

# ***BARANOGALE HELBINGI* KORMOS, 1934 (MUSTELIDAE, CARNIVORA) FROM THE LATE PLIOCENE SITE WĘŻE 1 (POLAND)**

**Adrian MARCISZAK<sup>1\*</sup>, Grzegorz LIPECKI<sup>2</sup> & Mieczysław WOLSAN<sup>3</sup>**

<sup>1</sup> Department of Palaeozoology, University of Wrocław,  
Sienkiewicza 21, 50-335 Wrocław, Poland;  
e-mail: [adrian.marciszak@uwr.edu.pl](mailto:adrian.marciszak@uwr.edu.pl);

<sup>2</sup> Institute of Systematics and Evolution of Animals, Polish Academy of Sciences,  
Sławkowska 17, 31-016 Kraków, Poland;

<sup>3</sup> Museum and Institute of Zoology, Polish Academy of Sciences,  
Twarda 51/55, 00-818 Warszawa, Poland;

\* Corresponding author

Marciszak, A., Lipecki, G. & Wolsan, M., 2024. *Baranogale helbingi* Kormos, 1934 (Mustelidae, Carnivora) from the late Pliocene site Węże 1 (Poland). *Annals Societatis Geologorum Poloniae*, 94: yy–zz.

**Abstract:** The ancient and archaic mustelid *Baranogale helbingi* is a European endemit. Its occurrence is characteristic for the Pliocene, but the species occurred also during the early Pleistocene. Among 30 sites, where its occurrence is documented, 8 are located in Poland. Among them, the most abundant material was found at Węże 1, dated at 3.6–3.2 Myr. The newly described remains, with two relatively well preserved skulls, broadly expand knowledge about the species. Morphometrical analysis showed the important role of sexual dimorphism in the variability of the species. Like other European Ictonychini, *B. helbingi* vanished during the early Pleistocene, owing to competition with small Mustelinae that were extremely adaptable in terms of ecology.

**Key words:** *Baranogale*, ecological niche, competition, *Mustela*, sexual dimorphism.

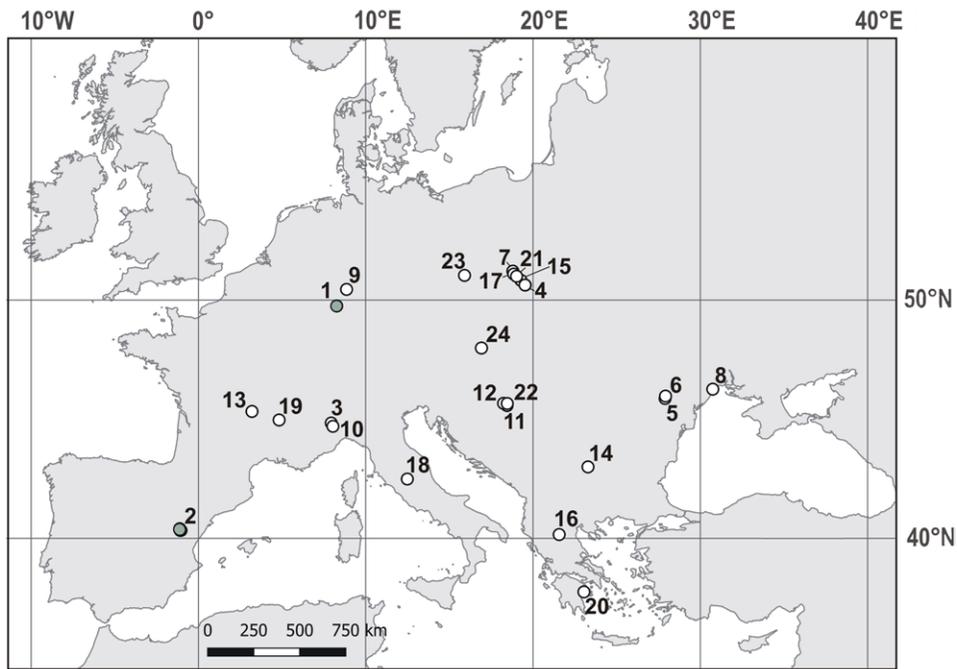
Manuscript received 22 March 2024, accepted 23 May 2024

## INTRODUCTION

The genus *Baranogale* Kormos, 1934 is a characteristic member of Pliocene and early Pleistocene European faunas, the occurrence of which is documented in the fossil record for more than 6 Myr (MN 11–18; Adrover *et al.*, 1986; Alcalá *et al.*, 1990; Alcalá and Montoya, 1990; Morlo and Kundrát, 2001; Spassov, 2001). Its origin and the earliest history of this ancient lineage is poorly documented. Most likely, this early genus of Ictonychini within the Ictonychinae Pocock, 1921 originated from Asiatic ancestors 9.5–8.9 Myr ago and was dispersed westwards to Europe (Sato *et al.*, 2012). Confusion about the evolution of *Baranogale* arose because the assignment of the late Miocene (8.7–6.2 Myr) forms, traditionally classified as *Baranogale adroveri* Petter, 1964, was questioned (Spassov, 2001). However, for the purpose of this article, the Miocene forms were assigned to *B. adroveri*, the Pliocene and the early Pleistocene individuals to *B. helbingi*.

Finds of *Baranogale* in central Europe (Hungary, Poland, Romania) always played the main role in the reconstruction of its evolutionary history (Kormos, 1934; Kowalski, 1959,

1964). The earliest appearance (4.9–4.2 Myr) of *B. helbingi* (Kowalski, 1959, 1964; Wolsan, 1989) was described from the Polish site Podlesice, which is important in a biochronological context. Only recently, the Italian site Moncucco Torinese (5.4–5.3 Myr; Colombero *et al.*, 2017) took on greater importance than this locality. The occurrence of *B. helbingi* within a timespan of ca. 4 Myr (5.4–1.2 Myr; Fig. 1; Tab. 1) was documented at 30 or more localities. These sites include Węże 1, where Stach (1961) described the damaged mandible of a young animal with erupted p3-p4, three fragments of a mandible body, two with p4 and one with p4-m1, and an isolated m1. Since that time, the material of *B. helbingi* from Węże 1 was mentioned many times (Kowalski, 1964, 1990; Wolsan, 1989), but nothing more was done with these remains. More than 60 yrs after the first description of these relics, much more abundant material, including two complete skulls, was found. This allows re-examination of the material of *B. helbingi* from Węże 1 in a broad, European, biochronological and evolutionary context, which is the main aim of this paper.



**Fig. 1.** Distribution of late Miocene to the early Pleistocene sites with *Baranogale* in Europe. For locality numbers, see Table 1.

**Table 1**

Occurrence of *Baranogale androveri* and *Baranogale helbingi* in the Miocene, Pliocene and the Pleistocene of Europe. Locality numbers (Map) correspond to those in Figure 1.

Map	Site	Country	Age (in mya)	Literature
<b><i>Baranogale androveri</i> Petter, 1964</b>				
1	Dorn-Dürkheim 1	Germany	8.7–7.8	Morlo, 1997; Franzen <i>et al.</i> , 2013
2	Puente Minero	Spain	8.7–7.8	Adrover <i>et al.</i> , 1986; Alcalá <i>et al.</i> , 1990
2	Vivero de Pinos	Spain	8.7–7.8	Adrover <i>et al.</i> , 1986; Alcalá and Montoya, 1990
2	Los Mansuetos	Spain	7.8–7.0	Petter, 1964, 1987; Adrover <i>et al.</i> , 1986
2	Rambla del Valdecebro	Spain	7.8–7.0	Petter, 1964, 1987; Alcalá <i>et al.</i> , 1990
2	Las Pedrizas	Spain	7.8–7.0	Alcalá, 1994
2	Cerro de la Garita	Spain	7.8–7.0	Alcalá, 1994
2	Las Casiones	Spain	6.3–6.2	Abella <i>et al.</i> , 2019
<b><i>Baranogale helbingi</i> Kormos, 1934</b>				
3	Moncucco Torinese	Italy	5.4–5.3	Colombero <i>et al.</i> , 2017
4	Podlesice	Poland	4.9–4.2	Kowalski, 1959, 1964
5	Beresti	Romania	4.9–4.2	Radulescu <i>et al.</i> , 2003
6	Malusteni	Romania	4.2–3.6	Radulescu <i>et al.</i> , 2003
7	Węże 1	Poland	3.6–3.2	Kowalski, 1959b, 1964; Stach, 1961
8	Odessa Catacombs	Ukraine	3.6–3.2	Vislobokova <i>et al.</i> , 2001; Nagel <i>et al.</i> , 2004
9	Wölfersheim	Germany	3.6–3.2	Morlo and Kundrát, 2001
10	Triversa	Italy	3.2–2.8	Alberdi <i>et al.</i> , 1997
11	Beremend 1, 2, 3	Hungary	3.2–2.8	Petényi, 1864; Kretzoi, 1956; Jánossy, 1986
12	Csarnóta 1, 2, 3, 4	Hungary	3.2–3.1	Kretzoi and Pécsi, 1982; Jánossy, 1986

Map	Site	Country	Age (in mya)	Literature
13	Perrier-Etouaires	France	2.8–2.7	Pomel, 1853; Schaub, 1949; Heller, 1967
14	Varshets	Bulgaria	2.5–2.4	Spassov, 1997, 2000, 2001, 2003
7	Węże 2	Poland	2.5–2.3	this work
15	Zamkowa Dolna	Poland	2.5–2.3	this work
16	Dafnero	Greece	2.4–2.3	Koufos <i>et al.</i> , 1991; Koufos, 1993, 2001, 2014, 2022; Koufos and Kostopoulos, 1997; Benammi <i>et al.</i> , 2020
17	Rębielice Królewskie 1A	Poland	2.4–2.2	Kowalski, 1964; Wolsan, 1989
18	Torre Picchio	Italy	2.2–2.1	Girotti <i>et al.</i> , 2003
19	Saint-Vallier	France	2.2–2.1	Viret, 1951, 1954
20	Karnezeika	Greece	2.1–2.0	Kokotini <i>et al.</i> , 2019; Sianis <i>et al.</i> , 2021, 2023
21	Kamyk	Poland	2.0–1.8	this work
22	Villány 3	Hungary	2.0–1.8	Kormos, 1934; Kretzoi, 1942, 1956
22	Villány 5	Hungary	1.8–1.6	Kretzoi, 1956
23	Południowa Cave	Poland	1.7–1.5	this work
4	Żabia Cave	Poland	1.7–1.5	this work
24	Deutsch Altenburg 4	Austria	1.4–1.2	Wolsan, 1993

## MATERIAL AND METHODS

The identification of mustelid remains analysed in the present account was performed using basic morphometric analysis. Measurements were taken point to point with the Landmark system to the nearest 0.01 mm (Fig. S1–S3 and Tab. S1–S3 in the Supplementary File). Measurements were taken using an Olympus set for image analysis (Olympus stereomicroscope ZSX 12, camera Olympus DP 71, program Cell D). A Canon EOS 5D camera was used in the photographic documentation of the fossil material. Statistical analysis was performed using “Statistica” (version 10.0 OL) software. Osteological and dental terminology follow Spassov (2001). Throughout the text, references to upper teeth are in capital letters (e.g., P4) and to lower teeth in lower-case letters (e.g., p4). The geologic time scale and its subdivisions were based on the International Chronostratigraphic Chart (v2018/08), approved by the International Commission on Stratigraphy.

### *Institutional abbreviations*

ISEA PAS: Institute of Systematics and Evolution of Animals, Polish Academy of Sciences in Kraków; MZ: The Museum of the Earth, Polish Academy of Sciences in Warsaw; ZP UW: Department of Paleozoology, University of Wrocław.

### *Anatomical abbreviations*

**B** – breadth; **B ta** – talonid breadth; **B tr** – trigonid breadth; **L** – length; **L ta** – talonid length; **L tr** – trigonid length; **max** – maximum value; **M** – mean; **min** – minimum

value; **mm** – millimetres; **N** – number of bones/individuals; **W1** – Węże 1.

The *Baranogale helbingi* material from Węże 1 was partially published by Stach (1961), which is revisited in this paper. Previously unpublished dentognathic material of this species also is included. All of the material examined amounts to 18 bones of *B. helbingi* (Tab. 2).

## GEOLOGICAL SETTING

Węże 1, known also as the Samsonowicz Cave (51°5′45″N, 18°47′21″E, 220 m a.s.l.), is located in an abandoned quarry in the village of Węże, near the small town of Działoszyn, Wieluń Upland, central Poland. The site was formed after the collapse of a large, vertical cave, which was filled with sediments. This 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. Intensive excavations were continued until the mid-1970s and resulted in the removal of most of the sediment from the site.

