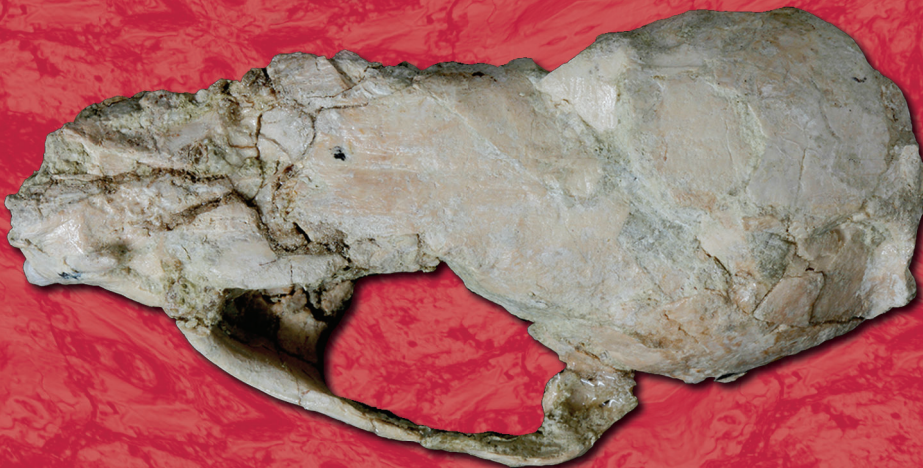
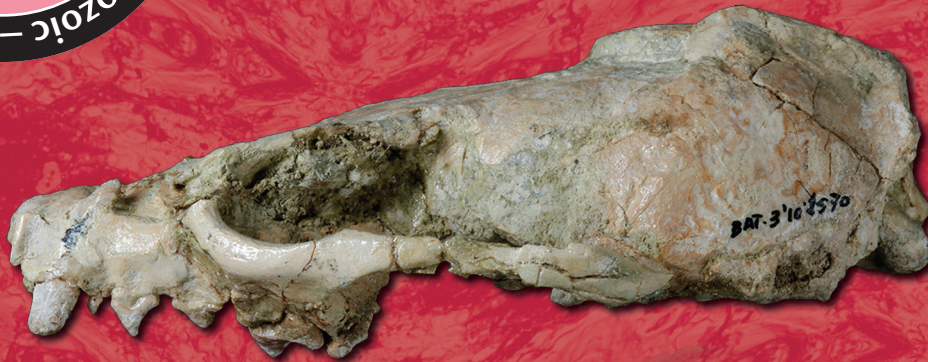


A new hypercarnivorous mustelid
(Mammalia, Carnivora, Mustelidae)
from Batallones, late Miocene (MN10),
Torrejón de Velasco, Madrid, Spain



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A new hypercarnivorous mustelid (Mammalia, Carnivora, Mustelidae) from Batallones, late Miocene (MN10), Torrejón de Velasco, Madrid, Spain

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ABSTRACT

We describe dentognathic remains of four individuals of the poorly known mustelid *Circamustela* Petter, 1967 from the late Miocene sites of Batallones-3 and 5 (MN10, Torrejón de Velasco, Madrid, Spain). These new fossils allow us to describe *Circamustela peignei* n. sp., a more primitive species than *Circamustela dechaseauxi* Petter, 1967 from Can Llobateres (MN9, Vallès Penedès Basin, Spain). *Circamustela peignei* n. sp. shows, among other features, an M1 with a more developed metacone, a smaller metastylar area, a mesially located protocone, and a more developed m1 metaconid compared to that of *C. dechaseauxi*. The new taxon differs from most Euroasian Miocene marten-like mustelids, such as the middle Miocene martens “*Martes*” *sansaniensis* (Lartet, 1851), and “*Martes*” *filholi* Depéret, 1887, the vallesian *Martes melibulla* Petter, 1963 and the Turolian/Ventian *Martes woodwardi* Pilgrim, 1931, *Martes ginsburgi* Montoya, Morales & Abella, 2011, *Pekania palaeosinensis* (Zdansky, 1924), and *Paramartes pococki* Kretzoi, 1952, in smaller size, a reduced lingual platform of the M1 and a more reduced m1 talonid and m2. However, *C. peignei* n. sp. is closer to the Chinese and Greek hypercarnivorous *Sinictis dolichognathus* Zdansky, 1924. *Circamustela* spp., and *Sinictis* Zdansky, 1924 can be interpreted as adapted to a more carnivorous diet than those of the more generalist martens, such as *Martes* spp., *Paramartes* Kretzoi, 1952 and *Pekania* spp.

KEY WORDS

Spain,
Carnivora,
Mustelidae,
Circamustela,
Sinictis,
Martes,
cooccurrence,
Neogene,
Mustelids,
new species.

RÉSUMÉ

Un nouveau mustélidé (*Mammalia*, *Carnivora*, *Mustelidae*) hypercarnivore de Batallones, Miocène supérieur (MN10), Torrejón de Velasco, Madrid, Espagne.

Les restes dentognathiques de quatre individus d'un mustélidé peu connu *Circamustela* Petter, 1967, sont décrits. Ces nouveaux fossiles provenant du Miocène supérieur de Batallones-3 et 5 (MN10, Torrejón de Velasco, Madrid, Espagne) nous permettent de définir une nouvelle espèce, *Circamustela peignei* n. sp., plus primitive que *Circamustela dechaseauxi* Petter, 1967 de Can Llobateres (bassin de Vallès Penedès, MN9, Espagne). Comparé à *C. dechaseauxi*, *C. peignei* n. sp. possède, entre autres, une M1 avec le métacone plus développé, une plus petite zone métastylaire et un protocone situé mésialement et une m1 dont le métaconide est plus développé. Cette nouvelle espèce diffère de la plupart des mustélidés du Miocène euroasiatique de type martre, comme "*Martes*" *sansaniensis* (Lartet, 1851) et "*Martes*" *filholi* Depéret, 1887 du Miocène moyen, *Martes melibulla* Petter, 1963 du Vallesien et *Martes woodwardi* Pilgrim, 1931, *Martes ginsburgi* Montoya, Morales & Abella, 2011, *Pekania palaeosinensis* (Zdansky, 1924) et *Paramartes pococki* Kretzoi, 1952 du Turolien /Ventien par sa taille moindre, la réduction de la plate-forme linguale de la M1 et un talonide de la m2 plus petit. *Circamustela peignei* n. sp. est plus proche de l'espèce hypercarnivore *Sinictis dolichognathus* Zdansky, 1924 de Chine et de Grèce. En ce sens, *Circamustela* spp. et *Sinictis* Zdansky, 1924 peuvent être interprétés comme étant adaptés à un régime plus carnivore que celui des martres les plus généralistes telles que *Martes* spp., *Paramartes* Kretzoi, 1952 et *Pekania* spp.

MOTS CLÉS

Espagne,
Carnivora,
Mustelidae,
Circamustela,
Sinictis,
Martes,
cooccurrence,
Néogène,
Mustélidés,
espèce nouvelle.

INTRODUCTION

Living martens are small to medium-sized gulonines with quite homogeneous, primitive and not very specialized skull, mandible and dentition (Larivière & Jennings 2009). This low intraspecific variability makes taxonomic studies of extinct martens difficult. However, Neogene marten-like mustelids forms a more heterogeneous group of small to medium-sized carnivorans with a wide-ranging fossil record in Europe, Asia and North America (e.g., Zdansky 1924; Baskin 1998; Ginsburg 1999; Morales *et al.* 2015), being its presence in Africa (Ginsburg 1977) anecdotal. Most of the extinct species are diagnosed based on fragmentary remains, where only the lower or the upper dentition is known, but rarely both, which makes morphological study at the species level problematic. This issue was pointed out by Werdelin & Peigné (2010), who stated that the genera *Martes* Pinel, 1792 and *Mustela* Linnaeus, 1758, has become a wastebasket *nomen* for various small mustelids of uncertain relationship to each other. Notable exceptions are the middle Miocene "*Martes*" *sansaniensis* (Lartet, 1851) from Sansan, MN6 (France) (Ginsburg 1961; Peigné 2012) and the late Miocene *Pekania palaeosinensis* (Zdansky, 1924) from China (Zdansky 1924; Wang *et al.* 2012), which are known from several individuals. The genus *Martes* is incredibly diverse in the Miocene of Europe with more than a dozen species distributed from mammal biozones MN3 to MN14 (Morlo 1997; Ginsburg 1999; Nagel *et al.* 2009; Montoya *et al.* 2011; Peigné 2012), being its origin quite controversial (Anderson 1994; Sato *et al.* 2003; Samuels & Cavin 2013; Li *et al.* 2014). In view of this, abundant small marten-like mustelids from the early and

middle Miocene of Eurasia and North America, which have been ascribed to "*Martes*", but show a different morphology are in need of thorough revision. This is partially in consonance with Li *et al.* (2014) who suggested that fossils older than Turolian/Ventian (late late Miocene) do not represent *Martes*, and they excluding from this genus its putative members from the Early, Middle, and early Late Miocene (Vallesian). However, we consider the vallesian *Martes melibulla* Petter, 1963 from Can Llobateres, MN9, (Vallès-Penedès Basin, Catalonia, Spain) as a real marten. Through late Miocene the diversity of these Euroasiatic mustelids increased, comprising hypercarnivorous genera such as *Circamustela* Petter, 1967 in Can Llobateres, Catalonia, Spain (Vallesian, MN9) and *Sinictis* Zdansky, 1924 in the Baodean (c. Turolian) of China, as well as more generalist forms as *Pekania* Gray, 1865 also in China (Baodean) and *Paramartes* Kretzoi, 1952 in Polgárdi, Hungary (Ventian, MN13).

