A reappraisal of *Sarmatosminthus*, the earliest European lophocricetine jerboa (Rodentia, Dipodidae), with comments on systematics and evolution of Neogene Lophocricetinae

Andrian Delinschi, Dumitru-Daniel Badea, Bogdan Ratoi & Maxim V. Sinitsa

The subfamily Lophocricetinae is a diverse group of fossil dipodids, with the earliest known records dating back to the late Oligocene and Early Miocene of Central Asia. Most members of the group are known from Asia, with only a few taxa documented from the Late Miocene of Eastern Europe. Currently, the earliest known genus of European lophocricetines is *Sarmatosminthus*, first described in 1981 from the Late Miocene of Moldova. The status and validity of the genus have remained elusive for decades, as it has been either neglected or synonymized with *Heterosminthus*. We examined the type material of *Sarmatosminthus*, as well as new lophocricetine material from Vallesian sites in Moldova, Romania, and Ukraine, and compared it with other lophocricetine taxa. We suggest that *Sarmatosminthus* is a valid genus characterized by moderately high-crowned cheek teeth with weak ridges; massive protostyle, reduced mesoloph, and the hypocone connected to the posterocone in M1; complete mesoloph of M2; and m1 with the hypoconid connected to a salient mesoconid and lacking the ectomesolophid and pseudomesolophid. • Key words: Lophocricetinae, *Sarmatosminthus*, jerboas, Late Miocene, Eastern Europe.

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The family Dipodidae (jerboas) has an intriguing evolutionary history, especially during the Neogene. This period, associated with the increasing aridification of Eurasia, is significant for many groups of small mammals, including jerboas, and is marked by changes in their development and adaptation to changing environmental conditions.

The evolutionary history of the group is well-represented by a rich and relatively well-studied Asian Neogene fossil record (*e.g.* Schlosser 1924, Savinov 1970, Qiu 1985, Zazhigin & Lopatin 2000b, Qiu & Li 2016). In contrast, the European members of Dipodidae remain poorly known. Our current knowledge of the systematics and distribution of Neogene jerboas from Europe is mostly limited to a series of snapshots, interrupted by vast temporal and geographical gaps. Most of these snapshots are from Eastern Europe, revealing several species of five-toed *Allactaga* jerboas (Nesin & Kovalchuk 2017), lophocricetine jumping mice (Lungu 1981, Topachevsky *et al.* 1984, Delinschi 2014), and the genus *Eozapus*, a common member of European faunas of late Vallesian and Turolian from Caucasus to Spain (van de Weerd 1976, Topachevsky *et al.* 1998, Nesin & Nadachowski 2001, Daxner-Höck & Höck 2015, Tesakov *et al.* 2017).

Referring to the presence of dipodids in the faunas of small mammals from the Late Miocene of the Dniester-Prut Interfluve, Lungu (1981) described a new genus and species –*Sarmatosminthus gabunii,* based on M1, M2 and m2 from the Bujor 1 site in western Moldova. Based on eleven m1s of the same species, Lungu (1981) also proposed another new genus and species *Bujoromys olarensis*, originally attributed to Muridae. The pronounced development of conids of *Sarmatosminthus* has been suggested as a unique character distinguishing it from *Sicista*, *Pliozapus*, and *Heterosminthus*, which

exhibit a more complex, ridge-like structure on the occlusal surface.

Topachevsky *et al.* (1984) reclassified *Sarmatosminthus* within the subfamily Lophocricetinae and revised the validity of *Bujoromys olarensis* by demonstrating its synonymy with *S. gabuniai*. Additionally, several differences between the lophocricetines described by Lungu and *Lophocricetus* have been noted, concluding that *Sarmatosminthus* is a valid genus within the subfamily Lophocricetinae.

Zazhigin & Lopatin (2000b) suggested that the dental structure of *S. gabuniai* closely resembles that of late representatives of the genus *Heterosminthus*, such as *H. gansus*. As a result, they proposed that the names *Sarmatosminthus* and *Bujoromys* should be considered junior synonyms of *Heterosminthus*.

Lungu (2008a, b) acknowledged the synonymization of *Bujoromys* with *Sarmatosminthus*, but disagreed with the synonymisation of *Sarmatosminthus* with *Heterosminthus* and continued to use *Sarmatosminthus* for the Vallesian lophocricetines of Moldova (Lungu & Rzebik-Kowalska 2011). For several decades, *Sarmatosminthus* has remained one of the most controversial extinct dipodids, largely due to the incomplete and scarce nature of its fossil record.

This research was initiated by the discovery of additional lophocricetine fossils collected between 2022 and 2024 at Bujor, Moldova. The study of specimens from the two fossiliferous layers at Bujor and the integration of previously unstudied remains from the Vallesian Bohotin-Moșna 1 and Țibana 1 fossil sites in Romania. The study allowed us to refer the material to *Sarmatosminthus gabuniai*. Here, we revise the lophocricetine material from the Vallesian of Eastern Europe and provide the first detailed description of *Sarmatosminthus*.

Geological setting

Fossil material from three sections, namely Bujor (Moldova), Bohotin-Moșna and Țibana (Romania), has been included in the present study. Bujor (also known as Bujoru, Bujory, Būzhor, Buzhory, Bužory), Hînceşti District, Republic of Moldova (Fig. 1) is a well-known vertebrate site that has been documented and extensively studied by Lungu (1981, 1990, 2000, 2008a, b) and Lungu & Rzebik-Kowalska (2011). Two outcrops, Bujor 1 and Bujor 2, have been described in Lungu & Rzebik-Kowalska (2011). The stratigraphic relationship of the sites remains somewhat unclear, although Bujor 1 appears to underlie Bujor 2. Lungu & Rzebik-Kowalska (2011) mentioned Bujor 1 as the "*Congeria* Beds", whereas Bujor 2 lies above the "*Congeria* Beds". The vertebrate community of Bujor 1 has originally been referred to the Vallesian by Lungu (1981) and later to the late Vallesian by Topachevsky *et al*. (1998) based on the mammals listed by Lungu (1981), Sinitsa & Delinschi (2016), referencing Vasiliev *et al*. (2011), argue that the absolute age of Bujor 1 should be significantly younger than 11.2 Ma. This view is supported by biochronological markers, such as the presence of *Neocricetodon*, two murid genera, and sciurid *Csakvaromys turolensis*, along with the absence of *Democricetodon*, *Megacricetodon*, and *Microtocricetus* (Sinitsa & Delinschi 2016), suggesting the late Vallesian (MN 10) age of the Bujor 1 assemblage. Since the precise geographic position of Bujor 1 and 2 localities is unclear, restudy of these sections remains impossible.

