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Systematic Palaeontology (Vertebrate Palaeontology)

Meles iberica n. sp., a new Eurasian badger (Mammalia, Carnivora, Mustelidae) from Fonelas P-1 (Plio-Pleistocene boundary, Guadix Basin, Granada, Spain)

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Abstract

This paper reports a new species of ancient badger – *Meles iberica* n. sp. – discovered at the Fonelas P-1 Plio-Pleistocene site (Cuenca de Guadix, Granada, Spain). The anatomical features of its fossils, which identify it as a new species of *Meles*, include: the great robustness and small size of the specimens found, orbits nearly closed by well-developed zygomatic processes of the frontal bone, very small and rounded infraorbital foramens that open above the fourth upper premolar metacone, upper carnassial teeth with a concave linguodistal outline, the reduction of the talon of the first upper molar, a very deep masseteric fossa, whose anterior margin reaches the mesial limit of the second lower molar, an extensive horizontal platform at the base of this fossa, and a very long and narrow angular apophysis. This species is the most ancient of the genus recorded for the Iberian Peninsula. ***To cite this article: A. Arribas, G. Garrido, C. R. Palevol 6 (2007).***

Résumé

Meles iberica* n. sp., un nouveau blaireau (Mammalia, Carnivora, Mustelidae) du gisement de Fonelas P-1 (limite Pliocène-Pléistocène, bassin de Guadix, Grenade, Espagne).** Cet article rapporte l'existence d'une nouvelle espèce de blaireau ancien –*Meles iberica* n. sp.– découverte sur le site plio-pléistocène de Fonelas P-1 (Cuenca de Guadix, Grenade, Espagne). Les caractéristiques anatomiques de ses restes fossiles, qui permettent de l'identifier comme une nouvelle espèce de *Meles*, incluent : la grande robustesse et la petite taille des spécimens trouvés, des orbites presque fermées par des processus zygomatiques de l'os frontal, bien développés, des petits foramens infraorbitaux qui s'ouvrent au-dessus du métacône de la quatrième prémolaire supérieure, une carnassière supérieure, à contour linguodistal concave, la réduction du talon de la première molaire supérieure, une fosse de masséter très profonde, dont la marge atteint la limite mésiale de la deuxième molaire inférieure, une plateforme extensive horizontale à la base de cette fosse et une apophyse angulaire très longue et étroite. Cette espèce est la plus ancienne du genre répertoriée dans la péninsule Ibérique. ***Pour citer cet article : A. Arribas, G. Garrido, C. R. Palevol 6 (2007).

Keywords: Mustelidae; *Meles*; Plio-Pleistocene; Fonelas P-1; Guadix Basin; Spain

Mots clés : Mustelidae ; *Meles* ; Plio-Pléistocène ; Fonelas P-1 ; Bassin de Guadix ; Espagne

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1. Introduction

The Fonelas P-1 site, which was discovered in 2000 and has been explored since 2001 as part of the *Proyecto Fonelas* [1], has become the most important site in the Iberian Peninsula with respect to research into the Plio-Pleistocene transition in a continental setting (http://www.igme.es/internet/museo/investigacion/paleontologia/fonelas/index.htm).

The sedimentary environment and the genetic model of the site (*Sondeo B*) have been established [26], and the biological processes associated with the genesis of its fossil association (a den/eating place of hyenids belonging to the species *Pachycrocuta brevirostris*) and the structure of the sedimentary matrix surrounding the fossils have been characterised. The large mammals represented [2,7] include native European species (*Mammuthus meridionalis*, *Stephanorhinus etruscus*, *Eucladoceros* sp., *Metacervoceros rhenanus* cf. *phillisi*, *Gazellospira torticornis* ssp., *Homotherium latidens*, *Acinonyx pardinensis*, *Megantereon cultridens* ssp., *Croizetoceros ramosus* ssp., *Lynx pardinus spelaeus*, *Vulpes alopecoides*, *Canis* n. sp. and *Meles iberica* n. sp.), as well as immigrant species from Asia and Africa (*Leptobos etruscus*, *Equus* cf. *major*, *Canis etruscus*, *Mitilanotherium* n. sp., *Praeovibos* sp., *Hyaena brunnea*, *Potamochoerus* n. sp., *Pachycrocuta brevirostris*, *Canis falconeri* and *Capra* n. sp.). No other such palaeobiological association is known in Eurasia.

Analysis of the last and first appearance data (LADs and FADs) for the site's most important taxa assign the fossil association a position between the Olivola and Tasso Faunal Units (FU) [20], or, if the indications of other authors regarding French fossil associations [15] are taken into account, in zone MNQ-18. Irrespective of the biochron used, the Fonelas P-1 site dates from the Plio-Pleistocene transition; i.e., it is some 1.7–1.9 million years old. However, the fossil association of the Fonelas P-1 site does not exactly match the associations of large mammals characteristic of any of the above-mentioned FUs or MNQs [2].

Eleven species of carnivores are found at the site, among which there is a single mustelid – a Eurasian badger – identified from three fossils representing two adults. The genus *Meles* arose in Asia [22] and reached Europe at the beginning of the Pliocene. The species *Meles gennevauxi* Viret, 1939, is the most ancient member of the genus known in Europe; a fossil from the Lower Pliocene was found in Montpellier (France). Some authors, however, include it in the genus *Arctomeles* [8,21]. In contrast to that indicated by Pilgrim [17], some authors [13,16] propose the genus *Meles* to have developed from the genus *Melodon* during the Upper Miocene.

