

The Early Pliocene small mammals (Eulipotyphla, Rodentia, Lagomorpha) from Berești and Mălușteni (eastern Romania): a fresh look at old collections

Vicente D. CRESPO^{1,2} , Ștefan VASILE^{3,4*} , Alexandru PETCULESCU^{4,5} , Bogdan G. RĂȚOI^{6,3}  and Bogdan S. HAIDUC³ 

¹ Departamento de Ciências da Terra, FCT-UNL Faculdade de Ciências E Tecnologia, GeoBioTec, Universidade Nova de Lisboa, 2829-516 Caparica, Portugal.

² GIUV2016-303 Grup d'Investigació en Paleontologia de Vertebrats Del Cenozoic PVC-GIUV, Àrea de Palaeontologia, Universitat de València, Dr. Moliner 50, E-46100 Burjassot, Spain.

³ Faculty of Geology and Geophysics, University of Bucharest, 1 Nicolae Bălcescu Avenue, 010041 Bucharest, Romania.

⁴ “Emil Racoviță” Institute of Speleology, Romanian Academy, 13-15 Calea 13 Septembrie, 050711 Bucharest, Romania.

⁵ Romanian Institute of Science and Technology, 3 Virgil Fulicea Street, 400022 Cluj-Napoca, Romania.

⁶ Department of Geology, “Alexandru Ioan Cuza” University, 22 Carol I Avenue, 700505 Iași, Romania.

*Corresponding author. Email: yokozuna_uz@yahoo.com

ABSTRACT: The neighbouring sites of Berești and Mălușteni (Eastern Carpathian Foreland, eastern Romania) have yielded the most abundant and taxonomically diverse Pliocene vertebrate assemblages described so far from the entire country. Some of the small mammals found here were described as new taxa, and occasionally reassessed during the past one hundred years, but most of the material collected initially remained unrevised. Here, we provide a taxonomic revision of all the small mammal material (insectivores, rodents, and lagomorphs) that could be found in three main collections. The studied specimens were assigned to the insectivore families Desmanidae (*Desmana verestchagini* and *Talpa* sp.), and Erinaceidae (*Erinaceus* sp.); to the rodent families Muridae (*Mimomys* sp. or *Promimomys* sp.; *Allocricetus* sp.), Sciuridae (*Spermophilus* cf. *nogaici*), Spalacidae (*Pliospalax macoveii*), and Castoridae (*Trogotherium minus*, *Castor fiber*); and to the lagomorph families Leporidae (*Trischizolagus dumitrescuae*) and Ochotonidae (*Ochotona ursui*). Compared to the faunal assemblages described from Central-Eastern Europe, the identified taxa (some confirmed, others reassessed as synonyms) support an Early Pliocene age for the vertebrate assemblages from Berești and Mălușteni. Both faunal assemblages are assigned to the Ruscinian, with the faunas from Berești being considered geologically slightly older than the ones from Mălușteni.



KEY WORDS: Eastern Carpathian Foreland, insectivores, lagomorphs, rodents, Ruscinian.

1. Introduction

Pliocene deposits are widely exposed in various areas of the Scythian Platform, a unit of the Eastern Carpathian Foreland, located in eastern Romania (Săndulescu 1984). These deposits were described as being part of the last sedimentary megacycle of the platform, which accumulated during the Badenian–Pleistocene interval (Ionesi 1994). The Pliocene fossil assemblages of Mălușteni and Berești (Fig. 1) have been known since the beginning of the 20th century, (Athanasiu 1915; Simionescu 1930, 1932), remaining to this day the richest continental Pliocene sites of the Dacian Basin (for an updated description of the Plio–Pleistocene units of the basin, see Andreescu *et al.* 2013), and of all Romania, in both large and small mammals.

The site of Mălușteni, the more productive of the two, is located along the Româneasca Creek, immediately under the Lacului Hill. According to Ghenea (1968), the Pliocene of Mălușteni includes fluvio-lacustrine deposits dominated by sands, where vertebrate fossils accumulated in some channel

deposit lenses. Aside from the small mammal taxa (reassessed in this paper), Simionescu (1930) describes from Mălușteni fossil vertebrate remains, assigning them to various large mammal groups, such as primates (*Macacus florentinus* and *Dolichopithecus ruscinensis*), carnivores (*Vulpes donnezani*, *Lutra rumana*, *Lynx issiodorensis*, *Promephitis malustenensis*, *Mustella* aff. *martes*, *Mustella* aff. *robusta*, *Mustella* aff. *putorius*, and *Phoca* sp.), perissodactyls (*Tapirus arvernensis*, *Rhinoceros* sp., *Hipparion gracile*, and *Equus* cf. *robustus*), artiodactyls (*Sus provincialis*, *Camelus bessarabensis*, *Capreolus australis*, *Cervus cusanus*, *Cervus buladensis*, *Cervus* cf. *ramosus*, *Cervus* cf. *arvernensis*, and *Palaeoryx athanasiui*), proboscideans (*Mastodon arvernensis* and *Mastodon borsoni*), as well as to reptiles (the chelonians *Testudo* sp., *Clemmys* sp., and *Trionyx* sp.; the snake *Coelopeltis* cf. *laurenti*; the lizard *Lacerta* sp.), and to fishes (*Acipenser* sp., *Esox* sp., *Lamna* sp., *Dentex* sp., *Sargus* sp., *Chrysophrys* sp., and *Myliobatis* sp.). Except for the chelonians, assigned by Macarovic & Vancea (1960) to *Testudo pregraeca ibera*, *Testudo grandis*,

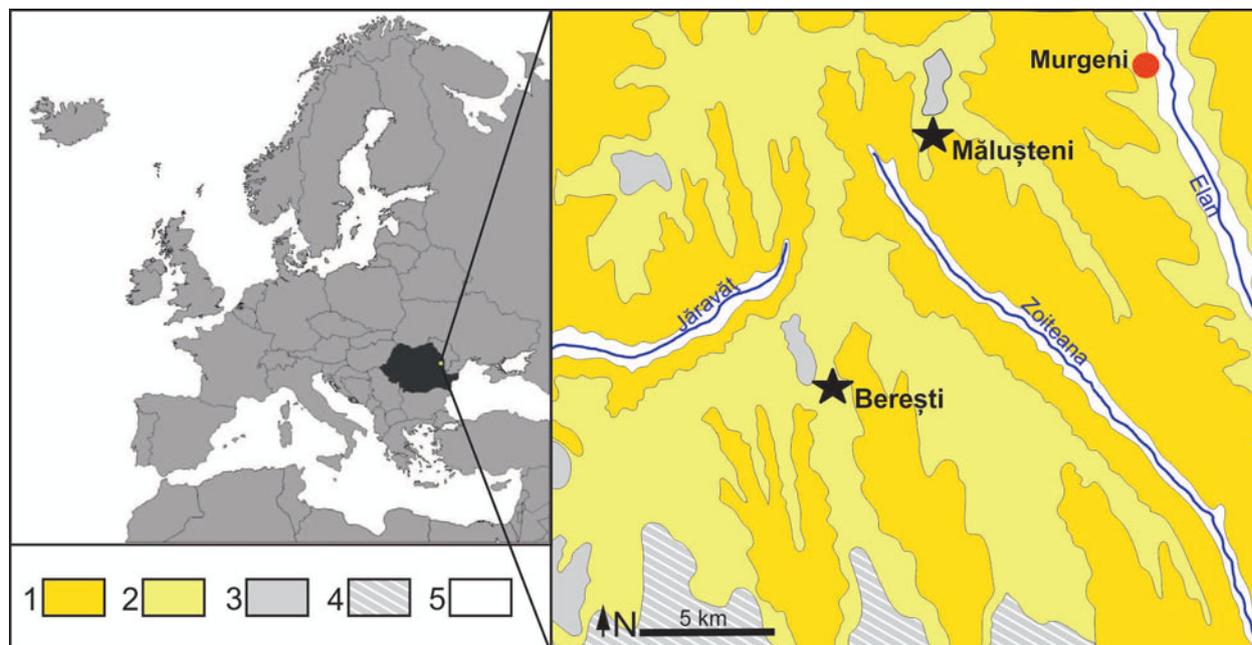


Figure 1 Geographical position of the fossil sites Berești and Mălușteni in eastern Romania, and the general geological map of the area (after Saulea *et al.* 1967). Colour legend: (1) Lower Pliocene; (2) Upper Pliocene; (3) Lower Pleistocene; (4) Middle–Upper Pleistocene; and (5) Holocene.

and *Clemmys malustensis*, and further reassigned by Młynarski (1969) to *Testudo macaroviczii*, *Geoemyda malustensis*, *Geoemyda* cf. *mossoczyi*, and Chelydridae gen. et sp. indet., the above-listed vertebrates from Mălușteni were never thoroughly revised, and their occurrence at the site should not be taken for granted until such a revision takes place.

The palaeontological site of Berești is located in the Porcului Ravine, near the railway station. From the lower part of the succession, Macarovici (1960) described white sands bearing several bivalve species of the genus *Prosodacna* (of Dacian, i.e., Early Pliocene, age), but also sands with microconglomerate-like sandstone concretions bearing vertebrate fossils (especially chelonian fragments) from the upper part of the succession. Except for the small mammals (revised in this paper), Simionescu (1932) describes large mammals' remains from Berești, assigning them to primates (*Macacus florentinus*), carnivores (*Machairodus* cf. *cultridens*, *Lutra rumana*, *Vulpes* sp., *Canis* sp., *Mustella* aff. *martes*, and *Mustella* sp.), perissodactyls (*Hipparion gracile* and *Equus* sp.), artiodactyls (*Sus* sp., *Capreolus australis*, *Cervus* cf. *arvernensis*, and *Cervus* sp.), proboscideans (*Mastodon* sp.), as well as to reptiles (the chelonians *Clemmys* sp., *Testudo* sp., and *Trionyx* sp.), and to fishes (*Scardinus* sp., *Barbus* sp., *Carpis* sp., and *Tinca* sp.). As is the case for the material from Mălușteni, the above-listed specimens from Berești were never revised, so their occurrence should be considered only tentative, until a proper revision of the specimens takes place.

