



HERPETOTHERIIDAE, TALPIDAE, AND ERINACEIDAE FROM THE EARLY MIOCENE FISSURES OF MOKRÁ-QUARRY (SOUTH MORAVIA, THE CZECH REPUBLIC)

ISAAC BONILLA-SALOMÓN^{1,2,*}, FLORENTIN CAILLEUX^{1,3}, PETER JONIAK¹, MARTIN IVANOV⁴, MARTIN SABOL¹

¹Comenius University, Faculty of Natural Sciences, Department of Geology and Paleontology, Mlynská dolina, Ilkovičova Str. 6, SK-84215 Bratislava, the Slovak Republic; e-mail: salomon1@uniba.sk, peter.joniak@uniba.sk, martin.sabol@uniba.sk.

²Institut Català de Paleontologia Miquel Crusafont, Universitat Autònoma de Barcelona, Edifici ICTA-ICP, c / de les Columnes, s/n, Campus de la UAB, 08193 Cerdanyola del Vallès, Barcelona, Spain.

³Naturalis Biodiversity Center, Darwinweg 2, 2333 CR Leiden, the Netherlands; e-mail: florentin.cailleux@naturalis.nl.

⁴Masaryk University, Faculty of Science, Department of Geological Sciences, Kotlářská 267/2, 611 37 Brno, the Czech Republic; e-mail: mivanov@sci.muni.cz.

*corresponding author

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Abstract: Fossils of Metatheria and Eulipotyphla from the karstic fissures MWQ2/2003, MCQ3/2005 and MWQ4/2018 of Mokrý-Quarry (South Moravia, the Czech Republic) are studied. These Early Miocene fissures have yielded remains of the herpetotheriid *Amphiperatherium frequens*, together with the erinaceids *Amphechinus* cf. *baudeloti*, *Galerix exilis*, and *G. symeonidisi*. The talpid *Talpa* sp. has also been identified. The rare remains of *Amphiperatherium frequens* represent the first description of this species from the Early Miocene of the Czech Republic. The erinaceid *Amphechinus* cf. *baudeloti* could be a convenient structural ancestor of *A. baudeloti*, although the scarcity of remains hampered a clear taxonomic verdict. In addition, the relatively abundant remains of Galericinae in the studied fissures made it possible to identify a mixture of two *Galerix* species, *G. exilis* and *G. symeonidisi*. Their cooccurrence is evidenced at least in MWQ2/2003. The dentognathic and postcranial remains of Talpidae clearly point to *Talpa* sp. The relatively low diversity of insectivores recovered from Mokrý-Quarry fissures agree with previous studies concerning the paleoenvironmental reconstruction, depicting Mokrý-Quarry as a dry karst plateau close to water bodies and patches of woodland. The wide range of small mammal species found in Mokrý-Quarry fissures suggests a diverse regional environment, making Mokrý-Quarry a reference locality in the Early Miocene of Central Europe.

Key words: Metatheria, Eulipotyphla, Burdigalian, Moravian Karst

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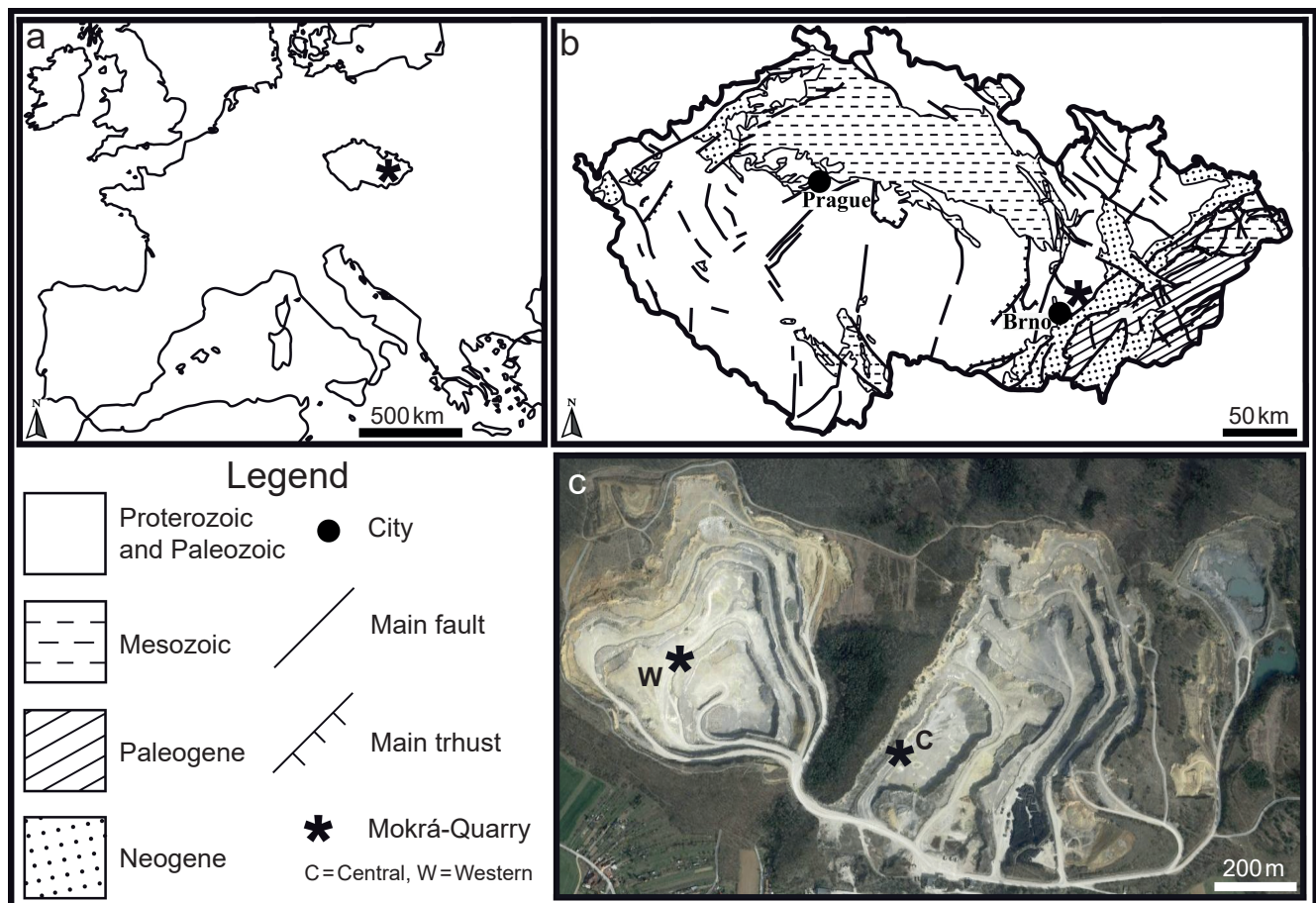
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Introduction

Among small mammals, the study of rodent remains is of great value, thanks to its biochronological purposes (van der Meulen et al. 2011). Rodentia allow establishing robust correlations between assemblages from different regions. By contrast, non-rodent small mammals, like Metatheria, Lagomorpha, Eulipotyphla and Chiroptera receive less attention, because of their lower abundance. Therefore, the taxonomic study of these groups is often neglected in favor of rodents. The identification of Eulipotyphla taxa is partly based on a subtle combination of characters and size ratios (van den Hoek Ostende and Fejfar 2006), making taxonomic verdicts heavily dependent on the amount of collected material. The

same is true for Metatheria, which are rather scarce in the fossil record (Bennet et al. 2018). Thus, the rare localities in which those requirements are met (i.e., large amounts of material, combination of characters and size ratios) are of particular importance. The study of Eulipotyphla and Metatheria is necessary to obtain a complete taxonomic overview of small mammal assemblages but is also motivated by their role as paleoecological and paleoenvironmental indicators.

