaro 3) with extant *U. thibetanus* sample from Pappa et al., 2019.

similarity between *U. praekudarensis/kudarensis* and *U. thibetanus* is driven by a high number of fine scratches and a low number of coarse scratches, resulting in an SWS of 0 for both populations. In contrast, *U. praekudarensis* and *U. kudarensis* display a significantly lower number of fine scratches and a higher number of coarse scratches, with higher SWS values. Furthermore, they exhibit the presence of puncture pits, which are absent in both *U. praekudarensis/kudarensis* and *U. thibetanus* (Table 1).

The microwear pattern observed in *U. praekudarensis/kudarensis* and in *U. thibetanus* reveals similar dietary characteristics within the predominantly herbivorous diet ecological niche (Furusaka et al., 2017; Panthi et al., 2019; Basnett et al., 2021).

5. Discussion

The dental microwear of *U. praekudarensis*, *U. praekudarensis/kudarensis*, and *U. kudarensis* indicates an omnivorous diet for all three populations.

However, there are differences in the preferred food items between the three cave bear species studied. The Middle Pleistocene *U. praekudarensis* displays an omnivorous diet with its individuals exhibiting a highly variable diet, encompassing soft and hard mast items, while still predominantly favouring a hard mast diet, while *U. praekudarensis/kudarensis* presents a different microwear pattern with an omnivorous diet dominated by soft mast highly abrasive items. Finally, the Late Pleistocene *U. kudarensis* is characterised by an omnivorous diet strongly dominated by hard mast consumption. This can be related to climatic changes experienced in the southern Greater Caucasus during the Pleistocene, as well as the mortality profile and season of accumulation of the three cave bear populations (Lisiecki and Raymo, 2005; Baryshnikov, 2020b). Furthermore, the presence of varying rates of hypercoarse scratches indicates the strong possibility of vertebrate intake and carnivorous behaviour, although in different proportions among the three species.

5.1. Palaeoenvironmental data from Kudaro caves during the Middle and Late Pleistocene

The Middle Pleistocene *U. praekudarensis* lived in very warm and stable climatic conditions during MIS 11 (Likhvian Interglacial) (Lioubine, 1998), as assessed by thermophilous mammalian fauna such as *Macaca* sp. and large and small porcupines found in the same stratigraphic horizon (Loutre and Berger, 2003; Nitychoruk et al., 2006; Baryshnikov, 2011). Moreover, the palynological analysis of the oldest Acheulean layer 5c supported these very warm temperature conditions, which oscillate from dry to very wet conditions during MIS 11 (Fig. 9; Lioubine, 2002). In the dry stage, which occupies most of layer 5c where *U. praekudarensis* remains were recovered, there was a mosaic landscape composed of mixed forests of xerophilous species, those formed by broad-leaved trees and warm Pinidae family conifers, as well as more open areas of shrubs and grasses (Lioubine, 2002), a landscape dominated by warm forest-steppe landscapes with savanna-like areas (Lioubine, 2002). Although there is a poor record of pollen and spores in the second half of the stratigraphic package due to conservation constraints (Lioubine, 2002), the remains of arboreal-adapted *U. thibetanus* suggests the existence of dense and tall forest vegetation not far from the cave during the formation of layer 5c (Baryshnikov, 2010). The presence of wooded areas is further supported by the fact that during the subsequent wetter phases, at the beginning of layer 5b, the caves were surrounded by a thick forest, composed of broad-leaved trees, similar to the vegetation found in lowland modern Colchian forests (Lioubine, 2002). The *U. praekudarensis* remains from layer 5c are composed mostly of females and young individuals that died due to natural causes during hibernation (Baryshnikov, 2020b). They would have inhabited a very diverse landscape, encompassing densely forested areas of deciduous trees and more open landscapes, including conifers, woodlands and meadows. These diverse biotopes would have provided a wide variety of plants, comprising soft foodstuffs such as leaves in the forest understorey, and forbs and grasses in more open areas, as well as hard objects such as hard-shelled fruits like chestnuts, beechnuts, acorns, or pinecones from forested areas. Therefore, the prevalence of hard mast items in the diet of *U. praekudarensis* before dormancy could be attributed to the search

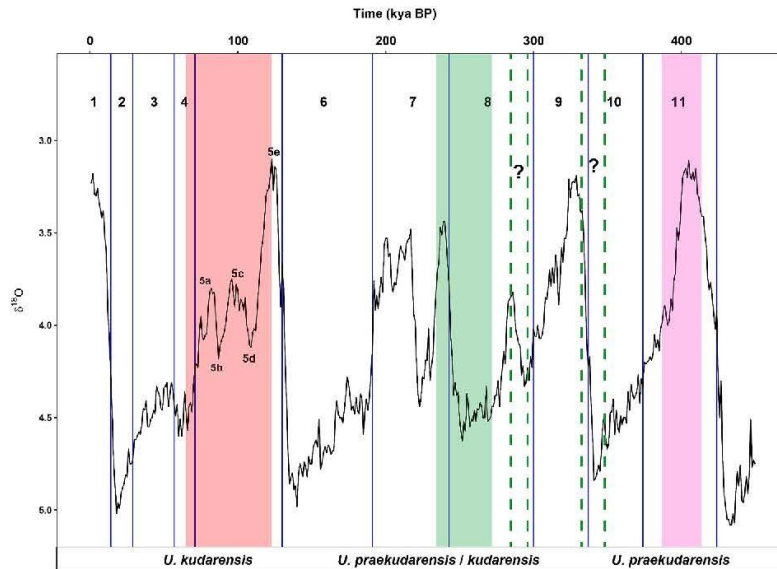


Fig. 9. Chronological time-range of the Kudaro cave bear populations in relation to the isotopic oxygen ($\delta^{18}\text{O}$) curve by Lisiecki and Raymo (2005) and Ruan et al. (2016). *U. praekudarensis* accumulated during a warm interstadial (MIS 11). *U. praekudarensis/kudarensis* accumulated during a cold to temperate interstadial, most likely at the end of MIS 8 / MIS 7 transition, although older periods such as the mid-MIS 8 warm event the transition from the MIS 10 stadial to the MIS 9 interstadial might also be considered. Finally, *U. kudarensis* remains accumulated during a temperate interstadial transitioning to a cold stadial (MIS 5 / MIS 4).

for high-calorie resources to survive hibernation (Duñó-Iglesias et al., 2024). However, the diversification of their diet, in search of alternative means to accumulate reserves, may be associated with challenges in accessing abundant enough resources solely from forested items. In extant bears the hyperphagia period is characterised by a narrowing of their dietary niche to single patches of landscape (e.g. Soofi et al., 2017; Ogurtsov, 2018). Usually, only those bears who are not storing enough reserves diversify their diet to include other foods (Wiegand et al., 2008).

The palynological studies of layer 5 (Kudaro 3) have recorded the presence of an open landscape with alpine herbaceous vegetation transitioning to an open spruce forest, because of a colder to a more temperate period at the end of the layer (Baryshnikov, 1998; Lioubine, 2002). The end of layer 5 from Kudaro 3, has been correlated with layer 5a from Kudaro 1 based on pollen analysis (Lioubine and Bosinski, 1995; Baryshnikov, 1998; Lioubine, 2002). Therefore, pollen analysis suggests that *U. praekudarensis/kudarensis* population inhabited the region from end-MIS 8 and the beginning of MIS 7 (Fig. 9; Baryshnikov, 1998; Lisiecki and Raymo, 2005). During this period, the palaeoclimatic records, spanning from Western Europe to Siberia, revealed a prevalence of open vegetation dominated by grassland communities, due to the prevailing cold and arid climatic conditions, which resulted in the retreat of temperate woodlands (Prokopenko et al., 2001; Desprat et al., 2007; Roucoux et al., 2008). Similarly, the palaeoecological records of the Southern Caucasus using small mammals, amphibians, and gastropods indicate a highly arid environment with a meadow steppe and alpine grasslands around 1000 m a.s.l. (Blain, 2016; Sevilla, 2016; Richter et al., 2020; Rey-Rodríguez et al., 2022). This arid period is evidenced by an unprecedented peak in herbaceous vegetation and a significant decline in woodlands, as recorded in the pollen analysis of layer 5 (Lioubine, 2002).

The assemblage of *U. praekudarensis/kudarensis* bones accumulated throughout the year, probably brought to the cave by predators or dying there due to disease (Baryshnikov, 1999). Arid and open habitat conditions in high altitudes could explain the soft mast and highly abrasive diet of *U. praekudarensis/kudarensis*, characterised by a high number of

fine scratches, as having relied most of the year on its preferred forage of short steppe grasses mostly composed of Gramineae plants rich in phytoliths. Therefore, it resembles the diet of the ultra-phytophagous giant panda, with an obligate bamboo diet (Goillot et al., 2009; Wei et al., 2015). A very abrasive diet based on grasses has also been observed in *U. karivetz* populations from the Urals inhabiting a mammoth steppe biome (Ramírez-Pedraza et al., 2022). Furthermore, isotopic analysis on Late Pleistocene cave bears have also suggested the prevalence of a vegetarian diet throughout the year as an adaptation to the mammoth steppe biome (Bocherens, 2015, 2019).

Finally, the studied *U. kudarensis* individuals inhabited the cave from 110 ± 10 kyr B.P., during the MIS 5 substage 5e (Eemian) until the beginning of MIS 4 (around 80 kyr B.P.) (Čerdyntsev et al., 1959; Baryshnikov, 2002). This corresponds with the transition from a relatively warm and humid interstadial (Odderade), characterised by the development of temperate deciduous forests in the region, to an overall drier and cooler phase (Fig. 9; Dansgaard et al., 1993; Sanchez Goñi et al., 2013; Helmens, 2014; Pickarski et al., 2015). This last stage is defined by the expansion of open vegetation that became predominant in the south of the Caucasus mountains around 70 kyr B.P. (Pickarski et al., 2015). This climatic transition was determined by the pollen record of layer 4 (Kudaro 3) (Lioubine et al., 1985). During the initial phase of stratigraphic unit formation, wooded areas were the dominant feature, with deciduous trees reaching the cave in a more closed landscape, while in the second half of the layer, open landscapes began to expand up the mountain, with a forest belt descending to the bottom of the valley (Lioubine et al., 1985). The assemblage of *U. kudarensis* bones suggests death by natural causes by mainly old adult male individuals that could not endure the harsh climate during hibernation (Baryshnikov, 1999; Baryshnikov, 2020b). These cave bears must have inhabited a temperate woodland and would have had access to hard-shelled fruits such as beechnuts, hazelnuts and acorns before dormancy. This is supported by a microwear pattern similar to that of *U. arctos* from Central Europe, with an omnivorous diet based on hard food from temperate forests (Rigg and Gorman, 2005; Bojarska and Selva, 2012). This similarity is confirmed by high amounts of puncture pits and gouges, which are

defining features of hard-object consumers (Solounias and Semperebon, 2002; Godfrey et al., 2004; Semperebon et al., 2004; Williams and Geissler, 2014). In particular, puncture pits are presented by carnivore clade omnivores consuming fruit coverings and seed coats in temperate deciduous woodland environments (Xafis et al., 2017). A similar microwear pattern, with a high presence of puncture pits and gouges, has been previously observed in the pre-dormancy diet of Romanian Carpathian omnivorous *U. spelaeus*, which inhabited a broad-leaf glacial refugia throughout MIS 3 (Duñó-Iglesias et al., 2024).

For the last two populations, another hypothesis for their food evolution can be proposed. *U. praekudarensis/kudarensis* or early *U. kudarensis* might have evolved in other conditions and then settled in the area of the Kudaro caves, retaining their mainly herbivorous feeding habits. Late *U. kudarensis* might have already adapted to life in the mountains of the Greater Caucasus and acquired feeding habits reminiscent of those of *U. praekudarensis*.

5.2. Vertebrate consumption for cave bear populations at Kudaro

Hypercoarse scratches, which are unique to hyper-carnivores and bone consumers like polar bears (Pappa et al., 2019) and hyenas (*Crocuta* spp.; Rivals et al., 2022), were observed in all three fossil populations. These microwear features were previously observed in low numbers in MIS 3 cave bears from the Urals; six specimens of *U. kanivetz* from Secrets Cave, two of *U. ingressus* from Shiriaev 1 Cave, and one of *U. rossicus* from Kizel Cave (24%, 28.5%, and 5.5% of the studied specimens, respectively; Ramírez-Pedraza et al., 2022). The authors of this study attributed the observed microwear features to an extreme environment, given that among the extant populations used as reference only the arctic dwelling polar bear exhibited them, and that hypercoarse scratches had so far not been observed in other extant or fossil bears in southern latitudes (Pappa et al., 2019; Ramírez-Pedraza et al., 2019, 2020, 2022). However, in other microwear studies, such features were observed in omnivorous carnivores inhabiting temperate latitudes and related to the contact of the enamel surface with bones (Goillot et al., 2009; Semperebon et al., 2011). Furthermore, a high number of hypercoarse scratches on the grinding area of the m1 was associated with species exhibiting a piscivorous diet, exemplified by the European river otter (*Lutra lutra*), malacophagy observed in the sea otter (*Enhydra lutris*), and a carnivorous diet represented by the Malagasy civet (*Fossa fossana*) and serval (*Leptailurus serval*) (Goillot et al., 2009). Additionally, species with a carnivorous diet exhibit predominantly coarse scratches compared to fine ones (Xafis et al., 2017). These piscivorous/carnivorous microwear patterns are exhibited by *U. kudarensis* and *U. praekudarensis*, which have a high number of hypercoarse scratches with 83% ($n = 10$) and 47% ($n = 7$), respectively, together with high numbers of coarse scratches in comparison to low counts of fine scratches. On the other hand, *U. praekudarensis/kudarensis* present a prevalence of fine scratches over coarse ones and only 14% ($n = 2$) of specimens exhibited hypercoarse scratches.

Previous isotopic studies of carbon ($\delta^{13}\text{C}$), nitrogen ($\delta^{15}\text{N}$), and sulphur ($\delta^{34}\text{S}$) in Kudaro yielded no evidence of a long-term fish or meat-based diet for the Late Pleistocene *U. kudarensis* (Bocherens et al., 2014b). However, this study primarily analysed individuals from MIS 3 layer 3 ($n = 6$), dated between 42 and 48 kyr B.P. (Baryshnikov, 2011), and layer 2 ($n = 2$) of Kudaro 3, which yielded dates around 30 kyr B.P. (Baryshnikov, 2002). These are from much younger layers than the individuals analysed in this work, with only one individual of *U. kudarensis* coming from layer 4, the same layer sampled for *U. kudarensis* in the present study (Bocherens et al., 2014b). Therefore, due to the relatively small sample size, predominantly derived from younger layers, and the different temporal resolutions of stable isotopes and microwear methods, we state that the intake of animal protein cannot be ignored for *U. praekudarensis*, *U. praekudarensis/kudarensis*, and *U. kudarensis* populations coming from older layers, although within a plant-dominated diet. It is important to remark that, while the two populations that

died during hibernation show significant amounts of vertebrate intake before dying (*U. praekudarensis* and *U. kudarensis*), *U. praekudarensis/kudarensis* teeth, which accumulated all year around, display fewer individuals with traces of animal protein consumption. Hence, the differences in the degree of vertebrate intake between the three populations could be related to the season of death, as microwear infers the diet of the last weeks before dying. Since *U. praekudarensis* and *U. kudarensis* died before entering dormancy, their dental microwear would be displaying hyperphagia. On the other hand, *U. praekudarensis/kudarensis* remains were mainly accumulated throughout the year by predators; consequently, its microwear signal would portray different seasons of death, and therefore the hypercoarse mean of the population would reflect a dietary signal representative of the mean annual diet (i.e. with a seasonal intake of vertebrates within an overall plant-based diet).

U. praekudarensis separated from *U. deningeri* around 800 kyr B.P. (Stiller et al., 2014; Barlow et al., 2021). This is the earliest divergence among the cave bear lineage (Knapp et al., 2009). *U. praekudarensis* remains are only found in Kudaro caves, hence, it is a species that evolved in the high-altitude environments of the Caucasus in isolation from European cave bears (Baryshnikov, 1998; Baryshnikov, 2007). Consequently, we can hypothesize that carnivorous behaviour during certain seasons might have been a plesiomorphic characteristic of this early cave bear, while more advanced species specialised towards herbivory as reflected in the evolution of cheek teeth morphology (Baryshnikov and Puzachenko, 2020).

During the formation of Kudaro 1 layer 5c, the cave was used as a maternity den during winter hibernation, as suggested by the accumulation of females and first-year cubs that probably did not reach the requirements in energy reserves to endure it, although their death would not be due to harsh winters as in this layer winters were short and mild (Levkovskaya, 1980; Baryshnikov, 2020b). Therefore, different explanations based on ecological niche competition with other species could explain this dietary behaviour in which *U. praekudarensis* would have had a carnivorous diet as fall-back food during certain seasons of the year. The presence of three plant-dominated omnivorous species might have shaped the ecology of the *U. praekudarensis* bear. Moreover, the hunting activities of two felids and human populations, which inhabited the cave more or less regularly, would have also contributed to the forming of *U. praekudarensis*' dietary niche before dormancy.

5.3. Intra-specific niche competition by *U. thibetanus*

First, the presence of *U. thibetanus* (subspecies *mediterraneus*, Forsyth Major, 1873) in the same layer (Baryshnikov, 2010), is a factor that should be considered to understand the reasons that could have driven *U. praekudarensis* to its dietary niche. The Asian black bear is a species with a highly variable omnivorous diet, almost completely based on plant resources, that varies seasonally from hard to soft mast, as well as invertebrates and with occasional intake of vertebrates (Hwang et al., 2001; Huygens et al., 2009; Furusaka et al., 2017; Panthi et al., 2019; Basnett et al., 2021). Furthermore, as stated before, the Asian black bear from layer 5c has been found to have had an arboreal lifestyle (Baryshnikov, 2010). The plant-based dietary niche of *U. thibetanus* might have overlapped to some degree with that of *U. praekudarensis* populations, with a highly variable diet, with a predominance of hard mast items, but also with soft mast consumption. The existence in the same landscape of two plant-dominant bear species, which are within a similar dietary niche, would have certainly created high competition for resources during the most energy demanding season of the year, i.e. during the period before dormancy.

Ecologically similar species can coexist by selecting different habitats or resources within a shared landscape (Schoener, 1974). Moreover, morphology and behaviour might influence resource and habitat partitioning (Rosenzweig, 1991; Wisheu, 1998). For example, in North America, brown bears mainly obtain their food in open habitats, whereas American black bears prefer densely forested areas for foraging

(Aume, 1994; Apps et al., 2006; Belant et al., 2006). This might be the case of *U. thibetanus*, well-adapted to dwelling high in the trees, favoured by its lighter weight and curved claws which allowed it to easily climb and reach places with high fruit concentration. This would be their preferred location in which they would have dwelled the most, as bears inhabit landscape areas with high food availability, and those which allow them to minimize their fitness requirements, especially during the hyperphagia period (Clark et al., 1994; Ruiz-Villar et al., 2019). Furthermore, minimizing their exposure to the risk of predation by other animals represents the second factor considered by a species when selecting a preferred area (Brown, 1988). Hence, the presence of two large felids in layer 5c, *P. gombaszoegensis* and *P. pardus*, as well as human populations, would have further shaped the forested and tree niche for *U. thibetanus* (Lioubine, 1998; Baryshnikov, 2011). In direct competition would be the two bear species inhabiting similar niches, at least during seasons low in resources, as smaller carnivores tend to distance themselves from larger ones (Creel et al., 2001). For example, in the tropical forest mosaics of Southeast Asia, sun bears (*Helarctos malayanus*, Raffles, 1821) systematically avoid eating in places where *U. thibetanus* recently exploited to avoid confrontation (Steinmetz et al., 2011). When food sources are concentrated in certain areas of the landscape, like in colder environments, competition by interference happens more frequently, for example, large brown bears from North America are reported to exclude the American black bear from places where salmon aggregate (Belant et al., 2006). Hence, as in the case of American bears, *U. thibetanus* from the Kudaro caves, with its smaller size and better adaptations to forest exploitation, could have been pushed by *U. praekudarensis* to forested areas, at least during times of the year with more diminished resources. In addition, another way in which niche displacement occurs is through exploitation competition, which tends to favour those morphologically better adapted to exploit a particular resource, e.g. Asian black bears avoid locations already harvested by sun bears because of the lower fruit density (Welch et al., 1997; Steinmetz et al., 2011). This scenario could apply to *U. praekudarensis*, which might have avoided the forested patches more effectively exploited by *U. thibetanus* due to the low availability of fruit, particularly during energetically demanding periods of the year, such as times of hyperphagia when energy reserves are stored in preparation for hibernation, and high food availability is needed (Coogan et al., 2014, 2018).

The hypothesis of niche partitioning with sympatric *U. thibetanus* during certain seasons is supported by the comparison of *U. praekudarensis* with extant *U. thibetanus* (Fig. 6; Fig. 8). The microwear analysis suggests a different dietary ecology for *U. praekudarensis* compared to the plant-based diet of *U. thibetanus*. Taking into account that the accumulation happened due to deaths during dormancy (Baryshnikov, 2020b), we can reinforce the idea that *U. praekudarensis* had a more carnivorous diet during hyperphagia, the reason which was niche partitioning with plant-based diet of *U. thibetanus*.

5.4. Competition for soft mast and underground vegetation

The presence of two porcupine species (*H. cf. refossa* and *H. brachyura*) in the same layer as *U. praekudarensis* suggests direct competition for herbivore resources. Porcupines have an opportunistic diet, considered strictly herbivorous, which changes according to food availability, shaped by seasonal variations, habitat diversity, and other factors, resulting in high ecological flexibility (Bruno and Ricciardi, 1995; Chaudhary et al., 2015; Khan et al., 2022). Their diet is mainly based on bulbs, tubers, and roots, excavated with their limbs adapted for digging, but also includes soft and hard mast items such as forbs, grasses, leaves, and fleshy fruits as well as woody plants and hard-shelled and seeded fruit such as bark, twigs, and wild berries, corns, and seeds (Hafeez et al., 2011; Akram et al., 2017). However, their diet may include insects (Mori et al., 2020), and some species have been recorded to exhibit highly infrequent scavenger behaviour (Coppola et al., 2020).

Furthermore, porcupines are known for gnawing bones as a source of calcium and phosphorus, which is consistent with the abundance of gnawing marks observed on bear bones from layer 5c (Duthie and Skinner, 1986; Baryshnikov, 2010, 2020a,b). Furthermore, the presence of *Macaca* sp. has also been recorded in layer 5c (Baryshnikov, 2002, 2020a). Macaques are generalist primates that have flexible foraging strategies that allow them to adapt to different environments, more specifically to northern latitudes and to higher altitudes (Cui et al., 2018, 2019; Zhang et al., 2023). Macaques living at high altitudes have been found to prefer herbaceous plants and leaves during the warm season (spring to summer) (Cui et al., 2019), but also fruit and seeds, although in lower proportions (Zhang et al., 2023). However, during autumn and winter, they mainly feed on plant roots, which is their dominant food during the cold season, followed by bark and fallen leaves as fallback foods (Cui et al., 2019; Zhang et al., 2023). Plant roots, as their principal fallback food, represent a key item for their survival in high-altitude severe winters (Zhang et al., 2023).

Therefore, both porcupines and macaques tend to adopt a generalist diet dominated by plant-based foods, which includes both soft and hard mast items. This diet overlaps with *U. praekudarensis*' dietary niche in layer 5c, consequently intensifying competition with omnivorous guild, mirroring the situation observed with *U. thibetanus*. Moreover, the preference for roots and tubers by porcupines year-round, and the utilization of plant roots and bark as fallback food by macaques living at high altitudes during the cold season indicate a niche overlap with the predominantly vegetarian diet of the European cave bear lineage (*Ursus spelaeus - deningeri*). Morphological studies on European cave bears have suggested the inclusion of underground storage organs of plants, such as roots and tubers, in their diets (Kurten, 1976; Mattson, 1998; Athen, 2006). This assumption is indirectly supported by the very high frequency of canine breakage in cave bears, which exceeds that of aggressive hypercarnivores such as the extant polar bear and the extinct American lion (Van Valkenburgh, 2009; Prilepskaya et al., 2022), as well as microwear analysis (Ramírez-Pedraza et al., 2022; Duñó-Iglesias et al., 2024). Hence, during the hyperphagia period, *U. praekudarensis* might have faced limited access to underground resources, which could have been more efficiently exploited by porcupines and macaques, similar to how *U. thibetanus* better exploited hard mast items from treetops of forested areas. During the period of hyperphagia, *U. praekudarensis* would probably need to broaden its diet by exploiting food areas that could offer abundant resources while also being energetically rich enough to survive the winter dormancy.

5.5. Female bear salmon exploitation and carcass scavenging during the hyperphagia period

Taphonomy of the *U. praekudarensis* accumulation of Kudaro 1 layer 5c, resembling a catastrophic mortality profile, indicates that their death occurred due to natural causes during the hibernation period (Baryshnikov, 2020a, 2020b). This is further supported by sex and age ratios, as females and young individuals are predominant in layer 5c. This has been explained by how in warm periods males do not need to hibernate, only females and their cubs do (Baryshnikov, 2020b). If so, males may have died in Kudaro 1 during the warm season, as shown for *U. kudarensis* during MIS 3 (Prilepskaya et al., 2022). Cave bear females probably died due to not being able to fulfil the energetic requirements associated with reproduction and lactation (Farley and Robbins, 1995; López-Alfaro et al., 2013), while the young individuals could have died (in addition to nourishment deficiencies) due to a high predatory environment in which they were attacked in the den by large felids, such as jaguars and leopards (Baryshnikov, 2020b). Salmon (*Salmo* spp.) represents one of the most nutritionally rich resources available for bears to accumulate protein and fat reserves before entering dormancy (Hilderbrand et al., 1999). The spawning season, which coincides with hyperphagia in bears, results in salmon concentrating in certain shallow rivers or streams, which makes them easier to hunt by bears (Gende et al.,

2001; Belant et al., 2006). Therefore, given the presence of a river at the bottom of the valley, just 260 m below the Kudaro caves at present, and in the past much less, where humans had exploited fish resources during the latter Late Pleistocene layers (Baryshnikov, 1999; Bocherens et al., 2014b), we suggest the possibility of *U. praekudarensis* females exploiting this source during the hyperphagia period before dormancy. Bears display notably greater consumption rates when catching salmon compared to foraging for berries or herbaceous vegetation, leading to larger body sizes and higher reproductive rates in females, as the reproductive success of female bears is directly linked to sufficient body fat before entering dormancy (Samson and Petteorelli, 1995; Gende and Quinn, 2004). Salmon intake could have been driven by the need to accumulate energy reserves in a season with high competition for resources within the omnivorous guild, in which other species capitalised on plant resources. However, the analysed bears were unsuccessful in their attempt to achieve their energy requirements through salmon as they died in the den. This phenomenon may be attributed to the fact that access to salmon is constrained by socially dominant larger bears (potentially males), which significantly reduces the salmon intake of subordinates, and therefore their reproductive and survival success through confrontation in the salmon-rich streams (Gende and Quinn, 2004).

Furthermore, there is significant human occupation during the formation of layer 5c, due to the recurrent presence of Acheulean artifacts (Lioubine, 1998). However, there is no evidence of cut marks on *U. praekudarensis* bones, indicating the alternation between humans and bears in the cave. The age and sex profile of leopard remains suggest that *P. pardus* used the cave as a temporary shelter as well as to hide carcasses from its prey from other predators (Baryshnikov, 2020a, 2020b). While fossil jaguar remains are limited to layer 5c, leopards appear in all levels, which suggest that this would have held the same top predator niche (Baryshnikov, 2011). Moreover, two canid species (*Canis kudarensis* and *C. mosbachensis*) were also recorded in layer 5c (Baryshnikov, 2002). The Middle Pleistocene *C. mosbachensis* had a predominantly carnivorous diet, although with the capacity to diversify into an omnivorous diet (Flower and Schreve, 2014). In landscapes with high competition for animal resources, *C. mosbachensis* scavenged ungulate carcasses already hunted by large felid predators (Courtenay et al., 2023), while coyotes were also social hunters with a meat-based diet (Hayward et al., 2023). Hence, the presence of three top large predators, humans, jaguars, and leopards, together with two different canid species with predatory behaviour suggests that hunting competition was very high. So, carcasses would have been regularly found in the cave and its surroundings benefiting scavengers (Elbroch et al., 2017). The intense competition for dietary resources among the carnivore guild may explain the absence of specialised scavengers like hyenas (except for the vultures) while boosting the available carcasses for multiple facultative scavengers (Levi and Wilmers, 2012; Pereira et al., 2014; Sivy et al., 2018). Moreover, the absence of hyenas could have allowed the cave bear *U. praekudarensis* to occupy the scavenger niche seasonally, during the hyperphagia period, in a way to further supplement its diet. Being the largest specimen with facultative scavenger behaviour (Rabal-Garcés et al., 2012), *U. praekudarensis* could have potentially out-competed smaller mesocarnivores like canids and the smaller Asian black bear in carcass scavenging (Allen et al., 2015; Inagaki et al., 2023). The partitioning of scavenger niches seasonally by different species while coexisting could be possible as observed in other ecosystems (Selva et al., 2005).

U. praekudarensis/kudarensis individuals displayed a much more plant-based diet in the weeks before their death, while still overlapping with northern omnivore populations in the CA and some of its individuals presented hypercoarse scratches. Therefore, this suggests a lower protein intake for *U. praekudarensis/kudarensis* in comparison to *U. praekudarensis*. However, it is important to note that *U. praekudarensis/kudarensis* populations probably accumulated throughout the year after being hunted by *P. pardus* or having died due

to disease (Baryshnikov, 1999). Their mortality throughout the year could explain the low percentage of hypercoarse scratches, as only the individuals displaying those would have died during hibernation and therefore showed evidence of a hyperphagia diet. Hence, we cannot discard a carnivorous diet during specific moments of the year by *U. praekudarensis/kudarensis* populations, as the climate was more rigorous and access to plant foods would have been harder during certain seasons (Bojarska and Selva, 2012). Moreover, its year-round very abrasive diet could be also explained by a cold and arid environment, and the presence of grasslands through this period.

The accumulation of *U. kudarensis* bones suggests death by natural causes during hibernation, in which mostly old male cave bears occupied the cave and died due to not being able to endure harsh winter conditions (Baryshnikov, 2020b). Hence, as in *U. praekudarensis*, the microwear would portray their diet before entering dormancy. Their hard mast-dominated pattern would be related to the hyperphagia period as observed in Romanian cave bears (Duñó-Iglesias et al., 2024). A diet almost completely based on hard mast could be easier as competitors such as *Macaca* and *U. thibetanus* were no longer present in the landscape, and only porcupines remained, but in declining numbers and only during the initial MIS 5 warmer phases and finally disappearing during subsequent substages of layer 4 characterised by colder conditions (Baryshnikov, 1999). Their carnivorous microwear pattern, which is the highest among the three populations, could be explained by colder climatic conditions. Recent studies on isolated extant brown bear populations have suggested a transition towards more carnivorous behaviour in alpine cold high-altitude environments (García-Vázquez et al., 2023). This shift is likely influenced by the limitations on plant-based resources due to increased snowfall at higher altitudes (Bojarska and Selva, 2012). This adaptation could also apply to *U. kudarensis* populations, especially considering the increasingly harsher winters they had to endure during the end of MIS 5 and the beginning of MIS 4. We can consider that, as large old bears, they would have had the ability to consume higher quantities of salmon (and their better-quality parts) as well as carrion, as seen in extant bears (Creel et al., 2001; Gende et al., 2001). Furthermore, human populations are recorded to have an increasing role in the accumulation of ungulate bones in the cave throughout layer 4 (Baryshnikov, 1999, 2020b). Hence, numerous carcasses would have been found in the cave too, much more than in older layers. This is recorded, for example, with red deer (Baryshnikov, 1999). In summary, we cannot discount fish consumption and scavenging of abandoned carcasses by *U. kudarensis* bears during hyperphagia as alternative food, as plants were increasingly restricted during colder phases in high-altitude environments of the Caucasus. This high-altitude adaptation would have resembled the diet of the Middle Pleistocene *U. praekudarensis*.

6. Conclusion

The Caucasian cave bears are a singular case of evolution in high-altitude isolation. The dental microwear analysis of the Kudaro cave bear populations reveals a complex and varied dietary adaptation influenced by climatic changes and ecological pressures throughout the Middle and Late Pleistocene. These findings highlight the complexity of Pleistocene ecosystems and the adaptive responses of early cave bears to climatic and environmental changes over time. Moreover, the resilience of the Kudaro bears underscores the capacity of cave bears to endure climatic shifts, although they were vulnerable to the presence of other omnivorous guild competitors, which could have been the driving force in shaping their dietary niche throughout the Pleistocene. Hence, it is important to consider the possibility of large omnivores (humans and other bear species) shaping the cave bear diet over time (Medin et al., 2019). Nevertheless, this suggests that their disappearance would have not only been through direct hunting (Toninato et al., 2024; Verheijen et al., 2023), but also through ecological exclusion during harsher climatic conditions.

Ethics approval/declarations

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CRediT authorship contribution statement

Paulo Duñó-Iglesias: Writing – original draft, Visualization, Investigation, Formal analysis, Data curation, Conceptualization. Iván Ramírez-Pedraza: Writing – original draft, Formal analysis, Data curation. Florent Rivals: Writing – original draft, Supervision, Funding acquisition, Formal analysis, Data curation, Conceptualization. Natalya E. Prilepskaya: Conceptualization, Writing – review & editing. Ruslan I. Belyaev: Writing – review & editing, Visualization. Gennady F. Baryshnikov: Writing – original draft, Visualization, Funding acquisition, Formal analysis, Data curation, Conceptualization.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have influenced the work reported in this paper.

Data Availability

Datasets related to this article can be found at <https://doi.org/10.5281/zenodo.11237694>, an open-source online data repository hosted at Zenodo (Duñó-Iglesias, 2024).

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References

- Akram, F., Ilyas, O., Haleem, A., 2017. Food and feeding habits of indian crested porcupine in Pench tiger reserve, Madhya Pradesh, India. *Amb. Sci.* 4 (1) <https://doi.org/10.21276/ambi.2017.04.1.ra02>.
- Alekseeva, L.I., 1977. Theriofauna of early anthropogene of Eastern Europe. *Trudy Gedogicheskogo Instituta SSSR* 30, 214.
- Allen, M.L., Ebberich, L.M., Wilmers, C.C., Wittmer, H.U., 2015. The comparative effects of large carnivores on the acquisition of carrion by scavengers. *Am. Nat.* 185 (6), 822–833. <https://doi.org/10.1086/681004>.

- Apps, C., Mdellan, B., Woods, J., 2006. Landscape partitioning and spatial inferences of competition between black and grizzly bears. *Ecography* 29, 561–572. <https://doi.org/10.1111/j.0906-7590.2006.04564.x>.
- Athen, K., 2006. Biostatistical investigation of long bones and metapodial bones of *Ursus spelaeus* and *Ursus deningeri*. *Sci. Annals. Geol. School. AUTH. special* 98, 159–162.
- Aune, K.E., 1994. Comparative ecology of black and grizzly bears on the Rocky Mountain Front. *Montana. Bears: Their Biology and Management* 9, 365–374. <https://doi.org/10.2307/3872723>.
- Azzaroli, A., 1983. Quaternary mammals and the “end-Villafranchian” dispersal event — a turning point in the history of Eurasia. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 44 (1–2), 117–139. [https://doi.org/10.1016/0031-0182\(83\)90008-1](https://doi.org/10.1016/0031-0182(83)90008-1).
- Barlow, A., Pajmans, J.L.A., Alberti, F., Gasparyan, B., Bar-Oz, G., Pinhasi, R., Foronova, I., Puzachenko, A., Pachet, M., Dalén, L., Baryshnikov, G.F., Hofreiter, M., 2021. Middle Pleistocene genome calibrates a revised evolutionary history of extinct cave bears. *Curr. Biol.* 31 (8), 1771–1779. <https://doi.org/10.1016/j.cub.2021.01.073>.
- Baryshnikov, G.F., 1998. Cave bears from the Paleolithic of the Greater Caucasus, in: Saunders, J.J., Styles, B.W., Baryshnikov, G.F. (Eds.). *Quaternary paleozoology in the Northern hemisphere*, Illinois State Museum Scientific Papers 27, 69–118.
- Baryshnikov, G.F., 1999. Bone assemblage from Acheulean and Mousterian levels in the Kudaro caves in the Caucasus mountains. *Römisch-Germanisches Zentralmuseum Monographien* 42, 237–253.
- Baryshnikov, G.F., 2002. Local biochronology of the Middle and late Pleistocene mammals from Caucasus. *Russ. J. Theor. Biol.* 1 (1), 61–67.
- Baryshnikov, G.F., 2007. Fauna of Russia and neighbouring countries. *Mammals. Ursidae*. Nauka, Saint Petersburg 541 (in Russian).
- Baryshnikov, G.F., 2010. Middle Pleistocene *Ursus thibetanus* (Mammalia, Carnivora) from Kudaro caves in the Caucasus. *Tr. Zool. Inst. RAS* 314 (1), 67–79. <https://doi.org/10.31610/trudyzin/2010.314.1.67>.
- Baryshnikov, G.F., 2011. Pleistocene Felidae (Mammalia, Carnivora) from the Kudaro Paleolithic cave sites in the Caucasus. *Tr. Zool. Inst. RAS* 315, 197–226. <https://doi.org/10.31610/trudyzin/2011.315.3.197>.
- Baryshnikov, G.F., 2020a. Large mammals of Kudaro Pleistocene fauna from Caucasus. *Tr. Zool. Inst. RAS* 9, 1–399 (in Russian).
- Baryshnikov, G.F., 2020b. Kudaro cave bear: evolution, taphonomy, extinction. *Transactions of the institute for the history of material culture RAS* 22, 158–175. <https://doi.org/10.31600/2310-6557-2020-22-158-175>.
- Baryshnikov, G.F., Puzachenko, A.Y., 2020. Morphometry of lower cheek teeth of cave bears (Carnivora, Ursidae) and general remarks on the dentition variability. *Boreas* 49 (3), 562–593. <https://doi.org/10.1111/bor.12447>.
- Baryshnikov, G.F., Gimranov, D.O., Kosintsev, P.A., 2019. Variability of the upper incisors in the cave bears (Carnivora, Ursidae) from the Caucasus and Urals. *Comptes Rendus Palevol* 18 (2), 209–222. <https://doi.org/10.1016/j.crpw.2018.08.001>.
- Basnet, R., Kumar, A., Vishwakarma, A., Boro, B., 2021. Seasonal diets of Asiatic black bear (*Ursus thibetanus*) in the Khangchendzonga National Park, Eastern Himalaya India. *J. Nat. Hist.* 55, 163–175. <https://doi.org/10.1080/00222933.2021.1899324>.
- Belant, J.L., Kielland, K., Follmann, E.H., Adams, L.G., 2006. Interspecific resource partitioning in sympatric ursids. *Ecol. Appl.* 16 (6), 2333–2343. [https://doi.org/10.1890/1051-0761\(2006\)016\[2333:irpisu\]2.0.co;2](https://doi.org/10.1890/1051-0761(2006)016[2333:irpisu]2.0.co;2).
- Bergman, S., 1936. Observations on the Kamchatka Bear. *J. Mammal.* 17 (2), 115–120. <https://doi.org/10.2307/1374183>.
- Blain, H.A., 2016. Amphibians and Squamate Reptiles from Azokh 1. In: Fernández-Jalvo, Y., King, T., Yepiskoposyan, L., Andrews, P. (Eds.), *Azokh Cave and the Transcaucasian Corridor*, *Vertebr. Springer, Paleobiol. Pa. Ser.*, pp. 191–210.
- Bocherens, H., 2015. Isotopic tracking of large carnivore palaeoecology in the mammoth steppe. *Quat. Sci. Rev.* 117, 42–71. <https://doi.org/10.1016/j.quascirev.2015.03.018>.
- Bocherens, H., 2019. Isotopic insights on cave bear palaeodiet. *Hist. Biol.* 31 (4), 410–421. <https://doi.org/10.1080/08912963.2018.1465419>.
- Bocherens, H., Grandal d'Anglade, A., Hobson, K.A., 2014a. Pitfalls in comparing modern hair and fossil bone collagen C and N isotopic data to reconstruct ancient diets: a case study with cave bears (*Ursus spelaeus*). *Isot. Environ. Health* 50 (3), 291–299. <https://doi.org/10.1080/10256016.2014.890193>.
- Bocherens, H., Baryshnikov, G.F., Van Neer, W., 2014b. Were bears or lions involved in salmon accumulation in the Middle Palaeolithic of the Caucasus? An isotopic investigation in Kudaro 3 cave. *Quat. Int.* 339–340, 112–118.
- Bojarska, K., Selva, N., 2012. Spatial patterns in brown bear *Ursus arctos* diet: the role of geographical and environmental factors. *Mammal Rev.* 42, 120–143. <https://doi.org/10.1111/j.1365-2907.2011.00192.x>.
- Brown, J.S., 1988. Patch use as an indicator of habitat preference, predation risk, and competition. *Behav. Ecol. Sociobiol.* 22 (1), 37–47. <http://www.jstor.org/stable/4600116>.
- Bruno, E., Ricciardi, C., 1995. The diet of the Crested porcupine *Hystrix cristata* L., 1758 in a Mediterranean rural area. *Z. Säugetierkunde* 60, 226–236. <https://api.semanticscholar.org/CorpusID:130088299>.
- Čerdyneev, V.V., Strašnikov, N.S., Poljakova, L.M., Borisenko, T.I., Enikeev, R.S., Neufesov, S.N., 1959. Determination of the Absolute Age of Paleolithic Sites Kudaro and Kostenki. *Optics and Nuclear Processes* (Kazakh University Publishing, Alma Ata), pp. 59–63 (translated in English).
- Chaudhary, R., Khan, J., Zehra, N., 2015. Abundance and dietary composition of indian crested porcupine in western part of Gir National Park and Sanctuary, Gujarat, India. *Int. J. Ecol. Environ. Sci.* 41, 377–392.
- Clark, J.D., Clapp, D.L., Smith, K.G., Ederington, B., 1994. Black bear habitat use in relation to food availability in the Interior Highlands of Arkansas. *Ursus* 9 (1), 309–318. <https://pubs.usgs.gov/publication/70170455>.

