COMPLETE DESCRIPTION OF THE SKULL AND MANDIBLE OF THE GIANT MUSTELID
EOMELLIVORA PIVETEAU OZANSOY, 1965 (MAMMALIA, CARNIVORA, MUSTELIDAE),
FROM BATALLONES (MN10), LATE MIOCENE (MADRID, SPAIN)

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ABSTRACT—We describe cranial, mandibular, and dental remains of five individuals of the giant mustelid Eomellivora
piveteaui Ozansoy, 1965, from the late Miocene (MN10) site of Cerro de los Batallones (Madrid, Spain)—the first complete
cranial remains recorded for this species and the most complete remains of the genus. This new sample enables a review of
the systematic status of Eomellivora, leading us to accept as valid the species E. piveteaui Ozansoy, 1965, E. wimani Zdansky,
1924, E. ursogulo (Orlov, 1948), and E. hungarica Kretzoi, 1942. Our phylogenetic hypothesis indicates that Eomellivora is
the sister taxon of the extant Mellivora capensis and E. piveteaui had a common ancestor within the crown group E. wimani–
E. ursogulo. Eomellivora piveteaui was specialized for a more hypercarnivorous diet than the largest extant terrestrial
mustelids, although it also had some derived bone-crushing adaptations. Eomellivora piveteaui had an active predatory role
in the late Miocene carnivore faunas, exploiting both small and relatively large prey.

SUPPLEMENTAL DATA—Supplemental materials are available for this article for free at www.tandfonline.com/UJVP

INTRODUCTION

The Cerro de los Batallones fossil sites (late Miocene [MN10]) have yielded some of the most interesting, richest, and best-preserved Neogene mammal assemblages of the Iberian Peninsula (Morales et al., 2008). It is a system of nine distinct sites located on a structural butte in the south of the province of Madrid, Spain (Fig. 1). Fossil remains indicate a late Vallesian age (ca. 9 Ma), for all the sites. However, there are slight differences in composition in micro- and macromammals among the different fossil deposits that have been attributed to minor temporal differences indicating, for instance, that Batallones-10 is older than Batallones-3 (López-Antonanzas et al., 2010; Siliceo et al., 2014). All these Batallones sites were cavities that acted as natural traps for vertebrates. The fossiliferous deposits are embedded in marls and are composed of two types of assemblages: (1) subsurface cavities (e.g., Batallones-1 and Batallones-3) interpreted as carnivore traps and (2) doline-like depressions (e.g., Batallones-4 and Batallones-10) interpreted as herbivore traps. The two types differ in their stratigraphic relative position, internal stratigraphic architecture, taxonomic composition, and taphonomic features (Pozo et al., 2004, Morales et al., 2008; Abella, 2011; Abella et al., 2011; Domingo et al., 2011, 2013; Calvo et al., 2013).

The numerous excavation campaigns in the different Batallones localities have yielded a rich assemblage of vertebrate fossils, including fishes, amphibians, reptiles (small and giant tortoises, lizards), and predatory birds (Morales et al., 2008; Pérez-García and Murelaga, 2013), as well as micromammals (López-Antonanzas et al., 2010), herbivores (Morales et al., 2008; Sánchez et al., 2009, 2011; Ríos et al., 2013), and carnivores, with the latter constituting the most diverse sample (e.g., Antón et al., 2004a, 2004b; Peigné et al., 2005, 2008; Salesa et al., 2006, 2008, 2010, 2012; Abella, 2011; Abella et al., 2011, 2013; Valenciano et al., 2012, 2013).

The giant mustelid was identified from Batallones-3 by Valenciano et al. (2012) as Eomellivora piveteaui Ozansoy, 1965. The richness of this sample is remarkable in that it includes relatively complete cranial and postcranial material, representing the most complete remains known of the genus. The craniodental specimens belong to at least five individuals and include two skulls, eight hemimandibles, and several isolated teeth (Figs. 2, 3). Eomellivora played an important role in the late Miocene Hippotherium faunas, being one of the largest and most hypercarnivorous mustelids ever known, larger and more hypercarnivorous than the extant wolverine Gulo gulo (Valenciano et al., 2013).

Eight species of Eomellivora have been described from 18 different localities in the Old and New World (e.g., Tobien, 1955;
Lupták, 1995; Wolsan and Semenov 1996; Morlo, 1997; Morales and Pickford, 2005; Koufos, 2012), spanning the middle (MN8) to late (MN13) Miocene. However, Wolsan and Semenov (1996) considered only a single valid species (*E. wimani* Zdansky, 1924), which they subdivided into two chronosubspecies: the Vallesian (MN9–10) *E. w. piveteaui* and the Turolian/Ventian (MN11–13) *E. w. wimani*. The aim of the present paper is to describe in detail the morphology of the complete skull, mandible, and dentition of *Eomellivora* from Batallones (including a three-dimensional [3D] digital model that removes some of the taphonomic distortion) and to study the systematic position of *Eomellivora* and its included taxa.

**MATERIALS AND METHODS**

**Nomenclature and Measurements**

Dental nomenclature follows Ginsburg (1999) and Smith and Dodson (2003). Anatomical descriptions are based primarily on Scapino (1968), Turnbull (1970), Barone (1999, 2000), Waibl et al. (2005), Evans and de Lahunta (2010, 2013), and Hartstone-Rose et al. (2012). The terminology conforms to the standard of the Nomina Anatomica Veterinaria (NAV; Waibl et al., 2005), with the exception of the masseter and temporalis muscle complexes for which we follow Hartstone-Rose et al. (2012). We provide a description of the main craniodental features of *Eomellivora* from Batallones, with emphasis on the traits that may indicate its systematic affinities. The Batallones material (Figs. 2, 3) has been compared with all the other material of *Eomellivora* on the basis of published descriptions, figures, measurements, and photographs (Figs. 4–8). For context, we compared *Eomellivora* with the extant terrestrial mustelids *Eira barbara*, *Gulo gulo*, *Martes martes*, *Mellivora capensis*, and *Pekania pennanti*, as well as the extinct giant mustelids *Ekorus ekkeran*, *Megalictis ferox*, and *Plesiogulo crassa*, described or studied by Matthew (1907), Werdelin (2003), and Koufos (2006). Measurements were made using Mitutoyo Absolute digital calipers to the nearest 0.1 mm (Tables 1, 2).

**Abbreviations**

**Institutional Abbreviations**—AMNH, American Museum of Natural History, New York, U.S.A.; BAT-3, Batallones-3 locality collection from MNCN; BAT-10, Batallones-10 locality collection from MNCN; IPS, collection from Institut Catalá de Paleontologia Miquel Crusafont (ICP), Universitat Autònoma de Barcelona, Barcelona, Spain; MFGI, Geological and Geophysical Institute of Hungary, Budapest, Hungary; MNCN, Museo Nacional de Ciencias Naturales, Madrid, Spain; MNHN, Muséum national d’Histoire naturelle, Paris, France; PIN, Palaeontological Institute, Russian Academy of Sciences, Moscow, Russia; PMU, Palaeontological Museum, University of Uppsala, Uppsala, Sweden; UST, Tiraspol State University, Chisinau, Moldova; VAL, Anatomical Museum of Valladolid University, Valladolid, Spain.