The field research of Ghenea (1968) represents the last attempt of systematic fossil collection from these sites. Following their original description, the initial fossil material, deposited in the collections of several institutions (see below, section 2. Material and methods) has not been studied intensely, only some small mammal taxa being occasionally reassessed, or just mentioned in general syntheses on Pliocene faunas of Romania (e.g., Radulescu & Samson 1967a, b; Samson & Radulescu 1973; Radulescu & Samson, 1989a, b; Rădulescu & Samson 1995; Terzea 1997, 2005; Radulescu *et al.* 2003, but see below, section 3. Systematic palaeontology, for additional references). Very little novel large vertebrate material has been described since the early days of research in the area – only some new rhinocerotid fossil material was more recently published in several papers (e.g., Codrea 1993; Codrea & Costănel 2003).

The faunal lists including small mammals from Berești and Mălușteni were published by Simionescu (1930, 1932), and by other authors, in subsequent syntheses presenting Pliocene continental mammal faunas from Romania (e.g., Terzea 1997, 2005; Radulescu *et al.* 2003), and they include many taxa that are new to science. Since the two sites have produced the most diverse Pliocene taxonomic assemblages of Romania, they are extremely important in understanding the palaeogeographical and stratigraphical ranges for the small mammal taxa of Central-Eastern Europe, in general, and of Romania, in particular. The aim of this work is to study all available small mammal specimens collected from the above-mentioned sites, now divided into three main collections (see below, section 2. Material and methods), to reassess the taxonomic validity of the taxa described so far from these sites, and to reassess the age of the faunal assemblages by comparing it to updated research on the biostratigraphy of Pliocene small mammal assemblages.

2. Material and methods

The fossils studied here are currently deposited at the Laboratory of Palaeontology, Faculty of Geology and Geophysics, University of Bucharest (Romania) – LPB (FGGUB), at the 'Emil Racoviță' Institute of Speleology, Romanian Academy (Bucharest, Romania) – ISER, and at the Department of Geology, 'Alexandru Ioan Cuza' University of Iași (Romania) – UAIC.

The followed terminologies are: Ziegler (1990) and Furió (2007) for erinaceids, Oliver & Peláez-Campomanes (2013) for 'cricetids', Cuenca-Bescós (1988) for sciurids, Sarica & Sen (2003) for spalacids, Huguency (1999) for castorids, and López Martínez (1984, 1989), with modifications by Hordijk (2010) for lagomorphs. We follow the measuring schemes proposed by Doukas (1986) for erinaceids, by Oliver & Peláez-Campomanes (2013) for 'cricetids', by Cuenca-Bescós (1988) for sciurids, by Sarica & Sen (2003) for spalacids, by Rekovets *et al.* (2020) for castorids, and by Hordijk (2010) for lagomorphs.

Scanning electron micrographs were taken at the Arheoinvest Research Center (Iași, Romania), using a VEGA II LSH scanning electron microscope (SEM) produced by TESCAN, coupled with a QX2 QUANTAX EDX detector produced by

BRUKER/ROENTEC. Larger specimens, that did not fit inside the SEM, were photographed with an Axiocam 105 colour microscopy camera, mounted on a Zeiss Stemi 305 trino stereomicroscope (at LPB[FGGUB] and at UAIC), and, in the sole case of a castorid hemimandible (the largest of all specimens), with a Nikon D7200 DSLR camera (at LPB[FGGUB]).

3. Systematic palaeontology

Phylum CHORDATA Bateson, 1885

Class MAMMALIA Linnaeus, 1758

Order EULIPOTYPHILA Waddell *et al.* 1999

Family Talpidae Fischer, 1814

Subfamily Desmaninae Thomas, 1912

Desmana Gueldenstaedt, 1777

Desmana verestchagini Topachevski, 1961

Myogale sp. in Simionescu (1932)

Desmana verestchagini amutriensis in Radulescu *et al.* (1989)

Desmana amutriensis in Rădulescu *et al.* (1992)

Occurrence: Early Pliocene (MN14)

Site: Mălușteni

Material: one left p4 (ISER MI/007a), one left hemimandible with p4–m2 (ISER MI/007b; Fig. 2A), one right humerus (LPB[FGGUB] 109 – Fig. 2B, C)

Measurements: See Table 1

Description: Material is described in Rădulescu *et al.* (1992)

Remarks:

These specimens were described by Simionescu (1932) as *Myogale* sp., but they were later used by Radulescu *et al.* (1989) as a basis for the description of a new subspecies, *Desmana verestchagini amutriensis*. Nevertheless, it was finally described by Rădulescu *et al.* (1992) as a separate species, *Desmana amutrensis* (Rzebik-Kowalska 2005). The genus *Desmana*, following the amended diagnosis made by Minwer-Barakat *et al.* (2020), is characterised by its medium–large size, by the different sizes and morphology of the incisors, as well as by the relative length between the different premolars. Since the incisors are not preserved in the materials studied here, we can only confirm assignment to the genus by using the relative sizes of the p2 and p3 alveoli, with p2 being larger than p3. Moreover, the size of the specimen indicates that it belongs to the medium-sized desmanine group, as already indicated by Rzebik-Kowalska (2002).

The holotype of *D. amutrensis* consists of a single broken M2, in which the parastyle and metastyle are broken (Radulescu *et al.* 1989; Rădulescu *et al.* 1992). In spite of the material being incomplete, close morphological similarities to *D. verestchagini*

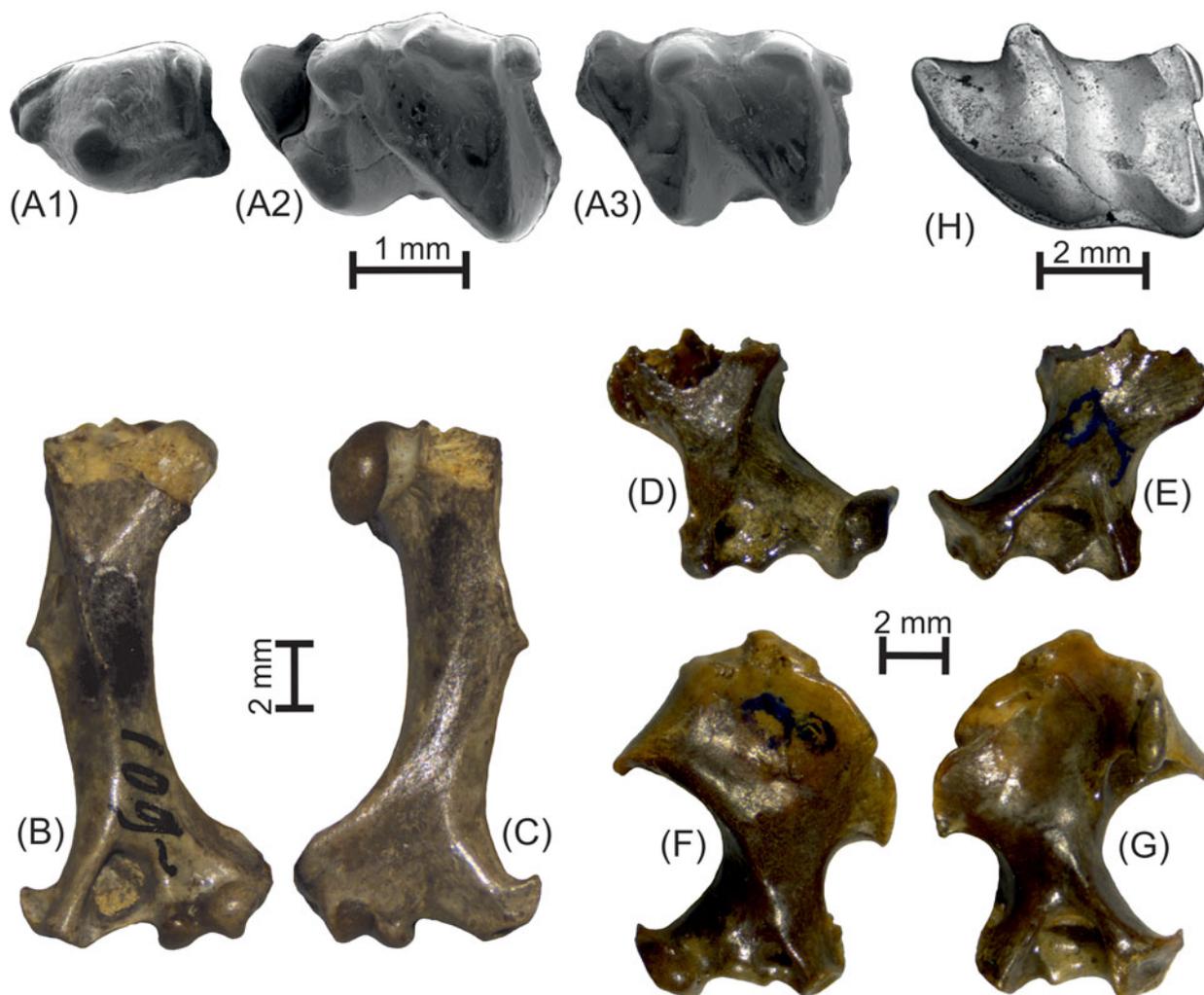


Figure 2 Eulipotyphla from Berești and Mălușteni. *Desmana verestchagini*: (A1–A3) left p4–m2 from Mălușteni, in occlusal view; (B, C) left humerus from Mălușteni, in anterior (B), and posterior (C) views. *Talpa* sp.: (D, E) left humerus from Mălușteni (holotype of *Talpa neagui* after Radulescu & Samson 1989b), in anterior (D), and posterior (E) views; (F, G) complete right humerus from Mălușteni, in anterior (F), and posterior (G) views. *Eri-naecus* sp.: (H) left m1 from Berești, in occlusal view.

