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A review of the evolution, systematics, distribution, dispersal, and ecology of the Holarctic ground squirrels, tribe Marmotini (Rodentia: Sciuridae: Xerinae), in Europe

Maxim V. Sinitsa

ABSTRACT. Recent advances in studying the fossil record and systematics of the Holarctic ground squirrels (tribe Marmotini) have prompted a revision of their evolution to refine the biogeography and adaptive trends within the clade. Their known fossil record — starting from the Oligocene of Western Europe — shows a rapid diversification into a range of adaptations to semiarboreal and strictly terrestrial lifestyles. This review aims to summarize the recent advances in studies of the marmotine fossil record, highlighting the lifestyle interpretations, geographic and temporal distribution, and phylogenetic relationships of these rodents. The recent phylogenetic inferences reconstructed two oldest genera of European marmotines from the Oligocene and Neogene, namely *Palaeosciurus* and *Csakvaromys*, as grouped with extinct North American *Protospermophilus* and living *Sciurotamias* and forming a subtribe Sciurotamiina, basal to all other Marmotini. The remainder of marmotines were segregated between chipmunks (subtribe Tamiina) and derived Holarctic ground squirrels (subtribe Marmotina, including sousliks, marmots, and prairie dogs). The fossil members of Sciurotamiina are believed to represent a semiarboreal and arboreal sciurids. The terrestriality evolved late in the evolution of the ground squirrels, most probably among the members of Marmotina. It has been suggested that Marmotini originated in North America. The major evolutionary events that affected the European ground squirrel communities were associated with at least three migration waves from North America through Asia during the Early Oligocene to Late Pliocene time interval.

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KEY WORDS: Holarctic ground squirrels, Europe, Marmotini, evolution, biogeography, autecology.

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Обзор эволюции, систематики, распространения, биогеографии и экологии голарктических наземных беличьих трибы Marmotini (Rodentia: Sciuridae: Xerinae) в Европе

М.В. Синица

РЕЗЮМЕ. Недавние достижения в изучении палеонтологической летописи и систематики голарктических наземных (трибы Marmotini) побудили пересмотреть их эволюцию с целью уточнения их биогеографии и адаптивных тенденций. Палеонтологическая летопись группы, берущая начало с олигоцена Западной Европы, показывает быструю диверсификацию в ряд адаптаций к полудревесному и строго наземному образу жизни. Данный обзор призван обобщить результаты новейших исследований палеонтологической летописи Marmotini, уделив особое внимание интерпретации их образа жизни, географическому и временному распространению, а также филогенетическим связям этих грызунов. Согласно современным филогенетическим реконструкциям, два древнейших рода европейских Marmotini олигоцена и неогена — *Palaeosciurus* и *Csakvaromys* — объединяются с вымершим североамериканским родом *Protospermophilus* и современным родом *Sciurotamias* в подтрибу Sciurotamiina, занимающую базальное положение по отношению ко всем Marmotini. Остальные представители трибы Marmotini подразделяются на бурундуков (подтриба Tamiina) и более продвинутые группы голарктических наземных беличьих (подтриба Marmotina, включающая сусликов, сурков и луговых собачек). Предполагается, что ископаемые представители Sciurotamiina вели полудревесный или древесный образ жизни. Переход к наземному образу жизни произошёл на поздних этапах эволюции этой группы, вероятнее всего, в пределах подтрибы Marmotina. Триба Marmotini предположительно возникла в Северной Америке. Ключевые эволюционные события, определившие состав европейских сообществ наземных беличьих, были связаны как минимум с тремя мигра-

ционными волнами из Северной Америки через Азию и Атлантику в период от раннего олигоцена до позднего плиоцена.

КЛЮЧЕВЫЕ СЛОВА: Голарктические наземные беличьи, Европа, Marmotini, эволюция, биогеография, аутэкология.

Introduction

The late Cenozoic has been one of the most important periods of climate and landscape change that reshaped terrestrial environments and biotas over local to global scales. The late Oligocene warming and Mid-Miocene Climatic Optimum were major events during this interval, which were followed by persistent cooling throughout the remainder of the Neogene and Quaternary (Zachos *et al*., 2001). These resulted in a gradual transition from forested ecosystems to C4 grasslands, which dominate the temperate zones of the Northern Hemisphere today (Edwards *et al*., 2010) and had a profound effect on terrestrial mammal communities. The first part of the late Cenozoic saw the disappearance of many Paleogene relics, which were replaced by various "modern" mammal groups that were suited to open environments. Among the primary beneficiaries of these events were ground squirrels (Xerinae). They rapidly diversified and became one of the dominant rodent groups for the second half of the Cenozoic (Anderson, 2008; Goodwin, 2008; Ge *et al*., 2013). Holarctic ground squirrels (Marmotini) were the most diverse and geologically earliest group of Eurasian xerines. The tribe includes 65 species of rock squirrels, chipmunks, sousliks, prairie dogs, and marmots, which are divided into 13 living genera (Thorington *et al*., 2012). Its evolutionary success is likely linked to morphological and functional adaptations, such as complex social behaviors, terrestrial locomotion, and burrowing associated with the ability to hibernate, as well as food hoarding using cheek pouches. Through these adaptations, the group has been able to exploit various biomes in both Eurasia and North America, including temperate and arctic habitats, as well as the tropics of Southern China (Gromov *et al*., 1965; Thorington & Hofmann, 2005; Thorington *et al*., 2012). Understanding these characteristics of early ground squirrels is of key importance for the evolutionary biology of sciurids.

The tribe has a long and complicated evolutionary history, which is believed to stem back to the early Oligocene of Eurasia. Its fossil record includes about twelve genera with 25–30 recognized species, whose phylogenetic relationships and interregional dispersals remain puzzling (Thorington & Hofmann, 2005; Goodwin, 2008; Thorington *et al*., 2012). Adapted to a wide range of environments, these rodents played an important role in many late Oligocene to Pleistocene mammal communities, and therefore any novel results on their taxonomy and paleobiogeography are important for studies of entire mammalian faunal turnovers and the evolution of terrestrial ecosystems.

In North America, the evolutionary history of the tribe's members is relatively accurately depicted by a wealth of well-preserved fossils (Bryant, 1945; Black, 1963; Goodwin, 2008). In contrast, Eurasian and, particularly, European taxa have not historically received the same level of attention. At this point, most of what we know about the systematics, phylogenetic position, and distribution of extinct Marmotini from Europe comes from a few snapshots that are separated by large gaps in time and space. This is even though the sciurid fossil record of Europe is one of the most diverse and rich currently recorded worldwide (see, e.g., de Bruijn, 1999). It encompasses both the most plesiomorphic and derived ground squirrels (Vianey-Liaud, 1974; Thorington *et al*., 2012) and consequently provides an important opportunity to examine key stages in their evolution and use them for intercontinental correlations and paleoenvironmental reconstructions. This review aims to summarize current knowledge on the European Marmotini fossil record, paleobiology, and paleogeography.

Institutional abbreviations

LACM, Natural History Museum of Los Angeles County, Los Angeles, USA; ML, Musée des Confluences, Lyon, France; NMB, Naturhistorisches Museum Basel, Switzerland; NMNHU-P, Department of Paleontology, National Museum of Natural History, National Academy of Sciences of Ukraine, Kiev; ZIN, Zoological Institute, Russian Academy of Sciences, Saint Petersburg, Russia.

