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Valenciano, Alberto; Morales, Jorge; Azanza, Beatriz; [et al.]. «Aragonictis araid, gen. et sp. nov., a small-sized hypercarnivore (Carnivora, Mustelidae) from the late middle Miocene of the Iberian Peninsula (Spain)». *Journal of vertebrate paleontology*, (January 2022). DOI 10.1080/02724634.2021.2005615

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1 *Aragonictis araid* gen. et sp. nov., a small-sized hypercarnivore (Carnivora, Mustelidae)  
2 from the late middle Miocene of the Iberian Peninsula (Spain)

3

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18 RH: VALENCIANO ET AL.—A NEW SMALL MIDDLE MIOCENE MUSTELID

19

20 ABSTRACT—Small to medium-sized mustelids from the last 18 million years

21 represent a heterogeneous group of carnivorans with a wide-ranging record in the

22 northern hemisphere. They were first referred to the genera *Mustela* and *Martes*, but

23 lately ascribed to the latter, and hence considered as the longest-lived genus within

24 Mustelidae. However, a great many of these forms have been based upon fragmentary

25 material and *Martes* has conformed progressively to a wastebasket *nomen* for species of

26 uncertain relationships. Here, we describe dentognathic material of a small-sized  
27 mustelid from three middle Miocene (MN7+8, latest Aragonian) localities of the Iberian  
28 Peninsula that constitutes a new genus and species. *Aragonictis araid* gen. et sp. nov.  
29 represents a distinct taxon if compared to early/middle Miocene forms ascribed to  
30 “*Martes*” spp., especially the similar-sized early Miocene *Circamustela? laevidens* and  
31 the middle Miocene “*Martes*” *caedoti* and “*Martes*” *delphinensis*. The finding of  
32 particular features in *A. araid* (low p2-3, loss or reduction of the p4 accessory cuspid  
33 with its main cuspid centrally located, presence of a sharp, beveled and lingually open  
34 m1 talonid, and reduction of M1 lingual platform) indicates affinities with the late  
35 Miocene *Circamustela* in the range of hypercarnivory. Our reassessment of “*Martes*”  
36 indicates possible evidence of cladogenesis for Miocene mustelidae with, at least, two  
37 different events being recognized in Europe—the latter during MN7+8 to MN9 with  
38 presence of *Aragonictis* and *Circamustela*. The finding of *A. araid* further confirms the  
39 presence of more densely forested environments than expected in inner Iberia during the  
40 latest middle Miocene.

41

42

## INTRODUCTION

43

44 Small to medium-sized mustelids from the early and middle Miocene are a  
45 heterogeneous group of carnivorans with a wide-ranging record in Europe, Asia, and  
46 North America (e.g., Baskin, 1998; Ginsburg, 1999; Peigné, 2012; Valenciano et al.,  
47 2020a). They were conventionally referred to both extant genera *Mustela* Linnaeus,  
48 1758 (Mustelinae) and *Martes* Pinel, 1792 (Guloninae), albeit since the last century they  
49 have been classified as *Martes* (Lartet, 1851; Depéret, 1887; Mayet, 1908; Hughes,  
50 2012 and references herein). Accordingly, it represents the genus with the longest fossil

51 record in Mustelidae with more than 18 million years of duration from its emergence  
52 (e.g., Dehm, 1950; Ginsburg, 1999; Peigné, 2012; Hughes, 2012).

53         However, the classification of a great many of these fossil forms has been based  
54 upon fragmentary or incomplete material and have numerous plesiomorphic  
55 traits/convergences with *Martes*, which makes of this genus a wastebasket *nomen* for  
56 various small mustelids of uncertain relationships (Werdelin and Peigné, 2010; Samuels  
57 et al., 2018). It remains to be discussed whether these Miocene forms should be  
58 assigned to *Martes* (e.g., Jiangzuo et al., 2021), and emerges as an urgent task to  
59 perform a comparison with the type species of the genus. While some of these forms  
60 have morphological features closely related to Guloninae, others could instead represent  
61 stem groups outside of the crown clade Guloninae (Anderson, 1970, 1994; Sato et al.,  
62 2003; Wang et al., 2012; Li et al., 2014; Samuels and Calvin, 2013; Samuels et al.,  
63 2018). For instance, Anderson (1994) proposed *Martes laevidens* Dehm, 1950 from the  
64 early Miocene (MN3) of Wintershof-West (Germany) as the earliest member of the  
65 genus, but such assignation to *Martes* has been recently discarded (Sato et al., 2003)—  
66 though it is not fully discussed (as occur with the remaining European middle Miocene  
67 species, Valenciano et al., 2020a). Within this complex scenario, it is debatable whether  
68 the early late Miocene *Martes melibulla* Petter, 1963 from the Vallès-Penedès and  
69 Madrid basins (Spain) represents the first true *Martes* (Valenciano, 2017; Valenciano et  
70 al., 2020a), or it is instead the late Pliocene *Martes wenzensis* Stach, 1959 from Węże 1  
71 (Poland) (Sato et al., 2003). Unfortunately, this systematics issue is far to be fully  
72 clarified with the known mustelid material.

73         Herein, we report and describe new dentognathic remains of a small-sized  
74 mustelid from three late middle Miocene Iberian localities (Aragonian, MN7+8, G3  
75 local zone) (Fig. 1). This material greatly differs from that considered to date for *Martes*

76 and the other Miocene species included in the same genus. With the view to address this  
77 challenge about this genus, the discovery of this new mustelid has the potential to shed  
78 light on the obscure history and systematic intricacies of the genus *Martes*.

79

## 80 **Geological Context and Age**

81 We include material from the fossil sites of Andurriales and Toril 3A, which are  
82 located in the Daroca area (province of Zaragoza, Spain) —one of the regions with the  
83 highest concentration of mammalian fossil localities from Spain (Alcalá et al., 2000).  
84 Both localities are magnetostratigraphically dated at 11.33 and 12.65 Ma, respectively,  
85 hence belonging to local zone G3 (MN unit 7+8, upper Aragonian, middle Miocene)  
86 (van Dam et al., 2014). The geology of the sites has been interpreted as an alluvial fan  
87 that alternate with lake deposits (Alcalá et al., 2000; Azanza et al., 2004; van Dam et al.,  
88 2014; Barasoain and Azanza, 2018). Toril 3A exhibit an exceptional and abundant fauna  
89 of vertebrates including amphibians, reptiles and birds, aquatic chelonians, small size  
90 hornless ruminants, rhinos, cricetid species, and beavers, among others. This fauna  
91 reveals the existence of areas of permanent or temporary fresh water and humid  
92 conditions (Azanza et al., 2004; DeMiguel et al., 2011). The locality of Escobosa de  
93 Calatañazor locality is a karstic infilling placed in the northern border of the Almazán  
94 Basin (province of Soria, Spain). The micromammal association is correlated with local  
95 zone G3 (as Nombrevilla 2), dated at 11.9 Ma (van Dam et al., 2014; Morales et al.,  
96 2018).

97

## 98 **MATERIAL AND METHODS**

99

### 100 **Nomenclature and Measurements**

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

104

## 105 **Abbreviations**

106 **Institutional Abbreviations**—**SNSB-BSPG**, Staatliche Naturwissenschaftliche  
107 Sammlungen Bayerns - Bayerische Staatssammlung für Paläontologie und Geologie,  
108 Munich, Germany; **FMNH**, Field Museum of Natural History Chicago, Illinois, USA;  
109 **IPS**, collection of the Institut Català de Paleontologia Miquel Crusafont (ICP),  
110 Universitat Autònoma de Barcelona, Spain; **MGUV**, Museu de Geologia de la  
111 Universitat de València, Burjassot; **MNCN**, Museo Nacional de Ciencias Naturales,  
112 Madrid, Spain; **MNHN**, Muséum national d’Histoire naturelle, Paris, France; **MPZ**,  
113 collection of the Museo de Ciencias Naturales de la Universidad de Zaragoza  
114 (MCNUZ), Zaragoza, Spain; **NMA**, Naturmuseum Augsburg, Germany; **NMB**,  
115 Naturhistorisches Museum Basel, Switzerland; **PMU**, Palaeontological Museum,  
116 University of Uppsala, Uppsala, Sweden; **SMF**, Senckenberg Forschungsinstitut und  
117 Naturmuseum, Frankfurt, Germany; and **UCBL-FSL**, Université Claude Bernard Lyon  
118 1 Lyon, France.

119 **Other Abbreviations**—**c**, lower canine; **L**, maximum length; **M**, upper molar; **m**,  
120 lower molar; **P**, upper premolar; **p**, lower premolar; and **W**, maximum width.

121

## 122 **Study Material**

123 The study material includes unpublished dentognathic remains from the Spanish  
124 localities of Andurriales and Escobosa de Calatañazor housed in the MNCN, and Toril  
125 3A housed in the MCNUZ. The comparative material includes fossils of

126 “*Martes*” *sanjoni* (Mayet, 1908) and “*Martes*” *burdigaliensis* Beaumont, 1974 from  
127 Artesilla (early Miocene, MN4, Spain) (Azanza et al., 1993) housed in the MCNUZ;  
128 “*Martes*” sp., from La Barranca (middle Miocene, MN6, Spain) (Peigné et al., 2006)  
129 housed in the MNCN; *Martes ginsburgi* Montoya, Morales and Abella, 2011 from  
130 Venta del Moro (late Miocene, MN13, Spain) housed in the MGUV; “*Martes*”  
131 *sansaniensis* (Lartet, 1851) from Sansan (middle Miocene, MN6, France) housed at  
132 MNHN; *Martes melibulla* Petter, 1963 from the localities of Can Llobateres (late  
133 Miocene, MN9, Spain) and Trinxera Nord de l’Autopista (late Miocene, MN10, Spain)  
134 housed in the ICP; *Martes* aff. *anderssoni* from Can Poncic 1 (late Miocene, MN9)  
135 (Petter, 1967) housed in the ICP; “*Martes*” *munki* Roger, 1900 from Sant Quirze del  
136 Valles (middle Miocene, MN7+8, Spain) and *Circamustela dechaseauxi* Petter, 1967  
137 from Can Llobateres housed in the ICP; *Circamustela peignei* Valenciano et al., 2020a  
138 from Batallones-3 and 5 (late Miocene, MN10, Spain) housed in the MNCN; and both  
139 *Sinictis dolichognathus* Zdansky, 1924 from Loc.108 of Zdansky (1924) (late Miocene  
140 c. Turolian/Ventian, China), and *Pekania palaeosinensis* from localities 11, 30, 30 (5),  
141 31, 108 and 111 of Zdansky (1924) (late Miocene c. Turolian/Ventian, China) housed in  
142 the PMU. We also established comparisons with casts of “*Martes*” *delphinensis*  
143 Depéret, 1892, “*Martes*” *filholi* (Depéret, 1887) and “*M.*” *munki* from La Grive (middle  
144 Miocene, MN7+8, France) housed in the MNCN. Additionally, we examined  
145 photographs of specimens of the following taxa: “*M.*” *laevidens* from Wintershof-West  
146 (early Miocene, MN3, Germany) (Dehm, 1950) housed in the BSPG; five marten-like  
147 taxa from Vieux-Collonges (middle Miocene, MN5, France) (“*Martes*” *collengensis*  
148 Roth and Mein, 1987, “*Martes*” *cadeoti* Mein, 1958, “*M.*” *burdigaliensis*, “*M.*” *munki*  
149 and “*M.*” *filholi*) housed in the UCBL; “*M.*” *munki* from Häder (middle Miocene, MN5,

