

2D Geometric morphometrics of the first lower molar of the genus *Meles* Brisson, 1762 including new badger evidence from the Lower Pleistocene Quibas site (Murcia, Spain)

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ABSTRACT

Badgers belong to the genus *Meles* Brisson, 1762, which comprise four extant species (*M. anakuma* Temminck, 1844, *M. leucurus* (Hodgson, 1847), *M. canescens* Blanford, 1875, and *M. meles* (Linnaeus, 1758)). The genus is included in the subfamily Melinae Bonaparte, 1838, a polyphyletic group of Eurasian mustelids whose evolutionary relationships need further clarification. The evolutionary relationships of the genus are complex and far from being resolved. This work aims to describe a nearly 1 Ma unpublished badger mandible from the Sierra de Quibas (Murcia) and to help clarify the evolutionary patterns of Euroasiatic badgers. To this end, we used 2D geometric morphometric techniques to measure 57 landmarks and semilandmarks in 79 first lower molars (m1) of *Meles*, ranging from Pleistocene to extant species. Our results show evidence for differentiating between primitive badgers and living species of *Meles*. The new m1 of *Meles* from the Quibas site is more gracile (relatively narrower and longer) than the other Eurasian extinct species, and shows that this specimen can be placed in the subspecies *M. meles meles* (Linnaeus, 1758). Our results also show that the denomination of *M. meles atavus* Kormos, 1914 as a related subspecies with a primitive morphology is morphologically supported. Therefore, we conclude that the living subspecies of badger *M. meles meles* was already differentiated in the south of the Iberian Peninsula at around 1 Ma, but some primitive remnant populations persisted in the north of the Iberian Peninsula, for which we recognize the subspecies *M. meles atavus*.

KEY WORDS

Badgers,
lower first molar,
Iberian Peninsula,
2D geometric
morphometrics.

RÉSUMÉ

Morphométrie géométrique 2D de la première molaire inférieure du genre Meles, incluant de nouvelles preuves de la présence de blaireaux sur le site de Quibas du Pléistocène inférieur (Murcie, Espagne).

Les blaireaux sont un groupe polyphylétique de mustélidés au sein duquel on retrouve le genre *Meles* Brisson, 1762. Il appartient à la sous-famille Melinae Bonaparte, 1838 de distribution eurasienne, actuellement composée de quatre espèces vivantes (*M. anakuma* Temminck, 1844, *M. leucurus* (Hodgson, 1847), *M. canescens* Blanford, 1875 et *M. meles* (Linnaeus, 1758)). Les relations évolutives du genre sont complexes et loin d'être résolues. L'objectif de ce travail est de décrire une mandibule de blaireau inédite de près de 1 Ma de la Sierra de Quibas (Murcie) et d'aider à clarifier les schémas évolutifs des blaireaux euroasiatiques. À cette fin, nous avons utilisé des techniques morphométriques géométriques 2D pour mesurer 57 repères et semi-repères dans 79 premières molaires inférieures (m1) de *Meles*, allant du Pléistocène aux espèces existantes. Nos résultats montrent des preuves solides de la différenciation entre les blaireaux primitifs et les espèces vivantes de *Meles*. Le nouveau m1 de *Meles* du site de Quibas est plus gracile (relativement plus étroit et plus long) que les autres espèces eurasiennes éteintes, et montre que ce spécimen peut être placé dans la sous-espèce *M. meles meles* (Linnaeus, 1758). Nos résultats montrent également que la dénomination de *M. meles atavus* Kormos, 1914 en tant que sous-espèce apparentée avec une morphologie primitive est étayée morphologiquement. Par conséquent, nous concluons que la sous-espèce vivante de blaireau *M. meles meles* était déjà différenciée dans le sud de la péninsule Ibérique à environ 1 Ma, mais certaines populations relictuelles persistent dans le nord de la péninsule Ibérique, pour lesquelles nous reconnaissons la sous-espèce *M. meles atavus*.

MOTS CLÉS
Première molaire
inférieure,
péninsule Ibérique,
morphométrie
géométrique 2D.

INTRODUCTION

The phylogeny of the genus *Meles* Brisson, 1762, known as the Eurasian badger, is complex and still largely unresolved, probably because the family Mustelidae Fischer, 1817 is a clear example of adaptive radiation (Koepfli *et al.* 2008). European badgers occupy a great variety of habitats, including forests, grasslands, agricultural areas, and urban areas (Proulx *et al.* 2016), which has given rise to a large variety of local specializations. The genus *Meles* is thought to have originated in Asia from the genus *Melodon* Zdansky, 1926 in the Upper Miocene-Lower Pliocene (Arribas & Garrido 2007; Del Cerro Márquez 2011; Madurell-Malapeira *et al.* 2011a, b; Abramov & Puzachenko 2013; Mecozzi *et al.* 2019), and paleontological evidence points to the species *M. thoralis* Viret, 1951 as the ancestor of the extant Asian and European *Meles* lineages (Baryshnikov *et al.* 2002; Abramov & Puzachenko 2005; Del Cerro Márquez 2011; Madurell-Malapeira *et al.* 2011a, b; Mecozzi *et al.* 2019). Currently, four species are distinguished within the genus *Meles*: *M. meles* Linnaeus, 1758 (Europe), *M. canescens* Blanford, 1875 (Caucasus-East Asia), *M. leucurus* Hodgson, 1847 (Asia), and *M. anakuma* Temminck, 1844 (Japan) (Sato 2016; Kundu *et al.* 2019; Kinoshita *et al.* 2020), while *M. atavus* is currently considered an extinct subspecies of *M. meles* (Madurell-Malapeira *et al.* 2011a). As a result of its wide variety of geographic and ecological settings, according to Proulx *et al.* (2016), species of genus *Meles* can be further subdivided into several subspecies. There are three recognized subspecies of *M. meles* (*M. meles meles*, *M. meles taxus*, and *M. meles milleri*) distributed along the entire European territory reaching the north of the Caucasus and the Volga river, where we find the geographical boundary between *M. meles* and *M. leucurus*.

Within the general debate about the precise time and place of emergence of the different lineages within *M. meles*, the Iberian Peninsula has a significant role. The potential oldest representative of *M. meles meles* in the Iberian Peninsula comes from the Lower Pleistocene of Fuente Nueva 3 site (Orce, Granada, Spain), dated in around 1.4–1.2 Ma (Duval *et al.* 2012; Toro-Moyano *et al.* 2013). However, in more recent chronologies (c. 1 Ma), some authors have proposed the presence of a different subspecies, *M. meles atavus*, in Vallparadís fossil site (Barcelona, Spain) (Madurell-Malapeira *et al.* 2011a, b), based on their primitive morphology.

Taking advantage of the recent recovery of a right hemimandible with a complete lower first molar (m1) from a badger fossil from the Quibas site (Murcia, Southern Iberian Peninsula) (Montoya *et al.* 1999) dated around 1 Ma (Piñero *et al.* 2020), we address the morphological evolution in the Iberian Peninsula badgers using 2D geometric morphometric techniques on the m1 crown variation (through its occlusal side). It has been previously established that the m1 of the badgers has great taxonomic importance within the genus (e.g. Madurell-Malapeira *et al.* 2011a) and the use of the 2D geometric morphometric (GM) may help to clarify the similarities between living and extinct forms of badgers.

THE QUIBAS SITE

On the SE slope of the Sierra de Quibas (Abanilla, Murcia, Spain) is located an abandoned limestone quarry (location coordinates 38°18'51"N, 1°4'42"W) including a karstic complex of cavities filled by sediments of Pleistocene age rich in paleontological remains. The chronology of the infilling has recently been established as between 1.2 and 0.78 Ma (Piñero

TABLE 1. — Comparative sample for the Quibas fossil m1, including information of the species, geographical origin, chronology, and data origin.

