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https://doi.org/10.1007/s12542-025-00747-8

RESEARCH PAPER

First description of fossil remains of the giant mustelid *Eomellivora* (Mammalia, Carnivora) from the Late Miocene of the Shouyang Basin (China)

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Received: 16 January 2025 / Accepted: 1 August 2025

Abstract

We describe three unpublished *Eomellivora* cranial specimens from the Late Miocene (ca. MN12–13) sites of Ta Tung Kou and Nan Ho, both in the Shouyang Basin (Shanxi Province, China), uncovered by Frick collectors (reposited in the fossil mammal collections of the American Museum of Natural History) between 1933 and 1936. The specimens consist of a fragmented cranium (AMNH F:AM 50570), a maxilla (AMNH F:AM 50569), and a nearly complete cranium (AMNH F:AM 144525). By means of morphological comparison and multivariate analysis (PCA with Mosimann-transformed dentition variables), AMNH F:AM 50570 is identified as *E. wimani*, exhibiting a relative elongation of the premolars. This finding enhances the understanding of intraspecific variability within the species. Specimens AMNH F:AM 50569 and AMNH F:AM 144525 are classified conservatively as *Eomellivora* sp., as they lack diagnostic features at the species level. These new discoveries contribute to a deeper understanding of the Late Miocene fauna of the Shouyang Basin, an area that has been less extensively studied in China compared to the nearby Baode and Yushe Basins. In addition, a re-examination of the dental remains from the earlier sites of Zhupeng and Xiaohe (Yunnan Province, China, ca. MN11), which had previously been identified as *Eomellivora* cf. *wimani*, permits their reclassification as *Eomellivora* cf. *E. piveteaui*.

Keywords Neogene · Mustelidae · Mellivorinae · Eomellivorini

Introduction

The extinct mustelid *Eomellivora* Zdansky, 1924 was a large caniform species known from the Middle-Late Miocene boundary to the end of the Miocene as a member of the carnivoran guild of the '*Hipparion* fauna' of Eurasia and North America (e.g., Alba et al., 2022; Kargopoulos et al., 2022; Kretzoi, 1942; Lavrov & Gimranov, 2018; Orlov, 1948; Pia, 1939; Simionescu, 1938; Stock & Hall, 1933; Valenciano et al., 2015, 2017; Wolsan & Semenov, 1996; Zdansky, 1924). It pertains to the subfamily Mellivorinae, which currently comprises a single representative, the honey badger (*Mellivora capensis* Schreber, 1776). Within this subfamily, Valenciano and Govender (2020a) proposed the tribes Eomellivorini Zdansky, 1924, and Mellivorini Gray, 1865. Eomellivorini are entirely extinct, and the tribe includes the Miocene taxa *Eomellivora*, the giant African mustelid *Ekorus ekakeran* Werdelin, 2003, and the North American *Moralesictis intrepidus* Valenciano & Baskin, 2022. These species were comparable in size to wolves and leopards

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Communicated by Irina Ruf.

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and exhibited a combination of primitive and derived traits relative to other mustelids. Primitive features included the presence of p1 and m2 and an enlarged stylar area on M1 (except in *Ekorus*). Derived traits comprised multicuspid premolars and a reduced m1 talonid with a central hypoconid. Additionally, they display postcranial skeleton adaptations reflecting a cursorial lifestyle (Valenciano & Govender, 2020a; Werdelin, 2003). On the other hand, Mellivorini exhibits semifossorial adaptations and includes the extant *Mellivora* in addition to several small to medium-sized Miocene genera from Africa and Asia (e.g., *Howellictis* Bonis et al., 2009; *Erokomellivora* Werdelin, 2003, *Promellivora* Pilgrim, 1932).

Eomellivora was first described by Zdansky (1924) in central China based on a fragmented skull with an associated mandible from Shangyingou, Xin'an County (locality 12 in Zdansky, 1924, Henan Province), (lectotype), and another fragmented cranium from Liuwangou, Baode County (locality 31 in Zdansky, 1924), Shanxi Province. Since then, this giant-sized mustelid with robust dentition has been described from numerous Miocene sites in Eurasia and North America (see Wolsan & Semenov, 1996). In most cases, the remains are very fragmentary, consisting mainly of craniodental elements. However, there also have been some finds of very complete skeletons, such as those from the Spanish site of Batallones-3 (Late Miocene, MN10, Torrejón de Velasco, Madrid) (Valenciano et al., 2015).

Historically, the taxonomy of *Eomellivora* has been debated. Wolsan and Semenov (1996) proposed the existence of a single lineage of *Eomellivora* based on the large sample of specimens from the locality of Gritsev, MN9, Ukraine. They identified only one species, *Eomellivora wimani*, which they separated into two chronosubspecies: *Eomellivora wimani piveteaui* from the Vallesian (MN9–10) of Europe and *Eomellivora wimani wimani* from the Turolian and Ventian (MN11–13) of Eurasia and North America. Although this classification was accepted by subsequent workers (e.g., Koufos, 2012; Morlo, 1997; Qiu, 2003; Werdelin, 2003), the initial description of the Gritsev fossils was not published accurately. The authors observed remarkably high intraspecific variability among Gritsev specimens, overlapping with other previously described species of the genus. However, their publication lacked images and precise measurements of the material from Gritsev. Consequently, the hypothesis of a single species could not be tested by others (Valenciano et al., 2015). Two decades later, Valenciano et al., (2015, 2017) and Alba et al. (2022) proposed the existence of at least six distinct Miocene *Eomellivora* species: *Eomellivora moralesi* Alba et al., 2022 (MN7/8), *Eomellivora fricki* (Pia, 1939) (MN9), *Eomellivora piveteaui* Ozansoy, 1965 (MN9–10), *Eomellivora ursogulo* (Orlov, 1948) (MN11–13), *E. wimani* Zdansky, 1924 (MN12–13), and *Eomellivora hungarica* Kretzoi, 1942 (MN13). This hypothesis remains the most widely accepted (e.g., Alba et al., 2022; Jiangzuo et al., 2023a; Kargopoulos et al., 2022; Lavrov & Gimranov, 2018; Spassov et al., 2018). Thus, the origin of the genus can be traced back to *E. moralesi*, which is the oldest, phylogenetically most basal, and anatomically most primitive species. *Eomellivora moralesi* was originally described from the Aragonian of Can Mata, Catalonia, Spain (11.21 Ma, MN7/8), and has recently been found in Hammerschmiede, Germany (11.62 Ma, MN7/8; Kargopoulos et al., 2022).

The fossil record of *Eomellivora* from China is limited compared to the rest of Eurasia. Since the initial description of *E. wimani* based on fossils from Shangyingou and Liuwangou (Zdansky, 1924), only a few additional specimens have been published or illustrated. These include specimens from Zhupeng (ca. MN11) in Yunnan Province, attributed to *E.* cf. *wimani* (Zong, 1997; Zong & Jiang, 1991), and from the Qingbushan Fauna, Linxia Basin (ca. MN12–13) in Gansu Province, assigned to *E. wimani* (Jiangzuo et al., 2023a). Additionally, this genus has been cited, but not described in the faunal lists, from the Late Miocene sites of Shihuiba, Yunnan Province (Qi, 1985; Qiu & Qiu, 1995) and Daijagou, Shanxi Province (Qiu & Qiu, 1995). Therefore, the description of the unpublished fossils from China studied in this paper, one hundred years after the first publication of *Eomellivora*, aims to shed light on the diversity of this giant mustelid in Asia.

Geological and geographical setting

The new *Eomellivora* specimens come from two different fossil sites and expeditions funded by Childs Frick which were later donated to and reposited in the fossil mammal collections of the American Museum of Natural History (AMNH). AMNH F:AM 50570 was uncovered in 1933 at the Ta Tung Kou site in Shouyang County, eastern Shanxi Province, China. AMNH F:AM 50569 and AMNH F:AM 144525 were found in 1936 at the Nan Ho site, next to the Pai Tao Tsun site, 17 miles west of Shouyang City in the same county and province as the Ta Tung Kou site (Fig. 1) (Tseng & Wang, 2007). Shanxi Province is traditionally known for the abundance of so-called 'Dragon Bones' in the area (Qiu & Tedford, 2013). The Shouyang Basin, to which these deposits belong, is dated to the Late Miocene-Early Pliocene and overlaps temporally with the deposits of the Baode and Yushe Basins (200 km to the northwest and 90 km to the south, respectively, both in Shanxi Province). These basins have been the subject of more detailed study, and their stratigraphic sequences have been used to define the Baodean and Yushean Asian land mammal 'ages', which correspond to the European Turolian and Ruscinian-Villafranchian (e.g., Qiu & Qiu, 1995; Qiu et al., 2013; Tseng & Wang, 2007). The Baodean encompasses five individually

Fig. 1 Map of East Asia showing the localities where *Eomellivora* remains have been identified. The stars represent the localities of the fossils studied in this paper (Shouyang County, Shanxi Province), the blue star being Ta Tung Kou (AMNH F:AM 50570) and the red star being Nan Ho (AMNH F:AM 50569 and AMNH F:AM 144525), near the better-known locality of Pai Tao Tsun. The triangles represent the other localities where *Eomellivora* has been found and described: orange, Shangyingou (locality 12 in Zdansky, 1924, type locality of *E. wimani*; Xin'an County, Henan Province); green, Liuwangou (locality 31 in Zdansky, 1924; Baode County, Shanxi Province); light blue, Qingbushan, Hezheng County, Gansu Province (Jiangzuo et al., 2023a); pink, Zhupeng and Xiaohe, Yuanmou County, Yunnan Province (Dong et al., 2003; Zong, 1997; Zong & Jiang, 1991)

diachronous faunas, extending from the Tsaidam Basin in Qinghai Province to the Ertemte Basin in Inner Mongolia, both located in China (Qiu & Qiu, 1995).

During this time, the tectonic uplift of the Tibetan Plateau resulted in the aridification of the broader region, relegating forests to the eastern part of the country. However, increased wetting in northeast Asia in the Late Miocene led to an expansion of the forest area of the continent, facilitating faunal exchange between Asia and North America (Deng et al., 2023; Jiangzuo & Wang, 2023; Jiangzuo et al., 2023b).

