



A DETAILED DESCRIPTION OF *CRICETODON HUNGARICUS* (KORDOS, 1986) (RODENTIA, MAMMALIA) FROM HASZNOS (N. HUNGARY, NÓGRÁD COUNTY)

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Abstract: The large-sized cricetid rodents (Tribe Cricetodontini) are of primary importance in the biostratigraphy of the Middle Miocene in Hungary. *Cricetodon hungaricus* is especially remarkable due to its original morphology and stratigraphic range. New excavations in the type locality of the species, namely Hasznos (Nógrád County, Hungary; Middle Badenian, MN 6) resulted in the acquisition of important new fossil material. The aim of this contribution in honor of Prof. O. Fejfar is to provide a detailed description, emended diagnosis and detailed comparison of the *Cricetodon* material with a taxonomical, biogeographical and paleoenvironmental context.

Key words: Rodentia, Cricetidae, Cricetodontini, Rodentia, middle Miocene, Badenian, Central Paratethys

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Introduction

Cricetodontini (Rodentia) are common elements of the Miocene fossil record from Europe, Asia and Africa. The species diversity, as well as the morphological plasticity of the tribe is indicative of biostratigraphical and palaeoecological changes. In France and in Spain the study of Cricetodontini has a long tradition from 19th century (e.g., Lartet 1851).

In sharp contrast, the early and middle Miocene sedimentation in the Carpathian Basin is represented mainly by marine complexes. As a result, the limnic, marshy and lagoon deposits, which are bedded into these marine sections, had not been seen as relevant by vertebrate palaeontologists. Indeed, the first Cricetodontini were unearthed only at the end of the 1970's. These historical localities were Hasznos in Hungary (Kordos 1981, 1986) and Comănești in Romania (Feru et al. 1980).

During the last decade a new intensive investigation of Cricetodontini has been undertaken in Europe with more detailed morphology being presented (López-Guerrero et al. 2008, 2013, 2014a, b, 2015, López-Antoñanzas and Mein 2009, 2011). In the present paper the author gives an accurate description which is comparable with the publications cited above.

Hasznos locality

The section of whitish-light gray unconsolidated diatomaceous earth exposed on the southern foothill of the

Vár-hegy (= Castel Hill) is west of the village of Hasznos (which is now part of the town of Pásztó), in close vicinity to the artificial lake and waterworks. Underlying this bed of sediment is the Nagyhársas Andesite Formation (Zelenka 2010, Gyalog et al. 2010). The K/Ar ages of the piroxandesites in the Nagyhársas Andesite Formation are between 14.5 and 16.3 My (Zelenka 2010). Paleomagnetic investigation of the andesites detected reversed polarity and rotation to the West (Márton and Márton 1996).

Overlying the diatomite complex at Hasznos is the alluvial fan of the Gombás-tető which was classified as part of the Sarmatian Sajóvölgy Formation (Hámor 1985). Strong erosional discordancies may occur between the beds.

The section at Hasznos belongs to the diatomites of the Western part of the Mátra Mountains which were classified as the Szurdokpüspöki Formation by Gyalog and Budai (2004). Varga et al. (1975) determined the age of the diatomite complex as Badenian following the results of Hajós (1968) using siliceous algae.

Hasznos was the first middle Miocene non-karstic vertebrate locality identified in Hungary. It was sampled by screenwashing (Kordos 1981, 1986). The marine fishes of Hasznos were studied by Solt (1991). With regard to mammals, a taxonomic study of the locality was completed by Prieto et al. (2015; Eulipotyphla), Hír and Pászti (2012; *Palaeosciurus*) and Rosina et al. (2015; Chiroptera). These data have been compiled and emended by Hír et al. (2016, 2017). The locality was studied from a sedimentological point of view by Vereb (2013).

Problem defining

The large-sized *Cricetodontini* from Hasznos was first assigned to the species *Deperetomys hagni* (FAHLBUSCH, 1964) described as *Deperetomys hagni hungaricus* by Kordos (1986). Later De Bruijn et al. (1993) proposed a closer relationship to *Cricetodon*.

A new description is necessary because neither Kordos (1986), nor De Bruijn et al. (1993) produced a detailed description, and new material was collected in 2012 and 2013 at the type locality (Hír and Pászti 2012).

A new extended differential diagnosis is also needed because Kordos (1986) made a comparison with only *Deperetomys* species. In addition, during the last decades significant progress has been made and it is now relevant to review the relationship between *C. hungaricus* and other species of *Cricetodon*, *Hispanomys* and *Byzantinia*.

Material and methods

Material used in this study: the original findings collected and described by Kordos (1986) and stored in the Geological Museum of the Hungarian Geological and Geophysical Institute (V 13033, V 13034, V 13035, V 13037, V 13038). Additional material was collected by the author and stored in the Natural History Collection of the Municipal Museum of Pásztó (P.2017.1. – P. 2017.6.).

Measurements were made using the ocular micrometer of a MBS-9 stereomicroscope. The measurements are given in mm.

We used the terminology of Mein and Freudenthal (1971b) and Rummel (1998) with some modifications. The numbers in Tables 7–27 refer to the numbers of teeth.

Systematic palaeontology

Family Cricetidae FISCHER, 1817

Subfamily Cricetodontinae SIMPSON, 1945

Tribe Cricetodontini SIMPSON, 1945

Genus *Cricetodon* LARTET, 1851

***Cricetodon hungaricus* (KORDOS, 1986)**

1986 *Deperetomys hagni hungaricus* n. ssp.; Kordos, p. 524, pl. 1, figs 1–9, pl. 2, figs 1–9, pl. 3, figs 1–6.

1993 *Cricetodon hungaricus*; De Bruijn et al., p. 208, pl. 18, figs 1–9, pl. 19, figs 1–9.

Original diagnosis. “Subspecies based on a specimen of great size with lengthy teeth and with a complicated structure of tooth elements slightly different from the type of *Deperetomys hagni* (FAHLBUSCH). The anterocone is always bifid, the anterolophule connects the antero- and posterocones. The mesoloph is short, it does not extend up to the labial margin of the tooth, closing a small island at the medial base of the paracone.” (Kordos 1986: 539).

Emended diagnosis. Large sized *Cricetodon* species with divided anterocone, frequent funnel structure, lingual transversal spur II and frequent short and thin

Table 1. Individual measurements of *Cricetodon hungaricus* M1 finds from Hasznos.

Inv. no.	Tooth	L [mm]	W [mm]	Published figures
V.13033.4	M1	3.57	2.27	De Bruijn et al. 1993: pl. 18, fig. 1
V.13033.11	M1	3.65	2.27	De Bruijn et al. 1993: pl. 18, fig. 4
V.13033.17	M1	3.27	2.20	De Bruijn et al. 1993: pl. 18, fig. 7; De Bruijn and Ünay 1996: fig. 17.2
V.13033.1	M1	3.42	2.20	
V.13033.2	M1	3.70	2.37	
V.13033.3	M1	3.62	2.17	
V.13033.5	M1	3.45	2.15	
V.13033.6	M1	3.42	2.17	
V.13033.7	M1	3.40	2.15	
V.13033.8	M1	3.50	2.17	Kordos 1986: pl. I, fig. 3
V.13033.9	M1	3.25	2.22	
V.13033.10	M1	3.40	2.15	Kordos 1986: pl. I, fig. 2
V.13033.12	M1	3.60	2.30	
V.13033.13	M1	3.52	2.25	
V.13033.14	M1	3.45	2.22	
V.13033.15	M1	–	2.25	
V.13033.16	M1	3.45	2.37	
V.13033.22	M1	3.50	2.25	
V.13033.23	M1	3.50	2.30	Kordos 1986: pl. I, fig. 1
V.13033.24	M1	3.77	2.25	
V.13033.25	M1	3.57	2.22	
V.13033.26	M1	–	2.15	
P.2017.1.1	M1	3.17	2.15	
P.2017.1.2	M1	3.55	2.20	
P.2017.1.3	M1	3.52	2.20	
P.2017.1.4	M1	3.37	2.05	
P.2017.1.5	M1	3.62	2.25	
P.2017.1.6	M1	3.30	2.12	
Min.		3.17	2.05	
Max.		3.77	2.37	
Mean		3.62	2.22	