In the framework of ongoing studies, we have discovered and studied an abandoned sand pit in the vicinity of Bujor village (46.91183 N, 28.28006 E). The section in the pit records a deltaic sequence with two fossiliferous horizons, named Bujor 3a (lower) and Bujor 3b (upper). Throughout the section, a marine upper Bessarabian mollusc assemblage *sensu* Lazarev *et al.* (2025) with *Mactra fabreana*, *M. podolica*, *Plicatiforma fittoni*, and *Solen subfragilis* has been found. Based on this fauna, an age of approximately 11–9.9 Ma is suggested. Bujor 1 and 3 are likely similar in age, as the sections contain comparable molluscan assemblages. A detailed study of the geology, stratigraphy, biostratigraphy, and chronostratigraphy of the Bujor 3a and 3b sites will be published elsewhere.

The Țibana section in Romania (47.00065 N, 27.36548 E) represents an alternation of marine, lagoonal (freshwater to brackish), and deltaic deposits. An assemblage of small mammalian fauna, including *Crusafontina endemica*, *Ochotona* sp., *Myomimus dehmi*, *Eomyops catalaunicus*, *Megacricetodon* sp., *Byzantinia bayraktepensis*, and *Progonomys cathalai*, has been found in the lagoonal deposits, which are overlain by a deltaic sequence containing upper Bessarabian molluscs, closely resembling that of Bujor 3. Thus, a similar age for this fauna can be suggested (Badea 2025).

The Bohotin-Moșna outcrop, Romania (46.93606 N, 27.95808 E) represents another sequence with deltaic deposits that contains a vertebrate horizon (Bohotin-Moșna 1). No marine molluscs have been found in the section. The age of the assemblage is based on the biochronology of the small mammals, among which are *Crusafontina endemica*, *Ochotona kalfense*, *Paraglirulus werenfelsi*, and *Progonomys cathalai*, the taxa characteristic of the late Vallesian (Badea 2025).

Material and methods

All specimens studied in this research were collected through surface surveying and screen-washing of dried

sediment at the localities of Bujor 1, 3a, 3b, Bohotin-Moșna 1, and Țibana 1. The material from Bujor 1 is stored at the "Ion Creangă" State Pedagogical University, Chișinau, Moldova; that from Buzhor 3a and 3b is stored at the Laboratory of terrestrial vertebrates, Institute of Zoology, Moldova State University, Chișinau, Moldova. The specimens from Bohotin-Moșna 1 and Țibana 1 are stored at the Museum of Natural History, Iași, Romania. The lophocricetine specimens from the early Vallesian locality Grytsiv are housed at the Department of Paleontology, National Museum of Natural History of the National Academy of Sciences of Ukraine, Kyiv, Ukraine.

Measurements were made using a Leica DVM500 microscope (Porrentruy, Switzerland) with an accuracy of 0.01 mm. The SEM images were taken using a Hitachi S-3400N II scanning electron microscope, a facility of the RAMTECH (Research Center on Advanced Materials & Technologies) at "Alexandru Ioan Cuza" University of Iași (Iași, Romania). The photographic images of specimens from Grytsiv were taken from ammonium

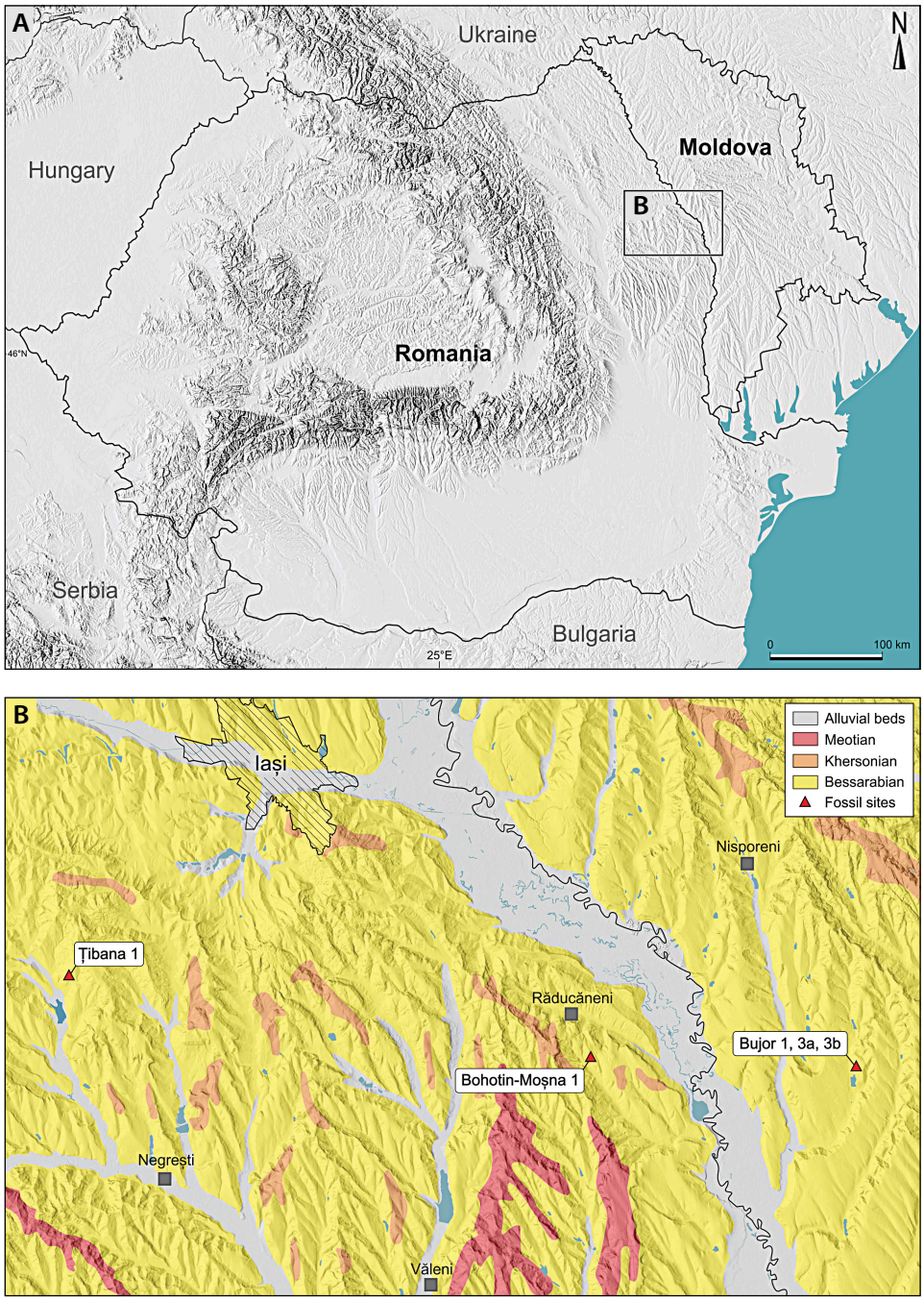

Figure 1. Geographic locations of the study area and geological map of the Late Miocene terrestrial sediments of Moldavian Platform.