A new interesting assemblage of extinct medium-sized mustelids from the late Miocene (MN10) of Cerro de los Batallones (Spain) was been found very recently (Morales *et al.* 2008; Valenciano 2017). This sample includes several skulls, mandibles and postcranial remains of at least two taxa: cf. *Martes melibulla* in Batallones-1 and Mustelidae gen. et sp. indet. aff. *Circamustela dechaseauxi* Petter, 1967 in Batallones-3 and 5 (Valenciano 2017). These undescribed samples of mustelids provide us with an excellent opportunity to increase our knowledge of Miocene martens and related forms. The main goal of the present paper is to describe the dentognathic remains of the hypercarnivorous marten-like mustelid from Batallones-3 and 5, as well as to compare them in the context of late Miocene martens from Eurasia.

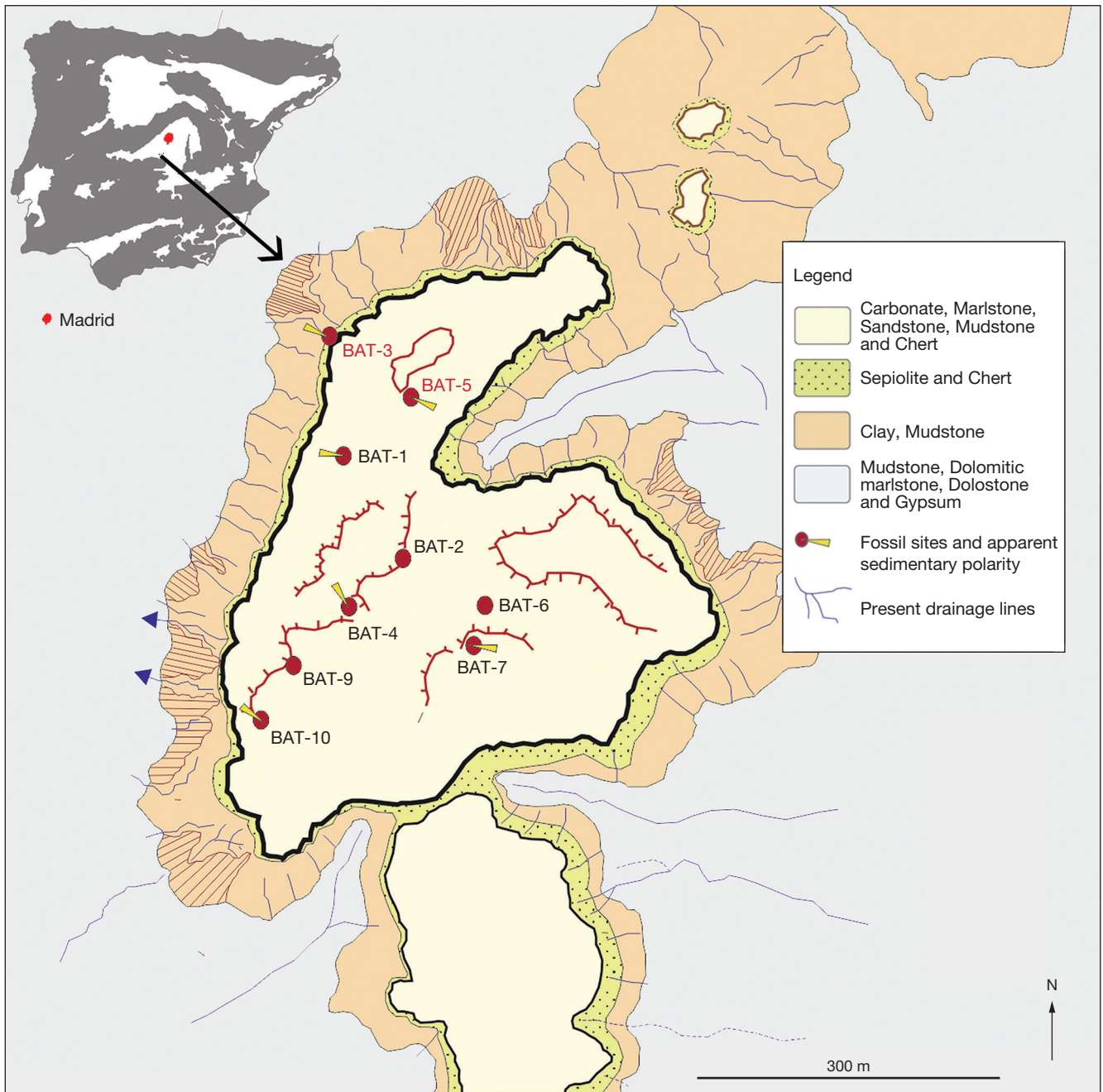


FIG. 1. — Simplified geographic map of the Iberian Peninsula with the Tertiary basins shaded and Madrid Province outlined, including a detailed map of the Cerro de los Batallones fossil complex with the sites with presence of *Circamustela peignei* n. sp., Batallones-3 and 5 designated in red. Modified from Calvo *et al.* (2013).

BATALLONES LOCALITIES

The Cerro de los Batallones fossil sites (late Miocene, MN10) have yielded some of the most interesting and richest Neogene mammal assemblages of the Iberian Peninsula (Morales *et al.* 2008; Morales 2017). The Cerro de los Batallones is located in the Madrid Basin on a structural butte in the south of the province of Madrid (Spain) (Fig. 1). It consists of a system of nine distinct sites, which were cavities that acted as natural traps for vertebrates (Pozo *et al.* 2004, Morales *et al.* 2008; Domingo *et al.* 2011,

2013a; Calvo *et al.* 2013; Abella *et al.* 2017). The fauna allowed us to assign all the sites to the late Miocene (Vallesian, *c.* 9.6-9.3 Ma) (Peláez-Campomanes *et al.* 2017). However, there are slight differences in the micro- and macromammal taxonomic composition among the different fossil deposits that have been attributed to minor temporal differences. Indications are that Batallones-10 is older than Batallones-1, and that Batallones-1 is older than Batallones-3 (López-Antoñanzas *et al.* 2010; Siliceo *et al.* 2014), whereas the difference in age between Batallones-2, 3 and 5 are unknown.

The numerous field seasons in the different Batallones localities since 1991 have yielded a rich and diverse assemblage of vertebrate fossils including freshwater fishes, amphibians and sauropsids (testudines, squamata and predatory birds) (Morales *et al.* 2008; Pérez-García & Murelaga 2013; Pérez-García & Vlachos 2014; Morales 2017; Vila *et al.* 2018). Micromammals (López-Antoñanzas *et al.* 2010, 2014; Álvarez-Sierra *et al.* 2017), equids, bovids, mosquids, giraffes, rhinoceroses, proboscids, suids (Morales *et al.* 2008; Sánchez *et al.* 2009, 2011; Pickford 2015; Ríos *et al.* 2017; Sanisidro 2017; Morales 2017; Domingo *et al.* 2018; Ríos & Morales 2019), and carnivorans comprising the most diverse sample, have also been recovered. Among the carnivorans the most abundant are the saber-tooth cats, a primitive hyaenid, two species of very derived amphicyonids, an ailuropod ursid, a large ailurid, mephitids and mustelids, all of them represented by a large sample of skulls, mandibles and nearly complete skeletons (e.g., Antón *et al.* 2004a, b; Peigné *et al.* 2005, 2008; Salesa *et al.* 2006, 2008, 2010, 2012, 2019; Abella 2011; Abella *et al.* 2013, 2015; Domingo *et al.* 2013b, 2016; Monesillo *et al.* 2014; Siliceo *et al.* 2014, 2015, 2017; Fabre *et al.* 2015; Valenciano *et al.* 2015; Fraile 2017; Valenciano 2017; Abella & Valenciano 2017; Morales *et al.* 2017).

MATERIAL AND METHODS

NOMENCLATURE AND MEASUREMENTS

Dental nomenclature follows Ginsburg (1999) and Smith & Dodson (2003). Anatomical descriptions are based primarily on Waibl *et al.* (2005), and Evans & de Lahunta (2010, 2013). Measurements were made using Mitutoyo Absolute digital caliper to the nearest 0.1 mm.

ABBREVIATIONS

Institutional abbreviations

BAT-3	Batallones-3 locality collection from MNCN;
BAT-5	Batallones-5 locality collection from MNCN;
IPS	Collection from Institut Català de Paleontologia Miquel Crusafont (ICP), Universitat Autònoma de Barcelona, Spain;
FMNH	Field Museum of Natural History, Chicago;
MGUV	Museu de Geologia de la Universitat de València, Burjassot;
MNCN	Museo Nacional de Ciencias Naturales, Madrid;
MNHN	Muséum national d'Histoire naturelle, Paris;
PMU	Palaeontological Museum, University of Uppsala, Uppsala.