In Central Europe, the study of Eulipotyphla and Metatheria has improved considerably in the last decades (e.g., Ziegler 1983, 1990, 2006, Mészáros 1999, Ziegler and Daxner-Höck 2005, Ziegler et al. 2005, van den Hoek Ostende and Fejfar 2006, Prieto 2007, Kliemann 2013,



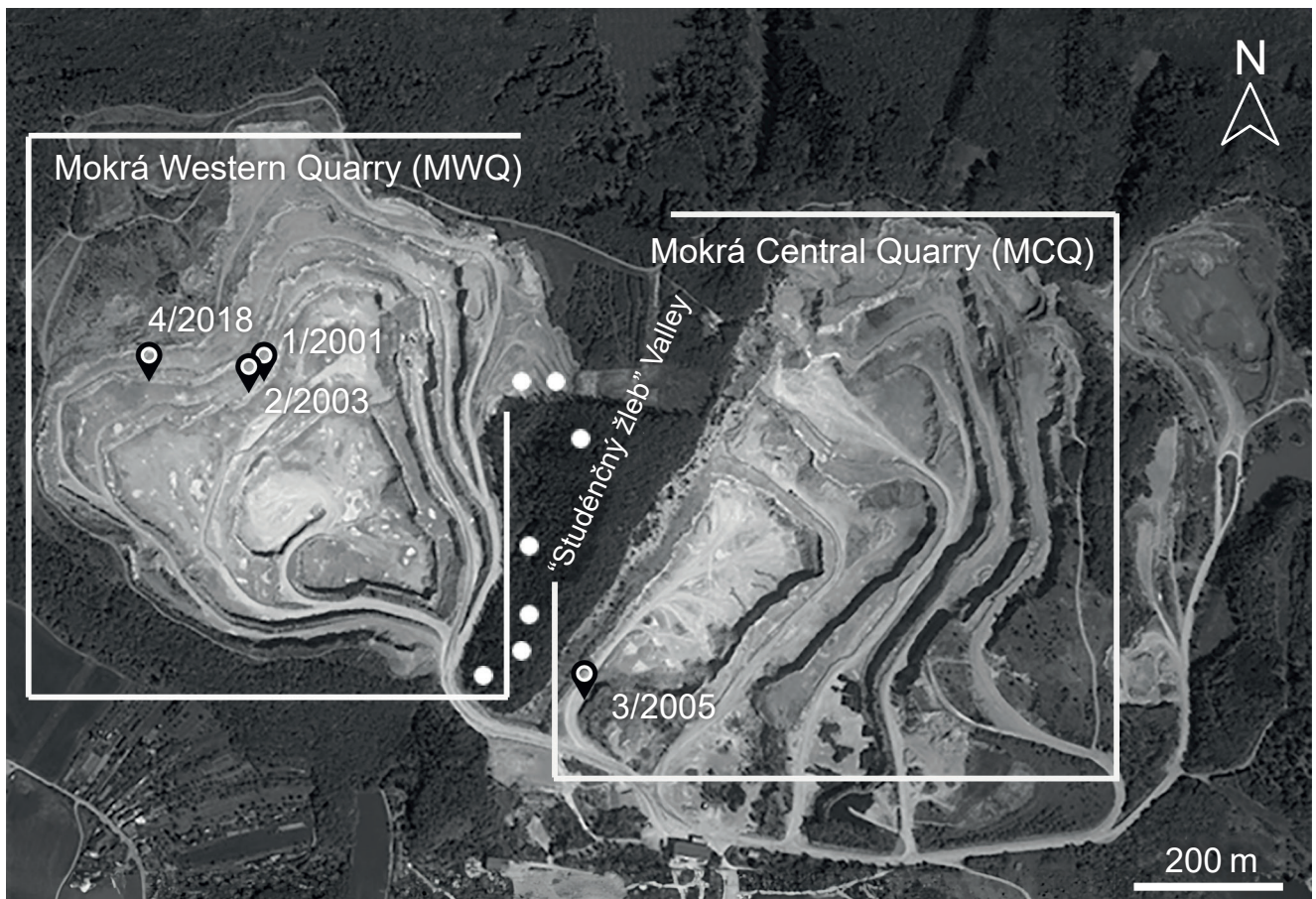
Text-fig. 1. Location of Mokra-Quarry. a: Geographical position of Mokra-Quarry in Europe. b: Schematic geological map of Czech Republic. c: Position of Western and Central Quarries. Modified from Lujan et al. (2021).

Daxner-Hock et al. 2016, Cailleux et al. 2023, 2024, in press). Regarding the territory of the Czech Republic, Fejfar and Sabol (2005) published preliminary faunal lists of Eulipotyphla from Czech and Slovak Neogene assemblages. In that work, remains from several Early Miocene localities are listed, but no detailed descriptions and measurements were provided. The most recent detailed descriptions of Eulipotyphla assemblages from the Early Miocene of the Czech Republic come from the MN 3 site of Ahnikov I (also known as Merkur-North; van den Hoek Ostende and Fejfar 2006, 2015). A single species of erinaceid, five species of Talpidae and four species of Dimylidae were described in these works. As for other MN 3 sites in the Czech Republic, such as Tuchoice, no detailed descriptions have been published so far.

Regarding MN 4 sites, Fejfar and Rocek (1988) indicated that a detailed paper on the Eulipotyphla from Dolnice sites was in preparation. Several years later, Fejfar and Sabol (2005) mentioned that this work was still in progress. However, no complete descriptions of the Eulipotyphla material from Dolnice has been published to date. The same is true for Orechov, the other remarkable MN 4 locality in the Czech territory, where its Eulipotyphla are still unstudied. As for Metatheria assemblages in the Early Miocene of the Czech Republic, no comprehensive studies have been published so far. The only exception constitutes the work of Fejfar (1966) in which a succinct description of *Peratherium* sp. from Dolnice and Orechov are included.

One of the latest sites of Early Miocene age to be discovered in the Czech Republic is Mokra-Quarry. The open-cast limestone mine of Mokra-Quarry is located 12 km ENE of Brno (Text-fig. 1), and it is situated on the Mokra Plateau, in the SE of the Moravian Karst (see Ivanov et al. 2006, for a detailed geological context). Mokra-Quarry consists of three separate quarry sites, the Western (MWQ), the Central (MCQ) and the Eastern (MEQ). Since commercial extraction works started at the beginning of the 21st century (Ivanov and Musil 2004, Ivanov et al. 2006), several karst fissures have been located in the Western and Central Quarries: 1/2001 Turtle Joint (hereafter MWQ1/2001), 2/2003 Reptile Fissure (hereafter MWQ2/2003), Turtle Cave (hereafter MWQ-TC4 2001) and 4/2018 (hereafter MWQ4/2018) in the Western Quarry; and 3/2005 (hereafter MCQ3/2005) in the central part of the Quarry (Text-fig. 2).

Most of the research on Mokra-Quarry localities has focused on the herpetofauna from different fissures (Ivanov et al. 2006, 2018, 2020, Ivanov 2008, Lujan et al. 2017, 2021). As for mammals, the first preliminary descriptions of medium-sized specimens were conducted by Ivanov and Musil (2004). The first faunal list of medium and large mammals was published by Ivanov et al. (2006), without providing measures or detailed descriptions of the fossil material. Regarding small mammals, Sabol et al. (2007) published a preliminary study on the fauna from MWQ1/2001. More recently, Bonilla-Salomon et al. (2021a) described for the first time the small mammal



Text-fig. 2. Position of Mokrá-Quarry fissures and locations of boreholes (white dots) along Studénčský žleb valley (source Mapy.cz; modified).

remains from MWQ1/2001, including the scarce non-rodent assemblage. Bonilla-Salomón et al. (2021b) also published the sciurid remains from MWQ2/2003, MCQ3/2005 and MWQ4/2018. However, non-rodent small mammal remains from MWQ2/2003, MCQ3/2005 and MWQ4/2018 have not been studied in detail, as only preliminary results have been published (Bonilla-Salomón et al. 2022a). The present work constitutes the first research conducted in which measurements and detailed descriptions of remains of Metatheria and Eulipotyphla from an Early Miocene (MN 4) site in the Czech Republic are published. Moreover, the material from MWQ1/2001 has been redescribed and new, previously undescribed material has been studied as well. Furthermore, the paleoenvironmental reconstruction is revised based on the hypothesised paleoecology of the taxa described here.

Material and methods

The small mammal faunas from MWQ1/2001, MWQ2/2003 and MCQ3/2005 were discovered during field campaigns led by M. Ivanov and R. Musil (Masaryk University, Brno, the Czech Republic) during the years 2002–2005 (Ivanov and Musil 2004). More recently, Mokrá-Quarry has yielded another mammal-bearing fissure: MWQ4/2018, from which small mammal remains have also been recovered. The fossil remains, mixed in clays and sands, were obtained by washing in sieves of 0.5 mm mesh

(see Ivanov et al. 2006, Luján et al. 2021). The material is currently housed in the collections of the Department of Geological Sciences (Faculty of Science, Masaryk University) under the inventory numbers SMM/009-09-11/372,009, Pal. 3000–4100. The upper cheek teeth are indicated by upper case letters (P3, DP4, P4, M1, M2, M3, M4), and the lower cheek teeth by lower case letters (p1, p2, dp4, p4, m1, m2, m3, m4). When the distinction between first and second molars is doubtful, they are indicated as M1/2 or m1/2.

The measurement protocol for Erinaceidae has yet to be standardized. We follow here the measurement methods of Prieto and Rummel (2009) instead of traditional perpendicular methods (e.g., de Jong 1988, Engesser 2009, Klietmann et al. 2014). Postcranial measurements of Talpidae follows Klietmann et al. (2015a). Measurement methodology for *Amphiperatherium* follows Crochet (1980), Klietmann et al. (2014) and Gernelle et al. (2024). Measurements of teeth were taken with a Carl Zeiss Stemi 305 microscope, a Carl Zeiss W-PI 10×/23 Microscope Focusable Eyepiece, and a calibrated micrometer eyepiece on a Leica MZ75 stereomicroscope. All measured data are given in millimetres (mm). Micrographs were taken using a Quanta FEG 250 Scanning Electron Microscope (SEM) at Institute of Electrical Engineering of the Slovak Academy of Sciences (SAS) in Bratislava (Slovakia).



