



# *Microchoerus hookeri* nov. sp., a new late Eocene European microchoerine (Omomyidae, Primates): New insights on the evolution of the genus *Microchoerus*



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## ABSTRACT

The study of Eocene primates is crucial for understanding the evolutionary steps undergone by the earliest members of our lineage and the relationships between extinct and extant taxa. Recently, the description of new material from Spain has improved knowledge of European Paleogene primates considerably, particularly regarding microchoerines. Here we describe the remains of *Microchoerus* from Sossís (late Eocene, Northern Spain), consisting of more than 120 specimens and representing the richest sample of *Microchoerus* from Spain. This primate was first documented in Sossís during the 1960s, on the basis of scarce specimens that were ascribed to *Microchoerus erinaceus*. However, the studied material clearly differs from *M. erinaceus* at its type locality, Hordle Cliff, and shows some characters that allow the erection of a new species, *Microchoerus hookeri*. This new species is characterized by its medium size, moderate enamel wrinkling, generally absent mesoconid and small hypoconulid in the M<sub>1</sub> and M<sub>2</sub>, single paracone in the upper molars and premolars and, particularly, by the lack of mesostyle in most M<sup>1</sup> and M<sup>2</sup>, a trait not observed in any other species of *Microchoerus*. Some specimens from Eclépins B (late Eocene, Switzerland), determined previously to be *Microcherus* aff. *erinaceus*, are also ascribed to *M. hookeri*. *M. hookeri* represents the first step of a lineage that differentiated from *Necrolemur antiquus* and, later, gave rise to several unnamed forms of *Microchoerus*, such as those from Euzet and Perrière, finally leading to *M. erinaceus*. This discovery sheds new light on the complex evolutionary scheme of *Microchoerus*, indicating that it is most probably a paraphyletic group. A detailed revision of the age of the localities containing remains of *Microchoerus* and the description of the still unpublished material from some European localities, are necessary to clarify the phylogenetic relationships among the members of this microchoerine group.

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## 1. Introduction

The Eocene documents the first occurrence of Euprimates in North America, Europe and Asia (Bloch et al., 2007), with several other orders of modern mammals appearing alongside them (Silcox

and Gunnell, 2008). It was one of the warmest epochs of the Cenozoic, especially during the Paleocene/Eocene Thermal Maximum and the subsequent sustained period of global warmth, the Early Eocene Climatic Optimum (Zachos et al., 2001). During the Eocene, primates underwent a very important radiation favored by the development of dense forests that provided suitable habitats for them. Through this epoch, primates were mainly represented by two groups, adapiforms and omomyiforms, which reached great abundance and diversity throughout the Northern Hemisphere and

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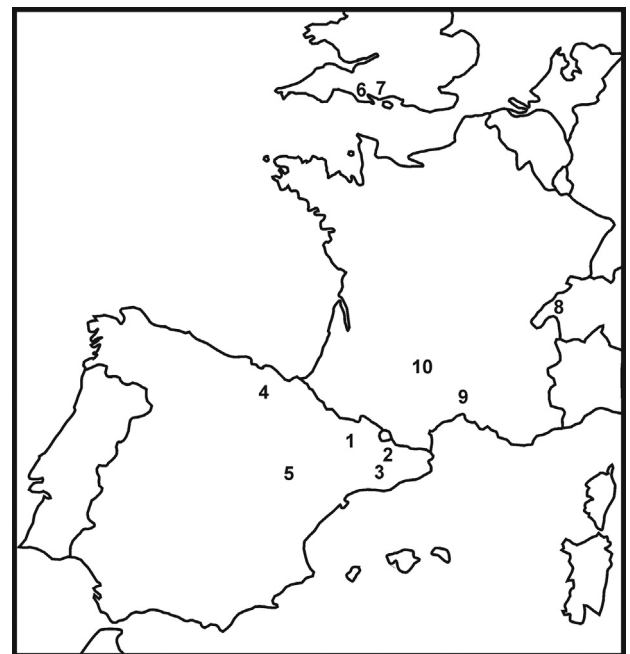
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declined at the end of the Eocene as a consequence of global cooling (Covert, 2002; Gebo, 2002; Gunnell and Rose, 2002; Gingerich, 2012; Godinot, 2015). Adapiforms and omomyiforms are related to the main clades of living primates (haplorrhines and strepsirrhines, respectively). Hence, the study of these first members of the Order helps understand the relations between extinct and extant primate groups. The first record of anthropoids is also documented in the Eocene, so studying new material of this epoch is essential for determining the evolutionary steps undergone by the earliest members of our lineage. During their evolutionary history, primates have developed a wide array of trophic, locomotor and cognitive adaptations that make them a very interesting subject for research. Fossils represent the basic source of information about the steps that this group followed during its evolution. For this reason, each new discovery of these early primates represents a valuable tool for improving our knowledge about the origin of the group to which we belong.

