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ORIGINAL PAPER

New Early Miocene Material of *Iberictis*, the Oldest Member of the Wolverine Lineage (Carnivora, Mustelidae, Guloninae)

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Abstract

We describe new dental remains of the genus *Iberictis* (Carnivora: Mustelidae) from the late early Miocene of the Iberian Peninsula. The new fossils of *Iberictis azanzae* from Artesilla (16.5–16.3 Ma, MN4; Calatayud-Teruel Basin, Zaragoza, Spain) add important morphological information about this species. Material from another species, *Iberictis buloti*, is described from els Casots (16.5–16.3 Ma, MN4; Vallès-Penedès Basin, Barcelona, Spain). This material constitutes the most complete sample of *Iberictis* and the first record of *I. buloti* in the Iberian Peninsula. Our analyses confirm the taxonomic validity of both species, and confirm the more plesiomorphic status of *I. buloti* compared to *I. azanzae*. Re-examination of large mustelid Miocene genera (*Dehmictis, Ekorus, Eomellivora, Hoplictis, Iberictis*, *Ischyrictis*, and *Plesiogulo*) and their inclusion for the first time in a cladistic analysis indicate that *Iberictis* is the sister taxon of *Plesiogulo*, and that these genera constitute the sister group of the extant wolverine (*Gulo gulo*). Our analysis thus confirms a close relationship between the early Miocene *Iberictis*, the late Miocene *Plesiogulo*, and the Plio-Pleistocene *Gulo*. *Iberictis* is the oldest member of Gulonini, the total clade of wolverines, thereby tracking the fossil record of this clade back to the early Miocene. We further propose a new systematic arrangement for the aforementioned large Miocene mustelids into the subfamilies Guloninae, Mellivorinae, and Mustelinae.

Keywords Mustelidae · Neogene · Gulo · Wolverine · Plesiogulo · Iberictis · Guloninae

Introduction

The subfamily Guloninae is currently composed of generalist and hypercarnivorous mustelids, distributed over much of North America and Eurasia, and with a single genus in Central and South America. The extant members of this clade are included in three main groups: (1) a heterogeneous group of small- to medium-sized taxa,

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comprised of the fisher (*Pekania* Gray, 1865) and martens (*Martes* Pinel, 1792, and *Charronia* Gray, 1865); (2) the medium-sized Latin American tayra (*Eira* Smith, 1842); and (3) the large-sized wolverine (*Gulo* Pallas, 1780). This subfamily was formerly referred to as the Martinae but Guloninae has priority (Sato et al. 2009; Samuels and Cavin 2013). Gulonines have a conservative morphology that hinders morphology-based studies of their phylogenetic relationships (Anderson 1970; Samuels and Cavin 2013).

This study focuses on the lineage of the wolverine, the largest terrestrial extant mustelid and one of the most iconic members of this family. It is restricted to mature conifer forests in the taiga and the treeless tundra from the North Holarctic region (Larivière and Jennings 2009). The origin of the wolverine lineage remains obscure, but according to recent molecular analyses the lineage of *Gulo* diverged from *Martes* 7.6–5.5 Ma (Li et al. 2014; Malyarchuk et al. 2015). A sister group relationship between *Gulo* and *Martes* is supported by Samuels et al. (2018) using evidence of a new species of *Gulo* from the early Pliocene (4.9–4.5 Ma) of Tennessee. However, this time interval also coincides with the expansion of the wolverine-like extinct mustelid *Plesiogulo* Zdansky, 1924, characterized by a large to giant body size. *Plesiogulo* has been found in Eurasia, North America, and Africa (e.g., Zdansky 1924; Viret 1939; Teilhard de Chardin 1945; Kurtén 1970; Hendey 1978; Harrison 1981; Alcalá et al. 1994; Sotnikova 1995; Haile-Selassie et al. 2004; Morales et al. 2005, 2016; Montoya et al. 2011), spanning from the late Miocene (MN10) to the early Pliocene (MN14). Viret (1939), Kurtén (1970), and Kurtén and Anderson (1980) supported a direct relationship between *Plesiogulo* and *Gulo*, based on general dental similarities, whereas other authors considered that *Plesiogulo* constitutes a distinct phylogenetic lineage without living descendants (Zdansky 1924; Hendey 1978; Harrison 1981; Xiaofeng and Haipo 1987; Alcalá et al. 1994; Sotnikova 1995; Montoya et al. 2011). Samuels et al. (2018) also considered *Plesiogulo* to be convergent with *Gulo*. However, the cladistic analysis of Valenciano et al. (2017) on some living and extinct gulonines and mellivorines grouped *Plesiogulo* and *Gulo* as the sister taxon to the beech marten, *Martes foina* (Erxleben, 1777) and the fisher, *Pekania pennanti* (Erxleben, 1777).

Iberictis Ginsburg and Morales, 1992, is a medium-size mustelid known from scarce remains from the early Miocene (MN4) of Europe. This genus comprises two species: *Iberictis azanzae* Ginsburg and Morales, 1992, from Artesilla (MN4, Spain) and *Iberictis buloti* Ginsburg and Morales, 1992, from Pellecahus (MN4, France). According to Ginsburg and Morales (1992), *Iberictis* shows strong affinities with *Plesiogulo*, despite the significant temporal gap between them. Here, we report new material of *I. azanzae* from the early Miocene (MN4) of Artesilla (Calatayud-Teruel Basin, Zaragoza, Spain) and abundant new material of *I. buloti* from the early Miocene (MN4) site of els Casots (Subirats, Catalonia, Spain). These fossils provide novel information for *Iberictis* and shed new light on the phylogenetic relationships of large Miocene mustelids belonging to the wolverine lineage. The aims of this paper are threefold: (1) to describe the remains of *Iberictis* from Artesilla and els Casots, while justifying their taxonomic ascription to species rank; (2) to perform a cladistic analysis in order to test the hypothesis that *Iberictis* is related to *Plesiogulo* and/or *Gulo*; and (3) to evaluate the relationships of this wolverine group with most of the medium- to large-sized Miocene mustelids, in order to further clarify their evolutionary history.

Age and Geological Background of Els Casots

The presence of fossil vertebrate remains in the municipality of Subirats (Catalonia, Spain) has been known for many decades, but the site of els Casots was not discovered until 1989. Subsequently excavated until 1994, els Casots has yielded abundant micro- and macrovertebrate remains, including fishes, amphibians, reptiles, birds, and mammals (Moyà-Solà and Rius Font 1993; Agustí and Llenas 1993; Casanovas-Vilar et al. 2011a). However, except for crocodylians (Díez Aráez et al. 2016), some rodent species (Aldana Carrasco 1991, 1992; Ginestí 2008; Jovells-Vaqué et al. 2017), and various artiodactyl groups (Pickford and Moyà-Solà 1994, 1995; Duranthon et al. 1995; van der Made 1997; Orliac 2006; Alba et al. 2014), most of the fauna (carnivorans included) remains unpublished.

Els Casots is located in the Vallès-Penedès Basin (Fig. 1), an elongated semigraben delimited by the Catalan Coastal Ranges (Littoral and Prelittoral) in NE Iberian Peninsula (Cabrera et al. 2004; de Gibert and Casanovas-Vilar 2011). This basin has delivered a rich fossil vertebrate record ranging from the late Ramblian (MN3) to the middle Turolian (MN12), i.e., ca. 20–7 Ma (Casanovas-Vilar et al. 2011b, 2016). Els Casots represents an ancient lacustrine system overlying Mesozoic deposits and situated within the early Miocene Detritic-Carbonated Unit of Subirats, which corresponds to the Lower Continental Complexes of the Vallès-Penedès Basin (Moyà-Solà and Rius Font 1993; de Gibert and Casanovas-Vilar 2011; Casanovas-Vilar et al. 2011a, c). Mostly on the basis of small mammal biostratigraphy, the site is correlated to MN4 (early Aragonian, early Miocene) and, in particular, to local zone C of the Calatayud-Daroca Basin, with an estimated age of 16.5–16.3 Ma (Casanovas-Vilar et al. 2011a, b, c, 2016; Jovells-Vaqué et al. 2017).

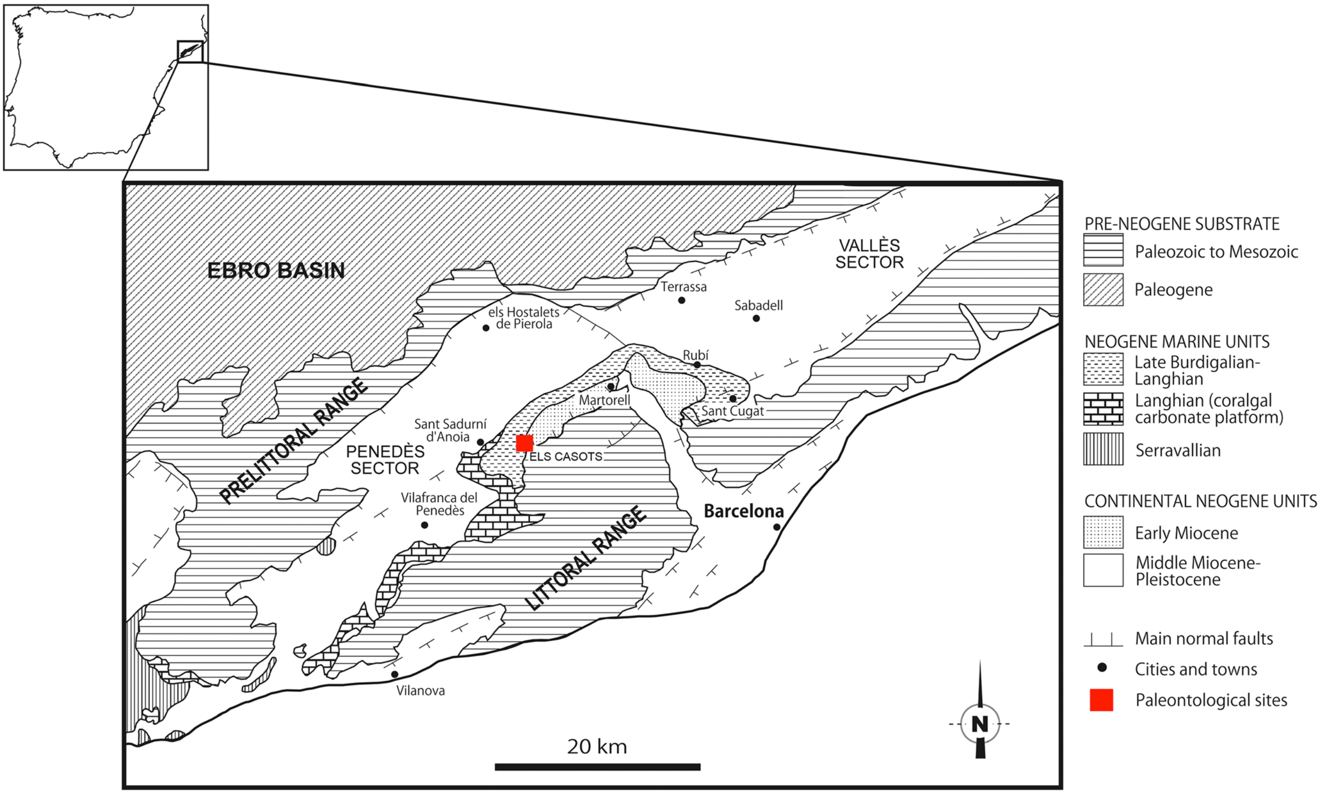

Fig. 1 Schematic geological map of the Vallès-Penedès Basin, showing the main geological units as well as the situation of els Casots. Modified from Alba et al. (2014)

Material and Methods

Nomenclature and Measurements

Dental nomenclature follows Ginsburg (1999) and Smith and Dodson (2003). Measurements were taken using a Mitutoyo Absolute digital caliper to the nearest 0.1 mm.

