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The earliest European badger (*Meles meles*), from the Late Villafranchian site of Fuente Nueva 3 (Orce, Granada, SE Iberian Peninsula)

Le blaireau européen le plus précoce (Meles meles) provenant du site Villafranchien supérieur de Fuente Nueva 3 (Orce, Grenade, Sud-Est de la Péninsule ibérique)

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ABSTRACT

Paleontological and molecular data suggest that the divergence of the European and Asian badgers (*Meles meles* and *Meles leucurus*, respectively) from their ancestor *Meles thorali* might have taken place in the Middle to Late Villafranchian boundary (ca. 1.8 Ma). However, the available record of Late Villafranchian European badgers is scanty and poorly known, and this hypothesis needs more paleontological data in order to be tested. The badger hemimandible from the Iberian locality of Fuente Nueva 3, a locality placed in the beginning of the Late Villafranchian, supports the idea of an early divergence between European and Asian badgers.

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R É S U M É

Les données paléontologiques et moléculaires suggèrent que la divergence des blaireaux européens et asiatiques (respectivement *Meles meles* et *Meles leucurus*) de leur ancêtre (ca. 1,8 Ma) *Meles thorali* aurait pu avoir lieu à la limite entre le Villafranchien moyen et supérieur. Toutefois, le registre disponible des blaireaux du Villafranchien supérieur européen est rare et mal connu, et cette hypothèse nécessite plus de données paléontologiques afin d'être testée. L'hémi-mandibule de blaireau de la localité ibérique de Fuente Nueva 3, une localité située au début du Villafranchien supérieur, soutient l'idée d'une divergence précoce entre les blaireaux européens et asiatiques.

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1. Introduction

The living Eurasian badgers (*Meles* sp.) have a Palearctic distribution, ranging from the Iberian Peninsula in the west, to the Japanese Islands in the east, including the British Islands, Scandinavia, Palestine, Iran and southern China. Throughout this wide distribution area, there is a remarkable geographic variation in both the osteological characters and the external appearance of these carnivores (Abramov and Medvedev, 2003; Abramov et al., 2009; Baryshnikov et al., 2002). Recently, several researchers have suggested that European, Asian and Japanese badgers may represent two or even three separate species. For example, Baryshnikov et al. (2002) recognized two distinct species on the basis of dental morphology: *Meles meles* Linnaeus, 1758 (Europe, south-western and central Asia) and *Meles anakuma* Temminck, 1844 (rest of Asia). Nevertheless, cranial morphology, coloration patterns of face marks and baculum structure support at least three distinct species (Abramov, 2001, 2002, 2003; Abramov and Medvedev, 2003): *M. meles* (in Europe and south-western and central Asia), *M. anakuma* (in Japan) and *M. leucurus* Hodgson, 1847 (in the rest of continental Asia).

On the basis of paleontological data, it has been suggested that the *Meles* lineage appeared in Asia, during the Early Pliocene, from a species of the genus *Melodon* Zdansky, 1924 (Neal and Cheeseman, 1996; Petter, 1971). In addition, paleontological evidence has confirmed that *Meles* reached the Iberian Peninsula before the beginning of the glacial-interglacial cycles in the northern hemisphere (ca. 2.6 Ma) (Madurell-Malapeira et al., 2009), thus indicating that this genus was widely distributed during the Early Villafranchian, soon after its first appearance in eastern Asia.

Even though the Plio-Pleistocene fossil record of European badgers is scanty and poorly known, six *Meles* species are historically recognized in this continent from the Late Pliocene to the Middle Pleistocene (Madurell-Malapeira et al., 2009, 2011). Nevertheless, in a recent review of the genus *Meles* based on the extensive fossil record from the Epivillafranchian localities of the Vallparadís section (Terrassa, Catalonia, Iberian Peninsula) (Madurell-Malapeira, 2010; Madurell-Malapeira et al., 2011), we suggested that the Early to Middle Villafranchian European badger remains might correspond to a single species, *M. thoralis*, and the Late Villafranchian remains must be assigned to the extant species, *M. meles*. Following this hypothesis, *M. thoralis* might have been the ancestor from which extant Asian and European badger species originated through vicariance during the Middle to Late Villafranchian boundary (ca. 1.8 Ma). This inference is supported by mtDNA and nuclear DNA data, which indicate that the divergence between both lineages might have occurred in the top of the Olduvai subchron (ca. 1.8 Ma) or before (Marmi et al., 2006; Sato et al., 2003).