Text-fig. 3. Scanning electron micrographs of *Amphiperatherium frequens* from MWQ2/2003 and MWQ4/2018 in occlusal view. **a:** Left M2 (Pal. 3546). **b:** Right M4 (Pal. 3547). **c:** Left p1 (Pal. 3511). **d:** Fragment of right m4 (Pal. 3512). **e:** Fragment of left mandible with m3 and m4 (Pal. 4204). All teeth are figured as left elements. From Bonilla-Salomón et al. (2022a). Scale bar = 1 mm.

Systematic paleontology

Infraclass Metatheria HUXLEY, 1880

Family Herpetotheriidae TROUESSART, 1879

Genus *Amphiperatherium* FILHOL, 1879

***Amphiperatherium frequens* (VON MEYER, 1846)**

Text-fig. 3

Studied material and measurements.

MWQ2/2003: one P3 (Pal. 3538: 1.76×0.68); one fragment of upper premolar (Pal 3542); one left M2 (Pal. 3546: 2.05×2.15); one right M4 (Pal. 3547: 1.95×2.45); one left p1 (Pal. 3511: 1.47×0.67); one left p2 (Pal. 3515: 1.83×0.85); one left p3 (Pal. 3513: 1.9×0.89); one fragment of right m4 (3512).

MWQ4/2018: one fragment of left mandible with fragment of m3 and m4 (Pal. 4204: m4: 2×0.93).

Description. **P3.** The tooth is labiolingually compressed. The main cusp is in a central position. The anterior cuspule is small. There is a well-developed crest that connects the main cusp to the posterior margin of the tooth. A posterior cingulum is present.

M2. The tooth has a subtriangular outline in occlusal view. The ectoflexus is concave between the antiparacone and antimetacone; there is no anticone between both cusps (Text-fig. 3a). The parastyle is distinct and isolated from the antiparacone. The metacone is higher than the paracone, and both cusps are connected by the premetacrista and the slightly shorter postparacrista. The postmetacrista is elongated and curved. The metastyle is indicated. The paracingulum is straight. The trigon basin is wide. The protocone is connected to the base of the paracone and metacone by two almost symmetrical crests. Three roots are preserved; the lingualmost is the thickest.

M4. The two-rooted tooth has a triangular outline in occlusal view and is strongly reduced in length. The paracone is conical and elongated. From it, the preparacrista runs labially to the parastyle. The parastyle is elongated lingually. The postparacrista and the premetacrista are connected. The metacone is small, protruding posteriorly. The protocone

is the largest cusp (Text-fig. 3b). The preprotocrista runs labially, ending at the base of the paracone. There is a postprotocrista running towards the metacone, without reaching it. The paracingulum begins near the very base of the paracone and joins the parastyle.

p1. The tooth has two roots. The main cuspid is in anterior position. The posterior cristid starting from this cuspid is labially oriented and turns posterolingually to reach the posterior talon, where a small cuspid is visible (Text-fig. 3c).

p2. The posterior cingulid is large. Its lingual side is wider and concave. There is a small but distinct posterior cuspid.

p3. The two-rooted tooth has a thick main cuspid and a short postcingulid. There is no anterior bulge.

m3. The protoconid is the only preserved cuspid of the trigonid. The protolophid appears to be complete. The hypoconid is anterior to the entoconid. The postcristid runs slightly posteriorly.

m4. In Pal. 3512, only the elongated talonid is preserved. The entonid is well-preserved, as an enlargement of the entocristid. The postentocristid is low and connects to a strong hypoconulid (Text-fig. 3d). The hypoconid is worn. The postcristid is oblique, connecting the two posterior cuspid. Pal 4204 m4 shows a well-developed anterior cingulid. The paraconid is well-developed. The paralophid shows a moderate central notch. The talonid is much narrower than the trigonid (Text-fig. 3e). The hypoconid is in a slightly more anterior position than the entoconid. The entocristid and the oblique crista run anteriorly, the first one ending at the base of the metaconid and the second one at the meeting point of protoconid and metaconid.

Fragment of mandible. Pal. 4204 preserves part of the mandible carrying m3 and m4. The ramus horizontalis is high, with flat sides. It shows a wide lingual foramen below the posterior root of the m3.

Remarks. The Herpetotheriidae TROUESSART, 1879 is a fossil family of the infraclass Metatheria, with no extant relatives. This family ranges from the Late Cretaceous to the Middle Miocene (for a complete literature review of the Herpetotheriidae, see Klietmann 2013). Herpetotheriids

were classically placed within the Didelphidae GRAY, 1821 until Kirsch et al. (1997) gave them a family rank within Marsupialia. Lavedèze et al. (2012) considered that the morphological characters that differentiate *Amphiperatherium* from *Peratherium* AYMARD, 1850 are very variable, and consequently not diagnostic enough, as already noted by von Koenigswald (1970). Later, Lavedèze et al. (2020) reviewed the relationship between both genera, and its phylogenetic analysis suggests a close relationship between *Amphiperatherium* and *Peratherium*, establishing the subfamily Peratheriinae to include both genera.

Of all the Herpetotheriidae, *Amphiperatherium* is the only genus that occurs in Early Miocene European localities. *Amphiperatherium* was first recorded in Europe during the Eocene, a period when the genus reached its highest specific diversity (Crochet 1980). After that, the genus gradually lost diversity, finally becoming extinct during the Middle Miocene (Furió et al. 2012). The presumed last occurrence of this genus was reported from Ergeten (MN 7+8, Switzerland; Kälin and Kempf 2009). However, as discussed by Prieto and Rummel (2015), the faunal lists provided by Kälin and Kempf (2009: 124) “do not reflect reality”. Therefore, Prieto and Rummel (2015) consider that the last occurrence of *Amphiperatherium* in Swiss territory belongs to the *Megacricetodon gersii*-*M. similis* interval zone, between 14 and 14.2 Ma ago, which is in agreement with the German findings.

Amphiperatherium frequens has been recorded in many Central European localities from the Miocene, when environmental conditions were rather humid, although remains of the species have also been found in humid Spanish localities (Furió et al. 2012). However, based on Crespo et al. (2020), *Amphiperatherium* might also have survived in rather dry environments.

Regarding MN 4 sites in Central Europe, remains of *Amphiperatherium frequens* have been found in several localities (Ziegler and Fahlbusch 1986, Ziegler 1998a). In Czech sites, *A. frequens* has been found in Tuchořice and Ahníkov I, both MN 3 sites (Fejfar et al. 2003) and Dolnice 1–3 (MN 4; Fejfar and Roček 1988). However, no detailed descriptions of the species in these assemblages have been ever published. Therefore, the *Amphiperatherium* remains from Mokrý-Quarry constitutes the first detailed description of the genus in the Czech Republic.

The marsupial species from MWQ2/2003 and MWQ4/2018 clearly belong to *Amphiperatherium frequens*, which can be distinguished by the presence of a slender cristid in the talonid basin only interrupted by a small notch between entoconid and hypoconulid (Text-fig. 3d, e), among other traits. The measurements fit well within the material from other Central European localities, such as Erkersthofen, Wintershof-West and Petersbuch 2 (all Germany; see Klietmann 2013: fig 5). Based on the size differences and morphological variability of *A. frequens* during the Early Miocene, von Koenigswald (1970) erected three subspecies, which were not followed by Crochet (1980). Furthermore, Ziegler and Fahlbusch (1986) pointed out several dental characters, which together with size reduction indicate evolutionary degrees in *A. frequens*. Later, Ziegler (1990) used these subspecies as chronosubspecies. The omnipresence of a conical antimetacone on the M2, as observed in Pal. 3546 (Text-fig. 3a) in the entire population

instead of only a bicuspid one, is a tendency observed in the population sequence of Wintershof-West – Petersbuch 2 – Erkersthofen 1. Moreover, the M2 from MWQ2/2003 resembles morphologically, as in size, the single M2 recovered from Oberdorf 4 (Ziegler 1998a: pl. 3, fig. 6). However, the scarcity of the remains found in the assemblage MWQ2/2003 hampers any inference of its evolutionary stage.

Infraclass Eutheria HUXLEY, 1880

Order Eulipotyphla WADDELL, OKADA et HASEGAWA, 1999

Family Erinaceidae FISCHER [DE WALDHEIM], 1814

Subfamily Erinaceinae FISCHER [DE WALDHEIM], 1814

Genus *Amphechinus* AYMARD, 1850

***Amphechinus* cf. *baudeloti* GIBERT, 1974**

Text-fig. 4

Studied material and measurements. MWQ2/2003: one I1 (Pal. 3398: 1.60×1.18); one P2 (Pal. 3544: 1.64×1.13); one left M1 (Pal. 3504: 3.32×3.46×3.65); one fragment of right M1 (Pal. 3505); two left M2 (Pal. 3396: 2.65×3.24×2.40; Pal. 3507: 2.45×3.19×2.43); one right M2 (Pal. 3506: 2.60×3.20×2.46).