Species	Geographical origin	Chronology	Data Origin
<i>Meles meles meles</i> (Linnaeus, 1758) (n = 54)	Spain	Current	MNCN
<i>Meles meles</i> (Linnaeus, 1758) (fossil) (n = 1)	Unikoté 1 Cave, France	Upper Pleistocene	Mallye 2018
<i>Meles meles</i> (fossil) (n = 6)	Laceduzza Cave, Italia	Upper Pleistocene	Mecozzi <i>et al.</i> 2019
<i>Meles meles</i> (fossil) (n = 3)	Kudaro Cave, Georgia	Middle Pleistocene	Baryshnikov 2009
<i>M. meles atavus</i> Kormos, 1914 (n = 2)	Vallparadís, Spain	1.0 Ma	Madurell-Malapeira <i>et al.</i> 2011
<i>Meles magnus</i> Jiangzou, Liu, Wagner & Chen, 2018 (n = 3)	Liucheng Gigantopithecus Cave, China	2.48-2.0 Ma	Jiangzou <i>et al.</i> 2018
<i>Meles teihardi</i> Qiu, Deng & Wang, 2004 (n = 1)	Ningyang, China	Lower Pleistocene	Jiangzou <i>et al.</i> 2018
<i>Meles chiai</i> Teilhard de Chardin, 1940 (n = 1)	Localidad 18 de Zhoukoudian, China	2.0 Ma	Jiangzou <i>et al.</i> 2018
<i>Meles thoralis</i> Viret, 1951 (n = 1)	Saint-Vallier, France	Upper Pleistocene	Mallye 2007
<i>Meles leucurus</i> Hodgson, 1847 (n = 3)	Zoological Institute, Beijing, China	Current	Jiangzou <i>et al.</i> 2018
<i>Meles leucurus</i> (n = 4)	Bliznets Cave, Russia	Early Holocene	Alekseeva & Baryshnikov 2020
<i>Arctonyx albogularis</i> (Blyth, 1853) (n = 3)	Zoological Institute, Beijing, China	Current	Jiangzou <i>et al.</i> 2018

et al. 2020). The site has yielded fossil remains of more than 70 species of both vertebrates and invertebrates from the late early Pleistocene (Montoya *et al.* 1999, 2001; Carlos-Calero *et al.* 2006; Made *et al.* 2007; Alba *et al.* 2011; Blain *et al.* 2014; Pérez-García *et al.* 2015; Piñero & Alberdi 2015; Piñero *et al.* 2015; Blain & Bailon 2019; among others). The main structures of this karstic complex with a paleontological record consist of a gallery called Quibas-Cueva (QC; up to 5 m wide, 9 m high, and more than 30 m in length) and a vertical shaft known as Quibas-Sima (QS; 12 m deep and up to 2 m wide), separated by 3-m-thick calcitic speleothems but connected internally. The stratigraphic sequence of the Quibas-Sima has been divided into seven distinct detritic units: QS-1 to QS-7. The interval QS2 to QS5 has been chronologically constrained to the Jaramillo Subchron (1.07–0.99 Ma) (Piñero *et al.* 2020). The fossil badger labeled Q'18/QS4-1/P19/10 (Fig. 1) comes from Quibas-Sima level 4 (sublevel 1) and was found in the 2018 field season.

MATERIAL AND METHODS

The m1 from the badger mandible Q'18/QS4-1/P19/10 was compared to 79 m1 teeth from different species of extant and extinct *Meles*: current *M. meles* (n = 54), fossil *M. meles* (n = 10) *M. meles atavus* (n = 2), *M. teihardi* Qiu, Deng & Wang, 2004 (n = 1), *M. chiai* Teilhard de Chardin, 1940 (n = 1), *M. leucurus* (n = 7), *M. magnus* Jiangzou, Liu, Wagner & Chen, 2018 (n = 3), *M. thoralis* (n = 1) (see Appendix 1). Even though the genus *Meles* has been described as highly dimorphic (Lüps and Roper 1988; Abramov & Puzachenko 2005; Bútorá *et al.* 2018), this aspect could not be analyzed in living specimens because of a lack of data. In addition, we included specimens from the genus *Arctonyx* F.G.Cuvier, 1825 (*A. albogularis* (Blyth, 1853); n = 3) as an external morphological reference for comparisons. Most of the teeth from extant species were photographed for this study at the Museo Nacional de Ciencias Naturales (MNCN-CSIC, Madrid, Spain), while others were taken from the literature (Table 1). For the 2D GM analyses, the individuals were grouped in “current *M. meles*”, “fossil *M. meles*” (including specimens from the

Caucasus, Italic Peninsula, and Central Europe)”, “*M. meles atavus*”, “*M. teihardi*”, “*M. chiai*”, “*M. leucurus*”, “*M. magnus*”, “*M. thoralis*”, “*A. albogularis*” and “*Meles* from Quibas site”.

Following the requirements of 2D geometric morphometrics (2D GM) methods (Zelditch *et al.* 2012), standardized photographs of the teeth were used, taken with a Canon EOS 70D camera, with a 0.39 m/1.3 ft EFS 18-135 mm Macro lens. The teeth were placed so that the plane of the cement-enamel contact was parallel to the camera lens at a fixed distance of 20 cm. In addition, a scale was placed at the height of the plane of the amelocementary junction of the teeth.

2D GEOMETRIC MORPHOMETRICS OF THE M1 BADGER TEETH

After photographing, the images were processed with Viewbox4 software (dHAL software, Kifissia, Greece; Bastir *et al.* 2019). The photographs were correctly scaled using the scales placed on them, for the subsequent digitization of the landmarks and semi-landmarks. A total of 17 landmarks were collected in each photograph of an m1 in occlusal view at the: mesial-most point, distal-most point, paraconid cuspid, paraconid-protoconid notch, protoconid cuspid, protoconid-metacnid notch, metacnid cuspid, metacnid-entoconid notch, entoconid cuspid, entoconid-entoconulid notch, entoconulid cuspid, hypoconulid cuspid, hypoconulid-hypoconid notch, hypoconid cuspid, metacnid base at the teeth “valley”, hypoconid base at the teeth “valley”, and hipoconulid base at the teeth “valley”. In addition to those landmarks, two curves of 20 semilandmarks were measured at the buccal and lingual contours (Fig. 2). Because of uncertainty as to their locations along the curves, semilandmarks were slid along their corresponding curves concerning the fixed landmarks to minimize bending energy following standard procedures (Gunz *et al.* 2005; Bastir *et al.* 2013; Gunz & Mitteroecker 2013). Each tooth in occlusal view was represented by 57 landmarks and sliding semilandmarks, so a total of 8778 cartesian coordinates were analyzed.

DATA ANALYSES

We carried out a Procrustes fit to remove the effect of rotation, translation and scaling of the coordinates (Bookstein



FIG. 1. — Badger (*Meles meles meles* (Linnaeus, 1758)) right hemimandible from the Quibas Sima site (Q'18/QS4-1/P19/10): **A**, lingual view of the hemimandible; **B**, buccal view of the hemimandible; **C**, occlusal view of the hemimandible; **D**, close up of the occlusal view of the first right lower molar. Scale bars: 1 cm.

