

FIRST REVIEW OF LYNCODONTINI MATERIAL (MUSTELIDAE, CARNIVORA, MAMMALIA) FROM THE LOWER PLEISTOCENE ARCHAEO-PALAEONTOLOGICAL SITES OF ORCE (SOUTHEASTERN SPAIN)

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Abstract: Two archaeo-palaeontological Lower Pleistocene sites of Orce (Baza Basin, SE Spain), Fuente Nueva 3 (1.3 Ma) and Barranco León (1.4 Ma), preserve some of the earliest evidences of human presence in the European continent. During the 2013 field season, a small Lyncodontini mustelid mandible was found at Fuente Nueva-3. This finding was accompanied by a lower canine (c1), also from the same site, and a lower fourth premolar (p4) from Barranco León. Here, we report on the morphological and biometrical study of these materials, in comparison to other Eurasian Pliocene-Pleistocene species of the tribe Lyncodontini. The analyses revealed an affinity between the taxon from Fuente Nueva-3 and Barranco León with the small-sized European species *Martellictis ardea* (Gervais, 1848-1852), allowing us to ascribe the described material to the latter species. The presence of *M. ardea* in the sites of Orce is the southernmost occurrence of the species in the Iberian Peninsula and an important finding in the scarce fossil record of Lyncodontini in Europe.

INTRODUCTION

Mustelid remains are relatively scarce in the fossil record unearthed from the upper Lower Pleistocene Orce site complex. Previous systematic

studies of the faunal assemblages of Level D from Barranco León (BL-D) and Fuente Nueva-3 (FN-3) mentioned the presence of the genus *Meles* Brisson, 1762 (Martínez-Navarro et al. 2010; Madurell-Malapeira et al. 2011) and also noted the record of other mustelid remains, tentatively attributed to *Pannonictis* cf. *nestii* (Martelli, 1906) in FN-3 and to cf. *Pannonic-*

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tis and Mustelidae indet. in BL Level D (Madurell-Malapeira et al. 2014).

This work focuses on the study of a few remains of a small mustelid unearthed from FN-3 and BL-D.

The record of *Pannonictis* Kormos, 1931, and of Lyncodontini Pocock, 1921 in general, is scarce and scattered in time and space across Eurasia (see Bartolini Lucenti 2018, and references there in). Five genera from the Old-World stock of Lyncodontini are currently known. In addition to *Pannonictis*, there are: (i) the large-sized and stoutly-built *Eirictis* Qiu, Tao, Wang, 2004; (ii) the insular endemic *Enhydriictis* Forsyth Major, 1901; (iii) the primitive-like *Martellictis* Bartolini Lucenti, 2018; and (iv) the eastern Asian *Oriensictis* Ogino & Otsuka, 2008. Considering this diversity and an utterly poor record, the taxonomical status of several species of these fossil mustelids is a harshly-debated issue. Yet, recent research has provided new and interesting insights on these mustelids. Geraads (2016) reported the first occurrence of a Lyncodontini in the African continent, opening to new biogeographic scenarios. This group of fossil mustelids received much attention in recent year (Bartolini Lucenti 2018; Rook et al. 2018). And lastly, not for importance, Jiangzuo et al. (2019) hypothesized biogeographical dispersal events and the existence of palaeoecological conditions previously undetected, and probably underestimated, in eastern Eurasia.

Figure 1 shows the known occurrences of Lyncodontini across the Old-World. According to several authors (Kormos 1931; Pilgrim 1932; Schreuder 1935; Rook 1995; García & Howell 2008; Bartolini Lucenti 2018), the earliest record of this group in Eurasia is that of Mustelidae gen. indet. sp. indet. by Zdansky (1927), which correlates to “*Hipparion* beds” from China (Late Miocene) and probably represents the oldest occurrence of *Pannonictis*. Other Early Pliocene scattered occurrences of this genus are those of Gaotege (4.5-4.1 Ma, Inner Mongolia, China; Li et al. 2003; Fig. 1) and the earliest European one of Wölfersheim (Germany; Morlo & Kundrát 2001). Sotnikova et al. (2002) reported also *Pannonictis* sp. from Etulia (Moldova). All these Eurasian records are too few to confidently ascribe the samples to a particular species. More or less coeval to Wölfersheim and Etulia, there is also the earliest record of another European taxon, *Martellictis ardea* (Gervais, 1848-1852). Its oldest record is in the Slo-

vakian site of Ivanovce (MN15, Fejfar et al. 2012; Fig. 1). After this initial occurrence, no record of *M. ardea* has been found in deposits related to the first half of the early Villafranchian, with the only exception of the type locality of Perrier-Les Etouaires (France).

During the Early Pleistocene this species became a common element of European Villafranchian assemblages. In Asia, Lyncodontini is represented in the Late Pliocene and Early Pleistocene by the genus *Eirictis*. Qiu et al. (2004) erected this genus on the material from the Early Pleistocene of Longdan (Dongxiang, Gansu, China). Among the diagnostic features that allow discriminating *Eirictis* from *Pannonictis* there is the absence of a hypocone on the P4. Qiu et al. (2004) included in the new genus the species *Eirictis robusta* Qiu, Tao, Wang, 2004 from Longdan, as well as “*Pannonictis*” *pachygnatha* (Teilhard de Chardin & Leroy, 1945) from Shamar (Sotnikova 1980) and Nihewan Basin (Teilhard de Chardin & Leroy 1945). Recently, *Eirictis variabilis* Jin & Liu, 2009 was described from the Lower Pleistocene site of Renzidong Cave (Eastern China). The Early Pleistocene was an interval of intense radiation of Lyncodontini especially for *Pannonictis* (as evident from Fig. 1). Several different species have been described from central and southern Europe (García & Howell 2008; Colombero et al. 2012). For example, *Pannonictis nestii* (Martelli, 1906) is reported from a number of Italian sites, including Upper Valdarno, Pietrafitta in Umbria (Rook 1995) and Pirro Nord, Apulia (Colombero et al. 2012), and also from the Spanish locality of Sima del Elefante (Sierra de Atapuerca; García & Howell 2008). The type species of the genus, *Pannonictis pliocaenica* Kormos, 1931, comes from the complex of cavities of Villany-Kalkberg (Hungary). Kormos (1933) described also another species, the small-sized *Pannonictis pilgrimi* Kormos, 1933. The identity and validity of these three European species (*i.e.*, *P. nestii*, *P. pliocaenica* and *P. pilgrimi*) is debated in literature. Several hypotheses were put forward: some authors (*e.g.* García et al. 2008 and reference therein) suggested grouping *P. nestii* with the critical “*Mustela*” *ardea*, whereas other scholars adverse this proposal (*e.g.* Viret 1954; Ficcarelli & Torre 1967; Rook 1995; Sotnikova et al. 2002). Viret (1954) synonymized *P. pilgrimi* to “*M.*” *ardea*. In contrast, Ficcarelli & Torre (1967) suggested synonymizing the former with *P. nestii*. García & Howell (2008) favored the inclu-

