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# *Martes wenzensis* Stach, 1959 within the early history of the genus *Martes* Pinel, 1792

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## ABSTRACT:

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*Martes wenzensis* Stach, 1959 is the only European Pliocene marten and possible ancestor of an evolutionary lineage leading through *Martes vetus* Kretzoi, 1942 to *Martes martes* Linnæus, 1758. Its occurrence ranged between c. 3.6–2.2 Ma and its presence is recorded herein from four sites: three Polish and one Bulgarian (Varshets). The oldest record from Węże 1, dated to 3.6–3.2 Ma, is also the most abundant and the type locality for this species. Only isolated teeth came from two other Polish sites, Węże 2 and Rębielice Królewskie 1A, dated to 2.5–2.2 Ma. The visceocranium from Varshets (c. 2.5 Ma) shows intermediate features between the type specimen from Węże 1 and the Early Pleistocene *M. vetus*, its possible descendant. The palaeontological records corroborate well with molecular data. The comparison of marten crania from Węże 1 and Varshets shows decrease in size and massiveness of teeth during the evolution of the species. *Martes wenzensis* shows an admixture of features inherent to *M. vetus*, *M. martes*, and *M. foina* Erxleben, 1777. The species resembles more *M. vetus* and *M. martes* than *M. foina*. It is described as a large, robust marten, with a flat forehead, short and broad viscerocranium, wide snout, robust canines, elongated and narrow premolars and enlarged carnassials.

**Key words:** *Martes*; Evolution; Dentition; Lineage; Pliocene; Pleistocene.

## INTRODUCTION

The genus *Martes* Pinel, 1792 comprises seven species and is placed in the Guloninae J.E. Gray, 1825 (*sensu* Sato *et al.* 2012). Previously, this genus was referred to the Martinae Wagner, 1841, and both these subfamilies were linked in the past into one monophyletic group (Anderson 1970). Although it resembles the synchorological genus *Pekania* J.E. Gray, 1865 in its dental and cranial morphology, robust molecular evidence has demonstrated that the genus *Martes* is more diverse than previously thought. Some recent studies have placed *Martes americana* (Turton, 1806) outside the genus and allied it with *Eira barbara* (Linnæus, 1758) and *Gulo gulo* (Linnæus, 1758), i.e., forming a new clade (Flynn *et al.* 2005; Koepfli *et al.* 2008; Samuels *et al.* 2018).

The origin of the genus *Martes* has been uncertain for a long time, however new findings have substantially improved the understanding of the martens' evolution. 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 Ma; 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). Recently, the feature is regarded as a plesiomorphic trait shared by different mustelids (Hughes 2012). Numerous forms formerly classified as early *Martes* species are known from the Early and Middle Miocene of Eurasia, North America, and North Africa. However, their taxonomical position need verification, since most of them were described based on quite fragmentary material (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 caused by their ecomorphological convergence or retention of plesiomorphic traits (Samuels *et al.* 2018). Taking into account a high level of polymorphism observed in these early taxa, comparable with the highly polymorphic dentition of extant taxa and the scarcity of fossil material, a broad revision is needed to fully understand their taxonomical position (Samuels *et al.* 2018).

Among gulonines, the genus *Martes* has been consistently found to be most closely related to the genus *Gulo* Pallas, 1780, and as a sister group to *Pekania pennanti* (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 Ma (12.5–9.4 Ma), while Sato *et al.* (2012) – at c. 12.7 Ma (14.7–10.8 Ma). Examination of mitochondrial genomes of gulonines shows that the *Martes*–*Gulo* clade diverged from *Pekania* around 7.6 Ma (8.9–7.1 Ma) (Li *et al.* 2014). Splitting of the genus *Martes* from the genus *Gulo* was assessed on 6.4–6.3 Ma (7.6–5.3 Ma) (Li *et al.* 2014), while Malyarchuk *et al.* (2015) suggested an age of 5.6 Ma (6.3–4.9 Ma).

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 Ma (Stach 1959; Wolsan 1989; Anderson 1994; Sato *et al.* 2003; Montoya *et al.* 2011).

The state of knowledge and the understanding of stages and dynamics of the dispersion and changes of particular faunal elements in areas north of the Carpathians has significantly increased over the last two decades. It was due to new chronological evidence, a broad revision of historical collections, as well as new excavations allowing to re-examine old and describe new material which particularly increased our knowledge about the formation of fauna in this region. However, data from Central Europe, including the modern territory of Poland, still seem to be incomplete and in need of revision.

One of such examples is the early history of martens, which is one of the most recognisable member of the mustelids. The main goal of this paper is the re-examination of old and description of new material of *M. wenzensis*, the only Pliocene marten from Europe. Since almost all material of this species was described from Poland, reconstruction of the history of this species within this territory is especially noteworthy. In addition, the find from Varshets sheds new light on the Late Pliocene–Early Pleistocene evolution of the genus *Martes*. The Polish and Bulgarian finds also confirm the evolutionary lineage *M. wenzensis* => *M. vetus* and document its probable evolution *in situ* within Europe. In this aspect, the fossil record corresponds well with molecular data.

The Middle–Late Miocene history of the possible ancestors of genus *Martes* is full of marten-like species and forms, often of debatable and unclear taxonomical position. The most numerous were described from Spain, e.g., *M. sainjoni* (Mayet, 1908) and *M. burdigaliensis* Beaumount, 1974 (Artesilla, MN 4; Azanza *et al.* 1993); *Martes* sp. (La Barranca, MN 6; Peigné *et al.* 2006); *M. ginsburgi* Montoya, Morales and Abella, 2011 (Venta del Moro, MN 13); *Circamustela dechaseauxi* Petter, 1967 (Can Llobateres, MN 9); *M. melibulla* Petter, 1963 (Can Llobateres, Trinxera Nord de l'Autopista, MN 9–10); *M.* aff. *anderssoni* Schlosser, 1924 (Can Poncic 1, MN 9; Petter 1967); *M. munki* Roger, 1900 (Sant Quirze del Vallès, MN 7–8); *Circamustela peignei* Valenciano, Pérez-Ramos, Abella and Morales, 2020 (Batallones-3 and 5, MN 10); and *Aragonictis aradis* Valenciano, Morales, Azanza and Demiguel, 2021 (Escobosa de Calatañazor, Toril 3A, and Andurriales, MN 8; Valenciano *et al.* 2021). The list count incudes also: *Martes sansani*-

*ensis* (Lartet, 1851) (Sansan, MN 6); *M. delphinensis* Depéret, 1892; *M. filholi* (Depéret, 1887) and *M. munki* (La Grive, MN 7–8), all from France; *Sinictis dolichognathus* Zdansky, 1924, from locality 108 (MN 13–14), *M. palaeosinensis* from localities 11, 30, 30 (5), 31, 108 and 111, all from China (Zdansky 1924); *M. laevidens* (Wintershof-West, Germany, MN 3; Dehm 1950); *M. collengensis* Roth and Mein, 1987; *M. cadeoti* Mein, 1958; *M. burdigaliensis*, *M. munki*, and *M. filholi* (Vieux-Collonges, France, MN 5; Mein 1958); *M. munki* (Häder, Germany, MN 5; Roger 1900); and *Circamustela* sp. (Dorn-Dürkheim 1, Germany, MN 11; Morlo 1997).

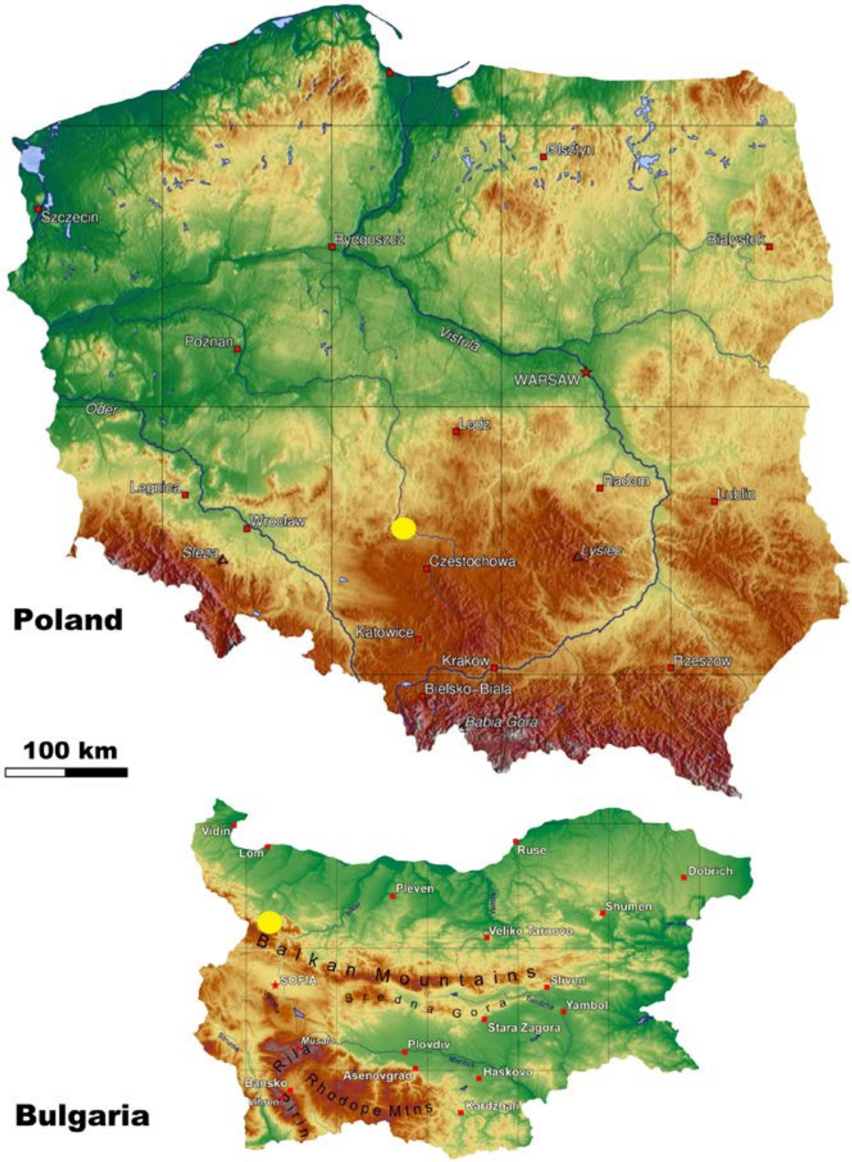
Mostly their description has been based upon fragmentary or incomplete material and classification of most of them is problematic. Their morphology is characterised by numerous plesiomorphic convergences (Werdelin and Peigné 2010; Samuels *et al.* 2018). Anderson (1994) proposed *M. laevidens* as the earliest member of the genus *Martes*, but later this assignation was rejected (Sato *et al.* 2003; Valenciano *et al.* 2021). It is debatable whether the early Late Miocene (MN 9–10) *M. melibulla* or Late Pliocene (MN 15) *M. wenzensis* represents the first true *Martes* (Valenciano 2017; Valenciano *et al.* 2020, 2021).

Contrary to the Miocene, the Eurasian Pliocene history of the genus is considerably weakly documented. Since Stach's (1959) description, *M. wenzensis* has been regarded as the only European Pliocene marten; no new remains have been described in detail so far. The Early Pleistocene martens are represented by *M. vetus* Kretzoi, 1942 (2.2–0.6 Ma; 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) and *M. crassidens* Jiangzuo, Gimranov, Liu, Liu, Jin and Liu, 2021 (2.2–1.7 Ma; Jiangzuo *et al.* 2021). Although most authors tentatively interpret *M. wenzensis* as the most probable ancestor of the *Martes* lineage, no unambiguous evidence of it has been published till now. A detailed revision of the remains described by Stach (1959) together with newly discovered material from Węże 1, and the younger sites Węże 2, Rębielice Królewskie 1A, all from Poland, and Varshets from Bulgaria, allow to shed new light on this matter.

## LOCALITIES AND STRATIGRAPHY

Locality Węże 1 (W1), sometimes called Samsonowicza Cave (51º5'45"N, 18º47'21"E, 220 m a.s.l.) is located in an abandoned quarry in the village of Węże near the small town of Działoszyn, in the Wieluń Upland, central Poland (Text-fig. 1). The site was formed after the collapse of a large, vertical cave which was filled with sediments. The locality was mentioned for the first time before World War 2 (Samsonowicz 1934). Later, in the late 1940s and 1950s, further research was conducted by an interdisciplinary team (researchers from the Institute of Systematics and Evolution of Animals Polish Academy of Sciences in Kraków – ISEZ, Museum of the Earth, Polish Academy of Sciences in Warszawa – MZ, and Department of Palaeozoology, University of Wrocław – ZP). Intensive excavations were continued until the mid-1970s and resulted in the removal of most sediment from the site. Samsonowicz (1934) divided the deposits into red and grey breccia, while Głazek *et al.* (1976) distinguished three main sedimentary intervals. The oldest layers, dating back to the Upper Miocene (6.0–5.5 Ma; MN 13) covered the cave bottom. They comprised residual red clay with an admixture of pinkish limestone rubble, covered by a thick layer of light flowstone calcite, covering almost the entire cave bottom. The layer was almost sterile from bones. The second sedimentary interval (c. 3.6–3.2 Ma; MN 15b), included thick deposits of red sandy clay with an addition of small concretions and bones. The clay gradually passed into a thick grey breccia. The layers of the second interval were laminated on the surface, while deeper in the profile the lamination gradually disappeared. The surface was covered with sandy and clayey deposits with an admixture of fragmented calcite and limestone. The youngest sedimentary series, dated at 1.0–0.8 Ma, comprised periglacial deposits developed as yellowish clay sands cemented with rock rubble (Głazek *et al.* 1976). Likewise, there were almost no bones there. A detailed analysis of the faunal assemblage failed to confirm this subdivision and now the main fauna from W1 is dated to 3.6–3.2 Ma. The site yielded 115 species and forms of vertebrates, with 9 amphibians, 15 reptiles, 4 birds, 30 insectivores, 11 bats, 1 lagomorph, 27 rodents, 14 carnivores, 2 perissodactyls and 2 artiodactyls (Samsonowicz 1934; Stach 1959; Sulimski 1962; Kowalski 1989a, b, 1990; Nadachowski *et al.* 1989; Rzebik-Kowalska 1989, 2009, 2014; Wolsan 1989, 1990; Wołoszyn 1989; Szynkiewicz 1993, 2015; Stefaniak 2015; Marciszak and Lipecki 2020; Czernielewski 2021, 2022, 2023).

