



Pliocene carnivorans from Jradzor, Armenia

Saverio Bartolini-Lucenti^{1,2}, Joan Madurell-Malapeira¹, Adrian Marciszak³, Marie Meyer⁴, Damien Becker^{5,6}, Davit Vasilyan^{5,6}

¹ Dipartimento di Scienze della Terra, Paleo[Fab]Lab, Università degli Studi di Firenze, Via La Pira 4, I-50121 Firenze, Italy

² Institut Català de Paleontologia Miquel Crusafont (ICP-CERCA), Universitat Autònoma de Barcelona, Edifici ICTA-ICP, c/ Columnes s/n, Campus de la UAB, 08193 Cerdanyola del Vallès, Barcelona, Spain

³ Department of Palaeozoology, University of Wrocław, Sienkiewicza 21, 50–335 Wrocław, Poland

⁴ Ecole Nationale Vétérinaire de Toulouse, 23 Chemin des Capelles, 31076 Toulouse Cedex 03, France

⁵ JURASSICA Museum, Route de Fontenais 21, 2900 Porrentruy, Switzerland

⁶ Department of Geosciences, University of Fribourg, Chemin du Musée 6, 1700 Fribourg, Switzerland

<https://zoobank.org/12CD63D3-C720-4C99-A50A-2E27FB23403C>

Corresponding author: Saverio Bartolini-Lucenti (saverio.bartolinilucenti@unifi.it)

Academic editor: Sergei Lazarev ♦ Received 24 November 2025 ♦ Accepted 18 March 2026 ♦ Published 24 April 2026

Abstract

The Jradzor locality (Armenia, South Caucasus) provides a stratigraphically constrained Pliocene carnivoran record spanning 4.16–3.98 Ma and 3.3 ± 0.03 Ma. Here we report new material of five taxa: *Nyctereutes urartuensis*, *Chasmaporthetes lunensis* and *Pliocrocota perrieri* from the horizon JZ–7, *Baranogale helbingi*, and a lynx-sized felid from three older layers (JZ–3s, JZ–13 and JZ–15). Dental and mandibular morphology, together with morphometric analyses, indicate a guild combining an omnivorous raccoon dog, an archaic ictonychid mustelid and two large hyaenids representing distinct feeding strategies (cursorial hunting vs. bone cracking). The Jradzor assemblage documents carnivoran diversity and ecological structure at the biogeographic junction between Europe and Asia especially along the southern margin of the Eastern Paratethys and contributes to understanding dispersal and community dynamics during the Pliocene.

Keywords

Armenia, Biogeography, Carnivora, faunal turnover, Jradzor, morphometrics, palaeoecology, Pliocene

Introduction

The Pliocene Epoch, spanning approximately 5.33 to 2.58 Ma, represents a pivotal transitional phase in Earth's climatic history, bridging the relatively warm conditions of the Miocene with the pronounced cooling and glacial–interglacial oscillations of the Pleistocene (Salzmann et al. 2011; Fedorov et al. 2013). During this epoch, global climates underwent a gradual yet sustained shift towards increased seasonality, continental aridification and polar cooling. This transformation was driven by a complex interplay of tectonic activity—alongside changes in oceanic circulation and long-term variations in atmospheric greenhouse

gas concentrations. Collectively, these processes reshaped global heat distribution and contributed to the emergence of modern climate patterns, including the intensification of latitudinal thermal gradients and the establishment of permanent polar ice sheets in the Northern Hemisphere by the end of the epoch (Fedorov et al. 2013; Haywood et al. 2016; Karas et al. 2017; Burke et al. 2018). A particularly significant interval within the Pliocene is the Mid-Pliocene Warm Period (MPWP), occurring between approximately 3.3 and 3.0 Ma. During this time, global mean annual temperatures are estimated to have been 2 to 4 °C higher than pre-industrial levels, with atmospheric CO₂ concentrations ranging between 350 and 450 ppm—values comparable

to or even lower than those observed today (Fedorov et al. 2013). The Earth's climate system responded to this modest rise in CO₂ with pronounced polar amplification, resulting in notably warmer conditions at high latitudes and a dramatic reduction in Arctic Sea ice. Consequently, sea levels during the MPWP are estimated to have been 15 to 25 metres higher than at present, implying substantial reductions in the Greenland and West Antarctic Ice Sheets and possibly partial melting of the East Antarctic Ice Sheet as well (Fedorov et al. 2013; Prescott et al. 2014; Haywood et al. 2016). Despite elevated global temperatures and CO₂ levels, the MPWP was not marked by extreme climatic instability, making it a valuable palaeoclimatic analogue for assessing the potential long-term equilibrium responses of Earth's climate system to sustained warming. Unlike current anthropogenic climate change, the conditions of the MPWP developed over geological timescales, allowing the Earth's system—including ocean currents, vegetation, cryosphere and ecosystems—to gradually adjust to shifting energy balances. Nevertheless, the MPWP demonstrates that even moderate increases in CO₂ can trigger large-scale environmental transformations, including irreversible ice sheet loss and significant sea-level rise. This period thus provides a critical baseline for evaluating long-term thresholds and feedback mechanisms in a warming world, such as polar amplification, albedo effects and the response of terrestrial carbon sinks (Burke et al. 2018).

A broader overview of Pliocene climate, vegetation and continental-scale faunal turnover is provided in Suppl. material 1: text S1. In this framework, the South Caucasus sits at the biogeographic junction between Europe and Asia and likely acted as a dispersal corridor during the Pliocene, yet well-dated carnivoran assemblages from this region remain rare. Here, we document new occurrences of carnivorans from the Jradzor locality (Armenia) across multiple fossil horizons and use dental and mandibular functional morphology, together with morphometrics, to discuss trophic ecology and community structure of the Jradzor carnivoran guild in a regional biogeographic framework. Additionally, your study demonstrates the importance of the south of Eastern Paratethyan realm for the dispersal of vertebrate assemblages.

Geological and palaeontological setting

The Jradzor locality (Armenia, South Caucasus) comprises a stratigraphically constrained Pliocene vertebrate record with several fossiliferous horizons dated by Lazarev et al. (2023). The carnivoran material described here derives from horizons JZ–3s, JZ–13 and JZ–15 (4.16–3.98 Ma) and from horizon JZ–7 (3.3 ± 0.03 Ma) (Fig. 1). The horizon JZ–7 is interpreted as a lahar deposit, i.e. a high-energy volcanoclastic mudflow that transported remains over relatively short distances, whereas the remaining layers as medium tail of pyroclastic flow (Lazarev et al. 2023). The associated vertebrate assemblage is dominated by taxa typically linked to open habitats, suggesting predominantly open landscapes in the local catchment:

such as *Cremohipparion longipes* (Becker et al. in press), *Gazellospira* sp., Caprini indet. (cf. *Eosyncerus*), Caprini indet. (Bukhsianidze 2026), a new hyracoid (Becker et al. 2026). Further, two additional forms from the JZ–7 horizon, such as *Bufotes* sp. and *Mimomys* cf. *davakosi*, suggest also the presence of open-habitats.

Materials and methods

Referred and comparative specimens

This study is based on anatomic and taxonomic analysis of the Late Pliocene carnivoran fauna from Jradzor, Armenia. The referred material, including 15 specimens, is stored in the collections of the Institute of Geological Sciences of the National Academy of Sciences of Republic of Armenia. The extant and fossil specimens used for the comparative study are stored in the collections of the JURASSICA Museum, Porrentruy, Switzerland; the Naturhistorisches Museum of Basel, Switzerland; the Geological and Paleontological Museum of Florence, Italy; the Musée des Confluences, the Department of Geology of the University of Lyon, France; Museum national d'Histoire naturelle of Paris, France; and the Natural History Museum of Madrid, Spain. The comparative morphological analysis is completed with the relevant literature on Pliocene carnivores including Depéret (1890); Viret (1954); Vekua (1972); Qiu (1987); Kurtén and Werdelin (1988); Sotnikova (1989); Morlo and Kundrát (2001); Argant (2004); Vekua et al. (2005); Turner et al. (2008); Agustí et al. (2009); Tseng et al. (2013); Vinuesa et al. (2014); Sen and Saraç (2018); Marciszak et al. (2022, 2024).

Measurements and statistical analyses

The cranium and mandible measurements follow von den Driesch (1976), Kurtén and Werdelin (1988), Werdelin and Solounias (1991) and Spassov (2001). Measurements are taken with a digital caliper to the nearest 0.1 mm. We performed a Principal Component Analysis on the mesiodistal length and buccolingual width of the p3, p4 and m1 of the mandible of *Chasmaporthetes* of Jradzor, in comparison with extant hyaenids (*C. crocuta*, *H. hyaena*, *Pa. brunnea*) and selected fossil species (i.e. *P. brevirostris* from Eurasia, *Pl. perrieri* from Eurasia, *Ch. borissiakii* from Moldova and France, *Ch. gangsriensis* from Zanda Basin, *Ch. lunensis* from Eurasia, *Ch. ossifragus* from North America). The data on the fossil taxa were taken from Kurtén and Werdelin (1988), Tseng et al. (2013) and Lewis and Werdelin (2022). See Suppl. material 1 for additional information. We used the RStudio software (v. RStudio 2025.09.0+387 “Cucumberleaf Sunflower” Release af5fc22a687c0f462ee27c6afeeee38ee46507b9, 2025-09-11; RStudio Team (2025)) in the R environment v. 4.5.1, (R Core Team 2024) to perform our analyses and produce graphs. The PCA was performed with *prcomp()* (*'stats'* package v. 4.5.1). The plots were obtained using

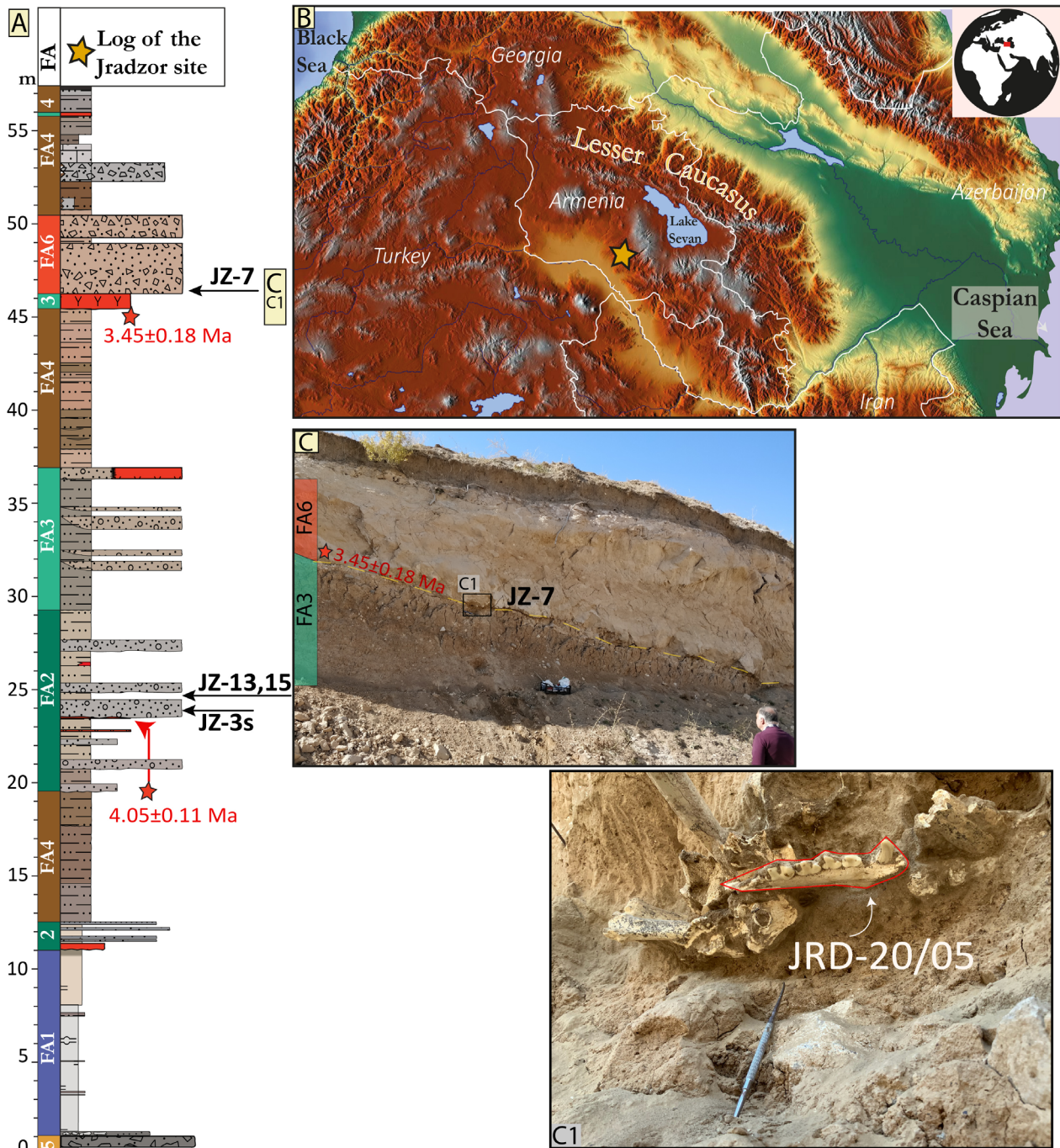


Figure 1. The log of the Jradzor section (modified from Lazarev et al. 2023) with indication of the fossiliferous horizons providing the carnivoran faunas (A); position of the site on the topographic map of the South Caucasus and selected outcrops (www.maps-for-free.com) (B); outcrop of the JZ–7 horizon (C) and field photograph of JRD–20/05 (C1).

the *ggplot()* (“*ggplot2*” package v.3.4.0; Wickham et al. (2016)). The deciduous premolar of hyaenid from Jradzor was compared with those of *Pl. perrieri* and *P. brevirostris* from the Late Pliocene–Early Pleistocene, using the dataset of Martínez-Navarro et al. (2025).

