Taphonomic Analysis of Early Pleistocene Fossil Localities of the Olteţ River Valley, Romania

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submitted: 2 May 2025; revised 11 November 2025; accepted: 12 November 2025

Handling Editor in Chief: Karen Ruebens

PaleoAnthropology **2026:1: 52–81** **https://doi.org/10.48738/2026.iss1.3892** **ISSN 1545-0031**
Paleoanthropology Society & European Society for the study of Human Evolution

ABSTRACT

Though the best documented first appearance of hominins in Eurasia is from Dmanisi, Georgia, there are several earlier sites with traces of hominin presence. Here we present taphonomic analyses of sites from the Olteţ River Valley in Romania, with particular attention to Grăunceanu, which preserves the current earliest evidence of hominins in Europe in the form of cut-marked bones. The Grăunceanu assemblage (n=4,524) is extremely well preserved with highly visible bone surfaces, very little weathering or reworking, and high numbers of nearly complete specimens. Large mammals, especially artiodactyls and perissodactyls, dominate the assemblage, though many smaller taxa are also represented. Carnivores are diverse and well represented, and there is evidence of carnivore modifications on 9.5% of the assemblage. Most specimens show some level of root etching and post-depositional damage; other taphonomic alterations are rare. There is evidence of density-mediated attrition, especially for the Artiodactyla, though in the Perissodactyla the pattern points toward utility-driven attrition. Sedimentological analysis indicates that sediments recovered inside bones from the assemblage are silty sands. Our analyses suggest that the Grăunceanu assemblage was likely accumulated near the paleo-Olteţ river in the Early Pleistocene, perhaps during overbank flooding events in an alluvial plain, capturing evidence of large ungulates, carnivores, and their food remnants, and even a small contribution from hominin activities.

INTRODUCTION

The Olteţ River Valley (ORV) of Romania includes multiple Early Pleistocene (Gelasian) fossil sites that inform our understanding of paleoenvironments in eastern Europe during the time hominins would have first been dispersing into this region. One of these sites, Valea Grăunceanului (hereafter Grăunceanu, abbreviated VGr), is extremely fossiliferous (n= ~5,000 inventoried specimens), with a biogeographically diverse fauna that may be reflective of the role of this region as a faunal crossroad (Croitor et al. 2024; Curran et al. 2021; Terhune et al. 2020; 2021). Recent work has identified multiple rare and unique species present at this site (e.g., pangolins, ostriches, primates) and has extended temporal and geographic ranges for previously identified species from Early Pleistocene Europe (Croitor et al. 2024; Terhune et al. 2020; 2021; Werdelin et al. 2023). Paleoecological reconstructions indicate an environment that was mostly open, with some water resources nearby; multiple indicators suggest the predominant taxon (cervids) at the site may have migrated seasonally (Curran et al. 2021). Radiometric (U-Pb) dates of 1.95 Ma, coupled with the presence of cut-marked bones from Grăunceanu (Curran et al. 2025), suggest that hominins were present in eastern Europe (and perhaps much of Eurasia) earlier than previously established. Here we present a detailed taphonomic analysis of the ORV sites, with a primary focus on the site of Grăunceanu. Understanding the taphonomy of the ORV sites is critical for interpreting site formation processes, abiotic and biotic contributors to the deposition of the remains, and the context for hominin activities at these localities.

BACKGROUND

The Olteţ River Valley of Romania (Figure 1) has yielded multiple fossil sites dated to the Early Pleistocene. These sites, originally discovered in the 1960s, are primarily located in the vicinity of the town of Tetoiu, approximately 50km south of the Carpathian Mountains. Multiple localities have yielded fossil remains, but the most fossiliferous of these localities are Grăunceanu, Fântâna lui Mitilan, and La Pietriș.

Geologically, the ORV is located in the Dacian Basin, a region defined by the Carpathian Mountains to the north and west, the Balkans to the south, and the Black Sea to the east. Deposits in the vicinity of the fossil sites are attributed to the Tetoiu Formation (Andreescu et al. 2011). This formation ranges in thickness across its extent but generally increases as it progresses south to a maximum of 150m. These sediments have predominantly sandy-pebbly facies and are typically richly fossiliferous (Andreescu et al. 1984; Lubenescu et al. 1987; Radulesco and Samson 1990; Samson and Radulesco 1973). Sediments from this formation extend from the base of the Pleistocene (2.588 Ma) to as young as ~1 Ma (Andreescu et al. 2011). The Olteţ River, which runs through this valley, is a tributary of the Danube River (via the Olt River). Importantly, the Danube Valley has been proposed to have been a dispersal corridor for mammals, including hominins, into Western Europe (Conard and Bolus 2003; Higham et al. 2012).

Materials recovered from the ORV fossil sites span a wide variety of mammalian and non-mammalian taxa. Previous work by Radulesco and Samson (1990) identified three faunal horizons (T-1, T-2, and T-3) in the Tetoiu region, which they describe as a fluvio-lacustrine sequence of over 100m in depth. The oldest horizon (T-1) includes the sites of Grăunceanu and La Pietriș, as well as Valea Roșcăi and Dealul Mijlociu. The middle horizon (T-2) includes the sites of Fântâna lui Mitilan, Fântâna Alortiței, La Seci, and Valea Mijlociei, while the youngest horizon (T-3) includes the sites of Dealul Viilor, Gorgonie, Dealul Șasei, Valea Omorîcea, Valea Râpei, Valea Caselor, Valea Teteșului, and Părăsiște.

At Grăunceanu, the most fossiliferous of the ORV sites, excavations were first conducted by Samson and Radulesco of the Emil Racoviţă Institute of Speleology of the Romanian Academy (henceforth ISER) in association with Necrasov from the University of Iași (Necrasov et al. 1961) in the

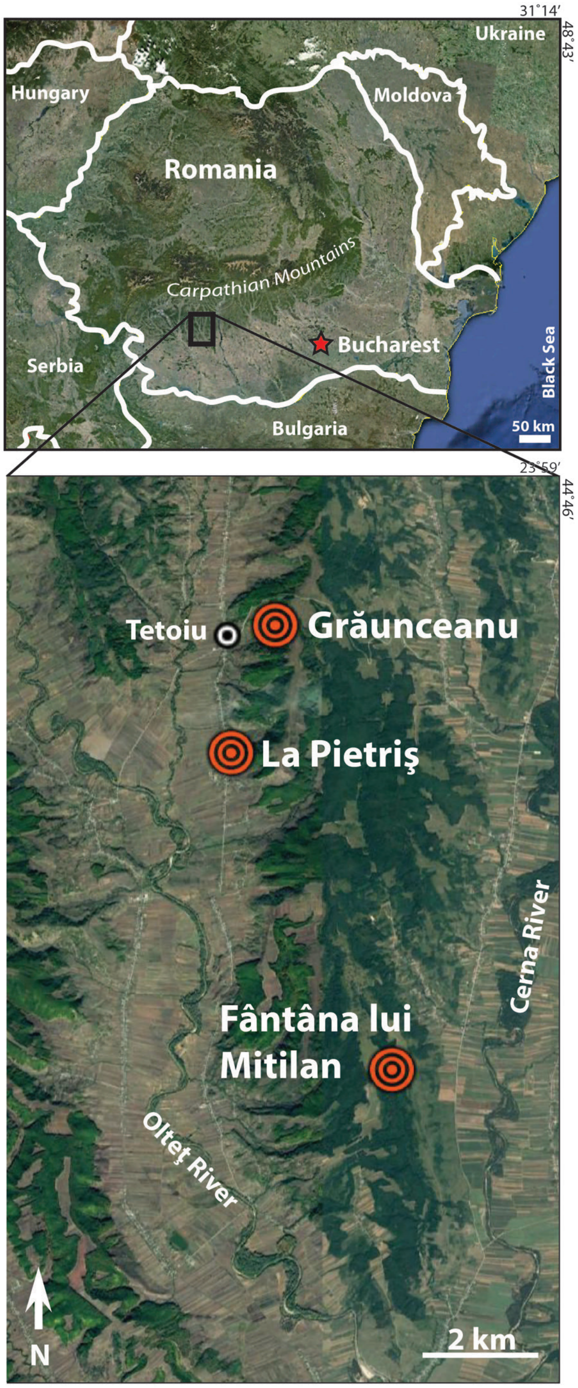


Figure 1. Overview map showing the location of the Olteţ River Valley (top) and overview of the Olteţ River Valley project area including relevant landmarks and fossil localities (bottom).

1960s. Work in the region was continued by Nicolaescu-Plopşor of the Archaeological Institute of the Romanian Academy. In the 1980s, excavations at Grăunceanu undertaken by the Natural History section of the Museum of Oltenia (Craiova, Romania) recovered further remains.

Our recent work in the ORV, which began in 2012, has successfully relocated several of the original sites and identified several small new localities, but has primarily focused on inventorying and analyzing previously excavated fossil materials from multiple localities, including Grăunceanu, Fântâna lui Mitilan, Fântâna Alortiței, La Pietriș, and others. Biochronological assessments of these previously excavated materials by our team (Terhune et al. 2020) suggested Grăunceanu is Late Villafranchian (~2.2–1.9 Ma) in age, while Fântâna lui Mitilan is likely younger (1.8 Ma to as young as 1.1 Ma). This is consistent with prior work suggesting dating of Grăunceanu to mammalian biostratigraphic zones MN17/MmQ1 (Bolomey 1965; Radulesco and Samson 1990; Radulescu et al. 2003). More recent U-Pb analyses indicate that Grăunceanu dates to at least 1.95 Ma, and Fântâna lui Mitilan is older than 1.63 Ma (Curran et al. 2025). Paleoecological analyses (Curran et al. 2021) suggest that Grăunceanu and La Pietriș were likely open grassland environments with some woodlands (forest steppe) and significant water sources nearby, though the carnivore guild aligns with somewhat more closed conditions (Werdelin et al. 2023). Isotopic analyses of equid dentition from Grăunceanu indicate higher annual rainfall amounts than present day and more pronounced seasonality, with increased winter and decreased summer precipitation (Curran et al. 2025). The younger Fântâna lui Mitilan is reconstructed to be slightly more closed than Grăunceanu.

Unfortunately, aspects of our ongoing work are hindered by a variety of unknowns. Though many of the sites of previous excavations have been relocated, surface surveys and limited subsurface testing by our team has not revealed any new fossil materials at the previously excavated localities; more extensive test digging at Grăunceanu by a joint American-Romanian team in the early 2000s confirms this (McNulty personal communication). Therefore, it is most likely that prior work fully removed the fossil deposits. Coupled with the loss of excavation notes from these sites, this obviously makes it difficult to accurately pinpoint the exact stratigraphic layers from which fossils were recovered or to know the exact excavation and collection strategies employed. Descriptions of the early 1960s excavations by Bolomey (1965) indicate that the fossil horizon from Grăunceanu was situated in sandy, yellow-ish gray clays and was densely concentrated in a 90m^2 area that was 0.75m thick (at least as of 1963, though excavations continued through at least 1965). Photographs presented in Bolomey (1965) and several archival photographs recovered by our team (Figure 2) show this dense concentration of bones and provide some glimpses into the excavation strategy of the original work.

Radulesco and Samson (1990) further describe the Grăunceanu deposits as situated at the base of a silty sand layer that was 1.5m thick; there was no mention of stratification in the fossil horizon, and many bones were found in articulation (see Figure 2). This suggests that the fossils were deposited over a relatively short period of time. Similar descriptions were provided for excavations at La Pietriș, where the fossils were concentrated in an area of about 50m^2 (Radulesco and Samson 1990). At Fântâna lui Mitilan, fossils seem to come from two faunal horizons (Radulesco and Samson 1990), perhaps indicating two distinct depositional events. Radulesco and Samson (1990) discuss a

Figure 2. Photographs showing the original Grăunceanu excavations in the 1960s. A) Photograph of two unidentified individuals standing in the excavation area; B) Another view of the excavation area showing the extent of excavations into the hillside; C) Photograph of the fossil beds as depicted in Bolomey (1965). Panels A and B are courtesy of the Emil Racoviță Institute of Speleology.

stratigraphically lower main fossil bed that was ~1.4–1.5m thick, while the higher fossil bed (situated 0.7–1.0m above the lower horizon) was only about 0.5m thick.

While we do not have the original excavation notes from this prior work, our observations of the Grăunceanu assemblage in particular suggest a comprehensive excavation and collection strategy. This is reflected in several lines of evidence: 1) the presence of many small specimens that were collected (e.g., isolated small carnivore teeth and phalanges) at Grăunceanu; 2) the publication of microfossil remains (e.g., shrew, rabbit, frog, and snake specimens; Bolomey 1965; Radulesco and Samson 1990) from La Pietriș; though we have not relocated these materials in our work in the collections, it is reasonable to assume they used the same collection strategies at these two closely situated localities; and 3) the presence of both remarkably complete specimens but also large numbers of fragmented remains with surfaces that are heavily taphonomically altered. All of these indicators suggest the retention of less-than-perfect specimens, rather than a collection strategy that focused only on large and complete/nearly complete specimens. Though we do not know for sure whether these original excavations included screening, given the prior lines of evidence presented we think it is probable. All of that said, while there is almost certainly some excavation and/or collection bias in this assemblage, it is not from a source that we can easily identify.

The aim of this study is to provide a detailed taphonomic assessment of the ORV fossil assemblages previously excavated in the 1960s. We mainly focus on the locality of Grăunceanu (VGr), though we also include summary results for two smaller localities, La Pietriș (LP) and Fântâna lui Mitilan (FM). We analyze patterns of skeletal element preservation, detail both abiotic and biotic factors that may have affected these assemblages, and present a sedimentological analysis for the site. Our goal is to shed additional light on site formation processes, including revealing the primary accumulators of materials at these sites, and the time depth across which fossils may have been deposited. These analyses are especially critical for putting the cutmarked bones reported from these sites by our research team (Curran et al. 2025) into a larger context.

MATERIALS AND METHODS

As of summer 2022, 5,527 inventoried items from all localities within the ORV research area have been cataloged. This number of identified specimens (NISP) was calculated from the ORV catalogs for specimens housed in Bucharest (ISER) and Craiova (Museum of Oltenia). For the Bucharest collection, every specimen was given an accession number

TABLE 1. CURRENT SPECIMEN AND TAXON COUNTS FOR THE THREE MOST FOSSILIFEROUS (NISP>100) SITES FROM THE OLTEȚ RIVER VALLEY.

		VGr*	**FM***	**LP***
	NISP*	**4,983**	**139**	**116**
Proboscidea	*Mammuthus* cf. *meriodionalis*	83	42	1
Artiodactyla	*Bison (Eobison)* sp.	4		
	Pliotragus ardeus	33		
	Megalovis latifrons		4	
	Gazellospira torticornis	7		
	Metacervocervus rhenanus	12		
	Dama sp.		1	
	Dama eurygonos	2		
	Eucladoceros sp.	333	17	26
	Eucladoceros dicranios	2		
	Eucladoceros ctenoides falconeri	3		
	Rucervus (Arvernoceros) radulescui	383		3
	Alces sp.	3		
	Praemegaceros obscurus		2	
	Praemegaceros cf. mosbachensis	?1	2	
	Mitilanotherium inexspectatum	26	1	
	Sus strozzi	1		
	Bovidae indet.	18	1	
	Cervidae indet.	216	11	7
	Artiodactyla indet.	1295	19	15
Perissodactyla	*Equus* sp. (cf. *livenzovensis*)	1045		
	Equus sp.		3	18
	cf. Equidae	5		
	Stephanorhinus sp.	102	1	
	cf. Rhinocerotidae	7		
	Perissodactyla indet.	9		

by our team in 2012–2022 using abbreviations for each collection locality (e.g., VGr= Grăunceanu, FM= Fântâna lui Mitilan, etc.). Specimens housed in Craiova had previously assigned accession numbers, though some of the materials (primarily bone fragments) were not previously accessioned. We made preliminary identifications of 106 of these unaccessioned specimens that were clearly attributable to the order Carnivora. These latter specimens were primarily identified to size categories such as felid/hyaenid/ursid or canid/mustelid; counts for these specimens are not included in the overall taxonomic list (or NISP counts, due to their preliminary identifications) but are included in the skeletal element frequency analysis below. Here, NISPs include specimens identified as specifically as possible to element and taxon, in addition to an unidentifiable category. Some catalog numbers include multiple elements or multiple unidentifiable fragments, and others currently await accessioning or are unaccounted for; thus, our current NISP is certainly an underestimate.

