

CARNIVORA FROM THE EARLY PLEISTOCENE OF GRĂUNCEANU (OLTEȚ RIVER VALLEY, DACIAN BASIN, ROMANIA)

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Abstract. The Grăunceanu site in the Olteț River Valley has yielded a rich carnivoran assemblage including at least 10, possibly 11 species: *Vulpes alopecoides*, *Nycteretes megamastoides*, *Ursus etruscus*, *Meles thoralis*, *Lutraeximia* sp., *Pliocrocuta perrieri*, *Lynx issiodorensis*, *Puma pardoides*, *Megantereon cultridens*, *Homotherium latidens* and possibly *Pachyrocata brevirostris*. The faunal assemblage is compared with approximately coeval sites Europe and western Asia. This comparative analysis shows that the Grăunceanu assemblage shows the greatest similarities with sites to the west such as Senèze and, particularly, Saint-Vallier, rather than more easternly ones such as Liventsovka and Dmanisi. The relative abundance of the taxa at Grăunceanu was compared to that of Saint-Vallier and broad similarities were found, except for the absence of some cursorially adapted taxa present at Saint-Vallier but absent from Grăunceanu. The absence at Grăunceanu of taxa with a reconstructed cursorial hunting strategy, such as *Chasmaporthetes* and *Acinonyx*, may suggest less open habitat at Grăunceanu than indicated in previous paleoenvironmental reconstructions.

INTRODUCTION

The Olteț River Valley in Romania occupies a strategic position for understanding mammalian dispersal patterns to, from, and within Eurasia across the middle-late Villafranchian transition (Terhune et al. 2020; Curran et al. 2021). This region is located

just south of the southern Carpathians in the Dacian Basin, and multiple localities in this area have yielded fossils dated to the Pleistocene. The sites in the Olteț River Valley (ORV) have been intermittently excavated since about 1960, producing extensive collections of large mammals (Necrasov et al. 1961; Bolomey 1965; Rădulescu & Samson 1990, 1991; Rădulescu et al. 2003). Of the known sites in this area, Valea Grăunceanului (Grăunceanu herein) is the richest. The location of this site, along with the locations of other sites discussed herein are shown in Fig. 1.

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Fig. 1 - Map showing part of southern Europe and southwestern Asia. Locations of sites mentioned herein are marked with red dots and Bucharest, the capital of Romania with a yellow dot.

Ongoing work over the last decade has updated prior taxon lists from Grăunceanu and other ORV sites (Terhune et al. 2020), with a current list that includes at least 37 mammalian and avian taxa from across all known localities. At Grăunceanu specifically we have identified 32 species. This assemblage is dominated by large cervids (e.g., *Eucladoceros* and *Rucervus*) and equids (*Equus* cf. *livenzovensis* Baigusheva, 1978), but also includes a wide variety of other artiodactyls, e.g., *Pliotragus ardens* (Depéret, 1884), *Mitilanotherium inexpectatum* Samson & Rădulescu, 1966, *Sus strozsi* Forsyth Major, 1881 (Croitor et al. 2023), mammoths (*Mammuthus* cf. *meridionalis*), rhinoceroses (*Stephanorhinus* sp.), primates (*Paradolichopithecus arvernensis geticus*), ostriches (*Pachystruthio* cf. *pannonicus*), carnivorans (described in detail here), and the latest occurring instance of pangolins in Europe (*Smutsia olteniensis* Terhune et al., 2021). Biochronological estimates date Grăunceanu to the late Villafranchian (~2.2 – 1.9 Ma, Rădulescu & Samson 1990; Rădulescu et al. 2003; Terhune et al. 2020), and paleoecological reconstructions suggest the site was relatively open, with some woodlands and water resources nearby (Curran et al. 2021).

The carnivoran assemblage of Grăunceanu is, as shown herein, exceptionally rich, equaling in species richness better known sites such as Saint-Vallier, Senèze, and Dmanisi. The carnivorans of Grăunceanu were first discussed by Bolomey (1965). She identified *Nyctereutes megamastoides*, *Ursus etrus-*

cus Cuvier, 1823, *Meles* sp., *Hyaena perrieri* Croizet & Jobert, 1828, *Felis (Lynx) issiodorensis* Croizet & Jobert, 1828, *Megantereon megantereon* Bravard, 1828, *Homotherium crenatidens* Fabrini, 1890, and *Felis* sp. in the material available to her. It is not clear what Bolomey (1965) meant by *Felis* sp., but all the other taxa she listed have been identified herein as well, albeit in some cases under slightly different names. It should be noted that of the four Grăunceanu specimens figured by Bolomey (1965), three are also included herein (the *Homotherium* mandibular corpus in her fig. 3, the *Homotherium* canine in her fig. 4, and the *Lynx* mandibular corpus in her fig. 5). The *Pliocrocuta* cranial fragment of her fig. 6 has not been relocated for this study. A preliminary list of carnivoran taxa was given in Terhune et al. (2020). Some reidentification of material has taken place subsequently and the present taxon list does not precisely match any previously published.

GEOLOGICAL SETTING

The site of Grăunceanu is situated in the Olteț River Valley (ORV) of Romania, approximately 175 km west-northwest of Bucharest (see Fig. 1 for geographic position). The site is located in the Dacian Basin, which is delimited to the north and west by the Carpathian Mountains and to the south and east by the Danube Valley and Dobrogea Plateau. Deposits in the ORV are attributed to

the Tetoiu Formation (Andreescu et al. 2011), the sediments of which are primarily of a sandy-pebbly facies and are fluvio-lacustrine in origin. The Tetoiu Formation extends from the base of the Pleistocene (2.588 Ma) to as young as ~1 Ma (Andreescu et al., 2011). During the Villafranchian (~3.5–1.0 Ma; Rook and Martínez-Navarro, 2010) this region was dominated by the presence of the Dacian Lake, which was connected to the Pannonian and Euxinic lakes to the northwest and east, respectively. Today, the Olteț River, a tributary of the Danube River (via the Olt River) crosscuts the valley.

MATERIAL AND METHODS

All material described and figured herein is housed in the Institutul de Speologie “Emil Racoviță” in Bucharest, Romania. Additional material from Grăunceanu, not described in this study but included in some calculations of faunal similarity, is housed in the Muzeul Olteniei in Craiova, Romania. These specimens were inventoried by the research team but not examined in person by the first author. The material there adds specimens to the existing species, but does not expand the list of species. All photographs were taken by the authors. Measurements were taken to the nearest 0.1 mm using digital calipers except as noted and are reported in mm. Comparative measurement data are from the files of L.W. Some additional data were kindly provided by Dr. Saverio Bartolini-Lucenti, University of Florence, Italy.

Abbreviations: VGr: prefix for Valea Grăunceanului specimens housed in the Institutul de Speologie “Emil Racoviță”; MO: prefix for Muzeul Olteniei specimens; NRM-PZ: acronym for specimens from the paleozoological collections of the Swedish Museum of Natural History, Stockholm; c/C, canine; p/P, premolar; m/M, molar; d, deciduous tooth. Upper dentition identified by upper case letters, lower dentition by lower case letters. L, greatest mesiodistal length; Lt, greatest mesiodistal length of m1 trigonid; Lpa, length of paraconid of m1; Lpr, length of protoconid of M1; W, greatest transverse width.

SYSTEMATIC PALEONTOLOGY

Order **Carnivora** Bowdich, 1821
Suborder **Caniformia** Kretzoi, 1943
Family **Canidae** Batsch, 1788
Genus *Vulpes* Garsault, 1764

Vulpes alopecoides (Del Campana, 1913)

Fig. 2a, b

Background. This small species of *Vulpes* from western Eurasia has been described under a variety of names, including *V. alopecoides*, *V. praecorsac*, and *V. praeglacialis*. Bartolini-Lucenti & Madu-

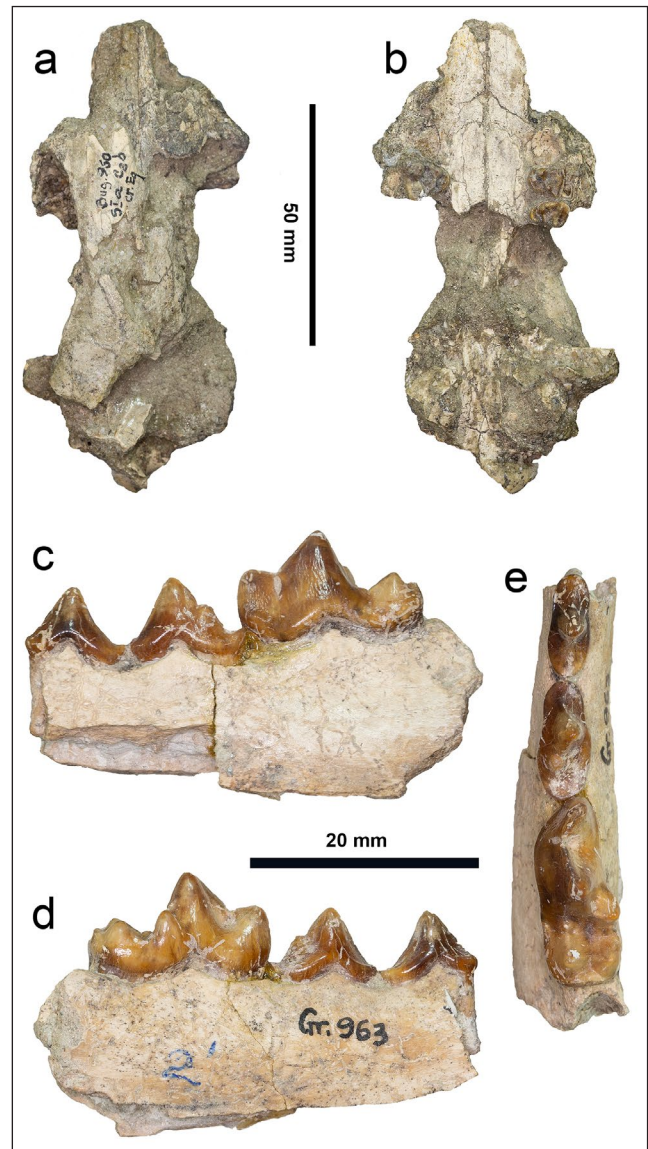


Fig. 2 - Specimens of Canidae from Grăunceanu. a-b) VGr.2334, cranium of *Vulpes alopecoides*; a: dorsal view; b: ventral view. c-e) VGr.0131, left mandible corpus with p3-m1 of *Nyctereutes megamastoides*; c: buccal view; d: lingual view; e: occlusal view.

rell-Malapeira (2020) have, however, convincingly argued that these are synonyms and that the valid name for all of them is *V. alopecoides*. The species is known from a number of sites ranging from early Villafranchian (MN 16) to late Galerian (MN 18), the time at which the extant *Vulpes vulpes* appears. *Vulpes alopecoides* is recorded (under the various names mentioned above) from numerous sites ranging from Georgia in the east to France and Spain in the west. Among Romanian sites, Terzea (1996) records its presence at Betfia-2 but it is not mentioned by Bolomey (1965), nor in other, later lists of specimens from the ORV.