The phylogenetic position of early European marmotine ground squirrels

The phylogenetic position of extinct European ground squirrels and their phylogenetic relationships are the questions that were addressed by Sinitsa (2022) and Sinitsa *et al*. (2022). The studies include a revision of the key Eurasian marmotine ground squirrel taxa, with particular attention to cranial features. It has revealed a monophyletic Xerinae clades Protoxerini (African tree squirrels), Xerini (African ground squirrels), and Marmotini (Holarctic ground squirrels) as successive sister taxa to the tree squirrel clades Ratufinae, Callosciurinae, and Sciurinae (Fig. 1). Several well-supported phylogenetic relationships emerged from the analyses: (1) a monophyletic subtribal clade, Sciurotamiina, composed of the basal Oligo-Miocene ground squirrels *Palaeosciurus*, *Csakvaromys*, and *Protospermophilus*, together with living *Sciurotamias*, assumed a basal position; (2) the Holarctic genus *Miospermophilus* and Eurasian *Sinotamias* are robustly grouped in a basal position with derived Holarctic ground squirrels, the Marmotina; (3) chipmunks, the subtribe Tamiina,

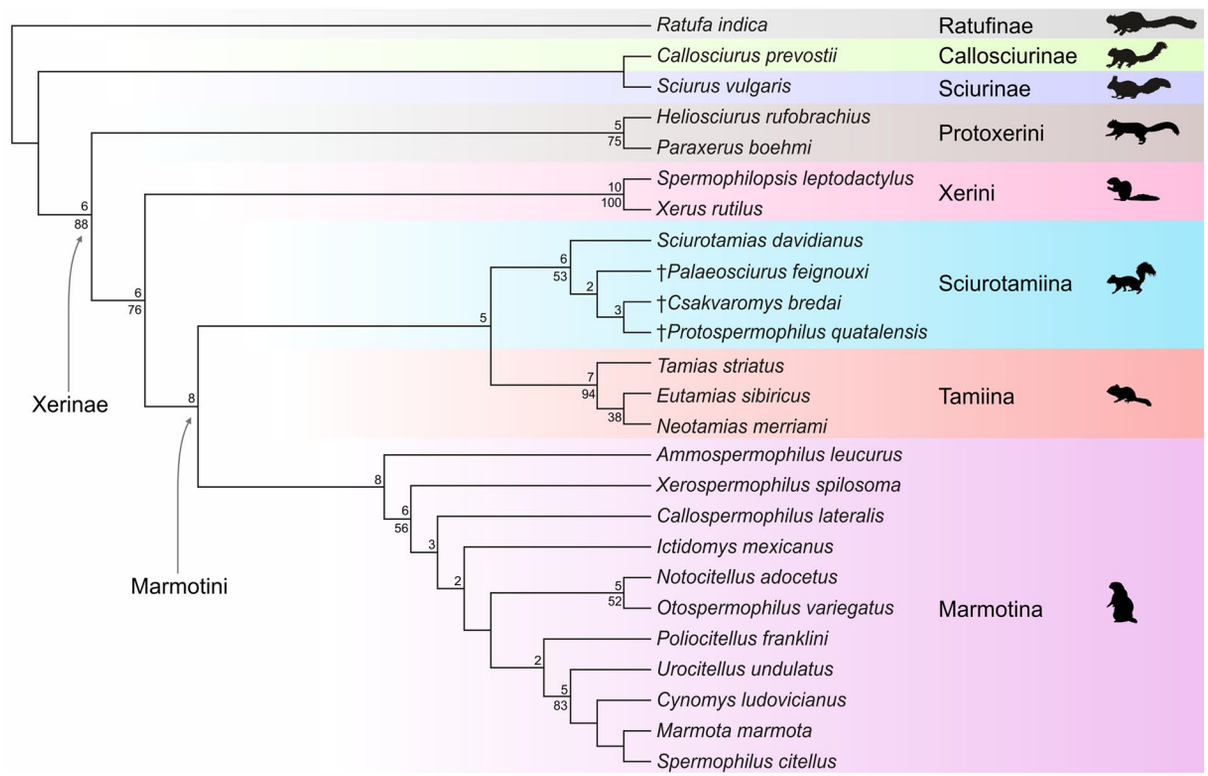

Fig. 1. Phylogenetic tree of Xerinae, after Sinitsa *et al*. (2022), showing the phylogenetic structure of Marmotini.

are found nested within stem ground squirrels as the sister clade to Sciurotamiina; and (4) the Early Pleistocene European ground squirrel species traditionally attributed to *Urocitellus* is placed within *Spermophilus*.

One of the novel findings of the studies (Sinitsa *et al*., 2022) was the identification of a clade that includes primitive extinct (*Palaeosciurus feignouxi*, *Protospermophilus quatalensis*, *Csakvaromys bredai*) and extant (*Sciurotamias davidianus*) marmotines. This clade is positioned as the sister group to Tamiina (chipmunks) and Marmotina (derived Holarctic ground squirrels) and diagnosed by four unequivocal synapomorphies (Fig. 2). These include a large lacrimal foramen occupying most of the orbital process of the lacrimal and contacting the orbital process of the maxilla; a gently swollen facial tuberosity with a crest for the aponeurotic origin of the superficial portion of the masseter muscle; a rudimentary ectopterygoid crest; and distinctly non-confluent anterior ends of the upper and lower masseteric crests separated by a depression posterior to the attachment area for the anterior fibers of the anterior deep masseter muscle.

The living Chinese rock squirrels have been historically affiliated with nearly all the major sciurid groups, including xerines (Trouessart, 1897), marmotines (Milne-Edwards, 1868; Ellerman, 1940; Ellerman & Morrison-Scott, 1951; Gromov *et al*., 1965; Thorington *et al*., 1998; Thorington & Hofmann, 2005), sciurines (Moore, 1959), ratufines (Callahan & Davis, 1982), and callosciurines (Allen, 1940; Simpson, 1945; Black, 1963). This disparity was partially the result of the evolving status and taxonomic structure of numerous sciurid groups, as well as the apparent challenges associated with interpreting the morphology of a primitive, generalized taxon like *Sciurotamias*. The application of molecular methods added little for resolving the problem, as the genus was either linked with the Protoxerini (Mercer & Roth, 2003; Ge *et al*., 2013) or the stem Marmotini (Steppan *et al*., 2004; Fabre *et al*., 2012; Zeldich *et al*., 2015). Thorington *et al*. (1998) contended that *Sciurotamias* is most appropriately classified in its own marmotine subtribe, Sciurotamiina, due to the presence of a suite of cranial and postcranial characters that support the remoteness of *Sciurotamias* from chipmunks (subtribe Tamiina). Although showing interesting and fairly convincing results, this concept has not received careful consideration from zoologists and molecular systematists. Recently, it has been independently revived by Kryštufek & Vohralík (2012), who erected the monotypic tribe Sciurotamiini. The morphology-based phylogenetic hypothesis proposed by Sinitsa *et al*. (2022) explicitly recovered *Sciurotamias* as a member of its own clade, sister to the Tamiina (the chipmunks). Based on this evidence, the authors argued that the subtribe Sciurotamiina should continue to be recognized. The inclusion of these extinct taxa in the subtribe has been supported by the unique combination of synapomorphies in *Palaeosciurus*, *Protospermophi-*