entomesoloph in M1. Mesoloph is short or medium-sized in M1–M2, but most often long in M3. In the upper molars, an entomesoloph is present, a complete anterior ectoloph is relatively rare, but a complete posterior ectoloph is frequent. Labial anterolophid and protosinusid are well developed in m1. Metalophulid I + II are developed in 50% of the m1, only metalophulid II is present in the other specimens. A short or medium developed ectomesolophid is frequent in m1 but less frequent in m2 and m3. A short mesolophid is characteristic for the lower molars. In juvenile and adult molars, the cusps and cuspids are higher than the lophids and lophids.

Description. M1. Anterocone consists of two conelets of equal size. There is a shallow and narrow groove between the cuspulas on the mesial surface. The labial conelet of the anterocone bears the remains of the labial anteroloph. The lingual conelet and the protocone are connected by the anterolophule. The labial conelet bears a

Table 2. Individual measurements of *Cricetodon hungaricus* M2 finds from Hasznos.

Inv. no.	Tooth	L [mm]	W [mm]	Published figures
V.13034.2	M2	2.67	2.17	
V.13034.3	M2	2.77	2.25	
V.13034.4	M2	2.52	2.05	
V.13034.5	M2	2.60	2.00	
V.13034.6	M2	2.52	1.92	
V.13034.8	M2	2.70	2.15	
V.13034.9	M2	2.60	2.07	
V.13034.10	M2	2.80	2.32	Kordos 1986: pl. II, fig. 5
V.13034.12	M2	2.60	2.40	
V.13034.13	M2	2.57	1.85	
V.13034.14	M2	2.95	2.20	
V.13034.15	M2	2.55	2.15	
V.13034.16	M2	2.62	2.15	
V.13034.17	M2	2.70	1.92	
V.13034.18	M2	2.52	1.97	
V.13034.19	M2	2.82	2.15	Kordos 1986: pl. II, fig. 4
V.13034.20	M2	2.60	1.87	
V.13034.21	M2	2.60	1.87	
V.13034.22	M2	2.77	–	
V.13034.23	M2	2.55	2.02	De Bruijn et al. 1993: pl. 18, fig. 5
V.13034.24	M2	2.77	2.40	De Bruijn et al. 1993: pl. 18, fig. 2
V.13034.25	M2	2.80	2.17	De Bruijn et al. 1993: pl. 18, fig. 8; De Bruijn and Ünay 1996: fig. 17.2
P.2017.2.1	M2	2.67	2.12	
P.2017.2.2	M2	2.52	2.12	
P.2017.2.3	M2	2.70	2.0	
P.2017.2.4	M2	2.75	2.12	
P.2017.2.5	M2	2.60	2.15	
P.2017.2.6	M2	2.62	2.27	
P.2017.2.7	M2	2.55	2.0	
P.2017.2.8	M2	2.32	1.90	
P.2017.2.9	M2	2.70	2.10	
Min.		2.32	1.85	
Max.		2.95	2.40	
Mean		2.65	2.10	

labial anterocone sporn, which is variable in length (Tab. 7). This anterior ectoloph is formed mainly by the anterocone sporn, the paracone anterior spur is distinguishable and forms part of the long anterior ectoloph in only 3 cases (3/26). The anterolophule frequently bears a lingual transversal spur II (Tab. 8). The lingual sinuses are closed by thick cingula, the labial sinuses are open. Protolophule I is developed in only one molar. A thin entomesoloph is frequent (Tab. 9), its length is variable. The mesoloph is short or medium-sized. The funnel structure is found in the majority of the molars (Tab. 10). The paracone posterior spur is long and frequently connects to the anterior spur of the metacone. The posterior ectoloph is complete in 24 molars. The labial outline of the toothcrown is straight (17/26) or undulated: the paracone and metacone are standing out from the labial outline (9/26). Four roots. Dimensions are given in Table 1.

Table 3. Individual measurements of *Cricetodon hungaricus* M3 finds from Hasznos.

Inv. no.	Tooth	L [mm]	W [mm]	Published figures
V.13035.1	M3	2.2	1.87	
V.13035.2	M3	2.25	2.00	
V.13035.3	M3	2.27	2.00	
V.13035.7	M3	2.32	2.30	Kordos 1986: pl. I, fig. 9
V.13035.8	M3	2.20	1.92	
V.13035.9	M3	2.02	1.97	
V.13035.12	M3	2.35	1.95	Kordos 1986: pl. I, fig. 8
V.13035.13	M3	2.35	2.07	
V.13035.14	M3	2.12	1.92	
V.13035.15	M3	2.37	2.22	Kordos 1986: pl. I, fig. 7
V.13035.16	M3	2.22	1.90	
V.13035.17	M3	2.30	2.0	
V.13035.17b	M3	2.42	2.12	
V.13035.18	M3	2.17	1.90	
V.13035.19	M3	2.30	2.10	
V.13035.20	M3	2.40	2.05	De Bruijn et al. 1993: pl. 18, fig. 9
V.13035.21	M3	2.0	1.90	De Bruijn et al. 1993: pl. 18, fig. 6
V.13035.22	M3	2.32	2.25	De Bruijn et al. 1993: pl. 18, fig. 3
P.2017.3.1	M3	2.45	2.0	
Min.		2.0	1.87	
Max.		2.45	2.30	
Mean		2.26	2.02	

M2. The labial anteroloph arm is thick, the lingual one is thin. In a few cases, the paracone anterior spur is connected to the lingual anteroloph arm (Tab. 11). A protocone spur is frequent (Tab. 12). The paracone posterior spur is long and reaches the anterior surface of the metacone in 17 molars. A mesoloph is found in 7/15 specimens. Its length is variable. The entomesoloph and the funnel structure are less frequent than in M1 (Tabs 13, 14). A remnant of the labial posteroloph is developed in one molar. The labial outline of the toothcrown is straight (9/31) or undulated: the paracone and metacone are standing out from the labial outline (22/31). A posteroloph is not developed. Four roots. Dimensions are given in Table 2.

M3. The anteroloph arm is developed as in M2. A labial anteroloph-paracone anterior spur connection is rare (Tab. 16). A protocone spur is normal (Tab. 15). The paracone posterior spur is long, in 18 molars it reaches the metacone. A short entomesoloph is rare (Tab. 17). A long mesoloph is found in 16 cases. A complete funnel structure is frequent (Tab. 18). Hypocone and metacone are reduced but distinct. Three roots. Dimensions are given in Table 3.

m1. The small and rounded anteroconid is unicuspid. In lateral view, it is lower than the protoconid and metaconid. The labial anterolophid is well developed, it reaches the anterior basis of the protoconid and closes the elliptical protosinusid. A very short lingual anterolophid is relatively frequent (Tab. 19). Metalophulid I and II are equally developed in 50% of the molars. Metalophulid II only is found in the other 50% (Tab. 20). Short mesolophids and

Table 4. Individual measurements of *Cricetodon hungaricus* m1 finds from Hasznos.