Anatomical abbreviations (see also Suppl. material 1)

H = height of the principal cusp/cuspid; **L** = mesiodistal length; **me** = metastyle; **pa** = paracone; **pr** = protocone;

tdm1 = m1 talonid; **trm1** = m1 trigonid; **W** = buccolingual width; **Wmax** = buccolingual width of the P4 across the protocone; **Wbl** = buccolingual width of the P4 between the paracone and the metastyle.

Institutional abbreviations

IGS - Institute of Geological Sciences of the National Academy of Sciences of Republic of Armenia; **MJSN** - Jurassica Museum (former Musée Jurassien Sciences Naturelles); **NMB** - Naturhistorisches Museum Basel.

Systematic Palaeontology

Order Carnivora Bowdich, 1821

Suborder Caniformia Kretzoi, 1945

Family Canidae Batsch, 1788

Subfamily Caninae Batsch, 1788

Tribe Vulpini Hemprich & Ehrenberg, 1832

Genus *Nyctereutes* Temminck, 1838

***Nyctereutes urartuensis* Bartolini-Lucenti et al., 2026**

Fossil horizons. JZ-7, 3.3 ± 0.03 Ma (Lazarev et al. 2023).

Holotype. JRD-20/03, skull with JRD-19/03, right lower jaw with c1, p3-m2 (Fig. 2).

Referred material. JRD-21/01, right P3, right P4, right M1; JRD-19/93, right i1; JRD-20/24, right i2; JRD-19/94, right P2/left p2; JRD-19/5, left P2/right p2.

Description. The detailed description of the specimens is published in Bartolini-Lucenti et al. (2026). The cranial specimen is fairly well preserved although the muzzle shows a right lateral compression and breakage due to taphonomic agents. The cranium is considerably elongated rostrocaudally and large. It is characterised by: a marked postorbital constriction; a vulpine crease on the dorsal surface of the zygomatic processes of the frontals; a marked parasagittal and sagittal crests; rugose parietals; squared-shaped nuchal crests; an evident subangular lobe; short canine crowns; enlarged crushing surface of the molars with additional or enlarged cusps/cusplids. The specimens show a similar degree of dental wear, belonging to a minimum of two young adult individuals.

Remarks. The attribution to the genus *Nyctereutes* is maintained by the presence of general features of Vulpini, for example, the vulpine crease and diagnostic ones for the genus, for example, the short-crowned canines and presence of a rounded and evident subangular lobe on the caudoventral side of the mandible. These morphologies contrast with those of *Vulpes* for the morphology of the canines and the presence of a subangular lobe. It lacks the derived features of *Otocyon megalotis*, for example, the duplication of the molars or the round-shaped expansion of the subangular lobe, but also *Nyctereutes* sp. from Jradzor differs from *Otocyon recki* as it does not possess reduction of premolar and carnassial blades. Compared to *Eucyon*, it possesses a vulpine crease obliterating the zygomatic process of the frontal, although a certain degree of frontal sinus is present (but this is a feature shared by extant and fossil *Nyctereutes*). The development of the features showed by the sample of from Jradzor is intermediate between primitive raccoon-dogs like *Nyctereutes tingi*-*N. donnezani* and more derived forms like *Nyctereutes sinensis*-*N. megamastoides*. The rostrocaudally elongated cranium and the poorly developed subangular lobe (in both dorsoventral sense and curvature) are features that resemble particularly *N. tingi* from China (Tedford and Qiu 1991) and *Nyctereutes* sp. from Çalta-1. The analyses of the morphological,

morphometric, endocranial and ecological parameters of the specimens from Jradzor suggest it belonged to a new species, described in Bartolini-Lucenti et al. (2026).

Family Mustelidae Batsch, 1788

Subfamily Ictonychinae Pocock, 1921

Genus *Baranogale* Kormos, 1934

***Baranogale helbingi* Kormos, 1934**

Fossil horizons. JZ-13 and JZ-15, 4.16–3.98 Ma (Lazarev et al. 2023).

Referred material. JRD-20/08, fragment of left maxilla with present infraorbital foramen and P3-P4 (JZ-13); JRD-19/239, fragment of left mandibular body with m1 (JZ-15) (Fig. 3, Table 1).

Description. The maxilla fragment (JRD-20/08) displays a large and round infraorbital foramen (Fig. 3A). The P2 alveolus is two-rooted indicating a moderately reduced tooth. The P2 is situated at an angle of 45° to the P3-P4. The P3 is located just after the P2 in a straight line. The tooth is elongated and irregularly oval-shaped. The prominent protocone is pushed slightly mesially and situated centrally. In front of the protocone, a centrally positioned, low and rounded paracone is located, which is strongly connected with the mesial cingulum. From the protocone apex, two thin crests run through elongated, mesial and distal cingular projections. Both ridges connect through the prominences of the cingulum. Behind the protocone, a second cuspid or at least a cuspid-like swelling is present, located slightly more lingually. This structure is low and oval, yet pronounced. 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, lingual moderately convex, like the distal half of the buccal margin. The distal half of the buccal margin is almost straight (Fig. 3).

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 moderately large and low protocone. The mesial margin of the protocone is aligned with that of the paracone. The long and rectangular protocone has straight mesial and distal margins, while its mesiolingual margin is blunt. The low metacone is blade-shaped, adjoining the paracone. The distal part of the metacone 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 (Fig. 3A).

The large and rather narrow m1 has a low and short paraconid and prominent and short protoconid (Fig. 3B). The length of the paraconid is nearly the same as that of the protoconid. Both main cusps are

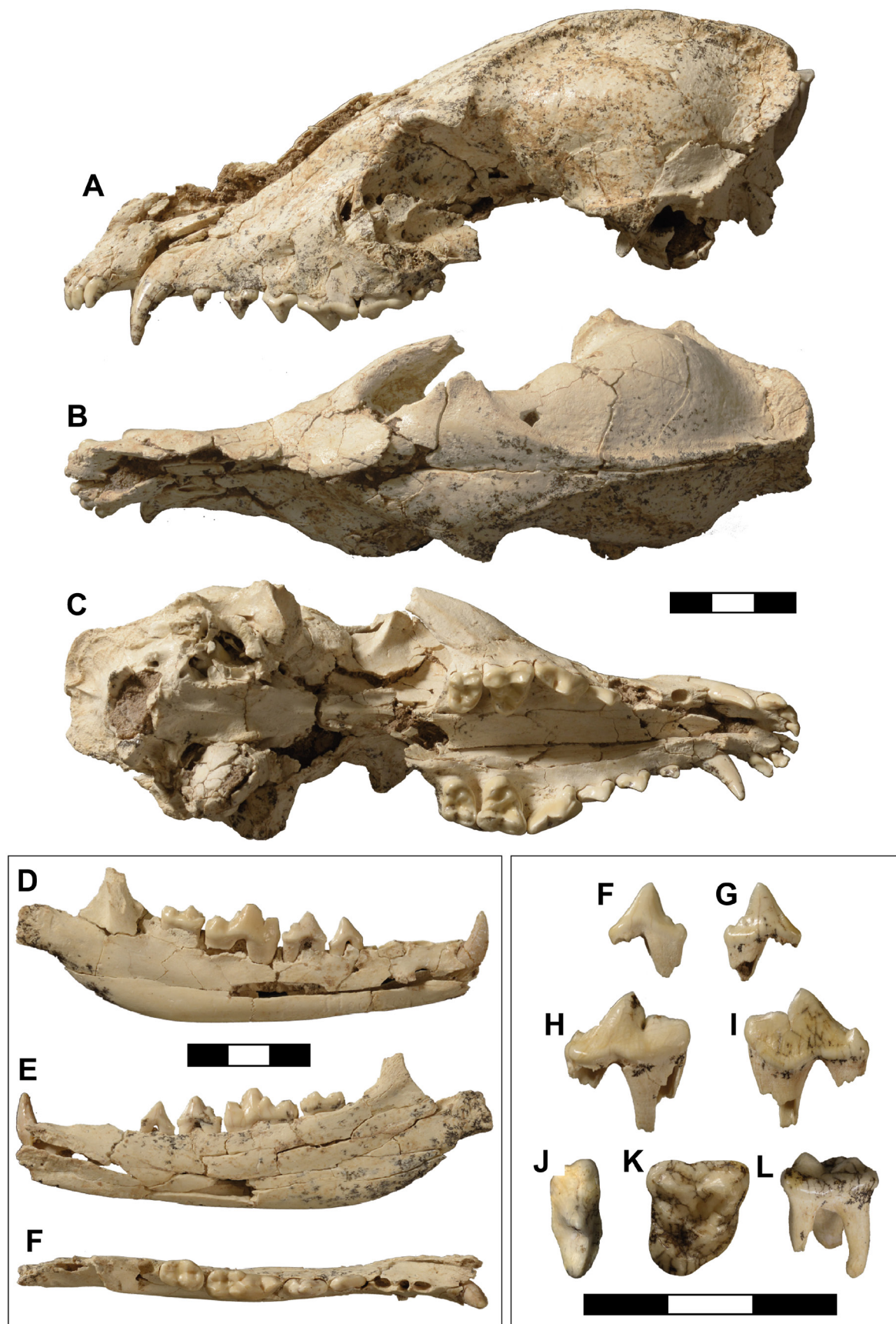


Figure 2. *Nyctereutes urartuensis* from Jradzor. JRD–20/03, cranium with left I1–M2 and right I1–C and P3–M2 in **A**. Left lateral; **B**. Dorsal and; **C**. Ventral views; **D–F**. JRD–19/03, right hemi-mandible with c, p3–m2 in **D**. Buccal; **E**. Lingual and **F**. Occlusal views; **F–L**. JRD–21/01 right P3 (**F**, **G**), right P4 (**H**, **J**), right M1 (**K**, **L**) in buccal (**F**), lingual (**G**), buccal (**H**), lingual (**I**), occlusal (**J**) and occlusal (**K**) buccal (**L**) views. Scale bars: 3 cm.

