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Multiproxy paleoenvironmental reconstruction of Early Pleistocene sites from the Olteţ River Valley of Romania

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ABSTRACT

The Early Pleistocene is recognized as a time of major global climatic and environmental change, including increasing aridity, significant spread of grasslands, and substantial faunal turnovers and dispersals. Importantly, this is the first time hominins are found in Eurasia. Reconstructing the types of environments that existed during this time is imperative for understanding mammalian, including hominin, dispersal patterns relative to climatic change. One proposed dispersal corridor across Europe is the Danube River. Here we characterize the 2.2 to ~1.1 million years ago (Ma) paleoenvironments surrounding one of the tributaries to the Danube, the Olteţ River, in southern Romania using a multiproxy approach, including taxonomic uniformitarianism, dental mesowear, dental microwear, enamel stable isotope (carbon and oxygen), and coprolite/palynology analyses, and compare our results to other penecontemporaneous Eurasian sites. Older sites from this region, Grăunceanu and La Pietriş, both dating to 2.2–1.9 Ma, are reconstructed as being primarily open, though with some nearby woodlands and significant water resources. Fântâna lui Mitilan, which is younger (1.8–1.1 Ma), is reconstructed as slightly more closed, though still relatively open in nature. These results are similar to reconstructions for other Early Pleistocene Eurasian sites, including ones with and without hominins, suggesting that hominins were likely not inhibited from dispersing across Eurasia due to environmental constraints at this time.

1. Introduction

Although there has been intensive exploration and excavation of Early Pleistocene paleontological localities across much of western Europe, there are fewer known sites in eastern Europe (Iovita et al., 2014). As a result, major temporal and spatial gaps exist in the paleoenvironmental record for the Early Pleistocene of Europe. A solid understanding of this time interval is critical due to major faunal turnovers that were occurring likely as a result of well-documented global climatic shifts from a warmer environment to more arid and cool environments

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(e.g., Ruddiman, 2006; Leroy et al., 2011). This shift has been linked to major changes in Eurasian faunal communities and has been implicated in the initial dispersal of hominins into Eurasia ca. 1.85 million years ago (Ma) (e.g., Ferring et al., 2011). With this in mind, the goal of this study is to present an updated paleoenvironmental reconstruction from the Olteţ River Valley (ORV) of southern Romania, using a multiproxy approach. The ORV region is represented by a rich collection of Early Pleistocene fossil materials and has the potential to shed light on this important time interval in human evolution.

1.1. *Hominin dispersal(s) into Eurasia*

Understanding the paleoenvironments of eastern Europe during the Early Pleistocene is critical because this is the time during which hominins were likely initially dispersing into Europe. The site of Dmanisi, Georgia demonstrates that hominins were present in Eurasia by at least ~1.85 Ma (Swisher et al., 1994; Ferring et al., 2011). This likely was part of a rapid radiation of hominins throughout Eurasia, as evidenced by other Asian sites (e.g., Swisher et al., 1994; Antón et al., 2002; Dennell, 2003; Morwood et al., 2003; Finlayson, 2005; Potts and Teague, 2010; but see Matsu'ura et al., 2020). Scattered evidence exists to suggest that hominins radiated into Eurasia even earlier, though this is debated (e.g., Riwat, India [Dennell et al., 1988] and Shangchen, China [Zhu et al., 2018]).

Several sites in Europe and southwestern Asia are purported to contain hominin remains and/or lithic materials, including Turkey (Kocabaş, 1.6–1.2 Ma [Vialet et al., 2018]), France (Lézignan-la-Cèbe, 1.3–1.1 Ma [Bourguignon et al., 2016]), Italy (Pirro Nord, 1.7–1.3 Ma [Arzarello et al., 2009]), and Montenegro (Trlica, 1.8–2.5 Ma [Vislobokova et al., 2020]) (Figs. 1 and 2); however, dating for these sites is controversial (Falguères, 2020). It is not until ~1.4 Ma at the site of Barranco León, Spain (Toro-Moyano et al., 2013), that there is well-accepted evidence for hominins in Europe, with a single deciduous hominin molar and thousands of Mode I stone tools recovered (Agustí et al., 2015). Given the scarcity of evidence for hominins in Europe between 1.85 and 1.4 Ma, it therefore remains unclear how and when hominins dispersed into Europe in the Early Pleistocene. Critically, the region under investigation here, the Olteţ River Valley of Romania, is one potential region through which hominins are hypothesized to have dispersed into the rest of Europe via the Danube River (Conard and Bolus, 2003; Higham et al., 2012; Parés et al., 2013; Iovita et al., 2014).

1.2. *The Olteţ River Valley (ORV)*

Located in the Dacian Basin of southern Romania, the Olteţ River (via the Olt River) is a tributary of the Danube River. During the 1960s and 1980s, expeditions in the ORV identified more than a dozen fossiliferous localities estimated to date to the Early Pleistocene (Samson, 1976; Rădulescu and Samson, 1990; Rădulescu et al., 2003). One locality, Grăunceanu (= Valea Grăunceanului, Fig. 3), has produced >5000 fossil specimens, making it an important site for understanding Villafranchian (MN 17/MmQ1) paleontology. Other important fossil localities in the ORV include La Pietriş, which is likely contemporaneous with Grăunceanu, and the younger site of Fântâna lui Mitilan (e.g., Rădulescu and Samson, 1990). Intriguingly, Mode I lithics were reported to have been recovered from two ORV localities (Pietrişu Vâjoieşti and Dealul Mjlociu; Rădulescu et al., 1998), though the anthropogenic origin of these lithics is unclear (Doboş, 2008). Expeditions by our research team since 2012 have relocated several of these original localities and identified new fossil-bearing deposits in the ORV. All ORV localities appear to be of fluvial and deltaic origin along the paleo-Olteţ River and a full taphonomic assessment of the faunal assemblages is currently underway. Previous paleoenvironmental reconstructions of Grăunceanu (primarily based on taxon presence/absence or ecomorphology) have indicated the presence of open ‘savannah’-like habitats (Ferretti and

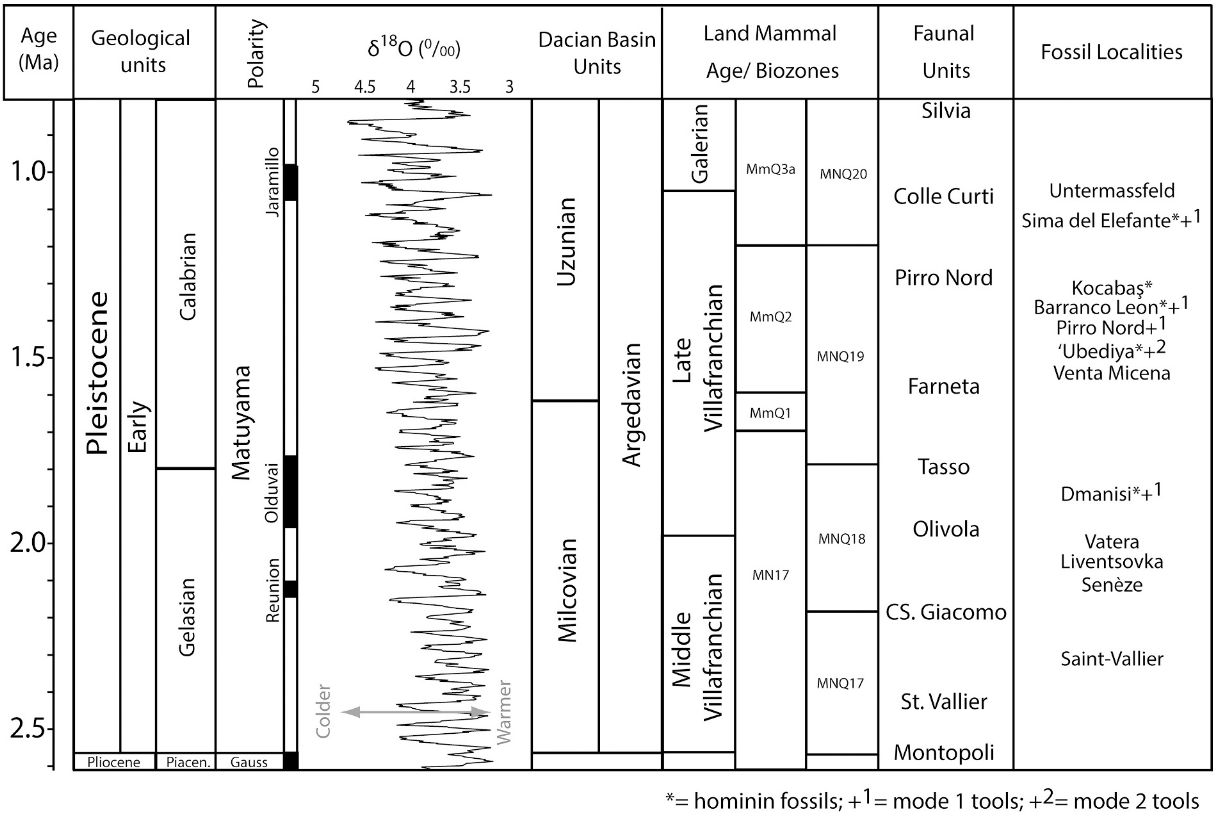

Fig. 1. Chart showing the temporal units discussed in the text and their relation to one another, including relevant faunal units and biozones/land mammal ages, and selected European and near eastern fossil localities. Mammal ages, Dacian Basin units, and oxygen isotope data are from Martínez-Navarro (2010), Oms et al. (1999), Andreescu et al. (2011), and Lisiecki and Raymo (2005).

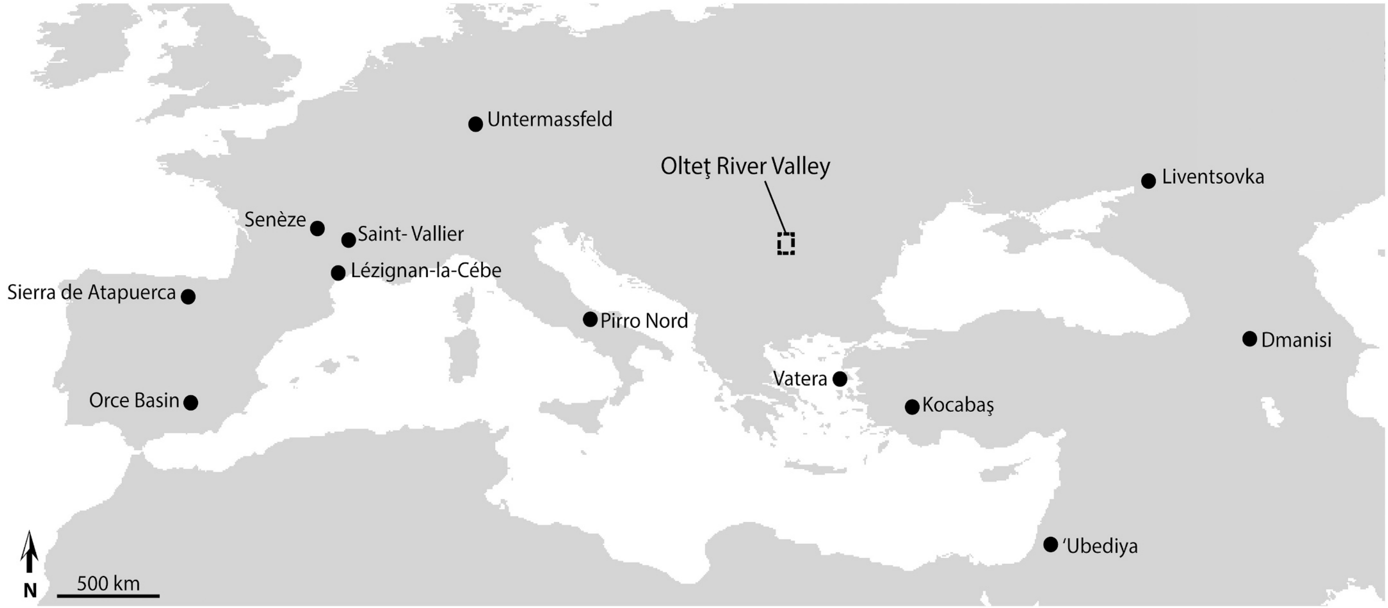

Fig. 2. Map of Europe and Southwest Asia showing fossil localities discussed in the text.

Croitor, 2001; Frost et al., 2005; Curran, 2009, 2015, 2018) with warm and humid conditions (Rădulescu et al., 2003) and some tree cover along a river (the paleo-Olteţ). This reconstruction is similar to those of other Early Pleistocene Eurasian sites, including Dmanisi, Georgia (Gabunia et al., 2000; Palmqvist, 2002), Vatera, Greece (Koufos, 2009), and Senèze, France (Delson et al., 2006; Curran, 2009).