Table 1 Measurements of the small mammals from Berești and Mălușteni (in mm).

Element	Site	Measurement	<i>n</i>	Minimum	Medium	Maximum
<i>Desmana verestchagini</i>						
p4	Mălușteni	Length (L)	2	1.94		2.07
		Width (W)	2	1.25		1.33
m1	Mălușteni	L	1		2.60	
		Trigonid width (Wtr)	1		1.58	
		Talonid width (Wtal)	1		2.09	
m2	Mălușteni	L	1		2.65	
		Wtr	1		1.92	
		Wtal	1		1.85	
<i>Erinaceus</i> sp.						
m1	Berești	L	1		5.42	
		Wtr	1		3.24	
		Wtal	1		3.41	
<i>Mimomys</i> sp. or <i>Promimomys</i> sp.						
m1	Mălușteni	L	1		≈2.79	
		W	1		≈1.43	
m2	Mălușteni	L	1		1.76	
		W	1		≈1.37	
M2	Mălușteni	L	1		2.12	
		W	1		1.55	
<i>Allocricetus</i> sp.						
m1	Berești	L	2	1.41		1.54
		W	2	1.01		1.07
m2	Berești	L	2	1.33		1.36
		W	2	1.11		1.2
m3	Berești	L	2	1.34		1.34
		W	2	1.10		1.17
<i>Spermophilus</i> cf. <i>nogaici</i>						
p4	Mălușteni	L	1		1.82	
		W	1		2.02	
m1,2	Mălușteni	L	1		2	
		W	1		2.51	
<i>Pliospalax macoveii</i>						
m1	Mălușteni	L	9	1.95	2.28	2.76
		W	9	1.4	1.97	2.48
m2	Mălușteni	L	11	1.8	2.25	2.5
		W	11	1.7	2.14	2.5
m3	Mălușteni	L	2	1.6		2.13
		W	2	1.4		1.83
M1	Berești	L	1		2.69	
		W	1		2.25	
M2	Berești	L	1		2.08	
		W	1		2.22	
<i>Trogotherium minus</i>						
p4	Mălușteni	L	4	3.87	5.21	6.7
		W	4	4.38	5.14	6.29
m1,2	Mălușteni	L	3	4.09	5.03	6.75
		W	3	4.3	4.95	6.03
m3	Mălușteni	L	1		7.02	
		W	1		6.12	
M1,2	Mălușteni	L	6	3.32	3.81	4.8
		W	6	3.95	4.56	5.5
M3	Mălușteni	L	7	4	4.83	6.02
		W	7	3.5	5.12	6.15
<i>Castor fiber</i>						
p4	Mălușteni	L	2	9.62		9.64
		W	2	6.84		7.86
m1	Mălușteni	L	1		8.25	
		W	1		7.75	
m2	Mălușteni	L	2	6.7		6.75
		W	2	6.03		8
m3	Mălușteni	L	1		6.62	
		W	1		6.44	
<i>Trischizolagus dumitrescuae</i>						
p3	Mălușteni	L	10	2.95	3.46	3.62
		W	10	2.88	3.19	3.73
p4/m1/m2	Mălușteni	L	72	2.42	3.08	3.95
		W	72	2.73	3.45	3.97

(Continued)

Table 1 Continued.

Element	Site	Measurement	<i>n</i>	Minimum	Medium	Maximum
P4/M1/M2	Berești	L	8	2.78	3.09	3.49
		W	8	3.34	3.6	3.96
	Mălușteni	L	32	2.05	2.95	3.66
		W	32	3.3	4.13	5.67
	Berești	L	6	2.46	2.63	3.02
		W	5	4.75	5.13	5.42
<i>Ochotona ursui</i>						
p3	Mălușteni	L	3	1.33	1.77	2.19
		W	3	1.39	1.71	1.94
p4/m1/m2	Mălușteni	L	76	1.44	1.87	2.51
		W	76	1.46	1.96	2.54
	Berești	L	14	1.23	1.74	2.12
		W	14	1.36	1.85	2.12
m3	Berești	L	1		0.68	
		W	1		1.4	
P3	Mălușteni	L	1		1.38	
		W	1		2.23	

can be observed, with the latter species being larger. The material found at Mălușteni only consists of lower dentition, the size of which is larger than that reported for the specimens described from Kosyakin quarry (Russia, type locality) and Kardia (Greece; Rümke 1985). However, in the extant species *Desmana moschata*, such a large variability in size is observed (Minwer-Barakat *et al.* 2020), that the previously-cited populations of *D. verestchagini* and those studied here could be included within the same species, each at opposite ends of the size range. Therefore, also taking into account the scarcity of remains, we propose the synonymy of *D. amutrensis* with *D. verestchagini*.

A humerus of this species was also found and described by Simionescu (1930) as *Sorex* sp. However, due to its close similarity to the humerus described by Rümke (1985) as *D. verestchagini* from Kardia, the humerus described by Simionescu (1930) as *Sorex* sp. is also assigned here to *D. verestchagini*.

Subfamily Talpinae Fischer von Waldheim, 1817

Genus *Talpa* Linnaeus, 1758

Talpa sp.

Talpa sp. in Simionescu (1930)

Talpa sp. in Simionescu (1932)

Talpa minor in Kowalski (1956)

Talpa minor in Sulimski (1959)

Talpa minor ssp. (partim) in Rabeder (1972)

Talpa sp. in Samson & Radulescu (1973)

Talpa neagui new species in Radulescu & Samson (1989b)

Occurrence: Early Miocene (MN2)–present

Sites: Berești and Mălușteni

Material: six humeri (ISER Br/001 – Fig. 2D, E; Br/002; MI/018 – Fig. 2F, G; MI/019; MI/020; MI/021)

Description: See Radulescu & Samson (1989b)

Remarks:

Based on the humeri found at Berești and Mălușteni, Radulescu & Samson (1989b) erected a new talpid species: *Talpa neagui*. The new species was defined, and humeri from a few European sites were assigned to it, based only on the relative width of the diaphysis, even in the absence of dentition. As it has no associated dentition, and the relative size of the diaphysis overlaps the ranges seen in other species, such as *Talpa minor* and *Talpa fossilis/Talpa europaea* (Rzebik-Kowalska 2013), we prefer to leave the species *T. neagui* as *nomen dubium*, and assign the material listed here to *Talpa* sp. until additional specimens will be found at Berești and Mălușteni.

Family Erinaceidae Fischer, 1817

Erinaceus Linnaeus, 1758

Erinaceus sp.

Erinaceus sp. in Simionescu (1930)

Occurrence: Late Miocene (MN10)–present

Site: Berești

Material: one left m1 (Fig. 2H; ISER, unnumbered specimen, labeled ‘*Erinaceus*’)

Measurements: See Table 1

Description: The outline of the occlusal surface is sub-rectangular. The V-shaped trigonid is slightly narrower and longer than the talonid. The paraconid is fairly lowered and lies at the end of a long and slightly curved paralophid. The hypolophid and the entocristid have an open V-shape, due to being worn. The anterior cingulum is narrow and connects the labial side of the paraconid to the posterior cingulum. The oblique cristid is straight. The posterior cingulid starts at the entoconid and it is connected to the anterior cingulum.

Remarks:

This molar was cited and preliminarily studied by Simionescu (1930). In this article, we describe and illustrate it for the first time. The classification made by the previous author is maintained, as the material is scarce and not very diagnostic. In terms of size, it is grouped with other medium-sized Plio–Pleistocene European species, such as *Erinaceus samsonowiczi*, *Erinaceus ostramosi*, *Erinaceus olgae*, and *Erinaceus lechei*, as well as with *Erinaceus* sp. 1 and 2 from Beftia, western Romania (Sulimski 1959; Rzebik-Kowalska 2000; Popov 2004). Due to the small size of the paraconid, species such as *E. lechei* and *E. samsonowiczi* can be discarded (Doukas *et al.* 1995; Rzebik-Kowalska 2000), while *E. olgae* can also be rejected as it has shorter trigonids (Flynn & Wu 2017).

Order Rodentia Bowdich, 1821

Family Muridae Illiger, 1811

Subfamily Arvicolinae Gray, 1821

Mimomys sp. or *Promimomys* sp.

Arvicola pliocenicus in Simionescu (1930)

Mimomys moldavicus n. sp., Kormos (1932)

Promimomys moldavicus in Kretzoi (1955)

Promimomys moldavicus in Samson & Radulescu (1973)

Mimomys silasensis n. sp. in Jánosy (1974)

Mimomys gracilis in Sen (1977)

Promimomys moldavicus moldavicus in Gromov (1977)

Mimomys davakosi n. sp. in van de Weerd (1979)

Promimomys moldavicus in Shushpanov (1985)

Promimomys moldavicus in Aleksandrova (1986)

Mimomys moldavicus in Radulescu & Samson (1989a)

Occurrence: MN14–early Middle Pleistocene

Sites: Mălușteni

Material: one left hemimandible with m1 + m2 (ISER, specimen not numbered – Fig. 3A–D), one right M2 (ISER, specimen not numbered – Fig. 3E, F)

Measurements: See Table 1

Description: See Radulescu & Samson (1989a).

