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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* Verestchagin, 1973) in the Ural Mountains. Researchers have shown that, with some regional deviations, these animals consumed mainly plant foods, including abresive 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 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.

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 (Alekseeva, 1977; Azzaroli, 1983; Zastrozhnov et al., 2018). Among the carnivorans, there are several felids, including leopard (*Panthera pardus*) and extinct jaguar (*Panthera gombaszoegensis*). 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

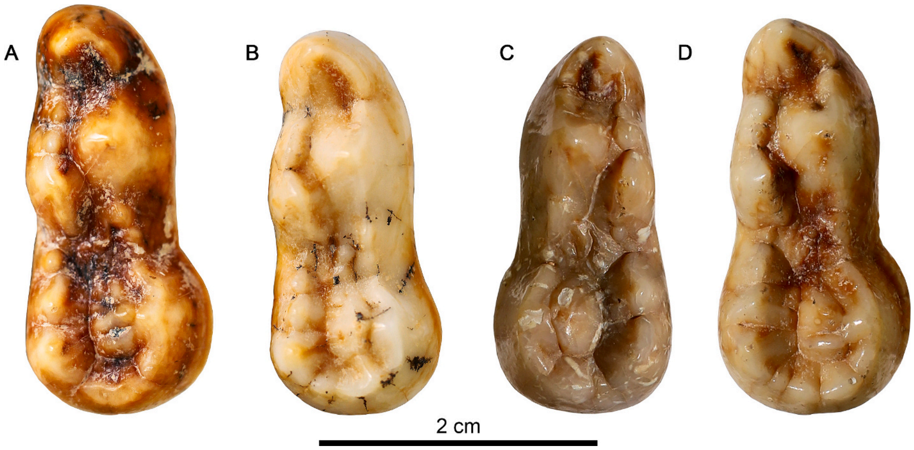

Fig. 1. Variation of the masticatory surface of m1 in cave bears from the Kudaro caves (top view). A–B: *Ursus praekudarensis*; C–D: *U. kudarensis*.

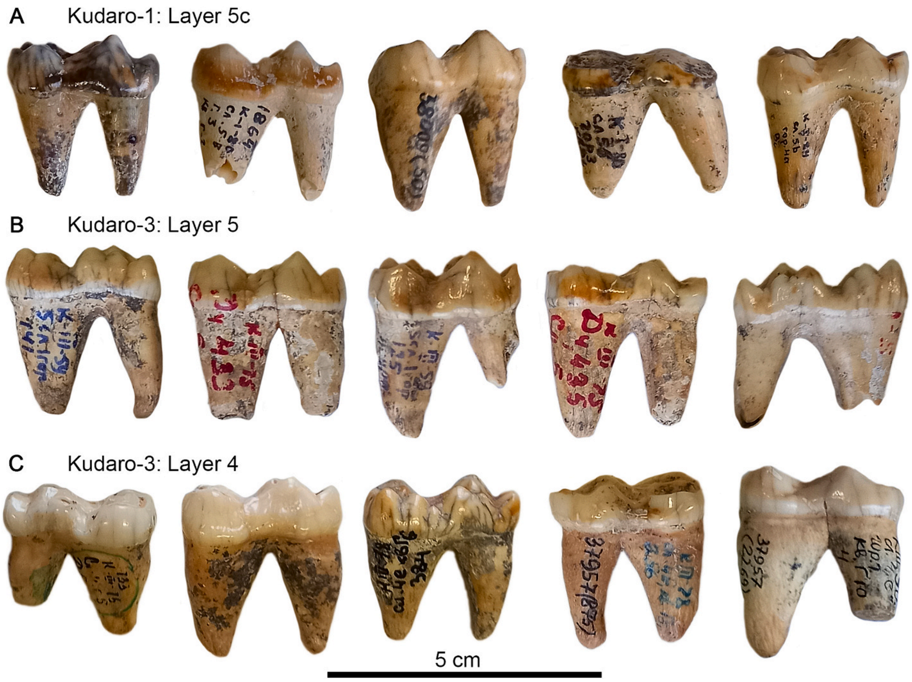

Fig. 2. Studied material. The first lower molar (m1) in cave bears from the Kudaro caves (side view). A: *Ursus praekudarensis*; B: *U. praekudarensis/kudarensis*; C: *U. kudarensis*.