Locality Węże 2 (W2; 51º5'53"N 18º47'20"E, 200 m a.s.l.) is situated on the NW slope of Zelce Hill, c. 200 m from and 20 m below W1 (Text-fig. 1). It is a vertical fissure, part of a buried and destroyed cave system of Late Jurassic origin. The fissure is SW-NE



Text-fig. 1. Location of sites with *Martes wenzensis* remains in Poland (Węże 1, Węże 2 and Rębielice Królewskie 1A) and Bulgaria (Varshets). Position of localities in both countries marked with a yellow dot.

oriented, 10 m long, 4 m wide and 3–5 m deep (its extension to the NE is a 5 m long collapsed corridor). In 1958, Sulimski found there karst forms with numerous remains of terrestrial vertebrates. The excavations carried out in 1958–1961 provided abundant remains of amphibians, reptiles and mammals (Sulimski 1962; Kowalski 1989a, b; Nadachowski *et al.* 1989; Stefaniak 1995). The skeletal remains of small animals were already examined by the discoverer (Sulimski 1962). The topmost sediments were formed of calcareous, sandy rubble, and bone-bearing breccia mixed with weathered material. The bottom clayey layers included sandy breccia, bones and weathered material (Sulimski 1962; Szynkiewicz 2015). The faunal assemblage of Węże 2 is less numerous than that from W1, being represented by 8 amphibian, 7 reptile and 51 mammal species. The faunal assemblage indicated a younger age compared to W1 and W2 is assigned to 2.5–2.2 Ma (Młynarski and Szyndlar 1989; Nadachowski 1989; Wołoszyn 1989; Kowalski 1990; Stefaniak 1995; Rzebik-Kowalska 2009; Bocheński *et al.* 2012; Sansalone *et al.* 2016).

Another Polish site, i.e., Rębielice Królewskie (50º59'16"N 18º50'38"E, 213 m a.s.l.), is situated on the western slope of Rębielska Hill (258.5 m a.s.l.; Text-fig. 1). The excavations in the 1970s and early 1980s provided abundant palaeontological material, mostly that of amphibians, reptiles, birds and small mammals (Kowalski 1990). A few faunal assemblages (of different species composition and period of occurrence) were distinguished. *Martes wenzensis* was found in Rębielice Królewskie 1A (RK1A) dated to 2.6–2.4 Ma (Kowalski 1990). The assemblage included 16 amphibians, 11 reptiles, 16 birds, 30 insectivores, 1 lagomorph, 26 rodents, 7 carnivores and 2 artiodactyls (Czyżewska 1989; Młynarski and Szyndlar 1989; Nadachowski 1989, 1990; Rzebik-Kowalska 1989, 2009; Szynkiewicz 1993; Bocheński *et al.* 2012; Stefaniak 2015).

The Bulgarian site Varshets (Va; 43º10'58''N 23º16'58''E, 359 m a.s.l.) is situated 6 km north-east of the town of Varshets (north-western Bulgaria) in the northern foothills of the Stara Planina Mts (Text-fig. 1). It represents a remnant of a diaclasic cavern, formed in Upper Jurassic limestones. The cavern walls are covered in several places by a 3 cm coating of aragonite and calcite limestones of a layered texture. The filling matter of the cavern consists of clay terra rossa, including fossil bones. The fauna of Varshets is slightly older than Saint Vallier (France) but slightly younger than Roca-Neyra, another French site (Spassov 2000, 2003). Recent estimates of the absolute age for the noted French landmark localities (Nomade *et al.* 2014) suggest an older age for Varshets of about at least 2.4 Ma (Spassov 2016). Keeping in mind that the age of Saint Vallier is estimated at about 2.5–2.4 Ma, and the age of Roca-Neyra at 2.6 Ma (Nomade *et al.* 2014), the age of Varshets should be around 2.5 Ma. The very abundant fauna consists of c. 133 species: amphibians (4), reptiles (7), birds (66), insectivores (13), bats (9), one lagomorph, rodents (14), carnivores (15), perissodactyls (2), and artiodactyls (4) (Spassov 1997, 1999, 2001, 2003, 2005, 2011, 2016; Spassov and Crégut-Bonnoure 1999; Popov 2001, 2003, 2004; Boev 2007, 2010, 2012, 2013, 2014, 2015a, b, 2016).

## MATERIAL AND METHODS

The identification of marten remains analysed in the paper was performed using a basic morphometric analysis. Measurements were taken point to point, with an electronic calliper, to the nearest 0.01 mm according to the scheme presented in Appendixes 1–3. Each value given here is the mean of three measurements. Additionally, some measurements were taken using a set for image analysis Olympus (Olympus stereomicroscope ZSX 12, camera Olympus DP 71, Cell D software). A Canon EOS 5D camera was used to prepare the photographic documentation of the fossil material. Statistical analysis was performed using 'Statistica' software (version 10.0 OL). Osteological and dental terminology follows Anderson (1970). Morphotype analyses were made according to Gimranov and Kosintsev (2015) and Jiangzuo *et al.* (2021). The age of the Mammal Neogene zones (MN) is based on the system of biostratigraphic zones in the stratigraphic record used to correlate mammal-bearing fossil localities of the Neogene period of Europe. Throughout the text, upper teeth are referred as capital letters (e.g., P4), while the lower ones as lowercase letters (e.g., p4).

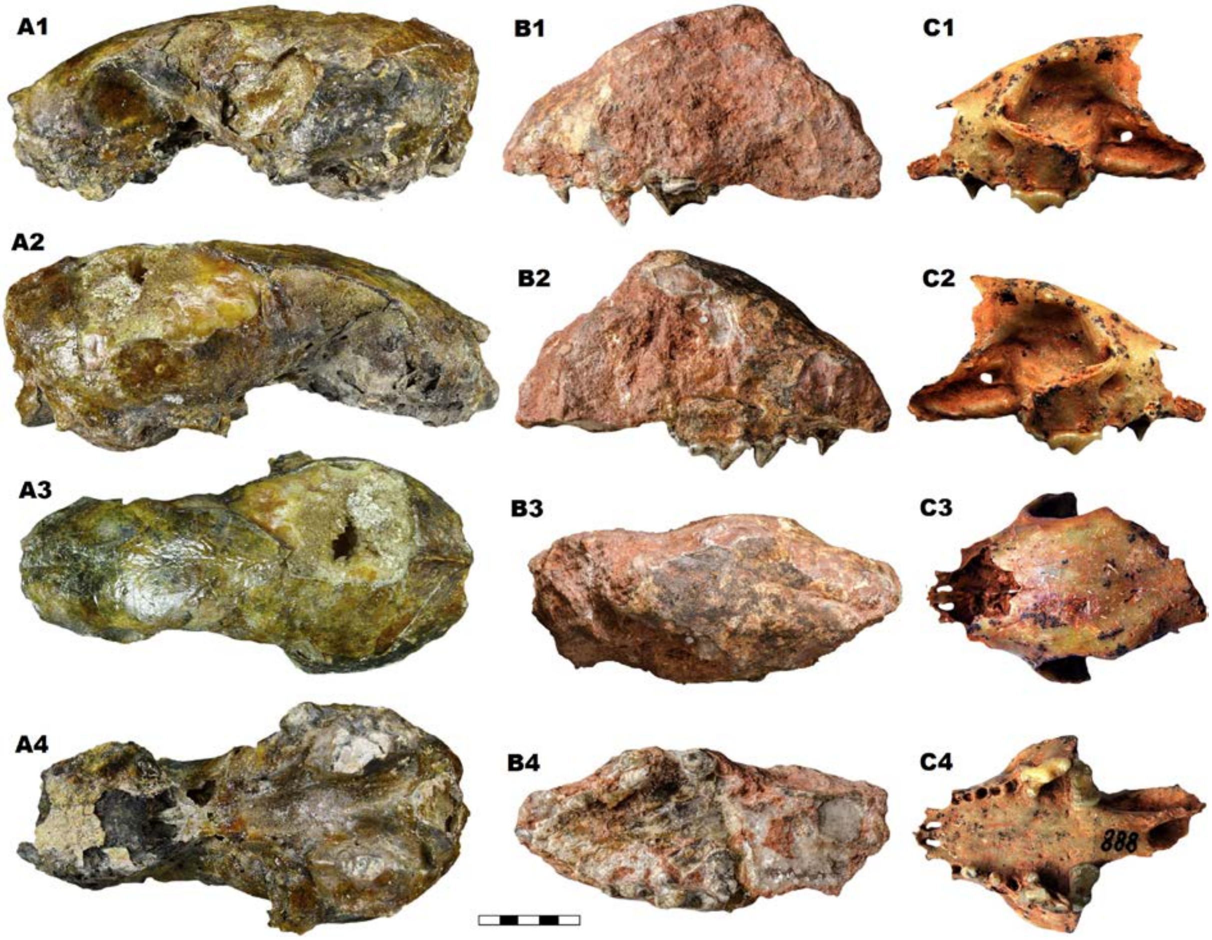
Morphometrical analysis is based on our own measurements. For comparison, we used the materials of *M. vetus*, and the extant *M. martes* and *M. foina* from the territory of Poland. The vast majority of *M. vetus* remains were measured by the authors and came from the following sites: Schernfeld (Germany; 1.9–1.6 Ma), Kamyk (Poland; 1.9–1.8 Ma), Żabia Cave (Poland; 1.7–1.5 Ma), Deutsch Altenburg (Austria; 1.4–1.2 Ma), Kielniki 1 (Poland; 1.3–1.1 Ma), Zalesiaki 1A (Poland; 1.3–1.1 Ma), Sackdilling Cave (Germany; 0.8–0.7 Ma), Stránská Skála (Czech Republic; 0.8–0.7 Ma), Kozi Grzbiet (Poland; 0.8–0.7 Ma) and Południowa Cave (Poland; 0.8–0.7 Ma). The data from Somssich Hill 2 (Hungary; 1.1–1.0 Ma) follow Gasparik and Panozyi (2018).

Abbreviations used in the text: B – breadth; Bp – distal breadth; B ta – talonid m1 breadth; B tr – trigonid m1 breadth; CBL – condylobasal length of the skull; FOR – mental foramens spacing; L – length; L pr – protocone length; L ta – talon/talonid length; L tr – trygon/trigonid length; max – maximum value; min – minimum value; n – number of bones/individuals; *s. l. – sensu lato*; *s. str. – sensu stricto.*

## SYSTEMATIC PALEONTOLOGY

Order Carnivora Bowdich, 1821
Family Mustelidae Fischer de Waldheim, 1817
Subfamily Guloninae J.E. Gray, 1825
Genus *Martes* Pinel, 1792
*Martes wenzensis* Stach, 1959
(Text-figs 2–7)

