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One or two species? Revision of fossil martens from the late Early Pleistocene sites Deutsch Altenburg 2 and 4 (Austria)

Adrian Marciszak and Doris Nagel

ABSTRACT

Marten fossils from the Austrian sites Deutsch Altenburg 2 and 4 have been revisited. Despite the previous view on the possible occurrence of two marten species, *Martes* cf. *zibellina* and *Martes vetus*, only the presence of the latter has been confirmed. Previous identifications of marten remains as *M. zibellina* are considered to be related to sexual dimorphism characteristic for *M. vetus*. The well-preserved viscerocranium and mandibles found at Deutsch Altenburg 2 and 4 are important materials in the European fossil record of this species. The revised material of *M. vetus* from Deutsch Altenburg 2 and 4 was compared with fossils from other European Early and early Middle Pleistocene sites, which showed that the species has intermediate features shared with *M. martes, M. zibellina,* and *M. foina*.

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INTRODUCTION

The origin of the genus *Martes* Pinel, 1792, has been uncertain for a long time, although new findings have substantially improved our understanding of the evolution of martens (Flynn et al., 2005; Koepfli et al., 2008; Samuels et al., 2018). The earliest species that has been referred to the Guloninae is *Martes laevidens* Dehm, 1950, from the German site Wintershof West, dated to the early Miocene (MN 3, 20–17 Mya; Dehm, 1950, 1953). However, based on basicranial anatomy, mainly on the incompletely ossified supramental fossa, this assignment was questioned (Wolsan, 1993; Sato et al., 2003), and the feature was regarded as a plesiomorphic trait shared by different mustelids (Hughes, 2012). Among gulonines, the genus *Martes* has been consistently found to be the most closely related to the genus *Gulo* Pallas, 1780, and a sister group to *Pekania pennanti*

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(Erxleben, 1777) (Koepfli et al., 2008; Wolsan and Sato, 2010; Sato et al., 2012; Li et al, 2014; Malyarchuk et al., 2015; Zhu et al., 2016; Samuels et al., 2018). Koepfli et al. (2008) estimated the time when the Guloninae diverged from the mustelid branch at c. 11.0 Mya (12.5–9.4 Mya), while Sato et al. (2012) at c. 12.7 Mya (14.7–10.8 Mya). The study of mitochondrial genomes of gulonines showed that the *Martes–Gulo* clade diverged from *Pekania* around 7.6 Mya (8.9–7.1 Mya) (Li et al., 2014). The split between the genus *Martes* and the genus *Gulo* was assessed to have occurred 6.4–6.3 Mya (7.6–5.3 Mya) (Li et al., 2014), while Malyarchuk et al. (2015) suggested a time of 5.6 Mya (6.3–4.9 mya). These molecular estimates corroborate well with the earliest records of definite true gulonines from the late Miocene, i.e., *Pekania occulta* Samuels and Cavin, 2013, from North America and *Martes palaeosinensis* Zdansky, 1924, from Asia (Wang et al., 2012; Samuels and Cavin, 2013). According to them, true martens from the genus *Martes* appeared even later, c. 4.2–4.0 Mya (Stach, 1959; Wolsan, 1989b; Anderson, 1994; Sato et al., 2003; Montoya et al., 2011).

The Middle–Late Miocene history of possible ancestors of the genus *Martes* is full of marten-like species and forms, often of debatable and unclear taxonomical position (Anderson, 1994; Baskin, 1998; Ginsburg, 1999; Hughes, 2012). Some of these forms show morphological features closely related to those in the Guloninae, but many others represent stem groups outside of the crown clade Guloninae (Anderson, 1994; Sato et al., 2003; Wang et al., 2012; Li et al., 2014). In addition, some of these *Martes*-like mustelids show some similarity to the ischyrictines (Ginsburg and Morales, 1992; Montoya et al., 2011) or even have been referred to the ischyrictine genera *Hoplictis* Ginsburg, 1961, *Plionictis* Matthew, 1924, and *Sthenictis* Peterson, 1910 (Anderson, 1994; Baskin, 1998; Hughes, 2012; Samuels and Cavin, 2013; Samuels et al., 2018). Morphological similarities of these *Martes*-like mustelids with members of the Guloninae are likely the result of their ecomorphological convergence or retention of plesiomorphic traits (Samuels et al., 2018). Considering the high level of polymorphism observed in these early taxa, comparable with the highly polymorphic dentition of extant taxa and the scarcity of fossil materials, a detailed revision is needed to fully understand their taxonomic position (Samuels et al., 2018).

It is debatable whether the early Late Miocene (MN 9–10) *Martes melibulla* Petter, 1963, or Late Pliocene (MN 15) *Martes wenzensis* Stach, 1959, is the first true *Martes* (Valenciano, 2017; Valenciano et al., 2020, 2021). Contrary to the Miocene, the Eurasian Pliocene history of the genus is considerably poorly documented. Since Stach's (1959) description, *M. wenzensis* has been regarded as the only European Pliocene marten (Anderson, 1970; Marciszak et al., 2024). The Early to the mid-Middle Pleistocene Eurasian martens are represented by *M. vetus* Kretzoi, 1942 (2.2–0.6 Mya; Heller, 1930, 1933, 1936; Brunner, 1933; Kretzoi, 1942, 1945; Dehm, 1962; Kurtén, 1968; Anderson, 1970; Wiszniowska, 1989; Ambros et al., 2005; Ambros, 2006; Marciszak, 2012; Marciszak et al., 2021, 2024) and *M. crassidens* Jiangzuo, Gimranov, Liu, Liu, Jin and Liu, 2021 (2.2–1.7 Mya; Jiangzuo et al., 2021). Although most authors tentatively interpret *M. wenzensis* as the most likely ancestor of the *Martes* lineage. The main goal of this paper is to revise old and to describe new materials of *M. vetus* from the famous paleontological site Deutsch Altenburg (Austria), the only Early Pleistocene site with marten fossils in Europe. The finds from this locality shed new light on the late Early Pleistocene evolution of the genus *Martes* and the relation of *M. vetus* with *M. martes* (Linnaeus, 1758) and *M. foina* (Erxleben, 1777). The article also tests the assumption about the hypothetical presence of a second European marten species, *M. zibellina*.

MATERIALS AND METHODS

All studied materials of *Martes vetus* are housed in the Department of Paleontology, University of Vienna, Austria. Measurements were taken with an electronic calliper to the nearest 0.01 mm, according to the schemes presented in Appendix 1 (Figures S1–S3). Each value given here is the mean of three measurements. Measurements were also taken using an Olympus set for image analysis (Olympus stereo microscope ZSX 12, Olympus DP 71 camera, and Cell D software). This set coupled with a Canon EOS 5D camera was also used to take photographs. The dental terminology and tooth morphotypes follow Anderson (1970) and Gimranov and Kosintsev (2015). For comparison, materials from the following sites were used (unless otherwise noted, measurements were made personally by A.M.): Kamyk (1.9–1.8 Mya), Schernfeld (1.9–1.6 Mya), Żabia Cave (1.7–1.5 Mya), Kielniki 1 (1.3–1.1 Mya), Zalesiaki 1A (1.3–1.1 Mya), Somssich Hill 2 (1.1–1.0 Mya; Gasparik and Pazonyi, 2018), Stránská Skála (0.9–0.8 Mya), Kozi Grzbiet (0.8–0.7 Mya), and Południowa Cave (0.8–0.7 Mya).

The site complex Deutsch Altenburg is located in the Hollitzer quarry (Pfaffenberg, the western foothill of the Hainburger Berge), where Mesozoic dolomites have been mined (Figure 1; Frank and Rabeder, 1997a, 1997b). It is near the Austrian–Slovak border (Bruck an der Leitha district, Lower Austria) (Figure 1). The first site discovered in 1900 was the Middle Pleistocene locality Deutsch Altenburg 1 (Toula, 1902, 1906; Freudenberg, 1914; Nagel and Rabeder, 1997). In 1908–1984, numerous crevices and caves were exposed during blasting (Pfeiffer-Deml, 2016). As a result, 52 localities were excavated in the quarry, each being referred to in chronological order of their discovery (Frank and Rabeder, 1997a, 1997b).

The most well-known site, Deutsch Altenburg 2 (DA2; 48°9'10" N, 16°55'2" E, c. 255 m a.s.l.), was discovered in 1971. The uppermost layers contain mostly microvertebrate remains (layer DA2A). Located below are brown coarse sands (layer DA2C). Layer DA2C1 consists of light brown grit interstratified with dolomite rubble and sandstone concretions. It is covered by sandstone slabs. The sands are of fluviatile origin and were probably sedimented by a precursor of the Danube. The karst cavity of the DA2C1 was connected to a wide shaft, which once passed the connection to the former surface of the Pfaffenberg. The shaft was filled mainly with rubble and blocks. Between them, partly hardened clay lenses were intercalated, which contained abundant molluscs and vertebrates. It consists also of fluviatile sand, which probably was delivered by the precursor of the Danube. The shaft was named Deutsch Altenburg 4 (280 m a.s.l.) and the clay deposits in the rubble were named layer DA4B. The *Martes vetus* remains analyzed in the paper were found in two horizons, DA2C1 and DA4B, which probably belonged to the same cave system. Previously it was connected to the surface of Pfaffenberg by a shaft of about 40 m wide (Rabeder et al., 2010).

Biochronological analysis of micromammals, mostly rodents, allow the age of the DA2C1 horizon to be estimated as 1.3–1.2 Mya (Rabeder et al., 2010). The dominance of the genus *Microtus* (*"Allophaiomys"*-horizon) with the basal species *Mimomys pliocaenicus* Forsyth-Major, 1902, but also other arvicolids such as *Lagurus arankae* Kretzoi, 1954, *Prolagurus pannonicus* Kormos, 1930, *Mimomys coelodus* Kretzoi, 1954, *Mimomys savini* Hinton, 1910, *Clethrionomys hintonianus* Kretzoi, 1958, *Pliomys episcopalis* Méhely, 1914, and *Ungaromys nanus* Kormos, 1932, stratigraphically position DA2C very well into the *Microtus pliocaenicus* zone (Table S1 in Appendix 1; Rabeder, 1976, 1981; Rabeder et al., 2010). The layer DA4B

FIGURE 1. Location of the Deutsch Altenburg site complex in the territory of Austria.

is younger by one *Microtus* zone and is estimated at about 1.1–1.0 Mya (Table S1 in Appendix 1; Rabeder, 1981; Rabeder et al., 2010).

In DA2C, 98 vertebrate taxa were identified, including seven amphibians, 11 reptiles, four birds, and 76 mammals. The latter are represented by 14 insectivorans, 18 bats, 21 rodents, two lagomorphs, 15 carnivorans, one proboscidean, two perissodactyls, two artiodactyls, and one primate. From DA4B, remains of 98 vertebrate taxa were identified, including four amphibians, 12 reptiles, 15 birds, and 67 mammals. The latter are represented by 10 insectivorans, 13 bats, 25 rodents, two lagomorphs, 12 carnivorans, one proboscidean, two perissodactyls, one artiodactyl, and one primate (Table S1 in Appendix 1; Ehrenberg, 1929; Mais, 1971, 1973, 1978; Rabeder, 1972a, 1972b, 1972c, 1973a, 1973b, 1974a, 1974b, 1974c, 1976, 1978, 1981, 1982; Mais and Rabeder, 1977a, 1977b, 1979, 1984, 1997; Jánossy, 1981; Fladerer, 1984; Frank and Rabeder, 1997a, 1977b; Sapper, 1997; Rabeder and Withalm, 2006; Rabeder et al., 2010).

