New Fossils of *Mellivora benfieldi* (Mammalia, Carnivora, Mustelidae) from Langebaanweg, ‘E’ Quarry (South Africa, Early Pliocene): Re-Evaluation of the African Neogene Mellivorines

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RH: VALENCIANO AND GOVENDER—PLIOCENE *MELLIVORA* FROM LANGEBAANWEG

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ABSTRACT—We describe abundant new remains of the medium-sized mustelid *Mellivora benfieldi* from the early Pliocene site of Langebaanweg (South Africa). The specimens are from the Muishond Fontein Pelletal Phosphorite Member (MPPM) and the Langeberg Quartz Sand Member (LQSM). Novel dentognathic – upper dentition, alveolus for m2– and postcranial –humerus, metacarpal V, femur and calcaneus– information is provided. This sample enables us to review the taxonomic status of Mio-Pliocene African mellivorines. *Mellivora benfieldi* is distinguished from the middle-late Miocene '*Eomellivora*' *tugenensis* from Ngorora Kenya by its smaller size, and a M1 protocone messially placed; from the late Miocene *Howellictis valentini* from Chad by bigger dental size with more crowded lower premolars, and p3 with distal accessory cuspid; and from the late Miocene *Erokomellivora lothagamensis* from Kenya, by shorter p4 and buccolingually shorter m1 protoconid. It also differs from *H. valentini* and *Er. lothagamensis* in absence or residual presence of the m2 alveolus. We infer *M. benfieldi* was an opportunistic, medium-sized carnivoran with semifossorial abilities, comparable to its living relative *Mellivora capensis*. A cladistics analysis was performed and our phylogenetic hypothesis places *M. benfieldi* as the sister group of *M. capensis*. Mellivorini contains *M. benfieldi, M. capensis* and *H. valentini*. Additionally, we also include *Er. lothagamensis* and the Indian *Promellivora punjabiensis*. We propose the creation of one new tribe within Mellivorinae: Eomellivorini (*Eomellivora* spp. + *Ekorus*). It shares a common ancestor with Mellivorini and is characterized by large size, a robust and sharp dentition, as well as a skeleton with cursorial adaptations.

INTRODUCTION

Mellivorinae Gray, 1865, is the subfamily of Mustelidae that contains *Mellivora capensis* (honey badger or ratel) as its single living member. *Mellivora capensis* is the largest African terrestrial mustelid, and is widespread in Africa, Southwest Asia, and the Indian subcontinent (Larivière and Jennings, 2009). The African fossil record of this subfamily is diverse and shows a relatively long evolutionary history (Werdelin and Peigné, 2010). It comprises the middle-late Miocene '*Eomellivora*' *tugenensis* Morales and Pickford, 2005a from the Ngorora Fm., Kenya (ca. 12 Ma); the late Miocene *Howellictis valentini* Bonis, Peigné, Guy, Likius, Makaye, Vignaud, and Brunet, 2009, from the locality Toros Menalla 192, Chad (ca. 7 Ma); three distinct forms in Lothagam, Kenya (Werdelin, 2003), including the very large *Ekorus ekakeran* Werdelin, 2003 from the Lower Nawata Fm. (ca. 7 Ma), smaller *Erokomellivora lothagamensis* Werdelin, 2003, and an indeterminate mellivorinae that may also be the same taxon (L. Werdelin, pers comm.) from the Upper member of the Nawata Fm. (6.5-5.5 Ma). Finally, the fossil record of *Mellivora* Storr, 1780, includes the Mio-Pliocene *Mellivora benfieldi* Hendey, 1978a from Langebaanweg, South Africa (early Pliocene, ca. 5.2 Ma), and doubtfully at the Middle Awash Fm. of Ethiopia, (ca. 6-5.5 Ma) (Haile-Selassie and Howell, 2009); and the late Pliocene/extant *Mellivora capensis* (Schreber, 1776). Outside Africa this subfamily occurs in Brisighella, Italy (MN13, ca. 5.4 Ma) (Rook et al., 1991), with the remains of *M. benfieldi*, and in Eurasia and North America with the remains of the giant mustelid *Eomellivora* Zdansky, 1924. Fragmentary remains have been described from India and Pakistan from the Siwaliks Hills, comprising three forms: (1) *Sivamellivora necrophila* (Pilgrim, 1932) from the Lower Siwaliks, Chinji Fm ca. 14–11.2 Ma (Patnaik, 2013), (2) *Promellivora punjabensis* (Lydekker, 1884), from the late Miocene sediments of the Dhok Pathan Fm, 10.2–5.3 Ma (Patnaik, 2013), and (3) *Mellivora sivalensis* (Falconer, 1868) from the upper part of the Siwaliks in the Pinjor Fm, Pleistocene (2.58–1.7 Ma) (Patnaik, 2013), which is morphologically similar to *M. capensis* (Falconer 1868; Lydekker, 1884; Pilgrim, 1932; Petter, 1987; Bonis et al., 2009).

Langebaanweg (LBW), 'E' Quarry, is a late Miocene – early Pliocene fossil site (Fig. 1) that has yielded one of the richest and best-preserved Neogene mammal assemblages in Africa (Hendey, 1981a; 1989). It is located within the West Coast Fossil Park near Vredenburg, Western Province, South Africa. Fossils were first discovered at 'E' Quarry in 1965 when phosphate mining started at the Varswater mine (Hendey, 1989). Langebaanweg has been interpreted as an estuary that formed during a transgressive phase with associated marine flooding of the coastal areas (Hendey, 1989; Roberts et al., 2011; Cohen et al., 2018). Repeated fluctuations in sea levels influenced the geology of Langebaanweg; and the depositional environments preserved there include shallow marine, estuarine, marsh and fluvial systems (Hendey, 1989; Roberts et al., 2011).

The fossils occur in the Varswater Fm., which is divided into four members that have different ages, spatial relationships, thickness, lithology, and depositional settings (Roberts et al., 2011): (1) Langeenheid Clayey Sand (LCSM), (2) Konings Vlei Gravel (KGM), (3) Langeberg Quartz Sand (LQSM) and (4) Muishond Fontein Pelletal Phosphorite Members (MPPM). The main fossil bearing deposits of the formation are the MPPM and LQSM. All the terrestrial carnivoran material from 'E' Quarry was found in these two members (Hendey, 1974, 1976, 1978a, 1978b, 1980, 1989). There are two different highly fossiliferous beds in the MPPM: Beds 3aN and Bed 3aS. These are interpreted as river channel deposits (Hendey, 1989), and are inferred as very close in age, with Bed 3aS slightly older (Hendey, 1981b). The ages of LQSM and MPPM were estimated by palaeomagnetic data and global sea level reconstructions as ~5.15±0.1 Ma, suggesting that the fossils accumulated at an early stage in the Early Pliocene transgression (Roberts et al., 2011). Baard's Quarry (Hendey, 1974, 1978c) is another fossil deposit in LBW that includes carnivoran fossils, but it is interpreted as much recent deposit (late Pliocene or early Pleistocene) (Hendey, 1978c).

Since Hendey completed a series of monographic studies on the LBW carnivorans (Hendey, 1972, 1974, 1976, 1978a, 1978b, 1980, 1981a, 1989), the LBW's fauna has been extensively cited and has become a reference fauna for Mio-Pliocene studies of carnivorans. Recent studies of the LBW carnivorans have focused on hyaenids (Werdelin et al., 1994), the saber toothed cats *Amphimachairodus* sp. and *Dinofelis* sp. (Werdelin and Lewis, 2001; Werdelin and Sardella, 2007), phocids (Govender et al., 2011, 2012; Govender, 2015), and recently the giant mustelids *Sivaonyx hendeyi* (Morales, Pickford and Soria, 2005) and *Plesiogulo* aff. *monspessulanus* (see Valenciano and Govender, 2020). Additionally, some ecological and biomechanical studies have been performed (Werdelin, 2006; Stynder, 2009; Tseng and Stynder, 2011; Oldfield et al., 2012; Stynder et al. 2012, 2018; Stynder and Kupczik, 2013; Hartstone-Rose and Stynder 2013; Hartstone-Rose et al., 2016).

The current study presents a review of the published and previously unpublished material referred to the mellivorine *Mellivora benfieldi* Hendey, 1978a from LBW, the type locality of this species. The goal of this study is to update our knowledge of this significant mustelid. It will be compared to other mellivorines from Eurasiatic and African Mio/Pliocene localities to better understand the taxonomy, paleobiology and ecology of this group of mustelids.

MATERIAL AND METHODS

Nomenclature and Measurements

Dental nomenclature follows Ginsburg (1999) and Smith and Dodson (2003). Anatomical descriptions are based primarily on Barone (1999, 2000), Waibl et al. (2005), Evans and de Lahunta (2010, 2013) and Ercoli et al. (2013, 2015), and the terminology conforms to the standard of the Nomina anatomica Veterinaria (NAV; Waibl et al., 2005). Measurements were taken using Mitutoyo Absolute digital calipers to the nearest 0.1 mm (Fig. 2; Tables 1-2; Table S1-2).

Abbreviations

Institutional Abbreviations—**AMNH**, American Museum of Natural History, New York, USA; **BAT-3**, Batallones-3 locality collection from MNCN; **BSPG**, Bayerische Staatssammlung für Paläontologie und Geologie, Munich, Germany; **F:AM**, collection housed in the Frick Collection of the Division of Paleontology, AMNH, New York, USA; **FCPT**, Fundación Conjunto Paleontológico de Teruel-Dinópolis, Museo Aragonés de Paleontología, Teruel, Spain; **FMNH**, Field Museum of Natural History Chicago, Illinois, USA; **FSL**, Université Claude Bernard Lyon 1 Lyon, France; **ICP**, Institut Català de Paleontologia Miquel Crusafont, Barcelona, Spain; **IPUW**, Institut für Paläontologie, Universität Wien, Vienna, Austria; **ISAM,** Iziko South African Museum, Cape Town, South Africa; **KNM**, Nairobi National Museum, National Museums of Kenya, Nairobi, Kenya;

MGUV, Museu de Geologia de la Universitat de València, Burjassot, Spain; **MNCN**, Museo Nacional de Ciencias Naturales Madrid, Spain; **MNHN**, Muséum national d'Histoire 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; **SAM-PQL**, Quaternary Palaeontology (Langebaanweg), Iziko South African Museum, Cape Town, South Africa; **SAM-ZM**, Zoology Mammals, Iziko South African Museum, Cape Town, South Africa; **SMNS**, Staatliches Museum für Naturkunde, Stuttgart, Germany; **USNM,** Smithsonian National Museum of Natural History (The Smithsonian Museum Support Center, Division of Mammals MSC, Suitland, USA).