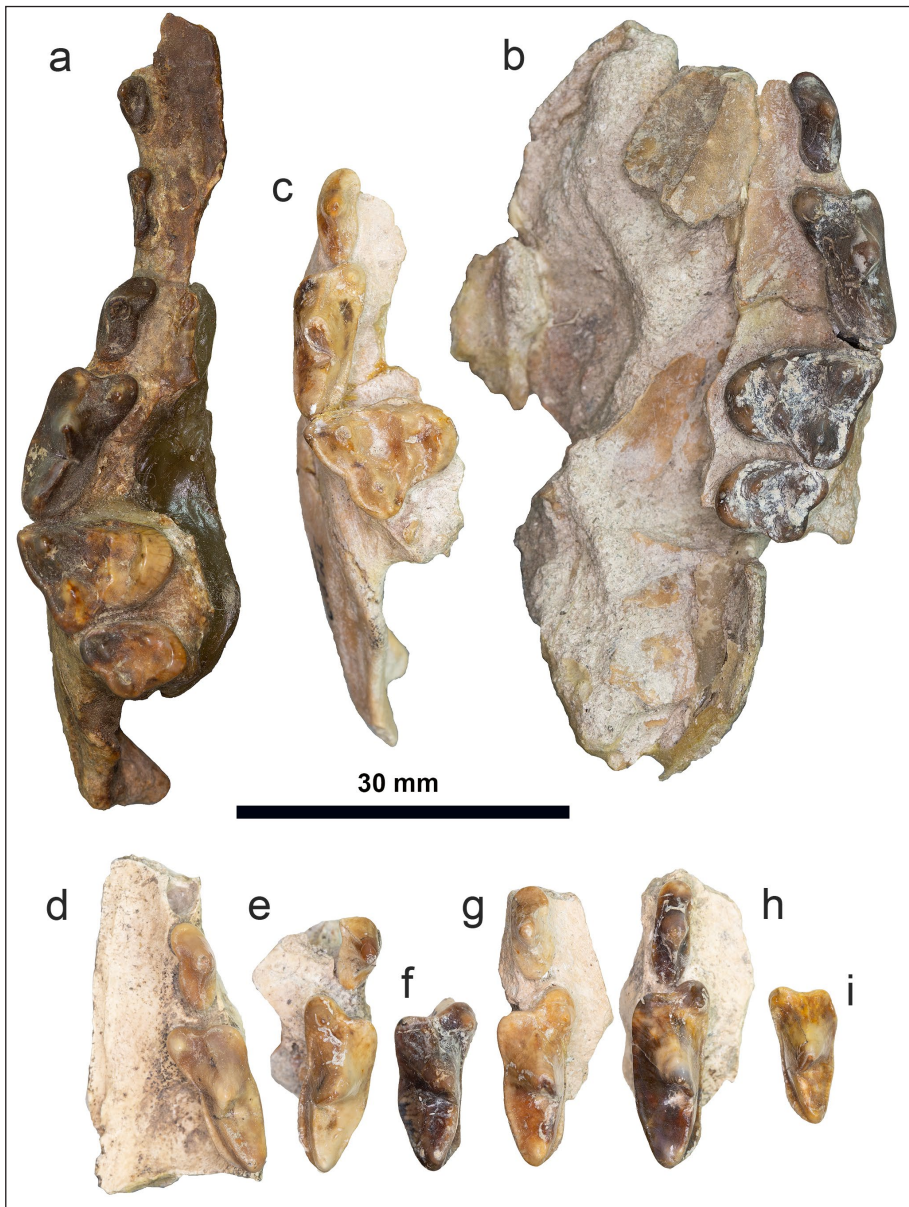


Fig. 3 - Specimens of *Nyctereutes megamastoides* from Grăunceanu. a-c) Maxillae in occlusal view; a: VGr.2298 right maxilla with P1-M2; b: VGr.0127, left maxilla with P3-M2; c: VGr.0205, right maxilla with P3-M1; d-i) isolated P4 or maxilla fragments with P4, showing variability in size and morphology of this tooth in Grăunceanu *N. megamastoides*; d: VGr.0142; e: VGr.0147; f: VGr.0213; g: VGr.0225; h: VGr.0227; i: VGr.0266.

Material: VGr.2334, laterally crushed and deformed cranium (Fig. 2a, b). In dorsal view retaining parts of both nasals and left maxilla, frontal, and parietal. In ventral view retaining a very fragmented basicranium and most of the left and right maxillae including complete right M1 and partial left M1 (buccal half) and complete M2. The markings on this specimen clearly identify it as coming from Grăunceanu.

Comments. Both in measurements and morphology this specimen conforms to published material of *V. alopecoides*. The cranium itself is too damaged to provide any additional information on the species.

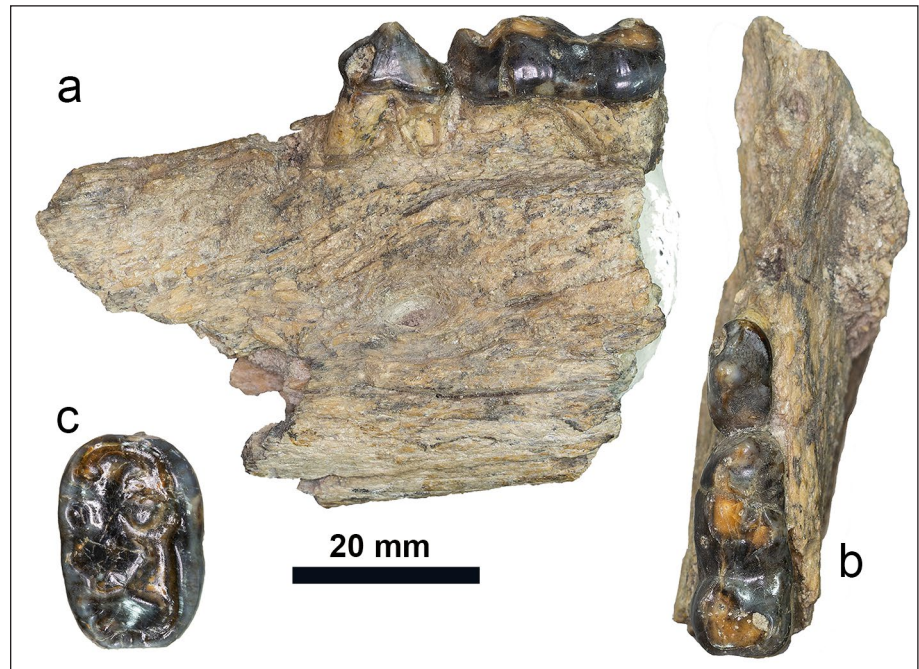
Genus *Nyctereutes* Temminck, 1838

Nyctereutes megamastoides (Pomel, 1842)

Fig. 2c-e, Fig. 3a-i

Background. This is the common raccoon dog species that is found at a number of sites across western Eurasia. It has a distribution similar to that of *V. alopecoides*, extending from Georgia in the east to France and Spain in the west (Bartolini-Lucenti 2018). Its temporal range extends in Europe from early Villafranchian or possibly late Ruscinian (see Bartolini-Lucenti et al. 2018) until at least the end of the middle Villafranchian (MN16/17 transition). It is preceded by the less derived *Nyctereutes donnezani*. A slightly more derived form, *Nyctereutes vulpinus*, may be present at Saint-Vallier (Soria & Aguirre 1976; Monguillon et al. 2004; Bartolini-Lucenti et al. 2018). Bolomey (1965) recorded *Nyctereutes megamastoides* as present at Grăunceanu and La Pietriș in Romania.

Fig. 4 - Specimens of *Ursus etruscus* from Grăunceanu. a-b) VGr.2315, left mandibular corpus fragment; a: buccal view; b: occlusal view; c: isolated left m2 in occlusal view.



