First occurrence of *Ischyrictis zibethoides* (Carnivora, Mustelidae, Guloninae) from the Middle Miocene of Southwestern Europe

by

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With 4 plates, 5 text-figures and 3 tables

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Abstract

This study describes the cranial remains of *Ischyrictis zibethoides* from the Middle Miocene of La Retama (MN5, Spain) and *Ischyrictis bezianensis* from the Early Miocene of Baigneaux (MN4, France). The presence of *I. zibethoides* in La Retama represents the first record of this species in the Iberian Peninsula, previously known exclusively from France and Germany. Additionally, we suggest that *I.* cf. *bezianensis* from Quinta de Farinheira (MN5, Portugal) should be reclassified as *I.* cf. *zibethoides*. *Ischyrictis zibethoides* from the localities of Sandelzhausen (MN5, Germany) and Sansan (MN6, France) exhibits significant variability in size and dental morphology, particularly in the first molars (M1/m1). The diversity of large-sized (over 10 kg) mustelids is a noteworthy feature of the carnivoran associations during the Middle Miocene in Europe. They almost exclusively occupied the mesocarnivore niche, which in North American faunas was shared by large mustelids and canids. The decline in diversity of large-sized mustelids coincided with the rise in size and diversity of hyaenid species, which was detected in European faunas towards the end of the middle Miocene.

Keywords: Carnivora; Arctoidea; Mustelidae; Iberian Peninsula; Neogene

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1. Introduction

Mustelidae show a significant adaptive radiation during the Early and Middle Miocene in Western Europe and Anatolia, with the emergence and diversification of species rooted in the living groups (GINSBURG 1999). Within the subfamily Guloninae (which includes extant wolverines and martens), there is a proliferation of forms close to the '*Martes'* group (e.g., VALENCIANO et al. 2022 and references therein), as well as the appearance of medium to large forms with affinities to Guloninae and Mellivorinae (honey badgers and relatives) (VALENCIANO et al. 2020a), such as *Ischyrictis* HELBING, 1930, *Laphictis* VIRET, 1933, *Hoplictis* GINSBURG, 1961, *Iberictis* GINSBURG & MORALES, 1992, *Dehmictis* GINSBURG & MORALES, 1992.

Ischyrictis HELBING, 1930 was the first genus defined for this group. HELBING (1930) took the species name of *Viverra zibethoides* (BLAINVILLE, 1842) from the classical locality of Sansan (MN6, France), which was placed in the family Mustelidae as *Mustela zibethoides* by FILHOL (1894). MAYET (1908) reassigned two different forms to the genus *Trochictis* VON MEYER, 1842: *Trochictis zibethoides* mut. *noueli* from

Artenay (MN4, France) and *Trochictis zibethoides* mut. *florancei* from Pontlevoy-Thenay (MN5, France). HELBING (1930) included these three forms in his generic diagnosis together with the one from the locality of Steinheim (MN7/8, Germany), originally identified as *Lutra dubia* by FRAAS (1870). He therefore attributed them to the species *Ischyrictis zibethoides* (BLAINVILLE, 1842). HELBING (1936) reclassified the Steinheim species as *Ischyrictis* (*Laphictis*) *mustelinus* VIRET, 1933, attributing them to the subgenus of *Ischyrictis* instead of the genus *Laphictis* as originally defined by VIRET (1933). This proposal was finally followed by VIRET (1951).

GINSBURG (1961) identified significant differences in the forms attributed to *Ischyrictis zibethoides*, dividing them into three different subgenera; i) *Ischyrictis (Ischyrictis) zibethoides* for the Sansan and Artenay forms; ii) *Ischyrictis (Hoplictis) florancei* from Pontlevoy (MN5, France). However, this author also implicitly included *Ischyrictis helbingi* from La Grive (MN7/8, France) (VIRET 1951), in this group, a suggestion accepted by CRUSAFONT-PAIRÓ (1972). A new species, *Ischyrictis (Hoplictis) anatolicus* SCHMIDT-KITTLER, 1976, was later erected from the locality of Çandir (MN6, Turkey) within this subgenus; and iii) *Ischyrictis (Laphictis) mustelinus* was named after the form from La Grive (type locality) and the Steinheim taxon mentioned above. DEHM (1950) doubtfully included two Early Miocene species from Wintershof-West (MN3, Germany) in *Laphictis*: *Laphictis? vorax* and *Laphictis? comitans*. The first of these species was later included in a new genus *Dehmictis* GINSBURG & MORALES, 1992.

GINSBURG & MORALES (1992) corrected the species determination from Artenay *Ischyrictis zibethoides noueli* to *Hoplictis noueli* (MAYET, 1908), and elevated the subgeneric ranks to the generic level in the group. In the same work, they defined a new genus, *Iberictis* GINSBURG & MORALES, 1992, for the Early Miocene forms from

Pellecahus (MN4, France) and Artesilla (MN4, Spain). Later, Ginsburg (1999) included *Laphictis mustelinus* in the genus *Ischyrictis*, synonymizing *Laphictis* with *Ischyrictis*.

According to Valenciano et al. (2020a), *Ischyrictis*, *Laphictis,* and *Dehmictis* are considered basal forms of Guloninae. Additionally, *Hoplictis* has been tentatively classified as a member of Mellivorinae. However, to clarify its systematic classification, additional cranial remains of *Hoplictis* are required. At present, the genus *Ischyrictis* consists of only two species: *Ischyrictis zibethoides* and *Ischyrictis bezianensis* Ginsburg & Bulot, 1982. The first species was first defined in Sansan (Blainville 1842; Helbing 1930; Ginsburg 1961; Peigné 2012). It has also been cited in Vieux-Collonges (MN5, France) (Mein 1958), Carrières de la Morfassiére (MN5, France) (Ginsburg 2001), Faluns d'Anjou (MN5, France) (Ginsburg 2002), Sandelzhausen (MN5, Germany) (Nagel et al. 2009), and La Retama (MN5, Spain) (Morales et al. 1993; Fraile et al. 1997). The second species of the genus *Ischyrictis*, *I. bezianensis,* has been discovered in various locations including Bézian (type locality, MN4, France) (Ginsburg & Bulot 1982), Pellecahus (Bulot & Ginsburg 1993), Baigneaux (MN4, France) (Ginsburg 2002) and Torrent de Vilaroc (MN4, Spain). An astragalus was initially described as belonging to *I. zibethoides* but was later reclassified as *I. bezianensis* (Crusafont-Pairó et al. 1955; Robles 2014). In addition, fragmentary remains of *Ischyrictis* cf. *bezianensis* have been described in Portugal at the fossil sites of Quinta de Farinheira (MN5), Quinta do Pombeiro (MN5), and Olival da Suzana (MN5) (Ginsburg & Antunes 1995; Pais et al. 2011).

However, the diversity of medium and large-sized mustelids is relatively smaller in the Iberian Peninsula than in other areas of Europe (Morales et al. 2015; Valenciano et al. 2020a). The Iberian fossil record only shows the presence of these carnivorans from the Lower Aragonian (MN4, Early Miocene) with *Iberictis azanzae* and *Iberictis* *buloti* (GINSBURG & MORALES 1992; VALENCIANO et al. 2020a). Apart from the few remains found in Portugal (GINSBURG & ANTUNES 1995; PAIS et al. 2011), there is a significant gap in the fossil record of these mustelids until the end of the Middle Aragonian (Middle Miocene, MN7/8) and the beginning of the Late Miocene of the Vallès-Penedès basin. In this area, *Laphictis mustelinus* was recorded in Can Mata (MN7/8) and *Hoplictis helbingi* in Castell de Barberà (MN9) (VILLALTA COMELLA & CRUSAFONT-PAIRÓ 1943; PETTER 1963; CRUSAFONT-PAIRÓ 1972, 1979; ALBA et al. 2019), along with the earliest Eomellivorini. These forms consist of *Eomellivora moralesi* from Can Mata (ALBA et al. 2022) and *Eomellivora fricki* from Can Llobateres I (MN9) (=*Ischyrictis [Ischyrictis] petteri* in CRUSAFONT-PAIRÓ [1972] and later synonymized as *E. fricki* in VALENCIANO et al. [2019]).

The fossil site of La Retama (MN5) is found within this temporal gap. *Ischyrictis zibethoides* has been cited in this locality by MORALES et al. (1993) and FRAILE et al. (1997), but the material had not been described. The purpose of this study is to describe these unpublished fossils, which represent the first record of *I. zibethoides* in the Iberian Peninsula and the most southwestern occurrence of this species in Europe. We also describe an unpublished hemimandible of *Ischyrictis bezianensis* from Baigneaux (GINSBURG 2001) for the first time.

1.1. Geological setting

The Miocene fossil site of La Retama (Loranca del Campo, province of Cuenca) is located in the Intermediate Basin, a long and narrow area of 10,000 km^2. It contains numerous vertebrate fossil sites from the Late Eocene to the Middle Miocene (DÍAZ MOLINA & LÓPEZ MARTÍNEZ 1979; TORRES et al. 1983; TORRES & ZAPATA 1986; MORALES et al. 1993, 1999; ARRIBAS et al. 1996) (Text-fig. 1). La Retama was discovered in 1988.

Excavations were carried out in 1988, 1989 and 1992 provided over 1400 large mammal specimens, mostly isolated bones and teeth, along with an abundant association of small mammals. The site is dated as Middle Aragonian, local biozone Db (15.9-16 Ma) (MN5, Middle Miocene) (Daams 1991; Daams et al. 1999; Álvarez-Sierra et al. 2006; van der Meulen et al. 2011, 2012). The Equidae *Anchitherium castellanum* is the most abundant taxon found in La Retama, accounting for approximately half of all fossils (Morales et al. 1993). The composition of the faunal list (Table 1) indicates a landscape dominated by bushes and low vegetation, with possible small semi-permanent lake. The climate has been inferred as subtropical dry (Morales et al. 1999; Álvarez-Sierra et al. 2006; Oliver & Peláez-Campomanes 2013; Sánchez et al. 2015; Valenciano et al. 2022).

Insert Text-fig. 1. about here

Insert Table 1 about here

1.2. Abbreviations

AD, Arrisdrift collection of the Museum of the Geological Survey of Namibia, Windhoek, Namibia; **AMNH**, American Museum of Natural History, New York, United States of America; **BSPG**, Bayerische Staatssammlung für Paläontologie und Geologie, Munich, Germany; **FSL**, collections of the Université Claude-Bernard Lyon 1, Lyon, France; **GPIT**, Palaeontological collection of the University of Tübingen, Tübingen, Germany; **ICP**, Institut Català de Paleontologia Miquel Crusafont, Universitat Autònoma de Barcelona, Spain; **IPS**, collections from the ICP (formerly Institut de Paleontologia de Sabadell); **IVPP**, Institute of Vertebrate Paleontology and Paleoanthropology, Chinese Academy of Sciences, Beijing, China; **MNCN**, Museo Nacional de Ciencias Naturales, Madrid, Spain; **MNHN**, Muséum National d'Histoire

Naturelle, Paris, France; **MPZ**, collections of the former Museo Paleontológico de la Universidad de Zaragoza, currently housed at the Museo de Ciencias Naturales Universidad de Zaragoza, Zaragoza, Spain; **NMB**, Naturhistorisches Museum Basel, Switzerland; **RET**, La Retama fossil site, Spain; **SMNS**, Staatliches Museum für Naturkunde Stuttgart, Stuttgart, Germany; **SO**, Sables de l'Orléanais fossil site, France.

2. Material and methods

The fossils from La Retama are housed at MNCN, and were described following the anatomical nomenclature of WAIBL et al. (2005) and EVANS & DE LAHUNTA (2010, 2013). Dental nomenclature follows GINSBURG (1999) and SMITH & DODSON (2003). Dental measures were taken using a Mitutoyo digital calliper with a resolution of 0.1 mm. The body weights of these extinct mustelids were inferred using the exponential regression model based on the m1 length by VAN VALKENBURGH (1990). However, it is important to note that the weight values we obtained are overestimated, as often occurs when inferring the body mass of extinct large mustelid from its m1 length (LEGENDRE & ROTH 1988; FORTELIUS 1990; BASKIN 1998).