Abbreviations

Institutional Abbreviations. AMNH: American Museum of Natural History, New York, USA; **BSPG**: Bayerische Staatssammlung für Paläontologie und Geologie, Munich, Germany; **FCPT**: Fundación Conjunto Paleontológico de Teruel-Dinópolis, Museo Aragonés de Paleontología, Teruel, Spain; **FSL**: Université Claude Bernard Lyon 1 Lyon, France; **ICP**: Institut Català de Paleontologia Miquel Crusafont, Universitat Autònoma de Barcelona, Spain; **IPS**: collections from the ICP (formerly 'Institut de Paleontologia de Sabadell'); **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; **MPZ**: collection of the former Museo Paleontológico de la Universidad de Zaragoza, currently housed at the Museo de Ciencias Naturales Universidad de Zaragoza, Zaragoza, Spain; **NHMW**: Naturhistorisches Museum Wien,Vienna, Austria; **NMB**: Naturhistorisches Museum Basel, Switzerland; **NRM**: Naturhistoriska rikmuseet, Stockholm, Sweden; **PMU**: Palaeontological Museum, University of Uppsala, Uppsala, Sweden; **SAM**: Iziko Museums of South Africa, Cape Town, South Africa; **SMNS**: Staatliches Museum für Naturkunde, Sttutgart, Germany; **USNM**: Smithsonian National Museum of Natural History, Washington, D.C., USA.

Studied Material

The fossil remains of *I. azanzae* from Artesilla are housed at the MPZ. The newly described sample includes: MPZ-2018/42, left P4 protocone; MPZ-2018/43, right fragment of M1 including the stylar area, the paracone, and the metacone; MPZ-2018/39, left c with the tip broken; MPZ-2018/40, crown of a left c; MPZ-2018/41, incomplete left p4. The fossil remains of *Iberictis* from els Casots are housed at the ICP. The studied sample includes: IPS10076, right fragment of cranium with I3, C, P2–M1; IPS10077, left maxillary fragment with P4–M1; IPS10083, right maxillary fragment with P2–P4; IPS24701, cranium fragmented in two pieces, the left one with the rostral part of the zygomatic arch, the ventral orbital area, and part of the maxillary bone (comprising the distal portion of the P3, the complete P4, and the broken M1, with the lingual platform and protocone), and the right fragment with P2 and P3 broken at the base of the root (the distal area of the P3 is preserved), the complete P4, and an almost complete M1 (missing the metacone and distal part of the tooth); IPS100599, left maxillary fragment with a complete P3 and the mesial part of the P4; IPS36425, isolated teeth of a single individual, comprising the left P3, P4 with a small portion of the maxillary bone, and an M1 fragment with the lingual platform and protocone; IPS10085, right C; ISP10086, left C; IPS24159, right C; IPS85598, right P4; IPS10072, left M1; IPS105255, left M1 fragment comprising the lingual platform and protocone; IPS24107, left mandibular fragment with isolated p4, fragmentary m1, and complete m2; IPS24700, mandible with left p3–p4 and right c and p2–m1; IPS85595, right mandibular fragment with fragmentary p4–m1; IPS10084, right mandibular fragment with p2–m1; IPS10069, left mandibular fragment with p4–m1; IPS24686, fragmentary mandible with right p4–m1 and left p4 (partial) and m1; IPS10079, right hemimandible with p3–m1; IPS10080, left hemimandible with p2–p4; IPS10066, left hemimandible with c, p2–m2; IPS10067, right hemimandible with c and p2–m1; IPS10068, right hemimandible with c and p2–m1; IPS10070, left p3, and a left mandibular ramus fragment with p4 broken at the level of the roots and partial m1 that only preserves part of the trigonid; IPS105256, left p4; IPS10088, right m2.

The comparative material of large Miocene mustelids consists of the following taxa: *Ekorus ekakeran* Werdelin, 2003 (cast), from Lothagam, Kenya, from the research collection of L. Werdelin housed at NRM; *Eomellivora piveteaui* Ozansoy, 1965, from Cerro de los Batallones, Spain (Valenciano et al. 2015), housed at MNCN; *Hoplictis noueli* (Mayet, 1908) from Artenay, France, housed at MNHN and NMB; the classic material of *Iberictis* described by Ginsburg and Morales (1992), including the type material of *I. azanzae* from Artesilla, Spain, housed at MPZ, and that of *I. buloti* from Pellecahus, France, housed at MNHN; *Ischyrictis mustelinus* (Viret, 1933), from Can Mata 1, els Hostalets de Pierola, Spain, housed at ICP (Villalta Comella and Crusafont Pairó 1943; Crusafont and Truyols 1954; Petter 1963); *Ischyrictis zibethoides* (Blainville, 1842) from Sansan, France, housed at MNHN; *Plesiogulo crassa* Teilhard de Chardin, 1945, from Localities 30, 108, and 111 from China (Kurtén 1970), housed at PMU; *Plesiogulo monspessulanus* Viret, 1939, from Montpellier, France, housed at FSL, also the specimens from Venta del Moro and Las Casiones, Spain, housed at MGUV and FCPT respectively, and the specimens from Langebaanweg, South Africa, housed at SAM; *Plesiogulo lindsayi* Harrison, 1981, from Wikieup, Old Cabin Quarry, and Redington Quarry in Arizona, USA, housed at AMNH; *Plesiogulo marshalli* (Martin, 1928) from Edson Quarry in Kansas, USA, Optima in Oklahoma, USA, Coffee Ranch in Texas, USA, Modesto reservoir in California, USA, San Juan Quarry in New Mexico, USA, and Boney Valley in Florida, USA housed at AMNH; and *Lartetictis dubia* (Blainville, 1842) from Sansan, France, housed at MNHN. We further inspected photographs of *Dehmictis vorax* (Dehm, 1950) from Wintershof-West, Germany, housed at BSPG; *Ischyrictis mustelinus* from La Grive-Saint-Alban, France, housed at FSL, and Erkertshofen 2, Germany (Viret 1933; Roth 1989), housed at FSL and SMNS; *Plesiogulo* sp. from Paşalar, Turkey (Schmidt-Kittler 1976), housed at BSPG; and *Paralutra jaegeri* (Fraas, 1862) from Ravensburg and Steinheim, Germany, housed at SMNS. *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). The extant comparative sample included the mustelids *Gulo gulo* Linnaeus, 1758, *Mellivora capensis* (Schreber, 1776), and *Mustela putorius* Linnaeus, 1758, the mephitid *Mephitis mephitis* (Schreber, 1776), and the procyonid *Bassariscus astutus* (Lichtenstein, 1830), housed at AMNH, MNCN, NRM, and USNM.

Cladistics Analysis

In order to better understand the phylogenetic relationships of *Iberictis* in relation to medium to large Miocene mustelids—*Dehmictis* Ginsburg and Morales, 1992, *Ekorus* Werdelin, 2003*, Eomellivora* Zdansky, 1924, *Hoplictis* Ginsburg, 1961, *Ischyrictis* Helbing, 1930, and *Plesiogulo*—as well as relative to selected extant mustelids, we performed a cladistic analysis including 18 taxa—*Iberictis buloti* is represented as two different operational taxonomic units (OTU), one for the previously-known remains of this taxon, and the other for the newly-described specimens from els Casots—and 76 equally-weighted and unordered dental characters (Appendix 1), based on Wolsan (1993), Bryant et al. (1993), Wesley-Hunt and Werdelin (2005), and Valenciano et al. (2015, 2016a, 2017). The musteloids *Mephitis mephitis* and *Bassariscus astutus* were included as outgroups. The data matrix was compiled in Mesquite 3.01 for Mac. Cladistics analysis was performed with PAUP* 4.0b10 (Swofford 2002), using the 'branch and bound' search command. Clade robusticity was assessed by means of bootstrap with 1000 replicates and Bremer support indices. The character/taxon matrix and character state definitions are reported in the Appendices 1-3. The distribution of character states for internal nodes was analyzed with Mesquite 3.01 and PAUP* 4.0b10.

The dataset generated and/or analyzed during the current study is available from the corresponding author on reasonable request.

Systematic Paleontology

Order **CARNIVORA** Bowdich, 1821
Suborder **CANIFORMIA** Kretzoi, 1943
Family **MUSTELIDAE** Fischer, 1817
Subfamily **GULONINAE** Gray, 1825

Genus ***IBERICTIS*** Ginsburg and Morales, 1992

Original diagnosis: (Reproduced from Ginsburg and Morales 1992: 116; our translation from the French original). "Mustelid of large size, P4–M1 close to those of *Plesiogulo* with a prominent P4 with protocone strong and very distinct, isolated from the mesial border of the paracone by a heavy concavity; M1 very elongated buccolingually with a short buccal wall and an enlarged lingual platform extended backward as in *Plesiogulo* and *Trochictis*. *Ischyrictis*-like lower teeth with a long m1 with a prominent entoconid; m2 longer than in *Ischyrictis*."

Emended diagnosis: Medium-sized gulonine mustelid with wrinkled enamel and a robust P4 that displays a concavity between parastyle and protocone; P4 with high and enlarged protocone, and variably developed lingual cingulum that thickens distally to protocone; M1 with distolingual enlargement of lingual platform (which possesses a concavity on its middle portion) and without hypocone; p4 with lingual bulge and entirely surrounded by stout cingulid with thickened mesial and distal cristids; m1 with protoconid higher than paraconid, pronounced metaconid (not entoconid as in original diagnosis), and beveled lingual wall of hypoconid; m2 plesiomorphic, with very pronounced metaconid and hypoconid, and with trigonid and talonid roots incompletely fused (resulting in a marked notch in the single m2 alveolus).

Differential diagnosis: Iberictis differs from the other gulonines *Plesiogulo*, *Gulo*, and *Ischyrictis* in having a smaller size, and more robust and higher P4 protocone that trends to form a lingual shelf. From *Plesiogulo* and *Gulo* in the presence of a P4 protocone mesially located, a higher and more massive M1 metacone, and in the presence of both metaconule and postprotocrista. It differs from *Plesiogulo* in the elongated P2; relatively higher and more slender lower premolars; a less developed m1 hypoconulid; and a more primitive m2 with hypoconid. It differs from *Gulo* in longer and slender premolars; shorter P4; longer M1 lingual platform with a small concavity on the middle part of the lingual platform; slender m1 trigonid, presence of m1 metaconid and longer talonid with more massive hypoconid; and less reduced m2. Compared to *Ischyrictis* and *Dehmictis* it differs in more developed M1 lingual platform. It differs from *Ischyrictis* in the presence of lingual concavity on M1 lingual platform; in more massive cingulids and cristids in lower premolars, without distal accessory cuspids; m1 with more developed metaconid and hypoconid, and relatively shorter talonid. It differs from *Dehmictis* in higher and robust P4 protocone that trends to form lingual shelf and shorter and less basined m1 talonid; and in bigger size. It differs from the basal mellivorine *Hoplictis* in the shorter P4; larger M1 with both a more developed metacone and lingual platform; in absence of accessory cuspids in the lower premolars; in more developed m1 metaconid and in longer m1 talonid. Besides, it differs from the primitive lutrines *Paralutra* Roman and Viret, 1934, *Lartetictis* Ginsburg and Morales, 1996, and *Siamogale* Ginsburg et al., 1983, in relatively longer P4 with lesser developed P4 lingual shelf and without hypocone; in M1 more mesiodistally constricted below paracone-metacone, with lesser mesiodistal expansion of lingual platform and absence of hypocone; and in more massive and beveled m1 hypoconid. It differs from *Paralutra* in wider M1 with less basined m1 talonid. It differs from *Lartetictis* and *Siamogale* in having smaller size, in shorter talon and talonid in M1 and m1, higher m1 crown, lesser m1 metaconid, and narrower m2. It differs from *Siamogale* in less bunodont and slenderer lower premolars; much smaller m1 metaconid and in smaller talonid with much slenderer and shorter m1 entocristid.

Type species: Iberictis azanzae Ginsburg and Morales, 1992

Other included species: Iberictis buloti Ginsburg and Morales, 1992

Iberictis azanzae Ginsburg and Morales, 1992

Holotype: MPZ-16522, left maxillary fragment with P4 and partial M1 with the lingual platform and protocone.

Type locality: Artesilla (Calatayud-Teruel Basin, Zaragoza, Spain).

Age: Early Miocene (MN4).

Remarks: In addition to the material described by Ginsburg and Morales (1992) from Artesilla, we describe new material from this locality obtained during screen-washing of sediments for micromammal sampling. The P4 protocone MPZ-2018/42 (Fig. 2a) is very similar to that of the holotype, except for a larger wear facet in the protocone. MPZ-2018/43 is a right buccal fragment of M1 (Fig. 2b)—missing in the holotype and previously unknown for the species. It possesses an enlarged stylar area with a stout cingulum. Both the paracone and the metacone have a wear facet. The paracone is the highest cusp and has a distal crista connecting with the metacone, which is located below the paracone. The presence of a metaconule cannot be ascertained because the tooth is broken in this area. The two canines have wrinkled enamel, are oval in cross-section, and markedly curved distally, and have a strong lingual cristid in contact with a stout cingulid (Fig. 2c, d). The left p4 MPZ-2018/41 (Fig. 2e) lacks its mesial portion. It is unicuspid and shows a strong wear facet on the tip of the cuspid. It possesses thick mesial and distal cristids, and a strong cingulid surrounding the whole crown, with an evident basal lingual bulge.