Study Material

We have re-analyzed the *Mellivora benfieldi* material described by Hendey (1974, 1978a) as well as new material housed in the Cenozoic collections at the Iziko South African Museum (ISAM). The comparative material includes original material of: *Zodiolestes daimonelixensis* Rigg, 1942 from the early-late Arikareean (c. 23 Ma) Harrison Formation, Sioux County, Nebraska (USA), housed at FMNH comprising a complete skeleton; dentition of *Iberictis buloti* Ginsburg and Morales, 1992 from els Casots (16.5–16.3 Ma, MN4, Vallès-Penedès Basin, Barcelona, Spain) housed at ICP (Valenciano et al., 2020); *Sthenictis* sp. (F:AM 25235 and 25236) from Burge Fauna, early Clarendonian (Valentine Formation, Nebraska, USA, 13-12 Ma, c. MN7/8) comprising a complete skeleton; *Laphictis mustelinus* Viret, 1933 from the localities of Can Mata 1 (MN7/8, els Hostalets de Pierola, Barcelona, Spain) comprising a skull and dentition housed at ICP (Villalta Comella and Crusafont Pairó 1943; Crusafont and Truyols 1954; Petter 1963), and by original photographs from La Grive-Saint-Alban (MN7/8, France) housed at FSL, Erkertshofen 2 (MN4, Germany) (Viret 1933; Roth 1989), housed at BSPG, and Steinheim (MN7, Germany), housed at SMNS (including some postcranial remains, see Helbing 1936); *Eomellivora piveteaui* Ozansoy, 1965 from Batallones-3, Spain (late Miocene, MN10, ca. 9 Ma), which is stored in the collections of the Department of Paleobiología at the MNCN and comprises cranial (Valenciano et al., 2015) and unpublished postcranial remains; *Eomellivora wimani* Zdansky, 1924 from Shangyingou and Liuwangou from China, MN12-13, housed at PMU, comprised of dentognathic material; *Plesiogulo monspessulanus* Viret, 1939, from Montpellier (MN14, France) housed at FSL, the dentognathic Spanish material from Venta del Moro (Montoya et al., 2011) and Las Casiones (Alcalá et al., 1994), housed at MGUV and FCPT respectively, as well as the cranial and postcranial fossils of *P*. aff. *monspessulanus* from Langebaanweg (Hendey, 1978a; Valenciano and Govender, 2020); and *Mellivora capensis* from the South African Pleistocene sites of Elandsfontein, 1-0.6 Ma (Klein et al., 2007), Swartklip 1 (0.1 Ma), and the Holocene sites of Tygerfontein and Sea Harvest (e.g., Hendey, 1974, 1978a) housed at ISAM. *Ekorus ekakeran* from Lower Nawata Fm., Lothagam, Kenya (late Miocene, c. a., 7 Ma) (Werdelin, 2003) from the research collection of L. Werdelin (cast) housed at NRM. The Pleistocene *Gulo schlosseri* Kormos, 1914, was also studied based on a cast of the holotype from Püspökfürdo, Hungary, housed at NHMW and the publications by Kormos (1914) and Bonifay (1971). We further examined photographs of the holotypes of *Dehmictis vorax* (Dehm, 1950) from Wintershof-West (MN3, Germany), housed at BSPG, *Ischyrictis zibethoides*

(Blainville, 1842) from Sansan (MN6, France) housed at MNHN, *Eomellivora ursogulo* (Orlov, 1948) from Grebeniki, Ukraine, MN11 housed at PIN (also available as a cast at IPUW and NHMW), and *Erokomellivora lothagamensis*, known from the Upper member of the Nawata Fm. Lothagan, Kenya (6.5–5.5 Ma) (Werdelin, 2003). Analyses of the Miocene '*Eomellivora*' *tugenensis*, from the Ngorora formation (Kenya), ca. 12 Ma (Morales and Pickford, 2005a) and the late Miocene *Howellictis valentini* from the locality Toros Menalla 192 (Chad), ca. 7 Ma (de Bonis et al., 2009) are based on published descriptions.

The extant specimens used for comparison are: *Martes foina* (Erxleben, 1777) (MNCN-3684, 3685, 21673, 3705), *Mellivora capensis* (AMNH-51952, 81232, 81848, 83450, 169085, 169088, 69499, 81831, 34263, 34264, 119622, 119949; USNM-270224; NRM-A582462, A583405, A591017, A605023, A580357, A591015, A584514; SAM-ZM-41483, 41666); *Pekania pennanti* (Erxleben, 1777) (FMNH-141987, 141989, 129326, 134449,134450, 203682, 160116, 153811, 165360, 165358, 6343, 165359, 10881, 89456, 72959, 129325, 81486, 6341, 6342; AMNH-121554, 121556); *Gulo gulo* Linnaeus (1758) (MNCN-16748; USNM 275160, 272316, A06231, 265649, 242705, 108654, 096147; NRMA825005, A845012, 20055154, 20115498, A815010, A587719, A885007, A795005, A825004; FMNH-151027, 129317).

Cladistic Analysis

In order to analyze the phylogenetic position of *Mellivora benfieldi* relative to better-known mellivorines, gulonines and primitive Miocene mustelids from Africa, Eurasia and North America, we performed a cladistics analysis of 18 operational taxonomic units (OTU), and 100 cranial, dental and postcranial characters. All characters were equally weighted and unordered. The complete list of taxa, characters and the character-taxon matrix are available in Supplemental File 1–2. We restricted our analysis to the early Miocene oligobunine *Zodiolestes daimonelixensis* (outgroup), *Dehmictis vorax* and *Iberictis buloti*, the middle Miocene medium-size *Ischyrictis zibethoides*, *Laphictis mustelinus* and *Sthenictis* sp., the late Miocene *Ekorus ekakeran*, *Eomellivora piveteaui*, *Eomellivora wimani*, *Eomellivora ursogulo*, *Howellictis valentini*, and *Plesiogulo monspessulanus* (including *P*. aff. *monspessulanus* from Langebaanweg), and the Pleistocene *Gulo schlosseri*. Additionally, the living mustelids *Mellivora capensis*, *Martes foina*, *Pekania pennanti* and *Gulo gulo* were analysed. We excluded the poorly known African '*Eomellivora*' *tugenensis* and *Erokomellivora lothagamensis*. The cladistic analysis was performed set using in PAUP*4.0b10 (Swofford, 2002). This analysis yielded 6 parsimonious trees with 247 steps by the branch-and-bound-search, with a consistency index (CI) of 0.4494, a homoplasy index (HI) of 0.5506 and a retention index (RI) of 0.6486. Clade support was calculated using bootstrap analysis with 1000 replicates, and a Bremer support values. Moreover, we obtained a Bootstrap 50% majority-rule consensus tree with 249 steps, a CI of 0.4458, HI of 0.5542 and a RI of 0.6434.

SYSTEMATIC PALEONTOLOGY

Order CARNIVORA Bowdich, 1821

Suborder CANIFORMIA Kretzoi, 1943

Family MUSTELIDAE Fischer, 1817

Subfamily MELLIVORINAE Gray, 1865

Genus *MELLIVORA* Storr, 1780

MELLIVORA BENFIELDI Hendey, 1978a

Mellivora aff. *punjabiensis* Hendey 1974 fig.6, (original description).

Holotype—SAM-PQL-42838, a left hemimandible with c, p2-4 and m1 figured by Hendey (1978a: fig.7).

Type Locality—Langebaanweg, MPPM.

Other Localities— Brisighella, MN13, Late Miocene, ca. 5.4 Ma (Italy), Rook et al. (1991); Middle-Awash, Ethiopia (Haile-Selassie and Howell, 2009), ca. 6-5.5 Ma (Haile-Selassie et al. 2004).

Referred Material from the Type Locality—In Hendey, (1978a): SAM-PQL-6385, left hemimandible with p4-m1; SAM-PQL-31273, right hemimandible with m1; SAM-PQL-50443, right hemimandible with p4-m1; SAM-PQL-50541, right M1; tentatively SAM-PQL-40080, left ulna, and SAM-PQL-45384, right radius. New Material: SAM-PQL-72167, right I3; SAM-PQL-69620C, left C; SAM-PQL-51386, left C; SAM-PQL-50107, right P3; SAM-PQL-72165, left P3; SAM-PQL- 72168, right P3 fragment; SAM-PQL-72227, right P4 fragment with missing protocone; SAM-PQL-72174, left hemimandible with p2-m1, and m2 alveolus; SAM-PQL-69620B, left fragmentary hemimandible with m1 and m2 alveolus; SAM-PQL-50002, left fragmentary hemimandible with m1; SAM-PQL-50105, left fragmentary hemimandible with broken p4-m1 at the base of the crown; SAM-PQL-50106, right fragmentary mandibular body with c, p2-p4 alveoli; SAM-PQL-50444, left p2; SAM-PQL-72176, left humerus fragment including the distal diaphysis and distal epiphysis; SAM-PQL-41875, right humerus fragment, including the distal part of the diaphysis; SAM-PQL-72175, complete right ulna; SAM-PQL-25606, right ulna fragment comprising the proximal epiphysis and two thirds of the diaphysis; SAM-PQL-69620A, right ulna fragment comprising the proximal epiphysis and one thirds of the diaphysis; SAM-PQL-69620E, right metacarpal V; SAM-PQL-42486, right proximal femur epiphysis; SAM-PQL-41513A, left distal femur epiphysis; SAM-PQL-69634B, right calcaneum.

Emended Diagnosis—Modified after Hendey (1978a). Smaller than the living *Mellivora capensis*. P3 slender, double-rooted and without accessory cusps; M1 with long parastyle, mesially oriented protocone, and a lingual platform relatively expanded, but without a prominent cingulum around the protocone; sharp lower premolars; p1 absent; p3 with distal accessory cuspid; slender p4 with mesial and distal accessory cuspids; m1 without metaconid, and with a narrow, sharp talonid that has a central, low hypoconid, and no hypoconulid; m2 absent or vestigial. Humerus with enlarged deltopectoral crest that exceeds the distal half of the diaphysis, enlarged supraepicondylar crest laterally projected, and the medial epicondyle, proximodistally and medially projected; Ulna with enlarged olecranon process medially projected; calcaneus with a short calcaneal tuber and the M. quadratus plantae process laterally expanded.

Differential Diagnosis—Differs from ‘*Eomellivora*’ *tugenensis* in smaller size, and M1 protocone more mesially placed. Differs from *Howellictis valentini* in larger teeth with more crowded premolars, mandibular condyle not elevated above the cheek teeth, p2 less buccolingually rotated, p3 with distal accessory cuspid, absent or residual m2, and deltoid crest of the humerus extends beyond the middle of the diaphysis. Differs from *Erokomellivora lothagamensis* in shorter p4, buccolingually shorter m1 protoconid, and absent or residual m2 alveolus. Differs from *Ekorus ekakeran* and *Eomellivora piveteaui* in much smaller size, absence of m2 and p1; in humerus with enlarged pectoral crest and medial epicondyle, distal epiphysis craniocaudally compressed; ulna with the tuber olecrani medially projected, and unreduced articular circumference; calcaneus more robust and shorter with sustentacular facet medially projected and groove for the M. quadratus plantae more developed. Differs from *Mellivora capensis* in slenderer P3, p4; M1 with longer parastyle, mesial protocone; absence of the distal accessory cusp on P3 and the mesial accessory cusp on p3; m1 talonid narrower, sharper and more reduced with a central hypoconid, and without a lingual basined depression; calcaneus with smaller sustentacular facet.

Description

SAM-PQL-72167—A caniniform, right I3 (Fig. 3A1-3; Table 1), with a single cusp that curves distally. There is a sharp crista as well as a distinct cingulum in the lingual face.

SAM-PQL-69620—Left C (Fig. 3B1-3; Table 1). It is oval in cross-section and worn, especially the tip, buccal and lingual sides. The root swells mesiodistally, and the root is encircled by concentric rings.

SAM-PQL-51386—Left C (Fig. 3C1–3; Table 1). Its cusp is curved distally. Like SAM-PQL-72167 (Fig. 3A1-3), it has a sharp crista from the tip to the lingual side, as well as a distinct lingual cingulum.