**Studied Material**

The fossil remains of *E. piveteaui* from Batallones are stored in the collections of the Department of Paleobiologia of the MNCN: BAT-3’09.1000 (Fig. 2A1–4; Supplementary Data 1, Fig. S1): skull with P2–M1 and its mandible with p2–m1 (Fig. 3C); BAT-3’13.185 (Fig. 2B1, 2): skull with P2–M1; BAT-3’09.688 (Fig. 2C1–2); 13; BAT-3’08.635 (Fig. 2D); C1; BAT-10’08-G4-102 (Fig. 2E1–3); P2; BAT-3’09.250; P3; BAT-3’09.2b; P4 very worn without protocone; BAT-3’09.2c: lingual half of M1 very worn and without protocone; BAT-3’08.526 (Fig. 3A1–3; Supplementary Data 1, Fig. S2): right hemimandible with c1 and p2–m1; BAT-3’13.230 (Fig. 3B1–3): left hemimandible with complete ascending ramus, partial p3, and complete p4–m1; BAT-3’12.1086: right hemimandible with complete ascending ramus and partial p4 and m1; BAT-3’09.2: right hemimandible fragment with alveolus for c1 and p1–p4 as well as a very worn m1; BAT-3’11.1180: left hemimandible fragment with p4; BAT-
Three-Dimensional Model

The skull of *E. piveteaui* from BAT-3 is almost complete, but crushed, due to the compaction of the sediments resulting in both fragmentation and deformation. This kind of distortion has been previously reported in the carnivoran cranial material from BAT-1 (Domingo et al., 2013). Although the exceptional preservation of the skull permits reliable observations of morphological details, the distortion makes it difficult or impossible to accurately interpret three-dimensional (3D) aspects (Antón et al., 2004a). The recovery of the original shape through 3D reconstruction of individuals with distortions improves overall morphological descriptions and constitutes a necessary first step toward a correct anatomical reconstruction. Two main deformation forces in BAT-3'09.1000 on the sagittal and coronal planes have been detected through observation of the relative position of symmetric structures. A surface 3D model has been obtained using a Next Engine 2020i scanner (Kuzminsky and Gardiner, 2012). In order to restore the original morphology, a shear deformation was applied to the sagittal plane of the 3D model through the CAD software Autodesk 3D Studio Max, with an angle of shearing of 18.3° estimated. Similarly, a 3.4° shearing deformation has been applied to the coronal plane. Both shearing amounts have been estimated based on realignment of paired structures. Although observed, the quantification of the minor dorsoventral distortion is difficult to estimate, thus preventing its correction. The corrected interactive 3D model has been created in PDF 3D format (which can be opened and manipulated in standard PDF viewers) for easy accessibility and comparison (Supplementary Data 1, Figs. S1, S2).

### SYSTEMATIC PALEONTOLOGY

Order CARNIVORA Bowdich, 1821
Suborder CANIFORMIA Kretzoi, 1943
Family MUSTELIDAE Fischer von Waldeheim, 1817
Subfamily MELLIVORINAE Gray, 1865
Genus *EOMELLIVORA* Zdansky, 1924
*EOMELLIVORA PIVETEAUI* Ozansoy, 1965

**Eomellivora piveteaui** Ozansoy, 1965: Pl II, fig. 1 (original description).

**Eomellivora wimani piveteaui**, Wolsan and Semenov, 1996 (emended diagnosis).

**Lectotype**—A partial right mandible with i2–p4 and m1 trigonid, figured by Ozansoy, 1965: Pl II, fig.1 (Wolsan and Semenov, 1996).

**Type Locality**—Yassiören (Turkey).

**New Localities**—BAT-3 and BAT-10.

### Description

**Skull and Upper Dentition**—Two skulls (BAT-3'09.1000 and BAT-3'13.185) of *Eomellivora* have been found at Batallones. BAT-3'09.1000 (Fig. 2A1–4) has an approximate basal cranial length of 182.52 mm. Its preservation is relatively good, despite the fact that it is compressed and warped approximately 18.3° in the sagittal plane and 3.4° in the coronal plane (Fig. 2). The nuchal and ventral regions are also quite damaged. BAT-3'13.185 (Fig. 2B1, 2) is lateromedially compressed, and the nuchal and ventral regions are quite damaged. The foramen magnum, occipital condyles, and basioccipital bones are missing in both specimens. The dentition of BAT-3'09.1000 is partially dissolved by soil acids, and also partially broken, with some of the cusps of the lower teeth being impacted into the upper dentition. The dentition of BAT-3'13.185 is relatively good and retains P2–M1.

Based on analysis of both specimens, the Batallones *Eomellivora* skull is triangular and has a massive aspect in both ventral and dorsal views. It has a dorsoventrally high snout, and the nasal bones are robust and rostrocaudally developed. The nasal aperture is large and slightly tilted caudally. The frontal region is weakly domed, becoming slightly flat above the orbit (Fig. 2A3). The interorbital region is broad. The postorbital processes are marked in BAT-
FIGURE 3. Mandibles and lower dentition of *Eomellivora piveteauxi* from Batallones. See Figure S2 (Supplementary Data 1) for a digital rendering of BAT-3’08.526 that can be manipulated in 3D space. **A1**, lateral view of mandible BAT-3’08.526; **A2**, medial view of mandible BAT-3’08.526; **A3**, occlusal view of mandible BAT-3’08.526; **B1**, lateral view of mandible BAT-3’13.230; **B2**, medial view of mandible BAT-3’13.230; **B3**, occlusal view of mandible BAT-3’13.230; **C**, lateral view of the right mandible associated with skull BAT-3’09.1000; **D1**, occlusal view of m1 and m2 associated with juvenile mandible BAT-10’12-G2-4; **D2**, lingual view of m1 and m2 associated with juvenile mandible BAT-10’12-G2-4; **D3**, buccal view of dp3 associated with juvenile mandible BAT-10’12-G2-4; **D4**, lingual view of dp3 associated with juvenile mandible BAT-10’12-G2-4; **D5**, occlusal view of dp3 associated with juvenile mandible BAT-10’12-G2-4; **D6**, buccal view of dp4 associated with juvenile mandible BAT-10’12-G2-4; **D7**, lingual view of dp4 associated with juvenile mandible BAT-10’12-G2-4; **D8**, occlusal view of dp4 associated with juvenile mandible BAT-10’12-G2-4. Scale bar for A1–3, B1–3, and C equals 5 cm and scale bar for D1–8 equals 2 cm.
3'13.185. On the maxillary bones, there is a moderately deep and rounded fossa in the rostral margin of the orbit that extends dorsally. The large infraorbital foramen (6.58 mm width and 12.83 mm height in BAT-3'13.185) is located under the frontal process of the maxilla and above the mesial edge of the P4 paracone. The rostral margin of the orbit ends at the level of the distal margin of the P4 paracone. BAT-3'09.1000 has a weak temporal crest and a well-developed sagittal crest that extends caudally towards the external occipital protuberance, where it divides into the nuchal crests, forming a ‘Y’ pattern. The external occipital protuberance does not exceed the nuchal region. In caudal view (Fig. 2A4), the nuchal area is triangular, rather flat, and has a large area of insertion on the supraoccipital bone.

