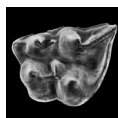# Middle Miocene *Plesiodimylus* from the Devínska Nová Ves-Fissures site (western Slovakia)

OLDŘICH FEJFAR & MARTIN SABOL

Two Middle Miocene forms of *Plesiodimylus* are described from the Devínska Nová Ves-Fissures site (the Middle Badenian, MN 6). Whereas the smaller form represents the typical individuals of *P. chantrei*, the larger one represents a different new species (*P. similis* sp. nov.) with an affinity to *P. crassidens* from the Anatolian Middle Miocene (MN 7/8). A phylogenetic relationship to *P. johanni* from the Swiss Late Miocene or to the finds of large m2s from the Polish site of Bełchatow A (*Plesiodimylus* sp., MN 9) is also not excluded. The process of parallelism, caused by both climatic and ecological factors, could play an important role too. The taphonomic origin of both found taxa of *Plesiodimylus* within the taphocoenosis of the Devínska Nová Ves-Fissures site is also considered. • Key words: *Plesiodimylus*, Middle Miocene, Badenian (MN 6), Devínska Nová Ves-Fissures, Slovakia.

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Plesiodimylus is the most widespread genus of the family Dimylidae and the one with the longest biostratigraphical range. Its fossils have been found in deposits from the Early to the Late Miocene in Europe and also in the Middle Miocene sediments of Turkey (western Asia). The genus displays the least specialized dentition within the dimylids and differs from all other species of the family in its morphology of the M1 (Ziegler 1999).

Apart from Turkish *P. crassidens*, described by Engesser (1980) from the MN 7/8 site of Sary Çay, six species of the genus have so far been distinguished in Europe. The earliest species is *P. huerzeleri* Müller, 1967, known from the Early Miocene (MN 3) sites of Germany and France. Its descendant is probably the endemic *P. helveticus* Bolliger, 1992, recorded only from the MN 4–5 sites of the Swiss Molasse. *Plesiodimylus bavaricus* Schötz, 1985, obviously also descended from the earliest species, is typical for MN 5 sites of Switzerland, Germany and Austria. However, the most common dimylid is *P. chantrei* Gaillard, 1897, ranging from MN 4 to MN 11 and recorded from Poland to Spain (Ziegler 1999). Its descendant is probably *P. johanni*, described by Kälin & Engesser (2001) from the MN 9 deposits of Nebelbergweg in Switzerland. The latest described species is *P. gaillardi* from the MN 7 deposits from the French site, La Grive-Saint-Alban, fissures L7 and M (Mein & Ginsburg 2002).

The species *P. chantrei* is also known from the territory of Slovakia, where it was recorded from the Middle Miocene sites of Devínska Kobyla Hill near Devínska Nová Ves village (Zapfe 1951, Sabol 2005). One of these sites is Devínska Nová Ves-Fissures (also known as Neudorf-Spalte, MN 6), located in the former Stockerau limestone quarry on the northern slope of Devínska Kobyla Hill (geographic co-ordinates of the site are 48° 12' N and 17° 01' E) (Fig. 1). Limestone was mined from the quarry from 1891 up to the 1970s (Bizubová & Minár 2005). During nearly a century of mining, some karst fissures were exposed, which yielded fossils of Miocene vertebrates. Most remains, including fossils of *Plesiodimylus*, have been described by Zapfe (1949, 1950a, b, 1951, 1954, 1976, 1983), Herre (1955), Wettstein-Wettersheimb (1955), and Fejfar (1974, 1990) from terrestrial deposits of the main fissure, also known as the classic fissure or as the Zapfe's fissure. The hitherto unpublished material on plesiodimylids presented here were also found in fissure deposits at this site.

Material and methods

The studied material was obtained by screen washing using 0.5 mm mesh seives during field work in the 1950s. It consists of 11 maxillary fragments with teeth, 24 toothed

hemimandibles or their fragments and 113 isolated teeth. Most of the 204 teeth are undamaged, belonging to young animals (juveniles to young adults). Only 12 teeth are worn, representing old(-er) individuals. The teeth crowns are coloured from light brown to black. Based on the number of the most represented tooth type (m2 sin.) within the studied sample, the minimum number of individuals (MNI) = 26.

The fossils were documented using a binocular magnifying microscope (Carl Zeiss, Jena) and scanned with a JEOL JSM-6380LV. They were measured according to Müller's methods (1967) using an eyepiece micrometer. All measured data are given in millimetres. For terminology of tooth crowns, Müller's (1967) paper was also followed. Since lengthratios between different elements are considered to have taxonomic value (van den Hoek Ostende 1995), the mean length P4 / mean length M1 (P4/M1 ratio) and the mean length m1 / mean length m2 (m1/m2 ratio) are also utilised in this paper.

Within the studied sample of dimylid fossils, two forms have been found – a smaller one representing the typical *Plesiodimylus chantrei*, and a somewhat larger form, closely related to the former species, but the data indicated this to be a separate species (*P. similis* sp. nov.). After finishing this research and the publication of the results, the fossil remains will be housed in the Slovak National Museum – Museum of Natural History in Bratislava.

Systematic palaeontology

Grandorder Lipotyphla Haeckel, 1866
Order Erinaceomorpha Gregory, 1910
Family Dimylidae Schlosser, 1887

Note. – Although Ziegler (1990) and van den Hoek Ostende (1995) did not state any criteria to justify a division of the Dimylidae into subfamilies, some different dental characteristics of known dimylids (see Wegner 1913, Hürzeler 1944, Müller 1967) indicate the possibility of dividing the family into minimally two subfamilies.

Genus *Plesiodimylus* Gaillard, 1897

Type species. – *P. chantrei* Gaillard, 1897.

Diagnosis. – The first lower molar (m1) is somewhat smaller or as large as m2, posteriorly as wide as its anterior part or slightly broader. The posteriorly expanded M1 has a longitudinal groove which is restricted labially (Müller 1967; translated from German).

Occurence. – Europe (MN 3–MN 11) and Turkey (MN 7/8).

Plesiodimylus chantrei Gaillard, 1897
Figures 5G, 6B

> 1851 *Mygale minuta*. – Lartet, p. 13.
> 1891 *Mygale minuta* Lartet. – Filhol, p. 26.
> 1892 *Dimylus paradoxus* Meyer. – Deperet, p. 47, taf. II, figs 10, 11.
> 1897 *Plesiodimylus chantrei* n. sp. – Gaillard, p. 1249.
> 1899 *Plesiodimylus chantrei* nov. sp. – Gaillard, p. 33, figs 21, 22.
> For a full detailed list of synonymy before 1967 see Müller (1967, p. 42); more recent data can be found in the NOW database (http://www.helsinki.fi/science/now/) or in van den Hoek Ostende et al. (2005).

Material. – 4 M1 dext. (733920, 734198, 7341104, 7341i); 3 M1 sin. (734199-100, 7341103); 2 M2 dext. (7341105-106); 2 m1 dext. (734184, 734193); 3 m1 sin. (734186, 734188, 734190); m1 sin. in hemimandible fragment (7341101); 3 m2 dext. (734191, 734195, 7341102); m2 sin. (734192); fragment of m2 sin. (7341af); m2 sin. in hemimandible fragment (734181); m2 sin. in mandible fragment with m1 alveoli (734182); fragment of right hemimandible with m1-2 (734179); fragment of left hemimandible with c-m1 (733917).

Diagnosis. – Müller (1967, translated from German): "An insectivore with dental pattern as follows: 3I/3i-1C/1c-4P/3p-2M/2m. p4 is large, unicuspulate. m1 and m2 slender and of approximately equal size, with two basins. Talonid only lingually opened. P4 is large and unicuspulate. M1 without a split mesostyle, longitudinally elongated. The hypocone is larger than the protocone. M2 is small with a simplified surface, without a split mesostyle."

