Special Issue: The Apidima Legacy Collections: New Analyses and Interpretations

Taphonomy of the Faunal Remains from Apidima Cave A (Mani Peninsula, Greece)

EFFROSYNI RODITI*
Paleoanthropology, Institute for Archaeological Sciences and Senckenberg Center for Human Evolution and Paleoenvironments, Eberhard Karls Universität Tübingen; GERMANY; effrosyni.roditi@uni-tuebingen.de

GEORGE E. KONIDARIS
School of Geology, Aristotle University of Thessaloniki, GREECE; and, Paleoanthropology, Institute for Archaeological Sciences, Department of Geosciences, Eberhard Karls University of Tübingen, GERMANY; gkonidaris@geo.auth.gr

VANGELIS TOURLOUKIS
University of Ioannina, School of Philosophy, Department of History and Archaeology, Ioannina, GREECE; Paleoanthropology, Institute for Archaeological Sciences, Eberhard Karls University of Tübingen, GERMANY; and, Museum of Anthropology, Medical School, National and Kapodistrian University of Athens, Athens, GREECE; vtourloukis@uoi.gr

NICHOLAS C. THOMPSON
Paleoanthropology, Institute for Archaeological Sciences, Department of Geosciences, Eberhard Karls Universität Tübingen, GERMANY; and, Museum of Anthropology, Medical School, National and Kapodistrian University of Athens, Athens, GREECE; nikothompso@yahoo.com

RAINER GRÜN
Research School of Earth Sciences, The Australian National University, Canberra, ACT, AUSTRALIA; School of Geography, Nanjing Normal University, Nanjing, 210023, CHINA; DFG Center for Advanced Studies 'Words, Bones, Genes, Tools', Eberhard Karls Universität Tübingen; and, HUMAN ORIGINS – Cluster of Excellence for Integrative Human Origins Studies (EXC 3101), Eberhard Karls University of Tübingen, GERMANY; rwgruen@gmail.com

QINGFENG SHAO
School of Geography, Nanjing Normal University, Nanjing, 210023, CHINA; qingfengshao@njnu.edu.cn

PANAGIOTIS KARKANAS
M.H. Wiener Laboratory for Archaeological Science, American School of Classical Studies at Athens, Athens, GREECE; tkarkanas@ascsa.edu.gr

VASSILIS G. GORGOULIS
Department of Histology and Embryology, Medical School, National and Kapodistrian University of Athens, Athens; Biomedical Research Foundation of the Academy of Athens, Athens, GREECE; and, Faculty of Biology, Medicine and Health, University of Manchester, Manchester, UNITED KINGDOM; vgorg@med.uoa.gr

KONSTANTINOS EVANGELOU
Department of Histology and Embryology, and Museum of Anthropology, Medical School, National and Kapodistrian University of Athens, Athens; GREECE; cnevagel@med.uoa.gr

KATERINA HARVATI
Paleoanthropology, Institute for Archaeological Sciences and Senckenberg Center for Human Evolution and Paleoenvironments, Eberhard Karls Universität Tübingen; DFG Center for Advanced Studies 'Words, Bones, Genes, Tools', Eberhard Karls Universität Tübingen; HUMAN ORIGINS – Cluster of Excellence for Integrative Human Origins Studies (EXC 3101), Eberhard Karls University of Tübingen, GERMANY; Centre for Early Sapiens Behaviour (SapienCE), University of Bergen, NORWAY; and, Museum of Anthropology, Medical School, National and Kapodistrian University of Athens, Athens, GREECE; katerina.harvati@ifu.uni-tuebingen.de

*corresponding author: Effrosyni Roditi; *effrosyni.roditi@uni-tuebingen.de*

submitted: 1 March 2025; revised 21 November 2025; accepted: 25 November 2025

Handling Editor in Chief: Karen Ruebens

PaleoAnthropology **2026:2: xxx–xxx** **https://doi.org/10.48738/2026.iss2.3867** **ISSN 1545-0031**
Paleoanthropology Society & European Society for the study of Human Evolution

ABSTRACT

The site of Apidima is a karstic complex of five caves (A–E) located on the western coast of Mani, Peloponnese, Greece. In the late 1970s–80s investigations by the Museum of Anthropology, School of Medicine, National and Kapodistrian University of Athens, revealed archaeological and paleoanthropological remains from the Middle and Late Pleistocene, including two hominin crania (Apidima 1 and Apidima 2) recovered in a block of breccia in the ceiling of Cave A. In addition to these finds, numerous faunal and some lithic remains were collected from the floor of Cave A, including from the excavation of test trenches, from surface finds, and from unprovenanced breccia deposits.

Expanding on earlier paleontological and preliminary taphonomic work, this study presents a detailed zooarchaeological analysis of the legacy faunal collection from Apidima Cave A, with the goal of deciphering its taphonomic history. We employ standard zooarchaeological and taphonomic methods to determine the presence and extent of anthropogenic, natural, and carnivore-induced damage on the specimens and identify the primary agents of accumulation and modification. In parallel, U-series dating was undertaken to provide an independent chronological framework for the assemblage.

Weathering processes, chemical alterations, manganese staining, and abrasion indicate subaerial exposure and water action to a certain degree. The bone preservation is further affected by high rates of fragmentation resulting in a low degree of specimen identifiability. Breakage patterns of long limb bones indicate that most of the fractures occurred at fresh stage, while dry fractures, although present, are less common. Cut marks, burning, and marrow extraction traces indicate that hominins likely played a primary role in bone modification. Nonetheless, the occasional presence of carnivore damage suggests periodic use of the cave by both human and non-human predators. The overall evidence points to a complex depositional history and time-averaged assemblage shaped by multiple biotic and abiotic agents.

INTRODUCTION

Caves have long been recognized as important repositories of archaeological and paleontological remains, especially for the Pleistocene. Functioning as natural shelters, traps, and prominent landscape features, they were repeatedly utilized by both animals and humans, often resulting in palimpsests that remained protected from erosive processes. Numerous cave sites in Greece have provided invaluable evidence for understanding Paleolithic subsistence strategies and facilitating the reconstruction of diachronic cultural and environmental changes (e.g., Bauer et al. 2018; Darlas and Psathi 2016; Harvati et al. 2003; 2009; 2011; 2013; Jacobsen 1973; Karkanas and Kyparissi-Apostolika 2024; Karkanas et al. 2004; Koumouzelis et al. 2001; Panagopoulou et al. 2013; Perlès and Vanhaeren 2010; Starkovich 2017; Starkovich et al. 2018a; 2018b; Stiner et al. 2010; Tourloukis and Harvati 2018 and references therein).

In the Peloponnese (southern Greece), cave sites such as Klissoura Cave 1, Lakonis Cave 1, Kephalari, and Franchthi have yielded well-studied faunal assemblages that document a shift in foraging behavior across the transition from the Middle to the Upper Paleolithic. The faunal records indicate that during the Middle Paleolithic, hominin subsistence primarily focused on hunting medium- and large-sized ungulates and sporadically included smaller prey taxa, such as slow-moving, easily collected tortoises. In the Upper Paleolithic, the dietary spectrum was more diversified, with increasing exploitation of smaller prey taxa—especially the fast-moving hares and birds, as well as marine resources (Starkovich 2017; Starkovich et al. 2018a; 2018b; Stiner et al. 2012). This pattern is also supported by faunal studies from other Eurasian sites (e.g., Marin-Arroyo 2011; Mata-González et al. 2022, 2023; Roditi and Starkovich 2022; Speth 2012; Stiner 2005, 2006, 2009, 2013) and has been largely attributed to increased hunting pressure due to human population growth in the Upper Paleolithic (Stiner et al. 1999; 2000).

Despite recent systematic research providing extensive zooarchaeological data, many archaeological and paleontological assemblages from Pleistocene caves in the Peloponnese remain understudied. This is especially true for legacy collections recovered without detailed documentation of stratigraphy or spatial distribution due to past excavation or collection practices. Such is the case of the archaeological collection from the excavations at the cave complex of Apidima, Peloponnese, conducted by Prof. Th. Pitsios of the Museum of Anthropology, School of Medicine (National and Kapodistrian University of Athens) in the late 1970s and 1980s (Pitsios and Liebhaber 1995). The Apidima Cave complex, situated on the limestone coastal cliffs of the western Mani Peninsula, has yielded some of Greece's most significant paleoanthropological discoveries (Harvati 2026; Harvati et al. 2019; 2026b [this issue]; Pitsios and Liebhaber 1995; Pitsios 1999). These findings have important implications for Pleistocene hominin dispersals and evolutionary dynamics, yet neither the cultural materials nor the faunal remains recovered from the site have been studied in detail.

This study focuses on the Pleistocene faunal assemblage from Apidima Cave A, which was recovered during the Pitsios test excavations on the floor of the cave, as well as from surface collection and from unprovenanced breccia sediments from Cave A. This work aims to provide a

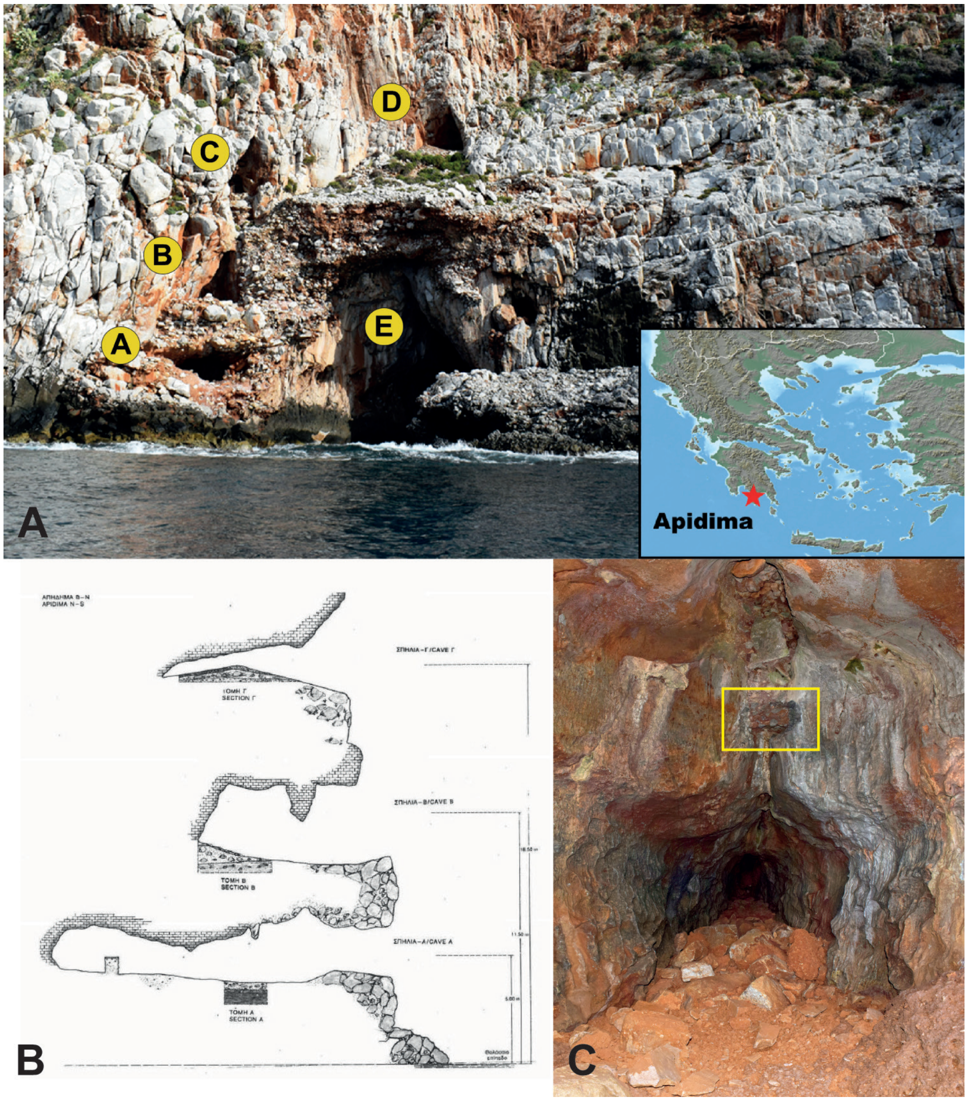

Figure 1. ***A)*** *Geographic position of Apidima (map taken from Copernicus Land Monitoring Service, https://land.copernicus.eu/) and view of the caves from the SW (labelled A–E);* ***B)*** *North–South section of Apidima caves A–C showing the excavation trenches and their stratigraphy (Pitsios and Liebhaber 1995);* ***C)*** *The interior of Apidima Cave A. The yellow box shows the original position of the two hominin crania (Apidima 1 and Apidima 2).*

detailed and systematic zooarchaeological and taphonomic re-investigation of this assemblage and to identify the agents that contributed to its formation, thereby shedding light on hominin activities at this site. Given the limited contextual background of the remains, our approach integrates the regional subsistence evidence into the interpretative framework to assess whether the taxonomic and taphonomic signatures are consistent with patterns documented in securely dated Middle or Upper Paleolithic contexts. In this way, the study serves not only to present new data on hominin subsistence patterns but also to assess the interpretive potential of a small and partially decontextualized faunal assemblage. Ultimately, we argue that the detailed investigation and re-examination of limited collections, such as this one, can help meaningfully contribute to the broader questions about past environments, biodiversity, site occupation, and use, thus augmenting the scarce and fragmentary Pleistocene records of the region.