SAM-PQL-50107—Right P3 (Fig. 3D1-3; Table 1). It is double rooted, elongate and unicuspid, with a lingual bulge. Its cusp is mesially located and shows wear. It has a well-developed cingulum.

SAM-PQL-72165—Left P3 (Fig. 3E1–2; Table 1). It belongs to a very young adult individual. No preserved roots or wear facets. Very similar to SAM-PQL-50107. It has a mesial and distal crista. Its distal cingulum is crowned.

SAM-PQL-72227—Right P4 (Fig. 3F1–3; Table 1). It is broken with a missing paracone. It is buccolingually robust. There is no parastyle. There is an inflection between the protocone and parastyle. The mesial side is worn. The protocone is missing, however, the remains suggest that it is in line with the parastyle, and is not mesiodistally reduced. There is no carnassial notch and the occlusal area is quite worn. There is a concavity in the buccal wall between the paracone and metastyle. A thick cingulum surrounds the entire crown.

SAM-PQL-72174—Left hemimandible with worn p2-m1, and an m2 alveolus (Fig. 3G1–4; Table 2). The mandibular corpus is tall and lateromedially broad. There are longitudinal cracks on the corpus (Fig. 3G1–2), as it was exposed prior to burial. The rostral part of the mandibular symphysis is missing as are the coronoid, articular and angular processes. The most caudal part of the mandibular symphysis reaches the distal position of p3. There are two mandibular foramina, one below p2 and the other below the junction of p3-4. Ventrally, there is a wide muscular attachment for the M. digastricus. The masseteric fossa is deep and in its ventral area has a large muscular attachment for M. masseter pars superficialis and M. masseter pars profunda. There is an alveolus for the C. There is no p1 alveolus. The p2 is buccolingually angled and unicuspid. Both p2 and p3 are double rooted, and distally wide. The main cuspid of the p3 is mesially located. There is a sharp cristid from the tip of this cuspid to the mesial part of the tooth. There is a small wear facet on the distal accessory cuspid, and the cuspid is smaller to those of the holotype SAM-PQL-42838. The p4 is elongated, subrectangular and distally broad.

It has a small mesial accessory cuspid. Its main cuspid is taller than the m1 paraconid. Its mesial cristid has a sharp edge. There is a worn distal accessory cuspid. A large cingulid surrounds the mesial and distal areas of p4. The occlusal surface of the m1 is worn. It is an elongate molar with a maximum width at base of the protoconid. The trigonid occupies more than three-fourths of the total length of the tooth. The protoconid is taller than the paraconid, and there is no metaconid. The talonid is low and buccolingually compressed. The only talonid cuspid is the hypoconid. There is a small, circular alveolus for the m2 (Fig. 3G3).

SAM-PQL-69620B—Left fragmentary hemimandible with m1 and m2 alveolus (Fig. 3I1–3; Table 2). The preserved mandibular corpus is very broad. It has longitudinal cracks on the corpus. The masseteric fossa is deeper than that of SAM-PQL-72174 and SAM-PQL-42836. The mandibular bone surrounding the m1 is very porous, indicating pathology. The m1 is larger than SAM-PQL-72174 and SAM-PQL-42836. There is a large wear facet on the distolingual part of the talonid. A low and centrally placed hypoconid is present. It has a large cingulid encircling the tooth. There is a small, circular alveolus for the m2.

SAM-PQL-50002—Left fragmentary hemimandible with m1 (Fig. 3J1–3; Table 2). The mandibular corpus is slender. The enamel of the m1 is partially dissolved and is missing on the mesial and distolingual area. The protoconid is taller than the paraconid. There are neither a metaconid nor an entoconid. The talonid has a low and centrally located hypoconulid. A distinct cingulid is present at the base of the entire tooth. There is no m2 alveolus.

SAM-PQL-50105—Large fragment of left hemimandible with p4-m1 broken at the base of the crown (Fig. 3K1–2; Table 2). The measurements of the teeth are the smallest of the entire sample from LBW (Table 2), but the absence of the crowns may underestimate the sizes of the actual teeth. There is no m2 alveolus.

SAM-PQL-50106—Right rostral mandibular corpus fragment with the alveolus for c, the distal root of p2, each of p3 and the mesial one of p4 (Fig. 3L1–2; Table 2).

SAM-PQL-50444—Left p2 (Fig. 3H1–3; Table 2), similar in the overall morphology to SAM-PQL-72174. It has long roots. The cuspid is tall and mesially situated. The distal cingulid is prominent.

SAM-PQL-72176—A partial humerus comprised of two thirds of the shaft, and the distal epiphysis (Fig. 4A–F; Table S1). Longitudinal cracks extend along the main axis of the bone and the surface is covered by root etching. The cortical bone of the diaphysis is thick (Fig. 4F). On the cranial surface, the pectoral and deltoid crests are present and are joined at the midpoint of the diaphysis (Fig. 4A). The pectoral crest projects medially. The distal epiphysis is very broad. The lateral epicondylar crest, onto which the M. anconeus and M. extensor carpi radialis attach, is expanded. The distal epiphysis is rectangular and craniocaudally compressed. The olecranon fossa is low, broad and proximodistally flattened. The caudal part of the capitulum is deep and lateromedially short. There is no a supratrochlear foramen. On the cranial side, the trochlea and the capitulum are proximodistally short and mediolaterally elongated. The medial epicondyle is dorsoventrally and medially enlarged, increasing the surface area for the attachment of M. pronator teres and M. flexor digitorum profundus. A large supracondylar (entepicondylar) foramen is present.

SAM-PQL-41875—Right humerus fragment, containing partial distal diaphysis (Fig. 4G–K; Table S1). The thick cortical bone and the large lateral epicondylar crest are very similar to SAM-PQL-72176. It also has longitudinal cracks along the main axis of the humerus. There are several pits and perpendicular bite marks, suggesting it was gnawed on.

SAM-PQL-72175—Complete right ulna (Fig. 4L–O; Table S1). It is robust, and sigmoid in cranial view. The olecranon is similar to SAM-PQL-40080, which is large and medially projected, without any tubercle on the cranial aspect of the olecranon. Thus, the attachment of the long head of the M. triceps brachii is also medially projected, more than that of SAM-PQL-40080. The trochlea is proximodistally short and craniocaudally deep. The anconeal process curves distally. The diaphysis is mediolaterally compressed but craniocaudally long. The proximal half of the diaphysis projects laterally, and the distal half projects medially. There is a prominent crest for the attachment of the M. pronator quadratus. The distal epiphysis is robust, with the articular circumference projecting cranially. The styloid process is large and round.

SAM-PQL-25606— Right ulna fragment (Fig. 4P; Table S1), comprised of the proximal epiphysis and two-thirds of the diaphysis. It is slightly smaller than SAM-PQL-40080 and SAM-PQL-72175, but larger than SAM-PQL-69620A.

SAM-PQL-69620A— Right ulna fragment (Fig. 4Q; Table S1), comprised of proximal epiphysis and one-third of the diaphysis. The olecranon is partially gnawed off. It may represent a young adult, because of its small size and porous nature.

SAM-PQL-69620E—Right fifth metacarpal (Mc V). A short and robust bone (Fig. 4R-W; Table S1). The dorsal surface of the metacarpal is rectilinear, but the palmar surface is slightly concave, because of the palmar projection of the proximal epiphysis. This epiphysis is subquadrangular, with the lateromedial axis longer than the dorsopalmar axis. There is a small hole in the middle of the proximal epiphysis. The lateral facet for the Mc IV is large and L-shaped. There is a relatively large and round groove for the attachment of the M. extensor carpi ulnaris on the lateral face of the metacarpal. The diaphysis is slightly dorsopalmarily flattened. The distal epiphysis is asymmetric, with the lateral margin larger than the medial.

SAM-PQL-42486— Right proximal femur epiphysis (Fig. 5A-E; Table S2). It is eroded and broken. There is bone regrowth and bone expose all over the surface. The head and greater trochanter are damage. The head is large and medially projected. The neck is short. The greater trochanter is relatively large and the trochanteric fossa is deep. In lateral view, the greater trochanter is craniocaudally wide, and has a rugose muscular attachment for the M. gluteus medius (Fig. 5D). The lesser trochanter is well developed and extends lateromedially. The rest of the diaphysis is missing.

SAM-PQL-41513A—Left distal femur epiphysis (Fig. 5F-I; Table S2), probably belonging to the same individual as SAM-PQL-42486. Part of the cortical bone is missing, like the area around the medial condyle. This epiphysis is subrectangular in distal view. The lateral condyle is lateromedially wider than the medial one. The trochlea is shallow. There are large scars for the attachment of the M. gastrocnemius on the caudolateral and caudomedial sides of the condyles.

SAM-PQL-69634B— Right calcaneum (Fig. 5J-O; Table S2). The entire bone shows secondary growth. It is nearly complete, with the exception of the most distodorsal part of the astragalar platform. The calcaneal tuberosity is robust, and lateromedially wide, with no process. The gastrocnemial groove on the proximal part of the tuberosity is shallow. There are lateral and medial bulges on the calcaneal tuberosity for the tendon of the M. superficial digital flexor. The body of the calcaneus is dorsoplantarily enlarged. The sustentaculum tali extends medially. In plantar view, there is a large falciform scar for the ligament of the M. long plantar, located lateral to the groove for the tendon of the M. flexor digitorum lateralis. On the laterodistal portion of the bone, there is a laterally extended quadratus plantae process. Additionally, there is a crest from that process to the ectal facet, to which the M. quadratus plantae is attached.

DISCUSSION

Mellivora benfieldi and Mio/Pliocene African and Indian Mellivorines

The mellivorine from LBW was first reported by Hendey (1974), who described a fragmentary mandible (SAM-PQL-6385) as *Mellivora* aff. *punjabiensis.* The material was collected from 'E' Quarry, MPPM, bed 3aS of the Varswater Fm. Later, he redefined this material and erected *M. benfieldi* from MPPM (bed 3aS and bed 3aN) based on several mandibles (SAM-PQL-42838, SAM-PQL-31273, SAM-PQL-50443, SAM-PQL-6385), an M1 (SAM-PQL-50541), and, tentatively on a complete ulna and radius (SAM-PQL-40080, SAM-PQL-45384) (Hendey, 1978a).

