

THE CARNIVORAN RECORD FROM THE NEOGENE OF EASTERN ROMANIA

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Abstract: The present work deals with the carnivorans found in five Neogene localities in eastern Romania: the Vallesian locality of Păun, the Turolian localities of Pogana 1 and Crețești 1, and the Ruscian localities of Berești and Mălușteni. The presented material includes cranial and postcranial specimens, some of which are herein described for the first time. This study includes a re-description and re-depiction of the type material of *Lutra rumana* Simionescu, 1922 and *Promephitis malustenensis* Simionescu, 1930, in order to clarify the taxonomic position of these two enigmatic taxa. The carnivoran faunal lists of all five localities are reviewed offering interesting insights into the temporospatial range of the discovered forms. Most localities have only yielded a limited number of species, except for Mălușteni, which shows evidence of at least nine different coexisting forms. Notable occurrences in terms of biostratigraphy include *Paludolutra* sp. in Pogana 1, *Protictitherium crassum* (Depéret, 1892) in Crețești 1, and a phocid from Mălușteni. This review aims to aid the understanding of the Neogene ecosystems in the north of the Paratethys in terms of faunal contents, biostratigraphy and palaeoecology.

INTRODUCTION

Published reports on the carnivorans from the Neogene of eastern Romania have been surprisingly scarce compared to the neighbouring Republic of Moldova (e.g., Lungu & Rzebik-Kowalska 2011) and Ukraine (e.g., Semenov

2001; Sotnikova 2008). However, this region is pivotal to the understanding of the evolution of mammal assemblages during these periods, because of its proximity to the Carpathians, which formed an overwhelming natural barrier affecting the distribution of species north of the Paratethys. The following paragraphs provide an overview of the published data concerning the carnivorans of this region.

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Macarovici (1957) published a partial skull of *Ictitherium hipparionum* (Gervais, 1846) from the Vallesian locality of Păun (Jassy). This specimen was later included by Semenov (1989) in the hypodigm of *Hyaenictitherium venator* Semenov, 1989. Werdelin & Solounias (1991) argued that the specimens under this name, as well as *Miohyaenotherium bessarabicum* Semenov, 1989, are very similar to *Lycyaena parva* Khomenko, 1914, and are intermediate in size between *Hyaenictitherium wongii* (Zdansky, 1924) and *Hyaenictitherium hyaenoides* (Zdansky, 1924), making their identification very problematic. This approach was furtherly followed by Tseng & Wang (2007), Turner et al. (2008), and Coca-Ortega & Pérez-Claros (2019). However, Semenov (2008) retained the names for these forms, without further justification.

Ursachi (2016) reported the presence of *Adcrocuta eximia* (Roth & Wagner, 1854) and *Yoshi* sp., as well as depicting a hemimandible of an icthid from the Turolian locality of Creţeşti 1. Recently, a fragmentary radius of a medium-sized terrestrial mustelid with affinities to Guloninae Gray, 1825, Melinae Bonaparte, 1838, or Mellivorinae Gray, 1865, was reported from the Turolian of Fălciu-Prut 1 (MN11-MN12, Eastern Romania, Vaslui County, Scythian Platform) (Bordeianu et al. 2022).

The two main Lower Pliocene localities in this region are Bereşti and Măluşteni (see below). Simionescu (1932) reported the presence of *Machairodus* cf. *cultridens* (Cuvier, 1824), *Lutra rumana* Simionescu, 1922, *Vulpes* sp., *Canis* sp., *Mustela* aff. *martes* (Linnaeus, 1758), and *Mustela* sp., from the Lower Pliocene of Bereşti. In a more recent synthesis, Radulescu et al. (2003) updated the taxon names of the carnivorans from Bereşti, listing *Agriotherium* sp., *Eucyon odessanus* (Odintsov, 1967), *Eomellivora* sp., *Baranogale* sp., and Mustelidae indet., without providing arguments to support their assignments. Simionescu (1922) provided a preliminary faunal list of the Pliocene locality of Măluşteni, including *Vulpes* cf. *donnezani* (Depéret, 1890), *Lu. rumana*, and *Mustela* sp. Some years later, he identified the canid mandible as *Vu. donnezani* and added *Lynx issiodorensis* (Croizet & Jobert, 1828), *Promephitis malustenensis* Simionescu, 1930, *Mustela* aff. *martes*, *Mustela* aff. *robusta* Newton, 1894, *Mustela* aff. *putorius* Linnaeus, 1758, *Phoca* sp. Linnaeus, 1758, and Carnivora indet., to the list of taxa (Simionescu 1930). Radulescu et al. (2003) provided an updated faunal list for the locality including the carnivorans: *Eu. odessanus*,

Lynx cf. *issiodorensis*, *Eomellivora rumana* Simionescu, 1938, *Baranogale* cf. *helbingi* Kormos, 1934, *Enhydriectis* sp., and Mustelidae indet., again without providing any detailed arguments about these assignments.

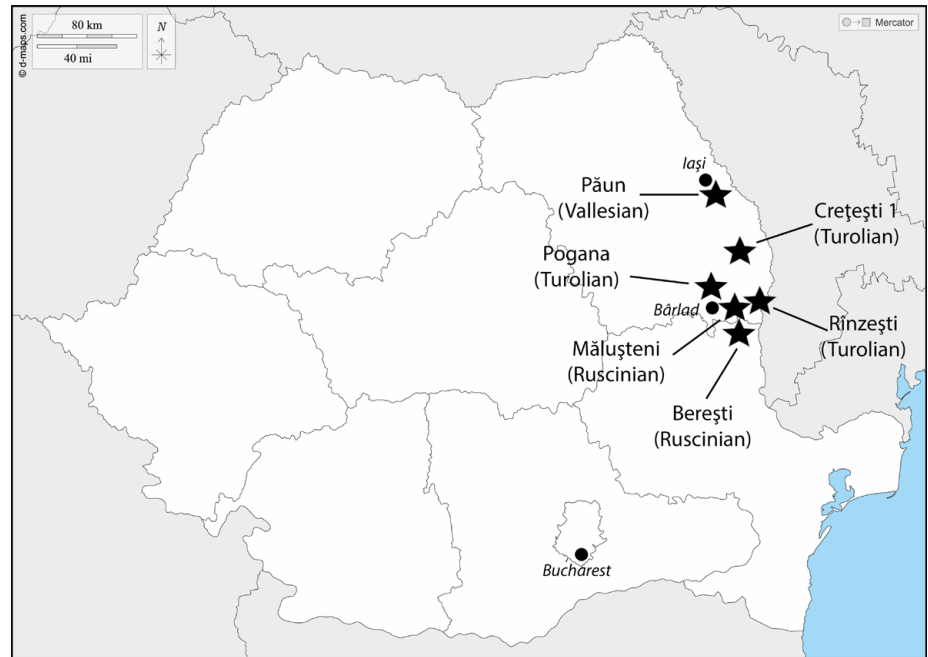
The aim of the present study is to revise the carnivoran material from the Neogene of eastern Romania, in order to clarify the taxonomic attributions and to understand the evolution of these forms in the region during the Miocene–Pliocene interval. A map of the fossiliferous sites, as well as the locations of the relevant collections can be seen in Figure 1.

GEOLOGICAL BACKGROUND

East of the folded units of the Carpathians, two major structural units are present in the Carpathian Foreland: the Moldavian and the Scythian platforms (e.g., Săndulescu 1984). Separated by the Bistriţa Fault, running approximately on the Fălciu-Bacău direction, the two major platforms differ in the evolution of their Precambrian and Palaeozoic basement and cover units, but share most of their post-Palaeozoic evolution (Săndulescu 1984). Most of the deposits cropping out in eastern Romania represent the Neogene and Quaternary cover of the two platforms mentioned above. Most of the Neogene is represented by Middle Miocene (Sarmatian) marine and deltaic deposits, continental sedimentation occurring mostly at the end of the Middle Miocene (during the Khersonian subage of the Sarmatian), and later on, during the Late Miocene, Pliocene, and Quaternary (e.g., Ionesi 1994). The south-eastern retreat of the Paratethys Sea constrained by the Middle Sarmatian uplift of the last Eastern Carpathians nappe led to the gradually emerging lands adjacent to the Dacian Basin (Palcu et al. 2019). A diverse terrestrial biota progressively colonized these Miocene lands, among which large mammals are common (Ursachi 2016).

The Khersonian deposits correspond to (1) a marine-brackish facies (Huşi Formation), developed between the Prut and Bârlad rivers, which includes clay, sand, and sandstone intercalations with some small bivalves of the genus *Macra* Linnaeus, 1767. At the top, the brackish facies are replaced by freshwater facies, as supported by the presence of *Unio* Philipsson, 1788, shells; (2) a fluvial-deltaic “facies” (Păun Formation) north and west of the

Fig. 1 - Map of the studied localities, and locations of the collections. Base map source: d-maps.com.



Bârlad River, composed mainly of sand with large cross-bedding and sandstone concretions with vertebrate remains and plant debris (Jeanrenaud 1971). In a previous sedimentological study of the Khersonian deposits from Monument open pits at Vaslui (Huși Formation), Rățoi & Brânzilă (2012) identified a series of sedimentary facies, which were assigned to a river delta system.

The Păun fossil locality was first described by Macarovici (Macarovici 1957; Macarovici & Paghida 1966). The deposits comprised 4 m of yellow sand interbedded by sandstone with leaf impressions, which can be interpreted as fluvial channel deposits. The early Khersonian age estimated for this site is due to its geometric position about the subjacent deposits marking the late Bessarabian / early Khersonian.

Crețești 1 is located on the right riverside of Lohan Stream, near Vaslui city in the framework of the Moldavian Platform. The fossil-bearing layers have been discovered during the works for the national road between Crasna and Huși localities (e.g., Ursachi et al. 2015). The Miocene sedimentary succession represents a floodplain built up of greenish mudstone of one up to two meters in height including only one thin silty sand layer. The fossiliferous deposits have yielded various vertebrate taxa (amphibians, reptiles, birds, and mammals) and lacustrine gastropods (Ursachi 2016). The initially considered older age (MN9; e.g., Ursachi et al. 2015) has been re-assessed to the late Khersonian (MN11)

due to the presence of geologically younger rodent taxa (Daniel Badea, pers. comm.).

The Pogana 1 outcrop is a local quarry near Pogana village (Vaslui County) confined to the westernmost part of the Scythian Platform. A detailed description of the geological setting of the locality can be found in Kampouridis et al. (2023) and references therein. The Maetian sedimentary succession seen in the quarry was deposited in a fluvial environment. It starts with trough cross-beds and convolute beds of sands unconformably overlain by coarser sands with angular mud clasts with extensive cross-stratification, and yellow sands with horizontal bedding and current-ripple lamination. The age of these deposits is middle Turolian (MN12) (Kampouridis et al. 2023).

The Pliocene continental deposits mostly crop out across the Scythian Platform, around the city of Bârlad. Here, several localities yielded vertebrate fossil remains (e.g., Simionescu 1930, fig. 2), but two of those, Mălușteni and Berești (Fig. 1), stand out from others in the high abundance of fossil specimens and the taxonomic diversity of continental vertebrate assemblages. Athanasiu (1912) was the first to report fossil vertebrate remains (primates and cervids) from Quaternary sands cropping out in the gullies crossing the slopes of Lacului Hill, north of Mălușteni. Athanasiu (1915), further investigated the area of Mălușteni, attempting to correlate the fossiliferous cross-bedded sands of this locality to the sand cropping out near the

town of Bereşti. He concluded that the sands from Măluşteni correlate to the sands from the top of the section exposed at Porcului Hill, in Bereşti, which represent the base of the Quaternary, because they overlay sands and claystones that are rich in Pliocene-indicative molluscs. Simionescu (1922, 1930) conducted further investigations of the fossil fauna from Măluşteni, significantly expanding the faunal list. Based on the composition of the faunal assemblage, Simionescu (1930) assigned the fossiliferous deposits from Măluşteni to the Pliocene. Further analyses of the small mammal faunas (Terzea 1997; Radulescu et al. 2003) considered that the faunal assemblage from Măluşteni can be dated as MN15a, based on the occurrence of the arvicolid *Mimomys moldavicus* Kormos, 1932. In the most recent revision of the small mammal assemblage, Crespo et al. (2023) argued that the presence of the talpid *Desmana verestchagini* Topachevski, 1961, is indicative for MN14b age, in the vicinity of the MN14/MN15 boundary. Herein, we follow this latter age determination for the locality of Măluşteni.

From similar fluviolacustrine sands cropping out along gullies next to the neighbouring town of Bereşti, Simionescu (1932) described a somewhat less diverse fossil vertebrate assemblage than that seen in Măluşteni. Nonetheless, he considered that the two assemblages were comparable and assigned Bereşti to the Pliocene, due to its geometric position on top of claystones that bear Pliocene-indicative molluscs. Based on the presence of the cricetine *Cricetulus simionescui* (Samson & Radulescu, 1973), Terzea (1997) and Radulescu et al. (2003) dated the assemblage from Bereşti to MN14b. Due to the occurrence of the castorid *Trogotherium minus* Newton, 1890, and of the spalacid *Pliospalax macoveii* (Simionescu, 1930), Crespo et al. (2023) reconsidered the age of the assemblage as spanning across the MN14–MN15 interval, encompassing the entire Early Pliocene; a conclusion we also follow in this study.

MATERIAL AND METHODS

The already published carnivoran material of the localities of Păun (Vallesian), Rînzeşti (Turolian), Creţeşti 1 (Turolian), Măluşteni (Ruscinian) and Bereşti (Ruscinian) is herein revised. Additionally, unpublished carnivoran specimens from the Turolian localities of Creţeşti 1 and Pogana 1 are presented enriching our knowledge on the Neogene carnivoran record of the region. The material is stored in four institutions: the Alexandru Ioan Cuza University Palaeontological

Museum, Iaşi (AICUPM), Alexandru Ioan Cuza University Natural Science Museum, Iaşi (AICUNSM), the Natural Science Branch of the Vasile Pârvan Museum, Bârlad (MVP-SN), and the Laboratory of Palaeontology, Faculty of Geology and Geophysics, University of Bucharest, abbreviated as LPB (FGGUB). AICUPM hosts specimens from Păun, Pogana 1, and Măluşteni, MVP-SN hosts specimens from Pogana 1 and Creţeşti 1, while LPB (FGGUB) hosts specimens from Măluşteni and Bereşti. A detailed list of the material can be found in the Appendix Table 1.

Dental nomenclature follows Kargopoulos et al. (2022). Measurements were taken using a digital calliper to the nearest 0.1 mm. Measurements' abbreviations: L – total proximodistal length, APDp – anteroposterior diameter of the proximal epiphysis, TDp – transverse diameter of the proximal epiphysis, APDm – anteroposterior diameter of the midshaft, TDm – transverse diameter of the midshaft, APDd – anteroposterior diameter of the distal epiphysis, TDd – transverse diameter of the distal epiphysis, APDd.ar – anteroposterior diameter of the articular surface of the distal epiphysis, TDd.ar – transverse diameter of the articular surface of the distal epiphysis, TDtr – transverse diameter of the trochlea. Statistical analyses were conducted in PAST 4.13 (Hammer et al. 2001).

SYSTEMATIC PALAEOLOGY

Order **Carnivora** Bowdich, 1821
 Suborder **Caniformia** Kretzoi, 1943
 Family **Canidae** Fischer von Waldheim, 1817
 Genus *Eucyon* Tedford and Qiu, 1996

cf. *Eucyon* sp.

Locality: Bereşti.

Age: Ruscinian, Early Pliocene.

Material: LPB (FGGUB) 10192, right C; LPB (FGGUB) 192, right c. Both are mentioned in Simionescu (1932: p. 217–218).

Description. The two discovered canines are very simple and very similar to each other (Figure 2). They have one long root, which is slightly wider in the upper tooth, and a long robust crown with slight signs of wear on its apex. The upper canine has a lingual crest that starts from the cingulum and ends near the tip of the tooth. It is followed distally by a smooth and shallow depression. This structure is faintly seen also in the lower canine, but its slightly damaged base conceals its exact morphology. The lower canine can be differentiated from the upper one by the presence of a distal heel in its base.

Comparisons. Simionescu (1932) assigned these canines to *Canis* sp., whereas Radulescu et al. (2003) likely assigned them to *Eu. odessanus*. The uncertainty arises from the lack of detailed catalogues in Radulescu et al. (2003). The identification of Simionescu (1932) was based on the then common conception that the large Upper Miocene and Plio-

Fig. 2 - Canines of cf. *Eucyon* sp. from Berești (Romania): (A) LPB (FGGUB) 10192 upper right canine in buccal (A1) and lingual (A2) views; (B) LPB (FGGUB) 192 lower right canine in buccal (B1) and lingual (B2) views.



Tab. 1 - Metrical comparison (in mm) of the canines of cf. *Eucyon* sp. from Berești (Romania) to that of selected *Eucyon* spp. Data sources: ¹Valenciano et al. (2022a), ²Montoya et al. (2009), ³Rook (1993).

	cf. <i>Eucyon</i> sp.		<i>Eu. khoikhoi</i>	<i>Eu. debonisi</i>	<i>Eu. adoxus</i>	<i>Eu. odessanus</i>	<i>Eu. monticinensis</i>
	LPB (FGGUB) 10192	LPB (FGGUB) 192	Langebaanweg ¹	Venta del Moro ²	Perpignan ³	Odessa Catacombs ²	Monticino Quarry ²
CL	10.7		6.8–7.7 7.1 (n=3)	7.0–7.1 7.1 (n=2)			
CW	7.5		4.8–5.4 5.1 (n=3)	5.4			
CW/L	0.70		0.70–0.75 0.72 (n=3)	0.77			
CH	20.2						
cL		10.0	5.8–7.2 6.7 (n=5)	6.3			
cW		7.1	4.2–5.1 4.6 (n=5)	4.4			
cW/L		0.71	0.65–0.72 0.70 (n=5)	0.70			
cH		19.9					
m1L			14.4–16.2 15.0 (n=6)	14.7–17.2 16.0 (n=12)	18.2–18.7 18.5 (n=2)	13.3–19.5 17.2 (n=12)	16.7–19.5 17.6 (n=5)

cene canids of the Old World belong to the genus *Canis*, whereas modern approaches classify them in the genus *Eucyon* Tedford & Qiu, 1996 (Rook 1993; Bartolini-Lucenti & Rook 2021; Valenciano et al. 2022a). The genus *Nyctereutes* Temminck, 1838, is another common canid from that period, but it can be differentiated from the present specimens by its smaller size and the slenderer and longer canines, as discussed below. Therefore, the material is herein attributed to the genus *Eucyon*. The comparison is based solely on metrical data as there are no published distinguishing characteristics in the canines of the species of the genus. Within this group, there are forms of varying size, as evidenced by the length of the lower carnassial (Table 1). The dimensions of the canines of species *Eucyon debonisi* Montoya et al., 2009, and *Eucyon khoikhoi* Valenciano et al., 2022a, suggest that the Berești specimens belong to a relatively larger species. During the Pliocene of Europe there are two species that could fit this size based on the m1L: *Eu. odessanus*, known from the Pliocene

of Odessa Catacombs in Ukraine (Odintsov 1967), and *Eucyon adoxus* (Martin, 1973), known from the Pliocene of Perpignan in France. Unfortunately, there are no criteria to distinguish between these two forms based on the canines. The geographical proximity favours *Eu. odessanus*, which would justify the assignment of Radulescu et al. (2003). However, it is herein preferred to follow a more cautious approach and identify these specimens as cf. *Eucyon* sp.