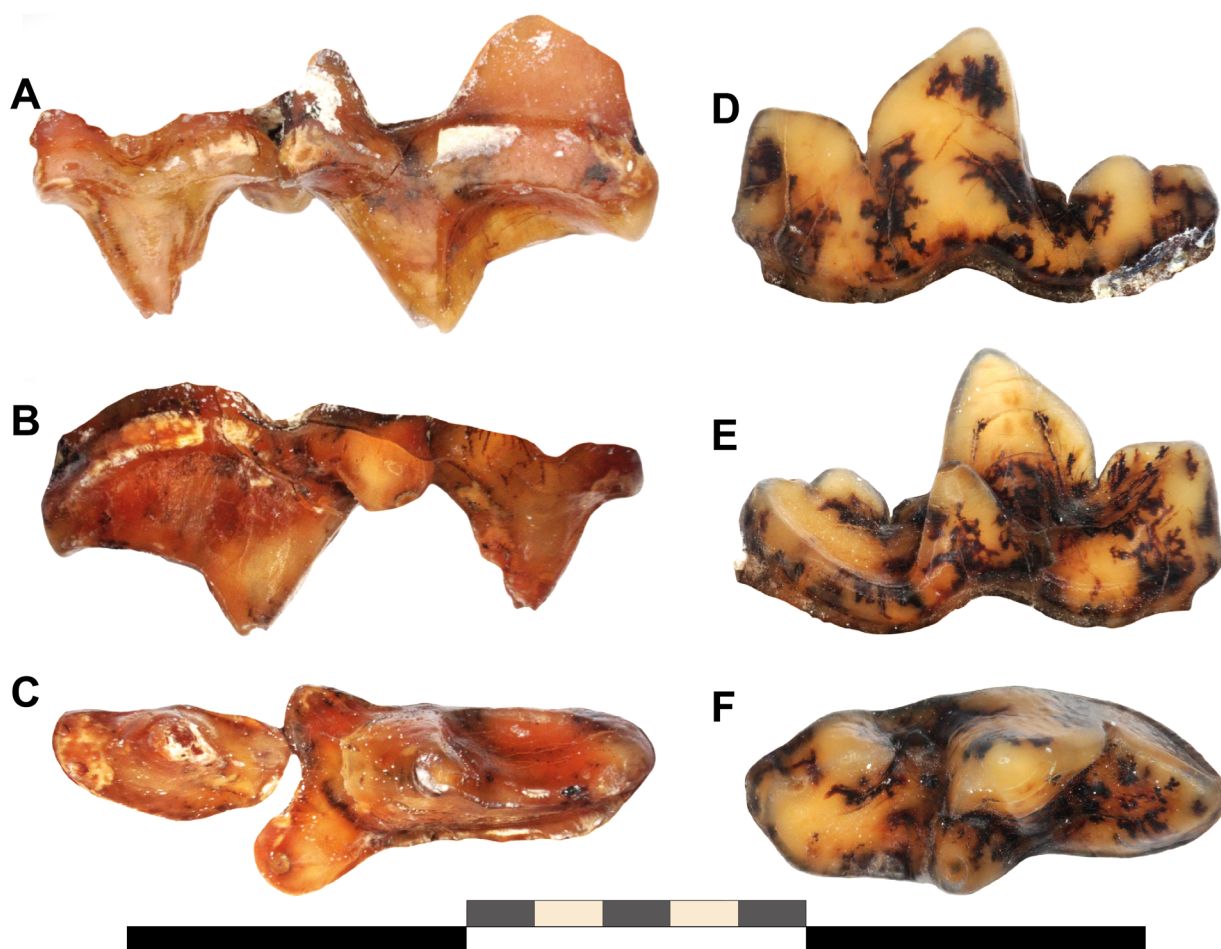


Figure 3. Teeth of *Baranogale helbingi* from Jradzor. JRD-20/08 left maxilla from JZ-13 in **A**. Buccal; **B**. Lingual and **C**. Occlusal views. JRD-19/239 left m1 from JZ-15 in **D**. Buccal; **E**. Lingual and **F**. Occlusal views. Scale bar is in mm: light yellow and grey smaller rectangles equal 1 mm each; black and white larger rectangles equal 5 mm.

Table 1. Measurements of the maxillary and m1 specimens of *Baranogale helbingi* from Jradzor (in mm).

	P3 L	P3 H	P3 Wa	P3 Wp	P4 L	P4 L pr	P4 H pa	P4 L me	P4 Wmax	P4 Wbl
JRD-20/08	3.6	2.5	1.6	1.7	5.7	1.8	3.2	2.9	3.2	2.5
	m1 L	trm1 L	trm1 W	tdm1 L	tdm1 W					
JRD-19/239	6.6	4.6	2.9	2.0	2.3					

separated by a deep valley. The distal wall of the paraconid and mesial wall of the protoconid form an open angle. The protoconid holds two thin crests running from the apex. The strongly developed and prominent metaconid is clearly separated from the protoconid. Its apex deviates from the latter in the lingual direction, pointing slightly distally, thus projecting backwards behind the distal wall of the protoconid. In lateral view, the metaconid is nearly vertical. The talonid is long and trenchant, narrower than the trigonid. The hypoconid occupies almost the entire buccal portion of the talonid and is associated with the nearby cingulum. It is an elongated, high and well-developed cusp, with a cutting, crest-like occlusal surface. Distal to the hypoconid, on the distobuccal edge of the talonid, a much smaller entoconid is situated. 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 and perpendicular valley. On the lingual edge, a series of cuspid-like swellings is located, which start from the metaconid base and 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 talonid. The trigonid buccal margin is arched, whereas the space between the trigonid and talonid is a moderately concave. The buccal margin of the talonid is arched and the strongest convexity occurs on the level of the hypoconid. The lingual margins of the paraconid and talonid are 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 (Fig. 3B).

Remarks. Two cranial fragments from Jradzor were assigned to a small mustelid, whose morphology allows us to assign the specimen to Ictonychinae. Few small species, morphologically comparable to Jradzor mustelid, have been described from the Pliocene and the Early Pleistocene of Europe. From the Austrian site Deutsch–Altenburg 2 (1.3–1.2 Ma), the enigmatic species *Psalidogale altenburgensis* Rabeder, 1976 was described, whose taxonomic status remains 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 the 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 Ma; Jánossy (1986)), it has not been found elsewhere in Eurasia. *P. altenburgensis* is referable to some Miocene Mustelini, if it is a truly independent species and not an atypical specimen, which cannot be yet confidently stated. This form should 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 Jradzor and Osztramos 7 specimens. *Psalidogale altenburgensis* can be distinguished from Jradzor mustelid by: its smaller size; the presence of diastemas between the 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 an extremely reduced protocone; and a considerably narrower m1 without metaconid and hypoconulid.

The Jradzor mustelid differs also distinctly from both species from the genus *Vormela* Blasius, 1884, the Pliocene–Early Pleistocene *Vormela petényii* Kretzoi, 1942 and its descendant *Vormela peregusna* (Güldenstädt, 1770). Both species are more highly specialised and their teeth are characterised by more evolved cutting and crushing capabilities (Figs 3, 4). In relation to both *Vormela* species, Jradzor mustelid possesses a larger size, less reduced and more oval P2, a more elongated and narrower P4 with a lower and shorter height and mesiodistally longer protocone, smaller, but higher parastyle and narrower and shorter metastyle, 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 (Figs 4, 5).

From the same Austrian site Deutsch–Altenburg 2 (1.3–1.2 Myr) where *P. altenburgensis* was described, another form *Oxyvormela maisi* Rabeder, 1973 has been also described. This fossil Ictonychini was described as a highly evolved form, characterised by: a size comparable with the extant *Vormela peregusna* (Güldenstädt, 1770); a short and robust rostrum; enlarged and robust canines; strongly to totally reduced P2 and 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; possessing a particularly robust symphyseal part, with mass 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 (Figs 4, 5; Rabeder (1973)).

The Jradzor mustelid represented an earlier stage of evolution, when compared with the highly evolved *O. maisi*. It differs from latter form by its lesser reduction of the P2; a narrower P4 with a longer and more prominent protocone; parastyle set at a 45° angle to the rest of the crown; considerably shorter metastyle; and archaic m1 with less developed cutting abilities for the less sharp cuspids. These characters are demonstrated in an elongated and narrow crown, lower and shorter main cusps (para- and protoconid), large and prominent metaconid and broad and elongated talonid, with large and high hypoconid positioned strongly buccally and still present small and well distinct entoconid, located lingually, just after the metaconid (Figs 4, 5).

Amongst other fossil Ictonychini, the Jradzor mustelid resembles closest the species of the genus *Baranogale*. *Baranogale balcanica* Spassov, 2001, described from Bulgarian site Varshets (2.5–2.4 Ma), differs from Jradzor mustelid in: its smaller dimensions and infraorbital foramen; strongly reduced P2 set straight to the P3–P4; and the protocone of the P4 not reaching frontally the level of the parastyle. In all features of the P3–P4 and m1 (Figs 4, 5), the Jradzor mustelid strongly resembles *Baranogale helbingi*. Features shared by specimens of *B. helbingi* include: the two-rooted and weakly reduced P2; narrow P3; P4 with an elongated and prominent protocone low; short metastyle, with strong lingual cingulum; the m1 with a short trigonid, broad and long talonid, prominent metaconid, elongated and laterally located hypoconid and elongated and low hypoconulid (Figs 4, 5).

The plotted index of the total length and trigonid breadth of the m1 of *B. helbingi* individuals showed the presence of three sets of data that do not overlap with each other (Fig. 6). One group is created by the very large (L m1 between 8.50 and 9.50 mm) individuals of *B. helbingi* from Karnezeika, Greece (2.1–2.0 Ma, Sianis et al. (2021, 2023)). 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, males (♂) were assigned with m1 length of 7.40–8.40 mm, while, for the second group of smaller females (♀), m1 length of 6.32–7.25 mm. In this context, *B. helbingi* from Jradzor can be interpreted as a female (Fig. 6). The intraspecific size variability of *B. helbingi* seems to be greater than that of the extant *V. peregusna*. It could be related to the lesser ecological specialisation and lesser evolutionary advanced level of *B. helbingi*, closer to its Miocene ancestors.

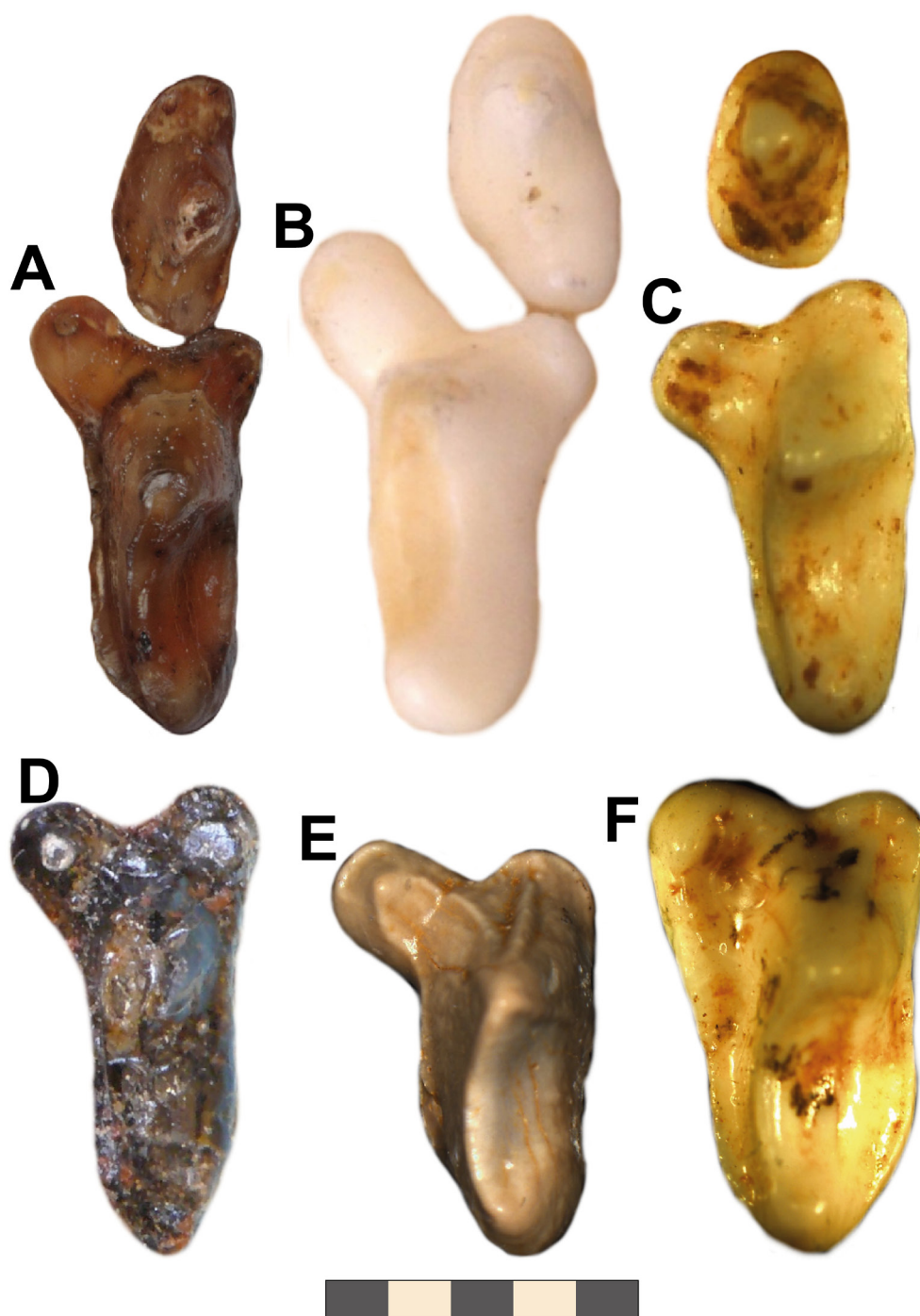


Figure 4. Comparison of the P4 of the different Ictonychini. **A.** *Baranogale helbingi* from Jradzor (4.16–3.98 Ma; JZ-13; JRD-20/08); **B.** *Baranogale helbingi* from Węże 1 (3.6–3.2 Ma; W1.7.1); **C.** Extant *Poecilogale albinucha* (Z.P.R.M.114); **D.** *Vormela* cf. *petényii* from Podlesice (4.9–4.2 Ma; PO.7.1); **E.** *Oxyvormela maisi* from Kielniki 1 (1.3–1.1 Ma; KI.5.1); **F.** *Vormela* cf. *peregrina* from Kozi Grzbiet (0.8–0.7 Ma; KZ.11.1). All teeth shown in the same proportions in the occlusal view, scale bars equal 1 mm for a total of 5 mm.

