Journal of Human Evolution 65 (2013) 313–321

Contents lists available at ScienceDirect

Journal of Human Evolution

journal homepage: www.elsevier.com/locate/jhevol

First record of the genus *Microchoerus* (Omomyidae, Primates) in the western Iberian Peninsula and its palaeobiogeographic implications

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ARTICLE INFO

Article history:
Received 17 February 2013
Accepted 10 July 2013
Available online 2 August 2013

Keywords:
Microchoerinae
Late Eocene
Headonian
Western Iberian bioprovince
Europe

ABSTRACT

In this paper we describe new material of *Microchoerus* (Microchoerinae, Omomyidae, Primates) from Zambrana (Miranda-Trebiño Basin, northern Iberian Peninsula, Spain), a locality assigned to Reference Level MP18 (middle Headonian, Late Eocene). The specimens studied consist of two mandibular fragments, bearing p3-m3 and p4-m3. The teeth resemble in size and morphology those of *Microchoerus erinaceus* from Hordle Cliff, England, although some differences prevent us from making a definitive ascription to this species. We therefore refer the material from Zambrana to *Microchoerus* aff. *erinaceus*. Some traits, such as the development of the mesoconid and hypoconulid in the m1 and m2, and the shape of the hypoconulid lobe in the m3, are intermediate between those of *M. erinaceus* and *Microchoerus edwardsi*. Thus, the material from Zambrana is very similar to other species of *Microchoerus* present in Europe, representing a transitional form between *M. erinaceus* and *M. edwardsi*.

The described material represents the first discovery of a primate from the Miranda-Trebiño Basin, and also the westernmost record of the genus *Microchoerus* in the Iberian Peninsula. Moreover, the identification of this microchoerine, with clear similarities to the representatives of this genus described from other European sites, reinforces the idea of the existence of connections between western Iberia and the rest of Europe in the Late Eocene, previously hypothesized after the discovery of typical European artiodactyls in the site of Zambrana.

Introduction

Primates underwent a great radiation during the Eocene. This was favoured by warm climates resulting from the increased global temperatures that marked the beginning of this epoch, known as the Paleocene–Eocene Thermal Maximum. Throughout the Eocene, primates were mainly represented by two groups, Adapoidea and Omomyoidea, which reached great abundance and diversity across the Northern Hemisphere. Both groups declined at the end of the Eocene as a consequence of global cooling (Covert, 2002; Gebo, 2002; Gunnell and Rose, 2002; Gingerich, 2012). Omomyoids were small-bodied primates, similar to living galagids in form and locomotor adaptations, generally nocturnal and with insectivorous–frugivorous diets (see Szalay and Delson, 1979; Ross et al., 1998; Ross and Covert, 2000; Strait, 2001; Tornow, 2008). The superfamily Omomyoidea includes a unique family (Omomyidae), currently divided into three subfamilies: Omomyinae and Anaptomorphinae, found in North America and Asia, and Microchoerinae, limited to Europe.

Microchoerines ranged from the Early to Late Eocene, with some genera (*Pseudoloris*, *Microchoerus*) lasting into the Early Oligocene in the Iberian Peninsula (Köhler and Moyà-Solà, 1999; Peláez-Campomanes, 2000). Their remains are relatively scarce in the fossil record, although recent discoveries in several European sites have increased our knowledge about this subfamily of primates (Hooker, 2007, 2012; Hooker and Harrison, 2008). The first described microchoerine was *Microchoerus erinaceus* from the Late Eocene (Headonian, MP17) site of Hordle Cliff in England, interpreted by Wood (1844) as a small suid. Later, remains of *Microchoerus* were found in other English sites, as well as in localities from France, Germany, Switzerland and Spain (see Hooker and Weidmann, 2000; Gunnell and Rose, 2002, and references therein), ranging in age from the Middle Eocene (Robiacian, MP 16) to the Early Oligocene (Suevian, MP 21). This genus is characterized by, among other traits, complex and rugose enamel in

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http://dx.doi.org/10.1016/j.jhevol.2013.07.002

the cheek teeth. Recent microwear analyses suggest a diet based on fruit and gum for this genus (Ramdarshan et al., 2012).

In the Iberian Peninsula, the study of Eocene primates started in the 1960s by Dr. M. Crusafont-Pairó, who discovered several fossil sites containing prosimian remains such as Sant Cugat de Gavadons, Les Saleres and Sossís (Crusafont-Pairó, 1967). In recent decades, the study of this group has received increased attention due to the existence of well-exposed Eocene continental series containing abundant vertebrate remains. More recently, studies carried out by the researchers of the Institut Català de Paleontologia Miquel Crusafont (ICP) have yielded new fossil sites, as well as detailed analysis of material from the classical collections housed at the ICP. The most relevant results include the description of several new forms of Adapoidea (Marigó et al., 2010, 2011, 2013) and the first record of Plesiadapiformes from Spain (Marigó et al., 2012), the latter considered a sister group of Euprimates or primates of 'modern aspect' (Silcox, 2001, 2003; Bloch and Silcox, 2001, 2006; Bloch and Boyer, 2002; Bloch et al., 2007; Silcox and Gunnell, 2008; Boyer, 2009). Regarding Microchoerines, the latest work analyzed several populations of the genus *Pseudoloris* (Minwer-Barakat et al., 2010, 2012, 2013). All of these cited studies deal with material recovered from the Duero, Ebro and Pyrenean basins.

