



REDESCRIPTION OF THE TYPE SPECIMEN OF *CSAKVAROMYS SCIURINUS* (RODENTIA, SCIURIDAE, XERINAE) FROM THE LATE MIOCENE OF HUNGARY AND ITS BEARING ON THE SYSTEMATICS OF EARLY GROUND SQUIRRELS

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Abstract: *Csakvaromys sciurinus* is an enigmatic stem ground squirrel from the Late Miocene of Hungary that has previously only been briefly described. The restudy of the holotype allows a detailed redescription and comparison with different xerines. *Csakvaromys sciurinus* is recognized as a junior synonym of *Csakvaromys bredai* and diagnosed by the following combination of characters: medium size, close to the maximum limits of *C. bredai*; massive body of the mandible with deep diastemal portion and shallow diastemal depression; elevated area of the mental foramen; nonconfluent lower and upper masseteric crests separated by the attachment area for the anterior fibers of the anterior deep masseter muscle; transversely compressed lower incisor with longitudinally striated anterior enamel face; and brachyodont cheek teeth with mesoconids, rudimentary entoconids, and well-developed anteroconulid of p4.

Key words: *Csakvaromys*, Sciuridae, ground squirrels, Miocene, taxonomy

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Introduction

In 1951, M. Kretzoi described a new sciurid genus and species “*Csákváromys sciurinus*” based on a single specimen – an incomplete mandible of an old individual found within the *Hipparion* fauna of the Csákvár fossil site near Budapest, Hungary (Kretzoi 1951). The specimen was only briefly described and not figured. Its sciurid affinities were explicitly recognized by the author three years later after the discovery of an isolated p4 purportedly belonging to the taxon (Kretzoi 1954).

Since the original description, the holotype has been restudied by Gromov et al. (1965) who, for the first time, illustrated the specimen and recognized its affinities with ground squirrels by tentatively ascribing *C. sciurinus* to the living South Asian rock squirrels of the genus *Sciurotamias* MILNE-EDWARDS, 1867, as *S. (Cszakvaromys) sciurinus*. Although lacking information on many significant regions of the mandible, this contribution remains the best description of *Cszakvaromys sciurinus*.

A new interest in the taxon was triggered by Kretzoi and Fejfar (2005) who synonymized *Cszakvaromys* and *Spermophilinus* DE BRUIJN et MEIN, 1968, a widespread European Neogene ground squirrel. This decision was questioned by De Bruijn and Bosma (2012), who, among other arguments against *Cszakvaromys* priority over *Spermophilinus*, mentioned that (De Bruijn and Bosma 2012: 319) “the type material of *Cszakvaromys sciurinus* is obviously too poor for identification at the species level”.

After Gromov et al.’s (1965) appraisal, no published source has considered the actual holotype. Almost sixty years later, *Cszakvaromys sciurinus* remains one of the most enigmatic fossil sciurids. It is also of great importance for resolving early ground squirrel systematics. This work requires the morphological and taxonomic reanalysis of the holotype as well as reexamination of the taxonomic assignments of *Cszakvaromys sciurinus*. The goal of the present contribution is to redescribe the original historic type specimen of *Cszakvaromys sciurinus* in a modern context, given our recent advances in paleontological data analyzes

and sciurid osteology and systematics, and to review the alpha taxonomy of this taxon.

Materials and methods

The specimen

The holotype of *Csakvaromys sciurinus*, a right mandible (SARA V 2024.11.1; originally catalogued as F.I.V. 6003) from the Late Miocene (presumably, late Tortonian) sediments of Esterházy-Cave near Csákvár, district Fejér, Hungary, is curated in the collections of the SARA Geological Survey, Budapest.

CT scanning and rendering

The specimen was CT-scanned in the Palaeontological department of the National Museum in Prague, using Nikon XTH 160 micro-CT scanner. The three-dimensional data sets were acquired with a source voltage of 70 kV, a source current of 141 μ Ae (Cu radiation, Al filter), an exposure time of 5.3 seconds, an image rotation angle of 0.4 deg, and a resolution of 13.55 μ m. The specimen was scanned in a three-slice mode. The final slices were combined during a single rotation using the NRecon software package. A total of 2211 individual transversal slices with a matrix size of 2000 \times 2000 pixels were exported into 8 bit TIFF image stacks. The post-processing of the two-dimensional raster images into three-dimensional reconstructions and segmentations was conducted using Avizo 8.1.1 and Slicer 5.2.2.

Measurements and terminology

Measurements were taken to the nearest 0.01 mm from original specimens using hand-held calipers or digital models using the measurement tool in Avizo 8.1.1., and follow the measurement methodology by Van de Weerd (1976) for dental specimens and Sinitsa et al. (2022) for the mandible. The dental nomenclature follows that employed by Sinitsa (2018) and Sinitsa and Pogodina (2019). The classification of Sciuridae follows Steppan et al. (2004) and Thorington and Hoffmann (2005). Subtribal- and generic-level systematics of Marmotini follow Sinitsa et al. (2022). The timescale and stratigraphic frameworks follow Hilgen et al. (2012).

Institutional abbreviations

ML, Musée des Confluences, Lyon, France; NMB, Naturhistorisches Museum Basel, Switzerland; NMNHU-P, Paleontological museum, National Museum of Natural History, National Academy of Sciences of Ukraine, Kyiv; SARA GS, Supervisory Authority for Regulatory Affairs – Geological Survey, Budapest, Hungary; ZIN, Laboratory of Theriology, Zoological Institute, Russian Academy of Sciences, Saint Petersburg, Russia.

