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Cricetid, Eomyid, and Murid fauna from the Middle Miocene site (MN6) of Devínska Nová Ves – Bonanza (Slovakia)

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Abstract

Rodents play an important role in all current and extinct ecosystems. In this study we present the fossil record of cricetids and eomyids from Devínská Nová Ves–Bonanza (Vienna Basin, Slovakia). A detailed morphometric analysis revealed the presence of *Eumyarion* cf. *latior*, *Democricetodon vindobonensis*, *Karydomys* sp., *Anomalomys* sp., *Neocometes* cf. *brunonis*, *Keramidomys carpathicus*, and *Eomyops* sp. This species association with other taxa available from the locality indicates an early MN6, probably slightly younger in age than the neighbouring locality Devínská Nová Ves–Štokeravská vápenka = Neudorf an dem March – die Spaltenfüllung or Zapfe's Fissures. Paleoenvironmental specificities of the locality dated after the peak of the Mid-Miocene Climatic Optimum are discussed. The faunal assemblage, together with geological setting, suggests a mixed insular or peninsular area with subtropical forests close to freshwater bodies in the vicinity of a saltwater sea.

Keywords:

Rodents
Cricetids
Eomyids
Central Europe
MN6
Late Badenian

1. Introduction

Small mammal fauna, especially rodent fauna, plays a very significant role in current and past ecosystems. They represent nowadays 40% of the mammal biodiversity worldwide (Pardiñas et al., 2017; D'Elía et al., 2019). Rodents are commonly characterized as small and diversified mammals, specialized in gnawing and with high reproductive rates. Their radiation includes different types of species from subterranean species to arboreal and cursorial forms (D'Elía et al., 2019). These characteristics make the rodent group one of the most adaptative groups across the globe. Rodent fossil fauna are common components of the mammalian fossil record in the Miocene terrestrial deposits in Europe. They also represent one of the most biochronologically significant groups of fossil mammals due to their rapid evolutionary rates and their wide geographical distributions. Therefore, the first and last appearances of determinate rodent taxa, such as cricetids and eomyids, mark 'the boundaries' between different biochronological units used in terrestrial record, including the Mammal Neogene (MN) zone system in Europe (Mein, 1975, 1990, 1999; Fahlbusch, 1976; Bruijn et al., 1992; Van Dam et al., 2001, 2006; Hilgen et al., 2012). Moreover, the cricetid and eomyid fauna along with other groups of rodents, such as glirids and sciurids, are also important for paleoecological and paleoenvironmental studies.

In Slovakia, the fossil record of rodents currently found in Miocene deposits is not as rich as in other parts of Europe, as they have been found only in eight out of at least 27 Miocene mammal sites (Sabol et al., 2021). The record for the fossil rodents in the Slovak territory begins during the Astaracian (Middle Miocene; MN6) since throughout the Early Miocene most of the territory was submerged by the vast inland Central Paratethys sea (Kováč et al., 2017, 2018).

This study focuses its attention on the cricetid and eomyid fauna from the Devínska Nová Ves–Bonanza site (DNV–Bonanza; Vienna Basin) correlated to the early Astaracian

(Middle Miocene, MN6; see Sabol and Holec, 2002; Sabol, 2005a,b; Sabol et al., 2021). DNV–Bonanza site is located in an area that had a peninsular to insular environment during the Badenian, based on the characteristics of the faunal and geological record (Sabol et al., 2021). The sedimentary record of DNV–Bonanza is related to paleobiogeographic changes that took place during the Middle Miocene in the Central Paratethys area (Kováč et al., 2017, 2018).

DNV–Bonanza site was discovered by amateur paleontologist Š. Meszároš in 1982. It is located in the former Štokeravská vápenka (= Stockerau limestone quarry), situated in the northern slope of Devínska Kobyla Hill near the Village of Devínska Nová Ves (Holec et al., 1987; Fejfar and Sabol, 2005; Sabol and Kováč, 2006; Mažgút, 2010). This site is a fissure filling with high probability of Badenian sediment infill. It contains a rich marine and terrestrial fossil fauna. DNV–Bonanza is known for its mammal fossil remains, especially for the primitive Miocene seals (Holec et al., 1987; Koretsky and Holec, 2002; Koretsky and Rahmat, 2015). These findings promoted new excavations in the area lead by a team from the Comenius University (Bratislava) and the Smithsonian Institution (Washington) in 1997–1998 (Holec et al., 1987), as well as by subsequent revision research teams in 2001–2022 (Sabol et al. 2021).

2. Geological setting

The DNV–Bonanza site is a broad karst fissure located at the eastern margin of the abandoned limestone quarry (the geographic coordinates of the site are 48°12’13” N and 17°00’11” E) but in the opposite quarry wall, as the most famous site of DNV – Štokeravská vápenka = Neudorf an dem March – die Spaltenfüllung or Zapfe’s Fissures (Holec et al., 1987). The site itself is situated in the protective wall of the Lower Jurassic dark limestone, oriented towards the railway line from Bratislava to Prague (Fig. 1(A–B)). Marine sands, sandstones, and large limestone boulders fill the fissure (Fig. 1(C)). Single layers of this sedimentary filling document change of coastal line position associated with several (possibly orbital) cycles and contain fossils of terrestrial (incl. freshwater), semi-aquatic, and marine vertebrates (Sabol and Kováč, 2006; Sabol et al., 2021). A detailed description of DNV–Bonanza site, including the most important sites for the interregional correlations in Central Europe, has been presented by Holec et al. (1987), Sabol and Kováč (2006), and Lehotský et al. (2009). The DNV–Bonanza site, is a type locality of four species (*Bufo priscus* Špinar, Klembara and Meszáros, 1993, *Gerhardstorchia meszaroshi* Sabol, 2005, *Devinophoca claytoni* Koretsky and Holec, 2002, and *D. emryi* Koretsky and Rahmat, 2015) and it forms a "transition" between DNV–Štokeravská vápenka and DNV–Sandberg sites from the biostratigraphic point of view (Sabol and Kováč, 2006; Sabol et al., 2021). Moreover, these sites show a direct relationship between the terrestrial and the marine record, based on the collected data published in Sabol et al. (2021). The DNV–Bonanza site is dated approximately around 13.8 Ma, while the oldest site of this area, i.e., DNV–Štokeravská vápenka, has an approximate time span from 14.7 to 13.8 Ma (early Badenian, Middle Miocene: Sabol et al., 2021). The remaining and youngest site of the area is DNV–Sandberg and dates back from 13.8 Ma to 12.8 Ma (Sabol et al., 2021). The correlation of these sites is important because it shows a complete record of terrestrial and marine fauna ranging from 14.7 to 12.8 Ma from the Central Paratethys area during a time of great changes, as was the Mid Miocene Climatic Optimum (MMCO; Steinthorsdottir et al., 2021).

3. Material and methods

The material from DNV–Bonanza is housed at the Faculty of Natural Sciences of the Comenius University in Bratislava (numbered as KGP-MSxx, KGP-xx.x and DB92xxxx), and at the Slovak Natural Museum – Natural History Museum (labelled as Zxxxx) in the same city. The micromammal assemblage described in this work comes from the thorough excavations that took place during the years 1997–1998, 2001, and 2002. Part of these materials was already figured in Sabol, Joniak and Holec (2004). The material numbered as DB92xxxx was recovered in 1991-1993 field campaigns by PJ. Dental terminology for the cricetid fauna follows Oliver and Peláez-Campomanes (2013), whereas the measurement method is after Daams and Freudenthal (1988: 42, fig. 1). The dental terminology for eomyid species follows Fahlbusch (1970) and Álvarez-Sierra (1987) for the measurements. The dental terminology for *Neocometes* follows Fahlbusch (1966). All measurements are given in millimetres and were taken with an optical micrometer to the nearest 0.01 mm. Estimated measurements, because of minor damage or distortion, are between brackets. Summary statistics and scatterplots were performed using the R software (R Core Team 2017). The biochronologic/biostratigraphic terminology and boundaries follow Steininger (1999) and Hilgen et al. (2012). Although the material under study stems from different layers of the same fissure deposited in the time horizon at approximately 13.8 Ma (Sabol et al., 2021), it is evaluated as a whole.

4. Systematic paleontology

Order Rodentia Bowdich, 1821

Family Cricetidae Fischer [von Waldheim], 1817

Genus ***Eumyarion*** Thaler, 1966

Type species: *Cricetodon medius* Lartet, 1851 (= *Cricetodon helveticus* Schaub, 1925).

Eumyarion cf. *latior* Schaub et Zapfe, 1953

Material and measurements: Partial skull with fragment of upper M1 (KGP-1: unmeasurable); left M1 (KGP-6a.4: L= 2.05, W= 1.48); right m1 (KGP-9.2: L= 2.14, W=

1.34); m1 fragment (KGP-MS60: unmeasurable); right m2 (KGP-6a.5: L= 1.65, W= 1.45); left m2 (KGP-6a.6: unmeasurable); fragment; left m3 (KGP-6a.9: L= [1.53], W= [1.29]), right m3 (KGP-9.3: L= 1.5, W= 1.32).