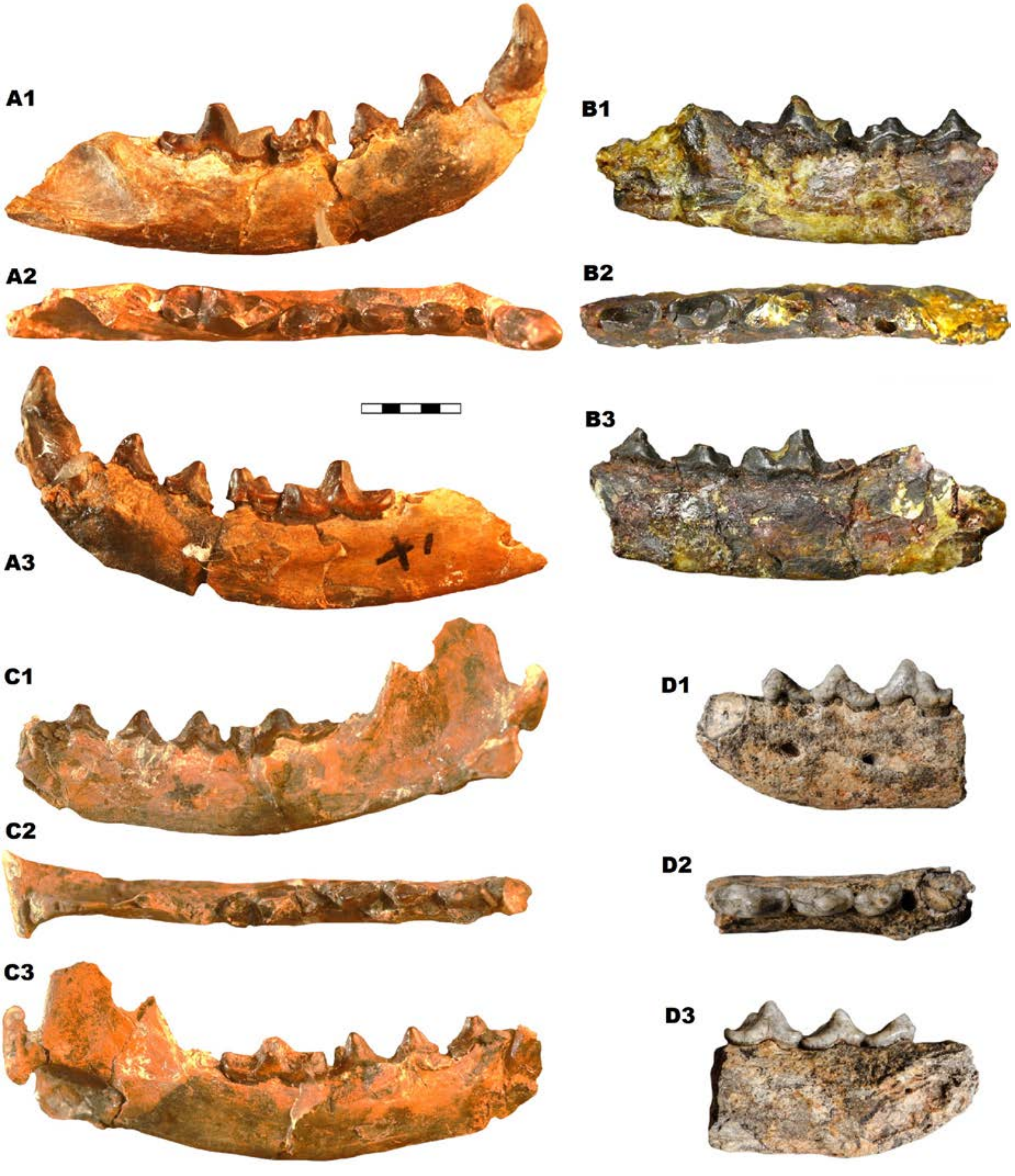
EMENDED DIAGNOSIS: Large, robust marten; cranium with a short and broad viscerocranium; broad incisor row moderately extended forward; flat forehead with a well-marked concavity in the mid-



Text-fig. 2. Skulls of *Martes wenzensis*. A – MZ VIII Vm-218; Węże 1; B – MF/342/1; Węże 1; C – FM/888; Varshets. All specimens shown in left (1), right (2), dorsal (3), and ventral (4) views, on the same scale. Scale bar equals 20 mm.

dle part; elongated and broad temporal region with a broad and long 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; the apex of cranial elevation situated almost at half length, muzzle area noticeably broadened at the canines; C1 with a broad and short crown; broad P2; narrow P3 with a gently concave buccal margin and weakly convex lingual margin; large and robust P4 longer than M1 breadth, with protocone length equal to the distal breadth and strong mesial and mesio-lingual cingulum; large M1 with trigon length equal to the talon length, moderately complicated microrelief on the occlusal surface and large metacone; mandible with an elongated and stout body, gently convex mandibular lower margin under m1, robust and large symphysis, triangular and deep masseteric fossa, mental foramens widely spaced; large and robust c1; large and narrow p2–p4; stout and large m1 with a proportionally short and robust trigonid and long and low talonid, which is narrower than the trigonid, and with large metaconid.

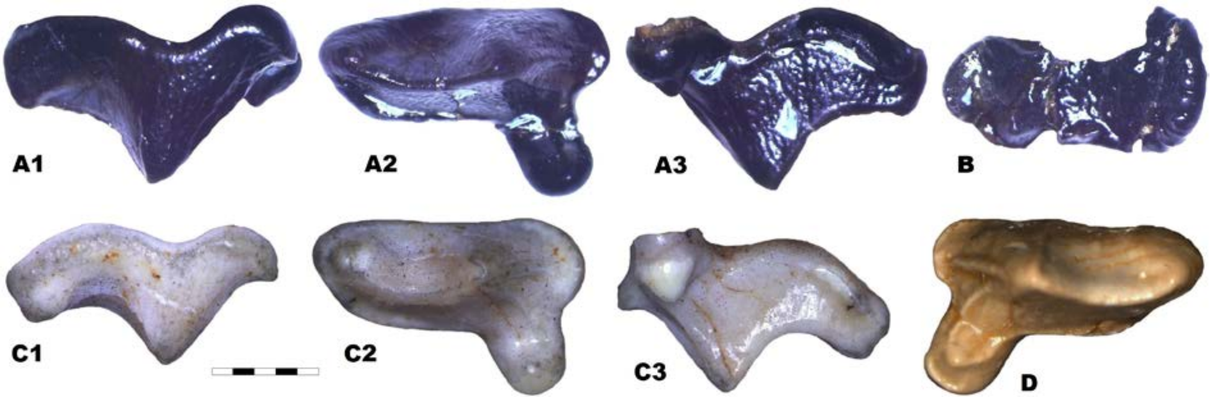
TYPES: Stach (1959) do not designate a holotype, while Anderson (1970) proposed the viscerocranium with preserved left, mesial part of P4, lingual part of M1, and right, distal part of P2 and P3–M1 (MF/342/1, stored in ISEZ) (Text-fig. 2B1–4) as type one. Adhering to this convention, this individual was designated as a neotype. The specimen was described in Stach (1959, pp. 101, 110–119, fig. 2.3, table 4) and in Anderson (1970, pp. 11, 22–24, figs 5b, 12, table 2). Additionally, we have designated a second neotype, a mesial part of the left mandible with p2–p4 (MF/342/2, stored in ISEZ) (Text-fig. 3D1–3). The specimen was described in Stach (1959, pp. 101, 110–119, fig. 2/2, table 5) in Anderson (1970, pp. 22–24, fig. 12, table 2).



Text-fig. 3. Mandibles of *Martes wenzensis* from Węże 1. A – right mandible (W1.5.2), B – right mandible (MZ VIII Vm-218), C – left mandible (W1.5.1), D – left mandible (MF/342/2). All specimens shown in buccal (1), occlusal (2), and lingual (3) views, on the same scale. Scale bar equals 10 mm.

MATERIAL: Only cranial material belonging to adult individuals was found. Most of the materials are incomplete, and some parts are missing. The teeth have a varying stage of wear, from almost intact to strongly worn. The most numerous remains were collected in W1:

(1) skull without zygomatic arches and rostral part, with partially damaged palatal region and without



Text-fig. 4. Upper teeth of *Martes wenzensis*. A – right P4 (W1.5.3) from Węże 1; B – right M1 (W1.5.3) from Węże 1; C – left P4 (W2.5.1) from Węże 2; D – left P4 from Rębielice Królewskie 1A. All specimens shown in buccal (1), occlusal (2), and lingual (3) views, on the same scale. Scale bar equals 5 mm.

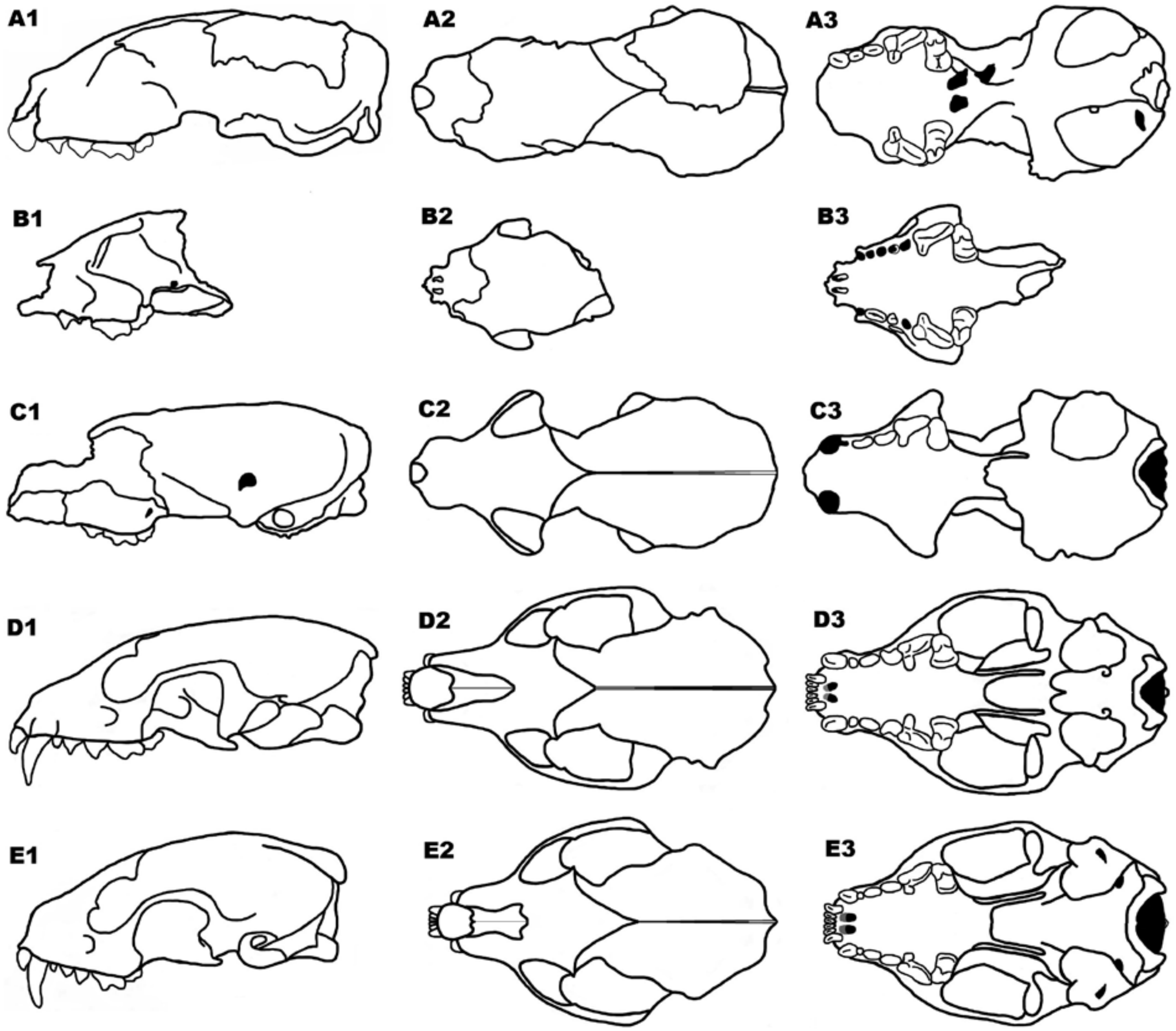
teeth (formerly skull with I1–M1 on both sides; Text-fig. 2A1–4; and permanently joined right mandible without ramus and with c1-m2; Text-fig. 3B1–3) (MZ VIII Vm 218, stored in MZ). Specimen described in Stach (1959, pp. 101, 110–119, fig. 2.4, table 4).
(2) neurocranium fragment with damaged tympanic bullae (MZ VIII Vm 355-9, stored in MZ);
(3) neurocranium (MZ VIII Vm 355-10, stored in MZ);
(4) right mandible without ramus and with p3–m1 (previously permanently joined with skull no. MZ VIII Vm-218, stored in MZ). Specimen described in Stach (1959, pp. 101, 110–119, fig. 2.4, table 5);
(5) left mandible with damaged symphysis and ramus and with c1 and p2–m1 (W1.5.1, stored in ZP) (Text-fig. 3A1–3);
(6) right mandible without symphysis and ramus, with c1 and p2-m1 (W1.5.2, stored in ZP) (Text-fig. 3C1–3);
(7) fragment of the right maxilla with P4 and worn M1 (W1.5.3, stored in ZP) (Text-fig. 4A1–3 and B);
(8) left C1 (W1.5.4, stored in ZP);
(9) crown of the left C1 (W1.5.5, stored in ZP);
(10) worn left C1 (W1.5.6, stored in ZP);
(11) right c1 (W1.5.7, stored in ZP);
(12) distal part of the right P3 (W1.5.8, stored in ZP);
(13) crow of the right p2 (W1.5.9, stored in ZP);
(14) left p4 (W1.5.10, stored in ZP);
(15) crown of the left p4 (W1.5.11, stored in ZP).

A fragment of the left maxilla with P4 (W2.5.1; Text-fig. 4C1–3) comes from Węże 2. We used two isolated teeth, left P4 (RK/1; Text-fig. 4D) and right c1 (RK/2), from RK1A. Finally, a viscerocranium without zygomatic arches, with damaged nasal aperture, and preserved whole palate, with left P4–M1 and right P2, mesial part of P3 and P4–M1 (FM/888; Text-fig. 2C1–4) was found in Varshets (Bulgaria).

DESCRIPTION: The most complete cranium (MZ VIII Vm-218) was described as the specimen of considerable size and robust build (Text-fig. 5A1–3; Table 1). The highest point of *M. wenzensis* is located on the vertical line drawn through the auditory bullae area (Text-fig. 5A1–3). The frontal line runs somewhat mesially to the nasal bones, and depresses slightly on the boundary between the cerebral and facial areas. The top of the skull forms an arch, uniformly domed mesially and distally (Text-fig. 5A1–3). The viscero- and neurocranium are nearly equal in length. The muzzle area is broadened at the canines, narrowed behind them and then gradually widened (Text-fig. 5A1–3). The rostral area is proportionally short and massive. The jaws are shorter and the nasal aperture is more vertical. As a result, the muzzle area is compact and short in lateral view. The incisors' region of the W1 specimen is strongly damaged, so any precise description is impossible. The nasals are large

| Measurements | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 10 | 11 | 13 | 14 | 15 | 17 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Value [mm] | 91.36 | 92.16 | 86.17 | 41.79 | 53.07 | 45.21 | 25.68 | 43.37 | 36.69 | 24.84 | 9.84 | 23.27 | 35.86 | 10.87 |
| | | | | | | | | | | | | | | |
| Measurements | 18 | 19 | 20 | 21 | 22 | 23 | 24 | 25 | 26 | 27 | 28 | 29 | 30 | 32 |
| Value [mm] | 28.92 | 29.64 | 33.18 | 24.11 | 37.89 | 42.17 | 21.64 | 12.18 | 12.05 | 10.54 | 12.26 | 22.17 | 14.86 | 34.36 |

Table 1. Measurements of *Martes wenzensis* cranium from Węże 1 (MZ VIII Vm 218). For measurements description see Appendix 1.



