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Initial Upper Paleolithic in the Zagros Mountains

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The Iranian Plateau and the Zagros Mountain chain, located at the crossroads of Africa and Eurasia, occupy a critical geographical position in out-of-Africa scenarios, sitting astride a major dispersal corridor into southern and central Asia. Yet, the region's role in human population expansions remains under-investigated. Here, we present findings from new excavations at Pebdeh Cave, a site located in the southern zone of the Zagros Mountains. Pebdeh contained a well-defined layer dating to ~42–40,000 years ago (ka), with Levallois elements alongside laminar reduction. This transitional feature in the Zagros was not dated and recorded before, and, given its similarity to Western and Central Asian industries with respect to chronology and technological features, we define it here as the Zagros Initial Upper Paleolithic (IUP). Although Late Middle Paleolithic and Early Upper Paleolithic technologies have been identified in the Zagros in the time period ranging between 50 and 40 ka, suggesting the presence of Neanderthals and modern humans in the mountainous region, the overall abrupt and constrained chronology of the IUP at Pebdeh, together with the penecontemporaneous appearance of other Upper Paleolithic sites in the Zagros Mountains, is compatible with a population expansion of *Homo sapiens* rather than an autochthonous development.

KEYWORDS

Zagros Paleolithic, modern humans, paleoecology, southern Zagros, Pebdeh Cave

1 Introduction

Despite the intense archaeological and paleoanthropological focus on studying the geographic expansion of *Homo sapiens* outside Africa during the Pleistocene, relatively little is known about the occupation history of humans across large parts of Asia. Current research suggests that the earliest dispersal of *H. sapiens* into Eurasia occurred between ~210 and 170 ka (Hershkovitz et al., 2018; Harvati et al., 2019), followed by multiple, later expansions (Groucutt et al., 2015) that involved interactions with resident archaic human populations (Hajdinjak et al., 2021). Growing evidence indicates that *H. sapiens* was widespread across Eurasia by ~40 ka (Shea, 2013; Hublin, 2015; Bae et al., 2017; Hublin et al., 2020), equipped with advanced forms of lithic technology and symbolic items (Kuhn, 2019; Kadowaki et al., 2021).

The modern country of Iran sits at the crossroads between Southwestern Asia, the Arabian Peninsula, and Central Asia, suggesting that the region would have played a key role in the territorial expansion of *H. sapiens* populations into Asia (Vahdati Nasab et al., 2013; Shoae et al., 2021). Demarcated by the Iranian Central Plateau, the Zagros Mountain chain, and the Alborz Mountains, the region experienced considerable Late Pleistocene environmental fluctuations (Shoae et al., 2023) that undoubtedly shaped human population expansions, connections, and demographic structure across the broader continent (Heydari-Guran et al., 2020). The Zagros Mountains have played a key role in archaeological and paleoanthropological research since the 1950s. However, most fieldwork has focused on the west-central Zagros region, owing to the presence of Neanderthal fossils and Middle Paleolithic (MP) and Upper Paleolithic (UP) assemblages.

There is an ongoing debate as to whether early UP assemblages evolved from the local Mousterian or whether they represent a population expansion related to *H. sapiens* movement across the region (Olszewski et al., 2006; Otte, 2014; Reynolds et al., 2018; Shidrang, 2018; Ghasidian et al., 2019; Shoae et al., 2021). Comprehensive lithic techno-typological analysis between UP sites in Zagros suggests an intrusive nature and regional variability for the Zagros UP lithic assemblages (Ghasidian, 2019; Ghasidian et al., 2019). The argument for a gradual regional development of the early UP from the MP is mainly based on evidence from the Warwasi rockshelter (Braidwood et al., 1961). Researchers have contended that the Warwasi lithic assemblages represented a local transition based on the existence of Mousterian elements in the early Zagros UP Baradostian layer, including truncated-facetted pieces, side scrapers, and small radial cores (Olszewski, 1993; Olszewski et al., 2006). Others have suggested that mid-layer assemblages at Warwasi may represent the IUP (Beshkani, 2018). However, evidence for a gradual transition from the late MP at Warwasi has not been widely accepted, given the imprecise excavation methods used in the early 1960s and the lack of stratigraphic sub-divisions with absolute ages (Tsanova, 2013; Reynolds et al., 2018; Shoae et al., 2021). Here, we summarize available dates from sites in the Zagros, examining the chronological picture of demographic and ecological events during the MP-to-UP transition in the region.

Indeed, the *in situ* development of the UP from the local Mousterian is not evidenced at dated sites that yielded both assemblages, such as at Shanidar (Solecki, 1964; Reynolds et al., 2018). Claims have been made that the Kaldar Cave assemblage

might represent this transitional phase, but due to a lack of clarity about the chronology and presentation of the lithic assemblages, this cannot yet be accepted (Bazgir et al., 2017). Currently, the only dated site with a continuous stratigraphy containing MP-to-UP transitional layers is Ghar-e Boof in southern and central Zagros (Conard et al., 2019), but owing to the low density of artifacts in the transitional layers, detailed assessments of the lithics cannot be made, other than noting the mixed characteristic artifacts from both the MP and the UP (Mata-González et al., 2023). Although dated MP sites in the Zagros are sparse, the early UP is better understood based on excavations at Shanidar, Yafteh, and Ghar-e Boof (Solecki, 1964; Conard et al., 2011; Otte et al., 2011). Late MP ecological conditions, coinciding with MIS 4, were shaped by a period of drastic climate shifts (Shoae et al., 2023), which may have been a factor in Neanderthal population extinctions or a factor driving Neanderthals to lower elevations, such as in the lower-lying southern Zagros zone (Heydari-Guran et al., 2023).