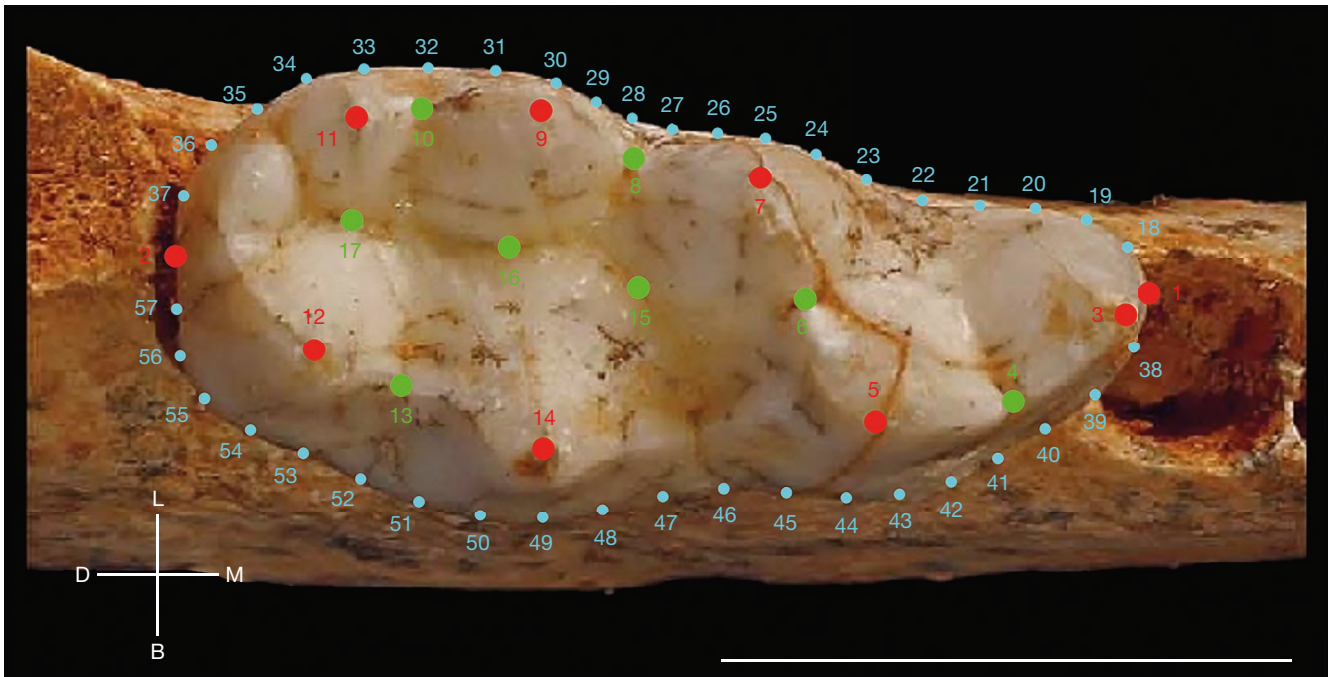


FIG. 2. — Set of landmarks and semilandmarks employed for the study of the badgers lower first molar (m1); the **red points** mark the landmarks corresponding to the ends of the tooth and the cusps: **1**, mesial point; **2**, distal point; **3**, paraconid; **5**, protoconid; **7**, metaconid; **9**, entoconid; **11**, entoconulid; **12**, hypoconulid; **14**, hypoconid; the **green points** correspond to the landmarks of the nodes between the cusps and the heel of the heel: **4**, para-protoconid notch; **6**, proto-metaconid notch; **8**, meta-entoconid notch; **10**, entoconid-entoconulid notch; **13**, hypoconulid-hypoconid notch; **15**, metaconid valley; **16**, hypoconid valley; **17**, hypoconulid valley; the **blue dots** mark the semi landmarks (**18-57**). Abbreviations: **B**, buccal; **D**, distal; **L**, lingual; **M**, mesial. Scale bar: 1 cm.

1991, 1996). The size variation was analyzed through the centroid size, which is defined as the square root of the sum of squared distances of all the landmarks of an object from their centroid (center of gravity) (Zelditch *et al.* 2012). For the shape analysis, the Procrustes coordinates were subjected to a principal component analysis (PCA) and then analyzed to explore the morphological variability of the sample. Once the shape variation was explored, we also carried out a regres-

sion analysis to test for shape differences explained by size variation. The allometric analysis was carried out for current and fossil *Meles meles* and the slopes of both allometric trajectories were compared.

Finally, a comparison between Iberian group means was carried out including living *M. meles* belonging to the MNCN ($n = 54$), the *M. meles atavus* ($n = 2$), and the *Meles* from Quibas Sima site ($n = 1$). Procrustes distance between

TABLE 2. — Centroid size results for the sample analyzed, including the 95% confidence interval for the current and fossil *Meles meles* Linnaeus, 1758.

	<i>Meles meles</i> (Linnaeus, 1758) (current)	<i>M. meles</i> (fossil)	<i>Meles</i> sp. (Quibas)	<i>M. meles</i> <i>atavus</i> Kormos, 1914	<i>M. magnus</i> Jiangzou, Liu, Wagner & Chen, 2018	<i>M. teihardi</i> Qiu, Deng & Wang, 2004	<i>M. chiai</i> Teilhard de Chardin, 1940	<i>M. leucurus</i> Hodgson, 1847	<i>M. thoralis</i> Viret, 1951
Mean	455.12	430.14	478.94	449.28	427.28	333.31	366.6	372.79	467.66
+95% CI	459.87	453.01	—	—	—	—	—	—	—
-95% CI	450.37	407.26	—	—	—	—	—	—	—

TABLE 3. — Procrustes distances between the different *Meles* groups analyzed. The numbers in **bold** with the symbol ** mean that the distance is statistically significant at level 0.01, whereas * means that it is only statistically significant at level 0.05 (permutation test (n = 1000) of the Procrustes distance between species means in MorphoJ (Klingenberg 2011)).

	<i>Meles meles</i> (Linnaeus, 1758) (current)	<i>M. meles</i> (fossil)	<i>Meles</i> Brisson, 1762 (Quibas site)
<i>M. meles</i> (current)	—	—	—
<i>M. meles</i> (fossil)	0.044**	—	—
<i>Meles</i> (Quibas site)	0.053	0.042	—
<i>M. meles atavus</i>	0.050*	0.058	0.064

means was calculated and tested by running a permutations test (n = 1000 permutations). All these analyses were carried out in MorphoJ software (Klingenberg 2011). Finally, the Procrustes distances matrix between the complete set of assessed species was subjected to a cluster analysis using the UPGMA algorithm (Unweighted Pair Group Method using Arithmetic averages) and running a Bootstrap test (Past4.01 software, n = 9999; Hammer *et al.* 2001), to observe the relationship between these different groups and the distances between them.

INTRA-OBSERVER ERROR

To ensure that the measurement error was reduced and did not significantly affect the results, permutations tests (Klingenberg 2011) were carried out. The intra-observer error was accepted after testing that the largest Procrustes distance within five measurements of the same individual was smaller than the smallest Procrustes distance between ten different teeth.

ABBREVIATIONS

2D GM	2D geometric morphometrics;
c	canine;
CS	centroid size;
GM	geometric morphometric;
m2	molar;
MNCN-CSIC	Museo Nacional de Ciencias Naturales, Madrid;
p	premolar;
PCA	principal component analysis;
QC	Quibas-Cueva;
QS	Quibas-Sima;
UPGMA	Unweighted Pair Group Method with Arithmetic.

SYSTEMATIC PALEONTOLOGY

Order CARNIVORA Bowdich, 1821
Suborder CANIFORMIA Kretzoi, 1943

Family MUSTELIDAE Fischer, 1817
Subfamily MELINAE Bonaparte, 1838
Genus *Meles* Brisson, 1762

Meles meles (Linnaeus, 1758)

LOCALITY. — Sierra de Quibas.

AGE. — 1 Ma (Piñero *et al.* 2020).

MATERIAL. — Q'18/QS4-1/P19/10 (Fig. 1), fragmentary right hemimandible, comprising a complete m1.

