Short Note

First record of *Megaviverra carpathorum* (Kretzoi and Fejfar, 1982) from Poland within Eurasian context

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Abstract

The first record of *Megaviverra carpathorum* from the Polish site of Węże 1, together with Slovak locality of Ivanovce 1, are the only two occurrences of large viverrids in Central Europe and are both dated at MN 15b (3.8–3.4 mya). Both records constitute an interesting and exotic event of a short-term eastern migration of a rare but successful carnivoran, which preceded the main wave of *Canis* dogs. This migration event of large viverrids of Asian origin is restricted spatially (Poland, Slovakia, and northern Italy) and temporarily (MN 15b–16a, 3.8–2.8 mya). It fills the gap between the disappearance of ictitheriids and the appearance of *Canis* dogs. The invasion of *Canis* dogs may be the main factor that led large European viverrids like *Megaviverra carpathorum* to extinction.

Introduction

The large European viverrids are among the most enigmatic and poorly known carnivorans. Their Pliocene occurrence is documented by scanty material from few localities, and so far, only two European records have been found from a roughly contemporaneous timespan (MN 15b–16a, 3.8–2.8 mya). These include remains of *Megaviverra carpathorum* (Kretzoi and Fejfar, 1982) from the oldest level (MN 15b) of Ivanovce 1 and a slightly smaller *Megaviverra apennina* Kretzoi and Fejfar (1982) from the Italian site of Arondelli-Triversa (MN 16a, 3.2–2.8 mya) (Kretzoi and Fejfar, 1982; Fejfar and Sabol, 2004).

Large viverrids have been more commonly reported from the Late Miocene of Africa, where the presence of two species has been detected. The remains from two Kenyan sites, Sahabi and Lower Nawata Formation at Lothagam, were assigned to *Viverra howelli* Rook and Martinez-Navarro (2004) (Howell, 1987; Rook and Martinez-Navarro, 2004). A second species, *Viverra leakeyi* (Petter, 1963), was erected based on a maxilla fragment from the Upper Unit of Laetoli Bed (3.8–3.5 mya; Petter, 1967, 1987; Werdelin, 2003); however, the presence of this form, or at least a form closely related, was already noted from the Upper Miocene lower Nawata Formation at Lothagam (7.4–6.5 mya; McDougall and Feibel, 1999; Werdelin, 2003). It is known also from other late Miocene sites, such as the Kapsomin Member of the Lukeino Formation (5.9–5.8 mya; Sawada et al., 2002; Morales et al., 2005), Amba East, lower Sagantole Formation in the Middle Awash (5.5–5.2 mya; Renne et al., 1999; Haile-Selassie and Howell, 2009), and from the Langebaanweg (5.2–5.1 mya; Hendey, 1974, 1981; Matthews et al., 2007). It is also present in later sites of the Pliocene and Pleistocene boundary, such as members C, E, and G of the Shungura Formation, Omo Group, Ethiopia (2.8–1.9 mya; Howell and Petter, 1976;

McDougall and Brown, 2008). A single record of *V. leakeyi* was also recorded from the Morocco site, Ahl al Oughlam (2.6–2.5 mya; Geraads, 1997; Peigné et al., 2008). Late Pliocene records of large viverrids from Africa are quite rare. Apart from the above mentioned, *V. leakeyi*, only *Pseudocivetta ingens* (Petter, 1967) and an undescribed species from Koobi Fora, which is not closely related to either of those species, have been reported from this period (Peigné et al., 2008).