According to Madurell-Malapeira (2010), the oldest European remains of *M. meles* might correspond to the localities of Pirro Nord (Italy) and Apollonia-1 (Greece). Unfortunately, the last two Late Villafranchian sites do not provide long stratigraphical sequences calibrated on the basis of magnetostratigraphical and biostratigraphi-

cal data, and the estimated age for the badger remains covers a wide chronological range (1.3–1.7 Ma) (Arzarello et al., 2007; Koufos, 1992). In this paper, we describe a badger remain from the Late Villafranchian Iberian locality of Fuente Nueva 3. This remain has a clear geological, magnetostratigraphical and biostratigraphical context, and additionally an absolute age was determined by the ESR method (Duval, 2008; Oms et al., 2010). The combinations of the former methods results in an estimated age of 1.3–1.4 Ma for the described badger remain. These data confirms that the extant European badgers were distributed throughout Europe by the Late Villafranchian, slightly later of their divergence from their ancestor *M. thoralis* in the Middle-Late Villafranchian boundary (ca. 1.8 Ma).

Abbreviations: L: mesiodistal length; Lext: mesiodistal length of m1 on the buccal side; Ltal: mesiodistal length of m1 talonid; Ltrig: mesiodistal length of m1 trigonid; W: buccolingual width of m1.

2. Systematic palaeontology

Carnivora Bowdich, 1821
 Mustelidae Fisher, 1817
 Melinae Bonaparte, 1838
Meles Brisson, 1762
Meles meles Linnaeus 1758
 (Table 1; Fig. 2)

Synonymy

Meles atavus Kormos, 1914: original description of the species.

Meles meles atavus Kormos, 1914: in Kretzoi (1938).

Meles hollitzeri Raebeder, 1976: original description of the species.

Meles n. sp.: in Mais and Raebeder (1984).

Meles dimitrius Koufos, 1992 (partim): original description of the species.

Meles meles sp. indet.: in Moullé (1992).

Meles atavus Kormos, 1914: in Wolsan (1993).

Meles hollitzeri Raebeder, 1976: in Baryshnikov (1993).

Meles hollitzeri Raebeder, 1976: in Wolsan (2001).

Meles meles Linnaeus, 1758: in Moullé et al. (2006).

Meles meles Linnaeus, 1758: in Petrucci (2008).

Meles Meles Linnaeus, 1758: in Madurell-Malapeira (2010).

Referred specimen: FN3 2005 V92 no. 142, partial right hemimandibular corpus with c1-m2, housed at the Museo de Prehistoria y Paleontología of Orce (Granada, Spain).

Stratigraphy, age and associated fauna: The Fuente Nueva 3 locality is placed in the village of Fuente Nueva, nearby to the town of Orce (Granada, SE Iberian Peninsula) (Fig. 1). The sediments in the locality consist in a 20 m-thick section mainly composed of three lacustrine carbonate layers interspersed by silty-calcareous beds. These Early Pleistocene deposits are arranged in an upward-shallowing sequence that represents a depositional unit with distinctive features in the tectosedimentary history of the Baza intramontane basin (García-Aguilar and Palmqvist, 2011). The combination of biochronological,

Table 1Dental measurements of *Meles meles* from the Late Villafrachian of Fuente Nueva 3.**Tableau 1**Mesures dentaires de *Meles meles* provenant du Villafranchien supérieur de Fuente Nueva 3.