Samsonowicz (1934) divided the deposits into red and grey breccias, while Głazek *et al.* (1976) assigned them to three main sedimentation periods. The oldest layers, dating back to the late Miocene (6.0–5.5 Myr; MN 13) covered the cave bottom. They were formed of 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 without any bones. The second deposition period, ca. 3.6–3.2 Myr (MN 15b), included thick deposits of red, sandy clay with the addition

**Table 2**

Cranium and upper dentition measurements  
of *Baranogale helbingi* from Węże 1.

		W1.7.1	W1.7.2	
Cranium measurements	1	71.78	69.34	
	2	71.08	69.31	
	3	64.72	64.84	
	4	31.64	31.75	
	5	40.02	39.78	
	6	33.52	33.41	
	7	21.78		
	8	26.98		
	9	31.05		
	10	22.54		
	11	17.48		
	13	7.41		
	14	14.97	13.96	
	15	22.69		
	19	16.07		
	21	14.22	14.36	
	23	27.32		
	24	30.46	29.34	
	28		7.25	
	29		7.36	
30	17.42	18.74		
31	11.61	11.42		
32	18.64			
33	19.36			
Teeth measurements	P2 L		3.89	3.82
	P2 B		1.78	1.71
	P3 L		4.42	
	P3 B		2.14	
	P4 L	7.24		
	P4 L pr	2.48		
	P4 Ba	4.26		
	P4 Bp	2.74		
	M1 B	7.14		
	M1 L tr	4.69		
	M1 L ta	4.04		

of small concretions and bones. The clay gradually passed into a thick, grey breccia. The layers of the second period were laminated on the surface, and the lamination disappeared gradually deeper in the profile. The surface was covered with sandy and clayey deposits, with an admixture of fragmented calcite and limestone. The youngest sedimentary series, 1.0–0.8 Myr, comprised periglacial deposits in the form of yellowish clay sands, cemented with rock rubble. Also, there were almost no bones (Głazek *et al.*, 1976; Głazek and Szykiewicz, 1987).

A detailed analysis of the faunal assemblage failed to confirm this subdivision and now the main fauna from Węże 1 is dated as 3.6–3.2 Myr. The site yielded 118 vertebrate species, with 9 amphibians, 11 reptiles, 4 birds, 35 insectivores, 10 bats, 1 lagomorph, 30 rodents, 14 carnivores, 2 perissodactyls and 2 artiodactyls (see Supplementary File; Marciszak *et al.*, 2024 and references therein).

## SYSTEMATIC PALAEOLOGY

Class Mammalia Linnaeus, 1758

Order Carnivora Bowdich, 1821

Family Mustelidae Fischer von Waldheim, 1817

Subfamily Ictonychinae Pocock, 1921

Genus *Baranogale* Kormos, 1934

**Type species:** *Baranogale helbingi* Kormos, 1934, pp. 145–148, tab. 2, figs 6, 7, by monotypy.

*Baranogale helbingi* Kormos, 1934

Figs 1–6, Tabs 1–5

1934 *Baranogale helbingi* – Kormos, pp. 145–148, tab. 2, figs 6, 7.

**Holotype:** Left mandible with damaged ramus and with p3-m1 (Kormos 1934: pp. 145–148, pl. 2, fig. 6a, b). Stored in the Hungarian Natural History Museum in Budapest (Hungary) under catalogue number V.61.1380 (former inventory number Nr. 3914).

**Type locality:** Villány 3 (= Villány-Kalkberg), Hungary, early Pleistocene, MNQ 17, 2.0–1.8 Myr.

**Material:** Partially damaged skull, without zygomatic arches and most of the ventral part of neurocranium, with present left P4-M1 (W1.7.1); strongly damaged skull, without zygomatic arches and most of the ventral and right parts of neurocranium, with present left P2 and right P2-P3 and P4 paracone (W1.7.2); left mandible with damaged symphysis missing most of the ramus, with present c1-p3, mesial fragment of p4 and m1 (W1.7.3); fragment of left body and ramus mandible with m1 (W1.7.4); left m1 (W1.7.5); fragment of left body mandible with m1 (W1.7.6); right, complete p3 (W1.7.7); left m1 without distal root (W1.7.8); right m1 with missing mesial root (W1.7.9); trigonid of the left m1 (W1.7.10); left c1 (W1.7.11); trigonid of left m1 (W1.7.12); left m1 (W1.7.13); right mandible with missing part of the ramus, present worn c1, erupted p3-p4 and m1 (MF/558/1); distal part of the right body mandible with ramus fragment, worn p4 and m1 (MF/558/2); fragment of left body mandible with p4 (MF/558/4); fragment of left body mandible with p4 (MF/558/5); fragment of left body mandible with m1 (MF/558/3); right mandible without most of the ramus and with preserved c1-m2 (MF/7933). Individuals W1.7.1–12 stored in ZP UW, specimens MF/558/1–5 and MF/7933 housed in ISEA PAS.

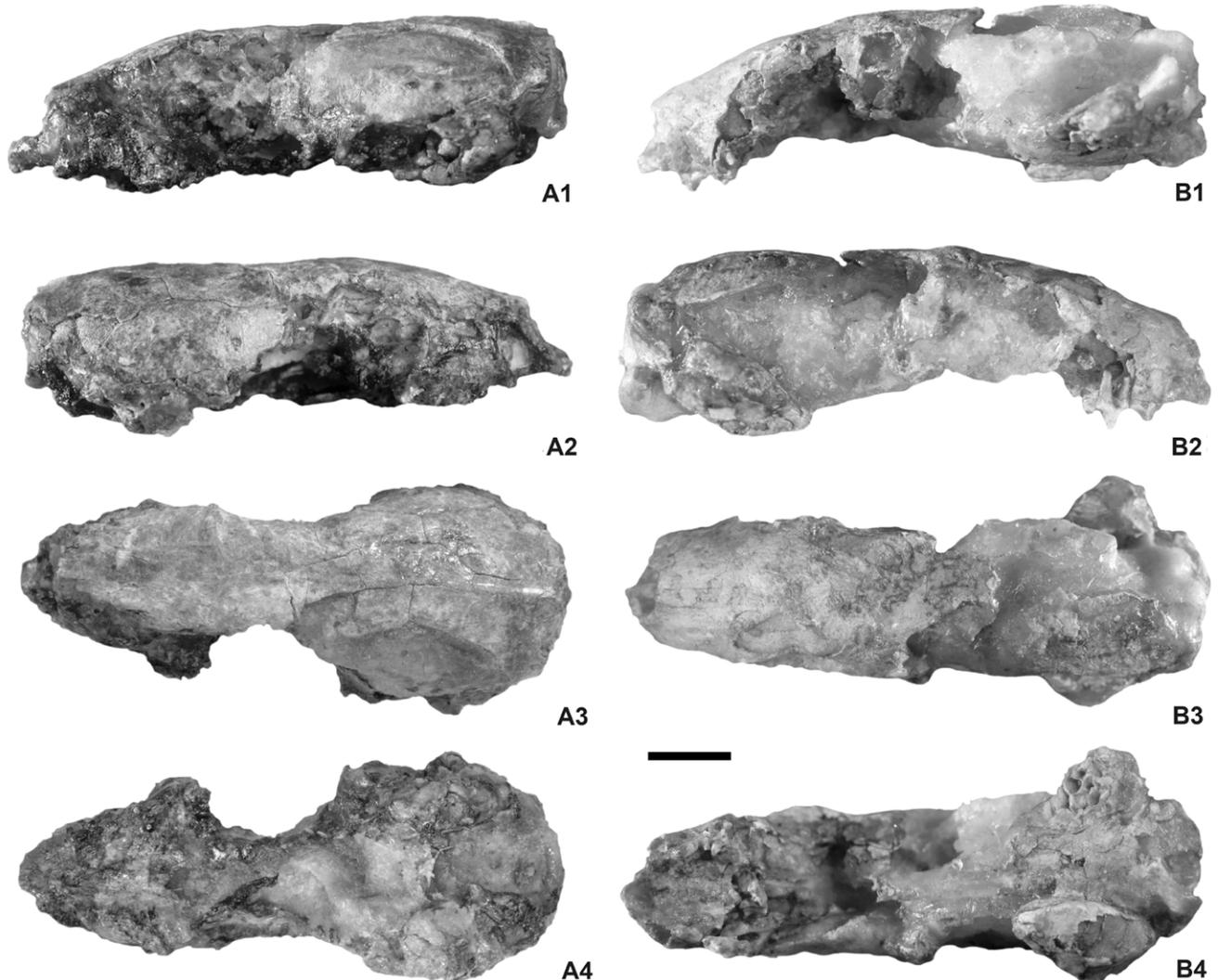
**Emended diagnosis:** Mustelid intermediate between *Mustela erminea* and *Mustela putorius*; narrow, short and triangular rostrum, moderately broadening at the canines level; elongated and wide temporal region; almost straight frontal profile, without any crossing between maxillae and

frontal region; widely spaced massive mastoid processes; large, strongly inflated and convex tympanic bullae with large tympanic chamber; straight and moderately robust C1; narrow P2-P3; P4 with an moderately long and high protocone, low and large paracone and low and short metastyle, with strong lingual cingulum; M1 situated obliquely in relation to P4, collared by a thick cingulum, with significant concavity at the border between the trigon and talon, high and large paracone, smaller and lower metacone, moderately broadened talon, with centrally located, high and large hypocone and minute hypoconule; elongated and moderately high mandibular body with constant lateral thickness; longitudinal, lingual furrow on the body weakly to moderately developed; deep and long masseteric fossa; long and narrow symphysis; lower teeth tightly set in the tooth row; curved, large and robust c1; large and oval p2; narrow p3-p4 with weak lingual bulge; m1 with a high and short trigonid, broad and long talonid, prominent metaconid, elongated and laterally located hypoconid and elongated and low hypoconulid; large and rounded m2.

**Description:** The viscerocranium is shortened and wide, with a moderate broadening at the canines level. In the dorsal view, it has a triangular shape. The frontal profile in the

lateral view is almost straight, without any marked crossing between the maxillae and the frontal region. The nasal aperture is rounded; its height is almost the same as the width (Tab. 2). The temporal region is broad and elongated, with a wide postorbital bar. The postorbital processes are positioned almost exactly in the middle of the temporal region (Fig. 2). The orbits are large and rounded (Fig. 2). The palate is proportionally short and broad. The tympanic bullae are convex, large, and strongly inflated, with a large tympanic chamber. The carotid canals are widely separated, ca. 2/3 of the distance between the distal lacerum foramen and the external auditory meatus (Fig. 2).

A strongly arched incisors row is exposed forward. There are no diastemas between I3 and C1 and C1 and P2, and the C1 is poorly exposed. There are no diastemas between P2, P3, P4 and M1. The P2 is a two-rooted, weakly reduced tooth, situated exactly parallel to the C1. The crown is elongated and narrow, with straight buccal and lingual margins. Its distal and mesial margins are blunt. From the apex of the protocone starting thin, but well recognised ridge running through to the base of this cusp. The protocone is located strongly mesially and slightly lingually. The crown has elongated, distal cingular projection, which has