MCQ3/2005: one left M2 (Pal. 3932: 2.74×3.37×2.50).

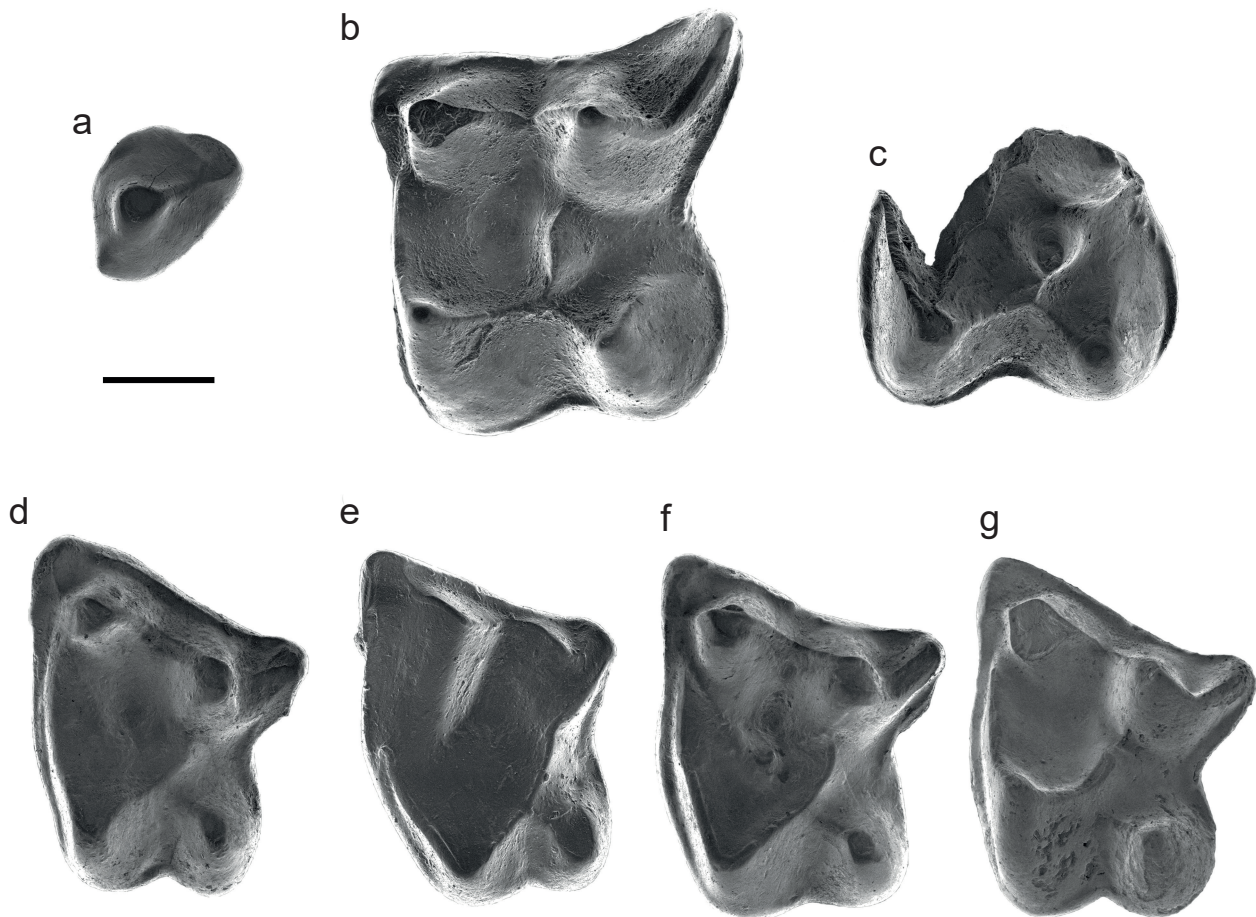
Description. **I1.** The incisor is large and robust, with a slightly caniniform morphology. The root is curved posteriorly.

P2. The tooth has two roots. The main cusp is placed in an anterolabial position (Text-fig. 4a). There is a short, central, posterior crest reaching the posterolabial edge of the tooth.

M1. Pal. 3504 is complete (Text-fig. 4b), whereas in Pal. 3505 only the lingual half of the tooth is preserved (Text-fig. 4c). The tooth has a quadrangular shape; all the cingulums are well-developed. The protocone is conical; the preprotocrista is thicker than the other crests and ends at the base of the paracone, without fusing with it. The protoconule is not distinguishable. The paracone is somewhat wider than the protocone. There is a small parastyle anterior to the paracone (Pal. 3504; Text-fig. 4b). The postprotocrista joins the prehypocrista and runs towards the metaconule, which is rounder in Pal. 3505 (Text-fig. 4c). There is a well-marked groove that separates the metaconule from the base of the high metacone. There is a well-developed postmetacrista, but a metastyle is absent. The posthypocrista is weak and short.

M2. These teeth are characterized by a shortening of the postmetacrista and an enlargement of the parastyle compared to M1 (Text-fig. 4d–g). Both the anterior and posterior cingulum are well-developed. There is a very large parastyle in Pal. 3506, whereas in Pal. 3507 it is much smaller. A low preprotocrista starts from the protocone, joining the base of the high paracone. The postprotocrista leads directly to the metacone. The metaconule is fused into the postprotocrista. There is a short prehypocrista and an incipient posthypocrista. The former ends below the postprotocrista.

Remarks. Erinaceinae remains in the fossil record are usually very rare and fragmented. Their phylogeny is poorly known (Ziegler 2005, Engesser 2009, van Dam et al. 2020, Cailleux et al. 2023). According to van Dam et al. (2020),



Text-fig. 4. Scanning electron micrographs of *Amphechinus* cf. *baudeloti* from MWQ2/2003 and MCQ3/2005 in occlusal view. **a:** Left P2 (Pal. 3544). **b:** Left M1 (Pal. 3504). **c:** Fragment of right M1 (Pal. 3505). **d:** Left M2 (Pal. 3396). **e:** Left M2 (Pal. 3507). **f:** Right M2 (Pal. 3506). **g:** Left M2 (Pal. 3932). All teeth are figured as left elements. Scale bar = 1 mm.

the scarcity of Erinaceinae remains is due to a combination of their overall rarity in the ecosystems compared to other small mammals and their lesser abundance in the diet of birds of prey (Corbet 1988).

Only three Erinaceinae genera are recorded from the Early Miocene of Europe. These include the genus *Dimylechinus* HÜRZELER, 1944, last recorded in MN 2 (Huguéney 1997, Huguéney and Maridet 2022), and the advanced genus *Mioechinus* BUTLER, 1948, first recorded in MN 4 of Spain (Crusafont et al. 1955). Many Early Miocene assemblages are attributed to several species of the genus *Amphechinus*, recorded in Europe from the late Oligocene to the Middle Miocene (e.g., Baudelot 1972, Gibert 1974, Ziegler 1990, 2005, Huguéney and Maridet 2022). The earliest Miocene species of *Amphechinus* (e.g., *A. arvernensis* BLAINVILLE, 1839, *A. edwardsi* FILHOL, 1879) were small, with typically insectivorous antemolars bearing many small sharp cusps and ridges (van Dam et al. 2020), together with rectangular M1 and uncompressed M2 (see Viret 1938, Ziegler 1998b, Ziegler et al. 2007). These characteristics are not consistent with those found in the assemblage from Mokra-Quarry.

Amphechinus is not recorded in Europe during the MN 3. The European forms identified in MN 4 sites show cranial and morphological characteristics that reflect a broadening of the dietary spectrum and are characterized by a more

squared M1 and a greater posterior reduction of the M2. In the Miocene of Spain, *Amphechinus* has been recovered from several sites (see van den Hoek Ostende and Furio 2005). Notably, *Amphechinus baudeloti* from MN 4 assemblages shares morphological similarities with the sample from Mokra-Quarry, despite its slightly larger size. Moreover, this species often shows a distinct metaconule and a hypocone connected to the postprotocrista, which is indicative of already modern *Amphechinus* species (Baudelot 1972, Gibert 1974, van Dam et al. 2020). This is also observed in the M1s from Mokra-Quarry.

Concerning MN 4 sites from Central Europe, remains of *Amphechinus* have been identified in the German localities of Petersbuch 2 and Erkertshofen 2 (Ziegler 2006). However, no descriptions, measurements or figures have been published. Regarding Czech sites, in the preliminary faunal lists of Fejfar and Rocek (1988) and Fejfar and Sabol (2005) about Dolnice, no remains of *Amphechinus* are listed. The same applies to the MN 3 sites of Ahnikov I and Tuchořice, in which the faunal list published by Fejfar et al. (2003), and the later description of Erinaceidae by van den Hoek Ostender and Fejfar (2006) mentions no remains of *Amphechinus*. Therefore, the case of Mokra-Quarry constitutes the only Czech site where remains of the genus have been found so far. Based on the evolutionary stage of

the morphological characteristics, the *Amphechinus* from Mokrá-Quarry probably represents an early occurrence of *A. baudeloti*. However, the scarcity of the recovered remains and the somewhat smaller size prevents a more confident statement about its taxonomical status. Therefore, it is referred to here as *Amphechinus* cf. *baudeloti*.

