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Early Pleistocene fauna of the Olteţ River Valley of Romania: Biochronological and biogeographic implications

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A R T I C L E I N F O

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A B S T R A C T

The Early Pleistocene of Eurasia is marked by significant climatic, environmental, and faunal shifts and is the time during which *Homo* first appears in the Eurasian fossil record. To better characterize the environments that were available to these hominins, accurate data regarding the faunal composition of eastern European sites are necessary, as this is the region through which *Homo* is hypothesized to have dispersed into Europe. Here we present updated and revised taxonomy and biochronology for sites in the Olteţ River Valley (ORV) of central Romania. The site of Grăunceanu is one of the most fossiliferous deposits from this time. Excavations and descriptions of the ORV sites took place during the 1960–1980s, but since that time many taxonomic revisions have been published. Here, we present a reassessment and update of the fauna from the ORV sites. We report several new taxa (e.g., *Pachystruthio*, *Smutsia*) and expand the known biogeographic range for other taxa (e.g., *Puma pardoides*). Our biochronological assessment of this updated taxonomy is consistent with previous reports, though with some refinement. We suggest Grăunceanu is Late Villafranchian (~2.2–1.9 Ma) and compositionally similar to the sites of Saint-Vallier (France) and Vatera (Greece). Similarly, the La Pietriş assemblage was likely deposited >1.7 Ma. The younger site of Fântâna lui Mitilan was deposited after 1.8 Ma, and perhaps as recently as 1.1 Ma. Thus, the ORV faunal assemblages provide an excellent record of nearly the entire span of the Late Villafranchian for both central Romania and eastern Europe.

1. Introduction

Paleontological work in the 1960s located a number of fossil sites in the Olteţ River Valley (ORV) of Romania that were identified as being Early Pleistocene in age (Necrasov et al., 1961; Bolomey, 1965; Rădulescu et al., 2003). The fossil assemblages are dominated by materials from the site of Valea Grăunceanului (henceforth called Grăunceanu), and to a much lesser extent the sites of La Pietriş and Fântâna lui Mitilan. Biochronological estimates for these sites suggest they are best attributed to the Late Villafranchian Land Mammal Age of Europe (MN17/MmQ1), with more specific comparisons made to the faunas from Saint-Vallier and Senèze (Bolomey, 1965; Rădulescu and Samson, 1990; Rădulescu et al., 2003). As such, these fossil sites have the ability to yield important insights into mammalian, and potentially hominin, dispersal patterns into Eurasia and paleoenvironments present in eastern Europe during this time. Though a number of publications have provided information on taxa recovered from these sites, changes to many taxonomic groups of the Early Pleistocene of Europe necessitate a reassessment of the ORV fossil assemblage. Here we present the results of new and ongoing work focused on reinventory of the ORV fossil assemblage, and we highlight changes and updates to prior taxonomic lists with the goal of improving biochronological estimates for the age of

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the ORV sites.

2. Background

2.1. The Villafranchian Land Mammal Age

The Villafranchian Land Mammal Age of Europe spans the Late Pliocene and Early Pleistocene, from approximately 3.5 to 1.0 million years ago (Ma) (Rook and Martínez-Navarro, 2010). It can be roughly split into Early (3.5–2.6 Ma), Middle (2.6–2.0 Ma), and Late (2.0–1.0 Ma) portions (Fig. 1; Azzaroli, 1983; Rook and Martínez-Navarro, 2010), with some authors identifying the time period between 1.2 and ~0.9 Ma as the Epivillafranchian (e.g., Bellucci et al., 2015). These portions of the Villafranchian are linked to a number of different faunal and geological units (Fig. 1). The Villafranchian roughly corresponds to parts of biochronological units MN15-17 and MmQ1-3a as defined by Agustí et al. (1987, 2001; dates following Oms et al., 1999, 2000) and the mammalian biozones MNQ16-19 defined by Guérin (1982) and Faure and Guérin (1992). This timeframe is marked by a number of faunal turnover events and the first appearance of *Homo* in Eurasia.

The faunas from the Early Villafranchian retain some subtropical affinities, as exemplified by the presence of tapirs (*Tapirus arvernensis*) and primates such as *Mesopithecus monspessulanus*, while also being associated with the appearance of a variety of new taxa linked to more wooded environments such as the primitive rhinocerotid species *Stephanorhinus elatus*, bovids such as *Leptobos stenometopon*, and a variety of carnivore species including *Pliocrocuta perrieri*, *Homotherium crenatidens*, and *Acinonyx pardinensis* (Rook and Martínez-Navarro, 2010). The Early Villafranchian also saw the appearance of the first mammoth species in Europe, *Mammuthus rumanus*, in the Dacian Basin of Romania at ~3.5 Ma (Lister and van Essen, 2003; Lister et al., 2005; Rook and Martínez-Navarro, 2010).

The Middle Villafranchian (the beginning of which is marked by the Gauss/Matuyama boundary at 2.588 Ma and the start of the Pleistocene Epoch) witnessed the disappearance of European fauna with subtropical affinities such as those listed above and the appearance of taxa that were more arid-adapted, including monodactyl horses and large deer and bovids (e.g., *Eucladoceros ctenoides vireti* and *Gazella borbonica*) (Rook and Martínez-Navarro, 2010). A number of new species appear during this time period, including *Stephanorhinus etruscus*, *Equus stenonis*, *Sus strozzii*, *Gallogoral meneghinii*, *Gazellospira torticornis*, and *Canis etruscus*. *Mammuthus meridionalis*, a well-known and widespread species of mammoth likely descended from *M. rumanus*, appears close to the onset of the Middle Villafranchian (Lister et al., 2005; Palombo and Ferretti, 2005).

Though there is considerable continuity with the Middle Villafranchian, the Late Villafranchian saw a number of important faunal dispersal events take place. Most significantly, this is the time period during which the genus *Homo* first appears in Eurasia, as evidenced by hominin remains from the sites of Dmanisi, Georgia at 1.85 Ma (Ferring et al., 2011) and the Gaudix-Baza Basin of Spain at 1.4 Ma (Toro-Moyano et al., 2013). The large hyaena *Pachycrocuta brevirostris* (which likely dispersed from Africa) first appears at or near the beginning of the Late Villafranchian, and the derived deer species *Eucladoceros ctenoides* and *Cervus nestii* are also present in the earliest faunal unit (Olivola) of the Late Villafranchian (Azzaroli and Mazza, 1992; Rook and Martínez-Navarro, 2010; Croitor, 2014). Toward the middle of the Late Villafranchian, species such as *Sus scrofa*, *Hippopotamus antiquus*, and the primate *Theropithecus oswaldi* also appear in Europe for the first time (Rook and Martínez-Navarro, 2010; Martínez-Navarro, 2010; Martínez-Navarro et al., 2015; Bellucci et al., 2015).

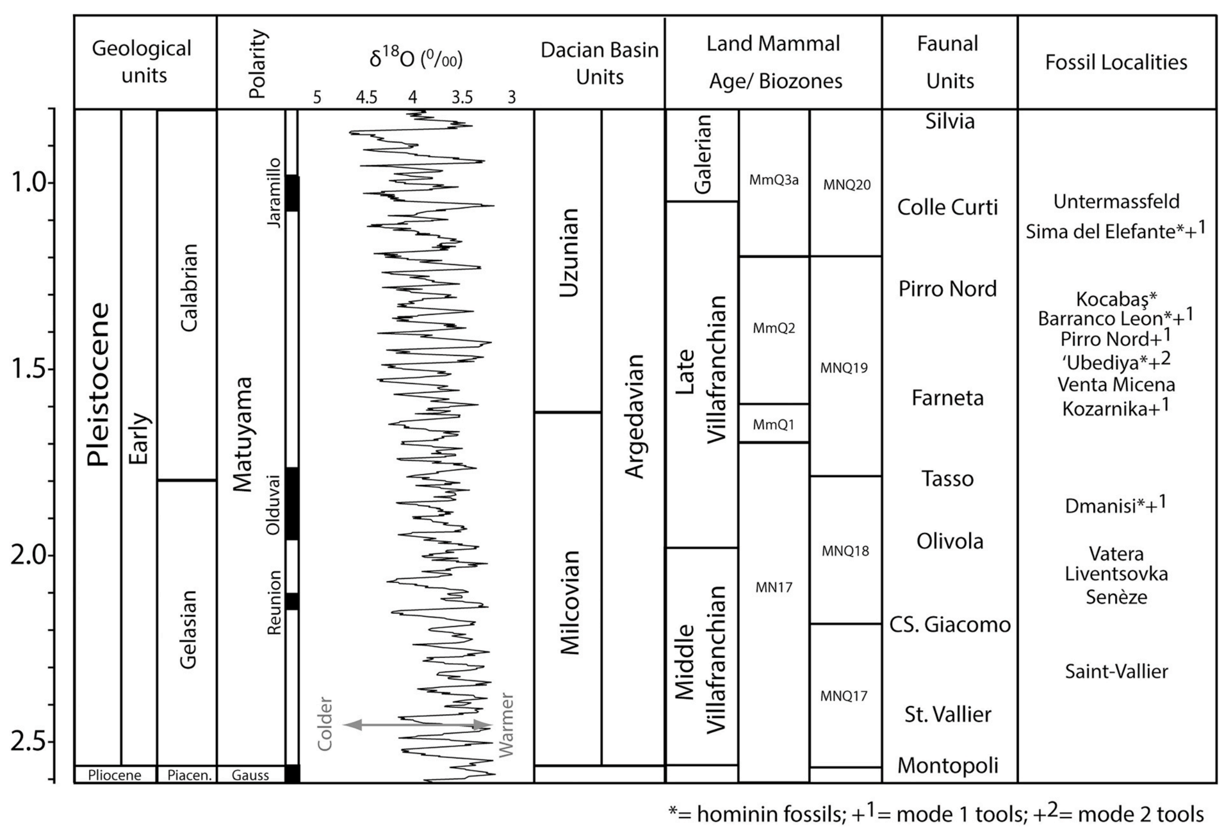

Fig. 1. Chart showing the temporal units discussed in the text and their relation to one another, including relevant faunal units and biozones/land mammal ages, and selected European and near eastern fossil localities. Mammal ages/biozones, Dacian Basin units, and oxygen isotope data are from Martínez-Navarro (2010), Oms et al. (1999), Andreescu et al. (2011), Nomade et al. (2014), and Lisiecki and Raymo (2005).

2.2. The Olteţ River Valley

The Olteţ River Valley (ORV) of Romania (Fig. 2) has yielded a series of fossil sites that has the potential to shed light on mammalian dispersal patterns into Europe during the Early Pleistocene (Rădulescu and Samson, 1990). Exploration of this region in the 1960s identified multiple fossil localities, several of which are among the most fossiliferous Pleistocene sites in Eastern Europe.

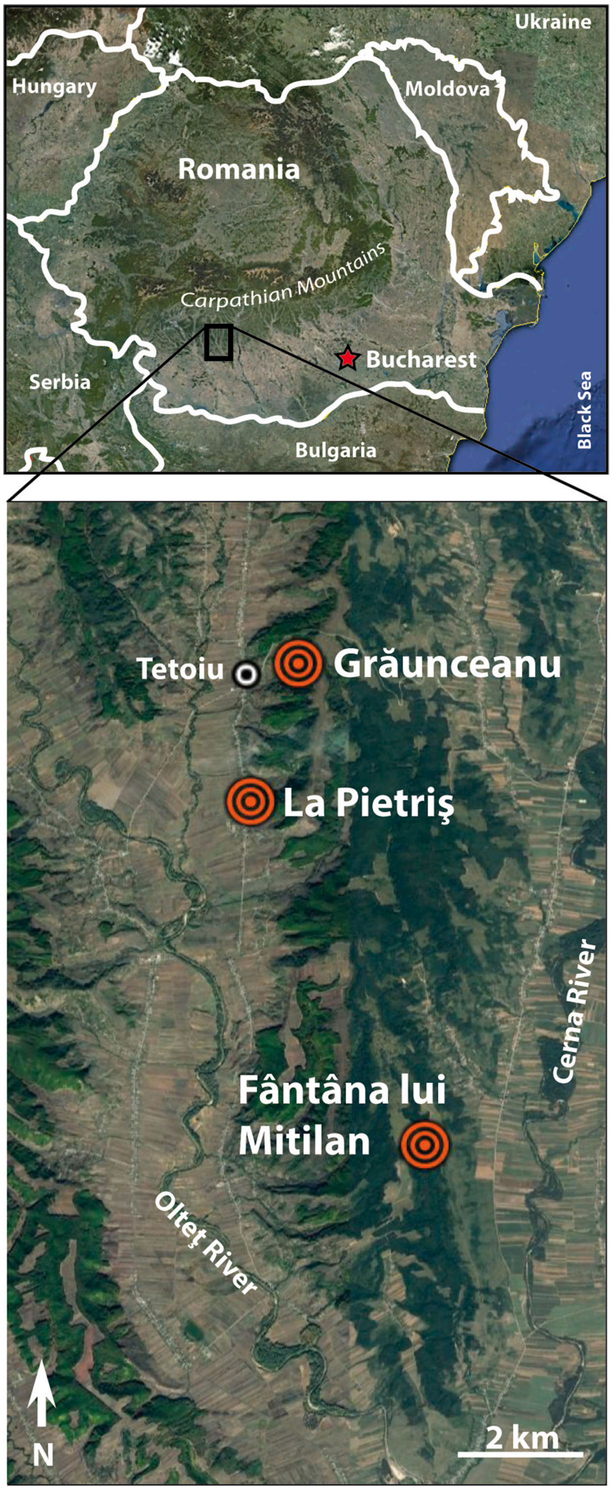

Fig. 2. Top: map of Romania showing the location of the Olteţ River Valley (ORV) project area. Bottom: overview of the ORV project area including relevant landmarks and fossil localities that have been relocated by our research team.