Nomenclatural background

The name-bearing eligibility of the holotype revised here has been the subject of much controversy and debate. This is especially true in the context of the genus *Spermophilinus*

described by De Bruijn and Mein (1968) with *Sciurus bredai* as type species and the subsequent synonymization of the species *sciurinus* with *bredai* by Kretzoi and Fejfar (2005).

The holotype was designated by Kretzoi (1951) when describing a new genus and species named *Csakvaromys sciurinus* from the Late Miocene locality of Csákvár (Hungary). The description fulfills the mandatory provisions of Articles 13.1 and 13.3 (ICZN 1999), and both species- and genus-group names are available. The type species of the genus is *C. sciurinus* fixed by monotypy (Article 68.3; ICZN 1999). *Csakvaromys* and/or *sciurinus* have/has often been used as valid (i.e., as the oldest available names applied to the taxon; Article 23.1 of ICZN 1999) in the literature; e.g., in Kretzoi (1954, 1987), Gromov et al. (1965), Topachevsky (1971), Kretzoi et al. (1976), Gromov and Baranova (1981), Lungu (1981), Rabeder (1985, 1989), Kretzoi and Fejfar (2005), Hulva et al. (2007), Nicoara (2011), Sinitsa (2011), Kryštufek and Vohralík (2013).

The turning points, however, were the aforementioned work by De Bruijn and Mein (1968), in which they erected a new genus, *Spermophilinus*, with *Sciurus bredai* as the type species, and the subsequent revision of the sciurid material from Rudabanya (early Vallesian ELMA, Hungary) by Kretzoi and Fejfar (2005), in which they synonymized the species *sciurinus* with *bredai* and the genus *Spermophilinus* with *Csakvaromys*.

The description of the genus *Spermophilinus* fulfills the mandatory provisions of Article 13.3 (ICZN 1999) and the genus-group name is available. The first usage of the species group name “*bredai*” is in Meyer (1848: 472) and has been taken as available by many authors. However, this mention lacks any description, definition, or indication. Meyer (1848) only reports the presence of a new rodent “*Sciurus Bredai*” [sic] from “Oeningen”. Therefore, this usage fails to conform to Article 12 of ICZN (1999) and the name must be regarded as a nomen nudum. The name was first made available in the sense of Article 12 (ICZN 1999) by Schlosser (1884: 88), who provided dimensions and a brief description of the original specimen from Meyer’s van Breda collection (Major 1899). The availability of the name in Schlosser (1884) was noted by Black (1966: 52). The species was established based on a single specimen, a partially articulated skeleton (Major 1899: pl. XVII), which, in accordance with Article 73.1.2 (ICZN 1999), is to be regarded as the holotype fixed by monotypy. The type specimen should currently be curated in the collections of the British Natural History Museum (Lydekker 1885, Major 1899, Black 1966). For a considerable period, the name “*bredai*” was combined with the genus-group name *Sciurus* LINNAEUS, 1758 (Lartet 1851, Schlosser 1884, Lydekker 1885, Depéret 1887, 1892, Major 1893, Dechaseaux 1946, Wilson 1960, Black 1963, 1966, Sulimski 1964, Kowalski 1967, Engesser 1972) or *Heterosciurus* TROUESSART, 1880 (Trouessart 1897). After the description of the genus *Spermophilinus* by De Bruijn and Mein (1968), the name was often used in combination with this generic name (e.g., Bachmayer and Wilson 1970, Daxner-Höck 1975, 2010, Van de Weerd 1976, De Bruijn et al. 1980, Cuenca Bescós 1988, Flynn and Jacobs 1990, Aldana Carrasco 1992, Adrover et al. 1993, De Bruijn 1995, 1998, 1999, Kálin and Engesser 2001, Casanovas-Vilar 2007, Bosma et al. 2013, 2019,



Text-fig. 1. *Csakvaromys* “*sciurinus*”, holotype, SARA V 2024.11.1, right mandible from Csákvár, Late Miocene, Hungary. a: Lateral view. b: Medial view. c: Dorsal view. d: Ventral view. e: Lower incisor whitened with ammonium chloride in ventral view. f: Lower tooththrow (p4–m3) whitened with ammonium chloride in direct occlusal view. g: Original label associated with the specimen.

Maridet et al. 2014, Freudenthal and Martín-Suaréz 2015, Qiu and Li 2016, Hír et al. 2016, Li et al. 2020, Prieto et al. 2020, Gusovsky and Sinitsa 2021).

The “usage” of the generic name *Csakvaromys* was questioned by De Bruijn and Bosma (2012). The ambiguities pertaining to the validity of the generic name *Csakvaromys* were discussed in detail and elucidated by Sinitsa et al. (2022). Within the present taxonomic state of the art, the genus-group name *Csakvaromys* has to be regarded, in the sense of the Principle of Priority (sensu Article 23.1, ICZN 1999), as the oldest available name applicable to the genus; which means, it is valid. In other words, the name *Spermophilinus* DE BRUIJN ET MEIN, 1968 has to be regarded as a subjective junior synonym of *Csakvaromys* KRETZOI, 1951.

