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Multiproxy evidence for environmental stability in the Lesser Caucasus during the Late Pleistocene

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ABSTRACT

The Lesser Caucasus, situated between Asia and Europe, has long been recognised as a key region for the study of human evolution in terms of the timing and routes of dispersal, as well as, ecological adaptations. In particular, scholars have argued whether stable environments persisted in the region throughout the last glaciation, serving as a refugium for temperate biota, likely attracting human settlement and use. Here, we present the results of a multidisciplinary study of Karin Tak Cave, which contains sediments that accumulated between 48,000 and 24,000 cal yr BP. We examined biostratigraphic changes at the site by looking at the composition of fauna, which we hypothesise to be naturally accumulated, in different stratigraphic phases using traditional zooarchaeological approaches combined with collagen fingerprinting (ZooMS, Zooarchaeology by Mass Spectrometry). To gain further insights into regional palaeoenvironmental conditions, we also applied stable carbon and oxygen isotope analyses to faunal tooth enamel. The obtained results suggest that the onset of the last glaciation did not cause dramatic changes in regional environments, indicating that the Lesser Caucasus was a climatically and ecologically stable region despite significant global climatic changes during this period.

1. Introduction

The Lesser Caucasus, a mountainous region that stretches between the Black and Caspian seas, has long been recognised as a key area for the study of human evolution, the timing and routes of human dispersals, and ecological adaptations (Fernández-Jalvo et al., 2016; Gabunia et al., 2000; Gasparyan and Arimura, 2014). Scholars have hypothesised that the region experienced relatively stable environmental conditions throughout the Pleistocene, due to the ameliorating effects of its maritime location and the Caucasus Mountains serving as a climatic and topographical barrier. Today, the mountainous nature of the region results in a mosaic landscape, with different geological substrates, soils, water resources, and microclimates (Volodicheva, 2002) stimulating biodiversity richness. The geographic location, complex

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geological composition, and the presence of a wide range of ecosystems and microclimates, rich floral and faunal resources, and an abundance of raw materials suitable for manufacture of stone artefacts are all factors assumed to have attracted mobile groups of humans to the region far back into the deep past (e.g. Bertacchi et al., 2021; Frahm et al., 2020; Kandel et al., 2017).

Though the early human occupation throughout the Pleistocene of this area has been extensively explored (e.g. Ferring et al., 2011; Lordkipanidze et al., 2013; Asryan et al., 2016; Mgeladze and Moncel, 2016; Moncel et al., 2015; Adler et al., 2014; Frahm et al., 2020), the Late Pleistocene period remains to be studied from the perspective of human-environmental interactions. Several regional archaeological sites dated between ca. 65-30 ka BP cover this crucial time span – a period that includes the disappearance of Neanderthals, the expansion of anatomically modern humans (AMH), and major climatic fluctuations (Bar-Yosef et al., 2006, 2011; Cullen et al., 2021; Egeland et al., 2016; Frahm et al., 2016; Gasparyan and Arimura, 2014; Ghukasyan et al., 2010; Glauberman et al., 2020a; Kandel et al., 2017; Kot et al., 2021; Moncel et al., 2015; Pinhasi et al., 2012, 2014; Pleurdeau et al., 2016). These sites indicate that groups producing Upper Paleolithic (UP) material culture (generally accepted to be AMH) arrived in the region after the local disappearance of bearers of late Middle Paleolithic (MP) technology (associated with Neanderthals), with apparently little possibility for contact between the two groups (Adler et al., 2006, 2008; Bar-Yosef et al., 2011; Golovanova and Doronichev, 2012; Kandel et al., 2017; Margherita et al., 2017; Meshveliani et al., 2004; Pinhasi et al., 2012; Pleurdeau et al., 2016; Tushabramishvili et al., 2011). The apparent lack of overlap in occupation between Neanderthals and AMH argues against the idea that the Neanderthal demise, at least in this region, depended on the arrival of modern humans.

The earliest direct evidence of the presence of AMH in the Caucasus comes from a human tooth found in Bondi Cave, dated to 38.7–35.3 cal ka BP (Douka and Higham, 2017; Pleurdeau et al., 2016; Tushabramishvili et al., 2012). A recently-revised chronology from Ortvale Klde, located in modern day west-central Georgia, suggests that the late MP locally ends between ca. 47.5–44.2 cal ka BP and the early UP begins at 46.7–43.6 cal ka BP, providing the earliest evidence for the early UP in the Caucasus. Additionally, the heterogeneity of MP technologies and the cultural unity of the early UP found in both the Northern and Southern Caucasus suggest that AMH crossed the Greater Caucasus Mountain range, which appears to have been impenetrable for Neanderthals (Adler and Tushabramishvili, 2004). Thus, the colonization of the Southern Caucasus by AMH seems to have been a rather rapid and widespread process (Adler et al., 2014; Goder-Goldberger and Malinsky-Buller, 2022; Lordkipanidze et al., 2013). However, the tempo of subsequent human occupation and its relationship to major Late Pleistocene climate change following this initial colonization remains under-studied. Well-stratified UP sequences are represented by only a handful of archaeological assemblages, restricted to the Imereti region of Georgia and Southern Armenia. In the sites of Ordvale Klde, Dzudzuana, Satsurblia, Aghitu-3 and Kalavan-1, radiocarbon dates suggest a break in occupation between ca. 24–18 cal ka BP, overlapping with the peak of the LGM (26–19 ka BP). Between ca. 20–11 ka BP, a new industry with geometric microliths emerged in both the Southern and Northern Caucasus. This may suggest a human recolonization or adaptation to new environmental conditions of these regions at the end of the LGM (Montoya et al., 2013). The 6000-year hiatus during the LGM is part of a wider pattern of reduction in human presence attested also more broadly across southwest Asia (Düring, 2010; Matthews and Nashli, 2022). However, sporadic human settlement during the LGM is recorded at the low-elevation sites of Akhshtyrskaya and Navalishenskaya, suggesting potential presence of refugia that sheltered human groups during harsh climatic conditions (Doronichev and Golovanova, 2019).

To test hypotheses of human-environmental interactions in this important region for human evolutionary studies, there is a great need for systematic excavations and detailed chronologies from additional sites. This will allow us to arrive at a more robust understanding of the environmental backdrop of human occupation and the potential role of climatic conditions on population dynamics over the last 50,000 years. In this paper, we aim to characterise distinct types of environments that humans might have encountered by presenting the results of our multidisciplinary analyses of faunal remains discovered and studied from Karin Tak Cave.

In a previous study (Antonosyan et al., 2019), some of the current authors focused on the fragmented bone specimens recovered from the site, and applied a novel bulk bone metabarcoding (BBM) genetic approach to identify the animal taxa present in different layers. Building on the previous analyses to fine tune our understanding of the paleoenvironmental conditions in the region during the Late Pleistocene, we applied further zooarchaeological, taphonomic, stable isotope, palaeobotanical, and typological analyses to the materials recovered from the 2017–2019 excavations of Karin Tak.

2. Study site

Karin Tak Cave is located at the southeastern end of the Lesser Caucasus mountain range at an elevation of 1396 m a.s.l., within the Karintak forest, on the east bank of the Karkar River (Antonosyan et al., 2019; Avagyan et al., 2022, Fig. 1). The cave system contains two separate passages (termed Caves 1 and 2; Fig. 2). Cave 1 is considerably longer, with a ca. 2-metre-high chamber that extends northeast for at least 66 m, along a geologic joint system that begins at an opening partially hidden by a rock fall. Cave 1 narrows and widens (constricting and expanding) several times along its length producing a set of small 'sub-chambers'. The passageways vary from <1 m to 3 m wide and trend straight for several metres before taking abrupt 60–90° turns. A preliminary geological survey suggested the former presence of an open chimney in the inner chamber of Cave 1 before the collapse of the cave system. A boulder collapse in the mid-section of Cave 1 has created a steep slope on parts of the floor filling sediments. Cave 2 extends from the entrance in a westerly direction for only roughly 10 m before turning 90° in a southerly direction for another 5 m. The positioning of this pronounced inflection in Cave 2 appears to align with a conspicuous (nearly right-angled) inflection in the trend of one of the inner sub-chambers of Cave 1. A potential (buried and inaccessible) link between these two caves is tentatively suggested on the map in Fig. 2.

Geophysical survey using ground-penetrating radar was conducted throughout the interior of the cave system, revealing an accumulation of up to 4 m of sediment infill. In the main chamber of Cave 1, excavations revealed infill consisting of ca. 2 m of loamy sediments deposited over a limestone bedrock, with eight distinct layers (see Fig. 2). Avagyan et al. (2022) conducted a detailed geological study of the sedimentary fill of Karin Tak, a summary of which can be found in the Supplementary data.

3. Materials and methods

3.1. Excavations

The first brief scientific description of the cave was completed in 2011, followed by preliminary archaeological surveys in 2014 and 2015. Excavations at the site started in 2016 and continued until 2020. The fossil materials presented here were recovered during the 2019–2020 field seasons. The excavation of a 3 × 2 × 2 m pit, subdivided into different excavation units (C1, C2, C3 and C4; Fig. 2), was undertaken in the inner chamber of Cave 1.

Bones and other fossils recovered during excavation were collected *in situ* and their stratigraphic position recorded. Excavated sediments were removed (in 5 cm spits) for dry sieving with 2- and 0.5-mm sieves to recover small specimens. Additionally, to recover botanical remains, 100 L of sediment were floated and screened through 125 μm mesh geological sieves. The overview of the archaeobotanical remains is

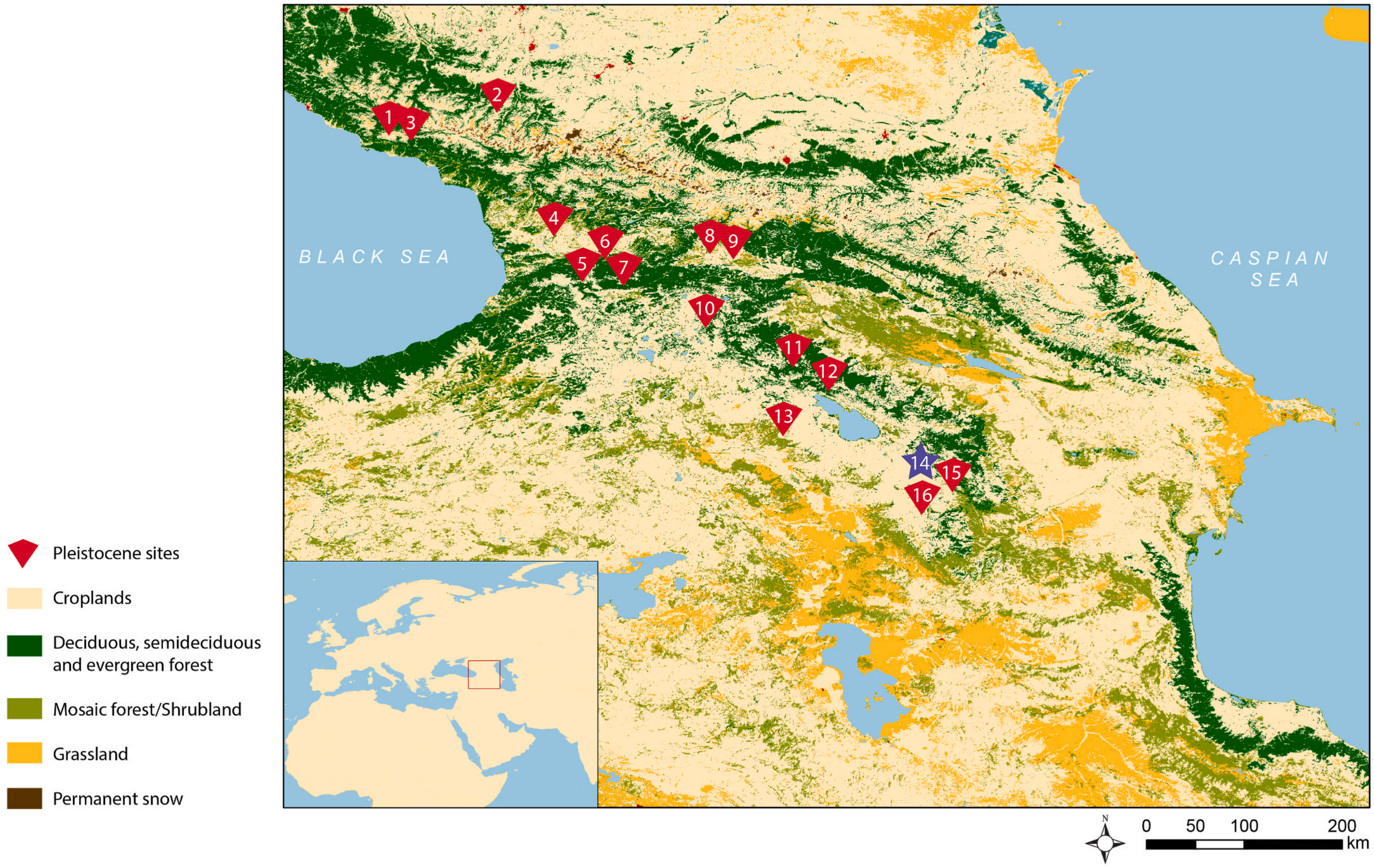

Fig. 1. Map of the region and discussed archaeological sites: 1 - Akhshtyrskaya cave; 2 - Mezmaiskaya Cave; 3 - Navalishenskaya Cave; 4 - Satsurblia Cave; 5 - Ortvale Klde; 6 - Bondi Cave; 7 - Dzudzuana Cave; 8 - Tsona; 9 - Koudaro I, III; 10 - Dmanisi; 11 - Hovk-1; 12 - Kalavan-1 and Kalavan-2; 13 - Nor Geghi-1; 14 - Karin Tak Cave; 15 - Azokh Cave; 16 - Aghitu-3 Cave. [colour used in print; single fitting image].

available in Table S2, with selected species illustrated in Figs. S1 and S2. All finds were brushed and dry cleaned in a field laboratory and stored in airtight, opaque bags.