- Coogan, S.C.P., Raubenheimer, D., Stenhouse, G.B., Nielsen, S.E., 2014. Macronutrient optimization and seasonal diet mixing in a large omnivore, the grizzly bear: a geometric analysis. *PLoS One* 9 (5), e97968. <https://doi.org/10.1371/journal.pone.0097968>.
- Coogan, S.C.P., Raubenheimer, D., Stenhouse, G.B., Coops, N.C., Nielsen, S.E., 2018. Functional macronutritional generalism in a large omnivore, the brown bear. *Ecol. Evol.* 8 (4), 2365–2376. <https://doi.org/10.1002/ece3.3867>.
- Coppola, F., Guerrieri, D., Simoncini, A., Varuzza, P., Vecchio, G., Felicioli, A., 2020. Evidence of scavenging behaviour in crested porcupine. *Sci. Rep.* 10 (1), 12297. <https://doi.org/10.1038/s41598-020-69252-z>.
- Courtenay, L.A., Yravedra, J., Herranz-Rodrigo, D., Rodríguez-Alba, J.J., Serrano-Ramos, A., Estaca-Gómez, V., González-Aguilera, D., Solano, J.A., Jiménez-Arenas, J.M., 2023. Deciphering carnivorous competition for animal resources at the 1.46 Ma early Pleistocene site of Barranco León (Orce, Granada, Spain). *Quat. Sci. Rev.* 300, 107912. <https://doi.org/10.1016/j.quascirev.2022.107912>.
- Creel, S., Spong, G., Creel, N., 2001. Interspecific competition and the population biology of extinction-prone carnivores. In: Gitterman, J.L., Funk, S.M., Macdonald, D., Wayne, R.K. (Eds.), *Carnivore conservation*. Cambridge University Press, Cambridge, pp. 35–36.
- Cui, Z., Wang, Z.L., Shao, Q., Raubenheimer, D., Lu, J.Q., 2018. Macronutrient signature of dietary generalism in an ecologically diverse primate in the wild. *Behav. Ecol.* 29 (4), 804–813. <https://doi.org/10.1093/beheco/ary003>.
- Cui, Z., Shao, Q., Grueter, C.C., Wang, Z., Lu, J., Raubenheimer, D., 2019. Dietary diversity of an ecological and macronutritional generalist primate in a harsh high-latitude habitat, the Taihangshan macaque (*Macaca mulatta tcheliensis*). *Am. J. Primatol.* 81 (4), e22965. <https://doi.org/10.1002/ajp.22965>.
- Dansgaard, W., Johnsen, S., Clausen, H., Dahl-Jensen, D., Gundestrup, N., Hammer, et al., 1993. Evidence of general instability of past climate from a 250-kyr ice-core record. *Nature* 364, 218–220. <https://doi.org/10.1038/364218a0>.
- Desprat, S., Sanchez Goñi, M., Jean Louis, T., Duprat, J., Malaizé, B., Peyrouquet, J.P., 2007. Climatic variability of Marine Isotope Stage 7: direct land-sea-ice correlation from a multiproxy analysis of a north-western Iberian margin deep-sea core. *Quat. Sci. Rev.* 1010–1026. <https://doi.org/10.1016/j.quascirev.2006.01.001>.
- Duñó-Iglesias, P., 2024. Dental microwear raw data for cave bears from Kudaro 1 and Kudaro 3 caves [Data set]. Zenodo. <https://doi.org/10.5281/zenodo.11237694>.
- Duñó-Iglesias, P., Ramírez-Pedraza, I., Rivals, F., Mirea, I.C., Faur, L.M., Constantin, S., Robu, M., 2024. Palaeodiet during the pre-dormancy period of MIS 3 Romanian cave bears as inferred from dental microwear analysis. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 636, 111988. <https://doi.org/10.1016/j.palaeo.2023.111988>.
- Duthie, A.G., Skinner, J.D., 1986. Osteophagia in the Cape porcupine *Hystrix africaeaustralis*. *S. Afr. J. Zool.* 21 (4), 316–318. <https://doi.org/10.1080/02541858.1986.11448005>.
- Elbroch, L.M., O'Malley, C., Pezold, M., Quigley, H., 2017. Vertebrate diversity benefiting from carrion provided by pumas and other subordinate, apex felids. *Biol. Conserv.* 215, 123–131. <https://doi.org/10.1016/j.biocon.2017.08.026>.
- Elmork, K., Kaasa, J., 1992. Food habits and foraging of the brown bear *Ursus arctos* in Central South Norway. *Ecography* 15 (1), 101–110. <http://www.jstor.org/stable/3682968>.
- El-Zaatari, S., 2010. Occlusal microwear texture analysis and the diets of historical/prehistoric hunter-gatherers. *Int. J. Osteoarchaeol.* 20, 67–87. <https://doi.org/10.1002/oa.1027>.
- Farley, S.D., Robbins, C.T., 1995. Lactation, hibernation, and mass dynamics of American black bears and grizzly bears. *Can. J. Zool.* 73 (12), 2216–2222. <https://doi.org/10.1139/z95-262>.
- Flower, L.O.H., Schreve, D.C., 2014. An investigation of palaeodietary variability in European Pleistocene canids. *Quat. Sci. Rev.* 96, 188–203. <https://doi.org/10.1016/j.quascirev.2014.04.015>.
- Furusaka, S., Kozakai, C., Nemoto, Y., Umemura, Y., Naganuma, T., Yamazaki, K., Koike, S., 2017. The selection by the Asiatic black bear (*Ursus thibetanus*) of spring plant food items according to their nutritional values. *ZooKeys* 672, 121–133. <https://doi.org/10.3897/zookeys.672.10078>.
- García-Vázquez, A., Crampton, D.A., Lamb, A.L., Wolf, G.A., Kiriakoulakis, K., Guidarelli, G., Loy, A., Ciucci, P., Groff, C., Pinto-Illona, A.C., Grandal-d'Anglade, A., Meloro, C., 2023. Isotopic signature in isolated south-western populations of European brown bear (*Ursus arctos*). *Mamm. Res.* 68 (1), 63–76. <https://doi.org/10.1007/s13364-022-00654-2>.
- Gende, S.M., Quinn, T.P., 2004. The relative importance of prey density and social dominance in determining energy intake by bears feeding on Pacific salmon. *Can. J. Zool.* 82 (1), 75–85. <https://doi.org/10.1139/z03-226>.
- Gende, S.M., Quinn, T.P., Willson, M.F., 2001. Consumption choice by bears feeding on salmon. *Oecologia* 127 (3), 372–382. <http://www.jstor.org/stable/4222942>.
- Godfrey, L.R., Semperebon, G.M., Jungers, W.L., Sutherland, M.R., Simons, E.L., Solounias, N., 2004. Dental wear in extinct lemurs: evidence of diet and niche differentiation. *J. Hum. Evol.* 47 (3), 145–169. <https://doi.org/10.1016/j.jhevol.2004.06.003>.
- Goillot, C., Blondel, C., Peigné, S., 2009. Relationships between dental microwear and diet in Carnivora (Mammalia) — Implications for the reconstruction of the diet of extinct taxa. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 271 (1–2), 13–23. <https://doi.org/10.1016/j.palaeo.2008.09.004>.
- Grandal-d'Anglade, A., López-González, F., 2005. On factors that influence the morphology of the cave bear dentition and a study of the geographical variation in the lower carnassial. *Mitteilungen Der Kommission Für Quartärforschung* 14, 41–52.
- Hafeez, S., Khan, G., Ashfaq, M., Khan, Z., 2011. Food habits of the indian crested porcupine (*Hystrix indica*) in Faisalabad. *Pakistan. Pak. J. Agric. Sci.* 48, 205–210.
- Hatler, D.F., 1967. Some Aspects in the Ecology of the Black Bear (*Ursus americanus*) in Interior Alaska. University of Alaska, Master of Science. <http://hdl.handle.net/11122/5224>.
- Hayward, M.W., Mitchell, C.D., Kamler, J.F., Rippon, P., Heit, D.R., Nams, V., Montgomery, R.A., 2023. Diet selection in the Coyote *Canis latrans*. *J. Mammal.* 104 (6), 1338–1352. <https://doi.org/10.1093/jmammal/gyad094>.
- Helmens, K.F., 2014. The Last Interglacial–Glacial cycle (MIS 5–2) re-examined based on long proxy records from central and northern Europe. *Quat. Sci. Rev.* 86, 115–143. <https://api.semanticscholar.org/CorpusID:54791099>.
- Hilderbrand, G., Schwartz, C., Robbins, C.T., Jacoby, M.E., Hanley, T.A., Arthur, S., Servheen, C., 1999. The importance of meat, particularly salmon, to body size, population productivity, and conservation of north American brown bears. *Can. J. Zool.* 77, 132–138. <https://doi.org/10.1139/cjz-77-1-132>.
- Huygens, O., Manen, F., Martorello, D., Hayashi, H., Ishida, J., 2009. Relationships between Asiatic black bear kills and depredation costs in Nagano Prefecture, Japan. *Ursus* 15, 197–202. [https://doi.org/10.2192/1537-6176\(2004\)015<0197:RBABBB>2.0.CO;2](https://doi.org/10.2192/1537-6176(2004)015<0197:RBABBB>2.0.CO;2).
- Hwang, M.H., Garshelis, D., Wang, Y., 2001. Diets of Asiatic black bears in Taiwan, with methodological and geographical comparisons. *Ursus* 13, 111–125.
- Inagaki, A., Allen, M.L., Tochigi, K., Maruyama, T., Koike, S., 2023. Evidence for interspecific modulation of carcass consumption among facultative scavengers in Asian temperate forest. *Food Webs* 37, e00324. <https://doi.org/10.1016/j.fooweb.2023.e00324>.
- Iurino, D.A., Meozzi, B., Iannucci, A., Moscarella, A., Strani, F., Bona, F., Gaeta, M., Sardella, R., 2022. A Middle Pleistocene wolf from Central Italy provides insights on the first occurrence of *Canis lupus* in Europe. *Sci. Rep.* 12 (1), 2882. <https://doi.org/10.1038/s41598-022-06812-5>.
- Khan, M.B., Irshad, H., Ahmed, B., Khan, M.R., Minhas, R.A., Ali, U., Mahmood, M., Muhammad, A., Sheikh, A.A., Ashraf, N., 2022. Food habits of indian crested porcupine (*Hystrix indica*) (Kerr 1792), in district Bagh, Azad Jammu and Kashmir. *Braz. J. Biol.* 82. <https://doi.org/10.1590/1519-6984.243063>.
- King, T., Andrews, P., Boz, B., 1999. Effect of taphonomic processes on dental microwear. *Am. J. Phys. Anthropol.* 108 (3), 359–373. [https://doi.org/10.1002/\(SICI\)1096-8644\(199903\)108:3<359::AID-ajpa10968644\(199903\)108:3:359-373>3.0.CO;2-9](https://doi.org/10.1002/(SICI)1096-8644(199903)108:3<359::AID-ajpa10968644(199903)108:3:359-373>3.0.CO;2-9).
- Kistchinski, A.A., 1972. Life history of the brown bear (*Ursus arctos* L.) in North-East Siberia. *Bears: Their Biology and Management* 2, 67–73. <https://doi.org/10.2307/3872570>.
- Knapp, M., Rohland, N., Weinstock, J., Baryshnikov, G.F., Sher, A., Nagel, D., Rabeder, G., Pinhasi, R., Schmidt, H., Hofreiter, M., 2009. First DNA sequences from Asian cave bear fossils reveal deep divergences and complex phylogeographic patterns. *Mol. Ecol.* 18, 1225–1238. <https://doi.org/10.1111/j.1365-294X.2009.04088.x>.
- Kosintsev, P.A., Simonova, G.V., Konovalova, K.Y., 2023. First data on nutrition of the ural cave bear *Ursus (Spelaeoartos) karavetzi* Vereshchagin, 1973 (Mammalia, Carnivora, Ursidae) as based on ^{13}C and ^{15}N isotope analyses. *Dokl. Biol. Sci.* 510 (1), 160–162. <https://doi.org/10.1134/S0012496623700357>.
- Kosintsev, P.A., Konovalova, K.Y., Simonova, G.V., 2024. Diet of the small cave bear *Ursus (Spelaeoartos) rossicus* Borissak, 1930 (Mammalia, Carnivora, Ursidae) as revealed by ^{13}C and ^{15}N isotope analyses in bone collagen. *Dokl. Biol. Sci.* 513. <https://doi.org/10.1134/S0012496623700825>.
- Krechmar, M.A., 1995. Geographical aspects of the feeding of the brown bear (*Ursus arctos* L.) in the extreme northeast of Siberia. *Russ. J. Ecol.* 26 (6), 436–443. <http://eurekamag.com/research/002/852/002852483.php>.
- Kurten, B., 1976. *The Cave Bear Story*. Columbia University Press, Life and death of a vanished animal, p. 163.
- Levi, T., Wilmers, C.C., 2012. Wolves–coyotes–foxes: a cascade among carnivores. *Ecology* 93 (4), 921–929. <https://doi.org/10.1890/11-0165.1>.
- Levkovskaya, G.M., 1980. Palynological characterization of deposits in caves Kudaro I and Kudaro III. In: Ivanova, I.K., Chernyakhovsky, A.G. (Eds.), *Kudaro Cave Paleolithic Sites in South Ossetia*. Nauka, Moscow, pp. 128–151.
- Louibine, V.P., 1989. Paleolithic of the Caucasus. In: Boriskovsky, P.I. (Ed.), *Paleolithic of the Caucasus and North Asia*. Nauka, Leningrad, pp. 7–142 (In Russian).
- Louibine, V.P., 1998. *The Acheulian Epoch on the Caucasus*. Publishing house of IHMC RAS, Saint Petersburg, 192 pp. (In Russian).
- Louibine, V.P., 2002. La grotte de Kudaro 1, in: *L'Acheuléen du Caucase*, Liège. ERAUL 93, 41–59 (In French).
- Louibine, V.P., Bosinski, G., 1995. The earliest occupation of the Caucasus region. In: Roebroeks, W., van Kolfschoten, T. (Eds.), *The Earliest Occupation of Europe*. University of Leiden, Leiden, pp. 207–253.
- Louibine, V.P., Tcherniakovski, A.G., Baryshnikov, G.F., Levkovskaia, G.M., Seivanova, N.B., 1985. La grotte de Kudaro 1 (Résultats de recherches pluridisciplinaires). *L'Anthropologie (Paris)* 89, 159–180 (In French).
- Lisiecki, L.E., Raymo, M.E., 2005. A Pliocene-Pleistocene stack of 57 globally distributed benthic ^{18}O records. *Paleoclimatology* 20, PA1003. <https://doi.org/10.1029/2004PA001071>.
- López-Alfaro, C., Robbins, C., Zedrosser, A., Nielsen, S., 2013. Energetics of hibernation and reproductive trade-offs in brown bears. *Ecol. Modell.* 270, 1–10. <https://doi.org/10.1016/j.ecolmodel.2013.09.002>.
- Loutre, M.F., Berger, A., 2003. Marine Isotope Stage 11 as an analogue for the present interglacial. *Glob. Planet. Change.* 36, 209–217. [https://doi.org/10.1016/S0921-8181\(02\)00186-8](https://doi.org/10.1016/S0921-8181(02)00186-8).
- Mattson, D.J., 1998. Diet and morphology of extant and recently extinct northern bears. *Ursus* 10, 479–496. <http://www.jstor.org/stable/3873160>.
- Medin, T., Martínez-Navarro, B., Madurell-Malapeira, J., Figueirido, B., Kopalani, G., Rivals, F., Kiladze, G., Palmqvist, P., Lordkipanidze, D., 2019. The bears from

- Dmanisi and the first dispersal of early *Homo* out of Africa. *Sci. Rep.* 9 (1), 17752. <https://doi.org/10.1038/s41598-019-54138-6>.
- Micó, C., Blasco, R., Muñoz Del Pozo, A., Jiménez-García, B., Rosell, J., Rivals, F., 2024. Differentiating taphonomic features from trampling and dietary microwear, an experimental approach. *Hist. Biol.* 1–23. <https://doi.org/10.1080/08912963.2023.2184690>.
- Mori, E., Di Gregorio, M., Mazza, G., Ficetola, G.F., 2020. Seasonal consumption of insects by the crested porcupine in Central Italy. *Mammalia* 85. <https://doi.org/10.1515/mammalia-2020-0131>.
- Mowat, G., Heard, D., 2011. Major components of grizzly bear diet across North America. *Can. J. Zool.* 84, 473–489. <https://doi.org/10.1139/z06-016>.
- 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. *Quat. Int.* 339–340, 148–163. <https://doi.org/10.1016/j.quaint.2013.10.020>.
- Nitychoruk, J., Bińka, K., Ruppert, H., Schneider, J., 2006. Holsteinian Interglacial = Marine Isotope Stage 11? *Quat. Sci. Rev.* 25, 2678–2681. <https://doi.org/10.1016/j.quascirev.2006.07.004>.
- Ogurtsov, S., 2018. The diet of the brown bear (*Ursus arctos*) in the Central Forest Nature Reserve (West-European Russia), based on scat analysis data. *Biol. Bull.* 45, 1039–1054. <https://doi.org/10.1134/S1062359018090145>.
- Panthi, S., Aryal, A., Coogan, S.C.P., 2019. Diet and macronutrient niche of Asiatic black bear (*Ursus thibetanus*) in two regions of Nepal during summer and autumn. *Ecol. Evol.* 9 (7), 3717–3727. <https://doi.org/10.1002/eec3.4926>.
- Pappa, S., 2016. Palaeoecology and Palaeodiet: Reconstructing Adaptations in the Middle and Late Pleistocene Ursidae through Dental Microwear and Geochemistry. PhD thesis. Royal Holloway University of London.
- Pappa, S., Schreve, D.C., Rivals, F., 2019. The bear necessities: a new dental microwear database for the interpretation of palaeodiet in fossil Ursidae. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 514, 168–188. <https://doi.org/10.1016/j.palaeo.2018.10.015>.
- Peigné, S., Merceron, G., 2017. Palaeoecology of cave bears as evidenced by dental wear analysis: a review of methods and recent findings. *Hist. Biol.* 31, 1–13. <https://doi.org/10.1080/08912963.2017.1351441>.
- Peigné, S., Goillot, C., Germonpré, M., Blondel, C., Bignon, O., Merceron, G., 2009. Predomancy omnivory in European cave bears evidenced by a dental microwear analysis of *Ursus spelaeus* from Goyet, Belgium. *Proc. Natl. Acad. Sci.* 106 (36), 15390–15393. <https://doi.org/10.1073/pnas.0907373106>.
- Pereira, L., Owen-Smith, N., Molón, M., 2014. Facultative predation and scavenging by mammalian carnivores: Seasonal, regional and intra-guild comparisons. *Mammal Rev.* 44, 44–55. <https://doi.org/10.1111/mam.12005>.
- Persson, I., Wikan, S., Swenson, J., Myrsetrud, I., 2001. The diet of the brown bear *Ursus arctos* in the Pasvik Valley northeastern Norway. *Wildl. Biol.* 7, 27–37. <https://doi.org/10.2981/wlb.2001.006>.
- Pickarski, N., Kwicien, O., Langgut, D., Litt, T., 2015. Abrupt climate and vegetation variability of eastern Anatolia during the last glacial. *Clim. Past* 11 (11), 1491–1505. <https://doi.org/10.5194/cp-11-1491-2015>.
- Prilepskaya, N.E., Bachura, O.P., Baryshnikov, G.F., 2022. Season-of-death and age-at-death of the easternmost European cave bears: Cementum and dentine increment analysis provides new insight into the cave bear ecology. *Boreas* 51, 810–823. <https://doi.org/10.1111/bor.12590>.
- Prokopenko, A.A., Karabanov, E.B., Williams, D.F., Kuzmin, M.I., Shackleton, N.J., Crowhurst, S.J., Peck, J.A., Gvozdkov, A.N., King, J.W., 2001. Biogenic silica record of the Lake Baikal response to climatic forcing during the Brunhes. *Quat. Res.* 55 (2), 123–132. <https://doi.org/10.1006/qres.2000.2212>.
- Rabal-Garcés, R., Cuenca-Bescós, G., De Canudo, J.I., Torres, T., 2012. Was the European cave bear an occasional scavenger? *Lethaia* 45, 96–108.
- Raine, R.M., Kansas, J.L., 1990. Black bear seasonal food habits and distribution by elevation in Banff National Park, Alberta. *Bears: Their Biology and Management* 8, 297–304. <https://doi.org/10.2307/3872932>.
- Ramírez-Pedraza, I., Tornero, C., Pappa, S., Talamo, S., Salazar-García, D.C., Blasco, R., Rosell, J., Rivals, F., 2019. Microwear and isotopic analyses on cave bear remains from Toll Cave reveal both short-term and long-term dietary habits. *Sci. Rep.* 9 (1), 5716. <https://doi.org/10.1038/s41598-019-42152-7>.
- Ramírez-Pedraza, I., Pappa, S., Blasco, R., Arilla, M., Rosell, J., Millán, F., Maroto, J., Soler, J., Soler, N., Rivals, F., 2020. Dietary habits of the cave bear from the late Pleistocene in the northeast of the Iberian Peninsula. *Quat. Int.* 557, 63–69. <https://doi.org/10.1016/j.quaint.2019.09.043>.
- Ramírez-Pedraza, I., Baryshnikov, G.F., Prilepskaya, N.E., Belyaev, R.I., Pappa, S., Rivals, F., 2022. Paleodiet and niche partitioning among the easternmost European cave bears based on tooth wear analysis. *Hist. Biol.* 34 (6), 1063–1071. <https://doi.org/10.1080/08912963.2021.1960324>.
- Rey-Rodríguez, I., López-García, J.M., Stoetzel, E., Denys, C., Arnaud, J., Parfitt, S., Fernández-Jalvo, Y., King, T., 2022. Palaeoecological reconstructions of the Middle to late Pleistocene occupations in the Southern Caucasus using rodent assemblages. *Archaeol. Anthropol. Sci.* 14 (5), 96. <https://doi.org/10.1007/s12520-022-01555-w>.
- Richter, C., Wolf, D., Walther, F., Meng, S., Sahakyan, L., Hovakimyan, H., Wolpert, T., Fuchs, M., Faust, D., 2020. New insights into Southern Caucasian glacial-interglacial climate conditions inferred from Quaternary gastropod fauna. *J. Quat. Sci.* 35 (5), 634–649. <https://doi.org/10.1002/jqs.3204>.
- Rigg, R., Gorman, M., 2005. Diet of brown bears (*Ursus arctos*): new results from the Tatras region and a comparison of research methods. *Výskum a Ochrana Geovcov Na Slovensku* 7, 61–79.
- Rivals, F., Solounias, N., Mithlacher, M.C., 2007. Evidence for geographic variation in the diets of late Pleistocene and early Holocene *Bison* in North America, and differences from the diets of recent *Bison*. *Quat. Res.* 68 (3), 338–346. <https://doi.org/10.1016/j.yqres.2007.07.012>.
- Rivals, F., Baryshnikov, G.F., Prilepskaya, N.E., Belyaev, R.I., 2022. Diet and ecological niches of the late Pleistocene hyenas *Crocuta spelaea* and *C. ultima ussura* based on a study of tooth microwear. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 601, 111125. <https://doi.org/10.1016/j.palaeo.2022.111125>.
- Rosenzweig, M.L., 1991. Habitat selection and population interactions: the search for mechanism. *Am. Nat.* 137, S5–S28. <http://www.jstor.org/stable/2462286>.
- Rouxoux, K.H., Tzedakis, P.C., Frogley, M.R., Lawson, I.T., Preece, R.C., 2008. Vegetation history of the marine isotope stage 7 interglacial complex at Ioannina, NW Greece. *Quat. Sci. Rev.* 27 (13–14), 1378–1395. <https://doi.org/10.1016/j.quascirev.2008.04.002>.
- RStudio Team, 2021. RStudio: Integrated Development Environment for R. <http://www.rstudio.com/>.
- Ruan, J., Kherbouche, F., Genty, D., Blamart, D., Cheng, H., Dewilde, F., Hachi, S., Edwards, R.L., Régnier, E., Michelot, J.L., 2016. Evidence of a prolonged drought ca. 4200 yr BP correlated with prehistoric settlement abandonment from the Guedaman GLD1 Cave, Northern Algeria. *Clim. Past* 12 (1), 1–14. <https://doi.org/10.5194/cp-12-1-2016>.
- Ruiz-Villar, H., Morales-González, A., Bombieri, G., Zarzo-Arias, A., Penteriani, V., 2019. Characterization of a brown bear aggregation during the hyperphagia period in the Cantabrian Mountains, NW Spain. *Ursus* 29 (2), 93. <https://doi.org/10.2192/URSU-D-29-1.1>.
- Samson, C., Pettordelli, J., 1995. Reproductive biology of female black bears in relation to body mass in early winter. *J. Mammal.* 76, 68–77. <https://doi.org/10.2307/1382315>.
- Sanchez-Guñ, M., Bard, E., Landais, A., Rossignol, L., d'Errico, F., 2013. Air-sea temperature decoupling in western Europe during the last interglacial-glacial transition. *Nat. Geosci.* 6, 837–841. <https://doi.org/10.1038/ngeo1924>.
- Schoener, T.W., 1974. Resource partitioning in ecological communities. *Science* 185 (4145), 27–39. <https://doi.org/10.1126/science.185.4145.27>.
- Selva, N., Jędrzejewska, B., Jędrzejewski, W., Wajrak, A., 2005. Factors affecting carcass use by a guild of scavengers in European temperate woodland. *Can. J. Zool.* 83 (12), 1590–1601. <https://doi.org/10.1139/z05-158>.
- Sempere, G.M., Godfrey, L.R., Solounias, N., Sutherland, M.R., Jungers, W.L., 2004. Can low-magnification stereomicroscopy reveal diet? *J. Hum. Evol.* 47 (3), 115–144. <https://doi.org/10.1016/j.jhevol.2004.06.004>.
- Sempere, G.M., Sise, P.J., Coombs, M.C., 2011. Potential bark and fruit browsing as revealed by stereomicroscopic analysis of the peculiar dived herbivores known as Chalicotheres (Perissodactyla, Chalicotherioidea). *J. Mamm. Evol.* 18 (1), 33–55. <https://doi.org/10.1007/s10914-010-9149-3>.
- Sevilla, P., 2016. Bats from Azokh Caves. In: Fernández-Jalvo, Y., King, T., Yepiskoposyan, L., Andrews, P. (Eds.), *Azokh Cave and the Transcaucasian Corridor*. Vertebr. Paleobiol. Pa. Ser. Springer, pp. 177–189. https://doi.org/10.1007/978-3-319-24924-7_8.
- Siviy, K.J., Pozzanghera, C.B., Colson, K.E., Mumma, M.A., Prugh, L.R., 2018. Apex predators and the facilitation of resource partitioning among mesopredators. *Oikos* 127 (4), 607–621. <https://doi.org/10.1111/oik.04647>.
- Solounias, N., Sempere, G., 2002. Advances in the reconstruction of ungulate ecomorphology with application to early fossil equids. *Am. Mus. Novit.* 3366, 1–49. [https://doi.org/10.1206/0003-0082\(2002\)366<0001:AITROU>2.0.CO;2](https://doi.org/10.1206/0003-0082(2002)366<0001:AITROU>2.0.CO;2).
- Soofi, M., Qashqaei, A., Aryal, A., Coogan, S., 2017. Autumn food habits of brown bear *Ursus arctos* in the Golestan National Park: a pilot study in Iran. *Mammalia* 82. <https://doi.org/10.1515/mammalia-2016-0051>.
- Steinmetz, R., Garshelis, D.L., Chutipong, W., Seutaurien, N., 2011. The shared preference niche of sympatric asiatic black bears and sun bears in a tropical forest mosaic. *PLoS One* 6 (1), e14509. <https://doi.org/10.1371/journal.pone.0014509>.
- Stiller, M., Molak, M., Prost, S., Rabeder, G., Baryshnikov, G.F., Rosendahl, W., Münzel, S., Bocherens, H., Grandal-d'Anglade, A., Hilpert, B., Germonpré, M., Stasyk, O., Pinhasi, R., Tintori, A., Rohland, N., Mohandesan, E., Ho, S.Y.W., Hofreiter, M., Knapp, M., 2014. Mitochondrial DNA diversity and evolution of the Pleistocene cave bear complex. *Quat. Int.* 339–340, 224–231. <https://doi.org/10.1016/j.quaint.2013.09.023>.
- Toniato, G., Russo, G., Verheijen, I., Serangedi, J., Conard, N., Leder, D., Terberger, T., Starkovich, B., Münzel, S., 2024. A diachronic study of human-bear interactions: An overview of ursid exploitation during the Paleolithic of Germany. <https://doi.org/10.1016/j.quascirev.2024.108601>.
- Tsepkin, E.A., 1980. Remains of fish from the Kudaro cave 1. In: Ivanova, I.K., Chernyakhovsky, A.G. (Eds.), *Paleolithic Sites in Kudaro Cave in South Ossetia (Questions of Stratigraphy, Ecology, Chronology)*. Nauka, Moscow, pp. 90–97 (In Russian).
- Ungar, P.S., Teaford, M.F., 1996. Preliminary examination of non-occlusal dental microwear in anthropoids: implications for the study of fossil primates. *Am. J. Phys. Anthropol.* 100 (1), 101–113. [https://doi.org/10.1002/\(SICI\)1096-8644\(199605\)100:1<101::AID-AJPA10>3.0.CO;2-4](https://doi.org/10.1002/(SICI)1096-8644(199605)100:1<101::AID-AJPA10>3.0.CO;2-4).
- Ungar, P.S., Brown, C.A., Bergstrom, T.S., Walkers, A., 2003. Quantification of dental microwear by tandem scanning confocal microscopy and scale-sensitive fractal analyses. *Scanning Microsc.* 25 (4), 185–193. <https://doi.org/10.1002/scs.4950250405>.
- Uzunidis, A., Pineda, A., Jiménez-Manchón, S., Xafis, A., Ollivier, V., Rivals, F., 2021. The impact of sediment abrasion on tooth microwear analysis: an experimental study. *Archaeol. Anthropol. Sci.* 13 (8), 134. <https://doi.org/10.1007/s12520-021-01382-5>.
- Van Valkenburgh, B., 2009. Costs of carnivory: tooth fracture in Pleistocene and recent carnivores. *Biol. J. Linn. Soc.* 96, 68–81.

- Vereshagin, N.K., 1976. The brown bear in Eurasia, particularly the Soviet Union. *Bears: Their Biology and Management* 3, 327–335. <https://doi.org/10.2307/3872784>.
- Verheijen, I., Starkovich, B.M., Serangeli, J., van Kolfschoten, T., Conard, N.J., 2023. Early evidence for bear exploitation during MIS 9 from the site of Schöningen 12 (Germany). *J. Hum. Evol.* 177, 103294. <https://doi.org/10.1016/j.jhevol.2022.103294>.
- Wei, F., Hu, Y., Yan, L., Nie, Y., Wu, Q., Zhang, Z., 2015. Giant pandas are not an evolutionary cul-de-sac: evidence from multidisciplinary research. *Mol. Biol. Evol.* 32 (1), 4–12. <https://doi.org/10.1093/molbev/msu278>.
- Welch, C.A., Keay, J., Kendall, K.C., Robbins, C.T., 1997. Constraints on frugivory by bears. *Ecology* 78 (4), 1105–1119. <https://doi.org/10.2307/2265862>.
- Wiegand, T., Naves, J., Garbulsky, M.F., Fernández, M., 2008. Animal habitat quality and ecosystem functioning: exploring seasonal patterns using NDVI. *Ecol. Monogr.* 78 (1), 87–103. <http://www.jstor.org/stable/27646120>.
- Williams, F.L., Geissler, E., 2014. Reconstructing the diet and paleoecology of plio-pleistocene *Cercopithecoides williamsi* from Sterkfontein, South Africa. *PALAIOS* 29 (9), 483–494. <https://doi.org/10.2110/palo.2014.046>.
- Wisheu, I.C., 1998. How organisms partition habitats: different types of community organization can produce identical patterns. *Oikos* 83 (2), 246. <https://doi.org/10.2307/3546836>.
- Xafis, A., Nagel, D., Bastl, K., 2017. Which tooth to sample? A methodological study of the utility of premolar/non-carnassial teeth in the microwear analysis of mammals. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 487, 229–240. <https://doi.org/10.1016/j.palaeo.2017.09.003>.
- Zastrownov, A., Danukalova, G., Shick, S., van Kolfschoten, T., 2018. State of stratigraphic knowledge of Quaternary deposits in European Russia: Unresolved issues and challenges for further research. *Quat. Int.* 478, 4–26. <https://doi.org/10.1016/j.quaint.2017.03.037>.
- Zhang, K., Karim, F., Jin, Z., Xiao, H., Yao, Y., Ni, Q., Li, B., Pu-Cuo, W., Huang, Z., Xu, H., 2023. Diet and feeding behavior of a group of high-altitude rhesus macaques: high adaptation to food shortages and seasonal fluctuations. *Curr. Zool.* 69 (3), 304–314. <https://doi.org/10.1093/cz/zoac047>.

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journal homepage: www.elsevier.com/locate/palaeoDental microwear of cave bear (*Ursus spelaeus*) reveals locally adapted foraging strategies in South-Eastern Europe during late MIS 3

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ABSTRACT

Cave bears (*Ursus spelaeus* sensu lato) represent a remarkable example of Late Pleistocene megafauna, whose ecology and extinction dynamics remain a subject of intense debate. This study investigates the short-term dietary ecology of Late Pleistocene (mainly late MIS 3) South-Eastern European cave and brown bear populations ($n = 316$) using dental microwear analysis (DMA) on specimens from Romanian Carpathians ($n = 160$), Moldavian Plateau ($n = 58$), Western Balkans and Western Rhodopes ($n = 65$) and Central Balkans ($n = 32$). By analysing and quantifying microwear features, this research captures the final days-to-weeks dietary behaviour prior to death, offering a high-resolution perspective complementary to isotopic and morphological analyses. Complementing the prevailing view of cave bears as highly specialized herbivores, our results suggest a seasonal ecology more comparable to that of extant northern hemisphere ursids, characterized by landscape-based dietary opportunism. This inferred dietary flexibility is further supported by local-scale niche partitioning, and possible regional niche overlap with contemporaneous southern refugia dwellers *U. arctos* populations. Evidence of dietary flexibility, closely tied to their immediate environment, supported by new radiocarbon dates ($n = 16$), with the youngest at 35 ka cal BP (Butești), calls for a reassessment of cave bear extinction dynamics. Ecological specialisation, particularly during resource-scarce seasons and in refugia areas, combined with pre-hibernation ecological pressures, likely contributed to a gradual, multifactorial extinction process. This localized dietary endemism may have limited the species' ability to adapt when climatic conditions deteriorated during MIS 3.

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1. Introduction

The *Ursus spelaeus* (order Carnivora) transitioned from an omnivorous diet towards a specialized herbivory during the Pleistocene (Jiangzuo and Flynn, 2020); a clear pattern inferred from both morphological traits (e.g., Mazza and Rustioni, 1994; van Heteren and Figueirido, 2019) and stable isotope analyses (e.g., Bocherens et al., 1994, 1997, 2006, 2011, 2014; Nelson et al., 1998; Vila-Taboada et al., 1999; Fernández-Mosquera et al., 2001; Münzel et al., 2011; Krajcarz et al., 2016; Naito et al., 2016; Bocherens, 2019; Ramírez-Pedraza et al., 2019; Kosintsev et al., 2024). Consequently, its ecology has been proven to have been plant-based, with a heavy year-round reliance on plant matter. Numerous stable isotopes studies involving large sample sizes have concluded that the cave bear's diet was relatively uniform over its lifespan (e.g., Bocherens, 2015; Krajcarz et al., 2016). This level of insight has been possible because cave bears hibernated in deep karstic cave systems, and their remains are among the most frequently recovered from cave fossil assemblages across Europe, likely due to individuals dying during dormancy (Kurtén, 1976; Rabeder, 1999; Rabeder et al., 2000; Grandal-d'Anglade et al., 2019). However, the seasonal ecology of cave bears differed from their overall annual dietary patterns (e.g., Ramírez-Pedraza et al., 2019). Individuals that died during hibernation reflect the physiological need for high caloric intake prior to dormancy, which resulted in a broadening of their diet before hibernation (e.g., Duñó-Iglesias et al., 2024a, 2024b). The pre-hibernation period is a key period for bears that determines the survival or extinction of offspring (Gende and Quinn, 2004). Interferences, such as competition for caves, hunting, or human presence might cause a shrinking of the regional population and even of a species (Stiller et al., 2010; Fortes et al., 2016; Robu et al., 2024).

The extinction of the cave bear has been mainly attributed to a decline in the availability of high-quality vegetation approaching the

Last Glacial Maximum (LGM) (Pacher and Stuart, 2009). The presence of other bears in the same landscapes have suggested local niche partitioning through both stable isotopes (e.g., Bocherens et al., 2011; Münzel et al., 2011; Frémonteau et al., 2020) and dental microwear analysis (e.g., Pappa, 2016; Ramírez-Pedraza et al., 2020, 2022; Duñó-Iglesias et al., 2024a, 2024b). The influence of other bear species on the decline of cave bears has been considered negligible based on life-span dietary proxies (i.e., stable isotopes) (Münzel et al., 2011); however, they may have exerted an ecological pressure at a seasonal scale (Duñó-Iglesias et al., 2024b).

In this study, we present a regional-scale dental microwear analysis of both *U. spelaeus* and *U. arctos* in South-Eastern Europe, including the Romanian Carpathians, expanding upon the dataset of Duñó-Iglesias et al. (2024a) with newly analysed individuals from Cioclovina and additional specimens from Urşilor and Muierilor caves, as well as newly sampled populations from the Moldavian Plateau, the Western Balkans, the Western Rhodope Mountains, and the Central Balkans regions.

The aim of this work is to assess the extent of seasonal dietary flexibility in *U. spelaeus* during the pre-hibernation period, and to evaluate niche relationships with *U. arctos*, in order to better understand ecological pressures that may have contributed to the decline of cave bears in South-Eastern Europe glacial refugias during the MIS 3.

2. Geographical context

This study includes populations from the Southeastern regions of the European continent (Fig. 1); from the Romanian Carpathians, Moldavian Plateau, Western Balkan Mountains and Western Rhodopes, and Central Balkans. The populations were grouped by regions based on geographical coherence. All populations are chronologically associated to the latter half of the Late Pleistocene, primarily during late MIS 3.

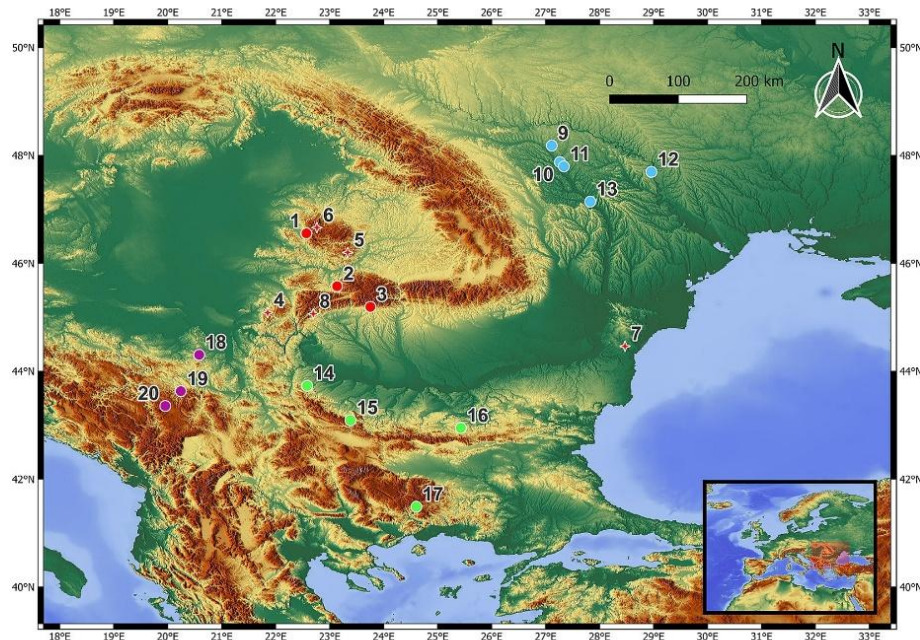


Fig. 1. Map of the sampled populations. *Romanian Carpathians* (red): 1. Urşilor, 2. Cioclovina Uscată, 3. Muierilor, 4. Oase, 5. Biseriçuța, 6. Onceasa, 7. Adam, 8. ACCG. *Moldavian Plateau* (blue): 9. Trinca I, 10. Duruitoarea Veche, 11. Butești, 12. Saharna, 13. Buzdjueni. *Western Balkan Mountains and Western Rhodopes* (green): 14. Magura, 15. Lakatnik, 16. Bacho Kiro, 17. Borikovska. *Central Balkans* (purple): 18. Risovača, 19. Hadži Prodanova, 20. Ušacka. Stars indicate previously published sites, included for comparative purposes. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

2.1. Romanian Carpathians

Urșilor Cave (46° 55' 37" N, 22° 56' 92" E), located on the western slope of the Apuseni Mountains (Western Carpathians), contains a rich Late Pleistocene cave bear (*U. spelaeus*) assemblage dated to 47–27.1 ka cal BP (Constantin et al., 2014; Robu, 2016; Duňo-Iglesias et al., 2024a).

Cioclovina Uscată Cave (45° 34' 27" N, 23° 08' 10" E), in the Șureanu Mountains (Southern Carpathians), served as a hibernation site for *U. spelaeus* between 44.2 and 31.4 ka cal BP (Soficaru et al., 2007; Robu et al., 2019). Fauna includes *U. arctos*, *Canis lupus*, and *Panthera spelaea* (Rădulescu and Samson, 1959; Păunescu, 1980).

Muierilor Cave (45° 11' 29" N, 23° 45' 14" E), in the Parâng Mountains (Southern Carpathians), yielded a diverse MIS 3 faunal assemblage (ca. 51–29 ka cal BP), dominated by *U. spelaeus* but also including *P. spelaea*, *C. lupus*, and *Cervus elaphus* (Mirea et al., 2021; Duňo-Iglesias et al., 2024a; Robu et al., 2024).

Further details on previously published comparative sites can be found in Duňo-Iglesias et al. (2024a).

2.2. Moldavian Plateau

Trinca I Cave (48° 10' 55" N, 27° 06' 50" E), in the Edineț District, yielded *U. spelaeus*, and associated fauna (e.g., *U. arctos*, *P. spelaea*, *C. lupus*) of MIS 3 age, recovered from surface finds and old excavations.

Duruitoarea Veche Cave (47° 52' N, 27° 15' E), Râșcani District, includes a diverse MIS 3 faunal assemblage with *U. spelaeus* dominant, but also including other taxa such as *Equus* sp., *Bison* sp., *C. elaphus*, *Megaloceros giganteus*, *Rangifer tarandus*, *P. spelaea*, *Crocota crocota spelaea*, *C. lupus*, *Vulpes vulpes*, and *U. arctos*.

Butești Cave (47° 47' 46" N, 27° 20' 13" E) contains *U. spelaeus* specimens attributed to the Late Pleistocene.

Saharna Cave (47° 41' 40" N, 28° 57' 40" E), located near the Dniester River, is a karst containing Late Pleistocene *U. spelaeus* remains.

Buzdjueni I Cave (47° 08' 33" N, 27° 49' 40" E) has a Late Pleistocene faunal sequence dominated by *U. spelaeus*, with associated remains of *E. ferus*, *B. priscus*, as well as *C. c. spelaea*, among others (Croitor and Burlacu, 2020; Vishnyatsky et al., 2020). The faunal deposits correspond to Late Pleistocene.

2.3. Western Balkan Mountains and Western Rhodopes

Magura Cave (43° 43' 41" N, 22° 34' 57" E), in Western Balkan Mountains, preserves a Late Pleistocene assemblage dominated by *Ursus ingressus*, accompanied by *U. arctos*, *C. lupus*, *C. c. spelaea*, *P. spelaea*, *E. hydruntinus*, and *C. elaphus*, among others (Ivanova et al., 2016). The cave bear remains date from more than >50 ka to ca. 35 ka (Ivanova et al., 2016).

Lakatnik Cave (43° 05' 21" N, 23° 23' 05" E), in Western Balkan Mountains, includes Late Pleistocene *U. spelaeus* remains from Trench I, dating at between 40 and 31 ka BP (Ginter et al., 2000; Stuart and Lister, 2011).

Bacho Kiro Cave (42° 56' 48" N, 25° 25' 49" E), in the Balkan Mountains, yielded *U. spelaeus* remains, associated with a diverse Late Pleistocene fauna, *E. ferus*, *E. hydruntinus*, *Megaloceros giganteus*, *Capra ibex* and *Rupicapra rupicapra*, *Mammuthus primigenius* among others and dating to 61–51 ka BP (Fewlass et al., 2020; Pederzani et al., 2021; Martisius et al., 2022).

Borikovska Cave (41° 29' 08" N, 24° 36' 21" E), located in the Rhodope Mountains, preserves a rich MIS 3 faunal assemblage dominated by *U. spelaeus*, alongside *U. arctos*, *Lynx lynx*, and *C. c. spelaea*, belonging to MIS 3 (Petrov and Stoev, 2007; Boev, 2021).

2.4. Central Balkans

Risovača Cave (44° 18' 07" N, 20° 34' 56" E), in Šumadija (Balkans, central Serbia), near the city of Arandelovac, includes Late Pleistocene

faunal remains dominated by *U. spelaeus*, along with remains of *U. arctos*, *C. c. spelaea*, *P. spelaea*, *M. primigenius*, *Dicerorhinus hemitoechus*, *E. ferus*, *E. hydruntinus*, *Sus scrofa*, *C. elaphus*, etc. (Dimitrijević, 1997; Forsten and Dimitrijević, 1995).

Hadži Prodanova Cave (43° 37' 41" N, 20° 14' 25" E), central Serbia, near the city of Ivanjica, contains a faunal assemblage dominated by *U. spelaeus*, among other mammal species; *C. ibex*, *C. lupus*, *U. arctos*, *R. rupicapra*, *C. elaphus*, *L. lynx* and *C. c. spelaea* (Mihailović and Mihailović, 2006; Bogićević et al., 2017). The analysed cave bear specimens derive from upper stratigraphic levels assigned to late MIS 3 based on associated rodent and large mammal assemblages (Bogićević et al., 2017).

Usačka Cave (43° 21' 16.2" N, 19° 57' 15.2" E), part of the Usacki Cave System, southwestern Serbia, near the city of Sjenica, yielded abundant Late Pleistocene *U. spelaeus* remains, with few remnants of *U. arctos*, *C. c. spelaea* and *C. elaphus* (Dimitrijević, 1997).

3. Materials and methods

3.1. Dental microwear

A total of 495 lower first molars (m1; $n = 495$; published $n = 92$, from Duňo-Iglesias et al., 2024a, newly added $n = 403$) of different ursid species have been selected for this work, from a wide range of individuals, including juveniles, prime adults, and old adults of both sexes, hence, ensuring a comprehensive and reliable assessment of the population's variability. The m1 specimens comprise teeth preserved within mandibles as well as isolated teeth. The studied Pleistocene Ursidae fossil collection taxonomically contains two different species: *U. spelaeus* ($n = 489$), and *U. arctos* ($n = 6$). The specimens belong to 16 populations, from 15 different bone assemblages distributed across 4 different regions: Romanian Carpathians ($n = 246$; published $n = 92$, newly added $n = 154$), Moldavian Plateau ($n = 96$), Western Balkan Mountains and Western Rhodopes ($n = 99$), Central Balkans ($n = 54$) (see Table 1 in Supplementary Materials; see Duňo-Iglesias, 2025 for the raw data).

