

All time high: Dimylidae (Eulipotyphla, Mammalia) diversity in the early Miocene locality of Akníkov 1 (Czech Republic, MN 3)

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Abstract The locality of Akníkov 1 (Czech Republic, MN 3) has yielded the largest diversity of Dimylidae known from a single locality. Four species are recognised in the few dozen recovered fossils: *Dimylus* aff. *paradoxus*, *Plesiodimylus* sp., *Chainodus intercedens* and *Lacrimodon vandermeuleni* nov. gen., nov. sp. The high diversity supports the assumption of a humid palaeoenvironment for Akníkov 1.

Keywords Insectivores · Palaeoenvironment · Palaeodiversity · Evolution · Merkur-Nord

Introduction

Dimylidae are an extinct family of insectivores characterised by the loss of the last molars and very plump and bulbous (amblyodont) teeth, which to varying degrees overhang the dentary (exoedaenodont). This dentition is believed to be an

adaptation to shell-crushing predation (Müller 1967). Dimylids are generally considered to be malacophagous and as such associated with relatively humid environments that provide a year-round food source.

The family attained its highest diversity in the early Miocene of Central Europe (Ziegler 2006a) and, as a consequence, all monographs dealing with the family have been published in German (Hürzeler 1944; Müller 1967; Ziegler 1990). The family has also been found, albeit much rarer, in the early Miocene of the Mediterranean area. Gibert (1975) noted the presence of *Cordylodon* [= *Chainodus*] *intercedens* in Rubielos del Mora (Spain, MN 3), a species which was also listed for Alto de Ballester (Montoya et al. 1996). The designation was subsequently changed to *Chainodus* cf. *sulcatus* by Van den Hoek Ostende et al. (submitted). Doukas (1986) described *Plesiodimylus chantrei* from Aliveri, while Doukas and Van den Hoek Ostende (2006) described *P.* aff. *crassidens* from Karydia (both locations in Greece, MN 4). The easternmost known range of the family is formed by Anatolia where Van den Hoek Ostende (1995) described two species of *Turkodimylus* (Turkey, MN 1–3). In all these cases only one species of dimylid was recorded per locality, whereas contemporaneous German sites have been reported yielding several different forms (e.g. Ziegler 1990; Klietmann et al. 2014).

The diversity of Dimylidae is strongly reduced after the early Miocene (Furió et al. 2011a), with only the genera *Plesiodimylus* and *Metacordylodon* surviving [except for some records of *Chainodus* (aff.) *intercedens* from MN 5 (Rzebik-Kowalska 1996; Ziegler and Mörs 2000), the presumed ancestor of *Metacordylodon*]. Both genera survived into the middle Miocene and had a wide distribution, with records from Poland (Rzebik-Kowalska 1996) and Austria (Ziegler 2006b) to Spain (Engesser 1972; Agustí et al. 1984; Furió et al. 2011b) and Anatolia (Engesser 1980).

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In this paper, we describe the Dimylidae from the locality of Akníkov 1 (Czech Republic, MN 3; Fig. 1), a locality that was previously known under the name Merkur-Nord. Fossils were collected from the so-called “main seam member” in the open cast brown coal pit. Akníkov 1 is known for its excellent fossil preservation, the micromammals being often represented by complete mandibles. This certainly applies to the material described in this paper. The locality is also important for having preserved both macro- and micromammals, providing a complete view of the MN 3 mammalian fauna in the area (Fejfar et al. 2003; Table 1). Among insectivores, the Erinaceidae and Talpidae were described in an earlier paper (Van den Hoek Ostende and Fejfar 2006). Preliminary lists including the Dimylidae were provided by Fejfar et al. (2003) and Fejfar and Sabol (2005), but as the material had not yet been studied in detail at that time, we provide some emendations to these preliminary lists.

Material and methods

Dental elements were measured according to the orientation of Müller (1967), using an ocular micrometer on a bisecting microscope. All measurements are given in millimetres. The material is stored in the palaeontology collections of the National Museum in Prague.

Systematic palaeontology

Eulipotyphla Waddell, Okada and Hasegawa, 1999
Dimylidae Schlosser, 1887

Dimylus von Meyer, 1846

Dimylus aff. *paradoxus* von Meyer, 1846
(Fig. 2a–e)

Measurements: The measurements are listed in Table 2.

Description

Maxilla: In one specimen bearing P3–M1, part of the face has been preserved. There is a huge infraorbital foramen around the P4 that is as wide and as high as the length of the P4. Above and to the back of this foramen is a second, much smaller foramen. The zygomatic process is high and strongly built. It is free-ending and forked at its end.

P3: The enamel in the only available specimen is crenulated. The outline of the occlusal surface is rectangular. The main cusp lies in the anterolabial corner of the premolar. Its posterocrista runs straight back. The P3 is surrounded by a cingulum.

P4: Three P4 have been found. The only unworn specimen has a sub-triangular outline. The labial part of the premolar consists of the very large paracone, which has a rounded anterior face and a blunt posterocrista. Lingually of its tip lies a much smaller, conical protocone. The premolar is surrounded by a cingulum and its enamel is crenulated. The two worn specimens are markedly different. Here, the enamel is smooth, there is no trace of a protocone and instead a parastyle seems to have been present.

M1: The outline of the occlusal surface is roughly trapezoidal. The M1 is somewhat wider at its back than at its front. The posterior side is straight, but in one specimen it is slightly S-curved. The metacone is the largest cusp and its two arms stand at a wide angle. The paracone is the smallest of the main

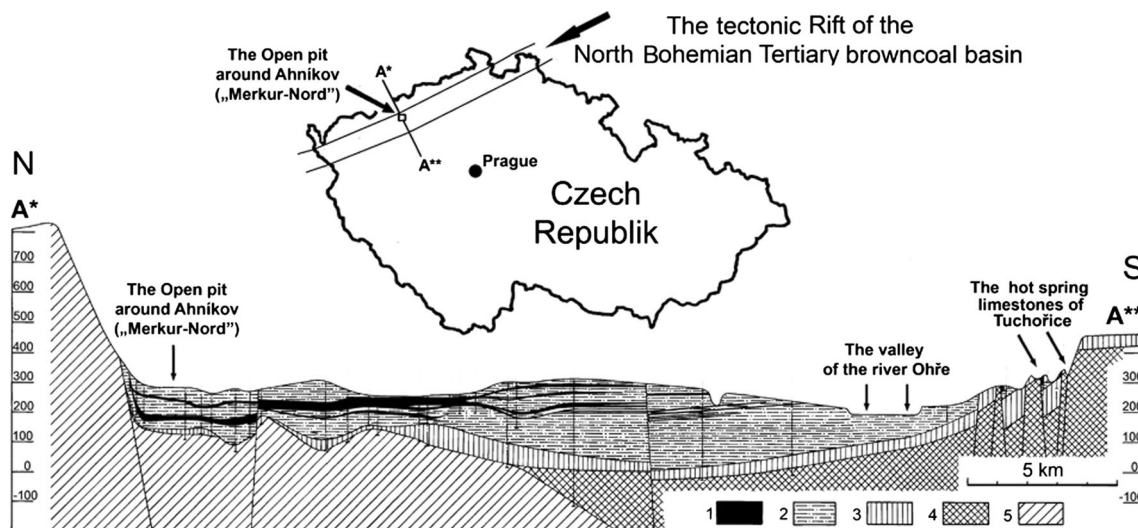


Fig. 1 The geographical position (*top*) and the geological setting (*bottom*) of the open pit around the site Akníkov (the mining area “Merkur-Nord”). *Bottom* North–south cross-section (A*–A*; *top*) through the North Bohemian Tertiary brown coal basin, showing the asymmetrical shape of the rift caused by the volcano–tectonic subsidence