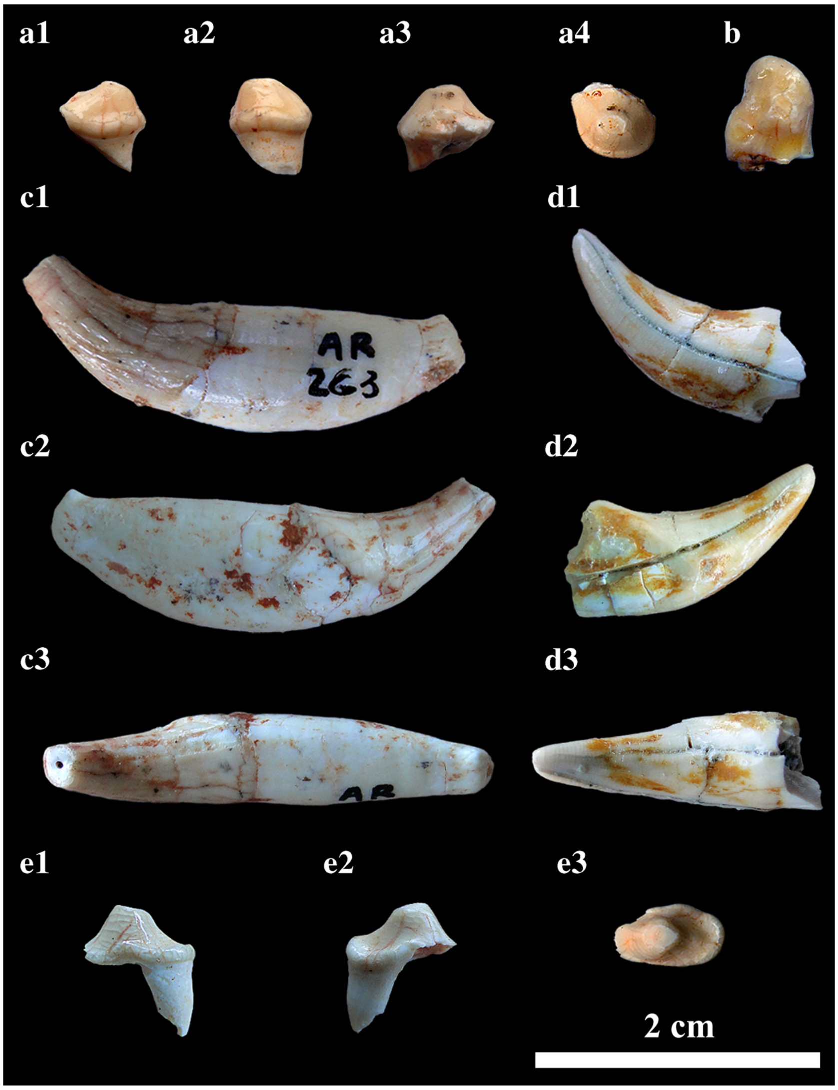

Fig. 2 New dental remains of *Iberictis azanzae*, from Artesilla. **a**. MPZ-2018/42, left P4 protocone. **a.1.** distal view, **a.2.** lingual view, **a.3.** buccal view, **a.4.** occlusal view; **b.** MPZ-2018/43, right fragment of M1, occlusal view; **c.** MPZ-2018/39, left c, **c.1.** buccal view, **c.2.** lingual view, **c.3.** distal view; **d.** MPZ-2018/40, left c, **d.1.** buccal view, **d.2.** lingual view, **d.3.** distal view; **e.** MPZ-2018/41, left p4, **e.1.** buccal view, **e.2.** lingual view, **e.3.** occlusal view

Iberictis buloti Ginsburg and Morales, 1992

Holotype: MNHN LRM 1044, right hemimandible with p3–m1 with worn dentition.

Type locality: Pellecahus (France).

Other localities: els Casots (Subirats, Vallès-Penedès Basin, Catalonia, Spain).

Age: Early Miocene (MN4).

Original diagnosis: (Reproduced from Ginsburg and Morales 1992: 116; our translation from the French original). "*Iberictis* smaller than *I. azanzae*. P4 protocone less distinct; M1 lingual platform less prominent."

Emended diagnosis: Iberictis species smaller than *I. azanzae*; P4 protocone not individualized, with lingual cingulum markedly thickened distal to protocone; p2–p4 stout and without accesory cuspids, surrounded by a stout cingulid with thickened mesial and distal cristids; m2 hypoconid very pronounced.

Differential diagnosis: It differs from *I. azanzae* in less distinct P4 protocone; relatively shorter P4; presence of postprotocrista in M1; lesser distolingual enlargement of M1; and more developed m2 hypoconid.

Description of the Material from Els Casots

Maxilla and Upper Dentition

The preserved maxillary specimens from els Casots (IPS85598, IPS10076, IPS24701, IPS100599, IPS36425, IPS10077, and IPS10083) are quite fragmentary (Fig. 3), but based on IPS10076, the muzzle appears to have been short, with the orbital shape and height of the nasal aperture resembling those of martens and fishers (*Martes* and *Pekania*). The infraorbital foramen is not preserved. The dentition possesses wrinkled enamel, which is most conspicuous in the C, the P4, M1, and the lower dentition. The preserved upper dentition includes the I1–I3, the C, and the P2–M1 row (Table 1). The I1 and I2 are quite damaged, but the I3 is not enlarged compared to the other incisors (Fig. 3a). The C is oval in cross-

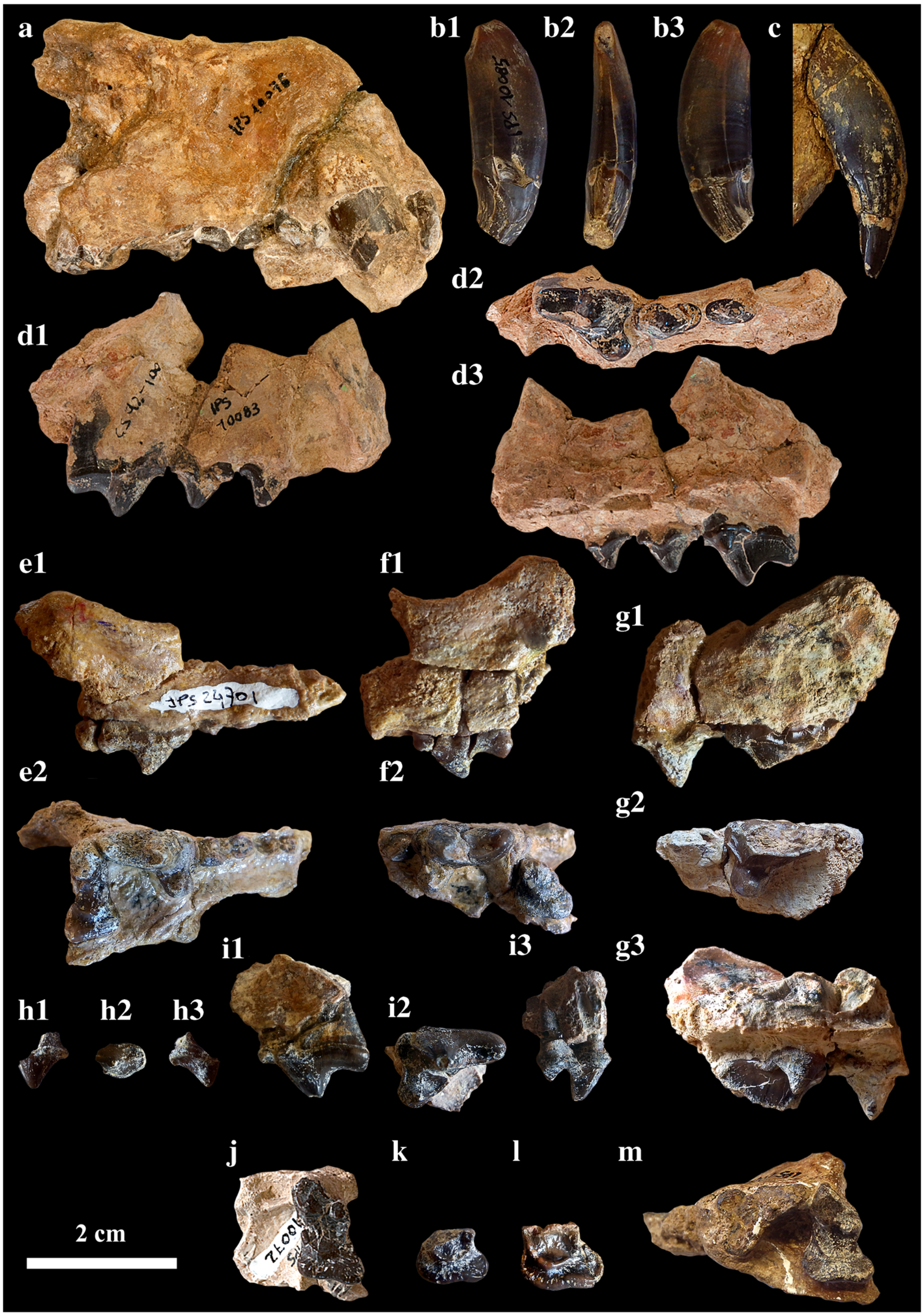

Fig. 3 Upper dentition of *Iberictis buloti* from els Casots. **a**. IPS10076, right maxillary fragment with I3, C, P2–P4, M1, buccal view; **b**. IPS10085, right C. **b.1.** buccal view, **b.2.** distal view, **b.3.** lingual view; **c.** IPS24159, right C, buccal view; **d.** IPS10083, right maxillary fragment with P2–P4, **d.1**. buccal view, **d.2.** occlusal view, **d.3.** lingual view; **e.** IPS24701, right maxillary fragment with P2–P3 roots and P4–M1 (partially broken), **e.1**. buccal view, **e.2.** occlusal view; **f.** IPS24701, left maxillary fragment with partial root of P3, a complete P4 and a lingual part of the M1, **f.1**. buccal view, **f.2.** occlusal view; **g**. IPS100599, left maxillary fragment with complete P3 and broken P4. **g.1.** buccal view, **g.2.** occlusal view, **g.3.** lingual view; **h**. IPS36425, left P3. **h.1.** buccal view, **h.2.** occlusal view, **h.3.** lingual view; **i**. IPS36425, left P4. **i.1.** buccal view, **i.2.** occlusal view, **i.3.** mesial view; **j.** IPS10072 left M1, occlusal view; **k**. IPS36425, partial left M1, occlusal view; **l**. IPS105255, partial left M1, occlusal view; **m**. IPS10077, left maxillary fragment with P4–M1, occlusal view

section, displays radial crenulations from the tip to the base of the crown, and has a strong cingulum (Fig. 3b, c). The presence or absence of P1 cannot be assessed based on the available material. The P2–P4 exhibit a strong cingulum that surrounds the whole crown. The P2 is elongated, oval in occlusal view, and unicuspid. The P3 is subrectangular in occlusal view, elongated, and unicuspid, with a buccodistal bulge and a pronounced concavity at the base of its buccal wall (Fig. 3d2). The P4 has a robust cingular parastyle located on the mesial cingulum. Mesially, there is an inflection between the protocone and parastyle, and the paracone and parastyle are connected by a thick crista. The protocone is stout, very high, conical, and projected mesiolingually, but aligned with the parastyle (Fig. 3d, e-g, i). There is a thick cingulum surrounding the whole crown, with a lingual shelf that runs from the base of the protocone to beneath that of the paracone. On this lingual shelf, next to the protocone, there is a concavity, more evident in IPS10083, IPS24701, and IPS36425 (Fig. 3d,

Table 1 Upper teeth measurements (in mm) of mesiodistal length (L) and buccolingual width (W) of *Iberictis buloti* from els Casots (C) and Pellecahus (P), and *Iberictis azanzae* from Artesilla (A). Estimated values are reported within parentheses