Inv. no.	Tooth	L [mm]	W [mm]	Published figures
V.13037.1	m1	2.85	1.92	Kordos 1986: pl. II, fig. 3
V.13037.2	m1	2.92	1.90	Kordos 1986: pl. II, fig. 1
V.13037.3	m1	2.90	1.92	Hír 2007: pl. I, fig. 13
V.13037.4	m1	2.95	2.0	Kordos 1986: pl. II, fig. 2
V.13037.5	m1	2.62	1.82	
V.13037.6	m1	2.67	1.80	De Bruijn et al. 1993: pl. 19, fig. 7
V.13037.7	m1	2.70	1.77	De Bruijn et al. 1993: pl. 19, fig. 4
V.13037.8	m1	2.62	1.82	
V.13037.9	m1	2.82	1.70	
V.13037.10	m1	2.72	-	
V.13037.11	m1	2.65	1.77	
V.13037.13	m1	2.72	1.87	
V.13037.14	m1	2.87	1.80	
V.13037.15	m1	2.90	1.85	
V.13037.16	m1	2.95	1.87	De Bruijn et al. 1993: pl. 19, fig. 1
V.13037.17	m1	2.85	1.67	
V.13037.18	m1	2.42	1.80	
P.2017.4.1	m1	2.87	1.80	
P.2017.4.2	m1	2.62	1.75	
Min.		2.42	1.67	
Max.		2.95	2.00	
Mean		2.77	1.82	

short ectomesolophids are frequent (Tabs 21, 22). Labial sinusids and the posterosinusids are closed by a cingulum, but lingual sinusids are open. Two roots. Dimensions are given in Table 4.

m2. Lingual anterolophid is absent. The labial anterolophid reaches the anterior basis of the protoconid and closes the deep protosinusid. Only metalophulid I is developed. The mesolophid is short, in a few molars it reaches the posterior basis of the metaconid (Tab. 23). Protosinusid, labial main sinusid and the posterosinusid are closed, the lingual sinusid is open. The occurrence of a short ectomesolophid is rare (Tab. 24). Two roots. Dimensions are given in Table 5.

m3. Lingual anterolophid is most usually absent. The labial anterolophid reaches the anterior basis of the protoconid and closes the deep protosinusid. In a few molars, a low remnant of the lingual anterolophid is found (Tab. 25). The mesolophid is short and frequently reaches the posterior basis of the metaconid (Tab. 26). The protosinusid is closed, the other sinusids are open. Two roots. Dimensions are given in Table 6.

Comparison. *Cricetodon hungaricus* from Hasznos differs from the early Miocene *Cricetodontini* from Anatolia

- *C. trallesensis* ÇINAR DURGUT et ÜNAY, 2016, Söke, Turkey, MN 4, local biozone E (Ünay et al. 2003),
- *C. fikreti* ÇINAR DURGUT et ÜNAY, 2016, Dededag, Turkey, MN 4, local biozone B (Ünay et al. 2003),

Table 5. Individual measurements of *Cricetodon hungaricus* m2 finds from Hasznos.

Inv. no.	Tooth	L [mm]	W [mm]	Published figures
V.13038.1	m2	2.67	2.07	Kordos 1986: pl. I, fig. 4
V.13038.3	m2	2.67	1.85	
V.13038.4	m2	2.75	2.0	
V.13038.5	m2	2.67	1.85	
V.13038.6	m2	2.75	2.0	
V.13038.10	m2	2.80	2.02	
V.13038.11	m2	2.65	1.95	
V.13038.15	m2	2.77	2.07	
V.13038.19	m2	2.77	1.90	
V.13038.20	m2	2.75	2.10	Kordos 1986: pl. I, fig. 5
V.13038.22	m2	2.67	1.95	
V.13038.23	m2	2.70	1.90	
V.13038.24	m2	2.82	2.02	
V.13038.25	m2	2.75	1.97	De Bruijn et al. 1993: pl. 19, fig. 5
V.13038.26	m2	2.72	1.95	De Bruijn et al. 1993: pl. 19, fig. 8
V.13038.27	m2	2.75	2.12	De Bruijn et al. 1993: pl. 19, fig. 2
V.13038.28	m2	2.55	1.90	
P.2017.5.1	m2	2.77	2.02	
P.2017.5.2	m2	2.37	1.80	
P.2017.5.3	m2	2.87	2.07	
P.2017.5.4	m2	2.80	2.10	
P.2017.5.5	m2	2.75	2.05	
Min.		2.37	1.80	
Max.		2.87	2.12	
Mean		2.72	1.99	

- *C. yapintiensis* ÇINAR DURGUT et ÜNAY, 2016, Yapinti, Turkey, MN 3–4, local biozone D or E (Ünay et al. 2003),
 - *C. magnesiensis* ÇINAR DURGUT et ÜNAY, 2016, Kinik, Turkey, MN 3, local biozone D (Ünay et al. 2003),
 - *C. kasapligili* DE BRUIJN, ÜNAY et HORDIJK, 1993, Keseköy, Turkey, MN 3, local biozone D (Ünay et al. 2003),
 - *C. versteegi* DE BRUIJN, ÜNAY et HORDIJK, 1993, Kilçak 3a, Turkey, MN 1, local biozone B (Ünay et al. 2003),
 - *C. tobieni* DE BRUIJN, ÜNAY et HORDIJK, 1993, Horlak 1a, Turkey, MN 3, local biozone D (Ünay et al. 2003),
 - *Cricetodon* n. sp. 1 in De Bruijn et al. (1993), Kilçak 3b, Turkey, MN 5, local biozone F (Ünay et al. 2003),
- in being larger, in having a higher degree of hypsodonty and in always having four roots in M1 and M2.

Cricetodon hungaricus differs from *C. aliveriensis* KLEIN HOFMEIJER et DE BRUIJN, 1988 from Aliveri, Greece, MN 4:

- in being larger and in having a higher degree of hypsodonty,
- in the better developed ectolophs and in the presence of the funnel structure in M1 and M2,
- in the presence of the anterior ectoloph, in the posteriorly directed metalophule in M3,

Table 6. Individual measurements of *Cricetodon hungaricus* m3 finds from Hasznos.

Inv. no.	Tooth	L [mm]	W [mm]	Published figures
V.13034.26	m3	2.72	1.80	De Bruijn et al. 1993: pl. 19, fig. 6
V.13034.27	m3	2.67	1.90	De Bruijn et al. 1993: pl. 19, fig. 9
V.13034.28	m3	2.57	1.77	De Bruijn et al. 1993: pl. 19, fig. 3
P.2017.6.1	m3	2.45	1.65	
V.13034.29	m3	2.67	1.85	Kordos 1986: pl. II, fig. 8
V.13034.30	m3	2.72	1.92	
V.13034.31	m3	2.77	1.90	
V.13034.32	m3	2.82	2.0	Kordos 1986: pl. I, fig. 7
V.13034.33	m3	2.80	1.80	
V.13034.34	m3	2.70	2.0	
V.13034.35	m3	2.90	2.07	
V.13034.36	m3	2.60	1.92	
V.13034.37	m3	2.85	1.97	Kordos 1986: pl. I, fig. 9
V.13034.38	m3	2.92	2.0	
V.13034.39	m3	2.50	1.75	
V.13034.40	m3	2.62	1.80	
Min.		2.50	1.75	
Max.		2.92	2.07	
Mean		2.74	1.91	

- in the less developed lingual arm of the anterolophid and in the absence of metalophulid I in 50% of the m1s.