(10-fold height exaggeration). 1 Brown coal seams, humolitic clays and claystones, 2 tertiary sands and clays, 3 Late Cretaceous deposits, 4 permocarboniferous deposits, 5 metamorphic rocks of the Krušné Hory Mts

Table 1

The mammalian fauna of Ahníkov 1

Marsupialia, Herpetotheriidae: *Amphiperatherium frequens* (H.v. Meyer).

Eulipotyphla, Erinaceidae: *Galerix aurelianensis* Ziegler; **Talpidae:** *Desmanella gudrunae* Van den Hoek Ostende and Fejfar, *Mygalea magna* Ziegler, *Myxomygale minor* Ziegler, *Talpa tenuidentata* Ziegler; Talpinae gen. et sp. indet., **Dimyidae:** *Dimylus* aff. *paradoxus* H.v. Meyer, *Plesiodimylus* sp., *Chainodus intercedens* (Müller), *Lacrimodon vandermeuleni* n. gen., n. sp.; **Metaconodontidae:** *Plesiosorex* cf. *soricinoides* (Blainville); **Soricidae:** cf. *Viretia* sp., *Miosorex desnoyrianus* (Lartet), *Soricella discrepans* Doben-Florin, *Paenelimoecus micromorphus* Doben-Florin, *Florinia stehlini* (Doben-Florin); **Heterosoricidae:** *Heterosorex neumayrianus* (Schlosser).

Rodentia, Aplodontidae: *Plesispermophilus descendens* (Dehm), *Plesispermophilus* sp. II., *Ameniscomys selenoides* Dehm, *Paracitellus eminens* Dehm; **Petauristidae:** *Miopetaurista* cf. *dehmi* De Bruijn, *Blackia miocaenica* Mein; **Sciuridae:** *Heteroxerus vireti* Black, *Sciurus costatus* Dehm; **Castoridae:** *Steneofiber depereti* Mayet, *Monosaulax minutus* (H.v. Meyer); **Eomyidae:** *Pentabuneomys* sp. I. und II., *Ligerimys lophidens* Fahlbusch, *Ligerimys* cf. *antiquus* Fahlbusch, *Pseudotheridomys* aff. *parvulus* (Schlosser); *Apeomys tuerkheimae* Fahlbusch; *Megapeomys lavocati* Fejfar et al.; **Gliridae:** *Heteromyoxus schlosseri* Dehm, *Myoglis antecedens* Mayr, *Glirudinus modestus* (Dehm), *Glirudinus gracilis* (Dehm), *Glirulus diremptus* (Mayr), *Microdyromys praemurinus* Freudenberg, *Peridyromys murinus* (Pomel), *Bransatoglis* sp., *Paraglis* sp.; **Cricetidae:** *Melissiodon dominans* Dehm.

Lagomorpha, Ochotonidae: *Ptychoprolagus* sp., *Amphilagus ulmensis* Tobien.

Carnivora, Mustelidae: *Martes laevidens* Dehm, *Broiliana nobilis* Dehm, *Stromeriella franconica* Dehm, *Plesictis humilidens* Dehm, *Laphycitis vorax* Dehm; **Viverridae:** *Palaeogale hyaenoides* Dehm, *Semigenetta elegans* Dehm; **Ursidae:** *Ballusia elmensis* (Stehlin), *Ursavus isorei* (Ginsburg and Morales); Amphicyonidae: *Amphicyon acutidens* Dehm, *Megamphicyon* “*maior – giganteus*”.

Perissodactyla, Rhinocerotidae: *Prosantorhinus laubei* Heissing and Fejfar, *Protaceratherium minutum* (Cuvier), *Plesiaceratherium* sp.; Chalicotheriidae: *Phyllotillon schlosseri* Heissing and Fejfar; Equidae: *Anchitherium aurelianense* H.v. Meyer; **Tapiridae:** *Tapirus intermedius* (Filhol).

Artiodactyla, Palaeomerycidae: *Palaeomeryx kaupii* H. v. Meyer; **Amphitragulidae:** *Amphitragulus boulangeri* Pomel; Suidae: *Aureliachoerus aurelianensis* (Stehlin).

cusps; its posterior arm ends against the end of the anterior arm of the metacone to form an undivided mesostyle. The parastyle is a small to very small conical cusp, which lies anterolingually of the paracone and protrudes slightly. The anterior arm of the protocone runs parallel to the anterior side of the molar and connects low to the parastyle. The posterior arm runs straight backwards, curves lingually of the mesostyle and ends freely directly adjacent to the tip of the hypocone, giving this cusp the appearance of having two tips. The conical hypocone, which is somewhat smaller than the protocone, bears a faint rib on its posterior flank, which continues as a ridge bordering the posterior side. A

weak labial cingulum is only discernable in two unworn specimens.

Mandible: The ramus horizontalis is only somewhat higher at its back than at its front. The only foramen mentale lies below the middle of the m1. The ramus ascendens stands at a right angle to the ramus horizontalis and rises up well behind the m2. The mandibular fossa forms a marked depression on the ramus ascendens. The condyle has not been preserved.

p4: The outline of the occlusal surface is sub-rectangular. The tip of the main cusp lies in the front part of the premolar. Its anterior face bears a blunt anterocristid. The posterior face slopes down. The enamel of this face is, particularly in unworn specimens, somewhat crenulated. The premolar is surrounded by a well-developed cingulum.

m1: The outline of the occlusal surface is sub-rectangular, with the lingual and labial sides nearly parallel. The talonid is only somewhat longer and wider than the trigonid. The protoconid and metaconid are of the same height. In unworn specimens, they are separated by a clear notch. The paraconid is much lower. It lies directly in front of the metaconid. The hypoconid is the largest cusp, though lower than the protoconid and metaconid. The oblique cristid slopes down toward the base of the protoconid. The hypolophid ends just short of the entoconid, where it meets the posterior arm of that cusp as well as the posterior cingulum. The entoconid is blade-like and closes the talonid basin. Directly behind the entoconid is a very small entostylid. A well-developed cingulum is present on all sides, except for the lingual side.

m2: The trigonid is wider and larger than the talonid. The protoconid and metaconid are of the same height. The paraconid is much lower and blade-like. It is incorporated in the curved paralophid and lies just short of the lingual border. In some specimens, the paralophid continues after the paraconid and it may even turn back to close part of the trigonid basin. Both protolophid and paralophid are relatively sharp. The cusps of the talonid are much reduced and are incorporated in a ridge consisting of the oblique cristid, hypolophid and entocristid. This ridge encircles the talonid basin. There is a narrow to well-developed cingulum on the anterior, labial and posterior sides. In one specimen, the posterior cingulum is missing.