150 Germany) (Roger, 1900) housed in the NMA; and *Circamustela?* from Dorn-Dürkheim  
151 1 (late Miocene, MN11, Germany) (Morlo, 1997) housed in the SMF.

152 The extant specimens used for comparison are the following: *Martes foina*  
153 (Erxleben, 1777) (MNCN); *Martes martes* Linnaeus, 1758 (MNCN); *Pekania pennanti*  
154 (Erxleben, 1777) (FMNH); *Mustela putorius* Linnaeus, 1758 (MNCN); and *Mustela*  
155 *nivalis* Linnaeus, 1766 (MNCN).

156

## 157 SYSTEMATIC PALEONTOLOGY

158

159 Order CARNIVORA Bowdich, 1821

160 Suborder CANIFORMIA Kretzoi, 1943

161 Family MUSTELIDAE Batsch, 1788

162 Subfamily GULONINAE Gray, 1825

163 Genus *ARAGONICTIS* gen. nov.

164

165 **Type and Only Included Species**—*Aragonictis araid*, gen. et sp. nov.

166 **Etymology**—Aragon-, for the autonomous community of Spain in where was

167 defined the Aragonian biozone (European Land Mammal Age: late early

168 Miocene/middle Miocene); -ictis, Greek suffix for weasel-like mammals.

169 **Diagnosis**—Mustelidae of small size. Slender dentition with narrow canines and

170 slender unicuspid premolars; p1 present; cuspids of p2-3 lower in height than the p4;

171 absence of diastema between p2-3; p4 long and unicuspid in the specimens from the

172 type locality, and with a very reduced distal accessory cuspid in the specimen from

173 Escobosa; m1 with subequal protoconid and paraconid, but slightly taller protoconid.

174 Small m1 metaconid. Sectorial and lingually open m1 talonid composed by a buccal



175 hypoconid relatively tall, beveled, lingually longer, with a reduced hypoconulid, and a  
176 very low entocristid reaching the basal level of the paraconid crown; trapezoidal m2  
177 with protoconid and metaconid of similar size, rectilinear buccal wall, and convex  
178 lingual wall; slender P4 protocone mesially placed, paracone-metastyle blade elongated;  
179 M1 mesiodistally narrow, with both mesial and distal walls straight but concave tooth  
180 profile in mesial view; large parastylar area, reduced metacone, mesial crest-like  
181 protocone, absent metaconule and short lingual platform.

182

183 *ARAGONICTIS ARAID* sp. nov.

184 (Figs. 2, 3)

185 *Martes delphinensis* Sesé 1980:133

186

187 **Holotype**—Left fragmentary hemimandible, MNCN 150.003, including the  
188 complete dental formula c, p1-4, and m1-2.

189 **Type Locality**—Andurriales, MN7+8, local zone G3 (11.33 Ma; Van Dam et al.,  
190 2014), Zaragoza, Spain.

191 **Other Localities**—Toril 3A, MN7+8, local zone G3 (12.65 Ma; Van Dam et al.,  
192 2014), Zaragoza, Spain and Escobosa de Calatañazor, MN7+8, local zone G3 (ca. 12  
193 Ma; Morales et al., 2018).

194 **Referred Material**—Andurriales: MNCN 150.004, right fragmentary  
195 hemimandible with p2-3 and m1 (found associated with MNCN 150.003, probably  
196 belonging to the same individual); Toril 3A: MPZ 2020/474, left dp4; MPZ 2020/482,  
197 left fragmentary M1; Escobosa de Calatañazor: MNCN 26577, right fragmentary  
198 hemimandible with p2, p4-m2 and MNCN 150.007, left fragmentary maxillary with P4-  
199 M1.

200           **Etymology**—After ARAID (acronym for the Fundación Agencia Aragonesa para  
201 la Investigación y el Desarrollo—in English, Aragonese Foundation for Research and  
202 Development), an agency created by the Government of Aragon with the aim of  
203 promoting research, development and innovation. In recognition of its implication in the  
204 research of vertebrate paleontology in Aragon.

205           **Diagnosis**—As for genus.

206           **Description**—The mandibular corpus is long and low (Fig. 2). Two mental  
207 foramina are present, one below the p2 and other at the level of the p3. The c is narrow.  
208 The lower premolars are elongated and unicuspid. There is not diastema between the  
209 lower premolars (Fig. 2A-C). The p1 is present. The cuspid of both p2-3 are lower than  
210 p4 and placed mesially. The p4 is tall with a cuspid situated in the middle of the tooth  
211 and reaches the high of the m1 paraconid. A low and reduced distal accessory cusp is  
212 present in the specimen MNCN 26577 (Fig. 2M-O). A mesial and distal crown  
213 cingulids are present. The m1 is long compared with the p4. The trigonid represents  
214 three fourths of the total length of the molar. The protoconid is the tallest cuspid,  
215 although the paraconid is relatively tall. It has a small metaconid, and a bucco-lingually  
216 reduced talonid. The hypoconid is clearly separated from the postprotocristid. It is  
217 buccally placed, and shows a beveled morphology, being bulbous in the buccal wall,  
218 and with a marked lingual slope in the lingual wall towards the entoconid crista. There  
219 are no entoconid or hypoconulid in the type, but a small hypoconulid is presents in  
220 MNCN 26577. The m1 entocristid is very low reaching the basal level of the paraconid  
221 crown, providing an open talonid valley (Fig. 2B-E-O). This area is broken in MNCN  
222 26577 (Fig. 2M-O). The m2 is trapezoidal. It has a protoconid and a metaconid of  
223 similar size. The trigonid is larger than the talonid. The buccal wall is rectilinear and  
224 includes the paraconid, protoconid and hypoconid. On the contrary, the lingual wall is

225 convex. The lower deciduous carnassial (dp4) (Fig. 2J-L) is very similar to that of the  
226 described m1. It differs in an acuter talonid, being relatively shorter and sharper with a  
227 smaller hypoconid. The P4 paracone-metastyle blade is elongated, compared with the  
228 M1 width (Fig. 3). The parastyle is very low and the protocone is mesially located and  
229 isolated. The M1 lacks the typical eight-shaped mustelid morphology and is reduced  
230 compared with extant gulonines (Fig. 3). The mesial and distal walls are rectilinear,  
231 although the tooth profile is concave in mesial view. It has a large parastylar area, and a  
232 reduced metacone compared to the paracone. There is not metaconule. The protocone is  
233 crest-like and mesially placed. The lingual platform is not mesiodistally expanded. The  
234 specimen MPZ 2020/482 is larger to MNCN 150.007, but morphologically similar,  
235 including a crest-like and mesially placed (Fig. 3B).

236 **Measurements**—Measurements are provided in Table 1.

237

238

## DISCUSSION

239

240 The new mustelid here reported from the latest middle Miocene of the Iberian  
241 Peninsula differs from the living genera *Mustela* and *Martes* in multiple morphological  
242 traits. It differs from *Mustela* (type species *Mustela erminea* Linnaeus, 1758), as well as  
243 other living *Mustela* spp., in a larger size, longer and slender mandible, presence of p1,  
244 longer lower premolars (especially the p4), taller m1 protocone, presence of m1  
245 metaconid, larger and wider m1 talonid with smaller hypoconid, and well-developed  
246 entocristid. M1 with both larger parastylar area and metacone, along with absence of  
247 narrowing of the crown at about mid-width.

248 The seven extant species of marten *sensu stricto* (*Martes*) are categorized among  
249 other traits by having long, relatively narrow skulls, a long auditory bulla, a large P4  
250 protocone (less developed in type species of the genus *M. foina*), an enlarged M1

251 lingual platform (inner lobe), and a relatively elongated and basined m1 talonid, with a  
252 conical hypoconid linking the metaconid by an entocristid (Anderson, 1970, 1994;  
253 Jiangzuo et al., 2021). The new Spanish mustelid also differs from *M. foina* and other  
254 living *Martes* spp. in a smaller size (Figs. 4-5), unicuspid and slenderer p4 comprising a  
255 centrally located cuspid, m1 without mesoconid, stronger metaconid, slenderer talonid,  
256 with much lower entocristid, and more open talonid valley, plus an absent or reduced  
257 hypoconulid. It also has a lesser subquadrangular talonid in occlusal view. The m2 is  
258 more asymmetric, and comprises a more developed talonid. The P4 protocone is  
259 slenderer and the M1 has a larger parastylar area, an absence of both metaconule and  
260 narrowing of the crown at about mid-width, besides of a much more reduced lingual  
261 platform. Therefore, this new form can be confidently described as a genus distinct of  
262 *Martes*. However, based on the hitherto known fossils of this new form, it is difficult to  
263 determine with accuracy its systematic position at the subfamily level. Accordingly, we  
264 provisionally place it into the extant subfamily Guloninae, whose early members, as  
265 *Dehmictis* Ginsburg and Morales, 1992, and *Iberictis* Ginsburg and Morales, 1992, are  
266 recorded in the early Miocene of Central and Western Europe (Valenciano et al.,  
267 2020b).