Text-fig. 5. Comparison of the skull morphology of European martens. A – *Martes wenzensis* (Węże 1); B – *Martes wenzensis* (Varshets), C – *Martes vetus* (Sackdilling Cave); D – *Martes martes*, 5 – *Martes foina*. All individuals drawn in left (1), dorsal (2), and ventral (3) views, on the same scale.

and rounded, and the nasal bones are broad, short and W-shaped. The temporal region is compressed, proportionally elongated and narrow, with moderately wide postorbital processes. The postorbital bar is narrow and V-shaped (Text-fig. 5A1). The semi-circular lines running from the frontal bones form an acute angle in distal direction and merge with the thick sagittal crest of moderate height. The oval, large orbits have minute lacrimal processes (Text-fig. 5A1). The infraorbital foramina are large and oval. The palate is long and proportionally broad at the base of canines and carnassials, while the post-molar part of the palatal lamina horizontalis is elongated and narrow. The spina nasalis caudalis is U-shaped and running slightly externally in distal direction. The auditory bullae are broad and elongated, moderately inflated, and located slightly distally. The internal part is swollen, while the external one is more flat. Both parts are separated by a slightly expanded depression running centrally along the whole length (Text-fig. 5A3). The second viscerocranium of *M. wenzensis* from W1 (MF/342/1) is very similar in morphology and size. The specimen from Va (FM/888) is smaller, but morphologically resembles both specimens from W1 (Text-fig. 5B1–3).

The upper tooth row is curved distally. The teeth are tightly set. The rounded alveolus for the absent P1 shows that it was one-rooted and moderately reduced.

| | | W1 | | | | W2 | Va | |
|---|---|---|---|---|---|---|---|---|
| | | MF/342/1 | MZ VIII VM 218 | W1.5.3 | W1.5.4 | W2.5.1 | FM 888 | |
| C1 | L | | 7.14 | 6.97 | 6.98 | | | |
| | B | | 4.46 | 4.34 | 3.97 | | | |
| P2 | L | 5.92 | 5.98 | | | | 4.90 | |
| | B | 2.89 | 3.14 | | | | 2.50 | |
| P3 | L | 7.03 | 6.94 | | | | | |
| | B | 3.37 | 3.27 | | | | | |
| P4 | L | 12.16 | 12.14 | 11.97 | | 11.17 | 9.40 | 9.40 |
| | L pr | 4.45 | 4.54 | 4.56 | | 3.78 | | |
| | Ba | 6.97 | 6.88 | 7.26 | | 6.89 | 5.80 | 6.00 |
| | Bp | 4.42 | 4.62 | 4.45 | | 3.87 | 3.80 | 3.80 |
| M1 | B | 10.41 | 10.56 | 10.64 | | | 9.20 | 9.20 |
| | L1 | 6.32 | 6.63 | 6.37 | | | 5.70 | 5.70 |
| | L2 | 4.45 | 4.49 | 4.56 | | | | |
| | L3 | 5.39 | 5.41 | 5.35 | | | | |

Table 2. Measurements of the upper dentition of *Martes wenzensis* specimens. For explanation of symbols see text.

This tooth was tightly squeezed between C1 and P2. The P2 is an elongated tooth, with a strong distal cingulum. The buccal margin is nearly straight and the lingual margin is gently convex in its middle part. The elongated, two-rooted P3 has the protocone situated more mesially than in P2 and rising gently buccally. The distal crown part is longer than the mesial one. The crown bears an elongated, distal cingular projection. The small mesio-lingual prominence of the cingulum forms a faint mesial crest to the apex of the protocone. The buccal margin is moderately concave, while the lingual one is moderately convex in its middle part. The mesial and distal cingulum ridges and both crests running from the protocone top are thick, high and well-developed.

The large and robust P4 is longer than M1 breadth (Table 2). The paracone and metacone form a nearly straight line (Text-fig. 4A1–3). The tooth is three-rooted and the external median rootlet is absent. The rounded protocone protrudes mesio-ligually at an angle of c. 60º to the mesio-distal axis. It is long and high, with a centrally placed top. Its length is equal to the distal breadth. The high, strong paracone has a convex, sharp cutting edge extending distally to the metacone. The mesial paracone border is rounded and oriented slightly mesio-buccaly. Three long and thick crests run mesially from the paracone top, with one of them connected with the protocone peak. The metacone is high and robust, with rounded distal edge. The cingulum is well-developed, with a notably thick ridge occurring in the mesial part. It surrounds the protocone and lingual and distal margins of the metacone.

The P4 from RK1A is similar to the P4 from W1, but it is smaller (Text-fig. 4D; Table 2). Three ridges running from the top of the paracone are thinner. The protocone is rectangular in occlusal view, notably elongated, and distinctly protruding from the rest of the crown. The high and well-developed protocone top is connected with the other ridges by a thick, long wall which connects with the mesial cingulum. The parastyle area is quite small, but not displaced as far mesially as in the P4 from W1. Apart the similarities to the older specimens from W1, there are some morphological differences recognised as progressive features. Apart from the smaller size, the disto-buccal cingulum is less pronounced. The buccal margin of the crown is also different. In the specimen from W1, the buccal margin is almost straight and slightly convex only in the middle. In the specimen from RK1A, the buccal margin is slightly concave in its middle part (Text-fig. 4D). The P4 from W2 (W2.6.1) metrically is similar to the P4 from RK1A, but differs morphologically (Text-fig. 4C1–3). The parastyle is larger and rounded, with a weakly developed mesial cingulum. The cingulum and three ridges running from the top of the paracone are thin and delicately marked. The paracone is lower than in the RK1A and W1 specimens. The protocone is significantly shorter, with a gently marked cusp, and it is poorly distinguishable from the rest of the crown. The buccal wall has a well-defined concavity in its middle part. In occlusal view, the outline looks more elongated and less robust than in the specimens from W1 and RK1A.

Both P4s from Va are similar to the P4 from W2 in having a short and low protocone, rounded and large parastyle area, only slightly marked crests running from the top of the paracone and a well-marked concavity on the buccal margin. The most obvious difference is the smaller size and the narrower blade part of the P4 in teeth from Va.

| | | MF/342/2 | MZ VIII Vm 218 | W1.5.1 | W1.5.2 | W1.5.7 |
|---|---|---|---|---|---|---|
| mandible | 4 | | 43.39 | 42.98 | 43.47 | |
| | 5 | | 35.69 | 35.64 | 35.71 | |
| | 6 | 22.08 | 22.48 | 22.56 | 21.93 | |
| | 7 | | 15.78 | 15.71 | 15.45 | |
| | 8 | 7.71 | 6.79 | 6.48 | 6.46 | |
| | 9 | | | 21.98 | | |
| | 12 | 10.64 | 10.02 | 9.94 | 9.97 | |
| | 13 | 5.44 | 5.09 | 5.16 | 5.14 | |
| | 14 | | 11.39 | 11.37 | 11.46 | |
| | 15 | | 5.11 | 5.04 | 5.06 | |
| | 16 | | | 4.47 | | |
| | 17 | | | 11.92 | | |
| | 18 | 17.84 | | | | |
| | 19 | 8.67 | | | | |
| c1 | L | | 6.97 | 6.94 | 6.77 | |
| | B | | 4.87 | 4.88 | 4.72 | |
| p2 | L | 5.37 | 5.59 | 5.68 | 5.47 | |
| | B | 2.74 | 2.73 | 2.79 | 2.78 | |
| p3 | L | 6.52 | 6.23 | 6.02 | 5.96 | |
| | B | 3.02 | 3.07 | 3.09 | 3.02 | |
| p4 | L | 7.94 | 7.38 | 7.28 | 7.29 | 7.31 |
| | B | 3.49 | 3.34 | 3.29 | 3.32 | 3.39 |
| m1 | L | | 11.44 | 11.49 | 11.27 | |
| | L tr | | 7.45 | 7.41 | 7.36 | |
| | L ta | | 4.11 | 4.14 | 4.07 | |
| | B tr | | 4.46 | 4.51 | 4.48 | |
| | B ta | | 4.08 | 4.09 | 4.04 | |

Table 3. Measurements of mandibles and lower dentition of *Martes wenzensis* specimens from Węże 1. For explanation of symbols see text and Appendix 1.

The M1 from W1 is large, even if its breadth is smaller than the P4 length (Table 3). The trigon and talon are similar in length and separated by a deep and broad depression running through the middle crown part. The trigon is moderately wide and long, with a strong and abrupt concavity of the buccal margin. Both main buccal cusps, paracone and metacone, are elongated and high, and the paracone is larger. They are well separated by a deep, narrow, V-shaped valley, while the apexes of both cusps are connected by a thin, long crest. The talon is longer than the trigon and 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 deep and broad valley in two parts of similar length and height. The moderately reduced metaconule is not connected with any other cusp or crest. This low and elongated cuspid is situated in the middle part of the crown. A long and thin crest corresponding to the buccal cingulum margin runs in parallel along the whole talon length. A dozen of short, thin lingually extending stretches raise vertically from this crest. The well-developed lingual cingulum forms a thick crest.

The mandibular body is long and stout (Text-fig. 3). Its height measured behind the m1 is equal to the m1 length (Table 3). Two rounded mental foramens are widely spaced. Both are similar in size, the mesial one situated under the distal root of p2, while the distal mental foramen is located under the distal root of p3, slightly lower than the mesial one (Text-fig. 3). The masseteric fossa is deep and reaches the m1 and m2 boundary. Its mesial edge is rounded. The mesial part narrows dorso-ventrally and its ventral margin only slightly exceeds the midline of the mandibular body in dorso-ventral direction. The large and massive condyle is situated at the level of m1. The lover mandibular body margin forms a gently curved arch, uniformly domed mesially and distally. The symphysis part is massive and elongated, well proportionate to the large size and robust canine.

The series of cheek teeth is almost straight and only the distal part of the p2 crown moderately arches lingually. In the tooth row, the premolars occupy a more buccal position in relation to the molars, so the lingual margin of the p4 roots is displaced by c. 5 mm buccally relative to the lingual border of the m1 root

(Text-fig. 3). The premolars and molars are set close together and there is no diastema between them. All teeth are situated at a similar level. The c1 is long and robust, with a proportionally short and strongly curved crown (Text-fig. 3). Two longitudinal grooves run on the buccal and lingual sides of the crown. The rounded alveolus of the absent p1 suggests that this small one-rooted tooth was tightly squeezed between c1 and p2. The two-rooted p2 is low-crowned, with the protoconid displaced more mesio-medially. Its occlusal outline is slightly arched, with an elongated distal part. Two thin crests run in the mesial and distal direction from the protoconid top. The distal cingulum forms a thick 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 its buccal margin slightly concave in the middle part. The lingual margin is slightly convex in the middle length. The mesial and distal margins are blunt. The protoconid is also displaced mesio-medially, however less 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 edges running from the protoconid top are strongly marked, especially the distal one. On the distal edge, a small tubercular convexity is present just behind the peak. The mesial and distal cingulum is well-developed. The two-rooted p4 is relatively high-crowned and has the protoconid placed almost exactly centrally. A relatively large cuspid is present after the disto-buccally situated protoconid. It is associated with the distal crest, running distally from the protoconid apex. 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 in the distal direction. A gentle, buccal convexity occurs in the middle part of the crown. The lingual margin is slightly arched. The mesial margin is blunt; the distal margin is rounded. The mesial and distal cingulum is well-developed, and forms thick and high ridges. On them, a delicate microrelief of horizontal thin ribs is recognisable. The distal, cingular projection is less elongated when compared to the rest of the crown. Collared by a thick cingulum, the inner surface of this projection is crescent-shaped and shallow. The stout and large m1 has a proportionally short and massive trigonid with a high protoconid and a low paraconid. The top of the strong metaconid is linked with the paraconid top by a thin crest. The long and low talonid is slightly narrower than the trigonid. A thick, high longitudinal ridge, surrounding the middle part, and ending on the metaconid base, runs from the elongated and low hypoconid. Behind the hypoconid (connected with it), a minute hypoconulid is present. The paraconid edge is weakly developed. The mesial margin is rounded, while the distal one is blunt. The buccal margin is almost straight, while the lingual margin holds a gentle concavity in its median part. The mesial and distal cingulum is strong. The alveolus for the absent m2 (alveolar length of c. 3.5–3.7 mm) shows that this was a moderately reduced, one-rooted tooth.