At present, 3,669 (66.4%) specimens are housed at ISER in Bucharest, while the remainder (1,858 or 33.6%) are housed at the Museum of Oltenia in Craiova (MO). The most fossiliferous site by far is Grăunceanu (NISP=4,983), followed by Fântâna lui Mitilan (NISP=139) and La Pietriș (NISP=116), while other localities have fewer than 100 specimens each. Due to the great difference in NISPs between Grăunceanu (VGr) and the other smaller localities, our main focus here is on VGr, though we report summary data for the smaller localities for comparison.

Distributions of specimens by taxon (and for additional localities) are shown in Table 1. Further detail is provided in prior publications (Croitor et al. 2024; Curran et al. 2025;

TABLE 1. CURRENT SPECIMEN AND TAXON COUNTS FOR THE THREE MOST FOSSILIFEROUS (NISP>100) SITES FROM THE OLTEŢ RIVER VALLEY (continued).

		VGr*	**FM***	**LP***
	NISP*	**4,983**	**139**	**116**
Carnivora	*Megantereon cultridens*	9		
	Homotherium latidens	5		
	Puma pardoides	5		
	Lynx issiodorensis	1		
	Pliocrocuta perrieri	7		
	Pachycrocuta brevirostris	?1		
	Ursus etruscus	40		
	Meles thorali	17		
	cf. *Lutraeximia simplicidens*	2		
	Nyctereutes megamastoides	88		1
	Vulpes alopecoides	1		
	Canis etruscus			
	Canis sp.			
	Canidae indet.	28	1	
	Felidae indet.	10	1	
	Mustelidae indet.	2		
	Hyaenidae indet.	3		
	Carnivora indet.	83	1	
Primates	*Paradolichopithecus arvernensis geticus*	27		
Rodentia	*Hystrix refossa*	2		
	Castor fiber cf. plicidens		1	
	Trogonotherium sp.	5	2	
	Rodentia indet.	1		
Pholidota	*Smutsia olteniensis*	2		
	Mammalia indet.	357	27	18
Non-mammals	*Pachystruthio* cf. *pannonicus*	3		
	Aves indet.	1		
	Geoemyidadae indet.		2	
	Vertebrata indet.	692		27
Invertebrates	Bivalvia	1		

*NISP= Number of Identified Specimens; VGr= Grăunceanu; LP= La Pietriş; FM= Fântâna lui Mitilan

Terhune et al. 2020; 2021; Werdelin et al. 2023), with additional future analyses planned for some taxonomic groups (e.g., equids).

TAXON LIST AND AGE DATA

As part of our cataloging process, we first assigned specimens (where possible) to the following taxonomic categories: Class, Order, Family, Tribe, Genus, and species (see Terhune et al. 2020) and to element and side. Developmental age of each specimen was categorized as subadult (epiphyses were observable and either completely unfused or partially fused), adult (epiphyses were observable and fully fused), or indeterminate (epiphyses were not observable and/or the bone does not have epiphyses). Dental remains were identified as either subadult (i.e., deciduous and/or unerupted) or adult (permanent and erupted).

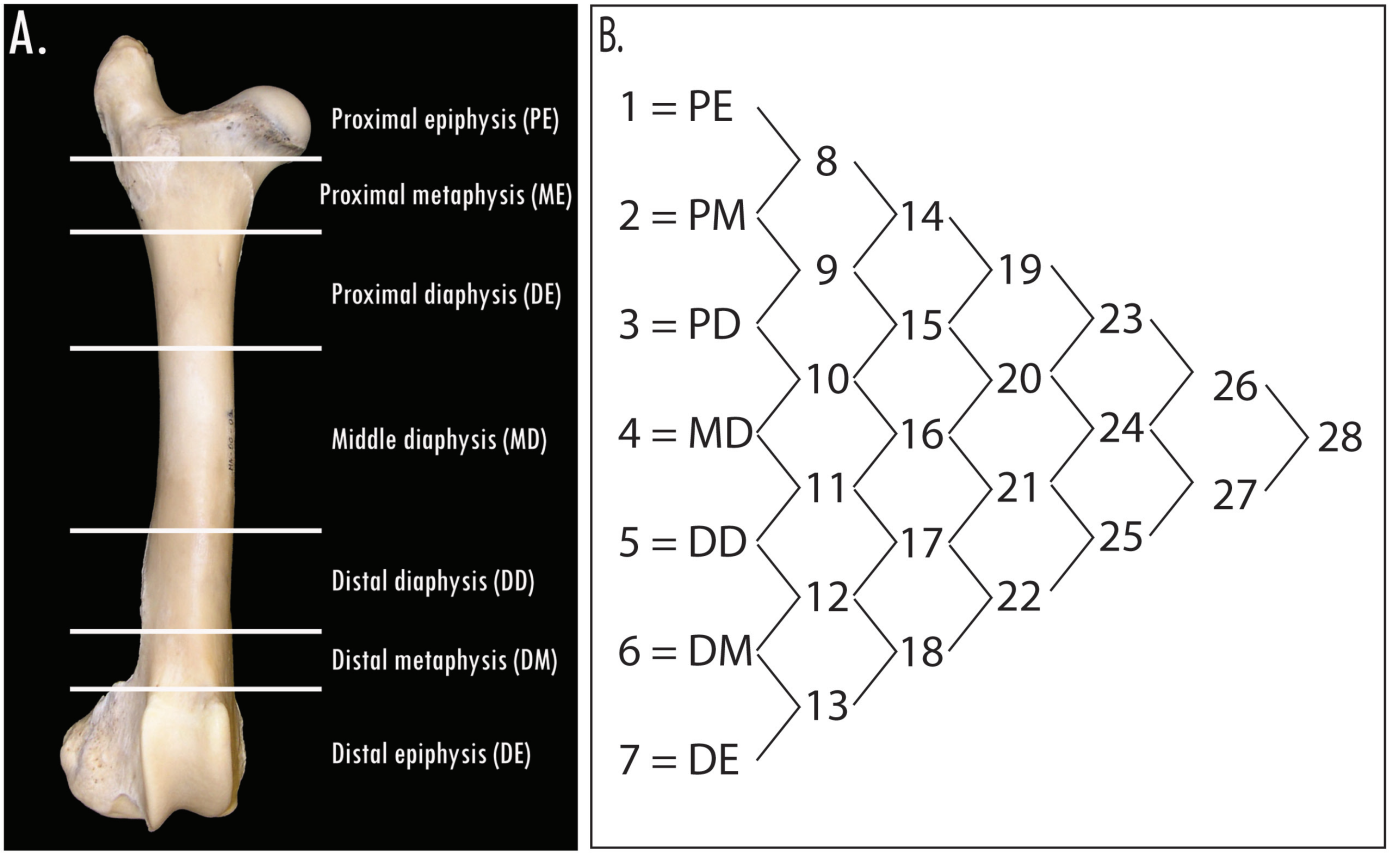


Figure 3. Long bone portions analyzed as part of this study. Typical long bones were divided into seven portions: the proximal epiphysis (PE), proximal metaphysis (PM), and proximal diaphysis (PD), the middle diaphysis (MD), and the distal diaphysis (DD), distal metaphysis (DM), and distal epiphysis (DE) (coded 1-7). For more complete remains, these portions can be combined in stages as shown here. For example, if the proximal portion of a femur is present (to the lesser trochanter), this would be scored as an 8 (PE + PM). If the specimen is missing just the proximal epiphysis (say the femoral head), then it would be scored as a 27 (PM + PD + MD + DD + DM + DE). A whole bone is coded as 28.

Our first goal was to update the ORV taxon list from prior publications (Curran et al. 2021; Terhune et al. 2020) based on new assessments (Croitor et al. 2024; Terhune et al. 2021; Werdelin et al. 2023) and additional specimens that were cataloged more recently. We then aggregated data on age data and skeletal element frequencies from the site of Grăunceanu, which is the only locality that has sufficient numbers of specimens for a thorough analysis. For age ratios, we compare the frequencies of subadult vs. adult specimens; where taxonomic identification was difficult to assess we also lumped some groups (i.e., Artiodactyla indet., large carnivore postcrania vs. canid/mustelid postcrania). Age data are reported only for long bones with at least one epiphysis observable and for mandibles and crania where the eruption sequence was discernible.

PATTERNS OF SKELETAL ELEMENT PRESERVATION

Skeletal Element Frequencies

We report skeletal element frequencies (SEF) across all taxonomic groups (mostly at the family level), though data were analyzed for combined taxonomic groups to maximize sample size (specifically Artiodactyla, Equidae, and small-sized and large-sized Carnivora). This approach allows us to assess the overall pattern of preservation at the sites and test if there are differences in preservation among taxa or different sized species. Long bones are reported to accurately reflect the relative abundance of skeletal elements in the assemblage (Marean and Cleghorn 2003).

Long Bone Portions and Circumference

For all identifiable long bones (i.e., any specimen or fragment that was able to be identified to skeletal element), the portion of each skeletal element present was recorded for all specimens using the coding system illustrated in Figure 3. Maximum circumference for long bones was recorded as 1=1–25% of the total circumference present, 2=26–50%, 3=51–75%, 4=76–99%, and 5=100% present (following Pobiner [2007]; modified from Bunn [1983] and Villa and Mahieu [1991]). Due to time and personnel constraints, full analysis of break morphology (e.g., Villa and Mahieu 1991) was not conducted, however, each taphonomist did record whether breaks appeared to be ancient, recent, both, or indeterminate. It should be noted that small, unidentifiable specimens were not included in this analysis, though it is likely that many of these specimens are fragments of long bones.

Analyses of Bone Mineral Density and Utility Indices

To assess if the Grăunceanu assemblage underwent density-mediated attrition, we calculated Pearson's r (in 'stats' package, R v. 4.3.2) for measures of bone mineral density (BMD; Lam et al. 1999) and proportional representation of long bones in the Grăunceanu assemblage. For each long bone fossil specimen, we recorded the portion(s) present (see Figure 3). Minimum number of elements (MNE) was calculated by summing all portions of each element from both sides (Lyman 1994; Stiner 1991), which was divided by two to calculate MAU (Minimum Animal Units, Binford 1978). For each taxon investigated, the highest MAU count was set to 100% and all other MAUs were adjusted according to that amount to calculate %MAU (Percent MAU; Lyman 1994; Tappen et al. 2022). Given restrictions in taxonomic identification of long bone elements, we calculated %MAU for Equidae as a group and Artiodactyla (excluding small and very large species) as a separate group. Bone mineral density (BMD) scan location data from Lam et al. (1999) align closely with our skeletal portion system. We calculated correlations for %MAU for each element region with Lam et al.'s (1999) data for *Equus* sp. for our Equidae group and *Rangifer tarandus* for our Artiodactyla group.

To assess whether skeletal portion representations were impacted by carnivore consumption, we also calculated correlations of %MAU against measures of food utility. Food utility index (FUI) data for *Rangifer tarandus* are from Metcalfe and Jones (1988, their Table 2) and standard FUI (S)FUI data for *Equus* are from Outram and Rowley-Conwy (1998, their Table 6). In order to match the portions in these utility indices, we report %MAU as the highest proportion in the proximal (PE, PM, or PD) and distal (DM, DE, or DD) regions.

Though these two sets of analyses attempt to measure different winnowing processes in the taphonomic history of an assemblage, destruction due to mainly mechanical processes (BMD and %MAU) versus biotic processes (FUI and %MAU), the two processes are not mutually exclusive. That is, a fossil assemblage can, and likely did, experience both processes. While there is no test to elucidate which process had more impact on an assemblage, context clues such as the amount of carnivore modifications (i.e., tooth scores and pits) present can help to identify the more dominant signal. It should also be noted that the two processes share a moderately strong negative relationship. Bone regions with lower densities tend to be those more easily chewed by carnivores to access bone grease (Blumenschine 1988). This relationship is stronger for *Rangifer tarandus* (r= -0.6, p=0.04) than *Equus* (r= -0.54, p=0.07) based on the data used in this study (Lam et al. 1999; Metcalfe and Jones 1988; Outram and Rowley-Conwy 1998), though this has also been abundantly demonstrated previously (Faith et al. 2007; Lyman 1992). Thus, it is imperative to take into consideration all contextual clues when determining agent(s) of assemblage accumulation, and especially bone surface modifications.

BONE SURFACE MODIFICATIONS (BSM)

Taphonomic alterations were assessed for a subset of the total specimens (dentition, antlers, and horn cores were excluded). Thus, counts included in the taphonomy analyses are lower than the cataloged counts. Out of the total NISP for Grăunceanu, La Pietriș, and Fântâna lui Mitilan (n=5,238), 4,706 specimens were examined for BSMs (VGr=4,524; LP= 114, FM=68).

All specimens analyzed were examined under strong, low-angled light from a gooseneck microscope light with a 10x hand-lens following the method outlined in Blumenschine et al. (1996). Specimens with potentially significant taphonomic alteration were further examined with a Dino-Lite Edge digital microscope. Taphonomic assessments were made by one of four individuals (SC, BP, SG, or CT) on our research team. Because this work was conducted by all researchers simultaneously, we frequently sought verification from each other when bone surface modifications were unclear. Particularly for potential hominin modifications, we discussed and viewed the modifications as a team and came to a consensus on BSM identifications (for more details, see Curran et al. 2025). Some fossils in the study were viewed multiple times (either by the same observer or different observer(s)); in the majority of these instances, we retained the most recent entry for analysis, except where records were incomplete for one entry and not the other.

Assessment of Bone Surface Condition

The approximate percentage of the specimen's surface that was visible for taphonomic inspection (that is, not obscured by adhering matrix or shellac/glue) was recorded as 1=0–25%, 2=26–50%, 3=51–75%, and 4=76–100% (following Monahan 1996). Weathering stage was recorded as between 0 and 5 (following Behrensmeyer 1978).

Bone Surface Modifications

Each specimen was inspected for a wide variety of BSMs, including abiotic alterations (bone surface pitting, erosion/dissolution, exfoliation/flaking, adhering matrix, smoothing, chipping, denting, cracking, sediment splitting), and biotic alterations (root/fungal rhizomorph etching, insect damage, rodent gnawing, digestion, notches and flake scars, cut marks, peeling, antemortem pathology, and carnivore modifications such as tooth pits and crenulated edges from chewing). Definitions employed for these categories of modifications are found in Supplementary Table 1 and largely follow the identification criteria in Fernandez-Jalvo and Andrews (2016). Following the original excavations, some specimens were glued, shellacked, or plastered during reconstruction processes, which was also noted in the data collection process. All data were input into a prepared Excel spreadsheet shared among the analysts.

Linear Marks

Any impression on a specimen's surface that was at least twice as long as it was wide was recorded as a linear mark. Linear marks can be biotic (carnivore tooth scores, cut marks from hominins using tools to remove soft tissue, trampling by large animals, preparators using tools to remove dirt/sediment/matrix, biochemical deterioration) or abiotic (e.g., scraping of a specimen during fluvial transport or while rolling down a steeply inclined surface) in origin. Though these sometimes can be difficult to distinguish, here the criteria of Domínguez-Rodrigo et al. (2009, 2010; Supplementary Table 2) were used for a visual, qualitative assessment. This method is likely to be conservative for identifying cut marks, since several of the features described, such as microstriations internally and on the shoulder of the mark, can be eroded away even after a short exposure to fluvial environments (Behrensmeyer et al. 1986) or in other depositional contexts and thus are not expected to be present in ancient specimens. For each mark, we also recorded taxon, skeletal element, and the location of the mark(s) on the specimen. We interpreted the origin of each mark whenever possible. Excavator and preparator-created marks were typically wide and U-shaped, and most significantly were a different color within the mark than the exterior of the fossil's surface. Sedimentary abrasion and trampling marks can mimic cut marks but are differentiated by usually having curved to sinuous trajectories, random orientations to the long axis of the bone, random distributions across a bone's surface, and overlapping striae external to the main mark (Domínguez-Rodrigo et al. 2009). Tooth scores were identified by U-shaped cross-sections with no internal or external striae.

In cases when modifications consistent with hominin alterations (cut and chop marks) were identified, marks were molded with Coltene President Jet light body dental molding material for further analysis. A sample of modifications identified as trampling and carnivore tooth marks were also molded for comparison to the suspected hominin alterations. These molds were sent to MP for analysis without any contextual or identifying information. Three-dimensional (3D) models were created from the molds using a Sensofar S-Neox optical profilometer and measured following methods described in Pante et al. (2017). Data collected through the analysis from the entire 3D model of the BSM were volume, surface area, maximum depth, mean depth, maximum length, and maximum width. Additional data were collected from a profile taken from the deepest point of the BSM including area of the hole, depth of the profile, roughness (Ra), opening angle, and radius of the hole.