			C		P2		P3		P4		M1	
Species	Locality	Catalog No.	L	W	L	W	L	W	L	W	L	W
I. buloti	C	IPS10085	9.5	6.5								
I. buloti	C	IPS10086	9.6	6.6								
I. buloti	C	IPS24159	9.9	6.8								
I. buloti	C	IPS10076			6.2	2.8	8.2	4.5	12	8.6	8.6	10.7
I. buloti	C	IPS10083			6.7	3.5	8.8	4.9	13.3	9.2		
I. buloti	C	IPS10077							12.5	8	9	11.9
I. buloti	C	IPS85598							13.6	9.4		
I. buloti	C	IPS10072									8.8	13.5
I. buloti	C	IPS105255									10	
I. buloti	C	IPS100599					9.2	5.3	(13.6)	10.2		
I. buloti	C	IPS36425						5.2	14.1	10.6	9	
I. buloti	C	IPS24701 left							13.4	9.4	8.29	
I. buloti	C	IPS24701 right			(6.9)	(3.7)	(8.6)	(4.6)	13.6	9.2	(7.7)	12.9
I. buloti	P	MNCN-74707					7.89	5.62	14.25	10.5		
I. buloti	P	MNHN LRM782							13	8.8		
I. buloti	P	MNHN LRM 789									9.6	(13.4)
I. azanzae	A	MPZ-16522							16	10.5	10.5	(16.0)

f2, i). The buccal wall between the paracone and metastyle is concave. The M1 is robust and subequal in size to the P4. The stylar area is large and has a swollen cingulum. The paracone is larger than the metacone, which is somewhat more lingually situated. There is a constriction in the crown mid-length. Mesially, the M1 has a small crest-shaped paraconule in contact with the protocone. On the distal corner of the crown there is also a small metaconule aligned with the paraconule, being more conspicuous in IPS10072, IPS36425, and IPS105255 (Fig. 3j, k, l). The protocone is crest-like and located on the lingual corner. It has a postprotocrista, more patent in IPS24701, IPS10072, IPS36425, IPS105255, and IPS10077 (Fig. 3e, j, k, l, m). The M1 shows an additional slender buccolingual crista connecting the paracone with the protocone. It has a mesiodistally enlarged lingual platform with a small concavity on the middle, and which is even more pronounced in the distolingual area (being particularly evident in IPS10077 and IPS105255; Fig. 3j, m).

Mandible and Lower Dentition

The mandibular corpus is high, with a very stout ventral edge. There is a single rounded mental foramen under the p2 and p3 (Fig. 4). The ramus is high. The postcanine tooth row is straight. The c is oval in cross-section and markedly curved distally (Fig. 4a, Table 2). There is a strong lingual cristid in contact with a stout cingulid. The p1 is absent (Fig. 4a3, e2). The p2–p4 have a single cuspid, thick mesial and distal cristids, and a strong cingulid surrounding the whole crown (Fig. 4). The p2 is slender and somewhat shorter compared to the p3, which slightly widens distally. The p4 has a noticeable basal lingual bulge (Fig. 4c3, d3, g3). The m1 is elongated. The protoconid is higher than the paraconid. The metaconid is robust. The hypoconid is low, pyramidal, stout, buccally located, and occupies an important area of the talonid. The lingual wall of the talonid is beveled, without entoconid, with a peripheral entocristid connecting the metaconid to the hypoconid (Fig. 4a3, b3). There is no hypoconulid. The alveolus of the m2 is oval and somewhat elongated. It is single-rooted, with a remarkable notch in the alveolus, indicating the somewhat incomplete fusion of the trigonid and talonid roots—unlike living mustelids, which have a reduced single root with no traces of fusion (Fig. 4a3). The m2 is oval, with well distinct cuspids (paraconid, protoconid, metaconid, and hypoconid; Fig. 4h, i). The trigonid is wider than the talonid. The paraconid is crest-shaped, and the protoconid, metaconid, and hypoconid are pyramidal. The protoconid and metaconid are the highest cuspids, particularly the protoconid. The internal cristids of these cuspids are thickened and connected in the middle of the tooth, producing a clear separation between the basins of the trigonid and the talonid. The hypoconid is centrally located and occupies the whole talonid, being most developed in IPS24107 and IPS10088. A continuous and strong cingulid is present.

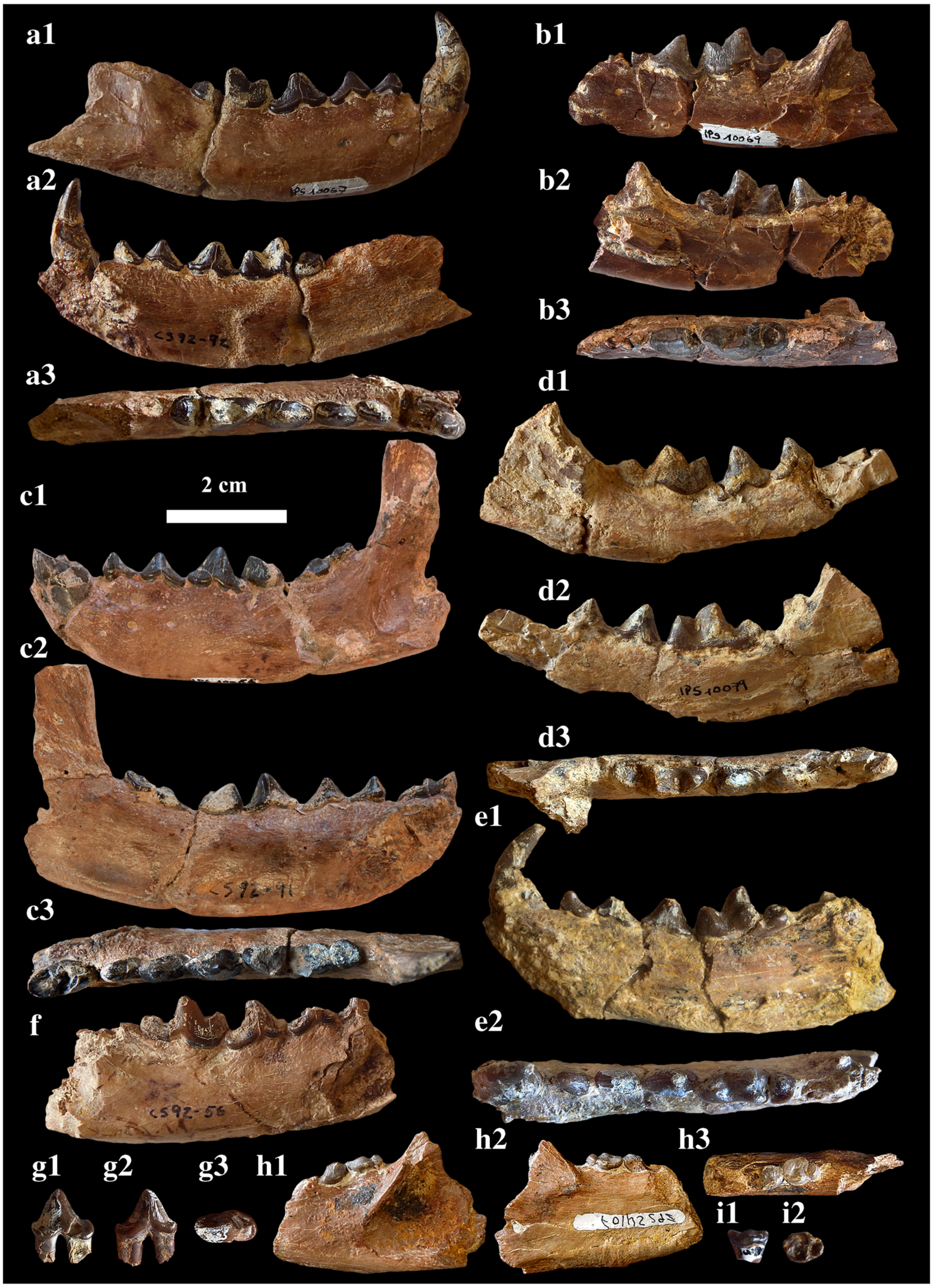

Fig. 4 Lower dentition of *Iberictis buloti* from els Casots. **a.** IPS10067, right hemimandible with c, p2–m1, **a.1.** buccal view, **a.2.** lingual view, **a.3.** oclussal view; **b.** IPS10069, left hemimandible with p4–m1, **b.1.** buccal view, **b.2.** lingual view, **b.3.** oclussal view; **c.** IPS10066, left hemimandible with c, p2–m2, **c.1.** buccal view, **c.2.** lingual view, **c. 3.** oclussal view; **d.** IPS10079, right hemimandible with p3–p4 and m1, **d.1.** buccal view, **d.2.** lingual view, **d.3.** oclussal view; **e.** IPS24700, right hemimandible with p2–p4 and m1, **e.1.** lingual view, **e.2.** occlusal view; **f.** IPS10084 right hemimandible with p2–p4 and m1, buccal view; **g.** IPS105256, left p4, **g.1.** buccal view, **g.2.** lingual view, **g.3.** oclussal view; **h.** IPS24700, left mandibular fragment with m1 talonid and m2, **h.1.** buccal view, **h.2.** lingual view, **h.3.** oclusal view; **i.** IPS10088, right m2. **i.1.** buccal view, **i.2.** occlusal view

Cladistic Results

Our cladistic analysis recovered three equally most-parsimonious trees, with a tree length of 187 steps, a consistency index (CI) of 0.4545, a rescaled consistency index (RC) of 0.2941, and a retention index (RI) of 0.6471. The apomorphies for each node are reported in Table 3. Our analysis only fails to resolve the relationships among some species of *Plesiogulo*. The strict consensus tree (Fig. 5) recovers two major clades: the Guloninae, composed of the monophyletic clade of *Iberictis*, *Plesiogulo*, *Gulo*, and *Dehmictis* + *Ischyrictis*; and a clade composed of the paraphyletic Mellivorinae—which include the living *Mellivora capensis* and the extinct mellivorines *Eomellivora piveteaui*, *Ekorus ekakeran*, and *Hoplictis noueli*—as well as the extant musteline *Mustela putorius*. Among the Guloninae, two different tribes (Gulonini and Ischyrictini) may be recognized: (1) the Gulonini, composed of *Iberictis* spp. (*I. buloti* and *I. azanzae*), *Plesiogulo* spp., and *Gulo* spp.; and (2) the Ischyrictini, including the genera *Dehmictis* and *Ischyrictis*. The monophyly of both the Gulonini

Table 2 Lower teeth measurements (in mm) of mesiodistal length (L) and buccolingual width (W) of *Iberictis buloti* from els Casots (C) and Pellecahus (P), and *Iberictis azanzae* from Artesilla (A). Estimated values are reported within parentheses

			c		p2		p3		p4		m1		m2	
Species	Locality	Catalog No.	L	W	L	W	L	W	L	W	L	W	L	W
I. buloti	C	IPS24107							10.7	5.4			6.4	5.1
I. buloti	C	IPS24700 left					7.5	4.2	10.3	5.2				
I. buloti	C	IPS24700 right	9.7	7.1	6.1	3.4	7.4	4	9.5	5	15.9	6		
I. buloti	C	IPS85595							9.6	4.8	14.79	4.8*		
I. buloti	C	IPS10084			6.1	3.3	8.1	4.2	10.5	5	14.92	6.1		
I. buloti	C	IPS10069							9.8	5.2	15.49	5.9		
I. buloti	C	IPS24686							9.8	4.9	14.32	6		
I. buloti	C	IPS10080			6.1	3.4	8.4	4.1	10.7	5.5				
I. buloti	C	IPS10079					8.4	4.3	11.1	5.5	16.42	6.1		
I. buloti	C	IPS10066	9.3	5.6	6.9	3.3	7.3	4.2	10.1	5.1	14.32	(5.4)	5.4	4.7
I. buloti	C	IPS10067	8.2	6.1	6.1	3.2	7.2	4.2	9.9	5.2	14.12	5.9		
I. buloti	C	IPS10068	7.9	5.2			7.3	4						
I. buloti	C	IPS 10088											7.1	5.6
I. buloti	C	IPS 10070					7.3	3.8	(9.2)	(5.2)				
I. buloti	C	IPS 105256							10.7	5.6				
I. buloti	P	MNHN LRM1044					7.5	4.1	10.2	5.1	14.7	6.2		
I. buloti	P	MNHN LRM1032							10.2	5.3	15.3	6.1		
I. azanzae	A	MPZ-2018/39	9.0	6.0										
I. azanzae	A	MPZ-2018/40	8.3	6.8										
I. azanzae	A	MPZ-2018/41							(9.9)	5.0				
I. azanzae	A	MPZ-16525	9	5.8										
I. azanzae	A	MPZ-16523							9.6	4.7				
I. azanzae	A	MPZ-16524									16	6.2		
I. azanzae	A	MPZ-16526											6.7	5.3

and of the genera *Iberictis*, *Plesiogulo*, and *Gulo* are supported by bootstrap results and Bremer indices (Fig. 5: Nodes B, D, F, and H). Our cladistic analysis therefore supports an *Iberictis* clade sister of *Plesiogulo*, with these clades jointly constituting the sister clade of the extant *Gulo*. The remains of *Iberictis* from els Casots are nested with those of *I. buloti* from the type locality (Pellecahus), in agreement with their attribution to the same species.