Cricetodon hungaricus differs from *C. caucasicus* ARGYROPULO, 1938, Belomechetskaya, Georgia, MN 6, after Pickford et al. (2000):

- in being larger and having a higher degree of hypsodonty,
- in the divided anterocone in M1,
- in the presence of the entomesoloph in upper molars,
- in the presence of metalophulid I + II in 50% of the m1s and in the presence of an ectomesolophid in the lower molars.

Cricetodon hungaricus differs from *C. meini* FREUDENTHAL, 1963, Vieux Collonges, France, MN 5, after Mein and Freudenthal (1971b):

- in being larger and having a higher degree of hypsodonty,
- in the more frequent and well-developed lingual transversal spur II,
- in the frequent occurrence of the mesoloph, entomesoloph and the funnel structure,
- in the better developed ectolophs in M1,
- in the presence of a protocone spur,
- in the better developed ectolophs in M2 and M3,
- in the more frequent occurrence of metalophulid I, in the presence of a very short lingual anterolophid arm in m1,
- in the occurrence of a short ectomesolophid in m2 and m3.

Cricetodon hungaricus differs from *C. aureus* MEIN et FREUDENTHAL, 1971b, Vieux Collonges, France, MN 5:

- in having larger mean measurements and a higher degree of hypsodonty,
- in the frequent and well-developed lingual transversal spur II,
- in the occurrence of the entomesoloph and funnel structure,
- in the better developed ectolophs in M1,
- in the occurrence of the entomesoloph and funnel structure,
- in the better developed ectolophs in M2,
- in the occurrence of the funnel structure in M3.

Cricetodon hungaricus differs from *C. jotae* MEIN et FREUDENTHAL, 1971a, Manchones, Spain, MN 6, local biozone G2, (López-Guerrero et al. 2014b):

- in being larger and having a higher degree of hypsodonty,
- in the frequent and well-developed lingual transversal spur II,
- in the frequent occurrence of the mesoloph, entomesoloph and the funnel structure in M1,
- in the more frequent occurrence of an entomesoloph and the presence of the funnel structure in M2,
- in the presence of the protocone sporn, entomesoloph, funnel structure and the frequently long mesoloph in M3,
- in the more frequent mesolophid and ectomesolophid, the less frequent co-occurrence of metalophulid I and metalophulid II in m1,
- in the occurrence of the short ectomesolophid in m2 and m3.

Cricetodon hungaricus differs from *C. jumaensis* RUMMEL, 2000, Petersbuch 18, 6, 35, Germany, MN 7 + 8 (Rummel 2000):

- in having larger mean measurements and a higher degree of hypsodonty,
- in the more deeply divided anterocone, and the absence of a labial transversal spur anteromesoloph in M1,
- in the presence of the funnel structure, and complete posterior ectoloph in the upper molars,
- in the regular presence of a metalophulid II in m1,
- in the presence of a short ectomesolophid in m2 and m3.

Cricetodon hungaricus differs from *C. bolligeri* RUMMEL, 1995, Petersbuch 10, Germany (originally the biochronological position was classified as MN 9, later it was emended by Prieto and Rummel (2016) to MN 7 + 8, close to the *Megacricetodon gregarius-Deperetomys hagni* interval zone of Kálin and Kempf (2009)):

- in having larger mean measurements and a higher degree of hypsodonty,
- in the more deeply divided anterocone, more frequent lingual transversal spur II, more frequent mesoloph, entomesoloph and complete posterior ectoloph in M1,

Table 7. Variations in the form of M1 labial anterocone spur (= anterocone posterior ectoloph) in *Cricetodon hungaricus* from Hasznos. A: not found; B: short or medium development but never reaching the anterior surface of the paracone; C: spur reaches the anterior surface of the paracone.







			
	A	B	C
Hasznos	3	17	7

Table 8. Variations in the form of M1 lingual transversal spur II (= lingual querspur II) in *Cricetodon hungaricus* from Hasznos. A: not found; B: interrupted; C: complete.

			
	A	B	C
Hasznos	4	1	22

- in the less variable anterior region of the M1: among the 12 morphotypes described by Rummel (1995) 4 morphotypes are found in *C. hungaricus*,
- in the more frequent mesoloph, entomesoloph and complete posterior ectoloph in M2,
- in the presence of the funnel structure in the upper molars,
- in the more frequent mesolophid, in the less variable anterior region of m1: among the 6 morphotypes described by Rummel (1995) 2 types are found in *C. hungaricus*, and in the less frequent ectomesolophid in m1.

Cricetodon hungaricus differs from *C. sansaniensis* LARTET, 1851, Sansan, France, MN 6, after the emended diagnosis and description of Maridet and Sen (2012):

- in having larger mean measurements,
- in the better developed and longer lingual transversal spur II,
- in the frequent presence of a funnel structure, in the presence of an entomesoloph, in the absence of a mesocone in M1,
- in the frequent presence of a funnel structure, in the presence of the entomesoloph, in the absence of a mesocone in M2 and M3,
- in the regular presence of metalophulid II,
- in the more frequent short mesolophid in m1,
- in the larger protosinusid in m2 and m3.

Table 9. Variations in the form of M1 entomesoloph in *Cricetodon hungaricus* from Hasznos. A: not found; B: developed (short, medium developed or long).






		
	A	B
Hasznos	11	16

Table 10. Variations in the form of M1 funnel structure in *Cricetodon hungaricus* from Hasznos. A, B: incomplete; C: complete.

			
	A	B	C
Hasznos	6		20

Cricetodon hungaricus differs from *C. albanensis* MEIN et FREUDENTHAL, 1971a, fissure L7, La Grive-Saint Alban, France, MN 7 + 8:

- in the presence of the mesoloph and funnel structure in the upper molars,
- in the regular presence of metalophulid II in m1,
- in the occurrence of a short ectomesolophid in the lower molars.

Cricetodon hungaricus differs from *C. engesseri* RUMMEL et KÄLIN, 2003, Chräzerentobel 523 m, MN 7; Schauenberg-Langriet 690 m, MN 6; Mettlen-Weid, Switzerland, *Megacricetodon similis*-*Megacricetodon gregarius* interval Zone, MN 6 (Kälin and Kempf 2009); Petersbuch 68, Germany, ~MN 6 (Prieto and Rummel 2009):

- in the presence of the funnel structure and entomesoloph in the upper molars,
- in the regular presence of metalophulid II in m1,
- in the occurrence of a short ectomesolophid in the lower molars.

Cricetodon hungaricus differs from *C. soriae* LÓPEZ-MARTÍNEZ, CÁRDABA, SALESA, HERNÁNDEZ FERNÁNDEZ, CUEVAS-GONZÁLEZ et FESHARAKI in Hernández Fernández et al. (2006), Somosaguas N, Spain, MN 5, Local biozone E:

- in being larger and having a higher degree of hypsodonty,
- in the presence of a lingual transversal spur II, in the presence of a labial anterocone spur (= anterocone posterior ectoloph), in the frequent funnel structure and in the frequent entomesoloph in M1,

Table 11. Variations in the form of M2 paracone anterior spur in *Cricetodon hungaricus* from Hasznos. A: not found; B: short, not connected to the labial anteroloph; C: connected to the labial anteroloph.






			
	A	B	C
Hasznos	21	1	11

Table 12. Variations in the form of M2 protocone spur in *Cricetodon hungaricus* from Hasznos. A: not found; B: short, or medium developed.

		
	A	B
Hasznos	7	25

- in the presence of a funnel structure, in the longer mesoloph, in the presence of an entomesoloph and in the presence of a protocone spur in M2,
- in the presence of a funnel structure, in the presence of an entomesoloph and in the presence of a protocone spur in M3,
- in the absence of metalophulid I in 50% of the m1s, in the regular presence of the lingual anterolophulid and protosinusid, in the absence of the labial posterolophid,
- in the absence of the labial posterolophid in m2,
- in the presence of an ectomesolophid in m3.