Recently, our team conducted a re-analysis of the ORV faunal assemblages (Terhune et al., 2020). This ongoing work identified a total of 38 unique taxa from 18 families (Table 1), several of which were either substantially revised taxonomically from previous publications or had not been previously identified in the ORV assemblage. The ORV assemblage is dominated by cervid and equid remains (roughly 55.2% and 26.5% of the number of identified specimens (NISP) in the Grăunceanu assemblage, respectively), and includes a high diversity of carnivore taxa (at least 11 species from 5 families). Further, the ORV assemblage and particularly that of Grăunceanu contains members of the orders Rodentia, Pholidota, and a large ostrich species (*Pachystruthio* cf. *pannonicus*). Consistent with previous work (e.g., Rădulescu and Samson, 1990; Rădulescu et al., 2003), our biochronological estimates suggest an age of ~2.2 to 1.9 Ma for Grăunceanu (and likely also La Pietriş), while the site of Fântâna lui Mitilan is younger (~1.8 to 1.1 Ma) (Terhune et al., 2020). Given this revised taxonomy, the generalized nature of previous paleoenvironmental reconstruction, and new techniques now available, the updated paleoenvironmental reconstruction and comparison to other penecontemporaneous localities presented here is warranted.

1.3. Paleoenvironmental conditions during the Early Pleistocene of western Eurasia

Paleoclimatological studies document substantial climate changes across the globe during the Early Pleistocene, creating increasingly cooler and more arid conditions in western Asia (Bradley, 1999; Ravelo et al., 2004; Carrion et al., 2011) with the onset of northern hemisphere glacial cycling (Ruddiman, 2006). Transitions between glacial and interglacial conditions resulted in shifts from forests to open woodlands and then to open vegetation landscapes, such as grasslands, with a 41,000 year or obliquity-dominated periodicity (Leroy et al., 2011). Expansions of grasslands in Eurasia may have created more favorable conditions for hominins and other grassland-adapted mammals to disperse into these areas (Antón et al., 2002; Tappen, 2009; Belmaker, 2010; Popescu et al., 2010; O'Regan et al., 2011; Berlioz et al., 2018). Support for this hypothesis is found at many of the earliest hominin sites in Asia, which have been reconstructed as open, grassland environments, broadly similar to contemporaneous hominin localities in Africa (Dennell, 2003; Dennell and Roebroeks, 2005). In Europe and southwest Asia (e.g., Israel) paleoenvironmental reconstructions also reflect a pattern of increasing aridity beginning in the Early Villafranchian. Here we briefly review paleoenvironmental reconstructions (summarized in Table 2) from a number of important faunal localities in western Eurasia from the Middle and Late Villafranchian; we limit our discussions to sites older than one million years with good reconstructions and paleoenvironmental data against which we can compare the ORV sites (Figs. 1 and 2).

1.3.1. Saint-Vallier, France (2.4–1.9 Ma, Valli, 2004)

Saint-Vallier is the reference locality for biozone MN17 (2.4–1.9 Ma) due to its rich and well-preserved fauna (Valli, 2004). It is an open-air site south of Lyon, France to the east of the Rhône River. Ecomorphological analyses of the cervid post-crania indicate that available habitats were open to intermediate-open in nature with mountainous relief nearby (Curran, 2009). Paleoecological reconstructions using taxon-based methods indicate that Saint-Vallier had a mosaic of warm open and wooded habitats along a lake or river (Valli, 2004).

1.3.2. Senèze, France (2.21–2.09 Ma, Pastre et al., 2015)

Senèze is the biochronological reference for MNQ18, in the Late Villafranchian (Delson et al., 2006). The Senèze faunal assemblage is comprised of remains from 34 mammalian species, many of which were first defined on the basis of the Senèze materials, including a wide variety of artiodactyls and carnivores, multiple equid species, and the primate *Paradolichopithecus arvernensis* (Delson et al., 2006). According to cervid ecomorphological analyses, Senèze was similar to Saint-Vallier in having mostly open to intermediate-open paleohabitats (Curran, 2009, 2018). A small palynological sample suggests the presence of a temperate mixed deciduous and coniferous forest in addition to more open habitats surrounding a lake (Delson et al., 2006).

1.3.3. Liventsovka Quarry, Russia (2.1–1.97 Ma, Sablin and Girya, 2010)

Fossils from the Liventsovka Quarry, located near Rostov-on-Don in southern Russia, belong to the Khapry Faunal Complex (Sotnikova et al., 2002). Specimens were recovered from the Khapry alluvium and represent 33 species of large mammals, many of which are associated with a dry

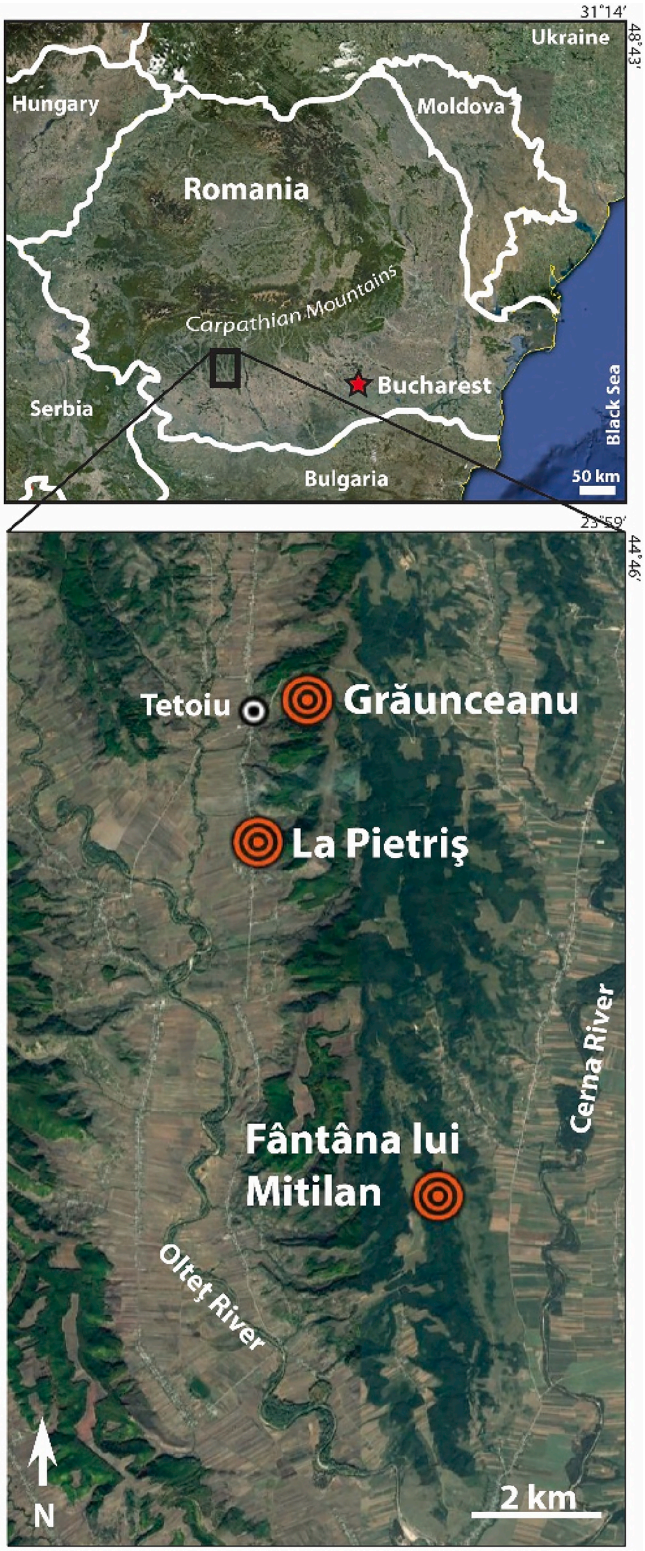

Fig. 3. Top: map of Romania showing the location of the Olteţ River Valley (ORV) project area. Bottom: overview of the ORV project area including relevant landmarks and fossil localities that have been relocated by our research team.

savannah environment (including *Equus livenzovensis*, *Archidiskodon meridionalis*, *Paracamelus alutensis*, *Struthio*, and *Palaeotragus*). The presence of the molluscan taxon, *Bogatschevia tamanensis* also suggests a hot and dry climate (Sablin and Girya, 2010).

Table 1
Olteţ River Valley sites and taxa present.

		VGr (*n* = 3132)	FM (*n* = 155)	LP (*n* = 112)	FA (*n* = 20)	Other
Proboscidea	*Mammuthus* cf. *meriodionalis*	X	X	X	X	DM, Olt, RA
Artiodactyla	*Bison (Eobison) sp.*	X				Olt
	Pliotragus ardeus	X				
	Megalovis latifrons		X			
	Gazellospira torticornis	X				
	Metacervocerus sp.	X				Olt
	Dama cf. *eurygonos*		X			
	Eucladoceros sp.		X	X	X	
	Eucladoceros dicranios	X				
	Eucladoceros ctenoides falconeri	X				
	Rucervus (Arvernoceros) radulescui	X		X		
	Croizetoceros ramosus	X				
	Alces sp.	X				
	Praemegaceros obscurus		X			Olt
	Praemegaceros cf. *mosbachensis*		X			Olt
	Mitilanotherium inexspectatum	X	X			
	Sus strozzi	X				
Perissodactyla	*Equus sp. (cf. livenzovensis)*	X				
	Equus sp.		X	X	X	RA
	Stephanorhinus sp.	X	X			
Carnivora	cf. *Acinonyx pardinensis*	X				
	Megantereon cultridens	X				
	Homotherium sp.	X				
	Puma pardoides	X				
	Lynx issiodorensis	X				
	Pachycrocuta brevirostris	X				
	Ursus etruscus	X			X	
	Meles cf. *thorali*	X				
	Nyctereutes megamastoides	X				
	Vulpes alopecoides	X				
	Canis etruscus				X	
	Canis sp.	X				
	Carnivora indet.	X	X			LS
Primates	*Paradolichopithecus arvernensis geticus*	X				
Rodentia	*Hystrix refossa*	X				
	Castor fiber cf. *plicidens*		X			
	Trogonotherium sp.	X	X			
Pholidota	*Smutsia* spp. *nov.*	X				
Non-mammals	*Pachystruthio* cf. *pannonicus*	X				
	Aves indet.	X				
	Geoemyidadae indet		X			
	Testudines indet					RA

VGr = Grăunceanu; LP = La Pietriş; FM = Fântâna lui Mitilan; FA = Fântâna Alortetei; LS = La Seci; RA = Râpa; DM = Dealul Mammut; Olt = Olteţ River Valley. Olt designation indicates specimens with uncertain provenience.

1.3.4. Vatera, Greece (~2 Ma, Sondaar and van der Geer, 2002)

Faunal remains from Vatera, located on Lesvos Island, Greece, were preserved in sandy clay layers in fluvial deposits (Lyras and van der Geer, 2007). Fauna from this site have been attributed to the early

Table 2
Summary of habitat reconstructions for Early Pleistocene Western Eurasian sites. See references below table. Dates in millions of years (Ma).

Site	Latitude/ Longitude[b]	Date range (Ma)	Habitat summary
Saint-Vallier, France	45°10′N/ 4°53′E	2.4–1.9	Mosaic of open & wooded[1,2,3]
Orce- Galeria 2, Spain	37°44′N/ 2°33′W	2.4–1.9	Mediterranean woodland[4]
Senèze, France	45°14′N/ 3°29′E	2.21–2.09	Mosaic of open & wooded[2,3,5]
Liventsovka Quarry, Russia	47°13′N/ 39°34′E	2.1–1.97	Open & arid[6]
Vatera, Greece	39°01′N/ 26°11′E	~2.0	Open & arid[7]
Orce- Barranco Conejo, Spain	37°44′N/ 2°28′W	1.9–1.6	Mosaic of open & wooded[4]
Dmanisi, Georgia[a]	41°19′N/ 44°12′E	1.85–1.78	Open on lower slopes, grading into forest on upper[8,9,10,11,12,13]
Pirro Nord, Italy[a]	41°48′N/ 15°23′E	1.7–1.3	Open & arid[14,15]
Orce- Venta Micena, Spain	37°43′N/ 2°23′W	1.6–1.4	Mosaic of open & closed[4,16]
‘Ubeidiya, Israel[a]	32°41′N/ 35°33′E	1.6–1.4	Mediterranean (mosaic of open, scrublands, and forest)[2,17,18]
Kocabaş, Turkey[a]	37°51′N/ 29°20′E	1.6 (1.4)- 1.2	Mediterranean (mosaic of open & wooded)[19]
Orce- Barranco Leon, Spain[a]	37°43′N/ 2°27′W	1.4–1.2	Mediterranean woodland[4,20]
Orce- Fuente Nueva 3, Spain[a]	37°43′N/ 2°24′W	1.4–1.2	Mediterranean woodland[4,20]
Orce- Huescar, Spain[a]	37°47′N/ 2°30′W	1.2–0.8	Wooded[4,21]

References cited include 1: Valli (2004); 2: Curran (2009); 3: Curran (2015); 4: Agustí et al. (2010); 5: Delson et al. (2006); 6: Sablin and Girya (2010); 7: de Vos et al. (2002); 8: Gabunia et al. (2000); 9: Gabunia et al. (2001); 10: Palmqvist (2002); 11: Lordkipanidze et al. (2007); 12: Messager et al. (2011); 13: Blain et al. (2014); 14: Arzarello et al. (2007); 15: Bedetti and Pavia (2013); 16: Palmqvist et al. (2003); 17: Dennell (2003); 18: Belmaker (2006); 19: Rausch et al. (2019); 20: Blain et al. (2016); 21: Alberdi et al. (2001).