BACKGROUND

The cave complex of Apidima is located on the western coast of Mani (Peloponnese) and consists of five karstic depressions (Caves A–E) arranged at different elevations on a south-facing (Caves A–C) and west-facing (Cave D and E) coastal escarpment (Figure 1A, B). Today, the site lies directly on the coast; however, based on geomorphological evidence from nearby contexts, during Pleistocene marine regressions, the Apidima caves would have been located several hundred meters to a few kilometers inland from the shoreline, overlooking a plateau (Basiakos 1993; Darlas 2012; Darlas and Psathi 2016; Tsartsidou et al. 2002).

In the late 1970s and 80s, investigations were conducted in Cave A, including a test excavation of the cave floor, as part of a larger research program at the site. Cave A is located at four meters above the current sea level, and revealed evidence of a Middle Paleolithic human presence, including two hominin crania (Apidima 1 and Apidima 2) discovered in a block of breccia found near the ceiling of Cave A (Harvati et al. 2026b [this issue]; Pitsios 1999; Pitsios and Liebhaber 1995; Figure 1B, C). Important cultural and faunal, as well as human skeletal remains, were retrieved also from Caves B, C, and D, referred to the Middle and Upper Paleolithic (Darlas 1995; Harvati et al. 2026a [this issue]; Karali-Gianakopoulou 1995; Lax 1995; Lombardo et al. 2026a; 2026b; Mompherratou and Pitsios 1995; Naumann et al. 2026 [this issue]; Roditi et al. in prep).

At Cave A, Pitsios (1979, 1985) originally reported a sequence of four stratigraphic horizons in the excavation of the cave floor—Layer 1, a thin crystalline layer; Layer 2, a 70cm thick light brown-reddish layer with coarse and hard texture, which contained large numbers of animal bones; Layer 3, a layer with finer texture and darker reddish color with little to no organic finds; and finally, Layer 4, a reddish compacted layer. Presumably referring to the latter two, a later publication (Pitsios 1985) describes a compacted and undisturbed layer from the trench ("A-IV") and an overlying layer of "*loose terrestrial materials that seemed to contain elements of sea sand* (A-III)". Potential traces of fire were also noted, and a few lithic artifacts were recovered from the surface, while two reportedly came from the trench excavation but without specific layer attribution (Pitsios 1979). However, since Pitsios notes that they were excavated close to bone fragments, it is likely that they derived from Layer 2.

Subsequent geoarchaeological investigations at the site and surrounding area indicate that the brecciated deposits, which are partly preserved on the cave walls and ceiling and contain the two hominin crania, represent remnants of earlier Middle Pleistocene infills of the cave. These sediments were likely extensively eroded during the Marine Isotope Stage (MIS) 5e and 5c highstands (Basiakos 1993; Darlas and Psathi 2016; de Lumley et al. 2024; Harvati et al. 2011), and potentially also earlier high sea-level stand periods. The cave floor sediments are hypothesized to have accumulated in subsequent low sea-level periods in the Late Pleistocene, probably during MIS 6 (Harvati et al. 2011) or between MIS 4 and 3 (de Lumley et al. 2024; Pitsios and Liebhaber 1995). Ongoing excavations and an extensive targeted dating program in the context of the ERC Advanced project FIRSTSTEPS aim to test these hypotheses on site formation.

Few attempts have been made at dating the Cave A deposits and finds. The hominin crania from the Cave A ceiling breccia have been dated directly using laser-ablation U-series. Bartsiokas et al. (2017) obtained a minimum age estimate of 172±11 ka years. More recently, Harvati et al. (2019) directly dated both crania using the same method. Apidima 1 was dated to >210 ka, whereas the Apidima 2 date was largely consistent with the previous date estimate at >170 ka. The consolidation of the surrounding breccia was dated to ca. >150 ka, while four unidentifiable bone fragments found within it yielded minimum dates of approximately 150 to 160 ka (samples 3757A and 3758) and ca. 240 ka (samples 3757B and C) (Harvati et al. 2019: Supplementary Information; see also Harvati et al. 2026a [this issue]). The chronology of the cave floor sediments and their potential association with the breccia deposits, however, is unclear. A calcite sample from a stalagmitic floor from Cave A was recently dated to 32,000±500 (de Lumley et al. 2024). Finally, our team recently undertook U-series dating of the flowstone capping the sedimentary sequence of the cave floor (see below).

The small collection of lithic artifacts recovered from the cave floor during the Pitsios excavations included several scrapers, points, and a Levallois core, which have been attributed to the Mousterian technocomplex (de Lumley et al. 2024; Harvati and Delson 1999). The taxonomic analysis of the faunal remains from Cave A identified the presence of red fox (*Vulpes vulpes*), fallow deer (*Dama dama*), wild goat (*Capra ibex*), and hippopotamus (*Hippopotamus* sp.) (Tsoukala 1999; see also Athanassiou 2022 for hippopotamus), while preliminary taphonomic and zooarchaeological analyses suggested a complex interaction between anthropogenic and non-anthropogenic factors at the site (Lax 1995; Tsoukala 1999). However, since the stratigraphic and spatial provenience of the faunal remains, as well as their association with the lithic artifacts and the hominin crania, remain unclear across the assemblage, an attribution to the Middle Paleolithic can only be considered a working hypothesis.

MATERIALS AND METHODS

The analyzed sample includes presumably all specimens recovered during the 1970s–80s fieldwork, which are housed at the Museum of Anthropology of the National and Kapodistrian University of Athens. Contextual information was available only for a small portion of the material (ca. 30%), for which a comparison between surface finds and excavated remains—recovered from the test trench at 0.74–1.15 meters below datum—was possible. The analysis followed standard zooarchaeological and taphonomic procedures (Gifford-Gonzalez 2018; Grayson 1984, Lyman 1994, 2008; Reitz and Wing 2008, Stiner 2005). Specimens were examined macroscopically under 20× magnification using a hand-held lens. Identifications (besides those made by Tsoukala 1999) were conducted to skeletal element and to the lowest taxonomic level possible based on available literature (e.g., Di Stefano 1996; Fernàndez 2001; Lister 1996; Pales and Lambert 1971) and unpublished virtual manuals. Results are reported using NISP (Number of Identified Specimens) and NUSP (Number of Unidentified Specimens) as the main quantification units, while MNE (Minimum Number of Elements) is employed to describe skeletal element representation (after Lyman 2008). Minimum Animal Units (MAU) have been also calculated following Stiner (1991) and are provided in Supplemental Information (SI) Table 2. Minimum Number of Individuals (MNI) is used to report data on species mortality (Hillson

2005, Stiner 1994). Age-at-death estimations were generated on the basis of tooth eruption and wear stages using the dp4-P4 sequence, as well as on long bone epiphyseal fusion. Criteria for ontogenetic age attributions of *Capra ibex* relied on Pérez Ripoll (1988) for teeth and Phoca-Cosmetatou (2005) for teeth and bones. Age assessment of *Dama dama* was based on tooth wear stages by Bowen et al. (2016).

Taphonomic observations include anthropogenic and non-anthropogenic damage, as well as post-depositional alterations. Burned bones were recorded based on coloration into the seven categories of Stiner et al. (1995): 0) unburned (cream/tan); 1) slightly burned bones, sometimes localized; 2) lightly burned, more than half of the fragment is carbonized; 3) fully carbonized (completely black); 4) localized grey/white coloration; 5) extended grey or white tonalities through more than half of the fragment; 6) fully calcined bones. Anthropogenic and carnivore-inflicted bone surface damage, such as tool marks and gnawing marks, respectively, are documented based on established criteria by Blumenschine and Selvaggio (1988), Capaldo and Blumenschine (1994), Domínguez-Rodrigo et al. (2009), Fernández-Jalvo and Andrews (2016), Haynes (1983), Pickering and Egeland (2006), Sala and Arsuaga (2018), and Stiner (1994). Percussion marks were recorded following the definitions of Vettese et al. (2020). An array of modifications pertaining to carnivore damage were considered, including pits, punctures, scores, furrowing, notches, edge crenulation, and digestion (Binford 1981). Rodent gnawing was identified following the description of Gifford-Gonzalez (2018: 275–276). With respect to abiotic alterations, specimens were classified into weathering stages following Behrensmeyer (1978), while other types of modifications, such as abrasion and oxide staining, were recorded based on Domínguez-Rodrigo et al. (2009), Fernández-Jalvo and Andrews (2016), and Olsen and Shipman (1988). For abraded specimens, the presence of polishing was noted, and the degree of rounding was documented based on the three categories of Shipman et al. (1981): 1) light abrasion with fragments retaining fresh sharp edges; 2) moderate abrasion where edges or breaks exhibit some rounding; 3) heavy abrasion with well-rounded fragment edges.

Mean fragment length and fragment-size categories were employed to infer fragmentation intensity (Lyman 1994; Stiner 1994). Fragment length was measured lengthwise to the nearest millimeter with a digital caliper on all identifiable specimens that have not been subjected to recent fragmentation, while frequencies of 10mm fragment-size categories were used for unidentifiable specimens. Preliminary results on the mode of fragmentation are reported for medium-sized mammal diaphyseal fragments with ancient and unaltered breakage. Following the protocol by Villa and Mahieu (1991), fracture outline (curved/V-shaped, longitudinal, and transverse), fracture angle (right, oblique or intermediate), and degree of completeness of the diaphyseal circumference (splinters - less than half of the shaft cylinder, more than half of the total circumference, or complete diaphysis/cylinder) were recorded, to assess the condition of the bones (fresh versus dry) during fracturing and, subsequently, determine whether the breakages occurred during the nutritive phase of the bones, i.e., when the bones retain edible tissue, or not (Domínguez-Rodrigo et al. 2022). These data were combined with observations on fracture edge morphology (jagged, smooth, mixed), wherein smooth edges are characteristic of fresh/green breaks and jagged edges of dry fractures (Johnson 1985; Morlan 1984).

Finally, two speleothem samples, APU1 and APU2, were collected from Cave A. They were dated with U-series analysis. These were carried out at the U-series Dating Laboratory at Nanjing Normal University following the routine analysis for calcitic speleothems; for details, see Jin et al. (2022).

RESULTS

FRAGMENTATION

The total number of recorded specimens is 2881, of which 230 could be identified to specific skeletal element. The overall degree of specimen identifiability is 9% (NISP/NSP*100). The mean fragment length for 124 identifiable specimens (excluding small mammals and birds) that have not been subjected to modern breakage is 28.4mm. Most of the unidentifiable specimens (*n*=1602, 60%) measured less than 20mm, while 16% measured between 20–30mm, 5% between 30–40mm, and only 3% more than 40mm. Results on the mode of fragmentation indicate that 42% of the studied long bone fragments exhibit curved and V-shaped breakage plains, 33% present fractures with a longitudinal outline, while transverse breaks occurred to a lesser degree (20%) (Figure 2A). Additionally, the high percentage of fractures with smooth edges (66%) and the increased presence of breaks with oblique angles (48%) suggest the predominance of fresh fractures. However, right angles (44%) and jagged edges (21%) were also identified, indicating dry breakage to a certain degree. In addition, the vast majority (*n*=216; 93%) of the long bone fragments are represented by less than half of the diaphysis, whereas complete cylinders are extremely rare (*n*=2, 1%) (SI Table 1).

ANTHROPOGENIC AND CARNIVORE-INDUCED MODIFICATIONS

Modifications from biotic agents are relatively scarce (Tables 1 and 2). The most frequent type of anthropogenic damage is thermal alteration, with a total of 595 fragments (21%) affected. The collection from the test trench demonstrates higher frequencies of burning (18%; 44 out of 244 fragments) compared to the material from the cave's floor surface (8%; 46 out of 611 specimens) (see Table 2). Overall, most burned specimens underwent scorching or carbonization (*n*=444), whereas calcined specimens have been identified to a lesser extent (*n*=151). Ten specimens, one caprine metacarpal and nine long bone shaft fragments, exhibit linear striations that represent toolmarks (Figure 3A–D). Several specimens demonstrate a non-uniform color distribution (e.g., Figure 4C–D, Figure 5B, Figure 6).