2.2.1. Geological history

The ORV is located in the Dacian Basin, which is delimited by the Carpathian Mountains to the north and west, the Balkan Mountains to the south, and the Black Sea to the east. Deposits in the vicinity of our study area are attributed to the Tetoiu Formation (Andreescu et al., 2011); sediments in this formation have a predominantly sandy-pebbly facies, and tend to be richly fossiliferous (Andreescu et al., 1984; Lubenescu et al., 1987; Samson and Rădulescu, 1973; Rădulescu and Samson, 1990). Molluscan remains recovered from the Tetoiu formation suggest an attribution to the Milcovian and Uzunian substages of the Argedavian Stage (Fig. 1), with sediments extending 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), which has been proposed to have been a dispersal corridor for mammals, including humans, into Western Europe (Conard and Bolus, 2003; Higham et al., 2012). It is worth noting that during the Villafranchian this region was dominated by the presence of the Dacian Lake, interconnected to the Pannonian and Euxinic lakes to the west and east, respectively.

2.2.2. Existing paleontological sites

In the 1960s, numerous fossil localities in the ORV were identified, primarily in the vicinity of the town of Tetoiu (formerly Bugiuleşti) (Samson, 1975; Rădulescu and Samson, 1990). The most prolific site in this area is Grăunceanu (Fig. 2), which was first excavated by Samson and Rădulescu under the auspices of the Emil Racoviţă Institute of Speleology of the Romanian Academy (henceforth ISER) in conjunction with Necrasov from the University of Iași (Necrasov et al., 1961), and then continued by Nicolăescu-Plopşor under the auspices of the Archaeological Institute of the Romanian Academy. Although unclear from existing resources (unfortunately, records describing the excavation of the ORV materials and any prior specimen inventories have been lost), it is likely that excavations were halted when no fossils remained *in situ*. Subsequent investigations at Grăunceanu were undertaken by the Natural History section of the Museum of Oltenia (Craiova, Romania) in the 1980s, which recovered a number of faunal remains now housed at that institution (in addition to a portion of the materials from the original excavations). Most recently (2004), excavations were conducted at Grăunceanu by a joint Romanian and American team, but no fossil remains were recovered (McNulty, pers. comm.).

As many as 15 smaller localities in the Olteţ River Valley (Samson, 1975; Rădulescu and Samson, 1990) have also yielded fossil remains. In addition to Grăunceanu, the most notable of these sites include Fântâna lui Mitilan and La Pietriş (Fig. 2). Materials recovered from Grăunceanu and the ORV more generally include well-preserved fossil remains from multiple mammalian taxa (Table S1; Necrasov et al., 1961; Bolomey, 1965; Rădulescu and Samson, 1990, 1991; Rădulescu et al., 1998, 2003). Analyses by Rădulescu and Samson (1990) suggest that there are several faunal horizons represented by these sites, with Grăunceanu and La Pietriş in the oldest horizons, and Fântâna lui Mitilan being somewhat younger. Previous biochronological assessments suggest that Grăunceanu is best attributed to the Late Villafranchian (MN17/MmQ1), being similar to Saint-Vallier and Senèze (Bolomey, 1965; Rădulescu and Samson, 1990; Rădulescu et al., 2003). However, dating for these localities is uncertain, as no radiometric dating of the ORV sites has been conducted. Further, taxonomic designations have shifted considerably since initial publications describing taxa recovered from the ORV (Table S1).

2.2.3. Archaeological remains

Of particular interest for the ORV sites are reports of archaeological materials recovered from this region. The earliest archaeological materials in Romania have been tentatively assigned to the Lower Paleolithic, although the lack of excavation records and doubts regarding the

Table 1
Taxa identified from the Olteţ River Valley sites by our research team.

		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.*[a]	X				Olt
	Pliotragus ardeus	X				
	Megalovis latifrons		X			
	Gazellospira torticornis	X				
	Metacervocerus sp.[a]	X				Olt
	Dama cf. *eurygonos*[a]		X			
	Eucladoceros sp.		X	X	X	
	Eucladoceros dicranios	X				
	Eucladoceros ctenoides falconeri	X				
	Rucervus (Arvernoceros) radulescui[a b]	X		X		
	Croizetoceros ramosus[a]	X				
	Alces sp.[a]	X				
	Praemegaceros obscurus[a]		X			Olt
	Praemegaceros cf. *mosbachensis*[a]		X			Olt
	Mitilanotherium inexspectatum	X	X			
	Sus strozzi	X				
Perissodactyla	*Equus* sp. (cf. *livenzovensis)* [b]	X				
	Equus sp.		X	X	X	RA
	Stephanorhinus cf. *etruscus*	X	X			
Carnivora	cf. *Acinonyx pardinensis*[a]	X				
	Megantereon cultridens[b]	X				
	Homotherium sp.	X				
	Puma pardoides[a]	X				
	Lynx issiodorensis	X				
	Pachycrocuta brevirostris[a b]	?				VH
	Pliocrocuta perrieri	?				
	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.*[a b]	X				
Non-mammals	*Pachystruthio* cf. *pannonicus*[a b]	X				
	Aves indet.[a]	X				
	Geoemyidadae indet[a]		X			
	Testudines indet[a]					RA

VGr = Grăunceanu; LP = La Pietriş; FM= Fântâna lui Mitilan; FA= Fântâna Alortetei; LS = La Seci; RA = Râpa; DM = Dealul Mammut; VH= Valea Homorecia; Olt = Olteţ Valley (designation indicates specimens with uncertain provenience).
[a] Newly identified taxon.
[b] Taxonomy revised.

anthropogenic origin of these materials make the existence of a Lower Paleolithic record in this country questionable (see Doboş [2008] for an extensive review). Materials recovered from *in situ* contexts primarily derive from excavations undertaken in the Olteţ River Valley and surrounding counties in the 1960s (Rădulescu et al., 1998; Doboş, 2008). Recovered lithics have largely been attributed to the "Pebble Culture", a term used to designate Mode 1 industries; these specimens, along with several unworked cobbles of exotic origin and a single quartzite chopper, represent the bulk of the purported evidence for human activity at this site. Two additional sites in the vicinity of Tetoiu (Pietrisu Vijoiesti and Dealul Mjlociu) also yielded lithic materials that were attributed to hominins (Rădulescu et al., 1998), although the anthropogenic origin of these materials is also questionable (Doboş, 2008; Doboş and Iovita, 2016).

2.2.4. *Previous paleoenvironmental reconstructions*

Sedimentological data suggest that the Grăunceanu deposits were accumulated in a fluvial-lacustrine environment (Samson and Rădulescu, 1973). Rădulescu et al. (2003) reconstructed Grăunceanu as being humid and warm, based on the abundance of cervid specimens, though subsequent research (Curran, 2009, 2015) has shown that the most abundant taxon from the ORV fauna, *Rucervus* (formerly *Eucladoceros*), was most likely adapted to open habitats. Frost et al. (2005) suggested a savanna woodland setting based on *Paradolichopithecus* postcranial morphology, and Ferretti and Croitor (2001) reported a savanna 'parkland' environment based on the presence of *Mammuthus meridionalis*. Thus, these prior analyses indicate that Grăunceanu was likely a relatively open habitat with some tree cover available near a river (the paleo-Olteţ). This preliminary reconstruction suggests an environment similar to that of Dmanisi (Gabunia et al., 2001; Palmqvist, 2002; Lordkipanidze et al., 2007), Vatera (Koufos, 2009), and Senèze (Curran, 2009, 2015, 2018). However, it is important to emphasize that the faunal list from the site has not previously been updated based on current taxonomic designations, and the original specimens have in many cases not been analyzed since they were originally recovered in the 1960s, which makes this paleoenvironmental reconstruction tentative.

3. The ORV assemblage

Olteţ River Valley materials recovered in the 1960s through the 1980s are currently split between two collections: ISER (Bucharest) and the Museum of Oltenia (Craiova). We estimate that the entire collection is represented by ~5000–6000 specimens, not including unidentifiable bone fragments that have not been individually accessioned. The present analysis includes only specimens from the collections in Bucharest, though these analyses will be expanded in the near future to include the collections in Craiova. The work presented here builds on previous taxonomic lists created by prior researchers working with these materials (Supplemental Table 1; Necrasov et al., 1961; Bolomey, 1965; Rădulescu and Samson, 1990, 1991; Rădulescu et al., 1998; Rădulescu et al., 2003).

3.1. Revised taxonomy

To date, 3634 specimens have been catalogued by our team, 3132 of which are from Grăunceanu (Table 1). At present we have identified a total of 38 separate taxa from the ORV sites, several of which had not been previously identified from this region. Here we briefly describe the composition of each of the taxonomic groups present in the assemblage; additional more detailed descriptions and analyses for some taxonomic groups (e.g., Artiodactyla, Carnivora, Pholidota) will be provided in subsequent publications.

3.1.1. Proboscidea

There is abundant evidence for the presence of proboscideans in the ORV assemblage, remains of which are found at nearly all identified localities. These remains are assigned here to *Mammuthus* cf. *meridionalis* (Nesti, 1825); there is no evidence to suggest that *Anancus*

Fig. 3. Photographs of representative cervid and bovid remains from the Olteţ River Valley assemblage. A = *Croizetoceros ramosus* mandible (VGr.2435), B = *Dama* cf. *eurygonos* maxilla (FM.0092), C= *Praemegaceros obscurus* mandible fragment (FM.0136), D = *Eucladoceros ctenoides falconeri* shed antler (VGr.2373), E = *Alces* sp. shed antler (VGr.2374), F= *Gazellospira torticornis* metatarsal (VGr.0655), G = *Pliotragus ardeus* metacarpal (VGr.0383), H = *Megalovis latifrons* metacarpal (FM.0154). Scale bars for each specimen = 1 cm.

arvernensis is present in the assemblage (contra Necrasov et al., 1961). Many of the dental remains are from subadult *Mammuthus*, including specimens from La Pietriş and two nearly intact subadult mandibles for which the specific ORV provenience is unknown (three-dimensional [3D] models of these specimens are available via Morphosource.org). Though no adult teeth are fully intact, the juvenile teeth present between 7 and 10 plates. Enamel thickness of the adult molar fragments identified in the assemblage ranges from 2.28 to 3.7 mm with a mean of 3.12 mm. This is consistent with an average enamel thickness of 3.2 mm reported for *Mammuthus meriodionalis* (Palombo and Ferretti, 2005).

3.1.2. Artiodactyla

The artiodactyl remains from the ORV represent the largest portion by far of the identified faunal remains. From Grăunceanu alone, of the 2191 specimens identified to order or below 68.7% are identified to Artiodactyla. At the family level, approximately 55.2% are identified to Cervidae, 2.6% to Bovidae, 1.5% to Giraffidae, and just a single specimen (0.1%) is identified to Suidae. Contra Bolomey (1965) and consistent with all subsequent publications (Table S1), our analyses find no evidence for the presence of *Hippopotamus* at Grăunceanu.

3.1.2.1. Cervidae. The ORV cervid materials have been poorly understood due to multiple unresolved taxonomic identifications of deer species from the Early Pleistocene of Europe. The present study reveals a more complex and diversified character to the cervid communities from the ORV (Table 1), especially Grăunceanu, than previously reported (Table S1). Although a detailed analysis of the Artiodactyla assemblages is forthcoming (Croitor et al., in prep.), here we present a summary of the new taxonomic assignments for the ORV specimens.

The identification of *Eucladoceros* in the ORV has not been previously contested, as these remains are similar in body size and dental morphology to other cervid species present in Plio-Pleistocene Europe; however, the specific attribution of the Grăunceanu remains have previously been uncertain. Recent systematic revision has attributed the large deer from Grăunceanu (as well as several specimens from the site of La Pietriş) to the earlier evolutionary radiation of *Rucervus* (*Arvernoceros*) represented by *R.* (*Arvernoceros*) *ardei* from the Pliocene of Europe and the giant *R.* (*Arvernoceros*) *verestchagini* from the Early Pleistocene of Southeastern Europe (Croitor, 2018a). The large cervid from Grăunceanu is clearly distinguished from the above-mentioned forms and belongs to *R.* (*Arvernoceros*) *radulescui* (Croitor, 2018a). It is likely that most of the large-sized deer from Grăunceanu belong to this taxon.