Suborder Feliformia Kretzoi, 1945
Family Felidae Fischer von Waldheim, 1817
Genus *Lynx* Kerr, 1792

cf. *Lynx* sp.

Fossil horizons. JZ-3s, 4.16–3.98 Ma (Lazarev et al. 2023).

Material. One mandibular corpus with c and p3–p4 (JRD-18/65) and one isolated m1 (JRD-24/01).

Description. Specimen JRD-18/65 in a corpus preserving c1 and p3–p4, whereas JRD-24/01 is an isolated lower first molar. The corpus is stout and high below the premolars. Between the canine and the premolars, there is a mesiodistally short diastema. The m1 is sharp, buccolingually compressed and with an absent metaconid/talonid.

Remarks. The size and morphology of the mandibular corpus and the lower carnassial are consistent with

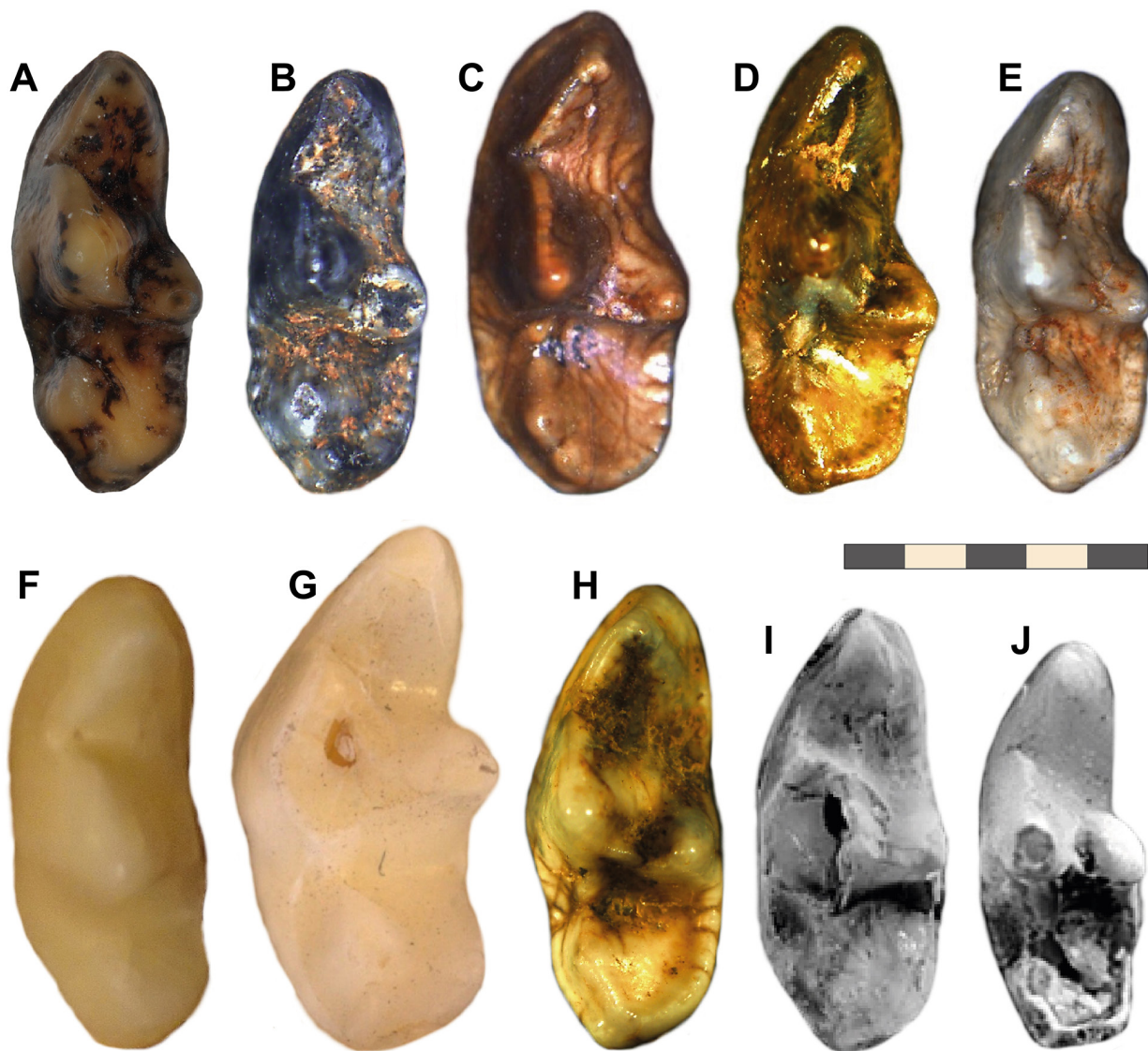


Figure 5. Comparison of the m1 of the different Ictonychini. **A–E.** *Baranogale helbingi*. **A.** Jradzor (4.16–3.98 Ma; JZ–15, JRD–19/239); **B.** Południowa Cave (JP.14.1); **C** Węże 1 (W.7.13); **D.** Węże 1 (W1.7.6); **E.** Węże 1 (MF/558/3); **F.** *Oxyvormela maisi* from Deutsch–Altenburg 2 (1.3–1.2 Ma; UWPI 2277/4/5); **G.** Extant *Vormela peregrusna* from Ukraine (ZP.R.M.Vp.1); **H.** *Vormela petényii* from Żabia Cave (1.7–1.5 Ma; JZ.14.1); **I.** *Vormela petényii* from Varshets (2.5–2.4 Ma; Spassov (2001: 91), Fig. 2); **J.** *Baranogale balcanica* from Varshets (2.5–2.4 Ma; Spassov (2001: 97), Fig. 6). All teeth shown in the same proportions in the occlusal view, scale bars equal 1 mm for a total of 5 mm. Specimens in B, D, I and J are mirrored.

a lynx-sized felid. However, the fragmentary nature of the material does not allow a confident species-level attribution; we therefore refer it to cf. *Lynx* sp. pending additional material and a dedicated taxonomic treatment.

Family Hyaenidae Gray, 1821
Subfamily Hyaeninae Gray, 1821
Genus Chasmaporthetes Hay, 1921

***Chasmaporthetes lunensis* (Del Campana, 1914)**

Fossil horizon. JZ–7, 3.3 ± 0.03 Ma (Lazarev et al. 2023).

Referred material. JRD–20/04, right hemi-mandible with i2, c–m1; JRD–20/05, left hemi-mandible fragment with i3–m1 (Fig. 7, Table 2); both belong to the same individual.

Description. Two specimens from Jradzor show virtually identical morphology and a comparable degree of dental wear, so it is very likely that both hemi-mandibles belong to the same individual. The hemi-mandibles are well-preserved, only lacking the right ramus. Both hemi-mandibles display a single mental foramen located below the p2. In buccal view, the ventral margin is straight. In occlusal view, the tooth row is slightly lingually curved, especially at p3–p4. The masseteric fossa is deep, extending mesially, almost reaching the distal level of the m1 talonid. The crowns of the i2 and i3 are asymmetric as they bear an enlarged main cuspid with two distinct secondary mesial and distal cuspidulids. The c1 is mesiodistally wide with a round cross-section at the base of the crown. The premolars are slightly tilted backwards and display a sharp protoconid.

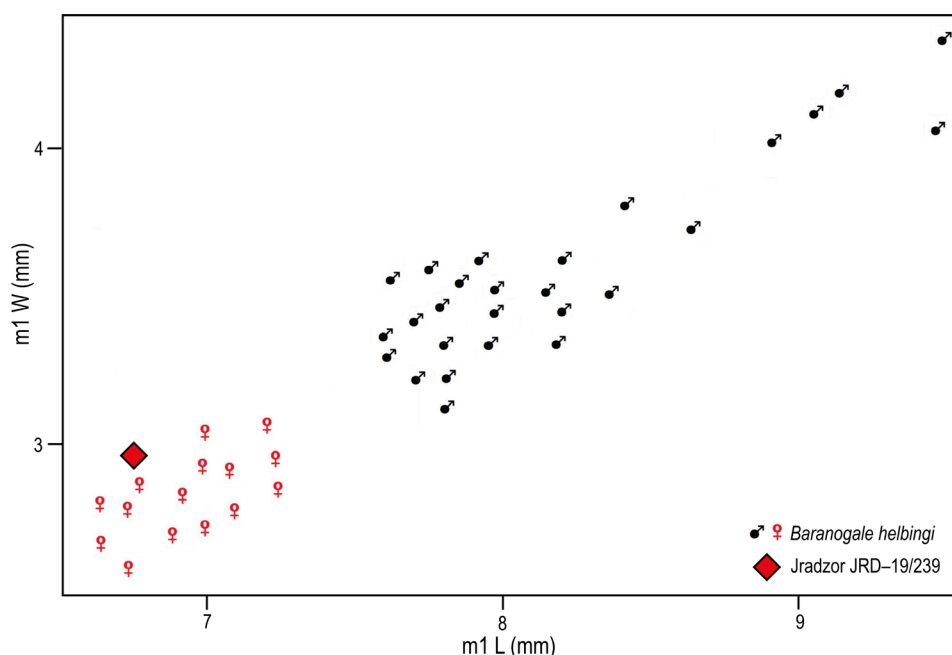


Figure 6. Graph showing the relationship between the crown length (L m1) and breadth (W m1) of m1 of *Baranogale helbingi*. Data from Marciszak et al. (2024) and references therein.

Table 2. Measurements of *Chasmaporthetes lunensis* from Jradzor (in mm).

		i2 L	i2 W	i3 L	i3 W	c L	c W	p2 L	p2 W	p3 L	p3 W	p4 L	p4 W	m1 L	m1 W
JRD-20/04	L	5.4	4.4	6	6.1	16.5	11	17.3	9.1	20.5	10.5	24.5	11.7	25.6	11
JRD-20/05	R	–	–	6	6.2	17.1	11.9	16.5	9.1	20.5	10.6	24.3	11.5	26.1	11.4

The p2 is separated from the canine by a 5.8–7.3 mm long diastemata. All premolars bear two accessory cusps, separated from the main cuspid by a notch. The mesial accessory cuspid (mac) is small and lingually placed on the p2, while the distal accessory cuspid (dac) is comparatively larger and situated in line with the protoconid. On the p3, they are almost equal size and position, but with the dac slightly larger. The p4's mac and dac are equally developed. The p4 also displays a strong distal cingulum and a second reduced distal accessory cuspid. The m1's metaconid is vestigial, while its paraconid and protoconid are developed. It displays a slight mesial cingulum. The m1 talonid is mesiodistally reduced. The hypoconulid is well developed.

Remarks. The genus *Chasmaporthetes* includes several species customarily recorded from the Turolian (Late Miocene) to the Calabrian (Early Pleistocene) in Europe, Asia, Africa and North America. Compared to the stoutly built extant hyaenas, the representatives of the genus *Chasmaporthetes* display more slender dentition and more elongated and slender post-cranial bones. Werdelin and Solounias (1991) and Turner et al. (2008) included this genus in the category of 'hunting hyaenas' for its inferred cursorial abilities. Morphologically, *Chasmaporthetes* species, are characterised by a narrow m1 without a metaconid. Its short talonid does not have a basin and consists of a single shearing blade, which is formed by a hypoconid.