Additionally, one double overlapping notch, five com-

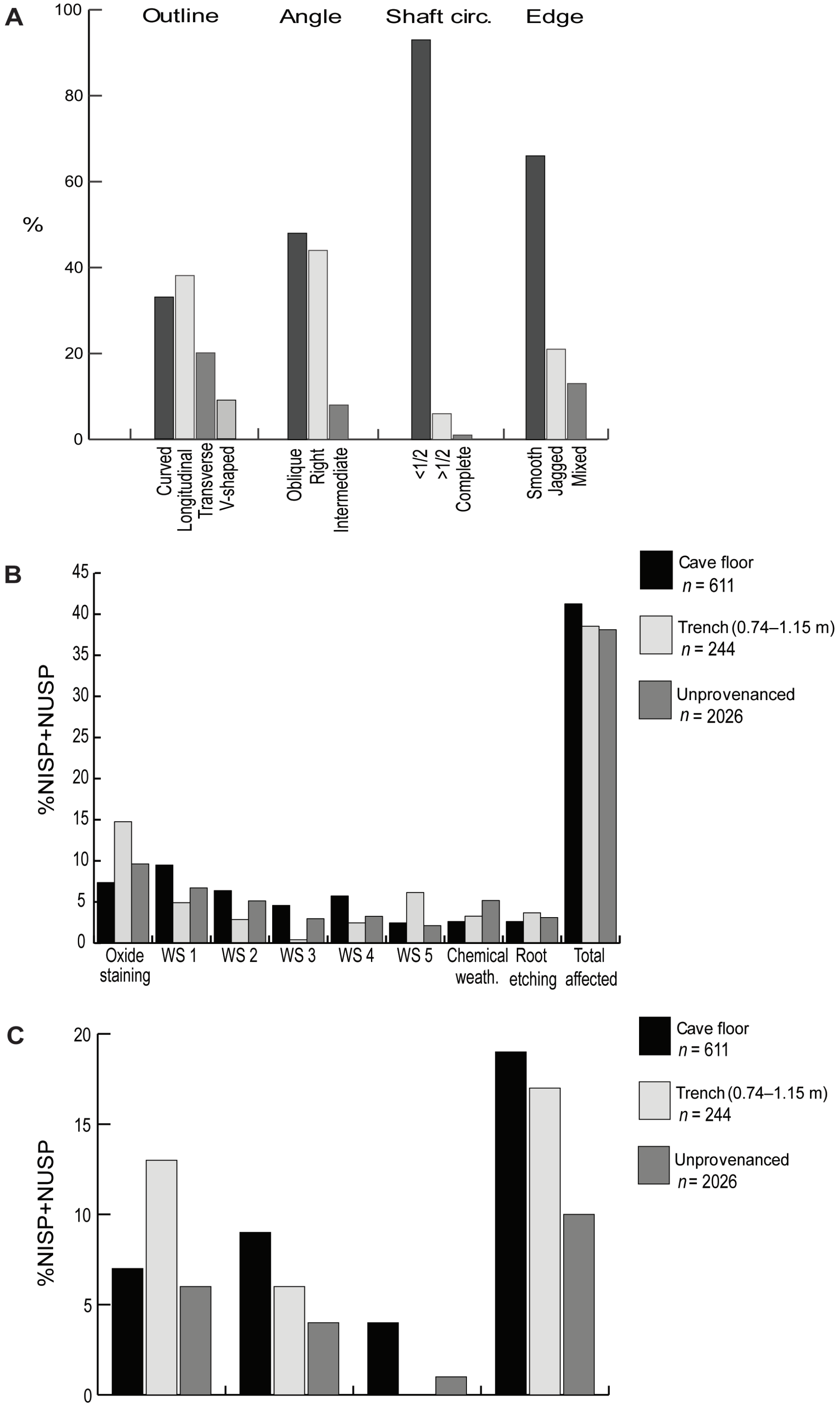

Figure 2. ***A)*** *Relative frequencies of fracture angle, fracture outline, fracture edge, and shaft circumference for medium-sized mammal diaphyseal fragments with ancient, unaltered breakage according to Villa and Mahieu (1991);* ***B)*** *relative frequency of natural alterations by context;* ***C)*** *proportion and degree of abrasion by context.*

TABLE 1. SUMMARY OF SURFACE MODIFICATIONS FOR ALL NON-IDENTIFIABLE AND IDENTIFIABLE SPECIMENS.*

Modifications		NUSP	%NUSP	NISP	%NISP	All	%All
Biotic							
	Anthropogenic						
	BS 1	45	1.7	7	3.1	52	1.8
	BS 2	127	4.8	10	4.4	137	4.8
	BS 3	249	9.4	6	2.6	255	8.9
	BS 4	91	3.4	4	1.8	95	3.3
	BS 5	38	1.4	2	0.9	40	1.4
	BS 6	16	0.6	0	-	16	0.6
	Total	566	21.3	29	12.7	595	20.7
	Toolmarks	9	0.3	1	0.4	10	0.3
	Carnivore-induced						
	Digestion	2	0.1	2	0.9	4	0.1
	Puncture	0	-	5	2.2	5	0.2
	Pits	2	0.1	2	0.9	4	0.1
	Scores	0	-	2	0.9	2	0.1
	Notches	0	-	3	1.3	3	0.1
	Total	3	0.1	12	5.3	15	0.5
	Rodent gnawing	2	0.1	1	0.4	3	0.1
Abiotic							
	Weathering						
	WS 1	175	6.6	31	13.6	206	7.2
	WS 2	143	5.4	7	3.1	150	5.2
	WS 3	86	3.2	3	1.3	89	3.1
	WS 4	96	3.6	11	4.8	107	3.7
	WS 5	69	2.6	4	1.8	73	2.5
	Chemical weathering	96	3.6	33	14.5	129	4.5
	Other						
	Root etching	85	3.2	3	1.3	88	3.1
	Oxide staining	252	9.5	24	10.5	276	9.6
	Total	1002	37.8	116	50.9	1118	38.8
	Abrasion/Rounding						
	Light	165	6.2	31	13.6	196	6.8
	Moderate	134	5.1	9	3.9	143	5.0
	Heavy	33	1.2	0	-	33	1.1
	Total	332	12.5	36	15.8	368	12.8
	Abrasive linear marks	3	0.1	1	0.4	4	0.1
Grand Total		2653	100.0	228	100.0	2881	100.0

*BS: Burning stage; WS: Weathering stage

plete notches, two outer conchoidal flake scars, as well as four bone impact-flakes (bone splinters bearing the basic technological features of a stone flake, such as a platform or ripple marks, usually occurring as by-products of percussion [after Vettese et al. 2020]; Figure 4F–G), were recorded on long bone fragments and indicate attempts of intentional breakage to access the marrow content (Binford 1978; Stiner 1994). This is further corroborated by the characteristic anthropogenic breakage in three artiodactyl hemimandible fragments (Figure 4A–B), in which the base of the corpus is split away from the tooth row (Fernández-Jalvo and Andrews 2016: Figure A.986; Morin 2012: Figure 9.17; Rosell et

TABLE 2. SUMMARY OF SURFACE MODIFICATIONS BY CONTEXT
(NSP refers to the total number of specimens and includes NISP and NUSP).*

Modifications	**Cave floor**		**Trench**		**Unprovenanced**	
	NSP	%NSP	NSP	%NSP	NSP	%NSP
Biotic						
Anthropogenic						
BS 1	2	0.3	3	1.2	47	2.3
BS 2	9	1.5	15	6.1	113	5.6
BS 3	14	2.3	13	5.3	228	11.3
BS 4	10	1.6	8	3.3	77	3.8
BS 5	7	1.1	5	2.0	28	1.4
BS 6	4	0.7	0	0.0	12	0.6
Total Burned	46	7.5	44	18.0	505	24.9
Toolmarks	3	0.5	3	1.2	4	0.2
Carnivore-induced						
Digestion	0	-	0	-	4	0.20
Puncture	0	-	0	-	5	0.25
Pits	0	-	0	-	4	0.20
Scores	0	-	0	-	2	0.10
Notches	0	-	0	-	3	0.15
Total affected	0	-	0	-	15	0.74
Rodent gnawing	0	-	0	-	3	0.15
Abiotic						
Weathering						
WS 1	58	9.5	12	4.9	136	6.7
WS 2	39	6.4	7	2.9	104	5.1
WS 3	28	4.6	1	0.4	60	3.0
WS 4	35	5.7	6	2.5	66	3.3
WS 5	15	2.5	15	6.1	43	2.1
Chemical weathering	16	2.6	8	3.3	105	5.2
Other						
Root etching	16	2.6	9	3.7	63	3.1
Oxide staining	45	7.4	36	14.8	195	9.6
Total affected	252	41.2	94	38.5	772	38.1
Abrasion/Rounding						
Light	43	7.0	32	13.1	121	6.0
Moderate	53	8.7	14	5.7	76	3.8
Heavy	22	3.6	0	-	11	0.5
Total affected	118	19.3	46	18.9	208	10.3
Abrasive linear marks	0	-	0	-	4	0.1
Grand Total	611	100.0	244	100.0	2026	100.0

*BS: Burning stage; WS: Weathering stage

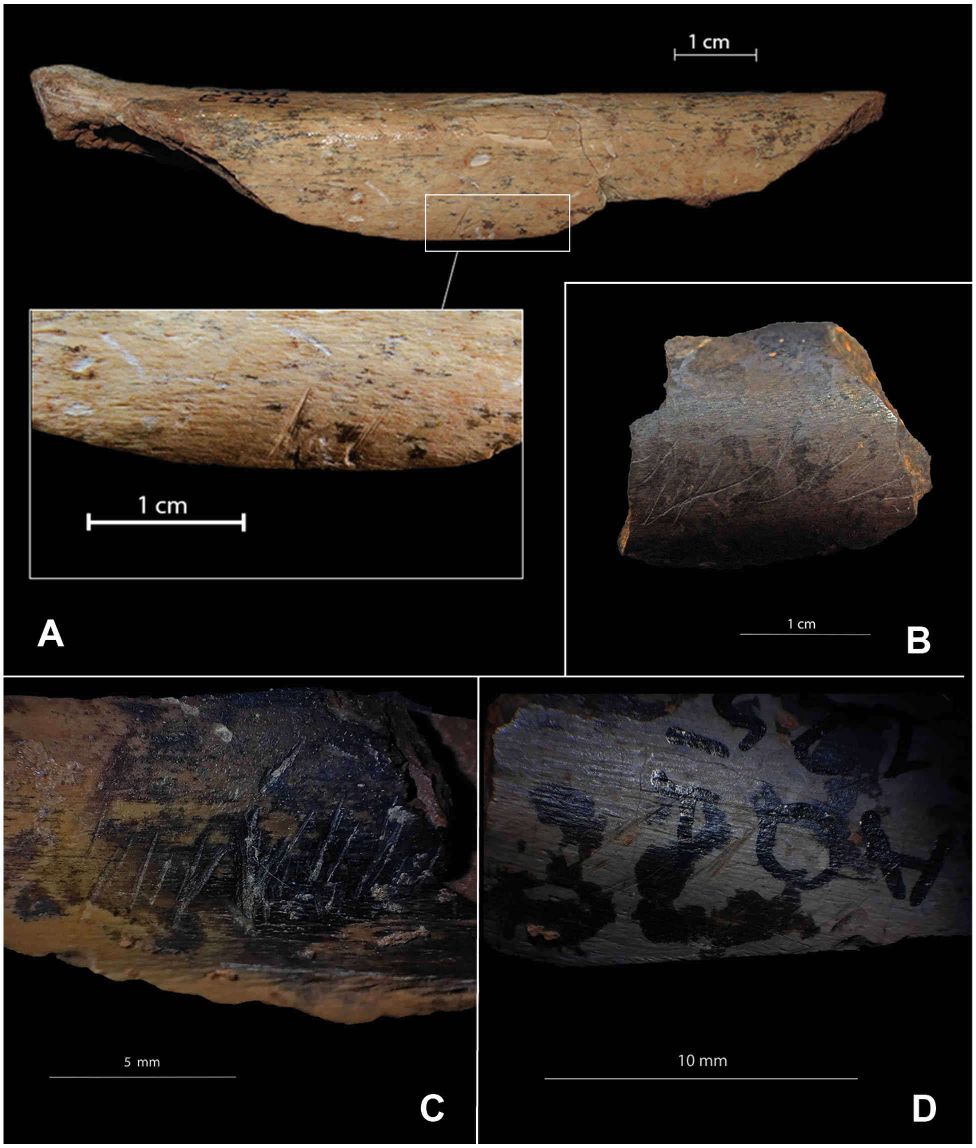

Figure 3. Examples of anthropogenic modifications: ***A)*** *cutmarks on the shaft of a caprine metacarpal;* ***B)*** *cutmarks on a burned, unidentifiable shaft fragment;* ***C-D)*** *cutmarks and oxide staining on unidentifiable shaft fragments.*

al. 2012; Stiner 1994: Figures 5.23, 5.25C, 5.28), as well as by the longitudinal fracturing of phalanges and metapodials (Figure 4C–E; Jin and Mills 2011; Stiner 1994: Figure 5.22).