COMPARISON OF THE SKULL MORPHOLOGY: *Martes wenzensis* was described as an ancestor of *M. vetus*, and is larger than its presumed descendant (Text-fig. 5A1–3). The cranium of the type specimen of *M. vetus* from Sackdilling Cave (H Sa 80-1; stored at the GeoZentrum Nordbayern, Lehrstuhl Paläoumwelt, Friedrich-Alexander-Universität Erlangen-Nürnberg) was described as having the size of *M. martes* and *M. foina* (Heller 1930, 1933; Anderson 1970; Marciszak *et al.* 2021; Text-fig. 5C1–3). With the CBL of 85 mm, the size of the specimen falls into the range of variation of males of both species. The mean CBL of *M. martes* ♂♂ is 86.26 mm (81.84–94.43 mm, n = 69), while the CBL of *M. foina* ♂♂ is 85.64 mm (82.43–91.49 mm, n = 57). The Sackdilling marten is smaller than *M. wenzensis* (CBL = 92.36 mm). Two other crania of *M. vetus* from Deutsch Altenburg 2 (1.4–1.2 Ma) and Południowa Cave (0.8–0.7 Ma) are incomplete and slightly larger than the type specimen. Even so, both specimens (MZ VIII Vm-218, MF/342/1) of *M. wenzensis* from W1 are larger than *M. vetus*.

The size of *M. wenzensis* exceeds the mean of the extant *M. martes* ♂♂ and *M. foina* ♀♀ and is more comparable with the mean of the Late Pleistocene *M. martes* ♂♂ (CBL = 96.74 mm, 88.97–112.74 mm, n = 9), which is regarded as an exceptionally large marten (Anderson 1970). The size of *M. wenzensis* clearly exceeds the values obtained for ♀♀ of both extant martens (the mean CBL of ♀♀ of *M. martes* is 78.96 mm, 74.75–81.65 mm, n = 80 and CBL of ♀♀ of *M. foina* is 78.01 mm, 74.59–80.75 mm, n = 57). The Va marten is slightly smaller than individuals from W1, although still larger than *M. vetus* (Text-fig. 5B1–3).

*Martes wenzensis* resembles *M. vetus* in the short and broad viscerocranium, and less extended forward, broad incisor row. Both species also have a short and broad palate, especially in its distal part. Their snout is noticeably broadened at the canines and P4 level. The frontal profile (in lateral view) of *M. wenzensis* is almost straight, with a poorly marked crossing between the maxillae and the frontal region. In *M. vetus*, the frontal profile (in lateral view) is strongly convex, with a well-marked concavity in the middle of the frontal part. *Martes wenzensis* possesses an elongated and broad temporal region with a broad and long postorbital bar situated almost exactly in the middle of the temporal region. The temporal region of *M. vetus* is compressed, short and broad. The broad and short postorbital bar is situated slightly mesially. In both species, the tympanic bullae are large and strongly inflated, with large tympanic chamber. The bony choana are distally extended, with a well-marked middle spur. They also have a convex median indentation of the palate (Text-fig. 5).

The cranial morphology of *M. wenzensis* shows an admixture of features inherent to both extant marten species. The rostral area is similar to that of *M. foina*, proportionally shorter and more massive (Text-fig. 5E1–3). The jaws are shorter and the nasal aperture is more vertical. As a result, the muzzle area is compact, high and short in lateral view. The muzzle area in *M. wenzensis* is broadened at the canines, narrowed behind them and then gradually widened (Text-fig. 5A1–3). In *M. martes*, the snout is proportionally longer but narrower, and its shape is almost triangular, with its facial part only gently widening at the canine level (Text-fig. 5D1–3). Two indexes showed that in the wide snout *M. wenzensis* strongly resembles *M. foina* and differs considerably from *M. martes*. The C1–C1 B to CBL ratio of *M. wenzensis* (25.2) matches with values obtained for *M. foina* (23.4, 20.8–26.3, n = 169) and notably exceeds those of *M. martes* (20.1, 19.1–21.9, n = 169). The same results were obtained to the second ratio of the breadth on P4–P4 to CBL. The value of this index in *M. wenzensis* (38.9) fits to those of *M. foina* (35.7, 34.1–39.3, n = 169) and is higher than those of *M. martes* (32.7, 29.8–36.1, n = 164). The nasal bones are similar, i.e., broad, short and W-shaped.

*Martes wenzensis* also shares some similarities with *M. martes* in cranial morphology. The temporal region is narrow and elongated. The index of the interorbital length (the distance between frontal postorbital processes to the postorbital constriction) to the postorbital breadth well illustrate this feature. The distal part of the sagittal crest is less developed and low. The oval, large orbits possess minute lacrimal processes. In addition, the infraorbital foramens resemble those of *M. martes* in their large size and oval shape. The caudal nasal spine is U-shaped as in *M. martes*, instead of V-shaped as in *M. foina*. The B/L ratio of the auditory bullae is closer to the *M. martes* than to the *M. foina* mean. The B/L of auditory bullae in *M. wenzensis* is 67.0, while the mean of *M. martes* is 64.9 (58.9–67.8, n = 164) and of *M. foina* is 59.6 (52.9–63.9, n = 169; Table 4).

The cranium of *M. wenzensis* holds also features typical only for this species. The apical point of cranial elevation in *M. martes* is situated at half-length of occipital bones (Text-fig. 5D1), while in *M. foina* it is located somewhat more mesially (Text-fig. 5E1). The highest point of *M. wenzensis* is located on the

| | *Martes wenzensis* | | *Martes vetus* | | *Martes martes* | | *Martes foina* | |
|---|---|---|---|---|---|---|---|---|
| ratio | M | min–max (n) | M | min–max (n) | M | min–max (n) | M | min–max (n) |
| B/L of palate | 28.2 | | | | 24.9 | 21.2–27.8 (164) | 26.3 | 22.8–29.4 (169) |
| B/L of auditory bullae | 67.0 | | | | 64.9 | 58.9–67.8 (164) | 59.6 | 52.9–63.9 (169) |
| C1–C1 B/CBL | 25.2 | | 23.4 | | 20.1 | 19.1–21.9 (164) | 23.4 | 20.8–26.3 (169) |
| P4–P4 B/CBL | 38.9 | | 34.9 | | 32.7 | 29.8–36.1 (164) | 35.7 | 34.1–39.3 (169) |
| C1/C1 B/P4–P4 B | 64.9 | | 67.0 | | 60.6 | 50.3–62.9 (164) | 65.9 | 54.4–69.4 (169) |
| IOL/POB | 82.4 | | | | 79.2 | 64.3–92.3 (164) | 64.9 | 49.7–71.6 (169) |
| B/L P2 | 50.7 | 48.8–52.5 (2) | 46.3 | 43.2–47.8 (11) | 51.1 | 46.3–58.7 (366) | 51.7 | 46.8–60.5 (321) |
| B/L P3 | 47.5 | 47.1–47.9 (2) | 50.3 | 46.2–55.3 (21) | 59.6 | 51.4–67.2 (366) | 50.9 | 47.1–56.1 (321) |
| L pr/Bp P4 | 100.5 | 98.3–102.5 (3) | 78.2 | 70.6–87.9 (42) | 95.5 | 81.3–116.9 (366) | 68.5 | 56.1–81.3 (321) |
| M1 B/L P4 | 87.2 | 85.6–88.9 (3) | | | 94.2 | 85.4–111.1 (366) | 91.9 | 82.0–98.8 (321) |
| L tr M1/L P4 | 53.3 | 52.0–54.6 (3) | | | 77.9 | 63.6–89.0 (366) | 58.5 | 40.0–67.3 (321) |
| FOR/L m1 | 57.7 | 56.4–59.4 (3) | 47.8 | 39.4–58.2 (24) | 58.4 | 54.5–66.3 (164) | 29.3 | 21.4–36.6 (169) |
| B/L p2 | 50.3 | 49.1–51.0 (3) | 55.6 | 50.0–59.1 (26) | 55.0 | 47.7–60.0 (366) | 57.9 | 50.0–65.4 (321) |
| B/L p3 | 49.5 | 46.3–52.5 (4) | 50.4 | 44.7–55.3 (26) | 51.8 | 45.3–60.0 (366) | 54.7 | 49.0–60.1 (321) |
| B/L p4 | 45.8 | 44.0–48.0 (5) | 50.1 | 45.4–54.8 (27) | 51.2 | 46.3–56.9 (366) | 53.6 | 47.6–60.0 (321) |
| L ta/L tr m1 | 53.9 | 53.1–55.5 (3) | 40.5 | 32.7–51.2 (58) | 43.5 | 34.4–52.3 (366) | 34.2 | 33.0–48.8 (321) |
| B ta/B tr m1 | 90.8 | 90.2–91.5 (3) | 102.8 | 97.3–105.7 (58) | 104.9 | 100.9–108.3 (366) | 95.8 | 91.7–103.1 (321) |

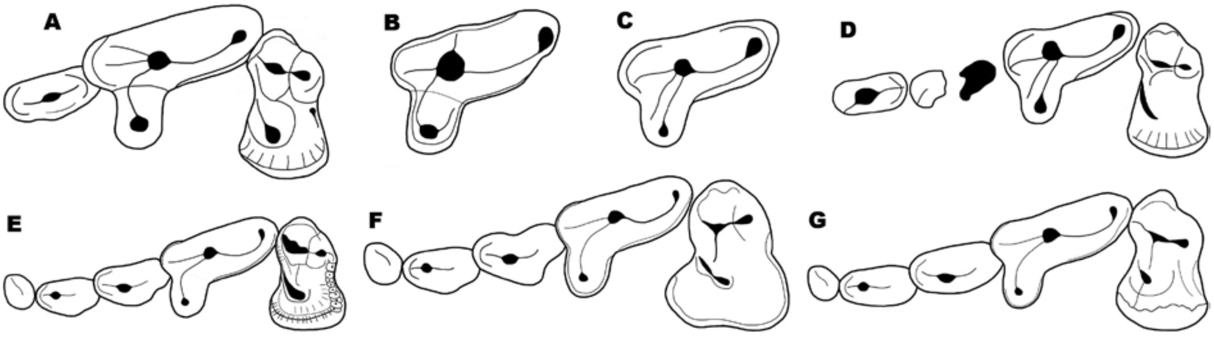
Table 4. Ratios distinguishing the different species of European martens (for abbreviations and measurements schema see Appendixes 1–3).

vertical of the auditory bullae area (Text-fig. 5A1). The viscero- and neurocranium in *M. wenzensis* are nearly equal in length, while in *M. martes* and *M. foina* the neurocranium seems to be longer. The post-molar part of the horizontal plate of palate is elongated and broad. The B/L of palatae ratio of *M. wenzensis* (28.2) exceeds the values obtained for *M. martes* (24.9, 21.2–27.8, n = 164) and falls into the upper part of the range variability of *M. foina* (26.3, 22.8–29.4, n = 169).

COMPARISON OF THE UPPER DENTITION MORPHOLOGY: The P2 of *M. wenzensis* is similar to that of *M. vetus* in weakly marked lingual convexity, but is broader. The P2 B/L mean ratio for *M. wenzensis* is 50.7 (48.8–52.5, n = 2) and is higher than that of *M. vetus* (46.3, 43.2–47.8, n = 11; Table 4). Contrary to that, *M. wenzensis* has a slightly narrower P3 (B/L = 47.5, 47.1–47.9, n = 2) than *M. vetus* (B/L = 50.3, 36.2–55.3, n = 21). This is due to the stronger developed of a lingual convexity in the second species. Both P3 of *M. wenzensis* from W1 represent morphotype A2 with a small lingual bulge. This morphotype is also typical for *M. martes* (73%) (Gimranov and Kosintsev 2015). For *M. vetus*, typical is morphotype A1 without the lingual bulge, which is also characteristic for *M. foina* (97%). This morphotype rarely (19%) occurs in *M. martes* (Text-fig. 6A–D).

The P4 of *M. wenzensis* is particularly large and robust. Apart from the larger size, the main distinctness from *M. vetus* is the longer and higher protocone. Its length in *M. wenzensis* is comparable with the distal breadth of P4. The L pr/Bp P4 index in *M. wenzensis* is much higher (100.5, 98.3–102.5, n = 3) than that of *M. vetus* (94.5, 82.6–99.4, n = 45; Table 4). *Martes vetus* has a moderately long and low protocone, which is slightly shorter than the distal breadth of the crown. The three P4 of *M. wenzensis* from W1 and two from Va represent morphotype A2, with a notch between the protocone and parastyle, non-protruding protocone and concave buccal outline. This morphotype is also quite common in *M. foina* (33%) and *M. martes* (24%) (Gimranov and Kosintsev 2015). The P4 from RK1A represents morphotype A3, with a notch between the protocone and parastyle, the protocone pushing mesially to the parastyle and without buccal concavity. The specimen from W2 was assigned to morphotype A1, with a notch between the protocone and parastyle, the protocone shifted mesialy to the parastyle, and concave buccal outline. This morphotype is also characteristic for *M. vetus*. This is the most common morphotype in extant martens (in both 58%; Gimranov and Kosintsev 2015). The P4 of *M. wenzensis* from RK1A resembles the P4 of *M. vetus* in smaller size, less pronounced disto-buccal cingulum and slightly concave buccal margin in its middle part.

The P4 of *M. wenzensis* from W2 resembles the P4 of *M. vetus* even more in: (1) smaller dimensions; (2) larger and rounded parastyle with a weak mesial cingulum; (3) weaker developed cingulum and the presence of three ridges running from the top of the paracone; (4) lower and shorter paracone, which is also poorer distinguishable from the rest of the crown and (5) narrower distal part. These features are stronger developed in both P4 from Va. Their size (L = 9.40 mm) is within the size variability of *M. vetus* (8.25 mm, 6.87–9.54 mm, n = 55) and fairly below the values of *M. wenzensis* from W1 (12.09 mm, 11.97–12.16 mm, n = 3). In occlusal outline it looks more elongated and less robust. The P4s of *M. wenzensis* from Va are also characterised by a short and low protocone, rounded and large parastyle, weakly marked crests running from the top of the paracone and a well-marked concavity along the buccal margin. All these features are typical for *M. vetus*. The



Text-fig. 6. Comparison of the upper dentition of European martens. A–D – *Martes wenzensis* (A – Węże 1, B – Rębielice Królewskie 1A, C – Węże 2, D – Varshets), E – *Martes vetus* (Żabia Cave), F – *Martes martes*, G – *Martes foina*. All individuals drawn in occlusal view on the same scale.

