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RESEARCH ARTICLE

Revision of *Dinosorex* (Heterosoricidae, Eulipotyphla), with special reference to Slovak and Swiss material

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ABSTRACT

Dinosorex is an emblematic representative of the European Miocene small mammal community. Despite a relatively well-known fossil record, previous works pointed out the ambiguous definition of several species, accentuating the need for a taxonomic revision. The present work provides a comprehensive study of the highly specialised heterosoricid genus *Dinosorex*, including the description of well-preserved Slovak material from Devínska Nová Ves – Bonanza (MN6), Borský Svätý Jur (MN9), Studienka A (MN9), and Pezinok (MN10). The use of micro-computed tomography has shed light on the peculiarities of the basal *Dinosorex zapfei*, and material from numerous localities have been compared and restudied. As a result, we provide here an updated morphological comparison of all *Dinosorex* species and discuss the variability and resolving power of all morphological and morphometrical features used in the taxonomy of the genus. Our phylogenetic reconstruction confirms the strong role of geological basins in the evolutionary history of *Dinosorex*. The detailed study of European and Anatolian *Dinosorex* material led to the identification of a new species, *Dinosorex kaelini* sp. nov. from the Swiss locality of Nebelbergweg (MN9). The history of *Dinosorex* is driven by local evolution and dietary specialisation, which led to a trophic dead end in the earliest Turolian.

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Introduction

The family Heterosoricidae is a common member of eulipotyphlan communities in the Palaeogene and Neogene of Eurasia and North America. The first discovery of a member of this family dates from the middle of the 19e century, when Lartet (1851) described *Sorex sansaniensis* from the MN6 locality of Sansan, now the type species of the genus *Dinosorex*. A century later, Viret and Zapfe (1952) created the subfamily Heterosoricinae. This taxon is now often considered a family (following Reumer, 1987) because of its ambiguous relationship with Soricidae and Nyctitheriidae (see Klietmann et al., 2014a for discussion). The most recent phylogenetic analysis by Yuan et al. (2024) is in strong support of the family rank.

The fossil record of the Heterosoricidae goes back to the Eocene of North America with *Domnina*, a genus of unusual longevity (Cope, 1873; Gunnell et al., 2008; Yuan et al., 2024). In North America, the family is lastly recorded in the Middle Miocene. The oldest Eurasian heterosoricid species are recorded in the Early Oligocene in Europe (Smith & Van den Hoek Ostende, 2006; Ziegler, 2009) and Asia (Bendukidze et al., 2009; Ziegler et al., 2007). The assemblages from the lowermost Oligocene of Belgium, initially attributed to a new genus, *Belgicasorex* Smith & Van den Hoek Ostende, 2006, have been reattributed to *Quercysorex herrlingensis* by Ziegler (2009). Thus, the European record consists of three genera: *Quercysorex*, identified during the Oligocene (Engesser, 1975; Ziegler, 2009), *Heterosorex*, identified in Europe from the Late Oligocene to the Middle Miocene (Gaillard, 1915; Klietmann, 2013), and *Dinosorex*, the predominant heterosoricid genus in the Miocene of Europe.

The 'Terror-Shrew' *Dinosorex* is a specialised genus that is frequently recorded in European Miocene assemblages. However, despite a relatively high number of known species and a rather complete fossil record, most *Dinosorex* materials are left in open nomenclature (e.g. Prieto et al., 2010; Rabeder, 1998; Rzebik-Kowalska, 1994; Sabol, 2005) or show ambiguous morphological variability (Ziegler 2005; Furió et al., 2015; Seehuber, 2008). This is shedding doubts on the actual number of European species and on the robustness of several, commonly used diagnostic features. For instance, only two phylogenies are known to include *Dinosorex*. The first phylogenetic reconstruction of *Dinosorex* was made by Engesser (1975) at a time when only three species had been identified. The second, made by Ziegler (2009), resulted in the soft polytomy of four species and the curious proximity of distant species (e.g. *D. anatolicus* and *D. pachygnathus*), a consequence of using characters that are only relevant at a higher taxonomic rank.

The original purpose of the present work was the description of the Late Miocene Heterosoricidae from Slovakia, as part of a general study of the Late Miocene insectivore faunas of the country (Cailleux et al., 2023, 2024, in press). However, it soon became necessary to carry out a more detailled investigation of the taxonomy and phylogeny of *Dinosorex*. Therefore, we undertook a re-examination of numerous localities to provide a global revision of the genus. Our main objectives were as follows: (1) identify or re-identify all Slovak *Dinosorex* material; (2) provide an updated

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morphological comparison of European *Dinosorex* remains based on direct observation; (3) evaluate the strength of the morphological and metric features used in the taxonomy of *Dinosorex*; (4) provide a phylogenetic reconstruction of *Dinosorex* based on the most reliable characters, which should be parsimonious from a biochronological and biogeographical perspective.

Materials and methods

The present revision is based on European and Anatolian assemblages extracted from the localities shown in Figure 1. When possible, localities are divided into layers, fissures, or subareas. Additionally, we have described material from one Middle Miocene and three Late Miocene Slovak localities (Figure 1, underlined): Devínska Nová Ves (DNV) – Bonanza (MN6), Borský Svätý Jur (MN9), Studienka A (MN9) and Pezinok (MN10) (Cailleux et al., 2023; Joniak, 2005, 2016; Sabol, 2005; Sabol et al., 2021). These sites are located in the Vienna and Danube Basins. Geological settings are summarised in Sabol (2005) and Cailleux et al. (2023).

The dental terminology of the Heterosoricidae is unstable. Engesser (1980, 2009) used the terminology of Hutchison (1968) made for Talpidae, while Van den Hoek Ostende (1995) used the terminology of Reumer (1984) made for Soricidae. Klietmann et al. (2014a) also provided a more detailed terminology for *Heterosorex* and Soricidae, based on Reumer (1984). For descriptive purposes and as shown in Figure 2, the present study provides a new extended dental terminology for Heterosoricidae. The main difference from previous terminologies is about the term ‘hypoloph’, which is used in the literature to designate the crest sometimes found labial to the hypocone on the M1-M2, following Rabeder (1998). As an exception, in Klietmann et al. (2014a), the term hypoloph designates the posterolingual cingular crest. Since loph/lophid refers to a crest connecting two cusps/cuspids, we designate the labial crest of the hypocone as the prehypocrista. The posthypocrista designates the crest usually fused with the posterior cingulum in the P4-M3 of *Dinosorex*. Similarly, the prefixes pre- and post- refer to crests and cristids attached anteriorly and posteriorly to cusp/cuspids (Figure 2). Apart from the incisors, the teeth found anteriorly to the M1/m1 are called antemolars. The posteriormost antemolar corresponds to the P4/p4. The position of the teeth found between the A1 and the P4 is difficult to identify in the case of isolated fragments (Van den Hoek Ostende, 1995). Such elements are morphologically and morphometrically variable and their number seems to differ between the *Dinosorex* species. Consequently, we have used the abbreviation A2/A3, for example, to qualify upper antemolars corresponding to the A2 or to the A3. Upper dental elements are mentioned in the text with uppercase letters, unlike lower elements.

Dinosorex species are traditionally characterised by several diagnostic features, notably the presence of a prehypocrista on M1-M2, the number of lower antemolars, the degree of reduction of the entocristid on m1-m2, the configuration of the postcristid on m1-m2 (modus A or B, sensu Engesser, 1975) and the degree of separation of the condylar facets. As explained in this work, several of these features were overestimated. The identification of several morphotypes is also subject to clear observational biases. In order to

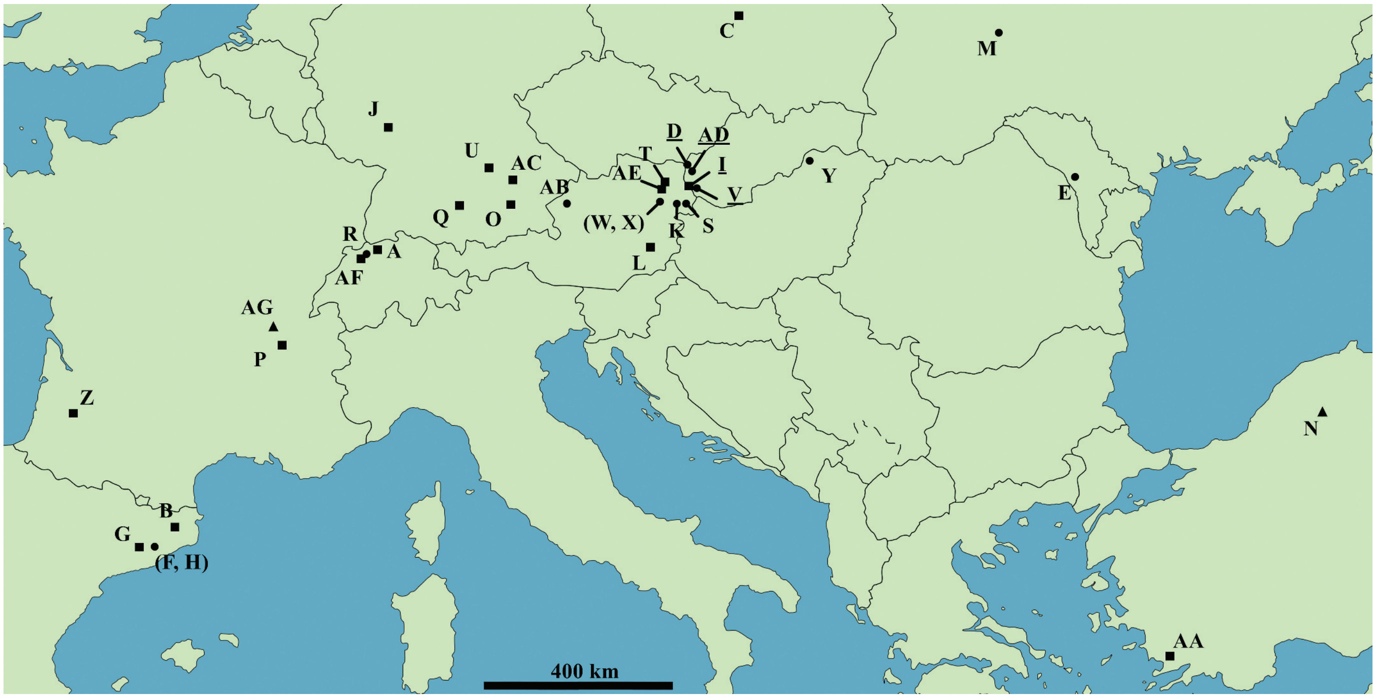

Figure 1. Map of western Eurasia showing the *Dinosorex* localities mentioned in the present work. (A) Anwil (Engesser, 1972); (B) Barranc de Can Vila (Furió et al., 2015); (C) Bełchatów (Rzebik-Kowalska, 1994); (D) Borský Svätý Jur (this work); (E) Bužor (Rzebik-Kowalska & Lungu, 2009); (F) Can Llobateres (Furió et al., 2015); (G) Can Mata (Furió et al., 2015); (H) Castell de Barbera (Furió et al., 2015); (I) Devínska Nová Ves (Sabol, 2005; this work); (J) Dorn-Dürkheim (Storch, 1978); (K) Götzendorf (Rabeder, 1998; Ziegler, 2006); (L) Gratkorn (Prieto et al., 2010); (M) Grytsiv (Rzebik-Kowalska & Topachevsky, 1997); (N) Keseköy (Van den Hoek Ostende, 1995); (O) Kleineisenbach (Prieto, 2007); (P) La Grive Saint-Alban (Hugueney et al., 2012); (Q) Mörgen (Seehuber, 2008); (R) Nebelbergweg (Kälin & Engesser, 2001; this work); (S) Neusiedl am see (Ziegler, 2006); (T) Obergänserndorf (Rabeder, 1998); (U) Petersbuch (Ziegler, 2003); (V) Pezinok (this work); (W) Richardhof-Golfplatz (Ziegler, 2006); (X) Richardhof-Wald (Ziegler, 2006); (Y) Rudabánya (Ziegler, 2005); (Z) Sansan (Engesser, 2009); (AA) Sarıçay (Engesser, 1980); (AB) schernham (Ziegler, 2005); (AC) Sandelzhausen (Ziegler, 2000); (AD) Studienka (this work); (AE) Teiritzberg (Rabeder, 1998); (AF) Vermes (Ziegler, 2000); (AG) Vieux-collonges (Hugueney et al., 2012). Early, Middle and Late Miocene localities are indicated by black triangles, squares and circles, respectively. Only underlined localities are formally described.