The fauna associated with Ta Tung Kou and Nan Ho sites is not well-documented and there is a paucity of published material from them. The Ta Tung Kou site, as proposed by Tseng and Wang (2007), would include the hyaenid *Hyaenictitherium hyaenoides* Zdansky, 1924, and the unpublished material also would include the fox *Vulpes* Frisch, 1775, the rhinocerotid *Chilotherium* Ringström, 1924 and the giraffid *Samotherium* Forsyth-Major, 1888 (X. Wang, pers. comm.). The Nan Ho site, according to Tseng and Wang (2007) and Wang and Qiu (2004), includes the hyaenids *H. hyaenoides* and *Hyaenictitherium wongii* (Zdansky, 1924) and the skunk *Promephitis hootoni* Şenyürek, 1954. Those species suggest the dating of these sites as Late Baodean, which is equivalent to the European MN12–13 zones (Late Turolian), between 8–5.3 Ma (Qiu et al., 2013; Tseng & Wang, 2007). This biochronology allows us to estimate the age of the Ta Tung Kou and Nan Ho sites to be within the MN12 biozone, with a possibility of extending into the beginning of MN13 (Tseng & Wang, 2007).

Material and methods

Studied material

The fossil of *Eomellivora* here described are reposited in the fossil mammal collections of the Division of Paleontology at the American Museum of Natural History (AMNH), New York, USA: AMNH F:AM 50570, rostral fragment of a cranium with left I1, C, P1–4 and M1 and right P2–4 and M1 from Ta Tung Kou, Shanxi Province, China; AMNH F:AM 50569, fragment of right maxilla with I1–3, C, P1–4 and M1 from the Nan Ho site, Shanxi Province, China; AMNH F:AM 144525, cranium with left I1–3 and P4 and right I1–3 and P1–3 from the Nan Ho site, Shanxi Province, China. For comparison, we studied all *Eomellivora* species known to date. The comparative sample comprises original fossils of: *E. moralesi* from Abocador de Can Mata (MN7/8, Spain) (Alba et al., 2022), housed at ICP; *E. fricki* from Wien XII-Altmannsdorf (MN9, Austria) (Pia, 1939; Valenciano et al., 2017), housed at NHMW, Los Valles de Fuentidueña (MN9, Spain) (Alba et al., 2022; Crusafont-Pairó & Ginsburg, 1973), housed at ICP, and Can Llobateres (MN9, Spain) (Crusafont-Pairó, 1972; Valenciano et al., 2019), housed at ICP; *E. piveteaui* from Batallones-3 (MN10, Spain) (Valenciano et al., 2015) housed at MNCN; *E. wimani* from Shangyingou (MN12–13, China) (Zdansky, 1924) and from Liuwangou (MN12–13, China) (Zdansky, 1924), housed at PMU, Kern River Formation site 50 (MN12–13, California, USA) (Stock & Hall, 1933) housed at LACM; and *E.* cf. *wimani* from Zhupeng and Xiaohe (MN11, China) (Zong, 1997) housed at IVPP. In addition, we examined photographs of the originals of *E. piveteaui* from Yassiören (MN9, Turkey) (Ozansoy, 1965), housed at MNHN, and from Kalfa (MN9, Moldova) (Lungu, 1978), housed at UST; *E. ursogulo* from Grebeniki (MN11, Ukraine) (Orlov, 1948), housed at PIN (as well as a cast of this specimen in the fossil mammal collections at AMNH); and *E. hungarica* from Polgárdi 2 (MN13, Hungary) (Kretzoi, 1942), housed at MFGI. Finally, we studied by their original publications: *E. ursogulo* from Taralik-Cher (MN12–13, Russia) (Lavrov & Gimranov, 2018); *E. wimani* from Cimişlia (MN12, Moldova) (Simionescu, 1938), and Pannonhalma 2 (= Györszentmárton 2)

(MN12, Hungary) (Kretzoi, 1965); *E.* cf. *E. wimani* from Karaslari (MN12, North Macedonia) (Spassov et al., 2018); and *Eomellivora* sp. from Gritsev (MN9, Ukraine) (Wolsan & Semenov, 1996), and Csákvár (MN11, Hungary) (Kretzoi, 1942).

Nomenclature and measurements

Dental nomenclature follows Ginsburg (1999) and Smith and Dodson (2003). Anatomical descriptions are based primarily on Waibl et al. (2005) and Evans and Lahunta (2010, 2013). Measurements were taken to the nearest 0.1 mm using a Mitutoyo Absolute digital calliper (Fig. 2).

Abbreviations

Institutional Abbreviations: AMNH: American Museum of Natural History, New York, USA; **AMNH F:AM**: Frick Collection (Fossil Mammals), Division of Paleontology, AMNH, New York, USA; **BSPM**: Bayerische Staatssammlung für Paläontologie und Historische Geologie, Munich, Germany; **ICP**: Institut Català de Paleontologia Miquel Crusafont, Universitat Autònoma de Barcelona, Spain; **IPS**: collections from the ICP (formerly 'Institut de Paleontologia de Sabadell'); **IVPP**: Institute of Vertebrate Paleontology and Paleoanthropology, Chinese Academy of Sciences, Beijing, China; **LACM**: Department of Vertebrate Palaeontology, Natural History Museum of Los Angeles County, Los Angeles, USA; **LGPUT**: Laboratory of Geology and Palaeontology, University of Thessaloniki, Greece; **MFGI**: Geological and Geophysical Institute of Hungary, Budapest, Hungary; **MNCN**: Museo Nacional de Ciencias Naturales-CSIC, Madrid, Spain; **MNHN**: Muséum national d'Histoire naturelle, París, France; **NHMW**: Naturhistorisches Museum Wien, Vienna, Austria; **NRM**: Naturhistoriska rikmuseet, Stockholm, Sweden; **PIN**: Paleontological Institute, Russian Academy of Sciences, Moscow, Russia; **PMU**: Museum of Evolution (formerly 'Palaeontological Museum'), University of Uppsala, Uppsala, Sweden; **SAM-ZM**: Iziko South African Museum, Cape Town, South Africa; **USNM**: Smithsonian National Museum of Natural History, Washington, D.C., USA; **UST**: Universitatea de Stat din Tiraspol, Chisinau, Moldova.

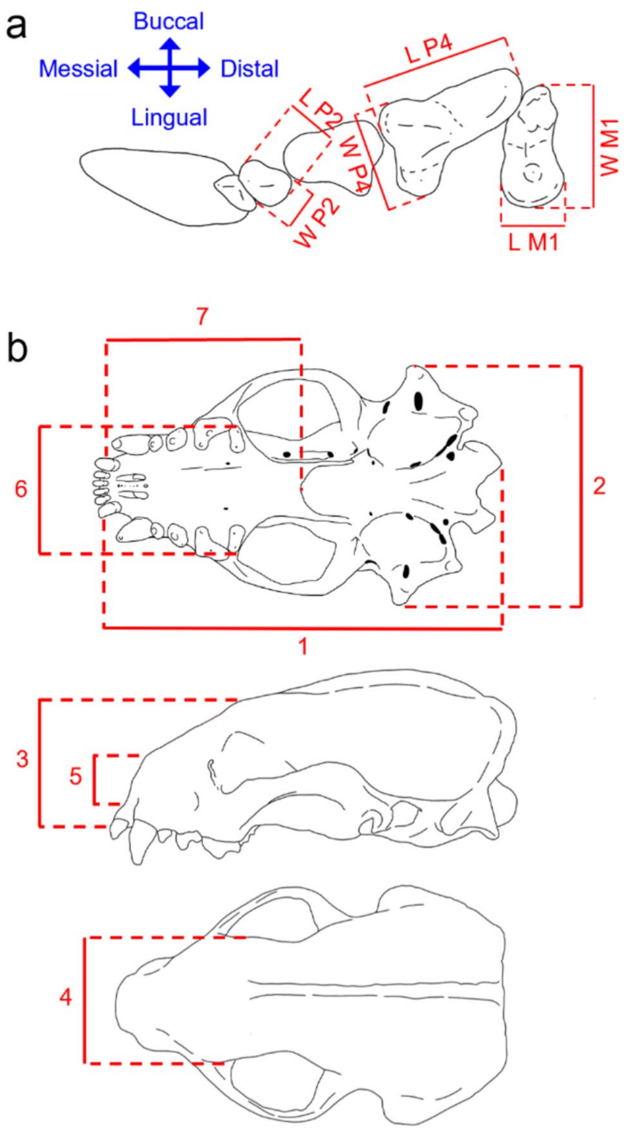

Fig. 2 Schematic drawings of the measurements taken for this work. **a** Dentition of *Eomellivora* AMNH F:AM 50570 in occlusal view showing the measurements of maximum length (L) and maximum width (W) of the upper dentition; **b** skull of *Mellivora capensis* showing cranial measurements: 1. condyle-basal length; 2. width between the mastoid processes; 3. height of the cranium between the maxilla and the frontal bones; 4. maximum width between the zygomatic postorbital processes; 5. height of the nostrils; 6. maximum width of the maxilla between M1's (including alveoli); 7. length of the maxilla

Multivariate analysis

We performed a principal component analysis (PCA) to aid in the classification of the most complete specimen of *Eomellivora* (AMNH F:AM 50570) comparing it with extinct and extant genera of mustelids. For this purpose, eight linear measurements of the upper dentition (maximum length and width of P2, P3, P4 and M1) were used from that specimen and comparator information from our own database. These linear measurements were then transformed from their geometric mean according to Mosimann (1970), which reduces allometry caused by size difference (e.g., Cuccu et al., 2023; Ercoli et al., 2019; Morales & Giannini, 2021; Mosimann, 1970; Rabe et al., 2022; Smart & Sakamoto, 2024). This type of analysis from transformed measurements has been demonstrated to be effective in improving the taxonomic determination of fossil remains (e.g., Cuccu et al., 2023; Ercoli et al., 2019; Smart & Sakamoto, 2024; Valenciano & Baskin, 2022).

The sample used in this PCA consists of 76 mustelids (55 extant and 21 extinct) corresponding to: *Moralesictis intrepidus* (1 specimen; Valenciano & Baskin, 2022), *Eomellivora wimani* (2 specimens; Zdansky, 1924), *Eomellivora piveteaui* (2 specimens; Valenciano et al., 2015), *Eomellivora ursogulo* (1 specimen; Orlov, 1948), *Eomellivora moralesi* (1 specimen; Alba et al., 2022), *Eomellivora* AMNH F: AM 50570 (1 specimen), *Ekorus ekakeran* (1 specimen; Werdelin, 2003), *Plesiogulo lindsayi* Harrison, 1981 (1 specimen; Harrison, 1981), *Plesiogulo crassa* Teilhard de Chardin & Leroy, 1945 (5 specimens; Koufos, 2006; Zdansky, 1924), *Plesiogulo marshalli* (Martin, 1928) (3 specimens; Harrison, 1981), *Sthenictis* sp. (1 specimen: AMNH F:AM 25134), *Ischyrictis zibethoides* (Blainville, 1842) (1 specimen; Peigné, 2012), *Hoplictis anatolicus* (Schmidt-Kittler, 1976) (1 specimen; Schmidt-Kittler, 1976), *Mellivora capensis* (17 specimens), *Gulo gulo* Linnaeus, 1758 (20 specimens) and *Martes foina* Erxleben, 1777 (18 specimens). These specimens are in the collections of the following museums and institutions: AMNH, PIN, NRM, USNM, USNM, ZM, MNCN, ICP, PMU, LGPUT, MNHN and BSPM. The PCA and the scatter plots were performed using the paleontological statistics software package PAST 4.17 (Hammer et al., 2001).