Material: *Nyctereutes megamastoides* is the most common carnivoran at Grăunceanu. A total of 43 craniodental specimens are recorded here (with a minimum of 18 additional specimens housed at the Muzeul Olteniei), as well as many postcranial elements. VGr.0127, left maxilla fragment with complete P3-M2 (Fig. 3b); VGr.0128, right maxilla with complete P2-P3, P4 with damaged paracone and protocone, and complete M1-M2; VGr.0129, left maxilla fragment with P4 metastyle, complete M1-M2; VGr.0130, isolated right m1; VGr.0131, left mandible corpus fragment with complete p3-m1 (Fig. 2c-e); VGr.0132, left mandible corpus fragment with complete m1, mesial root of m2; VGr.0133, C; VGr.0134, c; VGr.0142, left maxilla fragment with complete P3-P4 and associated isolated P2 and incisors (Fig. 3d); VGr.0143, isolated incisors; VGr.0144, isolated incisor; VGr.0145 and VGr.0146, cranial fragments; VGr.0147, left maxilla fragment with damaged P3, complete P4, associated isolated left M1-M2, left C, right c (Fig. 3e); VGr.0149, cranial fragments and teeth; VGr.0156, associated isolated C, left P1-P3, left M2 fragment; VGr.0157, c; VGr.0158, c; VGr.0159, C; VGr.0160, C; VGr.0161, c; VGr.0205 right maxilla fragment with complete P3-M1 (Fig. 3c); VGr.0208, right M1; VGr.0213, right P4 (Fig. 3f); VGr.0219, left M1; VGr.220, left M2; VGr.0225, right maxilla fragment with P3-P4, associated isolated right C, I3, M1, buccal half of M2, P3, c, left C (Fig. 3g); VGr.0226, right M1 with damaged paracone, complete M2; VGr.0227, right maxilla fragment with P3-P4, associated isolated C (Fig. 3h); VGr.0228, cranial fragment with associated isolated left M1, M2, right m2, c; VGr. 263, right maxilla fragment with C-P3, mesial half of P4; left maxilla fragment with complete P1-P2 alveoli, complete P3, P4 with damaged metastyle, M1-M2 with damaged buccal halves; VGr.0264, left maxilla fragment with alveoli for P1-P2, complete P3-P4, broken M1, complete M2; VGr.0266, isolated left P4 (Fig. 3i); VGr.2298, right maxilla fragment with complete P1, damaged P2, complete P3-M2 (Fig. 3a); VGr.3135, right mandibular corpus with c-m1 and isolated elements including left c and incisors; VGr.3137, left mandibular corpus with p2-m2; VGr.3140, left mandibular corpus with p1, p3, m1-m2; VGr.3141, right mandibular corpus in two pieces broken at protocone of m1, with p1-m2; VGr.3142, right mandibular corpus with p1-m2; VGr.3143, cranial fragment with right I1-I3, left I1-I3, P2-M2; VGr.3147, maxilla in two pieces with right I1-P1, P3-M2, left I1 (a second fragment with right C-P1

is also present under this number); VGr.3148, right maxilla fragment with P3-P4; VGr.3149, edentulous cranial fragment; VGr.3150, edentulous partial cranium lacking anterior part of snout; VGr.3152, edentulous cranial fragment; VGr.3164, mandibular corpus fragment with left m1 talonid.

Comments. The large sample of *Nyctereutes* from Grăunceanu shows great variability in both morphology and metrics (e.g., Fig. 3d-i). This raises questions regarding the taxonomic distinction of *N. vulpinus* from *N. megamastoides* (Soria & Aguirre 1976; Monguillon et al. 2004), but this issue requires a deeper analysis than is possible here. Grăunceanu may be one of the latest occurrences of *N. megamastoides* in Europe. A closely related, possibly conspecific taxon, *Nyctereutes sinensis*, survives later in China (Tedford & Qiu 1991).

Family Ursidae Batsch, 1788
Genus *Ursus* Linnaeus, 1758

Ursus etruscus Cuvier, 1823

Fig. 4a-c

Background. *Ursus etruscus* is the common bear of the western European Plio-Pleistocene. It had its main center of distribution in western and southwestern Europe (France, Spain, Italy), but is also known from Romania, Bulgaria, Georgia, and as far east as China (Wagner 2010). Bolomey (1965) listed *U. etruscus* from Grăunceanu.

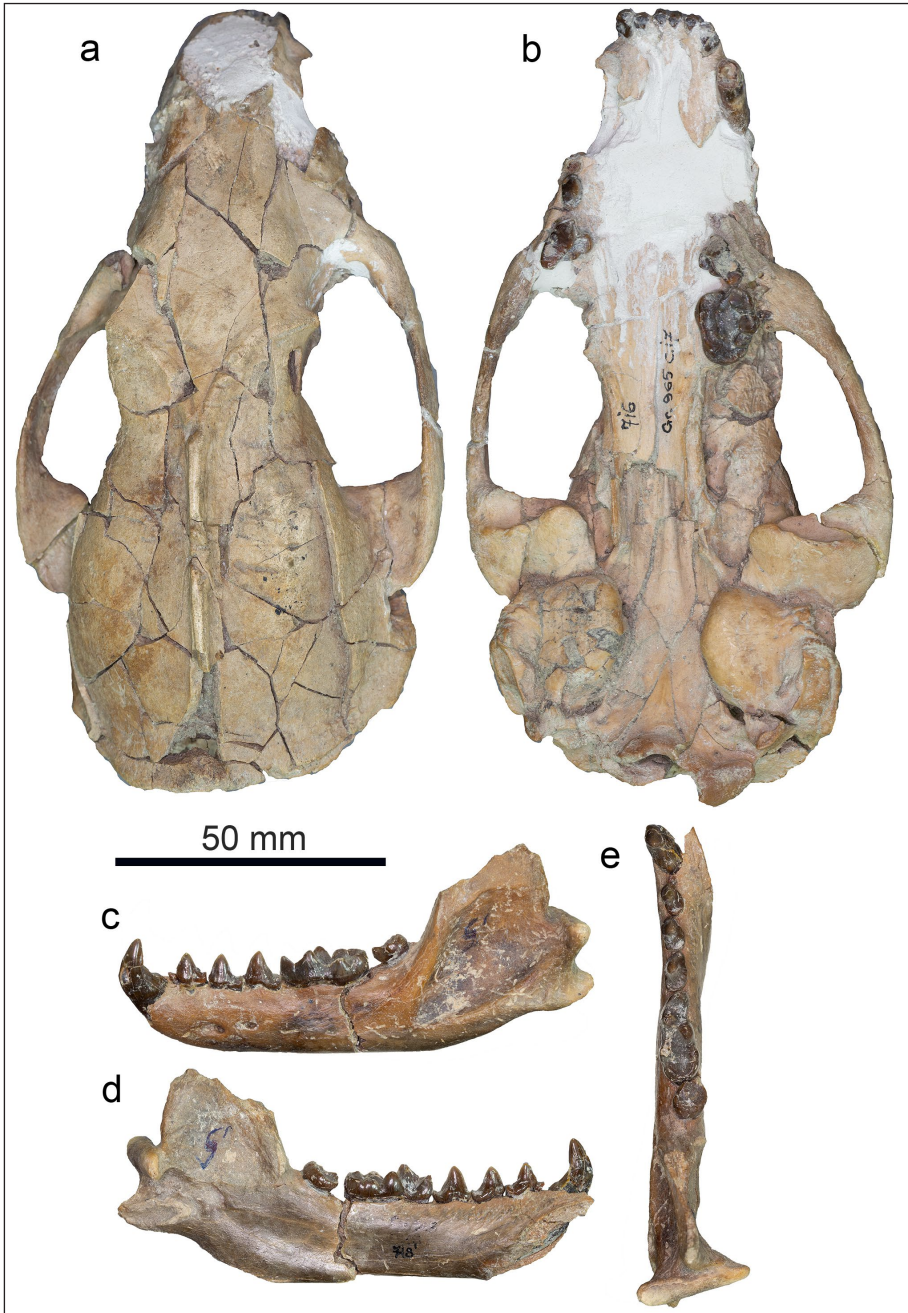


Fig 5 - Specimens of Mustelidae from Grăunceanu. a-b) VGr.2333, cranium of *Meles thorali*; a: dorsal view; b: ventral view. c-e) VGr.2319, left mandibular corpus with c-m2. c: buccal view; d: lingual view; e: occlusal view.

Material: VGr.2315, left mandibular corpus fragment with p4-m1 (Fig. 4a, b); VGr.2330, left m2 (Fig. 4c). A further 24 specimens from Muzeul Olteniei (almost all craniodental) were documented and included in the representativity calculations below, but not directly studied herein.

Comments. The identification of these specimens presents no difficulties. They are typical of *U. etruscus* in morphology and proportions. They are slightly smaller than average among a sample of *U. etruscus* from western Europe and may possibly belong to a female individual or individuals.

Family Mustelidae Batsch, 1788

Genus *Meles* Brisson, 1762

Meles thorali Viret, 1950

Fig. 5a-e

Background. Madurell-Malapeira et al. (2011) revised the taxonomy of European Plio-Pleistocene badgers, leaving two species (one of these with two subspecies). In this view, the earlier species, *Meles thorali*, is ancestral to the extant *Meles meles* and is found in the early and middle Villafranchian. *Meles thorali* here includes *M. iberica* Arribas & Garrido, 2007 and *Meles dimitrius* Koufos, 1992 (specimens

from Gerakarou, Greece). *Meles thorali* gives rise to *M. meles atavus*, which is found in the late Villafranchian and Epivillafranchian, subsequently evolving into the extant subspecies. In the view of Madurell-Malapeira et al. (2011), *Meles hollitzeri* Rabeder, 1976 is considered a junior subjective synonym of *M. meles atavus*, as are specimens from Apollonia-1 (Greece) previously assigned to *M. dimitrius* by Koufos & Kostopoulos (1997). Bolomey (1965) recorded *Meles* sp. from Grăunceanu.

Material: VGr.2296, left maxilla fragment with M1; VGr.2312, isolated right M1; VGr.2319, left mandibular corpus with c-m2 (Fig. 5c-e); VGr.2320, right mandibular corpus with c-m2; VGr.2323, left mandibular corpus with c-m2; VGr.2326, isolated left M1; VGr.2327, isolated left M1; VGr.2328, isolated right P4; VGr.2329, isolated right P4; VGr.2333, near complete cranium with left I1-c, P4-M1, right I1-I3, P2-P4 (Fig. 5a, b); VGr.3139, left mandibular corpus fragment with m1-m2; VGr.3186, left mandibular corpus fragment with p4-m2.