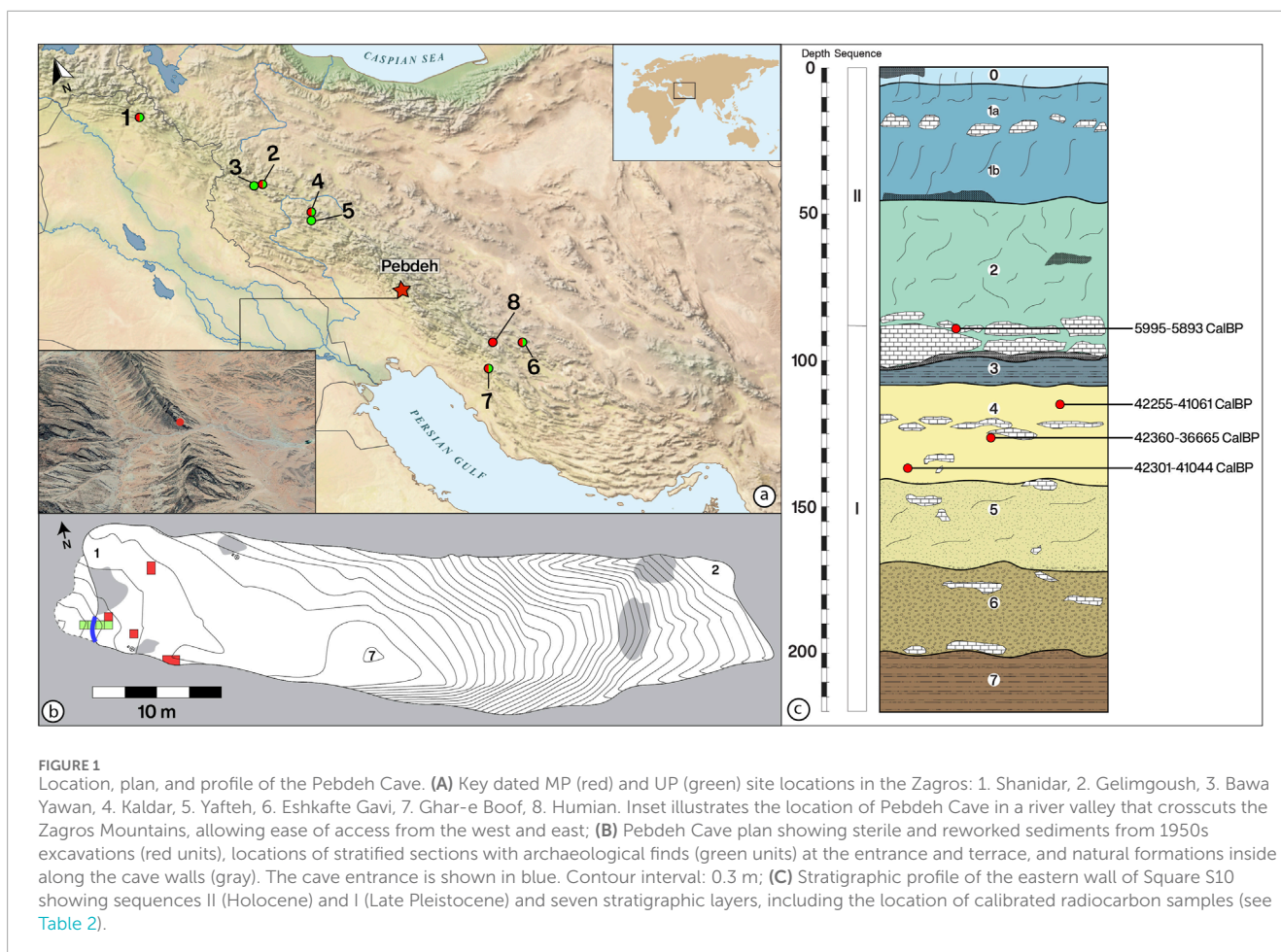
Researchers have contended that UP assemblages reflect the expansion of incoming populations of *H. sapiens* from an external source (Ghasidian et al., 2019; Shoae et al., 2021). Early UP assemblages have been variably referred to as the Baradostian, the Zagros Aurignacian, and the Rostamian (Solecki, 1964; Olszewski et al., 2006; Ghasidian et al., 2018; Shidrang, 2018), which the Rostamian itself is considered to be late Baradostian by other researchers (Shidrang, 2018). The diversity of early UP assemblages has been viewed as a product of adaptive variation and cultural diversification of *H. sapiens* populations throughout the Zagros Mountains (Mirazón Lahr, 2016; Ghasidian et al., 2019).

The crucial period of transition from the late MP to Early UP in the region is not understood thoroughly due to the lack of sites containing transitional features. Here, we report on new excavations and findings from Pebdeh Cave, situated in the southern flanks of the Zagros Mountains (Figure 1). Pebdeh fills a geographic hiatus between the better-known west-central Zagros sites and the handful of sites known in the south. We show that in the regional scope, Pebdeh reveals new data concerning the transition between the late MP and the Early UP in the Zagros Mountains, and in a broader perspective, we suggest that Pebdeh may affiliate with IUP assemblages from Western and Central Asia.

2 Pebdeh Cave

Pebdeh Cave is located in the Lali region of the southern Zagros Mountains at an altitude of 660 m above sea level. The cave is in a karstic system located along the southernmost flank of the mountain chain, where it merges into the lowland plains. The accessibility to both mountain and lowland resources likely made the location desirable to foraging populations (Figure 1A). Although Roman Ghirshman reported Pebdeh Cave in 1949, noting large-scale excavations in the cave interior (Ghirshman, 1949), the resulting artifact assemblages were never described, and they cannot be located despite extensive searches.

The Pebdeh Cave chamber measures 110 m × 40 m × 30 m, making it one of the largest known caves in the Lali region. Our excavations were conducted in 2019 and initially involved the placement of five test squares within and at the entrance of the cave to define the boundaries of the 1949 excavations. Backfilled



and sterile sediments were evident in all four test squares in our 2019 excavations, indicative of Ghirshman's original work in the cave interior. A test unit (S7) was consequently placed at the cave entrance, revealing *in situ* lithics and fauna in stratified contexts. Test unit S7 was subsequently extended as a 4 m × 1-m trench (S7–S10) extending from the cave entrance and onto the terrace. Here, excavations reached a maximum depth of 2.20 m, and, although bedrock was not reached, the artifact density fell off considerably after 1.4 m–1.7 m below the surface (Figure 1C).

The eastern wall of the trench profile showed two main sedimentological deposits separated by a layer of thick calcified sediments. We labeled these two main deposits as sequences I and II in the field and considered them to represent the Holocene (Sequence II) and the Late Pleistocene (Sequence I) (Figure 1C). The eastern wall profile was then sub-divided into seven distinctive litho-pedostratigraphic layers, Layers 1–7. The layers showed a gradual transition, horizontally extending along the entire length of the trench (Figure 1; Supplementary Table S1). Sequence II was characterized by higher sand and loam content with well-sorted particles, while Sequence I was mainly composed of silt, with less well-sorted particles (Table 1; Supplementary Table S1). Artifacts were recorded in Layers 2 to 7, although the main artifact horizons were Layers 3 and 4, yielding more than 90% of the lithic and fauna assemblages collectively.

Above the Pleistocene Layer 3 is a horizon of abundant calcareous clasts, probably contemporaneous with an episode of cryoturbation, representing an erosional surface. Other coarse-grained materials include bones, and millimetric and centimetric charcoal flecks adjacent to yellowish brown (10YR 4/4) zones with common redoximorphic features. A high organic content and frequent bioturbation (e.g., krotovina bores) were found at the top of Layer 3 (Table 1; Supplementary Table S1).

The sediments of Layer 4 are well-sorted, and the finer fraction is almost entirely comprised of loess-like silt or very fine sand with visible but weak stratification (Supplementary Figure S3). Anthropogenic sedimentation, consisting of the combustion of wood and bones and the accumulation of ash, was also responsible for the formation of the deposit. The formation of Layer 4 is indicative of a relatively dry and cold episode, owing to silty sediments, while Layer 3 was deposited in a more humid period due to the abundance of calcareous clasts and signs of cryoturbation. The skewness and sorting appear moderately correlated, with some outliers exhibiting higher than usual skewness, notably the thin gravelly bedding at the interface of Layers 3 and 4 (Table 1, Supplementary Text S1).