Cricetodon hungaricus differs from *C. nievei* LÓPEZ-GUERRERO, ÁLVAREZ-SIERRA, GARCÍA-PAREDES et PELÁEZ-CAMPOMANES, 2014a, Toril 3A, Spain, MN 7 + 8, Local biozone G3:

- in being larger and having a higher degree of hypsodonty,
- in the less developed (only a remnant) lingual anteroloph,
- in the better developed and longer lingual transversal spur II,
- in a frequent funnel structure,
- in a more frequent entomesoloph in M1,
- in the longer mesoloph, in the frequent funnel structure and in a more frequent entomesoloph in M2,
- in the higher frequency of a long mesoloph and in the presence of a funnel structure in M3,

Table 13. Variations in the form of M2 entomesoloph in *Cricetodon hungaricus* from Hasznos. A: not found; B: short, or medium developed.






		
	A	B
Hasznos	19	13

Table 14. Variations in the form of M2 funnel structure in *Cricetodon hungaricus* from Hasznos. A, B: incomplete; C: complete.

			
	A	B	C
Hasznos	14		18

- in the better developed labial anterolophulid which always reaches the protoconid and closes the protosinusid, in the regular presence of metalophulid II and in the short and less frequent ectomesolophid in m1,
- in the short and less frequent ectomesolophid in m2.

Cricetodon hungaricus differs from *Hispanomys castelnovi* AGUILAR, CALVET et MICHAX, 1994, Castelnou 6, France, MN 6:

- in having larger mean measurements,
- in the presence of a lingual transversal spur II in M1,
- in the presence of the mesoloph, entomesoloph and funnel structure in the upper molars,
- in the presence of the protocone spur in M2 and M3,
- in the better developed labial anterolophid arm and closed protosinusid, and in the regular presence of metalophulid II in m1,
- in the presence of an entomesoloph in the lower molars.

Cricetodon hungaricus differs from *Hispanomys bijugatus* MEIN et FREUDENTHAL, 1971a, Fissure L3, carrière Lechartier, La Grive-Saint Alban, France, MN 7 + 8 (for detailed description see López-Antoñanzas and Mein (2009)):

- in having larger mean measurements,
- in the presence of the mesoloph and funnel structure in M1,
- in the better developed and more frequent anterior ectoloph, in the presence of the mesoloph and funnel structure in M2 and M3,

Table 15. Variations in the form of M3 protocone spur in *Cricetodon hungaricus* from Hasznos. A: not found; B: short, or medium developed.





		
	A	B
Hasznos	3	15

Table 16. Variations in the form of M3 paracone anterior spur in *Cricetodon hungaricus* from Hasznos. A: not found; B: well developed, connected to the labial anteroloph.

		
	A	B
Hasznos	15	4

- in the absence of metalophulid I in 50% of the m1s. In the presence of a short mesolophid and more frequent ectomesolophid in m1,
- in the occurrence of an ectomesolophid in m2 and m3.

Cricetodon hungaricus differs from *Hispanomys aguirrei* SESÉ-BENITO, 1977, Escobosa de Calatañazor, Nombrevilla 2, Spain, MN 7 + 8, local biozone G3 (for detailed description see López-Guerrero et al. (2008)):

- in being larger,
- in the presence of a lingual transversal spur II in M1,
- in the more frequent anterior ectoloph, in the presence of the mesoloph, funnel structure and entomesoloph in M2 and M3,
- in the regular presence of metalophulid II in m1,
- in the better developed labial anterolophulid arm and the closed protosinusid, in the presence of an ectomesolophid in the lower molars.

Cricetodon hungaricus differs from *Hispanomys decedens* SCHAUB, 1925, La Grive-Saint Alban, Fissure L5', France, MN 7 + 8 (for detailed description see López-Antoñanzas and Mein (2011)):

- in having larger mean measurements,
- in the absence of the additional conelets on the mesial surface (prelobe) of the anterocone in M1,
- in the absence of metalophulid I in 50% of the m1s,
- in the more frequent ectomesolophid in m1,
- in the occurrence of an ectomesolophid in m2 and m3.

Table 17. Variations in the form of M3 entomesoloph in *Cricetodon hungaricus* from Hasznos. A: not found; B: short, or medium developed.






		
	A	B
Hasznos	13	6

Table 18. Variations in the form of M3. Funnel structure in *Cricetodon hungaricus* from Hasznos. A, B: incomplete; C: complete.

			
	A	B	C
Hasznos	3		16

Cricetodon hungaricus differs from *Hispanomys daamsi* (AGUSTI, CASANOVAS-VILAR et FURIO, 2005), Can Missert, Spain, Late Aragonien, MN 7+8, “just before the entry of the *Hipparion*” (Agusti et al. 2005) (later the chronological position of Can Missert was modified by Alba et al. (2006) as “undetermined age between late Aragonian and early Vallesian”):

- in having larger mean measurements,
- in the presence of the lingual transversal spur II, funnel structure, mesoloph and entomesoloph in M1,
- in the presence of the mesoloph, funnel structure and entomesoloph in M2 and M3,
- in the better developed labial anterolophid arm and protosinusid, in the absence of metalophulid I in 50% of the m1s, in the more frequent ectomesolophid in m1,
- in the better developed labial anterolophulid arm and protosinusid, in the occurrence of an ectomesolophid in m2 and m3.

Cricetodon hungaricus differs from *Hispanomys lavocati* FREUDENTHAL, 1966, Hostalets de Pierola, Spain, MN 7 + 8 (Agusti 1980):

- in having larger mean measurements,
- in the presence of the mesoloph, funnel structure and entomesoloph in M1 and M2,
- in the higher frequency of a long mesoloph and the presence of an entomesoloph in M3,
- in the regular presence of metalophulid II in m1,
- in the more frequent mesolophid and the presence of an ectomesolophid in m2 and m3.

Table 19. Variations in the form of m1 remnant lingual anterolophid arm in *Cricetodon hungaricus* from Hasznos. A: not found; B: developed.





		
	A	B
Hasznos	7	10

Table 20. Variations in the form of m1 metalophulids in *Cricetodon hungaricus* from Hasznos. A: only posterior one is developed; B: anterior and posterior metalophulids are equally developed.

		
	A	B
Hasznos	9	9

Cricetodon hungaricus differs from the late Miocene *Hispanomys* species,

H. adroveri AGUSTI, 1986, Casa del Acero, Spain, MN 12 and MN 13,

H. freudenthali VAN DE WEERD, 1976, Masada del Valle 2, Spain, MN 12,

H. baixasi AGUILAR, MICHAUX et LAZZARI, 2007, Lo Fournas 16-M, France, MN 11,

H. peralensis VAN DE WEERD, 1976, Peralejos, Spain, MN 10,

H. moralesi LÓPEZ-ANTOÑANZAS, PELÁEZ-CAMPOMANES, ÁLVAREZ-SIERRA, GARCÍA-PAREDES, 2010, Batallones 10, Spain, MN 10,

H. mediterraneus AGUILAR, 1982, Montredon, France, MN 10,

H. thaleri (HARTENBERGER, 1965), Can Llobateres, MN 9,

H. aragonensis (FREUDENTHAL, 1966), Pedregueras 2C, MN 9,

H. nombrevillae (FREUDENTHAL, 1966), Nombrevilla H, MN 9,

- in the lower degree of hypsodonty,
- in the lower value of the LM1/LM3 and Lm1/Lm3 ratios,
- in the less frequent complete anterior ectoloph in the upper molars,
- in the presence of a lingual transversal spur II, mesoloph, funnel structure and entomesoloph in M1,
- in the regular metalophulid II in m1,

Table 21. Variations in the form of m1 mesolophid in *Cricetodon hungaricus* from Hasznos. A: not found; B: short mesolophid developed.