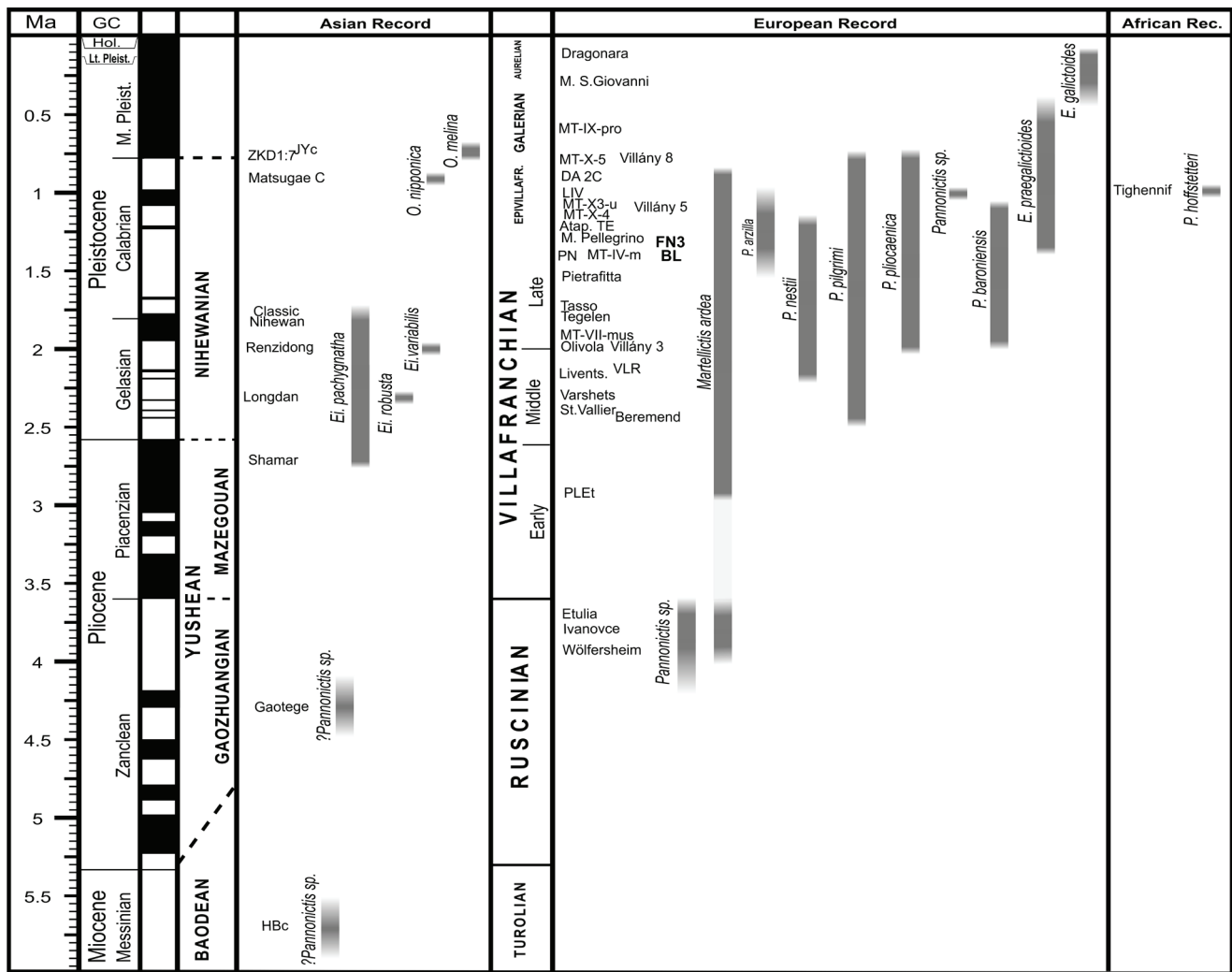


Fig. 1 - Chronological scheme of the known occurrences of *Lyncodontini* in the fossil record of the Old World. Data from: Forsyth Major (1901); Martelli (1906); Pei (1934); Teilhard de Chardin & Leroy (1945); Schaub (1949); Villalta (1952); Viret (1954); Rabeder (1976); Jánossy (1986); Willemsen (1988); Ferrandini & Salotti (1995); Masseti (1995); Rook (1995); Burgio & Fiore (1997); Spassov (2000); Morlo & Kundrát (2001); Sotnikova et al. (2002); Li et al. (2003); Abbazzi et al. (2004); Qiu et al. (2004); García & Howell (2008); García et al. (2008); Ogino & Otsuka (2008); Jin & Liu (2009); Colombero et al. (2012); Fejfar et al. (2012); Koufos (2014); Madurell-Malapeira et al. (2014); Geraads (2016); Bartolini Lucenti (2018); Rook et al. (2018); Jiangzuo et al. (2019). Abbreviations – Atap. TE, Atapuerca Trincheras Elefante (Spain); BL: Barranco León (Spain); DA 2C, Deutsch Altenburg 2C (Austria); FN3, Fuente Nueva-3 (Spain) HBC, Hipparion Bed (China); JYc, Jinyuan Cave (China); LIV, Livakkos (Greece); Livents, Liventsoska (Russia); MT, Monte Tuttavista (Italy); PLEt, Perrier-Les Etouaires (France); VLR, Villarroya (Spain); ZKD, Zhoukoudian (China).