Eurasian large viverrids from the Late Miocene are relatively more common, but due its scarcity and incompleteness of their remains, they were described under several forms and species. In many cases, these were of uncertain taxonomic affinities and position. *Viverra howelli* is not only known from the African sites of Lothagam and Sahabi, but also from the Italian site of Baccinello V3 (6.7–6.4 mya; Rook and Martinez-Navarro, 2004; Rook et al., 2011). The closely related forms, *Civettictis howelli* Morales, Pickford, Soria, 2005, and *Pseudocivetta ingens* Petter (1967), known from the Early Pliocene (4.9–4.4 mya) sites like Magabet Formation (Tugen Hills, Kenya; Morales et al., 2005), are characterised by more bunodont dentition (Leakey, 1965; Petter, 1967). Multiple species were erected from Middle Miocene to Pleistocene sediments in the Siwaliks of India and Pakistan. Among them are *Viverra chinjiensis* Pilgrim, 1932 and *Viverra hasnoti* from the Chinji and Nagri Formations (14.2–9.5 mya) (Pilbeam et al., 1979; Sahni and Tiwari, 1979; Barry et al., 2002). *Vishnuictis salmontanus* Pilgrim, 1932 was found in the early Dhok Pathan Formation of the Middle Siwaliks (8.7–8.5 mya), while remains of *Viverra bakerii* Bose, 1880 and *Vishnuictis durandi* (Lydekker, 1884) came from the Pinjor stage of the Upper Siwaliks (3.5–3.2 mya) (Matthew, 1929; Pilgrim, 1932; Barry, 1995; Peigné et al., 2008). From Cap Travertine at Zhoukoudian, another form *Viverra peii* Qiu, 1980 was described Qiu (1980) and was dated from 3.6–3.2 mya. Hunt (1996), however, considers *V. peii* as a synonym of *V. durandi*. Fossil material of *Hyaenictitherium intuberculatum* (Ozansoy, 1965) from the Turkish site of

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Yassiören (7.4–7.1 mya), originally classified as *Ictitherium* (Ozansoy, 1965), was regarded by Fejfar and Sabol (2004) as the largest viverrid *Hesperoviverra intertuberculata* (Ozansoy, 1965); however, this opinion was later rejected (De Bonis, 2004; Peigné et al., 2008).

We present the first record of *M. carpathorum* from the Polish site of Węże 1. The spatial and temporal fit with other European occurrences from Ivanovce 1 and Arondelli-Triversa. These Late Pliocene large viverrids represent a dispersal of one genus of Asian origin (Kretzoi and Fejfar, 1982; Fejfar and Sabol, 2004).

Material and methods

The identification of the fossilis analysed in the paper was performed using the basic morphometric analysis. Measurements were taken point to point with the Landmark system to the nearest 0.01 mm. Measurements were taken using a set for image analysis with an Olympus (Olympus stereomicroscope ZSX 12, camera Olympus DP 71, program Cell D). A Canon EOS 5D camera was used to prepare the photographic documentation of the fossil material. Throughout the text, upper teeth are referred to as capital letters (e.g. P4) and the lower as lower-case letters (e.g. p4). The geologic timescale and subdivisions were based on the International Chronostratigraphic Chart (v2018/08), approved by the International Commission on Stratigraphy (http://www.stratigraphy.org/index.php/ics-chart-timescale). Abbreviations used in the text are as follows: B – breadth, B ta – talonid m1 breadth, B tr – trigonid m1 breadth, L – length, L ta – talonid m1 length, L tr – trigonid m1 length, mya – million years ago, W1 – Węże 1.

The material of *M. carpathorum* from Węże 1 was never mentioned or studied, and the material described here is the first Polish record of this species. All of the fossil material is stored in the Institute of Systematics and Evolution of Animals, Polish Academy of Sciences in Kraków.

Geological settings

Węże 1 (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 (Fig. 1). 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). From the late 1940's until the mid-1970's, intensive excavations were conducted, resulting in the removal of most of the sediment from the site. Samsonowicz (1934) divided the deposits into red and grey breccia, while Głazek et al. (1976) assigned them to three main sedimentation periods. The oldest layers (6.0–5.5 mya) 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 that covered almost the entire cave bottom. The layer was almost sterile from fossils. The second deposition period (3.6–3.2 mya) included thick deposits of red, sandy clay with the addition of small concretions and fossils. The clay gradually passed into a thick grey breccia. The layers were laminated on the surface, and the lamination gradually disappeared deeper into the profile. The surface was covered with sandy clay deposits with an admixture of fragmented calcite and limestone. The youngest sedimentary series (1.0–0.8 mya) comprised periglacial deposits in the form of yellowish clay sands, cemented with rock rubble. In addition, there were almost no fossils (Głazek et al., 1976; Głazek and Szynkiewicz, 1987). A detailed analysis of the abundant faunal assemblage showed that the main fauna from Węże 1 is dated at 3.8–3.4 mya. 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 (Table S1; Marciszak et al., 2024 and references therein).