Systematic Paleontology

Order **Carnivora** Bowdich, 1821
Suborder **Caniformia** Kretzoi, 1943
Family **Mustelidae** Batsch, 1788
Subfamily **Mellivorinae** Gray, 1865
Tribe **Eomellivorini** Zdansky, 1924

Genus ***Eomellivora*** Zdansky, 1924

Eomellivora wimani Zdansky, 1924
Figure 3, Table 1

Diagnosis. In Zdansky (1924) and Wolsan and Semenov (1996) (for *E. wimani wimani*).

Emended diagnosis. *Eomellivora* of large size, with a prominent forehead and short muzzle; P1–P2 with distal area buccolingually enlarged; P2 with a triangular occlusal morphology, a single cusp in mesial position, and with a marked concavity in the buccal wall; P2–P4 with strong cingula; P3 with one mesial and distal accessory cusps; P4 with two well-marked buccal concavities, one at the paracone level and a secondary one in the metastyle distal to the paracone-metastyle border; M1 with vestigial metacone, and centrally positioned conical protocone surrounded by an circular lingual platform that completely enclosed it; p1–p3 distally broadened; p3–p4 with marked lingual expansion (less marked in the p3 than in *E. ursogulo*); p4 with well-developed mesial accessory cuspid; m1 trigonid mesiodistally enlarged, especially the paraconid, and talonid relatively reduced in width with a more isolated central hypoconid.

Lectotype. PMU-21824 (formerly PMU-M3692, Ex. 1), fragment of skull with complete dentition, and a fragmentary mandible (formerly PMU-M3693, Ex. 1) with complete dentition except for the right m2.

Type locality. Shangyingou (Henan province, China, MN12–13), also known as locality 12 (Zdansky, 1924).

Other localities. Liuwangou (Shanxi province, China, MN12–13), also known as locality 31 (Zdansky, 1924); Kern River Formation site 50 (California, USA, MN12–13) (Stock & Hall, 1933); Cimişlia (Moldova, MN12) (Simionescu, 1938); Pannonhalma 2 (= Györszentmárton 2) (Hungary, MN12) (Kretzoi, 1965); Novaya Emetovka (Ukraine, MN12) (Orlov, 1948).

Temporal distribution. ca. 7.2–5.23 Ma, MN12-13, Late Miocene (Valenciano et al., 2015).

New material. AMNH F:AM 50570, rostral fragment of a cranium with left I1, C, P1–4 and M1, and right P2–4 and M1 from the Ta Tung Kou site, near Shouyang, Shanxi Province, China, Turolian, ca. MN12–13.

Description. AMNH F:AM 50570 is an anterior fragment of a very-well preserved cranium with minimal deformation (Fig. 3). The nasal, frontal, and part of the palatine bones (including a portion of the hamulus processes) are present. The interior of the cranium is filled with hardened clay sediment, as seen in the nasal cavity and the endocranium. In general, the cranium has a robust appearance, with a prominent forehead and short muzzle, with dorsoventrally developed maxilla and nasal bones, and with a large nasal aperture that is slightly inclined caudally. The frontal bone is broad and possesses postorbital processes. The infraorbital foramen has a large opening and lies above the parastyle of P4. The anterior margin of the orbits is at the same dorsoventral level with the paracone of P4. The zygomatic arches are fragmented, with only the anterior part preserved to the frontal process of the zygomatic bone, although their robust appearance, thickened dorsoventrally, is clear.

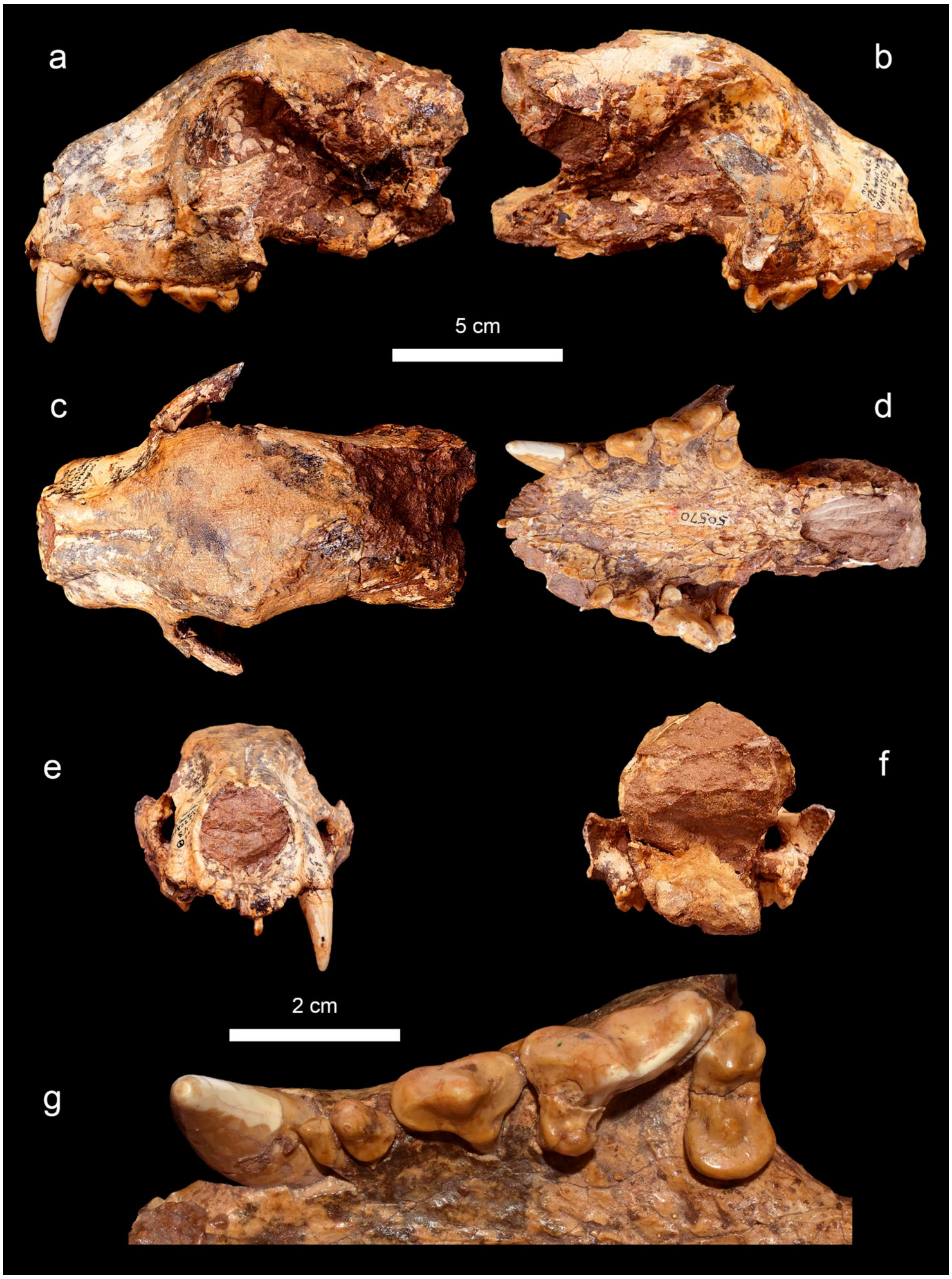

Fig. 3 Cranium of *Eomellivora wimani,* AMNH F:AM 50570, from the Ta Tung Kou site (Shouyang County, Shanxi Province, China): **a** left lateral view; **b** right lateral view; **c** dorsal view; **d** ventral view; **e** rostral view; **f** caudal view; **g** detail view of left dentition; **a–f** share the same 5 cm scale; **g** is a 2 cm scale

Table 1 Maximum length (L) and maximum width (W) (in mm) of the upper dentition of the specimens of *Eomellivora* described in this paper (measurements as in Fig. 2a)

Specimen	I1		I2		I3		C		P1		P2		P3		P4		M1	
	L	W	L	W	L	W	L	W	L	W	L	W	L	W	L	W	L	W
AMNH FM:50569	4.0	2.6	4.8	3.2	8.0	5.2	10.1	9.0	3.4	4.2	6.4	6.0	11.7	8.6	19.9	12.9	–	–
AMNH FM:50570 (left)	4.8	2.7	–	–	–	–	13.5	11.1	3.6	5.5	8.1	6.2	15.5	10.5	23.1	15.6	11.2	20.4
AMNH FM:50570 (right)	–	–	–	–	–	–	–	–	–	–	8.1	6.2	15.3	10.4	23.4	16.5	–	–
AMNH FM:144525 (left)	–	–	–	–	9.0	6.2	–	–	–	–	–	–	–	–	(19.0)	(14.7)	–	(21.9)
AMNH FM:144525 (right)	–	–	–	–	9.2	5.6	(11.9)	(9.9)	–	–	9.1	5.8	14.6	10.0	–	–	–	–

Measurements in parentheses are approximate, as they were taken between the alveoli or from fragmented pieces

Regarding the dentition, the right side preserves P2, P3, P4 with fragmented protocone, and fragmented M1 without the lingual platform. The left side preserves I1, C, P1, P2, P3, P4, and M1, all in good condition. I1 is small, elongated and lingually expanded at its base. The C is large, separated from the alveolus of I3 by a diastema, has a marked distal ridge, is oval in section, and is slightly compressed laterally. All premolars and M1 have a robust and thickened cingulum. P1 is smaller than the rest of the premolars, broad in appearance, and buccolingually rotated. P2 has a triangular occlusal morphology, a single cusp in mesial position, and a marked concavity in the buccal wall, and also is buccolingually rotated. P3 is a robust tooth, with three roots, almost triangular in occlusal view, with a well-marked lingual expansion; it has a poorly developed mesial and distal accessory cusp, and a marked concavity in the buccal wall. P4 also is robust, with a hemispherical protocone distally located in line with a strong cingulum at the parastyle area; there are two buccal concavities, one at the paracone level and a secondary one in the metastyle, as well as a strong basal cingulum surrounding the whole tooth. The M1 is robust, with a large parastylar area, a reduced metacone, and a widely extended oval-shaped lingual platform surrounding the cone-shaped protocone, centred in the middle of the talon and connected to the paracone by a faint ridge.

Eomellivora sp.
Figures 4, 5, Table 1, 3

New material. AMNH F:AM 50569, fragment of right maxilla with I1–3, C, P1–4 and M1 from the Nan Ho site, near the Pai Tao Tsun site, near Shouyang, Shanxi Province, China, Turolian, ca. MN12–13; AMNH F:AM 144525, cranium with left I1–3 and P4 and right I1–3 and P1–3 also from the Nan Ho site.