The zygomatic arches are robust in their rostral and caudal areas and are especially robust near the glenoid cavity. Both M. masseter pars superficialis and M. masseter pars profunda have their origin on the ventrolateral side of zygomatic arch. The frontal processes of the zygomatic arches are triangular, high, and rostrocaudally broad.

Ventrally, the tooth rows are rectilinear between C1 and P4. A diastema separates I3–C1. Neither the pterygoid region nor the hamulus pterygoideus processes are well preserved. The tympanic bulla is partially inflated, with a rugose ventral surface and a large and rounded external auditory meatus. The ventral parts of the nuchal crest in conjunction with the mastoid process are well developed and are rostrocaudally widened. The nuchal crest is concave and projects laterally, which creates large attachment areas for M. zygomatic temporalis on the dorsal side and M. obliquus capitis cranialis on the caudal side. The mastoid process is robust and is situated lateral to the tympanic bulla. The paroccipital process is caudal to the auditory bulla. BAT-3'09.1000 possesses a medium-sized paroccipital process, narrow, triangular in section, and projecting laterocaudally. The M. digastricus originates on the lateral side of the process.

The preserved upper dentition includes I3, C1, P2, P3, P4, and M1. The I3 BAT-3'09.688 (Fig. 2C1–2) is caniniform, with a single cusp curved distally. On the lingual side, there is a sharp cusp as well as a marked cingulum. It has a massive root that is oval in cross-section. The C1 BAT-3'08.635 (Fig. 2D) has a long
crown, wide at the base. The mesial and distal cristae are cor-
roded. The crown has a small distal cingulum, and the root is
robust and buccolingually wide near the cementoenamel junc-
tion. BAT-3’13.185 has an alveolus for P1 (Fig. 2B2); the P2 is
two rooted and has a high and mesially oriented single cusp
(Fig. 2B1, E1, 2). It is buccolingually rotated relative to the tooth
row. The mesial and distal cristae have sharp edges. It widens
distally and has a marked distolingual cingulum. The P3
(Fig. 2B2) is triangular in occlusal view, bicuspid, and two
rooted. Its cusps are distolingually oriented. The main cusp is
very high, and the distal accessory cusp is not very prominent.
There is a marked lingual expansion, a broad lingual cingulum,
and a concavity in the buccal wall. The P4 of BAT-3’13.185
(Fig. 2B2) is triangular, and robust. It has a very small and low
parastyle located on its mesial cingulum (Fig. 2B1). The proto-
cone is subconical, robust, and located in line with the parastyle.
There is a slight mesial inclination between the paracone and the
parastyle. There is a poorly developed concavity in the buccal
wall. The paracone and metastyle form an elongate blade. The
paracone is the highest and largest cusp, occupying over half of
the total length of the tooth. It is triangular and distally inclined.
The distal crista of the paracone has a somewhat concave slope
that fuses to the mesial crista of the metastyle via a ‘U’-shaped
valley. The M1 (Fig. 2B2) is rectangular, with the buccal wall
narrower than the lingual one. The paracone is conical and sit-
uated on the mesiobuccal corner. It is the highest and most robust
cusp, although the metacone is also quite well developed. There
is a markedly swollen buccal cingulum. The stylar area of the M1
is enlarged. The protocone is robust, subconical, and mesiolvingu-
ally located. There is a very swollen lingual platform that does
not completely enclose the protocone.

**Mandible and Lower Dentition**—The mandible of the
Batallones *Eomellivora* is long and robust (Fig. 3A1–3, B1–
2, C). The specimens BAT-3’08.526 (Fig. 3A1–3) and BAT-
3’09.1000 (Fig. 3C) have a total length of 120.79 and
134.16 mm, respectively. The tooth row is straight and
aligned with the articular process. The mandibular corpus is
deep, approximately twice the height of the m1, and is
mediolaterally widened at the level of the paraconid of m1.
The ventral margin is convex at the level of the ascending
ramus and the mandibular symphysis, but it is concave from
the p3 to the trigonid of m1. On the lateral side, there are
two rounded mental foramina, one beneath p2 and the
other beneath p3. The mandibular symphysis is rather verti-
cal, being more evident in the larger hemimandibles
(Fig. 3C). The muscle attachment of M. digastricus is on the
caudoventral edge of the mandibular corpus and reaches rostra-
lly beneath the m1 trigonid.

The ascending ramus is rostrocaudally broad. Its dorsal border
is sharp and vertically oriented. The coronoid process is laterally
rotated with an angle of ~75° with respect to the articular
process. The M. temporalis pars profunda and the M. temporalis
pars superficialis have their areas of insertion on the medial and
lateral sides of the ascending ramus, respectively. The masseteric
fossa is large, oval, and relatively deep. Its rostral margin lies
at the level of the m2. Inside the masseteric fossa, there is a notice-
able and deep insertion area for the M. zygomaticomandibularis.
The M. masseter pars superficialis inserted on the ventrolateral
edge of the angular process, which also has a large insertion for
the M. masseter pars profunda near its ventrolateral margin. The
articular process is large and is widely separated from the angu-
lar process. The angular process is robust, caudally directed, and
on its medial side has a well-developed muscular attachment for
M. pterygoideus medialis.