[a] Sites where hominin remains or lithics have been reported.

[b] Coordinates may be estimated based on published descriptions of site localities.

portion of the Middle Villafranchian (MN17) (Sondaar and van der Geer, 2002; de Vos et al., 2002). Most of the larger fauna, and especially the bovids, indicate that Vatera was an open and dry landscape (de Vos et al., 2002), which is similar to other Greek sites (e.g., Vólax, Dafneró, and Sésklo) from the Middle Villafranchian (de Vos et al., 2002; Koufos, 2014).

1.3.5. Dmanisi, Georgia (1.85–1.78 Ma, Ferring et al., 2011)

Located in the Mashavera River Valley of the Georgia Caucasus region, Dmanisi is well known for having the earliest well-dated hominins with associated stone tools in Eurasia and a very well-preserved and rich faunal assemblage (Ferring et al., 2011; Lordkipanidze et al., 2007). Several types of habitats are represented by the fauna at Dmanisi and indicate that there was likely a vertical zonality to the vegetative structure (Gabunia et al., 2000). Forest, forest-steppe, and steppe habitats are represented by various types of animal remains, predominantly cervids. The cervid assemblage suggests a wet river valley with gallery forests (Lordkipanidze et al., 2007, supplementary information). The taxa represent a Eurasian faunal assemblage, with *Homo erectus* being the only certain African migrant (Tappen et al., 2007). Palynological evidence shows a wide variety in species representation from forest to more brush vegetation (Gabunia et al., 2000). Pollen remains also indicate an increase in aridity in this region at the time of deposition (Gabunia et al., 2001), which is further supported by phytolith evidence (Messager et al., 2011). The herpetological fauna indicate open and dry environments, though likely with seasonal rather than continuous water stress (Blain et al., 2014). Community analyses of faunal locomotor and trophic adaptations suggest Dmanisi was relatively open, dominated by grasslands and shrublands, similar to modern African savannas, though forests likely existed on higher slopes (Palmqvist, 2002).

1.3.6. Pirro Nord, Italy (1.7–1.3 Ma, Pavia et al., 2012)

The rich fossil vertebrate assemblage from the site of Pirro Nord in southern Italy is dated on the basis of biochronology to the very end of the Late Villafranchian, approximately 1.7–1.3 Ma (Pavia et al., 2012; Bertok et al., 2013) and the large mammalian assemblage from this site has been designated as the reference faunal unit for the latest Villafranchian. Analysis of the faunal assemblage indicates that Pirro Nord was likely an open and arid landscape, with locally available humid (Arzarello et al., 2007) and aquatic areas (Bedetti and Pavia, 2013). This is evidenced by the presence of mixed feeding and grazing taxa in the Pirro Nord assemblage (Manzi et al., 2011). A lithic assemblage showing affinities with Mode 1 tools from sites in Europe and Africa has also been recovered from this site, potentially representing some of the earliest evidence of hominin activity in western Europe (Arzarello et al., 2015).

1.3.7. ‘Ubeidiya, Israel (1.6–1.4 Ma, Shea, 1999)

The site of ‘Ubeidiya is located in the Jordan River Valley of Israel; fauna from this site are a mix of both African and Eurasian species. Though most strata are dominated by cervids (*Pseudodama* sp., *Capreolus* sp., and *Praemegaceros obscurus*), African taxa are represented by 11 species, including *Homo* sp. (Belmaker et al., 2002), indicating an open and arid landscape (Dennell, 2003). However, in an examination of the full faunal assemblage, Belmaker (2006) concludes that ‘Ubeidiya was a closed Mediterranean biome (i.e., forests to scrublands characterized by warm, dry summers and rainy winters). Ecomorphological analyses of cervid post-cranial elements suggest that the paleoenvironment of ‘Ubeidiya was of an intermediate-open nature with a mixture of more open and more closed regions and nearby water resources (Curran, 2009).

1.3.8. Kocabaş, Turkey (1.6–1.2 Ma, Rausch et al., 2019)

Mammalian remains (including *Homo erectus*) were preserved in lacustrine and fluvial deposits and suggest a heterogeneous environment with a mix of ample open habitats and some wooded patches. Preserved macro and microbotanicals point to a flora with a warm, Mediterranean nature (Rausch et al., 2019).

1.3.9. Orce Region Sites, Spain (2.4–0.8 Ma, Agustí et al., 2010)

Sites from the Orce region in the Gaudix-Baza Basin of southeast Spain, span a time range from the Early to Middle Pleistocene and show a trend of increasing aridity over time. Microfaunal assemblages from the Galera 2 site (2.4–1.9 Ma) are indicative of mild, humid Mediterranean woodlands (Agustí et al., 2010). Environmental conditions then became more arid at the Barranco Conejo site (1.9–1.6 Ma) with scrublands and dry meadows appearing (Agustí et al., 2010). The site of Venta Micena (1.6–1.4 Ma, Agustí et al., 2010), which was likely accumulated primarily by the large hyena, *Pachycrocuta brevirostris* (Arribas and Palmqvist, 1999), has been well-studied and was likely a mosaic of open and more closed habitats (Agustí et al., 2010), though community analyses suggest that the site accumulated in a savanna-like (tall grass, low tree cover) environment (Palmqvist et al., 2003).

Records of hominin presence have been recovered from the nearly contemporaneous sites of Barranco León (hominin fossil remains and lithics) and Fuente Nueva 3 (lithics), dating to 1.4–1.2 Ma (Toro-Moyano et al., 2013). These sites both demonstrate a shift to warmer and more humid conditions that supported a Mediterranean woodland (Agustí et al., 2010; Agustí et al., 2015; MacDonald et al., 2012; Blain et al., 2016). Wooded, though more arid (perhaps even approaching open and arid) conditions persisted during 1.2–0.8 Ma at the Huescar 1 site (Alberdi et al., 2001; Hernández Fernández et al., 2006; Agustí et al., 2010).

1.4. Research goals for this study

Here we provide an updated paleoenvironmental interpretation for localities from the Olteţ River Valley. To this end, we assess the habitat preferences of the ORV taxa, and analyze the dental microwear, mesowear, and stable carbon and oxygen isotopic composition of tooth enamel of the ORV fossil ungulates. Lastly, we evaluate the palynology of coprolites presumed to be from hyaenids present at the ORV sites. We compare the results of this multiproxy analysis to previous paleoenvironmental reconstructions for the ORV and for other penecontemporaneous sites across western Eurasia during the Early Pleistocene.

2. Materials and methods

Specimens excavated from ORV localities between the 1960s and 1980s are housed in the "Emil Racoviţa" Institute of Speleology (ERIS; Bucharest) and the Museum of Oltenia (Craiova) in Romania. Of the ~6000 identifiable fossil remains collected from the ORV localities, more than half (3634 specimens inventoried, not including unidentifiable bone fragments) are in the ERIS collections and are the samples included in this study. The majority of the remains were recovered from Grăunceanu (*n* = 3132), though smaller assemblages from La Pietriş (*n* = 112) and Fântâna lui Mitilan (*n* = 155) are also included (Table 1). Localities with fewer specimens are not included here. For several of the proxies used in this study, sample sizes from these assemblages are low and thus caution is advised against over interpreting results. Nevertheless, we present these results here to provide preliminary characterizations of paleoecological conditions at these localities.

In general, the ORV materials are in very good condition and taphonomic alterations within each assemblage are extremely similar in character. There is little evidence of carnivore ravaging, weathering, or water transportation. Multiple specimens were excavated in articulation with other bones from the same individual (e.g., entire hock joints). A complete taphonomic analysis of the assemblage is ongoing.

2.1. Taxon-based environmental reconstruction

Taxon-based methods, such as taxonomic uniformitarianism (Andrews, 1995; Faith and Lyman, 2019) or taxonomic analogy (Reed, 1998) draw ecological correlations between fossil taxa and their extant counterparts (be they the same or very closely related genera and species) and utilize all available paleoecological data on extinct taxa to reconstruct a species' ecological adaptations. Using this approach, one assumes niche stasis across space and time, an assumption that has been shown to be invalid in some taxa (Solounias and Dawson-Saunders, 1988; Curran, 2015). However, this method is used widely and provides a good starting point for paleoenvironmental reconstructions. Further, since all taxa from an assemblage that have been identified are included, the method is relatively robust to the particular tolerances of a single taxon, although resulting reconstructions are often of lower resolution than other methods (Faith and Lyman, 2019). Nevertheless, we include this method here to pull in information regarding all taxa from the ORV sites, since several of the other proxies used here are focused on artiodactyls and especially cervids. We use the newly updated taxonomic identifications for the ORV assemblage (Terhune et al., 2020) and associate them with published ecological data available for each taxon. We then estimate paleoenvironmental parameters for each faunal assemblage from the ORV localities.

2.2. Mesowear

The surface of an animal's dentition is worn down over time due to mastication of food items, materials adhering to the food (abrasion), and dental attrition (Fortelius and Solounias, 2000). The overall macromorphology of dental wear during an animal's lifetime is thus associated with its adaptation to particular diets and has been demonstrated to be a proxy for the type of vegetation matter consumed during life (Rivals et al., 2010). Browsers tend to maintain discrete wear facets throughout most enamel loss caused by tooth-tooth attrition and have high occlusal relief with sharp cusps. Grazers, consuming tough grasses that frequently have gritty adhering particles, quickly abrade and wear down their enamel ridges and have low occlusal relief and blunt cusps, though typically have very high crowned, or hypsodont, dentition (Fortelius, 1985; Janis, 1986).

A total of 81 fossil specimens from the ORV were analyzed for mesowear by SCC. These specimens included all second molars for which mesowear could be assessed: a large sample from Grăunceanu (*n* = 69) and smaller samples from the sites of Fântâna Alortiţei (n = 3), Fântâna lui Mitilan (n = 6), La Pietriş (n = 3). These samples represent a variety of cervid and bovid taxa, as well as a small sample of *Equus*.

Dental mesowear was evaluated for the sharpest buccal cusp of all second molars of all ungulates (e.g., all artiodactyl and perissodactyl dental remains) by scoring occlusal relief (1 = low, 2 = high) and cusp shape (1 = sharp, 2 = round, 3 = blunt), using the methods and data in Fortelius and Solounias (2000) and Rivals et al. (2007). Scores were combined to create a mesowear score (Table 3; Rivals and Semprebon, 2006). Scores for all ungulate specimens (grouped by taxon) from the ORV assemblages were compared to the mean scores of extant taxa (grouped by dietary category) as presented by Fortelius and Solounias (2000).

2.3. Microwear

All available first and second molars (whether upper/lower, left/right) were vetted initially for suitability for microwear analysis. Candidate teeth lacking clear taphonomic damage were cleaned with alcohol-soaked cotton swabs to remove sediment and dust on occlusal surfaces prior to molding. Molds of the entire occlusal surface were made using President's Jet regular body polyvinylsiloxane dental impression material (Coltène-Whaledent Corp.), then replicas were poured using Epotek 301 epoxy resin and hardener (Epoxy Technologies Corp). Taphonomic damage is common for fossil ruminant molars because their thin enamel bands are especially susceptible to chipping and fracture. In this case, we originally generated replicas for 57 individual teeth, but clear unobscured antemortem dental microwear was evident only for 10 specimens, all of which were cervids (*n* = 1 *Dama* cf. *eurygonos* from Fântâna lui Mitilan; *n* = 9 *Rucervus radulescui* from Grăunceanu).