Genus *Nyctereutes* Temminck, 1838

Nyctereutes donnezani (Depéret, 1890)

Locality: Mălușteni.

Age: Ruscinian, Early Pliocene.

Material: AICUPM-754-SM-31, right hemimandible (Simionescu 1922: p. 452, 1930: p. 90–91).

Description. The specimen AICUPM-754-SM-31 is a right hemimandible, which is bro-



Fig. 3 - Right hemimandible of *Nyctereutes donnezani* (AICUPM-754-SM-31) from Măluşteni (Romania) in (A) lateral, (B) occlusal, and (C) lingual views. A2, B2 and C1 are non-scaled close-ups of p4 and m1 for A1, B1 and C2, respectively.

ken at the mesial plane of p2 and preserves p2–m1 and the alveoli of m2 and m3 (Figure 3). The mandibular corpus is notably slender. There are two mental foramina. The distal one is situated below the third premolar. The distal part of the mesial mental foramen is retained below the mesial part of p2. There are clear diastemata between the premolars, especially between p2 and p3. The subangular lobe is faintly present. The angular process is damaged, but the remaining part of its base attests to its relatively large size and its ventrolateral direction. The masseteric fossa is relatively deep. It extends distally near the mesial border of the mandibular condyle, and mesially until the level of m3. It is separated from the angular process by a thin ridge. The coronoid process is relatively low and distally inclined.

The second and third premolars are very simple, lacking any accessory cusps and having faint cingulids. They are asymmetrical, as their distal end is more elongated than the mesial one, forming a gradual heel. The fourth premolar has a strong distal accessory cuspid and a more developed cingulid, especially in its distal part. All premolars exhibit moderate dental wear, but their outline indicates that they were relatively high and acute. The lower carnassial is damaged by a crack that splits it in two. It shows considerable dental wear, especially in the talonid. The trigonid is relatively high, much higher than p4, with the protoconid being significantly higher than the paraconid. The mesial base of the paraconid is mesially extended towards p4. The metaconid is large, situated at the distolingual base of the protoconid and

detached from it. The talonid is slightly wider than the trigonid and shows a clear valley. However, the extreme wear does not allow the description of any cusps or cristids.

Comparisons. The present hemimandible was identified as “*Vu. donnezani*” by Simionescu (1922, 1930), whereas Radulescu et al. (2003) probably assigned it to the species *Eu. odessanus*. However, the latter authors did not provide a detailed synonymy correspondence, but, since *Eu. odessanus* is the only canid in their faunal list for Măluşteni, it is herein considered that this assignment most probably refers to the present specimen. Although the dimensions and age of AICUPM-754-SM-31 are similar to that of *Eu. odessanus*, initially found in the neighbouring Ukraine, the relatively wider teeth, the presence of a faint subangular lobe, and the absence of a secondary cuspid detached from the distal cingulid of p4 indicate that this specimen cannot be assigned to the genus *Eucyon*.

The genus *Nyctereutes* is represented by numerous species in the fossil record that have been found in Asia, Europe, and Africa (Daguenet & Sen 2019, and references therein). Among these species *N. donnezani* is one of the most prevalent, and was originally described from the Lower Pliocene of Perpignan (France). This species has been found in several other localities, including Layna (Lower Pliocene of Spain; Soria & Aguirre 1976; Bartolini-Lucenti et al. 2018), La Gloria 4 (Lower Pliocene of Spain; Alcalá 1994), and Çalta (Lower Pliocene of Turkey; Ginsburg 1998; Daguenet & Sen 2019) among others. The oldest fossils of this genus are from the latest Miocene to earliest Plio-

Tab. 2 - Metrical comparison (in mm) of the *Nyctereutes donnezani* hemimandible from Mălușteni (Romania) and *Nyctereutes* sp. from Berești (Romania) to that of other localities. Data sources: ¹Monguillon et al. (2004), ²Bartolini-Lucenti et al. (2018), ³Daguenet & Sen (2019), ⁴Tedford & Qiu (1991).

Species		<i>N. donnezani</i>				<i>N. tingi</i>	<i>N. vulpinus</i>	<i>N. megamastoides</i>	<i>Nyctereutes</i> sp.
Locality		Mălușteni	Perpignan ¹	Layna ²	Çalta ³	Yushe ⁴	Saint-Vallier ¹	Various ¹	Berești
C	L		5.8–7.1 6.5 (n=4)	7.2	7.1	6.6–8.5 7.5 (n=2)	5.6–6.5 6.1 (n=6)	5.8–6.4 6.1 (n=2)	7.6
	H								20.0
p2	L	7.7	7.0–7.4 7.2 (n=3)	6.1	8.2–8.5 8.3 (n=3)	8.2–9.4 8.6 (n=8)	6.2–7.8 6.9 (n=13)	6.0–6.9 6.5 (n=7)	
	W	3.2	2.8–3.1 3.0 (n=4)	2.5	3.3–3.4 3.3 (n=3)	3.6–4.1 3.8 (n=8)	2.8–3.2 3.0 (n=11)	2.7–3.0 3.0 (n=7)	
p3	L	8.3	7.7–8.6 8.1 (n=6)	7.1–7.5 7.3 (n=2)	8.4–9.0 8.8 (n=3)	9.0–10.6 9.8 (n=9)	7.5–9.2 8.5 (n=13)	7.2–8.0 7.7 (n=7)	
	W	3.4	2.8–3.1 3.0 (n=5)	2.1–2.7 2.4 (n=2)	3.4–3.6 3.5 (n=3)	3.8–4.5 4.1 (n=9)	3.0–3.6 3.3 (n=11)	2.9–3.3 3.1 (n=7)	
p4	L	9.7	8.6–10.7 9.7 (n=4)	9.0–9.1 9.1 (n=3)	9.8–10.2 10.0 (n=3)	10.2–12.1 11.2 (n=11)	9.0–10.3 9.7 (n=16)	7.0–9.6 8.7 (n=7)	
	W	5.6	3.6–4.1 3.8 (n=4)	3.5–3.9 3.7 (n=2)	6.5–8.0 4.4 (n=3)	4.9–5.9 5.2 (n=11)	3.7–4.7 4.2 (n=16)	3.7–3.9 3.8 (n=8)	
m1	L	16.8	14.6–17.3 15.7 (n=7)	13.6–17.0 15.4 (n=7)	15.4–17.6 16.3 (n=4)	17.5–19.3 18.2 (n=9)	14.7–16.8 15.9 (n=20)	13.8–16.5 15.1 (n=9)	
	W	6.9	5.8–6.8 6.3 (n=7)	5.2–6.8 6.3 (n=8)	6.5–8.0 7.2 (n=4)	6.9–8.3 7.7 (n=9)	5.8–7.1 6.4 (n=20)	5.6–7.1 6.3 (n=7)	

cene of Yushe, China (Tedford & Qiu 1991; Tedford et al. 2009) with the species *Nyctereutes tingi* Tedford & Qiu 1991, which has also been reported in the locality of Megalo Emvolon in Greece (Koufos 1997). This form can be differentiated from the present specimen and the other material of *N. donnezani*, based on its larger size, the hook-like angular process and the slightly wider premolars. These two species are very similar, and although a question of their distinctiveness has been raised (Koufos 1997; Tedford et al. 2009), recent studies have shown that they are indeed different (Daguenet & Sen 2019).

Nyctereutes sinensis (Schlosser, 1903) has been found in the Upper Pliocene of East Asia. This species can be distinguished from *N. donnezani* by the prominent subangular lobe and the broadened premolars and m1 talonid. These criteria are also applicable to other Upper Pliocene and Pleistocene species, including *Nyctereutes vulpinus* Soria & Aguirre, 1976, and *Nyctereutes megamastoides* (Pomel, 1843) (Monguillon et al. 2004; Bartolini-Lucenti 2017; Bartolini-Lucenti et al. 2018; Daguenet & Sen 2019). The trend of *Nyctereutes* during the Pleistocene was characterized by a gradual decrease in size (Table 2). This was accompanied by broadened dentition, which was better suited for opportunistic omnivory, and enlargement of the subangular lobe (Tedford et al. 2009; Bartolini-Lucenti 2017, 2019; Bartolini-Lucenti et al. 2018; Daguenet & Sen 2019). The hemimandible from Mălușteni exhibits intermediate size, a restricted subangular lobe, and narrow premolars and m1 talonid, which allow for its taxonomic assignment as *N. donnezani*.



Fig. 4 - Right C (LPB (FGGUB) 194) of *Nyctereutes* sp. from Berești (Romania) in mesial (A) and buccal (B) views.

Nyctereutes sp.

Locality: Berești.

Age: Ruscianian, Early Pliocene.

Material: LPB (FGGUB) 194, right C (Simionescu 1932: p. 217).

Description. The specimen LPB (FGGUB) 194 is a broken upper right canine (Figure 4). Its

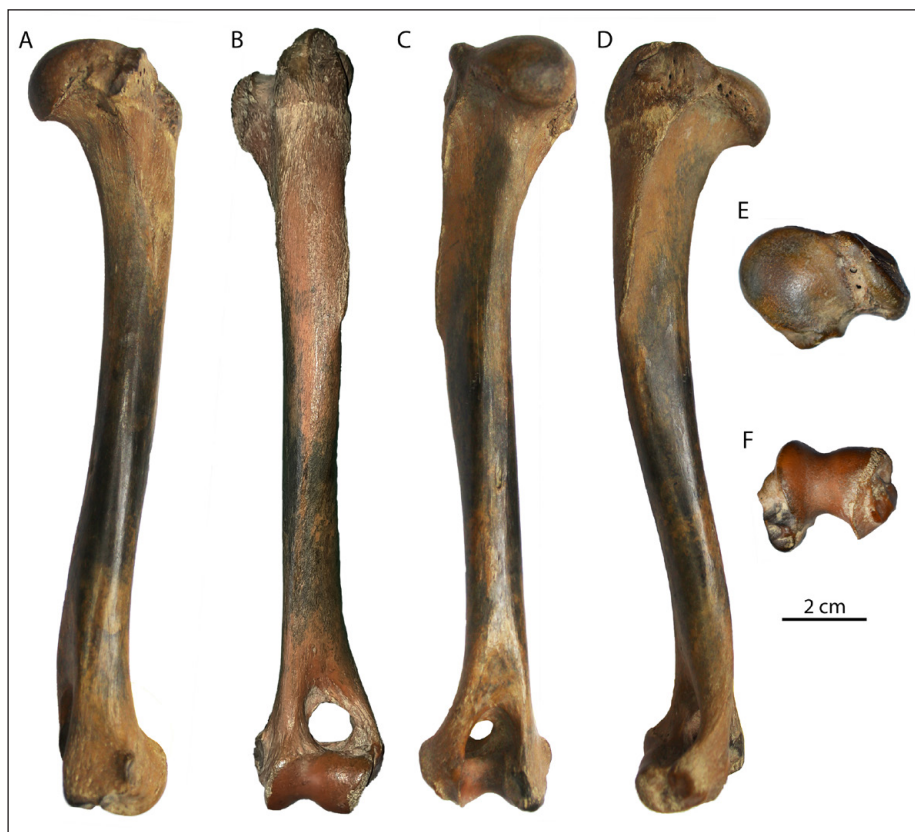


Fig. 5 - Left humerus of Canidae indet. (AICUPM-SM-108) from Măluşteni (Romania) in (A) medial, (B) anterior, (C) posterior, (D) lateral, (E) proximal and (F) distal views.

crown is broken in its middle sagittal plane. The remaining buccal shows that there is no cingulum, whereas the crown is considerably high and moderately curved.

Comparisons: Compared to the canines of cf. *Eucyon* sp. mentioned above from the same locality, this specimen is shorter in length, but respectively higher, resembling the canines of modern foxes. In contrast, the aforementioned specimens of cf. *Eucyon* sp. are stouter, having a larger base and being shorter in height. Therefore, the present canine resembles those of the genera *Vulpes* and *Nyctereutes*, rather than *Eucyon*. This specimen is, most probably, the one that Simionescu (1932) referred to as *Vulpes* sp., in the same manner that he attributed the hemimandible from Măluşteni to *Vu. donnezani*. However, the specimen is too long and slender to belong to *Eucyon*, but its preservation does not allow for a specific allocation (as shown in Table 2). It clearly belongs to an animal that is larger than the known species of *Vulpes* from this time period (e.g., Odintsov 1965; de Bonis et al. 2007; Bartolini-Lucenti & Madurell-Malapeira 2021), being herein identified as *Nyctereutes* sp. It should be noted that more derived species of the genus have relatively smaller (and shorter) upper canines, such as *N. me-*

gamastoides (e.g., Koufos 1993, fig. 3). However, the Pliocene representatives have longer canines, like *N. donnezani* (e.g., Bartolini-Lucenti et al. 2018, fig. 2C; Dagueneat & Sen 2019, fig. 2D). Specific attribution is avoided due to the poor condition of the specimen.

Canidae indet.

Locality: Măluşteni.

Age: Ruscinian, Early Pliocene.

Material: AICUPM-SM-108, left humerus.

Description. The specimen AICUPM-SM-108 is a complete left humerus (Figure 5). The proximal epiphysis has a large globular head, a developed, lip-shaped greater tuberosity and a more distally placed lesser tuberosity. The shaft is very long and slender, and the deltoid crest is faint. The distal half of the shaft is relatively straight. A large, round supratrochlear foramen is present at the distal end of the shaft, covering most of the width of the bone. The olecranon fossa is relatively deep, despite the expansion of the supratrochlear foramen. The entepicondylar foramen is absent. The medial and lateral epicondyles of the distal epiphysis are rela-

tively small, even though the latter is well-developed posteriorly. The trochlea is distinctly longer than the capitulum, even though it is relatively narrow. The two latter structures are separated by a faint groove. The capitulum is not differentiated in two distinct parts, but it retains a rather smooth distal and anterior surface.

Comparisons. The long shaft, the big supratrochlear foramen, the absence of the entepicondylar foramen, the small medial epicondyle and trochlea, as well as the non-differentiated capitulum indicate that the specimen belongs to a canid. Its slender shaft, the faint deltoid crest and the relatively small trochlea and epicondyles suggest that it does not belong to a relatively robust animal, but rather resembles more the morphology of the specimens published by Depéret (1890) and Bartolini-Lucenti et al. (2018) as *N. donnezani* and by Tong et al. (2023) as *Nyctereutes* sp. However, based on metrical data, it appears that AICUPM-SM-108 is larger than the size range of *N. donnezani* or *Eu. kboikboi* (Table 3), particularly in the distal epiphysis. Rook et al. (1991) depicted a complete humerus of *Eu. monticinensis* (then known under the name *Canis* sp.) that appears sturdier than that of *Nyctereutes*. Even though the relative proportions of this form are similar to that of the humerus from Mălușteni (Table 3), its dimensions are considerably smaller. Therefore, the specimen from Romania must belong to a relatively larger canid species. In the absence of directly comparable data, this specimen is herein attributed to Canidae indet.

Species Measurement /Locality	Canidae indet.	<i>N. donnezani</i>		<i>Eu. kboikboi</i>	<i>Eu. monticinensis</i>
	Mălușteni	Roussillon	Layna	Langebaanweg	Monticino
L	148.0				120.6
APDp	27.5		25.5–29.3 27.4 (n=2)		19.4
TDp	33.9				23.2
APDm	13.9			9.0–9.2 9.1 (n=3)	8.9
TDm	12.0			8.9–9.3 9.1 (n=3)	9.0
APDd	24.3			16.5–17.2 16.8 (n=3)	16.8
TDd	30.7	22.0	20.4–25.5 22.9 (n=4)	21.8–24.4 22.9 (n=3)	21.0
TDtr	21.7			12.6–13.7 13.0 (n=3)	12.2

Tab. 3 - Metrical comparison (in mm) between the humeri of *Nyctereutes donnezani* from Mălușteni (Romania), Roussillon (France; Depéret 1890), Layna (Spain; Bartolini-Lucenti et al. 2018), and *Eucyon kboikboi* from Langebaanweg (South Africa; Valenciano et al. 2022a).

Family Mustelidae Batsch, 1788
Subfamily Lutrinae Bonaparte, 1838
Genus *Paludolutra* Hürzeler & Engesser, 1976

Paludolutra sp.

Locality: Pogana 1.

Age: Turolian, Late Miocene.

Material: MVP-SN-PG67, partial maxilla with right P4.

Description. The specimen MVP-SN-PG67 is a small part of a right maxilla that preserves only the upper carnassial and part of the region where the M1 would be (Figure 6). The latter is absent and the surface of the maxilla in its place is particularly rugose with small pores. The P4 is complete with signs of dental wear in the carnassial blade and the protocone region. The cingulum is very robust, especially in its mesiobuccal part. The outline of the tooth is sub-triangular to quadrate. The paracone is the largest cusp in all dimensions and forms a semi-lunar/angular carnassial blade with the very restricted metastyle. There are no signs of a parastyle. The lingual part of the tooth is considerably developed, being expanded almost until the distal end of the blade, forming a large valley. A significantly developed and worn protocone is present in the most mesial part of the valley, detached from all the other cusps, but very closely positioned to the paracone. The lingual border of the valley hosts two additional cusps: a well-developed hypocone, approximately at the middle plane of the paracone, and a hypoconule, at the mesial plane of the metastyle.