Most of the new specimens of *M. benfieldi* described in the present study are from the MPPM (bed 3aS and N), and for the first time this taxon is reported from the LQSM (Table S3). The minimum number of individuals known from MPPM and LQSM, based on the m1, is eight. This sample of *M. benfieldi* from LBW displays wide biometric and morphological variability in dentition and in the postcranial bones (Figs. 3–6; Tables 1–2, Table S1-2). This variability includes: a better developed distal accessory cuspid on p3 of SAM-PQL-42838 (holotype) in relation with SAM-PQL-72174; and a better developed mesial accessory cuspid on p4 of SAM-PQL-50443 and SAM-PQL-42836 compared to the other specimens. However, the most noteworthy variation is on the lower molars. The specimens with preserved lower molars come from Beds 3aN and Bed 3aS of MPPM (Table S3). The m1 of SAM-PQL-72174 and SAM-PQL-6385 have a relatively wide protoconid and talonid compared to SAM-PQL-42836 and the extremely slender SAM-PQL-50002, which has damaged or dissolved enamel. SAM-PQL-72174 and SAM-PQL-69620b have the first documented m2 alveolus in *M. benfieldi*. The retention of the m2 alveolus in two specimens from the relatively older Bed 3aS, represents 25% of the entire sample of *M. benfieldi*. This also means 50% of the mandibles from Bed 3aS had m2s (Table S3). This study suggests that this trait is variable, although the low occurrence in the LBW population points toward the m2 disappearing in this mustelid through the time. Some intraspecific variation in *M. benfieldi* may be explained by sexual dimorphism, with large specimens interpreted as males and smaller ones as females, as is the case in *M. capensis* (Begg et al., 2003; Larivière and Jennings, 2009). This extensive variability should be taken into account when interpreting other African mellivorines from the fossil record. For instance, the occurrence of m2 in the late Miocene *Howellictis* Bonis, Peigné, Guy, Likius, Makaye, Vignaud, and Brunet, 2009 and *Erokomellivora* Werdelin, 2003 is interpreted as a primitive trait for the group, and has been used to separate it from *Mellivora*, where it disappeared (Werdelin, 2003; Werdelin and Peigné, 2010). Additional traits are needed to distinguish between these genera.

Mellivora benfieldi has also been described from: Brisighella, Italy (late Miocene, MN13, ca. 5.4 Ma) represented by a mandible fragment with p3-m1

(Rook et al., 1991) and Middle Awash Fm. of Ethiopia (ca. 6-5.5 Ma), represented by a hemimandible with worn dentition, a broken m1 and a lower canine (Haile-Selassie and Howell, 2009), though this referral is dubious. The mellivorine from Brisighella can undoubtedly be attributed to *M. benfieldi*, as its morphological traits conform to the known variability of this taxon. However, the Middle Awash specimen AMW-VP-1/40 is different. Haile-Selassie and Howell (2009) suggested that the Middle Awash species is likely to be ancestral to the South African *M. benfieldi*. It has a relatively longer p4 (Table S4) and a m1 with a wider trigonid and a more robust talonid to those from LBW. These traits are more comparable to those of *Er. lothagamensis* from Lothagam (Werdelin, 2003), which lived at the same time in Kenya. The absence of an m2 alveolus in AMW-VP-1/40 could be explained as intraspecific variability in *Erokomellivora*, as it occurs in *M. benfieldi* from LBW. *Erokomellivora lothagamensis* and AMW-VP-1/40 are worn and incomplete specimens, we therefore consider the designation of AMW-VP-1/40 as *M*. aff. *benfieldi* as valid until more material is available.

‘*Eomellivora*’ *tugenensis* from the Ngorora formation in Kenya (Morales and Pickford, 2005b) represents the oldest African mellivorine, ca. 12 Ma. It is a poorly known mustelid of medium size, known from a fragmentary skull with a broken P4 and a complete M1, which could constitute an ancestral form of *Eomellivora* (Valenciano et al., 2015, 2017a). *Mellivora benfieldi* shares some primitive traits with ‘*E*’. *tugenensis*, such as a double rooted P3, and an M1 with an enlarged parastyle, and a relatively well-developed metacone. However, *M. benfieldi* is distinguished from ‘*E*’. *tugenensis* by its smaller size, and a messially placed M1 protocone.

Howellictis valentini from the late Miocene locality of Toros Menalla 192 from Chad (ca. 7 Ma), is known from several specimens including skulls, mandibles and some fragmentary postcranial remains (Bonis et al., 2009). It has been interpreted as a basal mellivorine (Valenciano et al., 2017a), which is partially in agreement with Bonis et al. (2009). *Mellivora benfieldi* also shares primitive traits with *H. valentini* such as an elongated P3, a well- developed M1 parastyle, and a slender p4. Additionally, both taxa have m1s with a low and reduced talonid. *Mellivora benfieldi* differs from *H. valentini* by having a mandibular condyle that is not elevated above the cheek teeth, larger teeth with more crowded premolars, p2 with less buccolingually rotation, p3 with a distal accessory cuspid, and absent or residual m2. The fragmentary nature of the postcrania of *H. valentini* does not allow a direct comparison to the postcrania of *M. benfieldi*, except for the humerus, and the calcaneus. The deltoid crest of the humerus does not extend beyond the middle of the diaphysis, and the calcanei of both small mellivorines are robust and have similar proportions. *Howellictis valentini* is interpreted as a fully plantigrade carnivore with a gait comparable to that of the ambulatory ones (Bonis et al., 2009), but has not be reconstructed as fossorial. In contrast, we suggest *M. benfieldi* was semifossorial.

Promellivora punjabensis was originally described as *Mellivora punjabiensis* by Lydekker (1884), from the late Miocene sediments of the Dhok Pathan Fm., in India (Pilgrim, 1932), based on an extremely fragmentary mandible with worn dentition that has p2 and m1 alveoli and broken c, p3-p4. Pilgrim (1932) erected the genus *Promellivora* based on this mandible, and described the presence of a p1 alveolus. Rook et al. (1991) distinguished *P. punjabensis* from *M. benfieldi* by its much sturdier mandibular corpus, its relatively broader premolars and by the presence of the p1. In our opinion, this material is very fragmentary, and a detailed comparison cannot be made with *M. benfieldi*. More complete material of *Promellivora* might clarify its relationship with other mellivorines.

The late Miocene Nawata Formation from Kenya has yielded two distinct mellivorines, *Ekorus ekakeran* in the Lower Nawata Fm. ca. 7 Ma, and *Erokomellivora lothagamensis* in the Upper member, ca. 6.5–5.5 Ma (Werdelin, 2003; Werdelin and Peigné, 2010), of which only *Er. lothagamensis* is a form close to *Mellivora benfieldi*. *Erokomellivora lothagamensis* is only known from a mandibular corpus with a broken p4 and a worn m1. It has the longest p4 in relation to the m1 of the mellivorines analyzed for this study (Table S4). The size of the m1 of *Er. lothagamensis* overlaps with the larger specimens of *M. benfieldi* from LBW (Fig. 6). Werdelin (2003) noted the similarities of *Er. lothagamensis* and *M. benfieldi* from LBW but distinguished it as a new mellivorine that is more primitive than *M. benfieldi*, because of its considerably longer p4, the more obliquely set and shorter m1 trigonid, and, primarily because the retention of m2 (Fig. 7A-I). Only SAM-PQL69620 of *M. benfieldi* (Figure 3I1-3) is close to *Er. lothagamensis* in having a similar m1 morphology and retaining m2 alveolus. However, the less obliquely set m1 trigonid, the shorter m1 talonid, and the reduced m2 alveolus in SAM-PQL-69620 distinguishes these taxa.

The mellivorine from LBW can be ascribed to the genus *Mellivora* based on several dental traits shared with *M. capensis* (Fig. 7; Table S5). These are a short P4 with a buccal concavity between the paracone and the metastyle; a mandibular condyle not elevated above the cheek teeth; presence of a distal accessory cuspid on the p3; a mesial accessory cuspid on the p4; and the loss of m2. Furthermore, several postcranial features, place the LBW taxon within *Mellivora*, such as a humerus with craniocaudally compressed distal epiphysis, an ulna with medially projected tuber olecrani and a medial projection of the M. pronator quadratus. The oldest specimen of *M. capensis* in the fossil record comes from the middle Pliocene of Laetoli (Tanzania, ca. 3.5 Ma) (Petter, 1987). It is fragmentary and poorly preserved, which raises doubts about its specific assignation. Its presence is more confident in the late Pliocene of Ahl al Oughlam (Morocco) ca. 2.5 Ma (Geraads, 1997). This taxon was abundant in Africa during the Pleistocene, especially in South Africa (Hendey, 1974, 1978a; Werdelin and Peigné, 2010; Geraads, 2016). It appears in the Cradle of Humankind World Heritage Site localities of Komdraai B, 2-1 Ma (Gommery et al., 2008), and Cooper's D, 1.4-1.5 Ma (De Ruiter et al., 2009; O´Regan et al., 2013). It is better represented at Elandsfontein, 1-0.6 Ma (Klein et al., 2007), Swartklip 1 (0.1 Ma), and the Holocene sites of Tygerfontein and Sea Harvest (e.g., Hendey, 1974, 1978a). These middle-late Pleistocene/Holocene remains of *M. capensis* are nearly identical to those of the living populations, overlapping in the wide range of variability observed in the dentition of *M. capensis* (Fig. 6; Table S5).

Mellivora benfieldi has a mosaic of primitive and derived traits. It is a more primitive mellivorine than *M. capensis* by having less robust premolars (P3, p3-4), double rooted P3; M1 with longer parastyle; M1 with a mesial protocone and with a relatively smaller and weak lingual platform; smaller and fewer accessory cusps (e.g., absence of the mesial and distal ones on the P3, and the mesial one in the p3), m1 protoconid taller than the paraconid and a reduced sustentacular facet of the calcaneus. The m1 is different, interpreted here as derived, being narrower, sharper and with a more reduced talonid to that of *M. capensis*. It has a central hypoconid, and has lost the hypoconulid and the lingual basin depression of the talonid, which are present in *M. capensis*. The distinction between *M. benfieldi* and *M. capensis* and their phylogenetic affinities have been questioned in the past (Petter, 1987; Werdelin and Dehghani, 2011) as a result of the previously fragmentary material of *M. benfieldi*, the similarities of the Pleistocene *M. capensis* with the living ones, and because *M. capensis* is a highly plastic taxon in terms of dental variability (A.V. pers. observ.). Hendey (1978a) indicated that *M. benfieldi* is suitable to be ancestral to *M. capensis*, while Petter (1987) compared the classic material of *M. benfieldi* (Hendey, 1974, 1978a) with the living *M. capensis*, and stated that neither the measurements nor proportions of the teeth clearly separate the Langebaanweg specimens from the extant *M. capensis*. Petter (1987) proposed that *M. benfieldi* might represent the ancestral starting point of the *M. capensis* lineage, instead of two separated taxa, with an increase in size in *M. capensis* through the Pliocene. However, based on the updated sample of *M. benfieldi* and the discussed morphological differences between both, we support their taxonomic differentiation.