Description

The specimen SARA V 2024.11.1 is represented by an incomplete right mandible (dentary) belonging to an old individual with heavily worn cheek teeth, corresponding to the wear stage of a two and a half – three years old individual in red squirrels (*Sciurus vulgaris*). It lacks the anteriormost tip of the diastemal portion, the main parts of the coronoid, condylar, and angular processes (Text-fig. 1a–d). Both the incisor and the cheek teeth have suffered some post-burial damage.

The mandibular body consists of a sturdy cheek teeth-bearing part and an elongated diastemal portion, which

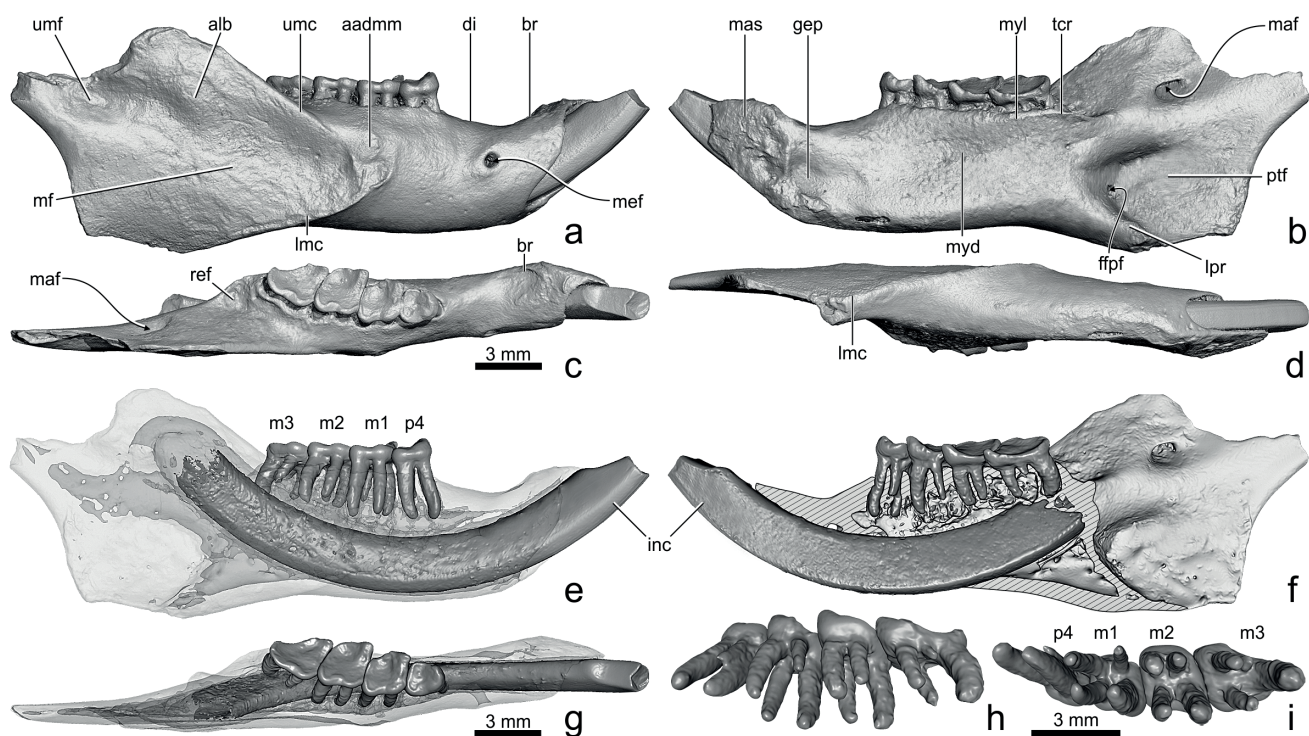
constitutes 49.3 % of the entire mandibular body length measured from the anteriormost tip of the mandible to the posterior rim of the ultimate m3 alveolus. The body is deepest beneath p4 (5.81 mm measured on the medial side of the mandible); the posterior portion of the body, beneath m3 is somewhat shallower (5.12 mm). In lateral view (Text-fig. 2a), the ventral margin of the body is sinuous: convex ventrally in the anterior half and concave dorsally in the posterior half. The diastemal portion of the mandible is moderately elongated (7.90 mm long) and relatively deep. The difference in depth between the deepest (5.48 mm dorsoventrally) and the shallowest (4.42 mm) parts of this area of the mandible is 19.3 %, which results in a relatively shallow diastemal depression. The dorsal margin of the diastemal portion is a crescent concavity that slopes gently anteroventrally away from p4 and does not possess the pronounced step that marks the posterior end of the diastema in most sciurids. Anteriorly, the dorsal side of the diastema bears a clearly discernible horseshoe-shaped scar for the anterior mandibular portion of the buccinator muscle. Seen dorsally (Text-fig. 2c), the scar appears as an indentation accentuated anteriorly by a prominent ridge that gradually diminishes posteriorly before reaching the mid-length of the diastema. The most conspicuous structure on the lateral side of the diastemal area is a single mental foramen located slightly dorsal to the mid-depth level and mid-way between the rim of the incisor alveolus and p4 (Text-fig. 2a). The opening is almost circular in outline (although slightly