Remarks:

Simionescu (1930) described two arvicolid hemimandibles from Mălușteni, classifying them as *Arvicola pliocenicus*, later synonymised to *Mimomys pliocaenicus*. One of them, which is not in the collection under study and is probably lost, was used by Kormos (1932) to establish the species *Mimomys moldavicus* Kormos, 1932 (or *Promimomys moldavicus* according to some authors). While Radulescu & Samson (1989a) revised the material in order to confirm the validity of the species, several attempts have been made to synonymise it to *Promimomys cor* (Suata-Alpaslan 2015), or to *Mimomys davakosi* (Fejfar *et al.* 1998, 2011), using as type material a mandible with very worn teeth. In addition, Radulescu & Samson (1996) describe further material assigned to this species in Drănic 0 (*M. moldavicus* group) and 1 (*Mimomys moldavicus/Propiomys*), but this material does not fit with the type material of the species in the number of triangles of m1.

The mandible available for this study is characterised by having narrower reentrant angles than the holotype of *M. moldavicus* described by Kormos (1932) and by Radulescu & Samson (1989a), as well as presenting an islet on the anteroconid, characters that do not appear in the holotype of *M. moldavicus*, if the species were to be considered valid. For these reasons, and until they can be compared to each other, we consider that the mandible included in this study could belong to a different species than the former. According to Hordik & de Bruijn (2009), the genera *Promimomys* and *Mimomys* are differentiated by 'A weak or relatively well-developed and persistent LRA4 on m1, a *Mimomys*-kante on m1 and development of dentine tract ea on m1'. Because of the high degree of digestion by a predator, these characters do not appear in the material under study, making it impossible to assign it to a genus. In any case, more material from this site, other than from senile individuals, will allow further studies aiming to synonymise or better characterise *M. moldavicus*.

Subfamily Cricetinae Fischer, 1817

Genus *Allocricetus* Schaub, 1930

Allocricetus sp.

Cricetulus simionescui sp. nova in Schaub (1931)

Cricetulus simionescui in Simionescu (1930)

Occurrence: Late Miocene (MN9)–Early Pleistocene

Site: Berești

Material: Two hemimandibles bearing m1–m3 (ISER NN1; NN2 – Fig. 3G)

Measurements: See Table 1

Description: The m1 has a slightly bifid anteroconid which is connected to the junction of the protoconid–metaconid by a thick, probably double, anterolophulid, resulting in a very worn area of the tooth. The mesolophid is absent and the thick

posterolophid is connected to the distal base of the entoconid. The m2 and m3 have the protosinusid as deep as the sinusid; the labial anterolophid is strong, and the lingual one is reduced. The m2 has a short mesolophid, which is more robust than the one found on M3, and is directed forward.

Remarks:

Two mandibles belonging to a medium-sized cricetine, deposited in the ISER collections, were classified by Simionescu (1932) as *Cricetulus simionescui* Schaub, 1932. The identification of cricetines from the Miocene-to-Pleistocene interval is very complicated, as some authors list more than 20 genera, but many of them are morphologically very similar, and, probably, after being revised, many of them will end up being synonymised (McKenna & Bell 1997; De Bruijn *et al.* 2012). Simionescu (1990) cites a *Cricetus* sp. from Mălușteni but it is not known what material was identified as such.

Thanks to their size, and stratigraphical distribution, the hemimandibles available for this study could be not assigned to practically all genera except *Allocricetus* and *Neocricetodon*. Sen *et al.* (2019) morphologically differentiate the two genera, the former being characterised by narrow lower molars, single anterolophulids connected to the protoconid, narrow and slightly bifid anteroconid and finally absent or weak mesolophids, but in the case they should possess these structures they should have a greater size of the molar series. On the other hand, according to the same authors, *Neocricetodon* is characterised by molars bearing broad anteroconids, well-developed mesolophids, and usually double anterolophulids, characters that differ from the material under study, thus making it more similar to *Allocricetus*. Within *Neocricetodon*, the following Pliocene species can be excluded: *Allocricetus bursae* Schaub, 1930, the most common species in the Plio–Pleistocene of Europe, although it has a similar size to the material studied here, can be discarded because of its large m1 anteroconid; *A. primitivus* Wu & Flynn, 2017, from China, is also very similar, but has a wider m1; and *Allocricetus ehiki* Schaub, 1930 can also be excluded because of its large size (Wu & Flynn 2017; Sen *et al.* 2019). Therefore, the species most similar to the material under study is *Allocricetus primitivus*, of Chinese origin and primitive morphology.

Family Sciuridae Fischer, 1817

Subfamily Xerinae Osborn, 1910

Tribe Marmotini Pocock, 1923

Genus *Spermophilus* Cuvier, 1825

Spermophilus cf. *nogaici* (Topachevsky, 1957)

Spermophilus sp. in Simionescu (1930)

Spermophilus sp. in Simionescu (1932)

Occurrence: Late Pliocene–Middle Pleistocene

Site: Mălușteni

Material: two hemimandibles with a p4 (LPB[FGGUB] 110 – Fig. 3H), one m1/2 (ISER, not registered specimen – Fig. 3I)

Measurements: See Table 1

Description: The p4 is premolariform. The trigonid is moderately labiolingually compressed, which results in the occlusal outline of the tooth crown being subtriangular (in one of the specimens) to subrectangular (in the other). From the main cusps, the anterior two (i.e., the metaconid and the protoconid) are the tallest, and are closely situated; the metaconid is slightly taller than the protoconid. The anterolophid is well developed, but does not close the anterior basin. There is no labial anterolophid and the metalophid is low and well developed. One of the specimens presents a low mesolophid which resembles an elongated cusp and has no contact with the entoconid. The mesoconid is

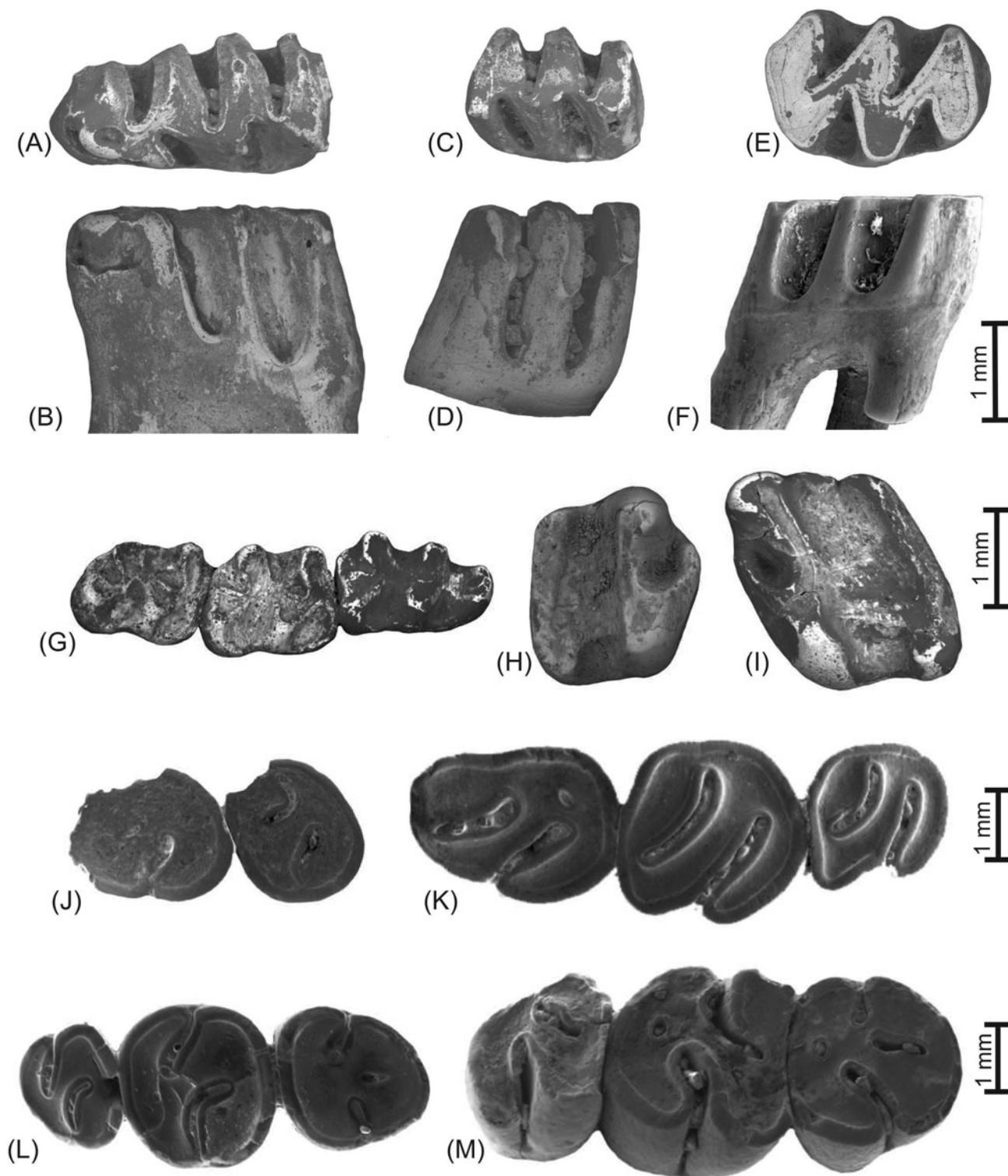


Figure 3 Rodents (except castorids) from Berești and Mălușteni, in occlusal view, except B, D, and F in labial view. *Mimomys* sp. or *Promimomys* sp.: (A, B) left m1; (C, D) left m2, (A–D) from the same hemimandible from Mălușteni; (E, F) right M2 from Mălușteni. *Allocricetus* sp.: (G) right m1–3 from Berești. *Spermophilus* cf. *nogaici*: (H) right p4 from Mălușteni; (I) left m1/2 from Mălușteni. *Pliospalax macoveii*: (J) left m1,2 from Mălușteni with advanced wear; (K) left m1–3 from Mălușteni (holotype? of *Prospalax rumanus* after Simionescu 1930); (L) right m1–3 from Berești; (M) right m1–3 from Mălușteni (holotype? of *Prospalax macoveii* after Simionescu 1930).

not present, and the entoconid is poorly developed. The entolophid is absent, whereas the hypoconulid is small. Finally, one of the specimens has a straighter posterolophid than the other.