Emended diagnosis. – An insectivore with dental formula as follows: 3I/2i-1C/1c-4P/4p-2M/2m. P4 is large with two cusps. M1 is without the split mesostyle, simplified, longitudinally elongated, with the hypocone being larger than the protocone. M2 is small, with a simplified surface and without a split mesostyle. p4 is large and unicuspulate. m1 and m2 are slender, of approximately equal size, with two basins and a lingually opened talonid.

Description. – M1 – The paracone is tall, but also the smallest of all the main cusps, it is conical and pointed, with a distinct postparacrista. The latter connects the paracone with the metacone, but a mesostyle is absent; the parastyle is small, situated on the triangular, rounded anterolabial crown protuberance with or without a conspicuous posterior crest and distinctly separated from the paracone by a notch (rarely it appears to be connected with the paracone by a faint labial crest); the metacone is the tallest and the

largest, a conical, pointed cusp, with its tip faintly projected posteriorly and passing into the long postmetacrista, which is probably terminated by the crest-shaped metastyle; the protocone can be as large as the hypocone, relatively wide, conical, protruding more anteriorly (or with anterior swelling?), with a distinct posterior crest (an inner crest may also be developed), passing into the cusp-shaped metaconule, which is also connected with the hypocone by a short crest (prehypocrista?); the hypocone only has a most conspicuously developed prehypocrista (an inner crest may also be present); the two lingual main cusps are more robust than the two labial ones, which are more slender and taller; all three lingual cusps are separated from the labial ones by a distinct longitudinal notch (notch-shaped valley), opening posteriorly into the deep talon basin; the crown base is almost completely bordered by a cingulum.

M2 – Both second upper molars have a drop-shaped outline to the crown. The rarely crest-shaped paracone is as tall as, or taller, than the protocone, but not as robust; its distinct preparacrista is curved posteriorly and ends next to the small cusp-shaped or crest-shaped parastyle or passes into a crest-shaped labial and anterior cingulum; the conspicuous postparacrista passes into the crest-shaped metacone, forming the posterior edge of the crown; the protocone is low and wide, but pointed with some crests; anteriorly it borders the shallow, semi-lunar basin; the mesostyle is confluent; the cingulum is mainly developed around the parastyle and it may be less conspicuously present at the anterior and lingual margins of the protocone; the teeth have three roots.

dc – The crown of deciduous lower canine is "premolarised", longitudinally oval, with a small main cusp on its anterior part with anterior and posterior crests, with a lingual and posterior basal cingulum, and with a small bumpy posterior area. The tooth is situated together with the milk premolars (dp1–dp4) and permanent m1 in a fragment of the left hemimandible (No. 733917; Fig. 2B).

dp1 – The double-rooted deciduous first lower premolar with an irregular shaped outline is relatively large; its crown is almost completely broken off; the protoconid was anteriorly shifted and a conspicuous cingulum is preserved only at the base on the lingual side.

dp2 – The extremely tiny dp2 has a heart-shaped crown; the small, anteriorly situated protoconid has a short anterior crest, the posterior one is divided into posterolabial and posterolingual parts; the conspicuous cingulum borders the whole crown base; only one root is developed.

dp3 – The single-rooted dp3 is larger than dp2, but smaller than dp1; the round crown consists only of one cusp (a low, blunt protoconid with a short anterior crest), situated almost on its anterior margin, and with a relatively large talonid area, which is faintly wrinkled; the cingulum borders the whole crown base.
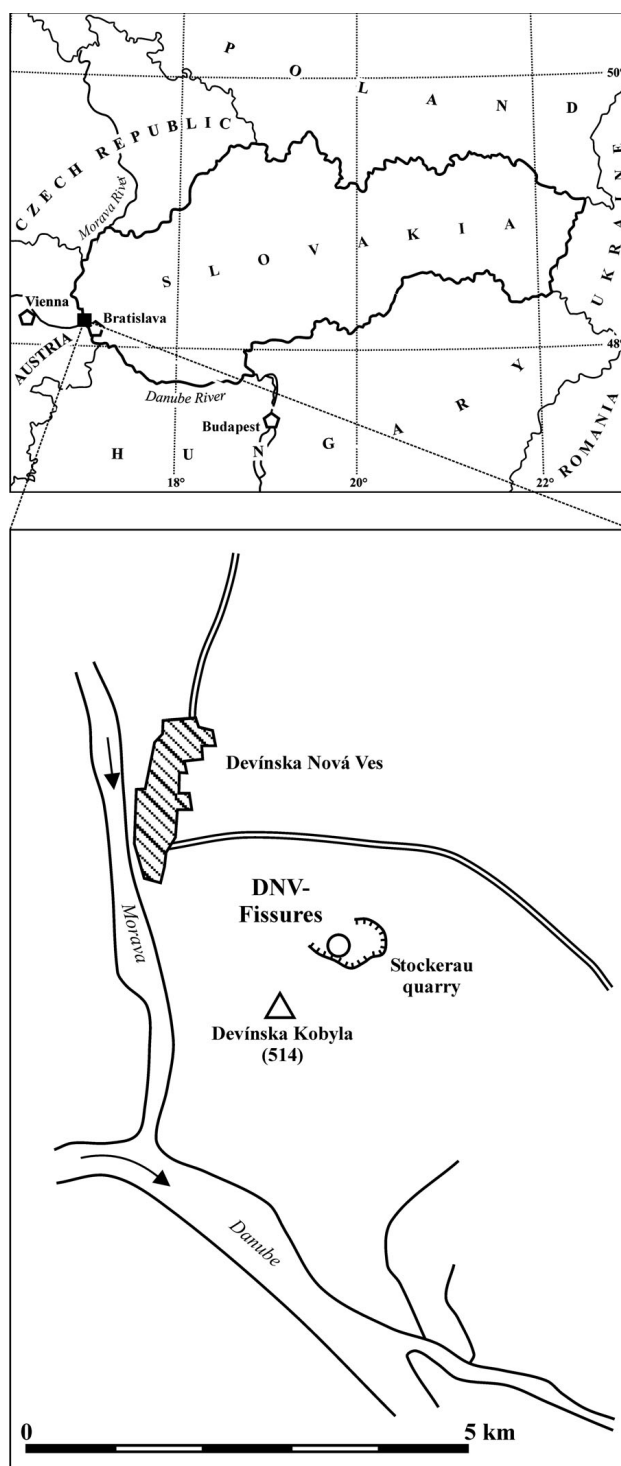

Figure 1. Location of the Devínska Nová Ves-Fissures site.

dp4 – The crown of the double-rooted dp4 with an irregular shaped outline is the largest of lower premolars; the distinct, anteriorly shifted protoconid dominates the crown and its anterior crest, passing into a anterolingual cingulum, is curved lingually, whereas the posterior one is directed towards the posterior basal cingulum, dividing the
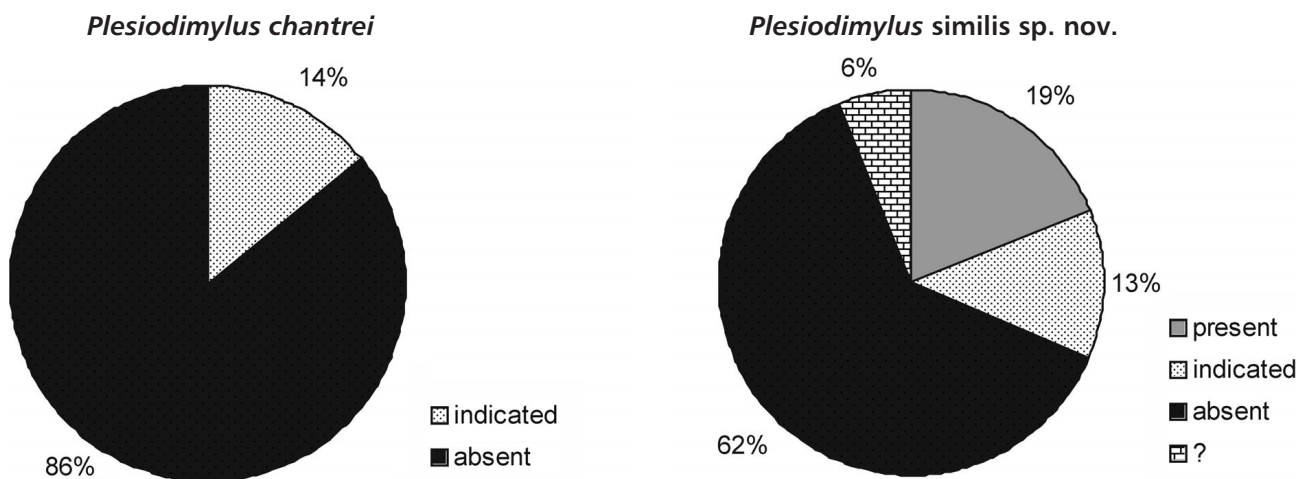
Plesiodimylus chantrei

Plesiodimylus similis sp. nov.