Although represented by only a few specimens (Fig. 3), other highly diagnostic materials attest to the presence of both *Eucladoceros ctenoides falconeri* (= *Eucladoceros senezensis* [Deperet and Mayet, 1910]) and *E. dicranios* in the cervid sample from Grăunceanu, though likely in much lower proportions than previously thought. We retain the designation of *Eucladoceros* sp. for remains from Fântâna lui Mitilan based on the presence of a right hemimandible (FM.0091) with complete lower cheek tooth row; morphology and proportions of the premolars for this specimen clearly distinguish it from *R.* (*Arvernoceros*) *radulescui.* However, the absence of antler remains precludes species determination for the *Eucladoceros* specimens from Fântâna lui Mitilan.

The fallow deer-sized *Croizetoceros ramosus* from Grăunceanu is represented by a single mandible fragment (VGr.2435) with a highly molarized P_4 and a relatively long premolar series (premolar/molar length ratio is 62.5%) (Fig. 3). This premolar/molar ratio is close to the lowest values of *Croizetoceros* samples from Western Europe (Heintz, 1970). The mandible from Grăunceanu is slightly larger than the largest specimens from the Early Villafranchian of Villarroya (Spain) and is substantially larger than the mandible from Sésklo (Greece) described by Kostopoulos and Athanassiou (2005) as *C. ramosus gerakarensis*.

Metacervocerus sp. is an *Axis*-like deer represented by antler fragments and a few dental and postcranial remains from Grăunceanu. The antlers are characterized by a rather high position of the first ramification and morphologically are similar to *Metacervocerus rhenanus* from western Europe, but are somewhat larger, corresponding in size to '*Axis*' *shansius* from the Late Neogene of China and '*Cervus*' *punjabiensis* from the Upper Sivaliks (Croitor and Robinson, 2020). One mandible fragment (VGr.2436) from Grăunceanu metrically corresponds to the largest specimens of *Metacervocerus rhenanus* from Senèze and Saint-Vallier (Heintz, 1970) and is somewhat smaller than the sole complete lower jaw ascribed by Teilhart and Trassaert (1937) to '*Axis*' *shansius*.

Alces sp. from Grăunceanu is represented by a single, atypical, almost complete shed antler (VGr.2374, Fig. 3). The distal palmation is not developed, and the antler is terminated by three tines that form a three-lined bauplan, characteristic of Capreolinae, with a short distance between the first and second bifurcations. The undeveloped distal palmation could be an idiosyncratic feature due to age (juvenile or senile) and/or poor physical state of the animal (Sokolov, 1959). The antler beam is shorter and more robust than in typical *Alces gallicus* and thus may belong to *Alces carnutorum*. However, considering the peculiar individual character of this specimen, we prefer to identify it as *Alces* sp. for now.

Three additional cervid species not present at Grăunceanu were identified in the assemblage from Fântâna lui Mitilan. *Dama* cf. *eurygonos* is represented by an upper right maxilla (FM.0092, Fig. 3) and is metrically similar to *Dama eurygonos* from the Upper Valdarno (Croitor, 2018b). The length of the upper molar series falls within the size range of Early Pleistocene fallow deer from western Europe (Croitor, 2006a, 2014). *Praemegaceros obscurus* is a large-sized deer represented by a left mandibular ramus fragment (FM.0136, Fig. 3) and an isolated P_4 (FM.0137); this dentition is characterized by the advanced molarization of P_4. In addition, a more advanced form of *Praemegaceros obscurus, Praemegaceros* cf. *mosbachensis* (Soergel, 1927) is identified from a single antler fragment (FM.0024) from the upper level of Fântâna lui Mitilan. This specimen is characterized by the progressive reduction of the basal tine and by the pronounced anteroposterior compression of the antler beam.

3.1.2.2. Bovidae. Pliotragus ardeus is the most common bovid in the Grăunceanu assemblage, represented by both craniodental and postcranial remains (Fig. 3). The horn cores of *P. ardeus* from Grăunceanu are short, cone-shaped, slightly bent and compressed from the sides, and do not show any torsion. The dental morphology of *P. ardeus* from Grăunceanu may be regarded as archaic: the molars are characterized by the presence of small basal pillars, while the posterior lobe of P_4 is more strongly developed than in the sample from Senèze (Duvernois and Guérin, 1989).

Gazellospira torticornis is represented by several gracile postcranial remains from Grăunceanu, including a complete long and slender metatarsal (VGr.0655, Fig. 3) with a nearly symmetric diaphyseal outline in cross-section. The remains of this long-limbed bovid are somewhat larger than postcranial elements of *Pontoceros ambiguus* from Apollonia-1 and stand closer to *G. torticornis* from Senèze. The length of the metatarsal (249 mm) falls within the range of variation for *G. torticornis* from western Europe (247-267 mm) reported by Duvernois and Guérin (1989).

Subfamily Bovinae is represented by a few poorly diagnostic remains: a proximal fragment of horn core (VGr.1989) and two damaged astragali (VGr.2292 and VGr.2123) from Grăunceanu, and a distal fragment of a metacarpal from an unspecified location in the Olteț River Valley. The shape and size of the horn core from Grăunceanu is very close to the type specimens of *Bison* (*Eobison*) *tamanensis* and *B.* (*Eobison*) *georgicus*, as well as to *Bison* (*Eobison*) sp. from Italy (Capena) and southeastern Europe (Dolinskoe, Semibalki).

Megalovis latifrons is a large ovibovine represented by a series of well-preserved skeletal remains from Fântâna lui Mitilan. The right metacarpal (FM.0154, Fig. 3) was originally described by Rădulescu and

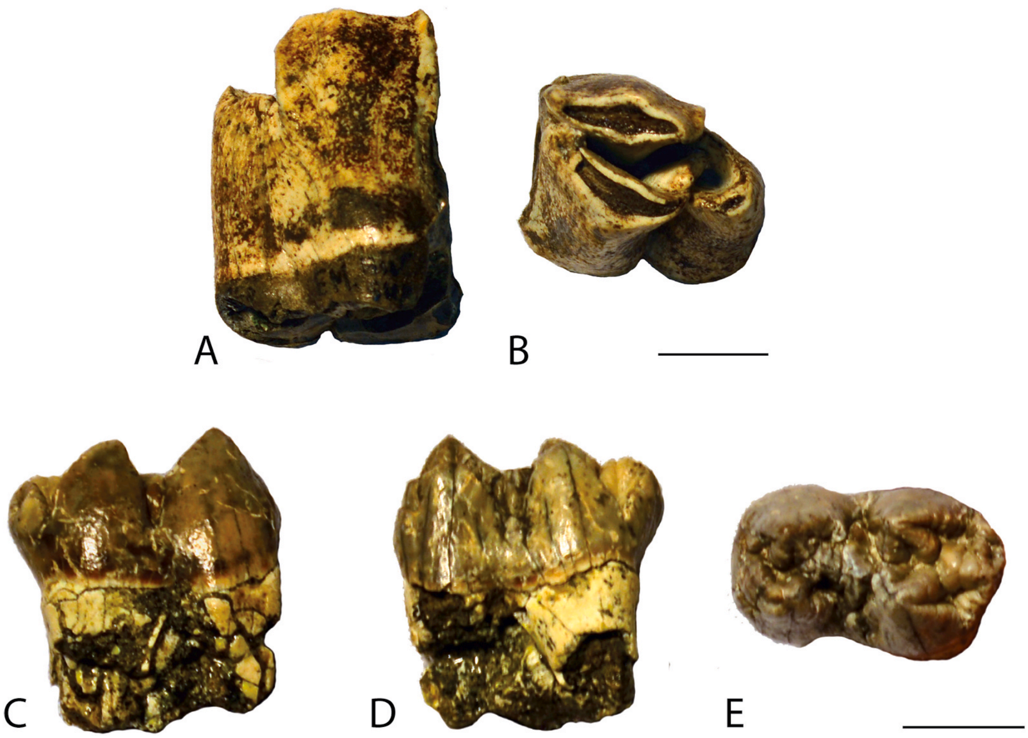

Fig. 4. Top: Photograph of specimen FM.0002, a partial third lower molar and the type specimen of *Mitilanotherium inexspectatum*. A = buccal view, B = occlusal view. Bottom: Photograph of specimen VGr.0879, lower left first molar identified to *Sus strozzi*. C = buccal view, D = lingual view, E = occlusal view. Scale bar = 1 cm.

Samson (1962) who noticed the peculiar robustness and accentuated dorsoplantar compression of this specimen. The distal part of the horn core is strongly compressed dorsoventrally and terminates with a rounded apex. A left complete radius from Fântâna lui Mitilan (FM.0094) is relatively slender and resembles the proportions of modern *Ovibos moschatus* and is less robust than radii of *Leptobos* and *Bison* (*Eobison*).

3.1.2.3. Giraffidae. The type specimen of the giraffid species *Mitilanotherium inexspectatum* is a distal lower M_3 (Fig. 4) described by Samson and Rădulescu (1966) from Fântâna lui Mitilan. Other than the type specimen, there are no giraffid craniodental remains known from the ORV sites. All postcranial specimens are derived from Grăunceanu and they are all podials, metapodials, and phalanges (other than one distal tibia and an os malleolus). Given that the postcranial material morphologically and metrically matches *Mitilanotherium* specimens from other sites, we maintain the attribution of *Mitilanotherium inexspectatum* as originally proposed by Samson and Rădulescu (1966). Specifically, the tibia (VGr.0961), which preserves the distal articular surface and approximately 2/3 of the shaft, is approximately the same size as the *Mitilanotherium* specimen from Dafnero (Kostopoulos and Athanassiou, 2005) and morphologically matches it and the one other distal tibia specimen of this taxon from Sésklo, Greece (Athanassiou, 2014).

3.1.2.4. Suidae. Only a single suid specimen has been identified by our team from the ORV collections, which we tentatively attribute to the site of Grăunceanu due to the absence of markings on the specimen. Previous publications identified *Sus* sp. from Grăunceanu (Bolomey, 1965) or *Sus strozzi* from Fântâna lui Mitilan (Rădulescu and Samson, 1990, 1991) but more recent publications (e.g., Rădulescu et al., 1998, 2003) have not included suid remains in their species lists (Table S1). Specimen VGr.0879 (Fig. 4) is an essentially unworn suid mandibular left M_1 (likely from a juvenile individual) with a small hypoectoconulid and a well-developed pentaconid and hypopreconulid. The two most likely candidate taxa for this specimen, the Plio-Pleistocene Eurasian *Sus* species *S. arvernensis* and *S. strozzi*, are thought to differ primarily in size (Pickford, 2013; Pickford and Obada, 2016; Cherin et al., 2018) with the M_3s, for example, being approximately 30% larger in *S. strozzii* (Cherin et al., 2018). This specimen is longer than any M_1 of either of these species but is closest in length to *S. strozzii* and is substantially longer than *Sus arvernensis* lower M_1s (Pickford and Obada, 2016) (Fig. S1). Compared to *S. strozzi* specimens the ORV specimen is relatively narrow for its length (see Fig. S1). Based on these metrics we assign this specimen to *Sus strozzi*.

3.1.3. Perissodactyla

A large portion of the specimens from the ORV assemblage were assigned to the order Perissodactyla. At Grăunceanu alone, 20% (n = 439) of the specimens identified were assigned to this order, and when the entire Grăunceanu sample is broken down by family, 26.5% (n = 383) of the specimens were identified to the family Equidae and 3.7% (n = 53) to Rhinocerotidae.

3.1.3.1. Equidae. The taxonomy of the equid sample from the ORV sites has changed considerably since the first faunal lists for the ORV sites in the 1960s (Table S1). Initial publications (Necrasov et al., 1961; Bolomey, 1965) placed all of the equid remains into *Equus stenonis*, but subsequent work by Samson (1975) identified multiple species of equid from the ORV, most of which he placed in the genus *Allohippus*, later *Plesippus*. However, current taxonomy for Pleistocene European equids places all species into the genus *Equus* (Bernor et al., 2019; Rook et al., 2019). Importantly, Samson (1975) named the species *Equus* (*Allohippus) athanasiui* on the basis of fossil remains from Grăunceanu, citing similarities to *E. stenonis*, but larger proportions, in this new species. As reviewed by Forstén (1999), it is clear that specimens attributed by Samson to *E. athanasiui* are larger on average than *E. stenonis* but share similar proportions, at least for the metapodials and proximal phalanges.