Systematic Paleontology

Order Carnivora Bowdich, 1821
Suborder Feliformia Kretzoi, 1945
Infraorder Aeluroidea Flower, 1869
Parvorder Viverroidea Gray, 1821
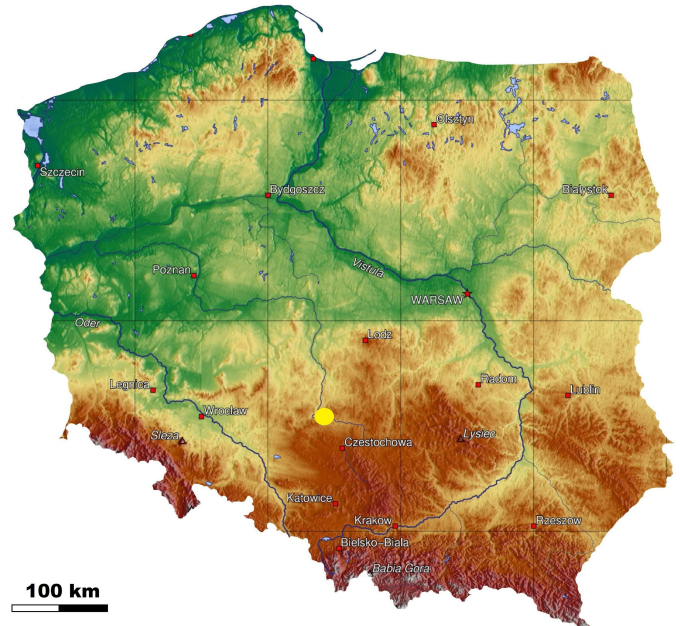Family Viverridae Gray, 1821

Figure 1 – Location of Węże 1 site within territory of Poland.

Subfamily Viverrinae Gray, 1821
Genus *Megaviverra* (Kretzoi and Fejfar, 1982)
Megaviverra carpathorum (Kretzoi and Fejfar, 1982)

Material: right C1 (MF/7935; L - 10.44 mm, B - 6.87 mm); left mandibular fragment with p1–p3 (MF/7936; p1: L - 5.27 mm, B - 3.44 mm; p2: L - 10.47 mm, Ba - 4.34 mm, Bp - 5.14 mm; p3: L - 13.78 mm, Ba - 5.44 mm, Bp - 6.88 mm, mandibular body height × thickness after the p4 is 24.8911.57 mm); left mandibular fragment with p4 (MF/7937; L p4 - 15.56 mm, Ba - 7.54 mm, Bp - 8.89 mm, mandibular body height × thickness after the p4 is 26.8412.23 mm); trigonid of left m1 (MF/7938; L tr - 13.14 mm, B tr - 11.45 mm).

Diagnosis: large and stout species, P4 with a well-developed parastyle, m1 with a weak hypoconulid.

Description: the canine is elongated and narrow, with a lateral, strongly arched and flattened profile. The crown and the root are similar in length. The buccal and lingual surfaces are smooth. The mandibular body is elongated, high and robust, and its height increases distally(Fig. 2). Two similarly sized, oval, mental foramens are located on the buccal side. The mesial one is situated below the p1, while the distal one is below the mesial root of p3 and is slightly higher than the mesial one. The longitudinal, lingual groove of the mandibular body is strongly developed. The tooth row is almost straight in the occlusal view. The teeth between c1–p1 and p2 and p3 are tightly positioned, and there are no diastemas between them. The relatively long diastema is present between p1 and p2. The apexes of all three conical premolars, namely p2, p3, and p4, are located nearly at the same level (Fig. 2).

The proportionally large p1 fits tightly to the c1. The mesial, steep edge is strongly convex, while the distal ridge is distinctly longer. From the apex of p1 runs a delicate, thin crest, which reaches the weak, distal cingulum. The mesial and distal margins are blunt and the lingual is weakly convex, while the buccal one is strongly convex. The two-rooted p2 are elongated and oval and bear an elongated, distal, singular projection. The crown has an apex that is positioned strongly forward with the straight buccal and lingual margins. The mesial and distal margins are blunt. The crown expands gradually and uniformly distally. Located just after the protoconid is a minute, but well-recognised metaconid. It is low and rounded and separated from the main cuspid and from the moderately developed distal cingulum. The elongated and narrow p3 is tear-shaped in the occlusal view. The apex of the moderately prominent protoconid is moved forward, but not as strongly as in p2. Distally to the protoconid there is a low-situated, elongated, and an oval metaconid. This cuspid is well-separated from the protoconid by a narrow, deep, and V-shaped valley. The distal metaconid is sep-