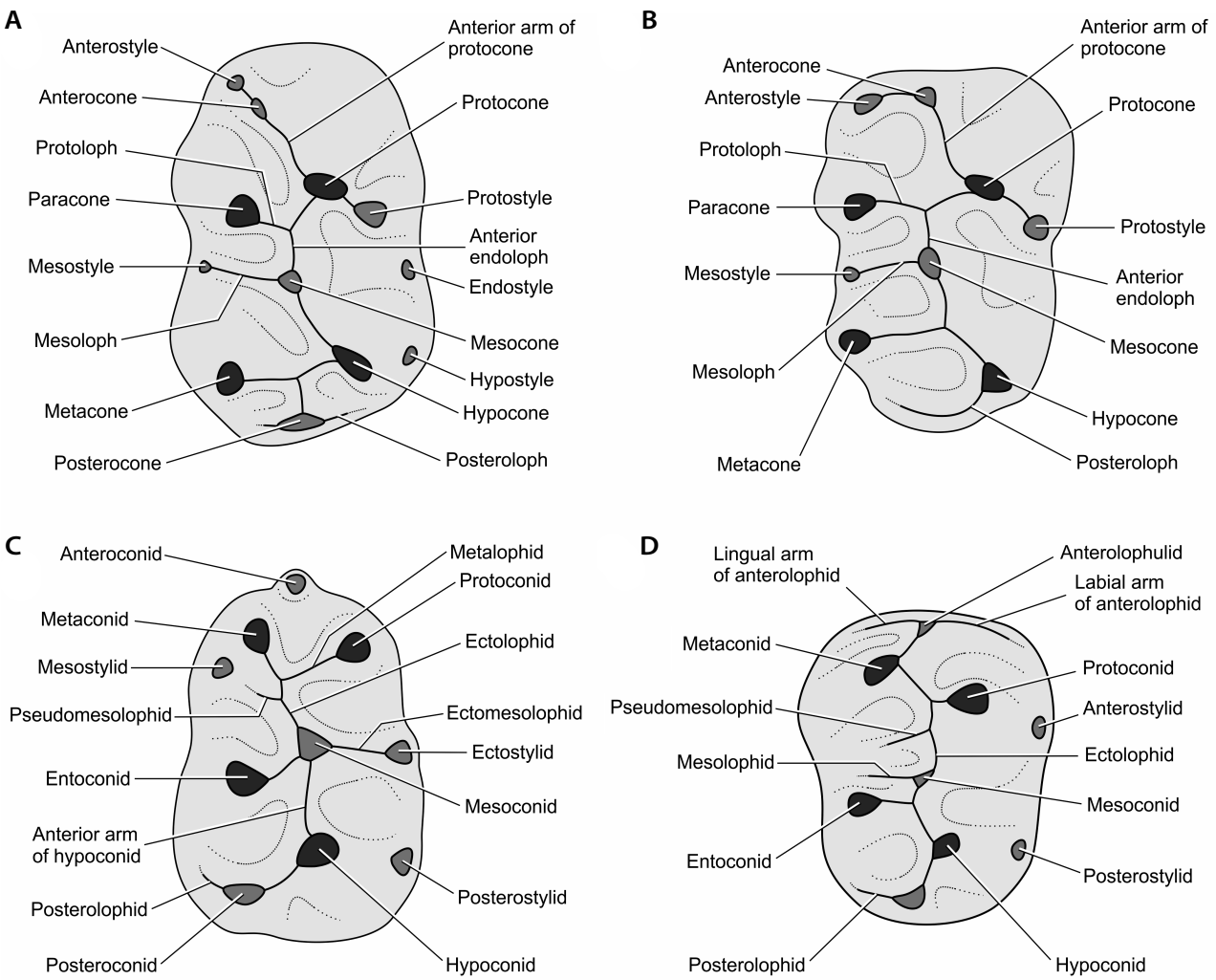

Figure 2. Upper M1 (A) and M2 (B), and lower m1 (C) and m2 (D) lophocricetine cheek teeth illustrating the terminology employed here.

chloride-coated high-resolution resin casts using a Canon MP-E 65 mm macro lens with a DSLR camera.

Dental terminology used in this study (Fig. 2) follows Delinschi (2014) with modifications. Upper teeth are indicated by capital letters (M1–M3) and the lower teeth by lower-case ones (m1–m3).

The higher-level taxonomic classification of dipodids remains a subject of debate, particularly regarding the fossil taxa. In this paper, we follow the classification proposed by Zazhigin & Lopatin (2000b) and Lebedev *et al*. (2013), assigning dipodids to the superfamily Dipodoidea. The classification within the family follows Zazhigin & Lopatin (2000b).

Institutional abbreviations. – IZRM-V – Laboratory of terrestrial vertebrates, Institute of Zoology, Moldova State University, Chișinau, Republic of Moldova; MNHI – Museum of Natural History of Iași, Romania; NMNHU-P – Department of Paleontology, National Museum of Natural History of the National Academy of Sciences of Ukraine, Kyiv, Ukraine; TSU – "Ion Creangă" State Pedagogical University, Chișinau, Republic of Moldova.

Systematic palaeontology

Order Rodentia Bowdich, 1821
Family Dipodidae Fischer, 1817
Subfamily Lophocricetinae Savinov, 1970

Genus *Sarmatosminthus* Lungu, 1981

1981 *Sarmatosminthus*; Lungu, p. 75.
1981 *Bujoromys*; Lungu, p. 86.
2000b *Heterosminthus*. – Zazhigin & Lopatin, p. 93.
2011 *Sarmatosminthus*. – Lungu & Rzebik-Kowalska, p. 22.
2014 *Heterosminthus*. – Delinschi, p. 10.

Type species. – *Sarmatosminthus gabuniai* Lungu, 1981. Late Miocene, late Vallesian, Moldova.

Diagnosis. – Emended: Medium-sized lophocricetine: length of M1 1.50—1.77 mm. Cheek teeth moderately high-crowned with buno-lophodont occlusal pattern. Alternation of cusps moderately expressed, ridges (except M2 mesoloph) weak to absent. M1 with massive protostyle, but lacking mesoloph, hypocone connected to posterocone. Mesoloph on M2 complete. Ectomesolophid on m1 weak or absent, pseudomesolophid absent, ectostylid always present and well-developed, hypoconid massive and connected to salient mesoconid. On m2, anterior arm of protoconid and mesoconid weak, pseudomesolophid absent, posterostylid rudimentary to absent.

Differential: *Sarmatosminthus* differs from *Heterosminthus* in lacking mesoloph on M1, having a strong protostyle on M1 and M2, a different configuration of anterior main cusps of M2 with paracone adjoining protocone via protoloph, rudimentary pseudomesolophid and ectomesolophid, and stronger posterostylid of m1, and m2 that lacks the pseudomesolophid. It differs from *Lophocricetus* by weak ridges on molars and less alternating cusps, lack of direct connection between posteroloph and metacone, strong M2 mesoloph, weaker ectomesolophid, and presence of hypoconid-mesoconid connection on m1, weaker anterior arm of protoconid, and stronger mesoconid on m2. Differs from *Lophosminthus* by varying degrees of development in main cones/conids on more bunodont cheek teeth, proportionally narrower anterior portion, weaker mesocone and posterocone, and well-developed arms of the posteroloph of M1. Further, *Sarmatosminthus* differs from *Sibirosminthus* in having substantially smaller, bunodont, and low-crowned cheek teeth with complex occlusal morphology retaining discernible cusps, labial arm of the posteroloph of M1, and mesoloph of M2 (Tab. 1).