The recovery of a mellivorine clade partially agrees with the phylogenetic relationship supported by Valenciano et al. (2015, 2017), according to which *Eomellivora piveteaui* and *Ekorus ekakeran* would be allied with the living honey badger (*Mellivora capensis*). The early Miocene *Hoplictis noueli* is recovered as a stem mellivorine. Both the *Ekorus* + *Mellivora* and *Eomellivora* + (*Ekorus* + *Mellivora*) clades are well supported (Fig. 5). The position of *Mustela putorius* in the recovered strict consensus is controversial (see the Discussion for more details).

Discussion

Taxonomic Attribution

Iberictis was considered to be closely related to *Plesiogulo* by Ginsburg and Morales (1992). These authors erected two species of this genus, both from the early Miocene (MN4) of Europe, based on the then available scarce material: the type species, *I. azanzae*, from Artesilla (Zaragoza, Spain; Fig. 6a); and *I. buloti* from Pellecahus (France; Fig. 6b, E1–E3). Since their description, no further fossil remains of *Iberictis* have been described. The new sample of *I. azanzae* from Artesilla adds very important information about the M1 morphology, complementing the information provided by the holotype (Fig. 6a) and corroborating a close relationship between *I. azanzae* and *I. buloti*.

The new fossils described here from the MN4 of els Casots are assigned to *Iberictis* because they display the diagnostic features of this genus (e.g., lingual platform of the M1 distolingually enlarged, and unicuspid p4 with lingual bulge

Table 3 Synapomorphies for selected nodes (see Fig. 5), as indicated by character numbers followed by character states within parentheses. Italics denote ambiguous synapomorphies

Node	Character (state)
A	7 (0); 34 (1), *37 (1)*
B	17 (1); 18 (1); *21 (1)*; 26 (1); 27 (1); 45 (1); 46 (1); *50 (1)*; 51 (1); 52 (1); 54 (1); 56 (1); *60 (0)*; *69 (0)*
C	*8 (0)*; 29 (1); *35 (1)*; 38 (1); 39 (1); *62 (0)*
D	*11 (0)*; *21 (0)*; 22 (1); 23 (1); 25 (1); 32 (0); *44 (0)*; *50 (0)*; 76 (0)
E	26 (0); *35 (0)*; *36 (0)*
F	66 (1); *69 (1)*
G	13 (1)
H	*19 (0)*; 28 (2); 30 (0); *37 (0)*; 59 (1); 61 (1); 67 (2); 71 (2); 74 (1)
I	*11 (0)*; 49 (0); 57 (0); *62 (2)*; 66 (1)
J	33 (1); 48 (0); 67 (2)
K	31 (1); 35 (1); *48 (0)*; *60 (1)*; *64 (1)*; 65 (1); 67 (1); 68 (1); *70 (2)*; 71 (2)
L	*33 (1)*; 59 (1); 63 (1); 73 (1); 74 (1)
M	1 (1); 13 (1); 16 (0); *17 (1)*; 18 (1); *27 (1)*; *37 (1)*; *50 (1)*; 61 (1); 75 (1)
N	15 (1); *24 (2)*; 26 (1); 42 (1); 43 (1); 47 (1); 53 (1); 64 (0)

as well as thickened mesial and distal cristids; see our emended diagnosis above for further details). The sample from els Casots is considerably larger than that previously known for *Iberictis* (Tables 1 and 2), being composed of the remains from at least seven individuals (based on right hemimandibles), and thus it allows us to expand greatly the

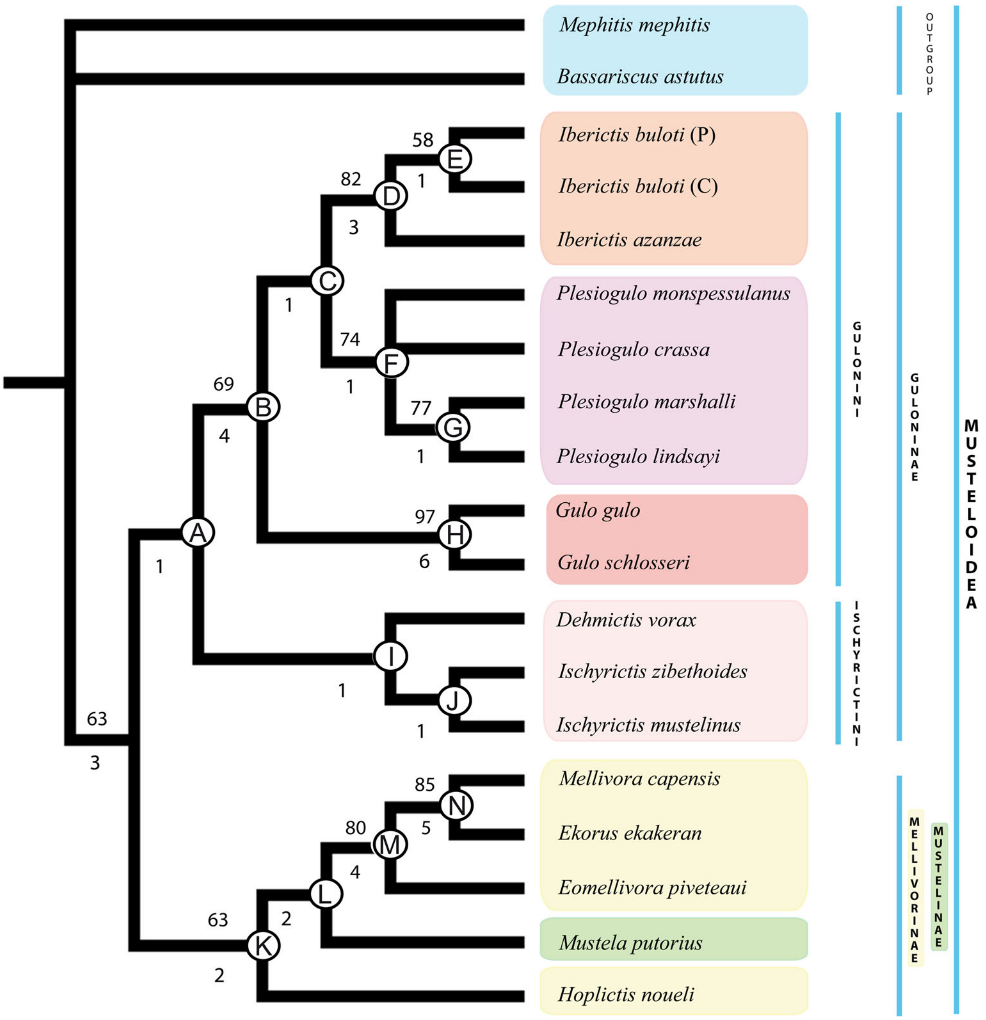

Fig. 5 Results of the cladistic analysis performed in this paper to decipher the phylogenetic relationship of *Iberictis buloti* (P = Pellecahus, C = els Casots) with selected extinct large Neogene mustelids and living musteloids. The cladogram depicts the strict consensus of the three most parsimonious trees (see main text for further details). Numbers below nodes are Bremer indices, and numbers above nodes are Bootstrap support percentages (only shown when ≥50). Apomorphies for each node are reported in Table 3

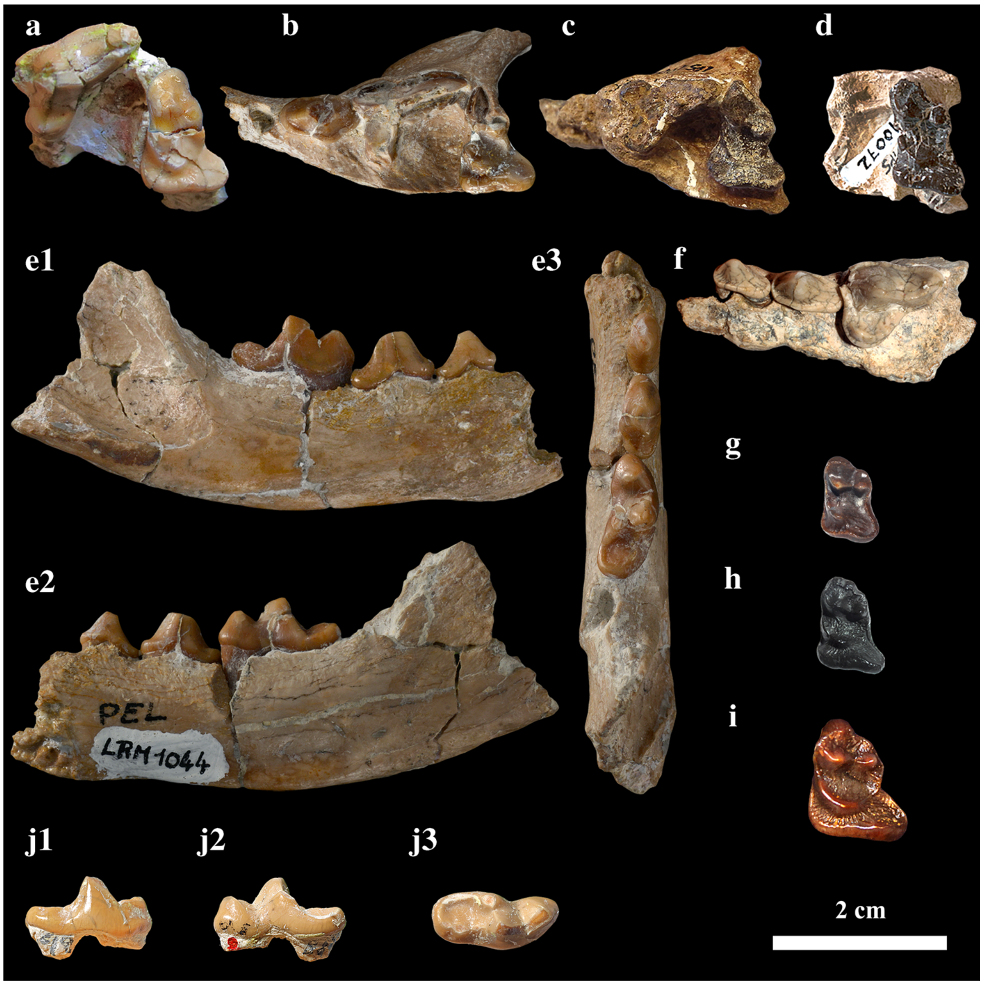

Fig. 6 The dentition of *Iberictis* compared with that of other early and middle Miocene mustelids. **a.** Composed maxillary specimen of *Iberictis azanzae* from Artesilla, comprised by MPZ-16522 (holotype, left maxillary fragment with P4 and partial M1) and by MPZ-2018/43 (buccal part of a right M1, mirrored specimen for comparison), occlusal view; **b.** MNHN LRM 782 and MNHN LRM 789, paratypes of *Iberictis buloti* from Pellecahus (composed specimen), left maxillary fragment with P3–P4 (MNHN LRM 782), and left M1 fragment (MNHN LRM 789); **c.** IPS10077, *Iberictis buloti* from els Casots, left maxillary fragment with P4–M1, occlusal view; **d.** IPS10072, *Iberictis buloti* from els Casots, left M1, occlusal view; **e.** MNHN LRM 1044, holotype of *Iberictis buloti* from Pellecahus, right hemimandible with p3–m1, **e.1.** buccal view, **e.2.** lingual view, **e.3.** occlusal view; **f.** SMNS 4082, left maxillary with P2–P4 of *Paralutra jaegeri* from Steinheim (see also Helbing 1936: fig. 1), occlusal view; **g.** SMNS 16816, left M1 of *Paralutra jaegeri* from Steinheim (see also Helbing 1936: fig. 2), occlusal view; **h.** SMNS T.D. 537, left M1 of *Paralutra jaegeri* from Ravensburg, described initially by Helbing (1928) as cf. *Lutra lorteti* (see also Helbing 1928: fig. 3), and subsequently synonymized by him (Helbing 1936) with *Pa. jaegeri*, occlusal view; **i.** MNHN Sa 843, left M1 of *Larteticti*s *dubia* from Sansan, occlusal view; **j.** BSPG Nr 645 right m1 of Guloninae indet.,described as *Plesiogulo* sp. by Schmidt-Kittler (1976) from Paşalar, **j.1.** buccal view, **j.2.** lingual view, **j.3.** occlusal view

knowledge about this genus. The ranges of variation observed within the described sample agree with those ascertained for extant large mustelids such as *Mellivora capensis* and *Gulo gulo* (Figs. 3, 4, 7, and 8). The P4s from els Casots show a variable development of the lingual shelf that runs from the base of the protocone to beneath that of the paracone as well as of the concavity situated on this lingual shelf. In particular, specimens with a larger lingual shelf have a larger concavity as well (e.g., IPS10083 and IPS36425; Fig. 3d, i). Another variable feature is the differential degree of development of the M1 metaconule and postprotocrista, which are more remarkable in IPS10072, IPS36425, and IPS105255 (Fig. 3j, k, l). Two (out of the seven available) M1s are completely preserved (IPS10077 and IPS10072; Fig. 6c, d), and display some morphological differences relative to one another. In particular, IPS10077 (Fig. 6c) displays a more symmetrical lingual platform than IPS10072 (Fig. 6d), whose platform is larger distolingually. Another example of variability is the very reduced bulge (IPS10067), or even the small convexity (IPS10069), present on the distal cristid of the p4, which reflects the reduction of the distal accessory cuspid on this tooth (Fig. 3a2, b2). The remains of *Iberictis* from els Casots most closely resemble those of *I. buloti* from Pellecahus, including a similar size and an almost identical morphology of the