To date, the Eurasian badgers of the Plio-Pleistocene transition were known only by the species *Meles thorali* Viret, 1950, which has only been found at the Upper Pliocene sites of Saint-Vallier (France) and Vatera (Greece), and *Meles dimitrius* Koufos, 1992, discovered at the Upper Pliocene site of Gerakarou and the Lower Pleistocene site of Apollonia-1, both in the Mygdonian basin (Greece). In the Iberian Peninsula, the only known specimen of *Meles* for this period comes from the Lower Pleistocene site of Venta Micena. This citation of Cf. *Meles* sp. [18] was possible due to the finding of a canine tooth and a fragment of humerus; unfortunately, both

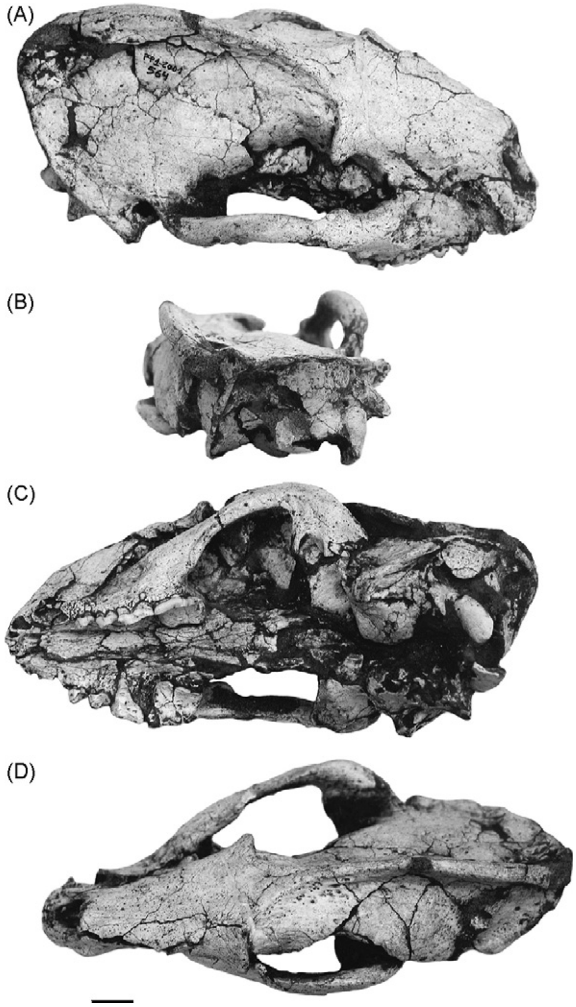

Fig. 1. The skull of *Meles iberica* n. sp., holotype FP1-2001-0564. (**A**): Oblique, right lateral view; (**B**): caudal view; (**C**): oblique left ventral view; (**D**): sagittal view. Scale bar = 1 cm.

Fig. 1. Crâne de *Meles iberica* n. sp., holotype FP1-2001-0564. (**A**) : Vue oblique latérale droite. (**B**) : vue caudale ; (**C**) : vue oblique ventrale gauche ; (**D**) : vue sagittale. Barre d'échelle = 1 cm.

have been lost. Recently, *Meles* sp. has been cited at the Fuente-Nueva-3 and Barranco León-5 [14] sites, but no description nor figure of the material evidence has been published.

2. Systematic palaeontology

Order CARNIVORA Bowdich, 1821
Family MUSTELIDAE Fischer, 1817
Subfamily MELINAE Bonaparte, 1838
Genus *Meles* Brisson, 1762
Meles iberica n. sp.

Etymology. From *Iberica* [coming from Iberia], a Greek word used as a toponym by Herodotus (5th century B.C.) to designate the Iberian Peninsula, currently occupied by Spain and Portugal, and home to the Fonelas P-1 site.

Holotype. FP1-2001-0564, skull with P2-M1 in both dental series (Figs. 1–3). Held at the *Museo Geominero* (*Instituto Geológico y Minero de España, Ministerio de Educación y Ciencia*), Madrid, Spain.

Paratypes. FP1-2001-0704, left hemimandible with i1, c, p2-m1 (Fig. 4); FP1-2002-1446, fragment of left mandible with right i1 and left i1-i3, c, p1-m1 (Fig. 5). Held at the *Museo Geominero* (*Instituto Geológico y Minero de España, Ministerio de Educación y Ciencia*), Madrid, Spain.

Fig. 3. Upper left dentition of *Meles iberica* n. sp., holotype FP1-2001-0564. Scale bar = 1 cm.
Fig. 3. Dentition supérieure gauche de *Meles iberica* n. sp., holotype FP1-2001-0564. Barre d'échelle = 1 cm.

Type locality. Fonelas P-1, Guadix Basin, Granada, Spain. See [1,26] for details.

Stratigraphic level. Facies association E (*Sondeo B*), Unit VI (*Sistema Axial*) at the Guadix Formation, in accordance with [26].

Geological age. Plio-Pleistocene boundary, c1.7–1.9 Ma, based on comparisons of the faunal association with older faunas from the Upper Pliocene of Saint-Vallier (MNQ-17) or Senèze (MNQ-18), contemporaneous faunas from the Plio-Pleistocene boundary (Olivola-Tasso Italian FUs), and younger faunas from the Lower Pleistocene (MNQ-19) [1,2,7].