P4s from Va show intermediate features between *M. wenzensis* and *M. vetus*. It can be regarded as a proof for the single evolutionary lineage of these species (Text-fig. 6D).

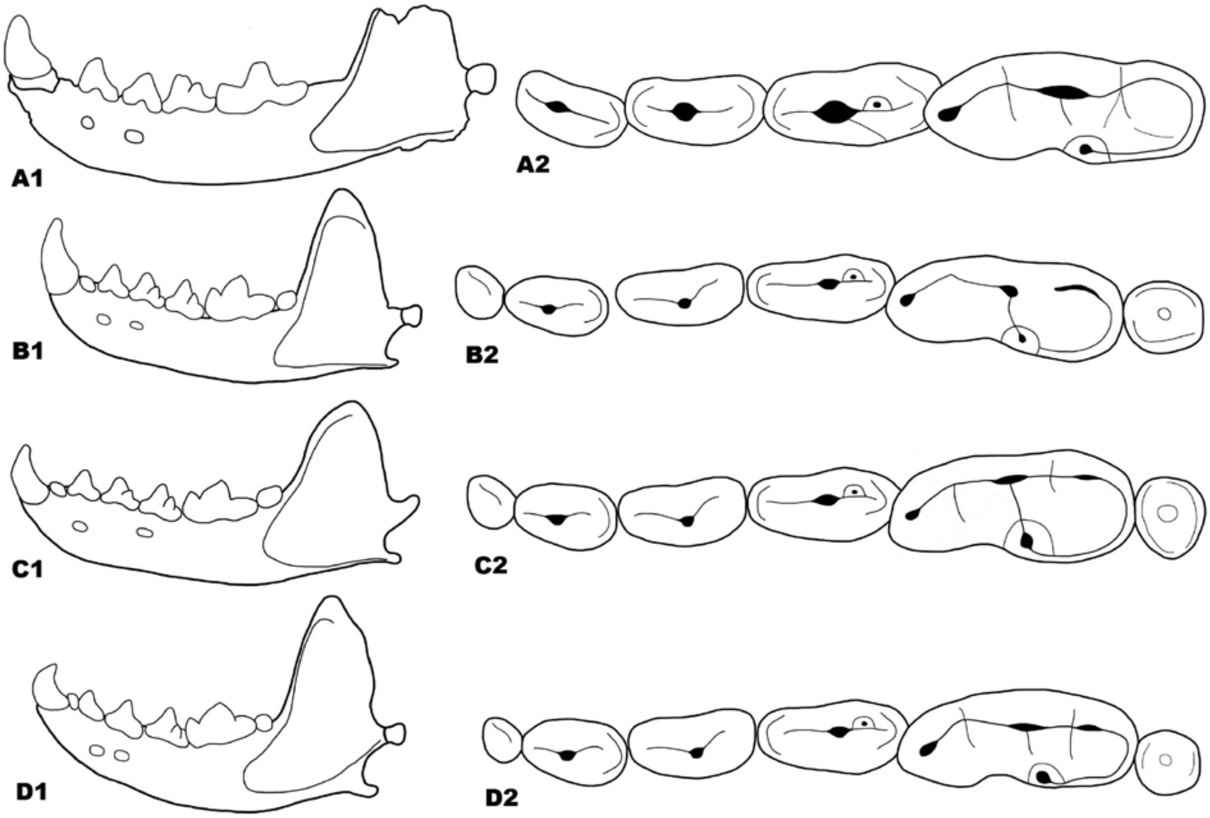
The occlusal outline of M1 of *M. wenzensis* from W1 is similar to that of *M. vetus*, although the microrelief is less complicated. Both species have a moderately wide trigon. The M1 L tr/B ratio mean in *M. vetus* is 66.8 (59.2–76.1, n = 58). The mean of the index is slightly higher than the mean for *M. wenzensis* from W1 (61.1, 59.9–62.8, n = 3). However, the range of *M. wenzensis* is placed within the lower part of the variability of *M. vetus*. Another difference is the larger size of the metaconule in *M. wenzensis*. The M1s of *M. wenzensis* from W1 were assigned to morphotype C3, with a straight lingual and rounded buccal outline, where the preprotocrista bears two small cusps and a metaconule is present. For *M. vetus*, characteristic are morphotypes from group D, with the most common morphotype D2. It possesses a straight lingual and rounded buccal outline, a preprotocrista with two small cuspids, and the hypocone and metaconule are present (Gimranov and Kosintsev 2015). In *M. foina*, only morphotypes from group B occur, with a deep groove between the paracone and metacone (Gimranov and Kosintsev 2015). This is a reliable specific character for this species, which was already pointed by Wolsan *et al.* (1985) and Wolsan (1988). For *M. martes*, the most typical are morphotypes A1 (32%) and A2 (55%), while the other occur only rarely (Gimranov and Kosintsev 2015; Text-fig. 6F, G).

Similarly to the cranium, the morphology of the upper dentition of *M. wenzensis* also shows an admixture of features characteristic for *M. martes* and *M. foina*. The massiveness of P2 does not show any particular differences between all three species (Table 4). Contrary to that, the P3 of *M. wenzensis* is notably narrower from the P3 of both extant martens. The B/L index mean for *M. wenzensis* (47.5, 47.1–47.9, n = 2) is distinctly lower than that of *M. martes* (59.6, 51.4–67.2, n = 366) and matches only with the narrowest P3 of *M. foina* (50.9, 47.1–56.1, n = 321; Table 4). The narrow crown of P3 in *M. wenzensis* is mostly related with the poorly developed median lingual bulge, which is weak in *M. foina* and particularly well developed in *M. martes*.

The P4 morphology of *M. wenzensis* in some respects is closer to *M. martes* and *M. foina*, but it also differs notably in any features. First of all, the protocone is even higher and comparatively long as in *M. martes*. The mean of the L pr P4/Bp index of *M. wenzensis* (100.5, 98.3–102.5, n = 3) slightly exceeds the mean of *M. martes* (95.5, 81.3–116.9, n = 366). Both martens differ also notably from *M. foina* in this matter (68.5, 56.1–81.3, n = 321). The protocone is situated more disto-lingually, the parastyle is noticeably larger and expanded mesially, and crests running from the paracone apex as well as cingulum are much stronger. These differences in the P4 morphology between *M. wenzensis*, *M. martes* and *M. foina* are especially well-visible on the teeth from W1 and RK1A. Specimens from W2 and Va showed the morphology closer to *M. martes*, mainly in the lower protocone, rounded and smaller parastyle, weakly marked crests running from the top of the paracone and a well-marked concavity on the buccal margin. Contrary to the P4, the morphology of M1 of *M. wenzensis* is closer to *M. foina* than to *M. martes*. The M1 is smaller than P4, as in *M. foina*. The M1 B/P4 L ratio of *M. wenzensis* (87.2, 85.6–88.9, n = 3) is closer to *M. foina* (91.9, 82.0–98.8, n = 321) than to *M. martes* (94.2, 85.4–111.1, n = 366). The trigon is moderately expanded and the L tr M1/L P4 index of *M. wenzensis* (53.3, 62.0–54.6, n = 3) fits well within the ratio of *M. foina* (58.5, 40.0–67.3, n = 321). The values of this index for *M. martes* are distinctly higher (77.9, 63.6–89.0, n = 321). The occlusal outline is similar as in *M. foina*, with a strong and abrupt concavity of the contour. The M1 of *M. wenzensis* is distinguished from that of *M. martes* and *M. foina* in a less reduced metaconule and more complicated microrelief in occlusal view.

Wolsan (1988) assigned the microrelief at the occlusal surface of M1 to many morphotypes. The microrelief of the teeth from Va is similar to his morphotypes E1 and D (morfotype D1 in Wolsan *et al.* 1985). These morphotypes are the most common in *M. martes* and *M. foina*, and are found in all the Holarctic species investigated by Wolsan (1988). One of the teeth, the M1 from Va shows slight resemblance to morphotype E2 (most common in *M. martes*), but the tendency is too weak and almost negligible. Compared to *M. martes* and *M. foina*, the M1 from Va is more enlarged bucco-lingually. The double pinching (concave mesial and distal surfaces) of the tooth is less marked. The trigon length is not much greater than the talon length, and the enlargement of the buccal surface is still not so marked. In respect of all these proportions, the M1 from Va distinctly differs from the teeth of *M. martes.* It is slightly closer to the M1 morphology of *M. foina* and especially to the relatively small M1 of *M. flavigula* Boddaert, 1785, but the M1 of this species is less extended lingually.

An important feature in *Martes* is the shape of the occlusal outline of the buccal cingulum of M1.



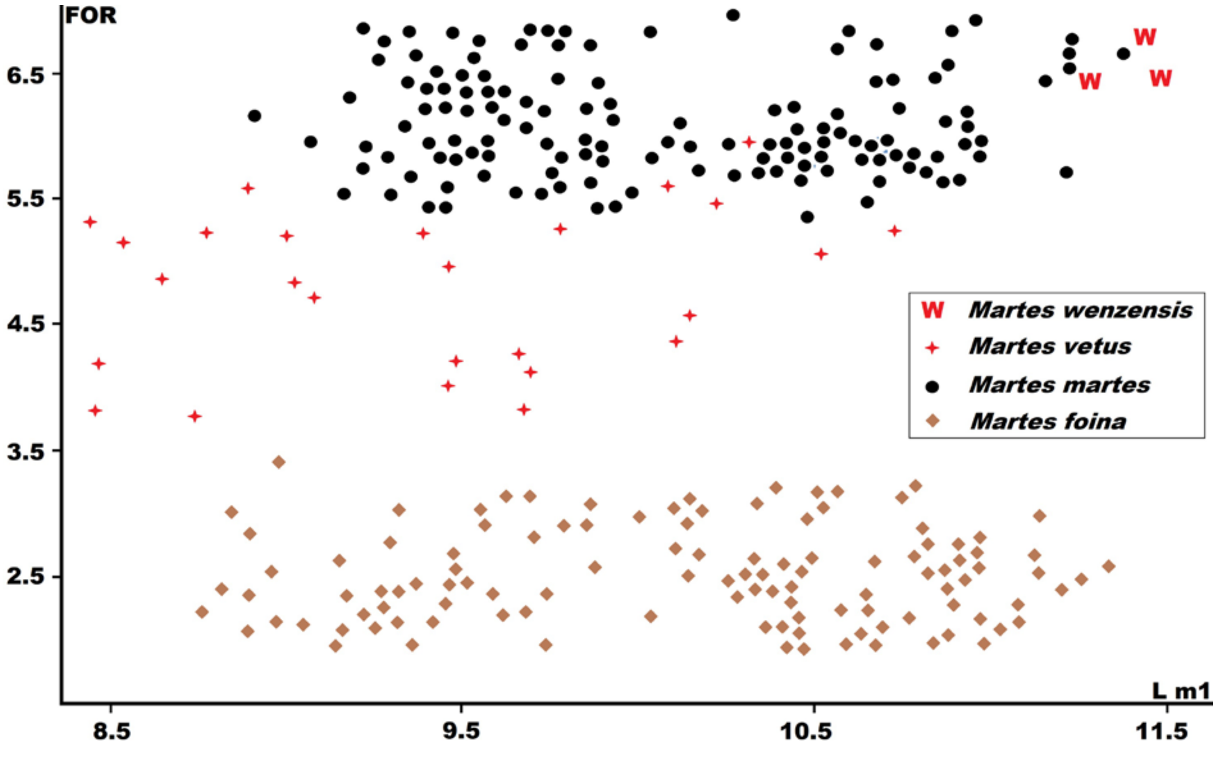
Text-fig. 7. Comparison of the mandible morphology (1 – buccal view) and lower dentition (2 – occlusal view) of European martens. A – *Martes wenzensis* (Węże 1), B – *Martes vetus* (Żabia Cave), C – *Martes martes*, D – *Martes foina*. All individuals drawn on the same scale.

Wolsan *et al.* (1985) distinguished three morphotypes: C1 (continuous, fully convex), C2 (slightly concave) and C3 (with a strong and abrupt concavity of the contour). The buccal surface of the M1 from Va is almost without concavity of its outline and thus more similar to *M. martes* than to *M. foina*. In *M. martes*, c. 80% of individuals have a completely continuous contour (morphotype C1), and the rest are assigned to morphotype C2 (n = 412). In *M. foina*, the labial surface of the tooth has a strong concavity between the paracone and the metacone (corresponding to morphotype C3) in nearly 80% of cases, type C2 is found in 18%, and type C1 in about 2% (n = 79; Wolsan *et al.* 1985). The buccal contour in both M1 from W1 is close to morphotype C3, typical of *M. foina*, and has a strong depression. The double pinching in the middle part is quite symmetrical. Besides, with its large, double protocone, the M1 from W1 represents morphotype E2, while the ancestral morphology of the mesio-lingual surface indicates morphotype Dc (Wolsan 1988). The M1s from Va and W1 look similar, but with some minor differences, i.e., a smaller depression and more asymmetrical pinching in the middle crown part in the M1 from Va (Text-fig. 6A–D).

