Re-evaluation of the very large *Eomellivora fricki* (Pia, 1939) (Carnivora, Mustelidae, Mellivorinae) from the Late Miocene of Austria

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ABSTRACT

We re-evaluated the Austrian material for *Hadrictis fricki* Pia, 1939, from the localities Wien XII-Altmannsdorf and Gaiselberg (MN9, Vallesian, Late Miocene), concluding that *Hadrictis* can be considered as a synonymy of *Eomellivora* Zdansky, 1924; we therefore named it as *Eomellivora fricki*. This species is one of the earliest representatives of the genus, together with *E. piveteaui* Ozansoy, 1965. Our phylogenetic analyses indicate that *Eomellivora* forms a monophyletic group, establishing the sister clade of the large and derived Late Miocene *Ekorus ekakeran*. *Eomellivora fricki* shows a primitive dental morphology and is the largest species of the genus. This species shows the complexity of the genus *Eomellivora*, in which large and small species coexisted since the beginning of the Late Miocene.

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INTRODUCTION

Mustelidae is the most diverse family within the currently existing Carnivora, comprising 57 extant species of weasels, martens, polecats, badgers and otters (Larivière and Jennings, 2009). The Mellivorinae Gray, 1865, is the subfamily containing *Mellivora capensis* (Schreber, 1776) as the only living representative, commonly known as the ratel, or honey badger. It is the largest African terrestrial mustelid, weighing between 6.2 and 13.6 kg, and with a distribution range from Africa to India (Larivière and Jennings, 2009). It is a generalist and opportunistic predator, with a wide range of prey; it presents clear regional differences in its diet, which mostly involves rodents, other carnivorans (e.g., *Suricata, Felis, Cynictis, Ictonyx*), amphibians, reptiles, birds and invertebrates, but also includes roots, berries and fruits (Begg et al., 2003; Larivière and Jennings, 2009). Notwithstanding the fact that only one monospecific genus has survived up to the present, this subfamily was more diversified in the past. This mellivorine diversity is well reflected in the Neogene fossil record, although the remains are mostly fragmentary (Baskin, 1998; Morales et al., 2015, Werdelin and Peigné, 2010). The origin of the subfamily is unclear, but most likely arose in Eurasia or Africa, during the Middle Miocene and early Late Miocene with *Sivamellivora* Kretzoi, 1942, *Mellalictis* Ginsburg, 1977 and *Eomellivora* ?*tugenensis* Morales and Pickford, 2005. *Sivamellivora necrophila* (Pilgrim, 1932) comes from the Lower Siwaliks (India), Chinji formation ca. 14-11.2 m.y.a. (Patnaik, 2013) and is based on very few teeth and an edentulous mandible. *Mellalictis mellalensis* Ginsburg, 1977 from Beni Mellal (Morocco) ca. 12.5-11.2 m.y.a. (Werdelin and Peigné, 2010) is known by its isolated teeth and postcranial fragments. It is uncertain, however, whether it is a Mellivorinae or a mustelinae (Bonis et al., 2009). *Eomellivora* ?*tugenensis* Morales and Pickford, 2005 from the Ngorora formation (Kenya), ca. 12 m.y.a., is a poorly known mustelid of medium size that could constitute an ancestral form of *Eomellivora* (Valenciano et al., 2015).

Since the beginning of the Late Miocene, new genera of mellivorines radiated throughout Eurasia and Africa, e.g., *Ekorus* Werdelin, 2003 (assigned to Mellivorinae in this manuscript), *Eomellivora* Zdansky, 1924, *Erokomellivora* Werdelin, 2003, *Hadrictis* Pia, 1939, *Howellictis* Bonis et al., 2009, *Mellivora* Storr, 1780 and *Promellivora* Pilgrim, 1932. Some of them, such as *Ekorus* and *Eomellivora* (=*Hadrictis*), reached a significantly large size, which is why they are considered as giant mustelids. *Eomellivora* and *Ekorus* were one of the largest and most hypercarnivorous mustelids ever known; they were larger than the extant wolverine, *Gulo gulo*, but according to their cranium dimensions, they were smaller than the Oligobuninae *Megalictis ferox* (Werdelin, 2003; Valenciano et al., 2015, 2016). *Eomellivora* has been described in Asia, North America, Europe and Africa (e.g., Wolsan and Semenov 1996; Morales and Pickford, 2005; Valenciano et al., 2015), spanning from the Middle (MN8) to the Late Miocene (MN13). The first complete review of the genus was conducted by Wolsan and Semenov (1996); it concluded that this genus represents a single lineage of *E. wimani* Zdansky, 1924, which they subdivided into the chrono-subspecies *E. wimani piveteaui* for the Vallesian (MN9-10) specimens, and *E. wimani wimani* for the Turolian/Ventian (MN11-13) ones. More recently, a sample of *E. piveteaui* Ozansoy, 1965, from Batallones (Late Miocene, MN10, Madrid, Spain) has been described by Valenciano et al. (2015); this has enabled *E. piveteaui*, *E. wimani*, *E. ursogulo* (Orlov, 1948) and *E. hungarica* Kretzoi, 1942, to be accepted as valid species. However, neither Wolsan and Semenov (1996) nor Valenciano et al. (2015) analyzed the very large-sized mustelid *Hadrictis fricki* Pia, 1939.

Hadrictis fricki was described by Pia (1939) from the Austrian locality of Wien XII-Altmannsdorf, Late Miocene (MN9), by a largely fragmented skull that includes a worn P4-M1. Subsequently, Zapfe (1948) described a hemimandible with a worn dentition as *H. fricki* from Gaiselberg (Austria), Late Miocene (MN9). The systematic position of *Hadrictis* is doubtful - it constitutes a valid genus for some authors (Pia, 1939; Zapfe, 1948; Kretzoi 1942, 1965; Ozansoy, 1965; Webb, 1969; Ginsburg, 1977), whereas for others it is a synonym of *Eomellivora* (Werdelin, 1996, 2003; Peigné et al., 2006). However, the mandible of *H. fricki* described by Zapfe (1948) has been ignored and never compared with any other species of *Eomellivora*. The
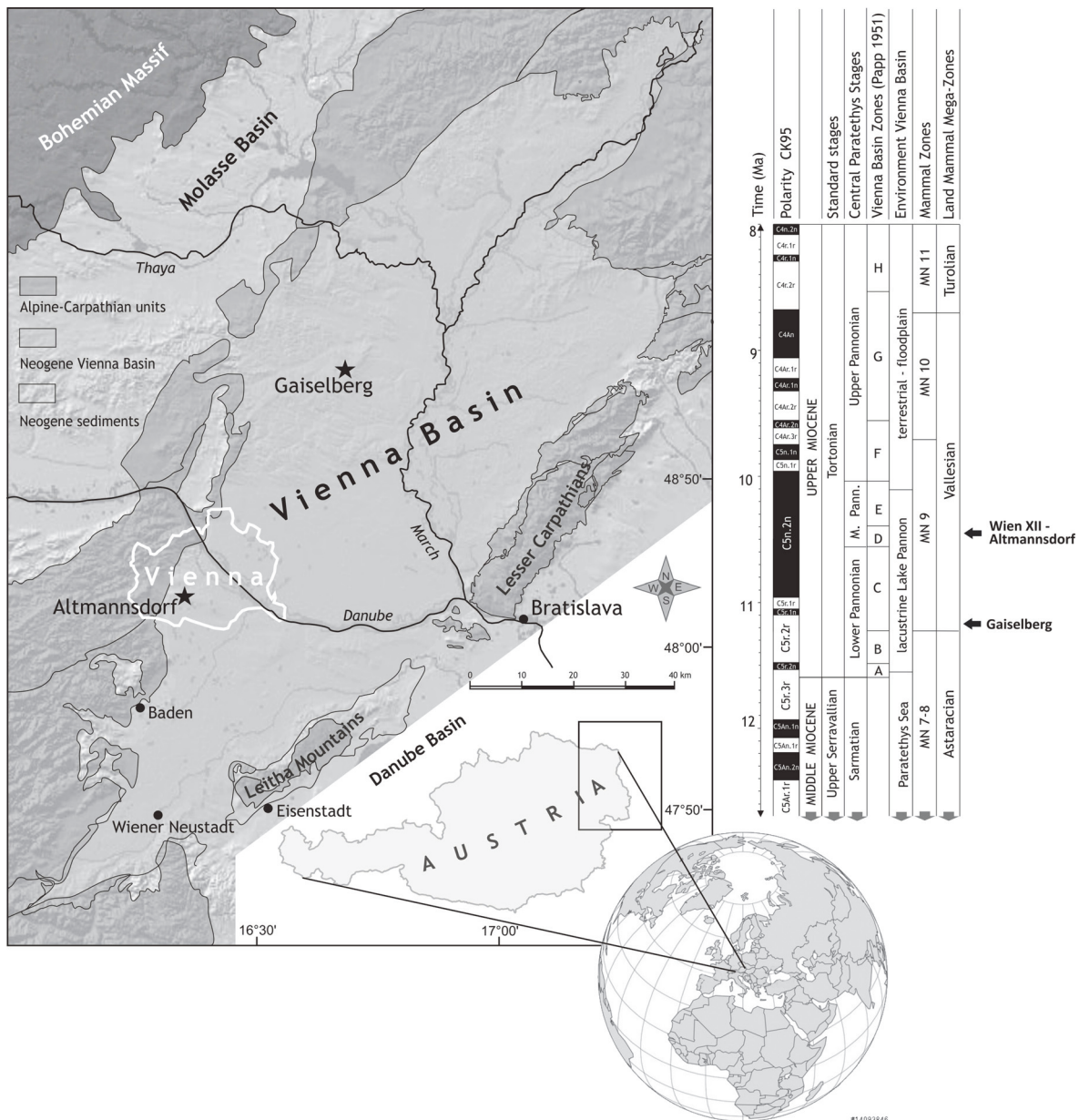
FIGURE 1. Vienna Basin with geographic and stratigraphic position of localities (asterisks) (modified after Harzhauser et al., 2004, figures 1 and 2).

objectives of the present manuscript are twofold: (1) to re-describe and re-measure the material described by Pia (1939) and Zapfe (1948), and (2) to re-evaluate the systematic position of *H. fricki* in the light of the new evolutionary framework of *Eomellivora* proposed by Valenciano et al. (2015).