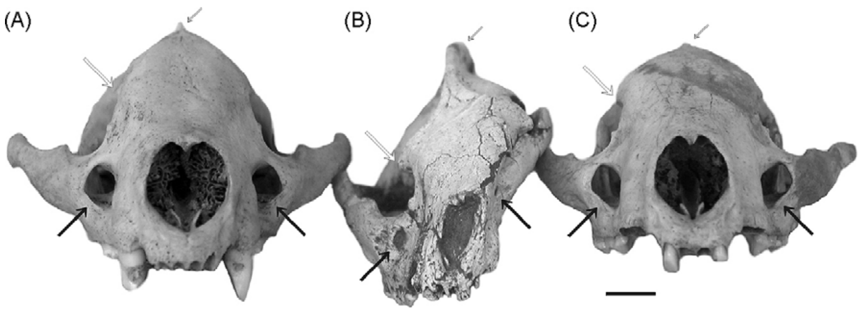

Fig. 2. Comparison (frontal view) of the skull of *Meles iberica* n. sp. (**B**) with one of modern-day *M. meles* (**A**) from Granada (Spain) and one of a fossil *M. meles* (**C**) (Holocene) from the Cueva de Los Torrejones (Guadalajara, Spain). Black arrows indicate the position of the infraorbital foramens (note the large size of these structures in the representatives of *M. meles* and the small dimensions in *Meles iberica* n. sp.). White arrows indicate the position of the zygomatic process of the frontal bone; note the great development and projection of this process in the badger from Fonelas P-1. The small arrow indicates the position of the sagittal crest (note the height reached by this crest and, especially, its great width in *Meles iberica* n. sp.). Specimens **A** and **B** represent senile individuals with a great degree of tooth wear, while specimen **C** represents a senile individual with moderate dental wear. Scale bar = 1 cm.
Fig. 2. Comparaison (vue frontale) du crâne de *Meles iberica* n. sp. (**B**) avec des crânes de *M. meles* actuel (**A**) de Grenade (Espagne) et de *M. meles* fossile (**C**) (Holocène) de la Cueva de los Torrejones (Guadalajara, Espagne). Les flèches noires indiquent la position des foramens infraorbitaux (à noter le grande taille de ces structures chez *M. meles* et leurs faibles dimensions chez *Meles iberica* n. sp.). Les flèches blanches indiquent la position du processus zygomatique de l'os frontal ; à noter le grand développement et la projection de ce processus chez le blaireau de Fonelas P-1 La petite flèche indique la position de la crête sagittale (à noter la hauteur atteinte par cette crête et tout spécialement sa grande largeur chez *Meles iberica* n. sp.). Les spécimens (**A**) et (**B**) représentent des individus séniles avec un grand degré d'usure dentaire, alors que le spécimen (**C**) représente un individu sénile à usure dentaire modérée. Barre d'échelle = 1 cm.

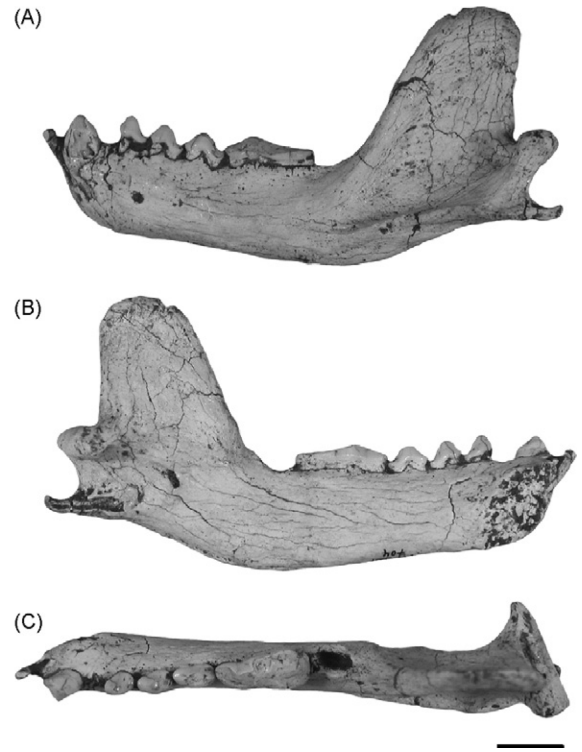

Fig. 4. Hemimandible showing lower left dentition of *Meles iberica* n. sp., paratype FP1-2001-0704. (**A**): Labial view; (**B**): lingual view; (**C**): occlusal view. Scale bar = 1 cm.
Fig. 4. Hémimandibule montrant la dentition inférieure gauche de *Meles iberica* n sp., paratype FP1-2001-0704. (**A**) : Vue labiale ; (**B**) : vue linguale ; (**C**) : vue occlusale. Barre d'échelle = 1 cm.

Diagnosis. A small very robust badger; the skull possesses a broad sagittal crest with a strongly convex curvature; frontonasal profile mildly concave; orbits nearly closed by well-developed zygomatic processes of the frontal bone; infraorbital foramens very small and circular and open above the fourth upper premolar metacone; zygomatic arches with a mild curvature and close to the skull; palatine fissures in a very forward position. Presence of P1/p1. p2 with two roots. Noticeable in the upper dentition are a linguodistally concave P4, a short M1 with a paracone clearly larger than the metacone, a lingual notch between the protocone and hypocone, a labial notch between the metacone and metaconule, and a talon, little developed in its distal region. The jaw of this new species shows a deep, very well developed masseteric fossa, the anterior margin of which reaches the mesial limit of the second lower molar and at its base has a bony crest that forms an extensive horizontal platform. The angular apophysis is very large and narrow. The coronoid process is very graceful with very fine edges. No supernumerary cusps are seen for the first lower molar.

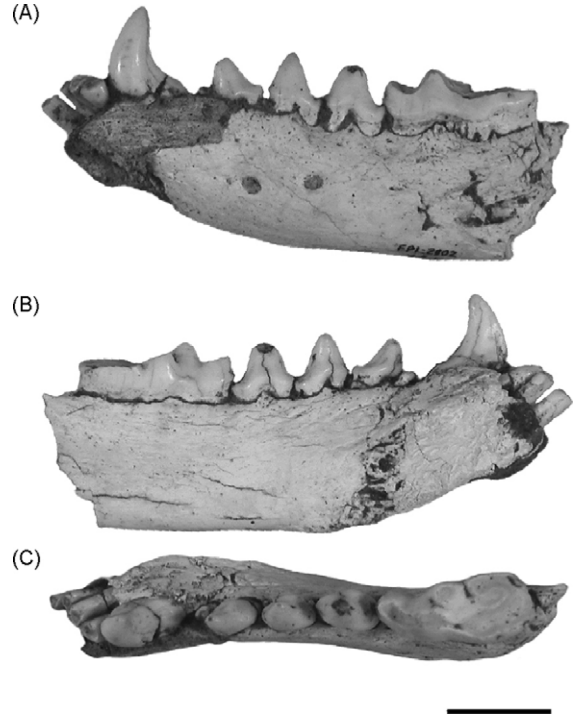

Fig. 5. Fragment of a hemimandible and lower left dentition of *Meles iberica* n. sp., paratype FP1-2002-1446. (**A**): Labial view; (**B**): lingual view; (**C**): occlusal view. Scale bar = 1 cm.
Fig. 5. Fragment d'une hémimandibule et de la dentition de *Meles iberica* n. sp. Paratype FP1-2002-1446. (**A**) : Vue labiale ; (**B**) : vue linguale ; (**C**) : vue occlusale. Barre d'échelle = 1 cm.