Subfamily Galericinae POMEL, 1848

Genus *Galerix* POMEL, 1848

Galerix exilis DE BLAINVILLE, 1839

Text-fig. 5a–e

Studied material and measurements. MWQ2/2003: one right P3 (Pal. 3543: 1.69×1.37); one damaged left M2 (Pal. 3519).

MCQ3/2005: one fragment of right M1 (Pal. 3909).

MWQ4/2018: one right M1 (Pal. 4201: 2.56×2.82×3.06); one right M2 (Pal. 4200: 2.13×2.68×2.62).

Description. P3. The tooth has one main lingual cusp (Text-fig. 5a) and is subtriangular in shape. The protocone is connected to a small parastyle. There is a slightly curved and moderately high crest starting from the paracone and ending at the posterolabial margin of the tooth. This crest ends into a small thickening.

M1. The paracone and metacone are connected by a thin metaloph. The parastyle is well-developed and is connected to the base of the paracone. Pal. 3909 shows a distinguishable protoconule (Text-fig. 5b), absent in Pal. 4201 (Text-fig. 5c). Pal. 3909 also shows a connection between the postprotocrista and the metaconule (Text-fig. 5b). This connection is absent in Pal. 4201 (Text-fig. 5c). The metaconule is connected to the base of the metacone through the premetaconule crest. The postmetaconule crest runs posteriorly in Pal. 4201 (Text-fig. 5c) and posterolabially in Pal. 3909 (Text-fig. 5b). In both cases, the postmetaconule crest ends freely before the posterior cingulum. An anterior cingulum is also present.

M2. The preprotocrista ends without connecting to the paracone. There is no clear protoconule. The paracone and metacone are connected by a straight loph. The postmetacrasta is almost labially oriented. On the lingual side, the postprotocrista reaches the metaconule in Pal. 3519 (Text-fig. 5d), whereas in Pal. 4200 (Text-fig. 5e) it does not fully connect to the conule. The metaconule connects to the metacone through the premetaconule crest. The postmetaconule crest runs posteriorly along the base of the metacone without joining it, nor does it connect to the posterior cingulum. Anterior and labial cingulums are also present.

Galerix symeonidisi DOUKAS, 1986

Text-fig. 5f–g

Studied material and measurements. MWQ2/2003: one right P3 (Pal. 3525: 1.44×1.2×1.43); one left M1 (Pal. 3517: 2.21×2.36×2.72).

Description. P3. The tooth is trapezoidal with two well-developed lingual cusps. The protocone is placed slightly anteriorly to the robust paracone. There is a low anterior cingulum running from the protocone to the base of the paracone. The hypocone is somewhat larger and

placed more lingually than the protocone (Text-fig. 5f). The posterior cingulum runs from the posterior side of the hypocone towards the posterior edge of the tooth, where it ends in a well-marked crest departing from the paracone.

M1. The protocone is directly connected to the paracone by the preprotocrista. The postprotocrista and prehypocrista are broad and fused in a single loph. A thin and low crest connects this loph to the well-developed metaconule (Text-fig. 5g). The premetaconule crest reaches the base of the metacone, whereas the postmetaconule crest runs along the lingual side of the metacone and ends freely before the cingulum. The postmetacrasta runs posterolabially, but does not end into a cusp-like metastyle. The paracone is connected to both the hypocone and the metaconule by a broad loph. An incipient posthypocrista is visible (Text-fig. 5g).

Galerix exilis seu *Galerix symeonidisi*

Text-fig. 6

Studied material and measurements. MWQ1/2001: one right M2 (Pal. 3016: 2.10×2.50×2.39); one damaged left M2 (Pal. 3017), two left m2 (Pal. 3018: 2.56×1.46×1.54; 3019: 2.72×1.73×1.77).

MWQ2/2003: one upper incisor (Pal. 3397: 1.02×0.73); one upper canine (Pal. 3534: 1.39×0.65); one fragment of upper canine (Pal. 3539); one P1 (Pal. 3530: 1.30×0.63); one P2 (Pal. 3399: 1.65×0.83); one fragment of P4 (Pal. 3510); one right P4 (Pal. 3503: 2.44×2.11×2.48); one right M1 (Pal. 3518: 2.30×2.73×2.87); two right M3 (Pal. 3520: 1.34×1.57×1.89; 3521: 1.29×1.57×1.87); one p2 (Pal. 3400: 1.35×0.83); one left p2 (Pal. 3545: 1.51×0.82); one p3 (Pal. 3523: 1.39×0.80); one fragment of p3 (Pal. 3535: -×0.97); one left p4 (Pal. 3541: 1.82×1.21); two left m1 (Pal. 3508: 2.70×1.64×1.85; Pal. 3509: 2.91×1.61×1.85); one fragment right m1 (Pal. 3401: -×-×1.81); five left m2 (Pal. 3402: -×1.45×1.49; 3403: 2.34×1.53×1.61; 3531: 2.46×1.64×1.67; 3532: -×1.54×-; 3533: -×1.68×-).

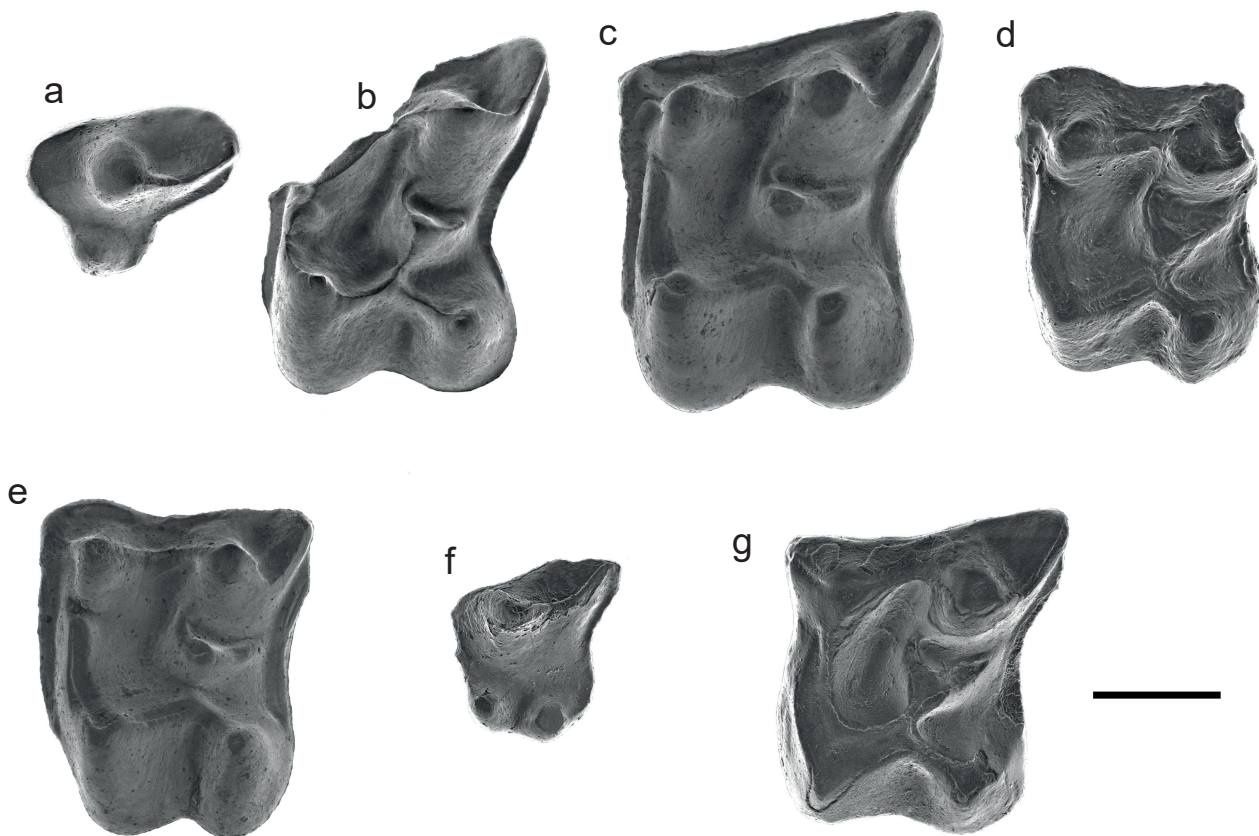
MCQ3/2005: one right p4 (Pal. 3908: 1.94×1.21); one left m2 (Pal. 3934: 2.41×1.47×1.60); one left M2 (Pal. 3933: 2.05×2.62×2.35).

Description. Upper incisor. The monocuspid tooth has a large and posteriorly curved root. **Upper canine.** The tooth shows two roots. It is very narrow, and its main cusp is anterior. The posterior talon is slightly elongated.

P1. The tooth has two roots and small dimensions. The main cusp is in a central position. A posterior cingulum is present.