Comments. *Meles thorali* differs in a number of respects from extant *M. meles*. The extant species is somewhat smaller on average. In *M. thorali* the buccal margin of M1 is shorter than the lingual margin and the latter bulges out beyond the buccal margin both mesially and distally. In the extant species they are more similar in length. In these characteristics the Grăunceanu specimens match *M. thorali*. Bolomey (1965) reported two specimens of *Meles* from Grăunceanu, a left mandibular corpus with very worn teeth, which is likely to be specimen VGr.2323 herein, and a second corpus that cannot be identified based on Bolomey's (1965, p. 84) description. Bolomey (1965) presented evidence for derived characteristics in the Grăunceanu *Meles*, including a trigonid that is tall and longer than the talonid. It is not clear how this was measured, but there is no certain evidence for this characteristic in the material available here. Bolomey also stated (p. 84): "The shape of the mandible separates it significantly from *Meles meles* and from *M. thorali*..." (our translation from the original German). Applied to VGr.2323, available to Bolomey, this is correct to some degree by comparison both with the illustration in Viret (1950) and with the other Grăunceanu specimens; VGr.2323 is more robust, with a deeper corpus and larger and deeper coronoid process. However, VGr.2323 represents an aged individual with very worn teeth and changes with usage in life may have remodeled the mandible in this specimen. The other specimens available are young, with little dental wear, show no such changes, and do not differ from published specimens of *M. thorali*.

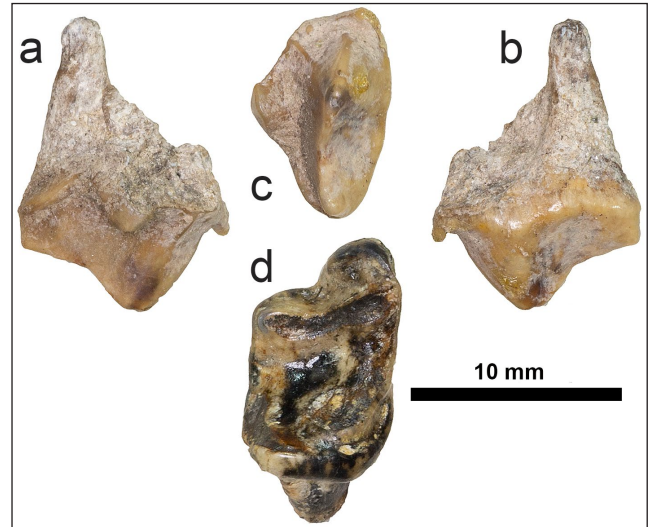


Fig. 6 - Specimens of *Lutraeximia* sp. from Grăunceanu. a-c) VGr.2297, damaged left P4; a: buccal view; b: lingual view; c: occlusal view. d: VGr.2331, right M1 of *Lutraeximia* sp. in occlusal view.

Subfamily Lutrinae Bonaparte, 1838
Genus *Lutraeximia* Cherin et al., 2016

Lutraeximia sp.

Fig. 6a-d

Background. Recent work has solidified the importance of '*Lutra simplicidens*' to the evolution of otters in the European Pleistocene. Key to this has been the description of upper dentition material of the species (Cherin & Rook 2014; Cherin 2017). This work suggests transfer of the species to the recently erected *Lutraeximia* Cherin et al., 2016 and also a link between that genus and the extant *Lutrogale*. *Lutraeximia* spp. are known from a small number of sites in Europe dating from the late Early to the Middle Pleistocene (see list in Cherin 2017).

Material: VGr.2297, damaged left P4 (Fig. 6a-c); VGr.2331, right M1 (Fig. 6d).

Comments. Lutrinae are generally rare in Villafranchian faunas and Grăunceanu is no exception. Only two teeth of this taxon are known from there. In both morphology and metrics the M1 shows similarities to that of *Le. simplicidens* from Voigtstedt illustrated by Cherin (2017, fig. 2), although the Grăunceanu tooth is more worn. The P4 is damaged but what is available is also similar to the Voigtstedt specimen in size and morphology. The main distribution of the genus is in western Europe (Germany,

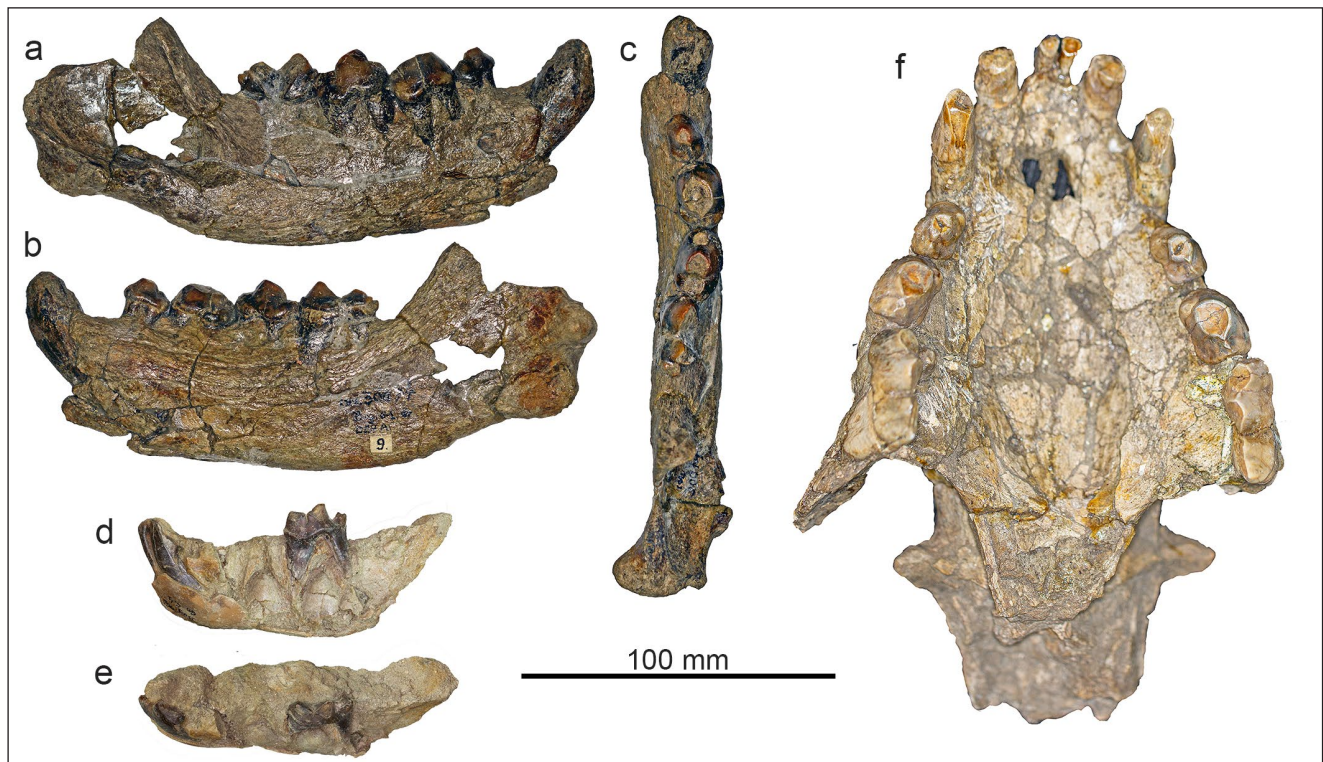


Fig. 7 - Specimens of Hyaenidae from Grăunceanu. a-c) VGr.3145, right mandibular corpus of *Pliocrocuta perrieri* with c-m1; a: buccal view; b: lingual view; c: occlusal view. d-e) VGr.2314, left juvenile mandibular corpus fragment of *Pliocrocuta perrieri*, with dp4 and p3-p4 in crypt; d: buccal view; e: occlusal view. f) VGr.0878, partial cranium of *Pachycrocuta brevirostris* in ventral view.

England, Italy) and the Grăunceanu specimens, which are among the oldest *Lutraeximia* are the first recorded from Romania.

Suborder **Feliformia** Kretzoi, 1945
 Family Hyaenidae Gray, 1821
 Genus *Pliocrocuta* Kretzoi, 1938

Pliocrocuta perrieri (Croizet & Jobert, 1828)

Fig. 7a-c

Background. *Pliocrocuta perrieri* was the first extinct hyaenid to be described, at a time when most members of the family were assigned to the genus *Hyaena*. It was not reassigned to *Pliocrocuta* until much later (Kretzoi 1938). It shares a number of features with the extant brown hyaena, but these are plesiomorphic and several apomorphic features link this species to the derived hyaenas in the *Crocuta* clade (Werdelin & Solounias 1991). *Pliocrocuta perrieri* is the common Eurasian hyaenid in the Pliocene and earliest Pleistocene and is replaced by *Pachycrocuta brevirostris* at the ‘*Pachycrocuta*-event’ around 2 Ma (Martínez-Navarro 2010; Rook & Martínez-Navarro 2010). Bolomey (1965) reported *Hyaena perrieri* from Grăunceanu.

Material: VGr.2314, juvenile left mandibular corpus with dp4, emerging c, and p3, p4 in crypt (Fig. 7d-e); VGr.3144, left mandibular corpus with p2-m1; VGr.3145, right mandibular corpus with c-m1 (Fig. 7a-c). VGr.3144 and VGr.3145 likely come from the same individual.