Microwear texture data were collected following previously established procedures for ruminant molars (Ungar et al., 2007a; Merceron et al., 2010; Scott, 2012; Ungar et al., 2012). First, point clouds were generated for the Facet 1 surface on the anterobuccal enamel band of the paracone for upper first or second molars or the posterobuccal enamel band on the protoconid for lower molars. The center of the facet or the field closest to it that preserved antemortem microwear was sampled. The Sensofar PLμ Standard confocal profiler fitted with a 100× objective lens was used for data collection. Surface elevations were sampled at a lateral (x, y) interval of 0.18 μm, a vertical step of 0.2 μm and a published resolution of 0.005 μm. The work envelope was 102 × 138 μm in

Table 3
Mesowear scoring protocol used in this study (following Rivals and Semprebon, 2006).

Relief	Shape	Score
2	1	0
2	2	1
1	2	2
1	3	3

For Relief, 1 = low, 2 = high; for Shape, 1 = sharp, 2 = round, 3 = blunt. Score is assigned on the basis of relief and shape.

the horizontal plane, for a total of nearly 435,000 sampled points. Individual point clouds were converted to surface files in Solarmap Universal software (Solarius Development Corp.) and leveled prior to analysis. Identifiable defects, such as adherent dust particles, were excluded from analysis using the "erase defects" operators in Solarmap. Resultant files for each surface were then analyzed using ToothFrax software (SurFract Corp) following standard microwear texture analysis protocol (Scott et al., 2006). Both area-scale fractal complexity (*Asfc*), and length-scale anisotropy of relief (*epLsar*) were recorded for each specimen. Complexity was calculated for scales ranging from 7200 μm^2 to 0.02 μm^2, and anisotropy was calculated at the 1.8 μm scale following previous studies of ruminant microwear textures (Scott, 2012). These two attributes provide a robust characterization of change in surface roughness across scales of observation and directionality of texture. Complexity and anisotropy are standards suggested to reflect the hardness and toughness, respectively, of foods eaten (Ungar et al., 2007b). Surfaces covered in pits of varying shapes and sizes tend to be highly complex, whereas those dominated by aligned striations are more anisotropic. These have proven especially useful for distinguishing extant ruminants on the basis of diet, with harder, more three-dimensional browse items leaving relatively complex surfaces, and tougher grasses consistent with more anisotropic surfaces (Scott, 2012; Merceron et al., 2014). Indeed, microwear texture patterns of fossil ruminants have been interpreted and shown to differ in ways typical of extant grazers and browsers (Ungar et al., 2007a, 2012, 2016; Merceron et al., 2014, 2016).

Data for the ORV cervids were compared with data published by Scott (2012) for a baseline of extant ruminants with known differences in diet. Scott's original baseline includes 575 specimens from 25 modern bovid species spanning the diet categories defined by Gagnon and Chew (2000). Individual extant species are divided into: 1) obligate grazers (>90% monocots, with no seasonal or geographic variability); 2) variable grazers (60–90% monocots, but with seasonal and geographic variability); 3) browser-grazer intermediates (30–70% monocots and dicots, but always <20% fruits); 4) generalists (>20% of all three food types – monocot, dicot leaves, fruit); 5) browsers (>70% dicots); and 6) frugivores (>70% fruits, with little or no monocots). Data for both *Asfc* and *epLsar* were rank-transformed to mitigate violation of assumptions inherent in parametric statistical analyses (Conover and Iman, 1981). A multivariate analysis of variance model with *Asfc* and *epLsar* as the variables was used to determine whether groups (the ORV cervids and individuals in each diet category) varied in microwear surface texture. Individual ANOVAs and pairwise Tukey's honestly significant difference (HSD) test were used to determine the sources of significance as appropriate. Tukey's tests were limited to comparisons of the ORV cervid sample with each of the extant groups given our interest in assessing diets of the fossil taxa.

2.4. Stable carbon and oxygen isotopic composition of tooth enamel

The carbon and oxygen isotopic compositions of mammalian tooth enamel are proxies for diet and climatic conditions during the time of enamel deposition (Koch, 1998; Lee-Thorp and Sponheimer, 2007). Fifty-one fossil artiodactyl dental specimens were analyzed to evaluate signatures of diet (carbon isotopes or $\delta^{13}C$) and local hydroclimate (temperature and/or precipitation; oxygen isotopes or $\delta^{18}O$). Specimens were primarily from Grăunceanu ($n = 44$), though several specimens were from other ORV sites (La Pietriş = 3, Fântâna lui Mitilan = 1, Fântâna Alortitei = 3). Specimens are mostly attributed to the large cervid species *Rucervus radulescui* (Croitor, 2018a), with a few specimens of *Eucladoceros* and *Pliotragus ardeus*, as well as a single indeterminate cervine. For each specimen, a hand-held Dremel fitted with a diamond burr and running at the lowest speed was used to collect enamel powders from each sampled tooth; samples were preferentially taken from the lingual surface of the distal loph of the second molar (both upper and lower dentition). Samples were taken along the entirety of the height of the crown and therefore represent a time-averaged signal (e.g., Merceron et al., 2020).

Following Koch et al. (1997), all sample enamel powders were reacted with 1 M acetic acid with a 1 M calcium acetate buffer (pH: 5) for 24 h to remove any exogenous carbonate. Samples were rinsed three times with distilled, deionized water and then dried in a 60 °C oven for 48+ hours to remove any remaining water. A preliminary sample of ten specimens were processed at the University of Minnesota Stable Isotope Lab. The cleaned enamel samples and approximately 2 cm of silver thread (to react with any SO_2 generated during acidification) were reacted with 100% phosphoric acid in a Kiel automatic carbonate extraction device at 71 °C. A Finnigan MAT 252 Isotope Ratio Mass Spectrometer was used to measure the carbon and oxygen isotopic composition of the resulting CO_2. Samples and standards (NBS-19, $\delta^{13}C = +1.95‰$, $\delta^{18}O = -2.20‰$, both V-PDB) were run identically and analytical precision for both oxygen and carbon is <0.1‰ based on repeated analyses of NBS-19 over the time during which the samples were analyzed.

The remaining samples ($n = 41$), which were collected separately but prepped identically to those above, were analyzed at the University of Arkansas Stable Isotope Lab (UASIL). The cleaned samples were weighed into exetainers that were flushed with helium (~100 ml/min for 10 min). The flushed vials were acidified with phosphoric acid (105%) and allowed to react for at least 18 h at 25 °C in a GasBench II sample preparation device coupled to a Thermo Delta V Advantage IRMS. NBS-19 and two in-house standards (UASIL22 [$\delta^{13}C = -35.6‰$ V-PDB, $\delta^{18}O = +13.31$ V-SMOW] and UASIL23 [$\delta^{13}C = -0.6‰$ V-PDB, $\delta^{18}O = +15.75$ V-SMOW]) were analyzed within the same runs as the samples. Data distributions from the University of Minnesota and University of Arkansas isotope labs are statistically indistinguishable.

Carbon isotope values are reported on the VPDB scale, while oxygen isotope values were expressed and are reported on the VSMOW scale, following eq. 11 of Coplen (1988: 295), and oxygen isotope values from each lab are corrected for the differences in acid digestion temperature. All $\delta^{13}C$ values of fossils are expressed as modern equivalents (shifted by −1.7‰) based on the estimated mean $\delta^{13}C$ value of Neogene and Quaternary (1.99–1.00 Ma;) atmospheric CO_2 of −6.3 ± 0.2‰ and the modern $\delta^{13}C$ value of −8.0‰ (Passey et al., 2009; Tipple et al., 2010).

2.5. Coprolite pollen analysis

Eleven round coprolites, tentatively attributed to Hyaenidae based on their morphology, from Grăunceanu ($n = 3$) and Fântâna lui Mitilan ($n = 8$) were analyzed for their pollen content. Coprolite surfaces were cleaned to avoid contamination from modern pollen. Samples were prepared using standard methods for pollen extraction from sediments (Faegri and Iversen, 1989), including treatment with HCl (35%), HF (40%), and heavy liquid separation ($ZnCl_2$). After each step, the samples were centrifuged and the supernatant removed, except following the heavy liquid separation, where the resulting organic ring was retained. Residues were mounted in glycerin on glass slides for identification. Pollen and spore taxa were identified using keys and illustrations in Reille (1995, 1998, 1999). Tree taxa were identified at the genus level because the morphology and structure of pollen is generally specific to each genus. In the case of herbaceous taxa, the pollen identification was possible at genus level, or in some cases only at family level due to similarities of pollen morphology within some families.

3. Results

3.1. Taxon-based environmental reconstruction

The majority of taxa from the ORV sites occupied habitats on the open end of the spectrum (grasslands through open woodlands) with few species associated with forests (Table 4). At Grăunceanu and La Pietriş, specimens of taxa associated with more open habitats are most numerous and are primarily comprised of artiodactyls such as *Gazellospira torticornis* (Croitor and Brugal, 2007), *Rucervus radulescui* (Curran, 2009, 2015, 2018; Croitor, 2018a), and *Mitlanotherium inexspectatum*, which likely preferred open and/or arid conditions (van der Made and Morales, 2011). While its specific taxon is uncertain, the equid (*Equus* sp.) was likely open adapted and was a grazer. Open-adapted carnivores include the sprinter cf. *Acinonyx pardinensis* (Hemmer et al., 2011), *Vulpes alopecoides*, which preferred open steppe habitats (Hemmer et al., 2011), and *Canis* sp., which likely was cursorial in open landscapes (Kahlke et al., 2011). *Homotherium* sp. may have been a social and semi-cursorial hunter in more open habitats (Anton et al., 2005), though others have suggested that they preferred more forested environments (Marean, 1989; Palmqvist et al., 2007). *Pachystruthio pannonicus*, like most ostrich species, likely inhabited open shrublands (Boev and Spassov, 2009).

Taxa occupying slightly more closed habitats, such as open woodlands, comprise the second most frequent ecological category from Grăunceanu and La Pietriş. *Eucladoceros dicranios* inhabited open ‘savanna-like’ to sparsely wooded landscapes (Croitor and Popescu, 2011). *Paradolichopithecus arvernensis geticus* was a large terrestrial primate and likely preferred more open savannah woodland (Frost et al., 2005). *Mammuthus* cf. *meriodionalis* inhabited ‘parkland’ environments comprising grasses, shrubs, and trees (Ferretti and Croitor, 2001) from which it browsed (Haiduc et al., 2018). The porcupine, *Hystrix refossa*, preferred a mosaic of open and woodland habitats (Lazaridis et al., 2019), as did the raccoon dog, *Nyctereutes megamastoides* (Kahlke et al., 2011). The majority of carnivores from Grăunceanu, such as *Megantereon cultridens*, *Puma pardoides*, *Lynx issiodorensis*, and *Ursus etruscus* were likely ambush hunters that required varying degrees of cover and some open habitats (Marean, 1989; Anton et al., 2005; Palmqvist et al., 2007; Kahlke et al., 2011).

Table 4
Habitat assignments for Olteţ River Valley taxa (see text for references).

Habitat type	Taxon	ORV locality
Open:	*Alces* sp.	FM
	Rucervus (Arvernoceros) radulescui	VGr, LP
	Gazellospira torticornis	VGr
	Mitilanotherium inexspectatum	VGr, FM
	Equus sp. (cf. *livenzovensis)*	VGr
	Equus sp.	FM, LP, FA, RA
	cf. *Acinonyx pardinensis*	VGr
	Vulpes alopecoides	VGr
	Canis etruscus	FA
	Canis sp.	VGr
	Pachystruthio pannonicus	VGr
Open-Woodland:	*Mammuthus* cf. *meriodionalis*	VGr, FM, LP, FA, DM, Olt, RA
	Dama cf. *eurygonos*	FM
	Eucladoceros sp.	FM, LP, FA
	Eucladoceros dicranios	VGr
	Praemegaceros cf. *mosbachensis*	FM, Olt
	Megantereon cultridens+	VGr
	Homotherium sp.	VGr
	Puma pardoides	VGr
	Lynx issiodorensis	VGr
	Pachycrocuta brevirostris	VGr?, VH
	Pliocrocuta perrieri	VGr?
	Ursus etruscus	VGr, FA
	Meles cf. *thorali*	VGr
	Nyctereutes megamastoides	VGr
	Paradolichopithecus arvernensis geticus	VGr
	Hystrix refossa	VGr
Woodland:	*Metacervocerus sp.*	VGr, Olt
	Megalovis latifrons	FM
Woodland-Forest:	*Praemegaceros obscurus*	FM, Olt
Forest:	*Sus strozzi*	VGr
	Eucladoceros ctenoides falconeri	VGr
Non-forest:	*Croizetoceros ramosus*	VGr
Riparian:	*Castor fiber* cf. *plicidens*	FM
	Trogontherium sp.	VGr, FM

VGr = Grăunceanu; LP = La Pietriş; FM = Fântâna lui Mitilan; FA = Fântâna Alorti̦ei; LS = La Seci; RA = Râpa; DM = Dealul Mammut; VH = Valea Homorâcea; Olt = Olteţ Valley (designation indicates specimens with uncertain provenience).