sion of *P. pilgrimi* in *P. pliocaenica*, considering the marked size difference as a strong sexual dimorphism: in their opinion, *P. pliocaenica* would represent the larger male individuals, whereas *P. pilgrimi* the smaller females. Another species of *Pannonictis* was described from the African site of Tighennif, *Pannonictis hoffstetteri* (Geraads, 2016), ascribed to *Enhydriactis* by Geraads (2016) considering this genus as inclusive of all taxa of *Lyncodontini*. Later, Bartolini Lucenti (2018) reascribed it to *Pannonictis*. *Pannonictis* was also present in the Mediterranean islands. An interesting and still unclear record is that of the *Pannonictis arzilla* (De Gregorio, 1886) from

Monte Pellegrino (Sicily), uncertainly correlated to the Calabrian stage (Fig. 1). Several dentognathic features suggest a clear relationship between this taxon and the other continental *Lyncodontini*, most probably with the continental *P. nestii* (see Rook 1995). Nevertheless, Burgio & Fiore (1997) maintained the name *Mustelercta* De Gregorio, 1886, originally used by De Gregorio, as a subgenus, stressing its peculiarity compared to the continental species. Further studies might clarify the taxonomical identity of this taxon in relation to the other Pleistocene circum-Mediterranean species. An unidentified species of *Pannonictis* was reported

by Abbazzi et al. (2004) from the sedimentary infillings of the fissure of the Monte Tuttavista site complex (Nuoro, Sardinia), which was recently described as *Pannonictis baroniensis* Rook, Bartolini Lucenti, Tuveri, Arca, 2018. One of the most peculiar taxon within the European record is by far *Enhydriactis*. The genus was erected for the mustelid recovered from the Middle Pleistocene deposits of the locality of Monte S. Giovanni (Sardinia) and described as *Enhydriactis galictoides* Forsyth Major, 1901. According to Forsyth Major (1901), the form had a strong affinity with the extant South American Ictonychinae, *Galictis cuja* (Molina, 1782) and *Galictis vittata* (Schreber, 1776). *Enhydriactis* is more elusive than *Pannonictis*, and it is only known from few other Sardinian and Corsican localities. Among these, there is the outstanding record of Monte Tuttavista, described as *Enhydriactis praegalictoides* Rook, Bartolini Lucenti, Tuveri, Arca, 2018. Many peculiar features that typify this genus (e.g. a strong postorbital constriction and a shorter muzzle) probably resulted from endemism and some researchers regarded them as adaptations to an aquatic lifestyle (Forsyth Major 1901; Pilgrim 1932; Ficcarelli & Torre 1967). The Middle Pleistocene of eastern Asia was characterized by the presence of *Oriensictis*. This Lyncodontini was recorded in Japan, *Oriensictis nipponica* (Naora, 1968), and from Chinese localities (e.g. Zhoukoudian 1), *Oriensictis melina* (Pei, 1934). Recently, Jiangzuo et al. (2019) described a well-preserved specimen of *O. melina* from Jinyuan cave (Middle Pleistocene; Puwan, Danlian, China). In their analysis, the authors suggested to include the genus *Oriensictis* in *Enhydriactis* considering the cranial similarities between the Chinese skull and the Sardinian species. This grouping challenges the present hypotheses on the origin, radiation and dispersal of the clade Lyncodontini. Unfortunately, at present there is no strong supporting evidence for the intercontinental dispersion of these mustelids, or of their ancestors. Moreover, the marked dental differences between *O. nipponica* (the most primitive of the species of *Oriensictis*, see Ogino & Otsuka 2008; Jiangzuo et al. 2019) and *Enhydriactis* (both the primitive-like *E. praegalictoides* and the derived *E. galictoides*), cannot be ruled out as interspecific variability. The lack of any record of *Enhydriactis/Oriensictis* out of their area of description (i.e., Sardinia and eastern Asia, respectively) does not favor the inclusion of the latter genus in *Enhydriactis*.

The cranial similarities of *Enhydriactis* and *Oriensictis* might actually be the result of adaptations to similar environments and selective pressures. Until new evidence from central Asia or eastern Europe is found, we deem more prudent to leave the genera separated.

In this wide and complex scenario, the findings of the Orce sites add valuable information on these poorly known species, regarding their geographic distribution and biostratigraphic range. To serve this purpose, the bone and dental mustelid remains from Fuente Nueva-3 and Barranco León were revised, and most of them were taxonomically classified.

GEOLOGICAL AND PALAEOANTHROPOLOGICAL SETTING

FN-3 and BL are located in the vicinity of the town of Orce (Fig. 2), in the northeastern sector of the lacustrine Baza Basin (Granada, Andalusia, Spain). The research in this area started during the seventies of the XX Century by a team led by Prof. Josep Gibert (see Martínez-Navarro 1993).

From a stratigraphic point of view, FN-3 records the presence of two sedimentary cycles, composed of clastic sediments (shales, marls and sandstones) with carbonate levels at the top of the sequence, which would correspond to shallow lacustrine deposits (Turq et al. 1996; Anadón et al. 2003; Duval et al. 2010). This section is divided in six archaeological levels. These levels show taphonomic differences mainly due to the stage of preservation of the bones and differences in the usage intensity produced by hominins and carnivores (Espigares 2010; Espigares et al. 2013, 2019).

The BL section includes a succession predominantly composed by reddish and whitish clayish marlstones (Red Detritic Member), which are present in the lower parts of the ravine, and other carbonate layers with intercalations of quartzitic sandstones and shales, which constitute the most pronounced upper escarpments of the ravine (Vera et al. 1985; Soria et al. 1987; Anadón et al. 2003; Oms et al. 2010). In this site, most of the palaeontological and archaeological record comes from Level D, previously named BL-5 (Arribas & Palmqvist 2002), including the earliest human fossil of Europe, a lower deciduous first premolar of a juvenile