SYSTEMATIC PALEONTOLOGY

Class MAMMALIA Linnaeus, 1758
Order CARNIVORA Bowdich, 1821
Suborder CANIFORMIA Kretzoi, 1943
Infraorder ARCTOIDEA Flower, 1869
Parvorder MUSTELIDA Tedford, 1976
Superfamily MUSTELOIDEA Fischer, 1817
Family MUSTELIDAE Fischer, 1817
Genus *MARTES* Pinel, 1792
Martes vetus Kretzoi, 1942
Figures 2–7; Tables 1–3

Material. *Deutsch Altenburg 2C*: a viscerocranium with a small part of the left neurocranium and preserved left I1, I3, C1, P2–P4, and right I1–M1; right P4; three M1 (2 left, 1 right); a left mandible without most of the ramus and present i3–m2; a right mandible without the ramus, with c1, p2–m3, and m1 (DA/2275/14/77); a right complete mandible with i3–c1 and p2–m2; a right c1; two trigonids, of the left and right m1. *Deutsch Altenburg 4B*: a left mandible with missing symphyseal part and with p2 and p4; a right mandibular body fragment with m1.

Emended diagnosis. Marten of about the size of *Martes martes* and *M. foina;* cranium with a short and broad viscerocranium; broad incisor row moderately extended forward; moderately convex frontal profile with gently marked concavity in the middle part; compressed, short, and broad temporal region with a broad and short postorbital bar situated almost exactly in the middle of the temporal region; large, inflated, and strongly convex tympanic bullae; short and broad palate, especially in its distal part; V-shaped and convex median indentation of palate; C1 with broad and short crown; large and oval P1; narrow P2; narrow P3 with weakly marked convex margin; P4 with short and low protocone, whose length is smaller than the distal breadth of P4; M1 with trigon length slightly greater than the talon length, highly complicated microrelief on the occlusal surface and moderately large metacone; mandible with a long and slim body, gently convex mandibular lower margin under m1 and vertical edges of the ramus; triangular and shallow masseteric fossa; moderately spaced mental foramens; large p1; m1 with a short trigonid and small metaconid; oval m2; postcranial bones morphologically resembling those of *M. martes.*

Description. The viscerocranium is short and wide, with a well-marked broadening at the level of canines and P4. The frontal profile in lateral view is moderately convex, with a well-marked concavity in the middle of the frontal part. The frontal line runs somewhat mesially to the nasal bones and depresses slightly on the boundary between the cerebral and facial areas. The muzzle area is broadened at the canines, narrowed behind them, and then gradually widened (Table 1). The rostral area is proportionally short and massive. The nasal aperture is large and rounded, and the nasal bones are broad, short, and W-shaped. The oval and large orbits have minute lacrimal processes. The infraorbital foramina are large and oval. The upper tooth row is curved distally. The teeth are loosely arranged with short diastemas between I3 and C1, P1 and P2, and P2 and P3; the longest one is between I3 and C1. The broad and curved incisor row is moderately extended forward (Figure 2).

The simple build I1 is relatively short mesiodistally and moderately developed bucco-lingually. The crown is asymmetric, and its main axis runs obliquely from the upper-lingual to the lower-buccal side. The apex of the crown is oriented mesio-buccally and forms an asymmetric triangle. The mesial edge is larger than the distal one. The mesial valley between them is V-shaped, shallow, and both edges are connected to each other. The I2 has a massive and compact crown with a tip directed distally and slightly buccally. The buccal part of the crown is concave and separated from the convex lingual side by a thin and V-shaped cingulum, almost evenly developed mesially and distally. The large, canine-like I3 has a crown placed at an

FIGURE 2. Skull of *Martes vetus* from Deutsch Altenburg 2AC. **A**, left view. **B**, ventral view. **C**, right view. **D**, dorsal view. Scale bar is 10 mm.

angle of 40° to the root axis. The crown, ovoid or oval in cross-section, is also flattened on both sides, especially on the lingual side. The top of the crown is twisted disto-lingually. Two edges extend from it, mesial and distal, which at the base of the crown connect with the moderately developed lingual cingulum, forming a thin ridge around the crown. The C1 are flattened laterally and relatively short mesio-distally; weak mesial and distal crests run from their apex to the base. The oval-shaped P1 is a small, monocuspid, single-rooted tooth. Its buccal and lingual margins are convex, and the lingual one is developed more strongly.

The P2 is an elongated tooth, with a stronger distal cingulum. The buccal margin is straight, and the lingual margin is slightly convex in its middle part. The mesial and distal margins are blunt. The protoconid is situated more mesially. Two thin edges run from the apex of the protoconid, the mesial one in a mesio-lingual direction. The distal edge ends exactly medially and is connected with the distal cingulum. The P3 is elongated and narrow. The crown bears an elongated distal cingular projection. The small mesio-buccal prominence of the cingulum forms a faint mesial crest to the apex of the protoconid. This main cusp is located medially and slightly mesially. The two edges running from the apex of the protoconid are thick and sharp. The distal one is not connected with the distal cingulum, and its end forms a small, swelling-like bulge. The cingulum is weakly developed on the lingual side. The mesial and distal margins are blunt or rounded, while the buccal margin bears a moderately developed, median concavity. There is a moderate convexity at the same level, but on the lingual margin.

The long and narrow P4 has straight buccal and lingual margins of the talon. The mesial and

TABLE 1. Measurements of *Martes vetus* cranium from Deutsch Altenburg 2.

Measurements	9	10	13	14	15	21	27	28	34
Value (mm)	33.36	20.16	8.24	14.94	23.94	21.94	10.62	8.62	19.94

FIGURE 3. Mandibles of *Martes vetus* from Deutsch Altenburg 2AC. **A**, right mandible. **B**, left mandible. **C**, right mandible. 1, buccal view; 2, lingual view; 3, occlusal view. Scale bar is 10 mm.

distal margins are blunt or rounded. The moderately high paracone bears a thin crest across the mesial border from the apex to the base of the crown. It is separated from the moderately long and low protocone, whose mesial margin is aligned with that of the paracone. Its length is, on average, smaller than the distal breadth of the crown (Table 2). The metacone is separated from the paracone by a deep valley. The cingulum is more strongly developed on the lingual margin of the metacone. The M1 is large, its breadth is smaller than the length of P4 (Table 2). The trigon is moderately wide and short, with a moderate and abrupt concavity of the buccal margin. The paracone and the

TABLE 2. Measurements (mm) of *Martes vetus* upper dentition from Deutsch Altenburg 2 and 4.

		1	2	3	4	5	6
I1	L	1.92	1.88				
	B	1.14	1.04				
I2	L		2.04				
	B		1.17				
I3	L	2.67	2.74				
	B	1.49	1.69				
C1	L	4.58	4.66				
	B	3.16	3.27				
P1	L		2.74				
	B		1.91				
P2	L	4.32	4.32				
	B	2.23	2.24				
P3	L	5.09	5.08				
	B	2.58	2.56				
P4	L	7.49	7.59	7.54			
	L pr	2.56	2.79	2.84			
	Ba	4.68	4.74	4.43			
	Bp	2.66	2.89	2.88			
M1	B		7.33		7.44	7.78	7.68
	L tr		5.24		5.39	5.94	5.88
	L ta		4.27		4.39	4.52	4.46

metacone are elongated and well developed; the paracone is larger. They are well separated by a deep, narrow, V-shaped valley. Apexes of both main cusps are connected by a thin, long crest. The talon is shorter than the trigon and they are separated by a deep and broad depression running through the middle part of the crown. The protocone is low and long. It is divided by a shallow and wide valley into two parts of similar length and height. The reduced metaconule is not connected with any other cusp or crest, and is a low, elongated cuspid situated in the middle part of the crown. A long and thin crest corresponding to the buccal margin of the cingulum runs in parallel along the whole talon length. The well-developed lingual cingulum forms a thick crest.

The mandibular body is long and moderately high (Figure 3). Its height measured behind the m1 is comparable to the m1 length (Table 3). Two rounded mental foramens are moderately spaced and similar in size. The mesial one is situated under the p2, while the distal mental foramen is located under the distal root of p3, slightly lower than the mesial one (Figure 3). The masseteric fossa is moderately deep and its rounded, mesial edge reaches the m1 and m2 boundary. The mesial part narrows dorso-ventrally and its ventral margin only slightly exceeds the midline of the mandibular body in dorso-ventral direction. The lover mandibular body margin forms a gently curved arch, uniformly domed mesially and distally, with the strongest curvature under m1. The symphysial part is moderately massive and elongated. The row of cheek teeth is almost straight and only the distal parts of the p2–p3 crowns moderately arch lingually. In the tooth row, the premolars are located more buccaly in relation to the molars. As a result, the lingual margin of the p4 is displaced more buccally relative to the lingual border of the m1 (Figure 3).

The premolars are loosely arranged with diastemas between c1 and p1, p2 and p3, and p3 and p4. All teeth are situated at a similar level. The triangular crown of the i3 is double cusped, with the main protoconid occupying a larger surface. It is slightly asymmetrical, being more developed on the lingual side. Its vertical top is massive and rather blunt. The distoconid, located laterally to it on the buccal side, has the top of the crown directed slightly disto-buccally. It is a well-developed cuspid, although its shape and size are subject to considerable variability. It is separated from the protoconid by a thin and deep medial notch running almost to the base of the crown, which, in fact, divides the crown into two parts. The c1 is long and robust, with a proportionally short and hook-shaped crown (Figure 3; Table 3).

Two longitudinal grooves run on the buccal and lingual sides of the c1 crown. The relatively large and weakly reduced p1 is an oval, small, and one-rooted tooth. It is tightly squeezed between c1 and p2. Contrary to other premolars, the axis of its crown runs in an arrangement from mesio-lingual to bucco-distal. The two-rooted p2 is low-crowned, with the protoconid strongly displaced mesially. Its occlusal outline is almost rectangular, with an elongated distal part. Two thin crests run in the mesial and distal direction from the top of the protoconid. The distal cingulum forms a thin ridge, collaring the smooth area in the distal part. The mesial part of the crown is longer than the distal one. It bears an elongated distal cingular projection. The mesial and distal margins are blunt, while the buccal and lingual margins are almost straight. The larger p3 has a similar outline in occlusal view, with straight buccal and lingual margins. The mesial and distal margins are blunt. The protoconid is also displaced mesio-medially, although to a lesser degree than in p2. The distal part of p3 is shorter than the mesial one. An elongated distal, cingular projection is oriented slightly disto-buccally. Two thin edges run from the apex of the protoconid. On the distal edge, a small tubercular convexity is present just behind the top. The mesial and distal cingulum are relatively strongly developed. The two-rooted p4 is relatively high-crowned and has the protoconid placed almost exactly centrally and pushed slightly mesially. A relatively large hypoconid is present behind the protoconid. It is associated with the distal crest, running distally from the apex of the protoconid. The mesial ridge is thinner than the distal one. The mesial and distal halves of the tooth are equal in length. The mesial part is narrower than the distal one. The crown is slightly broadened distally. There is a gentle lingual convexity in the middle part of the crown. The lingual margin is straight. The mesial margin is blunt, while the distal one is rounded. The mesial and distal cingulum are relatively strongly developed. The distal, cingular projection is less elongated compared to the rest of the crown. Collared by a thick cingulum, the inner surface of this projection is crescent-shaped and shallow.