Comparisons. The genus *Paludolutra* Hürzeler & Engesser, 1976, belongs to the group of bunodont otters. This group is characterized by the very wide and robust dentition with additional cusps in the P4 and M1 (e.g., Willemsen 1992; Morales & Pickford 2005; Pickford 2007; Kargopoulos et al. 2021b, 2022). In Europe it includes the genera *Paludolutra*, *Tyrrhenolutra* Hürzeler, 1987, *Sivaonyx* Pilgrim, 1931, *Vishnuonyx* Pilgrim, 1932, and *Enhydriodon* Falconer, 1868. The species within these genera can be differentiated by metrical criteria. However, due to the high number of the species in some genera, it is simpler to base intergeneric comparison on morphological characteristics, because the P4 is a diagnostic element for the four of them. The specimen described here differs from *Vishnuonyx* on the more distally expanded lingual part of the tooth, the absence of a parastyle, the protocone not being situated right next to the hypocone and the more developed cingulum (Pilgrim

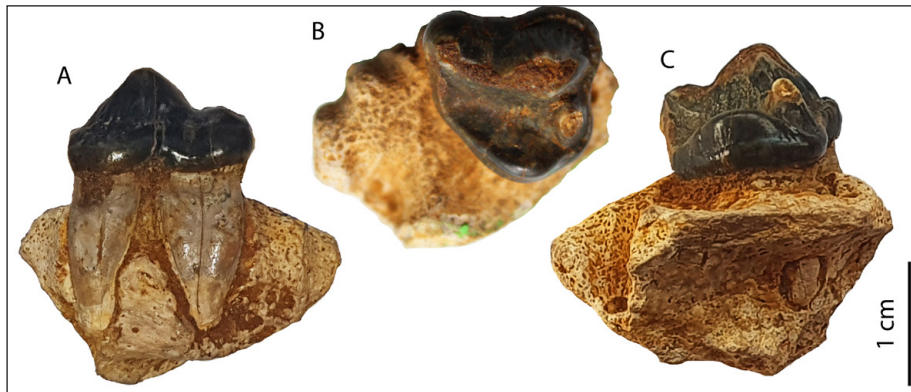


Fig. 6 - Maxilla of *Paludolutra* sp. (MVP-SN-PG67) from Pogana 1 (Romania) in (A) buccal, (B) occlusal and (C) lingual views.

1931; Pickford 2007; Grohé et al. 2020; Kargopoulos et al. 2021b, 2022). *Tyrrhenolutra helbingi* Hürzeler, 1987, is the only species of its genus. It was found in the latest Miocene of Montebamboli (Italy), and co-existed with *Paludolutra*. However, it can be differentiated from *Paludolutra* and the described specimen by its less developed lingual part of the tooth, the smaller and less individualised protocone and the absence of a hypocone. *Sivaonyx* is primarily identified by its lower teeth. However, when upper carnassials are assigned to this genus, they usually have low lingual cusps, a present parastyle, and a protocone situated near the hypocone (Pickford 2007; Grohé et al. 2013; Valenciano & Govender 2020). Finally, *Enhydriodon* is the most derived genus of this group, exhibiting significant adaptations in its postcanine teeth. Typically, its P4 is very wide, with a hypocone larger than the protocone, additional cusps on the lingual side, a concave buccal outline, and an enlarged parastyle (Pickford 2007; Geraads et al. 2011; Grohé et al. 2022). However, *Paludolutra* is distinguished by a relatively longer P4 with sub-triangular shape, a distinct angle in the carnassial blade, the absence of a parastyle, and a protocone attached to the distolingual end of the paracone (Hürzeler 1987; Morales et al. 2005). These traits align perfectly with the morphology of the described specimen.

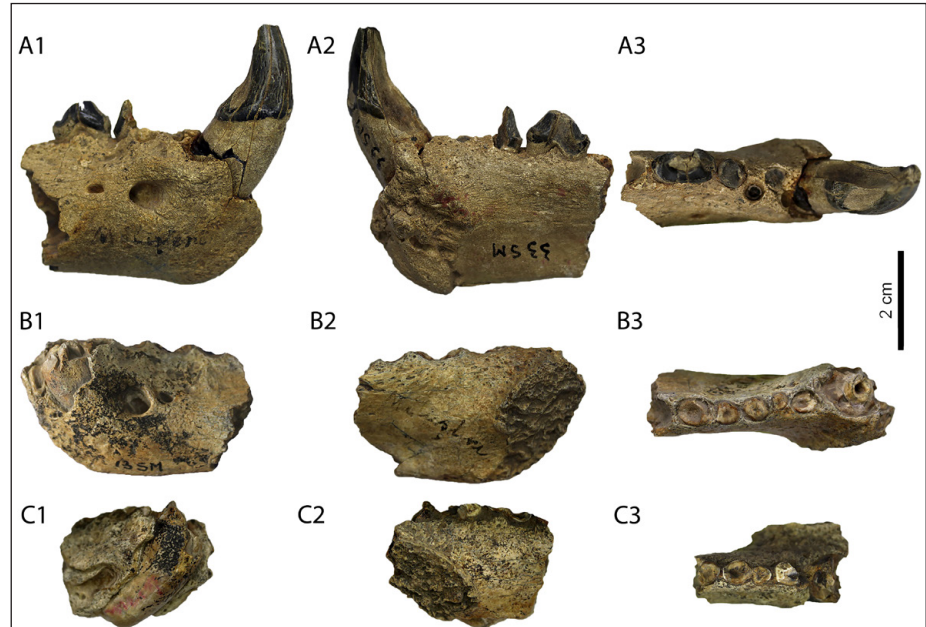
The genus *Paludolutra* is only known from limited material, which is restricted to the Upper Miocene of Europe. The type species, *Paludolutra campanii* (Meneghini, 1863), is known from the Upper Miocene of Montebamboli (Baccinello) in Italy (Hürzeler & Engesser 1976; Hürzeler 1987). Another species of the same genus, *Paludolutra maremmana* Hürzeler, 1987, is also found at the same locality. The species *Paludolutra lluecai* (Villalta Comella & Crusafont-Pairó, 1945), originally described from Los Algezares (Spain), has also been represented by an upper carnassial from the locality of Rambla de Valdecebro II

(= El Arquillo in Alcalá, 1994; Spain). This specimen was initially described as a new species, *Sivaonyx lebrmani* Crusafont-Pairó & Golpe-Posse, 1962b. *Paludolutra lluecai* is also present in the upper Turolian Spanish localities of Los Mansuetos and Conclud (Cerro de la Garita) (Crusafont-Pairó & Golpe-Posse 1962a; Alcalá 1994; Fraile et al. 1997). This Spanish form is characterised by a less developed lingual part of the upper carnassial, which ends distally at approximately the middle plane of the metastyle (Crusafont-Pairó & Golpe-Posse 1962b; Alcalá 1994). On the other hand, *Pa. campanii* has a more developed lingual side of the tooth, with a strong protocone and a hypocone that is more developed than the hypocone. Additionally, it has a more developed cingulum that covers a larger area in the buccal and mesial part of the tooth (Hürzeler 1987). The species *Pa. maremmana* seems to fit better with the morphology of the specimen from Pogana 1, having an intermediately developed lingual region that reaches the end of the metastyle and a restricted buccal cingulum. The only difference between the specimens is that the hypocone is larger than the hypocone in the specimen from Pogana 1, whereas the opposite is seen in the Montebamboli specimen (Hürzeler 1987). Metrical comparison between the three species can be seen in Table 4. Even though the three forms are comparable in size, with *Pa. lluecai* being slightly smaller than

Species	<i>Paludolutra</i> sp.	<i>Pa. maremmana</i>	<i>Pa. campanii</i>	<i>Pa. lluecai</i>
Locality	Pogana 1	Montebamboli ¹	Montebamboli ¹	Rambla de Valdecebro II ² Cerro de la Garita ³
P4L	14.5	15.1	14.0–16.1 15.4 (n=3)	13.0–13.1 13.1 (n=2)
P4W	12.5	12.8	14.5–15.2 14.9 (n=3)	12.8–13.7 13.3 (n=2)
P4W/P4L	0.86	0.85	0.93–1.04 0.97 (n=3)	0.98–1.05 1.02 (n=2)

Tab. 4 - Metrical comparison (in mm) of the P4 of *Paludolutra* sp. from Pogana 1 (Romania) to *Paludolutra* spp. from Italy and Spain. Data sources: ¹Hürzeler (1987), ²Crusafont-Pairó & Golpe-Posse (1962b), ³Alcalá (1994).

Fig. 7 - Mandibular remains of *Lutra? rumana* from the Lower Pliocene of Mălușteni (Romania): (A) AICUPM-759-SM-33, right fragmentary hemimandible with c, p3 and p4 in buccal (A1), lingual (A2), and occlusal (A3) views; (B) AICUPM-753-SM-13, left fragmentary hemimandible in buccal (B1), lingual (B2), and occlusal (B3) views; (C) AICUPM-SM-105, right fragmentary hemimandible in buccal (C1), lingual (C2), and occlusal (C3) views.



the other two, the P4W/P4L ratio can differentiate the species *Pa. maremmana* which has a value of 0.85 compared to the > 0.90 values of the other forms.

However, there are some noted differences between the present specimen and *Pa. maremmana*. These include the more developed lingual cingulum of the former and the more distantly placed hypocone and hypoconule. Additionally, although the metrical comparison between the different species shows a closer resemblance to *Pa. maremmana*, it must be noted that the P4 of the holotype is broken, and there are no known complete specimens or any reliable statistically significant samples of this form. Finally, *Pa. maremmana* is a species that belongs to the Tusco-Sardinian palaeobioprovince (Rook et al. 2006; Abazzi et al. 2008), which is characterized by interesting evolutionary traits that have been connected to insular endemism. Any report of this species outside its known range should be based on more complete specimens. Therefore, due to these uncertainties, even though there is some similarity to *Pa. maremmana*, it is preferred to assign the premolar from Pogana 1 to *Paludolutra* sp.

Genus *Lutra* Brünnich, 1772

Lutra? rumana Simionescu, 1922

Locality: Mălușteni.

Age: Ruscinian, Early Pliocene.

Material: Mălușteni: AICUPM-759-SM-33, right fragmentary hemimandible with complete c, fragmented p3 and a nearly complete p4; AICUPM-753-SM-13, left fragmentary hemimandible;

AICUPM-SM-105, right fragmentary hemimandible. All three are mentioned in Simionescu (1922: p. 452) and Simionescu (1930: p. 91–92).

Remarks. These three fragments consist of the type material initially mentioned by Simionescu (1922) and then described further by Simionescu (1930).

Description. The symphysis of the mandible is rostrocaudally long and mediolaterally robust, forming a faint mandibular flange below the c (Figure 7). The distal part of the symphysis reaches the p3. There are two mental foramina on the mandibular corpus. The most rostral one is very large, rounded, and placed below the p3. The caudal one is much more reduced (circa two thirds) and located below the p4. The lower canines are conical and distally curved, exhibiting a conspicuous cingulid in their distal part (Figure 7A). There is no evidence of p1. There seems to be a noted degree of variability in the orientation of the alveoli of the premolars. In AICUPM-759-SM-33 the alveoli of both p2 and p3 are turned buccolingually, contrary to the specimens AICUPM-753-SM-13 and AICUPM-SM-105, in which alveoli are more in line with the toothrow, even though they are still crowded. All the preserved lower premolars are double rooted. The p3 has no distal accessory cuspid. The preserved p4 shows that there are no mesial nor distal accessory cuspid. It is oval and shows a high crown with a marked distal cingulid. Both AICUPM-759-SM-33 and AICUPM-753-SM-13 preserve a portion of the mesial m1 alveolus.

Species	<i>Lutra? rumana</i>			<i>Lu. cf. bravardi</i>	<i>Lu. affinis</i>	<i>En. praegalictoides</i>	<i>Pa. maremmana</i>	<i>T. helbingi</i>
	SM-33	SM-13	SM-105	Hajnáčka ¹	Maramena ²	Monte Tuttavista ³	Montebamboli ⁴	Baccinello V1 ⁴
p2L	(8.6)	(7.4)	(7.4)			4.4–5.2 4.6 (n=6)		5.7
p2W	(5.5)	(4.4)	(4.6)			3.0–3.6 3.4 (n=5)		3.7
p3L	(11.3)	(9.3)	(9.8)	5.8	4.5–4.9 4.7 (n=2)	5.5–6.4 6.0 (n=10)	9.0	7.4
p3W	(6.5)	(5.1)	(4.9)	3.2	2.7 (n=2)	3.6–4.1 3.9 (n=8)		4.2
p4L	12.7	(12.7)		6.2–8.0 7.1 (n=2)	6.4	6.2–7.2 6.7 (n=10)	12.7	9.4
p4W	7.3	(5.5)		3.5–3.8 3.7 (n=2)	3.3	3.9–4.3 4.0 (n=8)	8.0	5.3

Tab. 5 - Metrical comparison (in mm) of the material of *Lutra? rumana* from Măluşteni (Romania) to that of other otter-like taxa from the Pliocene of Eurasia. Data from: ¹Fejfar & Sabol (2004), ²Schmidt-Kittler (1995), ³Rook et al. (2018), ⁴Hürzeler (1987).

Comparisons. The taxonomic affinities of the described material are difficult to ascertain due to the absence of diagnostic dentition in the described material. However, the robustness of the mandible, the large mental foramina, the developed mandibular symphysis, the crowded premolars, the apparent absence of p1, the robust dentition, the developed cingulids, and the absence of accessory cuspids in p3 and p4 support the assignment of the three hemimandibles to the subfamily Lutrinae.

These specimens are distinguishable from *Lutra bravardi* Pomel, 1843, and *Lutra affinis* Gervais, 1859, due to their large size, as can also be seen in Table 5, based on the specimens from Hajnáčka in Slovenia (Fejfar & Sabol 2004) and Maramena in Greece (Schmidt-Kittler 1995). The same applies to most of the known otter-like ictonychine species that are known from the Pliocene and Lower/Middle Pleistocene of Eurasia, such as *Enhydriactis melina* (Pei, 1934), *Enhydriactis praegalictoides* Rook et al., 2018, and *Martellictis ardea* (Gervais, 1850) (Willemssen 1992). However, the hemimandible of *Pa. maremmana*, and in a lesser degree *T. helbingi*, could potentially match the Romanian specimens (Hürzeler 1987). Therefore, in the absence of diagnostic dentition, it is preferred to refer to these specimens as *Lu.? rumana*, until more material is uncovered.

Subfamily Guloninae Gray, 1825

Genus *Martes* Pinel, 1792

Martes cf. wenzensis Stach, 1959

Locality: Măluşteni.

Age: Ruscinian, Early Pliocene.

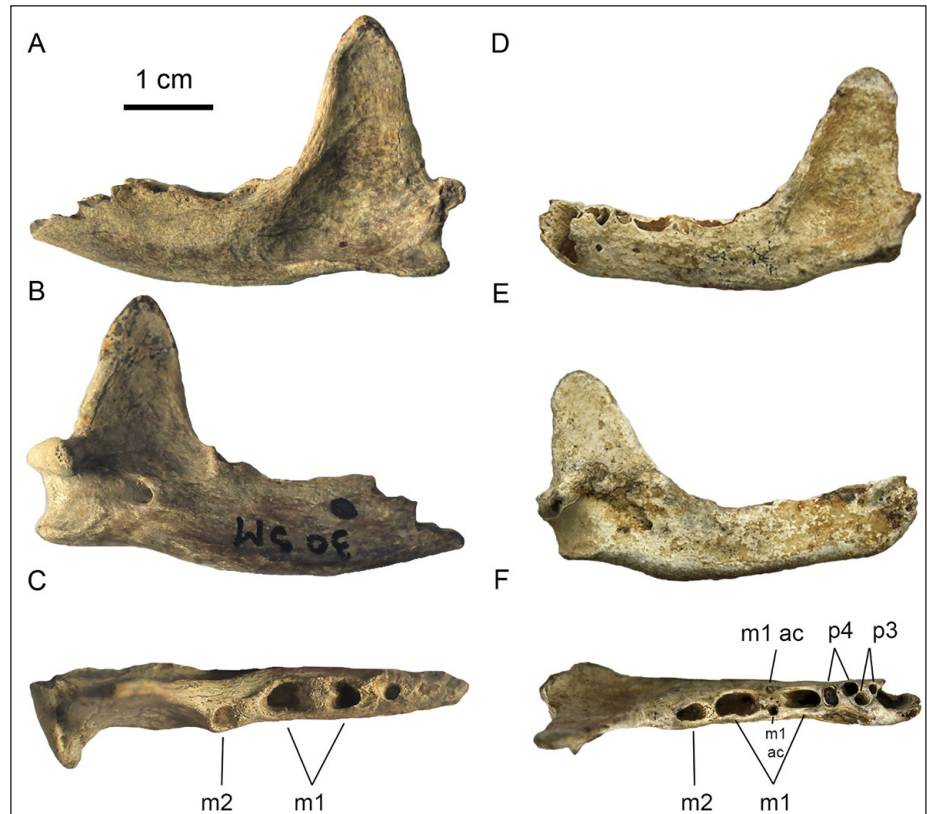
Material: AICUPM-753-SM-30, left hemimandible (Simionescu 1930: p. 95).

Description. The specimen AICUPM-753-SM-30 is a fragmentary and edentulous hemi-

mandible retaining the distal alveolus of the p4, and the complete alveoli of m1 (m1L=10.9 mm; m1W=3.9 mm) and m2 (m2L= 2.0 mm; m2W=1.5 mm) (Figure 8A–C). The ventral part of the mandibular corpus is slightly concave. The coronoid process is straight and high. The masseteric fossa is deep, and its rostral end reaches the plane of the m2 alveolus. Most of the angular process is preserved and located in line with the tooththrow. It has a well-developed angular process. The m1 possesses two alveoli with a regular development, whereas the m2 just one.

Comparisons. Simionescu (1930) assigned AICUPM-753-SM-30 to *Mustela* aff. *martes*, due to some similarities with the pine marten (*Martes martes*). However, the size of its alveoli in relation to of the tooththrow and the length of the preserved mandible exclude its classification in the mustelid genera *Mustela* (weasels), *Meles* Brisson, 1762 (badgers), and *Lutra* (otters). Instead, it suggests that it belongs to a member of the genus *Martes*. During the Pliocene, various extinct martens are known, highlighting the Upper Miocene/Lower Pliocene *Martes lefkonensis* Schmidt-Kittler, 1995, from Maramena (Turolian–Ruscinian interval, Greece) (Schmidt-Kittler 1995) and the lower Upper Pliocene *Martes wenzensis* Stach, 1959, from Weże-1 (Poland), dated in 3.8–3.4 Ma (Stach 1959; Stefaniak et al. 2020; Marciszak et al. 2023). Some authors (Sato et al. 2003) consider this species as the first true marten, while others suggest that the genus has been present since the Late Miocene (Valenciano et al. 2020, 2022b). The alveolar dimensions of the specimen from Măluşteni are closer to that of *Martes wenzensis* (m1L=11.0; m1W=4.5; n=1) than to those of *Martes lefkonensis* (m1L=7.2–7.6; m1W=2.8–3.2; n=4). It must be noted that the measurements of the two latter species concern the teeth and not the alveoli, so the alveolar dimensions should be slightly lower. However, it is impossible to be more specific in the

Fig. 8 - Hemimandibles of *Martes* cf. *wenzensis* (AICUPM753-SM30, A-C) and *Mustela* sp. (AICUPM-SM-110, D-F) from Mălușteni (Romania) in buccal (A, E), lingual (B, E), and occlusal (C, F) views. m1 ac= accessory root of m1.



metrical comparison without knowing the morphology of the dentition. In any case, it is justifiable to conclude that the current specimen belongs to the range of *Martes wenzensis* and not to that of *Martes lefkonensis*. However, as there is no evidence of diagnostic dentition, it is herein preferred to attribute this hemimandible to *Martes* cf. *wenzensis*.