Record No.	c/1		p/2		p/3		p/4		m/1		m/2		L	Ltrig	Ltal	W	L	W	
	L	W	L	W	L	W	L	W	L	W									
FN3 2005 V92 142	7.9	5.9	4.7	3.3	6.4	3.3	6.4	4.2	17.6	9.9	7.8	7.5	5.6	5.8					

magnetostrigraphic data and ESR results allows estimating an age range of 1.3–1.4 for these sediments (Duval, 2008; Martínez-Navarro et al., 1997; Oms et al., 2000, 2010). The mammalian assemblage of Fuente Nueva 3 includes the following species: *Homo* sp. (only lithic artefacts), *Ursus* sp., *Canis mosbachensis*, *Lycaon* cf. *lycaonoides*, *Vulpes* cf. *praeglacialis*, *Meles* sp., *Pannonictis* cf. *nestii*, Mustelidae indet. (small size), *Pachycrocuta brevirostris*, *Lynx* sp., Felidae indet., *Mammuthus meridionalis*, *Stephanorhinus* cf. *hundsheimensis*, *Equus altidens*, *Equus sussenbornensis*, *Hippopotamus antiquus*, *Bison* sp., *Ammotragus europaeus*, *Hemitragus* cf. *albus*, *Praemegaceros* cf. *verticornis*, *Metacervoceros rhenanus*, Erinaceneae indet., *Crociodura* sp., *Sorex minutus*, *Sorex* sp., *Allophaiomys* cf. *lavocati*, *Allophaiomys*

sp., *Mimomys savini*, *Castillomys crusafonti*, *Apodemus* aff. *mystacinus* and *Hystrix* sp. (Abbazzi, 2010; Alberdi, 2010; Agustí and Madurell, 2003; Furió-Bruno, 2003; Locombat, 2010; Martínez-Navarro et al., 1997, 2003, 2004, 2010; Moullé et al., 2004; Oms et al., 2010).

Description: See Table 1 and Fig. 2 for measurements.

The specimen displays three mental foramina: one below the mesial margin of the p2, another below the p3 and the third one below the distal margin of the p4. The corpus shows a slightly convex profile in lateral view. The masseteric fossa reaches only the distal margin of the m2, showing a marked crest in the ventral margin. The specimen preserves the alveolus of p1. The p2 bears two unfused roots. The p3 and p4 have two roots and display