arated from the cingulum by a crescent, shallow, and wide valley. The width of the tooth increases notably distally. The buccal margin is almost straight, similar to the first half of the lingual margin. A moderate convexity occurs on the distal half. The mesial and distal margins are blunt. A distal, strong cingulum forms a thick wall (Fig. 2).
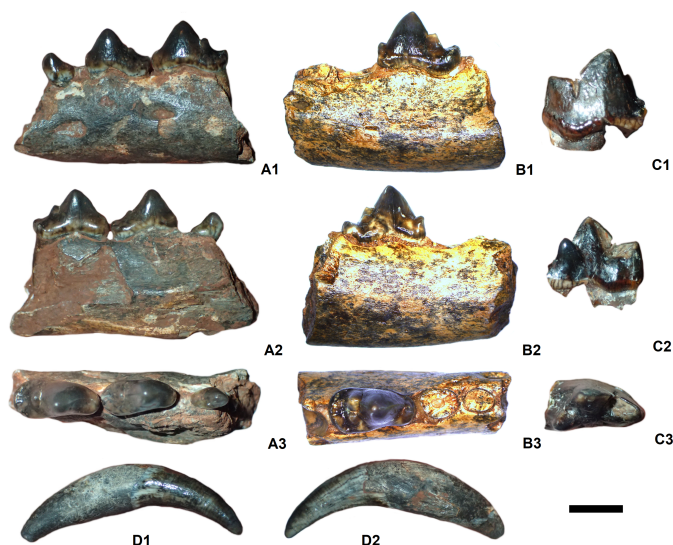

Figure 2 – Remains of *Megaviverra carpathorum* from Wȩże 1: A - left mandible (MF/7936), 2 - left mandible (MF/7937), C - left ml (MF/7938), D - right Cl (MF/7935). All individuals showed on the same scale (10 mm), 1 - buccal view, 2 - lingual view, 3 - occlusal view.

The two-rooted p4s have a compact build, with the crown strongly broadening distally. A high and prominent protoconid is centrally positioned and has a particularly robust cuspid, occupying almost the entire surface of the crown on which it is located. From its apex starts two thin but well-recognised ridges, which run up to the cusp base. Mesial to the protoconid there is a relatively large and distinct paraconid. The cuspid apex is oriented strongly mesially and slightly lingually. The elongated paraconid is rectangular and located perpendicular to the crown axis. Surprisingly, after the protoconid there is a large hypoconid. It is an elongated, low, and oval-shaped cuspid. It is separated by a wide, U-shaped groove, and runs parallel to the tooth axis. Distal to this cuspid there is a crescent, shallow, and moderately wide valley. After this cuspid is a crescent, shallow, and moderately wide valley. The distal margin is collared by a wall of thick cingulum. The mesial and distal margins are blunt. The mesial half of the lingual margin is straight, while the distal half is moderately convex. The buccal margin is moderately arched with a gentle, median concavity on the transition between the proto- and hypoconid.

The preserved trigonid of m1 is long and robust and is moderately arched. A strong, mesio-lingual mesial margin is triangular in the occlusal view, and a relatively low paraconid is oriented and sharpened. The prominent and voluminous protoconid has a convex buccal margin. It is well-separated from the paraconid by a notably deep and V-shaped valley, running diagonally between both main cusps. A distinct and large metaconid is oriented strongly disto-lingually, and creates an angle of 45º with the protoconid. The lingual margin possesses only a moderate, median convexity at the metaconid level. The mesial and buccal margins are collared by a thick cingulum.

