Macaca (Primates, Cercopithecidae) from the Late Miocene of Spain

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Introduction

Extant Old World monkeys (Cercopithecidae) are nearly absent from the European continent, but five fossil genera have been recorded from the European Miocene through Pleistocene (Delson, 1974, 1975; Arditto & Motura, 1987; Andrews *et al.*, 1996). Even though fossil remains of *Macaca* belonging to the *M. sylvanus* complex of (sub?)species are well known in Europe from the Early Pliocene to the Late Pleistocene (Delson, 1974, 1980; Szalay & Delson, 1979; Ardito & Mottura, 1987), until 1989 only colobines had been recorded from the Miocene of this continent (Andrews *et al.*, 1996; Köhler *et al.*, 1999). Here we describe in detail the cercopithecid remains from the locality of Almenara-M (Castellón, Spain), formerly also called Casablanca-M, which is dated to the MN13 (Late Miocene) of the Mediterranean Neogene (Moyà-Solà *et al.*, 1989/1990). These remains, which include a mandibular fragment found in November 1987 and a first lower deciduous premolar (dp_3) found two weeks later during sediment washing, are described and assigned to the genus *Macaca*. This is one of the two oldest *Macaca* records from the whole Eurasian continent, and therefore the biogeographic and taxonomic implications of this find deserve further discussion.

The locality: stratigraphy and age

The locality of Almenara-M is a karstic fissure filling belonging to the great karstic complex of Almenara (=Casablanca) (Agustí *et al.*, 1989), which is situated in a calcareous massif near the Mediterranean coastal margin between Castellón and Valencia (eastern Spain), next to the town of Almenara (Figure 1). Almenara-M is the oldest fissure filling of this complex, which ranges from the Late Miocene to the Middle Pleistocene (Agustí & Galobart, 1986; Agustí *et al.*, 1989).

Almenara-M is not a rich locality, being particularly poor in macromammals, which apart from the primate remains include only *Pliohyrax graecus* (Pickford *et al.*, 1997), cf. *Nyctereutes* sp., Felidae indet. and Bovidae indet. On the other hand, micromammals are very abundant and diversified (Agustí *et al.*, 1989; Agustí, 1990), including: *Protatera almenarensis*, *Pseudomeriones abbreviatus*, *Blancomys* sp., *Myocricetodon* cf. *parvus*, *Calomyscus* sp., *Ruscinomys lasallei*, *Cricetus kormosi*, *Apodemus gudrunae*, *Occitanomys* cf. *adroveri*, *Castillomys crusafonti gracilis*, *Paraethomys miocaenicus*, *Stephanomys ramblensis* and *Eliomys truci*. The most outstanding feature of this fauna is the presence of some rodents of Asian or African origin, like *Protatera*, *Myocricetodon*, *Pseudomeriones* and *Calomyscus*, whereas the rest of the rodent assemblage clearly indicates a Late Miocene age (MN 13) for this karstic deposit (Agustí & Galobart, 1986; Agustí, 1989). The presence of the murid *Paraethomys* is especially relevant, since the entry of this Asiatic immigrant into the Iberian Peninsula corresponds to the lower part of subchron C3An.1n, ca. 6·1 Ma

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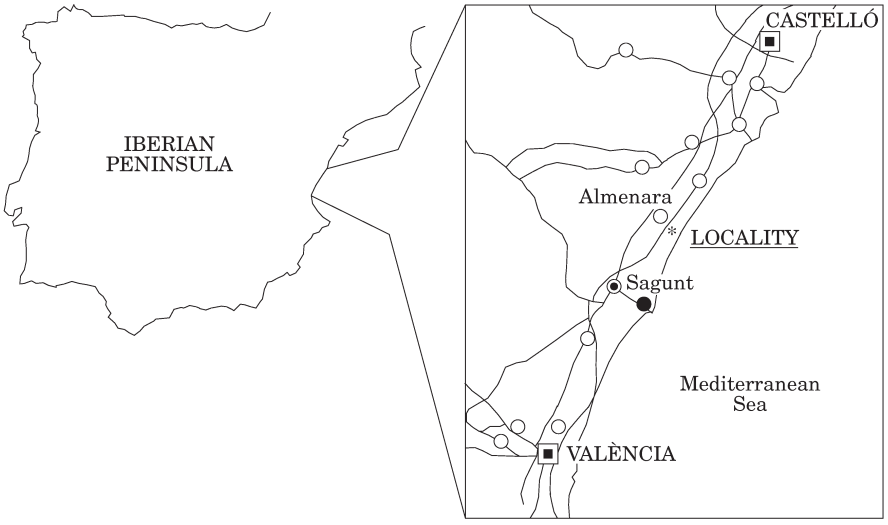

Figure 1. Map showing the location of the locality of Almenara-M.