Figure 2. The occurrence of a mesostyle in M1s of both plesiodimyline forms from the site under study – *Plesiodimylus chantrei*: N = 7 M1 (indicated in 1 M1, absent in 6 M1); *Plesiodimylus similis* sp. nov.: N = 16 M1 (present in 3 M1, indicated in 2 M1, absent in 10 M1, ? in 1 M1).

talonid area into two approximately equal parts; the basal cingulum borders almost the whole of the crown base, with a cingular cusp-shaped hump in front of the protoconid.

m1 – The paraconid is a small (almost crest-shaped) cusp integrated into the long, lingually curved paralophid which borders the large, wide, lingually opened trigonid basin; the protoconid is as tall as the metaconid or slightly taller; both cusps are conical, but rather slender and so relatively more distant from each other, they are connected by a crest, which is divided in the middle by an indistinct notch (or they are divided only by a notch); the hypoconid is lower than the entoconid, but more robust, with a conspicuous posterior crest, running directly towards the entoconid (this crest may be divided from the entoconid posterior crest by a notch); the oblique cristid is lingually curved, abruptly ending behind the protoconid near the middle of the trigonid posterior wall (or rarely, it continues to the posterior side of the protoconid); the entoconid is conical and relatively slender, with a cingulum at the base on its outer posterior side; the postcristid runs obliquely downwards, from the entoconid to the posterolabial crown base, where it passes into a basal cingulum; it is mainly developed on the labial, mesial and mesiolingual sides (in molar No. 734179, a small mesoconid is present between the metaconid and the entoconid at the lingual margin of the crown); the talonid basin, open lingually, is larger and deeper than the trigonid basin.

m2 – The second lower molars are longer than m1s; the crest-shaped paraconid, situated on the anterior crown margin, is integrated into the lingually curved (or refracted) paralophid, bordering the relatively large and deep trigonid basin; the conical protoconid is taller and usually more robust than the conical metaconid and both cusps, forming a distinct posterior border of the trigonid (with a syncline in the middle of molar No. 79); the protoconid medial crest in unworn teeth (*e.g.*, No. 734181) is divided from the meta-

conid one by a slight notch; the hypoconid is not very conspicuous and it is connected with the distinct entoconid by a posterior crest; the relatively short oblique cristid is curved lingually towards the protoconid-metaconid posterior wall (or towards the middle of this wall, No. 734181), where it ends abruptly; the entoconid crest is conspicuous, faintly curved lingually; the talonid and its basin are smaller than the trigonid and its basin, and only somewhat more elongated than in the m2s of larger *Plesiodimylus*-form (see below); only the anterior and labial cingula are distinctly developed; near the paraconid, a small cingular accessory cusp is developed on the lingual side.

Mandible – Only the horinzontal rami of the dentaries are preserved. The mandible symphysis is oval and smooth; the *foramen mentale* is large, situated below the protoconid or the hypoconid of the m1.

Occurrence. – Europe (MN 4–MN 11).

Plesiodimylus similis sp. nov.
Figures 5A–F, H–K, 6A, C–E

Holotype. – Left hemimandible with c-m2 (No. 733921; Fig. 6A). Measurements of teeth: c – 1.40 × 0.93 mm, p1 – 1.92 × 1.30 mm, p2 – 0.56 × 0.71 mm, p3 – 0.62 × 0.65 mm, p4 – 1.71 × 1.18 mm, m1 – 2.73 × 1.52 × 1.55 mm, m2 – 2.73 × 1.55 × 1.24 mm.

Paratype. – Fragment of right maxilla with C-M2 (No. 733911), divided into an anterior part with C-P3 and a posterior part with P4-M2 (Fig. 5E).

Measurements of teeth: C – 1.49 × 1.18 mm, P1 – 1.09 × 1.09 mm, P2 – 0.78 × 0.99 mm, P3 – 1.09 × 0.93 mm, P4 – 2.23 × 2.17 mm, M1 – 3.60 × 2.39 × 2.64 mm, M2 – 1.98 × 2.88 mm.

Type horizont and locality. – Devínska Nová Ves-Fissures, Middle Miocene, Middle Badenian, Early Astaracian, lower part of MN 6 zone.

Material. – 4 C dext. (7339j, 7339l-m, 7339p); 3 C sin. (7339k, 7339n-o); 2 c dext. (7339v-w); 2 c sin. (7339t-u); 5 P4 dext. (733970, 733974, 733976, 7339h-ch); P4 sin. (733067); 2 p1 dext. (7339ai-aj); 4 p1 sin. (7339ah-ach, 7339al-am); 5 p4 dext. (733972, 7339ak, 7339ap, 7339at-au); 4 p4 sin. (7339ao, 7339aq-as); 4 M1 dext. (733961, 7339a-c); 3 M1 sin. (733919, 733960, 7339d); M1 sin. in fragment of maxilla (733954); M1 sin. in maxilla fragment with labial alveolus of M2 (733966); M2 dext. (7339g); 5 M2 sin. (733977-78, 7339e-f, 734197); M2 sin. in maxilla fragment (733968); 7 m1 dext. (733940, 733042, 733957, 733959, 7339y-aa); fragment of m1 dext. (7339ae); 3 m1 sin. (733938-39, 7339x); 3 fragments of m1 sin. (7339ab, 7339ad, 7339ag); 3 m2 dext. (733941, 734187, 734194); 8 m2 dext. in fragment of hemimandible (733929, 733931, 733934-35, 733943, 733946-47, 733971); 2 m2 dext. in fragment of hemimandible with m1 alveoli (733927, 733973); m2 dext. in hemimandible fragment with m1 alveoli (733944); 4 m2 sin. (733956, 734183, 734189, 734196); fragment of m2 sin. (7339ac); 6 m2 sin. in fragment of hemimandible (733937, 733948, 733951, 733953, 733963, 734185); m2 sin. in hemimandible fragment with m1 alveoli and posterior root of p4 (733928); 2 m2 sin. in hemimandible fragment with m1 alveoli (733949, 733965), 2 m2 sin. in hemimandible fragment with posterior alveolus of m1 (733932, 734180); fragment of right maxilla with I3 – P2 (7339q); fragment of right maxilla with C-M2 (733911); fragment of right maxilla with P4-M2 (733913); fragment of right maxilla with P4 and M1 (733952); fragment of right maxilla with M1-2 (733914); fragment of left maxilla with I2–P3 and with alveolus of I1 (7339r); fragment of left maxilla with C and with I1-3 roots (7339s); fragment of left maxilla with P3-4 (733964); fragment of left maxilla with P3-M1 (733912); 2 fragments of left maxilla with P4 and M1 (733945, 733955); fragment of right hemimandible with c and p1, and with p2-4 alveoli (733962); fragment of right hemimandible with c and p1 (7339an); fragment of right hemimandible with c-p4 (733918); fragment of right hemimandible with p1, p2, p4 and m1 (733933); fragment of right hemimandible with p4-m2 (7339bc); fragment of right hemimandible with p4 (7339ba); fragment of right hemimandible with p4 and alveoli of p2-3 and m1 (7339az); fragment of the hemimandible with damaged p4 and worn m1 (7339bb); fragment of right hemimandible with p4 and m1 anterior alveolus (7339ay); fragment of right hemimandible with m1-2 and with p4 alveoli (733016); fragment of right hemimandible with m1-2 (733936); 2 fragments of left mandible with still unerupted p4 without roots (7339av-aw); left hemimandible with c-m2 (733921); fragment of left hemimandible with p4 and roots of p1-3 (7339ax); fragment of
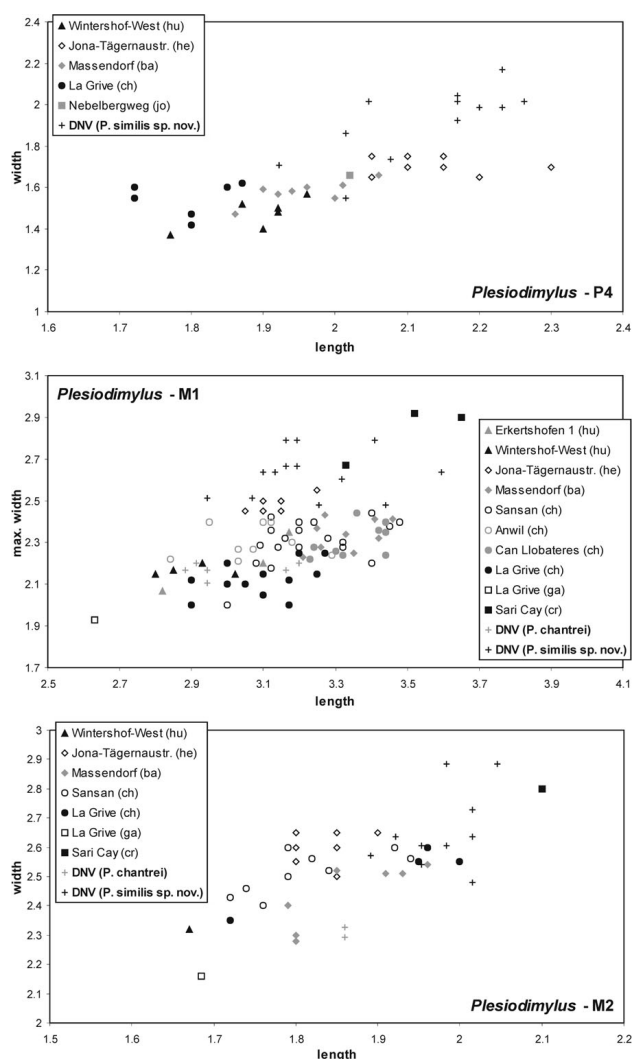