Description. AMNH F:AM 50569, a fragment of a right maxilla, preserves I1, I2, I3, C, P1, P2, P3, P4, and a fragmented M1 (Fig. 4). I1and I2 are of similar size and morphology, elongated and lingually expanded at their base. I3 is larger, caniniform, surrounded by a well-marked cingulum, and its cusp is worn. The C is large, with a very pronounced distal ridge, oval in cross-section, and slightly compressed laterally; it is separated from I3 by a diastema. Both the upper premolars (P1-P4) and the M1 have a very robust cingulum. P1 is smaller than the rest of the premolars, broad in appearance, and buccolingually rotated relative to the main tooth row line. P2 is unicuspid and has a triangular occlusal morphology, with a convex margin on the buccal wall and buccolingually rotated. The P2 cusp is mesially located, providing a hooked appearance, and is surrounded by a marked cingulum. P3 is a very robust tooth, almost triangular in occlusal view. It has a very pronounced lingual expansion with a third root underneath, and possesses mesial and distal accessory cusps and a straight buccal margin. P4 is robust, with a conical protocone in line with the parastyle area. There is a marked concavity in the buccal wall between the paracone and the metastyle, with a strong basal cingulum surrounding the entire tooth. M1 retains the parastylar area, a reduced metacone in relation to the paracone, and an oval lingual platform surrounding the protocone, which is conical in shape and in a central position; part of this lingual platform is broken at the mesial margin.

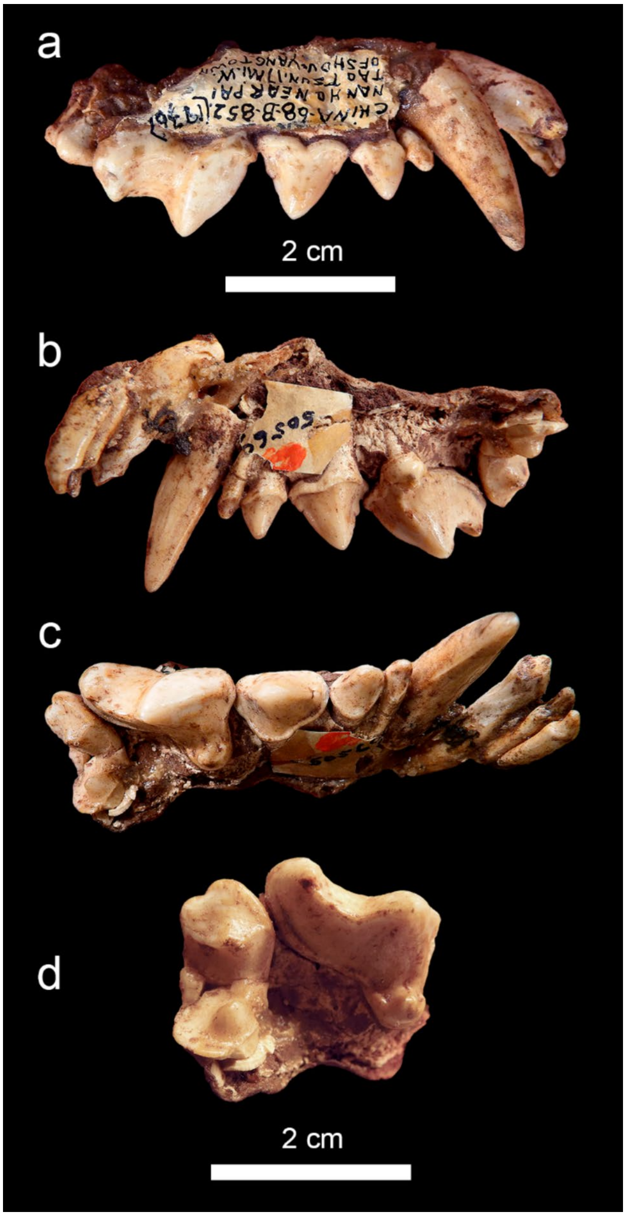

Fig. 4 Maxilla of *Eomellivora* sp., AMNH F:AM 50569, from the Nan Ho site, near the Pai Tao Tsun site (Shouyang County, Shanxi Province, China): **a** buccal view; **b** lingual view; **c** occlusal view; **d** detail of P4 and M1 in lingual-occlusal view; **a–c** share the same 2 cm scale

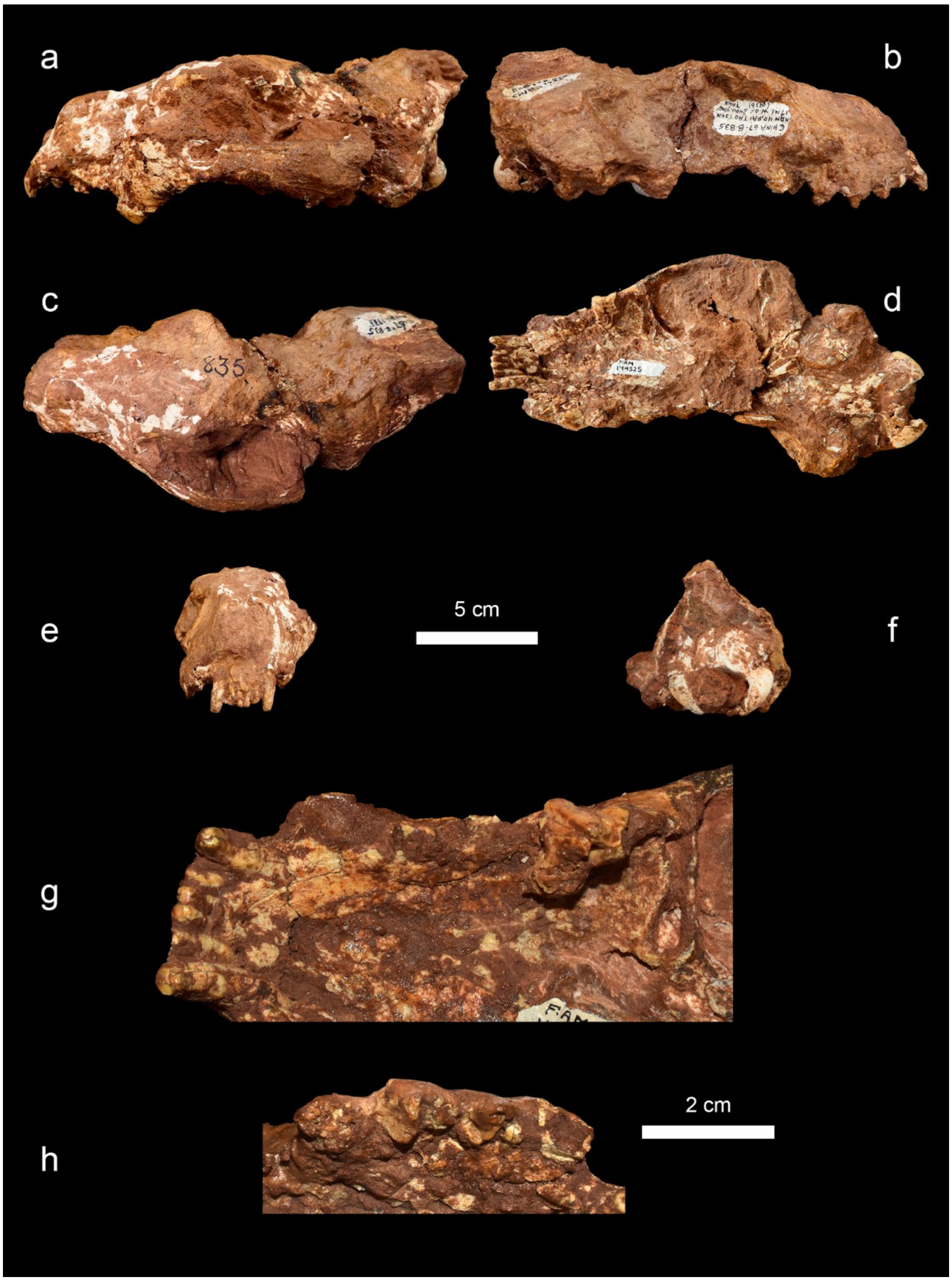

Fig. 5 Cranium of *Eomellivora* sp., AMNH F:AM 144525, from the Nan Ho site, near the Pai Tao Tsun site (Shouyang County, Shanxi Province, China): **a** left lateral view; **b** right lateral view; **c** dorsal view; **d** ventral view; **e** rostral view; **f** caudal view; **g** detail of the left dentition in occlusal view; **h** detail of the right dentition in occlusal view. **a–f** share the same 5 cm scale; **g** and **h** share the same 2 cm scale

AMNH F:AM 144525, a nearly complete cranium except for the missing right zygomatic arch and part of the right maxilla, remains partially embedded in a very hard red clay matrix (Fig. 5). It preserves all the incisors and parts of the right premolars, as well as the mesial part of the left P4. As in other mustelids, the splanchnocranium is relatively short, exhibiting a somewhat prominent forehead and a short muzzle, with a nasal aperture that is partially inclined, while the neurocranium is elongated and low. The frontal bone is broad and becomes flat above the orbit, showing the postorbital processes. There is a well-developed sagittal crest, broken at the anterior level of the parietal bone, and its continuation in the nuchal crests is inferred. A complete left zygomatic arch is preserved; it is robust and dorsoventrally developed, especially in its distal part. The cranium preserves the globular tympanic bullae, as well as both occipital condyles. The left mastoid process projects laterally. The paraoccipital processess are not observed. The entire row of incisors is relatively well preserved, whereas the rest of the dentition is either very fragmented or missing, hampering a detailed description. The incisors are arranged in a straight line, with I1 and I2 of similar size. I3 is larger, caniniform, and protrudes into the row of incisors. On the right side P1-3 are very fragmented and surrounded by sediment;

the morphology of P3 is better distinguished, being triangular in occlusal view, with a very marked lingual expansion. It has mesial and distal accessory cusps surrounded by a well-defined cingulum. On the left side, the P4 is very fragmented, preserving only the paracone and the base of the protocone, which is located mesially and in line with the parastylar area. A left M1 alveolus is present.