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

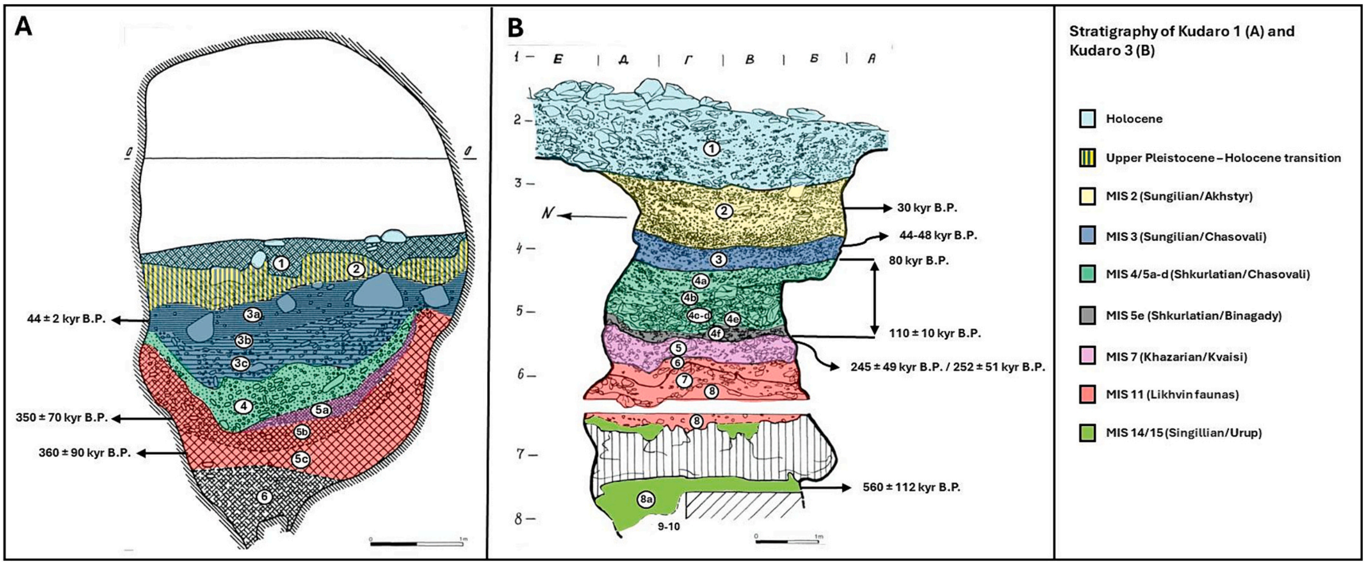

Fig. 4. Stratigraphic sequence of Kudaro 1 (A) and Kudaro 3 (B) caves, extracted and modified from Lioubine and Bosinski (1995). Chronology has been established based on thermoluminescence/uranium-thorium dating and biostratigraphy correlations (mammal age/faunal units) and further supported by pollen analysis (Ĉerdyncev 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 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; 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. (Ĉerdyncev 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 Semprebon, 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 mm^2 (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-Zaatari, 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/praekudarensis* 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)	*N*	NFS	NCS	NTS	SWS	NLP	NSP	NPP	NTP	NG	NHC%
Extinct											
U. praekudarensis	15	5.67	8.57	14.07	1.53	2.00	35.10	0.40	37.10	0.20	47%
U. praekudarensis/kudarensis	14	17.36	1.50	18.89	0.00	0.79	20.93	0.00	21.71	0.21	14%
U. kudarensis	12	7.46	11.25	18.63	1.75	2.50	33.38	0.83	35.88	2.38	83%
Extant											
U. americanus (North America)	9	13.56	2.56	16.12	0.00	5.44	19.00	3.00	27.44	0.00	0%
U. arctos (Greece)	4	13.00	7.00	20.00	0.5	9.25	8.50	2.25	20.00	2.00	0%
U. arctos (Central Europe)	10	17.50	3.40	20.90	0.00	5.4	22.50	8.30	36.20	2.10	0%
U. arctos (North America)	8	18.25	3.00	21.25	0.00	6.75	18.38	3.25	28.38	0.25	0%
U. arctos (Kamchatka)	23	16.22	3.83	20.05	0.10	6.96	19.78	4.78	31.52	0.35	0%
U. arctos (Northern Europe)	9	15.78	3.78	19.56	0.00	6.44	23.33	2.67	32.44	0.22	0%
A. melanoleuca	4	19.25	0.00	19.25	0.00	8.50	46.25	0.00	54.75	0.00	0%
U. maritimus	13	11.00	3.21	14.23	2.79	4.50	16.21	0.07	20.15	0.00	100%
U. thibetanus	6	14.33	3.33	15.33	0.00	4.50	15.33	0.00	20.33	17.67	0%