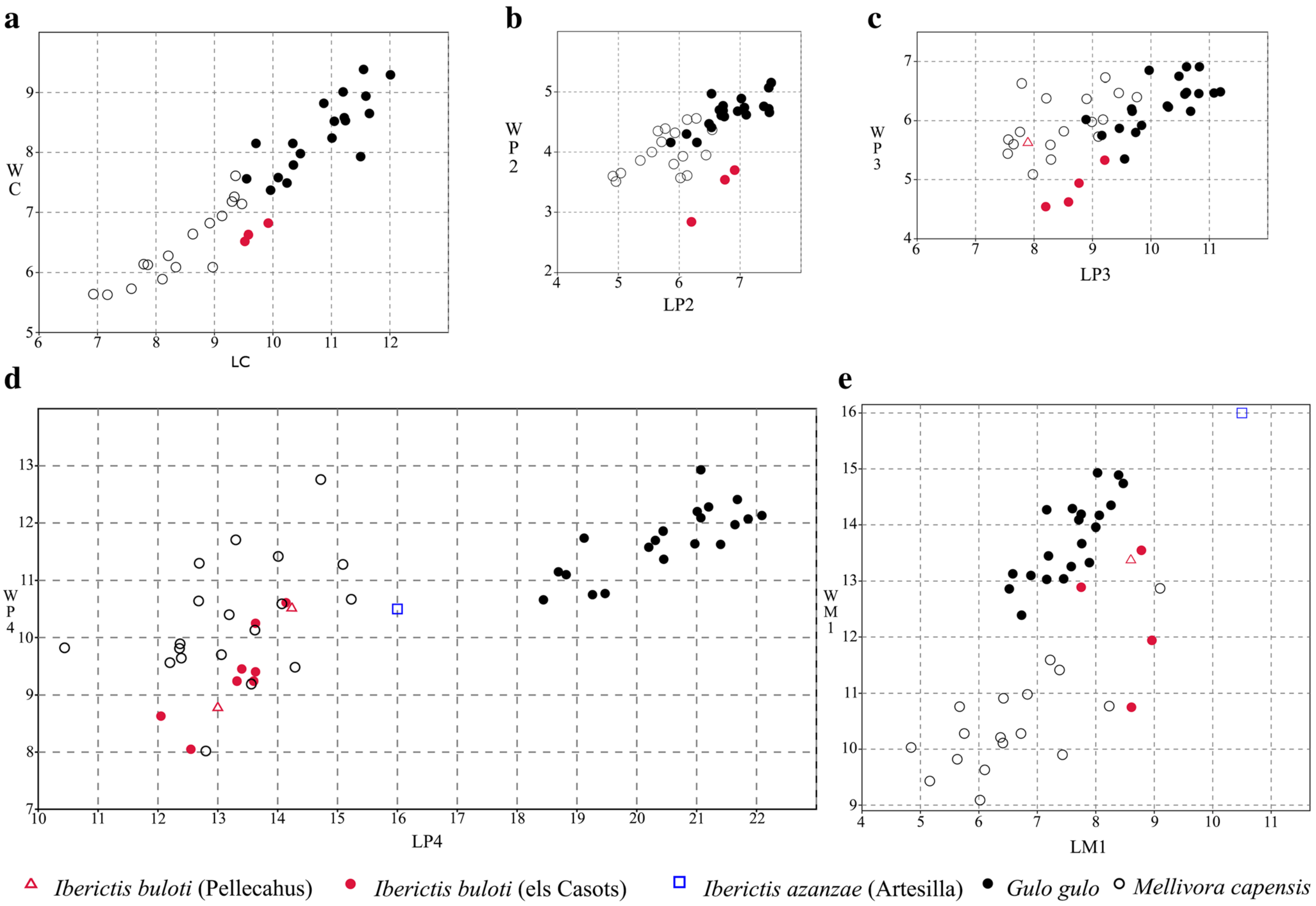

Fig. 7 Measurements (mm) of the upper dentition of *Iberictis* spp., *Gulo gulo*, and *Mellivora capensis*, as depicted by bivariate plots of buccolingual width (W) vs. mesiodistal length (L). **a.** C; **b.** P2; **c.** P3; **d.** P4, **e.** M1

premolars as compared with the type species—with the exception of the more pronounced buccal concavity in the P3 and the more primitive morphology of the p4, which retains a vestigial distal accessory cuspid in the els Casots sample. The specimens from els Casots display some minor differences in dental proportions as compared to those of *I. buloti* from Pellecahus for some tooth loci (e.g., the P3), but nevertheless these differences can be easily accommodated within the variability range of a single species (Figs. 7 and 8), particularly taking into account the small sample size previously available for *I. buloti* from the type locality. Given the lack of relevant morphological differences between these two samples, we formally assign the sample from els Casots to *I. buloti*. In contrast, the sample from els Casots differs from *I. azanzae* in the lack of the derived traits characteristic of the latter: enlarged cutting edge of the P4, better individualized P4 protocone, greater distolingual enlargement of the M1, absence of postprotocrista in M1, and the lesser development of cuspids in m2. Therefore, the new material from els Casots and Artesilla described here fills an important gap in the knowledge of this mustelid genus *Iberictis* and confirms the distinctiveness of the two originally described species. The presence of both species in the Iberian Peninsula during the early Miocene might be attributable to paleogeographical factors. Both localities are correlated to MN4, and in particular to local zone C of the Calatayud-Daroca Basin (Azanza et al. 1993; Casanovas-Vilar et al. 2011a, b, c), but they belong to different sedimentary basins (the Vallès-Penedès and the Calatayud-Teruel basins, respectively).

One of the most striking morphological characters of *Iberictis* and other gulonines (e.g., *Dehmictis*, *Plesiogulo*) is the distolingual expansion of the M1, which is also present in some Neogene lutrines such as *Siamogale thailandica* Ginsburg et al., 1983, *Paralutra jaegeri*, and *Larctetictis dubia*, as well as melines such as *Parataxidea* Zdansky, 1924, and *Melodon* Zdansky, 1924 (Ginsburg and Morales 1992, 2000; Grohé et al. 2010). Although the dentition of *Iberictis* is very different from that of these early-middle Miocene lutrines, isolated M1 of *Iberictis* could be easily mistaken for those of the lutrines *Paralutra jaegeri* (also present at Pellecahus) and *Lartetictis dubia* (Fig. 6f–i). However, the M1 of these lutrines is less mesiodistally constricted, displays a smaller stylar area, and a more developed paracone with a stouter cingulum, and it further retains the hypocone.

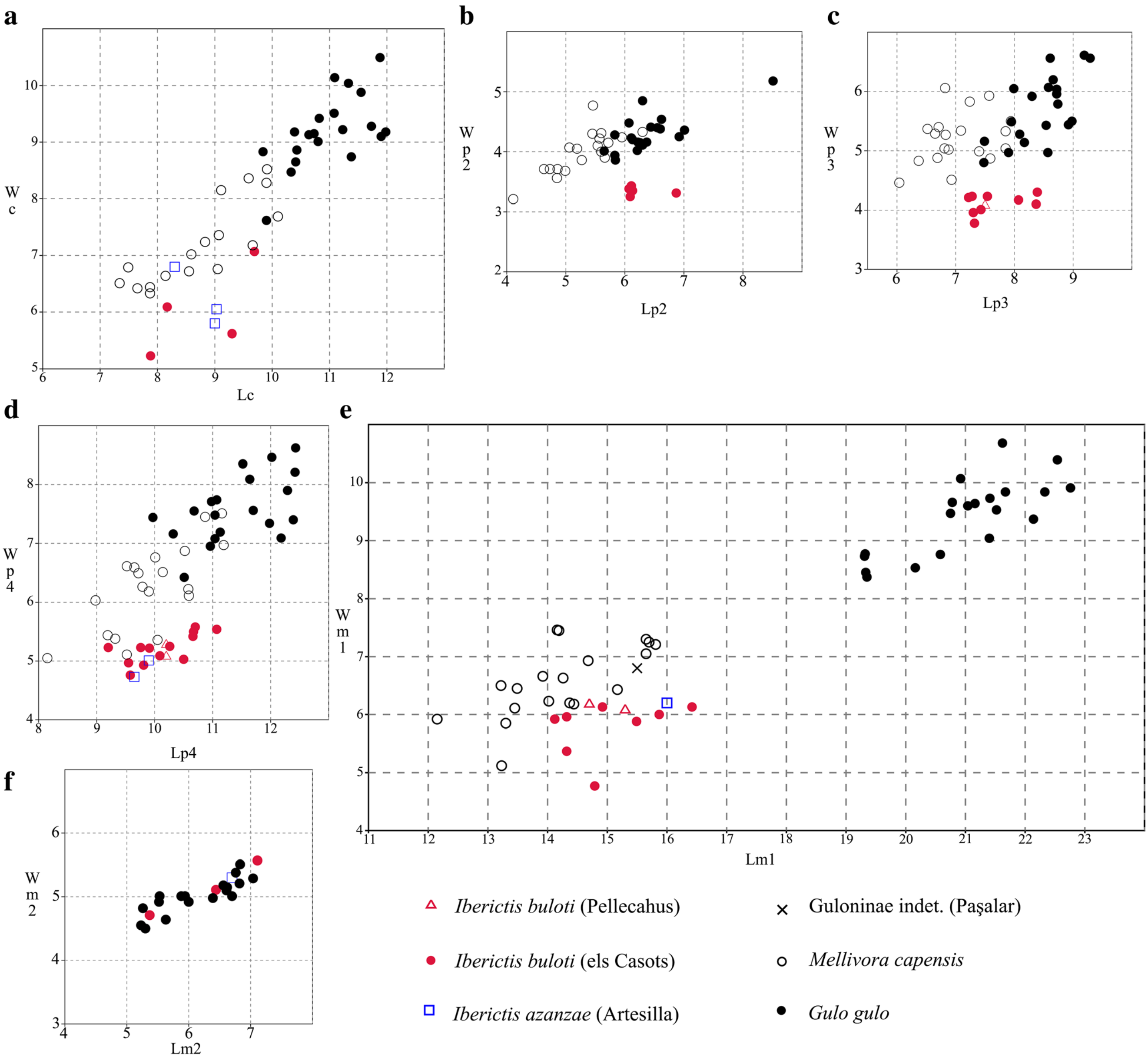

Fig. 8 Measurements (mm) of the lower dentition of *Iberictis* spp., Guloninae indet. from Paşalar, *Gulo gulo*, and *Mellivora capensis*, as depicted by bivariate plots of buccolingual width (W) vs. mesiodistal length (L). **a.** c; **b.** p2; **c.** p3; **d.** p4, **e.** m1; **f.** m2

A worn m1 BSPG Nr 645 (Fig. 6j1–3) from the early middle Miocene of Paşalar (MN5, Turkey) was described and assigned to *Plesiogulo* sp. by Schmidt-Kittler (1976). However, this designation is questionable in terms of morphology and age, with BSPG Nr 645 being much older than other remains of *Plesiogulo* spp., which range from the late Miocene to the early Pliocene (MN10–MN14). Furthermore, the Turkish mustelid does not match with the morphology of *Plesiogulo*, with the former possessing a much more developed m1 metaconid, a protoconid much higher than the paraconid, a relatively longer talonid with a longer hypoconulid, and a deeper valley. Due to the scarcity of the material and the above-mentioned morphological differences, we consider that the m1 from Paşalar should be excluded from *Plesiogulo*. Although BSPG Nr 645 shows some similarities with the m1 of *Iberictis*, the former specimen is more robust, possesses a more developed metaconid, and displays a different talonid morphology (longer talonid, non-beveled lingual wall of the hypoconid, deeper talonid valley, higher entocristid, and lower hypoconid). These features indicate that an assignment to *Iberictis* also can be discounted for the indeterminate Turkish specimen, while its assignment is feasible within the subfamily Guloninae.