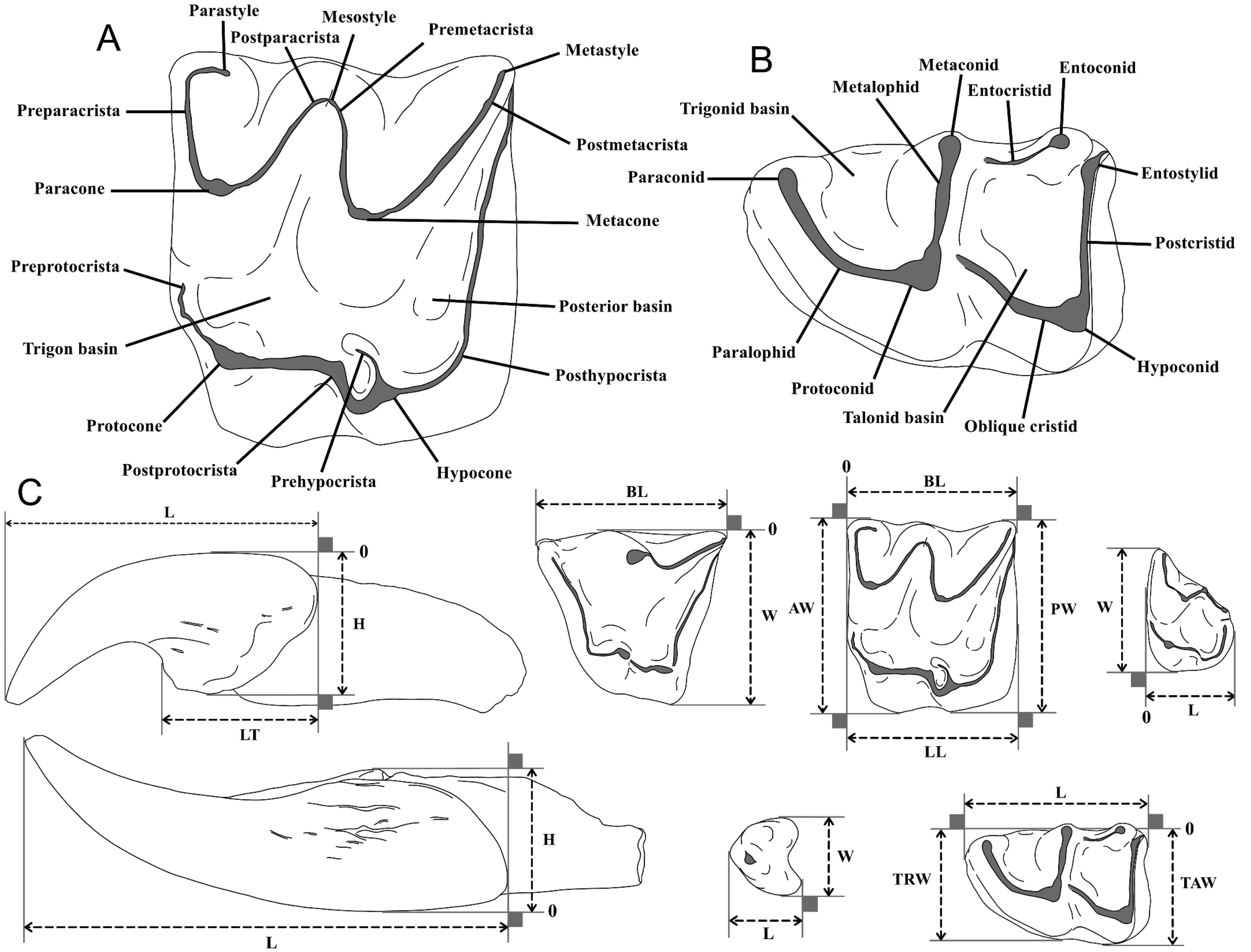

Figure 2. (A–B) Terminology used for the M1 (A) and m1 (B) of *Dinosorex*; (C) measurements protocol for I1, P4, M1, M3, i1, p4 and m1. AW: anterior width; BL: labial length; H: height; L: length; LL: lingual length; LT: length of the talon; PW: posterior width; TAW: talonid width; TRW: trigonid width; W: width.

reduce these, several morphotypes identified in the present work are schematised in Figure 3. Namely, the structural configuration of the A1 and P4, the degree of development of the entocristid on m1-m2, and the mode of the postcristid of m1-m2. For the latter, two examples are given for both modus A and modus B. There are no distinct morphotypes on the lower molars but only morphological gradients. Therefore, intermediate configurations are particularly ambiguous.

When materials without direct observation are mentioned, the terms ‘predominant’, ‘variable’ and ‘negligible’ are used to describe the frequency of morphotypes based on the original description of the material and figures. These terms are deliberately vague due to the paucity of data, but roughly correspond to 100%–66%, 66%–33%, and 33%–0% of representation, respectively. Otherwise, the morphotype frequencies given in this work are new and may differ slightly to greatly from the original descriptions.

The measurement protocol used for *Dinosorex* is shown in Figure 2 and follows Furió et al. (2015). The reference line is indicated by a ‘0’ (Figure 2). For antemolars (except P4), the reference line is the anteroposterior axis of symmetry. The width was measured for both the anterior and the posterior parts of the molars. Considering the fragmentary state of several Slovak specimens, we also provided both labial and lingual lengths for M1-M2. We used the abbreviations of Reumer (1984) to distinguish the different measurements, which are given in millimetres (mm).

The dental elements were measured using a digital measuring microscope with a mechanical stage and digital measuring clocks. The identification numbers, laterality and measurements of the Slovak specimens are given in Supplementary Data 1. Except for CT-scanned elements, specimens in figures are represented in left orientation. A specimen was scanned using a Zeiss Xradia 520 X-ray CT, at the Naturalis Biodiversity Center, Leiden, The Netherlands, and virtually segmented with the Avizo software (v. 2020.3.1; https://www.thermofisher.com/). Drawings were made using a graphics tablet (Wacom Intuos Pro) and the Autodesk SketchBook software (v. 8.7.1; https://www.sketchbook.com/). The material described from DNV – Bonanza is housed in the Natural History Museum of Bratislava, Slovakia. The materials from Borský Svätý Jur, Studienka and Pezinok are housed at the Department of Geology and Paleontology of Comenius University, Bratislava, Slovakia.

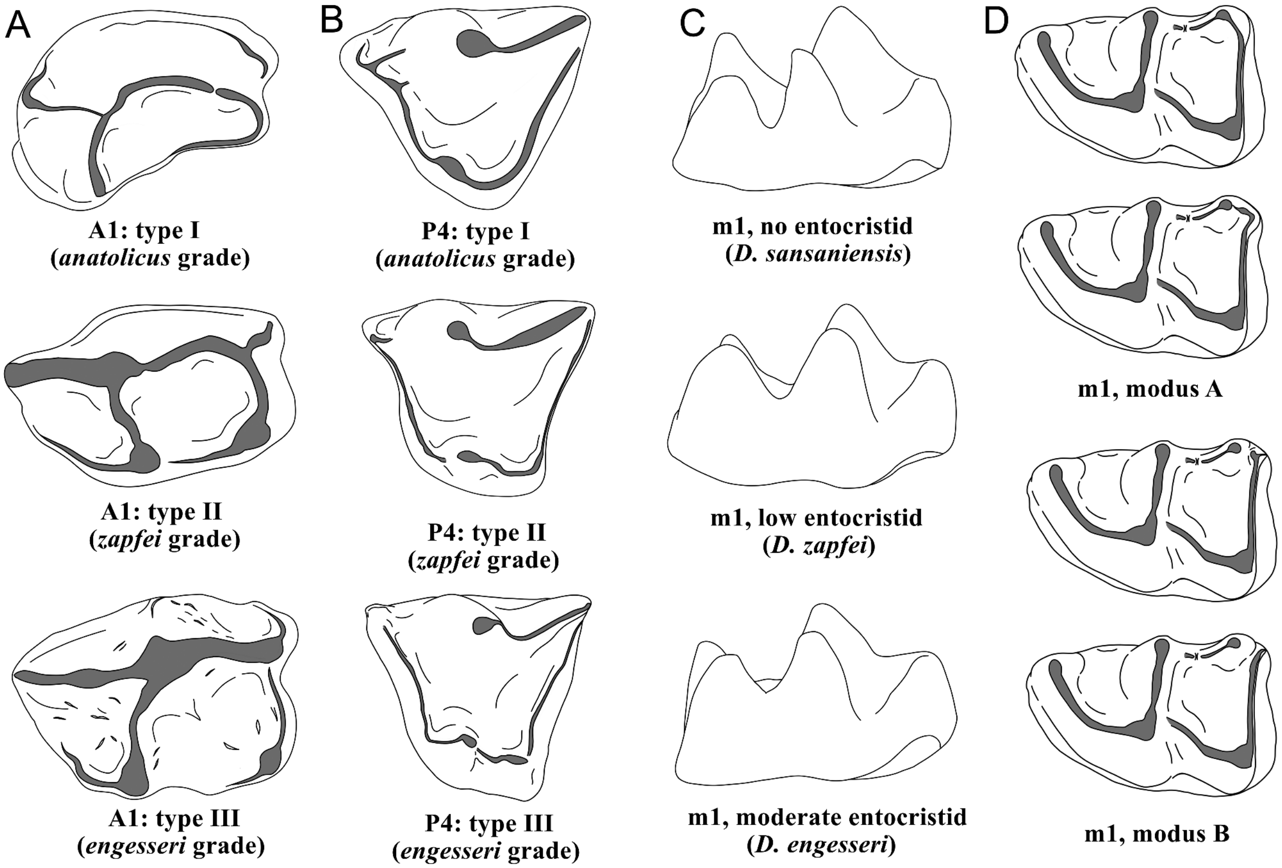

Figure 3. Morphotypes and modes used in the present work. (A) structural configuration of the A1, occlusal view; (B) structural configuration of the P4, occlusal view; (C) height development of the entocristid on m1, lingual view; (D) identification of modus a and modus B postcristid on m1, occlusal view. Dental elements are schematised and unscaled.

List of abbreviations

AW, anterior width; **BL**, labial length; **H**, height; **L**, length; **LL**, lingual length; **LT**, length of the talon; **N**, number of specimens; **PW**, posterior width; **TAW**, talonid width; **TRW**, trigonid width; **W**, width.

List of institutions

BSPG, Bayerische Staatssammlung für Paläontologie und Geologie, München, Germany; **CU**, Department of Geology and Paleontology of Comenius University, Bratislava, Slovakia; **HGI**, Hungarian Geological Institute, Budapest, Hungary; **ICP**, Institut Català de Paleontologia Miquel Crusafont, Cerdanyola del Vallès, Spain; **ISEZ PAN**, Institute of Systematics and Evolution of Animals, Polish Academy of Sciences, Cracow, Poland; **LMJG**, Landesmuseum Joanneum of Graz, Germany; **NHMV**, Natural History Museum of Vienna, Austria; **NMA**, Naturmuseum Augsburg, Germany; **NMB**, Natural History Museum of Basel, Switzerland; **NMNHU-P**, Palaeontological Museum, National Museum of Natural History, National Academy of Sciences of Ukraine, Kiev, Ukraine; **SMF**, Senckenberg Research Institute and Natural History, Frankfurt, Germany; **SNM-NHM**, Slovak National Museum, Natural History Museum, Bratislava, Slovakia; **TSU**, Tiraspol State University, Kišinev, Moldova; **UCBL**, University of Lyon 1 (Claude Bernard), France.

List of localities

BZ, (DNV) Bonanza; **BJ**, Borský Svätý Jur; **DNV**, Devínska Nová Ves; **Nbw.**, Nebelbergweg; **PK**, Pezinok; **ST**, Studienka.

Systematic palaeontology

Order **Eulipotyphla** Waddell, Okada and Hasegawa, 1999
Family **Heterosoricidae** Viret and Zapfe, 1952
Genus ***Dinosorex*** Engesser, 1972

Type species

Sorex sansaniensis Lartet, 1851.

Other referred species

Dinosorex pachygnathus Engesser, 1972; *D. zapfei* Engesser, 1975; *D. anatolicus* Van den Hoek Ostende, 1995; *D. grycivensis* Rzebik-Kowalska and Topachevsky, 1997; *D. engesseri* Rabeder, 1998.

Diagnosis (emended)

Heterosoricidae characterised by a slightly to moderately reduced dental formula (I1/1, A5-?/4–2, M3/3) and the combination of: large size (mean Lm1: 2.5–3.0 mm); mainly type II A1; mainly types II and III P4; acuspulate and strongly elongated i1 (Li1/Lm1 >2.30); slightly reduced m2 (Lm1/Lm2 >1.10) and moderately reduced m3 (Lm1/Lm3 >1.50); often pigmented dental elements; massive anterior part of the mandibular body; the mandibular foramen is located between the posterior root of m1 and the anterior root of m2; the masseteric fossa is divided by a low ridge; strongly separated condylar facets, or at least vestigial connection.

Distribution

MN1–3, MN5 and MN7/8 of Anatolia (Begun et al., 2003; Engesser, 1980; Van den Hoek Ostende, 1995), and from MN4 to MN11 of Europe (Engesser, 1972, 1975; Storch, 1978; Ziegler & Fahlbusch, 1986; Franzen & Storch, 1999; Ziegler, 2000, 2003; Ziegler, 2006; Prieto et al., 2010; Furió et al., 2015; this paper).

Dinosorex zapfei Engesser, 1975 (Figure 4)

Diagnosis (emended)

Species of *Dinosorex* characterised by the combination of: smooth surface on A1 (type II); trapezoidal P4 with a weak to absent parastyle and no hypocone (type II); no prehypocrista on M1-M2; rather elongate M1; 3 or 4 lower antemolars; on m1-m2, low entocristid and high predominance of modus A postcristid; high Lm1/Lm3 ratio (~1.63 to 1.92).