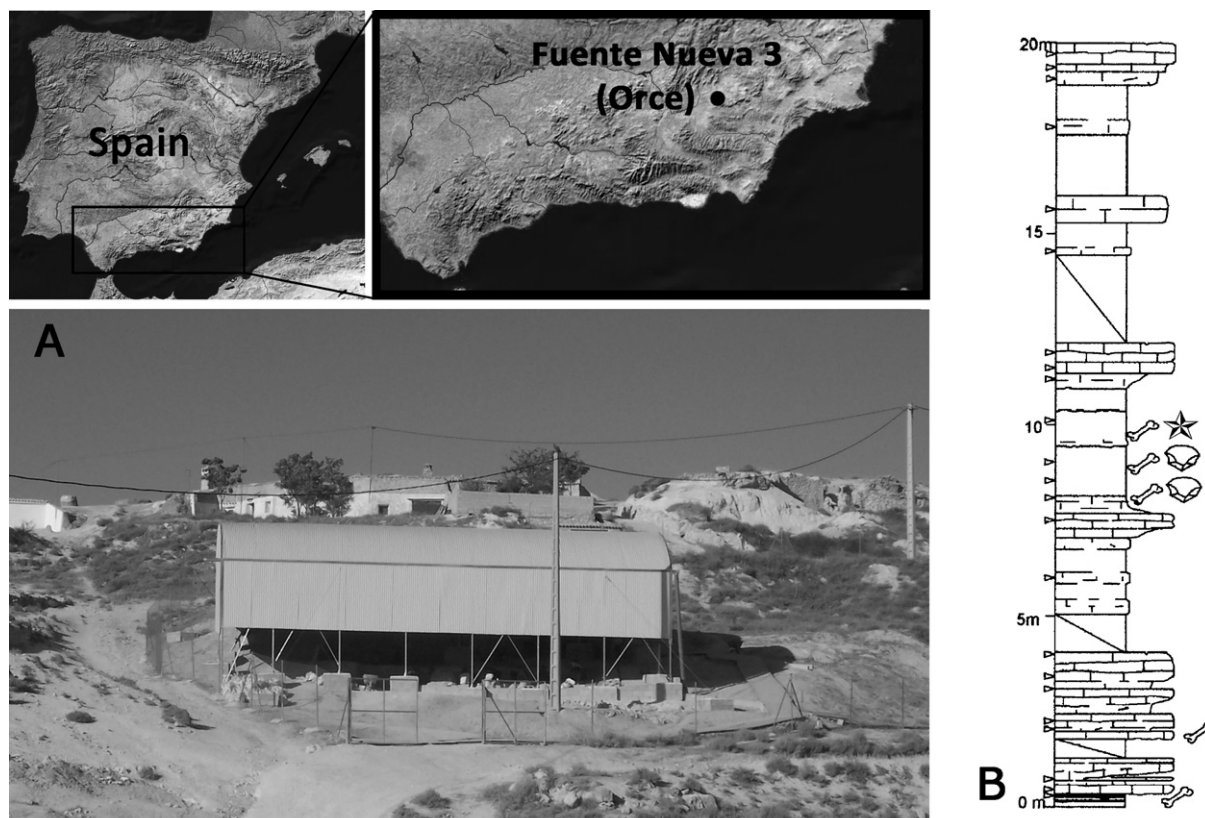


Fig. 1. A. Geographic location and external view of the Fuente Nueva 3 locality (Orce, Granada, SE Iberian Peninsula). B. Stratigraphic section of the Fuente Nueva 3 locality, modified from Oms et al. (2010). Note: the whole stratigraphic section has negative magnetic polarity and the star marks the layer on which the *Meles meles* specimen was recovered.

Fig. 1. A. Localisation géographique et une vue extérieure de la localité de Fuente Nueva. 3 (Orce, Grenade, Sud-Est de la Péninsule ibérique). B. Coupe stratigraphique de la localité de Fuente Nueva 3, modifiée d'après Oms et al. (2010). À noter que l'ensemble de la section stratigraphique a une polarité magnétique négative et l'étoile marque la couche dans laquelle le spécimen de *Meles meles* a été prélevé.

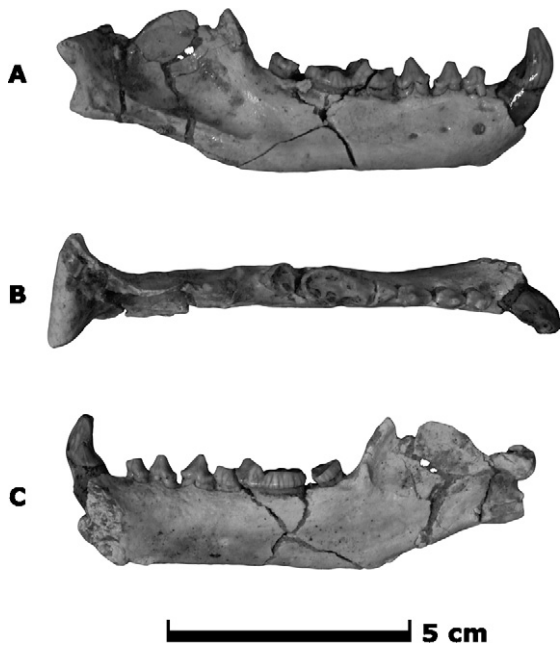


Fig. 2. Right hemimandible of *Meles meles* from Fuente Nueva 3 (FN3 2005 V92 142). A. Buccal view. B. Occlusal view. C. Lingual view.