Comments. The juvenile corpus VGr.2314 is clearly hyaenid and can be assigned to *Pl. perrieri* based on the size of the dp4 (Baryshnikov & Averianov 1995). The two adult corpuses match other *Pl. perrieri* in size and dimensions, as well as in morphology.

Genus *Pachycrocuta* Kretzoi, 1938

Pachycrocuta brevirostris (Gervais, 1850)

Fig. 7f

Background. *Pachycrocuta brevirostris* is another species with a Eurasian distribution, although unlike *P. perrieri* it was also distributed across Africa (Ewer 1954; Werdelin 1999). The African forms are sometimes classified as a separate species, *Pachycrocuta bellax* (Ewer 1954). The author of the name *Pachycrocuta* was previously thought to be Aymard (1846) but Alba et al. (2015) have shown that no

Fig. 8 - Specimen of *Lynx issiodorensis* from Grăunceanu. a-c) VGr.2332, right mandibular ramus; a: buccal view; b: lingual view; c: occlusal view.



such publication exists and that the earliest record of the name is Gervais (1848-1852). *Pachycrocuta* may have an African origin and appeared in and spread rapidly throughout Eurasia around 2 Ma (the aforementioned ‘*Pachycrocuta*-event’). It became extinct sometime in the late Middle Pleistocene.

Material: VGr.0878, anterior cranium lacking most of neurocranium, with left i1-P4, right i3-P4, fragments of M1 crown (Fig. 7f).

Comments. It is important to note, first of all, that the exact provenance of this specimen is not known. This means that it may come from a slightly younger deposit, suggesting that the ‘*Pachycrocuta*-event’ horizon is not present at Grăunceanu. The cranium is large, although not among the largest *Pachycrocuta*, which are found in the later part of the early Pleistocene. Nevertheless, in size and metrics, as well as in morphology, it falls well within the range of *Pa. brevirostris*. In Romania, the species has been reported from La Seci (Rădulescu & Samson 1990) and from Fîntîna Alortîței (Rădulescu & Samson 1991, 2001).

Family Felidae Batsch, 1788
Genus *Lynx* Kerr, 1792

Lynx issiodorensis (Croizet & Jobert, 1828)

Fig. 8a-c

Background. There is general agreement that *Lynx issiodorensis* is the sister taxon to the four extant species of *Lynx* (Werdelin 1981; Lorfèvre 2009). Its antecedents are less clear, but appear to lie in North America, possibly with ‘*Felis*’ *proterolyncis* Savage, 1941 or ‘*Felis*’ *longignathus* Shotwell, 1956. The evolution of the genus *Lynx* subsequent to *L. issiodorensis* is less clear, with several fossil species named, e.g., *Lynx spelaeus*, *Lynx shansius*, and *Lynx variabilis* (Lorfèvre 2009) but no consensus has been reached regarding their validity or place in the phylogeny. *Lynx issiodorensis* appears in the Early Pliocene of Europe (Montoya et al. 2001), becomes widespread at the beginning of the Villafranchian (Late Pliocene) in Europe and survives there approximately to the end of the Villafranchian (late Early Pleistocene), when it is ostensibly replaced by *Lynx spelaeus* and subsequently by the extant *Lynx pardinus*. In Romania, *L. issiodorensis* is also known from La Pietriș (Bolomey 1965).

Material: VGr.2332, right mandibular corpus with c-m1 (Fig. 8a-c); (Bolomey 1965, fig. 5). The canine was separated from the corpus but has been glued back.

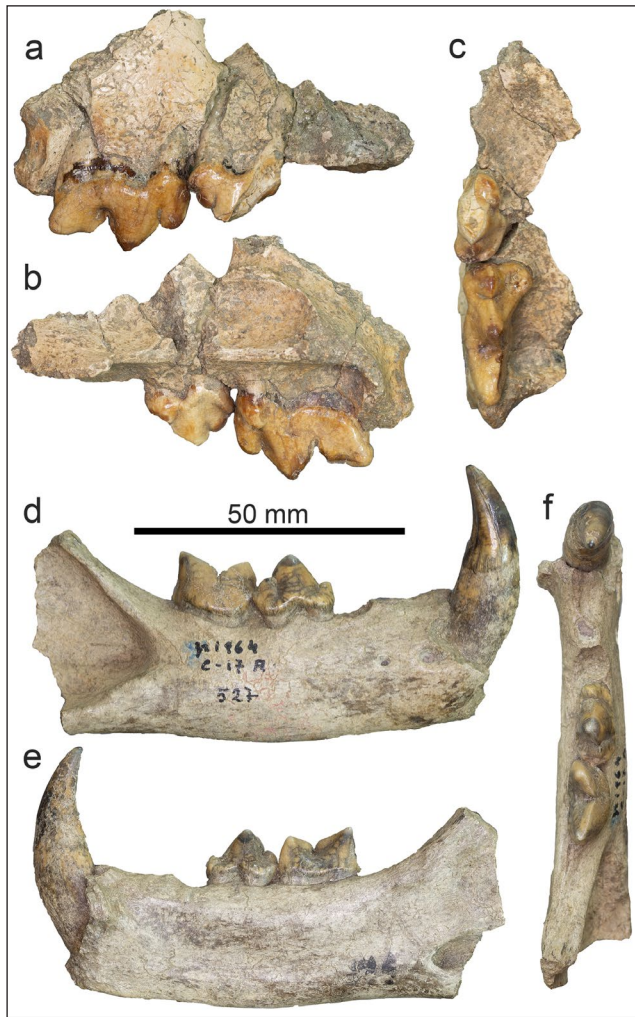


Fig. 9 - Specimens of *Puma pardoides* from Grăunceanu. a-c) VGr.2295, right maxilla fragment with P3-P4; a: buccal view; b: lingual view; c: occlusal view. d-f) VGr.1808, right mandibular corpus with c, p4-m1; d: buccal view; e: lingual view; f: occlusal view.

Comments. The Grăunceanu specimen is relatively large, with wide premolars, but in morphology is typical of *L. issiodorensis*. The illustration in Bolomey (1965, fig. 5) shows that the canine was still attached to the corpus at that time.

Genus *Puma* Jardine, 1834

Puma pardoides (Owen, 1846)

Fig. 9a-f

Background. This is a problematic taxon that has been published under a variety of names since Owen (1846) described the first specimen, a single lower carnassial from the Red Crag Formation, southeast England. Material currently thought

to pertain to this species was described by Viret (1954) as *Panthera schaubi* and later ascribed to *Viretailurus schaubi* by Hemmer (1965). In subsequent publications Hemmer (2001; Hemmer et al. 2004) has argued that the species belongs in the genus *Puma*. Addressing this phylogenetic issue is beyond the scope of this paper and we here accept the generic attribution to *Puma*. The species ranges temporally from the later part of the early Villafranchian to at least the latest Villafranchian and possibly into the earliest Galerian. Its geographic distribution extends from westernmost Europe (Britain) to Mongolia in the east.

Material: VGr.1808 right mandibular corpus with c, p3 alveolus, p4-m1 (Fig. 9d-f); VGr.1809 left mandibular corpus with left c-p4. VGr.1808 and VGr.1809 likely come from the same individual; VGr.2294, left maxilla with P3-P4; VGr.2295, right maxilla with P3-P4. Dental morphology indicates that these two specimens probably derive from different individuals. (Fig. 9a-c); VGr.2304, left p4.

Comments. In both morphology and metrics, the Grăunceanu specimens are a good match for *P. pardoides* from other sites in Eurasia (Hemmer 2001; Hemmer et al. 2004; Madurell-Malapeira et al. 2010; Cherin et al. 2013). Variation within the Grăunceanu sample appears to be about as great as between the remaining known specimens, but the overall variation is quite small in most characters. This is the first record of the species from Romania.

Genus *Megantereon* Croizet & Jobert, 1828

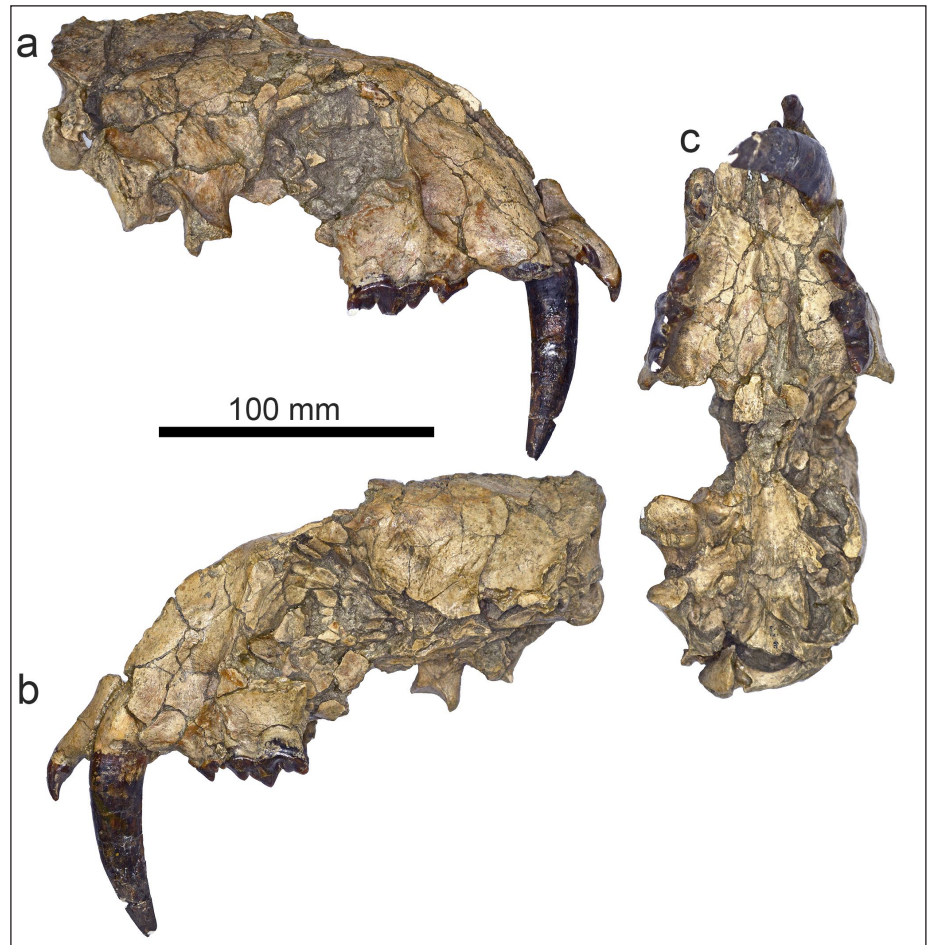
Megantereon cultridens (Cuvier, 1824)

Fig. 10a-c, Fig. 11a-c

Background. The taxonomy of *Megantereon* in Europe is a matter of debate. Most authorities agree that there are two temporally successive species present. The older of these, by all commentators listed as *Megantereon cultridens*, was present until some time between 2 and 1.5 Ma. The younger species, appearing after 2 Ma, is regarded by some as the European endemic *Megantereon adroveri* (Hemmer 2001) and by others as being a late immigration of the African species *M. whitei* (Martínez-Navarro & Palmqvist 1995, 1996).