3. Description

3.1. Skull (Figs. 1 and 2)

(Measurements: see Table 1). The skull (specimen FP1-2001-0564) is probably that of an old individual; this would seem evident from the extreme development of the sagittal crest and the wear shown by the teeth, which on their occlusal side have lost much of their enamel. This prevented the position of the majority of the cusps and their development from being determined. Although the skull is that of an adult, it is very small (total length = 121.02 mm; condylobasal length = 114.77 mm).

This fossil underwent a great deal of lateral diagenetic compression. This inclined the sagittal axis of the skull towards the left (as seen in caudal view), leaving this side completely deformed. In contrast, the right side conserves its original proportions; the following anatomical notes therefore refer to this side. From a dorsal view, the most obvious anatomical feature is the great height (maximum: 7.7 mm) and thickness (maximum: 4.4 mm) of the sagittal crest, the lateral profile of which is strongly convex. In its anterior region, this crest gives rise to two

Table 1
Comparison of the condylobasal length of the skull of *Meles iberica* nov. sp. with that of modern-day *M. meles* from Europe (in mm)
Tableau 1
Comparaison des mesures de longueur condylobasale du crâne (en mm) chez les espèces *Meles iberica* nov. sp. et *M. meles* actuel d'Europe

	Origin	*n*	Min	Max	$\bar{x}$	S.D.
Meles iberica n. sp.	Fonelas P-1	1			114.77	
Meles thorali	Saint-Vallier[a]	1			120	
Meles dimitrius	Apollonia 1[b]	1			125	
Meles meles	Sierra de Aralar (Spain)[c]	19	120.6	135.7	127.27	4.1
	Doñana (Spain)[d]	63			125.90	
	Ciudad Real (Spain)[d]	28			126.5	
	Lugo–Santander (Spain)[d]	30			125.6	
	Great Britain (♂)[e]	14	121.69	136.74	127.7	4.41
	Great Britain (♀)[e]	9	116.97	133.99	125.73	6.25
	Ireland (♂)[e]	21	122.99	132.92	126.92	2.61
	Ireland (♀)[e]	31	114.63	132.61	125.39	4.18
	Poland[d]	32			130.87	
	Switzerland[d]	54			132.96	
	Italy[d]	11			125.4	

[a] From [24]; d'après [24].
[b] From [11]; d'après [11].
[c] From [30]; d'après [30].
[d] From [25]; d'après [25].
[e] From [6]; d'après [6].

prominent frontal crests. On its back edge, the sagittal crest is continuous, with a well-developed nuchal crest. The profile of the cranial case cannot be traced accurately, since compression caused the collapse of part of this region.

The zygomatic processes of the frontal bone are very developed and project strongly towards the lateral region, leaving at least three quarters of the orbit closed. From a dorsal view, the zygomatic arch has a mildly convex profile and lies relatively close to the skull. Behind this arch lies the opening of the external ear canal. The frontonasal profile forms a subtly concave plane. The infraorbital foramen, which is circular in shape, is very small (transversal width: 2.8 mm; dorsoventral height: 3.3 mm) and opens above the metacone of P4.

The tympanic bullae appear too collapsed to infer any details of their morphology, although the right tympanic bulla is triangular-shaped. The main axis is oblique to the sagittal axis of the skull. The postglenoid (retroarticular or tympano-occipital) foramen opens anterior to the external ear canal. The rest of the ventral foramens cannot be seen due to the great compaction of the skull in this region. The *foramen magnum* appears too deformed for its perimeter to be described.

The palatine bone, which also appears very compressed, shows two fissures close to the sockets of the first incisors.

3.2. Upper dentition (Figs. 3 and 6)

(Measurements: see Table 2). The upper dentition shows a great deal of wear, rendering it impossible to recognise the morphotypes of P4 and M1 established for the genus [3]. However, M1 shows a well-developed labial incision between the metacone and the metaconule (morphotypes B1 or B2 according to [3]). This wear is particularly true of P4 and M1, which have completely lost the enamel of their occlusal surfaces [*L* (length) C-M1: 39.0 mm; *L* P2-M1: 30.6 mm; *L* P2–P4: 18.9 mm]. Neither the canines nor the incisors have been preserved. The first upper premolar is also missing, although a very small socket corresponding to it is visible. The remaining premolars show two roots, except for P4, which has three.

The second upper premolar is narrow, with a pyriform outline, and is mesially thickened. It has a high protocone in its mesial portion. The third upper premolar has an oval outline and a high protocone that is more centred than that of P2, and a well-developed linguodistal cingulum that forms a small platform. The distribution of the cusps in the upper carnassial (which has a triangular outline) cannot be made out, although three smooth notches can be seen at the tooth perimeter that serve to separate them. One of these notches lies in a labial position approximately at the centre of the tooth, separating the paracone and metacone; another lies in a mesial position between the paracone and protocone, and one lies

Table 2
Comparison of dimensions (in mm) of the upper teeth of *Meles*
Tableau 2
Comparaison des mesures dentaires (en mm) chez les espèces de *Meles*