The m1/2 is similar to the p4, but has a more rectangular occlusal outline; the trigonid is shorter, the anterolophid is connected to the metaconid, and the metalophid is less developed.

Remarks:

Two hemimandibles retaining the p4s, and an isolated m1/2, all belonging to a species of ground squirrel, are deposited in the collections of ISER and LPB(FGGUB). One of the p4-bearing hemimandibles was already published by Simionescu (1930) as *Spermophilus* sp., whereas the remaining specimens remained unpublished, until now. Kormos (1940; as cited by Samson & Radulesco 1973) assigns one of the hemimandibles to *Citellus primigenius*, whereas Samson & Radulesco (1973) reinterpreted that

specimen as *Citellus* sp., and the other p4-bearing hemimandible as *Pliosciuropterus* sp. The material studied here presents similarities to *S. nogaici*, species described by Sinita & Pogodina (2019) from the uppermost Pliocene–Lower Pleistocene deposits of Ukraine. It is worth mentioning that the basalmost and first known species of the genus in Eurasia, *Spermophilus praecox*, described from the Late Pliocene–Early Pleistocene interval, differentiates itself by having a larger overall size, a p4 that is more trapezoidal due to its triangular trigonid, and, in general, by lacking the metalophid in the m1/2. It also differs from the other primitive species present in the Late Pliocene, such as *Spermophilus polonicus*, by having a less triangular p4 (Popova et al. 2021). Therefore, this would be the first finding of this genus in Europe, outside of Ukraine, making their migration patterns occur earlier than the Late Pliocene, as it was previously established (Sinita et al. 2019).

Family Spalacidae Gray, 1821

Pliospalax Kormos, 1932

Pliospalax macoveii (Simionescu 1930)

Prospalax rumanus n. f. in Simionescu (1930) (in part)

Prospalax Macoveii n. f. in Simionescu (1930) (in part)

Spalax (*Pliospalax* Kormos n. g.) *Macoveii* in Simionescu (1932)

Occurrence: Late Miocene (MN13)–Late Pliocene (MN15)

Sites: Berești and Mălușteni

Material: One M1 (LPB[FGGUB] 225-1), one M2 (ISER NN), three hemimandibles m1–m3 (ISER 112.17 – Fig. 3K; ISER, specimen not numbered – Fig. 3L; LPB[FGGUB] 117-3 – Fig. 3M), six hemimandibles m1–m2 (LPB[FGGUB] 117-1; LPB[FGGUB] 117-2; UAIC SM-8-3 – Fig. 3J; UAIC SM-8b; ISER 116-15), three m1 (LPB[FGGUB] 107-11; UAIC SM-8-4; ISER 116-16) and two m2 (UAIC SM-8-1; UAIC SM-8-2; ISER 116-17).

Measurements: See Table 1

Description:

M1: subquadrate occlusal shape, with three labial folds and one lingual reentrant fold. One small labial anteroloph is present, connected to the protocone and the paracone. The mesoloph is connected to the metacone. The posteroloph is long and narrow.

M2: subtriangular occlusal shape, with one labial and one lingual reentrant fold. The anteroloph is connected to the paracone, isolating an islet, which in turn is located in the continuation of the sinus. The mesosinus is L-shaped, and posteriorly directed.

m1: the tooth may be subtriangular in occlusal view (nine out of 11), or it may appear as more rounded (two out of 11); the protosinusid may be curved and directed to the anterior side of the tooth (seven out of 11), it may be straight (two out of 11), or it may appear in the form of an islet (two out of 11). In two specimens, a small labial protosinusid is present. The sinusid may be straight (eight out of 11), it may be curved (two out of 11) and directed to the posterior side, or it may only appear as an islet (one out of 11). An islet may (eight out of 11) or may not (three out of 11) be present on the lingual side of the sinusid.

m2: It is similar to m1, but has a more quadrate outline, and the islet may (four out of 10) or may not (five out of 10) be present.

m3: It is similar to m2, but the tooth may be narrower (one out of three), or it more triangular (two out of three).

Remarks:

Two species of spalacids belonging to the genus *Prospalax* were described by Simionescu (1930) from Mălușteni (*Prospalax macoveii* and *Prospalax rumanus*). Subsequently, Kormos (1932) defined the genus *Pliospalax* based on this material, separating it from the genus *Prospalax*, which nowadays is considered an anomalomyid (Nesin & Kovalchuk 2021). From that

moment on, there has been a large amount of literature doubting whether the two species are different, and many authors synonymise *Pr. rumanus* with *Pl. macoveii* (e.g., Hordik & de Bruijn 2009). This all came from the fact that the two species are separated by size (Simionescu 1930), but, after comparing their measurements, they are not sufficiently different to make such separation. On the other hand, some authors, such as Popov (2017), following Topachevskyi (1969), place this species within the genus *Microspalax*. Other authors, such as Sulimski (1964), synonymise both species with *Prospalax priscus*, although with some doubts.

Rădulescu & Samson (1995) describe a new hemimandible belonging to *Pl. macoveii*, and another one, bearing only two molars, assigned to *Microspalax* cf. *odessanus*. However, these specimens are not among the material found by us in the three collections investigated, and, therefore, could not be studied.

One of the major problems of the family Spalacidae is the great variability in their dental morphology, which depends on wearing degree. Although the typical S-form occurs in the extinct genus *Pliospalax*, as well as in juveniles of the current genus *Nannospalax*, the two genera can be differentiated by the number of reentrants on the m1's lingual and labial faces, with other characters that can be used for their identification as well (de Bruijn & van der Meulen 1975; Sarica & Sen 2003; Sen & Sarica 2011; Popov 2017; Erdal et al. 2018). Despite the large amount of described material, no specimens have been found to have little wear, which makes comparison between specimens, and to specimens belonging to other species difficult. Therefore, taking into account the wide range of different morphologies, and the similar size between *Pr. rumanus* and *Pl. macoveii*, we here decided to group both previously-described species into a single one, *Pliospalax macoveii*.

Family Castoridae Gray, 1821

Genus *Trogotherium* Newton, 1890

Trogotherium minus Newton, 1890

Steneofiber covurluensis n. f. in Simionescu (1930) (in part)

Castor sp. in Simionescu (1930) (in part)

Steneofiber covurluensis n. f. in Simionescu (1932) (in part)

Castor sp. in Simionescu (1932) (in part)

Zamolxifiber covurluensis n. sp. in Radulescu & Samson (1967b) (in part)

Romanocastor filipes n. sp. in Radulescu & Samson (1967b) (in part)

Occurrence: Early Pliocene (MN14)–Early Pleistocene

Sites: Berești and Mălușteni

Material: five M1/2 (UAIC SM-7-1 – Fig. 4B; UAIC SM-7-3 – Fig. 4D; ISER 27; UAIC SM-7-4 – Fig. 4E; ISER 14), eight M3 (UAIC SM-14-5; ISER 23; ISER 24; ISER 25; ISER 26; ISER 10; ISER 11; ISER 13), five p4 (LPB[FGGUB] 195; UAIC SM14-3; UAIC SM-7-2 – Fig. 4C; ISER 22; ISER 12), one m1/2 (LPB[FGGUB] 104-1), one m3 (UAIC SM-14-4), and one hemimandible m1-2 (UAIC SM-14-1 – Fig. 4A).

Measurements: See Table 1

Description:

M1/2: subquadrangular tooth, with a narrow posterior side. The metafossette and the parafossette are narrow and long, the mesoflexus and the hypoflexus are open and shorter than the fossettes; and a mesofossette is present in one of the specimens. Two roots are present. One unworn specimen has a wide flexus and an anterior islet.