***Sarmatosminthus gabuniai* Lungu, 1981**
Figures 3–4

1981 *Sarmatosminthus gabunii*; Lungu, p. 75, pl. 12, figs 6–8b.
1981 *Bujoromys olarensis*; Lungu, p. 86, pl. 12, fig. 1a–v.
2000b *Heterosminthus gabuniai* Lungu. – Zazhigin & Lopatin, p. 93.
2011 *Sarmatosminthus gabuniai* Lungu. – Lungu & Rzebik-Kowalska, p. 22.
2014 *Heterosminthus gabuniai* Lungu. – Delinschi, p. 10.

Nomenclatural remarks. – The species name "*gabuniai*" proposed by Zazhigin & Lopatin (2000b) is an unjustified emendation in the original spelling of the specific name "*gabunii*". However, this emendedation has been cited by virtually all subsequent authors, including the author of the original name (*e.g.* Daxner-Höck 2001, López-Antoñanzas & Sen 2006, Lungu & Rzebik-Kowalska 2011, Delinschi 2014, Qiu & Li 2016), which makes "*gabuniai*" a justified emendation under the Article 33.2.3.1. (ICZN 1999).

Type locality. – Bujor 1, Hîncești District, Republic of Moldova, early Late Miocene, late Vallesian.

Holotype. – Holotype originally comprised of three isolated specimens: the M1, TSU Buj Coll. No. 2 (243);

Table 1. Morphological comparison of *Heterosminthus*, *Sarmatosminthus*, and *Lophocricetus*.

		Heterosminthus	*Sarmatosminthus*	*Lophocricetus*
M1	Protocone-paracone connection	present	absent	absent
	Protocone-protoloph connection	absent	present	present
	Protostyle	weak	strong	strong
	Mesoloph	present	absent	absent
	Posteroloph-metacone connection	present	present	absent
	Posteroloph-hypocone connection	absent	absent	present
M2	Protostyle	weak	strong	strong
	Mesoloph	present	present	absent
m1	Ectomesolophid	weak	weak	strong
	Hypoconid-mesoconid connection	present	present	absent
	Hypoconid-entoconid connection	absent	absent	present
m2	Pseudomesolophid	present	absent	absent
	Posterostylid	absent	absent	present

Table 2. Measurements of upper and lower teeth (in mm) of *Sarmatosminthus gabuniai*.

	Bujor 1	Bujor 3a	Bujor 3b	Țibana 1	Bohotin-Moșna
Length	1.67; 1.71	1.63–1.77	1.63–1.17	1.51	1.58
M1	n = 2	n = 5	n = 7	n = 1	n = 1
Width	1.15	1.15–1.23	1.134–1.21	1.07	1.10
Length	1.41; 1.46	1.39–1.49	1.38; 1.39	1.39; 1.50	–
M2	n = 2	n = 5	n = 2	n = 2	
Width	1.00; 1.05	1.01–1.07	1.01; 1.02	0.81; 1.00	–
Length	–	–	–	–	–
M3					
Width	–	–	–	–	–
Length	1.38–1.48	1.38–1.62	1.31–1.584	1.59	–
m1	n = 3	n = 14	n = 10	n = 1	
Width	0.98–1.03	1.03–1.16	0.93–1.05	1.07	–
Length	1.39; 1.41	1.36–1.50	1.31–1.46	–	–
m2	n = 2	n = 5	n = 12		
Width	1.12; 1.14	1.04–1.19	0.98–1.19	–	–
Length	–	0.87; 0.89	–	–	–
m3		n = 2			
Width	–	0.74; 0.87	–	–	–

M2, TSU Buj Coll. No. 2 (244); and m2, TSU Buj Coll. No. 2 (245). Based on different wear stages and preservation, we suggest that TSU Buj Coll. No. 2 (244) and TSU Buj Coll. No. 2 (245) derive from different individuals. Therefore, under the Article 73.1.5 (ICZN 1999), TSU Buj Coll. No. 2 (244) and TSU Buj Coll. No. 2 (245) are here excluded from the holotype. The isolated M1, TSU Buj Coll. No. 2 (243), remains the sole name-bearing component of the holotype.

Dimensions. – See Table 2.

Material. – Bujor 1: 2 M1, 2 M2, 3 m1, 2 m2 (TSU Coll. No. 2, 243–251); Bujor 3a: 5 M1, 3 M2, 14 m1, 5 m2, 3 m3 (IZRM-V-77/100 – 132); Bujor 3b: 7 M1, 2 M2, 10 m1, 12 m2 (IZRM-V-78/100 – 131); Bohotin-Moșna 1: 1 M1 (MNHI-225-12-18); Țibana 1: 1 M1 (MNHI-224 9-12b), 2 M2 (MNHI-224-8-65 and MNHI-224-9-16), 1 m1 (MNHI-224-16-12).

Diagnosis. – As for the genus.

Description. – The M1 (Fig. 3A–N) has a rounded-rectangular outline with a slightly narrowed anterior portion, prominent cusps, although crests are poorly developed or completely absent. The protostyle is well-developed and located approximately level with the paracone. The anterostyle is weak to medium in size and is connected to the protocone via a thin anteroloph. A rudimentary anterocone is observed in four teeth. The protocone-paracone connection shows varying degrees of development (in two specimens, it is missing). The mesocone is relatively well-developed. In all specimens, the mesoloph and mesostyle are absent. The hypostyle is absent. In most specimens, the posterocone is connected to the metacone and, in one specimen (IZRM-V-78/105), it is shifted towards the hypocone (Fig. 3M). MNHI-225-12-18 lacks the posterocone (Fig. 3E). The labial posteroloph is well-developed in all specimens and, in two teeth from Bujor 3b (IZRM-V-78/105, IZRM-V-78/108), the lingual posteroloph is also present (Fig. 3M). The tooth is four-rooted.