3.2. *Dating*

The chronology is based on Accelerator Mass Spectrometry (AMS) ^{14}C ages, performed on bone collagen at the Scottish Universities Environmental Research Center (SUERC) Radiocarbon Laboratory in the University of Glasgow. Detailed descriptions of the methods employed by the SUERC Radiocarbon Laboratory can be found in Dunbar et al. (2016). Twelve bone specimens from Layers 3–6 in excavation units C2 and C4 were selected for ^{14}C dating. These units yielded the most animal remains, including those considered in the current study. Six of the samples returned ^{14}C dates that allowed us to refine the chronostratigraphy of the site (Table S1). The dates were calibrated in OxCal v.4.4, using the IntCal20 calibration curve (Ramsey, 2009; Reimer et al., 2020).

3.3. *Morphology and taphonomy of faunal material*

To minimise bias in the chronology, which might be caused by mixed sediments, faunal material was sampled exclusively from units C2 and C4, given our focus on the dating of these units. A total of 6202 faunal specimens consisting of skeletal ($n = 5793$; 93.4%) and isolated dental ($n = 409$; 6.6%) remains wasanalyzed in the current study. These consist of all faunal materials (excluding microfauna, i.e. remains of animals <1 kg) recovered from excavations of Units C2 ($n = 2202$) and C4 ($n = 4000$; see Table S5). Results of the in-depth zooarchaeological analyses, including detailed zooarchaeological counts (body part representation, minimum number of individuals, etc.), will be detailed in a forthcoming publication. The current study also does not include analyses of microfaunal remains such as those of murids and cricetids ($n =$ ca. 4000). Instead, here we focus on preliminary identification of intermediate and large-size mammals, as well as the taphonomy of the faunal materials from the site.

All fragments were sorted, cleaned to allow for observation of bone surface modifications, measured using a digital caliper, and identified to the highest possible taxonomic classification using modern comparative materials maintained at the Max Planck Institute of Geoanthropology (MPI GEA) and the Laboratory of Comparative Anatomy of the French National Museum of Natural History (MNHN). All specimens were examined for natural – including weathering (Behrensmeyer, 1978; Andrews, 1990), animal and anthropic modifications, such as abrasion (Shipman and Rose, 1988), burning, staining, and butchery marks (Fernandez-Jalvo and Andrews, 2016). We used the criteria detailed by Fernandez-Jalvo and Andrews (2016) in identifying marks made by non-human predators. For weathering and abrasion, we applied a modified classification (see: Amano et al., 2016), wherein fragments with minimal weathering (stages 0–1 following Behrensmeyer, 1978) were assigned a score of 0 and heavily weathered bones (i.e. with longitudinal cracking and exfoliation of the cortical bone surface) a score of 4. The completeness of the skeletal element was recorded as well as the fracture patterning (Reitz and Wing, 1999) considering the characteristics of fracture surfaces, its position and orientation. All specimens were classified to size based on live weight following a modification of the criteria established by Thomas (1969) and Grayson (1984): small mammals (1 kg–10 kg); intermediate mammals (>10 kg-<100 kg) and

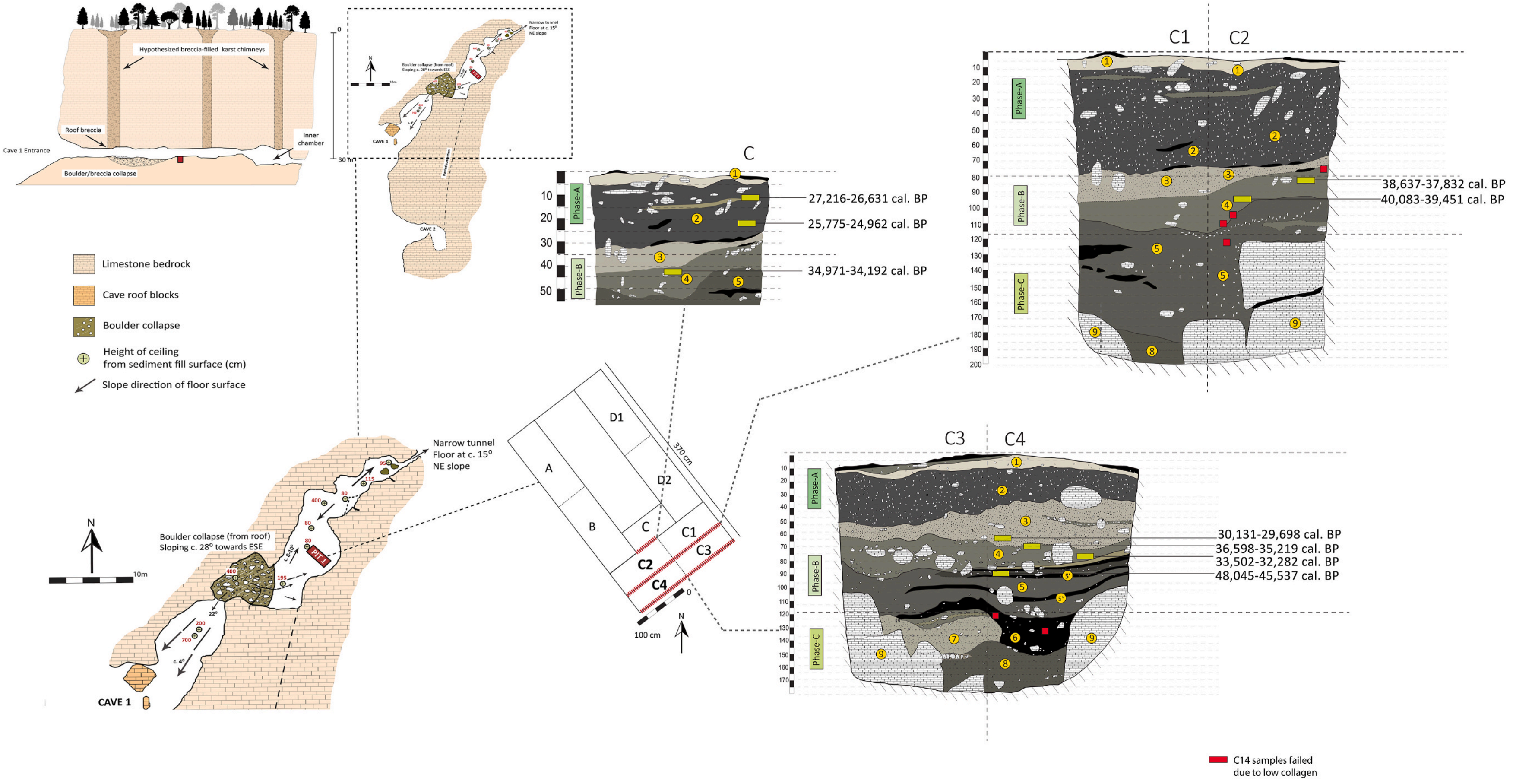

Fig. 2. General map, excavation plan and stratigraphy of Karin Tak. The dates are detailed in Table S1. [colour used in print; 2-column fitting image].

large mammals (>100 kg). Bone fragments that could not be assigned to a taxon but could be identified to a skeletal element were also assigned to a size class considering the relative size of the element (e.g. cortical bone thickness).

3.4. Zooarchaeology by mass spectrometry (ZooMS)

ZooMS or collagen peptide mass fingerprinting, is a novel cost-effective proteomic approach that allows taxonomic identification of morphologically ambiguous bones through MALDI-TOF mass spectrometry. The method is based on taxon-specific amino acid sequence variations within collagen type I, the most abundant protein in bone material, allowing for the consideration of the latter as a molecular barcode to read the taxonomic identity of bones (Buckley et al., 2009; Buckley, 2023). We applied ZooMS to 400 bone fragments recovered from different stratigraphic phases in excavation units C2 and C4. The bones of large/intermediate-size mammals, mainly ungulates, along with fragments with high porosity (among other possible indicators outlined in Hillier and Bell, 2007) were sampled, to explore the possibility of identifying human remains. We acknowledge that this could introduce a bias, specifically the overrepresentation of large mammals in the ZooMS NISP count. To partially address this, we also randomly sampled non-diagnostic bone fragments (N = 78; 3–5 cm in length), in order to try to produce data representative of the diversity of animal sizes found at the site (i.e. regardless of body size see Discussion below). ZooMS analysis was carried out at the dedicated ZooMS laboratory at the MPI GEA following the Acid insoluble protocol (Buckley et al., 2009; Brown et al., 2020). In brief, this involved acid demineralization of 20–30 mg bone chips, isolation and enzymatic (trypsin) digestion of collagen followed by ZipTip purification of the resulting peptides. Samples were run on a Bruker Autoflex Speed MALDI-TOF mass spectrometer (Bruker Daltonics) to produce spectra/fingerprints for taxonomic identification. Extraction blanks were included throughout all stages to monitor the introduction of potential contamination, the blanks were empty of collagen type I, pointing to the absence of protein contamination in the laboratory. The resulting peptide markers were identified via mMass software (v5.5.0; Strohalm et al., 2010; Wang et al., 2021), and the registered collagen fingerprints of each specimen are presented in Table S15.

For taxa that exhibited an identical series of markers, taxonomic identifications were assigned considering the current range of fauna in the study region and the archaeological records from the area. This is the case for many wild bovids and cervids that share many of the same peptide markers. For instance, *Ovis* sp., *Rupicapra* sp., and *Nesotragus* sp. have an identical set of markers; however, considering that *Nesotragus* sp. and *Rupicapra* sp. have not been reported in the study region (i.e. outside the biogeographic range of modern and fossil specimens), the attribution to *Ovis* sp is more probable.

Discriminating gazelles (*Gazella* sp.) from deer (*Cervus* sp.) is less straightforward, as both taxa are common in the region and display a similar set of markers. However, a recent study by Janzen et al. (2021) suggested new markers to separate members of Antilopini tribe, these are COL1A2 375 and α2 889 that, for Antilopini, display m/z 1182, 2056, 2072 and 1532, respectively. At the same time, m/z 3227 was suggested as a potential marker for gazelles (Desmond et al., 2018) while m/z 2216 was reported as being specific to red deer (Jensen et al., 2020; Janzen et al., 2021). We used these new findings to guide our identifications, with samples which had at least three of the above-mentioned markers identified as gazelle or deer. If the markers were absent, the identification was restricted to *Gazella/Cervus*. Similarly, sheep and goat exhibit almost identical peptide markers with exception of markers COL1α2 757 (+16; m/z 3017.4, 3033.4 for sheep and m/z 3077.4, 3093.4 for goat: Buckley et al., 2009, 2010) and a recently identified COL1α2 375 (m/z 1154, 2028 and 2044; Janzen et al., 2021) that facilitate the identification of caprines.

3.5. Stable isotope analyses

We studied $\delta^{13}C$ and $\delta^{18}O$ values from faunal dental enamel, mostly from ungulates, as a proxy for paleoenvironmental conditions around Karin Tak during the last ca. 45,000 years. 127 faunal dental elements from different chronological phases of the site were selected (Table S16). We tried to sample as many dental elements as possible from the different phases. However, we avoided teeth that showed evidence of remineralization or alteration (i.e. burning) and those with severe calcium carbonate/mineral concretions. The fragmentary nature of the dental elements limited taxonomic identification (i.e. to genera/species), and we opted for a conservative approach, grouping together specimens into families/subfamilies.

Caprines/Antilopines (n = 42) included goat (*Capra* cf. *aegagrus*), mouflon (*Ovis* cf. *gmelini*) and goitered gazelle (*Gazella* cf. *subgutturosa*). Cervids (n = 10), on the other hand, included both the red deer (*Cervus elaphus*) and the roe deer (*Capreolus capreolus*). We also sampled, albeit in low frequency because of the rarity of dental remains, equids (n = 3), suids (n = 1), and canids (n = 1). Our analyses also included a total of 71 dental elements, mostly fragments, that we were unable to confidently identify to taxon (considering the applied conservative approach), which we designated as ‘artiodactyls’. The details of the specimens analyzed in this study are presented in Table S16, including the specimen number, excavation context, associated chronology, taxon identification, and skeletal element.

We followed the standard protocol used at the Stable Isotope Laboratory of the MPI GEA for the analyses of $\delta^{13}C$ and $\delta^{18}O$ from the carbonate portion of tooth enamel bioapatite. We employed bulk sampling of the dental enamel by abrading the complete length of the buccal surface of the teeth with a diamond-tip drill to ensure a representative sample for the whole axis of enamel mineralization. Where this was not preserved, we sampled the lingual aspect. Organic and secondary contaminants were removed from the obtained enamel powder following an established protocol (adapted from Lee-Thorp et al., 2012; Sponheimer et al., 2005; Ventresca Miller et al., 2018), which involved: pretreating the samples with 1% NaOCl for 60 min; followed by repeated rinsing with purified water and then 0.1M acetic acid for 10 min; and again by repeated rinsing with purified water. Samples were then frozen and transferred to a freeze dryer until fully dry. Roughly 2 mg of the dried samples were then weighed into glass vials and left to react with 100% phosphoric acid at 70 °C for 1 h. The resulting gases were measured using a Thermo Gas Bench 2 connected to a Thermo Delta V Advantage Mass Spectrometer. The obtained $\delta^{13}C$ and $\delta^{18}O$ values were corrected using a three-point calibration against international standards (IAEA-603 ($\delta^{13}C = 2.5‰$; $\delta^{18}O = -2.4‰$); IAEA-CO-8 ($\delta^{13}C = -5.8‰$; $\delta^{18}O = -22.7‰$); IAEA-NBS 18 ($\delta^{13}C = -5.014‰$, $\delta^{18}O = -23.2‰$)). USGS44 ($\delta^{13}C = -42.2‰$) was run as an in-house standard. External reproducibility was c. + 0.2‰ for $\delta^{13}C$ and +0.2‰ for $\delta^{18}O$, as determined by replicate analysis of an in-house bovine enamel standard.