Very few taxa at Grăunceanu are associated with more closed-cover habitats. These include *Metacervocerus* sp. (Kaiser and Croiter, 2004; Croitor, 2006a) and *Sus strozzi*, which likely inhabited forests and forest ecotones (Faure, 2004; Iannussi et al., 2020). *Trogontherium* sp., like other beavers, likely lived in riparian habitats, though may have been slightly more terrestrial than *Castor* (Mayhew, 1978; Fostowicz-Frelik, 2008; Rekovets et al., 2009; Kahlke et al., 2011).

The fossil assemblage from the younger site of Fântâna lui Mitilan is considerably smaller, though the taxonomic composition illustrates a similar range of habitats as the older ORV sites. Again, open-adapted taxa are most frequent and are represented by similar ungulates such as *Mitilanotherium inexspectatum*, *Equus* sp., *Alces* sp. (Croitor, 2018b; Croitor and Brugal, 2007; Croitor and Popescu, 2011) and the newly appearing *Megalovis latifrons*, which has been reported to be cursorial (Spassov and Crégut-Bonnoure, 1999), though given its large body size and very short metapodia was more likely a woodland inhabitant. Taxa adapted to slightly more closed habitats include *Mammuthus* cf. *meriodionalis*, *Dama* cf. *eurygonos*, and *Praemegaceros* sp. (Croitor, 2001; Palmqvist et al., 2003; Croitor, 2005; Croitor, 2011). The only species in the Fântâna lui Mitilan assemblage that might be considered to be forest-adapted, is *Praemegaceros obscurus*, though it is known to be ecologically flexible, being found in deposits from ‘Ubeidiya, Israel to the Forest Bed Formation in England (Kaiser and Croiter, 2004; Croitor, 2005, 2006b). The two beaver species, *Trogontherium* sp. and *Castor fiber* cf. *plicidens* both occupied riparian areas, though were likely partitioned by the former being more cursorial than the latter (Mayhew, 1978; Fostowicz-Frelik, 2008; Rekovets et al., 2009; Kahlke et al., 2011).

3.2. Mesowear

All cervid and bovid remains had a mean mesowear score of ≤ 1 (Table 5), suggesting similarity to extant leaf and/or fruit browsers and mixed feeders (Fig. 4). In contrast, all equids analyzed showed a mean mesowear score of 3, as expected of grazers. Thus, with the exception of the equids, all specimens from the ORV deposits indicate that browse resources (trees, bushes, shrubs, etc.) were in high availability.

3.3. Microwear

Representative photosimulations of microwear surfaces are illustrated in Fig. 5. Raw values for the ORV cervid sample, both in its entirety and broken down by locality and species, are presented in Tables 6. Summary statistics for both the extant comparative sample (i.e. data from Scott, 2012) and fossil samples are presented in Table 7. Compared to extant taxa, *Asfc* values (i.e., complexity) for all ORV specimens are low, consistent only with known grazers; this is true regardless of locality or species (Figs. 6). Values of *epLsar* (i.e., anisotropy of relief) are more variable across the ORV sample, and are most consistent with extant variable grazer and generalist groups (Fig. 6). Notably, the single specimen from Fântâna lui Mitilan, identified as *Dama* cf. *eurygonos* (Table 6), is different in both *Asfc* and *epLsar* from the samples from Grăunceanu (all of which are attributed to *Rucervus* cf. *radulescui* or *Rucervus radulescui*), perhaps reflecting differences in species and/or paleoenvironment between these two localities. However, sample sizes for all taxa are small, cautioning against over interpretation of results.

Results of the MANOVA test evince significant variation in microwear textures between samples (Wilk's $\lambda = 0.193$, F-ratio = 104.8, df = 14, 1150, $p < 0.0001$). Individual ANOVAs (where only specimens from Grăunceanu are compared to extant groups) for *Asfc* (F = 218.7, $p < 0.0001$) and *epLsar* (F = 144.62, $p < 0.0001$) indicate differences in both complexity and anisotropy. Tukey's HSD test results (Table 8) show that

Table 5
Mesowear results by Olteţ River Valley locality and taxon. Extant data are from Fortelius and Solounias (2000). Counts (n) for extant data are number of species and number of specimens for fossils.

Diet category/taxon/locality	n	Mean
Leaf browser (extant)	14	0.33
Fruit browser (extant)	12	0.85
Mixed feeder (extant)	29	0.78
Grazer (extant)	14	1.67
Fântâna Alortiţei	3	1.00
cf. *Eucladoceros*	3	1.00
Fântâna lui Mitilan	6	0.67
cf. *Eucladoceros*	3	0.33
Dama cf. *eurygonos*	1	1.00
Bovidae indet.	1	1.00
Cervidae indet	1	1.00
La Pietriş	3	0.00
cf. *Eucladoceros*	3	0.00
Grăunceanu	69	0.64
cf. *Eucladoceros*	35	0.43
Croizetoceros ramosus	1	0.00
Metacervocerus sp.	1	0.00
Rucervus radulescui	18	0.39
Cervidae indet	5	0.80
Pliotragus ardeus	3	0.67
Bovidae indet.	1	1.00
Equus sp.	5	3.00

the fossils have significantly lower average *Asfc* values than nearly all extant samples ($p < 0.0001$) except for obligate grazers ($p = 0.994$) and variable grazers ($p = 0.078$). The fossil samples also differ significantly in *epLsar* from browsers and frugivores ($p < 0.001$), as well as obligate grazers ($p < 0.001$). Their values overlap with those of mixed feeders (variable grazers, browser-grazer intermediates, and generalists) ($p > 0.05$).

3.4. Stable carbon and oxygen isotopes

Specimens analyzed from all ORV sites have relatively low δ^{13}C values (Table 9; Figs. 7 and 8). The mean δ^{13}C value from Grăunceanu is −14.6‰, with a range from −16.81‰ to −12.2‰. When data for Grăunceanu are broken down by genus, *Eucladoceros* has the lowest mean δ^{13}C values, followed by *Rucervus* and then the bovid species *Pliotragus ardeus* (Fig. 8); however, ranges for all genera overlap considerably and sample sizes are small for *Eucladoceros* ($n = 4$) and *Pliotragus* ($n = 2$). Values from the rest of the ORV sites fall within the range observed for Grăunceanu, including the likely contemporaneous site of La Pietriş (−15.2‰, −15.3‰, and −14.4‰), the younger site of Fântâna lui Mitilan (−14.5‰), and a mean of −14.6‰ (range: −14.8‰ to −14.5‰) for Fântâna Alortiței. These results are consistent with these animals primarily consuming C_3 resources from a range of forest habitats, with the lowest δ^{13}C values possibly corresponding to closed canopy forests.

The mean δ^{18}O value for Grăunceanu is 21.8‰ with a range of 18.9‰ to 25.3‰. As with the carbon isotope values, *Pliotragus* shows the highest mean values while means for *Eucladoceros* and *Rucervus* at Grăunceanu are lower (Fig. 8). Additionally, values from La Pietriş (21.1‰, 21.91‰, and 23.4‰) fit within the observed range from Grăunceanu. However, values for Fântâna lui Mitilan (18.6‰) and Fântâna Alortiței (mean = 19.8‰, range: 18.6‰-21‰) are lower on

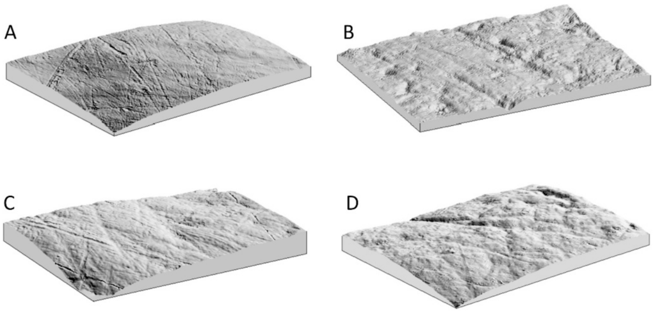

Fig. 5. Photosimulations of representative fossil specimens. A) FM.0092 (*Dama* cf. *eurygonos*), B) VGr.0891 (*Rucervus* cf. *radulescui*), C) VGr.0885 (*Rucervus* cf. *radulescui*), D) VGr.0844 (*Rucervus* cf. *radulescui*). All surfaces represent areas 102 × 138 μm and each vertical axis is exaggerated 10× for visualization.

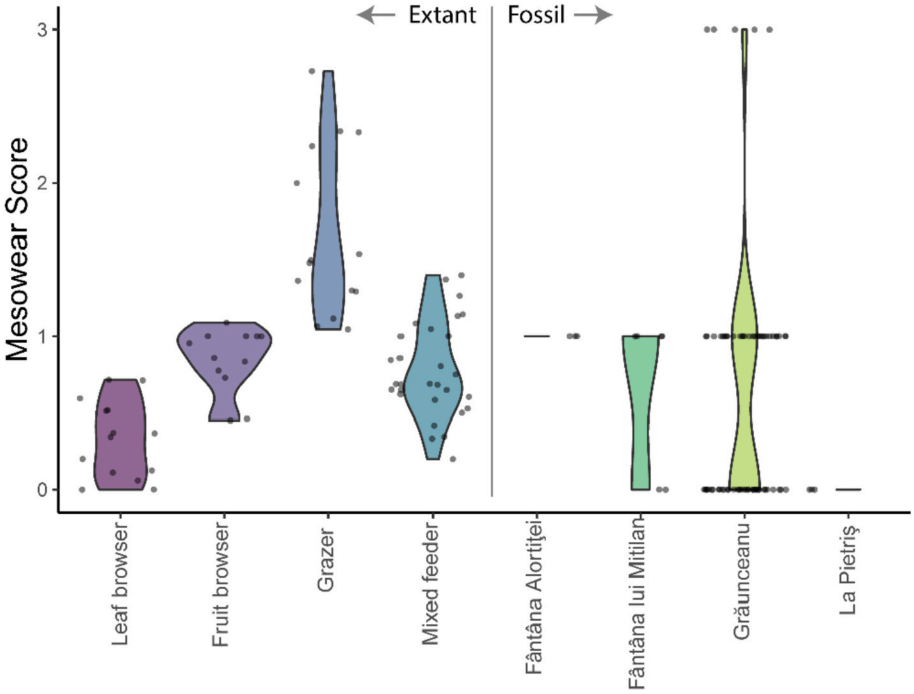

Fig. 4. Distribution of mesowear scores from extant dietary categories (from Fortelius and Solounias, 2000) and Olteţ River Valley localities. Data are shown as violin plots where width of the distribution represents the probability density of data at different values. Dots represent data points for each species (for extant data) and specimen (for fossil data) that have been jittered to maximize visibility.

Table 6
Raw microwear values for the fossil cervid sample analyzed here.

Specimen	Taxon	*Asfc*	*epLsar* (x 1000)
FM.0092	*Dama* cf. *eurygonos*	1.086	7.464
VGr.0002	*Rucervus* cf. *radulescui*	0.958	3.737
VGr.0032	*Rucervus* cf. *radulescui*	0.858	3.183
VGr.0077	*Rucervus* cf. *radulescui*	0.559	5.226
VGr.0812	*Rucervus radulescui*	0.855	3.231
VGr.0844	*Rucervus* cf. *radulescui*	0.772	5.934
VGr.0885	*Rucervus* cf. *radulescui*	0.642	6.253
VGr.0890	*Rucervus radulescui*	0.879	3.341
VGr.0891	*Rucervus* cf. *radulescui*	1.166	3.395
VGr.0895	*Rucervus radulescui*	0.978	5.374

FM = Fântâna lui Mitilan; VGr = Grăunceanu.

average.