A computed tomography of the hemimandible of La Retama was conducted at MNCN to be able to describe the non-emerged teeth. We used a NIKON CT-SCAN XT H-160 micro-X-ray computed machine with an X-ray voltage of 105 kV resulting in over 990 images of 1008x1008 pixels and 0.056861 (X, Y, Z) voxels. The images were calibrated to eliminate the background noise with the ImageJ v.1.50e software (PERTUSA 2010; PÉREZ-RAMOS et al. 2020). The segmentation and construction of the three-dimensional (3D) mesh were carried out with the Avizo Lite ® version 9.2 and Geomagic Wrap ® software (3D System, NC, USA).

The comparative sample comprises original fossils of: *Ischyrictis zibethoides* from La Retama (Morales et al. 1993; Fraile et al. 1997), housed at MNCN; from Sansan (MN6, France) (Blainville 1842; Ginsburg 1961; Peigné 2012) housed at MNHN; *Laphictis mustelinus* from Hostalets de Pierola (MN7/8, Spain) (Villalta Comella & Crusafont-Pairó 1943; Petter 1963) housed at ICP; *Iberictis buloti* Ginsburg & Morales, 1992 from els Casots (MN5, Spain) (Valenciano et al. 2020a; Casanovas-Vilar et al. 2022) housed at ICP; *Iberictis azanzae* Ginsburg & Morales, 1992 from Artesilla (MN4, Spain) (Ginsburg & Morales 1992; Valenciano et al. 2020a) housed at MPZ; *Hoplictis helbingi* from Castell de Barberà (MN9, Spain) (Crusafont-Pairó 1972) housed at ICP; *Hoplictis* sp. from Love Bone Bed (Cl2-Hh1, United States) (Baskin 2005) housed at AMNH; and *Namibictis senuti* Morales et al., 1998 from Arrisdrift (Early-Middle Miocene, Namibia) (Morales et al. 1998, 2003) housed at AD. Furthermore, we also studied casts of *I. zibethoides* from Carrières de la Morfassiére (MN5, France) (Ginsburg 2001) housed at MNCN; *Ischyrictis bezianensis* from Pellecahus (MN4, France) (Bulot & Ginsburg 1993) housed at MNCN; *Hoplictis noueli* from Artenay (MN4, France) (Mayet 1908; Helbing 1930) housed at NMB; *Hoplictis florancei* from Pontlevoy-Thenay (MN5, France) (Mayet 1908) housed at MNHN; and *Hoplictis grangerensis* (Bryant, 1968) from Granger Clay Pit (Cl2-Cl3, United States) (Bryant 1968) and from Mixson's Bone Bed (Hh1, United States) (Baskin 2005) housed at AMNH. In addition, we examined photographs of the originals of *I. zibethoides* from Sandelzhausen (MN5, Germany) (Nagel et al. 2009) housed at BSPG; *I. bezianensis* from Baigneaux (MN4, France) (Ginsburg 2002) housed at NMB; *L. mustelinus* from La Grive-Saint-Alban (MN7/8, France) (Viret 1933, 1951; Peigné 2012) housed at FSL, from Steinheim (MN7/8, Germany) (Viret 1933; Helbing 1936; Peigné 2012), housed at SMNS, and from Hammerschmiede 4 (MN7/8, Germany)

(Kargopoulos et al. 2022) housed at GPIT; *Dehmictis vorax* from Wintershof-West (MN3, Germany) (Dehm 1950) housed at BSPG; *Ib. buloti* from Pellecahus (France, MN4) (Ginsburg & Morales 1992) housed at MNHN; *H. helbingi* from La Grive-Saint-Alban (Viret 1951) housed at FSL; *H. florancei* from Erkertshofen 2 (MN4, Germany) (Roth 1989) housed at BSPG; *Hoplictis anatolicus* (Schmidt-Kittler, 1976) from Çandir (MN5-MN6, Turkey) (Schmidt-Kittler 1976) housed at BSPG; and *Hoplictis baihu* Valenciano et al., 2019 from Tieersihababe (MN5-MN6, China) and *Hoplictis* cf. *helbingi* from Duolebulejin (MN7/8, China) (Valenciano et al. 2019) housed at IVPP. Finally, we studied by their original publications *I. zibethoides* from Vieux-Collonges (MN5, France) (Mein 1958); *I. bezianensis* from Bézian (France, MN4) (Ginsburg & Bulot 1982); *Ischyrictis* cf. *bezianensis* from Quinta de Farinheira (MN5, Portugal) (Ginsburg & Antunes 1995); *L. mustelinus* from Vieux-Collonges (Mein 1958) and from Erkertshofen 2 (Roth 1989).

3. Systematic palaeontology

Order Carnivora Bowdich, 1821

Family Mustelidae Batsch, 1788

Subfamily Guloninae Gray, 1825

Diagnosis. In Ginsburg (1999, p.124): Mustelidae larger than Mustelinae, with tendency of M1 to enlarge.

Emended diagnosis. Mustelidae larger than Mustelinae; males with enlarged and straight sagittal crest (contrary to Melinae and Mellivorinae, which are convex), with the external occipital protuberance surpassing the occipital condyles; P3 elongated; tendency of M1 lingual platform to enlarge, and presence of a slender buccolingual crista in the M1 extending from the paracone to the protocone; m1 with medium-sized metaconid in the older species, and tendency of a subquadrangular talonid with a buccally-placed hypoconid and a shallow valley.

Included genera. *Gulo* PALLAS, 1780, *Martes* PINEL, 1792, *Pekania* GRAY, 1865, *Charronia* POCOCK, 1941, *Dehmictis* GINSBURG & MORALES, 1992, *Iberictis* GINSBURG & MORALES, 1992, *Ischyrictis* HELBING, 1930, *Laphictis* VIRET, 1933, *Plesiogulo* ZDANSKY, 1924, *Paramartes* KRETZOI, 1952, *Legionarictis* TSENG et al., 2009.

Remarks. GINSBURG (1999) excluded all species of *Martes* from this subfamily (placing them within Mustelinae), while including the extinct *Trochictis*, *Hoplictis* and *Eomellivora* ZDANSKY, 1924 (=*Hadrictis*). However, DNA-based phylogenetic studies (e.g., SATO et al. 2003; LI et al. 2014) have identified the extant *Gulo*, *Martes*, *Pekania*, and *Charronia* as a monophyletic group, thereby placing all these genera within Guloninae. The Late Miocene *Circamustela* PETTER, 1967 has also been proposed for inclusion in Guloninae (VALENCIANO et al. 2020b; KARGOPOULOS et al. 2022). Nevertheless, *Eomellivora* and *Hoplictis* have recently been reclassified as Mellivorinae (VALENCIANO et al. 2015, 2017, 2020a), while the inclusion in Guloninae of *Trochictis* and *Circamustela* remains unresolved. Given the high level of polymorphism observed in the Miocene *Martes*-like early taxa, comparable with the highly polymorphic dentition of extant Guloninae and the scarcity of fossil materials, a detailed revision is required to fully understand their taxonomic position (SAMUELS et al. 2018).

Genus *Ischyrictis* HELBING, 1930

Type species: *Ischyrictis zibethoides* (BLAINVILLE, 1842)

Type locality: Sansan (France), Middle Miocene (MN6).

Other species: *Ischyrictis bezianensis* GINSBURG & BULOT, 1982

Diagnosis. HELBING (1930, p.644) proposed the diagnosis of the genus *Ischyrictis* based on species currently classified in different genera, in particular in the sample from Artenay, now considered as *Hoplictis noueli*.

Emended diagnosis: Medium to large sized Guloninae; P1 present; P4 with moderately-sized protocone placed in line with a poorly-developed parastyle; M1 with non-reduced metacone; presence of metaconule variable, when present it has an enlarged cingulum surrounding it; protocone mesially positioned, round lingual platform with moderate mesiodistal expansion, and presence of hypocone variable; p1 present; p4 with well-developed distal accessory cuspid; m1 with protoconid taller than paraconid and including a prominent metaconid; talonid moderately wide and comprising one third of the total length of the tooth; well-developed and labially placed hypoconid, and well-developed entocristid surrounding a shallow talonid basin; m2 subquadrangular with protoconid, metaconid and hypoconid.

Differential diagnosis: *Ischyrictis* differs from *Hoplictis* in having a relatively shorter P4 with a more robust protocone, a M1 with a non-reduced metacone, a metaconule (variable), and a more developed lingual platform. The m1 has a more developed metaconid, a more robust talonid with a smaller hypoconid placed in labial position and non-imbricated toward the protoconid. It differs from *Laphictis* in having a P4 with a less robust protocone and parastyle, a smaller lingual platform on the M1, a shorter p3 and p4, a less massive m1 metaconid and a shorter and slenderer m1 talonid with both smaller hypoconid and entocristid. It differs from *Iberictis* in a larger size, in lacking a P4 lingual platform, in a much smaller and rounded M1 lingual platform with no postprotocrista. Regarding lower dentition, it differs in the possession of accessory cuspids in p3 and p4, and slenderer cingulids and cristids in their premolars, and m1 with a reduced metaconid and hypoconid, and a more reduced m2 talonid. It also differs from *Dehmictis* in being larger in size, with a relatively buccolingually wider M1 with a more conical protocone and a more reduced and rounded lingual platform. Additionally, it has a larger and more developed distal accessory cusp in the p4, and a taller crown of the m1 with both a smaller metaconid and talonid.

Ischyrictis zibethoides (Blainville, 1842)

Lectotype: Sa 373, fragmentary right hemimandible with p4-m1 (Peigné 2012)

Type locality: Sansan (France), Middle Miocene (MN6).

Other localities: Vieux-Collonges (MN5, France), Carrières de la Morfassiére (MN5, France), Faluns d'Anjou (MN5, France), Sandelzhausen (MN5, Germany), La Retama (MN5, Spain).

Age: Middle Miocene, MN5 – MN6.

Emended diagnosis: *Ischyrictis* of large size; M1 with thick crista from the paracone to the parastylar area; metaconule variable, when present it has an enlarged cingulum surrounded it; lingual platform with moderate mesiodistal expansion and hypocone absent; m1 talonid narrower than the protoconid-metaconid width.

Studied material from La Retama: RET-1501, skull with left P3-M1; RET-220, right P4; RET-818, left M1; RET-1502, right M1; RET-712, left hemimandible with c and p3-m1; RET-558, right m1. The MNI (minimum number of individuals) is 2, based on the two left M1s.

Description: RET-1501 is an incomplete and slightly deformed cranium that retains part of the nasal, frontal, parietal and maxillary bones (Plate 1, Fig. 1 to 5). The nasal bones are wide, and the frontal bone exhibits very robust temporal ridges and thick and prominent zygomatic processes like in extant large mustelids. The temporal ridges converge at the rostral end of the sagittal crest, which is very prominent (Plate 1, Fig. 2).