After comparing of the available postcrania of *M. benfieldi* and *M. capensis*, we confirm that the ulna and radius (SAM-PQL-L40080 and SAM-PQL-45384) figured by Hendey (1978a) belongs to *M. benfieldi*. The long bones of both *Mellivora* species (*M. benfieldi* and *M. capensis*) are quite similar. The humerus has a deltopectoral crest that exceeds the distal half of the diaphysis, a well-developed pectoral crest that enlarges laterally, a supraepicondylar crest that projects laterally, and a well-developed medial epicondyle, which is proximodistally expanded and projected medially. These structures serve as areas of attachment for various muscles that flex, pronate and supinate the forearm and flex and extend the wrist (e.g., Gambaryan, 1974; Schutz and Guraznik, 2007; Samuels et al., 2013; Ercoli et al., 2015, 2016; Fabre et al., 2015). These large epicondyles increase the muscle mass located in the medial and distal segments of the forelimb and increase the force produced when digging (Hildebrand 1985; Moore et al., 2013, Rose et al., 2014) as observed in caviomorph rodents (Elissamburu and Vizcaíno, 2004; Elissamburu and De Santis, 2011; Rose et al., 2014). *Mellivora benfieldi* has a relatively narrow trochlea on the caudal part of the distal epiphysis of the humerus compared to *M. capensis*. We calculated the index of fossorial ability (OLI sensu Samuels et el., 2013 and IFA sensu Rose et al., 2014), and the index of ulnar robustness (URI) of *M. benfieldi* ulnae and compared them with a broad sample of living carnivorans. The index of fossorial ability, a recognized metric of fossoriality, indicates the relative mechanical advantage for the elbow extensors (M. triceps brachii, M. anconeus, and M. epitrochlearis) by an enlargement of the olecranon process to apply a large force to the substrate during elbow joint extension (Schutz and Guralnick, 2007; Moore et al., 2013; Samuels et al., 2013; Rose et al., 2014). The values of OLI and IFA in SAM-PQL-72175 and SAM-PQL-40080 are relatively high compared with the living carnivorans families but slight lower than the badgers *Melogale moschata*, *Melogale personata*, and *M. capensis*, being closer to the generalist mustelid *Galictis vittata* or the herpestid *Crossarchus obscurus*, both with recognized digging abilities (e.g., Larivière and Jennings, 2009; Gilchrist et al., 2009). These high values indicate a relatively large olecranon process in *M. benfieldi*, which suggests that it also had some digging abilities, although not as progressive as living badgers (e.g., *Melogale* spp., *Meles* spp., *Taxidea taxus*, *M. capensis*). The URI indicates the degree of robustness of the ulna and its ability to resist bending and shearing stresses and the relative area available for the origin and insertion of forearm and manus flexors, pronators and supinators

(Hildebrand, 1985; Elissamburu and Vizcaíno, 2004; Elissamburu and De Santis, 2011; Samuels et al., 2013; Rose et al., 2014). *Mellivora benfieldi* is amongst the highest values for the carnivoran sample of Samuels et al. (2013) and Rose et al. (2014) indicating a very robust ulna. This index increases with fossorial ability in scratch-digging rodents (Elissamburu and Vizcaíno, 2004; Lagaria and Youlatos, 2006), yet, we cannot rule out that the large curvature of the ulna overestimated this index. The proximal epiphysis of the femur of *M. benfieldi* (SAM-PQL-42486; Fig. 5A-E) has a shorter neck than *M. capensis*, which could suggest lower degree of mobility of the femur, with restriction to the parasagittal plane. This specimen, however; has pathological regrown bone, which hides the real length of the femoral neck. Finally, *M. benfieldi* has a robust Mc V (Fig. 4R-W) and robust calcaneus (Fig. 5J-O) like *M. capensis*.

Based on the above observations, we conclude that *M. benfieldi* was a more hypercarnivorous mustelid than *M. capensis*, with semifossorial abilities. We infer *M. benfieldi* was an opportunistic carnivoran of medium size in the carnivore guild of LBW. Two additional species of mustelid have been found at LBW, including the giant gulonine *Plesiogulo* aff. *monspessulanus*, a species related to the living wolverine (Valenciano et al., 2020a; Valenciano and Govender, 2020), and the large, bunodont otter *Sivaonyx hendeyi* (Hendey, 1974, 1978a; Morales et al., 2005; Morales and Pickford, 2005b; Valenciano and Govender, 2020). It is notable that small musteloids are absent from LBW, when compared with other Mio/Pliocene Eurasian localities, in which small martens, weasels, and skunks are present (e.g., Ginsburg, 1999; Montoya et al., 2011; Morales et al., 2015; Valenciano et al., 2020b). The only Mio-Pliocene small mustelid described in Africa is *Prepoecilogale* Petter and Howell, 1985, which occurred in late Pliocene localities of Morocco, Tanzania and South Africa (Werdelin and Peigné, 2010), but is absent from LBW. Small musteloids may be absent in Africa during this time because small carnivore niches were occupied by small herpestids and viverrids, which are also very common at LBW, with at least two small taxa for each family (Hendey, 1974, Werdelin, 2006; Werdelin and Peigné, 2010).

Phylogenetic Analysis

Suprageneric taxonomy can be a critical problem for the fossil taxa due to the fragmentary dental, cranial and postcranial material, and the presence of primitive and derived characters (Valenciano et al., 2017a). The systematics of Mellivorinae and the tribe Mellivorini have been extensively discussed in the past (e.g., Pia, 1939; Tobien, 1955; Webb 1969; Ginsburg, 1977; Ginsburg and Morales, 1992; McKenna and Bell, 1997; Ginsburg, 1999; Valenciano et al., 2015, 2017a, 2020a). Pia (1939) used comparative morphology to subdivide the Mellivorinae in the "sub-subfamilies": Mellivorini (*Mellivora*, *Promellivora* Pilgrim, 1932, and *Eomellivora* Zdansky, 1924), Ischyrictini (*Ischyrictis* Helbing, 1930, *Laphictis* Viret, 1933, *Hadrictis* Pia, 1939, and the North American endemic megalictine *Megalictis* Matthew, 1907, *Aulurocyon* Peterson, 1907, *Oligobunis* Cope, 1881). Later, Tobien (1955) reclassified these groups at the tribe rank and added *Hoplictis helbingi* (Viret, 1951) into Ischyrictini. Webb (1969) introduced several changes to the tribes within Mellivorinae with his final tribes resolved as: (1) Mellivorini (*Mellivora*, *Promellivora*, *Eomellivora*, *Perunium* Orlov, 1948, *Megalictis* and *Aelurocyon*), (2) Gulonini (*Ischyrictis*, *Hadrictis*, *Plesiogulo* Zdansky, 1924 and *Gulo* Pallas, 1780), (3) Brachypsalini (*Brachypsalis* Cope, 1890, *Paroligobunis* Peterson, 1910, *Sthenictis* Peterson, 1910, and *Brachypsaloides* Webb, 1969). New relationships are being assessed using cladistics methods for Miocene mustelids. Thus, Valenciano et al. (2020a) resolved Guloninae as comprised of the tribes Gulonini (*Gulo*, *Plesiogulo* and *Iberictis* Ginsburg and Morales, 1992) and Ischyrictini (*Ischyrictis*, *Laphictis*, and *Dehmictis* Ginsburg and Morales, 1992). In Valenciano et al. (2015, 2017a, 2020a) Mellivorinae includes the genera *Mellivora*, *Eomellivora* (=*Perunium*, and *Hadrictis*), *Ekorus* Werdelin, 2003, *Howellictis*, and possibly *Hoplictis* Ginsburg, 1961. Valenciano et al. (2016), interpreted the North American Oligobuninae as containing among others *Oligobunis*, and *Megalictis* (=*Aelurocyon,* and *Paroligobunis*) (Valenciano et al., 2016).

Our cladistics analysis recognizes two main clades: Mellivorinae and Guloninae (Fig. 8). Synapomorphies for each node are reported in Table S5. The relationship of the medium size mustelid *Sthenictis* sp, *Ischyrictis zibethoides* and *Laphictis mustelinus* are not resolved by our phylogenetic analysis. In the previous analysis of Valenciano et al., (2020a) both *I. zibethoides* and *L. mustelinus* were nested with *Dehmictis vorax* in the tribe Ischyrictini, however they appear herein in a polytomy. The primitive morphology of *Sthenictis* sp, *I. zibethoides* and *L. mustelinus*, which share several symplesiomorphies, may support their potential Guloninae affinity, therefore we interpreted them as stem Guloninae. The clade Gulonini is very-well supported (Fig. 8). It is located as the sister group of the living *Martes foina*-*Pekania pennanti*, in agreement with molecular data based phylogenies (Koepfli et al., 2008; Sato et al., 2012; Li et al., 2014; Zhu et al., 2016), where wolverines (*Gulo*) is always closely related to martens (*Martes*) and fisher (*Pekania*).The gulonini show minor differences to the one from Valenciano et al., (2020a). Here, *Plesiogulo monspessulanus* nests with *Gulo* spp., rather with the early Miocene *Iberictis*. This difference in the new phylogeny, stresses the importance of the inclusion of postcranial characters in phylogenies. The incorporation of more postcrania data of the early Miocene *Iberictis*, the middle Miocene *Sthenictis* sp, *I. zibethoides* and *L. mustelinus* and the late Miocene *Plesiogulo* spp., are needed to refine their evolutive relationships. Our phylogenetic analysis suggests a new evolutionary framework in Mellivorinae, which two mains clades, interpreted as a tribe level, are distinguished within this subfamily: Eomellivorini Zdansky, 1924 (new rank) (*Eomellivora* spp. + *Ekorus*) and Mellivorini Gray, 1865 (*Howellictis* + *Mellivora* spp.). We identify for the first time the clade Eomellivorini, defined by the common ancestor of *Eomellivora piveteaui* and *Ekorus ekakeran* and all of its descendants. This clade is strongly supported (Fig. 8). It comprises very large mellivorines from the late Miocene of Eurasia, North America, and Africa that are characterized by both primitive dentition—presence of p1 and m2, enlarged M1 stylar area—and derived dentition—slender and multicuspid premolars and m1 talonid reduced to a single cuspid placed directly distal to the trigonid blade. The postcranial skeleton includes cursorial adaptations (Werdelin, 2003; Valenciano et al., 2015, 2017b) observed in canids or hyaenids, but not seen in Mustelidae. Some of this traits are a small-size supraepicondilar crest, a distinct reduction in the medial epicondyle, and a sub-quadrangular distal epiphysis of the humerus; ulna with a rectilinear tuber olecrani, and a reduced articular circumference integrated in the styloid process, and lastly an elongated calcaneus with a reduced sustentacular facet and a reduced process for the M. quadratus plantae. Here the tribe Mellivorini encompasses *Mellivora* spp. (*M. benfieldi* + *M. capensis*) plus *H. valentini*. They are small- to medium mellivorines with P4 protocone mesially placed, M1 with a reduced metacone and with a lingual platform enclosed by the protocone, P1-p1 absent, and a robust calcaneal tuber among other traits (Table S5). According to this, *Erokomellivora* and the late Miocene *Promellivora* from the Dhok Pathan in Siwalik, India (Pilgrim, 1932) are likely part of Mellivorini. Eomellivorini is the sister group of the African Mellivorini. It has also been proposed that *Mellivora* probably evolved in the latest Miocene from *Er. lothagamensis*, *H. valentini* or a similar form (Werdelin, 2003; Werdelin and Peigné, 2010; Werdelin and Dehghani, 2011). Our phylogenetic analysis (Fig. 8) suggests *Howellictis* is the sister taxon of *Mellivora*, though more fossils of Mio-Pliocene mellivorines – especially *Erokomellivora* – are necessary to fully resolve the origins of *Mellivora*.

CONCLUSIONS

We describe abundant new fossils of *M. benfieldi,* including several hemimandibles, and previously unknown upper dentition C, I3, P3 and P4, as well as remains of the forelimb, and hind limb. These new specimens of *M. benfieldi* expands our knowledge of its intraspecific variability, paleobiology, and distribution in the LBW´s members, being reported for the first time in LQSM (SAM-PQL 25606 and 51386). *Mellivora benfieldi* also occurred in the late Miocene of Italy and Ethiopia, and is clearly distinguished from other African mellivorines, such as the middle-late Miocene '*Eomellivora*' *tugenensis* from Ngorora, Kenya, and the late Miocene *Howellictis* from Chad, and *Erokomellivora* from Kenya, and the living honey badger *M. capensis* by the overall morphology and proportions of the dentition and postcranial skeleton. The postcranial remains of *M. benfieldi* indicate semifossorial abilities, similar to those of *M. capensis*. We infer *M. benfieldi* was an opportunistic, medium-sized carnivoran in the carnivore guild of LBW. This is the first cladistics analysis to include these taxa, and a sister-group relationship between *M. benfieldi* and *M. capensis* is confirmed. We create a tribe within Mellivorinae: Eomellivorini (*Eomellivora* spp.+ *Ekorus*) and suggest Mellivorini includes *M. benfieldi*, *M. capensis, H. valentini, Er. lothagamensis* and the Indian taxon *Promellivora punjabiensis*.