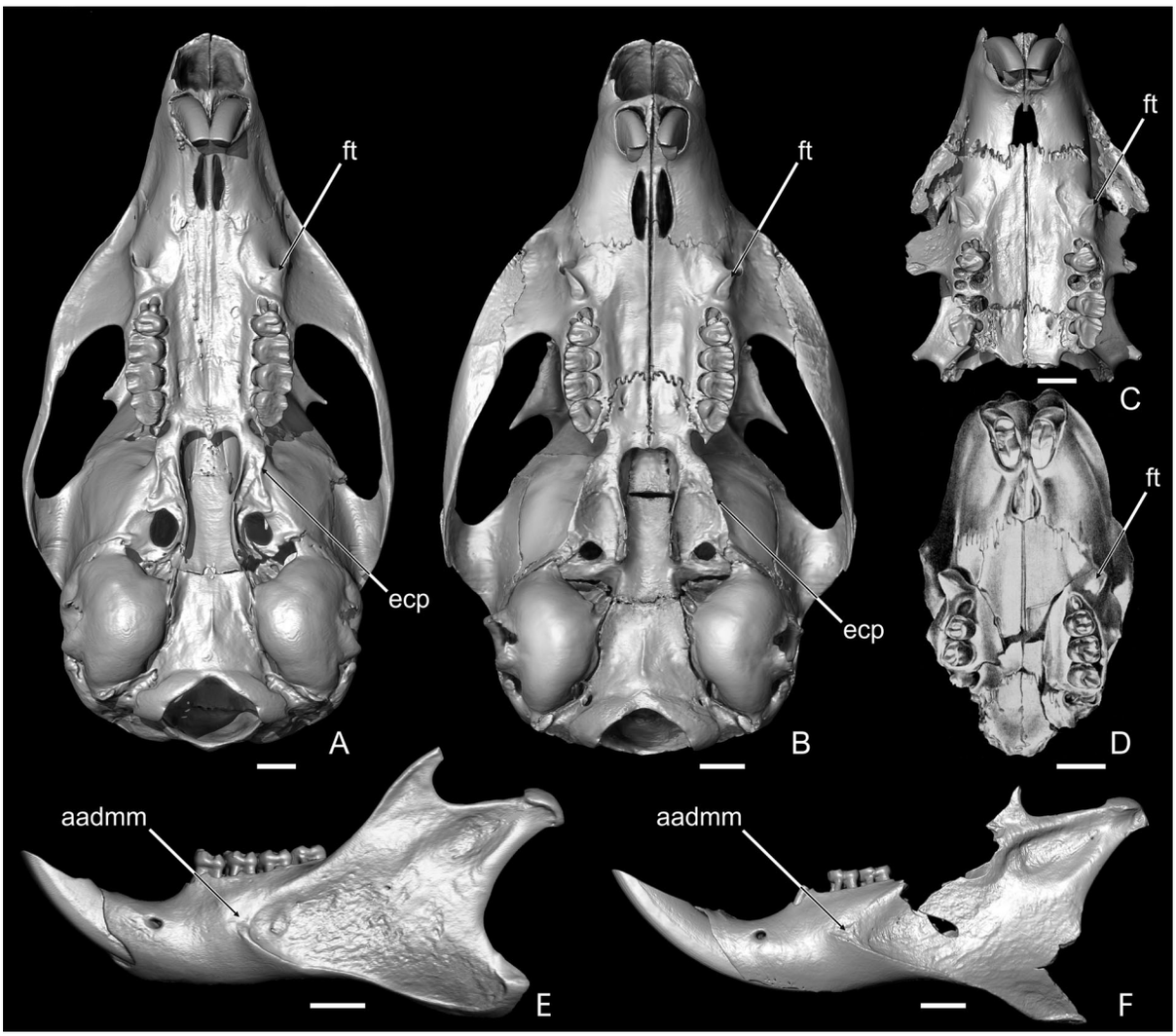

Fig. 2. Skulls (A–D) and mandibles (E, F) of the representatives of subtribe Sciurotamiina in ventral (A–D) and lateral (E, F) views. A — *Sciurotamias davidianus*, Recent, China (ZIN 3585); B, E — *Palaeosciurus feignouxi*, Early Miocene, Montaigule-Blin, France (B — composite reconstruction of the skull based on several fragmentary specimens, E — mandible, NMB M.A. 5290); C, F — *Csakvaromys bredai*, Late Miocene, Grytsiv, Ukraine (C — facial skull, NMNHU-P 22–2706, F — mandible, NMNHU-P 22–2718) (after Sinitsa *et al*., 2022); D — *Protospermophilus quatalensis*, Late Miocene, Quatall Canyon, USA (LACM (CIT) 30) (after Black, 1963). Abbreviations: aadmm — attachment area for anterior fbers of anterior deep masseter muscle; epc — ectopterygoid crest; ft — facial tuberosity. Scale bars equal 3 mm.

lus, and *Csakvaromys*, which indicated a sister-group relationship. This defined Sciurotamiina beyond the initial definition proposed by Thorington *et al*. (1998). Within Sciurotamiina, *Sciurotamias davidianus* was plesiomorphic for most cranial features analyzed here and placed as the basalmost member of the clade.

The monophyly and phylogenetic structure of the ground squirrels (Xerinae)

Since Osborn (1910) created the subfamily, which was originally designed to include only the two genera — the giant squirrels (*Ratufa*, which is now classified in its subfamily, the Ratufinae) and the African sun squirrels (*Xerus*) — the monophyly and taxonomic content of Xerinae have been a source of controversy. The status of the subfamily was slightly altered by other specialists, most of whom, however, treated it in a narrow sense, as a tribe-level group restricted to several genera of African (*Atlantoxerus*, *Xerus*) and Asian (*Spermophilopsis*) sun squirrels (see, e.g., Pocock, 1923; Ellerman, 1940; Simpson, 1945; Moore, 1959; Black, 1963; McKenna & Bell, 1997). Molecular-based research conducted in recent decades has significantly broadened and reinterpreted the subfamily's range, leading to the identification of a sizable mono-

phyletic clade that includes both African (Protoxerini, Xerini) and Holarctic (Marmotini) terrestrial squirrels (Mercer & Roth, 2003; Steppan *et al*., 2004). Although the monophyletic status of Xerinae is firmly established by molecules, it remains unsupported by morphological traits. Neither the major studies of cranial (Moore, 1959) or bacular (Pocock, 1923; Didier, 1952, 1953) morphology nor the studies of external characters (Ellerman, 1940) indicated a close relationship among the three terrestrial squirrel clades that are currently united as xerines.

One of the outcomes of Sinitsa *et al*. (2022) was the recognition of morphological synapomorphies of xerines. The phylogenetic analysis recovers Xerinae as a well-supported monophyletic clade that is diagnosed by four unequivocal synapomorphies: (1) a large orbital process of the lacrimal extending ventrally close to the maxillary foramen, (2) a well-developed and laterally projected facial tuberosity with its posterior end terminating just anterior to the P3 alveolus, (3) a horizontally oriented condylar process with its posterior end being situated level with or slightly above the level of the lower tooth row, and (4) the metaloph and protoloph of P4-M2 convergent toward the protocone. This morphology-based phylogeny (Sinitsa *et al*., 2022) is congruent with previous molecular phylogenies (Mercer & Roth, 2003; Steppan *et al*., 2004; Zeldich *et al*., 2015), thereby providing an encouraging proof of the reliability of these morphological characters for phylogenetic analyses.

