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# Palaeoecological implications of the sympatric distribution of two species of *Machairodus* (Felidae, Machairodontinae, Homotherini) in the Late Miocene of Los Valles de Fuentidueña (Segovia, Spain)

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## ABSTRACT

In this paper, we study a sample of cranial, mandibular and dental remains of two species of the machairodontine felid genus *Machairodus* from the Early Vallesian (MN 9, around 10 Ma) site of Los Valles de Fuentidueña (Segovia, Spain): the tiger-sized *Machairodus aphanistus*, and the smaller and more primitive *M. alberdiae*; a species which is only known from this site. The fossils of these two sympatric populations are compared with the most abundant samples of *M. aphanistus* from the Late Vallesian (MN 10), younger sites of Batallones-1 and Batallones-3 (Torrejón de Velasco, Madrid, Spain). The results support the specific separation of *M. alberdiae* from *M. aphanistus* based on several differences in teeth size and proportions. Besides this, we observed differences among the analysed samples of *M. aphanistus*, indicating a differentiation between the older and more primitive form from Los Valles de Fuentidueña, and the younger and more derived one from the two Batallones sites. These differences fit well with the morphological evolution of this lineage towards the more derived Turolian *Amphimachairodus giganteus*. Finally, a relatively structured, patched habitat, combining the presence of open landscapes with shrubby and wooded areas, is inferred to explain the sympatric distribution of these two large machairodontines in Los Valles de Fuentidueña.

## ARTICLE HISTORY

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Vallesian; Miocene;  
Felidae; Machairodontinae;  
*Machairodus*; Spain

## Introduction

The sabre-toothed felid *Machairodus aphanistus* entered Europe in the Early Vallesian (MN 9), as a part of an immigration event from Asia known as the ‘*Hipparion datum*’, which involved the dispersal of several other large mammals (Berggren and Van Couvering 1974; Bernor et al. 1988; Steininger et al. 1996; Lunkka et al. 1999; Antón et al. 2004; Koufos et al. 2005). *Machairodus aphanistus* played the role of top predator in the European mammalian faunas of the Late Miocene, and its presence seems to have displaced other large carnivores such as amphicyonids and barbooufelids (Agustí and Antón 2002). At the end of the Vallesian, *M. aphanistus* itself is replaced in the faunas by the more derived, similarly sized *Amphimachairodus giganteus*, although the phylogenetic relationships between them are still not clear, and the origin of *M. aphanistus* is virtually unknown (de Beaumont 1975; Ginsburg et al. 1981; Antón et al. 2004, 2013; Turner et al. 2011). Sotnikova (1992) summarized the set of morphological features defining *M. aphanistus*: (i) small lower incisors arranged in a straight row; (ii) large lower canines; (iii) large premolars with a complete set of additional cusps; (iv) m1 with a well-developed metaconid, talonid complex, and a strong protoconid; (v) absence of mandibular flange; and (vi) low mandible height. In contrast, *A. giganteus* showed more derived cranial

and dental traits, such as: (i) more flattened upper canines; (ii) reduced lower canines; (iii) larger carnassial teeth; (iv) reduced coronoid process; and (v) moderately developed mandibular flange. It is widely accepted that both genera *Machairodus* and *Amphimachairodus* can be included within the same clade of relatively primitive machairodonts (Ginsburg et al. 1981; Morlo and Semenov 2004; Werdelin and Sardella 2006; Werdelin et al. 2010; Antón et al. 2004, 2013; Turner et al. 2011).

The Early Vallesian (MN 9) fossil site of Los Valles de Fuentidueña (Segovia province, Spain) was excavated as early as 1940 (Almela et al. 1944), yielding an interesting association of vertebrates dominated by large mammals (Meléndez et al. 1944; Crusafont-Pairó and Ginsburg 1973; Ginsburg et al. 1981; Morales and Soria 1981). Among them, there is a relatively rich fauna of carnivores, including one of the last known European Amphicyonidae (*Magericyon castellanus*) and two species of large machairodontine felids: *Machairodus aphanistus* and the smaller *M. alberdiae* (Alberdi et al. 1981; Ginsburg et al. 1981; Peigné et al. 2008).

The Cerro de Los Batallones palaeontological complex is located near the village of Torrejón de Velasco (Madrid province, Spain), on a low hill of around 700 m of elevation, located around 30 km south of Madrid city. Nine fossil localities have been found

over more than 25 years of excavations (Morales et al. 2008; Calvo et al. 2013). All the localities were formed as hourglass-shaped cavities up to 15 m deep, non-connected but some of them very closely located, and hosted in mudstone (mostly sepiolite), chert and carbonate bedrock (Calvo et al. 2013). These cavities acted as natural traps for the animals inhabiting the area, and thus many predators and scavengers were attracted by an easy meal. But, once into the trap, the slippery walls of sepiolite hindered any attempt to escape from the hole, and the carnivorans were

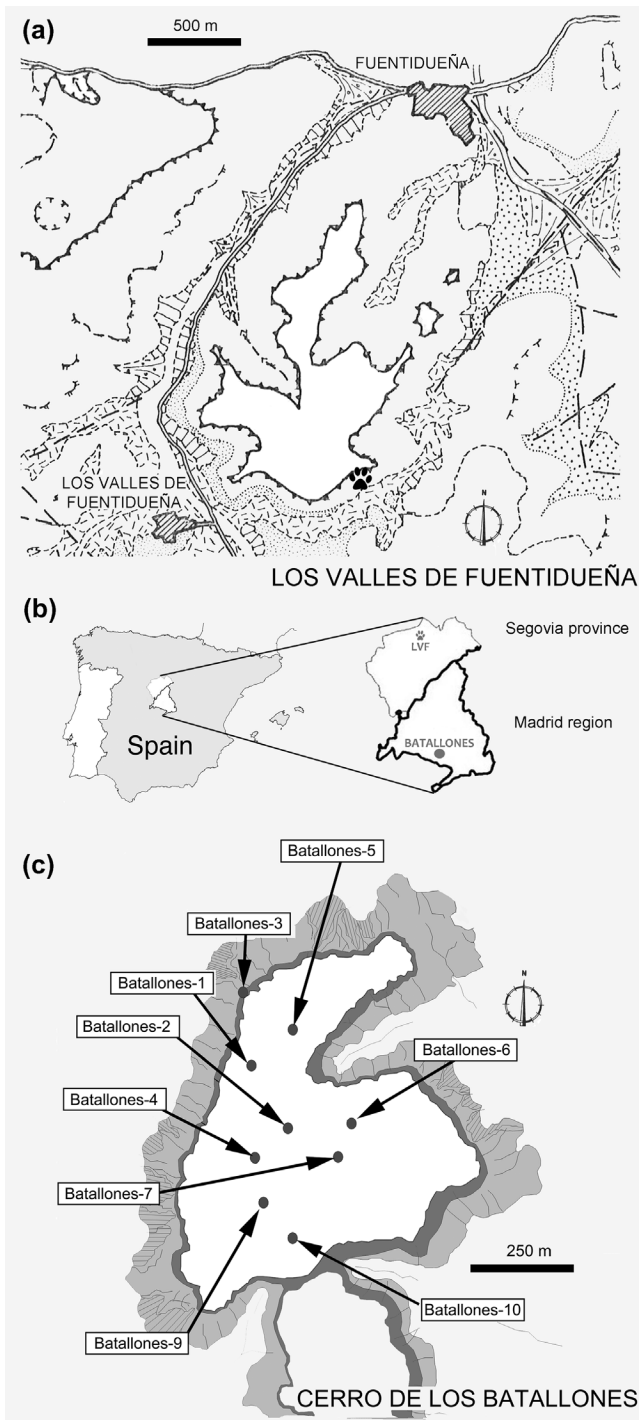
also entrapped (Antón and Morales 2000; Morales et al. 2008). This entrapping lasted for a relatively short time, as the cavity was gradually filled with sediments (mainly greenish clay and carbonates) (Antón and Morales 2000; Calvo et al. 2013). This recurrent event produced one of the richest accumulations of Miocene carnivorans in the World. Among these carnivorans, two species of sabre-toothed felids are especially abundant in the Batallones sites, the leopard-sized *Promegantereon ogygia*, and the much larger, lion-sized *Machairodus aphanistus* (Antón et al. 2004; Salesa et al. 2005; 2006, 2010a, 2010b; Monescillo et al. 2014; Siliceo et al. 2014). Previous studies on the samples of these two taxa from the localities of Batallones-1 and Batallones-3 have shown several morphological differences between them, supporting the existence of some temporal separation between the two sites (Monescillo et al. 2014; Siliceo et al. 2014).