Figure 3. Scatter diagram of the length and width of upper teeth (P4 – M2) of *Plesiodimylus* species: hu – *P. huerzeleri*, he – *P. helveticus*, ba – *P. bavaricus*, ch – *P. chantrei*, ga – *P. gaillardi* (mean), jo – *P. johanni*, cr – *P. crassidens* (data source: Gaillard 1899; Hürzeler 1944; Zapfe 1951; Müller 1967; Engesser 1972, 1980; Schötz 1985; Bolliger 1992; Kälin & Engesser 2001; Mein & Ginsburg 2002).

left hemimandible with p4-m2 (733975); fragment of left mandible with p4 and m1 (733958); 2 fragments of left hemimandible with m1-2 (733930, 733950); fragment of left hemimandible with m1-2 and with p1-4 alveoli (733969); fragment of left hemimandible with very damaged m2 (7339bd).

Etymology. – The species name is derived from the Latin word *similis*, indicating a simililarity of the new species with *Plesiodimylus chantrei* and *Plesiodimylus crassidens*.

Diagnosis. – A form closely related to *P. chantrei*, differing from typical representatives of the species by its larger, swollen (more amblyodont) teeth.
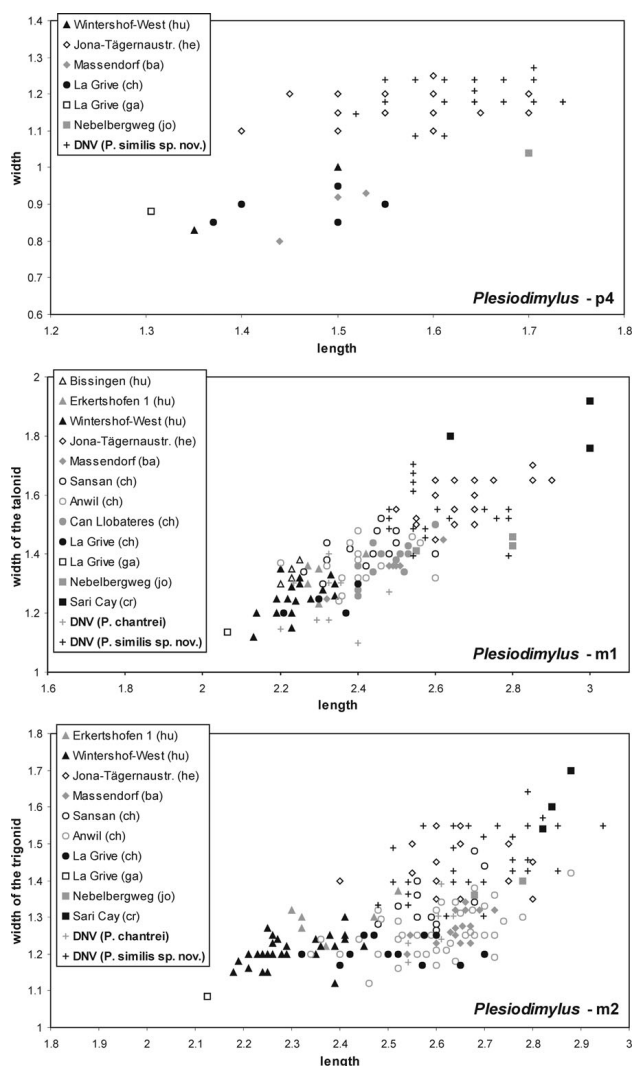
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Figure 4. Scatter diagram of the length and width of lower teeth (p4–m2) of *Plesiodimylus* species: hu – *P. huerzeleri*, he – *P. helveticus*, ba – *P. bavaricus*, ch – *P. chantrei*, ga – *P. gaillardi* (mean), jo – *P. johanni*, cr – *P. crassidens* (data source: Zapfe 1951; Müller 1967; Engesser 1972, 1980; Schötz 1985; Bolliger 1992; Kälin & Engesser 2001; Mein & Ginsburg 2002).

Description. – I1 – Based on measurements of the root which has a circular cross-section, the first upper incisors are the largest of the upper incisors.

I2 – The crown is longitudinally oval, larger than that of the I3s, rotated about 90° towards the other post-incisor teeth in the tooth row, with a relatively pointed cusp with anterior crest in the posteromesial part of the crown and with a small shallow basin in the anterodistal part of the crown.

I3 – The crown is longitudinally oval, knob-shaped and also rotated about 90° towards the other post-incisor teeth in the tooth row.

C – The crown is high, conical, faintly posteriorly pointed with a distinct posterior crest (can be lingually curved), passing into a blunt cusplet near to the posterior margin of the crown or only abruptly ending before the basal cingulum; the crown outline is oval (more convex on the labial side than on the lingual one); the teeth are double-rooted.

P1 – The occlusal outline is between almost triangular with rounded corners to round; the relatively low paracone is situated in a central position with an indistinct anterior ridge and more conspicuous one at the back; the basal cingulum borders the crown base and distolingually borders on where there is a hint of a small longitudinal basin.

P2 – The P2 crown is the smallest of all the upper premolars; its occlusal outline is rounded square to circular, and its base is bordered by a distinct cingulum; the paracone is a low, blunt cusp with a rather inconspicuous anterior crest and short distinct posterior one.

P3 – The third upper premolars are rounded with a more distolingual projection; the paracone is relatively tall, situated somewhat anteriorly, with a distinct posterior crest (a short basal anterior crest may also be developed, passing into the mesial cingulum); on the distolingual side of the crown, a flat shelf-shaped basin is present between the paracone and the basal cingulum, which borders the entire crown base.