STUDIED MATERIAL

The fossil remains of *Circamustela peignei* n. sp. from Batallones are stored in the collections of the Department of Paleobiología of the MNCN. For comparison we studied:

Circamustela dechaseauxi Petter, 1967 from Can Llobateres, Vallès Penedès Basin, Catalonia (Spain, late Miocene,

MN9) including the lectotype (IPS-2016) and the M1 IPS-28086 housed at ICP;

C. dechaseauxi MNCN-79043 from Los Valles de Fuentidueña (Segovia, Spain, MN9) studied by Ginsburg *et al.* (1981) housed at MNCN;

Martes melibulla (IPS-2047, lectotype) from Can Llobateres (type locality) and IPS-29308 from Trinxera Nord de l'Autopista (Vallès-Penedès Basin, Catalonia, Spain, late Miocene, MN10) described by Pons-Moyà (1990) housed at ICP;

Martes cf. *anderssoni* IPS-37686 from Can Ponsic (Vallès-Penedès Basin, Catalonia, Spain, MN9) described by Petter (1967);

Siniectis dolichognathus Zdansky, 1924 PMU M3791 (cranium) and M3792 mandibles of the same specimen (lectotype) from Loc.108 of Zdansky (1924) (late Miocene c. Turolian/Ventian) from Shanxi Province, China housed at PMU;

Pekania palaeosinensis PMU M3793, cranium (lectotype) and mandibles (PMU M3794-3795) from Loc.111 (ex1 of Zdansky 1924), and PMU M6, M7-8, M10-12, M13-14 and M3798 [= ex 2-7 from classical localities 30, 30 (5), 31, 108 and 11 of Zdansky 1924] (late Miocene c. Turolian/Ventian), Shanxi Province, China housed at PMU;

The holotype and type material of *Martes ginsburgi* Montoya, Morales & Abella, 2011 from Venta del Moro (Ventian, MN13), Spain described by Montoya *et al.* (2011) housed at MGUV;

The type material of "*Martes*" *sansaniensis* from Sansan (middle Miocene MN6, France) housed at MNHN;

The holotype of "*Martes*" *filholi* Depéret, 1887 from La Grive (middle Miocene, MN7/8, France) by a cast housed at MNCN;

and *Paramartes pococki* Kretzoi, 1952 from Polgárdi, Hungary, *Martes woodwardi* Pilgrim, 1931 from Pikermi (MN12), and *Pekania occulta* Samuels & Cavin, 2013 from Rattlesnake Fm, in Oregon (United States, c. 7 Ma) by their original descriptions (Pilgrim 1931; Kretzoi 1952; Samuels & Cavin 2013).

The studied extant mustelids were *Martes foina* (Erxleben, 1777), *Martes martes* Linnaeus, 1758, *Martes americana* (Turton, 1806), and *Pekania pennanti* Erxleben, 1777 housed at MNCN and FMNH.

3-D MODELS

BAT-3'10.1570, BAT-3-'10.1246, BAT-3'10.1570A and BAT-5'10.G14.129 were CT-scanned at the Servicio de Técnicas No Destructivas: Microscopía Electrónica y Confocal y Espectroscopía del MNCM-CSIC, Madrid. Scan Tomographic images were obtained by VGStudio MAX® 3.0 software. We used a MicroCT with a voxel size of 42.7 µm. We processed the stack of the obtained images of BAT-3'10.1246 with the free software ImageJ® v1.50e to proceed with the application of different filters to remove the noise generated in the process of Micro-CT, as diffraction rings or



FIG. 2. — Cranium and upper dentition of *Circamustela peignei* n. sp. from Batallones-3: **A-E**, cranium BAT-3'10.1570 (Holotype); **A**, lateral view; **B**, dorsal view; **C**, occlusal view of the Micro CT-scan reconstruction; **D**, rostral view; **E**, caudal view; **F-L**, fragmentary cranium BAT-3'11.1041, comprising the muzzle (**F-G**), a left fragment of the maxillary with a fragmented P3 and a complete P4 (**H-I**) and an isolated right P4 (**J-L**); **F**, dorsal view; **G**, rostral view; **H**, buccal view; **I**, occlusal view; **J**, buccal view; **K**, lingual view; **L**, occlusal view. Scale bar: 20 mm.

outliers elements in the sample generated by heavy elements or minerals immersed in the fossil (Pertusa Grau 2003). This data was imported to the software 3D Slicer® for the segmentation of the model using the thresholding method (Abel *et al.* 2012). We followed Sutton *et al.* (2014) for generating the individual element virtual models. We used the software Geomagic Wrap® (3D analysis and visualization model software) for further processing and finally, for the virtual reconstruction of the craniodental and mandibular elements, each dental piece was exported separately to the program designer 3DMaxStudio® V.

SYSTEMATIC PALEONTOLOGY

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

Genus *Circamustela* Petter, 1967

TYPE SPECIES. — *Circamustela dechaseauxi* Petter, 1967 by original designation.

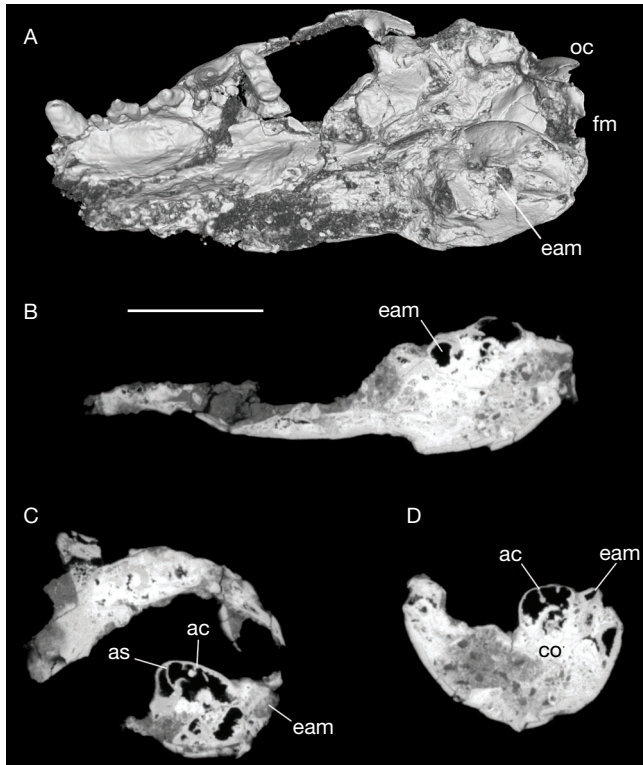


FIG. 3. — Micro CT-scan reconstruction of the fragmentary cranium BAT-3'10.1246 of *Circamustela peignei* n. sp. from Batallones-3: **A**, Ventral view; **B**, sagittal slice; **C**, horizontal slice; **D**, transversal slice. Abbreviations: **ac**, accessory crest; **as**, accessory septum; **co**, cochleae; **eam**, external auditory meatus; **fm**, foramen magnum; **oc**, occipital condyle. Scale bar: 20 mm.

TYPE LOCALITY. — Can Llobateres, Vallès Penedès Basin, Catalonia (Spain, late Miocene, MN9).

INCLUDED SPECIES. — *Circamustela peignei* n. sp., from Batallones; *Circamustela* sp. from Dorn-Dürkheim.

AGE. — Late Miocene Vallesian and early Turolian (MN9-11).

DIAGNOSIS. — American marten-sized mustelid with a hypercarnivorous dentition, including a reduction of upper and lower molars; M1 mesiodistally narrow, with both mesial and distal walls straight, small metacone and short lingual platform, such as a crest-like protocone; m1 shows a higher protoconid than paraconid, and a reduced m1 talonid in both length and width, with a low entocristid; low and lingually bevelled m1 hypoconid.

DIFFERENTIAL DIAGNOSIS. — Differs from *Martes*, and the late Miocene *Pekania*, and *Paramartes* in smaller size, reduced lingual platform of the M1, and more reduced m1 talonid comprising a very shallow basin, and a reduction of both m1 entocristid and the m2; Differs from *Sinictis* in a more developed P4 protocone; M1 with enlarged styler area, smaller and cuspid-like protocone; lower and smaller p4 distal accessory cuspid; m1 with shorter paraconid-protoconid edge; and relatively more robust hypoconid and entocristid.

Circamustela peignei n. sp.
(Figs 2-6; 7A-D)

[urn:lsid:zoobank.org:act:5FE42B44-EAD1-404B-9858-F3E546C99B03](https://doi.org/10.21203/rs.3.rs-1234567/v1)

Mustelidae gen. et sp. indet. aff. *Circamustela dechaseauxi* – Valenciano 2017: 331.

HOLOTYPE. — BAT-3'10.1570, complete cranium with C, P1-4 and M1 (Fig. 2A-E).

PARATYPE. — BAT-3'13.1048, nearly complete left hemimandible with p2-m2 (Fig. 5D-F).

ETYMOLOGY. — In memory of Dr Stéphane Peigné, expert on Neogene carnivorans from Eurasia and Africa.

HYPODIGM. — BAT-3'11.1041 (Fig. 2F-L): fragmentary cranium, comprising the muzzle, a left fragment of the maxillary with a fragmented P3 and a complete P4 and isolated right P4; BAT-3'10.1246: fragmentary cranium, comprising the muzzle and attached mandible, including C, P1-4, M1 and i1-3, c, p2-4, m1-2 (Fig. 3); BAT-3'13.1086: nearly complete right hemimandible with p2-m2 (Fig. 5A-C) (same individual as the paratype); BAT-3'10.1570A (Fig. 5J-L): fragmentary left hemimandible with p4 and m1 (same individual as the holotype); BAT-3'10.1570B (Fig. 5G-I): fragmentary right hemimandible with a broken p2 and complete p3-m1 (same individual as the holotype); Bat5-'10.G14.129: right m1 (Fig. 6).

TYPE LOCALITY. — Batallones-3 (late Miocene, Vallesian, MN10).

OTHER LOCALITY. — Batallones-5 (late Miocene, Vallesian, MN10).

AGE. — Late Miocene, Vallesian, MN10.

DIAGNOSIS. — Mustelid of a size comparable to *Circamustela dechaseauxi*. Relatively long muzzle; P1 present; P2-3 unicuspid and elongated; P3 distally widened; P4 long with conical and slender protocone mesially located, low parastyle and lingual cingulum; M1 buccolingually elongated and mesiodistally reduced, with a large parastylar area, paracone larger than metacone, the latter being distinctive, high mesially located protocone; long and low mandibular corpus; high coronoid process and shallow masseteric fossa; p2-4 elongated; p2-3 unicuspid; p4 with low distal accessory cuspid; m1 metaconid lingually expanded; oval and short m2 with small protoconid and metaconid.