longer than wide), about 0.7 mm in maximum diameter, and opens anterolaterally. The bony surface around the foramen is notably elevated (Text-fig. 2a, c). A smooth, albeit wide, longitudinal eminence extends anterodorsally from the dorsal rim of this elevation towards the anterodorsal aspect of the diastemal portion. On the ventrolateral side of the diastemal portion, there are several tiny (less than 0.1 mm in diameter) nutritive foramina. The medial side of the diastemal portion is dominated by an extensive facet of the mandibular symphysis, which occupies about half of its surface (Text-fig. 2b). The facet is comma-shaped, with a vast, elliptical body anteriorly and an elongate, narrowing tail extending posteroventrally from the ventral side of the head along the ventral margin of the diastemal portion. Adjacent to the dorsal edge of the tail is a pronounced depression of a genioglossal pit (Text-fig. 2b), located approximately at the mid-length of the diastemal region. The specimen lacks a scar for the anterior mandibular portion of the buccinator muscle that is generally present anteromedial to the p4 alveolus in most Marmotini xerines, including some specimens of *C. bredai* (Sinitsa et al. 2022). The main, cheek teeth-bearing part of the mandibular body is roughly rectangular in lateral view, with straightened dorsal and ventral margins (Text-fig. 2a). The masseteric fossa is a moderately excavated depression delimited dorsally and ventrally by well-developed upper and lower masseteric crests that converge anteriorly at an angle of 54°. The obtuse anterior edge of the fossa, defined by a prominent lower masseteric crest, ends level with the anterior portion of m1. The anterior 1.7 mm of the masseteric fossa, confined between the anteriormost areas of the lower and upper masseteric crests, is an attachment area for the anterior fibers of the anterior deep masseter muscle. It is slightly taller than long and consists of a roughly equally elevated dorsal half and depressed ventral half. Apart from a barely discernible dorsal concavity at the contact with the upper masseteric crest, the lower masseteric crest is gently convex ventrally and robust. Viewed dorsally (Text-fig. 2c), the lower crest appears about three times taller on the lateral side of the mandible than the upper crest. The latter is subvertical in its anterior part and oblique in its posterior part, with a 138° angle between them. Extending posterodorsally, the crest passes uninterrupted along the anterior margin of the coronoid process. The bottom of the masseteric fossa is rugose and bears several vascular foramina associated with posteriorly directed grooves and subhorizontal smooth crests left by fibers of the posterior deep masseter muscle roughly at the transition between the mandibular body and angular process. On the medial side of the mandibular body is the smooth, anteroposteriorly long and vast area of the mylohyoid depression (Text-fig. 2b). The concavity is approximately 7 mm long and 3.5 mm deep. The ventral border of the depression is smooth to almost indiscernible, whereas its dorsal limit is somewhat accentuated by a mylohyoid line. Extending posteriorly, the line becomes sharper and stretches along the ventral slope of a prominent temporal crest. The crest extends posteriorly from the posterolingual side of m3 towards the masseteric foramen thus forming the medial wall of a well-excavated retromolar triangle (fossa). The fossa is roundly triangular in dorsal view (Text-fig. 2c). Its lateral wall is formed by the medial face of the coronoid process. The process is

not well preserved in SARA V 2024.11.1. The straight anterior margin of the process rises gently lateral to m3 at a 145° angle between the anterior edge of the process and the base of the tooth row. The lateral and medial sides of the preserved part of the process are slightly depressed by the attachment areas for the zygomaticomandibularis and temporal muscles respectively. The depression on the lateral surface of the process is delimited ventrally by a smooth and shallow alveolar bulge. Posteriorly, the bulge extends onto the condylar process. The entire lateral side of the preserved part of the process is occupied by a vast and deep upper masseteric fossa (Text-fig. 2a). The medial surface of the process is gently elevated. Some 4.20 mm posterior to the ultimate m3 alveolus is an elliptical, anteroposteriorly elongated (about 1.4 mm long and 0.75 mm tall) mandibular foramen (Text-fig. 2b). The opening is directed posteroventrally and slightly medially, so its posteroventral rim appears relatively smooth when compared with the sharp anterodorsal rim that forms the medial wall of the mandibular canal at its posteriormost aspect. As is typical for generalized marmotines, the angular process of SARA V 2024.11.1 is somewhat anteroposteriorly shortened and slightly deflected medially. In lateral view (Text-fig. 2a), the virtually straight anterior side of the process is defined by the sharp posterior half of the lower masseteric crest. Apart from the crest, the remainder of the preserved lateral side of the process appears featureless. The medial surface of the process is dominated by an expansive pterygoid fossa (Text-fig. 2b). Ventrally, the fossa is contoured by a massive lower pterygoid ridge. The ridge expands anteriorly and seamlessly continues into the mandibular body. Anterodorsally, the ridge connects with the smooth upper pterygoid crest that fades out about half way to the angular incisure. The anterior corner of the pterygoid fossa is pierced by a circular nutritive foramen, probably accompanied by smaller openings not discernible in mCT images.

The lower incisor is almost complete, only its anteriormost tip is broken off. The incisor is narrow transversely and flattened anteriorly and medially (L – 2.51 mm, W – 1.44 mm). The lateral and posterior walls are evenly convex. A thin enamel layer covers the anterior side, extending up to about one-third of the lateral side; it has a very short overlap onto the medial wall (Text-fig. 2a, b). The enamel surface is complicated by four complete and one incomplete thin enamel ridges extending parallel to the labial side of the anterior wall (Text-fig. 1e). The remainder of the enamel surface is featureless. Based on the CT scans, the incisor extends posteriorly to the level of mandibular foramen, where its alveolar capsule forms a smooth alveolar bulge visible on the lateral surface of the mandible (Text-fig. 2e–g).