In the present paper, we compare the dental samples of *M. aphanistus* from Los Valles de Fuentidueña, Batallones-1 and Batallones-3 to assess their intraspecific variability, checking if all these populations show similar degree of variability. Also, we have compared these samples to the dental material of the much more poorly known species *M. alberdiae*, to elucidate its actual systematic status. We found statistically significant differences between *M. aphanistus* and *M. alberdiae*, supporting the taxonomic validity of the latter as a more primitive form.

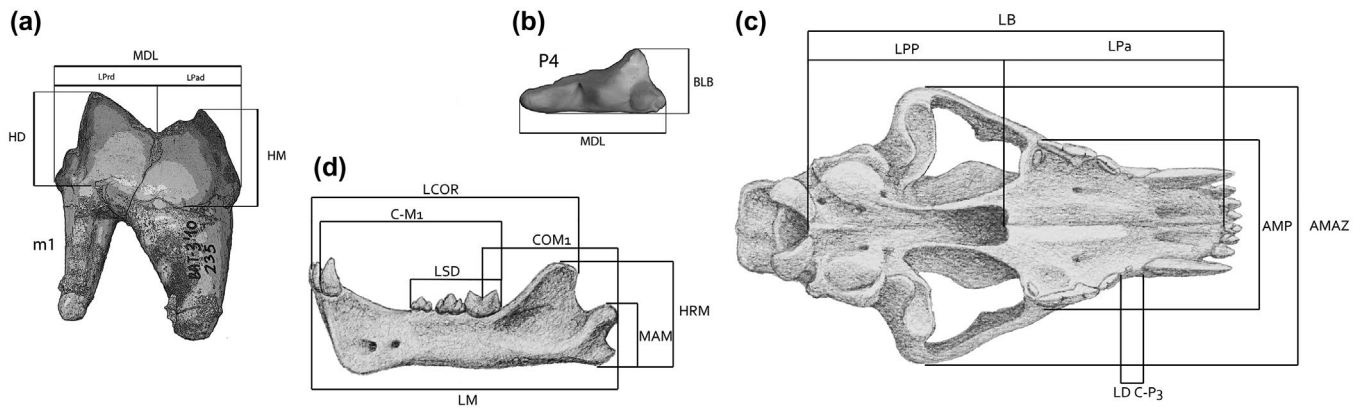
## Material and methods

Samples of the genus *Machairodus* are housed at the collections of the Museo Nacional de Ciencias Naturales-CSIC (Madrid, Spain). Fossils of *M. aphanistus* from Cerro de los Batallones sites come from the excavation campaigns of 1991–2008 (Batallones-1) and 2005–2011 (Batallones-3) (Figure 1(a)–(b), all of them directed by Prof. J. Morales (MNCN-CSIC). On the other hand, Los Valles de Fuentidueña (MN 9, Segovia, Spain) site is known from the 1940s (Almela et al. 1944; Meléndez et al. 1944; Villalta and Crusafont 1948) (Figure 1(b)–(c), and was exhaustively excavated during the campaigns of 1978–1981 carried out by the Unidad Estructural de Paleontología, Instituto de Geología de Madrid (CSIC) (Alberdi et al. 1981).

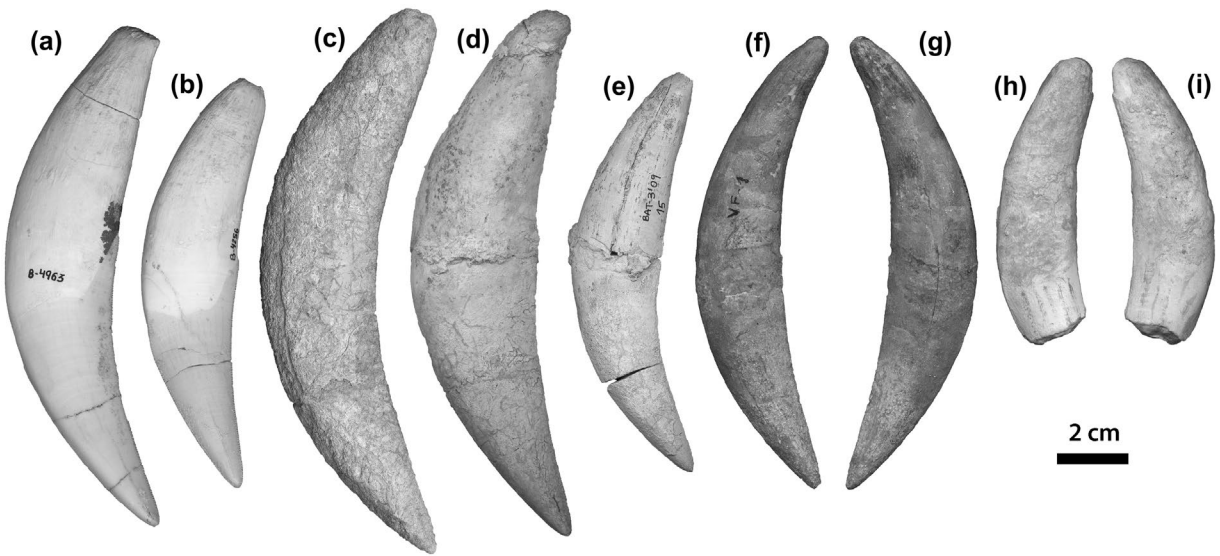
Anatomical descriptions follow the terminology of Barone (2010) and the Nomina Anatomica Veterinaria (Waibl et al. 2005). Measurements were taken with a digital calliper of 150 mm, and with a manual precision calliper of 500 mm, they are shown in Figure 2 and in Table 3. Quantitative data were analysed using the Student t and Welch tests using the statistic software package IBM SPSS Statistic 19.0 (results in Tables 1–3). To keep the independence of data between the two studied populations, the paired fossils of the same individual (e.g. right and left P4 from the same skull) were considered as a unique data, using the mean between both values. Finally, a principal component analysis (PCA) was performed to assess the total explained variance, using the three main measurements taken for each piece (MDL, BLW and H; except for the m1 sample, which did not include HD, HM, LPad, LPrd or MDL due to the worn of the cuspids) (see Measurements Abbreviations). The first component (PC1) of the PCA was analysed using Student t and Welch tests (see Table 3). Minimal number of individuals (MNI) was estimated on the base of adult cranial, mandibular and dental material: MNI = 15 for *M. aphanistus* from Batallones-1, MNI = 5 for *M.*



**Figure 1.** Los Valles de Fuentidueña, Segovia, Spain (a) schematic map, modified from Mazo (1981); Spain map showing (b) the location of Segovia and Madrid provinces; Cerro de los Batallones (Torrejón de Velasco, Madrid, Spain) (c) schematic map, showing the location of the nine fossiliferous sites found in the area.