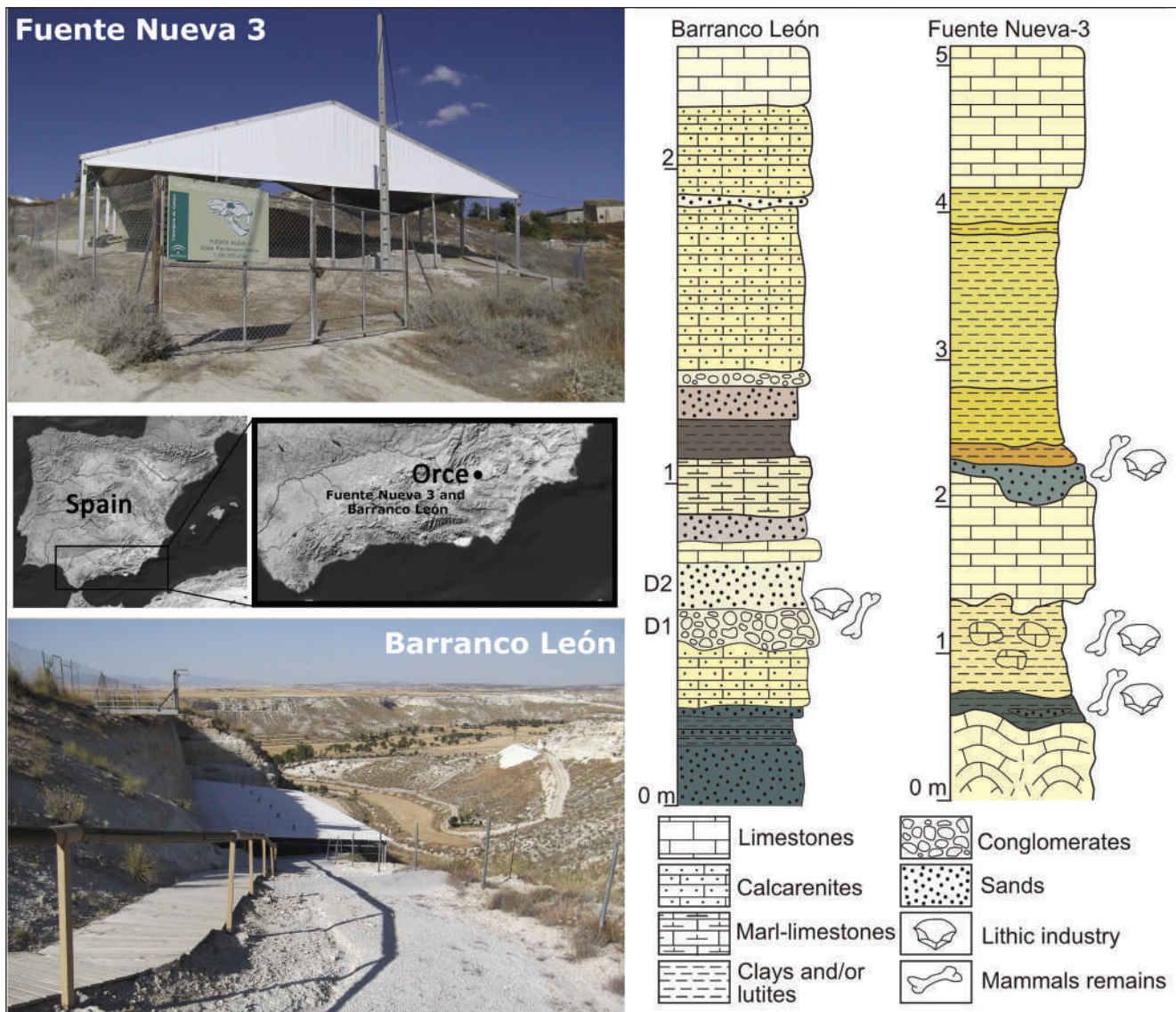


Fig. 2 - Left: geographic situation of the archeo-paleontological sites of Fuente Nueva-3 and Barranco León (Granada, Spain). Right: stratigraphic columns (modified from Espigares et al. 2019).

hominin, about ten years old (Toro et al. 2013). This tooth, together with the presence in this site and also in FN-3 of abundant Oldowan lithic artifacts, cut and percussion marks on the bones, represent the earliest evidence of human presence in Western Europe (see reviews in Martínez-Navarro et al. 1997, 2014; Arribas & Palmqvist 1999, 2002; Oms et al. 2000c; Palmqvist et al. 2005, 2014, 2016; Toro et al. 2009, 2011; Espigares et al. 2013, 2019; Toro et al. 2013; Barsky et al. 2015; Tilton et al. 2020).

BL-D and FN-3 have similar faunal assemblages of large mammals, although there are differences in their abundance. For example, hippo remains are particularly well represented in BL-D (Palmqvist et al. 2005; Espigares 2010), while elephant remains are abundantly preserved in FN-3

(Ros-Montoya 2010; Espigares et al. 2013). The faunal assemblage of these sites consists of the following species: one proboscidean [*Mammuthus meridionalis* (Nesti, 1825)], three perissodactyls [*Equus altidens* von Reichenau, 1915, *Equus sussenbornensis* Wüts, 1901, and *Stephanorhinus cf. hundsheimensis* (Toula, 1902)], one hippo (*Hippopotamus antiquus* Desmarest, 1822), three bovids (*Bison* sp., *Hemitragus cf. albus* (Moyà-Solà, 1987), and *Ammotragus europaeus* Moullé, Echassoux, Martínez-Navarro, 2004), two cervids [*Praemegaceros verticornis* (Dawkins, 1872) and *Metacervoceros rhenanus* (Dubois, 1904)], one ursid (*Ursus etruscus* Cuvier, 1823), three canids [*Canis mosbachensis* Soergel, 1925, *Lycaon lycaonoides* (Kretzoi, 1938) and *Vulpes alopecoides* (Del Campaña, 1913)], two mustelids (*Pannonictis* sp., *Meles me-*

les Linnaeus, 1758), three felids [*Lynx* cf. *pardinus* Temminck, 1824, *Homotherium* cf. *latidens* (Owen, 1846), *Megantereon whitei* (Broom, 1937)], one hyaenid [*Pachycrocuta brevirostris* (Gervais, 1850)] and one primate (*Homo* sp.; in FN-3 recorded only by lithic artifacts and anthropic marks on large mammals bones) (Martínez-Navarro et al. 1997, 2003, 2004, 2010; Alberdi 2010; Abbazzi 2010; Lacombat 2010; Madurell-Malapeira et al. 2011; Moullé et al. 2004; Ros-Montoya 2010; Boscaini et al. 2015; Bartolini Lucenti et al. 2017; Medin et al. 2017; Espigares et al. 2019; Bartolini Lucenti & Madurell-Malapeira 2020).