The phylogenetic position of the genus *Csakvaromys*

Being the most abundant genus in the Western Eurasian Neogene fossil record, *Csakvaromys* (=*Spermophilinus*) is one of the earliest and most geographically widespread sciurids. The genus includes six species from the Miocene and Early Pliocene of Europe and Asia (Qiu & Li, 2016; Bosma *et al*., 2019; Li *et al*., 2020; Sinitsa & Čermák, 2024) and is characterized by a combination of dental features, including massive incisors bearing longitudinally striated enamel and primitively low-crowned cheek teeth with a rudimentary P3 and weakly developed additional cusps in both the upper and lower dentitions (de Bruijn & Mein, 1968; Cuenca Bescós, 1988). As early as the mid-nineteenth century, when the taxon "*Sciurus*" *bredai* was first described, it was regarded as potentially significant as a link between the tree and the ground squirrels (Depéret, 1887, 1892; Major, 1893). A brief description of the cranial morphology of *Csakvaromys bredai* based on a partial facial skull from the classic late Middle Miocene site La Grive Saint-Alban was published by de Bruijn & Mein (1968). They assigned this specimen to the recently described genus *Spermophilinus* and proposed that the genus is distinguishable from the morphologically similar *Palaeosciurus* due to its chipmunk-like characteristics. While de Bruijn & Mein (1968) provided a relatively informative description, the phylogenetic position of *Csakvaromys* in relation to potentially closely related taxa remained controversial, and the majority of the cranial anatomy that is now considered phylogenetically significant was not documented.

Using a well-preserved facial skull and related cranial specimens from the early Late Miocene (11.1–9.7 Ma) Grytsiv fauna in western Ukraine, further supplemented by the mandible from the late Miocene Csákvár locality in Hungary, Sinitsa *et al*. (2022) and Sinitsa & Čermák (2024) provided bone-by-bone description of the cranial anatomy of the type species of the genus, *Csakvaromys bredai* (Fig. 2C,F). Notable cranial features of *C. bredai* include (1) a shallow, broad, and elongated facial skull with a straight dorsal profile; (2) a massive rostrum; (3) a deeply concave lateral lip of the infraorbital foramen; (4) a shortened infraorbital canal; (5) a large lacrimal foramen; (6) an elongated anteromedial edge of the zygomatic arch extending onto the premaxilla; (7) a broad and fat interorbital region with closed supraorbital foramina; and (8) non-elevated supraorbital margins. *Csakvaromys bredai* exhibits synapomorphies of Marmotini in its cranial osteology and dentition. These features include a rostrum with depressions for the cheek pouch muscles, a deeply excavated sphenopalatine fossa, a moderately anteromedially extended jugal wedged between the maxilla and lacrimal, and an elongated diastemal portion of the mandible with a mental foramen located near the dorsal edge of the bone. As in most other marmotines, the upper and lower teeth of *Csakvaromys* lack distinct hypocones and entoconids, respectively.

The phylogenetic analysis of Sinitsa *et al*. (2022) supported the hypothesis of Sciurotamiina affinities for *Csakvaromys* by identifying a suite of craniodental resemblances between *Csakvaromys* and *Sciurotamias* that the present phylogenetic reconstruction has shown to be synapomorphies (Fig. 2). These comprize a large lacrimal foramen and sizeable lacrimal fenestra whose dorsolateral rim confluents with a foramen for the malar branch of the infraorbital artery; a slightly swollen facial tuberosity bearing a crest for the aponeurotic origin of the superficial portion of the masseter muscle; nonconfluent lower and upper masseteric crests of the mandible separated by an extensive attachment area for the anterior fibers of the anterior deep masseter muscle; and the presence of a supraorbital foramen. A crown clade of the Sciurotamiina, comprising *C. bredai* and *Protospermophilus quatalensis*, depicted as the sister group to *Palaeosciurus*, was recovered in the most parsimonious topology of this analysis. The clade that includes *Csakvaromys* and *Protospermophilus* was characterized by six synapomorphies, including the muscle origin of the anterior deep masseter expanding onto the premaxilla, a well-developed concavity for the superficial masseter muscle on the ventral surface of the angular process, incisor enamel striated with three to five longitudinal ridges, a short anteroloph of P4, the bottom of the posterior valley of M3 being rugose, and an elongated m3 with its talonid portion shifted later-

ally relative to the trigonid. Within the aforementioned clade, *C. bredai* was diagnosed by the possession of a deeply concave lateral lip of the infraorbital foramen, weak to almost fully reduced entoconids, and mesostylids in m1–2. *Csakvaromys* lacks critical derived characters of living Tamiina but demonstrates derived features of Sciurotamiina. The phylogenetic analysis by Sinitsa *et al*. (2022) reconstructed the taxon as a member of the sciurotamiine rock squirrel clade, albeit a distinctive one.

Implications for the relationships of the North American basal Marmotini

Several early ground squirrels from North America's Oligo-Miocene have been described, though their systematic positions remained largerly unclear (Bryant, 1945; Black, 1963). Among them is *Protospermophilus*, which represents one of the most abundant and, at the same time, one of the most problematic extinct Nearctic sciurids (Fig. 2D). The genus is currently composed of six species of medium-sized generalized marmotines. These species are characterized by a distinctively robust rostrum, primitively compressed incisors with a longitudinally striated enamel, and heavily built low-crowned cheek teeth with distinct hypocones and entoconids on the upper and lower molars, respectively (Bryant, 1945; Black, 1963; Goodwin, 2008). Although they were only briefly described and illustrated, the genus is known from reasonably informative cranial materials, such as an almost complete facial skull of *Pr. angusticeps* (Gazin, 1930, 1932; Matthew & Mook, 1933; Bryant, 1945; Black, 1963). The combination of supposedly primitive and derived morphological features of *Protospermophilus* led Black (1963) to consider it to be an aberrant marmotine, possibly ancestral to marmots. Based on similarities in dental morphology, Bosma *et al*. (2019) considered the genus to be closely related to European *Palaeosciurus*, implying close phylogenetic affinities between the earliest Eurasian Marmotini and *Protospermophilus*.

The reevaluation of the craniodental morphology of *Protospermophilus* (Sinitsa *et al*., 2022) revealed that *Protospermophilus* possesses numerous derived craniodental characters that are not documented in *Palaeosciurus*. Additionally, the dental similarities cited by Bosma *et al*. (2019) are indicative of shared primitive features. The phylogenetic results based on craniodental features (Sinitsa *et al*., 2022) support a close phylogenetic relationship between *Protospermophilus* and *Csakvaromys*; both genera are more closely allied to one another than to other marmotines (Fig. 1). They genera possess a set of derived conditions that unite them in a separate clade and that differentiate this clade from all more basal marmotines, including *Palaeosciurus*. These shared synapomorphic characters include (1) a widened rostrum with the muscle origin of the anterior deep masseter expanded onto the premaxilla; (2) a pronounced concavity for the superficial masseter muscle on the ventral surface of the angular process; (3) striated incisor enamel; (4) a rudimentary anterior lobe of P4; (5) a well-defined M3 talon portion with a strong metaconule and, in the Late Miocene species, rugose enamel; (6) a reduced anteroconule of p4; and (7) an anteroposteriorly elongated m3 crown having a laterally shifted talonid portion. In terms of cranial and, to a lesser extent, dental morphology, *Protospermophilus* and *Csakvaromys* together manifest a roughly similar evolutionary grade, as implied by their adjacent positions on the topology. This could imply a common ancestry for the genera from some mid-Oligocene marmotine. Using the current phylogenetic structure, it's interesting to think that European *Palaeosciurus* might be the best structural ancestor for North American *Protospermophilus* and Eurasian *Csakvaromys*.