**Figure 2.** Measurements for each studied cranial, mandibular and dental element. (a) labial view of the m1, (b) occlusal view of the P4, (c) labial view of the mandible, (d) ventral view of the skull.



**Figure 3.** Upper canines of *Machairodus aphanistus* from BAT-1, BAT-3 and from Los Valles de Fuentidueña. (a) left C (B-4963) in labial view, (b) right C (B-4256) in lingual view, (c) left C (BAT-3'07 981) in labial view, (d) left C (BAT-3'09 82) in labial view, (e) left C (BAT-3'09 15) in labial view; (f, g) left C (MNCN-46577) in (f) labial and (g) lingual view respectively; (h, i) cast of right C (MNCN-46578) in (h) lingual and (i) labial view respectively.

*aphanistus* from Batallones-3, MNI = 4 for *M. aphanistus* from Los Valles de Fuentidueña, and MNI = 3 for *M. alberdiae* from Los Valles de Fuentidueña.

For our study, we considered the different sites (Batallones-1, Batallones-3 and Los Valles de Fuentidueña) as independent populations of *M. aphanistus*, as only in the population from Los Valles de Fuentidueña there is evidence of sympatry with another species of the genus *Machairodus* (*M. alberdiae*).

### Abbreviations

**Institutional Abbreviations:** BAT-1 and B, Batallones-1; BAT-3, Batallones-3; B/S, fossils from Batallones-1 not found *in situ*; MNCN, Museo Nacional de Ciencias Naturales-CSIC; LVE, Los Valles de Fuentidueña.

**Anatomical Abbreviations:** C, upper canine; c, lower canine; I, upper incisor; i, lower incisor; P, upper premolar; p, lower premolar; m, lower molar; M, upper molar.

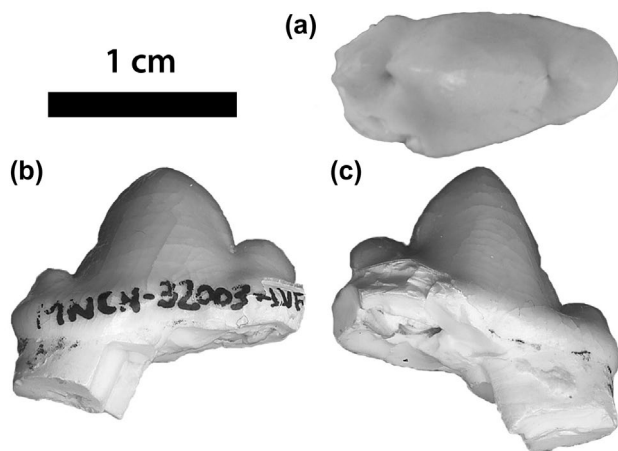
**Measurements Abbreviations:** BLW, bucolingual width; H, main crown height; HD, m1 protoconid height; HM, m1 paraconid height; LPad, m1 paraconid length; LPrd, m1 protoconid length; MDL, mesiodistal length.

### Systematic palaeontology

Class Mammalia Linnaeus, 1758  
 Order Carnivora Bowdich, 1821  
 Suborder Feliformia Kretzoi, 1945  
 Family Felidae Fischer, 1817  
 Subfamily Machairodontinae Gill, 1872  
 Genus *Machairodus* Kaup, 1833  
*Machairodus aphanistus* Kaup 1832

Figure 3(f)–(i), Figure 4(a)–(c), Figure 5(a)–(c), Figure 6(a)–(f).

Referred material: the list of fossils from Batallones-1, Batallones-3 and from Los Valles de Fuentidueña are included in Supplementary Material 1.



**Figure 4.** Lower left p3 of *Machairodus aphanistus* from Los Valles de Fuentidueña. (a–c) lower p3 (MNCN-32003). (a) occlusal, (b) labial, and (c) lingual view respectively.

**Table 1.** Summarized results of the Student *t* tests or Welch test, showing the variables that showed significant differences in the comparison of *Machairodus alberdiae* from Los Valles de Fuentidueña with *Machairodus aphanistus* from both Batallones-1 and Batallones-3.

Site compared	Piece	Variable	<i>p</i>	Comments
BAT-1	I3	MDL	0.005	<i>M. alberdiae</i> shows shorter I3
BAT-1	I3	BLW	0.008	<i>M. alberdiae</i> shows narrower I3
BAT-1	I3	H	0.013	<i>M. alberdiae</i> shows lower I3
BAT-1	I3	MDL/BLW	0.041	<i>M. alberdiae</i> shows relatively wider I3
BAT-1	P3	MDL	0.004	<i>M. alberdiae</i> shows shorter P3
BAT-1	P3	BLW	0.025	<i>M. alberdiae</i> shows narrower P3
BAT-1	c	MDL	0.027	<i>M. alberdiae</i> shows shorter c
BAT-1	c	BLW	0.029	<i>M. alberdiae</i> shows shorter c
BAT-1	p3	BLW	0.016	<i>M. alberdiae</i> shows narrower p3
BAT-1	p4	MDL	0.002	<i>M. alberdiae</i> shows shorter p4
BAT-1	p4	BLW	0.000	<i>M. alberdiae</i> shows narrower p4
BAT-3	I3	MDL	0.039	<i>M. alberdiae</i> show shorter I3
BAT-3	c	BLW	0.045	<i>M. alberdiae</i> show narrower c
BAT-3	p3	BLW	0.012	<i>M. alberdiae</i> show narrower p3
BAT-3	p4	MDL	0.009	<i>M. alberdiae</i> show shorter p4
BAT-3	p4	BLW	0.002	<i>M. alberdiae</i> show narrower p4

## Description and comparisons

Cranial, mandibular and dental material from BAT-1 was described by Antón et al. (2004), and that from BAT-3 by Monesillo et al. (2014). Material from Los Valles de Fuentidueña was partially described by Ginsburg et al. (1981), we only provide a description of the material not included in that paper.

## Upper Dentition

Ginsburg et al. (1981) assigned two upper canines from Los Valles de Fuentidueña (MNCN-46577 and MNCN-46578) to *Machairodus alberdiae* (Figure 3(f)–(i)) based on their lesser degree of flattening and their smaller size when compared to those of other populations of *M. aphanistus* known at that time. Nevertheless, when compared with those from BAT-1 and BAT-3, these two upper canines from LVF show a similar size to that of the smallest individuals of both samples, and most likely to belong to *M. aphanistus*. Therefore, this is the reason why these canines do not fit with the outstandingly small size of the rest of the upper teeth of *M. alberdiae*.

## Lower dentition

The p3 MNCN-32003 (Figure 4) has three non-crenulated cusps, the main one, and two accessories mesial and distal both lower than the former. According to its morphology and measurements, this p3 is considered as belonging to *M. aphanistus* rather than to *M. alberdiae*. In this latter species, there is a high variation between the height of the mesial and distal accessory cusps, with the mesial much lower. Due to the breakage of the distal part of the teeth, the distal cingulum is missing.