There are two deciduous teeth (dp3 and dp4) associated with
BAT-10’12-G2-4 (Fig. 3D1–8). The dp3 (Fig. 3D3–5) is sigmoi-
dal, two rooted, and tricuspidate. The mesial accessory cuspid is
very low; there is a small notch between it and the main cusp.
The main cuspid is high, lingually widened at the base and some-
what mesially placed, with two sharp cristids. The distal acces-
sory cuspid is located on a cingulid. It is the lowest cuspid and
has a large valley between it and the main cuspid. The dp4
(Fig. 3D6–8) is fragmentary. It is also two rooted, elongated, and
much larger than dp3. It preserves the buccal wall of the para-
conid, a complete protoconid, and a small fragment of the hypoco-
nid with a tiny linguoocclusal wall. The trigonid is similar to that
of the m1; it has no metaconid and possesses a convex buccal
wall. The paraconid is low and reduced relative to the protocon-
id. The protoconid is the highest cuspid. There is a wide valley
between the trigonid and the talonid. The adult lower dentition
includes the c1, p2–p4, and m1–m2. All the cusps are aligned
on the longitudinal axis. No lower incisors are preserved. The
lower canine of BAT-3’08.526 (Fig. 3A 1–3) is robust and conical
and has heavy occlusal wear. It has an oval cross-section, slightly

**FIGURE 5.** Relationships between lengths (L) and widths (W) of the lower dentition in
*Eomellivora*. Legend and sources, the same as Figure 4.
FIGURE 6. Main comparative material of species of *Eomellivora* recognized in this paper. **A1**, MNHN-TRQ-1005, *Eomellivora piveteaui* from Yassiören (YAS), occlusal view of maxilla fragment with P4 and M1; **A2**, MNHN-TRQ-1004, lectotype of *Eomellivora piveteaui* from YAS, lateral view of mandible fragment; **A3**, MNHN-TRQ-1004, occlusal view; **B1**, PMU-M3692, lectotype of *Eomellivora wimani* from Shangyingou (SH), lateral view of skull fragment with complete upper dentition; **B2**, PMU-M3692, ventral view; **B3**, PMU-M3693, holotype of *Eomellivora wimani* from SH, lateral view of mandible fragment with complete lower dentition; **B4**, PMU-M3693, occlusal view; **C1**, PIN-No. 268 holotype of *Eomellivora ursogulo* from Grebeniki (GRE), occlusal view; **C2**, PIN-No. 269a, holotype of *Eomellivora ursogulo* from GRE, lateral view of mandible with complete lower dentition; **C3**, PIN-No. 269a, occlusal view; **D1**, MFGI-Ob-2676, holotype of *Eomellivora hungarica* from Polgárdi 2 (POL), lateral view of mandible with fragmentary p3, p4, and m1; **D2**, MFGI-Ob-2676, occlusal view. Scale bar equals 5 cm.
broader at the base and curved distally. Some longitudinal lines radiate from the apex to the crown. The p1 is not preserved, but there is a single small alveolus in the larger mandibles. The p2 (Fig. 3A1–3, C) is two rooted, with elliptical shape formed by one cuspid mesially displaced. It is buccolingually rotated relative to the tooth row and is elongated but with a slight distal widening. It has small mesiobuccal and noticeable distobuccal cingulids. The p3 (Fig. 3A1–3) is bicuspidate. It has a pronounced buccolingual widening. The main cuspid is elongated and buccolingually compressed; its mesial and distal cristids have sharp edges. The distal accessory cuspid is low and has a blunter morphology. The mesial, buccal and lingual cingulids are well developed. The p4 (Fig. 3A1–3, B1–3, C) has three cuspids and is subrectangular with a slight distal broadening. It is a relatively long tooth compared with the total length of m1. It has a very small mesial accessory cuspid. Its main cuspid is buccolingually compressed; the crown of p4 is higher than that of the m1 paraconid. Its mesial and distal cristids have sharp edges. There is a noticeable intercuspis notch between the main cuspid and the distal accessory cuspid. The distal accessory cuspid is high, and
blunt in BAT-3'09.1000, and low in BAT-3'13.230, suggesting some degree of variability in this feature. Its main cusp is inclined distally toward the m1 (see Appendix 1). There is an occlusally projected mesial cingulid and a larger cingulid surrounding the distal accessory cusp. The m1 (Fig. 3A1–3, B1–3, D1, 2) is elongated and with a buccolingually compressed talonid. The trigonid is a trenchant blade that occupies almost three-fourths of the total length of the tooth and has a prominent

FIGURE 8. Ratio diagram of all *Eomellivora* described in the bibliography. The dental measurements of *Gulo gulo* B.1280 serve as the standard for comparison (solid line at Y axis equal to 100). Legend and sources, the same as Figure 4.
TABLE 1. Upper tooth measurements (in mm) of Eomellivora piveteaui from Batallones localities.

| Specimen          | L    | W    | L    | W    | L    | W    | L    | W    | L    | W    |
|-------------------|------|------|------|------|------|------|------|------|------|------|
| BAT-3’09.1000 (left) | 8.7  | 5.9  | 14.5 | 10.5 | 21.3 | —    | 11.6 | 22.1 |
| BAT-3’09.1000 (right)| —    | —    | —    | —    | —    | 21.2 | 14.2 | 10.9 | 20.5 |
| BAT-3’13.185 (left) | 7.7  | 5.1  | 13.1 | 8.3  | 21.3 | 15.4 | 10.8 | 18.3 |
| BAT-3’13.185 (right)| 7.8  | 5.2  | 12.9 | 8.4  | 21.4 | 14.8 | 10.5 | 19.1 |
| BAT-3’08.635        | 7.2  | 5.5  | —    | —    | —    | 13.3 | 8.1  | —    | —    |
| BAT-10-08-G4-102    | 7.2  | 5.5  | 13.4 | 10.5 | —    | —    | —    | —    | —    |
| BAT-3’09.250        | —    | —    | 13.3 | 8.1  | —    | —    | —    | —    | —    |

TABLE 2. Lower tooth measurements (in mm) of Eomellivora piveteaui from Batallones localities.

| Specimen          | c    | p2   | p3   | p4   | m1   | m2   |
|-------------------|------|------|------|------|------|------|
| BAT-3’08.526      | 12.0 | 9.3  | 8.2  | 4.7  | 10.7 | 7.3  |
| BAT-3’09.1000 (left) | —    | —    | 8.2  | 5.3  | 11.8 | 8.4  |
| BAT-3’09.1000 (right)| —    | —    | 8.3  | 5.5  | 11.8 | 8.3  |
| BAT-3’13.230      | —    | —    | —    | —    | 15.4 | 8.2  |
| BAT-3’11.1180     | —    | —    | —    | —    | 13.7 | 7.3  |
| BAT-3’09.688      | —    | —    | —    | —    | 19.7 | 8.5  |
| BAT-3’12.1086     | —    | —    | —    | —    | 22.2 | 8.1  |
| BAT-10-12-G2-4    | —    | —    | —    | —    | 20.6 | 8.6  |

Systematic Discussion

The taxonomy of the genus Eomellivora has remained problematic because a substantial number of species have been named based on very scarce remains and the range of dental variation is largely unknown. For this reason, we believe that the completeness of the sample of Eomellivora from Batallones (Figs. 4–9) presents a great opportunity to shed light on the systematics of the genus (Table 3).