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FIGURE CAPTIONS

FIGURE 1. Location of the Langebaanweg fossil site. **A,** Silhouette of Africa, indicating the position of Langebaanweg (gray star); **B**, Simplified geographic map of South Africa. Modified from Govender (2019). **Abbreviations**: WCFP, West Coast Fossil Park. [planned for column width]

FIGURE 2. Postcranial measurements used in this work, based on *Mellivora capensis* (ZM-41666 and ZM-41483). Humerus in cranial (**A**), and lateral (**B**) views; Radius in proximal (**C**), distal (**D**), caudal (**E**), and medial (**F**) views; Ulna in cranial (**G**), and medial (**H**) views; Metacarpal V in medial (**I**) and dorsal (**J**) views; Femur in cranial (**K**), proximal (**L**), and distal (**M**) views; Calcaneus in dorsal (**N**), lateral (**O**), and distal (**P**) views. **Description of the measurements**: **Humerus**. lateromedial width of the diaphyseal shaft measured at the last third of the bone, where the lateral crest of *M. anconeus* finish (**1**), height of the medial epicondyle (**2**), height (**3**) and length (**4**) of the humeral condyle (trochlea + capitulum), maximum lateromedial width of the distal epiphysis (**5**), craniocaudal

width at the point where measurement 1 was collected (**6**), and craniocaudal width of the lateral epicondyle (**7**); **Radius**. total length (**1**), lateromedial (**2**), and craniocaudal (**3**) widths of the proximal epiphysis, lateromedial (**4**) and craniocaudal (**5**) widths of the middle point of the diaphysis, lateromedial (**6**) and craniocaudal (**7**) widths of the distal epiphysis; **Ulna**. Total length (**1**), maximum lateromedial width of the olecranon tuber (**2**), maximum craniocaudal width of the olecranon tuber (**3**), proximodistal height of the proximal epiphysis of the ulna, measured from the proximal edge of the olecranon to the distal edge of the radial notch (**4**), proximodistal height of the trochlear notch (**5**), proximodistal height of the olecranon (**6**), lateromedial width of the radial notch, comprising both medial and lateral coronoid processes (**7**), lateromedial (**8**) and craniocaudal widths of the middle point of the diaphysis (**9**), craniocaudal width of the distal epiphysis at the level of the articular circumference (**10**), craniocaudal (**11**) and lateromedial (**12**) widths of the styloid process; **Metacarpal V**. dorsopalmar (**1**) and lateromedial (**2**) widths of the distal epiphysis, total length (**3**), dorsopalmar (**4**), and lateromedial (**5**) widths of the middle point of the diaphysis, dorsopalmar (**6**) and lateromedial (**7**) widths of the proximal epiphysis**; Femur**. Lateroproximal-mediodistal width of the articular head (**1**), craniocaudal width of the articular head (**2**), maximum lateromedial width of the proximal epiphysis (**3**), lateromedial width of the distal epiphysis (**4**), and craniocaudal length of the distal epiphysis (**5**); **Calcaneus**. Total length (**1**), maximum width (**2**), maximum height (**3**), proximodistal length of the articular surface (**4**), proximodistal (**5**) and lateromedial (**6**) widths of the *tuber calcanei*, dorsoplantar (**7**) and lateromedial (**8**) lengths of the cuboid facet. [planned for page width]

FIGURE 3. New dental and mandibular material of *Mellivora benfieldi* from Langebaanweg (South Africa). **A**. SAM-PQL-72167, right I3 in distal (**A1**), buccal (**A2**), and mesial (**A3**) views; **B**. SAM-PQL-69620C, left CX in buccal (**B1**), distal (**B2**), and lingual (**B3**) views; **C**. SAM-PQL-5138B, left CX in buccal (**C1**), distal (**C2**), and lingual (**C3**) views; **D**. SAM-PQL-50197, right P3 in buccal (**D1**), lingual (**D2**), and occlusal (**D3**) views; **E**. SAM-PQL-72165, right P3 in buccal (**E1**), and occlusal (**E2**) views; **F**. SAM-PQL-72227, fragmentary right P4 in buccal (**F1**), lingual (**F2**), and occlusal (**F3**) views; **G**. SAM-PQL-72174, fragmentary left hemimandible in buccal (**G1**), lingual (**G2**), occlusal (**G3**) and ventral (**G4**) views; **H**. SAM-PQL-50444, left p2 in buccal (**H1**), lingual (**H2**), and occlusal (**H3**) views; **I**. SAM-PQL-69620B, fragmentary left hemimandible in buccal (**I1**), lingual (**I2**), and occlusal (**I3**) views; **J**. SAM-PQL-50002, fragmentary left hemimandible in buccal (**J1**), lingual (**J2**), and occlusal (**J3**) views; **K**. SAM-PQL-50105, fragmentary left hemimandible in buccal (**K1**), and occlusal (**K2**) views; **L**. SAM-PQL-50106, fragmentary right hemimandible in buccal (**L1**), and occlusal (**L2**) views. Scale bar equals 2 cm. [planned for page width]

FIGURE 4. New postcranial material of the forelimb of *Mellivora benfieldi* from Langebaanweg (South Africa). **A-F**. SAM-PQL-72176, left fragmentary humerus in cranial (**A**), lateral (**B**), caudal (**C**), medial (**D**), distal (**E**), proximal (**F**) views; **G-K**. SAM-PQL-41875, right fragmentary humerus diaphysis in distal (**G**), rostral (**H**), lateral (**I**), caudal (**J**), and medial (**K**) views; **L-O**. SAM-PQL-72175, right ulna in cranial (**L**), medial (**M**), caudal (**N**), and lateral (**O**) views; **P**. SAM-PQL-25606, right fragmentary ulna in rostral view; **Q**. SAM-PQL-69620A, right fragmentary ulna in rostral view; **R-W**. SAM-PQL-69620E, right fifth metacarpal

(Mc V) in proximal (**R**), distal (**S**), dorsal (**T**), lateral (**U**), ventral (**V**), and medial (**W**) views. Scale bar equals 2 cm. [planned for page width]

FIGURE 5. New postcranial material of the hind limb of *Mellivora benfieldi* from Langebaanweg (South Africa). **A-E**. SAM-PQL-42486, femur, right proximal epiphysis in rostral (**A**), medial (**B**), caudal (**C**), lateral (**D**), and proximal (**E**) views; **F-I**. SAM-PQL-41513A, femur, left distal epiphysis (belonging to the same specimen than SAM-PQL-42486) in rostral (**F**), medial (**G**), caudal (**H**), and distal (**I**) views; **J-O**. SAM-PQL-69634, right calcaneum in dorsal (**J**), medial (**K**), plantar (**L**), lateral (**M**), proximal (**N**), and distal (**O**) views. Scale bar equals 2 cm. [planned for page width]

FIGURE 6. Measurements (mm) of the lower carnassial (m1) of African and Eurasian mellivorines as depicted in bivariate plots of maximum mesiodistal length (L) vs. maximum buccolingual width (W). Sources: Hendey, 1974; Rook et al., 1991; Geraads, 1997; Werdelin, 2003; Bonis et al., 2009; Haile-Selassie and Howell, 2009; Geraads, 2016, and this work. [planned for page width]

FIGURE 7. Main comparative material of mellivorines from Africa herein analyzed. **A-C**. SAM-PQL-42838, holotype of *Mellivora benfieldi* from Langebaanweg described by Hendey (1978a), fragmentary right hemimandible in buccal (**A**), lingual (**B**), and occlusal (**C**) views; **D-F**. SAM-PQL-50443, *Mellivora benfieldi* from Langebaanweg described by Hendey (1978a), fragmentary right hemimandible in buccal (**D**), lingual (**E**), and occlusal (**F**) views; **G-I**. KNM-LT 23926, *Erokomellivora lothagamensis* Lothagam, upper member of the Nawata

Formation, Kenya, Late Miocene, fragmentary left hemimandible in buccal (**G**), lingual (**H**), and occlusal (**I**) views; **J-L**. SAM-ZM-41666, *Mellivora capensis*, living honey badger, left hemimandible in buccal (**J**), lingual (**K**), and occlusal (L) views. Scale bar equals 2 cm. [planned for page width]

FIGURE 8. Phylogenetic relationships of *Mellivora benfieldi* within selected Mustelidae. Bootstrap 50% majority-rule consensus (length 249 steps; consistency index (CI) = 0.4458, homoplasy index (HI) = 0.5542, and retention index (RI) = 0.6434) was obtained using PAUP*4.0b10 (Swofford, 2002). The outgroup is *Zodiolestes daimonelixensis*. The numbers below nodes are Bremer support, and the numbers above nodes are Bootstrap support percentages (only shown if ≥ 50). Letters (A-E) indicated selected nodes. The synapomorphies for each node are reported in Table S5. [planned for column width]