Fig. 2. Héli-mandibule droite de *Meles meles* provenant de Fuente Nueva 3 (V92 142). A. Vue buccale. B. Vue occlusale. C. Vue linguale.

a clearly asymmetric protoconid in lateral view. The m1 shows a talonid relatively longer than the trigonid, a feature characteristic of *M. meles*. No supernumerary cusplids are present between the m1 protoconid and hypoconid. The m2 has an advanced wear stage with a clear rounded occlusal outline

3. Discussion

3.1. Attribution of the Fuente Nueva 3 specimen

On the one hand, the hemimandible described in this paper shares many morphological traits with extant *M. meles*, features that are also displayed by the Late Villafranchian specimens of *M. meles* from the Vallparadís section, Pirro Nord, Apollonia 1, Vallonnet and Untermassfeld (Koufos, 1992; Madurell-Malapeira, 2010; Madurell-Malapeira et al., 2011; Moullé, 1992; Petrucci, 2008; Wolsan, 2001). These traits include the unfused roots of the p2 (which are usually fused in a single root in the living Asian badgers [Baryshnikov et al., 2002]), and the m1 talonid relatively longer than the trigonid (*M. thoralis* has a m1 trigonid more developed than the talonid [Madurell-Malapeira, 2010; Madurell-Malapeira et al., 2011]). On the other hand, the position of the mesial end of the masseteric fossa is variable in the genus *Meles* and has no taxonomical significance, reaching the mesial margin of the m2 in some cases, but in others situating at the distal margin of this tooth, as happens with several specimens of the species *M. thoralis* and of Pleistocene *M. meles* (Madurell-Malapeira, 2010).

In which concerns the morphometric comparisons, a scatter diagram for the mesiodistal length and the buccolingual width of the first lower molar (Fig. 3), which includes data from all Villafranchian *Meles* remains (Arribas and Garrido, 2007; Bonifay, 1971; Kormos, 1914; Koufos, 1992; Moullé, 1992; Petrucci, 2008; Rabeder, 1976; Viret, 1951; Wolsan, 2001) and measurements from one hundred extant European badgers from the Iberian Peninsula (Madurell-Malapeira, 2010), shows that nearly all Villafranchian badgers are included in the interspecific variability of the living badgers. It is worth noting, however, that the Late Villafranchian specimens show higher values on average for the m1 mesiodistal length than the living badgers. Finally, the remains of *M. thoralis* from Saint-Vallier and Fonelas P-1 have lower values of mesiodistal and buccolingual length.

Fig. 4 shows the results obtained in a principal components analysis of cheek teeth measurements (i.e., mesiodistal length and buccolingual width of p2, p3, p4 and m1) in extant and extinct *Meles*. These measurements were selected as they allow including most fossil specimens in the statistical comparisons. Unfortunately, this is not the case for other teeth (e.g., the lower canine) or measurements (e.g., trigonid and talonid length for the lower carnassial) that could have also provided relevant information. This figure shows the distribution of the specimens on the first three components, which jointly account for more than 65% of the original variance of the eight metric variables. According to the factor loadings of the variables, which were logarithmically transformed prior to the analysis, the first component may be interpreted in an *ad hoc* manner as a size vector, because all variables show positive loadings. In contrast, the variables take both positive and negative loadings on the second and third components, which indicates that these are shape vectors. Specifically, the second component distributes the specimens according to the development of p2 and p3 (positive loadings) relative to the dimensions of m1 (negative ones). Concerning the third component, this vector arranges the specimens according to the width of p3 and p4, which score negatively on this axis.

The scatter of the measured specimens on the plot for the first three components (Fig. 4) shows that the mandibles of *M. meles* have a relatively homogeneous distribution, in which no differences between both sexes were detected, and that the five fossil specimens of Late Villafranchian age (i.e., FN3 2005 V92 142 from Fuente Nueva; 118 and 14/117 from Deutsch-Altenburg-2; AP-15 and AP-546 from Apollonia) are enclosed in the cloud of extant *M. meles*. In contrast, the Early to Middle Villafranchian specimens (i.e., SV-555 and SV-574 from Saint-Vallier; FP1-2001-074 and FP1-2002-1446 from Fonelas) scatter on a different region of this morphospace, especially as a result of their more positive scores on the second component, which confirms that they belong to a different badger species, *M. thoralis*.