Linear marks suspected to be of anthropogenic origin were considered to be of special interest and were evaluated both qualitatively and quantitatively. Qualitative assessments were conducted directly on the specimens and by referring to photos and 3D scans. For each mark, we recorded a range of attributes describing the mark location, trajectory, orientation relative to the long axis of the bone, cross-sectional shape, coloration, and other features (e.g., barbs, shoulder effects, etc.) after Domínguez-Rodrigo et al. (2009). Quantitative assessments were based upon a statistical comparison with a sample of 898 BSMs of known origin, including 405 cut marks from a variety of stone tool types and raw materials (Keevil 2018; Keevil et al. 2025), 275 tooth marks from crocodiles and five species of mammalian carnivores (Muttart 2017), 130 trample marks produced by cows on substrates including sand, gravel, and soil (Orlikoff et al. 2017), and 88 percussion marks from both anvils and hammerstones (Tolley et al. 2019). Surface area and depth of the profile were excluded from the statistical analyses because they are correlated with volume and maximum depth, respectively, which can lead to overfitting of data. All experimental data were transformed using the Box-Cox method to normalize the distributions for each variable and the same transformations were applied to the archaeological data. Comparisons were carried out using the quadratic discriminant analysis function from the MASS package (Venables and Ripley 2002) in R (version 4.4.1). The accuracy of the quadratic discriminant model in correctly classifying the experimental BSMs was 82% using a leave-one out cross-validation method. Prior probabilities were set proportional to the occurrence of each mark type in the dataset to offset the disproportionate representations of each mark type in the experimental sample. The final attribution to mark type was assigned based on a combination of primary visual assessment of qualitative attributes, microscopic visualizations using the Dino-Lite images, and the confidence of the quadratic discriminant model in the identification of each mark, which was assessed by the resulting posterior probabilities with values closer to one indicating higher confidence. When our qualitative and quantitative analyses returned conflicting results on the nature of the marks, the qualitative analysis was given higher weight due to the human observer being able to more fully contextualize the bone surface modification in question (see Curran et al. 2025 for detailed analyses of these marks).

Quantification of BSMs

Bone surface modifications were tallied from the Excel spreadsheet shared among the analysts and counts were created for each modification type. Frequencies of specimens presenting each type of modification were calculated by dividing the tally of each modification type by the total number of specimens analyzed for the assemblage. Many specimens present multiple BSMs and thus the number of BSMs is far greater than the NISP for each locality. To more effectively present and discuss the results of our analysis, we combined data for some types of BSM categories; for example, post-depositional damage, all linear marks, and carnivore alterations. Since there is likely to be much overlap in data types in each of the combined categories (that is, many specimens are likely to present multiple forms of BSMs related to the category), we sorted the Excel spreadsheet by the relevant BSMs and tallied the number of specimens that present any of the BSMs in the category so as to not overcount specimens. For example, if a specimen presented two different types of post-depositional damage, the specimen was counted only once in the post-depositional BSM category.

We further examined carnivore modifications and their impacts on skeletal element frequencies in Artiodactyla (excluding Giraffidae) and Perissodactyla (excluding Rhinoceratidae) from Grăunceanu by quantifying the percent of carnivore modifications (tooth scores and pits) per NISP for each skeletal element by taxon. This allowed us to assess whether particular skeletal elements were under- or over-represented relative to the amount of carnivore modifications in the assemblage. Elements that show low frequencies in the assemblage but high levels of carnivore modifications would then suggest that carnivores may have disproportionately contributed to their destruction.

GRAIN SIZE ANALYSIS

Grain size distribution of the matrix in which the bones were found was determined using five sediment samples retrieved from the interior of bone shafts of specimens VGr.0276 (femur, cf. *Eucladoceros*; see Supplemental Figure 1), VGr.0972 (metacarpal, Girrafidae), VGr.1250 (radius, *Equus* sp.), VGr.1964 (radius, *Equus* sp.), and VGr.2184 (long bone shaft fragment, cf. Proboscidea). Analysis was performed according to the ISO 17892-4:2016 standard "Laboratory testing of soil – Determination of particle size distribution." Initial wet sieving was performed on a 0.063mm sieve to separate the coarse fraction from the fine fraction. The fine fraction was analyzed using the hydrometer method and the coarse particles by dry sieving.

RESULTS

Note that each analysis may have different counts of total specimens included either due to the type of analysis or to missing data. There are 5,527 cataloged entries for the ORV remains, of which 5,238 are from the three sites included here (VGr, FM, and LP). Taphonomic analyses were conducted only on non-dental and non-horn/antler remains, for a total of 4,706 analyzed specimens (VGr=4,524, FM=68, LP=116). Long bone portion analyses were on identifiable long bones only and thus have lower counts than the other analyses.

TAXON LIST AND AGE DATA

Previous publications (Terhune et al. 2020) provided taxonomic data only for that portion of the ORV collections housed at ISER and were published prior to several taxonomic revisions (Croitor et al. 2024; Werdelin et al. 2023); we therefore update this taxon list here and provide current specimen counts for each taxon (see Table 1). Notable differences in the species list include the addition of *Lutraeximia* sp. and the removal of *Acinonyx pardinensis* and *Croizetoceros ramosus*. There were also several shifts to the percentages attributable to taxonomic groups at Grăunceanu (Figure 4) such as an increase in the percent of equids (previously 12% of our original NISP, now 21%). Artiodactyla account for 47% of the VGr assemblage, Carnivora for 6%, Rhinocerotidae for 2%, and *Mammuthus* for 1.7%. The remaining specimens are either unidentifiable (21%) or rare taxa such as primates, pangolins, ostriches, or porcupines.

Age data by taxonomic group for Grăunceanu are presented in Table 2 and Figure 5. In general, there are a fair number of subadult individuals in the sample. This is especially true for artiodactyl remains that were not attributable to family (28% subadult; almost all are likely from either Cervidae or Bovidae), Cervidae (20% subadult), and Rhinoceratidae (37% subadult). However, for equids, only 10.7% of the NISP are subadult and none of the 11 giraffid specimens are juveniles, so this does not appear to be a strictly size-based bias. That is, we do not find primarily younger individuals of larger taxa. Further, in large carnivores for which we have a good sample size, there are very few juvenile specimens (7.7% of felids and 5.6% of ursids), and there are no juveniles of small carnivores, though small carnivores are well represented (especially by small skeletal elements).

PATTERNS OF SKELETAL ELEMENT PRESERVATION

Skeletal Element Frequencies

Skeletal element frequencies for Grăunceanu are presented in Supplementary Table 3. For ease of comparison, we will discuss the %NISP for Artiodactyla Indet/Cervidae/Bovidae (i.e., all ruminants except giraffes) vs. Equidae and Felidae/Hyaenidae/Ursidae (i.e., larger carnivores) vs. Mustelidae/Canidae (i.e., smaller carnivores) remains.

The skeletal element distributions for artiodactyls vs. equids are shown in Figure 6 by NISP. Disproportionately more cranial remains of artiodactyls than equids are represented in our sample. We also observe that distal limb elements (carpals, tarsals, metapodials, phalanges) are heavily represented. This was true for both ruminants and equids, though equids have proportionally more tarsals and phalanges than ruminants.

Similarly, for both the Artiodactyla and Equidae analysis by long bone MNE, the stylopodia (femur, humerus) are the least represented, followed by the zeugopodia (radius, ulna, tibia), and finally the autopodia (manus, pes elements) are best represented (Table 3), a pattern that is likely a product of density-mediated attrition (see below). However, in the Equidae, the MNE of the forelimb (based on the metacarpal count; MNE=71) and hindlimb (based on the metatarsal count; MNE=69) are nearly equal, a pattern that has been interpreted to suggest that equids entered the assemblage as whole or nearly whole individuals (Tappen et al. 2022). In the Artiodactyla sample the hindlimb (metatarsals; MNE=156) outnumber the forelimb (metacarpals; MNE=117), which could indicate that hindlimbs were preferentially transported to and/or preserved in the assemblage.

In comparison, carnivores were more frequently represented by craniodental remains (see Figure 6), for both large and small carnivore groups. However, we observe a large proportion of phalanges for smaller carnivores.

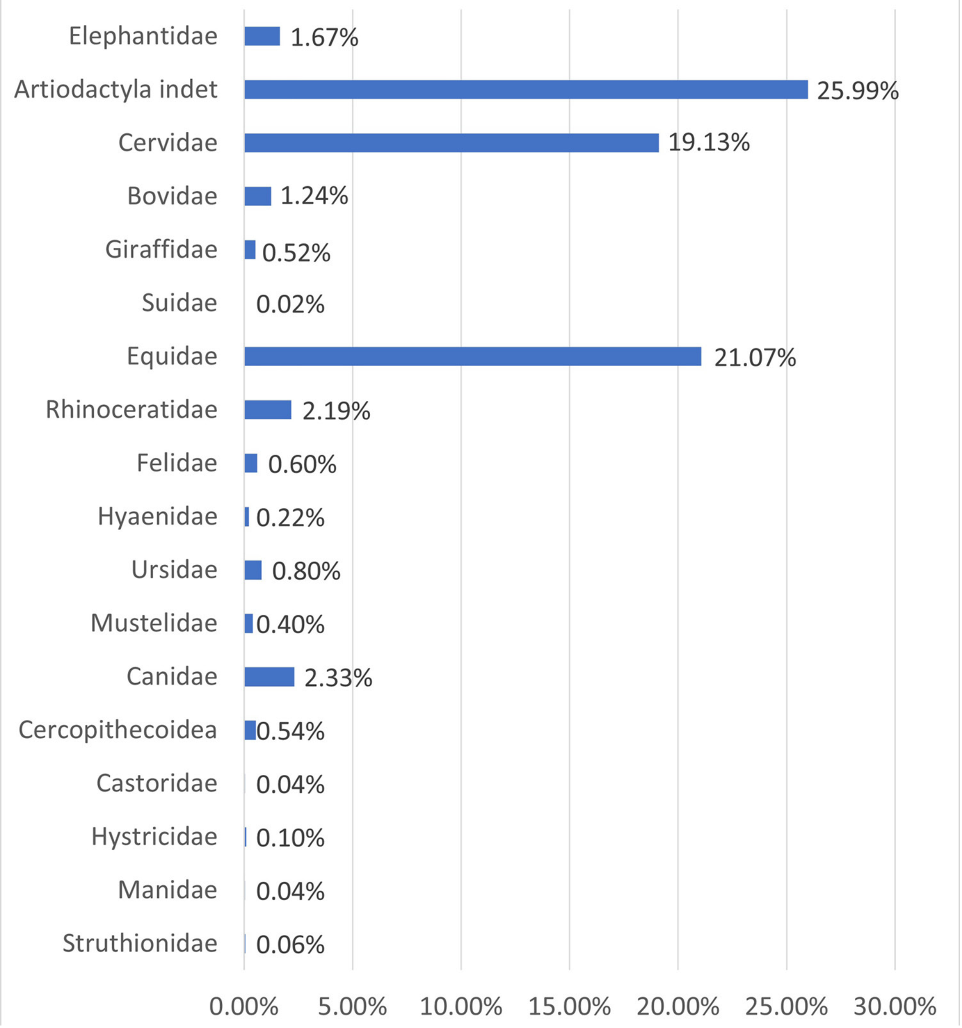


Figure 4. Chart showing percentage NISP for each family (plus indeterminate Artiodactyla, which are mostly likely a combination of cervids and bovids) in the Grăunceanu inventory.

Long Bone Portions and Circumference

Although there is breakage in the Grăunceanu assemblage, the extremely good state of preservation overall allows for a significant number of specimens to be identified to element (3,989 of 4,983; 80%). Many of the unidentifiable fragments appear to be of long bones and likely broke post-depositionally.

Of the 1,354 identifiable VGr long bone specimens in the analysis, 1,050 (77.5%) are half or more of the bone, and 203 (15%) of those are complete (Supplementary Table 4). Only 304 (22.5%) specimens are less than half of the element's original length. In addition to having high representations of fairly complete bone lengths, complete circumferences are found in 84.3% of the Grăunceanu long bone specimens analyzed (Supplementary Table 5).

Long bone specimens occur in far lower frequencies at other ORV localities (FM=11, LP=16). FM is somewhat similar to VGr in that 81.8% of the identifiable specimens are represented by half or more of the bone. Specimens from LP are more fragmentary in nature, with only 31.3% of the specimens half or more complete (see Supplementary Table 4). FM (n=11) and LP (n=11) have more specimens with incomplete circumferences; only 63.6% of specimens from these two sites have complete circumferences. The discrepancy in LP specimens is due to several of the long bones being only epiphyses and thus they cannot be included in circumference calculations.

Analyses of Bone Mineral Density and Utility Indices

In the VGr Artiodactyla (excluding small artiodactyls and Giraffidae), there is a moderate and statistically significant correlation (r=0.55, p=0.001) between bone mineral density (BMD) and %MAU, indicating that higher density bones have higher presentation at VGr. This relationship is driven by the high proportion of metapodia, and radii to a lesser extent, in the assemblage (Table 4, Figure 7). However, density-mediated attrition cannot fully account for the long bone portions in the assemblage, since several high-density element portions (proximal tibiae metaphysis, femora, and humeri distal metaphysis) have relatively low proportional

TABLE 2. AGE DATA FOR SKELETAL ELEMENT BY TAXONOMIC GROUP FOR GRĂUNCEANU.

		Cranium	Mandible	Humerus	Radius	Ulna	Radius/ulna	Metacarpal	Pelvis	Femur	Tibia	Calcaneus	Metatarsal	Metapodial	Proximal phalanx	Intermediate phalanx
Proboscidea	Ad*			1				1	1	1					3	1
	Sub*			1						1				1		
Artiodactyla Indet	Ad		1	20	47	12		21	4	9	47	7	28	25	96	73
	Sub			1	15			3		15	33	1	3	33	31	19
Cervidae	Ad	26	52	22	35	1		59		1	32	49	87	38	35	21
	Sub	10	22		5			11			6	31	12	11	5	1
Bovidae	Ad		2		2			6					8			
	Sub	1	2													
Giraffidae	Ad						1	3			1	1	2		3	
	Sub															
Equidae	Ad	8	7	36	43	7	4	62	2	7	33	33	104	25	49	45
	Sub	1	2	1	3	1		2		4	3	35		2	1	1
Rhinocerotidae	Ad		1	3	6	4		4		4	2	1	2		5	1
	Sub			2	4	1			1	3	6	1		1		
Felidae	Ad	3	6								2	1				
	Sub		1													
Hyaenidae	Ad	1	3													
	Sub		1													
Ursidae	Ad	5	9	1					1	1						
	Sub											1				
Large Carnivore Postcrania	Ad															
	Sub									1	2					
Canidae	Ad	15	7													
	Sub															
Mustelidae	Ad	1	5													
	Sub															
Canid/Mustelid Postcrania	Ad				1			4			2	1	11	1	16	34
	Sub															
Cercopithecoidea	Ad	5		3	1	1										
	Sub	1	2							1						
Rodentia	Ad		4													
	Sub		1													

*Ad=adult (epiphyses observable and fully fused or teeth fully adult); Sub=subadult (epiphyses observable and either unfused or partially fused or evidence of deciduous dentition).

representation (<30%). Unsurprisingly, the lowest density bone portions also have the lowest proportional %MAU representation.

The correlation in the Artiodactyla group between food utility index (FUI) and %MAU is moderately strong and statistically significant (r= -0.77, p=0.004), demonstrating that the skeletal element portions with the highest utility have the lowest representation in the VGr assemblage (Table 5).

