Journal of Human Evolution 83 (2015) 74–90

Contents lists available at ScienceDirect

Journal of Human Evolution

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

New material of *Pseudoloris parvulus* (Microchoerinae, Omomyidae, Primates) from the Late Eocene of Sossís (northeastern Spain) and its implications for the evolution of *Pseudoloris*

Raef Minwer-Barakat [a, *], Judit Marigó [a, b], Joan Femenias-Gual [a], Salvador Moyà-Solà [c]

[a] Institut Català de Paleontologia Miquel Crusafont, Universitat Autònoma de Barcelona, 08193, Cerdanyola del Vallès, Barcelona, Spain
[b] Department of Evolutionary Anthropology, Duke University, 130 Science Drive, 27708, Durham, NC, USA
[c] ICREA at the Institut Català de Paleontologia Miquel Crusafont, Universitat Autònoma de Barcelona, 08193, Cerdanyola del Vallès, Barcelona, Spain

ARTICLE INFO

Article history:
Received 31 August 2014
Accepted 1 April 2015
Available online 8 May 2015

Keywords:
Paleogene
Headonian
Pyrenean Basins
Iberian Peninsula
Europe

ABSTRACT

The species *Pseudoloris parvulus*, identified in several Middle and Late Eocene European sites, was previously known in the Iberian Peninsula by a single mandible preserving P_4–M_3 from Sossís (Southern Pyrenean Basins, northeastern Spain), described in the 1960s. Further field work at this Late Eocene site has led to the recovery of a large number of mammal remains, including the additional material of *P. parvulus* described in this paper. Some specimens of *P. parvulus* from this locality have also been recently found in the collections of the Naturhistorisches Museum Basel, Switzerland. The whole sample consists of 11 mandible fragments including several teeth, three upper dental series and nearly 80 isolated teeth including all of the dental elements, and represents the most complete sample of the genus described from the Iberian Peninsula. This abundant material allows us to provide an emended diagnosis for the species and to observe several directional changes in the dental morphology of the lineage including the species *Pseudoloris saalae*, *Pseudoloris isabenae*, *Pseudoloris pyrenaicus* and *P. parvulus*. These directional changes include the progressive reduction of the paraconid in the lower molars and the increase in size of the hypocone, metaconule and paraconule in the upper molars. Moreover, despite the overall resemblance among all of the samples ascribed to *P. parvulus*, we also recognize some differences, particularly an increase in size and better development of the hypocone from the oldest populations of the species, such as Le Bretou, to the most recent ones, like Sossís and Perrière. Therefore, this study sheds new light on the evolution of this genus, which inhabited Europe from the Middle Eocene to the Early Oligocene.

1. Introduction

The Eocene is of particular interest for the study of the evolutionary history of primates, since this epoch records the first remains of Euprimates and evidences the early division between strepsirrhines and haplorhines. The first studies of Eocene primates from the Iberian Peninsula occurred in the Institut de Paleontologia de Sabadell (now called Institut Català de Paleontologia Miquel Crusafont, ICP) during the 1960s by M. Crusafont-Pairó, who discovered several fossil sites containing prosimian remains, such as Sant Cugat de Gavadons, Les Saleres and Sossís (Crusafont-Pairó, 1967). Recent studies carried out by the research team of the ICP have involved the discovery of new fossil sites, as well as the detailed analysis of the material from the classical collections housed at the ICP (Marigó et al., 2010, 2011, 2012, 2013, 2014). Specifically, several works have been focused on the study of omomyids from some Spanish localities such as Sant Jaume de Frontanyà, Mazaterón, Sant Cugat de Gavadons and Zambrana (Minwer-Barakat et al., 2010, 2012, 2013a, 2013b, respectively).

The family Omomyidae includes some early primates that radiated during the Eocene, becoming abundant and diverse in the Northern Hemisphere. Omomyids were small-bodied, generally nocturnal primates, similar to living galagids, dwarf and mouse lemurs in morphology and locomotor adaptations (Gunnell and Rose, 2002), with insectivorous or frugivorous diets (Tornow, 2008; Ramdarshan et al., 2012). The subfamily Microchoerinae is

* Corresponding author.
E-mail address: raef.minwer@icp.cat (R. Minwer-Barakat).

http://dx.doi.org/10.1016/j.jhevol.2015.04.002
0047-2484/

exclusively recorded 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). *Pseudoloris* is a very small microchoerine, similar in some morphological features to the living *Tarsius*, with whom it shares strong dental convergences (Szalay and Delson, 1979). It is particularly well represented in France, but is also found in Spain, England and Germany. The recent description of relatively rich samples from the Iberian Peninsula has notably increased our knowledge of its dental morphology, including a description of the anterior dentition (Minwer-Barakat et al., 2010, 2012), which was previously nearly unknown. Here we describe new material of *Pseudoloris* from Sossís, one of the most important Eocene sites from the Iberian Peninsula.

This site is located close to the village of Sossís (Conca de Dalt, Lleida Province), in the Southern Pyrenean Basins. Geologically, this fossil site is part of the Collegats Formation, a 1000 m thick conglomeratic unit with clayey intercalations that lies unconformably over Late Cretaceous marine deposits. The fossiliferous level is found in the so-called Sossís Member, corresponding to a lacustrine intercalation within the Collegats Formation and consisting of a 100 m thick succession of limestones, marls, clays and lignites (see López-Martínez, 1998 and references therein).