(Garcés *et al.*, 1998). This is the oldest possible age for Almenara-M; the youngest one is more difficult to determine, although it is certainly older than 5·33 Ma, which corresponds to the Miocene–Pliocene boundary (Krijgsman *et al.*, 1999; McKenzie, 1999).

The primate material

The primate remains from Almenara-M are very scarce, consisting only of a mandibular fragment with dP_4–M_1 (IPMC-11676), and another isolated dP_4 (IPMC-11675) (Figure 2; see measurements in Table 1). The lower first molar has a "brachydont" morphology, lacking the high relief typical of Colobinae. The lingual notch is shallow; the trigonid is slightly larger than the talonid; the mesial and distal foveae are subequal; the protoloph and hypoloph are high; an accessory cusp is present on the lingual side, between the metaconid and the entoconid, and the buccal cleft between the protoconid and the hypoconid does not reach the crown base. The morphology of the two deciduous premolars is similar to that of M_1, but the premolars are narrower.

Some characters (low crown relief with low cusps and shallow foveae, large mesial fovea, and shallow lingual notch) permit the distinction from Colobinae, and moreover, the morphology of these dental remains is clearly papionin, especially resembling the conservative genus *Macaca*. In particular, both size and morphology are very similar to *M. sylvanus prisca*, from the Early Pliocene of Montpellier (France), which was the oldest European *Macaca* previously recorded (Delson, 1980; Ardito & Mottura, 1987), and also to the extant *M. sylvanus sylvanus* from Africa and Gibraltar. Two other papionin genera are known from the Plio-Pleistocene of Spain: *Paradolichopithecus* from several Pliocene (MN16 and MN17) and perhaps also Early Pleistocene localities (Moyà-Solà *et al.*, 1989/1990, and references therein); and *Theropithecus* from the Early Pleistocene of Cueva Victoria (Gibert *et al.*, 1995). However, the smaller size of the remains here described is enough to distinguish them from both *Theropithecus*

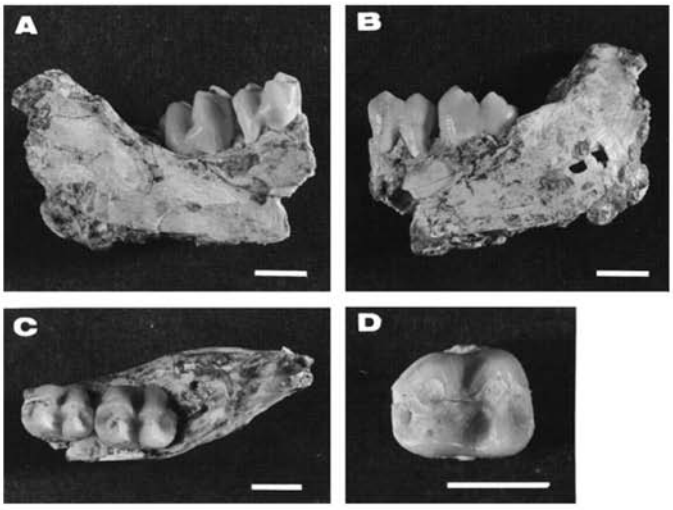

Figure 2. Photographs of the specimens attributed to *Macaca* sp. from Almenara-M: mandibular fragment IPMC-11676, showing dP_4 and M_1 (A: buccal view; B: lingual view; C: occlusal view), and isolated dP_4 IPMC-11675 (D: occlusal view). Scale bar=0·5 cm.

Table 1 **Dental measurements (in mm) of *Macaca* sp. from Almenara-M**

	M_1 (IPMC 11676)	dP_4 (IPMC 11676)	dP_4 (IPMC 11675)
Length	8·0	7·3	7·1
Mesial width	6·2	5·3	5·6
Distal width	6·1	5·2	5·7

and *Paradolichopithecus*. We therefore attribute the remains from Almenara-M to the genus *Macaca*.