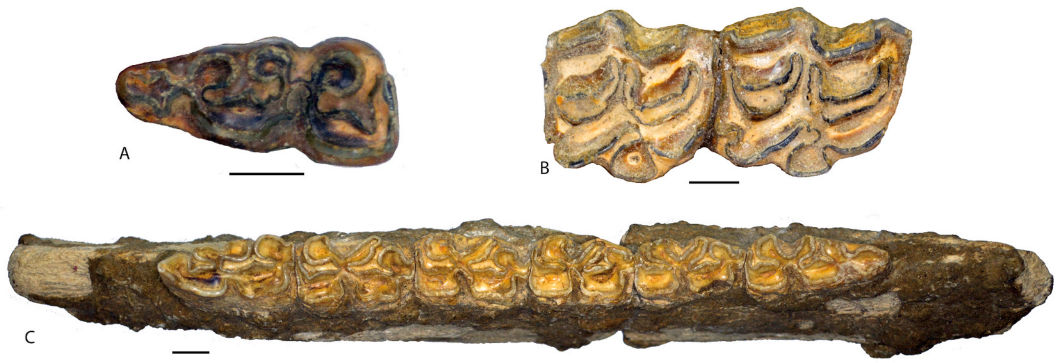

Fig. 5. Photographs of *Equus* sp. (cf. *livenzovensis*) dental remains from Grăunceanu. Top left = VGr.0071, a lower right third molar; top right = VGr.0022, upper first and second molars; bottom = VGr.0023, left mandibular tooth row including the second premolar through the third molar (anterior is to the left of the image). Scale bars for each specimen = 1 cm.

Work by Alberdi et al. (1998) included *E. athanasiui* in *E. livenzovensis,* describing this species as similar to *E. stenonis* but larger.

Our ongoing analyses show that *Equus* remains are found at nearly all sites across the ORV. Craniodental remains of *Equus* from Grăunceanu indicate that these fossils are consistent with stenonid dental morphology, including lower molars with a typical double knot, deep v-shaped lingual groove, and rounded metaconid (Fig. 5; Alberdi et al., 1998; Bernor et al., 2019). The Grăunceanu materials further display pointed metastylids and ectoflexids that do not enter the isthmus on the premolars but do penetrate the isthmus on the molars. The protocone is linked to the protoloph and is short, though in at least one specimen the protocone becomes more elongate and pinched moving posteriorly along the tooth row. Enamel margins on the upper and lower teeth are relatively simple, and the presence of the pli caballin and pli caballid is variable (terminology following Alberdi and Palombo, 2013).

The majority of the equid materials from the ORV are postcranial elements that are not easily identifiable to species. Metric analysis of the intact metacarpals, metatarsals, and proximal phalanges (all from Grăunceanu) indicate that these specimens are on average larger than *E. stenonis* or *E. stehlini*, and have different proportions than *E. altidens* (data from Forstén, 1999; Fig. S2), though there is considerable variation within this sample. The Grăunceanu specimens are most consistent in size with specimens identified by Forstén (1999) as *E. ? athanasiui* (including previous measurements of Grăunceanu materials by Samson, 1975) and with specimens identified to *E. livenzovensis* from the sites of Liventsovka, Russia and Montopoli, Italy (Forstén, 1999; Bernor et al., 2018). Metric comparison to Italian fossils of *E. altidens* and *E. sussenbornensis* (data from Alberdi and Palombo, 2013; Fig. S3) identify a similar pattern. As reviewed recently by several authors (Bernor et al., 2019; Boulbes and van Asperen, 2019) considerable work remains to sort out the taxonomy and biochronology of large and very large stenonid horses from the early and middle Pleistocene of Europe. We therefore identify the ORV equid material as *Equus* sp., though we note size similarities to *E. livenzovensis* for equid materials from Grăunceanu. Further analysis of the equid remains from the ORV is clearly warranted.

3.1.3.2. Rhinocerotidae. The rhinocerotid material from the ORV collections in Bucharest consists mainly of postcranial specimens, with most limb elements represented by at least one specimen. Only a few fragmentary teeth and one partial mandible were assigned to this family. Previous publications have included *Stephanorhinus etruscus* in the faunal assemblage from La Pietriş and *Stephanorhinus* sp. (large species) from Grăunceanu (Rădulescu et al., 2003). Nearly all of the rhinocerotid material that has been identified in the collections in Bucharest is from Grăunceanu, with one specimen from Fântâna lui Militan and two more generally from the ORV (i.e., exact provenience unknown). Two rhinocerotid species are commonly preserved at European Late Pliocene and Early Pleistocene sites, *Stephanorhinus elatus* and *Stephanorhinus etruscus*, with the latter being smaller than the former but similar in proportions (Ballatore, 2016; Ballatore and Breda, 2016, 2019; Pandolfi et al., 2019). While many authors prefer to use the name *Stephanorhinus jeanvireti* for the *S. elatus* material, Ballatore and Breda (2016) provide a detailed argument for the priority of *Stephanorhinus elatus* (although Pandolfi et al. (2019), following Guérin (1972) and Guérin and Tsoukala (2013) contend that *S. elatus* is a *nomen dubium*). For now, we retain the name *S. elatus*.

A fragmented mandible (VGr.2052) from Grăunceanu partially preserves both the left and right corpus, including premolar roots on both sides along with an intact left M_1. The dimensions of the tooth are similar to those of *Stephanorhinus etruscus* specimens from Senèze and the Upper Valdarno (Table S2). The M_1 length is at the lower end of the *S. elatus* range, but at the upper end of that species' range for maximum breadth. The Grăunceanu molar exhibits the large difference in height between the bottoms of the V-shaped valleys on the lingual side of the tooth that is distinctive of *S. etruscus* (Pandolfi and Petronio, 2011; but see Guérin and Tsoukala, 2013). Mandibular depth at P_4/M_1 is in the middle of the range for *S. etruscus* and just below the lower end of the range for *S. elatus* (Table S2). These data suggest that the mandible can likely be attributed to *S. etruscus*.

The large number of postcranial remains of *Stephanorhinus* are harder to attribute to species. Ballatore and Breda (2019) differentiate *S. elatus* and *S. etruscus* from the site of Perrier-Étouaires, France on the basis of a number of qualitative characters of the postcrania. However, in our investigation the remains from the ORV show either a mixture of features of the two taxa or have morphologies and dimensions that are intermediate between those described for *S. etruscus* and *S. elatus* (Table S2). For example, of the four proximal radii from Grăunceanu, three exhibit a lateral ulnar facet that is medio-laterally enlarged like the depiction of *Stephanorhinus etruscus* (Ballatore and Breda, 2019); however, this facet is also inferiorly extended like in *S. elatus*, but not as far as in the lectotype (Ballatore and Breda, 2016). One specimen (VGr.1895) that, unfortunately, has a break on the postero-lateral edge of its lateral ulnar facet, has a narrower and more inferiorly extended facet. It also appears to be unlike *S. etruscus* in the weakly oblique angle of the proximal articular surface palmar edge, although another specimen from Grăunceanu (VGr.1887) combines a weak angle with a medio-laterally expanded lateral ulnar facet, which suggests that there may be more variation in these characters than observed by Ballatore and Breda (2019). The proximal articular surface breadth of the radii from Grăunceanu overlaps with the upper end of the *S. etruscus* range and the lower end of the *S. elatus* range (Table S2). Similar patterns and intermediate dimensions were observed for the second and third metatarsals, tibiae, and calcanei (Table S2). These findings could either suggest that postcranial morphology varies more than previously identified in studies of relatively small samples of the two species (Ballatore and Breda, 2019) such that they are not distinguishable, and/or that observations of rhinocerotid species from France are not applicable to the eastern European representatives of this genus. We assign the rhinocerotid specimens from the ORV and Grăunceanu to *Stephanorhinus* cf. *etruscus* pending further, more detailed analyses.

3.1.4. *Carnivora*

The carnivoran assemblage from the ORV includes at least 11 species from 5 families, nearly all of which are from Grăunceanu. Of the Grăunceanu materials identified to order approximately 9.3% (204) are attributed to Carnivora. Most of the material consists of isolated teeth or postcranial (most often limb) elements, but complete skulls and mandibles as well as partial skeletons are also present. We present a preliminary assessment of these remains here with more detailed analyses to follow (Werdelin et al., in prep).

3.1.4.1. Canidae. The most abundant canid at Grăunceanu, and the most abundant carnivoran overall, is the early raccoon-dog *Nyctereutes megamastoides*. This species is commonly found in Late Pliocene and Early Pleistocene faunas of southern Europe, such as Perrier-Étouaires and Senèze (France), and the Lower Valdarno (Italy) (Lucenti, 2017). At Grăunceanu this species is represented by an abundance of material including skull, mandible, and postcranial material. It shows all the typical features of the genus and species, including the broad molars and the well-developed subangular lobe of the mandible (Lucenti, 2017). Also included in the Grăunceanu material is a fairly well-preserved skull of a vulpine (VGr.2334) attributed to *Vulpes* cf. *alopecoides*. One or two dental elements that are too large to represent either of the species mentioned above attest to the rare presence of *Canis* (likely *C. etruscus*) at Grăunceanu. A nearly complete, though partially crushed, cranium (FA.0019) and a poorly preserved mandible (FA.0003) of *Canis etruscus* are identified from Fântâna Alortitei.

3.1.4.2. Mustelidae. Several well-preserved skulls and mandibles are attributable to the genus *Meles*. The remains are most similar to the Early and Middle Villafranchian *M. thorali*, which is present at sites such as Saint-Vallier, France and Vatera, Greece (Madurell-Malapeira et al., 2011). Pending further study the Grăunceanu remains are here assigned to *M.* cf. *thorali*.

3.1.4.3. Ursidae. A few remains (n = 10) of isolated teeth and postcranial elements (pelvis, femur) are evidence of the presence of an ursid at Grăunceanu, and a single isolated lower third incisor suggests the presence of this taxon at Fântâna Alortitei. This ursid can most likely be identified as *U. etruscus*, which is also known from Betfia, Romania (Terzea, 1996).

3.1.4.4. Hyaenidae. Hyenas are rare in the ORV samples, for reasons that are not entirely clear. The family is primarily represented by coprolites and by a nearly complete, massive skull attributable to *Pachycrocuta brevirostris* (VGr.0878). Unfortunately, the provenience of this specimen is somewhat unclear; markings on the skull suggest that it was recovered in 1961 from the site of Valea Homorecia (i.e., Homorîcea Valley, the location of which is unknown although it would be geographically close to Grăunceanu), while other original packaging of the specimen listed it as being from Grăunceanu. Notably, previous publications list only *Pliocrocuta perrieri* as being present at Grăunceanu (Table S1), though *P. brevirostris* has been listed as present at the sites of La Seci and Fântâna Alortetei (Rădulescu and Samson, 1990, 1991). Additionally, a juvenile mandibular corpus (VGr.2314) and several isolated teeth attest to the presence of hyaenas at Grăunceanu, but further analyses are necessary to determine the exact taxon present.

3.1.4.5. Felidae. The cats are the best represented family of carnivoran at Grăunceanu in terms of diversity, with five species identified, although all five are uncommon in the collections (total felid n = 20). *Homotherium* is represented by a left mandibular corpus fragment with P_4 and M_1 and a right isolated M_1 that may belong to the same individual (specimens VGr.2317 and VGr.2318, respectively). The carnassials show the highly characteristic *Homotherium* morphology, with a dental wear facet that extends from the distal end of the M_1 all the way to the mesial end of the main cusp of P_4. At this time we identify this only to *Homotherium* sp. pending resolution of the species-level taxonomy for this taxon. *Megantereon* is represented by a nearly complete skull (VGr.2378)

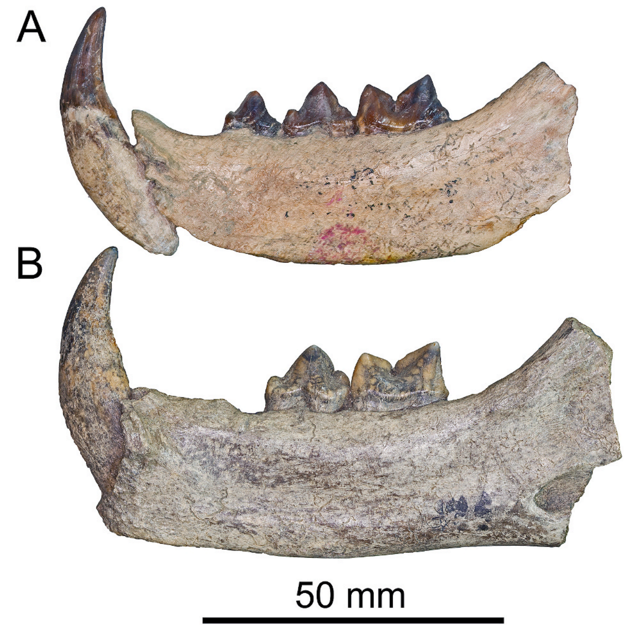

Fig. 6. Two right mandibular corpora of Felidae from Grăunceanu. A = *Lynx issiodorensis* (VGr.2332); B= *Puma pardoides* (VGr.1808). Note the development of an incipient M_1 metaconid/talonid complex characteristic of *Lynx* in (A) that is absent in (B).