Kurtén and Werdelin (1988) made the only existing review specifically focused on this genus. The former authors provided a revised diagnosis of the genus *Chasmaporthetes* namely: an elongated p4 with large accessory cuspid; a m1 lacking metaconid and with a unicuspid talonid. Slightly later, Werdelin and Solounias (1991) described two other main morphological characters for the genus: a straight or slightly concave mesial face of the p3 and a p4 anterior accessory cuspid not attached to the protoconid.

In general terms, the Jradzor specimen can be distinguished from the *Pliocrocota perrieri* by: the presence of the mesial accessory cuspid in the p2 and p3 (Vinuesa et al. 2014); the m1 morphology without metaconid and with unicuspid talonid; and finally by the slender and low mandibular corpus. *Pliocrocota perrieri* co-exists with *Chasmaporthetes* during the most of its known chronological range in Europe (Turner et al. 2008).

The studied specimens from Jradzor differ from most of the previously described Eurasian species. Indeed, they differ from *Ch. melei* and *Ch. gangsriensis* by larger dimensions (Table 2) and from *Ch. gangsriensis* and *Ch. borissiakii* by the number of cuspid on the talonid. As described earlier, the mandible found in Jradzor only bears one developed cusp on its talonid. Moreover, the tooth row of *Ch. borissiakii* is straight (Werdelin and Solounias 1991), while the mandible found in Jradzor has a slightly curved tooth row. *Chasmaporthetes exitelus* is



Figure 7. *Chasmaporthetes lunensis* from Jradzor. JRD–20/04, right hemi-mandible with i2, c–m1 in **A**. Buccal; **B**. Lingual; **C**. Occlusal (**B**) and **G**. Zoomed occlusal views. JRD–20/05, left hemi-mandible with i3–m1 in **D**. Buccal; **E**. Lingual; **F**. Occlusal and **H**. Zoomed occlusal views.

only known from one specimen (Kurtén and Werdelin 1988), represented by a palate and cannot be compared to the mandible found in Jradzor. The studied specimens, however, display several morphological affinities with *Ch. lunensis*, namely: curved tooth row; unicuspid talonid; large mesial accessory cuspid on the p4 (Werdelin and Solounias 1991); and presence of mesial accessory cuspid on the p2. According to Kurtén and Werdelin (1988), the p2 mesial accessory cuspid is normally very small or absent within *Chasmaporthetes*, except for two species: *Ch. nitidula*, whose mesial accessory cuspid is well-developed and *Ch. lunensis*, whose mesial accessory cuspids are smaller, but present. Based on morphological and morphometric data, the studied specimen can be ascribed to the species *Chasmaporthetes lunensis*. Even in morphometric terms, the mandibles from Jradzor are consistent with the attribution to *Ch. lunensis* (Fig. 8). Indeed, two specimens fall perfectly within the variability of *Ch. lunensis*. In the PCA on lower teeth, the PC1 explains 76.69% and the PC2 only about 9.17% of the variability. They both are respectively influenced by the tooth size and by the size of the p4 and length of the m1. In Fig. 8, the species are fairly well separated from each other into specific groups. The most variable seems to be

the extant spotted hyaena, *C. crocuta*, that is also largely represented in the used dataset. *Chasmaporthetes* spp. occupies an intermediate position in the scatterplot, for their medium size and less-specialized dentition towards durophagy as opposed to other taxa (e.g. *Parahyaena*, *Hyaena*, *Pliocrocata* and *Pachycrocata*).

Genus *Pliocrocata* Kretzoi, 1938

Pliocrocata perrieri (Croizet & Jobert, 1828)

Fossil layers. JZ–7, 3.3 ± 0.03 Ma (Lazarev et al. 2023).

Referred material. JRD–20/06 right p4 and m1; JRD–19/04, right dp4 (Fig. 9, Table 3).

Description. The occlusal outlines of the p4 and m1 are buccolingually wide. The p4 displays a high protoconid and two accessory cuspids. The paraconid is small, but well individualised and lingually deflected, while the hypoconid is developed. They are separated from the main cusp by a slight notch. On its distal part, the crown of the p4 displays a large, mainly lingually developed cingulum. The m1 bears a large paraconid and large protoconid of equal height and an individualised,

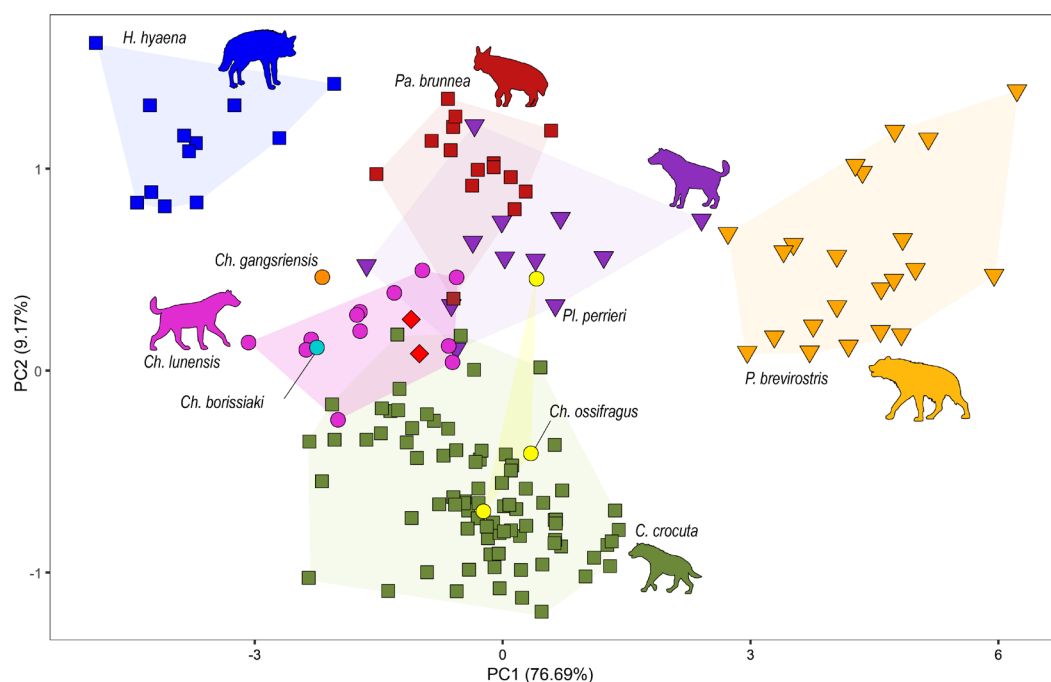


Figure 8. Principal Component Analysis performed on mandibular specimens for selected species of Hyaenidae, both extant and fossil ones and the specimens JRD-20/04 and JRD-20/05 (red diamonds) based on the length and width of p3–m1. The considered species include the extant *Crocota crocuta*, *Hyaena hyaena*, *Parahyaena brunnea*; the fossil *Chasmaporthetes borissiakii*, *Chasmaporthetes gangsriensis*, *Chasmaporthetes lunensis*, *Chasmaporthetes ossifragus*, *Pachycrocota brevirostris* and *Pliocrocota perrieri*. See Suppl. material 1 for the loadings.

but small metaconid. On its mesial face, the m1 bears a cingulum. The mesiodistally reduced talonid displays a well-developed hypoconid, while the hypoconulid and entoconid seem merged into a ridge. Finally, the dp4 displays a high protoconid and a mesiodistally long paraconid. The metaconid, on the lingual side, is smaller than the buccal cusps, but still sharp. The reduced talonid displays a broad, but low hypoconid, a hypoconulid and a high entoconid, all connected into a crest.

Remarks. *Pliocrocota perrieri* is a large bone-cracking hyaena commonly recorded in Early to Middle Villafranchian European assemblages, being also customarily recorded together with the less common hunting hyaena *Chasmaporthetes lunensis*. The known chronological range of *P. perrieri* is from 4.2 to 2.0 Ma (Turner et al. 2008) being distributed in Europe, Asia and Africa. From a phylogenetic viewpoint, *Pliocrocota* is considered as a sister-taxon of *Pachycrocota brevirostris* (Turner et al. 2008). *Pliocrocota* is dentally characterised by a non-reduced P4 protocone, as well as a short and massive m1 with normally no metaconid, but with a wide talonid, in which both the entoconid and hypoconid are normally present (Vinuesa et al. 2014). The m1 metaconid is present in different percentages within fossil populations, being more common in Pliocene forms (Martínez-Navarro et al. 2025). The morphology of the m1 talonid also varies between more primitive and derived forms with one or two cuspidals (Kurtén and Poulanos 1981; Sotnikova 1989). The morphometric data reported in Table 3 show an increase in the general size of the teeth within *P. perrieri*. By their dimensions,

Table 3. Measurements of *Pliocrocota perrieri* from Jradzor (in mm).

		p4 L	p4 W	m1 L	m1 W	L	W
JRD-20/06	L	21.9	12	23.1	11.3	–	–
JRD-19/04	L	–	–	–	–	19.6	7.8

the teeth found in Jradzor resemble the *P. perrieri* individuals from the Zanda Basin, China (MN14), but also from the Odessa Catacombs, Ukraine (MN15).

The morphological characteristics of deciduous teeth do not possess reliable diagnostic characters (Qiu 1987; Moullé et al. 2006; Martínez-Navarro et al. 2025). The morphology of the dp4 has a simple morphology, but with a fairly extended talonid and evident cuspidals on it. These morphologies contrast with the generalised ones of the deciduous dentition of *P. brevirostris*. According to Qiu (1987), the dp4 of *Pliocrocota* generally has a short talonid and a reduced metaconid, if not absent, although these features are somewhat variable (see Qiu (1987)). In contrast to this morphology, the dp4 of *Pachycrocota*, being in some way more stable in its morphology, generally retains a mesiodistally short talonid without metaconid (Fig. 9; Viret (1954); Howell and Petter (1980); Qiu (1987); Argant (2004)). Martínez-Navarro et al. (2025) showed that the combination of the mandibular and dental parameters (e.g. height and breadth of the juvenile mandible at or below the dp4, together mesiodistal length and width of deciduous dentition) is more diagnostic. In Jradzor, only the single specimen JRD-19/04 is available; thus its ascription to a certain

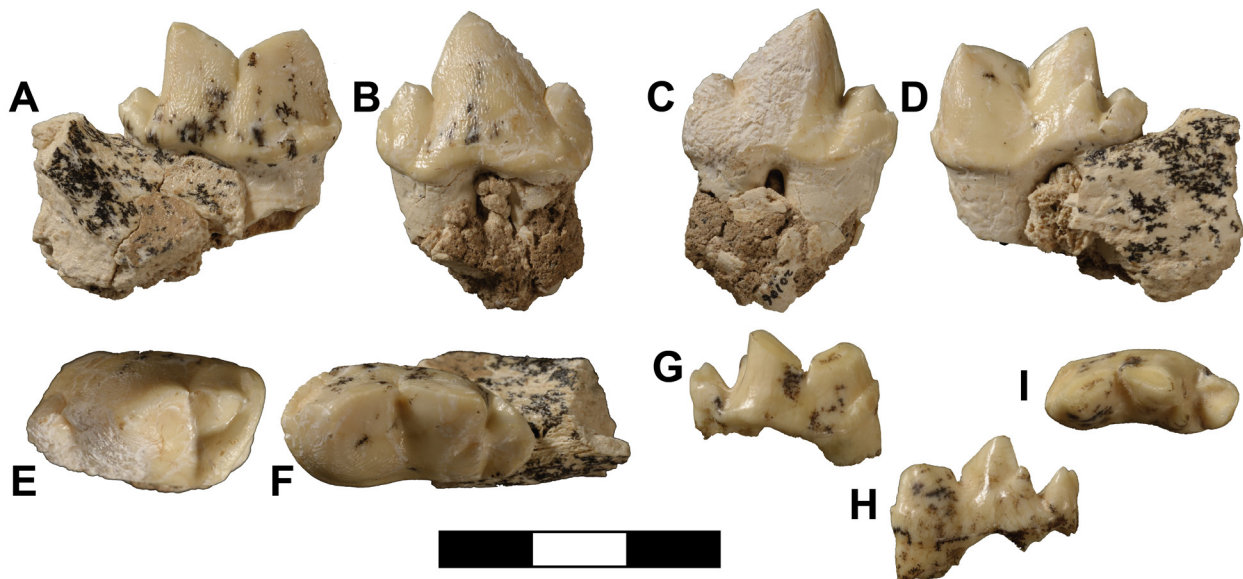


Figure 9. *Pliocrocuta perrieri* from Jradzor. JRD–20/06, right p4 and m1 displayed as in anatomical position, in buccal (A – m1; B – p4), lingual (C – the p4; D – the m1) and occlusal (E – the p4, F – the m1) views. JRD–19/04, right dp4 in G buccal, H lingual and I occlusal views.

taxon is difficult. Considering the morphological features of the adult dentition of JRD–20/06, consistent with *Pliocrocuta*, we suggest that JRD–19/04 belongs to the same species. Metrically, this seems to be confirmed if compared to other deciduous premolars of *Pliocrocuta* and *Pachycrocuta* (Fig. 10).