The specimen MNCN-32000 (Figure 5(a)–(c)) consists of a left mandibular fragment with p4 and m1. The height of the body is similar to those of the mandibles of *M. aphanistus* from BAT-1 and BAT-3. The p4 has three non-crenulated cusps, the main one being well developed, whereas the distal and mesial cusps, much lower than the former, are similarly sized. There is a marked distal cingulum. In occlusal view, the mesial cuspid is curved lingually, whereas the distal one is slightly located buccally. There is no buccal cingulum, whereas the lingual face shows a faint lingual cingulum; the distolingual face of the distal cingulum is bulkier than that of the buccal face. The m1 is partially broken and very worn. The paraconid is slightly mesiodistally shorter than the protoconid. There is no trace of cingula. The talonid is very reduced, but it consists of a small cuspid, with a very similar morphology to that seen in the specimens from BAT-1 and BAT-3. There are another two p4 in the sample from LVF (MNCN-46552 and MNCN-46561) similar to each other (Figure 6(a)–(c) and (d)–(f)), both much larger than MNCN-32000. In occlusal view, these former teeth are distally much wider than those from BAT-1 and BAT-3, showing a bulky mesiolingual expansion also seen in some specimens from BAT-3, but absent in those from BAT-1. The smallest p4 from LVF (MNCN-32000) lacks this later feature, and therefore it is more similar in morphology to the p4 from BAT-1, and to the specimen BAT-3'08 92 (Figure 6(g)–(i)) from BAT-3.

## Statistical results

Dental remains of *M. aphanistus* from LVF, BAT-1 and BAT-3 show statistically significant differences in several measurements (Table 1). Thus, the population from LVF has relatively mediolaterally longer c, relatively bucolingually wider p4, and bucolingually narrower m1 than those from BAT-1, and relatively

**Table 2.** Summarized results of the Student *t* tests or Welch test, showing the variables that showed significant differences in the comparison of *Machairodus aphanistus* from Los Valles de Fuentidueña with *Machairodus aphanistus* from Batallones-1, *Machairodus aphanistus* from Batallones-3, and *Machairodus alberdiae* from Los Valles de Fuentidueña.

Site compared	Piece	Variable	<i>p</i>	Comments
BAT-1	c	MDL/BLW	0.013	<i>M. aphanistus</i> from LVF shows relatively longer c
BAT-1	p4	BLW/H	0.020	<i>M. aphanistus</i> from LVF shows relatively wider p4
BAT-1	m1	BLW	0.015	<i>M. aphanistus</i> from LVF shows narrower m1
BAT-3	c	MDL/BLW	0.042	<i>M. aphanistus</i> from LVF shows relatively shorter c
LVF	P3	BLW	0.039	<i>M. aphanistus</i> from LVF shows wider P3
LVF	p4	BLW	0.035	<i>M. aphanistus</i> from LVF shows wider p4

mediodistally shorter c than those from BAT-3. Unfortunately, the scarcity or absence of some elements hinder other comparisons that would be very interesting, such as those concerning the m1, C or P4 (see Table 4). In general, despite the existence of significant differences, it is clear that the LVF, BAT-1 and BAT-3 compared populations of *M. aphanistus* show similar size and proportions, different from those of *M. alberdiae*, as discussed below.

## Discussion

Both p4 of *M. aphanistus* from LVF shows a very different size, in comparison with BAT-1 population, the bigger p4 from LVF (MNCN-46552) shows a medium range distribution with MDL and BLW; while the lower p4 (MNCN-32000) shares the lowest MDL and BLW both BAT-1 or BAT-3 population (Figure 7). In addition, the morphological comparison with the former population shows a lingually expanded distal end, with the distal cuspid clearly buccally displaced, different from the morphology seen in smaller specimens, whereas in the p4 from BAT-1, this expansion is clearly reduced, and this part is much buccolingually narrower. Also, the distal cuspid of these large specimens from LVF is more centrally located than in the p4 from BAT-3 (Figure 6(h)–(i)). Thus, in occlusal view, the crown of the largest p4 from LVF is triangular instead of the much more elongated shape of the p4 from BAT-3. This feature should be considered as a primitive character, as it is present in the Middle Miocene felids *Miomachairodus pseudoailuroides* (see Schmidt-Kittler 1976), *Diamantofelis ferox* (Morales et al. 2003), *Miopanthera lorteti*, and *Pseudaelurus quadridentatus* from Sansan (MS personal observations). Nevertheless, the m1 of this specimen is really small, being clearly outside the size distribution of this tooth in the populations of *M. aphanistus* from both Batallones sites. In fact, the results of the statistical analysis show that the m1 of *M. aphanistus* from LVF have a shorter MDL than those from the younger localities of BAT-1 and BAT-3. This suggests that the lower carnassial of LVF had a more primitive morphology, besides a less efficient cutting ability (Tables 1 and 2). On the other hand, m1 from BAT-1 are significantly narrower (more trenchant); an indication of an enhanced cutting action.

**Table 3.** Summarized results of the Student *t* tests or Welch test for the PC1, showing the variables that showed significant differences, in the comparison to *Machairodus alberdiae* from Los Valles de Fuentidueña with *Machairodus aphanistus* from Batallones-1.

Piece	Variable	<i>p</i>	Comments
I3	PC1	0.008	PC1 explain the 83.19% of the variance. The order of the importance of the measurement to create the PC1 is BLW, MDL and H
p4	PC1	0.012	PC1 explain the 83.84% of the variance. The order of the importance of the measurement to create the PC1 is MDL, BLW and H

Moreover, the m1 MNCN-32000 is outside the size range of the m1 from the Batallones sites, even when considering the smallest specimens from BAT-3. This can be considered, as discussed for the p4, as an indication of the high sexual dimorphism within this species, one of the highest for a member of the Felidae (Salesa et al. 2006; Monesillo et al. 2014).

The two upper canines from LVF (MNCN-46577 and MNCN-46578) (Figure 3(f)–(i)) show a similar morphology than those of *M. aphanistus* from BAT-1 and BAT-3, although from Figure 3 it is evident the strong variability in both shape and size existing in the sample of upper canines from these two latter populations (Figure 3(a)–(f)). This is explained in part by the strong sexual dimorphism exhibited by *M. aphanistus* (Salesa et al. 2006). In addition, the measurements of the upper canines from LVF do not show statistically significant differences with those from BAT-1 and BAT-3, so, although Ginsburg et al. (1981) assigned them to *M. alberdiae*, we have to consider them as part of the *M. aphanistus* sample from LVF. In fact, given the sizes of the rest of the cheek teeth of *M. alberdiae*, these upper canines from LVF are much larger than expectable. Also, the differences described by Ginsburg et al. (1981) between the upper canines from LVF and those from other localities are now better understood, thanks to the good samples from BAT-1 and BAT-3. In fact, Monesillo et al. (2014) recognised two different upper canine morphotypes, independent from size, within the BAT-3 sample, as some specimens have a relatively mesiodistally longer crown than others. The two upper canines of *M. aphanistus* from LVF are more similar to the morphotype with the mesiodistally shortest crown length, which interestingly is the only one observed in the BAT-1 sample (Figure 3).

Another remarkable difference between the *M. aphanistus* of LVF and BAT-1/BAT-3 is the absence of crenulations in the teeth from LVF, except in the upper canines, whereas in the samples from BAT-1 and BAT-3, the crenulations are observed in the I3, upper canines, lower canines and premolars (Antón et al. 2004; Monesillo et al. 2014). The presence of such crenulations in the dentition is typical of machairodontine felids of the tribe Homotherini (Turner and Antón 1997; Antón et al. 2004; Antón 2013), and it has been explained as an ecological advantage that increases the efficiency when hunting and consuming the prey, as it improves the cutting action of canines and carnassial teeth (Akersten 1985; Anyonge 1996; Turner and Antón 1997; Salesa et al. 2005; Antón 2013). The absence of crenulations in most of the *M. aphanistus* teeth from LVF suggests a more primitive stage of this feature in this geologically earlier population (dated as MN 9), in contrast to those younger populations from the MN 10 (BAT-1 and BAT-3), which show a derived dentition, with crenulations in most of the teeth. This difference agrees with

**Table 4.** Summary of the measurements, in mm, of the dental remains of *M. aphanistus* from Batallones-1 and Batallones-3, and Los Valles de Fuentidueña; and of *Machairodus alberdiae* of Los Valles de Fuentidueña.