P2. The tooth shows two roots, the posterior one being thicker. It is more robust in shape than the P1. The cusp is conical. A thin ridge connects its tip to a barely visible posterior cingulum.

P4. The paracone is massive and occupies the labial half of the tooth. A parastyle is present, but it is not connected to the paracone or to the protocone. The latter is about the same size as the hypocone, and both cusps are isolated from each other. There is a crest running labially from the protocone that ends before reaching the paracone (Text-fig. 6a). A cingulum runs from the base of the hypocone along the posterior side of the tooth. It ends below the posterolabial crest of the paracone.



Text-fig. 5. Scanning electron micrographs of *Galerix* taxa from Mokrá-Quarry fissures in occlusal view. a–e: *Galerix exilis*; a – right P3 (Pal. 3543), b – damaged right M1 (Pal. 3909), c – left M1 (Pal. 4201), d – left M2 (Pal. 3519), e – Right M2 (Pal. 4200). f–g: *Galerix symeonidisi*; f – right P3 (Pal. 3525), g – left M1 (Pal. 3517). All teeth are figured as left elements. Scale bar = 1 mm.

M1. The protocone connects directly to the paracone through the preprotocrista; the protoconule is absent. The parastyle is a weak cusplule. A short and straight crest is present between the postparacrista and the premetacrista. The postmetacrista does not end in a clear metastyle. The metaconule is large (Text-fig. 6b) and attached to the base of the metacone through the premetaconule crest. The metaconule is also connected by a low crest to the protocone-hypocone loph. The postmetacrista ends freely near the posterior cingulum.

M2. Pal. 3016 is quite worn (Text-fig. 6c), Pal. 3017 is damaged (Text-fig. 6d), whereas Pal. 3933 is well preserved (Text-fig. 6e). Yet, like in the M1s, its morphology prevents an attribution to the species level. The overall morphology of M2 resembles that of M1. It differs in a more rounded outline in occlusal view, a shorter postmetacrista, a less posterolingual position of the hypocone, and overall by slightly smaller dimensions. There is also a thin crest connecting the metaconule to the protocone-hypocone loph in Pal. 3933, but not Pal 3016-3017 (Text-fig. 6c–e).

M3. The tooth is small and triangular. It is characterized by the presence of three cusps (protocone, metacone, paracone) at the three corners of the tooth, delimitating a rather rounded and shallow basin. The M3 also shows a well-developed parastyle (Text-fig. 6f–g). The metaloph is short. Only the anterior cingulum is present.

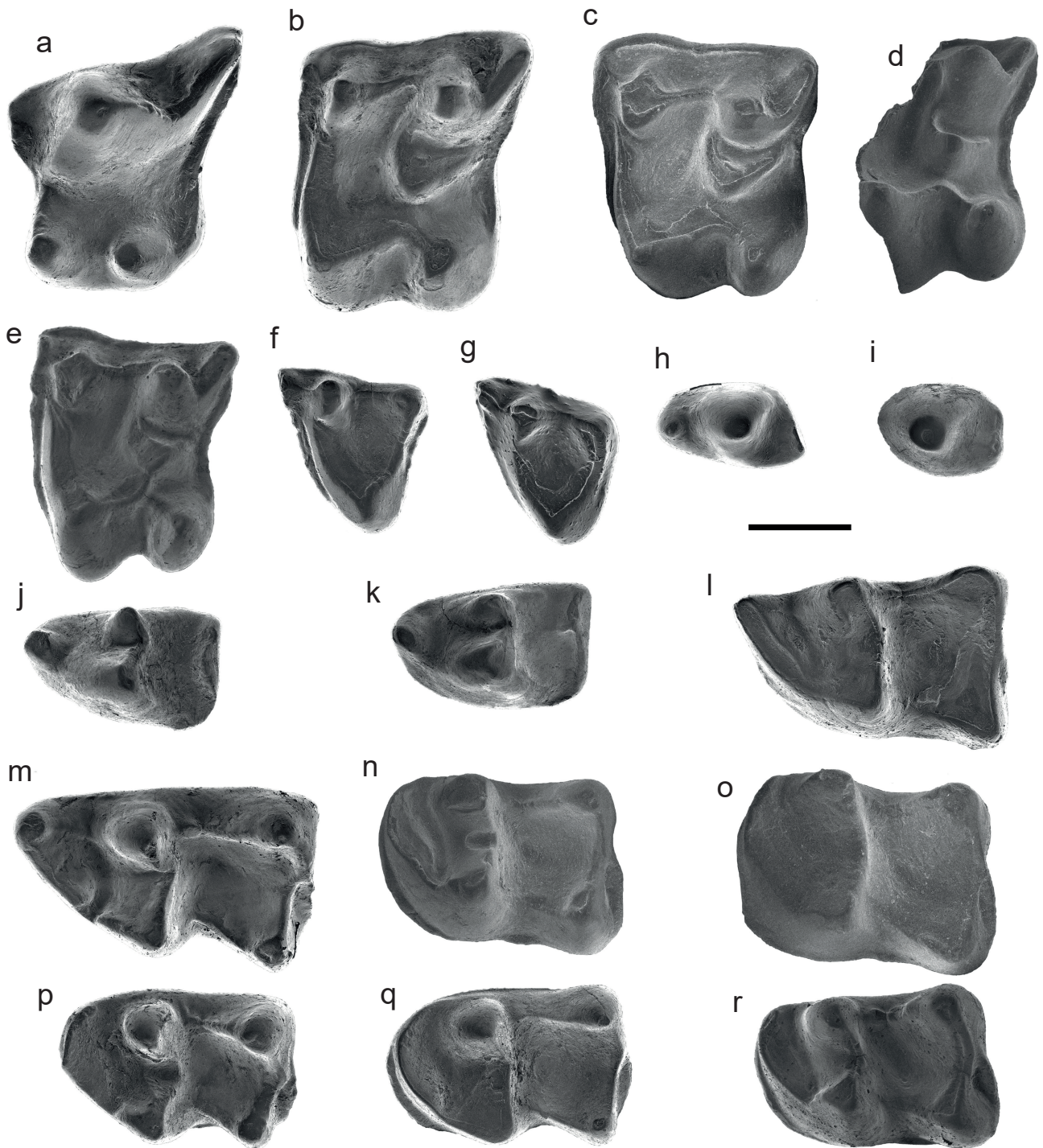
p2. The tooth is two-rooted. The cuspid is more conical than the one in P2. Moreover, it shows a small anterior bulge attached to the base (Text-fig. 6h).

p3. The tooth shows a wider and more compact shape than the p2. The protoconid is placed in a central position. The paraconid is low but clearly defined (Text-fig. 6i). There is a well-defined postcrisid of the posterior lingual side of the tooth.

p4. The tooth is subtriangular. The paraconid is the most anterior cuspid and is isolated from the protoconid (Text-fig. 6j–k). The protoconid is the highest cuspid. It is connected lingually to the metaconid, which is about the same height as the paraconid. The talonid is noticeably lower than the trigonid. There is only an incomplete posterior cristid, which ends before reaching the lingual side of the tooth.

m1. The first lower molars have a trigonid and a talonid of similar length. The protoconid has a triangular shape, while the metaconid is more conical. Both cusps are faintly connected by a metalophid divided into two short cristids. The protoconid also connects to the paraconid, the most anterior cuspid. There is a clear notch anterior to the protoconid (Text-fig. 6l). The talonid displays a high entoconid. It shows a low anterior cristid running lingually toward the trigonid, interrupted by a superficial notch (Text-fig. 6m). The hypoconid is lower and connects to the trigonid through an oblique cristid. The postcrisid connects both trigonid cusps.

m2. The m2 differs from the m1 in the anterior compression of the trigonid, resulting in a more curved paralophid, completely including the paraconid and a shorter length. Also, the postcingulid is more strongly reduced (Text-fig. 6n–r).



Text-fig. 6. Scanning electron micrographs of *Galerix exilis* seu *G. symeonidisi* from Mokra-Quarry fissures in occlusal view. a: Right P4 (Pal. 3503). b: Right M1 (Pal. 3518). c: Right M2 (Pal. 3016). d: Left M2 (Pal. 3017). e: Left M2 (Pal. 3933). f: Right M3 (Pal. 3520). g: Right M3 (Pal. 3521). h: Left p2 (Pal. 3545). i: Left p3 (Pal. 3535). j: Left p4 (Pal. 3541). k: Right p4 (Pal. 3908). l: Left m1 (Pal. 3508). m: Left m1 (Pal. 3509). n: Left m2 (Pal. 3018). o: Left m2 (Pal. 3019). p: Left m2 (Pal. 3403). q: Left m2 (Pal. 3531). r: Left m2 (Pal. 3934). All teeth are figured as left elements. Scale bar = 1 mm.