Discussion

Comparison

Three mandibular body fragments from Wȩże 1 and Ivanovce 1 (SNM-MNH, Z 26386/65261) reveals several similarities. The massiveness and stoutness of the mandibular body, the spacing and shape of the mental foramens are well-documented. In addition, the teeth morphology is similar. There are some differences between the p4 of Wȩże 1 and Ivanovce 1. The main feature is the presence of a double hypoconid after the protoconid, with the larger part on the buccal side and the smaller part on the lingual side. It is quite unusual that an additional

Figure 3 – Size comparison of Megaviverra carpathorum from Wȩże 1 with German shepherd *Canis familiaris* (shoulder height 70 cm). Drawing by W. Gornig. .

cuspid is bipartite. In Ivanowce, the p4 possesses only an elongated and high metaconid, which runs obliquely to the crown axis and from the disto-lingual to the mesio-buccal direction. We interpreted this not as a diagnostic feature, rather as a dental abnormality. Such characteristics are not common, but are regularly noted in carnivores (Wolsan, 1984a,b). The m1 trigonid of the Wȩże 1 and Ivanovce 1 individuals are almost indistinguishable metrically and morphologically.

Megaviverra apennina was identified from a single, right mandibular body with c1 and p3–m1 from Arondelli-Triversa. The species is smaller than the Wȩże 1 and Ivanovce 1 individuals and has a less-massive build. The mandibular body is less stout and is on the lingual side, possessing a longitudinal, lingual furrow that is especially strong in the first half of its length. This structure is absent in *M. carpathorum*. The premolars of *M. apennina* are narrower (massiveness indexes (Bp/L). In Arondelli-Triversa, the premolars are 42.4 for p2, 42.1 for p3, and 42.9 for p4, while for *M. carpathorum* from Wȩże 1, the premolars are 49.1 for p2, 49.9 for p3, and 57.1 for p4. In the occlusal, the transition between the mesial and distal crown parts are less marked. In the p3-p4 protoconid, the main cuspid is lower and less robust. In m1 of *M. apennina*, the paraconid is less expanded mesially, while the particularly strong metaconid is more vertical with a smaller angle between the protoconid and metaconid.

Viverra howelli also cannot be taken into consideration, since the trigonid length of m1 (13.14 mm) considerably exceeds the length of the complete m1 of this species (10.4–11.2 mm) (Howell, 1987; Rook and Martinez-Navarro, 2004)) or is at least similar in length (13.7 mm; Peigné *et al.* 2008).

Based on the analysis conducted here, the large viverrid from Wȩże 1 was determined to be *M. carpathorum,* especially by its metrical and morphological similarity to the fossil material from the Slovak site Ivanovce 1. Based on these comparisons, the remains show some affinities to the material from Arondelli-Triversa. Given the wide geographical and stratigraphical gap that exists between the different forms and species, a specific distinction cannot be ruled out. African and Asian species are probably closely related; however, some of those forms might in fact belong to different hypercarnivorous viverrid lineages (Hunt, 1996). A thorough analysis of the whole African taxa, but also of the Eurasian material, will be necessary to determine the systematic position of those large viverrids.

In the described material from Wȩże 1, the large dimensions and robust build of those remains are notable. This is especially visible when compared the individual from Wȩże 1 to the extant *Civettictis civetta* (Schreber, 1776). This largest African viverrid, is an animal with a head and body length of 70–100 cm, shoulder height 40–50 cm and of 8–20 kg weight (Ray, 1995). When comparing the teeth size of *C. civetta* (L p4 10.6, 10.1–11.2 mm, L m1 14.07 mm, 13.70–14.40 mm; Peigné et al. (2008)) with those of the Wȩże 1 viverrid (L p4 15.56 mm, estimated L m1 of ca. 20 mm), it is clear that we are dealing with an animal that is 1/3 larger (Fig. 3).

In the literature, there is some confusion regarding the names, *Megaviverra* and *Hesperoviverra* (Peigné et al., 2008)). In their first publication, Fejfar (1961) described material from Ivanovce 1 as being close to *V. durandi*, and classified it as *Viverra* sp. Later, Kretzoi and Fejfar (1982) determined this material as *M. carpathorum*. For the first time, the name *H. carpathorum* appears in a faunal list from the Ivanovce site (Kretzoi and Fejfar, 1982). Just one year later, Kretzoi (1986), who be-