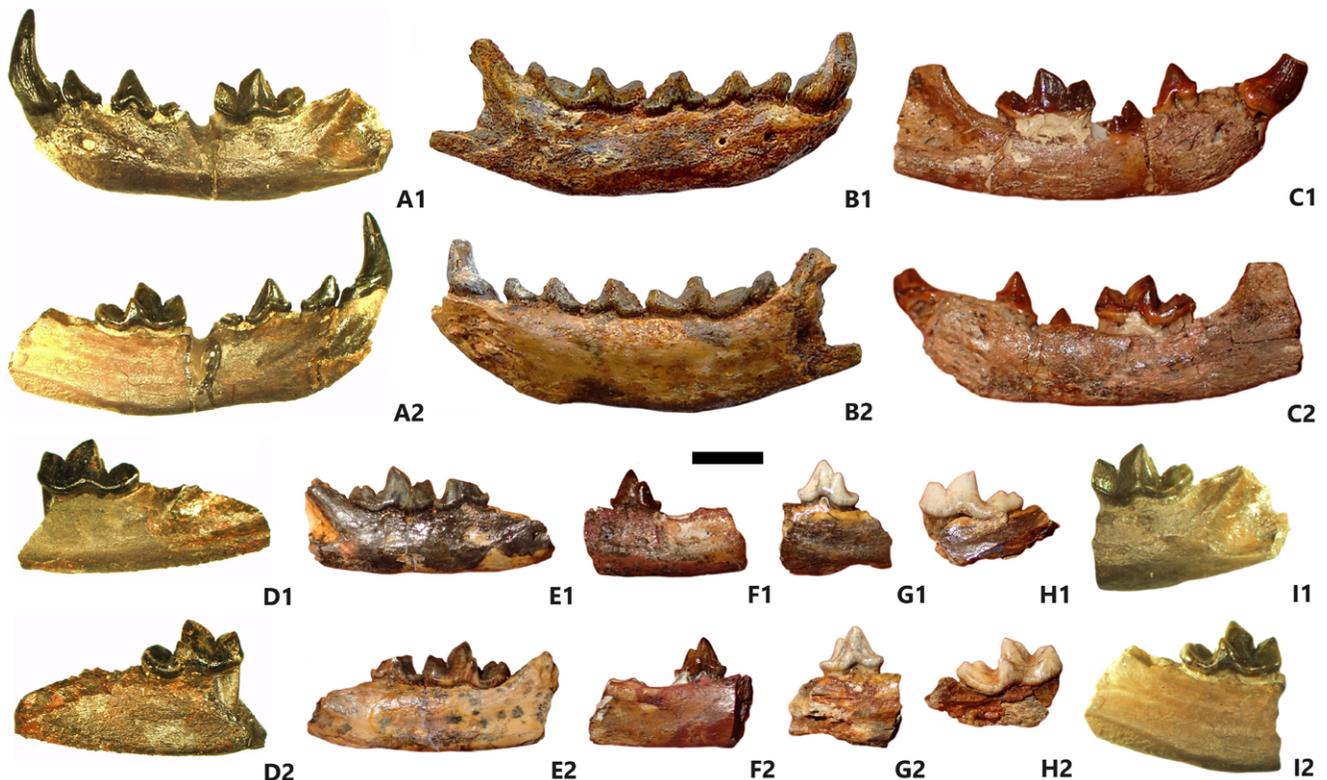
**Fig. 2.** Skulls of *Baranogale helbingi* from Weże 1 site. A. W1.7.1. B. W1.7.2. Both individuals shown on the same scale; a, b, lateral view; c, dorsal view; d, ventral view; scale bar 10 mm.

a smooth, internal surface. Relatively strong cingulum collars the mesial and distal margins. The P3 is located just after the P2 in a straight line. The tooth is elongated and irregularly oval-shaped. The prominent protocone is strongly pushed mesially and situated centrally. In front of the protocone is located a centrally positioned, low and rounded paracone, which is strongly connected with the mesial cingulum. From the protocone apex starts a thin crest, which runs through an elongated, distal cingular projection. This ridge connects with the mesio-lingual prominence of the cingulum. Parallel, behind the protocone a second cuspid or at least a cuspid-like swelling is present, located slightly more buccally. This structure is low and oval, but well displayed. The thick cingulum collared most of the crown, and is especially strongly developed on the mesial and distal sides. The mesial and distal margins are blunt, buccal straight, similar to the mesial half of the lingual margin. The distal half of the lingual margin is weakly convex.

The elongated and narrow P4 has a straight crown, with the narrowest part of the transition between the paracone and metacone. The buccal and lingual margins are straight, while the distal margin is rounded. A moderately high paracone bears a thin ridge, running across the mesial border, extending from its apex to the base of the crown. It is poorly separated from the low and moderately large protocone, the mesial margin of which is aligned with that of the paracone. The short and rounded protocone has straight mesial and distal margins, while its mesio-lingual is blunt. The low metacone is blade-shaped, adjoining the paracone its distal part is slightly curved buccally. The thick cingulum is most developed along the lingual margin. A strong cingulum is present also on the mesial wall of the paracone.

The breadth of the M1 is comparable to the P4 length. The crown is moderately curved within a median longitudinal axis. The trigon and talon are separated by a broad, deep and U-shaped depression, running through the transitional part of the crown. The relatively narrow talon is comparably long with respect to the trigon, with a strong mesial and lingual cingulum. The buccal cingulum on the moderately short and wide trigon is strongly developed. The buccal and distal margins of the trigon are convex, while the mesial convexity is moderately developed. The distal and mesial margins of the talon are moderately convex. The moderately high and rounded paracone occupies ca. 70% of the trigon surface. A lower and more oval metacone is strongly associated with it. It is separated from the paracone by a narrow, V-shaped valley. The talon bears a centrally positioned, low and elongated protocone. From its apex a thin ridge running in a disto-lingual direction (Fig. 2).

The mandibular body is elongated and moderately high and has a constant lateral thickness (Tab. 3). The ventral margin is gently arched with a maximum curve up to the middle length of m1 (Fig. 3). The symphyseal area is elongated and narrow. Two oval mental foramina are located on the buccal side. A larger, mesial one is situated below the distal root of p2, while the distal one is below the mesial root of p4, slightly lower than the mesial one. The longitudinal, lingual furrow of the mandibular body is weakly to moderately developed. The deep masseteric fossa has a rounded, mesial margin, which in its maximal extent reaches the m1 and m2 border (Fig. 3). The tooth row is almost straight in the occlusal view. Only the distal parts of p2-p3 are oriented disto-lingually. The teeth are mostly tightly positioned there are no diastemas between them. The only short diastemas



**Fig. 3.** Mandibles of *Baranogale helbingi* from Węże 1. **A.** W1.7.3. **B.** MF/7933. **C.** MF/558/1. **D.** W1.7.4. **E.** MF/558/2. **F.** MF/558/4. **G.** MF/558/5. **H.** MF/558/3; **I.** W1.7.6. All individuals shown on the same scale (5 mm); 1 – buccal view; 2 – lingual view.

Table 3

Mandible measurements of *Baranogale helbingi* from Węże 1.

Coll. no.	Measurements								
	4	5	6	7	8	12	13	14	15
W1.7.3						5.77	2.87	6.68	3.11
MF/7933	25.13	20.82	11.59	9.48	3.25	6.49	3.65	6.76	4.11
MF/558/1					2.06			6.13	2.62
MF/558/2					2.46			6.13	3.28

are present in some, but not all, individuals, between p2 and p3. The apexes of all three conical premolars, namely p2, p3 and p4, are located nearly at the same level (Fig. 4).

The c1 is quite slender and strongly curved. The crown is flattened laterally and relatively short, mesio-distally. Its tip points slightly obliquely upwards and backwards, with a strong bend on the mesial edge. A strong, lingual cingulum is located in the base of the crown. The cingulum continues up the lingual surface, thus forming a strong vertical, longitudinal crest. This crest has a distinctly marked distal contour, thus being strongly separated distally from the c1 surface. The elongated and oval, two-rooted p2 is large and weakly reduced. The crown has an apex moved strongly forward and the straight buccal and lingual margins. The mesial and distal margins are blunt. The two-rooted p3 is low and narrow and bears an elongated, distal cingular projection. The apex of the moderately prominent protoconid is also moved forward, but not so strongly as in p2. It is located in ca.  $\frac{1}{3}$  of the length of the crown. A thin ridge runs in a distal direction from the protoconid apex to its base. In front of and behind the protoconid shallow, moderately wide, crescentic valleys are located. A moderately developed cingulum is present only on the mesial and partially on the distal

margins. The buccal and lingual margins are straight, while the mesial and distal margins are blunt or rounded (Tab. 5).

The p4 is two-rooted and narrow. The mesial and distal margins are blunt. The margins of the mesial half of the crown are almost straight. The crown broadens moderately distally and the transition between both halves is well developed. The margins of the distal half are moderately curved and the lingual convexity is usually more strongly marked. A centrally positioned, high and prominent protoconid is well-separated from the strong, mesial and distal cingulum by shallow, wide, U-shaped valley. From its apex, a thin, but well-developed ridge, runs up to the crescent wall of the strong, mesial cingulum. Likewise strongly developed is a distal cingulum, which forms a semicircular wall. In front of and behind the protoconid, are located shallow, moderately wide, crescent valleys. Behind the protoconid, strongly associated with it, there is a low and rounded hypoconid. This accessory cuspid is shifted disto-buccally.

The large and rather narrow m1 has an elongated and prominent paraconid and protoconid (Fig. 5). The length of the paraconid is nearly the same as that of the protoconid (Tab. 4). Its apex is situated notably lower than the apexes of both the protoconid and p4. The distal wall of

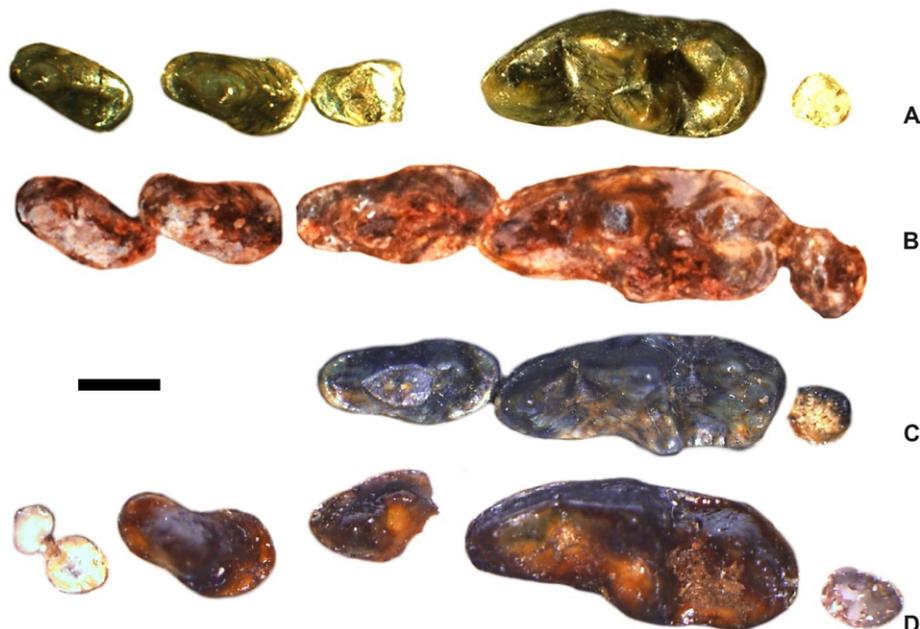
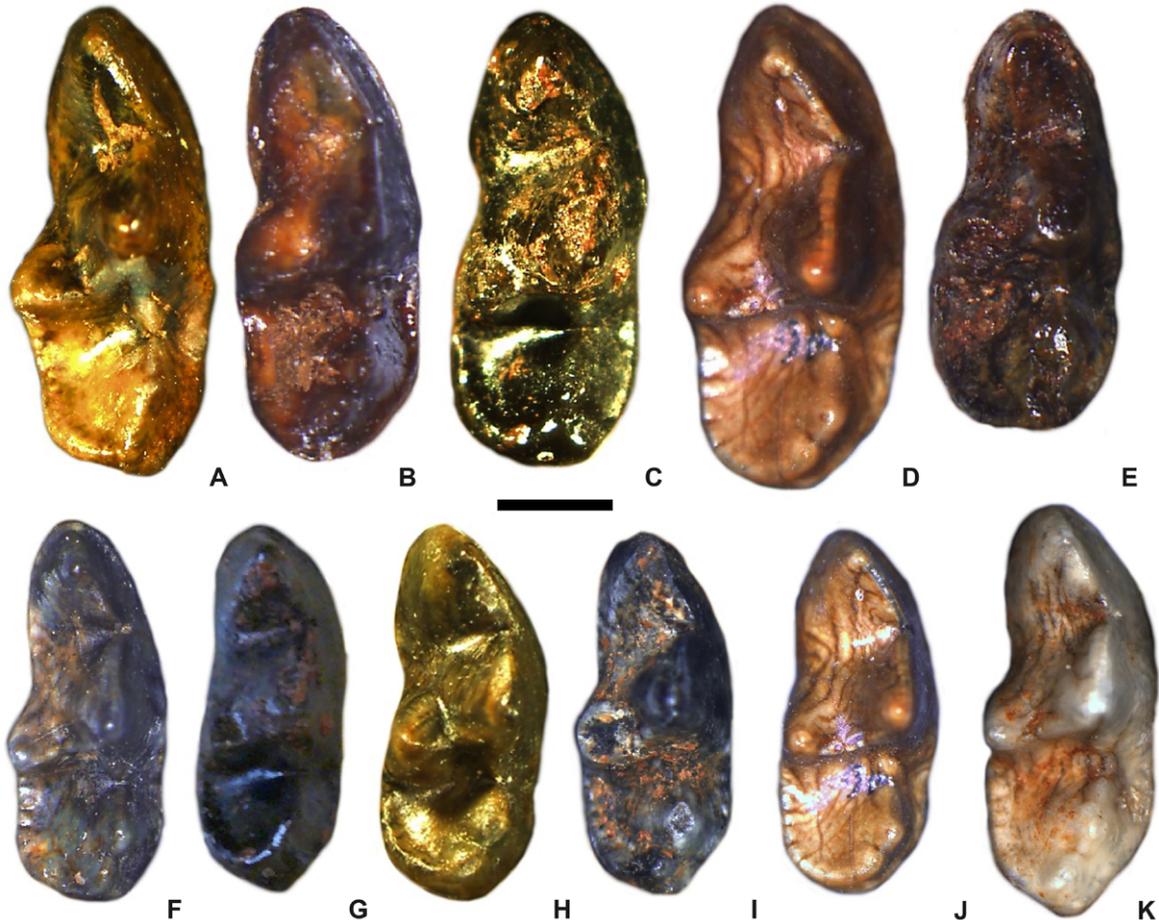


Fig. 4. Lower teeth row of *Baranogale helbingi* from Węże 1 in the occlusal view. A. W1.7.3. B. MF/7933. C. MF/558/2. D. MF/558/1. All individuals shown on the same scale (2 mm).