Discussion

Several forms of giant musteloids, such as the mustelids *Eomellivora*, *Plesiogulo* Zdansky, 1924, and *Siamogale* Ginsburg et al., 1983, as well as the ailurid *Simocyon* Wagner, 1858, occurred during the Late Miocene of China (e.g., Ginsburg et al., 1983; Grohé et al., 2020; Koufos, 2006; Peigné et al., 2005; Teilhard de Chardin & Leroy, 1945; Valenciano & Govender, 2020b; Valenciano et al., 2015; Wang, 1997; Wang et al., 2017; Zdansky, 1924). *Siamogale melilutra* is a large bunodont otter in the subfamily Lutrinae, and is found at the Shuitangba and Dapinggou sites (Wang et al., 2017). Its dentition differs significantly from AMNH F:AM 50570. *Siamogale melilutra* presents a much shorter and more robust snout, P1 absent, a much shorter P4 with a more developed protocone (giving it the shape of an equilateral triangle in occlusal view), a subquadrangular M1 with a highly developed metacone and metaconule, and a greatly expanded lingual platform (Wang et al., 2017). Therefore, *Siamogale* is excluded as a potential taxon to which these fossils can be attributed. With regard to *Plesiogulo*, it is a member of the subfamily Guloninae (comprising extant wolverines and martens) (Harrison, 1981; Valenciano et al., 2020; Zdansky, 1924). This genus is relatively common in the Upper Miocene deposits of China (Kaakinen et al., 2013; Teilhard de Chardin & Leroy, 1945; Wang et al., 2013; Woodburne et al., 2013; Zdansky, 1924). The robust dentition and its M1 morphology, characterised by the typical mustelid ‘8’ shape (with a mesiodistal narrowing at the midpoint of the tooth), show a closer resemblance to AMNH F:AM 50570 than the previously discussed genera. However, *Plesiogulo* also exhibits numerous differences from the new material described herein, including an oval-shaped P3 that lacks lingual widening, the absence of accessory cusps, a more robust P4 (paracone and metastyle) with a rounded protocone that is expanded linguodistally, and an M1 with a metacone thickened by a cingulum, presence of a metaconule, and possessing a highly enlarged and distally projected lingual platform (Harrison, 1981; Koufos, 2006; Teilhard de Chardin & Leroy, 1945; Valenciano & Govender, 2020b; Valenciano et al., 2020; Zdansky, 1924). These pronounced disparities exclude the possibility that these newly described Chinese specimens can be assigned to *Plesiogulo*.

The three new fossils share notable traits with *Eomellivora* such as the presence of a P1, P3 thickened distally with one or two distal accessory cusps, and P4 including a subconical protocone located in line with the parastyle area, and with a concavity in the buccal wall between the paracone and the metastyle. M1 further similarly exhibits an expanded stylar area, a prominent metacone in the more primitive species or a markedly smaller (inferred to be reduced) one in the more derived species, accompanied by a moderate mesial and distal expansion of the talon. These characters have been included in the amended diagnoses of Alba et al. (2022) and Valenciano et al. (2017), allowing these specimens to be unequivocally assigned to *Eomellivora*.

To aid in determining the taxonomic placement of AMNH F:AM 50570, the most complete of the three specimens, we performed a multivariate analysis (PCA). Figure 6 shows that the upper dentition clearly distinguishes among extant and extinct mustelids analysed at the genera level. When we plotted the scores of PC1 against PC2 (together explaining 82.01% of the variance) (Fig. 6a, Table 2), all genera are separated, forming distinct and non-overlapping morphospaces. More positive PC1 axis loading values differentiate specimens according to P4 length, whereas more negative values separate specimens according to M1 length (dependent on lingual platform size). Thus, the Guloninae taxa *Ma. foina* and *Plesiogulo* spp. are distributed on the left and the Guloninae species *G. gulo* and the Eomellivorini species *Ek. ekakeran* on the right, with all *Eomellivora* species situated somewhere in between those end members. As for the PC2 axis loading values, the most positive ones again separate the specimens according to the length of P4, while the most negative ones separate the specimens according to the widths of both P3 and P4. This splits all the *Eomellivora* species analysed, together with the *M. capensis* specimens, from the rest of the taxa. When PC1 and PC3 are considered (Fig. 6b, Table 2; together accounting for 56.72% of the variance), the separation of taxa is similar. The most positive loading values on the PC3 axis separate specimens according to the width of M1, whereas the most negative values do so according to the length of P2. Overall, AMNH F:AM 50570 is located close to the most complete specimens of *E. wimani* from China—the lectotype PMU-21824 (Fig. 7f) from the Shangyingou (locality 12) and the specimen PMU-21825 (Fig. 7g) from the Liuwangou (locality 31) (Zdansky, 1924)—and to *E. piveteaui* from Spain (Valenciano et al., 2015). However, it is closer to the latter species, specifically to the specimen Bat-3´13.185, characterized by slender premolars.

Morphologically, AMNH F:AM 50570 is most similar to *E. wimani* (see Figs. 7f–j), exhibiting a markedly high nasal and a relatively high frontal bones. AMNH F:AM 50570, PMU-21824 and PMU-21825 also share pronounced concavities in the buccal wall of P2–P4, P2 distally widened,

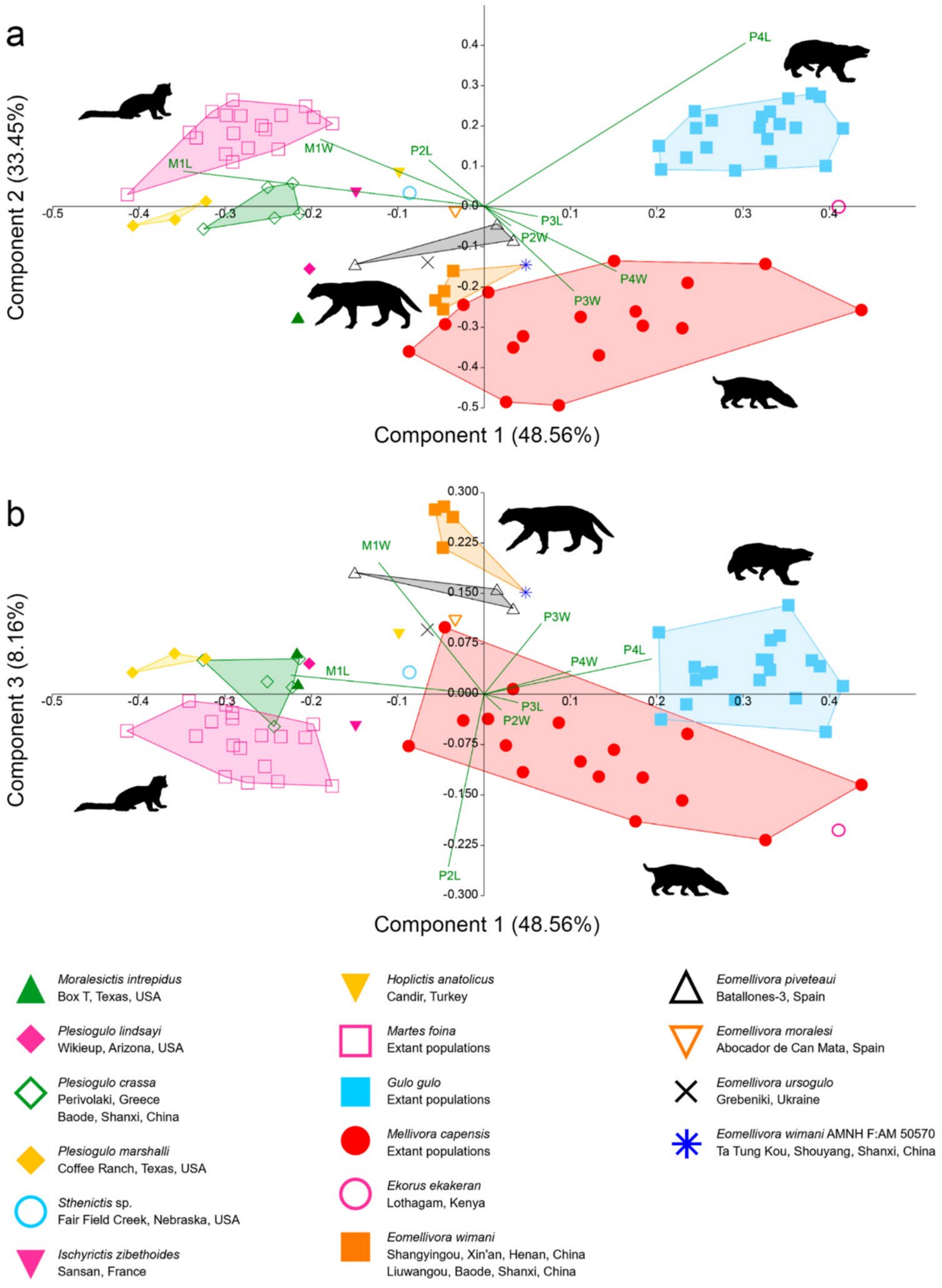

Fig. 6 Principal component analysis (PCA) of the 8 selected dental measurements (width and length of P2-M1), transformed according to the methods of Mosimann (1970), of various extinct and extant mustelid species. **a** plot of components 1 and 2, whose sum explains 82.01% of the variance; **b** plot of components 1 and 3, whose sum explains 56.72% of the variance. Silhouettes from PhyloPic (http://phylopic.org)

P3 with mesial and distal accessory cusps, and M1 with a reduced metacone relative to the paracone and a rounded lingual platform completely surrounding the centrally positioned cuspid-like protocone. In addition, AMNH F:AM 50570 shows proportions of the C and M1 resembling *E. wimani* (Fig. 8d) (Kretzoi, 1965; Simionescu, 1938; Stock & Hall, 1933; Zdansky, 1924). However, AMNH F:AM 50570 shows some qualitative morphological and metric differences, such as the greater relative length of the premolars (P2–P4; Fig. 6), especially in the relatively longer metastyle of P4, less developed accessory cusps of P3, and a simplified M1 without a thickening in the metaconule area (thickening visible in PMU-21825; Fig. 7g). The overall appearance of the M1 of AMNH F:AM 50570, including the degree of development of the metacone, is much more similar to that of the *E. wimani* lectotype PMU-21824 (Fig. 7f). This feature indicates that the M1 of *E. wimani* is a tooth that shows some intraspecific variability, as can be seen in comparisons to the specimen LACM CIT 1210 from Kern River, California, USA (Stock & Hall, 1933), whose metacones are greatly reduced relative to other specimens of this species (Fig. 7h–j).