Rodent gnawing was observed on three specimens, while one or more types of carnivore damage in the form of punctures, pits, digestive etching, and overlapping and opposing notches (Figure 5), were recorded on 14 specimens. Five of these belong to birds, one to fallow deer, and six were generally attributed to medium-sized ungulates. Damage overprinting is evident on three specimens that demonstrate signs of burning together with carnivore bitemarks (see Figure 5B).

Finally, a well-preserved diaphyseal fragment of a medium-sized mammal demonstrates multiple defects resembling flaking scars and could potentially represent an expedient bone tool (see Figure 6; Doyon et al. 2021; Lyman 1984; Ma et al. 2023). The fragment shows traces of combustion and diagonally oriented linear striations, possibly toolmarks, on its surface. The detachments are contiguous, extending along one lateral edge to the proximal end of the specimen and located on the cortical surface (see Figure 6). These characteristics are consistent with the criteria described by Doyon et al. 2021 and Mateo-Lomba et al. 2023 for the identification of retouched/knapped bone blanks.

ABIOTIC ALTERATIONS

Abiotic processes have affected 1118 specimens (39%) in total (see Table 1). The most common type of damage is oxide staining (*n*=276; 10%). The latter appears more frequently in the sample derived from the test trench (15%) in contrast to the surface material, constituting 7% of the affected fraction (see Table 2). Fine linear cracks, corresponding to weather-

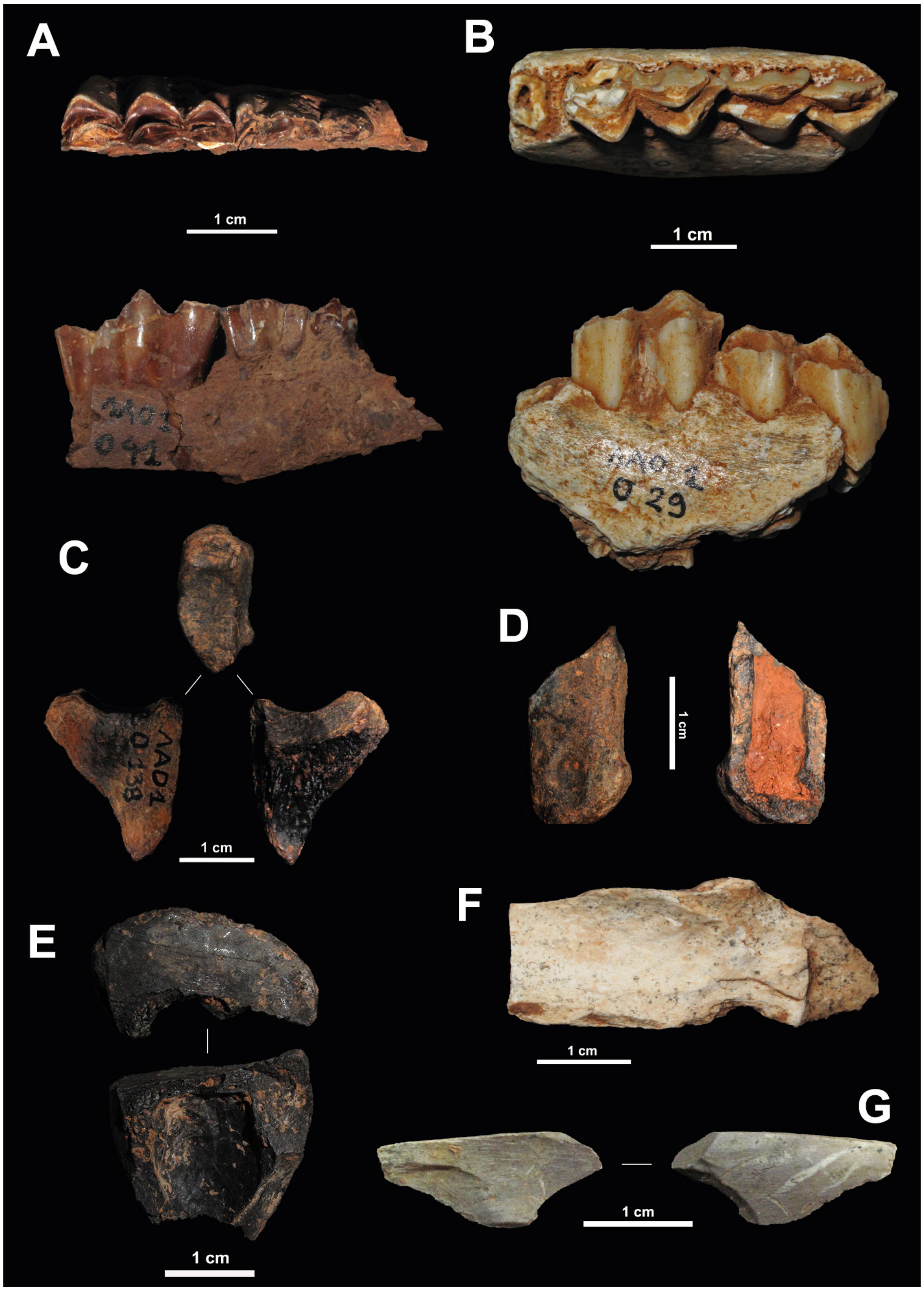

Figure 4. Examples of anthropogenic fractures: ***A)*** *mandible fragment of a juvenile wild goat (Capra ibex);* ***B)*** *mandible fragment of a young caprine with signs of abrasion and dissolution;* ***C)*** *cervid burned proximal fragment of a first phalanx;* ***D)*** *burned distal fragment of a phalanx with longitudinal split fractures;* ***E)*** *burned and split artiodactyl proximal metatarsal fragment;* ***F)*** *indeterminate long bone fragment with opposite percussion notches;* ***G)*** *bone impact flake****.***

ing stages 1 and 2, occur on 12% of the material, followed by exfoliation (6%). Chemical weathering was observed in 129 specimens (4%), predominantly in the form of dissolution or decalcification, with bones demonstrating shallow cupules and white, chalky appearance (see Figure 4B).

Abrasion has altered approximately 13% of the faunal collection, with specimens collected from the surface demonstrating a slightly higher percentage of abraded edges (19%; 118 out of 611 fragments) than the excavated remains (17%; 42 out of 244 fragments) (see Table 2). Differences could also be observed in the degree of rounding between the two contexts, where bones from the test trench show predominantly signs of light abrasion (13%; 32 out of 244), whereas abraded surface materials are distributed between all three categories, including higher proportions of moderate and severely rounded bones (9% and 4% respective-

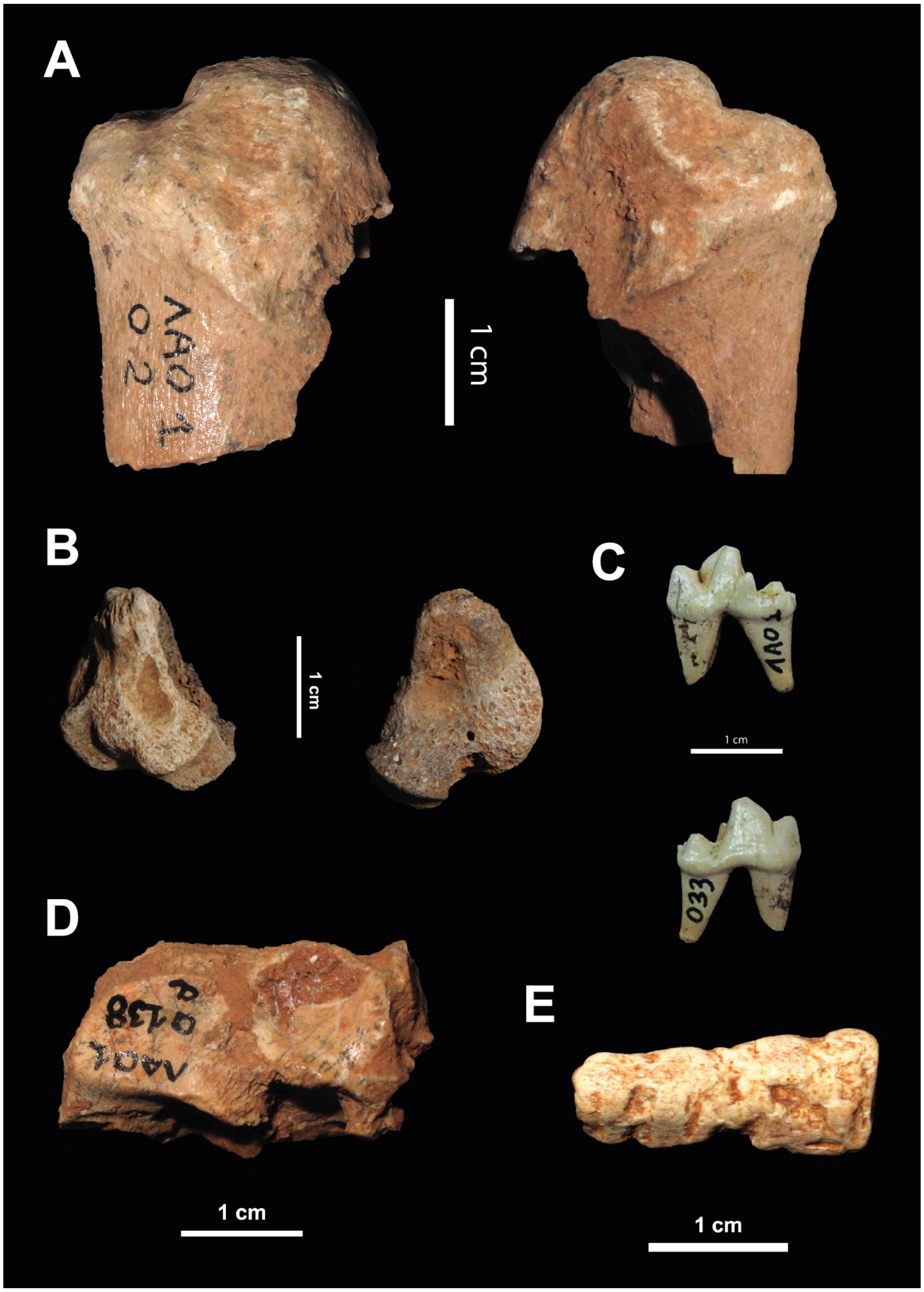

Figure 5. Evidence of carnivore activity: ***A)*** *cervid calcaneus with overlapping and opposing notches possibly caused by carnivore gnawing;* ***B)*** *burned distal metapodial epiphysis of an ungulate with bite marks and digestive etching;* ***C)*** *first lower molar of red fox (Vulpes vulpes);* ***D)*** *distal radius epiphysis with salivary rounding and edge crenulation;* ***E)*** *multiple carnivore tooth marks on an unidentifiable bone fragment; the bone appears rounded perhaps as a result of digestion.*

ly) (see Figure 2C; see Table 2). The effects of weathering and abrasive processes have caused, in many cases, partial or complete loss of the bone's cortex, and therefore have significantly reduced the visibility of observable surfaces. Moreover, a large part of the assemblage is still embedded in heavily compacted sediment. The aforementioned could provide a plausible explanation for the low percentage of identified bone surface marks in the assemblage.

TAXONOMIC ABUNDANCE AND ONTOGENETIC AGE DISTRIBUTION

Regarding taxonomic representation, the majority of the identified specimens belongs to ungulates (53%), of which 31% could be attributed to caprines (the wild goat *Capra ibex* or Caprinae indet., presumably belonging to the latter species) and 8% to cervids (the fallow deer *Dama dama* or Cervidae indet., presumably belonging to the latter spe-

Figure 6. Possible anthropogenic flaking scars and toolmarks on an undiagnostic long bone shaft fragment. The specimen could represent an expedient bone tool.

cies). Red fox (*Vulpes vulpes*; see Figure 5C), hippopotamus (*Hippopotamus* sp.), and possibly wild boar (a distal metapodial fragment tentatively attributed to cf. *Sus* sp.) are represented by one specimen each. Testudines comprised 10% of the assemblage, while birds (12%), rodents (7%), leporids (3%), and small-sized carnivorans (2%; some of the specimens may belong to *Vulpes*) are also present. The rest of the remains could only be identified to broader taxonomic categories (e.g., medium-sized mammal) (Table 3).

Data from tooth eruption and wear using the dp4 (lower fourth deciduous premolar) and p4 (lower fourth premolar) sequence indicate the presence of at least two juvenile and one adult ibex individuals, represented by two dp4s and one p4, respectively. A young adult fallow deer is represented by an unworn p4. Only one early-fusing landmark, an unfused caprine distal tibia epiphysis, allowed an age estimation using bone epiphyseal fusion. The specimen supports the previous data for the presence of a juvenile *Capra ibex* individual, in this case below the age of 1.5–2 years (Phoca-Cosmetatou 2005). An isolated dp4 and a mandible preserving the m1 (first molar) and an erupting m2 (second molar) attributed to *Capra ibex* permitted some seasonality inferences, in accordance with the stages described by Pérez Ripoll (1988) for Iberian ibex (*Capra pyrenaica*). Both were classified to phase 2D, placing the time of death of the two individuals around autumn. These seasonality results should be considered with caution due to limited sample size, which precludes further discussion of species mortality.