DESCRIPTION

It is a fragmentary right hemimandible with alveoli for c (canine), p2-p4 (second to the fourth premolar), and m2 (second molar), and a complete m1 (Fig. 1). It belongs to a young adult, as shown by the small worn area over the cusps of the m1, and the mild scars of the muscles masseter pars superficialis and pars profunda over the cranioventral part of the masseteric fossa. The coronoid process is missing and the angular process is broken. The horizontal ramus is dorsoventrally short. The alveolus for the c is distally broken, making it impossible to confirm the presence of the p1 (first premolar) alveolus. Both p2-p3 (third premolar) alveoli are buccolingually turned, indicating a shorter teeth row, and a shortening of the mandible. The m1 (maximum length = 18.6 mm; maximum width = 8.5 mm) has a typical *M. meles* morphology, comprising a longer talonid compared with the trigonid. The protoconid is the tallest cuspid of the trigonid, the paraconid, and the metaconid having similar heights. The metaconid is well developed and is buccolingually broad. The maximum width of the teeth is located at the hypoconid-entoconid level. Both cusps are well developed, the hypoconid being the largest one. The talonid's valley is mesiodistally long and shallow. There is a well-developed hypoconulid (buccal) and entoconulid

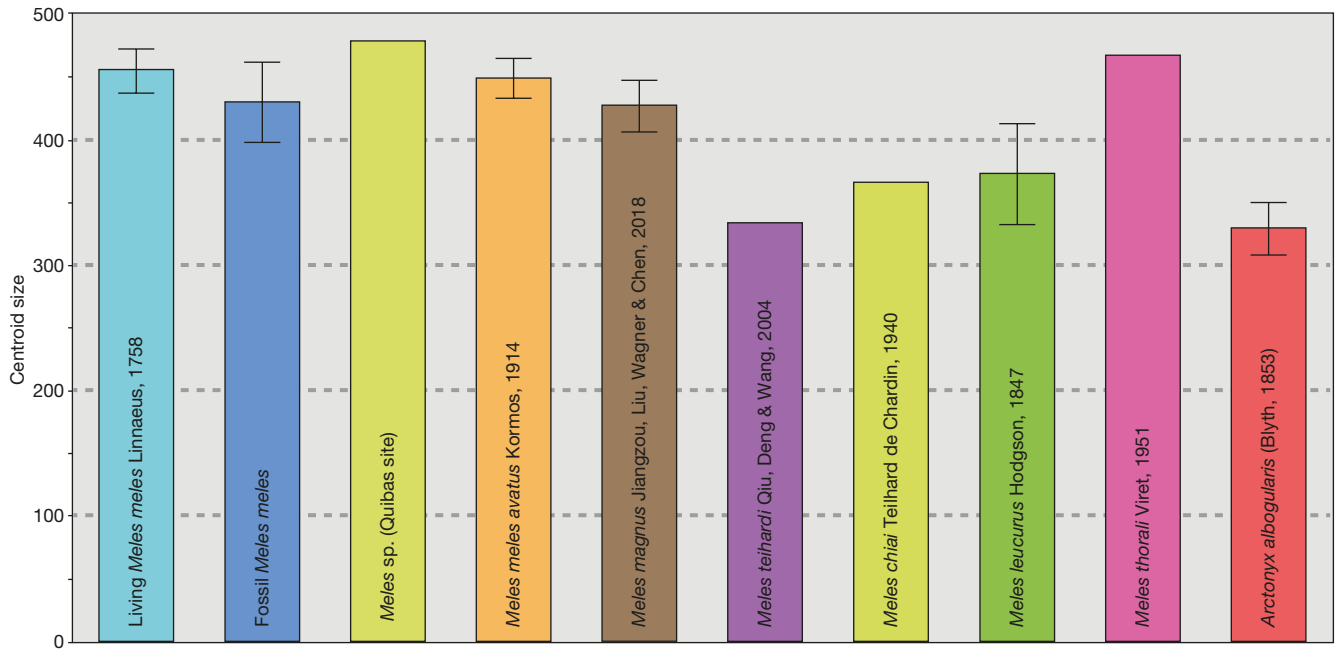


FIG. 3. — Centroid size analysis, showing a histogram bar graphic with the 95 confidence interval for the mean.

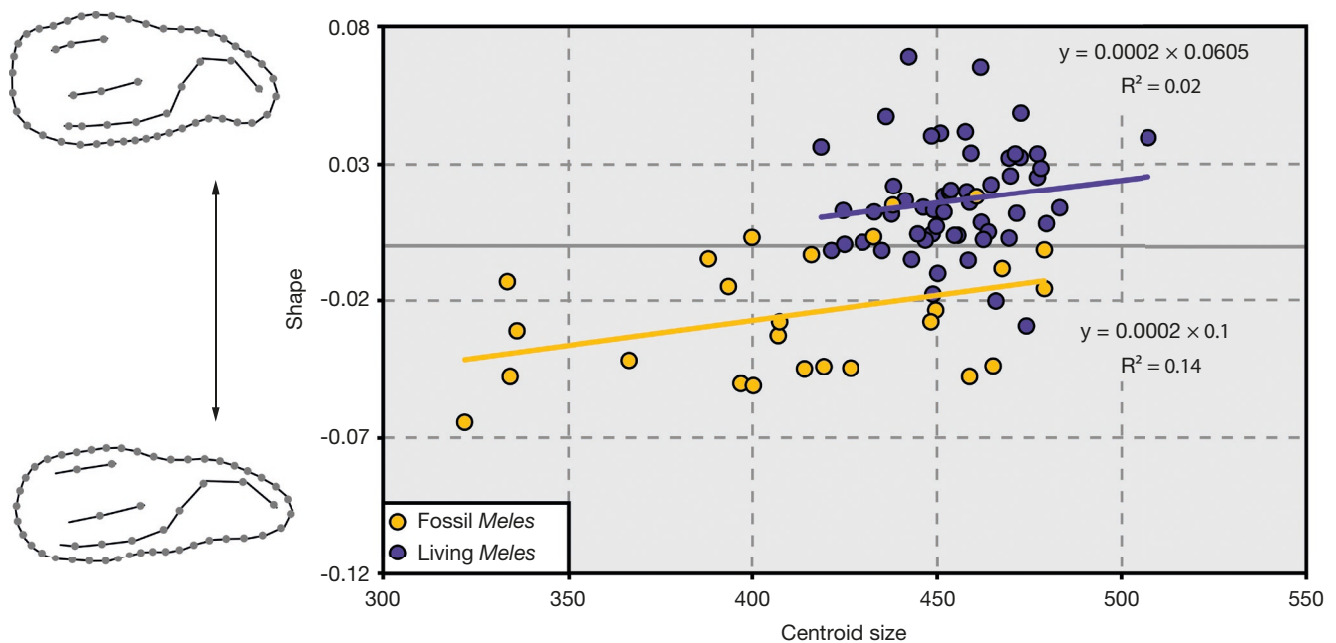


FIG. 4. — Allometric analysis for the size and shape variation of both current and fossil *Meles meles* (Linnaeus, 1758). The allometric trajectories in terms of slope and intercept are compared. Both trajectories are statistically significant but explain a little percentage of variation.

(lingual). A post entoconid cuspid is located in the most distal part of the tooth, closing the talonid. The alveolus of the m2 indicates the presence of a regular m2. The preserved portion of the masseteric fossa is shallow.

CENTROID SIZE (CS) ANALYSIS

The size analysis shows that the Quibas specimen is one of the largest specimens from the sample, being out of the confidence interval for the CS of both current and fossil

M. meles, being even larger than *M. meles atavus* and the rest of the fossils (Table 2; Fig. 3).

Using the *Meles meles* sample, we also did a Kolmogorov-Smirnov test to study the normality of the sample. After rejecting the normality of the sample (K-S test; $p < 0.05$), we carried out a Mann-Whitney test to test for size differences, finding that the current *M. meles* sample presented statistically larger values than the fossil *M. meles* sample (U: 148; z: 2.25; p : 0.02).