The elongated and large m1 has a proportionally short and massive trigonid with a low paraconid and high protoconid. The long and low talonid is similar in breath to the trigonid. The medium-sized, but well-recognized metaconid is connected

TABLE 3. Measurements (mm) of *Martes vetus* mandibles and lower dentition from Deutsch Altenburg 2 and 4.

		1	**2**	**3**	**4**	**5**	**6**	**7**	**8**
mandible	1					51.97			
	2					50.51			
	3				35.16	31.02			
	4				33.68	33.62			
	5		26.45		28.51	27.71			
	6	15.67	16.17		17.04	16.54	16.23		
	7		10.94		11.64	11.39			
	8	5.44	4.02		5.23	5.22			
	9					17.76			
	10					21.87			
	11					24.81			
	12	6.97	7.62		7.44	7.66			
	13	4.08	3.36		3.78	3.54			
	14	8.16	7.49		8.62	9.22			
	15	3.24	3.41		3.42	3.38			
	16								
	17								
	18	5.84			6.25	6.38			
	19	13.66			14.57	14.33			
i3	L				1.62	1.68			
	B				1.64	1.57			
c1	L				5.04	5.27	5.02	4.52	
	B				3.78	3.69	3.38	3.11	
p1	L				2.27				
	B				1.54				
p2	L	4.62			4.39	4.24	4.06		
	B	2.34			2.27	2.32	2.16		
p3	L				4.94	4.89	4.65		
	B				2.51	2.47	2.35		
p4	L	5.86			5.56	5.67			
	B	2.54			2.66	2.71			
m1	L		7.97		8.78	8.37	8.47		
	L tr		5.24	5.91	5.65	5.61	5.48		6.54
	L ta								
	B tr		3.14	3.61	3.54	3.56	3.59		3.54
	B ta		3.24		3.53	3.69	3.69		
m2	L				3.16	3.14			
	B				2.78	2.84			

with the protoconid. A thin, longitudinal ridge surrounds the talonid field, ends on the metaconid base, and runs from the elongated and low hypoconid. The edge of the paraconid is weakly developed. The mesial margin is rounded, while the distal one is blunt. The buccal margin is almost straight, with a gentle concavity at the transition between the trigonid and talonid. The lingual margin of the paraconid and half of the protoconid is straight, while there is a moderate convexity more distally. The cingulum is moderately developed. The m2 is a moderately reduced, one-rooted tooth. The crown has a slightly irregular, rounded occlusal outline, with a length slightly exceeding the

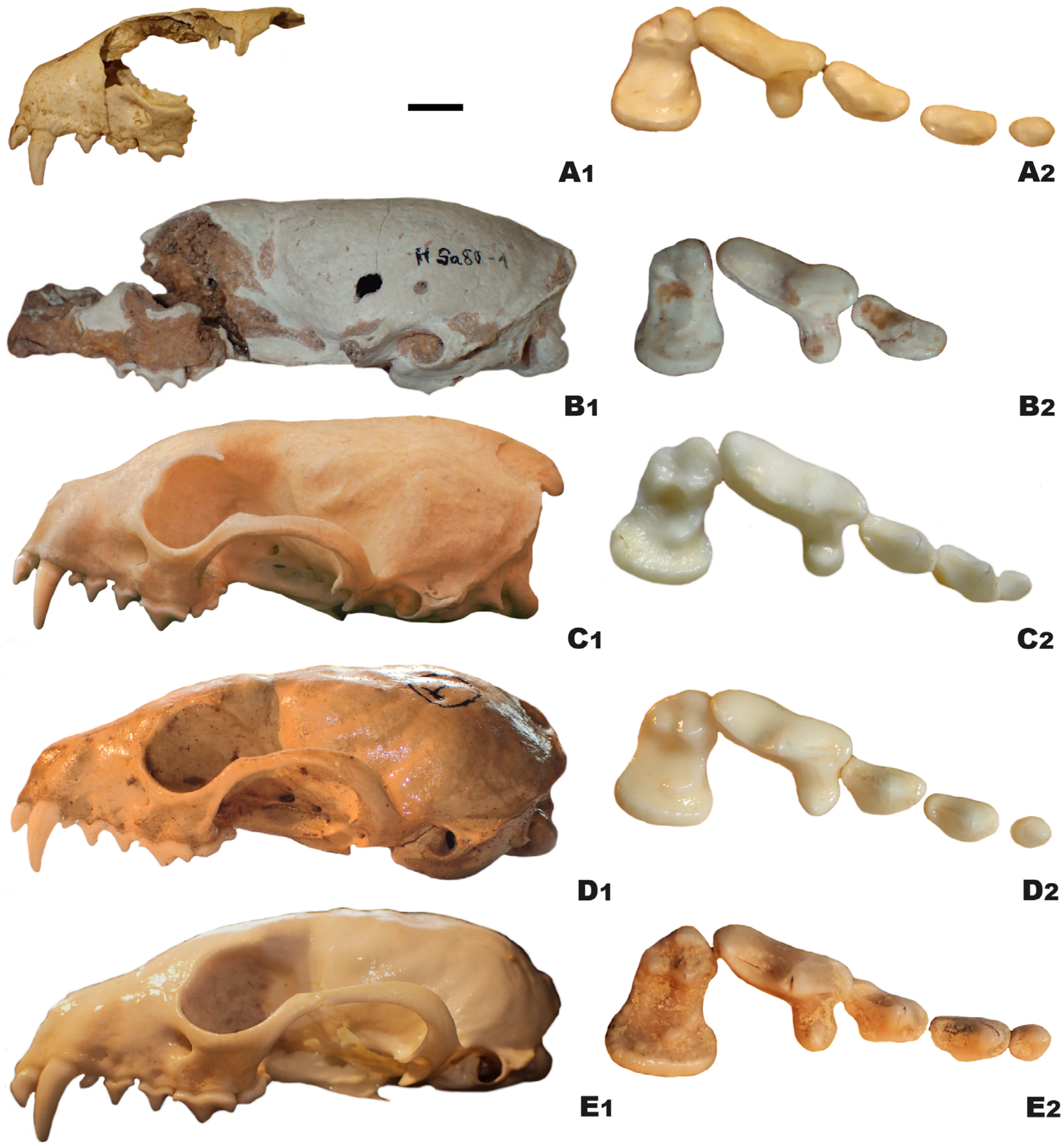

FIGURE 4. Comparison of the morphology of the skull (1) and upper dentition (2) of European martens: **A**, *Martes vetus* (Deutsch Altenburg 2AC). **B**, *Martes vetus* (Sackdilling Cave). **C**, extant *Martes foina*. **D**, extant *Martes zibellina*. **E**, extant *Martes martes*. All individuals are drawn on the same scale; skulls are shown in lateral view; dentition is shown in occlusal view. Scale bar is 10 mm for skulls and 4 mm for dentition.

breadth. On the trigonid are located the large and low paraconid and protoconid. The larger paraconid is located mesio-buccaly, while the smaller, but not lower protoconid is situated medially and lingually. The talonid is narrower, with a conical and low hypoconid. The moderately developed cingulum is stronger only on the distal margin.

Comparison. Being the same metrically, the DA2 marten morphologically differs more from *Martes martes* than from *M. foina.* The viscerocranium is short and broad as in *M. foina,* with a broad and less extended forward incisor row. In lateral view, the frontal profile is weakly convex, with a slightly marked crossing between the maxillae and frontal region (Figure 4). In *M. martes,* the rostrum is proportionally longer and narrower, with a similarly less marked widening of the facial part at the level of canines.

No particular differences were found in the morphology of the upper incisors and canines. The C1 of all three marten species are comparable dimensionally, where males are larger than females. On average, the C1 of *Martes vetus* is slightly more robust, but the ranges of variation strongly overlap. Morphologically, the C1 of *M. vetus* is characterised by a more curved, shorter and wider crown, which resembles more the C1 of *M. foina* than the more elongated and narrower C1 of *M. martes.* The right P1 of the DA2C marten measured 2.74 mm, which falls well into the range of variability of *M. vetus* (2.69 mm, 2.46–2.94 mm, n = 13) and *M. martes* (2.59 mm, 2.29–3.21 mm, n = 129), but distinctly exceed values obtained for *M. foina* (1.97 mm, 1.78–2.49 mm, n = 114). The P1 of *M. vetus* is not only larger, but also more robust, and the B/L index for this species is 68.5 (62.4–72.8, n = 13) compared to 69.7 in the DA2 marten. The P1 of *M. martes* is even more massive (71.9, 66.4–77.8, n = 129), while that of *M. foina* is notably narrower and more reduced (55.6, 52.9–64.3, n = 114). The P3 of *M. vetus* is similar to that of *M. foina* in having a narrow crown, with a weakly-marked convex margin (Figure 4). The P3 B/L mean ratio for *M. vetus* (48.7) is similar to that of *M. foina* (47.7). Morphotype A1, which is characteristic for *M. foina* (97%), without the lingual bulge, occurs also in the DA2 marten. This morphotype rarely occurs in *M. martes* (19%), for which the morphotype A2 is the most typical, with a small to moderate lingual bulge (73%). This species possesses much broader P3 (B/L = 62.4), which is consistent with the strongly developed lingual convexity.

The P4 of the DA2 marten is moderately long and low, and it is slightly shorter than the distal breadth of the crown (Figure 4). The protocone length to the distal breadth (L pr/Bp) index in the DA2 specimens (97.1, 96.2–98.6, n = 3) corresponds well with the data obtained for *Martes vetus* (94.5). *Martes foina* has distinctly shorter protocone (80.8), while its length in *M. martes* exceeds the distal breadth of P4 (L pr/Bp = 105.7). The P4 of the DA2 marten represents morphotype A2, with a notch between the protocone and parastyle, non-protruding protocone, and a concave buccal outline. This morphotype often occurs in *M. foina* (33%) and *M. martes* (24%). The P4 from the Sackdilling holotype belong to morphotype A1, with a notch between the protocone and parastyle, the protocone being shifted mesialy to the parastyle, and a concave buccal outline (Marciszak et al., 2021). This is also the most common morphotype in extant martens (58% in both). Other morphotypes are much rarer (Gimranov and Kosintsev, 2015).

The M1 of the DA2 marten has a relatively wide trigon, visibly broader than that in the Sackdilling holotype. The index of the trigon length to the M1 breadth (L ta/L tr) in DA2 is higher (78.7, 75.9–81.4, n = 4) than that obtained for the Sackdilling marten (69.0, 65.5–72.5, n = 2) (Marciszak et al. 2021). Data from both localities coincide with values of this index for *Martes vetus* (66.8, 59.2–76.1, n = 58). In this matter, *M. vetus* shows intermediate values between *M. foina* (62.6, 58.0–67.5, n = 114) and *M. martes* (75.4, 68.3–85.3, n = 129). The outline is irregular, and the occlusal surface is more complicated than in most specimens of *M. foina* and *M. martes.* The single M1 of the DA2 marten was assigned to morphotype A2, with straight lingual and rounded buccal outline and the preprotocrista bearing two small cusps. This morphotype (55%), together with A1 (32%), is the most common for *M. martes,* while others occur only rarely (Gimranov and Kosintsev, 2015). In *M. foina,* only group B morphotypes occur, with a deep groove between the paracone and metacone (Gimranov and Kosintsev, 2015). This is a reliable specific feature for *M. foina,* which was already pointed out by Wolsan et al. (1985) and Wolsan (1988, 1989a). The sole M1 from Sackdilling represents morphotype D2, with a straight lingual and rounded buccal outline, where the preprotocrista possesses two small cuspids and the hypocone and metaconule are present.