268         The described specimens of *Aragonictis araid* shown a range of variability in  
269 dental size and morphology comparable to those of marten-like mustelids found in the  
270 localities of Wintershof-West (Dehm, 1950) and Sansan (Peigné, 2012), being also  
271 similar to living *Martes foina* (Figs. 4-5). *Aragonictis araid* specimens from Escobosa  
272 are easily recognized by being the smaller ones, whereas specimens from Toril 3A  
273 represent the largest in size among the sample (Figs. 4-5, Table 1). However, the fact of  
274 sharing a lower p2, p4 with the main cuspid centrally located, together with a great  
275 reduction of the p4 accessory cuspid, a similar m1 talonid (lingually broken in the one

276 from Escobosa), and a reduced M1 lingual platform with a crest-like protocone, allows  
277 the assignment of all these fossils into the same taxon.

278 Over the course of the 19th and 20th centuries, fourteen species of *Martes* have  
279 been described in the Miocene of Europe, ranging from MN3 to MN13 (Ginsburg,  
280 1999; Montoya et al., 2011; Peigné, 2012; Hughes, 2012). They represent a group  
281 widely heterogeneous and unevenly known, which has led researchers to often place  
282 their mustelid material of small size and marten-like morphology inside of the  
283 wastebasket name of *Martes*. Sato et al. (2003) specified *Martes wenzensis* from the late  
284 Pliocene of Weże 1 (Poland) as the oldest known *Martes*. This taxon is very similar in  
285 morphology to living *Martes martes*, but larger in size (Anderson, 1970), and its  
286 assignment to the genus is not questionable. Despite this, *Martes* remains can be found  
287 in older sediments than late Pliocene. Several key features of marten are already present  
288 in late Miocene forms such as *Martes melibulla* from the Vallès-Penedès localities of  
289 Can Llobateres (late Miocene, MN9) and Trinxera Nord de l'Autopista (late Miocene,  
290 MN10) (Petter, 1963; Pons-Moyà, 1990), as well as the early late Miocene *Martes* aff.  
291 *anderssoni* of Can Poncic 1 (MN9), also in the Vallès-Penedès Basin (Petter, 1967).  
292 These traits are the enlargement of the M1 lingual platform, and a relatively elongated  
293 and basined m1 talonid with a conical hypoconid connected with the metaconid by an  
294 entocristid. More complete material of these forms would be needed to further  
295 investigate the validity of this hypothesis.

296 Independent of which taxa represent the oldest record of *Martes*, there are  
297 findings that clearly indicate that abundant small marten-like mustelids from the early  
298 and middle Miocene of Eurasia ascribed to “*Martes*” show a dissimilar morphology  
299 with *Martes* and stand in need of thorough revision (e.g., Hughes, 2012; Peigné, 2012).  
300 Among these heterogeneous sample, four distinct groups can be distinguished:

301 (1) “*Martes*” spp. that are close to *Martes* but exhibit primitive traits which  
302 distinguished them from this genus. This group is composed by the small-sized “*M.*”  
303 *cadeoti* (Fig. 6A-D) and “*M.*” *collongensis* from Vieux-Collonges (middle Miocene,  
304 MN5, France) (Mein, 1958; Roth and Mein, 1987), “*M.*” *burdigaliensis* from Vieux-  
305 Collonges, Artesilla and Artenay (early and middle Miocene, MN4-MN5) (Beaumont,  
306 1974; Azanza et al., 1993; Ginsburg, 2002), and by the large-sized “*M.*” *munki* from  
307 Häder, Sandelzhausen, Sant Quirze del Vallès, La Grive (middle Miocene, MN5-  
308 MN7+8) (Roger, 1900; Villalta Comella and Crusafont Pairó 1943; Viret 1951; Mein,  
309 1958; Nagel et al., 2009) and “*Martes*” *sansaniensis* from Sansan (middle Miocene,  
310 MN6) (Peigné, 2012). All the above include taxa that resemble *Martes* in having a  
311 similar carnassial and M1; a p4 distal accessory cuspid; a relatively elongated and  
312 basined m1 talonid (shorter in “*M.*” *burdigalensis*) with a conical hypoconid linking the  
313 metaconid by an entocristid; a large P4 protocone; an enlarged M1 lingual platform; and  
314 presence of a narrow M1 crown at about mid-width (Fig. 6A-D). Furthermore, all of  
315 these extinct forms share several primitive traits: diastema between p2-3, presence of a  
316 m1 protoconid very tall, m1 metaconid well developed and tall (especially in “*M.*”  
317 *cadeoti*, and “*M.*” *collongensis*), M1 with distinct proportions (being more elongated  
318 buccolingually, Fig. 5) with a M1 parastyle and metacone more developed, a  
319 metaconule, and a protocone located more buccally compared with living *Martes*.  
320 *Aragonictis araid* is different from this group having a lower p2-3; absence of diastema  
321 in the lower dentition; absence or reduction of the distal accessory p4; m1 paraconid and  
322 protoconid close in high, m1 talonid mesiodistally and buccolingually shorter with a  
323 beveled hypoconid, a lower entocristid, reduced hypoconulid and distal cingulid, and a  
324 more open valley; reduced m2; slenderer P4 protocone; and M1 with larger parastyle

325 area, reduced metacone, absent metaconule, absence of narrowing of the crown at about  
326 mid-width, and a much reduced lingual platform.

327 (2) “*Martes*” *sainjoni* from Artenay (type locality), Artesilla and Bezia (Mayet,  
328 1908; Ginsburg and Bulot, 1982; Azanza et al., 1993; Ginsburg, 2002), for which only  
329 the lower dentition is known. This early-middle Miocene mustelid is different from  
330 *Aragonictis* and *Martes* in being a more robust form, and having a distinct m1 talonid  
331 including a massive hypoconid, centrally positioned, and a strong cingulum. More  
332 specifically, *A. araid* differs from “*M.*” *sainjoni* in a smaller size; slenderer mandibular  
333 corpus; lower p4; absence of cingulid in both p4 and m1; shorter length of the trigonid  
334 and less conical m1 hypoconid. Thus, “*M.*” *sainjoni* emerges as closer to basal Miocene  
335 gulonines such as *Dehmictis* Ginsburg and Morales, 1992, *Laphictis* Viret, 1933, and  
336 *Ischyriictis* Helbing, 1930.

337 (3) “*Martes*” *filholi* from La Grive (type locality), Viex-Collonges (Depéret, 1887;  
338 Viret, 1951; Mein, 1958), and (albeit with certain doubts) Rudabánya (Werdelin, 2005).  
339 It has diastema in the lower dentition; higher p2-3; longer m1 talonid; much developed  
340 m2; shorter P4; and a much more distinct M1 with reduced parastyle, enlarged  
341 metacone, a much-enlarged lingual platform and a very marked narrowing of the crown  
342 at about mid-width than *A. araid*. It is clearly different from *Martes*, being probably  
343 more related to *Trochictis* Meyer, 1842, or related genera (see Morlo et al., 2021).

344 (4) Small sized-mustelids with slender dentition comprising “*Martes*”  
345 *delphinensis* and “*Martes*” *laevidens*. The former, which conforms the smallest mustelid  
346 among the analyzed sample (Fig. 4), is recorded throughout the middle Miocene of  
347 Western Europe, in the fossil sites of La Grive (type locality), Vieux-Collonges,  
348 Manchones (MN6, Calatayud-Daroca Basin, Spain), Hostalets de Pierola (MN7+8,  
349 Vallès-Penedès Basin, Spain) (Depéret, 1892; Villalta Comella and Crusafont Pairó

1943; Viret, 1951; Mein, 1958; Petter, 1976), and in all probability La Barranca (MN6,  
Calatayud-Daroca Basin, Spain) (described previously as *Martes* sp. by Peigné et al.,  
2006). “*Martes*” *delphinensis* is represented only by mandibles and lower dentition, so  
it has been scarcely studied in the past. Nevertheless, Mein (1958) described and figured  
a maxillary with a complete M1 (Mein, 1958;fig. 56) for which a re-examination allows  
us to confirm that it may belong to the stem mephitid *Proputorius* Filhol, 1890 which  
also occurs in the locality (*Proputorius pusillus* [Viret, 1951]). The dimensions of *A.*  
*araid* and its superficial similarities with the small-size mustelid “*M.*” *delphinensis*  
makes its comparison somewhat intricate. Indeed, the mandible MNCN 26577 from  
Escobosa was previously described as “*M.*” *delphinensis* in Sesé (1980). *Aragonictis*  
*araid* differs from “*M.*” *delphinensis* in a larger size; a lower p2-3; a central position of  
the main cuspid of the p4; an absence/reduction of the p4 distal accessory cuspid; a m1  
paraconid higher; and a more open and longer m1 talonid with a much lower entocristid.  
With regard to “*Martes*” *laevidens* from the early Miocene (MN3) of Wintershof-West  
(Germany) (Dehm, 1950), this can be considered as the oldest species in the group. Sato  
et al. (2003) discarded its assignation to *Martes* based on the basiocranial fragment  
described by Dehm (1950:fig. 130), but they did not analyze its dentition. The sample  
described in Dehm (1950) has some size variability (Figs. 4-5). The lower dentition is  
slender, and has a diastema between p2-3, a well-developed distal accessory cuspid in  
p4, and a buccolingually reduced m1 talonid. The P4 protocone is relatively robust  
when compared with *A. araid*, and the M1 (although it shows some variability, see Fig.  
6E-N) is characterized by an elongated parastylar area, a reduced metacone (almost  
absent in SNSB-BSPG 1937 II 13372, see Fig. 6L), and a reduced lingual platform with  
some degree of expansion. It must be emphasized that the original ascription by Dehm  
(1950) of the M1 SNSB-BSPG 1937 II 13723 (Fig. 6O) with mustelid features to “*M.*”



375 *laevidens*, must be discarded due to its distinct morphology. *Aragonictis araid* differs  
376 from “*M.*” *laevidens* in having a less sigmoid dp4 with a less developed metaconid;  
377 absence of both diastema between p2-3 and lower cuspids; p4 with less crowned mesial  
378 and distal cingulids; absence or reduction of p4 distal accessory cuspid; beveled m1  
379 hypoconid, slenderer P4; as well as smaller M1 parastylar area with more developed M1  
380 metacone. The extremely reduced metacone in the M1 SNSB-BSPG 1937 II 13372  
381 (Fig. 6L) of “*M.*” *laevidens* is almost fused in a crista with the paracone (Schmidt-  
382 Kittler, 1981). This feature is shared with *Circamustela dechaseauxi* (type species of  
383 *Circamustela* Petter, 1967) from Can Llobateres (late Miocene, MN9, Vallès-Penedès  
384 Basin). The m1 of both species—which is the only possible additional comparison—  
385 shows the same morphological pattern in which the metaconid is reduced and the  
386 talonid is narrow (Petter, 1967, 1976; Valenciano et al., 2020a). For all these reasons,  
387 and considering the limitation of comparisons in the rest of the dentition and the  
388 important separation in age between these two species, it seems convenient to reclassify  
389 the Wintershof-West species as *Circamustela? laevidens* (Dehm, 1950).