The age of these sites has been estimated by micro- and macromammals biostratigraphy, palaeomagnetism, and combined U-series/ESR dating methods at 1.43 ± 0.38 Ma for BL-D and at 1.19 ± 0.21 Ma for FN-3, respectively (Duval et al. 2012; Toro et al. 2013), and there is also an age estimate of 1.50 ± 0.31 Ma for FN-3 derived from cosmogenic nuclides (Álvarez et al. 2015). In this context, it is important to note the absence of suids in all the Lower Pleistocene sites of Orce. Species of the genus *Sus* disappeared in Europe after 1.8 Ma and reappeared at around 1.2 Ma, marking the beginning of the Epivillafranchian biochron (Martínez-Navarro et al. 2015; Cherin et al. 2020). Its first record in the Iberian Peninsula is at the level TE9 of Atapuerca Sima del Elefante, dated by cosmogenic nuclides to 1.22 ± 0.16 Ma (Carbonell et al. 2008), but it is absent from both BL-D and FN-3 (Martínez-Navarro et al. 2015).

MATERIALS AND METHODS

The studied material was held at the Museo de Prehistoria y Paleontología of Orce. Since 3rd November 2016, all the Orce collections, including the materials described here, are housed at the Museo Arqueológico y Etnológico of Granada.

This material has been compared with the record of Lyncodontini from Eurasia. We used specimens from the collections of the Natural History Museum of the University of Florence (IGF; see the institutional abbreviations below), the Museum of Geology and Palaeontology of the University of Turin, the Musée des Confluences, the Université Claude Bernard of Lyon (France), the Hungarian Museum of Natural History in Budapest (Hungary), and the Fossil Mammal collections of the American Museum of Natural History in New York as comparative fossil materials. These fossil comparative samples included specimens of *P. pliocenica* from Villány-Kalkberg; *P. pilgrimi* from Villány and Beremend; *P. nestii* from Upper Valdarno and Pirro Nord; *P. hoffstetteri* from Tighennif; *P. baroniensis* and *E. praegalictoides* from Monte Tuttavista deposits; *E. galictoides* from Monte S. Giovanni; and *M. ardea* from Olivola,

Perrier-Les Etouaires and St. Vallier. All the relevant literature on the Pliocene-Pleistocene Lyncodontini was also inspected (Viret 1954; Ficcarelli & Torre 1967; Rabeder 1976; Willensen 1988; Rook 1995; Morlo & Kundrát 2001; Sotnikova et al. 2002; Qiu et al. 2004; García & Howell 2008; García et al. 2008; Ogino & Otsuka 2008; Jin & Liu 2009; Colombero et al. 2012; Fejfar et al. 2012; Geraads 2016; Jiangzuo et al. 2019). Extant specimens from the Zoology section of the Museum of Natural History of the University of Florence were also used for morphological and morphometric comparisons. The extant comparative sample includes specimens of *G. cuja*, *G. vittata*, *Mustela putorius* Linnaeus, 1758, and *Eira barbara* Linnaeus, 1758, housed in the MZUF.

Craniodental measurements were taken to the nearest 0.1 mm with a digital caliper, following Driesch (1976) for anatomical nomenclature.

Institutional abbreviations

AMNH, American Museum of Natural History, New York, United States of America; HMHN, Hungarian Museum of Natural History, Budapest, Hungary; IGF, Museum of Natural History, Geological and Palaeontological section, the University of Florence (Italy); MZUF, Museum of Natural History, “La Specola” Zoology section, University of Florence (Italy).

Anatomical abbreviations

L: Length, W: Width, LTRI: m1 trigonid length, WTRI: m1 trigonid width, LTAL: m1 talonid length, WTAL: m1 talonid width, HMdbM/1: mandibular height at M/1, and WMdbM/1: mandibular width at M/1.

SYSTEMATIC PALAEOLOGY

Order **Carnivora** Bowdich, 1821

Family **Mustelidae** Fischer, 1817

Subfamily **Ictonychinae** Pocock, 1921

Tribe **Lyncodontini** Pocock, 1921

Genus *Martellictis* Bartolini Lucenti, 2018

Martellictis ardea (Gervais, 1848-1852)

Fig. 3

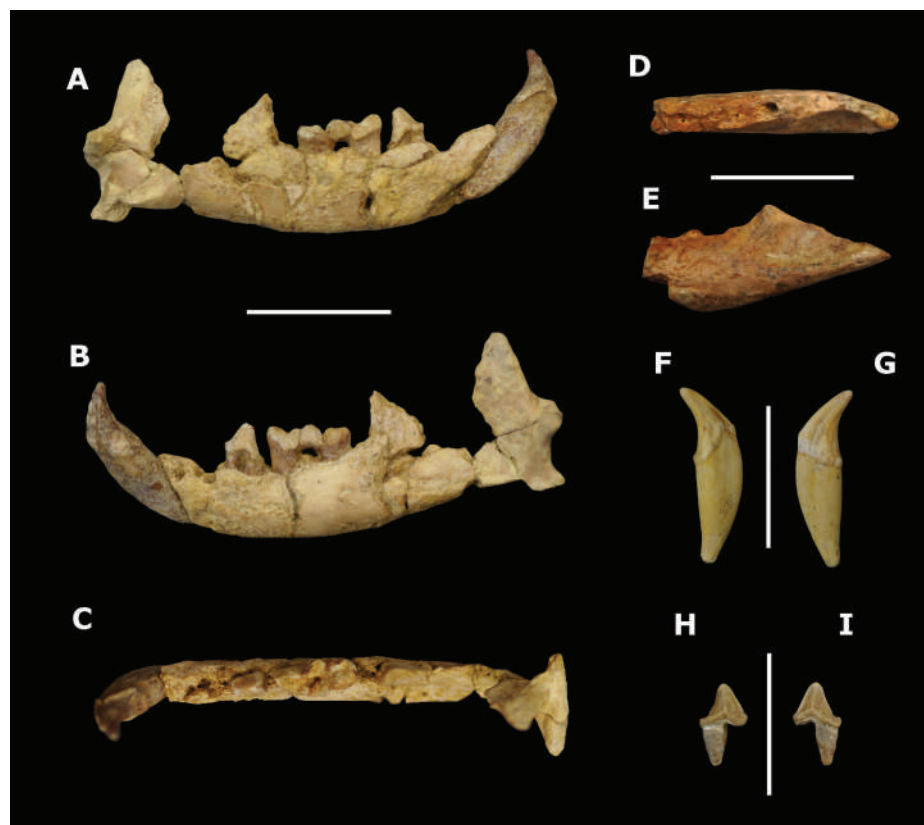
Holotype: MNHN.EPET 2008, left hemimandible fragment with m1, recovered from Côte de Ardé (Perrier-Les Etouaires, Puy-de-Dôme, Auvergne-Rhône-Alpes, France).