Previous authors, e.g., Heller (1930, 1933, 1936), Brunner (1933), or Dehm (1962), who described and studied remains of *Martes vetus,* practically did not deal with the mandible morphology. Only Anderson (1970) noted that the mandibular body is relatively shallow, the masseteric fossa reaches its maximum at the m1/m2 border, and the mental foramens are situated relatively far apart. She noted that the distance between them in *M. vetus* is 4.96 mm (3.70–6.10 mm, n = 13), while the mental foramens spacing ranged between 3.70–7.40 mm in *M. martes* and 2.00–3.40 mm in *M. foina.* A detailed revision showed that this feature is the most useful for taxonomic classification of European martens. The obtained results are close to the data presented by Anderson (1970), where the spacing of the mental foramens in the DA2 marten is 4.98 mm (4.02–5.74 mm, n = 5), and well corroborates with that of *M. vetus* (4.77 mm, 3.78–5.94 mm, n = 28). This measurement shows intermediate values between that of *M. foina* (2.53 mm,

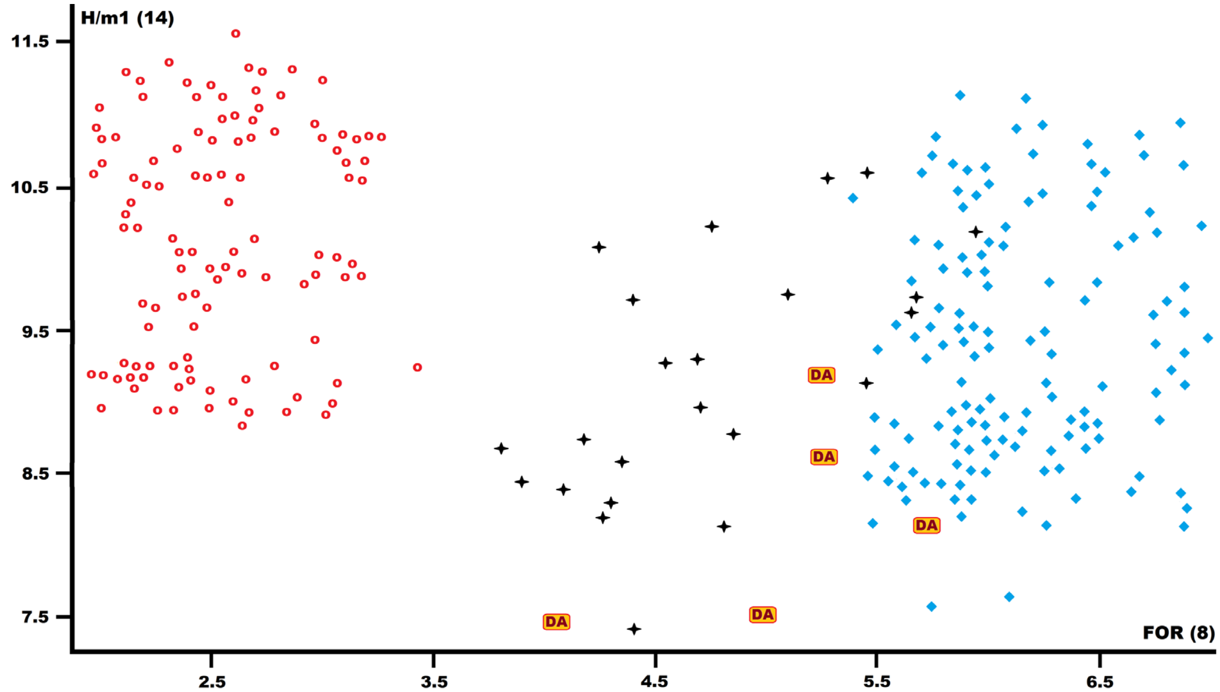

FIGURE 5. Graph showing the relationship between the height of the mandibular body measured behind m1 (H/m1, no. 14) and the spacing of mental foramens (FOR, no. 8) in European martens. For references see the Materials and Methods section.

1.97–3.41 mm, n = 114) and *M. martes* (6.13 mm, 5.36–7.97 mm, n = 129) (Figure 5).

Considering other features as well, the mandible of *Mares vetus* is morphologically more similar to that of *M. martes* in having an elongated and moderately high mandibular body, the condyloid processes located slightly below or at the level of p4/m1, and a similar shape of the mandibular ramus. In *M. vetus* and *M. martes,* the mesial and distal edges of the coronoid process are approximately of the same length and form a not fully isosceles triangle. In *M. foina,* the mesial edge of this process is more inclined than the distal one, which is almost vertical and therefore considerably shorter. That is why, in relation to the mandibular body, the ramus is proportionally shorter and more vertical.

The morphology of the angular process is more variable; however, there are some differences (Figure 6). The morphology of the angular process in the DA2 marten strongly resembles that in *Martes vetus* and *M. martes,* which is longer and hooked, contrary to the short and straight angular process of *M. foina.* There are also some differences in the shape of the masseteric fossa, which, on average, is shallower with a more triangular mesial edge in *M. vetus* and *M. martes.* In *M. foina,* this structure is usually slightly deeper, with a more rounded mesial edge. However, the shape of the masseteric fossa is also highly variable. It is rather more related to age and sex (in males and older individuals the masseteric fossa is deeper), than to species-specific characteristics. Therefore, the diagnostic values of this feature is limited and cannot be taken into consideration during species discrimination. The mandible of *M. vetus* resembles that of *M. foina* and differs from that of *M. martes* simultaneously in having a strongly curved mandibular body, with a notably marked curvature of the lower margin under m1. In contrast, the mandibular body of *M. martes* is straighter, with a lower margin having no or only a gentle curvature. The variability of all the above features is relatively smaller than in most teeth, but still relevant and therefore diagnostic value of those characters should be considered with caution.

There are also some differences between the studied martens in the morphology of the lower dentition. Our studies confirmed all previously known differences and revealed a few others. The great size variability of the c1 of *Martes vetus* was already highlighted by Heller (1933). When comparing size values of different marten species, differences seemingly result from sexual dimorphism. The c1 of *M. vetus* is on average slightly narrower than c1 of *M. martes* and *M. foina.* However, the

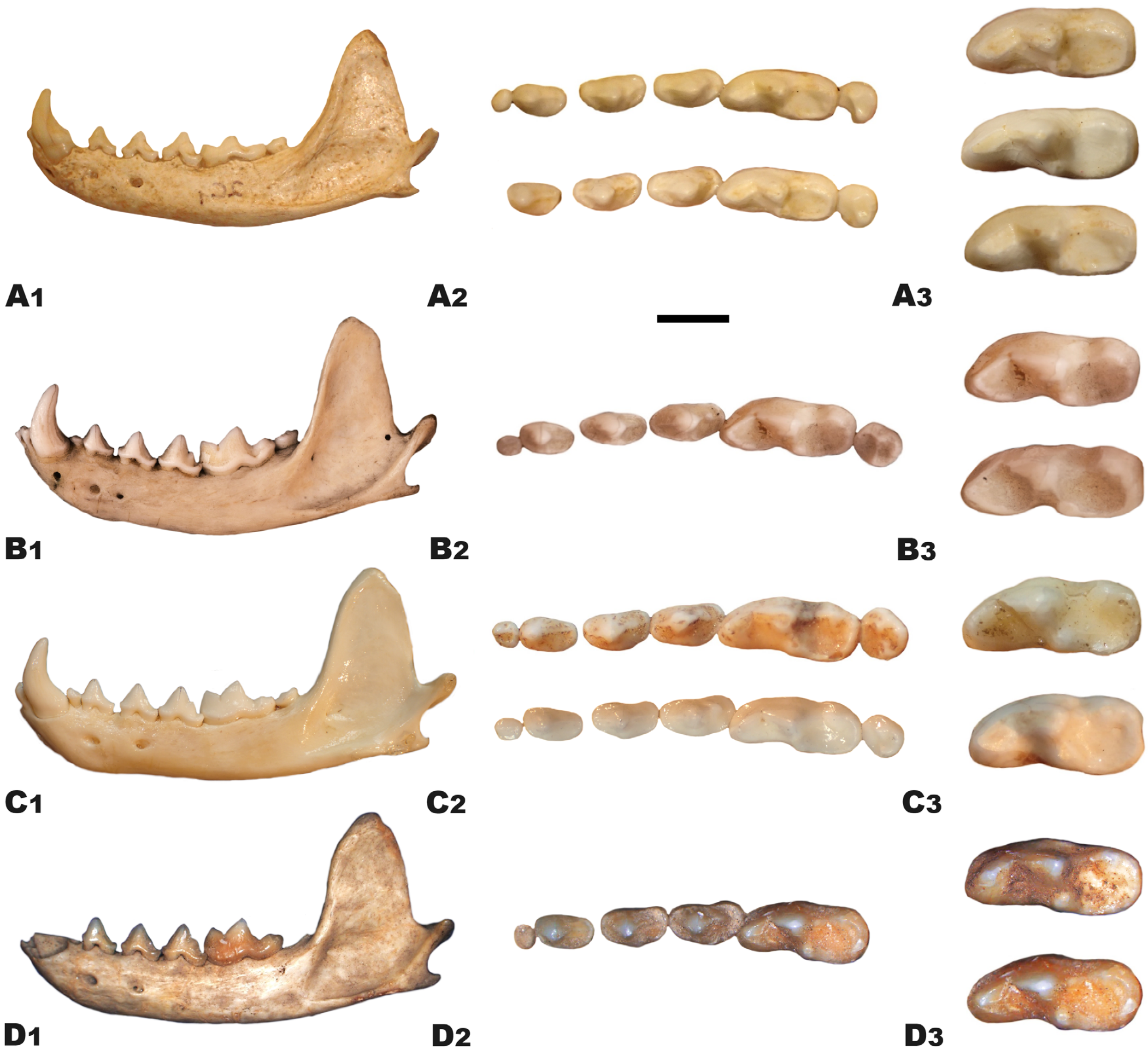

FIGURE 6. Comparison of the morphology of the mandible (1), lower dentition (2), and m1 (3) of European martens. **A**, *Martes vetus* from Deutsch Altenburg 2AC. **B**, extant *Martes foina*. **C**, extant *Martes martes*. **D**, extant *Martes zibellina*. All individuals are drawn on the same scale; mandibles are shown in the lateral view; dentition is shown in occlusal view. Scale bar is 10 mm for skulls and 4 mm for dentition.

ranges of variation are almost the same, and c1 of all three martens also do not differ morphologically. The p1 of *M. vetus* tends to be larger and less reduced (2.67 mm, 2.32–3.14 mm, n = 33) than in *M. foina* (2.21 mm, 1.79–2.56 mm, n = 114), and shows great similarity to p1 of *M. martes* (2.54 mm, 2.14–3.19 mm, n = 129).