Upper teeth		P2		P3		P4		M1		
		L	*w*	*L*	*w*	*L*	*w*	*L*	L_{ext}	*w*
Meles iberica n. sp.	FP1-2001-0564	4.4	2.9	5.1	3.6	8.9	7.9	12.7	8.7	11.2
Meles thorali[a]	QSV 1	5.3	3.7	5.5	4.5	10.6	8.5	14.5	9.6	12.3
	QSV 2	5.1	3.8	6.1	3.9	9.2	7.9	13.5	9.1	12.9
	QSV 3							13.4	8.2	11.8
	QSV 17	6	3.5	6	4.9	10.5	8.5	15	9.2	12
	QSV 18							14.2	8.9	12
	QSV 1052							13.3	8.8	12
	QSV 1055							15	9	12.3
	QSV 1056							13.1	8.5	12
Meles thorali spelaeus[b]	LV. 92.930	5	3.2	6.2	4.1	10.5	7.5	12.8	9.3	12
Meles dimitrius[c]	GER-159					8	7.8	13.3	8.5	12.1
	GER-160			5.9	3.9	8.2	8.2	13		
	GER-163					7	5			
Meles dimitrius[d]	APL-544			6.2	4.1	8.8	8.1	13.6	8.8	12
	APL-545			5.7	4.2	8.9	7.8	13.5	8.5	12
Meles hollitzeri[e]	IQW 24619	5.1	2.6			8.3	6.8	13.3		9.7
	($n=3$)					8.6	9.3	16.4	10.6	12.7
Meles meles ($\bar{x}$)[f]										
Meles meles ($\bar{x}$) [g]	($n=23$)					8.8	7.5	13.9		11.8

L = total length; *w* = maximum width; L_{ext} = external length.
L = longueur totale ; *w* = largeur totale ; L_{ext} = longueur externe.
[a] Saint-Vallier, France [24].
[b] Lunel Viel, France [4].
[c] Gerakarou, Greece [10] ; Gerakarou, Grèce [10].
[d] Apollonia, Greece [11] ; Apollonia, Grèce [11].
[e] Untermassfeld, Germany [29] ; Untermassfeld, Allemagne [29].
[f] Cueva de Los Torrejones (Holocene), Spain [5] ; Cueva de Los Torrejones (Holocène), Espagne [5].
[g] Current, Sierra de Aralar, Spain [30] ; actuel, Sierra de Aralar, Espagne [30].

in a more linguodistal position between the protocone and metacone. The protocone is very well developed lingually and slightly individualized with respect to the other cusps due to the above-mentioned notches. The profile of its linguodistal edge is concave. A labial cingulum can be seen, which at its mesiolabial edge forms a minuscule cusp continuous with the mesial cingulum.

The first molar has a nearly square outline with a short, distal projection. The distribution of its cusps can be appreciated because of the notches that separate them. That which separates the paracone from the protocone is well marked at the base of the tooth, while that which separates the protocone from hypocone is less pronounced. Although the paracone and metacone are clearly separated, as are the metacone and the metaconule, the responsible notches disappear at the base of the tooth. It is important to note that the paracone is larger than the metacone, appreciably so from a labial view. The only cingulum that can be seen is in a labial position; the rest of the tooth is so worn that, if there ever were any other features, they have disappeared. The distal edge of the tooth is straight.

3.3. Lower jaw (Figs. 4 and 5)

The preserved hemimandibles belong to the left side of two individuals at different stages of development. The teeth of specimen FP1-2001-0704 are much worn (*L* c-m1: 41.3 mm; *L* p2-m1: 31.2 mm; *L* p2–p4: 16.7 mm), as seen in the fossil skull FP1-2001-0564; they are also of matching size and therefore probably belong to the same animal (indeed, both fossils were recovered at the contact between excavation grid squares E2 and E3). Fossil jaw FP1-2002-1446 shows teeth that are not very worn (*L* c-m1: 37.4 mm; *L* p2-m1: 29.0 mm; *L* p2–p4: 15.9 mm). A biostratinomic breakage after m1 prevents observation of the ascending branch's anatomical features. However, hemimandible FP1-2001-0704 is completely preserved. In general, the badgers to which these jaws belonged were of robust composition

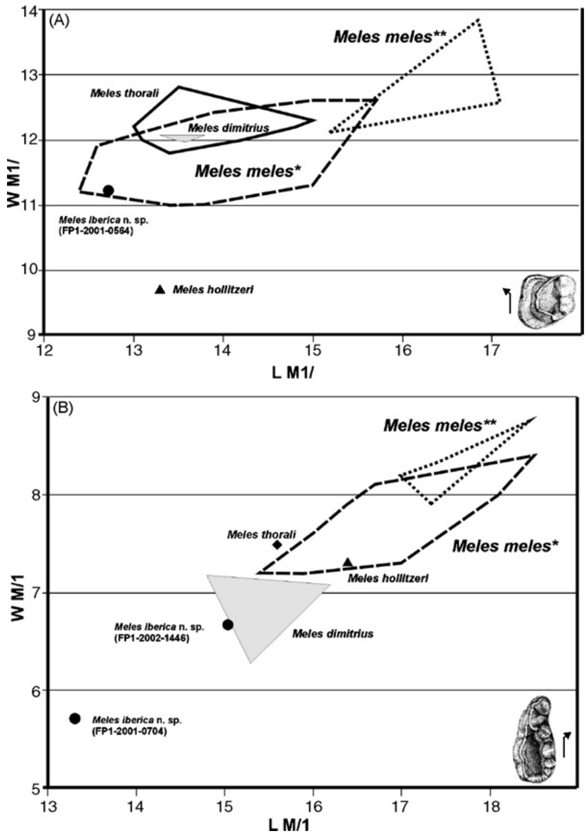

Fig. 6. Graphs comparing the total length (*L*) and maximum width (*w*) of the first upper molar (**A**) and first lower molar (**B**) of the Fonelas P-1 specimens, the fossil species *M. thorali*, *M. dimitrius* and *M. hollitzeri*, and two Iberian specimens of *M. meles* (one modern-day, one fossil). The hemimandible FP1-2001-0704 belongs to the same individual as skull FP1-2001-0564. The representation of *M. thorali* is based on data from Saint-Vallier [24] and Vatera [27], *M. dimitrius* on data from Gerakarou [10] and Apollonia [11], and *M. hollitzeri* on data from Untermassfeld [29]. The data for *M. meles** come from modern-day populations in the Sierra de Aralar [30], and those for *M. meles*** from Holocene fossils found in the Cueva de Los Torrejones [5].