P4 – The occlusal outline is triangular or irregularly rounded; the crown is dominated by the conical paracone with its relatively blunt, posteriorly pointed/projected tip and distinct posterior crest with a cusp-shaped hump at the base (not always developed; frequently the paracone posterior crest can also pass into the basal cingulum or it ends abruptly at the base, near the cingulum); the protocone, distinctly separated from the main cusp by a conspicuous notch, is conical and distinctly smaller than the paracone, it is situated on the lingual side of the crown; no parastyle is present and a distinct cingulum borders the crown base, or almost the whole crown base respectively (in this case, the anterolingual cingulum runs towards the protocone, where it ends abruptly); in the area among the paracone, protocone and the posterolingual cingulum (in some cases serrated), a very shallow basin is developed (very rarely with the indication of a tiny accessory cusp on the posterior margin).

M1 – The paracone is the smallest of all the main cusps, conical, with a short postparacrista, passing into the typical cusp-shaped mesostyle in only three teeth (in the remaining 13 M1s, the mesostyle is absent or only indicated); the parastyle is small, situated on the triangular or rounded anterolabial crown protuberance, with or without a conspicuous posterior crest and distinctly separated from the paracone by a notch; the metacone is the tallest, conical (or sporadically pointed) cusp with a tip faintly projected posteriorly and passing into the long postmetacrista which ends in the crest-shaped (rarely cusp-shaped) metastyle; the protocone is relatively wide, conical, with indistinct

posterior and inner cristae (in some cases, an anterior or lingual crista can also be present); the hypocone is one of the largest cusps on the crown and is morphologically similar to the protocone, but usually with an inner blunt crest only and/or with a faint prehypocrista, curved labially towards the metaconule; both lingual main cusps are more robust than the labial ones; in the inner area between the protocone and the hypocone, a very small, blunt metaconule is usually present, sometimes also developed as a crest-shaped blunt cusp on the antero-inner side of the hypocone (in a few specimens only a crest is present); all three lingual cusps are separated from the labial ones by a distinct longitudinal notch, opening posteriorly into the relatively deep talon basin; the crown base is almost completely bordered by a cingulum; in a few cases, the labial sides of both the paracone and the metacone are wrinkled; a very tiny accessory cusp is occasionally developed between the protocone and the hypocone near the lingual basal cingulum.

M2 – The occlusal outline is drop-shaped; the paracone is as tall as, or taller than the protocone, but not as robust, with a distinct preparacrista curved posteriorly and terminated by the small cusp-shaped or crest-shaped parastyle, and with a conspicuous postparacrista passing into a crest-shaped metacone, forming the posterior edge of the crown; the protocone is low, wide, blunt, with some (blunt) crests and anteriorly bordering the shallow, semi-lunar (relatively wide and deep) basin; the mesostyle is confluent; the cingulum is mainly developed around the parastyle and it can be less conspicuously present on the anterior and lingual margins of the protocone; in one molar, a tiny cingular cusp is situated near the parastyle; three roots are present.

c – A robust cingulum is developed on the posterior and posterolingual part of the lower canine crown base; the pointed cusp is faintly curved lingually, with a short crest on its posterior side (sometimes at its base only) and with another one on the anterolingual side.

p1 – The robust crown consists of a massive, but relatively blunt or only faintly pointed (depending on the state of abrasion) protoconid, shifted somewhat anteriorly, with a short, lingually curved anterior crest and a blunt, but massive posterior one, abruptly ending even before reaching the posterior basal cingulum; apart from on the posterior side, the cingulum can be present on the lingual and posterolabial crown base; one indistinct crest is sporadically developed on the inner (lingual) side of the protoconid which is not as convex as the outer (labial) protoconid side; the shape of the crown from an occlusal view resembles a "gothic window".

p2 – The oval second lower premolars, clearly wider than long, are the smallest of the lower premolars; the central robust, but blunt protoconid dominates the crown, the base of which is bordered by a massive cingulum; only one root is developed.

Table 1. The teeth measurements of *Plesiodimylus chantrei* from the Devínska Nová Ves-Fissures site. Abbreviations: L – length, W – width, WA – anterior width, WP – posterior width, TRW – trigonid width, TAW – talonid width.

Plesiodimylus chantrei		N	min.	max.	mean
dc	L	1	–	–	1.085
	W	1	–	–	0.62
dp1	L	1	–	–	1.302
	W	0	–	–	–
dp2	L	1	–	–	0.465
	W	1	–	–	0.62
dp3	L	1	–	–	0.62
	W	1	–	–	0.558
dp4	L	1	–	–	1.333
	W	1	–	–	0.93
M1	L	5	2.883	3.162	2.9698
	WA	6	1.829	1.922	1.8652
	WP	6	2.015	2.201	2.139
M2	L	2	1.86	1.86	1.86
	W	2	2.294	2.325	2.3095
m1	L	8	2.201	2.48	2.3178
	TRW	8	0.992	1.24	1.1625
	TAW	8	1.147	1.4	1.26
m2	L	7	2.542	2.666	2.6084
	TRW	8	1.178	1.395	1.2865
	TAW	7	0.93	1.147	1.0363

p3 – The single-rooted third lower premolars are similar to the p2, but they are larger and more robust, with an indication of a posterior crest.

p4 – The irregularly oval crown of the double-rooted fourth lower premolars is bordered by a distinct cingulum; it is the largest (most robust) lower premolar with a robust protoconid, situated somewhat anteriorly and mostly with a conspicuous posterior crest (occasionally, it can be faintly arched labially), which can in some specimens be divided in the lower part into two branches, running towards the posterolabial crown corner, or posterolingual one; in the posterolingual area, between the protoconid and basal cingulum, blunt, tiny accessory cusps (1–2) may be situated, or a cingular cusp is developed on the posterolingual cingulum; the anterior root is arched posteriorly, the posterior root is straight.

m1 – The small paraconid is short, relatively blunt, situated in the anteriormost part of the crown, with a very short paralophid (sometimes it is curved lingually, otherwise it runs directly towards the protoconid, or towards the medial side of the protoconid); it borders the very small, shallow,

narrow, lingually opened trigonid basin; the protoconid and the metaconid are of approximately equal size and they are situated very close to each other, separated only by an indistinct notch in some teeth and together forming a robust posterior "wall" of the trigonid, inclining steeply downwards; both cusps are conical and robust; very rarely, the protoconid can be shifted more posteriorly than the metaconid; the hypoconid is blunt and small (lower than entoconid) with a direct oblique cristid running towards the protoconid, where it usually abruptly terminates (in a few cases, it is lingually curved and continues towards the posterior side of the protoconid), and with a posterior crest connecting the cusp with a similar crest from the entoconid (very rarely, both crests may be divided by a slight notch or the posterior entoconid crest is not developed); the entoconid is pointed (or conical), with a blunt, relatively conspicuous anterior crest, which can be curved (or orientated) more labially (in some molars, this anterior entoconid crest is not developed or it is indistinct); the postcristid is developed on the crown's distal wall; the shallow talonid basin, open lingually, is larger than the trigonid one, but, the trigonid of the m1s is larger than their talonid; the cingulum is only developed in the anterior and labial parts of the crown base, and it passes into the postcristid on the posterior side. Generally, these molars are larger and wider than molars of *P. chantrei* from the same site.

m2 – The crest-shaped paraconid, situated on the anterior crown margin, is integrated into the lingually curved paralophid, bordering the relatively large and open trigonid basin; the conical protoconid is taller and mostly more robust than the conical metaconid (with a swelling at the back) and both cusps are connected by a crest (protolophid?), forming a distinct posterior border of the trigonid; the hypoconid is not very conspicuous and it is connected with the distinct entoconid by a posterior crest; the relatively short oblique cristid runs directly towards the protoconid, where it abruptly ends (it can also be separated by a notch) or continues to the posterior side of the protoconid; the entoconid crest is conspicuous [in one m2 sin. (No. 733930; Fig. 6E), a tiny humpy accessory cusp (entostylid?) is situated at the end of the entoconid crest]; the talonid is smaller than the trigonid; only anterior and labial cingula are distinctly developed (a small cingular accessory cusp near the paraconid on the lingual side, or cusp-shaped termination of the anterolingual cingulum can

also be present); in molar No. 733927, the postcristid is indicated on the distal wall of the crown. These molars are faintly rotated towards m1s (or tooth row).