The p1 of *Martes vetus* is not only larger, but also more robust, with a B/L index of 73.8 (66.2–80.2, n = 33), while this ratio is 72.9 (64.9–84.6, n = 129) in *M. martes* and 54.1 (53.2–63.9, n = 114) in *M. foina.* The p1 of the DA2 marten is relatively small (L = 2.27 mm), but rather wide (B/L = 67.8), and the robustness index falls into the range of variability of *M. vetus.* Metrically, the p2, p3, and p4 of all three martens are similar, only *M. foina* tends to show slightly higher values. Morphologically, those lower premolars showed some tendency to variability, although its range is not so wide. The p2 and p4 of *M. vetus* are narrower than that of *M. martes* and *M. foina.* In *M. vetus,* the B/L index of p2 is 50.7 (46.8–56.8, n = 29) and 45.2 (41.6–48.6, n = 38) in p4. Values of this ratio are 54.8 (48.9–61.1) for p2 and 53.2 (48.2–57.6) for p4 in *M. martes* (n = 129). In *M. foina* (n = 114), it is 54.9 (48.7–64.3) for p2 and 54.5 (48.8–61.6) for p4. The robustness index of p3 is almost the same for all three martens. Of the three p3 from DA2, two were assigned to morphotype A2, where a small distal additional cuspid is present on the distal ridge of the protoconid. The third p3 represents morphotype A1, where this cuspid is absent, and which is the dominant morphotype in *M. foina* (97%) and *M. zibellina* (82%) (Gimranov and Kosintsev, 2015). In *M. martes,* the most numerous is morphotype A2 (73%), but A1 also occurs relatively often (17%). Two p4 from DA2 were assigned to morphotype A3, where a small distal additional cuspid is present on the distal ridge of the protoconid, at lower level. This morphotype occurs in all three extant martens, but in low proportion: *M. foina* (3%), *M. zibellina* (9%), and *M. martes* (10%). Much more numerous in those species are morphotypes A1 (58% in *M. foina* and *M. martes,* and 40% in *M. zibellina),* without the additional cuspid, and A2 (33% in *M. foina,* 24% in *M. martes* and *M. zibellina),* where this cuspid is located high in relation to the protoconid (Gimranov and Kosintsev, 2015).

In the morphology of the lower dentition, most authors focused on m1. Dehm (1962) and Anderson (1970) highlighted the larger value of the mean size of m1. Additionally, Anderson (1970) and Wiszniowska (1989) mentioned that the m1 of *Martes vetus* has a proportionally short trigonid as in *M. martes,* and a small metaconid as in *M. foina.* Rabeder (1976) noted the lack of the so-called “paraconid edge”, a strong, median concavity situated between the disto-lingual margin of the paraconid and the mesio-lingual margin of the metaconid. When dealing with the DA2 material, it shows to be small marten, dimensionally smaller from other populations and species. The mean of L m1 in DA2 is 8.38 mm (7.97–8.78 mm, n = 5), which is clearly smaller than in extant martens, where L m1 in *M. martes* is 10.71 mm (10.08–11.38 mm, n = 63) in males and 9.64 mm (9.16–10.27 mm, n = 75) in females. Similarly, in *M. foina,* L m1 has higher values in males (L m1 = 10.64 mm, 10.04–11.34 mm, n = 68) compared to females (9.35 mm, 8.76–9.88 mm, n = 44). When comparing the DA2 material with two relatively numerous populations from Schernfeld and Żabia Cave, differences seemingly result from sexual dimorphism. In Schernfeld, *M. vetus* is larger (L m1 = 10.76 mm, 10.17–11.89 mm, n = 23 in males, and 9.44 mm, 8.74–9.89 mm, n = 17 in females) than in the Żabia Cave (L m1 = 9.87 mm, 9.57–10.52 mm, n = 7 in males, and 8.78 mm, 7.98–9.47 mm, n = 15 in females). The DA2 marten is relatively small, but its dimensions fall into the range of size variability of *M. vetus* females, and indicates a predominance of females at this locality. Only a single, incomplete m1 documents the presence of a larger male.

The general morphology of m1 in *Martes vetus* is typical for the genus *Martes*, with a proportionally broad and trenchant talonid, comparable in width with the trigonid. This is well illustrated by the talonid (B ta) to trigonid breadth (B tr) index. The mean value of this ratio is 98.9 (94.1–103.1, n = 83) in *M. vetus,* 106.1 (103.1–116.9, n = 139) in *M. martes,* and 93.4 (87.5–103.1, n = 114) in *M. foina.* It has been also found that *M. vetus* has not only a moderately narrow talonid, but also a relatively short trigonid. The mean ratio of the talonid (L ta) to trigonid length (L tr) is 46.9 (36.2–58.1, n = 86) in *M. vetus,* while 56.8 (41.5–72.3, n = 139) in *M. martes* and 37.6 (26.7–47.5, n = 114) in *M. foina.* In both indexes (L ta/L tr and B ta/B tr), the m1 of *M. vetus* shows intermediate values between *M. martes* and *M. foina.* The same was obtained for the material from DA2, where the mean of L ta/L tr is 52.6 (49.2–55.4, n = 4) and the mean of B ta/B tr is 98.8 (98.1–99.7, n = 5). Two m1 of DA2 were assigned to morphotype A1, were the distinct and robust hypoconid, as a sole cusp, occupies approximately half of the talonid basin. Two other m1 represents morphotype A2, where the small, but well-recognizable hypoconulid is adjacent to the robust hypoconid. Finally, the last tooth belongs to morphotype B2, where the hypoconulid is adjacent to the relatively small-sized hypoconid. The frequency of occurrence of particular morphotypes in extant martens is highly variable. There is, however, a noticeable difference between *M. foina,* in which group A morphotypes predominate (55% A1, 40% A2), *M. martes,* for which group B morphotypes are typical (24% B1, 67% B2), and *M. zibellina,* in which morphotypes B2 (44%) and C2 (45%) are the most common (Gimranov and Kosintsev, 2015). Other morphotypes occur only rarely.

In this aspect, the DA2 marten resembles the most *Martes foina,* because group A morphotypes also predominate. But the limited number of specimens should also be taken into account, especially considering that other morphotypes in the much more numerous populations of Schernfeld and Żabia Cave occurred also relatively often. Anderson (1970) noted some differences in the morphology of m2, being long and narrow in *M. vetus,* slightly broader than longer in *M. martes,* and nearly round in *M. foina.* Both preserved m2 from DA2 were assigned to morphotype A2, where the closely spaced protoconid and metaconid form a crest. This is also the dominant morphotype in *M. foina* (83%) and *M. zibellina* (96%), but occurs rarely (9%) in *M. martes.* For this species, morphotype A1 is typical (91%), where the protoconid and metaconid are separated from each other (Gimranov and Kosintsev, 2015). When comparing the B/L index of m2, both teeth from DA2 (89.2, 87.9–90.5, n = 2) corroborate well with the data obtained for *M. vetus* (92.7, 84.5–99.5, n = 46). The m2 of this marten tends to be narrower than in extant martens, in which the mean B/L ratio is higher, approximately 107.4 (94.5–112.4, n = 138) in *M. martes* and 99.7 (91.6–102.5, n = 112) in *M. foina* (83%).

In sum, the analyzed marten material from the DA2 locality both metrically and morphologically corroborates well with the respective dentognathic material of *Martes vetus,* which allows assigning it to this species. The comparison with two extant martens, *M. martes* and *M. foina,* showed a similar number of differences and similarities between these three species. Moreover, many of those features and indexes of *M. vetus* showed intermediate values between *M. martes* and *M. foina.* A concluded list of differences and similarities between those three martens is given below.

Comparison with *Martes martes*. Individuals of *M. vetus* from DA2 differ from *M. martes* in: (1) shorter and broader viscerocranium; (2) broader and less extended forward row of incisors; (3) strongly convex frontal profile in lateral view, with well-marked concavity in the middle part; (4) shorter, wider, and more strongly curved crown of C1; (5) narrower P2; (6) narrower P3 with weakly marked convex margin; (7) shorter and lower protocone and stronger lingual cingulum of P4; (8) less expanded trigon of M1 with more complicated microrelief on the chewing surface and less reduced metacone; (9) narrower spacing of mental foramens on the mandibular body; (10) slightly narrower c1; (11) narrower p2; (12) narrower p4 with an additional cuspid located low in relation to the protoconid; and (13) narrower m2 with closely spaced protoconid and metaconid that form a crest (Figure 7).

Individuals of *Martes vetus* from DA2 resemble *M. martes* in: (1) larger, less reduced, and robust P1; (2) elongated and moderately high mandibular body; (3) condyloid processes located slightly below or at the level of p4/m1; (4) shape of the mandibular ramus, where the mesial and distal edges of the coronoid process are approximately of the same length and form a not fully isosceles triangle; (5) longer and hooked angular process;

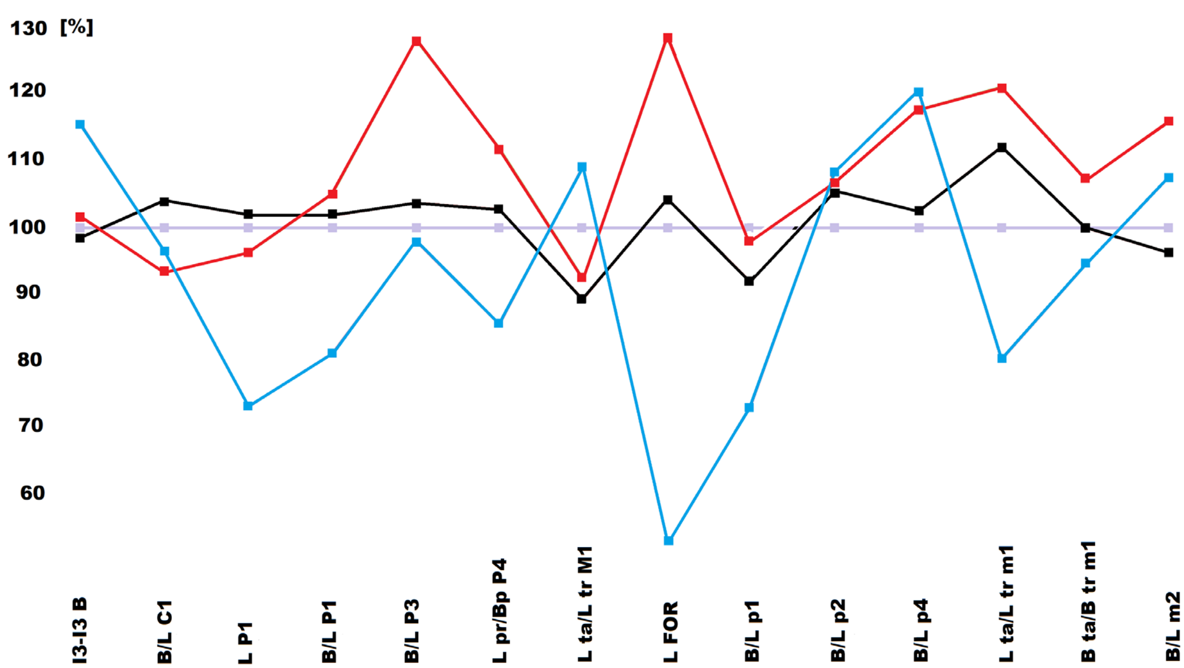

FIGURE 7. A list of selected features of the morphology of European martens, shown as a percentage of the base population of *Mates vetus* (purple line), for which the values of all features are presented as 100%. Black line — *Martes vetus* from Deutsch Altenburg; red line — extant *Martes martes*; blue line — extant *Martes foina*. For references see the Materials and Methods section.

(6) larger, less reduced, and robust p1; and (7) m1 with short trigonid (Figure 7).