Localities and Geological Setting

Both Austrian localities, Wien XII-Altmannsdorf and Gaiselberg, are situated in the Vienna Basin, which forms the northwestern part of the Pannonian Basin (Figure 1). During the Pannonian

stage the foregone disintegration of the Central Paratethys has restricted Lake Pannon to the Pannonian Basin system. The first brackish-lacustrine and subsequent fluvial-influenced deposits of Lake Pannon are biostratigraphically subdivided into the Pannonian A to H biozones, based on molluscs (Papp, 1951). Both sites yielded a Late Miocene (Pannonian) vertebrate fauna (e.g., Pia, 1939; Thenius, 1948; Zapfe, 1949) including fossils of the three-toed horse *Hippotherium* sp., which FAD (First Appearance Datum) is MN9.

TABLE 1. Fossil vertebrate fauna Wien XII-Altmannsdorf (Griesergasse, Oswaldgasse) (updated by U.B.Göhlich, based on Pia (1939) and Thenius (1948)).

Wien XII-Altmannsdorf

Carnivora

    Eomellivora fricki (formerly *Hadrictis*)

    Lycaena chaeretis

Perissodactyla

    Aceratherium incisivum

    Hippotherium sp.

Artiodactyla

    Miotragocerus pannoniae

    Propotamochoerus palaeochoerus

Proboscidea

    Deinotherium giganteum

TABLE 2. Fossil vertebrate fauna from Gaiselberg (uddated by U.B. Göhlich, based on Zapfe (1949), Thenius (1950), Pickford (2016) and J. Giaourtsakis (personal commun., Athens, 2014).

Gaiselberg

Carnivora

    Eomellivora fricki (formerly *Hadrictis*)

    Amphicyon sp.

    Felidae indet.

Perissodactyla

    Aceratherium incisivum

    Hoploaceratherium sp.

    Hippotherium sp.

    Anchitherium aurelianense

    Chalicotherium goldfussi

Artiodactyla

    Conohyus doati (formerly *Hyotherium palaeochoerus*)

    Dorcatherium naui

    Miotragocerus pannoniae

    Bovidae indet (smaller than *M. pannoniae*)

Proboscidea

    Deinotherium giganteum

    Tetralophodon longirostris

Wien XII-Altmannsdorf (Grießergasse clay and sand pit). Altmannsdorf is a quarter in the 12th urban district (Wien XII-Meidling) in the southwest of the city of Vienna. Vertebrate fossils in this area have been found mostly in historic sand and clay pits, in which the so-called "Congerientegel" (Schaffer, 1904) was exploited for brick production. Two nearby clay pits, one located in Grießergasse Street and the other in Oswaldgasse Street, have been active until about 1926 (Pia, 1939). At present, all the clay and sand pits have disappeared, and the area has become densely built up. Pia (1939) pointed out that the names of the nearby pits "Grießergasse," "Oswaldgasse," and even the general term "Altmannsdorf," as the provenance for the vertebrate fossils, were used arbitrarily by the clay pit workers. However, the outcropping deposits in these nearby pits can be expected to be the same.

The fossil of *Hadrictis fricki* from Altmannsdorf was bought together with other vertebrate fossils (Table 1) by the Naturhistorisches Museum Wien (Vienna, Austria) in 1912 from a clay pit worker, who indicated the precise locality as "Grießergasse" (Pia, 1939). Due to the presence of the snail *Melanopsis fossilis pseudoimpressa* Papp, 1953, in the deposits of the "Oswaldgasse" pit (Papp, 1953), these deposits can be correlated with the biozone Pannonian D (Middle Pannonian), corresponding to the Mammalian Neogene Unit MN9 (Figure 1).

Gaiselberg. The Late Miocene deposits of Gaiselberg near Zistersdorf (Lower Austria) belong to the Hollabrunn-Mistelbach Formation, which represents sediments of a braid-delta system dis-charged by the paleo-Danube in the Vienna basin into Lake Pannon (Nehyba and Roetzel, 2004). Three sand pits in the village of Gaiselberg yielded an early Vallesian vertebrate assemblage (Table 2), which was studied by Zapfe (1949). The presence of the bivalve *Congeria partschi,* the more plesiomorphic dental morphology of *Hippotherium* sp. (Woodburne, 2009), and the co-occurrence of the two equids, *Hippotherium* (FAD) and *Anchitherium* (LAD), in Gaiselberg (Thenius, 1950; Daxner-Höck and Bernor, 2009) indicate an early Pannonian age, corresponding to the biozones earliest Pannonian C and earliest MN9, respectively (Figure 1).

MATERIAL 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), and Evans and de Lahunta (2010, 2013).

Measurements were made with Mitutoyo Absolute digital calipers accurate to 0.1 mm.

Institutional Abbreviations

AMNH, American Museum of Natural History, Division of Mammalogy, New York, USA; **BAT**, Batallones localities collection from the MNCN; **IPUW**, Institut für Paläontologie, Universität Wien, Vienna, Austria; **MFGI,** Geological and Geophysical Institute of Hungary, Budapest, Hungary*;* **MNCN**, Museo Nacional de Ciencias Naturales, Madrid, Spain; **MNHN**, Muséum National d´Historie Naturelle, Paris, France; **NHMW**, Naturhistorisches Museum Wien, Vienna, Austria; **NRM**, Naturhistoriska Rikmuseet, Stockholm, Sweden; **PIN**, Palaeontological Institute, Russian Academy of Sciences, Moscow, Russia; **PMU**, Palaeontological Museum, University of Uppsala, Uppsala, Sweden.

Studied Material

The fossil remains of *E. fricki* from Austria are stored in the fossil vertebrate collections of the Department of Geology and Palaentology at the NHMW, Austria: NHMW 2016/0065/0001: very fragmented skull with P4-M1 from Wien XII-Altmannsdorf, Vienna, Austria, MN9; NHMW 1977/1948/0130: partial hemimandible with broken c, alveoli of p1 and p2, a complete p4 and m1 and an alveolus for m2 from Gaiselberg, Lower Austria, Austria, MN9. For comparison we studied the lectotype of *E. piveteaui* (MNH-TRQ-1004), and *E. piveteaui* (MNH-TRQ-1005), both from Yassiören, Turkey, MN9, housed at MNHN; *E. piveteaui* from Batallones (see Valenciano et al., 2015), Spain, MN10, housed at MNCN; the holotype of *E. ursogulo* (PIN-No.268) from Grebeniki, Ukraine, MN11 housed at PIN (available as a cast at IPUW and NHMW); the holotype of *E. hungarica* (MFGI-Ob-2676) from Polgárdi 2, Hungary, MN13, housed at MFGI; the lectotype of *E. wimani* from Shangyingou (PMU-M3692 and PMU-M3693) and *E. wimani* from Liuwangou (PMU-M3847), both from China, MN12-13, housed at PMU; a cast of the holotype of *Ekorus ekakeran* from Lothagan, Kenya, (~MN12-13), housed at NRM (Lars Werdelin´s collection); *Ischyrictis zibethoides* (Blainville, 1842) from Sansan, France, MN6, housed at MNHN; *Plesiogulo crassa* Teilhard de Chardin, 1945, from Localities 30, 108 and 111, China, MN10-12 (Kurtén, 1970) housed at PMU. The fossils from *Howellictis valentini* from Toros Menalla 192 (Chad) (~MN12), were studied based on the publication of Bonis et al. (2009). The studied extant carnivorans were the mustelids *Mellivora capensis*, *Pekania pennanti*, *Martes foina*, *G. gulo* and the canid *Canis lupus*, housed at AMNH, NRM and MNCN.

Cladistic Analysis

We performed a cladistic analysis to better assess the relationships of *E. fricki* with other large Middle and Late Miocene taxa presenting similar hypercarnivorous dentition and with nearly complete remains, such as *Ek. ekakeran*, *E. piveteaui*, *E. wimani*, *E. ursogulo*, *E. hungarica*, *H. valentini, I. zibethoides*, *P. crassa*, and the living gulonines *Martes foina*, *Pekania pennanti*, *G. gulo*, the mellivorine *M. capensis* and the canid *Canis lupus*. We did not include in the analysis the African species of *Eomellivora ?tugenensis* or other mellivorines (e.g., *Mellalictis*, *Promellivora*, *Erokomellivora*, *Mellivora benfieldi*) due to the incompleteness of the preserved remains. The cladistic analysis includes 14 taxa and 70 equally weighted and unordered dental and cranial characters generated by us; some of them were modified from Bryant et al. (1993), Wolsan (1993), Baskin (2004) and Valenciano et al. (2015, 2016; Appendix 1). The matrix can be observed in Appendices 2 and 3. The analysis was performed using PAUP*4.0b10 (Swofford, 2002).