In the present work, we describe two mandibles preserving p3-m3 and p4-m3, assigned to the genus *Microchoerus*, from the Late Eocene (Headonian, MP 18) site of Zambrana (Miranda-Trebiño Basin, Basque-Cantabrian region, Spain). This discovery represents the first record of a primate from the Miranda-Trebiño Basin, and also the westernmost record of the genus *Microchoerus* in the Iberian Peninsula.

The mammalian fossil assemblage from Zambrana has significant implications for Iberian and wider European mammalian palaeoecology and palaeobiogeography (Badiola et al., 2009a). The first description of a primate from this fossil site not only increases the knowledge about this group of mammals in the Eocene of the Iberian Peninsula, but also contributes to a better understanding of the faunal differentiation between the central and western Iberian basins during the Eocene and the interchanges of mammals between Iberia and the rest of Europe (see next sections).

Geographical, geological and biochronological context

The Zambrana site is situated about 70 km south of Bilbao in the province of Araba (Basque Country). Geologically, it is located in one of the oldest lacustrine systems of the Miranda-Trebiño Basin (Basque-Cantabrian region; Fig. 1). The fossiliferous strata consist of palustrine–lacustrine coal-bearing marls and marlstones, which have yielded fossil seeds of aquatic plants, charophyte oogonia, remains of invertebrates such as ostracods and gastropods, and vertebrate fossils. The latter come from black marls, corresponding to deposits rich in organic matter (Badiola et al., 2009b: Fig. 2). The depositional setting was a shallow and low-gradient freshwater lake margin with a peripheral swamp (Iriarte et al., 2003; Badiola et al., 2009b). To date, 27 fossil vertebrate taxa have been recovered, 23 of which are mammals. Table 1 shows the updated faunal list of the site, which includes anurans, squamates, chelonians, crocodilians and mammals (Astibia et al., 2000; Badiola et al., 2002, 2005, 2009a; Badiola, 2004; Badiola and Cuesta, 2007, 2008).

Zambrana is the first Late Eocene locality in the Iberian Peninsula to have yielded a fossil mammal assemblage belonging to the MP18 mammal reference level (Schmidt-Kittler, 1987; updated by Aguilar et al., 1997). We use reference levels in the same way as assemblage biozones, which can be calibrated to marine biochronological scales and to the geomagnetic polarity time scale (Luterbacher et al., 2004; Vandenberghe et al., 2012). According to the latter authors, the mammal reference levels MP17, MP18 and MP19 of the Headonian European Land Mammal Age can be correlated to the Priabonian (37.8–33.9 Ma [millions of years ago]).

Material and methods

The sample studied consists of a right mandible fragment with p3-m3 (MCNA 14518) and a right mandible fragment with p4-m3 (MCNA 14519), stored at the Museo de Ciencias Naturales de Álava/Arabako Natur Zientzien Museoa/(MCNA/ANZM), in Vitoria-Gasteiz (province of Araba, Basque Country, Spain).

The nomenclature used in the descriptions of the teeth is that of Hooker (1986). Measurements have been taken as defined by Godinot (2003) using an optic caliper (Nikon measuroscope 10) connected to a monitor (Nikon SC112). Micrographs were taken using the Environmental Scanning Electron Microscope (ESEM) of the Universitat de Barcelona (UB).

Systematic palaeontology

Order Primates Linnaeus, 1758
Suborder Haplorhini Pocock, 1918
Infraorder Tarsiiformes Gregory, 1915
Family Omomyidae Trouessart, 1879
Subfamily Microchoerinae Lydekker, 1887
Genus *Microchoerus* Wood, 1844
Microchoerus aff. *erinaceus* Wood, 1844
(Figs. 2 and 3)

Locality and horizon

Zambrana (Araba, Spain), Iberian Peninsula; Basque-Cantabrian region, Miranda-Trebiño Basin, middle Headonian (MP18) Z4 bed (Badiola et al., 2009b: Fig. 2).

Referred specimens

Right mandible fragment with p3-m3 (MCNA 14518); right mandible fragment with p4-m3 (MCNA 14519).

Measurements

See Table 2.

Description of the specimen MCNA 14518

p3: The dental pattern of this premolar is difficult to observe owing to the poor preservation of the tooth, which is fragmented mesially. The dimensions and disposition of the paraconid, protoconid and metaconid (if present) are impossible to determine because of the breakage of the enamel. No metaconid seems to be present, since a cristid directed distally, without any distinct cuspid, can be observed on the lingual part of the tooth. A well-marked, continuous cingulid surrounds the buccal base of the tooth and continues bordering the distal part, delimiting a short talonid basin. In addition, there is another prominent cingulid at the lingual border.

p4: The tooth is broken mesiolingually, so the paraconid cannot be observed. There are three cristids starting at the protoconid, which is the highest cuspid of the tooth. The paracristid is directed mesially towards the position of the now missing paraconid; this cristid continues around the mesial part of the lingual border but does not reach the metaconid, which is separated from the paraconid. Another cristid is directed distally, reaching the buccal part of the talonid. The third cristid runs distolingually from the protoconid and joins the buccal base of the metaconid, which is a well-