ANATOMICAL REPRESENTATION AND BONE SURVIVORSHIP

Anatomical profiles were generated for medium-sized ungulates and demonstrate that dental remains (MNE=41), mostly isolated, dominate the collection. Few postcranial elements have been identified (MNE=33), mainly from the foot region (Table 4). All major limb elements are fragmented and most of them (humerus, tibia, calcaneum, and metapodials) are represented largely by epiphyseal ends. Foot bones, such as phalanges, are also mostly incomplete. The over-representation of dental elements, which are more resistant to post-depositional destruction and density-mediated attrition, as well as the fragmentation of smaller, compact bone (e.g., carpal and tarsal elements), hints that such processes may have affected the assemblage. However, the presence of less dense and structurally fragile limb bone ends indicates that an interplay of forces may be at play, including mechanical, chemical, and post-excavation damage, as well as past biotic activity, which presumably introduced further identification biases.

U-SERIES DATING

The first speleothem sample, APU1, was taken close to the one reported by de Lumley et al. 2024. It produced a date of 17.9±01 ka. The second sample, APU2, yielded an age of 21.3±0.3 ka (Table 5).

TABLE 3. TAXONOMIC COMPOSITION OF THE APIDIMA CAVE A FAUNAL REMAINS.

Taxon	NISP	%NISP
Ungulates		
Hippopotamus (*Hippopotamus* sp.)	1	0%
Wild boar (*Sus* sp.)	1	0%
Fallow deer (*Dama dama*)	15	7%
Ibex (*Capra ibex*)	26	11%
Caprinae indet.	45	20%
Large-sized cervid	5	2%
Small-sized ungulate	1	0%
Medium-sized ungulate	26	11%
Large-sized ungulate	1	0%
Indet. ungulate	4	2%
Carnivora		0%
Red fox (*Vulpes vulpes*)	1	0%
Small carnivoran	4	2%
Carnivora indet.	1	0%
Small mammals		0%
Leporidae indet.	6	3%
Rodentia indet.	16	7%
Aves		0%
Large-sized	1	0%
Medium-sized	6	3%
Small-sized	21	9%
Reptilia		0%
Tortoise (*Testudo graeca*)	22	10%
General		0%
Medium-sized mammal	25	11%
Small-sized mammal	1	0%
Small mammal or bird	3	1%
Total	230	100%

TABLE 4. SKELETAL ELEMENT REPRESENTATION FOR MEDIUM-SIZED UNGULATES.

Skeletal element	NISP	MNE	Skeletal element	NISP	MNE
Skull			**Upper dentition**		
Horn	1	1	P2	2	2
Antler	1	1	P3	2	2
Partial cranium	2	1	P4	1	1
Hemimandible	4	2	M1	2	2
Axial skeleton			M2	1	1
Thoracic vertebra	1	1	M3	4	4
Rib	2	1	M (indet.)	9	5
Innominate	4	2	DP4	1	1
Front limb			**Lower dentition**		
Humerus	3	3	p2	1	1
Radius	1	1	p3	2	2
Hind limb			p4	2	2
Femur	1	1	m1	4	3
Tibia	1	1	m2	3	3
Calcaneum	1	1	m3	1	1
Metatarsal	3	2	m (indet.)	9	5
Foot			dp2	1	1
Phalanx 1	3	2	dp3	2	2
Phalanx 2	1	1	dp4	4	3
Phalanx 3	6	3	Total	51	41
Aux. phalanx 3	1	1			
Cuneiform	1	1			
Scaphoid	1	1			
Unciform	1	1			
Sesamoid	2	2			
Other					
Metapodial	6	2			
Aux. metapodial	1	1			
Total	48	33			

TABLE 5. U-SERIES RESULTS ON SPELEOTHEM SAMPLES FROM APIDIMA (all errors are 2-σ; the ages are corrected for detrital Th).

Sample Name	Sample ID	U (ppb)	Th (ppb)	^{234}U/^{238}U	^{230}Th/^{238}U	^{230}Th/^{232}Th	Age (ka)	initial ^{234}U/^{238}U	corrected Age (ka)
APU1	9392	121.4±0.1	4.98±0.02	1.109±0.002	0.169±0.001	12.9±0.1	17.9±0.1	1.114±0.002	16.9±0.5
APU2	9640	48.7±0.2	0.73±0.02	1.136±0.006	0.203±0.003	41.1±1.4	21.3±0.3	1.145±0.007	20.9±0.4

DISCUSSION

Given the nature of the collection, the integrity of the faunal assemblage is a critical factor in assessing the reliability of subsequent zooarchaeological and taphonomic interpretations. Based on the available archives, including published stratigraphic and geomorphological field observations (compiled in the Background Section), we consider the examined remains to represent a Pleistocene accumulation. No deposits of Holocene age, architectural features, or the recovery of any materials associated with Late Prehistoric or Historical periods (e.g., pottery) have been reported in the original excavation reports for Apidima Cave A, or our more recent research at the cave. This has also been confirmed through our extensive inventory of the Apidima legacy collection, which found no evidence of artifacts that would suggest intrusions or admixtures from more recent periods. Moreover, the broader condition of the faunal remains (based on macroscopic observations) indicates a high degree of mineralization/fossilization for almost all studied specimens. Few small-sized avian remains displayed minimal weathering or surface damage, suggesting a more recent accumulation and were, therefore, excluded from further analyses.

Overall, the faunal assemblage from Apidima Cave A demonstrates a low degree of specimen identifiability to skeletal element and species. This could be explained by the high rates of fragmentation, evident through both the average fragment length and the fragment size distribution index. The fracture analysis suggested that some degree of post-depositional breakage has occurred, based on the increased presence of dry fractures. Nonetheless, the predominance of fresh bone fractures and the prevalence of shaft splinters, in addition to the high intensity of fragmentation, are consistent with the patterns typically observed in anthropogenically-derived assemblages (e.g., Stiner 1994; Villa and Mahieu 1991; Villa et al. 2004). Moreover, overall higher proportions of hominin-induced damage, such as burning, tool marks, and characteristic fracture morphotypes, such as the splitting of the mandibular corpus and the longitudinal fracturing of phalanges and metapodials (see, e.g., Stiner 1994), suggest that hominins were the primary biotic modifiers of the large mammal assemblage.

The superposition of burning and gnawing traces offers direct evidence for the alternating presence of hominins and carnivorans. Stiner (1994) has previously reported such patterns in Italian Paleolithic faunal assemblages, for instance, at levels S0-3 of Sant' Agostino, where hominin and canid damage overprinting was evident. Based on the pronounced influence of weathering processes in Sant' Agostino (analogous to our results/observations for the faunal collection discussed here), it was proposed that animal bones remained exposed for prolonged periods of time, thereby attracting scavenging predators. Hence, it should be noted that, despite attestation of the two modifying agents in Apidima Cave A, their presence at the cave may not have been simultaneous, but instead short-term and alternating, or even occasional in the case of carnivores.

Multiple types of evidence support the influence of water action on the remains. Superficial, patchy black oxide coatings, presumably of manganese dioxide, typically occur in humid environments and likely indicate water percolation (Fernández-Jalvo and Andrews 2016; López-González et al. 2006; White et al. 2009). Abrasion and weathering patterns, including chemical alterations in the form of dissolution or corrosion, likely highlight slow burial rates, long exposure of the remains to water activity, or both. In addition, the presence of specimens with different stages of weathering within the same context indicates either different time of exposure to atmospheric conditions, likely related to the palimpsest nature of the sequence, or variable microenvironmental conditions in the cave. Finally, the taphonomic comparison between specimens from the cave floor and those recovered from the test trench revealed minor differences between the two contexts, suggesting minimal waterborne alterations for the latter. Specimens collected from the surface display pronounced bleaching and advanced rounding, which has been elsewhere described as an outcome of marine immersion (Pokines and Higgs 2015). One likely explanation for these differences is that the materials labeled as originating from the surface of the cave floor were actually collected from exposed blocks of lithified sediment that had eroded or detached from the surrounding *in situ* brecciated deposits and were subsequently exposed to wave action, which still occurs today during the winter months. Noteworthy is also the identification of a bone refit, involving two unprovenanced, taxonomically unidentifiable long bone fragments with good cortical preservation. The transverse fractures demonstrate green breakage planes with lithified sediment attached to them. These observations suggest that at least some part of the assemblage may be spatially and/or temporally coherent and possibly originated from a context that was not significantly subjected to material displacement during water activity in the cave.

Regarding taxonomic abundance, the faunal composition of Apidima Cave A, which comprises sizeable proportions of caprines, fallow deer, and tortoise, resembles those reported in other Middle and Upper Paleolithic sites of the Peloponnese. Within this region, the Mani peninsula demonstrates the highest density of Paleolithic localities, many of which share contextual and/or topographic affinities with the site of Apidima, i.e., cave sites or rockshelters in a coastal habitat (Tourloukis and Harvati 2018; Tourloukis et al. 2016). Therefore, the following comparisons focus on sites from this geographic zone. Tortoise and fallow deer are dominant at the Middle Paleolithic cave of Kalamakia, while ibex and wild boar contribute to the assemblage to a lesser extent (Darlas and Psathi 2016). Similarly, at the site of Lakonis Cave 1, the faunal collection includes high frequencies of medium-sized ungulates, possibly belonging to fallow deer; tortoise, red deer, wild boar, and horse were also identified (Panagopoulou et al. 2013; Starkovich et al. 2018a). At the Middle Paleolithic Mavri Spilia, the preliminary zooarchaeological study documented the presence of abundant remains of small- to medium-sized bovids and cervids, among them caprines and fallow deer, together with few specimens of wolf and bear (Tourloukis et al. 2016). At the nearby site of Melitzia, the faunal assemblage of the stratigraphically lower units (units I–III), which have been dated between ca. 46,448–44,553 and 32,155–31,470 cal BP, appears similar in composition to the assemblage from Apidima Cave A, consisting of several fallow deer remains and fewer specimens of ibex, as well as a limited number of large-sized carnivoran remains (Tzortzi et al. 2024a,b). In the Upper Paleolithic, preliminary results from recently excavated sites on the western coast of the area report once again the dominance of *Dama dama* and caprines in the archaeological sequence of Kolominitsa cave, spanning from the Middle/Upper Paleolithic transition to the Mediterranean Gravettian, as well as a significant proportion of tortoise remains in the older phase; red deer and roe deer are present in lower proportions, while few specimens of large bovids, wild boar, hare and large carnivorans complete the faunal list (Darlas and Psathi 2016). On the other hand, at Skini 4, the red deer is the most common species. The site further includes a noteworthy abundance of *Capra*, besides leporids, wild boar, and small carnivorans, such as fox (Darlas and Psathi 2016). The zooarchaeological collection from Tripsana is very similar in composition but differs from the other sites in the abundance of European hare (*Lepus europaeus*) (Darlas and Psathi 2016). Finally, a gradual increase in the abundance of red deer and a higher taxonomic diversity—including leporids, wild boar, horse, small carnivorans, as well as the unusual for the area occurrence of *Bison* sp. and *Megaloceros* sp.—both these genera are possibly observed in the faunal collection from the upper stratigraphic units IV–VII of Melitzia (Tzortzi et al. 2024a, b), and *Megaloceros* is also identified at Apidima Cave C (Tsoukala 1999).

Taphonomic similarities can also be observed between the Paleolithic sites of Mani and Apidima Cave A. High-intensity fragmentation, cutmarks, cones (defined as the scar of a Hertzian cone fracture caused by direct pressure or impact *sensu* Stiner 1994), and abundance of burned fragments have been previously reported at Lakonis Cave 1. The total percentage of burned bones in the Apidima Cave A assemblage approximates that being observed in the lower bone breccia of Lakonis Cave 1, which has been interpreted as a palimpsest refuse deposit that has experienced post-depositional hydrological alterations (Starkovich et al. 2018a). Comparable observations have been made for the faunal assemblage of Mavri Spilia, which, in addition to having elevated proportions of burned and fragmented remains, also exhibits cutmarks and characteristic marrow-yielding split fractures of the mandibular corpus, as well as a specimen with possibly anthropogenic flaking scars, similar to the one presented here (Tourloukis et al. 2016: Figure 8V). Finally, noteworthy is the taphonomic interpretation of the Kalamakia assemblage, which parallels the situation of Apidima Cave A. The researchers report the periodic use of the cave by humans, who exploited both medium-sized ungulates and tortoises; in addition, carnivore scavenging, predominantly by canids, and short-term use of the cave by non-human predators has also been identified (Darlas and Psathi 2016; Kolendrianou et al. 2020). Carnivore-inflicted damage has also been found on one of the Neanderthal specimens from the site (Camarós 2017; Harvati et al. 2013). Further comparison with the remaining Upper Paleolithic sites of the area is currently not possible due to the lack of detailed taphonomic descriptions.