DIFFERENTIAL DIAGNOSIS. — Differs from *Circamustela dechaseauxi* in more developed M1 metacone, lesser developed metastylar area, higher and mesially located protocone, lesser development of the cingulum on the lingual platform; more developed m1 metaconid, and a more conical hypoconid; Differs from *Martes melibulla* in the shorter mandibular corpus, reduced m1 talonid with a much shallower talonid basin, with reduced m1 entocristid and reduced m2; Differs from “*Martes*” *sansaniensis*, “*Martes*” *filholi*, *Martes woodwardi*, *Martes ginsburgi*, *Pekania palaeosinensis*, *Pekania occulta*, and *Paramartes pococki*, in smaller size, reduced lingual platform of the M1 and more reduced m1 talonid.

DESCRIPTION

Cranium and upper dentition

Circamustela peignei n. sp., has a medium-sized cranium about as large as that of the American marten (*Martes americana*) and a long rostrum similar to that of the North American fisher (*Pekania pennanti*). Three fragmentary skulls have been found at Batallones-3. Specimen BAT-3'10.1570 (Fig. 2A-E) is the most complete, and with a basal cranial length of 80.7 mm. It is dorso-ventrally compressed and the left frontal bone is collapsed. The cranium is partially crystallized in its interior, affecting the internal cavities and roots, and some superficial bone, such as of the right maxilla and pre-maxilla is dissolved. The nuchal and ventral regions are also damaged. The right zygomatic arch, left

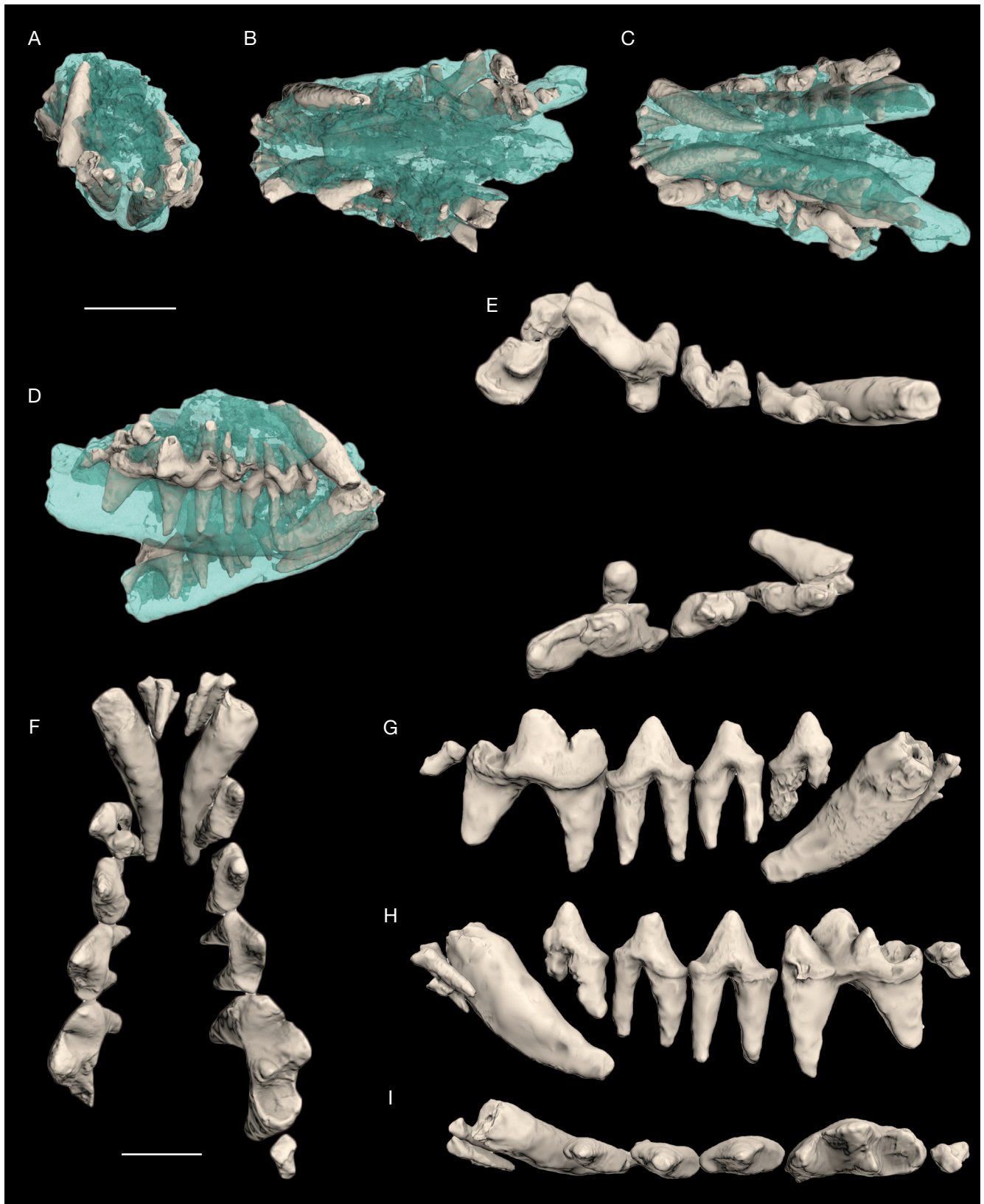


FIG. 4. — Micro CT-scan reconstruction of the fragmentary cranium BAT-3'10.1246 of *Circamustela peignei* n. sp. from Batallones-3: **A-D**, the skull and jaw are shown in semitransparent turquoise and the dentition in grayscale; **A**, rostral view; **B**, dorsal view; **C**, ventral view; **D**, lateral view; **E**, upper dentition, occlusal view; **F**, lower dentition, occlusal view; **G-I**, left hemimandible; **G**, buccal view; **H**, lingual view; **I**, occlusal view. Scale bars: A-D, 10 mm; E-I, 5 mm.

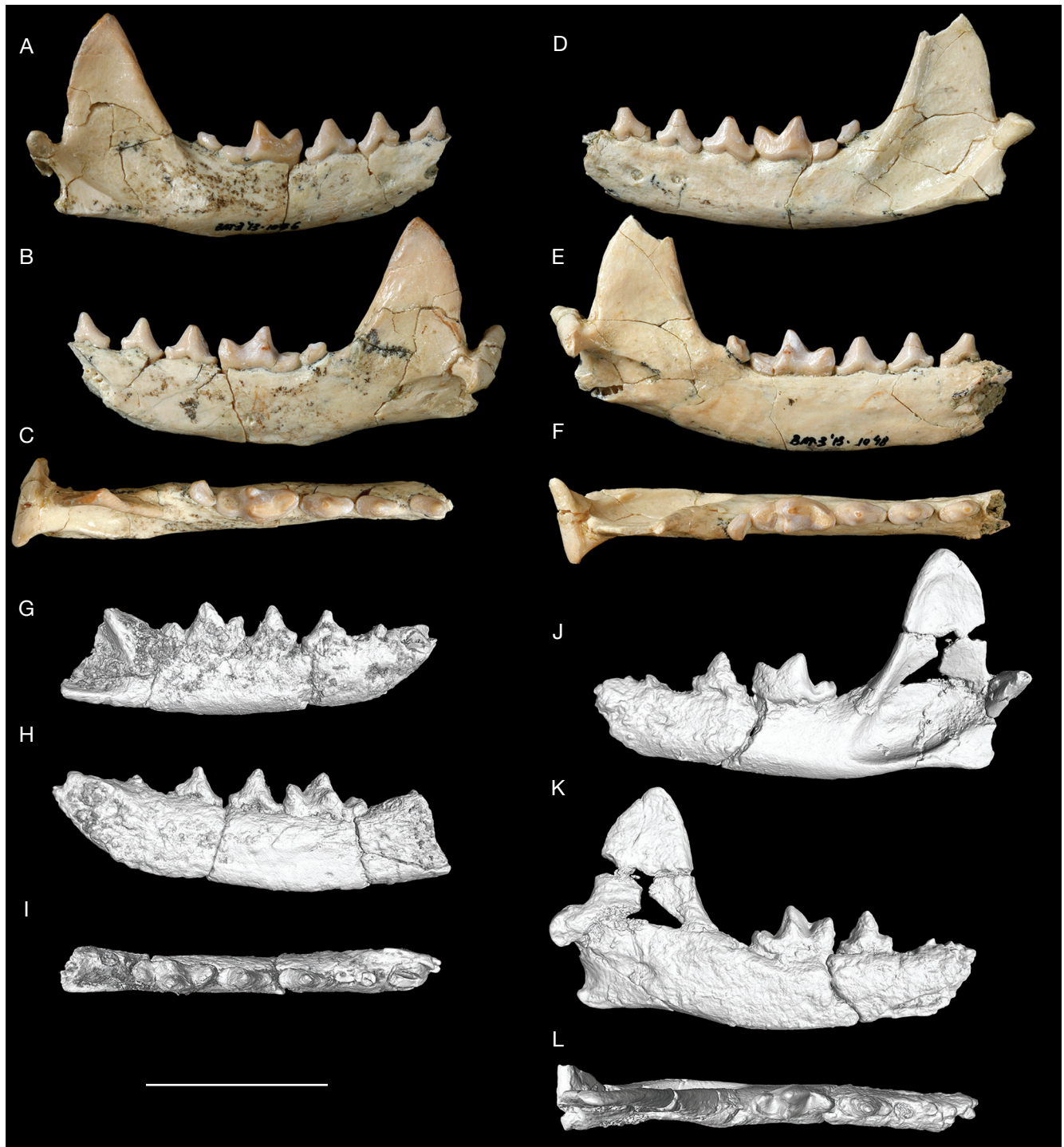


FIG. 5. — Mandibles and lower dentition of *Circamustela peignei* n. sp. from Batallones-3: **A-C**, right hemimandible BAT-3'13.1086; **A**, buccal view; **B**, lingual view; **C**, occlusal view; **D-F**, left hemimandible BAT-3'13.1048 (paratype); **D**, buccal view; **E**, lingual view; **F**, occlusal view; **G-Q**, Micro CT-scan reconstruction; **G-I**, right hemimandible BAT-3'10.1570B; **G**, buccal view; **H**, lingual view; **I**, occlusal view; **J-L**, left hemimandible BAT-3'10.1570A; **J**, buccal view; **K**, lingual view; **L**, occlusal view. Scale bar: 20 mm.