Discussion

The European Pliocene—often referred to as the “dark epoch”—remains comparatively less understood than the preceding Miocene and the subsequent Pleistocene, both of which are represented by numerous fossil-rich sites across Mediterranean Europe (see Haneda et al. (2019)). The number of Pliocene localities with abundant fossils and well-documented ecological diversity is limited, and those with a clearly defined carnivoran guild are virtually non-existent or were excavated in the 19th century without proper stratigraphic control. In this context, the carnivoran assemblage from Jradzor offers an important perspective on the dynamics of carnivore communities during the middle and late phases of the epoch. Although comprehensive reviews of the European Pliocene carnivorans are scarce, literature confirms the existence of several sites in Spain, France, Italy, Greece and Ukraine. Unfortunately, many of these were discovered over a century ago and lack numerical dating or clear stratigraphic frameworks. The carnivoran guild of the European Pliocene is, thus, characterised by the genera, such as *Megantereon*, *Dinofelis*, *Lynx*, *Felis*, *Ursus*, *Pliocrocuta*, *Chasmaporthetes*, *Eucyon*, *Vulpes*, *Nyctereutes*, *Baranogale*, *Lutra*, *Martellictis* and *Pannonictis*. From the latest Pliocene (Early Villafranchian), the gradual transition to more open environments and increased climatic seasonality facilitated the dispersal of new forms better adapted

to open habitats, including *Homotherium*, *Acinonyx*, *Viretailurus*, *Xenocyon* and *Canis*. The recorded species and their taxonomical adscriptions vary considerably in the palaeontological literature. However, description and comparison of the specific forms recorded in the European Pliocene is outside the scope of this paper (Viret 1954; Kurtén and Crusafont 1977; Kurtén and Werdelin 1988; Sotnikova 1994; Morales et al. 2003; Turner et al. 2008; Sen and Saraç 2018; Bartolini-Lucenti and Spassov 2022; Marciszak et al. 2023; Bartolini-Lucenti et al. 2025).

The entire vertebrate remains of the JZ–7 horizon are interpreted to be confined to lahar deposit. This depositional environment represents rapid and high-energy mudflow made predominantly of pyroclastic material transporting the remains at a relatively small distance from the drowning place (Lazarev et al. 2023). The faunistic assemblage of the JZ–7 is dominated by forms characteristic to herbivores and open environments. The carnivorans recorded in Jradzor are not in contrast with this interpretation. The presence of a primitive form of *Nyctereutes* at Jradzor is particularly noteworthy. The results presented in the descriptive paper (Bartolini-Lucenti et al. 2026) suggest an ecological profile distinct from that of the solitary extant raccoon dog, more consistent with jackal-like canids such as the golden jackal (*Canis aureus*), potentially capable of forming transient foraging groups. The ecological and palaeoenvironmental implications of this species within the Jradzor community remain difficult to interpret. While extant *Nyctereutes* species prefer forested environments, the consistency of this preference amongst fossil representatives is far from established and often assumed without direct evidence. An additional consideration that can be made regarding *Nyctereutes urartuensis* from Jradzor is its possible ecology. To compare and estimate dietary differences amongst extant raccoon dog species, Asahara and Takai (2017) used the molar ratio method (see the cited

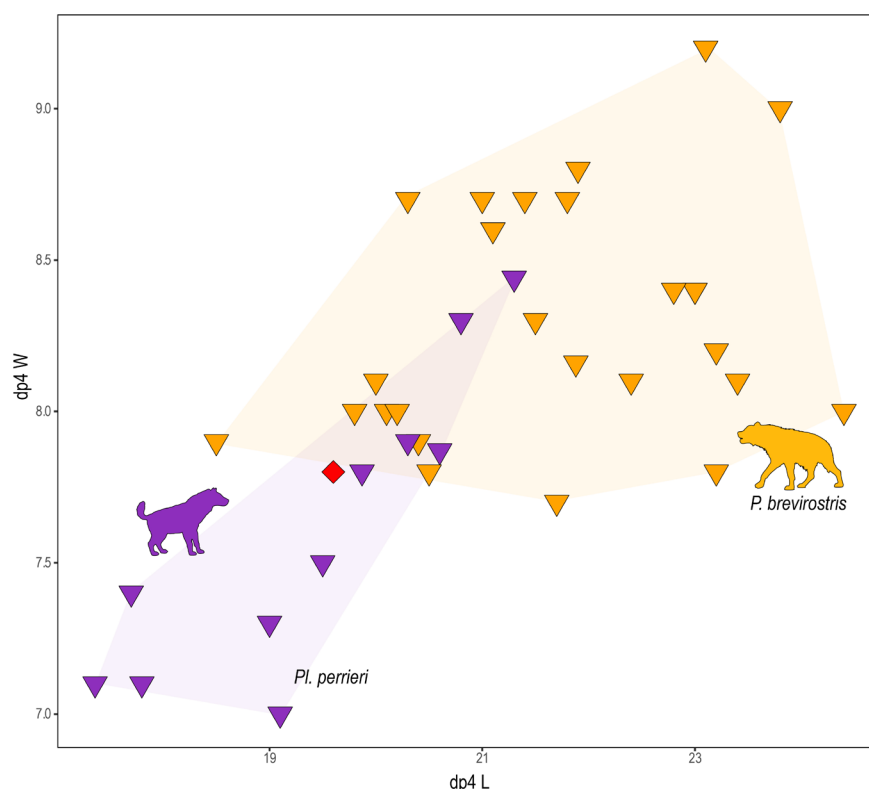


Figure 10. Plot of the length and width of the dp4 in *Pliocrocuta* (from various localities of Eurasia), *Pachycrocuta* (from Dmanisi, Untermassfeld, Upper Valdarno, Vallonnet) and the specimen (red diamond) from Jradzor.

reference for the methodology). This method has proved to be interestingly suggestive of possible dietary preferences in fossil raccoon dogs (Bartolini-Lucenti et al. 2018; Bartolini-Lucenti 2019; Tamvakis et al. 2023). Particularly higher molar ratios would imply a more omnivorous diet than lower ones. Carnivorous taxa have an average $m2/m1$ score of 0.48–0.49, for example, *N. tingi* and *N. vulpinus*. In contrast, more omnivorous taxa have higher average values > 0.55 , like *N. megamastoides* and *N. sinensis* (see Bartolini-Lucenti (2019) and Tamvakis et al. (2023)). Calculation for the *Nyctereutes urartuensis* from Jradzor is considerably high (i.e. $m2/m1$ ratio 0.62), but consistent with the range of individual variance of the omnivore species, as visible in Tamvakis et al. (2023). This value fits with the morphological features of *Nyctereutes urartuensis* from Jradzor and gives us hints on its position in the Pliocene trophic chains of this part of western Asia.

The described record of *Baranogale helbingi* from Jradzor significantly increases our knowledge of this species, both temporally and spatially. Regarded so far as a European endemic, this ancient and archaic mustelid has a much broader geographical scope than previously thought. The Jradzor material is the earliest from the Caucasus and Asia in the overall record of the species and the easternmost occurrence of this species. It is also one of the oldest records, but younger than that of Italian Moncucco Torinese (5.4–5.3 Ma; Colombero et al. (2017)), Polish Podlesice (4.9–4.2 Ma; Kowalski (1959, 1964)) and two Romanian sites of Beresti and Malusteni (4.9–4.2 Ma; Radulescu et al. (2003)). It is also older than most of the other records of this species, slightly predating such sites dated on MN15b

(3.6–3.2 Ma), as Węże 1 (Poland; Kowalski (1959, 1964); Marciszak et al. (2024)), Odessa Catacombs (Ukraine; Vislobokova et al. (2001)) or Wölfersheim (Germany; Morlo and Kundrát (2001)). The temporal occurrence of *B. helbingi* covers the whole Pliocene and the Early Pleistocene (5.4–1.5 Ma) and it is limited mostly on the Eastern Paratethyan regions. Like other European Ictonychini, *B. helbingi* vanished during the Early Pleistocene, most likely due to competition with small Mustelinae that were highly plastic ecologically (Marciszak et al. 2024).

Several scholars conducted comprehensive reviews of the evolution and fossil record of the genus *Chasmaporthetes* (Qiu 1987; Kurtén and Werdelin 1988; Sotnikova 1994; Antón et al. 2006; Turner et al. 2008). The former authors agreed to include the specimens traditionally included in *Euryboas*, *Lycyaena* and *Ailuraena* in this genus. *Chasmaporthetes* is characterised by a wide rostrum, sharp dentition as compared with extant hyaenas and cursorial adaptations in the limbs (Kurtén and Werdelin 1988). *Chasmaporthetes* is known in Asia and Europe from the latest Miocene to the Pleistocene (Calabrian), whereas, in North America, from the latest Pliocene to the Early Pleistocene. The taxonomy of Eurasian forms of *Chasmaporthetes* remained a considerable debate over the last decades. The main works on this (Kurtén and Werdelin 1988; Turner et al. 2008) considered the validity of two species in Europe—*Ch. lunensis* and *Ch. borissiakii*—and two in Asia—*Ch. exitelus* and *Ch. lunensis*. Other authors, like Qiu (1987), however, insisted on the validity of the Asian species *Ch. kani* with at least two subspecies. More recently, Rook and colleagues (2004) erected *Ch. melei*,

an endemic form of Sardinia. Finally, Tseng et al. (2013) erected a new species, *Ch. gangsriensis*, from the Early Pliocene of Tibet. The most widely distributed European species *Ch. lunensis* was erected by Del Campana (1914) on the basis of specimens from Olivola, Tuscany (ca. 2.0 Ma). Nowadays, this species is known in the fossil record of Spain, France, Germany, Greece, Ukraine, China, Russia and Turkey (Turner et al. 2008), again as *B. helbingi* has mostly found in the Eastern Paratethys region. *Ch. lunensis* is overall larger than other species of the genus. Its lower premolars are buccolingually narrow with small mesial accessory cusplids, except for the p2. The P2 and P3 are buccolingually wider at the paracone level and without mesial accessory cusps in older forms which can be present in Gelasian and Calabrian ones. The P4 has a well-developed protocone and mesiodistally elongated metastyle. These former characters perfectly fit with the mandibular specimen from Jradzor (Fig. 7).

In turn, the taxonomic status and phylogenetic affinities of *Pliocrocota perrieri* have also been a matter of hot debate over the last decades. The species *Hyaena perrieri* was erected by Croizet and Jobert (1828), based on the specimens from the Mount of Perrier in Auvergne, France. Kretzoi (1938) erected the genus *Pliocrocota*, which was subsequently synonymised with *Pachycrocota* by some authors (Ficcarelli and Torre 1970; Howell and Petter 1980). Later on, Turner (1990) and Werdelin and Solounias (1991) resurrected the genus *Pliocrocota* and further noted that both *Pliocrocota pyrenaica* (Depéret 1890) and *Hyaena arvernensis* (Croizet and Jobert 1828) must be considered as junior subjective synonyms of *Pl. perrieri*. *Pliocrocota* is the most common Pliocene and Gelasian bone-cracking hyaena, first recorded during the Early Pliocene of China (ca. 5 Ma; Qiu (1987)) and slightly later in Europe and Africa. Its record suggests a fast dispersal of this large hyaenid alongside the most derived members of the *Chasmaporthetes* lineage. *Pliocrocota* is considered as a sister taxon of *Pachycrocota* and is deemed by several authors to be its direct ancestor (Turner et al. 2008). *Pliocrocota perrieri* is a large-bodied hyaenid dentally characterised by a non-reduced P4 protocone, as well as a short and massive m1 normally with no metaconid (in the derived forms), but with a wide talonid, in which both the entoconid and hypoconid are present (Werdelin and Sanders 2010).