Table 2 Eigenvalues, % variance and factor loadings for each dental measure analysed for the first four principal components of the PCA

	PC 1	PC 2	PC 3	PC 4
Eigenvalue	0.06	0.04	0.01	0.01
% variance	48.56	33.45	8.16	5.67
P2L	-0.1183	0.2124	-0.7380	0.2523
P2W	0.0572	-0.0886	-0.0676	-0.0774
P3L	0.1144	-0.0457	-0.0367	0.4238
P3W	0.1915	-0.3875	0.3031	0.0988
P4L	0.5589	0.7492	0.1505	-0.2337
P4W	0.2895	-0.3351	0.0995	-0.3319
M1L	-0.6433	0.1616	0.0812	-0.5726
M1W	-0.3508	0.3083	0.5644	0.4984

With regard to the Eurasian *Eomellivora piveteaui* (Fig. 7c–d) (MN9–10) (Lungu, 1978; Ozansoy, 1965; Tobien, 1955; Valenciano et al., 2015; Wolsan & Semenov, 1996), morphological differences preclude assignment of AMNH F:AM 50570 to this species (Figs. 7, 8). *E. piveteaui* is characterized by a more slender P2 with a poorly developed lingual cingulum, a shorter and more slender P3 with a poorly developed mesial accessory cusp, and a more slender P4 with a less pronounced buccal wall concavity. Additionally, its M1 is typically shorter mesiodistally—though similar in buccolingual width—features a more well-developed metacone, and has a more slender, mesially displaced, and non-centrally positioned protocone (Lungu, 1978; Ozansoy, 1965; Tobien, 1955; Valenciano et al., 2015). Although AMNH F:AM 50570 falls near one end of the dental metric range observed for *E. piveteaui* from Batallones-3 (Valenciano et al., 2015), particularly in the relatively slender P2 and P3, and the less enlarged M1 platform (Figs. 6, 8), its overall morphology more closely aligns with that of *E. wimani*, as previously discussed.

Notable differences are evident when AMNH F:AM 50570 is compared to the older, more anatomically primitive *Eomellivora* species from the early Late Miocene (*E. moralesi*, MN7–8; *E. fricki*, MN9). *Eomellivora moralesi* (Fig. 7a) (MN7/8 from Europe) is known from a partial cranium and some lower dentitions from Can Mata (Spain) and Hammersmiede (Germany) (Alba et al., 2022; Kargopoulos et al., 2022). In comparison to AMNH F:AM 50570, *E. moralesi* exhibits a greater degree of gracility in its premolars, characterised by the absence of concavities in the buccal walls. Additionally, that species displays a subrectangular P2, P3 with a poorly developed cingulum, relatively shorter P4 that lacks a distinct basal cingulum, and more slender M1 with a larger parastylar area, more pronounced metacone, and lower protocone situated mesiolingually. The species *E. fricki* is known from the early Late Miocene (Vallesian, MN9) of Wien XII-Altmannsdorf (Fig. 7b) and Gaiselberg (Austria), besides Los Valles de Fuentidueña and Can Llobateres (Spain) (Alba et al., 2022; Pia, 1939; Valenciano et al., 2017, 2019; Zapfe, 1948). It possesses the largest known P4 and M1 for any species of *Eomellivora*. Its P4 possesses a relatively subtle concavity in the buccal wall, and its M1 has a large metacone and a slightly cuspidate protocone, forming an arch, with a large mesiodistal expansion of the lingual platform (Pia, 1939; Valenciano et al., 2017). Some of the specimens from Gritsev (MN9, Ukraine) initially identified as *Eomellivora wimani piveteaui* by Wolsan and Semenov (1996), but later reassigned to *Eomellivora* sp. (Alba et al., 2022; Valenciano et al., 2017), exhibit a notably large dentition, although not as large as in *E. fricki*. However, other than size, the dental morphology of the Gritsev material is unknown and the original description does not include images of these fossils.

AMNH F:AM 50570 shows greatest similarities to the other younger and more anatomically-derived Late Miocene *E. ursogulo* (MN11–13, Ukraine and Russia) (Lavrov & Gimranov, 2018; Orlov, 1948) and *E. hungarica* from Polgárdi 2 (MN13, Hungary) (Kretzoi, 1942). The holotype of *E. ursogulo* (Fig. 7e) (MN11) from Grebeniki, Ukraine (Orlov, 1948) indicates that it has a shorter and more slender C than that of AMNH F:AM 50570. Furthermore, in the holotype of *E. ursogulo* the P3 is shorter with two distal accessory cusps, P4 is shorter with a similar width and a less marked concavity in the buccal wall, and M1 is distinctive. M1 of the holotype of *E. ursogulo* displays a highly developed metacone, a markedly expanded lingual platform with a midline incisure, and a greater width between the distal and mesial walls in the middle of the tooth (Orlov, 1948; Valenciano et al., 2015). A poorly figured M1 is the only known specimen of the upper dentition of *E. hungarica* (MN13, Hungary), which makes comparison with that specimen challenging. However, a less expanded lingual platform and a less reduced metacone are visible in *E. hungarica*.

Therefore, based on a comprehensive assessment of morphology, morphometrics, and multivariate analysis, AMNH F:AM 50570 is assigned to *E. wimani* (e.g., Kretzoi, 1965; Simionescu, 1938; Spassov et al., 2018; Stock & Hall, 1933; Zdansky, 1924), thereby expanding the known intraspecific variability and geographic distribution of this species.

The two newly described specimens from the Nan Ho site (MN12–13), AMNH F:AM 50569 and AMNH F:AM 144525, exhibit a series of characteristics that complicate their precise taxonomic determination. The maxilla AMNH F:AM 50569 presents a notably smaller dentition relative to other material of *Eomellivora*, displaying the lowest values of length and width of the C and premolars (P2–P4) among the entire set of species in the database. Furthermore, its M1 is fragmented, and although some measurements can be taken, the morphology of the lingual platform, which is a particularly useful diagnostic character, cannot be

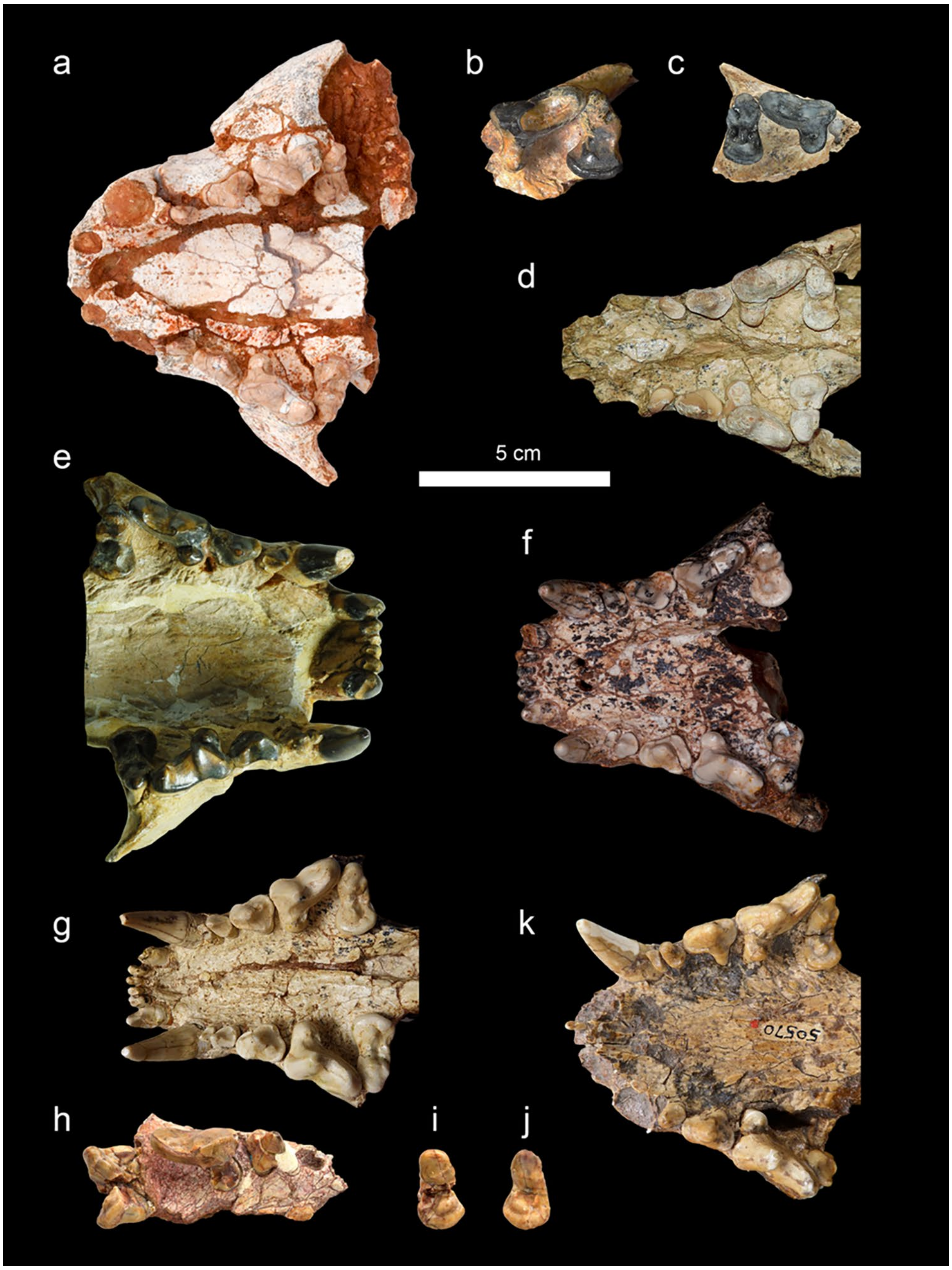

Fig. 7 Upper dentitions of *Eomellivora* spp. in occlusal view. **a** *Eomellivora moralesi*, IPS122262 (holotype) from Abocador de Can Mata (Spain); **b** *Eomellivora fricki*, NHMW 2016/0065/0001 (holotype) from Wien XII-Altmannsdorf (Austria); **c** *Eomellivora piveteaui*, MNHN-TRQ-1005 (lectotype) from Yassiören (Turkey); **d** *Eomellivora piveteaui*, BAT-3′13.185 from Batallones-3 (Spain); **e** *Eomellivora ursogulo*, PIN-No.268 (holotype) from Grebeniki (Ukraine); **f** *Eomellivora wimani* PMU-21824 (lectotype, formerly M3692, Ex. 1 in Zdansky, 1924) from Shangyingou, Xin'an County (Henan Province, China); **g** *Eomellivora wimani*, PMU-21825 (formerly M3847, Ex. 2 in Zdansky, 1924) from Liuwangou, Baode County (Shanxi Province, China); **h** *Eomellivora wimani*, LACM CIT 1210 from Kern River Fm., California (USA). **i**. Detail of M1 from LACM CIT 1210 from the Kern River Fm., California (USA); **j** Right M1 associated with LACM CIT 1210 from the Kern River Fm., California (USA); **k** *Eomellivora wimani*, AMNH F:AM 50570 from Ta Tung Kou, Shouyang County (Shanxi Province, China). **a–k** all share a 5 cm scale

determined. Notably, the metacone of M1 is present as a ridge (rather than a distinct cusp as in other *Eomellivora* species), a derived character state for *Eomellivora*. In addition to the general reduction in size of the entire dentition relative to other *Eomellivora* species, it exhibits several other distinctive characteristics, such as the small mesial accessory cusp of P3 (reduced relative to other species) and the absence of concavity at the buccal margin of P2–P4 (present in other species). These are diagnostic features of *E. wimani* and are clearly present in the cranium of *E. wimani* AMNH F:AM 50570. In the specimen AMNH F:AM 50569, the triangular margin of P2 in occlusal view and the well-developed premolar cingulae rule out the possibility of assigning this specimen to *E. moralesi*. The small size of M1, although incomplete, and the presence of a cuspidate protocone (Fig. 4d), serve to differentiate it from *E. fricki*. Compared to *E. piveteaui*, AMNH F:AM 50569 P2 exhibits a more robust morphology, P3 is slender but shorter, and P4 is short and slender. However, the concavity of the buccal wall of the P4 bears a resemblance to the *Eomellivora* from Zhupeng (Zong, 1997). Yet, there is a very considerable difference in size between these two specimens. The contrasting proportions of all teeth, and the M1 with a small metacone, also serve to exclude assignment of AMNH F:AM 50569