Referred Material: Left hemimandible (FN-3 2013 X96 N°84), left hemimandible (FN-3 1995 S11 NC), left C/1 (FN-3-1026, FN-3 2002 V96 ume 1 nc), and left P/4 (BL-1001 BL 2002 N55 nc).

Description

Mandible – The left hemimandible FN-3 2013 X96 n°84 is incomplete, lacking part of the masseteric fossa, but preserves c1, p4 and m1. The bi-rooted alveoli of p2 and p3, and the single-rooted alveolus of the m2 are all visible. Considering the degree of tooth wearing, the mandible would correspond to an adult individual. Its corpus is rather

Fig. 3 - Dentals remains of *Martellictis ardea* from FN-3 and BL-D. A–C) left hemimandible (FN-3 2013 870 X96 N°84) in lingual (A), labial (B), and occlusal (C) view; D–E) left hemimandible (FN-3 1995 S11 NC) 871 in occlusal (D) and labial view (E); F–G) left lower canine (FN-3 2002 V96 ume 1 nc, FN-3-1026) in lingual (F) and labial view (G), and H–I) left lower fourth premolar (BL 2002 N55 nc, BL-1001) in lingual (H) and labial view (I). Scale bars equals 20 mm.



low, and not particularly robust. The angular process of the FN-3 specimen is short and pointy. Although the masseteric fossa is not complete, it appears deep, reaching mesially the level of the m2 alveolus. Although the coronoid process is incomplete, it is possible to see that it is reduced in height. The other left hemimandible fragment (FN-3 1995 S11 NC) preserves the m1 roots, the single-rooted m2 alveolus, and the lower part of the masseteric fossa, which begins at the m2 distal margin.

Lower teeth – The lower canines, both FN-3 2002 V96 nc-FN-3-1026 and FN-3 2013 X96 n°84, are curved (hook-like) and wrinkled by a thin groove above the crown base. The advanced wear of FN-3 2002 V96 nc-FN-3-1026 indicates that it belonged to an adult individual. The p4 of FN-3 2013 X96 n°84 is complete, bi-rooted and with a well-developed protoconid, with a bean-like shape, in occlusal view, for the basal swelling of the enamel. The left p4 of BL 2002 N55 nc, BL-1001 has lost its anterior root. The crown cusp is well marked, with the tip centrally situated. The m1 is mostly complete, showing a pronounced wear in the trigonid. The protoconid, the paraconid and the metaconid are well differentiated. The talonid is concave downwards and represents a third of the total molar length.

Discussion

Comparison with Eurasian and African *Lyncodontini*

In size and morphology, the material from Barranco León and Fuente Nueva-3 is consistent with its attribution to a single taxon. For instance, the fourth premolar of BL-D is very similar to that of the FN-3 mandible, so it is the lower canine found in FN-3 compared to that preserved in FN-3 2013 X96 n°84. The sample described above corresponds to a minimum of three adult individuals, two in FN-3 and one in BL-D.

Nevertheless, the scanty nature of the material recovered from BL-D and FN-3 complicates their taxonomic attribution. There are, though, some dentognathic features suggestive of a plausible attribution to *M. ardea*. The slender and shallow mandibular corpus does not resemble any other European or Asian taxon (Fig. 4). Indeed, it markedly differs from *Eirictis* spp., in which the mandible is stout and high. The same can be said for several *Pannonictis* species, like *P. pliocaenica* from Villány, *P. nestii* from Upper Valdarno, Pirro Nord or Atapuerca TE, *P. baroniensis* from Mt. Tuttavista (Fig. 4). Even species of *Enhydriactis* from Sardinia and *Oriensictis* from China and Japan have deeper and more robust mandibles (Fig. 5). The mandibles of