Site	Spc	Element	N	MDL (Mean)	MDL (SD)	BLW (Mean)	BLW (SD)	H (Mean)	H (SD)
BAT-1	<i>M. aphanistus</i>	I3	11	10.26	0.84	12.34	0.59	18.01	1.25
BAT-3	<i>M. aphanistus</i>	I3	4	10.33	0.83	12.06	0.55	18.34	1.98
LVF	<i>M. alberdiae</i>	I3	2	8.04	0.40	10.94	0.13	15.06	0.21
BAT-1	<i>M. aphanistus</i>	C	15	29.85	2.50	12.80	0.92	65.57	6.88
BAT-3	<i>M. aphanistus</i>	C	6	30.75	4.01	14.08	1.68	72.21	7.07
LVF	<i>M. aphanistus</i>	C	2	26.36	2.49	12.74	0.66	61.51	–
BAT-1	<i>M. aphanistus</i>	P3	20	23.62	1.44	11.76	1.01	11.37	0.57
BAT-3	<i>M. aphanistus</i>	P3	3	22.19	1.50	10.22	1.79	10.28	1.30
LVF	<i>M. aphanistus</i>	P3	2	24.21	–	12.04	0.66	12.77	–
LVF	<i>M. alberdiae</i>	P3	3	20.71	0.05	10.21	0.51	10.58	0.90
BAT-1	<i>M. aphanistus</i>	P4	24	38.35	2.85	17.89	1.10	17.60	0.93
BAT-3	<i>M. aphanistus</i>	P4	7	37.15	1.96	17.55	1.31	16.84	2.76
LVF	<i>M. aphanistus</i>	P4	1	–	–	17.34	–	–	–
BAT-1	<i>M. aphanistus</i>	c	15	17.78	0.15	11.34	0.65	29.43	3.54
BAT-3	<i>M. aphanistus</i>	c	6	17.27	0.96	11.31	0.54	30.22	2.36
LVF	<i>M. aphanistus</i>	c	3	18.79	1.12	11.38	0.55	–	–
LVF	<i>M. alberdiae</i>	c	1	14.7	–	9.61	–	–	–
BAT-1	<i>M. aphanistus</i>	p3	15	19.12	0.86	8.73	0.52	10.98	0.51
BAT-3	<i>M. aphanistus</i>	p3	4	17.88	1.16	8.71	0.20	10.93	0.38
LVF	<i>M. aphanistus</i>	p3	2	–	–	8.79	1.11	11.05	–
LVF	<i>M. alberdiae</i>	p3	2	17.05	–	7.68	0.42	–	–
BAT-1	<i>M. aphanistus</i>	p4	20	25.11	1.38	11.44	0.66	15.48	1.27
BAT-3	<i>M. aphanistus</i>	p4	5	24.24	1.08	10.64	0.28	14.44	0.81
LVF	<i>M. aphanistus</i>	p4	3	23.62	1.30	11.47	1.02	13.98	0.45
LVF	<i>M. alberdiae</i>	p4	2	20.86	0.06	8.48	0.54	11.99	–
BAT-1	<i>M. aphanistus</i>	m1	24	30.46	1.30	13.40	0.74	17.92/17.28*	1.20/1.05*
BAT-3	<i>M. aphanistus</i>	m1	3	29.58	29.58	11.91	0.47	16.45/17.06*	0.19/0.11*
LVF	<i>M. aphanistus</i>	m1	3	24.72	–	12.10	1.40	–	–

\*First measurement refers to Paraconid height, second measurement refers to Protoconid height and in italic the measurement with just one sample.

the mosaic evolution of this species through the Late Miocene, already pointed out by Antón et al. (2004).

## Systematic paleontology

### *Machairodus alberdiae*

Figure 8(a)–(g), Figure 9(a)–(c).

Referred material. The list of fossils from Los Valles de Fuentidueña is included in Supplementary Material 2.

## Description

Here we only provide a description of new dental material that was not included in Ginsburg et al. (1981).

### Upper dentition

The two available I3 from LVF (MNCN-46563 and MNCN-46557) (Figure 8(a)–(b) and (c)–(d), respectively) have a caniniform crown with a pointed main cusp and a mesiolingually located accessory cusp, with a cutting edge which runs mesiolingually until the crown base. The main cusp has two cutting edges, the larger one running distolingually, whereas the other one, around half as long as the former, is mesially located and markedly curved. In lingual view, the larger edge of the main cusp and the cutting edge of the accessory cusp are placed in parallel. In labial view, the base of the crown is markedly inflated. The root is distolingually curved, with a groove occupying most of the mesial face.

The P3 (MNCN-67370) (Figure 8(e)–(g)) has three non-crenulated cusps: the main one is well developed, the distal one is

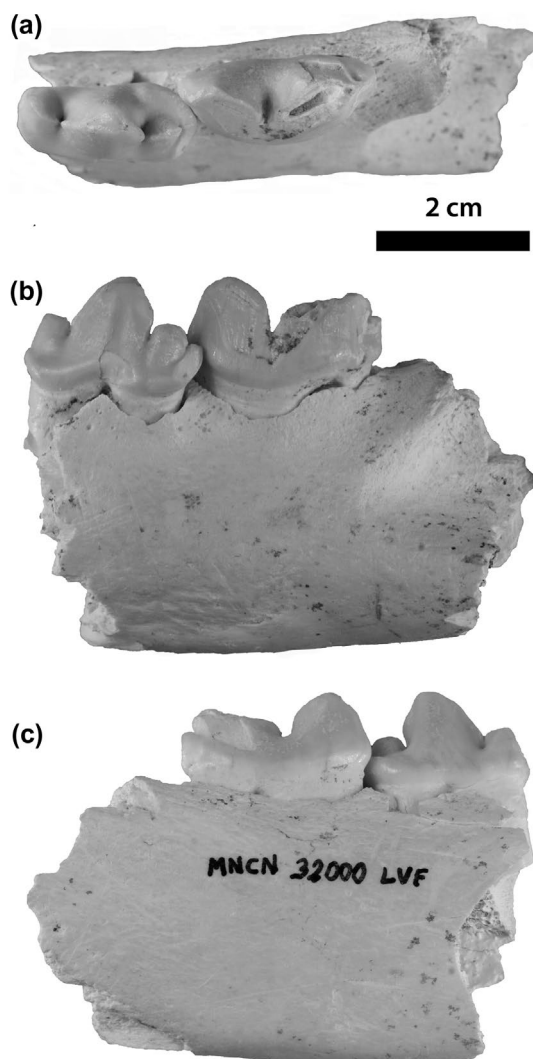
much lower, and the mesial cusp is very little but present. There is also a distal cingulum, well developed and ending in a little central tip. In occlusal view, the crown has a broad disto-lingual surface beginning from the end of the disto-lingual side of the cingulum, and reaching the top of the main cusp.