Overall, the taxonomic and taphonomic signature of the Apidima Cave A faunal collection seemingly presents more similarities to Middle Paleolithic assemblages from the Mani region. This aligns with the presence of Mousterian lithic artifacts at the cave floor deposits (Background Section above; de Lumley et al. 2024; Harvati and Delson 1999) and is consistent with the available U-series dates of the stalagmitic floor capping the Cave A sedimentary sequence, including the new dates reported here, which provide a *terminus ante quem* for the sequence ca. 17 ka.

In terms of subsistence practices and hominin behavior in the Mani Peninsula, our taphonomic study implies that ungulate carcasses were processed for meat and marrow extraction. Oblique cut marks found on the diaphysis of a metapodial indicate skinning practices (e.g., Blasco et al. 2019, Soulier and Morin 2016), while oblique slicing marks long bone diaphyseal fragments possibly occurred during defleshing (Soulier and Costagmano 2017). Marrow processing seems to have predominantly employed cold extraction techniques directed at the medullary marrow of ungulate limbs and mandibles, as indicated by the presence of impact marks and impact flakes (Stiner 2005; Vettese et al. 2020; 2022). Differential burning distribution and carbonization of the medullary cavity (as in the case of the fragmented ungulate phalanges; see Figure 5C–D) likely indicate that bones were broken open first and were subsequently exposed to fire. Burned bones primarily exhibited scorching or carbonization, suggesting that they were exposed to relatively low heating temperatures (Munro et al. 2007; Shipman et al. 1984; Stiner et al. 1995).

Finally, one of the most significant finds of this study was the identification of a likely bone implement among the unprovenanced faunal sample. The specimen's morphology is consistent with experimentally established morphological criteria for the identification of osseous artifacts (Doyon et al. 2021; Mateo-Lomba et al. 2023) and is similar to other archaeological examples of flaked/retouched bones from the Middle Paleolithic, including an excavated artifact from the Middle Paleolithic site Mavri Spilia, located nearby in the Mani peninsula (Doyon et al. 2021; Ono 2006; Romandini et al. 2015; Tourloukis et al. 2016). While we recognize the interpretative limitations imposed by the absence of contextual information and the isolated occurrence of the find, it remains an important addition to the behavioral repertoire of the Cave A hominins.

CONCLUSION

The present study provided a detailed assessment of the faunal remains collected during the 1970s–80s test excavations at Apidima Cave A. Our results confirm the contribution of multiple biotic, i.e., hominins and carnivorans, and abiotic agents (e.g., water) and provide a new minimum age for the deposits of ca. 17 ka based on U-series dating of flowstone capping the sediments. The multivariate taphonomic investigation of the remains successfully discerned hominins as the primary modification agents and provided evidence for the occasional presence of carnivorans at the cave. However, traces of differential preservation and weathering between bones occurring within the same context suggest that the assemblage may be time-averaged and/or mixed, most likely due to erosional processes but also due to post-excavation curation of the materials. Given the complex taphonomic history of the remains, as well as the lack of detailed contextual information, on-site investigations, and the implementation of further interdisciplinary laboratory techniques are necessary to understand potential differences in spatial or temporal contextual provenance. Despite the aforementioned limited amount of available material and the contextual challenges, the faunal assemblage discussed here exhibits common attributes with other Paleolithic sites from the region. This fact highlights the potential of further addressing hominin site use in the wake of future work aiming to obtain a more representative and carefully contextualized faunal sample from the site, but also contributing further data to explorations of hominin activity and subsistence in the Peloponnese.

ACKNOWLEDGMENTS

We thank the three anonymous reviewers for their constructive feedback, which helped improve our manuscript. We extend our gratitude to the Ephorate of Paleoanthropology and Speleology (Hellenic Ministry of Culture) for awarding us permission to study the materials (permit nr. 6Σ0Σ46NKOT-44Z) and to Dr. Myrsini Kouloukoussa (Museum of Anthropology, Medical School, National and Kapodistrian University of Athens) for her support and collaboration. This research was supported by the ERC Consolidator Grant ERC-CoG-724703 ("CROSSROADS"), the ERC-AdG-101019659 ("FIRSTSTEPS"), and the German Research Foundation (DFG FOR 2237), all awarded to K. Harvati. E.R., G.E.K., V.T., and K.H. were also supported by the Deutsche Forschungsgemeinschaft (DFG Project no. 463225251). K.H. is also supported by the Carl Friedrich Siemens Foundation. We also thank the three anonymous reviewers whose comments greatly improved the manuscript.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available on request from the corresponding author.

CONFLICT OF INTEREST

The authors declare no conflict of interest.

AUTHOR CONTRIBUTIONS

ER: Conceptualization, Formal analysis, Investigation, Visualization, Writing- Original draft, Writing – Review & Editing; **GEK**: Validation, Supervision, Writing - Review & Editing; **VT**: Writing - Review & Editing; **NCT:** Writing - Review & Editing; **RG:** Investigation, Writing- Review & Editing; **QS:** Investigation, Writing- Review & Editing; **PK:** Writing - Review & Editing; **VGG:** Resources, Writing - Review & Editing; **KE:** Resources, Writing - Review & Editing; **KH:** Conceptualization, Resources, Project administration, Supervision, Funding acquisition, Writing – Original draft, Writing – Review & Editing.

REFERENCES

Athanassiou, A., 2022. The fossil record of continental hippopotamids (Mammalia: Artiodactyla: Hippopotamidae) in Greece. In: Vlachos, E. (Ed.), Fossil Vertebrates of Greece Vol. 2: Laurasiatherians, Artiodactyles, Perissodactyles, Carnivorans, and Island Endemics. Springer International Publishing, Cham, pp. 281–299.

Bartsiokas, A., Arsuaga, J.L., Aubert, M., Grün, R., 2017. U-series dating and classification of the Apidima 2 hominin from Mani Peninsula, Southern Greece. J. Hum. Evol. 109, 22–29.

Basiakos, Y., 1993. Dating of Fossils from Caves and Speleothems: Evidence from Electron Spin Resonance (ESR) Technique, the Study of Underground Karst Morphology and the Relevant Radiometric and Geological Conditions in Speleoenvironments of Dyros, Mani. Ph.D. Dissertation. National and Kapodistrian University of Athens.

Bauer, C.C., Benazzi, S., Darlas, A., Harvati, K., 2018. Geometric morphometric analysis and internal structure measurements of the Neanderthal lower fourth premolars from Kalamakia, Greece. Quatern. Int. 497, 14–21. https://doi.org/10.1016/j.quaint.2018.01.035

Behrensmeyer, A.K., 1978. Taphonomic and ecologic information from bone weathering. Paleobiology 4(2), 150–162. https://doi.org/10.1017/S0094837300005820

Binford, L.R., 1978. Nunamiut Ethnoarchaeology. Academic Press, New York.

Binford, L.R., 1981. Bones: Ancient Men and Modern Myths. Academic Press, New York.

Blasco, R., Rosell, J., Arilla, M., Margalida, A., Villalba, D., Gopher, A., Barkai, A., 2019. Bone marrow storage and delayed consumption at Middle Pleistocene Qesem Cave, Israel (420 ka to 200 ka). Sci. Adv. 5, eaav9822.

Blumenschine, R.J., Selvaggio, M.M., 1988. Percussion marks on bone surfaces as a new diagnostic of hominid behaviour. Nature 333(6175), 763–765. https://doi.org/10.1038/333763a0

Bowen, F., Carden, R.F., Daujat, J., Grouard, S., Miller, H., Perdikaris, S., Sykes, N., 2016. *Dama* dentition: a new tooth eruption and wear method for assessing the age of fallow deer (*Dama dama*). Int. J. Osteoarchaeol. 26(6), 1089–1098. https://doi.org/10.1002/oa.2523

Camarós, E., C.M., Rosell, J., Díez, J.C., Blasco, R., Duhig, C., Darlas, A., Harvati, K., Jordá, J., Montes, L., Villaverde, V., Rivals, F., 2017. Hunted or scavenged Neanderthals? Taphonomic approach to hominin fossils with carnivore damage. Int. J. Osteoarchaeol. *27*, 606–620.

Capaldo, S.D., Blumenschine, R.J., 1994. A quantitative diagnosis of notches made by hammerstone percussion and carnivore gnawing on bovid long bones. Am. Antiq. 59(4), 724–748. https://doi.org/10.2307/282345

Darlas, A., 1995. Τα λίθινα εργαλεία του σκελετού ΛΑΟ 1/Σ 3 (Απήδημα – Μάνη). Acta Anthropol. 1, 59–62.

Darlas, A., 2012. Geomorphological evolution and occupation of the caves of the western coast of Mani during the late Pleistocene and Holocene. In: Zacharias, N., Georgakopoulou, M., Polykreti, K., Fakorellis, G., Vakoulis, T. (Eds.), Proceedings of the 5th Symposium of the Greek Archaeometry Society. Papazisi, Athens, pp. 237–253.

Darlas, A., Psathi, E., 2016. The Middle and Upper Paleolithic on the western coast of the Mani Peninsula (southern Greece). In: Harvati, K., Roksandic, M. (Eds.), Paleoanthropology of the Balkans and Anatolia. Vertebrate Paleobiology and Paleoanthropology. Springer, Dordrecht, pp. 95–117.

de Lumley, H., Darlas, A., Cauche, D., Perrenoud, C., Saos, T., Falguères, C., Voinchet, P., de Lumley, M.-A., Guipert, G., Matzanas, C., 2024. Réflexions sur la datation des deux crânes humains Apidima 1 et Apidima 2 découverts dans la cavité Apidima A, Aréopoli, péninsule du Mani, Laconie, Péloponnèse, Grèce. L'Anthropologie 128(1), 103239.

Di Stefano, G., 1995. Identification of fallow deer remains on the basis of its skeletal features: taxonomical considerations. Boll. Soc. Paleontol. Ital. 34, 323–331.

Domínguez-Rodrigo, M., de Juana, S., Galán, A.B., Rodríguez, M., 2009. A new protocol to differentiate trampling marks from butchery cut marks. J. Archaeol. Sci. 36(12), 2643–2654. https://doi.org/10.1016/j.jas.2009.07.017

Domínguez-Rodrigo, M., Egeland, C.P., Cobo-Sánchez, L., Baquedano, E., Hulbert, R.C., 2022. Sabertooth carcass consumption behavior and the dynamics of Pleistocene large carnivoran guilds. Sci. Rep. 12(1), 6045. https://doi.org/10.1038/s41598-022-09480-7

Doyon, L., Li, Z., Wang, H., Geis, L., d'Errico, F., 2021. A 115,000-year-old expedient bone technology at Lingjing, Henan, China. PLoS One 16(5), e0250156. https://doi.org/10.1371/journal.pone.0250156

Fernàndez, H., 2001. Ostéologie comparée des petits ruminants eurasiatiques sauvages et domestiques (genres *Rupicapra, Ovis, Capra* et *Capreolus)*: diagnose différentielle du squelette appendiculaire. Ph.D. Dissertation. University of Geneva.

Fernández-Jalvo, Y., Andrews, P., 2016. Atlas of Taphonomic Identifications: 1001+ Images of Fossil and Recent Mammal Bone Modification. Springer, Dordrecht.

Gifford-Gonzalez, D., 2018. An Introduction to Zooarchaeology. Springer, Cham.

Grayson, D.K., 1984. Quantitative Zooarchaeology: Topics in the Analysis of Archaeological Faunas. Academic Press, Orlando.

Harvati K., 2026. The role of the Eastern Mediterranean in human evolution: recent results from Greece. J. R. Anthropol. Inst. https://doi.org/10.1111/1467-9655.70138

Harvati, K., Darlas, A., Bailey, S.E., Rein, T.R., El Zaatari, S., Fiorenza, L., Kullmer, O., Psathi, E., 2013. New Neanderthal remains from Mani peninsula, southern Greece: the Kalamakia Middle Paleolithic cave site. J. Hum. Evol. 64(6), 486–499. https://doi.org/10.1016/j.jhevol.2013.02.002

Harvati, K., Delson, E., 1999. Conference report: paleoanthropology of the Mani Peninsula (Greece). J. Hum. Evol. 36(3), 343–348.

Harvati, K., Douka, K., Shao, Q., Grün, R., Thompson, N., Tourloukis, V., Gorgoulis, V., Evangelou, K., Karkanas, P., 2026a. New radiometric dates for the Apidima Caves C and D (Greece) Upper Paleolithic Legacy Collections. PaleoAnthropology 2026:2.