		
	A	B
Hasznos	7	11

Table 22. Variations in the form of m1 ectomesolophid in *Cricetodon hungaricus* from Hasznos. A: not found; B: developed.

		
	A	B
Hasznos	5	13

- in the better developed labial anterolophid and protosinusid in the lower molars,
- in the occurrence of an ectomesolophid in the lower molars.

Cricetodon hungaricus differs from *Cricetodon* cf. *hungaricus* from Sámsonháza, Hungary, MN 6, (Hír and Mészáros 2002):

- in the presence of the entomesoloph, funnel structure and posterior ectoloph in M1,
- in the presence of the mesoloph and entomesoloph in M2,
- in the always open anterosinusid, in the presence of metalophulid I and short mesolophid in m1.

Cricetodon hungaricus differs from *Cricetodon* sp. from Mátraszőlös 2, Hungary, MN 7 + 8, (Hír and Kókay 2004):

- in the occurrence of a long lingual querspur II in M1,
- in the occurrence of an entomesoloph in the upper molars,
- in the better developed labial anterolophid arm and larger protosinusid in m2 and m3.

m1 is not represented in the limited material from Mátraszőlös.

Cricetodon hungaricus differs from *Cricetodon* sp. from Tășad, Romania, MN 7 + 8, (Hír et al. 2001):

- in the occurrence of a lingual querspur II, and in the continuous protocone-anteterolophule-lingual

Table 23. Variations in the form of mesolophid in m2 in *Cricetodon hungaricus* from Hasznos. A: short, does not reach the posterior surface of the paracone; B: reaches the posterior surface of the paracone.





		
	A	B
Hasznos	16	9

Table 24. Variations in the occurrence of m2 short ectomesolophid in *Cricetodon hungaricus* from Hasznos. A: not found; B: developed.

		
	A	B
Hasznos	18	5

anterocone connection in M1 (in the M1 from Tășad the anterolophule is divided from the lingual anterocone by a narrow trench; Hír et al. 2001: pl. IV, fig. 5),

- in the occurrence of the mesoloph, entomesoloph and funnel structure in the upper molars,
- in the presence of a labial anterolophid and protosinusid in m3.

m1 and m2 are not represented in the limited material from Tășad.

Cricetodon hungaricus differs from “*Cricetodon*” *klariankae* Hír, 2007, Felsőtárkány-Felnémet 2/3, Hungary, MN 7 + 8:

- in having smaller mean M2 measurements and in the lower degree of hypsodonty,
- in the presence of the lingual transversal spur II, mesoloph and funnel structure in M1,
- in the presence of the mesoloph and funnel structure in M2 and M3,
- in the less reduced hypocone and metacone in M3,
- in the more frequent mesolophid, the better developed labial anterolophid arm, protosinusid and in the less frequent metalophid I in m1,
- in the presence of an ectomesolophid in m2 and m3.

Cricetodon hungaricus differs from “*Cricetodon*” *fandli* PRIETO, BÖHME et GROSS, 2010, Gratkorn, Austria, early late Sarmatian, MN 7 + 8:

Table 25. Variations in the occurrence of remnant lingual anterolophid in m3 in *Cricetodon hungaricus* from Hasznos. A: not found; B: developed.





		
	A	B
Hasznos	13	3

Table 26. Variations in the form of the mesolophid in m3 in *Cricetodon hungaricus* from Hasznos. A: short, does not reach the posterior surface of the paracone; B: short, or middle developed, but reaches the posterior surface of the metaconid.

		
	A	B
Hasznos	6	10



- in being larger,
- in the less frequent complete anterior ectoloph, in the presence of the mesoloph and funnel structure in M1,
- in the less frequent complete anterior ectoloph, in the presence of the mesoloph and funnel structure and in the presence of the entomesoloph in M2,
- in the presence of the mesoloph, funnel structure, as well as entomesoloph in M3,
- in the better developed labial anterolophid arm, the closed and nonreduced protosinusid, in the more frequent presence of a short mesolophid and ectomesolophid in m1,
- in the better developed labial anterolophid arm and the closed and nonreduced protosinusid, in the presence of a short ectomesolophid in m2 and m3.

Cricetodon hungaricus differs from *Byzantinia* sp. or div. sp., Comănești 1, Romania, early late Sarmatian, MN 7 + 8 (first described as *Hispanomys* cf. *lavocati* and *Hispanomys* cf. *bijugatus* by Feru et al. (1980), later this classification was emended by Hír et al. (2011, 2016, 2017)):

- in the nearly equal anterior and posterior width in M2,
- in the presence of the mesoloph, entomesoloph, and funnel structure in M2 and M3,
- in the better developed labial anterolophid arm and protosinusid and in the occurrence of short mesolophid and ectomesolophid in m1 and m3.

M1 and m2 are not represented in the material from Comănești.

Table 27. Variations in the occurrence of remnant ectomesolophid in m3 in *Cricetodon hungaricus* from Hasznos. A: not found; B: developed.

		
	A	B
Hasznos	14	2

Cricetodon hungaricus differs from *Hispanomys* cf. *bijugatus* from Gaweinstal, Austria, MN 9 (Harzhauser et al. 2011):

- in the presence of the mesoloph, entomesoloph and funnel structure in M1.
- Only one M1 is recorded from Gaweinstal.

Cricetodon hungaricus differs from *Hispanomys* sp. from Nebelberg TGL II and III, Switzerland, MN 9 (it was first published as *Cricetodon* sp. by Rummel and Kálin (2003); later the classification was emended by Engesser and Kálin (2005)):

- in having larger mean measurements,
- in the occurrence of lingual querspur II in M1,
- in the occurrence of better developed anterior ectoloph, mesoloph, funnel structure, protocone spur in upper molars,
- in the presence of the lingual anteroloph in M2 and M3.

Cricetodon hungaricus differs from *C. pasalarensis* (TOBIEN, 1978), Paşalar, Turkey, originally published as MN 6, later the biochronological position was revised as MN 5, local biozone F (Ünay et al. 2003) (for detailed description see Ünay (1990)):

- in being larger,
- in the more frequent complete anterior ectoloph, in the more frequent long mesoloph and in the more frequent complete funnel structure in M1,
- in the more frequent complete anterior ectoloph, in the more frequent long mesoloph and funnel structure, in the presence of the entomesoloph in M2,
- in the presence of the entomesoloph in M3,
- in the more frequent ectomesolophid and in the presence of a short mesolophid in m1,
- in the more frequent short mesolophid in m2,
- in the less frequent lingual anterolophid arm, in the more frequent short mesolophid in m3.

Cricetodon hungaricus differs from *C. candirensis* (TOBIEN, 1978), Çandır, Turkey, originally MN 6, later the biochronological position was revised as MN 5, local biozone F (Ünay et al. 2003) (for detailed description see Rummel (1998) and De Bruijn et al. (2003)):

- in having larger mean measurements,

- in the more frequent lingual transversal spur II (Tab. 28) and in the occurrence of entomesoloph in M1,
- in the presence of the anterior ectoloph, the more frequent long mesoloph and funnel structure in M3 (Tab. 28),
- in the significantly better developed labial anterolophid arm and protosinusid, in the more frequent metalophulid I, in the occurrence of the short mesolophid and ectomesolophid in m1 (Tab. 28),
- in the occurrence of the ectomesolophid in m2,
- in the occurrence of the ectomesolophid, and in the less reduced hypoconid in m3.