Material

DNV – Bonanza: SNM-NHM Z-14589, a crushed fragment of skull with right P4 (L = 2.08, W = 2.02), right M1 (BL = 2.00, LL = 2.04, AW = 2.29, PW = 2.27), right M2 (BL = 1.92, LL = 1.99, AW = 2.17, PW = 1.80), left P4 (L = 2.31, W = 2.24), left M1 (BL = 2.22, LL = 2.27, AW = 2.46, PW = 2.43) and left M2 (BL = 2.07, LL = 2.16, AW = 2.32, PW = 1.96), and an almost complete right mandible with i1 (L = 6.82), m1 (L = 2.46, TRW = 1.49, TAW = 1.59), m2 (L = 2.06, TRW = 1.37, TAW = 1.37) and m3 (L = 1.51, W = 1.04).

Distribution

Dinosorex zapfei is commonly identified in MN5 and MN6 localities of central Europe (Engesser, 1975; Rabeder, 1998; Rzebik-Kowalska, 1994; Sabol, 2005; Ziegler, 2000).

Description

As shown in Figure 4(B), the two maxillaries are damaged and not virtually extractable. No teeth are preserved posterior to the P4. The left P4-M2 are longer, about 10%, than the right P4-M2. The right dental row preserves four alveoli (Figure 4(D,E)), corresponding to the A1 (marked in green), the A2 (marked in pink), the A3 (marked in light blue) and the A4 (marked in yellow). Therefore, each upper antemolar has a single root. The alveole of the A2 is the smallest. The alveoles have different degrees of obliquity, that of the A4 being the straightest, and that of the A1 the most oblique.

The P4 is trapezoidal and is as long as it is wide. The paracone is massive and positioned anterolabially. There is no distinct parastyle but a narrow extension at the anterolabial corner (Figure 4(D–G)). The postparacrista is sharp and slightly curved. The rounded lingual area is simple. It is bordered by a robust, continuous cingular crest extending from the anterolingual corner to the posterolingual corner. This crest is damaged in our left specimen (Figure 4(F,G)). This crest is thicker and higher in its most lingual part, where it bears a low protocone in an anterolingual position. The M1 is a stout element. The heavy paracone is slightly more compressed than the metacone. The preparacrista is short and the parastyle is

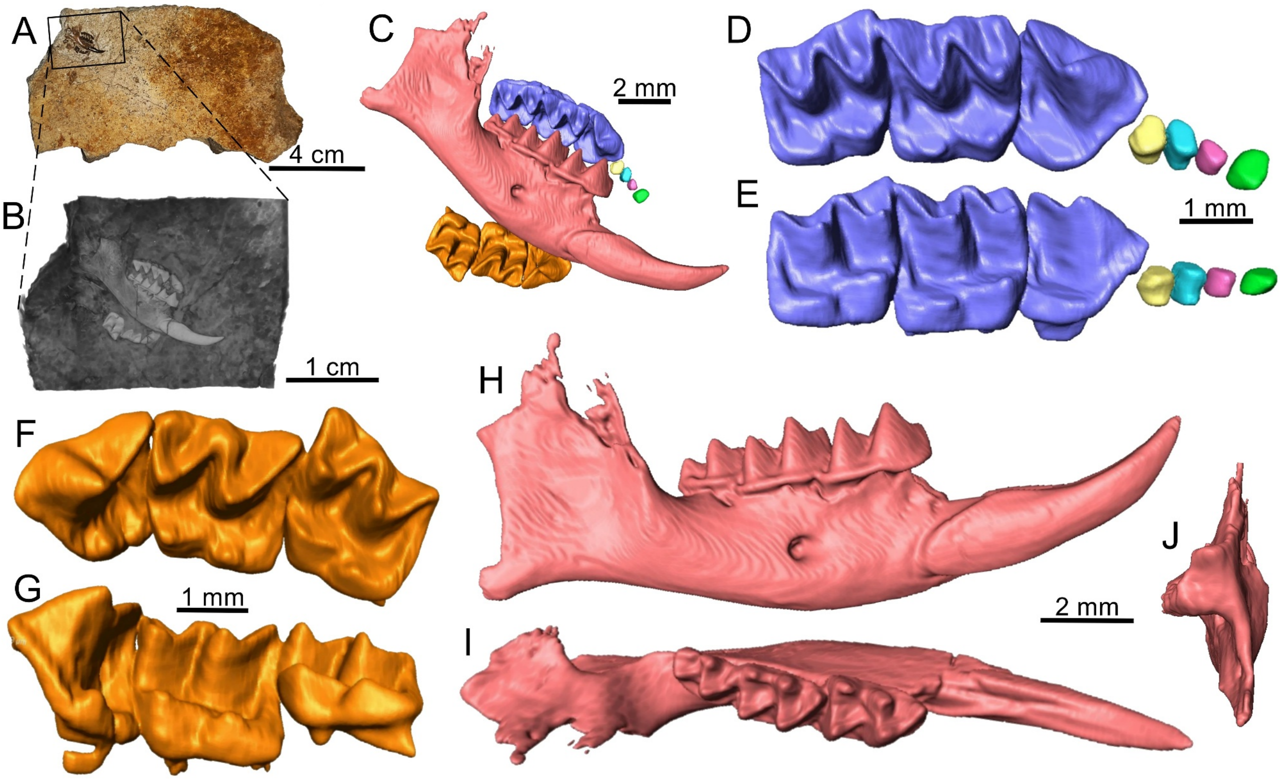

Figure 4. *Dinosorex zapfei* from DNV – Bonanza, SNM-NHM Z-14589. (A) enclosing rock with the specimen; (B) extracted fragment of the enclosing rock; (C) interpretation after ct-scan segmentation; (D–E) extracted right upper dental row with P4-M2 (purple) and the filled alveoli of the A4 (yellow), A3 (light blue), A2 (pink) and A1 (green), in occlusal (D) and occluso-lingual (E) views; (F–G) extracted left upper dental row with P4-M2 (orange), in occlusal (F) and occluso-lingual (G) views; (H–J) extracted right mandible with i1, m1-m3 (red), in labial (H), occlusal (I) and posterior (J) views.

low. The postparacrista is longer than the premetacrista. The postmetacrista is the longest labial crest. The metastyle is only slightly lower than the undivided mesostyle. On the lingual side, a straight preprotocrista extends from the broad protocone and touches the lingual base of the paracone. The postprotocrista is S-shaped and is superficially divided near the low hypocone. There is no prehypocrista. The posthypocrista connects the hypocone to the posterolabial margin, thus forming a broad and relatively deep posterior basin. The M2 is slightly smaller than the M1 and has a less square shape (Figure 4(D–G)). It is characterised by a moderate transverse compression of the posterior side, resulting in a short postmetacrista and posthypocrista. The preparacrista is longer and the parastyle is found in a more labial position. In addition, the lingual outline is slightly more curved than that of the M1.

The mandibular body is robust and especially high below the m1 because of the extension of the lower incisor to below the anterior root of the m1. The height then decreases posteriorly, creating an S-shaped ventral line in the labial view (Figure 4(H)). A relatively broad space separates the i1 from the m1. At least three alveoli are clearly visible. The mandibular foramen is found below the anterior root of m2. The posterior part of the mandible shows a narrow masseteric region. In the labial view, a thin blade cuts the shallow masseteric fossa in half. The angular process is elongated. The condylar process of the specimen is damaged. The two condylar facets are strongly divided. A thin ridge connects the base of the two facets (Figure 4(J)).

The i1 is an elongated incisor with a single bent tip. The labial side is largely extended posteriorly and bears a distinct cingulid. There is no rough surface on the posterolabial side. The m1 has a trigonid of similar length to the talonid. The robust protoconid is connected to the paraconid by a curved, angular paralophid. The metaconid is slightly higher than the paraconid. The trigonid basin is deep and open lingually. The entoconid is laterally compressed. The entocristid is low. The hypoconid is lower and more conical than the entoconid. The oblique cristid connects the hypoconid to the base of the trigonid wall, slightly lingual to the base of the protoconid. The postcristid extends from behind the entoconid and joins the posterolingual flank of the hypoconid (modus A). The anterior, labial and posterior cingulum are not connected to each other. The m2 differs from the m1 in that it has a slightly more compressed trigonid and a protoconid in a more labial position. The paralophid and metalophid are therefore longer. The talonid of m2 is similar to m1 but is less broad, resulting in a more squared shape. The small m3 has a slightly reduced trigonid, with all trigonid cuspid being relatively low. The paralophid is longer than the metalophid. The talonid is narrow and strongly reduced. The entoconid and hypoconid are still distinct and are connected to each other by a barely visible postcristid. The oblique cristid is parallel to the entocristid. There is a broad and continuous cingulid on the lingual side.

Remarks

The present specimen, recovered from the fissure of DNV – Bonanza in 2002, has been previously described by Sabol (2005) and attributed to *Dinosorex* cf. *zapfei*. The spatial configuration of the specimen within the enclosing rock did not allow a clear taxonomic verdict. The scan (Figure 4) revealed features characteristic of *Dinosorex zapfei*. These are: a weak/absent parastyle and no hypocone on P4, no prehypocrista on M1-M2, a poorly posteriorly compressed M2, a relatively large space between i1 and m1, an inflated mandible below the m1, and a reduced entocristid and a modus A postcristid on m1-m2. This specimen shows no significant morphological differences from the nearby-type locality of DNV – Štokeravská vápenka.

The insertion of the mandible between the two upper dental rows is explained by mechanical compression related to avian predation. Fractured skulls and inserted mandibles are common observations in the pellets of birds of prey (Czaplewski, 2011; F.C., pers. obs.). There is a moderate fracture of the skull and no visible digestion marks (sensu Fernández-Jalvo et al., 2016). The specimen shows severe secondary damages. Namely, whereas its overall structure is recognisable in scans, its reconstruction is impossible because of the highly fragmented nature of the superficial bone. The cracking, flaking and general degradation of the bone is very typical of aerial weathering (Czaplewski, 2011), supporting that a relatively long time elapsed between the regurgitation of the individual and its cover by sediment. This could also account for the absence of most antemolars.

Dinosorex engesseri Rabeder, 1998 and ***Dinosorex* cf. *engesseri*** Rabeder, 1998 (Figure 5, Table 1)

Diagnosis (emended)

Species of *Dinosorex* characterised by the combination of: clearly wrinkled surface on A1 (type III); two cuspules on A1; trapezoidal P4 with a robust parastyle and a low hypocone (type III); extremely frequent presence of prehypocrista on M1-M2; three lower antemolars; moderately high entocristid and frequent modus A postcristid on m1-m2.

Material

Borský Svätý Jur (*D. engesseri*), 73 elements: seven I1, four A1, one A2/3, two A4, four P4, two M1, nine M2, six M3, ten i1, three a3, one p4, one fragment of mandible with m1–2, twelve m1, seven m2, four m3. The dental measurments are provided in Table 1.

Studienka A (*D. engesseri*), 43 elements: one I1, one A1, four P4, six M1, three M2, five M3, two i1, two a1, five m1, nine m2, five m3. The dental measurments are provided in Table 1.

Pezinok (*D.* cf. *engesseri*), five elements: one I1 (L = 4.28, LL = 2.46, H = 1.87), one fragment of P4, one fragment M1 (LL = 2.35), one fragment M3, one fragment m2.

Distribution

Dinosorex engesseri is restricted to MN9 and MN10 of Austria (Rabeder, 1998; Ziegler, 2006) and Slovakia (this paper), and MN9 of Hungary (Ziegler, 2005).

Description

The different colouring of the apexes of several teeth specimens from the three described assemblages indicates a moderate dental pigmentation. The I1 is a massive incisor with a bent, shovel-like apex (Figure 5(A)). A superficial central apical notch is present on the apex ridge. The central side is flat and ends before the large incisor canal. The labial side is extended posteriorly where the surface is creased. It bears an irregular cingulum which forms a distinct median talon. The A1 is especially robust. The tooth is surrounded by a continuous cingulum and bears a labiolingually compressed cusp in the labial position. From its tip, three crests emerge: one reaching the anterolabial margin, one reaching the posteriolabial margin and a third one descending as a perpendicular crest and touching the most lingual border as a minute cuspule (Figure 5(C–D)). The posterior margin is bilobed. While the labial lobe bears only a posterior crest, the lingual lobe bears a relatively robust cuspule connected to the cingulum, thus forming an incipient basin. Between the two previously mentioned cuspules, a third, smaller one is sometimes found. The A2/A3 is the smallest upper antemolar. The single cusp has a slightly labial