Results for the VGr Equidae assemblage BMD analysis are quite different from the Artiodactyla. There is a non-significant correlation between BMD and %MAU (r=0.29, p=0.1). This may be driven in part by the low representation of mid-shaft portions of humeri, radii, and femora, all

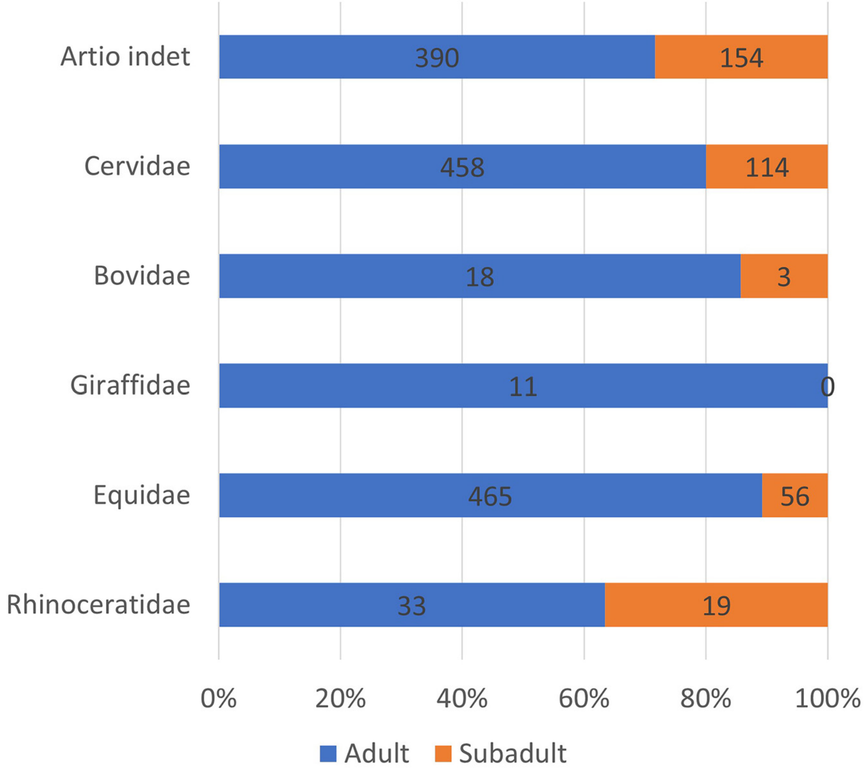


Figure 5. Bar chart showing the proportion of adult vs. subadult remains (when possible to determine) at Grăunceanu for selected taxonomic groups.

of which have high BMD. There are also many complete metacarpals (70.3% are whole) and metatarsals (73.2% are whole), which drives up their proportional representation (see Table 4).

Like the Artiodactyla, the correlation in the Equidae between (S)FUI and %MAU is moderately strong and significant (r= -0.72, p=0.008), once again driven by the high representation of metapodia, and low representation of femora and proximal humeri (see Table 5).

BONE SURFACE MODIFICATIONS

In general, the Grăunceanu assemblage can be characterized as being heavily altered by post-depositional processes, especially root-etching and abiotic damage associated with burial and fossilization (Figure 8). Though present, pre-burial alterations (e.g., carnivore and hominin modifications) are far rarer. Representative bone surface modifications are shown in Figures 9–12 and 14 (below) and summarized in Table 6. Also of note is the consistency in the

TABLE 3. NISP, MNE, %MNE OF LONG BONE ELEMENTS FOR ARTIODACTYLA AND EQUIDAE FROM GRĂUNCEANU*.

	Artiodactyla			Equidae		
Element	NISP	MNE	%MNE	NISP	MNE	%MNE
Humerus	61	50	9.8	20	19	8.0
Radius	118	86	16.9	30	24	10.1
Metacarpal	137	117	23.0	74	71	29.8
Femur	25	20	3.9	8	5	2.1
Tibia	101	80	15.7	54	50	21.0
Metatarsal	187	156	30.6	71	69	29.0

*NISP= Number of Identified Specimens; MNE= Minimum Number of Elements

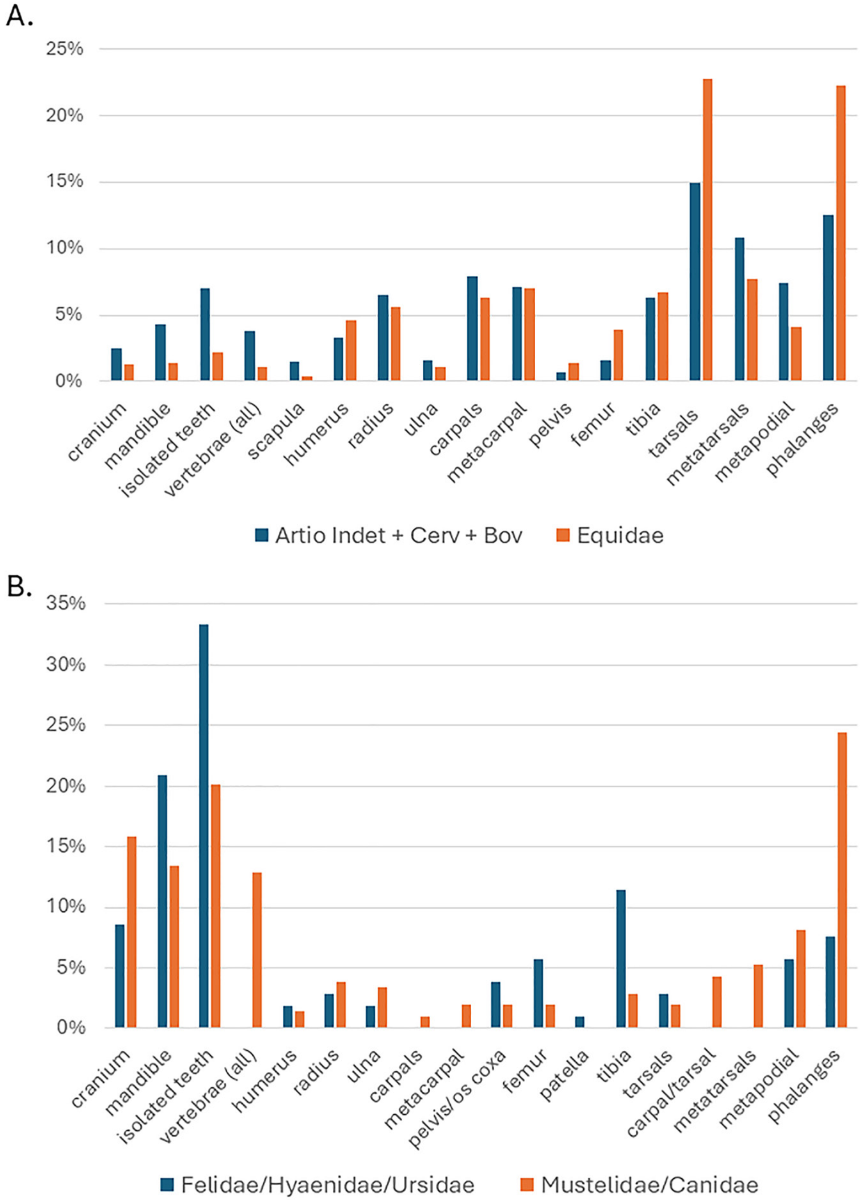


Figure 6. Bar charts showing skeletal element frequencies for indeterminate artiodactyls as well as cervids and bovids (blue) and equids (orange) (A), and for large (Felidae, Hyaenidae, and Ursidae; blue) vs. small (Mustelidae, Canidae; orange) carnivores (B) at Grăunceanu.

surface preservation from each locality; only rarely did any specimen deviate in presentation of overall preservation and in such cases, the deviation (such as having a chalky surface) was noted.

Bone surface visibility is high for the Grăunceanu specimens, with 72.2% (3,268 of 4,524) of the specimens analyzed having 75–100% surface visibility. For the remainder of the assemblage, 12.1% are 51–75% visible, 6.6% are 26–50% visible, and 8.0% are 0–25% visible (with 52 specimens for which data were not recorded; Supplementary Table 6). Bone surface visibility is relatively lower for specimens from the other ORV sites: at FM=44.1% (30 of 68) and LP=45.6% (52 of 114) of specimens have 76–100% surface visibility. This pattern appears to be driven by more extensive post-depositional alterations (specifically, adhering matrix) at these sites.

Weathering

Grăunceanu specimens were not subjected to heavy weathering, with 3,762 (83.2%) in WS 0, 12.2% in WS 1, 2.2% in WSs 2–4, and 2.5% for which WS data were not able to be collected (Supplementary Table 7). The other ORV localities also have high frequencies of low weathering stages: WS0=82.4% (56 of 68 at FM), and 87.2% (95 of 109 at LP) and WS1=13.2% (9 of 68 at FM) and 10.1% (11 of 109 at LP).

TABLE 4. LONG BONE PORTION DATA (MNE, MAU, %MAU) AND BONE MINERAL DENSITIES (BMD; from Lam et al. 1999) FOR GRĂUNCEANU ARTIODACTYLA AND EQUIDAE SPECIMENS.

		Artiodactyla				Equidae				Lam et al.
Element	Portion*	MNE*	MAU*	%MAU	BMD	MNE*	MAU*	%MAU	BMD	(1999) site
Humerus	PE	2	1	1.3	0.26	1	0.5	1.4	0.23	HU1
	PM	5	2.5	3.4	0.44	5	2.5	7.0	0.33	HU2
	MD	32	16	21.5	1.12	13	6.5	18.3	1.1	HU3
	DM	50	25	33.6	1.08	15	7.5	21.1	1.05	HU4
	DE	35	17.5	23.5	0.48	19	9.5	26.8	0.36	HU5
Radius	PE	67	33.5	45.0	0.53	11	5.5	15.5	0.37	RA1
	PM	78	39	52.3	1.08	13	6.5	18.3	1.04	RA2
	MD	86	43	57.7	1.09	18	9	25.4	1.08	RA3
	DM	47	23.5	31.5	0.97	18	9	25.4	1	RA4
	DE	43	21.5	28.9	0.49	24	12	33.8	0.42	RA5
Metacarpal	PE	108	54	72.5	0.92	69	34.5	97.2	0.55	MC1
	PM	114	57	76.5	1.08	71	35.5	100.0	1.03	MC2
	MD	117	58.5	78.5	1.1	69	34.5	97.2	1.1	MC3
	DD	98	49	65.8	1.01	66	33	93.0	0.71	MC4
	DM	71	35.5	47.7	0.48	59	29.5	83.1	0.56	MC5
	DE	47	23.5	31.5	0.68	56	28	78.9	0.6	MC6
Femur	PE	5	2.5	3.4	0.39	4	2	5.6	0.35	FE1
	PM	6	3	4.0	0.52	2	1	2.8	0.3	FE2
	PD	6	3	4.0	0.74	4	2	5.6	0.99	FE3
	MD	12	6	8.1	1.15	5	2.5	7.0	1.09	FE4
	DM	14	7	9.4	0.61	3	1.5	4.2	0.51	FE5
	DE	20	10	13.4	0.32	1	0.5	1.4	0.3	FE6
Tibia	PE	9	4.5	6.0	0.35	6	3	8.5	0.32	TI1
	PM	12	6	8.1	1.01	14	7	19.7	0.77	TI2
	MD	45	22.5	30.2	1.13	41	20.5	57.7	1.07	TI3
	DM	67	33.5	45.0	1.12	50	25	70.4	1.05	TI4
	DE	80	40	53.7	0.73	48	24	67.6	0.45	TI5
Metatarsal	PE	135	67.5	90.6	0.9	66	33	93.0	0.59	MR1
	PM	138	69	92.6	1.1	67	33.5	94.4	1.07	MR2
	MD	149	74.5	100.0	1.08	68	34	95.8	1.1	MR3
	DD	117	58.5	78.5	1.08	65	32.5	91.5	0.71	MR4
	DM	72	36	48.3	0.41	60	30	84.5	0.58	MR5
	DE	44	22	29.5	0.59	56	28	78.9	0.6	MR6

*MNE= Minimum Number of Elements; MAU= Minimum Animal Units; PE= Proximal Epiphysis; PM= Proximal Metaphysis; MD= Middle Diaphysis; DD= Distal Diaphysis; DM= Distal Metaphysis; DE= Distal Epiphysis

Root Etching

By far, the most frequent bone surface alteration to the Grăunceanu materials is root etching, with 81.7% (3,698 of 4,524) of the specimens analyzed showing some trace of root etching. Root etching is also frequently found on specimens from other localities (FM=23.5% and LP=64.9%), though not nearly as commonly as at VGr. These BSMs range from just a few pits to complete obliteration of the surface. In Figure 9, a recent specimen from a root etching experiment (by SC; images A and B) is compared to fossil specimens with various degrees of root etching. Even with the root etching, other BSMs are still visible on these specimens. For example, in Figure 9C there are two marks visible that have both root etching and adhering matrix on top of them. Thus, while root etching can potentially remove prior evidence of taphonomic alterations, in many cases, those alterations are still visible, though the BSMs may experience some changes to their texture. In some cases, root

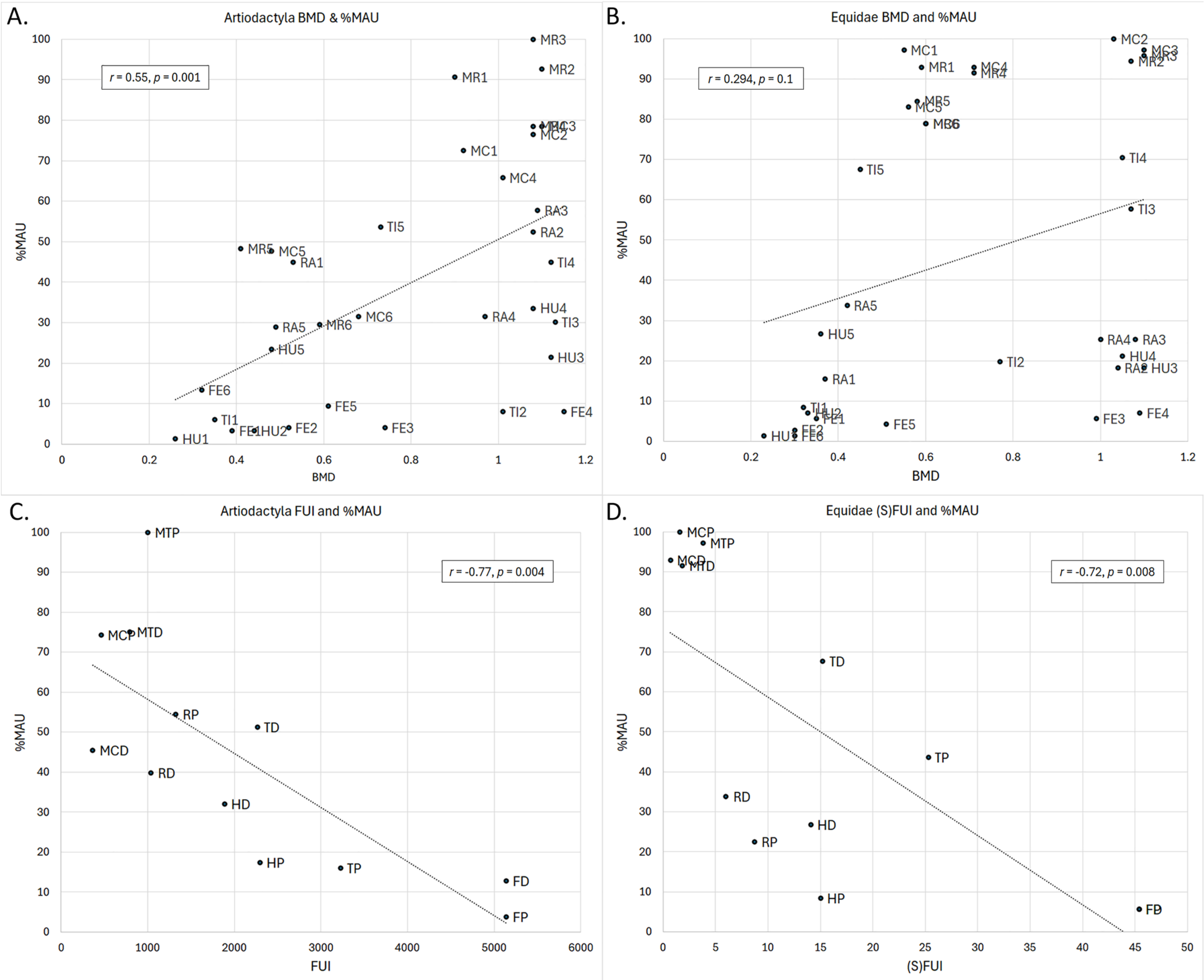


Figure 7. Bivariate plots of A) Bone Mineral Density (BMD) and Percent Minimum Animal Units (%MAU) from Grăunceanu. For Artiodactyla long bones, B) BMD and %MAU for Equidae long bones, C) Food Utility Index (FUI) and %MAU for Artiodactyla long bones, and D) Standard Food Utility Index ((S)FUI) for Equidae long bones. BMD from Lam et al. (1999: Table 1); FUI from Metcalfe and Jones (1988: Table 3), (S)FUI from Outram and Rowley-Conwy (1998: Table 6). Element and portion abbreviations can be found in Tables 6 and 7.

etching extended into linear marks making them difficult to digitize and produced unreliable scans and those linear marks were removed from our quantitative analysis.