Description: **M1** (Fig. 2(A)). The roots are not preserved in specimen KGP-6a.4. The anterocone is simple and well developed and has a labial position compared to the rest of the tooth. The labial part of the anteroloph presents a bifurcated spur that occupies most of the anterosinus but does not connect with the spur of the paracone. The lingual part of the anterocone connects with the protocone by the anterolophule. The anterolophule presents two little spurs strongly directed to the anterosinus, but they do not show any connection. The paracone is well-developed and presents three different spurs: the first one is located in the lower anterior part of the protolophule; the second one is a small spur directed to the labial anterocone spur, but it does not show any connection; and the third one, the ectoloph, is a ridge that follows the margin of the tooth and is directed to the mesoloph but without reaching it. The mesoloph is long but does not reach the labial edge. The sinus is deep and anteriorly directed. There is no presence of an entomesoloph in these specimens. The metalophule is simple and connects anteriorly to the hypocone. The posteroloph is long and well-developed, reaching the metacone in its posterior part: this results in a narrow and deep posterosinus.

m1 (Fig. 2(B)). There are two roots in these specimens: the anterior one is smaller and located below the anteroconid, while the posterior one is more robust. The anteroconid is simple and round-shaped. The anterosinusid is open and narrower than the protosinusid, which is closed by a low cingulid that emerges from the anteroconid and would correspond to the labial anterolophid. There is also a small protostylid at the end of the labial anterolophid. The metalophid is double; the anterior arm connects just before the protoconid and the posterior arm behind it. There is a short anteriorly directed mesolophid in the specimen KGP-9.2 (Fig. 2(B)), the other specimen (KGP-MS60) is broken, being only the anterior part of the tooth present, but a short mesolophid is preserved. The sinusid is wide and open and there is a faint presence of an ectomesolophid. The hypolophulid is simple and connects anteriorly the entoconid with the hypoconid. The posterolophid is well-developed and encloses a wide posterosinusid.

m2 (Fig. 2(C)). There are two roots in these teeth, being the anterior smaller and less robust. The lingual anterolophid is reduced and barely present. It is directly connected with the metaconid, resulting in a very narrow and reduced anterosinusid as is shown in specimen KGP-6a.5 (Fig. (2C)). The labial anterolophid is more developed than the lingual one and encloses a narrow protosinusid. Anterior to the mesoconid, there are two ridges: the former is posteriorly directed and corresponds to the protoconid hind arm, whereas the latter is smaller and shorter, corresponds to the mesolophid, and connects to the lingual end of the protoconid hind arm. The metalophulid is simple and anterior. The posterolophid is well-developed and connects with the posterior part of the entoconid, resulting in a closed posterosinusid. The sinusid is posteriorly directed and closed by a low cingulid. There is a faint presence of the extomesolophid.

m3 (Fig. 2(D)). There are two specimens available in the DNV–Bonanza site material. These teeth present two roots, one located in the anterior position, just below the anterolophids, and the other in the posterior part of teeth. The anterolophids are well-developed, being the lingual anterolophid more reduced than the labial anterolophid, resulting in a barely present anterosinusid and a small protosinusid. The mesolophid is medium-sized, but it does not reach the lingual margin of the tooth in both preserved specimens (KGP-6a.9 and KGP-9.3; Fig. 2(D)). The hypolophulid is single and connects the entoconid with the hypoconid. The posterolophid is well-developed enclosing a wide posterosinusid, whereas the sinusid is narrow and posteriorly oriented.

Remarks: This genus has a combination of primitive dental characteristics that make them easily identifiable from other Miocene cricetids (see Bruijn, 2009). The specimens recovered in the DNV–Bonanza site, show several diagnostic features that allow to refer them to the *Eumyarion* genus, such as the labial position of the anterocone and the bifurcated anteroloph in the M1.

Apart from the isolated check teeth, a partial skull with the rostrum, part of the palatine and the maxilla with an upper left M1 fragment was recovered as well (KGP-1; Fig. 3(A–B)). The presence of this tooth fragment allows the adscription of this skull to the genus *Eumyarion* and most likely to *Eumyarion* cf. *latior* species due to the morphology of the anterocone, anterolophule, and part of the metacone.

The genus *Eumyarion* is characterized by an archaic tooth morphology showing similarities with some Oligocene cricetids such as *Eucricetodon* (Kälin, 1999). Several species of the genus have been described during the Early and Middle Miocene in Europe, which are the following: *Eumyarion weinfurteri* (Schaub and Zapfe, 1953), *E. bifidus* (Fahlbusch, 1964), and *E. latior* (Schaub and Zapfe, 1953). The validity of both taxa *E. latior* and *E. weinfurteri* has already been discussed by several authors (e.g., Engesser, 1972; Bruijn and Saraç, 1991; Bruijn, 2009). In fact, the different size ranges for *Eumyarion* species is depicted in Figure 4 as well, being *E. weinfurteri* the smaller species within the genus *Eumyarion*. That figure further shows that there is great homogeneity among the *Eumyarion* populations from DNV sites. Both *Eumyarion weinfurteri* and *E. latior* were described by Schaub and Zapfe (1953) from the same fissures, being size the only remarkable difference between the two species. From then on, smaller sized specimens of the genus *Eumyarion* from the Early Miocene European fossil record were assigned to *E. weinfurteri* based solely on this character (Fejfar, 1974; Bolliger, 1992; Daxner-Höck, 1998). Even though it is not within the scope of this paper to elucidate the controversy regarding *E. weinfurteri* and *E. latior*, some authors of this work are working on a revision of the populations of *Eumyarion* from DNV sites, which may shed light on the subject. For the time being, the material is here referred to as *Eumyarion* cf. *latior*.

Genus ***Democricetodon*** Fahlbusch, 1964

Type species: *Democricetodon crassus* Freudenthal in Freudenthal and Fahlbusch, 1969 (=*Cricetodon minor* Lartet, 1851 sensu Fahlbusch 1964).

Democricetodon vindobonensis (Schaub et Zapfe, 1953)

Holotype and type locality: Originally described as *Cricetodon brevis vindobonensis* nov. ssp. (Schaub and Zapfe, 1953); holotype: mandible fragment with m1 and m2 sin.; type locality: DNV–Štokeravská vápenka (originally, Horizont B der Neudorfer Spalte, Helvétien).

Material and measurements: partial skull; right maxillary fragment with M1-M3 KGP-17 (M1, L: 1.62, W: 0.87; M2, L: 1.32, W: 1.10; M3, L: 1.02, W: 0.85); M1: (left KGP-6a.7 (L: 1.92, W: 1.32), right KGP-6a.8 (L: 1.87, W: 1.30), right KGP-MS29 (L: 1.65, W: 1.10), right KGP-MS30 (L: -, W: 1.10); M2: (left KGP-6a.12 (L: 1.37, W: 1.25), left KGP-MS31 (L: 1.4, W: 1.22); M3: (right KGP-MS34 (L: 0.95, W: 1.23)); m1: (left KGP-6a.10 (L: 1.52, W: 1.12)), right KGP-MS35 (L: 1.52, W: 1.05), right KGP- MS36 (L: 1.47, W: 1.00), right KGP-MS37 (unmeasurable), left Z14597 (L: 1.27, W: 0.90); m2: (left KGP-6a.11 (L: 1.37, W: 1.12), left KGP-6a.13 (L: 1.32, W: 1.15), left KGP-6a.14 (L: 1.23, W: 0.95), right KGP-MS38 (L: 1.37, W: 1.00), left KGP-MS39 (L: 1.37, W: 1.10), left KGP-MS40 (L: 1.37, W: 1.08), left Z14597 (L: 1.28, W: 1.10), left Z14598 (L: 1.43, W: 1.12); m3: (left KGP-MS61 (L: 1.08, W: 0.97), left KGP-MS62 (L: 1.20, W: 0.97), left Z14597 (L: 1.22, W: 0.86)).

Description: **M1** (Fig. 2(E–G)). There are three roots available in the M1 specimens. The larger ones are located under the labial and the lingual part of the tooth respectively, whereas the third one is located under the anterocone. The anterocone is simple and well-developed and has a labial position compared to the rest of the tooth. As is seen in unworn specimens (e.g., Fig. 2(F–G)), the anterolophule shows a labial long spur that reaches the margin of the teeth dividing the anterosinus into two small valleys. The protolophule is double in KGP-6a.7 (Fig. 2(E)), whereas in the other specimens studied it is simple, being the anterior arm connected with the basis of the anterolophule labial spur (KGP-6a.14; Fig. 2(F)). The protolophule hind arm connects with the entoloph posteriorly to the protocone. The mesoloph is long but ends before connecting to a small mesostyle. The metalophule is simple and connects directly to the posteroloph, except for the specimen KGP-6a.14 (Fig. 2(F)). The posterosinus is narrow and deep, closed by the posteroloph. The sinus is narrow and deep and is closed by a small cingulum.