Eomellivora piveteaui Ozansoy, 1965, was first described on the basis of a partial right hemimandible with i2–p4 and m1 trigonid, a fragment of maxilla with P4 and M1, and an isolated M1 from Yassiören (Turkey), MN9 (Fig. 6A1–3). Wolsan and SemeNov (1996) included this taxon in Eomellivora piveteaui at the sub-specific rank of E. wimani piveteaui, and they chose the Yassiören hemimandible MNHN-TRQ-1004 as lectotype (Table 3). The similarities between the material from Batallones and the Yassiören Eomellivora are striking (Valenciano et al., 2012), especially BAT-3’09.1000, which has dentition of similar size and morphology (Figs. 4–6) to the material described by Ozansoy (1965). However, there are some differences between the material, such as the smaller size of the p2 and M1 and the more robust p3 in the Batallones-3 specimens (Fig. 8).

The Eomellivora from Batallones includes five individuals (four from Batallones-3 and one from Batallones-10) and shows great variation (Figs. 4, 5, 8, Tables 1, 2). This variability reaches up to 20% of the tooth length (e.g., m1) and appears to indicate the existence of marked sexual dimorphism in the genus, as occurs in other extant and extinct mustelids (e.g., Zakrzewski, 1967; Moors, 1980; Hunt and Skolnick, 1996; Baskin, 1998; Ewer, 1998; Larivière and Jennings, 2009). Thus, we believe that sexual dimorphism can help us to interpret the systematics of Eomellivora, and explain the larger size of some Batallones specimens in relation to the material from Turkey. The two samples are similar in the absence of a p2 distal accessory cusp, and slight mesial accessory cusp in p3; similar robustness in p4 and P4; P4 shows a similar concavity in its buccal wall, with a robust protocone in line with the parastyle; and the M1 has a conical paracone and a well-developed metacone, with a robust, subconical, and mesiolingually located protocone as well as buccal and lingual cingula. Therefore, the Eomellivora from Batallones-3 is conspecific with E. piveteaui from Yassiören (Fig. 7). The specimen of Eomellivora from Batallones-10 cannot be completely compared with the Yassiören sample because the only comparable element, the m1 trigonid, is insufficient for comparative assessment. However, this specimen is metrically and morphologically similar to the Batallones-3 specimens; therefore, we are confident in identifying it as E. piveteaui. An isolated m1 without roots belonging to a young adult described as Mellivorine, gen. et sp. indet., from the Wissberg locality (Germany), MN9 (Tobien, 1955), was considered to belong to E. wimani piveteaui by Morlo (1997). This m1 is similar in size to the largest teeth of the E. piveteaui sample from Batallones-3, and the morphology of the m1 talonid is similar to the m1 from Batallones-10; thus, we assigned it to E. piveteaui (Fig. 7, Table 3).
Lungu (1978) ascribed a complete dental sample of one individual from Kalfa (Moldova), MN9, to *E. piveteaui*. With the exception of Wolsan and Semenov (1996) paper, no other papers seem to have taken this description into account. This material is comparable to the lectotype of *E. piveteaui* from Yassiören, except for the ascribed m2 (UST-CLF-N1-2027) that actually belongs to a hyaenid. The dentition from Kalfa is similar to that of *E. piveteaui* from Batallones, only differing in the more developed M1 distal platform and a larger length of M1, p3, and p4, and more robust M1 and m1 in the *Eomellivora* from Moldova (Figs. 4–8). Due to the larger size of the *E. piveteaui* from Kalfa and the older age of this locality in relation to *Eomellivora* from Batallones, these differences can be explained in terms of temporal differences or sexual dimorphism, and we agree with the taxonomic determination of Lungu (1978) (Table 3). Crusafont-Pairó and Ginsburg (1973) described very fragmentary material of the taxon *Eomellivora ligurior*, from the late Miocene (MN9) locality of Los Valles de Fuentidueña (Spain), consisting of an isolated M1 and a P4 without its protocone (Ginsburg et al., 1981). This species was synonymized with *E. wimani piveteaui* by Wolsan and Semenov (1996). The dentition is similar in size to *E. piveteaui* from Kalfa and *E. wimani* from China, but based on the remains of Kalfa, we think this Spanish material should be assigned to *E. piveteaui* (Table 3). Koufos (2012) described and classified an isolated and worn M1 from Ravin de la Pltie, Greece, MN10, as *E. wimani*. However, it is metrically and morphologically similar to the M1 from Kalfa; thus, we reclassified it as belonging to *E. piveteaui* (Table 3).

Of particular interest is the large sample of *Eomellivora* from the Ukrainian site of Gritsev, MN9, identified by Wolsan and Semenov (1996) as *E. wimani piveteaui* and more recently assigned to *E. wimani* (Morlo and Semenov, 2004; Vangengeim et al., 2006) (Table 3). According to the biometric data provided by Wolsan and Semenov (1996), the P2, M1, p2, and m1 are especially large, and in some cases (P3, P4, and p2) relatively more slender than those of *E. piveteaui* from Batallones (Figs. 4, 5). However, without a full description, it is difficult to say more about the taxonomic assignment of this material, and the assignment of this sample seems open to question until more information is available.

Zdansky (1924) described the first fossil of *Eomellivora* under the name of *E. wimani* based on one fragmentary skull and associated mandible from Shangyingou or locality 12, Honan Province, China, and another fragment of skull from Liuwangou or locality 31, Shansi Province, China (Figs. 4–8, Table 3).

TABLE 3. Taxonomic concordance of *Eomellivora*.