The posterior part of the M2 (Fig. 3O–T) is slightly narrowed and rounded. In most specimens, the protostyle is well-developed and connected to the protocone. The anteroloph is practically absent, but the anterocone is prominent in most cases. The well-developed anterostyle joins the anterocone in heavily worn teeth (Fig. 3R). The well-developed protocone and paracone are connected by the protoloph. The anterior endoloph is connected to the protoloph in most specimens (Fig. 3P, S) or missing in two M2s (Fig. 3O). In two out of nine specimens, a small mesocone is present (Fig. 3Q). The strong mesoloph reaches the labial edge of the tooth and ends with a mesostyle in five out of nine specimens (Fig. 3R). In slightly worn teeth, the posteroloph is solitary (Fig. 3P). In moderately worn ones, the posteroloph is united with the hypocone (Fig. 3S), and it is fused with both the

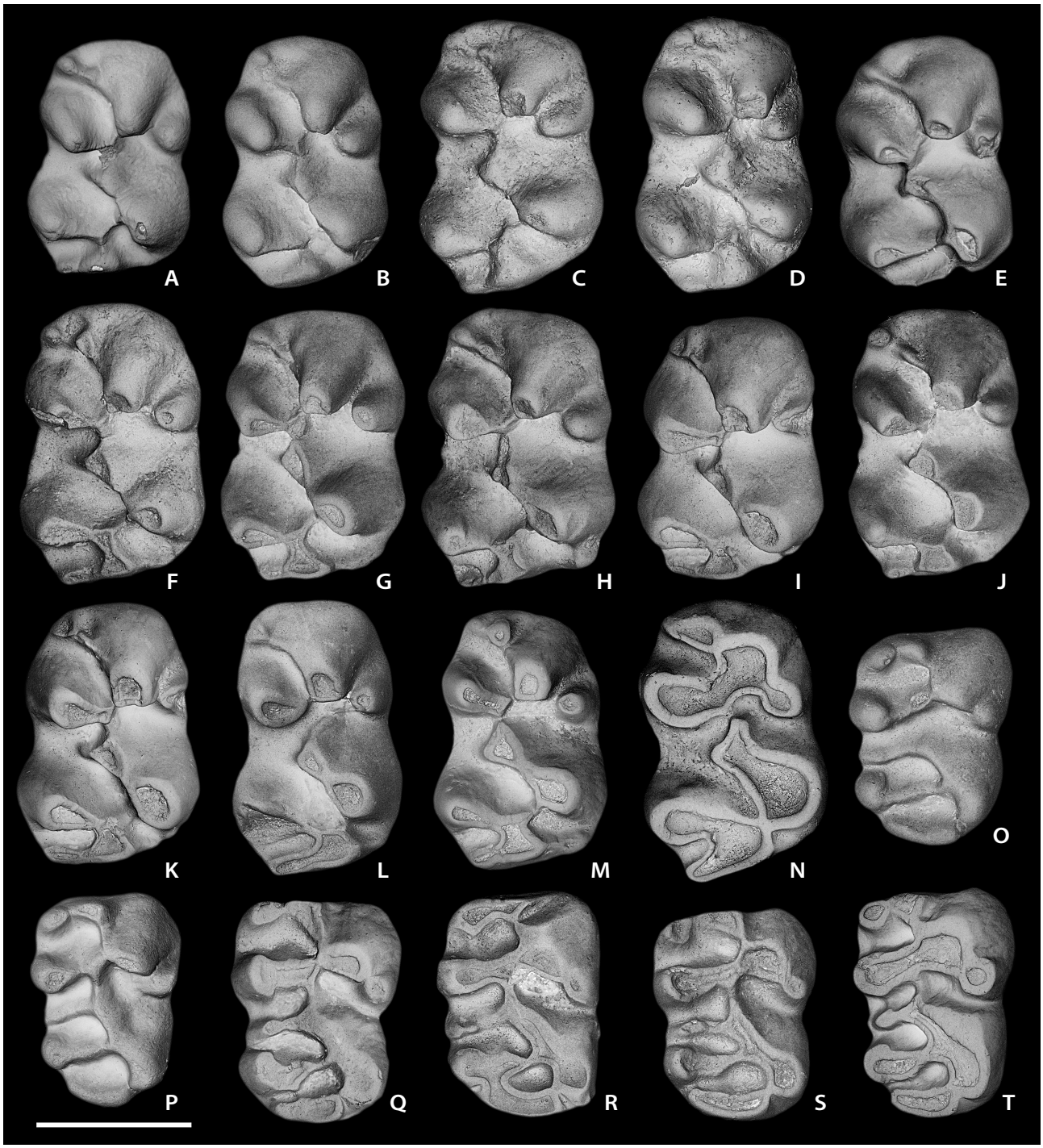

Figure 3. *Sarmatosminthus gabuniai* Lungu, 1981; M1 (A–N) and M2 (O–T) in occlusal view. C, F – Bujor 1; H, I, J, K, O, Q, R – Bujor 3a; B, D, G, L, M, N, S – Bujor 3b; E –Bohotin-Moșna 1; A, P, T – Țibana 1. A – MNHI-224-9-12b; B – IZRM-V-78/100; C – TSU Coll. No. 2, 243 (holotype); D – IZRM-V-78/101; E – MNHI- 225-12-18; F – TSU Coll. No. 2, 248; G – IZRM-V-78/102; H – IZRM-V-77/100; I – IZRM-V-77/101; J – IZRM-V-78/107; K – IZRM-V-77/103; L – IZRM-V-78/103; M – IZRM-V-78/104; N – IZRM-V-78/106; O – IZRM-V-77/105; P – MNHI-224-8-65; Q – IZRM-V-77/106; R – IZRM-V-77/107; S – IZRM-V-78/107; T – MNHI-224-9-16; (B–F, L, P, R–T – inverted). Scale bar equals 1 mm.

hypocone and metacone in heavily worn specimens (Fig. 3R). The M2 has four roots.

The m1 (Fig. 4A–K) is relatively elongated. The development of the anteroconid is variable. It is well-developed as a separate cusp in five (Fig. 4B, D–F, K), poorly developed, but still discernible in fifteen (Fig. 4A, C, H–J), and completely absent in six specimens (Fig. 4G). In nine cases, the protoconid is isolated (Fig. 4A, D).

The anterior ectolophid connects the protoconid, metaconid, and mesoconid in three specimens. In fifteen specimens, the protoconid joins the metaconid by a thin ridge (Fig. 4G), and, in eighteen, the metaconid joins the mesoconid via a thin ectolophid. The m1 lacks a pseudomesolophid. However, four specimens possess a barely discernible swelling on the anterior part of the ectolophid, interpretable as a base of pseudomesolophid (Fig. 4B, E, F, J). The mesoconid is well-developed and fused with a rudimentary ectomesolophid, which ends with a strong ectostylid (Fig. 4I). In six specimens, the ectomesolophid is missing, and the mesoconid remains isolated from the ectostylid. In five teeth from Bujor 3b (IZRM-V-78/110, IZRM-V-78/113, IZRM-V-78/114, IZRM-V-78/115, IZRM-V-78/116, IZRM-V-78/118), the ectostylid consists of two cusps (Fig. 4B, E, F, K). The connection between the hypoconid and entoconid is not developed, and the former is connected to the mesoconid. Five m1s bear a weak cusp- or crest-like posterostylid on the labial slope of the hypoconid (Fig. 4A, B, H–J). The posteroconid (hypoconulid *sensu* Zazhigin & Lopatin 2000b) varies in its configuration; however, it is always connected to the hypoconid. The posterolophid joins the hypoconid and entoconid in nine specimens. The posterolophid is shaped like a crest (Fig. 4A, D, G), like a conid (Fig. 4G, I, J), or is composed of two separate (Fig. 4B, C) or joined conids (Fig. 4F). The m1 possesses two roots.