SYSTEMATIC PALAEONTOLOGY

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

Type species. *Eomellivora wimani* Zdansky, 1924 by original designation.
Included species. *Eomellivora wimani* Zdansky, 1924; *Eomellivora fricki* (Pia, 1939); *Eomellivora hungarica* Kretzoi, 1942; *Eomellivora ursogulo* (Orlov, 1948); *Eomellivora piveteaui* Ozansoy, 1965; *Eomellivora ?tugenensis* Morales and Pickford, 2005.
Diagnosis. Modified after Wolsan and Semenov (1996) and Werdelin and Peigné (2010). Mellivorine mustelid of large size; P1 present; P3 with one or two distal accessory cusps; P3 with the distal area thickened; P4 with a subconical protocone, and with paracone-protocone and paracone-parastyle crests; P4 protocone located in line with the parastyle; P4 parastyle poorly-developed but thickened; buccal wall of P4 with a concavity in the base of the crown between the paracone and the metastyle, exhibiting a variable degree of development; stylar area of M1 enlarged; M1 with a non-reduced metacone in the earlier species and a reduced one

in the Turolian-Ventian; M1 with an arched ridge-shaped or conical protocone continuing into the mesial protocone crest, and a talon relatively equally expanded mesially and distally; premolar teeth crowned; p1 present; p2 turned buccolingually from the tooth row; p3 with a distal accessory cuspid and with the distal area thickened; p4 enlarged with a distal accessory cuspid and with a backward inclination of the main cuspid towards the m1; m1 enlarged with the m1 metaconid residual in some of the earliest species and absent in the others, in which it is replaced by a distinct crest; m1 talonid with single but strong, high and centrally positioned hypoconid; m2 elongated mesiodistally with a low crown surrounded by a cingulum and a central protoconid.

Eomellivora fricki (Pia, 1939)
Figure 2, Table 3

1939   *Hadrictis fricki* Pia, p. 538, figures 1-5.
1942   *Hadrictis fricki* Kretzoi, p. 319.
1948   *Hadrictis fricki* Zapfe, p. 244, figure 1.
1965   *Hadrictis fricki* Ozansoy, p.25.
1965   *Hadrictis fricki* Kretzoi, p.131.

Holotype. NHMW 2016/0065/0001, comprising several small fragments of a cranium, including a portion of maxilla with P4 and M1.

Type locality. Wien XII-Altmannsdorf (Vienna, Austria).

Other locality. Gaiselberg (Lower Austria, Austria).

Stratigraphical distribution. Late Miocene (MN9).

Diagnosis. For cranium and upper dentition in Pia (1939) and for mandible and lower dentition in Zapfe (1948).

Emended diagnosis. *Eomellivora* of very large-size, with a relatively large P4 and M1. M1 with an enlarged stylar area, metacone not reduced, protocone ridge-edge located mesially with a prominent lingual platform. Very robust mandible, with a large c, presence of p1, rectangular p4 without a mesial accessory cuspid, a large m1, and a relatively large m2, according to its alveolus.

Differential diagnosis. Differs from all the species of *Eomellivora* in a larger dentition, in the presence of a residual m1 metaconid and in a stouter mandibular corpus. Differs from *E. piveteaui* in a bigger M1 metacone, in a larger distal platform in M1 and in a shorter mandible. Differs from *E. wimani* in a less concave buccal base of the P4, in a more developed M1 metacone and a non-cuspid-like M1 protocone; Furthermore, it differs in the absence of a mesial accessory cuspid in p4 and a shorter

mandible. Differs from *E. ursogulo* in a better developed M1 metacone and a non-cuspid-like protocone; additionally it differs in the absence of a mesial accessory cuspid in p4, in possessing only one distal accessory cuspid in p4 and in a shorter mandible. Differs from *E. hungarica* in a much more developed M1 with a larger metacone and larger distal platform in M1 and in the absence of a mesial accessory cuspid in p4.

Description. NHMW 2016/0065/0001 comprises five little fragments of an incomplete cranium from Wien XII-Altmansdorf previously described by Pia (1939): (1) a fragment of the left maxilla with the distal part of the P3 alveoli and a worn P4-M1 (Figure 2.1-4; Table 3). It also shows the most rostral portion of the zygomatic arch and the ventral part of the infraorbital foramen; (2) an homologous edentulous fragment of the right maxilla (Figure 2.5-6) with the distal part of the P3 alveolus, the alveoli of P4 and one broken root of the M1; (3) a small fragment of the left zygomatic arch, fitting the frontal process of the zygomatic (Figure 2.7); (4) a small fragment of the left temporo-mandibular joint with a partial glenoid cavity (Figure 2.8); and (5) a fragment including the right mastoid process, the ventral part of the nuchal crest, the external auditory meatus and part of the glenoid cavity (Figure 2.9-10). Neither the alisphenoid canal nor a suprameatal fossa can be observed.

The distal part of the P3 alveolus is very wide, which indicates that the distal end of the P3 is wide. The P4 is strongly worn in the distal and occlusal area (Figure 2.1-4). It displays a very low but robust parastyle and a paracone-parastyle crest. The protocone, which is strongly worn, is subconical, robust and located in line with the mesial corner of the P4. Despite this wear, an inflection between the protocone and parastyle is visible. There is also a concavity in the buccal wall between the paracone and the metastyle. The M1 is a very large tooth with a typical morphology of *Eomellivora*, with the buccal wall narrower than the lingual one. It shows an enormous wear facet in the paracone, in the metacone and in the mesial part close to the protocone, as well as in the most distal corner of the tooth (Figure 2.2, 2.4). The mesial wear facet of the M1 is caused by the occlusion with the metaconid area of the m1, and the distal wear facet is produced by the occlusion with the m2. The stylar area is greatly enlarged. The paracone is conical and situated in the mesiobuccal corner. The metacone is also quite well developed and is surrounded by a distal expansion. The protocone is ridge-shaped, and it is mesiolingually
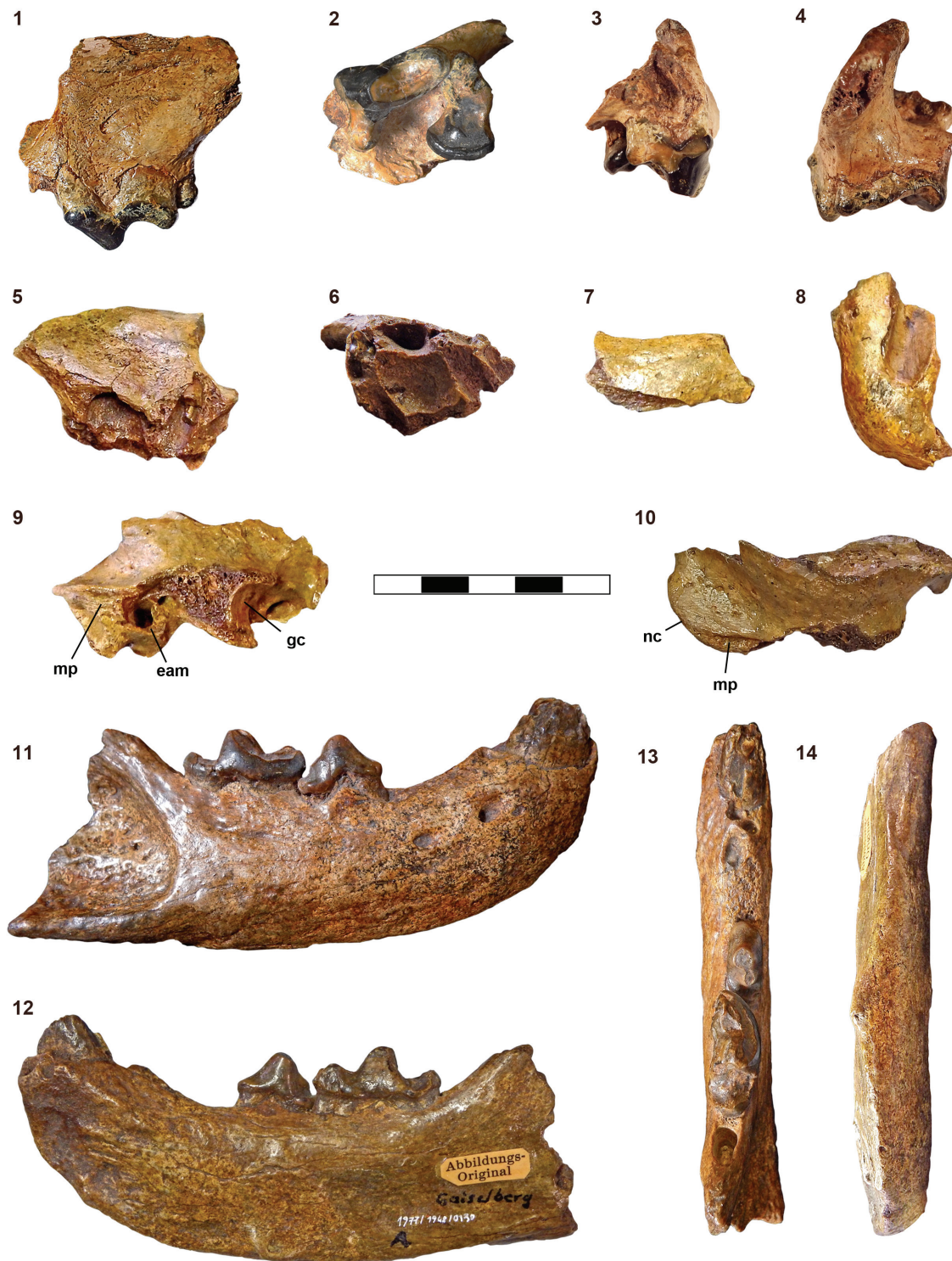
FIGURE 2. Fossil remains of *Eomellivora fricki* (Pia, 1939) from Wien XII-Altmannsdorf and Gaiselberg. **1-4,** Holotype NHMW 2016/0065/0001 from Wien XII-Altmannsdorf, left maxilla fragment, **1,** lateral view, **2,** occlusal view, **3,** rostral view, **4,** caudal view; **5-6,** right maxilla fragment, **5,** lateral view, **6,** occlusal view; **7,** fragment of the left zygomatic arch; **8,** fragment of the left temporo-mandibular joint; **9-10,** fragment with the right mastoid process (mp), the ventral part of the nuchal crest (nc), the external auditory meatus (eam), and part of the glenoid cavity (gc), **9,** lateral view, **10,** dorsal view; **11-14,** NHMW 1977/1948/0130 right hemimandible from Gaiselberg. **11,** lateral view, **12,** medial view, **13,** occlusal view, **14,** ventral view. Scale bar equals 5 cm.