390         Additionally, albeit *A. araid* shares several dental traits (including a slender  
391 dentition, a similar P4, and a reduced M1 lingual platform; Valenciano et al., 2020a)  
392 with the early late Vallesian *Circamustela* spp., it is different in many others. For  
393 instance, the new species is smaller in size, and it has absence of diastema between p2-  
394 3, as well as lower p2-3, presence of m1 metaconid (quite reduced in *C. dechaseauxi*),  
395 slenderer m1 talonid with lower entocristid and more open valley, M1 more concave in  
396 distal view with deeper trigone valley, and more developed metacone than the type  
397 species. Moreover, a similar sized M1 of *Circamustela?* appeared in younger (early  
398 Turolian, MN11) sediments of Dorn-Dürkheim 1 (Germany) (Morlo, 1997). Despite its  
399 small size, (closer to *A. araid* than to *Circamustela* spp., Fig. 5), its reduced parastylar

400 area, and the narrowing of the crown at about mid-width, as well as the less reduced  
401 lingual platform, allows us to propose that the German M1 is closer related to  
402 *Circamustela* than to *Aragonictis*.

403 An overview of the described groups suggests the inclusion of *Aragonictis* within  
404 the “*M.*” *delphinensis* and *C.?* *laevidens* group, being probably related to *Circamustela*.  
405 However, more dentognathic material is necessary in order to further determine its  
406 systematic affinities and verify whether these similarities are a consequence of a  
407 convergence towards hypercarnivorism or are instead result of close evolutionary  
408 relationships

409

#### 410 **Paleobiological Insights**

411 Compared with small to medium-sized living gulonines (e.g., stone marten, beech  
412 marten, fisher) of omnivore diets (Larivière and Jennings, 2009) and with Miocene  
413 forms of “*Martes*” from Europe (Fig. 4), *A. araid* shares similarly narrower teeth (e.g.,  
414 m1, P4 and M1) to those of the early Miocene *Circamustela?* *laevidens* and the late  
415 Miocene *Circamustela* (Vallesian, MN9-10) and *Sinictis* (Turolian, MN11-MN13).  
416 Because these late Miocene mustelids have been customarily interpreted as  
417 hypercarnivores (Valenciano et al., 2020a), we interpret *A. araid* as a hypercarnivore  
418 form as well.

419 It is remarkable how the discovery of this new Iberian mustelid and our review of  
420 Miocene “*Martes*” suggest the occurrence of several cladogenesis events in Central and  
421 Western Europe in this epoch. A first event took place at the end of the early Miocene  
422 (MN3-4) and the beginning of the middle Miocene (MN5) in both Central (Germany)  
423 and Western (France and Iberian Peninsula) Europe. During such a relatively long  
424 event, roughly coinciding with the Miocene Climatic Optimum (Zachos et al., 2008),

425 members of the group of “*Martes*” appeared. An increase in the carnivoran’s Spanish  
426 turnover rate during the late Aragonian MN7+8, as noticed by Morales et al. (2015),  
427 informs about a second cladogenesis event. It was probably triggered, among other  
428 factors, by an increase of the precipitation levels compared to the previous biozone (Van  
429 Dam, 2006), thus increasing the forest areas of the region. The presence of small  
430 mustelids has been traditionally considered as indicative of forested habitat (Ginsburg  
431 and Morales, 1992; Baskin, 1998). Therefore, the large diversity of small mustelids in  
432 Toril 3A, which comprises several species of “*Martes*” and the new form *A. araid*,  
433 might suggest the presence of forest patches embedded in a mosaic environment for this  
434 locality at ca. 12.65 Ma. This fits well with the hypothesis of a climate change towards  
435 more humid conditions and increased canopy cover by the latest Aragonian in the  
436 Daroca-Nombrevilla area (DeMiguel et al., 2011, 2012; García Paredes et al., 2016).  
437 Such kind of habitats would have probably been suitable for other contemporaneous  
438 mammals from the same basin customarily interpreted as forest-dwellers. Therefore, the  
439 discovery of *A. araid* strongly indicates that a cladogenesis event for small to medium-  
440 sized mustelids of hypercarnivorous dentition took place, at least at a regional scale, at  
441 the end of the Aragonian (ca. 12.65 Ma). As such, some of these clades seem to have  
442 increased in size during the late Miocene, as occurred for the Vallesian *Circamustela*  
443 (Vallès-Penedès and Tagus Basins, Spain) (Valenciano et al., 2020a), and for later  
444 forms such as the Turolian *Sinictis* (China and Greece) (Zdansky, 1924; Valenciano et  
445 al., 2020a). An in-depth review of marten and weasel-like forms from other  
446 contemporaneous localities from Eurasia would be the logical next step to further  
447 investigate this cladogenesis event at a more global scale during the latest Aragonian.

448

449

## CONCLUSIONS

450

451 We describe new mustelid material from the latest middle Miocene sites of  
452 Andurriales, Toril 3A and Escobosa de Calatañazor (Iberian Peninsula). This form  
453 constitutes a new genus and species that we name as *Aragonictis araid*.

454 Our analyses show that *A. araid* is morphologically different from living *Mustela*  
455 and *Martes*, and also differs from the early and middle European Miocene forms of  
456 Europe ascribed *sensu lato* to “*Martes*” spp., thus rejecting the conventional view that  
457 all small to medium-sized Miocene mustelids belong to *Martes*. A preliminary  
458 reassessment of these heterogenous taxa (formerly considered as *Martes*) allows us to  
459 distinguish four different groups: (1) early to middle Miocene “*Martes*” spp.—distinct  
460 from *Martes sensu stricto*—including “*M.*” *collongensis*, “*M.*” *cadeoti*, “*M.*”  
461 *burdigaliensis*, “*M.*” *munki* and “*M.*” *sansaniensis*; (2) early to middle Miocene  
462 “*Martes*” *sainjoni* from Western Europe—much closer to basal Miocene gulonine (such  
463 as *Dehmictis*, *Laphictis*, and *Ischyriactis*) than to *Martes*; (3) middle Miocene “*Martes*”  
464 *filholi*—a form probably related with *Trochictis*; and (4) early Miocene “*Martes*”  
465 *delphinensis*” and “*Martes*” *laevidens*—the latter being herein reassessed as  
466 *Circamustela*?

467 Finally, from a paleobiological viewpoint, we interpreted the new Iberian  
468 *Aragonictis araid* as a hypercarnivorous mustelid that lived in forest patches of mosaic  
469 environments.

470

471

#### ACKNOWLEDGMENTS

472

473 We thank the following colleagues for kindly providing us comparative material  
474 and photographs of fossil mustelids: P. Mein and E. Robert (UCBL, France), C. Argot  
475 (MNHN), G. Rössner and M. Schellenberger (BSPG, Germany), M. Morlo, O. Kullmer

476 and C. Hemm (SMF, Germany), M. Rummel (Naturmuseum Augsburg, Germany), S.  
477 Fraile and A. Garvía (MNCN, Spain), J. M. Robles and D. M. Alba (ICP, Spain), I.  
478 Canudo (MCNUZ, Spain), L. Costeur (NMB, Switzerland), J. O. R. Ebbestad and V.  
479 Berg-Madsen (PMU, Sweeden), and the staff of Servicio de Técnicas No Destructivas:  
480 Microscopía Electrónica y Confocal y Espectroscopía del MNCN-CSIC. We also thank  
481 C. Langa for finding the fossils from Andurriales, and E. Cantero (MNCN) for the  
482 preparation of the material. We are indebted to the editor T. Martin and the reviewers L.  
483 Werdelin and M. Morlo for their useful comments and suggestions, which made  
484 meaningful improvements to the original manuscript. This study was supported by the  
485 Government of Aragon (Group ref. E33\_20R), the Research Group UCM 910607, the  
486 Spanish Ministry of Economy and Competitiveness and FEDER funds (Research  
487 Projects PGC2018-094122-B-100 and PID2020-116220GB-I00), and the Spanish  
488 Ministry of Science, Innovation, and Universities (“Juan de la Cierva Formación”, ref.  
489 FJC2018-036669-I).

490

#### 491 LITERATURE CITED

492

493 Alcalá, L., A. M. Alonso-Zarza, M. A. Álvarez, B. Azanza, J. P. Calvo, J. C. Cañaveras,  
494 J.A. van Dam, M. Garcés, W. Krijgsman, A. J. van der Meulen, J. Morales, P.  
495 Peláez, A. Pérez-González, S. Sánchez, R. Sancho, and E. Sanz. 2000. El registro  
496 sedimentario y faunístico de las cuencas de Calatayud-Daroca y Teruel. Evolución  
497 paleoambiental y paleoclimática durante el Neógeno. *Revista de la Sociedad*  
498 *Geológica de España*13:323–343.  
499 Anderson, E. 1994. Evolution, prehistoric distribution and systematics of *Martes*;  
500 pp.13–25 in S. W. Buskirk, A. S. Harestad, Raphael and R. A. Powell (eds.),

501 Martens, Sables and Fishers: Biology and Conservation. Cornell University Press,  
502 Ithaca, New York.

503 Anderson, E. 1970. Quaternary evolution of the genus *Martes* (Carnivora, Mustelidae).  
504 Acta Zoologica Fennica 130:1–132.