The outline of the m2 (Fig. 4L–T) shows distinct variation. The labial arm of the anterolophid is long and turns posterobucally but does not join with the protoconid. In one tooth (IZRM-V-78/122), a fine and low lingual arm of the anterolophid is observed (Fig. 4M). The protoconid is connected to the metaconid by a weak crest in three teeth from Bujor 3b (IZRM-V-78/121, IZRM-V-78/130, IZRM-V-78/131), whereas, in most specimens, the cusps are separated. The protoconid and entoconid are united by a well-developed ectolophid. The pseudomesolophid (posterior arm of protoconid *sensu* Zazhigin & Lopatin 2000b) is absent. The hypoconid is connected to the entoconid by a fine, short anterior arm of the hypoconid in seven teeth (Fig. 4O). The junction between the anterior arm of the hypoconid and the anterior arm of the entoconid is complicated by a weak mesoconid, well-discernible in worn specimens (Fig. 4Q–T). The posterolophid joins the hypoconid in all specimens. In seven teeth, there is a small, separate anterostylid labial to the protoconid (TSU Coll. No. 2, 350, IZRM-V-77/110, IZRM-V-77/125, IZRM-V-77/128, IZRM-V-78/121, IZRM-V-78/130, IZRM-V-78/131) (Fig. 4M, P, S). The posterostylid also appears in seven specimens (TSU Coll. No. 2, 350, IZRM-V-77/126, IZRM-V-77/128, IZRM-V-78/129, IZRM-V-78/120, IZRM-V-78/122, IZRM-V-78/123) (Fig. 4L, N, S, T). The m2 has two roots, with the anterior root often subdivided into two smaller roots.

The m3 has a triangular shape, with the metaconid joining the anteroloph and forming a single ridge. The massive protoconid joins the entoconid. The elongated posteroloph is present. The m3 has two roots.

Comparisons. – Among about thirty recognized species of four genera of Lophocricetinae, there are several taxa attributed to the derived *Heterosminthus* and primitive *Lophocricetus* morphologically similar to *Sarmatosminthus* and, therefore, deserving a direct comparison with the genus. *Sarmatosminthus gabuniai* differs from:

"*Heterosminthus*" *gansus* Zheng, 1982 (Builstyn Khudag, Mongolia, Late Miocene; Daxner-Höck 2001) by the following combination of characters: the absence of the protocone–protostyle connection and the mesoloph (whereas, in "*H.*" *gansus,* the mesoloph shows variable development) and weaker posterocone of M1; the rudimentary anteroloph of M2; m1 possessing weaker ectomesolophid and stronger labial arm of metaconid (metalophid *sensu* Qiu & Li 2016); the m2 having stronger mesoconid, while lacking the connection between the labial arm of the anterolophid and the protoconid, as well as the hypoconid-entoconid connection.

Heterosminthus mugodzharicus Zazhigin & Lopatin, 2000 (Shet-Irgiz, Kazakhstan, Late Miocene; Zazhigin & Lopatin 2000b) in having a stronger protostyle isolated from the protocone, reduced mesoloph, and a well-developed mesocone of M1; the m1 anteroconid is always isolated from the metaconid, a weaker ectomesolophid, and proportionally smaller posterolophid with a distinct lingual arm.

Heterosminthus saraicus Zazhigin, Lopatin & Pokatilov, 2002 *in* Zazhigin *et al.* (2002) (Olkhon 1, Russia, Late Miocene) in having smaller molars, reduced mesoloph and mediolaterally narrower posterocone of M1, stronger protostyle and a complete mesoloph of M2, a thinner m1 ectomesolophid and the m2 with the hypoconid connected to the mesoconid.

Lophocricetus minuscilus Savinov, 1977 (Petropavlovsk 1A, Kazakhstan, Late Miocene; Savinov 1977, Zazhigin *et al.* 2002) in having: the M1 completely lacking the mesoloph and showing a less derived posterior portion with the posteroloph connected to hypocone; m1 possessing the weaker anteroconid not connected to the metaconid, well-developed mesoconid, and the presence of the entoconid-hypoconid connection.

Lophocricetus xianensis Qiu, Zheng & Zhang, 2008 (Bahe Formation, China, Late Miocene; Qiu *et al.* 2008, Qiu & Li 2016) by its larger size and the following dental features: M1 with narrower anterior portion, smaller protostyle, complete absence of the mesoloph and a more prominent anterostyle; M2 with a more anteroposteriorly elongated crown, well-developed protostyle connected