We tested whether there were significant differences in $\delta^{13}C$ and $\delta^{18}O$ values between different time periods and for the different faunal groups. The $\delta^{13}C$ and $\delta^{18}O$ values were tested for normality using the Shapiro-Wilk test. Following observation of non-normality, we employed Kruskal-Wallis tests to examine the significance between the values in the different phases of the site. If significant, the tests were followed by a post hoc Dunn test to determine which phases/faunal groups were significantly different from each other. Analysis of variance (ANOVA) followed by post hoc Bonferroni/Tukey pairwise comparisons were conducted in cases where normality was observed. All statistical analyses were conducted using R (R Core Team, 2013).

4. Results and interpretations

4.1. Chronology

Previous dating efforts from excavation unit C0 suggest that the first four layers of the sediments of Karin Tak formed between ca. 24–34 ka cal BP. In particular, two bone fragments from Layer 2 returned ^{14}C dates of 27,216–26,631 cal yr BP and 25,775–24,962 cal yr BP, while a bone fragment from Layer 4 was dated to 34,971–34,192 cal yr BP (Antonosyan et al., 2019).

Our current dating efforts add to this picture with six new radiocarbon dates from excavation units C2 and C4 (see Fig. 2; Table S1). A suid third metatarsal from the previously undated Layer 3 returned a ^{14}C date of 30,131–29,698 cal yr BP. Four samples from Layer 4 yielded dates between ca. 40,000–32,000 cal yr BP, aligning with the previous dates from Layer 4 of excavation unit C0. A gazelle mandible and suid patella from Layer 4 in C4 returned ^{14}C dates of 33,502–32,832 cal yr BP and 36,598–35,219 cal yr BP, respectively. Likewise, two caprine phalanges from Layer 4 in C2 were dated to 38,637–37,832 cal yr BP and 40,083–39,451 cal yr BP. A bear basal phalanx from Layer 5 in C4 was dated to 48,045–45,537 cal yr BP, the oldest date for the site thus far. Other samples from the layer, as well as from Layer 6 (see Fig. 2), did not preserve sufficient collagen for dating.

Considering these dates and the different layers of infill identified, we propose three sedimentary phases for Karin Tak (Phases A, B, C). All the materials studied were grouped into these three phases. Although there are some date inversions in the uppermost Layer 2, our now well-established chronology suggests that there is no mixing between the Phases; the dates align in a clear, stratigraphic order from bottom to top. To avoid any issues of taphonomic movement, we focus our interpretations of the methods applied at the resolution of Phase rather than Layer.

Phase A, comprising Layers 1, 2 and 3, dates to the last ca. 30,000 years and represents MIS 2 at Karin Tak. Currently there are no dates for Layer 1, but previous dates coupled with new dates generated by this study suggest that Layer 2 was deposited between ca. 24,000–27,000 cal yr BP and Layer 3 between ca. 29,000–30,000 cal yr BP. We suspect that humans occupied the site during this time period, most likely utilizing the parts of the cave closer to daylight (near the opening of the cave or on the terrace in front of the cave), as evidenced by a handful of lithic materials recovered during the excavation of these layers (Tables S3 and S4; Figs. S3 and S4). The few artefacts found in the excavated deposits from deep within the cave probably represent finds people discarded when they (occasionally) entered the area. However, it remains difficult to judge the nature of this occupation given the sparse archaeological dataset. The details on typo-morphological characteristics of artefacts can be found in the Supplementary data.

Phase B, comprising Layers 4 and 5, dates to ca. 32,000–48,000 cal yr BP and represents MIS 3 at the site. No evidence of human presence/activity is recorded in this phase.

Phase C represents the undated layers of the site (presumably >48,000 cal yr BP) and consists of Layers 6, 7 and 8. Similar to Phase B, these layers lack evidence of human occupation.

4.2. Taphonomy

The faunal materials from Karin Tak exhibited a very high degree of fragmentation, with 85.2% of the long bone fragments analyzed preserving less than 25% of the complete length (Fig. S5; Table S6). Only 0.96% of the long bone fragments in the assemblage preserved more than 75% of the complete element length. Fragments preserving less than a quarter (ca. <25%) of the original length account for 80.5% of the appendicular skeletal elements in Phase A, 93.8% in Phase B and 95.1% in Phase C. We observed the same pattern in circumference completeness, with 83.6% of the specimens analyzed preserving less than a quarter of the bone's original circumference (Fig. S4; Table S7). There is no significant difference in terms of fragmentation as indicated by length and circumference completeness between the different phases of the site ($F(11) = 0.854$, $p < 0.05$ for length; $F(11) = 0.888$, $p < 0.05$ for circumference) and the high degree of fragmentation made the assignment of the specimens to taxon difficult (see below).

We recorded the patterns of fragmentation of the bone specimens (e.g. spiral, transverse, stepped, etc.), as well as the orientation (oblique, perpendicular, intermediate) and shape of the fracture edge (e.g. jagged, peeled, smooth or flaked), with the aim of identifying the agent and/or taphonomic processes that caused/affected the accumulation of bones in the site. As pointed out by numerous researchers (e.g. Johnson et al., 2016; Karr, 2015; Karr and Outram, 2012; Rabett, 2004), identifying the causal agent(s) responsible for bone fragmentation based on these characteristics is not, however, straightforward, since different agents/behaviours could fragment bones in similar ways (and vice versa). In all phases of Karin Tak, bones with transverse fracture (70.5% in the Phase A to 65.5% in the Phase C) dominate the assemblage followed by specimens with spiral fracture (12.4% in the Phase A to 8.1% in the Phase C) (Fig. 3, Table S8).

Bone fragments with intermediate (i.e. between oblique and perpendicular) fracture angles are the most common in all phases of the site (57.1% in the Phase B to 43.1% in the Phase C) followed by fragments exhibiting perpendicular fractures (32.2% in the Phase C to 28.4% in the Phase B; Fig. 3, Table S9). With regards to fracture edge shape, fragments exhibiting smooth fracture are dominant (ca. 65.4% in total) followed by specimens with jagged edges (ca. 29.5%; Fig. 3, Table S10).

In terms of bone surface alteration, the majority of the bone fragments examined exhibited little weathering and abrasion. Considering all the fragments analyzed, 96.6% exhibited stages 0–1 weathering (i.e. no cracks or at the very least minimal flaking of the bone) and only 3.2% exhibited pitting and cracks (stages 2–3; Fig. 4 and Table S11). A similar pattern was observed with regards to abrasion, with more than 95% of the bone fragments examined exhibiting stages 0–1 (Fig. 4, Table S12). ANOVA tests show that there is no significant difference in the degree of weathering ($F(14) = 1.169$, $p < 0.05$) and abrasion ($F(14) = 0.456$, $p < 0.05$) of bone fragments between the different phases in Karin Tak. Calcium carbonate concretion ($CaCO_3$) was recorded in some bone fragments from the site, albeit heavy concretion (e.g. covering >50% of the bone surface) was rare (ca. 1%, Fig. 4 and Table S13). Only 2% of the bone fragments analyzed for each phase exhibited slight (e.g. <25% coverage) $CaCO_3$ concretion and the rest (i.e. 96.8% in the Phase C and 96.7% in the Phase A) exhibited no concretion.

There is no clear evidence for butchery (i.e. cutmarks or chopmarks) in any of the skeletal specimens analyzed ($n = 5793$). By contrast, trampling marks were recorded in a total of 209 bone fragments, representing 3.6% ($n = 126$) of the non-dental elements examined in Phase A, 3.5% ($n = 55$) in Phase B and 3.9% ($n = 28$) in Phase C. Possible anthropogenic signatures are limited to burning, which was observed in a total of 91 specimens from Phase A (1.9%, $n = 70$) and Phase B (1.2%, $n = 21$), and flaking and percussion marks were recorded in 1.5% of the bone fragments from Phase A ($n = 59$), 1.9% in Phase B ($n = 55$) and 0.9% in Phase C ($n = 7$; Table S14). Burning is not necessarily evidence for human activity as bones burnt by natural causes (i.e. forest/grassland fires) could have been transported into the cave, particularly considering the lack of burning features/hearths in the site. Percussion marks and flaking could also be caused by non-human agents including carnivores.

Indeed, carnivores appear to have been a major taphonomic agent in the site (Table S14). A total of 201 bone fragments (3.6% of non-dental specimens analyzed) exhibited evidence of carnivore modification, including 39 fragments with tooth grooves/scores, 42 fragments with punctures (in compact bone/broken edges and articular surfaces), 48 fragments with evidence of chewing and 46 specimens exhibiting corrosion consistent with carnivore digestion (pitting, etc. See: Fernandez-Jalvo and Andrews, 2016). The rest showed multiple alterations attributable to carnivores (i.e. both punctures and grooves, etc.). Examples of carnivore-modified bone fragments are shown in Fig. 5. Determination of the carnivore taxa/taxon responsible for the observed taphonomic signatures is beyond the scope of the current paper and is the focus of an ongoing study. Nonetheless, comparison with published

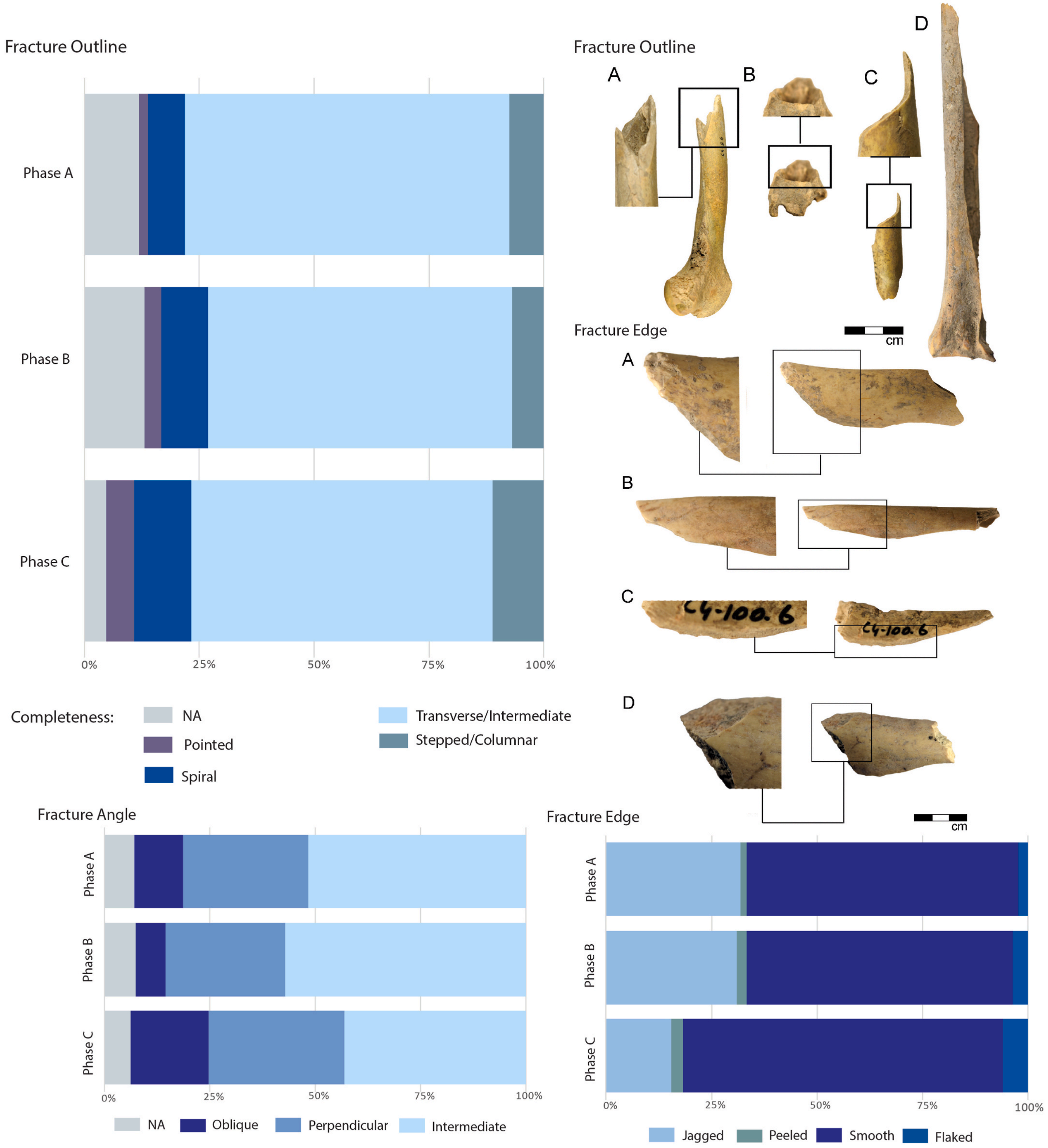

Fig. 3. Bone fragmentation patterns (fracture outline, edge and angle) observed in the specimens from Karin Tak. For examples of specimens with different fracture outline, A: pointed; B: transverse/intermediate; C: spiral; D: stepped/columnar; for fracture edge, A: jagged; B: smooth; C: peeled; D: flaked. [colour used in print; single fitting image].

data (Arilla et al., 2014; Sala and Arsuaga, 2013; 2014; Saladié et al., 2013), in addition to evidence for their presence in the site (see below), leads us to hypothesise that bears (*Ursus* sp.) and/or wolves (*Canis lupus*) (or both) were the key taphonomic agent(s) at the site.