Milk dentition

Three deciduous elements (d3, d4, D4) have been found, which may possibly belong to one individual. On the basis of their morphology, we consider these best referable to *Dimylus*. However, as four species of dimylid are present, and the milk dentition of many genera is as yet unknown, they could theoretically also belong to one of the other genera.

d3: The outline of the occlusal surface is sub-triangular, with a narrow anterior end. The main cusp has a rounded anterior face. At the back there is a blunt posterocrista. There is a

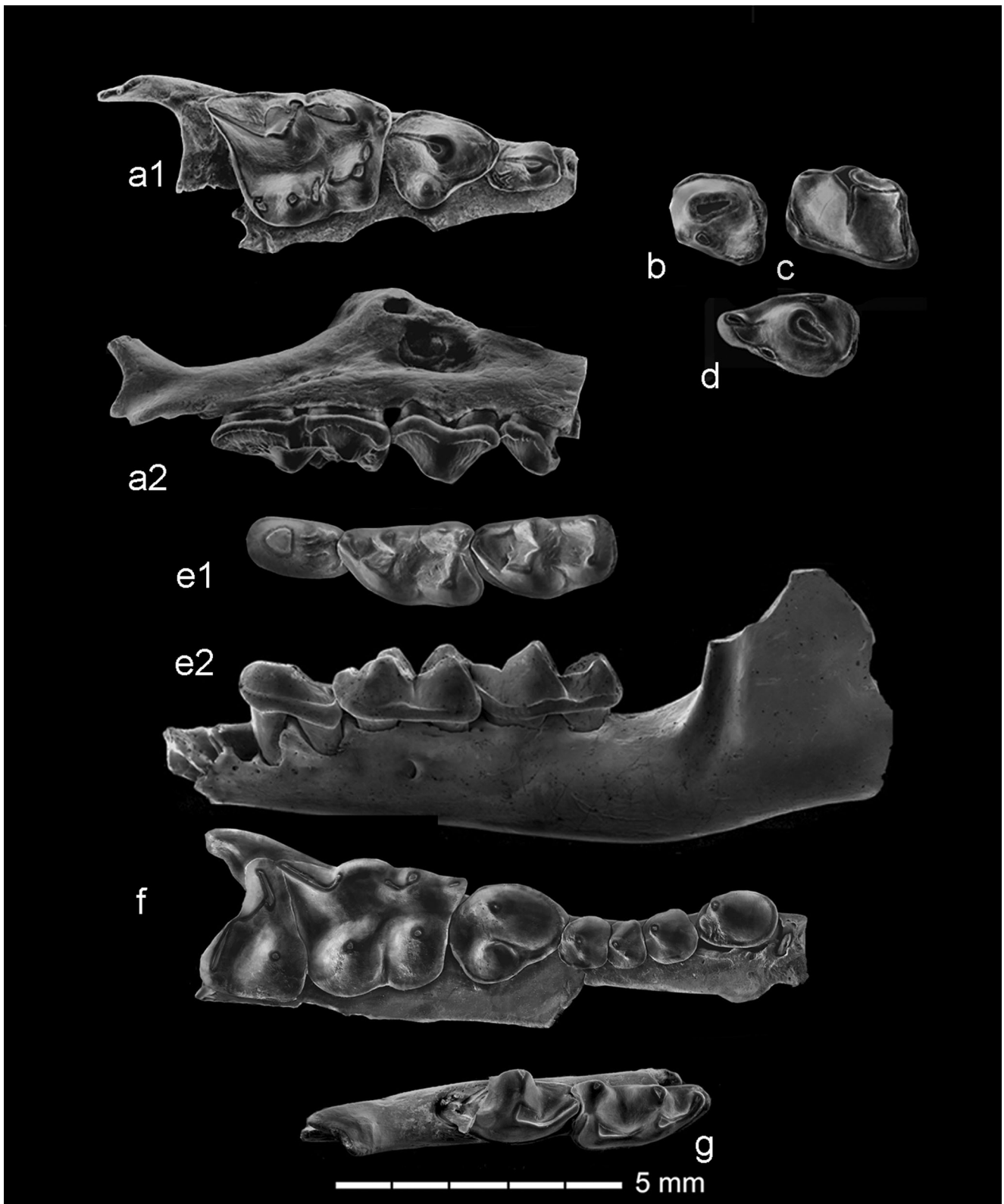


Fig. 2 Dimylidae from Ahnikov 1. **a–e** *Dimylus* aff. *paradoxus*: **a** Pv 10001, maxillary with P3, P4 and M1 dext. (**a1** occlusal view, **a2** labial view), **b** Pv 10002 d3 sin., **c** Pv 10003 d4 sin., **d** Pv 10004 D4 sin., **e** Pv 10005, mandibular tooth row with p4, m1 and m2 sin., e1 occlusal view,

e2 labial view. **f, g** *Plesiodimylus* sp.: **f** no number, maxillary with C-M3 dext, occlusal view, **g** Pv 10006, mandible with m1 and m2 (damaged) dext., occlusal view

Table 2 Measurements of the dentition of *Dimylus* aff. *paradoxus* from Ahníkov 1

Dental element	N	Length (mm)		Width (mm)	
		Range	Mean	Mean	Range
D4	1		1.81		1.54
P3	1		1.32		0.85
P4	3	1.92–2.09	2.00	1.43–1.70	1.58
M1	4	3.19–3.79	3.46	1.91–2.42	2.21
d3	1		2.53		1.59
d4	1		2.58		1.43
p4	3	1.76–1.84	1.80	1.04–1.15	1.10
m1	9	2.36–2.58	2.47	1.51–1.70	1.58
m2	12	2.25–2.69	2.53	1.21–1.54	1.41

small, round cusp at the anterior end. The cingulum is well developed on the posterior and anterolingual sides, but much weaker along the labial flank of the main cusp.

d4: The outline of the occlusal surface is sub-rectangular, the tooth being labially somewhat longer than lingually. The labial side is clearly lower than the lingual side. The tip of the main cusp lies in the middle of the d4, close to the lingual side. From the tip four ridges run in all directions, producing an irregular cross. The lingual ridge is short and curves slightly backwards. The anterior ridge connects to the front at about one-fourth the width of the molars. The posterior ridge is slightly curved and connects to the postero-lingual corner. The labial ridge curves somewhat backwards and ends near the labial border at about two-thirds the length of the molars. The d4 is surrounded by a cingulum, which is interrupted at the anterior side.