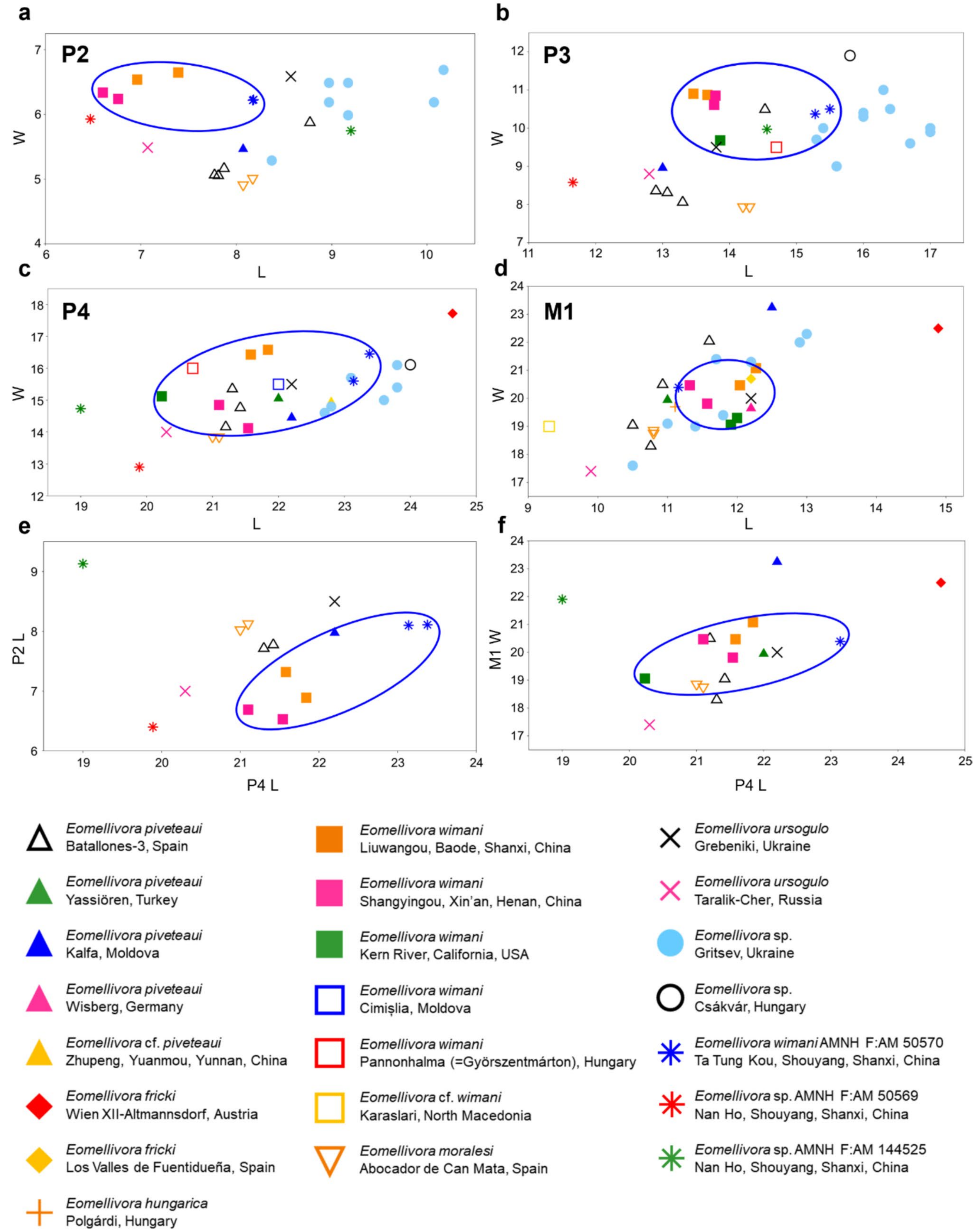

Fig. 8 Scatter plots of maximum length (L) and maximum width (W) in mm of the upper dentition of different species of *Eomellivora*: **a** P2; **b** P3; **c** P4; **d** M1; **e** length of P4 vs. length of P2; **f** length of P4 vs. width of M1. The blue ellipse indicates the range of variability of *E. wimani*

to *E. ursogulo*. The disparity in size, the anomalous values in dental proportions, and the distinct morphological characteristics described above prevent the assignment of AMNH F:AM 50569 to any known species of *Eomellivora*. However, the aforementioned characteristics are not sufficiently diagnostic to establish a new species, and for this reason, we conservatively classify AMNH F:AM 50569 as *Eomellivora* sp.

With regard to the cranium AMNH F:AM 144525, also discovered at Nan Ho, despite being almost complete, its dentition is incomplete and fragmented, making it challenging to determine its morphology in detail and to obtain dental measurements. For instance, the length of P4 was measured from the distal alveolus, as only the mesial half is preserved. This resulted in a notably small value compared to its width. Similarly, the width of M1 could only be measured at the alveoli, as the tooth crown is not preserved. This resulted in only a minimum estimate, representing a smaller measurement than the tooth itself would have possessed. The values of both P2 and P3 are higher than those of the maxilla AMNH F:AM 50569 from the same site (Fig. 8a–b). These differences in size may be attributed to intraspecific variability, potentially indicative of sexual dimorphism. This phenomenon has been observed in extant mustelids, wherein males tend to be larger than females (Larivière & Jennings, 2009; Law & Mehta, 2018; Law et al., 2016; Noonan et al., 2016; Sánchez et al., 2024). Given the lack of diagnostic dental features preserved in specimen AMNH F:AM 144525, we also have opted to classify it conservatively as *Eomellivora* sp., as for AMNH F:AM 50569. However, the preserved cranial morphology of this specimen is noteworthy, representing one of the most complete skulls of *Eomellivora* (Fig. 9a, Table 3). Only three other almost complete crania for species of this genus have been described in the fossil record, one of *E. ursogulo* (Fig. 9b) from Grebeniki and two of *E. piveteaui* from Batallones-3 (Fig. 9c) (Orlov, 1948; Valenciano et al., 2015). Other crania of *E. wimani* are more incomplete (e.g., PMU-21825, Ex. 2 of Zdansky, 1924) (Fig. 9d). Recently, Jiangzuo et al. (2023a) figured a fairly complete cranium from Qingbushan attributed to *E. wimani* that has not yet been described but presents a relatively prominent forehead, a short muzzle, and a nasal aperture partially inclined. In terms of maximum length, AMNH F:AM 144525 has a similar size to *E. ursogulo*, even exceeding it in some dimensions, with comparable values for maximum width between the mastoid processes and maxillary length, but lower values for the height of the cranium between the maxilla and frontal, and for the height of the nostrils (Table 3). In comparison to *E. piveteaui*, the cranium of AMNH F:AM 144525 is generally larger, with the exception of the width of the mastoid processes and the height of the cranium between the maxilla and the frontal bone. It is possible that the observed lower height can be attributed to dorsoventral deformation of this fossil.

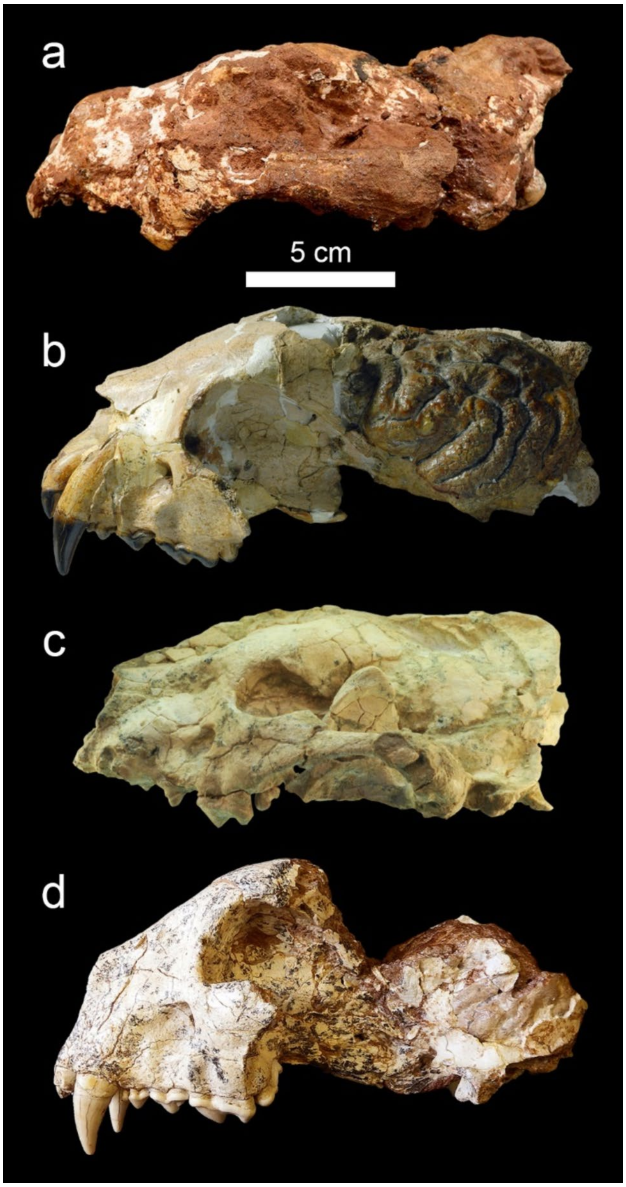

Fig. 9 Crania of *Eomellivora* in lateral view: **a** *Eomellivora* sp., AMNH F:AM 144525 from Nan Ho, Shouyang County (Shanxi, Province China); **b** *Eomellivora ursogulo*, PIN-No.268 (holotype) from Grebeniki (Ukraine); **c** *Eomellivora piveteaui*, BAT-3′09.1000 from Batallones-3 (Spain); **d** *Eomellivora wimani*, PMU-21825 (formerly M3847, Ex. 2 in Zdansky, 1924) from Liuwangou, Baode County (Shanxi Province, China). **a–d** All share a 5 cm scale

Additional lesser-known Chinese material of *Eomellivora* was described by Zong (1997: Pl. 26, figs. 8a–c), who attributed to *Eomellivora* cf. *wimani* isolated teeth from two sites from Yuanmou (Yunnan Province, China) of similar age to the European MN11 biozone. That material included a complete P4 and a lingual platform of an M1 from Zhupeng site 8603, and a complete m1 from Xiaohe site 8801 (Fig. 10).