Mandible – The lower jaw is long and slender, with a more posteriorly protruded posterior part of the mandible ramus, with distinctly bordered symphysis, and with relatively large *foramen mentale* below the m1 protoconid or shifted more posteriorly; *fossa mandibularis externa* is relatively deep, nearly reaching up to the area behind m2; there was also a long angular process (?).

Occurrence. – Slovakia (MN 6).

Discussion

So far, six species of *Plesiodimylus* are known from the European Miocene (*P. huerzeleri*, *P. helveticus*, *P. bavaricus*, *P. chantrei*, *P. gaillardi*, and *P. johanni*). Some of them, however, are considered as non-valid species. According to Engesser (1976, 1980) and Doukas (1986) *P. huerzeleri* is synonymous with *P. chantrei*, although Schötz (1985) showed that *P. huerzeleri* and *P. chantrei* are separate species. In addition, according to van den Hoek Ostende (1995), *P. bavaricus* from German Middle Miocene sites is not a well-defined species, showing no great differences from *P. chantrei* or *P. huerzeleri*. The latter species, moreover, probably represents the ancestor of *P. bavaricus*, *P. chantrei*, and maybe *P. helveticus* is also derived from it (Ziegler 1999).

For exact species determination, the morphology of M1 is of paramount importance. Based on this feature, it is possible to divide the species of the genus into two groups – a group with a mesostyle in M1 (*P. huerzeleri*, *P. helveticus*, and *P. bavaricus*) and a group without a mesostyle in M1 (*P. chantrei*, *P. gaillardi*, and *P. johanni*). The Turkish species *P. crassidens* from the late Middle Miocene (MN 7/8) can also be assigned to the latter group. The presence and shape of the mesostyle, however, is a relatively variable primitive character and it can occasionally occur in *P. chantrei* as well. Based on this fact, its form and frequency within the sample under study is very important (Fig. 2) and during the course of geological time, it decreases as from *P. huerzeleri* to *P. chantrei* (Ziegler & Mörs 2000).

Figure 5. Upper dentition of plesiodimyline dimylids from the Middle Badenian deposits of the Devínska Nová Ves-Fissures site (MN 6) in Slovakia. • A–F, H–K – *Plesiodimylus similis* sp. nov. A – fragment of the right maxilla with M1-2 of juvenile to young adult (No. 733914, invert.). B – fragment of the right maxilla with P4-M2 of juvenile to young adult (No. 733913, invert.). C – fragment of the left maxilla with P3-M1 of juvenile to young adult (No. 733912). D – M1 sin. in maxilla fragment of young adult animal (No. 733966). E – posterior fragment of the right maxilla with P4-M2 of juvenile to young adult (No. 733911, paratype; invert.). F – M1 sin. (No. 733960) and M2 sin. (No. 733977) of juveniles. H – M1 sin. from young animal (No. 733919). I – P4 dext. of young animal (No. 733970). J – P4 dext. of young animal (No. 733974). K – P4 dext. of young animal (No. 733976); all in occlusal view. • G – *Plesiodimylus chantrei* Gaillard, 1897 – M1 dext. of young animal in occlusal view (No. 733920, invert.).
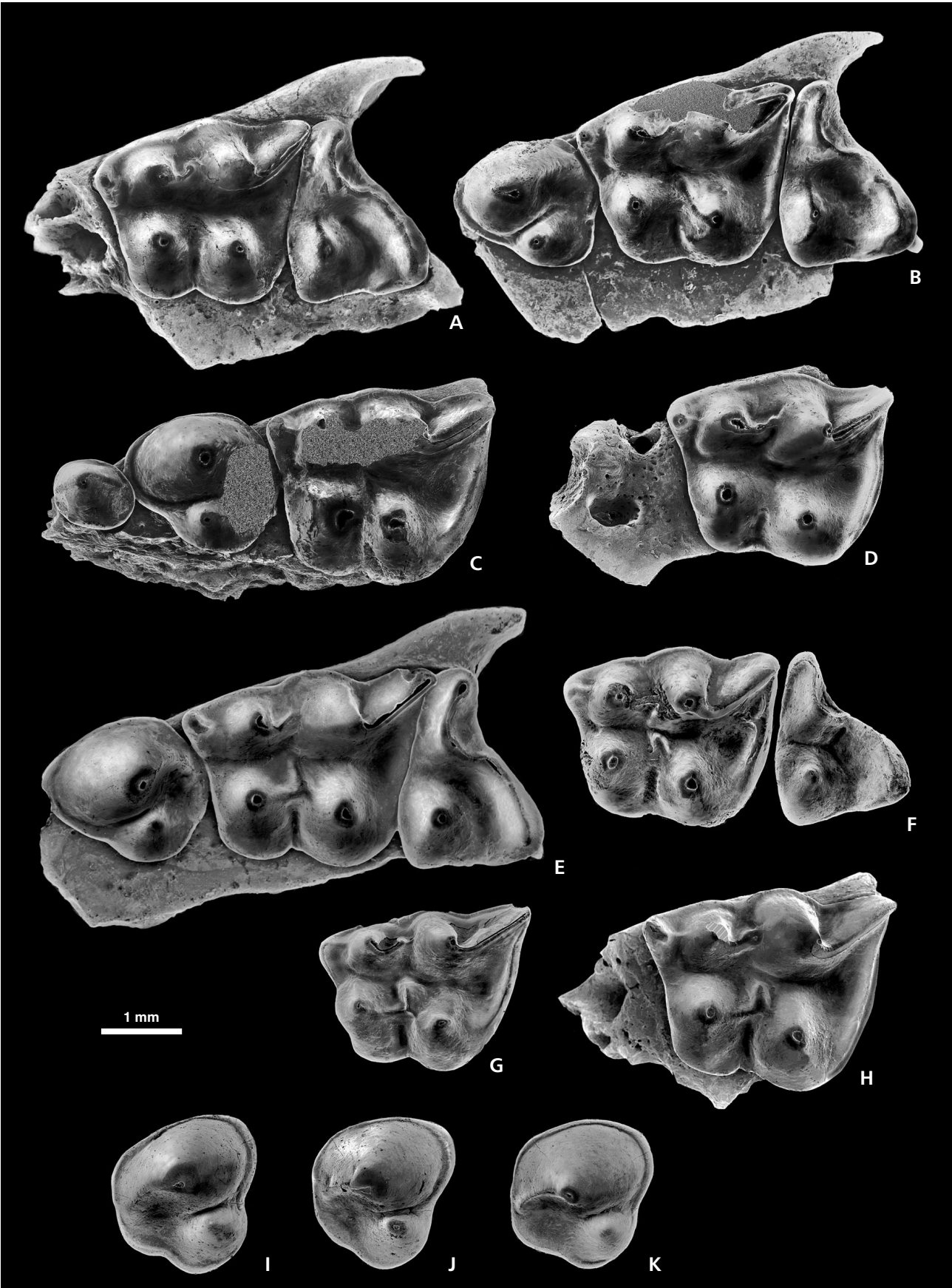
P. chantrei was a relatively conservative species with many local populations during the period of its existence. Apart from their stratigraphical position, these populations differ from one another also in certain morphological differences or measurements. Overall, *P. chantrei* shows a larger morphological variability (Ziegler & Fahlbusch 1986) and based on general opinion, the species did not increase in size during evolution (Rzebik-Kowalska 1996).

The stratigraphical range of *P. chantrei* is from MN 4 (Petersbuch 2) up to MN 11 (Dorn-Durkheim) and its fossils have been found from Poland in the north down to Spain in the south of Europe.