bullae, and both right mastoid process and occipital condyle are missing. The nasal aperture is broken. The orbit is large. The rostral margin of the orbit ends at the level of the mesial margin of the P4 parastyle. The postorbital processes are not preserved. The infraorbital foramen is located above the P3 and P4. It has a well-developed sagittal crest (Fig. 2A), which suggests that it

was a male individual (Larivière & Jennings 2009). In caudal view (Fig. 2E), the nuchal area is triangular, rather flat, and no muscular attachments are preserved on the supraoccipital bone. The left zygomatic arch is similar to that of living martens, so it is not especially robust. The frontal process of the zygomatic arch is triangular and of moderate size. On the palate, the incisive

foramina are not preserved. There is an oval concavity in the left maxilla from the canine at the P3 level. The right bulla is preserved. It is swollen, oval and rostrocaudally larger. It has three small perforations on its surface due to erosion. The scan images show a highly septate tympanic bulla, with a more developed anterior septum that partially divide the bulla (Fig. 3B-D), as it happens in the late Miocene African mustelid *Howellictis valentini* (de Bonis *et al.* 2009). No additional features or foramina from the basicranial area are preserved.

Specimens BAT-3'11.1041 (Fig. 2F-L) and BAT-3'10.1246 (Fig. 4) preserve the anterior part of the rostrum. Both show signals of dissolution by soil acids. BAT-3'11.1041 is not distorted. It shows a higher than broad nasal aperture and a high and relatively robust muzzle (Fig. 2F-G). The rostral part of the cranium BAT-3'10.1246 has both hemimandibles attached, as seen in the virtual reconstruction (Fig. 4).

The preserved upper dentition comprises the C, P1-4 and M1 (Figs 2-4; Table 1). Most teeth show signs of dissolution. The C is oval and long. Both BAT-3'10.1570 and BAT-3'10.1246 have a large wear facet on the tip. There are diastemata between all the upper premolars. The P1 is robust and unicuspid. Both P2 and P3 are elongated, unicuspid and show a concave buccal wall. The P3 is distally widened. The P4 is relatively long. It possesses an eroded parastyle in BAT-3'10.1570 (Fig. 2C). There is an inflection between the parastyle and the protocone. The protocone is very isolated and mesially located. Additional P4s associated with the crania BAT-3'11.1041 (Fig. 2H-L) and BAT-3'10.1246 (Fig. 4E) indicate that the parastyle is of moderate size. The protocone is conical and slender with moderate height. A lingual cingulum is present on the whole length of the lingual wall (Fig. 2K-L). Two M1 are preserved in the crania BAT-3'10.1570 and BAT-3'10.1246. The M1 BAT-3'10.1570 is buccolingually elongated and mesiodistally reduced (Fig. 2C). It has a large parastylar area. The paracone is larger than the metacone. Both mesial and distal walls are very straight. The protocone is high and mesially located. The lingual platform is reduced in comparison with living gulonines (e.g., *Martes martes*, *Martes foina*, *Pekania pennanti*). The CT-scan allowed us to examine the M1 BAT-3'10.1246 (Fig. 4E). It is broken at the paracone-metacone level and the metacone is dissolved. Its overall morphology is close to BAT-3'10.1570, showing a short lingual platform and a high and distally placed protocone (Figs 2C; 4E).

Mandibles and lower dentition

Three incomplete mandibles have been found in Batallones-3 comprising i1-3, c, p2-4 and m1-2 (Figs 4, 5; Table 2). Both BAT-3'10.1570A and B are poorly preserved and the mandibular corpus and teeth are dissolved and carbonated, having several small concretions on the surface (Fig. 5G-K).

The mandible of *C. peignei* n. sp. is slender with a low mandibular corpus. Laterally, there are two rounded mental foramina, one under the distal part of the p2 and the other beneath the middle cuspid of the p3. The mandibular symphysis is elongated and curved (Fig. 5G-H). Its medial surface is rough, and the attachment of the fibrocartilage pad reaches the mesial part of the p3. The coronoid process is high, sharp and vertically oriented. The masseteric fossa is shallow, although in BAT-3'10.1570A

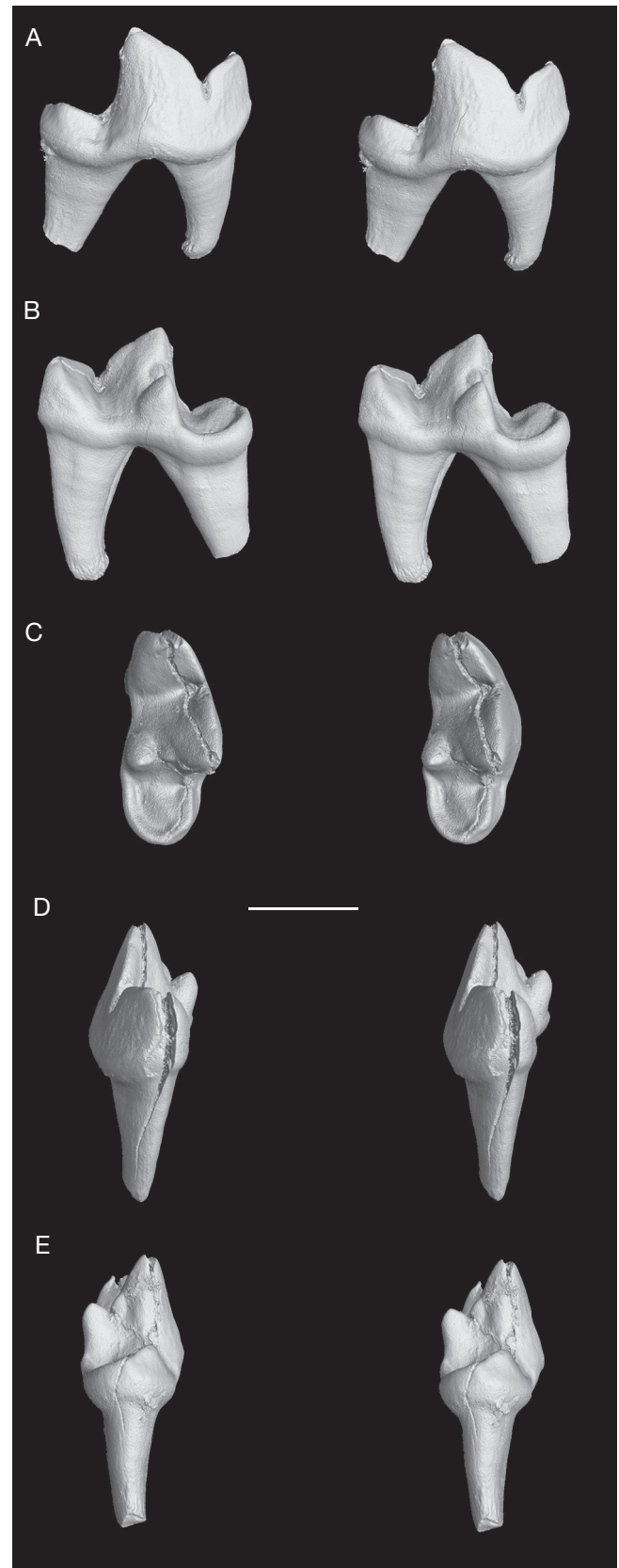


FIG. 6. — Stereo view of the right m1 BAT-5'10.G14.129 of *Circamustela peignei* n. sp. from Batallones-5: **A**, buccal view; **B**, lingual view; **C**, occlusal view; **D**, mesial view; **E**, distal view. Scale bar: 5 mm.

TABLE 1. — Upper teeth measurements (in mm) of mesiodistal length (L) and buccolingual width (W) of *Circamustela peignei* n. sp. from Batallones-3. Estimated values are reported within parentheses. Abbreviations: *, micro CT measurements; lf, left; r, right.

	C		P1		P2		P3		P4		M1	
	L	W	L	W	L	W	L	W	L	W	L	W
BAT-3'10.1570	4.2	3.1	1.7	1.4	4.4	1.8	5.4	2.6	7.9	4.9	3.8	8.5
BAT-3'11.1041 lf	(4.6)	(3.5)	—	—	—	—	—	—	8.1	4.9	—	—
BAT-3'10.1246 lf *	—	—	1.6	1.3	4.3	1.9	4.9	2.4	(8.6)	—	—	—
BAT-3'10.1246 r *	4.2	3.3	1.6	1.4	4.2	1.8	4.7	(2.7)	8.3	4.3	3.9	(8.8)

TABLE 2. — Lower teeth measurements (in mm) of mesiodistal length (L) and buccolingual width (W) of *Circamustela peignei* n. sp. from Batallones-3 and Batallones-5. Estimated values are reported within parentheses. Abbreviations: *, micro CT measurements from the right hemimandible; lf, left; r, right.

	i1		i2		i3		c		p2		p3		p4		m1		m2	
	L	W	L	W	L	W	L	W	L	W	L	W	L	W	L	W	L	W
BAT-3'10.1246 lf *	0.7	1.9	1.4	1.6	1.4	1.6	4.2	3.1	—	—	5.1	2.5	6.1	2.9	—	—	—	—
BAT-3'10.1246 r *	—	—	1.4	1.7	1.3	1.4	3.9	3.1	4.3	2.0	5.0	2.5	6.2	2.8	10.0	4.1	(2.4)	(1.7)
BAT-3'13.1056	—	—	—	—	—	—	—	—	4.2	2.1	4.8	2.5	6.0	2.9	9.2	3.8	3.5	2.8
BAT-3'13.1048	—	—	—	—	—	—	—	—	4.5	2.1	5.3	2.4	5.8	2.9	9.4	3.9	3.4	2.7
BAT-3'10.1570A	—	—	—	—	—	—	—	—	—	—	—	—	6.5	3.0	9.4	3.6	—	—
BAT-3'10.1570B	—	—	—	—	—	—	—	—	—	—	5.2	2.6	6.1	2.8	9.1	3.7	—	—
BAT-5'10.G14.129	—	—	—	—	—	—	—	—	—	—	—	—	—	—	9.0	4.1	—	—

it is deeper. Its rostral margin lies at the level of the m2. The tooth row is straight and is aligned with the articular process. The articular process is large and close to the angular process. The angular process is robust and caudally directed. It is more developed in BAT-3'10.1570A.