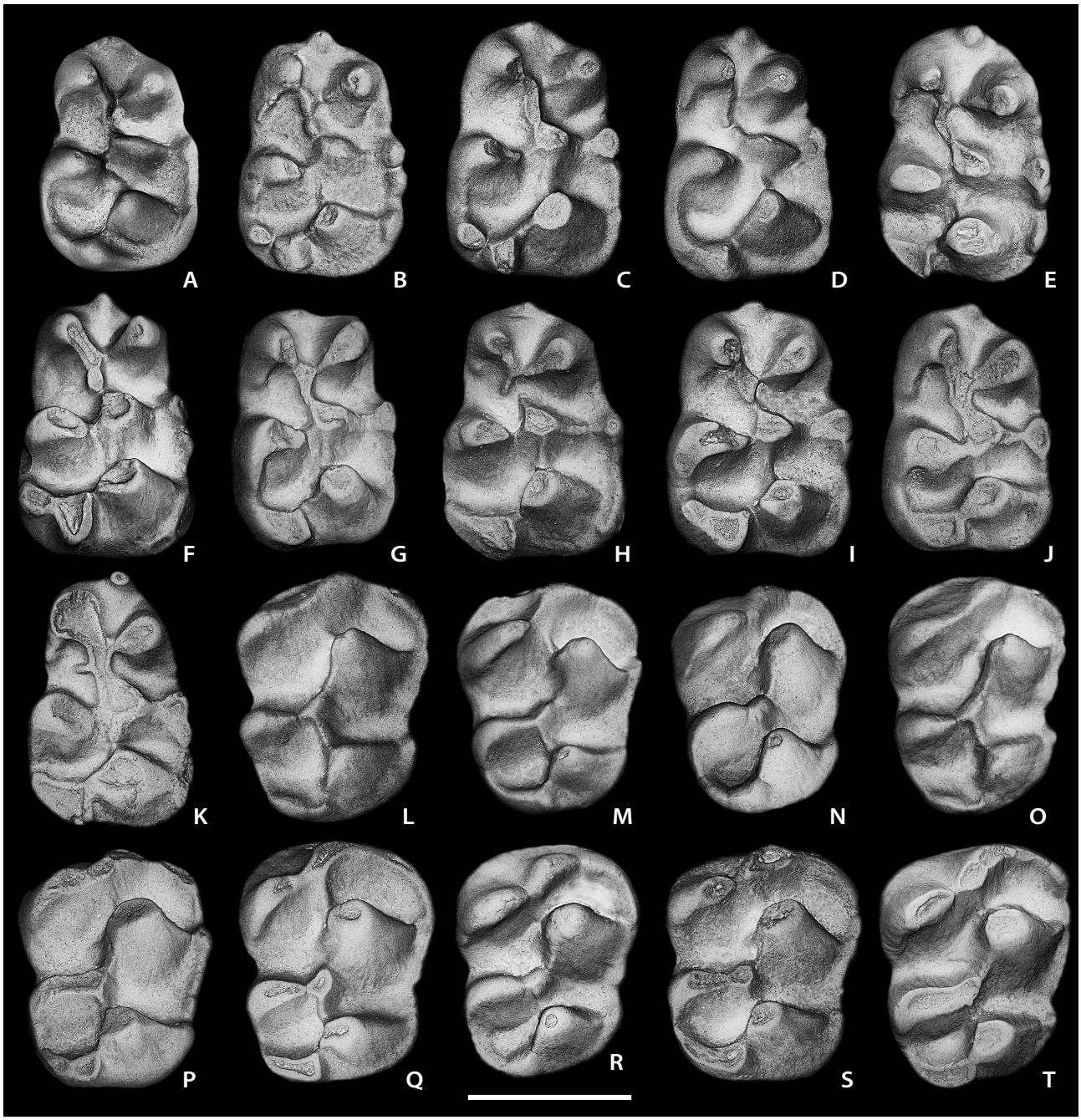

Figure 4. *Sarmatosminthus gabuniai* Lungu, 1981; m1 (A–K) and m2 (L–T) in occlusal view. J, S – Bujor 1; A, D, G, H, P– Bujor 3a; B, E, F I, K, L, M, N, O, Q, R, T – Bujor 3b; C –Țibana 1. A – IZRM-V-77/110; B – IZRM-V-78/109; C – MNHI-224-16-12; D – IZRM-V-77/111; E – IZRM-V-78/110; F – IZRM-V-78/111; G – IZRM-V-77/112; H – IZRM-V-77/114; I – IZRM-V-78/112; J – TSU Coll. No. 2, 251; K – IZRM-V-78/120; L – IZRM-V-78/121; M – IZRM-V-78/122; N – IZRM-V-78/123; O – IZRM-V-78/124; P – IZRM-V-77/110; Q – IZRM-V-78/124; R – IZRM-V-78/128; S – TSU Coll. No. 2, 250; T – IZRM-V-78/119; (A, C, D, F, I, H, L–N, O, R – inverted). Scale bar equals 1 mm.

to the protocone, the presence of a mesostyle and a complete mesoloph; m1 with a different configuration of the protoconid (isolated only in nine specimens of *S. gabuniai*, while, in *L. xianensis,* it is consistently isolated) and a rudimentary ectomesolophid; the m2 hypoconid is connected to a discernible mesoconid and not to the labial arm of entoconid, as in *L. xianensis*.

Lophocricetus cimishliensis Delinschi, 2014 (Gura Galbenei, Moldova, Late Miocene; Delinschi 2014) by its smaller size, the complete absence of the mesoloph on M1, the absence of the protocone–protostyle connection, the presence of a rudimentary anterocone and the metacone-posteroloph connection; the M2 has a complete mesoloph; on m1 and m2, the hypoconid is connected to mesoconid.

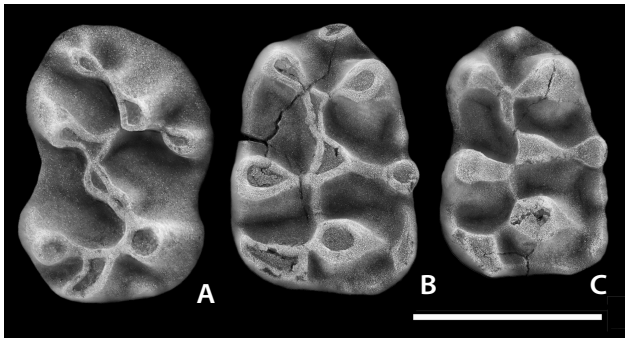

Figure 5. Lophocricetinae gen. et sp. indet., Grytsiv. A – M1, NMNHU-P 22-3125; B – m1, NMNHU-P 22-3126; C – m1, NMNHU-P 22-3127 (C – inverted). Scale bar equals 1 mm.

Remarks. – The teeth from Bujor, Bohotin-Moșna, and Țibana 1 exhibit minor variations in size and morphology, yet they share several common characteristics. These include the presence of a well-defined protostyle on the M1, the presence of the mesocone, and the absence of the mesoloph on the M1, a long M2 mesoloph, and the connections between the hypocone and posterocone of M1 and the hypoconid and mesoconid in m1. Additionally, all m2s lack the pseudomesolophid. Further, the m2 from Bujor, Bohotin-Moșna, and Țibana 1 demonstrate either a distinct two-rooted morphology or a tendency for division of the anterior root.

The early Late Miocene evidence of Eastern European lophocricetines is not limited to the specimens described above. Three isolated teeth of a problematic "*Lophocricetus* sp." have been reported from the early Vallesian of Grytsiv in western Ukraine (Topachevsky *et al*. 1996). We had the opportunity to study this material (Fig. 5), which includes one M1 (NMNHU-P 22-3125) and two m1s (NMNHU-P 22-3126 and NMNHU-P 22-3127). These specimens belong to a small-sized lophocricetine (M1 length = 1.55 mm, width = 1.05 mm) with an elongated, relatively low M1 and anteriorly tapered m1, crowned by a pronounced anteroconid. The specimens exhibit a rather *Lophocricetus*-like occlusal pattern, with anteriorly widened M1 having a massive protostyle, reduced mesoloph and mesostyle, and the hypoconid of m1 is connected to the anterior arm of the entoconid. Further, the m1s possess posterostylids and well-developed ectomesolophids, while lacking the pseudomesolophids (Fig. 5B, C). However, the teeth strikingly differ from those of *Lophocricetus* by a narrow posterocone connected to the hypocone, as in *Heterosminthus*. Given these uncertainties and the limited data available, we refrain from assigning the lophocricetine from Grytsiv to any existing genus. Most probably, this form would represent either a transitional taxon morphologically similar, but somewhat more derived than *Sarmatosminthus* or an evolutionary offshoot of Late Miocene *Heterosminthus* with no known derivatives.

Occurrence. – Early Late Miocene, late Vallesian, Republic of Moldova and Romania.

Results and discussion

Comments on the systematic position of *Sarmatosminthus*

Based on diagnostic characters traditionally used to distinguish *Heterosminthus* and *Lophocricetus* (see, for instance, Zazhigin *et al.* 2002), *Sarmatosminthus* occupies an intermediate position between these two genera (Tab. 1). Additional characters proposed by Qiu *et al*. (2008), Qiu & Li (2016), and Ma *et al*. (2024), such as the degree of development of the parastyle on the M1 and the presence or absence of the pseudomesolophid on the m2, further confirm that *Sarmatosminthus* shares features with *Heterosminthus* and *Lophocricetus*, yet remains distinct from both.