Post-Depositional Damage

We recorded the presence of many other types of abiotic, post-depositional damage, such as surface exfoliation, chipping, pitting, etc. (Figure 10). Rather than discuss each type independently (though see Supplementary Table 8), here we present these as a combined total of all post-depositional damage to the ORV specimens. At Grăunceanu, post-depositional alterations are present on 41.5% of specimens (1,877 of 4,524) (see Figure 8). Specimens from other ORV localities incurred proportionally higher post-depositional damage than those in the VGr assemblage (FM=73.5% (50 of 68 specimens) and LP=49.1% (56 of 114 specimens)), a pattern which is mainly driven by adhering matrix on specimens.

Of the post-depositional BSMs, adhering matrix/manganese staining is the most frequent in the Grăunceanu assemblage, occurring on 26.8% (1,210 of 4,524) specimens. While manganese staining does not inhibit the ability to read bone surfaces, adhering matrix can cover prior taphonomic alterations. In most cases, matrix was easily removed without damaging surfaces, though it was impossible to remove from some specimens (e.g., Figure 10A).

Some excavator and/or preparator damage was noted in the Grăunceanu assemblage, especially recent breaks (Figure 10D). Some (5.9%) VGr specimens exhibited evidence of reconstruction in the form of glue or shellac. Spec-

TABLE 5. LONG BONE PORTION DATA (MAU and %MAU) AND FOOD UTILITY INDICES FOR ARTIODACTYLA AND EQUIDAE FROM GRĂUNCEANU.

	Artiodactyla			Equidae		
Element and Portion	FUI[a]	%MAU	MAU*	(S)FUI[b]	%MAU	MAU*
HP (Proximal humerus)	2295	17.3	13.5	15	8.5	3
HD (Distal humerus)	1891	32.1	25	14.1	26.8	9.5
RP (Proximal radius)	1323	54.5	42.5	8.7	22.5	8
RD (Distal radius)	1039	39.7	31	6	33.8	12
MCP (Proximal metacarpal)	461	74.4	58	1.6	100	35.5
MCD (Distal metacarpal)	364	45.5	35.5	0.7	93.0	33
FP (Proximal femur)	5139	3.8	3	45.4	5.6	2
FD (Distal femur)	5139	12.8	10	45.4	5.6	2
TP (Proximal tibia)	3225	16.0	12.5	25.3	43.7	15.5
TD (Distal tibia)	2267	51.3	40	15.2	67.6	24
MTP (Proximal metatarsal)	1003	100.0	78	3.8	97.2	34.5
MTD (Distal metatarsal)	792	75.0	58.5	1.8	91.6	32.5

*MAU= Minimum Animal Unit

[a]FUI= Food Utility Index; Metcalf and Jones (1988: Table 2)

[b](S)FUI= Standardized Food Utility Index; Outram and Rowley-Conwy (1998: Table 6)

imens from other ORV localities have very low frequencies (2.5–3.5% of the assemblages) of excavator/preparator damage (2 from FM and 4 from LP).

Rounding/Smoothing

Rounding and smoothing of bone can indicate if an assemblage was affected by fluvial or lacustrine processes, which tend to produce rounding on the edges of bones (Griffith et al. 2016). Though paleoecological analysis (Curran et al. 2021) indicates that the paleo-Olteţ river likely ran close to the depositional area of Grăunceanu, there is little evidence of fluvial transport on the specimens, as only 0.46% (21/4,524) present any smoothing. Thus, the main accumulator for Grăunceanu was unlikely to be fluvial transport, though burial in point bar or overbank deposits along the river remains a possibility due to their potentially low ve-

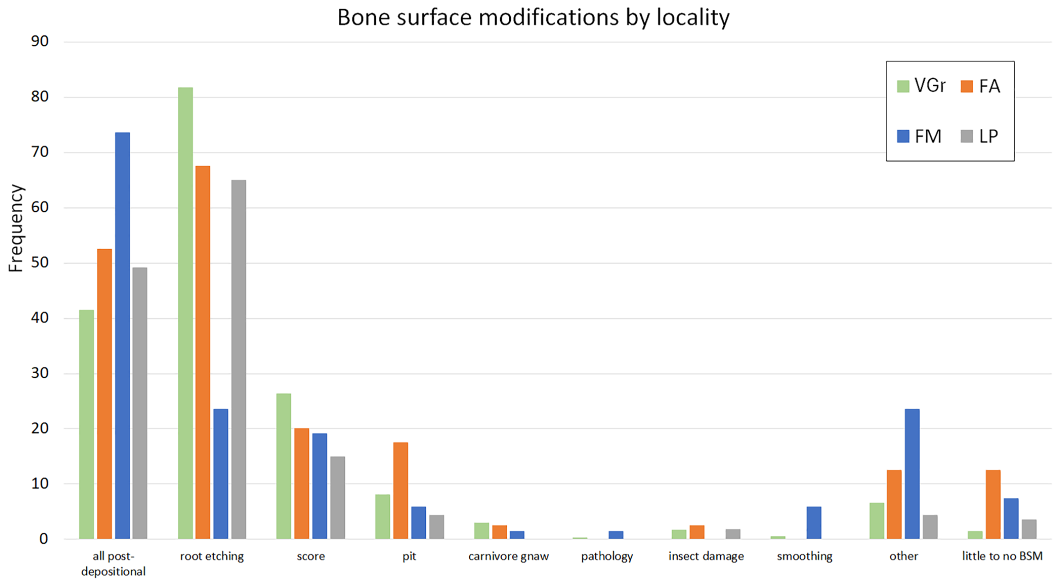


Figure 8. Bone surface modifications by type as percentage of assemblage for Fântâna lui Mitilan (FM), La Pietriş (LP), and Grăunceanu (VGr).

TABLE 6. SIMPLIFIED BONE SURFACE MODIFICATION TYPES ON FOSSILS FROM THE OLTEŢ RIVER VALLEY LOCALITIES.

	VGr* (n=4,524)		FM* (n=68)		LP* (n=114)	
BSM*	n	%	n	%	n	%
any post-depositional	1877	41.5	50	73.5	56	49.1
root etching	3698	81.7	16	23.5	74	64.9
any score	1189	26.3	13	19.1	17	14.9
any pit	366	8.1	4	5.9	5	4.4
carnivore gnaw	133	2.9	1	1.5	0	0
pathology	11	0.2	1	1.5	0	0
insect damage	74	1.6	0	0	2	1.8
smoothing	21	0.5	4	5.9	0	0
other	299	6.6	16	23.5	5	4.4
little to no BSM	68	1.5	5	7.4	4	3.5

*BSM= Bone surface modification; VGr= Grăunceanu; FM= Fântâna lui Mitilan; LP= La Pietriş

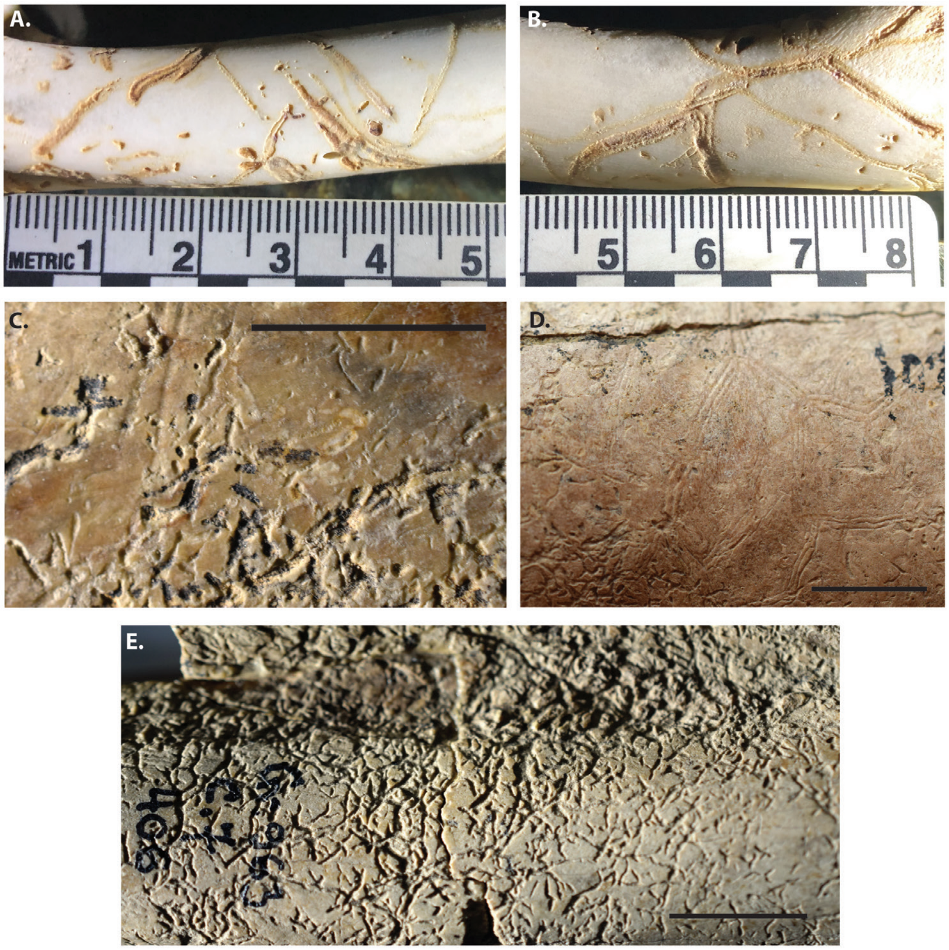


Figure 9. Examples of root etching. A-B) Recent root-etching on a juvenile Odocoileus virginianus *humerus (Curran, in prep); C) Ancient root-etching of moderate intensity on VGr.1485;* Equus *sp. tibia (with two marks in the upper left-hand corner that has some etching and adhering matrix); and, D) MO.8603;* Equus *sp. humerus, E) Extreme root etching on VGr.1723; Artiodactyla left radius (black scale bar=1cm).*

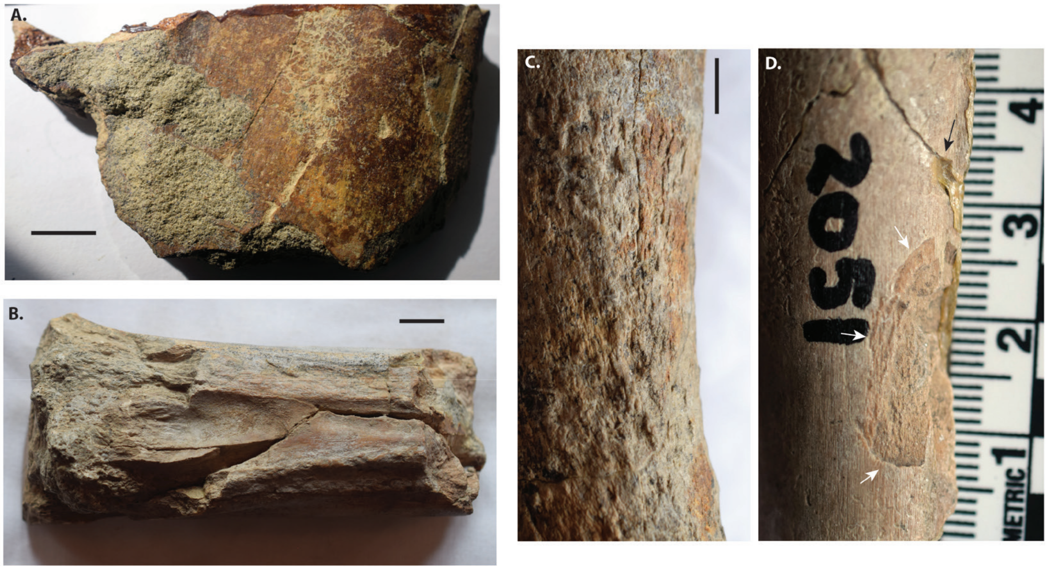


Figure 10. Examples of several types of post-depositional bone surface modifications. A) Adhering matrix (VGr.1695), B) Matrix infill of post-deposition cracks (MO.9318), C) Erosion of cortical surface (MO.9196), D) Excavation damage (MO.2051) (black scale bar=1cm).

locity. Only one other ORV assemblage (FM) displays any rounded or smooth bone surfaces, and those specimens only account for 5.9% of that assemblage (4 of 68 specimens).

Pre-Depositional Damage

Other than carnivore modifications (addressed below), pre-depositional alterations (Figure 11) are found in relatively low frequencies at Grăunceanu. Insect damage is present on 74 specimens (1.64%), rodent gnawing is found on 24 specimens (0.53%), and pathologies were observed on 11 specimens (0.24%).

Pre-depositional modifications to remains from other ORV sites are extremely infrequent. Insect damage is only found on two specimens from LP, rodent gnawing is absent, and pathology was only found on a single specimen from FM.

Linear Marks

A total of 1,189 specimens with linear marks were identified in the Grăunceanu assemblage (26.3% of the total VGr assemblage). Of these, 411 could not be identified to mark type, 296 were identified as excavator or preparator damage, 290 were identified as carnivore tooth scores, 172 were identified as sedimentary abrasion/trampling, and 20 specimens were identified as having cut marks. We return to carnivore and hominin modifications below.

Other ORV localities presented far fewer linear marks. From FM there are 9 unidentified marks, 3 excavator/preparator marks, and a single high confidence cut mark. Specimens from LP have 9 unidentified marks, 4 excavator/preparator marks, 3 sedimentary abrasion/trampling marks, and a single carnivore tooth score.

Carnivore Modifications

Carnivore damage (Figure 12) is present on 430 specimens from Grăunceanu (9.5% of the assemblage) in the form of tooth scores, pits, crenulated break edges, or any combination of these three BSMs. Specifically, we recorded tooth scores on 290 specimens, tooth pits on 147 specimens, and crenulated/chewed break edges on 133 specimens. Of these, 26 specimens had all three carnivore modifications, 45 had both tooth pits and scores, 12 specimens had tooth pits and crenulated break edges, and 31 specimens had tooth scores and crenulated breaks. A further 188 specimens had tooth scores only, 64 had tooth pits only, and 64 had only crenulated breaks. Carnivore modifications are most frequently found on Perissodactyla remains (35%, 150 of 430 specimens), specifically Equidae (with 134 carnivore-damaged specimens), as well as Artiodactyla remains (32%, 136 of 430 specimens). Only 1.2% (5 specimens) of the carnivoran assemblage presented any carnivore alterations. One specimen each of *Castor*, *Paradolichopithecus*, and Aves had carnivore damage, accounting for a summed total of 0.7% of the assemblage. The remaining 32% (136 specimens) of the carnivore-modified VGr specimens could not be identified to taxon.

Percent carnivore modifications (tooth scores and pits) from Grăunceanu relative to NISPs per skeletal element for Artiodactyla and Perissodactyla are shown in Figure 13. These patterns reveal that multiple elements that are underrepresented in NISP show disproportionately high levels of carnivore modifications. These include the humerus, femur, and pelvis which are high meat-bearing and low-density bones. Carnivore modifications are unexpectedly low for Artiodactyla tibiae, which are marrow-rich bones that are often targeted by carnivores, but in expected pro-

Figure 11. Examples of pre-depositional BSMs. A-B) Pathology- possible healed fracture of proximal phalanx (MO. 9451), C) Suspected insect boring (VGr.0068), D) Rodent gnawing (MO.9604), E) Small pits and arrows indicating sedimentary abrasion (VGr.2722), F) Root etching and arrows indicating sedimentary abrasion (VGr.1769) (black scale bar=1cm).

portions for Perissodactyla.

Carnivore-modified specimens are relatively uncommon in other ORV localities. One crenulated break edge was found in the FM assemblage. Specimens with tooth pits are somewhat more frequent, with 4 from FM and 2 from LP.