D4: The outline of the occlusal surface is sub-square. The posterior side is somewhat wider than the anterior side. The main cusp lies just in front of the centre of the tooth and has a backwards-directed wear facet. There is a well-developed cingulum on all sides of the milk molar except for the anterior side.

Remarks: The lineage *Dimylus paradoxus*–*Plesiodimylus huerzeleri*–*P. chantrei* is well recorded in southern Germany (Müller 1967; Ziegler 1990). Müller (1967, p. 37) extensively listed the differences between the various species. From this listing, it is clear that the Ahníkov species takes a somewhat intermediate position between *D. paradoxus* and *P. huerzeleri*. In the width/length ratio of the m1 (0.62–0.68), the Ahníkov species resembles *D. paradoxus*. Furthermore, as in typical *Dimylus* assemblages, the protoconid and metaconid stand well apart, and an entostylid is present, though relatively smaller. However, the m2 is longer than the m1 in all but one of nine specimens (m1/m2 length ratio varying between 0.91 and 1.05), a character that is considered typical for *Plesiodimylus*. *Plesiodimylus*-like characters in the M1 are

the straight posterior side, which is somewhat wider than the anterior side, the undivided mesostyle and the slightly protruding parastyle. By contrast, the protocone with two arms and somewhat larger than the hypocone and the double tip on the latter cusp are features found in *Dimylus*.

We have decided to classify the Ahníkov species as *Dimylus* rather than *Plesiodimylus*, because we feel that genera should be recognisable by easily identifiable characters. The wider m1 and the protocone of the M1 with arms which are rather ridge-shaped than blunt are easy to observe, even to the layman's eye. Although, from a morphological point of view, the Ahníkov 1 assemblage is clearly intermediate, biometrically it is not. The lineage *Dimylus*–*Plesiodimylus* is characterised by a slight size decrease. A comparison of our measurements with the scatter diagrams and measurements provided by Ziegler (1990: figs. 3, 4; table 6) shows that in size the Ahníkov *Dimylus* falls in the upper part or even above the variation of the German localities. The record from Ahníkov 1 is the youngest record of *Dimylus*, thereby extending the range of the genus into the early part of MN 3.

Plesiodimylus Gaillard, 1897

Plesiodimylus sp.

(Fig. 2f, g)

Material and measurements: one maxillary with P1–M2 (C=1.68×1.16; P1=1.04×1.10; P2=0.81×0.98; P3=1.10×1.04; P4=2.42×2.02; M1=3.81×2.77; M2=2.19×2.89); one mandible dext. with p4–m2 (p4=1.24×0.82; m1=2.25×1.26; m2=2.64×1.26); one mandible dext. with m1 and fragmentary m2 (m1=2.53×1.32)

Description

C: The outline of the occlusal surface is rectangular. The main cusp lies in the front of the canine, its tip is slightly inclined backwards. There is a low cusp in the posterolingual part of the tooth. The canine is surrounded by a well-developed cingulum.

P1–P3: The first three premolars are quite similar, with a sub-square outline. The P2 is the smallest of this series. The tip of the main cusp lies in the anterior part of the elements. The cingula are less well-defined than in the canine.

P4: The P4 is only somewhat longer than wide. The labial part of the premolar consists of the large paracone. In our hardly worn specimen, only a faint posterocrista can be discerned. The conical protocone is about half the length of the paracone, and clearly lower. The premolar is surrounded by a strong cingulum, which is slightly concave at the anterolingual side. At the posterior side, a small basin is bordered by the protocone, paracone and posterior cingulum.

M1: In our unworn specimen, the lingual cusps have a very conical appearance. Protocone and hypocone are of similar size. A faint ridge on the lingual side of the protocone betrays the direction of its anterior arm towards the valley separating parastyle and paracone. The parastyle is ridge-shaped, directed to the front and protrudes. The paracone is the smallest of the four main cusps. A mesostyle could not be discerned, but could perhaps develop with advanced wear. The long posterior arm of the metacone extends to the posterolabial corner of the molar. The posterior basin is bordered by a posterior cingulum.

M2: The outline of the occlusal surface is subtriangular. The large M2 is dominated by the conical protocone. In our unworn specimens, the position of the anterior arm is only indicated by a faint ridge directed towards the base of the paracone. The paracone and metacone form an undulating posterlabial ridge. A small thickening at the base of the metacone indicates the position of the hypocone, which is nearly completely incorporated into the metacone.

Mandible: The ramus horizontalis is slender. The foramen mentale lies in a shallow sulcus on the upper part of the ramus horizontalis below the middle of the m1. The ramus ascendens is positioned at a right angle to the ramus horizontalis.

p4: The outline of the occlusal surface is rectangular. The main cusp is very slender for a dimyloid, tri-faced, with crenulations on its posterior flank. The premolar is surrounded by a cingulum.

m1: The trigonid is somewhat longer than the talonid. The protoconid and metaconid appear as two rather small tips on the backwall of the trigonid. The paraconid is much lower and lies at the end of a long paralophid, anteriorly to the metaconid. The hypoconid and entoconid are triangular in cross-section and about the same size. There is no entostylid. A cingulum is present on the anterior, labial and posterior sides, with lingually a short stretch along the trigonid basin.

m2: The trigonid is clearly longer and somewhat wider than the talonid. The protoconid and metaconid are small tips on top of the trigonid posterior wall. The ridge connecting them is sharp, as is the paralophid. The paraconid is low and blade-like. It lies far to the front of the molar, lingually of its median. A shallow ridge borders the talonid basin. The molar is nearly completely surrounded by a cingulum, which is only missing on the lingual side of the talonid.

Remarks: The two mandibles of *Plesiodimylus* were initially interpreted as separate individuals, with an advanced morphology in the *Dimylus* assemblage. The general morphology of the molars is rather similar. However, the very slender p4 cannot possibly be connected to the much larger and heavier p4 of the *Dimylus*. Moreover, the two m1 are clearly narrower than those of *Dimylus* ($W/L=0.52–0.56$), and the m1/m2 ratio is much lower (0.85). The lower molars are less amblyodont than in *Dimylus*.

Morphologically, our M1 fits best with the morphotype I (*huerzeleri* type) of Klietmann et al. (2014). There are only two basins, a central and a posterior one, the parastyle is ridge-shaped and the cusps are rounded. It is, however, clearly larger than the *Plesiodimylus* finds from Petersbuch 28. Klietmann et al. (2014) clearly showed that morphological variability within the genus is large. For that reason, and considering the limited material available from Ahníkov 1, we deem it prudent not to assign the material to any known species.