Comparison with *Martes foina*. Individuals of *M. vetus* from DA2 differ from *M. foina* in: (1) less massive crown of C1; (2) smaller, narrower, and less reduced P1; (3) M1 with more complicated microrelief on the chewing surface and less reduced metacone; (4) wider spacing of mental foramens on the mandibular body; (5) elongated and moderately high mandibular body; (6) condyloid processes located slightly below or at the level of p4/m1; (7) shape of the mandibular ramus, where the mesial and distal edges of the coronoid process are approximately of the same length and form a not fully isosceles triangle (in *M. foina,* the mesial edge is more inclined than the distal one, which is almost vertical and thus considerably shorter); (8) longer and hooked angular process (short and straight in *M. foina);* (9) slightly narrower c1; (10) larger, less reduced, and broader p1; (11) narrower p2; (12) narrower p4 with an additional cuspid located usually low in relation to the protoconid; (13) shorter trigonid of m1; and (14) narrower m2 (Figure 7).

Individuals of *Martes vetus* from DA2 resemble *M. foina* in: (1) shorter and broader viscerocranium; (2) broader and less extended forward row of incisors; (3) strongly convex frontal profile in lateral view, with well-marked concavity in the middle part; (4) shorter and broader crown of C1; (5) narrow P2; (6) narrow P3 with weakly marked convex margin; (7) P4 with short and low protocone, which length is smaller than the distal breadth; (8) M1 with less expanded trigon and irregular occlusal outline; (9) strongly curved mandibular body, with notably marked curvature of the lower margin under m1; (10) m1 with a small metaconid and a talonid slightly narrower than the trigonid; and (11) morphology of m2, where the closely spaced protoconid and metaconid are connected by a distinct crest (Figure 7).

Possible occurrence of *Martes zibellina* at DA2. Rabeder (1976) described a right mandible body with the ramus fr. and present c1, p2–p3, and m1 (collection no. UWPI 2275/14/77) from DA2 as *Martes* cf. *zibellina.* He classified this specimen to this species according to its small size, lower crowns of c1, p2, and p3, and the small metaconid and broad talonid of m1. Among other features of this individual, he also noted the low mandibular body, the two mental foramens being located under p2 and p3, the moderately elongated and curved c1, the p1 alveolus directed distally, the low m1 without median concavity situated between the disto-lingual margin of the paraconid and the mesio-lingual margin of the metaconid, the trigonid slightly narrower than the talonid, the low hypoconid located on the trenchant talonid, and the minute hypoconulid. All these features are also characteristic for the morphology of *M. vetus.*

Rabeder (1976) did not discuss the differences between mandibles classified as *Martes* cf. *zibellina* and those of *M. vetus.* Only when describing the trigonid of the isolated m1 as *M*. cf. *vetus*, he concluded that this tooth cannot be assigned to *M. zibellina,* which differs in having smaller size and more strongly reduced metaconid of m1. He compared both specimens with the mandible (L m1 = 9.28 mm) from Sackdilling Cave, which was studied before by Brunner (1933), Anderson (1970), and Marciszak et al. (2021). More recently, Jiangzuo et al. (2021) agreed with Rabeder's (1976) original classification as *M.* cf. *zibellina*. However, they also pointed out some differences, such as the relatively wide m1 talonid and the presence of an additional small cuspid in the talonid basin or in the entoconid ridge, which is not present in the analyzed specimen.

Rabeder (1976) also highlighted his doubts about the correctness of the identification of this particular specimen. Considering that *Martes zibellina* is unknown from the European fossil record and that its extant populations show a remarkable geographic variability, this determination is even less probable. Of course, we cannot fully reject the possible presence of other marten species at DA2, but, based on our current state of knowledge, it is highly unlikely. There are no clear differences between *M. zibellina* and *M. martes* in the structure of the skull and teeth. As it was already pointed out above, the morphology of *M. vetus* showed intermediate values by many features and indexes between *M. martes* and *M. foina,* which makes unambiguous classification extremely difficult or even impossible. Additionally, the presence of small specimens, metrically and morphologically indistinguishable from the DA2 specimen, was also reported from the Schernfeld and Żabia Cave populations. All of them were, after detailed and careful revision, identified as females of *M. vetus.*

DISCUSSION

Contrary to a widespread view (Kurtén, 1968; Kaiser, 1999), there is no evidence of survival of *Martes vetus* beyond to the mid-Middle or even late Middle Pleistocene of Europe. All mentioned records, especially those post-Elsterian (MIS 12) and later, are highly uncertain and based on fossil materials of doubtful taxonomic value. *Martes vetus* is regarded as a typical Early and early Middle Pleistocene (2.2–0.6 Mya) component of the fauna (Kurtén, 1968; Anderson, 1970; Wiszniowska, 1989; Kot et al., 2022; Marciszak et al., 2021, 2024). Marten remains from the mid-Middle Pleistocene are most often described as displaying intermediate features and are classified differently. The main issue with those remains is that they are fragmentary, which does not allow for comparison with materials from other sites. Therefore, their taxonomic assignment remains unresolved. Many previous authors, including Miller (1912), Kurtén (1965, 1968), and Anderson (1970), tried to single out specific metric and morphological characters to distinguish the species *M. martes, M. foina,* and *M. vetus.* However, due to those attempts, there is a large overlap between their ranges of variation. As a result, it is difficult to make a specific attribution based on isolated teeth alone, and when species-specific characters are not observable in poorly preserved materials recovered from mid-Middle Pleistocene European sites, such as Cerè Cave (Ghezzo et al., 2014), it is preferred only to attribute such fragments to the genus *Martes*.

Among the European sites dated to the mid-Middle Pleistocene (MIS 16–12), there many examples. One of the most fascinating and long-lasting examples is the Spanish site Sima de los Huesos (MIS 13–12). García et al. (1997, 2023), based mostly on the proportions of P4 and M1, identified the marten fossils unearthed at this site as *Martes* sp. Later, however, after a detailed morphometric comparison, García (2003) classified those remains as *Martes* cf. *martes*, which was followed by later authors (García and Arsuaga, 2011; García et al., 2023). She highlighted some features, including the elongated protocone of P4, which length exceeds the distal breadth of P4, the large and broad M1, the distinct transition between the trigon and talon marked by two concavities, especially the distal one, the moderately developed metacone and protocone, the considerably expanded and wide trigon, and the m1 lacking the median concavity between the disto-lingual margin of the paraconid and the mesio-lingual margin of the metaconid. Simultaneously, all those authors (García, 2003; García and Arsuaga, 2011; García et al., 2023) highlighted the intermediate features and proof for the evolutionary lineage of *M. martes* → *M. vetus.* Part of a right mandibular body of a marten was illustrated and mentioned from the West Runton Freshwater Bed (MIS 19; England) (Stuart and Lister, 2010). Originally classified as *Martes sylvatica* (Newton, 1880), it was soon re-identified as *M. martes* (Newton, 1880, 1882, 1891; Reynolds, 1912; Kurtén, 1968; Stuart, 1974, 1975, 1981, 1982, 1988, 1992, 1996). It was never, however, described in detail, and even a provisional look at the relatively narrowly spaced mental foramens or the weak metaconid of m1 allows this determination to be seriously doubted. Similarly, Kaiser (1999) mentioned the presence of *M.* cf. *vetus* at the German locality Breitscheid-Erdbach 1 Cave, dated provisionally to the Middle Pleistocene. Jánossy (1969) briefly described a complete humerus (60 mm long) from the Hungarian site Tarkő (MIS 15–13) and a few postcranial remains from Uppony 5 (MIS 11). In both cases, it was impossible to exactly determine the marten species. He noted, however, the greatest similarity of the humerus from Tarkő to that of *M. martes* by its gracile structure. Ghezzo et al. (2014) described in detail a distal fragment of a left mandible from Ceré Cave (MIS 15–13) as *Martes* sp.

At least MIS 12 is the time of the first appearance of *Martes martes.* The earliest, undoubted occurrence of the species is known from Polish site Tunel Wielki Cave (Kot et al., 2022). A faunal turnover took place in the cold period of MIS 12. It was the time when tundra species expanded to southern and south-western Europe, entering the newly formed tundra-steppe ecosystem. At the same time, Asian steppe species dispersed to the north and north-west. The changes led to the formation of the earliest pan-Eurasian Mammoth fauna c. 460 kya, which dominated the late Middle Pleistocene and Late Pleistocene mammal assemblages (Kahlke, 2014; Kot et al., 2022). From the same horizon came also remains of two other, cold adapted mustelid species, *Gulo gulo* (Linnaeus, 1758) and *Mustela nivalis* Linnaeus, 1758. *Martes martes* appeared after the *Mimomys–Arvicola* transition (Koenigswald and Heinrich, 1999; Marciszak, 2012; Marciszak et al., 2021). The mid-Middle Pleistocene changes in mustelid paleoassemblages corroborate well with the evolution of rodents (Horáček and Ložek, 1988; Horáček et al., 2004; Horáček, 2008). It shows that the main rearrangement of rodent communities in Central Europe took place at the same time, between MIS 17 and 15. From this perspective, the evolution of these mustelids could be interpreted as a result of the selective pressure of the onset of environmental deterioration. In this model, the main selective pressure would be related to specialization in a different spectrum of prey and a life strategy associated with open grasslands (in case of *Mustela* *palerminea* (Petényi, 1864) → *Mustela erminea* Linnaeus, 1758, and *Mustela praenivalis* Kormos, 1934 → *Mustela nivalis* Linnaeus, 1758) and forests (in case of *Martes vetus* → *Martes martes).* As documented by Marciszak et al. (2021) and Kot et al. (2022), the earliest occurrence of *M. martes* in Europe is younger than MIS 16/15, and all of the earlier published records of this species are either a result of misidentification or based on material with no diagnostic characters.

Similarly to *Martes martes, M. zibellina* also evolved from *M. vetus* during the Middle Pleistocene (0.6–0.55 Mya), probably in western Eurasia (Figure 8; Ishida et al. 2013). This hypothesis has been, however, poorly supported so far by fossil and mitochondrial data. Remains of *M. zibellina* older than the Late Pleistocene (~100 kya) are unknown. Additionally, the time of divergence from the most recent common ancestor was estimated for this species as c. 250 kya, with 95% confidence interval between 330–180 kya (Hope et al., 2013; Li et al., 2021). The extant *M. zibellina* is better adapted to cold environments than other *Martes* species (Davison et al. 2001). Accordingly, it was suggested that it could have first dispersed to eastern Eurasia during the glacials/stadials (Li et al., 2021). This is also supported by results obtained from the revision of the fossil material from the DA2 and DA4 localities, namely the absence of *M. zibellina* at both of these sites.

CONCLUSIONS

The Early Pleistocene marten fossils from the Austrian sites Deutsch Altenburg 2 and 4 showed a strong similarity to *Martes vetus*. As a result of a detailed revision, all marten remains have been assigned to this species, despite previous statements about the possible occurrence of another marten species, *Martes* cf. *zibellina.* The supposed earlier presence of *M. zibellina* is regarded as a result of misidentification due to sexual dimorphism. Thanks to their good state of preservation, the viscerocranium and mandibles from Deutsch Altenburg 2 and 4 are important materials in the European fossil record of *M. vetus*. A comparison with marterns from other European Early and early Middle Pleistocene sites showed the studied materials have intermediate features shared with *M. martes*, *M. zibellina*, and *M. foina*.