Both large hyaena species recorded from Jradzor are known to have different dietary habits. Indeed, although both are hypercarnivores, *Chasmaporthetes lunensis* was a hunting hyena (Kurtén and Werdelin 1988; Antón et al. 2006), while *Pliocrocota perrieri* was a bone-cracking species (Werdelin and Solounias 1996). Antón et al. (2006) suggested that the limited fossil record of *Ch. lunensis* could reflect its solitary lifestyle, while *P. perrieri* is more abundant and its fossil record could reflect a group-denning scavenger. However, based on the shape of the muzzle and the elongated and gracile fore-limbs, the authors suggest that *Chasmaporthetes* would “still require group action in order to kill medium and large prey”. Considering the similarities in their body size and the presence of adaptations

for bone cracking in both species, Antón et al. (2006) point out the problem of the competition between two species for the carcasses. If *Pl. perrieri*, due to its greater bone-cracking abilities, it did not hunt as it was well adapted to scavenging the carcasses of animals, *Ch. lunensis* would have used its crushing premolars on its own prey and “not so much to consume scavenged carrion”. This could explain why *P. perrieri* has been more abundantly found in sites where the presence of hyaenids is correlated to their capacity to scavenge carcasses of other animals.

Conclusions

The carnivoran assemblage from Jradzor represents a significant contribution to our understanding of Pliocene faunal dynamics in western Asia and, more broadly, within the framework of European palaeobiogeography. The discovery and analysis of taxa, such as *Nyctereutes urartuensis*, *Baranogale helbingi*, *Chasmaporthetes lunensis* and *Pliocrocota perrieri*, not only expand the known geographic and temporal ranges of these genera, but also provide critical insights into their ecological roles and evolutionary histories during a period of pronounced climatic and environmental transition.

The Jradzor locality, with its well-preserved and stratigraphically constrained fossil record, offers a rare opportunity to examine carnivoran guild structure during the Pliocene—a time often referred to as the “dark epoch” due to the relative scarcity of well-documented sites. The presence of a primitive-like form of *Nyctereutes* is particularly noteworthy. Morphological and morphometric analyses suggest that this species occupied a more omnivorous niche than its extant relatives, as evidenced by its high m2/m1 ratio and cranial features consistent with jackal-like canids. This ecological inference challenges traditional assumptions about the genus’ habitat preferences and underscores the importance of integrating dental metrics with broader anatomical and palaeoenvironmental data.

Equally significant is the record of *Baranogale helbingi*, which extends the known distribution of this archaic mustelid into the Caucasus and marks its easternmost occurrence. The Jradzor specimens, being amongst the oldest record of the species, provide valuable data on intraspecific variation, sexual dimorphism and evolutionary conservatism within the genus. The persistence of *B. helbingi* throughout the Pliocene and its eventual disappearance in the Early Pleistocene likely reflect competitive displacement by more ecologically plastic mustelines—a pattern consistent with broader trends in carnivoran evolution during this interval.

The identification of *Chasmaporthetes lunensis* and *Pliocrocota perrieri* further enriches the carnivoran profile of the site. These two large-bodied hyaenids, representing distinct ecological strategies—cursorial hunting and bone-cracking scavenging, respectively—illustrate the functional diversity within the guild and raise important questions about niche partitioning and interspecific competition. The morphological features of

the Jradzor specimens align closely with those of other Eurasian populations, reinforcing their taxonomic assignments and providing new data on regional variation. Their co-existence supports hypothesis of ecological complementarity, wherein *Chasmaporthetes* may have relied more heavily on active predation, while *Pliocrocota* exploited carcasses through its enhanced durophagy.

Taken together, the carnivore fauna of Jradzor offers a compelling snapshot of Pliocene ecosystems in a region historically under-represented in palaeontological research. The assemblage reflects a transitional phase in carnivore evolution, marked by increasing specialisation, geographic dispersal and adaptation to changing environmental conditions. The integration of morphological, morphometric and ecological data in this study underscores the value of multidisciplinary approaches in palaeontology and highlights the potential of Jradzor as a reference locality for future research on Pliocene faunal dynamics. These findings not only fill critical gaps in the fossil record, but also contribute to broader discussions on the biogeographic and ecological processes that shaped Eurasian carnivore communities during the Neogene. Furthermore, the comparison of the Jradzor carnivore assemblage with large scale regional records suggests its strong links with Eastern Paratethys record as well as the south margin of the Eastern Paratethys in the dispersal of the vertebrate assemblages between Asia and Europe.

Acknowledgements

The authors are thankful to the kindness and availability of E. Cioppi and P. Agnelli, curators of the IGF and of the MZUF, respectively; M. Bukhsianidze of the GNM; E. Robert of the “Laboratoire de Géologie”, Université Claude-Bernard–Lyon 1; D. Berthet of the Musée des Confluences; S. Fraile and J. Morales of the CSIC-MNCN of Madrid. The authors thank Lilit Sahakyan (IGS deputy director, Yerevan, Armenia) for the scientific, administrative, and logistic support of our studies in Armenia. We are grateful Nikolai Spassov for fruitful discussions on the fauna. We would also like to thank Renaud Roch

(JURASSICA Museum, Porrentruy, Switzerland), who took part in the excavations at Jradzor and performed the preparation of the studied specimen (JURASSICA Museum, Porrentruy, Switzerland). We would also like to thank the staff of the diatomite mine for their hospitality, administrative and logistic support during all fieldwork. We would like to thank all participants in excavations at the Jradzor site since 2007. SBL thanks CERCA Programme/Generalitat de Catalunya.

Additional information

Conflict of interest

The authors have declared that no competing interests exist.

Ethical statement

No ethical statement was reported.

Use of AI

No use of AI was reported.

Funding

This research has been funded by the Swiss National Science Foundation project (197323).

Author contributions

SBL, JMM and AM wrote the main manuscript text; MM, DB and DV revised and improved the first draft of the text; SBL and AM prepared the figures; JMM and AM prepared the files for analysis. SBL and AM performed the analyses. All authors reviewed and approved the final version of the manuscript.

Author ORCIDs

Saverio Bartolini-Lucenti  <https://orcid.org/0000-0003-1280-5378>

Adrian Marciszak  <https://orcid.org/0000-0002-1472-6553>

Damien Becker  <https://orcid.org/0000-0002-2226-9946>

Davit Vasilyan  <https://orcid.org/0000-0001-8712-0678>

Data availability

All of the data that support the findings of this study are available in the main text or Supplementary Information.

References

- Agustí J, Vekua A, Oms O, Lordkipanidze D, Bukhsianidze M, Kiladze G, Rook L (2009) The Pliocene-Pleistocene succession of Kvabebi (Georgia) and the background to the early human occupation of Southern Caucasus. *Quaternary Science Reviews* 28: 3275–3280. <https://doi.org/10.1016/j.quascirev.2009.09.001>
- Antón M, Turner A, Salesa MJ, Morales J (2006) A complete skull of *Chasmaporthetes lunensis* (Carnivora, Hyaenidae) from the Spanish Pliocene site of La Puebla de Valverde (Teruel). *Estudios Geológicos* 62(1): 375–388. <https://doi.org/10.3989/egol.0662132>
- Argant A (2004) Les Carnivores du gisement Pliocène final de Saint-Vallier (Drôme, France). *Geobios* 37: S133–S182. [https://doi.org/10.1016/s0016-6995\(04\)80013-5](https://doi.org/10.1016/s0016-6995(04)80013-5)
- Asahara M, Takai M (2017) Estimation of diet in extinct raccoon dog species by the molar ratio method. *Acta Zoologica* 98: 292–299. <https://doi.org/10.1111/azo.12179>
- Bartolini-Lucenti S, Rook L, Morales J (2018) Nyctereutes (Mammalia, Carnivora, Canidae) from Layna and the Eurasian raccoon-dogs: an updated revision. *Rivista Italiana di Paleontologia e Stratigrafia* 124: 597–616.
- Bartolini-Lucenti S (2019) “Measure my teeth and you’ll know what I ate”: The molar ratio method and an updated interpretation of the diet of *Nyctereutes sinensis* (Carnivora, Canidae). *Acta Zoologica* 100(2): 211–215. <https://doi.org/10.1111/azo.12232>
- Bartolini-Lucenti S, Spassov N (2022) Cave canem! The earliest *Canis* (*Xenocyon*) (Canidae, Mammalia) of Europe: Taxonomic affinities