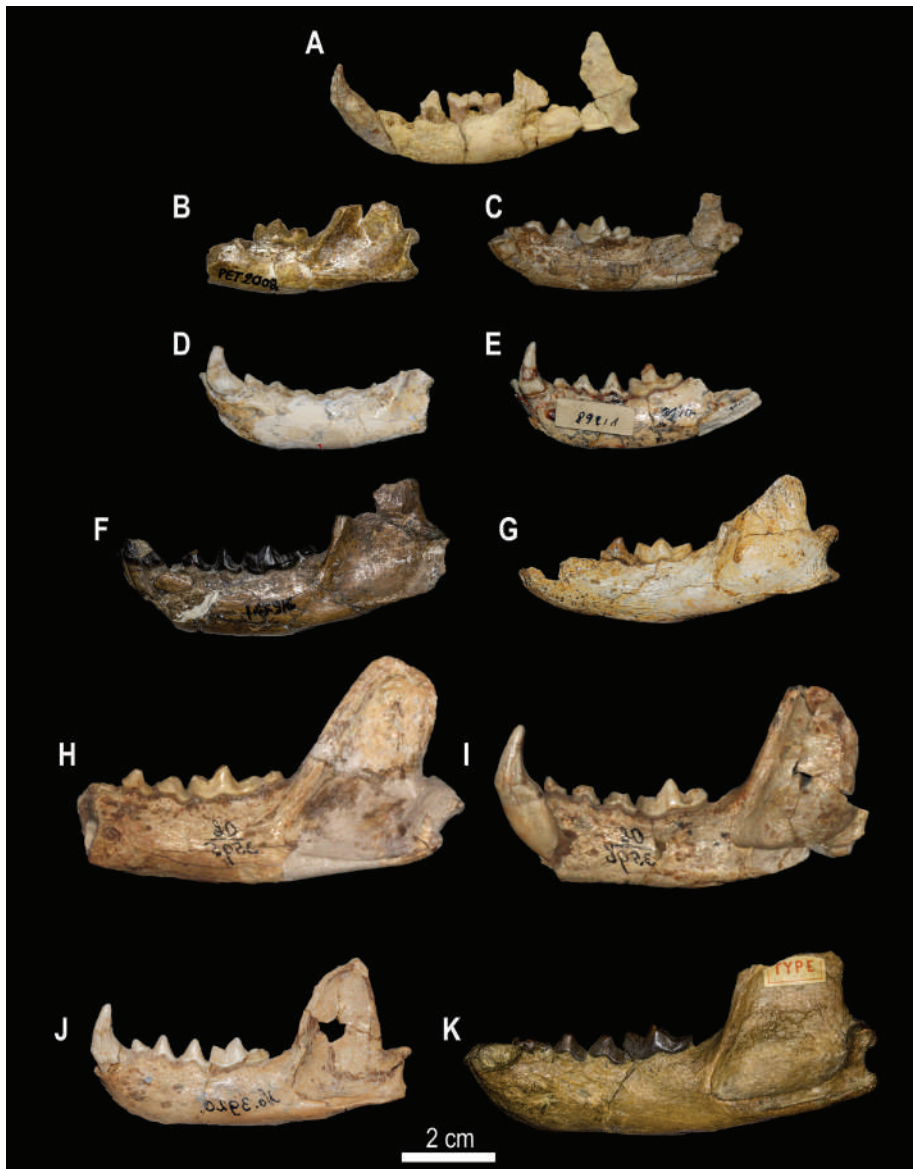


Fig. 4 - Comparison of hemimandibles of selected species of Lyncodontini from Eurasia. A) FN-3 2013 X96 N°84, left hemimandible from Fuente Nueva-3. B–D) *M. ardea*. B, MNHN.F.PET2008, left hemimandible from Perrier-Les Etouaires; C, IGF 4297, right hemimandible (reversed) from Olivola; D, MHNL 20161911, right hemimandible (reversed) from St. Vallier. E) *P. pilgrimi*, V.61.1368, left hemimandible from Villány. F–G) *P. nestii*. F, IGF 916, left hemimandible from Upper Valdarno; G, MGPT-PU120257, left hemimandible from Pirro Nord. H–J) *P. pliocaenica* from Villány. H, OB3596, right hemimandible (reversed); I, OB3595, right hemimandible (reversed); J, V.61.1369, right hemimandible (reversed); K) *Ei. pachygnatha*, MNHN.F.NIH 177, left hemimandible from Nihewan Basin.

M. ardea from Olivola, Perrier-Les Etouaires and St. Vallier are instead considerably shallow and slender (Fig. 4). Focusing on the European record, the lower carnassial tooth of *P. nestii* from Upper Valdarno, Pirro Nord and Atapuerca TE is proportionally stouter compared to that of FN-3 2011 X96 N°84. *Pannonictis pliocaenica* from Hungary and both *P. nestii*

and *P. pilgrimi* from Hungary have wider and longer talonids, about one half of the length of the carnassial. The distal cingulids on the m1 of *P. nestii* and *P. pilgrimi* differ from the one of FN-3 2011 X96 N°84, which is less distally expanded, whereas the comparison with *P. pliocaenica* shows that the hypoconid and metaconid are both proportionally

	c			p4		m1				Mandible		
	L	W	L	W	L	LTRI	WTRI	LTAL	WTAL	L	HMdbM/I	WMdbM/I
FN-3 2011 X96 N°84	6.2	5.2	6.0	3.4	11.5	6.2	5.3	5.1	4.2	65.1	11.6	5.9
FN-3 2002 V96 ume 1 nc	6.5	5.1	-	-	-	-	-	-	-	-	-	-
BL 2002 N55 nc	-	-	6.5	3.9	-	-	-	-	-	-	-	-

Tab. 1 - Anatomical measurements of dentognathic remains attributed to *Martellictis ardea* from FN-3 and BL-D.

larger. In *Enhydriactis*, the m1 metaconid tends to be reduced, whereas the hypoconid and the distal cingulid, which is cuspid-like, are prominent. In both *E. praegalictoides* and *E. galictoides* the talonid is long, similar to *Pannonictis* spp. In contrast, *M. ardea* from Olivola and Perrier-Les Etouaires has a shorter talonid, which is less than half of the total length of the m1, similar to that of FN-3 2011 X96 N°84. Bi-plots on selected dentognathic variables of the Old-World taxa confirm the morphological evidence (Fig. 5). The first scatterplot (Fig. 5A) compares the height and the breadth of the mandible at the level of the carnassial. The second compares the length of the carnassial with the height of the mandible (Fig. 5B), and with the greatest width of the m1 (Fig. 5C). Basically, two principal groups can be identified in all plots: one includes the largest species and is composed of *Eirictis* spp. and *P. pliocaenica*. The second, more numerous, is made up by the small- to medium-sized species, *Enhydriactis* spp., *P. hoffstetteri*, *P. nestii*, *P. pilgrimi*, *M. ardea* and *Oriensictis* (although a specimen of *O. melina* scatters within the cluster of the large-sized lyncodontini). The insular *P. baroniensis* appears to be intermediate in size between the two groups. The specimens from Fuente Nueva-3 cluster in the second group, particularly within the variability of *M. ardea*, and their measurements are among the smallest of all, close to the small specimens of *P. pilgrimi*, *P. nestii* and *E. galictoides*. The plot that better discriminates the known species appears to be the first one (Fig. 5A). It shows that the small mandibles FN-3 2011 X96 N°84 and FN-3 1995 S11 NC are clearly included in the variance of *M. ardea*, that lies in the bottom-left corner of the variability of Lyncodontini, separated from the other species (except a single specimen of *P. nestii* from Pietrafitta). Similarly, in the proportion of the lower molars (Figs. 5B-C), the specimens from Fuente Nueva-3 lie closest to *M. ardea*. Considering both biometric and morphological evidence, the specimens recovered from BL-D and FN-3 can be confidently ascribed to *M. ardea*.