On the basis of these shared morphological characters, as well as taking into consideration the root morphology of p2 and the relatively proportions of the m1 trigonid and talonid, we attribute the Fuente Nueva 3 hemimandible to *M. meles*.

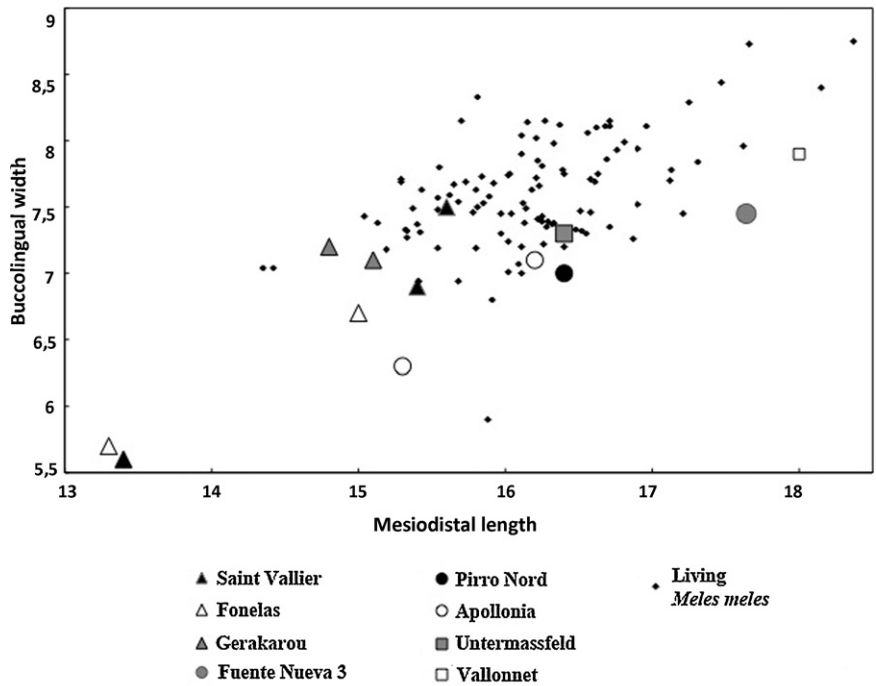


Fig. 3. Dental proportions of the first lower molar of *Meles meles* from Fuente Nueva 3, compared with other specimens from Villafranchian European localities and with a sample of extant European badgers.
Fig. 3. Proportions dentaires de la première molaire inférieure de *Meles meles* de Fuente Nueva 3, comparées à celles de spécimens provenant d'autres localités villafranchiennes européennes et d'un blaireau européen actuel.