BAT-3'10.1246 preserves all the lower incisors on both sides (Fig. 4). The i1 is very small and peg-like. The right i1 only preserves part of the root. The i2 and i3 are bilobed, with i3 mesiodistally wider. The root of the i2 is imbricated between the i1 and the i3. The canine is large and has a lingual cingulid (Fig. 4F-I). BAT-3'10.1570A also shows an alveolus for p1. The p2-3 are elongated and unicuspid. The cuspid of p2 is placed mesially, but in the p3 it is located in the middle portion of the tooth. Both p3-4 have high mesial and distal cingulids. The p4 has a tiny distal accessory cuspid (Fig. 4F-I, 4A-F), which is more developed in BAT-3'10.1570A (Fig. 5J-L). The m1 is long; its trigonid forms more than two thirds of the total length of the tooth; the protoconid is higher than the paraconid. The metaconid is distinct, attached to the protoconid but not exceeding its posterior edge. It is lingually extended (Figs 4F, H-I; 5Q; 6), and is more developed in BAT-3'13.1086 (Fig. 5A-C), and in the specimen from Batallones-5 (Fig. 6). The maximum width is located at the protoconid-metaconid level. The talonid is reduced in length. The hypoconid is low and lingually bevelled (Figs 4F-I; 5C, E). There is no entocristid; instead a posterior cristid of the metaconid extends along the lingual edge of the talonid, reaching the hypoconulid. Between the hypoconid and the aforementioned edge there is a shallow basin. The hypoconulid is more developed in BAT-3'10.1570A (Fig. 5J-L) and BAT-5'10.G14.129 (Fig. 6). The m2 is reduced and oval. Its protoconid and metaconid are of similar height (Fig. 5A-C).

DISCUSSION AND CONCLUSIONS

Two species of medium-sized mustelids have been found in Batallones comprising cf. *Martes melibulla* in Batallones-1 and Mustelidae gen. et sp. indet. aff. *Circamustela dechaseauxi* in both Batallones-3 and 5 (Valenciano 2017). The most significant feature of the latter form is the reduction of the M1 and m1, which undoubtedly match the late Miocene mustelid *Circamustela* (Fig. 7A-H). Previously, the only species within *Circamustela* was *C. dechaseauxi*. This species is exclusively known from Can Llobateres, Vallès Penedès Basin, Catalonia (Spain, late Miocene, MN9) (Petter 1967) by an isolated m1 (lectotype) and by an M1 assigned, with reservations, by Petter (1976) to the same species (Fig. 7E-H). Additionally, some specimens have been described tentatively to *Circamustela*, on the basis of a fragmentary M1 lingual platform from Los Valles de Fuentidueña (Segovia, Spain MN9) (Ginsburg *et al.* 1981) and a small complete M1 with an associated mandibular fragment with p4 from Dorn-Dürkheim 1 (Germany, MN11) determined by Morlo (1997) as ?*Circamustela*. Thus, this new sample from Batallones is considerably more extensive than that of the remaining finds of the genus. It includes remains of at least four individuals (three in Batallones-3 and one in Batallones-5) (Tables 1 and 2), and in consequence it allows us to greatly improve the knowledge about *Circamustela*.

The associated upper and lower dentition of *Circamustela peignei* n. sp. from Batallones-3 allows us to confirm that the reduced M1 described by Petter (1976) from Can Llobateres (Fig. 7E) belongs to *C. dechaseauxi*. *Circamustela peignei* n. sp. shares with the latter a similar size, a reduced lingual platform of the M1, and a reduced m1 talonid (Figs 7A-H;

FIG. 7. — Main comparative material of species of late Miocene martens and marten-like mustelids from Eurasia analysed herein: **A**, BAT-3'10.1570, micro CT-scan reconstruction of the left upper dentition of *Circamustela peignei* n. sp. (holotype) from Batallones-3, occlusal view; **B-D**, left hemimandible BAT-3'13.1048 of *Circamustela peignei* n. sp. (paratype) from Batallones-3; **B**, buccal view; **C**, lingual view; **D**, occlusal view; **E**, IPS-28086, left M1 of *Circamustela dechaseauxi*



Petter, 1967 from Can Llobateres MN9; **F-H**, IPS-2016, left fragmentary hemimandible with fragmentary p4 and complete m1 of *Circamustela dechaseauxi* (lectotype) from Can Llobateres; **F**, buccal view; **G**, lingual view; **H**, occlusal view; **I-K**, IPS-2047, right hemimandible comprising p4-m2 of *Martes melibulla* Petter, 1963 (lectotype) from Can Llobateres; **I**, buccal view; **J**, lingual view; **K**, occlusal view; **L-O**, *Pekania palaeosinensis* (Zdansky, 1924) PMU M3793 cranium (lectotype) and PMU M3795 left hemimandible from Loc.111, Baode Fm, Shanxi Province, China; **L**, occlusal view; **M**, buccal view; **N**, lingual view; **O**, occlusal view; **P-S**, *Sinictis dolichognathus* Zdansky, 1924 PMU M3791 (cranium) and M3792 mandibles of the same specimen (lectotype) from Loc.108; **P**, occlusal view; **Q**, buccal view; **R**, lingual view; **S**, occlusal view. Scale bar: 20 mm.

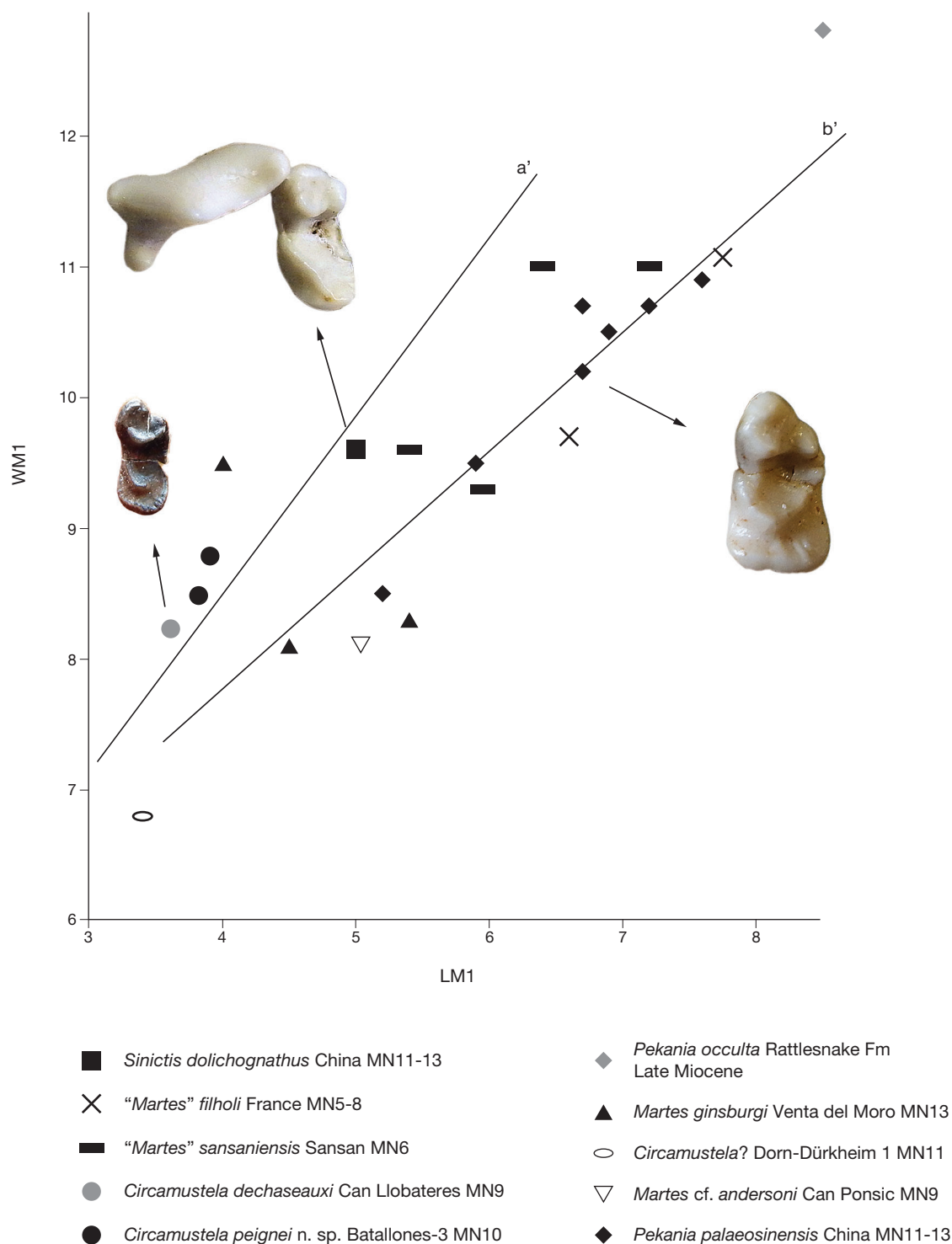


FIG. 8. — Bivariate plot of the length (L) and with (W) of the M1 of Neogene martens. The linear regression a' ($r^2 = 0.73$) is defined by relatively hypercarnivorous martens, characterized by short M1 talon and comprise *Circamustela* spp., and *Sinictis*. The linear regression b' ($r^2 = 0.75$) is defined by more generalist taxa, characterized by longer M1 talon, comprising *Pekania* Gray, 1865, *Paramartes* Kretzoi, 1952 and *Martes* Pinel, 1792. The values are given in mm. Abbreviations: r^2 , coefficient of determination. M1s pictures are showed scaled between them. Sources: Zdansky (1924); Viret (1951); Mein (1958); Petter (1976); Schmidt-Kittler (1995); Morlo (1997); Montoya *et al.* (2011); Wang *et al.* 2012; Peigné (2012); Samuels & Cavin (2013).