Material: VGr.0140, right P3; VGr.0164, left p4; VGr.0863, left p4; VGr.2335, right mandibular corpus fragment with dp4, emerging m1 (Fig. 11a-c); VGr.2378, near complete cranium with complete left I3-P4, right C fragment, complete P3-P4 (Fig. 10a-c).

Fig. 10 - Specimens of *Megantereon cultridens* from Grăunceanu. a-c) VGr.2378, nearly complete cranium with I2-P4, right C root, P3-P4; a: right lateral view; b: left lateral view; c: ventral view.



Comments. With its relatively large anterior premolars the Grăunceanu material conforms in all respects to the morphology of *M. cultridens*. *Megantereon megantereon* (a junior subjective synonym of *M. cultridens*) was recorded from Grăunceanu by Bolomey (1965).

Two specimens of *Megantereon* from Grăunceanu stand out as exceptional. One is the nearly complete cranium VGr.2378 and the second the mandibular corpus fragment VGr.2355 that includes a dp4 that represents the first definitely identified dp4 of *Megantereon*. Because of the special interest of the latter specimen, it is here described in detail and compared with the dp4 of *Smilodon* sp., the sister taxon to *Megantereon*.

The cranium VGr.2378 adds to the small collection of crania of *Megantereon* from the Villafranchian of Europe. The bone is cracked into many pieces and the frontal in particular is flattened, but the overall shape of the cranium is intact. In dental metrics it is approximately average among European *Megantereon*, being a little larger than specimens from Les Étouaires and Perrier (France), approxi-

mately equal in size to specimens from Saint-Vallier (France), and smaller than specimens from Olivola and Figline (Italy).

In dental metrics the juvenile specimen VGr.2335 is within the range of European *M. cultridens* (Lm1 VGr.2335 18.7; mean for European sample = 19.8, range = 18.3 – 23.0, N = 14) although on the smaller side. The permanent carnassial is only partly erupted and seemingly unworn. The paraconid is shorter and lower than the protoconid (Lpa = 8.3; Lpr = 9.9). There is no metaconid or talonid. The enamel is vertically wrinkled as well as being grooved horizontally ventral to the carnassial notch. In the basal part of the leading edge of the m1 there are very minute serrations, similar to but slightly more prominent than those sometimes seen in unworn teeth of extant Felidae.

The dp4 (Ldp4 16.2M Wdp4 5.9; Ltdp4 14.4) is 87% the length of the m1. Unlike the m1, the paraconid and protoconid are nearly equal in length (Lpa = 6.2; Lpr = 6.3). The protoconid is nevertheless the taller of the two. The metaconid is set very slightly lingual to a line through the protoconid

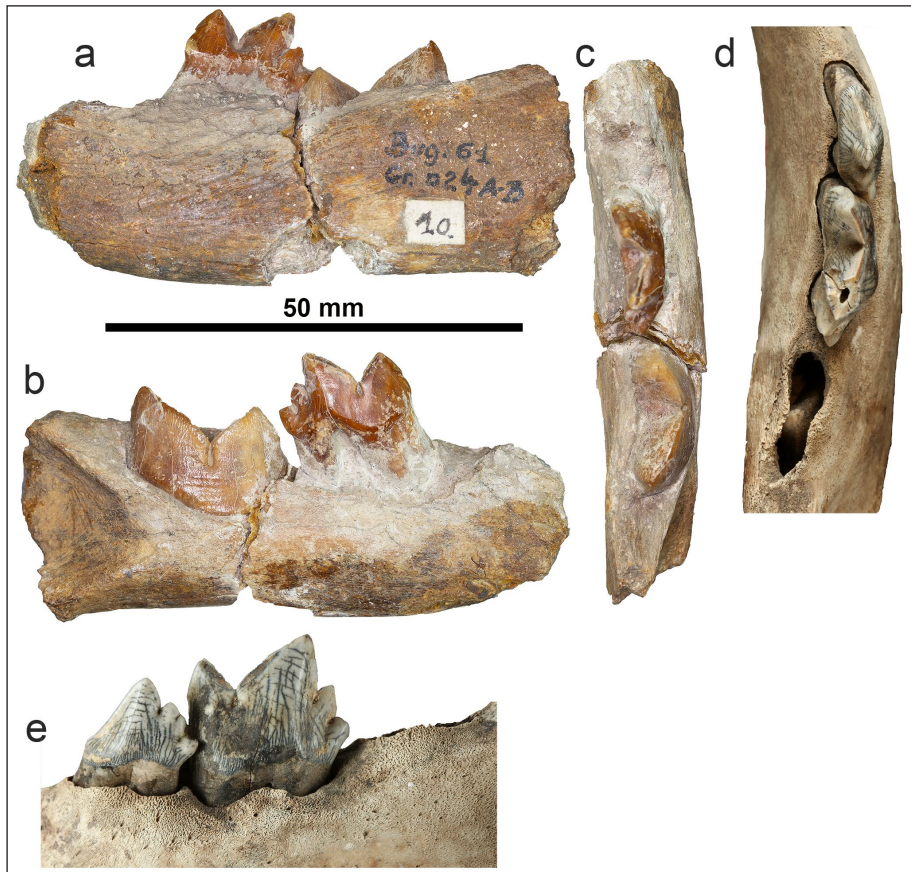


Fig. 11 - Juvenile specimen of *Megantereon cultridens* from Grăunceanu compared with a juvenile specimen of *Smilodon* sp. from Tarija, Bolivia. a-c) VGr.2335, juvenile *Megantereon* right mandibular corpus fragment with dp4, emerging m1; a) lingual view; b) buccal view; c) occlusal view; d-e) juvenile *Smilodon* mandible corpus NRM-PZ M8157b with left and right dp3-dp4, m1 in crypt; d) left side buccal view; e) right side occlusal view.

shear facet. The talonid is short, more crest- than cusp-like and comes to a point at the distal end of the tooth.

The dp4 of *Smilodon* (Fig. 11D-E) is similar in structure to that of *Megantereon*. Differences include that the paraconid is shorter and lower relative to the protoconid in *Smilodon* than in *Megantereon*. Also, in *Smilodon* the metaconid-talonid complex is more mesiodistally compressed than in *Megantereon*. A comparison of the length of this dp4 (Ldp4 mean of left and right = 20.0) with that of m1 (Lm1 mean of left and right = 28.2; measured on screen, based on a CT-scan of the specimen) shows it to be 71% of the length of m1, i.e., substantially less than in *Megantereon*. Thus, either the dp4 of *Smilodon* has evolved to be relatively smaller or the m1 to be relatively larger, or both.

Genus *Homotherium* Fabrini, 1890

Homotherium latidens (Owen, 1846)

Fig. 12a-d

Background. The genus *Homotherium* is present on all continents with the exception of Australia and Antarctica. It is characterized by moderately en-

larged but very narrow and serrated upper canines, a very long, low cranium, and a slightly sloping back, somewhat reminiscent of hyaenas. The sister taxon to *Homotherium* as presently known is *Lokotunjailurus* from the late Miocene of Kenya (Werdelin 2003) and this, together with a very early presence of *Homotherium* in the Lonyumun Member of the Koobi Fora Formation, Kenya (Werdelin & Sardella 2006; Werdelin & Lewis 2013) suggests an African origin. However, an equally early record of *Homotherium* from the Odessa Caves, Ukraine (Sotnikova et al. 2002) means that this issue remains open.

In Europe, *Homotherium* has been at times subdivided into two species, with *Homotherium crenatidens* Fabrini, 1890 being an earlier, slightly more robust form and *H. latidens* a later, more gracile form. Current consensus, however, is that only one species, *H. latidens*, encompasses all European material (Antón et al. 2013). Bolomey (1965) recorded *H. crenatidens* from Grăunceanu.

Material: VGr.0558, patella; VGr.2317, left mandibular corpus fragment with p4-m1; VGr.2318, right m1 (part of VGr.3134); VGr.3133, right C (Fig. 12d-e), (Bolomey 1965), fig. 4; VGr.3134, right mandibular corpus with i1-m1 (Fig. 12a-c), (Bolomey 1965), fig. 3.