Remarks. The genus *Galerix* is the most common insectivore in Early Miocene fossil sites in Europe. Although its first records come from the earliest Miocene of Anatolia (de Bruijn et al. 1992, van den Hoek Ostende 1992), it is first identified in Europe in MN 3 localities. To date, four species have been identified in the Early Miocene: *Galerix remmertii* VAN DEN HOEK OSTENDE, 2003, *G. aurelianensis* ZIEGLER, 1990, *G. symeonidisi*, and *G. exilis*. To this is also included “*Galerix*” *kostakii* DOUKAS et VAN DEN HOEK OSTENDE, 2006,

although several authors include this taxon to the genus *Parasorex* VON MEYER, 1865, due to the advanced state of its metaconule on M1–2 (Doukas and van den Hoek Ostende 2006, Prieto et al. 2012, Zijlstra and Flynn 2015). *G. remmertii* is mostly found in Spanish assemblages (van den Hoek Ostende and Furio 2005) and is considered to be closely related to the Central European *G. aurelianensis* (Ziegler 1990), based on the less derived morphology and the high-crested pattern on upper molars. The main

Table 1. Measurements (in mm) of ulnae of *Talpa* sp. from Mokrá-Quarry. 1 – maximal length, 2 – minimum diameter of processus anconeus, 3 – distal diameter, 4 – distal width, 5 – length of incisura, 6 – olecranon length, 7 – olecranon width, 8 – minimum diaphysis diameter (MDD).

Locality	Collection Number	1	2	3	4	5	6	7	8
MWQ1/2001	Pal. 3040	15.02	2.32	3.47	1.32	1.80	5.03	3.37	1.60
MWQ1/2001	Pal. 3048					1.80			1.57
MWQ2/2003	Pal. 4019					1.79			
MWQ2/2003	Pal. 4020					1.78	4.61		
MCQ3/2005	Pal. 4422		2.44			1.71	4.62		1.44
MCQ3/2005	Pal. 4423		2.36			1.77	4.41		1.54
MCQ3/2005	Pal. 4424								
MCQ3/2005	Pal. 4425		2.46			1.77			1.62
MCQ3/2005	Pal. 4426					1.71			
MCQ3/2005	Pal. 4427		2.32			1.71			1.57

difference between them is the slightly smaller size of *G. remmertii* (van den Hoek Ostende 2003). Both species are larger than our specimens. Regarding *G. symeonidisi* and *G. exilis*, the main differences between them reside in the morphology of P3 (Doukas 1986, van den Hoek Ostende and Doukas 2003). The assemblage from Mokrá-Quarry yielded two different P3 morphologies, one that shows a well-developed hypocone and attributed to *G. symeonidisi*, and another that lacks a developed hypocone, referred to *G. exilis* (Ziegler 1983). Despite *G. exilis* rarely possessing a hypocone on P3 (Ziegler 1983), this cusp is weakly developed and the parastyle is still relatively prominent, which is not the case here. In addition, the morphometric variability of the assemblage is consistent with a mixture of *G. symeonidisi* and *G. exilis*, at least in MWQ2/2003. This mixture of two distinct *Galerix* species has been identified in late MN 4 and earliest MN 5 of central Europe thanks to the in-depth study of van den Hoek Ostende and Doukas (2003). Most recovered upper molars resemble *G. exilis*, based on size similarity, a reduced protoconule, and the frequent presence of protoconule-metaconule connection. Pal. 3517 (Text-fig. 5g) constitutes the only exception. The small size, reduced parastyle, and thin posthypocrista more

closely resemble *Galerix symeonidisi*. Although most of the *Galerix* assemblage cannot be attributed to the species level, the overall morphological characteristics suggest that *G. exilis* was more abundant than *G. symeonidisi*.

Family Talpidae FISCHER [VON WALDHEIM], 1814
Subfamily Talpinae FISCHER [VON WALDHEIM], 1814

Genus *Talpa* LINNAEUS, 1758

***Talpa* sp.**
Text-figs 7, 8

Studied material and measurements.
MWQ1/2001: two ulnae (Pal. 3040, Pal. 3048).

MWQ2/2003: one fragment of mandible (Pal. 3404); one right lower premolar (Pal. 3522, 1.53×0.68); five humeri (Pal. Pal. 4014–4018) two ulnae (Pal. Pal. 4019, 4020).

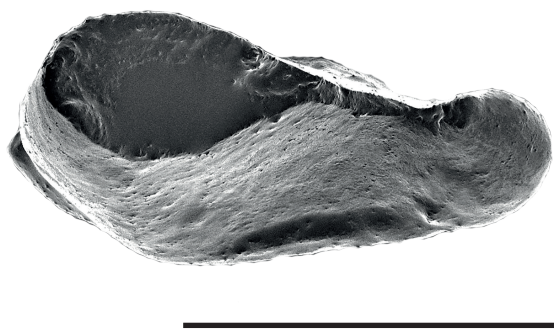
MCQ3/2005: 4 humeri (Pal. 4418–4421); five ulnae (Pal. Pal. 4422–4427).

Measurements. see Tabs 1, 2.

Description. **Lower premolar.** It has two roots. It is much longer than wide. There is a very small cuspule at the anterior edge, isolated from the rest of the tooth. The tip

Table 2. Measurements (in mm) of humeri of *Talpa* sp. from Mokrá-Quarry. 1 – maximal length, 2 – length to tuberculum teres proximal, 3 – length to tuberculum teres distal, 4 – length to pectoral tubercle, 5 – length to tuber maior, 6 – length to processus deltoideus, 7 – distal width, 8 – proximal width, 9 – width capitulum to fossa, 10 – minimum diaphysis diameter (MDD), 11 – MDD parallel to reference line, 12 – width tuber minor to tuber major.

Locality	Collection Number	1	2	3	4	5	6	7	8	9	10	11	12
MWQ2/2003	Pal. 4014	11.51	7.96	4.73	4.507	10.62		7.29	8.86	6.96	3.50	3.28	7.87
MWQ2/2003	Pal. 4015	11.87	8.55	5.03	4.695	10.57	7.43	7.43	9.37	7.09	3.63	3.56	8.51
MWQ2/2003	Pal. 4016	11.41	7.93	4.70	4.527	10.28		7.24		6.88	3.32	3.21	
MWQ2/2003	Pal. 4017										3.55		
MWQ2/2003	Pal. 4018							6.87		6.39	3.58	3.41	
MCQ3/2005	Pal. 4418	10.91		5.09						6.42	3.62	3.57	
MCQ3/2005	Pal. 4419										3.54		
MCQ3/2005	Pal. 4420									6.56	3.63	3.45	
MCQ3/2005	Pal. 4421									6.64	3.69		



Text-fig. 7. Scanning electron micrograph of *Talpa* sp. from MWQ2/2003 in occlusal view. Right premolar (Pal. 3522). Tooth figured as left element. Scale bar = 1 mm.

of the cuspid is in an anteriormost position. From it runs a slender cristid connected to a posterior cuspid (Text-fig. 7). There is a short labial cingulid between the main cuspid and the posterior one. The labial margin is slightly concave.

Fragment mandible. The fragment of the mandible is edentulous. There are two alveoli for the m3 roots, as well as a partial ramus. The condylar process is low and elongated. The masseteric fossa is moderately deep.

Humeri. The pectoral area is large. There is a shallow notch between the tuber major and the crista pectoralis, which continues along the pectoral margin before reaching the crista humeri (Text-fig. 8a). The caput humeri has an elongated drop-like shape (Text-fig. 8b). Attached to its inner base, a short and very thin ridge is found in one of five specimens. The fossa brachialis is deep. The bicipital groove is marked and the musculus flexor digitorum ligament fossa is deep. The supratrochlear fossa and the olecranon fossa are wide (Text-fig. 8a, b).

Ulnae. The diaphysis is almost straight (Text-fig. 8c, d). Below the incisura radialis ulnae there is a deep, elongated basin reaching the base of the olecranon, which is robust and strongly developed. The basin is surrounded by a high posterior ridge. In medial view, the subtriangular basin is found between the incisura and the base of the olecranon.

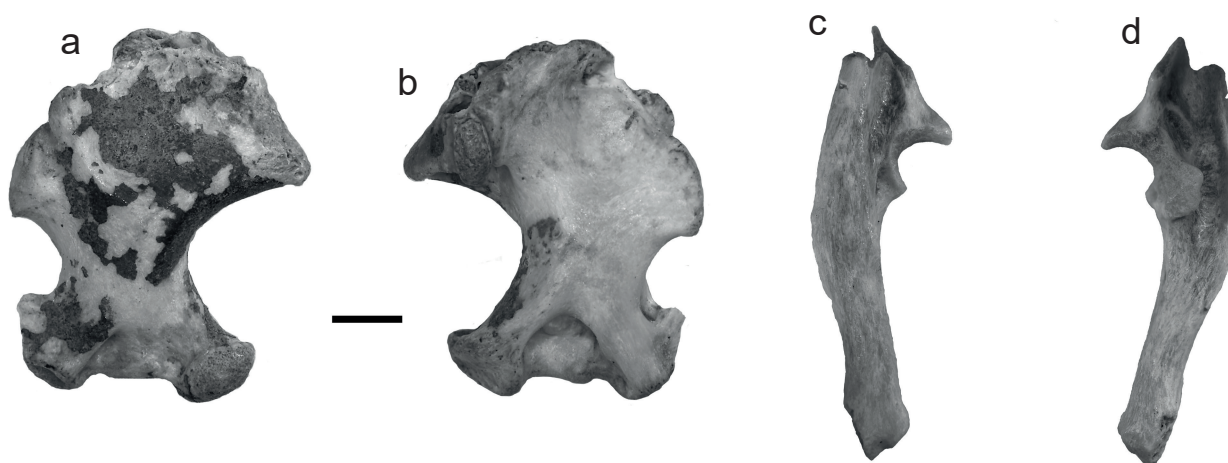
The incisura trochlearis is thick and semicircular (Text-fig. 8d). On the lateral face near the trochlea, there is a short central crest.