The systematics and diversity of the Neogene European Marmotina

Marmotina, Scirotamiina, and Tamiina compose the Marmotini tribe (Holarctic ground squirrels) of Xerinae, which comprises the majority of living marmotine ground squirrels. Despite the existence of molecule-based phylogenies (Mercer & Roth, 2003; Steppan *et al*., 2004), the morphological monophyly of this tribe has only recently been demonstrated (Sinitsa, 2018; Sinitsa *et al*., 2022). Among extinct taxa of European ground squirrels, only derived Late Pliocene and Quaternary forms, such as sousliks (*Spermophilus*) and marmots (*Marmota*), were traditionally included in the tribe. There are, however, a number of small, dentally generalized ground squirrel species from Southern and Eastern Europe's Neogene that were previously classified as either *Tamias* s.l. (de Bruijn, 1995; Bosma & de Bruijn, 2013) or *Sciurotamias* (Topachevsky, 1971). A reexamination of the Late Miocene "*Sciurotamias*" *gromovi* from Ukraine and "*Tamias*" *atsali* from Greece (Sinitsa, 2018) showed them to be the members of the genus *Sinotamias* previously documented only from the middle–upper Miocene of Asia (Qiu, 1991, Qiu & Li, 2016). Four species-level taxa within eastern European *Sinotamias* were identified in a revision of rich dental materials from thirteen Late Miocene (Turolian) localities of Moldova and Ukraine (Sinitsa & Delinschi, 2023): *S. gromovi* (latest Miocene, latest mid-Turolian to the terminal Turolian), *S. topachevskyi* (Late Miocene, middle Turolian to the latest mid-Turolian), *S. lungui* (Late Miocene, early Turolian to the middle Turolian), and *Sinotamias* sp. from the early Turolian of Frunzovka 2 (Fig. 3). The two latter taxa are evidently among the basal members of the genus, followed by *S. topachevskyi*. The geologically youngest species, *S. gromovi,* is further derived regarding *S. topachevskyi*. Out of these taxa, only *S. gromovi* possesses autapomorphies (entoconulids in m1 and m2), and *S. lungui* and *S. topachevskyi* may both be recognized as metaspecies. This suggests that eastern European species of the genus may form a single evolving lineage. This assertion is corroborated by a comprehensive analysis of the morphological and size changes that have occurred

in the evolution of eastern European *Sinotamias* species (Sinitsa & Delinschi, 2023). Along with *S. primitivus* and *S. anatoliensis*, *S. lungui* partially bridges the gap between more derived species of the genus and basal members of Marmotina.

Sinotamias topachevskyi is roughly intermediate in size between *S. lungui* and *S. gromovi*. Geologically older P4, M1, M2, M3, and m3 specimens of *S. topachevskyi* are slightly smaller than younger ones, suggesting a gradual size increase, and demonstrated stronger metaconules on the upper cheek teeth and weaker mesoconids on p-m3. Although the overall sample size for the species is too restricted to postulate a firm conclusion about cheek teeth size change throughout the temporal distribution of *S. topachevskyi*, one can suggest that for most tooth loci the species seems to continue the size trend observed in *S. lungui*. The terminal eastern European species *Sinotamias gromovi* continues several morphological (enlargement of the metaconules and reduction of mesoconids) and morphometrical morphoclines evident in *S. topachevskyi*.

With three recognized temporally successive species, the genus *Sinotamias* represents the most frequent and, consequently, biochronologically useful Neogene sciurid of Eastern Europe. The occurrence of *S. lungui*, *S. topachevskyi*, and *S. gromovi* in Southern Ukraine and Moldova strongly supports the hypothesis of faunal provincialism among the Late Miocene mammal faunas of Eastern Europe. All three *Sinotamias* species documented from this fauna are endemic, having never been recorded from the relatively well-known small mammal assemblages of Anatolia, Southern, and Central Europe, despite the fact that our knowledge of the Miocene sciurid fauna from most eastern European