It must be noted that Simionescu (1932) reported an additional hemimandible with a m1 from the Pliocene locality of Berești as *Mustella* aff. *martes* (sic; m1L=11.5 mm). The development degree of the m1 talonid, as well as the dimensions of the complete tooth suggest affinities with the central European *Martes wenzensis*. Unfortunately, this specimen is currently lost, making it impossible to confirm the presence of this species from this locality.

Subfamily Mustelinae Batsch, 1788

Genus *Mustela* Linnaeus, 1758

Mustela sp.

Locality: Mălușteni.

Age: Ruscinian, Early Pliocene.

Material: AICUPM-SM-110, a broken left hemimandible with the alveoli of c, p3–m2 (Simionescu 1922: p. 452, 1930: p. 95).

Remarks. Simionescu (1930) assigned a left hemimandible (AICUPM-SM-110), as well as a fragmentary ulna (AICUPM-SM-111) and a sacrum (AICUPM-SM-112) to *Mustela* aff. *robusta*. The original description of this material is controversial. The left hemimandible (AICUPM-SM-110) figured and briefly described by Simionescu (1930: fig. 15, and Pl. II, fig.18) had a single, low and unicuspid p3. However, in the same work, an edentulous left hemimandible virtually identical to AICUPM-SM-110 was attributed to *Mustela* aff. *martes* (Simionescu 1930: Pl. II, fig.19, 19a). A fragmented lower premolar, which likely represents the missing one from AICUPM-SM-110 was found with the specimen. Thus, after reviewing the material, we conclude that during the manuscript writing process of Simionescu (1930), the premolar was broken off from the mandible. This resulted in a repetition of the same hemimandible in Simionescu (1930), and we confirm that all figures represent the same specimen (Simionescu 1930:Pl. II, fig. 18, 19, 19a). Furthermore, due to the position in the tooththrow and the morphology of the broken premolar, it is re-interpreted as a p4.

Description. The hemimandible AICUPM-SM-110 preserves the alveoli for c, p3 (p3L=3.0 mm; p3W=1.4 mm), p4 (p4L=4.0 mm; p4W=2.2

mm), m1 (m1L=11.7 mm; m1W=3.6 mm), and m2 (m2L=2.7 mm; m2W=1.4 mm) (Figure 8D–F). The mandibular corpus is low, and its ventral profile is almost straight. The coronoid process is high and somewhat tilted distally. The masseteric fossa is shallow. There is no sign of the p1 and p2 alveoli. However, due to the fragmentation of the symphysis and the area of the canine alveolus, we cannot discard the presence of at least a tiny p2 alveolus. Both p3 and p4 alveoli are double-rooted and imbricated in relation to the tooth row. The m1 is very elongated. It shows the typical two large alveoli (mesial and distal) of most carnivorans. However, there are two extra accessory roots at the level of the m1 protoconid, placed lingually and buccally respectively. The m2 alveolus is single, oval, and relatively elongated.

Comparisons. The hemimandible can be linked to the genus *Mustela* due to the relatively long m1 and the short tooth row with imbricated mesial premolars. Additionally, the very large size of the m1 alveoli rules out its assignment to other typical Pliocene mustelids from the subfamily Ictonychinae Pocock, 1921 (*Baranogale* Kormos, 1934, and *Vormela* Blasius, 1884) (Spassov 2001). The existence of accessory roots in the m1 of mustelids is not a common trait but has been reported in both badgers and weasels (e.g., Hugueney 1975; García-Martínez et al. 2020). Among weasels, it has only been cited in the living stoat *Mustela erminea* Linnaeus, 1758 (Hugueney 1975; Baryshnikov 2009; Marciszak, 2016). However, based on our own personal observations, polecats (*Mustela putorius* Linnaeus, 1758) and stoats possess two well-developed accessory roots in both lingual and buccal sides at the base of the m1 protoconid. The specimen from Măluşteni also exhibits the same accessory roots, indicating strong affinities with extant *Mustela* species.

Simionescu (1930) determined AICUPM-SM-110 as *Mustela* aff. *robusta* based on Pleistocene fossils of *Mustela robusta* Newton, 1894, from England (Reynolds 1912). However, such attribution is not followed herein, due to the significant temporal gap between the localities. Subsequent discoveries from the Lower Pliocene (Ruscinian, MN 15) of Central and Eastern Europe revealed the existence of small-sized weasels (*Mustela plioerminea* Stach, 1959, and *Mustela pliocaenica* Stach, 1959) during that period (Stach 1959; Morlo & Kunderát 2001; Fejfar & Sabol 2004). The remarkable size of the m1 al-

veoli of AICUPM-SM-110 (m1L= 11.7 mm) shows that the hemimandible cannot belong to *Mu. plioerminea* (m1L=5.4 mm; m1W=2.3 mm; n=1) or *Mustela pliocaenica* (m1L=4.8–5.5 mm; m1W=1.6–1.8 mm; n=3) (Stach 1959; Morlo & Kunderát 2001). Its size also exceeds the extant values for *M. putorius* (m1L=6.9–8.9 mm; m1W=2.9–3.6 mm; n=6; A.V. pers. data), although the values for p3–p4 fall within the range of variation of *M. putorius*. The relatively large *Mustela* from Măluşteni may be related to the lineage of the subgenus *Putorius* Cuvier, 1817, which includes the largest extant representatives of *Mustela*: *Mu. putorius* (European polecats), *Mustela eversmannii* (Lesson, 1827) (steppe polecats) and *Mustela nigripes* (Audubon & Bachman, 1851) (black-footed ferrets). However, without knowing the morphology of the dentition, we cannot provide more specific information, and we assign this material to *Mustela* sp.

Another potential small-sized mandible with complete p2–p3 and m1 was also described from Măluşteni as *Mustela* aff. *putorius* (Simionescu 1930: fig.17). Regrettably, this specimen is missing, making it impossible to compare the two specimens.

Family Mephitidae Bonaparte, 1845
Genus *Promephitis* Gaudry, 1861

'*Promephitis*' *malustenensis* Simionescu, 1930

Locality: Măluşteni.

Age: Ruscinian, Early Pliocene.

Material: AICUPM-734-SM-12, a left hemimandible with c, p2, m1 and the alveolus of p3 (Simionescu, 1930: p. 93–94).

Remarks. This is the holotype of the species, originally described by Simionescu (1930).

Description. The hemimandible is broken just distally of the lower carnassial (Figure 9). The ventral border of the mandibular corpus is also damaged ventrally to the m1. The mandibular corpus is relatively short in height and length. It exhibits a broadening at the mesial plane of p3, whereas the remaining undamaged part ventrally of p3, p4 and m1 is relatively straight. The alveolar plane, on the other hand, creates an arched line, reaching its lowest point at the level of p4. A mental foramen is present ventrally of the distal part of p2. The mandibular symphysis is short, extended until the distal end of p2. There are no visible diastemata between the alveoli or the remaining teeth.

The lower canine is long and high, and its tip is slightly worn. Its mesial part is relatively straight, whereas the distal part is hook-shaped, ending distally to a basin-like slope. This slope is marked lingually and buccally by two strong cristids, and medially by two fainter cristids. A cingulid is present at the perimeter of the tooth, being stronger in its buccal side and more bulbous in its lingual side. There are no indicators of a p1. The second premolar is relatively simple, having only the main cuspid, followed distally by a lobe that ends in a small basin. The cingulid is moderately developed, forming a small cuspid at its distal lip. The tooth is mesially inclined and is oblique in comparison to the tooththrow line. The alveolus of p3 shows that the tooth had two roots and that its distal part was much longer and wider than its mesial part. Its orientation is oblique to the tooththrow axis. The alveoli of p4 are almost completely covered by secondary ossification. It is possible that the tooth may have fallen off during the life of the individual and the trauma was then healed. The lower carnassial is complete with dental wear on the trigonid cuspid. A cingulid is present in the perimeter of the base of the tooth, being more prominent in its mesiobuccal part. It has two roots, one below the trigonid and one below the talonid. The protoconid is the highest cuspid, being considerably higher than the other trigonid cuspid. Its tip is distally inclined. The paraconid is relatively long and it is also distally inclined. The metaconid is well developed, but much lower than the other two trigonid cuspid. It is more distally situated than the protoconid and its base is relatively detached from the base of the latter. The talonid is enlarged, broader than the trigonid, with a clear valley covering most of it. The hypoconid is relatively large, covering most of the buccal part of the talonid rim. No other clear cuspid are present in the talonid.

Comparisons. The generic status of this small-sized musteloid from Mălușteni has been considered as questionable in previous works (Pilgrim 1933; Wang & Qiu 2004; Geraads & Spassov 2016), a viewpoint that is also adopted herein. Simionescu (1930) attributed it to *Promephitis* (Mephitidae), making it the single Pliocene form of the genus in Europe. However, Pilgrim (1933) noted that the mandibular ramus and the premolars were too long to belong to this genus. Metrically, the m1 of AICUPM-734-SM-12 is proportionally comparable to some species of *Promephitis* from the Upper Miocene



Fig. 9 - Hemimandible of *Promephitis* *malustenensis* (AICUPM-734-SM-12) from Mălușteni (Romania).

of Eurasia (e.g., *Promephitis bootoni* from several Chinese localities and *Promephitis lartetii* Gaudry, 1861, from several localities in Greece), but smaller and slenderer than that of the Turolian/Ventian *Promephitis alexejewi* and *Promephitis maeotica* (e.g., Wang & Qiu 2004; Montoya et al, 2011; Geraads & Spassov 2016) (Table 6). However, the presence of a simple lingual rim in the m1 talonid with absent entoconid and entoconulid, as well as a relatively large p4 (inferred from the long space for the p4 in the mandible), argue against its classification as a *Promephitis*. Several features of this genus are convergent with members of the subfamily Ictonychinae, which includes, among others, the extant marbled polecats and grisons. Those are the curvature and morphology of the canine, and the size and shape of the p2 and m1 (e.g., Spassov & Spiridonov 1993; Spassov 2001). Therefore, this species could alternatively be a member of Ictonychinae, possibly similar to *Vormela prisca* Teilhard de Chardin & Leroy, 1945, from the Pliocene of China, even though the m1 talonid of *Prom.* *malustenensis* is comparatively longer. Therefore, in the absence of clear results, the original genus is retained until more material is available to make a more certain assignment.

	'Prom. <i>malustenensis</i>	Prom. <i>hootoni</i> ¹	Prom. <i>larteti</i> ²	Prom. <i>alexjewi</i> ^{2,3}	Vo. <i>prisca</i> ⁴
cL	4.0		3.1–4.5 3.8 (n=6)		
cW	3.2		2.1–3.7 2.9 (n=4)		
p2L	2.5				
p2W	2.0				
m1L	9.1	7.8–10.0 9.0 (n=15)	8.5–9.3 8.7 (n=6)	10.4–10.6 10.5 (n=3)	7.0
m1W	3.4	3.6–4.6 4.0 (n=14)	3.6–4.4 3.9 (n=4)	4.3–4.8 4.6 (n=3)	

Tab. 6 - Metrical comparison (in mm) of the hemimandible (AI-CUPM-734-SM-12) of '*Promephitis malustenensis* from Măluşteni (Romania) to other related forms. Data from: ¹Wang & Qiu (2004), ²Geraads & Spassov (2016), ³Montoya et al. (2011), ⁴Teilhard de Chardin & Leroy (1945).

Family Ursidae Fischer von Waldheim, 1817
Genus *Ursus* Linnaeus, 1758

Ursus sp.

Locality: Măluşteni.

Age: Ruscinian, Early Pliocene.

Material: LPB (FGGUB) 1066, left MtIII.

Description. The specimen LPB (FG-GUB) 1066 is a complete left third metatarsal of a bear (Figure 10). It is generally robust and stout. The proximal articular surface is the dorsoplantarly longest part of the bone. Its dorsal part is trapezoidal in shape, with the medial part being wider than the lateral. This is followed plantarly by a constricted neck that gradually ends in a wider platform. The overall shape of the articular surface resembles a notched hook. The articulation with the MtII is formed by two surfaces: a dorsal

oval articular surface that is slightly curved proximally, a plantar triangular articular surface (smaller than the dorsal one), which is followed distally by a deep notch than slopes into a protruding lip. The articulation for the MtIV includes a similar overall view to that for the MtII. However, the two proximal articular surfaces are much more restricted proximodistally (almost linear), and instead of a plantar notch, there is a more centrally placed pit. The shaft is short and wide, reaching its narrowest point just distally to the lip of the articulation with MtII. The distal part of the shaft, just before the distal articular surface, shows one medial and one lateral protrusion. The former is proximodistally longer, but mediolaterally shorter than the latter. Additionally, the plantar and dorsal parts of the shaft at this plane are slightly remodeled, quite possibly due to the attached tendons. The distal articular surface resembles a proximodistally compressed sphere, and it exhibits a sagittal crest that almost reaches the shaft on its plantar side.

Comparisons. The morphology of the specimen is very similar to that of the MtIII of *Ursus arctos* Linnaeus, 1758, demonstrating their close affinities. However, there are some minor differences that are worth mentioning. The plantar part of the proximal epiphysis is more developed, being wider and more curved. The shaft is more robust, and has wider mediolateral protrusions at its border with the proximal and distal epiphyses. Additionally, the articular surfaces for the MtII and MtIV are less pronounced.

Despite being morphologically similar to the brown bear MtIII, the specimen is consider-

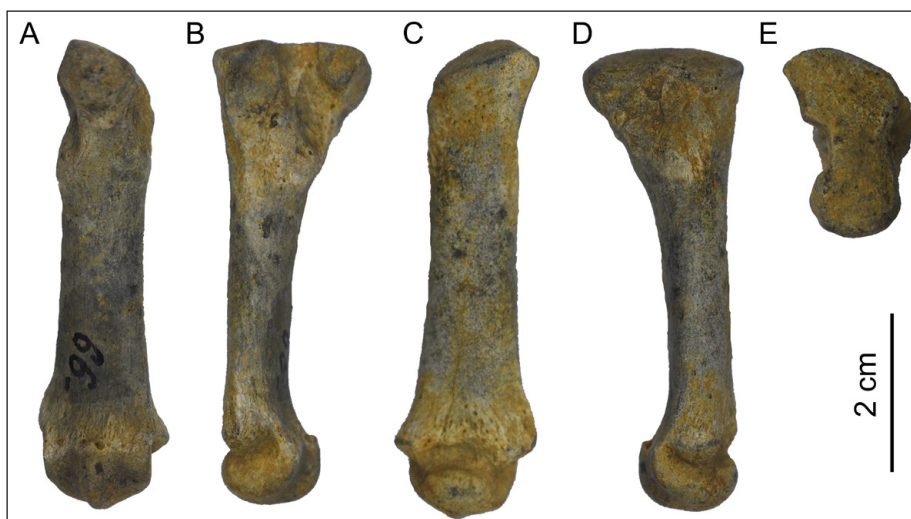


Fig. 10 - Left MtIII (LPB (FG-GUB) 1066) of *Ursus* sp. from Măluşteni (Romania) in (A) plantar, (B) medial, (C) dorsal, (D) lateral, and (E) proximal views.

MtIII	L	APDp	TDp	APDm	TDm	APDd	TDd	APDd.ar	TDd.ar
<i>Ursus</i> sp.	56.4	20.1	12.6	8.0	10.6	12.1	16.8	12.1	13.2

Tab. 7 - Measurements (in mm) of the *Ursus* sp. MtIII (LPB (FGGUB) 1066) from Mălușteni (Romania).

ably smaller than in the latter species (e.g., Table 7; Baryshnikov & Puzachenko 2017). It is also significantly smaller than the MtIII of *Indarctos arctoides* Depéret, 1895, from Batallones-3 (Abella 2011). Members of the genus *Agriotherium* that are present in Europe during the Early Pliocene are very large, far exceeding the estimated size of the present specimen (e.g., Montoya et al. 2006).

A species that could match the size and the ursine morphology of the MtIII from Mălușteni is *Ursus boeckhi* Schlosser, 1899. This species was initially reported by Schlosser (1899) from the then Hungarian locality of Baróth-Köpec (presently found in Romania and named Baralot-Căpeni) (Radulescu & Kisgyörgy 1970; Radulescu et al. 2003), but it has also been found in other Pliocene localities in Europe (e.g. Morlo & Kunderát 2001; Montoya et al. 2006). However, the relationships of this species to other Pliocene and Pleistocene ursids are not very clear and the taxonomic framework is still unclear (Morlo & Kunderát 2001; Wagner 2010; Wagner et al. 2011). Another possible attribution could be *Ursus minimus* Devèze & Bouillet, 1827, which has been found in localities of relatively younger age (Wagner et al. 2009). Therefore, due to the apparent absence of data on the metatarsals of these bears, we prefer to refer to the present specimen as *Ursus* sp.

Family Phocidae Gray, 1821

Phocidae indet.

Locality: Mălușteni.

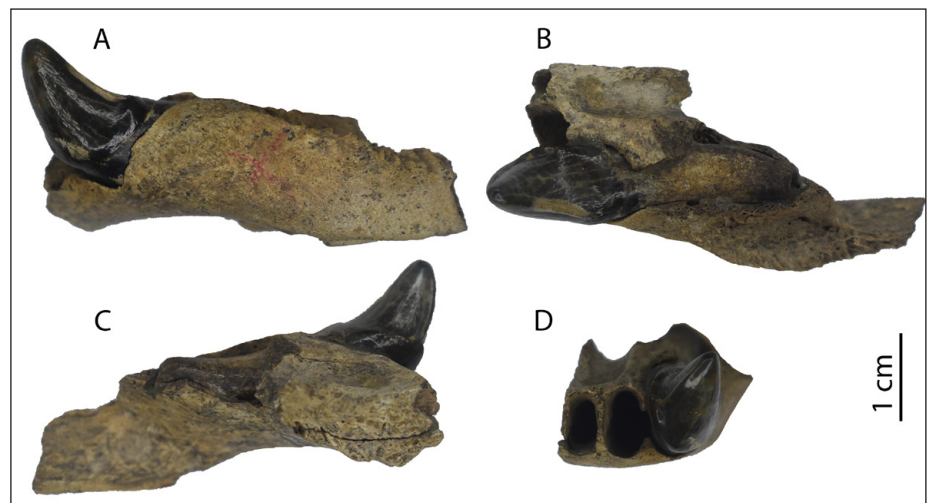
Age: Ruscinian, Early Pliocene.