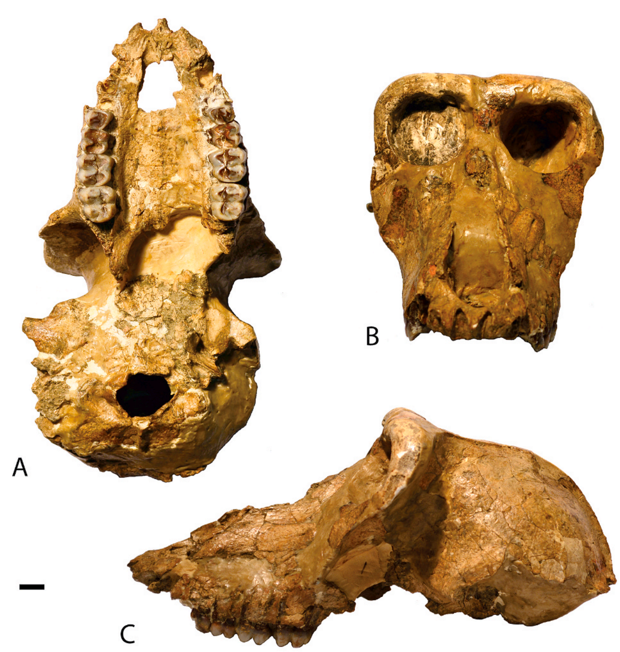

Fig. 7. Photographs of specimen VGr.0345, a male *Paradolichopithecus* cranium recovered from Grăunceanu. A) inferior view, B) anterior view, C) left lateral view. Scale bar = 1 cm.

with complete left dentition and right C-P4, as well as a small number of other craniodental specimens. The skull was identified as *M. megantereon* by Bolomey (1965). The P3 is unreduced relative to P4, indicating that the skull represents *M. cultridens* (typical form) of Sardella (1998). *Puma pardoides* is represented by two partial mandibular corpora, right (VGr.1808; Fig. 6B) and left (VGr.1809), that because of poor fit and different preservation are unlikely to be from the same individual. These specimens are a close match in morphology and metrics to that from Untermassfeld, Germany illustrated by Hemmer (2001, Pl.141:1–3). They are larger than *Lynx issiodorensis* and smaller than *Panthera gombaszoegensis* (not represented at Grăunceanu). This is the first record of *Puma pardoides* from Romania. *Lynx issiodorensis* is represented by a well preserved right mandibular corpus lacking ramus but with complete dentition. This specimen (VGr.2332; Fig. 6A) is clearly smaller than those of *P. pardoides* and has the characteristic bulging distal M_1 (incipient talonid), thus representing a typical *L. issiodorensis* very similar to those of Perrier-Étouaires and Saint-Vallier, France (Werdelin, 1981). The fifth felid species is represented by a P_3, VGr.2304, tentatively referred to cf. *Acinonyx pardinensis*.

3.1.5. Primates

Perhaps the best studied taxon from the ORV (Grăunceanu) is the large-bodied terrestrial papionin of the genus *Paradolichopithecus*. This species is represented by at least 16 specimens including several partial crania (e.g., Fig. 7) and multiple postcranial bones (several of which refit and/or likely belong to the same individual). The genus *Paradolichopithecus* has been recovered from France, Spain, Greece, Romania, Serbia, and perhaps as far east as Tajikistan and China (Deperet, 1929; Necrasov et al., 1961; Delson, 1971; Trofimov, 1977; Aguirre and Soto, 1978; Sondaar and Van Der Geer, 2002; Qiu et al., 2004; Delson et al., 2014; Radović et al., 2019). The first specimens attributed to *Paradolichopithecus* (initially attributed to a colobine species, *Dolichopithecus arvernensis*, Deperet, 1928) were recovered from Senèze, France. Specimens recovered from Grăunceanu, originally assigned to the species *Paradolichopithecus geticus* (Necrasov et al., 1961), were also first thought to be colobine. Subsequent work by Delson (Delson, 1973; Delson and Nicolăescu-Plopşor, 1975) attributed these taxa to a single cercopithecine species, *Paradolichopithecus arvernensis*, with *P. geticus* commonly considered a subspecies. A detailed description and comparative study of *Paradolichopithecus* remains from Europe is forthcoming (Delson et al., in prep).

3.1.6. Small mammals

Only a handful of small mammal remains from the ORV have been reidentified by our research team. Though previous faunal lists indicate the recovery of rabbit (*Hypolagus brachygnathus*) and shrew (*Beremendia* cf. *fissidens*) from the site of La Pietriş, materials from these taxa have not been reidentified in the existing collections housed in Bucharest.

Remains from several rodent species are present at both Grăunceanu and Fântâna lui Mitilan, including one porcupine, *Hystrix refossa*, and two beaver species, *Trogontherium* sp. and *Castor fiber* cf. *plicidens*. These species are represented by only a handful of fossils, all of which are craniodental remains (Table 2; 3D models available via Morphosource.org). Measurements and occlusal patterns of the single *Hystrix* mandibular fragment and cheek teeth fit comfortably in the ranges presented for *Hystrix refossa* in van Weers (1994) and Rook and Sardella (2005). Similarly, the single *Castor* mandible fragment (recovered from the site of Fântâna lui Mitilan) with intact incisor and three postcanine teeth compares favorably to those described in Barisone et al. (2006) and exhibits complex secondary enamel folds on the premolar and molar occlusal surfaces that are characteristic of *C. fiber plicidens* (Fig. 8). This specimen is slightly smaller, however, than those reported from the site of Pietrafitta, Italy (Farneta Faunal Unit), perhaps representing geographic or temporal variation (Barisone et al., 2006). Finally, four specimens from both Fântâna lui Mitilan and Grăunceanu (a nearly complete cranium that is heavily encrusted with matrix, one nearly complete mandible, one mandible fragment including cheek teeth, and one isolated lower molar) are identified to the genus *Trogontherium*. Occlusal patterns and in particular the relative enlargement of the P4 and "cone-shaped" upper third molars (Mayhew, 1978:426) are

Fig. 8. Rodent specimens from the ORV sites. A) *Trogontherium* sp. mandible (VGr.2365); B) *Trogontherium* sp. maxillary tooth row (FM.0155); C) *Hystrix refossa* mandibular toothrow (VGr.2381); D) *Castor fiber* cf. *plicidens* partial mandible (FM.0001). Scale bar = 1 cm.

Table 2
Dental measurements for rodent specimens from the ORV assemblage. All measurements are in millimeters (mm).

Specimen	Taxonomic attribution	Description	Incisor width	P4 length	P4 width	M1 length	M1 width	M2 length	M2 width	M3 length	M3 width
FM.0001	*Castor fiber* cf. *plicidens*	Right mandible fragment including part of incisor and p4-m2	9.26	10.65	7.68	7.96	8.29	6.59	7.91	–	–
VGr.2381	*Hystrix refossa*	Right mandible fragment including p4-m2	7.09	10.52	8.35	9.57	8.13	9.97	8.55	–	–
FM.0155	*Trogontherium* sp.	Nearly complete cranium heavily encrusted with matrix	–	11.88	11.5	8.24	11	8.2	9.07	10.63	8.12
VGr.2363	*Trogontherium* sp.	Isolated right lower molar	–	–	–	6.9	6.8	–	–	–	–
VGr.2364	*Trogontherium* sp.	Right mandible fragment including all postcanine teeth and part of incisor	6.86	7.74	6.86	6.54	6.33	6.4	6.41	5.89	5.77
VGr.2365	*Trogontherium* sp.	Nearly intact mandible including left and right tooth rows; missing most of gonial angle and ascending ramus on both sides. (measurements are for right side)	6.94	9.41	7.85	7.74	6.57	7.25	7.44	7.46	6.35

diagnostic of this genus. We make no attempt to assign representatives of this genus to the species level, given the considerable debate regarding the taxonomy of *Trogontherium* (e.g., Mayhew, 1978; Fostowicz-Frelik, 2008; Stefen, 2011), though measurements of the skull and dimensions of the upper P^4 are consistent with *T. cuvieri* as described by Fostowicz-Frelik (2008), and measurements of the mandibular P_4 and M_1 are considerably larger than those reported for *T. minutum* by Giersch et al. (2010) and Apoltsev and Rekovets (2015).

3.1.7. Pholidota

One notable inclusion in prior faunal lists for Grăunceanu is *Manis* cf. *hungarica*, a species of pangolin that was interpreted to suggest a relatively warm environment in the ORV during the Early Pleistocene (Rădulescu and Samson, 1990). Previous publications on the ORV fauna do not describe the materials attributed to *Manis* cf. *hungarica*, and thus it is unclear on what basis this taxon was identified and how many specimens of this species may be present. That this species was named originally by Kormos (1934) on the basis of a single distal phalanx from the site of Villány, Hungary, causing some to suggest that this species is taxonomically invalid (Koenigswald, 1999; Gaudin et al., 2009), presents an additional challenge. During our reinventory and analysis of the ORV materials housed at ISER we identified a single pangolin specimen, a nearly completely intact right humerus. This specimen, measuring approximately 104.2 mm in length, shows a mixture of metric and non-metric traits that more closely align it with the genus *Smutsia* than with *Manis*, and that suggest a morphology and size intermediate between the two living species of *Smutsia* (i.e., the giant pangolin, *S. gigantea*, and the ground pangolin, *S. temminckii*). Further, additional characters differ from both extant *Smutsia* species. We thus place this specimen preliminarily into the taxon *Smutsia* sp. nov. with additional descriptions forthcoming (Gaudin et al., in prep).

3.1.8. Non-mammals

A handful of non-mammalian specimens have been identified from the ORV assemblage, including two turtle and four avian specimens. The turtle remains (represented by multiple shell fragments) were recovered from the site of Fântâna lui Mitilan. Previous researchers working with the collections identified these remains as belonging to *Geoemyda* cf. *mossoczyi*, though this genus of freshwater turtles has now been subdivided into several genera (Danilov et al., 2012). Here we identify these remains as only Geoemydidae indet.

The four avian specimens all originate from Grăunceanu and include one unidentified carpometacarpus (VGr.2368) that measures at least 100 mm in length (the proximal end of the bone is missing) (Fig. 9). The remaining three specimens are all identified by our research team as ostrich; these include two proximal phalanges (both rights; VGr.2366 and VGr.2367) that are clearly attributable to this taxon and another heavily gnawed and eroded specimen (VGr.2148) that is identified as the distal end of an ostrich tibiotarsus (Fig. 9; 3D models available via Morphosource.org). Though ostrich is not included in previous species lists for the ORV sites (Table S1), Rădulescu and Samson (2001: 289) do say (presumably in regard to the ORV fauna) “the occurrence of a large-

Fig. 9. Avian remains from the ORV sites. A) Specimen VGr.2368, an unidentified carpometacarpus. B and C) Specimen VGr.2148, a distal tibiotarsus fragment attributed to *Pachystruthio pannonicus* (shown in anterior and posterior views, respectively). Bottom: specimen VGr.2367, a right third proximal pedal phalanx attributed to *Pachystruthio pannonicus* shown in anterior (D), lateral (E), and posterior (F) views. All scale bars = 1 cm.