M2 (Fig. 2(H–I)). There are two roots in the preserved two samples: one of them root is placed labially and the other one on the lingual part of the tooth. The labial anterolophule is well-developed enclosing a narrow anterosinus. Similarly, the lingual anteroloph is well developed and encases a narrow and small protosinus. The protolophule is double following the same pattern described for the M1 specimens (Fig. 2(E–G)). The mesoloph is long and reaches the margin of the tooth forming a small mesostyle on the mesosinus. The sinus is narrow and is closed by a low cingulum. The metalophule is simple and connects with the entoloph posteriorly to the mesoloph as is seen in specimen KGP-6a.12 (Fig. 2(I)), the metalophule is simple and is connected with the mesoloph through the entoloph. The posteroloph is well-developed and encloses a deep and narrow posterosinus.

M3 (Fig. 2(J)). Two M3 were recovered from the DNV–Bonanza site, being the specimen (KGP-17) the only attached to a maxilla fragment that contains the complete tooth row (M1 to M3). The other specimen (i.e., KGP-MS34; Fig. 2(J)) is a single right M3. The root of KGP-MS34 is not preserved, whereas in KGP-17 it is not visible as it is attached to the maxilla in its natural position. The general morphology of both M3 is rounded. The lingual and labial anterolophs are well-developed, enclosing the anterosinus and the protosinus respectively. The sinus is closed by a low cingulum. The paracone is connected to the anterolophule by a single protoloph arm. The metaloph is simple. The posteroloph is well-developed and reaches the posterior part of the metacone, enclosing the posterosinus.

Moreover, a partial skull embedded into sandstone matrix was also recovered from DNV–Bonanza site. Only part of the skull is visible, including the right tooth row (KGP-17; Fig. 3(C–D)). The latter can refer to *Democricetodon vindobonensis* due to the occlusal morphology of the M1-M3 cheek teeth. Apart from the tooth row, the right incisor is also present. Regarding the skull, the rostrum is preserved along with the right zygomatic arch, the frontal bone, and the parietal bones. This skull is flattened dorsally (Fig. 3(C–D)).

m1 (Fig. 2(K–M)). The m1 specimens have two roots; the former is located on the anterior part of the tooth and the latter is on the posterior part. Both roots have similar dimensions. The anteroconid is simple and small compared to the anterocone of M1s. The lingual anterolophid is short and defines a small round-shaped anterosinusid as shown in specimen KGP-6a.10 (Fig. 2(K)). On the contrary, the labial anterolophid is longer and more developed than the lingual one, which results in the enclosing of the protosinusid. The metaconid presents two anterior spurs: the lingual one merges with the lingual anterolophid, except in specimen KGP-MS36 (Fig. (2M)); and the labial one would correspond to the protolophulid, which is simple and connects to the anterolophulid, leaving the protoconid isolated from the metaconid and anteroconid. The mesolophid is long and reaches the lingual margin of the tooth. The metalophulid is simple and anterior. The posterolophid is long and well-developed, and merges with the entoconid resulting in a closed posterosinusid. The sinusid is also closed by a low cingulid.

m2 (Fig. 2(N–S)). These specimens have two roots. The lingual anterolophid is very short and almost absent in some cases (e.g., KGP-6a.13; Fig. (2O)); in fact, this results in very reduced and in some cases absent anterosinusid. On the contrary, the labial anterolophid is well-developed enclosing the protosinusid. The mesolophid is long and reaches the lingual margin of the tooth. Both the metalophulid and hypolophulid are simple and anterior. As in seen in the m1, the posterolophid is well-developed and enclosing the posterosinusid. The sinusid is closed by a low cingulid as well.

m3 (Fig. 2(T)). There are three m3 available from DNV–Bonanza, all of them with two roots. The lingual and labial anterolophids are well-developed, being the lingual one smaller than the labial one: this results in a small anterosinusid and a longer, but narrow protosinusid. There is no mesolophid in these specimens (Fig. 2(T)). The posterolophid is well-developed and encloses a wide and deep posterosinusid. The sinusid is wide and enclosed by a low cingulid.

Remarks: The specimens recovered from DNV–Bonanza site were originally named *Cricetodon brevis vindobonensis* by Schaub and Zapfe (1953). However, they are here referred to *Democricetodon vindobonensis* in having a long mesoloph/id that extends to the margin of the teeth in both upper and lower molars forming a mesostyle/id, as well as the presence of a long labial spur of the anterolophule which divides the anterosinus into two smaller valleys (also called as “anteromesoloph” in Sabol, 2005a). *Democricetodon vindobonensis* mainly differs from *D. franconicus* by the presence of a long mesoloph reaching the margin of the teeth, and longer anteromesoloph.

As is depicted in Figure 5, the material recovered from DNV–Bonanza, despite scarce, fits well within the size range of *Democricetodon vindobonensis*, especially regarding the upper and lower M1/m1, which can be compared with the already published data from DNV–Štokeravská vápenka (see Fejfar, 1974). Moreover, we included more data from other

Democricetodon species such *D. franconicus* from Dolnice 1-3 and Ořechov (Fejfar, 1974), *D. gracilis* and *D. mutilus* from Sandelzhausen (Wessels and Reumer, 2009) and other Central European localities to compare our specimens with these other assemblages. We concluded that *D. vindobonensis* material from DNV–Bonanza site coincides in size within the range for the *D. vindobonensis* from DNV–Štokeravská vápenka, as well it is quite similar in size with *D. franconicus* from the Czech sites of Dolnice 1-3 and Ořechov (Fig. (5)), despite showing clear morphological differences (see above).

Genus ***Karydomys*** Theocharopoulos, 2000

Type species: *Karydomys symeonidisi* Theocharopoulos, 2000. Karydia 1, Early Miocene, Greece.

Karydomys sp.

Material and measurements: right M2 (KGP-MS63: L=2.50, W=2.05)

Description: **M2** (Fig. 2(U)). There is only one single specimen represented by an isolated upper M2 (KGP-MS63). The tooth is quite worn and makes it difficult to describe and evaluate with confidence. It is square-shaped with a well-developed labial anteroloph that follows the margin of the tooth and encloses the labial anterosinus. Similarly, the lingual anteroloph is also well-developed and encloses the protosinus with a low ridge. The protolophule is double. The anterior arm connects with the anterolophule right before the protocone. The protolophule posterior arm connects directly to the mesocone and the lower part of the mesoloph. The mesoloph is long and almost reaches the labial margin of the tooth, but without the presence of mesostyle. Instead, the mesoloph connects directly with an anterior metacone spur. The metaloph is simple and is joined directly with the posteroloph just behind the hypocone. The posteroloph is well-developed and enclose the posterosinus.

The sinus is narrow and straight, enclosed by a low cingulum on the lingual margin of the tooth, and with no endostyle present in the sinus.

Remarks: The solely recovered specimen shows high crown wear, which renders difficult its taxonomical attribution. Despite this, it still retains several morphological characteristics that allow for its tentative attribution to a genus level. Based on the dimensions of the M2, together with some specific morphological characteristics (i.e., square-shaped morphology of the teeth with the rounded edges of its crown, and long mesoloph without mesostyle at the labial margin of the teeth and the absence of endostyle), we concluded that KGP-MS63 belongs to *Karydomys* sp. Moreover, the dimension of this tooth fits within the *Karydomys* previously reported from DNV–Štokeravská vápenka published by Fejfar (1974) as *Lartetomys* cf. *zapfei*. Later, Mörs and Kalthoff (2004) re-assigned the specimens found in DNV–Štokeravská vápenka to *Karydomys wigharti* (Prieto, 2012). Anyhow, KGP-MS63 constitutes one of the largest cricetids recovered from DNV–Bonanza site.

Family Eomyidae Winge, 1887

Genus ***Keramidomys*** Hartenberger, 1966

Type species: originally described as *Pseudotheridomys carpathicus* nov. sp.; holotype: maxilla dext. with P4 and M1; type locality: DNV–Štokeravská vápenka (originally, Horizont D der Neudorfer Spalte, Helvétien: Schaub and Zapfe, 1953).

Keramidomys carpathicus Schaub and Zapfe, 1953

Material and measurements: two right M1 (KGP-MS69: L=0.85, W=0.90 and KGP-6a.18: L=0.85, W=0.80).

Description: **M1** (Fig. 2(V–W)). There are only two specimens available from DNV–Bonanza site, and both correspond to the right M1. KGP-MS69 (Fig. 2(V)) is almost complete while KGP-6a.18 (Fig. 2(W)) is quite damaged, with the labial part of the tooth completely eroded. Both molars show a well-developed anteroloph that encloses the anterior syncline in KGP-6a.18, yet remains open in KGP-MS69. The protoloph is thick in both molars reaching the paracone. The mesoloph is long and well-developed reaching the lingual margin of the teeth. There is no longitudinal crest connecting the mesoloph and the protoloph. Only a small spur emerging from the mesoloph is discerned, thus resulting in an open labial syncline that divides the molar into two parts. The base of the mesoloph is in contact with the hypocone. The metaloph is also well-developed and connects the hypocone with the metacone. The posteroloph is thick and follows the posterior margin of the tooth. In KGP-MS69, the posterior syncline is left open, while in KGP-6a.18 is closed by the connection between the posteroloph and the metacone probably due to the wear.