| Locality                     | MN zones | Original taxon / Author                | Wolsan and Semenov (1996) | This paper                      |
|------------------------------|----------|----------------------------------------|---------------------------|--------------------------------|
| Ngogora (Kenya)              | MN8      | *Eomellivora tugenensis* / Morales and Pickford (2005) | —                         | *Eomellivora tugenensis*        |
| Yassören (Turkey)            | MN9      | *Eomellivora piveteaui* / Ozansky (1965) | *Eomellivora wimani piveteaui* | —                              |
| Wissberg (Germany)           | MN9      | Melivorine, gen. et sp. indet. / Tobien (1955) | *Eomellivora wimani piveteaui* | —                              |
| Kalfa (Moldova)              | MN9      | *Eomellivora piveteaui* / Lungu (1979) | *Eomellivora wimani piveteaui* | —                              |
| Los Valles de Fuentidueña    | MN9      | *Eomellivora ligurior* / Crusafont-Pairó and Ginsburg (1973) | *Eomellivora wimani piveteaui* | —                              |
| Gritsev (Ukraine)            | MN9      | *Eomellivora wimani piveteaui* / Wolsan and Semenov (1996) | *Eomellivora wimani piveteaui* | —                              |
| Borsky Svät Jur (Slovakia)   | MN9      | *Eomellivora wimani wimani* / Luptáč (1995) | *Eomellivora wimani sp.* | *Eomellivora wimani* |
| Batallones - 3 and - 10 (Spain) | MN10 | *Eomellivora piveteaui* / Valenciano et al. (2012) | —                         | *Eomellivora piveteaui*        |
| Ravin de la Pltie (Greece)    | MN10     | *Eomellivora wimani* / Koufos (2012) | —                         | *Eomellivora piveteaui*        |
| Grebeník (Ukraine)           | MN11     | *Perunium ursogulo* / Orlov (1948) | *Eomellivora wimani ursogulo* | —                              |
| Čsákvar (Hungary)            | MN12     | *Eomellivora hungarica altera* / Kreitsoi (1942) | *Eomellivora hungarica sp.* | —                              |
| Nováva Emetovka (Ukraine)    | MN12     | *Eomellivora aff. wimani* / Orlov (1948) | *Eomellivora wimani wimani* | —                              |
| Győrszentmárton 2 (Hungary)   | MN12     | *Eomellivora orlovii* / Kreitsoi (1965) | *Eomellivora wimani wimani* | —                              |
| Čimisla (Moldova)            | MN12     | *Eomellivora rumana* / Simionescu (1938) | *Eomellivora wimani wimani* | —                              |
| Liuwangou + Shangyingou (China) | MN12–13 | *Eomellivora wimani Zdansky (1924) | *Eomellivora wimani wimani* | —                              |
| Kern River Formation site 50 (California, U.S.A.) | MN12–13 | *Eomellivora cf. wimani* / Stock and Hall (1933) | *Eomellivora wimani wimani* | —                              |
| Polgáról 2 (Hungary)         | MN13     | *Eomellivora hungarica* / Kreitsoi (1942) | *Eomellivora wimani wimani* | *Eomellivora hungarica*        |
Although there have not been any geological surveys of Shangyingou in recent years, their assemblage is similar to the lower fossiliferous bed of Baode (T. Deng, pers. comm.). The updated biostратigraphy and paleomagnetic dating (Zhu et al., 2008; Kackén et al., 2013) of the sequence in the Baode area place locality 31 and very probably locality 12 at 7.2 Ma. This is roughly correlated in Europe with late MN12–lower MN13. *Eomellivora wimani* is the type species of the genus and the remains from Shangyingou are the lectotype (Fig. 6B1–4).

The two individuals from China are very similar, but the lectotype is slightly larger. On the other hand, the largest P3–P4 and p3–m1 from Batallones-3 are similar in size to the lectotype of *E. wimani*. (Figs. 4, 5, 8). However, the two species possess many morphological differences that clearly distinguish them (Fig. 6): *Eomellivora wimani* has a slightly shorter muzzle and more robust dentition, specifically its P2 and p2. It also has a more pronounced concavity in the buccal wall of its P2–P4, a strong mesial cingulum in P2, a mesial accessory cusp in P3 with a more developed mesial cingulum, together with a more reduced M1 metacone and a more robust M1 protocone than in *E. piveteaui*. *E. wimani* also has a centrally located M1 protocone, where the lingual platform completely encloses the protocone, being mesiodistally larger than the *E. piveteaui* from Batallones. The mesial accessory cusp is more developed in the p4; it has a more robust m1 talonid with a more massive hypoconid, and the m2 of *E. wimani* seems more derived than the m2 of *E. piveteaui*, with a single buccal cuspid in a central position. Nevertheless, due to the fact that the Chinese specimen is worn, this last interpretation might be questionable.

Other localities with *E. wimani* (Table 3) are Kern River Formation site 50, California, U.S.A. (Hemphillian, Hh2), according to Tedford et al., 2004, and correlated to late MN12–lower MN13 according to Woodburne, 2010, described as *E. cf. wimani* by Stock and Hall (1933); Novaya Emotovka, Ukraine (MN12 according to Semenov, 2001), described by Orlov (1948) as *E. aff. wimani* and Györgyszentmárton 2, Hungary (MN12 according to Nargolwalla et al., 2006), described by Kretzoi (1965) as *E. orlovii*, and *E. rumana* from Cimisia, Moldova (MN12, according to Lungu and Rzebik-Kowalska, 2011), studied by Simionescu (1938).

*Perunium ursogulo* from Grebeniki (Ukraine) was described by Orlov (1948), based on a fragment of skull and two mandibles (Fig. 6C1–3). The age of this locality is MN11 (Hir and Kókay, 2010), based on three isolated teeth (P3, P4, and m1). Wolsan and Semenov (1996) synonymized it with *E. wimani wimani*. Despite substantial differences such as large upper dentition and a P3 with large lingual projection, there is not enough material to compare it with the other species of *Eomellivora*. We believe this material likely represents a distinct taxon, and yet because of the scarcity of the material and its lack of definitive diagnostic features, we assign them for now simply to *Eomellivora* sp. (Figs. 4, 5, 8, Table 3).

In their review of the Eurasian and North American *Eomellivora* material, Wolsan and Semenov (1996) considered this material to represent a single lineage of *Eomellivora*, subdivided into two chronospecies: one Vallesian (MN9–10) *E. wimani piveteaui* (including the material previously assigned to *E. liguriort Crasafont-Pairó and Ginsburg, 1973, from Los Valles de Fuentiduena) and another Turolian/Ventian (MN11–13) *E. wimani wimani*, including the specimen of *E. ursogulo* (Orlov, 1948) from Grebeniki. *E. hungarica* Kretzoi, 1942, from Polgárdi 2, *E. orlovii* Kretzoi, 1965, from Györgyszentmárton 2, and *E. rumana* Simionescu, 1938, from Cimisia. Although the taxonomic proposal put forth by Wolsan and Semenov (1996) has been accepted by several authors (e.g., Morlo, 1997; Qiu, 2003; Werdelin, 2003; Koufos, 2012), in view of the distinct morphological differences between the samples, it seems more reasonable to consider the existence of at least four species (*E. piveteaui, E. wimani, E. ursogulo*, and *E. hungarica*) as discussed above (Figs. 4–8, Table 3).

More recently, Morales and Pickford (2005) described the African *E. tugenensis*, from Ngorora Formation (Kenya), dated to about 12 Ma. This species is based on a fragmentary skull that contains a P4 with broken protocone and a complete M1. It is a primitive *Eomellivora* morphologically similar to *E. wimani* but much smaller (Werdelin and Peigne, 2010), being approximately intermediate in size between the extant *G. gulo* and *M. capensis*. The proportions of the P4 of *E. tugenensis* are similar to *G. gulo*, and thus very different than the other species of *Eomellivora*, but the proportions of the M1 are similar to the species of this genus (Figs. 4, 5, 7, 8), suggesting that these African remains could correspond to an ancestral form of the genus, although more material is needed to address this hypothesis.
FIGURE 10. Sequential reconstruction of the head of *Eomellivora piveteaux* from Batallones in lateral view. **A**, life appearance; **B**, reconstructed skull and mandible; skull and mandible, BAT-3-09.1000. Artwork by Adam Hartstone-Rose.
Phylogenetic Analysis