3.5. *Coprolite pollen analysis*

Eight coprolite specimens from Fântâna lui Mitilan and three from Grăunceanu were analyzed for pollen and spores. All samples contained few pollen grains, the number of palynomorphs extracted from the coprolites ranging between 0 and 21 grains. Pollen preservation was generally good, allowing reliable pollen identifications, with few indeterminable grains (Table 10). Palynomorph taxonomic diversity is low, with 18 types in total, exceeding 10 types in four samples. There was no relationship between polliniferous character and macroscopic appearance of the coprolite (e.g., color, size, presence of surface cracks). The tree and shrub pollen types present in the coprolites are *Pinus*, *Picea*, *Alnus*, *Betula*, *Corylus*, *Ulmus*, *Tilia*, *Carpinus*, *Fagus*, and Ericaceae. Herbaceous taxa are represented by pollen of Poaceae, *Artemisia*, *Centaurea*, Asteroideae, Chenopodiaceae, Apiaceae, Rosaceae, Urticaceae, Polygonaceae, *Plantago* sp., and several fern and *Sphagnum* spores.

Due to the low number of pollen grains in these samples, it is difficult to render a comprehensive paleoecological reconstruction for the ORV sites based on palynology, though some insights are possible. For coprolites from Fântâna lui Mitilan, the presence of taxa like *Alnus*, *Betula*, and ferns suggest wetter conditions or the presence of humid zones (ponds, marshes, rivers). One testate amoeba (*Archerella flavum*) that lives on plants in wet areas (ponds, marshes) was found in a single sample from Fântâna lui Mitilan. The presence of pollen of meso-thermophilous taxa (*Ulmus*, *Tilia*, *Corylus*, and *Carpinus*), coming from slightly higher altitudes, could indicate a warmer period (probably an interglacial/interstadial). For Grăunceanu, only two microbotanicals were recovered- *Tilia* pollen, and a *Sphagnum* spore, indicating temperate conditions with a nearby water source. Most samples contain microcharcoal remains that may indicate vegetation fires.

4. Discussion

Understanding the paleoenvironments present in Early Pleistocene Europe is crucial for assessing the challenges hominins may have faced as they first dispersed into Eurasia. The Olteţ River Valley of Romania is uniquely situated to help in this regard, as this may have been one of the geographic regions through which hominins traveled into Europe. The goal of the present study was to undertake a series of paleoecological analyses of the ORV sites with the ultimate aim of providing an updated paleoenvironmental reconstruction for this region during the Early Pleistocene, and to compare these results to other Early Pleistocene sites in Europe and western Asia.

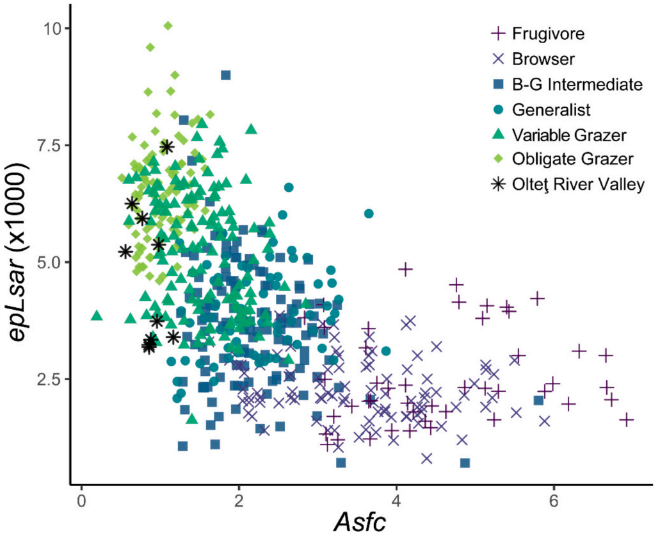

Fig. 6. Bivariate plot of area-scale scale fractal complexity (*Asfc*) and length-scale anisotropy of relief (*epLsar*) (magnified by 1000). Samples include extant bovids (Scott, 2012) in a variety of dietary categories and specimens from the Olteţ River Valley (black stars). All ORV specimens are from the site of Grăunceanu except one, which is from Fântâna lui Mitilan (represented by the black star symbol with the highest *epLsar* value).

Table 8
Results of Tukey HSD between Grăunceanu microwear and all extant comparative groups for microwear data (the single specimen from Fântâna lui Mitilan was excluded from these analyses).

Group	*Asfc*	*epLsar*
Obligate grazer	0.994	**<0.0001**
Variable grazer	0.078	0.439
Generalist	**<0.0001**	0.945
Browser-grazer Intermediate	**<0.0001**	0.516
Browser	**<0.0001**	**<0.0001**
Frugivore	**<0.0001**	**0.0002**

Table 7
Summary statistics of extant and fossil microwear data. Extant data are from Scott (2012).

Group	n	*Asfc*			*epLsar* (x 1000)		
		Median	Mean	SD	Median	Mean	SD
Browse-Graze Intermediate	131	2.063	2.182	0.663	3.700	3.676	1.359
Frugivore	46	4.399	4.575	1.153	2.300	2.554	1.032
Obligate Grazer	95	0.985	1.015	0.263	6.450	6.501	1.098
Variable Grazer	136	1.502	1.522	0.488	5.279	5.185	1.311
Browser	95	3.612	3.510	0.994	2.155	2.285	0.664
Generalist	71	2.255	2.225	0.651	3.819	3.986	1.030
Entire ORV sample	10	0.869	0.875	0.186	4.482	4.714	1.536
Fântâna lui Mitilan (*Dama* cf. *eurygonos*)	1	–	1.086	–	–	7.464	–
Grăunceanu (*Rucervus radulescui*)	9	0.858	0.852	0.181	3.737	4.408	1.267

Table 9
Carbon and oxygen isotope values from the Olteţ River Valley sites.

Specimen #	Site	Taxon	$\delta^{13}C$ (‰ VPDB)	$\delta^{18}O$ (‰ VSMOW)
FA.0009	Fântâna Alorti̦tei	*Rucervus* cf. *radulescui*	−14.47	21.00
FA.0010	Fântâna Alorti̦tei	*Rucervus radulescui*	−14.77	19.92
FA.0012	Fântâna Alorti̦tei	*Rucervus* cf. *radulescui*	−14.49	18.61
FM.0091	Fântâna lui Mitilan	cf. *Eucladoceros*	−14.56	20.26
LP.0065	La Pietriş	*Rucervus* cf. *radulescui*	−14.38	23.4
LP.0066	La Pietriş	*Rucervus* cf. *radulescui*	−15.13	21.91
LP.0067	La Pietriş	*Rucervus radulescui*	−15.16	21.08
VGr.0001	Grăunceanu	*Rucervus radulescui*	−14.33	20.64
VGr.0002	Grăunceanu	*Rucervus* cf. *radulescui*	−14.78	22.98
VGr.0003	Grăunceanu	*Rucervus radulescui*	−13.70	20.62
VGr.0004	Grăunceanu	*Rucervus* cf. *radulescui*	−14.92	19.41
VGr.0008	Grăunceanu	*Rucervus radulescui*	−14.96	20.17
VGr.0011	Grăunceanu	*Rucervus radulescui*	−14.44	20.48
VGr.0018	Grăunceanu	*Rucervus radulescui*	−15.13	23.6
VGr.0019	Grăunceanu	*Rucervus radulescui*	−16.05	24.8
VGr.0032	Grăunceanu	*Rucervus* cf. *radulescui*	−14.54	20.74
VGr.0035	Grăunceanu	*Rucervus* cf. *radulescui*	−14.42	22.84
VGr.0036	Grăunceanu	*Rucervus radulescui*	−15.49	22.32
VGr.0061	Grăunceanu	*Rucervus radulescui*	−14.24	23.12
VGr.0063	Grăunceanu	*Rucervus* cf. *radulescui*	−13.82	24.49
VGr.0077	Grăunceanu	*Rucervus* cf. *radulescui*	−12.22	25.4
VGr.0078	Grăunceanu	*Rucervus radulescui*	−16.81	22.8
VGr.0079	Grăunceanu	*Rucervus radulescui*	−14.32	24.4
VGr.0080	Grăunceanu	*Rucervus* cf. *radulescui*	−13.98	25
VGr.0082	Grăunceanu	*Rucervus radulescui*	−15.18	25.1
VGr.0083	Grăunceanu	*Rucervus radulescui*	−13.97	22.4
VGr.0085	Grăunceanu	*Rucervus* cf. *radulescui*	−14.14	20.8
VGr.0086	Grăunceanu	*Rucervus radulescui*	−14.19	20.08
VGr.0087	Grăunceanu	*Rucervus radulescui*	−14.42	19.81
VGr.0350	Grăunceanu	*Rucervus radulescui*	−14.41	20.52
VGr.0831	Grăunceanu	*Rucervus* cf. *radulescui*	−14.43	23.69
VGr.0833	Grăunceanu	*Rucervus radulescui*	−14.76	20.02
VGr.0834	Grăunceanu	*Rucervus radulescui*	−14.69	18.90
VGr.0835	Grăunceanu	*Rucervus radulescui*	−15.12	19.03
VGr.0836	Grăunceanu	*Eucladoceros sp.* (?)	−15.19	19.85
VGr.0838	Grăunceanu	Cervinae gen. et sp. (juv.)	−14.47	20.31
VGr.0839	Grăunceanu	*Rucervus radulescui*	−14.78	20.11
VGr.0841	Grăunceanu	*Eucladoceros sp.* (?)	−14.29	19.70
VGr.0844	Grăunceanu	*Rucervus* cf. *radulescui*	−14.40	21.62
VGr.0847	Grăunceanu	*Rucervus radulescui*	−14.06	21.83
VGr.0880	Grăunceanu	*Rucervus radulescui*	−14.85	20.53
VGr.0883	Grăunceanu	*Rucervus radulescui*	−13.94	21.61
VGr.0884	Grăunceanu	*Rucervus radulescui*	−14.97	19.88
VGr.0885	Grăunceanu	*Rucervus* cf. *radulescui*	−14.11	20.51
VGr.0886	Grăunceanu	*Rucervus* cf. *radulescui*	−15.13	20.96
VGr.0889	Grăunceanu	*Eucladoceros sp.*	−14.95	24.66
VGr.0891	Grăunceanu	*Rucervus* cf. *radulescui*	−14.45	21.80
VGr.0905	Grăunceanu	*Pliotragus ardeus*	−13.39	23.69
VGr.0918	Grăunceanu	cf. *Eucladoceros*	−14.83	21.23
VGr.0920	Grăunceanu	*Rucervus radulescui*	−14.86	21.69
VGr.0922	Grăunceanu	*Pliotragus ardeus*	−14.87	25.53

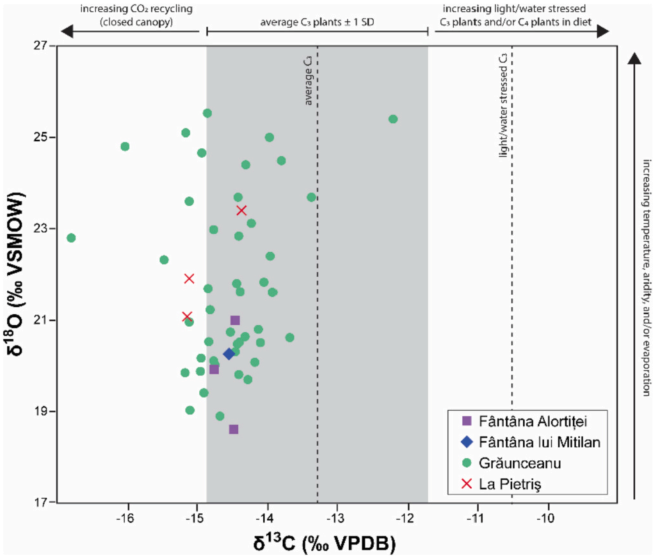

Fig. 7. Bivariate plot of the carbon (x-axis) and oxygen (y-axis) isotope data for the Olteţ River Valley localities. Refer to Table 9 for a breakdown of values by taxon.