Material: LPB (FGGUB) 81, left hemimandible with c and the alveoli of i2 and i3 (Simionescu, 1930: p. 96).

Description. The herein described hemimandible is very fragmentary (Figure 11). Only part of the symphysis, the alveoli of the two incisors, and the canine are present. The symphysis is long and flat, but it is broken just distally of the plane of the canine. It has a longitudinal depression distodorsally of the alveolus of i2. There are only two incisors. The alveolus of i2 is relatively smaller and narrower than the one of i3. The canine is short and robust, with a moderately developed cingulid and a well-developed cristid in its mesiolingual part. Its crown is slightly curved and exhibits faint signs of wear on its tip and its distolingual part. Measurements of the alveoli and the canine can be found in Table 8.

Comparisons. Unfortunately, specimen LPB (FGGUB) 81 is not sufficiently preserved to allow for a definite assignment. The presence of only two incisors in the hemimandible, and the flat and elongated symphysis clearly attribute it to the Phocidae, excluding the subfamilies Cystophorinae Gray, 1866,

Fig. 11 - Left hemimandible of the phocid from Mălușteni (LPB (FGGUB) 81) in (A) buccal, (B) occlusal, (C) lingual, and (D) mesial views.



	i2L	i2W	i3L	i3W	cL	cW	cH
LPB (FGGUB) 81	(8.6)	(4.2)	(9.4)	(5.9)	11.0	9.1	15.1

Tab. 8 - Measurements (in mm) of the canine and the alveoli of the incisors of the phocid hemimandible (LPB (FGGUB) 81) from Măluşteni (Romania).

and Devinophocinae Koretsky & Holec, 2002, which have only one lower incisor in their hemimandibles (Koretsky & Holec 2002; Koretsky & Rahmat 2013, 2015). However, the subfamilies Phocinae Gray, 1821, and Monachinae Trouessart, 1897, both have two lower incisors. Interestingly, although there are many references to phocids from the Miocene of the Eastern Paratethys (e.g. Koretsky 2001), there are no records of this group during the Pliocene. In fact, Pliocene seal occurrences are very infrequent in general in Europe. The monachine *Homiphoca* de Muizon & Henedy, 1980, has been found in Spain with only one innominate (Rahmat et al. 2020). The phocine species *Pliophoca etrusca* Tavani, 1941, has been found in the Pliocene of the northwestern Mediterranean (e.g., Berta et al. 2015). However, several phocid species have been described from the North Sea (Van Beneden 1876; Koretsky et al. 2015; Dewaele et al. 2018). Since many of the forms are only known from postcranial material, the present specimen cannot be identified below the family rank until more material from the region comes to light.

Suborder **Feliformia** Kretzoi, 1945
 Family Felidae Fischer von Waldheim, 1817
 Subfamily Felinae Fischer von Waldheim, 1817
 Genus *Pristifelis* Salesa et al., 2012

Pristifelis attica (Wagner, 1857)

Locality: Creţeşti 1.

Age: Turolian, Late Miocene.

Material: MVP-SN-C5664, left hemimandible with p3–m1.

Description. The specimen MVP-SN-C5664 is a partial left hemimandible that retains part of the mandibular ramus and the p3–m1 (Figure 12). The ramus is short and slender. It shows a marked elevation just mesially of p3. There is only one mental foramen, which is situated below the p3–c diastema. The p3 is short with a high main cuspid. The mesial accessory cuspid is absent and the distal accessory cuspid is very faint. The fourth premolar is much longer, having a clear distal accessory cuspid and mesial and distal cuspid-like elevations on the cingulid. The lower carnassial is long and narrow. The protoconid is considerably higher than the paraconid. There are no signs of a metaconid. The talonid is very reduced to practically absent.

Comparisons. Only two small felids are known from the Upper Miocene of Europe: *Leptofelis vallesiensis* (Salesa et al., 2012) from the Vallesian



Fig. 12 - Hemimandible of *Pristifelis attica* (MVP-SN-C5664) from Creţeşti 1 (Romania) in (A) buccal and (B) lingual views.

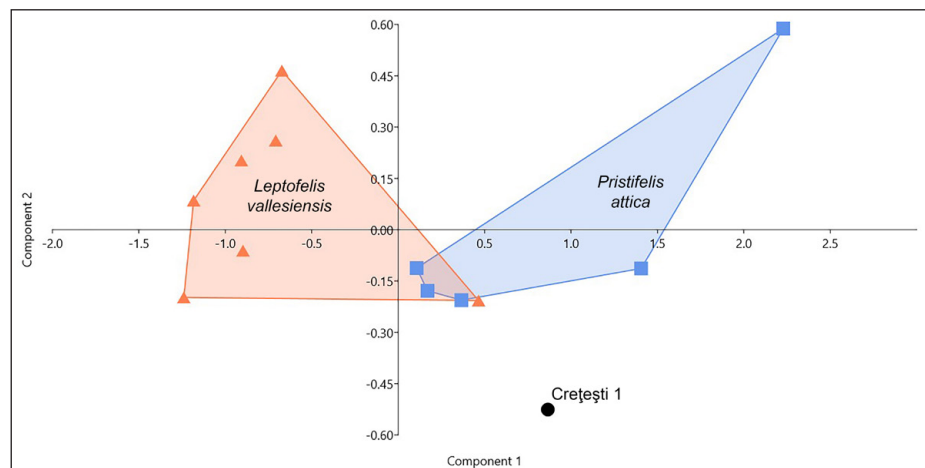
	MVP-SN-C5664	<i>Pristifelis attica</i>	<i>Leptofelis vallesiensis</i>
p3L	6.4	7.1–8.0 7.6 (n=2)	6.0–6.7 6.4 (n=7)
p4L	9.0	8.5–9.8 9.2 (n=3)	7.4–8.5 7.8 (n=6)
m1L	10.8	10.2–11.0 10.6 (n=5)	9.1–10.5 9.5 (n=7)

Tab. 9 - Metrical comparison (in mm) of the hemimandible from Crețești 1 (Romania) to that of known specimens of *Pristifelis attica* and *Leptofelis vallesiensis*. Data from Salesa et al. (2012a).

of Spain and *Pristifelis attica* (Wagner, 1857) from the Turolian of Greece, Turkey, and Spain (Salesa et al. 2012a, 2012b). According to Salesa et al. (2012a), these two forms can be differentiated by the larger size, the absence of mesial accessory cuspid on p3 and the reduced m1 talonid in the latter species. All of these traits can clearly be seen in the specimen from Crețești 1 as shown in Table 9 and Figure 13. This also fits with the distinct temporal ranges of the two species.

The values of Table 9 were directly used for the PCA shown in Figure 13. The PC1 is the main axis of the analysis, explaining 89.5% of the total variance, whereas the respective percentage for PC2 is 7.5%, resulting in a total of 97%. The first principal component is mainly affected by the length of the p4 and m1, whereas the second principal component is affected by the length of the p3 and m1. With the exception of one specimen of *Le. vallesiensis* (BAT-1'03 D4-265) that is slightly larger than its conspecifics, there is practically no overlap between the two species. Even though there is some differentiation in the PC2 axis, the values of the main PC1 axis show that the specimen from Crețești 1 clearly falls into the range of *Pri. attica*.

Fig. 13 - Principal components analysis including the hemimandible of *Pristifelis attica* (MVP-SN-C5664; black dot) from Crețești 1 (Romania) and known specimens of *Leptofelis vallesiensis* (orange triangles) and *Pristifelis attica* (blue squares). Data sources as in Table 9.



Felinae indet.

Locality: Mălușteni.

Age: Ruscinian, Early Pliocene.

Material: AICUPM-726-SM-4, left m1 (Simionescu 1930: p. 93).

Remarks. Simionescu (1930) published a pair of left p4 and m1 under the name *Lynx issiodorensis*. However, there are no taphonomic notes that can prove that these two specimens belong to the same individual. Even though the m1 exhibits a typical morphology, the absence of a mesial accessory cuspid and the low and robust remaining cuspids of the premolar show that it does not belong to a felid. Therefore, the two specimens are dealt with separately.

Description. The m1 (Figure 14) is complete with moderate signs of wear. Its cingulid is faint to moderately developed, being more marked in its distobuccal part. The protoconid is much higher than the paraconid, which is only faintly expanded mesially of the most distal part of the tooth base. The two cuspids have approximately the same length and are separated by a marked incision. A small talonid with a very small metaconid is present at the distal part of the tooth. The metaconid is adjacent to the distolingual end of the protoconid.

Comparisons. The Lower Pliocene of Europe has yielded a relatively limited diversity of felids compared to that of the Upper Miocene. The few sabertooth cats present during that time are relatively derived, with serrated teeth and relatively large size. The primitive cheetah *Acinonyx pardinensis* (Croizet & Jobert, 1828) is relatively larger than the specimen described here (e.g., Cherin et al. 2014). However, there are three medium-sized lynx/cara-



Fig. 14 - m1 (AICUPM-726-SM-4) of Felinae indet. from Măluşteni (Romania) in buccal (A), occlusal (B) and lingual (C) views.

cal-like forms in Europe during this period, which will be the focus of the present comparison.

The most common felid of this period probably is *Lynx issiodorensis* (Croizet & Jobert 1828), which has been found in multiple Upper Pliocene and Pleistocene localities of Eurasia (e.g., Kurtén 1978; Werdelin 1981; Kurtén & Werdelin 1984; Mecozzi et al. 2021; Cuccu et al. 2023). This form is gradually larger and more derived than the two species discussed below, with a smaller metaconid and talonid on the lower carnassial, although there appears to be considerable variability in the known dataset.

The species *Caracal depereti* Morales et al., 2003, was first described from the Lower Pliocene localities of Layna in Spain (MN 15, Spain; Morales et al. 2003) and Serrat d'en Vaquer in France (MN 15, France; Depéret 1890; Morales et al. 2003), and later from La Gloria 4 and La Calera (MN 14, Spain; Alcalá 1994; Morales 2016). These specimens are relatively smaller than the average material of *Lynx issiodorensis*, and they exhibit some postcranial features that suggest affinities with the extant caracal (Morales et al. 2003). However, there is no consensus on whether this taxon is indeed different from *Lynx issiodorensis* or whether it represents an earlier smaller form of the latter (Morales et al. 2003; Cipullo 2010; Boscaini et al. 2016; Mecozzi et al. 2021).

The species *Felis christoli* Gervais, 1849, has been found in the Lower Pliocene of Montpellier (type locality, MN 14, France) (Ficarelli & Torre 1975) and Cava Monticino (Brisighella, MN 14, Italy) (Rook et al. 1991; Bartolini-Lucenti et al. 2022). It is only known from mandibles, lower dentition, and postcranial bones.

Unfortunately, the fact that the Măluşteni felid is represented only by one lower carnassial is not ideal for such a homogenous set of comparative species. The only means of differentiation are the size of the tooth and the morphology of the metaconid and the talonid. In terms of size, *Lynx issiodorensis* usually is larger than the other two species. In this sense AICUPM-726-SM-4 is slightly smaller than the average values of *Lynx issiodorensis* and fits better into the range of *Ca. depereti* and *F. christoli*. However, there seems to be a considerable overlap between the three forms, especially when considering the age of the material (Table 10).

The most derived specimens of *Lynx issiodorensis* have a markedly small metaconid and talonid, whereas these structures are more developed in *F. christoli*, which retains a more plesiomorphic state. The species *Ca. depereti*, as well as the earlier specimens of *Lynx issiodorensis* (including the specimens from its type locality: Etouaires, early Villafranchian, 2.6 Ma) show an intermediate state. In AICUPM-726-SM-4, the metaconid is large and well-differentiated from the protoconid, and the talonid is also more distinctly developed by felid standards. In this sense, it mostly resembles *F. christoli*. However, *Ca. depereti* from Layna (Morales et al. 2003) also has an m1 metaconid and a relatively well-developed bulbous m1 talonid.

	Măluşteni	<i>F. christoli</i>	<i>Ca. depereti</i>	<i>Ly. issiodorensis</i>
m1L	14.0	12.4–14.2 13.1 (n=5)	12.0–15.9 13.9 (n=7)	13.1–16.5 14.8 (n=51)
m1W	5.8	5.2–5.7 5.4 (n=3)	5.2–7.7 6.1 (n=7)	5.5–8.2 6.5 (n=48)

Tab. 10 - Metrical comparison (in mm) of the m1 of the feline from Măluşteni (Romania) to *Felis christoli*, *Lynx issiodorensis* and *Caracal depereti*. Data from Rook et al. (1991) and Cuccu et al. (2023).

Therefore, although important, the presence of the m1 metaconid in these medium-sized felids is variable and plesiomorphic.

Even though the initial attribution of Simionescu (1930) to *Lyn. issiodorensis* has merit, the discrimination of this species from *F. christoli* and *Ca. depereti* is nearly impossible on the basis of a single tooth. Therefore, due to the great morphological and metrical overlap, it is herein preferred to refer to the present specimen as Felinae indet. until more material is found.

Subfamily Machairodontinae Gill, 1872

Genus *Dinofelis* Zdansky, 1924

cf. *Dinofelis* sp.

Locality: Berești.

Age: Ruscianian, Early Pliocene.

Material: LPB (FGUUB) 86, right C (Simionescu 1932: p. 217).

Description. The specimen LPB (FGUUB) 86 is a very fragmentary right C that retains the crown and part of the root (Figure 15). However, the crown shows extreme wear and part of the remaining enamel is taphonomically deformed, partly by root etching. The base of the crown is oval with a mesiodistal length of 21.1 mm, and a buccolingual width of 14.9 mm. Therefore, the W/L ratio is 0.71. The cingulum is absent. There are no signs of serrations or crenulations on the remaining part of the tooth. The crown is markedly curved.

Comparisons. Even though the tooth is in poor condition, the curved and buccolingually compressed crown indicates that it is an upper canine of a sabertoothed cat. However, the W/L ratio is relatively high, making the attribution to *Megantereon* Croizet & Jobert, 1828, as suggested by Simionescu (1932), highly improbable (e.g., Palmqvist et al. 2007). However, there are numerous other taxa of sabertooths that are present during that time, showing variable dimensions and canine compression (e.g., Werdelin et al. 2010). The most likely attribution is that of *Dinofelis* Zdansky, 1924, which fits in both dimensions and geological age. The species *Dinofelis diastemata* (Astre 1929) has been found in several localities in France, including Perpignan. Other tentative reports of *Dinofelis* in eastern Europe include the localities of Zemo Melaani (Georgia; Gabunia & Vekua 1998) and Novaya Etulia 2 (Republic of Moldova; Aver-



Fig. 15 - Right upper canine (LPB (FGUUB) 86) of cf. *Dinofelis* sp. from Berești (Romania) in (A) buccal, (B), lingual, and (C) distal views.

anov & Baryshnikov 1999) (Werdelin & Lewis 2001). Due to the poor condition of the present specimen, it is preferable to attribute it to cf. *Dinofelis* sp.

Family Hyaenidae Gray, 1821

Subfamily Hyaeninae Gray, 1821

Genus *Adcrocuta* Kretzoi, 1938

Adcrocuta eximia (Roth & Wagner, 1854)

Locality: Crețești 1.

Age: Turolian, Late Miocene.

Material: MVP-SN-C5697, a partial right hemimandible (Ursachi 2016: p. 98 and 163).

Description. The specimen MVP-SN-C5697 is a broken right hemimandible with the p1–p2, the root of c and the mesial root of p3 (Figure 16). The mandibular corpus is broken at the middle plane of p3 and at the lingual side of the canine. The remaining part is considerably deep and includes a large mental foramen ventrally to the p2. No diastemata are present between the remaining premolars. The p1 is small and sub-globular. It has only one cuspid that is considerably worn. No clear cingulid is present, even though the base of the tooth is slightly inflated. The p2 is asymmetrical, with its distal part being longer and wider than its mesial one. A faint cingulid runs the perimeter of the tooth, being slightly damaged in its distobuccal part. Only the one main cuspid is present, which is heavily worn, so the presence of a small distal accessory cuspid

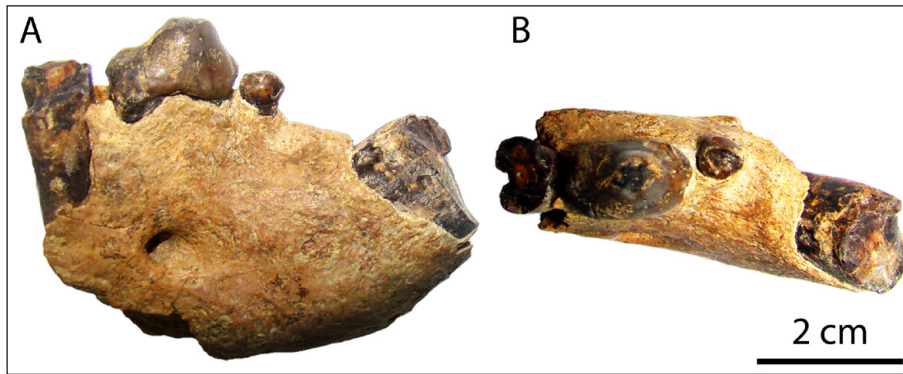


Fig. 16 - Hemimandible (MVP-SN-C5697) of *Adcrocuta eximia* from Creţeşti 1 (Romania) in (A) buccal and (B) occlusal views.

cannot be excluded. However, its mesial part is more restricted and unworn and there are no signs of a cuspid or cristid in this region.

Comparisons. The partial hemimandible (MVP-SN-C5697) can be attributed to a large hyaenid, based on the wide premolars with present cingulid and robust enamel that are characteristic of the bone-cracking large hyenas. The Turolian of Eurasia is dominated by only one form of such a large hyena, the species *Ad. eximia* (Roth & Wagner, 1854), which has been discovered in high numbers in numerous localities from Spain to China (Werdelin & Solounias 1990, 1991). During the Turolian, the only other hyaenid that can reach comparable sizes is *Hyaenictis graeca* Gaudry, 1861. This species has mainly been found in Pikermi (Greece) and possibly in other MN12 localities of southern Europe with just a handful of specimens (Paparizos et al. Submitted). *Hyaenictis graeca* can be distinguished from the former by its slenderer premolars, among other characteristics (e.g., Howell & Petter, 1985),

as shown in Table 11. This distinction is very clear for the two genera, as presented by Vinuesa et al. (2017). Therefore, based on the relatively wider p2 of the specimen from Creţeşti 1 and the extreme rarity of *Hyaenictis* Gaudry, 1861, compared to *Adcrocuta*, we attribute the Romanian material to the latter.

Genus *Chasmaporthetes* Hay, 1921

Chasmaporthetes sp.

Locality: Măluşteni.