Finding *Dimylus* and *Plesiodimylus* in the same locality is surprising, as the latter is generally considered to be a descendant of the first. A possible explanation would be that the two mandibles are an admixture of younger deposits. As the degree of fossilisation of the two specimens agrees well with those from the other fossils in the locality, we consider such a contamination an unlikely solution.

The transition from *Dimylus* to *Plesiodimylus* possibly took place in another part of the molasse basin. The high diversity of dimyloids in Central Europe certainly suggests that speciation could occur within the area. A theoretical objection against such a scenario would be that two such similar forms would be in strong competition, which is bound to lead to displacement of one or the other species. However, the co-occurrence of two species of *Plesiodimylus* is known from Belchatow A (Rzebik-Kowalska 1996), Petersbuch 31 (Ziegler 2005) and Devínska Nová Ves (Fejfar and Sabol 2009), showing that there is ecological room even for such similar forms among dimyloids. In this scenario, the large size of the *Plesiodimylus* could be explained by interspecific competition with the other, less specialised dimyloid in the assemblage.

Chainodus Ziegler, 1990

Chainodus intercedens (Müller, 1967)

(Fig. 3a–e)

Measurements: The measurements are listed in Table 3.

Description

M1: The metacone is by far the largest cusp. Its posterior arm bends just behind the tip and extends to the posterolabial corner. In contrast, the paracone is very small and hardly larger than the parastyle. The posterior arm of the paracone ends low against the anterolabial side of the metacone. The parastyle is a conical cusp. It does not protrude. The protocone is larger than the hypocone. Its anterior arm ends low against the parastyle. Its posterior arm bends lingually off the mesostyle and ends against the anterolabial corner of the hypocone. The latter cusp is conical, with an elliptical wear facet. It has a faint posterocrista, which continues as a low ridge along the slightly undulating posterior side. There is a narrow labial cingulum, and a small patch of lingual cingulum between the protocone and the hypocone.

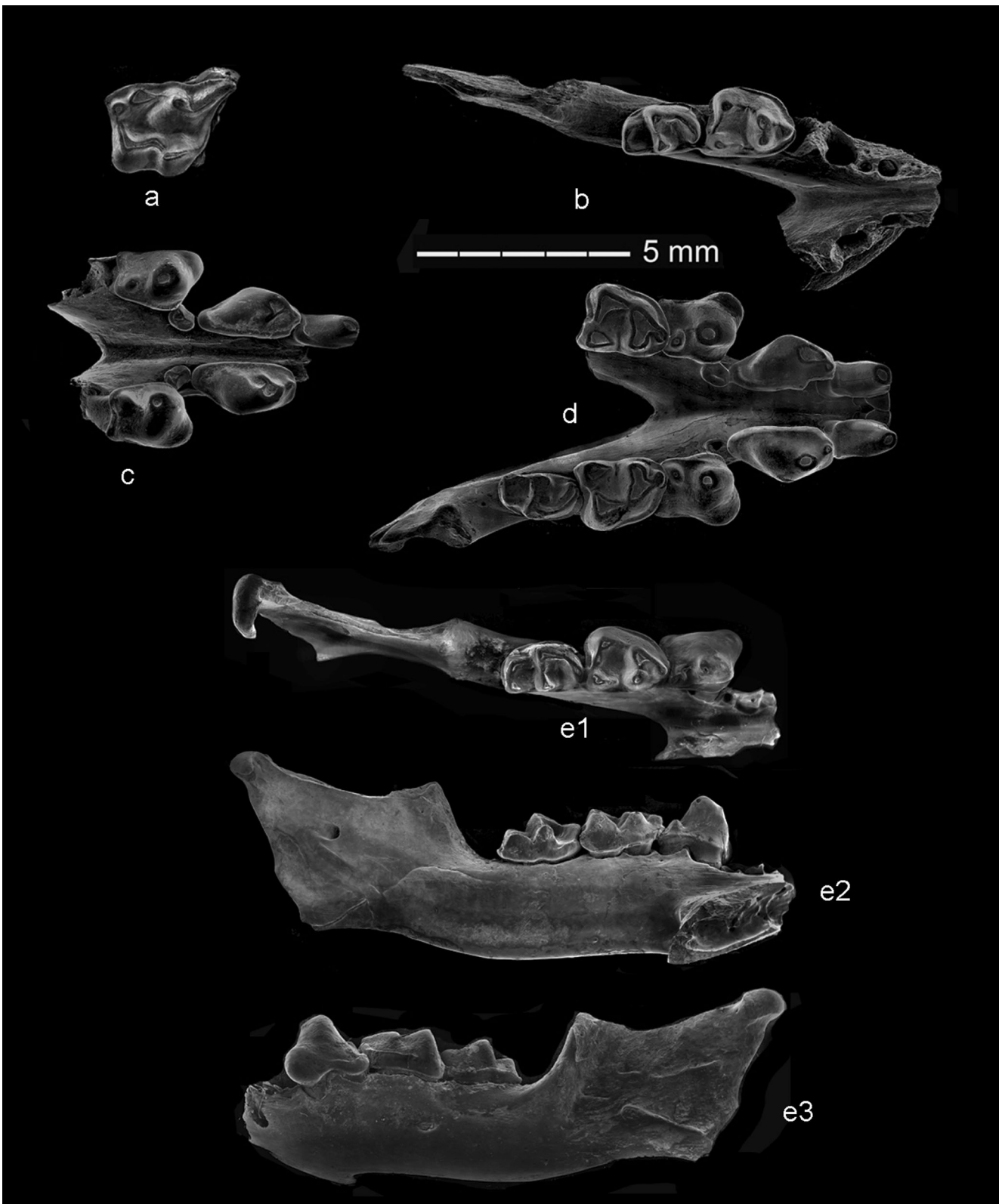


Fig. 3 Dimylidae from Ahníkov 1. *Chainodus intercedens*: **a** Pv 10007, M1 sin., **b** Pv 10008, lower jaw with m1 and m2 sin, **c** Pv 10009, lower jaw with c, p1, p3 and p4 dext. and p1, p3 and p4 sin., **d** Pv 10010, lower jaw with c, p1, p4, m1 and m2 dext. and c, p1, p3, p4 and m1 sin., **e** Pv 10011, lower jaw with p4-m2 sin. (**e1** occlusal view, **e2** lingual view, **e3** labial view)

Table 3 Measurements of the dentition of *Chainodus intercedens* from Ahníkov 1

Dental element	N	Length (mm)		Width (mm)	
		Range	Mean	Range	Mean
M1	1		2.80		2.14
c	1		1.43		0.88
p1	3	2.31–2.53	2.42	1.21–1.54	1.34
p3	2	0.55–0.63	0.59	0.49–0.55	0.52
p4	4	2.03–2.14	2.08	1.51–1.79	1.63
m1	8	2.03–2.28	2.13	1.54–1.79	1.63
m2	7	1.92–2.09	2.02	1.10–1.43	1.23