The generally distinct upper and lower boundaries of Layer 4 reinforce its integrity as a discrete sedimentary unit. The layer also contains an abundance of lithic artifacts and faunal remains,

TABLE 1 Sedimentological features of excavated layers at the Pebdeh Cave. Thickness, color, texture, and sedimentological characteristics of layers 2 to 7 (Supplementary Text S1).

Layer	Thickness (cm)	Color	Texture	Description
2	~40	Brown to dark brown	Clayey silt	Humic soil, characterized by the presence of an Fe/Mn segregation zone at its base, features interspersed charcoal fragments, and delicate organic layers measuring mere millimeters in thickness. The irregular lower boundary is delineated by a prominent layer of cobble-sized clast, predominantly composed of elongated subangular calcareous clasts
3	~22	Light brown to yellowish brown	Slightly clayey silt	Common bone fragments and charcoal pieces ranging from millimeters to centimeters in size are frequently observed adjacent to yellowish-brown Fe/Mn oxide concentration zones, particularly beneath the calcareous clasts. The layer also contains calcareous clasts predominantly concentrated near the surface. Evidence of bioturbation, such as krotovina bores, is present, mostly at the top. The upper boundary of Layer 3 displays significant irregularities along the trench wall, likely indicating a depositional hiatus
4	~35	Light brown	Slightly gravelly silt	This layer exhibits crudely stratified calcareous clasts primarily concentrated near the upper portion. The deposit contains thin organic lenses composed of dark organic substances blended with loam. Millimetric- and centimetric-sized charcoals are present. Bioturbation was not observed. The layer contained the highest number of archaeological finds, including lithics and faunal remains
5	~30	Light brown	Slightly gravelly silt	Within this layer, the coarse fraction comprises rounded detrital granules, coarse sands, and subangular calcareous clasts. The sediments predominantly consist of well-sorted silt with a light brown hue. Although the boundaries of this layer are laterally traceable throughout the trench wall, its upper limit displays irregularities. Bioturbation is visible at the border with the layer below
6	~30	Brown	Slightly sandy gravelly silt	This layer exhibits a porphyric structure composed of gravel interspersed within well-sorted fine silt. The coarse fraction displays poor sorting, with the sand/gravel ratio increasing toward the bottom. Notably, it contains prominently hydromorphic calcareous pebbles and cobbles. Rodent activity is recorded as burrows
7	~20	Dark brown	Slightly gravelly silty clay	The clay content in this layer is notably higher than in the layers above. It is distinguished by the presence of rounded to sub-rounded gravels. Soil peds appear compact yet brittle, displaying a weak blocky structure. This layer also exhibits the highest amount of organic material due to heavy burrowing activity by rodents

with over 95% of the artifacts occurring in a horizontal orientation, indicating minimal disturbance. The primary nature of Layer 4 is therefore indicated by its stratigraphic consistency, the consistent ages obtained from various depths within the layer, and its significant archaeological contents.

2.1 Chronology

Four charcoal samples from Layers 2 and 4 resulted in viable accelerator mass spectroscopy (AMS) radiocarbon measurements (Figure 1C; Table 1). Bone and charcoal samples from Layers 3 and 5 did not yield suitable carbon for AMS measurement. An age of ~6 ka cal BP was obtained from the base of Layer 2, sitting on and overlying rockfall, indicating a stratigraphic hiatus at the transition to Layer 3 (Figure 1C).

Three samples from the main cultural deposit, Layer 4, produced consistent conventional uncalibrated ages of $36,870 \pm 500$ years, $34,800 \pm 1500$ years, and $36,920 \pm 540$ years BP (Table 2). To better constrain the chronology of Layer 4, the three radiocarbon ages were subject to Bayesian modeling, yielding a more precise estimate for the occupation period, falling between ~42 and 40 cal BP (68.3% C.I. modeled) (Table 2, Supplementary Text S2).

2.2 Human activities and paleoecology

A total of 542 animal bones and teeth were recovered during the Pebdeh excavations, 60.9% of which were from Layer 4 ($n = 330$), the main cultural horizon (Figure 2). Faunal remains were highly fragmented and heavily covered in calcium carbonate (CaCO_3), with poor collagen preservation (Supplementary Text S4).

TABLE 2 Radiocarbon results, Pebdeh Cave. OxCal 4.4 Bayesian chronological software and the IntCal 20 calibration curve were used for calendar calibration (Ramsey, 2009; Reimer et al., 2020). Calibration results are reported as 68.3% and 95.4% credible intervals for individual (unmodeled) calibrations and for modeled calibration within a Bayesian model that included the stratigraphic sequence.

Laboratory no.	Layer	Depth (cm)	Conventional ^{14}C age (yrs uncal BP)	Calibrated ^{14}C ages (yrs cal BP - 68.3% C.I.)	Calibrated ^{14}C ages (yrs cal BP - 95.4% C.I.)	Modeled calibrated ^{14}C ages (yrs cal BP - 68.3% C.I.)
OxA - 40,148	2	-89	5163 ± 28	5985–5900	5995–5893	6000–5900
OxA - 39,588	4	-115	36,870 ± 500	42,025–41,385	42,255–41,061	42,00–41,300
OxA - 40,147	4	-124	34,800 ± 1500	41,405–38235	42,360–36,665	42,200–40,400
OxA - 39,589	4	-137	36,920 ± 540	42,065–41,390	42,301–41,044	42,000–41,300

A total of 191 specimens from Layer 4 were assigned to taxa (Supplementary Table S15), comprising three major groups: rodents, birds, and antilopines/caprines (gazelle, sheep, and/or goat). Identification of the taxa of 120 specimens was attempted using collagen fingerprinting/Zooarchaeology by Mass Spectrometry (ZooMS) following several protocols (van der Sluis et al., 2014; Welker et al., 2015; Brown et al., 2021; Naihui et al., 2021), but the specimens yielded insufficient collagen for analysis. The faunal remains are mainly long bones (78.3%) and rib and skull fragments from medium-sized ungulates. These fragments mainly derive from antilopines/caprines, or 80.3% of the identifiable taxa. Anthropogenic modifications were recorded on dental and skeletal elements of these taxa. Burning was recorded for 28.9% of the specimens identified as caprine and gazelle/sheep/goat-sized ungulates. Butchery marks were recorded on two long bone shaft fragments of sheep/goat-sized ungulates, consisting of cutmarks with V-shaped cross sections (Figure 2B) and shouldering (Supplementary Text S4). In addition, six long bone fragments, three of which derived from Layer 4, exhibited evidence of flaking resulting from direct percussion. Taken together, and alongside the notable absence of carnivore modifications, these findings indicate that the caprine remains were brought into the cave and processed anthropogenically.

