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Macaque remains from the early Pliocene of the Iberian Peninsula

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ABSTRACT

Macaques dispersed out of Africa into Eurasia in the framework of a broader intercontinental faunal exchange that coincided in time with the sea level drop associated with the Messinian Salinity Crisis. They are first recorded in Europe (Italy and Spain) by the latest Miocene, being subsequently recorded all over Europe, albeit sparsely, throughout the Pliocene and Pleistocene. These fossil European macaques are attributed to several (sub)species of the extant Barbary macaque (*Macaca sylvanus*). In Iberia, fossil macaques are best documented by *Macaca sylvanus florentina* from various Early Pleistocene sites, whereas their published Pliocene record is very scarce. Here we report the oldest post-Messinian occurrence of macaques in the Iberian Peninsula, based on the description and metrical comparisons of two upper teeth (a male canine and a third molar of two different individuals) from the early Pliocene (MN14, 5.0–4.9 Ma) site of Puerto de la Cadena (Murcia, SE Spain). The male C^1 is fully comparable in morphology with those of extant and fossil *M. sylvanus*, and larger than those of *Mesopithecus*. The M^3, in turn, displays the typical papionin morphology that characterizes the dentally-conservative genus *Macaca*—thereby discounting an alternate assignment to either the extinct colobine monkey *Mesopithecus* or the more dentally-derived papionin *Theropithecus*. Dental size and proportions of the M^3 further support an attribution to an extinct subspecies of *M. sylvanus* instead of the larger papionin *Paradolichopithecus*. Mostly on biochronologic grounds, the two macaque teeth from Puerto de la Cadena are here assigned to *Macaca sylvanus* cf. *prisca*, albeit tentatively, given the lack of clear-cut criteria to distinguish this subspecies from the younger *Macaca sylvanus florentina*. The described material represents the oldest well-dated Pliocene record of macaques in Iberia, predating the record of *Paradolichopithecus* by almost 1.5 million years.

1. Introduction

1.1. Puerto de la Cadena

Continental fossil vertebrates from the late Neogene fossiliferous outcrops of the Puerto de la Cadena area (Murcia, SE Iberian Peninsula) have been known for many decades, particularly on the basis of two sites (La Alberca and La Paloma) correlated to the latest Miocene Mammal Neogene (MN) unit MN13 (Montenat and Crusafont, 1970; Mein et al., 1973; Aguirre et al., 1974; de Bruijn et al., 1975; Morales, 1984; López Martínez, 1989; Freudenthal et al., 1998; Mancheño Jiménez and Fierro Bandera, 2011; Pérez-García et al., 2011; Morales et al., 2013). The location in 2008 of a new site, due to the construction of highway MU-31 in the area of Puerto de la Cadena, led to the discovery of more than 2000 fossil remains during successive emergency paleontological works in the

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following three years (Mancheño Jiménez and Fierro Bandera, 2011; Piñero et al., 2017). This fossil vertebrate assemblage from Puerto de la Cadena was recently described by Piñero et al. (2017). Although preliminary accounts suggested a latest Miocene age for this site (Mancheño et al., 2013), Piñero et al. (2017) conclusively correlated it to the early Pliocene. Among the 26 reported species, Piñero et al. (2017) noted the presence of a cercopithecine, which on the basis of the two available teeth was assigned to *Macaca* sp.

1.2. The fossil macaques from the Iberian Peninsula

Macaques are first recorded in Eurasia by the latest Miocene (MN13), based on fossil remains from Almenara-Casablanca M, Spain (Köhler et al., 2000) and Moncucco Torinese, Italy (Alba et al., 2014), all assigned to cf. *Macaca* sp. The remains from Moncucco Torinese are confidently dated to 5.41–5.33 Ma (Colombero et al., 2017), whereas those from Almenara-Casablanca M are roughly contemporaneous with the Messinian Salinity Crisis (ca. 5.9–5.3 Ma; Agustí et al., 2006; Minwer-Barakat et al., 2009; Alba et al., 2014). Coupled with the lack of papionin remains from older localities in Eurasia as a whole, this evidence suggests that macaques probably did not disperse out of Africa until the sea level drop associated with the Messinian Salinity Crisis (Agustí et al., 2006; Alba et al., 2014, 2015; Colombero et al., 2017).

It is uncertain whether macaques dispersed into Europe through southern Iberia or followed the Middle East route that was already available from pre-Messinian times (Alba et al., 2015). In any case, the dispersal of macaques coincides with a major mammalian turnover that took place ca. 5.5–5.3 Ma and involved multiple intercontinental dispersals between Africa and Europe—the so-called 'Gerbil Event' (Agustí et al., 2006) or 'Third African-Iberian Dispersal' (Gibert et al., 2013). Subsequently, during the Plio-Pleistocene, European fossil macaques are represented by several taxa that belong to the lineage of *Macaca sylvanus* (Linnaeus, 1758), the extant Barbary macaque from northern Africa (Delson, 1974, 1980; Szalay and Delson, 1979; Alba et al., 2011, 2014, 2016), which on phylogenetic evidence is considered the basal-most member of the genus (e.g., Springer et al., 2012). The Plio-Pleistocene remains of European macaques are customarily attributed to chronologically successive subspecies of *M. sylvanus*, which due to the lack of cranial remains are not particularly well characterized (Szalay and Delson, 1979; Delson, 1980; Alba et al., 2008, 2011, 2016; Marigó et al., 2014). Only the endemic macaque from Sardinia, *Macaca majori* Azzaroli, 1946, is customarily considered distinct enough from extant *M. sylvanus* to be considered a separate species (Zanaga, 1998; Rook and O'Higgins, 2005; Smith et al., 2014).