The large size of the sagittal crest suggests that the cranium could have belonged to an adult male, as both extant and extinct mustelids show sexual dimorphism in this trait anatomical trait, which also grows in size during the ontogeny (LARIVIÈRE & JENNINGS 2009; LAW et al. 2016; NOONAN et al. 2016; LAW & MEHTA 2018). Neither of the parietal bones are complete, although a larger portion of the left one has been preserved. The parietal bones and the sagittal crest have a rough texture due to the temporal muscle insertion. Sediment covers the ventral side of the cranium, except for the palate and the caudal ends of the maxillary bones (Plate 1, Fig. 3). The right maxillary preserves the P3 alveolus, while the left maxillary has nearly complete P3, P4 and M1. The P3 (Plate 1, Fig. 3 and 6) is fragmented at its main cusp and widened at its length midpoint. Additionally, it has a distal cingulum larger than its mesial one. The P4 (Plate 1, Fig. 3 and 6) has a triangular shape, and its paracone is broken at its base due to a fracture that also affects the mesial end of the metastyle. Furthermore, the P4 also has a lingually-projected protocone placed in situ (Plate 1, Fig. 7). It also has a small parastyle, and a robust cingulum that encircles the teeth in all of it buccal length. The M1 (Plate 1, Fig. 3 and 6) is nearly the same size as the P4. The paracone (which shows signs of wearing in its apex) is slightly larger than the metacone, and they are connected by a crista. Two cristae run from the paracone to the parastylar area, and the trigone basin shows a circular wear caused by the occlusion with the m1 hypoconid (Plate 1, Fig. 7). The metaconule is absent. The protocone is pyramidal and has a mesial position. The M1 also has a moderately-developed lingual platform. Sings of wearing can be seen in the mesial region of the tooth and in the protoconule zone. The M1 is narrowest at its midpoint, having an approximate an "8" shape, which is a common trait in mustelids. The P4 RET-220 (Plate 1, Fig. 8 to 10) is shorter than the P4 of the cranium and shows a significant wear across the entire occlusal area. This P4 has lost its protocone, but it retains the paracone and the parastyle, which is formed by a low and robust cingulum. The M1 RET-1502 (Plate 1, Fig. 11 and 12) and the M1 RET-818 (Plate 1, Fig. 13 and 14) are fragmented and only retain the lingual platform, the protocone and the protoconule, united by the preprotocrista.

The specimen RET-712 (Plate 2, Fig. 1 to 3) consists of an incomplete left hemimandible that has lost the mandibular symphysis as well as the coronoid, condylar and angular processes. This hemimandible belonged to a juvenile individual that had not yet reached sexual maturity, as not all pieces of the definitive dentition had emerged at the time of death. The c and the m1 were going through the eruption process, while the dp4 (lower decidual carnassial) is the only remaining tooth of the deciduous dentition. The p3 and p4 are not visible, but their morphology can be observed through the micro-computerized tomography (Plate 2, Fig. 4 to 9). The dp4 and p4 are affected by a significant fracture that split both of them. The c has longitudinal grooves from the apex to the base of the crown, and is distally deformed. The p3 (Plate 2, Fig. 7 to 9) is long and almost quadrangular, maintaining a constant width along its entire length. It only has a prominent main cuspid, and its mesial and distal cingulids are of similar size. The p4 (Plate 2, Fig. 7 to 9) has a main cuspid and a well-developed distal accessory cuspid located near the buccal edge of the tooth. Additionally, it is mesially fragmented. The m1 (Plate 2, Fig. 7 to 9) is labio-lingually compressed, with its trigonid being two-thirds longer than the talonid. The protoconid is the tallest cuspid, while the metaconid is shorter, sharp and situated slightly distal to the protoconid. The carnassial notch is partially filled by sediment. The talonid has a hypoconid, that is similar in height to the metaconid, and also has a hypoconulid that is more reduced in size and is placed in a distal position. The metaconid and the hypoconulid are lingually connected by an entrocristid, forming a shallow talonid basin. The dp4 (Plate 2, Fig. 4 to 6) is also fragmented, but it preserves the paraconid (with a buccal wear facet) and a low hypoconid. In occlusal view, it has a sigmoid shape. The right m1 RET-558 (Plate 2, Fig. 10 to 13) only retains the trigonid, which shows a buccal wearing facet. Table 2 shows the length and width of all the teeth from La Retama.

Ischyrictis bezianensis GINSBURG & BULOT, 1982

Holotype: Be 7545, right M1.

Type locality: Bézian (France), Early Miocene (MN4).

Other localities: Baigneaux (MN4, France), Pellecahus (MN4, France).

Age: Early Miocene, MN4.

Diagnosis: In GINSBURG & BULOT (1982, p. 63).

Emended diagnosis: *Ischyrictis* smaller than *I. zibethoides* and similar in size to the living *Pekania pennanti*; M1 mesiodistally longer with more rectilinear mesial and distal walls than *I. zibethoides*, and with an additional distolingual cusp close to the protocone (hypocone after GINSBURG & BULOT 1982); m1 talonid relatively broader with a smaller hypoconid than *I. zibethoides*.

Remarks: *Ischyrictis bezianensis* was first described by GINSBURG & BULOT (1982) based on an almost complete right M1 from Bézian (MN4, France) which presents differential traits with *I. zibethoides*. Subsequently, BULOT & GINSBURG (1993) mention the species in the Early Miocene locality of Pellecahus (MN4, France). GINSBURG (2002) reported the species in the locality of Baigneaux (MN4, France) based on a left fragmentary hemimandible (SO 4095), providing its measurements but no descriptions. Interestingly, GINSBURG & ANTUNES (1995), published a fragmentary hemimandible with a broken m1, as well as scarce postcranial remains of *I.* cf. *bezianensis* in three Portuguese localities from the Middle Miocene (MN5). They compared it with *I.*

bezianensis from Pellecahus and *I. zibethoides* from Sansan. Based on the pictured m1 from GINSBURG & ANTUNES (1995), the m1 talonid from Quinta de Farinheira seems to be wider than the ones from Sansan and La Retama, being more similar to the one from Baigneaux, but much larger in size to that of the specimens from Baigneaux and from Pellecahus. When GINSBURG & ANTUNES (1995) described the Portuguese material the intraspecific variability of *I. zibethoides* was less known, as the sample from Sandelzhausen was not published yet. According to its length and width proportions, it fits better as *I.* cf. *zibethoides*, as it falls within the known variability range of *I. zibethoides*, suggesting a possible relationship with this species rather than with *I. bezianensis*. This may suggest that La Retama is not the only record of *I. zibethoides* in the Iberian Peninsula, but a more detailed study of the morphology of the m1 from Quinta de Farinheira is necessary to confirm its suitable identity.

Description of the material from Baigneaux: The hemimandible SO 4095 (Text-fig. 2A, 2B) preserves a worn p4 and m1, along with the most rostral part of the masseteric fossa. The p4 has a well-developed accessory distal cuspid, with both the main and the accessory cuspid showing wear patterns. The m1 is also worn (Text-fig. 2C) and has a well-developed metaconid. The talonid represents one third of the total length of the molar. The tooth is relatively broad, being almost as wide as the protoconid-metaconid complex throughout the whole talonid. The hypoconid and entocristid are not observable. Table 2 shows the measurements of the teeth (GINSBURG 2002).

Insert Text-fig. 2 about here.

Insert Table 2 about here.

4. Discussion

In general, the tooth measurements from La Retama fall within the range of variability of the populations of *Ischyrictis zibethoides* from Sansan and Sandelzhausen. The P4 from La Retama (Text-fig. 3A) is situated closer to the lower end of the variability range, similar to the smaller individuals of this species. The M1 (Text-fig. 3B) differs from most of the Sansan values, instead being closer in size to the individuals from Sandelzhausen and Carrières de la Morfassiére. The p4 (Text-fig. 4A) has the smallest length and width of all the p4s assigned to *I. zibethoides*. It is important to note that the tooth is unerupted, and the 3D model indicates a mesial fracture on the p4. Therefore, the dimensions provided are only approximate. The m1 (Text-fig. 4B) falls within the range of variability of *I. zibethoides,* although it is among the most gracile specimens of the species. The sample from Sansan has a wider range in the m1 proportions than the sample from Sandelzhausen. PEIGNÉ (2012) explained this difference as a possible case of sexual dimorphism, as occurs in extant mustelids (GITTLEMAN & VAN VALKENBURGH 1997). The length of P3 in La Retama is shorter than in Sansan (Text-fig. 5A), and the ratio of P3/P4 lengths is also lower in La Retama than in Sansan. The ratio of p4/m1 lengths in La Retama (Text-fig. 5B) is slightly different from that in the other *I. zibethoides* populations. The scarcity of available data from other fossil sites where *I. zibethoides* has been cited (Vieux-Collonges and Carrières de la Morfassiére) means that metric and morphological comparisons with these sites are not significant. Morphologically, the dentition from La Retama fits the diagnosis of the genus *Ischyrictis* and is most similar to *Ischyrictis zibethoides*, while differing from *I. bezianensis* in its size and in all the features that characterise the smaller species. The fossils from La Retama are closer in size those from the German site, which is consistent with La Retama and Sandelzhausen belonging to the same biozone (MN5), and both being older than Sansan (MN6). Although the sample from la Retama is too limited to give a reliable interpretation, it may suggest that the population of *I. zibethoides* had more hypercarnivorous traits than the French and German samples (NAGEL et al. 2009; PEIGNÉ et al. 2012), but not as hypercarnivorous as those present in some species of the genus *Hoplictis* (*H. florancei* and *H. helbingi*). Instead, it is comparable to the traits exhibited in the older *Hoplictis noueli* from Artenay.

Insert Text-fig. 3. about here.

Insert Text-fig. 4. about here.

Insert Text-fig. 5 about here.

With regards to *I. bezianensis*, both the M1 from Bézian (Plate 4, Fig. 1) and the hemimandible from Baigneaux (Text-fig. 2) clearly differ from *I. zibethoides*. This is evident from the presence of a M1 hypocone and a broader m1 talonid. The width of the M1 from Bézian (holotype) is estimated and falls within the variability range of *I. zibethoides*, similar to the M1 from La Retama and Sandelzhausen (Text-fig. 3B). However, the p4 and m1 of *I. bezianensis* from Baigneaux (Text-fig. 4) are significantly smaller than the dentition of *I. zibethoides*. The m1 from Quinta de Farinheira assigned to *I.* cf. *bezianensis* falls within the variability range of *I. zibethoides* (Text-fig. 4B), suggesting that it could be reassigned to *I.* cf. *zibethoides*. However, a detailed analysis of this specimen should be carried out to reach a more definitive conclusion.

The morphological variability in the dentition of *I. zibethoides* has also been recognised by other authors (NAGEL et al. 2009; PEIGNÉ 2012). NAGEL et al. (2009) identified variability in the dentition of *I. zibethoides* from Sandelzhausen and described two morphotypes of the m1 talonid. In our comparisons, we find that there are indeed some forms with a robust talonid, an enlarged entocristid, and a more buccally positioned hypoconid (BSPG 1959 II 8039, 8047 and 8042; Plate 3, Figs. 7 and 8), while others have a slenderer talonid and a lingual flexo at the level of the metaconid (BSPG 1959 II 8041, 8038 and 8040; Plate 3, Figs. 6, 9, 10 and 11). These two morphotypes also occur in Sansan, with the broader one identified as MNHN Sa 15517 (Plate 3, Figs. 3 and 12) and the slender one as MNHN Sa 375 (Plate 3, Fig. 13). The m1 RET-712 from La Retama (Plate 3, Fig. 14) fits into the slender talonid morphotype (Plate 3, Fig. 14), even having a more advanced degree of slenderness. Furthermore, we observed additional variability in the M1s of Sansan and Sandelzhausen (Plate 3), distinguishing two morphotypes: one with a metaconule and a robust cingulum surrounding it (MNHN Sa 15519 and BSPG 1959 II 8044; Plate 3, Figs. 15 and 18), and another lacking the metaconule and cingulum in this area (MNHN Sa 4677 and BSPG 1959 II 8072; Plate 3, Figs. 16 and 19). The M1 from La Retama (Plate 1, Fig. 3 and 6) and that from Carrières de la Morfassiére (Plate 3, Fig. 20) exhibit the morphotype without metaconule. Another variable feature of *I. zibethoides* is the presence of a rudimentary distal accessory cuspid in the p3, which is present only in some specimens from Sansan (Plate 3, Figs. 1 to 3), as noted by Peigné (2012), but is absent in the p3 of the hemimandible RET-712.

Insert Table 3 about here.