4.3. *Morphological taxonomic identification*

The high degree of fragmentation of the faunal remains from all phases of the site severely limited the identification of the specimens to taxon through traditional means. Of the 6202 tooth and bone fragments analyzed in the study, only 373 specimens (6%) could be confidently

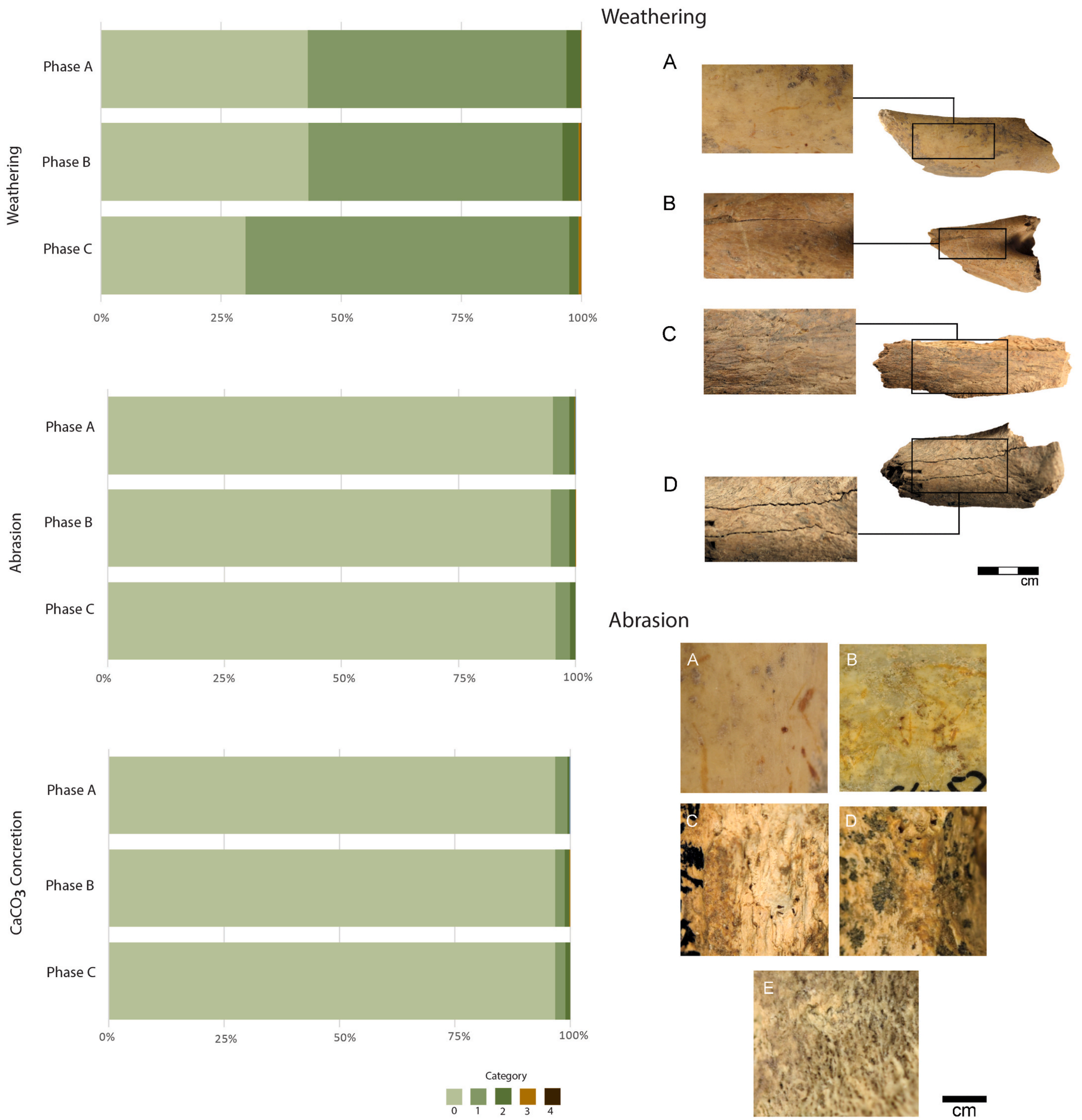

Fig. 4. Bone surface alterations (weathering, abrasion and calcium carbonate concretion) observed in the specimens from Karin Tak. Image insert for weathering, A: Stage 0; B: Stage 1; C: Stage 2; D: Stage 3, Image insert for abrasion, A: Stage 0; B: Stage 1; C: Stage 2; D: Stage 3; E: Stage 4. [colour used in print; single fitting image].

assigned to taxon (family/genus/species; Table 1, Fig. 6). Identification rate is slightly higher in Phase C (7.3%, n = 56) than in Phase A (5.9%, n = 224) and Phase B (5.5%, n = 93), but this could be due to the smaller number of fragments recovered from the layers. In all phases, bovids dominate the assemblage (mean = 62%), specifically caprines (*Capra* sp./*Ovis* sp.), representing 57.6% of the identified specimens in Phase A, 53.8% in Phase B and 57.1% in Phase C. Although these specimens most likely represent wild goat (*Capra aegagrus*) and mouflon (*Ovis gmelini*), the fragmentary nature of the specimens obscured the morphological features that allow for identification to species. Remains of gazelle (most likely *Gazella subgutturosa*) were also recorded in all phases, albeit in very low frequency (~1–3%).

Cervids represent the second most common group at the site, with 34 fragments (15.2%) identified in Phase A, 23 (24.7%) in Phase B and 10 (17.9%) in Phase C. Two species can be confidently identified based on antler fragments and isolated teeth, red deer (*Cervus elaphus*) and roe deer (*Capreolus capreolus*), with the former (15.1% in the Phase B) being more common than the latter (only securely identified in the Phase A at

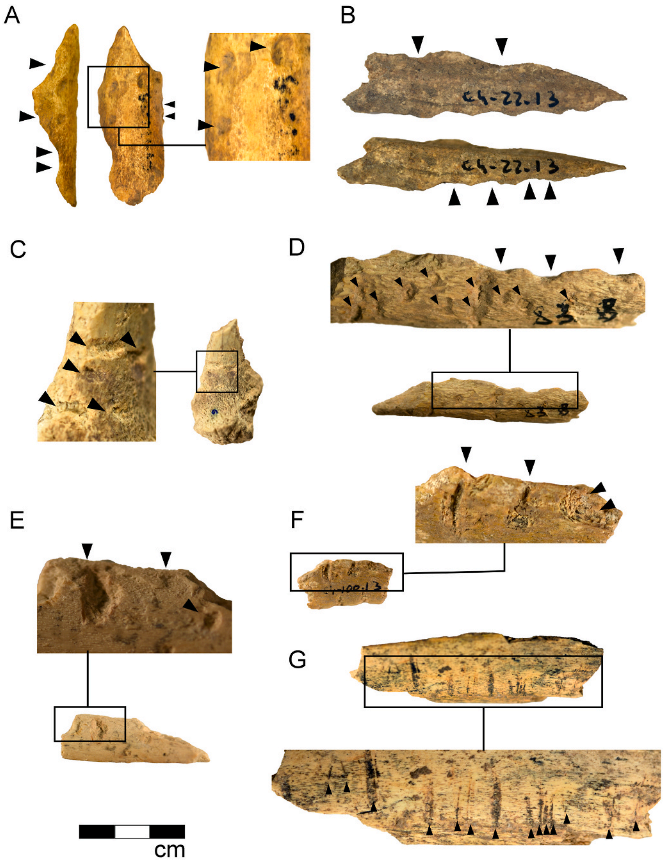

Fig. 5. Examples of carnivore modified bones showing chewing (A–D), punctures (E–F) and grooves/scores (G). [colour used in print; single fitting image].

1.8%).

Other ungulates identified at the site include wild boar (Sus scrofa), with 18 identified specimens (4.8%), and equids (*Equus* sp.), with eight identified specimens (2.1%). Carnivores including mustelids (*Martes martes* and *Meles* sp.) and canids, notably red fox (*Vulpes vulpes*) and wolf (*Canis lupus*), were also identified in the assemblage though in limited numbers (≤3%). Bears (most likely the brown bear *Ursus arctos*) were also identified, with six fragments of mostly isolated teeth and phalanges recorded in the Phase A (2.7%) and three fragments identified in the Phase B (3.2%).

Considering body size, intermediate-size taxa (i.e. weighing >10 kg < 100 kg) dominate the Karin Tak faunal assemblage. Intermediate-size mammals represent 85.9% of the identified mammalian taxa in Phase A, 89.8% in Phase B and 98.1% in Phase C. We made similar observations for the non-identified taxa, with 99.3% of the bone fragments having cortical bone thickness suggestive of intermediate-size mammals. By contrast, small (>10 kg, i.e. rabbit or fox-size) and large (>100 kg, i.e. horse or bear-size) account for only 0.18% and 0.42% of the non-classifiable bone fragments, respectively.

4.4. ZooMS identification

In order to complement morphological identifications and refine the taxonomic composition of ungulates, including species that are difficult to distinguish morphologically, as well as to explore the potential for identifying human remains, we applied ZooMS to bone fragments recovered from the different stratigraphic phases in excavation units C2 and C4.

Of the 400 screened Karin Tak samples, 339 (84.7%) generated collagen (I) peptide mass fingerprints sufficient for reliable taxonomic identification (Table S15, Fig. 7). Only 61 specimens failed to generate enough collagen due to poor preservation, most of these were recovered from lowermost Phase C. The preservation of collagen (intensity of peaks and the number of diagnostic markers) varied considerably between the samples, with the bones from deeper layers being more degraded.

A suite of wild fauna, as well as human bones, were identified by

Table 1
Number of Identified Specimens (NISP) of different animal taxa (excluding micromammals) recorded in the different phases of Karin Tak Cave.

Class/Order	Family	Taxon	Common name	Phase A		Phase B		Phase C	
				N	(%)	N	(%)	N	(%)
Aves	–	–	birds	3	1.3	1	1.1	1	1.8
Passeriformes	–	–	passerines	2	0.9	0	0.0	0	0.0
	Corvidae	–	crow/raven/magpie/jay	4	1.8	1	1.1	2	3.6
	Hirundinidae	–	swallow	2	0.9	0	0.0	0	0.0
Falconiformes	Falconidae	–	hawk/eagle/kite	0	0.0	2	2.2	0	0.0
Lagomorpha	Leporidae	–	rabbit/hare	6	2.7	0	0.0	0	0.0
Carnivora	Mustelidae	*Martes martes*	pine marten	1	0.4	1	1.1	0	0.0
		Martes sp./*Meles* sp.	marten/badger	2	0.9	0	0.0	0	0.0
	Canidae	–	dog-like carnivores	1	0.4	1	1.1	1	1.8
		Canis lupus	wolf	5	2.2	0	0.0	1	1.8
		Vulpes vulpes	red fox	0	0.0	1	1.1	2	3.6
	Ursidae	*Ursus* sp./*Ursus* (cf. *arctos*)	bear/brown bear	6	2.7	3	3.2	0	0.0
Artiodactyla	Bovidae	*Bos*/*Bison* sp.	aurochs/bison	5	2.2	1	1.1	0	0.0
		Capra (cf. *aegagrus*)/*Ovis* (cf. *gmelini*)	wild goat/mouflon	129	57.6	50	53.8	32	57.1
		Gazella sp./*Gazella* (cf. *subgutturosa*)	goitered gazelle	4	1.8	1	1.1	2	3.6
		Capra/*Ovis*/*Gazella*		3	1.3	1	1.1	3	5.4
	Cervidae	–	deer	11	4.9	9	9.7	8	14.3
		Cervus sp./*Cervus* cf. *elaphus*	deer/red deer	19	8.5	14	15.1	2	3.6
		Capreolus capreolus	deer/roe deer	4	1.8	0	0.0	0	0.0
	Suidae	*Sus scrofa*	wild boar	13	5.8	3	3.2	2	3.6
Perissodactyla	Equidae	*Equus* sp.	onager/horse	4	1.8	4	4.3	0	0.0
			TOTAL NISP	**224**		**93**		**56**	
Unidentifiable	Small mammal (<10 kg)			6		5		0	
	Intermediate mammal (>10 kg- <100 kg)			3495		1602		706	
	Large mammal (>100 kg)			12		3		0	
			TOTAL Unidentified	**3513**		**1610**		**706**	
			GRAND TOTAL	**3737**		**1703**		**762**	

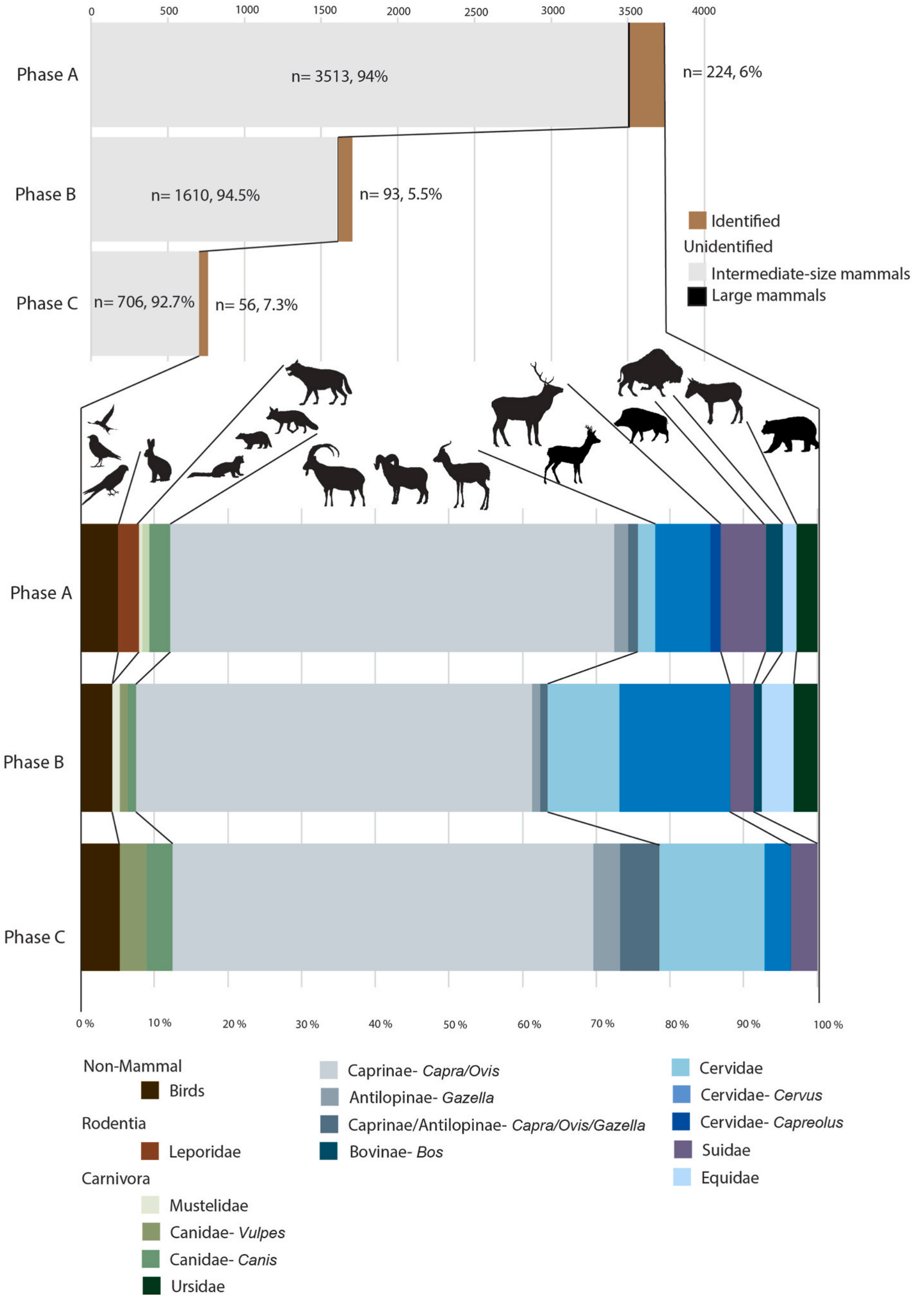

Fig. 6. Distribution of animal taxa identified in different phases of Karin Tak. [colour used in print; 1.5 column fitting image].