8; 9). However, several differences exist between the two forms. For instance, a more developed M1 metacone, and a higher and mesially located protocone compared to those of *C. dechaseauxi*, in which the protocone is centrally placed on

the talon of the molar, and lesser development of the cingulum on the lingual platform (Fig. 7A, E). Besides, although *C. dechaseauxi* possesses a much-reduced metacone, it has a more developed metastylar area compared to that of *C. peig-*

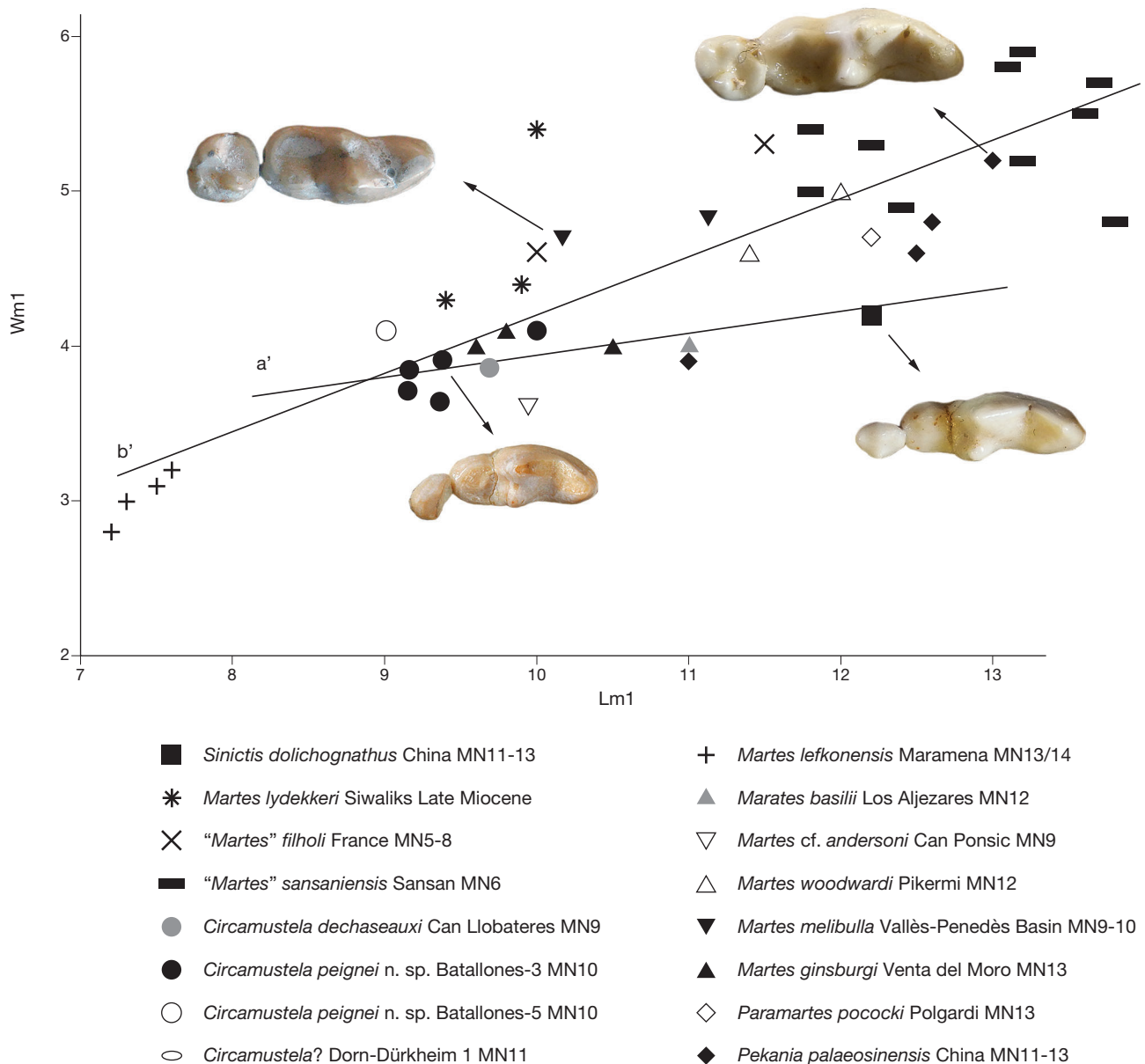


FIG. 9. — Bivariate plot of the length (L) and with (W) of the m1 of Neogene martens. The linear regression **a'** ($r^2 = 0.37$) is defined by relatively hypercarnivorous mustelids, characterized by slender m1 and comprise *Circamustela* spp., and *Sinictis*. The linear regression **b'** ($r^2 = 0.73$) is defined by more generalist taxa, characterized by robust m1 talonid, comprising *Pekania* Gray, 1865, *Paramartes* Kretzoi, 1952 and *Martes* Pinel, 1792. The values are given in mm. Abbreviations: r^2 , coefficient of determination. Same legend than Figure 6 and m1s pictures are showed scaled between them. Source: Zdansky (1924); Pilgrim (1931); Colbert (1933, 1935); Viret (1951); Kretzoi (1952); Mein (1958); Petter (1963; 1964, 1967); Pons-Moyà (1990); Schmidt-Kittler (1995); Roussiakis (2002); Ghaafar *et al.* (2004); Montoya *et al.* (2011); Wang *et al.* (2012); Peigné (2012); Samuels & Cavin (2013).

nei n. sp., including a distinct lobe that surrounds it. Another difference lies in the more developed m1 metaconid and more conical hypoconid in *C. peignei* n. sp. than the more reduced metaconid and crest-like hypoconid of *C. dechaseauxi*. These differences indicate more primitive morphological features in *C. peignei* n. sp. In relation to the M1 ascribed tentatively to *C. dechaseauxi* from Los Valles de Fuentidueña by Ginsburg *et al.* (1981), it differs from *C. peignei* n. sp. in a more centrally located protocone and a distinct cingulum on the lingual platform, but because of the fragmentary nature of the material we still follow the designation of Ginsburg *et al.* (1981). The complete M1 from Dorn-Dürkheim 1 is too

small to be assigned to *C. dechaseauxi* or *C. peignei* n. sp. (Fig. 8). However, its inclusion in this genus is consistent with its morphology.

Martes melibulla represents a true marten in the early late Miocene (Vallesian). It is coeval with *Circamustela* and is restricted to the localities of Can Llobateres and Trinxera Nord de l'Autopista in the Vallès-Penedès Basin, Catalonia, Spain, from MN9-10 respectively. It is known only from the lower dentition and some long bones (Petter 1963; Pons-Moyà 1990). The undescribed marten from Batallones-1 matches the overall morphology of this taxon well (Valenciano 2017). The mandibles of *C. peignei* n. sp. differ from the lectotype of

M. melibulla (IPS-2047, Fig. 7I-K) in the lower mandibular corpus, and a reduced m1 talonid with a much shallower talonid basin and a reduction of both m1 entocristid and m2. *Circamustela peignei* n. sp. also differs from the middle Miocene martens “*Martes*” *sansaniensis* from Sansan (MN6, France) (Ginsburg 1961; Peigné 2012) and “*Martes*” *filholi* from La Grive (MN7/8, France) (Viret 1951), as well as the late Miocene *Pekania palaeosinensis* from Shanxi Province (Fig. 7L-O) and Inner Mongolia in China, c. 7-5.7 Ma (equivalent to MN12-13 in Europe) (Zdansky 1924; Zhu *et al.* 2008, Wang *et al.* 2012), *Pekania occulta* Samuels & Cavin, 2013 from Rattlesnake Fm, in Oregon (United States), 7.3-7.05 Ma, *Martes woodwardi* Pilgrim, 1931 from Pikermi (MN12), *Paramartes pococki* Kretzoi, 1952, late Miocene, MN13 and *Martes ginsburgi* from Venta del Moro, MN13 (Valencia, Spain) (Montoya *et al.* 2011) in smaller size, a reduced lingual platform of the M1 and a more reduced m1 talonid (Figs 8; 9). However, the Ventian *M. ginsburgi* shows a mosaic of features, having a similar overall morphology of the lower dentition, including the m1, but with a completely different enlarged M1 lingual platform (Montoya *et al.* 2011).