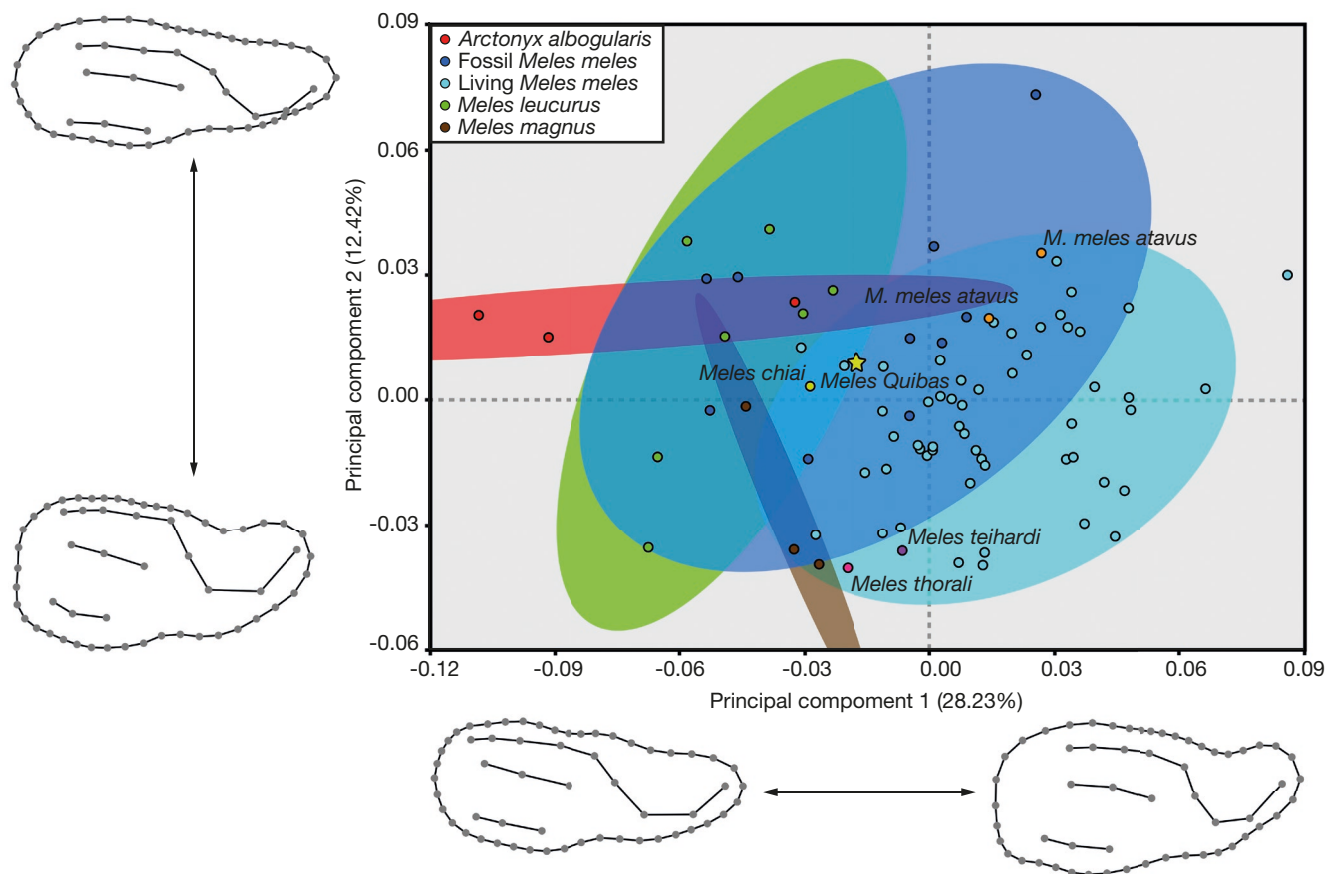


FIG. 5. — Graphic representation of the two principal components from the PCA, which explains 40% of the variability of the sample. We also include the 95% confident ellipses of the current and fossil *Meles meles* (Linnaeus, 1758), as well as *Arctonyx albogularis* (Blyth, 1853), *M. leucurus* (Hodgson, 1847), and *M. magnus* Jiangzou, Liu, Wagner & Chen, 2018. Close to the axes of variation, we show the percentage of variance absorbed (%) and the landmark morphologies (wireframe) associated with the extreme of the PC scores variation. **Green points:** current *Meles meles meles*.

ALLOMETRIC ANALYSIS

The variation of size and shape shows a statistically significant but slight association between both variables, both for the current ($r^2 = 0.02$) and fossil *M. meles* ($r^2 = 0.14$). It is interesting to note that the size variation is larger in the fossil *M. meles* than in the current ones. In addition, it is observed that the allometric trajectory between both is parallel, presenting identical slopes (0.0002) but different intercepts (Fig. 4).

MEAN COMPARISONS AND PERMUTATIONS TEST

We compared the mean of the extant *M. meles* with the means of the remaining *M. meles*: *M. meles* fossils, *M. meles atavus*, and the *Meles* from the Quibas site. Our results show that the *Meles* from Quibas were not significantly different from the extant *M. meles*, but the *M. meles* fossil group and the group of *M. meles atavus* were statistically significant, despite having a smaller Procrustes distance compared to the current *M. meles* (Table 3).

PRINCIPAL COMPONENT ANALYSIS (PCA, SEE Appendix 2 FOR MORE INFORMATION)

The projection of PC1 vs PC2 (40.65 % of variability; Fig. 5) shows that the negative scores of PC1 (28.23 % of variability),

where *M. leucurus* and *Arctonyx albogularis* plot, represent a trend of slender m1 that are buccolingually narrow, with a trigonid and talonid about the same length. They also have a wide space between the cusps of paraconid, protoconid, and metaconid, and reduced space between the cusps of the entoconulid and hypoconulid to the mesial-most point of the tooth. In the positive scores, we observe the reverse trend, with a more robust morphology of m1 caused by quadrangular talonid and a shortened trigonid. This also causes a re-arrangement of the cusps, since the talonid cusps are far from the mesial-most point and the trigonid cusps are closer to each other. Regarding the extinct specimens, most of them (including the Quibas one) fall into the variability of *Meles*, but it is possible to observe a trend in which most of them fall at the more negative part of the distribution, as in more slender morphologies.

The PC2 (12.42 % of variability; Fig. 5) distinguishes less between groups or species. In the negative-most end of the axis, we observe a robust morphology, teeth with a globular shape, in which the trigonid and talonid are about the same length, with little separation of the cusps between the metaconid, entoconid, and entoconulid to the lingual edge, in contrast to the wide separation of hypoconid, hypoconulid, and protoconid to the buccal edge. On the other hand, at

the opposite end of the axis (positive scores), we find teeth of elongated morphology, with talonid of larger length than the trigonid. Regarding the separation of the cusps and the edges of the tooth, we observed a wide separation between metaconid, entoconid, and entoconulid to the lingual, and a close location of the hypoconid, hypoconulid, protoconid, and paraconid to the buccal edge. Also, we can observe a greater amplitude in the distal area of the tooth due to the separation between entoconulid and hypoconulid and the distal point of the tooth. Regarding the fossils, *M. leucurus* and *A. albogularis* fall in the positive scores, linked to slender morphologies, but a fair amount of extant *M. meles* fall as well (Fig. 5). The different fossils are spread along the variability in PC2, but it could be important to mention that *M. meles atavus* falls at the upper extreme of the *M. meles* variability, characterized by a slender morphology, as in the case of *M. leucurus* and *A. albogularis*. However, other species such as *M. magnus*, *M. thoralis*, or *M. teihardi* fall at the opposite extreme of the variability, thus having a more robust (quadrangular-shaped) morphology.

CLUSTERS UPGMA

We did two different clusters using the UPGMA analysis, the first one (UPGMA1; Fig. 6) using all the shape variation comprised by all the different PCs, and the second one (UPGMA2; Fig. 7) also adding the CS to the shape variation. When the size is included, we observe a large cophenetic correlation (0.88), and large values for the different nodes associations (>67). In this UPGMA1 we can see two separated branches, one containing the Asiatic species except for *M. magnus* and the other one with all of the European species plus *M. magnus*. These results show us that size has a great influence on the relationships of this cluster because the first branch comprises the groups with smaller teeth and the second one the groups with larger teeth, as demonstrated also by the previously shown CS. This way we can also observe a tendency in the European groups of larger teeth compared to the majority of Asiatic groups.