For the microwear analysis, the preparation of the sample followed the protocol developed by Solounias and Semprebon (2002) and Semprebon et al. (2004). For a detailed visual description of the process see Supplementary Materials, section 2.1. The features examined include counts of fine (characterized by narrow and shallow marks) and coarse (characterized by wider and deeper marks) scratches, small and large pits (circular or semicircular shapes of similar length and width, which can be classified as either small pits, which are characterized by being shallow and appearing as shiny, bright, white dots, or large pits, which are wider and deeper, and reflect less light), puncture pits (very deep and symmetrical crater-like morphology with regular edges), gouges (crater-like but with irregular edges), SWS (0 = predominant fine scratches, 1 = mixed of fine and coarse, 2 = predominantly coarse scratches) and hypercoarse scratches (very deep and wider than fine and coarse scratches, resulting in very low reflectivity and appearing as dark features, they have a distinctive "trench-like" shape with symmetrical edges; presence counted from >4).

Our findings were compared with the reference dataset of extant bear species established by Pappa et al. (2019) to reconstruct the palaeodiet of the fossil populations. The reference collection allowed us to directly compare extinct ursids with their closely related living counterparts, such as *U. arctos* from different regions including Kamchatka, Greece, Central Europe, Northern Europe, and North America, as well as *Ursus americanus* from North America. Both species show a wide range of dietary preferences, which include the consumption of vertebrates and invertebrates as well as a hard mast and soft mast diet. In addition, the hyper-carnivorous *Ursus maritimus* and the hyper-herbivorous *Ailuropoda melanoleuca* were added to the comparison. To avoid the possibility of inter-observer error, a single observer (PDI) performed the analysis on all specimens.

Photomicrographs were captured using an Invenio 5SII digital

Table 1
Samples which were AMS ¹⁴C dated (mandible bone). The radiocarbon dates were calibrated using the IntCal13 calibration dataset (Reimer et al., 2013). The table includes data from multiple sites (e.g., Duruitoarea Vechie, Butești, Buzdjujeni, Saharna, and Urșilor), with most samples identified as *U. spelaeus* and one as *U. arctos* (Butești). Collagen yield (%), and calibrated radiocarbon ages (median, mean, and 2σ/95.4 % ranges in cal BP), C:N ratio and Cb% and Nb% are reported where available.

#Collection	#FTMC	#IPHES	Species	Material	Bone type	Site	Coll. Yield (%)	cal BP age (median)	Age range cal BP (2σ; 95.4 %)	C:N ratio	%Cb	%Nb
Valid												
Bx8.63.5	FTMC-SI30-6		<i>U. spelaeus</i>	Bone	Mandible	Duruitoarea Vechie	6.71	42,585	42,891	3.18	44.81	16.43
669	FTMC-NO87-5	23	<i>U. spelaeus</i>	Bone	Mandible	Duruitoarea Vechie	4.98	42,464	42,723	3.15	30.09	11.15
671	FTMC-TW42-3	24	<i>U. spelaeus</i>	Bone	Mandible	Duruitoarea Vechie	2.67	40,044	40,534	3.11	31.93	11.96
10,704/149	FTMC-TW42-2	73	<i>U. spelaeus</i>	Bone	Mandible	Butești	2.96	41,704	41,985	3.18	41.6	15.26
10,704/185	FTMC-TW42-3	79	<i>U. arctos</i>	Bone	Mandible	Butești	4.17	41,333	41,702	3.19	34.21	12.53
10,704/147	FTMC-TW42-6	75	<i>U. spelaeus</i>	Bone	Mandible	Butești	1.37	34,972	35,298	3.27	45.76	16.33
GB/2	FTMC-PH50-2	33	<i>U. spelaeus</i>	Bone	Mandible	Buzdjujeni	7.15	43,713	44,350	3.18	40.13	14.71
GB/5	FTMC-TW42-8		<i>U. spelaeus</i>	Bone	Mandible	Buzdjujeni	12.37	43,599	44,145	3.18	46.9	17.23
GB/7	FTMC-PH50-1		<i>U. spelaeus</i>	Bone	Mandible	Buzdjujeni	3.7	43,508	44,161	3.19	42.39	15.52
GB/1	FTMC-TW42-7		<i>U. spelaeus</i>	Bone	Mandible	Buzdjujeni	1.58	42,399	42,582	3.19	47.18	17.26
GB/4	FTMC-NO87-2	32	<i>U. spelaeus</i>	Bone	Mandible	Buzdjujeni	2.5	40,557	40,974	3.13	34.5	12.86
GB/21	FTMC-PH50-3		<i>C. c. spelaea</i>	Bone	Mandible	Buzdjujeni	3.59	46,576	47,776-45,725	3.14	31.29	11.63
SH/8	FTMC-TW42-11		<i>U. spelaeus</i>	Bone	Mandible	Saharna	3.54	42,960	43,228	3.18	48.06	17.65
SH/4	FTMC-TW42-10	15	<i>U. spelaeus</i>	Bone	Mandible	Saharna	2.9	42,353	42,517	3.2	46.87	17.09
SH/31	FTMC-TW42-13		<i>U. spelaeus</i>	Bone	Mandible	Saharna	6.84	41,313	41,700	3.2	46.26	16.86
SH/18	FTMC-TW42-12		<i>U. spelaeus</i>	Bone	Mandible	Saharna	3.18	41,306	41,712	3.2	47.11	17.15
Discarded												
674	FTMC-NO87-4	22	<i>U. spelaeus</i>	Bone	Mandible	Duruitoarea Vechie	1.73	40,603	41,035	3.1	15.03	5.65
670	FTMC-SI30-4		<i>U. spelaeus</i>	Bone	Mandible	Duruitoarea Vechie	2.14	36,677	37,101	3.16	23.76	8.76
60 Kg2511-75	FTMC-SI30-2		<i>U. spelaeus</i>	Bone	Mandible	Duruitoarea Vechie	1.54	36,249	36,724	3.18	24.28	8.91
673	FTMC-SI30-3		<i>U. spelaeus</i>	Bone	Mandible	Duruitoarea Vechie	1.16	31,859	32,224	3.23	26.03	9.39
Kg 28 I12	FTMC-SI30-1		<i>U. spelaeus</i>	Bone	Mandible	Duruitoarea Vechie	1.36	31,020	31,161	3.24	13.45	4.85
SH/11	FTMC-PH50-5	2	<i>U. spelaeus</i>	Bone	Mandible	Saharna	0.78	27,620	27,790	3.21	11.56	4.2
SH/10	FTMC-PH50-4		<i>U. spelaeus</i>	Bone	Mandible	Saharna	2.02	37,228	37,737	3.13	17	6.33
GB/3	FTMC-TW42-9		<i>U. spelaeus</i>	Bone	Mandible	Buzdjujeni	0.29	40,883	41,222	3.23	44.51	16.09
10,704/180	FTMC-TW42-1	57	<i>U. spelaeus</i>	Bone	Mandible	Butești	0.41	37,432	38,240	3.17	21.18	7.8
10,704/189	FTMC-TW42-5	65	<i>U. spelaeus</i>	Bone	Mandible	Butești	1.05	38,066	39,008	3.13	12.41	4.62
10,704/168	FTMC-TW42-4	61	<i>U. spelaeus</i>	Bone	Mandible	Butești	1.31	35,335	35,713	3.2	18.71	6.83

camera in extended focus mode and the Helicon Focus software to combine the images acquired at different focal planes to create a single image with an increased depth of field. The scale bars were incorporated using ImageJ software. Maps were generated using ArcGIS version 10.6.1 (Esri, 2018), while graphs, statistical tests, and analyses were performed using RStudio version 4.1.2 (RStudio Team, 2021).

3.2. Radiocarbon dating

For radiocarbon dating, we sampled cave bear ($n = 25$), brown bear ($n = 1$) and cave hyena ($n = 1$) mandible bones from: Butești ($n = 6$: *U. spelaeus*, $n = 5$, *U. arctos*, $n = 1$), Buzdujeni ($n = 6$: *U. spelaeus*, $n = 5$, *C. c. spelaea*, $n = 1$), Saharna ($n = 6$) and Duruitoarea Veche ($n = 9$). The AMS ^{14}C dating was performed at the Center for Physical Sciences and Technology (FTMC), in Vilnius (Lithuania). The preparation of bone samples involved standard acid-base-acid (ABA) procedure and collagen extraction. Firstly, bone samples were ultrasonicated in ultrapure water, dried, grinded and sieved to get the appropriately sized sample fraction (0.5–1 mm). Then samples were treated with 0.5 M hydrochloric acid (~18 h), 0.1–0.2 M sodium hydroxide (30 min–1 h), and 0.5 M hydrochloric acid (1 h). Bone collagen gelatinization was performed in pH 3 solution at 70 °C for 20 h. Gelatine solution was filtered using a cleaned Ezeefilter and freeze-dried. As quality of collagen is a critical factor in radiocarbon dating, it was monitored by carbon and nitrogen content in collagen, atomic C/N ratio determination and collagen yield. Samples were dated if the collagen yield was above 1 % and the C:N ratio of the collagen was between 2.9 and 3.5. The samples that deviate from these ratios were discarded. The obtained radiocarbon data were calibrated using the OxCal v4.4 software (Bronk Ramsey, 2009, 2020) against the IntCal20 radiocarbon calibration curve (Reimer et al., 2020).

4. Results

4.1. Radiocarbon dating

A total of 27 AMS radiocarbon dates were obtained from the Moldavian Plateau region, including specimens of *U. spelaeus* ($n = 25$), *U. arctos* ($n = 1$), and *C. c. spelaea* ($n = 1$). Of these, 24 radiocarbon dates yielded sufficient collagen (≥ 1 %) for reliable analysis, while 3 were discarded due to insufficient yield (< 1 %) or unavailable yield data (van Klinken, 1999; Brock et al., 2010). Moreover, of the remaining 24 dated samples, 8 exhibited poor chemical preservation, evidenced by %Cb values below 30 % and %Nb below 12 %, the lower thresholds for valid AMS collagen dating as recommended by van Klinken (1999) and van der Plicht and Palstra (2016), and were therefore discarded. Hence, 16 dates were thus retained as valid (Table 1; Fig. 2). Calibrated valid ages range from ca. 46 ka cal BP (Buzdujeni site) to ca. 35 ka cal BP (Butești).

4.2. Dental microwear

A total of 315 lower first molars (m1) were selected for analysis out of 495 examined specimens from four regions across South-Eastern Europe (Table 2; Fig. 3). From the Romanian Carpathians, 160 m1s were suitable, including *U. spelaeus* from Urșilor ($n = 54$), Cioclovina ($n = 35$), Muierilor ($n = 32$), Oase ($n = 26$), Biserița ($n = 5$), Onceasa ($n = 3$), and La Adam ($n = 2$), as well as *U. arctos* from Biserița ($n = 1$) and ACCG ($n = 2$). In the Moldavian Plateau, 58 m1s were included, comprising *U. spelaeus* from Trinca ($n = 16$), Saharna ($n = 18$), Buzdujeni ($n = 11$), Duruitoarea Veche ($n = 6$), Butești ($n = 2$), and *U. arctos* from Trinca ($n = 5$). Western Balkan Mountains and Western Rhodopes yielded 65 suitable m1s, from *U. spelaeus/ingressus* individuals at Borikovska ($n = 48$), Magura ($n = 8$), Bacho Kiro ($n = 5$), and Lakatnik ($n = 4$). In Central Balkans, 32 m1s were included from *U. spelaeus* specimens at Ušacka ($n = 11$), Hadži Prodanova ($n = 11$), and Risovača ($n = 10$). Across all regions, 180 specimens were excluded due to the absence of wear facets in juvenile individuals (Rivals et al., 2007) or due to

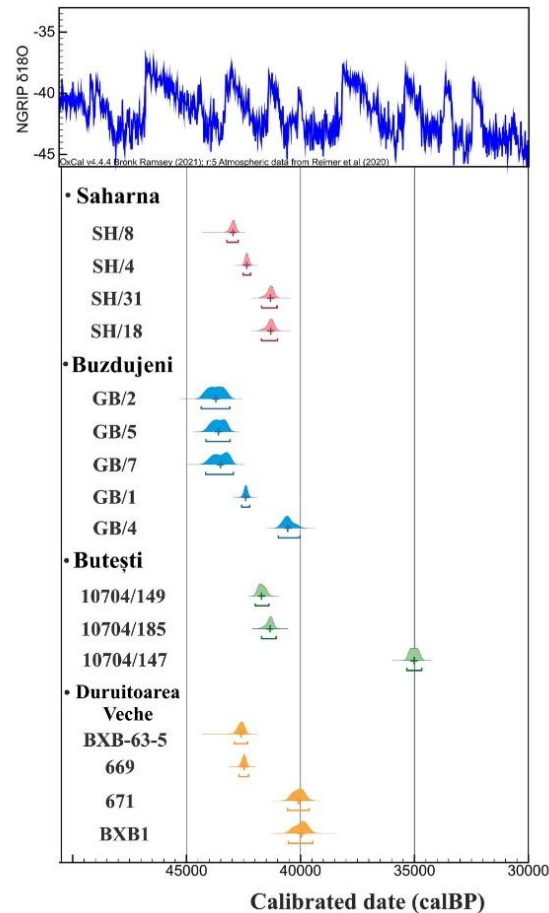


Fig. 2. Posterior probability distributions of calibrated AMS ^{14}C dates for *U. spelaeus* and *U. arctos* specimens from four key sites in Moldavian Plateau: Saharna (red), Buzdujeni (blue), Butești (green), and Duruitoarea Veche (orange). Calibrations were performed using OxCal v4.4 and the IntCal20 atmospheric curve (Reimer et al., 2020). The top panel shows the NGRIP $\delta^{18}\text{O}$ climate record as a proxy for palaeo-temperatures. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

significant taphonomic damage affecting occlusal surfaces (King et al., 1999; El-Zaatari, 2010; Uzunidis et al., 2021; Micó et al., 2024). Excluded samples included *U. spelaeus* from Urșilor ($n = 16$), Cioclovina ($n = 12$), Muierilor ($n = 44$), Oase ($n = 8$), Onceasa ($n = 3$), ACCG ($n = 3$) Saharna ($n = 3$), Buzdujeni ($n = 8$), Duruitoarea Veche ($n = 4$), Butești ($n = 23$), Borikovska ($n = 28$), Magura ($n = 4$), Bacho Kiro ($n = 1$), Lakatnik ($n = 1$), Ušacka ($n = 7$), Hadži Prodanova ($n = 3$), and Risovača ($n = 12$).

The cave bear populations exhibit regional variation (Table 2; Fig. 3). A description of microwear patterns and their comparison with the reference dataset established by Pappas et al. (2019), organised by geographic region, is presented below, while a detailed population-level analysis is provided in the Supplementary Materials (section 3).

4.2.1. Romanian Carpathians

Microwear analysis of *U. spelaeus* from the Romanian Carpathians reveals notable variability among sites, for both number of total scratches (NTS) and number of total pits (NTP) (Fig. 4A). Furthermore,

Table 2

Comparison of the dental microwear results of the fossil populations of cave bear (*U. spelaeus*) and brown bear (*U. arctos*) from the Romanian Carpathians, Moldavian Plateau, Western Balkan Mountains and Western Rhodopes and Central Balkans with the reference dataset of extant bear species of *U. arctos*, *U. americanus*, *A. melanoleuca* and *U. maritimus* established by Papp et al. (2019). Abbreviations: N = number of specimens, NFS = number of fine scratches, NCS = number of coarse scratches, NTS = number of total scratches, SWS = scratch width score, NLP = number of large pits, NSP = number of small pits, NPP = number of puncture pits, NTP = number of total pits, NG = number of gouges.

Region	Site	Species	N	NFS	NCS	NTS	SWS	NLP	NSP	NPP	NTP	NG
Extinct												
Romanian Carpathians												
	Urşilor	<i>U. spelaeus</i>	54	10.58	8.84	19.55	1.04	2.31	20.04	1.27	23.59	0.94
	Cioclovina	<i>U. spelaeus</i>	35	15.29	5.33	20.88	0.37	1.67	27.17	2.34	31.3	1.03
	Muierilor	<i>U. spelaeus</i>	32	16.75	3.81	21.24	0.22	1.64	30.34	3.14	35.17	1.34
	Oase	<i>U. spelaeus</i>	26	13	10.05	23.05	1.04	3.6	19.35	2.87	25.81	1.12
	Bisericuța	<i>U. spelaeus</i>	5	14.27	9.1	23.37	0.8	2.8	19.03	2.5	24.33	0.6
		<i>U. arctos</i>	1	6	21	27	2	27	9	2	38	1
	Onceasa	<i>U. spelaeus</i>	3	15.17	10	25.17	1	5	17.33	1	23.17	0
	La Adam	<i>U. spelaeus</i>	2	16	4	20	0.5	2	25	2	29	0
	ACCG	<i>U. arctos</i>	2	10.5	14.75	25.25	1.5	5.5	14.25	1.5	21.25	1
Moldavian Plateau												
	Trinca	<i>U. spelaeus</i>	16	19.91	0.63	20.53	0	0.5	11.05	0.44	11.99	0.09
		<i>U. arctos</i>	5	16.7	3.6	20.2	0.4	2	18.8	0.4	21.2	1.7
	Saharna	<i>U. spelaeus</i>	18	16.54	1.97	18.45	0.06	0.5	33.4	3.11	36.47	0.28
	Buzdujeni	<i>U. spelaeus</i>	11	17.41	3.82	27.45	0.36	0.68	24.59	2.59	27.45	0.14
	Duruitoarea Veche	<i>U. spelaeus</i>	6	19	3	22	0.29	2.42	30.21	0.64	33.28	0.57
	Butești	<i>U. spelaeus</i>	2	19.25	5	24.25	0.5	0.5	36.5	0.25	37.25	0
W-Balkans and W-Rhodopes												
	Borikovska	<i>U. spelaeus</i>	48	11.53	2.55	14.07	0.19	2.34	30.63	0.64	33.61	1.48
	Magura	<i>U. ingressus</i>	8	11.94	4.38	15.06	0.38	1.44	25.4	1.31	28.15	1.29
	Bacho Kiro	<i>U. spelaeus</i>	5	10	3.6	14.1	0.2	2	31.67	1.7	35.37	0.9
	Lakatnik	<i>U. spelaeus</i>	4	11.88	0.38	12.5	0	0.25	20.63	0.13	21	0.5
Central Balkans												
	Ušacka	<i>U. spelaeus</i>	11	10.41	5.14	15.48	0.64	1.09	20.14	0.05	21.27	0.27
	Hadzi Prodanova	<i>U. spelaeus</i>	11	13.86	2.27	16.29	0	1.23	22.02	0.14	23.38	0.59
	Risovača	<i>U. spelaeus</i>	10	17.35	0.9	18.15	0	0.65	28	0.3	28.95	0.4
Extant												
	North America	<i>U. americanus</i>	9	13.56	2.56	16.12	0	5.44	19	3	27.44	0
	Greece	<i>U. arctos</i>	4	13	7	20	0.5	9.25	8.5	2.25	20	2
	Central Europe	<i>U. arctos</i>	10	17.5	3.4	20.9	0	5.4	22.5	8.3	36.2	2.1
	North America	<i>U. arctos</i>	8	18.25	3	21.25	0	6.75	18.38	3.25	28.38	0.25
	Kamchatka	<i>U. arctos</i>	23	16.22	3.83	20.05	0.1	6.96	19.78	4.78	31.52	0.35
	Northern Europe	<i>U. arctos</i>	9	15.78	3.78	19.56	0	6.44	23.33	2.67	32.44	0.22
	Eastern Asia	<i>A. melanoleuca</i>	4	19.25	0	19.25	0	8.5	46.25	0	54.75	0
	Polar circle	<i>U. maritimus</i>	13	11	3.21	14.23	2.79	4.5	16.21	0.07	20.15	0

all populations presented puncture pits (NPP) and gouges (NG) (Fig. 3A–B–C). A detailed description of dental microwear patterns can be found in the Supplementary Materials, section 3.1., along with extended population-level comparisons. Multivariate analysis of microwear patterns (i.e., NFS, NCS, NSP, NLP, SWS, NG and NPP) using PERMANOVA revealed significant differences between populations from the Romanian Carpathians ($R^2 = 0.276$, $p = 0.001$), indicating marked dietary variation across sites. Importantly, the lack of significant differences in within-group dispersion ($p = 0.174$) suggests that these differences reflect genuine shifts in population-level dietary preferences rather than variation in dietary breadth within populations. Permutation-based tests further confirmed that no individual population exhibited unusually high or low intra-population variability (all $p > 0.1$), reinforcing the conclusion that dietary divergence occurred primarily between, rather than within, populations in the Romanian Carpathians (see Duñó-Iglesias (2025) for underlying statistical information).

When compared with extant bear populations, the microwear scores (NTS, NTP, NG, NPP) and the distribution of scratches (coarse vs fine) and pits (small vs large) size are similar to omnivorous *U. arctos* from Greece, Central and Northern Europe, Kamchatka and North America as well as *U. americanus* from North America (a detailed population by population description of similarities with reference dataset bear populations can be found in Supplementary Materials, section 3.1.1.).

The Pleistocene *U. arctos* from Bisericuța displays notable differences with contemporaneous *U. spelaeus* populations as well as with reference ursids, due to displaying a predominance of coarse over fine scratches (opposed to *U. spelaeus* and extant omnivorous bears). Finally, the two

Holocene-age *U. arctos* from ACCG, present similarities with fossil *U. spelaeus*, due to a predominance of fine scratches over coarse and small pits over large ones (see Supplementary Materials, Fig. 3).

The fossil populations occupy distinct eco-regions within the bivariate plot (Fig. 4A). Urşilor, Bisericuța, and Oase are primarily distributed within the soft mast-dominated region, situated near the omnivorous *U. arctos* population from Greece. However, their error bars extend into regions associated with omnivorous bears exhibiting vertebrate-dominated diets, overlapping with populations from northern latitudes, such as *U. arctos* from North America. Notably, Oase displays the most extensive extension into the vertebrate-dominated region, overlapping with *U. arctos* populations from Kamchatka and Northern Europe. The Cioclovina population falls within the vertebrate-dominated region but its error bars extend into both the soft mast- and hard mast-dominated regions, exhibiting the most extensive variability among populations. This wide range mirrors the dietary breadth displayed by *U. arctos* from Kamchatka and Northern Europe, which are characterized by highly variable omnivorous diets. Finally, the Muierilor population is located within the vertebrate-dominated eco-region, overlapping with northern omnivorous bears, while its error bars extend significantly into the hard mast-dominated region, overlapping with *U. arctos* from Central Europe.

The extinct ursid populations exhibit distinct distributions within the CA plot (Fig. 4B). The *U. spelaeus* from the Romanian Carpathians displays a wide range of distribution, in comparison to any other species represented in the analysis. The different *U. spelaeus* populations show variability in their placement on the plot, reflecting differences based on

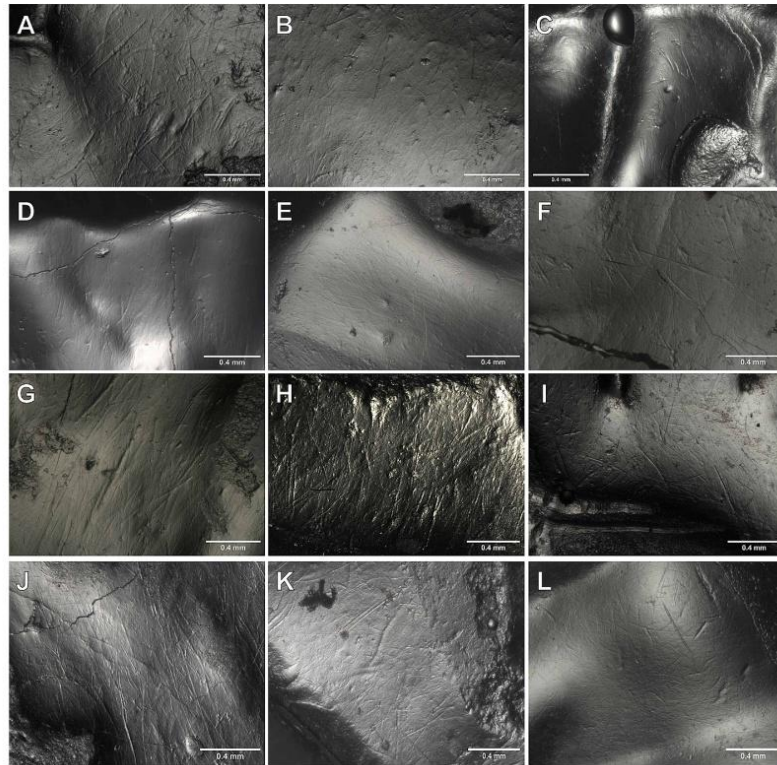


Fig. 3. Photomicrographs (at $\times 35$ magnification) of the grinding non-faceted enamel surface of selected fossil individuals of *U. spelaeus* sensu lato from: Romanian Carpathians. A: Muierilor (#PM/R6-0-I-X6) individual displaying gouges; B: Cioclovina (#18il/107) individual displaying puncture pits; C: Cioclovina (#18il/101) individual displaying puncture pits. Moldavian Plateau. D: Trinca (#Tr-I-80-41) individual displaying puncture pits and a pattern dominated by fine over coarse scratches; E: Saharna (#SH/3-31/55) individual exhibiting puncture pits and predominantly fine scratches; F: Buzdijeni (#ERIS-25) individual displaying high counts of coarse scratches as well as presence of gouges. Western Balkan Mountains and Western Rhodopes. G: Borikovska (#116C) individual displaying hypercoarse and coarse scratches, along with small and large pits; H: Magura (#MII/53) individual exhibiting gouges, large pits and a clear predominance of coarse over fine scratches; I: Magura (#M3/1532) individual exhibiting both coarse and fine scratches, along with large and small pits, and gouges. Central Balkans. J: Risovača (#RIS92/284) individual, displaying fine and coarse scratches. K: Ušacka (#85/1048) specimen displaying a mix of coarse and fine scratches, as well as gouges. L: Hadži Prodanova (#HPP04/172/5) specimen, exhibiting fine and coarse scratches and one hypercoarse scratch. Scale bar = 0.4 mm.

their cave of origin. Within each cave population, some groups cluster tightly, indicating more uniform diets, while others are more dispersed, suggesting greater dietary diversity. The fossil *U. arctos* populations, are positioned to the right along the x-axis and above the y-axis (Fig. 4B). This placement indicates a higher number of coarse scratches relative to fine scratches, and a relatively high number of large pits in comparison to most *U. spelaeus* individuals. However, there is a certain degree of overlap between MIS 3 *U. arctos* and *U. spelaeus* from the Romanian Carpathians.

When compared to extant bear populations, the majority of *U. spelaeus* specimens from the Urşilor and Oase populations cluster on the right side of the x-axis, separating from the extant omnivorous bear populations (*U. arctos* and *U. americanus*) while some of them display an overlap with *U. maritimus* (Fig. 4B). This positioning can be attributed to their higher number of coarse scratches and, consequently, a higher SWS compared to the omnivorous reference bears, i.e., a higher preference for hard object consumption. However, a significant portion of the individuals from the Urşilor ($n = 6$: 11.1 %) and Oase ($n = 6$: 23.1 %) populations overlap with extant omnivorous bear species.

Although there is a certain degree of differentiation from extant bears, and some populations overlap with *A. melanoleuca* (with a graminivorous tough diet), a significant proportion of *U. spelaeus* individuals fall within the range of *U. americanus* and *U. arctos* populations

from Kamchatka, North America, and the northern regions of Europe, as well as with the central European population (Fig. 4B); all with a shared omnivorous nature including a wide range of items in their diets (soft and hard mast plants, as well as vertebrates). Finally, some individuals overlap with *U. maritimus* with a higher number of coarse scratches (see Supplementary Materials, section 3.1.3. for a detailed population by population description).

The *U. arctos* individual from Biseriçuța ($n = 1$; dating to the Pleistocene), plot on the right side, overlapping with certain Oase and Urşilor cave bear individuals (Fig. 4B). Among extant reference bears, this directional placement is exclusively associated with the hypercarnivorous *U. maritimus*, whose diet is characterized by a high proportion of vertebrates. Thus, we infer that the *U. arctos* individual analysed here similarly consumed a diet rich in hard objects, as driven by their high SWS. Nevertheless, two individuals from ACCG ($n = 2$) which date of medieval times, present a more diverse distribution, with one falling closer to the left side of the plot, while the other falls not far from the Pleistocene *U. arctos* from Biseriçuța within the right side of the plot (Fig. 4B). Nevertheless, all *U. arctos* analysed tend to differentiate from Pleistocene cave bears and extant reference bears. Furthermore, due to their statistically null ($n = 1$) in case of Biseriçuța and statistically insignificant ($n = 2$) due to low number of ACCG, their ecological niche cannot be inferred properly as lacking more individuals.

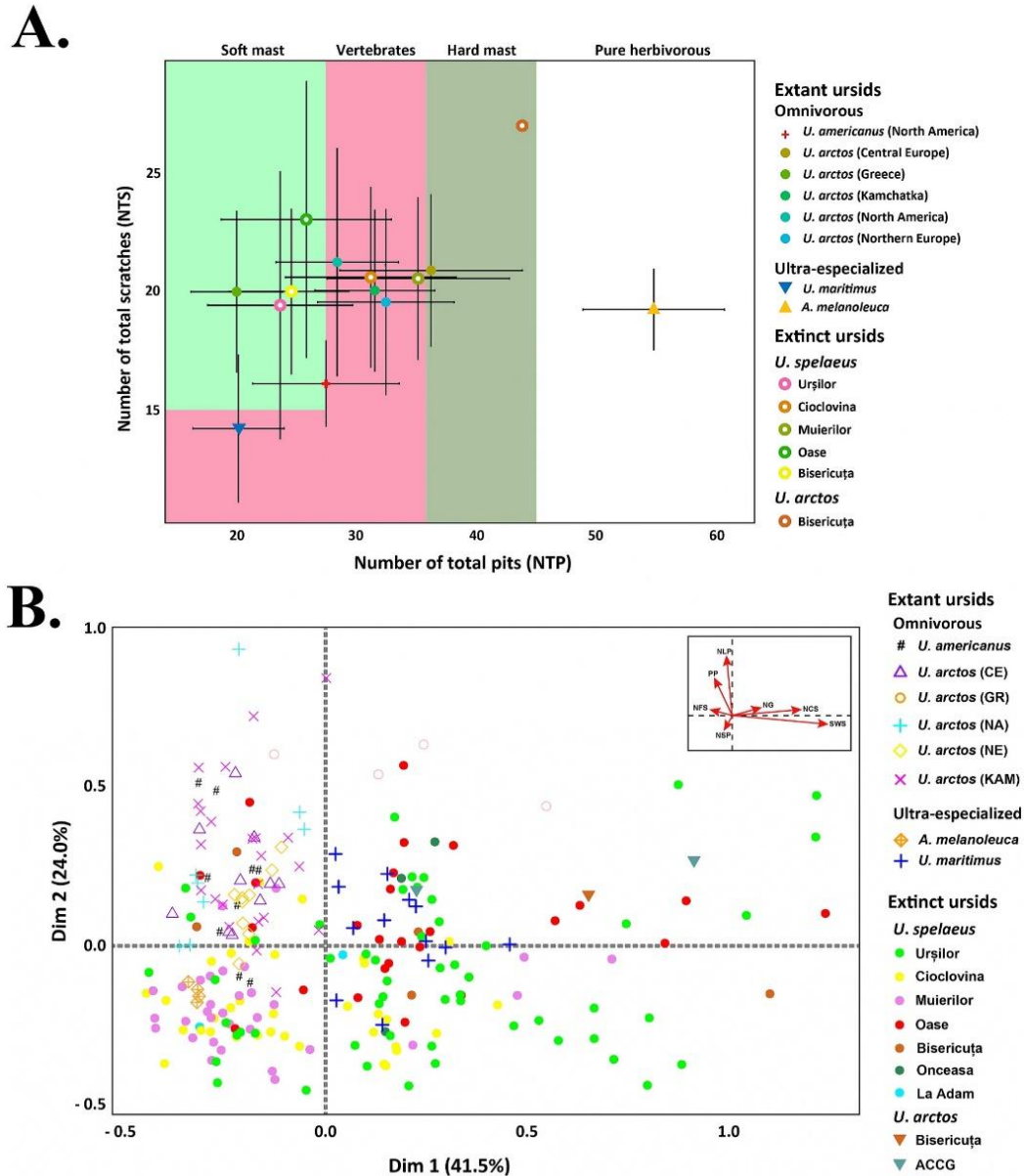


Fig. 4. Romanian Carpathians: A. Bivariate plot of the number of total pits (NTP) and the number of total scratches (NTS) comparing the extant bear populations and the fossil populations. Highlighted are four distinct eco-regions (soft mast, hard mast, vertebrates, and pure herbivorous) based on the predominant diet of extant bear populations as established by Papp et al. (2019). B. Correspondence analysis (CA) based on seven microwear variables: number of fine scratches (NFS), coarse scratches (NCS), small pits (NSP), large pits (NLP), gouges (NG), puncture pits (NPP), and the scratch width score (SWS). The analysis compares fossil populations of *U. spelaeus* and *U. arctos* from the Romanian Carpathians with a reference dataset of extant ursids established by Papp et al. (2019). Auxiliary plot in the upper right illustrates variable loadings, with red vectors depicting the direction and relative contribution of each microwear variable to the first two CA dimensions. Abbreviations: CE = Central Europe; GR = Greece; NA = North America; NE = Northern Europe; KAM = Kamchatka. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

4.2.2. Moldavian Plateau

Microwear analysis of *U. spelaeus* from Moldavian Plateau reveals notable differences between cave sites, regarding NTS and NTP (Table 2). However, the predominance of fine over coarse scratches results in consistently low SWS across all populations (Table 2). Microwear analysis of fossil bear populations from the Moldavian

Plateau also reveals substantial inter-population variability in both the total number of scratches (NTS) and total number of pits (NTP). A detailed description of dental microwear patterns can be found in the Supplementary Materials, section 3.2, along with extended site-level comparisons.

Multivariate analysis of microwear variables (NFS, NCS, NSP, NLP,

SWS, NG, and NPP) using PERMANOVA showed statistically significant differences between populations ($R^2 = 0.412$, $p = 0.001$), suggesting marked dietary variation across sites. However, the test for homogeneity of dispersion yielded significant results ($p = 0.021$), implying that differences among populations may be partially influenced by variation in dietary breadth. Nevertheless, post hoc permutation tests for intra-population variance revealed that none of the individual populations displayed significantly high or low variability (all $p > 0.1$), suggesting that the observed differences likely reflect genuine shifts in dietary preferences across sites. These findings highlight the complexity of ecological behaviours among fossil bear populations in the region (see Duñó-Iglesias (2025) for underlying statistical information).

Regarding puncture pits, Saharna (NPP = 3.11) and Buzdujeni (NPP = 2.59) recorded high values, while Duruitoarea Veche (NPP = 0.64), and Butești (NPP = 0.25) also displayed them. Regarding gouges, all populations exhibit values ranging from low gouge counts, such as Duruitoarea Veche (NG = 0.57) and Saharna (NG = 0.28), to negligible levels: Trinca (NG = 0.09), Buzdujeni (NG = 0.14). While no gouges were observed in Butești (NG = 0.00). The microwear patterns of *U. spelaeus* populations from the Moldavian Plateau exhibit strong similarities to those of omnivorous bears, specifically *U. americanus* and *U. arctos* from North America, Kamchatka, and Central Europe (see Supplementary Materials, section 3.2. for a more detailed site by site description).

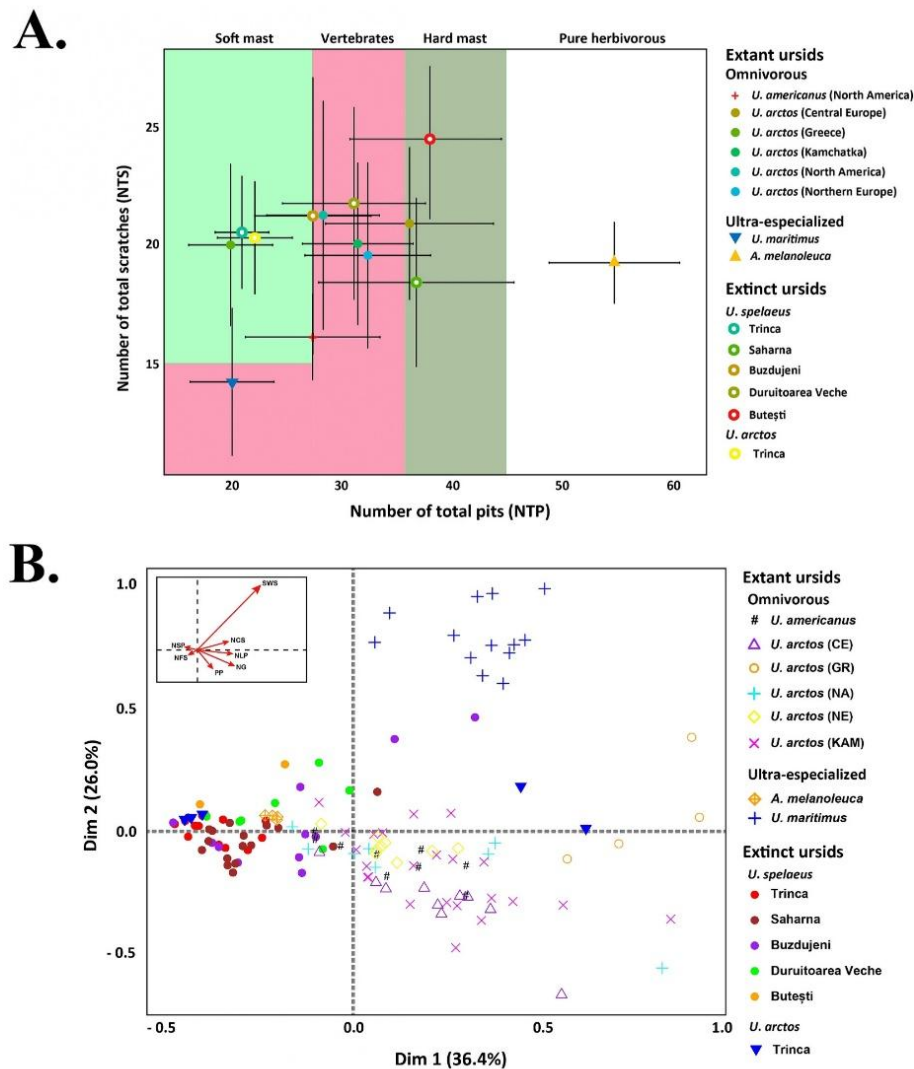


Fig. 5. Moldavian Plateau: A. Bivariate plot of the number of total pits (NTP) and the number of total scratches (NTS) comparing the extant bear populations and the fossil populations. Highlighted are four distinct eco-regions (soft mast, hard mast, vertebrates, and pure herbivorous) based on the predominant diet of extant bear populations as established by Pappa et al. (2019). B. Correspondence analysis (CA) based on seven microwear variables: number of fine scratches (NFS), coarse scratches (NCS), small pits (NSP), large pits (NLP), gouges (NG), puncture pits (NPP), and the scratch width score (SWS). The analysis compares fossil populations of *U. spelaeus* and *U. arctos* from the Moldavian Plateau with a reference dataset of extant ursids established by Pappa et al. (2019). Auxiliary plot in the upper left illustrates variable loadings, with red vectors depicting the direction and relative contribution of each microwear variable to the first two CA dimensions. Abbreviations: CE = Central Europe; GR = Greece; NA = North America; NE = Northern Europe; KAM = Kamchatka. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Despite the limited sample size ($n = 5$), the *U. arctos* population from Trinca shows a different microwear pattern than co-occurring *U. spelaeus* from Trinca (regarding SWS and NTP), but comparable with contemporaneous populations of *U. spelaeus* of the same region. In comparison to referential bears, it shows similar values to omnivorous *U. arctos* populations.

The fossil populations from the Moldavian Plateau are distributed across distinct ecological regions in the bivariate plot (Fig. 5A). *U. spelaeus* and *U. arctos* from Trinca fall within the soft mast-dominated

region, closely aligning with omnivorous *U. arctos* from Greece. *U. spelaeus* from Buzdujeni lies near the soft mast–vertebrate boundary, close to *U. arctos* from Kamchatka, which consumes high amounts of vertebrates within a soft mast-based omnivorous diet. Buzdujeni overlaps with *U. americanus* from North America, with an omnivorous diet including soft mast and vertebrates, particularly fish. *U. spelaeus* from Duruitoarea Veche is positioned in the vertebrate-dominated region, overlapping with *U. arctos* from Northern Europe and Kamchatka, with error bars extending into the soft and hard mast regions, overlapping

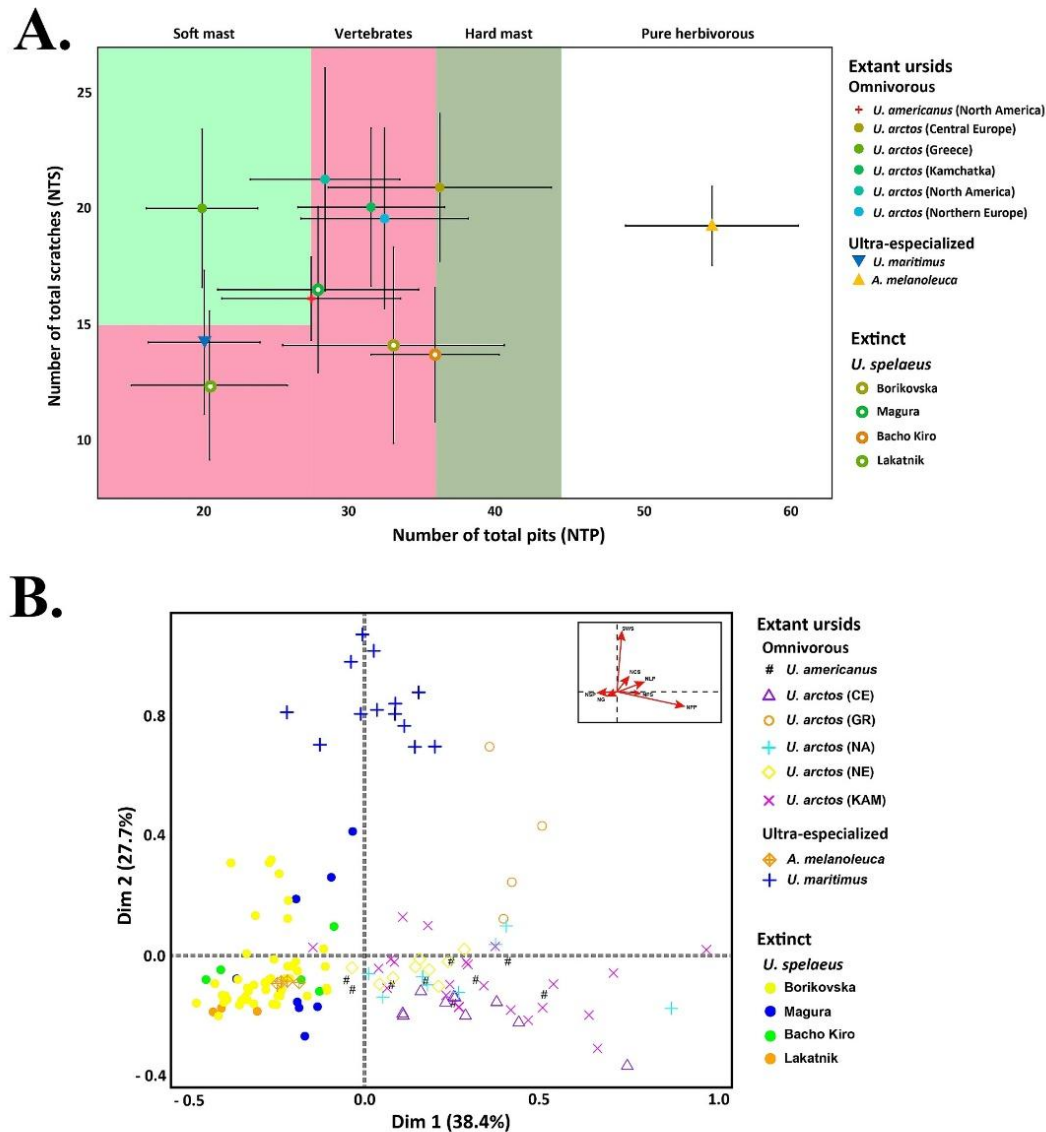


Fig. 6. Western Balkan Mountains and Western Rhodopes: A. Bivariate plot of the number of total pits (NTP) and the number of total scratches (NTS) comparing the extant bear populations and the fossil populations. Highlighted are four distinct eco-regions (soft mast, hard mast, vertebrates, and pure herbivorous) based on the predominant diet of extant bear populations as established by Pappas et al. (2019). B. Correspondence analysis (CA) based on seven microwear variables: number of fine scratches (NFS), coarse scratches (NCS), small pits (NSP), large pits (NLP), gouges (NG), puncture pits (NPP), and the scratch width score (SWS). The analysis compares fossil populations of *U. spelaeus* from the Western Balkan Mountains and Western Rhodopes with a reference dataset of extant ursids established by Pappas et al. (2019). Auxiliary plot in the upper right illustrates variable loadings, with red vectors depicting the direction and relative contribution of each microwear variable to the first two CA dimensions. Abbreviations: CE = Central Europe; GR = Greece; NA = North America; NE = Northern Europe; KAM = Kamchatka. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

with *U. arctos* from Central Europe, with variable omnivorous diet rich in vertebrates. *U. spelaeus* from Saharna and Butești fall within the hard mast-dominated region, overlapping with *U. arctos* from Central Europe and extending into the vertebrate region, with omnivorous northern hemisphere bears with high vertebrate intake. While Saharna aligns more closely with *U. americanus*. Despite the small sample size ($n = 2$), the elevated scratch counts and high pit density of the Butești population suggest a hard mast-based omnivorous diet (Fig. 5A).