M3: triangular tooth. The anterior lobe of the tooth may be long (three out of seven), or short (four out of seven). The hypoflexus and the paraflexus may be curved (five out of seven), or straight (two out of seven) and in line. The mesoflexus and the

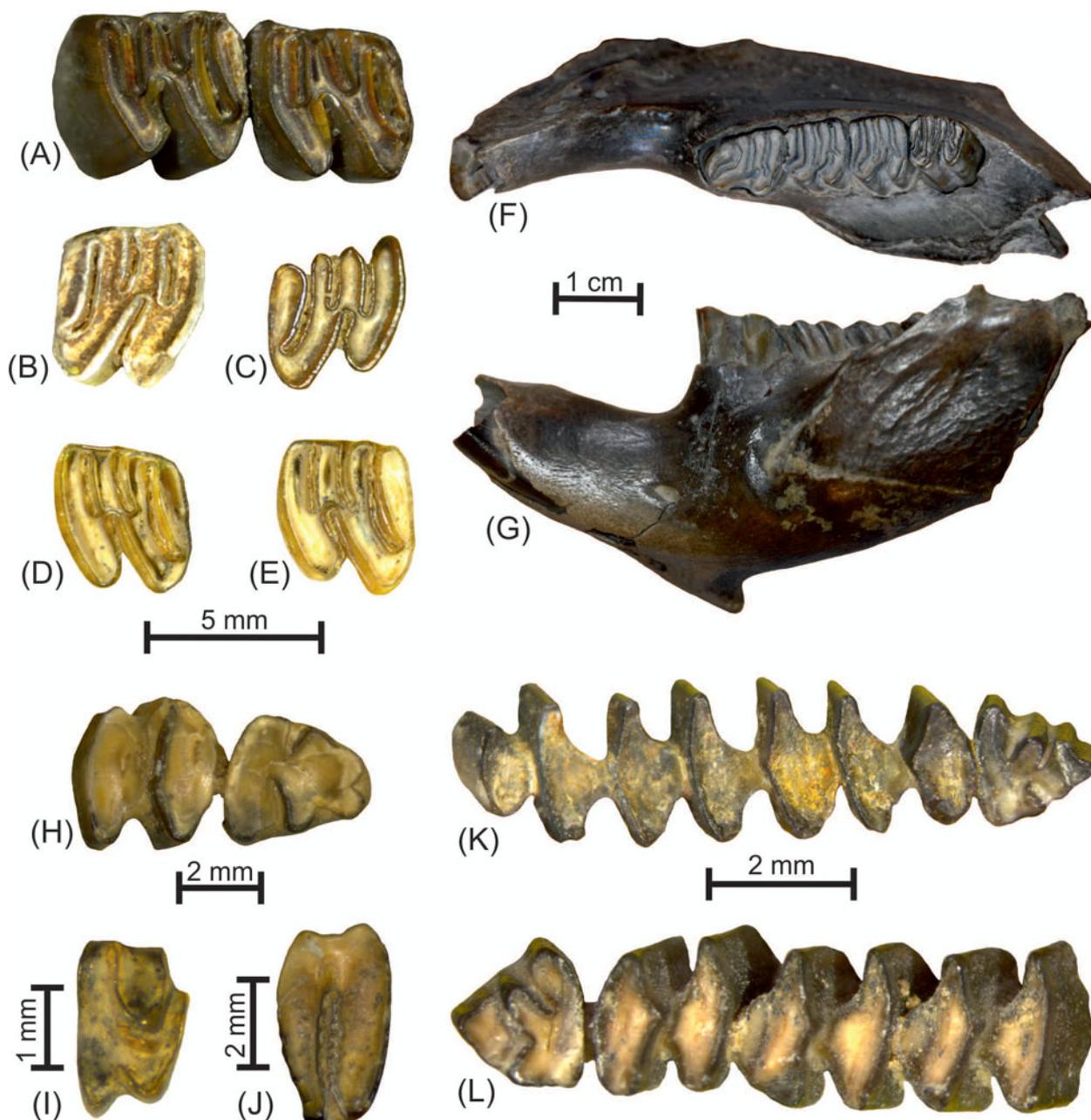


Figure 4 Castorids and lagomorphs from Berești and Mălușteni in occlusal view, except G, in labial view, mirror-image, to correspond to the orientation in F. *Trogontherium minus*: (A) left m1,2 from Mălușteni (probably partial holotype of *Steneofiber covurluiensis* after Simionescu 1930); (B) right M1,2 from Mălușteni; (C) right p4 from Mălușteni; (D) left M1,2 from Mălușteni; (E) left M1,2 from Mălușteni. *Castor fiber*: (F, G) left hemimandible bearing p4–m3 from Mălușteni. *Trischizolagus dumitrescuae*: (H) right p3–4 from Mălușteni; (J) left upper molariform from Mălușteni. *Ochotona ursui*: (I) right P3 from Mălușteni; (K) left hemimandible bearing p3–m3 from Mălușteni (holotype?); (L) left hemimandible bearing p3–m2 from Mălușteni.

metaflexus may be curved and extend themselves along the tooth (three out of seven), or fossettes may be present (three out of seven). Two small islets may (one out of seven) or may not (five out of seven) be present on the labial side. One of the M3s has divided central lobes. An extra flexus (one out of seven), a fossette (five out of seven), or none of these elements (one out of seven) may exist at the posterior side. Two roots are present.

p4: subrectangular to suboval tooth with narrow and long labial flexids. One of the specimens does not present fossetids, the other two contain the parafossettid and the metafossettid. The paraflexid is the longest flexid, and it is slightly curved. The hypoflexid is short. There are three roots.

m1/2: similar to, but shorter than p4; the paraflexid and the metaflexid are parafossettid and metafossettid.

m3: similar to m1/2, but more quadrangular in occlusal view.

Castor Linnaeus, 1758

Castor fiber Linnaeus, 1758

Castor fiber in Simionescu (1930)

Castor praefiber in Radulesco & Samson (1967b)

Occurrence: Pliocene–present

Sites: Berești and Mălușteni

Material: one M1/2 (LPB[FGGUB] 104-3), one p4 (LPB[FGGUB] 104-2) and one hemimandible bearing the p4–m1 (UAIC SM-6 – Fig. 4F, G).

Measurements: See Table 1

Description:

M1/2: broken tooth, with the connection between the protoloph and the anteroloph at the middle of the tooth. The paraflexus and the hypoflexus are near continuous. The mesoflexus and the metaflexus are connected in a Y-shaped form. There are no roots.

p4: subtrapezoidal tooth with a very long and more irregular flexus than in *T. minus*. The hypoflexus is short and wide.

m1: similar to p4, but with a shorter and longer hypoflexus.

m2: similar to, but shorter than m1.

m3: similar to m2, but with a less quadrate occlusal shape, and having a more irregular flexus.

Remarks:

Abundant material belonging to beavers has been found at the two sites under study. This material has a long taxonomic history, being first described from Mălușteni (Simionescu 1930) as *Steneofiber covurluiensis* Simionescu, 1930, *Castor fiber* and *Castor* sp., and from Berești (Simionescu 1932) as *Steneofiber covurluiensis* and *Castor* sp. Subsequently, Radulesco & Samson (1967b) move from *Castor* sp. to *C. praefiber*, and define the genus *Zamolxifiber*, for *S. covurluiensis* (in part), and *Romanocastor filipescai* (Simionescu 1930) from Berești as part of *S. covurluiensis*. Subsequently, this material has been reinterpreted several times, and all reinterpretations agree that *Zamolxifiber* and *Romanocastor* should be synonymised to a single, already existing, genus. Thus, Mayhew (1978) synonymises the two Romanian species and genera to *Trogotherium minutum* (von Meyer, 1838), but, eventually, a subgenus was created for the latter species (*Euroxenomys*), which Huguency & Duranthon (2012) subsequently elevate to genus status. Another less approved interpretation of this material is the one proposed by Korth (2001), who discusses that the morphology of these remains is similar to that of *Steneofiber*, but, not having studied mandible morphology, he only comments on its synonymy. On the other hand, the species *T. minutum* has been restricted to the Miocene, while its possible descendant, *T. minus*, has been restricted to the Pliocene, the taxonomy of these species remaining, however, under discussion (Huguency *et al.* 1989), and for this reason the material studied here has been assigned to *T. minus*. The holotypes of the genera and species *Zamolxifiber covurluiensis* and *Romanocastor filipescai* are not found among the material studied. Furthermore, Simionescu (1990) mentions *C. fiber* and *C. cf. praefiber* Schreuder, 1928 from Mălușteni, but without stating clearly on what material he based these identifications. On the other hand, the species described as *Castor praefiber*, was synonymised to *C. fiber* by van der Weerd (1979).

Lagomorpha Brandt, 1855

Family Leporidae Fischer de Waldheim, 1817

Genus *Trischizolagus* Radulesco & Samson, 1967a

Trischizolagus dumitrescuae Radulesco & Samson, 1967a

Lepus valdarnensis in Simionescu (1930)

Alilepus sp. in Dice (1931)

Lepus valdarnensis in Simionescu (1932)

Alilepus sp. in Kormos (1934)

Alilepus sp. in Schreuder (1937)

Alilepus sp. in Dietrich (1942)

Alilepus sp. (= ? *A. dietrichi*) in Fejfar (1961)

Alilepus sp. in Samson & Radulesco (1963)

Trischizolagus dumitrescuae n. g. n. sp. in Radulesco & Samson (1967a)