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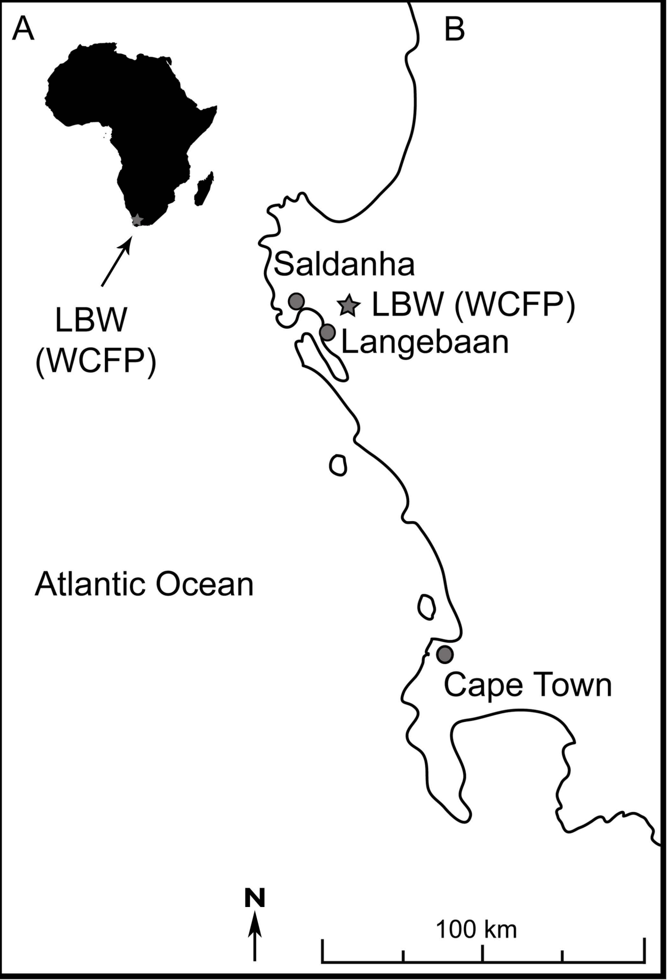
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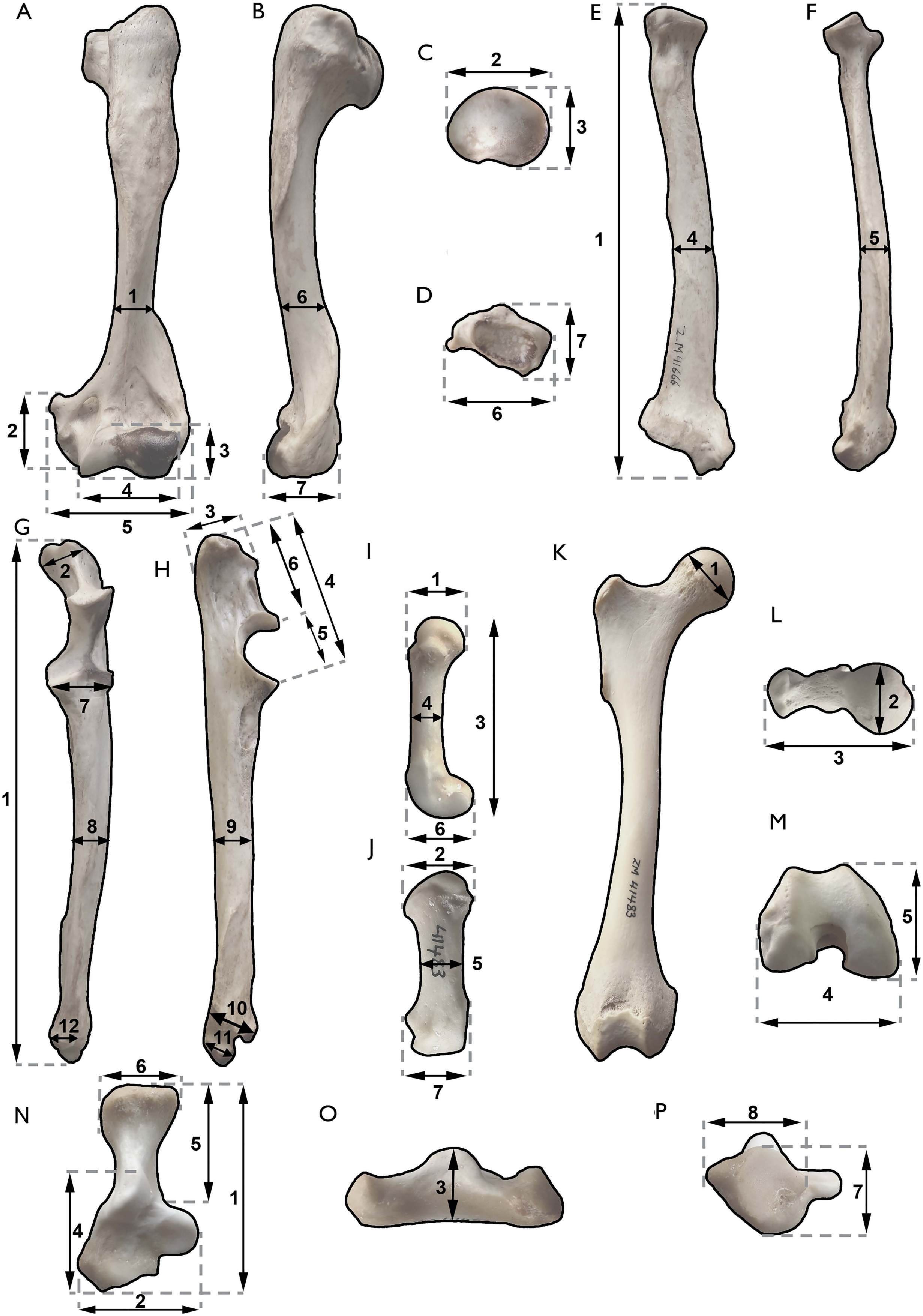
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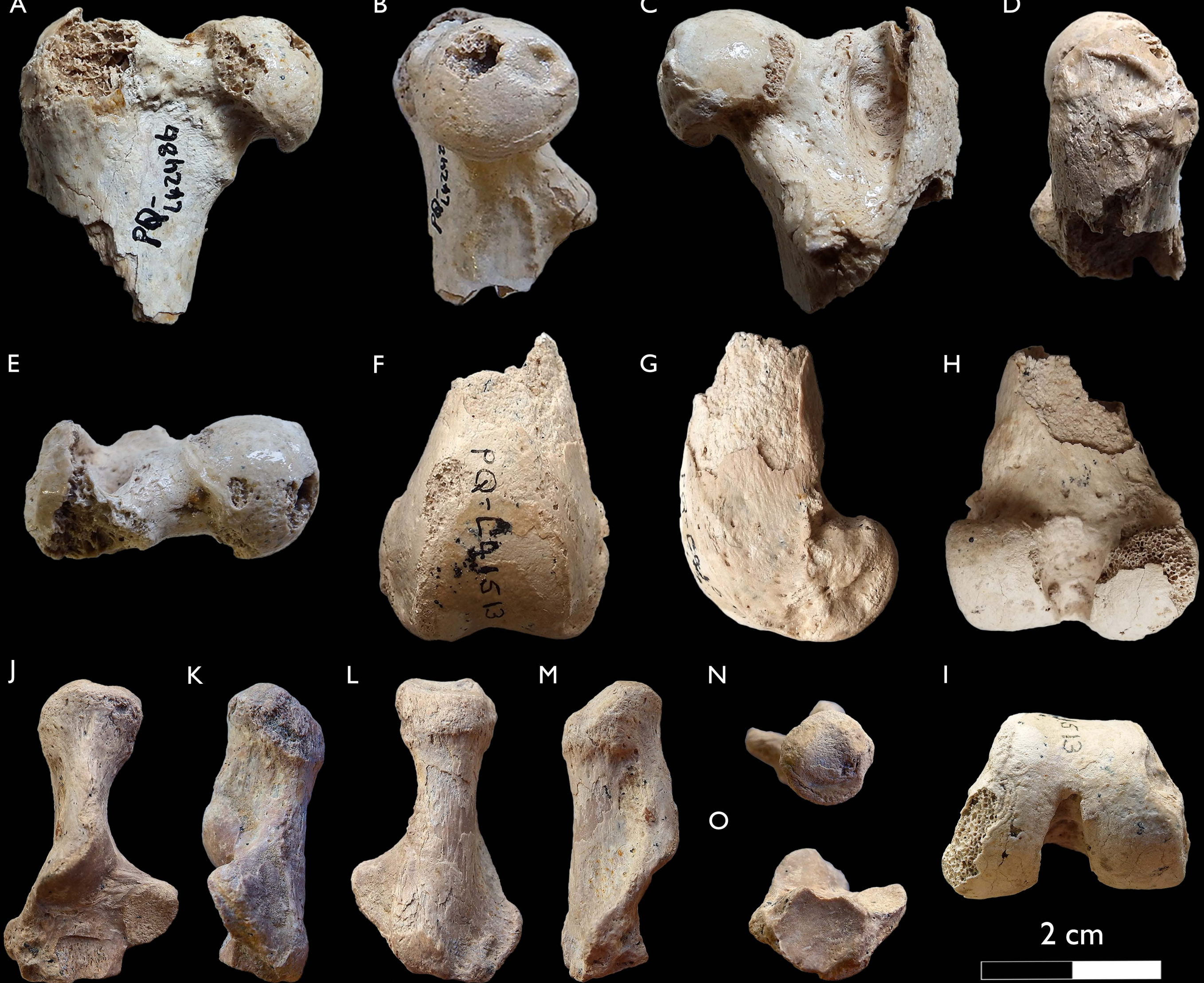
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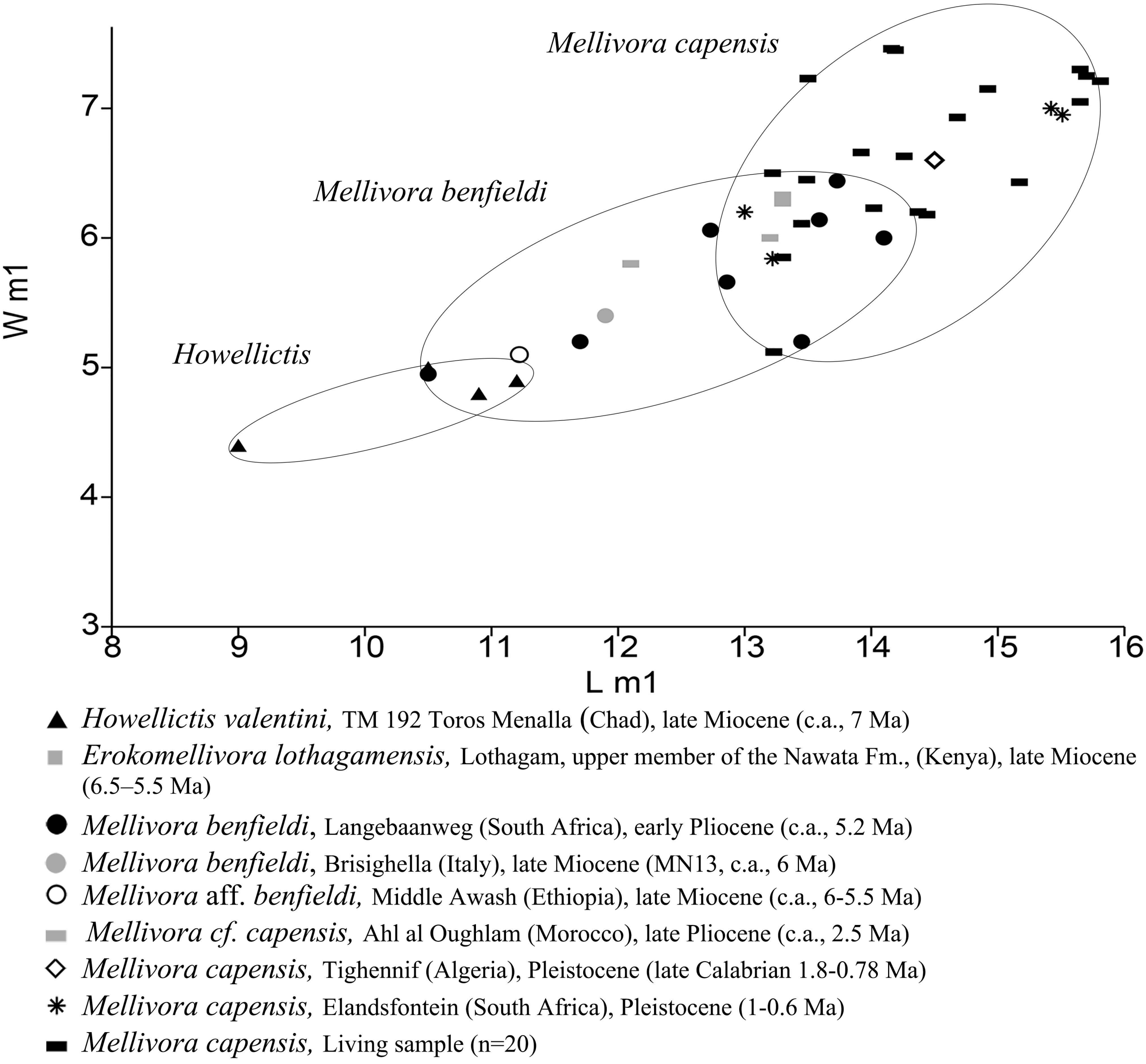
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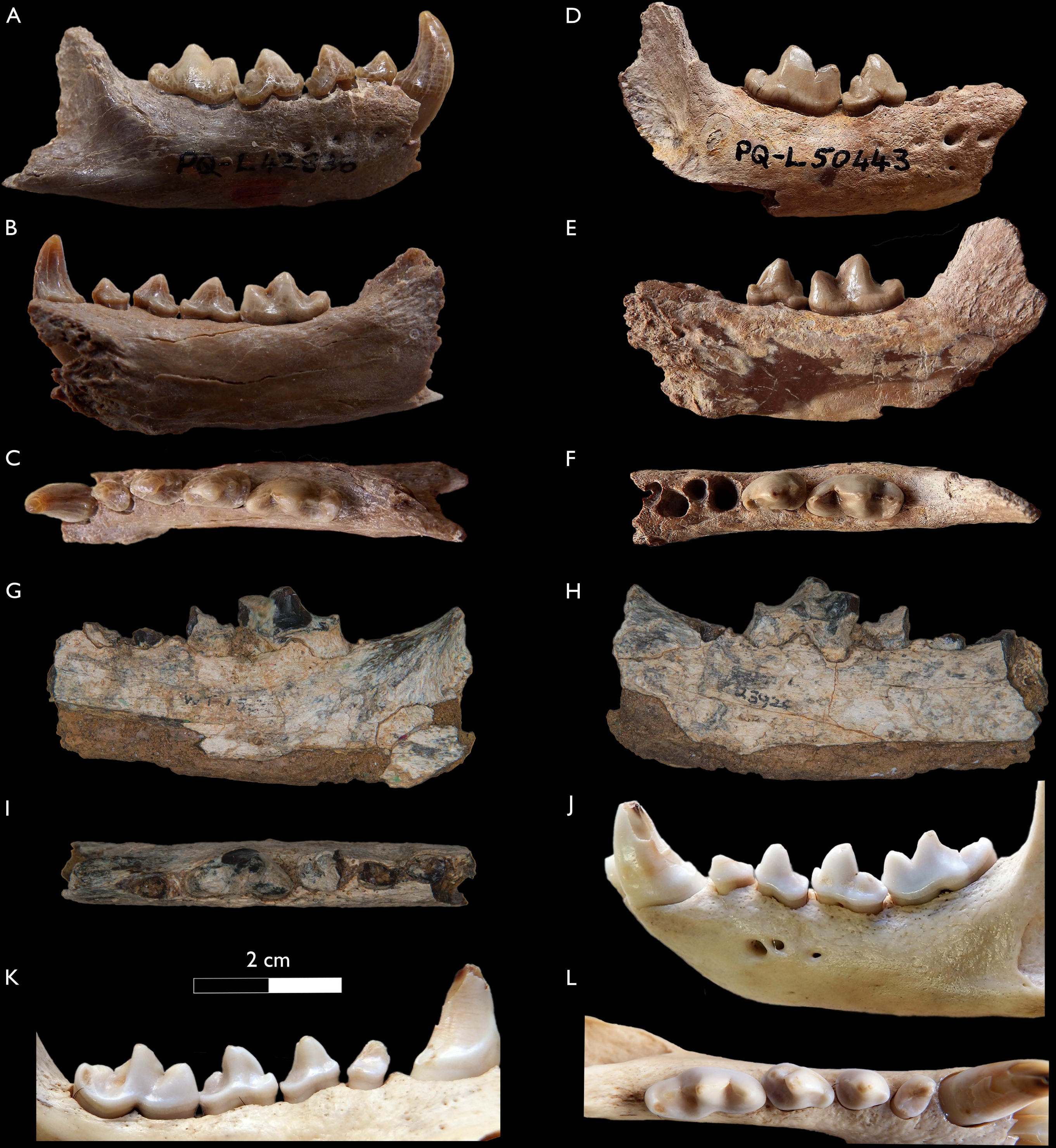
▲ Howellictis valentini, TM 192 Toros Menalla (Chad), late Miocene (c.a., 7 Ma)
■ Erokomellivora lothagamensis, Lothagam, upper member of the Nawata Fm., (Kenya), late Miocene (6.5–5.5 Ma)
● Mellivora benfieldi, Langebaanweg (South Africa), early Pliocene (c.a., 5.2 Ma)
● Mellivora benfieldi, Brisighella (Italy), late Miocene (MN13, c.a., 6 Ma)
○ Mellivora aff. benfieldi, Middle Awash (Ethiopia), late Miocene (c.a., 6-5.5 Ma)
▬ Mellivora cf. capensis, Ahl al Oughlam (Morocco), late Pliocene (c.a., 2.5 Ma)
◇ Mellivora capensis, Tighennif (Algeria), Pleistocene (late Calabrian 1.8-0.78 Ma)
✳ Mellivora capensis, Elandsfontein (South Africa), Pleistocene (1-0.6 Ma)
▬ Mellivora capensis, Living sample (n=20)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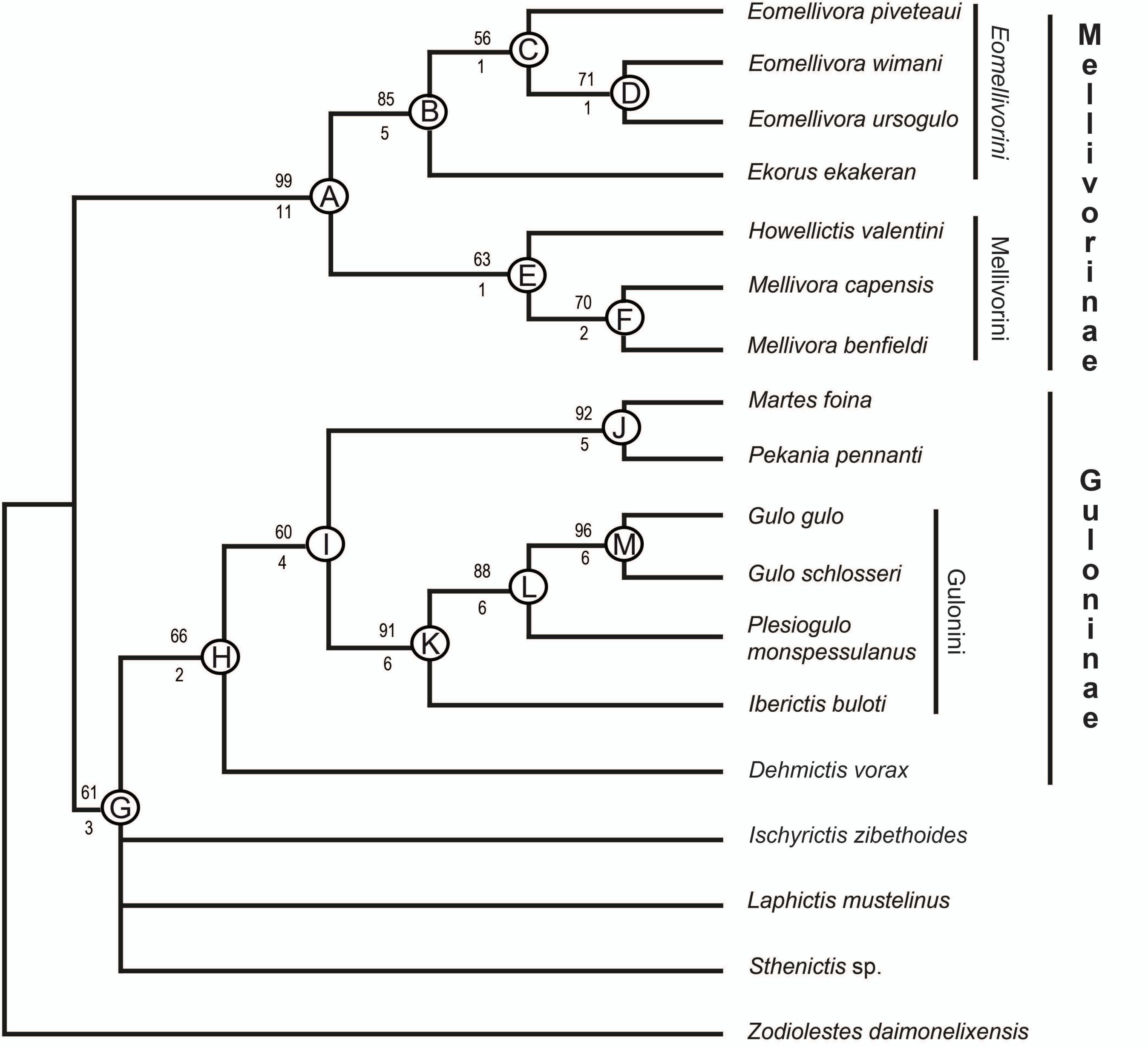
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Eomellivora wimani
Eomellivora ursogulo
Ekorus ekakeran
Howellictis valentini
Mellivora capensis
Mellivora benfieldi
Martes foina
Pekania pennanti
Gulo gulo
Gulo schlosseri
Plesiogulo monspessulanus
Iberictis buloti
Dehmictis vorax
Ischyrictis zibethoides
Laphictis mustelinus
Sthenictis sp.
Zodiolestes daimonelixensis
Eomellivorini
Mellivorini
Gulonini
Mellivorinae
Guloninae