Evolutionary History

Phylogenetic Relationships of the Guloninae, Mellivorinae, and Mustelinae

During the Miocene, large terrestrial mustelids exhibited a wide taxonomic diversity in Eurasia, Africa, and North America, being represented by genera such as *Dehmictis*, *Ekorus, Eomellivora*, *Hoplictis, Iberictis*, *Ischyrictis,* and *Plesiogulo* (Zdansky 1924; Teilhard de Chardin 1945; Baskin 1998; Ginsburg 1999; Werdelin and Peigné 2010; Fig. 9). Historically, these mustelids have been assigned to the extant subfamilies Guloninae, Mellivorinae (honey badger), and Mustelinae (including weasels, polecats, minks, and relatives; Baskin 1998; Ginsburg 1999; Werdelin and Peigné 2010). However, the phylogenetic relationships among these genera and relative to extant mustelids remained elusive (e.g., Ginsburg and Morales 1992; Baskin 1998; Ginsburg 1999; Werdelin and Peigné 2010). Our cladistic analysis helps to unravel the relationship between these extinct and extant taxa (Fig. 5), by showing that the genera *Dehmictis, Iberictis*, *Ischyrictis*, and *Plesiogulo* belong to the Guloninae clade. The systematics of these extinct mustelids has been controversial (e.g., Pia 1939; Webb 1969; Ginsburg 1977; Ginsburg and Morales 1992; McKenna and Bell 1997; Baskin 1998; Ginsburg 1999), not only due to the scarce and fragmentary craniodental remains available for many extinct genera, but also to the presence of a mixture of primitive and derived characters (Valenciano et al. 2017). Valenciano et al. (2017) performed a cladistic analysis of some living and extinct large gulonines and mellivorines, and concluded that the beech marten (*Martes foina*) and the fisher (*Pekania pennanti*), together with *Gulo*, *Plesiogulo*, and the ischyrictin *Ischyrictis zibethoides* may be considered gulonines. The inclusion of additional Miocene taxa in the present study further supports the distinction of two subclades within the Guloninae, which

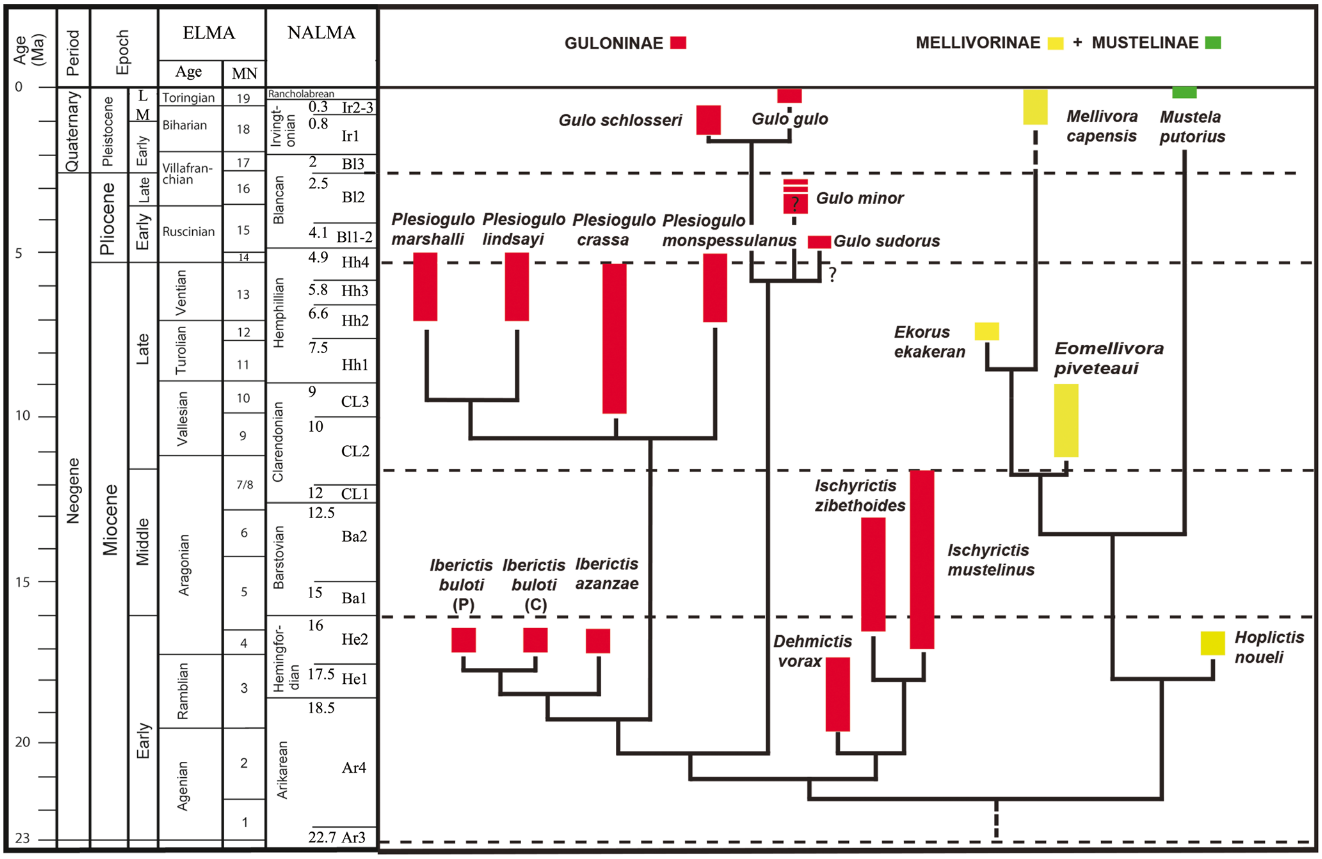

Fig. 9 Calibrated phylogenetic hypothesis based on our cladistic analysis. Chronostratigraphical and biochronological correlations of North American land mammal age (NALMA) based on a Tedford et al. (2004), Albright et al. (2008), and Hilgen et al. (2012); European Mammal Neogene Units (MN) based on Hilgen et al. (2012) and Morales et al. (2013). Stratigraphic ranges of the taxa based on Kormos (1914), Zdansky (1924), Viret (1933, 1939), Helbing (1930, 1936), Teilhard de Chardin (1945), Petter (1963), Kurtén (1970), Bonifay (1971), Hendey (1978), Harrison (1981), Roth (1989), Ginsburg and Morales (1992), Alcalá et al. (1994), Sotnikova (1995, 2008), Ginsburg (1999), Werdelin (2003), Montoya et al. (2011), Sher et al. (2011), Peigné (2012), Wolsan and Sotnikova (2013), and Valenciano et al. (2015). *Gulo sudorus and G. minor* are placed here based on Sotnikova (1982, 2010) and Samuels et al. (2018), although they were not included in our cladistics analysis. Abbreviations: ELMA, European land mammal ages; NALMA, North American land mammal ages (units defined by inmigrant taxa); E, early, M, middle; L, late

we distinguish at the tribe rank: the Gulonini (*Iberictis*, *Plesiogulo*, and *Gulo*) and the Ischyrictini (*Dehmictis* and *Ischyrictis*). These family-group taxa were originally erected as "sub-subfamilies" by Pia (1939), with the Ischyrictini including the extinct large mustelids *Ischyrictis*, *Laphictis*, and *Hadrictis* (within subfamily Mellivorinae), and the Gulonini including *Gulo* and *Plesiogulo* (within the Mustelinae). Subsequently, the Ischyrictini and the Gulonini were considered at the tribe rank by Tobien (1955) and Webb (1969), respectively. Different authors (Pia 1939; Tobien 1955; Webb 1969; Ginsburg 1977, 1999) have included these tribes into the Mellivorinae and the Guloninae, comprising the genera *Eomellivora* (=*Hadrictis*)*, Hoplictis*, *Iberictis, Gulo, Ischyrictis* (=*Laphictis*), *Mellalictis*, *Mellivora*, and *Plesiogulo*.

Based on the results of the cladistic analysis reported in this paper, the Guloninae clade (Figs. 5 and 9, Table 3) is defined, by the following synapomorphies: (1) I3 spread out laterally in relation to the I1-I2; (2) presence of a slender buccolingual crista in the M1 from the paracone to the protocone (1 and 2 unambiguous synapomorphies); and (3) relatively enlarged M1 lingual area (ambiguous synapomorphy). The Guloninae also are characterized by the following traits: (1) P2 with a robust cingulum, absence of distal accessory cuspid in P3; (2) stout P4 cingular parastyle; and (3) a relatively reduced p2. The subclade of *Dehmictis* + *Ischyrictis* is distinguished here as a tribe (Ischyrictini) of more basal Guloninae, depicted by a more primitive dentition (e.g., slender premolars) and with a relatively enlarged m1 talonid (excluding *Izchyrictis zibethides*). The closer phylogenetic relationships between *Iberictis*, *Plesiogulo*, and *Gulo* are reflected in the strict tree obtained (Figs. 5 and 9), in which these genera conform the monophyletic tribe Gulonini (the total clade of wolverines), characterized by the possession of wrinkled enamel and a robust premolar morphology (Fig. 10). In particular, the Gulonini are defined (Table 3) by the following unambiguous synapomorphies: (1) P3 with a stout cingulum and a distinct buccal concavity; (2) P4 with both a strong buccal concavity and a stout cingulum surrounding the whole tooth; (3) p2-p4 with strong cingula; absence of mesial and distal accessory cuspids, with the exception of the p4, whose distal accessory cuspid is vestigial or absent —some specimens of *Plesiogulo* not analyzed herein from the Turolian of Russia ascribed to *Plesiogulo* cf. *P. brachygnathus* and *Plesiogulo* ex gr. *P. minor* possess a small distal accessory cuspid in the p4; see Sotnikova (1995)— and thickening on the mesial and distal cristids; and (4) m1 hypoconulid reduced or absent. It is also defined by the following ambiguous synapomorphies: (1) P4 protocone distally displaced; and (2) m1 metaconid individualized with a moderate size in the older taxa (*Iberictis* and *Plesiogulo*), and lost in the living genera *Gulo*. The members of the clade *Iberictis* + *Plesiogulo* (Figs. 5, 9 and 10) share more derived characters towards a *Canis*-like dentition, with a prominent crushing area in the upper and lower molars. In addition, they are characterized by the possession of an enlarged M1 in relation to the P4, and a mesiodistal enlargement of the M1 lingual platform, which possesses a concavity on the lingual edge. The late Miocene species of *Plesiogulo* are large to giant-sized mustelids, characterized by a more robust dentition than in *Iberictis* and the possession of other more derived traits (e.g., shorter lower premolars, trend to enlarge the m1 talonid, by the presence of a crestiform m1 hypoconid, and a hypoconulid, as well as a derived m2 that has lost the hypoconid).