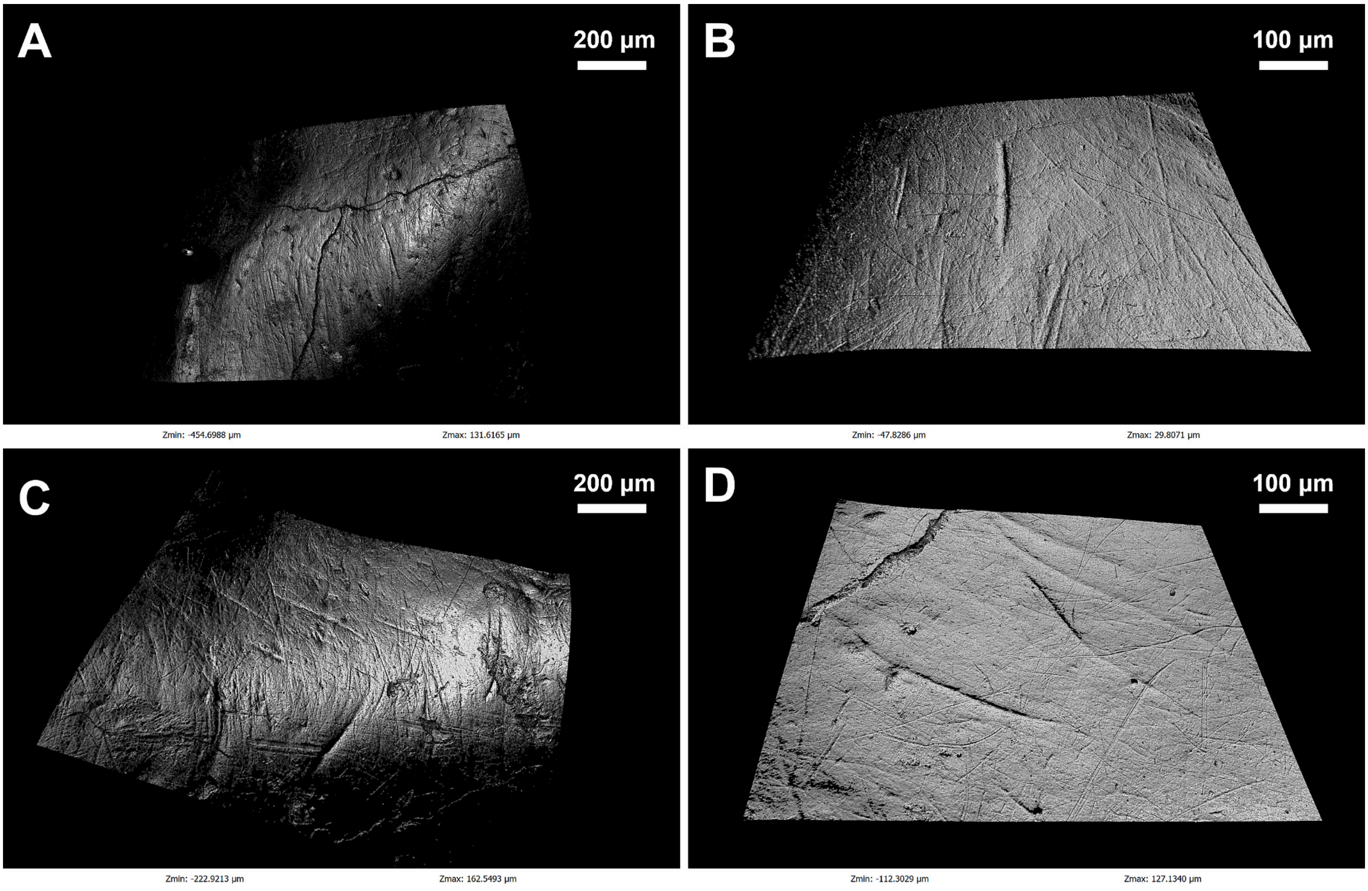

Fig. 5. Three-dimensional scans of the occlusal surface of the talonid of the lower first molar (m1) of different cave bear specimens from the Kudaro caves performed by a Sensofar® S Neox microscope. A: Surface topography (employing a × 10 lens) of the occlusal surface of *U. kudarensis/praekudarensis* (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 × 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 × 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 × 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 (Solounias and Semprebon, 2002), and falls within the lower part of the plot.