TABLE 1. Upper teeth measurements (in mm) of the new specimens of *Mellivora benfieldi* from Langebaanweg.

Taxa	I3		CX		P3		P4	
Mellivora benfieldi	L	W	L	W	L	W	L	W
SAM-PQL-72167	6.7	4.7	—	—	—	—	—	—
SAM-PQL-69620C	—	—	8.5	6.5	—	—	—	—
SAM-PQL-51386	—	—	7.0	5.4	—	—	—	—
SAM-PQL-72165	—	—	—	—	8.0	4.8	—	—
SAM-PQL-50107	—	—	—	—	7.2	4.1	—	—
SAM-PQL-72227	—	—	—	—	—	—	12.6	—

TABLE 2. Lower teeth measurements (in mm) of the new specimens of *Mellivora benfieldi* from Langebaanweg. Parenthesis means measurements on alveoli or at the base of the broken crown. * = new measurement or re-measured after Hendey (1978a); ** = holotype.

Taxa	c1		p2		p3		p4		m1			m2	
Mellivora benfieldi	L	W	L	W	L	W	L	W	L	W	Wtl	L	W
SAM-PQL-72174	—	—	4.7	3.6	6.3	4.3	8.2	4.6	12.9	5.7	4.4	(1.7)	(1.6)
SAM-PQL-50444	—	—	5.7	3.8	—	—	—	—	—	—	—	—	—
SAM-PQL-69620B	—	—	—	—	—	—	—	—	13.7	6.4	5.1	(1.7)	(1.7)
SAM-PQL-50002	—	—	—	—	—	—	—	—	13.4	5.2	4.2	—	—
SAM-PQL-50105	—	—	—	—	—	—	(6.7)	(3.7)	(10.5)	(4.9)	(3.9)	—	—
SAM-PQL-50106	—	—	—	—	(6.7)	(4.2)	—	—	—	—	—	—	—

SAM-PQL-6385*	—	—	—	—	—	—	9.7	5.3	14.2	6.2	5.0	—	—
SAM-PQL-42838**	6.6	5.3	4.9	3.4	6.4	4.4	8.5	4.8	11.7	5.2	4.5	—	—