Table 4

Lower dentition measurements of *Baranogale helbingi* from Węże 1.

Coll. no.	Measurements																
	c1 L	c1 B	p2 L	p2 B	p3 L	p3 Ba	p3 Bp	p4 L	p4 Ba	p4 Bp	m1 L	m1 L tr	m1 L ta	m1 B tr	m1 B ta	m2 L	m2 B
W1.7.3	4.46	2.73	3.13	1.57	3.68	1.66	1.91				7.06	4.77	2.29	2.88	2.83		
W1.7.4											6.32	4.43	2.11	2.57	2.58		
W1.7.6											8.31	5.54	2.81	3.42	3.37		
W1.7.7					3.74	1.84	2.01										
W1.7.8											6.88	4.56	2.21	2.72	2.66		
W1.7.9											6.73	4.57	2.16	2.61	2.57		
W1.7.10											8.14	5.66	3.06	3.44	3.37		
W1.7.11	3.97	1.98															
W1.7.12												4.99		3.31			
W1.7.13											7.25	4.88	2.37	3.18	3.12		
MF/558/5								5.11	1.86	2.26							
MF/558/4								4.55	1.75	2.01							
MF/558/2								4.43	1.61	2.02	6.93	4.54	2.39	2.79	2.72		
MF/558/3											8.29	5.45	2.75	3.22	3.16		
MF/558/1	4.61	2.27			3.99	1.79	2.02				7.78	5.01	2.77	3.06	2.97		
MF/7933	4.71	3.06	3.35	1.63	3.58	1.71	1.93	6.33	1.84	2.37	7.97	5.44	2.78	3.31	3.29	2.25	2.32



**Fig. 5.** Lower carnassials (m1) of *Baranogale helbingi* from Węże 1 in the occlusal view. A. W1.7.6. B. MF/558/1. C. W1.7.5. D. W1.7.13. E. MF/7933. F. MF/558/2. G. W1.7.8. H. W1.7.3. I. W1.7.9. J. W1.7.4. K. MF/558/3. All individuals shown on the same scale (3 mm). Specimens C, D, G, H, J and K are duplicated.

Table 5

Morphological comparison of the mandible and lower dentition characters among known specimens of *Baranogale helbingi* (modified from Sianis *et al.*, 2023, p. 49, tab. 2).

		Węże 1	Podlesice	Karnezeika	Saint Vallier	Villány 3	Etouaries	Dafnero
man- dible	mesial margin of the masseteric fossa	to m1/m2 border		to m2 or m1/m2 border				
c1	angle between the crown axis and the mandibular body axis	acute			almost right		almost right	
	angle between the base crown axis and the mandibular body axis	acute			almost parallel		parallel	
	mesial margin	smooth		smooth	smooth		angular	
	distal margin	smooth		step-like structure	step-like structure		step-like	
p2	p2/m1	41.5			46.0	36.5	42.3	27.3
p3	lingual ridge	strong	weak	weak	strong	strong	strong	
	high/short	short	high	high	high	high	high	short
	cingulid protrusions	weak	only distal strong	strong	strong	strong	strong	only distal strong
p4	diastema	absent	absent	absent	absent	absent	absent	present
	shape	elongated	less elon- gated	elongated	elongated	elongated	elongated	elongated
	cingulid protrusions	strong	only distal strong	strong	strong	strong	strong	only distal strong
m1	accessory cuspid	weak	weak	strong	strong	strong	strong	weak
	notch depth	deep		deep	deep	deep	less deep	shallow
	hypoconid- hypoconulid	independent		almost fused	almost fused	almost fused	independent	
	talonid	elevated	flattened	elevated	elevated	elevated	elevated	flattened
m2	m2/m1	28.2			33.3		27.1	39.0

the paraconid and mesial wall of the protoconid form an open angle. Both main cusps are separated by a deep valley. The protoconid holds two thin crests running from the apex. A very prominent metaconid is well-developed, and clearly separated from the protoconid. Its apex deviates from the latter in a lingual direction, pointing slightly distally thus projecting backwards behind the distal wall of the protoconid. The talonid is moderately long and trenchant, almost as wide as the trigonid. The hypoconid occupies almost the entire buccal portion of the talonid and is well separated from the nearby cingulum. It is an elongated, high and well-developed cusp, with a cutting, crest-like occlusal surface. After this, on the peripheral, disto-buccal edge of the talonid, is situated a much smaller entoconid. It is much lower than the hypoconid, and forms a raised and cutting ridge. The surface of the talonid, closed between the hypo- and entoconid, resembles a deep valley. On the lingual edge is located a series of cuspid-like swellings, which start from the metaconid base, distally decreasing in size. The internal, talonid surface is fully closed and developed in the form of

a smooth, shallow and rectangular area. A second, smaller, smooth and shallow, fan-shaped external surface is located on the buccal side on the transition between the trigonid and the talonid. The buccal margin is almost straight or weakly arched. The lingual margins of the paraconid and talonid are also straight. Only the metaconid lingual ridge is considerably convex, forming a median, lingual bulge. The mesial margin is oblique, while the distal one is blunt. A stronger cingulum is present on the distal margin. The weakly reduced m2 is a one-rooted, rounded tooth, collared by a thick cingulum. This proportionally large tooth is situated somewhat obliquely, in relation to m1. The main cusps, namely the proto- and metaconid, are low, but large and well-developed. The occlusal surface is flat and smooth.

**Comparison:** Stach (1961), who described *Baranogale helbingi* from Węże 1, stated that beyond any doubt, the analysed material is characterised by a set of morphological features, indistinguishable from those of the remains from other sites. In this matter, the material from Węże 1 showed some not very strong, morphological differences between

individuals. However, according to Stach (1961), these are within the intraspecific range of variability. The main problem is that most of the European material of *B. helbingi* is still quite scarce and mostly represented by fragmentary or incomplete mandibles (Kowalski, 1959; Stach, 1961). More numerous relics from one locality are rare, and among them only the Polish site Węże 1, the French Saint Vallier (Viret, 1954) and the Greek Karnezeika (Sianis *et al.*, 2021, 2023) provided more abundant material that made it possible to trace, to some extent, intraspecific variability.

Few small specimens, dimensionally comparable to *Baranogale helbingi* have been described from the Pliocene and the early Pleistocene of Europe. From the Austrian site Deutsch-Altenburg 2 (1.3–1.2 Myr), the enigmatic species *Psalidogale altenburgensis* Rabeder, 1976 was described; its taxonomic status is unclear. Rabeder (1976) described this form as metrically intermediate between *Mustela erminea* Linnaeus, 1758 and *Mustela nivalis* Linnaeus, 1766, with an extremely reduced and short protocone of P4, a bizarre arrangement of the M1 buccal cusps and a considerably elongated and narrow m1. Apart from a strongly doubtful record of this species from the Hungarian site Osztramos 7 (2.0–1.8 Myr; Jánossy, 1986), it has not been found in Europe. Morphologically, *P. altenburgensis* is referable to some Miocene Mustelini. If it is a truly independent species, not an atypical specimen, which is not so clear, it therefore must be regarded as a highly specialised representative of a previously unknown musteline form (Rabeder, 1976; Spassov, 2001).

The comparison showed the morphological distinctiveness of both forms. *Psalidogale altenburgensis* distinguished from *Baranogale helbingi* from Węże 1 by its distinctly smaller size, the presence of diastemas between C1, P2 and P3, one-rooted and notably stronger reduced P2, located at an angle of 45° in relation to the P3, more elongated and narrower P4 with extremely reduced protocone, morphology of M1, where the metacone forms a ridge that curves inwards with the parastyle, and where the paracone is only a mesial, second cusp, related to the metacone, a considerably narrower m1 without metaconid and hypoconulid and a highly trenchant talonid with centrally positioned hypoconid, and a strongly reduced, one-rooted m2 with a simple, occlusal relief.

From the same as *Psalidogale altenburgensis* Austrian site Deutsch-Altenburg 2 (1.3–1.2 Myr), another form, *Oxyvormela maisi* Rabeder, 1973, was described. This fossil Ictonychini was described as a highly evolved form, characterised by a size comparable with the extant *Vormela peregusna* (Güldenstädt, 1770), with a short and robust rostrum, enlarged and robust canines, strongly to totally reduced P2/p2, a more elongated and narrower P4 with a shorter protocone, a more strongly reduced and narrower M1, a considerably more massive and thicker mandible, with a particularly robust symphyseal part, with massiveness of the body mandible decreasing distally, a narrower m1 with a shorter and more reduced talonid and without a metaconid and with a considerably reduced m2 (Rabeder, 1973).

*Baranogale helbingi* from Węże 1 represented a lower stage of evolution, when compared with the highly evolved *Oxyvormela maisi*, and differs with respect to its

less massive rostrum, lower and less massive body mandible with constant lateral thickness, narrower canines, lesser reduction of the P2/p2, a more robust P4 with a longer protocone and shorter metastyle, a larger and broader M1 with more complicated relief, the presence of the hypoconid on p4, a more robust and plesiomorphic m1, with an unreduced metaconid and its more archaic and elongated talonid, and a considerably larger m2.

From Deutsch-Altenburg 2 also a few isolated teeth of an undetermined *Vormela* sp. (Rabeder, 1976) were described. The material was studied by one of us (AM) and it seems clear that it should be classified as *Vormela petenyii* Kretzoi, 1942, a closely related mustelid, mostly contemporary with *Baranogale helbingi* (Kormos, 1934; Kretzoi, 1942). A set of morphological differences was found between *B. helbingi* from Węże 1 and *V. petenyii* and the extant *V. peregusna*. In relation to members of the genus *Vormela*, *B. helbingi* from Węże 1 possesses a larger size, a longer and narrower rostrum, a proportionally longer neurocranium, narrower and a row of incisors pushed more forward, a larger diastema between I3 and C1, a less massive and higher upper dentition, a narrower C1 with a strong longitudinal furrow on the lingual surface, a notably less reduced and more oval P2, a more elongated and narrower P4 with a higher and longer protocone, which is oriented at an angle of 60–70° in relation to the rest of the crown, a distinctly less reduced M1, with a much broader talon and more complicated relief on the chewing surface, a considerably more gracile mandible, with a more elongated and lower body mandible, a much less massive and more oblique symphysis, less tightly compressed lower teeth in the row, a narrower and more curved c1, less robust and higher crowns of p2–m2, a two-rooted, oval-shaped and notably less reduced p2 positioned less disto-lingually, a narrower p4 with a higher, elevated metaconid, a more elongated and narrower m1, with a proportionally larger metaconid, a shorter and lower trigonid, with an oblique mesial margin, a longer, more concave and less trenchant talonid with a longer and higher hypoconid and a larger hypoconulid, and a more plesiomorphic and rounded m2, with stronger main cusps.

Among other fossil Ictonychini, the material from Węże 1 most resembles three species from the genus *Baranogale*, the taxonomic position of which, with the exception of *B. helbingi*, is still strongly unclear. Assignment of the Turolian *B. adroveri* to the genus is questioned (Spassov, 2001). Its occurrence is mostly restricted to the Iberian Peninsula (Petter, 1964, 1987; Adrover *et al.*, 1986; Alcalá *et al.*, 1990; Alcalá and Montoya, 1990; Abella *et al.*, 2019), although a single, not fully certain record came from Germany (Morlo, 1997; Franzen *et al.*, 2013) and temporally to the late Miocene (8.7–6.2 Myr). Spassov (2001) described *B. adroveri* as a form, characterised by an early Turolian age and a very large size. When the dimensions of this species are compared with the range of variability of *B. helbingi*, especially with the material from the Greek site Karnezeika (Sianis *et al.*, 2021, 2023), it matches metrically the size of this species. The main problem with *B. adroveri* is that it is known only from two mandible fragments; such scarce material cannot be used to demonstrate a full range of variability.