Stable isotope analysis of plant biomarkers from the cave sediments revealed that vegetation and hydrological conditions remained relatively stable throughout site occupation (Supplementary Text S5). Plant wax normal (*n*-)alkane abundances and carbon ($\delta^{13}\text{C}$) and hydrogen (δD) isotope ratios of the C_{27} - C_{31} *n*-alkanes suggest a C_3 -dominated, woody biome with an overall wet and cool climate (Dansgaard, 1964) (Supplementary Figure S29). The coupled $\delta^{13}\text{C}$ and δD data suggest a C_3 -dominated woodland environment under the direct influence of steady Indian Ocean weather cycles and precipitation patterns during the Layer 4 occupation. $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ data from caprine and porcupine teeth further support a woody environment and a relatively mesic climate. Tooth enamel $\delta^{13}\text{C}$ values range from -12.3‰ to -7.8‰ , indicating the dominance of C_3 resources in caprine and porcupine diets during the Layer 4 occupations. This aligns well with known caprine browsing preferences and highlights the presence of shrubs and trees, as indicated by the biomarker work, in the vicinity of the site. Values between -10.0‰ and -7.8‰ potentially

indicate some limited contribution of C_4 plants (Cerling et al., 1997; Levin et al., 2008), likely grasses, into the animal diets, perhaps supported by Indian Ocean summer rainfall in the warm season (Supplementary Figure S30). Although elevated $\delta^{13}\text{C}$ could also be linked to impacts of aridity or temperature on consumed C_3 vegetation, this does not seem to be indicated by the biomarker data and wider paleoenvironmental picture of the region.

2.3 Stone tool assemblages

A total of 611 lithic artifacts were recorded from Trench 1 (200 pieces are >20 mm), 85% of which were made on high-quality cherts, followed by siltstone (5%), calcareous sandstone (5%), limestone (3.5%), and mudstone (1.5%). Layer 4 yielded the highest count of stone artifacts ($n = 481$; 78.72% of the lithic assemblage), followed by Layer 3 ($n = 77$; 12.6%). The lithic counts for other layers were low: 23 from Layer 2, 16 from Layer 5, 9 from Layer 6, and 5 from Layer 7 (Supplementary Text S3).

In Layer 2, the lithic debitage primarily consists of small flakes with plain striking platforms, suggesting a simple reduction sequence. Among the four tools identified, a side-retouched piece and a notched-naturally backed knife stand out. The presence of multiple small flake scars on the core fragment suggests intensive core reduction activities. Layer 3 presents a higher proportion of debitage, with flakes and blades dominating the assemblage. Seven tools were identified, including flake tools such as sidescrapers, retouched pieces, and a carinated endscraper/core with a blade tool that has an elongated Levallois-like point.

Layer 4, which will be described in detail below, is dominated by debitage and contains flakes, blades, and bladelets. A range of typologically defined tools are present, accompanied by core reduction and maintenance activities. Layer 5 exhibits a notable presence of blades, indicating a focus on blade production. Seven tools were identified, including scrapers, burins, and points, indicating diverse tool functions. The systematic reduction process is evident from the presence of unidirectional subparallel scars on the dorsal face of the artifacts. Layers 6 and 7 contain fewer lithic artifacts, possibly due to intrusion from post-depositional processes. The persistence of elongated/laminar forms and subparallel scars shows similarity in lithic reduction strategies, similar to Layer 4.

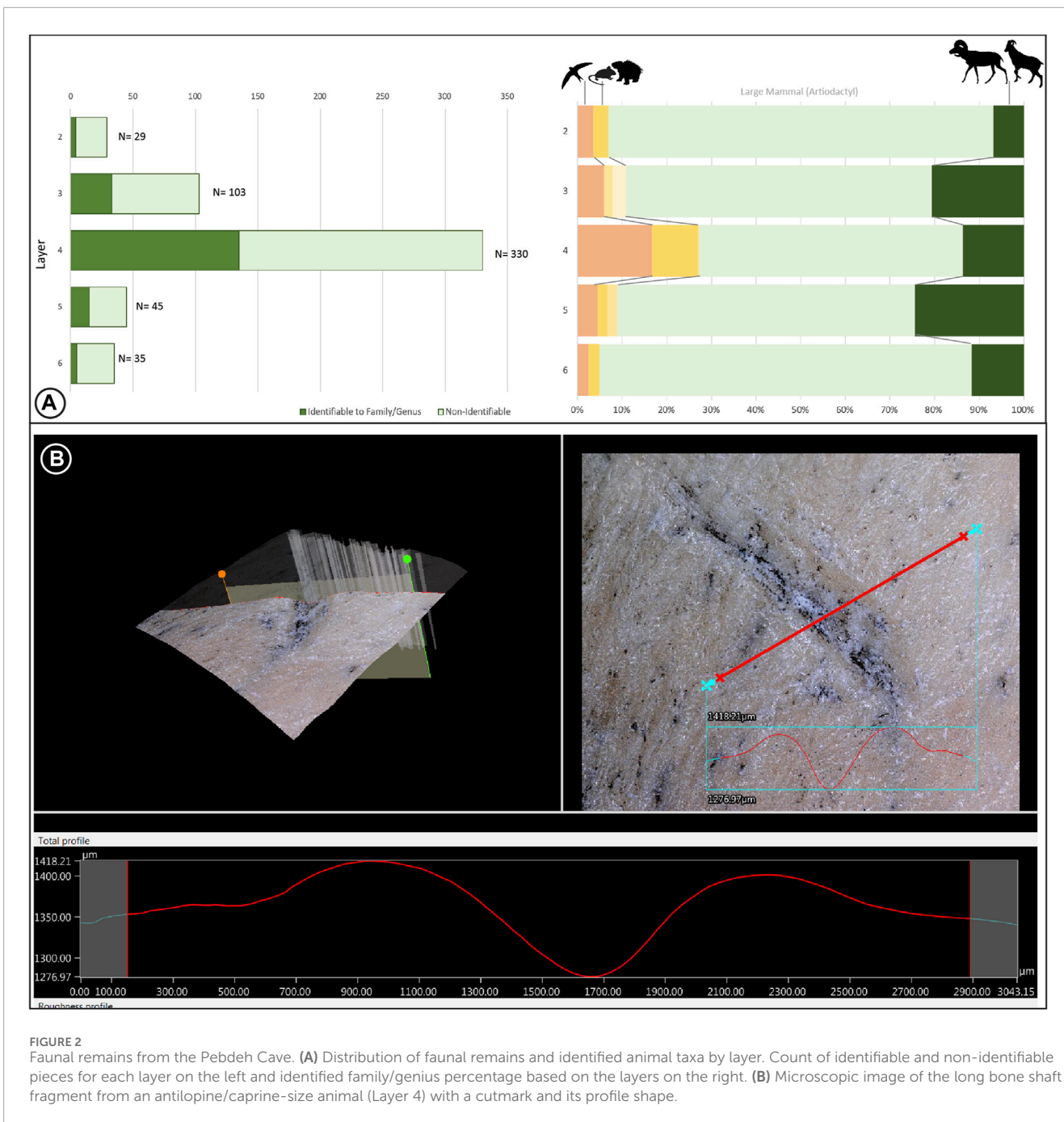


FIGURE 2 Faunal remains from the Pebdeh Cave. **(A)** Distribution of faunal remains and identified animal taxa by layer. Count of identifiable and non-identifiable pieces for each layer on the left and identified family/genus percentage based on the layers on the right. **(B)** Microscopic image of the long bone shaft fragment from an antelope/caprine-size animal (Layer 4) with a cutmark and its profile shape.