Mandible: The ramus horizontalis is quite sturdy. The only foramen mentale lies below the talonid of the m1. The symphysis is fully merged and reaches to the trigonid of the m1. A specimen which preserves the anterior left and right dentition shows a tiny alveole below the canine, indicating the presence of one incisor. The ramus ascendens stands at a slight angle to the ramus horizontalis. The fossa mandibularis is shallow. There are two conspicuous ridges in the lower part. The condyle is small and its end stands well above the tooth row.

c: The lower canine is procumbant. Its tip lies far to the front of the tooth. There is a sharp ridge at the front of the canine. The posterior face slants down and is bordered by a strong cingulum.

p1: The p1 is elongated with a straight lingual side and a rounded labial side. It has a single, bulbous cusp, with a wear facet on its anterolingual flank. In some specimens, this facet has a short, posterolingually direct spur. In front of the wear facet, a short ridge connects to the front of the premolar. There is a well-developed cingulum on the lingual and posterior sides.

p3: The p3 is a small and low element, somewhat longer than wide. A faint crest runs over its median, and halfway there is a short posterolingually directed off-shoot of this crest, which ends before reaching the lingual side.

p4: The outline of the occlusal surface is irregularly quadrangular due to the large anterolabial extension (“Vorderlappen” in the German literature). The main cusp lies in the anterolingual corner and is slightly inclined backwards. There is a small, comma-shaped cusplet in the posterolingual corner, with the tail of the comma connecting to the posterior side of the main cusp. There is a well-developed cingulum along the lingual and posterior sides. At its labial end, the posterior cingulum becomes ridge-shaped.

m1: The trigonid is much smaller than the talonid. The protoconid and metaconid stand close together and are the same height. The paraconid is much lower and smaller and lies in a median position. The hypoconid is bulbous; the entoconid is ridge-shaped. The oblique cristid ends low against the base of the protoconid. The talonid basin is closed by an entocristid which is merged with the entoconid. The

posterior cingulum is rather narrow. There is a lingual cingulum along the trigonid, which may or may not be interrupted at the paraconid before continuing as the labial cingulum. This cingulum ends at the base of the hypoconid.

m2: The trigonid is wider and longer than the talonid. In contrast to the m1, the protocone and metacone stand well apart. The paraconid is blade-like and totally incorporated in the long, curved paralophid. Oblique cristid, hypolophid and entocristid have merged into a ridge encircling the shallow talonid basin. The hypoconid and entoconid appear as elevations in this ridge. There is a narrow to well-developed cingulum, starting at the base of the protoconid and running along the anterior side until it tapers out at the base of the hypoconid. In one specimen, there is also a posterior cingulum.

Remarks: The genus *Chainodus* was introduced by Ziegler (1990). Rediscovery of the holotype of *Cordylodon haslachensis*, the type species of its genus, showed that some species were incorrectly attributed to *Cordylodon*. *Cordylodon intercedens* Müller, 1967 and *C. sulcatus* Stephan-Hartl, 1972 were certainly not related to *C. haslachensis*, leading to the proposal of a new name for these species. While doing so, Ziegler (1990) also introduced two new species for that genus, *Chainodus ulmensis* and *C. eggingensis*.

The p4, with its anterolabial extension is one of the typical characters of *Chainodus*. The only other genus with a similar p4 is *Metacordylodon*. Another typical feature of *Chainodus* is the presence of a similarly sized paracone and parastyle on the M1. These characters are also found in the Ahníkov dimyloid, making it clear the species is referable to *Chainodus*.

There can be no doubt regarding species identification. The form of *Chainodus intercedens* is quite different than that of the other species included in the genus. It does not have the strong reduction of the m2, and its molars are less bulbous (amblyodont). All other species are also larger than *C. intercedens*. In addition, Ziegler (1990) showed that *C. eggingensis* has a loose symphysis and assumed the same for *C. sulcatus* on the basis of a hemimandible imbedded in the sediment. In contrast, the symphysis of *C. intercedens* is fully joined, as is also clear from the new finds from Ahníkov. The symphysis of *C. ulmensis* is, unfortunately, unknown.

The dental formula implied in our descriptions (1.1.3.2) differs from that in the original diagnosis (2.1.2.2). The difference lies only in the interpretation of the large element which Müller (1967) still assumed to be the canine, but was subsequently shown by Schmidt-Kittler (1973) to represent the p1.

Lacrimodon nov. gen.

(Fig. 4a–e)

Derivatio nominis: The genus is named after its most characteristic element, the tear-shaped p4 (Lacrima=tear L., odous, odontos=tooth Gr.)