Mustelids are characterised by great intraspecific variability and overlap. This is a result of sexual dimorphism, local climatic and environmental conditions and individual variation. For this reason, size difference cannot be used as a stand-alone tool for species discrimination. In comparison with *Mustela* species, characterised by extreme sexual dimorphism (Kratochvíl, 1951, 1977a, b; Erlinge, 1975, 1979, 1987; King, 1989; Abramov and Baryshnikov, 2000; Spassov, 2001; King and Powell, 2007; Marciszak and Socha, 2014; Marciszak *et al.*, 2021), Ictonychini exhibits less variability between the sexes (Rozhnov and Abramov, 2006; Puzachenko *et al.*, 2017). The sexual dimorphism index for extant *Vormela peregusna* is only 6–8% (Rozhnov and Abramov, 2006; Puzachenko *et al.*, 2017), compared with 18–25% in *Mustela* species (Kratochvíl, 1951, 1977a, b; Erlinge, 1975, 1979, 1987; King, 1989; Abramov and Baryshnikov, 2000; Spassov, 2001; King and Powell, 2007; Marciszak and Socha, 2014; Marciszak *et al.*, 2021).

The plotted index of the total length and trigonid breadth of the m1 of *Baranogale* individuals showed the presence of four sets of data that do not overlap with each other (Fig. 6). One set is the huge specimen (♂?) from Rambla del Valdecebro (L m1 is 10.6 mm; Petter, 1964, 1987), comparable in size to very large males of *Mustela eversmanii* (Lesson, 1827) and *M. putorius*. A second group is created by the also very large (L m1 between 8.50–9.50 mm) individuals of *B. helbingi* from Karnezeika (Sianis *et al.*, 2021, 2023) and a single specimen of *B. adroveri* from Los Mansuetos (L m1 is 9.00 mm; Petter, 1964, 1987; Adrover *et al.*, 1986). The other two sets grouped “normal-sized” individuals of *B. helbingi* from the rest of the localities. There is a noticeable difference in size between them, which may be interpreted as sexual dimorphism. For the first group, ♂♂ were assigned with L m1 of 7.40–8.40 mm, while for the second group of smaller ♀♀ with L m1 of 6.32–7.25 mm (Fig. 6). In this context, *B. helbingi* from Węże 1 also can be differentiated in terms of gender, where ♂♂ (L m1 between

7.78–8.31 mm) are clearly larger than ♀♀ (L m1 of 6.32–7.25 mm). The only outstanding, problematic specimens are two very small individuals from Varshets, classified as a separate species, *Baranogale balcanica* Spassov, 2001, which is discussed below. The intraspecific size variability of *B. helbingi* seems to be greater than that of the extant *Vormela peregusna*. It could be related to the lesser ecological specialisation and lower evolutionary level of *B. helbingi*, closer to its Miocene ancestors.

Regarding *Baranogale adroveri*, Spassov (2001) stated that features, like great size, absence of the strongly outlined distal edge of the longitudinal crest on the lingual surface of the c1, the apomorphic morphology of p4 being long and robust, with reduced metaconid and m1 with a larger metaconid and a more reduced taloned, are typical for *Baranogale*. However, as was mentioned above, the fossil material of *B. adroveri* is scarce and it is very risky to use it as a basis for creating definitive opinions. At this point, the present authors are guessing that these differences are related to specific level and the Miocene and Pliocene forms are rather closely related.

*Baranogale balcanica* mentioned above was determined as a separate species, which differs from *B. helbingi* in its smaller dimensions and an admixture of plesiomorphic (more conical, short and high p3–p4, highly positioned and distinctly separated metaconid on p4 and m2 with a vestigial paraconid) and apomorphic (shortening of the rostral parts of the skull and mandible, more tightly pressed lower teeth in rows formed in straight lines without diastemas, a notably strong longitudinal lingual furrow on the C1 and a strongly reduced p2) features (Spassov, 2001). He stated that the demonstration of too great metric differences between *B. balcanica* and *B. helbingi* should be regarded mostly as taxonomic and not an individual or sexual feature. He also added that the values of the dimensional variability in *Baranogale* indicate the existence of more than one species. The present authors currently accept this statement

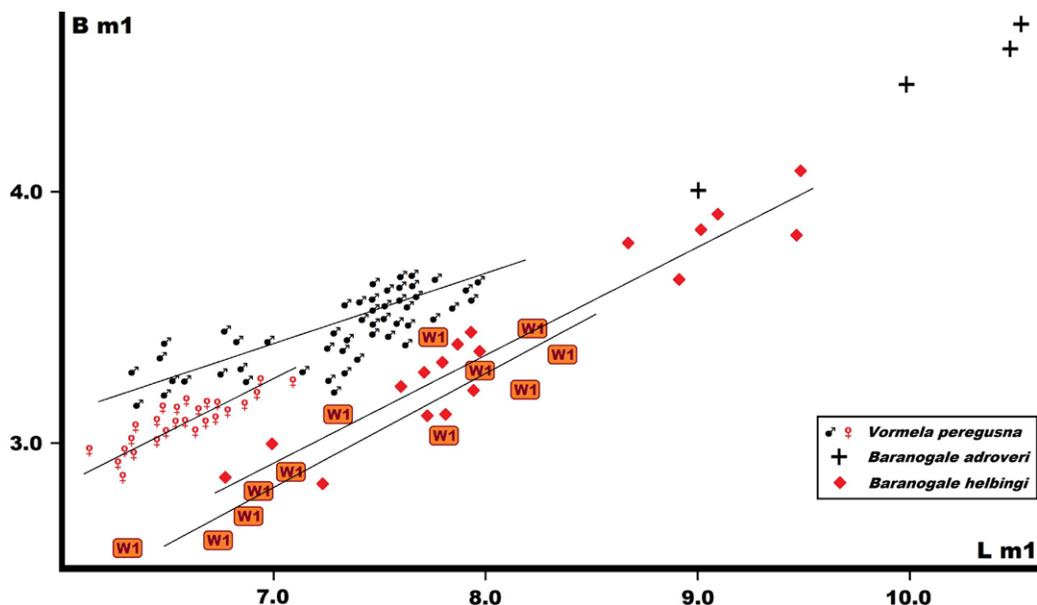


Fig. 6. Graph showing the relationship between the crown length (L m1) and breadth (B m1) of ml of European species of the genus *Baranogale*. For citation, see the chapter Material and Methods.

and regard *B. balcanica* as a separate species, although the aforementioned differences also might be related to the sub-specific level.

## DISCUSSION

Individuals of *Baranogale helbingi* showed relatively broad variation in metrical and morphological differences. Some previous authors (e.g., Kowalski, 1959, Spassov, 2001 and Sianis *et al.*, 2023), mentioned that those inhomogeneous characters are beyond the variability of a normal population, thus pointing to the possible co-occurrence of different subspecies. However, it should be strongly highlighted that in comparison with mustelids from the genus *Martes* Pinel, 1792 and *Mustela* Linnaeus, 1758, the remains of *B. helbingi* are much rarer and mostly incomplete. Except for at sites like Karnezeika and Węże 1, material of this species is represented by one or two mandibles, sometimes also with the addition of other material. Such scarce material does not reflect the full temporal, intraspecific and geographical variability of the species. The real degree of intraspecific variation is not fully known and still there is not enough evidence to support fully some hypotheses. Thus, new finds will provide possible guidelines for future studies (Sianis *et al.*, 2023; Tab. 5).

*Baranogale helbingi* from Węże 1 showed great metrical and morphological similarity to most of the specimens from other European localities. Some among them, like the individuals from Dafnero, Karnezeika and Saint-Vallier, are larger; some, like the holotype from Villány, are smaller. But all of the specimens are within the range of variability for the species and cannot be used as a discriminative feature. Furthermore, the “enormous” size of some specimens can be easily explained by the presence of abnormally sized individuals, the presence of which is noted regularly in the fossil material of different carnivores. Compared to those from Karnezeika and Saint-Vallier, they have more weakly developed cingulid protrusions in p3, a weaker accessory cuspid in p4, and greater independence of the hypoconulid from the hypoconid. The angular orientation of the c1 in relation to the main mandible axis is acute (Sianis *et al.*, 2023). In other specimens, the angle between the c1 crown axis and the mandibular body axis is almost a right angle, while the c1 base crown axis and the mandibular body axis are almost parallel. In the Perrier-Etouaries and Saint-Vallier specimens, the mesial and distal margins have a significantly stronger morphology, with a step-like structure developed (Sianis *et al.*, 2023).

From the entire known material of *Baranogale helbingi*, the most outstanding feature is the robust Dafnero mandible (2.4–2.3 Myr; Koufos and Kostopoulos, 1997). Compared with *B. helbingi* from Węże 1, the Dafnero individual possesses more conical premolars, separated by a diastema and with a more reduced mesial cingulum, a stronger reduced secondary cuspid in p4, a higher paraconid in m1, and a non-elevated talonid. Interestingly, the greatest morphological similarity to the Dafnero specimen is shown by a much smaller and far more ancient mandible from Podlesice, one of the oldest occurrences of the species (Kowalski, 1959;

Spassov, 2001). The Podlesice individual has more conically shaped premolars, a less developed distal cingulum of p4, a flattened and not elevated talonid of m1, with a hypoconulid less independent from the hypoconid and a less deep carnassial notch.

Leaving dimensions aside, since size is not good taxonomic indicator, as was shown already above, an evolutionary scenario can be proposed, in which the present authors generally agree with Sianis *et al.* (2023). Even if owing to the scarcity of the material, the full evolutionary history cannot be reconstructed, certain basic elements make up a logical whole. The oldest (4.9–4.2 Myr) record from Podlesice represented a different stock of Asian or African origin, which might have given rise to the European *B. helbingi* lineage. The morphology of this specimen contains an admixture of traits, typical for the species, but also some more archaic features. The much younger (2.4–2.3 Myr), but morphologically similar Dafnero individual could reflect its Asian or African descendant, which re-invaded Europe during the earliest Pleistocene (Sianis *et al.*, 2023).

Specimens dated as early Pleistocene (2.5–1.6 Myr), like those from Karnezeika, Saint-Vallier, and Villány 3 and 5, represented the same form, widespread across European territory. Their morphology is strongly homogeneous and characterised by the presence of more progressive features, like almost a right angle between the c1 main axis and the mandibular corpus axis, an almost parallel relationship between the c1 base crown and the mandibular corpus axis, a smooth mesial margin of c1 with a tendency to create a step-like structure on its distal margin, a high p3, strong cingulum protrusions in the premolars, an elongated p4 with a strong accessory cuspid, an m1 with a deep carnassial notch, a hypoconulid almost fused with the hypoconid, and an elevated talonid. The middle-late Pliocene (3.6–2.7 Myr) specimens from Beremend, Csarnóta, Odessa Catacombs, Perrier-Etouaries and Węże 1, younger than those at Podlesice, but older than the early Pleistocene, show similar characteristics to those mentioned above, being, however, more primitive. They may represent an ancestral form of *Baranogale helbingi*, the morphology of which is characterised by a mosaic of intermediate features between the middle-late Pliocene and the early Pleistocene. They belong to the one, evolutionary lineage, represented by a monospecific genus. The taxonomic status of *B. balcanica* is still highly uncertain, since scarce material from only one locality (Varshets), was described (Spassov, 2001). It can be assumed with caution that *B. balcanica* really belongs to a separate species, but more material is needed to verify this hypothesis. In this matter, sites like Węże 1, with more numerous and relatively well-preserved material, are especially important in showing in a broader context a wide range of intraspecific variability. On the basis of such material, some aspects like sexual dimorphism, which so far has received no attention, can be also highlighted.

The origin of the Pleistocene *Mustela* is highly unclear, since the late Miocene and early Pliocene history of this genus remains poorly documented. Only a few sites of this age yielded scarce material. In addition, the uniform morphology, strongly pronounced sexual dimorphism and limited

number of finds do not make the task easier. The remains of the small Pliocene *Mustela*, dated between 5–3 Myr, are very rare in Europe and poorly represented (Kormos, 1934; Kowalski, 1962, 1973; Stach, 1959; Vangengeim *et al.*, 1998; Morlo and Kundrát, 2001). Most of these records were assigned to *M. plioerminea*, *M. pliocaenica* or *Mustela* sp. They were regarded as a stem form of the genus *Mustela* and ancestors of Pleistocene forms *M. palerminea* and *M. praenivalis* (Sato *et al.*, 2012). The morphological results obtained were corroborated with the molecular data, which indicated that the separation of the *erminea* lineage and the *nivalis* lineage took place between 3.9–3.4 Myr (Sato *et al.*, 2012).

However, last year this schema that was accepted so far was undermined and the American species recently formed a monophyletic clade *Neogale* Gray, 1865, distinct from other Mustelinae species. It was found that this clade diverged from *Mustela* between 13.4–11.8 Myr (Patterson *et al.*, 2021). Previously, most species were determined as *Mustela* (Koepli *et al.*, 2008; Law *et al.*, 2018; Law, 2019). Additionally, data inferred from mitochondrial genomes showed that the genus *Mustela* already had appeared 11.8–10.3 Myr (Hassanin *et al.*, 2021), much earlier than previously believed (Koepli *et al.*, 2008; Sato *et al.*, 2012; Law *et al.*, 2018).