Cricetodon hungaricus differs from *C. cariensis* SEN et ÜNAY, 1979, Sariçay, Turkey, MN 7 + 8, local biozone H (Ünay et al. 2003) (for detailed description see Rummel (1998)):

- in having smaller mean measurements,
- in the longer mesoloph, in the larger funnel structure and in the more frequent entomesoloph in M1,
- in the better developed labial anteroloph arm, in the longer mesoloph and in the more frequent entomesoloph in M2,
- in the better developed anteroloph arm, in the more frequent long mesoloph and funnel structure in M3,
- in the position of the anteroconid, which is situated on the longitudinal axis of the tooth crown and not pushed to the labial side, in the better developed labial anterolophid arm and protosinusid, in the more frequent metalophulid I, mesolophid and ectomesolophid in m1.

Cricetodon hungaricus differs from *Byzantinia eskihisarensis* (TOBIEN, 1978), Bayraktepe 1, Turkey, MN 7 + 8, local biozone H (Ünay et al. 2003) (for detailed description see Rummel (1998)):

- in having larger mean measurements, in the lower degree of hypsodonty and in the flat occlusal surface,
- in the narrower anterocone, in the narrower groove between the cusps of the anterocone, in the more frequent lingual transversal spur on the anterolophule, in the absence of a labial-transversal spur on the anterolophule, in the presence of an entomesoloph in M1,
- in the less frequent complete anterior ectoloph, in the less elongated shape, in the more frequent funnel structure, in the almost identical anterior and posterior width in M2,
- in the less reduced posterior part of the tooth crown, in the presence of long mesoloph, funnel structure and entomesoloph in M3,
- in the larger anteroconid, in the better developed lingual anterolophid arm and protosinusid, in the regular presence of metalophulid II, in the more frequent mesolophid in m1,
- in the less elongated shape and in the presence of an ectomesolophid in m2,
- in the less reduced hypoconid and in the presence of an ectomesolophid in m3.

Cricetodon hungaricus differs from *Byzantinia bayraktepensis* ÜNAY, 1980, Bayraktepe I, Turkey, MN 7 + 8,

local biozone H (Ünay et al. 2003) (for detailed description see Rummel (1998)):

- in having larger mean measurements, in the lower degree of hypsodonty, in the flat wear surface,
- in having a narrower groove between the conelets of the anterocone, in the higher frequency of a lingual transversal spur on the anterolophule, in the presence of the mesoloph and funnel structure, in the lower frequency of complete anterior ectoloph in M1,
- in the non-elongated shape, in the better developed lingual anteroloph arm, in the presence of a mesoloph and funnel structure in M2 and M3,
- in the better developed lingual anterolophulid arm and protosinusid, in the regular presence of a metalophulid II, in the more frequent short mesolophid in m1,
- in not being elongated, in the presence of an ectomesolophid, in the absence of a lingual anterolophid arm in m2 and m3.

Cricetodon hungaricus differs from *Byzantinia ozansoyi* ÜNAY, 1980, Bayraktepe I, Turkey, MN 7 + 8, local biozone H (Ünay et al. 2003) (for detailed description see Rummel (1998)):

- in being larger, in the lower degree of hypsodonty, in the flat wear surface,
- in having a narrower groove between the cusps of the anterocone, in the more frequent lingual transversal spur II and funnel structure, in the less frequent complete anterior ectoloph and in the presence of an entomesoloph in M1,
- in the almost identical anterior and posterior width, in the less frequent complete anterior ectoloph and in the more frequent funnel structure in M2,
- in the better developed lingual anteroloph arm, in the less frequent complete anterior ectoloph, in the presence of mesoloph, funnel structure and entomesoloph in M3,
- in the stronger labial anterolophulid arm and protosinusid, in the longer anterolophulid, in the regular presence of a metalophulid II, in the absence of “X-structure” (the junction of metalophulid II, hypolophulid I, protoconid posterior arm and hypoconid anterior arm in the sense of Rummel (1998: 105), in the presence of an ectomesolophid in m1,
- in the less elongated shape, in the presence of an ectomesolophid in m2,
- in the less reduced hypoconid and entoconid, in the presence of an ectomesolophid in m3.

Cricetodon hungaricus differs from *Byzantinia dardanellensis* ÜNAY, 1980, Bayraktepe II, Turkey, MN 9, local biozone I (Ünay et al. 2003):

- in having a lower degree of hypsodonty, in the flat wear surface, in the narrower groove, between the cusps of the anterocone, in the presence of a lingual transversal spur II, mesoloph, funnel structure and entomesoloph, in the less frequent complete anterior ectoloph in M1,
- in the almost identical anterior and posterior width, in the less frequent complete anterior ectoloph in M2,

- in the less elongated shape in M2 and M3,
- in the better developed lingual anteroloph arm in M3,
- in the stronger labial anterolophulid arm and protosinusid, in the regular presence of metalophulid II, in the presence of an ectomesolophid in m1,
- in the less elongated shape, in the narrower metalophulid and hyplophulid, in the presence of an ectomesolophid in m2 and m3,
- in the less reduced hypoconid, in the presence of an ectomesolophid in m3.

Cricetodon hungaricus differs from *Byzantinia nikosi* DE BRUIJN, 1976, Biodrak, Greece, MN 10, local biozone I (Ünay et al. 2003):

- in having larger mean measurements, in the lower degree of hypsodonty, in the flat wear surface,
- in the narrower groove between the cusps of the anterocone, in the less frequent complete anterior ectoloph, in the presence of an entomesoloph in M1,
- in the almost identical anterior and posterior width, in the less frequent complete anterior ectoloph, in the presence of an entomesoloph in M2,
- in the less frequent complete anterior ectoloph, in the presence of mesoloph and entomesoloph in M3,
- in the ridge-like (not cusp-like) mesolophid,
- in the regular presence of metalophulid II, in the narrower metalophulid and hypolophulid in m1,
- in not being elongated, in the narrower metalophulid and hypolophulid, in the presence of an ectomesolophid in m2,
- in the less reduced hypoconid, in the presence of an ectomesolophid in m3.

Cricetodon hungaricus differs from *Byzantinia uenayae* RUMMEL, 1998, Karaözü, Turkey, MN 10 – MN 13, local biozones J, K, L (Ünay et al. 2003):

- in having larger mean measurements, in the lesser degree of hypsodonty, in the flat wear surface, in the narrower and less deep groove between the conelets of the anterocone, in the presence of mesoloph and entomesoloph in M1,
- in the almost identical anterior and posterior width in M2, in the presence of short anterolophule and lingual anteroloph arm, in the presence of anterior ectoloph, mesoloph, entomesoloph, in the presence of a funnel structure in M2 and M3,
- in the better developed labial anterolophulid arm and protosinusid, in the narrower metalophulid and hypolophulid, in the presence of an ectomesolophid in m1,
- in not being elongated, in the presence of better developed labial anterolophulid arm and protosinusid, in the narrower metalophulid and hypolophulid, in the presence of an ectomesolophid, in the less reduced hypoconid in m2 and m3.