The morpho-metric analysis of records from the terrestrial deposits of karst fillings near Devínska Nová Ves, dated the Middle Miocene (the Middle Badenian, lower part of MN 6), shows the occurrence of two forms of the genus *Plesiodimylus*, differing from each another mainly in size and massiveness of teeth (Tables 1, 2). Whereas the smaller form with its morphological characters (such as the absence of the mesostyle in the upper molars, slender lower molars and m1s which are smaller or alternatively almost as large as m2s) and teeth measurements (Figs 3, 4) represents the typical individuals of *P. chantrei*, comparable with type material from the French site of La Grive St. Alban, the larger form represents a different species, closely related to the above-mentioned species, differing mainly in larger size of teeth, partly overlapping with tooth measurements of *P. helveticus* and *P. johanni* (Figs 3, 4). The contrast can also be seen in different indices of lengthratios between P4/M1 and m1/m2 (Table 3), suggesting their possible taxonomic relevance not only for distinguishing of genera (van den Hoek Ostende 1995) but also for distinguishing of species within a genus. From this viewpoint, the P4/M1 ratio could be of significant interest for species separation of the two *Plesiodimylus* forms from Devínska Nová Ves, the larger form exhibiting a distinctly higher index (0.66) than indices of *P. chantrei* (0.57–0.59).

From a morphological viewpoint, the teeth of *P. similis* sp. nov. show the basic model of *P. chantrei* teeth, but they are more amblyodont (Figs 5, 6), resembling also teeth of *P. crassidens*. The teeth of this Anatolian species, however, are slightly larger (Figs 3, 4).

The remains of a larger new species from Devínska Nová Ves differ from the various Miocene species of *Plesiodimylus* in several morphological and metric characters and are as follows:

– it differs from *P. huerzeleri* by the predominant absence of a mesostyle in M1, the presence of a confluent mesostyle in M2, and in larger dimensions;

– it differs from *P. helveticus* by the predominant absence of a mesostyle in a wider M1, the presence of a confluent mesostyle in a larger M2, a different structure of the paraconid-paralophid complex of m1, and in having a more limited talonid basin in m2;

– it differs from *P. bavaricus* by a predominant absence of a mesostyle in M1 and the presence of a confluent mesostyle in M2, a more shallow trigonid basin in m1, and, generally, in its larger dimensions;

– it differs from typical individuals of *P. chantrei* by its larger (particularly regarding width) and more amblyodont teeth;

– it differs from *P. gaillardi* in its larger dimensions, proportionally less robust metaconid on the lower molars, and generally more massive teeth;

– it differs from *P. johanni* in its protoconid, usually separated from an oblique cristid in m1 and in having more robust teeth;

– it differs from *P. crassidens* in having smaller tooth measurements (mainly M1 and m1), which are also less amblyodont.

The comparison indicates that the larger form from Devínska Nová Ves, as a representative of *Plesiodimylus*, is a close relative to *P. chantrei*, but has been determined as a new species (*P. similis* sp. nov.). Its teeth are also larger and morphologically slightly different (*e.g.*, oblique cristid of m1 abruptly terminates on the posterior side of the protoconid) from teeth of the forms described by Ziegler (2006) as *P.* aff. *chantrei* from the Austrian sites of Schernham (MN 10), Richardhof-Wald (MN 10) and Richardhof-Golfplatz (MN 9). This new species of *Plesiodimylus* from Devínska Nová Ves shows a certain similarity with a phylogenetic line, terminating in *P. crassidens*. It is however not possible to exclude a phylogenetic relationship with species of *P. johanni* or to finds of large m2s from the Polish site of Bełchatow A (MN 9), described as *Plesiodimylus* sp. only (Rzebik-Kowalska 1996). This similarity may, however, also be the result of parallelism, caused by climatic and ecological factors.

The origin of both forms (*P. chantrei* and *P. similis* sp. nov.) in the taphocoenosis of the site under study is also questionable. The common occurrence of two forms of *Plesiodimylus* in one locality is very rare, known so far

Figure 6. Lower dentition of plesiodimyline dimylids from the Middle Badenian deposits of the Devínska Nová Ves-Fissures site (MN 6) in Slovakia. • A, C–E – *Plesiodimylus similis* sp. nov. A – left hemimandible with c-m2 of young animal in occlusal and lateral view (No. 733921, holotype). C – fragment of the right mandible with p1, p2, p4 and m1 of adult animal in occlusal and lateral view (No. 733933, invert.). D – fragment of the left mandible with p4 and m1 of young adult animal in occlusal and lateral view (No. 733958). E – fragment of the left hemimandible with m1 and m2 of young animal in occlusal and lateral view (No. 733930). • B – *Plesiodimylus chantrei* – fragment of the left hemimandible with dc, dp1–dp4, and m1 of juvenile in occlusal and lateral view (No. 733917).
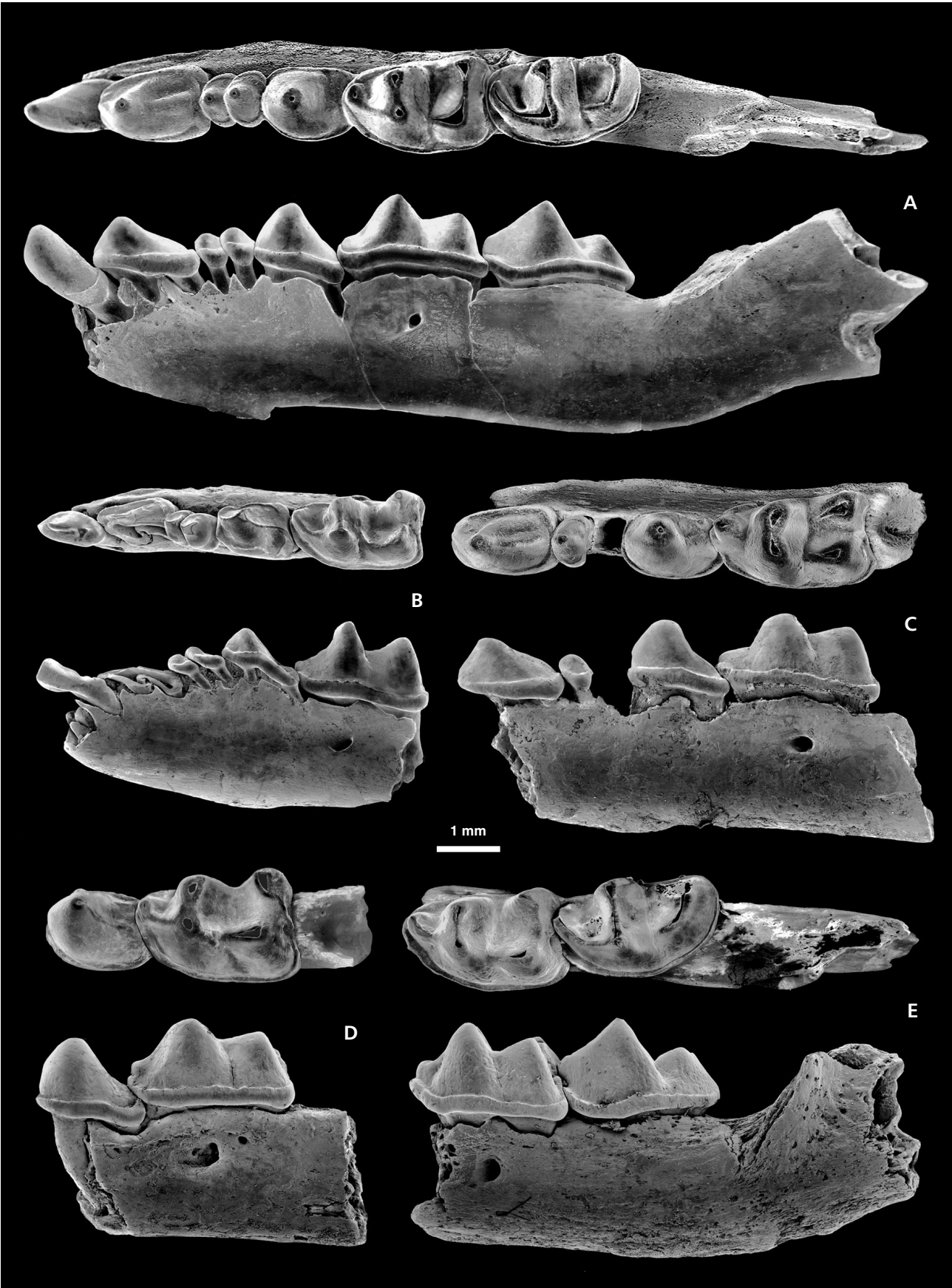
Table 2. The teeth measurements of *Plesiodimylus similis* sp. nov. from the Devínska Nová Ves-Fissures site. Abbreviations: L – length, W – width, WA – anterior width, WP – posterior width, TRW – trigonid width, TAW – talonid width.