- and paleoecology of the fossil wild dogs. *Quaternary Science Reviews* 276: 107315. <https://doi.org/10.1016/j.quascirev.2021.107315>
- Bartolini-Lucenti S, Madurell-Malapeira J, Garrido G, Rook L, Arribas A (2025) Early dispersal and niche partitioning in Canidae from an Early Pleistocene site of Spain (Fonelas P-1, Guadix-Baza basin, Granada). *Bollettino della Società Paleontologica Italiana* 64(1): 47–67.
- Bartolini-Lucenti S, Meyer M, Frosali S, Madurell-Malapeira J, Liu W, Costeur L, Becker D, Vasilyan D (2026) Systematics and paleoneurology of a new Pliocene raccoon dog (*Nyctereutes*) from Jradzor (Armenia). *Swiss Journal of Paleontology* 145: 213–249.
- Batsch AJGC (1788) Versuch einer Anleitung zur Kenntniss und Geschichte der Thiere und Mineralien: für akademische Vorlesungen entworfen, und mit den nöthigsten Abbildungen versehen. Akademischen Buchhandlung, Jena, Germany, 528 pp. <https://doi.org/10.5962/bhl.title.79854>
- Becker D, Mouhat Bourquard M, Maridet O, Vasilyan D (in press) The Hipparionini horses (Equidae, Perissodactyla, Mammalia) from the Late Pliocene of Jradzor (Armenia). *Swiss Journal of Paleontology*.
- Becker D, Lefebvre R, Saulnier M, Vasilyan (2026) A new genus and species of Pliohyracidae (Hyracoidea, Mammalia) from the Pliocene of Jradzor, Armenia. *Swiss Journal of Palaeontology* 145: 179–198. <https://doi.org/10.3897/sjp.145.181371>
- Burke KD, Williams JW, Chandler MA, Haywood AM, Lunt DJ, Otto-Bliesner BL (2018) Pliocene and Eocene provide best analogs for near-future climates. *Proceedings of the National Academy of Sciences* 115(52): 13288–13293. <https://doi.org/10.1073/pnas.1809600115>
- Bukhsianidze M (2026) Fossil ruminants from the Pliocene site of Jradzor, Armenia. *Swiss Journal of Paleontology* 145: 199–211. <https://doi.org/10.3897/sjp.145.177453>
- Colombero S, Alba DM, D'Amico C, Delfino M, Esu D, Giuntelli P, Harzhauser M, Mazza PPA, Mosca M, Neubauer TA, Pavia G, Pavia M, Villa A, Carnevale G (2017) Late Messinian mollusks and vertebrates from Moncucco Torinese, north-western Italy. *Paleoecological and paleoclimatological implications. Palaeontologia Electronica* 20.1.10A: 1–66. <https://doi.org/10.26879/658>
- Croizet J-B, Jobert A (1828) Recherches sur les ossements fossiles de département du Puy-de-Dôme. Les Principaux Libraires, Paris, France.
- Del Campana D (1914) La *Lycyaena lunensis* n. sp. dell'ossario pliocenico di Olivola (Val di Magra). *Palaeontographia Italica* 20: 87–104.
- Depéret C (1890) Les animaux pliocènes du Roussillon. *Mémoires de la Société géologique de France, Paléontologie* 3: 195.
- von den Driesch A (1976) A guide to the measurement of animal bones from archaeological sites (Vol. 1). Peabody Museum Press, 136 pp.
- Fedorov AV, Brierley CM, Lawrence KT, Liu Z, Dekens PS, Ravelo AC (2013) Patterns and mechanisms of early Pliocene warmth. *Nature* 496(7443): 43–49. <https://doi.org/10.1038/nature12003>
- Ficcarelli G, Torre D (1970) Remarks on the taxonomy of Hyaenids. *Palaeontographia Italica* 66: 1–32.
- Haneda Y, Suganuma Y, Okada M, Head MJ (2019) Integrated stratigraphy of the Pliocene and lower Pleistocene at Chiba composite section, central Japan: A reference for the GSSP of the Chibanian Stage (Middle Pleistocene Subseries). *Quaternary International* 519: 12–27.
- Haywood AM, Dowsett HJ, Dolan AM (2016) Integrating geological archives and climate models for the mid-Pliocene warm period. *Nature Communications* 7: 10646. <https://doi.org/10.1038/ncomms10646>
- Howell FC, Petter G (1980) The *Pachycrocuta* and *Hyaena* lineages (Plio-Pleistocene and extant species of the Hyaenidae). Their relationships with Miocene icittheres: *Palhyaena* and *Hyaenictitherium*. *Geobios* 13(4): 579–623. [https://doi.org/10.1016/s0016-6995\(80\)80004-0](https://doi.org/10.1016/s0016-6995(80)80004-0)
- Jánossy D (1986) Pleistocene vertebrate faunas of Hungary. Akadémiai Kiadó, Budapest, 226 pp.
- Karas C, Nürnberg D, Bahr A, Groeneveld J, Herrle JO, Tiedemann R, Demenocal PB (2017) Pliocene oceanic seaways and global climate. *Scientific reports* 7(1): 39842. <https://doi.org/10.1038/srep39842>
- Kormos T (1934) Neue und wenig bekannte Musteliden aus dem ungarischen Oberpliozän. *Folia Zoologica et Hydrobiologica* 5: 129–158.
- Kowalski K (1959) *Baranogale helbingi* Kormos and other Mustelidae from the bone breccia in Podlesice near Kroczyce (Poland). *Acta Palaeontologica Polonica* 4(1): 61–69.
- Kowalski K (1964) Paleokologia ssaków pliocenu i wczesnego plejstocenu Polski. *Acta Theriologica* 8(4): 73–88.
- Kretzoi M (1938) Die Raubtiere von Gombaszög nebst einer Übersicht der Gesamtfauuna (Ein Beitrag zur Stratigraphie des Altquartärs). *Annales historico-naturales Musei Nationalis Hungarici* 31: 88–157.
- Kurtén B, Crusafont-Pairó M (1977) Villafranchian carnivores (Mammalia) from La Puebla de Valverde (Teruel, Spain). *Commentationes Biologicae* 85: 1–39.
- Kurtén B, Werdelin L (1988) A review of the genus *Chasmaporthetes* Hay, 1921 (Carnivora, Hyaenidae). *Journal of Vertebrate Paleontology* 8(1): 46–66. <https://doi.org/10.1080/02724634.1988.10011683>
- Kurtén B, Poulanos AN (1981) Fossil Carnivora in Petralona Cave. Status of 1980 in The Third European Congress of Anthropology. *Anthropos. Etesio Organo tes Anthropologikes Etaireias Ellados Athinai* 8: 9–56.
- Lewis M, Werdelin L (2022) A revision of the genus *Crocota* (Mammalia, Hyaenidae). *Palaeontographica. Abteilung A, Paläozoologie, Stratigraphie* 322(1–4): 1–115. <https://doi.org/10.1127/pala/2022/0120>
- Lazarev S, Maul LC, Kuiper K, Becker D, Bukhsianidze M, Hovakimyan H, Sahakyan L, Vasilyan D (2023) Pliocene volcanic terrain of the South Caucasus as a missing link in Eurasian palaeobiogeography: Dating and palaeoenvironments of vertebrate assemblages of the Jradzor locality, Armenia. *Palaeogeography, Palaeoclimatology, Palaeoecology* 625: 111685. <https://doi.org/10.1016/j.palaeo.2023.111685>
- Marciszak A, Gornig W, Kropczyk A, Rössner GE (2022) The latest European record of *Chasmaporthetes lunensis lunensis* (Del Campana, 1914) from Schernfeld (Bavaria, Germany) in terms of the changes in the European carnivore paleoguilds. *Stratigraphy & Timescales* 7: 137–156. <https://doi.org/10.1016/bs.sats.2022.09.003>
- Marciszak A, Kropczyk A, Gornig W, Kot M, Nadachowski A, Lipeczki G (2023) History of Polish Canidae (Carnivora, Mammalia) and their biochronological implications on the Eurasian background. *Genes* 14(3): 539. <https://doi.org/10.3390/genes14030539>
- Marciszak A, Lipeczki G, Wolsan M (2024) *Baranogale helbingi* Kormos, 1934 (Mustelidae, Carnivora) from the Late Pliocene site Węże 1 (Poland). *Annales Societatis Geologorum Poloniae* 94(3): 255–272. <https://doi.org/10.14241/asgp.2024.09>
- Martínez-Navarro B, Madurell-Malapeira J, Bartolini-Lucenti S, Lordkipanidze D, Rook L (2025) The giant short-faced hyaena from Dmanisi: taxonomy and palaeobiology. *Bollettino della Società Paleontologica Italiana* 64: 107–131.
- Morlo M, Kundrát M (2001) The first carnivoran fauna from the Ruscinium (Early Pliocene, MN15) of Germany. *Paläontologische Zeitschrift* 75: 163–187. <https://doi.org/10.1007/BF02988011>
- Morales J, Soria D, Montoya P, Pérez B, Salesa MJ (2003) *Caracal depéreti* nov. sp. y *Felis* aff. *silvestris* (Felidae, Mammalia) del Plioceno inferior de Layna (Soria, España). *Estudios geológicos* 59(1–4): 229–247. <https://doi.org/10.3989/egcol.03591-4101>

- Moullé PE, Tréguier J (2006) Comparaison des dents déciduales de *Pachycrocuta brevirostris* et de *Crocota crocuta spelaea*. Bulletin du Musée d'Anthropologie préhistorique de Monaco 46: 21–33.
- Prescott CL, Haywood AM, Dolan AM, Hunter SJ, Pope JO, Pickering SJ (2014) Assessing orbitally-forced interglacial climate variability during the mid-Pliocene Warm Period. Earth and Planetary Science Letters 400: 261–271. <https://doi.org/10.1016/j.epsl.2014.05.030>
- Qiu Z (1987) Die Hyaeniden aus dem Ruscium und Villafranchium Chinas. Münchner Geowissenschaftliche Abhandlungen A 9: 1–108.
- Rabeder G (1973) Ein neuer Mustelidae (Carnivora) aus dem Altpleistozan 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: 1–119.
- Radulescu C, Samson PM, Petculescu A, Stiuca E (2003) Pliocene large mammals of Romania. Coloquios de Paleontologia 1: 549–558.
- R Core Team (2024) R: A language and environment for statistical computing, Vienna, Austria. <https://www.R-project.org/>
- RStudio Team (2025) RStudio: integrated development environment for R. Boston, MA. <http://www.rstudio.com/>
- Salzmann U, Williams M, Haywood AM, Johnson ALA, Kende S, Zalasiewicz J (2011) Climate and environment of a Pliocene warm world. Palaeogeography, Palaeoclimatology, Palaeoecology: 309(1–2): 1–8. <https://doi.org/10.1016/j.palaeo.2011.05.044>
- Sen S, Saraç G (2018) Hyaenidae (Carnivora, Mammalia) from late Miocene and Pliocene of Çalta (Ankara, Turkey). Revue de Paleobiologie 37(2): 561–575.
- Sianis PD, Kostopoulos DS, Roussiakis SJ, Koufos GD, Iliopoulos G (2021) New Baranogale (Mammalia, Mustelidae) finds from the Middle Villafranchian of Southern Greece. In: Belvedere M, Diez Diaz V, Mecozzi 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), 1–151.
- Sianis PD, Kostopoulos DS, Roussiakis S, Iliopoulos G (2023) Carnivora from the Early Pleistocene locality of Karnezeika (Southern Greece). Geobios 79: 43–59. <https://doi.org/10.1016/j.geobios.2023.06.002>
- Sotnikova MV (1989) Carnivores Mammals of the Pliocene–Early Pleistocene: Stratigraphic Implications. Moscow, Russia: Nauka.
- Sotnikova M (1994) The genus *Chasmaporthetes* Hay, 1921 from the Pliocene of Russia, Ukraine, Mongolia and Tadzhikistan. In: Tatarinov LP (Ed.) Palaeotheriology. Moscow, Russia: Nauka, Vol. 139, 113–139.
- 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.
- Tamvakis A, Savvidou A, Spassov N, Youlatos D, Merceron G, Kostopoulos DS (2023) New insights on Early Pleistocene *Nyctereutes* from the Balkans based on material from Dafnero-3 (Greece) and Varshets (Bulgaria). Palaeoworld 32(3): 555–572. <https://doi.org/10.1016/j.palwor.2022.09.006>
- Tedford RH, Qiu Z (1991) Pliocene *Nyctereutes* (Carnivora: Canidae) from Yushe, Shanxi, with comments on Chinese fossil racoon-dogs. Vertebrata Palasiatica 29(3): 176–189.
- Turner A (1990) The evolution of the guild of larger terrestrial carnivores during the Plio-Pleistocene in Africa. Geobios 23: 349–368. [https://doi.org/10.1016/0016-6995\(90\)80006-2](https://doi.org/10.1016/0016-6995(90)80006-2)
- Turner A, Antón M, Werdelin L (2008) Taxonomy and evolutionary patterns in the fossil Hyaenidae of Europe. Geobios 41(5): 677–687. <https://doi.org/10.1016/j.geobios.2008.01.001>
- Tseng ZJ, Li Q, Wang X (2013) A new cursorial hyena from Tibet, and analysis of biostratigraphy, paleozoogeography, and dental morphology of *Chasmaporthetes* (Mammalia, Carnivora). Journal of Vertebrate Paleontology 33(6): 1457–1471. <https://doi.org/10.1080/02724634.2013.775142>
- Vekua A (1972) Kvabebi Fauna of Akchagylian Vertebrates. Moscow, Russia.
- Vekua A, Lordkipanidze D, Agustí J, Oms O (2005) The Pliocene mammal site of Kvabebi (Eastern Georgia): new field-campaigns and age determination. Quaternary Science Reviews 28: 8450.
- Vinuesa V, Madurell-Malapeira J, Ansón M, Alba D (2014) New cranial remains of *Pliocrocuta perrieri* (Carnivora, Hyaenidae) from the Villafranchian of the Iberian Peninsula. Bollettino della Società Paleontologica Italiana 53(1): 39–47.
- Viret J (1954) Le lœss à bancs durcis de Saint-Vallier (Drôme), et sa faune de mammifères villafranchiens (avec une analyse granulométrique et une analyse pollinique). Nouvelle Archives du Muséum d'Histoire Naturelle de Lyon 4: 1–258. <https://doi.org/10.3406/mhnl.1954.986>
- Vislobokova I, Sotnikova M, Dodonov A (2001) Late Miocene – Pliocene mammalian faunas of Russia and neighbouring countries. Bollettino della Società Paleontologica Italiana 40(2): 307–313.
- Werdelin L, Solounias N (1991) The Hyaenidae: Taxonomy, systematics and evolution. Fossils and Strata 30: 1–104. <https://doi.org/10.18261/8200374815-1991-01>
- Werdelin L, Sanders WJ (2010) Cenozoic Mammals of Africa. In: Werdelin L, Sanders WJ (Eds) University of California Press. Berkeley, California, USA: University of California Press. <http://books.google.cz/books?id=vKlQQAACAAJ>
- Werdelin L, Solounias N (1996) The Evolutionary History of Hyaenas in Europe and Western Asia during the Miocene. In: Bernor RL, Fahlbusch V, Rietschel S (Eds) Later Neogene European biotic evolution and stratigraphic correlation. Columbia University Press, New York, 290–306.
- Wickham H, Chang W, Wickham MH (2016) Package ‘ggplot2’. Create elegant data visualisations using the grammar of graphics. Version 2: 1–189.

Supplementary material 1

Additional information

Authors: Saverio Bartolini-Lucenti, Joan Madurell-Malapeira, Adrian Marciszak, Marie Meyer, Damien Becker, Davit Vasilyan

Data type: docx

Copyright notice: This dataset is made available under the Open Database License (<http://opendatacommons.org/licenses/odbl/1.0>). The Open Database License (ODbL) is a license agreement intended to allow users to freely share, modify, and use this Dataset while maintaining this same freedom for others, provided that the original source and author(s) are credited.

Link: <https://doi.org/10.3897/sjp.145.180311.suppl1>