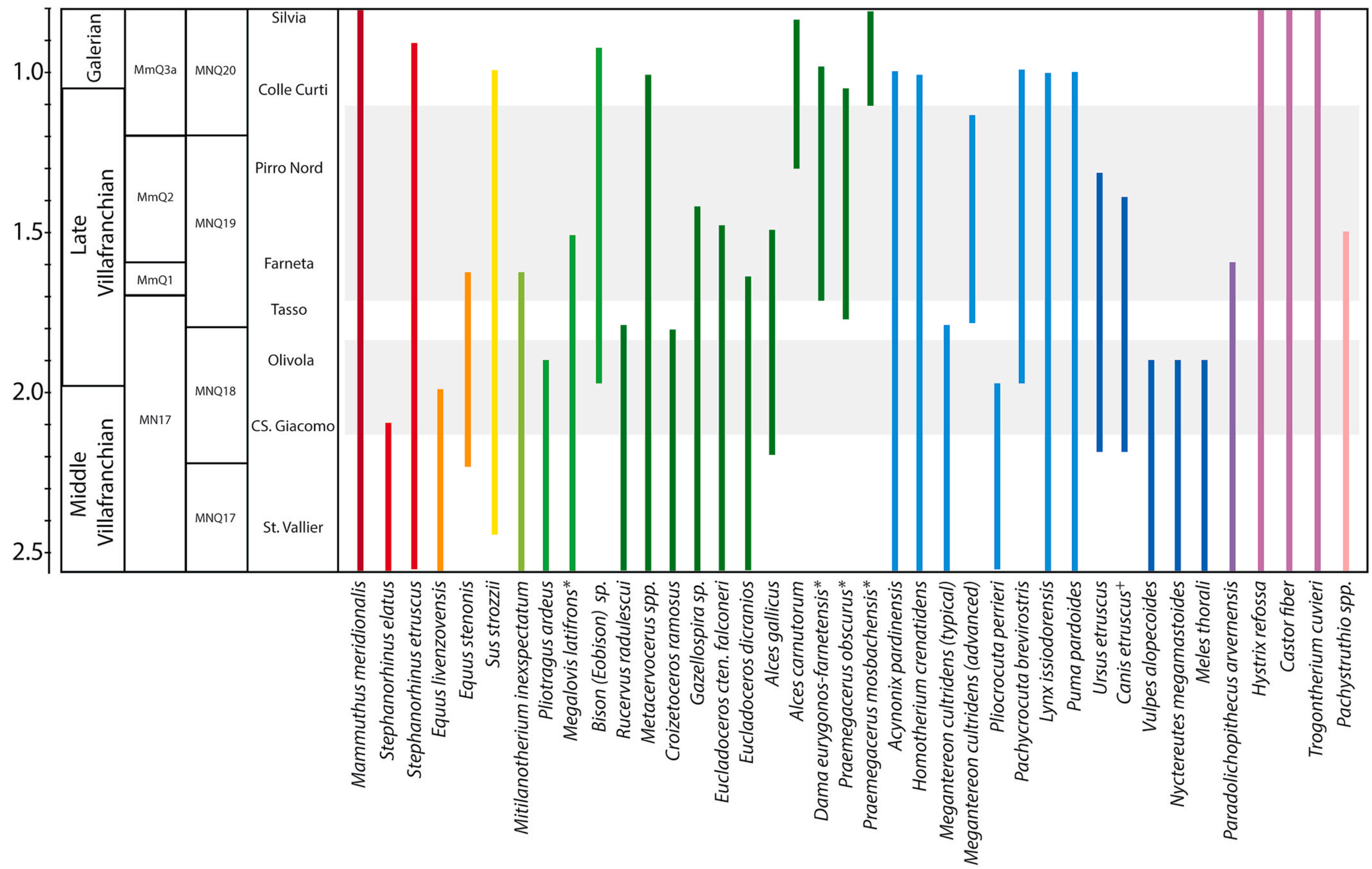

Fig. 10. Chronology chart showing the temporal ranges of relevant taxa from the Olteţ River Valley assemblage. Gray boxes represent estimated temporal ranges for Grăunceanu (lower box) and Fântâna lui Mitilan (upper box), as discussed in the text.

sized ostrich (*Pachystruthio* sp.), probably of African origin, is also characteristic of this fauna." Thus it is unclear if this taxon has previously been identified from the ORV sites or if this is a new addition. Regardless, the specimens from Grăunceanu are most appropriately attributed to *Pachystruthio* cf. *pannonicus* based on their overall dimensions and similarity to measurements published by Kretzoi (1954) and reviewed by Boev and Spassov (2009) (Fig. S4). As discussed by Zelenkov et al. (2019), it is possible that *Pachystruthio* materials from the site of Dmanisi are also from this species, though at present these materials are assigned to *P. dmanisensis*. Since the Dmanisi remains are represented by different skeletal elements than those of *P. pannonicus*, direct comparison is not presently possible.

3.2. Biochronology and paleobiogeography

One primary goal of our reanalysis of the ORV fossil assemblage is to generate updated estimates of the age of the ORV localities. To that end, here we review the biochronology and paleobiogeography of the taxa listed above. Approximate first and last appearance (FAD/LAD) dates for each of these taxa (or other closely related species) are provided in Fig. 10.

3.2.1. Proboscidea

Mammuthus meriodionalis as a species is well represented from the Pliocene and Pleistocene of Europe and is one of the most widespread and longest lived (~2.6–1 Ma) species of *Mammuthus* (Palombo and Ferretti, 2005). However, considerable chronological variation exists in this lineage, with archaic forms perhaps represented by *M. rumanus* (identified on the basis of remains from the Dacian Basin of Romania [Rădulescu and Samson, 1995, 2001]) and/or *M. gromovi* (from the Khapry Faunal Complex of Russia [Alexeeva and Garutt, 1965]) (Lister et al., 2005).

3.2.2. Artiodactyla

E. ctenoides falconeri is a specialized form of *Eucladoceros* from the Saint-Vallier and Senèze type faunas of western Europe. The occurrence of *E. ctenoides falconeri* in southern Romania is interesting paleobiogeographically, because it implies a direct biogeographic connection of the area under study with western Europe and its relative isolation from the Italian Peninsula. *Eucladoceros dicranios* is a more advanced form that evolved in the more continental conditions of eastern Europe, appearing first in the fauna of Khapry (as *E. dicranios tanaitensis* Baigusheva and Titov, 2013), and then in the Late Villafranchian of Italy, France, and England, where this species is scarce and younger. The Early Pleistocene site of Leu (Oltenia, Romania), which yielded an antler fragment ascribed by Croitor and Popescu (2011) to *E. dicranios*, is correlated with the Olivola Faunal Unit and Senèze fauna (Popescu, 2004). The remains of *Rucervus radulescui* from Khapry indicate a rather early appearance of this cervid roughly coeval with the Saint-Vallier stage (MNQ17) and then later (MNQ18) in the Balkans at the site of Gerakarou, Greece. No similar cervid forms are found in the Late Villafranchian of western Europe, though *R. ardei* from Perrier-Étouaires (Early Villafranchian) is fairly close and most probably is a direct ancestor of *R. radulescui*. The latter species thus is a Pliocene survivor with a restricted area of distribution in southeastern Europe, but which disappeared before the end-Villafranchian event, since it is not known from younger Late Villafranchian faunas (Croitor, 2018a).

The finding of *Croizetoceros ramosus* from Grăunceanu is of interest since this species is not common in the paleontological record of the Balkan-Carpathian Area. Remains of *C. ramosus* are abundant in the Early and Middle Villafranchian of western Europe, become rare in the Late Villafranchian, and are unknown in the Villafranchian faunas younger than Senèze (Heintz, 1970). The richest Late Villafranchian sample of *Croizetoceros* comes from the fauna of Gerakarou dated to MNQ18 (Koufos and Kostopoulos, 1997) where they are particularly small in body size and identified to the subspecies *C. ramosus gerakarensis* (Kostopoulos and Athanassiou, 2005). *Croizetoceros* from Grăunceanu is not identical with *C. ramosus gerakarensis,* and its systematic and biogeographic affinities remain unclear.

Praemegaceros obscurus from Fântâna lui Mitilan is a South Asian large-sized ruminant that dispersed into the European subcontinent during the Early Pleistocene (Croitor, 2006b, 2018b). The oldest remains of *P. obscurus* are known from Dmanisi, Georgia (Vekua et al., 2010) and Izvoru-1, southern Romania (Rădulescu and Samson, 1986). *Praemegaceros* cf. *mosbachensis* is an advanced form of *P. obscurus* that does not belong to the core faunal assemblage from Fântâna lui Mitilan and instead likely comes from younger levels. A similar cervid is found at the sites of Chițcani (Moldova) and Alexandria (Romania). The Chițcani site is an outcrop of the VII-th terrace of the Dniester River, characterized by the Jaramillo paleomagnetic event (0.98–1.07 Ma) in the upper alluvium (Chepalyga et al., 2012). *Dama* cf. *eurygonos*, also from Fântâna lui Mitilan, is a peculiar faunal element of the Mediterranean Villafranchian. The primitive fallow deer *Dama eurygonos* becomes an important Villafranchian faunal element starting from the Tasso Faunal Unit from Upper Valdarno in Italy (Rook et al., 2013) and becoming more abundant in the Farneta Faunal Unit (Gliozzi et al., 1997).

Pliotragus ardeus is an old species that had its first appearance in the Early Villafranchian of Perrier-Étouaires, France (Depéret, 1884). The geographic distribution of *Pliotragus* during MN17 was vast, ranging from Spain to Bulgaria and Romania (Crégut-Bonnoure and Guerin, 1996; Spassov, 2005), and possibly Turkey (Kostopoulos and Sen, 1999). *Pliotragus* survived until the Middle Pleistocene of Petralona where it is represented by *Pliotragus macedonicus* (Crégut-Bonnoure and Tsoukala, 2005). *Gazellospira* is another successful Eurasian bovid genus with a vast Late Villafranchian distribution from western Europe to the Near East and Tajikistan (Hooijer, 1958; Duvernois and Guérin, 1989; Athanassiou, 2005). The genus includes two lightly built spiral-horned species: *G. torticornis* from western Eurasia and *G. gromovae* from central Asia and the Khapry fauna (Titov, 2008). The earliest record of *Bison* (*Eobison*) in western Eurasia comes from Dmanisi (Georgia), ca 1.8 Ma (Bukhsianidze, 2005). According to Kostopoulos et al. (2018), the early bison form similar to *Bison degiulii* from Pirro Nord (Italy) dispersed into the southern Balkans and Italian Peninsula between 1.7 and 1.5 Ma. It is noteworthy that the rich fossil material from Grăunceanu does not contain remains of *Leptobos etruscus*, which is present in the fauna of Leu (Croitor and Popescu, 2011). The coexistence of *Leptobos* and *Bison* was reported from Tsiotra Vryssi (ca. 1.8–1.5 Ma), Greece (Kostopoulos et al., 2018) and the lower faunal level of Trlica (MN18), Montenegro (Vislobokova and Agadjanyan, 2016).

The bovid species *Megalovis latifrons* is a characteristic Late Villafranchian faunal element with an earliest occurrence in Europe at Varshets, Bulgaria (Spassov and Crégut-Bonnoure, 1999). *Megalovis* is an ovibovine genus of Asian origin that is also present in the Early and Middle Pleistocene of China (Louys et al., 2007). It seems that the dispersal of *Megalovis latifrons* westwards is a part of a larger dispersal event of ovibovines into western Eurasia and Africa (Gentry, 1970). A species closely related to *M. latifrons, Makapania broomi,* was found below tuff G at Omo, Ethiopia (2.6–1.8 Ma) and in the Makapansgat Limeworks Quarry, South Africa (Gentry, 1970), thus suggesting an exceptional case of dispersal of the *Makapania-Megalovis* lineage over a vast Euro-African area.

The giraffid genus *Mitilanotherium* is known primarily known from western Asia and eastern Europe in the Pleistocene (e.g., Sharapov, 1974; Rădulescu et al., 1998; de Vos et al., 2002; Rădulescu et al., 2003; Kostopoulos and Athanassiou, 2005; Lyras and van der Geer, 2007; Kahlke et al., 2011), although there are specimens attributed to this genus from Spain as well (Arribas et al., 2001; Arribas et al., 2009; van der Made and Morales, 2011). The earliest site from which *Mitilanotherium* has been recovered is Gülyazi, Turkey dated to approximately 2.5 Ma, while its current last appearance is 1.6 Ma at Libakos, Greece (Kostopoulos and Athanassiou, 2005; Kahlke et al., 2011).

Sus strozzii is thought to be the larger descendant of *Sus arvernensis* and is known from the later portions of the Villafranchian (Azzaroli, 1975; Pickford and Obada, 2016; Cherin et al., 2018), extending temporally from MN17 to MNQ19 and geographically from Spain to the Azov Sea area of Russia (Cherin et al., 2018) and into the Middle East at 'Ubeidiya (Pickford and Obada, 2016; van der Made et al., 2017). The earliest specimen tentatively attributed to *Sus strozzi* is currently known from Saint-Vallier, France at approximately 2.4 Ma and the most recent specimen attributed to this species is from the Arda River (Italy), which is dated to approximately 0.99 Ma (Bona and Sala, 2016; Cherin et al., 2018).

3.2.3. Perissodactyla

Typical monodactyl stenonid horses appear in the European fossil record at the end of the Pliocene/beginning of the Middle Villafranchian, where they ultimately replace the preceding hipparionine equids (Azzaroli, 1983). The earliest stenonid horse and the species believed by some authors to be ancestral to all other European stenonid species (Azzaroli, 2003; Alberdi and Palombo, 2013; Rook et al., 2019; Boulbes and van Asperen, 2019), is *E. livenzovensis*, which first appears at the site of Montopoli, Italy approximately 2.6 Ma (Bernor et al., 2018). This species ranges across Europe and is also identified from Khapry, near the Azov Sea (Gromova, 1949), and Liventsovka near Rostov-on-Don, Russia (Baigusheva, 1971, 1978). However, there is considerable debate regarding the taxonomy of European stenonid horses, and particularly regarding the taxonomy and biogeography of *E. livenzovensis* (e.g., Boulbes and van Asperen, 2019). Appearing slightly later in time, *E. stenonis* is better understood in terms of its morphology and biogeography. The earliest record of this species comes from the site of Saint-Vallier, France in the Middle Villafranchian (Eisenmann, 2004), with a last well-established appearance in the Tasso Faunal Unit (Alberdi and Palombo, 2013; Bernor et al., 2019), though some authors suggest this *E. stenonis* sensu lato extends to 1.2 Ma at Ceyssaguet, France (Boulbes and van Asperen, 2019).