The occurrence of *Ischyrictis zibethoides* from La Retama and the classification of the material from Portugal as *Ischyrictis* cf. *zibethoides* (previously classified as *I.* cf. *bezianensis*) indicate that it was widespread in Western Europe during the Middle Miocene. Relatively close genera such as *Dehmictis*, *Hoplictis*, *Laphictis* and *Iberictis* (see Valenciano & Govender 2020; Valenciano et al. 2020a; Plate 4) occur in European fossil sites of the same age and later spread to Eastern Europe (Pickford et al. 2000), and Asia (Schdmidt-Kittler 1976; Valenciano et al. 2019). However, coexistence between species of these genera is rare. For instance, *Iberictis buloti* and

Ischyrictis bezianensis were found together in Pellecahus (Ginsburg & Bulot 2000), *Laphictis mustelinus* and *Hoplictis florancei* in Erkertshofen-2 (Roth 1989), *Hoplictis florancei* and *Ischyrictis zibethoides* in Faluns d'Anjou and Touraine (Ginsburg 1989) and Faluns de Savigné-sur-Lathan (Ginsburg 2001), *Laphictis mustelinus* and *Hoplictis helbingi* in La Grive (Viret 1933, 1951). This diversity of large mustelids (more than 10 kg) can be considered a characteristic of Middle Miocene carnivoran associations in Europe. The estimated weight range for these species (Table 3) places them in the category of medium-size carnivorans (10-60 kg following Viranta 2003), but within the family Mustelidae they would occupy the highest values, close to the extant *Gulo gulo*. The only exception would be *Hoplictis helbingi*, which surpasses all terrestrial mustelids in size. Overall, the dentition of this group shows unreduced premolars, with low-crowned lower carnassials, with robust trigonid and functional talonid, while the P4 tends to reinforce the paracone-metastyle cutting blade, while retaining a strong protocone. These features are congruent with a mesocarnivorous dentition model defined by Crusafont-Pairó & Truyols-Santonja (1956). Close to the Middle-Late Miocene boundary, these forms nearly disappear (only *Hoplictis helbingi* survives at Castell de Barberá in the Vallès-Penedès Basin), coinciding with the appearance of the first species of *Eomellivora* (Valenciano et al. 2019; Alba et al. 2022; Kargopoulos et al. 2022). It is possible that this group of mustelids played a role analogous to that of the Canidae in North American faunas before the Late Miocene, as they share the mesocarnivorous dental adaptations, whereas in Europe this role was shared by Mustelidae and Hyaenidae (Viranta 2003). However, other medium-to-large-sized mustelids of uncertain affinities but morphologically similar to extant Guloninae were present in North America during that period. Among these stand out *Sthenictis* spp. (e.g., *Sthenictis lacota* from Cañón of Little White, Claredonian, South Dakota in

MATTHEW & GIDLEY [1904], *Sthenictis dolichops* from Sheep Creek, Hemingfordian-Barstovian, Nebraska in MATTHEW [1932], and the undescribed *Sthenictis* sp. AMNH F:AM 25235 from the Burge Fauna of Nebraska, Early Clarendonian, ca. 12 Ma), as well as the marten-sized *Dinogale siouxensis* from Stonehouse Draw, Later Hemingfordian (equivalent to the European MN4-5), Nebraska (COOK & MACDONALD 1962). In VALENCIANO & GOVENDER (2020), VALENCIANO et al. (2020a) and VALENCIANO & BASKIN (2022) *Sthenictis* sp. (AMNHN F:AM 25325) is discussed. The relationship between this species and the crown clade of Guloninae remains unresolved, but it is nested with other Middle Miocene mustelids of large size from Europe (*Ischyrictis zibethoides* and *Laphictis mustelinus*). Consequently, further investigation into the systematic and paleobiology of these North American forms is required in order to substantiate this hypothesis.

Insert Text-fig. 6. about here.

During the end of the Middle Miocene in Europe, a general increase in size and diversity was observed within the Hyaenidae family (e.g., GINSBURG 1999; ROBLES 2014; MORALES et al. 2015) (Text-fig. 6), which could have contributed to the decline of these large Middle Miocene mustelids.

5. Conclusions

The discovery of *Ischyrictis zibethoides* in the Iberian Peninsula extends the geographical range of this species. This finding suggests that large mustelids were common elements in the faunal associations of Europe during the Middle Miocene. The *Ischyrictis* genus consist of two species*:* *I. zibethoides* and *I. bezianensis*. They share a dental morphology similar to other large mustelids weighing over 10 kg, such as *Iberictis*, *Laphictis*, and *Hoplictis*. Although a thorough review of the phylogenetic relationships of this group is necessary, its species may have played similar ecological roles. During the Middle Miocene, these large-sized mustelids would have occupied the mesocarnivore niche in the European carnivore associations, which in North America was shared by mustelids and canids. The increase in size and diversity of the Hyaenidae family since the end of the Middle Miocene (MN 7/8) may have caused the decline of these large mustelids.

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Text-figures captions

Text-fig. 1. Geographical and geological context of La Retama fossil site within the Intermediate Basin; modified from SÁNCHEZ et al. (2015).

Text-fig. 2. Fossils and casts of *Ischyrictis bezianensis* from Baigneaux. A. Left hemimandible SO 4095 from Baigneaux, buccal view. B. Left hemimandible SO 4095 from Baigneaux, lingual view. C. Left hemimandible SO 4095 from Baigneaux, occlusal view. All figures use the same scale (10 mm).

Text-fig. 3. Bivariate plot of the logarithmic values of length (L) and width (W) of the P4 (A) and M1 (B) of selected large-sized mustelids from the Early and Middle Miocene. *Ischyrictis* cf. *bezianensis* from Quinta de Farinheira is listed as *I.* cf. *zibethoides*. Values given in mm. The ellipse indicates the variability range of published *Ischyrictis zibethoides*. Metric data from: VIRET (1933, 1951); VILLALTA COMELLA & CRUSAFONT-PAIRÓ (1943); DEHM (1950); MEIN (1958); SCHMIDT-KITTLER (1976); GINSBURG & BULOT (1982); BULOT & GINSBURG (1993); NAGEL et al. (2009); PEIGNÉ (2012); VALENCIANO et al. (2020a); KARGOPOULOS et al. (2022).

Text-fig. 4. Bivariate plot of the logarithmic values of length (L) and width (W) of the p4 (A) and m1 (B) of selected large-sized mustelids from the Early and Middle Miocene. *Ischyrictis* cf. *bezianensis* from Quinta de Farinheira is listed as *I.* cf. *zibethoides*. Values given in mm. The ellipse indicates the variability range of published *Ischyrictis zibethoides*. Metric data from: MAYET (1908); HELBING (1930); VIRET (1933); VILLALTA COMELLA & CRUSAFONT-PAIRÓ (1943); DEHM (1950); MEIN (1958); BRYANT (1968); CRUSAFONT-PAIRÓ (1972); SCHMIDT-KITTLER (1976); ROTH (1989); BULOT & GINSBURG (1993); GINSBURG & ANTUNES (1995); GINSBURG (2002); MORALES et al. (2003); BASKIN (2005); NAGEL et al. (2009); PEIGNÉ (2012); VALENCIANO et al. (2019, 2020a).

Text-fig. 5. Bivariate plot of the logarithmic values of length (L) of the P3-P4 (A) and of the p4-m1 (B) of selected large-sized mustelids from the Early and Middle Miocene. *Ischyrictis* cf. *bezianensis* from Quinta de Farinheira is listed as *I.* cf. *zibethoides*. Values given in mm. The ellipse indicates the variability range of published *Ischyrictis zibethoides*. Metric data from: MAYET (1908); HELBING (1930); VIRET (1933); VILLALTA COMELLA & CRUSAFONT-PAIRÓ (1943); DEHM (1950); MEIN (1958); BRYANT (1968); CRUSAFONT-PAIRÓ (1972); SCHMIDT-KITTLER (1976); ROTH (1989); GINSBURG & ANTUNES (1995); GINSBURG (2002); MORALES et al. (2003); BASKIN (2005); NAGEL et al. (2009); PEIGNÉ (2012); VALENCIANO et al. (2019, 2020a).

Text-fig. 6. Biochronological distribution of the European Middle and Late Miocene medium and large-sized mustelids (red) and hyaenids (green). The hyaenid-like viverrid *Semigenetta grandis* is also included with the hyaenids. The light blue bar indicates the transition between the end of the Middle Miocene (Aragonian, MN7/8) and the beginning of the Late Miocene (Vallesian, MN9). ELMA (European Land Mammal Ages) and MN (Mammal Neogene units) are based on HILGEN et al. (2012) and MORALES et al. (2013). Sources for the biochronological distribution of the different taxa: GINSBURG et al. (1981), ROBLES (2014), MORALES et al. (2015), and references in this work.

Plates 1-4 and explanation of plates

Plate 1

Fig. 1.	Cranium RET-1501 of *Ischyrictis zibethoides* from La Retama; dorsal view.
Fig. 2.	Ditto; left lateral view.
Fig. 3.	Ditto; occlusal view.
Fig. 4.	Ditto; rostral view.
Fig. 5.	Ditto; caudal view
Fig. 6.	Ditto; occlusal view obtained by CT scan (stereo pair).
Fig. 7.	Ditto; dorsal plane view at the level of the roots, showing that the P4 protocone root is not displaced and confirming the measurement of the P4 width.
Fig. 8.	Right P4 RET-220 of *Ischyrictis zibethoides* from La Retama; buccal view.
Fig. 9.	Ditto; lingual view.
Fig. 10.	Ditto; occlusal view.

Fig. 11. Right M1 RET-1502 of *Ischyrictis zibethoides* from La Retama; occlusal view.

Fig. 12. Ditto; anterior view.

Fig. 13. Left M1 RET-818 of *Ischyrictis zibethoides* from La Retama; occlusal view.

Fig. 14. Ditto; anterior view.

Fig. 1 – 5 use the same scale (10 mm). Fig. 6 – 14 use the same scale (10 mm).

Plate 2

Fig. 1. Left hemimandible RET-712 of *Ischyrictis zibethoides* from La Retama; buccal view.

Fig. 2. Ditto; lingual view.

Fig. 3. Ditto; occlusal view.

Fig. 4. 3D model of RET-712 obtained by CT scan; buccal view.

Fig. 5. Ditto; lingual view.

Fig. 6. Ditto; occlusal view.

Fig. 7. 3D model of RET-712 obtained by CT scan, with both the mandibular bone and deciduous tooth dp4 digitally removed; buccal view.

Fig. 8. Ditto; lingual view.

Fig. 9. Ditto; occlusal view.

Fig. 10. Right m1 RET-558 of *Ischyrictis zibethoides* from La Retama; buccal view.

Fig. 11. Ditto; lingual view.

Fig. 12. Ditto; occlusal view.

Fig. 13. Ditto; distal view.

All Figs. of this Plate use the same scale (10 mm).

Plate 3

Fig. 1. Left hemimandible MNHN Sa 15517 of *Ischyrictis zibethoides* from Sansan; buccal view.

Fig. 2. Ditto; lingual view.

Fig. 3. Ditto; occlusal view.

Fig. 4. Right hemimandible BSPG 1959 II 8041 of *Ischyrictis zibethoides* from Sandelzhausen; buccal view.

Fig. 5. Ditto; lingual view.

Fig. 6. Ditto; occlusal view.

Fig. 7. Right m1 BSPG 1959 II 8039 of *Ischyrictis zibethoides* from Sandelzhausen; occlusal view. Mirrored.

Fig. 8. Right m1 BSPG 1959 II 8037 of *Ischyrictis zibethoides* from Sandelzhausen; occlusal view. Mirrored.

Fig. 9. Right m1 BSPG 1959 II 8041 of *Ischyrictis zibethoides* from Sandelzhausen; occlusal view. Mirrored.

Fig. 10. Left m1 BSPG 1959 II 8038 of *Ischyrictis zibethoides* from Sandelzhausen; occlusal view.