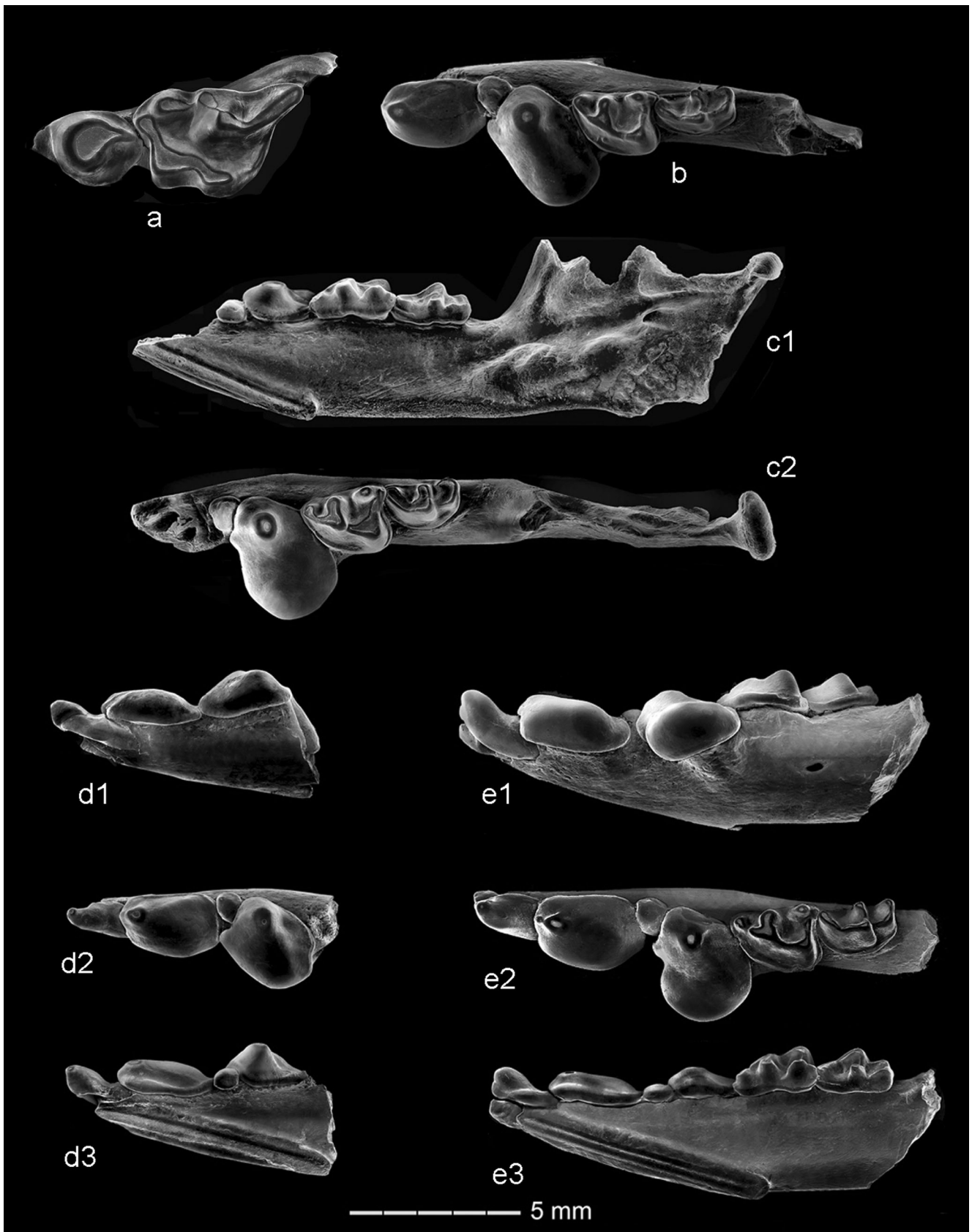


Fig. 4 Dimylidae from Ahnikov 1. *Lacrimodon vandermeuleni*: **a** Pv 10012, maxillary with P4, M1 sin., **b** Pv 10013, mandible with p1-m2 sin., **c** Pv 10014, mandible with p3-m2 sin. (**c1** lingual view, **c2** occlusal view), **d** Pv 10015, anterior part mandible with i1-p4 sin. (**c1** labial view, **c2** occlusal view, **c3** lingual view), **e** Pv 10016, mandible with i1-m2 sin. (holotype) (**e1** labial view, **e2** occlusal view, **e3** lingual view)

Table 4 Measurements of the dentition of *Lacrimodon vandermeuleni* nov. gen. nov. sp. from Ahníkov 1

Dental element	N	Length (mm)		Width (mm)	
		Range	Mean	Mean	Range
P4	1		1.81		1.55
M1	1		3.52		2.75
c	2	1.76–1.76	1.76	0.85–1.24	1.05
p1	8	2.53–3.13	2.87	1.65–1.98	1.82
p3	13	0.71–1.04	0.83	0.82–0.99	0.90
p4	32	2.53–3.74	3.01	2.03–2.86	2.40
m1	25	2.14–2.64	2.37	1.59–2.06	1.79
m2	22	1.98–2.47	2.24	1.15–1.48	1.32

Diagnosis: Medium-sized dimyloid ($m1 \approx 2.4$) characterised by a large posterolabial extension on the p4, supported by an outgrowth on the mandible. Lower dental formula 1.1.3.2, with a small p3. Molars are moderately amblyodont. The m2 is not very reduced ($m2/m1 \approx 0.95$). The P4 has no protocone. The lingual cusps of the M1 bear relatively sharp ridges. The symphysis is loose, long and bears a ridge-shaped structure.

Differential diagnosis: The large p4 with its posterolabial extension that is supported by a mandibular outgrowth distinguishes *Lacrimodon* from all known dimyloid genera. Moreover, *Lacrimodon* is the only dimyloid that lacks a protocone on the P4.

Type species: *Lacrimodon vandermeuleni*

Diagnosis: As *Lacrimodon* is monospecific, the diagnosis is the same as for the genus.

Derivatio nominis: The species is named in honour of our friend and colleague Albert van der Meulen.

Holotype: Pv 10016, ramus horizontalis sin. with the entire tooth row preserved ($c=1.76 \times 1.24$; $p1=2.86 \times 1.92$; $p3=0.88 \times 0.99$; $p4=2.75 \times 2.47$; $m1=2.47 \times 1.73$; $m2=2.17 \times 1.57$) (Fig. 4e).

Type locality: Ahníkov 1, Czech Republic (MN 3).

Measurements: The measurements are listed in Table 4.

Description

P4: The outline of the occlusal surface is sub-elliptical. The P4 consists almost completely of the large and bulbous paracone, which has a tear-shaped wear facet. In front of the paracone, there is a large flattening without the formation of a parastyle. A protocone is also absent. The lingual and posterolabial cingulums are bordered by low ridges.

M1: The metacone is the largest cusp, covering two-thirds of the length of the molar and over half its width. Its sharp ridges

produce a shallow V-shape, the tip of the cusp being placed in the anterior arm of the V. The anterior arm ends with a small thickening; the posterior arm extends to the posterolabial corner. The paracone is small. It has a short posterocrista which ends low against the anterior arm of the metacone, just lingually of the thickening at its end. The parastyle is a small conical cusp, positioned anterolingually of the paracone. It protrudes, causing a clear bulge in the anterior outline. The two arms of the protocone are sharp and stand roughly perpendicular to each other. The anterior arm connects to the posterolingual side of the parastyle. The posterior arm runs straight backwards. It connects to the anterior arm of the hypocone. The hypocone is somewhat smaller than the protocone. It is crescent-shaped, the anterior arm meeting with the posterior arm of the protocone, the posterior arm continuing as a posterior ridge which ends against the flank of the metastyle. There are no cingula.

Mandible: The ramus horizontalis is sturdy and strongly tapers to the front. It thickens slightly below the p1 and shows a marked outgrowth below the p4. The only foramen mentale lies below the m1/m2. The symphysis is loose. Along its length, it has a structure consisting of two parallel lines bordering a shallow groove within a somewhat rugose area. The symphysis reaches all the way up to below the trigonid of the m1. The ramus ascendens stands at a slight angle to the ramus horizontalis. The fossa mandibularis is deepest at its front. The rather small condyle lies just above the level of the tooth row, somewhat above the tips of the molars.

i1: The only incisor has a small, spade-shaped crown. The element is directed forward and lies underneath the canine so that the cutting edges of both elements are in line.

c: The crown of the canine starts underneath the front part of the p1 and is directed straight forward. Halfway along its length, it slopes up to form a slightly lingually inclined tip. The anterior edge of the c, from its tip downwards, is sharp.

p1: The first premolar is a very large, sub-elliptical element. The anterior part, where it partly overgrows the canine, is rather straight. The wear-facet lies close to the front edge in median position.

p3: The p3 is a small, lozenge-shaped element, which mainly seems to serve as a wedge between the p1 and p4.