The fossil populations of *U. spelaeus* exhibit a clustered (and concentrated) distribution within the CA plot, with most *U. spelaeus* individuals positioning in the lower-left quadrant of the plot, distinguishing them from extant omnivorous bears and overlapping them close to *A. melanoleuca* with a graminivorous diet based on abrasive foliage. While the *U. spelaeus* population from Trinca clusters close to *A. melanoleuca* (Fig. 5B), indicating a uniform diet focused on soft mast consumption, the populations from Saharna, Duruitoarea Veche, and particularly Buzdujeni exhibit a broader distribution, extending towards the right side of the plot, overlapping with the dietary range of omnivorous bear species (Fig. 5B; see Supplementary Information, section 3.2.3. for a detailed comparison). This distribution further supports the presence of dietary variability within the *U. spelaeus* populations from Moldavian Plateau. The fossil *U. arctos* population from Trinca exhibits a broad distribution on the CA plot (Fig. 5B). While three individuals cluster near *A. melanoleuca*, alongside other *U. spelaeus* specimens, two individuals deviate significantly towards the lower-right region of the plot, overlapping with the dietary range of omnivorous bear species. The *U. arctos* population from Trinca ($n = 5$) displays a microwear pattern distinct from the coexisting *U. spelaeus*, with notably higher values in scratch width (SWS), number of pits (NTP), and gouges (NG), despite similar total scratch counts. These results suggest dietary differences between the two taxa at the same site, as can be observed in the CA plot (Fig. 5B; see Supplementary Information, section 3.2.2 and 3.2.3. for a detailed comparison).

4.2.3. Western Balkan Mountains and Western Rhodopes

The microwear analysis of the cave bear populations from Western Balkan Mountains and Western Rhodopes reveals that the total number of scratches (NTS) and the total number of pits (NTP) varies significantly among the different cave populations, likewise in puncture pits (NPP) and gouges (NG) (Table 2; see Supplementary Materials, section 3.3. for a more detailed site by site description). It is important to note that the Borikovska cave bear specimens exhibited a notable presence of hypercoarse scratches (Fig. 3G), with a mean value of 0.5, observed in 30 % of the individuals ($n = 48$).

Microwear analysis of fossil bear populations from the Western Balkans and Western Rhodopes reveals considerable variability in both total scratches (NTS) and pits (NTP) (Fig. 6A). Multivariate analysis of microwear features (NFS, NCS, NSP, NLP, SWS, NG, and NPP) using PERMANOVA identified statistically significant differences between populations ($R^2 = 0.195$, $p = 0.003$), suggesting notable dietary divergence across sites. Importantly, the test for homogeneity of dispersions was not significant ($p = 0.156$), indicating that these differences are unlikely to result from variation in dietary breadth within populations. This interpretation is supported by permutation-based tests of intra-population variance, which showed no population exhibited significantly high or low variability (all $p > 0.1$). While the degree of inter-population divergence is slightly lower than that observed in the Romanian Carpathians and Moldavian Plateau, the results nonetheless point to consistent patterns of regional dietary differentiation among *U. spelaeus* populations (see Duñó-Iglesias (2025) for underlying statistical information).

Regarding the comparison with the extant bears reference dataset, the *U. spelaeus* populations from the Western Balkans and Western Rhodopes most closely resemble extant *U. arctos* from Central, Northern Europe, Kamchatka, and Greece, particularly in their high pit counts and moderate to high coarse scratch and gouge values, indicating similar

omnivorous diets including hard and soft mast, while vertebrate consumption cannot be ruled out. Additionally, their low NTS and NFS counts align them more closely with *U. maritimus*, suggesting reduced abrasive plant matter consumption relative to the compared extant omnivorous bears (see Supplementary Materials, section 3.3.1. for a more detailed population by population description).

The cave bear populations from Western Balkan Mountains and Western Rhodopes display intra-population variability among them (Fig. 6A), although they predominantly cluster within the vertebrate-dominated region of the bivariate plot (see Supplementary Materials, section 3.3.2. for a more detailed site by site description). Regarding the CA plot, the fossil cave bear populations from this region are clustered in the lower-left region of the plot, occupying the negative space along both the x- and y-axes (Fig. 6B). This placement differentiates them from extant omnivorous bears and makes them fall close to *A. melanoleuca* and *U. arctos* from Northern Europe and *U. americanus*. Nevertheless, those exhibit partial overlap along the y-axis (explaining 27.7 % of the variance) with omnivorous bear populations such as *U. arctos* from Kamchatka, Central Europe, North America, Northern Europe and *U. americanus* (see Supplementary Materials, section 3.3.3. for a more detailed site by site description).

4.2.4. Central Balkans

Microwear analysis of *U. spelaeus* populations from the Central Balkans reveals that the total number of scratches (NTS) and pits (NTP) varies among different cave populations (Table 2). Variation is also observed in the scratch width, pit size, puncture pits (NPP), and gouges (NG). PERMANOVA results reveal statistically significant differences between populations ($R^2 = 0.522$, $p = 0.001$), indicating the strongest inter-population divergence observed among the regions analysed. Importantly, the test for homogeneity of dispersion was not significant ($F = 0.38$, $p = 0.687$), confirming that the observed differences reflect genuine shifts in population-level dietary preferences, rather than variation in dietary breadth within populations. This interpretation is further supported by permutation-based tests for intra-population variance, which showed that no population exhibited significantly high or low variability (all $p > 0.05$). Notably, while the Romanian Carpathians, Moldavian Plateau as well as the Western Balkans and Western Rhodopes also exhibited significant dietary variation with similarly non-significant dispersion (i.e., all populations showed comparable levels of within-group dietary consistency). These findings position the Central Balkans as a region of strong dietary differentiation among fossil bear populations while dietary consistency was maintained within the same localities (see Duñó-Iglesias (2025) for underlying statistical information).

Finally, regarding hypercoarse scratches, those were only displayed by Risovača population specimens, although in low numbers ($n = 3$: 30 %), as well as for Ušacka ($n = 1$: 9 %; Fig. 3K). The *U. spelaeus* populations from the Central Balkans show the greatest similarity in microwear scores with *U. americanus*, and *U. arctos* from Greece, Kamchatka, and Central Europe, as well as with *U. maritimus* (see Supplementary Materials, section 3.4.1. for a more detailed population by population description).

The *U. spelaeus* populations from Central Balkans exhibit a degree of intra-population variability (Fig. 7A); however, their distribution on the bivariate plot remains clustered near the boundary between vertebrate-dominated and soft-mast-dominated dietary regions (see Supplementary Materials, section 3.4.2. for a more detailed population by population description).

The *U. spelaeus* populations from Hadži Prodanova and Ušacka are positioned in the lower-most section of the soft-mast-dominated region, with total pit values (x-axis) overlapping those of *U. arctos* from Greece and *U. maritimus* (Fig. 7A). Additionally, the error bars for Hadži Prodanova extend into the range of *U. americanus* within the soft-mast-dominated region. Despite this, their relatively low total scratch counts (y-axis) bring them closer to *U. maritimus*, while their error bars

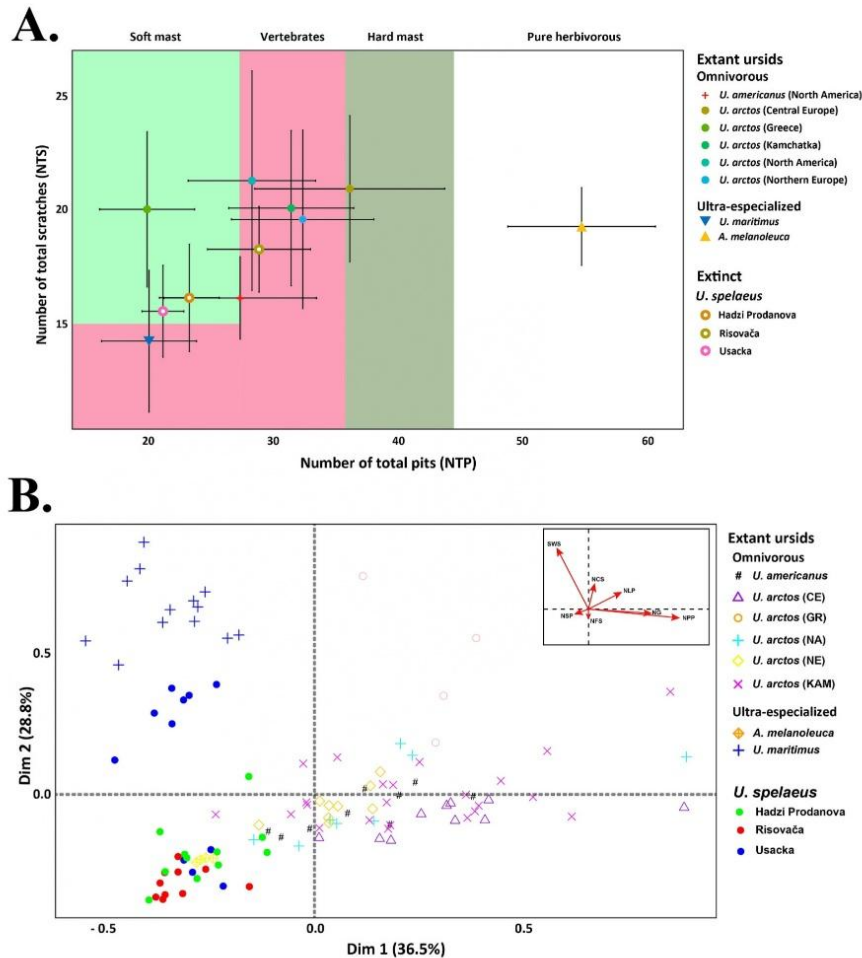


Fig. 7. Central Balkans: A. Bivariate plot of the number of total pits (NTP) and the number of total scratches (NTS) comparing the extant bear populations and the fossil populations. Highlighted are four distinct eco-regions (soft mast, hard mast, vertebrates, and pure herbivorous) based on the predominant diet of extant bear populations as established by Pappa et al. (2019). B. Correspondence analysis (CA) based on seven microwear variables: number of fine scratches (NFS), coarse scratches (NCS), small pits (NPS), large pits (NLP), gouges (NG), puncture pits (NPP), and the scratch width score (SWS). The analysis compares fossil populations of *U. spelaeus* from the Central Balkans with a reference dataset of extant ursids established by Pappa et al. (2019). The direction and contribution of the variables in the CA plot are depicted in the top-right inset of the figure. Auxiliary plot in the upper right illustrates variable loadings, with red vectors depicting the direction and relative contribution of each microwear variable to the first two CA dimensions. Abbreviations: CE = Central Europe; GR = Greece; NA = North America; NE = Northern Europe; KAM = Kamchatka. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

extend towards the vertebrate-dominated region. In contrast, the Risovača population falls within the vertebrate-dominated region, positioned higher on the y-axis, overlapping with *U. arctos* from Northern Europe, Kamchatka, and North America, as well as with *U. americanus* (Fig. 7A).

The fossil *U. spelaeus* populations from Central Balkans exhibit a clustered distribution in the lower-left region of the plot, occupying negative values along both the x- and y-axes (Fig. 7B). This placement differentiates them from extant omnivorous bears, positioning them closer to *A. melanoleuca*, *U. arctos* from Northern Europe, and *U. americanus*. However, some individuals from Hadzi Prodanova ($n = 3$; 27.27 %) extend towards the cluster of omnivorous bears from the northern-most hemisphere such as *U. arctos* from North America and Northern Europe, as well as *U. americanus* (Fig. 7B). Hence, Hadzi Prodanova exhibits a degree of intra-population variability, which is associated with the presence of gouges and puncture pits, which are more

characteristic of extant omnivorous bears. Furthermore, most of the Usacka population ($n = 7$; 63.63 %) deviates from this main cluster, positioning itself closer to *U. maritimus*. This differentiation is primarily driven by a higher scratch width score (SWS), indicating higher counts of coarse to fine scratches in comparison to other Central Balkans *U. spelaeus* populations (Fig. 7B).

4.2.5. Interregional analysis

In the interregional correspondence analysis of all populations (CA; Fig. 8A-B), the Romanian Carpathians exhibit the broadest distribution, indicating the highest degree of variability in the microwear pattern. This is clearly visible in the convex hulls plot (Fig. 8B), where all regional ellipses are nested within the Romanian Carpathians hull, although some individuals extend beyond its boundaries at the lower extremes. Furthermore, considerable overlap exists among the regions of Moldavian Plateau, Western Balkan Mountains and Western

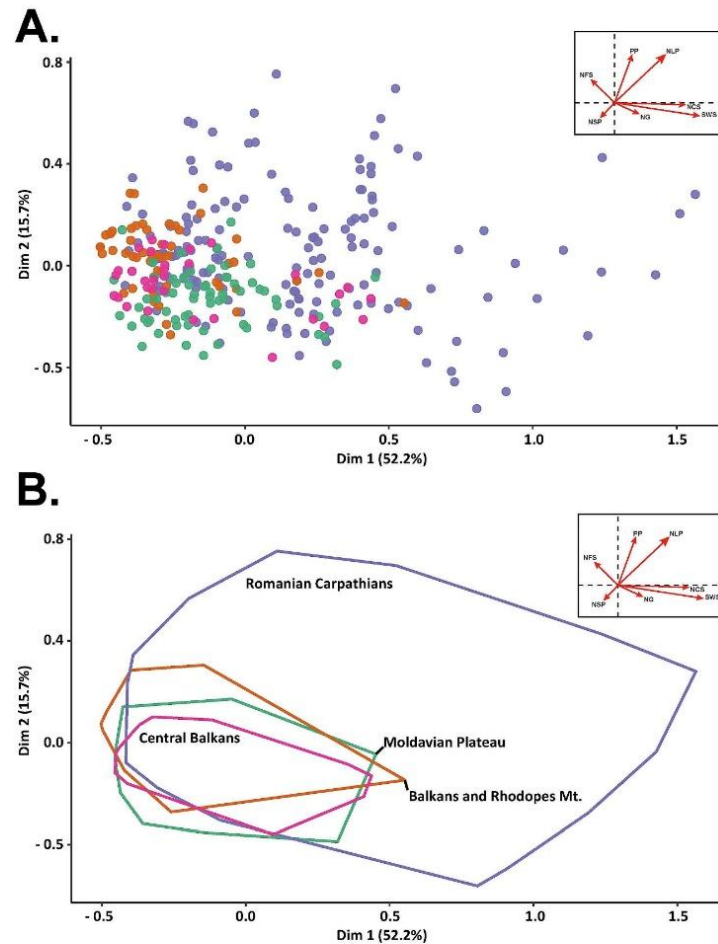


Fig. 8. Correspondence analysis (A) based on seven microwear variables: number of fine scratches (NFS), coarse scratches (NCS), small pits (NSP), large pits (NLP), gouges (NG), puncture pits (NPP), and the scratch width score (SWS). The analysis compares cave bear (*U. spelaeus* sensu lato) populations from different regions: Romanian Carpathians (purple), Moldavian Plateau (green), Western Balkan Mountains and Western Rhodopes (orange) and Central Balkans (pink). A) Individual-level CA coloured by region. B) Same plot with group outlines (convex hulls) highlighting regional populations. Auxiliary plots in the upper right illustrate variable loadings, with red vectors depicting the direction and relative contribution of each microwear variable to the first two CA dimensions. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Rhodopes, and Central Balkans (Fig. 8B; see Supplementary Materials section 3.5. for a more detailed description).

The left area of the plot, where the bulk of Moldavian Plateau, Western Balkan Mountains and Western Rhodopes and Central Balkans cluster is characterized by a high number of small pits (NSP) and fine scratches (NFS), coupled with a relatively low number of coarse scratches (NCS), resulting in a low scratch width score (SWS). Additionally, puncture pits (NPP), gouges (NG), and large pits (NLP) exhibit moderate to low frequencies in this area, indicative of diets dominated by soft mast items. In contrast, some individuals of this populations partially extend towards the right side of the plot (Fig. 8). This right-side region is characterized by a higher prevalence of coarse scratches (NCS), thus resulting in elevated SWS values.

Finally, it is noteworthy that several individuals from the Romanian Carpathians extend into the uppermost area of the plot. This pattern reflects elevated values for puncture pits (NPP) and large pits (NLP), features that characterize and distinguish Romanian Carpathians cave bears from those of other regions. This microwear signature likely corresponds to a diet enriched with hard mast resources, such as seeds and

tough-coated fruits, a pattern characteristic of some Romanian Carpathian populations.

4.2.6. *U. spelaeus* and *U. arctos* dental microwear comparison during the MIS 3

To assess dietary differences and ecological interactions between cave bears (*U. spelaeus*) and brown bears (*U. arctos*) during MIS 3, as well as the dietary evolution of *U. arctos* from the Pleistocene to the Holocene, microwear patterns were analysed across all studied populations. These populations included *U. spelaeus* ($n = 307$) and *U. arctos* from MIS 3 ($n = 6$), as well as Holocene *U. arctos* from Romanian Carpathians ($n = 2$). Given the very limited sample size for *U. arctos*, these results must be interpreted with caution and should be considered preliminary.

Two correspondence analyses were performed, one with population averages and the other with individual species level (for more details about the CA see Supplementary Materials section 3.6.). When examining the correspondence analysis based on population averages, a clear pattern emerges (Fig. 9). Holocene *U. arctos* plots in proximity to large pits (NLP), coarse scratches (NCS), and scratch width score (SWS),

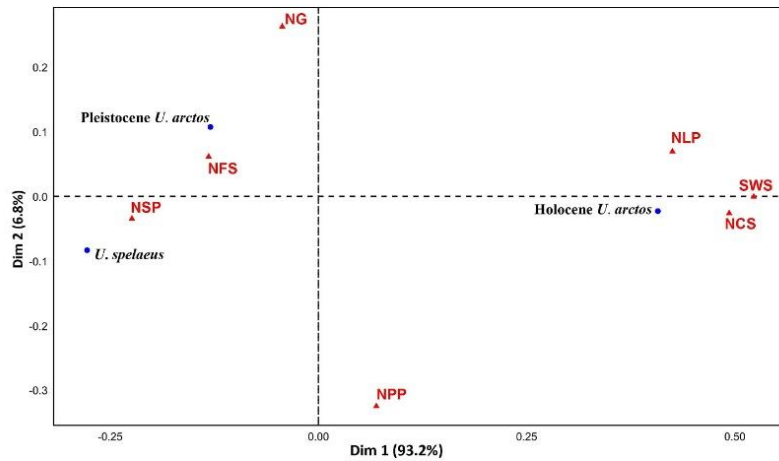


Fig. 9. Correspondence analysis (CA) showing the relationships between microwear variables (red triangles) and population means (blue circles) for *U. spelaeus* and *U. arctos* specimens. The analysis includes seven microwear variables: number of fine scratches (NFS), coarse scratches (NCS), small pits (NSP), large pits (NLP), gouges (NG), puncture pits (NPP), and the scratch width score (SWS). Population means were calculated using averaged individual scores per group. The plot includes Late Pleistocene *U. spelaeus* ($n = 307$), *U. arctos* from the same period ($n = 6$), and Holocene *U. arctos* ($n = 2$) from South-Eastern Europe (Romanian Carpathians). Dim 1 explains 93.2 % of the variation and primarily reflects the contrast between coarse/fine scratches and pit sizes (i.e., small versus large pits), while Dim 2 explains only 6.8 %, as the number of gouges and puncture pits contribute very little to the distribution of the populations in the space. Auxiliary plot in the upper right illustrates variable loadings, with red vectors depicting the direction and relative contribution of each microwear variable to the first two CA dimensions. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

suggesting an association with harder or more resistant food items. However, the limited sample size ($n = 2$) precludes generalization and may instead reflect local dietary behaviour in the Romanian Carpathians, where Holocene *U. arctos* have been observed to consume harder items (Fig. 9). Furthermore, Pleistocene *U. arctos* and *U. spelaeus* cluster

in distinct regions, although both lie near fine scratches (NFS), more so in *U. arctos*, while small pits (NSP) are more frequent in *U. spelaeus*. Late Pleistocene *U. arctos* plots closer to gouges (NG), possibly reflecting a harder diet relative to *U. spelaeus*. Although the sample size remains statistically insufficient, it reflects the constraints of the Pleistocene

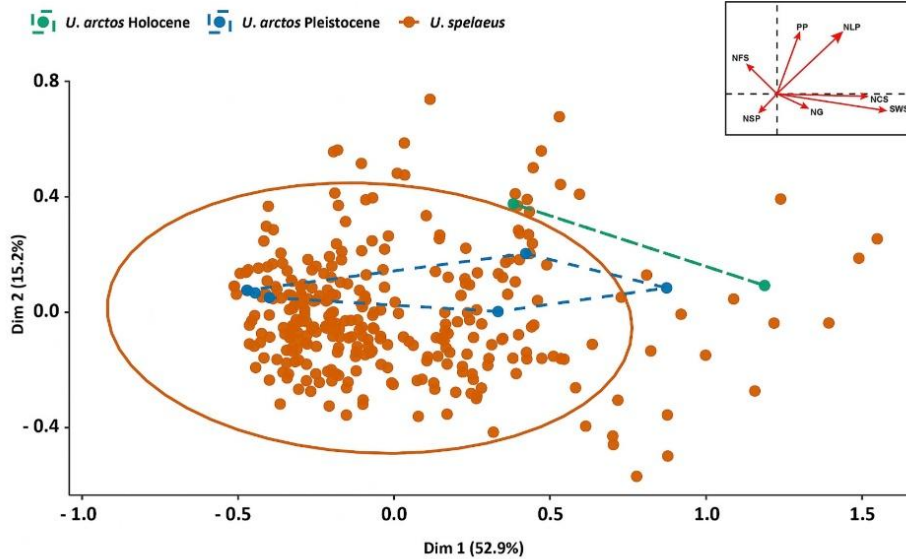


Fig. 10. Correspondence analysis (CA) at the species level comparing *U. spelaeus* (sensu lato) and *U. arctos* based on seven dental microwear variables: number of fine scratches (NFS), coarse scratches (NCS), small pits (NSP), large pits (NLP), gouges (NG), puncture pits (NPP), and scratch width score (SWS). Each point represents an individual specimen. *U. spelaeus* individuals (in orange) are enclosed by a 98 % confidence ellipse, illustrating the range of dietary microwear variation in this fossil taxon. *U. arctos* individuals are represented in two groups: Pleistocene populations (in blue) and Holocene populations (in green), each enclosed within convex hulls to highlight group spread. Auxiliary plot in the upper right illustrates variable loadings, with red vectors depicting the direction and relative contribution of each microwear variable to the first two CA dimensions. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

fossil record and includes individuals from several localities across South-Eastern Europe, offering limited yet potentially informative insights into regional dietary trends. Nonetheless, a larger and more balanced sample of Late Pleistocene *U. arctos* is required to robustly support these preliminary observations.

When correspondence analysis is performed at the individual level, the resulting distribution of all specimens (Fig. 10) suggests a potential niche overlap between *U. spelaeus* and *U. arctos* during MIS 3, where 5 out of 6 *U. arctos* specimens from MIS 3 (83.3 %) fall within the 98 % confidence ellipse of the *U. spelaeus* cluster (Fig. 10). Only one pre-LGM *U. arctos* individual (16.6 %) plots closer to the post-LGM *U. arctos*, though it still overlaps with the *U. spelaeus* distribution. In contrast, Holocene *U. arctos* individuals occupy the margins of the overall distribution, lying outside the 98 % confidence ellipses of both *U. spelaeus* and Pleistocene *U. arctos*, thereby indicating a distinct dietary niche (Fig. 10).

However, conclusions regarding niche relationships between *U. spelaeus* and *U. arctos* must be interpreted with caution due to the substantial imbalance in sample sizes, particularly the limited representation of *U. arctos*. Additional specimens are needed to strengthen the analysis in future studies. The suggested regional niche overlap between Pleistocene *U. arctos* and *U. spelaeus* should be considered tentative. In contrast, Holocene *U. arctos* cannot be meaningfully evaluated, as the sample size ($n = 2$) is both minimal and geographically restricted to a single region.

5. Discussions

5.1. Romanian Carpathians

With the expansion of the sample set, including new site of Cioclovina, and new sampled individuals for the populations of Urşilor and Muierilor and taking into account the populations from previously published sites across a broader temporal and spatial range within the Romanian Carpathians, the results remain consistent with those previously reported at Duñó-Iglesias et al. (2024a). The new data confirm the initial observations of pronounced inter-population dietary flexibility in *U. spelaeus* during the pre-dormancy phase (Duñó-Iglesias et al., 2024a). While statistical analyses reveal that the Romanian Carpathians exhibited distinct, localized dietary adaptations. Each population likely relied on specific food resources available in its region, leading to clear differences in feeding patterns across sites. These dietary differences were locally structured, not mainly driven by variability among individuals within the same population, suggesting that local ecological factors shaped population-level dietary strategies during the Late Pleistocene. Therefore, the expanded dataset reinforces the interpretation that dietary diversity in Carpathian cave bears reflects a sustained local-adapted omnivorous feeding strategy linked to the ecological stability and persistent availability of plant-based resources in the region throughout the MIS 3 period (e.g., Richards et al., 2008; Robu et al., 2013, 2018; Duñó-Iglesias et al., 2024a).

However, an alternative explanation may lie in the inheritance of foraging behaviours through social learning in cave bears. A recent study by Meleg et al. (2024), which correlated isotopic signals from bone collagen with geographic location, sex, and genetic data (DNA) at the individual level, revealed that cave bears adapted their feeding strategies primarily through individual experience rather than being constrained by genetic or environmental factors.

Finally, the presence of puncture pits and gouges remained consistently observable across individuals from the Romanian Carpathians, even with an increased sample size, reinforcing the interpretation that hard-object consumption was a persistent dietary trait of cave bears in this region during MIS 3, potentially indicative of its role before dormancy in Romanian Carpathians glacial refugia (Duñó-Iglesias et al., 2024a).

5.2. Moldavian Plateau

The microwear analysis of *U. spelaeus* populations from Moldavian Plateau reveals notable dietary variability, indicating both specialized and more generalized feeding strategies. The Trinca population exhibits a highly specialized soft mast-dominated diet (Table 2; Fig. 5). Conversely, the Buzdujeni population demonstrates a more variable omnivorous diet, primarily incorporating soft mast and vertebrates (Fig. 5). The Duruitoarea Veche population also follows a diverse dietary pattern, including vertebrates as well as both soft and hard mast. Similarly, the Saharna population exhibits an omnivorous diet with a mix of hard and soft mast, without the possibility to discard the inclusion of vertebrates. The Buteşti population, though based on a small sample size ($n = 2$), presents a high density of pits, suggesting a diet dominated by hard mast. Overall, these *U. spelaeus* populations exhibit distinct dietary strategies, with Trinca showing a specialized reliance on soft mast, while Buzdujeni, Duruitoarea Veche, Saharna, and possibly Buteşti display greater dietary flexibility within predominantly soft-mast-based diets.

5.2.1. Palaeoenvironment of Moldavian Plateau during the late MIS 3: A mix of tundra-steppe and forest refugia

The dietary flexibility observed in some of these populations aligns with the environmental diversity of the Moldavian Plateau region during MIS 3, which supported a mosaic of landscapes ranging from tundra-steppe to forested environments (Gerasimenko, 2006). This period, preceding the LGM, was characterized by significant climatic fluctuations that shaped the regional faunal composition (e.g., David and Lungu, 1972; Markova, 2007; Puzachenko and Markova, 2019). The region generally featured a mix of steppe habitats supporting Mammuthus faunas; including *M. primigenius*, *Coelodonta antiquitatis*, *R. tarandus*, *Megaloceros giganteus* and *Ovibos moschatus*; alongside open-landscape taxa such as *Bison* sp. and *Equus* sp. Additionally, more temperate and forest-adapted species, including *Capreolus capreolus*, *S. scrofa*, and the ecologically flexible *C. elaphus*, indicate the persistence of wooded refugia (e.g., Croitor, 2008; Demay et al., 2019, 2024). The Moldavian Plateau region's proximity to the Carpathians has been linked to the existence of glacial refugia, which may have provided habitat stability for certain taxa during the climatic oscillations of MIS 3 (Sommer and Benecke, 2005; Sommer and Nadachowski, 2006; Sommer and Zachos, 2009; Stewart et al., 2010). This can be linked to the observed consumption of hard objects (such as nuts and hard-shelled fruits) for some population of the region (Xafis et al., 2017). Saharna (43–41 ka cal BP), Duruitoarea Veche (42.6–40 ka cal BP) and Buteşti (41.7–35 ka cal BP), dating to the MIS 3, representing late cave bear populations in the region and notably, both exhibit microwear patterns consistent with hard-mast consumption within a forested glacial refugium.

The faunal assemblage from Buzdujeni, dominated by *Equus* sp. and *Bison* sp., suggests an open tundra-steppe environment at the time of bone accumulation (Croitor and Burlacu, 2020), which is supported by the climatically-cold moment of accumulation, between 43.7 and 40.5 ka cal BP. However, the presence of *C. elaphus* (albeit in low numbers), might indicate patches of forested habitat, as its occurrence during cold phases of MIS 3 typically correlates with forest refugia (Croitor and Burlacu, 2020; Sommer, 2020). The *U. spelaeus* population from Duruitoarea Veche displays individual variation in microwear patterns, with some bears consuming hard objects and others relying more on soft mast. This variability likely reflects environmental conditions shaped by alternating cold and temperate phases, supporting a mosaic landscape of open and forested habitats, along with tundra-steppe biomes during colder periods, as inferred from the site's faunal assemblage (Robu et al., 2025.).

Hence, the microwear analysis from Moldavian Plateau populations displays flexibility that can be linked to alternance of cold and temperate cycles during MIS 3, as well as reinforces the notion of the existence of

some vegetation and tree refugia in Moldavian Plateau before the faunal turnover that happened around ca. 20 ka BP, during the LGM (Willis and Vanandel, 2004; Stuart and Lister, 2011). These refugia likely provided suitable habitats for bear species such as *U. spelaeus* and *U. arctos*, which may have survived in isolated forested patches. From these refugia, brown bear populations are thought to have expanded post-LGM, facilitating the recolonization of northern Europe (Sommer and Bencke, 2005).

5.2.2. Local niche partitioning between *U. spelaeus* and *U. arctos* from Trinca

The *U. spelaeus* individuals from Trinca represent the only cave bears among Moldavian Plateau populations exhibiting a clearly specialized soft-mast diet. This dietary specialisation was likely driven by their coexistence with *U. arctos* at the same locality and the resulting necessity for niche differentiation within an eco-region marked by progressively limited vegetation resources and the total disappearance of temperate forest cover as the LGM approached (Willis and Vanandel, 2004). Moreover, the *U. arctos* from the Moldavian Plateau has a microwear pattern linked to hard object consumption, potentially including hard-shelled fruits or bone (Godfrey et al., 2004; Goillot et al., 2009). Niche partitioning between MIS 3 *U. spelaeus* and *U. arctos* has previously been inferred from microwear analyses in the Carpathians (Duñó-Iglesias et al., 2024a), and this may also apply to the site of Trinca. In contrast, the other Moldavian Plateau *U. spelaeus* populations from MIS 3 exhibit scratch-width patterns comparable to those of contemporary MIS 3 *U. arctos*, indicating a more flexible dietary strategy (see Supplementary Materials, section 3.2.). Such variability in microwear features underscores distinct ecological adaptations among cave bear populations within the same region, likely influenced by local environmental conditions, resource availability, and niche partitioning.

5.3. Western Balkan Mountains and Western Rhodopes

The sites of Lakatnik and Borikovska lack a well-defined stratigraphic context. Lakatnik exhibits a soft mast diet with some possible variation towards vertebrate consumption. Borikovska, in contrast, exhibited a predominantly vertebrate-based diet, overlapping with *U. maritimus* along the y-axis of the bivariate plot. Borikovska exhibits a high number of pits, a feature associated with elevated plant intake in bear microwear analyses (Münzel et al., 2014), likely reflecting occupation of more vegetated habitats relative to Arctic environments. The correspondence analysis further differentiates this population from typical omnivores, with some individuals clustering near *A. melanoleuca* and others near *U. maritimus*. Although hypercoarse scratches are uncommon in herbivorous diets, they have been documented in omnivorous carnivores from temperate environments, where they are linked to bone processing (Goillot et al., 2009; Semperebon et al., 2011). Their presence in Borikovska supports dietary flexibility, including potential consumption of animal matter.

5.3.1. Refugia mosaic environments in mountain ranges from Western Balkan Mountains and Western Rhodopes during the MIS 3

Among the sites where paleoenvironmental data is available, Magura provides evidence of a mosaic environment. In particular, stable isotope analyses on herbivore taxa from Magura, as well as pollen extracted from hyenas' coprolites (Ivanova et al., 2016; Frémontdeau et al., 2020), indicate the presence of steppe vegetation interspersed with patches of taiga and more humid aquatic environments. Isotopic analysis of cave bear remains reveals long-term dietary homogeneity, with all individuals exhibiting low nitrogen ($\delta^{15}\text{N}$) values, and thus herbivory (Frémontdeau et al., 2020). While the co-occurrence of *U. arctos* alongside cave bears in some layers suggests niche partitioning based on the same stable isotope analysis (Frémontdeau et al., 2020). Notably, the isotopic results match with microwear results in some aspects, the Magura cave bear population exhibits a preference for soft mast foods, although certain

individuals show a dietary shift towards harder objects consumption (Fig. 6; for a detailed explanation Supplementary Materials, section 3.3.2.). The diversification towards harder resources, which could be linked to hard-shelled fruits, roots, or animal matter (Goillot et al., 2009; Xafis et al., 2017) might have responded to the necessity to fulfil the energetic requirements of hibernation (Farley and Robbins, 1995; López-Alfaro et al., 2013; Coogan et al., 2014).

Bacho Kiro also reflects a mosaic environment, evidenced by the co-occurrence of steppe-adapted and woodland fauna, and a cold, continental climate inferred from $\delta^{18}\text{O}$ stable isotope analysis indicating marked seasonal temperature variation (Pederzani et al., 2021). The dietary pattern of *U. spelaeus* suggests a predominantly herbivorous diet with notable hard-object consumption. This inference is consistent with the presence of forested environments in the region that would have supported hard-shelled and seeded plant resources. This diversification towards hard-object consumption may reflect the targeting of carbohydrate-rich resources prior to hibernation, a behaviour typical of ursids (Bojarska and Selva, 2012; Coogan et al., 2018) and previously documented in MIS 3 cave bear populations from the Carpathians (Duñó-Iglesias et al., 2024a).

The Balkan Mountains are recognized, through genetic, pollen and mammal fossil analyses, as a refuge from which temperate species expanded throughout Eastern Europe after the Last Glacial Maximum (e.g., Hewitt, 2000; Tzedakis et al., 2002; Sommer and Zachos, 2009; Sadori et al., 2016; Lang et al., 2023). Recent palynological analyses of sediments and coprolites, combined with vegetation reconstructions from Pešturina in the Central Balkans of Serbia (integrated with other paleoenvironmental data of the area, such as northern Balkan slopes and south-west of Southern Carpathians), have suggested a mosaic landscape characterized by dense patches of temperate woodland with high botanical diversity (Carrión et al., 2024; Ochando et al., 2024). Specifically, these studies reported a diverse assemblage of woody taxa persisting continuously throughout the Late Pleistocene, particularly during the final phases of MIS 3 (Ochando et al., 2024). This assemblage includes *Pinus*, *Juniperus*, deciduous *Quercus*, *Acer*, *Alnus*, *Betula*, *Carpinus*, *Corylus*, *Tilia*, *Ulmus*, *Buxus*, *Genisteae*, and *Cistus*, confirming that the Central Balkans served as a refugial area for meso-thermophilic vegetation during MIS 3, with a mosaic landscape encompassing open habitats in high altitude with densely forested patches in the valleys (Jarrión et al., 2024). The microwear results, which highly diverge from one population to the other, support the presence of mosaic environments in the Western Balkan Mountains and Western Rhodopes territory during MIS 3, particularly in the northern slopes of the Western Balkan Mountains ranges and the Western Rhodope Mountains.

Finally, the Borikovska population, dwelling high altitude environments (ca. 1250 m a.s.l.) might have had to rely to other resources, specifically to a higher component of vertebrates and soft mast vegetation, moved by scarcity of plant resources in the alpine areas (Ochando et al., 2024). This dietary adaptation might reflect limited plant-based resource availability resulting from increased snowfall at higher altitudes, as documented for extant *U. arctos* populations (Bojarska and Selva, 2012).

The diversity of dietary signals among cave bear populations reflects occupation of ecologically heterogeneous landscapes, where steppe, boreal taiga, and temperate refugia coexisted. This environmental mosaic likely supported varied pre-hibernation foraging strategies. Such flexibility suggests cave bears adapted their diets to distinct biomes within dynamic environments.

5.4. Central Balkans

The microwear analysis of *U. spelaeus* populations from Central Balkans reveals some-degree of dietary homogeneity (soft-mast dominated) for Hadži Prodanova and Risovača, while Ušacka population differentiates from the former two.

5.4.1. Soft mast diets with evidence of diversification

Hadži Prodanova cave individuals exhibit a general tendency towards a soft-mast-dominated diet, however, three individuals overlap with omnivorous bear populations from northern latitudes, suggesting room for dietary flexibility. Therefore, while the primary diet of this population appears to have been based on soft mast and abrasive plants items, some individuals might have diversified towards a diet that included the consumption of hard objects. The Hadži Prodanova faunal assemblage suggest that Late Pleistocene layers formed during a humid and relatively warm period within MIS 3, characterized by dense forest cover (Bogićević et al., 2017), conditions that are consistent with dietary diversification towards the foraging of hard-shelled and seeded fruits, and underground plant resources such as roots.

The presence of *U. arctos* suggests niche partitioning with *U. spelaeus* (Bogićević et al., 2017), as supported by isotopic (Bocherens et al., 2011) and dental microwear evidence through other sites (Duñó-Iglesias et al., 2024a), wherein *U. spelaeus* maintained a largely plant-based diet, while *U. arctos* exhibited more carnivorous tendencies. At Hadži Prodanova, microwear data for *U. arctos* are needed to further substantiate this dietary partitioning, however, *U. spelaeus* also consumed hard foods, likely reflecting pre-hibernation energetic requirements, as observed for MIS 3 Carpathian populations (Duñó-Iglesias et al., 2024a).

The cave bear population from Risovača predominantly exhibits a diet similar to northern latitude omnivorous bears, soft-mast-dominated, albeit with occasional hard-object consumption. Moreover, the occasional (although scarce) presence of hypercoarse scratches within the Risovača population ($n = 3$: 30 %) further supports a casual inclusion of hard items in their diet; although with a low frequency, the presence of hypercoarse scratches may suggest occasional consumption of vertebrate prey, as such features are otherwise only documented in reference bears for *U. maritimus* (Pappa et al., 2019). Hypercoarse scratches have also been documented in bone-consuming carnivores such as *Crocota* spp. (Rivals et al., 2022), in omnivorous carnivores from temperate regions, where they are linked to enamel contact with bone during feeding (Goillot et al., 2009; Sempere et al., 2011), and in carnivorous and piscivorous mammals inhabiting forested environments (Goillot et al., 2009; Xafis et al., 2017). The herbivore faunal assemblage of Risovača present a dominance of open-landscape species (i.e., *E. ferus*, *E. hydruntinus*, *Bos primigenius*, *Bison* sp.) (Forsten and Dimitrijevic, 1995), this landscape matches with a diet based on abrasive items for cave bear populations, while some individuals might have diversified towards hard-object consumption, in order to diversify the resources to survive hibernation as observed in extant bears from northern latitudes (e.g., Bojarska and Selva, 2012).

The Ušacka cave bear population displays a predominantly soft-mast diet, although vertebrate consumption cannot be ruled out due to overlap with northern latitude omnivorous bears. This soft-mast diet potentially reflects the high-altitude habitat (1200 m a.s.l.) they occupied. Such elevations likely imposed harsher conditions and favored access to more abrasive, open-habitat plant resources. The absence of hypercoarse scratches supports limited vertebrate consumption prior to death, consistent with an abrasive, predominantly herbivorous diet.

Dietary variability among the Hadži Prodanova, Risovača, and Ušacka cave bear populations reflects the ecological heterogeneity of the Central Balkans during MIS 3; a mosaic landscape of temperate woodlands and open steppe habitats (Argant and Dimitrijevic, 2007; Jovanović et al., 2022; Carrión et al., 2024). Open areas offered abundant soft mast (e.g., sprouts, grasses, flowers, leaves), while woodland patches supported occasional hard-mast consumption (e.g., hard-shelled fruits and nuts), likely supplementing herbivorous diets during seasonal scarcity or pre-hibernation.

5.5. Regional niche overlap between *U. arctos* and *U. spelaeus* in SE Europe during MIS 3

Dental microwear data suggests a certain overlap in short-term

dietary niches between Late Pleistocene *U. arctos* and *U. spelaeus* populations from South-Eastern Europe (Figs. 9 and 10). The dietary preferences reconstructed from our limited sample of *U. arctos* suggest a regional scale overlap at a short-term scale (e.g., seasonally) with *U. spelaeus* (Fig. 10). However, we did not find this overlap at the locality of Trinca, where these species co-existed. Hence, more data on *U. arctos* are needed to confirm our hypothesis of a seasonal niche overlapping.

The isotopic signatures (i.e., $\delta^{15}\text{N}$) of pre-Last Glacial Maximum (LGM) brown bears have been interpreted as indicative of a predominantly carnivorous diet (Münzel et al., 2011; Bocherens, 2015; Bocherens et al., 2015; Ersmark et al., 2019), the reported elevated $\delta^{15}\text{N}$ isotopic values may reflect adaptations to carcass scavenging in colder, more open environments (Marciszak et al., 2019). Additionally, high $\delta^{15}\text{N}$ values could result from the consumption of nitrogen-fixing plants (Schwartz et al., 1999; Hartman, 2011), such as grasses and sedges characteristic of the Mammoth Steppe, as observed in large herbivorous mammals of the Late Pleistocene, including *Mammuthus* sp. and *Megaloceros* sp. (e.g., Kuitens et al., 2015; Rey-Iglesia et al., 2021). Elevated nitrogen values may also be associated with physiological responses to water stress in particularly arid steppe environments (Bocherens, 2015). High $\delta^{15}\text{N}$ values were recorded in the steppe-adapted giant brown bear *U. arctos* “priscus,” which likely relied heavily on scavenging in the northern latitudes of Europe during MIS 3–2 and may have consumed up to 50 kg of meat daily to sustain its body size (Mattson et al., 1991; Schwartz et al., 2014; Marciszak et al., 2019). In contrast, smaller-bodied brown bears inhabiting temperate refugia may have maintained a more omnivorous diet with a substantial intake of plant matter (Sommer and Benecke, 2005). Local-scale niche partitioning between the two species appears to have occurred at least seasonally. Therefore, dental microwear patterns suggest the hypothesis that *U. arctos* populations from South-Eastern European refugia competed with *U. spelaeus* during the pre-dormancy period; a critical time for accumulating energy reserves for hibernation.

5.5.1. Localized foraging behaviour in *U. spelaeus*

This study reveals seasonal ecological flexibility in South-Eastern European cave bears, challenging the notion of a uniform herbivorous diet tied to the Mammoth Steppe biome. Different microwear patterns indicate dietary plasticity, comparable to that of extant omnivorous bears like *U. arctos*, suggesting an ability to exploit a broad range of resources. Furthermore, the similarity of microwear patterns to those of extant omnivorous species with broad dietary repertoires supports the interpretation of a flexible and opportunistic diet adapted to local ecological conditions of the time.