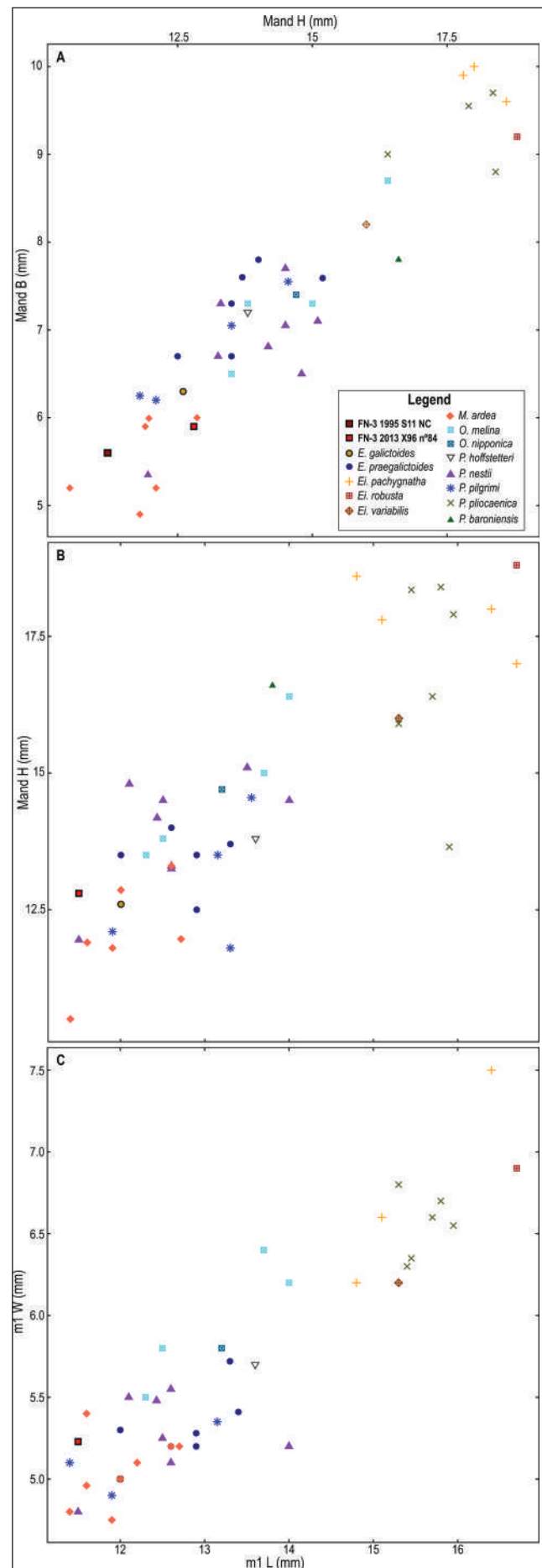


Fig. 5 - Plots of lower carnassial and mandibular variables (length of m1, height and breadth of the mandible at m1) in several fossil Lyncodontini. A) height vs. breadth of the mandible at m1. B) m1 length compared to mandible height distally to the m1. C) m1 length vs. m1 width.

Importance of the record of Lyncodontini from Orce

The Lyncodontini mustelids are represented in the Eurasian Pliocene-Pleistocene by five genera, *Eirictis*, *Enhydriactis*, *Martellictis*, *Oriensictis* and *Pannonictis*, whose record is scattered across Eurasia and Africa in the last five million years (Fig. 1). This fossil record is utterly scarce, which contributes to the high taxonomic complexity of the group. A detailed synthesis of these references is included in Bartolini Lucenti (2018), including the taxonomic issues of these taxa.

An important aspect to take into consideration is the palaeoecological inferences obtained from the presence of *M. ardea* in the fossil associations of Barranco León and Fuente Nueva-3 (Rodríguez-Gómez et al. 2016). As it has been published, during the Early Pleistocene a lake was installed in the Baza Basin, with the depocenter in the Orce region. Although it was not very deep, it had a large lateral extension, in excess of one thousand km². The sedimentary deposits in this region are closely related to this lacustrine context (Blain et al. 2016). Moreover, in the area an intense low-temperature hydrothermalism existed (García-Aguilar et al. 2014 and 2015), which allowed the maintenance of the water table, despite the balance between rainfall and water losses by evaporation, infiltration, etc., was negative.

In addition, the faunal association of these two sites presents several species of aquatic affinities, such as the hippopotamus *H. antiquus*, for which a strictly aquatic life style has been defined from the isotopic study of the $\delta^{15}\text{N}$ ratios in bone collagen (Palmqvist et al. 2003), and numerous elements of the herpetofauna, which allowed to obtain climatic data. Blain et al. (2016) concluded that during the late Early Pleistocene the Orce area was considerably more humid than today, with a warmer climate, temperate winters and a higher rainfall than today, especially during winter and spring. This conclusion was also reached using isotopic data from the nearby site of Venta Micena, slightly older (1.6-1.5 Ma) than BL and FN-3, which had an estimated annual rainfall of 780 mm (García-Aguilar et al. 2014, Fig. 7).

The ecology of the extant lyncodontini mustelids has been related, to a greater or lesser extent, with the presence of water, as the two extant species, *G. cuja* and *G. vittata*, inhabit humid environments. Rook (1995) discusses the possibility of an aquatic lifestyle for *P. nestii* based on an adaptation present

in *E. galictoides*, which could have been present in all the fossil representatives of the group. However, in most of the publications it is assumed that they are forms related to humid environments, although a strictly aquatic way of life seems unlikely. This argument is supported by additional evidence, as the presence in Pirro Nord of a complete humerus of *P. nestii*, which shows some “aquatic” characteristics that contrast with other “non-aquatic” features (Colombero et al. 2012).

In any case, the presence of *M. ardea* in the faunal associations of BL Level D and FN-3 fits with the evidence of the existence of humid environments in the Orce region 1.4 Ma ago (García-Aguilar et al. 2014; Blain et al. 2016). This Lyncodontini was a small-bodied carnivore, which probably had no significant impact on the ungulate prey that inhabited the palaeoecosystem of Orce (see discussion in Rodríguez-Gómez et al. 2016).

Specifically, a least-squares regression equation of Van Valkenburgh (1990) for body mass (BM) on lower carnassial length (LM1) derived using a wide sample of living carnivores [$\log_{10}(\text{BM}) = 2.72\log_{10}(\text{LM1}) - 2.03$] provides an estimate of only 6.83 kg for *M. ardea*. Such small-sized carnivores could have preyed on the abundant small vertebrate fauna (e.g. herpetofauna, Blain et al. 2011; 2016) dwelling on the shores of the Baza palaeolake.

CONCLUSIONS

The sites of Barranco León and Fuente Nueva-3 (Orce), with a chronology of ca 1.4 and 1.3 Ma, respectively, preserve a rich faunal assemblage of mammals that includes the record of a small-sized Lyncodontini, known since the early Villafanchian until the Epivillafranchian in Europe.

These remains recovered in the Orce sites, especially the right hemimandible of FN-3, show dimensions and morphology that favor an ascription to the species *Martellictis ardea*.

The fossil remains here described represent the first record of this taxon so far south in the Iberian Peninsula and, moreover, a new and reliable contribution to the scarce and fragmentary record of this group of mustelids, and may therefore contribute to the clarification of their evolutionary and biogeographical history.

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