Fig. 11. Left m1 BSPG 1959 II 8040 of *Ischyrictis zibethoides* from Sandelzhausen; occlusal view.

Fig. 12. Left m1 MNHN Sa 15517 of *Ischyrictis zibethoides* from Sansan; occlusal view.

Fig. 13. Right m1 MNHN Sa 375 of *Ischyrictis zibethoides* from Sansan; occlusal view. Mirrored.

Fig. 14. 3D model of left m1 RET-712 of *Ischyrictis zibethoides* from La Retama; occlusal view.

Fig. 15. Right P4 and M1 MNHN Sa 15519 of *Ischyrictis zibethoides* from Sansan, where the arrow points to the M1 metastyle; occlusal view.

Fig. 16. Left M1 MNHN Sa 4677 of *Ischyrictis zibethoides* from Sansan, which lacks a metastyle; occlusal view.

Fig. 17. Left P4 BSPG 1959 II 8044 of *Ischyrictis zibethoides* from Sandelzhausen; occlusal view.

Fig. 18. Right M1 BSPG 1959 II 8044 of *Ischyrictis zibethoides* from Sandelzhausen, where the arrow points to the metastyle; occlusal view.

Fig. 19. Right M1 BSPG 1959 II 8072 of *Ischyrictis zibethoides* from Sandelzhausen; occlusal view.

Fig. 20. Cast of a left M1 of *Ischyrictis zibethoides* from Carrières de la Morfassiére; occlusal view.

Fig. 1 – 14 use the same scale (10 mm). Fig. 15 – 20 use the same scale (10 mm).

Plate 4

Fig. 1. Left M1 Be 7545 of *Ischyrictis bezianensis* from Bézian; occlusal view.

Fig. 2 Left P4 BSPG 1937 II 13727 of *Dehmictis vorax* from Wintershof-West; occlusal view.

Fig. 3. Left M1 BSPG 1937 II 13374 of *Dehmictis vorax* from Wintershof-West; occlusal view.

Fig. 4. Left hemimandible BSPG 1937 II 13300 of *Dehmictis vorax* from Wintershof-West; buccal view.

Fig. 5. Ditto; occlusal view.

Fig. 6. Left P4 and M1 of the holotype of *Iberictis azanzae* from Artesilla; occlusal view.

Fig. 7. Left P4 and M1 (IPS10077) of *Iberictis buloti* from els Casots; occlusal view.

Fig. 8. Right hemimandible MNHN LRM 1044 of *Iberictis buloti* from Pellecahus; buccal view.

Fig. 9. Ditto; occlusal view.

Fig. 10. Right M1 NMB S.O. 5490 of *Hoplictis noueli* from Artenay; occlusal view.

Fig. 11. Right hemimandible NMB S.O. 4078 of *Hoplictis noueli* from Artenay; buccal view.

Fig. 12. Left m1 IPS 33105 of *Hoplictis helbingi* from Castell de Barberà; lingual view.

Fig. 13. Ditto; occlusal view.

Fig. 14. Right P3, P4 and M1 FSL 213784 of *Laphictis mustelinus* from La Grive-Saint-Alban; occlusal view.

Fig. 15. Right hemimandible IPS2043 of *Laphictis mustelinus* from Hostalets de Pierola; lingual view.

All Figs. of this Plate use the same scale (10 mm).

Table captions

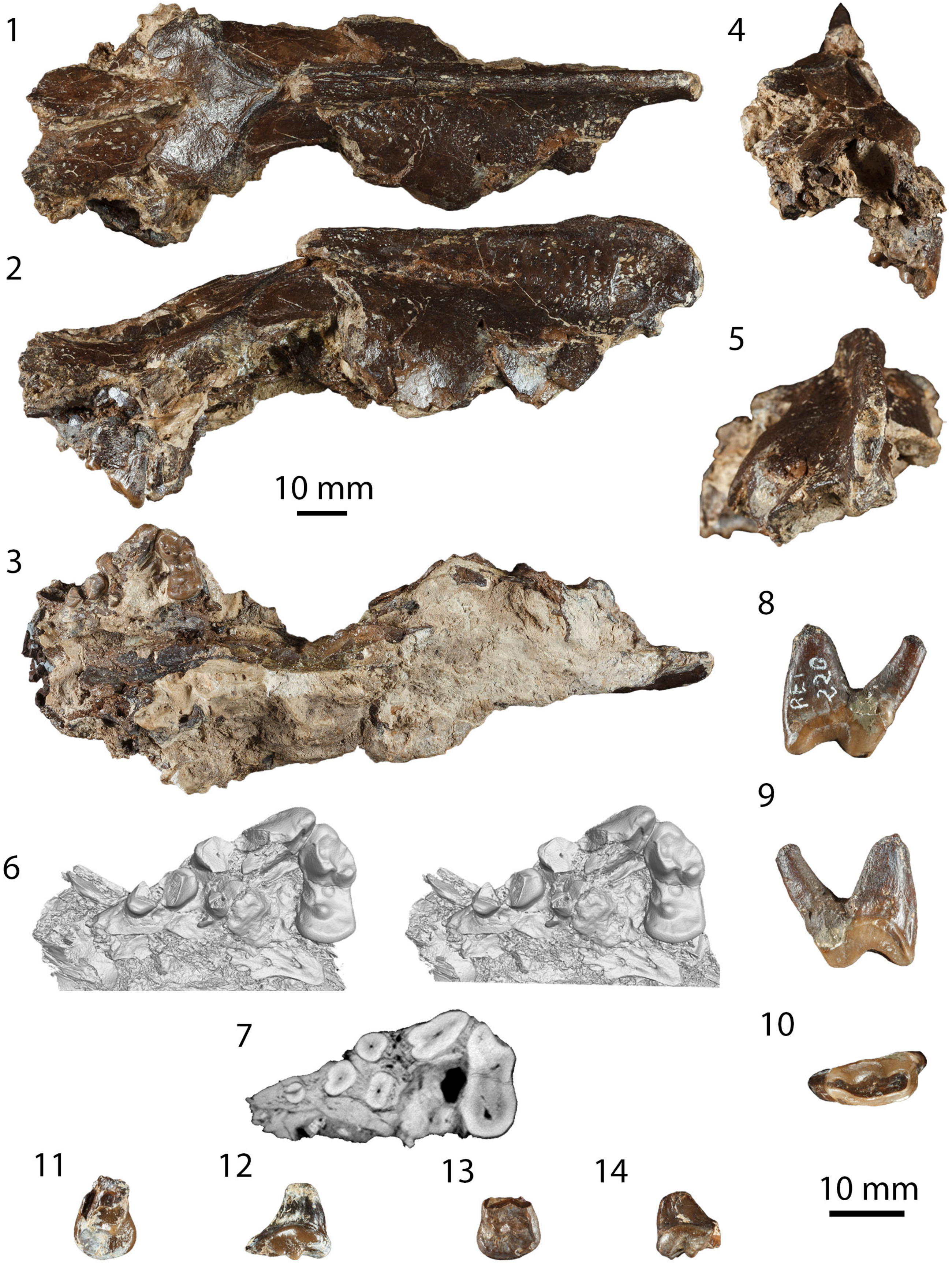
Table 1. Faunal list of La Retama fossil site (Morales et al. 1999; Álvarez-Sierra et al. 2006; Oliver & Peláez-Campomanes 2013; Sánchez et al. 2015; Valenciano et al. 2022).

Table 2. Length (L) and width (W), both given in mm, of the teeth belonging to *Ischyrictis zibethoides* from La Retama and to *Ischyrictis bezianensis* from Baigneaux. Measures of *I. bezianensis* from Ginsburg (2002).

Table 3. Inferred weight based on m1 length of *Ischyritctis zibethoides* and other Early and Middle Miocene mustelids, following the model of Van Valkenburgh (1990). The table includes the range and the mean of both m1 length and inferred weight, alongside the number of specimens whose m1 were taken into account to estimate the weight. *Ischyrictis* cf. *bezianensis* from Quinta de Farinheira is listed as *I.* cf. *zibethoides*. Length values given in mm and weight values given in kg. Metric data of extinct mustelids taken from: Mayet (1908); Helbing (1930); Viret (1933); Villalta Comella & Crusafont-Pairó (1943); Dehm (1950); Mein (1958); Crusafont-Pairó (1972); Schmidt-Kittler (1976); Roth (1989); Ginsburg & Antunes (1995); Ginsburg (2002); Nagel et al. (2009); Peigné (2012); Valenciano et al. (2019, 2020a).

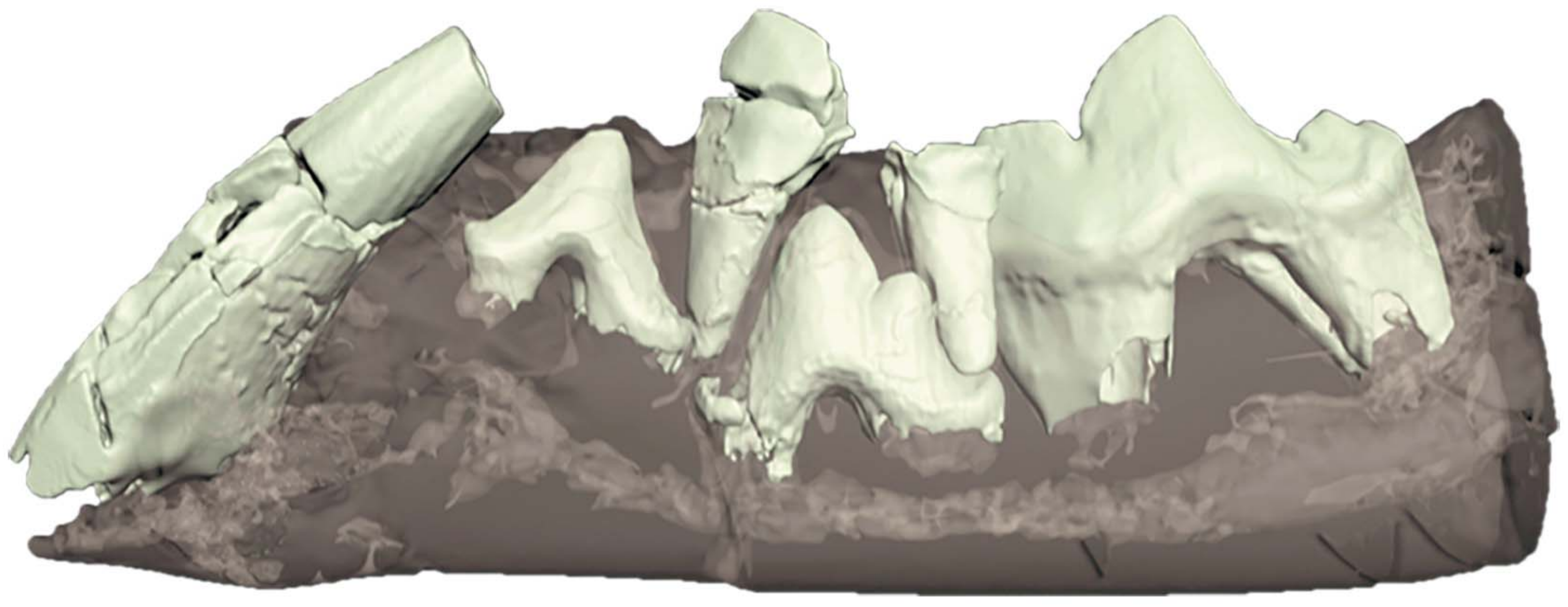
Rodentia	**Chiroptera**
Armantomys aragonensis	*Asellia mariaetheresae*
Armantomys jasperi	*Hipposideros (Brachipposideros) collongensis*
Democricetodon decipiens	*Hipposideros (Pseudorhinolophus)* sp.
Heteroxerus grivensis	*Myotis* sp.
Heteroxerus rubricati	*Tadarida* sp.
Megacricetodon primitivus	**Eulipotyphla**
Megacricetodon vandermeuleni	*Galerix* cf. *symeonidisi*
Microdyromys koenigswaldi	Soricidae indet.
Pseudodryomys ibericus	**Artiodactyla**
Pseudodryomys simplicidens	*Bunolistriodon lockharti*
Lagomorpha	*Cainotherium miocaenicum*
Lagopsis sp.	*Xenokeryx amidalae*
Carnivora	Cervidae indet.
Amphicyon olissioponensis	**Perissodactyla**
Hemicyon sansaniensis	*Anchitherium castellanum*
Ischyrictis zibethoides	*Hispanotherium matritense*
“*Martes*” sp.	*Lartetotherium sansaniens*
Plithocyon conquense	**Proboscidea**
Protictitherium crassum	*Gomphotherium angustidens*
Pseudaelurus sp.	