Their seasonal diet appeared to be closely tied to the local ecological and competitive pressures, reflecting an adaptable foraging strategy. While some regional consistency is observed, dietary patterns are more reliably maintained at the population level, suggesting behavioural inheritance, likely the result of foraging strategies transmitted across generations (Meleg et al., 2024). The present findings extend this pattern beyond the Romanian Carpathians, indicating that such ecological learning may have been a species-wide trait in *U. spelaeus*. The foraging behaviour of cave bears, particularly during the hyperphagic pre-hibernation phase, a period of heightened vulnerability to natural selection, became closely tied to the surrounding landscape, most probably due to ecological pressures. As a result, during the MIS 3 foraging strategies were closely shaped to local environmental conditions, reinforcing a strong ecological link to the immediate landscape. This is supported by the highly localized microwear patterns observed among populations, contrasting with species-level dietary uniformity.

6. Conclusion

This study demonstrates that *U. spelaeus* populations from South-Eastern Europe exhibited marked local-scale dietary flexibility during the MIS 3 pre-hibernation period, as reflected in highly variable dental

microwear patterns. Rather than supporting a uniform herbivorous diet across its range, our results reveal population-level dietary adaptations shaped by local environment and ecological settings. Microwear evidence from the Romanian Carpathians, Moldavian Plateau, and from Western and Central Balkan ranges as well as Western Rhodopes indicates that cave bear populations responded to locally specific ecological pressures, including resource availability and interspecific competition with *U. arctos*, through the development of distinct seasonal foraging strategies. In some cases, local niche partitioning, especially at Trinca where both bear species coexisted, suggests that *U. arctos* may have imposed ecological constraints on *U. spelaeus* during critical hyperphagic periods. These findings refine our understanding of the ecological dynamics that shaped *U. spelaeus*'s adaptive strategies prior to its extinction. Importantly, they underscore the need to interpret cave bear paleoecology at different temporal scales and point to the value of further integrating microwear data with stable isotopic studies to explore the mechanisms behind megafaunal persistence and extinction during the Late-Quaternary.

Ethics approval/declarations

Not applicable.

CRediT authorship contribution statement

Paulo Duñó-Iglesias: Writing – review & editing, Writing – original draft, Visualization, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Iván Ramírez-Pedraza:** Writing – review & editing, Visualization, Supervision, Data curation, Conceptualization. **Florent Rivals:** Writing – review & editing, Writing – original draft, Visualization, Supervision, Data curation, Conceptualization. **Ionuț-Cornel Mirea:** Writing – review & editing, Funding acquisition, Data curation. **Luchiana-Maria Faur:** Writing – review & editing, Data curation. **Marius Vlaicu:** Writing – review & editing, Data curation. **Theodor Obadă:** Writing – review & editing, Data curation. **Roman Croitor:** Writing – review & editing, Data curation. **Viorica Pascari:** Writing – review & editing, Data curation. **Elena Delinschi:** Writing – review & editing, Data curation. **Latinka Hristova:** Writing – review & editing, Data curation. **Nikolai Spassov:** Writing – review & editing, Data curation. **Marin Gospodinov:** Writing – review & editing, Data curation. **Vesna Dimitrijević:** Writing – review & editing, Data curation. **Sanja Alaburić:** Writing – review & editing, Data curation. **Katarina Bogičević:** Writing – review & editing, Data curation. **Ivan Stefanović:** Writing – review & editing, Data curation. **Marius Robu:** Writing – review & editing, Writing – original draft, Visualization, Supervision, Project administration, Investigation, Funding acquisition, Data curation, Conceptualization.

Consent to participate

Not applicable.

Consent for publication

Not applicable.

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Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have influenced the work reported in this paper.

Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.palaeo.2025.113200>.

Data availability

Datasets related to this article can be found at <https://doi.org/10.5281/zenodo.16793240>, an open-source online data repository hosted at Zenodo (Duñó-Iglesias, 2025).

References

- Argant, J., Dimitrijevic, V., 2007. Pollen analyses of Pleistocene hyaena coprolites from Montenegro and Serbia. *Geol. An. Balk* 68, 73–80. <https://doi.org/10.2298/GABP0701073A>.
- Bocherens, H., 2015. Isotopic tracking of large carnivore palaeoecology in the mammoth steppe. *Quat. Sci. Rev.* 117, 42–71. <https://doi.org/10.1016/j.quascirev.2015.03.018>.
- Bocherens, H., 2019. Isotopic insights on cave bear palaeodiet. *Hist. Biol.* 31 (4), 410–421. <https://doi.org/10.1080/08912963.2018.1465419>.
- Bocherens, H., Fizet, M., Mariotti, A., 1994. Diet, physiology and ecology of fossil mammals as inferred from stable carbon and nitrogen isotope biogeochemistry: implications for Pleistocene bears. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 107 (3), 213–225. [https://doi.org/10.1016/0031-0182\(94\)90095-7](https://doi.org/10.1016/0031-0182(94)90095-7).
- 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). *Quat. Res.* 48 (3), 370–380. <https://doi.org/10.1006/qres.1997.1927>.
- Bocherens, H., Drucker, D., Billiou, D., Geneste, J.-M., 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. *J. Hum. Evol.* 50, 370–376. <https://doi.org/10.1016/j.jhevol.2005.12.002>.
- Bocherens, H., Stiller, M., Hobson, K., Pacher, M., Rabeder, G., Burns, J., 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. *Quat. Int.* 245, 238–248. <https://doi.org/10.1016/j.quaint.2010.12.020>.
- 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* ROSENTHALLER, 1794) from Rochedane (France). *Quat. Int.* 339–340, 179–188. <https://doi.org/10.1016/j.quaint.2013.05.021>.
- Bocherens, H., Drucker, D.G., Germonpré, M., Láznicková Galetová, M., Naito, Y.I., Wissing, C., Brůžek, J., Oliva, M., 2015. Reconstruction of the Gravettian food-web at Predmostí I using multi-isotopic tracking (^{13}C , ^{15}N , ^{34}S) of bone collagen. *Quat. Int.* 359–360, 211–228. <https://doi.org/10.1016/j.quaint.2014.09.044>.
- Boev, Z., 2021. Past distribution of *Ursus arctos* in Bulgaria: fossil and subfossil records (Carnivora: Ursidae). *Lynx New Ser.* 51 (1), 5–18. <https://doi.org/10.37520/lynx.2020.001>.
- Bogičević, K., Nenadić, D., Milošević, S., Mihailović, D., Vlastić, S., Tosovic, R., 2017. A late Pleistocene rodent fauna (Mammalia: Rodentia) from Hadzi Prodanova Cave near Ivanjica (western Serbia). *Riv. Ital. Paleontol. Stratigr.* 123, 23–38.
- Bojarska, K., Selva, N., 2012. Spatial patterns in brown bear *Ursus arctos* diet: the role of geographical and environmental factors. *Mammal Rev.* 42, 120–143. <https://doi.org/10.1111/j.1365-2907.2011.00192.x>.
- Brock, F., Ilgham, T., Ramsey, C.B., 2010. Pre-screening techniques for identification of samples suitable for radiocarbon dating of poorly preserved bones. *J. Archaeol. Sci.* 37 (4), 855–865. <https://doi.org/10.1016/j.jas.2009.11.015>.

- Bronk Ramsey, C., 2009. Bayesian analysis of radiocarbon dates. *Radiocarbon* 51 (1), 337–360. <https://doi.org/10.1017/S0033822200033865>.
- Bronk Ramsey, C., 2020. OxCal online. <https://c14.arch.ox.ac.uk/oxcal.html>.
- Carrión, J., Amorós, G., Ochando, J., Magri, D., Marín-Arroyo, A.B., Sánchez-Giner, M.V., Amorós, A., Munuera, M., Di Rita, F., Michelangeli, F., Roksandic, M., Mihailović, D., 2024. Welcome to the forest theatre: Unveiling a Balkan refugium through paleoart. *Quat. Sci. Rev.* 338, 108829. <https://doi.org/10.1016/j.quascirev.2024.108829>.
- Constantin, S., Robu, M., Munteanu, C.-M., Petculescu, A., Vlaicu, M., Mirea, I., Kencs, M., Drăgușin, V., Hoffmann, D., Anecitei, V., Timar-Gabor, A., Roban, R.-D., Panaioiu, C.G., 2014. Reconstructing the evolution of cave systems as a key to understanding the taphonomy of fossil accumulations: the case of Ursilor Cave (Western Carpathians, Romania). *Quat. Int.* 339–340, 25–40. <https://doi.org/10.1016/j.quaint.2013.10.012>.
- Coogan, S.C.P., Raubenheimer, D., Stenhouse, G.B., Nielsen, S.E., 2014. Macronutrient optimization and seasonal diet mixing in a large omnivore, the grizzly bear: a geometric analysis. *PLoS One* 9 (5), e97968. <https://doi.org/10.1371/journal.pone.0097968>.
- Coogan, S.C.P., Raubenheimer, D., Stenhouse, G.B., Coops, N.C., Nielsen, S.E., 2018. Functional macronutritional generalism in a large omnivore, the brown bear. *Ecol. Evol.* 8 (4), 2365–2376. <https://doi.org/10.1002/ece3.3867>.
- Croitor, R., 2008. Giant deer *Megaloceros giganteus* (Cervidae Mammalia) from late Pleistocene of Moldova. *Oltenia J. Stud. Nat. Sci.* 24, 262–266.
- Croitor, R., Burlacu, V., 2020. The Middle Paleolithic site of Buzdujeni 1 (Northern Moldova): evidence on periodic occupation by cave hyena. *Rev. Arheol.* 16 (1), 136–144. <https://hal.science/hal-03126336>.
- David, A.L., Lungu, A.N., 1972. Mammal Remains from Karagash Quarry. In: *Neogene and Pleistocene Vertebrates of Moldavia*. Shtiintsa Press, pp. 19–24.
- Demay, L., Obadă, T., Păun, S., Prepelită, A., 2019. Utilization of mammoth resources and occupation of the Dniester Prut basin territory: the Upper Palaeolithic site of Valea Morilor (Republic of Moldova). *Quat. Sci. Rev.* 222, 105898. <https://doi.org/10.1016/j.quascirev.2019.105898>.
- Demay, L., Croitor, R., Covalenco, S., Obadă, T., Pascari, V., 2024. Zooarchaeological analysis of the Rasov 7 Upper Palaeolithic site (Republic of Moldova). *I'Anthropologie* 128 (4), 103299. <https://doi.org/10.1016/j.anthro.2024.103299>.
- Dimitrijević, V., 1997. Upper Pleistocene Mammals from the Cave Deposits of Serbia. *Geološki anali Balkanskog poluostrva*. Faculty of Mining and Geology.
- Duño-Iglesias, P., 2025. Dental microwear raw data for SouthEastern cave bears populations (Duño-Iglesias et al., 2025) [Data set]. *En J. Zenodo*. <https://doi.org/10.5281/zenodo.16793240>.
- Duño-Iglesias, P., Ramírez-Pedraza, I., Rivals, F., Mirea, I.C., Faur, L.M., Constantin, S., Robu, M., 2024a. Palaeodiet during the pre-dominance period of MIS 3 Romanian cave bears as inferred from dental microwear analysis. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 636, 111988. <https://doi.org/10.1016/j.palaeo.2023.111988>.
- Duño-Iglesias, P., Ramírez-Pedraza, I., Rivals, F., Prilepskaya, N.E., Belyaev, R.I., Baryshnikov, G.F., 2024b. Dental microwear analysis of Kudaro cave bears: Insights into dietary evolution from the Middle to late Pleistocene. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 653, 112417. <https://doi.org/10.1016/j.palaeo.2024.112417>.
- El Zaatari, S., 2010. Occlusal microwear texture analysis and the diets of historical/prehistoric hunter-gatherers. *Int. J. Osteoarchaeol.* 20, 67–87. <https://doi.org/10.1002/oa.1027>.
- Ersmark, E., Baryshnikov, G., Higham, T., Argant, A., Castaños, P., Döppes, D., Gasparik, M., Gernoux, P., Lidén, K., Lipecki, G., Marciszak, A., Miller, R., Moreno-García, M., Pacher, M., Robu, M., Rodríguez-Varela, R., Rojo Guerra, M., Sabol, M., Spassov, N., Stora, J., Valdiesera, C., Villalunga, A., Stewart, J.R., Dalén, L., 2019. Genetic turnovers and northern survival during the last glacial maximum in European brown bears. *Ecol. Evol.* 9 (10), 5891–5905. <https://doi.org/10.1002/ece3.5172>.
- Esri, 2018. *ArcGIS Desktop: Release 10.6.1*.
- Farley, S.D., Robbins, C.T., 1995. Lactation, hibernation, and mass dynamics of American black bears and grizzly bears. *Can. J. Zool.* 73 (12), 2216–2222. <https://doi.org/10.1139/z95.262>.
- Fernández-Mosquera, D., Vila-Taboada, M., Grandal-d'Anglade, A., 2001. Stable isotopes data ($\delta^{13}\text{C}$, $\delta^{15}\text{N}$) from cave bear (*Ursus spelaeus*): a new approach to its paleoenvironment and dormancy. *Proc. R. Soc. Lond. Ser. B Biol. Sci.* 268, 1159–1164. <https://doi.org/10.1098/rspb.2001.1639>.
- Fewlass, H., Talamo, S., Wacker, L., Kromer, B., Tuna, T., Fagault, Y., Bard, E., McPherron, S.P., Aldeias, V., Maria, R., Martisius, N.L., Paskulin, L., Rezek, Z., Sinet-Mathiot, V., Sirakova, S., Smith, G.M., Spasov, R., Welker, F., Sirakov, N., Tsanova, T., Hublin, J.J., 2020. A ^{14}C chronology for the middle to upper Palaeolithic transition at Bacho Kiro Cave, Bulgaria. *Nat. Ecol. Evol.* 4 (6), 794–801. <https://doi.org/10.1038/s41559-020-1136-3>.
- Forsten, A., Dimitrijević, V., 1995. The Paleolithic horses (genus *Equus*) from Risovaca, Arandjelovac, Serbia. *N. Jb. Geol. Paläont. (Abh.)* 196 (3), 395–409. <https://doi.org/10.1127/njgpa/196/1995/395>.
- Fortes, G., Grandal-d'Anglade, A., Kolbe, B., Fernandes, D., Meleg, I., García-Vázquez, A., Pinto-Illona, A., Constantin, S., Torres, T., Ortiz, J., Frischauf, C., Rabeder, G., Hofreiter, M., Barlow, A., 2016. Ancient DNA reveals differences in behaviour and sociality between brown bears and extinct cave bears. *Mol. Ecol.* 25 (19), 4907–4918. <https://doi.org/10.1111/mec.1119>.
- Frémonteau, D., Ottoni, C., Ivanova, S., Marinova, E., Spassov, N., Hristova, L., Konyovska, R., Van Neer, W., Lupianez, N., Gurova, M., 2020. New mtDNA and isotopic evidence on late Pleistocene cave bears in the Balkans: the case study of Magura Cave, NW Bulgaria. *Acta Zool. Bulg.* 72 (3), 461–478.
- Gende, S.M., Quinn, T.P., 2004. The relative importance of prey density and social dominance in determining energy intake by bears feeding on Pacific salmon. *Can. J. Zool.* 82 (1), 75–85. <https://doi.org/10.1139/z03.226>.
- Gerasimenko, N., 2006. Upper Pleistocene loess-palaeosol and vegetational successions in the Middle Dnieper Area, Ukraine. *Quat. Int.* 149, 55–66. <https://doi.org/10.1016/j.quaint.2005.11.018>.
- Ginter, B., Kozłowski, J.K., Guadelli, J.L., Laville, H., 2000. Temnata Cave. Excavations in Karlukovo karst area, Bulgaria. 2.1. Jagellonian University, Cracow. <https://shs.hal.science/halshs-00133843>.
- Godfrey, L.R., Semperebon, G.M., Jungers, W.L., Sutherland, M.R., Simons, E.L., Solounias, N., 2004. Dental use wear in extinct lemur: evidence of diet and niche differentiation. *J. Hum. Evol.* 47 (3), 145–169. <https://doi.org/10.1016/j.jhevol.2004.06.003>.
- Goillot, C., Blondel, C., Peigné, S., 2009. Relationships between dental microwear and diet in Carnivora (Mammalia) — implications for the reconstruction of the diet of extinct taxa. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 271 (1–2), 13–23. <https://doi.org/10.1016/j.palaeo.2008.09.004>.
- Grandal-d'Anglade, A., Pérez-Rama, M., García-Vázquez, A., González-Fortes, G.M., 2019. The cave bear's hibernation: reconstructing the physiology and behaviour of an extinct animal. *Hist. Biol.* 31 (4), 429–441. <https://doi.org/10.1080/08912963.2018.1468441>.
- Hartman, G., 2011. Are elevated $\delta^{15}\text{N}$ values in herbivores in hot and arid environments caused by diet or animal physiology? *Funct. Ecol.* 25, 122–131. <https://doi.org/10.1111/j.1365-2435.2010.01782.x>.
- Hewitt, G., 2000. The genetic legacy of the Quaternary ice ages. *Nature* 405 (6789), 907–913. <https://doi.org/10.1038/35016000>.
- Ivanova, S., Gurova, M., Spassov, N., Hristova, L., Tzankov, N., Popov, V., Marinova, E., Makedonska, J., Smith, V., Ottoni, C., Lewis, M., 2016. Magura Cave, Bulgaria: A multidisciplinary study of late Pleistocene human palaeoenvironment in the Balkans. *Quat. Int.* 415, 86–108. <https://doi.org/10.1016/j.quaint.2015.11.082>.
- Jiangzuo, Q., Flynn, J.J., 2020. The earliest ursine bear demonstrates the origin of plant-dominated omnivory in Carnivora. *iScience* 23 (6). <https://doi.org/10.1016/j.isci.2020.101235>.
- Jovanović, M., Bogićević, K., Nenadić, D., Agustí, J., Sánchez-Bandera, C., López-García, J.M., Blain, H.A., 2022. New paleoecological perspectives on late Pleistocene Neanderthals in northern Balkans: the rodent assemblages from Smolućka cave (Serbia). *Archaeol. Anthropol. Sci.* 14 (9), 169. <https://doi.org/10.1007/s12520-022-01624-0>.
- King, T., Andrews, P., Boz, B., 1999. Effect of taphonomic processes on dental microwear. *Am. J. Phys. Anthropol.* 108 (3), 359–373. [https://doi.org/10.1002/\(SICI\)1096-8644\(199903\)108:3<359::AID-ajpa10968644>3.0.CO;2-9](https://doi.org/10.1002/(SICI)1096-8644(199903)108:3<359::AID-ajpa10968644>3.0.CO;2-9).
- Kosintsev, P.A., Konovalova, K.Y., Simonova, G.V., 2024. Diet of the small cave bear *Ursus (Spelaeoceros) rossicus* Borissak, 1930 (Mammalia, Carnivora, Ursidae) as revealed by ^{13}C and ^{15}N isotope analyses in bone collagen. *Dokl. Biol. Sci.* 513. <https://doi.org/10.1134/S0012496623700825>.
- 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. *Quat. Sci. Rev.* 131, 51–72. <https://doi.org/10.1016/j.quascirev.2015.10.028>.
- Kuipers, M., van der Plicht, J., Drucker, D.G., Van Kolfschoten, T., Palstra, S.W.L., Bocherens, H., 2015. Carbon and nitrogen stable isotopes of well preserved Middle Pleistocene bone collagen from Schöningen (Germany) and their paleoecological implications. *J. Hum. Evol.* 89, 105–113. <https://doi.org/10.1016/j.jhevol.2015.01.008>.
- Kurtén, B., 1976. *The Cave Bear Story: Life and death of a vanished animal*. Columbia University Press.
- Lang, G., Anmann, B., van der Knaap, P., del Molino, C., Schwörer, C., Tinner, W., 2023. Regional vegetation history. In: Tinner, W. (Ed.), *Vegetation History and Archaeobotany of Europe*. Springer, pp. 150–248. <https://doi.org/10.1145/360061.360075>.
- López-Alfaro, C., Robbins, C., Zedrosser, A., Nielsen, S., 2013. Energetics of hibernation and reproductive trade offs in brown bears. *Ecol. Model.* 270, 1–10. <https://doi.org/10.1016/j.ecolmodel.2013.09.002>.
- Marciszak, A., Schouwenburg, C., Lipecki, G., Talamo, S., Shpansky, A., Malikov, D., Gornig, W., 2019. Steppe brown bear *Ursus arctos* “priscus” from the late Pleistocene of Europe. *Quat. Int.* 534, 158–170. <https://doi.org/10.1016/j.quaint.2019.02.042>.
- Markova, A.K., 2007. Pleistocene mammal faunas of Eastern Europe. *Quat. Int.* 160 (1), 100–111. <https://doi.org/10.1016/j.quaint.2006.09.011>.
- Martisius, N.L., Spasov, R., Smith, G.M., Endarova, E., Sinet-Mathiot, V., Welker, F., Aldeias, V., Horta, P., Marreiros, J., Rezek, Z., McPherron, S.P., Sirakov, N., Sirakova, S., Tsanova, T., Hublin, J.J., 2022. Initial Upper Palaeolithic bone technology and personal ornaments at Bacho Kiro Cave (Bulgaria). *J. Hum. Evol.* 167, 103198. <https://doi.org/10.1016/j.jhevol.2022.103198>.
- Mattson, D.J., Blanchard, B.M., Knight, R.R., 1991. Food habits of Yellowstone grizzly bears, 1977–1987. *Can. J. Zool.* 69, 1619–1629. <https://pubs.usgs.gov/publication/70125376>.
- Mazza, P., Rustioni, M., 1994. On the phylogeny of Eurasian Bears. *Palaeontogr. Abt. A* 230 (1–3), 1–38. <https://doi.org/10.1127/pala/230/1994/1>.
- Meleg, I., Alberti, F., Drucker, D., Năpăruș Aljancic, M., Feurdean, A., Robu, M., Vlaicu, M., Naito, Y., Boroneant, A., Marin, C., Nitu, E., Hofreiter, M., Bocherens, H., Barlow, A., 2024. Ancient biomolecules suggest learned foraging strategy in extinct cave bears. *BioRxiv*. <https://doi.org/10.1101/2024.09.23.614392>.
- Mico, C., Blasco, R., Muñoz Del Pozo, A., Jiménez-García, B., Rosell, J., Rivals, F., 2024. Differentiating taphonomic features from trampling and dietary microwear, an experimental approach. *Hist. Biol.* 36 (4), 760–782. <https://doi.org/10.1080/08912963.2023.2184690>.

- Mihailović, D., Mihailović, B., 2006. The palaeolithic site Hadži Prodan's Cave by Ivanjica. *Arheol. Pregl. Srpsk. Arheol. Druš* 1, 13–16.
- Mirea, I.C., Robu, M., Petculescu, A., Kenez, M., Faur, L., Arghir, R., Tecsă, V., Timar-Gabor, A., Roban, R. D., Panaïotu, C.G., Sharifi, A., Pourmand, A., Codrea, V.A., Constantin, S., 2021. Last deglaciation flooding events in the Southern Carpathians as revealed by the study of cave deposits from Muierilor Cave, Romania. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 562, 110084.
- Münzel, S.C., Stiller, M., Hofreiter, M., Mittnik, A., Conard, N.J., Bocherens, H., 2011. Pleistocene bears in the Swabian Jura (Germany): Genetic replacement, ecological displacement, extinctions and survival. *Quat. Int.* 245 (2), 225–237. <https://doi.org/10.1016/j.quaint.2011.03.060>.
- 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. *Quat. Int.* 339–340, 148–163. <https://doi.org/10.1016/j.quaint.2013.10.020>.
- Naito, Y.I., Geronpré, M., Chikaraishi, Y., Ohkouchi, N., Drucker, D., Hobson, K., Edwards, M., 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. *J. Quat. Sci.* 31, 598–606. <https://doi.org/10.1002/jqs.2883>.
- Nelson, D.E., Angerbjörn, A., Lidén, K., Turk, I., 1998. Stable isotopes and the metabolism of the European cave bear. *Oecologia* 116 (1), 177–181. <https://doi.org/10.1007/s004420050577>.
- Ochando, J., Carrión, J.S., Magri, D., Marín-Arroyo, A.B., Di Rita, F., Munuera, M., Michelangeli, F., Amorós, G., Milošević, S., Bogićević, K., Dimitrijević, V., Nenadić, D., Roksandic, M., Mihailović, D., 2024. Balkan Neanderthals: the late Pleistocene palaeoecological sequence of Pešturina Cave (Niš, Serbia). *Quat. Sci. Rev.* 330, 108600. <https://doi.org/10.1016/j.quascirev.2024.108600>.
- Pacher, M., Stuart, A.J., 2009. Extinction chronology and palaeobiology of the cave bear (*Ursus spelaeus*). *Boreas* 38 (2), 189–206. <https://doi.org/10.1111/j.1502-3885.2008.00071.x>.
- Pappa, S., 2016. Palaeoecology and Palaeodiet: Reconstructing Adaptations in the Middle and Late Pleistocene Ursidae through Dental Microwear and Geochemistry. PhD thesis. Royal Holloway University of London, p. 456.
- Pappa, S., Schreve, D.C., Rivals, F., 2019. The bear necessities: A new dental microwear database for the interpretation of palaeodiet in fossil Ursidae. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 514, 168–188. <https://doi.org/10.1016/j.palaeo.2018.10.015>.
- Păunescu, A., 1980. Evoluția istorică pe teritoriul României din paleolitic până la începutul neoliticului. *Stud. Cercet. Ist. Veche Arheol.* 31, 519–545.
- Pederzani, S., Britton, K., Aldeias, V., Bourgon, N., Fewlass, H., Lauer, T., McPherron, S. P., Rezak, Z., Sirakov, N., Smith, G.M., Spasov, R., Tran, N.H., Tsanova, T., Hublin, J. J., 2021. Subarctic climate for the earliest *Homo sapiens* in Europe. *Sci. Adv.* 7 (39). <https://doi.org/10.1126/sciadv.abi4642>.
- Petrov, B., Stoev, P., 2007. The Underground World of the Mountain Rhodopes. UNDP. Puzachenko, A.Y., Markova, A.K., 2019. Evolution of mammal species composition and species richness during the late Pleistocene - Holocene transition in Europe: a general view at the regional scale. *Quat. Int.* 530–531, 88–106. <https://doi.org/10.1016/j.quaint.2018.12.025>.
- Rabeder, G., 1999. Die Evolution des Höhlenbärengebisses. *Mitt. Konu. Quartärforsch.* Österr. Akad. Wiss. 11, 1–102.
- Rabeder, G., Nagel, D., Pacher, M., 2000. *Der Höhlenbär: Species 4*. Verlag Thorbecke, Stuttgart, p. 256.
- Rădulescu, C., Samson, P., 1959. Contribution à la connaissance de la dentition lactéale d'*Ursus spelaeus*. *Eiszeit. Al. Gegenw.* 10 (205), 16.
- Ramírez-Pedraza, I., Tornero, C., Pappa, S., Talamo, S., Salazar-García, D.C., Blasco, R., Rosell, J., Rivals, F., 2019. Microwear and isotopic analyses on cave bear remains from Toll Cave reveal both short term and long term dietary habits. *Sci. Rep.* 9 (1). <https://doi.org/10.1038/s41598-019-42152-7>.
- Ramírez-Pedraza, I., Pappa, S., Blasco, R., Arilla, M., Rosell, J., Millán, F., Maroto, J., Soler, J., Soler, N., Rivals, F., 2020. Dietary habits of the cave bear from the late Pleistocene in the northeast of the Iberian Peninsula. *Quat. Int.* 557, 63–69. <https://doi.org/10.1016/j.quaint.2019.09.043>.
- Ramírez-Pedraza, I., Baryshnikov, G.F., Prilepskaya, N.E., Belyaev, R.I., Pappa, S., Rivals, F., 2022. Palaeodiet and niche partitioning among the easternmost European cave bears based on tooth wear analysis. *Hist. Biol.* 34 (6), 1063–1071. <https://doi.org/10.1080/08912963.2021.1960324>.
- Reimer, P.J., Bard, E., Bayliss, A., Beck, J.W., Blackwell, P.G., Ramsey, C.B., Buck, C.E., Cheng, H., Edwards, R.L., Friedrich, M., Grootes, P.M., Guilderson, T.P., Hajdas, I., Heaton, T.J., Hogg, A.G., Hughes, K.A., Kromer, B., Manning, S.W., Muscheler, R., Palmer, J.G., Pearson, C., van der Plicht, J., Reimer, R.W., Richards, D.A., Scott, E.M., Southon, J.R., Staff, R.A., Turney, C.S.M., van der Plicht, J., 2013. IntCal13 and Marine13 radiocarbon age calibration curves 0–50,000 years cal BP. *Radiocarbon* 55 (4), 1869–1887. <https://doi.org/10.2458/azu.jr.55.16947>.
- Reimer, P.J., Austin, W.E.N., Bard, E., Bayliss, A., Blackwell, P.G., Bronk Ramsey, C., Butzin, M., Cheng, H., Edwards, R.L., Friedrich, M., Grootes, P.M., Guilderson, T.P., Hajdas, I., Heaton, T.J., Hogg, A.G., Hughes, K.A., Kromer, B., Manning, S.W., Muscheler, R., Palmer, J.G., Pearson, C., van der Plicht, J., Reimer, R.W., Richards, D.A., Scott, E.M., Southon, J.R., Turney, C.S.M., Wacker, L., Adolphi, F., Büntgen, U., Capano, M., Fahrni, S., Fogtmann-Schulz, A., Friedrich, R., Kohler, P., Kudsk, S., Miyake, F., Olsen, J., Reinig, F., Sakamoto, M., Sookdeo, A., Talamo, S., 2020. The IntCal20 northern hemisphere radiocarbon age calibration curve (0–55 cal kBP). *Radiocarbon* 62 (4), 725–757. <https://doi.org/10.1017/RDC.2020.41>.
- Rey-Iglesia, A., Lister, A.M., Stuart, A.J., Bocherens, H., Szpak, P., Willerslev, E., Lorenzen, E.D., 2021. Late Pleistocene palaeoecology and phylogeography of woolly rhinoceroses. *Quat. Sci. Rev.* 263, 106993. <https://doi.org/10.1016/j.quascirev.2021.106993>.
- Richards, M.P., Pacher, M., Stiller, M., Quilès, 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. *Proc. Natl. Acad. Sci. USA* 105 (2), 600–604. <https://doi.org/10.1073/pnas.0711063105>.
- Rivals, F., Solomias, N., Mählbacher, M.C., 2007. Evidence for geographic variation in the diets of late Pleistocene and early Holocene Bison in North America, and differences from the diets of recent *Bison*. *Quat. Res.* 68 (3), 338–346. <https://doi.org/10.1016/j.yqres.2007.07.012>.
- Rivals, F., Baryshnikov, G.F., Prilepskaya, N.E., Belyaev, R.I., 2022. Diet and ecological niches of the late Pleistocene hyenas *Crocuta spelaea* and *C. ultima ussuriica* based on a study of tooth microwear. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 601, 111125. <https://doi.org/10.1016/j.palaeo.2022.111125>.
- Robu, M., 2016. Age re-assessment of the cave bear assemblage from Urșilor Cave, North-Western Romania. *Int. J. Speleol.* 45 (2), 123–133. <https://doi.org/10.5038/1827-806X.45.2.1947>.
- 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*). *Can. J. Zool.* 91 (4), 227–234. <https://doi.org/10.1139/cjz-2012-0222>.
- Robu, M., Wynn, J.G., Mirea, I.C., Petculescu, A., Kenez, M., Pușcaș, C.M., Vlaicu, M., Trinkaus, E., Constantin, S., 2018. The diverse dietary profiles of MIS 3 cave bears from the Romanian Carpathians: insights from stable isotope ($\delta^{13}\text{C}$ and $\delta^{15}\text{N}$) analysis. *Palaeontology* 61 (2), 209–219. <https://doi.org/10.1111/pala.12338>.
- Robu, M., Wynn, J., Pușcaș, C.M., Meleg, I.N., Martin, J.E., Constantin, S., 2019. Palaeoecology and palaeoclimatic context of Romanian Carpathian MIS 3 cave bears using stable isotopes ($\delta^{13}\text{C}$ and $\delta^{18}\text{O}$). *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 534, 109288. <https://doi.org/10.1016/j.palaeo.2019.109288>.
- Robu, M., Marom, N., Mirea, I.C., Faur, L.M., Petculescu, A., Kenez, M., Shafir, R., Egiuez, N., Constantin, S., 2024. Intraguild interactions among carnivores of the last glacial: the case of wolves and bears from Muierilor Cave, Romania. *Quat. Sci. Rev.* 334, 108720. <https://doi.org/10.1016/j.quascirev.2024.108720>.
- Robu, M., Rivals, F., Vlaicu, M., Duñó-Iglesias, P., Ramírez-Pedraza, C., Croitor, R., Ionuț-Cornel, M., Marom, N., Egiuez, N., Denay, L., Obadă, T., Burlacu, V., Meloro, C., Martin, J.E., 2025. The paleoecology of the large mammals from Duruitoarea Veche Cave (Moldova).
- RStudio Team, 2021. RStudio: Integrated Development Environment for R. <http://www.rstudio.com/>.
- Sadori, L., Koutsodendris, A., Panagiotopoulos, K., Masi, A., Bertini, A., Combouret-Neubou, N., Francke, A., Kouli, K., Joannin, S., Mercuri, A.M., Peyron, O., Torri, P., Wagner, B., Zanchetta, G., Sinopoli, G., Donders, T.H., 2016. Pollen based palaeoenvironmental and paleoclimatic change at Lake Ohrid (South-Eastern Europe) during the past 500 ka. *Biogeosciences* 13 (5), 1423–1437. <https://doi.org/10.5194/bg-13-1423-2016>.
- Schwarz, H.P., Dupras, T.L., Fairgrieve, S.I., 1999. ^{15}N enrichment in the Sahara: in search of a global relationship. *J. Archaeol. Sci.* 26, 629–636. <https://doi.org/10.1006/jasc.1998.0380>.
- Schwartz, C.C., Fortin, J.K., Teisberg, J.E., Haroldson, M.A., Servheen, C., Robbins, C.T., Van Manen, F.T., 2014. Body and diet composition of sympatric black and grizzly bears in the Greater Yellowstone Ecosystem. *J. Wildl. Manag.* 78 (1), 68–78. <https://doi.org/10.1002/jwmg.633>.
- Sempere, G.M., Godfrey, L.R., Solomias, N., Sutherland, M.R., Jungers, W.L., 2004. Can low-magnification stereomicroscopy reveal diet? *J. Hum. Evol.* 47 (3), 115–144. <https://doi.org/10.1016/j.jhevol.2004.06.004>.
- Sempere, G.M., Sise, P.J., Coombs, M.C., 2011. Potential bark and fruit browsing as revealed by stereomicroscopy analysis of the peculiar clawed herbivores known as Chalicotheres (Perissodactyla, Chalicotherioidea). *J. Mamm. Evol.* 18 (1), 33–55. <https://doi.org/10.1007/s10914-010-9149-3>.
- Soficaru, A., Petrea, C., Dobos, A., Trinkaus, E., 2007. The human cranium from the Peștera Cioclovina Uscată, Romania. *Curr. Anthropol.* 48 (4), 611–619. <https://doi.org/10.1086/519915>.
- Solomias, N., Sempere, G., 2002. Advances in the reconstruction of ungulate ecomorphology with application to early fossil equids. *Am. Mus. Novit.* 3366, 1–49. [https://doi.org/10.1206/0003-0082\(2002\)366<0001:AITROU>2.0.CO;2](https://doi.org/10.1206/0003-0082(2002)366<0001:AITROU>2.0.CO;2).
- Sommer, R.S., 2020. Late Pleistocene and Holocene history of mammals in Europe. In: *Handbook of the Mammals of Europe*. Springer International Publishing, pp. 1–16. https://doi.org/10.1007/978-3-319-65038-8_3-1.
- Sommer, R.S., Benecke, N., 2005. The recolonization of Europe by brown bears *Ursus arctos* Linnaeus, 1758 after the last glacial maximum. *Manuscr. Rev.* 35, 156–164. <https://doi.org/10.1111/j.1365-2907.2005.00063.x>.
- Sommer, R.S., Nadachowski, A., 2006. Glacial refugia of mammals in Europe: evidence from fossil records. *Manuscr. Rev.* 36 (4), 251–265. <https://doi.org/10.1111/j.1365-2907.2006.00093.x>.
- Sommer, R.S., Zachos, F.E., 2009. Fossil evidence and phylogeography of temperate species: 'glacial refugia' and post-glacial recolonization. *J. Biogeogr.* 36 (11), 2013–2020. <https://doi.org/10.1111/j.1365-2699.2009.02187.x>.
- Stewart, J.R., Lister, A.M., Barnes, L., Dalén, L., 2010. Refugia revisited: individualistic responses of species in space and time. *Proc. R. Soc. Lond. B Biol. Sci.* 277 (1682), 661–671. <https://doi.org/10.1098/rspb.2009.1272>.
- Stiller, M., Baryshnikov, G., Bocherens, H., Grandal d'Anglade, A., Hilpert, B., Münzel, S. C., Pinhasi, R., Rabeder, G., Rosendahl, W., Trinkaus, E., Hofreiter, M., Knapp, M., 2010. Withering away 25,000 years of genetic decline preceded cave bear extinction. *Mol. Biol. Evol.* 27 (5), 975–978. <https://doi.org/10.1093/molbev/msq083>.

- Stuart, A., Lister, A., 2011. Extinction chronology of the cave lion *Panthera spelaea*. *Quat. Sci. Rev.* 30, 2329–2340. <https://doi.org/10.1016/j.quascirev.2010.04.023>.
- Tzedakis, P.C., Lawson, I.T., Frogley, M.R., Hewitt, G.M., Preece, R.C., 2002. Buffered tree population changes in a Quaternary Refugium: Evolutionary implications. *Science* 297 (5589), 2044–2047. <https://doi.org/10.1126/science.1073083>.
- Uzunidis, A., Pineda, A., Jiménez-Manchón, S., Xafis, A., Ollivier, V., Rivals, F., 2021. The impact of sediment abrasion on tooth microwear analysis: an experimental study. *Archaeol. Anthropol. Sci.* 13 (8), 134. <https://doi.org/10.1007/s12520-021-01382-5>.
- van der Plicht, J., Palstra, S.W.L., 2016. Radiocarbon and mammoth bones: What's in a date. *Quat. Int.* 406, 246–251. <https://doi.org/10.1016/j.quaint.2014.11.027>.
- van Heteren, A.H., Figueirido, B., 2019. Diet reconstruction in cave bears from craniodental morphology: past evidences, new results and future directions. *Hist. Biol.* 31 (4), 500–509. <https://doi.org/10.1080/08912963.2018.1547901>.
- van Klinken, G.J., 1999. Bone collagen quality indicators for palaeodietary and radiocarbon measurements. *J. Archaeol. Sci.* 26 (6), 687–695. <https://doi.org/10.1006/jasc.1998.0385>.
- Vila-Taboada, M., Fernández-Mosquera, D., González, F., Grandal d'Anglade, A., Vidal-Romani, J.R., 1999. Paleocological implications inferred from stable isotopic signatures ($\delta^{13}\text{C}$, $\delta^{15}\text{N}$) in bone collagen of *Ursus spelaeus*. *ROS-HEIN. Cadernos Lab. Xeolóxico Laxe* 24, 73–87.
- Vishnyatsky, L., Burlacu, V., Voskresenskaya, E., Nekhoroshev, P.E., 2020. New research at the Middle Palaeolithic cave site of Buzdujeni. *Stratum Plus* 1, 187–200.
- Willis, K., Vanandel, T., 2004. Trees or no trees? The environments of central and eastern Europe during the last Glaciation. *Quat. Sci. Rev.* 23 (23–24), 2369–2387. <https://doi.org/10.1016/j.quascirev.2004.06.002>.
- Xafis, A., Nagel, D., Bastl, K., 2017. Which tooth to sample? A methodological study of the utility of premolar/non-carnassial teeth in the microwear analysis of mammals. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 487, 229–240. <https://doi.org/10.1016/j.palaeo.2017.09.003>.

A.2 Appendix 2: Introduction

Table A1 – section 1.3.1.1: The following table compiles the length ratio between the second and first lower molars (m2L/m1L) in key fossil ursid taxa, spanning from the Early Miocene to the Late Pleistocene. This morphological metric is used to assess evolutionary trends in molar proportions that are closely linked to dietary adaptations across the ursid lineage. These data were used to construct Figure 1 in the main text, which illustrates a significant positive trend in m2L/m1L over time ($R^2 = 0.87$), suggesting a progressive increase in m2 length relative to m1, interpreted as an adaptation from early carnivory (e.g., *Ballusia elmensis*) to balanced omnivory (*Aurorarcos tirawa*, *Ursavus tedfordi*), and eventually toward a herbivorous diet in later taxa such as *Ursus spelaeus*.

Species	Age	m2L/m1L	References
<i>Ballusia elmensis</i>	20 Ma	0.71	Jiangzuo and Flynn, 2020
<i>Aurorarcos tirawa</i>	15–12.5 Ma	0.79	Jiangzuo and Flynn, 2020
<i>Ursavus tedfordi</i>	10 Ma	0.81	Jiangzuo and Flynn, 2020
<i>Ursus minimus</i>	4 or 3 Ma	0.98	Baryshnikov and Lavrov, 2013
<i>Ursus etruscus</i>	2-1 Ma	0.99	Jiangzuo and Flynn, 2020
<i>Ursus deningeri</i>	0.8 Ma	1	Jiangzuo and Flynn, 2020
<i>Ursus spelaeus</i>	0.4 Ma	1.15	Jiangzuo and Flynn, 2020

Table A2 – section 1.3.2.1: The following table compiles information used to generate the isotopic graphs presented in Figures 3 and 4. It includes radiocarbon dates (in years before present, B.P.), site names, altitudes (m a.s.l.), geographic coordinates, stable carbon ($\delta^{13}\text{C}$) and nitrogen ($\delta^{15}\text{N}$) isotope values, and the reference numbers for the original publications, for which the data was extracted from.