In the cluster UPGMA2, where only shape information is included, we can see that even slightly lower cophenetic correlation (0.78) compared to the UPGMA1. Also, the nodes associations are weaker than in the previous case, showing that size is an important driving factor for the associations. In this cluster, we observed two different branches: one including only the genus *Arctonyx* and the other one with all the *Meles* species. The *Meles* branch is also divided into two branches, being *M. chiai* in a different branch and leaving the rest of *Meles* divided into another two branches. The first branch groups all Asiatic fossils together, including the *M. thoralis*, and the second branch with all the current specimens grouped with the rest of the European fossils. The *Meles* fossil from the Quibas site is grouped in a branch with the *M. meles* fossils.

DISCUSSION

The evolution of badgers in Western Europe is still under debate, and new fossils such as the one from Quibas site

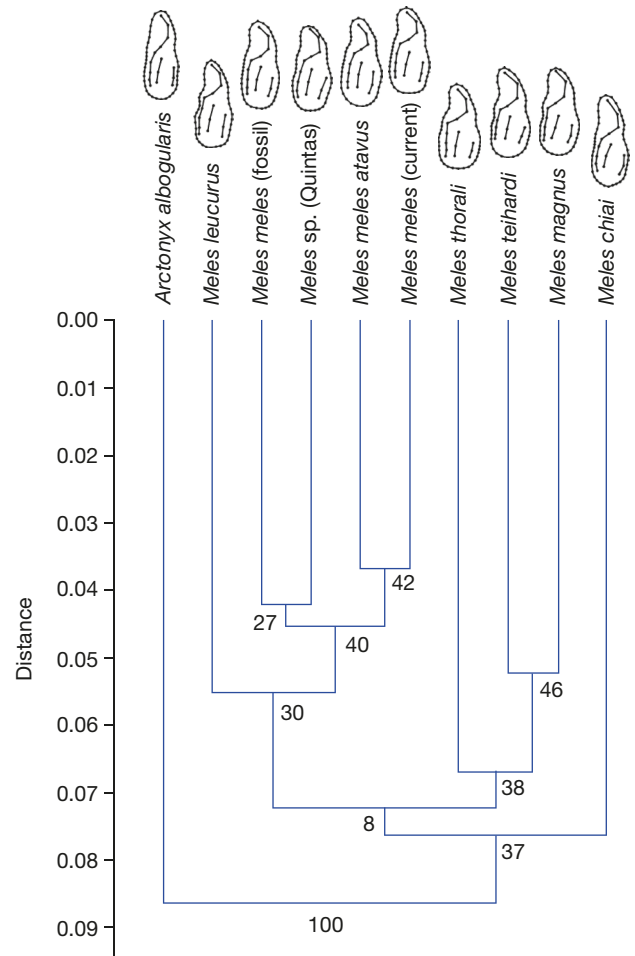


Fig. 6. — Graphic representation of the cluster analysis using the shape information coming from all the PCs. It has been carried out using a hierarchical method with the criterion (algorithm) of Unweighted Pair Group Method with Arithmetic mean (UPGMA). The landmarks representing the average of each group is shown at the end of the branches.

described herein add new data to the extensive record of Pleistocene-Holocene *M. meles* from the Iberian Peninsula (Baryshnikov *et al.* 2002; Madurell-Malapeira *et al.* 2009, 2011a, b; García-Martínez *et al.* 2020). Our 2DGM results take into account the morphology of the badger's lower first molar and corroborate its previously stated taxonomic informative value (Madurell-Malapeira *et al.* 2011a, b). It is important to state that we recognize that phenetic analysis such as the UPGMA or the mean comparisons is weak in supporting or rejecting phylogenies, but the knowledge provided here can complement other more strict phylogenetic analyses (Adams *et al.* 2011). To get a more complete approach to the badgers' taxonomy it may be necessary to analyze also other characters.

Nevertheless, the use of 2D GM allows for a good representation of morphological differences and affinities between different badger taxa with potential phylogenetic information. According to the overall morphology of the hemimandible and the m1, as well as the 2D GM analysis of a wide sample of Plio-Pleistocene and extant melinae badgers, the specimen Q'18/QS4-1/P19/10 from the Quibas site is determined as

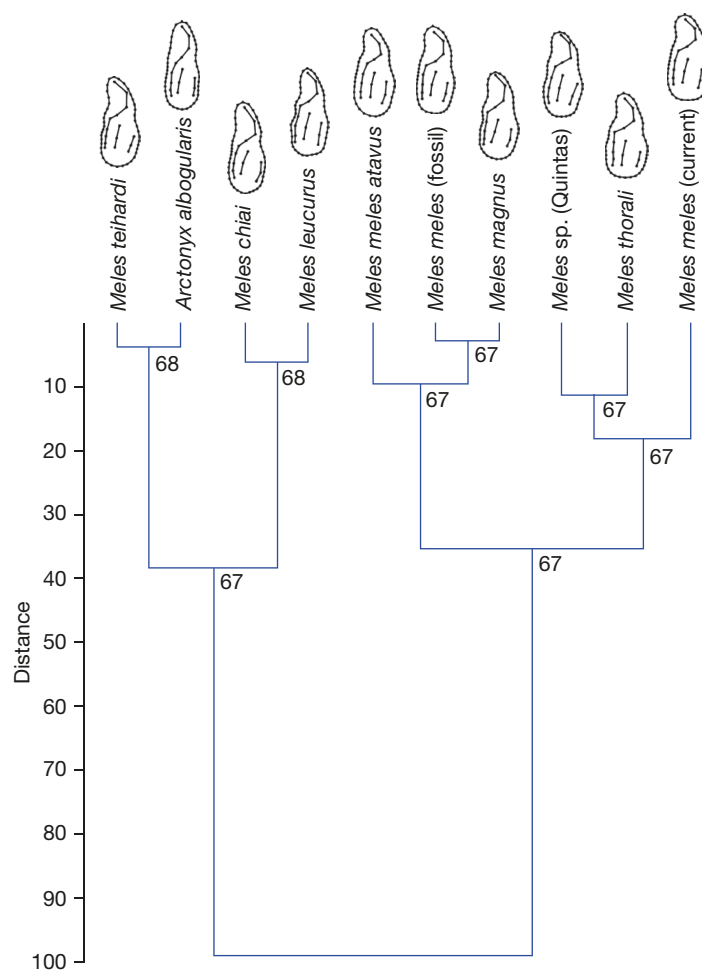


FIG. 7. — Graphic representation of the cluster analysis using the shape information coming from all the PCs plus the centroid size. It has been carried out using a hierarchical method with the criterion (algorithm) of Unweighted Pair Group Method with Arithmetic mean (UPGMA). The landmarks representing the average of each group is shown at the end of the branches.

M. meles meles. In the first place, the permutations tests carried out with the comparison of extant *M. meles* and *M. meles* from Pleistocene localities indicate that the differences between those groups were not significant, so they could be grouped within the same group. Similarly, when we observe the shape of the Quibas tooth and the average shape of the living *M. meles meles*, the morphological differences between them are very subtle and could fall within the great morphological variation observed in the species (Del Cerro Márquez 2011; Gasparik & Pazonyi 2018). Finally, supporting this taxonomic attribution, it is to be noted that these two taxa groups (fossil *M. meles* and *Meles* from Quibas) are together in the same cluster (Fig. 6).

The hypothesis of a single lineage of badgers in the Pleistocene of Western Europe may be supported in our analyses, which suggest a single cluster for the fossil *M. meles*, distinct to the Plio/Pleistocene Eurasian group comprised by the European *M. thoralis* from Saint Vallier (Viret 1954), and the Asiatic *M. magnus*, *M. theihardi* and *M. chiai* (see Jiangzou *et al.* 2018).