Occurrence: Late Miocene–Early Pliocene of Eurasia

Measurements: See Table 1

Sites: Berești and Mălușteni

Material: one hemimaxilla with two molariforms (UAIC NN-24), 19 upper molariforms (LPB[FGGUB] 245-5; LPB[FGGUB] 245-6.1; LPB[FGGUB] 245-6.2; LPB[FGGUB] 245-7.1 – Fig. 4J; LPB[FGGUB] 245-7.2; LPB[FGGUB] 245-8.1; LPB[FGGUB] 245-8.2; LPB[FGGUB] 245.9; LPB[FGGUB] 245-12; LPB[FGGUB] 107-13; LPB[FGGUB] 206; LPB[FGGUB] 211-2; LPB[FGGUB] 211-3; LPB[FGGUB] 211-4; LPB[FGGUB] 211-5; LPB[FGGUB] 211-6; LPB[FGGUB] 101-5; LPB[FGGUB] 101-7; UAIC NN18), four p3 (LPB[FGGUB] 245-1; LPB[FGGUB] 245-2; LPB[FGGUB] 245-3; LPB[FGGUB] 245-4), one hemimandible bearing the p3–p4 (LPB[FGGUB] 101-8 – Fig. 4H), four hemimandibles bearing the p3–m1 (UAIC SM9b1; UAIC NN03; UAIC NN08; UAIC NN10), two hemimandibles bearing the p3–m2 (UAIC SM11; UAIC NN14), 10 hemimandibles bearing the p4–m2 (LPB[FGGUB] 108-1; LPB[FGGUB] 108-2; LPB[FGGUB] 100-2; LPB[FGGUB] 101-11; UAIC NN01; UAIC NN02; UAIC NN06; UAIC NN07; UAIC NN13; UAIC NN39), 22 hemimandibles with two molariforms (LPB[FGGUB] NN2; LPB[FGGUB] 107-4; LPB[FGGUB] 100-1; LPB[FGGUB] 100-3; LPB[FGGUB] 211-7; LPB[FGGUB] 101-1; LPB[FGGUB] 101-2; LPB[FGGUB] 101-3; LPB[FGGUB] 101-4; LPB[FGGUB] 101-6; LPB[FGGUB] 101-10; LPB[FGGUB] 101-15; LPB[FGGUB] 101-16; UAIC NN04; UAIC NN05; UAIC NN09; UAIC NN11; UAIC NN12; UAIC NN15; UAIC NN17; UAIC NN25; UAIC NN40), 16 lower molariforms (LPB[FGGUB] 245-10; LPB[FGGUB] 245-11; LPB[FGGUB] 100-4; LPB[FGGUB] 211-1; LPB[FGGUB] 211-8; LPB[FGGUB] 211-9; LPB[FGGUB] 101-9; LPB[FGGUB] 101-12; LPB[FGGUB] 101-14; LPB[FGGUB] 101-17; LPB[FGGUB] 101-18; UAIC NN16; UAIC NN19; UAIC NN20; UAIC NN22; UAIC NN23).

Description: See Radulesco & Samson (1967a).

Family Ochotonidae Thomas, 1897

Genus *Ochotona* Link, 1795

Ochotona ursui Simionescu, 1930

Ochotona ursui n. f. in Simionescu (1930)

Ochotona ursui in Simionescu (1932)

Occurrence: Only Berești and Mălușteni, after Sen (2020)

Sites: Berești and Mălușteni

Material: One P3 (LPB[FGGUB] 245-13 – Fig. 4I), three hemimandibles bearing the p3–m3 (UAIC SM9b-2 – Fig. 4L; UAIC SM10-1; UAIC SM10-2 Fig. 4K), one hemimandible bearing the p3–m2 (LPB[FGGUB] 242-4), one hemimandible bearing the p4–m3 (LPB[FGGUB] 107-14), 15 hemimandibles bearing the p4–m2 (LPB[FGGUB] 107-1; LPB[FGGUB] 107-3; LPB[FGGUB] 106; LPB[FGGUB] 211-10; UAIC NN27; UAIC NN29; UAIC NN31; UAIC NN34; UAIC NN35; ISER 107-1; ISER 107-2; ISER 107-4; ISER 107-5; ISER 107-6; ISER 107-7), 14 hemimandibles with two molariforms (LPB[FGGUB] 107-2; LPB[FGGUB] 107-5; LPB[FGGUB] 107-9; LPB[FGGUB] 211-11; LPB[FGGUB] 211-13; UAIC NN21; UAIC NN26; UAIC NN28; UAIC NN30; UAIC NN32; UAIC NN33; UAIC NN37; UAIC NN38; ISER 107-3), and 13 lower molariforms (LPB[FGGUB] 107-6; LPB[FGGUB] 107-7; LPB[FGGUB] 107-8; LPB[FGGUB] 107-10; LPB[FGGUB] 107-12; LPB[FGGUB] 242-1; LPB[FGGUB] 242-2; LPB[FGGUB] 242-3; LPB[FGGUB] 211-12; LPB[FGGUB] 211-14; LPB[FGGUB] 211-15; LPB[FGGUB] 101-13; UAIC NN36).

Measurements: See Table 1

Description:

Table 2 Faunal list published by Simionescu (1930, 1932), Kormos (1940), Samson & Radulesco (1973), Radulescu & Samson (1989a, b), Rădulescu *et al.* (1992) and Rădulescu & Samson (1995) compared to the one published in this paper for small mammals; the presence of a '?' indicates that the material previously assigned to that species was not found in the studied collections; the presence of a '-' indicates the absence of this taxon in the site; when two cells in horizontal are joined together, it means the presence of that taxon in both sites; and when two or more upright cells are joined together, it signifies the synonymy of those taxa to a single taxon in the new taxonomic assignment.

Old taxonomic assignments		New taxonomic assignments	
Order Eulipotyphla			
Berești	Mălușteni	Berești	Mălușteni
	<i>Desmana amutriensis</i> ¹ (synonymised)	–	<i>Desmana verestchagini</i>
	<i>Talpa neagui</i> (nomen dubium)		<i>Talpa</i> sp.
	<i>Erinaceus</i> sp. ¹	<i>Erinaceus</i> sp.	–
–	<i>Sorex</i> sp. ¹	–	?
Order Rodentia			
–	<i>Mimomys moldavicus</i> (synonymised)	–	<i>Mimomys</i> sp. or <i>Promimomys</i> sp.
<i>Cricetulus</i> (<i>Moldavimus</i>) <i>simionescui</i> (synonymised)	<i>Cricetus</i> sp. ²	<i>Allocricetus</i> sp.	–
<i>Spermophilus</i> sp. ¹	–	?	–
–	<i>Citellus primigenius</i> ¹		?
–	<i>Pliosciuropterus</i> sp.		<i>Spermophilus</i> cf. <i>nogaici</i>
	<i>Pliospalax macoveii</i>		<i>Pliospalax macoveii</i>
	<i>Prospalax rumanus</i> (synonymised)		
<i>Microspalax</i> cf. <i>odessanus</i>	–	?	–
	<i>Zamolxifiber covurluensis</i> (synonymised)		<i>Trogotherium minus</i>
	<i>Romanocastor filipescui</i> (synonymised)		
	<i>Castor praefiber</i> (<i>C. cf. praefiber</i> ²) (synonymised)		<i>Castor fiber</i>
–	<i>Castor fiber</i> ²		
Gliridae gen. et sp. indet.	–	?	–
<i>Mus</i> sp. ¹	<i>Stephanomys donnezani</i> ¹	?	?
–	(<i>Myomys</i>) <i>moldavicus</i> ²	–	?
Order Lagomorpha			
	<i>Trischizolagus dumitrescuae</i>		<i>Trischizolagus dumitrescuae</i>
	<i>Ochotona ursui</i>		<i>Ochotona ursui</i>
–	<i>Lepus</i> cf. <i>timidus</i> ²		
–	<i>Lagomys corsicanus</i> ²		
–	<i>Lagomys rumanus</i> ²		
	<i>Proochotona gigas</i> ³	?	–

¹Material lost after Samson & Radulesco (1973).

²Cited in Simionescu (1990).

³*Pliolagomys* cf. *gigas* after Rădulescu & Samson (1995), but only present in Berești.

P3: molariform tooth, having a trapezoidal shape. Its mesial hyperloph is more or less convergent to the distal hyperloph, and the precone ends in front of a small mesoflexus. The mesial hyperloph is straight. The paraflexus is poorly developed and it has a distinctive J-shape. A secondary inverted J-shaped enamel wall appears at the lingual side of the paraflexus and extends to the posterior side. This secondary paraflexus has well-developed enamel on the lingual side. A very shallow mesoflexus is present, marking the distinctive well-developed lagicone and a broken postlobus. A shallow and wide hypoflexus is present. Crown cement is present only at the secondary paraflexus. The lagicone is large and oval, and lacks the lagiloph and the centrocone. It is oriented in a lingual direction. The postlobus is damaged.

p3: the anteroconid is diamond-shaped and well-developed. The paraflexid and the protoflexid may be well-developed and connected to each-other (one out of three), or may appear in a narrow anterolophid (two out of three), which in turn separates the antero-, the proto-, and the metaconid from each-other. The anteroconid is larger than the metaconid. The anteroflexid is shallow. The metaconid and the protoconid are small and oval in shape. The hypoconid is more developed than the entoconid. The mesoflexid is very shallow, well-developed in one specimen, and the hypoflexid is long and narrow. The isthmid is wide, and serves as connection for the protoconid and the metaconid with the entoconid–hypoconid lobe.

Lower molariforms: the trigonid and the talonid are of the same width (trigonid width = taloned width), but the trigonid is longer. The trigonid appears to be massive when compared to the talonid, as well as prominent, and with a rounded labial side. The connection between the trigonid and the talonid is narrow. The talonid labial reentrants at the m1,2 is more developed than the ones at p4. The enamel is more developed in the posterior side of the trigonid and talonid.

m3: this tooth is formed by only one lobe; it may be similar to the trigonid of the m2, but smaller (two out of six), or it may be rounded (four out of six).

Remarks:

Two species of lagomorphs are present in the available material, and can be clearly separated by their size, among other characteristics. Much of the material found at the studied sites, described or listed in previous papers, is lost. The two present species were already differentiated by Simionescu (1930) for Mălușteni, although they were described as *Lepus valdarnensis* (now *T. dumitrescuae*), and *O. ursui*. Both species were also identified at the locality of Berești (Simionescu 1932). Kormos (1934), describes a p3 as *Alilepus* sp. Later, based on the material of *L. valdarnensis* from both localities, Radulescu & Samson (1967a) described the new genus and species, *T. dumitrescuae*, and synonymised the former p3 of *Alilepus* sp. to this new species. This species was amended by Averianov (1995).