Fig. 6. Graphiques comparant la longueur totale (*L*) et la largeur maximum (*w*) de la première molaire supérieure (**A**) et de la première molaire inférieure (**B**) des spécimens de Fonelas P-1, des espèces fossiles *M. thorali*, *M. dimitrius* et *M. hollitzeri*, et de deux spécimens espagnols de *M. meles* (un actuel et un fossile). L'hémi-mandibule FP1-2001-0704 appartient au même individu que le crâne FP1-2001-0564. La représentation de *M. thorali* est basée sur les données de Saint-Vallier [24] et de Vatera [27], celle de *M. dimitrius* sur les données de Gerakarou [10] et d'Apollonia [11], et celle de *M. hollitzeri* sur les données d'Untermassfeld [29]. Les données relatives à *M. meles** proviennent de populations actuelles de la Sierra de Aralar [30], et celles relatives à *M. meles*** de fossiles holocènes trouvés dans la Cueva de Los Torrejones [5].

and were quite small [mandible height between p4-m1: 12.5 mm (FP1-2001-0704); 12.3 mm (FP1-2001-0564)].

Along the ventral edge of the jaw, and in the area where the ascending branch begins, the horizontal branch shows a curvature with an inflexion point at the distal limit of m2. The lingual face of the horizontal branch shows strong longitudinal thickenings for the insertion of the mylohyoid and digastric muscles, which are separated by a smooth furrow. Behind the socket of m2, there is a vertical lingual crest forming a small platform that increases the basal surface of the ascending branch (i.e., it forms a developed retromolar platform). The mandibular foramen lies at the central point of the main axis of the ascending branch. Labially, the horizontal branch shows a small mental foramen at the distal boundary of the second lower premolar. Specimen FP1-2002-1446 also shows a second mental foramen beneath the contact between the third and fourth lower premolars. The masseteric fossa is deep and its mesial margin lies below the mesial limit of the second lower molar. This fossa is limited in its upper region by a curved crest that follows the line of the coronoid apophysis. At its lower edge, the masseteric fossa appears to be bounded by a crest, very developed laterally, which forms a wide basal platform (deep: 5.4 mm). In its posterior region, this platform has an extensive concavity below the mandibular condyle where the pterygoid muscle was inserted. The latter must have been very developed, since the angular apophysis is very long (5.4 mm) and narrow (2.9 mm), and curves slightly upwards. The coronoid apophysis is very narrow and graceful, with very fine edges.

3.4. Lower dentition (Figs. 4–6)

(Measurements: see Table 3). The main observations on the lower dentition were made using the fossil whose cusps were least worn (FP1-2002-1446). The canine is robust, but its crown is very low (height: 8.5 mm). It is strongly curved and has a sharp vertical, linguodistal crest, and a less sharp mesiolingual crest. The base of this tooth is notably thickened mesiodistally. The first lower premolar is present in specimen FP1-2002-1446, in which it appears as a small, simple, vestigial tooth slightly displaced towards the lingual face of the jaw. Specimen FP1-2001-0704 shows an alveolus for p1. The second lower premolars show two roots. The second, third and fourth lower premolars each have a very high, acute protocone and a distal cingulum that forms a small platform. The third lower premolar has a medium-sized mesial cingulum; this is more developed in p4, but absent in p2. The second and third lower premolars are therefore very asymmetric teeth with mesial margins that fall more abruptly than that of p4, in which the mesial edge is softened by the presence of the cingulum. While p3 and p4 are implanted parallel to the

Table 3
Comparison of dimensions (in mm) of lower teeth of *Meles*
Tableau 3
Comparaison de mesures dentaires inférieures (en mm) chez les espèces de *Meles*

Lower teeth		p2		p3		p4		m1			
		L	*w*	*L*	*w*	*L*	*w*	*L*	L_{trig}	L_{tal}	*w*
Meles iberica n. sp.	FP1-2001-0704	4.7	3.5	5.6	3.6	6.1	3.8	15.0	8.8	6.2	6.7
	FP1-2002-1446	4.2	3.1	5.2	3.2	6.2	3.4	13.3	7.9	5.6	5.7
Meles thorali[a]	QSV 8	4.8	4.1	6.3	3.5	6.5	3.5	15.6			7.5
	QSV 13							16.4	9.4	7.2	
	QSV 16							16.2	9.5	7.1	
	QSV 19							16.6	9.5	7.7	
	QSV 1051							17	10	7.8	
Meles thorali[b]	PO 630 F							17.3	9.4	7	
Meles dimitrius[c]	GER-161	4.7	3.1			6.8	3.8	15.1	8.5		7.1
	GER-162							14.8	8.3		7.2
Meles dimitrius[d]	APL-15	4		5.5	3.3	6.3	3.4	15.3	8.5		6.3
	APL-546	5.4	3.2	5.8	3.5	7	3.9	16.2	8.8		7.1
Meles hollitzeri[e]	IQW 17971							16.4	9.6	7.4	7.3
	($n=4$)	4.6	4.0	5.5	3.6	6.5	4.1	17.5	9.3	8.5	8.3
Meles meles ($\bar{x}$) [f]											
Meles meles ($\bar{x}$) [g]	($n=26$)							16.7			7.7

L = total length; w = maximum width; L_{trig} = length of the trigonid; L_{tal} = length of the talonid.
L = longueur totale ; w = largeur totale ; L_{trig} = longueur du trigonide ; L_{tal} = longueur du talonide.
[a] Saint-Vallier, France [24].
[b] Vatera, Greece [27]; Vatera, Grèce [27].
[c] Gerakarou, Greece [10] ; Gerakarou, Grèce [10].
[d] Apollonia, Greece [11] ; Apollonia, Grèce [11].
[e] Untermassfeld, Germany [29] ; Untermassfeld, Allemagne [29].
[f] Cueva de Los Torrejones (Holocene), Spain [5] ; Cueva de Los Torrejones (Holocène), Espagne [5].
[g] Current, Sierra de Aralar, Spain [30] ; actuel, Sierra de Aralar, Espagne [30].

longitudinal axis of the jaw, p2 is slightly oblique to this, with its distal region displaced towards the lingual face.