The two most likely rhinocerotid species present in the ORV, *Stephanorhinus elatus* and *Stephanorhinus etruscus,* overlap temporally and geographically, with both taxa being present throughout much of Europe from the Late Pliocene to the Early Pleistocene. However, *S. etruscus* is much more common, especially during the Early Pleistocene (Guérin and Tsoukala, 2013; Pandolfi et al., 2017, 2019; Ballatore and Breda, 2019). *Stephanorhinus elatus* is currently known from strata dating to between the latter half of MN15 (approximately 3.6 Ma) at Musselievo, Bulgaria (although there is some question as to whether the material there can be attributed to that taxon) and the final part of MNQ17 or the first half of MNQ18 at Coltesti, Romania, with the species being most common during MN16 (Guérin and Tsoukala, 2013; Pandolfi et al., 2019). The earliest known appearance of *S. etruscus* is at Las Higueruelas, in Spain, which is dated to about 3.3 Ma (Mazo, 1995), while its latest appearance is currently cited as Gran Dolina TD4, 6, and 8, dated to about 800 ka (Pandolfi and Petronio, 2011; Pandolfi et al., 2017).

3.2.4. Carnivora

The most important carnivoran found in the ORV assemblage, biostratigraphically speaking, is *Pachycrocuta brevirostris*. The specimen, a sub-complete cranium, can be unequivocally assigned to this species. The taxon defines what has been called the "*Pachycrocuta*-event" (Rook and Martínez-Navarro, 2010), marking the beginning of the Olivola Faunal Unit of the Italian sequence, the base of which is suggested to be roughly 1.9 Ma or slightly older (Nomade et al., 2014; van der Made, 2018). If this species is indeed found at Grăunceanu, this would certainly make this assemblage no older than 2 Ma. Several of the carnivoran species also have last appearance datums around this time. Of these, *Nyctereutes megamastoides* is the best known, being recorded from numerous localities in Europe, as noted above. All of these are from sites close to the boundary between MNQ17 and MNQ18.

3.2.5. Primates

Paradolichopithecus was a wide-ranging taxon found throughout much of Europe and Asia in the Plio-Pleistocene and spanning much of the Villafranchian (Necrasov et al., 1961; Trofimov, 1977; Aguirre and Soto, 1978; Sondaar and Van Der Geer, 2002; Qiu et al., 2004; Delson et al., 2014; Radović et al., 2019). In Europe, fossils from this genus (as *P. arvernensis*) have been recovered from localities in Spain, France, Romania, and Greece, appearing first at approximately 3.2 Ma (Eronen and Rook, 2004; Kostopoulos et al., 2018). In Asia, *Paradolichopithecus* may range east to Tajikistan (*P. sushkini*) and likely to China (*P. gansuensis*); some authors have also suggested that the Asian Plio-Pleistocene primate taxon *Procynocephalus* is synonymous with *Paradolichopithecus* (Kostopoulos et al., 2018). *Paradolichopithecus/Procynocephalus* is typically identified as originating in Europe and dispersing eastward throughout the Plio-Pleistocene (Necrasov et al., 1961; Delson and Nicolăescu-Plopşor, 1975; Eronen and Rook, 2004; Takai et al., 2008; Nishimura et al., 2010), with a suggested disappearance from European faunas by perhaps 1.6 Ma (Kostopoulos et al., 2018). Thus, *Paradolichopithecus* may not extend into the latter half of the Late Villafranchian, and the disappearance of this genus has been linked to the onset of colder climates during this time period (Delson and Nicolăescu-Plopşor, 1975; Eronen and Rook, 2004).

3.2.6. Other mammals and non-mammals

None of the pangolin, rodent, avian, or turtle remains from the ORV are particularly informative from a biochronological standpoint. Both *Hystrix* and *Castor* appear early in the European fossil record, likely in the Late Miocene (Rook and Sardella, 2005; Rekovets et al., 2009) and are still present throughout Europe today. *Hystrix refossa* appears first in the Early Villafranchian (MN16a) at the site of Grevena, Greece and extends into the Late Pleistocene; this species is found at sites throughout Europe, Asia, and Africa (Lazaridis et al., 2019). Similarly, *C. fiber* likely appeared in the late Early Villafranchian and is present at the site of Saint-Vallier, France (Hugueney, 2004); however, debate exists regarding the systematics of European Pleistocene *Castor* (Barisone et al., 2006), with some authors identifying two species, *C. fiber* and *C. plicidens*, while others preferring to identify *C. plicidens* as a subspecies of *C. fiber*. Barisone et al. (2006) suggest that *C. fiber plicidens* is likely a subspecies largely endemic to the Italian peninsula. In contrast to *Castor* and *Hystrix*, the genus *Trogontherium* has no living representatives. However, this genus also was long-lived, with the best-known species, *T. cuvieri*, extending throughout Plio-Pleistocene Europe (Mayhew, 1978; Fostowicz-Frelik, 2008). Some authors suggest that *T. cuvieri*, as well as a smaller form, *T. minus* that was found in the Pliocene and earliest Pleistocene of Europe, represent a monophyletic lineage (Mayhew, 1978).

Though not previously identified as being present at any of the ORV sites, ostrich remains (i.e., *Struthio/Pachystruthio*) have been recovered from a number of Miocene, Pliocene, and Pleistocene sites across Eastern Europe (e.g., Kretzoi, 1954; Boev and Spassov, 2009; Zelenkov et al., 2019). Notably, *Struthio (Pachystruthio) pannonicus* was named by Kretzoi (1954) from several phalanges recovered from the site of Kislang, Hungary (~2.0–1.6 Ma). Other Pleistocene ostrich remains have been identified from the sites of Dmanisi, Georgia (~1.85 Ma) (Burchak-Abramovich and Vekua, 1990; Vekua, 2013), Taurida, Crimea (1.8–1.5 Ma) (Zelenkov et al., 2019), Liventsovka, Russia (2.1–1.97 Ma) (Kurochkin and Lungu, 1970; Baigusheva, 1971), and Sésklo, Greece (MNQ17) (Athanassiou, 2018). A recent review by Zelenkov et al. (2019) places materials from the former two of these localities into the taxon *Pachystruthio dmanisensis*. The specimens from Liventsovka (and by comparison the specimen from Sésklo which Athanassiou [2018] compares favorably to those from the Odessa Catacombs) are identified only as *Struthio* sp. on the basis of relatively smaller body sizes than *Pachystruthio* (Zelenkov et al., 2019). Thus, large ostrich species such *Pachystruthio* and *Struthio* may have had distributions throughout eastern Europe in the Late Pliocene and Early Pleistocene. However, no ostrich remains have been recovered from Plio-Pleistocene sites in western Europe.

4. Discussion

The large size and wide taxonomic diversity of the assemblage makes the ORV collection particularly valuable for evaluating hypotheses regarding paleoenvironmental reconstructions and biogeography in the Early Pleistocene, either just preceding or coincident with the earliest dispersal(s) of hominins out of Africa and into Eurasia (e.g., Ferring et al., 2011; Toro-Moyano et al., 2013). In particular, the large fossil assemblage from Grăunceanu has considerable significance, as it is one of only a handful of fossil localities from eastern Europe during this time frame. As a result, reevaluation and analysis of the ORV fauna, as we present here, is especially critical.

4.1. Taxonomy of the ORV vertebrates

Our reassessment of the ORV fossils reveals a number of important differences from faunal lists previously published for the ORV sites, and

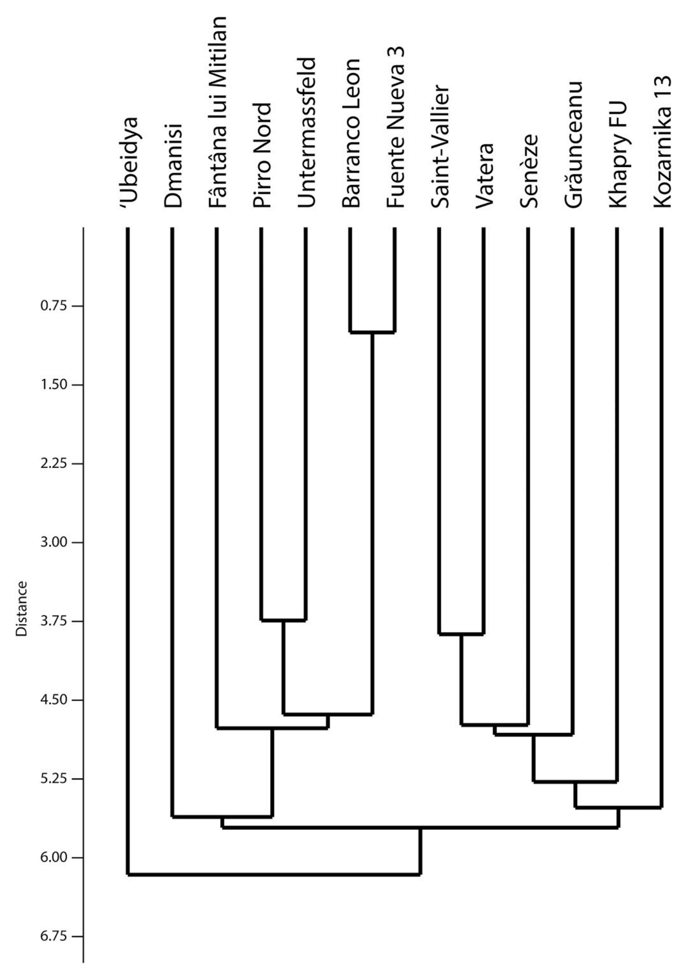

Fig. 11. Results of the cluster analysis comparing fauna (excluding Rodentia, Lagomorpha, and Pholidota) at major European and Western Asian localities from the Middle and Late Villafranchian. Analysis was conducted in the program PAST using the unweighted pair-group method with arithmetic mean (UPGMA). Data for this analysis can be found in Table S3.

Grăunceanu in particular. Some differences represent changes to taxonomic nomenclature (e.g., *Archidiskodon* vs. *Mammuthus*). Others allow us to verify the presence of a particular taxon that had been previously reported (e.g., *Pliotragus ardeus*, *Mitilanotherium inexspectatum*). Still other taxa represent entirely new additions to the species list for the ORV sites (e.g., *Acinonyx* cf. *pardinensis*, *Puma pardoides*, *Alces* sp., *Pachystruthio* cf. *pannonicus*), whereas we were unable to verify the presence of certain taxa (e.g., *Beremendia* cf. *fissidens*, *Hypolagus brachygnathus*). In some cases, our updated species list enables us to expand the known geographic range of fossil taxa; for example, this is the first identification of *Puma pardoides* from Romania. Finally, the reidentification of the pangolin from Grăunceanu and assignment of this specimen to a new taxon may represent the only solidly identified pangolin remains from the Pleistocene of Europe.

As might be expected given its geographic location, the faunal assemblage from Grăunceanu shows clear biogeographic connections with the faunas of the Late and Middle Villafranchian of western Europe (e.g., *Eucladoceros ctenoides falconeri*, *Gazellospira torticornis*) as well as contemporaneous faunas in eastern Europe/western Asia (e.g., *Bison*, *Pachystruthio*, *Mitilanotherium inexspectatum*, *Eucladoceros dicranios*, *Rucervus radulescui*). Cluster analysis (Fig. 11) suggests that the Grăunceanu assemblage is most similar to those of Saint-Vallier, Senèze, and Vatera, while also sharing some affinities with Khapry and Kozarnika, Bulgaria. Fântâna lui Mitilan is clearly differentiated from Grăunceanu and clusters more closely with later fossil sites, primarily from western Europe (with the exception of Dmanisi). These results suggest both biogeographic and biochronological differences between sites in the ORV assemblage that warrant further investigation and discussion.