COMPARISON OF THE MANDIBLE MORPHOLOGY: The mandible of *M. wenzensis* differs strongly from that of *M. vetus* (Text-fig. 7). The mandibular body is stout and elongated, while it is slimmer and shorter in *M. vetus*. The height of the mandibular body measured behind the m1 is equal to the m1 length in *M. wenzensis*. In *M. vetus*, the length of the m1 exceeds the height measured behind the m1. In *M. wenzensis*, the lower mandibular body margin forms a gently curved arch, uniformly domed mesially and distally. Mental foramens are widely spaced and the mesial edge of the masseteric fossa is more rounded. The mean of mental foramens spacing (FOR) to the L m1 index in *M. wenzensis* is 57.7 (56.4–59.4, n = 3). In *M. vetus*, the mean of this ratio is 47.8 (39.4–58.2, n = 25), and the mesial edge of the masseteric fossa is more triangular (Text-fig. 7). The mesial half of the mandibular body has an almost straight ventral margin, and is noticeably curved under the m1. The condyloid process is situated below the m1 level. The mandible of *M. vetus* has also a less massive symphysis. The lower teeth row is almost straight and only the distal part of the p2 crown moderately arches disto-lingually. In *M. vetus*, the deflection of the distal part of p2 is much less pronounced and it is situated almost exactly straight. The teeth are set more loosely.

The morphology of the *M. wenzensis* mandible resembles rather *M. martes* (Text-fig. 7C1) than *M. foina* (Text-fig. 7D1). The mandibular body is stout and elongated as in *M. martes*. The mandible of *M. wenzensis* possesses also features typical for this species and differ from both extant martens. The height of the mandibular body behind m1 is equal to the m1 length. In *M. martes* and *M. foina*, this ratio is lower, and the m1 length exceeds the height measured behind m1. The mental foramens are widely spaced and the distance between them fits within the range characteristic of *M. martes* and significantly exceeds the value for *M. foina* (Text-fig. 8). The mean of the FOR/L m1 index for *M. wenzensis* is 57.7 (56.4–59.4, n = 3) and is almost the same as that of *M. martes* (58.4, 54.5–66.3, n = 164). The ratios of both species considerably exceed that of *M. foina* (29.3, 21.4–36.6, n = 169). The masseteric fossa is mesially rounded and reaches the m1/m2 border, as in *M. martes* (Text-fig. 7A1 and A3). The condylar process is situated at the m1 level. Apart spacing of the mental foramen, the mandible of *M. wenzensis* can be distinguished from that of *M. foina* also in the shape of the masseteric fossa. In *M. foina*, it is displaced further mesially, often extends the m1 trigonid and talonid boundary and terminates in an acute angle. The lower margin of the mandible is noticeably curved under the m1 and this convexity is much strongly marked than in *M. wenzensis*. The condylar process is situated usually below the m1 level. The mandible of *M. wenzensis* from W1 differs also from mandibles of *M. martes* and *M. foina* in a more massive symphysis.

In the lower teeth row, the distal part of the p2 crown in *M. martes* and *M. foina* is situated almost exactly straight, while it arches disto-lingually in *M. wenzensis* (Text-fig. 7A1, B1, C1, D1). The c1 of *M. wenzensis*, proportionally long, robust and strong curved, shows intermediate features between the shorter and strongly curved c1 of *M. foina* and the elongated and narrower c1 of *M. martes*. The B/L ratio of *M. wenzensis* (70.0, 69.7–70.3, n = 3) is distinctly higher than ratios obtained for *M. martes* (B/L = 63.9, 51.5–77.0, n = 129) and *M. foina* (B/L = 63.0, 54.9–69.9, n = 114). It should be added, however, that the canine massiveness of all three marten species vary considerably and the range variations strongly overlap.



Text-fig. 8. Graph showing relationship between the length of m1 (L m1) and the spacing of mental foramens (FOR) of European martens. For data see text.

COMPARISON OF THE LOWER DENTITION MORPHOLOGY: The c1 of *M. wenzensis*, with a proportionally long, very wide and less curved crown differs from the shorter and narrower c1 of *M. vetus*. The B/L index of *M. wenzensis* (70.0, 69.7–70.3, n = 3) is distinctly higher than the ratio obtained for *M. vetus* (B/L = 60.2, 50.8–75.0, n = 68). On average, the premolars of *M. wenzensis*, i.e., p2, p3 and p4, are high-crowned, with a stronger cingulum and ridges running mesially and distally from the protoconid apex (Text-fig. 7A1, B1, C1, D1). Their distal cingular projection is more elongated and they are narrower than those of *M. vetus*, especially p2. The mean of the B/L ratio for p2 of *M. wenzensis* is 50.3 (49.1–51.0, n = 3), 49.5 for p3 (46.3–52.5, n = 4), and 45.8 for p4 (44.0–48.0, n = 5). The mean values of *M. vetus* in these teeth are 55.6 (50.0–59.1, n = 26) for p2, 50.4 (44.7–55.3, n = 26) for p3, and 50.1 (45.4–54.8, n = 27) for p4. The ranges of these indexes for all three teeth overlap, but the average values clearly indicate narrower crowns in *M. wenzensis*. The last characteristic of *M. wenzensis* is the shift of the protoconid far more mesially than in *M. vetus* (Text-fig. 7A1, B1, C1, D1).

On average, the p2, p3 and p4 of *M. wenzensis* are slightly narrower than those of *M. martes* and *M. foina*, especially p2. In *M. wenzensis*, the mean of the B/L ratio for p2 is 50.3 (49.1–51.0, n = 3), for p3 – 49.5 (46.3–52.5, n = 4), and for p4 – 45.8 (44.0–48.0, n = 5). The mean values of *M. martes* in these teeth are 55.0 (47.7–60.0, n = 366) for p2, 51.8 (45.3–60.0, n = 366) for p3, and 54.7 (49.0–60.1, n = 366) for p4. Slightly higher than those of *M. wenzensis*, they are still closer than the ratios obtained for *M. foina*, with 57.9 for p2 (50.0–65.4, n = 321), 54.7 for p3 (49.0–60.1, n = 321), and 53.6 for p4 (47.6–60.0, n = 321). The ranges of these indexes for all three teeth overlap, but the average values clearly indicate narrower crowns in *M. wenzensis*. The p2, p3 and p4 of *M. wenzensis* are distinguished from those of *M. martes* and *M. foina* also in a stronger cingulum and ridges running from the protoconid apex mesially and distally. Their distal cingular projection is more elongated, and their protoconid is shifted more mesially. In lateral view, they are also higher crowned (Text-fig. 7A2, B2, C2, D2).

The differences in the m1 morphology between *M. wenzensis* and *M. vetus* are well marked. The m1 of *M. wenzensis* is much larger (L m1 = 11.40 mm, 11.27–11.49 mm, n = 3) than the m1 of *M. vetus* (L m1 = 9.64 mm, 7.94–12.16 mm, n = 89). In the m1 of *M. wenzensis*, the protoconid is more prominent, while the metaconid is larger and higher situated. The paraconid edge is stronger developed. The mesial margin of m1 is more rounded. The buccal concavity on the trigonid and talonid transition is better marked. A minute hypoconulid is present and the hypoconid is situated more centrally. The mesial and distal cingulum is stronger developed. The mean proportions of the particular tooth parts differ slightly, but the ranges of both species strongly overlap. On average, *M. wenzensis* possesses a slightly shorter trigonid, which is narrower than the talonid. The L ta/ L tr m1 ratio in *M. wenzensis* is slightly lower (L tal/L tri = 53.9, 53.1–55.1, n = 3) than that of *M. vetus* (47.2, 36.1–58.1, n = 89). The B ta/B tr m1 index in *M. wenzensis* is lower (B tal/B tri = 90.8, 90.2–91.5, n = 3) than that of *M. vetus* (98.9, 94.1–103.1, n = 89). *Martes vetus* has a proportionally longer trigonid, comparable in breadth with the talonid.

The m1 morphology of *M. wenzensis* is closer to *M. martes* rather than to *M. foina*. It is larger (L m1 = 11.40 mm, 11.27–11.49 mm, n = 3) than the m1 of *M. martes* ♂♂ (L m1 = 10.74 mm, 10.28–11.38 mm, n = 53), and *M. foina* ♂♂ (L m1 = 10.73 mm, 10.14–11.34 mm, n = 57). However, despite being very large, the m1 of *M. wenzensis* is within the size variability and smaller than the mean of the particularly large Late Pleistocene *M. martes* ♂♂ (12.04 mm, 10.64–13.38 mm, n = 31). The m1 of *M. wenzensis* resembles that of *M. martes* in a large and prominent metaconid and proportionally short trigonid. The L ta/L tr m1 ratio in *M. wenzensis* (L ta/L tr = 53.9, 53.1–55.1, n = 3) is even higher than that of *M. martes* (43.5, 34.4–52.3, n = 366) and distinctly higher than that of *M. foina* (34.2, 33.0–48.8, n = 321). Simultaneously, the talonid of m1 is as long as that of *M. martes*, but is also as narrow as that of *M. foina*. The B ta/B tr m1 index in *M. wenzensis* is lower (B tal/B tri = 90.8, 90.2–91.5, n = 3) than that of *M. foina* (95.8, 91.7–103.1, n = 321) and notably lower than that of *M. martes* (104.9, 100.9–108.3, n = 366). The m1 of *M. wenzensis* resembles also *M. foina* in a stronger developed paraconid edge. It also differs from the m1 of *M. martes* and *M. foina* in the hypoconid situated more centrally, the presence of a minute hypoconulid (it occurs in extant martens very rarely), and a stronger developed cingulum.

COMPARISON SUMMARY: *Martes wenzensis* can be distinguished from *M. vetus* by its larger size, flat forehead, elongated temporal region, broader P2, narrower P3, P4 with a longer and higher protocone, smaller parastyle, and stronger developed crests and cingulum, M1 with a less complicated microrelief and larger size of the metaconule, more elongated body mandible with a straighter lower margin and widely spaced mental foramens, more massive c1, narrower p2, p3 and p4 with a stronger cingulum and ridges, and more elongated distal cingular projection, m1 with a more prominent protoconid, larger metaconid, stronger developed paraconid edge, proportionally shorter and narrower trigonid, stronger cingulum, and talonid without the minute hypoconulid.

The craniodental morphology of *M. wenzensis* shows an admixture of features of *M. martes* and *M. foina*. *Martes wenzensis* resembles *M. martes* in a narrow and elongated temporal region, a minute lacrimal processes on the orbits, large and oval infraorbital foramens, U-shaped caudal nasal spine, broader auditory bullae, elongated and flat forehead, P4 with a long protocone, elongated mandible body with widely spaced mental foramens, masseteric fossa reaching the m1/m2 border with a rounded mesial edge, and m1 with a proportionally short trigonid and prominent metaconid.

The morphological similarities between *M. wenzensis* and *M. foina* include a proportionally short and massive rostral area, more vertical nasal aperture, broad snout, wide, short and W-shaped nasal bones, narrow P3, breadth of M1 smaller than the length of P4 and moderately expanded trigon of M1, short and strongly curved crown of c1, and m1 with a narrow talonid and strongly developed paraconid edge.

*Martes wenzensis* differs from *M. martes* and *M. foina* in a distally located apical point of the cranial elevation, viscero- and neurocranium nearly equal in length, P4 with the protocone situated more distolingually, larger and expanded mesially parastyle and much stronger crests and cingulum, M1 with less reduced metaconule and more complicated microrelief in occlusal view, height of the mandible body measured behind m1 equal to the m1 length, more massive mandibular symphysis, narrower and higher crowned p2, p3 and p4 with stronger cingulum and ridges, more elongated distal cingular projection, more mesial protoconid shifting, m1 with the hypoconid situated more centrally, the presence of a minute hypoconulid, and a stronger developed cingulum.

## DISCUSSION

The fossil record of the genus *Martes* in Europe between 4.0–1.5 Ma is scanty and poorly known. So far, only one species was historically recognised in this continent both from the Early Pliocene and the Early Pleistocene (Stach 1959; Anderson 1970). Following this hypothesis, *M. wenzensis* might have been the ancestor of *M. vetus*, from which this species originated between 2.5–2.0 Ma (Sato *et al.* 2012). The geological range of *Martes* in Europe extends from the earliest Pliocene to the recent. The genus is most probably of Palaearctic origin. Miocene martens are poorly known and their relationships to *M. wenzensis* are unclear, even though their fossils are quite frequently encountered. Numerous species were described from that period based mostly on fragmentary cranial material, which was not sufficiently diagnostic (Stach 1959; Anderson 1970).

In this context, the only certain Pliocene European species, *M. wenzensis*, was regarded as the possible ancestor of the *M. martes* lineage. While the morphological features were often quite vague, the metrical values were among the most frequently used criteria for species determination. Some species can be regarded as ancestral forms of the Plio-Pleistocene species, but most authors agree that they are not directly related (Anderson 1970; Montoya *et al.* 2011). Among them, very large forms, larger than *M. wenzensis*, formed a group of great, primitive 'marten-like' forms, which existed in Eurasia during the Middle and Late Miocene. Most authors associate them with the so called 'Hipparion fauna'. The group included such species as *M. palaeosinensis*, *M. anderssoni*, *M. pentelici* (Gaudry, 1861), *M. woodwardi* (Pilgrim, 1931), and *M. ginsburgi* (Anderson 1970; Montoya *et al.* 2011). In addition to these large species, noticeably smaller *M. laevidens* was described from the Lower Miocene of Wintershof West (Dehm 1950, 1953). Most of these forms display ancestral features, different from that observed in later species. Among them, there are P4 with a very long protocone (its length is greater than the posterior breadth), an external medial rootlet, and a distinct shape of M1 and m1. In the Miocene marten-like forms, the metaconid is situated close to the protoconid. In Plio-Pleistocene martens, the buccal wall tends to be semi-circular, while the lingual wall is concave and discontinuous due to the lingual displacement of the metaconid base (Montoya *et al.* 2011).