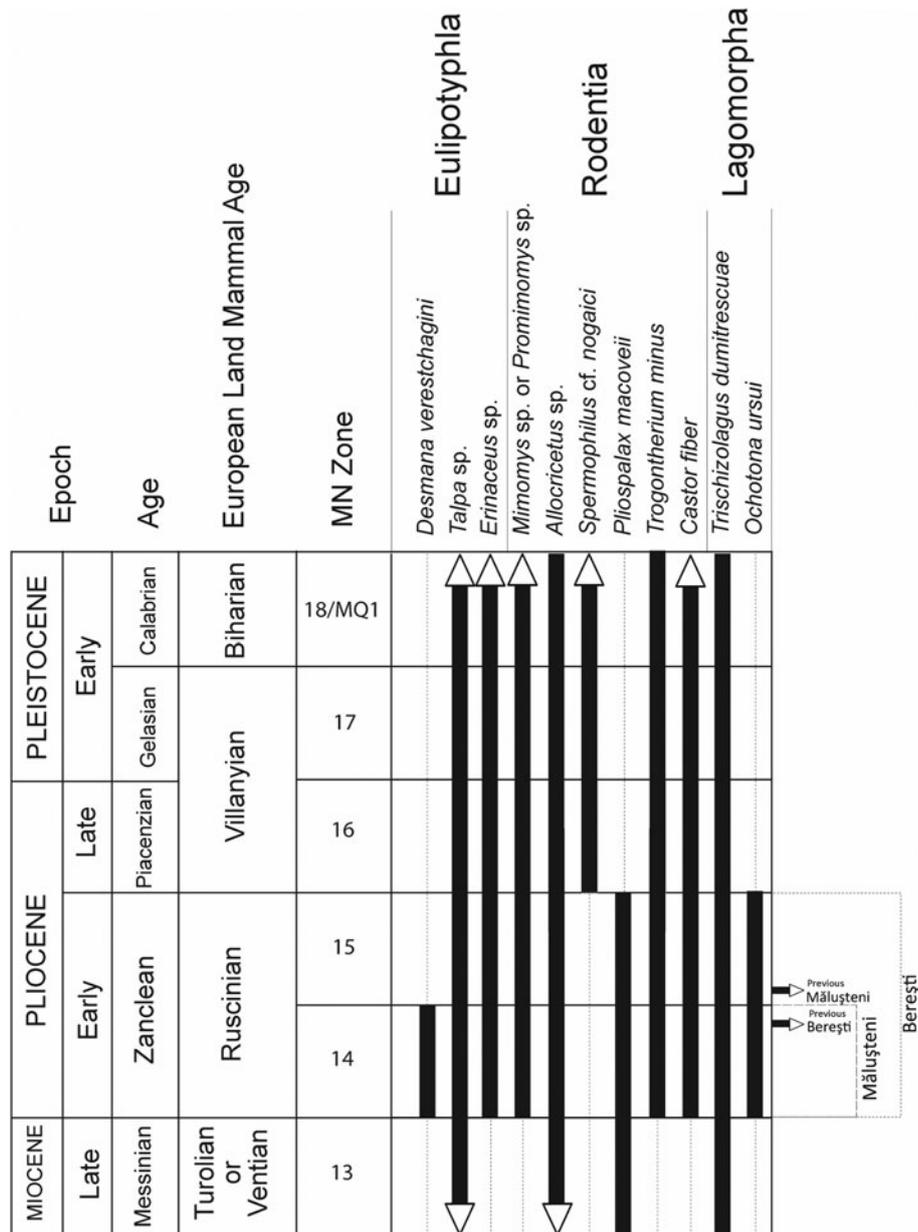


Figure 5 Stratigraphical range of the species studied here, and the traditional and new hypothesis of the stratigraphical position of the sites Berești and Mălușteni. Neogene Mammal (MN) zones follow Mein (1975).

Subsequently, Rădulescu & Samson (1995) based on the larger size of the specimen, identified another species at Berești, *Pliolagomys* cf. *gigas*, using a mandible that had been previously classified as *O. ursui*. Unfortunately, this mandible has not been found among the material studied. Although it is not known from which materials the descriptions have been made, Samson & Radulescu (1973) also cite *Proochotona gigas* (= *Pl. gigas*) for both sites, whereas Simionescu (1990) cites five species from Mălușteni: *T. dumitrescuae*, *O. ursui*, *Lepus* cf. *timidus*, *Lagomys corsicanus*, and *Lagomys romanus*.

While *T. dumitrescuae* is a well-characterised species, and is found in more than one site (e.g., Averianov 1995), *O. ursui* presents the opposite case, and it does not have a good photographic record (Sen 2020). Pidoplichko (1956; according to Samson & Radulescu 1973), suggests that synonymy exists between *O. ursui* and *Ochotona antiqua*. Subsequently, Čermák & Rekovets (2010) give three different possibilities: firstly, that *O. ursui* and *O. antiqua* are two different species; secondly that *O. ursui* is a subadult of *Pliolagomys* (these authors compared three mandibles without p3, but with their alveolus,

that had been deposited in the Natural History Museum of Basel); or, lastly, that *O. antiqua* and *O. ursui* are the same species. The lectotype is not in the collections being studied, but instead they contain three p3s. From the three options listed above, the hypothesis of them belonging to a representative of the genus *Pliolagomys*, due to having a paraflexid, can be discarded, as, in the latter genus, the paraflexid tends towards the anterior part (Čermák 2010) – this is not the case in the three studied specimens. One of the characters that can be used to discriminate *O. antiqua* from *O. ursui* is the size of the p3, as a similar morphology can be observed between both species; the remains under study have a larger size than in *O. antiqua*. There are specimens that fall within the size range of *O. antiqua*, and others are found to be larger; the P3R (p3 ratio = p3 length × 100/p3 width) is somewhat larger in *O. ursui* (104 in this species, and 96 in *O. antiqua*), although based on a poor sample (it may be altered by its low number of specimens). While *O. ursui* material has the MR (mandible ratio – buccal height of mandible at m² × 100/alveolar length of p3–m3) between 83.29 and 89.97, the *O. antiqua* from the

Novopetrovka site (Ukraine; Čermák & Rekovets 2010) has an MR of 66. Therefore, although both species are very similar in dental morphology, the mandibles of *O. ursui* are much more robust, confirming the first hypothesis, which supports that they are different species. Nonetheless, additional material from this species is needed for a clear conclusion to be drawn.

4. General discussion and conclusions

The site of Mălușteni is classically interpreted as being geologically younger than Berești due to the presence of the arvicolid *Mimomys moldavicus*, and Berești is interpreted to be older due to the presence of the cricetine *Cricetulus simionescui* (Samson & Radulescu 1973). According to Terzea (1997), and to Radulescu *et al.* (2003), although both sites have similar faunas, thanks to the presence of the above-mentioned arvicoline, Mălușteni could be dated as MN15a (final part of the Ruscinian), while Berești, taking into account the absence of the arvicoline and the presence of the cricetine, could be dated as MN14b (middle part of the Ruscinian). However, other authors, such as Simionescu (1990), group the faunas from both sites as late Early Pliocene, without specifying which of the two sites is older.

In our new review of the material (Table 2), both deposits can be grouped at a very similar age, within the Early Pliocene. This is because the cricetine and arvicoline genera present at both sites have a very broad biostratigraphical range, spanning the entire Pliocene. Thus, for Mălușteni, the presence of *Desmana verestchagini* indicates that this deposit accumulated during MN14, meaning that it belongs to the Early Pliocene, leaving *Spermophilus cf. nogaici* as the only taxon that does not fit within this age, as it belongs to the Late Pliocene (MN16). Nevertheless, more material would allow us to confirm or infirm the presence of this species, suggesting that the age of the deposits would be in the proximity of the MN14/15 transition. On the other hand, the site of Berești yielded specimens assigned to *Trogontherium minus* and *Pliospalax macoveii*, which allows us to place this site across MN14–15, a stratigraphical range that includes the entire Early Pliocene (Fig. 5).

In other Romanian and Ukrainian sites of similar age, the presence of sites belonging to MN15 is abundant (Ciuperceni 1 and 2, Drănic 1, 2, and 3, Lupoaia 8, and Odessa Catacombs, among others; Vislobokova *et al.* 1993; Rădulescu *et al.* 1997; Terzea 1997; Rădulescu & Samson 2001), the sites belonging to MN14 are very scarce (only Drănic 0, MN14-15; Rădulescu & Samson 2001). In general, the fauna studied here is characterised by a great diversity and/or abundance of talpids, lagomorphs, beavers, and spalacids, with scarce cricetines, arvicolids, sciurids, and other insectivores. Something similar occurs in Ciuperceni 2 (Terzea 1997), while in other sites such as Drănic 0, 1, 2, and 3, there is a great diversity of soricids and arvicolids, while the murines are present, although lagomorphs and beavers are scarcer (Rădulescu *et al.* 1997). In the other hand, the Odessa Catacombs site would have a combination of both types of sites, there neither soricids nor talpids are present, while there is a great diversity of lagomorphs, beavers, cricetines, and murines, but there are only a few species of arvicolids and spalacids (Vislobokova *et al.* 1993). This difference may be due to three reasons: for palaeoecological reasons – different types of the environments in which the sediments were deposited; for biostratigraphical reasons – all the sites are more modern than those studied here; or for methodological reasons – many of the missing species are small in size, and there may have been a bias in collecting the material. For this reason, the study of Berești and Mălușteni is very important, as it is a unique example for understanding the Early Pliocene small mammal faunal assemblages in the northern Black Sea region.

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7. Competing interests

None.

8. References

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