505 Azanza, B., E. Cerdeño, L. Ginsburg, J. Van der Made, J. Morales, and P. Tassy. 1993.  
506 Les grands mammifères du Miocène inférieur d’Artesilla, bassin de Calatayud-  
507 Teruel (province de Saragosse, Espagne). Bulletin du Museum National d’Histoire  
508 naturelle 15:105–153.

509 Azanza, B., A. M. Alonso-Zarza, M. A. Álvarez-Sierra, J. P. Calvo, S. Fraile, I. García-  
510 Paredes, E. Gómez, M. Hernández, A. van der Meulen, D. DeMiguel, P. Montoya, J.  
511 Morales, X. Murelaga, P. Peláez-Campomanes, B. Pérez, V. Quiralte, M. J. Salesa, I.  
512 M., Sánchez, A. Sánchez, and D. Soria. 2004. Los yacimientos de vertebrados  
513 continentales del Aragoniense superior (Mioceno medio) de Toril, Cuenca de  
514 Calatayud-Daroca. Geo-Temas 6:271–274.

515 Barasoain, D. and B. Azanza. 2018. Geoheritage and education: a practical example  
516 from the Rhinoceros of Toril 3 (Calatayud-Daroca Basin, Spain). Geoheritage  
517 10:363–374.

518 Baskin, J. A. 1998. Mustelidae; pp. 152-173 in C. M. Janis, K. M. Scott, L. L. Jacobs  
519 (eds.), Evolution of Tertiary Mammals of North America, Volume 1: Terrestrial  
520 Carnivores, Ungulates, and Ungulate-like Mammals. Cambridge University Press,  
521 Cambridge.

522 Batsch, A. J. G. C. 1788. Versuch einer Anleitung, zur Kenntniß und Geschichte der  
523 Thiere und Mineralien, für akademische Vorlesungen entworfen und mit den  
524 nöthigsten Abbildungen versehen. Erster Theil. Academische Buchhandlung, Jena.

525 Beaumont, G. de 1974. Un nouveau Mustélide (Carnivora), *Martes burdigaliensis* n.  
526 sp., du Miocène inférieur de Vieux-Collonges, Rhône. Comptes Rendus des Séances,  
527 Société de Physique et d'Histoire naturelle de Genève 9:81–83.

528 Bowdich, T. E. 1821. An Analysis of the Natural Classifications of Mammalia For The  
529 Use Of Students And Travelers. J. Smith, Paris, 115 pp.

530 Dehm, R. 1950. Die Raubtiere aus dem Mittel-Miocän (Burdigalium) von Wintershof-  
531 West bei Eichstätt in Bayern. Abhandlungen der Bayerischen Akademie der  
532 Wissenschaften. Mathematisch-naturwissenschaftliche Klasse, n. F. 58: 1-158.

533 DeMiguel, D., B. Azanza, and J. Morales. 2011. Paleoenvironments and paleoclimate of  
534 the Middle Miocene of central Spain: a reconstruction from dental wear of  
535 ruminants. *Palaeogeography, Palaeoclimatology, Palaeoecology* 302:452–463.

536 DeMiguel, D., I. M. Sánchez, D. M. Alba, J. Galindo, J. M. Robles, and S. Moyà-Solà.  
537 2012. First evidence of *Tethytragus* Azanza and Morales, 1994 (Ruminantia,  
538 Bovidae), in the Miocene of the Vallès-Penedès Basin (Spain). *Journal of Vertebrate*  
539 *Paleontology* 32:1457–1462.

540 Depéret, C. 1887. Recherches sur la succession des faunes de vertébrés miocènes de la  
541 vallée du Rhône. *Archives du Muséum d'Histoire naturelle de Lyon* 4:45–269.

542 Depéret, C. 1892. La faune des Mammifères miocènes de la Grive-Saint-Alban (Isère)  
543 et de quelques autres localités du bassin du Rhône. *Archives du Muséum d'Histoire*  
544 *naturelle de Lyon* 5:1–93.

545 Erxleben, J. C. P. 1777. *Systema regni animalis per classes, ordines, genera, species,*  
546 *varietates cum synonymia et historia animalium. Classis I. Mammalia.* Weigand,  
547 Leipzig: I-XLVII:1–636.

548 Filhol, H. 1890. Étude sur les mammifères de Sansan. *Bibliothèque des Hautes Études*  
549 *section des Sciences naturelles* 37:1–319.

550 García-Paredes, I., M. A. Álvarez-Sierra, L. W. Van den Hoek Ostende, V. Hernández-  
551 Ballarín, K. Hordijk, P. López-Guerrero, A. Oliver, and P. Peláez-Campomanes.  
552 2016. The Aragonian and Vallesian high-resolution micromammal succession from  
553 the Calatayud-Montalbán Basin (Aragón, Spain). *Comptes Rendus Palevol* 15:781–  
554 789.

555 Ginsburg, L. 1999. Order Carnivora; pp. 109–148 in G. E. Rössner, and K. Heissig  
556 (eds.), *The Miocene Land Mammals of Europe*. Friedrich Pfeil, München.

557 Ginsburg, L. 2002. Les carnivores fossiles des sables de l’Orléanais. *Annales de*  
558 *Paléontologie* 88:115–146.

559 Ginsburg, L. and C. Bulot. 1982. Les carnivores du Miocène de Bézian près de la  
560 Romieu. *Proceedings of the Koninklijke Nederlandse Akademie van Wetenschappen*  
561 *Serie B* 85:53–76.

562 Ginsburg, L., and J. Morales. 1992. Contribution à la connaissance des Mustéolidés  
563 (Carnivora, Mammalia) du Miocène d’Europe *Trochictis* et *Ischyrictis*, genres affines  
564 et genres nouveaux. *Comptes Rendus de l’Académie des Sciences* 315:111–116.

565 Gray, J. E. 1825. An outline of an attempt at the disposition of Mammalia into tribes  
566 and families, with a list of the genera apparently appertaining to each tribe. *Annals of*  
567 *Philosophy* 10:337–344.

568 Helbing, H. 1930. Zur Kenntnis der miocänen, “*Mustela*” *zibethoides* Blainville.  
569 *Eclogae Geologicae Helvetiae* 23:637–644.

570 Hughes, S. S. 2012. Synthesis of *Martes* evolutionary history; pp. 3–22 in K.B. Aubry,  
571 W. J. Zielinski, M. G. Raphael, G. Proulx, S. W. Buskirk (eds.), *Biology and*  
572 *Conservation of Martens, Sables, and Fishers*. Cornell University Press, New York.



573 Jiangzuo, Q.-G., D. Gimranov, J.-Y. Liu, S.-Z. Liu, C.-Z. Jin, and J.-Y. Liu. 2021. A  
574 new fossil marten from Jinyuan Cave, northeastern China reveals the origin of the  
575 Holarctic marten group. *Quaternary International* 591:47–58.

576 Kretzoi, M. 1943. *Kochictis centennii* n. g. n. sp. az egeresi felső oligocénből. *Földtani*  
577 *Közlöny* 73:10–17.

578 Larivière, S., and A. P. Jennings. 2009. Family Mustelidae (Weasels and Relatives); pp.  
579 564–656 in D. E. Wilson and R. A. Mittermeier (eds.), *Handbook of Mammals of the*  
580 *World*. 1. Carnivores. Lynx Editions, Barcelona, Spain.

581 Lartet, E. 1851. Notice Sur La Colline de Sansan, Suivie D’Une Recapitulation Des  
582 Diverses Espèces D’Animaux Vertébrés Fossiles, Trouvés Soit À Sansan, Soit Dans  
583 D’Autres Gisements Du Terrain Tertiaire Miocène Dans Le Bassin Souspyrénéen. J.  
584 A. Portes, Auch, 60 pp.

585 Li, B., M. Wolsan, D. Wu, W. Zhang, Y. Xu, and Z. Zeng. 2014. Mitochondrial  
586 genomes reveal the pattern and timing of marten (*Martes*), wolverine (*Gulo*), and  
587 fisher (*Pekania*) diversification. *Molecular Phylogenetics and Evolution* 80:156–64.

588 Linnaeus, C. 1758. *Systema Naturae Per Regna Tria Naturae, Secundum Classes,*  
589 *Ordines, Genera, Species, Cum Characteribus, Differentiis, Synonymis, Locis.*  
590 Laurentius Salvius, Stockholm, 823 pp.

591 Linnaeus, C. 1766. *Systema naturae per regna tria naturae, secundum classes, ordinus,*  
592 *genera, species, cum characteribus, differentiis, synonymis, locis. Tomus I. Editio*  
593 *duodecima, reformata.* Laurentius Salvius, Stockholm. 532 pp.

594 Mayet, L. 1908. Études de Mammifères miocènes des sables de l’Orléanais et des faluns  
595 de la Touraine. *Annales de l’Université de Lyon* 24:1–336.

596 Mein, P. 1958. Les mammifères de la faune sidérolithique de Vieux-Collonges.  
597 *Nouvelles Archives du Muséum d’Histoire naturelle de Lyon* 5:1–122.

598 Meyer von H. 1842. Mittheilungen an Professor Bronn gerichtet. Neues Jahrbuch für  
599 Geologie und Paläontologie 1842:583–589.

600 Montoya, P., J. Morales, and J. Abella. 2011. Musteloidea (Carnivora, Mammalia)  
601 from the late Miocene of Venta del Moro (Valencia, Spain). Estudios Geológicos  
602 67:193–206.

603 Morales, J., J. L. Cantalapiedra, A. Valenciano, D. Hontecillas, S. Fraile, B. A. García  
604 Yelo, P. Montoya, and J. Abella. 2015. The fossil record of the Neogene Carnivore  
605 Mammals from Spain. Palaeobiodiversity and Palaeoenvironments 95:373–386.

606 Morales, J., P. Peláez-Campomanes, P. Pérez, M. T. Alberdi, B. Azanza, M. Pickford,  
607 M. Ríos, O. Sanisidro, G. Alcalde, J. L. Cantalapiedra, S. Fraile, B. García Yelo, A.  
608 R Gómez Cano, V. Hernández-Ballarín, A. Oliver, E. Cantero, A. Valenciano, and P.  
609 Montoya. 2018. Neogene Mammal sites from Molina de Aragón (Guadalajara,  
610 Spain): correlation to other karstic sites of the Iberian Chain, and Geoheritage values.  
611 Geoheritage 10:353–362.