Harvati, K., Panagopoulou, E., Karkanas, P., 2003. First Neanderthal remains from Greece: the evidence from Lakonis. J. Hum. Evol. 45, 465–473.

Harvati, K., Panagopoulou, E., Runnels, C., 2009. The paleoanthropology of Greece. Evol. Anthropol. 18, 131–143.

Harvati, K., Röding, C., Bosman, A.M., Karakostis, F.A., Grün, R., Stringer, C., Karkanas, P., Thompson, N.C., Koutoulidis, V., Moulopoulos, L.A., Gorgoulis, V.G., Kouloukoussa, M., 2019. Apidima Cave fossils provide earliest evidence of *Homo sapiens* in Eurasia. Nature 571(7766), 500–504. https://doi.org/10.1038/s41586-019-1376-z

Harvati, K., Roditi, E., Grün, R., Thompson, N., Röding, C., Gorgoulis, V., Evangelou, K., 2026b. Middle Pleistocene funerary ritual at Apidima? An examination of the evidence. PaleoAnthropology 2026:2.

Harvati, K., Stringer, C., Karkanas, P., 2011. Multivariate analysis and classification of the Apidima 2 cranium from Mani, Southern Greece. J. Hum. Evol. 60, 246–250.

Haynes, G., 1983. A guide for differentiating mammalian carnivore taxa responsible for gnaw damage to herbivore limb bones. Paleobiology 9(2), 164–172. https://doi.org/10.1017/S0094837300007545

Hillson, S., 2005. Teeth (2nd edition). Cambridge University Press, Cambridge.

Jacobsen, T.W., 1973. Excavation in the Franchthi Cave, 1969-1971, part I. Hesperia 42(1), 45–88.

Jin, J.J.H., Mills, E.W., 2011. Split phalanges from archaeological sites: evidence of nutritional stress? J. Archaeol. Sci. 38(8), 1798–1809. https://doi.org/10.1016/j.jas.2011.03.013

Jin, M., Jiao, Y., Liu, Y., Shao, Q., Kong, X., Wang, Y., 2022. High-precision MC-ICP-MS static measurements of uranium isotopes using Faraday cups. Chin. Sci. Bull. 67, 2651–2661.

Johnson, E., 1985. Current developments in bone technology. In: Schiffer, M.B. (Ed.), Advances in Archaeological Method and Theory. Academic Press, San Diego, pp. 157–235.

Karali-Gianakopoulou, I., 1995. Preliminary report on malacological material found in Apidima (Laconia). Acta Anthropol. 1, 159–163.

Karkanas, P., Koumouzelis, M., Kozlowski, J.K., Sitlivy, V., Sobczyk, K., Berna, F., Weiner, S., 2004. The earliest evidence for clay hearths: Aurignacian features in Klisoura Cave 1, southern Greece. Antiquity 78(301), 513–525. https://doi.org/10.1017/S0003598X00113195

Karkanas, P., Kyparissi-Apostolika, N., 2024. Revisiting Palaeolithic combustion features of Theopetra Cave: a diachronic use of dung and peat as fuel. J. Archaeol. Sci. 165, 105958. https://doi.org/10.1016/j.jas.2024.105958

Kolendrianou, M., Ligkovanlis, S., Maniakas, I., Tzortzi, M., Iliopoulos, G., 2020. The Palaeolithic cave of Kalamakia (Mani Peninsula), Greece: new insights on the palaeoenvironment using microvertebrates and mesowear analysis of ruminant teeth. Heliyon 6(5), e03958. https://doi.org/10.1016/j.heliyon.2020.e03958

Koumouzelis, M., Ginter, B., Kozlowski, J.K., Pawlikowski, M., Bar-Yosef, O., Albert, R.M., Litynska-Zajac, M., Stworzewicz, E., Wojtal, P., Lipecki, G., Tomek, T., Bochenski, Z.M., Pazdur, A., 2001. The Early Upper Palaeolithic in Greece: the excavations in Klisoura Cave. J. Archaeol. Sci. 28(5), 515–539. https://doi.org/10.1006/jasc.2000.0599

Lax, E., 1995. Quaternary faunal remains from the cave site of Apidima (Laconia, Greece). Acta Anthropol. 1, 127–158.

Liritzis, Y., Maniatis, Y., 1989. ESR experiments on Quaternary calcites and bones for dating purposes. J. Radioanal. Nuclear Chem. 129(1), 3–21. https://doi.org/10.1007/BF02037564

Lister, A.M., 1996. The morphological distinction between bones and teeth of fallow deer (*Dama dama*) and red deer (*Cervus elaphus*). Int. J. Osteoarchaeol. 6(2), 119–143.

Lombardo, S., Thompson, N.C., Gorgoulis, V.G., Evangelou, K., Harvati, K., Tourloukis, V., 2026a. Early Upper Paleolithic technical behavior at Apidima (Peloponnese, Greece): technological analysis of the lithic assemblage from the Cave C legacy collection. PaleoAnthropology 2026:2.

Lombardo, S., Thompson, N.C., Roditi, E., Evangelou, K., Gorgoulis, V.G., Harvati, K., Tourloukis, V., 2026b. Apidima Cave at the Last Glacial Maximum: the lithic Legacy Collection of Cave D (Peloponnese, Greece). PaleoAnthropology 2026:2.

López-González, F., Grandal-d'Anglade, A., Vidal-Romaní, J.R., 2006. Deciphering bone depositional sequences in caves through the study of manganese coatings. J. Archaeol. Sci. 33(5), 707–717. https://doi.org/10.1016/j.jas.2005.10.006

Lyman, R.L., 1984. Broken bones, bone expediency tools, and bone pseudotools: lessons from the blast zone around Mount St. Helens, Washington. Am. Antiq. 49(2), 315–333. https://doi.org/10.2307/280021

Lyman, R.L., 1994. Vertebrate Taphonomy. Cambridge University Press, Cambridge.

Lyman, R.L., 2008. Quantitative Paleozoology. Cambridge University Press, Cambridge.

Ma, S., Doyon, L., Zhang, Y., Li, Z., 2023. Disentangling carcass processing activities and the state of worked hide from use-wear patterns on expedient bone tools: a preliminary experiment. J. Archaeol. Sci. Rep. 49, 104027. https://doi.org/10.1016/j.jasrep.2023.104027

Marin-Arroyo, A.B., 2011. Palaeolithic human subsistence in Mount Carmel (Israel). A taphonomic Assessment of Middle and Early Upper Palaeolithic faunal remains from Tabun, Skhul and el-Wad. Int. J. Osteoarchaeol. 23, 254–273.

Mata-González, M., Starkovich, B.M., Zeidi, M., Conard, N.J., 2022. New zooarchaeological perspectives on the early Upper Paleolithic Rostamian sequence of Ghar-e Boof (southern Zagros Mountains, Iran). Quatern. Sci. Rev. 279, 107350. https://doi.org/10.1016/j.quascirev.2021.107350

Mata-González, M., Starkovich, B.M., Zeidi, M., Conard, N.J., 2023. Evidence of diverse animal exploitation during the Middle Paleolithic at Ghar-e Boof (southern Zagros). Sci. Rep. 13, 19006. https://doi.org/10.1038/s41598-023-45974-8

Mateo-Lomba, P., Andreu, O., Isabel, C., 2023. Experimental bone toolmaking: a proposal of technological analytical principles to knapped bones. J. Lithic Stud. 10(2), 24

Mompherratou, E., Pitsios, T., 1995. Apidima Cave Gamma: the burial of female skeleton LAO 1/S 3. Acta Anthropol. 1, 27–51.

Morin, E., 2012. Testing the hypotheses. In: Morin, E. (Ed.), Reassessing Paleolithic Subsistence: The Neandertal and Modern Human Foragers of Saint-Césaire. Cambridge University Press, Cambridge, pp. 180–211.

Morlan, R.E., 1984. Toward the definition of criteria for the recognition of artificial bone alterations. Quatern. Res. 22(2), 160–171.

Munro, L.E., Longstaffe, F.J., White, C.D., 2007. Burning and boiling of modern deer bone: effects on crystallinity and oxygen isotope composition of bioapatite phosphate. Palaeogeogr. Palaeoclimatol. Palaeoecol. 249, 90–102.

Naumann, D., Gorgoulis, V.G., Evangelou, K., Harvati, K., 2026. New bio-anthropological insights on the possible Upper Paleolithic human remains from Apidima Cave C (Peloponnese). PaleoAnthropology 2026:2.

Olsen, S.L., Shipman, P., 1988. Surface modification on bone: trampling versus butchery. J. Archaeol. Sci. 15(5), 535–553. https://doi.org/10.1016/0305-4403(88)90081-7

Ono, A., 2006. Flaked bone tools and the Middle to Upper Paleolithic transition: a brief perspective. Archaeol. Ethnol. Anthropol. Eurasia 28, 38–47.

Pales, L., Lambert, C., 1971. Atlas ostéologique: pour servir à l'identification des mammifères du Quaternaire. Editions du Centre national de la recherche scientifique, Paris.

Panagopoulou, E., Karkanas, P., Tsartsidou, G., Kotjabopoulou, E., Harvati, K., Ntinou, M., 2013. Late Pleistocene archaeological and fossil human evidence from Lakonis Cave, Southern Greece. J. Field Archaeol. 29(3–4), 323–349. https://doi.org/10.1179/jfa.2004.29.3-4.323

Pérez Ripoll, M., 1988. Estudio de la secuencia del desgaste de los molares de la "*Capra pyrenaica*" de yacimientos prehistóricos. Arch. Prehist. Lev. 18, 83–127.

Perlès, C., Vanhaeren, M., 2010. Black *Cyclope neritea* marine shell ornaments in the Upper Palaeolithic and Mesolithic of Franchthi Cave, Greece: arguments for intentional heat treatment. J. Field Archaeol. 35(3), 298–309.

Phoca-Cosmetatou, N., 2005. Landscape use in northeast Italy during the Upper Palaeolithic. Preist. Alp. 41(2005), 23–49.

Pickering, T.R., Egeland, C.P., 2006. Experimental patterns of hammerstone percussion damage on bones: implications for inferences of carcass processing by humans. J. Archaeol. Sci. 33(4), 459–469. https://doi.org/10.1016/j.jas.2005.09.001

Pitsios, T., 1979. Palaeoanthropological finds of Inner Mani. Anthropos 6, 98–105.

Pitsios, T., 1985. Palaeoanthropological research in the Apidima site of Mesa Mani II. Archaeologia 15, 26–33.

Pitsios, T., 1999. Paleoanthropological research at the cave site of Apidima and the surrounding region (South Peloponnese, Greece). Anthropol. Anz. 57, 1–11.

Pitsios, T., Liebhaber, B., 1995. Research conducted in Apidima and the surrounding region. Acta Anthropol. 1, 175–179.

Pokines, J.T., Higgs, N., 2015. Macroscopic taphonomic alterations to human bone recovered from marine environments. J. Forensic Identif. 65(6), 953–984.

Reitz, E.J., Wing, E.S., 2008. Zooarchaeology (2nd edition). Cambridge University Press, Cambridge.

Roditi, E., Starkovich, B.M., 2022. Investigating Middle Palaeolithic subsistence: zooarchaeological perspectives on the potential character of hominin climate refugia in Greece. J. Quatern. Sci. 37, 181–193.

Romandini, M., Cristiani, E., Peresani, M., 2015. A retouched bone shaft from the Late Mousterian at Fumane cave (Italy). Technological, experimental and micro-wear analysis. C. R. Palevol 14(1), 63–72. https://doi.org/10.1016/j.crpv.2014.08.001

Rosell, J., Blasco, R., Huguet, R., Caceres, I., Saladie, P., Rivals, F., Bennasar, M., Bravo, P., Campeny, G., Esteban-Nadal, M., Fernández-Laso, C., Gabucio, M.J., Ibáñez, N., Martín, P., Muñoz, L., Rodríguez-Hidalgo, A., 2012. Occupational patterns and subsistence strategies in Level J of Abric Romaní. In: Carbonell i Roura, E. (Ed.) High Resolution Archaeology and Neanderthal Behavior. Vertebrate Paleobiology and Paleoanthropology. Springer, Dordrecht, pp. 313–372. https://doi.org/10.1007/978-94-007-3922-2_8

Sala, N., Arsuaga, J.L., 2018. Regarding beasts and humans: a review of taphonomic works with living carnivores. Quatern. Int. 466, 131–140. https://doi.org/10.1016/j.quaint.2016.03.011

Shipman, P., Foster, G., Schoeninger, M., 1984. Burnt bones and teeth: an experimental study of color, morphology, crystal structure and shrinkage. J. Archaeol. Sci. 11 (4), 307–325.

Shipman, P., Walker, A., Van Couvering, J.A., Hooker, P.J., Miller, J., 1981. The Fort Ternan hominoid site, Kenya: geology, age, taphonomy and paleoecology. J. Hum. Evol. 10(1), 49–72. https://doi.org/10.1016/S0047-2484(81)80025-5

Soulier, M.C., Costamagno, S., 2017. Let the cutmarks speak! Experimental butchery to reconstruct carcass processing. J. Archaeol. Sci. Rep. 11, 782–802.