Hominin Modifications

We identified 19 specimens with cut marks from Grăunceanu and one from FM (Figure 14), details of which are reported elsewhere (Curran et al. 2025). We observed no clear evidence of percussion marks in the assemblage. Of the linear marks that could be digitized, those identified as cut marks in the qualitative (visual) analysis were generally supported as cut marks in the quantitative (morphometric) analysis (75% or 12 of 16 scores), though a few were not. Most surprising of these was VGr.1483 (Figure 14A), which is the mark that has the highest visual confirmation of being a cut mark but was identified as a tooth mark in the quantitative analysis (Curran et al., 2025). The posterior probabilities for the identification of this mark indicate uncertainty with values of 0.52 for it being a tooth mark and 0.48 for a cut mark. The comparative dataset for the quantitative analysis includes marks on limb shafts, which tend to be relatively shallower than this mark (which is on a limb epiphysis), and the depth of the mark is closer to that of tooth marks. However, its v-shaped cross-section, indicated by an acute opening angle, is more typical of cut marks. Further, the mark is on the distal tibia, which is frequently cut during butchery (Pizarro-Monzo et al. 2021). Cut marks are found on 0.442% of the Grăunceanu and FM assemblages, which is similar to the frequency of cut marks at other early Pleistocene hominin Eurasian sites, such as Dmanisi, Georgia (Tappen et al. 2022) and 'Ubeidiya, Israel (Gaudzinski 2004).

GRAIN SIZE ANALYSIS

The grain size distribution of the five samples analyzed (Table 7, Supplementary Figure 2) is dominated by sands (50–86%) (especially medium and fine-grained sands) and silts (13–48%); clays and gravels were also present but at very low levels in all samples (1–2%). Of these samples, 3 were classified as silty sands, 1 was classified as a sandy silt, and 1 was classified as sand.

DISCUSSION

The goal of this study was to present taphonomic analyses of the ORV fossil assemblages, with a special focus on the site of Grăunceanu. Our analyses reveal a pattern of extremely good bone preservation, with highly visible bone surfaces, little evidence of weathering or reworking, and a high number of complete specimens. Large mammals dominate the assemblage, though the site of Grăunceanu in particular also shows evidence for a rich carnivore guild

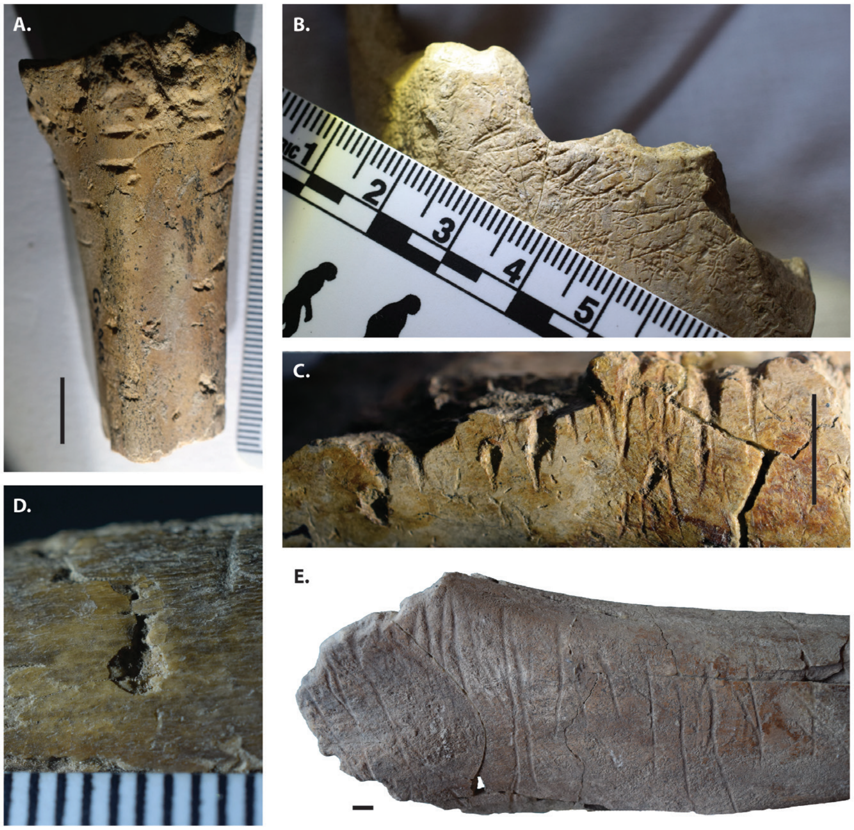


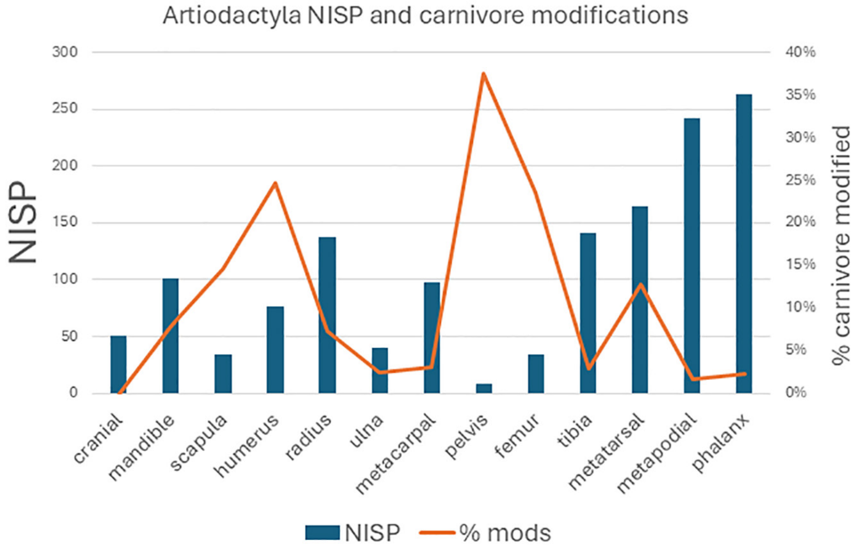
Figure 12. Examples of carnivore modifications. A) Tooth scores and gnawing (VGr.1492), B) Small tooth scores (MO.8626), C) Tooth scores and crenulated break edge (VGr.0847), D) Large tooth scores (MO.1947) (black scale bar=1cm).

(Werdelin et al. 2023). Bone surface modifications include root etching and post-depositional damage, as well as carnivore and hominin modifications. Our identifications of cut-marked fossils may constitute the earliest evidence for hominin activity (ca. 1.95 Ma) in Europe identified to date (Curran et al. 2025).

Unfortunately, these sites were originally excavated in the 1960s (Necrasov et al. 1961; Radulesco and Samson 1990) and relevant excavation notes are now lost. The detailed taphonomic investigation presented here therefore has the power to expand our knowledge of the history of these sites and shed new light on their formation processes. Publications around the time of excavation and in the intervening decades (Bolomey 1965; Radulesco and Samson 1990) describe Grăunceanu as a 1.5-meter-thick fossiliferous bone bed deposited over a relatively small area (90m^2) in silty sand, which matches adhering matrix on some of the fossils as described in the grain size analysis above. Several of the original excavation sites have been relocated based on published maps (Samson 1975), though the fossil deposits seem to have been entirely removed at the time of excavation. The bone surface modification analyses presented here suggest a cohesive assemblage with uniform surface preservation, and our skeletal element analysis does not reveal clear signs of specific collection bias. Lastly, there is excellent dating resolution placing Grăunceanu at ~1.95 Ma (Curran et al. 2025), which matches the stratigraphic description of the ORV sites (Radulesco and Samson 1990). All of these lines of data together give us high confidence in the fidelity of the ORV assemblages, particularly Grăunceanu, in terms of location, depositional type, and integrity of the fossil remains. Below we suggest ways to improve our understanding of the sites and region, but first, we compare the ORV sites, with a focus on Grăunceanu, to other Early Pleistocene Eurasian sites with reported taphonomic analyses. We finally present a summary of our hypothesis for the Grăunceanu taphonomy and deposition.

COMPARISONS TO PENECONTEMPORANEOUS LOCALITIES

Of the ORV specimens that can be taxonomically identified, there is a skew towards medium and larger taxa (size classes III and IV; Brain 1974), especially in the herbivore assemblage at Grăunceanu. While this could result from an excavation or collection bias, this seems relatively unlikely due to the collection of unidentifiable fragments and the high representation of smaller carnivores, such as *Nyctereutes megamastoides* and other canids and mustelids in the assemblage. The higher representation of medium to large size taxa at Grăunceanu is comparable to the representations reported for many Pleistocene Eurasian sites, including ones proposed to be hydraulically-accumulated



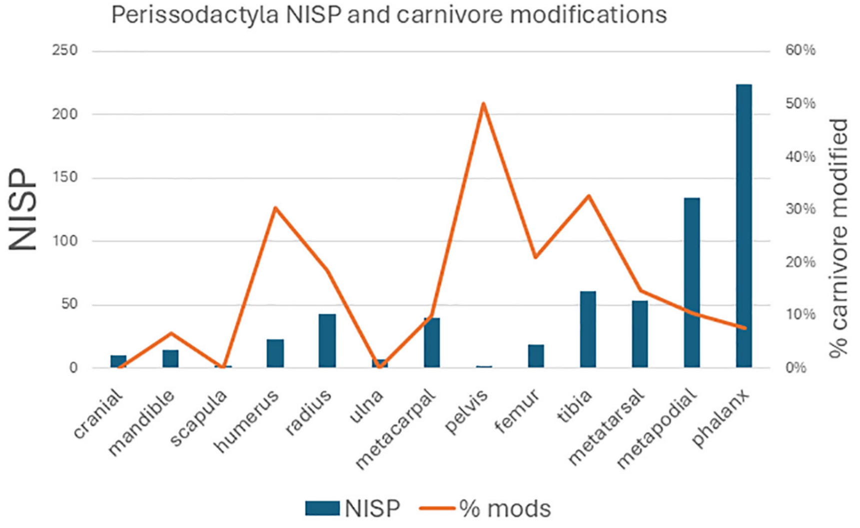


Figure 13. Histogram of number of identifiable specimens (NISP) per skeletal element for Artiodactyla (excluding Giraffidae) from Grăunceanu (left axis, blue bars) compared to percent of NISP for that category showing carnivore modifications (tooth pits, scores, and/or crenulated chewing) (line graph, right axis).

(Muhkai II, Russia (Sablin and Iltsevich 2021), Barranco León (Orce), Spain (Yravedra et al. 2022a), Fuente Nueva 3 (Orce), Spain (Yravedra et al. 2021)), cave/karst-accumulations (Trlica, Montenegro (Vislobokova et al. 2020), Pirro Nord, Italy (Cheheb et al. 2019), Sima del Elefante, Spain (Huguet et al. 2017)), hominin-accumulated (Bizat Ruhama, Israel (Yeshurun et al. 2011)) and hyena-accumulated (Dmanisi, Georgia (Tappen et al. 2022), Venta Micena, Spain (Palmqvist et al. 2022), Bois-de-Riquet/ Lezignan-la-Cebe, France (Bourguignon et al. 2016)). None of the ORV sites are speleological in origin, and both hyenas and hominins are relatively unlikely to be primary accumulators at Grăunceanu since they are poorly represented (either by remains or bone-surface modifications). Further, though there are many juveniles in the Grăunceanu assemblage, in the best-represented potential hyena prey categories for which age can be assessed, juveniles comprise 14.3–28.3% of the artiodactyl groups and only 10.7% of the equids (see Table 4). This is in contrast to the pattern at Venta Micena, hypothesized to be hyena-accumulated, where juveniles account for 42.9% of cervid specimens and 58.3% of equid specimens (Palmqvist et al. 2022).

The unlikelihood of a hyena accumulator is further supported by a relatively low level of fragmentation and the presence of many nearly complete skeletal elements in the Grăunceanu assemblage. In fact, due to the remarkable preservation in the Grăunceanu assemblage, the level of specimen identification (to element) is quite high (80%). This is unusual, as many comparable fossil assemblages are reported to be highly fragmented (including Pabbi Hills,

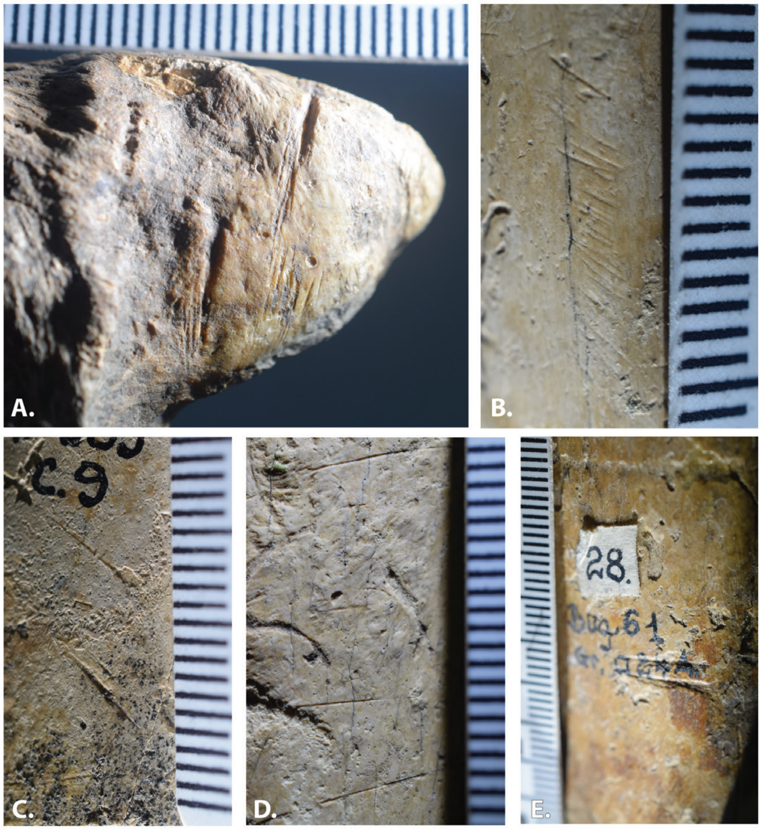


Figure 14. Examples of cut marks. A) VGr.1483, B) VGr.2186, C) VGr.2170, D) VGr.2004, E) VGr.0519 (black scale bar=1cm).

Pakistan (Dennell 2008), Ain Hanech, Algeria (Sahnouni and Heinzelin 1998), Bizat Ruhama, Israel (Yeshurun et al. 2011), Barranco León, Spain, with 13% identifiable (Yravedra et al. 2022a), Xiaochangling, China, with 10% identifiable (Peterson et al. 2003), Thomas Quarry, Morocco (Gallotti et al. 2021), Vallonnet Cave, France (Michel et al. 2017), and), Fuente Nueva 3, Spain, with 14% identifiable (Yravedra et al. 2021)). Thus, hyena do not appear to be a significant accumulator for the Grăunceanu assemblage, though carnivores were certainly involved in modifying some of the remains preserved in the assemblage.

Skeletal Element Representation

There is a clear pattern in the Grăunceanu skeletal element representation in the large herbivore assemblage, where more proximal elements are less represented and more distal elements are better represented. This is not a unique pattern in the paleontological record and is usually attributed to density-mediated attrition, either through post-depositional destruction or carnivore activity. In large herbivore assemblages there is typically a pattern of density bias with the small, dense bones of the limbs (especially tarsals and phalanges) greatly out-numbering long bones as well as

TABLE 7. GRAIN SIZE ANALYSIS RESULTS SHOWING DISTRIBUTION OF DIFFERENT GRAIN SIZES FOR EACH OF THE FIVE SAMPLES.