## Statistical results

Results of the statistical comparisons between the populations of *M. alberdiae* from LVF and *M. aphanistus* from BAT-1 show several significant differences in a number of measurements: MDL, BLW, H, and MDL/BLW index of I3; MDL and BLW of P3; MDL and BLW of lower c; MDL and BLW of p3; and MDL, BLW, H and MDL/BLW of p4 (Table 1). Significant differences between the population of *M. alberdiae* from LVF and *M. aphanistus* from BAT-3 are: MDL of I3; BLW of lower c; BLW of p3; MDL and BLW of p4 (Table 1). Significant differences between *M. alberdiae* and *M. aphanistus* from LVF has been previously discussed (Table 2). In general, for a given variable, the distribution of *M. alberdiae* is always below that of *M. aphanistus*, independently from the existence of significant differences. Also, we performed a set of Principal Component Analysis, PC1 of *M. alberdiae* with *M. aphanistus* from BAT-1 has been made, pursuant to requirements, just in two pieces the I3 and p4, in both cases the PC1 explain the variance with an 83% (Table 3).

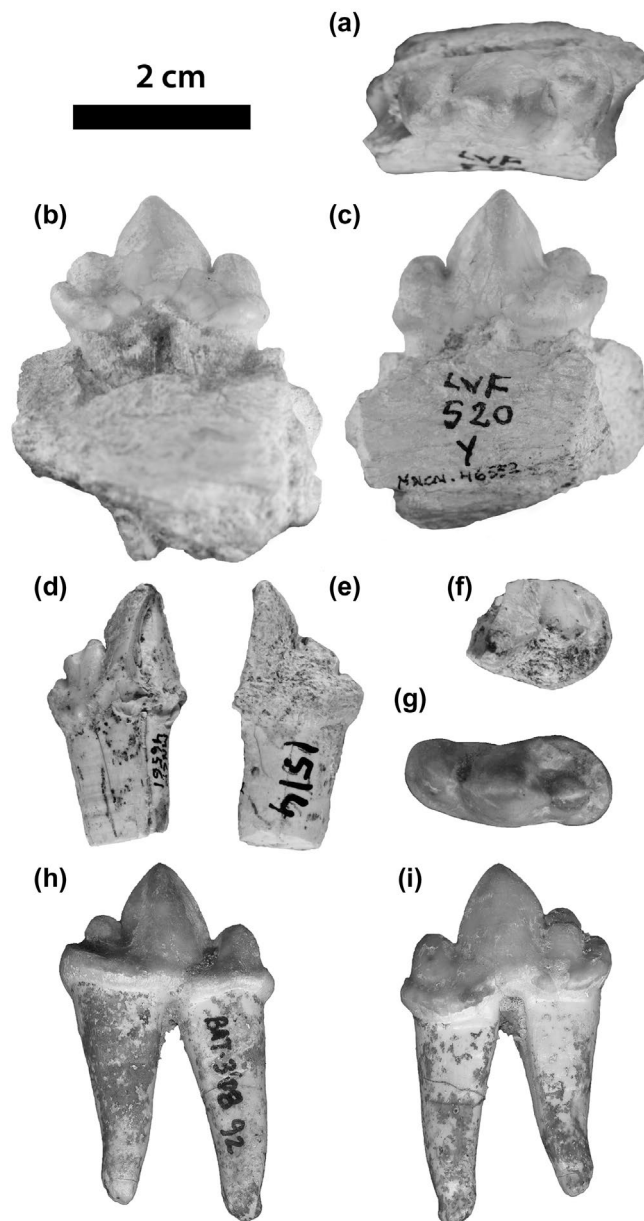
## Discussion

Following Ginsburg et al. (1981), the main features distinguishing *M. alberdiae* from *M. aphanistus* are the markedly smaller size and the more primitive dentition of the former species. Among these primitive characters is the presence of a small



**Figure 5.** Fragment of left hemimandible (a–c) (MNCN-32000) with p4-m1 of *Machairodus aphanistus* from Los Valles de Fuentidueña. (a) occlusal (b) labial, and (c) lingual view.

alveolus for p2 in the hemimandible MNCN-45860, a remarkable feature (de Beaumont 1975; Sotnikova 1992), absent in *M. aphanistus* (Antón et al. 2004). With the new descriptions provided in the present paper, we have clarified some dental features not included in the work by Ginsburg et al. (1981), such as the presence of a small mesial cusp in the P3, at least in the specimen MNCN-67370 (Figure 8 (a)–(c)), which also shows a slender distolingual protuberance. In this latter feature, MNCN-67370 resembles the P3 sample from BAT-3, which in occlusal view shows a rounded outline; different from the lingually pointed P3 from BAT-1, but also from other P3 of *M. alberdiae* from LVF, such as MNCN-46573) (Figure 9(a)–(c)). On the other hand, although Ginsburg et al. (1981) pointed out the absence of mesial cuspid on the p3 of *M. alberdiae*, at least in the specimen MNCN-45860 there is in fact a very reduced, mesiolingually located cuspid. Concerning the skull and mandible of *M. alberdiae*, few data are available due to the scarcity of these elements, but the mandible MNCN-35938 (see Ginsburg et al. 1981) shows a moderately verticalised symphysis, very similar to those of *M. aphanistus* from BAT-1 and BAT-3 (Antón et al. 2004; Monesillo et al. 2014).



**Figure 6.** Comparison between selected p4 of *Machairodus alberdiae* from Los Valles de Fuentidueña and of *Machairodus aphanistus* from BAT-3. (a–c) left p4 from LVF (MNCN-46552) in (a) occlusal, (b) labial, and (c) lingual view respectively; (d–f) left p4 from LVF (MNCN-46561) in (d) labial, (e) lingual, and (f) occlusal view respectively; (g–i) left p4 (BAT-3'08 92) from BAT-3 in (g) occlusal, (h) lingual, and (i) labial view respectively.

In summary, our results support the validity of *M. alberdiae* as a separate species from the larger and more derived *M. aphanistus*.

### Palaeobiology of the carnivoran community from Los Valles de Fuentidueña

The three localities included in our study, BAT-1, BAT-3 and LVF, have yielded a fossil sample with a high percentage of carnivorans. In the case of the two former sites, 98% of the fossils belong to Carnivora; including two species of machairodontine felids of strongly different body-mass, the lion-sized *M. aphanistus* and the leopard-sized *Promegantereon ogygia* (see Salesa et al.