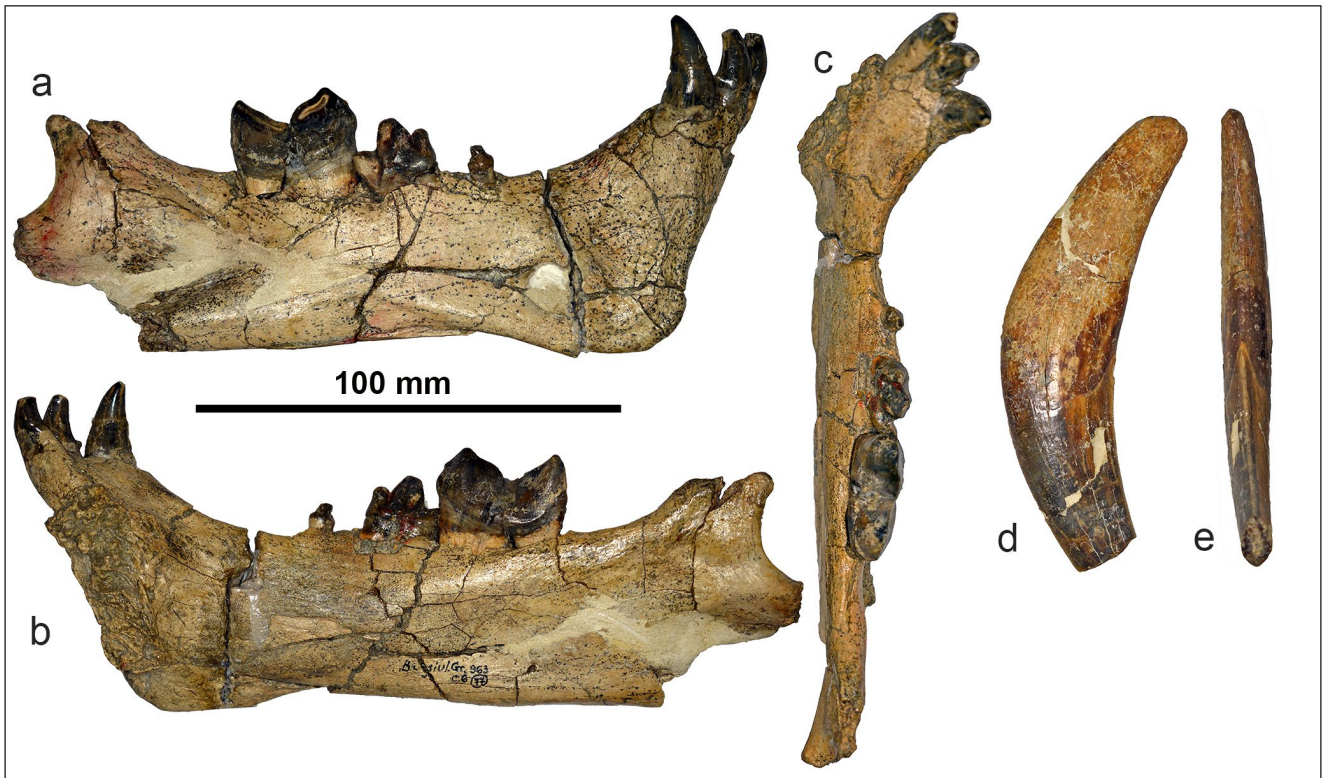


Fig. 12 - Specimens of *Homotherium latidens* from Grăunceanu. a-c) VGr.2317, left mandibular ramus fragment with p4-m1; a: buccal view; b: lingual view; c: occlusal view. d-e) VGr.3133, left C in d: medial view; e: lingual (distal) view.

Comments. The Grăunceanu material of *Homotherium* is limited. The craniodental material is readily attributable to *Homotherium*. The patella can be identified as pertaining to *Homotherium* by its size and because it conforms closely to the morphology of the patella of *Homotherium* illustrated by Balleisio (1963, fig. 46). All of the specimens can be assigned to the species *H. latidens*.

DISCUSSION

In this discussion we will place Grăunceanu in the context of a number of other western Eurasian carnivoran assemblages of approximately similar age (see Fig. 13 for an overview of absolute and relative stratigraphic positions of these assemblages.). These include the somewhat older Saint-Vallier, France, the approximately coeval Senèze, also from France, the slightly younger Olivola, Italy and Dmanisi, Georgia, and Liventsovka in Rostoc Oblast, Russia. The last mentioned of these sites may, like Senèze, be approximately coeval with Grăunceanu but span slightly more time. Another site of interest in this time span is Pantalla, Italy (Cherin et al. 2017, 2022), which is the only site among the ones listed

here that shares the presence of *Lutraeximia* with Grăunceanu. However, only five species of Carnivora are known from Pantalla and it is therefore not included in the analysis.

In addition to comparing faunas and discussing the reasons for similarities and differences, we can also make a crude comparison between Grăunceanu and Saint-Vallier in the individual representation of the different taxa thanks to the detailed study of material from recent excavations at the latter locality by Argant (2004).

The list of carnivoran taxa present at each of these sites is given in Table 1. It is immediately obvious that in terms of number of species, Grăunceanu is as rich or richer than those better-known sites. One species, *H. latidens*, is known from all six sites. This may be, either because it was very common and had a wide distribution, or because it is very easy to identify from even small fragments, being the largest felid species in Eurasia at the time. Two further species, *Pl. perrieri* and *L. issiodorensis*, are known from five of the six sites. All families are known from across Eurasia (not surprisingly). Mustelidae is the rarest of the families present at these sites, with only Grăunceanu and Saint-Vallier

Site	Senèze (c. 2.2 Ma)	Saint-Vallier (c. 2.4 Ma)	Olivola (c. 2.0 Ma)	Grăunceanu (c. 2.2-1.9 Ma)	Liventsovka (c. 2.3-1.9 Ma)	Dmanisi (c. 1.8 Ma)
Number of taxa shared with Grăunceanu	6/9	9/14	6/10		4/8	5/10
	<i>Nyctereutes megamastoides</i>	<i>Nyctereutes vulpinus</i>		<i>Nyctereutes megamastoides</i>		
					<i>Canis cf. senezensis</i>	
	<i>Canis etruscus</i>		<i>Canis etruscus</i>			<i>Canis mosbachensis</i>
						<i>Xenogyon lycaonoides</i>
	<i>Vulpes alpecooides</i>	<i>Vulpes alpecooides</i>		<i>Vulpes alpecooides</i>		<i>Vulpes alpecooides</i>
	<i>Ursus etruscus</i>	<i>Ursus etruscus</i>	<i>Ursus etruscus</i>	<i>Ursus etruscus</i>		<i>Ursus etruscus</i>
		<i>Meles thoralii</i>		<i>Meles thoralii</i>		
	<i>Martelliacis ardea</i>	<i>Martelliacis ardea</i>			<i>Pannoniacis nestii</i>	
		<i>Baranogale helbingi</i>				
		<i>Lutra cf. bravardi</i>		<i>Lutraeximia</i> sp.		
					<i>Lutra</i> sp.	
			<i>Felis silvestris</i>			
		<i>Lynx issiodorensis</i>	<i>Lynx issiodorensis</i>	<i>Lynx issiodorensis</i>	<i>Lynx issiodorensis</i>	<i>Lynx issiodorensis</i>
		<i>Puma pardoides</i>		<i>Puma pardoides</i>		
		<i>Achonyx pardinensis</i>			<i>Achonyx pardinensis</i>	<i>Achonyx pardinensis</i>
			<i>Panthera cf. gombaszoegensis</i>			<i>Panthera cf. gombaszoegensis</i>
	<i>Megantereon cultridens</i>	<i>Megantereon cultridens</i>	<i>Megantereon cultridens</i>	<i>Megantereon cultridens</i>		<i>Megantereon adroveri</i>
	<i>Homotherium latidens</i>	<i>Homotherium latidens</i>	<i>Homotherium latidens</i>	<i>Homotherium latidens</i>	<i>Homotherium latidens</i>	<i>Homotherium latidens</i>
	<i>Pliacocuta perrieri</i>	<i>Pliacocuta perrieri</i>	<i>Pliacocuta perrieri</i>	<i>Pliacocuta perrieri</i>	<i>Pliacocuta perrieri</i>	
	<i>Chasmaporthes lunensis</i>	<i>Chasmaporthes lunensis</i>	<i>Chasmaporthes lunensis</i>	<i>Pachycrocuta brevirostris</i> *	<i>Pachycrocuta brevirostris</i>	<i>Pachycrocuta brevirostris</i>

Tab. 1 - A compilation of carnivore taxa found at some representative Early Pleistocene sites in western Eurasia. The columns are organized based on the position of the sites on a west to east axis. Dates are very approximate. The absence of a west-east gradient in taxon representation is noteworthy. A distinct temporal difference can, however, be discerned between the two youngest sites (Olivola and Dmanisi) and the remaining sites. Non-Grăunceanu data from Viret (1954), Somikova et al. (2002), Argant (2004), and Bartolini-Lucenti et al. (2021). Species names in bold are those not present at Grăunceanu. The two *Nyctereutes* species are considered equivalent in the calculations. Although the presence of *Pachyonychia* at Grăunceanu is uncertain it has been included in the calculations.

Fig. 13 - Diagram showing the approximate absolute and relative stratigraphic positions of the faunal assemblages studied herein.

Epoch	Age	Chron	Mammal Age	Faunal unit	MNQ	Approximate age of sites included in this study
Pleistocene	Middle	BRUNHES	GALERIAN	Slivia	MNQ 20	
	Early	1.0	Jaramillo	EPIVILLA - FRANCHIAN	Pirro	
1.5		C.M.		Farneta	MNQ 19	
2.0		Matuyama	Villafranchian	Tasso		Dmanisi
2.0		Réunion Olduvai	Late	Olivola	MNQ 18	Olivola Grăunceanu Liventsovka
2.5			Middle	C. San Giacomo	MNQ 17b	Senèze
				Saint-Vallier	MNQ 17a	Saint-Vallier
				Montopoli		

having substantial samples of a mustelid (*M. thoralis*). This may be due to a size bias against smaller taxa at many of the sites.