4.2. Biochronology of the ORV localities

One major objective of this work was to obtain updated biochronological estimates for the ORV localities. For the most part, our estimates, described below, roughly align with those generated previously suggesting that Grăunceanu is most appropriately attributed to MN17/MmQ1, and that La Pietriş and Grăunceanu are similar in age, whereas Fântâna lui Mitilan is younger (Rădulescu and Samson, 1990). Rădulescu and Samson (1990) identify three faunal horizons (T-1, T-2, and T-3) in the Tetoiu region, the general geology of which they describe as a fluvio-lacustrine sequence of over 100 m. Their horizon T-1 (Lower Faunal Horizon) is a silty/sand layer with some gravel and pebbles and is represented principally by the sites of Grăunceanu and La Pietriş, as well as Valea Roşcăi and Dealul Mijlociu. The Middle Faunal Horizon (T-2) is predominantly a sand layer with gravel and pebble lenses as well as thin clay intercalations; this horizon includes the sites of Fântâna lui Mitilan,

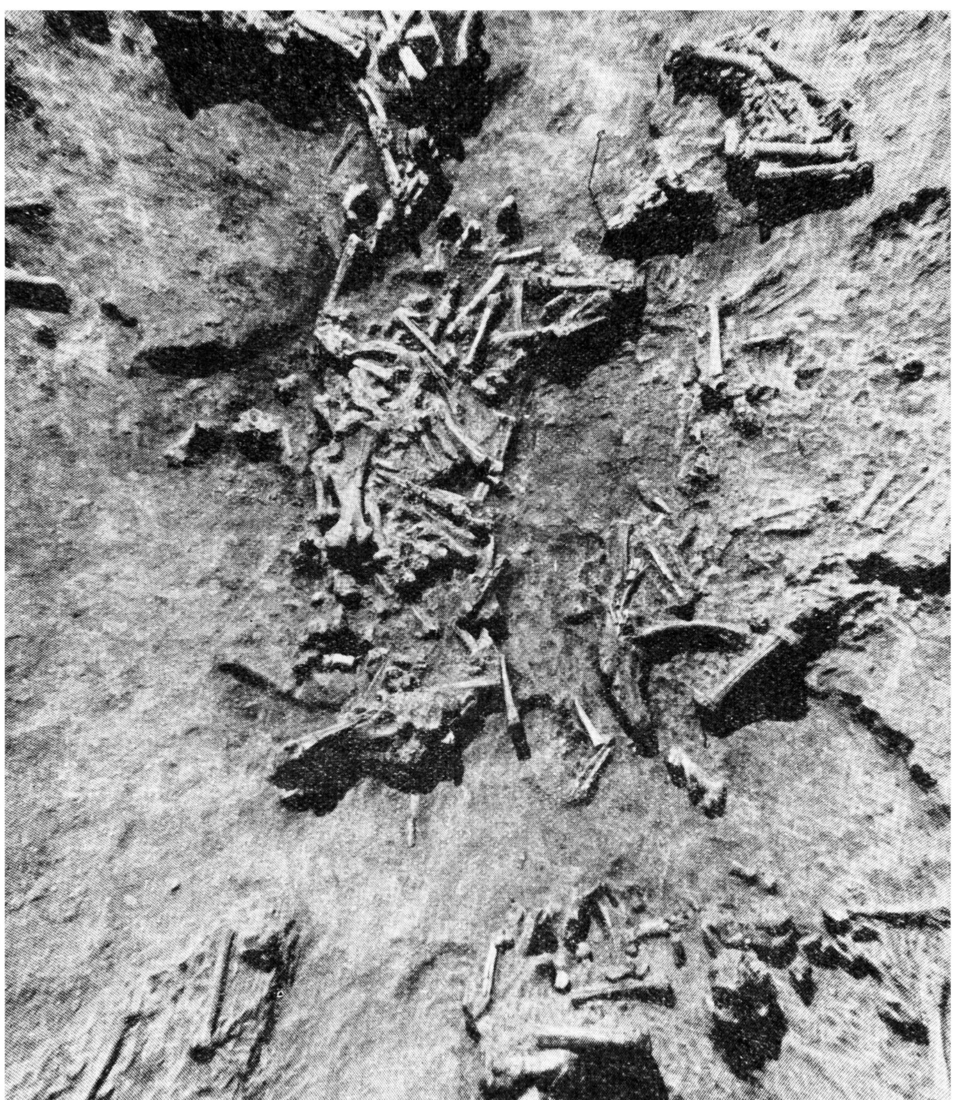

Fig. 12. Photograph of the fossil beds from Grăunceanu as depicted by Bolomey (1965).

Fântâna Alortitei, La Seci, and Valea Mijlociei. Finally, T-3, their Upper Faunal Horizon, is predominantly coarse sands and gravels; considerably fewer (and smaller) fossil localities are represented in this horizon, but include Dealul Viilor, Gorgonie, Dealul Şasei, Valea Omorîcea, Valea Râpei, Valea Caselor, Valea Teteşului, and Părăsişte.

4.2.1. *Grăunceanu*

The vast majority of the fossil taxa identified from Grăunceanu suggest a temporal distribution with a lower limit of ~2.2 Ma, as evidenced by the presence of *Alces* and potentially *C. etruscus* (though it is notable that the specific attribution of the *Canis* remains at Grăunceanu is unclear). Further, the fossil materials described above suggest that the deposits from Grăunceanu may potentially be as young as ~1.8 or 1.9 Ma, since multiple species present at Grăunceanu disappear around this time (e.g., *P. ardeus*, *R. radulescui*, *C. ramosus*, *M. cultridens* (typical form), *N. megamastoides*, *V. alopecoides*, *M. thorali*) and other species appear (*P. brevirostris*, *Bison (Eobison)*) (Fig. 10). A perhaps more restricted estimate for Grăunceanu would be 2.0–1.9 Ma, since it is only during this interval that *all* taxa found at Grăunceanu are documented within Europe (shifts in temporal distributions not withstanding). The potential cooccurrence of *Nyctereutes* and *Pachycrocuta* is particularly notable as these taxa are typically diachronous in the western European fauna, though they are also found together in the Khapry Faunal Unit of Russia (Sotnikova et al., 2002). Thus, consistent with previous descriptions for this site (e.g., Rădulescu and Samson, 1990), the faunal community from Grăunceanu bears similarities to the sites of Saint-Vallier and Senèze and the Costa San Giacomo Faunal Unit (as well as the eastern European Khapry Faunal Unit) of the Middle Villafranchian, but is particularly comparable to the Olivola Faunal Unit of the Late Villafranchian (Rook and Martínez-Navarro, 2010). These comparisons are thus most favorable to MNQ Units 17 and 18 (following Nomade et al., 2014).

Not much attention has been given to the time frame across which the assemblage from Grăunceanu was accumulated. Missing excavation records and lack of documentation for this site make directly assessing its stratigraphy impossible, though our ongoing analyses are focused on the stratigraphy immediately surrounding the site. Based on the limited data presented in previous publications, we do know that the fossil horizon was extensive (Bolomey, 1965; Rădulescu and Samson, 1990). Description of the excavations by Bolomey (1965) indicate that the fossils from Grăunceanu were densely concentrated in a ~0.75 m layer spread across a 90 m^2 area (at least as of 1963, though we know that excavations took place each year between 1961 and 1965) (Fig. 12). Rădulescu and Samson (1990) further describe the fossil deposits from Grăunceanu as being situated at the base of a silty sand layer that was approximately 1.5 m thick. Notably, there is no mention of any stratification within the fossil horizon. Many bones were found in articulation (e.g., complete or nearly complete hock joints) and our preliminary taphonomic observations suggest little transport or weathering of fossil materials. Combined, these data suggest that the Grăunceanu assemblage was deposited over a relatively short period of time, though our inability to directly examine the fossil deposits makes this interpretation tentative.

4.2.2. *La Pietriş*

There is little data that will help us infer the age of the deposits at La Pietriş, since our reinventory of the collections returned relatively few taxa from this site. Of those, the only taxon that is potentially useful here is *R. radulescui*. This species is typical of the pre-*Pachycrocuta* faunas of the Late Villafranchian and likely disappeared well before the end-Villafranchian event, potentially 1.7–1.6 Ma (Croitor, 2018a). This would suggest that La Pietriş might not be younger than this date. Referring to prior faunal lists, it is notable that several other taxa previously identified from this site also fit this time frame (i.e., >1.7 Ma) including *P. ardeus*, *V. alopecoides*, *N. megamastoides*. Thus, prior statements that La Pietriş and Grăunceanu are potentially of similar age (Rădulescu and Samson, 1990) are supported here, though additional inventory of the collections from Craiova are necessary. As with Grăunceanu, Bolomey (1965:78, translated from German) provides some clues as to the stratigraphic context of the fossil deposits at La Pietriş, stating: "The excavations carried out at La Pietriş in the years 1960–1961 exposed 126 m^2, in which the fossil remains were found concentrated only on 50 m^2. It is evident that the fossiliferous deposit was originally more extensive but was destroyed by the recent erosion of the valley that bounded it to the north." Rădulescu and Samson (1990:227) further note that the fossils from La Pietriş were recovered from "a sequence of sands and fine sands, 2 m thick".

4.2.3. *Fântâna lui Mitilan*

The estimated time range for this locality is rather broad. Based on the presence of *Praemegaceros obscurus* and *Dama* cf. *eurygonos* the locality is unlikely to be older than ~1.8 Ma and given the presence of *Praemegaceros* cf. *mosbachensis* the entire locality is potentially as young as 1.1 Ma. Previous publications provide some clues regarding this wide time frame, as there is clear evidence from this prior work that two faunal horizons are present at this site (Rădulescu and Samson, 1990). Specifically, Rădulescu and Samson (1990:228) note a "main fossil bed approximately 1.4–1.5 m thick at the top of a basal succession of clays and sands", represented by "alternating coarse sands and gravel lenses showing cross-bedding, surmounted by fine sands with small gravel lenses and portions of cemented silty sediment." They contrast this with a second fossil bed located 0.7–1.0 m above the main faunal level that consisted of sands and gravels and was approximately 0.5 m thick. Our research team saw this clearly reflected in labeling of some fossil specimens that included the words "niv. sup." (i.e., nivel superior or upper level). We can be reasonably confident that these specimens, at least, come from the upper faunal level identified by Rădulescu and Samson (1990). This includes the remains of multiple cervids preliminarily identified as *Eucladoceros*, one *Megalovis* specimen, the only specimen of *Praemegaceros* cf. *mosbachensis*, and at least one *Equus* and one cf. *Stephanorhinus* specimen, as well as a fragment of a mammoth tooth. Further, Rădulescu and Samson (1990) note the presence of *Militanotherium inexspectatum* from this upper level; importantly, this site is the type locality for this species. Based on the presence of *Praemegaceros* cf. *mosbachensis* in the upper level (but not in the lower level), we suggest that the upper faunal level is likely ~1.1 Ma or younger. If this is true, the LAD for *M. inexspectatum* may be younger by ~500 kyr, as the current LAD for this species is approximately 1.6 Ma (Kostopoulos and Athanassiou, 2005; Kahlke et al., 2011). The faunal assemblage from the lower (or main) level of Fântâna lui Mitilan better corresponds to the Farneta Faunal Unit from Italy, which is characterized by the presence of a *Eucladoceros*-like deer, *Praemegaceros obscurus* (= *Megaceroides boldrinii* Azzaroli and Mazza, 1992) and an advanced form of *Dama eurygonos* (= *Pseudodama farnetensis* Azzaroli, 1992) (Gliozzi et al., 1997). The coexistence of *P. obscurus* and a small-sized cervid similar to fallow deer is also reported from the Farneta Faunal Unit mammal assemblage from Ubeidya, Israel (Geraads, 1986).

4.2.4. *Fântâna Alortitei*

There is little data with which to assess the biochronology of this site other than the materials attributed to *Canis etruscus* and *Ursus etruscus* from this locality. Both of these taxa appear in the Middle Villafranchian at ~2.2 Ma and subsequently disappear in the Late Villafranchian (Rook and Martínez-Navarro, 2010; Medin et al., 2019), suggesting that the remains from Fântâna Alortitei could be from either of these time periods. Rădulescu and Samson (1990:227) note that fossils from this locality were recovered from "the base of a bed consisting of fine, partially consolidated sands, 0.7 m thick".

5. Conclusions and future directions

As demonstrated here, sites such as Grăunceanu show particular promise for elucidating the paleoenvironments of Early Pleistocene Europe. Situated in eastern Europe, the ORV may have represented an important dispersal corridor for mammals, potentially including hominins, moving into and out of Europe. Indeed, this is evidenced by the characteristic combination of typical western European Middle and Late Villafranchian faunas and those that are more typically found in eastern Europe/western Asia.

Considerable work remains if we are to better understand the specific paleoenvironments that may have been present in the ORV during the Middle and Late Villafranchian. Better biochronological estimates and updated taxonomic lists, such as we present here, are the first of multiple analyses that will shed further light on the significance of this region. Though the biochronological estimates provided here are largely consistent with previous estimates, our additions and refinements of the taxonomy lend more nuance to our understanding of the ORV sites. Additional analyses are planned in the near future to assess the taphonomy of the ORV remains, to inventory and analyze ORV remains housed at the Museum of Oltenia in Craiova, to conduct more detailed analyses of the taxonomic groups presented above (e.g., Carnivora, Artiodactyla, Pholidota), and to present a series of analyses designed to examine the paleoecology of the ORV localities. Importantly, attempts at radiometric and trapped charge dating of the ORV localities are currently underway, and we hope that these analyses will help us to validate the biochronological estimates presented here.

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Data availability

Three-dimensional scans of selected fossil materials are available via morphosource.org, under the project name “Oltet River Valley”.

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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Appendix A. Supplementary data

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