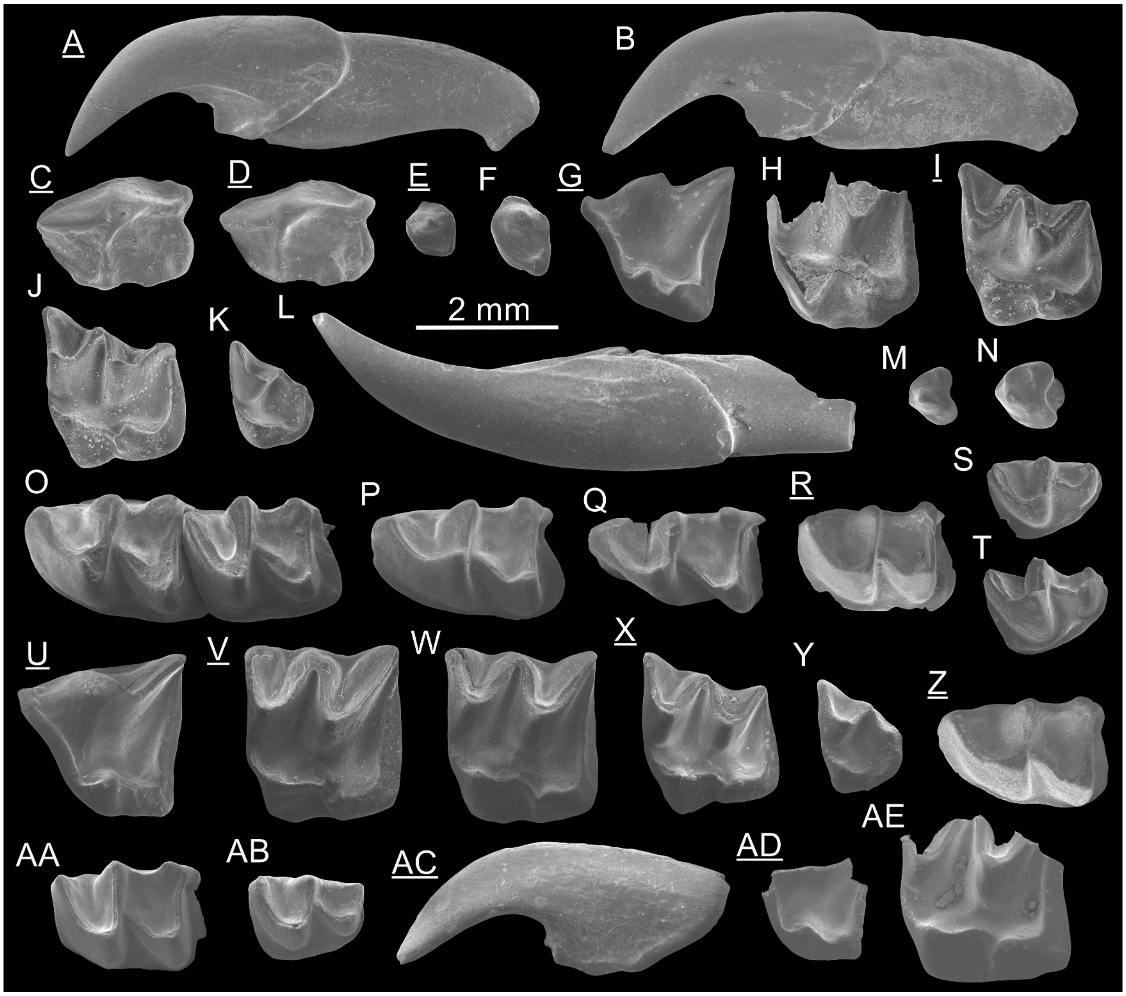

Figure 5. Sem pictures of *Dinosorex engesseri* from Borský Svätý Jur (A–T), Studienka A (U–AB) and Pezinok (AC–AE). (A) I1, BJ213504, labial view; (B) I1, BJ213504, labial view; (C) A1, BJ21310; (D) A1, BJ213511; (E) A2/3, BJ213591; (F) A4, BJ213590; (G) P4, BJ213514; (H) M1, BJ213520; (I) M2, BJ213525; (J) M2, BJ213530; (K) M3, BJ213535; (L) i1, BJ213540, labial view; (M) a3, BJ213597; (N) p4, BJ213594; (O) fragment of mandible with m1-m2, BJ213561; (P) m1, BJ213566; (Q) m1, BJ213567; (R) m2, BJ213576; (S) m3, BJ213584; (T) m3, BJ213586; (U) P4, ST214303; (V) M1, ST214307; (W) M1, ST214308; (X) M2, ST214312; (Y) M3, ST214317; (Z) m1, ST214329; (AA) m2, ST214335; (AB) m3, ST214344; (AC) I1, PK151004; (AD) P4, PK151006; (AE) M1, PK151005. Images with underlined numbers (A, C-G, I, R, U-V, Z, AC-D) are reversed.

position and is labiolingually compressed. There is a reduced buccal cingulum. There is a short lingual cingulum surrounding a protobasin. The A4 has an irregular outline and is wider than long. There is a low cusp almost in the middle of the tooth. A moderate posterolabial extension is present, delimited by a cingulum. The larger lingual extension is also delimited by a cingulum, but has a distinct, shallow basin. The P4 is a three-rooted tooth with a trapezoidal outline. The paracone is conical and weakly connected to a weak parastyle. The postparacrista is sharp and angular. The protocone is a robust cusp connected to the parastyle by a low preprotocrista and to the smaller hypocone by a thin and short postprotocrista. The hypocone is more lingual than the protocone (Figure 5(G,U,AD)). It is rarely distinguishable from the robust posthypocrista. The posterolingual basin is deep.

The M1 is a large, quadrangular tooth. On the labial side, the metacone and the paracone have roughly the same shape. The paracone is in a more labial position. The preparacrista turns posteriorly as a hook when reaching the anterolabial corner. The mesostyle is undivided. The postmetacrista is almost straight. The lower protocone is connected to the base of the paracone by a short, curved preprotocrista and to the lower hypocone by an angular postprotocrista. The prehypocrista is often present (2/2 in BJ; 4/6 in ST A). Figure 5(A,E) shows that it is absent in the single M1 from Pezinok. The posthypocrista is broad and reaches the posterolabial corner. A short cingulum is present between the protocone and the base of the hypocone. The M2 differs from M1 by a moderate labiolingual compression of the posterior side, resulting in a labial crest with a symmetrical shape and a more curved posthypocrista (Figure 5(I,X)). The hypocone is more reduced and the prehypocrista is less frequent (4/7 in BJ; 1/4 in ST A). The M3 is a reduced subtriangular tooth with a rounded posterior flank. The paracone and adjacent crests are robust. The premetacrista is thin and short. The metacone is low and bulbous. A robust and curved crest descends from it posterolingually and bears a barely distinguishable hypocone in two out of six specimens from Borský Svätý Jur. The protocone is slightly labially compressed. The preprotocrista touches the base of the paracone. The postprotocrista is connected to the posterior crest (three in BJ, two in ST A) or ends freely in front of it (two in BJ, three in ST A).

The mandible is strongly built. There are three alveoli between the alveoli of i1 and the alveoli of m1. The anterior one is the widest and corresponds to a1. The posterior one is smaller but more circular and corresponds to p4. Between these two alveoli, incorporated in the bony lamina separating the alveole of a1 and the alveole of p4, there is a reduced alveole interpreted as belonging to a3. The mandibular foramen is located below the anterior alveole of m2.

Table 1. Measurements (in mm) of *Dinosorex engesseri* from Borský Svätý Jur (MN9) and Studienka A (MN9), Slovakia.

Dinosorex engesseri, **Borský Svätý Jur**

	I1			**A1**		**A2/3**		**A4**		**P4**		**M1**	**M2**			
	L	**Lt**	**H**	**L**	**W**	**L**	**W**	**L**	**W**	**BL**	**W**	**Ll**	BL	**Ll**	**AW**	**PW**
N	3	3	5	3	3	1	1	1	1	3	3	2	5	5	5	5
Min	3.84	1.92	1.73	2.03	1.43					2.21	1.95	2.16	1.80	1.93	2.24	1.63
Max	4.00	2.03	1.83	2.07	1.55					2.28	2.08	2.19	1.87	2.02	2.34	1.68
Mean	3.93	1.99	1.76	2.05	1.47	0.66	0.82	0.81	1.09	2.25	2.03	2.18	1.84	1.97	2.28	1.66

	M3		**i1**	**a3**		**p4**		**m1**			**m2**			**m3**	
	L	**W**	**L**	**L**	**W**	**L**	**W**	**L**	**TRW**	**TAW**	**L**	**TRW**	**TAW**	**L**	**W**
N	6	6	5	2	3	1	1	9	5	5	5	5	6	4	4
Min	1.00	1.35	6.06	0.66	0.79			2.43	1.41	1.51	2.11	1.41	1.37	1.66	1.07
Max	1.10	1.55	6.47	0.68	0.83			2.69	1.57	1.67	2.25	1.53	1.52	1.73	1.10
Mean	1.05	1.46	6.25	0.67	0.80	0.89	0.95	2.57	1.47	1.55	2.18	1.46	1.44	1.68	1.08

Dinosorex engesseri, **Studienka A**

	A1	**P4**		**M1**				**M2**				**M3**		**i1**	**a1**	
	L	**BL**	**W**	**BL**	**LL**	**AW**	**PW**	**BL**	**LL**	**AW**	**PW**	**L**	**W**	**L**	**L**	**W**
N	1	2	2	2	3	2	2	2	3	2	2	5	3	1	2	2
Min		2.15	2.10	2.10	2.13	2.49	2.37	1.77	1.89	2.21	1.63	1.11	1.49		1.42	1.00
Max		2.32	2.10	2.14	2.18	2.51	2.47	1.79	2.00	2.29	1.64	1.15	1.60		1.42	1.01
Mean	2.34	2.24	2.10	2.12	2.16	2.50	2.42	1.78	1.95	2.25	1.63	1.13	1.54	6.65	1.42	1.00

	m1			**m2**			**m3**	
	L	**TRW**	**TAW**	**L**	**TRW**	**TAW**	**L**	**W**
N	3	3	2	7	3	6	5	4
Min	2.47	1.44	1.54	1.94	1.35	1.35	1.54	1.01
Max	2.60	1.47	1.56	2.19	1.47	1.50	1.64	1.19
Mean	2.54	1.46	1.55	2.08	1.43	1.42	1.61	1.08

The large i1 is acuspulate and has an upwards curved tip. In a way similar to the I1, the labial side is extended posteriorly whereas the medial side is interrupted by the incisor canal. The posterolabial area is creased and delimited by a distinct cingulum. The a1 is a flat element with a heart-shaped outline. The only cuspid is found anteriorly. A thin crest connects this cuspid to the pointy anterior margin. A second, less distinguishable crest is present and has a slight posterolabial orientation. Two elongated lobes are present posteriorly. The a3 is a very small element with a pointy anterior margin and two posterior lobes (Figure 5(M)). A pointy cuspid is present in anterobuccal position. There is a short and thin anterior crest and a thicker posterobuccal crest ending before the cingulid of the short buccal lobe. The short lingual lobe also bears a thin cingulid. The p4 is a larger and bulkier version of the a3. The cuspid is in a central position. There is no clear anterior crest, but a thin anterolingual crest that reaches the margin of the tooth. The cuspid also has a short posterobuccal crest attached to it. The two posterior lobes are poorly extended. Only the lingual lobe has a thin cingulid. The area between this cingulid and the cuspid forms a shallow basin (Figure 5(N)).

On m1, the trigonid is slightly longer than the talonid but narrower. The three trigonid cuspids are strong and form an almost equilateral triangular area. The paralophid is slightly curved. The trigonid basin is open, although there is a small anterolingual cingulum. The entoconid is high and the entocristid is moderately high. The postcristid starts from the tip of the hypoconid and is usually attached to the posterolabial flank of the entoconid (modus A). This is the case in 8/11 m1 from Borský Svätý Jur (e.g. Figure 5 (P)) and 4/4 m1 from Studienka A. The labial and posterior cingulid are broad, especially below the hypoconid. The m2 differs from the m1 by the shorter and broader trigonid, resulting in a quadrangular molar. The modus A is found in 6/7 m2 from Borský Svätý Jur (Figure 5(R)) and 6/7 m2 from Studienka A. The small m3 has a narrow talonid. The trigonid cuspids form an equilateral triangular area. The paraconid joins an incipient anterolingual cingulum, partially closing the trigonid basin. Both entoconid and hypoconid are distinguishable on the talonid. The oblique cristid is parallel to the labiolingual compression of the entoconid. A short lingual notch opens the talonid basin. There is no postcingulid but a large and rounded labial cingulid.

Remarks

The Late Miocene Slovak materials display all the morphological peculiarities of *Dinosorex engesseri*. Namely, the heavy A1, the presence of a low hypocone on P4, the high frequency of prehypocrista on M1 and M2 and the high frequency of m1 and m2 displaying the modus A. The omnipresence of prehypocrista on the M1-M2 is the sole morphological character of the diagnosis of Rabeder (1998). As discussed below, this omnipresence is found only in the type locality of Götzendorf. In the case of the material from Pezinok, despite the absence of prehypocrista on the only M1, the development of a hypocone on P4 supports an attribution to *Dinosorex* cf. *engesseri*.

Comparisons

In addition to the above description of the Slovak *Dinosorex*, a large number of assemblages have been re-examined. Table 2 summarises the main morphological and metric characteristics of 42 *Dinosorex* assemblages, 25 of which were directly compared. Notable is the unexpected number of variable and convergent features. *Dinosorex* species can only be distinguished from each other on the basis of a combination of several variable characteristics, making some diagnosis inadequate and requiring a certain amount of material before a clear taxonomic verdict can be made. Additionally, some of the data presented here are in contradiction

Table 2. Comparison of the dento-gnathic features of *Dinosorex* species. Modified after Engesser (1972, 1975, 1980, 2009), Storch (1978), Rzebik-Kowalska (1994), Van den Hoek Ostende (1995), Rzebik-Kowalska and Topachevsky (1997), Rabeder (1998), Ziegler (2000), 2003, Ziegler, 2005, Ziegler, 2006), Sabol (2005), Prieto (2007), Seehuber (2008), Prieto et al. (2010), Rzebik-Kowalska and Lungu (2009), Hugueney et al. (2012), Furió et al. (2015). Asterisk indicates type localities.