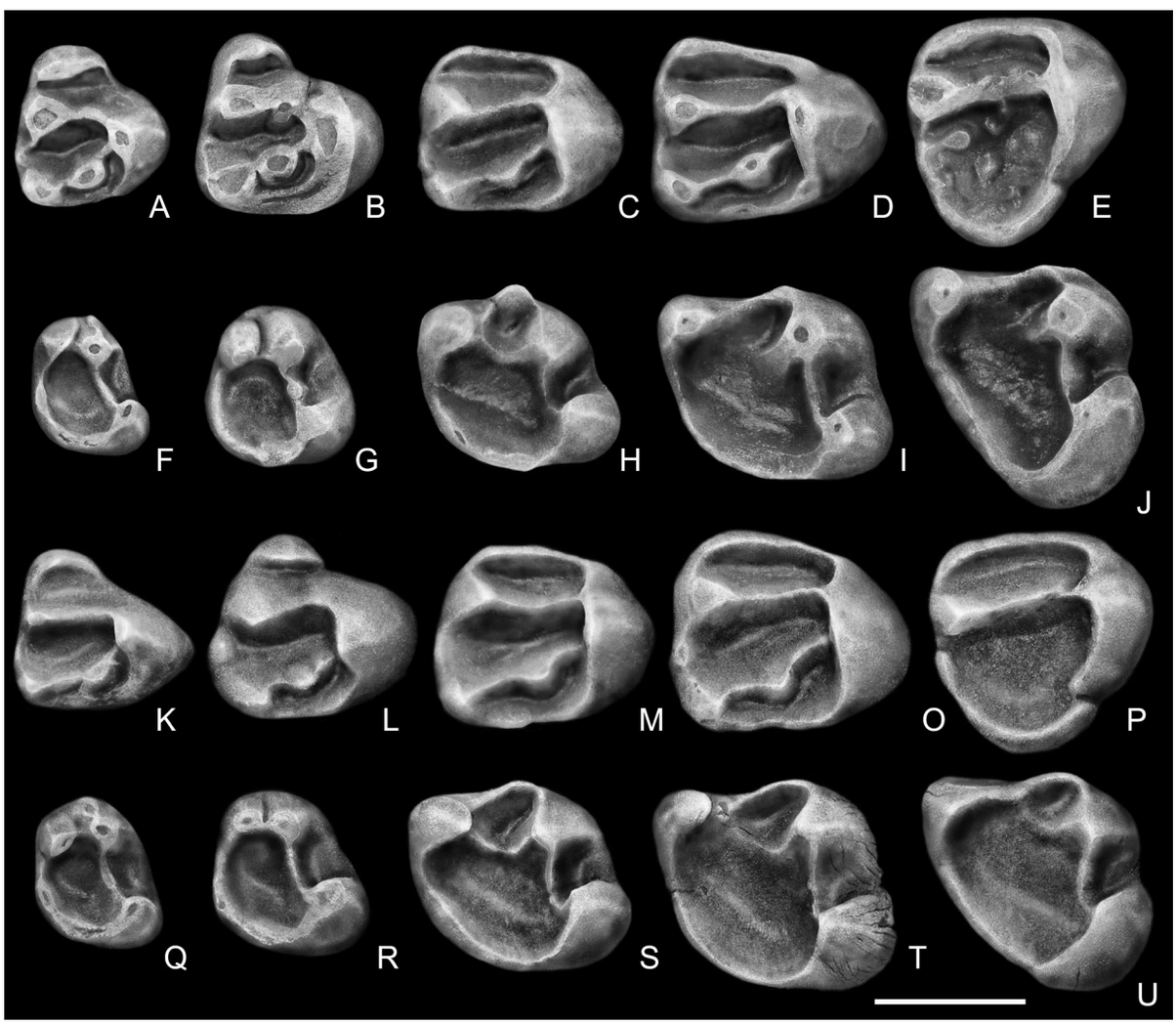

Fig. 3. Upper (A–E, K–P) and lower (F–J, Q–U) cheek teeth of *Sinotamias lungui* (A–J) and *Sinotamias topachevskyi* (K–U). A, C, E, H–J — Keinar, Moldova, early Turolian; D — Otradovo, Ukraine, early Turolian; F — Palievo, Ukraine, early Turolian; G — Novoelizavetovka 2, Ukraine, early Turolian; K, L, O, P, R–U — Cherevichnoe 3, Ukraine, middle Turolian; M — Kubanka 2, Ukraine, middle Turolian; Q — Chimishliya, Moldova, middle Turolian. Scale bars equal 3 mm. After Sinitsa & Delinschi (2023), with modifications.

realms remains rather limited and confined to the northern rim of the Eastern Paratethys.

The cranial morphology and phylogenetic position of *Sinotamias*

The representatives of the genus *Sinotamias* were arguably among the most successful and widespread Eurasian Neogene sciurids. However, despite their diversity and abundance, the cranial morphology of *Sinotamias* is still very poorly known. By contrast, complete or nearly complete skulls are known for most extinct ground squirrel genera. Mainly due to poor preservation and rarity in the fossil sites, skull materials of *Sinotamias* are limited to mandibular specimens of eastern European *S. gromovi* and Asian *S. primitivus* (Topachevsky, 1971; Sinitsa, 2018; Qiu & Li, 2023). No maxillary or other cranial elements of the genus have been reported.

This gap has been partially filled by studying cranial fragments of *Sinotamias* pertaining to *S. orientalis* from the latest Miocene (Baodean ALMA) fossil site Pavlodar 1A in Northern Kazakhstan (Sinitsa *et al*., 2023). The maxilla of *Sinotamias*, as evidenced by these specimens, is generalized in comparison to that of the majority of marmotines. It is characterized by a palatine process that is widened and flat, an expansive facial process, subparallel upper tooth rows, a weak zygomatic process, a shallow alveolar process, and a weak facial tuberosity. These features clearly distinguish *Sinotamias* from the majority of living Holarctic ground squirrels. In many ways, the maxilla of *Sinotamias* resembles that of the basal Marmotina, especially *Ammospermophilus*, and to a lesser degree, *Callospermophilus*, *Xerospermophilus*, and chipmunks (subtribe Tamiina). *Sinotamias* lacks the derived features of rock squirrels or chipmunks, such as a prominent aponeurotic scar of the superficial portion of the masseter muscle on the facial tuberosity and the enlarged infraorbital foramen with an incomplete lateral lip and shortened infraorbital canal. The majority of the characters that ally *Sinotamias* with Sciurotamiina and Tamiina represent retained primitive conditions. The overall morphology of the maxilla of *Sinotamias* is intermediate in grade of morphological evolution between that of basal Marmotini (the subtribes Sciurotamiina and Tamiina) and the derived Holarctic ground squirrels (subtribe Marmotina). This is consistent with the dental and mandible-based phylogeny, which places *Sinotamias* among the basalmost Marmotina (Sinitsa, 2018).

The origin of European Marmotina

The abrupt appearance of early Marmotina in the European fossil record, as evidenced by four cheek teeth of *Sinotamias* sp. from the earliest Turolian of Southern Ukraine (Sinitsa & Delinschi, 2023), suggests that it originated from a form of Asian marmotine and subsequently dispersed westward to Europe. The Oligo-Miocene marmotine genus *Plesiosciurus*, originally described from the Early Miocene Xiacaowan Formation of Sihong (Qiu & Lin, 1986), is the earliest undeniable representative of this group. Originally considered to be a primitive tree squirrel, it has been later reattributed to the ground squirrels with uncertain affinities (Qiu, 2015; Qiu & Jin, 2016). The recent phylogenetic analysis of Marmotini (Sinitsa, 2018) reconstructed *Plesiosciurus sinensis* as a sister taxon to the North American Early Miocene *Miospermophilus bryanti* and within the basal radiation of Marmotina. This reconstruction was based on the presence of shared-derived dental characters, such as the metaconules on M1 and M2, reduced mesoconids, entoconids, and metalophid of m2, and finely striated incisor enamel. The charac-

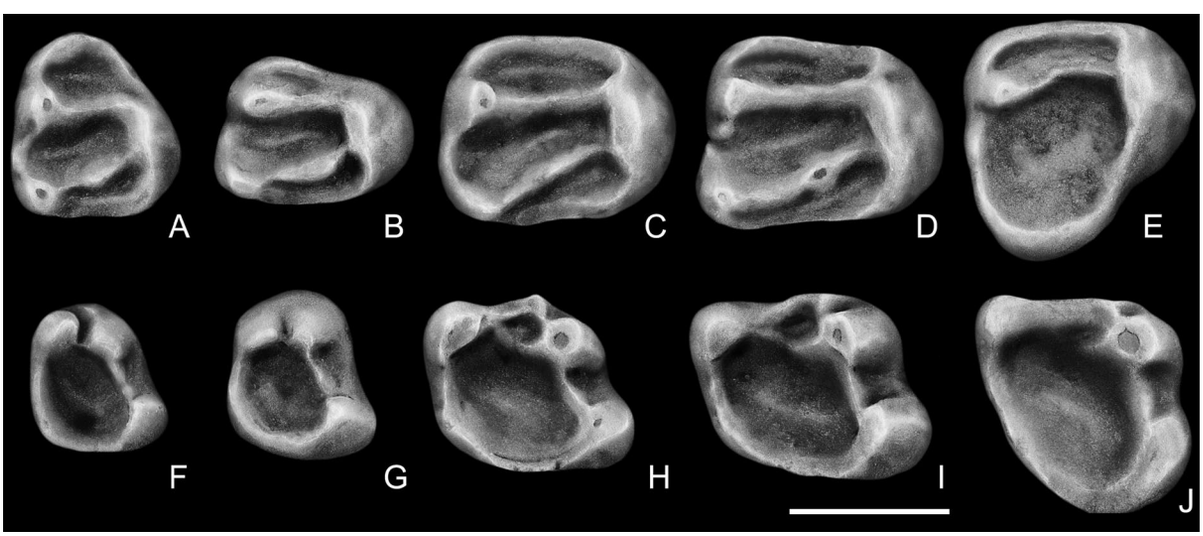

Fig. 4. Upper (A–E) and lower (F–J) of cheek teeth of *Miospermophilus debruijni*, Tagay, Russia, late Early Miocene. Scale bars equal 3 mm. After Sinitsa & Tesakov (2023), with modifications.