2.4 Layer 4 stone tool assemblage

Layer 4 is the richest deposit with lithics ($n = 481$), dated to between ~ 42 and 40 cal BP (Table 2). The debitage in Layer 4 constitutes 48.9% ($n = 235$) of the lithic assemblage, while the count of other debris and indeterminates ($n = 174$, 15.6%) is also considerable (Table 3). Of the identifiable debitage, flakes represent 40% ($n = 95$), while blades ($n = 35$) and bladelets ($n = 62$) collectively account for 41.5% of the debitage. A substantial portion (43.9%) of the tools ($n = 25$) are made on flakes. Flakes occasionally contain small, elongated, and atypical forms, which may be products of simple core preparation and rejuvenation within

a laminar reduction sequence. The removal of such atypical flakes within a laminar reduction sequence is evidenced by the frequent subparallel blade and bladelet scars on the dorsal face of many of the flakes. The debitage and tools are of various morphologies in plan and profile views along the technological axis (Figure 3; Supplementary Figure S15). With respect to the plan view, 21% of the flakes in Layer 4 are convergent, including subtriangular forms (Kozłowski, 2004); 73% of these flakes are also elongated in their dimensional ratio (length/width ≥ 1.5). Overall, 30% of the flakes in Layer 4 are elongated. The emphasis on elongated and larger blanks for blade production is one of the key characteristics of the IUP in the Levant and Central Asia (Meignen, 2012; Kuhn et al.,

TABLE 3 Lithic artifact types in the Pebdeh Cave by layer.

Layer	Debitage (%)	Tool (%)	Core & core fragments (%)	Debris (%)	Indeterminate (%)	Total (%)
2	13 (56.52)	4 (17.39)	0&1 (4.35)	3 (13.04)	2 (8.70)	23 (3.76)
3	50 (64.94)	7 (9.09)	2&1 (3.90)	8 (10.39)	9 (11.69)	77 (12.60)
4	235 (48.86)	57 (11.85)	9&6 (3.12)	75 (15.59)	99 (20.58)	481 (78.72)
5	8 (50)	7 (43.75)	- (0)	- (0)	1 (6.25)	16 (2.62)
6	8 (88.89)	1 (11.11)	- (0)	- (0)	- (0)	9 (1.47)
7	4 (52.05)	1 (20)	- (0)	- (0)	- (0)	5 (0.82)
Total	318	77	19	86	111	611 (100)

2014bib_kuhn_and_zwyns_2014; Leder, 2018; Zwyns, 2021; Goder-Goldberger et al., 2022bib_ggmb_2022) (Supplementary Text S3).

The main scheme of core reduction in Layer 4 was unidirectional blank removal (Figures 3K, M), the evidence for which is recorded on 26 artifacts (vs. eight lithics with bidirectional scars and three with multidirectional scars). The presence of unidirectional removals (Figures 3E, G, J) and rarer instances of multidirectional scars imply the more common use of the volumetric concept of core reduction and suggest entry into the UP. Both sub-convergent (Figure 3F) and subparallel (Figures 3D, J) negative scars and ridges are present on bladelets and microblades. The artifacts with such scars are usually laminar products (62%). While there are a considerable number of flakes with such scars (37%), they are mostly elongated or very small flakes. This suggests that they were serving as blade/let core-trimming and preparation elements and, hence, part of the laminar reduction sequence (Supplementary Text S3).

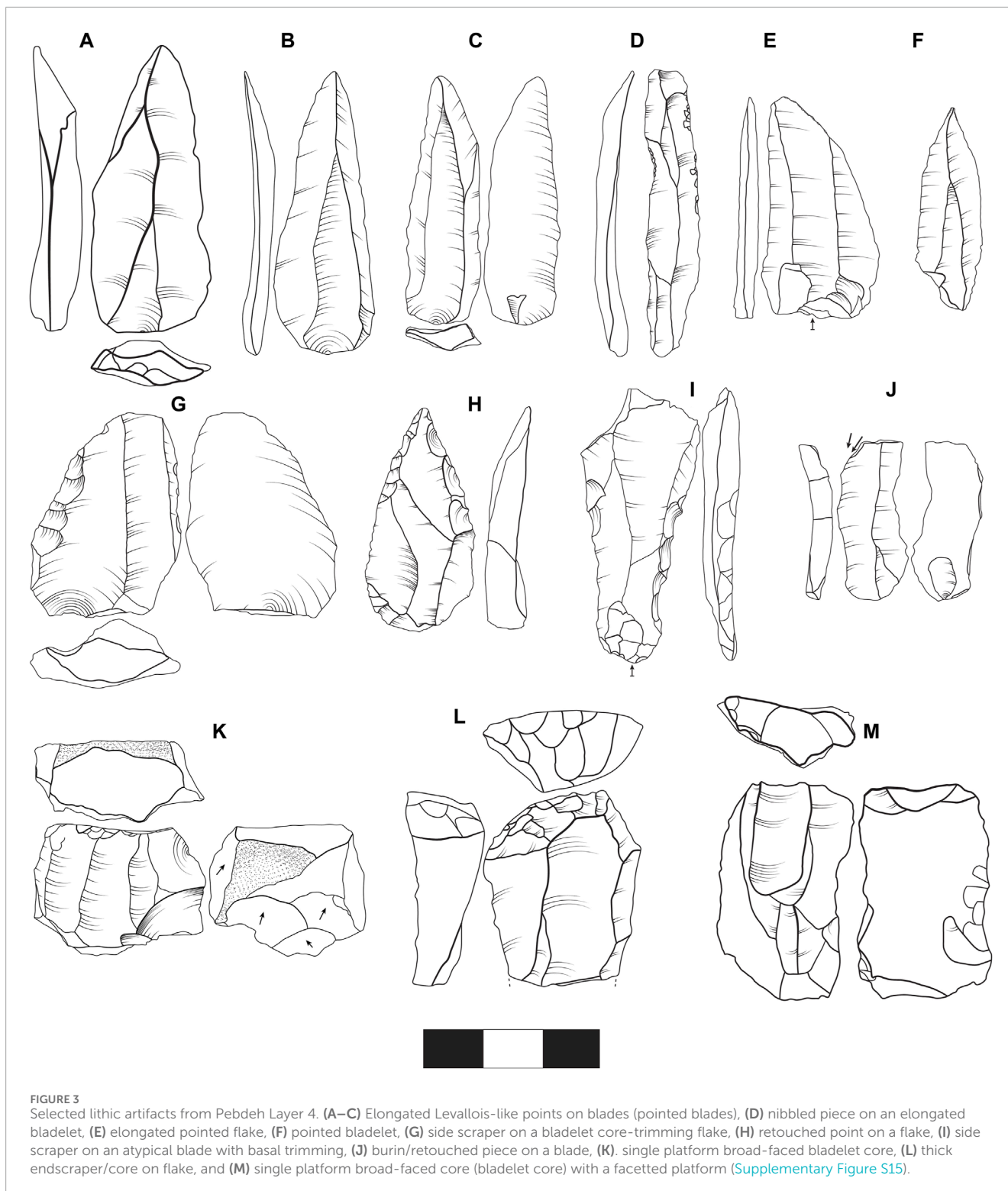
Faceted, dihedral, and *chapeau de gendarme* striking platforms constitute 10% of the striking platforms. While most platform preparations were used to detach flakes, blades with faceted platforms are also present, some of which are characteristic elongated Levallois-like points (Figures 3A–C). As expected with laminar products, punctiform and linear striking platforms are more numerous, representing 26% of the platform types. This could imply an increase in the share of soft hammer percussion in the reduction sequence, as was the case in the initial phases of the UP elsewhere (Ohnuma et al., 1990). Owing to the presence of bladelets, the percentage of punctiform/linear platforms is larger than the faceted/dihedral varieties (Supplementary Table S7). There are faceted/dihedral platforms in laminar removals (6 pieces, 10.17%, Supplementary Table S7), consistent with the earliest stages of the UP in southwest Asia (Meignen, 2012; Goder-Goldberger et al., 2022). In total, 19% of the laminar products (blade and bladelets) in Layer 4 are convergent, pointed, or in-between (Leder, 2014) in plan view morphology, while parallel- or subparallel-sided morphologies constitute 22.7% of the laminar artifacts.