	P3		**P4**		**M1**		**p3**		**p4**		**m1**		**dp4**	
	L	**W**	**L**	**W**	**L**	**W**	**L**	**W**	**L**	**W**	**L**	**W**	**L**	**W**
RET-1501	9.1	4.7	15.8	9.4	8.1	15.6								
RET-220			14.1	-										
RET-818					8.6	-								
RET-1502					8.4	-								
RET-712							9.1	3.8	11.4	4.7	18.4	7.3	10.1	-
RET-558											-	6.9		


1
4
2
5
10 mm
3
8
RET 220
9
6
7
10
11
12
13
14
10 mm

1

4



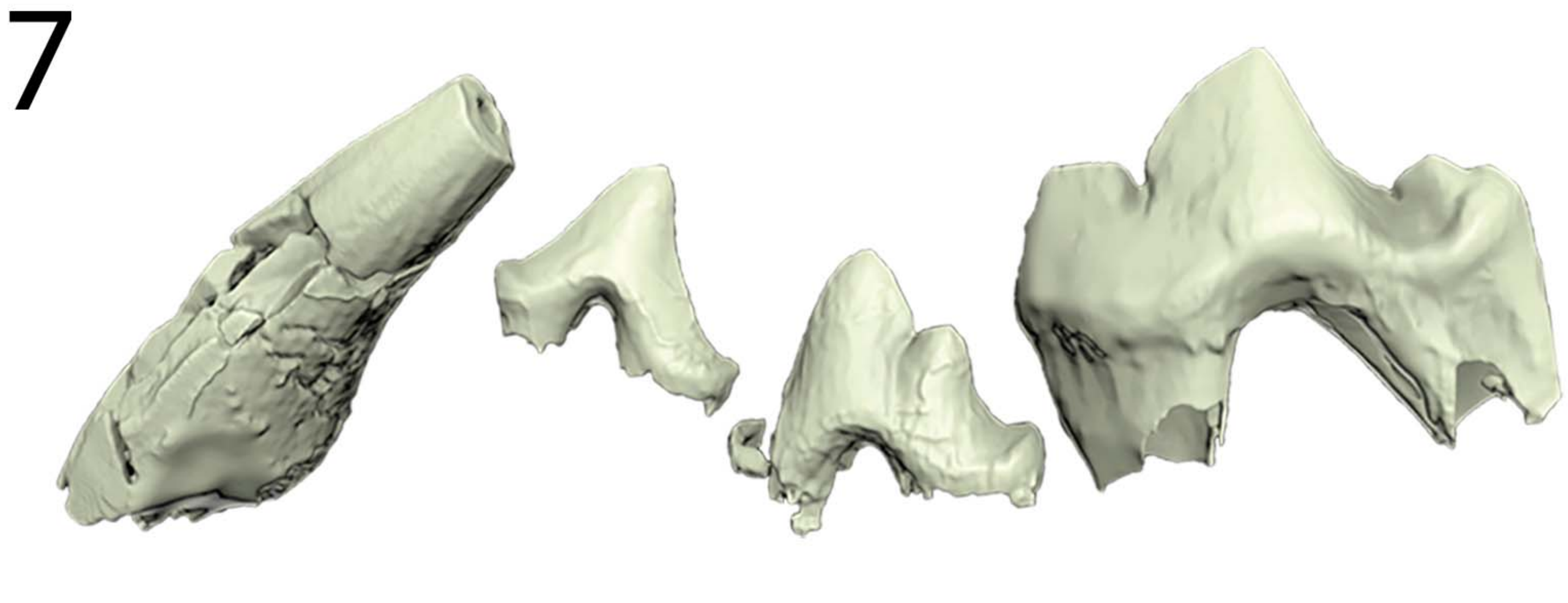
2

5

3

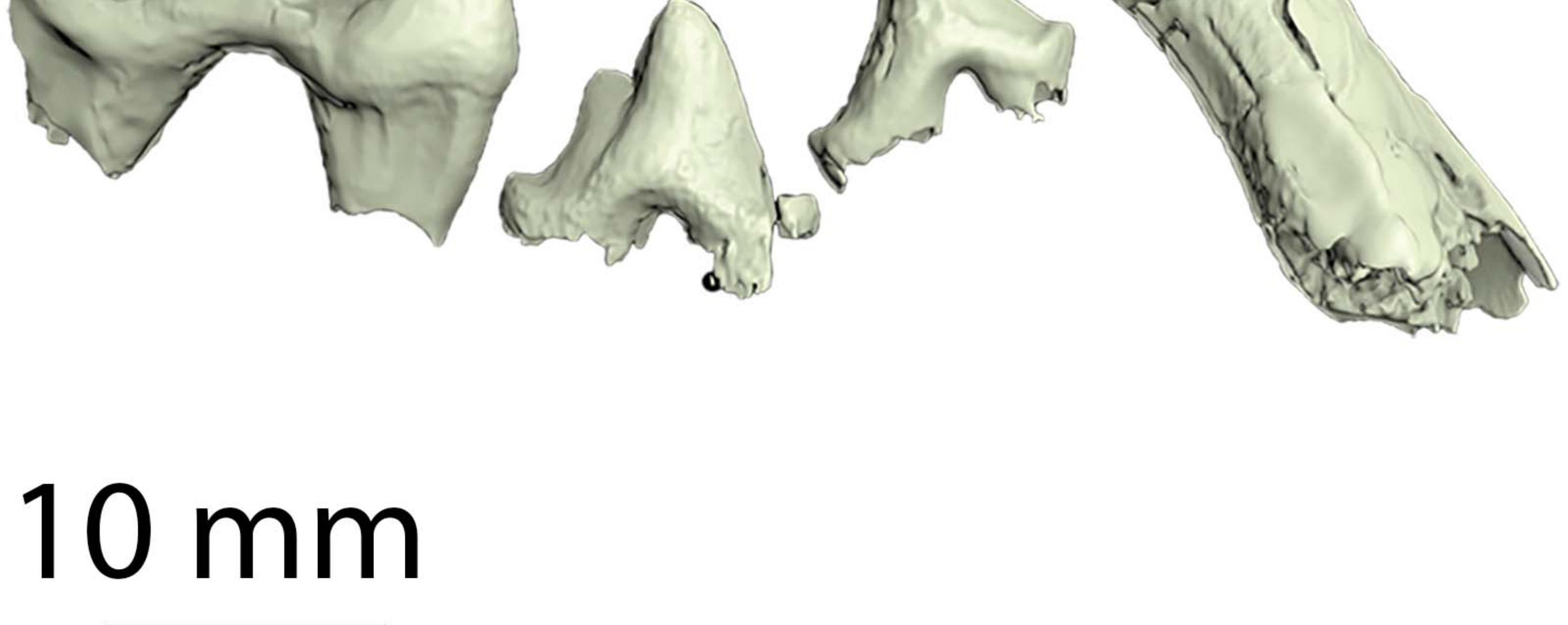
6

7



9

8



10 mm

10

11

12

13

1

2

3

4

5

6

7

8

9

10

11

12

13

14

15

16

17

18

19

20

1

2

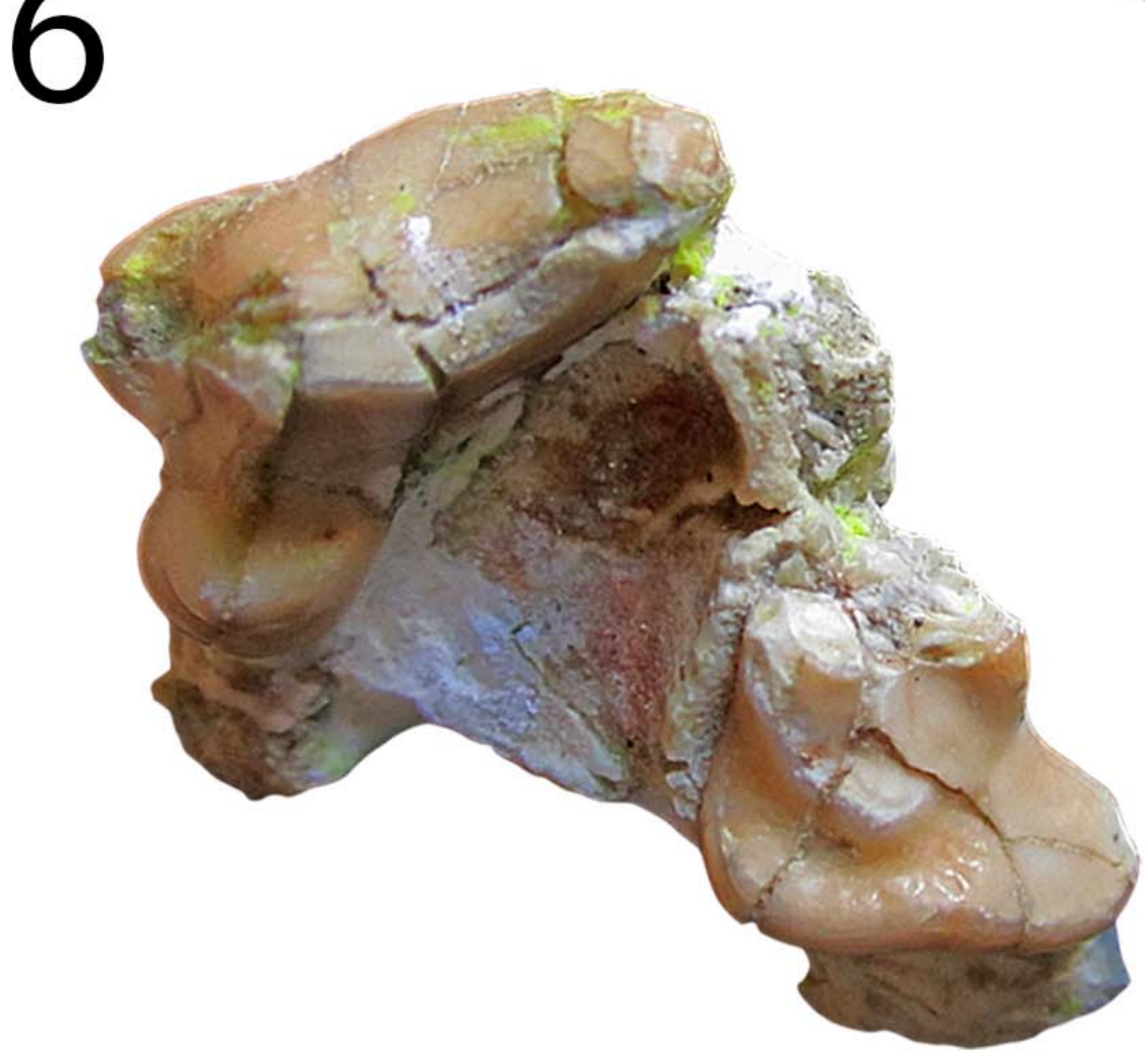
3

4

5

7

6



8

9

10

11

10 mm

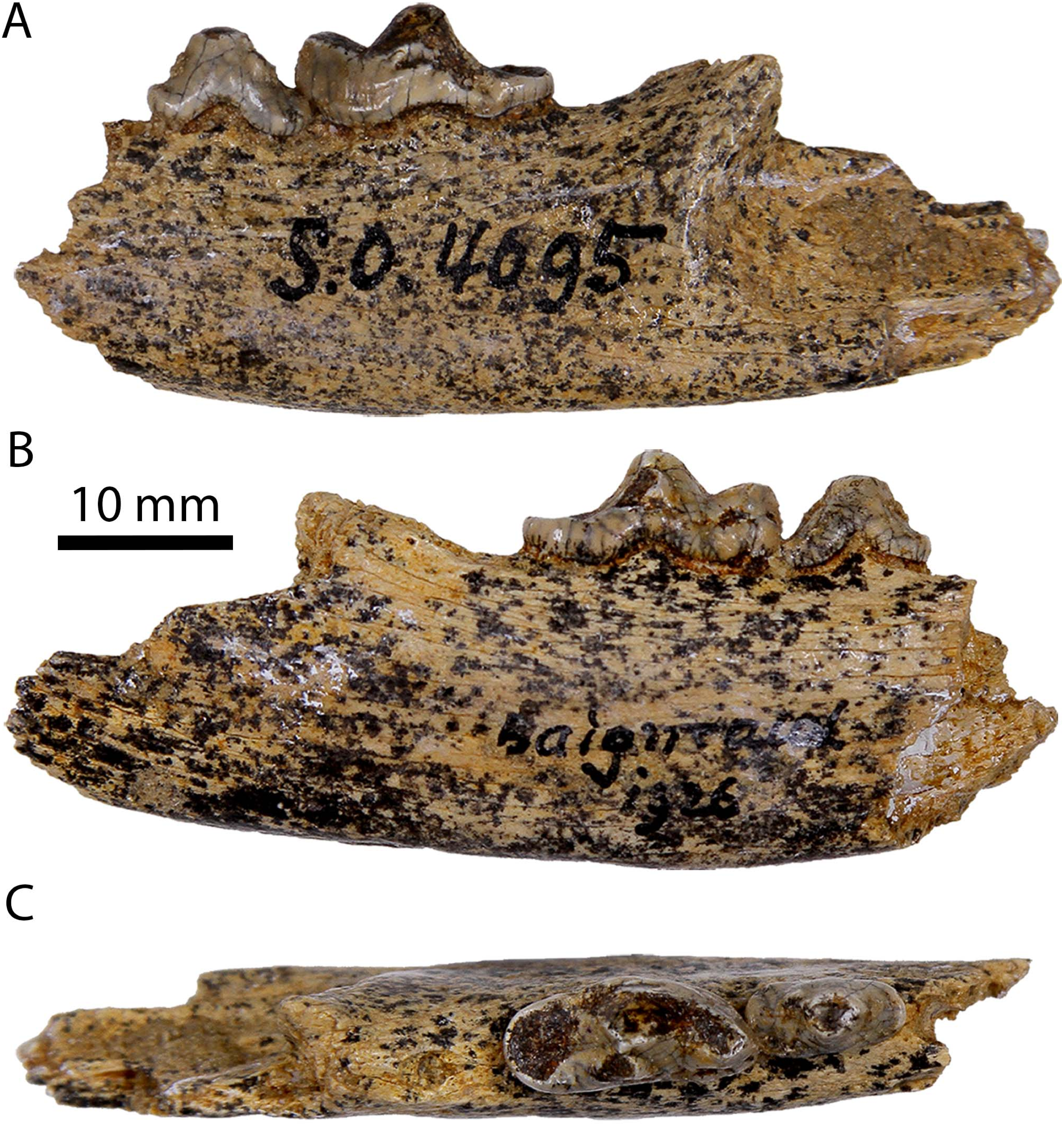
12

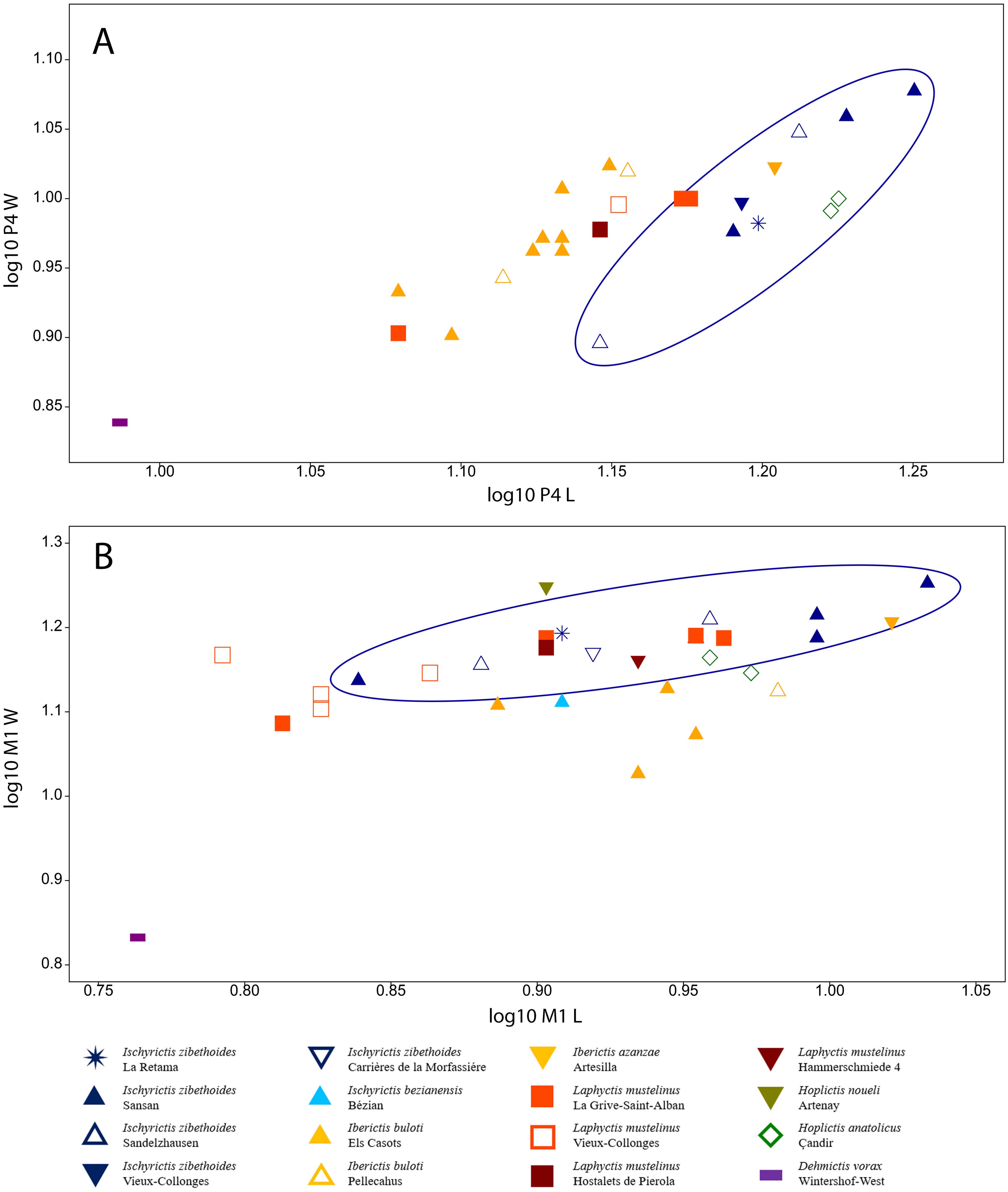
13

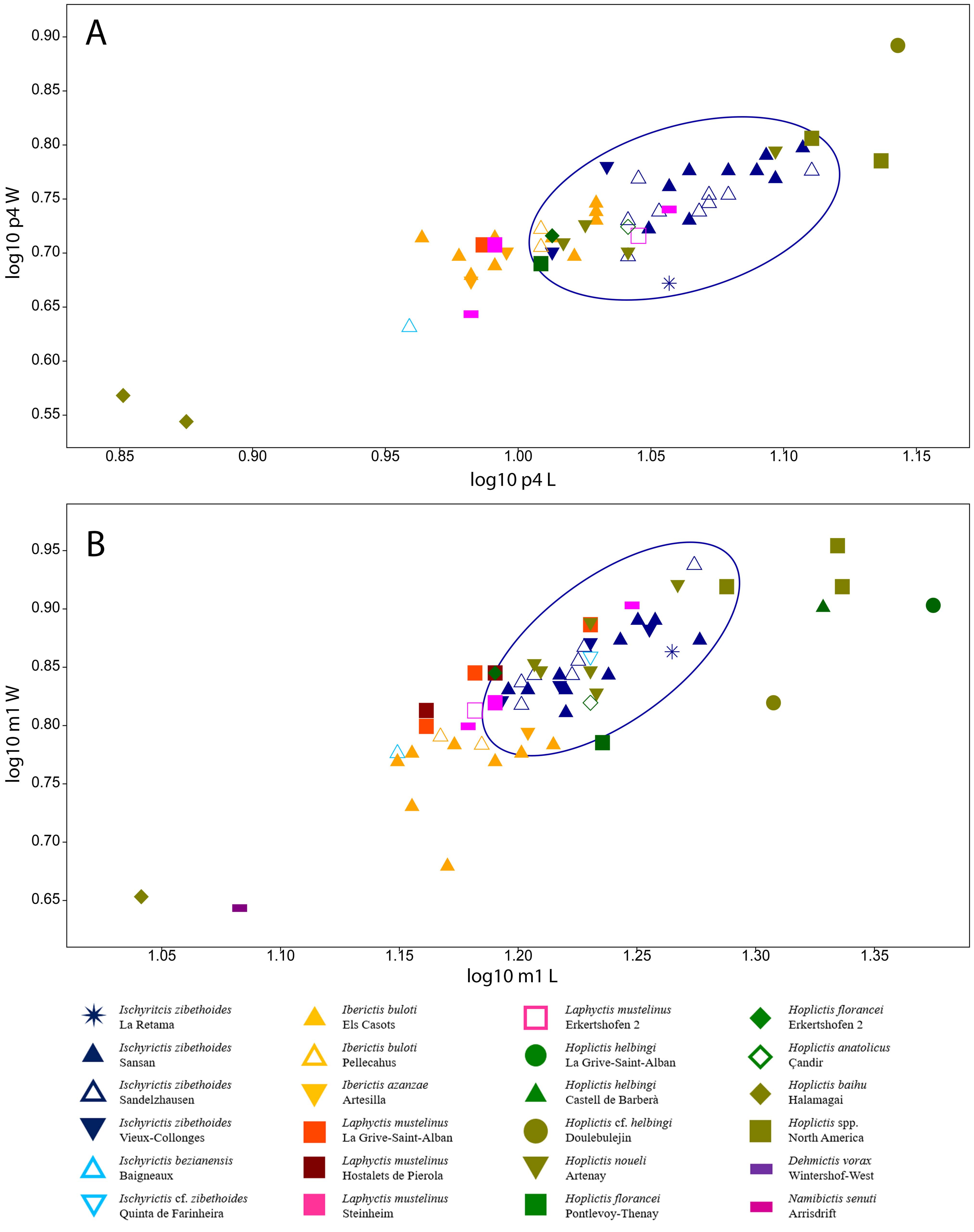
14

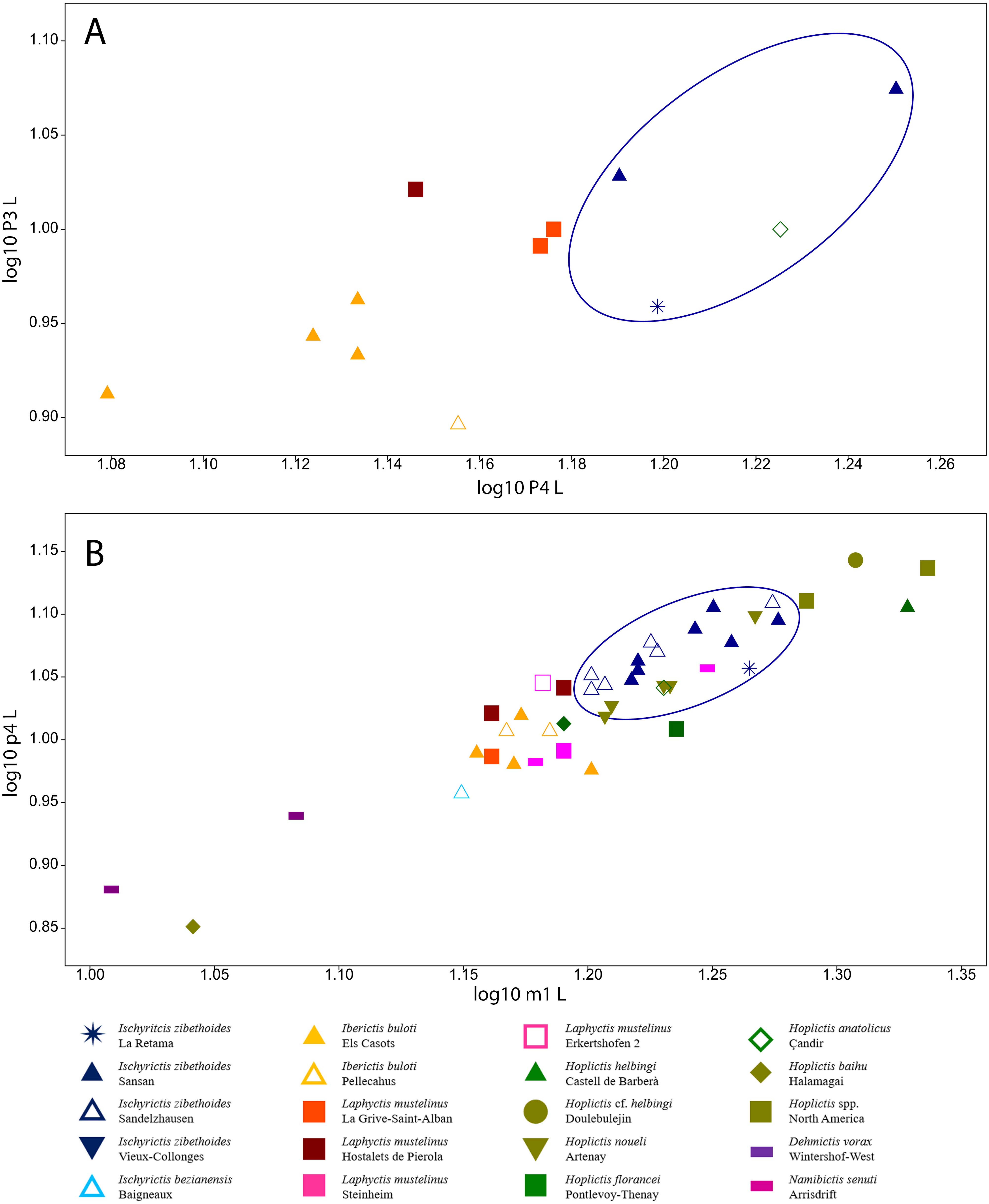
15

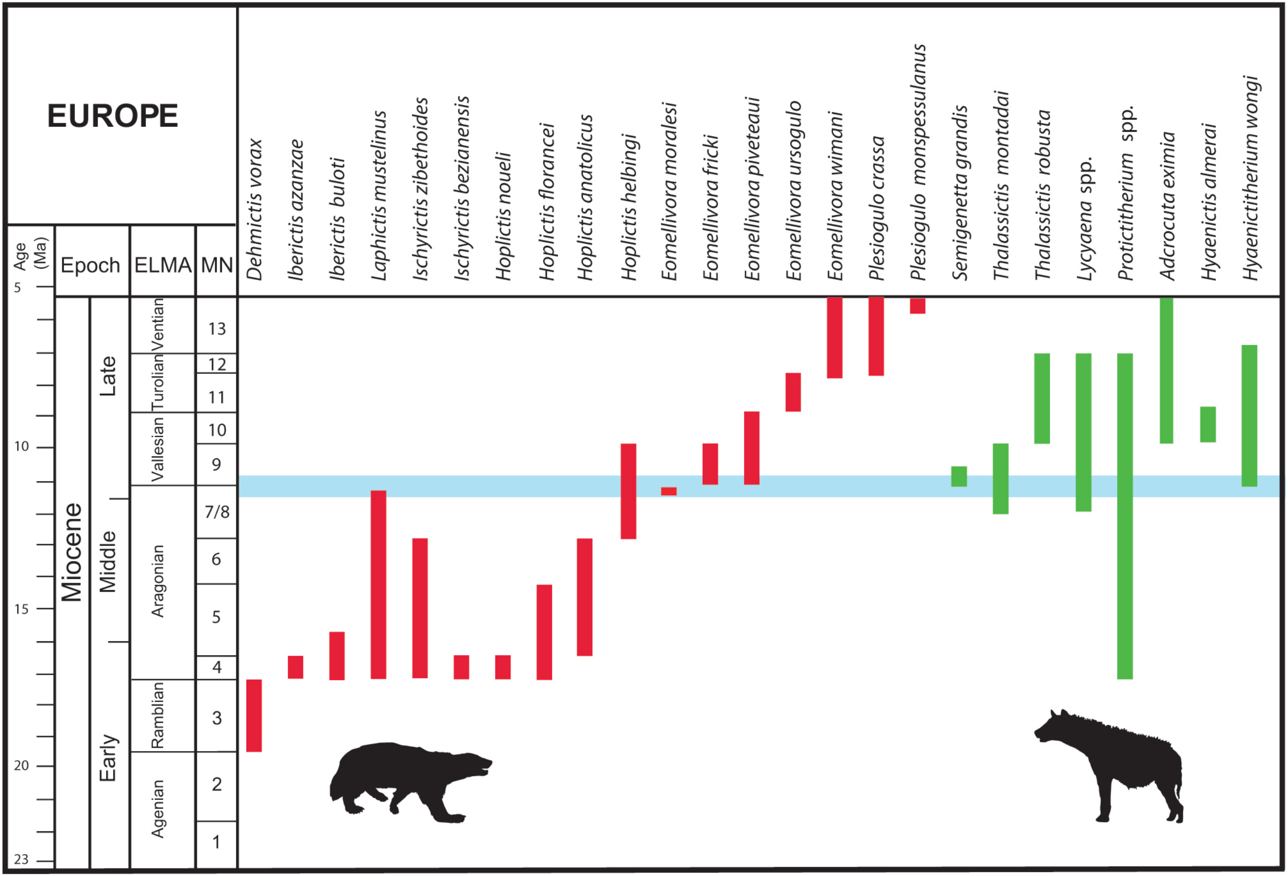

Mesozoic
Cenozoic
Entrepeñas dam
Guadiela river
Priego
Buendía dam
Tagus riv.
Guadamejud river
Altomira range
Mayor river
Cuenca
La Retama
Cigüela river
Loranca del Campo
Júcar river
Carrascosa del Campo
N
20 km


A
S.O. 4095
B
10 mm
baignead
1926
C


A
log10 P4 W
1.10
1.05
1.00
0.95
0.90
0.85
log10 P4 L
1.00
1.05
1.10
1.15
1.20
1.25
B
log10 M1 W
1.3
1.2
1.1
1.0
0.9
0.8
log10 M1 L
0.75
0.80
0.85
0.90
0.95
1.00
1.05
Ischyrictis zibethoides La Retama
Ischyrictis zibethoides Sansan
Ischyrictis zibethoides Sandelzhausen
Ischyrictis zibethoides Vieux-Collonges