Date	Site	m. a.s.l.	Coord.	C	N	Reference
36,667	Cioclovina	780	45°34'27"N, 23°08'11"E	-20.4	3.3	1
44,237	Cioclovina	780	45°34'27"N, 23°08'11"E	-20.3	3.1	1
44,372	Muierilor	645	45°11'29" N, 23°45'14" E	-20.3	6	1
44,467	Muierilor	645	45°11'29" N, 23°45'14" E	-20.3	3.7	1
46,182	Muierilor	645	45°11'29" N, 23°45'14" E	-20.2	3.4	1

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45,000	Oase	600	45° 05' N, 21°51' E	-20.8	8.3	1
42,450	Oase	600	45° 05' N, 21°51' E	-21	8.3	1
43,100	Oase	600	45° 05' N, 21°51' E	-20.8	7.4	1
37,450	Oase	600	45° 05' N, 21°51' E	-21.1	9.7	1
47,600	Oase	600	45° 05' N, 21°51' E	-21.1	7.8	1
46,800	Oase	600	45° 05' N, 21°51' E	-21.2	5.7	1
45,958	Oase	600	45° 05' N, 21°51' E	-21.5	7.7	1
42,900	Oase	600	45° 05' N, 21°51' E	-21.7	7.8	1
46,614	Oase	600	45° 05' N, 21°51' E	-21.4	7.5	1
51,453	Oase	600	45° 05' N, 21°51' E	-21.1	7.8	1
42,090	Oase	600	45° 05' N, 21°51' E	-21.1	9.7	1
32,990	Geissenklösterle	584	48°23'54"N, 9°46'20"E	-21	3.4	2
28,500	Geissenklösterle	584	48°23'54"N, 9°46'20"E	-20.3	3	2
31,710	Geissenklösterle	584	48°23'54"N, 9°46'20"E	-20.8	1.7	2
32,000	Geissenklösterle	584	48°23'54"N, 9°46'20"E	-20.9	1.1	2
34,400	Geissenklösterle	584	48°23'54"N, 9°46'20"E	-21.2	3.1	2
26,230	Geissenklösterle	584	48°23'54"N, 9°46'20"E	-21	4	2
27,720	Geissenklösterle	584	48°23'54"N, 9°46'20"E	-20.3	2.5	2
28,360	Geissenklösterle	584	48°23'54"N, 9°46'20"E	-20.8	2.9	2
28,360	Geissenklösterle	584	48°23'54"N, 9°46'20"E	-21	2.8	2
30,800	Geissenklösterle	584	48°23'54"N, 9°46'20"E	-20.8	1.8	2
27,090	Hohle Fels	550	48°22'45"N, 9°45'20"E	-20.6	2.8	2
30,370	Hohle Fels	550	48°22'45"N, 9°45'20"E	-21.1	2.7	2
27,440	Hohle Fels	550	48°22'45"N, 9°45'20"E	-20.6	4	2
28,200	Hohle Fels	550	48°22'45"N, 9°45'20"E	-20.8	3.2	2
28,250	Hohle Fels	550	48°22'45"N, 9°45'20"E	-20.4	2.9	2
28,330	Hohle Fels	550	48°22'45"N, 9°45'20"E	-20.9	3.7	2
28,750	Hohle Fels	550	48°22'45"N, 9°45'20"E	-20.7	4.2	2
23,900	Rochedane	700	47° 8' 21" N, 6° 8' 46" E	-21	4.6	3
30,360	Chauvet	120	44°23'14"N, 4°24'57"E	-21	4.8	4
30,690	Chauvet	120	44°23'14"N, 4°24'57"E	-20.8	3.9	4
35,160	Chauvet	120	44°23'14"N, 4°24'57"E	-20.8	2.4	4
30,350	Chauvet	120	44°23'14"N, 4°24'57"E	-20.8	4	4

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29,050	Chauvet	120	44°23'14"N, 4°24'57"E	-20.6	4.5	4
28,930	Chauvet	120	44°23'14"N, 4°24'57"E	-20.6	3.6	4
37,410	Chauvet	120	44°23'14"N, 4°24'57"E	-20.2	0.9	4
30,350	Chauvet	120	44°23'14"N, 4°24'57"E	-20.6	3.9	4
31,360	Chauvet	120	44°23'14"N, 4°24'57"E	-20.8	4.6	4
30,360	Chauvet	120	44°23'14"N, 4°24'57"E	-20.3	3.7	4
31,130	Chauvet	120	44°23'14"N, 4°24'57"E	-20.5	4.4	4
31,300	Chauvet	120	44°23'14"N, 4°24'57"E	-20.7	4.4	4
31,320	Chauvet	120	44°23'14"N, 4°24'57"E	-20.8	4.9	4
30,420	Chauvet	120	44°23'14"N, 4°24'57"E	-20.5	4.4	4
30,740	Chauvet	120	44°23'14"N, 4°24'57"E	-20.5	4.5	4
29,080	Chauvet	120	44°23'14"N, 4°24'57"E	-20.2	3.7	4
29,400	Chauvet	120	44°23'14"N, 4°24'57"E	-20.1	3.4	4
30,530	Chauvet	120	44°23'14"N, 4°24'57"E	-20.6	4.1	4
30,140	Chauvet	120	44°23'14"N, 4°24'57"E	-20.6	4	4
30,460	Chauvet	120	44°23'14"N, 4°24'57"E	-21	4.2	4
29,560	Chauvet	120	44°23'14"N, 4°24'57"E	-20.6	3.9	4
31,870	Chauvet	120	44°23'14"N, 4°24'57"E	-20.3	3.5	4
30,760	Chauvet	120	44°23'14"N, 4°24'57"E	-20.3	3.7	4
30,900	Chauvet	120	44°23'14"N, 4°24'57"E	-21.1	5.1	4
30,690	Chauvet	120	44°23'14"N, 4°24'57"E	-21.1	5	4
28,850	Chauvet	120	44°23'14"N, 4°24'57"E	-20.5	4.1	4
30,430	Chauvet	120	44°23'14"N, 4°24'57"E	-20.3	3.1	4
31,625	Pala de Rebolal	500	42°28'49"N, 6°50'08"W	-21.2	3.9	5
37,830	A Ceza 1	1004	42°40'38"N, 7°08'00"W	-21.5	4.8	6
46,560	Liñares	1110	42°40'38"N, 7°08'00"W	-20.9	1	6
49,140	Liñares	1110	42°40'38"N, 7°08'00"W	-20.8	1.9	6
29,710	Eirós	780	42°46'05" N, 7°12'40" W	-20.7	5.5	6
29,990	Eirós	780	42°46'05" N, 7°12'40" W	-21.8	6.1	6
25,592	Eirós	780	42°46'05" N, 7°12'40" W	-21.6	5.6	6
29,072	Eirós	780	42°46'05" N, 7°12'40" W	-20.4	4.3	6
29,245	Eirós	780	42°46'05" N, 7°12'40" W	-21.1	5.4	6
29,659	Eirós	780	42°46'05" N, 7°12'40" W	-21.1	4.8	6

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29,710	Eirós	780	42°46'05" N, 7°12'40" W	-20.7	5.5	6
29,990	Eirós	780	42°46'05" N, 7°12'40" W	-21.8	6.1	6
30,150	Eirós	780	42°46'05" N, 7°12'40" W	-21	3.8	6
30,655	Eirós	780	42°46'05" N, 7°12'40" W	-20	4.7	6
31,390	Eirós	780	42°46'05" N, 7°12'40" W	-21.5	4.7	6
31,680	Eirós	780	42°46'05" N, 7°12'40" W	-21.2	4.2	6
34,500	Urşilor	480	46° 55' 37" N, 22° 56' 92"E	-21.1	2.8	1
36,900	Urşilor	480	46° 55' 37" N, 22° 56' 92"E	-22.4	8.9	1
37,300	Urşilor	480	46° 55' 37" N, 22° 56' 92"E	-21.6	7.2	1
38,200	Urşilor	480	46° 55' 37" N, 22° 56' 92"E	-22.2	8.6	1

Table 10. References: (1) Robu, M., Wynn, J.G., Mirea, I.C., Petculescu, A., Kenesz, M., Puşcaş, C. M., Vlaicu, M., Trinkaus, E., Constantin, S., 2018. The diverse dietary profiles of MIS 3 cave bears from the Romanian Carpathians: insights from stable isotope ($\delta^{13}\text{C}$ and $\delta^{15}\text{N}$) analysis. *Palaeontology* 61(2), 209–219. <https://doi.org/10.1111/pala.12338> (2) Bocherens, H., Drucker, D.G., Germonpré, M., Lázníková-Galetová, M., Naito, Y.I., Wissing, C., Brůžek, J., Oliva, M., 2015. Reconstruction of the Gravettian food-web at Předmostí I using multi-isotopic tracking (^{13}C , ^{15}N , ^{34}S) of bone collagen. *Quat. Int.* 359–360, 211–228. <https://doi.org/10.1016/j.quaint.2014.09.044> (3) Bocherens, H., Bridault, A., Drucker, D.G., Hofreiter, M., Münzel, S.C., Stiller, M., van der Plicht, J., 2014a. The last of its kind? Radiocarbon, ancient DNA and stable isotope evidence from a late cave bear (*Ursus spelaeus* ROSENMÜLLER, 1794) from Rochedane (France). *Quat. Int.* 339–340, 179–188. <https://doi.org/10.1016/j.quaint.2013.05.021> (4) Bocherens, H., Drucker, D., Billiou, D., Geneste, J.M., 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. *J. Hum. Evol.* 50, 370–376. <https://doi.org/10.1016/j.jhevol.2005.12.002> (5) García-Vázquez, A., Pinto-Llona, A. C., Grandal-d’Anglade, A., 2018. Brown bear (*Ursus arctos* L.) palaeoecology and diet in the Late Pleistocene and Holocene of the NW of the Iberian Peninsula: A study on stable isotopes. *Quat. Int.* 481, 42–51. <https://doi.org/10.1016/j.quaint.2017.08.063> (6) Pérez-Rama, M., Mosquera, D., Grandal-d’Anglade, A., 2011. Effects of hibernation on the stable isotope signatures of adult and neonate cave bears. *Quaternaire Hors-série*, 79–88.

A.3 Appendix 3: Results

Table A2-Raw data. This table presents the raw count data for dental microwear features recorded in ursid specimens analysed in this study ($n = 375$). The column # indicates the specimen number assigned in this work, while **#Collection** refers to the identifier associated with the institutional collection where the specimen is curated. **Region** indicates the geographic region of origin (Romanian Carpathians, Moldavian Plateau, Western Balkans, Western Rhodopes Mountains, Central Balkans, Greater Caucasus and Northern Urals) and **Cave** specifies the site (i.e., population) to which the specimen belongs. **Species** denotes the taxonomic identification (e.g., *Ursus arctos*, *Ursus spelaeus*, *Ursus praekudarensis*). The microwear variables include, number of total scratches (NTS), number of total pits (NTP), number of fine scratches (NFS), number of coarse scratches (NCS), scratch width score (SWS), number of large pits (NLP), number of small pits (NSP), number of gouges (NG), number of puncture pits (NPP), and number of hypercoarse scratches (NHC).

#	#Collection	Region	Cave	Species	NTS	NTP	NFS	NCS	SWS	NLP	NSP	NG	NPP	NHC
1	PA/002	omanian Carpathians	Adam	<i>Ursus spelaeus</i>	22.50	32.00	20.00	2.50	0.00	0.00	29.00	0.00	3.00	0.00
2	PA/001	omanian Carpathians	Adam	<i>Ursus spelaeus</i>	17.50	26.00	12.00	5.50	1.00	4.00	21.00	0.00	1.00	0.00
3	PB/B1-X-XI	omanian Carpathians	Bisericuța	<i>Ursus arctos</i>	26.00	38.00	6.00	21.00	2.00	9.00	27.00	1.00	2.00	0.00
4	PB/C1-IX	omanian Carpathians	Bisericuța	<i>Ursus spelaeus</i>	22.00	29.00	12.00	10.00	1.00	1.00	25.00	1.00	3.00	0.00
5	PB/C1-XIV	omanian Carpathians	Bisericuța	<i>Ursus spelaeus</i>	29.00	33.50	27.00	3.00	0.00	6.00	26.00	0.00	1.50	0.00

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6	PB/C1-XVI-23	omanian Carpathians	Bisericuța	<i>Ursus spelaeus</i>	22.00	19.00	4.00	22.00	2.00	0.00	16.50	1.00	1.00	0.00
7	PB/A1-V	omanian Carpathians	Bisericuța	<i>Ursus spelaeus</i>	16.00	16.00	10.00	6.00	1.00	2.00	11.00	1.00	1.00	0.00
8	PB/A1-I-II-1	omanian Carpathians	Bisericuța	<i>Ursus spelaeus</i>	22.83	27.67	18.33	4.50	0.00	5.00	16.67	0.00	6.00	0.00
9	18II/96	omanian Carpathians	Cioclovina	<i>Ursus spelaeus</i>	22.00	32.50	13.00	9.00	1.00	0.50	32.00	0.00	0.00	0.00
10	18II/98	omanian Carpathians	Cioclovina	<i>Ursus spelaeus</i>	19.00	36.50	14.00	3.00	0.00	1.00	32.50	0.00	3.00	0.00
11	18II/101	omanian Carpathians	Cioclovina	<i>Ursus spelaeus</i>	16.50	28.50	11.00	7.00	1.00	0.00	26.00	1.50	2.50	0.00
12	18II/102	omanian Carpathians	Cioclovina	<i>Ursus spelaeus</i>	20.33	35.00	20.00	0.00	0.00	0.00	33.50	0.50	1.50	0.00
13	18II/103	omanian Carpathians	Cioclovina	<i>Ursus spelaeus</i>	20.00	24.50	12.00	8.00	1.00	0.50	24.00	0.00	0.00	0.00
14	18II/104	omanian Carpathians	Cioclovina	<i>Ursus spelaeus</i>	25.67	22.50	26.00	1.00	0.00	1.50	21.00	0.00	0.00	0.00
15	18II/106	omanian Carpathians	Cioclovina	<i>Ursus spelaeus</i>	19.50	33.00	16.50	3.00	0.00	4.00	26.00	0.50	3.00	0.00
16	18II/107	omanian Carpathians	Cioclovina	<i>Ursus spelaeus</i>	26.50	25.50	23.00	3.50	0.00	0.00	25.00	0.00	0.50	0.00
17	18II/108	omanian Carpathians	Cioclovina	<i>Ursus spelaeus</i>	26.00	31.50	20.00	6.00	0.00	0.00	28.50	1.50	3.00	0.00
18	18II/109	omanian Carpathians	Cioclovina	<i>Ursus spelaeus</i>	26.00	28.50	19.00	7.00	0.00	0.00	22.00	0.00	6.50	0.00
19	18II/110	omanian Carpathians	Cioclovina	<i>Ursus spelaeus</i>	25.00	18.50	10.50	7.00	0.00	0.00	17.50	2.00	1.00	0.00
20	23II/111	omanian Carpathians	Cioclovina	<i>Ursus spelaeus</i>	22.50	30.50	11.50	8.00	1.00	0.50	30.00	0.50	0.00	0.00
21	23II/112	omanian Carpathians	Cioclovina	<i>Ursus spelaeus</i>	21.50	25.50	19.00	2.50	0.00	4.00	21.50	0.00	0.00	0.00
22	23II/113	omanian Carpathians	Cioclovina	<i>Ursus spelaeus</i>	24.50	35.00	20.00	4.00	0.00	4.00	23.00	2.00	2.00	0.00
23	23II/115	omanian Carpathians	Cioclovina	<i>Ursus spelaeus</i>	17.00	31.50	11.50	4.50	0.00	5.50	22.00	3.00	4.00	0.00
24	18II/116	omanian Carpathians	Cioclovina	<i>Ursus spelaeus</i>	17.00	38.83	10.50	6.50	1.00	3.50	33.00	0.50	2.00	0.00
25	18II/117	omanian Carpathians	Cioclovina	<i>Ursus spelaeus</i>	16.50	30.00	16.50	0.00	0.00	3.00	26.00	0.00	1.00	0.00
26	18II/119	omanian Carpathians	Cioclovina	<i>Ursus spelaeus</i>	14.00	19.50	14.00	0.00	0.00	2.50	12.00	2.00	5.00	0.00
27	18II/120	omanian Carpathians	Cioclovina	<i>Ursus spelaeus</i>	15.00	27.17	5.00	10.00	2.00	0.00	22.67	0.00	4.50	0.00
28	18II/122	omanian Carpathians	Cioclovina	<i>Ursus spelaeus</i>	22.00	51.00	10.50	11.50	1.00	2.50	47.00	1.50	1.50	1.00
29	18II/123	omanian Carpathians	Cioclovina	<i>Ursus spelaeus</i>	22.00	30.50	10.00	11.00	1.00	0.00	28.00	0.50	2.50	0.00
30	18II/124	omanian Carpathians	Cioclovina	<i>Ursus spelaeus</i>	18.00	27.50	13.00	5.00	0.00	0.00	26.00	1.50	1.50	0.00
31	PC/126	omanian Carpathians	Cioclovina	<i>Ursus spelaeus</i>	20.50	38.50	15.00	5.50	0.00	0.00	34.00	0.00	4.50	0.00
32	PC/127	omanian Carpathians	Cioclovina	<i>Ursus spelaeus</i>	20.00	35.67	12.00	8.00	1.00	2.00	31.67	3.00	2.00	0.00
33	PC/128	omanian Carpathians	Cioclovina	<i>Ursus spelaeus</i>	21.67	31.83	19.00	2.50	0.00	0.00	28.33	1.50	3.50	0.00
34	PC/129	omanian Carpathians	Cioclovina	<i>Ursus spelaeus</i>	18.00	22.00	14.50	2.50	0.00	0.00	21.00	1.50	3.00	0.00
35	PC/133	omanian Carpathians	Cioclovina	<i>Ursus spelaeus</i>	16.00	32.00	15.00	1.00	0.00	0.00	28.00	0.00	4.00	0.00
36	PC/134	omanian Carpathians	Cioclovina	<i>Ursus spelaeus</i>	25.00	31.00	22.50	2.50	0.00	1.50	29.50	0.00	0.00	0.00
37	PC/135	omanian Carpathians	Cioclovina	<i>Ursus spelaeus</i>	21.50	52.50	10.50	9.00	1.00	5.50	41.00	3.50	6.00	0.00
38	PC/138	omanian Carpathians	Cioclovina	<i>Ursus spelaeus</i>	17.50	29.50	9.00	10.00	1.00	6.00	23.50	1.00	0.00	0.00
39	PC/141	omanian Carpathians	Cioclovina	<i>Ursus spelaeus</i>	19.50	36.17	13.50	8.00	1.00	3.50	28.67	3.00	4.00	0.00
40	PC/142	omanian Carpathians	Cioclovina	<i>Ursus spelaeus</i>	20.00	34.50	17.50	4.50	0.00	0.00	29.00	0.00	5.50	0.00
41	PC/144	omanian Carpathians	Cioclovina	<i>Ursus spelaeus</i>	31.00	24.00	25.00	6.00	0.00	4.00	16.00	2.50	4.00	0.00
42	PC/145	omanian Carpathians	Cioclovina	<i>Ursus spelaeus</i>	20.67	35.50	16.00	5.50	0.00	2.00	33.00	0.50	0.50	0.00
43	PC/146	omanian Carpathians	Cioclovina	<i>Ursus spelaeus</i>	23.00	29.00	19.00	4.00	0.00	1.00	28.00	2.00	0.00	0.00
44	CV/005	omanian Carpathians	ACCG	<i>Ursus arctos</i>	19.00	26.00	1.00	18.00	2.00	8.00	17.00	1.00	1.00	0.00
45	CV/009	omanian Carpathians	ACCG	<i>Ursus arctos</i>	31.50	16.50	20.00	11.50	1.00	3.00	11.50	1.00	2.00	0.00
46	PM/U6-I-41	omanian Carpathians	Muierilor	<i>Ursus spelaeus</i>	18.00	23.50	10.00	8.00	1.00	0.00	22.50	0.00	1.00	0.00
47	PM/O6-0-89	omanian Carpathians	Muierilor	<i>Ursus spelaeus</i>	17.00	19.67	4.00	12.00	2.00	1.00	15.67	3.00	3.00	0.00
48	PM/V6-IV-5	omanian Carpathians	Muierilor	<i>Ursus spelaeus</i>	25.50	23.50	7.00	10.00	2.00	1.00	20.00	2.00	2.00	0.00
49	PM/O6-0-I-17	omanian Carpathians	Muierilor	<i>Ursus spelaeus</i>	21.00	25.50	18.00	3.00	0.00	0.00	25.00	0.00	0.50	0.00
50	PM/O6-0-I-21	omanian Carpathians	Muierilor	<i>Ursus spelaeus</i>	22.00	42.50	18.50	3.50	0.00	4.00	34.00	2.50	4.50	0.00
51	PM/O6-I-II-18	omanian Carpathians	Muierilor	<i>Ursus spelaeus</i>	23.50	30.33	21.00	4.00	0.00	0.00	26.33	2.50	4.00	0.00
52	PM/O6-I-II-15	omanian Carpathians	Muierilor	<i>Ursus spelaeus</i>	18.50	29.00	16.50	2.00	0.00	0.00	28.00	0.50	1.00	0.00
53	PM/O6-0-I-27	omanian Carpathians	Muierilor	<i>Ursus spelaeus</i>	23.00	29.00	20.00	3.00	0.00	2.50	20.00	3.00	6.50	0.00
54	PM/O6-II-III-X3	omanian Carpathians	Muierilor	<i>Ursus spelaeus</i>	20.50	42.50	19.50	1.00	0.00	2.00	34.50	0.50	6.00	0.00
55	PM/O6-II-III-X9	omanian Carpathians	Muierilor	<i>Ursus spelaeus</i>	26.50	33.67	20.50	6.00	0.00	0.00	29.67	2.50	4.00	0.00
56	PM/Q6-0-I-1	omanian Carpathians	Muierilor	<i>Ursus spelaeus</i>	21.50	31.50	18.00	3.50	0.00	0.00	27.50	0.00	4.00	0.00
57	PM/Q6-I-II-22	omanian Carpathians	Muierilor	<i>Ursus spelaeus</i>	20.00	34.50	15.00	4.00	0.00	0.00	30.50	0.50	4.00	0.00
58	PM/Q6-I-II-24	omanian Carpathians	Muierilor	<i>Ursus spelaeus</i>	23.00	49.00	20.00	3.00	0.00	0.00	42.50	3.00	6.50	0.00
59	PM/P6-I-II-2	omanian Carpathians	Muierilor	<i>Ursus spelaeus</i>	22.00	48.00	20.00	2.00	0.00	4.00	41.00	0.50	3.00	0.00
60	PM/P6-I-II-3	omanian Carpathians	Muierilor	<i>Ursus spelaeus</i>	19.00	41.50	16.00	3.00	0.00	4.00	35.00	2.50	2.50	0.00
61	PM/P6-0-I-21	omanian Carpathians	Muierilor	<i>Ursus spelaeus</i>	20.50	31.83	18.50	2.00	0.00	2.50	26.33	1.50	3.00	0.00
62	PM/P6-II-III-X1	omanian Carpathians	Muierilor	<i>Ursus spelaeus</i>	20.50	29.00	20.00	0.50	0.00	1.00	24.50	0.00	3.50	0.00
63	PM/T6-I-II-8	omanian Carpathians	Muierilor	<i>Ursus spelaeus</i>	20.00	33.50	17.00	4.00	0.00	0.00	33.50	3.00	0.00	0.00

Appendix

64	PM/R6-0-I-X2	omanian Carpathians	Muierilor	<i>Ursus spelaeus</i>	27.00	50.00	24.00	3.00	0.00	1.50	43.00	0.50	5.50	0.00
65	PM/R6-0-I-X6	omanian Carpathians	Muierilor	<i>Ursus spelaeus</i>	17.00	37.50	3.50	13.50	2.00	3.50	29.00	4.00	5.00	0.00
66	PM/S6-0-I-6	omanian Carpathians	Muierilor	<i>Ursus spelaeus</i>	19.00	41.00	12.00	6.00	0.00	2.50	37.00	0.50	0.50	0.00
67	PM/S6-VI-VII-X1	omanian Carpathians	Muierilor	<i>Ursus spelaeus</i>	19.00	34.83	17.00	2.00	0.00	2.00	32.33	0.00	0.50	0.00
68	PM/S6-XI-XII-X5	omanian Carpathians	Muierilor	<i>Ursus spelaeus</i>	31.50	41.00	27.50	4.00	0.00	4.50	34.50	1.50	2.00	0.00
69	PM/S6-II-III-X6	omanian Carpathians	Muierilor	<i>Ursus spelaeus</i>	29.33	28.50	18.00	2.00	0.00	1.50	26.00	1.00	1.00	0.00
70	PM/U6-I-II-3	omanian Carpathians	Muierilor	<i>Ursus spelaeus</i>	29.50	37.50	18.00	4.00	0.00	0.00	33.00	3.50	4.50	0.00
71	PM/U6-I-II-2	omanian Carpathians	Muierilor	<i>Ursus spelaeus</i>	21.00	42.00	17.00	5.00	0.00	10.00	29.50	1.50	2.50	0.00
72	PM/U6-I-II-X1	omanian Carpathians	Muierilor	<i>Ursus spelaeus</i>	19.50	28.50	19.50	0.00	0.00	0.00	26.00	1.00	2.50	0.00
73	PM/W6-0-I-1	omanian Carpathians	Muierilor	<i>Ursus spelaeus</i>	19.00	43.50	14.00	5.00	0.00	0.50	41.50	0.00	1.50	0.00
74	PM/V6-0-I-2	omanian Carpathians	Muierilor	<i>Ursus spelaeus</i>	18.00	33.50	18.00	0.00	0.00	0.50	29.00	0.00	4.00	0.00
75	PM/V6-III-IV-X2	omanian Carpathians	Muierilor	<i>Ursus spelaeus</i>	16.50	38.00	15.50	1.00	0.00	4.00	31.00	0.50	3.00	0.00
76	PM/U6-III-14	omanian Carpathians	Muierilor	<i>Ursus spelaeus</i>	18.50	34.50	17.50	1.00	0.00	0.00	30.00	1.00	4.50	1.00
77	PM/U6-II-64	omanian Carpathians	Muierilor	<i>Ursus spelaeus</i>	13.00	37.00	15.00	1.00	0.00	0.00	32.50	0.50	4.50	0.00
78	N34.139	omanian Carpathians	Oase	<i>Ursus spelaeus</i>	23.00	19.50	15.00	8.00	1.00	2.00	17.00	0.00	0.50	0.00
79	O34.180	omanian Carpathians	Oase	<i>Ursus spelaeus</i>	21.00	22.50	19.00	2.00	0.00	6.00	15.50	0.50	1.00	0.00
80	N32.27	omanian Carpathians	Oase	<i>Ursus spelaeus</i>	20.50	28.00	15.00	5.50	0.00	1.00	24.00	3.00	3.00	0.00
81	N37.152	omanian Carpathians	Oase	<i>Ursus spelaeus</i>	30.50	24.50	19.00	12.00	1.00	7.00	14.50	0.00	3.00	0.00
82	O36.50	omanian Carpathians	Oase	<i>Ursus spelaeus</i>	16.50	22.00	1.00	13.50	2.00	3.00	17.00	2.00	2.00	0.00
83	N35.244	omanian Carpathians	Oase	<i>Ursus spelaeus</i>	21.00	15.50	14.00	7.00	1.00	7.00	6.00	3.00	2.50	0.00
84	N34.101a	omanian Carpathians	Oase	<i>Ursus spelaeus</i>	21.67	33.50	18.00	3.70	0.00	1.00	30.50	0.00	2.00	0.00
85	O35.138	omanian Carpathians	Oase	<i>Ursus spelaeus</i>	17.50	25.50	9.50	8.00	1.00	1.50	19.00	1.00	5.00	0.00
86	O36.94	omanian Carpathians	Oase	<i>Ursus spelaeus</i>	22.67	20.00	12.67	10.00	1.00	3.00	17.00	0.00	2.00	0.00
87	O35.264	omanian Carpathians	Oase	<i>Ursus spelaeus</i>	41.00	38.00	25.00	15.00	1.00	3.00	32.00	3.00	3.00	0.00
88	N36.955	omanian Carpathians	Oase	<i>Ursus spelaeus</i>	35.00	31.00	6.00	28.00	2.00	6.00	22.00	1.50	3.00	0.00
89	O36.327	omanian Carpathians	Oase	<i>Ursus spelaeus</i>	20.67	10.00	3.67	17.00	2.00	1.50	7.50	0.50	1.00	0.00
90	N36.962	omanian Carpathians	Oase	<i>Ursus spelaeus</i>	24.17	25.00	8.67	14.50	2.00	3.50	18.50	3.00	3.00	0.00
91	N36.961	omanian Carpathians	Oase	<i>Ursus spelaeus</i>	27.00	18.50	21.50	5.50	0.00	2.00	14.50	0.00	2.00	0.00
92	O33/L.1/hde/62	omanian Carpathians	Oase	<i>Ursus spelaeus</i>	25.00	23.50	20.00	5.00	0.00	7.00	12.00	0.50	4.50	0.00
93	N33.d/I.26/147	omanian Carpathians	Oase	<i>Ursus spelaeus</i>	23.50	28.50	11.00	12.50	1.00	6.50	17.00	0.00	5.00	0.00
94	N37.555	omanian Carpathians	Oase	<i>Ursus spelaeus</i>	29.00	33.00	14.00	15.00	1.00	2.50	29.50	1.00	1.00	0.00
95	O36.354	omanian Carpathians	Oase	<i>Ursus spelaeus</i>	19.33	24.50	12.33	7.00	1.00	3.00	19.00	2.00	2.50	0.00
96	N36.956	omanian Carpathians	Oase	<i>Ursus spelaeus</i>	19.00	44.00	11.00	8.00	1.00	4.00	37.00	1.00	3.00	0.00
97	O34.487	omanian Carpathians	Oase	<i>Ursus spelaeus</i>	21.67	25.00	14.67	7.00	1.00	4.00	19.00	1.00	2.00	0.00
98	N35.475	omanian Carpathians	Oase	<i>Ursus spelaeus</i>	22.50	32.00	12.00	10.50	1.00	3.50	25.00	3.00	3.50	0.00
99	N37.545	omanian Carpathians	Oase	<i>Ursus spelaeus</i>	16.17	30.33	7.67	7.50	1.00	5.00	20.33	0.00	5.00	0.00
100	N336/I.2/216	omanian Carpathians	Oase	<i>Ursus spelaeus</i>	15.83	18.00	12.33	3.50	0.00	3.00	12.00	0.00	3.00	0.00
101	O34.454	omanian Carpathians	Oase	<i>Ursus spelaeus</i>	26.50	23.50	8.50	16.50	2.00	2.00	16.00	2.00	5.50	0.00
102	N34.395	omanian Carpathians	Oase	<i>Ursus spelaeus</i>	27.50	26.17	16.50	11.00	1.00	4.50	16.67	0.00	5.00	0.00
103	N36.1027	omanian Carpathians	Oase	<i>Ursus spelaeus</i>	18.00	27.17	10.00	8.00	1.00	1.00	24.67	1.00	1.50	0.00
104	POc/003	omanian Carpathians	Onceasa	<i>Ursus spelaeus</i>	21.50	19.00	13.50	8.00	1.00	5.00	13.00	0.00	1.00	0.00
105	POc/016	omanian Carpathians	Onceasa	<i>Ursus spelaeus</i>	32.00	29.00	18.00	14.00	1.00	10.00	18.00	0.00	1.00	0.00
106	POc/018	omanian Carpathians	Onceasa	<i>Ursus spelaeus</i>	22.00	21.50	14.00	8.00	1.00	0.00	21.00	0.00	0.50	0.00
107	PACC/001	omanian Carpathians	Avenul Mățului	<i>Ursus arctos</i>	25.00	33.00	4.00	20.00	2.00	10.00	20.00	0.00	3.00	0.00
108	PU/A-III-8b	omanian Carpathians	Urșilor	<i>Ursus spelaeus</i>	15.50	27.00	12.50	3.00	0.00	3.00	20.50	1.50	3.50	0.00
109	PU/E1-II-080	omanian Carpathians	Urșilor	<i>Ursus spelaeus</i>	28.00	16.50	26.00	2.00	0.00	0.00	15.00	0.00	1.50	0.00
110	PU/F-I-12b	omanian Carpathians	Urșilor	<i>Ursus spelaeus</i>	26.00	23.50	15.00	11.00	1.00	3.00	18.50	0.00	2.00	0.00
111	PU/D2-XI-045	omanian Carpathians	Urșilor	<i>Ursus spelaeus</i>	21.50	32.00	13.50	8.00	1.00	4.00	25.50	1.00	2.50	0.00
112	PU/D1-VIII-116	omanian Carpathians	Urșilor	<i>Ursus spelaeus</i>	23.50	33.50	15.00	10.00	1.00	1.00	29.00	2.00	3.50	0.00
113	PU/G-II-10.9	omanian Carpathians	Urșilor	<i>Ursus spelaeus</i>	22.33	20.00	4.30	16.00	2.00	9.00	10.00	0.00	1.00	0.00
114	PU/D1-VIII-099	omanian Carpathians	Urșilor	<i>Ursus spelaeus</i>	24.00	20.00	14.00	10.00	1.00	3.00	14.00	2.00	3.00	0.00
115	PU/D1-X-036	omanian Carpathians	Urșilor	<i>Ursus spelaeus</i>	23.00	26.50	13.00	9.00	1.00	6.00	18.50	1.00	2.00	0.00
116	PU/E1-III-125	omanian Carpathians	Urșilor	<i>Ursus spelaeus</i>	24.00	14.50	15.00	9.00	1.00	3.00	9.50	1.00	2.00	0.00
117	PU/E1-III-808	omanian Carpathians	Urșilor	<i>Ursus spelaeus</i>	24.00	29.00	4.00	19.00	2.00	3.00	21.00	2.00	5.00	0.00
118	PU/B1-II-005	omanian Carpathians	Urșilor	<i>Ursus spelaeus</i>	19.50	14.00	1.00	17.50	2.00	5.00	6.00	2.00	3.00	0.00
119	PU/C1-IV-063	omanian Carpathians	Urșilor	<i>Ursus spelaeus</i>	18.50	17.00	10.50	8.00	1.00	3.00	13.00	0.00	1.00	1.00
120	PU/D1-IV-013	omanian Carpathians	Urșilor	<i>Ursus spelaeus</i>	36.00	15.00	21.00	15.00	1.00	0.00	15.00	0.00	0.00	0.00
121	PU/E-II-5a	omanian Carpathians	Urșilor	<i>Ursus spelaeus</i>	13.00	18.50	9.00	4.00	1.00	0.00	15.50	1.00	5.00	0.00

Seasonal insights into the dietary ecology of Eastern European cave bears

122	PU/D2-XI-086	omanian Carpathians	Urşilor	<i>Ursus spelaeus</i>	22.50	23.00	20.00	2.00	0.00	3.00	17.00	1.00	3.00	0.00
123	PU/B-I-14	omanian Carpathians	Urşilor	<i>Ursus spelaeus</i>	25.50	13.50	14.00	11.50	1.00	1.00	11.50	0.00	1.00	0.00
124	PU/E1-III-004	omanian Carpathians	Urşilor	<i>Ursus spelaeus</i>	20.50	23.50	12.50	8.00	1.00	0.00	22.50	0.00	1.00	0.00
125	PU/A-IV-10	omanian Carpathians	Urşilor	<i>Ursus spelaeus</i>	28.50	23.00	4.00	24.50	2.00	5.00	17.50	0.50	0.50	0.00
126	PU/E2-III-1164	omanian Carpathians	Urşilor	<i>Ursus spelaeus</i>	34.00	20.33	20.00	14.00	1.00	1.00	18.33	0.00	1.00	0.00
127	PU/E2-III-969	omanian Carpathians	Urşilor	<i>Ursus spelaeus</i>	18.00	41.50	10.00	8.00	1.00	6.00	33.00	2.00	2.50	0.00
128	PU/B-V-a1	omanian Carpathians	Urşilor	<i>Ursus spelaeus</i>	23.00	23.17	14.00	9.00	1.00	7.00	12.67	0.00	3.50	0.00
129	PU/D1-V-146	omanian Carpathians	Urşilor	<i>Ursus spelaeus</i>	15.50	15.50	9.50	6.00	1.00	4.00	10.50	0.00	1.00	0.00
130	PU/G-I-13a	omanian Carpathians	Urşilor	<i>Ursus spelaeus</i>	27.00	31.00	14.00	13.00	1.00	2.00	28.00	2.00	1.00	0.00
131	PU/D1-VI-135	omanian Carpathians	Urşilor	<i>Ursus spelaeus</i>	19.00	26.00	10.00	8.00	1.00	6.00	18.00	2.00	2.00	0.00
132	PU/F(037)	omanian Carpathians	Urşilor	<i>Ursus spelaeus</i>	23.50	14.50	3.00	20.50	2.00	5.00	8.00	0.00	1.50	0.00
133	PU/F(036)	omanian Carpathians	Urşilor	<i>Ursus spelaeus</i>	27.67	20.00	24.70	3.00	0.00	4.00	14.00	0.00	2.00	0.00
134	PU/D1-II-039	omanian Carpathians	Urşilor	<i>Ursus spelaeus</i>	19.00	35.33	7.50	11.50	1.00	4.00	28.33	2.00	3.00	0.00
135	PU/E1-11-080	omanian Carpathians	Urşilor	<i>Ursus spelaeus</i>	24.50	32.50	17.50	7.00	1.00	4.00	24.00	1.00	4.50	0.00
136	298	omanian Carpathians	Urşilor	<i>Ursus spelaeus</i>	22.50	18.00	10.50	12.00	1.00	0.00	18.00	0.00	0.00	0.00
137	310	omanian Carpathians	Urşilor	<i>Ursus spelaeus</i>	14.50	33.00	6.00	9.00	2.00	2.00	27.50	2.50	3.50	0.00
138	196	omanian Carpathians	Urşilor	<i>Ursus spelaeus</i>	22.50	27.00	10.50	10.50	1.00	2.00	24.50	4.00	0.50	0.00
139	307	omanian Carpathians	Urşilor	<i>Ursus spelaeus</i>	18.50	23.00	15.50	3.00	0.00	1.00	22.00	0.50	0.00	0.00
140	290	omanian Carpathians	Urşilor	<i>Ursus spelaeus</i>	17.50	23.50	1.50	16.00	2.00	0.00	23.50	0.50	0.00	0.00
141	305	omanian Carpathians	Urşilor	<i>Ursus spelaeus</i>	15.50	21.50	3.50	12.00	2.00	0.00	21.50	2.00	0.00	0.00
142	296	omanian Carpathians	Urşilor	<i>Ursus spelaeus</i>	13.00	22.67	7.00	6.00	1.00	0.00	22.67	0.00	0.00	0.00
143	309	omanian Carpathians	Urşilor	<i>Ursus spelaeus</i>	18.50	25.50	12.00	6.50	1.00	0.00	25.50	0.50	0.00	0.00
144	301	omanian Carpathians	Urşilor	<i>Ursus spelaeus</i>	14.50	22.50	5.00	9.50	2.00	1.50	20.50	0.50	0.50	0.00
145	295	omanian Carpathians	Urşilor	<i>Ursus spelaeus</i>	22.50	19.50	15.00	7.50	1.00	1.00	18.50	0.50	0.00	0.00
146	291	omanian Carpathians	Urşilor	<i>Ursus spelaeus</i>	14.50	28.50	10.50	4.50	0.00	0.00	28.50	1.00	0.00	0.00
147	188	omanian Carpathians	Urşilor	<i>Ursus spelaeus</i>	15.50	27.00	7.50	8.00	1.00	1.50	25.50	0.50	0.00	0.00
148	300	omanian Carpathians	Urşilor	<i>Ursus spelaeus</i>	13.50	18.50	4.00	9.50	2.00	1.50	17.00	2.50	0.00	0.00
149	297	omanian Carpathians	Urşilor	<i>Ursus spelaeus</i>	15.50	19.50	13.50	2.00	0.00	0.00	19.50	0.00	0.00	0.00
150	183	omanian Carpathians	Urşilor	<i>Ursus spelaeus</i>	13.50	20.00	11.50	2.00	0.00	1.00	19.00	2.00	0.00	0.00
151	304	omanian Carpathians	Urşilor	<i>Ursus spelaeus</i>	13.00	29.50	7.50	5.50	1.00	3.50	24.50	3.00	1.50	0.00
152	306	omanian Carpathians	Urşilor	<i>Ursus spelaeus</i>	19.50	21.00	17.00	2.50	0.00	2.50	18.50	0.00	0.00	0.00
153	303	omanian Carpathians	Urşilor	<i>Ursus spelaeus</i>	13.00	20.83	6.50	6.50	1.00	0.50	20.33	0.00	0.00	0.00
154	166	omanian Carpathians	Urşilor	<i>Ursus spelaeus</i>	14.50	20.50	12.50	2.00	0.00	1.00	19.50	1.00	0.00	1.00
155	174	omanian Carpathians	Urşilor	<i>Ursus spelaeus</i>	14.00	28.67	1.50	12.50	2.00	2.00	26.67	2.50	0.00	0.00
156	155	omanian Carpathians	Urşilor	<i>Ursus spelaeus</i>	13.50	24.33	0.50	13.00	2.00	0.00	24.33	0.50	0.00	0.00
157	302	omanian Carpathians	Urşilor	<i>Ursus spelaeus</i>	14.50	30.33	9.50	5.00	1.00	2.00	28.33	1.50	0.00	0.00
158	299	omanian Carpathians	Urşilor	<i>Ursus spelaeus</i>	12.50	20.50	11.00	1.50	0.00	0.00	20.50	0.00	0.00	0.00
159	292	omanian Carpathians	Urşilor	<i>Ursus spelaeus</i>	13.00	27.50	2.50	10.50	2.00	2.00	25.50	1.50	0.00	0.00
160	292	omanian Carpathians	Urşilor	<i>Ursus spelaeus</i>	17.00	30.67	14.00	2.00	0.00	3.00	27.67	0.00	0.00	0.00
161	181	omanian Carpathians	Urşilor	<i>Ursus spelaeus</i>	12.00	20.50	1.00	11.00	2.00	2.00	18.50	0.00	0.00	0.00
162	674	Moldavian Plateau	Duruitoarea Veche	<i>Ursus spelaeus</i>	23.50	39.00	21.50	2.00	0.00	0.50	37.50	0.00	1.00	0.00
163	1353	Moldavian Plateau	Duruitoarea Veche	<i>Ursus spelaeus</i>	18.50	30.50	15.00	3.50	1.00	3.50	27.00	0.00	0.00	0.00
164	10H/1	Moldavian Plateau	Duruitoarea Veche	<i>Ursus spelaeus</i>	22.00	34.00	21.00	1.00	0.00	4.50	29.00	2.50	0.50	0.00
165	C-D-II-41	Moldavian Plateau	Duruitoarea Veche	<i>Ursus spelaeus</i>	23.00	27.00	20.00	3.00	0.00	0.50	25.50	0.00	1.00	0.00
166	Y326	Moldavian Plateau	Duruitoarea Veche	<i>Ursus spelaeus</i>	27.50	35.50	26.50	1.00	0.00	3.50	32.00	0.00	0.00	0.00
167	IOW/1; N=10	Moldavian Plateau	Duruitoarea Veche	<i>Ursus spelaeus</i>	16.00	21.00	12.00	4.00	0.00	0.50	20.00	0.00	0.50	0.00
168	GB/4	Moldavian Plateau	Buzdujeni	<i>Ursus spelaeus</i>	21.00	36.00	15.50	5.50	1.00	0.50	33.50	0.00	3.00	0.00
169	17	Moldavian Plateau	Buzdujeni	<i>Ursus spelaeus</i>	15.00	26.50	4.50	10.50	2.00	1.50	25.00	0.00	3.50	0.00
170	19	Moldavian Plateau	Buzdujeni	<i>Ursus spelaeus</i>	15.00	30.50	11.00	4.00	0.00	1.50	26.00	0.00	3.00	0.00
171	24	Moldavian Plateau	Buzdujeni	<i>Ursus spelaeus</i>	19.00	21.00	11.50	7.50	1.00	1.50	19.00	0.00	0.50	0.00
172	20	Moldavian Plateau	Buzdujeni	<i>Ursus spelaeus</i>	20.50	26.50	18.50	2.00	0.00	0.50	22.50	1.50	3.50	0.00
173	26	Moldavian Plateau	Buzdujeni	<i>Ursus spelaeus</i>	19.00	21.00	15.50	3.50	0.00	0.00	17.50	0.00	3.50	0.00
174	23	Moldavian Plateau	Buzdujeni	<i>Ursus spelaeus</i>	16.00	34.50	15.00	1.00	0.00	0.00	31.00	0.00	3.50	0.00
175	25	Moldavian Plateau	Buzdujeni	<i>Ursus spelaeus</i>	35.00	27.50	29.00	6.00	0.00	2.00	23.00	0.00	2.50	0.00
176	30	Moldavian Plateau	Buzdujeni	<i>Ursus spelaeus</i>	26.00	32.00	25.00	1.00	0.00	0.00	29.50	0.00	2.50	0.00
177	32	Moldavian Plateau	Buzdujeni	<i>Ursus spelaeus</i>	24.00	22.00	23.00	1.00	0.00	0.00	19.00	0.00	3.00	0.00
178	29	Moldavian Plateau	Buzdujeni	<i>Ursus spelaeus</i>	23.00	24.50	23.00	0.00	0.00	0.00	24.50	0.00	0.00	0.00
179	31/41	Moldavian Plateau	Saharna	<i>Ursus spelaeus</i>	17.00	46.50	16.00	1.00	0.00	1.00	45.00	0.00	3.00	0.00