If we compare our cluster (Fig. 6) with the phylogenetic hypothesis proposed by Jiangzou *et al.* (2018), we can see some differences in the relationships between the non-*M. meles* fossil species. In their work, they all share a common

ancestor but they are divided into two groups. The first one, where *M. theihardi* is nested with *M. chiai* and *M. leucurus* appears jointed with *M. magnus*; and the second one, where *M. thoralis* is placed alone. However, our results, although they also nest the extinct Asiatic species and *M. thoralis* together, show minor differences, placing *M. chiai* as the most different group, pairing *M. magnus* and *M. theihardi*, and leaving *M. thoralis* close to this branch. The most striking difference in our results is the position of *M. leucurus*, contrary to Jiangzou *et al.* (2018), where *M. leucurus* nests with *M. magnus*. We have to take into account that our cluster is based on the differences between the m1 morphology whereas the analysis by Jiangzou *et al.* (2018) is made using both lower and upper teeth. It would be interesting for a future project to use 2D GM methods to analyze the upper dentition to see if the results are similar to the ones given by Jiangzou *et al.* (2018).

The oldest record of *M. meles* in the Iberian Peninsula comes from Fuente Nueva 3 site within the Orce Paleontological complex (Granada, Spain), dated 1.3-1.4 Ma (Madurell-Malapeira *et al.* 2011a, b), which places the species on the peninsula up to 0.3-0.4 Ma before the record correspond-

ing to the Quibas site. It was not possible to analyze the Orce complex fossil using the 2D GM methods due to the lack of preservation of the m1 cuspids. However, Madurell-Malapeira *et al.* (2011a, b) have proposed the presence of a different subspecies, *M. meles atavus* in Vallparadís (Barcelona, Spain), dated to *c.* 1 Ma, based on their primitive morphology. Our morphometric data seem to support this assignment and consequently provide the basis for a new evolutionary hypothesis. If we accept that the Quibas tooth is representative of the species *M. meles meles*, then we might recognize that two different subspecies of *M. meles* coexisted on the east coast of the Iberian Peninsula approximately 1 Ma. On the other hand, the abovementioned *M. meles meles* from Quibas (Murcia, southeast of the Iberian Peninsula) and *M. meles atavus* in Vallparadís (Catalonia, northeast of the Iberian Peninsula) appear in similar chronologies (Madurell-Malapeira *et al.* 2011a, b). Initially, *M. atavus* was described by Kormos (1914) as a different fossil species from *M. meles*, but later on, various authors such as Kretzoi (1938) agreed that it should be recognized as a subspecies of the species *M. meles* since certain morphological features of *M. atavus* that originally led to a specific distinction (the presence of an accessory cusp between the m1 protoconid and hypoconid) were also found in some specimens of *M. meles*.

As mentioned, our results support the consideration of *M. meles atavus* as a subspecies since the cluster obtained (Fig. 6) shows *M. meles atavus* at the base of the core of *M. meles* analyzed. According to Madurell-Malapeira *et al.* (2011b), the main differences between *M. meles* and the extant *M. meles atavus* are dental proportions. The latter displays intermediated conditions between *M. thoralis* and the extant *M. meles*. Our analysis also supports the results provided by Madurell-Malapeira *et al.* (2011b) where *M. meles atavus* shows intermediate characteristics between *M. thoralis* and the extant *M. meles*. Likewise, it is nested with *M. meles* from the Middle Pleistocene of Kudaro Cave (Georgia) in the same branch. It is important to highlight that Georgian specimens were described as *M. meles* (see Baryshnikov 2009) before *M. canescens* was considered a different species (Abramov & Puzachenko 2013). According to Baryshnikov (2009), there were no noticeable differences between the Kudaro fossils and the extant *M. (meles) canescens*. Recent mtDNA data analysis suggested that *M. canescens* and *M. meles* diverged between 2.37 and 0.45 Ma (Abramov & Puzachenko 2013). Therefore, it is potentially possible that the fossil *M. meles* from Georgia belong to *M. canescens* since this fossil comes from the Middle Pleistocene Caucasus, the current habitat of that species. This fact could give us to understand that *M. meles atavus* is a primitive form of the species *M. meles* similar to the Middle Pleistocene *Meles* from Georgia. However, to test this hypothesis, it would be necessary to analyze m1 of *M. canescens*.

We are conscious that some limitations can be found in our study, some of them resulting from a bias in the fossil record and some of them caused by to availability of some samples. For example, the absence of two extant species in the analysis (*M. anakuma* and *M. canescens*) and the limited number of

specimens sampled from seven of the six species limits the confidence in the results obtained. In addition, this limited number of specimens can cause that the statistical significance for some values is not strong.

Despite those limitations, we can infer that there must be a subspeciation process in the Iberian Peninsula towards *M. meles meles* around 1.5 Ma, as represented by the Fuente Nueva 3 (Orce) evidence, persisting until the present day, as it can be tracked throughout Quibas fossil and a series of later Pleistocene evidence. Interestingly, relic morphologies such as those represented by the *M. meles atavus* of Vallparadís (Barcelona), more similar to primitive forms such as *M. thoralis*, persist in some other areas. These data suggest that the phylogenetic origin of *M. meles meles* could be geographically located in the southeastern area of Iberia.

CONCLUSIONS

Based on the morphology of the m1, analyzed with 2D GM methods, the 1 Ma badger fossil from the Quibas Sima site is classified as *M. meles meles*. This species was already present in the Iberian Peninsula around 1.3-1.4 Ma in Fuente Nueva 3. Furthermore, our results support the denomination of *M. meles atavus* as a subspecies, which we relate to a primitive morphology close to one of *M. meles* from the Caucasus (potentially *M. canescens*). The proposition of a phylogenetic origin of *M. meles meles* in the southeastern area of Iberia might be tested with further evidence using complementary analysis apart from the UPGMA or mean shape comparisons.

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Authors' contribution

Antonio Rosas, Ana Soler-Fajardo and Daniel García-Martínez contributed equally to the manuscript.

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APPENDICES

APPENDIX 1. — Details of the comparative (current) *Meles meles meles* (Linnaeus, 1758) sample.

Species	ID	Side	Geographical origin	Chronology	Data housing
<i>Meles meles</i> (Linnaeus, 1758)	MNCN 15988	Left	Burgos, Spain	Current, 1977	MNCN
	MNCN 15992	Right	Burgos, Spain	Current, 1977	MNCN
	MNCN 16105	Right	Oviedo, Spain	Current, 1982	MNCN
	MNCN 16097	Left	Oviedo, Spain	Current, 1982	MNCN
	MNCN 16101	Right	Barcelona, Spain	Current, 1981	MNCN
	MNCN 16106	Left	Tarragona, Spain	Current, 1981	MNCN
	MNCN M22065	Right	Barcelona, Spain	Current, 1991	MNCN
	MNCN 15989	Right	Ávila, Spain	Current, 1979	MNCN
	MNCN 16100	Right	Oviedo, Spain	Current, 1982	MNCN
	MNCN 16095	Left	Asturias, Spain	Current, 1977	MNCN
	MNCN 16096	Left	Asturias, Spain	Current, 1977	MNCN
	MNCN M22068	Right	Córdoba, Spain	Current, 1986	MNCN
	MNCN 15990	Left	Almería, Spain	Current, 1979	MNCN
	MNCN M21636	Right	Madrid, Spain	Current, Indet.	MNCN
	MNCN M21709	Left	Madrid, Spain	Current, 2006	MNCN
	MNCN 15998	Left	Asturias, Spain	Current, 1977	MNCN
	MNCN 16020	Right	Asturias, Spain	Current, 1978	MNCN
	MNCN 15997	Right	Gerona, Spain	Current, 1981	MNCN
	MNCN 16014	Left	Soria, Spain	Current, 1974	MNCN
	MNCN 16008	Left	Navarra, Spain	Current, 1978	MNCN
	MNCN 16022	Right	Navarra, Spain	Current, 1976	MNCN
	MNCN 16016	Right	Burgos, Spain	Current, 1973	MNCN
	MNCN 16010	Left	Santander, Spain	Current, 1980	MNCN
	MNCN 16071	Right	Burgos, Spain	Current, 1974	MNCN
	MNCN 16002	Left	Santander, Spain	Current, 1980	MNCN
	MNCN 16009	Right	Soria, Spain	Current, 1974	MNCN
	MNCN 16023	Right	Lérida, Spain	Current, 1973	MNCN
	MNCN 16038	Right	Ciudad Real, Spain	Current, 1974	MNCN
	MNCN 16048	Right	Ciudad Real, Spain	Current, 1978	MNCN
	MNCN 16043	Right	Ciudad Real, Spain	Current, 1978	MNCN
	MNCN 16034	Right	Cáceres, Spain	Current, 1976	MNCN
	MNCN 16025	Left	Oviedo, Spain	Current, 1976	MNCN
	MNCN 16045	Right	Ciudad Real, Spain	Current, 1978	MNCN
	MNCN 16044	Right	Toledo, Spain	Current, Indet.	MNCN
	MNCN 16039	Right	Toledo, Spain	Current, 1979	MNCN
	MNCN 16047	Right	Toledo, Spain	Current, 1980	MNCN
	MNCN 16050	Right	Toledo, Spain	Current, 1981	MNCN
	MNCN 16054	Right	Cáceres, Spain	Current, 1975	MNCN
	MNCN 16057	Right	Lugo, Spain	Current, 1974	MNCN
	MNCN 16061	Right	Indet, Spain	Current, 1976	MNCN
	MNCN 16055	Right	Toledo, España	Current, Indet.	MNCN
	MNCN 16075	Right	León, Spain	Current, 1979	MNCN
	MNCN 16072	Right	Pontevedra, Spain	Current, 1975	MNCN
	MNCN 16079	Right	Ciudad Real, Spain	Current, 1975	MNCN
	MNCN 16049	Right	Ciudad Real, Spain	Current, Indet.	MNCN
	MNCN 16074	Right	Lérida, Spain	Current, 1977	MNCN
	MNCN 16063	Right	Lérida, Spain	Current, 1972	MNCN
	MNCN 16078	Right	Indet, Spain	Current, 1975	MNCN
	MNCN 16076	Right	Asturias, Spain	Current, 1978	MNCN
	MNCN 16059	Right	Burgos, Spain	Current, 1975	MNCN
	MNCN 16037	Right	Oviedo, Spain	Current, 1979	MNCN
	MNCN 16080	Right	Lérida, Spain	Current, 1974	MNCN
	CSIC 1	Right	Indet, Spain	Current, Indet.	MNCN
	CSIC 2	Right	Indet, Spain	Current, Indet.	MNCN