Ischyrictis zibethoides Carrières de la Morfassiére
Ischyrictis bezianensis Bézian
Iberictis buloti Els Casots
Iberictis buloti Pellecahus
Iberictis azanzae Artesilla
Laphyctis mustelinus La Grive-Saint-Alban
Laphyctis mustelinus Vieux-Collonges
Laphyctis mustelinus Hostalets de Pierola
Laphyctis mustelinus Hammerschmiede 4
Hoplictis noueli Artenay
Hoplictis anatolicus Çandir
Dehmictis vorax Wintershof-West


A
0.90
0.85
0.80
0.75
0.70
0.65
0.60
0.55
log10 p4 W
0.85
0.90
0.95
1.00
1.05
1.10
1.15
log10 p4 L
B
0.95
0.90
0.85
0.80
0.75
0.70
0.65
log10 m1 W
1.05
1.10
1.15
1.20
1.25
1.30
1.35
log10 m1 L
Ischyritcis zibethoides La Retama
Ischyrictis zibethoides Sansan
Ischyrictis zibethoides Sandelzhausen
Ischyrictis zibethoides Vieux-Collonges
Ischyrictis bezianensis Baigneaux
Ischyrictis cf. *zibethoides* Quinta de Farinheira
Iberictis buloti Els Casots
Iberictis buloti Pellecahus
Iberictis azanzae Artesilla
Laphyctis mustelinus La Grive-Saint-Alban
Laphyctis mustelinus Hostalets de Pierola
Laphyctis mustelinus Steinheim
Laphyctis mustelinus Erkertshofen 2
Hoplictis helbingi La Grive-Saint-Alban
Hoplictis helbingi Castell de Barberà
Hoplictis cf. *helbingi* Doulebulejin
Hoplictis noueli Artenay
Hoplictis florancei Pontlevoy-Thenay
Hoplictis florancei Erkertshofen 2
Hoplictis anatolicus Çandir
Hoplictis baihu Halamagai
Hoplictis spp. North America
Dehmictis vorax Wintershof-West
Namibictis senuti Arrisdrift


A
log10 P3 L
1.10
1.05
1.00
0.95
0.90
log10 P4 L