Soulier, M.C., Morin, E., 2016. Cutmark data and their implications for the planning depth of Late Pleistocene societies. J. Hum. Evol. 97, 37–57.

Speth, J., 2012. Middle Palaeolithic subsistence in the Near East: zooarchaeological perspectives—past, present and future. Before Farm. 2, 1–45.

Starkovich, B.M., 2017. Paleolithic subsistence strategies and changes in site use at Klissoura Cave 1 (Peloponnese, Greece). J. Hum. Evol. 111, 63–84. https://doi.org/10.1016/j.jhevol.2017.04.005

Starkovich, B.M., Elefanti, P., Karkanas, P., Panagopoulou, E., 2018a. Site use and maintenance in the Middle Palaeolithic at Lakonis I (Peloponnese, Greece). J. Paleolit. Archaeol. 3(2), 157–186. https://doi.org/10.1007/s41982-018-0006-x

Starkovich, B.M., Munro, N.D., Stiner, M.C., 2018b. Terminal Pleistocene subsistence strategies and aquatic resource use in southern Greece. Quatern. Int. 465, 162–176. https://doi.org/10.1016/j.quaint.2017.11.015

Stiner, M.C., 1991. Food procurement and transport by human and non-human predators. J. Archaeol. Sci. 18 (4), 455–482.

Stiner, M.C., 1994. Honor Among Thieves: A Zooarchaeological Study of Neandertal Ecology. Princeton University Press, Princeton.

Stiner, M.C., 2005. The Faunas of Hayonim Cave, Israel: A 200,000-year Record of Paleolithic Diet, Demography, and Society (No. 48). Harvard University Press, Cambridge, MA.

Stiner, M.C., 2006. Middle Paleolithic subsistence ecology in the Mediterranean region. In: Hovers, E., Kuhn, S.L. (Eds.), Transitions Before the Transition. Interdisciplinary Contributions to Archaeology. Springer, Boston, MA, pp. 213–231. https://doi.org/10.1007/0-387-24661-4_12

Stiner, M.C., 2009. Prey choice, site occupation intensity & economic diversity in the Middle–Early Upper Palaeolithic at the Üçağizli Caves, Turkey. Before Farm. 2009(3), 1–20.

Stiner, M.C., 2013. An unshakable Middle Paleolithic? Trends versus conservatism in the predatory niche and their social ramifications. Curr. Anthropol. 54(S8), S288–S304.

Stiner, M.C., Kozłowski, J., Kuhn, S.L., Karkanas, P., Koumouzelis, M., 2010. Klissoura Cave 1 and the Upper Paleolithic of southern Greece in cultural and ecological context. Eur. Prehist. 7(2), 309–321.

Stiner, M.C., Kuhn, S.L., Weiner, S., Bar-Yosef, O., 1995. Differential burning, recrystallization, and fragmentation of archaeological bone. J. Archaeol. Sci. 22(2), 223–237. https://doi.org/10.1006/jasc.1995.0024

Stiner, M.C., Munro, N.D., Starkovich, B.M., 2012. Material input rates and dietary breadth during the Upper Paleolithic through Mesolithic at Franchthi and Klissoura 1 Caves (Peloponnese, Greece). Quatern. Int. 275, 30–42. https://doi.org/10.1016/j.quaint.2011.08.006

Stiner, M.C., Munro, N.D., Surovell, T.A., 2000. The tortoise and the hare: small-game use, the broad-spectrum revolution, and Paleolithic demography. Curr. Anthropol., 41(1), 39–79.

Stiner, M.C., Munro, N.D., Surovell, T.A., Tchernov, E., Bar-Yosef, O., 1999. Paleolithic population growth pulses evidenced by small animal exploitation. Science 283(5399), 190–194.

Tourloukis, V., Harvati, K., 2018. The Palaeolithic record of Greece: a synthesis of the evidence and a research agenda for the future. Quatern. Int. 466, 48–65. https://doi.org/10.1016/j.quaint.2017.04.020

Tourloukis, V., Thompson, N., Garefalakis, C., Karkanas, P., Konidaris, G.E., Panagopoulou, E., Harvati, K., 2016. New Middle Palaeolithic sites from the Mani Peninsula, Southern Greece. J. Field Archaeol. 41(1), 68–83. https://doi.org/10.1080/00934690.2015.1125223

Tsartsidou, G., Gaki-Papanastasiou, K., Maroukian, H., 2002. Coastal evolution of the inner Lakonic Gulf in the late Pleistocene-Holocene period. Proceedings of the 6th Pan-Hellenic Geographical Conference of the Hellenic Geographical Society, Thessaloniki, Greece, pp. 380–387.

Tsoukala, E., 1999. Quaternary large mammals from the Apidima caves (Lakonia, S. Peloponnese, Greece). Beitr. Paläontol. 24, 207–229.

Tzortzi, M., Arvanitis, A., Iliopoulos, G., Darlas, A., 2024a. The fossil record of ungulates from the late Pleistocene locality of Melitzia cave, Mani Peninsula, Greece. PalZ. 98(4), 603–636. https://doi.org/10.1007/s12542-024-00704-x

Tzortzi, M., Sianis, P.D., Iliopoulos, G., Darlas, A., 2024b. Carnivores from the late Pleistocene locality Melitzia Cave (Mani peninsula, Greece). Hist. Biol. 36(2), 266–284. https://doi.org/10.1080/08912963.2022.2161380

Vettese, D., Blasco, R., Cáceres, I., Gaudzinski-Windheuser, S., Moncel, M.-H., Hohenstein, U.T., Daujeard, C., 2020. Towards an understanding of hominin marrow extraction strategies: a proposal for a percussion mark terminology. Archaeol. Anthropol. Sci. 12(2), 48. https://doi.org/10.1007/s12520-019-00972-8

Vettese, D., Borel, A., Blasco, R., Chevillard, L., Stavrova, T., Thun Hohenstein, U., Arzarello, M., Moncel, M.H., Daujeard, C., 2022. New evidence of Neandertal butchery traditions through the marrow extraction in southwestern Europe (MIS 5–3). PLoS One 17(8), e0271816.

Villa, P., Castel, J.-C., Beauval, C., Bourdillat, V., Goldberg, P., 2004. Human and carnivore sites in the European Middle and Upper Paleolithic: similarities and differences in bone modification and fragmentation. Rev. Paleobiol. 23(2), 705–730.

Villa, P., Mahieu, E., 1991. Breakage patterns of human long bones. J. Hum. Evol. 21(1), 27–48. https://doi.org/10.1016/0047-2484(91)90034-S

White, W.B., Vito, C., Scheetz, B.E., 2009. The mineralogy and trace element chemistry of black manganese oxide deposits from caves. J. Cave Karst Stud. 71(2), 136–143.

Special Issue: The Apidima Legacy Collections: New Analyses and Interpretations

Supplement 1 to Taphonomy of the Faunal Remains from Apidima Cave A (Mani Peninsula, Greece)

EFFROSYNI RODITI
Paleoanthropology, Institute for Archaeological Sciences and Senckenberg Center for Human Evolution and Paleoenvironments, Eberhard Karls Universität Tübingen; GERMANY; effrosyni.roditi@uni-tuebingen.de

GEORGE E. KONIDARIS
School of Geology, Aristotle University of Thessaloniki, GREECE; and, Paleoanthropology, Institute for Archaeological Sciences, Department of Geosciences, Eberhard Karls University of Tübingen, GERMANY; gkonidaris@geo.auth.gr

VANGELIS TOURLOUKIS
University of Ioannina, School of Philosophy, Department of History and Archaeology, Ioannina, GREECE; Paleoanthropology, Institute for Archaeological Sciences, Eberhard Karls University of Tübingen, GERMANY; and, Museum of Anthropology, Medical School, National and Kapodistrian University of Athens, Athens, GREECE; vtourloukis@uoi.gr

NICHOLAS C. THOMPSON
Paleoanthropology, Institute for Archaeological Sciences, Department of Geosciences, Eberhard Karls Universität Tübingen, GERMANY; and, Museum of Anthropology, Medical School, National and Kapodistrian University of Athens, Athens, GREECE; nikothompso@yahoo.com

RAINER GRÜN
Research School of Earth Sciences, The Australian National University, Canberra, ACT, AUSTRALIA; School of Geography, Nanjing Normal University, Nanjing, 210023, CHINA; DFG Center for Advanced Studies 'Words, Bones, Genes, Tools', Eberhard Karls Universität Tübingen; and, HUMAN ORIGINS – Cluster of Excellence for Integrative Human Origins Studies (EXC 3101), Eberhard Karls University of Tübingen, GERMANY; rwgruen@gmail.com

QINGFENG SHAO
School of Geography, Nanjing Normal University, Nanjing, 210023, CHINA; qingfengshao@njnu.edu.cn

PANAGIOTIS KARKANAS
M.H. Wiener Laboratory for Archaeological Science, American School of Classical Studies at Athens, Athens, GREECE; tkarkanas@ascsa.edu.gr

VASSILIS G. GORGOULIS
Department of Histology and Embryology, Medical School, National and Kapodistrian University of Athens, Athens; Biomedical Research Foundation of the Academy of Athens, Athens, GREECE; and, Faculty of Biology, Medicine and Health, University of Manchester, Manchester, UNITED KINGDOM; vgorg@med.uoa.gr

KONSTANTINOS EVANGELOU
Department of Histology and Embryology, and Museum of Anthropology, Medical School, National and Kapodistrian University of Athens, Athens; GREECE; cnevagel@med.uoa.gr

KATERINA HARVATI
Paleoanthropology, Institute for Archaeological Sciences and Senckenberg Center for Human Evolution and Paleoenvironments, Eberhard Karls Universität Tübingen; DFG Center for Advanced Studies 'Words, Bones, Genes, Tools', Eberhard Karls Universität Tübingen; HUMAN ORIGINS – Cluster of Excellence for Integrative Human Origins Studies (EXC 3101), Eberhard Karls University of Tübingen, GERMANY; Centre for Early Sapiens Behaviour (SapienCE), University of Bergen, NORWAY; and, Museum of Anthropology, Medical School, National and Kapodistrian University of Athens, Athens, GREECE; katerina.harvati@ifu.uni-tuebingen.de

SUPPLEMENT 1
This supplement contains: Supplementary Information Tables 1–2.

PaleoAnthropology 2026:2 supplement to Roditi et al. 2026:2 OPEN ACCESS ISSN 1545-0031
Paleoanthropology Society & European Society for the study of Human Evolution

Supplementary Table 1. Quantification of bone breakage patterns following the recording system established by Villa and Mahieu (1991).

Outline		Longitudinal		Curved/V-shaped		Transverse	
		n	%	*n*	%	*n*	%
Angle	Right	41	46%	29	29%	33	70%
	Oblique	36	40%	63	64%	14	30%
	Intermediate	13	14%	7	7%	0	0%
Edge	Smooth	48	53%	69	70%	40	85%
	Jagged	25	28%	17	17%	6	13%
	Mixed	16	18%	13	13%	0	0%
	Total	90	100%	99	100%	47	100%

Supplementary Table 2. Anatomical distribution of medium-sized ungulate remains from Apidima Cave A (after Stiner 2005).

Ungulate Skeleton	MNE in Skeleton	NISP	MNE	MAU
Antler/Horn	2	2	2	1.00
1/2 Cranium	2	2	1	0.50
Mandible	2	4	2	1.00
Atlas	1	0	0	0.00
Axis	1	0	0	0.00
Cervical	5	0	0	0.00
Thoracic	13	1	1	0.08
Lumbar	7	0	0	0.00
Rib	26	2	1	0.04
Sacrum	1	0	0	0.00
Innominate	2	4	2	1.00
Scapula	2	0	0	0.00
Humerus	2	3	3	1.50
Radius	2	1	1	0.50
Ulna	2	0	0	0.00
Metacarpal	2	0	0	0.00
Femur	2	1	1	0.50
Tibia	2	1	1	0.50
Astragalus	2	0	0	0.00
Calcaneum	2	1	1	0.50
Metatarsal	2	3	2	1.00
Phalanx 1	8	3	2	0.25
Phalanx 2	8	1	1	0.13
Phalanx 3	8	6	3	0.38
Total	**106**	**33**	**22**	**0.21**

Ungulate Skeleton	MNE in Skeleton	NISP	MNE	MAU
Antler/Horn	2	2	2	1.0
Head	4	6	3	0.8
Neck	7	0	0	0.0
Axial	49	0	4	0.1
Upper Front	4	3	3	0.8
Lower Front	6	1	1	0.2
Upper Hind	2	1	1	0.5
Lower Hind	8	5	4	0.5
Feet	24	10	6	0.3
Total	106	33	22	0.2