Similarly, *C. peignei* n. sp. is close to *Sinictis*, a larger-sized and younger mustelid (MN11-13) that appears in localities of China and Greece (Zdansky 1924, Koufos 2011). It is important to note that the cranium of *Sinictis dolichognathus* PMU M3791 (lectotype, Fig. 7P) has an extra right P1, showing five premolars on the right side. However, other parts of the dentition does not shown signs of teratological features. The two forms share relatively slender premolars, such as M1, m1-2 with reduced talon and talonid respectively (Figs 7P-S; 8; 9). Conversely, *Sinictis* has a more reduced P4 protocone, more reduced M1 styler area, an enlarged, crested and higher M1 protocone, an nearly lost lingual platform, a higher p4 distal accessory cuspid, an m1 with a larger paraconid-protoconid edge, and a more reduced hypoconid and entocristid compared with those of *Circamustela*. All these features can be linked to a more hypercarnivorous diet in both *Circamustela* spp. and *Sinictis*, that is more evident in the latter. Thus, a remarkable trend in the overall morphology of the dentition of these two mustelids, can be interpreted in terms of adaptation to a more carnivorous diet than those of the more generalist martens such as *Martes* spp., *Paramartes* and *Pekania* spp. This trend is observable in Figures 8 and 9, where linear regression a' involving *Circamustela* spp., and *Sinictis*, shows a coefficient of determination (r^2) = 0.73 for the M1 and 0.37 for the m1, and is characterized by both short M1 talon and m1 talonid. Linear regression b' is quite different, and includes the middle and late Miocene martens *Pekania*, *Paramartes* and *Martes* (r^2 = 0.75 for the M1 and 0.73 for the m1), which are defined by a longer M1 talon, including a relatively long lingual platform, and wider and more basined m1 talonid compared to that of *Circamustela* spp., and *Sinictis*. These features are more similar to those of living martens, which exemplify more generalist taxa (Larivière & Jennings 2009). Additionally, *Sinictis* (?) *pentelici* (Gaudry 1861a, b) from Pikermi, Attica, Greece (middle Turolian, MN 12) is present in the late Miocene of Europe at the same time as the Chinese form. It was described

as *Mustela pentelici* by Gaudry (1861a, b) and later transferred questionably to *Sinictis* by Pilgrim (1931) according to Koufos (2011). A comparison of both *Sinictis* species suggests that both the overall morphology and size of the Greek mustelid are nearly the same as *S. dolichognathus*, and the minor differences between the two can be explained by intraspecific variability. Thus, we consider *Sinictis* (?) *pentelici* a junior subjective synonym of *S. dolichognathus*.

REMARKS ON THE BATALLONES MUSTELOID GUILD

The guild of musteloids from Batallones comprises a very diverse assemblage including the giant ailurid *Simocyon batalleri* (Viret, 1929), the giant mustelid *Eomellivora piveteaui* Ozansoy, 1965, and a wide sample of undescribed, small to medium-sized carnivores including martens, badgers, and mephitids (Peigné *et al.* 2005, Salesa *et al.* 2006, 2008; Valenciano *et al.* 2015, Valenciano 2017; Table 3). A faunal comparison of the carnivorans using common taxa of some of the most important localities of the Vallesian of the Iberian Peninsula (MN9-10) – Can Llobateres (CLL) in the Vallès-Penedès Basin, Catalonia (MN9), Los Valles de Fuentidueña (LVLL) in the Duero Basin, Segovia (MN9) and the localities of Batallones (BAT) in the Madrid Basin (MN10) – indicate more derived states in the species of the latter, including *Indarctos* Pilgrim, 1913, *Machairodus* (Kaup, 1832), *Magericyon* Peigné, Salesa, Antón & Morales, 2008, *Thaumastocyon* Stehlin & Helbing, 1925, and *Eomellivora* Zdansky, 1924 (Fernández-Monescillo *et al.* 2017; Peláez-Campomanes *et al.* 2017; Morales *et al.* 2017; Valenciano *et al.* 2017, 2019). Can Llobateres has been interpreted as having a humid forested environment (Marmi *et al.* 2012), and the habitat of BAT has been inferred to include more open woodland than CLL. However, the extent of vegetation cover at BAT is unclear, due to the absence of significant botanical remains. Herbivore and carnivore $d^{13}C$ and $d^{18}O$ values for medium and large-sized mammals suggest a similar woodland to mesic C3 grasslands, without significant changes in either the vegetation cover or the hydrological regime during the time separating LVF and BAT-1 and 3 (Domingo *et al.*, 2016, 2017). Among musteloids – ailurids, mustelids and mephitids – the samples of ailurids and mephitids are completely different between CLL and BAT at the generic level (Table 3). The small-sized shared mustelid genera between CLL and BAT – *Circamustela* and *Martes* (Table 3) – do not indicate a trend in the more derived states in the species from BAT as suggested by larger one (*Eomellivora*). In fact, we found the relatively primitive species *C. peignei* n. sp. in BAT. In order to extend the comparison of these faunas of small musteloids, it is necessary a deep review of both localities.

The presence of two different marten-like mustelids in BAT is not exceptional, with the coexistence of two or more species of martens in other European localities of the middle Miocene such as Vieux-Collonges (MN5; Mein 1958) and La Grive (MN7+8; Viret 1951), having been documented as well as

TABLE 3. — Faunal list of the musteloids from Can Llobateres (CLL), Los Valles de Fuentidueña (LVF) and Batallones (BAT) localities. Sources: Crusafont-Pairó & Ginsburg 1973; Ginsburg *et al.* 1981; Peigné *et al.* 2005; Robles 2014; Valenciano *et al.* 2015; Valenciano 2017; Valenciano *et al.* 2019; and this manuscript. Abbreviations: *, type locality.

Family	Taxa	MN9		MN10				
		CLL	LVF	BAT-10	BAT-1	BAT-2	BAT-3	BAT-5
Ailuridae	<i>Protursus simpsoni</i>	*	—	—	—	—	—	—
	<i>Simocyon batalleri</i>	—	—	—	×	—	—	—
Mustelidae	<i>Eomellivora fricki</i> (syn. of <i>Hoplictis petteri</i>)	×	—	—	—	—	—	—
	<i>Eomellivora piveteaui</i> (syn. of <i>E. liguritor</i>)	—	×	×	—	—	×	—
	<i>Circamustela dechaseauxi</i>	*	—	—	—	—	—	—
	<i>Circamustela cf. dechaseauxi</i>	—	×	—	—	—	—	—
	<i>Circamustela peignei</i> n. sp.	—	—	—	—	—	*	×
	<i>Martes melibulla</i>	*	—	—	—	—	—	—
	cf. <i>Martes melibulla</i>	—	—	—	×	—	—	—
	<i>Marcetia santigae</i>	*	—	—	—	—	—	—
	? <i>Marcetia santigae</i>	—	×	—	—	—	—	—
	<i>Trocharion albanense</i>	×	—	—	—	—	—	—
	<i>Trochictis narcisoni</i>	*	—	—	—	—	—	—
	aff. <i>Adroverictis ginsburgi</i>	—	×	—	—	×	×	—
Mephitidae	<i>Promephitis pristinidens</i>	×	—	—	—	—	—	—
	<i>Sabadellictis crussafonti</i>	*	—	—	—	—	—	—
	<i>Mesomephitis medius</i>	*	—	—	—	—	—	—
	" <i>Promephitis</i> n. sp."	—	—	—	×	—	×	—
	" <i>Mephitidae</i> n. gen. et sp."	—	—	—	×	×	×	×
	<i>Mephitinae</i> indet.	—	×	—	—	—	—	—

in the late Miocene of Can Llobateres (MN9; Robles 2014 and references herein), which represents the type locality of both *C. dechaseauxi* and *M. melibulla*. This also the case today in ecosystems of the Northern Hemisphere, where several sympatric hypercarnivorous and more generalist mustelids occur in the same area (e.g., *Pekania pennanti* and *Martes americana* in North America; *Mustela putorius* Linnaeus, 1758 and *Martes foina* in Europe) (Larivière & Jennings 2009; Ryšavá-Nováková & Koubek 2009). Thus, the occurrence of some martens in the same region can be explained from a partitioning perspective. *Circamustela* spp., could be interpreted as a relatively hypercarnivorous mustelid, and *Martes melibulla* as a more generalist marten.

In relation to the relative chronology of the localities of BAT, Vallesian, c. 9.6-9.3 Ma (Peláez-Campomanes *et al.* 2017), only three of the nine localities have been dated based on their fauna, being BAT-10 being the oldest, BAT-1 intermediate and BAT-3 the youngest. According to the musteloids found, the presence of similar taxa in BAT-3, 2 and 5 in comparison to BAT-1 (Table 3), may suggest that BAT-3, 2 and 5 are close in age. Nevertheless, the presence of *E. piveteaui* in BAT-10 and 3 may contradict this hypothesis, since it is found in the oldest and younger deposits, and, besides, there are common carnivores in most of them, such as *Machairodus aphanistus* (Kaup, 1832), *Promegantereon ogygia* (Kaup, 1832), and *Proictitherium crassum* (Depéret, 1892) (Morales 2017). With the exception of the undescribed mephitids from Batallones, there is not a wide sample to compare populations of the different Batallones sites in terms of variability, as have been done with some micro-mammals, hyenas and saber-tooth cats (López-Antoñanzas *et al.* 2010, 2014; Siliceo *et al.* 2014; Monesillo *et al.* 2014; Fraile 2017; Álvarez-Sierra *et al.* 2017). The differential presence of Musteloidea in BAT-1 and 3,

which are the best sampled localities from BAT, along with the small temporal gap between them might indicate changes in the dynamics of entry and exit of species in the Basin of Madrid during the time elapsed between the two (Valenciano 2017). Alternatively, these differences could be random, under the hypothesis that these species coexisted at the same time during the formation of the traps, but without being trapped.

Thus, the presence or absence of these small to medium sized musteloids must be cautiously analysed and cannot be interpreted exclusively as due to temporal differences in time in the filling in of the cavities between Batallones-10, 1, and 3-2-5.

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