Age: Ruscinian, Early Pliocene.

Material: AICUPM-SM-100, partial left maxillary with right I1–2 and left I1–P2; AICUPM-SM-101, right P2; LPB (FGGUB) 66, right McII (Simionescu 1930: p. 90).

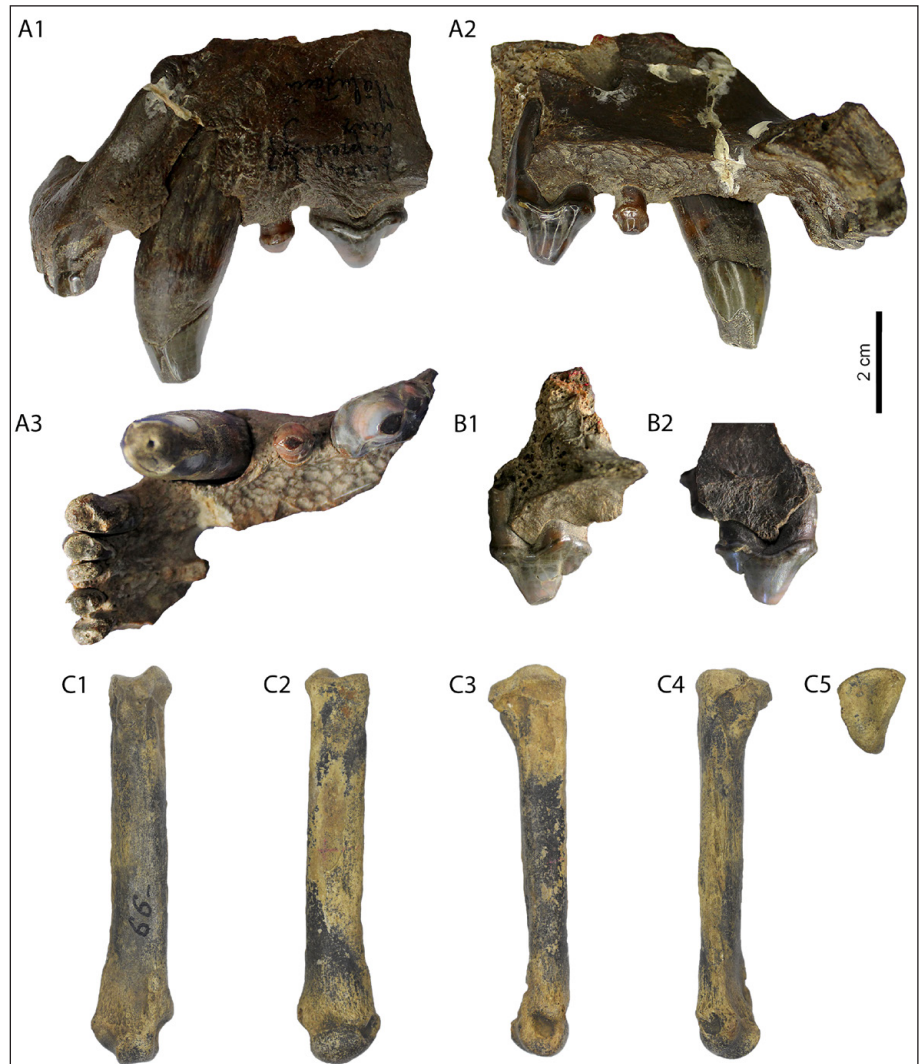
Description. The specimen AICUPM-SM-100 preserves the right I1–2, the left I1–P2, and part of the nasal aperture (Figure 17A), whereas AICUPM-SM-101 is an isolated right P2, still attached to the surrounding maxilla (Figure 17B). The anterior palatine foramina end rostrally at the middle plane of the upper canine. The incisors are placed in line on the premaxilla. The I3 is markedly larger than the other two. There are clear diastemata between I3–C, C–P1 and P1–P2. The dentition is moderately worn and is characterized by a generally wrinkled enamel, being more notable in the canine and the P2. The P1 is large, unicuspid, round and has a single cusp that is slightly bent lingually. The P2 is rhomboidal with a slight distal broadening and possesses a well-developed distal accessory cusp. The cingulum is moderately developed.

The specimen LPB (FGGUB) 66 is a complete right second metacarpal (Fig. 17C). The proximal epiphysis is sub-triangular with the anterior and the medial sides being arched, whereas the lateral side is

	<i>Adcrocuta eximia</i>		<i>Hyaenictis graeca</i>
	Creţeşti 1	Various ^{1,2}	Pikermi ²
p1L	5.3	4.6–6.2 5.6 (n=21)	
p1W	5.5	5.–7.0 5.8 (n=21)	
p2L	16.4	14.8–17.7 16.0 (n=26)	17.9
p2W	9.8	9.5–13.3 11.3 (n=32)	9.0
p2W/L	0.60	0.62–0.75 0.69 (n=21)	0.50

Tab. 11 - Metrical comparison (in mm) of the specimen from Creţeşti 1 (Romania) to material of *Adcrocuta eximia* from other localities, as well as with *Hyaenictis graeca*. Data sources: ¹Werdelin & Solounias (1990), ²Howell & Petter (1985).

Fig. 17 - Dentognathic and postcranial material of *Chasmaporthetes* sp. found in Mălușteni (Romania): (A) AICUPM-SM-100, maxilla with right I1–I2 and left I1–P2 in buccal (A1), lingual (A2), and occlusal (A3) views; (B) AICUPM-SM-101, right P2 in lingual (B1) and buccal (B2) views; (C) LPB (FGGUB) 66, right McII in anterior (C1), posterior (C2), lateral (C3), medial (C4), and proximal (C5) views.



straighter, and its lip is elevated proximally in comparison to the other two sides. The lateral face of the proximal part has an oval articular surface for the McIII situated anteriorly, just distally to the highest elevation of the lateral lip. The posterior part of the same side presents an arched articular surface that starts from the posteriormost point of the proximal triangle and extends distally on the side of the midshaft. The medial side of the proximal part of the bone hosts two surfaces: one triangular to oval just below the posterior end of the proximal epiphysis, and a more rectangular one in its anterior part. The distal parts of the two surfaces are separated by a small pit. The midshaft is long and narrow for hyaenid standards. It remains straight for most of its part, and it starts to widen near its distal end, causing a faint medial bending. The distal epiphysis is asymmetrical and ovoid. The distal end of the articular surface for the first digit is extended more distally on the lateral side in comparison to the medial one. Ad-

ditionally, the small tuberosity above the articular surface is situated much higher on the lateral side of the bone, whereas on the medial side, it almost touches the articular surface. The sagittal crest of the articular surface is slightly damaged but it seems like it was not reaching the midshaft.

Comparisons. The hyaenids have been one of the groups that were affected the most during the transition from the Late Miocene to the Early Pliocene and they never managed to reach the same diversity as in the Vallesian or the Turolian (Werdelin 1991; Werdelin & Solounias 1991; Turner et al. 2008). The only large hyaenids that have been found in Europe during the Pliocene are *Pliocrocota perrieri* (Croizet & Jobert, 1828), *Chasmaporthetes borissiakii* (Khomenko, 1932), *Chasmaporthetes lunensis* (Del Campana, 1914), and possibly *Lycyaenops rhomboideae* Kretzoi, 1938, whereas the appearance of the giant hyenas and the cave hyenas comes much later (Werdelin & Solounias 1991; Turner et al. 2008). The species *Lycyaenops*

Dental	AICUPM-SM-100	AICUPM-Sm-101	<i>Ch. borissiaki</i> ¹	<i>Ch. lunensis</i> ¹	<i>Plioc. perrieri</i> ²	Postcranial	LPB (FGGUB) 66
CL	14.9		14.5	14.6–17.9 16.7 (n=6)	15.9–18.8 17.8 (n=5)	L	76.3
CW	12.2			11.0–13.9 12.7 (n=6)	11.9–14.2 13.0 (n=5)	APDp	15.5
P1L	7.4		8.2–8.5 8.4 (n=2)	7.0–9.7 8.7 (n=4)		TDp	13.3
P1W	7.3		6.8–7.9 7.4 (n=2)	7.4–8.4 7.8 (n=3)	5.8–6.7 6.3 (n=2)	APDm	8.8
P1W/L	0.99		0.83–0.93 0.88 (n=2)	0.80–0.89 0.85 (n=3)		TDm	10.8
P2L	20.1	20.8	17.9–18.6 18.3 (n=2)	16.4–20.6 18.3 (n=9)	17.0–18.9 17.8 (n=9)	APDd	12.1
P2W	12.1	12.9	10.0–10.5 10.3 (n=2)	10.5–12.1 11.3 (n=9)	10.2–13.1 11.7 (n=8)	TDd	15.0
P2W/L	0.60	0.62	0.56 (n=2)	0.59–0.67 0.63 (n=8)	0.60–0.70 0.66 (n=7)	TDd.ar	12.6

Tab. 12 - Metrical comparison (in mm) of the teeth and McII of *Chasmaporthetes* sp. from Măluşteni (Romania) to that of previously published hyacnids. Data from: ¹Kurtén & Werdelin (1988); ²Howell & Petter (1980).

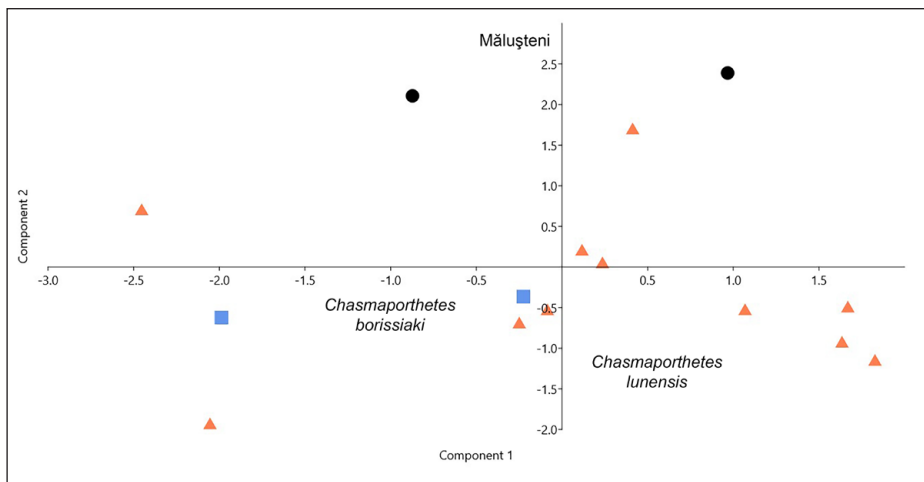


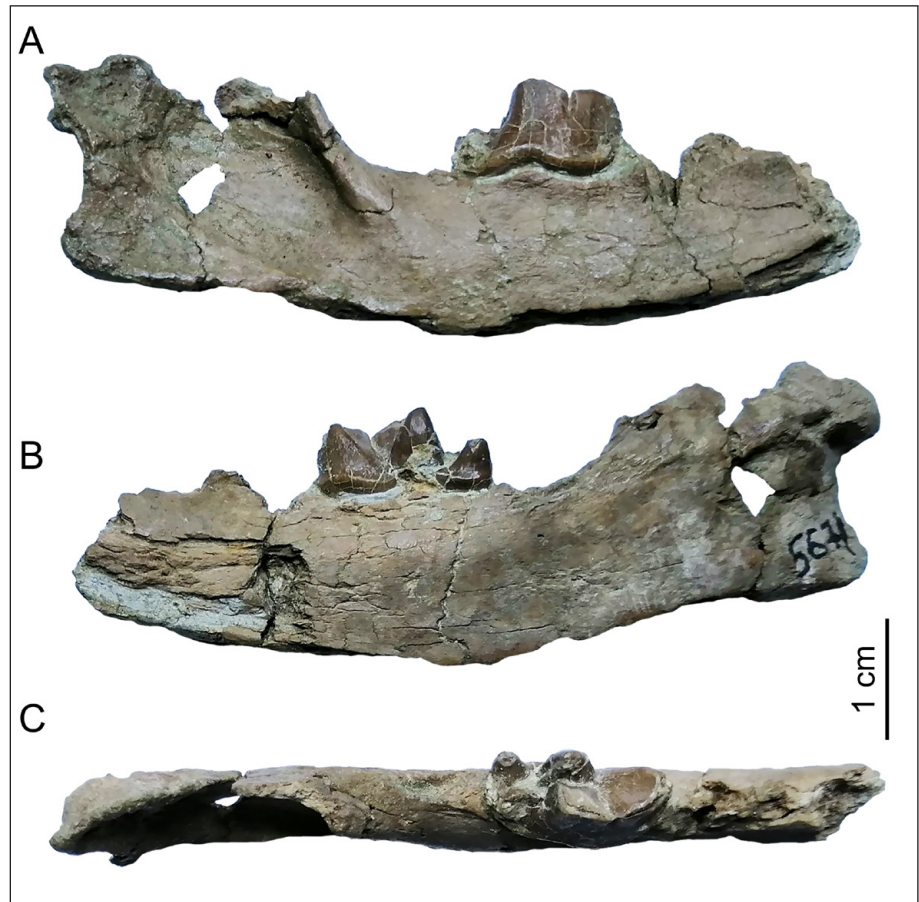
Fig. 18 - Principal component analysis including the upper teeth of *Chasmaporthetes* sp. found in Măluşteni (Romania; black dots), *Chasmaporthetes borissiaki* (blue squares), and *Chasmaporthetes lunensis* (orange triangles). Comparative data from Kurtén & Werdelin (1988).

rhomboideae is known from very scarce material and the age of the locality is not clear, but it can easily be differentiated from the described specimens by the much wider premolars with marked broadened distal ends (Werdelin 1999). Even though the dimensions of the teeth between *Plioc. perrieri* and the two species of *Chasmaporthetes* are similar (Table 12; Figure 18), the P2 of the former is much more rectangular and has a small mesial accessory cusp (Howell & Petter 1980; Vinuesa et al. 2014), which is absent from the latter genus, as well as from the specimens from Măluşteni. The measurements of Table 12 were directly used for the PCA shown in Figure 18. The PC1 and PC2 explain 45.8% and 37.1% of the total variance respectively, resulting in a combined 82.9% total percentage. PC1 is mainly affected by the two dimensions of the canine, whereas PC2 is mostly affected by the dimensions of the P2. The plot shows that the values of *Ch. borissiaki* fall in the range of *Ch. lunensis*, with the values from Măluşteni being close to the known values of the latter species' range.

The two European species of *Chasmaporthetes* Hay, 1921, are both represented in the MN15 of Eastern Europe, as *Ch. borissiaki* has been found in the "Roussillon-fauna" of Dermedzhi in the Republic of Moldova (Khomenko 1932) and *Ch. lunensis* has been found in Odessa Catacombs (Sotnikova 1994). It must be noted that Sotnikova (1994) argues that the age of the holotype of *Ch. borissiaki* is in fact Late Miocene. Based on the comparisons of Qiu (1987), Kurtén & Werdelin (1988), Sotnikova (1994), and Tseng et al. (2013), these two species are very similar, but *Ch. borissiaki* is slightly smaller, with narrower premolars and shorter forearm. However, as seen in Table 12, the metrical differences between them are not so evident when only the studied dentition is considered. Therefore, the material is provisionally referred to as *Chasmaporthetes* sp.

The McII is tentatively attributed to the same form, since the measurements fit very well for an animal of this size and because of the relatively

Fig. 19 - Right hemimandible of *Protictitherium crassum* (MVP-SN-C5671) from Crețești 1 (Romania) in (A) buccal, (B) lingual, and (C) occlusal views.



slender shaft that fits better to the cursorial *Chasmaporthetes* than to the more crocutoid *Plioc. perrieri*.

Subfamily Ictitheriinae Trouessart, 1897
Genus *Protictitherium* Wagner, 1848

Protictitherium crassum (Depéret, 1892)

Locality: Crețești 1.

Age: Turolian, Late Miocene.

Material: MVP-SN-C5671, right hemimandible with m1 (Ursachi 2016: p. 163).

Description. The preserved hemimandible is very fragmented, retaining only part of the mandibular ramus and a damaged m1 (Figure 19). However, the dimensions and the retained morphological features of the lower carnassial allow a short description and a tentative identification. The remaining part of the mandibular ramus is relatively slender. It has a deep masseteric fossa, and the occipital condyle must have been higher than the toothrow level. The angle of the ascending ramus is rather steep. The lower carnassial is damaged on the tips of the protoconid and paraconid, as well as in the lingual side of

the talonid. It is surrounded by a marked cingulid, which is stronger on its buccal side. The protocone is the largest cuspid, followed by the paraconid and the notably large metaconid, which is relatively well-individualised from the protoconid. The entoconid is very large and slightly bent distally. The distal part of the talonid is damaged, but the remaining part of the talonid basin indicates that it was large and clearly separated from the trigonid.

Comparisons. The present specimen is relatively smaller than the known species of the genera *Ictitherium* Wagner, 1848, and *Hyaenictitherium* Kretzoi, 1938 (Table 13; Figure 20). It can be further differentiated from the latter by the slender mandibular ramus, the steep ascending ramus, the large m1 talonid and the large metaconid and talonid cuspids (Semenov 2008; Kargopoulos et al. 2023). Therefore, based on its small size, the large talonid, the high and wide metaconid and the relatively high protoconid and paraconid, the specimen can be confidently assigned to the genus *Protictitherium* Kretzoi, 1938.

Most of the species of *Protictitherium* are considerably smaller than the present specimen, as seen in Table 13 for *Protictitherium gaillardii* (Forsyth Major,

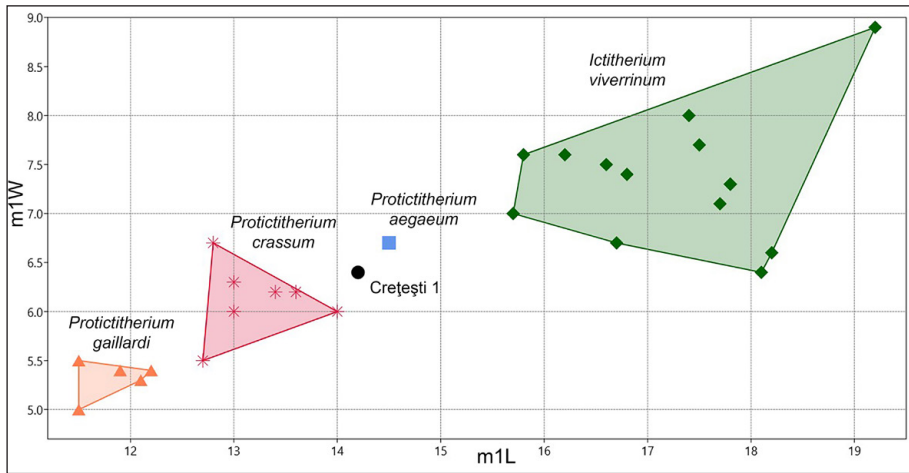


Fig. 20 - Scatter plot of m1W vs. m1L including the right hemimandible of *Protictitherium crassum* (MVP-SN-C5671) from Creţeşti 1 (Romania; black dot), *Protictitherium gaillardi* (orange triangles), *Protictitherium crassum* (red stars), *Protictitherium aegaeum* (blue square), and *Ictitherium viverrinum* (green diamonds). Data for *Prot. gaillardi* and *Prot. crassum* from de Bonis & Koufos (1991), for *Prot. aegaeum* from Kaya et al. (2005) and from personal data for *I. viverrinum*.