612 Morlo, M. 1997. Die Raubtiere (Mammalia, Carnivora) aus dem Turolium von  
613 Dorn-Dürkheim 1 (Rheinessen). Teil 1: Mustelidae, Hyaenidae, Percrocutidae,  
614 Felidae. Courier Forschungs-Institut Senckenberg 197:11–47.

615 Morlo, M., A. Le Maitre, K. Bastl, T. Engel, H. Lutz, B. Lischewsky, A. von Berg,  
616 and D. Nagel. 2021. First record of the mustelid *Trochictis* (Carnivora,  
617 Mammalia) from the early Late Miocene (MN 9/10) of Germany and a re-  
618 appraisal of the genus *Trochictis*. Historical Biology 33:1183–1195.

619 Nagel, D., C. Stefen, and M. Morlo. 2009. The carnivoran community from the  
620 Miocene of Sandelzhausen (Germany). Paläontologische Zeitschrift 83:151–174.

621 Peigné, S. 2012. Les Carnivora de Sansan; pp559–660 in: S. Peigné, and S. Sen (eds.),  
622 Mammifères de Sansan. Mémoires du Muséum national d'Histoire naturelle. Paris:  
623 Publications du Muséum, 203.

624 Peigné, S., M. J. Salesa, M. Antón, and J. Morales. 2006. New data on carnivores from  
625 the Middle Miocene (Upper Aragonian, MN6) of Arroyo del Val area (Villafeliche,  
626 Zaragoza Province, Spain). *Estudios Geológicos* 62:359–373.

627 Petter, G. 1963. Contribution à l'étude des Mustélidés des bassins néogènes du Vallès-  
628 Penedès et de Calatayud-Teruel (Espagne orientale). *Mémoires de la Société*  
629 *géologique de France* 43:1–44.

630 Petter, G. 1967. Mustélidés nouveaux du Vallésien de Catalogne. *Annales de*  
631 *Paléontologie* 53:93–113.

632 Petter, G. 1976. Étude d'un nouvel ensemble de petits carnivores du Miocène  
633 d'Espagne. *Géologie Méditerranéenne* 3:135–154.

634 Pinel, P. 1792. Recherches sur une nouvelle méthode de classification des quadrupèdes,  
635 fondée sur la structure mécanique des parties osseuses qui servent à l'articulation de  
636 la mâchoire inférieure. *Actes de la Société d'Histoire naturelle de Paris* 1:50–60.

637 Pons-Moyà, J. 1990. Presencia de carnívoros turolenses en el Vallesense terminal  
638 (MN10) de Terrassa (Catalunya). *Paleontologia i Evolució* 23:199–203.

639 Roger, O. 1900. Wirbeltierreste aus dem Dinotheriensande. *Naturwissenschaftlichen*  
640 *Vereins für Schwaben und Neudorf in Augsburg* 34:53–70.

641 Roth, C. and P. Mein. 1987. *Martes collongensis* n. sp. aus der miozänen Fundstelle  
642 Vieux-Collonges (Dépt. Rhône, Frankreich). *Mainzer geowissenschaftliche*  
643 *Mitteilungen* 16:157–164.

- 644 Samuels, J. X. and J. Cavin. 2013. The earliest known fisher (Mustelidae), a new  
645 species from the Rattlesnake Formation of Oregon. *Journal of Vertebrate*  
646 *Paleontology* 33: 448-454.
- 647 Samuels, J.X., K. E. Bredehoeft, and S. C. Wallace. 2018. A new species of *Gulo* from  
648 the early Pliocene Gray fossil site (eastern United States); rethinking the evolution of  
649 wolverines. *PeerJ* 6: p.e4648.
- 650 Schmidt-Kittler, N. 1981. Zur Stammesgeschichte der marderverwandten  
651 Raubtiergruppen. *Eclogae Geologicae Helvetiae* 74:753–801.
- 652 Smith, J. B., and P. Dodson. 2003. A proposal for a standard terminology of anatomical  
653 notation and orientation in fossil vertebrate dentitions. *Journal of Vertebrate*  
654 *Paleontology* 23:1–12.
- 655 Stach, J. 1959. On some Mustelinae from the Pliocene bone breccia of Węże. *Acta*  
656 *Palaeontologica Polonica* 4:101–117.
- 657 Sato, J. J., T. Hosoda, M. Wolsan, K. Tsuchiya, M. Yamamoto, and H. Suzuki. 2003.  
658 Phylogenetic relationships and divergence times among mustelids (Mammalia:  
659 Carnivora) based on nucleotide sequences of the nuclear interphotoreceptor retinoid  
660 binding protein and mitochondrial cytochrome b genes. *Zoological Science* 20:243–  
661 264.
- 662 Sesé, C. 1980. Mamíferos del Mioceno de Escobosa de Calatañazor (Soria). Ph.D.  
663 dissertation, Universidad Complutense de Madrid, Madrid, 388 pp.
- 664 Valenciano, A. 2017: Mofetas, martas, tejones y rateles gigantes del Cerro de los  
665 Batallones; pp. 322–336 in J. Morales (ed), *La Colina de los Tigres Dientes de Sable.*  
666 *Los Yacimientos Miocenos del Cerro de los Batallones* (Torrejón de Velasco,  
667 Comunidad de Madrid). Museo Arqueológico Regional, Madrid.

668 Valenciano, A., A. Pérez-Ramos, J. Abella, and J. Morales. 2020a. A new  
669 hypercarnivorous mustelid (Mammalia, Carnivora, Mustelidae) from Batallones, late  
670 Miocene (MN10), Torrejón de Velasco, Madrid, Spain. *Geodiversitas* 42:103–121.

671 Valenciano, A., J. Abella, D. M. Alba, J. M. Robles, M. A. Álvarez-Sierra, and J.  
672 Morales. 2020b. New early Miocene material of *Iberictis*, the oldest member of the  
673 wolverine lineage (Carnivora, Mustelidae, Guloninae). *Journal of Mammalian*  
674 *Evolution* 27:73–93.

675 Van Dam, J. A. 2006. Geographic and temporal patterns in the late Neogene 12-3Ma  
676 aridification of Europe: the use of small mammals as paleoprecipitation proxies.  
677 *Palaeogeography, Palaeoclimatology, Palaeoecology* 238:190–218.

678 Van Dam, J. A., W. Krijgsman, H. Abels, M. A. Álvarez-Sierra, I. García-Paredes, P.  
679 López-Guerrero, P. Peláez-Campomanes, and D. Ventrà. 2014. Updated chronology  
680 for the Middle to Late Miocene mammal sites of the Daroca Area (Calatayud-  
681 Montalbán Basin, Spain). *Geobios* 47:325–334.

682 Villalta Comella J. F. de, and M. Crusafont Pairó. 1943. Los vertebrados del Mioceno  
683 continental de la cuenca del Vallès-Penedès (provincia de Barcelona). I. Insectívoros.  
684 II. Carnívoros. *Boletín del Instituto Geológico y Minero de España* 56:145–336.

685 Viret, J. 1933. Contribution à l'étude des Carnassiers miocènes de La Grive-Saint-  
686 Alban (Isère). *Travaux du Laboratoire de Géologie de la Faculté des Sciences de*  
687 *Lyon* 21:1–31.

688 Viret, J. 1951. Catalogue critique de la faune des Mammifères miocènes de La Grive  
689 Saint-Alban (Isère). Première partie. Chiroptères, Carnivores, Édentés pholidotes.  
690 *Nouvelles Archives du Muséum d'Histoire naturelle de Lyon* 3:1–104.

691 Wang, X., Z. J., Tseng, and G. T. Takeuchi. 2012. Zoogeography, Molecular  
692 Divergence, and the Fossil Record-the Case of an Extinct Fisher, *Pekania*

693 *palaeosinensis* (Mustelidae, Mammalia), from the Late Miocene Baogeda Ula  
694 Formation, Inner Mongolia. *Vertebrata Palasiatica* 50:293–307.

695 Werdelin, L. 2005. The carnivores of Rudabánya; pp. 163–180 in: R. L. Bernor, L.  
696 Kordos and L. Rook (eds.), *Multidisciplinary Research at Rudabánya*.  
697 *Palaeontographia Italica* 90, Italy.

698 Werdelin, L., and S. Peigné. 2010. Carnivora; pp. 603–657 in L. Werdelin and W.  
699 Sanders (eds.), *Cenozoic Mammals of Africa*. University of California Press,  
700 Berkeley, California.

701 Zachos, J.C., Dickens, G.R., and Zeebe, R.E. 2008. An early Cenozoic perspective on  
702 greenhouse warming and carbon-cycle dynamics. *Nature* 451:279–283.