APPENDIX 2. — PC scores (PC1-PC6) from the PCA analysis, explaining. PC1-PC4 are shown after carrying out the scree plot.

	PC1 (28.23%)	PC2 (12.42%)	PC3 (9.02%)	PC4 (8.51%)
<i>Arctonyx albogularis</i> (Blyth, 1853)	-0.108410	0.020135	0.018050	0.008444
	-0.032454	0.023268	-0.030173	0.002667
	-0.091646	0.014806	0.016737	0.011227
<i>M. meles atavus</i> Kormos, 1914	0.026795	0.035083	-0.012693	-0.000523
	0.014267	0.019402	-0.012123	-0.007705
<i>Meles chiai</i> Teilhard de Chardin, 1940	-0.028800	0.003053	0.013991	0.048391
<i>Meles leucurus</i> (Hodgson, 1847)	-0.058216	0.037928	0.009112	0.034417
	-0.023334	0.026102	-0.043172	-0.015400
	-0.049175	0.015011	-0.045607	0.001664
	-0.038515	0.040799	0.023364	0.038707
	-0.067472	-0.035641	0.017134	-0.009946
	-0.030495	0.020503	-0.004191	0.027703
	-0.065248	-0.013810	-0.030547	-0.020554
<i>Meles magnus</i> Jiangzou, Liu, Wagner & Chen, 2018	-0.044165	-0.001748	-0.009114	-0.033911
	-0.026666	-0.039710	-0.009687	0.062013
	-0.032658	-0.036121	0.006002	0.041261
<i>Meles meles</i> (Linnaeus, 1758) (current)	0.041833	-0.019851	0.012366	0.001196
	0.007870	-0.001472	-0.029847	0.007661
	0.047742	0.000367	-0.027657	0.006729
	0.026632	0.017241	0.001275	0.024386
	0.007616	0.004481	0.008633	-0.014611
	-0.008500	-0.008929	-0.016715	-0.003191
	0.085898	0.029711	-0.004056	0.001079
	0.048196	-0.002597	-0.006729	0.009927
	0.030452	0.033093	-0.005871	-0.016422
	-0.000236	-0.000675	-0.015515	-0.004324
	0.032733	-0.014378	0.002950	0.004905
	0.033117	0.017231	0.027179	-0.006690
	-0.002207	-0.011924	-0.001920	-0.007320
	-0.002717	-0.011017	-0.003237	0.006693
	0.037114	-0.029759	-0.012073	0.032326
	0.044459	-0.033031	0.004973	0.009864
	0.009782	-0.020078	-0.011321	0.003525
	-0.027475	-0.032618	-0.005480	-0.016323
	0.007018	-0.039302	0.013471	-0.004873
	0.012809	-0.039924	-0.004904	-0.002848
	0.002599	0.009299	0.004830	0.017480
	0.036076	0.016149	-0.003043	0.002560
	0.011148	-0.012227	0.019059	-0.021824
	0.039546	0.002926	-0.009970	0.008739
	0.007172	-0.006467	0.003682	-0.016408
	-0.010270	-0.016706	-0.000549	-0.017227
	-0.011191	-0.002896	0.022332	-0.013382
	0.047677	0.021885	0.021314	-0.005594
	0.008406	-0.008252	-0.020594	-0.009727
	-0.000538	-0.013499	-0.014120	-0.003637
	0.066333	0.002545	-0.000743	0.007983
	0.034421	-0.013870	-0.007516	0.022196
	0.031355	0.020214	-0.006779	0.014597
	0.011801	0.002285	-0.041036	-0.008230
	0.005347	0.000020	-0.035267	-0.022213
	-0.010979	0.007800	-0.017160	-0.010629
	-0.030950	0.012330	0.018475	-0.003258
	0.034064	-0.005850	-0.009386	-0.008907
	0.013229	-0.036894	0.041810	-0.017583
	0.000816	-0.012209	-0.000321	-0.020591
	0.019665	0.015754	0.005288	0.002217
	0.000863	-0.011366	0.003932	-0.031436
	-0.015414	-0.017588	0.013304	-0.027481
	0.002652	0.000669	0.018780	-0.007924
	0.034003	0.025703	-0.027435	0.002340
	-0.011184	-0.032239	0.038790	-0.000992
	0.023295	0.010560	0.006152	0.001317
	-0.006857	-0.030752	0.009746	-0.013009
	0.012502	-0.014270	0.008506	-0.012381
	0.013333	-0.015821	0.005692	0.001377
	0.015391	0.018384	0.026210	-0.023726
	0.019855	0.006206	-0.022458	0.005371
	-0.020635	0.007988	-0.013839	-0.024726
	0.046692	-0.021865	0.000278	-0.002358

APPENDIX 2. — Continuation.

	PC1 (28.23%)	PC2 (12.42%)	PC3 (9.02%)	PC4 (8.51%)
<i>Meles meles</i> (fossil)	-0.004739	-0.004008	0.030330	-0.016621
	-0.029289	-0.014305	0.006913	0.021557
	-0.052745	-0.002700	-0.012890	-0.005097
	0.008901	0.019669	0.006271	0.046909
	-0.004630	0.014530	0.037114	-0.021046
	0.025456	0.073041	0.058783	-0.006838
	0.001096	0.036682	0.016306	0.011534
	0.003028	0.013443	-0.001477	0.002226
	-0.046083	0.029312	0.000181	-0.029442
	-0.053556	0.028910	-0.027528	-0.016883
<i>Meles</i> sp. (Quibas site)	-0.017387	0.008819	0.007042	0.001561
<i>Meles teihardi</i> Qiu, Deng & Wang, 2004	-0.006464	-0.036418	-0.003599	0.027942
<i>Meles thoralis</i> Viret, 1951	-0.019759	-0.040555	0.011984	0.001119