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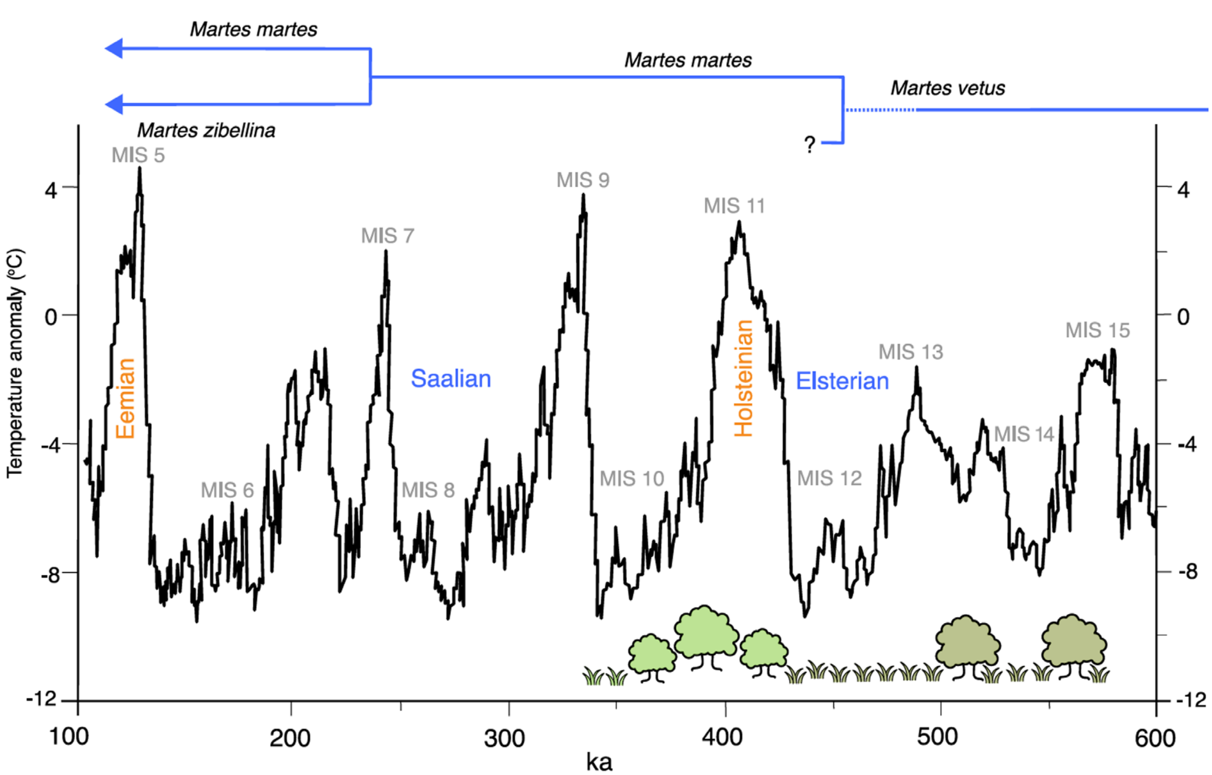

FIGURE 8. Schematic representation of the time of separation of martens from the *Martes* genus and the environmental conditions accompanying them.

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APPENDIX 1

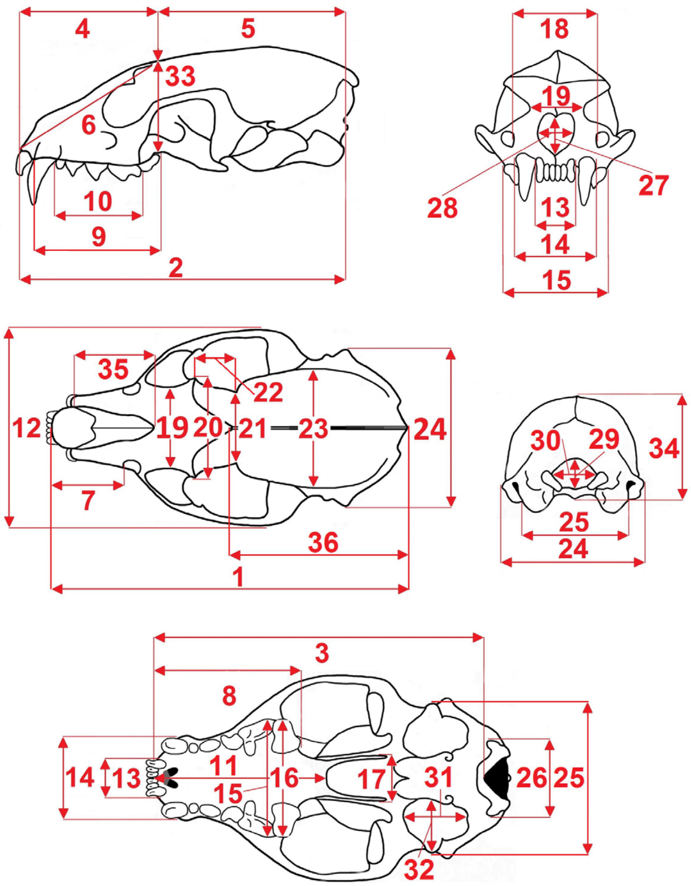
Supplementary tables and figures.

TABLE S1. List of taxa from Deutsch Altenburg 2C and 4B (Rabeder, 1972a-c, 1973a-b, 1974a-c, 1976, 1978, 1981, 1982; Mais and Rabeder, 1977a-b, 1979, 1984, 1997; Jánossy, 1981; Frank and Rabeder, 1997a-b; Rabeder and Withalm, 2006; Rabeder et al., 2010; Jiangzuo et al., 2021; Marciszak et al., 2021).

Deutsch Altenburg 2C (DA2C)	Deutsch Altenburg 4B (DA4B)
Amphibia Gray, 1925	
Pelobates fuscus (Laurenti, 1768)	*Pelobates fuscus* (Laurenti, 1768)
Pelobates sp.	*Bufo viridis* (Laurenti, 1768)
Pelodytes sp.	*Rana arvalis* Nilsson, 1842
Bufo viridis (Laurenti, 1768)	*Rana* sp.
Bufo bufo (Linnaeus, 1758)	
Rana arvalis Nilsson, 1842	
Rana sp.	
Reptilia Laurenti, 1768	
Zootoca vivipara (Lichtenstein, 1823)	*Ophisops elegans* Ménétries, 1832
Lacerta viridis (Laurenti, 1768)	*Zootoca vivipara* (Lichtenstein, 1823)
Lacerta agilis Linnaeus, 1758	*Lacerta viridis* (Laurenti, 1768)
Lacerta sp.	*Lacerta agilis* Linnaeus, 1758
Podarcis praemuralis Rauscher, 1992	*Dalmatolacerta oxycephala* Duméril & Bibron, 1839
Podarcis altenburgensis Rauscher, 1992	*Lacerta* sp.
Anguis fragilis Linnaeus, 1758	*Podarcis praemuralis* Rauscher, 1992
Pseudopus pannonicus Kormos, 1911	*Podarcis altenburgensis* Rauscher, 1992
Natrix natrix (Linnaeus, 1758)	*Anguis fragilis* Linnaeus, 1758
Coluber sp.	*Natrix natrix* (Linnaeus, 1758)
Elaphe quatuorlineata (Lacépède, 1789)	*Coluber* sp.
	Elaphe quatuorlineata (Lacépède, 1789)
Aves Linnaeus, 1758	
Francolinus capeki Lambrecht, 1933	*Falco tinnunculus atavus* Jánossy, 1972
Perdix perdix jurcsaki Kretzoi, 1962	*Francolinus capeki* Lambrecht, 1933
Athene cf. *veta* Jánossy, 1974	*Perdix perdix jurcsaki* Kretzoi, 1962
Turdus cf. *viscivorus* Linnaeus, 1758	*Glaucidium passerinum* (Linnaeus, 1758)
	Dendrocopos major submajor Jánossy, 1974
	Hirundo cf. *rustica* L. Linnaeus, 1758
	Sylvia cf. *atricapilla* (Linnaeus, 1758)
	Turdus cf. *viscivorus* Linnaeus, 1758
	Turdus cf. *philomelos* Brehm, 1831
	Turdus cf. *musicus* Linnaeus, 1758
	Sitta cf. *europaea* Linnaeus, 1758
	Sitta sp. (small form)
	Serinus cf. *serinus* (Linnaeus, 1766)
	Pinicola cf. *enucleator* (Linnaeus, 1758)
	Garrulus cf. *glandarinus* (Linnaeus, 1758)

Deutsch Altenburg 2C (DA2C)	Deutsch Altenburg 4B (DA4B)
Mammalia Linnaeus, 1758	
Eulipotyphla Waddell et al., 1999	
Erinaceus sp.	*Erinaceus* sp.
Talpa fossilis Petényi, 1864	*Talpa* cf. *europaea* Linnaeus, 1758
Talpa minor Freudenberg, 1914	*Desmana nehringi* Kormos, 1913
Desmana thermalis Kormos, 1930	*Sorex runtonensis* Hinton, 1911
Desmana nehringi Kormos, 1913	*Sorex minutus* Linnaeus, 1766
Sorex runtonensis Hinton, 1911	*Drepanosorex margaritodon* Kormos, 1930
Sorex praealpinus Heller, 1930	*Dimylosorex tholodus* Rabeder, 1972
Sorex minutus Linnaeus, 1766	*Episoriculus gibberodon* (Petényi, 1864)
Drepanosorex margaritodon Kormos, 1930	*Crocidura kornfeldi* Kormos, 1934
Dimylosorex tholodus Rabeder, 1972	*Beremendia fissidens* (Petényi, 1864)
Petenyia hungarica Kormos, 1934	
Beremendia fissidens (Petényi, 1864)	
Episoriculus gibberodon (Petényi, 1864)	
Crocidura kornfeldi Kormos, 1934	
Chiroptera Blumenbach, 1779	
Rhinolophus ferrumequinum (Schreber, 1774)	*Rhinolophus ferrumequinum* (Schreber, 1774)
Rhinolophus mehelyi Matschie, 1901	*Rhinolophus mehelyi* Matschie, 1901
Rhinolophus euryale (Blasius, 1853)	*Miniopterus schreibersii* (Kuhl, 1819)
Rhinolophus hipposideros Bechstein, 1800	*Myotis blythi* Tomes, 1857
Miniopterus schreibersii (Kuhl, 1819)	*Myotis bechsteini* (Kuhl, 1818)
Myotis blythi Tomes, 1857	*Myotis* cf. *emarginatus* (Geoffroy, 1806)
Myotis cf. *dasycneme* (Boie, 1825)	*Myotis* cf. *nattereri* (Kuhl, 1818)
Myotis oxygnathus (Monticelli, 1885)	*Myotis* cf. *exilis* Heller, 1936
Myotis bechsteini (Kuhl, 1818)	*Myotis* cf. *mystacinus* (Kuhl, 1819)
Myotis cf. *emarginatus* (Geoffroy, 1806)	*Plecotus abeli* Wettstein-Westersheim, 1923
Myotis cf. *nattereri* (Kuhl, 1818)	*Barbastella schadleri* Wettstein-Westersheim, 1923
Myotis sp.	*Eptesicus* cf. *praeglacialis* (Kormos, 1930)
Myotis cf. *exilis* Heller, 1936	*Nyctalus* sp.
Myotis cf. *helleri* Kowalski, 1962	
Plecotus abeli Wettstein-Westersheim, 1923	
Paraplecotus crassidens (Kormos, 1930)	
Barbastella schadleri Wettstein-Westersheim, 1923	
Eptesicus cf. *praeglacialis* (Kormos, 1930)	
Rodentia Bowdich, 1821	
Marmota sp.	*Spermophilus primigenius* (Kormos, 1934)
Spermophilus primigenius (Kormos, 1934)	*Sciurus* sp.
Sciurus sp.	*Myoxus sackdillingensis* (Heller, 1930)
Myoxus sackdillingensis (Heller, 1930)	*Muscardinus dacicus* Kormos, 1930
Muscardinus dacicus Kormos, 1930	*Lagurus arankae* Kretzoi, 1954
Cricetus nanus Schaub, 1930	*Prolagurus pannonicus* (Kormos, 1930)
Cricetulus bursae (Schaub, 1930)	*Mimomys coelodus* Kretzoi, 1954
Lagurus arankae Kretzoi, 1954	*Mimomys pusillus* (Méhely, 1914)
Prolagurus pannonicus (Kormos, 1930)	*Mimomys tornensis* Jánossy and van der Meulen, 1975