ZooMS (Fig. 8). In most of the cases, the identification was performed to genus level (250 specimens). In some samples, however, insufficient preservation of collagen restricted identifications to subfamily (70) or family level (17). The most frequent taxa identified were artiodactyls, with representatives of the Bovidae family (79% of the successful ZooMS identifications) dominating the assemblage (Fig. 8). This pattern is reflective of the sampling strategy we employed, with the main target being large mammals. In most cases, ZooMS confirmed previous morphological identifications and facilitated refinement of taxonomic identification of bones, with only 5% of the studied assemblage being incorrectly identified by morphology.

In total, 217 bones were selected from Phase A for ZooMS identification (118 from C2 and 99 from C4), of these 139 were unidentifiable fragments morphologically grouped within large mammals, 41 identified to family and 27 to subfamily level, with only 10 specimens to genus level. ZooMS screening revealed that the taxonomic composition of the assemblage was dominated by ungulates (Fig. S5) among which *Capra* sp. (n = 74) and *Ovis* sp. (n = 50) constituted the two most abundant groups.

For 15 specimens, discrimination between sheep and goat was not possible, due to absence of diagnostic peptide marker (COL1α2 757–789) and identification was restricted to the sub-family (Caprinae) level.

This assemblage also includes identical proportions of *Bos* sp./*Bison* sp. (n = 16) and *Gazella* sp. (n = 16). Other ungulates, such as *Sus* sp. (n = 4), *Cervus* sp. (n = 4), *Capreolus* sp. (n = 5), and *Equus* sp. (n = 6) were less common. Two samples lacked diagnostic markers to differentiate between *Cervus* sp. and *Gazella* sp. The carnivore component of the assemblage is represented by *Ursus* sp. (n = 1). Notably, the ZooMS analysis identified one specimen as *Castor* sp., previously unknown for the site, further demonstrating the capability of this method to provide taxonomic identification where morphological approaches fail. Beavers,

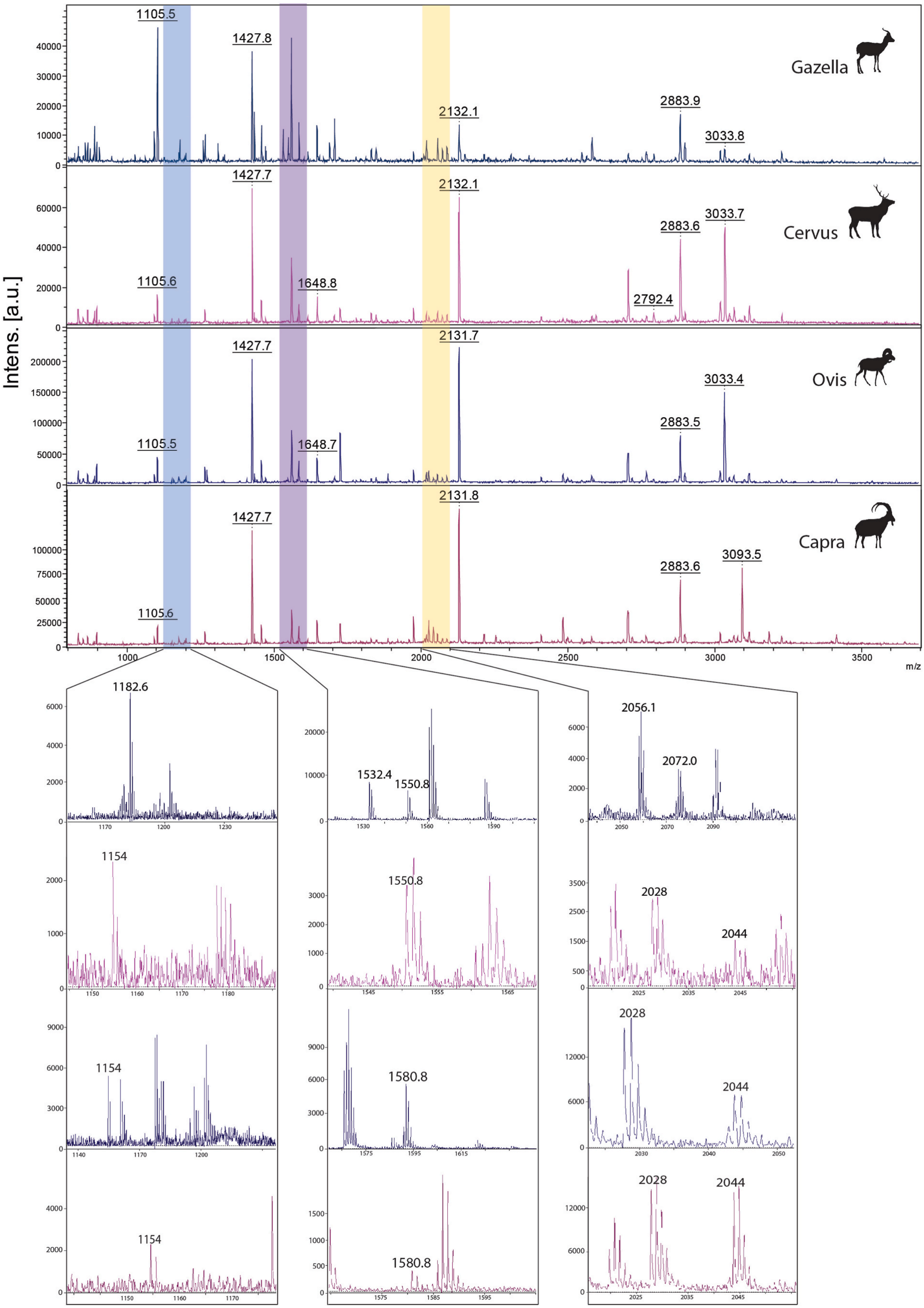

Fig. 7. Examples of peptide markers that distinguish ungulates. [colour used in print; 1.5 column fitting image].

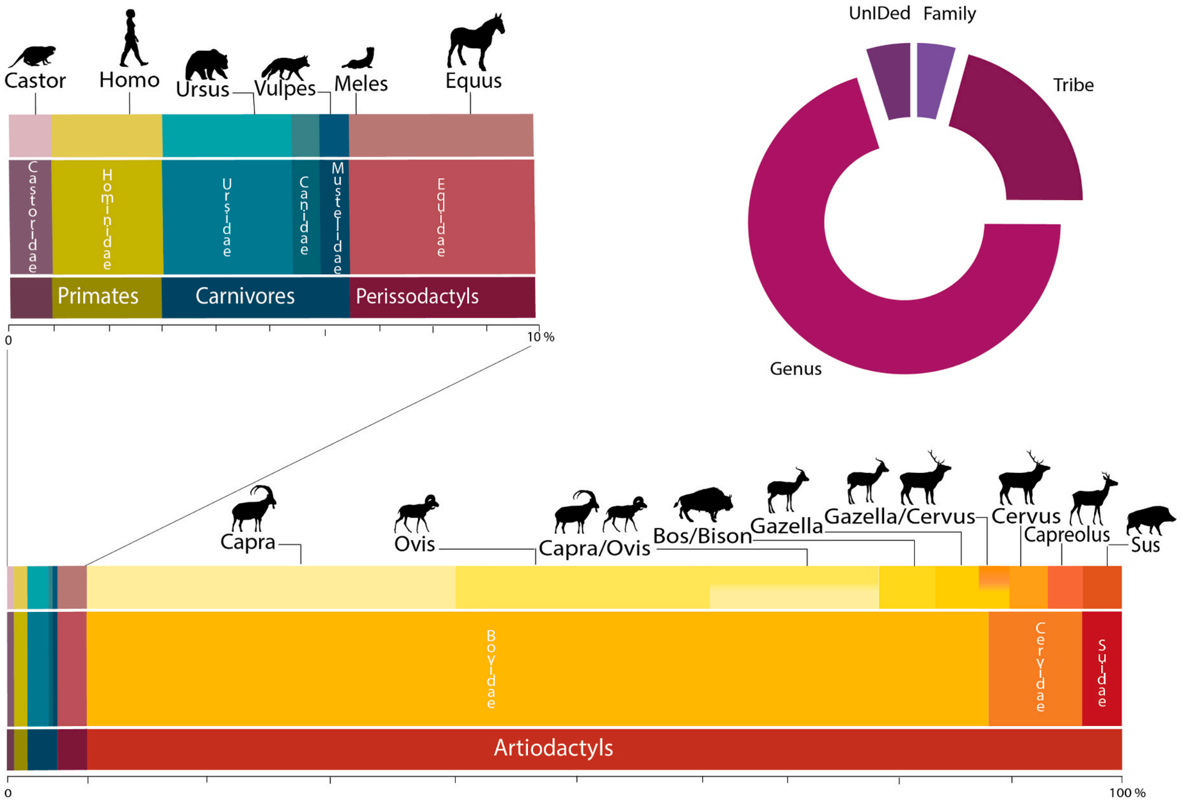

Fig. 8. Taxa identified using ZooMS method. [colour used in print; double column fitting image].

currently absent from the area, were previously recorded in late Middle to Late Pleistocene assemblages from the region (Baryshnikov, 2002; Pinhasi et al., 2014) and are known to have survived in the Caucasus until the 19th century (Vereshchagin and Burchak-Abramovich, 1958).

ZooMS screening allowed for identification of seven human bone fragments (from Phase A), which are currently being screened for whole genome analysis. The human bone fragments were amongst the unidentified remains, which were morphologically classified as large mammals. The human presence is restricted to the Phase A, and is accompanied by a handful of lithics recovered from the same layers.

ZooMS also allowed us to refine the morphological identification as was the case of samples C2-18 and C3-61 that were morphologically assigned to *Cervus* sp., but appeared to be *Capra* sp. based on collagen fingerprints. For seven samples it was not possible to narrow the identification any lower than family level, due to poor preservation. Additionally, five specimens failed to produce any collagen to provide taxonomic identification.

The ZooMS samples from Phase B include 138 bones (66 from Part C2 and 72 from Part C4) and, of these, 71 were unidentifiable fragments, morphologically grouped within large mammals, 17 were identified to order and 35 to subfamily level, with only 3 specimens assigned to genus level based on morphological features. Similar to the Phase A, the faunal composition in the Phase B as revealed by ZooMS shows a predominance of caprines, mainly represented by *Capra* sp. (31), *Ovis* sp. (25), and ‘Caprini’ (38), while other bovids are considerably less common (*Gazella* sp. (n = 3), and *Bos* sp./*Bison* sp. (n = 1); Fig. S5). The identified assemblage includes specimens of *Cervus* sp. (n = 2) and *Capreolus* sp. (n = 3). Three samples lacked the necessary peptide markers to distinguish between gazelle and deer, restricting identification to *Gazella/Cervus*. A single specimen was assigned to *Sus* sp. and six bones were identified as *Equus* sp. We also identified one bone belonging to *Castor* sp. Due to insufficient collagen preservation, six specimens could not be identified further than the order level (Artiodactyla). Carnivores were represented by *Ursus* sp. (n = 2), *Vulpes* sp. (n = 1), and *Meles* sp. (n = 1). In this assemblage (Phase B), 12 specimens failed to provide sufficient collagen for identification. Similar to the Phase A, some samples were incorrectly identified morphologically; for instance, sample C4-88 was morphologically assigned as gazelle. However, based on ZooMS results, this specimen represents sheep (*Ovis* sp.).

Fifty samples were selected from the Phase C for ZooMS screening, however, all the samples failed to generate collagen fingerprints sufficient for taxonomic identification.

Overall, the results from phases A and B record almost the same set of taxa (with an exception of presence of human bones in Phase A); although samples from Phase B were considerably less well-preserved compared to those from Phase A, which most likely reflects the different ages of the samples. The outcomes demonstrate the potential of ZooMS when applied to heavily-fragmented faunal assemblages from regional Pleistocene sites to improve the taxonomic level of identification.