Cricetodon hungaricus differs from *Byzantinia pikermiensis* DE BRUIJN, 1976, Pikermi, Greece, MN 12, detailed description given by Rummel (1998):

- in having larger mean measurements, in the lesser degree of hypsodonty, in the flat wear surface, in the

narrower anterocone, in the narrower groove between the cusps of the anterocone, in the presence of funnel structure and entomesoloph in M1,

- in not being elongated, in the almost identical anterior and posterior width, in the better developed lingual anteroloph arm, in the presence of a funnel structure and entomesoloph in M2,
- in not being elongated, protocone not incorporated into the anteroloph, hypocone and metacone not incorporated into the posteroloph in M3,
- in the narrower metalophulid and hyplophulid, the longer anterolophulid, in the presence of an ectomesolophid, in the better developed labial anterolophid arm and protosinusid in m1,
- in the narrower metalophulid and hyplophulid, in the presence of an ectomesolophid, in the better developed labial anterolophid arm and protosinusid,
- in the less elongated shape, in the presence of an ectomesolophid, in the better developed labial anterolophid arm and protosinusid in m3.

Discussion

A comparison of *Cricetodon hungaricus* with the Anatolian Cricetodontini *Cricetodon pasalarensis*, *Cricetodon candirensis* and *Cricetodon cariensis* is of particular interest, De Bruijn et al. (1993, 2003) recognised that *C. hungaricus* from Hasznos strongly resembles *C. candirensis* in size as well as in dental morphology. De Bruijn et al. (1993, 2003) questioned if *C. hungaricus* could be the junior synonym of *C. candirensis*. The only reason to maintain *C. hungaricus* as a separate species is that the mesolophid on the m1 is on average better developed in *C. hungaricus* than in *C. candirensis*. This assumption was rejected by Prieto et al. (2010) and López-Guerrero et al. (2015).

Cladistic analyses (Sen and Erbaeva 2011, Álvarez-Sierra et al. 2014, Çinar-Dirgut and Ünay 2016) also revealed the close relationship between the above mentioned Anatolian species and *C. hungaricus*.

Some researchers defined a number of morphological groups within Cricetodontini. De Bruijn and Ünay (1996) described five groups and they placed *C. hungaricus* into Cricetodontini type 3. Due to the four roots in M1 and M2, the divided anterocone in M1 and the double metalophulid and short mesolophid on m1. *C. pasalarensis* and *C. candirensis* are classified as the same type.

Prieto et al. (2010) suggested six groups. They classified *C. hungaricus*, *C. cf. hungaricus* from Sámsonháza (Hír and Mészáros 2002), *Cricetodon* sp. from Mátraszőlös (Hír and Kókay 2004) and the Anatolian species *C. candirensis*, *C. pasalarensis* and *C. cariensis* into Group 2. However they first described the morphological differences between the Hungarian and Anatolian species: the almost straight labial margin of the M1 in *C. hungaricus* contrary to the sinuous labial contour of the M1 of the Turkish species, and the better developed labial anterolophulid in the m1 of *C. hungaricus*.

López-Guerrero et al. (2014a, b) introduced a three phase model for the description of the morphological evolution of European Cricetodontini. They classified *C. hungaricus* as

Table 28. A comparison of the frequencies of some morphologic elements in *C. candirensis* and *C. hungaricus*.

Character	<i>C. candirensis</i>	<i>C. hungaricus</i>
M1		
Lingual transversal spur II	33%	79%
Funnel structure	82%	77%
M2		
Funnel structure	39%	56%
M3		
Funnel structure	30%	84%
Long mesoloph	30%	84%
m1		
Labial anterolophid arm and protosinusid	missing	well developed
Mesolophid, ectomesolophid	missing	frequent

a phase of basal morphology together with *C. meini* from Mühlbach and Grund (Daxner-Höck 2003), Litke (Hír 2013) and *C. cf. hungaricus* from Sámsonháza (Hír and Mészáros 2002). López-Guerrero et al. (2014b) explained this grouping as being due to the low development of ectolophs and absence of metalophulid I in *C. hungaricus*. However, the last statement is not true. The placing of *C. hungaricus* and *C. meini* in the same morphological group is questionable because of the substantial morphological differences which are described above in the comparison. The differences between the two species are also clearly mirrored in the cladistic analyses (Sen and Erbaeva 2011, Çinar Durgut and Ünay 2016).

In addition to Hasznos, *C. hungaricus* was also reported from Szentendre, Hungary (Kordos 1986), Brajkovac, Serbia (Marković and Milivojević 2010) and recently from Zambal, Turkey (De Bruijn et al. 2013). *Cricetodon cf. hungaricus* from Sámsonháza (Hír and Mészáros 2002) differs from the type material from Hasznos only in some of the above described morphological details. The measurements of the finds from Sámsonháza are very similar to the dimensions of the population from Hasznos. Hír and Mészáros (2002) explained the Sámsonháza material as a local descendant of the typical *C. hungaricus*. The two localities are close to each other in time (middle Badenian) and in space (10 km).

With regard to the palaeoenvironmental condition in Hasznos, it is worth mentioning that *Cricetodon* teeth are the dominant elements in the fossil rodent assemblage. In addition the forest elements (glirids, flying squirrels) are very rare and eomyids are almost completely absent. The preference for an arid climate is generally attributed to *Cricetodon* (De Bruijn and Ünay 1996, Daxner-Höck 2003). However, the insectivores are very diverse. According to Prieto et al. (2015) “the assemblage does not indicate very moist conditions”. The eulipotyphlan fauna of Sámsonháza 3 points to a humid, though not overly wet environment (Prieto et al. 2012).

The possibility of a semiarid climate with more than 6 dry months/year during the early- and middle Badenian of the Pannonian region is supported by the herpetofaunas of Litke (Venczel and Hír 2015).

Prieto et al. (2015) and Hír et al. (2016, 2017) postulated a westward shifting of some faunal elements because some rodent (e.g. *Palaeosciurus ultimus*) and insectivore species (e.g. *Desmanodon* aff. *crocheti*) and bats (e.g. *Myotis bavaricus*) (Rosina et al. 2015) already present in the Middle Badenian of Hungary (Hasznos and Sámsonháza) are also found as far as western Europe in the late Badenian.

It seems that *Cricetodon hungaricus* did not take part in this migration. Up to the present time no possible candidate is known among the *Cricetodon* species in Germany, Switzerland and in Western Europe which could be regarded as a descendant of *Cricetodon hungaricus*.

Conclusions

Cricetodon hungaricus (KORDOS, 1986) is the only Cricetodontini from the middle Badenian of Hungary. The species shows a mosaic of primitive (cusps and cuspids are more highly developed than lophs and lophids, the regular presence of metalophulid II in m1 and presence of mesolophs, mesolophids, entomesolophs, ectomesolophids, non reduced M3 and m3, distinct hypocone and metacone in M3), and progressive characters (divided anterocone in M1, frequent posterior ectoloph in upper molars, relative large dimensions).

Earlier researchers (De Bruijn et al. 1993, 2003, Sen and Erbajeva 2011, Álvarez-Sierra et al. 2014, Çinar Durgut and Ünay 2016) emphasised the close relationship between *Cricetodon hungaricus* and the Middle Miocene Anatolian *Cricetodon* species, especially with *Cricetodon candirensis*. De Bruijn et al. (1993, 2003) went as far as to suggest that *C. hungaricus* should be synonymised with *C. candirensis*.

The detailed morphological study presented herein allows us to recognise that there are significant morphometric differences which discriminate between the two species. It can be concluded that *C. candirensis* and *C. hungaricus* are close relatives, but a direct ancestor-descendant connection or even a conspecific relationship is not probable.

C. hungaricus is the dominant element of the Hasznos fauna which indicates the climate was not very moist or could even have been semiarid. A similar conclusion was drawn from the study of insectivores (Prieto et al. 2015, Hír et al. 2016).

C. hungaricus probably migrated from Asia Minor into the Carpathian region across the Balkans. At present, no data indicates any further westward migration of the species.

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