To better assess the relationships of *E. piveteaui* to other species of *Eomellivora* and within Mustelidae, we performed a cladistic analysis of nine taxa and 43 dental characters, being equally weighted and unordered (Figs. 7, 9). The complete list of taxa, characters, and character-taxon matrix are available in Appendices 1 and 2. We restricted our analysis of the fossils to *E. piveteaui* from Batallones, *E. wimani* from Shangyingou, and *E. ursogulo* from Grebeni—only the specimens with complete dental remains. Cladistic analysis was performed on this data set using PAUP*4.0b10 (Swofford, 2002). A bootstrap analysis was performed using 1000 replicates to test for resulting clade support. This analysis yielded a bootstrap tree of 98 steps, with a consistency index (CI) 0.5408, a homoplasy index (HI) 0.3977, and a retention index (RI) 0.4592, a homoplasy index (HI)

The cladogram shows that *Eomellivora* is the sister taxon of the extant *Mellivora capensis* (bootstrap 65%); thus, it is consistent to include it in the subfamily Mellivorinae (Fig. 9). This subfamily is characterized by a robust P3, with a high crown and marked buccal concavity, long relative to the P4; robust P4 with longer protocone; P4 relatively long and inclined backward; and M1 without metaconid, with a narrow talonid composed of a central hypoconid. Additionally, the monophyletic group *Eomellivora* is a well-supported clade (71% bootstrap support) (Fig. 9) characterized by a relatively slender M1 with an enlarged stylar area, and a very swollen lingual cingulum; M1 trigonid occupying almost three-fourths of the total length of the tooth, with a high talonid composed of a buccolingually compressed hypoconid; and M2 without metaconid. *E. wimani* and *E. ursogulo* form a well-supported crown group (91% bootstrap support) (Fig. 9) characterized by a triangular P2 with a strong lingual cingulum and a buccal concavity on the wall; P3 with mesial accessory cuspid present and very marked mesial cingulum; lingual platform of M1 completely enclosing the protocone; P2 very robust; P3 with a buccolingual platform; and P4 with a high mesial accessory cuspid.

Our phylogenetic hypothesis (Figs. 7, 9) indicates that *E. piveteaui* (MN9–10) had a common ancestor with the crown group *E. wimani*–*E. ursogulo* (MN11–13). *Eomellivora piveteaui* is found in Eurasia during biozones MN9 and MN10, being present in Western Europe (Los Valles de Fuentidueña and Batallones, Spain), Central Europe (Wissberg, Germany), Oriental Europe (Kalpa, Ukraine), Greece (Rabin de la Plui), and Turkey (Yasşören). During the Turonian, MN11–12, there appeared two more robust species of *Eomellivora*: *E. ursogulo* from Grebeni, only found in Ukraine, and the more common *E. wimani*, found in Oriental Europe (Novaya Emetovka 2, Ukraine and Cmišla, Moldova), China (Shangyingou and Liuwangou), and North America (Kern river Formation). Finally, the age of the genus extends to the end of the Miocene, Ventian, MN13 (Morales et al. 2013), with a large and robust species (*E. hungarica*) that has only been recorded in Polgárdi 2 (Hungary).

INSIGHTS INTO THE DIET OF EOMELLIVORA

The dentition of *E. piveteaui* has a mixture of features that can help us to interpret the feeding habits of this species. On the one hand, *E. piveteaui* possesses traits that can be interpreted as hypercarnivorous, based on features that emphasize the shearing function: (1) straight dental series; (2) long and buccolingually compressed m1 trigonid; and (3) loss of the m1 metaconid. All of these are features it shares with the extant *Gulo gulo* and *Mellivora capensis* and as well as with the extinct *Ekorus ekakeran*, *Megalictis ferox*, and the other species of *Eomellivora*; (4) the presence of a trenchant hypoconid centrally located on the m1 talonid, shared with all species of *Eomellivora*, that show a higher and more buccolingually compressed hypoconid than *M. ferox* and *Ekorus ekakeran*; and (5) m1 and m2 cuspsids in line with the dental series, thereby increasing the length of the cutting edges. In contrast, *Eomellivora piveteaui* possesses other characteristics that could be interpreted as adaptations to durophagy and/or carcass processing: (1) p3–p4 blunt posterior accessory cuspsids; (2) P4 protocone robust; (3) robust M1 lingual cingulum; and (4) distal widening of P3 and p3. Lungu (1978) considers *E. piveteaui* to be a smaller-sized *Eomellivora* with a more slender dentition than *E. wimani*, *E. ursogulo*, *E. hungarica*, and *Eomellivora* from Csákvár being a more primitive and less specialized species for crushing bones. Consequently, the complete sample of *E. piveteaui* from Batallones has allowed us to distinguish the existence of two dietary ecomorphotypes in the genus: (1) a group of smaller-size *Eomellivora* adapted to a more hypercarnivorous diet composed of *E. piveteaui* (Fig. 8), similar to that of the hypercarnivorous *Ekorus ekakeran*; and (2) a larger and robust *Eomellivora* composed of *E. wimani*, *E. ursogulo*, *E. hungarica*, and *Eomellivora* sp. from Csákvár characterized by having greater dimensions, and a higher and a greater number of blunt accessory cusps (Fig. 8), that may be adapted to a diet with a higher proportion of bone, similar to the extant durophage *G. gulo* (Larivière and Jennings, 2009) (although the higher number of accessory cusps would indicate greater hypercarnivory by some metrics; Hartstone-Rose, 2011; Hartstone-Rose and Synder, 2013). The widening of some premolars, together with the more sectorial dentition in *E. piveteaui*, could be considered a hypercarnivorous specialization towards a more hypercarnivorous canid-like animal, capable of processing bones with its molars to maximize access to the available food.

*Eomellivora piveteaui* (Fig. 10) could have accessed a wide variety of prey items present in the fauna of Batallones. It likely occupied an ecological niche of an active predator of medium to large prey such as moschids, small- to medium-sized bovids, and young suids or cervids, while maintaining the ability to hunt small prey such as reptiles, birds, and lagomorphs. It may have occupied an intermediate ecological role between the opportunist extant *Mellivora capensis* and the predominantly scavenging extant *G. gulo*. Moreover, *E. piveteaui* may have used its dentition to more fully process carcasses of its own prey, as happens with *M. capensis*, which is capable of consuming prey completely, including small bones (e.g., large lizards, snakes, or small mammals), but not so much as the efficient scavenger *G. gulo* (Ewer, 1998; Begg et al., 2003; Larivière and Jennings, 2009). Moreover, preliminary observations of the postcranial remains of *E. piveteaui* from Batallones show that the taxon had relatively long fore- and hind limbs, similar to extant canids that tend to have a high proportion of meat in their diet (e.g., *Canis lupus*). This could suggest possible cursorial adaptations in *E. piveteaui*. Future study of the postcranial remains could help determine whether this taxon was a pursuit predator and shed light on our understanding of its role in the Batallones ecosystem.