Locality	Country	Repositeries	Units	Attribution	Morphotype of A1	P4 shape	Hypocone on P4	Prehypocrista M1	Prehypocrista M2	Modus A on m1	Modus A on m2	mean i1 lenght
Keseköy	Turkey	NMB	MN3	D. anatolicus*	I	triangular	absent	negligible	negligible	variable	variable	6.84
Obergänserndorf 2	Austria	NHMV	MN4/5	D. cf. zapfei	II	trapezoid	absent	0/7	0/8	2/5	3/5	7.09
Teiritzberg (1, 2)	Austria	NHMV	MN4/5	D. cf. zapfei				1/2	0/3	4/5	2/4	6.20
Vermes (1, 2, 5)	Switzerland	NMB	MN5	D. zapfei	II	trapezoid		0/1	0/2	4/4	1/1	
Sandelzhausen	Germany	BSPG	MN5	D. cf. zapfei	II	trapezoid	low	negligible	negligible	predominant	predominant	6.50
Bełchatów B	Poland	ISEZ PAN	MN6	D. cf. zapfei			low			predominant	predominant	
DNV – Štokeravská vápenka	Slovakia	NHMV	MN6	D. zapfei*	II		absent	0/1		2/2	2/2	
DNV – Bonanza	Slovakia	SNM-NHM	MN6	D. zapfei		trapezoid	absent	0/2	0/2	1/1	1/1	6.82
Vieux-Collonges	France	UCBL	MN5	D. sansaniensis								
Sansan	France	NMB	MN6	D. sansaniensis*	II	trapezoid	low	1/2	0/2	4/7	4/7	7.02
Saricay	Turkey	NMB	MN7/8	Dinosorex sp.				0/1	0/1	1/1	2/2	
Petersbuch 6	Germany	NMA	MN7/8	D. aff. pachygnathus						predominant	predominant	8.33
Petersbuch 10	Germany	NMA	MN7/8	D. aff. pachygnathus	III	trapezoid				predominant	predominant	
Petersbuch 31	Germany	NMA	MN7/8	D. aff. pachygnathus						predominant	predominant	8.37
Petersbuch 35	Germany	NMA	MN7/8	D. aff. pachygnathus						predominant	predominant	7.80
Petersbuch 48	Germany	NMA	MN7/8	D. aff. pachygnathus						predominant	predominant	7.41
Anwil	Switzerland	NMB	MN7/8	D. pachygnathus*	III	trapezoid	rare	2/11	1/20	15/25	14/33	7.45
La Grive Saint-Alban L7	France	NMB	MN7/8	D. pachygnathus	III					variable	variable	
Kleineisenbach	Germany	BSPG	MN7/8	D. pachygnathus								7.2
Gratkorn	Austria	LMJG	MN7/8	D. cf. kaelini		trapezoid	absent?			1/1	1/1	8.00
Nebelbergweg	Swiss	NMB	MN9	D. kaelini*	III	trapezoid	low	3/4	3/4	2/6	1/3	8.07
Bełchatów A	Poland	ISEZ PAN	MN9	D. cf. kaelini	?	trapezoid	low	predominant	predominant	variable	variable	8.16
Mörgen	Germany	NMA	MN7/8	D. cf. grycivensis	III	trapezoid	absent	negligible	variable	1/2		7.70
Barranc de Can Vila 1	Spain	ICP	MN7/8	D. grycivensis	II-III	trapezoid		3/6	1/3	2/2	4/5	6.46
Can Mata (C4-A1)	Spain	ICP	MN7/8	D. grycivensis	II	trapezoid		3/6	4/10	14/18	14/18	6.63
Can Mata (C5-D1)	Spain	ICP	MN7/8	D. grycivensis		trapezoid		4/11	1/6	8/9	6/6	6.67
Can Llobateres (C19-21, D21, D32-33, D60)	Spain	ICP	MN9	D. grycivensis	II	trapezoid	rare	3/9	0/2	11/11	8/8	6.65
Castell de Barbera (D51, C42-45)	Spain	ICP	MN9	D. grycivensis		trapezoid	rare	0/3	3/8	9/11	7/11	6.85
Buzor 1	Moldova	TSU	MN9	D. grycivensis						predominant	predominant	7.20
Grytsiv	Ukraine	NMNHU-P	MN9	D. grycivensis*	II-III	trapezoid	rare	negligible	negligible	predominant	predominant	7.77
Götzendorf	Austria	NHMV	MN9	D. engesseri*	III	trapezoid	low	10/10	4/4	3/5	3/8	6.99
Borský Svätý Jur	Slovakia	CU	MN9	D. engesseri	III	trapezoid	low	2/2	4/7	8/11	6/7	6.25
Richardhof-Golfplatz (RH-A/2)	Austria	NHMV	MN9	D. engesseri	III			2/2	2/3	2/4	0/2	
Richardhof-Golfplatz (RH-A/7)	Austria	NHMV	MN9	D. cf. engesseri	III					0/1		
Rudabánya	Hungary	HGI	MN9	D. engesseri				predominant	predominant	predominant	predominant	7.84
Studienka A	Slovakia	CU	MN9	D. engesseri	III	trapezoid	low	4/6	1/4	4/4	6/7	6.65
Neusiedl am See	Austria	NHMV	MN10	D. cf. engesseri				0/1				
Pezinok	Slovakia	CU	MN10	D. cf. engesseri		trapezoid	low	0/1				
Richardhof-Wald (RH-94/1)	Austria	NHMV	MN10	D. engesseri	III			1/1	1/1	1/1	1/1	7.48
Richardhof-Wald (RH-94/5A)	Austria	NHMV	MN10	D. cf. engesseri	III					1/1	1/1	
Schernham	Austria	NHMV	MN10	D. engesseri	III	trapezoid		2/3	3/3	1/2	7/9	
Dorn-Dürkheim	Germany	SMF	MN11	Dinosorex sp.	III					1/1		

(Continued)

(Continued)

m1 mean lenght	m2 mean lenght	m3 mean lenght	m1/m2 lenght ratio	m1/m3 lenght ratio	i1/m1 lenght ratio	Nb of lower antemolars	Nb of upper antemolars	Height of entocristids on m1-m2	Dental pigmentation	Foramen below:	Condylar facets
2.49	2.13	1.59	1.17	1.57	2.75	4?		moderate		m1, posterior	
2.62	2.15	1.61	1.22	1.63	2.71		4	low		m2, anterior	
2.61	2.21	1.67	1.18	1.56	2.38						
2.72	2.48	1.60	1.10	1.70		4		low			
2.74	2.22	1.60	1.23	1.71	2.37	3	4	low/absent		between m1 and m2	
2.57	2.08	1.51	1.24	1.70							
2.80	2.14	1.52	1.31	1.84		3		low			separated or vestigial connection
2.46	2.05	1.51	1.20	1.63	2.77	3?	5	low		m2, anterior	separated
2.75	2.40	1.7	1.15	1.62					Yes		
3.01	2.53	1.72	1.19	1.75	2.33	4	5	absent	Yes	between m1 and m2	separated
2.68	1.98		1.35					moderate			
2.45	2.22	1.86	1.10	1.32	3.40				Yes		
2.72								moderate?	Yes	m2, anterior	
	2.24	1.84							Yes		
2.68	2.30	1.84	1.17	1.46	2.91				Yes		
2.66	2.34	1.84	1.14	1.45	2.79				Yes		
2.72	2.18	?	1.25		2.74	2		moderate	Yes	m2, anterior	separated; heavy lower facet
2.59	2.35	1.7	1.10	1.52				moderate	Yes		separated; heavy lower facet
2.73	2.25	1.73	1.21	1.58	2.64					m2, anterior	
2.5	2.07	1.68	1.21	1.49	3.20	3?		moderate	Yes	m2, anterior	separated
2.66	2.21	1.71	1.20	1.56	3.03	4		moderate	Yes		
2.64	2.25	1.7	1.17	1.55	3.09			low?			
2.58	2.37	1.69	1.09	1.53	2.98		4 ?	low			
2.53	2.09	1.6	1.21	1.58	2.55				Yes		
2.54	2.16	1.68	1.18	1.51	2.61	3			Yes		
2.53	2.18	1.59	1.16	1.59	2.64				Yes		
2.63	2.17	1.66	1.21	1.58	2.53			low	Yes		
2.62	2.25	1.63	1.16	1.61	2.61	3					
2.75	2.36	1.70	1.17	1.62	2.62						
2.63	2.30	1.74	1.14	1.51	2.95	4		low		m1, posterior to m2, anterior	separated
2.74	2.41	1.76	1.14	1.56	2.55	3		moderate	Yes	m2, anterior	vestigial connection
2.57	2.18	1.68	1.18	1.53	2.43	3		moderate	Yes	m2, anterior	
2.73	2.51	1.77	1.09	1.54				moderate	Yes		
2.73								moderate	Yes		
2.70	2.19	1.83	1.23	1.48	2.90	2?		moderate	Yes	m2, anterior	
2.54	2.07	1.61	1.23	1.58	2.62			moderate	Yes		
									Yes		
									Yes		
2.84	2.28	1.76	1.25	1.61	2.63			moderate	Yes		
2.82	2.21	1.74	1.28	1.62				moderate	Yes		
2.67	2.26	1.78	1.18	1.50				moderate	Yes	m2, anterior	
2.48	2.08	1.56	1.19	1.59				low/moderate			

with previous statements and comparisons, mainly because of observational and methodological biases.

Number of upper antemolars

The number of upper antemolars in *Dinosorex* species is barely known. Apart from the skull from DNV – Bonanza, displaying five antemolars (Figure 4), only Mörgen (Seehuber, 2008), Obergänserndorf 2 (Rabeder, 1998) and Sansan (Engesser, 2009) have delivered preserved maxillaries, with four, four, and five antemolars, respectively. It is worth noting that, whereas the specimens from DNV – Bonanza can be attributed without reservation to *D. zapfei*, this is not the case for the material from Obergänserndorf 2, which has been attributed to *D.* cf. *zapfei*. Additionally, the specimens from Mörgen are not consistent with *D. zapfei* (see below). Therefore, the number of upper antemolars seems to be subject to intraspecific variation but this cannot be firmly established.

Development of A1

The A1 displays three different grades. The most ancestral morphology, type I, includes a short anterior crest, an elongated posterior crest, two low minute cusps on the posterior and lingual sides and a smooth surface (Figure 3(A)). This type is found in *Dinosorex anatolicus* and in older heterosoricid species. In type II, the A1 is slightly more angular, with a stronger anterior crest and a slightly shorter posterior crest. Additionally, the posterolingual basin is clearly visible. This grade is found in *D. zapfei* and *D. sansaniensis*. The type III shows a more massive A1, with thicker minute cusps and crests. The surface is also rougher, i.e. the antemolar is covered by low, crest-like protuberances. This is attested in *D. pachygnathus*, *D. kaelini* sp. nov., *D. engesseri*, *D.* aff. *pachygnathus* from at least Petersbuch 10 (Ziegler, 2003: fig. 1.4), and the assemblage from Mörgen (Seehuber, 2008). Some of the specimens attributed to the *D. grycivensis* have an intermediate grade, with a slightly wrinkled surface (Rzebik-Kowalska and Topachevsky (1997): fig. 2.B.; Furió et al. (2015): fig. 2.14.). The massive A1 of *Dinosorex* sp. from Dorn-Dürkheim (Storch, 1978) corresponds to type III, but the minute cusps are particularly low.

Development of P4

The P4 became more molarized during the evolution of *Dinosorex*. *Dinosorex anatolicus* has a subtriangular P4 with only three cuspids, which defines the type I (Figure 3(B)). All other members acquired trapezoidal P4 (types II and III). In addition, the P4 became more complex with the appearance of a low hypocone (type III), strengthening the short anterolingual cingulid of the m1. The hypocone is absent in *D. anatolicus* and *D. zapfei*, is rarely present in *D. pachygnathus* and *D. grycivensis* and is frequently present in *D. sansaniensis*, *D. kaelini* sp. nov. and *D. engesseri*. In the latter species, the hypocone is always present in unworn specimens.

Prehypocrista on M1-M2

The taxonomic understanding of the Late Miocene species *D. engesseri* and *D. grycivensis* have suffered greatly from a lack of comparisons (see Furió et al., 2015). The main difference between these two species was apparently the presence/absence of prehypocrista on M1–2. As shown in Table 2, only the type material of *D. engesseri* always displays strong prehypocrista on M1 and M2, and only the type material of *D. grycivensis* apparently display a complete lack of prehypocrista. Moderately developed prehypocrista on M1-M2 are often present in *D. kaelini* sp. nov. and are also recorded, although rarely, in *D. sansaniensis*, *D. pachygnathus* and even in *Dinosorex* cf. *zapfei* from Teiritzberg (Table 2).