Tool types in Layer 4 are diverse, with points and simple side-retouched pieces being the most frequent (each contributed to 22.81% of the tools; Supplementary Table S6; Figure 3). Burins and burin spalls are present, including two multiple burins and two simple examples (Figure 3J). Endscrapers (15.8%, n = 9)

are present, and side scrapers exist, although rare (Figure 3G; Supplementary Table S6). Three carinated endscrapers on flakes were recovered, all with negative scars of microblades and bladelets (Figure 3L). Classic Arjeneh points and Dufour bladelets are absent in the assemblage, indicating differences in comparison to the Early Upper Paleolithic (EUP) assemblages in the Zagros (Olszewski et al., 2006; Tsanova, 2013). The presence of UP tool types (37%) (burins, burin spalls, endscrapers, retouched pieces on non-Levallois blades, a carinated endscrapers, tools on bladelet blanks; 37% of the tools in Supplementary Table S6) alongside Zagros MP tool types (15%) (side scrapers, denticulates on flakes) appears to indicate a departure from the MP and entry into the UP (Kuhn et al., 1999; Kozłowski, 2004; Meignen, 2012; Kuhn et al., 2014).

With respect to the 13 point tools from Layer 4, two are Levallois-like points made on a blade and an elongated flake. One of the Levallois-like points is convergent, and the other is pointed in morphology (Kuhn et al., 2014) with unidirectional sub-convergent negative scars on their dorsal face (Figures 3A–C). Nearly all of the points have such scars on their dorsal face, consistent with observations relating to IUP assemblages from elsewhere (Škrdla, 2003; Belfer-Cohen et al., 2012; Meignen, 2012; Kuhn et al., 2014). Most of the points are made using hard hammer percussion, with plain, faceted, and dihedral platforms, while three show signs of soft hammer percussion. Apart from the Levallois-like points, one elongated Mousterian point on a Levallois flake, and one *deje* point-scraper, all the other points are the simple retouched varieties, made on all types of blanks and with direct retouching.

In terms of techno-typology, the Pebdeh Layer 4 lithic assemblage is not comparable to what is currently recorded in the late MP in the Iranian Plateau and the Zagros Mountains. The rare MP sites in the Iranian Plateau with absolute chronology are all placed in the late MP; therefore, there is no distinction between the MP facies in the Zagros Mountains. In the Zagros, the so-called Zagros Mousterian radically differs from what is seen in Pebdeh Layer 4. In the Zagros Mousterian toolkit, there are flake-based side-, double side-, and convergent scrapers/retouched points together with retouched “rods,” transverse scrapers, demi Quina scrapers, and typical and atypical Levallois flakes. Although notches and denticulates are typically part of the Zagros Mousterian, burins



and endscrapers are very few (Skinner, 1965; McBurney, 1970; Bewley et al., 1984; Dibble, 1984; Baumler et al., 1993; Dibble et al., 1993). The late MP sites of the northern Iranian Central Plateau, such as Mirak, have a comparable toolkit, albeit with less intensive retouching and a higher participation of the Levallois method in the assemblage (Vahdati Nasab et al., 2019; Hashemi et al., 2021).

Apart from Iran, the Levantine late MP features high variability in terms of lithic techno-typology (Goder-Goldberger et al., 2020), but generally, unidirectional convergent preparation dominates, with flakes in significantly high frequencies and being usually wide and thin, and blades generally in low frequencies. In these techno-complexes, Levallois points, pseudo-Levallois points, blades, and

naturally backed knives are seen, and the role of the Levallois method is significantly more important than what is the case in the later Levantine industries. Some points are typical broad-based Levallois points, commonly with *chapeau de gendarme* striking platforms. Retouched tools are usually rare, especially in the later part of the late MP, but when present, the common types are simple side scrapers and elongated points, and burins and endscrapers are rare. Although elongated blanks are common in the IUP, the dominant typical production in the late MP is composed of subtriangular short blanks, although long narrow flakes produced by unidirectional convergent flaking are present (Meignen, 1992; Bar-Yosef et al., 2001; Richter et al., 2001; Bar-Yosef, 2002; Meignen, 2012; Shea, 2013; Rose et al., 2014).

Our overall evaluation is that Pebdeh's Layer 4 assemblage represents an *in situ* layer with characteristic pieces and technological traits that are a mixture of technologies from the MP and UP contexts of the Zagros Mountains, which, to some extent, fills the gap between unknown late MP industries of the Zagros and Early UP sites. This is based on its combined nature of both MP and UP techno-typological features and some characteristics shared with the wide and general definitions of the IUP in regions such as the Levant. More specifically, the IUP attribution is based on a combination of attributes: the coexistence of flake and laminar reduction with the dominance of a unidirectional scheme, the existence of volumetric core exploitation, the concurrence of faceted/dihedral and punctiform/linear striking platforms with signs of both hard and soft hammer percussion (albeit hard hammer percussion dominates), the combination of MP and UP tool types, and elongated convergent blanks alongside non-standardized bladelet production (Supplementary Text S3).

3 Implications of the Initial Upper Paleolithic in the Zagros Mountains

We have reported on the identification of a transitional lithic assemblage at Pebdeh Cave in the southern Zagros Mountains, similar to the IUP of Western Asia. The primary nature of human activities on the cave terrace is supported by fine-grained sedimentary deposits, the consistent radiocarbon ages of 42–40 cal BP (68.3% C.I. modeled), and the high frequency of lithic and faunal remains in Layer 4. The geographic location of Pebdeh Cave in the southern flanks of the Zagros provides novel information on settlement history as most previous Paleolithic research has been centered on well-known caves (e.g., Shanidar, Warwasi, and Yafteh) in the northern and central regions of the mountain chain. The location of Pebdeh complements research at the UP site of Ghar-e Boof, which is also situated in the southern Zagros zone (Conard et al., 2019).