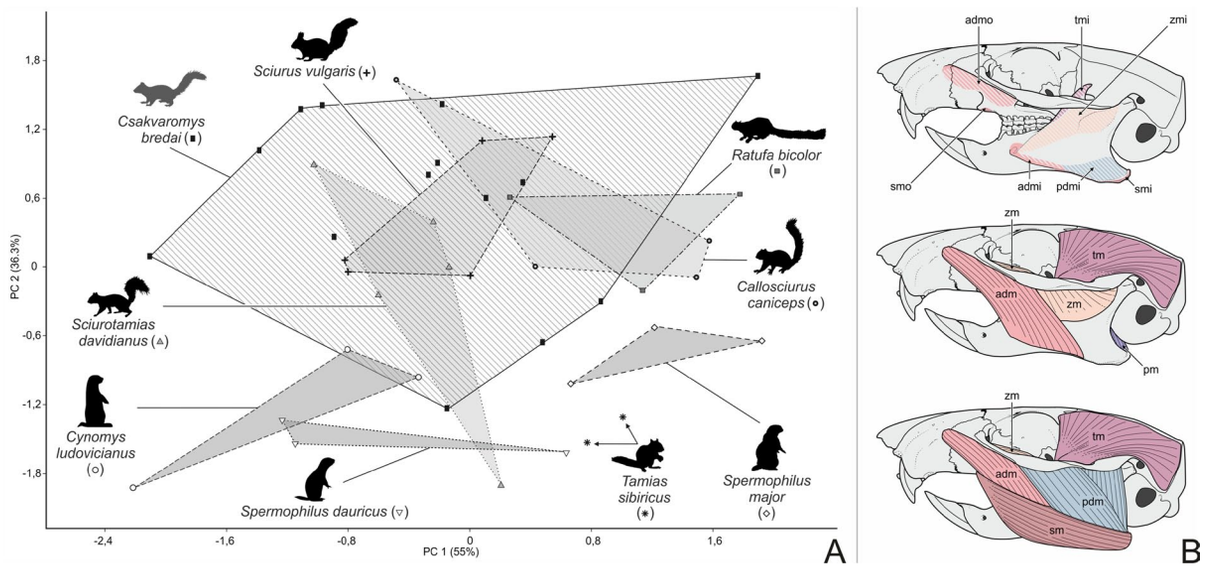

Fig. 5. A — PCA diagram for dental microwear analysis of *Csakvaromys bredai* and living sciurids (after Gusovsky & Sinitsa (2023), with modifications). B — reconstruction of chewing musculature of *C. bredai* (after Sinitsa *et al*. (2022), with modifications). Abbreviations: adm — anterior deep masseter; admi — insertion of anterior deep masseter; admo — origin of anterior deep masseter; pdm — posterior deep masseter; pdmi — insertion of posterior deep masseter; pm — pterygoideum; sm — superficial masseter; smi — insertion of superficial masseter; smo — origin of superfacial masseter; tmi — insertion of temporal muscle; zm — zygomaticomandibularis; zmi — insertion of zygomaticomandibularis.

ters distinguishing these two strikingly similar forms include more distinct metaconules, the partial loss of the P4 metastyle, a shortened anteroloph of P4, more arched ectolophids of m1 and m2, and more reduced m3 mesoconids in *P. sinensis* when compared with *M. bryanti*.

The re-evaluation of *P. sinensis* (Sinitsa & Delinschi, 2023) and the analysis of a large sample (Sinitsa & Tesakov, 2023) relating to a small primitive marmotine that was previously assigned to *Spermophilinus* (=*Csakvaromys*) as "*S.*" *debruijni* (Daxner-Höck *et al*., 2022) from the late Early Miocene Tagay vertebrate fauna (Olkhon Island, Lake Baikal, Russia) reveals a number of previously unidentified characteristics that clearly associate them with early members of the North American Oligo-Miocene genus *Miospermophilus*. These are a shortened and molariform P4 with a strongly anteroposteriorly compressed anterior valley and a lingually placed anterostyle, a pointed protocone of M1–2, and a rudimentary four (entoconid) root of M1–2 (Fig. 4). Consequently, *Plesiosciurus* has been considered a junior synonym of *Miospermophilus*, and "*S.*" *debruijni* has been reclassified as *M. debruijni* within *Miospermophilus*. The results of the phylogenetic reconstructions (Sinitsa, 2018) indicate its basalmost position of *Miospermophilus* among the rest of the Marmotina. This supported the hypothesis that the genus may represent the most plausible candidate for the ancestry of all other Marmotina, including the Eurasian representatives of this group (Sinitsa & Tesakov, 2023)

The paleobiology of basal Marmotini

The importance of basal marmotines in paleobiology is clear. The group played an important role in the late Cenozoic small mammal communities throughout the Holarctic. Until recently, however, our understanding of the autecology and paleobiology of the extinct European marmotines has been based on indirect evidence and, primarily, on a purported analogy with an "average" living ground squirrel presumably adapted to a terrestrial lifestyle and foraging on the ground (Bernor *et al*., 2004; Agustí *et al*., 2005; van der Meulen *et al*., 2005; Casanovas Vilar *et al*., 2006; Casanovas-Vilar, 2007; Casanovas-Vilar & Agustí, 2007; Prieto *et al*., 2008; Daxner-Höck, 2010; Harzhauser *et al*., 2011; Ginsburg & Mein, 2012). The dental microwear of *Csakvaromys bredai* was the subject of a recent study (Gusovsky & Sinitsa, 2021), which revealed that the rodent was a fruit and nut eater that was connected to forest biomes (Fig. 5A). This evidence has been recently supplemented by the cranial data based on the skull of this rodent (Sinitsa *et al*., 2022). The study of the functional anatomy of the feeding apparatus did not find any strong evidence that *Csakvaromys* is a green matter and seed feeder that lives in open areas (Fig. 5B). While facultative herbivory and granivory, as well as opportunistic insectivory, cannot be entirely disregarded, the cranial morphology of *Csakvaromys* suggests a specialization in hard-nut and fruit feeding, which is associated with the arboreal or semi-arboreal locomotor habit. In this respect, *Csakvaromys* has no

analogue among living marmotines, both generalized and derived, which highlights an adaptation to either a granivorous or herbivorous feeding habitat and a terrestrial lifestyle.

Evidence suggests that *Csakvaromys* was similar to extant frugivorous squirrels in terms of feeding preferences, although it was not as specialized for this feeding mode as typical nut-eaters like the living members of the genus *Sciurus*. This may offer a glimpse into the broader issues of sciurid evolution by corroborating the hypothesis of an arboreal common ancestor of ground squirrels and the theory that terrestriality evolved in parallel in Marmotini and Xerini. Furthermore, it implies that the transition from a primitively arboreal to a fully terrestrial lifestyle likely occurred relatively late in the evolutionary history of the Old World Marmotini and presumably was associated with the appearance of derived Marmotina.