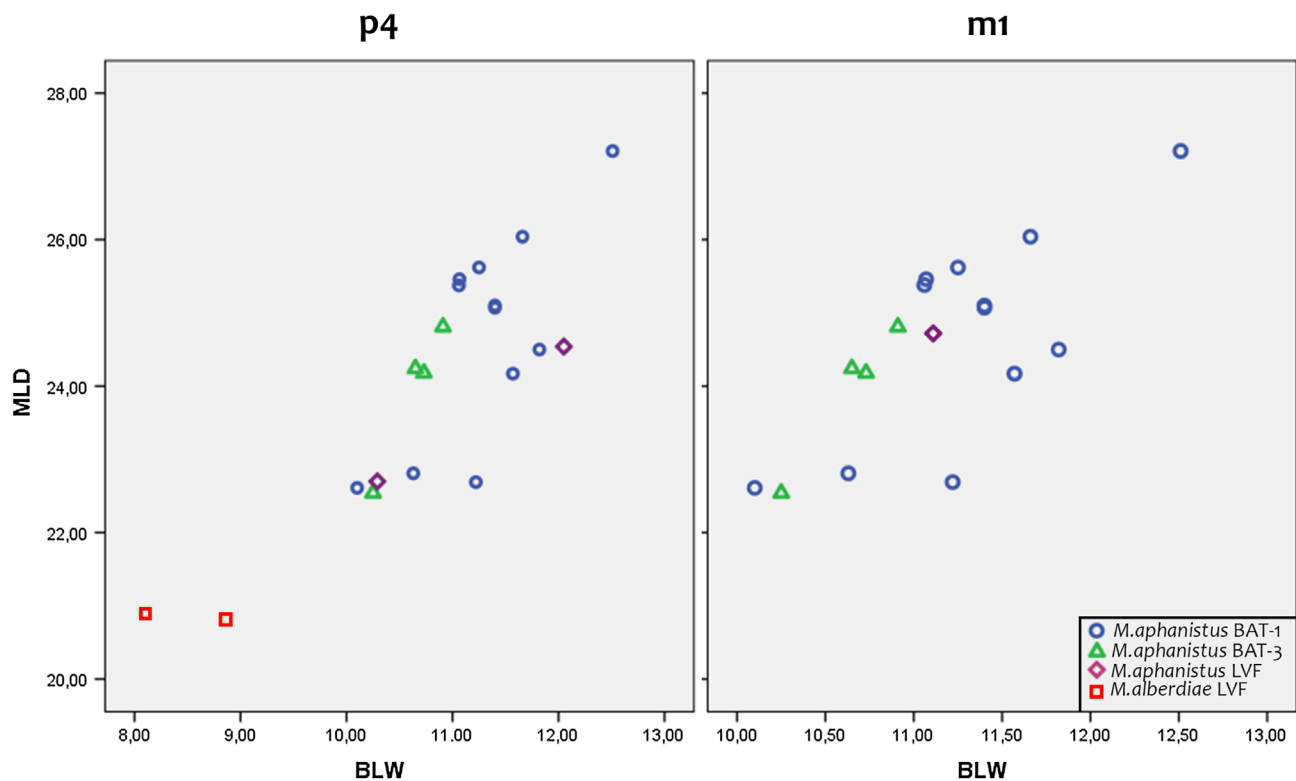
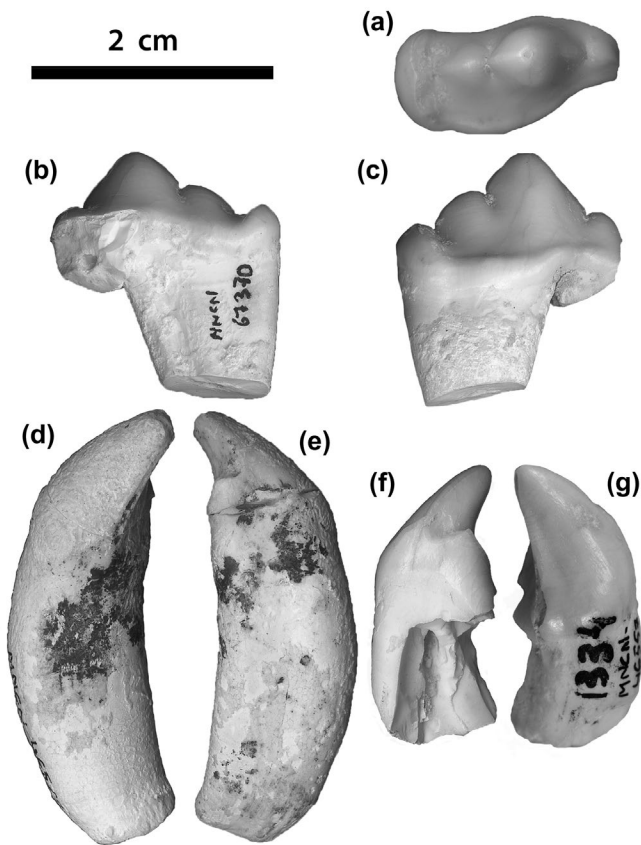


Figure 7. Graph of distribution showing the *Machairodus aphanistus* measurements of p4 and m1 BLW from BAT-1, BAT-3 and Los Valles de Fuentidueña.

2005 for the palaeoecological implications of this sympatry). In the case of LVF, up to 15 carnivorous species are included in the community of carnivorous from this site; with three amphicyonids (*Amphicyon major eppelsheimensis*, *Magericyon castellanus* and *Thaumastocyon dirus*), four mustelids (*Eomellivora liguritor*, *Circumstela dechaseauxi*, *Marcetia santigae* and a Mephitinae indet.), three hyaenids (*Protictitherium crassum*, *Lycyaena* aff. *L. chaeritis* and *Plioviverrops* sp.), and five felids (*M. aphanistus*, *M. alberdiae*, *Pseudaelurus quadridentatus*, *Sansanosmilus jourdani* and a Felidae indet.) (Alberdi et al. 1981; Ginsburg et al. 1981; Peigné et al. 2008). Such carnivorous richness suggests the existence of different habitats allowing the coexistence of species that would strongly compete for resources if they were occupying the same spaces. Thus, the sympatry of two large species of sabre-toothed felid such as *M. aphanistus* and *M. alberdiae* would be only possible if a sort of ecological segregation existed between them. There are different possibilities that explain this segregation in extant sympatric carnivorous, such as differences in body size, activity patterns, habitat choice, or degree of sociality (Linnell and Strand 2000; Hayward et al. 2006; McDonald et al. 2008). The ecological separation of sympatric felids is highly favoured when a structurally complex habitat exists, which generally supports a more abundant and diverse prey guild than less structured habitats do (Sunquist and Sunquist 2009). Modern ecosystems with two species of sympatric large felids are characterised by the presence of enough woodland areas so that the smaller species can escape from the attack of the large one (Morse 1974; Seidensticker 1976; Bailey 1993). In addition, the high carnivorous diversity in LVF would also suggest a relatively highly-structured habitat, with a great number of available niches, but a deeper

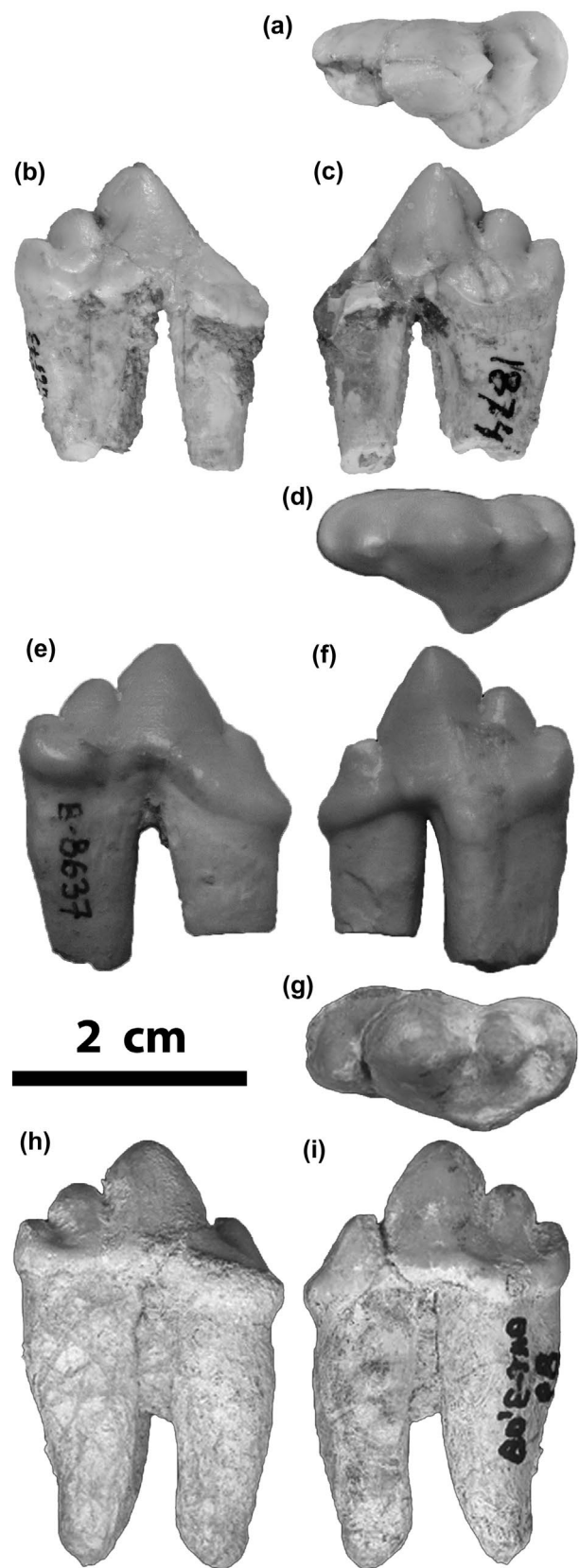
study on the locomotor adaptations of these species should be necessary for supporting the presence of a specific environment.