7

TABLE 3. Upper and lower teeth measurements (in mm) of *Eomellivora fricki* (Pia, 1939). L (length) and W (Width). The measurements for the p2 and m2 of NHMW 1977/1948/0130 are based on its alveolus.

	P4		M1		c		p2		p4		m1		m2	
	L	W	L	W	L	W	L	W	L	W	L	W	L	W
NHMW 2016/0065/0001	24.6	17.7	14.9	22.5										
NHMW 1977/1948/0130					15.1	10.8	11.5	5.7	17.9	8.7	26.5	10.5	9	5.6

located. There exists a swollen lingual platform that completely encloses the protocone.

The right hemimandible NHMW 1977/1948/0130 comes from Gaiselberg (Lower Austria) and was previously described by Zapfe (1948). The fragment has a total length of 123.37 mm. The mandible is very short, robust and dorsoventrally deep (Figure 2.11-14; Table 3). The height of the ramus, ventral to the m1, is 31 mm, and maximum width is 16.6 mm. The surface of the mandibular corpus is quite smooth, indicating some degree of alteration in its original morphology, likely due to a process of erosion by transport. The ventral margin is convex, with a medial bulge ventral to the distal part of the p4 on the ventromedial margin of the mandibular corpus. There are two rounded mental foramina, one ventral to the p2 and another ventral to the distal area of the p3. The mandibular symphysis is rather vertical and stout. The preserved dentition comprises c, p4 and m1 and the alveoli for i2-3, p1-2 and m2. The c is robust and elliptical in cross section, but the tip is broken off. The alveolus of the p1 is rounded. The p2 is two-rooted. The alveoli for the p2 are buccolingually rotated relative to the tooth row. The length of its alveoli suggests a long p2. This hemimandible has no alveoli for the p3; rather, there is a porous surface over the mandible, indicating that the tooth was lost when the animal was alive and reflects a complete closure of the alveoli. The p4 is long and sub quadrangular with a slight distal broadening. It presents no mesial accessory cuspid. The main cuspid is well worn and is inclined distally toward the m1. The distal accessory cuspid is high but also worn. The distal cingulum is high and shows a wear facet in the distobuccal corner of the p4, resulting from the occlusion with the P4. The m1 is very large and well worn. The trigonid occupies two-thirds of the total length of the tooth and bears a buccal wear facet on the trenchant blade. Between the paraconid and the protoconid there is a lingual concavity at the base of the crown. A residual metaconid can be observed (Figure 2.12). The talonid appears to have been high; however, due to its degree of wear this cannot be assured. The hypoconid is in a cen-

tral position. The oval alveolus for m2 indicates a relatively large m2. It has a buccolingual constriction between the roots.

RESULTS

The results of our cladistics analysis provide one single most parsimonious tree (Figure 3). Apomorphies for each node are reported in Table 4. The topology of the tree clearly indicates the presence of two major clades corresponding to the subfamily Guloninae Gray, 1825, and Mellivorinae. The clade Mellivorinae comprises the taxa *E. fricki*, *E. piveteaui*, *E. hungarica*, *E. wimani*, *E. ursogulo*, *Ek. ekakeran*, *M. capensis* and *H. valentini*. This clade shares among others, the following traits (Table 4): (1) posterior lacerate foramen and jugular foramen with separate openings, the jugular foramen being in a distolateral position in relation to the lacerate foramen; (2) rostrolateral enlargement of the mastoid process; (3) high and thick mandibular corpus; (4) M1 metacunule absent; (5) p2 buccolingually rotated in relation to the tooth row; (6) p4 relatively long, with a backward inclination of the main cuspid towards the m1; (7) m1 hypoconid enlarged; and (8) absence of m1 entoconid or entocristid. Among the Mellivorinae, our analysis therefore reinforces the monophyly of *Eomellivora*, now also represented by *E. fricki* (Figure 3). We detected a Vallesian clade of *Eomellivora* consisting of the Euroasiatic *E. piveteaui* and the Centro-European *E. fricki* which conform the sister group of the Ventian *E. hungarica*. These three taxa are allied as a sister group of the Turolian/Ventian clade comprising the Euroasiatic *E. wimani* and the East-European *E. ursogulo* (Figure 3). The African *Ekorus* is nested as the sister group of *Eomellivora*. These two mustelids are associated with the following synapomorphies (Table 4): (1) straight shape of the upper incisor row; (2) position of the infraorbital foramen situated below the P4 parastyle; (3) P3 with a conspicuous concavity in the buccal wall; (4) enlarged M1 stylar area; (5) m1 hypoconid in a central position; and (6) m1 talonid without a basin, in which the hypoconid is orientated toward the m1 protoconid. Both
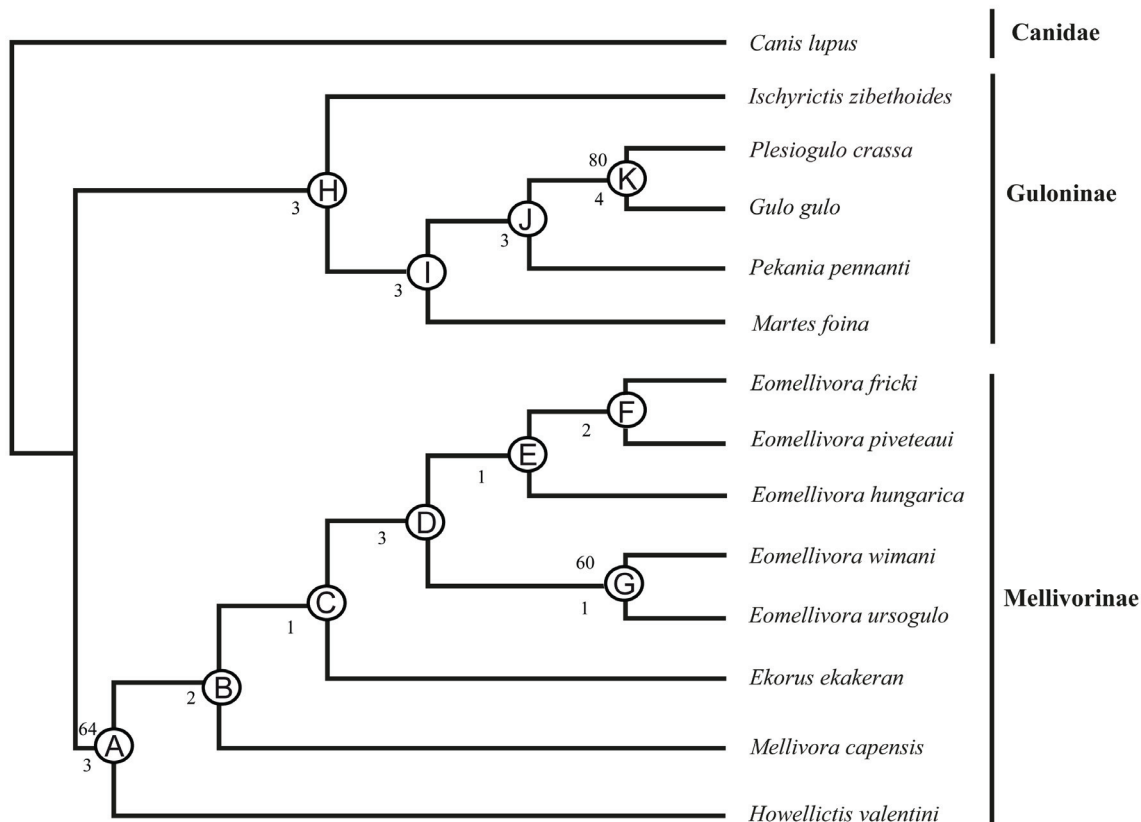
FIGURE 3. Phylogenetic relationship of *Eomellivora fricki* within *Eomellivora*, and of some extinct Neogene mustelids and living carnivorans. *Canis lupus* is the outgroup. Searches were performed by means of the Branch and Bound and a Bootstrap analysis through 1000 replicates. A single tree is obtained (length 172 steps, consistency index (CI)=0.4593, retention index (RI)=0.5811). The numbers below nodes are Bremer indices, and the numbers above nodes are Bootstrap support percentages (only shown ≥ 50). Letters (A-K) indicated selected nodes. The synapomorphies for each node are reported in Table 4.

Eomellivora and *Ekorus* appear as the sister group of the extant *M. capensis*, sharing a robust P3 with a strong cingulum, such as a widened p3. *Howellictis valentini* is placed in our tree as a primitive and basal mellivorine, which is in agreement with Bonis et al. (2009). The Guloninae clade (Table 4, node H), which in our analysis comprises *M. foina*, *P. pennanti*, *G. gulo*, *P. crassa* and *I. zibethoides*, shares among others, the following traits: (1) absence of the P3 distal accessory cusp; (2) length of the p2 relatively not reduced in relation to p3; and (3) m1 with an open and shallow talonid, with a low entocristid and a beveled lingual wall of the talonid (less marked in *G. gulo*). There is a significantly well-supported node composed of *Plesiogulo crassa* and the living wolverine *G. gulo.*

Ischyrictis zibethoides is placed in the tree as a basal Guloninae.

DISCUSSION

Eomellivora (*Hadrictis*) *fricki* is one of the largest extinct mustelids from Europe, together with the gulonine *Plesiogulo monspessulanus* Viret, 1939, from Montpellier (France, MN14); they both remarkably exceed the size of the wolverine, the largest living terrestrial mustelid. Since Zapfe (1948), nobody has appropriately considered the giant Austrian taxon within the broader context of the large Miocene mustelids. *Eomellivora fricki* possesses a clearly *Eomellivora*-like morphology in its dentition, which relates it to the species of the genus *Eomellivora* (Figures 4, 5, Table 4), more than with other extinct genera. It shares with the

TABLE 4. Synapomorphies for selected nodes, with associated character numbers and states (in parenthesis). Italics denote ambiguous synapomorphies.