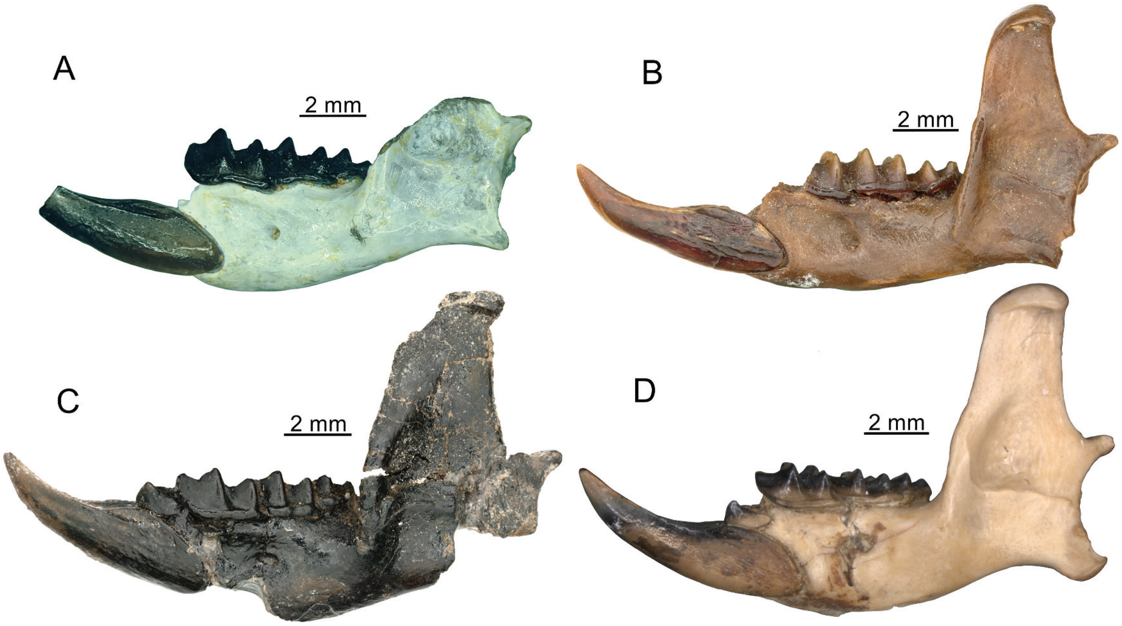

Figure 6. Mandibles of *Dinosorex* species, in labial view. (A) *D. zapfei*, DNV - štokeravská vápenka (MN6), 1975/1712/1 (holotype); (B) *D. sansaniensis*, Sansan (MN6), Ss. 603; (C) *D. pachygnathus*, Anwil (MN7/8), Al. 104; (D) *D.* cf. *kaelini* sp. nov., Gratkorn (MN7/8), LMJG 204.004.

Number of lower antemolars

The evolution of *Dinosorex* is characterised by a progressive shortening of the mandible and, consequently, a very slow reduction in the number of lower antemolars. The basal character in *Dinosorex* consists of four antemolars, the a1 being the largest and the p4 being rather bulky. *Dinosorex anatolicus* and *D. sansaniensis* have four antemolars; *Dinosorex* (cf.) *zapfei*, *D. kaelini* sp. nov. and *D. grycivensis* have three or four antemolars; *Dinosorex engesseri* has a relatively strong anteroposterior compression of the antemolars and seems to have three antemolars. As an exception, Ziegler (2006) identified only two alveoli in the material from Rudabánya. In all the previous examples, the reduction of the number of antemolar is related to the loss of the a3. Finally, *D. pachygnathus* displays the most derived state and has only two lower antemolars (a1 and p4).

Entocristid of m1-m2

The degree of development of the entocristid on the m1-m2 is highly dependent on the observer and the degree of wear. This led Rzebik-Kowalska and Topachevsky (1997) to correct the observation that the *Dinosorex* species from Bełchatów A had entocristids, as had been previously stated by Rzebik-Kowalska (1994). A similar case occurred with the development of entocristid in *D. grycivensis* from Grytsiv, which was considered as absent by Rzebik-Kowalska and Topachevsky (1997), but weak by Furió et al. (2015). The figured material from Grytsiv shows a structure that is considered here to be a low entocristid (Figure 3(C)). This structure is not comparable to *D. engesseri*, despite Ziegler (2006) mentions that the Austrian samples do not have distinct entocristid. New observation of this material reveals the presence of a moderately high entocristid, as in the Late Miocene Slovak material, and indeed in most *Dinosorex* species. Similarly, Storch (1978) mentioned a lack of entocristid in *Dinosorex* sp. from Dorn-Dürkheim, but the figured m1 (Storch (1978): fig. 20) shows at least a low entocristid. The only species displaying a clear lingual opening of the talonid basin without entocristid is *D. sansaniensis* (Figure 3(C)).

Postcristid of m1–2

Two morphotypes of the postcristid on m1–2 were identified by Engesser (1975), which has been widely used in the literature and is considered as a strong diagnostic element. The modus A (postcristid-entoconid connection) and B (postentoconid valley) are greatly dependent on the degree of wear and on the development of the accessory cusplet (Figure 3(D)). Moreover, as Engesser (1975) did not provide figures representing these two modes, the evaluation of this character varies according to the observer. For instance, Rabeder (1998) stated that the m1-m2 of *D. engesseri* from Götzendorf mostly display the modus B, whereas Ziegler (2006) included them in the modus A, arguing for artefacts of representation. We agree with Ziegler (2006) that the figures of Rabeder (1998) are imprecise, but his work accurately describes the very intermediate development state of the postcristid, even based on our own terminology (Figure 3(D)). In a similar way, Engesser (1975) considered the lower molars of the *Dinosorex* from Can Llobateres to display the modus B, whereas both the study of Furió et al. (2015) and our direct observation did not reveal any specimen displaying the modus B in the bulk sample housed at the ICP. Overall, this mode is especially present in *D. pachygnathus* and *D. kaelini* sp. nov.

Dental ratio

Apart from the slightly larger *D. sansaniensis*, all *Dinosorex* species have molars with greatly overlapping measurements (Table 2). This includes the m1/m2 and the m1/m3 length ratios. *Dinosorex zapfei* was originally described as having a stronger reduction of the m2 and the m3 (Engesser, 1975) but, as shown in Table 2, only the type material displays such peculiarity, which is solely caused by the relatively large dimensions of a single m1. The m1 from DNV – Štokeravská vápenka is actually found within the variability of the assemblages from Sandelzhausen and Vermes 1 (Ziegler (2000): fig. 3). The length of the incisor and the i1/m1 ratio is relatively similar in all *Dinosorex* material, apart from the material from Bełchatów A, Gratkorn and Nebelbergweg, identified here as *D.* (cf.) *kaelini* sp. nov.; and the ambiguous *D.* aff. *pachygnathus* from Peterbuch 6 and 31.

Tooth pigmentation

Most *Dinosorex* species are known to possess tooth pigmentation (colouring of the dental tips), which has been used as a diagnostic character for the genus (Engesser, 1972). However, this character can hardly be used because its preservation in fossils is not systematic. At least, dental pigmentation has been attested in *D. sansaniensis* (based on the material from Vieux-Collonges and Sansan; Engesser (2009); Hugueney et al. (2012)), *D. grycivensis* (based on the material from the Vallès-Penedès Basin; Furió et al. (2015)), *D. pachygnathus* (based on the material from Anwil and La Grive Saint-Alban; Engesser (1972); Hugueney et al. (2012)), *D.* aff. *pachygnathus* from the fissures of Petersbuch (Ziegler, 2003), *D. engesseri* (based on Austrian and Slovak finds; Ziegler, 2006; this work) and *D. kaelini* nov. sp. (based on the material from Nebelbergweg and Gratkorn; Kälin and Engesser (2001); Prieto et al. (2010); this work). To date, dental pigmentation has not been reported in *Dinosorex anatolicus* and *Dinosorex zapfei*.

Position of the mandibular foramen

The position of the foramen mandibulae may have been an indicator of the progressive shortening of the face. Table 2 shows that all species actually have a foramen mandibulae between the posterior root of m1 and the anterior root of m2. Whereas the position of the foramen mandibulae in *D. engesseri* seems to be consistent, its position in the type material of *D. grycivensis* is extremely variable (see Rzebik-Kowalska & Topachevsky, 1997). As Grytsiv is one of the rare localities having delivered several mandibles, the position of the foramen mandibulae is not considered a good intrageneric character.

Condylar facets

The separation of the condylar facets is subject to intraspecific variation within *Dinosorex*. Several mandibles with preserved condyles are known, but only *Dinosorex zapfei* is known from several specimens, including two from the type locality of DNV - Štokeravská vápenka. Only the condyles of the mandible 1975/1972/2 were figured by Engesser (1975), fig. 3B). This specimen

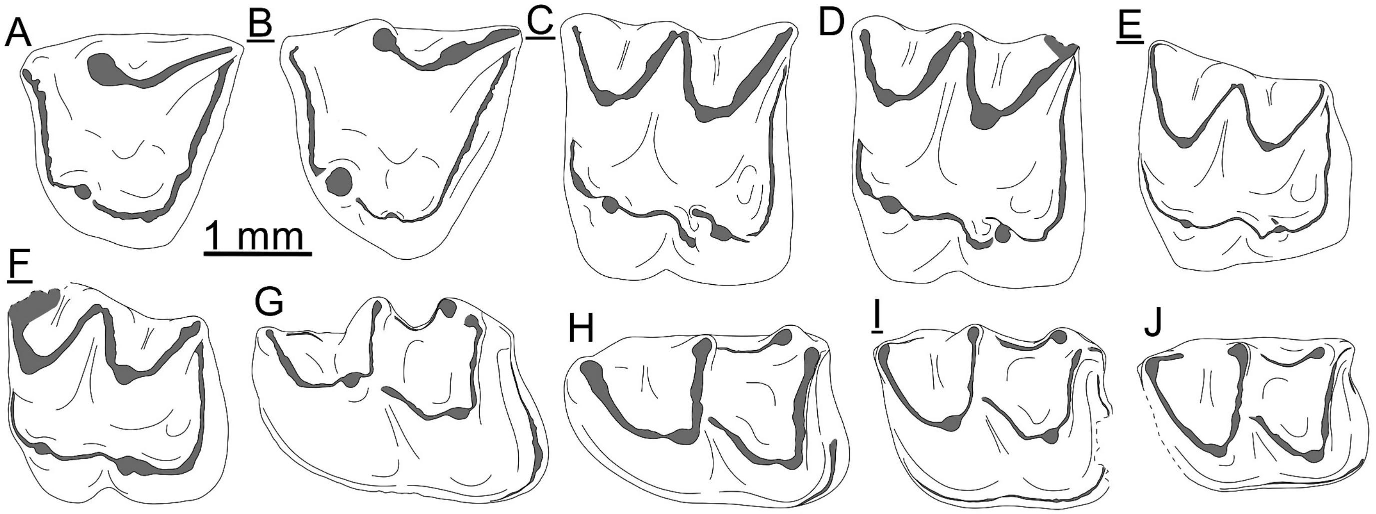

Figure 7. Line drawings of *Dinosorex kaelini* sp. nov. From Nebelbergweg. (A) P4, NMB Nbw. 150; (B) P4, NMB Nbw. 151; (C) M1, NMB Nbw. 9 (holotype); (D) M1, NMB Nbw. 153; (E) M2, NMB Nbw. 10; (F) M2, NMB Nbw. 156; (G) m1, NMB Nbw. 168; (H) m1, NMB Nbw. 14; (I) m2, NMB Nbw. 177; (J) m2, NMB Nbw. 12. Images with underlined numbers (C, I) are reversed.

shows a short medial connection between the two facets, motivating Furió et al. (2015) to consider here a strong distinction with the Spanish *D. grycivensis*. The second mandible and holotype of *D. zapfei* (1975/1712/1) does not display such a strong connection. Although there is a ridge connecting the two facets, this ridge is not part of the articulation: it is slightly lower than the facets and does not show the roundish aspect of condyles, as in the mandible from DNV – Bonanza (Figure 4). As in all *Dinosorex* species, the connection between facets is non-functional. Based on the literature, only *D. engesseri* might appear as an exception (Rabeder, 1998), but the articular condyle preserved in the type material from Götzendorf (NHMW1998z0046/001/53) is actually worn, possibly because of digestive acids or post-fieldwork treatment. Although Rabeder (1998), fig. 5) illustrated a moderate connection between the two facets, this connection was weaker and rather similar to the configuration found in *Dinosorex zapfei*. The two facets are also more elongated than in the representation of Rabeder (1998). Finally, it is worth noting that the two facets are particularly robust in *D. pachygnathus*.

Overall development of the mandible

The strengthening of the mandibular body is partly related to the strengthening of the lower incisor root. *Dinosorex anatolicus* has a relatively slender body and a narrow ascending ramus in labial view. *Dinosorex zapfei* also has a narrow ascending ramus, but the mandible is inflated below the m1 (Figures 4(H) and 6(A)). Figure 6 (B) shows that such inflation is not present in *Dinosorex sansaniensis*, which has a poorly curved mandible in the labial view. In *D. engesseri*, the mandibular body is slightly stronger than in *D. zapfei*. The ascending ramus is overall narrow, except for the most apical part that is wider. *Dinosorex* cf. *kaelini* sp. nov. from Gratkorn is similar to *D. engesseri*, but the part of the ramus anterior to the masseteric fossa is thicker, resulting in a swelling visible in labial view. The body is also more curved. The ascending ramus is overall high and straight, which is a feature also mentioned in *D.* aff. *pachygnathus* from the fissures of Petersbuch (Ziegler, 2003). *Dinosorex pachygnathus* has the most massive mandible and displays a marked enlargement of the masseteric region. In the labial view, the anterior ridge of the ascending ramus is strongly

Table 3. Measurements (in mm) of *Dinosorex kaelini* sp. nov. From Nebelbergweg (MN9), Switzerland.