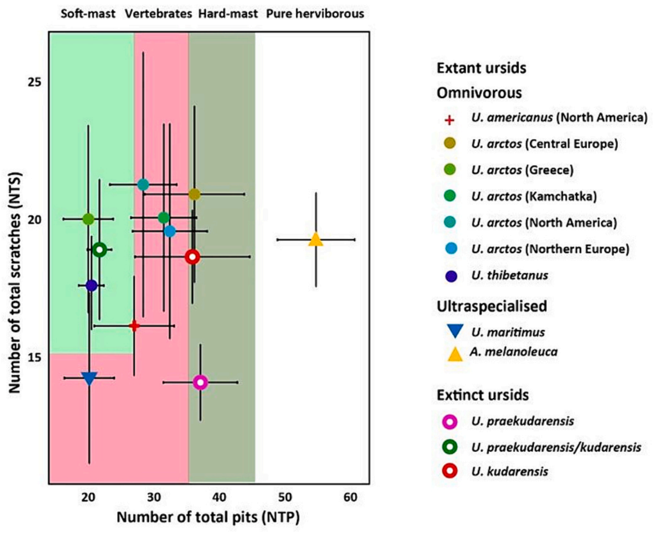

Fig. 6. Bivariate plot of the average number of total pits (NTP) and the number of total scratches (NTS) comparing the extant bear populations and the fossil populations. Error bars representing the standard deviation within the populations were added. Highlighted are four distinct eco-regions (soft mast, hard mast, vertebrates, and pure herbivorous) based on the predominant diet of extant bear populations as established by Pappa et al. (2019).

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

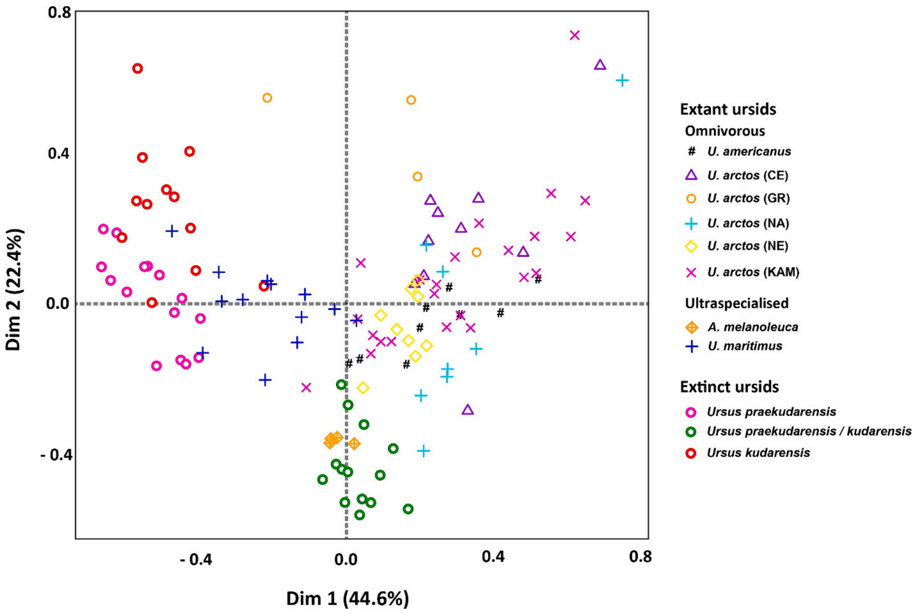

Fig. 7. Correspondence analysis using seven microwear variables, namely the number of fine and coarse scratches, small and large pits, gouges, puncture pits, and the scratch width score. Comparison of the fossil populations of the Kudaro caves, including the Middle Pleistocene *U. praekudarensis* (layer 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/praekudarensis 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). 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