703 Zdansky, O. 1924. Jungtertiäre carnivoren Chinas. *Palaeontologica Sinica* 2:1–149.

704 Submitted July 27, 2021; revisions received August 27, 2021; accepted Month DD,  
705 YYYY

#### 706 FIGURE CAPTIONS

707 FIGURE 1: Geographic location of fossil localities with *Aragonictis araid* gen. et sp.  
708 nov. in the Iberian Peninsula. **Abbreviations:** **1**, Escobosa de Calatañazor (Almazan  
709 Basin); **2**, Toril 3A (Calatayud-Daroca Basin); and **3**, Andurriales (Calatayud-Daroca  
710 Basin). Modified from Morales et al. (2018). [planned for 2/3 page width]  
711

712 FIGURE 2: Mandibles and lower dentition of *Aragonictis araid* gen. et sp. nov. from  
713 Andurriales, Toril 3A, and Escobosa de Calatañazor. **A–C**, MNCN 150.003 (holotype)  
714 from Andurriales, left fragmentary hemimandible in **A**, buccal, **B**, lingual and **C**,  
715 occlusal views; **D–I**, MNCN 150.004, right fragmentary hemimandible with m1 (**D–F**)  
716 and p2-3 (**G–I**) from Andurriales in **D**, buccal, **E**, lingual, **F**, occlusal, **G**, buccal, **H**,  
717 lingual, and **I**, occlusal views; **J–L**, MPZ 2020/474, left dp4 from Toril 3A in **J**, buccal,  
718 **K**, lingual, and **L**, occlusal views; **M–O**, MNCN 26577, right fragmentary

719 hemimandible, screenshots of the 3D model of the CT scans from Escobosa de  
720 Calatañazor in **M**, buccal, **N**, occlusal, and **O**, lingual views. [planned for full-page  
721 width]

722

723 FIGURE 3: Maxillary and upper dentition of *Aragonictis araid* gen. et sp. nov. from  
724 Escobosa de Calatañazor and Toril 3A. **A** MNCN 150.007, left fragmentary maxillary  
725 from Escobosa de Calatañazor. Screenshots of the 3D model from CT scans in stereo  
726 occlusal views; **B**, MPZ 2020/482, left fragmentary M1 from Toril 3A in occlusal view.  
727 [planned for column width]

728

729 FIGURE 4: Bivariate plot of the length (L) and width (W) of the m1 of Neogene  
730 marten-like mustelids and the extant *Martes foina* (type species of *Martes*). The linear  
731 regression a' ( $r^2 = 0.90$ ) is defined by Miocene "*Martes*", *Martes melibulla* and *Pekania*  
732 *palaeosinensis*, mostly characterized by their robust m1 talonid. The linear regression b'  
733 ( $r^2 = 0.04$ ) is defined by a sample of 19 specimens of *M. foina*. The linear regression c'  
734 ( $r^2 = 0.85$ ) is defined by relatively hypercarnivorous mustelids, characterized by slender  
735 m1 and comprises *Aragonictis araid*, *Circamustela* spp., and *Sinictis dolichognathus*.  
736 Values given in mm (Log). **Abbreviations:** **r2**, coefficient of determination; **Log**,  
737 logarithm; **1**, variability range of selected *M. foina*; **2**, variability range of "*Martes*"  
738 *munki* from numerous localities of Europe (MN4-MN8). The m1s pictures are showed  
739 unscaled between them. Metric data from: Mayet (1908); Zdansky (1924); Villalta  
740 Comella and Crusafont Pairó (1943); Dehm (1950); Viret (1951); Mein (1958); Petter  
741 (1963,1967, 1976); Beaumont (1974); Ginsburg and Bulot (1982); Roth and Mein  
742 (1987); Pons-Moyà (1990); Azanza et al. (1993); Ginsburg (2002); Peigné et al. (2006);  
743 Nagel et al. (2009); Peigné (2012); Valenciano et al. (2020a) and this work. [planned for  
744 full-page width]

745

746 FIGURE 5: Bivariate plot of the length (L) and width (W) of the M1 of Neogene  
747 marten-like mustelids and the extant *Martes foina* (type species of *Martes*). Values  
748 given in mm (Log). The ellipse marks the variability range of selected living *M. foina*  
749 based on 20 specimens. Metric data from: Zdansky (1924); Dehm (1950); Viret (1933,  
750 1951); Mein (1958); Petter (1976); Morlo (1997); Peigné (2012); Valenciano et al.  
751 (2020a), and this work. [planned for full-page width]

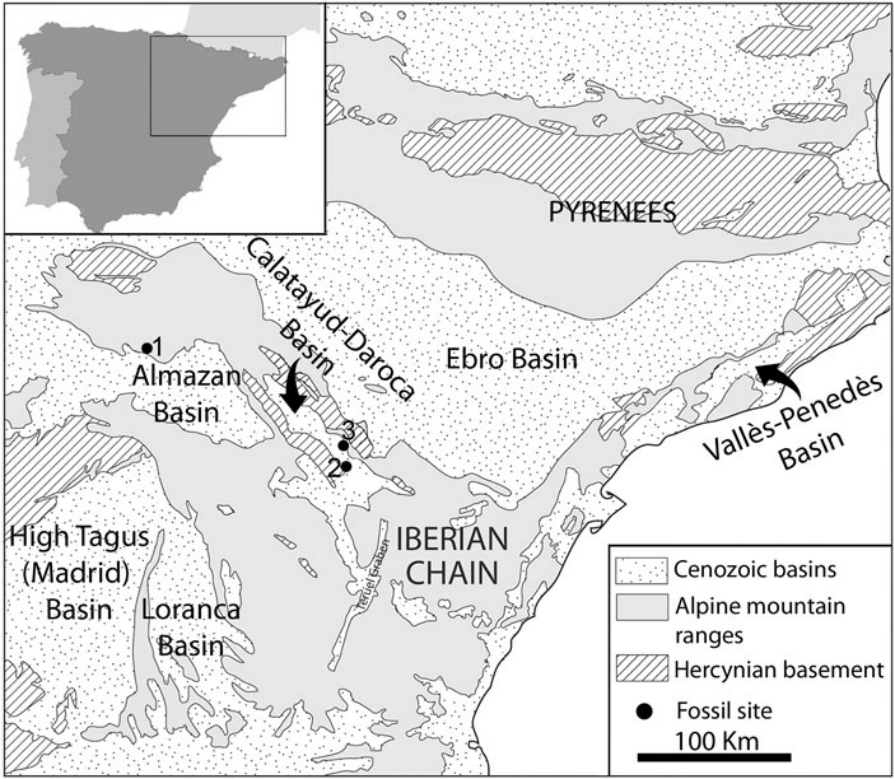
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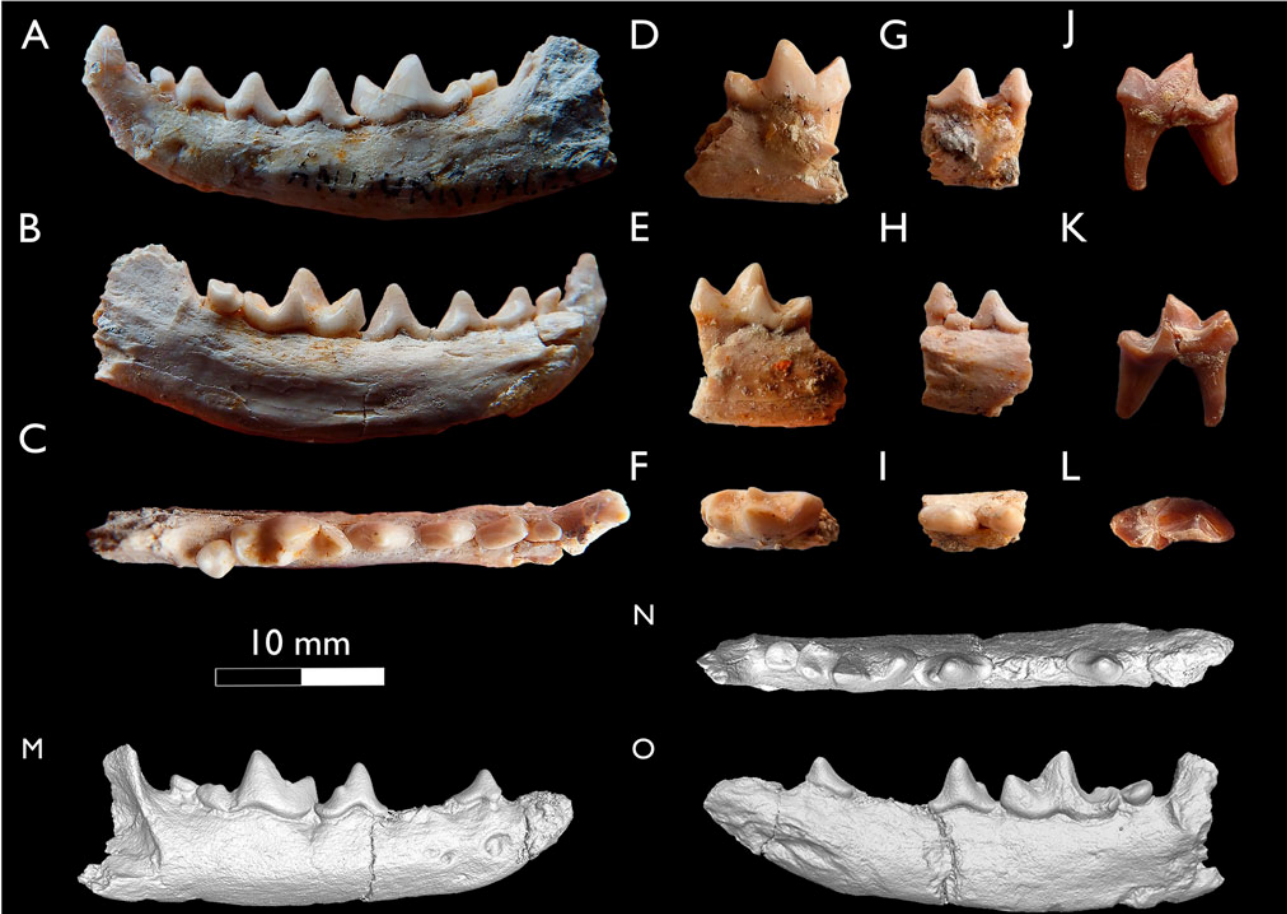
753 FIGURE 6: Dentognathic remains of “*Martes*” *cadeoti* from Vieux-Collonges (middle  
754 Miocene, MN5, France) and both *Circamustela? laevidens* and unknown Mustelidae  
755 indeterminate from Wintershof-West (early Miocene, MN3, Germany). A–D, “*Martes*”  
756 *cadeoti* from Vieux-Collonges. A–C, UCBL-FSL 65759, right m1 (holotype) in A,  
757 buccal, B, lingual and C, occlusal views; D, UCBL-FSL 65758, left M1 (paratype) in  
758 occlusal view; E–N, *Circamustela? laevidens* from Wintershof-West. E–G, SNSB-  
759 BSPG 1937II 13306, right hemimandible with p4-m1 (holotype) in E, buccal, F, lingual  
760 and G, occlusal views; H–J, SNSB-BSPG 1937II 13307, left hemimandible with p2, p4-  
761 m1 in H, buccal, I, lingual and J, occlusal views; K, SNSB-BSPG 1937II 13902, right  
762 hemimandible with p2-4, and a fragmented m1; L. SNSB-BSPG 1937II 13372, right  
763 maxillary with P4-M1 in occlusal view; M. SNSB-BSPG 1937II 13722, left P4 in  
764 occlusal view; N. SNSB-BSPG 1937II 13724, left M1 in occlusal view; O. Unknown  
765 Mustelidae from Wintershof-West. SNSB-BSPG 1937II 13723, right M1 in occlusal  
766 view. [planned for full-page width]