	I1			A1		A2/3		A4		P4		M1			
	L	LT	H	L	W	L	W	L	W	BL	W	BL	LL	AW	PW
N	3	2	4	1	1	3	3	1	1	4	4	3	4	4	4
Min	4.12	2.36	2.11			0.77	0.97			2.11	1.81	2.09	2.16	2.46	2.17
Max	5.09	2.73	2.56			0.84	1.16			2.25	2.18	2.20	2.23	2.59	2.43
Mean	4.61	2.54	2.33	2.39	1.68	0.82	1.08	0.6	0.98	2.19	2.01	2.14	2.20	2.51	2.31
	M2				i1	a1		a2		a3	p4		m1		
	BL	LL	AW	PW	L	L	W	L	W	W	L	W	L	TRW	TAW
N	5	6	2	5	2	2	2	1	1	1	2	2	5	5	5
Min	1.80	1.88	2.25	1.65	7.93	1.56	1.20				1.02	0.83	2.55	1.48	1.62
Max	1.99	2.15	2.28	2.09	8.22	1.59	1.24				1.10	0.95	2.83	1.66	1.76
Mean	1.89	2.05	2.27	1.81	8.09	1.57	1.22	0.68	0.76	0.95	1.06	0.89	2.66	1.58	1.70
	m2			m3											
	L	TRW	TAW	L	W										
N	3	3	3	6	7										
Min	2.14	1.50	1.48	1.60	1.06										
Max	2.35	1.55	1.51	1.84	1.29										
Mean	2.21	1.53	1.50	1.71	1.18										

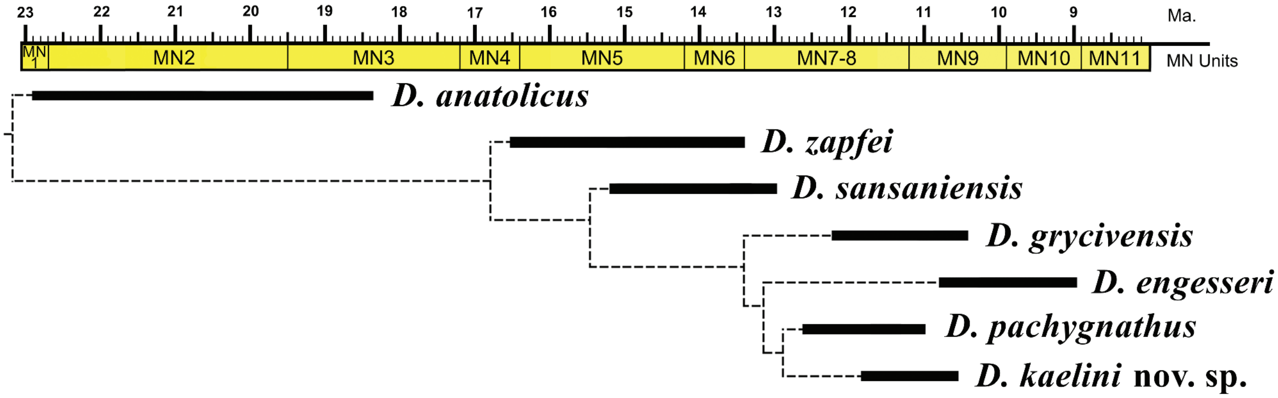

Figure 8. Reconstruction of *Dinosorex* hypothetical phylogeny, based on Table 2. Biostratigraphic chart created with the software TimeScale Creator (MN units modified after Van Dam et al., 2023).

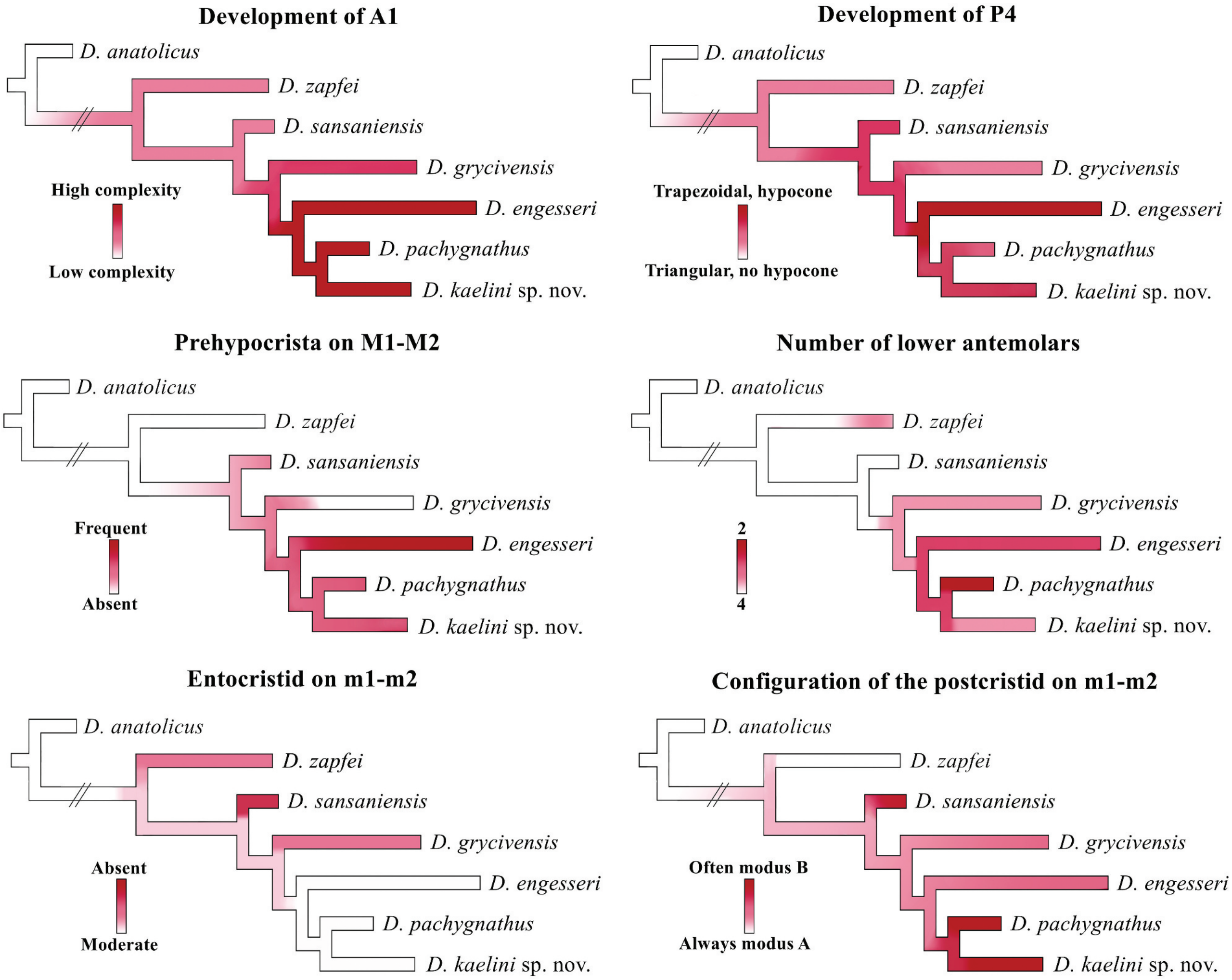

Figure 9. Interpretation of the evolution of the diagnostic features of *Dinosorex* species, reconstructed from Table 2 and Figure 8. Coloured areas represent the progressive acquisition of a derived morphological state.

curved (Figure 6(C)). The body is comparable to *D. kaelini* sp. nov., but it has a narrower mandibular bone between the i1 and the m1 (Figure 6(D)).

Discussion

Taxonomic implications

Despite being always close to the basal tribosphenic pattern, the dental configuration of eulipotyphlan species is highly adaptable. Species are characterised by a combination of variable features and each of them can appear or reappear in completely different lineages or assemblages, often leading to confusion about the taxonomic status of species known from limited sample sizes. In addition, morphological variability is still rarely described with *Dinosorex* being a typical case. Due to the high frequency of possible permutations, any tentative species-level phylogeny based solely on species diagnosis and type material should be avoided. Based on the morphological comparisons above, between five and seven characters are relevant to the study of *Dinosorex* phylogeny, all of them indicating a mosaic evolution. Consequently, phylogenetic reconstructions are tentative as they can drastically change depending on which character is considered as more reliable, particularly when the biogeographic parsimony is not taken into consideration. This said, a few conclusions can still be drawn.

There is a significant gap between *Quercysorex pusillus*, *Quercysorex huerzeleri*, and the Miocene *Dinosorex*. The Oligocene forms have a significantly smaller size, poorly reduced m2 and m3, a mandibular foramen in a relatively anterior position and five lower antemolars. *Dinosorex anatolicus* already has the size and the mandibular configuration of *Dinosorex*, although the A1 and P4 are still ancestral in shape (Van den Hoek Ostende, 1995). We thus follow the generic classification of Ziegler (1998) and additionally consider *Quercysorex pusillus* as a member of *Quercysorex*. Moreover, we follow the view of Smith and Van den Hoek Ostende (2006) in considering the taxon from the Late Oligocene of Cournon – Les Souméroux and Boudry – Trois – Rods as not belonging to *Dinosorex*. In adition, the structural differences found between *Dinosorex* and Miocene European *Heterosorex* (e.g. cuspulate i1, division of the masseteric fossa) preclude a European origin for *Dinosorex* (Klietmann, 2013; Van den Hoek Ostende, 1995). The first firm occurrence of *Dinosorex* is in MN1 of Anatolia (Van den Hoek Ostende, 1995) and its first firm European occurrence is in MN4 of Germany (Ziegler, 1998; Ziegler & Fahlbusch, 1986; Ziegler et al., 2005). This echoes with the biogeographic history of several other small mammal lineages (see Van den Hoek Ostende et al., 2015), making *Dinosorex* a likely member of the Asia-Europe small mammal migration events that occurred at the end of the Early Miocene.

On the basis of *Quercysorex pusillus*, *Q. huerzeleri*, and *Dinosorex anatolicus*, several morphological features can be clearly identified as derived in *Dinosorex* species: the rougher surface on A1, the trapezoidal outline of P4, the hypocone on P4, the prehypocrista on M1-M2, the smaller number of antemolar, the loss of the entocristid and the high frequency of modus B postcristid on m1-m2. *Dinosorex zapfei* stand as the most basal European species. A high number of these derived features are found in *D. engesseri*, *D. pachygnathus*, and *D. kaelini* sp. nov. These species represent the most advanced group of *Dinosorex*.

Attribution of material to *Dinosorex zapfei* without reservation are excessively rare in the literature. This is a consequence of the limited-type material and the unusual measurements of the holotype (Table 2). The studied assemblages attributed to *Dinosorex* cf. *zapfei* (Obergänserndorf, Teiritzberg, Bełchatów B) are consistent with a single species having a relatively high morphological variability, which is common in *Dinosorex* species. *Dinosorex* aff. *zapfei* from Sandelzhausen (Ziegler, 2000) is here reattributed to *Dinosorex* cf. *zapfei*, as the peculiarities of this material (lower Lm1/Lm2 ratio, mesostyle structure, modus A sensu lato) are minor differences related to morphological or morphometric variability. The lack of direct comparisons hampers a firm attribution. Studying the variability of the assemblages from Sandelzhausen or other rich assemblages are expected to resolve most taxonomic verdicts. Finally, the well-preserved material from Mörgen has been originally attributed to *Dinosorex* aff. *zapfei* by Seehuber (2008). The overall morphology of the material is rather basal but the more compressed M1 and the slightly wrinkled A1 completely exclude *D. zapfei*. Based on Table 2, the material from Mörgen better fit *D. grycivensis*, but Seehuber (2008) was likely not aware of the existence of this species. It is worth mentioning that few of the measured lower incisors are particularly long, which is unusual. Consequently, this assemblage is reclassified as *Dinosorex* cf. *grycivensis*.

Dinosorex sansaniensis has been used as a 'wastebasket' taxon of the genus, explaining its broad temporal distribution. This has been well documented by Furió et al. (2015) in the case of the Late Miocene material from Spain. There is no evidence for the presence of *D. sansaniensis* in the Late Miocene. The material from Vösendorf (Austria, MN9), only mentioned in a faunal list by Bachmayer and Wilson (1985), is reattributed to *Dinosorex* sp. Similarly, *Dinosorex* cf. *pachygnathus* has been identified at Douvre and Soblay (France, MN10; Mein 1999), but the material from the former locality has never been described and the identification of the species from Soblay by Ménouret and Mein (2008) is based on six undescribed and unmeasured specimens. There is little doubt that this attribution is risky, and the two materials are better reclassified as *Dinosorex* sp. pending on a published taxonomic description.

Despite the higher entocristid, the few specimens of *Dinosorex* sp. from Sariçay (MN7/8, Turkey) are similar to *Dinosorex zapfei*. This form displays basal features despite the relatively young age of the locality. It is very unclear how continuous the presence of *Dinosorex* was in Anatolia. The *Dinosorex* sp. from Dorn-Dürkheim (MN11) displays a much more advanced morphology. The combination of type III A1 and modus A postcristid on m1 suggests affinities with *D. engesseri*, but since only one specimen of both elements is known, the phylogenetic position of this form cannot be evaluated. It should also be noted that the A1 from Dorn-Dürkheim is exceptionally large and the m1 is particularly short (Table 2). Therefore, it cannot be excluded that the specimens from Dorn-Dürkheim represent an unknown, extremely advanced species. It could be equivalent to '*Dinosorex* n. sp'., mentioned by Fejfar and Sabol (2005) in the faunal list of Suchomasty (Czechia, MN10).