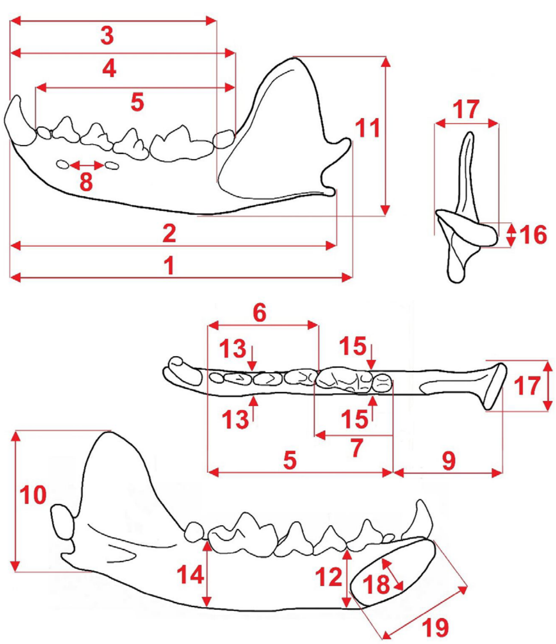
Deutsch Altenburg 2C (DA2C)	Deutsch Altenburg 4B (DA4B)
Mimomys coelodus Kretzoi, 1954	*Microtus praehintoni* Rabeder, 1981
Mimomys pusillus (Méhely, 1914)	*Microtus hintoni* Kretzoi, 1941
Mimomys tornensis Jánossy and van der Meulen, 1975	*Microtus superpliocaenicus* Rabeder, 1981
Mimomys pliocaenicus Forsyth-Major, 1902	*Mimomys savini* Hinton, 1910
Mimomys savini Hinton, 1910	*Clethrionomys hintonianus* Kretzoi, 1958
Mimomys ostramosensis Jánossy and van der Meulen, 1975	*Mimomys ostramosensis* Jánossy and van der Meulen, 1975
Clethrionomys hintonianus Kretzoi, 1958	*Pliomys episcopalis* Méhely, 1914
Pliomys episcopalis Méhely, 1914	*Pliomys hollitzeri* Rabeder, 1981
Pliomys simplicior Kretzoi, 1914	*Ungaromys nanus* Kormos, 1932
Ungaromys nanus Kormos, 1932	*Lemmus* cf. *lemmus* (Linnaeus, 1758)
Apodemus cf. *atavus* Heller, 1936	*Apodemus* cf. *atavus* Heller, 1936
Pusillomimus pusillus Kormos, 1930	*Sicista praeloriger* Kormos, 1930
	Pusillomimus pusillus Kormos, 1930
	Mimomys savini Hinton, 1910
	Cricetus nanus Schaub, 1930
	Cricetulus bursae (Schaub, 1930)
Lagomorpha Brandt, 1855	
Hypolagus beremendensis (Petényi, 1864)	*Hypolagus beremendensis* (Petényi, 1864)
Ochotona terraerubrae Kretzoi, 1956	*Ochotona terraerubrae* Kretzoi, 1956
Carnivora Bowditch, 1821	
Lycaon lycaonoides (Kreztoi, 1938)	*Cuon* sp.
Canis mosbachensis Soergel, 1925	*Canis mosbachensis* Soergel, 1925
Vulpes praeglacialis (Kormos, 1932)	*Vulpes praeglacialis* (Kormos, 1932)
Ursus arctos suessenbornensis Soergel, 1926	*Ursus arctos suessenbornensis* Soergel, 1926
Meles meles atavus (Kormos, 1914)	*Meles meles atavus* (Kormos, 1914)
Pannonictis ardea (Gervais, 1859)	*Mustela strandi* Kormos, 1934
Pannonictis pliocaenicus Kormos, 1934	*Martes vetus* Kretzoi, 1942
Martes vetus Kretzoi, 1942	*Vormela petenyi* Kretzoi, 1942
Vormela petenyi Kretzoi, 1942	*Mustela palerminea* (Petényi, 1864)
Oxyvormela maisi Rabeder, 1973	*Mustela praenivalis* Kormos, 1934
Psalidogale altenburgensis Rabeder, 1976	*Homotherium latidens* (Owen, 1846)
Vormela petenyi Kretzoi, 1942	*Panthera* sp.
Mustela palerminea (Petényi, 1864)	
Mustela praenivalis Kormos, 1934	
Felis cf. *lunensis* Martelli, 1906	
Proboscidea Illiger, 1811	
Mammuthus meridionalis (Nesti, 1825)	
Perissodactyla Owen, 1848	
Rhinocerotide indet.	*Equus* cf. *wuesti* (Musil, 2001)
Equus sp.	*Stephanorhinus etruscus* (Falconer, 1868);
Artiodactyla Owen, 1848	
Bison cf. *menneri* Sher, 1997	*Bison* cf. *menneri* Sher, 1997
Cervus sp.	
Primates Linnaeus, 1758	
Macaca sylvanus (Linnaeus, 1758)	*Macaca sylvanus* (Linnaeus, 1758)



The cranial measurements were made according to the scheme:

(1) total length (Prosthion-Akrokranion; TOT)
(2) condylobasal length (Prostion-occipital condyles; CBL)
(3) basal length (Prosthion-Basion; BAS)
(4) viscerocranium length (Prosthion-frontal midpoint)
(5) neurocranium length (frontal midpoint-Akrokranion)
(6) facial length (Prosthion-frontal midpoint)
(7) snout length (Prosthion-Infraorbital)
(8) rostrum length (mesial margin of I1 to distal margin of M1)
(9) C1-M1 length on alveoli (mesial margin of C1 to distal margin of M1)
(10) P1-P4 length on alveoli (mesial margin of P1 to distal margin of P4)
(11) palatal length (Prosthion-Staphylion)
(12) breadth at zygomatic arches (Zygion-Zygion)
(13) incisor row breadth (I3-I3 breadth)
(14) maximum breadth at canine alveoli (C1-C1 breadth)
(15) maximum breadth at P4 alveoli (P4-P4 breadth)
(16) maximum breadth at M1 alveoli (M1-M1 breadth)
(17) least palatal breadth
(18) least distance between infraorbital foramina
(19) least distance between orbits (Entorbital-Entorbital)
(20) frontal breadth (Ectorbital-Ectorbital)
(21) postorbital least breadth (postorbital bar; POB)
(22) distance between ectorbital and postorbital bar (IOL)
(23) maximal neurocranium breadth (Euryon-Euryon)
(24) mastoid breadth (Otion-Otion)
(25) maximal breadth on tympanic bullae
(26) maximum breadth of occipital condyles
(27) nasal aperture height
(28) nasal aperture breadth
(29) height of foramen magnum (basion-opisthion)
(30) breadth of foramen magnum
(31) tympanic bullae length
(32) tympanic bullae breadth
(33) skull length (prosthion-acrocranion)
(34) maximum cranial height (staphylion-frontal)
(35) maximum length of nasal bones
(36) maximum length of sagittal crest

FIGURE S1. Measurements scheme of a marten skull.



The mandibular measurements:

(1) total length (infradentale to condyle)
(2) length from infradentale to angular process
(3) length infradentale to mesial margin of masseteric fossa
(4) c1-m2 length (mesial margin of c1 to distal margin of m2)
(5) p2-m2 length (mesial margin of p1 to distal margin of m2)
(6) p2-p4 length (mesial margin of p1 to distal margin of p4)
(7) m1-m2 length (mesial margin of m1 to distal margin of m2)
(8) distance between mental foramina (FOR)
(9) length from distal margin of m2 to condyle
(10) ramus height (base of angular process - apex of coronoid process)
(11) mandible maximum height
(12) mandibular body height between p3 and p4
(13) mandibular body thickness between p3 and p4
(14) mandibular body height between m1 and m2
(15) mandibular body thickness between m1 and m2
(16) condyle height
(17) condyle breadth
(18) symphysis maximum diameter
(19) symphysis minimum diameter

FIGURE S2. Measurements scheme of a marten mandible.

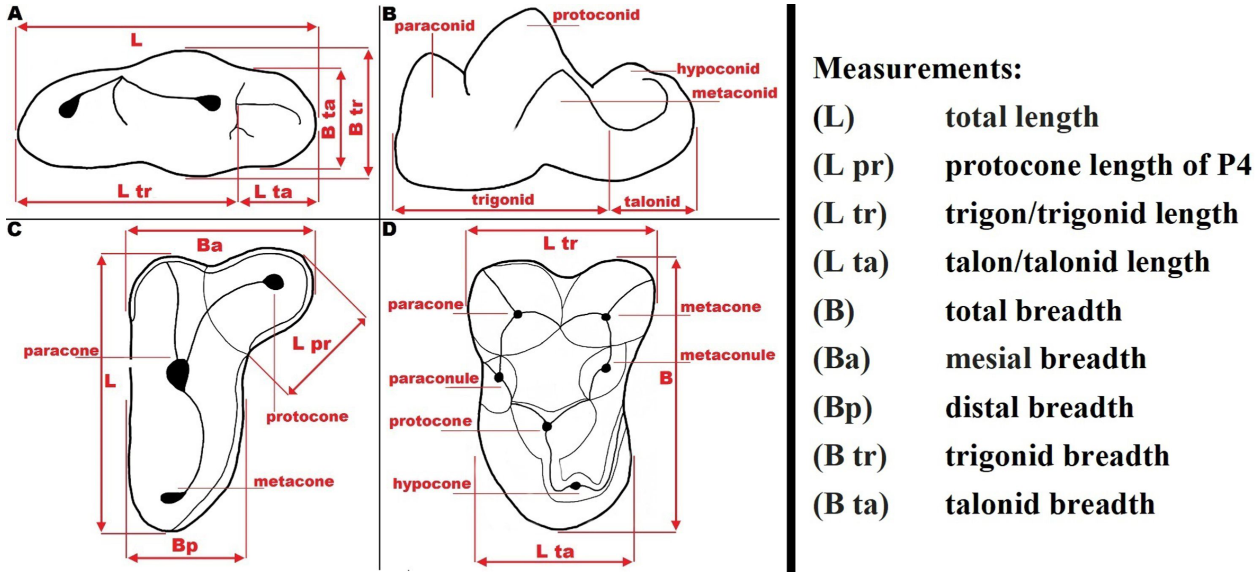


FIGURE S3. Measurements scheme and dental terminology of a marten teeth.

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