Paleobiogeography

Even though the Paleogene species of *Palaeosciurus*, which are representative of the early ground squirrels, were initially documented in Western Europe at 32 Ma, the results of the phylogenetic and biogeographic analyses (Sinitsa *et al*., 2022) indicate that an early Oligocene dispersal event from North America to Eurasia may have occurred via the North Atlantic Land

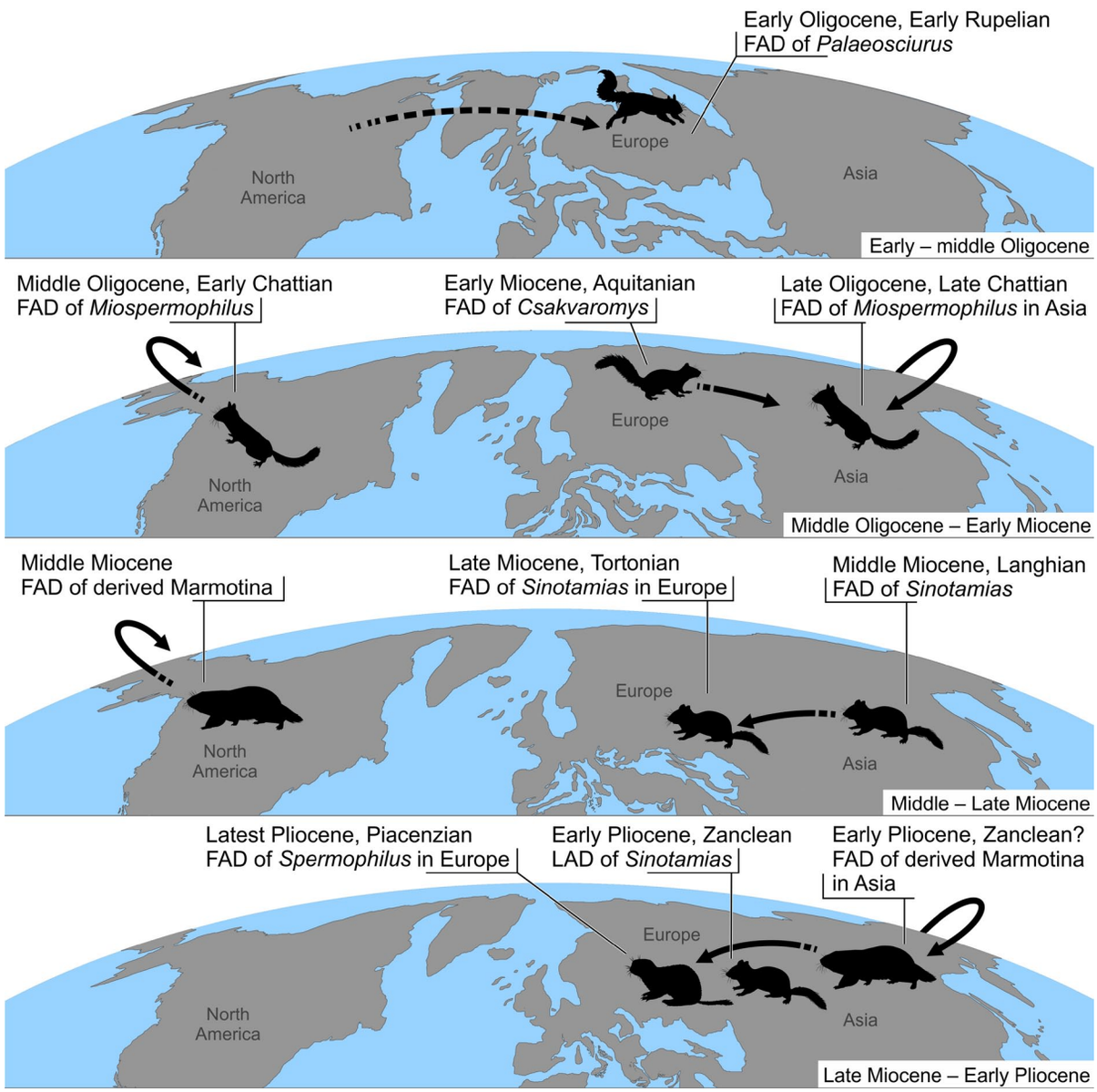

Fig. 6. Paleogeographic maps of the Northern Hemisphere during the Oligocene and Neogene showing hypotheses for intercontinental migrations and dispersals of Marmotini. Maps from Rob Blakey CPGeosystems, with modifications.

Bridge (Fig. 6). According to the craniodental morphology data of the basal Marmotini genera, *Palaeosciurus* gradually evolved into *Csakvaromys* (Sinitsa *et al*., 2022). This was followed by cladogenesis among the European (*C. besana*, *C. bredai*, *C. turolensis*, and *C. giganteus*) and Asian (*S. kumkolensis* and *S. mongolicus*) representatives of the genus. The Marmotini migration event was followed by several migration waves across the Bering Land Bridge that occurred during the late Oligocene and the Early Miocene and resulted in the sudden appearance of *Miospermophilus* in the Eurasian fossil record (Sinitsa, 2018; Sinitsa *et al*., 2022). The oldest-known Asian *Sinotamias*, *S. primitivus*, comes from the late Middle Miocene beds of the Tunguur Formation in China (Qiu, 1996). This first occurrence of *S. primitivus* is followed by the appearance of *S. anatoliensis* in the early Late Miocene of Turkey (Bosma *et al*., 2013). These temporal evidences imply that the East Asian records are somewhat older than the European ones. Ancestry-descendant relationships between *Sinotamias* and Asian *Miospermophilus* (Sinitsa & Delinschi, 2023; Sinitsa & Tesakov, 2023) provide a strong indication that the genus originated in Asia and point to a connection to the eastern Asian basal Marmotina. The earliest appearance of European *Sinotamias* is an unnamed species at Frunzovka 2 (Southern Ukraine), which is dated as early Turolian, indicating a slightly younger age when compared with records of *S. primitivus* and *S. anatoliensis*. This temporal distribution, combined with the lack of pre-Turolian European records of *Sinotamias*, implies that the immediate ancestry of *Sinotamias* in Europe may have been Asian. By analogy with other taxa that first appear in the early Turolian of Southeastern Europe, these specimens indicate that *Sinotamias* was among the many mammalian immigrants to Europe at the Vallesian–Turolian boundary. The early accounts of these immigrant taxa in eastern European assemblages are not unexpected and are consistent with a significant shift in the vegetation, which saw the disappearance of forested environments and their replacement by open grassland, savannah-type environments. The fossil record of *Sinotamias* in southeastern Europe and Greece is rather complete. A persistent, albeit never dominant, component of the Turolian rodent communities in Moldova, Southern Ukraine, and southwestern Russia were three species: *S. lungui*, *S. topachevskyi*, and *S. gromovi*. The first appearance of the genus in southeastern Europe is documented by the specimens of *Sinotamias* sp. from the middle Turolian of Samos. *Sinotamias atsali* appeared in southeastern Europe only in the late Turolian, evidently as a result of dispersal from Anatolia, where the species was present at least since the early Late Miocene (Bosma *et al*., 2013; Sinitsa, 2018; Sinitsa & Delinschi, 2023). In Asia the genus persisted into the Early Pliocene. The scarce remains from the terminal Miocene Bobrik site in Southern Ukraine may represent the latest occurrence of *Sinotamias* in Europe.

The subsequent evolutionary history of Marmotini in Europe is associated with the appearance of the modern genus *Spermophilus*, followed by the marmots (Fig. 6). Their appearance was preceded by a vast period of European "marmotine vacuum" spanning around 2.2 Ma and coincided with the arrival of jerboas of the genus *Plioscirtopoda,* which dispersed into southeastern Europe from the east (Sinitsa & Pogodina, 2019). The appearance of marmots and sousliks in Eurasia, in turn, manifests the third marmotine dispersal event from North America across the Bering land bridge at the Miocene-Pliocene boundary.

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