*Mustela* is an old and diverse genus, as noted by Izor and de la Torre (1978): “*Mustela* is in many respects a primitive mustelid, retaining most of the family’s basic characters. For this reason, care must be exercised so that it does not become a catchall genus, collecting diverse, structurally generalized species without true phylogenetic affinities”. This also has been confirmed by molecular phylogenies, which showed it to be an old and disparate group, characterised by many pleiomorphisms (Koepli *et al.*, 2008; Sato *et al.*, 2012; Law *et al.*, 2018; Hassanin *et al.*, 2021).

In the evolution of the Mustelidae, one of the most crucial periods is the Mid-Miocene Climate Transition (MMCO, 16.1–11.6 Myr; Edwards *et al.*, 2010; Strömberg, 2011; Law, 2019). The period was characterised by massive expansion of the Antarctic ice sheet and global cooling, which resulted in an increase of grasslands (Flower and Kennett, 1994; Böhme, 2003; Doláková *et al.*, 2020). Associated with it, the diversification of rodents and lagomorphs during that period led to increases in many clades among the mustelids, particularly forms like the Mustelinae (Finarelli and Badgley, 2010; Fabre *et al.*, 2012; Samuels and Hopkins, 2017). The carrying capacity of various mustelines for those environmental changes involved decreases in size and shifts towards small, elongate bodies (King, 1989; Koepli *et al.*, 2008; Edwards *et al.*, 2010; Strömberg, 2011; Law *et al.*, 2018; Law, 2019). Evolutionary plans during that time may have facilitated diversification by allowing mustelids to chase prey in tight burrows and tunnels and small crevices (Law *et al.*, 2018; Law, 2019; Liu *et al.*, 2023). During the MMCO, small Mustelinae extensively diversified and differentiated in a stepwise fashion, being able to occupy various habitats, ranging from tropical rainforests to tundra and from steppe and desert to riparian biotopes and to coastal waters, mostly in Asia (Sato *et al.*, 2012). The Eurasian continent itself was shown to have been involved in the

species diversification (Hosoda *et al.*, 2000; Law, 2019; Liu *et al.*, 2023).

The attempts of Mustelidae to create extra small, dwarf carnivore forms started as early as ca. 25–24 Myr, e.g., *Plesictis julieni siccaulensis* Viret, 1929 (Spasov, 2001). However, the real intensity of this phenomenon is observed in the late Miocene, and later, in the Pliocene. It results from an enlargement of the open grasslands, the so-called Microtinae habitat. It stimulated evolution by creating a new ecological niche for a number of small carnivores (King, 1989). The limb shortening and reduction of the body size was one of the main directions for specialisation of the Mustelidae (Spasov, 2001). It allowed small Mustelinae to hunt rodents in their burrows and tunnels. Parallel to the Mustelinae, such specialisation evolved simultaneously in the Ictonychini (Spasov, 2001).

During a long timespan, covering almost the whole Pliocene and the earliest Pleistocene (~4.9–2.0 Myr), the Mustelinae coexisted with the Ictonychini. Their co-occurrence is documented at 14 European sites (Kormos, 1934; Viret, 1954; Kretzoi, 1956, 1959a, b; Kowalski, 1959, 1962, 1973; Stach, 1961; Heintz *et al.*, 1974; Azzaroli, 1977; Jánossy, 1986, 1996; Kotsakis, 1986; Wolsan, 1989; Alberdi *et al.*, 1997; Koufos and Kostopoulos, 1997; Morlo and Kundrát, 2001; Radulescu *et al.*, 2003; Guérin *et al.*, 2004; Marciszak, 2012; Koufos, 2022). However, since the beginning of the Pleistocene (2.6–2.2 Myr), members of the genus *Baranogale* and *Vormela* started to be rare, until the final disappearance of the genus *Baranogale* in the early Pleistocene. Probably better adapted and ecologically more flexible Mustelinae, outcompeted the Ictonychini across most of their Eurasian range. Żabia Cave (1.7–1.5 Myr) seems to be the last and the youngest site with the documented co-occurrence of *Baranogale* and *Mustela* species (Marciszak, 2012). The extant *Mustela* is one of the most widespread genera in the Mustelidae. Members of this genus occur in Eurasia, North Africa, North America, and northern parts of South America (Law, 2019; Liu *et al.*, 2023).

The size variability of *Baranogale helbingi* is also one of the manifestations of evolutionary adaptation, though not the only one. Dwarfing was not observed in the evolution of this species, but some strong differences occur between specimens from various sites. Those from Węże 1, Csarnóta, Villány 3, and Perrier-Etouaires are of moderate size, while those from Dafnero, Karnezeika and Saint-Vallier appear to be larger than the rest. Palaeoecological conditions and the resulting competition in the environments inhabited by *B. helbingi* are still poorly understood and are based largely on comparison with the environmental conditions of today. Although this provides a certain picture, it does not allow us to draw any clear conclusions, but rather constitutes a background for certain hypothetical considerations. In this matter, the significant variation in the size of *B. helbingi* is partly the result of sexual dimorphism as well as the influence of the environmental conditions and the climate, in which a given population lived.

However, another explanation is also possible. In comparison with other small mustelids, *Baranogale helbingi* shows a relatively lower evolutionary level, which is clearly

visible in their dentognathic material. In relation to species like *Vormela peregusna*, but also those from genus *Mustela*, features adapted to catching and killing relatively large prey are more weakly developed. It is especially well documented in comparison with highly specialised hunters of the large, steppe rodents, like *M. eversmanii* and *V. peregusna*. The high development level of hypercarnivorous features in both species are expressed in strongly developed muscle attachments that are wide spacing. They have massive zygomatic arches, strongly expanded and flattened at the rear, and the shortening and expansion of the rostrum. These features shorten the length of the lever arm and compress the force, exerted by pressing the jaws over a shorter length (Poljakova, 1978; Spassov and Spidorov, 1993). The strongly marked postorbital narrowing is related to the strong development of the occipital muscle, occupying the entire distal part of the skull. The mandibular body is massive and short, the mandibular fossa long and deep. These features generate a high bite force and at the same time demonstrate resistance to high mechanical stress (Poljakova, 1978; Spassov and Spidorov, 1993).

There was a reduction in the number and size of the extreme teeth, like the disappearance of P1/p1 and a notable reduction in the size of P2/p2, M1 and m2. They are more strongly reduced than in the case of other species of the Ictonychini tribe. There has been a strong development of I3, where the crown is longer and more massive than that of I3 species of the genus *Mustela*. The incisor line is moved more forward, and the existing diastema between I3 and the canine is larger. These features result in the more effective use of the length of the canine crown: the remote crown I3 does not block the penetrating canines, and at the same time is an additional factor in holding and injuring the victim. Long and massive canines are characterised by massive roots. This allows better anchoring of the canines in the jaw and greater resistance to the mechanical stress exerted, when pressing the jaws and holding a struggling prey. This massiveness of the canines results from the method of killing prey by *V. peregusna* and allows them to pierce the thick bones of the braincase of large steppe rodents, like gophers and hamsters (Spassov and Spiridonov, 1993; Spassov, 2001). There was also an increase in the massiveness of P3/p3 and P4, the distal parts of their crown were expanded, and a number of premolars were shortened, compressed and arcuate. The long hypocone and large metacone M1 form additional cutting edges.

The same, even more strongly developed features were found in the evolution of *M. eversmanii*. A strong bite and massive teeth are necessary to kill large, aggressive prey, mainly the steppe rodents, which were the basis of its diet. The strongly arched line of moderately sized incisors is another expression of this specialisation. Carnivores that kill large prey through deep bites, like large felids and species of the *Mustela* genus, have smaller incisors in proportion to body size. Their smaller crowns are less involved in catching and killing prey and are generally not tools for inflicting large wounds, but for cleaning meat from the bones of hunted prey. The incisors have become strongly compressed and the I2/i2 is often moved to the second, rear row. Reducing the size of the incisor crowns allows the formation of a

diastema between them and the canines and allows better projection and, consequently, better use of the entire length of the canine crown and deeper penetration into the prey's body. The size of the incisors of *Mustela* species reflects the specialisation of hunting for prey, similar in size to or larger than the hunter. Moving the incisor line backwards and shortening the lever arm causes greater force generated by the jaw muscles to be concentrated in a shorter distance. This translates significantly into an increase in the bite force, necessary to pierce the bones of victims (Greaves, 1983; Van Valkenburgh and Ruff, 1987; Van Valkenburgh, 1988; Biknevičius and Ruff, 1992; Biknevičius et al., 1996; Biknevičius and Van Valkenburgh, 1996).

The massive canines of *Mustela eversmanii* are characterised by a weakly curved crown. They evolved as long, massive, straight blades, used to pierce the thick skulls and strongly muscled necks of prey. The canines of *M. eversmanii* and *Vormela peregusna*, which specialised in hunting large prey, are analogous to those of felids, with long, dagger-like canines with a straight, long crown, designed for piercing and deep penetration into the bodies of the prey. The elongated and robust m1 trigonid is characterised by a long, mesial, cutting edge, created by a protoconid and strongly accentuated broadening of the m1 crown at the level of the protoconid. There was also a particularly marked reduction of P2/p2, M1, the talonid of m1 and m2.

In comparison with *Mustela eversmanii* and *Vormela peregusna*, *Baranogale helbingi* definitely represents a lower stage of evolutionary development. It is well documented in a proportionally more elongated and narrower rostrum, less widely spaced zygomatic arches, less developed muscle attachments, like sutures and the sagittal crest, a more elongated and slender mandibular body, a shorter and shallower masseteric fossa, loosely positioned in almost a straight tooth row premolars and molars, less exposed forward and smaller incisors, narrower and more curved canines, relatively weak reduction of P2/p2, M1 and m2. Such a mixture of features is typical for mustelids, which regularly hunted prey smaller than themselves. Those species do not need such massive teeth and jaw muscles as those of *M. eversmanii* and *V. peregusna*, for example. This may mean that there is a similar situation in the case of *B. helbingi*. Anyway, the larger dimensions of specimens from Dafnero, Karnezeika and Saint-Vallier can be related to possibly less competition pressure of large *Mustela* species. It is especially the case with highly specialised *M. eversmanii*, the occurrence of which so far was not documented from Greek territory (Koufos, 2022), the area for most records of large *B. helbingi*. The lack of such competitors allowed this ancient and less specialised mustelid to hold the niche, occupied in other, more northern areas by ecologically more flexible and expansive *Mustela* species.

## CONCLUSIONS

The presence of a European endemit, *Baranogale helbingi*, was documented from 30 sites, of which 8 are located in Poland. The occurrence of this ancient and archaic

mustelid is characteristic for the Pliocene, but the species occurred also during the early Pleistocene. Among those records, especially noteworthy is the Polish site Węże 1, dated at 3.6–3.2 Myr. From this locality abundant material is known, represented among other specimens by two relatively well-preserved skulls. Studies of these remains broadly expand knowledge about the species. Morphometrical analysis showed the important role of sexual dimorphism in the variability of the species. During the early Pleistocene, like other European Ictonychini, *B. helbingi* became extinct, probably owing to competition with small Mustelinae that were extremely adaptable in terms of ecology.

### ACKNOWLEDGMENTS

We would like to thank Oleksandr Kovalchuk for proofreading the English text. We are also very grateful for the remarks from Martina Robličková (Moravské Zemské Muzeum, Brno) and one anonymous reviewer, which enabled us to improve the text and clarify the argumentation.