1.08
1.10
1.12
1.14
1.16
1.18
1.20
1.22
1.24
1.26
B
log10 p4 L
1.15
1.10
1.05
1.00
0.95
0.90
0.85
log10 m1 L
1.00
1.05
1.10
1.15
1.20
1.25
1.30
1.35
Ischyritcis zibethoides La Retama
Ischyrictis zibethoides Sansan
Ischyrictis zibethoides Sandelzhausen
Ischyrictis zibethoides Vieux-Collonges
Ischyrictis bezianensis Baigneaux
Iberictis buloti Els Casots
Iberictis buloti Pellecahus
Laphyctis mustelinus La Grive-Saint-Alban
Laphyctis mustelinus Hostalets de Pierola
Laphyctis mustelinus Steinheim
Laphyctis mustelinus Erkertshofen 2
Hoplictis helbingi Castell de Barberà
Hoplictis cf. *helbingi* Doulebulejin
Hoplictis noueli Artenay
Hoplictis florancei Pontlevoy-Thenay
Hoplictis anatolicus Çandir
Hoplictis baihu Halamagai
Hoplictis spp. North America
Dehmictis vorax Wintershof-West
Namibictis senuti Arrisdrift


EUROPE
Age (Ma)
Epoch
ELMA
MN
Dehmictis vorax
Iberictis azanzae
Iberictis buloti
Laphictis mustelinus
Ischyrictis zibethoides
Ischyrictis bezianensis
Hoplictis noueli
Hoplictis florancei
Hoplictis anatolicus
Hoplictis helbingi
Eomellivora moralesi
Eomellivora fricki
Eomellivora piveteaui
Eomellivora ursogulo
Eomellivora wimani
Plesiogulo crassa
Plesiogulo monspessulanus
Semigenetta grandis
Thalassictis montadai
Thalassictis robusta
Lycyaena spp.
Protictitherium spp.
Adcrocuta eximia
Hyaenictis almerai
Hyaenictitherium wongi
5
10
15
20
23
Miocene
Late
Middle
Early
Ventian
Turolian
Vallesian
Aragonian
Ramblian
Agenian
13
12
11
10
9
7/8
6
5
4
3
2
1