The lower dentition of SARA V 2024.11.1 is heavily worn and, therefore, provides rather limited information on the cheek teeth morphology of the specimen (Text-fig. 1f). The p4 has roundly triangular outlines, with a rounded anterior side, flattened posterior and lingual sides, and laterally expansive labial side (L – 1.72 mm, W – 1.50 mm). The anterior, trigonid portion of the crown is 13.5 % narrower than the talonid portion (trigonid W – 1.28, talonid W – 1.48). The four principal cusps, namely the metaconid, protoconid, hypoconid, and entoconid are discernible.



Text-fig. 2. *Csakvaromys "sciurinus"*, holotype, SARA V 2024.11.1, digitally restored right mandible from Csákvár, Late Miocene, Hungary. a: Lateral view. b: Medial view. c: Dorsal view. d: Ventral view. e: Dentition inside translucent mandible in lateral view. f: Mandible with virtually removed medial side showing the incisor and cheek teeth. g: Dentition inside translucent mandible in dorsal view. h: Lower tooththrow in oblique ventromedial view. i: Same as (h) in a direct ventral view. Abbreviations: aadmm – attachment area for anterior fibers of anterior deep masseter muscle, alb – alveolar bulge, br – buccinator ridge, di – lower diastema, ffpf – foramina in anteromedial corner of pterygoid fossa, gep – genioglossal pit, inc – lower incisor, lmc – lower masseteric crest, lpr – lower pterygoid ridge, maf – mandibular foramen, mas – mandibular symphysis, mef – mental foramen, mf – masseteric fossa, myd – mylohyoid depression, myl – mylohyoid line, ptf – pterygoid fossa, ref – retromolar fossa, tcr – temporal crest, umc – upper masseteric crest.

The trigonid is approximately 30 % taller than the talonid (Text-fig. 2a, b, e, f). The metaconid is the anteriormost and the tallest cusp with a fairly rounded anterolingual side. Laterally, the cusp abuts a circular protoconid, positioned slightly more posteriorly than its lingual counterpart. The sharply defined remnant of the trigonid basin exhibits a prominent peg-like anteroconulid. The cuspid is free and does not form either labial or lingual anterolophids. Another deep reentrant, the sinusid, is evident between the protoconid and the hypoconid. The bottom of the sinusid is smooth. The opposite, lingual side of the crown shows a somewhat narrower, albeit deep, lingual sinusid that partially divides the bases of the metaconid and entoconid. A low entoconid forms the posterolingual corner of the occlusal surface. There are two major roots supporting the crown: the taller anterior root and the somewhat shorter, but transversely wider posterior root (Text-fig. 2e–i). The medial wall of the latter bears the third vestigial root partially divided from it by a smooth vertical groove.

The m1 is rectangular in occlusal view (Text-fig. 1f). The crown gently tapers anteriorly (L – 1.92 mm, W – 2.09 mm), being slightly wider posteriorly. The anterior and labial walls of the crown are concave, the posterior wall is straight. The metaconid is the tallest cusp, about 30 % higher than the protoconid and 35% higher than the hypoconid (Text-fig. 2a, b, e, f). The entire anterior wall of the crown is formed by a relatively thin anterolophid connecting the metaconid

and the protoconid. The ridge continues seamlessly into an anteroposteriorly compressed and triangular metaconid, whereas the area of the contact between the anterolophid and protoconid is complicated by a weak anterosinusid on the anterolabial corner of the occlusal surface. The labial pair of cusps, namely the protoconid and the hypoconid, are subcircular and equally large when viewed from the occlusal aspect. A smooth sinusid indents the labial side of the crown. There is a barely discernible labial protrusion of the ectolophid indicating the presence of a mesoconid on m1. The central part of the occlusal surface is heavily worn, but does exhibit smooth enamel in the talonid basin and a tiny enamel island on the anterior aspect of the occlusal surface that represents the remains of a trigonid basin. This basin was delimited posteriorly by a thin and, purportedly, weak metalophid. The tooth has four distinct roots: three equally developed long roots supporting the metaconid, protoconid, and hypoconid, and a weaker fourth root beneath the entoconid (Text-fig. 2e–i).

The m2 is substantially wider than m1, mediolaterally widened in occlusal view (Text-fig. 1f), with almost equal trigonid and talonid halves (L – 2.06 mm, W – 2.51 mm; trigonid W – 2.30 mm, talonid W – 2.37 mm). The posterolingual corner of the crown is not reduced, whereas the entoconid is discernible neither in occlusal nor in lingual views. The metaconid is the tallest cusp, followed by the hypoconid and the protoconid (Text-fig. 2a, b, e, f). The two

labial cusps are almost identical in overall shape and height (Text-fig. 2a, e). The anterolophid is more robust than in m1. Extending laterally from an anteroposteriorly compressed metaconid, the ridge widens gradually to fuse with the lingual side of the protoconid. There are no discernible remnants of the trigonid basin or metalophid on the occlusal surface of m2. The sinusid appears somewhat wider and deeper than in m1. The ectolophid is devoid of the distinguishable traits of the mesoconid. The posterolingual side of the occlusal surface is formed by a complete posterolophid, which extends onto the lingual wall of the crown and continues anteriorly as a prominent entoconid ridge, and, finally, fuses with an elliptical mesostylid. A vast and essentially featureless talonid basin opens medially via a narrow lingual sinusid. The root structure of m2 is similar to that of the first molar (Text-fig. 2e–i). The only real distinctions between these molars are in the relatively weaker metaconid root and a somewhat more robust entoconid root in m2.