### REFERENCES

- Abella, J., Hontecillas, D., Valenciano, A., Montoya, P., Morales, J., Pesquero, M. D. & Alcalá, L., 2019. The last record of an ailuroprocyonid bear from the Iberian Peninsula. In: de Bonis, L. & Werdelin, L. (eds), *Memorial to Stéphane Peigné, carnivores (Hyaenodonta and Carnivora) of the Cenozoic. Geodiversitas*, 41: 797–809.
- Abramov, A. V. & Baryshnikov, G. F., 2000. Geographic variation and intraspecific taxonomy of weasel *Mustela nivalis* (Carnivora, Mustelidae). *Zoosystematica Rossica*, 8: 365–402.
- Adrover, R., Martínez, L. A., Mein, P., Moissenet, E. & Orrios, J., 1986. Mamíferos del turolense medio en la Rambla de Valdecebro (Teruel). *Estudios Geológicos*, 42: 495–510.
- Alberdi, M. T., Azanza, B., Cerdeño, E. & Prado, J. L., 1997. Similarity relationship between mammal faunas & biochronology from latest Miocene to Pleistocene in the Western Mediterranean area. *Ecologiae Geologicae Helvetiae*, 90: 115–132.
- Alcalá, L. A., 1994. *Macromamíferos neógenos de la fosa de Alfambra-Teruel*. Museo Nacional de Ciencias Naturales, Teruel, 563 pp.
- Alcalá, L. & Montoya, P., 1990. Las faunas de macromamíferos del Turolense inferior español. *Paleontologia i Evolució*, 23: 111–119.
- Alcalá, L., Morales, J. & Soria, D., 1990. El registro fósil neógeno de los carnívoros (Creodonta y Carnivora, Mammalia) de España. *Paleontologia i Evolució*, 23: 55–74.
- Azzaroli, A., 1977. The Villafranchian stage in Italy and the Plio-Pleistocene boundary. *Giornale di Geologia*, 41: 61–79.
- Benammi, M., Aidona, E., Merceron, G., Koufos, G. D. & Kostopoulos, D. S., 2020. Magnetostratigraphy and chronology of the Lower Pleistocene primate bearing Dafnero fossil site, N. Greece. *Quaternary*, 22: 1–15.
- Biknevicius, A. R. & Ruff, C. B., 1992. The structure of the mandibular corpus and its relationship to feeding behaviour in extant carnivores. *Journal of Zoology*, 228: 479–507.
- Biknevicius, A. R. & Van Valkenburgh, B., 1996. Design for killing, craniodental adaptations of predators. In: Gittleman, J. L. (ed.), *Carnivore Behaviour, Ecology, and Evolution*, Vol. 2. Cornell University Press, Ithaca, pp. 393–428.
- Biknevicius, A. R., Van Valkenburgh, B. & Walker, J., 1996. Incisor size and shape, implications for feeding behaviours in saber-toothed “cats”. *Journal of Vertebrate Paleontology*, 16: 510–521.
- Bowdich, T. E., 1821. An analysis of the natural classifications of Mammalia: for the use of students and travellers. J. Smith, Paris.
- Böhme, M., 2003. The Miocene Climatic Optimum, evidence from ectothermic vertebrates of Central Europe. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 195: 389–401.
- Colombero, S., Alba, D. M., D’Amico, C., Delfino, M., Esu, D., Giuntelli, P., Harzhauser, M., Mazza, P. P. A., Mosca, M., Neubauer, T. A., Pavia, G., Pavia, M., Villa, A. & Carnevale, G., 2017. Late Messinian mollusks and vertebrates from Moncucco Torinese, north-western Italy. Paleocological and paleoclimatological implications. *Palaeontologia Electronica*, 20.1.10A: 1–66.
- Doláková, N., Kováčová, M. & Utescher, T., 2020. Vegetation and climate changes during the Miocene climatic optimum & Miocene climatic transition in the northwestern part of Central Paratethys. *Geological Journal*, 56: 729–743.
- Edwards, E. J., Osborne, C. P., Strömberg, C. A. E., Smith, S. A. & Consortium, C. G., 2010. The origins of C4 grasslands, integrating evolutionary and ecosystem science. *Science*, 328: 587–591.
- Erlinge, S., 1975. Feeding habits of the weasel (*Mustela nivalis*) in relation to prey abundance. *Oikos*, 26: 378–384.
- Erlinge, S., 1979. Adaptive significance of sexual dimorphism in weasels. *Oikos*, 33: 233–245.
- Erlinge, S., 1987. Why do European stoats *Mustela erminea* not follow Bergmann’s rule? *Holarctic Ecology*, 10: 33–39.
- Fabre, P.-H., Hautier, L., Dimitrov, D. & Douzery, E. J. P., 2012. A glimpse on the pattern of rodent diversification, a phylogenetic approach. *BMC Evolutionary Biology*, 12: 88.
- Finarelli, J. A. & Badgley, C., 2010. Diversity dynamics of Miocene mammals in relation to the history of tectonism and climate. *Proceedings of the Royal Society B: Biological Sciences*, 277: 2721–2726.
- Fischer de Waldheim, G., 1817. *Adversaria zoologica. Mémoires de la Société Impériale des Naturalistes de Moscou*, 5: 357–472.
- Flower, B. P. & Kennett, J. P., 1994. The Middle Miocene climatic transition, East Antarctic ice sheet development, deep ocean circulation and global carbon cycling. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 108: 537–555.
- Franzen, J. L., Pickford, M. & Costeur, L., 2013. Palaeobiodiversity, palaeoecology, palaeobiogeography & biochronology of Dorn-Dürkheim 1: a summary. *Palaeobiodiversity and Palaeoenvironments*, 93: 277–284.
- Girotti, O., Capasso Barbato, L., Esu, D., Gliozzi, E., Kotsahis, T., Martinetto, E., Petronio, C., Sardella, R. & Squazzini, E., 2003. The section of Torre Picchio (Terni, Umbria, central Italy), a Villafranchian site rich in vertebrates, molluscs, ostracods and plants. *Rivista Italiana di Paleontologia e Stratigrafia*, 109: 77–98.
- Głazek, J., Sulimski, A. & Wysoczański-Minkowicz, T., 1976. On the stratigraphic position of Węże I locality, Middle Poland.

- In: Panoš, V. (ed.), *Proceedings of the 6<sup>th</sup> International Congress of Speleology, Olomouc – CSSR*. Academia, Praha, pp. 435–442.
- Głazek, J. & Szyrkiewicz, A., 1987. Stratygrafia młodo- trzeciorzędowych i wczesnoczwartorzędowych osadów krasowych i jej paleogeograficzne implikacje. In: Jahn, A. & Dyjor, S. (eds), *Problemy młodszego neogenu i eoplejstocenu w Polsce. Materiały Konferencji Naukowej Pliocena i eoplejstocena sieć rzeczna i związane z nią kompleksy osadów gruboklastycznych w Polsce*. Ossolineum, Wrocław, pp. 113–130. [In Polish.]
- Greaves, W. S., 1983. A functional analysis of carnassial biting. *Biological Journal of the Linnean Society*, 20: 353–363.
- Guerin, C., Faure, M., Argant, A., Argant, J., Cregut-Bonnoure, E., Debard, E., Delson, E., Eisenmann, V., Huguency, M., Limondin-Lozouet, N., Martin-Sufirez, E., Mein, P., Mourer-Chauviree, C., Parenti, F., Pastreh, J.-F., Seng, S. & Vallia, A., 2004. Le gisement pliocene superieur de Saint-Vallier (Drome, France) synthese biostratigraphique et paleoecologique. *Geobios*, 37: 349–360.
- Güldenstädt, A. I., 1770. Peregusna nova mustelae species. *Novi Commentari Academiæ Scientiarum Imperialis Petropolitanae*, 14: 441–455.
- Hassanin, A., Véron, G., Ropiquet, A., van Vuuren, B. J., Lécuyer, A., Goodman, S., Haider, J. & Nguyen, T. T., 2021. Evolutionary history of Carnivora (Mammalia, Laurasiatheria) inferred from mitochondrial genomes. *PLoS One*, 16: e0240770.
- Heintz, E., Guérin, C., Martin, R. & Prat, F., 1974. Principaux gisements villafranchiens de France, listes fauniques et biostratigraphie. *Mémoires du Bureau de Recherches géologiques et minières*, 78: 169–182.
- Heller, F., 1967. Die Altersstellung des Villafranchium und seiner Fauna. *Quartär*, 18: 9–23.
- Hosoda, T., Suzuki, H., Harada, M., Tsuchiya, K., Han, S. H., Zhang, Y., Kryukov, A. P. & Lin, L. K., 2000. Evolutionary trends of the mitochondrial lineage differentiation in species of genera *Martes* and *Mustela*. *Genes and Genetic Systems*, 75: 259–267.
- Izor, R. J. & De La Torre, L., 1978. A new species of weasel (*Mustela*) from the highlands of Colombia, with comments on the evolution and distribution of South American weasels. *Journal of Mammalogy*, 59: 92–102.
- Jánossy, D., 1986. *Pleistocene Vertebrate Faunas of Hungary*. Akademiai Kiado, Budapest, 226 pp.
- Jánossy, D., 1996. Lower Pleistocene vertebrate faunas from the localities 16 and 17 of Beremend (southern Hungary). *Fragmenta Mineralogica et Paleontologica*, 18: 91–102.
- King, C. M., 1989. The advantages and disadvantages of small size to weasels, *Mustela* species. In: Gittleman, J. L. (ed.), *Carnivore Behaviour, Ecology, and Evolution*. Springer, Boston, pp. 302–334.
- King, C. M. & Powell, R. A., 2007. *The Natural History of Weasels and Stoats. Ecology, Behaviour, and Management*. Oxford University Press, New York, 456 pp.
- Koepfli, K.-P., Deere, K. A., Slater, G. J., Begg, C., Begg, K., Grassman, L., Lucherini, M., Veron, G. & Wayne, R. K., 2008. Multigene phylogeny of the Mustelidae, resolving relationships, tempo and biogeographic history of a mammalian adaptive radiation. *BMC Biology*, 6: 10.
- Kokotini, M., Kargopoulos, N., Iliopoulos, G., Roussiakis, S., Skalos, P., Michailidis, D., Svorligkou, G., Kampouridis, P. & Theodorou, G., 2019. Karnezeika (Argolis, Peloponnese), preliminary data concerning a new Villafranchian locality of Southern Greece. In: Kranis, H. (ed.), *Proceedings of the 15th International Congress of the Geological Society of Greece, Athens, Greece, 22–24 May 2019*. Athens, pp. 39–40.
- Kormos, T., 1934. Neue und wenig bekannte Musteliden aus dem ungarischen Oberpliozän. *Folia Zoologica et Hydrobiologica*, 5: 129–158.
- Kotsakis, T., 1986. Elementi di paleobiogeografia dei mammiferi Terziari della Italia. *Hystrix*, 1: 25–68.
- Koufos, G. D., 1993. Late Pliocene carnivores from Western Macedonia (Greece). *Paläontologische Zeitschrift*, 67: 357–376.
- Koufos, G. D., 2001. The Villafranchian mammalian faunas and biochronology of Greece. *Bollettino della Società Paleontologica Italiana*, 40: 217–223.
- Koufos, G. D., 2014. The Villafranchian carnivoran guild of Greece, implications for the fauna, biochronology and paleoecology. *Integrative Zoology*, 9: 444–460.
- Koufos, G. D., 2022. The fossil record of mustelids (Mammalia, Carnivora, Mustelidae) in Greece. In: Vlachos, E. (ed.), *Fossil Vertebrates of Greece Vol. 2. Laurasiatherians, Artiodactyles, Perissodactyles, Carnivorans, and Island Endemics*. Springer, Cham, pp. 641–659.
- Koufos, G. D. & Kostopoulos, D. S., 1997. New carnivore material from the Plio-Pleistocene of Macedonia (Greece) with the description of a new canid. *Müncher Geowissenschaftliche Abhandlungen, Reihe A, Geologie und Paläontologie*, 34: 33–63.
- Koufos, G. D., Kostopoulos, D. S. & Koliadimou, K. K., 1991. Un nouveau gisement de mammifères dans le Villafranchien de Macédoine occidentale (Grèce). *Comptes Rendus de l'Académie des Sciences*, 313: 831–836.
- Kowalski, K., 1959. *Baranogale helbingi* Kormos & other Mustelidae from the bone breccia in Podlesice near Kroczyce (Poland). *Acta Palaeontologica Polonica*, 4: 61–69.
- Kowalski, K., 1962. Les micro-mammifères du Pliocène et du Pléistocène inférieur de la Pologne. In: Savage, R. J. G. (ed.), *Problèmes Actuels de Paléontologie (Évolution des Vertébrés), Paris, 29 Mai – 3 Juin, 1961. Colloques Internationaux du Centre National de la Recherche Scientifique*, 104: 409–416.
- Kowalski, K., 1964. Paleocology of mammals from the Pliocene and Early Pleistocene of Poland. *Acta Theriologica*, 8: 73–88. [In Polish, with English summary.]
- Kowalski, K., 1973. Rozwój fauny w czwartorzędzie Polski. In: Rühle, E. (ed.), *Metodyka badań osadów czwartorzędowych*. Wydawnictwa Geologiczne, Warszawa, pp. 110–111. [In Polish.]
- Kowalski, K., 1990. Stratigraphy of Neogene mammals of Poland. In: Lindsay, E. H., Fahlbusch, V. & Mein, P. (eds), *European Neogene Mammal Chronology*. Plenum Press, New York, pp. 193–209.
- Kratochvíl, J., 1951. Kolčavy a kolčavky v Československu. *Sborník Vysoké školy zemědělské v Brně*, 1: 61–148. [In Czech.]
- Kratochvíl, J., 1977a. Studies on *Mustela erminea* (Mustelidae, Mammalia) I. Variability of metric and mass traits. *Folia Zoologica*, 26: 291–304.