Node	Character: state
A	6 (1), *11 (1), 20 (1),* 32 (1), 35 (1), *40 (1),* 41 (1), 52 (1), 57 (2), *58 (1),* 59 (1), *62 (1), 63 (2), 64 (2), 70 (1)*
B	*12 (1), 13 (1),* 16 (1), *22 (1);* 26 (2), *27 (1), 28 (1), 42 (1), 46 (1);* 48 (1), 50 (1), 56 (1)
C	2 (1), 3 (1), *11(1), 17 (1),* 19 (1), 31 (1), 61 (1)
D	*13 (0),* 24 (1), 26 (1), *27 (0), 42 (0),* 54 (1), 60 (1)
E	*17 (0), 30 (1),* 36 (0), *69 (0)*
F	32 (0), 35 (0), 50 (0)
G	14 (1), 15 (1), 38 (2), 43 (2)
H	*3 (1), 7 (1),* 18 (1), *38 (2),* 52 (0),55 (1), 65 (1), 66 (0), 67 (1)
I	*8 (0),* 21 (1), *27 (1),* 36 (0), *43 (0), 47 (1),* 49 (0), 51 (1)
J	23 (0), 24 (1), 25 (1), 26 (1), 28 (1), *32 (1)*
K	1 (0), 6 (1), *7 (0), 8 (1),* 9 (0), 15 (1), 19 (1), 20 (1), 41 (1), 43 (2), 45 (1), 48 (1), 51 (2), 53 (1), 56 (1)

Eomellivora species the following characters: distal area of P3 thickened distally; P4 robust with a sub-conical protocone; M1 with an enlarged stylar area; M1 protocone higher than the metacone, with a lingual M1 platform mesiodistally enlarged; p4 relatively enlarged, main cuspid noticeably inclined towards the m1, and the distal area of p4 thickened buccolingually with a quadrangular shape in the occlusal view; narrow m1 talonid with an m1 hypoconid centrally positioned and orientated toward the m1 protoconid. According to all the features shared, and supported by our cladistics results, we conclude that *Hadrictis* is a synonymy of *Eomellivora*, and we therefore named it as *Eomellivora fricki.* However, *E. fricki* presents several diagnostic traits that make it a valid species of *Eomellivora*, e.g., a longer dentition (Figure 6), the presence of a residual m1 metaconid and a stouter mandibular corpus. Due to the very early Vallesian age of the Austrian species, the residual m1 metaconid is considered to constitute a primitive trait, which is lost in the other species of the genus. Such a loss is a very common feature along the evolution of mustelids, also occurring in some other genera (e.g., *Hoplictis*, *Plesiogulo* or *Megalictis*) in which some of their species became more hypercarnivorous (e.g., Hendey, 1978; Harrison, 1981; Ginsburg, 1999; Valenciano et al., 2016).

During the early Vallesian (MN9) *E. fricki* coexists in Central Europe with *E. piveteaui,* spanning from Europe and Turkey during the MN9-10. Both large mustelids are nested in the same clade (Figure 3), and share a primitive dentition, e.g., the two lack a marked concavity in the buccal base of the P4, which is present in the other species of *Eomellivora*; a M1 metacone not reduced, with an M1 protocone ridge-shaped and mesiolingually

located, and absence of a mesial accessory cuspid in the p4 (Figures 2, 4.2, 5.3-4). Nonetheless, *E. fricki* differs from *E. piveteaui* in a shorter mandible and in an M1 with a stronger developed metacone and with a larger distal platform. *Eomellivora fricki* from Wien XII- Altmannsdorf is the largest *Eomellivora* (Figure 6), whereas the one from Gaiselberg overlaps with the size range of the larger specimens from Gritsev (Ukraine), MN9, which are only known by their dental dimensions (Wolsan and Semenov, 1996) (Figure 6). The dental sample of *Eomellivora* from Gritsev is the largest of the genus, even more so than the sample from Batallones (Wolsan and Semenov, 1996; Valenciano et al., 2015), and only a complete description and figuration of these fossils could elucidate the relationship between the Vallesian *E. fricki* and *E. piveteaui*; this would provide valuable data on the intraspecific variability of *Eomellivora*.