The morphological analysis of *M. wenzensis* shows that the species has some ancestral characters. Large size is regarded as an ancestral feature, characteristic of the Miocene forms. Although in the late Middle and Late Pleistocene, representatives of *M. martes* were also very large and their dimensions often exceeded those of *M. wenzensis*, their large size may have been associated with climatic conditions. The size of *M. martes* follows the Bergmann rule and in cold climate tends to grow larger and decreases in size during warmer periods. The decreasing size tendency can be regarded as one of the trends in the *Martes* lineage (assuming that the concept of *M. wenzensis* => *M. vetus* => *M. martes* is correct). The largest specimens, forming a fairly homogenous group, are known from the Upper Pliocene site Węże 1, dated as 3.6–3.2 Ma. Large but somewhat smaller individuals of *M. wenzensis* come from the younger sites Węże 2 (2.5–2.2 Ma), Rębielice Królewskie 1A (2.6–2.2 Ma) and Varshets (c. 2.5 Ma). The single Early and early Middle Pleistocene species, *M. vetus*, is approximately as large as the medium-sized extant martens. This might suggest rather stable and warm climatic conditions in areas where the species occurred during the Pleistocene. Size fluctuations within the genus *Martes* became more pronounced since the mid Middle Pleistocene (Anderson 1970; Marciszak 2012).

The cranial morphology of *M. wenzensis* is closer to *M. martes* than to *M. foina*. However, the rostral part is shorter and more massive, similarly as in *M. foina*. The palate is broadened, especially at the canine's level. However, for such a large marten, the sagittal crest and the muscle protuberances are only moderately marked, as in *M. martes*. Canines and carnassials are very large and robust, while premolars are long but narrow compared to *M. vetus* and *M. martes* rather than to *M. foina*. P3 representing the advanced morphotype A2 is one of them. Wolsan *et al.* (1985) showed that the general trend in the P3 evolution was a progressive simplification of the crown. The shape of this tooth evolved from the buccally extremely concave and lingually convex (morphotype A4) in *M. martes* to the biconvex in *M. foina* (morphotype A1). With its only slightly concave buccal margin and the rather moderately convex lingual margin, *M. wenzensis* resembles *M. foina* rather than *M. martes*.

All similarities between the Polish material of *M. wenzensis* and the specimen from Bulgaria allow for assignment to this species. In relation to the Polish material, the marten from Varshets demonstrates M1 with more smooth microrelief, with weaker depression and slightly more asymmetric double pinching. The protocone of P4 is shorter and more mesially protruded (Spassov 1999). The differences with the material from Węże 1 may be explained by the younger age and the different geographical location of the Bulgarian material. The evolutionary link of *M. wenzensis* with the younger *M. vetus* is also probable.

Some papers provided a new insight into the general phylogeny of the family Mustelidae. They are based mainly on a nearly complete generic-level data matrix comprising gene segments analysed with maximum parsimony, maximum likelihood and Bayesian inference methods. Koepfli *et al.* (2008) showed that there were two main diversification peaks in the history of mustelids. The first occurred over a 3.7 myr long period within the time span from 12.5 to 8.8 Ma, and gave rise to most of the recently known main clades and lineages. The second was even larger and occurred in the Pliocene and the earliest Pleistocene, between 5.3 and 1.8 Ma, when 20 lineages appeared. It started when a marked global climate cooling occurred in the Late Miocene, which continues (with longer or shorter periods of warming, however) till today. Besides, several large decreases in sea level took place during that period which caused global terrestrial aridity and seasonality. Palaeontological data from the Late Miocene show that the Eurasian habitats were generally more heterogeneous than those during the early and middle Miocene. These palaeoenvironmental changes, mainly due to ecological opportunity through the creation of new niches and/or reorganisation of the existing ones, had a great impact on the faunal assemblages, including mustelids. Among the extinct carnivores, nearly half included mustelids, which opened new ecological niches and triggered the diversification of recent mustelid lineages (Koepfli *et al.* 2008; Law *et al.* 2018).

Global warming, coupled with increase in precipitation, during the Middle Pliocene (3.5–3.0 Ma), caused the expansion of deciduous forests in southern and middle Eurasia and taiga-type forests at high latitudes. Diversification of prey species (rodents and passerine birds), which came to live in the new habitats, was associated with these changes. It was also the time when the split of martens closely associated with taiga-type forests, started across the northern hemisphere. As observed by Koepfli *et al.* (2008, p. 12): "[…] taxa ancestral to these living species primarily evolved in forested habitats."

The finds from Węże 1 represent the earliest known, well-dated presence of true martens of the genus *Martes* in Europe, predating the former by more than 1.5 myr. Ancestral-state reconstructions based on molecular data suggest that the genus *Martes* has a Eurasian origin (Koepflii *et al.* 2008; Sato *et al.* 2012). Analysis with parsimony and Bayesian inference indicates Asia as the probable ancestral area, while maximum likelihood points to Asia and North America. It is likely that the genus *Martes* evolved *in situ* in Europe, especially considering the occurrence of other marten-like forms in the Late Miocene (Dehm 1950; Anderson 1970; Sotnikova 1995; Nagel 2009; Wang *et al.* 2012).

The fossil record corroborates well with the results of molecular studies, which have estimated the divergence dates of particular members of *Martes* from other forms of the Guloninae. Sato *et al.* (2012) estimated the divergence between *M. foina* and the group of the so called 'pine martens' (*M. americana*, *M.*

*martes*, *M. melampus*, *M. zibellina*) at 3.63 Ma (95% distal interval: 4.84–2.61 Ma) and the divergence of *M. foina* at 2.46 Ma (95% distal interval: 3.08–1.85 Ma) based on nine nuclear genes and one mitochondrial gene, using multitime analysis. In the group of 'pine martens', the separation between these four species took place at 1.72 Ma (95% distal interval 2.50–1.10 Ma; Sato *et al.* 2012). The age of *M. wenzensis* is close to the estimates based on molecular data, and inclusion of this form as a calibration point in future research would improve the estimates of the timing of splits within the family Mustelidae (Law *et al.* 2018).

## CONCLUSIONS

The fossil material of *Martes wenzensis* was revised and its taxonomical status was re-evaluated. Analysis showed that morphologically this marten shows a mixture of features characteristic for *M. vetus*, *M. martes*, and *M. foina*. The studied species resembles more *M. vetus* and *M. martes* rather than *M. foina*. *Martes wenzensis* is described as a large, robust marten, whose cranium has a flat forehead and short broad viscerocranium. The temporal region is elongated and broad, while the muzzle area is noticeably broadened at the canines. *Martes wenzensis* had robust canines, and elongated and narrow P2/p2, P3/p3 and p4 and enlarged carnassials. Large and robust P4 is longer than the M1 breadth, with a long and high protocone, and strong cingulum. Large M1 possesses a moderately wide trigon and a large metacone. The mandible has an elongated and stout body, with a robust symphysis and widely spaced mental foramens. The stout m1 possesses a short and robust trigonid, as well as a long talonid, narrower than the trigonid and prominent metaconid.

*Martes wenzensis* is so far the only Pliocene marten known from Europe and a possible ancestor of an evolutionary lineage leading through *M. vetus* to *M. martes*. Its timespan ranged between c. 3.6–2.2 Ma and its occurrence was recorded from three Polish and one Bulgarian sites. The oldest record is Węże 1 (3.6–3.2 Ma), from where also the most abundant material came. It is also a type site for the species. Two other Polish sites, Węże 2 and Rębielice Królewskie 1A, are similarly dated to 2.5–2.2 Ma. The Bulgarian record from Varshets (c. 2.5 Ma) is especially noteworthy. The preserved viscerocranium shows a number of intermediate features between the type specimen from Węże 1 and Early Pleistocene *M. vetus*, its possible descendant. The palaeontological records corroborate well with molecular data.

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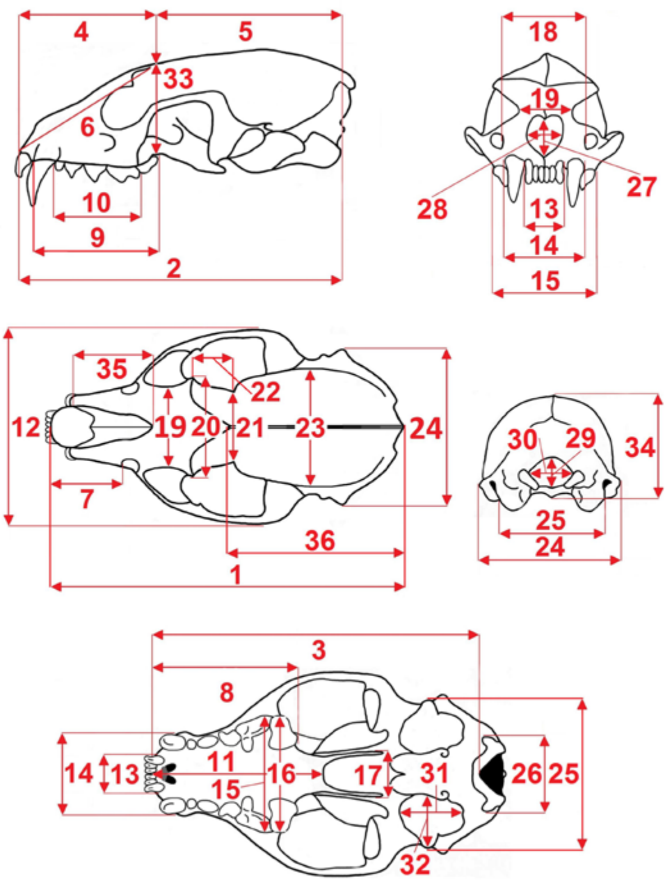
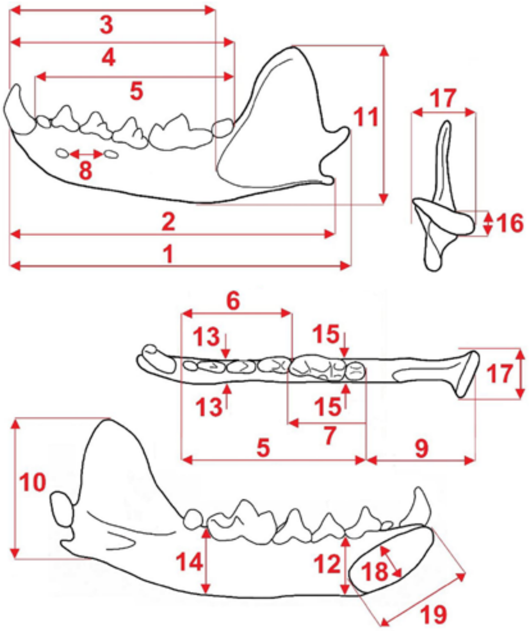
## Appendix 1. Scheme of measurements of the marten skull.



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

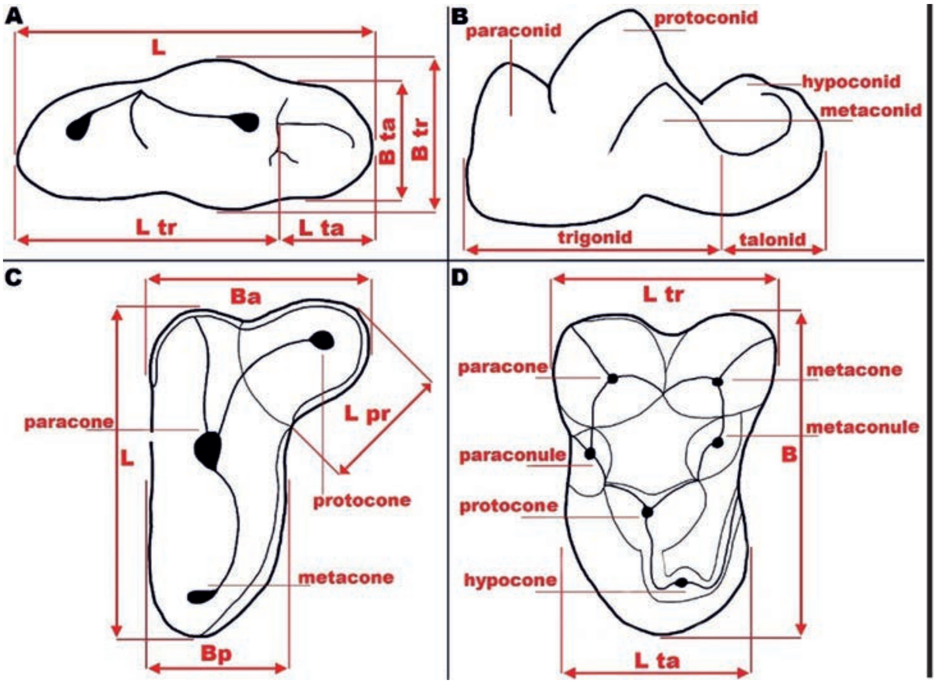
## Appendix 2. Scheme of measurements of the marten mandible.



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

## Appendix 3. Scheme of measurements and cusps terminology of marten teeth: m1 (A, B), P4 (C) and M1 (D).



**Measurements:**

| | |
|---|---|
| (L) | total length |
| (L pr) | protocone length of P4 |
| (L tr) | trigon/trigonid length |
| (L ta) | talon/talonid length |
| (B) | total breadth |
| (Ba) | mesial breadth |
| (Bp) | distal breadth |
| (B tr) | trigonid breadth |
| (B ta) | talonid breadth |