- Kratochvíl, J., 1977b. Sexual dimorphism & status of *Mustela nivalis* in Central Europe (Mammalia, Mustelidae). *Acta Scientiarum Naturalium Bohemoslovaca Brno*, 11: 1–42.
- Kretzoi, M., 1942. Tigeriltis, Iltis und Nerz im ungarischen Pleistozän. *Földtani Közlöny*, 72: 323–344.
- Kretzoi, M., 1956. Die altpleistozänen Wilberltierfaunen des Villanyer Gebirges. *Geologica Hungarica, Seria Paleontologia*, 27: 1–264.
- Kretzoi, M., 1959a. A Csarnotai fauna es faunaszint. *Földtani évi Jelentese*, 17: 297–395. [In Hungarian.]
- Kretzoi, M., 1959b. Insectivoren, Naugetierte und Lagomorphen der jüngstpliozänen Fauna von Csarnota in Villanyer Gebirge (Südungarn). *Vertebrata Hungarica*, 2: 237–246.
- Kretzoi, M. & Pécsi, M., 1982. A Pannóniai-medence pliocén és pleisztocén időszakának tagolása. *Földrajzi Közlemények*, 106: 300–326. [In Hungarian.]
- Law, C. J., 2019. Evolutionary shifts in extant mustelid (Mustelidae, Carnivora) cranial shape, body size and body shape coincide with the Mid-Miocene Climate Transition. *Biology Letters*, 15: 20190155.
- Law, C. J., Slater, G. J. & Mehta, R. S., 2018. Lineage diversity and size disparity in Musteloidea, testing patterns of adaptive radiation using molecular and fossil based methods. *Systematic Biology*, 67: 127–144.
- Lesson, R. P., 1827. *Manuel de mammalogie, ou Histoire naturelle des mammifères*. J. B. Baillière, Paris, 441 pp.
- Linnaeus, K., 1758. *Systema naturae per regna tria naturae: secundum classes, ordines, genera, species, cum characteribus, differentiis, synonymis, locis, Tomus I. Laurentii Salvii, Holmiae* [Stockholm], 824 pp.
- Linnaeus, K., 1766. *Systema naturae per regna tria naturae: secundum classes, ordines, genera, species, cum characteribus, differentiis, synonymis, locis, Tomus I. Laurentii Salvii, Holmiae* [Stockholm], 532 pp.
- Liu, Y., Pu, Y., Chen, S., Wang, X., Murphy, R. W., Wang, X., Liao, R., Tang, K., Yue, B. & Liu, S., 2023. Revalidation and expanded description of *Mustela aistoodonnivalis* (Mustelidae, Carnivora) based on a multigene phylogeny and morphology. *Ecology and Evolution*, 13: e9944.
- Marciszak, A., 2012. *Mustelids (Mustelidae, Carnivora, Mammalia) from the Pleistocene of Poland*. Unpublished Ph.D. Thesis, University of Wrocław, Wrocław, 1078 pp. [In Polish, with English abstract.]
- Marciszak, A., Ambros, D. & Hilpert, B., 2021. Mustelids from Sackdilling Cave (Bavaria, Germany) and their biostratigraphic significance. *Geobios*, 68: 83–107.
- Marciszak, A. & Socha, P., 2014. Stoat *Mustela erminea* Linnaeus, 1758 and weasel *Mustela nivalis* Linnaeus, 1766 in palaeoecological analysis, a case study of Biśnik Cave. *Quaternary International*, 339–340: 258–265.
- Morlo, M., 1997. Die Raubtiere (Mammalia, Carnivora) aus dem Turolium von Dorn-Dürkheim 1 (Rheinhausen). Teil 1, Mustelidae, Hyaenidae, Percrocutidae, Felidae. In: Franzen, J. L. (ed.), *Die Säugetiere aus dem Turolium von Dorn-Dürkheim 1 (Rheinhausen, Deutschland)*. Courier Forschungsinstitut Senckenberg, 197: 11–47.
- Morlo, M. & Kundrát, M., 2001. The first carnivoran fauna from the Ruscium (Early Pliocene, MN 15) of Germany. *Paläontologische Zeitschrift*, 75: 163–187.
- Nagel, D., Pronin, K., Pytlik, I., Urbanek, C., Ivanoff, D. & Semenov, Y., 2004. Die Pliozäne Fauna der Katakomben von Odessa (Ukraine). *Berichte des Institutes für Geologie und Paläontologie der Karl-Franzens-Universität Graz*, 9: 278–280.
- Patterson, B. D., Ramírez-Chaves, H. E., Vilela, J. F., Soares, A. E. R. & Grewe, F., 2021. On the nomenclature of the American clade of weasels (Carnivora, Mustelidae). *Journal of Animal Diversity*, 3: 1–8.
- Petőnyi, S. J., 1864. *János hátrahagyott munkái*. Eggenberger, Pest, 141 pp. [In Hungarian.]
- Petter, G., 1964. Deux Mustélidés nouveaux du Pontien d'Espagne orientale. *Bulletin du Muséum National d'histoire Naturelle*, 36: 270–278.
- Petter, G., 1987. Small carnivores (Viverridae, Mustelidae, Canidae) from Laetoli. In: Leakey, M. & Harris, J. (eds), *A Pliocene Site in Northern Tanzania*. Clarendon Press, Oxford, pp. 194–234.
- Pinel, P., 1792. Recherches sur une nouvelle classification des quadrupèdes, fondée sur la structure mécanique des parties osseuses qui servent à l'articulation de la mâchoire inférieure. *Actes de la Société d'Histoire Naturelle de Paris*, 1: 50–60.
- Pocock, R. I., 1921. On the external characters and classification of the Mustelidae. *Proceedings of the Zoological Society of London*, 1921: 803–837.
- Poljakova, R. S., 1978. O neprijamon opredelnii cili zhevatel'noy muskulaturi nekotorykh kunich (Mustelidae). *Trudy Zoologicheskava Istituta, Sbornik Sistematika i Morfologija Mlekopitajuscich*, 75: 106–118. [In Russian.]
- Pomel, A., 1853. *Catalogue méthodique et descriptif des vertébrés fossiles découverts dans le bassin hydrographique supérieur de la Loire, et surtout dans la vallée de son affluent principal l'Allier*. Baillière, Paris, 198 pp.
- Puzachenko, A. Y., Abramov, A. V. & Rozhnov, V. V., 2017. Cranial variation and taxonomic content of the marbled polecat *Vormela peregusna* (Mustelidae, Carnivora). *Mammalian Biology*, 83: 10–20.
- Rabeder, G., 1973. Ein neuer Mustelidae (Carnivora) aus dem Altpleistozän von Deutsch Altenburg 2 (Niederösterreich). *Neues Jahrbuch für Geologie und Paläontologie München*, 11: 674–689.
- Rabeder, G., 1976. Die Carnivore (Mammalia) aus dem Altpleistozän von Deutsch-Altenburg 2. Mit Beiträgen zur Systematik einiger Musteliden und Caniden. *Beiträge zur Paläontologie von Österreich*, 1: 5–119.
- Radulescu, C., Samson, P.-M., Petculescu, A. & Stiuca, E., 2003. Pliocene large mammals of Romania. *Coloquios de Paleontologia*, 1: 549–558.
- Rozhnov, V. V. & Abramov, A. V., 2006. Sexual dimorphism of marbled polecat *Vormela peregusna* (Carnivora, Mustelidae). *Bulletin of the Russian Academy of Sciences*, 33: 144–148.
- Samsonowicz, J., 1934. Zjawiska krasowe i trzeciorzędowa brekcja kostna w Wężach pod Działoszynem. *Zabytki Przyrody Nieożywionej Ziemi Rzeczypospolitej Polskiej*, 3: 151–162. [In Polish.]
- Samuels, J. X. & Hopkins, S. S. B., 2017. The impacts of Cenozoic climate and habitat changes on small mammal diversity of North America. *Global & Planetary Change*, 149: 36–52.

- Sato, J. J., Wolsan, M., Prevosti, F. J., D'Elia, G., Begg, C., Begg, K., Hosoda, T., Campbell, K. L. & Suzuki, H., 2012. Evolutionary and biogeographic history of weasel-like carnivorans (Musteloidea). *Molecular Phylogenetics and Evolution*, 63: 745–757.
- Schaub, S., 1949. Révision de quelques carnassiers villafranchiens du Niveau des Étouaires (montagne de Perrier, Puy-de-Dôme). *Eclogae Geologicae Helvetiae*, 42: 492–506.
- Sianis, P. D., Kostopoulos, D. S., Roussiakis, S. & Iliopoulos, G., 2023. Carnivora from the Early Pleistocene locality of Karnezeika (Southern Greece). *Geobios*, 79: 43–59.
- Sianis, P. D., Kostopoulos, D. S., Roussiakis, S., Koufos, G. D. & Iliopoulos, G., 2021. New *Baranogale* (Mammalia, Mustelidae) finds from the Middle Villafranchian of Southern Greece. In: Belvedere, M., Díez Díaz, V., Mecozi, B. & Sardella, R. (eds), *Abstract Book of the XVIII Annual Conference of the European Association of Vertebrate Palaeontologists (5–9 July 2021, Benevento, Italy)*. *Palaeovertebrata (Special Volume)*, 1: 1–151.
- Spassov, N., 1997. Varshets and Slivnitsa, new rich localities of vertebrate fauna from Bulgaria (taxonomical composition, biostratigraphy, climatochronology). *Geologica Balcanica*, 27: 83–90.
- Spassov, N., 2000. Biochronology and zoogeographic affinities of the Villafranchian faunas of South Europe. *Historia Naturalis Bulgarica*, 12: 89–128.
- Spassov, N., 2001. Zorillas (Carnivora, Mustelidae, Ictonychini) from the Villafranchian of Bulgaria with a description of a new species of *Baranogale* Kormos, 1934. *Geodiversitas*, 23: 87–104.
- Spassov, N., 2003. The Plio-Pleistocene vertebrate fauna in south-eastern Europe and the megafaunal migratory waves from the east to Europe. *Revue de Paléobiologie*, 22: 197–229.
- Spassov, N. & Spiridonov, G., 1993. *Vormela peregusna*. In: Niethammer, J. & Krapp, F. (eds), *Handbuch der Säugetiere Europas. Band 5, Raubsäuger-Carnivora (Fissipedia). Teil 2. Mustelidae, Viverridae, Herpestidae, Felidae*. AULA-Verlag, Wiesbaden, pp. 817–855.
- Stach, J., 1959. On some Mustelinae from the Pliocene bone breccia of Węże. *Acta Palaeontologica Polonica*, 4: 101–117.
- Stach, J., 1961. On two carnivores from the Pliocene breccia of Węże. *Acta Paleontologica Polonica*, 6: 321–329.
- Strömberg, C. A. E., 2011. Evolution of grasses and grassland ecosystems. *Annual Review of Earth and Planetary Sciences*, 39: 517–544.
- Vangengeim, E. A., Vislobokova, I. A. & Sotnikova, M. V., 1998. Large Ruscinian Mammalia in the territory of the former Soviet Union. *Stratigraphy and Geological Correlation*, 6: 368–382.
- Van Valkenburgh, B., 1988. Trophic diversity in past and present guilds of large predatory mammals. *Paleobiology*, 14: 155–173.
- Van Valkenburgh, B. & Ruff, C. B., 1987. Canine tooth strength and killing behaviour in large carnivores. *Journal of Zoology*, 212: 379–397.
- Viret, J., 1929. Les faunes de mammifères de l'oligocène supérieur de la Limagne bourbonnaise. *Annales de l'Université de Lyon Nouvelle série, I Sciences, Médecine*, 47: 1–328.
- Viret, J., 1951. Catalogue critique de la faune des mammifères miocènes de la Grive Saint-Alban (Isère). Première partie, chiropères, carnivores, édentés pholidotes. *Archives du Muséum d'histoire naturelle de Lyon*, 3: 1–104.
- Viret, J., 1954. Le loess à bancs durcis de Saint-Vallier (Drôme) et sa faune de mammifères villafranchiens. *Nouvelles Archives de Museum Histoire de Naturelle de Lyon*, 4: 1–200.
- Vislobokova, I., Sotnikova, M. & Dodonov, A., 2001. Late Miocene–Pliocene mammalian faunas of Russia and neighbouring countries. *Bollettino della Società Paleontologica Italiana*, 40: 307–313.
- Wolsan, M., 1989. Drapieżne Carnivora. In: Kowalski, K. (ed.), *Historia i ewolucja lądowej fauny Polski. Folia Quaternaria*, 59–60: 177–197. [In Polish.]
- Wolsan, M., 1993. Évolution des Carnivores quaternaires en Europe centrale dans leur contexte stratigraphique et paléoclimatique. *Anthropologie*, 97: 203–222.