4.1. Results indicate open conditions and the presence of water in the ORV

The evolution of vegetation of the Early Pleistocene in Romania is not well known, and from the very few sequences analyzed from this period and assigned to the Tiglian period (Diaconeasa and Tovisi, 1971; Petrescu, 1978; Diaconeasa and Clichici, 1984), a precise succession cannot be established due to the lack of the radiometric dating of the sediments. This is the first palynological study in Romania that can assign the presence of several mesothermophilous tree taxa (e.g. *Ulmus*, *Tilia*, *Corylus*, *Carpinus*, and *Fagus*) in the vegetation from a precise period of the Early Pleistocene. Though very few pollen grains or other microbotanicals were recovered from the ORV coprolites, they do reinforce the hypothesis that aquatic resources were available in the

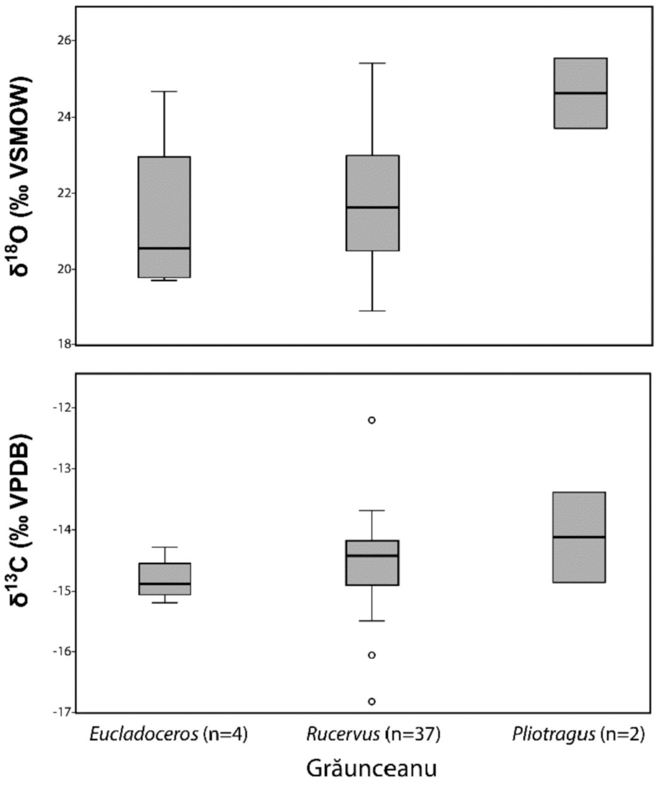

Fig. 8. Box plot showing the distribution of oxygen (top) and carbon (bottom) isotope values for the Grăunceanu sample only. Horizontal bars indicate the median, boxes represent the interquartile range, whiskers extend to the highest and lowest values that are no greater than 1.5× the interquartile range, and circles represent outliers.

vicinity of the sites as taxa such as *Alnus*, *Betula*, *Sphagnum*, and ferns all require the presence of water.

Results from the taxon-based paleoenvironmental reconstruction of the ORV sites (and especially Grăunceanu) clearly point to habitats that were open in nature, with some closed and dense areas nearby, perhaps existing in an altitudinal gradient similar to that reconstructed for Dmanisi (Gabunia et al., 2000). The majority of ungulates and several carnivore species from Grăunceanu, La Pietriş, and Fântâna Alortiţei preferentially occupied open habitats (see Table 4). Most carnivores are associated with open woodland habitats due to their preference for slightly more cover to practice ambush hunting. Only three relatively rare taxa from Grăunceanu likely preferred denser woodlands or forests. As evidenced by the presence of beavers in the assemblage, riparian areas were also available, and most fauna were likely dependent on the paleo-Olteţ River for water. The younger site of Fântâna lui Mitilan is slightly different in its taxonomic composition. Two species, *Metacervocerus* sp., which is represented by a few shed antlers and teeth, and the large bovid, *Megalovis latifrons*, likely inhabited denser woodlands (Croitor and Robinson, 2020), though the majority of fauna from Fântâna lui Mitilan are mainly open-adapted. Thus, the community of animals found in the ORV sites is demonstrative of more open habitat conditions with water access.

The numerous specimens from Grăunceanu with higher than average $\delta^{18}O$ values of tooth enamel (Figs. 7 and 8) are consistent with foraging or drinking water in open habitats, in which leaf water and surface waters would be subject to greater evaporative enrichment in ^{18}O than in more closed habitats. The isotopic range could also be expanded if some animals recovered from Grăunceanu seasonally migrated to higher elevation areas in the Carpathians, in which local precipitation would be isotopically lower than for lowland sites (Rozanski et al., 1993) and would likely not be subject to much evaporative enrichment in ^{18}O. We know of few sites of comparable age in southeastern Europe that have isotopic data from fossil mammal teeth. Kovács et al. (2015) published data for eight specimens of the rhinocerotid *Stephanorhinus jeanvireti* from Nová Vieska, Slovakia in the Pannonian Basin to the northwest of the ORV. This site is assigned to MN 17 (2.0–2.5 Ma) and so could potentially overlap in age with Grăunceanu. Mean $\delta^{13}C$ (−12.4‰) and $\delta^{18}O$ values (22.4‰) for Nová Vieska are similar to the means for Grăunceanu (−14.6 and 21.8‰, respectively), suggesting that the modal environments at both sites were similar. However, $\delta^{18}O$ values of the rhinos from Nová Vieska are far less variable (range: 21.4 to 22.9‰) than are the cervids from Grăunceanu (18.9‰ to 25.3‰), suggesting that the rhinos at Nová Vieska ingested food and water with much less oxygen isotopic variability than was available to the cervids at Grăunceanu. Based on the $\delta^{13}C$ values of all species at Nová Vieska, Kovács et al. (2015) suggest that the fauna occupied a woodland to mesic C_3 grassland or closed canopy forest. Other relevant isotopic data include three specimens of *Cervus* sp. from southern Slovakia (Szabó et al., 2021). The oldest site with isotopic data in their study, Gombasek, is assigned to early MN 20 (0.8–0.7 Ma) and so is considerably younger than Grăunceanu; these specimens exhibit somewhat higher mean $\delta^{13}C$ values (−10.1‰) but a very similar mean $\delta^{18}O$ value (21.7‰) relative to our samples from Grăunceanu. Variability is low for Gombasek, but the sample size is small.

One explanation for the contrast in oxygen isotope variability at Nová Vieska and Grăunceanu (i.e., many specimens with higher than average $\delta^{18}O$ values at Grăunceanu), is that some of the Grăunceanu cervids foraged in more open habitats that were subject to greater evaporation of leaf and surface waters than in the more closed parts of the landscape. A more seasonal climate at Grăunceanu, with a larger annual range in $\delta^{18}O$ values of precipitation could also have resulted in the increased variability in our sample. This increased oxygen isotope variability could also be a result of seasonal migration between higher elevation sites in the Carpathians and lower elevation sites in the Danube lowlands. Serial sampling of individual teeth and along tooth rows could reveal for intra- and inter-annual variations in $\delta^{18}O$ values implied by climatic seasonality or seasonal mobility; though such sampling was beyond the scope of this project these analyses are planned for the future. In sum, the oxygen isotope data are consistent with foraging across a gradient of habitat openness and are also permissive of seasonal effects.

4.2. Reconciling the mesowear, microwear, and isotopic data

Results from the mesowear, microwear, and carbon stable isotope analyses produced somewhat conflicting reconstructions of diet for the ungulate community from the ORV. Apart from the equids, all specimens studied in the mesowear analysis were artiodactyls, and primarily cervids. Further, cervids were the only group in the microwear analysis and dominated the isotope analyses. This sampling was a function of the composition of the ORV assemblage, which is dominated by cervid remains, and contains a considerably larger portion of postcranial elements rather than cranial or dental materials. Because the mesowear, microwear, and stable isotope analyses are focused primarily on cervids, one may expect that the three proxies would return similar results, but that was not the case.

The mesowear analysis indicates that the cervids were almost exclusively browsers and carbon isotope composition of tooth enamel indicates end-member C_3 diets (and some $\delta^{13}C$ values are permissive of closed canopy forests), consistent with browsing as the feeding mode for all specimens analyzed. While grazing on C_3 grasses cannot be ruled out, the $\delta^{13}C$ values would be unusually low for open-habitat C_3 grasses (but see below). However, cervid microwear textures strongly suggest the presence of, if not dominance by, grasslands. While texture anisotropy (*epLsar*) for the ORV sample is most consistent with a mixed diet, complexity values (*Asfc*) are more in line with a grazing diet. In aggregate, these texture attributes are inconsistent with a browse or frugivorous diet for the ORV

Table 10
Palynology of coprolites from Grăunceanu (VGr) and Fântâna lui Mitilan (FM).

Taxa	FM.0044	FM.0046	FM.0049	FM.0055	FM.0056	FM.0057	FM.0058	FM.0061	FM Total	VGr.1042	VGr.1043	VGr.2057	VGr Total
Trees and shrubs (subtotal)	**6**	**2**	**0**	**6**	**0**	**12**	**0**	**6**	**32**	**1**	**0**	**0**	**1**
Picea (spruce)						2		1	**3**				
Pinus (pine)	1					2		1	**4**				
Betula (birch)		1		1		1			**3**				
Alnus (alder)	2	1				3		1	**7**				
Corylus (hazelnut)	1			1		2			**4**				
Ulmus (elm)				1				1	**2**				
Tilia (linden)	1			1		1			**3**	1			**1**
Carpinus (hornbeam)				1		1		1	**3**				
Fagus (beech)				1				1	**2**				
Ericaceae (heath family)	1								**1**				
Herbaceous (subtotal)	**7**	**3**	**0**	**6**	**0**	**9**	**0**	**4**	**29**	**0**	**0**	**0**	**0**
Poaceae				5		4		1	**10**				
Artemisia	2	2		1		1			**6**				
Centaurea						1			**1**				
Polygonaceae								1	**1**				
Chenopodiaceae						1			**1**				
Rosaceae		1							**1**				
Plantago sp.	1							1	**2**				
Urticaceae						1		1	**2**				
Scrophulariaceae	3								**3**				
Brassicaceae	1								**1**				
Indeterminate						1			**1**				
Spores (subtotal)	**2**	**0**	**0**	**0**	**2**	**1**	**1**	**0**	**6**	**0**	**0**	**1**	**1**
Spores – triletes (Pterydophyta)					1				**1**				
Spores – monoletes (Polypodiaceae)	2				1	1			**4**				
Sphagnum (Bryophyta)							1		**1**			1	**1**
Other (subtotal)	**0**	**0**	**2**	**0**	**0**	**0**	**0**	**0**	**2**	**0**	**0**	**0**	**0**
*Sordaria (*coprophilous fungi)													**0**
TOTAL	**15**	**5**	**2**	**12**	**2**	**21**	**1**	**10**	**68**	**1**	**0**	**1**	**2**

fossil cervids, in contrast to the mesowear and isotope results. Given that complexity typically separates extant ruminants more "cleanly" than anisotropy, it seems most reasonable to infer that the ORV cervids had a diet dominated by grasses, at least based on the microwear results. Indeed, the range of variation in *Asfc* values for these specimens is low, suggesting a graze signal. However, variation in *epLsar* is consistent with at least some browse in the diet. While there is no one-to-one correspondence between diet and habitat, there is a reasonable association between grazing and grass availability and between browsing and the presence of woody cover (Estes, 1991; Kingdon, 1997; Sponheimer et al., 1999).

Microwear texture results presented here can be compared with values reported in a recent study by Berlioz et al. (2018) of fossil cervids (identified as *Eucladoceros*) from eight Early Pleistocene localities across Europe, representing both glacial and interglacial deposits. Their analyses identified variation in microwear textures that suggests a switch from browsing during interglacials, with complexity averages peaking above 3.0 during MNQ17 and MNQ19, to grazing during glacials, with *Asfc* average dipping nearly to 1.0 during MNQ18. Our mean *Asfc* value (0.875) for the ORV specimens is lower than the average for any of the fossil samples reported by Berlioz et al. (2018), though within the range of values for extant deer that mostly consume graze from the savannah-like habitat of Lugar Nuevo, Spain (Berlioz et al., 2017). Similarly, our *epLsar* average (4.714) is also within the range of the Lugar Nuevo cervids. We caution that the methods of analysis and instrumentation used differ between our study and those of Berlioz et al. (Leica Microsystems DCM8 confocal surface profilometer versus a Sensofar Plμ Standard), which can affect comparability of results (Arman et al., 2016). Nevertheless, if our results are compared directly with those of Berlioz et al. (2017, 2018), they remain most consistent with grazing for the Grăunceanu sample.

Another line of evidence regarding cervid behavior and the environment of the ORV during the Early Pleistocene is related to postcranial morphology and locomotor behavior. In this regard, prior ecomorphological studies (Curran, 2009, 2015, 2018) on the Grăunceanu cervid assemblage provide some evidence. Compared to recent cervids of known habitat preference, three-dimensional geometric morphometric comparisons of femoral, tibial, and calcaneal morphology of *Rucervus radulescui* specimens (formerly designated as *Eucladoceros* sp. in Curran, 2009, 2015, 2018) suggest that Grăunceanu cervids in the Early Pleistocene were adapted to open conditions. Further, their pedal morphology indicates adaptation to hard, dry ground with some topographic relief. These results therefore seem to be more in line with an open, perhaps grassland, environment as suggested by the microwear results.