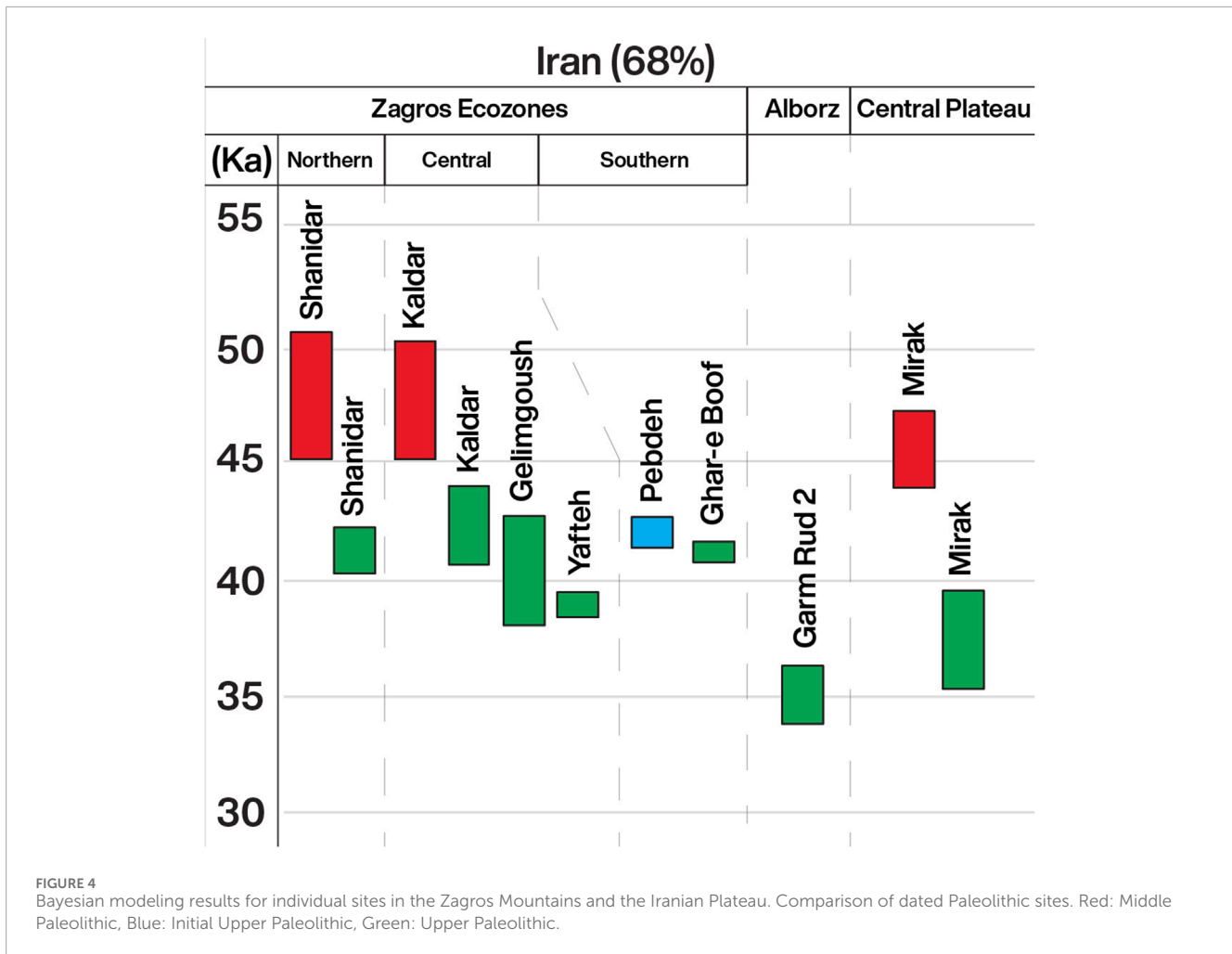
A mesic climate and a woody biome during the occupation of Pebdeh is indicated by isotope and biomarker analyses. However, harsh climatic fluctuations are recorded in lake cores during MIS 3, indicating that while the northern and west-central Zagros had steppe-like vegetation during cold and dry intervals of the Last Glacial (~44–29 ka) (Van Zeist et al., 1977; Djamali et al., 2008), the lower orography at Pebdeh in the southern Zagros resulted in a milder biome. The climatic difference between the central and southern Zagros is also reflected in the microvertebrate

remains from Kaldar (central) and Ghar-e Boof (southern) (Rey-Rodríguez et al., 2020; Blanco-Lapaz et al., 2022). Rodent remains from Kaldar suggest the Late Pleistocene environment was mainly open dry steppes with the presence of vegetation cover, while the rodent assemblage from Ghar-e Boof suggests a short-lived cold and dry phase between ~40–39 ka. Adding to this, stable isotope analysis of carbon and oxygen from tooth enamel of fauna collections from Shanidar in northern Zagros presents the occupation of both Neanderthals and *H. sapiens*, suggesting both species were exploiting the same resources in direct competition at about the same time (Ecker et al., 2023). The strategic placement of Pebdeh Cave, situated between the mountains and plains (Figure 1A), likely enabled hunter-gatherers to access a mosaic of ecosystems, including in the lower-elevation mountainous zone and the lowland plains. Indeed, the Pebdeh faunal remains and the lithic assemblage indicate that the cave was used as a temporary, special purpose site, a supposition supported by evidence for hunting-related activities, as evidenced by the targeting of ungulates, bones with butchery marks, and the high number of points.

The lithic collection from Pebdeh is a unique assemblage for the Zagros Paleolithic, combining elements representative of Zagros MP and UP technologies dating within a relatively brief interval between ~42–40 ka. The characteristics of the lithic assemblage in Layer 4 differ from the MP and UP collections at Yafteh, Ghar-e Boof, and Warwasi (Supplementary Text S3). Although the Pebdeh Layer 4 assemblage shows similarities with early UP Baradostian assemblages in the Zagros, there are clear technological divergences. The Zagros Baradostian is a laminar industry with a fully standardized bladelet production sequence, whereas the Pebdeh industry is composed of both flake and laminar reduction represented in nearly equal proportions and non-standardized laminar production with diverse bladelet morphologies and includes production of Levallois-like points, which the Baradostian lacks (Supplementary Text S3). The Levallois facies were not recorded in the MP assemblages of the southern Zagros region in excavated sites such as Ghar-e Boof (Mata-González et al., 2023).