4.5. *Stable isotope analyses*

Over the past four decades, stable carbon and oxygen isotope analyses of enamel of faunal teeth has become an increasingly standard approach for obtaining insights on the paleoecology of past animal communities, their diets and the types of environments they encountered (e.g. Roberts et al., 2023; Amano et al., 2023). Stable carbon isotope (δ^{13}C) values in tooth enamel reflect the type of vegetation consumed by an animal. The primary source of variation in terrestrial ecosystem δ^{13}C is brought about by the different pathways of carbon dioxide fixation by various plant clades during photosynthesis, with C_3 plants (which exhibit δ^{13}C values ranging from −31 to - 20 ‰) having lower values than C_4 plants (with δ^{13}C values from −16 to −12 ‰). The latter outcompete the former under conditions of lower atmospheric concentration of CO_2, and in warmer and drier conditions as they are able to photosynthesize without significant water loss (O’Leary, 1981, 1988; Farquhar et al., 1989).

The vegetation composition of the expanse surrounding Karin Tak Cave represents a mix of C_3 grasses, shrubs and trees along with C_4 grasses. Karin Tak is located close to the boundary between a semiarid subtropical climate characterised by steppe, and a region with a thermo-moderate humid climate that supports broad-leaved forest. The general pattern of present vegetation surrounding the cave is of hornbeam (*Carpinus caucasica*) and oak (*Quercus iberica*) woodland. At higher elevations (towards the cave entrance) the tree cover also includes ash (*Fraxinus excelsior*), maple (*Acer campestre*), juniper (*Juniperus* sp.) and plum (*Prunus* spp.). At lower elevations, towards river valley, the floral

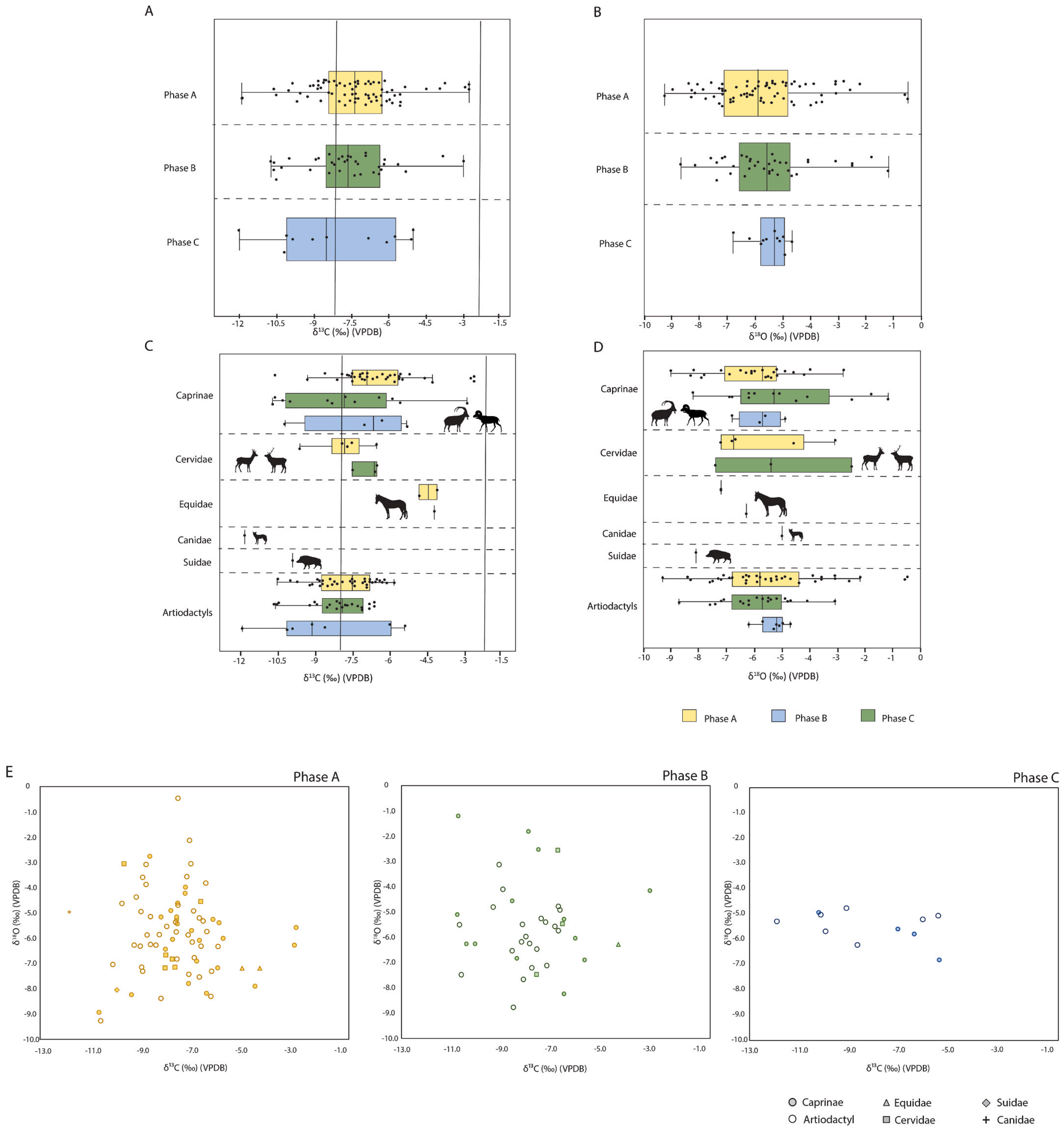

Fig. 9. Stable isotope measurements from dental enamel of different fauna from Karin Tak. A. δ^{13}C measurements of all taxa in different phases; B. δ^{18}O measurements of all taxa in different phases; C. δ^{13}C measurements of different groups of taxa in different phases; D. δ^{18}O measurements of different groups of taxa in different phases. E. Bivariate plots showing δ^{13}C and δ^{18}O data from different phases of Karin Tak. Boxplots show median and interquartile range, as well as data points including outliers. All data presented in detail in Table S17. Browsers usually have δ^{13}C values lower than −8‰ and grazers have δ^{13}C values higher than −2‰ (both indicated by vertical lines in Fig. 9A and C) and mixed feeders have δ^{13}C values falling in between (see: Cerling and Harris, 1999; Lee-Thorp et al., 2010). [colour used in print; double column fitting image].

biome changes towards a more open steppe environment, mostly dominated by C_3 shrubs (i.e. *Rubus* sp., *Rosa* sp.) together with C3 (i.e. *Stipa* sp.) and C_4 grasses (i.e. *Bothriochloa* sp.).

In this environment, pure C_3 consuming taxa (browsers or grazers) from the pre-industrial period (i.e. prior to significant amounts of fossil fuel burning and changes to the δ13C of the atmosphere; Keeling, 1979) are expected to have enamel $\delta^{13}C$ values lower than −10‰ for fossil ungulates, whereas pure C_4 grazers display enamel $\delta^{13}C$ values of higher than −2‰ (Cerling and Harris, 1999; Lee-Thorp et al., 2010). Intermediate $\delta^{13}C$ values are representative of C_3/C_4 mixed feeders.

Stable oxygen isotope ($\delta^{18}O$) values in tooth enamel, on the other hand, reflect the animal's diet, physiology and drinking behaviour often correlated with precipitation. The $\delta^{18}O$ values from animals that are obligate drinkers have been shown to closely reflect the $\delta^{18}O$ values of the water they imbibe, which is often strongly associated with the precipitation values. By contrast, the $\delta^{18}O$ values of non-obligate drinkers (i.e. animals that obtain water from the plants they consume) are generally higher as a result of higher $\delta^{18}O$ values in leaves brought about by environmental factors influencing transpiration (Kohn, 1996; Pederzani and Britton, 2019).

Of the 78 specimens analyzed from Phase A, 32% (n = 25) have $\delta^{13}C$ values that indicate a dominance of C_3 foods in the diet while the rest had values representative of more mixed C_3/C_4 feeding signatures (i.e. between −8.0‰ and −2.0‰) (Fig. 9). Caprines, with sheep being grazers and goats being mixed feeders, displayed a $\delta^{13}C$ range of −10.6 to −2.6‰ (n = 25, mean = −6.8‰), while cervids (red deer mixed feeder, roe deer browser) had $\delta^{13}C$ values ranging between −9.6 and −6.5‰ (n = 6, mean = −7.9‰). The two equid specimens (grazers) from Phase A returned $\delta^{13}C$ values of −4.8 to −4.1‰ and the suid (mixed feeder) and canid specimens had $\delta^{13}C$ values of −9.9‰ and −11.8‰, respectively. The unclassified 'artiodactyls' group (which included caprines, cervids and possibly bovines) had a range of −10.5 to −5.8‰ $\delta^{13}C$ (n = 43, mean = −7.6‰). In Phase B, 42% (n = 16) of the specimens had $\delta^{13}C$ values lower than −8‰ and the rest (n = 22) had values less than −2‰. Caprines had a range of −10.7 to −2.9‰ $\delta^{13}C$ (n = 13, mean = −7.8‰), cervids between −7.5 and −6.5‰ $\delta^{13}C$ (n = 3, mean = −6.9‰) and the unclassified artiodactyls had a range of −10.6 to −6.6‰ $\delta^{13}C$ (n = 21, mean = −8.0‰). The single equid specimen from Phase B returned a $\delta^{13}C$ value of −4.2‰. Lastly, in Phase C, 6 of the 11 specimens had $\delta^{13}C$ values indicative of predominance of C_3 biomass in the diets of studied ungulates. Caprines had an average $\delta^{13}C$ value of −7.2‰ (−10.2 to −5.3‰, n = 4) and the unclassified 'artiodactyls' group had an average $\delta^{13}C$ value −8.7‰ (−11.9 to −5.4‰, n = 7).

In terms of $\delta^{18}O$ values, the caprines from Phase A had an average value of −5.9‰ (−9.0 to −2.8‰, n = 25), while those from Phases B and C had average $\delta^{18}O$ values of −5.0‰ (−8.2 to −1.2‰, n = 13) and −5.8‰ (−6.8 to −4.9‰, n = 4), respectively. By comparison, the cervids from Phase A had a $\delta^{18}O$ range of −7.2 to −3.1‰ (n = 6, mean = −5.9‰) and those from Phase B had values between −7.4 and −2.5‰ (n = 3, mean = −5.1‰). Both equid samples from Phase A returned a $\delta^{18}O$ value of −7.2‰ and the equid specimen from Phase B had a $\delta^{18}O$ of −6.3‰. Excluding two outliers with $\delta^{18}O$ values of −0.6 and −0.5‰, the specimens of the artiodactyls group from Phase A have an average $\delta^{18}O$ of −5.7‰ (−9.3 to −2.2‰, n = 41). Meanwhile, the artiodactyls from Phase B and Phase C showed average $\delta^{18}O$ values of −5.9‰ (−8.7 to −3.1‰, n = 21) and −5.3 ‰ (−6.2 to −4.7‰, n = 7), respectively.

A Shapiro-Wilk test for normality indicates that the $\delta^{13}C$ ($p = <0.05$) of the dataset, when grouped according to phases, follows a normal distribution. An ANOVA test shows that considering all taxa, there is no significant difference in $\delta^{13}C$ values between the different phases of Karin Tak (F(126) = 1.03, $p < 0.05$; Fig. 9). The same is shown by the ANOVA test for the $\delta^{18}O$ values (F(126) = 0.76, $p < 0.05$). Comparisons of the $\delta^{13}C$ and $\delta^{18}O$ between the different phases, considering specific taxonomic groups, show similar patterns. ANOVA tests show no significant difference in the $\delta^{13}C$ (F(48) = 1.77, $p < 0.05$) and $\delta^{18}O$ (F(41) = 1.61, $p < 0.05$) values for caprines between the different phases. Similarly, T-tests for cervids from Phase A and B showed no significant difference in the $\delta^{13}C$ (df = 7, t = 1.55, $p > 0.05$) and $\delta^{18}O$ (df = 7, t = 0.79, $p > 0.05$) values. Likewise, ANOVA tests showed no significant difference in the $\delta^{13}C$ (F(70) = 1.69, $p < 0.05$) and $\delta^{18}O$ (F(70) = 0.56, $p < 0.05$) values of the unclassified artiodactyls group between Phases A, B and C.

Finally, there is no significant difference in the $\delta^{13}C$ (F(121) = 1.43, $p < 0.05$) and $\delta^{18}O$ 62(F(121) = 0.16, $p < 0.05$) values between the different phases of Karin Tak when all small artiodactyls (i.e. the caprines, cervids and unclassified artiodactyls) are grouped together. The only significant difference is observed in the $\delta^{13}C$ values when samples from different phases are grouped together according to taxon (F(122) = 6.362, $p < 0.05$). Tukey's pairwise comparison suggests that the $\delta^{13}C$ values for equids are significantly different from those of caprines, cervids and small artiodactyls, with the boxplot (Fig. 9) indicating higher $\delta^{13}C$ values.

5. Discussion

The late MIS 3 to early MIS 2 transitional period witnessed two major events in human history: the disappearance of the Neanderthals and the arrival and rapid dispersal of AMHs into Eurasia. These expansion and biological replacement/incorporation events were accompanied and followed by climatic fluctuations associated with the onset of the last glaciation, often suggested to be an influential factor in the apparent ecological downturn of the Neanderthals (e.g. Staubwasser et al., 2018; Wolf et al., 2018). Keeping in mind that the climatic fluctuations and human population dynamics followed a regionally-diverse pattern, rather than a uniform pan-continental one, it is important to focus on microscale studies within specific regions. This is also the case when exploring how AMH populations adapted to the varying impacts of the Last Glacial Maximum in different regions. The scarcity of suitable environmental archives within the Caucasus seriously hampers the evaluation of how Late Pleistocene climates were expressed locally and the significance of the climate for cultural transitions and population movements in the region. In this study we have sought to address this limitation and provide a palaeoenvironmental and palaeoecological background for the Late Pleistocene in the southeastern Lesser Caucasus via multiproxy analysis of a palaeontological fossil record, which includes some archaeological presence, in Karin Tak Cave.