The first lower molar is long and has an amoeboid outline; it is narrower in its mesial section. It has a trigonid with a labial protoconid that forms the highest cusp of the tooth, a mesial paraconid, and a well-developed lingual metaconid. No cusp is seen between the protoconid and the hypoconid. Between the paraconid and the metaconid, there is a wide space. The talonid of both specimens is worn, although a small, labial notch can be seen to separate the hypoconid and the hypoconulid. Lingually, the entoconid appears worn, as does the entoconulid and the characteristic small linguodistal cusps. Surrounded by the hypoconid, hypoconulid, entoconid, entoconulid, and the set of linguodistal cusps, there is an almost inappreciable depression due to the advanced wear suffered by the tooth. The second lower molar has not been preserved in either specimen, although in FP1-2001-0704 there is a long, mesiodistal socket that can hold a fused double root; the root in the mesial position is larger than that in the distal position (m2 alveolus L: 5.0 mm; w : 2.5 mm).

4. Comparisons and discussion

The badger fossils from the Fonelas P-1 site were compared with fossil and contemporary specimens of *Meles meles* Linnaeus, 1758 (which appears not to show sexual dimorphism in its jugal dentition [3]), and with fossils of *M. thorali* [23,24], *M. dimitrius* [10,11], *Meles hollitzeri* Rabeder, 1976 [19,29], *Meles thorali spelaeus* [4], and *Meles atavus* Kormos, 1914 [9,28].

The cranial profile of the studied skull, with its prominent frontal crests that join and continue as a powerful sagittal crest, its large and elongated cranial case, small orbits, subtriangular tympanic bullae, and a dentition clearly adapted to an omnivorous diet (dental formula 3-1-4-1/3-1-4-2) show its owner to have been a badger. In addition, the dentition has carnassial teeth that have lost their cutting function, the premolars are very small, the second and third lower and upper premolars have a mesial protocone/protoconid, P4 is triangular in section, and M1 rhomboid. The latter is larger than P4 and its labial face is shorter than its lingual face. The first lower molar is long and has a large talonid. These data further confirm the animal to belong to the genus *Meles*.

However, this animal shows certain peculiarities. The skull (FP1-2001-0564) has a substantially higher and thicker sagittal crest (Figs. 1B, 1D and 2B), which is more markedly convex than that seen in modern or fossil senile specimens of *M. meles* (sagittal crest, maximum height: 4.4, 7.3, 8.1 mm; maximum thickness: 2.2, 2.4, 2.7 mm; $n = 3$), or than that seen in fossil specimens of *M. thorali* [23] or *M. dimitrius* [11]. In addition, the great development shown by the zygomatic process of the frontal bone was not seen in any of the other current or fossil taxa analysed; certainly, *M. meles*, *M. thorali* and *M. dimitrius* have a more open orbit. Neither is the flattened, subtly concave frontonasal profile seen in any known fossil badgers, in which this region is slightly convex, as it is in the modern badger *M. meles*. In addition, the infraorbital foramens of the studied fossil are much smaller than those seen in senile *M. meles* (transversal width: 8.5, 7.3, 8.8 mm, $n = 3$; dorsoventral height: 9.2, 7.1, 8.9 mm, $n = 3$) or *M. thorali* [23], and the palatine fissures of FP1-2001-0564 are closer to the first incisors than in *M. meles* or *M. thorali* [23]. In *M. dimitrius*, this region could not be identified.

The studied skull also shows zygomatic arches with a smaller lateral projection than those seen in *M. meles* or *M. dimitrius* [11], although they resemble those of *M. thorali* [23,24]. A further similarity with the latter species is the double rooted P2; this is also seen in *M. hollitzeri* [29]. In the modern badger, and in *M. thorali spelaeus* [4], these roots are fused.

Given the deformation of the skull of *M. dimitrius* [11], the relative dimensions of the infraorbital foramens could not be determined, nor the position of the palatine fissures, nor the number of roots on P2.

It is difficult to determine the distribution of the cusps of the upper dentition due to their degree of wear. However, some differences can be seen between this ancient badger's dentition and that of other fossil badgers and of the modern Eurasian species. In the studied fossil, the linguodistal face of P4 is clearly concave, while those of *M. meles* and *M. thorali* are convex. In *M. dimitrius*, it is intermediate between the latter forms [11]; its profile is more or less straight, similar to that seen in *M. hollitzeri* [29]. In addition, the M1/P4 ratio is small in the Fonelas P-1 (*Meles iberica* n. sp.) compared to those seen in the other badger species analysed (Table 2).

The anatomical details of M1 are difficult to see; only the general shape can be appreciated due to the wear it suffered during the animal's lifetime. This prevents a proper appreciation of its cusp distribution. The main difference between this tooth in the studied fossil and that of *M. thorali* is the shape of the occlusal face. In the latter species, the talon is very well developed and projects distally, while in FP1-2001-0564 it is much shorter and more like that of *M. dimitrius* (Fig. 7). In general terms, the labial contact between the trigon and the talon is more similar to that seen in *M. thorali* (which has a well-defined notch) or *M. dimitrius* than to that seen in *M. meles* or *M. hollitzeri* (in which the contact is smoother and there is no notch) [19]. The studied M1 also shows a lingual notch between the protocone and hypocone that is hardly visible in *M. thorali*, yet quite visible in *M. dimitrius*. Another outstanding feature of this tooth in the studied fossil is that the paracone is much larger than the metacone, as seen in *M. hollitzeri* and in the modern *M. meles*. In contrast, in *M. thorali* and *M. dimitrius*, both cusps are about the same size (Fig. 7).