Remarks: The genus *Keramidomys* is one of the smallest eomyids known so far. This group shows a very lophodont tooth pattern with the cups incorporated into the ridges and very marked synclines between them. *Keramidomys* is also a biochronologically wide-ranged genus being present from MN2/3 to MN14, thus resulting in several evolutionary lines (Engesser, 1999; Kimura et al. 2019, Daxner-Höck et al. 2022). Originally erected by Schaub and Zapfe (1953) as *Pseudotheridomys carpathicus* based on the material from DNV–Štokeravská vápenka, *Keramidomys carpathicus* shares many features with *K. thaleri*, such as the long mesoloph/id. However, in *K. thaleri*, the longitudinal crest is always present and in many specimens this connection is complete, while in *K. carpathicus* this ridge is always interrupted (Mein, 2009). The teeth recovered from DNV–Bonanza (Fig. (6)) coincide in size with the *K. carpathicus* type material from DNV–Štokeravská vápenka published in Schaub and Zapfe (1953) and Fejfar (1974). However, the scarcity of the assemblage recovered in DNV–Bonanza is here referred to *K.* cf. *carpathicus.*

Genus ***Eomyops*** Engesser, 1979

Type species: *Eomyops catalaunicus* Hartenberger, 1966, Can Llobateres (Late Miocene), Spain.

Eomyops sp.

Material and measurements: right P4 (KGP-6a.17: L=0.80, W=0.75)

Description: **P4** (Fig. 2(X)). There is only one specimen available, but the poor state of preservation renders it difficult to give an exhaustive description of the tooth. KGP-6a.17 (Fig. 2(X)) has a well-developed anteroloph that encloses the anterior syncline, probably due to wear. The protoloph is well- developed and reaches the paracone. The mesoloph is short and is posteriorly directed almost reaching the metacone. There is an indication of the longitudinal ridge that connects the basis of the mesoloph with the protoloph. The metaloph is thick and connects the hypocone with the metacone. The posterior part of the tooth is highly worn so it is difficult to evaluate this area confidently. The labial syncline is wide and is anteriorly directed.

Remarks: The genus *Eomyops* is one of the stratigraphically long-ranged eomyids known so far in Europe. Its time span ranges from the Middle Miocene (MN5) to the Early Pleistocene (MN17; Engesser, 1999), registered little changes regarding the cheek teeth morphology. One of the main characteristics of *Eomyops* is its primitive bunodont cheek teeth structure (Engesser, 1999). Particularly, KGP-6a.17 shows some of the important characteristics of the genus *Eomyops,* such as a well-developed anteroloph and the presence of a second synclinal extending to the central part of the teeth. There is a lot of discussion regarding the validity of the genus *Eomyops*. Several authors, such as Engesser (1979) and Kimura et al. (2019), consider *Eomyops* and *Leptodontomys* to be two separate genera. However, other authors, (e.g., Kalthoff et al., 2022), consider these genera synonyms based mainly on the external morphology and microscopic structure of the incisors. The genus *Eomyops* sp. was already recovered in the nearby site DNV-Bonanza, DNV-Štokeravská vápenka (MN6; Schaub and Zapfe, 1953; Kälin, 1997; Prieto, 2011). Since the single tooth recovered from this site is very poorly preserved, a more precise attribution cannot be determined, therefore being referred to as *Eomyops* sp.

Family Muridae Illiger, 1811

Subfamily Platacanthomyinae Alston, 1876

Genus ***Neocometes*** Schaub et Zapfe, 1953

Type species: *Neocometes brunonis* Schaub et Zapfe, 1953; Neudorf Spalte 1, Middle Miocene, Slovakia.

Neocometes brunonis (Schaub and Zapfe, 1953)

Holotype and type locality: left mandible with m1-3 (O.E. 307; housed in the Natural History Museum Basel); Devínska Nová Ves “Spalte 1”, MN6. = DNV–Štokeravská vápenka (originally, Horizont D der Neudorfer Spalte, Helvétien).

Material and measurements: right M1 (KGP-6a.1: L=2.17, W=1.15); right M2 (KGP-6a.2: L=1.92, W=1.55); right m1-m3 (Z14596/1: m1 – L= -, W=1.23; m2 – L=1.71, W=1.24; m3 – L=1.36, W=1.16); left mandible fragment m2-m3 (DB920002, m2 – L=1.69, W=1.51; m3 – L=1.65, W=1.41) right m1 (KGP-MS64: L=2.18, W=1.28); right m2 (Z14596/2: L=1.81, W=1.56); left m3 (KGP-6a.3: L=1.65 ,W=1.32).

Description: **M1** (Fig. 7(A)). There is only one single M1 available in DNV–Bonanza site. This molar has an elongated overall morphology, with a rounded anterior part. The anteroloph is long and well-developed. Between the anterior transversal ridge and the anteroloph, the syncline Ia is left open. The paracone and protoloph are thick leaving a deep and narrow syncline I. The syncline II is deep and completely splits the tooth into two well-differentiated parts. The mesoloph is thick, structure anteriorly directed that reaches the margin of the tooth. The posteroloph is thin and connects directly with the metacone, thus resulting in a narrow and short IV syncline. All synclines are open labially.

M2 (Fig. 7(B)). There is only one M2 recovered from this site, and it shows a medium stage of wear. The syncline Ia is vaguely present, being completely closed and almost integrated into the anterior transversal ridge. The syncline I is deep and narrow. The protoloph connects the paracone and the protocone directly. The tooth is divided into two well-differentiated parts due to the deep and narrow syncline II, as seen in the M1. The posteroloph is partly broken in KGP-6a.2. It reaches the metacone, resulting in a closed syncline IV, probably due to its state of wear. The syncline III is short and open in its labial parts, as in the syncline II and I.

m1 (Fig. 7(C)). There are two m1 available from DNV–Bonanza: the specimen KGP-MS64 is well-preserved, whereas Z14596/1 presents a high level of wear, making it difficult an accurate description of its occlusal morphology. The m1 has a more elongated overall morphology compared to the upper molars. The syncline Ia and I are joined forming a loop in the anterior part of the tooth, which are closed labially. The anterior transversal ridge is narrow and connects with the labial margin of the tooth. The synclinal II and III are both open lingually and labially. The posterolophid is well-developed and encloses the synclinal IV by reaching the entoconid. The hypolophulid is indistinguishable from the entoconid and the posterolophid.

m2. One of the two m2 recovered is associated with a mandible (Z14596/1) with the m1 (previously mentioned) and m3. This tooth row shows a high level of wear. The other specimen available is Z14596/2: it also shows a high level of wear and therefore is difficult to evaluate properly its occlusal morphology. These teeth show an overall square-shaped morphology with rounded edges. Synclines I o IV are closed lingually due to the high level of wear. In both specimens, syncline Ia is not visible. Syncline III is open labially in Z14596/2.

m3 (Fig. 7(D)). There are two m3 available: the specimen associated with the mandible and show a high level of wear, whereas KGP-6a.3 is less worn. The anterolophid is well-developed following the anterior margin of the teeth. The syncline I is narrow, deep, and turns backwards on the lingual side. The synclines II and III also narrows and are only open labially. The posterolophid is well-developed and encloses the synclinal IV, reaching the entoconid.

Remarks: Although *Neocometes* has been reported in several Central European Early to Middle Miocene localities, it is still a rare genus. In DNV–Bonanza, just a few molars were recovered and ascribed to *Neocometes brunonis.* In fact, that genus does not register great changes in the morphologic pattern of the molars, and only a few differences have been proposed between *N. brunonis* and *N. similis* during the Middle-Late Miocene (Fejfar, 1999; Mörs, 2006; Pineker and Mörs, 2011). As for the upper molars of *N. brunonis*, the syncline Ia is not present and the anteroloph is being fused with the anteroloph transversal ridge. As a rule, the synclines I, II, III, and IV are open labially in the upper molars in the *Neocometes* genus (Fejfar, 1999; Mörs, 2006; Pineker and Mörs, 2011). The lower molars of *N. brunonis*, in turn, have a syncline Ia reduced and anteriorly opened. Conversely, in *N. similis* the syncline I and Ia are parallel, and they show no anterior opening (Schaub and Zapfe 1953; Fejfar, 1974, 1999). Concerning molar size, there is a significant gradual increase of size registered in this genus through the Miocene. As is seen in the Figure 8, the material recovered from DVN–Bonanza site coincide within the size range for the *N. brunonis* type material from DNV–Štokeravská vápenka and are larger compared with *N. similis* from Erkerstshofen used for comparison (Fejfar, 1974).