Our revised ^{14}C chronology at the site reveals the 24,000-year-long accumulation history of fossil material stretching from ca. 24–48 cal ka BP. Based on differences of sediment infill and obtained dates, three sedimentary phases were identified for the site (Phases A, B and C) spanning throughout late MIS 3 to early MIS 2 stages. These phases were taken as a basis for organising and conducting all the subsequent counts and analyses, thus minimising the effect of stratigraphic disturbances (potentially visible in some chronological inversions). Phase A reflects the MIS 2 stage at the site, spanning between ca. 24–30 cal ka BP and preserves records of short-term human occupation. Phase B, dated between ca. 32–48 cal ka BP represents MIS 3 at the site. Phase C represents the undated layers of the site (presumably >48,000 BP). This means that the site provides an important record of faunal accumulation, which extends from the earliest appearance of AMHs in the region, through the growing impacts of the Last Glacial Maximum around 24,000 years ago.

5.1. Fossil accumulation and faunal spectrum

We studied the fossil assemblage of Karin Tak using a combination of traditional zooarchaeological and novel biomolecular techniques, such as collagen fingerprinting, stable isotope analysis and bulk bone metabarcoding (BBM; published previously: Antonosyan et al., 2019). This multidisciplinary study is the first of its kind in the region. A significant number of bones from medium to large sized mammals and birds (ca. 15, 000 fragments), as well as abundant micromammal bones (ca. 1200 specimens), were recovered during excavations. The animal bones were uniformly distributed within the sediments and present in all stratigraphic levels. Although some of the bones recovered are well preserved, with complete skeletal elements with minimal to no breakage, a significant bulk of the faunal assemblage from Karin Tak consists of small fragments (0.5–5 cm) with extensive fracturing and including isolated vertebrate teeth and postcranial bones.

We were able to reconstruct the accumulation history of the fossil assemblage based on thorough taphonomic analysis of the material. The taphonomic signatures observed in the bone fragments suggest that the accumulation of faunal remains resulted from multiple processes. Evidence of human activity is sparse and limited to fragments of human bones and a small number of stone artefacts deposited during Phase A. Carnivores, possibly bear or wolf, clearly played a role in accumulation as evidenced by the moderate amount of carnivore damage including tooth marks and punctures, as well as acid digestion. The presence of fragments with pointed/irregular and jagged edges usually produced during chewing by carnivores further supports this suggestion. Diagenesis and sediment transport also contributed to the accumulation of the assemblage, albeit sediment abrasion of bone surfaces was rarely observed. The majority of the bone fragments analyzed exhibited smooth, transverse breaks that typically occur in fossilised bones during diagenesis, or resulting from sediment pressure. The limited extent of human impact on the accumulation of animal bones allows us to suggest that the cave reflects the faunal diversity at a time devoid of human-driven selection of prey taxa. This underscores the significance of the site as a valuable archive of ancient environmental conditions, free from bias in terms of human behaviour selectively favouring certain prey taxa.

Considering the fragmentary nature of the assemblage, zooarchaeological screening proved to be limited in most cases, especially in identification of closely related species that share almost identical postcranial morphological features (e.g. sheep, goat, gazelle). Novel molecular approaches, such as ancient DNA barcoding and ZooMS, address this limitation by allowing the retrieval of taxonomic information from highly fragmented bones. However, while these molecular techniques provide a higher resolution of taxonomic identification, they have limitations which prevent them being simply integrated in zooarchaeological counts (Murray et al., 2013; Silvestrini et al., 2022; Sinet-Mathiot et al., 2019). This illustrates that the best results are attained when combining traditional and novel methods of taxonomic identification (Fig. 10).

As anticipated, our ZooMS and BBM results noticeably increased species diversity when considered alongside the morphological results and contribute to increasing the number of identified species, while being consistent with the data obtained from the morphological analyses. Mammals are the richest and most diverse group in the record, whereas birds are less common. This can be explained by sampling bias

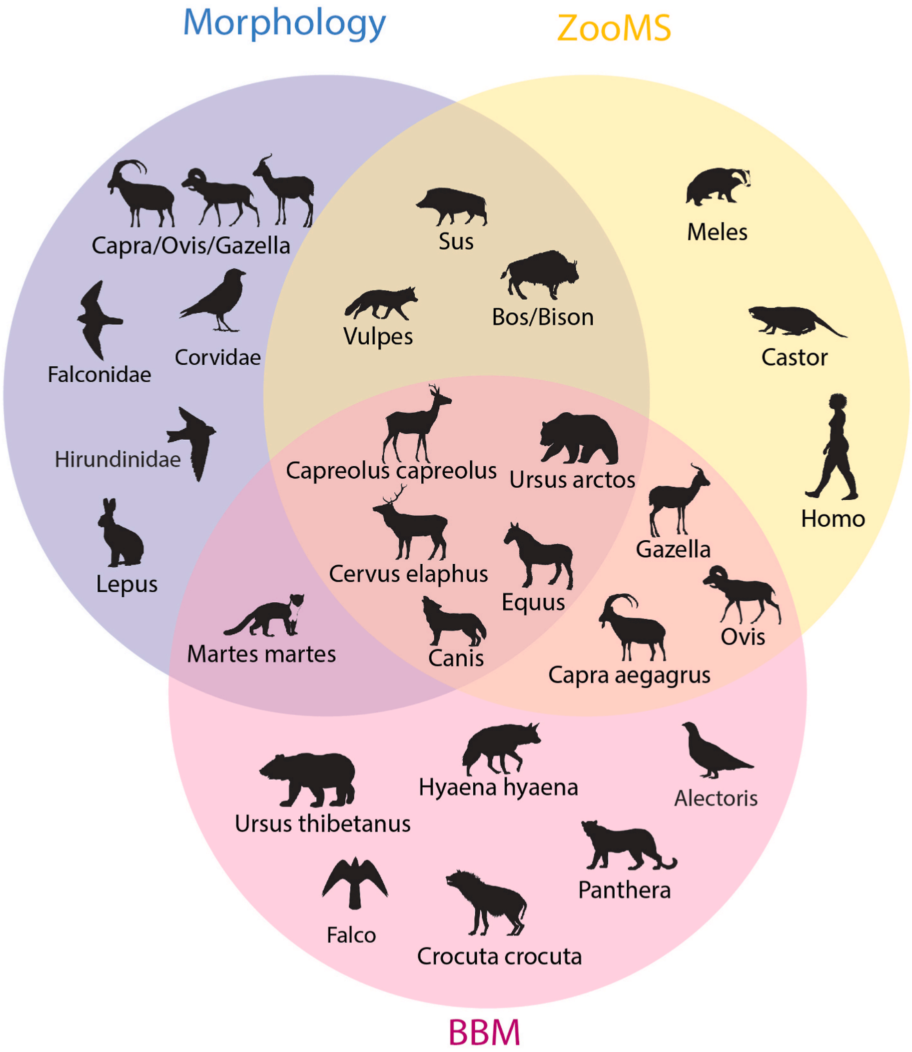

Fig. 10. Intermediate to large mammalian and avian composition of Karin Tak recovered by the three methods of taxonomic identification [colour used in print; single column fitting image].

as well as by differential preservation (fragile and hollow bird bones being less common). The recovered mammalian taxonomic composition is diverse and comprises predominantly extant wild species together with regionally extinct ones. In addition, the molecular approaches allowed us to identify several mammals that have not been previously described from the Late Pleistocene sites of the region (badger, spotted hyena, goitered gazelle and Asiatic black bear), along with human remains, most probably carried into the interior of the cave by carnivores.

Ungulates are the most commonly identified taxa throughout the record, with caprines, indicative of dry, open environments, dominating the assemblage. While in the case of morphological identification, a deeper taxonomic resolution within the subfamily was largely not possible, the integration of ZooMS allowed for successful differentiation between sheep and goat, with goat dominating the record. *Bos* sp./*Bison* sp., two taxa with very different ecological preferences, are the second most abundant group in the ZooMS-IDed portion of the assemblage, in contrast to morphological identification, which can be explained by higher numbers of fragments, related to big body size, inflating the NISP. It is worth noting that both *Bos* and *Bison* have been recorded in other Late Pleistocene regional sites, being identified as *Bos primigenius*, *Bison priscus* and *Bison bonasus* (Bar-Oz and Adler, 2005; Bar-Oz et al., 2008; Yeshurun et al., 2014). The other ungulate taxa identified are *Capreolus* and *Cervus*, genetically assigned to species level as *C. capreolus* and *C. elaphus*, known to be distributed in forested zones and shrublands.

The assemblage also includes gazelles that have been assigned to *G. subgutturosa* by BBM. The goitered gazelle is associated with a semi-arid steppe environment and mostly occurs in foothills and mountain valleys. It is extirpated from the southeastern Lesser Caucasus and appears only throughout Oman, across the Arabian Peninsula and into Southern Turkey, following the steppe of Central Asia into central Mongolia (Wacher et al., 2011). Although presumably hunted to extinction in the Near East by Neolithic hunter-gatherers, the species appears to have survived in Armenia until the Early Iron Age (Mirzoyan and Manaseryan, 2008). It is here worth mentioning that gazelles (bearing similar postcranial morphological features to caprines) were not found in any other Late Pleistocene archaeological sites of the region. This potentially highlights the importance and necessity of molecular screening of fossil bones that offers more precise taxonomic resolution, enabling identification between related species. Other ungulates such as *Sus* sp. and *Equus* sp. are less common. *Equus* sp. suggests the presence of an open plain close to the site, while *Sus* sp. is believed to occupy forests, with isotope values supporting the *Sus* environment in C_3 biome.

The carnivore assemblage is mostly represented by bear, wolf and fox, all being ecologically plastic species, which can inhabit a great variety of habitats (dry Asian steppes, Arctic shrublands and temperate forests). At the end of the LGM, brown bear is believed to have recolonized the glacial landscape of Central and Northern Europe faster than all other carnivorous mammal species, from Iberia and an eastern refuge (i.e., east of the Balkans; Sommer and Benecke, 2005). The genetically recovered carnivore composition includes *Panthera* sp. (*Panthera pardus* being critically endangered in Armenia); together with regionally extinct spotted hyena (*Crocuta crocuta*) and Asiatic black bear (*U. tibethanus*). These mammalian species have not been identified in any other Late Pleistocene sites of the region; although, they were recovered in Middle Pleistocene layers of nearby Azokh Cave (Van der Made et al., 2016). Thus, their identification at Karin Tak marks their last occurrence. Spotted hyena, typical for dry open habitats, was one of the first megafaunal carnivores to go extinct during the Last Glacial in Eurasia, with the latest record dated to about 30 ka BP (Stuart and Lister, 2014). They appear to have survived in the Lesser Caucasus region at Karin Tak Cave until at least ca. 34–33 cal ka BP. Similarly, following the last interglacial, the range of the Asiatic black bear, mostly associated with forested habitats, was significantly reduced. It disappeared from Europe, the Caucasus and northern Asia (Kosintsev et al., 2016), but clearly survived in the Karin Tak region until ca. 34–33 cal ka BP.

The assemblage includes rare occurrences of small mammals: *Martes martes* (species identified genetically) and *Meles* sp. that inhabit deciduous, mixed, and coniferous woodlands, as well as *Lepus* sp., indicative of a dry environment. The rodents found at the site were mainly identified using molecular techniques (with the morphological study in progress): *Arvicola amphibius*, commonly inhabiting territories around rivers and streams along with regionally extinct *Mesocricetus raddei*, associated with shrublands/open grassland (Antonosyan et al., 2019) and *Castor* sp. typical of wetlands and forests. Genetic screening also allowed for identification of bats: *Plecotus macrobullaris* (mountain long-eared bat) typical to oak shrub, as well as beech and pine forests, together with *Rhinolophus* sp. and *Myotis* sp., groups that include diverse populations inhabiting a variety of habitats. The recovered small assemblage of birds includes phasianids, falcons and passerines which are widely distributed through the region today. The birds were mostly identified to family level, with only two cases of more precise identification via DNA metabarcoding performed to genus level (*Falco* sp. and *Alectoris* sp.).

Overall, the identified fauna offers detailed insights into the MIS 3 to MIS 2 transition and onset of the LGM in the Lesser Caucasus. The majority of identified mammal species adapted to temperate environments (mixed woodlands or open mixed woodlands), such as red deer, roe deer, wild boar, beaver, or brown bear, are believed to be restricted to glacial refugia in southern European regions and to have recolonized Central and Northern European regions after the LGM (Sommer and Nadachowski, 2006; Sommer and Zachos, 2009). When the animal assemblage is considered in a diachronic perspective, no remarkable difference is observed through time in terms of faunal composition or habitat preference (Fig. S7). The reconstructed MIS 3 assemblage is rich with arid-adapted ungulates (e.g. *Capra*, *Ovis*, *Equus*) and their predators (wolves and hyenas), together with forest inhabitants, such as deer and bear. At the same time, the early MIS 2 collection comprises a similar set of both arid and humid-environment occupants. It includes species typical of forested zones (beaver, pine marten, badger) and open, dry landscapes (gazelle, hyena, Ciscaucasian hamster). In all the phases of Karin Tak the proportions of forest-adapted and arid-associated taxa are roughly equal, pointing to continuity of the same biota from late MIS 3 to early MIS 2, with species distinctive of broadleaved forest and arid steppe environments. This environmental pattern persists to the present day, with the cave currently surrounded by a thick forest on the mountain slopes and a steppe located in the lowland.