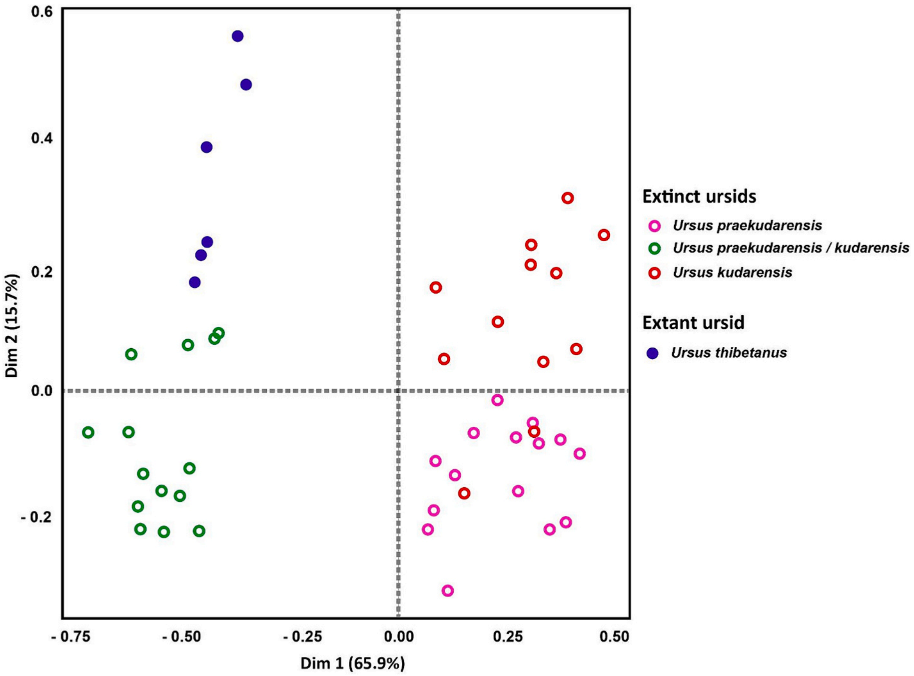

Fig. 8. Correspondence analysis employing the same seven variables as in Fig. 7. Comparison of the fossil populations of the Kudaro caves, including the Middle Pleistocene *U. praekudarensis* (layer 5c from Kudaro 1) and *U. praekudarensis/kudarensis* (layer 5 from Kudaro 3) populations, as well as the 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

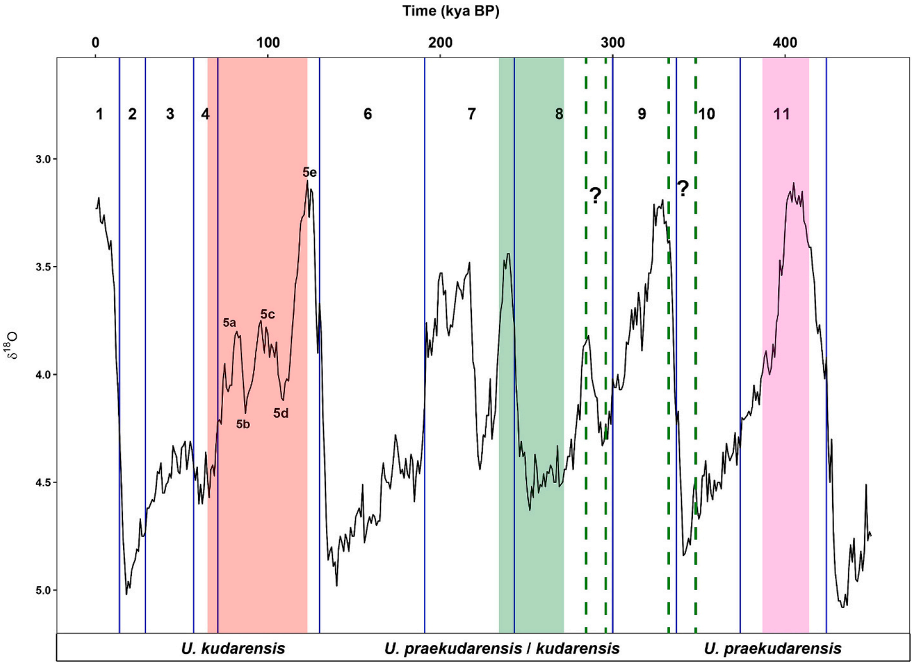

Fig. 9. Chronological time-range of the Kudaro cave bear populations in relation to the isotopic oxygen ($\delta^{18}O$) curve by Lisiecki and Raymo (2005) and Ruan et al. (2016). *U. praekudarensis* accumulated during a warm interstadial (MIS 11). *U. praekudarensis/kudarensis* accumulated during a 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. 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 kyr B.P., during the MIS 5 substage 5e (Eemian) until the beginning of MIS 4 (around 80 kyr B.P.) (Ĉerdyncev et al., 1959; Baryshnikov, 2002). This corresponds with the transition from a relatively warm and humid interstadial (Odderede), 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 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., 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 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 carnivorans 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 (*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 ($\delta^{13}C$), nitrogen ($\delta^{15}N$), and sulphur ($\delta^{34}S$) 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

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

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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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