1903). The only two species of the genus that have comparable size to the specimen from Creţeşti 1 are *Protictitherium crassum* (Depéret, 1892) and *Protictitherium aegaeum* Kaya et al., 2005. The only difference between the two species concerning the m1 is that the trigonid cuspids are higher in the latter. Kaya et al. (2005) noted a difference in the higher p4 of the latter species. However, it is unclear whether these differences are sufficient enough to separate these two forms. Our knowledge of the intraspecific variability of *Prot. crassum* is limited, and perhaps future specimens may link these diverging forms (Fraile 2017). However, Werdelin & Solounias (1991) noted a gap in the occurrences of *Prot. crassum* during the late Vallesian/early Turolian, which suggests that *Prot. aegaeum* may represent a distinct form present in the Turolian. In the absence of clearer data about the separation of the two species, it is preferable to ascribe the present specimen to *Prot. crassum*.

Genus *Hyaenictitherium* Kretzoi, 1938

Hyaenictitherium sp.

Locality: Păun.

Age: Vallesian, Late Miocene.

Material: AICUPM-MP1-1184, skull with left I3–M1 and right P2–M1 (Macarovici 1957: p. 144–147).

	MVP-SN-C5671	<i>Prot. crassum</i> ^{1,2,3}	<i>Prot. aegaeum</i> ⁴	<i>Prot. gaillardi</i> ²	<i>Ic. viverrinum</i> ¹
m1L	14.2	12.7–16.2 14.3 (n=16)	14.5	11.5–12.2 11.8 (n=5)	15.9–19.0 17.7 (n=22)
m1W	6.4	5.5–7.9 6.7 (n=16)	6.7	5.0–5.5 5.3 (n=5)	6.8–9.2 8.2 (n=21)

Tab. 13 - Metrical comparison (in mm) of the m1 (MVP-SN-C5671) of *Protictitherium crassum* from Creţeşti 1 (Romania) to that of other members of the genus. Data sources: ¹Semenov (1989), ²de Bonis & Koufos (1991), ³Koufos (2009), ⁴Kaya et al. (2005).

Description. The specimen AICUPM-MP1-1184 is a skull that is partially covered by sediment on its right and ventral parts of the braincase and exhibits some minor damage (Figure 21). The fragility of the specimen does not enable its safe isolation from the remaining sediment. However, no deformation is present in the skull.

The rostrum is relatively elongated, and it shows its narrowest constriction at the level of P1. Its tip shows a protuberance of secondary ossification above the alveoli of the right incisors, possibly a sign of a healed trauma. The pyriform is considerably oblique (due to the length of the rostrum) and its lateral borders are slightly diverging. The right infraorbital foramen is split in two smaller and closely situated foramina, whereas it is not present on the left side. A considerably notable thumbprint fossa is present between the upper carnassial and the orbit on both sides of the maxilla. An angle is formed between the end of the nasals, the nasion, and the forehead, creating a slightly domed profile of the skull. The orbit is oblique, and it is bordered by relatively well-developed postorbital processes of the frontal and the zygomatic, followed by a marked postorbital constriction. One temporal crest starts from the base of each frontal paraoccipital process, converging rather abruptly and merging into a well-developed sagittal crest that extends dorsally and ventrally of the braincase. The zygomatic is wide, robust and relatively high-placed in relation to the palate. Most of the ventral and distal parts of the skull are covered by sediment. However, the exposed part of the left side retains part of the auditory region. The auditory bulla is inflated with well-marked external distinction between the anterior and posterior chambers. A well-developed postorbital process can be seen distally of the auditory

bullae, despite its damage. Finally, part of a moderately-sized left occipital condyle is also preserved.

Only the alveolus of the left I2 is present to represent the morphology of this tooth. It is relatively mediolaterally compressed and considerably smaller than I3. The third upper incisor shows moderate signs of wear on its tip. Its crown is robust and slightly hook-like with a distal basin and a well-developed lingual crest. The canine is long and narrow. It is slightly curved, and it lacks any marked signs of crests or cingulum. The first premolar is represented by an exposed root. However, it can be inferred that it was single-rooted, relatively small and separated from the C and P2 by diastemata. The second premolar is relatively narrow and asymmetrical with its distal part being longer than the mesial one. The main cusp is relatively high, and it is followed mesially and distally by two crests. There are no signs of an accessory cusp. Its cingulum is more developed on its distal part. It is separated from the P3 by a small diastema. The third premolar is similar to the second one, but larger and it exhibits a small, slightly lingually placed mesial accessory cusp, as well as a distal one. Its lingual side is not too extended. The upper carnassial is better preserved on the right side of the toothrow. The paracone is the highest cusp, and it is separated from the significantly high parastyle and metastyle by two notches. It is surrounded by a cingulum that is more developed distobuccally and distolingually. The protocone is relatively small, narrow and it does not exceed the plane of the parastyle. Between the protocone and the paracone there is a D-shaped basin. The first upper molar is very simple, and it is closely attached to the upper carnassial. The paracone is the largest cusp, followed by a more lingually placed metacone. A narrow basin separates these two buccal cusps from a very small protocone. There are no signs of M2, even though the remaining sediment might conceal the presence of an alveolus, at least on the right part of the tooththrow.

Comparisons. The nomenclatural history of this specimen is rather problematic, because the *Lycyaena parva*/*Hyaenictitherium venator*/*Mi. bessarabicum* specimens fall within the overlapping metrical ranges of *Hyaenictitherium wongii* and *Hyaenictitherium hyaenoides* (Werdelin & Solounias 1991). This is evident in Table 14. The two latter species share similar morphology and their distinction is not always clear, particularly when the metrical data fall within their

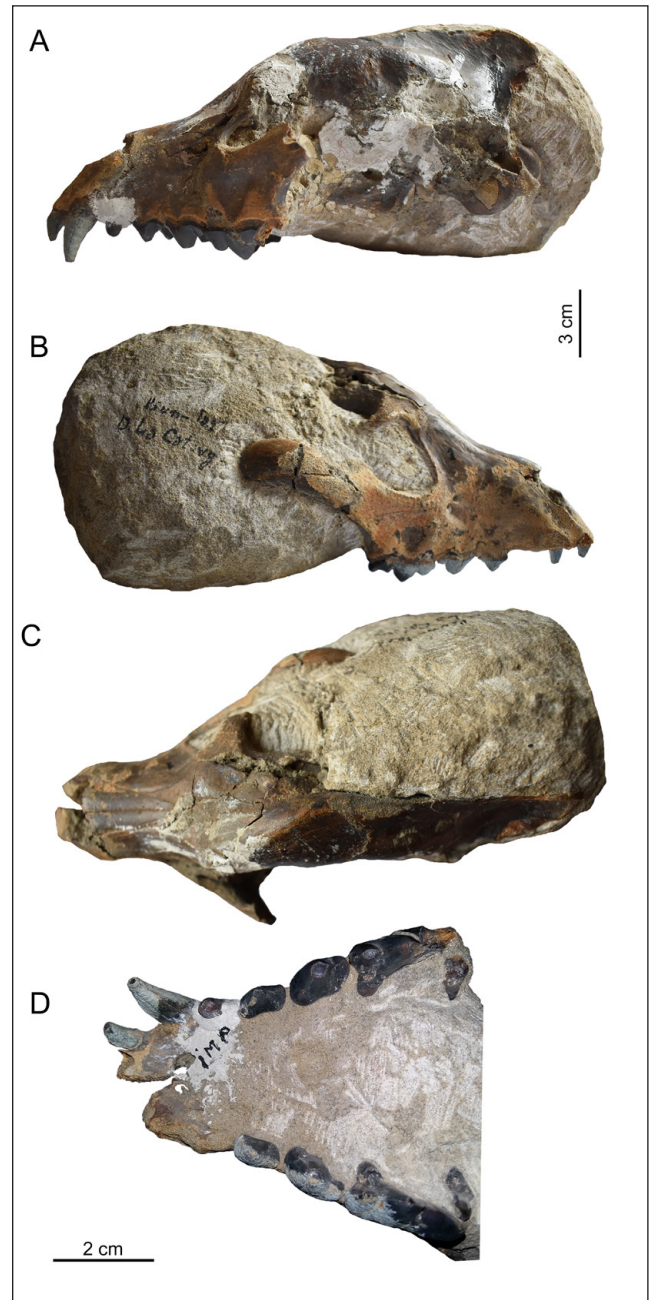


Fig. 21 - Skull (AICUPM-MP1-1184) of *Hyaenictitherium* sp. from Păun (Romania) in (A) left, (B) right, (C) dorsal, and (D) occlusal view. Scale 3 cm for A–C and scale 2 cm for D.

overlapping range. According to the comparisons of Tseng & Wang (2007), *Hyaenictitherium hyaenoides* can be distinguished by its wider premolars and its smaller upper molars. The ratio of P3W/P3L in the Păun specimen is 0.58 on the left side and 0.55 on the right side. On average, this ratio is 0.54–0.55 for *Hyaenictitherium wongii*, and 0.58 for *Hyaenictitherium hyaenoides* (Tseng & Wang 2007), and certainly there is considerable degree of variability. Additionally, the ratio P4L/M1W exceeds 2.0, in comparison to the val-

	<i>Hyaenictitherium</i> sp. (Păun)		Hyaenidae indet. (Pogana 1)		<i>Hyaenictith. wongii</i> ¹	<i>Hyaenictith. hyaenoides</i> ¹	<i>"Mi. bessarabicum"</i> ²	<i>L. chaeretis</i> ³
	L	R	AICUNSM 222-6	MVP-SN-PG66				
I3L	9.3							10.8
I3W	6.9							8.4
CL	12.1						12.2–15.0 13.2 (n=4)	10.4–10.6 10.5 (n=2)
CW	8.6						7.2–9.4 8.1 (3)	
P1L	6.4				4.8–6.2 5.4 (n=12)		6.8–8.0 7.3 (3)	7.0–7.2 7.1 (n=2)
P1W	5.5				3.8–4.8 4.4 (n=10)		5.0–6.0 5.5 (2)	5.8–6.1 6.0 (n=3)
P2L	13.9	13.7			11.1–15.1 13.3 (n=83)	14.0–17.2 15.4 (n=19)	13.0–17.5 14.6 (4)	15.7–16.8 16.4 (n=3)
P2W	8.0	7.9			5.4–7.7 6.5 (n=99)	7.4–10.0 8.6 (n=19)	6.8–7.6 7.3 (3)	9.3–9.4 9.4 (n=2)
P3L	18.2	18.1	19.3		14.3–19.0 16.7 (n=91)	18.0–22.5 19.7 (n=19)	18.0–19.5 18.7 (5)	19.6–21.0 20.3 (n=4)
P3W	10.6	10.0	9.6		7.4–10.8 9.0 (n=108)	9.8–13.1 11.4 (n=22)	10.0–10.9 10.6 (4)	12.8–13.0 12.9 (n=4)
P4L	(30.8)	29.0		32.6	23.1–29.2 25.5 (n=100)	27.4–33.4 30.0 (n=17)	26.9–33.5 28.6 (7)	31.0–33.0 31.5 (n=5)
P4W	14.5	13.6		18.2	11.2–16.8 14.0 (n=92)	15.5–19.2 17.0 (n=21)	13.8–16.5 15.3 (6)	16.9–17.5 17.2 (n=5)
M1L	7.5	7.6			6.0–9.2 7.9 (n=82)	7.0–8.9 8.0 (n=14)	8.0–9.4 8.9 (4)	6.2–8.5 7.6 (n=3)
M1W	11.9	13.0			13.2–18.1 15.0 (n=82)	14.3–18.7 16.3 (n=14)	11.0–16.2 14.2 (3)	17.5–18.3 17.8 (n=3)

Tab. 14 - Metrical comparison (in mm) of the upper dentition of hyaenids from Păun and Pogana 1 (Romania) to that of known hyaenid species. Comparative data from: ¹Werdelin (1988), ²Semenov (1989), ³Koufos (2021).

ues of 1.70 for *Hyaenictith. wongii* and 1.84 for *Hyaenictith. hyaenoides*. As a result, the described skull is attributed to *Hyaenictitherium* sp.

Hyaenidae indet.

Locality: Pogana 1.

Age: Turolian, Late Miocene.

Material: AICUNSM 222-6, left P3; MVP-SN-PG66, left P4; MVP-SN-C5677, right MtIII.

Description. The specimen AICUNSM 222-6 is a complete left P3 with faint signs of wear on its main cusp (Figure 22A). It is double-rooted and almost symmetrical, with the distal part being slightly longer than the mesial one. The outline of the tooth is relatively slender, and its periphery surrounded by a moderately developed cingulum. The main cuspid is relatively high and is marked by one mesial and one distal crista. The mesial one ends at the mesial cingulum, with just a very small elevation resembling a mesial accessory cusp. The distal one ends at the base of a well-individualized, moderately developed distal accessory cuspid. The lip of the distal cingulum creates a small elevation that resembles a secondary distal accessory cuspid. The enamel is wrinkled.

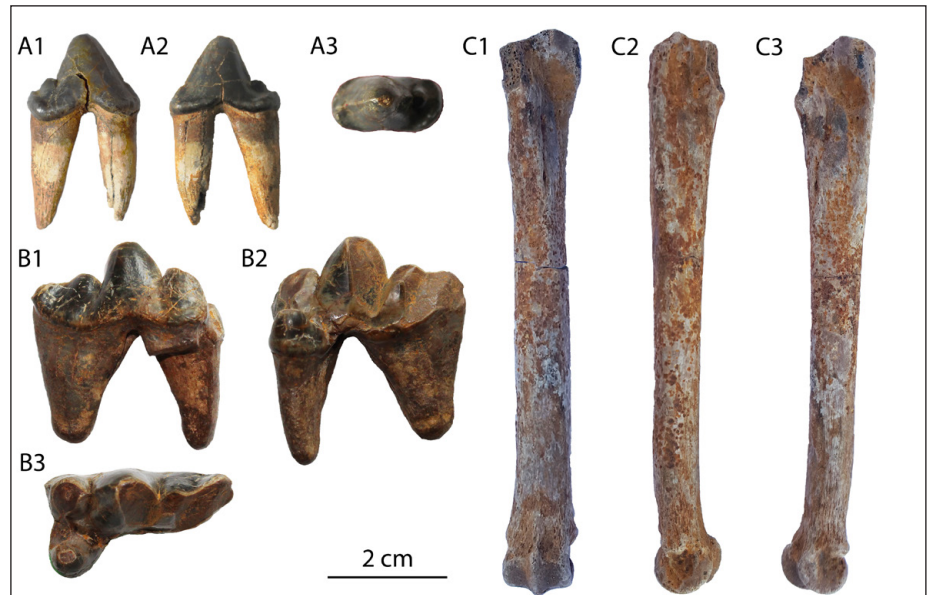
The specimen MVP-SN-PG66 is a complete left P4, lacking only the root above the parastyle, with advanced signs of wear (Figure 22B). The cingulum is relatively weak. However, the distolingual part of the tooth, where the cingulum is usu-

ally stronger in medium-sized hyenas, is completely worn down. The paracone is the highest cusp, even though it is relatively short in length, followed by the relatively large parastyle. The protocone is also well-developed, with a strong neck and its most mesial point is approximately level to that of the parastyle.

The right MtIII (MVP-SN-C5677) is almost complete with just a slight damage on the posterior part of the proximal epiphysis (Figure 22C). The proximal epiphysis has a characteristic T-like shape, with its posterior part forming a crest-like structure, whereas the anterior part is almost flat. The lateral part of the proximal epiphysis is more elevated than the medial one. It is marked by an arched groove that starts from the posterior end of the proximal epiphysis and runs through the proximal lateral side of the shaft. The shaft is long and narrow with almost parallel sides for most of its length. The distal epiphysis is asymmetrical, with the lateral extension being more marked and more proximally situated than the medial one. The distal articular surface is ovoid, and the sagittal crest reaches the shaft.

Comparisons. The morphology and the dimensions of the two teeth resemble those of *Hyaenictitherium* sp., from Păun, even though they are slightly larger. However, as seen in Table 14, they still fall within the range of medium- to large-sized hyaenids. The P3 differs from *Lycyaena chaeretis* (Gaudry, 1861) in the less developed lingual border of the tooth. In this genus both the mesial and distal ends of the lingual part of the tooth are arched

Fig. 22 - Material of Hyaenidae indet. from Pogana 1 (Romania): (A) AICUNSM 222-6, left P3 in buccal (A1), lingual (A2), and occlusal (A3) views; (B) MVP-SN-PG66, left P4 in buccal (B1), lingual (B2), and occlusal (B3) views; (C) MVP-SN-C5677, right MtIII in posterior (C1), medial (C2), and lateral (C3) views.



with a marked cingulum, creating a more rectangular outline. However, this tooth is notably narrow, with a robustness index ($P3W/L$) of 0.50, compared to other non-crocutoid hyenas of similar size that have an index of approximately 0.60. Even though the length of the teeth indicates that it could belong to an animal of the size of *Hyaenictith. hyaenoides* or *Lycyaena chaeretis*, its width is considerably smaller. The very worn upper carnassial and the isolated MtIII do not show any diagnostic features that could help with the identification. The latter is tentatively attributed to the same medium-sized hyaenid, based on its size (Table 15). Therefore, even though it is evident that there is a medium- to large-sized hyena present in Pogana 1, it is currently referred to as Hyaenidae indet.

Carnivora indet.

Localities: Mălușteni and Berești.

Age: Ruscianian, Early Pliocene.

Material: Mălușteni: AICUPM-SM-103, incisor; FG-GUB-189, right C; AICUPM-SM-113, premolar; AICUPM-SM-114, premolar; AICUPM-SM-115, premolar; AICUPM-SM-116, premolar; AICUPM-SM-109, premolar (Simionescu 1930: p. 93); AICUPM-SM-112, sacrum (Simionescu 1930: p. 95); AICUPM-SM-11, right proximal ulna (Simionescu 1930: p. 95); LPB (FGGUB) 98, right distal tibia. Berești: LPB (FGGUB) 213, right hemimandible with the alveoli of p1–p4; LPB (FGGUB) 86, canine (Simionescu 1932: p. 217); LPB (FGGUB) 215, premolar; LPB (FGGUB) 216, premolar; LPB (FGGUB) 217, premolar; LPB (FGGUB) 97, left astragalus.