Grăunceanu is most similar to the somewhat older Saint-Vallier, with nine of the 14 species at Saint-Vallier shared (nine of 11 if the three rare mustelids at Saint-Vallier are discounted). Five species at Saint-Vallier and two at Grăunceanu are not shared. Of these, three of the former and one of the latter are small mustelids that are exceedingly rare in the fossil record. In addition, one is the species of *Nyctereutes*, and the distinction between *N. megamastoides* and *N. vulpinus* is debatable. There remain two taxa at Saint-Vallier that are not shared with Grăunceanu, *Acinonyx pardinensis* and *Chasmaporthetes lunensis*. Both of these are reconstructed as open habitat pursuit predators and the difference between the sites may be indicative of less open habitat at Grăunceanu. The absence of *Canis* spp. at Grăunceanu may be another indication of more closed habitat there compared to, e.g., Senèze and Olivola, both of which include *Canis etruscus* in their faunal lists.

Looking geographically, it is clear that Grăunceanu is more similar to Senèze and Saint-Vallier to the west than it is to Dmanisi and Liventsovka in the east, despite the distances being approximately the same. This fits with a suggested opening up of the landscape from east to west

and through time (Curran et al. 2021 and citations therein). Given the absence of *Acinonyx*, *Chasmaporthetes*, and *Canis* at Grăunceanu an argument can be made that there was either less open habitat or that, if present, open habitat was more distant from the core habitat represented by the non-carnivoran remains at the Romanian site. The absence of open habitat carnivorans at Grăunceanu disagrees with the reconstruction of the habitat based on evidence from a variety of sources (Curran et al. 2021) and with the overwhelming dominance of open-habitat prey species (e.g., *Eucladoceros*, *Rucervus*, *Equus*) in the assemblage. One possible explanation may be related to the reconstruction by Curran et al. (2021) showing that there was also some locally available water source with nearby woodlands available, perhaps in the form of a gallery forest lining a river (i.e., the paleo-Oltet). This discrepancy between the paleoecological signals from predator vs. prey species at Grăunceanu cannot be resolved based on available data; analysis of δC^{13} isotope values in carnivoran teeth, and comparison to existing isotope data for Grăunceanu (Curran et al. 2021) may assist in a resolution. As Hopley et al. (2022) have shown, habitat inferences for carnivorans are not always what they are traditionally made out to be.

A comparison between Grăunceanu and Saint-Vallier in terms of number of specimens and MNI (minimum number of individuals mea-

Representation	<i>Nyctereutes megamastoides</i> *	<i>Ursus etruscus</i>	<i>Meles thorali</i>	<i>Puma pardoides</i>	<i>Homotherium crenatidens</i>	<i>Megaterion cultridens</i>	<i>Pliocrocuta perrieri</i>	<i>Lutraeximia</i> sp.	<i>Lynx issiodorensis</i>	<i>Vulpes alopecoides</i>	<i>Pachycrocuta brevirostris</i>	<i>Acinonyx pardinensis</i>	<i>Chasmodon lunsensis</i>
Grăunceanu raw data	43	26	11	5	5	5	4	2	1	1	1		
St. Vallier raw data	38	10	16	12	6	6	17		4	1		18	3
Grăunceanu MNI	9	4	4	2	2	3	2	1	1	1	1		
St. Vallier MNI	4	3	4	2	1	1	4		1	1		2	1
Grăunceanu raw %	41,3	25,0	10,6	4,8	4,8	4,8	3,8	1,9	1,0	1,0	1,0		
St. Vallier raw %	29,0	7,6	12,2	9,2	4,6	4,6	13,0	0,0	3,1	0,8	0,0	13,7	2,3
Grăunceanu MNI %	30,0	13,3	13,3	6,7	6,7	10,0	6,7	3,3	3,3	3,3	3,3	NA	NA
St. Vallier MNI %	16,7	12,5	16,7	8,3	4,2	4,2	16,7	0,0	4,2	4,2	0,0	8,3	4,2
Virot 1954 assessment	6	5	5	3	2	2	5		4	1		5	2

Tab. 2 - A comparison of relative proportions of taxa between Grăunceanu and Saint-Vallier. Data for Grăunceanu are based on craniodental material presented herein; data for Saint-Vallier are from Argant (2004), based on excavations carried out in the 1990s. These data do not include the material described by Virot (1954) but, unlike the Grăunceanu data, do include postcranial. Despite these differences, the general overall similarity in representation at the specimen level (except for the two taxa not found at Grăunceanu) suggests that the comparison has some validity. Thus, *Nyctereutes* (disregarding species) is the most commonly recorded taxon at both sites, with *M. thorali*, *P. pardoides*, *M. cultridens*, and *H. latidens* also well represented at both sites. The main difference lies in the relative commonness of *Pl. perrieri* and *U. etruscus* at Saint-Vallier. The first two rows are the raw numbers of specimens for each taxon and site. The following two are the MNI numbers based on max duplication of element. The following four rows are these numbers converted to percentages of the total number. Note that the two taxa furthest to the right are not represented at Grăunceanu. In addition to this, Virot (1954) describes material of three small mustelid taxa that are not represented in the 1990s excavations at the site, nor at Grăunceanu (cf. Table 1). The specimen count of *Nyctereutes megamastoides* does not include specimens from Muzeul Olteni, Craiova.

sured as greatest number of duplicated elements in a species sample) shows considerable similarities but also some glaring differences (Table 2). It should be noted here that this comparison concerns the excavations at Saint-Vallier by Faure and Guérin in 1996-1999 as reported by Argant (2004) and not the earlier excavations reported on by Virot (1954). The latter author did, however, provide a semi-quantitative assessment of commonness and rarity in the older excavations at Saint-Vallier (Virot 1954, p.184), which matches the relative position of species in Argant (2004) quite well (Table 2). Note also that the data of Argant (2004) include postcranial elements whereas the Grăunceanu data concern craniodental material only. Overall, a list of number of specimens per species in descending order shows the two to be quite similar. Indeed, they would be nearly identical except for the large number of specimens of *A. pardinensis* and *Pl. perrieri* at Saint-Vallier. Thus, *N. megamastoides*, *U. etruscus*, and *M. thorali* are common at both sites (not taking into account the putative species difference in *Nyctereutes* between the sites), followed by the large cats.

A similar pattern is seen when looking at MNI, although in this case Saint-Vallier has a more balanced fauna than Grăunceanu, with three species with equal MNI. Grăunceanu, on the other hand, is heavily dominated by *N. megamastoides*, even without including the Muzeul Olteniei specimens.

As noted above, the material from Grăunceanu ostensibly includes both *Pl. perrieri* and *Pa. brevirostris*. However, the exact provenance of the latter specimen is unclear given that it is recorded as coming from Valea Homorecia, an unknown site likely to be geographically close to Grăunceanu. Prior publications (Rădulescu & Samson 1990, 1991) noted the presence of *Pachycrocuta brevirostris* at two alternative sites in the ORV, La Seci and Fîntîna Alortîței, but no other publications list this taxon as being present either at Grăunceanu or the ORV more broadly. Unfortunately, no prior publications specifically describe the partial *Pa. brevirostris* cranium published here. Because of the uncertainty regarding provenance we therefore regard the attribution of *Pa. brevirostris* to Grăunceanu as tentative. The appearance of *Pa. brevirostris* is an important biostratigraphic marker event in the European Pleistocene at the middle-late Villafranchian transition (cf. Iannucci et al. 2021, 2023). The appearance of both hyaenid taxa may indicate that this datum event lies

within the Grăunceanu sequence. However, given the uncertainty regarding the provenance of the *Pa. brevirostris* specimen, it is perhaps more likely that Grăunceanu is slightly older than the ‘Pachyrocutea-event’ and therefore late middle Villafranchian rather than early late Villafranchian, as suggested by Rook & Martínez-Navarro (2010).

CONCLUSIONS

In terms of both specimens and number of species of carnivorans, Grăunceanu is one of the richest sites in the Early Pleistocene of Europe. We have here identified 11 species (or 10 depending on the status of *Pa. brevirostris*) in the Grăunceanu assemblage: 2 Canidae, 1 Ursidae, 2 Mustelidae, 2 Hyaenidae, and 4 Felidae. Things of note include the very large sample of *N. megamastoides*, the presence of the rare *Lutraeximia* sp., and the presence of a juvenile specimen of *Megantereon cultridens*.

Among more or less coeval sites in western Eurasia, the carnivoran assemblage from Grăunceanu shares more taxa with sites to the west than with sites to the east, and displays particular affinities with Saint-Vallier. All, or nearly all, carnivoran species found at Grăunceanu are also present at Saint-Vallier. The sequences of abundance measured as either number of specimens or MNI are also similar, although evenness is much greater at Saint-Vallier, whereas Grăunceanu is heavily dominated by the very large sample of *N. megamastoides*.

For habitat reconstruction the species that are not present at Grăunceanu may be more informative than those that are. Thus, three taxa that have generally been reconstructed as open habitat forms, *Canis* spp., *C. lunensis*, and *A. pardinensis* are all absent from Grăunceanu and a fourth, *Pl. perrieri*, is rare compared to its abundance at Saint-Vallier. This suggests that there may have been less open habitat at Grăunceanu than at Saint-Vallier, or that open habitat was more distant at Grăunceanu. This is not entirely compatible with multiproxy habitat reconstruction of Grăunceanu (Curran et al. 2021), and is especially at odds with the dominance of open-adapted prey species (e.g., *Eucladoceros*, *Rucervus*, *Equus*) found in the Grăunceanu assemblage. The discrepancy cannot be resolved on the basis of present evidence but requires new data sources, such as isotope analyses of carnivore teeth from Grăunceanu and other sites.

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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”.

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