Appendix

180	31/354	Moldavian Plateau	Saharna	<i>Ursus spelaeus</i>	17.50	30.00	17.00	0.50	0.00	0.50	29.00	0.00	0.50	0.00
181	31/352	Moldavian Plateau	Saharna	<i>Ursus spelaeus</i>	29.00	20.00	25.00	4.00	0.00	0.00	19.50	0.50	0.50	0.00
182	31/363	Moldavian Plateau	Saharna	<i>Ursus spelaeus</i>	16.50	26.33	16.50	0.00	0.00	0.00	24.33	0.00	2.50	0.00
183	31/161	Moldavian Plateau	Saharna	<i>Ursus spelaeus</i>	19.00	59.00	17.00	2.00	0.00	0.00	55.00	0.50	4.00	0.00
184	154	Moldavian Plateau	Saharna	<i>Ursus spelaeus</i>	19.00	36.50	18.00	2.00	0.00	0.50	34.00	1.00	2.00	0.00
185	31/440	Moldavian Plateau	Saharna	<i>Ursus spelaeus</i>	16.00	40.00	14.00	2.00	0.00	0.00	38.00	1.50	1.00	0.00
186	31/408	Moldavian Plateau	Saharna	<i>Ursus spelaeus</i>	17.50	33.50	16.50	1.00	0.00	1.50	29.50	0.50	2.50	0.00
187	31/398	Moldavian Plateau	Saharna	<i>Ursus spelaeus</i>	13.00	34.50	13.00	0.00	0.00	0.50	29.50	0.00	4.50	0.00
188	31/365	Moldavian Plateau	Saharna	<i>Ursus spelaeus</i>	20.00	34.67	14.50	5.50	0.00	0.00	32.67	0.00	3.50	0.00
189	SH/5	Moldavian Plateau	Saharna	<i>Ursus spelaeus</i>	16.00	38.00	12.00	4.00	0.00	4.00	33.00	0.00	4.50	0.00
190	SH/2021	Moldavian Plateau	Saharna	<i>Ursus spelaeus</i>	17.00	33.50	16.00	1.00	0.00	0.00	31.00	0.00	5.00	0.00
191	SH/4	Moldavian Plateau	Saharna	<i>Ursus spelaeus</i>	19.50	31.50	11.50	8.00	1.00	0.50	28.00	0.50	4.00	0.00
192	SH/40	Moldavian Plateau	Saharna	<i>Ursus spelaeus</i>	17.67	44.50	17.00	1.00	0.00	0.00	38.00	0.00	5.50	0.00
193	SH/2; 31/48	Moldavian Plateau	Saharna	<i>Ursus spelaeus</i>	17.50	45.00	16.50	1.00	0.00	0.00	41.00	0.00	4.00	0.00
194	SH/1	Moldavian Plateau	Saharna	<i>Ursus spelaeus</i>	17.00	36.00	17.00	0.00	0.00	0.00	31.00	0.50	5.00	0.00
195	SH/3; 31/55	Moldavian Plateau	Saharna	<i>Ursus spelaeus</i>	24.00	32.83	21.50	2.50	0.00	0.00	29.33	0.00	3.50	0.00
196	Tr I 80 n 4_1	Moldavian Plateau	Trinca	<i>Ursus arctos</i>	21.00	21.00	19.50	1.50	0.00	0.00	21.00	0.00	0.00	0.00
197	Tr I 80 n 4_2	Moldavian Plateau	Trinca	<i>Ursus arctos</i>	19.50	19.50	19.00	0.50	0.00	0.00	19.50	0.00	0.00	0.00
198	1994	Moldavian Plateau	Trinca	<i>Ursus arctos</i>	17.00	19.50	10.50	6.50	1.00	3.00	16.50	3.50	0.00	0.00
199	Tr I+II n 4	Moldavian Plateau	Trinca	<i>Ursus arctos</i>	23.50	23.50	22.50	1.00	0.00	0.00	23.50	0.00	0.00	0.00
200	Tr I 80	Moldavian Plateau	Trinca	<i>Ursus arctos</i>	20.50	27.50	12.00	8.50	1.00	7.00	20.50	5.00	2.00	0.00
201	Tr I n 4	Moldavian Plateau	Trinca	<i>Ursus spelaeus</i>	19.00	19.00	18.00	1.00	0.00	0.00	19.00	0.00	2.00	0.00
202	Tr I 80	Moldavian Plateau	Trinca	<i>Ursus spelaeus</i>	18.50	20.50	18.50	0.00	0.00	2.00	18.50	0.00	1.50	0.00
203	Tr I 80	Moldavian Plateau	Trinca	<i>Ursus spelaeus</i>	19.00	19.00	17.50	1.50	0.00	0.00	19.00	0.00	0.00	0.00
204	Tr I 80	Moldavian Plateau	Trinca	<i>Ursus spelaeus</i>	20.50	21.50	20.50	0.00	0.00	1.00	20.50	0.00	0.00	0.00
205	Tr I 80	Moldavian Plateau	Trinca	<i>Ursus spelaeus</i>	17.50	17.50	17.50	0.00	0.00	0.00	17.50	0.00	0.00	0.00
206	Tr I 80	Moldavian Plateau	Trinca	<i>Ursus spelaeus</i>	22.00	22.00	21.00	1.00	0.00	0.00	22.00	0.00	2.00	0.00
207	Tr II 1990	Moldavian Plateau	Trinca	<i>Ursus spelaeus</i>	23.50	24.50	23.50	0.00	0.00	1.00	23.50	0.00	0.00	0.00
208	Tr I 80	Moldavian Plateau	Trinca	<i>Ursus spelaeus</i>	19.00	19.00	17.00	2.00	0.00	0.00	19.00	0.00	0.50	0.00
209	Tr I 80	Moldavian Plateau	Trinca	<i>Ursus spelaeus</i>	23.00	23.00	23.00	0.00	0.00	0.00	23.00	0.00	1.00	0.00
210	Tr I 80	Moldavian Plateau	Trinca	<i>Ursus spelaeus</i>	18.50	18.50	18.00	0.50	0.00	0.00	18.50	0.00	0.00	0.00
211	Tr I 80	Moldavian Plateau	Trinca	<i>Ursus spelaeus</i>	17.00	18.00	15.00	2.00	0.00	1.00	17.00	0.50	0.00	0.00
212	Tr I 80	Moldavian Plateau	Trinca	<i>Ursus spelaeus</i>	21.00	21.00	19.50	1.50	0.00	0.00	21.00	0.00	0.00	0.00
213	Tr I 80	Moldavian Plateau	Trinca	<i>Ursus spelaeus</i>	24.00	24.00	24.00	0.00	0.00	0.00	24.00	0.00	0.00	0.00
214	Tr I 80	Moldavian Plateau	Trinca	<i>Ursus spelaeus</i>	21.50	21.50	21.50	0.00	0.00	0.00	21.50	0.00	0.00	0.00
215	Tr I 80	Moldavian Plateau	Trinca	<i>Ursus spelaeus</i>	20.00	22.00	19.50	0.50	0.00	2.00	20.00	1.00	0.00	0.00
216	Tr I 80	Moldavian Plateau	Trinca	<i>Ursus spelaeus</i>	24.50	25.50	24.50	0.00	0.00	1.00	24.50	0.00	0.00	0.00
217	10704/163	Moldavian Plateau	Butesti	<i>Ursus spelaeus</i>	26.50	42.50	19.00	7.50	1.00	1.00	41.50	0.00	0.50	0.00
218	10704/174	Moldavian Plateau	Butesti	<i>Ursus spelaeus</i>	22.00	33.00	19.50	2.50	0.00	0.00	33.00	0.00	0.00	0.00
219	K2313	Western Balkans	Bacho Kiro	<i>Ursus spelaeus</i>	8.50	31.00	7.00	1.50	0.00	1.50	29.50	0.00	0.00	0.00
220	6K 1824	Western Balkans	Bacho Kiro	<i>Ursus spelaeus</i>	12.50	35.50	9.00	3.50	0.00	1.50	34.00	1.50	0.00	0.00
221	K2941	Western Balkans	Bacho Kiro	<i>Ursus spelaeus</i>	16.50	35.00	12.50	4.00	1.00	3.00	29.50	0.50	2.50	0.00
222	6K2067	Western Balkans	Bacho Kiro	<i>Ursus spelaeus</i>	13.50	32.33	9.50	4.00	0.00	2.00	28.33	1.50	2.00	0.00
223	6K173	Western Balkans	Bacho Kiro	<i>Ursus spelaeus</i>	17.00	43.00	12.00	5.00	0.00	2.00	37.00	1.00	4.00	0.00
224	LK1	Western Balkans	Lakatnik	<i>Ursus spelaeus</i>	15.00	20.00	15.00	0.00	0.00	0.00	20.00	0.50	0.00	0.00
225	LK2	Western Balkans	Lakatnik	<i>Ursus spelaeus</i>	10.50	22.00	10.50	0.00	0.00	0.00	22.00	1.00	0.00	0.00
226	LK3	Western Balkans	Lakatnik	<i>Ursus spelaeus</i>	10.00	19.50	10.00	0.00	0.00	0.00	19.50	0.00	0.00	0.00
227	LK4	Western Balkans	Lakatnik	<i>Ursus spelaeus</i>	13.50	22.50	12.00	1.50	0.00	1.00	21.00	0.50	0.50	0.00
228	BP1	Western Balkans	Bashovishki Pech	<i>Ursus spelaeus</i>	17.00	38.50	13.00	4.00	0.00	6.50	23.00	3.00	9.00	0.00
229	BP2	Western Balkans	Bashovishki Pech	<i>Ursus spelaeus</i>	16.50	30.00	13.00	3.50	0.00	2.50	21.00	1.00	6.50	0.00
230	F938	Western Rhodopes Mountains	Triagalna	<i>Ursus spelaeus</i>	12.50	41.50	11.50	1.00	0.00	3.00	36.50	0.50	2.00	0.00
231	SM2177	Western Rhodopes Mountains	Triagalna	<i>Ursus spelaeus</i>	10.50	38.00	10.50	0.00	0.00	3.50	32.50	2.00	2.00	0.00
232	5	Western Rhodopes Mountains	Borikovska Cave	<i>Ursus spelaeus</i>	18.00	36.00	17.50	0.50	0.00	1.50	34.50	1.00	0.00	0.00
233	116F	Western Rhodopes Mountains	Borikovska Cave	<i>Ursus spelaeus</i>	14.50	37.50	11.00	3.50	0.00	0.50	35.50	1.00	1.50	0.00
234	0.20-0.25	Western Rhodopes Mountains	Borikovska Cave	<i>Ursus spelaeus</i>	18.50	34.00	14.00	4.50	0.00	2.50	31.50	1.00	0.00	0.00
235	627-34	Western Rhodopes Mountains	Borikovska Cave	<i>Ursus spelaeus</i>	18.00	35.50	14.00	4.00	0.00	3.50	31.50	1.50	0.50	0.00

Seasonal insights into the dietary ecology of Eastern European cave bears

236	x1	Western Rhodopes Mountains	Borikovska Cave	<i>Ursus spelaeus</i>	15.00	31.00	7.00	8.00	1.00	2.00	29.00	1.00	0.00	0.00
237	636-15	Western Rhodopes Mountains	Borikovska Cave	<i>Ursus spelaeus</i>	11.50	30.00	11.00	0.50	0.00	0.00	30.00	0.50	0.00	0.00
238	638-11	Western Rhodopes Mountains	Borikovska Cave	<i>Ursus spelaeus</i>	12.50	33.33	12.00	0.50	0.00	3.00	30.33	1.00	0.00	0.00
239	281	Western Rhodopes Mountains	Borikovska Cave	<i>Ursus spelaeus</i>	13.00	30.00	12.50	0.50	0.00	0.00	29.50	3.00	0.50	0.00
240	734-1	Western Rhodopes Mountains	Borikovska Cave	<i>Ursus spelaeus</i>	14.50	30.50	14.00	0.50	0.00	0.50	29.50	0.00	0.50	0.00
241	116I	Western Rhodopes Mountains	Borikovska Cave	<i>Ursus spelaeus</i>	15.50	36.00	14.00	1.50	0.00	1.50	34.50	4.50	0.00	0.00
242	116H	Western Rhodopes Mountains	Borikovska Cave	<i>Ursus spelaeus</i>	17.00	37.33	12.00	5.00	1.00	1.50	35.33	1.50	0.50	0.00
243	116A	Western Rhodopes Mountains	Borikovska Cave	<i>Ursus spelaeus</i>	13.00	34.50	9.50	3.50	0.00	4.50	29.50	3.00	0.50	0.00
244	151	Western Rhodopes Mountains	Borikovska Cave	<i>Ursus spelaeus</i>	14.50	32.00	11.50	3.00	0.00	2.50	29.00	3.00	0.50	0.00
245	627-39	Western Rhodopes Mountains	Borikovska Cave	<i>Ursus spelaeus</i>	13.00	30.50	11.00	2.00	0.00	1.50	29.00	0.50	0.00	0.00
246	851	Western Rhodopes Mountains	Borikovska Cave	<i>Ursus spelaeus</i>	13.50	36.50	13.00	0.50	0.00	1.00	35.00	0.00	0.50	0.00
247	116C	Western Rhodopes Mountains	Borikovska Cave	<i>Ursus spelaeus</i>	15.00	37.00	13.00	2.00	0.00	1.00	34.50	2.50	1.50	0.00
248	651	Western Rhodopes Mountains	Borikovska Cave	<i>Ursus spelaeus</i>	14.50	44.00	12.00	2.50	0.00	4.00	39.00	1.50	1.00	0.00
249	151B	Western Rhodopes Mountains	Borikovska Cave	<i>Ursus spelaeus</i>	13.00	35.50	11.00	2.00	0.00	3.50	31.50	2.00	0.50	0.00
250	627-53	Western Rhodopes Mountains	Borikovska Cave	<i>Ursus spelaeus</i>	13.00	33.50	11.00	2.00	0.00	3.00	28.50	1.50	2.00	0.00
251	116S	Western Rhodopes Mountains	Borikovska Cave	<i>Ursus spelaeus</i>	16.50	35.33	14.00	2.50	0.00	4.00	29.33	2.00	2.00	0.00
252	116M	Western Rhodopes Mountains	Borikovska Cave	<i>Ursus spelaeus</i>	15.50	32.00	12.50	3.00	0.00	2.00	29.00	0.50	1.00	0.00
253	151C	Western Rhodopes Mountains	Borikovska Cave	<i>Ursus spelaeus</i>	16.00	29.50	12.00	4.00	1.00	3.00	26.50	2.00	0.00	0.00
254	1000	Western Rhodopes Mountains	Borikovska Cave	<i>Ursus spelaeus</i>	14.00	35.00	12.50	1.50	0.00	7.50	27.50	2.00	0.00	0.00
255	627-33	Western Rhodopes Mountains	Borikovska Cave	<i>Ursus spelaeus</i>	13.00	28.00	6.50	6.50	1.00	2.00	26.00	1.50	0.00	0.00
256	1290	Western Rhodopes Mountains	Borikovska Cave	<i>Ursus spelaeus</i>	13.00	27.00	10.50	2.50	0.00	1.50	25.00	2.00	0.50	0.00
257	52/5	Western Rhodopes Mountains	Borikovska Cave	<i>Ursus spelaeus</i>	13.50	27.00	11.50	2.00	0.00	2.50	24.50	2.00	0.00	0.00
258	116D	Western Rhodopes Mountains	Borikovska Cave	<i>Ursus spelaeus</i>	12.00	32.00	11.00	1.00	0.00	1.50	30.50	2.00	0.00	0.00
259	415	Western Rhodopes Mountains	Borikovska Cave	<i>Ursus spelaeus</i>	13.50	34.00	12.00	1.50	0.00	2.00	30.50	2.50	1.50	0.00
260	116/61	Western Rhodopes Mountains	Borikovska Cave	<i>Ursus spelaeus</i>	13.00	38.00	9.00	4.00	1.00	2.00	32.00	2.50	4.00	0.00
261	x6	Western Rhodopes Mountains	Borikovska Cave	<i>Ursus spelaeus</i>	18.00	31.50	17.00	1.00	0.00	1.00	30.50	2.00	0.00	0.00
262	x7	Western Rhodopes Mountains	Borikovska Cave	<i>Ursus spelaeus</i>	14.50	37.00	11.50	3.00	0.00	2.00	33.00	3.00	2.00	0.00
263	x9	Western Rhodopes Mountains	Borikovska Cave	<i>Ursus spelaeus</i>	13.50	30.00	12.00	1.50	0.00	2.00	27.00	1.50	1.00	0.00
264	116/59	Western Rhodopes Mountains	Borikovska Cave	<i>Ursus spelaeus</i>	10.00	60.50	1.00	9.00	2.00	6.50	54.00	4.50	0.00	0.00
265	172/2	Western Rhodopes Mountains	Borikovska Cave	<i>Ursus spelaeus</i>	12.50	33.50	10.50	2.00	0.00	4.00	27.50	0.50	2.00	0.00
266	676-2	Western Rhodopes Mountains	Borikovska Cave	<i>Ursus spelaeus</i>	13.00	28.00	12.50	0.50	0.00	1.50	25.50	0.00	1.00	0.00
267	641-5	Western Rhodopes Mountains	Borikovska Cave	<i>Ursus spelaeus</i>	14.50	29.00	13.00	1.50	0.00	0.50	28.00	1.00	0.50	0.00
268	151D	Western Rhodopes Mountains	Borikovska Cave	<i>Ursus spelaeus</i>	11.50	32.00	7.50	4.00	0.00	2.50	29.50	1.00	0.00	0.00
269	1613	Western Rhodopes Mountains	Borikovska Cave	<i>Ursus spelaeus</i>	14.00	36.00	10.50	3.50	0.00	0.00	35.50	2.00	0.50	0.00
270	1643	Western Rhodopes Mountains	Borikovska Cave	<i>Ursus spelaeus</i>	15.50	34.00	14.50	1.00	0.00	4.50	29.50	0.00	0.00	0.00
271	982	Western Rhodopes Mountains	Borikovska Cave	<i>Ursus spelaeus</i>	12.00	26.17	8.00	4.00	1.00	2.50	23.67	0.50	0.00	0.00
272	170	Western Rhodopes Mountains	Borikovska Cave	<i>Ursus spelaeus</i>	15.00	31.50	14.00	1.00	0.00	0.50	31.00	0.50	0.00	0.00
273	2178	Western Rhodopes Mountains	Borikovska Cave	<i>Ursus spelaeus</i>	15.00	32.50	11.50	3.50	0.00	3.00	28.50	1.00	1.00	0.00
274	1500	Western Rhodopes Mountains	Borikovska Cave	<i>Ursus spelaeus</i>	13.50	33.50	11.50	2.00	0.00	2.00	30.50	1.00	1.00	0.00
275	1115	Western Rhodopes Mountains	Borikovska Cave	<i>Ursus spelaeus</i>	16.00	33.50	15.00	1.00	0.00	0.50	33.00	0.00	0.00	0.00
276	IV/221	Western Rhodopes Mountains	Borikovska Cave	<i>Ursus spelaeus</i>	12.50	44.00	8.00	4.50	1.00	5.00	37.50	2.00	1.50	0.00
277	2489	Western Rhodopes Mountains	Borikovska Cave	<i>Ursus spelaeus</i>	13.50	40.00	12.50	1.00	0.00	4.50	34.50	0.50	1.00	0.00
278	IV/190	Western Rhodopes Mountains	Borikovska Cave	<i>Ursus spelaeus</i>	11.50	24.00	10.50	1.00	0.00	1.50	22.50	0.00	0.00	0.00
279	2177	Western Rhodopes Mountains	Borikovska Cave	<i>Ursus spelaeus</i>	12.50	24.00	10.00	2.50	0.00	3.00	21.00	1.00	0.00	0.00
280	M3/813	Western Balkans	Magura	<i>Ursus spelaeus</i>	16.00	38.50	14.00	2.00	0.00	2.00	34.00	0.00	2.50	0.00
281	MII/53	Western Balkans	Magura	<i>Ursus spelaeus</i>	17.00	39.00	8.50	8.50	1.00	3.00	34.50	3.50	1.50	0.00

Appendix

282	M3/1061	Western Balkans	Magura	<i>Ursus spelaeus</i>	12.50	24.83	10.50	2.00	0.00	0.50	24.33	0.00	0.00	0.00
283	M3/1450	Western Balkans	Magura	<i>Ursus spelaeus</i>	13.50	26.50	6.50	7.00	1.00	1.50	23.00	1.50	2.00	0.00
284	M3/1032	Western Balkans	Magura	<i>Ursus spelaeus</i>	18.00	18.33	17.50	0.50	0.00	0.50	17.33	0.00	0.50	0.00
285	M3/1532	Western Balkans	Magura	<i>Ursus spelaeus</i>	14.00	23.83	14.00	0.00	0.00	0.50	21.33	2.50	2.00	0.00
286	M3/1582	Western Balkans	Magura	<i>Ursus spelaeus</i>	14.50	25.67	12.50	2.00	0.00	0.00	23.67	0.50	2.00	0.00
287	MIU/1495	Western Balkans	Magura	<i>Ursus spelaeus</i>	25.00	28.50	12.00	13.00	1.00	3.50	25.00	1.00	0.00	0.00
288	MK6/B19	Western Balkans	Mishin	<i>Ursus savini rossicus</i>	23.50	30.83	21.00	2.50	0.00	1.00	28.33	0.00	1.50	0.00
289	MK4/C20	Western Balkans	Mishin	<i>Ursus savini rossicus</i>	19.50	33.50	13.00	6.50	1.00	3.00	29.00	1.00	1.50	0.00
290	MK 1/20 F3J	Western Balkans	Mishin	<i>Ursus savini rossicus</i>	19.50	25.50	18.50	1.00	0.00	0.00	24.50	0.50	1.00	0.00
291	MK1/2137	Western Balkans	Mishin	<i>Ursus savini rossicus</i>	19.00	32.50	10.00	9.00	1.00	1.50	30.00	0.00	1.00	0.00
292	MK1/6 E37	Western Balkans	Mishin	<i>Ursus savini rossicus</i>	20.00	26.50	10.00	10.00	1.00	1.50	25.00	0.00	0.00	0.00
293	85/675	Central Balkans	Ušačka	<i>Ursus spelaeus</i>	16.00	18.00	15.50	0.50	0.00	0.00	18.00	1.50	0.00	0.00
294	85/943	Central Balkans	Ušačka	<i>Ursus spelaeus</i>	18.50	21.50	17.50	1.00	0.00	1.00	20.50	0.00	0.00	0.00
295	85/388	Central Balkans	Ušačka	<i>Ursus spelaeus</i>	17.50	20.50	9.50	8.00	1.00	0.00	20.50	0.00	0.00	0.00
296	85/1061	Central Balkans	Ušačka	<i>Ursus spelaeus</i>	13.50	20.83	6.00	7.50	1.00	2.00	18.33	0.50	0.50	0.00
297	85/1098	Central Balkans	Ušačka	<i>Ursus spelaeus</i>	16.50	21.00	9.50	7.00	1.00	0.50	20.50	0.50	0.00	0.00
298	85/1048	Central Balkans	Ušačka	<i>Ursus spelaeus</i>	14.00	19.67	12.50	1.50	0.00	1.00	18.67	0.00	0.00	0.00
299	85/1064	Central Balkans	Ušačka	<i>Ursus spelaeus</i>	13.00	23.83	11.50	1.50	0.00	2.50	21.33	0.50	0.00	0.00
300	45 4/5	Central Balkans	Ušačka	<i>Ursus spelaeus</i>	17.50	22.00	8.00	9.50	1.00	1.00	21.00	0.00	0.00	0.00
301	85/1073	Central Balkans	Ušačka	<i>Ursus spelaeus</i>	12.50	24.33	7.50	5.00	1.00	0.00	24.33	0.00	0.00	1.00
302	85/1066	Central Balkans	Ušačka	<i>Ursus spelaeus</i>	14.50	21.50	7.50	7.00	1.00	2.50	19.00	0.00	0.00	0.00
303	85/1071	Central Balkans	Ušačka	<i>Ursus spelaeus</i>	17.50	20.83	9.50	8.00	1.00	1.50	19.33	0.00	0.00	0.00
304	RIS92/284	Central Balkans	Risovača	<i>Ursus spelaeus</i>	18.50	26.50	18.50	0.00	0.00	0.50	26.00	0.00	0.00	0.00
305	RIS92/338	Central Balkans	Risovača	<i>Ursus spelaeus</i>	15.50	29.50	14.50	1.00	0.00	0.50	29.00	0.50	0.00	0.00
306	RIS92/283	Central Balkans	Risovača	<i>Ursus spelaeus</i>	20.50	27.00	18.50	2.00	0.00	0.00	27.00	0.00	0.00	0.00
307	RIS75/89	Central Balkans	Risovača	<i>Ursus spelaeus</i>	18.00	35.00	17.00	1.00	0.00	0.00	32.00	1.00	3.00	0.00
308	RIS92/497	Central Balkans	Risovača	<i>Ursus spelaeus</i>	16.00	25.50	16.00	0.00	0.00	0.00	25.50	0.50	0.00	0.00
309	RIS92/970	Central Balkans	Risovača	<i>Ursus spelaeus</i>	20.00	27.50	19.00	1.00	0.00	2.00	25.50	0.50	0.00	0.00
310	RIS92/681	Central Balkans	Risovača	<i>Ursus spelaeus</i>	18.50	25.00	18.50	0.00	0.00	0.50	24.50	0.50	0.00	0.00
311	RIS92/971	Central Balkans	Risovača	<i>Ursus spelaeus</i>	21.50	24.00	18.50	3.00	0.00	0.00	24.00	0.00	0.00	0.00
312	RIS92/973	Central Balkans	Risovača	<i>Ursus spelaeus</i>	17.50	33.50	17.50	0.00	0.00	0.50	33.00	0.50	0.00	0.00
313	RIS92/158	Central Balkans	Risovača	<i>Ursus spelaeus</i>	16.50	36.00	15.50	1.00	0.00	2.50	33.50	0.50	0.00	0.00
314	HPP04/100/3	Central Balkans	Hadži Prodanova	<i>Ursus spelaeus</i>	13.00	25.33	11.50	1.50	0.00	4.00	21.33	1.50	0.00	0.00
315	HPP04/172/5	Central Balkans	Hadži Prodanova	<i>Ursus spelaeus</i>	17.50	22.50	15.50	2.00	0.00	1.00	21.50	0.00	0.00	0.00
316	HPP04/76/1	Central Balkans	Hadži Prodanova	<i>Ursus spelaeus</i>	16.00	24.00	14.50	1.50	0.00	0.50	23.50	0.00	0.00	0.00
317	HPP04/172/4	Central Balkans	Hadži Prodanova	<i>Ursus spelaeus</i>	13.00	24.00	10.50	2.50	0.00	0.50	23.50	1.00	0.00	0.00
318	HPP04/213/5	Central Balkans	Hadži Prodanova	<i>Ursus spelaeus</i>	21.00	19.00	18.50	2.50	0.00	0.50	18.50	0.50	0.00	0.00
319	HPP04/95/8	Central Balkans	Hadži Prodanova	<i>Ursus spelaeus</i>	14.00	23.50	13.00	1.00	0.00	3.00	20.50	2.00	0.00	0.00
320	HPP04/173/4	Central Balkans	Hadži Prodanova	<i>Ursus spelaeus</i>	17.00	20.17	16.00	1.00	0.00	1.50	18.67	0.50	0.00	0.00
321	HPP03/96/2	Central Balkans	Hadži Prodanova	<i>Ursus spelaeus</i>	15.50	24.67	15.50	0.00	0.00	0.00	24.67	0.00	0.00	0.00
322	HPP03/103/1	Central Balkans	Hadži Prodanova	<i>Ursus spelaeus</i>	14.50	21.67	10.50	4.00	0.00	0.00	21.67	0.00	0.00	1.00
323	HPP03/77/1	Central Balkans	Hadži Prodanova	<i>Ursus spelaeus</i>	17.50	24.17	16.50	1.00	0.00	0.50	23.67	1.00	0.00	0.00
324	HPP03/68/2	Central Balkans	Hadži Prodanova	<i>Ursus spelaeus</i>	18.50	28.17	10.50	8.00	0.00	2.00	24.67	0.00	1.50	0.00
325	ZIN 37998 (83)	Greater Caucasus	Kudaro-1	<i>Ursus praekudarensis</i>	14.50	37.50	3.50	11.00	2.00	1.00	36.50	0.00	0.50	1.00
326	ZIN 38010 (1421)	Greater Caucasus	Kudaro-1	<i>Ursus praekudarensis</i>	13.50	33.50	7.00	6.00	1.00	0.00	33.50	0.00	0.00	0.00
327	ZIN 38010 (659)	Greater Caucasus	Kudaro-1	<i>Ursus praekudarensis</i>	13.00	28.50	7.50	6.50	1.00	1.00	27.50	0.00	1.00	1.00
328	ZIN 38010 (204)	Greater Caucasus	Kudaro-1	<i>Ursus praekudarensis</i>	16.50	35.50	3.50	13.00	2.00	2.00	33.50	0.00	0.50	0.00
329	ZIN 38010 (1108)	Greater Caucasus	Kudaro-1	<i>Ursus praekudarensis</i>	15.50	37.00	4.50	11.00	2.00	1.00	36.00	1.50	0.50	0.00
330	ZIN 38010 (1425)	Greater Caucasus	Kudaro-1	<i>Ursus praekudarensis</i>	12.50	33.00	5.50	7.00	1.00	3.00	30.00	0.00	0.00	1.00
331	ZIN 38010 (105)	Greater Caucasus	Kudaro-1	<i>Ursus praekudarensis</i>	13.00	31.00	7.50	5.50	1.00	1.00	30.00	0.00	0.00	0.00
332	ZIN 38010 (1116)	Greater Caucasus	Kudaro-1	<i>Ursus praekudarensis</i>	13.50	29.00	5.50	8.50	2.00	2.00	27.00	0.00	0.50	1.00
333	ZIN 38009 (50)	Greater Caucasus	Kudaro-1	<i>Ursus praekudarensis</i>	13.00	37.50	7.50	5.50	1.00	2.00	35.50	0.00	0.00	1.00
334	ZIN 38010 (669)	Greater Caucasus	Kudaro-1	<i>Ursus praekudarensis</i>	16.00	41.50	4.50	11.50	2.00	1.00	40.50	0.00	0.50	1.00
335	ZIN 38010 (1417)	Greater Caucasus	Kudaro-1	<i>Ursus praekudarensis</i>	15.00	43.50	5.00	10.00	2.00	3.00	40.50	0.00	1.50	0.00
336	ZIN 38010 (1427)	Greater Caucasus	Kudaro-1	<i>Ursus praekudarensis</i>	13.00	36.00	5.00	9.00	2.00	2.00	34.00	0.00	0.00	0.00
337	ZIN 38010 (1112)	Greater Caucasus	Kudaro-1	<i>Ursus praekudarensis</i>	15.00	47.50	8.50	6.50	1.00	4.00	43.50	0.00	0.00	0.00
338	ZIN 38010 (89)	Greater Caucasus	Kudaro-1	<i>Ursus praekudarensis</i>	15.00	44.00	5.00	10.00	2.00	3.00	41.00	1.00	0.50	1.00
339	ZIN 38010 (1419)	Greater Caucasus	Kudaro-1	<i>Ursus praekudarensis</i>	12.00	41.50	5.00	7.50	1.00	4.00	37.50	0.50	0.50	0.00

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340	ZIN 37958 (1130)	Greater Caucasus	Kudaro-3	<i>Ursus praekudarensis / kudarensis</i>	17.50	23.50	17.50	0.00	0.00	1.00	22.50	0.00	0.00	0.00
341	ZIN 37958 (1132)	Greater Caucasus	Kudaro-3	<i>Ursus praekudarensis / kudarensis</i>	23.00	22.00	18.00	3.50	0.00	1.00	21.00	1.50	0.00	0.00
342	ZIN 37958 (1203)	Greater Caucasus	Kudaro-3	<i>Ursus praekudarensis / kudarensis</i>	23.50	23.00	22.00	2.00	0.00	1.00	22.00	0.00	0.00	0.00
343	ZIN 37958 (911)	Greater Caucasus	Kudaro-3	<i>Ursus praekudarensis / kudarensis</i>	21.00	23.50	20.00	1.00	0.00	0.00	23.50	0.00	0.00	0.00
344	ZIN 37958 (902)	Greater Caucasus	Kudaro-3	<i>Ursus praekudarensis / kudarensis</i>	19.50	21.00	17.00	2.50	0.00	0.00	21.00	0.00	0.00	0.00
345	ZIN 37958 (1136)	Greater Caucasus	Kudaro-3	<i>Ursus praekudarensis / kudarensis</i>	17.50	23.50	16.00	1.50	0.00	1.00	22.50	0.00	0.00	0.00
346	ZIN 37958 (1135)	Greater Caucasus	Kudaro-3	<i>Ursus praekudarensis / kudarensis</i>	18.00	18.50	16.00	2.00	0.00	0.00	18.50	0.00	0.00	0.00
347	ZIN 37998 (1133)	Greater Caucasus	Kudaro-3	<i>Ursus praekudarensis / kudarensis</i>	18.00	18.50	18.00	0.00	0.00	1.00	17.50	0.00	0.00	0.00
348	ZIN 37958 (1127)	Greater Caucasus	Kudaro-3	<i>Ursus praekudarensis / kudarensis</i>	16.33	22.50	15.00	2.00	0.00	2.00	20.50	1.00	0.00	0.00
349	ZIN 37958 (918)	Greater Caucasus	Kudaro-3	<i>Ursus praekudarensis / kudarensis</i>	17.00	23.50	15.50	1.50	0.00	0.00	23.50	0.00	0.00	0.00
350	ZIN 37958 (1138)	Greater Caucasus	Kudaro-3	<i>Ursus praekudarensis / kudarensis</i>	22.50	19.50	19.50	2.50	0.00	2.00	17.50	0.00	0.00	1.00
351	ZIN 37958 (1134)	Greater Caucasus	Kudaro-3	<i>Ursus praekudarensis / kudarensis</i>	17.50	20.50	15.50	2.00	0.00	2.00	18.50	0.50	0.00	1.00
352	ZIN 37958 (572)	Greater Caucasus	Kudaro-3	<i>Ursus praekudarensis / kudarensis</i>	16.50	21.50	16.50	0.00	0.00	0.00	21.50	0.00	0.00	0.00
353	ZIN 37958 (1137)	Greater Caucasus	Kudaro-3	<i>Ursus praekudarensis / kudarensis</i>	16.67	23.00	16.50	0.50	0.00	0.00	23.00	0.00	0.00	0.00
354	ZIN 37957 (1350)	Greater Caucasus	Kudaro-3	<i>Ursus kudarensis</i>	20.00	39.50	9.00	11.00	1.00	2.00	37.50	3.00	1.00	1.00
355	ZIN 37957 (1581)	Greater Caucasus	Kudaro-3	<i>Ursus kudarensis</i>	16.50	45.50	11.50	5.00	1.00	4.00	41.50	3.00	2.00	1.00
356	ZIN 37957 (2014)	Greater Caucasus	Kudaro-3	<i>Ursus kudarensis</i>	14.50	43.00	4.00	10.50	2.00	2.00	41.00	3.00	1.50	1.00
357	ZIN 37957 (2269)	Greater Caucasus	Kudaro-3	<i>Ursus kudarensis</i>	19.00	35.00	10.50	9.50	1.00	2.00	33.00	2.00	0.00	1.00
358	ZIN 37954 (37)	Greater Caucasus	Kudaro-3	<i>Ursus kudarensis</i>	20.50	42.00	7.00	13.50	2.00	1.00	41.00	2.00	0.00	1.00
359	ZIN 37957 (1766)	Greater Caucasus	Kudaro-3	<i>Ursus kudarensis</i>	19.50	35.50	6.00	13.50	2.00	5.00	30.50	2.00	2.00	1.00
360	ZIN 37957 (1776)	Greater Caucasus	Kudaro-3	<i>Ursus kudarensis</i>	18.50	15.00	6.00	12.50	2.00	0.00	15.00	2.00	1.50	0.00
361	zin 27957 (1768)	Greater Caucasus	Kudaro-3	<i>Ursus kudarensis</i>	19.00	47.50	7.00	12.00	2.00	5.00	42.50	4.00	0.50	1.00
362	ZIN 37957 (2007)	Greater Caucasus	Kudaro-3	<i>Ursus kudarensis</i>	19.50	35.00	7.00	12.50	2.00	4.00	31.00	2.00	0.50	1.00
363	ZIN 37957 (1770)	Greater Caucasus	Kudaro-3	<i>Ursus kudarensis</i>	19.50	31.50	6.50	13.00	2.00	2.00	29.50	3.00	0.50	1.00
364	ZIN 37957 (1302)	Greater Caucasus	Kudaro-3	<i>Ursus kudarensis</i>	19.50	30.50	6.50	13.00	2.00	2.00	28.50	1.00	0.50	1.00
365	ZIN 37957 (611)	Greater Caucasus	Kudaro-3	<i>Ursus kudarensis</i>	17.50	30.50	8.50	9.00	2.00	1.00	29.50	0.00	0.00	0.00
366	ZIN 34756 - 138	Northern Urals	Medvezhiya	<i>Ursus kenivetz</i>	20.00	33.50	13.50	6.50	1.00	4.00	27.50	2.50	2.00	0.00
367	ZIN 34756 - 120	Northern Urals	Medvezhiya	<i>Ursus kenivetz</i>	17.00	26.50	12.50	4.50	0.00	2.00	22.50	2.50	2.00	0.00
368	ZIN 34756 - 110	Northern Urals	Medvezhiya	<i>Ursus kenivetz</i>	20.50	25.00	16.50	4.00	0.00	2.00	22.50	3.00	0.50	0.00
369	ZIN 34756 - 109	Northern Urals	Medvezhiya	<i>Ursus kenivetz</i>	14.50	25.00	11.50	3.00	0.00	3.00	21.50	1.00	0.50	0.00
370	ZIN 34756 - 124 A	Northern Urals	Medvezhiya	<i>Ursus kenivetz</i>	16.00	24.00	12.50	3.50	0.00	2.00	22.00	1.00	0.00	0.00
371	ZIN 34756 - 122	Northern Urals	Medvezhiya	<i>Ursus kenivetz</i>	16.00	31.50	13.00	3.00	0.00	4.00	27.50	3.00	0.00	0.00
372	ZIN 34756 - 134	Northern Urals	Medvezhiya	<i>Ursus kenivetz</i>	20.00	33.50	17.00	3.00	0.00	6.00	26.50	2.50	1.00	0.00
373	ZIN 34756 - 137	Northern Urals	Medvezhiya	<i>Ursus kenivetz</i>	16.00	36.00	12.50	3.50	0.00	7.00	29.00	2.00	0.00	0.00
374	ZIN 34756 - 121	Northern Urals	Medvezhiya	<i>Ursus kenivetz</i>	18.00	30.50	15.50	2.50	0.00	1.00	29.50	1.00	0.00	0.00
375	ZIN 34756 - 117	Northern Urals	Medvezhiya	<i>Ursus kenivetz</i>	15.00	33.00	13.00	2.00	0.00	4.00	29.00	0.00	0.00	0.00

A.3.1: Results of the correspondence analysis (CA) performed

Table A3 – CA results for the Romanian Carpathians region (section 6.1.3.2)

Axis	Eigenvalue	% total	% cumulative
1	0.12	41.38	41.82
2	0.07	23.88	65.70
3	0.04	13.46	79.16
4	0.03	9.07	88.23
5	0.02	6.47	94.70
6	0,01	5.30	100

Table A4 – CA results for the Moldavian Plateau region (section 6.2.3.2)

Axis	Eigenvalue	% total	% cumulative
1	0.10	36.38	36.38
2	0.07	25.99	62.37
3	0.03	11.76	74.13
4	0.03	10.88	85.02
5	0.02	8.60	93.62
6	0.02	6.38	100

Table A5 – CA results for the Western Balkans and Western Rhodopes region (section 6.3.2.2)

Axis	Eigenvalue	% total	% cumulative
1	0.09	37.54	37.54
2	0.07	27.53	65.07
3	0.03	13.67	78.74
4	0.02	9.04	87.78
5	0.02	6.52	94.30
6	0.01	5.70	100

Table A6. CA results for the Central Balkans region (section 6.4.2.2)

Axis	Eigenvalue	% total	% cumulative
1	0.10	36.47	36.47
2	0.08	28.82	65.29
3	0.03	11.10	76.39
4	0.02	9.18	85.56
5	0.02	8.74	94.30
6	0.01	5.70	100

Table A7 - CA results for the Northern Urals region (section 6.5.2.2)

Axis	Eigenvalue	% total	% cumulative
1	0.08	37.78	37.78
2	0.06	26.69	64.47
3	0.03	14.23	78.69
4	0.02	10.26	88.96
5	0.01	6.22	95.18
6	0.01	4.82	100

Table A8. CA results for the combined analysis of cave bears by population (section 6.6.5)

Axis	Eigenvalue	% total	% cumulative
1	0.12	49.92	49.92
2	0.04	17.66	67.58
3	0.03	13.21	80.79

4	0.02	11.61	92.41
5	0.01	6.25	98.67
6	0.01	1.32	100

Table A9. CA results for the Greater Caucasus region, dietary inference (section 6.7.1.5)

Axis	Eigenvalue	% total	% cumulative
1	0.13	44.63	44.63
2	0.06	22.44	67.07
3	0.04	13.32	80.39
4	0.02	8.45	88.84
5	0.02	6.75	95.59
6	0.01	4.41	100

Table A10 - CA results for the Greater Caucasus region, comparison with *U. thibetanus* (section 6.7.1.6)

Axis	Eigenvalue	% total	% cumulative
1	0.15	65.86	65.86
2	0.04	15.70	81.56
3	0.02	9.13	90.69
4	0.01	5.33	96.02
5	0.01	3.61	99.63
6	0.00	0.37	100

Table A11. CA results for the averages of brown bear and cave bear through time (section 6.7.2.2)

Axis	Eigenvalue	% total	% cumulative
1	0.11	93.9	93.9
2	0.01	6.1	100

Table A12. CA results for individuals of brown and cave bears through time (section 6.7.2.2)

Axis	Eigenvalue	% total	% cumulative
1	0.07	47.78	47.78
2	0.03	21.56	69.34
3	0.02	13.12	82.47
4	0.02	10.33	92.8
5	0.01	5.94	98.74
6	0	1.25	99.98

A.3.1.1 RStudio code employed for correspondence analysis (CA) on ursids

Appendix

```
# CORRESPONDENCE ANALYSIS (CA) CODE FOR MICROWEAR ANALYSIS ON URSIDS
# Load the required libraries
library(FactoMineR)
library(readxl)
library(ggplot2)
library(ggpubr)
library(dplyr)
library(factoextra)
# Step 1: Load and preprocess the data
# Please specify the path to your Excel file in the xlsx format. Make sure the file path is correctly defined for your system.
mydata <- read_xlsx("YOUR_PATH")
# Prepare data for analysis
# Create unique IDs by appending row numbers to the 'SPID' column
test <- mydata
test$id <- paste(test$SPID, 1:nrow(test), sep = "")
# Set the 'id' column as row names and remove the 'SPID' column from the data frame
mydata <- as.data.frame(mydata, row.names = test$id)
mydata <- subset(mydata, select = -SPID)
# Step 2: Run the Correspondence Analysis (CA) - Classic CA
# Perform the CA keeping the first five principal components, and do not display graphs immediately
myCA <- CA(mydata, ncp = 5, graph = FALSE)
# Step 3: Display eigenvalues and variance explained by each dimension
# Extract eigenvalues, which represent the variance explained by each dimension
eigenvalues <- as.data.frame(get_eigenvalue(myCA))
print("Eigenvalues and percentage of inertia explained by each dimension:")
print(round(eigenvalues, 2))
# Step 4: Display scree plot to visualize explained variance by dimension
# The scree plot helps to decide the number of dimensions to retain by showing the variance each dimension explains
fviz_screplot(myCA, addlabels = TRUE, ylim = c(0, 100)) +
  geom_hline(yintercept = 33.33, linetype = 2, color = "red") +
  labs(title = "Scree Plot: Explained Variance by Dimension")
# Step 5: Extract row coordinates from CA for plotting
# Get the coordinates for rows from the CA result and prepare data for plotting
row <- get_ca_row(myCA)
row_data <- data.frame(x = row$coord[, 1], y = row$coord[, 2], SPID = test$SPID)
# Define custom shapes and colors for each unique population (SPID)
# Customize shapes: Replace "Fossil population 1, 2, 3..." with the names of fossil populations as listed in your Excel file (e.g., "Oase",
"Toll", "Kudaro").
# Use filled shapes for fossil populations and unfilled shapes for extant reference populations for easy differentiation.
shape_mapping <- c("Fossil population 1" = 16, "Fossil population 2" = 16, "Fossil population 3" = 16,
  "Fossil population 4" = 16, "U. americanus" = 15, "U. arctos (GR)" = 1,
  "U. arctos (CE)" = 2, "U. arctos (NA)" = 3, "U. arctos (RU)" = 4,
  "U. arctos (NE)" = 5, "A. melanoleuca" = 6, "U. maritimus" = 7)
# Customize colors: Adjust the color of each population (both fossil and extant) to suit your preferences.
# Remove any "Fossil population" entries that are not needed.
color_mapping <- c("Fossil population 1" = "violet", "Fossil population 2" = "yellow", "Fossil population 3" = "green",
  "Fossil population 4" = "red", "U. americanus" = "black", "U. arctos (GR)" = "orange",
  "U. arctos (CE)" = "purple", "U. arctos (NA)" = "cyan",
  "U. arctos (RU)" = "magenta", "U. arctos (NE)" = "blue",
  "A. melanoleuca" = "darkgreen", "U. maritimus" = "pink")
# Step 6: Create the final CA scatter plot with custom shapes and colors
# Generate the scatter plot using ggplot2 with the specified shapes and colors for each SPID
ggplot(row_data, aes(x = x, y = y, color = SPID, shape = SPID)) +
  geom_point(size = 3) +
  scale_color_manual(values = color_mapping) +
  scale_shape_manual(values = shape_mapping) +
  theme_minimal() +
  labs(title = "Correspondence Analysis Plot", x = "Dimension 1", y = "Dimension 2")
```

A.3.2 No strong correlation between stable isotopes and microwear variables for Romanian Carpathian cave bears

In order to test for potential associations between short-term dietary traits captured by dental microwear and broader isotopic dietary signals, a Pearson correlation matrix was computed between the microwear variables (i.e., NTS, NTP, NFS, NCS, SWS, NLP, NSP, NG and NPP)

and stable isotope values of carbon ($\delta^{13}\text{C}$) and nitrogen ($\delta^{15}\text{N}$) (Table 11: Figure 83). Overall, the analysis revealed no strong or statistically significant correlations. The strongest apparent association was between the number of gouges (NG) and $\delta^{13}\text{C}$ ($r = 0.50$), which prompted further visual inspection through a linear regression plot (Figure 84).