Historically, it was accepted that the oldest known species of the extant genus *Gulo* was *Gulo minor* Sotnikova, 1982, originally described based on a hemimandible from the Lower Adycha River Basin (Arctic Siberia, Russia). These deposits were initially interpreted as Pliocene in age (Sotnikova 1982), but later reinterpreted as late middle Pleistocene (Sher et al. 2011). Subsequently, *G. minor* has been reported, based on mandibular remains, from Udunga (Transbaikal region of Siberia, Russia), dated between 3.1 and 3.6 Ma (MN15–MN16; Sotnikova 2008, 2010; Wolsan and Sotnikova 2013), thereby confirming an early late Pliocene age for this species (Fig. 9). Its lower dentition is clearly wolverine-like, being characterized by small size, elongated premolars without accessory cuspids, and an m1 similar in morphology to that of *Gulo gulo*. A more primitive species ascribed into the genus has recently been described from the early Blancan (early Pliocene, 4.9–4.5 Ma) of the Gray Fossil Site (Tennessee, USA). *Gulo sudorus* Samuels et al., 2018, is represented by a left maxillary fragment with the P2 and P4. This new wolverine represents the first datum of *Gulo*, being more than one million year older than *G. minor*. Its dentition is intermediate between fisher (*Pekania*) and later *Gulo* spp., suggesting that could represent an intermediate taxon, which could have evolved in North America and later dispersed to Eurasia (Samuels et al. 2018). Thus, *Gulo sudorus* fills a gap in the origin of the genus, emerging as a potential candidate to be the oldest member of *Gulo*, but the scarcity of its currently available fossil remains precludes confirming such a hypothesis. More recently, in the Pleistocene, *Gulo schlosseri* constitutes a better-known species from the early and middle Pleistocene of Eurasia (Kormos 1914; Bonifay 1971; Xiaofeng and Haipo 1987; Sotnikova 2010). It is also smaller and displays a less derived dentition than the living wolverine. *Gulo schlosseri* and *Gulo gulo* have a very robust P4 and m1 trigonid, and share derived characters towards a hypercarnivorous dentition, with a reduction in the expansion of the P4 protocone, the M1 talon, the m1 talonid, and the m2. In both species, the lower carnassial has lost the metaconid; the paraconid and protoconid are equal in height, and the talonid has been reduced (in height, length, and width), resembling a feloid-like tooth, in comparison with that of other mustelids. As discussed above, our phylogenetic results set back the origin

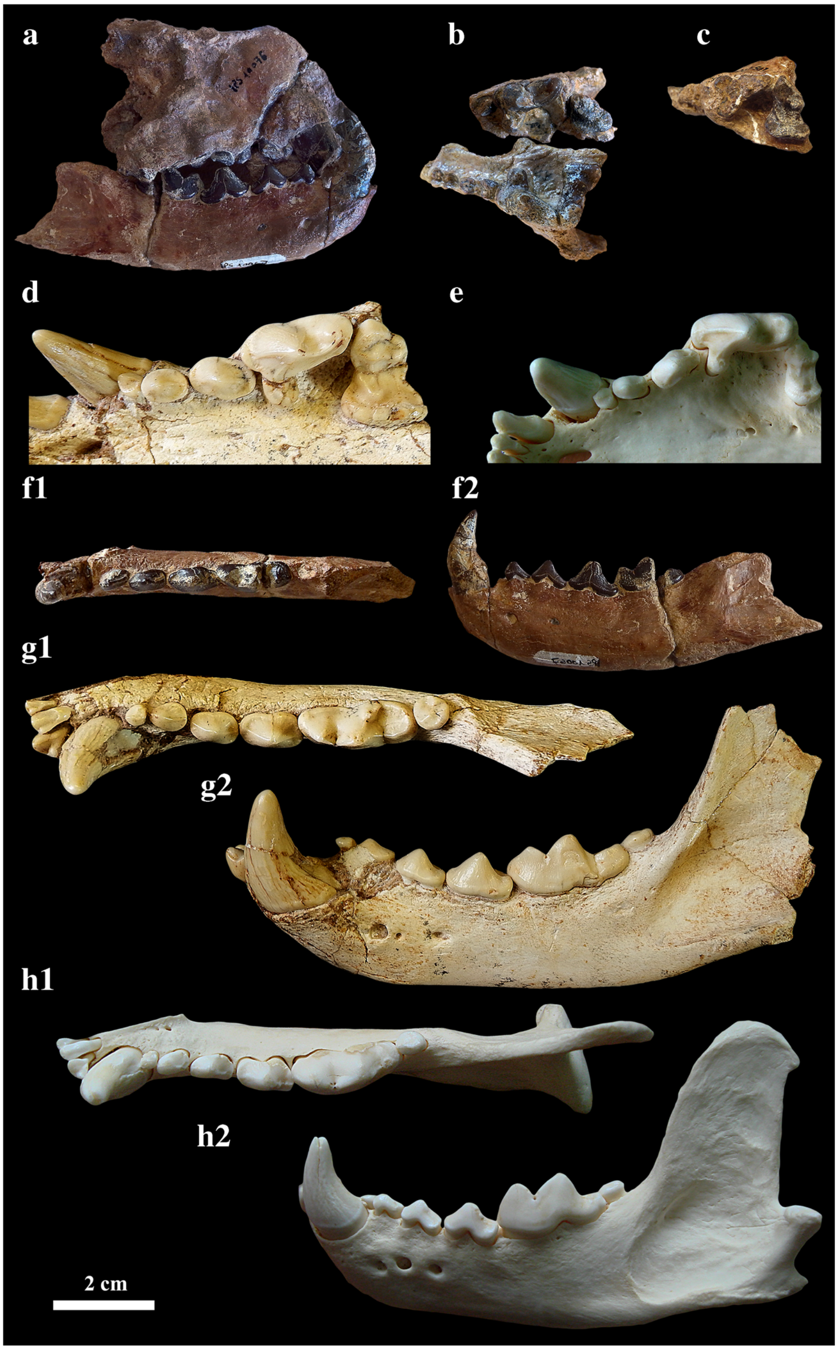

Fig. 10 The dentition of *Iberictis* compared with that of other members of the wolverine total clade. **a.** Fragment of the cranium IPS10076 of *Iberictis buloti* from els Casots with its mandible IPS10067, lateral view; **b.** IPS24701, partial maxilla of the same specimen of *Iberictis buloti* from els Casots, occlusal view; **c.** IPS10077 *Iberictis buloti* from els Casots, left maxillary fragment with P4–M1, occlusal view; **d.** PMU M3805, cranium of *Plesiogulo crassa* from Locality 108, China (specimen Ex. 8 of Zdansky 1924), occlusal view; **e**. Gulo gulo cranium, occlusal view; **f.** IPS10067, *Iberictis buloti* from els Casots, right hemimandible with c, p2–m1, mirrored specimen for comparison, **f.1.** occlusal view, **f.2.** buccal view; **g.** PMU M3806, mandible of *Plesiogulo crassa* from Locality 108, China (specimen Ex. 8 of Zdansky 1924; same individual as PMU M3805), **g.1.** occlusal view, **g.2.** buccal view; **h.** *Gulo gulo*, mandible (same individual as depicted in E), **h.1.** occlusal view, **h.2.** buccal view

of a total wolverine clade to the early Miocene, when *Iberictis* is recorded. This further indicates the existence of a ghost lineage in the wolverine lineage of at least 12 Myr (from MN4 to MN15), and that the genus *Gulo* (including *G. sudorus*, *G. minor*, *G. scholosseri,* and *G. gulo*) would have not derived from any of the *Plesiogulo* species included in our analysis (Fig. 9).

Our cladistic results also indicate that the giant mustelids *Eomellivora piveteaui* and *Ekorus ekakeran* are mellivorines, in agreement with Valenciano et al. (2015, 2017; Fig. 5). *Eomellivora piveteaui*, *Ekorus ekakeran*, and the living *Mellivora capensis* share among other synapomorphies the tendency of the posterior lacerate and jugular foramina to possess separate openings, the jugular foramen in a distolateral position in relation to the posterior lacerate foramen, as well as a robust P3 with a distal accessory cusp and a robust cingulum; a high m1 paraconid with a similar height to the m1 protoconid and a reduced m2, which is lost in the single living representative of the subfamily (Table 3). The living European polecat (*Mustela putorius*), which belongs to the subfamily Mustelinae, is nested in our analysis as the sister taxon of the clade composed of the three above mentioned species, but the node is only very weakly supported. Molecular phylogenetic analyses support mustelines as the sister group of lutrines (otters; e.g., Koepfli et al. 2008; Sato et al. 2012) instead of mellivorines, although it should be taken into account that the phylogenetic placement of *Mellivora capensis* (the only living mellivorine) is contentious (Sato et al. 2012), being generally considered to occupy a basal position within the Mustelidae (Koepfli et al. 2008; Sato et al. 2012). The primitive and hypercarnivorous *Hoplictis noueli* from Artenay (France, MN4), only know by mandibles and an isolated M1 (Mayet 1908; Helbing 1930; Ginsburg 1961), is recovered by our analysis as the basalmost taxon of the mellivorine clade (Fig. 9). However, the fact that it occupies a more basal position than *Mustela putorius*, even if this placement is weakly supported, does not allow us to conclusively discount the possibility that *Hoplictis* precedes the divergence between mellivorines and mustelines. The discovery of additional remains of the upper dentition of *Hoplictis noueli* might therefore contribute to clarify further the phylogenetic relationships between this basal form and other investigated taxa, thereby helping to decipher the relationships between the Mellivorinae and the Mustelinae.

Remarks on the Diet of the Gulonini

Both *Iberictis* and the more derived *Plesiogulo* are characterized by a robust dentition with a relatively long m1 as well as long and stout M1 and P4 (Fig. 10). These traits are useful for opportunistic foraging and also for crushing bones, as is the case among extant canids (Sillero-Zubiri 2009). This set of traits together (the possession of a mesiodistal enlargement of the M1 lingual platform and the presence of a concavity on the lingual edge) are also present in some lineages of Euroasiatic Miocene lutrines such as *Paralutra jaegeri*, *Larteticits dubia*, and *Siamogale thailandica*, which have been interpreted recently as badger-like otters (Wang et al. 2017) because their dentition is adapted for crushing food. Thus, the interpretation of these features found in these gulonines, lutrines, and also in melines as a convergence due to a dietary shift toward a more omnivorous or durophagous diet is reasonable. The characteristic shortening of the M1 talon and m1 talonid of *Gulo*, together with other craniodental features (thickening of the m1 trigonid and shortening of the muzzle), represent an alternative adaptation for crushing bones with the premolars and, especially, with the carnassials (Fig. 10). The diet of *Gulo gulo* includes the carcasses of large ungulates such as moose and reinder, as well as preying opportunistically on deer, sheep, and small vertebrates (Larivière and Jennings 2009). The shortening of the muzzle enabled the production of higher bite forces, thereby improving the efficiency for crushing bones, which constitute an important portion of the diet of this taxon (Larivière and Jennings 2009). Preliminary studies of the masticatory apparatus of large and giant mustelids suggested that *Gulo gulo* is able to produce relatively greater bite forces than *Plesiogulo crassa* (Valenciano et al. 2016b), although the estimates obtained for both taxa were quite high for a carnivoran of their size. Morphological similarities in the dentition of *Plesiogulo* and *Gulo,* such as the size and stoutness of the premolar series, suggest that *Plesiogulo* was similarly an opportunistic feeder able to process bone rather efficiently (Harrison 1981). The latter specialization is less evident in *Iberictis*, which might have been a more opportunistic feeder than *Plesiogulo* and *Gulo*. However, both the shape of the teeth and the horizontal wear pattern displayed by some specimens (e.g., Figs. 2a, b, e, 4a and 6e) support the consumption of hard food items such as bones (as in living jackals; Sillero-Zubiri 2009).

Summary and Conclusions

Based on previously unpublished remains from the early Miocene (MN4) of els Casots (Vallès-Penedès Basin), the extinct gulonine mustelid *I. buloti* is reported for the first time from the Iberian Peninsula, where only its sister species, *I. azanzae*, was previously known. The new material of both species described here fills an important gap in the knowledge of these mustelids and confirms the taxonomic validity of both species. The sample of *I. buloti* from els Casots includes more abundant material than that from the type locality (MN4 of Pellecahus, France), and therefore it enlarges the knowledge of this genus in relation to the wolverine lineage. A cladistic analysis of extinct and extant gulonines, mustelines, and mellivorines indicates that the wolverine lineage is much older that previously thought. In particular, *Iberictis* emerges as the oldest member of the Gulonini (the total clade of wolverines, currently represented only by the living *Gulo gulo*), thus allowing to track the fossil record of this clade back to the early Miocene (16.5–16.3 Ma). *Iberictis* is further nested as the sister group of the large late Miocene gulonine *Plesiogulo*, thereby indicating that none of the analyzed species of the latter genus is a likely direct ancestor of *Gulo*. The results of our phylogenetic analysis further allows us to rearrange the analyzed large Miocene genera into two distinct mustelid subfamilies: *Dehmictis* and *Ischyrictis* (Ischyrictini), together with the aforementioned genera *Iberictis* and *Plesiogulo* (Gulonini) are classified as gulonines; whereas *Ekorus*, *Eomellivora*, and *Hoplictis* are classified as mellivorines, being possibly more closely related to the Mustelinae (represented here by *Mustela*).

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