The m3 is the largest of the cheek teeth (L–2.45 mm; W–2.34 mm), roundly triangular to rectangular in occlusal view (Text-fig. 1f). The hypoconid is not shifted externally; the angle between the anterior and the labial walls of the crown is 86°. As in the preceding molars, the metaconid appears about 40 % taller than the labial cusps (Text-fig. 2a, b, e, f). Due to heavy wear, these latter cusps are not discernible in a direct lateral view (Text-fig. 2a, e). Viewed occlusally (Text-fig. 1f), they demonstrate rounded labial walls separated by a wide and nearly trapeziform sinus, which, in turn, shows no further morphological structures. The posterolingual side of the crown is broken off, so that the shape and size of the entoconid cannot be assessed. However, based on data from the m2, we assume that the entoconid was not discernible as a distinct cusp in m3. The anterolabial corner of the crown is notable due to a heavily worn metaconid and the remnant of a small cuspid interpreted here as a mesostylid. The enamel layer of the occlusal surface is worn away and preserved only on the anterior part of the crown as a triangular island between the trigonid cusp. The characteristic shape of the enamel island implies the absence of a metaloph in this specimen. The base of the crown is supported by a strong posterior root positioned roughly beneath the hypoconid, a very weak posterolingual root beneath the entoconid, and two moderately developed cylindrical roots representing the trigonid root system (Text-fig. 2e–i).

Comparisons

The results of this morphological description and analysis demonstrate that SARA V 2024.11.1 belonged to a marmotine ground squirrel, as evidenced by the following combination of characters: an elongated and moderately deep mandibular body with a stout diastemal portion having a shallow diastemal depression, nonconfluent lower and upper masseteric crests of the mandible separated by the attachment area for the anterior fibers of the anterior deep masseter muscle, transversely compressed lower incisor with longitudinally striated anterior enamel surface, brachyodont cheek teeth with rudimentary entoconid and well-developed mesoconid. In the following section, we compare SARA V 2024.11.1 to the currently known taxa of Eurasian stem Marmotini.

With *Palaeosciurus*

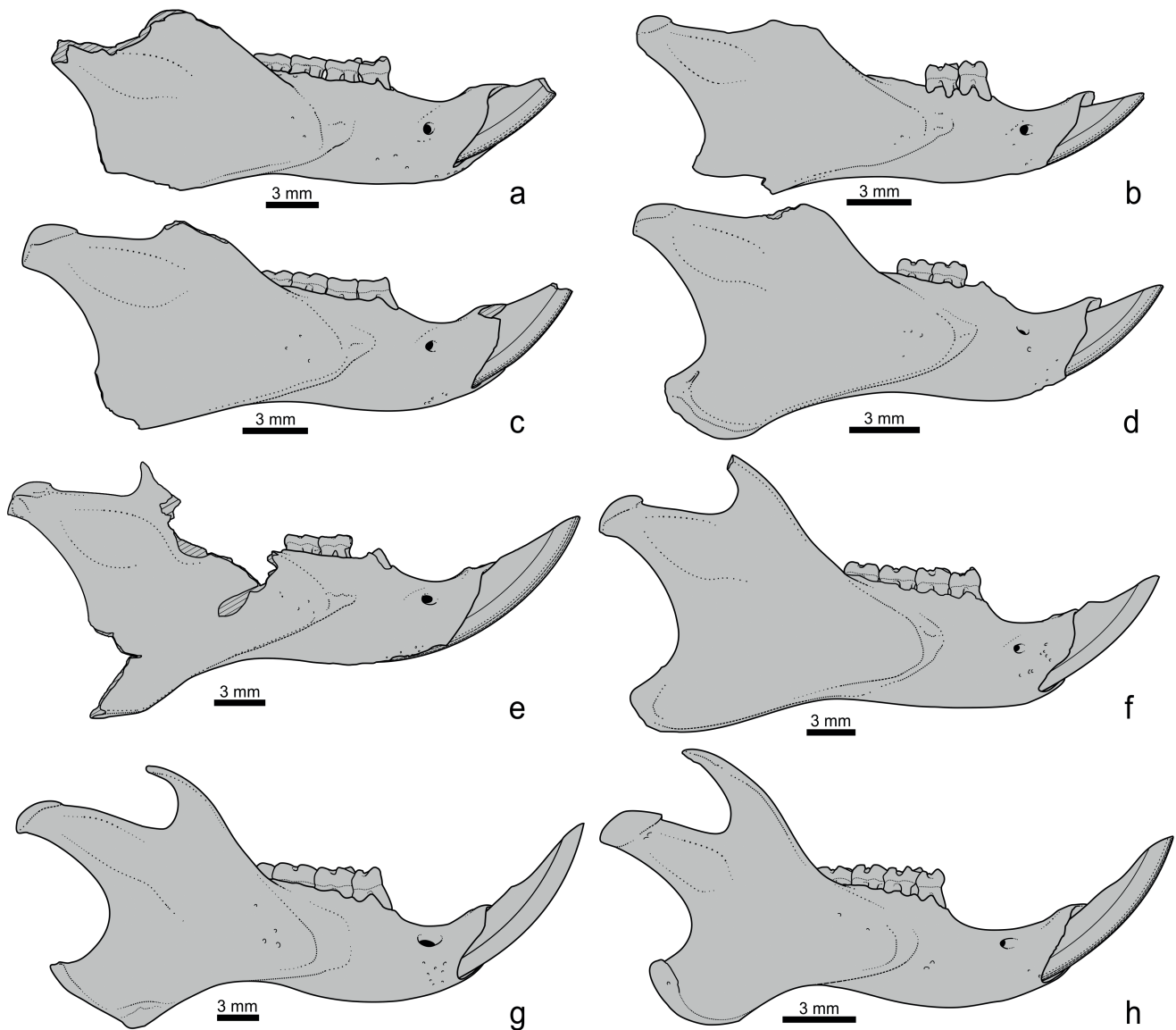
The rise of ground squirrels in Eurasia is associated with the genus *Palaeosciurus* POMEL, 1853 known from the early Oligocene – Middle Miocene of Europe and Eastern Asia (Vianey-Liaud 1974, De Bruijn 1999, Qiu and Li 2016, Bosma et al. 2019). The morphology of the mandible and lower dentition of the genus is illustrated by *P. goti* VIANEY-LIAUD, 1974 – the earliest representative of the genus from the early Oligocene (early Suevian ELMA) localities of Quercy, France (Vianey-Liaud 1974); and, more importantly, the exclusively well-preserved and abundant specimens of the type species *P. feignouxii* POMEL, 1853 from the Early Miocene (Agenian ELMA) of Allier fossil sites in central France (Filhol 1879, Dechaseaux 1946). Despite the obvious similarities between SARA V 2024.11.1 and *Palaeosciurus*, there are a number of striking differences (Text-fig. 3a, f). For example, compared to *Palaeosciurus* the mandible of SARA V 2024.11.1 has: a smaller size, a shallower mandibular body with a longer diastemal portion, and a shallower diastemal depression; a more prominent (anteroposteriorly longer) attachment area for the anterior fibers of the anterior deep masseter muscle; a more robust lower masseteric ridge; and a more inflated area of the mental foramen. The dental differences are: a prominent anteroconulid on p4, weaker mesostylid in m2, and, striated incisor enamel in SARA V 2024.11.1.