Sample ID	Sample Description	Gravel %	Coarse sand %	Medium sand %	Fine sand %	Silt %	Clay %
VGr.0276	Silty Sand	1.0	4.9	36.0	39.6	17.6	1.0
VGr.0972	Sandy silt	0.8	4.7	16.5	28.7	48.3	1.0
VGr.1250	Silty Sand	0.0	0.9	41.5	33.3	23.3	1.0
VGr.1964	Sand	0.0	2.3	62.2	21.1	13.1	1.0
VGr.2184	Silty Sand	0.0	4.3	38.3	24.4	32.3	1.0

cranial and axial elements. This is certainly the pattern we observe at Grăunceanu (see Figure 6) and is likely the result of a variety of causes including carnivore feeding and density-mediated attrition prior to or after burial (Brain 1981; Lam et al. 1998; Marean and Spencer 1991; Marean et al. 1992; Rogers 2000). Since there is little evidence of weathering and almost no evidence of fluvial transport, substantial abiotic damage prior to burial is not evident in the assemblage. More likely, the skeletal element pattern at Grăunceanu is the result of a combination of carnivore consumption of less-dense, fat-rich epiphyses and axial elements, preferential destruction of meat and marrow-rich bones, and post-depositional compaction and destruction of other less-dense elements (Faith and Thompson 2018). This interpretation is further supported by the moderately-strong positive correlation between bone mineral density (BMD) and %MAU in the Grăunceanu Artiodactyla assemblage, which is very similar to (though slightly stronger than) that found for *Cervus nestii* at Dmanisi, Georgia (Tappen et al. 2022). In the Dmanisi assemblage, forelimbs and hindlimbs were approximately equal in representation; this pattern, in combination with carnivore modifications, is interpreted as carnivore consumption of cervids *in situ*. Correlations between cervid BMD and skeletal element frequencies at ʻUbeidiya, Israel (I-15 and LF/I-16; Gaudzinski 2004) were also found to be moderate and positive, suggesting density mediated attrition there as well. However, low and non-significant correlations between ungulate BMD and bone portions were found for Bizat Ruhama, Israel (Yeshurun et al. 2011) and Barranco León, Spain (Espigares et al. 2019) indicating that a significant correlation between BMD and %MAU is not necessarily an expected feature of paleoanthropological sites.

Correlations between food utility index (FUI) and %MAU in Artiodactyla from Grăunceanu and *Cervus nestii* from Dmanisi are similar in that they both return moderate to moderately strong negative and significant results (Tappen et al. 2022). Correlations between ungulate marrow weight and bone portion were also strong, negative, and significant at Barranco León (Espigares et al. 2019). Only the analysis of ungulate %MAU and GUI (general utility index) at Bizat Ruhama did not return a significant relationship (Yeshurun et al. 2011). All of these sites are interpreted to have some degree of carnivore accumulation, though at Barranco León, Espigares et al. (2019) state that the pattern is more likely to be a product of hominins breaking open bones for marrow than carnivore activity.

The equid pattern at Grăunceanu differs both from the artiodactyl pattern at Grăunceanu and the equid pattern at Dmanisi. The correlation between BMD and %MAU for Grăunceanu is low and non-significant, while at Dmanisi it is moderate (Tappen et al. 2022). Further, the correlation between FUI and %MAU is stronger at Grăunceanu than at Dmanisi. Thus, the pattern of equid long bone preservation at Grăunceanu appears to be more driven by food utility than by density alone.

In contrast, the pattern of skeletal element representation is less clear for the carnivores, where not only are cranial elements far more represented overall, but there is also a difference in the representation of skeletal regions between large and small carnivores. Large carnivores are mostly represented by cranial elements and to a lesser extent, the hindlimb (femur and tibia). Small carnivores have a more even skeletal representation, though phalanges are the most frequent of their elements. It is not clear why these small skeletal elements in particular are so well preserved in the Grăunceanu small carnivore assemblage.

Bone Surface Modifications

At Grăunceanu, we observe a pattern of taphonomic alterations dominated by post-depositional changes (e.g., root etching and other changes associated with burial and fossilization), but punctuated by pre-depositional alterations such as trampling, carnivore, insect, and rodent damage. Of these, carnivore damage is found most frequently at 9.5% of the total NISP (if all carnivore modifications are included, or 8.09% if only tooth scores and pits are included). Either way, these frequencies exceed reported occurrences at most other sites, with the exceptions of Bois-de-Riquet, France (18%), and Dmanisi (9.85% for all carnivore modifications and 8.46% for only tooth scores and pits) (Supplementary Table 9), and are far less than the frequencies at hyena-accumulated Venta Micena-4 (at 29.4%; Palmqvist et al. 2022).

Carnivore tooth mark frequencies on medium and larger sized (2–4) artiodactyls and perissodactyl appendicular bones at Grăunceanu were compared to actualistic models for different sequences of carnivore and hominin access to carcasses (using data compiled and visualized in Yravedra et al. 2021: Figures 3 and 4). The tooth mark frequency from Grăunceanu is 10.11%, which is below the range of tooth mark frequencies associated with virtually all accumulations made primarily by carnivores, as well as accumulations from carnivore scavenging from human butchery refuse. Across the three categories of limb bones (stylopodium: 25.49%, zeugopodium: 10.02%, and autopodium: 6.96%), tooth mark frequencies are also much lower than would be expected when larger carnivores have primary access to medium and larger sized carcasses (Yravedra et al. 2021). Thus, while it is clear that carnivores were involved with the modification of remains at Grăunceanu, as discussed above, carnivores (and especially hyenas) were most likely not the main accumulator of the remains.

To a much smaller, though significant extent, hominins impacted the Grăunceanu assemblage, as evidenced by linear marks that we hypothesize were cut marks produced by hominins using lithic tools to deflesh and possibly disarticulate carcasses. Indeed, these cut marks may represent some of the earliest evidence of hominin activity in Eurasia documented to date (Curran et al. 2025). Though the count of identified cut marks is low, the rate of cut marks in the Grăunceanu assemblage is comparable to other Early Pleistocene Eurasian sites (Supplementary Table 9), most notably Dmanisi, where hominin remains and lithics also have been found (Tappen et al. 2022).

In sum, the Grăunceanu assemblage is remarkably well preserved, with highly visible bone surfaces, negligible weathering, and almost no smoothing or rounding that would indicate fluvial transportation. The fossils present frequent root etching and post-depositional alterations, and a moderate amount of carnivore modification. The assemblage contains a high frequency of identified long bones with half or more of their original length preserved and the majority of long bones have complete circumferences. There is a bias toward large herbivorous adult-aged mammals, which show a pattern of density-mediated preservation in their long bones. In the artiodactyl long bone counts, there is a moderate correlation between bone mineral density and representation, though this is not found for equids. There is a stronger relationship for both groups between representation and food utility indices. Most significantly, there are cut-marked bones in the Grăunceanu assemblage.

DEPOSITIONAL SCENARIOS FOR GRĂUNCEANU

Though we cannot say definitively what the main accumulating agent or depositional environment for the faunal assemblage from Grăunceanu was, we can rule out some scenarios. The general lack of weathering indicates that the bones were not left exposed on the surface for long, and the lack of rounding or smoothing suggests that they were not fluvially transported far (if at all). This is further supported by the fact that bones from the same individual are sometimes still in association/articulation (e.g., entire hock joints or multiple bones that articulate) (see Figure 2), and the comparatively low energy fluvial environment suggested by the grain size analysis. The overriding signal of root etching in the sample also suggests that the bones were buried relatively quickly and were accessible to plants near the surface not long after their deposition. Ongoing experimental analysis by one of us (SC) indicates that bones do not need to be fresh for root etching to occur, but in the ORV assemblage the vast majority of the root etching we observe shows the same coloration as the external bone surface, suggesting this root etching is ancient and occurred prior to fossilization.

Though there are some carnivore and hominin modifications present in the ORV assemblage and at Grăunceanu specifically, the low rates of both of these signatures and the general lack of fracturing of bones suggests that neither of these agents were likely to be the primary accumulators of the assemblage from Grăunceanu. The age ratios of the assemblage indicate there was not a single accumulating agent that targeted a specific age category. The lack of significant traces of clear carnivore-induced chewing damage and destruction on most of the ORV assemblage suggests that carnivores were also not major modifiers of the fauna either before or after it was accumulated. Although the presence of some tooth marks combined with many intact limb ends indicates that perhaps felids were the main carnivore modifying agent (Pobiner et al. 2020), it is possible that the multiple carnivores present in the assemblage, including sabertooths, bears, and smaller carnivores, all contributed lower 'background' levels of bone surface modifications to the ORV assemblage.

One depositional scenario we find plausible is that Grăunceanu was a catchment of primarily large-bodied mammals along the seasonally flooding paleo-Olteţ river. It is possible that gallery forests existed along the river course surrounded by more open grasslands, as is seen in modern forest-steppe habitats. This resolves some of the discrepancy between the paleoecological reconstruction by Curran et al. (2021), which indicated more open habitats (mostly for the Artiodactyla), and the more closed habitat preferences of the Carnivora (Werdelin et al. 2023). If gallery forests were present along the banks of the paleo-Olteţ, then the herbivores (including those from the outlying grassland/steppe) may have had to cross into or very near to the forests to drink, where carnivores would occasionally prey upon them. Given that the Olteţ originates in the Carpathian Mountains, there was likely substantial seasonal overbank flooding in the spring as snow melted. While the main channel of the Olteţ may have been high-energy during these times, the overbank flooding into the surrounding region may have had substantially lower energy. This could work to bring skeletal remains together without causing breakage or smoothing that is seen in more high-energy fluvial deposits. As the flood water receded back to the main channel, the skeletal remains would be buried in the silty sand brought by the overbank flooding; this interpretation is consistent with the fine-grained silty sands that still adhere to many of the Grăunceanu remains and are analyzed here. Plants would swiftly establish themselves in these rich deposits, which would then account for the ubiquitous root etching on the Grăunceanu remains. Repeated on an annual cycle, the deposits could have rapidly accumulated into the bone bed found at Grăunceanu, though the amount of time these types of deposits would represent is unknown.

Spring deposition is further supported by presence of the large Cervidae taxa, which have been proposed to utilize the Olteţ River Valley seasonally in the winter through early spring before migrating back to the Carpathian Mountains for the summer (Curran et al. 2021). These deer have C_3 isotopic signatures, indicating they were browsing during second molar growth (prior to 9 months of age; Merceron et al. 2021) and browsing mesowear morphology; however, the specimens at Grăunceanu have grazing microwear, suggesting that they were grazing just before death (Curran et al. 2021). There is a lack of neonate deer specimens, either because they were not preserved, or perhaps because they were born in the mountains before migration to the ORV. The assemblage also contains many antler sheds (21 of the 27 for which the coronet/burr was observable were shed) suggesting *in situ* loss, which occurs in late winter (Curran et al. 2021). Together, these lines of evidence point towards a depositional context that records aspects of life along the paleo-Olteţ river, where deer overwintered, carnivores hunted, and hominins occasionally visited and butchered animals approximately 2 million years ago.

There are several lines of evidence that could improve our understanding of the ORV sites and Grăunceanu in particular. Since the original excavation locations have been reidentified, detailed geophysical analyses would allow us to test hypotheses regarding the specific types of hydraulic deposition and the time span of accumulation. Analysis of break morphology (Villa and Mahieu 1991) and quantitative analyses of carnivore tooth scores and pits (Abellan et al. 2021; Herranz-Rodrigo et al. 2021; Yravedra et al. 2022b) could enable more specificity about carnivore-herbivore interactions. Further stable isotope analyses would better elucidate the amount of seasonality at the sites, and strontium isotope analysis would aid in understanding if regional migration occurred. And, of course, identifying new fossil localities would help to control for many of the unknowns discussed above. Though our research team has conducted several surveys of the region and has found various pockets of fossils, we have not yet identified any new fossil sites. However, given the richness of the fossiliferous deposits in the ORV, it is likely there are more *in situ* fossil sites to be found.

CONCLUSION

Taphonomic assessments such as the ones presented in this study have the ability to shed new light on fossil sites, including those, such as Grăunceanu, that were excavated decades ago. Our goal here is to present a detailed taphonomic assessment of the ORV sites, especially Grăunceanu, with a focus on identifying the primary agents of accumulation and modification in order to provide additional context to prior descriptions of cut marks from the ORV (Curran et al. 2025). The Grăunceanu assemblage has extremely good preservation with highly visible bone surfaces and many nearly complete bones. While it is likely that the paleo-Olteţ river was very near to the depositional site of Grăunceanu, the remains do not appear to be fluvial in accumulation, as there is very little smoothing to their surfaces. Further, the fossils have very little weathering, suggesting that they did not sit on the surface for very long prior to burial. The moderate incidence of carnivore modifications is testament to their involvement in modifying the remains present at Grăunceanu, in addition to the very small contribution from hominins. Grăunceanu most likely was accumulated in an alluvial floodplain, recording aspects of life and death along the paleo-Olteţ river.

ACKNOWLEDEMENTS

We thank the many people who helped with data collection, fieldwork, and provided valuable advice: Eric Delson, Kieran McNulty, Viorel Horoi, Silviu Constantin, Marius Robu, Martha Tappen, Răzvan Arghir, Amber Cooper, David Fox, Niki Garrett, Timothy Gaudin, Jenifer Hubbard, Lydia B. Ironside, Eric Mazelis, Ionuț Mirea, Ipyana Mwakyoma, Ashly Romero, Dana Stamatoiu, Cristina Stan, Emil Știucă, Ioan Tanțău, Peter Ungar, Laura Văcărescu, Caitlin Yoakum. We especially thank the people of the Olteț Valley and Tetoiu for their assistance during fieldwork and for initially locating many of these important fossils. Funding for this research was provided by The Leakey Foundation, National Science Foundation grant BCS-1636686, The Josiah Charles Trent Foundation and Duke University, The University of Arkansas, Ohio University, The University of California Santa Barbara, The Peter Buck Fund for Human Origins Research, and the Romanian Ministry of Education and Research, CNCS - UEFISCDI, project number PN-III-P4-ID-PCE-2020-2282 (ECHOES).

AUTHOR CONTRIBUTIONS

Conceptualization: S.C., C.T., C.R., B.P., A.Pe., V.D.; Methodology: S.C., C.T., B.P., V.D., M.P.; Investigation: S.C., B.P., S.G., V.D., M.P., R.C., A.Po., C.R., L.W., A.Pe., C.T.; Formal Analysis: S.C., C.T., B.P., M.P., V.D., T.K.; Visualization: C.T., V.D., S.C., M.P.; Data Curation: A.Po., A.Pe., C.T., S.C., V.D.; Resources: A.Pe., A. Po.; Funding acquisition: C.T., S.C., C.R., B.P., V.D., A.Pe; Project administration: CT, SC; Writing – original draft: S.C., C.T., V.D., M.P., BP; Writing – review & editing: S.C., B.P., S.G., V.D., M.P., R.C., T.K., A.Po., C.R., L.W., A.Pe., C.T.

DATA AVAILABILITY

All data are available in the main text or supplementary information. Data related to the cut marks can be found in Curran et al. (2025, https://doi.org/10.1038/s41467-025-56154-9). Fossil materials are housed at the "Emil Racoviţă" Institute of Speleology (ISER) in Bucharest, Romania, and the Museum of Oltenia (MO) in Craiova, Romania; access to these collections can be requested by contacting coauthors Petculescu (ISER) and/or Popescu (MO). Comparative data from the quantitative analysis of the cut marks is available upon request to Michael Pante.

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Supplement 1 to Taphonomic Analysis of Early Pleistocene Fossil Localities of the Olteţ River Valley, Romania

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SUPPLEMENT 1

This supplement contains: Supplementary Tables 1–9 and Supplementary Figures 1–2.

PaleoAnthropology 2026:1 supplement to Curran et al. 2026:1 ISSN 1545-0031
Paleoanthropology Society & European Society for the study of Human Evolution
OPEN ACCESS

Supplemental Materials

Supplementary Table 1. Definitions of abiotic and biotic bone surface modifications considered here.

Abiotic Modifications	
Pitting	Small round alterations randomly spread across the bone surface. These marks are possibly caused by contact with a low pH substrate (Barron et al., 2003; Dawes, 2003) and/or precipitation.
Matrix/ sediment adhering	Non-fossil material adhering to the specimen, including sedimentary matrix, precipitates such as carbonates, and manganese staining. When possible, adhering non-fossil material was removed.
Dissolution	Diagenetic alteration that occurs as a fossil surface erodes over time, typically while achieving equilibrium with an aqueous environment (Hedges, 2002). Similar to digestion, though dissolution is present on larger specimens while digestion is only on specimens small enough to have passed through the gastrointestinal tract.
Polishing/ smoothing/ rounding	Smoothing and polishing can be produced by a variety of influences, most importantly by water (e.g., transportation in a body of water or water moving across a specimen after it has been re-exposed; Shipman and Rose, 1983) and/or aeolian action (e.g., fine sediment blown across the specimen's surface).
Generalized post-depositional abiotic damage	This is a general descriptor for a specimen that exhibits one or more of the following: exfoliation/flaking (i.e., external-most layers of bone flaking off), crushing, denting, chipping, erosion (similar to exfoliation but extending deeper into the bone; can be confused for weathering), cracking/ expansion/ sediment infill (i.e., cracks that are in-filled with sediment whether or not the sediment infilling was the cause). The presence of each of these modifications was recorded for each specimen, though we collapse them here into a single category since they represent the same taphonomic process.
Biotic Modifications	
Tooth Pits	Round to slightly oval-shaped pits created by the compressive force of a carnivore's tooth (without dragging the tooth along the surface).
Root etching	Root etching takes the form of lightly incised lines or dots (typically with a u-shaped cross-section) across the bone surface; these appear in a dendritic pattern or may form a discontinuous trail across the bone. Early stages of root etching may result in the discoloration of the bone's surface, while more intense root activity may result in deep troughs that obliterate the bone's surface.
Insect modifications	Similar to root etching but may present as a series of semi-randomly distributed grooves. Termite damage is rather distinct, appearing in a distinct star-burst pattern (Kaiser, 2000; Backwell et al.; 2012) or as borrow-like features (Huchet et al., 2009).
Digestion	Erosion of bone surfaces caused by the low pH of stomach and intestinal acids, ranging from minor surface alterations to complete erosion of specimens to the point of being unrecognizable (as with some mammalian carnivores; Andrews, 1990). Indicators of digestion are "bones with thinned edges, pinholes, polish, and severe irregular erosion" (Tappen et al., 2007: 128).