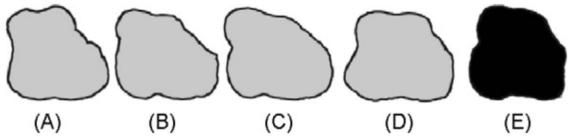

Fig. 7. Outlines of the occlusal faces of the first upper molars belonging to different members of the genus *Meles* and the new species from Fonelas P-1. (**A**): *M. thorali*; (**B**): *M. hollitzeri*; (**C**): *M. meles*; (**D**): *M. dimitrius*; (**E**): *Meles iberica* n. sp. Not to scale.

Fig. 7. Aspect des faces occlusales des premières molaires supérieures appartenant à différents membres du genre *Meles* et à l'espèce nouvelle de Fonelas P-1. (**A**) : *M. thorali* ; (**B**) : *M. hollitzeri* ; (**C**) : *M. meles* ; (**D**) : *M. dimitrius* ; (**E**) : *Meles iberica* n. sp. Pas à l'échelle.

The jaw of the proposed new species differs from those of other badgers in terms of the depth and degree of the mesial projection of the masseteric fossa. In the studied animal, this projection reaches the mesial limit of m2, while in *M. thorali*, *M. dimitrius* and *M. meles*, the fossa closes just after the distal boundary of m2 [11,23]. In *M. hollitzeri*, it ends under the mid point of m2 [29]. The extensive basal platform of this fossa is more developed in specimen FP1-2001-0704 than in *M. thorali* or *M. dimitrius*, and very much more developed than in fossil or current *M. meles* specimens. In addition, the mandibular foramen in the Fonelas P-1 fossil lies further forward than in *M. thorali* or *M. dimitrius* [11,23]. The labial face shows one or two mental foramens. *M. thorali* and *M. dimitrius* both show two aligned foramens, while in *M. meles* between 2 and 4 can be seen. The angular apophysis in the studied jaw fossils is very long and narrow, unlike in *M. thorali*, *M. dimitrius* or *M. meles* (fossil or present-day senile specimens: angular apophysis length: 2.2, 4.5, 2.8 mm; width: 4.5, 4.7, 5.1 mm; $n = 3$), in which it is short and wide.

The lower dentition of the studied animal bears no great morphological differences to that of the other badger species analysed; other authors also indicate m1 and m2 to be of little help in making diagnoses [3].

The *M. thorali* fossil from Saint-Vallier shows diastemas between p2 and p3, and between p3 and p4, which are not seen in the Fonelas P-1 animal, nor in *M. dimitrius* [11], nor in *M. meles* (either fossil or current). The presence of p1, and that of two roots for p2, are primitive characteristics shared with *M. thorali, M. hollitzeri*, and *M. meles* [3]. The accessory cusp between the protoconid and hypoconid of m1 in *M. atavus* [9,28] is not visible in the proposed new species. However, variability has been recorded in the absence/presence of this supernumerary cusp in specimens of *Meles* from Gombaszög [12]. Given that this is part of the normal variation seen in *M. meles*, it has been proposed that *M. atavus* be recognised as *M. meles atavus*, a subspecies of the nominal taxon. The socket of m2 in the studied animal is long; its mesiodistal diameter is greater than its buccolingual diameter, as seen in *M. thorali* [23]. In *M. thorali spelaeus* and *M. meles*, however, the reverse is true, and this tooth is much wider than it is long [4]. The same is seen in *M. hollitzeri* [29]. The presence of two fused roots, of which the more mesial is the larger, is very different to that seen in *M. meles*, which has three or more roots. In this respect, the studied animal is more like *M. thorali*.

In summary, the studied badger shows a number of cranial, mandibular, and dental features that allow it to be differentiated from other fossil or the modern Eurasian species *M. meles*, although it shows more anatomical resemblance to *M. thorali*. The new animal is the smallest fossil badger known to date (Tables 1–3, Fig. 6), even though its fossils are those of robust adults. This size difference is evident in terms of both the length of the skull (Table 1) and the dimensions of the upper and lower dentitions (Fig. 6). This contrasts with the similarity in size between the fossil species *M. dimitrius* and *M. thorali* (the latter is proposed as the ancestor of the nominal Euroasiatic species [3]) and the fossil and modern representatives of *M. meles*. The similarity in size between *M. thorali* (from the French Upper Pliocene) and *M. meles* was first mentioned in the former's original diagnosis [23].

5. Conclusions

This paper reports a new, ancient species of Eurasian badger classified as *Meles iberica*. This animal was particularly robust and small, much more so than any other European badgers from the Late Pliocene, from the Plio-Pleistocene boundary, or indeed than the modern Eurasian species *M. meles*. This new species shows primitive characteristics in common with *M. thorali*, from which it is descended (some of these characteristics are also shared with *M. meles*), along with a mosaic of specific characteristics very probably related to life in a warm environment and on soft ground. It has been known since the first half of the 20th century that, within the modern species *M. meles*, the Iberian representatives [which belong to the variety *M. meles marianensis* (Graells, 1897)] are smaller and more robust than their European counterparts, although they do not differ in terms of their cranial, mandibular or dental anatomy.

The fossil badger unearthed at Fonelas P-1 represents a new species, *Meles iberica*, the most ancient member of the genus known in the Iberian Peninsula. Until now, the oldest fossils of Eurasian badgers found in the Peninsula were of *M. meles* from karstic Mid-Pleistocene sites, 1.4 million years younger than the Fonelas P-1 population. The fossil record for this genus in the Iberian Peninsula (extension 582,925 km^2) suggests that the members of this species were genetically isolated from other European populations; *Meles iberica* n. sp. is therefore an endemic species of this Peninsula.

For the time being, the distribution of this new species is restricted to the Iberian Peninsula, its fossil remains forming part of the E facies fossil association (*Sondeo B*) of the Plio-Pleistocene boundary at the Fonelas P-1 site (Guadix Basin, Spain).

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