lieved that this name was a homonym of *Megaviverra* Qiu, 1980, proposed *Hesperoviverra* n. gen. as a replacement name for *Megaviverra* Kretzoi and Fejfar, 1982; however, Geraads (1997) pointed out that the genus *Megaviverra* Qiu, 1980 is a nomen nudum, since no definition or name was proposed expressly as a new replacement name and there was no fixation of a species type (Peigné et al., 2008). According to the Art. 13 in the International Code of Zoological Nomenclature, this action is not a valid nomenclatural act (ICZN, 1999). For the same reasons, the name *Hesperoviverra* Fejfar and Heinrich, 1985, used by Fejfar and Sabol (2004), was a nomen nudum (ICZN, 1999). Consequently, the term *Megaviverra* Kretzoi and Fejfar, 1982 is a valid name, of which *Hesperoviverra* Kretzoi, 1986 is a junior synonym. Peigné *et al.* (2008) do not agree with the assignment of *H. intuberculatum* to *Megaviverra* and to the Viverridae, since the studies of the holotype material from Yassiören show affinities of this species to the Hyaenidae Gray, 1821 (De Bonis, 2004). In this article, we do not re-open discussion about the taxonomic affinities and the position of particular findings. The material is still too scanty to give any definitive results, so further, more extensive research is needed when new material appears.

Importance of *Megaviverra* in the Pliocene carnivoran guild

Within the Central European biostratigraphy, the appearance of *M. carpathorum* constitutes an interesting and exotic event. Earlier, Late Miocene European faunas, so called Turolian *Hipparion* faunas, with prevailing species of the genus *Ictitherium* Trouessart, 1897 do not yet include the large viverrids (Kretzoi and Fejfar, 1982; Semenov, 2001; Fejfar and Sabol, 2004; Spassov et al., 2018; Sabol et al., 2021). The occurrence of *M. carpathorum* in Ivanovce 1 and Wȩże 1 represent an exceptional record of a short-term eastern migration event of a rare but successful carnivore, which preceded the main wave of the Canidae Fischer, 1817 (Fejfar and Sabol, 2004). During the Late Miocene and Early Pliocene in Africa (Toros Menalla, Langebaanweg) there were ictitheriids contemporary with giant viverrids (De Bonis et al., 2005; Peigné et al., 2008; Hendey, 1974). The presence of the large viverrids in Europe filled the gap after the disappearance of ictitheriids and just before the appearance of the true canids. This event was restricted spatially (northern Italy, Poland, Slovakia) and temporary (MN 15b–16a, 3.8–2.8 mya).

During this interval, those large viverrids co-existed with forms from the genus, *Eucyon* Tedford and Qiu, 1996, which appeared in Europe already ca. 7.9–7.4 mya ago, as is documented from the Iberian sites, Concud and Los Mansuetos, both near the city of Teruel (Crusafont Pairó, 1950; Pons Moyá and Crusafont Pairó, 1978; Rook et al., 1991; Rook, 1992, 1993, 2009; Torre et al., 1992; Alcalá Martínez, 1994). During the earliest Pliocene (5.2 mya) of Langenbaanweg (South Africa), co-occurred both, giant viverrids (*V. leakeyi*) (Hendey 1974) and jackal-sized canids (*Eucyon khoikhoi*) (Valenciano et al., 2022).

It was demonstrated however, that this Spanish form doesn't belong to *Eucyon* and was interpreted a "*Canis*" *cipio*, stating it is not *Canis* nor *Eucyon* (Valenciano et al., 2022). In Wȩże 1, *M. carpathorum* co-existed with *Eucyon odessanus* (Odintzov, 1967), which was a jackal-sized species that was widespread in Moldova, Ukraine, Greece, and Turkey (Rook, 1993, 2009; Marciszak et al., 2023). The records from MN 15b documented the latest occurrence of the genus *Eucyon* (Martin, 1973; Rook, 1992, 1993, 2009; Marciszak et al., 2023). The extinction of this canid in the latest Pliocene is correlated in time with the appearance of the first representatives of the genus, *Canis* and *Lycaon,* in Eurasia (Monguillon, 2005; Lacombat, 2006; Lacombat et al., 2008; Sotnikova and Rook, 2010). The westward invasion of *Canis* dogs put an end to the domination of eucyons, especially as they emerged in a larger, social, and much more advanced form (Marciszak et al., 2023). This was also probably the main factor that led slightly later large European viverrids like *M. carpathorum* to final extinction. After extinction, they never again appeared in the territory of Europe. ✐

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Supplemental information

Additional Supplemental Information may be found in the online version of this article:

Table S1 List of taxa from Węże 1.