CONCLUSIONS

The craniomandibular features of the material from Batallones is assigned to the *Eomellivora piveteaui*, Ozansoy, 1965, providing a fuller picture of this species, supplementing the previously known material from Yassióren and allowing the increased validation of the taxon at the specific level. The sample of *E. piveteaui* from Batallones permits the refinement of the diagnosis of the species, as well as expanding its age to MN10. Moreover, detailed comparisons with the rest of the species of *Eomellivora* show several morphological features that lead us to accept *E. piveteaui*, *E. wimani*, *E. ursogulo*, and *E. hungarica*. *Eomellivora* is the sister taxon of the extant *Mellivora capensis*, and *E. piveteaui* had a common ancestor with the crown group *E. wimani*–*E. ursogulo*. *Eomellivora piveteaui* was a large mustelid (Fig. 10) adapted to a more hypercarnivorous diet than the
largest extant terrestrial mustelids (e.g., *G. gulo* and *M. capensis*), and the other species of *Eomellivora* and also shows some bone-crushing or carcass-processing adaptations. In addition, we suggest that *E. piveteauii* may have had an active predatory role, exploiting both small and relatively large prey.

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APPENDIX 1. Description of characters used in phylogenetic analyses.

1. P1. Present (0); absent (1).
2. P2. The largest axis of P2 in line with P3 (0); the largest axis of P2 rotated (1).
3. P2. Distal accessory cusp of P2 present (0); absent (1).
4. P2. Occlusal morphology: subrectangular (0); triangular (1); oval (2).
5. P2. Marked concavity in the buccal wall: absent (0); present (1).
6. P2. Lingual cingulum weak (0); strong (1).
7. P3. Occlusal morphology: subrectangular with an absent or reduced lingual expansion (0); triangular with a well-developed lingual expansion (1).
8. P3. Robustness ratio [(maximum width/maximum length) × 100]; slender P3 (less than 50) (0); robust P3 (more than 50) (1).
9. P3. Maximum length of P3 in relation to maximum length of P4 ratio [(L P3/L P4) × 100]; P3 relatively reduced (less than 55) (0); P3 relatively long (more than 55) (1).
10. P3. Ratio between the height of P3 and P4 paracone [(maximum height P3/maximum height P4) × 100]; height P3 not enlarged (less than 65) (0); height P3 enlarged (more than 65) (1).
11. P3. Development of the mesial accessory cusp reduced or absent (0); present (1).
12. P3. At least one distal accessory cusp present (0); absent (1).
13. P3. Marked concavity in the buccal wall: absent (0); present (1).
14. P3. Mesial cingulum poorly developed (0); strong or very developed (1).
15. P4. Robustness ratio [(maximum width/maximum length) × 100] and size of the protocone: slender P4 with (less than 60) slender protocone (0); robust P4 (more than 60) with robust protocone (1).
16. P4. Protocone in line with the mesiobuccal corner or surpass the mesiobuccal corner of the tooth (0); protocone distal to the mesiobuccal corner (1).
17. P4. Without parastyle or poorly developed parastyle (0); strong parastyle (1).
18. P4. Mesial inflection between the paracorne and the paracone: deep (0); shallow (1).
19. P4. Pronounced concavity in the buccal wall: absent (0); present (1).
20. M1. Robustness ratio [(maximum width on the buccolingual area/matrix length) × 100]: slender M1 (from 130 to 150) (0); very slender M1 (more than 160) (1).
21. M1. Cingulum of M1 conspicuously swollen buccally: absent (0); present (1).
22. M1. Development of the styler area small (0); enlarged or very developed (1).
23. M1. Metacena not reduced (0); reduced (1).
24. M1. Protocone mesiolingually located (0); almost centrally on the middle of the talonid (1).
25. M1. Lingual platform not completely enclosing the protocone (0); completely enclosing the protocone (1).
26. p1. Present (0); absent (1).
27. p2. Development of the distal accessory cuspid present (0); reduced or absent (1).
28. p2. Robustness ratio [(maximum width/matrix length) ≤ 100]: slender p2 (less than 50) (0); robust p2 (from 50 to 70) (1); very robust p2 (more than 70) (2).
29. p3. Development of the distal accessory cuspid present and well developed (0); absent or poorly developed (1).
30. p3. Buccolingual platform of the crown absent (0); present (1).
31. p4. Length ratio in relation to m1 [(maximum length p4/matrix length m1) × 100]: p4 not reduced (from 50 to 60) (0); p4 relatively enlarged (more than 60) (1).
32. p4. Ratio between the height of p4 and m1 paraconid [(maximum height p4/matrix height m1 paraconid) ≤ 100]: p4 lower than m1 paraconid (less than 100) (0); p4 higher than m1 paraconid (more than 100) (1).
33. p4. Development of the mesial accessory cuspid absent or poorly developed (0); present with great height development (1).
34. p4. Development of the distal accessory cuspid present and well-developed (0); absent or vestigial (1).
35. p4. Development of a metaconid or labial accessory cuspid absent (0); incipient or developed (1).
36. p4. Development of a conspicuous buccodistal ledge absent (0); present (1).
37. p4. Backward inclination of the main cuspid: p4 practically vertical (90°–80°) (0); p4 with backward inclination (less than 80°) (1).
38. m1. Development of the metaconid present (0); absent (1).
39. m1. Relative length of talonid with respect the total m1 length: the talonid 1/3 of the total length (0); equal or less than 1/4 of the total length (1).
40. m1. Maximum buccolingual width of m1 located in talonid (0); narrow talonid without the maximum buccolingual width in the talonid (1).
41. m1. Height of hypoconid [(height of m1 hypoconid/height m1 protoconid) ≤ 100]: short hypoconid (equal or less than 50) (0); tall hypoconid (equal or more than 60) (1).
42. m1. Size and position of hypoconid: small size and labially located (0); strong and central position (1).
43. 2m2. Development of the metaconid present (0); absent (1).

APPENDIX 2. Character-taxon matrix used for phylogenetic analysis.

| Taxon                     | 10 | 20 | 30 | 40 |
|--------------------------|----|----|----|----|
| Eomellivora piveteai     | 01 | 01 | 01 | 11 |
| Eomellivora wimani       | 01 | 01 | 01 | 11 |
| Eomellivora ursogulo     | 01 | 01 | 01 | 11 |
| Gulo gulo                | 01 | 01 | 01 | 11 |
| Mellivora capensis       | 01 | 01 | 01 | 11 |
| Pekania pennanti         | 01 | 01 | 01 | 11 |
| Eira barbara             | 01 | 01 | 01 | 11 |
| Martes martes            | 01 | 01 | 01 | 11 |
| Canis lupus              | 01 | 01 | 01 | 11 |