The site was discovered in the 1940s when abundant and well-preserved vertebrate remains were found in a lignite mine (see Casanovas-Cladellas, 1998 for further details). The large amount of vertebrate material recovered from this locality has allowed the identification of more than 30 mammalian taxa, including marsupials, insectivores, rodents, carnivores, creodonts, perissodactyls, artiodactyls and primates (Table 1). Most of this material was studied in several unpublished dissertations, with only detailed descriptions of rodents (Crusafont-Pairó et al., 1963), insectivores (Sigé, 1997) and, more recently, artiodactyls (Cuesta Ruiz-Colmenares et al., 2006) being published. Besides mammals, the lizards from this fossil site have been recently described (Bolet and Evans, 2013; Bolet and Augé, 2014), leading to the identification of a rather diverse assemblage that includes a new genus. The study of the whole fauna allowed the assignment of the site to MP17a (Headonian, Late Eocene).

Regarding primates, Crusafont-Pairó (1967) documented the existence of three different taxa in Sossís, each of them represented by a few specimens. The published material consisted of two isolated teeth of the large adapine *Adapis* cf. *parisiensis*, a mandible and three maxillae with several teeth ascribed to '*Necrolemur erinaceus*' (including erroneously the species *erinaceus* in the genus *Necrolemur* instead of in the proper genus, i.e., *Microchoerus*) and, finally, a right mandible with P_4–M_3 assigned to *Pseudoloris parvulus*. Subsequent field work at Sossís led to the recovery of a large number of mammal remains, including additional specimens of the three primate taxa. Moreover, this new material has allowed the identification of a fourth taxon, an anchomomyin recently described as *Nievesia sossisensis* (Marigó et al., 2013). Here we present the new material of *P. parvulus* from Sossís housed in the ICP, consisting of 11 fragmentary mandibles bearing several teeth, three upper dental series and nearly 80 isolated teeth including all of the dental elements. In addition, we describe five isolated teeth of *P. parvulus* from Sossís recently found in the collections of the Naturhistorisches Museum Basel (NMB) in Switzerland. These specimens probably arrived in Basel as a result of the long-term collaboration between Dr. Crusafont-Pairó and Dr. Hürzeler, which included the exchange of fossil material for comparative purposes, as was the case for other primate remains from Spanish localities found in the NMB (Minwer-Barakat et al., 2013a). The material described here constitutes the most abundant sample of the genus *Pseudoloris* (or of any other omomyid) described to date from the Iberian Peninsula.

Table 1
Mammal faunal list of Sossís, after Casanovas-Cladellas (1998), Cuesta Ruiz-Colmenares et al. (2006) and Marigó et al. (2013).

Marsupialia	**Perissodactyla**
Peratherium lavergnense	*Palaeotherium magnum stehlini*
Peratherium perriense	*Palaeotherium medium euzetense*
Cimolesta	*Palaeotherium crassum sossisenses*
Apatemyidae indet.	*Plagiolophus annectens*
Lipotyphla	*Anchilophus dumasi*
Leptictis sp.	**Rodentia**
Saturninia pirenaica	*Treposciurus mutabilis*
Creodonta	*Estellomys ibericus*
Hyaenodon minor	*Paradelomys crusafonti*
Carnivora	*Theridomys euzetensis*
Miacis exilis	*Pseudoltinomys* cf. *phosphoricus*
Artiodactyla	*Elfomys parvulus*
Cebochoerus helveticus	*Gliravus robiaciensis*
Acotherulum sp.	**Primates**
Dacrytherium ovinum	*Adapis* cf. *parisiensis*
Leptotheridium lugeoni	*Nievesia sossisensis*
Haplomeryx euzetensis	*Microchoerus erinaceus*
Xiphodon intermedium	*Pseudoloris parvulus*

2. Material and methods

The described material (Tables 2 and 3) is housed in the collections of the Institut Català de Paleontologia Miquel Crusafont (Sabadell, Barcelona, Spain) and the Naturhistorisches Museum Basel (Basel, Switzerland).

The nomenclature used in the descriptions of the teeth is described in Figure 1. Following Hooker and Harrison (2008), the terms 'anterior' and 'posterior' are used specifically for the descriptions of the incisors because, whereas the posterior direction equates to distal, anterior does not equate with mesial. Measurements have been taken using an optic caliper (Nikon measuroscope 10) connected to a monitor (Nikon SC112), following the criteria explained in Figure 2. Micrographs were taken using the Environmental Scanning Electron Microscope (ESEM) at the Universitat de Barcelona (UB).

3. Systematic paleontology

Order Primates Linnaeus, 1758
Suborder Haplorhini Pocock, 1918
Infraorder Tarsiiformes Gregory, 1915
Family Omomyidae Trouessart, 1879
Subfamily Microchoerinae Lydekker, 1887
Genus *Pseudoloris* Stehlin, 1916
P. parvulus (Filhol, 1890)
(Figs. 3–6)

3.1. Original diagnosis (summarized from the description of Filhol, 1890)

Extremely small size, smaller than that of *Necrolemur zitteli*. Strong lower incisor. Third lower premolar high crowned and projected forward. Fourth lower premolar bilobulated, with the mesial lobe more developed than the distal one. Lower molars increasing in size from mesial to distal. First and second lower molars with a mesial lobe higher than the distal lobe; each lobe has two cuspids, the buccal cuspids are higher than the lingual ones. The mesial cuspids are connected to each other by a short crest; the distal cuspids are isolated. Third lower molar with three lobes, the distal one formed by a single central cuspid slightly curved forward.