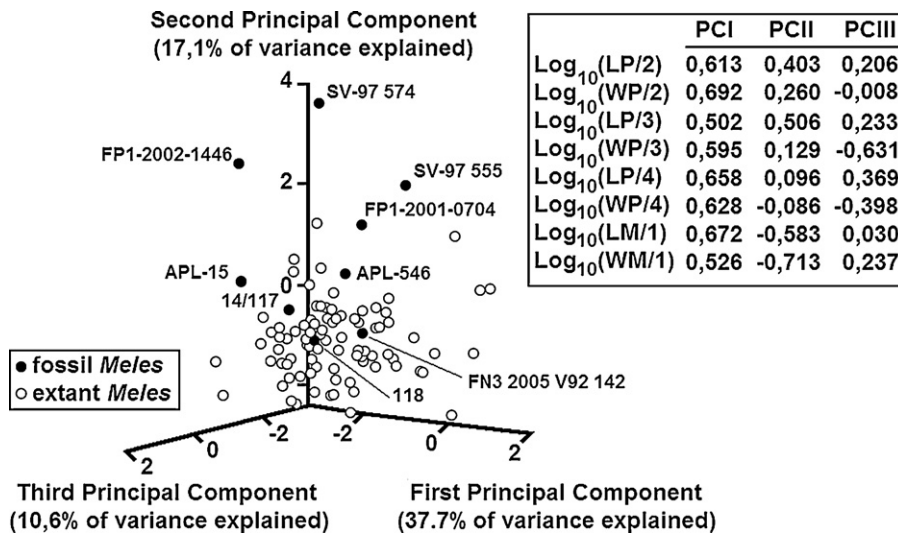


Fig. 4. Results of a principal components analysis of tooth measurements in extant *Meles meles* and several fossil specimens of *M. meles* and *M. thoralis* from Villafranchian localities (Apollonia: AP-15 and AP-546; Fonelas: FP1-2001-074 and FP1-2002-1446; Fuente Nueva: FN3 2005 V92 142; Deutsch-Altenburg-2: 118 and 14/117; Saint-Vallier: SV-555 and SV-574). The scatter plot shows the specimens' scores on the first three axes. The factor loading for the metric variables on each component is also shown.
Fig. 4. Résultats de l'analyse en composantes principales de mesures dentaires chez *Meles meles* actuel et chez différents spécimens fossiles en provenance de localités villafranchiennes (Apollonia : AP-15 et AP-546 ; Fonelas : FP1-2001-074 et FP1-2002-1446 ; Fuente Nueva : FN3 2005 V92 142 ; Deutsch-Altenburg-2 : 118 et 14/117 ; Saint-Vallier : SV-555 et SV-574). La répartition des points représentatifs des spécimens montre que ceux-ci sont centrés sur les trois premiers axes. La charge factorielle pour les variables métriques sur chaque composante est également indiquée.

3.2. Palaeobiogeographic implications

The presence of *M. meles* in Fuente Nueva 3 at 1.3–1.4 Ma is highly significant in order to date the divergence between the two living Eurasian badgers. In fact, the ancestor of the European and Asia badgers, *M. thoralis*, has a Palearctic distribution during the Early Villafranchian and later, during the Middle Villafranchian, this species is recorded in several localities around Europe, including Saint-Vallier, Fonelas, Vatera and Gerakarou. But afterwards, which is the first occurrence in the fossil record of the living European and Asian badgers? Several authors have suggested that both species originated in the Early-Middle Pleistocene from their possible ancestor, *M. thoralis* (Baryshnikov et al., 2002 and references therein), but alternatively other researchers have attributed several late Early Pleistocene badger remains to the living badger species (Moullé, 1992; Petrucci, 2008). In a recent taxonomical review of the Eurasian Plio-Pleistocene badgers (Madurell-Malapeira, 2010; Madurell-Malapeira et al., 2011), all Late Villafranchian European badger remains were assigned to the extant species, *M. meles*. We suggest that the split between the European and Asian badgers took place in the Middle to Late Villafranchian boundary (ca. 1.8 Ma) or slightly before, through a vicariance process prompted by palaeoclimatic changes. This interpretation is supported by molecular data (Del Cerro et al., 2010; Marmi et al., 2006).

Overall, the evidence available shows that *M. meles* was a distinct species in the Late Villafranchian according to the information from the localities of Pirro Nord and Apollonia. However, as a result of the wide chronological interval proposed for these localities, it is not possible to date with precision the moment from which *M. meles* was widely distributed around Europe. The material described in this paper sheds light into this issue, allowing to infer for the first time a precise age for the earliest remains of *M. meles*, and supporting the idea that the divergence from *M. thoralis* took place at the beginning of the Late Villafranchian (ca. 1.8 Ma) or even before.

4. Conclusion

In this article we describe dentognathic badger remains from the Late Villafranchian locality of Fuente Nueva 3 in south-eastern Iberian Peninsula. Morphological and morphometric comparisons with other European Late Villafranchian badgers show that these fossil remains share a set of characteristics with them as well as with extant European badgers. Accordingly, we attribute the described remains to the extant species, *M. meles*.

The Fuente Nueva 3 badger confirms that European badgers were widely distributed around Europe during the Late Villafranchian, thus supporting the idea that the divergence time for the two Eurasian species of living badgers took place previously or simultaneously to the Middle-Late Villafranchian boundary (ca. 1.8 Ma).

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