With *Sciurotamias*

A relationship between *Csakvaromys sciurinus* (SARA V 2024.11.1) and Chinese rock squirrels (genus *Sciurotamias*) has been proposed. In particular, Gromov et al. (1965) ascribed the species to *Sciurotamias* as *S. (Cskavaromys) sciurinus*. Although SARA V 2024.11.1 shares many mandibular features with *S. davidianus* (MILNE-EDWARDS, 1867) (Text-fig. 3g) and *S. forresti* (THOMAS, 1922), it clearly differs from these taxa in numerous ways, including: smaller size, a shallower diastemal depression, a less convex mandibular body, a mental foramen surrounded by an enlarged rim positioned approximately mid-depth on the diastemal portion (the opening in *Sciurotamias*, is placed more dorsally on the mandible), a more pronounced attachment area for the anterior fibers of the anterior deep masseter muscle, a more prominent lower masseteric ridge located more dorsally than in *Sciurotamias*, a masseteric fossa that sharply tapers anteriorly, a more horizontal anterior edge on the angular process, and a wider (dorsoventrally high) condylar process. The lower dentition of SARA V 2024.11.1, when compared with *Sciurotamias* (Text-fig. 3a, g) appears more generalized and has proportionally smaller dimensions (in both *S. davidianus* and *S. forresti*, the lower toothrow is larger so that the condyloid process overlays m3 in lateral aspect), less robust cheek teeth with wider sinusids and a more prominent anteroconulid of p4, and a narrower incisor with striated enamel.

With chipmunks

Living Tamiina, the chipmunks of North America and Eurasia, include 25 species in three genera: *Eutamias* TROUËSSART, 1880, *Neotamias* HOWELL, 1929, and *Tamias* ILLIGER, 1811 (Thorington et al. 2012). Both molecular and



Text-fig. 3. Mandibles of Eurasian stem marmotine ground squirrels, in right lateral view, scaled to approximately the same tooththrow length. a: *Cskvaromys* “*sciurinus*”, Late Miocene, Csákvár (SARA V 2024.11.1). b: *Cskvaromys bredai*, Middle Miocene, La Grive (ML LGR 97). c: *Cskvaromys bredai*, Middle Miocene, La Grive (ML LGR 93). d: *Cskvaromys bredai*, Middle Miocene, La Grive (ML, uncatalogued). e: *Cskvaromys bredai*, Late Miocene, Grytsiv (NMNHUP 22–2718). f: *Palaeosciurus feignouxii*, Early Miocene, Montaignu-le-Blin (NMB M.A. 5290). g: *Sciurotamias davidianus*, recent, China (ZIN 3585). h: *Eutamias sibiricus*, recent, Russia (ZIN 88523).

morphology-based analyses place chipmunks among the stem Marmotini (Piaggio and Spicer 2000, Zelditch et al. 2015, Patterson and Norris 2016, Sinitza et al. 2022). We made comparisons with *Eutamias sibiricus* (LAXMANN, 1769), the only Eurasian species of Tamiina with reasonably well-known craniodental morphology (Text-fig. 3h). Some characters present in *Eutamias* also occur in SARA V 2024.11.1: a shallow diastemal depression, low-crowned brachyodont cheek teeth, and striated incisor enamel. However, the mandible and dentition of SARA V 2024.11.1 clearly differ from those of *E. sibiricus* in: being larger, having a relatively shorter diastemal portion of the mandible with an elevated and less dorsally located mental foramen, a well-developed attachment area for the anterior fibers of the anterior deep masseter muscle, a more horizontally oriented angular process, and a deeper condylar process. In summary, the comparisons above show no specific similarities

between SARA V 2024.11.1 and the genera *Palaeosciurus*, *Sciurotamias*, and *Eutamias*.