The fossil material of *E. hungarica* from Polgárdi 2 (MN13) is poorly preserved (Figures 4.6, 5.9-10) and hinders comparisons with *E. fricki*. Both species have a large c, p4 and m1, showing a stout m1 talonid with a quadrangular shape in the occlusal view. *Eomellivora fricki,* however, differs from *E. hungarica* in a much more developed M1 with a bigger M1 metacone, in a larger distal platform in the M1 and in the absence of a mesial accessory cuspid in the p4. Our phylogenetic hypothesis suggests a closer relationship between *E. hungarica* and the Vallesian clade than with the latest *E. wimani* and *E. ursogulo* (Figure 3). *Eomellivora hungarica*, *E. fricki* and *E. piveteaui* possess the subsequent characters (Table 4): (1) a non-cusp-like M1 protocone (synapomorphy); (2) a relatively robust p2; and (3) m1 protoconid and paraconid similar in height. This phylogenetic
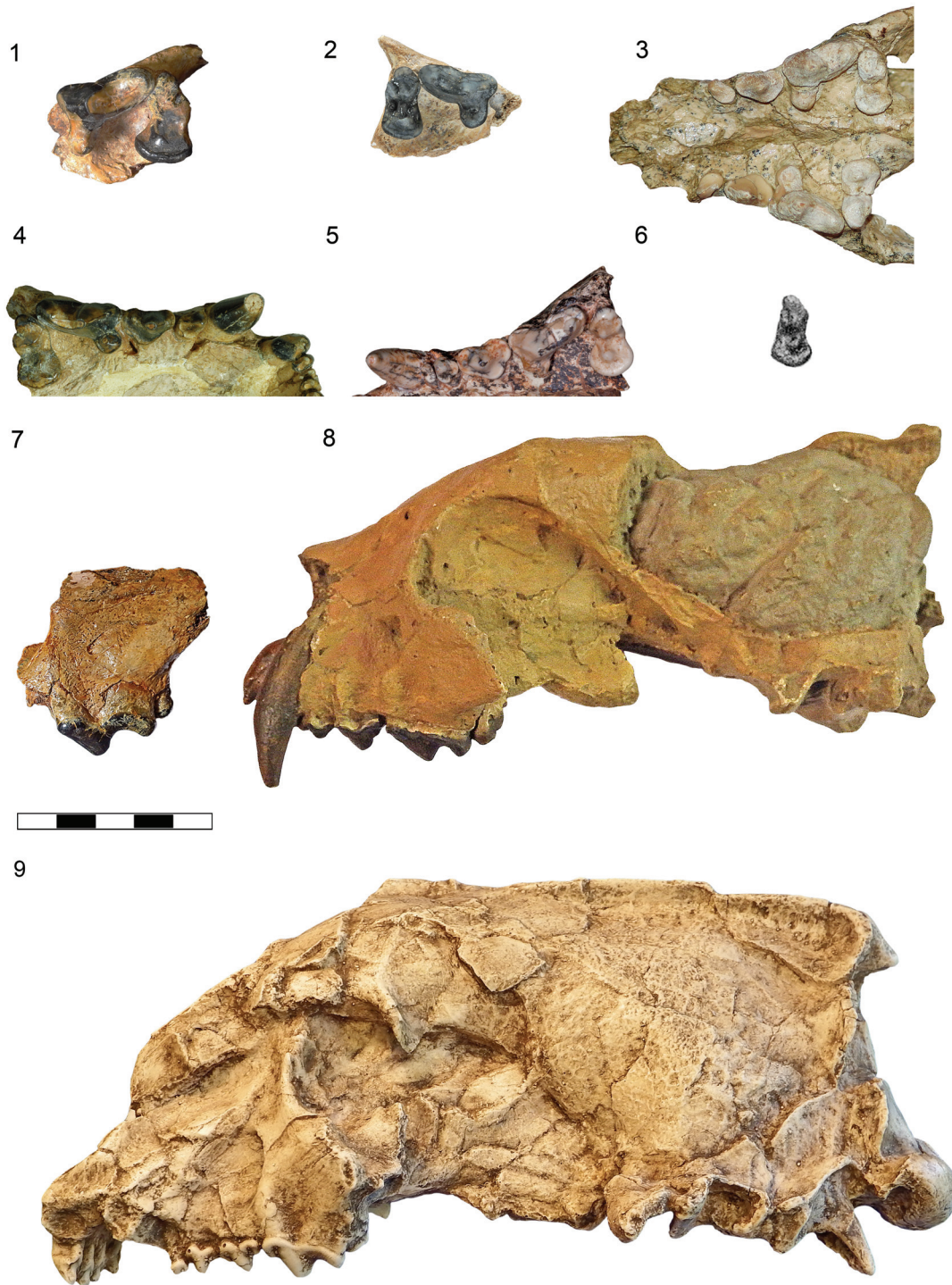
FIGURE 4. Main comparative material of the upper dentition of species of *Eomellivora* considered in the present manuscript. **1,** Holotype of *Eomellivora fricki* NHMW 2016/0065/0001 from Wien XII-Altmannsdorf (Austria), MN9; **2,** *Eomellivora piveteaui* MNHN-TRQ-1005 from type locality Yassiören (Turkey), MN9; **3,** *Eomellivora piveteaui* Bat-3´13.185 from Batallones (Spain), MN10; **4,** Holotype of *Eomellivora ursogulo* PIN-No.268 from Grebeniki (Ukraine), MN11; **5,** Lectotype of *Eomellivora wimani* PMU-M3692 from Shangyingou (China), MN12-13; **6,** Paratype (M1) of *Eomellivora hungarica* MFGI-Ob-3831 from Polgárdi 2 (Hungary), MN13; **8,** cast of the holotype of *Eomellivora ursogulo* NHMW 2016/0085/0001 from Grebeniki (Ukraine), MN11; **9,** cast of the holotype of *Ekorus ekakeran* KNM-LT 23125 from Lothagan (Kenya), 7 m.y.a. **1-6,** occlusal view, **7-9,** lateral view. Scale bar equals 5 cm.
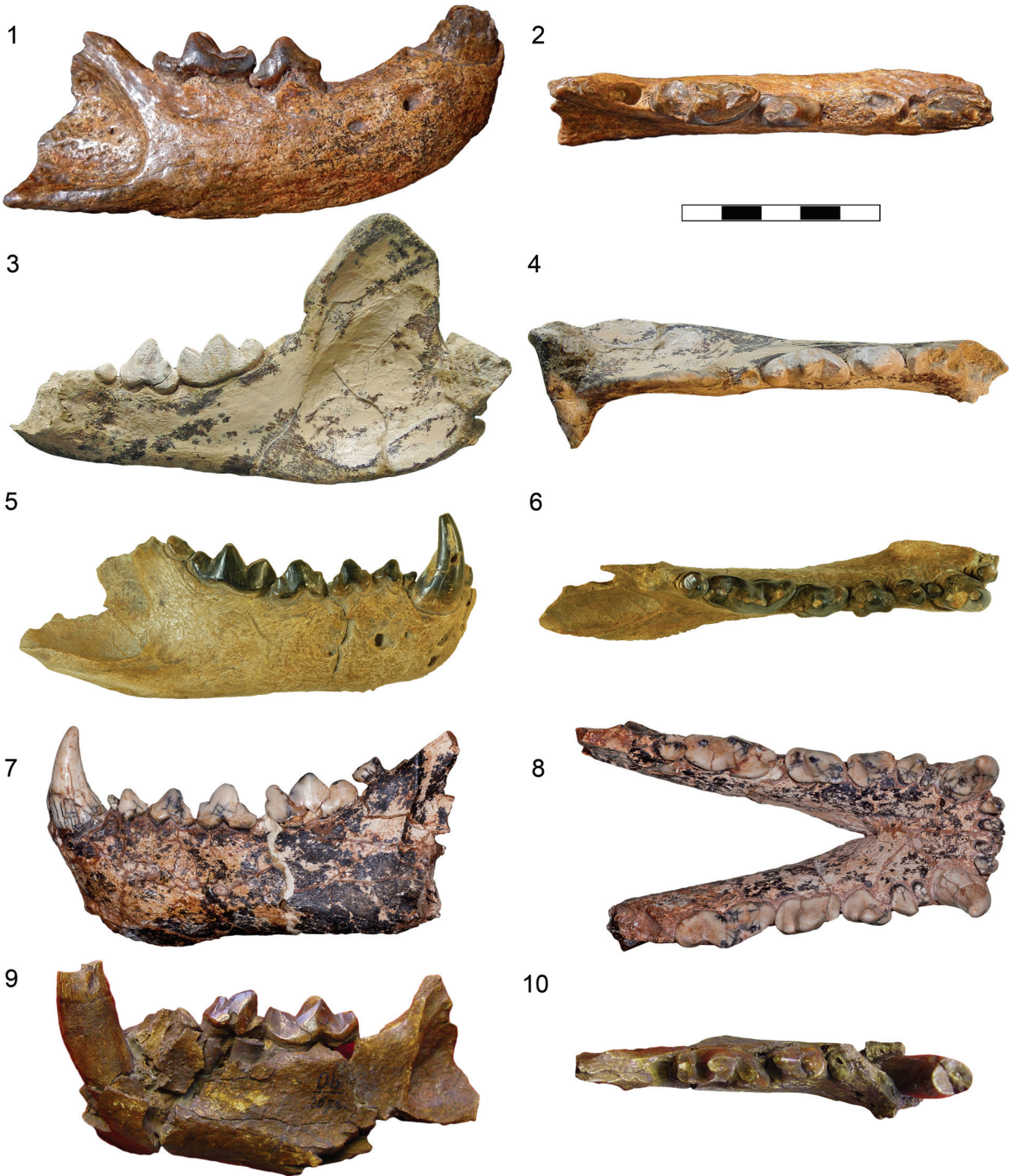
FIGURE 5. Main comparative material of mandible and lower dentition of species of *Eomellivora* considered in this manuscript. **1-2,** *Eomellivora fricki* NHMW 1977/1948/0130 from Gaiselberg (Austria), MN9.**1,** lateral view, **2,** occlusal view; **3-4,** *Eomellivora piveteaui* Bat-3´13.230 from Batallones (Spain), MN10. **3,** lateral view, **4,** occlusal view; **5-6,** *Eomellivora wimani* PMU-M3693 from Shangyingou (China), MN12-13 (same specimen as PMU-M3692). **5,** lateral view, **6,** occlusal view; **7-8,** Holotype of *Eomellivora ursogulo* PIN-No.269a from Grebeniki (Ukraine), MN11. **7,** lateral view, **8,** occlusal view; **9-10,** Holotype of *Eomellivora hungarica* MFGI-Ob-2676 from Polgárdi 2 (Hungary), MN13. **9,** lateral view, **10,** occlusal view. Scale bar equals 5 cm.
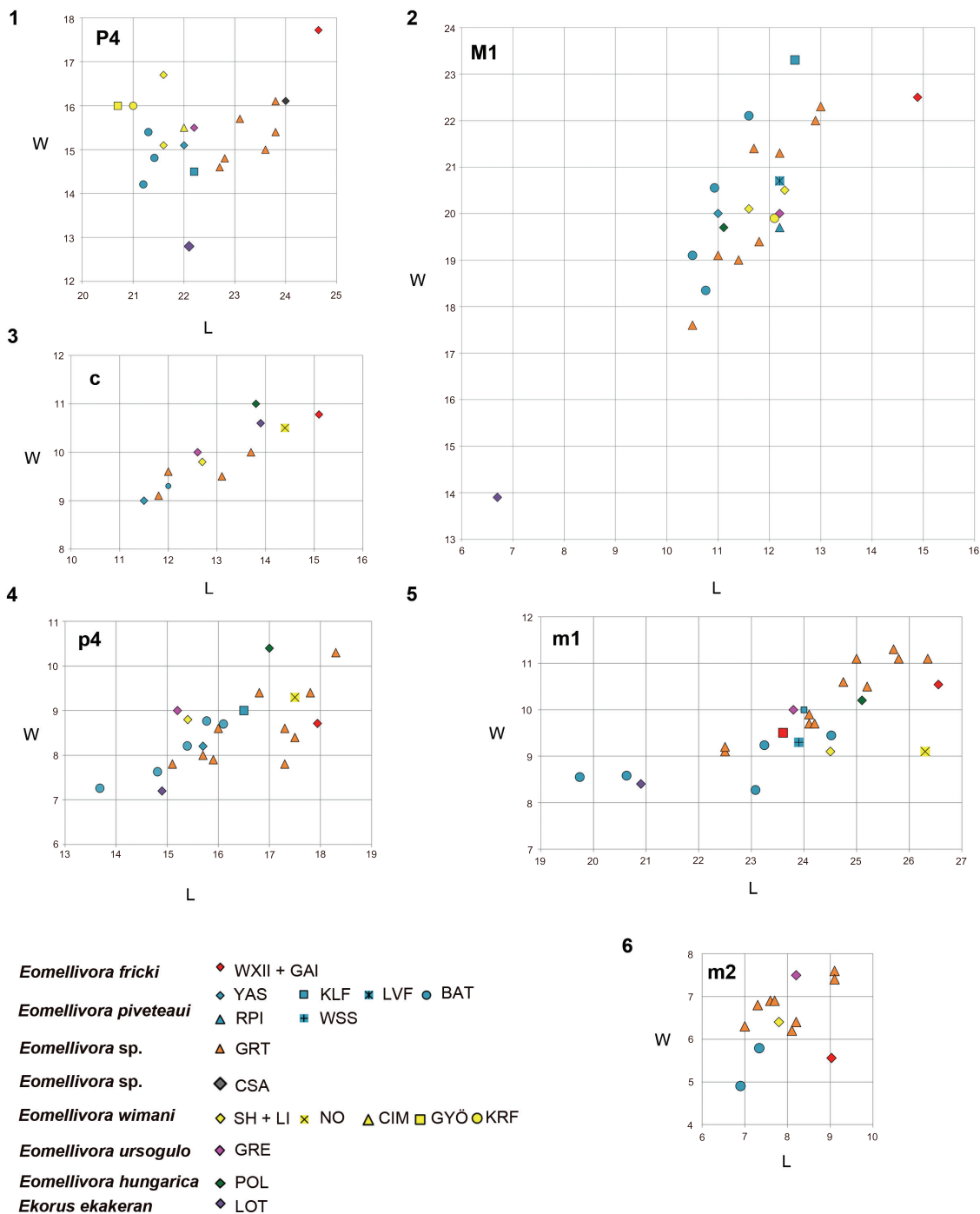
FIGURE 6. Scatter diagrams of measurements (mm) of the dentition of *Eomellivora* and *Ekorus ekakeran*. **1,** P4; **2,** M1; **3,** c; **4,** p4; **5,** m1; **6,** m2. Sources: **WXII** (Wien XII-Altmannsdorf) present manuscript; **GAI** (Gaiselberg) present manuscript; **SH** (Shangyingou), and **LI** (Liuwangou), Zdansky (1924); **GRT** (Gritsev), Wolsan and Semenov (1996); **NO** (Novaya Emetovka), Orlov (1948); **GYÖ** (Györszentmárton), Kretzoi (1965), **KRF** (Kern River Formation site 50), Stock and Hall (1933); **CIM** (Cimislia), Wolsan and Semenov (1996); **YAS** (Yassiören), Ozansoy (1965) and for P4 and M1, estimations based on pictures of MNHN-TRQ-1005, rather than the evidently confusing original data provided in Ozansoy (1965); **WSS** (Wissberg), Tobien (1955); **RPI** (Ravin de la Pluie), Koufos (2012); **BAT** (Batallones), Valenciano et al. (2015); **LVF** (Los Valles de Fuentidueña), Crusafont-Pairó and Ginsburg (1973) and for p2 Valenciano et al. (2015); **KLF** (Kalfa), Lungu (1978) and for M1 Valenciano et al. (2015); **GRE** (Grebeniki), Orlov (1948); **CSA** (Csákvár), Kretzoi (1942); **POL** (Polgárdi 2); **LOT** (Lothagam) Werdelin, 2003.

hypothesis could also be justified by the large size of the dentition and the apparently close morphology in the talonid of the m1 of *E. hungarica* and *E. fricki* and by the very similar morphology of the M1 between *E. hungarica* and *E. piveteaui*. Unfortunately, only a greater amount of material could clarify the systematic position of this *Eomellivora* from Polgárdi 2.