In the case of the Batallones localities, the presence of two sabre-toothed felids of such a different body mass as *M. aphanistus* and *P. ogygia* fits well with a scenario where the latter species is continuously avoiding the contact with the much larger *M. aphanistus* (Rabinowitz and Nottingham 1986; Nuñez et al. 2000; Salesa et al. 2006). With an estimated body weight of 100–240 kg for *M. aphanistus*, and 28–65 kg for *P. ogygia* (Salesa et al. 2006), an encounter with the former species would have been a serious situation for the latter. However, in the case of LVF the ecological relationships between *M. aphanistus* and *M. alberdiae* are more difficult to interpret, as in this case the differences in body weight between these species were not so marked. We cannot calculate the body weight of *M. alberdiae* due to the absence of skulls and long bones in the sample from LVF, but from an overall dental size comparison with the teeth of *M. aphanistus* from BAT-1, we can roughly estimate a body mass for *M. alberdiae* close to that of the smallest individuals of *M. aphanistus*, that is, around 100 kg. In extant ecosystems, there are few examples of two species of large, similarly-sized felids living in sympatry. One of the few comparable situations to LVF is some areas of South and Central America, where pumas (*Puma concolor*) and jaguars (*Panthera onca*) share the same habitats (Nuñez et al. 2000). In this case, the coexistence of these two felines is possible only when resources are rich enough to allow the maintenance of both species, but even in those cases, both species develop a marked ecological segregation based on the avoidance of adult encounters and the selection of different prey (Seidensticker 1976; Rabinowitz and Nottingham 1986; Nuñez et al. 2000). As pointed out above,



**Figure 8.** Upper dental remains of *Machairodus alberdiae* from Los Valles de Fuentidueña. (a–c) right P3 (MNCN-67370) in (a) occlusal view, (b) labial, and (c) lingual view; (d–e) right I3 (MNCN-46557) in (d) distal, and (e) mesial view; (f–g) left I3 (MNCN-46563) in mesial, and (g) distal view respectively.

the rich carnivoran community of LVF would be suggesting an abundance of resources (basically prey), and thus explaining the sympatry of *M. aphanistus* and *M. alberdiae* (besides that of other carnivorans). With *M. aphanistus* being larger, it would be dominant over *M. alberdiae*, and thus this latter species would avoid a direct confrontation with the former. Although this behaviour would be strongly dependent on the body proportions of this felid: if *M. alberdiae* was more robust than *M. aphanistus*, then it could occupy those areas with dense vegetal cover, where it could find refuge from the attack of its larger comrade. However if *M. alberdiae* was a slender sabre-toothed felid, it could have inhabited relatively open landscapes, hunting during the hours of maximum heat when *M. aphanistus* and other large predators would tend to be inactive and resting in the shade, as extant cheetahs do to avoid encounters with lions and hyenas (Hanby and Bygott 1979; Durant 2000). Until the postcranial adaptations of *M. alberdiae* are known, this matter will remain unclear, although the most likely possibility is that its body proportions will resemble those of other members of the genus *Machairodus*, such as *M. aphanistus* or the American *M. catocopis* (Antón et al. 2013), with a relatively unspecialized locomotor apparatus lacking clear adaptations for high speed running like those seen in the modern cheetah. In that case, seeking refuge among the vegetation would be the likely strategy used by *M. alberdiae* to avoid confrontation. Furthermore, considering the high diversity of the carnivoran guild, it is likely that the environment of LVF



**Figure 9.** Comparison between selected P3 of *Machairodus alberdiae* from Los Valles de Fuentidueña, and *Machairodus aphanistus* from BAT-1 and BAT-3. (a–c) left P3 from LVF (MNCN-46573) in (a) occlusal, (b) labial, and (c) lingual view respectively; (d–f) left P3 (B-8639) from BAT-1 in (d) occlusal, (e) labial, and (f) lingual view respectively; (g–i) right P3 (BAT-3'08 89) from BAT-3 showed reversed, in (g), occlusal, (h) labial, and (i) lingual view respectively.

included both wooded and open areas, this is, a highly-structured habitat where predators of different size and requirements were ecologically segregated. In the open areas of LVF, the most probably available prey would be the three-toed equid *Hipparion concudense* (Forstén 1982; Pesquero and Alberdi 2012), considered as a mixed-feeder or grazer, typical inhabitants of relatively open landscapes (Alberdi and Bonadonna 1990; Bernor et al. 1990; Forstén 1991), whereas the highly structured parts of this ecosystem (wooded and shrubby areas) would be the habitat of the bovid *Miotragocerus* sp., the giraffid *Decennatherium pachecoi*, the cervid *Euprox dicranocerus*, the tragulid *Dorcatherium naui*, and the moschids *Hispanomeryx duriensis* and *Micromeryx flourensianus*, all of them considered as herbivorous including a low percentage of grass on their diets, for example less than 10% in the case of and the bovid *Miotragocerus* sp. (Gentry and Kaiser 2009), and thus typical dwellers of close environments (Köhler 1993). Among them, the moschids and the tragulid would be too small to be regular prey of both *M. aphanistus* and *M. alberdiae* (see discussion in Salesa et al. 2006), but *Miotragocerus* sp. and *Euprox dicranocerus*, with body masses around 40–100 kg (Alcalá 1994; Salesa et al. 2006), would fit within the prey range of these predators. There are no published weight estimations for *Decennatherium pachecoi*, but from a rough comparison of the size of some postcranial elements (Bosscha Erdbrink 1976) this animal had a similar size to that of the extant giraffe, *Giraffa camelopardalis*, with a body mass range of 450–1980 kg (Skinner and Mitchell 2011). This animal would be probably too large to be part of the prey of *M. alberdiae*, at least the adult individuals, but younger animals could have been an easy prey for this felid. In the case of the larger *M. aphanistus*, it could have included this giraffid in its diet, hunting even adult individuals, resembling the behaviour observed in some populations of extant lions, which are able of bringing down regularly adult individuals of *G. camelopardalis* (Hirst 1969; Pienaar 1969; Strauss and Packer 2013).

In summary, the sympatry of two species of *Machairodus* in LVF, with *M. aphanistus* being dominant over *M. alberdiae*, suggests the existence of a relatively structured habitat, with open landscapes and other, much more vegetated areas, both inhabited by a rich community of herbivores, capable of sustaining a diverse guild of carnivorans.

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## Disclosure statement

The authors state that there is no potential conflict of interest derived from the present research.

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