In the evolutionary lineage of *Lophocricetus*, traits such as larger size, a prominent protostyle, absence of mesoloph, the endoloph connected to the paracone on M1, and the presence of ectostylids and ectocingulids on m1 and m2, are considered advanced features (Qiu & Li 2016). Conversely, characters like the long mesoloph, the endoloph connecting to the protoloph on the M1, the pseudomesolophid and the hypoconid connecting to the mesoconid on m1, along with the long pseudomesolophid on m2, are considered primitive traits and are frequently found in *Heterosminthus* (Qiu & Li 2016).

The only species of the genus *Sarmatosminthus* exhibits a reduction of the mesoloph on the M1, a lingual shift of the endoloph on both M1 and M2, strengthening of the protostyle on the M1, the retention of a complete mesoloph on the M2, a gradual disappearance of the pseudomesolophid on the m1 and the loss of the m2 pseudomesolophid. We interpret these traits as reflecting the evolutionary trend from *Heterosminthus* to *Lophocricetus*.

While *Sarmatosminthus* retains some characteristics typical of *Heterosminthus* – such as the connection between the hypocone and posterocone on the M1 and the connection between the hypoconid and mesoconid on the m1 – it also exhibits distinctive traits of *Lophocricetus*, such as a prominent protostyle on the M1 and M2, development of ectostylids on the m1 and m2, and the absence of the pseudomesolophid on the m2. The comparison of dental characteristics supports the hypothesis that *Sarmatosminthus* might have evolved from *Heterosminthus* during the Late Miocene and represents an intermediate form between *Heterosminthus* and *Lophocricetus*.

The reconstruction of phylogenetic relationships among Miocene dipodids from Eastern Europe remains

challenging, primarily due to the limited biostratigraphic range of the available material and the obvious rarity of lophocricetines in the Vallesian fossil sites. The regional diversity is currently restricted to two genera, *Sarmatosminthus* and *Lophocricetus*, yet several taxonomic uncertainties continue to obscure their evolutionary framework. Notably, the species *L. sarmaticus* and *L. maeoticus*, described by Topachevsky *et al.* (1984), have been variably interpreted: Zazhigin *et al*. (2002) considered them synonyms of *L. complicidens* and *L. minuscilus*, whereas Nesin (2013) retained them as valid taxa. The earliest record of dipodids in the region of the unidentified lophocricetine from Grytsiv also lacks a clear taxonomic placement, preventing its integration into broader phylogenetic hypotheses. Moreover, the absence of *Heterosminthus* or *Sarmatosminthus* in Ukrainian assemblages complicates attempts to evaluate the evolutionary connections between Eastern European and Asian lineages. As a result, any proposed phylogenetic reconstructions – whether placing *Sarmatosminthus* as the basal taxon leading to multiple *Lophocricetus* species or assuming it as an evolutionary dead-end offshoot *Heterosminthus* – remain provisional. Resolving these issues will require a comprehensive re-examination of all available Eastern European fossil material, particularly that from Ukraine, without which the phylogenetic history of European lophocricetines cannot be reliably established.

Palaeoenvironmental aspects

In the context of the European Late Miocene small mammal communities, the lophocricetines undoubtedly represented an Asian element whose westward dispersal was linked to dramatic climate change, driven by the replacement of forested areas by more open environments. However, details on lophocricetine ecology remain largely unknown.

The dental material alone does not provide sufficient information about their ecological preferences. One can suggest that they were typical open-grassland and semi-desert dwellers, similar to most living jerboas and jumping mice. Preliminary results of dental microwear analysis for the early Turolian *Lophocricetus complicidens* (Sinitsa 2015) indicate that the species was predominantly granivorous and insectivorous, resembling the five-toed pygmy jerboa (*Cardiocranius paradoxus*) in feeding preferences. This evidence aligns well with data on postcranial bones, particularly the calcaneus (Zazhigin & Lopatin 2000a), suggesting a five-toed rather than a three-toed foot for *Lophocricetus*, reminiscent of that of *Cardiocranius*. This indicates an adaptation for ricocheting locomotion, typical of jerboas (Zazhigin *et al.* 2002), and further suggests that *Lophocricetus* inhabited open biomes with xerophilous vegetation, where they could move efficiently by making short, bounding jumps.

Unfortunately, postcranial fossil remains of *Sarmatosminthus* have not been discovered thus far. However, the dentition of *Sarmatosminthus* shows more archaic dental features than those of *Lophocricetus*, such as lower-crowned teeth and less developed ridges (Qiu & Li 2016). These differences likely reflect a diet consisting of more succulent, herbaceous vegetation. Based on these dental characteristics, it is plausible that *Sarmatosminthus* lived rather in more forested savannah-like ecosystems during the Vallesian, which were gradually replaced by more open biomes by the beginning of the Turolian in the Eastern Paratethyan realm. Interestingly, the palaeogeographic history and fossil record of the genera can be directly compared with the palaeogeographic and climatic evolution of the Eastern Paratethys. All studied sites can be directly correlated with the upper Bessarabian, 11–9.9 Ma. The upper Bessarabian is characterized by ongoing aridification in comparison to lower Bessarabian, manifested by a desiccation event at the Bessarabian-Khersonian boundary (Lungu 1990, 2008a, b; Ionesi *et al.* 2005). The climate is thought to have been the cause of this event, forcing continentality in Central Eurasia. The expansion of drier environments should have favored the westward dispersal of open-landscape inhabitants, such as dipodids. Their subsequent diversification in Eastern Europe with local forms (Delinschi 2014) can be further explained by persistent and increasing aridification during the Khersonian.

Conclusions

This study provides a systematic analysis of lophocricetine dipodid fossils from five fossil-bearing layers (Bujor 1, Bujor 3a, Bujor 3b, Bohotin-Moșna 1, and Țibana 1), located on the Moldavian Platform (Republic of Moldova and Romania). The detailed taxonomic investigation confirms the validity of the genus *Sarmatosminthus*, represented by a single species, *S. gabuniai*. These new findings significantly enhance our understanding of the past dipodid diversity in Europe, clarify taxonomic interpretations from recent decades, and further underscore the importance of the Moldavian Platform in studying dipodid evolution in Eastern Europe.

The dental morphology of *S. gabuniai* exhibits characteristics shared with both *Heterosminthus* and *Lophocricetus*, placing it in an intermediate morphological position between these two genera.

The phylogenetic relationships of Miocene dipodids from Eastern Europe remain challenging to resolve due to the limited biostratigraphic range of the available material from other Eastern European fossil sites. Under such

constraints, any proposed phylogenetic reconstruction – whether positioning *Sarmatosminthus* as a basal taxon leading to multiple species of *Lophocricetus,* or suggesting an Asian origin for the latter via *Heterosminthus* – should be regarded as provisional.

Based on its dental features, it is likely that *Sarmatosminthus* inhabited predominantly wooded, savannah-like ecosystems during the Vallesian. These environments were gradually replaced by more open biomes towards the beginning of the Turolian in the eastern Paratethyan region, resulting in the appearance of the genus *Lophocricetus*.

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