Several Late Miocene localities (Menacer, Sahabi, Ongoliba, Wadi Natrun) have yielded remains of *Macaca* or other similar primitive papionins (Delson, 1975, 1980; Thomas & Petter, 1986; Geraads, 1987; Meikle, 1987), but they are all situated in Africa. Ongoliba and Menacer (ex-Marceau) are of Turolian age, but a more precise age determination is not possible; Geraads (1987) dates Menacer to the end of Turolian (ca. 5·5 Ma), but since there are not clear arguments for this attribution, it is preferable to assign this locality simply to the Turolian. Sahabi, on the other hand, although dated to the Early Pliocene by Boaz (1987), is probably Late Turolian, as suggested by Geraads (1987). In contrast, the oldest European *Macaca* dates from the Early Pliocene, whereas in Asia the record of this genus was thought until recently to begin with *M. palaeindica* from the Late Pliocene deposits of India (Delson, 1980). Delson (1996), however, reported two upper molars of cf. *Macaca* from the Mahui Formation of the Yushe Basin (China), dated at ca. 6–5·5 Ma.

The taxonomy of *Macaca* is very complex and unclear, at least with regard to fossil forms; according to Delson (1975, 1980) and Szalay & Delson (1979), most European *Macaca* could be considered

temporal–geographic subspecies of the extant species *M. sylvanus*, probably with the exception of the "dwarf" *M. majori* from Sardinia, which shows obvious differences (Azzaroli, 1946; Zanaga, 1998). However, given the scarcity of the macaque material from Almenara-M, which is insufficient for a systematic assessment at the species level, we simply attribute these teeth to *Macaca* sp. Be that as it may, this is one of the oldest records of a fossil cercopithecine monkey from Eurasia, extending backwards the first appearance of Cercopithecinae in Europe.

Biogeographic implications

The Mammal Neogene unit MN13 was a phase of intense faunal turnover for land mammals, being characterized by the arrival of many African and Asiatic immigrants into Europe (Main, 1999). Delson (1975) attributed the appearance of macaques in Europe by the earliest Pliocene to the desiccation of the Mediterranean during the so-called Messinian salinity crisis (Hsü *et al.*, 1973, 1977; Krijgsman *et al.*, 1999; McKenzie, 1999) of the Late Miocene. The beginning of this crisis was a synchronous event over the entire Mediterranean basin, which has been dated at 5·96 Ma, although isolation of the Mediterranean Sea from the Atlantic Ocean occurred only between 5·59 and 5·33 Ma (Krijgsman *et al.*, 1999; McKenzie, 1999).

The new evidence reported here supports a link between the dispersal of *Macaca* and the Messinian salinity crisis, but also permits a slightly older date of dispersal. This is in accordance with evidence from Spain (Garcés *et al.*, 1998) and especially North Africa (Benammi *et al.*, 1996), which indicates an intercontinental land mammal exchange between Africa and Europe at least 6·1 Ma, presumably by means of an ephemeral land bridge. This event antedates by at least 140 ka the onset of the evaporite deposition, although it was presumably made possible by the same tectonic processes that finally culminated in the Messinian salinity crisis (Krijgsman *et al.*, 1999). Alternatively, *Macaca* could have dispersed into the European continent during a later intercontinental exchange, corresponding to the salinity crisis. Current evidence therefore supports the view that *Macaca* entered into Europe from North Africa during the Late Miocene, just prior or during the Messinian salinity crisis.

A paleoecological analysis of the mammalian dispersal dynamics during the Late Miocene of the Mediterranean region (Moyà-Solà *et al.*, 1983, 1985) revealed that the partially desiccated Mediterranean basin acted as an ecological filter. This explains why "humid" forms were rare, whereas most of the taxa involved were "dry" or ubiquitous elements. *Macaca* is precisely a typically opportunistic primate, possessing an enormous geographic and ecological range of distribution. The presence of this genus also in Asia at 6–5·5 Ma (Delson, 1996) is remarkable because it appears to have spread across the whole Eurasian continent (Spain to eastern China), from one or perhaps two entry points, in a short interval of time. *Macaca* can be thus considered another form that, during the Late Miocene, settled on the Eurasian continent thanks to the new ecological and geographical conditions surrounding the Messinian salinity crisis.

Summary and conclusions

We report the oldest papionin fossil remains from Europe, thus dating the first appearance of the group in this continent to the Late Miocene (MN 13). The systematic affinities of these remains are discussed, being allocated to the extant genus *Macaca*. The dispersal of Cercopithecinae into Eurasia during the Late Miocene is briefly discussed in the light of information from other mammalian groups. It is concluded

that the appearance of *Macaca* during the Late Miocene in Europe, followed by rapid dispersal across the Eurasian continent, is related to the new geographical and ecological conditions that accompanied the Messinian salinity crisis and should not be considered in isolation, but in the context of other contemporaneous dispersal events that involved taxa from Europe, Africa and Asia at this time.

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