With the species of *Cskvaromys*

Of the six currently known species of *Cskvaromys*, *C. besanus* (CUENCA BESCÓS, 1988), *C. bredai* (SCHLOSSER, 1884), *C. giganteus* (DE BRUIJN, DAWSON et MEIN, 1970), *C. kumkolensis* (LI, ZHOU, NI, FU et DENG, 2020), *C. mongolicus* (QIU et LI, 2016), and *C. turolensis* (DE BRUIJN et MEIN, 1968), well-preserved, informative mandibles are known only from the type species, *C. bredai*. For the present comparisons, we had the opportunity to study the material of the species from the classical late Middle Miocene-aged (Astaracian ELMA) locality of La Grive M, France, and the early Late Miocene-aged (early Vallesian) locality of Grytsiv, Ukraine (Text-fig. 3b–e). The specimens within each sample demonstrate some intraspecific and ontogenetic variability. For example,

the ontogenetically younger specimens possess a shorter diastemal portion and, a possibly taller condylar process (Text-fig. 3d). The masseteric fossa varies in shape from relatively narrow and pointed anteriorly (Text-fig. 3b, e) to a wider area with a more blunt anterior edge, approaching the condition seen in most stem Marmotini (Text-fig. 3c, d). Additionally, the geologically older specimens from La Grive are somewhat smaller than those from Grytsiv; a difference that reflects a well-established general pattern of increased body sizes through time among the European species of the genus. Morphologically, the specimens from Grytsiv display a more prominent scar for the anterior mandibular portion of the buccinator muscle and a more distinctly elevated area of the mental foramen (Text-fig. 3e). In light of these differences, SARA V 2024.11.1 is certainly closer to the mandibular specimens of *C. bredai* from Grytsiv than those from La Grive. The morphological similarities are echoed by morphometric parameters: the cheek teeth of SARA V 2024.11.1 are slightly larger than those from La Grive M (m1–2 L – 1.41–1.87 mm; m1–2 W – 1.49–2.12 mm) and fit well within the size range of the population from Grytsiv (m1–2 L – 1.69–2.28 mm, m1–2 W – 1.82–2.55 mm), partially falling within the size distribution of *C. turolensis*. Based on the combination of the relatively large size of SARA V 2024.11.1 and geologically young age of the Csákvár locality, one can assume that the specimen represents a transitional form between *C. bredai* and *C. turolensis*, which has been documented from several latest Vallesian and early Turolian-aged localities in Austria (Daxner-Höck 1975, Van de Weerd 1976). Taking into account the obvious uncertainties in interpreting the specific attribution of SARA V 2024.11.1 based on its size, which are hampered by the gradual nature of the evolutionary changes in the *C. bredai*-*C. turolensis* lineage, we conservatively attribute the specimen to *C. bredai*. Such an attribution is further supported by the presence of a well-developed anteroconulid of p4, observable in about 78 % (n = 62) and 65 % (n = 23) of the fourth premolars from La Grive M and Grytsiv respectively, but rarely documented in specimens of *C. turolensis* (Van de Weerd 1976, De Bruijn 1995, MVS pers. obs.).

Summary and conclusions

In conclusion, the above can be summarized according to the standard convention of systematic paleontology, as presented in the following subsection:

Systematic paleontology

Order Rodentia BOWDICH, 1821

Family Sciuridae FISCHER, 1817

Subfamily Xerinae OSBORN, 1910

Tribe Marmotini POCKOCK, 1923

Genus *Csakvaromys* KRETZOI, 1951

Type species. *Csakvaromys sciurinus* KRETZOI, 1951.

Other species. *C. besanus* (Early Miocene, Europe), *C. bredai* (Middle to Late Miocene, Europe and Anatolia), *C. giganteus* (Early Pliocene, Greece), *C. kumkolensis*

(late Middle Miocene, China), *C. mongolicus* (late Middle Miocene – early Late Miocene, China), *C. turolensis* (Late Miocene – Early Pliocene, Europe and Anatolia).

Diagnosis. See Sinitza et al. (2022).

Stratigraphic and geographic distribution. Early Miocene – Early Pliocene of temperate Eurasia.

Csakvaromys bredai (SCHLOSSER, 1884)

Name-bearing type. Holotype fixed by monotypy (Article 73.1.2 of ICZN 1999); the partially articulated skeleton figured by Major (1899: pl. XVII).

Type locality and age. Oeningen (Öhningen), Baden-Württemberg, Germany (Upper Freshwater Molasse); late Middle Miocene; presumably early Astaracian.

Referred material in this study. Right mandible (SARA V 2024.11.1) from the Esterházy-Cave near Csákvár, Late Miocene (presumably, early Turolian).

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