In contrast to the rich and diverse material known from North America, the Eocene primate record from Europe is still relatively scarce. Therefore, studies of European Eocene primates are crucial to ascertain the biogeographical distribution of several groups, to identify intercontinental dispersal events (Smith et al., 2006), and to reconstruct the phylogenetic relationships among different taxa. In this sense, the advances made in the first years of the 21st century have notably improved knowledge of the Eocene primate faunas from Europe. Among other discoveries, the descriptions of several new genera and species of both microchoerines (Hooker, 2007, 2012; Hooker and Harrison, 2008; Minwer-Barakat et al., 2010, 2012a) and notharctids (Marigó et al., 2010, 2011, 2013; Femenias-Gual et al., 2016), some of them on the basis of exceptionally well-preserved material (Franzen et al., 2009), have allowed the reinterpretation of the phylogenetic relationships of several primate groups (for a detailed recent account of the Paleogene primate record from Europe, see Godinot, 2015). The description of new fossil material is essential for a better understanding of the evolution of the group, particularly in those geographic areas and time intervals in which the record is especially sparse.

Omomyids were small-bodied primates, similar to living galagids, dwarf and mouse lemurs in morphology and locomotor adaptations, generally nocturnal and with insectivorous or frugivorous diets (Strait, 2001; Gunnell and Rose, 2002; Tornow, 2008; Ramdarshan et al., 2012). Within this group, the subfamily Microchoerinae is recorded exclusively from Europe, ranging primarily 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). The first described microchoerine was *Microchoerus erinaceus* from the late Eocene (Headonian, MP17) site of Hordle Cliff in England, identified initially by Wood (1844) as a small suid. Later on, remains of *Microchoerus* were found in other English sites, as well as in localities from France, Germany, Switzerland and Spain (see Godinot, 1985; Hooker, 1986; Hooker and Weidmann, 2000; Gunnell and Rose, 2002; Minwer-Barakat et al., 2013a, 2016; Marigó et al., 2014, and references therein), ranging in age from the middle Eocene (Robiacian, MP16) to the early Oligocene (Suevian, MP21). This genus is characterized, among other traits, by complex and rugose enamel in the cheek teeth. Recent microwear analyses suggest a diet based on fruit and gum for this genus (Ramdarshan et al., 2012). *Microchoerus* is interpreted as a nocturnal primate on the basis of its orbit size, although a very recent analysis of its endocranial cast (Ramdarshan and Orliac, 2016) suggests the presence of relatively small olfactory bulbs, smaller than those of the diurnal coeval *Adapis parisiensis*. This pattern contrasts with those observed in living primates, where nocturnal taxa typically

have larger olfactory bulbs than diurnal species. In Spain, the genus *Microchoerus* was first documented at the locality of Sossís (Fig. 1), where Crusafont-Pairó (1965) mentioned the presence of *M. erinaceus*. Later works (Crusafont-Pairó, 1967) referred to this large microchoerine from Sossís as “*Necrolemur erinaceus*”. Crusafont-Pairó (1967) also reported a fragment of maxilla with two upper teeth from Sant Cugat de Gavadons (Fig. 1) that he ascribed to *Microchoerus ornatus*; however, Minwer-Barakat et al. (2016) demonstrated clear differences between the holotype of *M. ornatus* and the single specimen from Sant Cugat de Gavadons, suggesting that the latter specimen cannot be ascribed to any of the known species of *Microchoerus* and is best considered as *Microchoerus* sp. Peláez-Campomanes (2000) described an isolated lower molar of *Microchoerus* sp. from the early Oligocene site of Aguatón (Fig. 1), which represents the youngest known occurrence of the genus. Finally, the westernmost record of the genus in the Iberian Peninsula was recorded by Minwer-Barakat et al. (2013a), who described two mandibles with several teeth assigned to *Microchoerus* aff. *erinaceus* from the late Eocene of Zambrana in the Miranda-Trebiño Basin (Fig. 1). In contrast to the sparse remains from these localities, further fieldwork carried out at Sossís yielded abundant and well-preserved material of four different primates, two adapiforms and two omomyiforms (see next section). Among these primates, a rich and still undescribed sample of dental remains of *Microchoerus* is present, and described in the current paper. This material represents the richest collection of the genus recovered from Spain and includes almost all the dental elements, thus allowing detailed scrutiny of different anatomical traits, as well as thorough comparisons with other samples of the genera *Necrolemur* and *Microchoerus* from several European sites. The current study improves our knowledge of the composition of primate faunas during the late Eocene, at the time of their maximum diversity in southern Europe, before the crisis that dramatically



**Figure 1.** Location of some relevant European fossil localities yielding remains of the genera *Microchoerus* and *Necrolemur*. 1: Sossís; 2: Sant Jaume de Frontanyà; 3: Sant Cugat de Gavadons; 4: Zambrana; 5: Aguatón; 6: Creechbarrow; 7: Hordle Cliff; 8: Mormont fissure fillings (including, among others, the fossil sites of Eclépens B and Mormont Entreoches); 9: Euzet; 10: Quercy phosphorites (including many important Eocene sites such as Le Bretou, Lavergne, La Bouffie, Perrière and Malpérié).

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