5.2. The Karin Taks fauna in a regional context

The assemblage of Karin Tak is supplemented by regional contemporaneous sites of Ortvale Klde (Bar-Oz and Adler, 2005), Satsurblia (Pinhasi et al., 2014) and Dzudzuana (Bar-Yosef et al., 2011) in Georgia; and Hovk-1 (Pinhasi et al., 2011), Kalavan-2 (Ghukasyan et al., 2010; Malinsky-Buller et al., 2021) and Aghitu-3 (Kandel et al., 2017) in Armenia. The faunal composition found at these sites mainly results from the hunting activities of human groups providing snapshots of past biodiversity concerning the prey choices of prehistoric inhabitants. Karin Tak can provide a useful counterpoint here given that we suggest it is a primarily natural accumulation of animal bones by carnivores. Comparison with the faunal assemblages of regional Late Pleistocene sites reveals many mammalian species similar to the ones identified in Karin Tak. The cave deposits at Aghitu-3 have yielded both arid-zone (*Ovis, Capra, Equus, Bos/Bison*) and forest-associated (*C. elaphus, S. scrofa*) mammals from the 39-24,000 cal BP horizons. The same pattern is registered in the Kalavan-2 assemblage (59-36,000 BP) consisting mainly of *Bos/Bison, Equus, Capra/Ovis* and *Cervus*. Similarly, the largely non-anthropogenic faunal assemblage of Hovk-1 Unit 4 (35,000 cal BP) is dominated by forest taxa (*C. elaphus, C. capreolus, M. meles,* and *M. foina*) with few arid area representatives (*C. aegagrus* and *Lepus europaeus*). Likewise, the faunal assemblages of Georgian sites Dzudzuana (Unit D: 35-32,000 cal BP and Unit C: 27-24,000 cal BP), Satsurbia (Layers B/III and B/II: 26-24,000 cal BP) and Ortvale Klde (Layer 4: 40-26,000 cal BP, Layer 3: 26-22,000 cal BP) are often dominated by open-landscape taxa (*Capra, Ovis, Equus, and Bos/Bison*) together with forest associated ones, such as *U. arctos, C. elaphus,* and *C. capreolus*.

These studies, together with our results, demonstrate that Upper Palaeolithic hunters targeted both forest-dwelling and open landscape ungulates. The disparity in the taxonomic composition is probably due to different seasons of human occupation. The recovered animal diversity also indicates general continuity in the composition of fauna in the region throughout the Late Pleistocene. Most of the species persisted through the whole stretch of the Last Glaciation, with the exception of regionally extinct taxa. On the regional level, the large mammals in the assemblage include six extinct taxa, from which three (G. *subgutturosa, C. crocuta,* and *U. thibetanus*) were identified in Karin Tak, using a genetic approach. Another extinct species is *B. priscus* that was once widely distributed in Asia and across the exposed Bering Isthmus, surviving until about 5000 years ago in Alaska (Zazula et al., 2017). In the Caucasus, this species was last recorded in Dzudzuana Cave in 27-24,000 cal BP layers. The aurochs (*B. primigenius*) is currently extinct with the last representatives surviving until the 1st century BC (Kitchell, 2014). In the Caucasus, the last reports of the species come from Dzudzuana Cave in layers dated to 16-13,000 cal BP. The LGM layers of Bondi Cave contain remains of European bison (*B. bonasus*) that became extinct in much of Eurasia during the Middle Ages, persisting only in northern Europe and Northern Caucasus, where in the 20th century, it was hunted to extinction in the wild.

It is unclear whether human activity, climate change or a combination of the two caused this reduction in biodiversity. However, most of these species persisted until the onset of the LGM. They were last registered in archaeological horizons of the terminal LGM, suggesting that itsonset did not cause the demise of these animals in the region. Considering that large mammals occur in a relatively wide range of environments (allotropic species), it is worth focusing on micromammals that have narrow ecological tolerance limits. These can act as bioindicators for environmental changes, which allows fine-scale reconstructing of local ecology. Dzudzuana, Satsurblia, Aghitu-3, Hovk-1, Kalavan-2 and Karin Tak are the only sites in the region that have yielded micromammal assemblages with secure dating to allow robust palaeoecological analysis. A smaller assemblage of micromammals is available from Bondi Cave; although, the temporal distribution of these taxa is missing, and for that reason these data are not discussed here.

The aggregated assemblage of the micromammalian species from the Late Pleistocene sites of the region shows a congruence in the taxonomic structure of the fauna of the Eastern Mediterranean area and Asia Minor. The occurrence of *Cricetus cricetus, Dryomys nitedula, Sciurus anomalus, Microtus arvalis, Clethrionomys glareolus, Sorex satunini,* and *Plecotus macrobullaris* points to the presence of moist forest and shrubland areas. On the other hand, *Cricetulus migratorius, Mesocricetus raddei, Mesocricetus brandti, Ellobius lutescens,* and *Spalax nehringi* are indicative of grasslands, steppe and semi-deserts. At the same time, *Arvicola amphibious* and *Arvicola terrestris* point to the presence of wetland areas. This reflects the mosaic nature of habitat structure and supports continuity of the same biota from MIS 3 to early MIS 2, with species distinctive to the broadleaved forest and arid steppe environments.

The pockets of relatively stable warm climate are also distinguished by the presence of Colchis and Hyrcanian forests, which represent refugia for the Tertiary relict plants and animals (Akhani et al., 2010; Denk et al., 2001; Nakhutsrishvili et al., 2015). Additionally, the patches of mesophilic Cenozoic plants are currently sporadically dispersed between the Black and Caspian Seas (Mulkidjanyan, 1967), indicating the presence of spatially confined multiple refugia, where species survived the cold and aridity of the glacial period. A number of molecular studies and distribution analysis on Caucasian plants and animals (Tarkhnishvili et al., 2000, 2001, 2008, 2012; Murtskhvaladze et al., 2010; Orth et al., 2002; Perktaş et al., 2015; Pokryszko et al., 2011; Seddon et al., 2002) support the presence of multiple glacial forest refuges in the region.

5.3. Palaeoenvironmental reconstructions

Various proxies for palaeoclimate and palaeovegetation reconstruction have been applied to Late Pleistocene contexts in the region. These include exploration of soil archives (e.g. Malinsky-Buller et al., 2021; Ollivier et al., 2010; von Suchodoletz et al., 2016) and loess sequences (e.g. Richter et al., 2020; Trigui et al., 2019; Wolf et al., 2016, 2022), coupled with biochemical, palynological, and micromammal records of individual archaeological sites. Together, these proxies provide some insights into palaeoenvironmental conditions during the Late Pleistocene.

Regional MIS3 (57–29 ka BP) records suggest millennial-scale fluctuations in environmental conditions, with a highly fragmented mosaic of environments, including steppe, open grasslands, forests, and meadows (Belmaker et al., 2016; Kvavadze et al., 2012; Malinsky-Buller et al., 2021; Pleurdeau et al., 2016). A recent study of gastropod deposits linked to the last glacial period indicates that ecosystems during glacial periods experienced greater drought stress than cold stress (Richter et al., 2020). Pollen analysis combined with leaf wax analysis at the Kalavan-2 site points to grassy landscapes or a mix of deciduous and grassy environments between 60 and 45 ka BP and an open landscape between 51 and 36 ka BP, with low abundances of tree pollen (Malinsky-Buller et al., 2021). Sedimentological and biomarker data from Barozh-12 reflects increased aridity from 65 to 45 ka BP, followed by a relatively humid climate between 33 and 28 ka BP (Glauberman et al., 2020b). Recent analysis of sedimentary ancient DNA at Aghitu-3 combined with available environmental records from the site suggest that conditions were warm and humid from ca. 39–32 cal ka BP, while the climate was cooler and more humid than from ca. 32–30 cal ka BP. Further cooling was seen between ca. 30–29 cal ka BP, with a cold and dry period from ca. 29–26 cal ka BP, followed by relatively warmer conditions during ca. 26–24 cal ka BP (Kandel et al., 2017; ter Schure et al., 2022).

Our stable isotope data from MIS 3 levels adds to this picture with $\delta^{13}C$ values indicative of mixed forest/open environment foraging. In particular, caprines display a wide range of $\delta^{13}C$ values spanning between −10.7 and −2.9‰, while the values of cervids have a relatively narrow range (−7.5 to −6.5‰), with a slight tendency towards a C_3 dominated diet. The latter suggests the presence of forest, based on the habitat preference of deer. The unclassified artiodactyl group had values indicating a focus on C_3 biomass with $\delta^{13}C$ values ranging between −10.6 and −6.6‰. The single equid specimen has a $\delta^{13}C$ value of −4.2‰ suggesting a minor shift towards a drier and more open landscape, reflecting the animal's ecology, inhabiting grasslands environments. As with $\delta^{13}C$ the caprines also show a relatively high variability in $\delta^{18}O$ values. Conversely, cervids displayed a narrower range of $\delta^{18}O$ values. Being non-obligate (or at least semi-obligate) drinkers, caprines and cervids are reliant on water from the vegetation they consume, from shrubs to grasses, and the $\delta^{18}O$ values are therefore likely to be more indicative of the specific environmental conditions (e.g. more intense transpiration as a result of aridity) where these plants grow rather than the general precipitation patterns in the region.

Knowledge about the paleoenvironment of the region during MIS 2 (29–14 ka BP), which coincides with the LGM, remains limited. Currently available data come from a handful of palaeobotanical studies that suggest a cooler, but still moist, climate, with the presence of deciduous forest and steppe environments (Kandel et al., 2017; Pleurdeau et al., 2016). The pollen spectra of Unit C at Dzudzuana Cave, dated to 27–24 cal ka BP, indicate warm and wet conditions (even more than in Unit D dated to 34.5–32.2 cal ka BP) (Bar-Yosef et al., 2011). At the same time, sediment records from the Black Sea do not appear to indicate a clear temperature reduction during MIS 2, at least until about 20 ka BP (Wegwerth et al., 2015). Moreover, steadily increasing arboreal vegetation and strongly-reduced xerophytic vegetation along the southeastern shores of the Black Sea indicate higher humidity during the LGM compared to MIS 3. This strongly contrasts with palaeoenvironmental proxy data from more continental Central and Eastern Europe and the western and northern shores of the Black Sea (Shumilovskikh et al., 2014). Recently-studied loess deposits in Armenia show a lack of several MIS 2 Greenland Stadial and Heinrich events, raising the question of whether Last Glacial North Atlantic climate dynamics correspond to climatic and environmental changes in the Caucasus (Wolf et al., 2022).

These estimates align well with our $\delta^{13}C$ values of specimens from MIS 2 layers, which display the presence of C_3 and mixed C_3/C_4 environment, with the majority (70%) of the assemblage feeding on a mixture of C_3/C_4 plants. In detail, caprines and unclassified artiodactyls have a wider range of $\delta^{13}C$ values (−10.5 to −2.6‰), overlapping with a slightly narrower range of cervid values (between −9.6 and −6.5‰) and suggestive of a higher proportion of C_3 biomass in their diets. In contrast, equid specimens exhibited more open/grassland C_4 signature (−4.8 to −4.1‰). Single suid and canid specimens had values indicative of C_3 dominated diets (−9.9‰ and −11.8‰ respectively). Like the $\delta^{18}O$ data for samples from MIS 3, the oxygen isotopes values we obtained for specimens from MIS 2 corresponds to the $\delta^{13}C$ values, with caprines having a wider range of $\delta^{18}O$ values which is indicative of the wide range of environments where non-obligate (or semi-obligate) drinkers foraged.

Our statistical tests suggest no significant difference between the $\delta^{18}O$ values of specimens in MIS 2 and MIS 3 layers. But whether this indicates consistency in the precipitation patterns between late MIS 3 and early MIS 2 in the region remains to be fully elucidated perhaps using another proxy (i.e. $\delta^{18}O$ from speleothem). We interpret the $\delta^{18}O$ values we obtained as indicative of stability in vegetation cover in alignment with the $\delta^{13}C$ data. The isotope data highlights the persistence of a mosaic mixture of forest, woodland, shrubland, and grassland between late MIS 3 and early MIS 2 in the vicinity of the site.

Overall, the palaeoenvironmental assessments discussed above, coupled with the isotope data in this study, highlight the presence of regionally diverse microclimates within a wider mosaic of arid subtropical and humid climatic regions (with the latter supporting forests) throughout the Late Pleistocene. These results suggest that glacial and interglacial cycles and correlation between climatic fluctuations and human dispersals observed elsewhere do not necessarily apply to the Caucasus. The peculiarities of the mosaic of small ecozones in the Caucasus emphasises the importance of defining the local palaeoenvironmental setting in relation to human settlement and population patterns. Further studies of chronologically controlled palaeoenvironmental records focusing on climatic structure, biodiversity composition and human-environmental interactions are needed to determine whether, and to what degree, climate played a role on human population dynamics in the Lesser Caucasus.

6. Conclusion

Our multiproxy analysis of a 24,000-year-long fossil record contributes to our understanding of past biodiversity and extinction processes and provides novel insights into environmental conditions in the southeastern Lesser Caucasus during the Late Pleistocene. Morphological identifications combined with collagen fingerprinting (ZooMS) reveal a rich faunal composition at the site reflecting continuity of the same biota from late MIS 3 to early MIS 2, with species distinctive of both broadleaved forest and arid steppe environments. The isotope data similarly highlight the persistence of a mosaic mixture of forest, woodland, shrubland, and grassland in the vicinity of the site. A lack of major changes in species diversity, along with evidence of persistent environmental conditions based on isotopic measurements, suggests that climatic fluctuations did not cause a significant environmental change in the Lesser Caucasus. Future studies focusing on regional palaeoenvironmental conditions and human-environmental interactions are required to gain a more comprehensive understanding of the climatic background of AMH population expansion and the demise of Neanderthals in the region.

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Author contributions

The work presented in this manuscript represents original research that has not been previously accepted or published elsewhere. All authors have made substantial contributions to this submission.

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Declaration of competing interest

The authors declare no conflict of interest.

Data availability

MALDI-TOF-MS spectra of identified samples can be found at https://zenodo.org/records/8377104 an open-source online data repository hosted at Zenodo.

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Appendix A. Supplementary data

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