Eomellivora ursogulo from Grebeniki (Ukraine), MN11 (Figures 4.4, 4.8, 5.5-6) and *E. wimani* from Shangyingou (locality 12) (Figures 4.5, 5.7-8) and Liuwangou (locality 31) MN12-13 from China are characterized by a relatively stouter dentition (Figure 6), with more accessory cusps and cuspids, and herein they differ from the Vallesian species (*E. fricki* and *E. piveteaui*). *Eomellivora fricki* differs from the Holarctic *E. wimani* and the Ukrainian *E. ursogulo* in a more developed M1 metacone, in a non-cusp-like M1 protocone, in the absence of a mesial accessory cuspid in the p4 and by a shorter mandible. Furthermore, *E. fricki* differs from *E. wimani* in a weaker concavity in the buccal base of the P4 and from *E. ursogulo* by a single distal accessory cuspid in the p4, whereas *E. ursogulo* possesses two.

The suprageneric taxonomy of *M. capensis*, *G. gulo* and other living mustelids has been discussed over time (e.g., Pia, 1939; Webb, 1969; Ginsburg, 1977; Ginsburg and Morales, 1992; McKenna and Bell, 1997; Baskin, 1998; Ginsburg, 1999). *Mellivora capensis* is currently considered to be the only living representative of Mellivorinae, and the subfamily Guloninae (previously referred to as Martinae) comprises the extant martens (*Martes* Pinel, 1792 and *Charronia* Gray, 1865), the South American tayra (*Eira* Smith, 1842) and the wolverine *G. gulo* (Linnaeus, 1758). The suprageneric taxonomy becomes an acute problem for the fossil forms, in some cases due to the fragmentary dental and cranial representations, and in others due to the presence of a mixture of characters shared by both subfamilies. The position of the Mellivorinae and the Guloninae subfamilies as a sister clade in our cladistics analysis enters into conflict with a previous cladistics analysis based on molecular data (e.g., Koepfli et al., 2008; Sato et al., 2012), in which Guloninae appears as the sister group of Mustelinae (weasel and relatives) and Lutrinae (otters); furthermore, the position of Mellivorinae, even it is not clear, shows a more basal position within mustelidae than Guloninae (e.g., Koepfli et al., 2008; Sato et al., 2012). However, the main goal of the study involves establishing how *E. fricki* is related to some similar large Mio-

cene mustelids, and we therefore do not attempt to resolve the systematic position of the whole family.

The tree that we obtained reflects the evolutionary framework of *Eomellivora* proposed by Valenciano et al. (2015), in which *Eomellivora* is considered as a mellivorine. Werdelin (2003) noted that *Ekorus*, in spite of the differences in dental morphology between *Eomellivora* and *Ekorus*, could be in the same lineage. Our results confirm his idea and *Ekorus* is assigned to the Mellivorinae subfamily. The systematic position of the medium-sized ischyrictini *Ischyrictis zibethoides* from the middle Miocene of Europe has been ambiguous. The term Ischyrictini was erected by Pia (1939) as a "sub-subfamily," a group of large mustelids that included the genera *Ischyrictis*, *Laphictis* and *Hadrictis*. Subsequently, Tobien (1955) considered the Ischyrictini as tribal level, constituting a valid rank. Concerning different authors (Pia, 1939; Tobien, 1955; Webb, 1969; Ginsburg, 1977, 1999), this tribe has been assigned to Mellivorinae and Guloninae, with different degrees of relationship with the genera *Eomellivora*, *Hadrictis*, *Hoplictis*, *Iberictis*, *Gulo*, *Laphictis*, *Mellalictis*, *Mellivora* and *Plesiogulo*. Additionally, Ginsburg and Morales (1992) suggested a direct relationship between *Eomellivora* and *I. zibethoides*, a consideration that is rejected on the basis of our analysis. We considered *I. zibethoides* as a basal gulouinae without a sister group relationship with *Eomellivora*. Furthermore, the primitive dentition of *I. zibethoides* bears a resemblance to the living martens (e.g., *M. foina* or *M. martes*), with a close morphology in the P4-M1 and m1, but with a bigger size and a more primitive dentition within the guloninae clade (e.g., presence of a distal accessory cuspid in p3, a distal accessory cuspid in p4 not reduced, m2 paraconid present), including some derived traits such as a high mandibular corpus, a robust p2, a robust P4 or an enlarged M1 stylar area. The systematic relationship of the wolverine-like mustelid *Plesiogulo*, ranging in body size from large to gigantic, is controversial. Some authors (e.g., Viret, 1939; Kurtén, 1970; Kurtén and Anderson, 1980) considered it to be directly related to *G. gulo*, whereas others have seen it as a separate phylogenetic lineage without descendants (Zdansky, 1924; Hendey, 1978; Harrison, 1981; Xiaofeng and Haipo, 1987; Alcalá et al., 1994; Sotnikova, 1995; Montoya et al., 2011). The morphological similarities between *G. gulo* and *P. crassa*, suggest a close relationship between both genera, supported by the synapomorphy p2-4, which presents a strong cingula surrounding the entire tooth, with a thickening of the mesial and dis-

tal cristids of these teeth; as for several synapomorphies (Table 4), the most remarkable one involves a P4 more individualized protocone, located in a distal position in relation to the P4 parastyle. Nonetheless, further in-depth study of additional related taxa (e.g., other *Plesiogulo* species, *Iberictis*, *Dehmictis*, *Ischyritis*) are likely vital with regard to elucidating the relationship between the living wolverine and *Plesiogulo*.

CONCLUSIONS

The species *Hadrictis fricki* from the Austrian early Vallesian localities (MN9) can be referred to the genus *Eomellivora*, and we therefore synonymize *Hadrictis* with *Eomellivora.* This species represents the largest one, as well as one of the most primitive *Eomellivora,* which shows the complexity of the genus, in which larger (*E. fricki*) and relatively smaller (*E. piveteaui*) species coexisted since the early Vallesian. For the first time, the phylogenetic analysis resulted in the assignation of *Ek. ekakeran* to the Mellivorinae subfamily, and *Ekorus* is allied with *Eomellivora* as a sister genus. Additionally, we propose a new reassignment of some extinct large mustelids at the subfamily level, *I. zibethoides* being placed in our phylogeny as a basal guloninae, and *P. crassa* as sister to the extant wolverine.

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APPENDIX 1.

Descriptions of new dental characters employed in the phylogenetic analyses; some of them were modified from Bryant et al. (1993), Wolsan (1993), Baskin (2004) and Valenciano et al. (2015, 2016).
Characters and character states used in the phylogenetic analysis

(1)   Posterior lacerate and jugular foramina: "fused" into a single foramen (0); tendency to separate openings with the jugular foramen distolateral to the posterior lacerate foramen (1).

(2)   Shape of upper incisor row: parabolic (0); straight (1).

(3)   Position of the infraorbital foramen: above P3 (0); above P4 parastyle (1).

(4)   Incisive foramen: located at the level of C (0); located at the level of the diastema I3-C (1).

(5)   Mastoid process: reduced, located in dorsal view in line with the middle point of the orbit (0); enlarged, located laterally exceeding to the orbit (1).

(6)   Relative position of the mastoid and paroccipital processes: relatively close (0); mastoid process located mesially to the paroccipital process (1).

(7)   Paroccipital process: not reduced (0); reduced (1).

(8)   Height of the mandibular corpus: low and thin mandibular corpus (0); high and thick mandibular corpus (1).

(9)   Orientation of the I3 cusp: spreaded out laterally (0); in line with the cusps of I1-2 (1).

(10)   Orientation of Canine: spreaded out laterally, with an arrangement of the tip non parallel (0); ventrally directed, with a parallel arrangement of the tip (1).

(11)   P1. Present (0); absent (1).

(12)   P2. Mesiodistal axis of P2: in line with the tooth row (0); rotated buccolingually (1).

(13)   P2. Distal accessory cusp: absent (0); present (1).

(14)   P2. Occlusal shape: subrectangular (0); triangular (1).

(15)   P2. Buccal wall: rectilinear (0); conspicuous concavity (1).

(16)   P3. Robustness ratio [(maximum width/ maximum length) x 100]: slender P3 (less than 60) (0); Robust P3 (60 or more than 60) (1).

(17)   P3. Mesial accessory cusp: reduced or absent (0); present (1).

(18)   P3. Distal accessory cusp: present (0); absent (1).

(19)   P3. Buccal wall: rectilinear wall (0); conspicuous concavity (1).

(20) P3. Basal cingulum: weak (0); strong (1).

(21)   P4/3 length ratio. Maximum length of P4 in relation to maximum length of P3 ratio [(L P4/L P3) x 100]: less than 170 (0); more than 170 (1).

(22)   P4. Robustness ratio [(maximum width/ maximum length) x 100]: slender P4 (less than 60) (0); robust P4 (more than 60) (1).

(23)   P4 protocone: low (0); knoblike (1).

(24)   P4. Protocone cingulum: weak or absent (0); prominent and complete (1).

(25)   P4. Protocone: in front or anterior to the mesiobuccal corner (0); displaced distally (1).

(26)   P4. Parastyle: Absent or weak (0); Strong and low (1); Strong and high (2).