Subfamily Anomalomyinae Schaub, 1925

Genus ***Anomalomys*** Gaillard, 1900

Type species: *Anomalomys gaudryi* Gaillard, 1900. La Grive-Saint-Alban (Ìsere). Middle Miocene, France.

Anomalomys sp.

Material and measurements: right M2 (KGP-6a.21: L=1.62, W=1.20)

Description: **M2** (Fig. 7(E)). A single specimen was recovered from DVN–Bonanza site: it shows a medium stage of wear, but it still retains many occlusal morphological structures to allow an accurate description. KGP-6a.21 is square-shaped with a very high level of hypsodonty. The anteroloph is wide and occupies the anterior margin of the tooth from the protocone to the paracone. Due to the high degree of wear in the anterior part of the tooth, the anteromesoloph is almost and almost completely merged with the anteroloph. The anterior anterosinus is highly reduced and the posterior anterosinus is narrow and deep. The protoloph is wide and merges the paracone with the entoloph. The sinus is narrow and is anteriorly directed. The mesoloph is of medium length and does not merge with the paracone posterior spur, leaving the mesosinus open labially. The posteroloph is wide and merges in a continuous crest the hypocone and the metacone following the posterior margin of the tooth. The metaloph is connected with the metacone but does not reach the entoloph, leaving an open connection between the mesosinus and the posterosinus.

Remarks: The taxonomical position of the genus *Anomalomys* has been under discussion several times in the literature. Some authors considered *Anomalomys* to be part of the subfamily Anomalomyinae within the family Cricetidae (Mörs, 2008). However, Fejfar (1972) attributed this rodent clade within the family Spalacidae. Nowadays, *Anomalomys* is mostly considered as a member of the separate family Anomalomyidae (Bruijn and Saraç

1991; Bolliger, 1996, 1999; Kalthoff, 2000; Hír, 2001; Nesin and Kovalchuk, 2021). Although KGP-6a.21 found in DNV–Bonanza shows sufficient morphological characteristics that allow its attribution to the genus *Anomalomys*, an attribution at the species level is not possible.

5. Discussion

Devínska Nová Ves set of sites have a key role in understanding the biostratigraphy of the Badenian Paratethys regional stage (15.97-12.70 Ma, early Astaracian, MN6; Kováč et al., 2018; Sabol et al., 2021). Devínska Nová Ves is composed by three different sites DNV–Štokeravská vápenka, DNV–Sandberg and DNV–Bonanza. DNV–Štokeravská vápenka recorded terrestrial fossil vertebrates, DNV–Sandberg yielded predominantly a marine fossil record, while DNV – Bonanza shows a poor transition between the two different environments. DNV– Bonanza has a short mammal record, and in this work, we focused our attention on the cricetid and eomyid fauna recovered from this site, as well as on its biostratigraphic/biochronologic and paleoenvironmental implications.

The main cricetid representative in this site is *Democricetodon vindobonensis,* a small sized fossil rodent only known so far from the DNV–Štokeravská vápenka. The DNV–Bonanza remains of *D. vindobonensis* coincide in morphology and size with the specimens found in DVN–Štokeravská vápenka. This fact allows us to give an approximate correlation to the lower MN6. There is also the presence of ?*Megacricetodon* sp. in DNV–Bonanza, but only mandible fragments have been recovered so far (Sabol, 2005a).

The representatives of both genera (*Megacricetodon* and *Democricetodon*) represent, together with other rodent taxa such as *Eumyarion weinfurteri*, *Anomalomys* sp., and *Neocometes brunonis* the result of immigration waves from Asia into Europe during the Early Miocene (Kälin, 1999). The presence of these taxa in DNV–Bonanza is indicative of a great biodiversity of rodents, indicating a rich environment. In DNV–Bonanza there are several representatives of these genera (Sabol, 2005a; Mažgút, 2010), probably descendants of Early Miocene species. Some remains of *Neocometes brunonis* were also recovered from this site. The latter genus is recorded in Europe from the MN4, although there are some findings dated from the MN3 such as in Petersbuch 28 (Mörs, 2008) to the MN7/8: *N. brunonis* is well known from deposits dated from MN6-MN7/8; and *N.* aff. *brunonis* from MN5 site of Schellenfeld 2 (Ziegler, 1995). As to *Eumyarion,* several isolated teeth were found in DNV–Bonanza site and were referred to *Eumyarion* cf. *latior.* A sole specimen recovered from Bonanza was attributed to *Anomalomys* sp. *Karydomys,* is known in several localities from Central Europe during a short period of time, i.e., during the MN5 until MN6, corresponding to the Orleanian/Astaracian transition (Mörs and Kalthoff, 2004).

Concerning the eomyid fauna, two different taxa have been recovered in DNV–Bonanza: *Eomyops* sp. (one molar) and *Keramidomys carpathicus* (two molars). The latter taxon is well known in Central Europe during the MN6 (Sabol and Holec, 2002).

Based on the rodent assemblage from the DNV–Bonanza site, not limited to the cricetid and eomyid fauna, but also considering the presence of glirids such as *Myoglis meini* and *Muscardinus sansanensis,* among others (Sabol, 2005a; Sabol et al., 2021), as well as of the sciurid *Csakvaromys bredai* (Sabol, 2005a), the site can be correlated to the MN6 zone (see also Sabol et al., 2021). This is further supported by the insectivore records from the same site (Sabol, 2005b).

However, the rodent assemblage from DNV–Bonanza shows several differences with the fauna recorded at the nearby site of DNV–Štokeravská vápenka, therefore appearing to be a subset of the DNV–Štokeravská vápenka site (Sabol, 2005a,b; Mažgút, 2010; Sabol et al., 2021). As mentioned before, the Devínska Nová Ves set of sites are dated after the peak of the MMCO after which a major and permanent cooling step occurs. This was one of the major paleoclimatic events that took place in Europe at that time. Particularly, in Devínska Nová Ves this is reflected on a decrease in representation of open land elements recorded in the different sites (Sabol and Kováč, 2006).

When considering the paleoenvironmental aspects, the rodent assemblage suggests a forested environment, especially with the presence of the eomyids *Keramidomys carpathicus* and *Eomyops* sp., as well as a good assemblage of glirids, and the sciurid *Csakvaromys bredai* (Fejfar, 1974; Sabol 2005 a,b; Sabol et al., 2021). The presence of several taxa of cricetid rodents, which are characterized as generalist species (Kälin, 1999), cannot provide further information on the palaeoecology. Therefore, for a complete paleoenvironmental reconstruction, the whole fossil assemblage must be considered. The study of the Eulipotyphla depicted the palaeoenvironment as a forested area close to water bodies (Sabol, 2005b), which supports the results presented here. Moreover, the presence of several marine taxa, such as fish, sharks, seals, and marine bivalves, indicates a mixed insular or peninsular area, with subtropical forests close to freshwater bodies and in the vicinity of a saltwater sea (Sabol 2005a,b; Sabol et al., 2021).

6. Conclusions

The rodent assemblage of DNV– Bonanza site shows a significant number of cricetid and eomyid specimens. In this study, we were able to identify and describe several cricetid taxa such as *Eumyarion* cf. *latior, Democricetodon vindobonensis,* and *Karydomys* sp., together with *Anomalomys* sp. and *Neocometes brunonis.* A total of two eomyid species have been identified, being *Keramidomys carpathicus* and *Eomyops* sp. Apart from the described rodent taxa, DNV–Bonanza has a larger rodent assemblage with several taxa of glirid and sciurids. This association allows us to correlate this site, as well as its neighbouring locality, to the lower part of the MN6. In terms of the paleoenvironment, the rodent assemblage confirms a forested dominated environment, especially given the presence of eomyids such as *Keramidomys carpathicus,* and *Eomyops* sp., but also a good assemblage of glirids and the sciurid *Csakvaromys bredai.* Meanwhile, the cricetid fauna is considered to be generalist, so it cannot give further information on this behalf. Previous studies on the insectivore fauna of this locality further support the forested environment suggested.

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Figure captions

Fig. 1. A–B: Location of the DNV–Bonanza site on northern slopes of Devínska Kobyla Hill near Devínska Nova Ves – Štokeravská vápenka. C: Generalized section through the sediments of Bonanza (according to Ivanov, 1998). I – fine limestone debris; 2 – white lime sand; 3 – disaggregating sandstone with a higher content of muscovite; 4 – solid, light yellow marlstone with a great quantity of fossils; 5 – big boulders with white lime matter: 6 – greenish sand with interbeds of white lime matter; 7–11 – layers with coarse-grained, disaggregating sandstone without fossils to the fossiliferous marl, rich in fossils; 12 – white calciferous sandstone; 13 – yellowish-white sand with a large quantity of fauna; 14–17 – greenish to light sandstone, the biggest quantity of fossils are contained in the layer No. 17; a – Holocene humus-carbonate soil; b – Lias limestone; c – tectonic faults. Modified from Sabol (2005a).