Plesiodimylus similis sp. nov.		N	min.	max.	mean
I2	L	1	–	–	0.713
	W	1	–	–	0.558
I3	L	2	0.62	0.62	0.62
	W	2	0.434	0.465	0.4495
C	L	10	1.426	1.581	1.4889
	W	11	1.023	1.24	1.1132
c	L	3	1.054	1.395	1.178
	W	4	0.837	0.992	0.9223
P1	L	3	0.93	1.085	1.0023
	W	3	0.961	1.085	1.0127
P2	L	3	0.775	0.868	0.8267
	W	3	0.744	0.992	0.8577
P3	L	4	1.085	1.116	1.0928
	W	4	0.93	1.023	0.961
P4	L	12	1.922	2.263	2.1261
	W	12	1.55	2.17	1.9168
p1	L	11	1.705	1.922	1.7839
	W	11	1.147	1.302	1.2287
p2	L	3	0.527	0.62	0.5683
	W	3	0.713	0.992	0.837
p3	L	2	0.62	0.62	0.62
	W	2	0.651	1.085	0.868
p4	L	19	1.519	1.736	1.6348
	W	19	1.085	1.271	1.196
M1	L	13	2.945	3.596	3.2288
	WA	14	2.108	2.449	2.3029
	WP	14	2.48	2.79	2.6239
M2	L	10	1.891	2.046	1.9778
	W	10	2.48	2.883	2.6567
m1	L	20	2.48	2.79	2.6102
	TRW	22	1.395	1.612	1.5021
	TAW	21	1.395	1.705	1.5367
m2	L	37	2.48	2.945	2.6769
	TRW	37	1.178	1.643	1.4503
	TAW	37	0.93	1.333	1.1604

only from Bełchatów A (Rzebik-Kowalska 1996) or Petersbuch 31 (Ziegler 2005). And although van den Hoek Ostende (1995) suggested sexual dimorphism in dimylids,

Table 3. The P4/M1 and m1/m2 ratios of the various species of *Plesiodimylus*. (Apart from difference between indices of the both *P. chantrei* and *P. similis* sp. nov., note also the indices of *P. bavaricus*, indicating a possible dissolution its status of separate species as already assumed by van den Hoek Ostende in 1995; data source: Gaillard 1899; Seemann 1938; Hürzeler 1944; Zapfe 1951; Müller 1967; Engesser 1972, 1980; Schötz 1985; Ziegler & Fahlbusch 1986; Bolliger 1992; Rzebik-Kowalska 1996; Ziegler & Mörs 2000; Kälin & Engesser 2001; Mein & Ginsburg 2002.)

Plesiodimylus huerzeleri	P4/M1	m1/m2
Bissingen	0.60	–
Erkertshofen 1	0.58	0.97
Wintershof-West	0.65	0.98
Plesiodimylus helveticus		
Basel	0.69	1.02
Plesiodimylus bavaricus		
Massendorf	0.59	0.95
Plesiodimylus chantrei		
Anwil	–	0.93
Bełchatów A	–	0.84
Bełchatów B	0.57	0.94
Devínska Nová Ves-Fissures	–	0.90
La Grive	0.58	0.90
Langenmoosen	–	0.99
Hambach	0.57	0.95
Puttenhausen	0.59	0.99
Sansan	–	0.93
Viehhausen	0.59	0.91
Plesiodimylus gaillardi		
La Grive	–	0.97
Plesiodimylus johanni		
Nebelbergweg	–	0.99
Plesiodimylus crassidens		
Sari Çay	–	1.01
Plesiodimylus similis sp. nov.		
Devínska Nová Ves-Fissures	0.66	0.98

no fossil assemblages of *P. chantrei* indicates this to be the case. Futhermore, the ratio between smaller and larger forms from Devínska Nová Ves does not approach 50% as one would expect in dimorphism. Based on proportional representation of both these forms in the fossil record of the site under study, the larger form outnumbers (MNI = 22, MNE = 122, Number of teeth = 173) the smaller *P. chantrei* (MNI = 4, MNE = 24, Number of teeth = 31). On the other hand, the division into two groups within the scatter diagrams for P4, M2, and m2 of the new species could indicate sexual dimorphism in this larger form.

Due to the common occurrence of both dimilyds in the taphocoenosis, probably accumulated from raptor pellets, two possible interpretations can be put forward – either they represent forms, which commonly lived in the same territory, or they represent forms, which raptors hunted in the wider surroundings of the site. The local palaeogeographic situation during the Middle Badenian may also have played an important role. In this period, the area under study was part of an archipelago in the western part of the Central Paratethys (Kvaček *et al.* 2006) and the site under study was situated in the territory of Devínska Kobyla Hill which was an island during this time, isolated from the nearest land by a shallow isthmus (Sabol & Kováč 2006). In the case of co-occurrence of both forms in the area, it is possible to consider their probable sympatric relationship with different ecological conditions and food chains (?), with the dominance of the larger taxon (*P. similis* sp. nov.). However considering the differences in size of the determined taxa, their overall proportional representation in the taphocoenosis, as well as the palaeogeographic conditions, it cannot be excluded that the larger form represents an isolated insular (endemic?) population, evolved from the original land population of *P. chantrei* and the co-occurrence of both forms could be a result of raptor hunting not only on the island(-s), but also in the territory of the surrounding land. Circumstantial evidence for a proposed insular theory can also be found in the fossil record from the site. It contains some faunal elements (such as *Pliopithecus vindobonensis*, *Keramidomys carpathicus* or *Democricetodon vindobonensis*) indicating an isolated character of the assemblage over a critical time period (necessary for the evolution of endemic forms). The abundant record of approximately 60 individuals of *Chalicotherium grande* from the same site (Zapfe, 1976) is also interesting, pointing out the unique character of the whole assemblage from the site under study.

Generally, the dimylids are the most frequently represented within the insectivore taphocoenosis of Devínska Nová Ves-Fissures site, accounting for more than 50% of the fauna of this mammalian group. Similarly high proportions are observed in all Central European sites from the end of the Early Miocene (Ziegler 1998, Ziegler & Mörs 2000).

Conclussion

Dimylid fossils found in Middle Miocene terrestrial deposits of karst filling at the Devínska Nová Ves-Fissures site (MN 6) represent two distinct forms of *Plesiodimylus*, differing from each another mainly in size and massiveness of the teeth. The remains of the smaller form belong among typical individuals of *P. chantrei*, comparable with the type material. On the contrary, the larger form represents a different, new species (*P. similis* sp. nov.) with a similarity to

P. crassidens from the Middle Miocene of Turkey (MN 7/8), though some phylogenetic relationship with the Late Miocene species from Nebelbergweg in Switzerland (*P. johanni*) or from the Polish site of Bełchatow A (*Plesiodimylus* sp.) cannot be excluded. However, the process of parallelism, caused by both climatic and ecological factors, could also play a major role in evolution of the plesiodimyline taxa. Based on the assumption of raptor hunting in the wide surroundings of nesting sites, a different origin for both the found taxa of *Plesiodimylus* in the taphocoenosis of the Devínska Nová Ves-Fissures locality is suggested.

Acknowledgment

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