Early Pliocene macaques from Europe are customarily assigned to *M. sylvanus prisca* Gervais, 1859, which ranges from the earliest Ruscinian to the early Villafranchian (MN14–MN16; Szalay and Delson, 1979; Delson, 1980). The oldest record corresponds to the site of Montpellier, France (type locality; MN14, ~5 Ma), followed by Csarnota 2, Hungary (late MN15, ~3.6–3.2 Ma; Minwer-Barakat et al., 2012a) and several MN16 localities, such as Fornace RDB, Italy (early MN16, ~3.2–3.0 Ma; see Rook et al., 2001, and references therein). Although *M. s. prisca* was considered to be somewhat smaller than more recent and extant subspecies (Szalay and Delson, 1979; Delson, 1980), subsequent works have failed to substantiate such claims (Delson et al., 2000; Rook et al., 2001). Here we figure and describe in detail the fossil macaque remains from Puerto de la Cadena, which represent the oldest securely dated record of *Macaca* from the Iberian Pliocene, and tentatively one of the oldest occurrences of *M. s. prisca* in Europe.

2. Age and geological background

The site of Puerto de la Cadena is located 8 km SW of the city of Murcia (Fig. 1), close to the towns of La Alberca and El Palmar, on the northern flank of the Sierra de Carrascoy y el Valle. From a geological viewpoint, the fossiliferous outcrops of Puerto de la Cadena (Murcia-Carrascoy Basin) belong to the Cigarrón Unit, whose sediments were deposited under shallow marine conditions towards the bottom and within a continental setting towards the top (Piñero et al., 2017). The lower boundary of this unit consists of an erosional surface that has been correlated to the end-Messinian discontinuity, thus being interpreted as a post-Messinian regressive sequence (Piñero et al., 2017). The site of Puerto de la Cadena is located in the upper portion of the Cigarrón Unit, being composed of alternating sandstones and mudstones with some conglomeratic layers, indicative of a fluvial depositional environment with channels and floodplain development (Mancheño Jiménez and Fierro Bandera, 2011; Piñero et al., 2017).

Magnetostratigraphic analyses (Piñero et al., 2017) indicate that the short section from Puerto de la Cadena records a reverse magnetozone, which is also recorded in the upper portion of the nearby Barranco del Cigarrón section, being correlated to either C3n.3r (4.997–4.896 Ma; Ogg, 2012) or C3n.2r (4.799–4.631 Ma; Ogg, 2012). Correlation with the former has been favored on biostratigraphic grounds by Piñero et al. (2017:112), who further considered the fauna from Puerto de la Cadena to be "earliest MN14". These authors advocated for the placement of the MN13/MN14 boundary within C3n.3r (i.e., about 0.3 million years younger than the Miocene/Pliocene boundary at 5.33 Ma), in agreement with previous proposals by some authors (Opdyke et al., 1997; Agustí et al., 2001). However, such a proposal is at odds with the most common, recently strongly supported view that the MN13/MN14 boundary is somewhat older and might even roughly coincide with the Miocene/Pliocene boundary (García-Alix et al., 2008; Minwer-Barakat et al., 2012b; Piñero and Agustí, 2017; Piñero et al., 2018).

Piñero et al. (2017) did not provide positive evidence for their interpretation of Puerto de la Cadena as earliest MN14. They correctly indicated that it appears to be ca. 200 kyr younger than Sifón 413, which occurs just above the local end-Messinian erosion and thus must be within the Pliocene, at ca. 5.3 Ma, but they did not correlate Sifón 413 to a MN unit. Piñero and Agustí (2017) revised the rodent assemblages from the Sifón de Librilla section (Fortuna Basin) and made a good case that Sifón 413 yielded several taxa indicative of MN14, especially *Occitanomys brailloni*, which they suggested is the best marker for the beginning of MN14 in southern Spain. Therefore, Puerto de la Cadena does not represent the

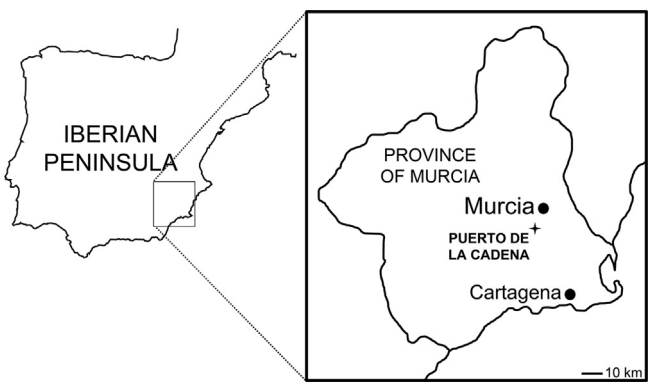

Figure 1. Location map of Puerto de la Cadena within the Iberian Peninsula (left) and within the province of Murcia (inset, right).

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