#	Cave	Species	NTS	NTP	NFS	NCS	SWS	NLP	NSP	NG	NPP	$\delta^{13}\text{C}$ (PDB)	$\delta^{15}\text{N}$ (AIR)
PB/B1-X-XI	Bisericuța	<i>U. arctos</i>	26	38	6	21	2	9	27	1	2	-21.4	6.8
PM/O6-0-89	Muierilor	<i>U. spelaeus</i>	17	20	4	12	2	1	16	3	3	-21.1	3.3
N34.139	Oase	<i>U. spelaeus</i>	23	20	15	8	2	2	17	0	1	-21.8	9.4
O34.180	Oase	<i>U. spelaeus</i>	21	23	19	2	0	6	16	1	1	-21.1	8.2
N37.152	Oase	<i>U. spelaeus</i>	31	25	19	12	1	7	15	0	3	-21.5	7.5
N34.101a	Oase	<i>U. spelaeus</i>	22	34	18	4	1	1	31	0	2	-22	9.5
PU/F-I-12b	Urșilor	<i>U. spelaeus</i>	26	24	15	11	1	3	19	0	2	-22	4.2
PU/B1-II-005	Urșilor	<i>U. spelaeus</i>	20	14	1	18	2	5	6	2	3	-21.4	9.6
PU/B-I-14	Urșilor	<i>U. spelaeus</i>	26	14	14	12	1	1	12	0	1	-21.6	7.2
PU/F	Urșilor	<i>U. spelaeus</i>	24	15	3	21	2	5	8	0	2	-22.5	11.5
PU/F	Urșilor	<i>U. spelaeus</i>	28	20	25	3	0	4	14	0	2	-22.3	7.9

Table 11. Summary of individual-level data for fossil bear specimens from Eastern Europe for which both dental microwear and stable isotope values were obtained. The table includes site of origin (Cave), taxonomic identification (Species), microwear variables—total scratches (NTS), total pits (NTP), fine scratches (NFS), coarse scratches (NCS), scratch width score (SWS), large pits (NLP), small pits (NSP), gouges (NG), and puncture pits (NPP)—and isotopic measurements of $\delta^{13}\text{C}$ (PDB) and $\delta^{15}\text{N}$ (AIR) derived from bone collagen.

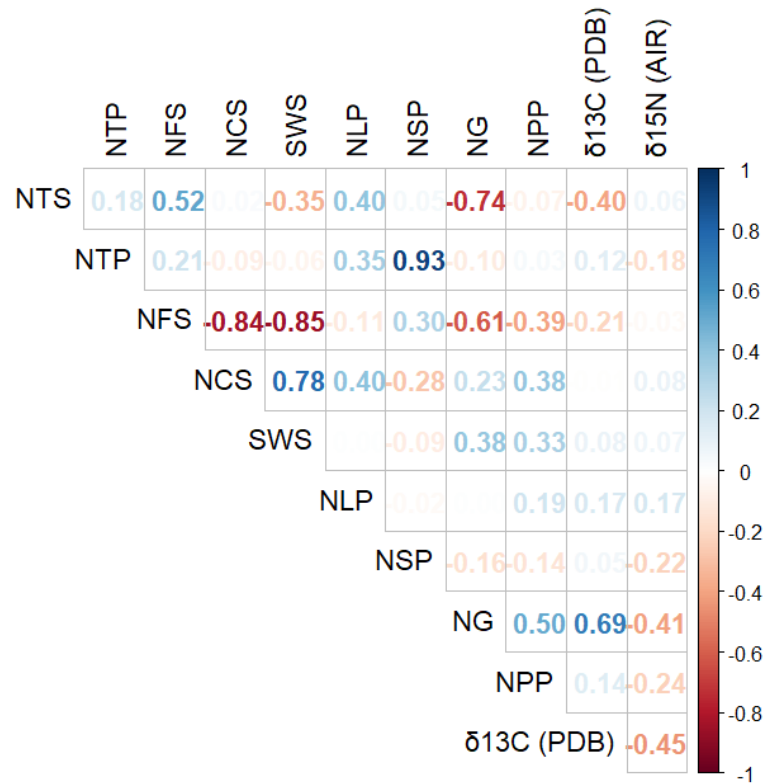


Figure 83. Correlation matrix of microwear variables (NTS, NTP, NFS, NCS, SWS, NLP, NSP, NG, and NPP) with $\delta^{13}\text{C}$ (PDB) and $\delta^{15}\text{N}$ (AIR) isotope values from the same individuals.

However, despite the moderate R^2 value (0.48), the visual distribution of points clearly reflects the low explanatory power of the model due to the large clustering of individuals at NG = 0, and only a few individuals with values above this threshold (Figure 84). The apparent correlation is thus heavily driven by a small subset of data points, limiting any meaningful biological interpretation. These results support the conclusion that microwear and isotopic proxies capture dietary signals at different temporal scales—lifespan average vs last week(s) before death, respectively—and should not be expected to correlate strongly.

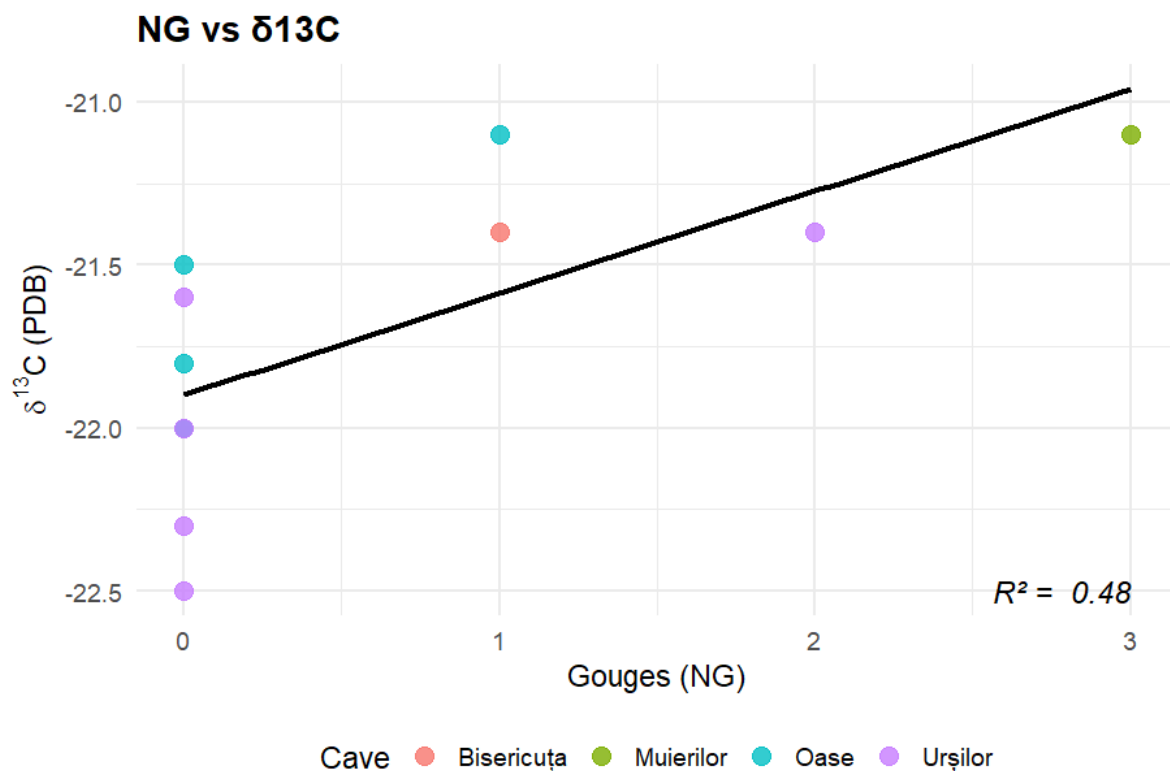


Figure 84. Linear regression plot showing the relationship between the number of gouges (NG) and $\delta^{13}\text{C}$ (PDB) isotope values for each individual. No significant correlation is observed.

A.3.2.1 Rstudio code employed

```
# Load necessary libraries
library(ggplot2)
library(readr)
library(corrplot)

# Load the data
data <- read_csv("C:/Users/paulo/Desktop/TFM/Results/Romanian_Carpathians/Correlation_microwear_isotopes_bo.csv")

# Select numeric columns for correlation
numeric_data <- data[, c("NTS", "NTP", "NFS", "NCS", "SWS", "NLP", "NSP", "NG", "NPP", "δ13C (PDB)", "δ15N (AIR)")]

# Compute and print correlation matrix
cor_matrix <- cor(numeric_data, use = "complete.obs")
```



```

print(cor_matrix)

corrplot(cor_matrix,
  method = "number",
  type = "upper",
  tl.col = "black",
  tl.cex = 1.1,
  number.cex = 1.1,
  diag = FALSE)

# Load necessary library
library(ggplot2)

# Calculate R-squared from a linear model
model <- lm(`δ13C (PDB)` ~ G, data = data)
r2 <- summary(model)$r.squared
r2_label <- paste("R² = ", round(r2, 2))

# Create the plot
ggplot(data, aes(x = NG, y = `δ13C (PDB)')) +
  geom_point(aes(color = Cave), size = 4, alpha = 0.8) +
  geom_smooth(method = "lm", se = FALSE, color = "black", linewidth = 1.2) +
  annotate("text", x = max(data$NG), y = min(data$`δ13C (PDB)`),
    label = r2_label, hjust = 1, size = 5, fontface = "italic") +
  labs(
    title = "NG vs δ13C",
    x = "Gouges (NG)",
    y = expression(delta^{13} * "C (PDB)")
  ) +
  theme_minimal(base_size = 14) +
  theme(
    legend.position = "bottom",
    plot.title = element_text(face = "bold")
  )

```

A.3.3 Pearson's r between microwear, climate and geographic factors

Variable 1	Variable 2	r value
Mean Annual Temp	Total Scratches	0.019573
Temp Seasonality	Total Scratches	0.119629
Max Temp Warmest Month	Total Scratches	0.064775
Min Temp Coldest Month	Total Scratches	-0.04846
Annual Temp Range	Total Scratches	0.090283
Annual Precipitation	Total Scratches	-0.12668
Latitude	Total Scratches	0.231393
Longitude	Total Scratches	-0.12746
Elevation	Total Scratches	-0.27722
Mean Annual Temp	Total Pits	0.017035
Temp Seasonality	Total Pits	-0.0189
Max Temp Warmest Month	Total Pits	0.043053
Min Temp Coldest Month	Total Pits	0.0445
Annual Temp Range	Total Pits	-0.02182
Annual Precipitation	Total Pits	-0.01783
Latitude	Total Pits	-0.13683
Longitude	Total Pits	0.13927
Elevation	Total Pits	0.12525
Mean Annual Temp	Fine Scratches	-0.03375
Temp Seasonality	Fine Scratches	0.174486
Max Temp Warmest Month	Fine Scratches	0.058774
Min Temp Coldest Month	Fine Scratches	-0.12337
Annual Temp Range	Fine Scratches	0.166617
Annual Precipitation	Fine Scratches	-0.34663
Latitude	Fine Scratches	0.17661
Longitude	Fine Scratches	-0.08997
Elevation	Fine Scratches	-0.31693
Mean Annual Temp	Coarse Scratches	0.060776
Temp Seasonality	Coarse Scratches	-0.07899
Max Temp Warmest Month	Coarse Scratches	0.000182
Min Temp Coldest Month	Coarse Scratches	0.0935
Annual Temp Range	Coarse Scratches	-0.09963
Annual Precipitation	Coarse Scratches	0.274788
Latitude	Coarse Scratches	0.030531
Longitude	Coarse Scratches	-0.01258
Elevation	Coarse Scratches	0.093677
Mean Annual Temp	Scratches Width Score	0.054987
Temp Seasonality	Scratches Width Score	-0.12301
Max Temp Warmest Month	Scratches Width Score	-0.03039
Min Temp Coldest Month	Scratches Width Score	0.117597
Annual Temp Range	Scratches Width Score	-0.14355
Annual Precipitation	Scratches Width Score	0.394393
Latitude	Scratches Width Score	-0.04989
Longitude	Scratches Width Score	0.088128

Elevation	Scratches Width Score	0.188703
Mean Annual Temp	Large Pits	-0.01091
Temp Seasonality	Large Pits	0.025049
Max Temp Warmest Month	Large Pits	0.01145
Min Temp Coldest Month	Large Pits	-0.01829
Annual Temp Range	Large Pits	0.026331
Annual Precipitation	Large Pits	0.029114
Latitude	Large Pits	0.067086
Longitude	Large Pits	0.013181
Elevation	Large Pits	0.081113
Mean Annual Temp	Small Pits	-0.00942
Temp Seasonality	Small Pits	-0.04078
Max Temp Warmest Month	Small Pits	-0.00186
Min Temp Coldest Month	Small Pits	0.035896
Annual Temp Range	Small Pits	-0.0394
Annual Precipitation	Small Pits	0.036696
Latitude	Small Pits	-0.17897
Longitude	Small Pits	0.200145
Elevation	Small Pits	0.168133
Mean Annual Temp	Gouges	-0.09512
Temp Seasonality	Gouges	0.021453
Max Temp Warmest Month	Gouges	-0.07981
Min Temp Coldest Month	Gouges	-0.07427
Annual Temp Range	Gouges	0.031684
Annual Precipitation	Gouges	-0.01893
Latitude	Gouges	0.007397
Longitude	Gouges	0.04864
Elevation	Gouges	0.100278
Total Scratches	Puncture Pits	0.249115
Mean Annual Temp	Puncture Pits	0.140678
Temp Seasonality	Puncture Pits	0.076036
Max Temp Warmest Month	Puncture Pits	0.20099
Min Temp Coldest Month	Puncture Pits	0.069049
Annual Temp Range	Puncture Pits	0.046081
Annual Precipitation	Puncture Pits	-0.25414
Latitude	Puncture Pits	0.081191
Longitude	Puncture Pits	-0.19681
Elevation	Puncture Pits	-0.26772
Mean Annual Temp	Hypercoarse Scratches	-0.1586
Temp Seasonality	Hypercoarse Scratches	-0.15938
Max Temp Warmest Month	Hypercoarse Scratches	-0.30043
Min Temp Coldest Month	Hypercoarse Scratches	-0.01385
Annual Temp Range	Hypercoarse Scratches	-0.16421
Annual Precipitation	Hypercoarse Scratches	0.522936
Latitude	Hypercoarse Scratches	-0.16444
Longitude	Hypercoarse Scratches	0.368696

Elevation	Hypercoarse Scratches	0.365965
-----------	-----------------------	----------

Table 12. Pearson's *r* values table of the correlation between climatic and geographic values and microwear variables.

A.3.4 Pearson's *r* between microwear and time

A.3.4.1 Calibrated years before present

Microwear variables	Pearson's <i>r</i> value
NTS	0.36751558
NTP	-0.08151594
NFS	0.02850379
NCS	0.16487426
SWS	-0.05636121
NLP	0.23639949
NSP	-0.13233196
NG	-0.30466273
NPP	-0.1932658

Table 13. Pearson's *r* values table of the correlation between calibrated dates (cal years B.P.) and microwear variables (*n* = 11).

The correlation analysis between microwear variables and calibrated dates (calibrated years before present) shows generally weak relationships (Table 13). No significant correlations (Pearson's *r* > 0.30) are observed for most variables. However, the number of total scratches (NTS) displays a Pearson's *r* value of 0.37, suggesting a weak positive trend.

However, when exploring the linear regression between NTS and calibrated age (Figure 85), the relationship appears highly scattered, with a wide confidence interval and poor model fit. This dispersion indicates that although the Pearson correlation is above 0.30, it is not robust or statistically meaningful. The visual inspection of the regression plot shows that outliers and the small sample size (*n* = 11) heavily influence the trend.

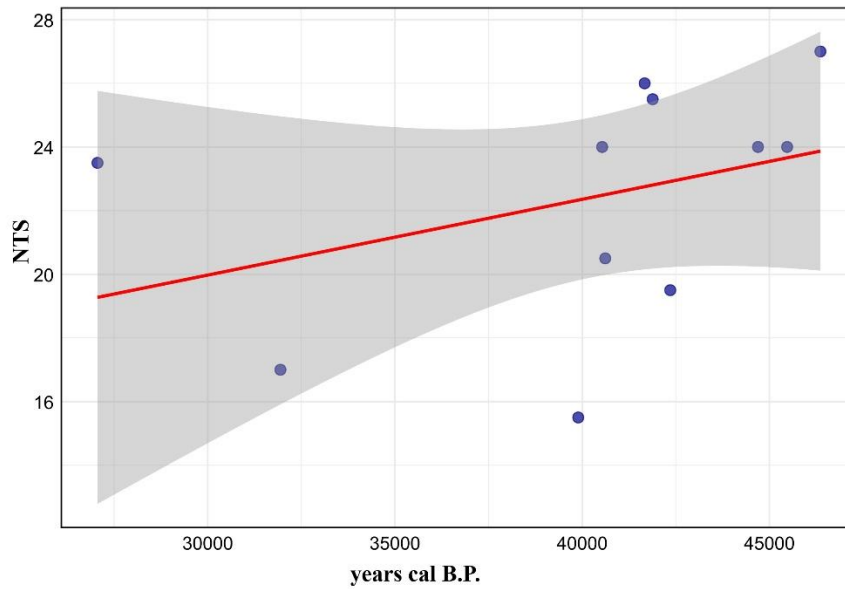


Figure 85. Linear regression between the number of total scratches (NTS) and calibrated age (years cal B.P.). Although a weak positive trend is observed ($r = 0.37$), the relationship is not statistically significant, with wide dispersion and a large confidence interval around the fitted line.

A.3.4.2 Mean horizon dates and calibrated individuals

Moreover, the same correlation analysis was performed not only using directly dated and calibrated cave bears ($n = 11$), but also using stratigraphic horizon mean dates ($n = 355$), excluding *U. arctos*, resulting in a total of $n = 366$ individuals of cave bears (*U. spelaeus sensu lato*).

Microwear variables	Pearson's r value
NTS	-0.15603538
NTP	0.09536479
NFS	-0.19305828
NCS	0.07719062
SWS	0.21945144
NLP	-0.05109911
NSP	0.16998092
NG	-0.17841115
NPP	-0.21698277
NHC	0.35893184

Table 14. Pearson's r values showing the correlation between both calibrated and mid-age of stratigraphic package estimates and microwear variables for *U. spelaeus sensu lato* ($n = 365$) individuals. Almost all correlations are weak ($r < 0.30$), indicating no strong relationship between microwear features and stratigraphic time in the studied populations.

The only correlation with an r value above 0.3 was observed for NHC. However, the regression plot revealed that the relationship was largely driven by a few scattered points (Figure 86), with

the majority of data clustered near zero. This pattern suggests that, despite the positive trend, the association between NHC and time (ka B.P.) is weak and not statistically robust.

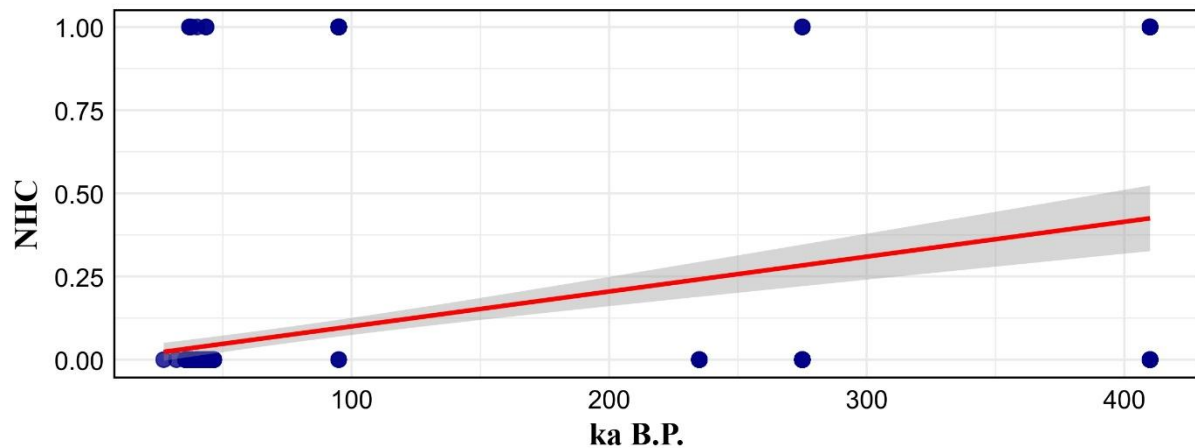


Figure 86. Linear regression between hypercoarse scratches (NHC) and time (ka B.P.). Despite a weak positive trend ($r = 0.36$), data points are highly dispersed with clustering near zero values. Hence, this trend is not statistically significant.

A.3.4.3 RStudio code employed for creating matrices and regression plots

```
# Load necessary libraries
library(tidyverse)
library(corrplot)

# Example: Load dataset
data <- read_csv("example_data.csv")

# Example: Filter or select variables
data_filtered <- data %>%
  filter(!is.na(variable_x), !is.na(variable_y))

# Simple linear regression model
model <- lm(variable_y ~ variable_x, data = data_filtered)

# Plot regression
ggplot(data_filtered, aes(x = variable_x, y = variable_y)) +
  geom_point() +
  geom_smooth(method = "lm") +
  labs(
    title = "Regression of Variable Y against Variable X",
    x = "Variable X",
    y = "Variable Y"
  )

# Create a correlation matrix for selected microwear and time or geographic variables
selected_vars <- data_filtered %>%
  select(variable_x, variable_y, variable_z)

# Calculate and plot correlation matrix
cor_matrix <- cor(selected_vars, use = "complete.obs", method = "pearson")
corrplot(cor_matrix, method = "color", type = "upper")
```

A.4 Appendix 4: Discussion

A.4.1 MIS 3 *U. arctos* and *U. spelaeus* compared to Holocene *U. arctos*

When the main microwear variables were compared between *U. spelaeus* ($n = 321$) and MIS 3 *U. arctos* ($n = 6$), and, finally, Holocene *U. arctos* ($n = 3$) from Romanian Carpathians, slightly

different dietary niches were identified, however partial overlap was also observed among groups. It is important to remark the very small sample size in both diachronic *U. arctos* populations.

The elevated average and distribution of NTP in *U. spelaeus*, combined with its relatively low NTS values, likely reflect a more herbivorous dietary regime, as the most herbivorous extant bear *A. melanoleuca* exhibits extremely high NTP counts (NTP = 54.00). An alternative hypothesis to explain the slightly higher number of pits in *U. spelaeus* is its low-ground foraging behaviour, specifically the search for roots, as originally proposed by morphological studies based on the species' snout morphology (Kurtén, 1976; Mattson, 1998; Athen, 2006). Similar microwear patterns—characterized by highly pitted surfaces—have been documented in omnivorous *S. scrofa*, where rooting in the forest understory generates comparable wear signatures (e.g., Duñó-Iglesias et al., 2023).

In contrast, *U. arctos* from both MIS 3 and the Holocene show similar NTP values, suggesting comparable levels of plant consumption or a foraging less centred in near -ground resources. However, they differ in NTS, with Holocene specimens displaying a higher distribution.

This divergence in NTS may be related to differing environmental contexts and landscape, as total number of scratches (NTS) appears to be a less reliable dietary discriminator than the total number of pits (NTP) (Münzel et al., 2014; Pappa et al., 2019). The overlap in fine scratch (NFS) values between MIS 3 *U. spelaeus* and *U. arctos* likely reflects broadly similar levels of soft plant consumption or abrasive diets during MIS 3, due to a shared landscape, particularly open in average.

The higher and more variable coarse scratch (NCS) values observed in Holocene *U. arctos*, in comparison to the MIS 3 bear groups, may indicate a shift toward the inclusion of hard-objects, consistent with increased ecological flexibility and adaptation to closer environments after the Last Glacial Maximum (LGM) in Central Europe (Bojarska and Selva, 2012).

Regarding the differentiation in pit size, the slightly higher NLP in *U. arctos* from MIS 3 in comparison to *U. spelaeus* suggests the inclusion of hard brittle items. However, the differences are not very strong, suggesting a high degree of overlap between species, even more if we consider the small sample size of MIS 3 *U. arctos* ($n = 6$). Furthermore, the high NLP values observed in Holocene *U. arctos*, diverging absolutely from MIS 3 cave and brown bears, may reflect the inclusion of high quantity of hard mast, as inferred for extant Romanian Carpathians Holocene bears, in a much forested environment than during the Pleistocene (Kalabér et al.,

1994; Frackowiak, 1997; Pop et al., 2018). The significantly lower NLP in MIS 3 *U. spelaeus* and *U. arctos* could indicate less frequent consumption of such hard mast, due to a more open landscape in MIS 3 Eastern Europe in comparison to nowadays Romanian Carpathians, (e.g., Willis and Vanandel, 2004).

The higher NSP in both *U. arctos* and *U. spelaeus* (which is, in turn, slightly higher), in comparison to Holocene *U. arctos*, suggests a higher reliance on abrasive plant-based diet for both Pleistocene ursids, as resembling *A. melanoleuca* (but not to the same extremes), which also display a high number of small pits (Pappa et al., 2019).

The elevated NPP values in Romanian Carpathians Holocene *U. arctos* likely reflect a greater reliance on hard-shelled fruits and other mechanically resistant plant resources, consistent with foraging in more forested landscapes (Kalabér et al., 1994). This interpretation aligns with ecological observations from Central-Eastern Europe, where modern brown bears exhibit extensive use of nut- and seed-bearing vegetation (Bojarska and Selva, 2012). While *U. spelaeus* displays a clear overlap in NPP values, with an even higher distribution, suggesting hard-shelled fruit consumption, during MIS 3. The lower NPP values in MIS 3 *U. arctos*, in comparison to the other two groups suggests a trend to more open landscape foraging.

As for gouges (NG) widest and highest distribution in *U. arctos*, their occurrence is not strongly diagnostic of specific dietary components, as they are produced by hard and brittle objects such as fruit hard mast or bone (e.g., Godfrey et al., 2004; Bastl et al., 2012). However, paired with low NPP in MIS 3 *U. arctos* suggests contact with hard, non-fruit materials, which could be linked to increased carnivorous diet in comparison to *U. spelaeus* or Holocene *U. arctos*, with slightly lower values.

However, caution is warranted, as these features alone are not definitive indicators of diet and, when studied in isolation, do not allow for precise dietary inference.

A.4.2 Comparison of microwear variables between regions

Regional and population-level trends in microwear features of *U. spelaeus* (sensu lato). The distribution of microwear variables across populations and regions may reflect differences in landscape use or dietary strategies. In this section, each variable is examined in detail.

A.4.2.1 NTS and NTP

The observed different degrees of variability in the total number of scratches (NTS) and the total number of pits (NTP) can be attributed to dietary differences among the studied

populations from different regions. The quantity of pits and scratches in low-magnification microwear have reflected distinct dietary regimes not only among herbivorous taxa (browser, grazer or mix feeder) (Solounias and Semprebon, 2002), but also across primates (tree-foliage browsers, grass consumers and hard-object specialists) (Godfrey et al., 2004), omnivorous carnivorans (i.e., bears, hard mast and soft mast; Münzel et al., 2014; Medin et al., 2017; Pappa et al., 2019), and strictly carnivorous species (e.g., durophagous and non- durophagous; Bastl et al., 2012). Hence, suggesting that the difference in the quantity of features, as NTS and NTP account for all features independently of their qualitative classification (fine or coarse in the case of scratches, small, large, or puncture in the case of pits), is directly related to different dietary preferences.

Specifically focusing on NTS, a greater variability as well as the highest values are observed for the Romanian Carpathians and secondly the Moldavian Plateau region. This could be related to a more diverse dietary niche, as observed through isotopic studies conducted on cave bears from Romanian Carpathians (Richards et al., 2008; Robu et al., 2013, 2018; Meleg et al., 2024). Additionally, unpublished, unusually high, and variable nitrogen values for Moldavian Plateau Duruitoarea Veche cave bears appear to follow the same trend as those observed in the Romanian Carpathians (Robu et al., in prep).

Regarding NTP, its higher variability compared to NTS across all regions (except for Central Balkans) may be attributed to the fact that, in Carnivora, the number of pits appears to be a better dietary discriminant than the number of scratches (Dewar, 2004; Goillot et al., 2009; Bastl et al., 2012; Xafis et al., 2017). In the case of bears, a low NTP can be related to soft mast omnivorous diet, as observed for the extant *U. arctos* from Greece, and a high NTP can be related to hard mast omnivorous diets, as observed by the extant *U. arctos* from Central Europe (Pappa, 2016; Pappa et al., 2019).

In the fossil sample studied, this pattern is also evident. Cave bear species from Romanian Carpathians, Moldavian Plateau, Western Balkans and Western Rhodopes Mountains, and the Greater Caucasus (diachronic lineage of *U. kudarensis*) exhibit high NTP variability associated with diverse omnivorous diets. Within these regions, some populations demonstrate a clear predominance of soft-mast consumption, as reflected by low NTP values; most notably in Trinca (Moldavian Plateau), Lakatnik (Western Balkans) and *U. praekudarensis/kudarensis* from the Greater Caucasus (MIS 8/7). While other populations within the same region display

a higher and wider array of NTP values, related to hard mast consumption, indicating a broader dietary spectrum at a regional scale.

Hence, the relatively low average NTP values and narrower distribution observed in Central Balkans populations likely reflect a diet primarily consisting of soft-mast and abrasive items, with limited dietary diversification, compared to other regions.

A.4.2.2 NFS and NCS

The scratch width, specifically the predominance of coarse or fine scratches in herbivorous species, is influenced by diet type (Semprebon et al., 2004). Fine scratches are more commonly associated with grazer species; in bears, this is exemplified by *A. melanoleuca* (giant panda), a bamboo specialist that feeds on a Gramineae plant (the bamboo leaves) extremely rich in phytoliths, and exhibits exclusively fine scratches without any coarse scratches. In contrast, coarse scratches are more prevalent in browser species (in herbivores), likely resulting from contact between the occlusal surface and twigs or branches of shrubs (Solounias and Semprebon, 2002; Semprebon et al., 2004).

In omnivorous bear species a high presence of coarse scratches can be found in *U. arctos* from Greece (NCS = 7.00), which has a soft mast diet based on green vegetation and soft fruits, with basically browsing tendencies. Its diet, in addition to wheat (Gramineae), includes *Prunus* sp. fruits, a diverse array of understory vegetation (i.e., browsing), acorns in forested areas, and ants (Giannakos, 1997; Vlachos et al., 2000; Paralikidis et al., 2010).

The dichotomy between forested and open habitats in coarse scratch proportions is evident in the studied cave bear sample. This suggests that cave bears from forested areas may have engaged more frequently in browsing on shrubs, resulting in higher numbers of coarse scratches. The Romanian Carpathians present the overall regional highest coarse scratches distribution, this might be related to the Carpathian Mountains being a large forest refugium, with patches of temperate species canopy forest (Jankovská and Pokorný, 2008; Tzedakis et al., 2013; Juříčková et al., 2014).

However, the high number of coarse scratches of Romanian Carpathian cave bears could not be explained by forest cover alone. As extant *U. maritimus* inhabiting Arctic landscapes presents also coarse scratches (NCS = 3.21), comparable to number of omnivorous bears from northern latitudes. Supporting this, the MIS 5/4 *U. kudarensis* from the Greater Caucasus displays the highest average and widest distribution of coarse scratches, including a notable presence of

hypercoarse scratches. Similarly, *U. praekudarensis* from MIS 11 also exhibits high counts of coarse scratches, with hypercoarse scratches observed in this population as well.

Given that hypercoarse scratches can be directly linked to a carnivorous diet (Goillot et al., 2009; Pappa et al., 2019), it raises the question of whether a high number of coarse scratches also results from tooth contact with bone, rather than with shrub twigs, as seen in herbivores. In the context of our fossil sample, this may indicate the presence of a more carnivorous dietary component, or alternatively, reflect a combination of interactions with both twigs and bone.

Nevertheless, the elevated and more variable $\delta^{15}\text{N}$ isotopic values observed exclusively in the Romanian Carpathians and, to date, in Moldavian Plateau (based on unpublished data from Duruitoarea Veche, Butești and Saharna; Robu et al., in prep) may be correlated to the higher and more variable distribution of coarse scratches in these regions. However, due to the differing temporal resolutions of stable isotope analysis—which reflects average diet over several years—and dental microwear analysis—which captures dietary signals from the final weeks before death—along with the limited number of cave bear individuals preserving both sufficient collagen for isotopic analysis and well-preserved lower first molars (m1's) for dental microwear study, this correlation may remain obscured.

A.4.2.3 NSP and NLP

The highest interregional variability observed in the number of large pits (NLP), compared to the number of small pits (NSP)—which shows greater within-region variability but remains relatively homogeneous at the regional scale—may be explained by the consistently high and relatively uniform number of small pits (NSP) observed across most individuals, as exemplified by reference collections of extant bears, all of which display similarly elevated NSP values (Pappa et al., 2019). Bastl et al., 2012 determined that in low magnification microwear analysis (Solounias and Semprebon, 2002), applied to carnivora mammals and performed in carnassial facets, the best dietary discrimination was obtained when small versus large pits were used. Much better than the number of total pits vs the number of total scratches (Bastl et al., 2012). A high number of small pits and a low number of large pits are characteristic of the bone-crushing (durophagous) *C. crocuta*, whereas the flesh-eating (non-durophagous) *A. jubatus* exhibits the opposite pattern, with a high number of large pits and fewer small pits (Bastl et al., 2012).

In contrast, among extant bears, large pits tend to occur uniformly across omnivorous species, with *U. arctos* from Greece displaying the highest average (NLP = 9.25), followed by *A.*

melanoleuca (NLP = 8.50). These two species share a predominantly herbivorous diet composed of hard and abrasive items (e.g., bamboo and twigs), with no evidence of vertebrate consumption. In our study, we are unable to establish a direct correlation between the presence of large pits and the consumption of specific food items. Moreover, as shown by Pappa et al. (2019), in bears the comparison of large versus small pits offers less dietary discrimination than total pits versus total scratches.

The high NLP distribution observed in Romanian Carpathians, Western Balkans and Western Rhodopes Mountains could initially be interpreted as indicative of increased consumption of coarse, forest-derived food items. However, this explanation is challenged by similarly high average NLP values in Medvezhyia, a locality associated with more open environments—potentially reflecting a herbivorous dietary regime. While this pattern appears consistent with extant herbivorous bears such as *A. melanoleuca* and *U. arctos* from Greece, both of which consume predominantly plant-based, abrasive diets, this hypothesis remains unproven. At present, the lack of a comprehensive reference dataset and controlled experimental studies on bears consuming different dietary items limits our ability to draw definitive conclusions. Future research should address this gap through targeted feeding experiments and expanded comparative datasets.

Similar NSP distribution in Romanian Carpathians, Moldavian Plateau and Western Balkans and Western Rhodopes Mountains, could be explained as these regions share (generally) temperate forested habitats where soft and abrasive vegetation may dominate the diet. Moldavian Plateau's slightly higher NSP average could reflect greater sample representation of such diets, while Western Balkans and Western Rhodopes Mountains' slight increase may be due to regional variability in plant material abrasiveness or localized ecological conditions. While Central Balkans's low NSP values and narrow distribution suggest a more uniform diet, likely dominated by soft-mast resources with limited abrasiveness. This dietary homogeneity could reflect specific ecological conditions or reduced resource diversity, as also supported by microwear homogeneity patterns in the region. Furthermore, Medvezhyia cave shows low values which may point toward a diet rich in soft-mast items, similar to the pattern seen in Central Balkans. The lower NSP in *U. kudarensis* (MIS 5/4) likely reflects a diet dominated by soft-mast resources. In contrast, higher NSP in *U. praekudarensis/kudarensis* (MIS 8/7) may reflect increased ingestion of abrasive plant material in more arid environments, supporting a more herbivorous diet. Based on these observations, a correlation between low NSP values and

colder and more arid environments can be proposed, however, environmental data needs to be retrieved to confirm this hypothesis.

Based on current data, a direct correlation between low NSP values and colder environments can be tentatively proposed, as both *U. kudarensis* and *Medvezhya* show low values and are linked to cold or open settings. However, more environmental and isotopic context is needed to confirm this hypothesis across broader samples.

A.4.2.4 NG and NPP

As for gouges and puncture pits, those are correlated with hard-object consumption (Solunias and Semprebon 2002; Godfrey et al., 2004; Semprebon et al., 2004; Williams and Geissler, 2014). Specifically, omnivorous carnivores dwelling temperate woodland environments (e.g., *V. vulpes*, *G. genetta* or *N. binotata*) present puncture pits, due to the consume of fruit coverings and seed coats (Xafis et al., 2017). Therefore, its number could be either related to seasonal hyperphagia dietary regimes, or landscape cover or resource availability.

Gouges predominance in Romanian Carpathians, Western Balkans and Western Rhodopes Mountains and *U. kudarensis* from Caucasus (MIS 5/4) suggests that bears had dominant hard object inclusion. However, gouges are not directly related to specific food items and appear similarly in bears feeding on hard-objects, either hard-mast *U. arctos* from Central Europe (NCS = 2.10) or browsing soft-mast Greece (NCS = 2.00). While the highest averages (NG = 17.67) are scored by extremely herbivorous and insect consumption *U. thibetanus* from Tibet and Japan temperate habitats (Pappa et al., 2019). Other omnivorous bears from northern latitudes (e.g., *U. americanus*, *U. arctos* from North America, Northern Europe, etc.), or hypercarnivorous *U. maritimus* (NG = 0.00) do not present them. This links gouges to herbivorous diets involving hard-mast consumption, rather than to specific food items. Consequently, the presence of gouges in these populations may reflect a reliance on habitats where such resources were seasonally or consistently available.

The uniform distribution of NPP (number of puncture pits) across Romanian Carpathians sites suggests a relatively consistent dietary behaviour among Romanian Carpathian cave bear populations before hyperphagia (Duñó-Iglesias et al., 2024a). Inhabiting a forested refugia and including hard-objects (e.g., seeds and hard-shelled fruits in their diets) before entering hibernation (Duñó-Iglesias et al., 2024a). Furthermore, the elevated NPP averages observed in Buzdujeni and Saharna (both in the Moldavian Plateau), and to a lesser extent in Magura, Bacho Kiro, and the MIS 7 *U. s. rossicus*, (all in Western Balkans) may be attributed to forest cover

and the availability of hard fruits, or alternatively, to seasonal pre-dormancy feeding strategy during hyperphagia. Notably, the exceptionally high averages recorded at Bashovishka Pech (Western Balkans) may reflect intense bulk intake prior to hibernation, potentially indicating an accumulation pattern during hibernation.

A.4.2.5 Correspondence analysis

The overall distribution of microwear variables suggests a general overlap in dietary patterns across Eastern European cave bear populations through time and geography, though subtle regional differences can still be discerned. These distinctions appear primarily driven by variation in the quantity of fine and coarse scratches, reflecting differences in the mechanical properties of consumed plant resources, ranging from softer mast to tougher harder plant items.

Despite this, a high degree of ecological overlap is evident among all populations, more specifically the Moldavian Plateau, Central Balkans, and Western Balkans–Southern Rhodopes present the highest overlap. Notably, the Romanian Carpathians exhibit the widest ecological breadth, encompassing all other regional dietary niches within its eco-region. This broad distribution implies a particularly high degree of dietary flexibility, as also infer through isotopic studies (Robu et al., 2013, 2018; Meleg et al., 2024).

END OF THE MANUSCRIPT

Reflections from my mentors

“Ha sido un verdadero placer acompañar a Paulo en su tesis de máster. Su dedicación y seriedad en la investigación facilitan el trabajo conjunto y generan un ambiente de auténtico intercambio científico. Colaborar con él siempre resulta estimulante y productivo. No tengo dudas de que sabrá aprovechar cada paso de su trayectoria científica”.

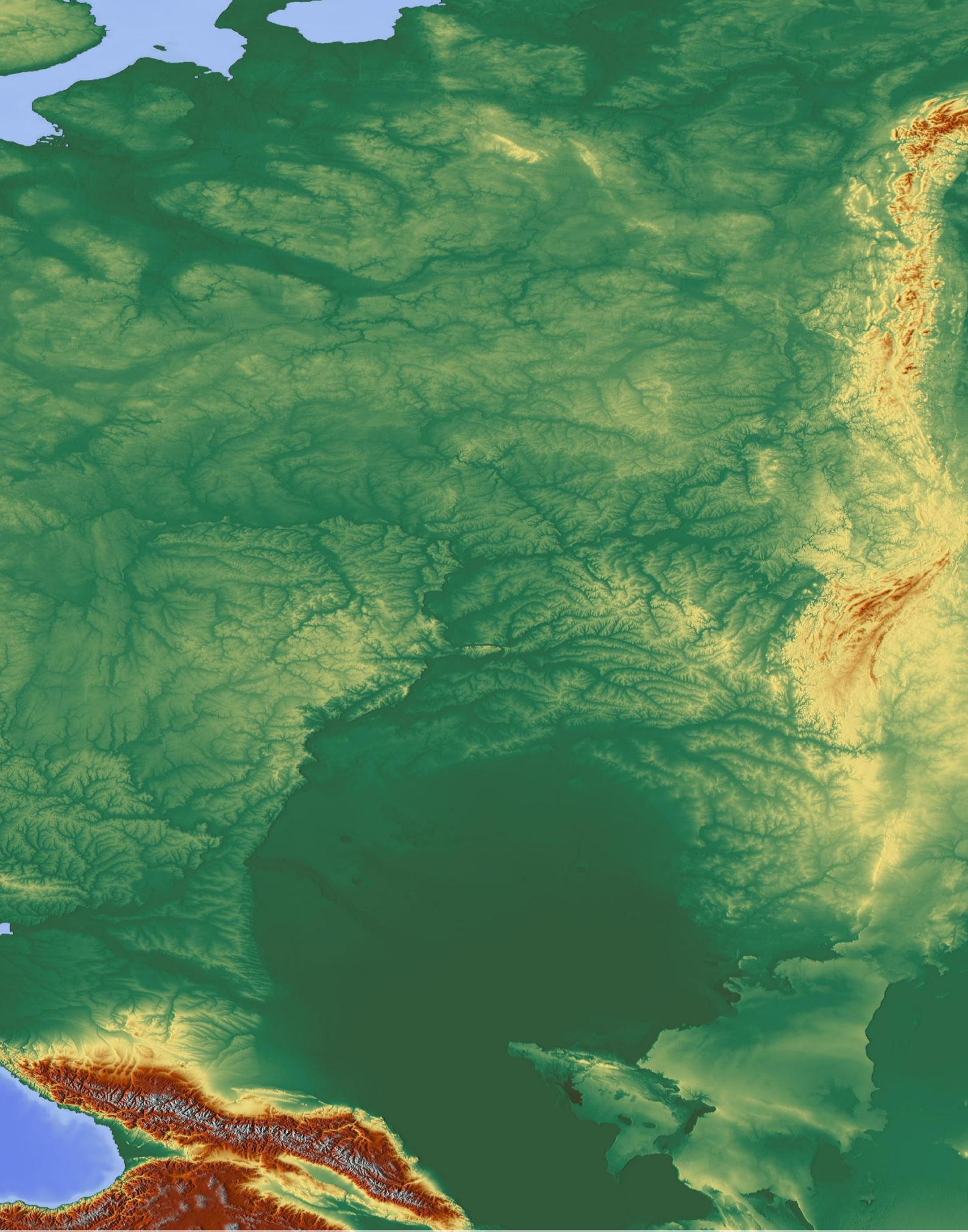
- Florent Rivals.

“Ha sigut un plaer acompanyar-te durant aquest treball. Realment, estic molt orgullós del resultat final. Jo també vaig fer el TFM sobre la dieta de l'os de les caveres, i entenc la complexitat de reconstruir la dieta d'un animal potencialment omnívor. Òbviament, has millorat tot el que jo vaig fer en qualitat i també amb un volum de mostres increïble (jo en vaig fer 12 i tu més de "500"). La veritat és que és molt fàcil ser el teu supervisor, amb la teva energia i ganes d'aprendre constants. I tinc moltes ganes de continuar treballant junts i reforçant el nostre vincle científic i d'amistat. Durant el teu primer mes de doctorat, ja hem visitat urgències, així que després d'aquesta experiència propera a la mort, estic segur que només podem anar a millor i que ens esperen molts èxits en aquesta nova etapa”.

- Iván Ramírez.

“Mr. Duño-Iglesias is one of the most promising young scientists I've met during my later scientific activity. I had the privilege to work with him both in Spain and Romania. He is ambitious and very prolific, curious and very focused, patient and dynamic in the same time. His Master thesis is a solid brick to the knowledge of the MIS 3 cave bear paleoecology. During his Master program he published a couple of seminal paper, in high-impact journals, a performance well beyond the students of his age. Only in a couple of years of training, supervised by Dr. Florent Rivals, he succeeded to master the microwear analyses on the MIS 3 cave bears and to answer palaeoecological questions that were not completely addressed by means of either stable isotopes or geometric-morphometrics. Given his performance during his early career so far, I have full confidence that Mr. Duño-Iglesias will become a distinguished scientist. I hope he will continue his scientific formation within the paleoecology of MIS 3 mammals, during a PhD program and beyond. I look forward to collaborate with him as he is a serious person and competitive scientist. I wish him all the best in his career and want to assure him that we'll continue strengthening our collaboration. Congratulations, Paulo!”

- Marius Robu.



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