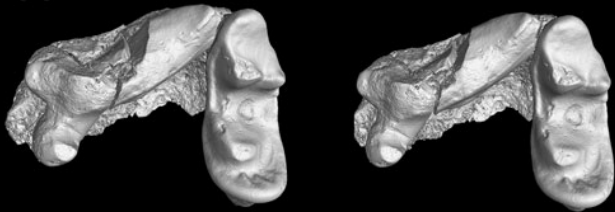
TABLE 1. Tooth measurements (in mm) of the specimens of *Aragonictis araid* gen. et sp. nov. from Andurriales, Toril 3A and Escobosa de Calatañazor.

	c		p1		p2		p3		p4		m1		m2		dp4		P4		M1	
	L	W	L	W	L	W	L	W	L	W	L	W	L	W	L	W	L	W	L	W
Andurriales																				
MNCN 150.003	2.9	2.4	1.3	1.7	3.0	1.6	3.7	1.7	4.5	1.8	7.1	3.0	2.1	2.2	—	—	—	—	—	—
MNCN 150.004	—	—	—	—	3.2	1.8	3.3	2.0	—	—	7.3	3.1	—	—	—	—	—	—	—	—
Escobosa de Calatañazor																				
MNCN 26577	—	—	—	—	2.9	1.5	—	—	4.3	1.9	6.5	2.6	1.6	1.7	—	—	—	—	—	—
MNCN 150.007	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	6.3	3.2	2.6	6.2
Toril 3A																				
MPZ 2020/482	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	3.0	—
MPZ 2020/474	—	—	—	—	—	—	—	—	—	—	—	—	—	—	7.6	3.0	—	—	—	—





A

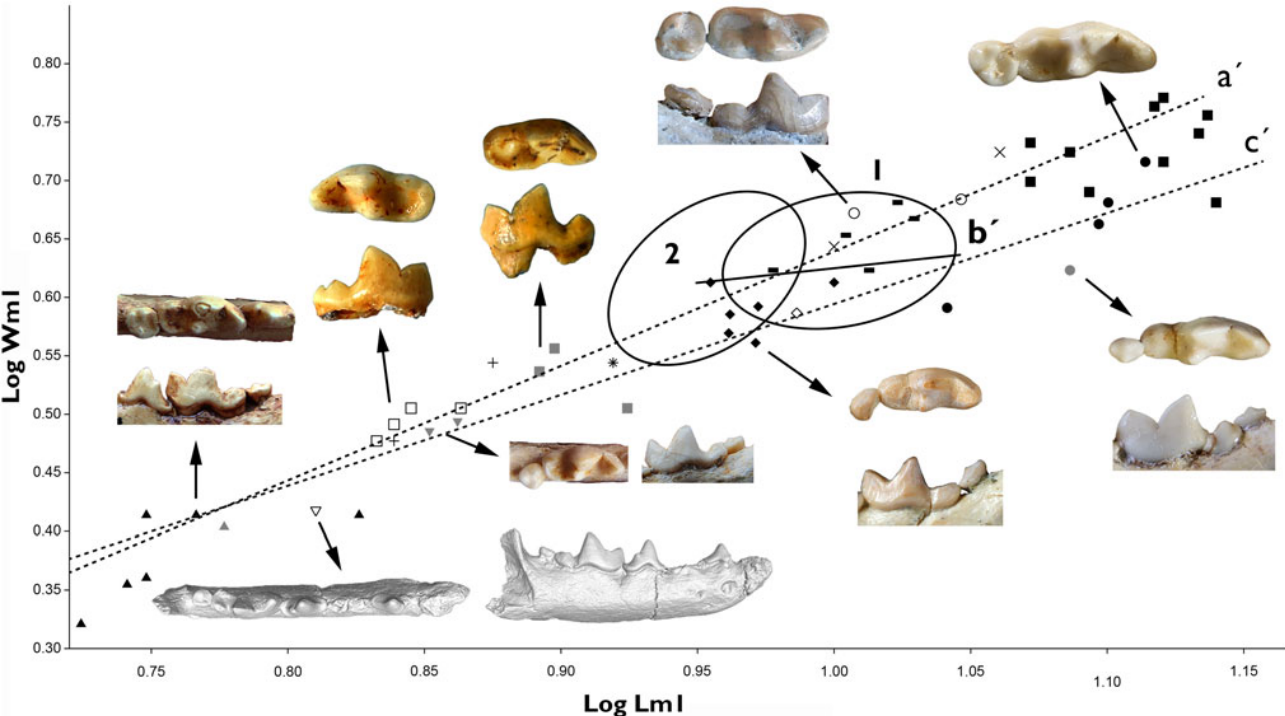


B



5 mm





+ *Circamustela? laevidens* MN3

■ “*Martes*” *sainjoni* MN4

■ “*Martes*” *burdigaliensis* MN4-MN5

□ “*Martes*” *cadeoti* Vieux-Collonges MN5

\* “*Martes*” *collongensis* Vieux-Collonges MN5

▲ “*Martes*” *delphinensis* MN5-MN8

× “*Martes*” *filholi* MN5-MN8

▲ “*Martes*” sp. La Barranca MN6

■ “*Martes*” *sansaniensis* sp. MN6

▼ *Aragonictis araid* Andurriales MN7+8

▽ *Aragonictis araid* Escobosa de Calatañazor MN7+8

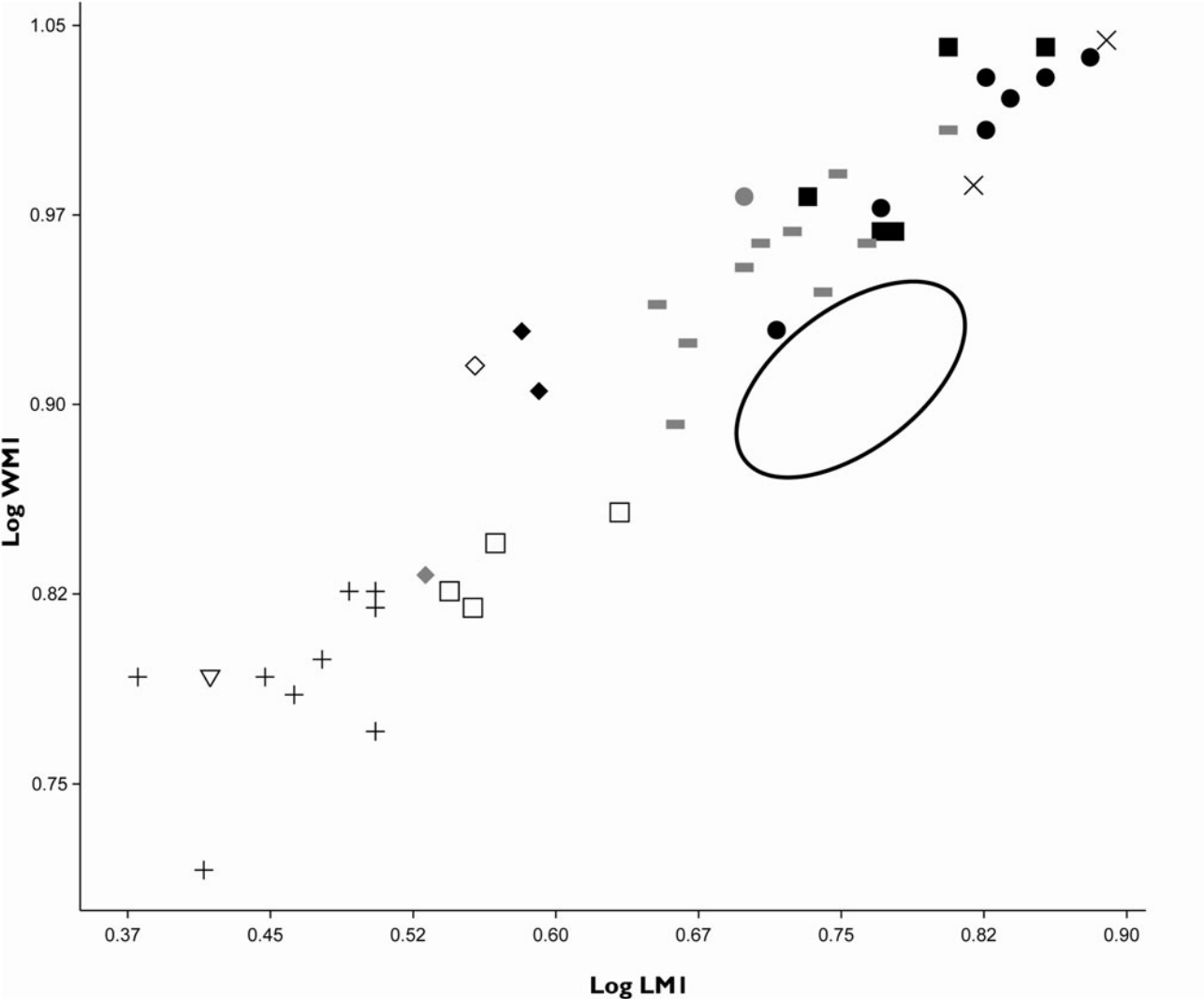
◇ *Circamustela dechaseauxi* MN9

◆ *Circamustela peignei* MN10

○ *Martes melibulla* MN9

● *Sinictis dolichognathus* MN11-MN13

● *Pekania palaeosinensis* MN11-MN13



+ *"Martes" laevidens* MN3

□ *"Martes" cadeoti* Vieux-Collonges MN5

■ *"Martes" sansaniensis* sp. MN6

× *"Martes" filholi* MN5-MN8

— *"Martes" munki* MN5-MN8

▽ *Aragonictis araid* Escobosa de Calatañazor MN7+8

◇ *Circamustela dechaseauxi* MN9

◆ *Circamustela peignei* MN10

◆ *Circamustela? sp.* Dorn-Dürkheim I MN11

● *Sinictis dolichognathus* MN11-MN13

● *Pekania palaeosinensis* MN11-MN13