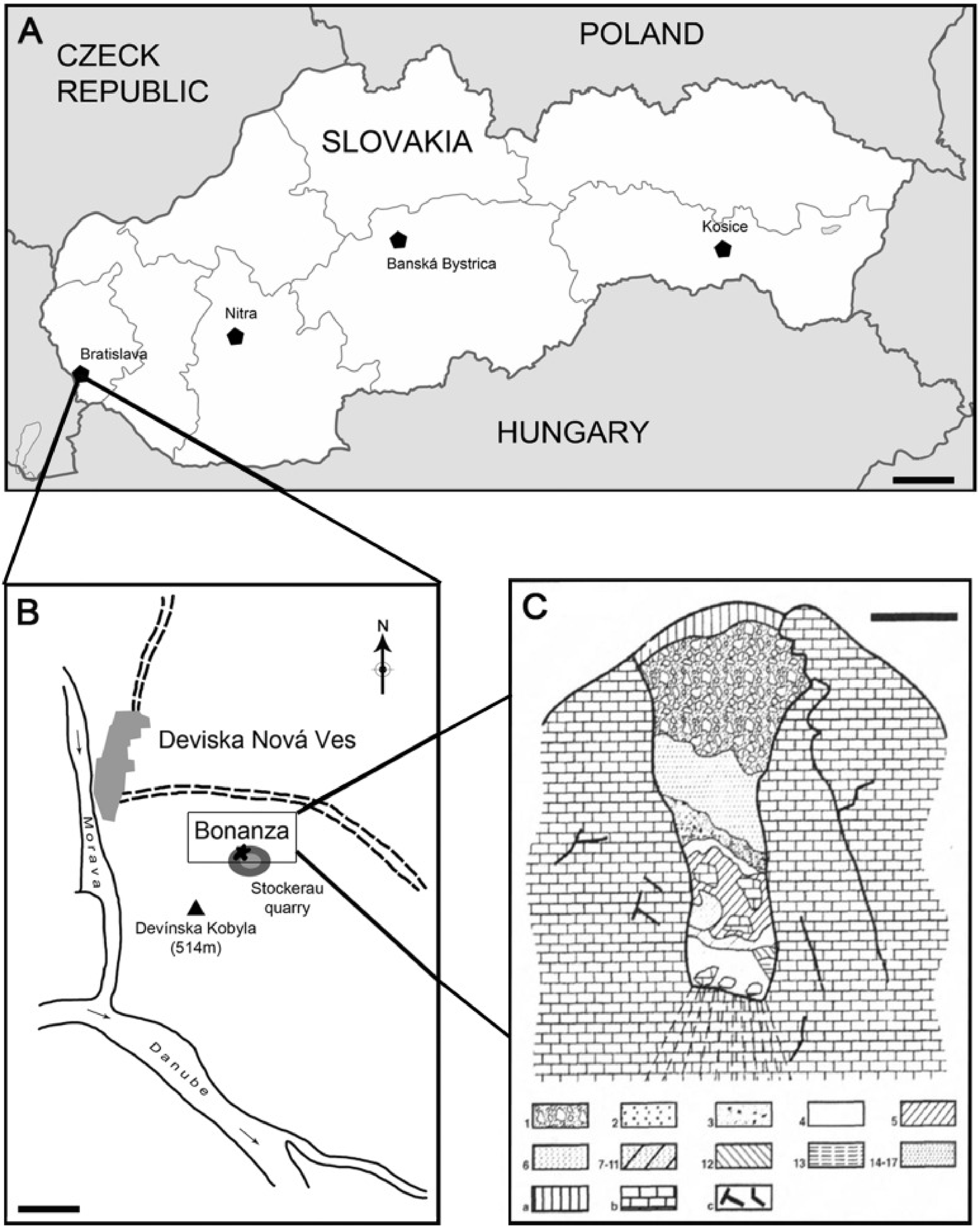

Fig. 2. Scanning electron microscope (SEM) micrographs. *Eumyarion* cf. *latior.* A: left M1 KGP-6a.4, B: right m1 KGP-9.2 (reversed), C: right m2 KGP-6a.5 (reversed), D: right m3 KGP-9.3 (reversed). *Democricetodon vindobonensis.* E: left M1 KGP-6a.7, F: right M1 KGP-6a.14 (reversed), G: left M1 KGP-MS29, H: left M2 KGP-MS31, I: left M2 KGP-6a.12, J:

right M3 KGP-MS34 (reversed), K: left m1 KGP-6a.10, L: right m1 KGP-MS35 (reversed), M: right m1 KGP-MS36 (reversed), N: left m2 KGP-6a.11, O: left m2 KGP-6a.13, P: left m2 6a.14, Q: right m2 KGP-MS38 (reversed), R: left m2 KGP-MS39, S: left m2 KGP-MS40, T: left m3 KGP-MS61. *Karydomys* sp. U: right M2 KGP-MS63 (reversed). *Keramidomys carpathicus.* V: right M1 KGP-MS69 (reversed), W: right M1 KGP-6a.18 (reversed). *Eomyops* sp. X: right P4 KGP-6a.17 (reversed).

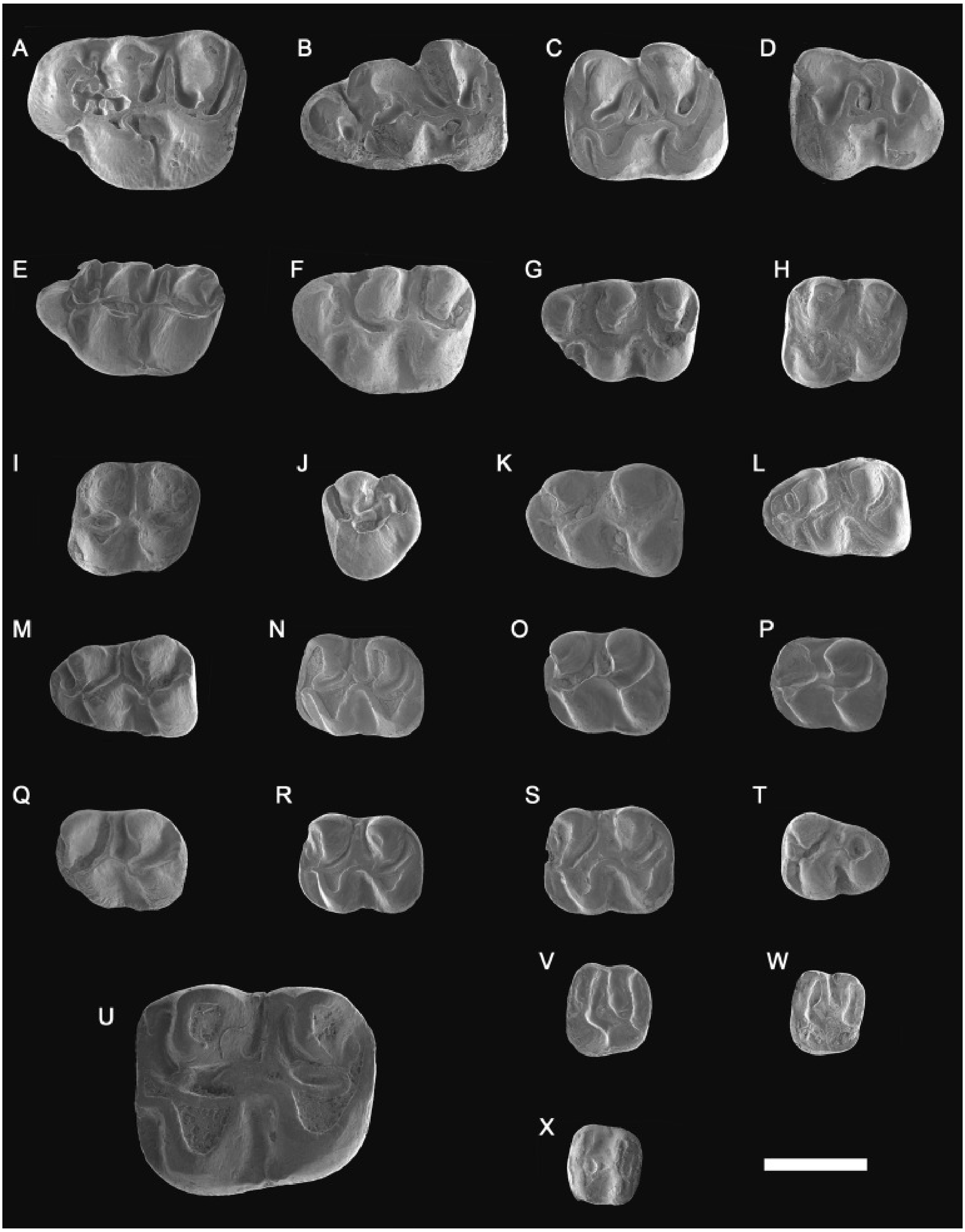

Fig. 3. Partial skull of *Eumyarion* cf. *latior* (KGP-1). A: left lateral view with M1 fragment. B: Ventral view of the skull with fragment of left M1. Partial skull remains of *Democricetodon vindobonensis* (KGP-17, C–D). C: dorsal view of the skull highly damaged. D: Ventral view of the skull with the right tooth row preserved.