Description. A single incisor is present in the sample (AICUPM-SM-103; Fig. 23A) from

MtIII	L	APDm	TDm	TDd	TDd.ar
MVP-SN-C5677	87.7	9.3	9.2	11.1	10.8
<i>Hyaenictith. wongii</i>	76.5–80.1 78.3 (n=2)	5.3–6.6 6.0 (n=3)		8.1–8.7 8.4 (n=2)	7.1–7.5 7.3 (N=2)
<i>Ad. eximia</i>	82.0–98.4 90.2 (n=2)	8.9		14.7	13.5–15.5 14.5 (n=2)

Tab. 15 - Metrical comparison (in mm) of the MtIII (MVP-SN-C5677) of Hyaenidae indet. from Pogana 1 (Romania) to those of *Hyaenictitherium wongii* (Samos; own data), and *Adcrocuta eximia* (Nikiti and Hadjidimovo; Koufos 2016).

Mălușteni. Unfortunately, it is too worn to enable a detailed description. The dental wear covers most of its lingual, buccal and occlusal views. Its base does not show any crests or heels, but there are remnants of a faint cingulum/cingulid.

Two canines are included in the indetermined material. The specimen LPB (FGGUB) 189 only retains part of the crown, which is relatively long and hooked and is marked by faint enamel grooves (Fig. 23B). The curvature indicates that it probably is an upper canine. The specimen LPB (FGGUB) 86 (Fig. 23C) is retaining part of the root. It is larger and with no grooves or crests, but it shows a heel at its base, indicating that it probably is a lower canine.

Eight isolated premolars with variable morphology and size are briefly described herein (Figs. 23D–H). Most of them are damaged and their preservation restrains their descriptions. Their crowns range from high and robust with no accessory cusps/cuspids (e.g., AICUPM-SM-113; Fig. 23F) to small and low with strong accessory cusps/



Fig. 23 - Indeterminate carnivoran material from Bereşti and Măluşteni (Romania): (A) AICUPM-SM-103, incisor; (B) LPB (FGGUB) 189, canine; (C) LPB (FGGUB) 86, canine; (D) AICUPMSM-115, premolar; (E) AICUPM-SM-114, premolar; (F) AICUPM-SM-113, premolar; (G) AICUPMSM-109, premolar; (H) LPB (FGGUB) 216, premolar; (I) LPB (FGGUB) 213, hemimandible; (J) AICUPM-SM-112, sacrum; (K) AICUPMSM-111, ulna; (L) LPB (FGGUB) 98, tibia; (M) LPB (FGGUB) 97, astragalus. All specimens are depicted to the same scale.

cuspid (e.g., LPB (FGGUB) 216; Fig. 23H) and intermediate ones (e.g., AICUPM-SM-115; Fig. 23D). The specimen AICUPM-SM-114 (Fig. 23E) shows an additional lingual cusp which could cor-

respond to a protocone of a carnassial, but it could also correspond to the same structure of the D3.

The preserved toothless hemimandible from Bereşti (LPB (FGGUB) 213; Fig. 23I) preserves the

alveolus of the canine, as well as seven post-canine alveoli, possibly corresponding to a one-rooted p1 and the two-rooted p2, p3 and p4. The alveoli of the incisors or the molars are not present. A large mental foramen can be seen below the alveoli of p2 and p3. The mandibular corpus is moderately high and wide.

The isolated sacrum (AICUPM-SM-112; Fig. 23J) is almost complete, with just some lateral apophyses being broken. It is formed by three vertebrae and shows a moderately developed sagittal crest. The cranial end is considerably broader than the caudal end.

The preserved ulna (AICUPM-SM-111; Fig. 23K) only retains its proximal part. The olecranon is relatively shallow and the articular surface for the radius is short. The shaft of the ulna is thin and slightly curved.

The broken tibia (LPB (FGGUB) 98; Fig. 23L) retains only its distal part. The shaft is wide and straight. The two parts of the distal articular surface for the astragalus have approximately the same size. The internal malleolus is well developed.

Finally, the isolated astragalus (LPB (FGGUB) 97; Fig. 23M) is very small with a long neck and a narrow head. The trochlear articular epiphysis with the tibia is larger in its medial side. The articular surface for the calcaneum has a longer part plantarly to the neck and a rounder part plantarly to the trochlea.

Comparisons. In total, there are eleven isolated teeth (one incisor, two canines and eight premolars), as well as one hemimandible and four post-cranial elements (one sacrum, one ulna, one tibia and one astragalus) that cannot be definitively assigned to any of the aforementioned taxa of Mălușteni and Berești, due to their fragmentary preservation, the lack of diagnostic features, their lack of association with more diagnostic material, and the relatively high carnivoran diversity of Mălușteni. However, they were described here for future reference. It should be noted that some specimens have been previously published. For instance, the canines identified as *Lynx issiodorensis* (LPB (FGGUB) 189; Mălușteni) and *L. rumana* (LPB (FGGUB) 86; Berești) by Simionescu (1930, 1932) are too fragmentary to allow for definite identifications and are therefore referred to as Carnivora indet. Some notes can be made someone certain specimens based on size. The sacrum (AICUPM-SM-112) and ulna (AICUPM-

SM-111) from Mălușteni (published as *Mustela* aff. *robusta* by Simionescu 1930), as well as the astragalus (LPB (FGGUB) 97) from Berești, are very small and slender, likely belonging to small-sized mustelids. The hemimandible (LPB (FGGUB) 213) may belong to the phocid present in Mălușteni, based on its size and the number and orientation of the alveoli. However, it is not possible to exclude the attributions of these specimens to other similar-sized taxa. Therefore, all of this material is included here as Carnivora indet. until more material from both localities comes to light and clarifies the taxonomic status of these specimens.

DISCUSSION

The present revision resulted in the carnivoran faunal lists as they are shown in Table 16 and Figure 24. An occurrence that may be added to this dataset is presented in Ghenea (1968: p. 108), who reported a fragmentary right hemimandible with significantly worn p4 and m1 from the Maeotian of Rânzești as *Ictitherium robustum* (Gervais, 1850). Unfortunately, this specimen has been lost since its description. More detailed data concerning the age of the locality are not known; therefore, this specimen is considered to be of Turolian age, without adding a more detailed attribution. However, it is possible that it could belong to *Ictitherium viverrinum* Roth & Wagner, 1854, since the former name was used for this taxon for a long time (Kurtén 1982), or to *Prot. crassum*, which is reported herein from Crețești 1.

Among the reported taxa, some are of special interest due to their temporal and spatial distribution. One such taxon is *Paludolutra* sp., which has been found for the first time in Pogana 1. The current understanding of the distribution and evolution of this genus begins with the species *Pa. lluecai* in the Turolian of Spain in the localities of Los Algezares (type locality; MN12; 7.18–7.09 Ma; van Dam et al. 2023), Rambla de Valdecebro II (=El Arquillo 1 following Alcalá 1994; MN13; 6.56–6.26 Ma; van Dam et al. 2023), Conclud (=Cerro de la Garita; MN12; 7.57–7.52 Ma, van Dam et al. 2023), and Los Mansuetos (MN12; 7.27–7.23 Ma; van Dam et al. 2023). The Messinian species *Pa. campanii* and *Pa. maremmana*, found in Baccinello (V2), are the next occurrences of *Paludolutra*. These species are part of the Tusco-Sardinian palaeobioprovince (Rook et

Păun	Creţeşti 1	Pogana 1	Măluşteni	Bereşti
Vallesian	Turolian	Turolian	Ruscinian	Ruscinian
<i>Hyaenictitherium</i> sp.	<i>Ad. eximia</i>	<i>Paludolutra</i> sp.	<i>N. donnezani</i>	cf. <i>Eucyon</i> sp.
	<i>Prot. crassum</i>	Hyaenidae indet.	Canidae indet.	<i>Nyctereutes</i> sp.
	<i>Pri. attica</i>		<i>Ursus</i> sp.	cf. <i>Dinofelis</i> sp.
			Phocidae indet.	Carnivora indet.
			<i>Lutra?</i> <i>rumana</i>	
			<i>Martes</i> cf. <i>wenzensis</i>	
			<i>Mustela</i> sp.	
			' <i>Prom.</i> ' <i>malustenensis</i>	
			Felinae indet.	
			<i>Chasmaporthetes</i> sp.	
			Carnivora indet.	

Tab. 16 - Overview of the herein reported occurrences in the eastern Romanian carnivoran Neogene record.

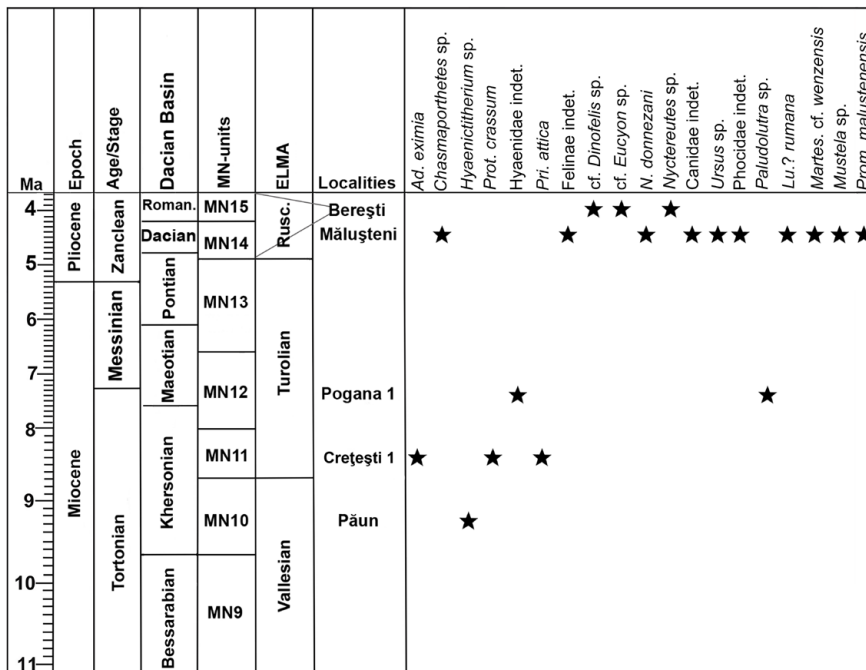


Fig. 24 - Stratigraphic occurrences of the discovered carnivorous mammals in the present work. Age correlations based on Van Baak et al. (2015), Palcu et al., (2017), Tesakov et al. (2017), and Crespo et al. (2023).

al. 2006; Abazzi et al. 2008). The present specimen indicates that these otters were also present in the Dacian Basin during the Turolian, covering a much larger area of the Paratethys than previously thought. This occurrence reveals a complex evolutionary pattern for *Paludolutra*, because Pogana 1 is contemporary to some of the mentioned localities from Spain. However, the tooth from Pogana appears to be different and more derived than the contemporary *Pa. lluecai*, resembling the subsequent MN13 Italian forms *Pa. maremmana* and *Pa. campanii*. Possibly, these morphological similarities could indicate an evolutionary connection between these species, suggesting that the Romanian representative of the genus may be a plausible ancestor for the Tusco-Sardinian species. This specimen is also interesting because it is possible that it shows signs of pathology. The area of the maxilla where the M1 should be located is highly porous and there is no indication of the molar or its alveolus (Fig. 6). This resembles the hyperplasia case

presented by Wang et al. (2023). Unfortunately, since only a limited part of the maxilla is preserved, it is not possible to make any definite assumptions on the factors that caused this abnormality. However, considering the amount of hard material consumed by otters, it cannot be ruled out that the preserved morphology resulted from the healing of dental trauma.

Another intriguing species is the small feline *Pri. attica*, previously only documented in Spain, Greece, and Turkey (Salesa et al. 2012a, 2012b). The discovery of this species in the Turolian of Creţeşti 1 indicates its presence in northern regions, reaching the northern borders of Paratethys. Creţeşti 1 is older than the localities of Pikermi (Böhme et al. 2017), Samos (Kostopoulos et al. 2009), and Vathyakkos (Koufos 2006) in Greece, Valdecebro 5 (Fraile et al. 1997) and Las Casiones (Salesa et al. 2012b) in Spain, and Akkaşdağı (de Bonis 2005; Karadenizli et al. 2005) in Turkey. The presence of *Pri. attica* in Creţeşti 1 represents its oldest validated known oc-

currence in the fossil record, as other identifications of material are not taxonomically certain (e.g., Peigné 2016).

Concerning the presence of *Protictitherium* in Crețești 1, this occurrence may be interpreted as a connection between the Vallesian and Turolian records of this species. Future material may show that in the bigger picture there is a virtually homogenous dataset that spans for a long period of time, as for example in *Semigenetta sansaniensis* (Lartet, 1851) (Kargopoulos et al. 2021a). Alternatively, it may indicate a transition towards a more derived species with higher p4 and m1 cuspids during the early Turolian. Although most reported occurrences of this taxon concern Vallesian localities, such as the neighbouring Kalfa (early Vallesian, MN9, Republic of Moldova; Lungu & Rzebik-Kowalska 2011), it is also present in the later stages of the Upper Miocene. For instance, it has been found in the MLN site in Samos (Greece, circa 7.5 Ma; Koufos 2009) and even in the MN13 locality of Dytiko 3 (Greece, 6.0–7.0 Ma; de Bonis & Koufos 1991; Koufos 2021). The presence of *Prot. crassum* in Crețești 1 indicates that this species was present in the central-eastern region of Europe after the transition from the Vallesian to the Turolian.

Aderocuta eximia is one of the most frequently occurring hyaenids of Eurasia during the Late Miocene (Werdelin & Solounias 1990, 1991). Recently, Rivals et al. (2024) investigated the role of this species in the Upper Miocene of the northern Black Sea region using a series of different methodologies based on material from the MN11 localities of Grebeniki (Ukraine) and Cioburciu 1 (Republic of Moldova). They concluded that the ecological niche of this species closely resembles that of the modern bone-cracking hyenas. This is a general trend that has been observed based on material from other regions as well (Werdelin & Solounias 1990, 1991; Turner et al. 2008; Kargopoulos 2019; Coca-Ortega & Pérez-Claros 2019).

Mălușteni has the highest diversity of carnivorans among all the localities analysed here, with at least nine taxa, whereas the other localities have yielded only one to four different taxa. Therefore, Mălușteni is a Pliocene locality that can be more broadly compared to other faunas of similar temporospatial range. Compared to the locality of Weże in Poland, which has been dated to 3.8–3.4 Ma for Weże 1 and 2.8–2.6 Ma for Weże 2 (Kow-

alski 1970; Marciszak et al. 2023), there are notable similarities and several shared taxa, such as *Martes wenzensis* (further details on this species are provided in the following paragraphs), *N. donnezani*, and possibly *Ursus* (Wolsan 1989). Kvabebi (3.07 Ma, Georgia) is another well-studied locality that shows four possible common taxa to the two Pliocene localities of Romania: *Eucyon* sp., *Lj. issiodorensis*, *Dinofelis* and *Chasmaporthetes* (Rook et al. 2017). The locality of Odessa Catacombs in Ukraine (MN 15; Pevzner et al. 1996) shares several possible carnivoran components with Mălușteni, including *Nycterentes*, *Eucyon*, *Ursus*, *Lynx* and *Chasmaporthetes* (Nagel et al. 2004). Some Pliocene localities from Greece are relevant to the carnivoran fauna of Mălușteni. The locality of Megalo Emvolon (MN15, Greece) is noteworthy for its occurrence of *N. tingi* (Koufos 1997), instead of the more commonly found *N. donnezani*, which is also present in Mălușteni. It is worth noting that the Grăunceanu locality (2.2–1.9 Ma; Terhune et al. 2020; Werdelin et al. 2023) has very limited similarities to that of Mălușteni, with the only possible shared taxa being *Ursus* and *Lj. issiodorensis*. These differences show that by that time the transition from a Ruscinian to a Villafranchian fauna had been completed.

The canids *Ny. donnezani* and *Eu. odessanus* are the most dominant species in the Pliocene of Eastern Europe (e.g., Marciszak et al. 2023). The former species, present in Mălușteni and possibly in Berești, has been found in many European and Anatolian sites, such as in Poland (e.g., Weże 1; Marciszak et al. 2023), Spain (e.g., Layna; Bartolini-Lucenti et al. 2018) and Turkey (Çalta-1; Dagueneet & Sen 2019). On the other hand, *Eu. odessanus* has been reported in several localities in Eastern Europe, including in the Republic of Moldova (e.g., Etulia; Nadochowski et al. 2006), Poland (e.g., Weże 1; Marciszak et al. 2023), and Ukraine (e.g., Odessa Catacombs; Odintsov 1967). The canines from Berești and the humerus from Mălușteni may also belong to this species. In certain instances, these species have been discovered in the same locality (e.g., Weże 1; Marciszak et al. 2023), indicating that their coexistence in Mălușteni and Berești cannot be disregarded.

The small mustelids found in Mălușteni, *Martes* cf. *wenzensis* and *Mustela* sp., are also of particular interest as they have not been reported in Romania until now (Stach 1959; Morlo & Kundrát 2001; Fjfar & Sabol 2004). The marten, in particular, holds

a crucial position in the evolution of extant European martens (Marciszak et al. 2024) and provides an intriguing connection with the locality of Weże (Poland). The age of this locality is slightly younger than that of Măluşteni, having an age of 3.8–3.4 Ma for Weże 1 and 2.8–2.6 Ma for Weże 2, according to Marciszak et al. (2023). Additionally, *Martes wenzensis* has also been reported from Rebielice Królewskie 1A (2.5–2.2 Ma, Poland) and Varshets (circa 2.5 Ma, Bulgaria) (Marciszak et al. 2024). Therefore, if the hemimandible from Măluşteni belongs to the species *Martes wenzensis*, it would be the oldest occurrence of the species in the fossil record. Even though the taxonomic status of the specimens from Măluşteni remains obscure, the reported specimens demonstrate that the small carnivorans of the locality exhibit great diversity that requires further study.

Finally, it is worth noting the interesting occurrence of the phocid from Măluşteni. While there are many Miocene seal forms found throughout the Paratethys, there are limited published data concerning the Pliocene, after the Messinian salinity crisis (Koretsky 2001). In this sense, it is interesting to determine if the seal found in Măluşteni corresponds to a form that survived during the Miocene/Pliocene transition or if it reflects a dispersal that occurred after the beginning of the Pliocene.

Concluding, the Neogene carnivoran record from Romania described herein remarks the importance of these localities from a palaeobiogeographical and evolutionary point of view. Further excavations are needed to provide additional insight into the faunal assemblages of the region during that period.

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