Rodent gnawing	Rodents, and especially porcupines, gnaw on dry bones in an effort to wear down their incisors, which continue erupting throughout their lives. This BSM is very distinctive and presents as discrete regions with many short parallel scores.
Carnivore chewing/ crenulated edges	Carnivore modifications were identified by the presence of tooth pits and tooth scores, and chewing of the epiphyses that typically results in the ends of the long bones having scalloped to crenulated furrows in them.
Peeling	Often a result of incomplete breakage where the cortical bone "peels off" of one side, as would happen if one tried to break a fresh tree branch (White, 1992). Resulting bones then have one side with a break that has bone that thins out to fibrous tendrils that typically curl back on themselves (which are unlikely to preserve) and another side that has a break with a beveled portion of cortical bone missing. Typically associated with hominin manipulation, though carnivores can also produce this modification (Pickering et al., 2011).
Pathology	Any antemortem morphology does not conform to the typical anatomy for that taxon. This includes congenital defects, disease (especially osteomyelitis and similar reactive bone growth associated with infections), and/or healed/healing injuries.

Supplementary Table 2. Score attributes recorded (modified from Dominguez-Rodrigo et al., 2009, 2010).

Trajectory	The gross morphology of the score. Recorded as 1) straight, 2) curved, or 3) slightly curved
Barb	Slight curve/hook to the shallower end of a score. Recorded as 1) presence or 2) absence
Orientation	Positioning of the score relative to the long axis of the bone. Recorded as 1) transverse, 2) oblique, 3) parallel, 4) transverse-oblique, or 5) all/indeterminate.
Cross-section	Internal morphology of the score. Recorded as 1) U-shaped, 2) V-shaped, 3) flat, or 4) indeterminate (when not visible).
Number of scores	Count of visible scores on a specimen
Symmetry	Symmetry of the cross-sectional morphology of the score. Recorded as 1) symmetrical or 2) asymmetrical
Shoulder effects	Presence (1) or absence (2) of striae and flaking visible along the edge of of the score
Microstriations	Presence (1) or absence (2) of striae within the score
Other striae	Presence (1) or absence (2) of striae away from the main score(s)
Color	Color of the internal surface of the score. Recorded as 1) same as external bone surface or 2) different from external bone surface.

Supplementary Figure 1. Specimen VGr.0276 (*Eucladoceros* sp. femur) showing sediments lodged in the bone shaft.

Supplementary Table 3. Skeletal element frequencies for Grăunceanu specimens.

	Proboscidea	Artiodactyla Indet	Cervidae	Bovidae	Giraffidae	Equidae	Rhinoceratidae	Felidae	Hyaenidae	Ursidae	Large Carnivore	Mustelidae	Canidae	Mustelid/ Canid	Cercopithecoidea	Castoridae	Hystricidae	Manidae	Struthionidae
horn core	na		na	7	na	na	na	na	na	na	na	na	na	na	na	na	na	na	na
antler	na		106	na	na	na	na	na	na	na	na	na	na	na	na	na	na	na	na
cranium		3	48	2		13		2	2	5		4	26	3	12	1			
mandible		4	83	5		14	1	7	5	10		5	23		2	3	2		
isolated teeth (incl frags)	10	13	134	12		22	4	11	4	20		11	27	4	1	1			
vertebrae																			
indet		16												25					
cervical		13		4		10								2					
thoracic		7																	
lumbar		35				1													
sacrum		5																	
caudal		2																	
rib	7																		
scapula		33				4													
humerus	8	45	26	1		46	7			1	1			3	3			1	
radius	3	92	45	3		52	11				3			8	1				
ulna		32	2			11	9	1		1				7	1				
radius & ulna			1		1	4													
carpals	6	163	8		4	63	20							2					
metacarpal	4	50	97	7	3	70	6							4					
pelvis/os coxa	3	16				14	2			1	3			4					
femur	2	32	3			39	9			1	5			4	2			1	
patella	5	1	1			0		1											
tibia	3	98	39		1	67	9	2			10			6					1
fibula/ os malleolus	2	26	2		1	0													
tibia & fibula together						0													
astragalus		11	48	6	3	97	7							2					
calcaneus		16	143	1	2	66	3	1		1				2					
cubonavicular		47	1	1	3	0													
misc tarsals	4	48			1	63	3	1											
metatarsals	1	87	137	8	3	77	2							11					
carpal/tarsal	5					1								9					
sesamoids		43				11													
metapodial	1	101	57	1		41	3				6			17					
accessory metapodial						49													
proximal phalanx	3	130			3	79	6				4			18					2
intermediate phalanx	1	97	2			69	2				2			31					
distal phalanx		40		1		73	2				2			2	1				

Supplementary Table 4. Long-bone portions for the Olteţ River Valley localities.

	Small fragment	Medium fragment	Half	>Half	Nearly whole	Whole
FM	18.2	0.0	9.1	36.4	0.0	36.4
LP	43.8	25.0	25.0	6.3	0.0	0.0
VGr	13.5	8.9	21.3	33.8	7.4	15.0

FM= Fântâna lui Mitilan; LP= La Pietriş; VGr= Grăunceanu

Supplementary Table 5. Long bone circumference for the Olteţ River Valley localities.

	0-25%	26-50%	51-75%	76-99%	100%
FM	0.0	18.2	9.1	9.1	63.6
LP	18.2	9.1	0.0	9.1	63.6
VGr	4.5	5.4	2.3	3.6	84.3

FM= Fântâna lui Mitilan; LP= La Pietriş; VGr= Grăunceanu

Supplementary Table 6. Surface visible on fossils for the Olteţ River Valley localities.

% visible	0-25%	26-50%	51-75%	76-100%	NA
FM	22.1	14.7	19.1	44.1	0.0
LP	27.2	10.5	16.7	45.6	0.0
VGr	8.0	6.6	12.1	72.2	1.1

FM= Fântâna lui Mitilan; LP= La Pietriş; VGr= Grăunceanu

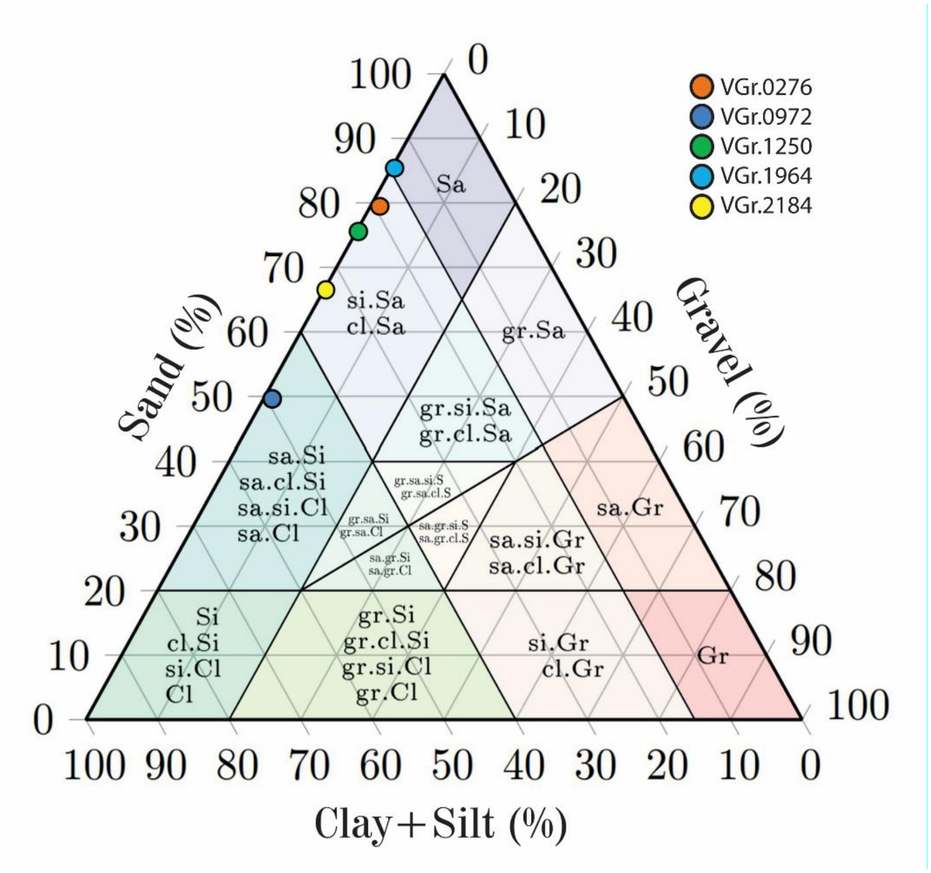
Supplementary Table 7. Weathering stages of fossils for the Olteţ River Valley localities.

	0	1	2	3	4	NA
FM	82.4	13.2	2.9	1.5	0	0
LP	87.2	10.1	2.8	0	0	0
VGr	83.2	12.2	1.3	0.7	0.2	2.5

FM= Fântâna lui Mitilan; LP= La Pietriş; VGr= Grăunceanu

Supplementary Table 8. Detailed bone surface modifications for the Olteţ River Valley localities.

		VGr (n=4,524)		FM (n=68)		LP (n=114)	
		n	%	n	%	n	%
Post-depositional	dissolution	139	3.1	9	13.2	0	0
	matrix/sediment/manganese	1210	26.7	32	47.1	49	43
	pitting	170	3.8	11	16.2	0	0
	exfoliation	345	7.6	15	22.1	9	7.9
	denting	46	1	0	0	0	0
	erosion	47	1	7	10.3	0	0
	cracking/expansion/sed infill	72	1.6	0	0	2	1.8
	crushing	16	0.4	2	2.9	1	0.9
	chipping/denting	195	4.3	0	0	3	2.6
	flaking	99	2.2	2	2.9	1	0.9
	general deterioration	15	0.3	0	0	0	0
root etching		3698	81.7	16	23.5	74	64.9
Scores	score- tooth	290	6.4	0	0	0	0
	score- excavator/prep	296	6.5	2	2.9	4	3.5
	score- sediment abrasion	151	3.3	0	0	3	2.6
	score- trampling	21	0.5	0	0	0	0
	score- CM uncertain	12	0.3	0	0	0	0
	score- CM certain	7	0.2	1	1.5	0	0
	score- undefined	411	9.1	9	13.2	8	7
Pits	tooth pits	147	3.2	4	5.9	2	1.8
	other pits	225	5	0	0	3	2.6
carnivore crenulations/gnaw		133	2.9	1	1.5	0	0
pathology		11	0.2	1	1.5	0	0
insect damage		74	1.6	0	0	2	1.8
polish/smoothing/rounding		21	0.5	4	5.9	0	0
Other	rodent gnawing	24	0.5	0	0	0	0
	peeling	3	0.1	0	0	0	0
	flake scar	5	0.1	0	0	0	0
	shellacked/glued/plaster	267	5.9	16	23.5	5	4.4
no to little visible surface/indet		29	0.6	0	0	0	0
no data recorded		39	0.9	0	0	0	0
none		132	2.9	5	7.4	4	3.5



Supplementary Figure 2. Ternary diagram showing proportions of sand (Sa), clay (Cl) and silt (Si), and gravel (Gr) in each of the samples analyzed as part of the grain size analysis.

Supplementary Table 9. Comparative data for cut marked and tooth marked specimens from other Early Eurasian Pleistocene sites.

Site	**Age (Ma)**	**CM#**	**CM%**	**TM#**	**TM%**	**NISP**	**Full taph?**[a]	**Reference**
Masol, India	2.6	3	0.204	12	0.817	1469	partial	Dambricourt Malassé et al. (2016)
Aïn Boucherit, Algeria	2.4-1.9	19	3.316	0/NS	0/NS	573	yes	Sahnouni et al. (2018)
Grăunceanu, Romania	1.95	8/21	0.177/0.46[b]	366/430[c]	8.09/9.5[c]	4524	yes	this study
Muhkai 2, Russia	2.1-1.77	1	0.04	0	0	2498	partial	Sablin and Iltsevich (2021)
Liventsovka, Russia	2.1-1.97	1	0.003	0/NS	0/NS	33000	partial	Sablin and Girya (2010)
Trlica, Montenegro	1.8-1.5	1	0.112	NR[d]	NR[d]	895	yes	Vislobokova et al. (2020)
Dmanisi, Georgia	1.8	30[e]	0.392	648/754[c]	8.46/9.85[c]	7658	yes	Tappen et al. (2022)
El-Kherba, Algeria	1.78	13	2.1	26	4.2	619	yes	Sahnouni et al. (2013)
Pirro Nord, Italy	1.6-1.3	14	1.089	22	1.71[f]	1285	yes	Cheheb et al. (2019)
Bizat Ruhama, Israel	1.6-1.2	1	0.709	1	0.709	141	yes	Yeshurun et al. (2011)
'Ubeidiya, Israel	1.5-1.2	16	0.262	NR[d]	NR[d]	6099	yes	Gaudzinski (2004)
Sangiran, Indonesia	1.45-0.79	2[g]	0.006	0	0	34000	partial	Choi and Driwantoro (2007)
Barranco León, Spain	1.4	82	0.856	183	1.912	9573	yes	Yravedra et al. (2022a)
Bois-de-Riquet, France	1.3-1.2	2	0.07	NR	18	2875	yes	Bourguignon et al. (2016)
Vallonnet Cave, France	1.2-1.1	12	0.021	NR[d]	NR[d]	57759[h]	yes	Michel et al. 2017 (SOM), Echassoux (2004)
Sima del Elefante, Spain	1.2-1.1	NR	5	NR	5	NR	yes	Huguet et al. (2017)
Fuenta Nueva 3, Spain	1.19	54	0.458	21	0.437	8653[i]	yes	Espigares et al. (2019), Yravedra et al. (2021)

Age (Ma) = Age of site in millions of years

CM= cut marks reported as either a raw number (CM#) or percentage (CM%)

TM= tooth marks reported as either a raw number (TM#) or percentage (TM%)

NISP= number of identified specimens

NR= not reported

0/NS= not specified (for tooth marks, this means the publication did not report any tooth marked bones, but also did not indicate explicitly that the authors looked for tooth marks or other carnivore damage but did not find any)

[a] Was a full taphonomic assessment reported for this locality? Yes= a full taphonomic analysis has been published; partial= taphonomy of some marks have reported

[b] Numbers for Grăunceanu indicate high certainty/ probable cut marks

[c] The first value reported is for specimens with tooth pits or scores and the second number is for all carnivore modifications

[d] Carnivore damage on bones is reported, but the number of tooth marked specimens is not given

[e] Exact number of specimens with marks (rather than total marks) not reported

[f] Our calculations are 22 tooth marked specimens with 26 total tooth marks (from Table 6), with 22/1285 total bones = 1.71%. However, this publication lists the proportion of tooth marked bones as 5.56%

[g] Reported as 18 cut marks on 2 specimens; likely made with clam shells

[h] total NISP analyzed for taphonomy unclear

[i] Part of this NISP (3,852, from Espigares et al. 2019) represents a subset of the larger assemblage. In Espigares et al. (2019) carnivore damage on bones is reported, but the number of tooth marked specimens is not given. Carnivore tooth mark % is reported only from Yravedra et al. (2022), in which the number of specimens reported with tooth marks (n = 21) is compared with the NISP studied (4,801, excluding teeth).