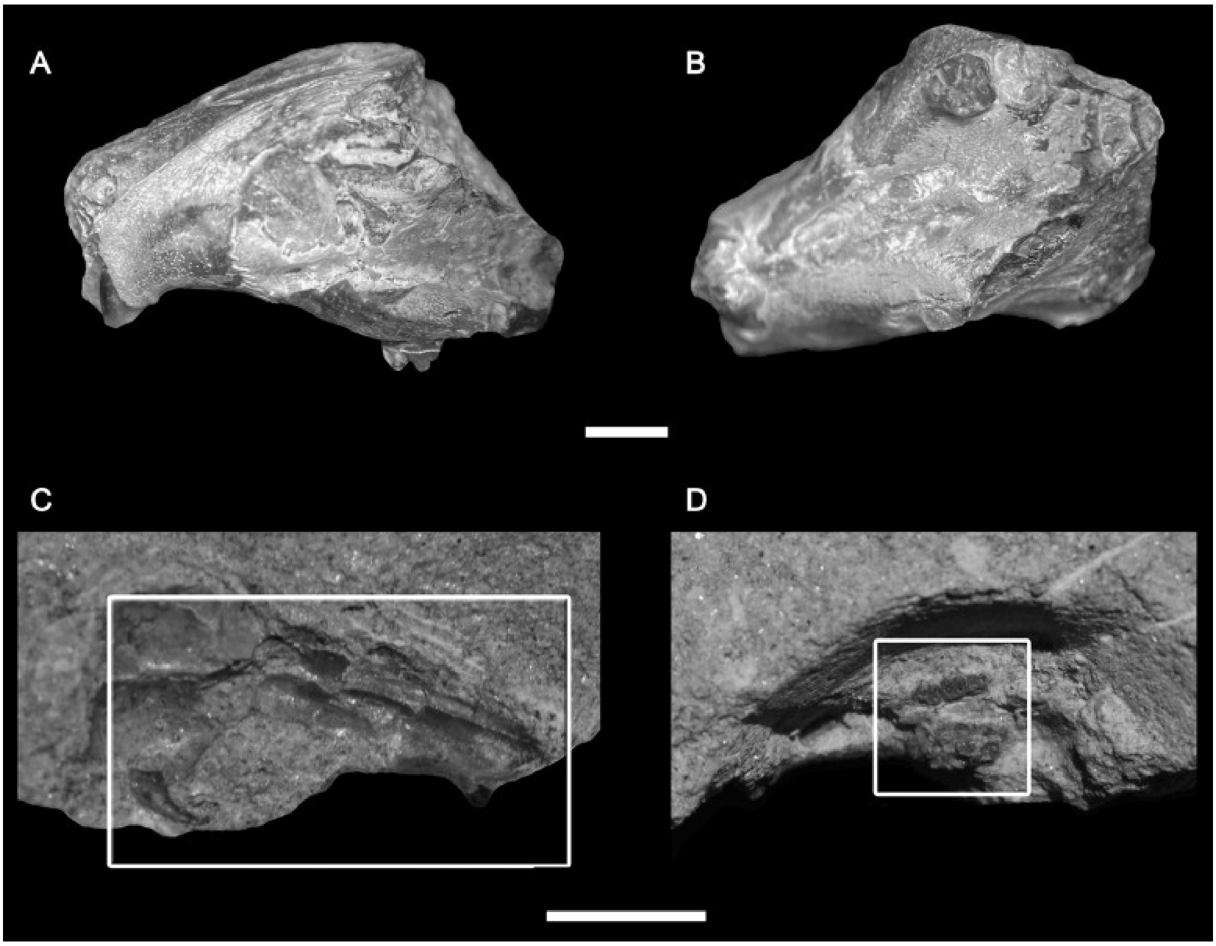

Fig. 4. Length/Width scatter plot of *Eumyarion* cf. *latior* from DNV- Bonanza site (black dots), DNV- Štokeravská vápenka (squares: material from Vienna Natural History Museum; triangles: material from Prague National Museum). The ellipses show the 95% confidence interval for *Eumyarion latior* (Anwil. Fejfar, 1974), *Eumyarion weinfurteri* (Sandelzhausen. Bruijn, 2009), and *Eumyarion bifidus* (Sandelzhausen, and other sites. Bruijn, 2009; Heissig, 1990).

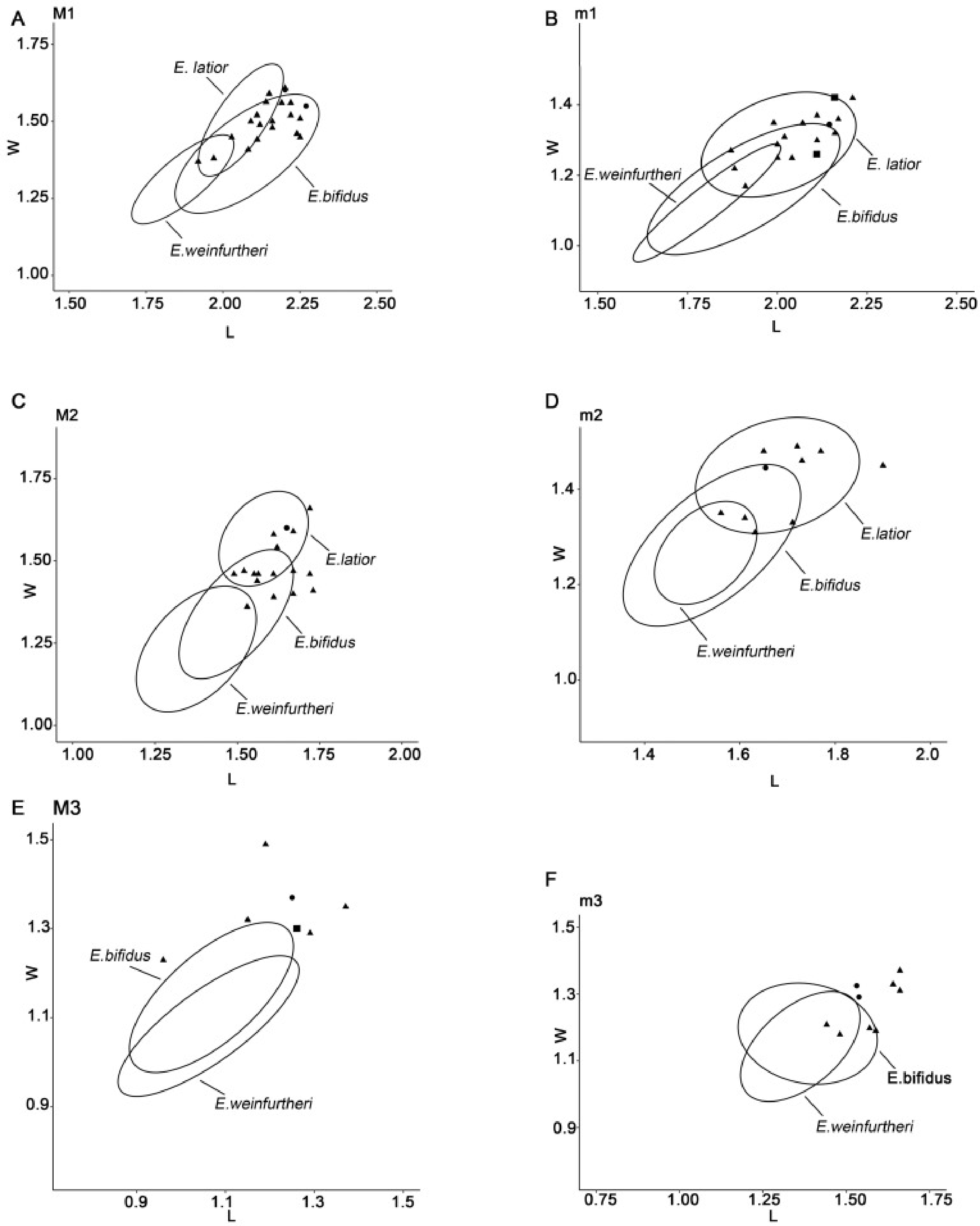

Fig. 5. Length/Width scatter plot of *Democricetodon vindobonensis* from DNV–Bonanza site (black dots), DNV–Štokeravská vápenka (squares: material from Vienna Natural History Museum; triangles: material from Prague National Museum). The ellipses show the 95% confidence interval for *Democricetodon gracilis* (Sandelzhausen. Wessels and Reumer,

2009), *Democricetodon franconicus* (Dolnice 1-3 and Ořechov. Fejfar, 1974), *Democricetodon mutilus* (Sandelzhausen. Wessels and Reumer, 2009), *Democricetodon vindobonensis* (DNV–Štokeravská vápenka, Neudorf. Fejfar, 1974).