In our analyses, three assemblages stand out by their peculiar combination of characters: 1) *Dinosorex* sp. from Gratkorn (MN7/8), described by Prieto et al. (2010), p. 2) *Dinosorex* sp. from Bełchatów A (MN9), described by Rzebik-Kowalska (1994) and reattributed to *Dinosorex grycivensis* by Rzebik-Kowalska and Lungu (2009), p. 3) *Dinosorex* aff. *pachygnathus* from Nebelbergweg (MN9), described by Kälin and Engesser (2001). The large sample from Nebelbergweg leaves no doubt that the unique morphological and size features of the assemblage justify the distinction of a separate species. Consequently, *Dinosorex* aff. *pachygnathus* is transferred into the newly described *Dinosorex kaelini* sp. nov. The specimens from Gratkorn are attributed to

Dinosorex cf. *kaelini* sp. nov. based on the small sample and the non-distinct hypocone on the single P4. The material from Bełchatów A has not been directly examined in the present study, therefore it is attributed to *Dinosorex* cf. *kaelini* sp. nov. with some reservations. The taxonomic information of *D. kaelini* sp. nov. is presented below.

Genus ***Dinosorex*** Engesser, 1972

***Dinosorex kaelini* sp. nov.** (Figure 7, Table 3)

LSID: https://zoobank.org/NomenclaturalActs/66ced819-fbc8-47c4-876d-3aacb8750f80

Holotype

Left M1 (BL = 2.20, LL = 2.16, AW = 2.54, PW = 2.43), NMB Nbw.9, Nebelbergweg, Switzerland (Figure 7(C)).

Paratypes

NMB Nbw.8–17 and NMB Nbw.145–184 (51 elements): four I1, one A1, three A2/3, one A4, four P4, three M1, six M2, three i1, two a1, one a2, two a3, two p4, five m1, three m2, seven m3. All dental measurements are provided in Table 3. Figures of the described dental elements are provided in Kälin and Engesser (2001: fig. 11) and in Figure 7.

Diagnosis

Species of *Dinosorex* characterised by the following combination of characters: rough surface on A1 (type III); trapezoidal P4 with a robust parastyle and a weak hypocone (type III); frequent presence of prehypocrista on M1-M2; strongly elongated i1 (Li1/Lm1 = 3.03–3.20 mm); 3 or 4 lower antemolars; bulky p4 with undivided postcristid; on m1-m2, moderately high entocristid and relatively high frequency of modus B postcristid.

Differential diagnosis

Differs from *Dinosorex anatolicus*, *D. zapfei*, *D. sansaniensis* and *D. grycivensis* by the always rough surface on A1; from *D. anatolicus*, *D. zapfei* and *D. grycivensis* by the common presence of hypocone on P4; from *D. anatolicus*, *D. zapfei*, *D. sansaniensis*, *D. pachygnathus* and *D. grycivensis* by the frequent prehypocrista on M1-M2; from *D. zapfei*, *D. grycivensis* and *D. engesseri* by the high frequency of modus B postcristid on m1-m2; from all *Dinosorex* by the extremely elongated i1.

Distribution

Identified in MN7/8 of Germany (Gratkorn), MN9 of Switzerland (Nebelbergweg) and MN9 of Poland (Bełchatów A).

Etymology

In honour of Dr. Daniel Kälin, who greatly contributed to the understanding of Swiss Neogene deposits and who first described the insectivore fauna from Nebelbergweg alongside Dr. Burkart Engesser.

Description

See Kälin and Engesser (2001).

Phylogenetic reconstruction

A tentative phylogenetic reconstruction is provided (Figure 8). The temporal range of the species excludes records that appear as outliers. Additionally, we provide the hypothetical evolution of several morphological characters (Figure 9) based on the aforementioned comparisons (Table 2). The development of A1 and P4 are strongly reliable and appear to be structural in our reconstruction of the phylogeny of *Dinosorex*. The frequency of the prehypocrista on M1-M2 and the modus B on m1-m2 are also quite reliable but require large samples. Engesser (1975) argued that the modus A is a derived feature within *Dinosorex*, which is in contradiction with our data. This is also contradicted by several Oligocene and Miocene heterosoricid materials displaying the modus A, such as *Quercysorex* (e.g. Klietmann et al., 2014a) and *Lusorex* (Storch & Qiu, 2004). The reduction of the number of lower antemolars is correlated with the development of A1 and P4, but its use as a marker is hampered by observational bias and also by interspecific variability related to the minor masticatory function of these elements. At least, we can confirm that the a2 disappeared first, followed by the a3.

The reduction of the entocristid appears as a weak phylogenetic signal, which is attributed to both convergent phenomenon and observational bias. If the reduction of the entocristid (low entocristid; Figure 3(C)) is truly attested in *Dinosorex zapfei* and *D. grycivensis*, this would imply three convergent phenomena. An alternative, as shown in Figure 9, is to consider a single event for the reduction of the entocristid, before *D. zapfei*, and a reverse adaptation in the *D. engesseri* + *D. pachygnathus* + *D. kaelini* group.

Dinosorex zapfei appears to be the most basal European species of *Dinosorex*, and the only species firmly identified in MN4 and in most MN5 localities. It constitutes a good structural ancestor for all younger species. However, it is unclear when the ancestor of the younger European species emerged, and the degree of paraphyly of *Dinosorex zapfei* can not be yet evaluated. It is possible that *D. sansaniensis* is an offshoot of a population of *D. zapfei*, whereas *D. grycivensis* evolved directly from *D. zapfei* as part of an anagenetic lineage. In any cases, the presence of dental pigmentation is attested in all European *Dinosorex* species except *D. zapfei*. The earliest case of dental pigmentation in the genus is recorded in *D. sansaniensis* from Vieux-Collonges (MN5; Hugueney et al., 2012).

The strongest current break in the understanding of *Dinosorex* phylogeny comes from the morphological variability of *D. grycivensis*. As already discussed (Furió et al., 2015), this species display strong similarities with *D. engesseri*, which was originally a consequence of a lack of comparisons in the works in which these species were described (Rabeder, 1998; Rzebik-Kowalska & Topachevsky, 1997; Ziegler, 2006). These similarities are even stronger than expected considering the variability of the prehypocrista in both species (Table 2). However, fundamental differences are found in the development of A1, the presence of a hypocone on P4 and the number of lower antemolars. These are structural evolutionary characteristics that make *D. grycivensis* a distinct species with less advanced features. It is worth noting that *D. grycivensis* sometimes displays intermediate grades. In Grytsiv, for instance, the A1 is partly wrinkled and the P4 sometimes possesses a hypocone (Rzebik-Kowalska & Topachevsky, 1997). The Spanish material (Furió et al., 2015) also contains M1-M2 with a weak prehypocrista. This also fit the characteristics of the assemblage from Mörgen (Seehuber, 2008).

The previous observations, the compared data (Table 2) and the phylogenetic reconstruction (Figure 8) have a major biogeographic implication: during early MN7/8, the ancestor of the *Dinosorex engesseri* + *D. pachygnathus* + *D. kaelini* group acquired a more robust dentition and emerged in central Europe, probably from the variable *D. grycivensis*, a species that was at that time present from Ukraine to Spain. This ancestor then diversified into three species occupying three regions: *D. pachygnathus* from eastern France to Germany, *D. kaelini* sp. nov. from Switzerland to Austria and Poland, and *D. engesseri* from Austria to Slovakia. This gives weight to the idea that geological basins have differently impacted the evolutionary dynamic of *Dinosorex* species, as hypothesised by Van den Hoek Ostende et al. (2016).

MN7/8 is a period of high diversity in *Dinosorex*, with the appearance of four of the seven identified species. Almost every MN7/8 assemblage has ambiguous features as Europe was the place of a largely spread species complex. Along with the Spanish material (Furió et al., 2015), this is illustrated by the material from Petersbuch 6, 10, 18, 31, 35 and 48 described by Ziegler (2003) and attributed to *D.* aff. *pachygnathus*. The material from Petersbuch 6 and 31 show morphometric similarities with *D. kaelini* sp. nov. (Table 2), but this is not the case for the material from Petersbuch 35 and 48. Likely, the description of Ziegler (2003) refers to a mixture of *Dinosorex* species and needs to be revised together with the nearby locality of Mörgen (Seehuber, 2008). This observation alone perfectly illustrates the complex study of insectivore taxa that are both conservative and highly variable.

Paleoenvironment and paleobiology

The ecological requirements of Heterosoricidae have been discussed by Klietmann et al. (2015), who concluded that *Dinosorex* preferred moderately humid environments. This preference is also supported here. While *Dinosorex* is moderately abundant in Borský Svätý Jur, it is the second most abundant eulipotyphlan species in the swamp deposits of Studienka A, surpassed only by the dimylid *Plesiodimylus chantrei*. Heterosoricidae and Dimylidae have a somewhat similar evolution in the Late Miocene of central Europe where, after a short period of abundance in MN9 localities (Cailleux et al., 2023; Ziegler, 2005, 2006), they rapidly went extinct in the earliest Turolian. There is little doubt that these two families were thriving in the same humid environments. While the Heterosoricidae extirpated from Slovakia in MN10, the last European occurrence of the family (*Dinosorex* sp.) is reported from MN11 of Dorn-Dürkheim, Germany, alongside the last Dimylidae (Storch, 1978). The reconstruction of Dorn-Dürkheim supports the presence of numerous aquatic habitats (Costeur et al., 2013; Franzen et al., 2013), which likely favoured the abundance of the invertebrates consumed by the last *Plesiodimylus* and *Dinosorex*. In the Pannonian region, the Turolian witnessed the progressive topographic reduction of humid forest environments and the overall success of the Soricidae (Cailleux et al., in press) and eurytopic taxa. This likely hastened the decline of the Heterosoricidae in Europe, whereas the final extinction of the family Heterosoricidae happened slightly later during the Turolian, as evidenced by the material from the MN12 locality of Lufeng, China, attributed to *Heterosorex wangi* (Storch & Qiu, 1991). Overall, central and eastern Asia were most likely areas of higher diversity for Neogene heterosoricids (based on Lopatin, 2004; Qiu, 1996; Storch & Qiu, 1991, 2004; Ziegler et al., 2007).

The postcranial elements of the Miocene heterosoricid *Lusorex* have been interpreted as indicating semifossoriality (Klietmann et al., 2015; Storch & Qiu, 2004). It is true that the reduced tail and overall compact body are good indicators, but the humerus seems ancestral in shape and indicates less fossorial locomotion than uropsiline talpid (Klietmann et al., 2014b) and semifossorial shrew (Woodman et al., 2019). Thus, although *Lusorex* shows adaptations to subterranean life, there is no clear evidence for burrowing ability. Therefore, pending on a detailled study of *Lusorex* postcranial elements, this taxon is interpreted as primarily terrestrial, and may have inhabited previously occupied burrows or karst habitats. In the absence of evidence to the contrary, an ancestral terrestrial locomotion is also interpreted for *Dinosorex*.

In *Dinosorex*, the presence of a hypocone on the P4 correlates with the frequency of prehypocrista on the M1-M2. These features are two answers to the same need: to increase the dental complexity and the occlusal contact with the lower dentition, i.e. the oblique cristid and trigonid posterior wall of the m1 (hypocone of the P4), m2 (prehypocrista of the M1) and m3 (prehypocrista of the M2). This results in a better delimitation of the dental basins. The acquisition of these features goes along with the more robust mandibles, including a stronger masseteric fossa (in *D. pachygnathus*) or a higher ascending ramus (in *D. engesseri* and *D. kaelini* sp. nov.). This implies a marked increase of hard object feeding. The broad and projected upper and lower incisors, together with the reduction of the number of premolars, result in a large empty volume in *Dinosorex* oral cavity, in a way even more marked than in *Beremendia fissidens* (as interpreted by Furió et al. (2010): fig. 8). With this reconstruction in mind, in which broad, shovel-like incisors are meant to immobilise preys rather than pierce through them, the role of the reinforced A1 would be to shatter shells and exoskeletons. The wrinkled surface on A1 likely had an additional biomechanical advantage, as such structures in mammals participate in reducing tensile stresses (Fiorenza et al., 2015) and thus help maintain dental structural integrity. This is very in line with the acquisition of pigmented teeth in *Dinosorex* during the Middle Miocene, Fe-rich enamel greatly increasing mechanical strength (see Dumont et al., 2014; Moya-Costa et al., 2019; Voyta et al., 2019). All things considered, there is little doubt that advanced *Dinosorex* species were extremely specialised durophagous invertivores.

Conclusion

The Heterosoricidae from the Middle and Late assemblages of Slovakia are attributed to *Dinosorex zapfei* and *Dinosorex* (cf.) *engesseri*. The described collection enabled a revision of both species, leading to an overall revision of the genus *Dinosorex*. An analysis of the dental and dentognathic elements of all *Dinosorex* species was carried out, revealing the large morphological variability of *Dinosorex* material. Our comparisons demonstrated the weak resolving power of several previously considered diagnostic features; the separation of the condylar facets and the reduction of the entocristid on the m1-m2. We provided an updated phylogeny of the genus according to the most reliable morphological characters (e.g. complexification of A1 and P4, prehypocrista on M1-M2, mode B postcristid on m1-m2). As a result, we have revealed the existence of a previously unnamed species in central Europe (Switzerland, Germany and Poland), *Dinosorex kaelini* sp. nov., described from the MN9 Swiss locality of Nebelbergweg.

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