Table 3 Cranial measurements (in mm) taken as shown in Fig. 2b from different specimens of *Eomellivora*, including AMNH F:AM 144525

Specimen	Locality	1	2	3	4	5	6	7
Eomellivora sp. AMNH F:AM 144525	Shouyang (China)	194	78.42	48.69	61.04	51.11	56.27	98.21
Eomellivora piveteaui BAT-3′09.1000	Batallones (Spain)	(170)	(87.73)	53.09	-	39.87	(57.14)	101.52
Eomellivora piveteaui BAT-3′13.185	Batallones (Spain)	(160)	-	66.59	-	37.97	-	98.22
Eomellivora ursogulo AMNH 99922 (cast)	Grebeniki (Ukraine)	192.5	88.63	68.12	61.11	43.42	77.14	100.99

The measurements correspond to: 1. condyle-basal length; 2. width between the mastoid processes; 3. height of the cranium between the maxilla and the frontal bones; 4. maximum width between the zygomatic postorbital processes; 5. height of the nostrils; 6. maximum width of the maxilla between the M1's (including alveoli); 7. length of the maxilla. Measurements in parentheses are approximate

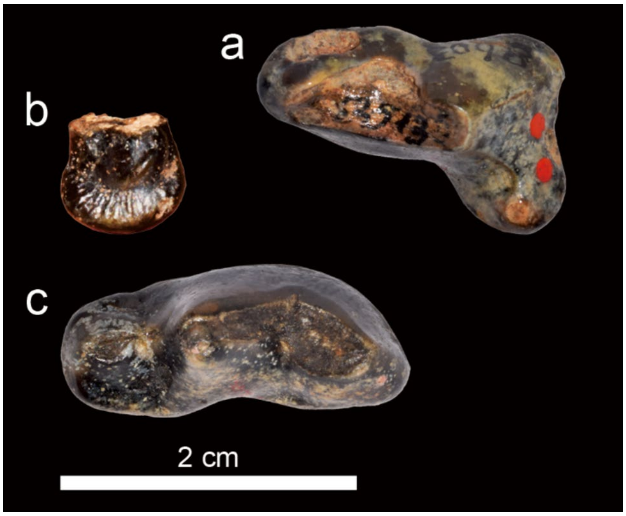

Fig. 10 *Eomellivora* dentition found in Yuanmou County (Yunnan Province, China), initially identified by Zong (1997) as *Eomellivora* cf. *wimani*, assigned in this paper to *Eomellivora* cf. *E. piveteaui*. **a** P4 in occlusal view from Zhupeng site 8603; **b** lingual platform of M1 in occlusal view from Zhupeng site 8603; **c**. m1 in occlusal view from Xiaohe site 8801. **a–c** Share the same 2 cm scale

Its P4 (L = 22.8 mm; W = 14.98 mm; Fig. 10a) exhibits a less pronounced concavity of the buccal wall than observed in other specimens of *E. wimani* (including AMNH F:AM 50570). In addition, it has a notable length, although its width is within the typical range, resulting in a more slender appearance than would be expected for *E. wimani*, instead being more similar to that of *E. piveteaui*. It also differs from *E. ursogulo* in the presence of a mesiodistally wider protocone, with a less pronounced mesial concavity (Lungu, 1978; Orlov, 1948; Ozansoy, 1965; Valenciano et al., 2015; Wolsan & Semenov, 1996; Zdansky, 1924). As for the M1 fragment (Fig. 10b), its lingual platform is morphologically more similar to *E. piveteaui*, with a ridge-shaped protocone located mesially, and a rounded and much less developed lingual platform than in *E. wimani* and *E. ursogulo* (Lungu, 1978; Orlov, 1948; Ozansoy, 1965; Valenciano et al., 2015; Wolsan & Semenov, 1996; Zdansky, 1924).

Regarding the m1 (L = 23.8 mm; W = 10.1 mm; Fig. 10c) of the Yuanmou material, its trigonid is not excessively long, and neither the lingual nor the buccal walls exhibit marked concavities. The lectotype of *E. wimani* PMU21824 (formerly M3693, Ex. 1 in Zdansky, 1924) from Shangyingou and *E. wimani* (No. 46) from Novaja Emetovka, Ukraine (Orlov, 1948) both possess an m1 with a proportionally longer trigonid than the one from Yuanmou and *E. piveteaui* (BAT-3′08.526) from Batallones-3 (Valenciano et al., 2015). The Shangyingou and Novaja Emetovka specimens of *E. wimani* have a notable enlargement of the m1 paraconid in a mesiodistal direction, giving them a more slender appearance than in *E. piveteaui*. Furthermore, the m1 of these specimens of *E. wimani* show a greater degree of concavity development in the lingual and mesial walls than in the Yuanmou specimen. With regard to *E. ursogulo* (MN11), its m1 also presents a relatively elongate trigonid, though with a width more akin to that of *E. piveteaui*, yielding a more robust appearance. It can thus be concluded that the Yuanmou m1 is more similar in appearance to the known material of *E. piveteaui* (Lungu, 1978; Ozansoy, 1965; Valenciano et al., 2015). We therefore propose that the teeth from Yuanmou, originally identified as *Eomellivora* cf. *wimani* by Zong (1997), instead should be reclassified as *E.* cf. *E. piveteaui* on the basis of their morphological similarities and proportions. This reassignment represents the first documented occurrence of the species in China, and the last known representative of the species worldwide, extending its temporal range to the MN11 zone and marking its easternmost record in Asia.

Conclusions

The description of the unpublished crania of *Eomellivora* from two Late Miocene sites in China in the Frick fossil mammal collections at the AMNH has enabled us to classify them as *E. wimani* (AMNH F:AM 50570) from the Ta Tung Kou site and *Eomellivora* sp. (AMNH F:AM 50569 and AMNH F:AM 144525) from the Nan Ho site. This work provides the first description of cranial material of *E. wimani* from China since the initial description of the genus and species by Zdansky (1924). These new Chinese specimens of *Eomellivora* expand the knowledge about the Upper Miocene fauna of the Shouyang Basin, which has been less extensively studied than the nearby Baode and Yushe Basins.

The specimen of *E. wimani* AMNH F:AM 50570 from Ta Tung Kou also contributes to a better understanding of intraspecific variability in the species. This is evidenced by the morphology of P3, different to the other known *E. wimani* specimens, with accessory cusps present but variable in size, and the variation in the proportions of the upper premolars. The generalised elongation of the upper premolars in AMNH F:AM 50570 may be indicative of a more derived condition within *E. wimani*.

The specimens of *Eomellivora* sp., AMNH F:AM 50569 and AMNH F:AM 144525, from Nan Ho site, exhibit a considerable degree of divergence from the known variability observed within other *Eomellivora* species. However, in spite of their distinctiveness, their taxonomic determination to species level or assignment to a new species has not been possible due to the poor preservation of the most diagnostic teeth.

The utility of multivariate analyses, using Mosimann-transformed linear measures to eliminate the sample size factor, for taxonomic studies was once more demonstrated. This analysis successfully separated all taxa at the genus level, establishing non-overlapping morphospaces, differentiating *Eomellivora* from other mustelids, and separating the species *E. piveteaui* from *E. wimani*.

Finally, we reassigned the known dentition of *Eomellivora* from Yuanmou (China), originally assigned to *Eomellivora* cf. *wimani,* to *Eomellivora* cf. *E. piveteaui*, extending the temporal range of that species to MN11. Furthermore, this also may represent the easternmost documented record of the species, suggesting the migration of the species during the Late Miocene from Europe to Asia, late in the history of this lineage.

Acknowledgements We thank the following curators and collections staff for allowing us access to the original fossils: Judy Galkin, Jin Meng, Ruth O'Leary, E. Westwig (AMNH); B. Kear (PMU); D. Kalthoff and L. Werdelin (NRM); S. Fraile, J. Morales, and A. Garvía (MNCN-CSIC); U.B. Göhlich (NHMW); C. Argot (MNHN); D. Lunde (USNM); X. Wang (LACM); and R. Robles and D.M. Alba (ICP). Our thanks also to our colleagues for kindly sharing original pictures of the following taxa: the late S. Peigné and P. Loubry (photographer UMR7207, MNHN), for the lectotype of *Eomellivora piveteaui* from Yassiören; M. Sotnikova (PIN), for the holotype of *E. ursogulo* from Grebeniki; L. Kordos and K. Palotás (MFGI), for the holotype of *E. hungarica* from Polgárdi 2; and S. Mayda (Ege University, İzmir, Turkey) for the specimen of *E. wimani* from Novaya Emetovka (Ukraine). We also thank Prof. X. Wang (LACM) for helping us to narrow down the dating of Ta Tung Kou and Nan Ho sites by providing access to unpublished faunal material from these localities. The authors also want to thank the editor M. Rasser as well as two anonymous reviewers for their valuable comments and suggestions, which helped to improve the quality of the manuscript. A. Valenciano received support for his research through the project SYNTHESYS3, http://www.synthesys.info/ (SYNTHESYS; AT-TAF-5457), financed by the European Community Research Infrastructure Action under the FP7 "Capacities" Programme, and the European Union´s Seventh Framework Programme (FP7/2007-2013) under grant agreement nº 226506 (SYNTHESYS; SE-TAF-3637), as well as founding from the AMNH Richard Gilder Graduate School through Collection Study Grants in 2014 and 2022 and a Theodore Roosevelt Memorial Grant 2022. This study was also supported by the research Group UCM910607, and the project PID2023-151089NB-I00 founded by MCIU /AEI/10.13039/501100011033/ FEDER, UE.

Funding Open Access funding provided thanks to the CRUE-CSIC agreement with Springer Nature.

Data availability All fossil specimens described in this study are housed in the American Museum of Natural History, New York, USA (AMNH). These materials are publicly available for study upon request to the curators of the respective collections.

Declarations

Conflict of interest The authors have no competing interests to declare that are relevant to the content of this article nor have financial or proprietary interests in any material discussed in this article.

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