p4: The p4 is characterised by its huge, drop-shaped posterolabial extension, which varies in size and shape. The wear-facet of the main cusp is situated on the anterolingual corner. An emargination is usually found just in front of this wear-facet, which holds the p3. At the back of the p4, along the part that is in contact with the m1, a low ridge is usually present. The p4 is partly supported by an outgrowth in the mandible. From the alveole pattern in an edentulous jaw it is clear that the p4 has four main roots, two of which have their alveoles in the outgrowth. A number of small alveoles are present which seem to belong to additional rootlets. In some specimens, such rootlets can indeed be observed.

m1: The outline of the occlusal surface is sub-triangular, with a rounded labial side. The trigonid is reduced. The protoconid and metaconid are of equal size and stand close together. The paraconid is lower and lies at the end of a long paralophid that is often interrupted. The hypocone is bulbous. The oblique cristid ends against the base of the protocone and lies in line with the paralophid. The hypolophid ends against the posterolabial side of the entoconid, or, when present, against the entostylid. The entoconid is blade-like and partly closes the talonid basin. On its posterior flank, it always shows a bulge, which in a number of specimens is developed into a true entostylid. There are cingulums on the labial and posterior sides. The labial cingulum may be interrupted at the base of the hypoconid.

m2: The outline of the occlusal surface is sub-rectangular. The trigonid is somewhat wider and about twice as long as the talonid. The protoconid is the largest cusp. The metaconid is somewhat lower and the paraconid is lower still. The latter cusp lies in the anterolingual corner of the m2. The protolophid is short and ends low against the metacone. The paralophid is long and curved. The talonid basin is bordered by the oblique cristid, hypolophid and entocristid; these three elements stand nearly perpendicular to one another. Only the entoconid is sometimes discernible as an elevation on this ridge. The labial cingulum is particularly pronounced along the base of the paralophid. In one specimen it ends at the base of the protoconid, but usually it runs to the posterolabial corner of the molar or continues as a weak posterior cingulum.

Remarks: The strong adaptations, which even involve additional support by a mandibular outgrowth, necessitate the description of a new genus. Given the amount of work done on Central European Dimylidae, it is somewhat surprising to find a new genus in a Czech locality. On the other hand, there are relatively few MN 3 localities known, and the one which would be closest to Ahníkov 1 in time, Stubersheim 3, has yielded very few dimylid remains (Ziegler 1990). The large collection from Wintershof-West, by contrast, has yielded ample fossils of Dimylidae (Müller 1967).

The relationships of the new form are unclear. The most plausible ancestor seems to be *Cordylodon*. This genus is known only from the type mandible of its type species, *C. haslachensis* from Haslach (Germany, MN 2; Ziegler 1990). *Cordylodon haslachensis* has the same dental formula as *Lacrimodon vandermeuleni*, a very small p3 and a mandible that tapers towards the front and has a loose symphysis. In contrast to *Lacrimodon*, all dental elements are neatly in a row, and the m2 is more reduced, in which it is more advanced than the Czech genus. However, the p4 is clearly enlarged and amblyodont, more so than, for example, in *Dimylus* and *Plesiodimylus*. Further enlargement with a sideways outgrowth would produce a dentition very similar to *Lacrimodon*.

Discussion and conclusion

The dimylid fauna from Ahníkov 1 contains four species: *Dimylus* aff. *paradoxus*, *Plesiodimylus* sp., *Chainodus intercedens* and *Lacrimodon vandermeuleni*. *L. vandermeuleni* is the most numerous dimylid from Ahníkov 1, making up more than 50 % of the assemblage. The species is represented by 38 mandibles and mandible fragments, whereas *Dimylus*, *Chainodus* and *Plesiodimylus* are represented by 13, ten and three specimens, respectively.

The evolutionary history of the Dimylidae is remarkable. On the one hand, it has produced some of the most bizarre dental morphologies in small mammals, with strongly amblyodont and exoedaenodont dentition. More importantly, however, most of the evolution took place in a restricted area and relatively short period of time. Well over 90 % of all dimylid fossils have been found in Central European localities, and most taxa are known from the early Miocene. The localities Lautern 2 (MN 1) and Ulm-Westtangente (MN 2) each have three species of the family (Ziegler 1990, 2006a; Ziegler and Werner 1994). Much of the evolution of the Dimylidae therefore seems to have taken place in the coastal areas of the western Paratethys. With four genera and an equal number of species, Ahníkov 1 has the highest recorded dimylid diversity. It is also the last time period that we see such a diversity. At MN 3 localities, such as Wintershof-West, Stubersheim and Petersbuch 28 (Ziegler 1990; Klietmann et al. 2014), only the genera *Plesiodimylus* and *Chainodus* are present.

The Ahníkov dimylids do not differ greatly in size, and the ecological differentiation is therefore mostly obtained by morphological disparity. This is best exemplified by the p4. *Plesiodimylus* sp. has an unspecialised, almost talpid-like p4. The last premolar in *Dimylus* is amblyodont and strong, but it does not have any extension. In *Chainodus*, the p4 has an anterolabial extension, whereas *Lacrimodon* is characterised by an extremely heavy p4 in which the extension is directed posterolabially. The latter two forms also differ markedly in terms of their symphysis, which is fully merged in *Chainodus* and loose in *Lacrimodon*. This construction must have had consequences on their feeding habits and, therefore, on their choice of prey.

Given the presumed palaeoenvironment of Ahníkov 1, it is not surprising that this locality holds the largest known diversity in Dimylidae. The facies itself, a lignite, is the first sign of humid surroundings, and Van den Hoek Ostende and Fejfar (2006) found that the most numerous mole was the desman *Mygalea magna*, confirming that conditions were indeed very wet. Such an environment would certainly support a rich malacofauna, presumably the main food source for Dimylidae. The loss of diversity towards the younger MN 3 localities suggests that conditions became less favourable, which led to the extinction of the specialised *Lacrimodon*.

The enormous number of dimylids in Peterbuch 28 suggests that conditions were once again more favourable at the end of MN 3, but at that time much of the disparity had been lost. Instead, we note here a high intraspecific variation in *Plesiodimylus* (Klietmann et al. 2014). A similar situation may have occurred in Devínska Nová Ves, where it even resulted in the presence of two *Plesiodimylus* species (Fejfar and Sabol 2009). The last stance of the family was in the early late Miocene of the Vallès-Penedès, when dimylids were again remarkably common (Casanovas-Vilar et al., research in progress). It can be no coincidence that this last period of relative bloom was again in a near-coastal basin. These were the areas where the family thrived and where it found the palustrine environments that provided an ample food source—conditions that also led to the all time high in dimylid diversity in Ahníkov 1.

Acknowledgements It is with the greatest pleasure that we dedicate this paper to Albert van der Meulen. Of course, this issue is there to honour his scientific achievements, but fond memories go beyond science, and in particular we remember the sound of his accordion, whether it was in the Lybian desert or during the field trips in his beloved Spain.

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