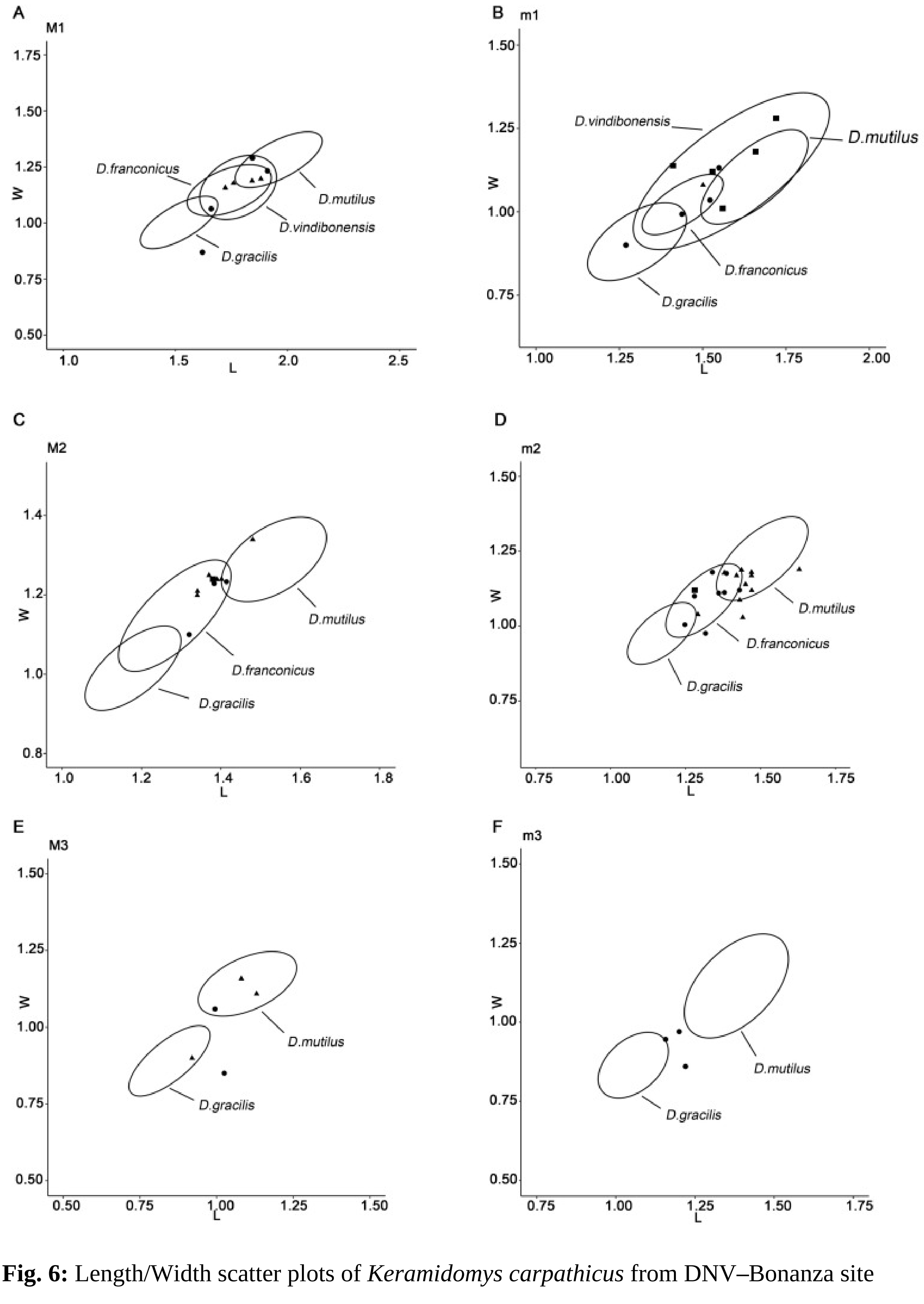

Fig. 6: Length/Width scatter plots of *Keramidomys carpathicus* from DNV–Bonanza site (black dots), DNV–Štokeravská vápenka (squares: material from Vienna Natural History Museum; triangles: material from Prague National Museum), and *Keramidomys thaleri* is

represented by blue dots. The ellipses show the 95% confidence interval for *Keramidomys carpathicus* from DNV–Štokeravská vápenka (Fejfar, 1974).

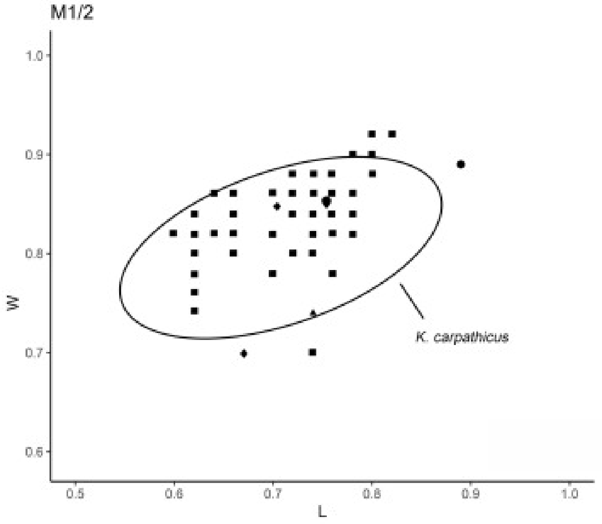

Fig. 7. Scanning electron microscope (SEM) micrographs. *Neocometes brunonis.* A: right M1 KGP-6a.1 (reversed), B: right M2 KGP-6a.2 (reversed), C: right m1 KGP-MS64 (reversed), D: left m3 KGP-6a.3. *Anomalomys* sp. E: right M2 KGP-6a.21 (reversed).

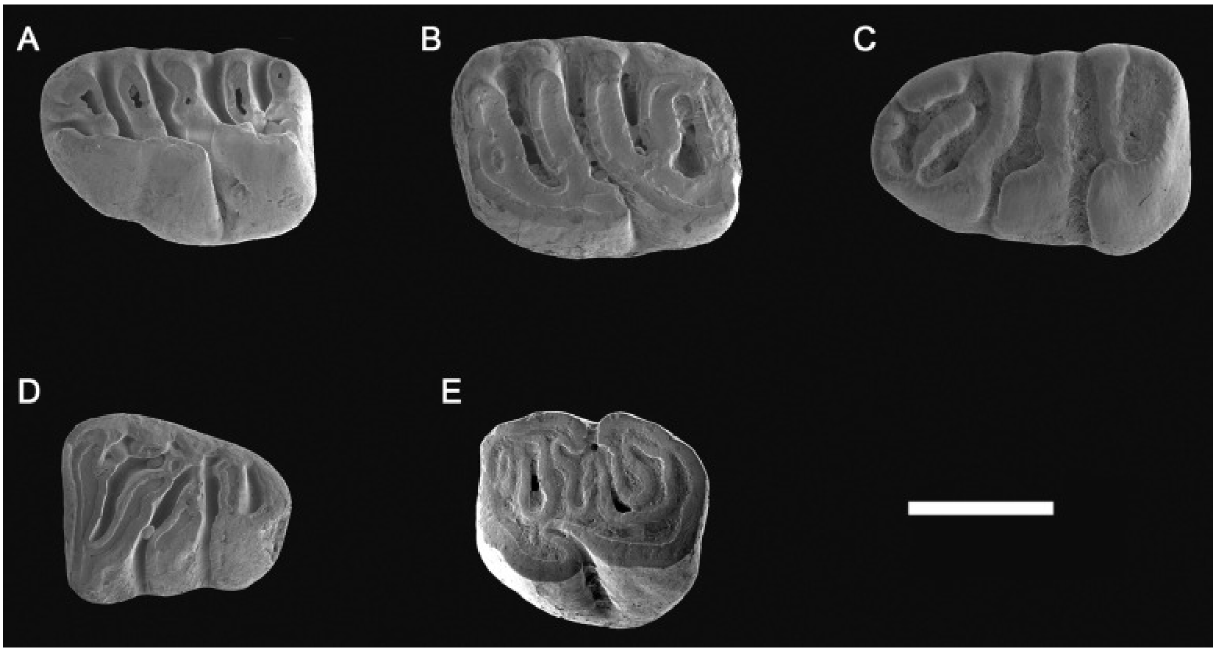

Fig. 8. Length/Width scatter plot of *Neocometes brunonis* from DNV- Bonanza site (black dots), DNV- Štokeravská vápenka (squares: material from Vienna Natural History Museum). The ellipses show the 95% confidence interval for *Neocometes brunonis* (DNV–Štokeravská

vápenka. Schaub and Zapfe, 1953; Fejfar, 1974), and *Neocometes similis* (Erkertshofen. Fahlbusch, 1966; Fejfar, 1974).