(27)   P4. Buccal wall: rectilinear (0); with a pronounced concavity between paracone and metastyle (1).

(28)   P4. Basal cingulum surrounding the tooth: weak (0); strong (1).

(29)   Relative size between maximum length of M1 and the maximum length of P4: M1 larger than or equal in size to P4 (values >100) (0); M1 smaller than P4 (values between 70-100) (1); M1 much smaller than P4 (values <70) (2).

(30)   M1. Robustness ratio [(maximum width on the buccolingual area/ maximum length) x 100]: relatively robust M1 (from 130 to 150) (0); slender M1 (more than 160) (1), very slender M1 (more than 200) (2).

(31)   M1. Stylar area: small (0); enlarged (1).

(32)   M1. Metacone related to paracone: normal size (0); very reduced (1).

(33)   M1. Metaconule: present (0); absent (1).

(34)   M1. Enlargement of the distal base of the metaconule: present (0); absent (1).

(35)   M1. Protocone position: mesolingually located (0); almost centrally on the middle of the talone (1).

(36)   M1. Protocone shape: ridge-shaped (0); conical cusp-like shape (1).

(37)   M1. Lingual platform: not completely enclose the protocone (0); completely enclose the protocone (1).

(38) M1. Length of the lingual wall: lesser than the buccal wall (unexpanded lingual platform) (0); longer than the buccal wall (moderately lingual platform) (1); much longer than the buccal wall (very expanded lingual platform) (2).

(39) M1. Lingual platform: oval shape (0); with a concavity in the middle point (1).

(40) p1. Present (0); absent (1).

(41) p2. Position of the mesiodistal axis of p2: in line with the tooth row (0); buccolingually rotated (1).

(42) p2. Distal accessory cuspid: absent (0); present (1).

(43) p2. Robustness ratio [(maximum width/ maximum length) x 100]: slender p2 (less than 50) (0); relatively robust p2 (from 50 to 70) (1); very robust p2 (more than 70) (2).

(44) p2 length compared to p3: p2 not reduced (0); p2 reduced (1).

(45) p2-4. Basal cingula with a mesial and distal thickened cristids: cingula and cristid weaks (0); complete and strong cingula and cristids (1).

(46) p3. Mesial accessory cuspid: absent (0); present (1).

(47) p3. Distal accessory cuspid: present (0); absent (1).

(48) p3. Distal thickened of p3: absent (0); present (1).

(49) p4. Length ratio in relation to m1 [(maximum length p4/ maximum length m1) x 100]: from 50 to 60, indicating a relatively not reduced p4 (0); more than 60, indicating a p4 relatively enlarged (1).

(50) p4. Mesial accesory cuspid: absent or poorly developed (0); present, well developed (1).

(51) p4. Distal accessory cuspid: High and well developed (0); low and reduced (1); Absent (2).

(52) p4. Backward inclination of the main cuspid: practically vertical (90º–80º) (0); with backward inclination (less than 80º) (1).

(53) p4, unworn principal cusp: equals or exceeds height of m1 paraconid (0); lower than m1 paraconid (1).

(54) p4. Distal area: not buccolingually thickened, oval shaped (0); buccolingually thickened, quadrangular shaped (1).

(55) p4. Lingual expansion or basal bulge: absent (0); present (1).

(56) m1. Height of protoconid in relation to paraconid: protoconid higher than paraconid (0); protoconid similar in height than the paraconid (1).

(57) m 1. Metaconid: individualized, with a moderate size (0); reduced (1); absent (2).

(58) 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).

(59) m1. Width talonid ratio [(maximum talonid width/ maximum width in the base of the protoconid-metaconid) x 100]: talonid not widened (values between 85-100) (0); reduced talonid (< 85) (1).

(60) m1. Height of hypoconid: low (0); high (1).

(61) m1. Position of hypoconid: labially located (0); centrally positioned or almost centrally positioned (1).

(62) m1. Orientation of the hypoconid: almost vertical (0); orientated towards the protoconid (1).

(63) m1. Entoconid: individualized (0); transform in an entocristid (1); absent (2).

(64) m1 talonid: closed and deep basin (0); open and shallow basin with a low entocristid and a beveled lingual wall of the talonid (1); basin lost (2).

(65) m1. Shape of the hypoconid: pyramidal (0); trending to a crest-like shape (1).

(66) m1. Hypoconid size: medium (0); enlarged (1); reduced (2).

(67) m1. Hypoconulid: very reduced to absent (0); present not reduced (1).

(68) (39) m2. Present (0); absent (1).

(69) m2 paraconid: present (0); (1) very week or absent (1).

(70) m2. Metaconid: present (0); absent (1).

APPENDIX 2.

Character-taxon matrix used for phylogenetic analyses.

Characters 1–40

Taxon / Character	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40
Eomellivora fricki	?	?	1	?	1	1	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	1	0	?	0	1	0	1	0	1	1	0	0	0	1	0	0	1	0	0
Eomellivora piveteaui	1	1	0	1	1	0	1	?	?	?	1	?	0	0	0	?	0	1	1	1	0	1	1	?	1	0	1	1	1	1	0	1	0	0	0	0	1	2	0	0
Eomellivora wimani	?	1	1	0	?	?	0	1	?	1	0	1	0	1	1	1	1	0	1	1	1	1	1	1	1	1	1	1	0	1	0	1	1	1	1	0	0	1	0	0
Eomellivora ursogulo	1	1	1	0	1	0	1	1	0	1	0	1	1	1	1	1	1	0	1	1	0	1	1	1	1	1	1	1	0	0	1	0	1	1	1	1	1	2	1	0
Eomellivora hungarica	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	1	1	?	?	1	?	?	1	1	2	0	?
Howellictis valentini	1	?	0	?	1	1	0	?	?	?	1	1	1	0	1	0	0	0	0	1	1	0	0	0	0	1	0	1	1	2	0	1	1	1	0	1	0	0	0	1
Ekorus ekakeran	?	1	1	1	1	1	1	0	1	1	1	1	1	0	0	0	1	1	1	1	0	1	0	2	1	2	0	2	2	2	1	0	1	1	1	0	0	0	0	0
Mellivora capensis	1	0	0	1	0	1	1	1	0	1	1	1	1	0	0	0	0	0	1	0	1	1	1	2	1	1	1	1	0	0	0	1	0	1	1	1	0	0	1	1
Martes foina	1	0	1	0	0	0	1	0	1	1	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	1	0	1	0	0	0	0	0	0	0	1	0	1	2	0
Pekania pennanti	1	0	1	0	1	0	1	0	1	1	0	1	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	1	0	0	1	0	1	0	0	0	0	1	2	0
Canis lupus	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0
Gulo gulo	0	1	0	1	0	1	0	1	0	1	0	1	0	0	1	0	0	1	1	1	0	1	1	1	1	1	0	1	2	1	0	1	0	1	0	1	0	1	0	1
Plesiogulo crassa	0	0	1	0	1	0	1	0	1	0	1	0	0	0	0	0	0	0	0	1	0	0	1	1	0	0	1	0	1	0	1	0	0	0	0	0	2	1	1	0
Ischyrictis zibethoides	?	1	?	?	?	1	1	0	1	1	1	0	0	0	0	1	0	1	0	1	0	0	0	0	0	1	0	1	1	1	0	0	1	0	1	0	1	2	0	0

Characters 41–70

Taxon / Character	41	42	43	44	45	46	47	48	49	50	51	52	53	54	55	56	57	58	59	60	61	62	63	64	65	66	67	68	69	70
Eomellivora fricki	1	?	?	?	?	?	1	0	0	1	0	0	?	1	0	?	1	0	?	?	1	1	2	0	1	?	0	?	0	?
Eomellivora piveteaui	1	0	1	1	0	0	1	1	0	0	1	0	1	0	1	0	1	1	1	1	1	1	2	0	1	0	0	0	0	1
Eomellivora wimani	1	0	2	1	0	0	1	1	0	0	0	1	0	1	0	1	0	1	1	1	1	2	2	0	1	?	0	1	1	1
Eomellivora ursogulo	1	1	2	1	0	1	1	1	0	1	0	1	0	1	0	0	1	1	1	1	2	2	2	0	1	0	0	1	0	1
Eomellivora hungarica	?	?	?	?	0	?	?	1	0	0	1	0	0	1	0	1	0	1	1	1	1	2	2	0	1	0	?	?	?	?
Howellictis valentini	1	0	1	1	0	0	0	0	1	0	0	1	0	0	0	0	0	0	0	0	1	1	2	0	1	0	0	0	?	?
Ekorus ekakeran	1	1	0	0	0	0	1	1	0	1	0	1	1	0	0	0	0	1	0	1	2	1	2	0	1	0	0	0	?	?
Mellivora capensis	1	1	1	0	1	0	1	1	1	1	0	1	0	0	0	0	1	1	0	1	2	1	2	0	1	0	0	?	?	1
Martes foina	0	0	1	0	0	1	0	0	0	0	1	0	0	0	0	1	0	0	0	0	0	0	1	0	0	1	1	–	–	0
Pekania pennanti	0	0	0	1	0	0	0	1	0	0	0	1	0	0	1	0	0	0	0	0	0	1	1	0	1	1	1	1	0	0
Canis lupus	0	1	0	0	0	0	0	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0
Gulo gulo	1	0	2	1	1	0	1	1	0	0	2	0	1	0	0	1	0	1	0	1	2	1	0	0	2	0	0	1	1	1
Plesiogulo crassa	1	0	2	1	1	1	0	1	1	0	0	2	0	1	0	1	1	0	0	0	0	1	1	0	1	1	0	1	0	0
Ischyrictis zibethoides	0	0	1	0	1	0	0	0	1	0	1	0	0	1	1	0	0	0	0	0	0	1	1	0	1	0	1	0	0	0

APPENDIX 3.

Character-taxon matrix in nexus format. (Available online in zipped format at palaeo-electronica.org/content/2017/1830-the-large-eomellivora-fricki