A comparison of Pebdeh's Layer 4 collection with the Levantine IUP and EUP (Ahmarian) assemblages shows some parallels to the former (Supplementary Figure S23). Layer 4 of the Pebdeh Cave features a *chaîne opératoire* with hard hammer percussion and platform faceting, moderate hints at soft hammer percussion with lipped platforms, linear and punctiform platforms, and diffuse bulbs. Moreover, the cores in Pebdeh are generally flat-faced (volumetric) platform cores (unidirectional), while both MP- and UP-related tool types made on laminar and elongated blanks exist (Supplementary Text S3).

The definition of the IUP has undergone changes and refinements over time, influenced by the specific contexts of research. The understanding of the IUP is not uniform across different regions, and its characterization can vary based on whether it is perceived as a technological taxonomy or a distinct chronological period (Kuhn et al., 2018; Kuhn, 2019; Goder-Goldberger et al., 2022; Goder-Goldberger et al., 2023). The evolving definition often centers around the transitional nature of lithic assemblages from the late MP to the UP. Broadly speaking, the IUP is characterized by the production of elongated triangular points, some of which exhibit typological Levallois characteristics, along with the presence of volumetric blade



production (Kuhn, 2019; Zwyns, 2021; Goder-Goldberger et al., 2022). This definition reflects the technological features that distinguish IUP assemblages from earlier MP ones, showcasing a shift toward more advanced lithic technologies associated with the UP. One notable aspect is the acknowledgment that the IUP was not a uniform phenomenon across Western and Central Asia. Researchers propose that the diversity in environmental settings influenced various adaptations, subsistence patterns, and strategies, leading to a range of IUP assemblages (Kuhn et al., 2018; Zwyns, 2021; Goder-Goldberger et al., 2022). The recognition of diverse environments underscores the impact of local conditions on the material culture left by hominin populations during this transitional phase. In addition, researchers have associated the IUP with a dispersal period of *H. sapiens* in Western and Central Asia between 50,000 and 40,000 years ago (Kuhn, 2019; Goder-Goldberger et al., 2023). This temporal association places the IUP within the broader context of hominin dispersals and expansions, linking changes in lithic technology to larger demographic and behavioral shifts. In essence, the evolving definition of the IUP reflects the dynamic nature of human cultural evolution and adaptation during a crucial period of technological innovation and behavioral change. Ongoing research and discussions surrounding the IUP contribute to a more nuanced understanding of the complexities inherent in the

archaeological record and the need to consider regional variations and environmental influences in interpreting Paleolithic cultures.

The identification of Pebdeh Cave as an IUP site, with a mix of MP and UP technological attributes, raises a question about the occupation history of indigenous Neanderthal populations and *H. sapiens* as they occupied and advanced across the Zagros and the wider region. The late MP in the Zagros is no younger than 45 ka on the basis of Bayesian modeling (Figure 4), although slightly younger at Mirak in the Iranian Central Plateau. MP technology, known as the Zagros Mousterian, is attributed to the Neanderthals, as supported by rare sites with fossils, such as at Shanidar and Bawa Yawan (Solecki, 1964; Heydari-Guran et al., 2021a). The earliest age for the UP in the Zagros is at Kaldar, with an onset of ~44 ka, although this early dating requires verification owing to the inconsistent nature of the dates in the stratigraphy and problems with the radiocarbon age limit (Bazgir et al., 2017). Otherwise, the IUP at Pebdeh (~42–40 ka) and the UP at Gelimgoush (~42–37 ka) (Heydari-Guran et al., 2021b) are among the earliest sites with regular blade assemblages (Figure 4), suggesting a significant technological transition during this period. The coexistence of MP and UP characteristics at Pebdeh Cave challenges our understanding of the dynamics between Neanderthals and *H. sapiens* in the Zagros Mountains. Further research and verification of early dates are

crucial for refining our comprehension of the precise timing and nature of these transformative events in the Paleolithic history of the Zagros region.

4 Conclusion

On the whole, the fossil and archaeological evidence from the Zagros Mountains indicates little chronological overlap between the MP and the UP, implying that Neanderthals and *H. sapiens* were not persistently using and cohabiting the same geographical locations (Figure 4). However, sporadic contact between these groups in the Zagros is reasonable, given evidence for interbreeding (Petr et al., 2020; Peyrégne et al., 2022) and for overlaps between late MP, IUP, and UP assemblages in the Levant between ~50 and 44 ka (Goder-Goldberger et al., 2023).

In contrast to the central Zagros, there is currently a lack of evidence for MP and Neanderthal occupations in the southern Zagros. This suggests that the southern Zagros may have served as a more favorable habitat for *H. sapiens* using UP toolkits. The MP characteristics observed in the Pebdeh assemblage may have either been influenced by Neanderthal occupations from the central Zagros or, alternatively, an influence from MP hominins occupying the periphery of the Iranian Central Plateau, which has been surmised to represent *H. sapiens* (Heydari-Guran et al., 2021c; Shoaei et al., 2023).

The acknowledgment of the Pebdeh Layer 4 lithic assemblage as an IUP entity in the Zagros Mountains represents a crucial development for understanding the Paleolithic history of the region. This recognition carries significant implications for contextualizing existing Paleolithic research, refining the timeline of *H. sapiens*' arrival into the Zagros Mountains, and shedding light on potential interactions between Neanderthals and *H. sapiens*. This also contributes to a more accurate reconstruction of the behavioral patterns and adaptive strategies employed by *H. sapiens* in response to the environmental conditions of the southern Zagros. Understanding the temporal dynamics of human occupation is fundamental for constructing a comprehensive narrative of population movements and demographic shifts in the Zagros Mountains. Further study is imperative to refine and substantiate our observations. Detailed investigations, including additional excavations, dating, and comprehensive analyses of lithic assemblages, will contribute to more precise and reliable results. This highlights the iterative and collaborative nature of interdisciplinary archaeological research, where each discovery opens new avenues for inquiry and prompts the need for continued exploration and scrutiny.

Author contributions

MS: conceptualization, data curation, formal analysis, investigation, methodology, project administration, resources, software, validation, visualization, writing—original draft, and writing—review and editing. HV: conceptualization, supervision, and writing—review and editing. MS: writing—review and editing, data curation, formal analysis, and visualization. PF: data curation,

formal analysis, and writing—review and editing. MA: formal analysis and writing—review and editing. RF: data curation, formal analysis, visualization, and writing—review and editing. SH: data curation, formal analysis, investigation, visualization, and writing—review and editing. MJ: writing—review and editing. NA: data curation, formal analysis, visualization, and writing—review and editing. BM: data curation, formal analysis, and writing—review and editing. MA: formal analysis, resources, and writing—review and editing. ML: formal analysis and writing—review and editing. SM: formal analysis and writing—review and editing. JI: formal analysis and writing—review and editing. RP: data curation, formal analysis, visualization, and writing—review and editing. PR: data curation, formal analysis, and writing—review and editing. NB: writing—review and editing. MP: conceptualization, funding acquisition, project administration, supervision, and writing—review and editing.

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Conflict of interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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Supplementary material

The Supplementary Material for this article can be found online at: <https://www.frontiersin.org/articles/10.3389/feart.2024.1352099/full#supplementary-material>

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