Remarks. The taxonomy of fossil Talpidae is not only based on the dentition, but also on the humeri (van den Hoek Ostende and Fejfar 2006). Fortunately, the presence of many postcranial remains in the Mokrá-Quarry fissures helped to identify the assemblage. Scalopini DOBSON, 1883 and Talpini are distinguished by the presence or absence of the “scalopine ridge” (Campbell 1939, van den Hoek Ostende and Fejfar 2006). The morphology of the humeri from Mokrá-Quarry clearly resembles that of Talpinae. More precisely, it is characterized by the absence of this ridge, and fits into the morphotype of *Talpa*. Moreover, it is more derived than the scalopine-like humerus of *Talpa tenuidentata* ZIEGLER, 1990 from the MN 3 Czech locality of Ahníkov I (van den Hoek Ostende and Fejfar 2006). In all, the dimensions of the humeri are larger than those of *Talpa minuta* BLAINVILLE, 1840 (Hutchison 1974, Ziegler 2000), but smaller than those of *Talpa* sp. from Petersbuch 28 (Klietmann et al. 2015a, b). As for the ulnae, their dimensions are between those of *T. minuta* and the extant *T. europaea* LINNAEUS, 1758 (Baudelot 1972, Sabol 2005), and only slightly smaller than those of *Talpa* sp. from Petersbuch 28 (Klietmann et al. 2015a, b). Consequently, the assemblage from Mokrá-Quarry is referred to as *Talpa* sp.

Discussion

Mokrá-Quarry is one of the most important Early Miocene sites of Central Europe. Its karst fissures have yielded a great diversity of small mammal taxa indicative of MN 4 faunas (see Bonilla-Salomón et al. 2021a, b, 2022a, b, c), and resembling other MN 4 Czech faunas, such as those from the Dolnice and Ořechov sites.

Previous studies on small mammals and herpetofauna described Mokrá-Quarry fissures as a karstic landscape with open dry steppes, close to more humid areas and large patches of woodland (Ivanov et al. 2006, 2018, 2020, Sabol et al. 2007, Ivanov 2008, Luján et al. 2017, 2021, Bonilla-



Text-fig. 8. Postcranial elements of *Talpa* sp. a, b: Right humerus Pal. 4419; a – anterior view, b – posterior view. c, d: Right ulna Pal. 4423; c – medial view, d – lateral view. All postcranial bones are figured as left elements. Scale bar = 2 mm.

Salomón et al. 2021a, b, 2022a, b, c). The data presented here, based on the Metatheria and Eulipotyphla, agree with these works.

Amphiperatherium remains are more common in Central European assemblages than elsewhere in the continent. Furió et al. (2012) correlated its higher abundance in Central Europe to more humid conditions, whereas Spanish assemblages containing *Amphiperatherium* are interpreted independently as representing wet environments. As an exception, Crespo et al. (2020) described *A. frequens* from a gypsum layer. This suggests that the species, although thriving in warm and humid environments, may have shown some drought tolerance. Overall, it has been traditionally linked with forested environments and nocturnal behaviors (Ziegler 1999a). Kurz (2005) considered *Amphiperatherium* a frugivore-omnivore taxon, with cursorial locomotion, based on a skeleton of *Amphiperatherium* cf. *maximum* CROCHET, 1979 from Mesel. Based on the redescription of Rose (2012), the presence of well-developed transverse processes in the lumbar vertebrae also suggests a more terrestrial adaptation than *Peradectes* GRANGER, 1921 considered more arboreal. All of the above could agree with the presence of *Amphiperatherium* in the vicinity of the karstic areas.

Regarding Erinaceinae, there is still discussion about their ecological preferences (van Dam et al. 2020, and references therein). *Amphichinus* is recorded in the late Oligocene and Early Miocene of several Central European localities, where conditions were more humid (van Dam et al. 2020). On the other hand, the entrance of *Amphichinus* in the Iberian Peninsula coincides with a transition to a drier condition (van der Meulen and Daams 1992). Furthermore, Furió et al. (2018) state that the less frequent occurrence of *Amphichinus* in the Iberian Peninsula fossil record during zone G (Middle Miocene) is coeval with an increase in precipitation. Besides the paleoenvironmental conditions debate, the genus *Amphichinus* is believed to have fed mainly on small invertebrates, based on its ancestral dental pattern (van Dam et al. 2020).

Regarding Galericinae, their closer relatives live in forested environments, near water bodies, where they feed on invertebrates, frogs, and some plant matter (Corbet 1988). However, modern gymnures display strong morphological differences from *Galerix*, and are rather distant phylogenetically. Therefore, the paleoecology of *Galerix* cannot be inferred from modern gymnures (van den Hoek Ostende and Doukas 2003, Klietmann et al. 2015a). The Miocene Galericipini, such as *Galerix*, were likely tolerant to a higher diversity of habitats (García-Alix et al. 2008, Furió et al. 2018), including notably drier conditions (Luis and Hernando 2000, Minwer-Barakat et al. 2009, Furió et al. 2011). As discussed by Klietmann et al. (2015b), based on the evolution and geographic distribution of *Galerix*, this genus is indicative of rather warm open, and slightly dry local environments. This is consistent with the reconstruction of Mokrà-Quarry. Regarding its diet, *Galerix* should be considered a generalist invertivore, whereas other Galericipini genera show clearer dietary adaptations (van den Hoek Ostende 2001). Given their close morphological and morphometric similarities, it is unclear whether *G. exilis* and *G. symeonidisi* are frequently co-occurring in MN 4 Central European assemblages. The slow replacement of *Galerix*

symeonidisi by *Galerix exilis* in the Daroca-Calamocho area, Spain (van den Hoek Ostende and Doukas 2003), suggests that these species partly avoided direct competition, and therefore occupied non-overlapping ecological niches. In this respect, the dominance of *G. exilis* in our samples suggests a correlation with the late MN 4, before the extinction of *G. symeonidisi*.

Fully fossorial moles are not direct competitors for resources with shrews, hedgehogs and other insectivorous species. Their specialized habitat makes them less easily caught by avian or scansorial mammalian predators (Klietmann et al. 2015b). In addition, these taxa required sufficiently humid soil. Their abundance in karstic sites and overall rocky areas are usually reduced. *Talpa* is rather abundant in Mokrà-Quarry, but this observation is based solely on postcranial elements. The faunal pattern observed in our assemblages based on dental elements only is typical of karst environments.

The Eulipotyphla specimens recovered from Mokrà-Quarry represent a minor part of the small mammal assemblages (bats excluded) in terms of relative abundance: 3.5% in MWQ1/2001, 15% in MWQ2/2003, 2.5% in MCQ3/2005 and 28.5% in MWQ4/2018, although the later consists only of 7 small mammal remains recovered so far (see a list of taxa with number of identified specimens in Bonilla-Salomón et al. 2022c). The number of identified specimens in the assemblages indicate that the picture of the eulipotyphlan diversity in Mokrà-Quarry is incomplete. Such relative abundance of Eulipotyphla is, however, also consistent with a low humidity rate, as already supported above. Further study is required to understand the local faunal evolution of eulipotyphlan and metatherian taxa in the late Early Miocene of Central Europe.

Conclusions

The Metatheria and Eulipotyphla faunas from MWQ2/2003, MCQ3/2005 and MWQ4/2018 are described for the first time, consisting of five different taxa: *Amphiperatherium frequens*, *Amphichinus* cf. *baudeloti*, *Galerix exilis*, *Galerix symeonidisi*, and *Talpa* sp. Mokrà-Quarry fissures contain a mixture of two *Galerix* species (i.e., *G. symeonidisi* and *G. exilis*) typical of late MN 4 assemblages. The occurrence of *Amphichinus*, rare in Early Miocene small mammal assemblages, is relevant. The sample from Mokrà-Quarry shows a characteristic set of features similar to those of *A. baudeloti*, never previously identified in Central Europe.

Finally, the genus *Talpa* is represented by a single premolar, an edentulous mandible fragment, and mostly postcranial material (i.e., several humeri and ulnae). The genus is also found in other Czech and Central European localities during the Early Miocene.

The non-rodent small mammal assemblage is consistent with previous paleoenvironmental reconstructions, depicting Mokrà-Quarry fissures as a karstic area, close to patches of woodland and small water bodies. Future studies of the Chiroptera and large mammals from all fissures will help to provide a more complete picture of Mokrà-Quarry assemblages.

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