There are several potential explanations for this seeming discrepancy between the results of the mesowear and isotope analyses, which indicate closed habitat conditions, and the microwear analyses and postcranial ecomorphology, which indicate open habitats. In prior research on the paleoecology of the large cervid *Eucladoceros,* conflicting dietary signals were found even using just a single paleoecological proxy such as microwear. As noted above, Berlioz et al. (2018) identified a browsing signal in *Eucladoceros* from the sites of Chilac (France), Varshets (Bulgaria), and Gerakarou (Greece) but a grazing signal at Saint-Vallier, Senèze, and Dafnero (Greece). Notably, the grazing signal from Saint-Vallier and Senèze identified by Berlioz et al. differs from prior reconstructions (Valli and Palombo, 2005) for these sites, which were based on cranial functional morphology as well as meso/microwear analysis and identified a browsing signal. Berlioz et al. (2018) suggest these conflicting interpretations and the variation in their sample reflects climatic fluctuations from glacial periods, when steppic conditions with grassy habitats predominated, to interglacial times, when there was higher tree cover, resulting in considerable dietary plasticity. However, deer that were habitually grazing should have a mesowear signal that indicates grazing, which is not the case for the ORV cervids. Thus, even if dietary flexibility may explain variation in signals among sites, it cannot fully explain the pattern we observe.

An alternative explanation may be that the microwear pattern associated with grazing we observe in the ORV sample was produced from grazing on C_3 grasses, which, as suggested above, could be consistent with the isotopic results. Indeed, C_4 grasses are rarely found in European Pleistocene paleontological sites, and multiple researchers have suggested that Pleistocene European environments may have instead been dominated by C_3 grasses (e.g., Venta Micena [Palmqvist et al., 2008]; Italian peninsula [Szabó et al., 2017]; central Europe [Kovács et al., 2012]). However, C_4 grasses have been recovered from sediments across Oligocene-Miocene southern Europe (Urban et al., 2010), indicating they were at least present in Europe earlier in the Cenozoic, well prior to the Early Pleistocene. In fact, several of the families of herbaceous pollen we identify from our coprolite sample here include representatives that can be either C_3 or C_4. However, the browsing mesowear patterns of the ORV cervids are inconsistent with grazing, whether on C_4 or C_3 grasses (e.g., Schubert, 2007).

Lastly, the grazing microwear pattern for the ORV may reflect seasonality in these large cervids, as has been found in other ungulates (Rivals and Deniaux, 2005; Semprebon and Rivals, 2007; Valli and Palombo, 2008; Rivals et al., 2009; Sánchez-Hernández et al., 2014, 2016; Amano et al., 2016; Rivals and Lister, 2016; Berlioz et al., 2017; Merceron et al., 2020; Rivals et al., 2020). In this scenario, the ORV large cervids (especially *Rucervus*) may have moved through different habitats on seasonal migrations between higher and lower elevations. The closest mountains to the ORV are the Carpathian Mountains, at ~50 km north, well within a migratory distance for a large-sized cervid (Benkobi et al., 2005; Beck et al., 2013). It is possible that the large ORV cervids migrated seasonally from summer habitats in the mountains to winter habitats at the lower elevations of the ORV to avoid dense snow cover and find forage, as some *Cervus elaphus* populations do today (Luccarini et al., 2006; Beck et al., 2013). However, *Cervus elaphus* cannot provide an exact model for ORV cervid behavior due to very different postcranial morphology. For example, the femoral head of *Cervus elaphus* is tapered in the lateral aspect, which is consistent with moving through more closed habitats while the single intact large cervid femoral head present in the ORV collections is greatly expanded in the lateral aspect, pointing to cursoriality in open landscapes (Kappelman, 1988; Curran, 2009, 2015, 2018). Further, the ORV cervids have unique pedal morphology suggesting adaptations to locomotion in both open and mountainous habitats (Curran, 2009, 2015, 2018). The ecomorphological signal of open and mountainous adaptations is consistent with the hypothesis that the ORV cervids may have migrated seasonally from the Carpathian Mountains to the Danube lowlands.

Thus, the differing signals recorded in the ORV cervid assemblage paleoecological proxies most likely reflect the temporal scale over which each proxy records. Microwear traces record a short period (a few days to a few weeks) just before the animal's death (Teaford and Oyen, 1989; Winkler et al., 2020). Carbon isotopic signatures are incorporated into enamel during tooth formation, capturing (for example in the second molar of *Cervus elaphus*) up to the first ~10 months of the animal's juvenile life (Rivera-Araya and Pilaar Birch, 2018; Merceron et al., 2020). In contrast, mesowear is a record of the attritional process between teeth and food created and maintained through an animal's lifetime (e.g., Fortelius and Solounias, 2000; Ackermans et al., 2020). Finally, ecomorphology represents the longest scale as the association between skeletal morphology and function and is the result of long-term adaptation (Wainwright and Reilly, 1994). Putting these proxies and scales together, we can construct a picture of how the ORV cervids, particularly *Rucervus radulescui*, may have used their environment. Based on ecomorphological analyses, we can hypothesize that the ORV cervids were primarily adapted to movement in open habitats, though they may have also migrated to more mountainous terrains seasonally, likely during the summer months, as some modern *Cervus elaphus* do (Luccarini et al., 2006; Beck et al., 2013). Mesowear analysis suggests the ORV cervids preferentially browsed throughout their life. Carbon isotope analysis indicates they fed on C_3 plants (minimally while their first and second permanent molars were forming), which could have been acquired from any form of C_3 foliage- whether the leaves of trees/shrubs or of grasses, or both. The high variability of the oxygen isotope data at Grăunceanu may indicate either mobility across the region from more closed to more open habitats or from lowlands to mountainous areas, and/or could suggest seasonal variability of the water ingested by the ORV cervids. Finally, microwear analyses indicate they grazed close to the time of death and deposition in the ORV. As the ORV sites would have been found in the lower elevation of this hypothetical migratory range, the ORV may represent the winter foraging/grazing grounds of these cervid taxa. This interpretation is supported by the large number of shed antlers recovered from the ORV localities, since antlers are typically shed in late winter (Miller, 2012) and the lack of neonatal to young juvenile cervid remains, which were likely born in the late spring to early summer (Whitehead, 1972; Nowak, 1999).

4.3. Situating the ORV sites in the Early Pleistocene of western Eurasia and implications for hominin dispersal

The Early Pleistocene is characterized as a time of global aridification and cooling initiated by northern Hemisphere glaciation (Flesche Kleiven et al., 2002; Lisiecki and Raymo, 2005, 2007; Lawrence et al., 2009; Tan, 2018). This climatic shift is evidenced by pollen records (Leroy et al., 2011; Alçiçek et al., 2017), isotopic shifts (Zachos et al., 2001; Lisiecki and Raymo, 2005), dust records (Denton, 1999; deMenocal, 2004), and faunal turnovers (Behrensmeyer et al., 1997; Bobe and Behrensmeyer, 2004; Martínez-Navarro, 2010; Palombo, 2018). There is little doubt that this climatic change is correlated with the onset of glacial cycling and this was likely the primary driver of environmental conditions starting at the beginning of the Pleistocene (deMenocal and Bloemendal, 1995). Specifically, growth of the Fennoscandian ice sheets commencing at 2.8 Ma would have started a high-pressure cell over the North Atlantic that would have forced cool, dry air out over Europe and Africa (deMenocal and Bloemendal, 1995). Temperatures continued to decline, and aridity increased as the glacial ice sheets grew larger into the Pleistocene. The onset of glacial cycling marked a significant change in climatic regime and would have affected local environmental conditions, likely resulting in habitat fragmentation, heterogeneity, and seasonality (Berlioz et al., 2018).

In western Eurasia, local environmental change due to new climatic conditions resulted in more open habitats than were found in the late Pliocene (Azzaroli et al., 1988). As reviewed above, these sites span across western Eurasia from Dmanisi in the east to the Orce region of Spain in the west. Although each site has its own unique environmental character, they all share a heterogeneous habitat structure that includes areas of open grasslands/steppe and open woodlands with near-by water sources. This description also characterizes the reconstruction for the ORV sites. This similarity is reflected in our prior comparisons of the taxonomic lists from other Early Pleistocene Eurasian sites that suggests affinities between Grăunceanu and Saint-Vallier and Senèze (France) and Vatera (Greece) (Terhune et al., 2020), which have also been reconstructed to have had relatively open environments. Importantly, this is also the paleohabitat reconstructed for the earliest hominin-bearing sites in Eurasia (see Table 2). Notably, in the sites reviewed here, there is little discernible difference between non-hominin and hominin sites in terms of environmental reconstructions. The time period just prior to the first well-documented appearance of *Homo erectus* in Eurasia at Dmanisi is reconstructed as being open and arid, which accords with other paleoclimatic proxies. Following this spike in openness, hominins are found in locations across Eurasia in heterogeneous open/wooded habitats (Dennell, 2010).

In almost all paleoenvironmental reconstructions for *H. erectus*, this species is associated with aquatic resources: fluvial, lacustrine, palustrine, or marine. Like modern humans and many other mammals, water was a limiting resource for *H. erectus*. Regardless of which continent *H. erectus* was living on, the paleoenvironmental evidence indicates that *H. erectus* inhabited primarily open but heterogeneous environments, generally near a water source. Habitat reconstructions from Africa, temperate Eurasia, and even more marine sites of Indonesia are all similar (Palmqvist et al., 2003; Bettis III et al., 2009; Messager et al., 2011; Bedetti and Pavia, 2013; Blain et al., 2014; Janssen et al., 2016; Roach et al., 2016). This suggests that *H. erectus* was not locked into the specific types of resources associated with each continent, but instead was adapted to exploit the variety of resources found in heterogeneous habitats in tropical through temperate regions (Potts, 2012; Antón et al., 2014).

It is evident that *H. erectus* represents an adaptive grade, both morphologically and behaviorally, distinct from all other hominins that preceded it. In fact, *H. erectus* is sometimes referred to as the first true member of the genus *Homo* (Wood and Collard, 1999). One distinguishing feature of *H. erectus* is its biogeographic range that extended far beyond that of any previous or contemporaneous hominin species. Across its huge range from South Africa (Herries et al., 2020) to Asia (Bettis III et al., 2009; Potts and Teague, 2010; Janssen et al., 2016), it undoubtedly encountered novel landscapes, flora, and fauna. Thus, while the initial evolution of *H. erectus* may have been due to the climatic change toward more arid conditions in the Early Pleistocene, selection that acted upon *H. erectus* continued to favor more generalist/versatilist traits (Potts, 1998, 2007) that allowed for occupation of a variety of habitats across Africa and into Eurasia.

It is unclear then why *H. erectus* does not appear in western Europe until relatively late (e.g., 1.4 Ma at Barranco León, Spain [Toro-Moyano et al., 2013]). The review of western Eurasian sites presented here clearly shows that heterogeneous habitats on the more open end of the spectrum were available across this region from the beginning of the Pleistocene through the time when hominin presence is well documented in Europe (~1.0 Ma and beyond). The new results reported here are no different: the habitat of the Olteţ River Valley of Romania in the Early Pleistocene was open and heterogeneous in nature. While hominins certainly encountered different fauna in Africa, SE Asia, and western Eurasia, they clearly were occupying these areas in the Early Pleistocene. As such, dispersal into western Europe does not seem to have been impaired by a lack of preferred habitat.

5. Conclusions

Using a multiproxy approach, this study demonstrates that the Early Pleistocene sites of the Olteţ River Valley of Romania were likely a mosaic of open grasslands and open woodlands, with limited areas of more closed woodlands and forests. Grăunceanu and La Peitriş were likely more open than the younger site of Fântâna lui Mitilan. These results accord well with the open habitats found in both previous reconstructions of the ORV sites and with reconstructions of paleoenvironmental conditions found at penecontemporaneous sites across western Eurasia. However, the small sample sizes analyzed here for several of the proxies studied caution against overinterpretation of these data.

Our team is currently extending our study of the ORV assemblages by investigating the taxonomic composition of the ORV remains housed in the Museum of Oltenia (Craiova, Romania), conducting detailed taphonomic analyses on all ORV fossils (with a special focus on potential hominin-generated modifications), evaluating the stratigraphy and sedimentology of the original depositional locations, and conducting surveys for new deposits in the ORV. To date, we have found several previously unreported localities with fossil remains, demonstrating the promise of continued research in the ORV deposits. This is likely to be the case for the many other tributaries to the Danube, a potential dispersal corridor into Europe. As suggested here, the preferred habitats of *H. erectus* at the time of its earliest dispersal into Eurasia were in place across much of Europe and western Asia, including modern-day Romania. Accordingly, expanding investigations into Early Pleistocene deposits across this region is encouraged to enhance our understanding of hominin dispersal(s).

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Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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